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The pea crab genus *Arcotheres* Manning, 1993 (Crustacea: Brachyura: Pinnotheridae) from Singapore and Peninsular Malaysia, with a reappraisal of diagnostic characters and descriptions of two new genera

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Abstract. Study of a large collection of pinnotherid crabs collected primarily from Singapore and Peninsular Malaysia revealed substantially more variation in the carapace shape, third maxilliped, and other taxonomic characters than previously acknowledged. While carapace shape and form, structures of the epistome (especially the posterior margin), antennal article 1, eyes (especially the cornea), third maxilliped, male and female chelae, ambulatory pereopods, male pleon, as well as features of the male first and second gonopods are useful taxonomic characters, the degree of variation must be better accounted for so that accurate species and genus assignments can be made. The female-to-male ratio is also indicative for several species. Also significant is that the host of the pinnotherid species is taxonomically correlated and many taxa are quite specific to the mollusc genus, family, or superfamily. As a result of this reappraisal of the taxonomic characters used, 14 names are synonymised under five taxa. The following new synonymies are recognised: *Pinnotheres hirsutissima* Johnson, 1963, a nomen nudum, under *Holotheres semperi* (Bürger, 1895); *P. rhombifer* Bürger, 1895, *P. latissimus* Bürger, 1895, *P. arcophilus* Bürger, 1895, *P. paralatissimus* Dai & Song, 1986, and *Arcotheres guinotae* Campos, 2001, under *Arcotheres palaensis* (Bürger, 1895); *P. modiolicola* Bürger, 1895, under *Arcotheres similis* (Bürger, 1895); *P. winckworthi* Gordon, 1936, *P. vicajii* Chhapgar, 1957, *P. casta* Antony & Kutyamma, 1971, and *P. obscuridentata* Dai & Song, 1986, under *Arcotheres exiguus* (Bürger, 1895); and *P. latus* Bürger, 1895, *P. borradailei* Nobili, 1906, and *P. ridgewayi* Southwell, 1911, under *P. globosum* Hombron & Jacquinot, 1846, which is referred to a new genus, *Magnotheres*. In addition, we establish a new genus, *Plenotheres*, for an unusual member of *Arcotheres* Manning, 1993, which lives in mangrove clams of the families Cyrenidae Gray, 1840, and Glauconomidae Gray, 1853. The poorly known Japanese species, *Pinnotheres corbiculae* Sakai, 1939, which lives in corbiculid clams and superficially resembles *Plenotheres coarctatus*, new combination, is redescribed from a male specimen and here referred to *Nepinnotheres* Manning, 1993. Likewise, *Pinnotheres tsingtaoensis* Shen, 1932, is also referred to *Nepinnotheres*.

Key words. systematics, Pinnotheroidea, Southeast Asia, new genera, synonymies, character states

INTRODUCTION

The earliest record of pinnotherid crabs from Singapore was by Hombron & Jacquinot (1846), who described *Pinnotheres globosum* from a "mussel". This was also the first brachyuran crab recorded from the island (see Ng & Corbari, 2019). Lanchester (1900) subsequently recorded four species: two, *P. semperi* Bürger, 1895, and *P. ortmanni* Bürger, 1895, from sea cucumbers; and two, *P. modiolicola* Bürger, 1895, and *P. arcophilus* Bürger, 1895, from bivalve molluscs. Gordon (1936) treated the taxonomy of three species from bivalves: *P. edwardsi* De Man, 1887, *P. similis* Bürger, 1895, and a new species, *P. spinidactylus*. In his book on the Malayan (including Singapore) seashore fauna, Chuang (1961) listed two species, *Pinnotheres palaensis* Bürger, 1895, and *Xanthasia whitei* De Man, 1888, from bivalves, and *P. semperi* from sea cucumbers.

The two pinnotherids associated with sea cucumbers (Echinodermata: Holothuroidea), *Holotheres semperi* (Bürger, 1895) and *Buergeres ortmanni* (Bürger, 1895), have been treated by Ng & Manning (2003) and Ahyong & Ng (2007b, 2020). The mollusc-associated pinnotherids, *Serenotheres* Ahyong & Ng, 2005, and *Tridacnatheres* Ahyong & Ng, 2005, with one species each from Singapore and Malaysia, have been revised by Ahyong & Ng (2005), so there is no need to elaborate on them here.

In his review of commensal and semi-parasitic decapod crustaceans of Singapore, Johnson (1963) expressed doubt about many of the old identifications. He commented: "The species which inhabitats [sic] the sea-cucumber *Holothuria*

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scabra is likewise very common. Usually a pair of individuals, male and female are present. This species is remarkable both for its unusual habitat and its extreme hairiness. Chuang records it as *P. semperi*. I have tentatively identified it as *P. hirsutissima*. Once again these identifications must be considered to be doubtful." (Johnson, 1963: 286). The source of Johnson's (1963) name "*P. hirsutissima*" is not known—there is no pinnotherid species with this name and perhaps he intended to eventually describe it as a new species. In any case, "*P. hirsutissima*" is not an available name as it has no description or diagnosis, and the name has never been used since. As noted above, Ng & Manning (2003) confirmed that Chuang's (1961) record is correctly identified as the species currently known as *Holotheres semperi* (Bürger, 1895). *Pinnotheres hirsutissima* Johnson, 1963, a nomen nudum, is here formally synonymised under *Holotheres semperi* (Bürger, 1895).

The Lee Kong Chian Natural History Museum (previously the Raffles Museum of Biodiversity Research) at the National University of Singapore has a large collection of pinnotherids dating back to the early 1900s, although many of the old specimens are in poor condition. Over the last decade, the first author actively collected and examined pea crabs (Pinnotheridae) in and around Singapore and Peninsular Malaysia, as well as neighbouring waters, to ascertain the regional diversity. Much of the recent material was obtained as a result of various malacological surveys around the island led by resident malacologist S. K. Tan and his colleagues, while others came from bivalves purchased from markets, most of which were harvested in nearby Peninsular Malaysia. Most of the species living in bivalves from Peninsular Malaysia and Singapore belong to the genus *Arcotheres* Manning, 1993a, with only a few species assigned to *Nepinnotheres* Manning, 1993b, *Serenotheres* Ahyong & Ng, 2005, and *Tridacnatheres* Ahyong & Ng, 2005 (see Ahyong & Ng, 2007b; Ng, 2018a; Ng et al., 2019a).

The present paper examines the taxonomy of the available specimens of *Arcotheres*, mainly from Singapore and Malaysia (except for *A. purpureus* (Alcock, 1900), which was covered in detail by Ahyong & Ng, 2021). The extensive material on hand for many of the species, including types and males, allows us to substantially reappraise the characters used thus far to differentiate species, clarifying the taxonomy of many species and resulting in many synonymies. We also show that two of the species formerly assigned to *Arcotheres* are referable to new genera.

MATERIAL AND METHODS

The terminology used follows Manning (1993b) and Davie et al. (2015) with the following abbreviations: cl = maximum carapace length; cw = maximum carapace width; MXP3 = third maxilliped; P2–P5 = pereopods 2–5 (first to fourth ambulatory legs), respectively; Gl = male first gonopod; and G2 = male second gonopod. Measurements provided, in millimetres (mm), are of the maximum carapace width and length, respectively. When the specimen is infected by epicaridean parasites and the carapace deformed, only the carapace length is provided.

Specimens examined are deposited in the Australian Museum, Sydney, Australia (AM); Institute of Zoology at the Chinese Academy of Science, Beijing, China (CAS); Natural History Museum and Institute, Chiba, Japan (CBM); Cambridge University Museum of Zoology, Cambridge, United Kingdom (CUMZ); Kanagawa Prefectural Museum of Natural History, Japan (KPM); Muséum national d'Histoire naturelle, Paris, France (MNHN); The Natural History Museum, London, United Kingdom (NHM); National Museum of Nature and Science, Tokyo, Japan (NSMT); Senckenberg Museum Forschunginstitut (including the Zoologisch Museum Göttingen collection), Frankfurt-am-Main, Germany (SMF-ZMG); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Natural History Museum of Denmark (formerly the Zoologisk Museum, Københavns Universitet, Copenhagen) (NHMD); Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore (ZRC); and Zoological Survey of India, Calcutta, India (ZSI).

Freshly collected pinnotherids should be carefully preserved. In the past, as with many parasites, they were often placed in 5–10% formalin (not always buffered), but nowadays, they are mostly preserved directly in 70–80% ethanol. For fresh specimens, it is useful to carefully clean them of mucus, debris, and mud prior to fixation. Otherwise, the mucus and mud can harden or become sticky in preservative, making subsequent cleaning more difficult and increasing the likelihood of damage to appendages, spines, and setae. Specimens of species with firmer and better chitinised exoskeletons can be directly preserved in 80% ethanol, leaving appendages sufficiently flexible for taxonomic examination, yet suitable for DNA extraction. Softer-bodied species, however, require more careful treatment. If collected alive, specimens can be euthanised slowly by refrigeration or freezing in water (preferably seawater), or rapidly (almost instantly) by immersion in ice water. Photography whilst fresh is also recommended to record not only colour in life, but also the natural form in case of carapace collapse during fixation. The use of high-concentration ethanol as a first step is not recommended because it can desiccate the specimens too rapidly, potentially collapsing the carapace and making the appendages stiff and brittle. Specimens will best retain their true shape and form if they are: 1) initially fixed in a 5–10% formalin-seawater solution with subsequent transfer to 80% ethanol, or; 2) preserved through an increasingly concentrated ethanol series (60% through 80%) over at least several hours (starting with as low as 60% diluted with seawater) to prevent rapid osmotic changes that lead to deformation or collapse, with final storage in 80% ethanol diluted with fresh water. Regardless of the method used, the legs, especially P5, tend to fold back on themselves and can become severely twisted as the preservative or fixative acts on the specimen. After about 5–10 minutes in the preservative, the legs of the specimen should be repositioned and spread out, and left for another 15–30 minutes to become "fixed" in place prior to the next preservation steps. If material is required for specialised molecular work, then whole individuals or a tissue sub-sample should be prepared from the outset for that purpose.

The taxonomy of the bivalves follows Huber (2010).

STATE OF PLAY

The foundations for pinnotherid taxonomy were primarily laid by Otto Bürger (1895) in his seminal paper on Southeast Asian pea crabs, which not only described many species but also introduced several important characters such as the segment proportions of MXP3. Although Bürger (1895) used the proportions of the P2–P5 to distinguish species, he did not realise that the ambulatory legs are naturally asymmetrical in some taxa, some markedly so. De Man (1921, 1929) discussed the matter and was the first to suggest that asymmetrical legs may not be an anomalous condition but a natural occurrence. In another major contribution, Gordon (1936) established the taxonomic reliability of asymmetry as expressed in species now assigned to *Arcotheres*, and Sakai (1939) reported on pereopodal asymmetry in *A. boninensis* (Stimpson, 1858). In the 1990s, Raymond Manning restarted work on their taxonomy and in two key papers (Manning, 1993a, b), he emphasised that the above characters allowed for more genera and species to be recognised. Over the last three decades, there has been a relative explosion of studies on pinnotherids, with numerous taxa described and systematic positions clarified (e.g., see Campos, 1989, 2009, 2013, 2016, 2017, 2018; Stevens, 1990; Pohle & Marques, 1998; Campos & Manning, 2001; Ng & Manning, 2003; Ahyong & Ng, 2005, 2007a, b, 2009, 2020, 2021; Komatsu & Ohtsuka, 2009; Komatsu & Takeda, 2009; Becker & Türkay, 2010; Campos & Hernández-Ávila, 2010; Ng & Ngo, 2010; Jiang & Liu, 2011; Ahyong et al., 2012; Ng & Kumar, 2015; Salgado-Barragán, 2015; Ng & Ho, 2016a, b; Ahyong, 2018, 2020a, b; Trivedi et al., 2018a, c, 2019, 2020; Campos & Hernández-Aguilera, 2019; Cuesta et al., 2019; Ng et al., 2019a, b; Felder & Palacios Theil, 2020a, b; Komai et al., 2020; Salgado-Barragán & Barragán-Zepeda, 2021; Salgado-Barragán et al., 2021). Molecular phylogenetic studies have been particularly useful in elucidating interrelationships and the higher classification of pinnotherids (e.g., Palacios-Theil et al., 2009; Ocampo et al., 2013; Palacios Theil et al., 2016; Tsang et al., 2018; Palacios Theil & Felder, 2019, 2020a, b).

Not surprisingly, given the poor state of knowledge of many pinnotherids, there is no good comprehensive key to the Pinnotheridae. Tesch (1918) was the last to attempt this, preparing a key to the known genera and 58 species of *Pinnotheres* that he regarded as valid at the time. Tesch (1918), however, did not actually examine types or material of many species, relying only on published accounts in most cases. During his time, the natural asymmetry in ambulatory legs in many species had also not yet been recognised. De Man (1921: 261, 262, 264) observed asymmetry but suggested that it was an abnormality due to parasitism by bopyrid isopods, an idea he later discarded (De Man, 1929: 14) when he had more specimens. Neither Bürger (1895) nor Tesch (1918) considered pereopodal asymmetry in their descriptions. Bürger's (1895) figures only show the ambulatory legs for the right side, while Tesch's (1918) figures do not mention or depict asymmetry at all. The carapace width-to-length ratio was used as diagnostic, but De Man (1929) challenged this given that the soft carapace is easily deformed. Gordon (1936: 163), Griffin & Campbell (1969: 160), and others also criticised the accuracy and usefulness of Tesch's key to *Pinnotheres*. Gordon (1936: 164, fig. 2a) even had doubts about the reliability of the proportions of the MXP3 propodus and dactylus as she noted that this character varies in some species.

Manning (1993b) provided a synoptic key to the known pinnotherid genera (with an emphasis on West African taxa), but did not distinguish between several genera due to a lack of characters. To date, no reliable generic key is available, and certainly no species key to genera such as *Pinnotheres*, *Arcotheres*, and *Nepinnotheres* has been attempted. For these large genera, many named taxa have yet to be redescribed and the types re-examined. In many cases, especially in the large genera, species are still being reassigned following redescription of type material and correction of errors (e.g., Ng et al., 2017; Trivedi et al., 2020; Ahyong & Ng, 2021; present paper).

From an ecological perspective, the latest review of symbiosis in the Brachyura (Castro, 2015: 558) noted that most pinnotherids can be treated as commensal symbionts, but observed ambiguity over whether some should be treated as parasites. Johnson (1963), for example, treats them as "semi-parasites", whereas some carcinologists regard them as true parasites (e.g., Silas & Alagarswami, 1967; Ng & Manning, 2003). While it is true that the ecology of many pinnotherid species is poorly studied and their effect on the host is not comprehensively known, a good body of data (mainly on European and American species) suggests that the relationship is usually detrimental to some degree for the host, whether they are molluscs or echinoderms (e.g., Seed, 1969; Kruczynski, 1972; Anderson, 1975; Bierbaum & Shumway, 1988; Tablado & López Gappa, 1995; Hamel et al., 1999, 2019; Cruz-Kaled et al., 2004; Narvarte & Saiz, 2004; Saeedi & Ardalan, 2010; Mena et al., 2014). For the time being, we regard them as symbionts.

AVAILABILITY OF SPECIMENS

Finding pinnotherids in bivalves is very much a hit-and-miss affair, with most bivalves not containing crabs. However, there have been a few cases where the relative incidence of pinnotherids was higher. For example, the presence of *Arcotheres placunicola* Ng, 2018a, in the window-pane oyster *Placuna ephippium* (Philippson, 1788) can be up to 70% in parts of Singapore, but in other parts of the world, there are almost no records of these crabs. As such, the infestation of pinnotherids in bivalves can be quite localised, possibly affected by season, water currents, habitat, host condition, etc. This is an important consideration because even *A. placunicola* did not seem to be so common in the

1950s and 1960s, when various molluscs were collected for malacological work and symbiosis studies, at least on the basis of published accounts and ZRC specimens. Yet over the last decade, *A. placunicola* has become very common in Singapore, with an infection rate of about 30–50% for the *Placuna* collected (unpublished data). Conversely, species such as *A. exiguus* (Bürger, 1895) are rarely seen, even when large numbers of their hosts, the venerid clams *Marcia recens* and *Paphia undulata*, are sampled. In some instances, a kilogram of these molluscs with some 50 clams can yield up to 10 crabs, but in most cases, there are no crabs at all. The same has been observed for *Plenotheres coarctatus* (Bürger, 1895) in the glauconomid clam *Glauconome rugosa* Hanley, 1843. This probably has much to do with where the clams were collected.

Almost universally, pinnotherid males are seldom found, but the incidence of males is dependent on the species. In the case of *A. placunicola*, a large number of males were collected and heterosexual pairs frequently obtained from one host. For species such as *A. similis* and *A. exiguus*, males are also not rare, and while not collected together, a good number of males are also collected when the females of the species are common. Males of *A. palaensis*, *Pl. coarctatus*, and *M. globosus*, on the other hand, are extremely rare, with only a few specimens known. We are of the opinion that males in *Arcotheres* are permanent entities and not a transitional ontogenic stage. There have been suggestions that at least some pinnotherids may be protandrous, starting as males and becoming female later in life. While this may be the case for some pinnotherids (see Ahyong & Ng, 2008), in *Arcotheres*, we do find small females that resemble males in habitus but do not have the associated gonopods (see Fig. 15A–C).

CHARACTERS

Pinnotherid crabs are in most cases morphologically conservative, so the paucity of taxonomic characters has always been one of the challenges of pinnotherid taxonomy. Historically, carapace shape, MXP3 features, and proportions of the ambulatory legs (P2–P5) have been the most important characters used because the majority of species are known only from females. Consequently, many important taxonomic characters used for other brachyuran groups, such as the male pleon and gonopods, are unavailable for most pinnotherid species and have not yet played a significant role in shaping the pinnotherid system. In addition, as most pinnotherids, particularly adult females, have poorly chitinised and weakly calcified carapaces and appendages, they are more susceptible to the vagaries of preservation than other, heavily chitinised crabs. The degree of variability in many diagnostic characters is often poorly understood, especially for pinnotherid species represented by only a few specimens. Many taxonomic studies use proportions of the MXP3 and P2–P5 to separate species, recognising new taxa for slight differences without knowledge of how much they may vary in life. As such, many of the characters that have been historically used as diagnostic need to be tested against good series of specimens to evaluate their taxonomic reliability. It helps when specimens are compared when fresh or very recently preserved, although this is often not possible with old type material. While many pinnotherid workers are aware of these problems, in lieu of determination of additional reliable alternatives, the suite of useful taxonomic characters remains limited.

The present study relies on a large series of specimens of several well-known species, obtained sometimes from many localities. In many cases, live specimens were studied and comparisons based on fresh material.

Female-to-male ratios. When there is a good series of specimens, the female-to-male ratio of many of the species treated here is noteworthy and has taxonomic significance. Although sampling bias cannot be excluded, the large series available to us suggests a real pattern is present. In species like *A. palaensis*, males are very rare—over 90 female specimens were examined, but only two males are known. The same is true for males of *Plenotheres coarctatus* (1:21), although proportionally more males are known. Males are more common in other species: *A. placunicola* (1:2), *A. similis* (1:5), *A. exiguus* (1:5), and *A. rayi* (1:8). Interestingly, in *Magnotheres globosus*, the male:female ratio across all lots is 1:11, but among Australian specimens, only 1:5. This difference is probably a sampling artefact given that Australian *M. globosus* is represented by only 12 specimens from four lots. Why the sex ratio in the Pinnotheridae is so skewed is not currently known, but males are usually less common than females. For this reason, unlike in most brachyurans, pinnotherid taxonomy is based mainly on female characters.

Male or female? In many pinnotherid species, and especially for the Indo-West Pacific taxa, subadult females closely resemble males superficially, with a more rounded carapace, well-developed front, eyes visible dorsally, and a narrow triangular pleon; so much so that they can be indistinguishable unless the pleopods are examined. We are of the opinion that some of the old records of "males" in the literature are actually juvenile females. At this early stage, the gonopods are usually undeveloped but the number and setation/form of pleopods are still visible. Several small specimens of *A. palaensis* and *P. coarctatus* (e.g., Fig. 15A) were originally identified as males, only to be confirmed to be subadult females on re-examination. As discussed above, males of *A. palaensis* are very rare and, as such, records such as those of De Man (1929: 14), which recorded two males among 11 females, require confirmation.

Christensen & McDermott (1958, as *Pinnotheres*) characterised postlarval ontogenetic growth stages for *Zaops ostreum* (Say, 1817), and Watanabe (2013, as *A. alcocki*) reported an additional stage in male *Arcotheres palaensis*. Although these stages might prove to have wider validity, especially in males, the life histories of too few species of pinnotherids, let alone males, are currently known. Although some studies have examined staging (e.g., Manning, 1993b; Komai et al., 2020), we do not attempt to correlate our examined specimens with the stages defined by Christensen & McDermott (1958) and Watanabe (2013). That being said, we certainly acknowledge that detailed life history studies of more pinnotherids will be extremely useful in better understanding their biology.

Carapace. The shape of the female carapace has been used as a major character in pinnotherid taxonomy, with the general shape as well as structures of the anterolateral margins and front often used as diagnostic features. Whether the dorsal surface is inflated or flat has also been used as a species character. While the carapace shape is a useful character if well preserved, the effects of suboptimal to poor preservation must also be considered in identifying specimens. Because the female carapace in most species is often poorly calcified and weakly chitinised, it can be soft and pliable, even in life. As such, depending on osmotic balance during the preservation process, effects of highly concentrated alcohol can rapidly dehydrate the specimen and cause deformation, causing the cephalothorax to change shape shortly after preservation. These effects are more serious if the specimen is preserved after a recent moult, when the cuticle is even softer. Likewise, poor initial preservation and/or long-term storage in unbuffered formalin can cause the cuticle to become frail and delicate. Also, if external osmotic conditions are too different from that of the specimen, significant deformity can result, either by swelling or shrivelling. In many female specimens with thin and soft cuticle, the dorsal surface of the carapace can collapse to differing degrees, with the lateral and posterior margins often folding in on themselves. In such cases, the female pleon sometimes folds inwards or appears shrivelled.

Beyond preservational effects, there can a substantial degree of natural carapace variation in some species. The excellent series of *A. palaensis* shows that female carapace shape alone is not a reliable feature in this species. The female carapace is typically transversely subovate with the front very low, barely protruding anteriorly, and the anterolateral margins evenly convex (Figs. 5A, 8A, 11A, B, D, F, 12F, 13A, B, C). The front, however, may be relatively more prominent in some specimens, with the anterolateral margins gently sloping posteriorly or evenly convex (Figs. 9A, 11E, G, H, 12B, C, E, G, H, 13E–H, 14A–G). Many female specimens also have a carapace that appears more subquadrate, with the anterolateral margins even appearing sinuous and the posterolateral margins more expanded laterally (Figs. 12G, H, 13D–H). One extreme example is seen in *A. rayi*. The type female specimen has a front that is in line with the truncate anterolateral margins, so much so that the anterior margin of the carapace is straight with the position orbits discernible as two clefts (Fig. 46A). In a series of fresh specimens, some have the frontal margin protruding anteriorly with the anterolateral margins gently convex (Figs. 47A, C, 48B, C, 49A), while others have the frontal margins at most weakly produced (Fig. 48B). Similarly, the frontal margins of female *A. palaensis* can vary from almost straight to gently convex or sinuous (Figs. 5A, 8A, 13, 14). Even from one lot (e.g., ZRC 2021.821), the front may be sunken in (Fig. 3G) or anteriorly produced (Fig. 3E, F). The posterior carapace margin also varies markedly, from gently sinuous to deeply concave (Figs. 13, 14). For these reasons, several species need to be synonymised under *A. palaensis* as the only differentiating character was the female carapace shape. In *A. palaensis*, the posterior margin is usually concave in fresh specimens (Fig. 3B, D–F), but is sometimes almost straight (Fig. 3A, H) to gently convex (Fig. 3C). One caution here is that in many of these specimens, the posterior margin becomes distinctly more concave after preservation. There are patterns in some species. In female *A. exiguus*, for example, the posterior carapace margin is usually straight to gently sinuous (e.g., Figs. 37A, C, 38A, B, 39D), but can sometimes be gently concave (Fig. 39A). In some poorly preserved specimens, however, the carapace can be badly deformed, making the posterior carapace margin artificially concave.

In species such as *A. exiguus* and especially *A. obesus*, the female carapace and even the pereopods are especially poorly chitinised, and after a few months in preservative, they become very fragile, sometimes almost membranous. This makes their study difficult.

The female carapace of *Magnotheres globosus* is interesting given the relative thinness of the cuticle. In live specimens, the carapace texture is crisp but firm. Within minutes of being placed in 70% alcohol, the carapace surface often starts to gently collapse, with folds or wrinkles forming and the firmness disappearing rapidly. If first preserved in strong alcohol (85% or more), the carapace often becomes brittle and fractures easily.

The carapace of males is a different matter. The cuticle is invariably thicker and more strongly chitinised, and the shape and proportions do not deform or change even after long preservation. As such, when available, male carapace shapes can be used to distinguish species. A good case in point pertains to two morphologically similar species, *A. similis* and *A. placunicola*. Adult male *A. similis* have a round or slightly longitudinally ovate carapace (Figs. 31A, D, 32A) and the dorsal surface is inflated, appearing distinctly convex (Fig. 31B). The carapace of *A. placunicola*, on the other hand, is always wider than long, appearing transversely ovate (Figs. 60A, D, 62A), and the dorsal surface is only gently convex, appearing almost flat in smaller specimens (Fig. 60B, E). These differences are consistent even for small specimens.

Many of these preservational challenges relating to the carapace shape are most apropos to the Indo-West Pacific and eastern Atlantic pinnotherids, where the fauna is dominated by pinnotherine species in which mature females have a delicate, weakly chitinised carapace and pleon. As a result, carapace and pleon shape must be used with care. Conversely, the American pinnotherid fauna includes a much larger proportion of pinnixines, which are typically much more stongly chitinised and for which carapace and pleon shape are reliably preserved by traditional methods. Certainly, soft-bodied pinnotherines also occur in the eastern Pacific and western Atlantic, but to a much lesser extent than in the Indo-West Pacific and eastern Atlantic.

Epistome. The structure of the posterior margin of the epistome is often useful to separate species, but is usually similar in close allies. It is useful for same-sex comparisons only, as males generally have a narrower carapace than females, which in turn affects epistome proportions. For example, in *A. similis* and *A. exiguus*, the posterior margin is relatively wider with the margins gently convex (Figs. 28D, 30K, 38C, 41C), but in *A. palaensis*, it is proportionately narrower with the margins only gently concave (Figs. 4, 8C, 9C, 17O, 18M).

Antennal article 1. A possibly phylogenetically informative feature highlighted by Campos (2009: 42) is the protuberance on the mesioventral margin of the epistome that he termed the basal antennal article. Ng et al. (2019b: 349), in their revision of *Orthotheres* Sakai, 1969, discussed this character at length, noting that the "basal antennal article" was antennal article 1, which carries the opening of the green gland, the nephridiopore. While antennal article 1 is often immovably fused to the epistome, the presence of the nephridiopore is always indicative. Ng et al. (2019b: 349) observed: "The fused articles 2 and 3 are usually demarcated by shallow grooves and article 1 is also immovably fused but positioned very low on the epistome such that its lower margin intrudes into, and forms part of, the margin of the buccal cavity. This lower margin of article 1 [as indicated by the nephridiopore] varies from indistinct to bluntly angular, appearing as a short lobe or protuberance, being most pronounced mesially. Among the species examined, the condition of this protuberance shows no obvious taxonomic pattern within or between genera, although it has a wider significance as a pinnotherid synapomorphy based on our consideration of all Brachyura. In *Orthotheres* s. str., the mesioventral angle of antennal article 1 is slightly projected and tubercle-like, with a small pore at the tip, almost certainly the nephridiopore. This mesioventral position of the presumed nephridiopore, readily observed in larger specimens of *Nepinnotheres* and *Arcotheres*, may well be the normal position in most, if not all, pinnotherines (and pinnotherids)." Although we have found the nephridiopore to be always present on the buccal margin in pinnotherids, making it useful at high taxonomic levels, we have not found this feature to be useful in separating species or genera.

Chela. The structure of the chela is relatively consistent within species for most taxa. Species such as *Arcotheres palaensis* and *Magnotheres globosus* have relatively short and stout adult female chelae (see Figs. 6F, 7B, 8D, 9D, 79D, 80D) with little variation. In *A. exiguus*, however, the proportions of the adult female chelae vary more than in the aforementioned species, from relatively short (e.g., Fig. 45B) to longer (e.g., Figs. 36F, 37E, 38D, 41E).

Pereopods (P2–P5). De Man (1921: 14) was the first to suggest that the asymmetry of the female ambulatory legs might prove to be a constant character in at least some species of *Pinnotheres* (sensu lato). Gordon (1936: 164) discussed this matter at length, noting that it was probably common in the genus but not evident in small specimens. Sakai (1939: 588, text-fig. 74) documented asymmetry of the ambulatory legs, particularly of P4, as a normal feature of *Arcotheres boninensis*. The proportions and symmetry of P2–P5 have become important features of pinnotherid taxonomy, especially in the Indo-West Pacific. A key character for *Viridotheres* Manning, 1996, for example, is that the female P3 (especially the merus and dactylus) is the longest of all the ambulatory legs (Manning, 1996). A major diagnostic feature of *Arcotheres* is that the female P4 is asymmetrical, with the longer leg being the longest of the ambulatory legs.

Compared to the carapace, the pereopods are relatively more robustly chitinised and as such are less vulnerable to poor preservation, although if preserved in acidic formalin and/or previously dried, they also become soft and the proportions and shape (especially the merus) may be affected. As the leg segment proportions are taxonomically effective, poor preservation may result in incorrect ratios and shapes. In cases where the specimens were previously desiccated and rehydrated, the appendages appear translucent and slightly distorted; for these cases, the proportions and exact features need to be interpreted more carefully.

The extent of asymmetry is not well known for males, notably in *Arcotheres*, mainly because they are generally rare. Previously, even when males were described, they were normally assumed to have symmetrical ambulatory legs. Neither De Man (1921) nor Gordon (1936) discussed male P2–P5 asymmetry; most papers do not discuss the matter. Ng (2018a: 478) noted that there was some degree of asymmetry in walking legs of male *A. placunicola*, and that the P4 dactylus on one side is slightly longer than the other. In the present material, there is slight asymmetry in the male P5 dactylus in *A. placunicola* (Fig. 62H versus Fig. 62L), and slight asymmetry in the P4 dactylus of *A. similis* (Fig. 32F versus Fig. 32J); while in *A. palaensis*, the left P4 dactylus is prominently longer than the right one (Fig. 22D versus Fig. 22H). No asymmetry was observed in the pereopods of male *A. exiguus*, *A. rayi*, or *Pl. coarctatus*, even in the P4 (Figs. 44A, F–I, 45C–F, 52A, F–I, 68A–H), although we note that the former two species are also somewhat unusual within the genus in other features (G1 and P5) as currently composed. This means that asymmetry is present in at least some male *Arcotheres*, albeit less distinctly than in females. The present observation presents major challenges for the taxonomy of some genera. While females with distinctly asymmetrical ambulatory legs are easy to assign to genera like *Arcotheres*, those with symmetrical legs are usually referred to *Pinnotheres* or *Nepinnotheres*; what do we do when only males are known for some described species? Which genus would they belong to if the differences in male ambulatory asymmetry is only slight (e.g., see Ahyong & Ng, 2021; discussion for *Magnotheres*, new genus)?

Why female ambulatory legs (notably the P4) are asymmetrical is not known and no studies have been done. It is interesting nevertheless to note that most *Arcotheres* live in bivalve species that have distinctly asymmetrical shells, and the longer P4 on one side may be associated with helping the crab reach the more elongate part of the bivalve. It is certainly not always easy for the whole crab to move around within the bivalve due to its swollen carapace and size. Also noteworthy is that in *Plenotheres coarctatus*, which is typically found in bivalves of the family Geloinidae and Glauconomidae with more symmetrical shells, the ambulatory legs show less pronounced asymmetry; and in *Magnotheres globosus*, which occurs in the symmetrical Pinnidae, the ambulatory legs show almost no asymmetry.

An important character first highlighted by Gordon (1936) is the presence, in some species, of small spinules on the subdistal flexor margin of the male and female P5 dactylus. These distoflexor spinules are distinct from the dense, short, soft setae that may be found along the margins, sometimes reaching the tip, being stiff and immobile. These spinules are often small, semi-transparent, and not easy to observe, so some degree of manipulation and adjusting of the light source is needed under high magnification. They may also be abraded or broken off, so care must be taken to ascertain this character. The row of spinules, when clearly present, are graded with the distal ones longest, becoming smaller proximally. The proximal spinules are often very small and low, appearing granuliform and not easy to see. One or two rows of spinules may be present, and when there are two, the upper row is usually the more pronounced with the spinules better developed and more numerous, but this can vary sometimes even in the same specimen (e.g., see *Magnotheres globosus*; Fig. 83D', D", H', H"). The length of the row varies between species, with one of the rows relatively long in *A. similis* (Fig. 30D', H'), but shorter in *A. placunicola* (Fig. 59G', K', K"). This character was used by Gordon (1936) to describe a new species, *A. spinidactylus* (a synonym of *A. similis*; Fig. 30L) (although she only recognised one row of spinules and did not notice the second, shorter row present in her specimens), and has since also been reported and used by other authors (e.g., see Griffin & Campbell, 1969; Dai et al., 1980; Takeda & Konishi, 1988; Ng, 2018a; Trivedi et al., 2018c, 2019; Ahyong & Ng, 2020, 2021). The presence of these spinules is useful to separate closely related species like *A. placunicola* and *A. palaensis*, being distinct in the former and absent in the latter. Two distinct rows of P5 distoflexor spinules are present in other Indo-West Pacific taxa like *A. boninensis* (Stimpson, 1858), *A. pernicola* (Bürger, 1895), and *A. purpureus* (Alcock, 1900) (see Trivedi et al., 2019; Ahyong & Ng, 2021). Some taxa like *Plenotheres coarctatus* have P5 distoflexor spinules that are relatively smaller, even for the distalmost ones (Fig. 66J, K), but they can be relatively large in *A. similis* (Fig. 30D', H', L). *Arcotheres exiguus* is not considered to possess P5 distoflexor spinules, although in a few specimens, one can discern a faint row of very low "prickles" or pointed granules, all of which are of similar size (Fig. 42M); in most specimens these are absent or only a few scattered, low "prickles" are visible. The same is true for *A. palaensis*; there are sometimes some scattered, low P5 distoflexor "prickles" or acute granules visible, but they are not arranged in rows (Fig. 18F').

The degree and type of setation on the margins of P4 and especially P5 also show some patterns. In species such as *A. exiguus*, *A. rayi*, and *Pl. coarctatus*, the flexor margin of the propodus and dactylus is densely lined with long setae with other surfaces largely glabrous (Figs. 41I, M, 42F, I, 49I, M, 66D, H), whereas in most other species, the setae are proportionately shorter, less dense, and not largely restricted to the flexor margins (e.g., in *A. palaensis*; Fig. 17D, J, N). The flexor margin of *A. palaensis* is densely covered with long and short stiff setae, which gives it a distinct bottle-brush appearance (Fig. 7C). In similar species like *A. placunicola* and *A. similis*, the setae are less dense and appear less bristly.

Another series of characters that may hold taxonomic potential is associated with the basis-ischium and merus of P5 in males. The articulation between the P5 ischium and merus is diagonal (oblique to the segment axis) in species like *A. exiguus*, *A. rayi*, and *Pl. coarctatus*, but is more perpendicular in other *Arcotheres* and *M. globosus* treated here. The P5 basis-ischium is distinctly elongate in species such as *A. ocularius* (Fig. 24G, K) and *M. globosus* (Fig. 83D, H), and slightly so in *A. similis* (Fig. 30D, H). In most of the other taxa treated in this paper, the P5 basis-ischium is more quadrate (e.g., Fig. 17D, H, J, N).

MXP3. The structure and proportions of the palp (carpus, propodus, and dactylus) are important in diagnosing genera and species. While the point of articulation of the dactylus on the propodus (whether proximal, median, or subdistal) appears to be consistent, the length of the dactylus is not always constant. Gordon (1936: 164, fig. 2a) first indicated issues with variation when she noted that in one specimen of *A. similis* (as *A. spinidactylus*), the dactylus on one side was distinctly shorter than that of the other side (Fig. 33A, B). Ng (2018b) discussed this further for the holothurian symbiont *Trichobezoares villosissimus* (Doflein, 1904), for which the dactylus was very short in several specimens. Ng (2018b: 621) suggested that a shorter dactylus may be due to damage and that the character must be used carefully, especially if there are few specimens. It is also important to always check the condition of the dactylus on both MXP3 to ensure the proportions of the left and right structures are the same. The structure of the fused ischiomerus is useful in some cases, but seems to be more or less consistent in members of one genus. It has been used to support the establishment of *Trichobezoares* Ng, 2018b, for *Pinnotheres villosissimus* Doflein, 1904 (Ng, 2018b); and a new genus, *Plenotheres*, for *Pinnotheres coarctatus* in the present study.

It is useful to note that some figures of the MXP3 dactylus and propodus are not comparable between publications because they may not have been drawn in the same plane; the entire structure should be on a level surface, especially the articles of the palp. Because the palp is articulated, it is important to ensure that the carpus, propodus, and dactylus are horizontal (as best as possible) before any figures are made. If the palp is tilted anteriorly with the dactylus and propodus not parallel, and more so if it is figured from the inner surface, the dactylus will appear to be longer than it is and reach beyond the tip of the propodus, even when it does not (e.g., see George & Noble, 1970: fig. 1). In one specimen of *Magnotheres globosus*, for example, the dactylus does not reach the tip of the propodus when drawn with the structure level (Fig. 84F), but when drawn at a slight angle, the dactylus appears to overreach the propodus apex (Fig. 84G). The same is true for the propodus, which may appear shorter or longer depending on the orientation of the structure when figured (e.g., Fig. 83J, K).

That being said, the shape of the MXP3 propodus is somewhat variable, with the apex appearing rounded to truncate in some species. Whether the dactylus is inserted submedially, slightly proximal to, or slightly distal to the midlength of the ventral margin of the propodus can vary. Although it is constant in most species, in at least *Arcotheres exiguus* and *Magnotheres globosus*, it can be inserted slightly distal to the midlength in the former, or slightly promixal in the latter. The relative length of the dactylus can also vary; in *A. exiguus* in particular, it is especially variable, from short to long (e.g., Figs. 36E, 41B, Q, 42A, L, 44B, 45A). Whether this variation reflects normal polymorphism or is due to damage and regrowth (as in *T. villosissimus*; see Ng, 2018b) cannot be determined at present.

Eyes. When present, the cornea of species of *Arcotheres* is always prominent and well pigmented, being especially distinct in fresh material (e.g., Figs. 2C, F, 4, 63C, D, 74C, D). The eyes, when present (absent in *A. latifrons* (Bürger, 1895)), although short and stout, fill the small orbit and are never fused to the carapace in any species we have examined. Whether the eyes are visible in dorsal view is a surprisingly useful character in adult females of some species. In *A. palaensis*, all female specimens unambiguously identified with this species never have the cornea substantially visible in dorsal view; in most cases, the eyes are not visible (Figs. 4A–D, 5A, 8A, 9A, 13, 14). Even when the eye can be extended anteriorly, only the edge of the cornea, at most, is visible in dorsal view. In contrast, the eyes in a few female *A. palaensis* are distinctly visible in dorsal view (e.g., Figs. 6A–D, 19A, M). In old and poorly preserved specimens, because of the poorly chitinised carapace that is easily shrivelled by preservation or drying, the true condition can be difficult to ascertain. The authors, however, have examined numerous live specimens of female *A. palaensis* and freshly preserved specimens, and find the visibility of the eye in dorsal view a very reliable character state. This is regardless of whether the frontal margin is more prominent and protruding anteriorly, or the carapace more inflated. The character has been shown to be reliable for *A. ocularius* from Fiji and Lombok, for which a large series of specimens is available with eyes that are always clearly visible in dorsal view (Fig. 23; see Komai et al., 2020).

Male pleon. The form of the male pleon has seldom been used in Indo-West Pacific pinnotherid taxonomy, mainly because of the rarity of males. As such, the degree of variation in this structure is not well known. As with other Brachyura, however, the available data suggests that pleonal morphology varies predictably in shape depending on the size and maturity of the specimen, especially in the appearance of somite 6 and the telson. Added to this, juvenile females can so closely resemble males in external appearance that the pleon must always be checked for gonopods (see above discussion). The pleon of early juvenile females can be near indistinguishable from that of size-matched males (Fig. 15C). Ng (2018a: 478) and Komai et al. (2020) noted that the shape of the male somite 6 and telson change allometrically and, as such, when only singletons are available, the character should be used with caution, considering the maturity of the specimen. Slight variation occurs even within species; in male *A. palaensis*, the telson varies from near semicircular to almost pentagonal (Fig. 22J, O). In *A. placunicola*, small males have a triangular telson with convex margins (Fig. 62B), which become more subquadrate in shape in larger specimens (Fig. 61B, C). Some differences, however, are significant; for example, the broadly trapezoidal male telson in *Magnotheres* is diagnostic (Figs. 85C, 86J).

Female pleon. The adult female pleon is almost never used in Indo-West Pacific pinnotherid taxonomy, mainly because there appears to be too much variation associated with growth and maturity. The pleon can change in shape substantially during growth and bulge due to the large egg mass when ovigerous. For example, in *A. similis*, smaller females have a regularly broad triangular telson (Fig. 27B), which becomes wider and more subtruncate in large individuals (Fig. 28B); in *A. exiguus*, the telson is broadly and unevenly fusiform in smaller specimens (Fig. 37B), becoming transversely ovate in large specimens (Fig. 39B). In *A. rayi*, on the other hand, the adult female pleon shape changes little, even in large specimens (Figs. 46B, 47B). The shape of the adult telson is generally consistent in shape, but not always. In *A. palaensis*, for example, the adult female telson is usually quite wide and triangular with the lateral parts tapering, appearing fusiform (Figs. 5B, 8B, 9B). In some specimens, however, the telson is distinctly narrower (Fig. 15D) or appears almost flattened (Fig. 15E). In addition, in some specimens, the telson is asymmetrical (e.g., see Fig. 15D), differing on either side in shape and proportions. We are confident that these represent intraspecific variations as most other specimens from the same lots have the more typical female telson condition. Some of the observed differences may also be due to preservational effects on the soft cuticle or poor condition prior to preservation, resulting in obvious deformations. We fully concede, however, that the shape of the adult female telson may prove to be taxonomically useful for some taxa.

Gonopods. Gonopod structures are not often used in pinnotherid taxonomy, especially so in *Arcotheres*, where males are generally rarer. The general pattern for many pinnotherid species, even across genera, is that the G1 is a gently curved structure, gradually tapering to a slender distal part which often has the tip gently deflected relative to the main plane of the gonopod. That being said, G1 structures can sometimes be very diagnostic at the genus and species levels. The case of *A. exiguus* is noteworthy; the G1 structure (Figs. 44K, L, 45H, I) is consistent across its very wide range, from the western Indian Ocean to the West Pacific. *Plenotheres*, for example, has the distal part ornamented with a prominent dorsal lobe that is very distinctive (Fig. 68N, P). *Magnotheres*, on the other hand, has the G1 very slender and long with the tip tapering (Fig. 86K). At the species level, the G1s of *A. exiguus* and *A. rayi* are diagnostic with a distinct subterminal projection (Figs. 44K, L, 45H, I, 52N, O). The tip of the G1 is more slender and gently upcurved in some species (e.g., in *A. similis*); this character varies in relative length (Figs. 32L–N, 33E–H, J, K) and can be affected by age (see Ng, 2018a: 478) as well as how well the specimen is preserved. In some specimens, the tip appears slightly twisted or shorter because the cuticle has slightly distorted.

The structure of the G2 endopod is relatively consistent, always short with the distal part spatuliform to subspatuliform. The presence of an exopod was only recently highlighted by Ahyong et al. (2012), but our observations suggest that it may be widely present in pinnotherids—it is present in all the species examined in this study. When present, the exopod is usually prominent, often as long as the endopod itself, although in some extreme cases, it is several times the length of the endopod, e.g., in *Tacitotheres glaber* (Bürger, 1895) and several species of *Viridotheres* (see Ahyong et al., 2012: fig. 2I; Ahyong, 2019: fig. 1K; Ng et al., 2019b: fig. 10L). The taxonomic value of this character will require further study.

Host records. Some pinnotherids have been recorded from a large number of hosts from different families (for reviews, see: Schmitt et al., 1973; Palacios Theil et al., 2016: supplementary material; De Gier & Becker, 2020). Many of the old host records for "well known" or "widespread" species should be considered doubtful and probably the result of misidentification of the pinnotherid and/or the host, at least until they can be substantiated. It is of course possible that some pinnotherid species are generalists and can live in many species of molluscs and other invertebrates, but we are of the opinion that this is not as common as it has been reported (e.g., Schmitt et al., 1973). Our studies show that *A. palaensis* is only known from arcids, but according to Schmitt et al. (1973: 65), it is also present in *Placuna* Lightfoot, 1786 (Placunidae), and *Mactra* Linnaeus, 1767 (Mactridae), records which we dispute. Ng (2018a) argued that Southeast Asian records from *Placuna* (originally from Bürger, 1895: 373) are almost certainly incorrect and belong to *P. placunicola* Ng, 2018a, instead. The record from *Mactra* was based on Chuang (1961: 188) and is likely to be *A. exiguus* instead (see present study), especially since the Mactridae is in the order Venerida. Many of the species found in Southeast Asia have more narrow host preferences than what the literature suggests. For example, Schmitt et al. (1973: 87) also listed a large number of hosts for the East Asian species, *Arcotheres sinensis* (Shen, 1932): Veneridae (*Tapes* Megerle von Mühlfeld, 1811, *Paphia* Röding, 1798, *Meretrix* Lamarck, 1799), Mytylidae (*Mytilus* Linnaeus, 1758, *Volsella* Scopoli, 1777), Pectenidae (*Chlamys* Röding, 1798), and Ostreidae (*Ostrea* Linnaeus, 1758, *Crassostrea* Sacco, 1897). Shen (1932: 135) himself had reported his species from an oyster (*Ostrea* sp.) and a clam (*Tapes variegatus* Sowerby, 1852, currently, *Venerupis aspera* (Quoy & Gaimard, 1835)). These seem doubtful and should all be rechecked. More recently, Jahangir et al. (2015) reported *Nepinnotheres villosulus* (Guérin-Méneville, 1832) from many species of venerid clams (*Meretrix casta* (Gmelin, 1791), *Callista umbonella* (Lamarck, 1818), *Protapes cor* (Sowerby, 1853), *Marcia recens* (Holten, 1802), *Gastrana multangula* (Gmelin, 1791), *Psammotreta angulata* (Linnaeus, 1767)) and arcid cockles (*Anadara antiquata* (Linnaeus, 1758)) from Pakistan. Jahangir et al.'s (2015: fig. 2B–E) figures of *N. villosulus*, however, depict two or possibly three different species from at least two genera. Moreover, from the variety of hosts alone, it can be inferred that the authors probably had at least two or three species of pinnotherids.

As such, host records, especially old records, must be treated very judiciously. In particular, historical changes in host taxonomy must be considered before accepting host records at face value. For instance, there was some confusion with the host identity of the poorly known species *Arcotheres pernicola* (Bürger, 1895), supposedly from the mytilid *Perna* Philipsson, 1788, and later shown to have come instead from the ostreid oyster *Magallana* Salvi & Mariottini, 2016 (Trivedi et al., 2019). This is significant as *A. pernicola* is actually morphologically closer to oyster-dwelling species such as *A. boninensis* (Stimpson, 1858) and *A. purpureus* (Alcock, 1900).

Accurate host records are much more useful in assisting identification of pinnotherid species than previously recognised. In our study, we find that pinnotherids that infest bivalves are usually host-specific, probably at least at the family or superfamily level, although some bivalves host more than one species of pea crab. In such cases, the pinnotherid species are usually very different in body form, such as *Xanthasia*, *Tridacnatheres*, and *Ostracotheres*, all of which infest tridacnid clams (Ahyong & Ng, 2005; Ahyong, 2018). For example, as noted above, all reliable records of *A. palaensis* are from arcoid clams, whilst *A. exiguus* is known from various related venerids. The unusual venerid, *Gafrarium*, hosts one species, *A. obesus* (Dana, 1852), with a wide range from Malaysia to Fiji (Komai et al., 2020). Noteworthy is that *Plenotheres coarctatus* occurs in two outwardly very different looking mangrove bivalves in different families, *Geloina coaxans* (Gmelin, 1791) (Cyrenidae) and *Glauconome* spp. (Glauconomidae Gray, 1853), but the clams are phylogenetically related (both belong to the superfamily Cyrenoidea). Similarly, *Magnotheres globosus* is known reliably only from fan shells of the family Pinnidae.

Host records are often confounded by the fact that pea crabs are incidentally found by malacologists as part of their work, and it has not always been possible to accurately associate hosts with the crab symbiont. In large-scale expeditions, particularly when large amounts of material are collected, some of the pinnotherids have no host records and/or the records are doubtful because of errors made while processing the volume of specimens collected. Also problematic with older host records is that they often come from markets where many bivalve species are sold together, and, unless the crabs were directly removed from the shells by the collector, records may be dubious. We have seen and collected pinnotherids

Table 1. List of species in *Arcotheres* and related genera.

***Arcotheres* Manning, 1993**	
Arcotheres alcocki (Rathbun, 1909) [*Pinnotheres*]	= *Pinnotheres parvulus* De Man, 1887 (pre-occupied name)
Arcotheres atrinae (Sakai, 1939) (*Pinnotheres*)	
Arcotheres boninensis (Stimpson, 1858) [*Pinnotheres*]	
Arcotheres cyclinus (Shen, 1932) (*Pinnotheres*)	
Arcotheres exiguus (Bürger, 1895) [*Pinnotheres*]	= *Pinnotheres winckworthi* Gordon, 1936 = *Pinnotheres vicajii* Chhapgar, 1957 = *Pinnotheres casta* Antony & Kuttyamma, 1971 = *Pinnotheres obscuridentata* Dai & Song, 1986
Arcotheres lanensis (Rathbun, 1909) [*Pinnotheres*]	
Arcotheres latifrons (Bürger, 1895) [*Xenophthalmus*]	
Arcotheres nudifrons (Bürger, 1895) [*Pinnotheres*]	
Arcotheres obesus (Dana, 1852) [*Pinnothera* (sic)]	
Arcotheres ocularius Komai, Kawai & Ng, 2020	
Arcotheres palaensis (Bürger, 1895) [*Pinnotheres*]	= *Pinnotheres arcophilus* Bürger, 1895 = *Pinnotheres rhombifer* Bürger, 1895 = *Pinnotheres latissimus* Bürger, 1895 = *Pinnotheres paralatissimus* Dai & Song, 1986 = *Arcotheres guinotae* Campos, 2001
Arcotheres pernicola (Bürger, 1895) [*Pinnotheres*]	
Arcotheres placunae (Hornell & Southwell, 1909) [*Pinnoteres*]	
Arcotheres placunicola Ng, 2018	
Arcotheres pollus Ahyong & Ng, 2020	
Arcotheres purpureus (Alcock, 1900) [*Pinnoteres* (sic)]	= *Pinnotheres nigrans* Rathbun, 1909
Arcotheres quadratus (Rathbun, 1909) [*Pinnotheres*]	
Arcotheres rayi Ahyong & Ng, 2007	
Arcotheres rotundatus (Bürger, 1895) [*Pinnotheres*]	= *Pinnotheres consors* Bürger, 1895
Arcotheres shahi Trivedi, Campos & Vachhrajani, 2018	
Arcotheres similis (Bürger, 1895) [*Pinnotheres*]	= *Pinnotheres modiolicola* Bürger, 1895 = *Pinnotheres kamensis* Rathbun, 1909 = *Pinnotheres spinidactylus* Gordon, 1936
Arcotheres sinensis (Shen, 1932) [*Pinnotheres*]	
Arcotheres tivelae (Gordon, 1936) [*Pinnotheres*]	
***Plenotheres*, new genus**	
Plenotheres coarctatus (Bürger, 1895), new combination [*Pinnotheres*]	
***Magnotheres*, new genus**	
Magnotheres globosus (Hombron & Jacquinot, 1846), new combination [*Pinnotheres*]	= *Pinnotheres meleagrinae* Hilgendorf, 1869 (nomen nudum) = *Pinnotheres latus* Bürger, 1895 = *Pinnotheres tenuipes* Borradaile, 1903 (pre-occupied name) = *Pinnoteres borradailei* Nobili, 1906a (replacement name) = *Pinnoteres ridgewayi* Southwell, 1911

from the bottoms of aquaria and display tables of markets where various bivalves were sold together and sometimes deshelled for customers. In such circumstances, host records can only be inferred at best.

TAXONOMY

Family Pinnotheridae De Haan, 1833

Genus *Arcotheres* Manning, 1993a

Type species. *Pinnotheres palaensis* Bürger, 1895, by original designation.

Diagnosis. MXP3 dactylus slender (digitiform), inserted on proximal one-third or near midlength of ventral margin of propodus, variable length; propodus linear, usually spatuliform, 2.5–3.0 times longer than wide; inner margin of widest part of ischiomerus rounded to gently angular; exopod relatively slender with proximal part of exopod not especially wide. Female P4 asymmetrical, with one side distinctly longer (usually merus, propodus, and dactylus); longer P4 and both P5 dactyli longer, different in structure than those of P2 and P3; P5 dactylus elongate, linear; ischiomeral articulation perpendicular to segment axis. Male pleon broadly triangular, telson subhexagonal, subpentagonal to broadly triangular or semicircular, widest basally near midlength. G1 relatively stout, arcuate, with or without subdistal ventral projection; G2 with exopod.

Remarks. *Arcotheres* must be attributed to Manning (1993a) even though the name was first used in 1880 by Nauck in an unpublished note and later cited by Bürger (1895: 361), although he did not recognise the genus. Manning (1993a: 524) diagnosed the genus in a short note, attributed the authorship to Bürger (1895) and assigned *Pinnotheres palaensis* Bürger, 1895, as the type species (see also Manning, 1993a: 127, 128). Campos & Manning (2001) clarified the nomenclature of the genus (see also Ng et al., 2008: 252).

Arcotheres is a large genus with over 30 species, with Ahyong & Ng (2021) having recently transferred another five to the genus. Ng et al. (2017) questioned the monophyly of *Arcotheres* (see also Ahyong & Ng, 2007b) given the diversity in form in the large genus, and singled out *A. borradailei* (Nobili, 1906a) and *A. ridgewayi* (Southwell, 1911) as being different in several features of the pereopods. Both species are here synonymised with *Magnotheres globosus* (Hombron & Jacquinot, 1846) (see later). The carapace, MXP3, and pereopods of *A. coarctatus* (Bürger, 1895) are also quite different from those of typical *Arcotheres*, so *A. coarctatus* is also referred here to its own genus, *Plenotheres*, new genus. As redefined in this study, *Arcotheres* now contains 23 valid species (Table 1).

Arcotheres palaensis (Bürger, 1895)
(Figs. 1A–C, 2–22)

Pinnotheres obesus — Miers, 1880: 314, pl. 4 fig. 4 (not *Pinnothera obesa* Dana, 1852).

Pinnotheres palaensis Bürger, 1895: 372, 373, pl. 9 fig. 12, pl. 10 fig. 12 [type locality: Palau]; Tesch, 1918: 249 (list); De Man, 1921: 260 (Amboina, Indonesia); 1929: 14, pl. 2 fig. 5, 5a, b (Indramaju, Java, Indonesia); Perez, 1921: 59 (Amboina, Indonesia) (parasitised by epicaridean); Gordon, 1936: 64 (discussion); Estampador, 1937: 547 (list); Miyake, 1939: 221 (list); Chuang, 1961: 189, pl. 94 fig. 1 (Singapore, Malaysia); Silas & Alagarswami, 1967: 1205 (list); Serène, 1968: 94; Schmitt et al., 1973: 64 (list).

Pinnotheres rhombifer Bürger, 1895: 374, pl. 9 fig. 15, pl. 10 fig. 14 [type locality: Ubay, Philippines]; Serène, 1968: 94. [New synonymy]

Pinnotheres latissimus Bürger, 1895: 373, pl. 9 fig. 13a, b, pl. 10 fig. 13 [type locality: Manila, Philippines]; Gordon, 1936: 176, fig. 6; Serène, 1968: 94. [New synonymy]

Pinnotheres arcophilus Bürger, 1895: 371, pl. 9 fig. 10, pl. 10 fig. 10 [type locality: Ubay, Philippines]; Lanchester, 1900: 762 (Singapore); Tesch, 1918: 248 (list); De Man, 1921: 260, pl. 8 figs. 1–7 (Lombok, Indonesia); Perez, 1921: 61 (Lombok, Indonesia) (parasitism by epicaridean); Gordon, 1936: 164 (discussion); Silas & Alagarswami, 1967: 1196 (list); Schmitt et al., 1973: 39.

Pinnoteres palaensis — Balss, 1957: 1418 (list).

Pinnotheres paralatissimus Dai & Song, 1986: 55, 61, 62, text-fig. 2 [type locality: Beihai, Guangxi, China]; De Gier & Becker, 2020: tab. 1. [New synonymy]

?*Arcotheres alcocki* — Takeda & Konishi, 1988: 138, figs. 1, 2f–h, 3; Watanabe, 2013: 47 (not *Pinnotheres alcocki* Rathbun, 1909).

Arcotheres guinotae Campos, 2001: 494, figs. 1, 2 [type locality: Thailand]; Ng et al., 2008: 248; De Gier & Becker, 2020: tab. 1. [New synonymy]

Arcotheres palaensis — Pohle & Marques, 1998: 231 (part); Ahyong & Ng, 2007b: 200, fig. 9 (types); Ng et al., 2008: 248 (list); Ng et al., 2017: 1094; Trivedi et al., 2018a: 197; De Gier & Becker, 2020: tab. 1; Komai et al., 2020: 222.

Arcotheres rhombifer — Ahyong & Ng, 2007b: 205, fig. 12; Ng et al., 2017: 1094.

Arcotheres arcophilus — Ahyong & Ng, 2007b: 194, fig. 2; Ng et al., 2008: 248; Ng et al., 2017: 1093; De Gier & Becker, 2020: tab. 1.

?*Arcotheres* sp. — Watanabe & Henmi, 2009: 217, figs. 2, 3.

Arcotheres acrophilus — Trivedi et al., 2018a: 197 [misspelling].

Type material. Lectotype: female (10.2 × 8.4 mm) (SMF-ZMG 948a), Palau, coll. C. Semper. Paralectotypes: 3 poorly preserved females (10.3 × 8.3–10.8 × 8.9 mm; 1 with epicaridean) (SMF-ZMG 948b), same data as lectotype; 1 female (10.0 × 7.0 mm, shrivelled) (SMF-ZMG 947), same data as lectotype. **Philippines:** 4 females (9.5 × 7.4–11.8 × 8.3 mm, shrivelled) (SMF-ZMG 177) (paralectotypes of *Pinnotheres palaensis* Bürger, 1895), Ubay, from "*Placuna sella*", coll. C. Semper; 1 ovigerous female (8.5 × 6.8 mm) (SMF-ZMG 179a) (simultaneous lectotype of *Pinnotheres rhombifer* Bürger, 1895, and neotype of *Pinnotheres latissimus* Bürger, 1895), Ubay, from *Pectunculus aurifluus*; 1 ovigerous female (7.4 × 5.7 mm) (SMF-ZMG 179b) (paralectotype of *Pinnotheres rhombifer* Bürger, 1895), same

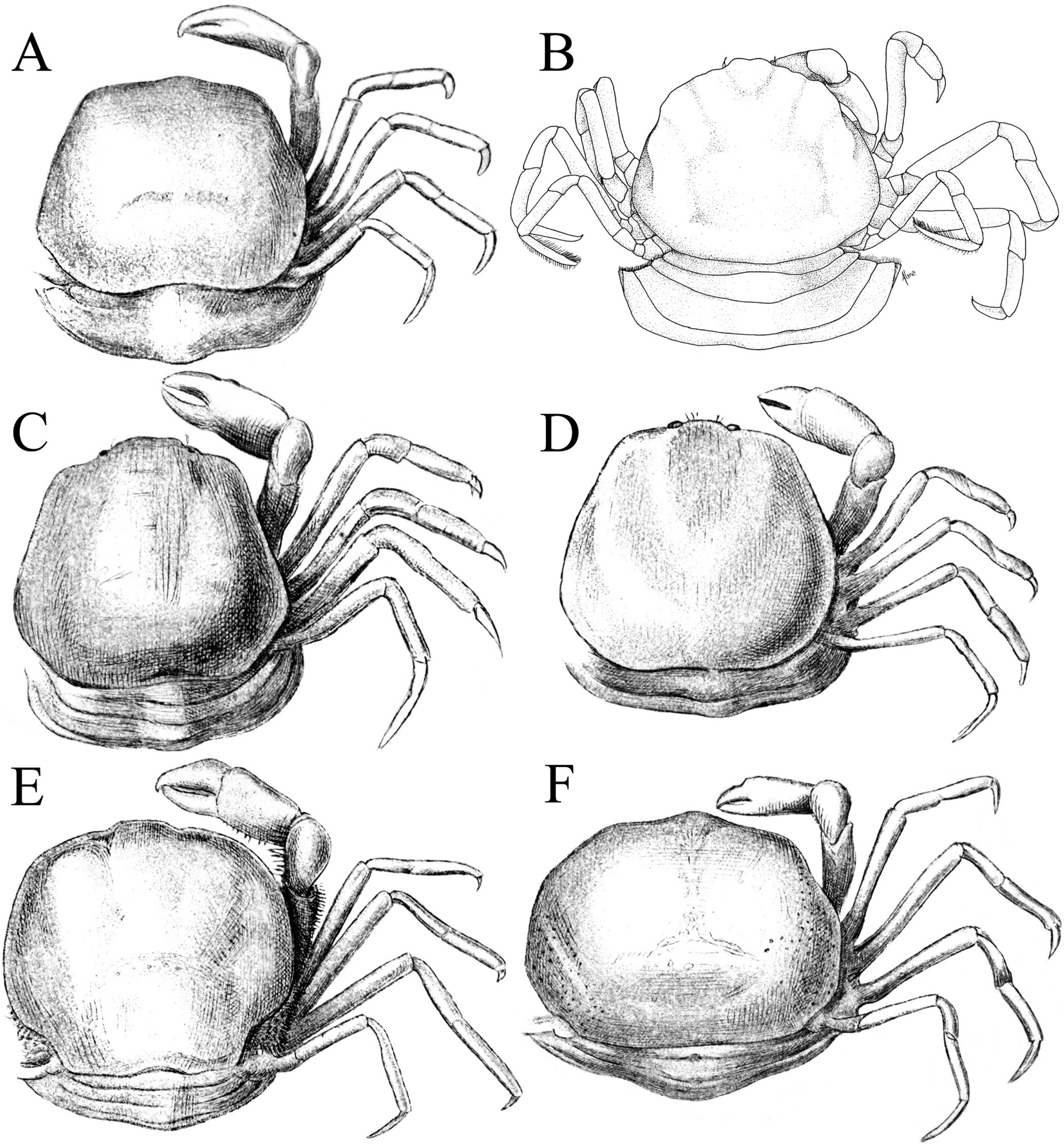

Fig. 1. Original figures of selected species. A, *A. palaensis* (Bürger, 1895), after Bürger (1895: pl. 9 fig. 12); B, *A. guinotae* Campos, 2001, after Campos (2001: fig. 1A); C, *A. arcophilus* (Bürger, 1895), after Bürger (1895: pl. 9 fig. 10); D, *A. modiolicola* (Bürger, 1895), after Bürger (1895: pl. 9 fig. 9); E, *Pl. coarctatus* (Bürger, 1895), after Bürger (1895: pl. 9 fig. 7); F, *M. latus* (Bürger, 1895), after Bürger (1895: pl. 9 fig. 16).

data as lectotype; 1 female (5.3 × 4.7 mm) (SMF-ZMG 172a) (lectotype of *Pinnotheres arcophilus* Bürger, 1895), Ubay, Philippines, from *Arca*, C. Semper, 1863–1864; 1 male (2.8 × 2.5 mm), 1 shrivelled female (5.1 × 4.5 mm) (SMF-ZMG 172b) (paralectotypes of *Pinnotheres arcophilus* Bürger, 1895), same data as lectotype. **Thailand:** 1 female (6.4 × 5.8 mm) (MNHN-B9498) (holotype of *Arcotheres guinotae* Campos, 2001) [photographs examined], from *Barbatia* sp., coll. R. Serène.

Other material examined. Peninsular Malaysia: 1 female (8.1 × 6.6 mm) (ZRC 2017.1252), Peninsular Malaysia or Singapore, from practical class, coll. 30 August 1967; 1 ovigerous female (7.3 × 5.8 mm), 1 non-ovigerous female (carapace length 6.0 mm; with bopyrid on right side of carapace), 1 non-ovigerous female (carapace length 5.7 mm; with bopyrid on left side of carapace) (ZRC 1987.537–539), in *Tegillarca granosa*, from markets, coll. P. K. L. Ng, 29 November 1986; 1 female (6.1 × 5.2 mm) (ZRC 1993.119),

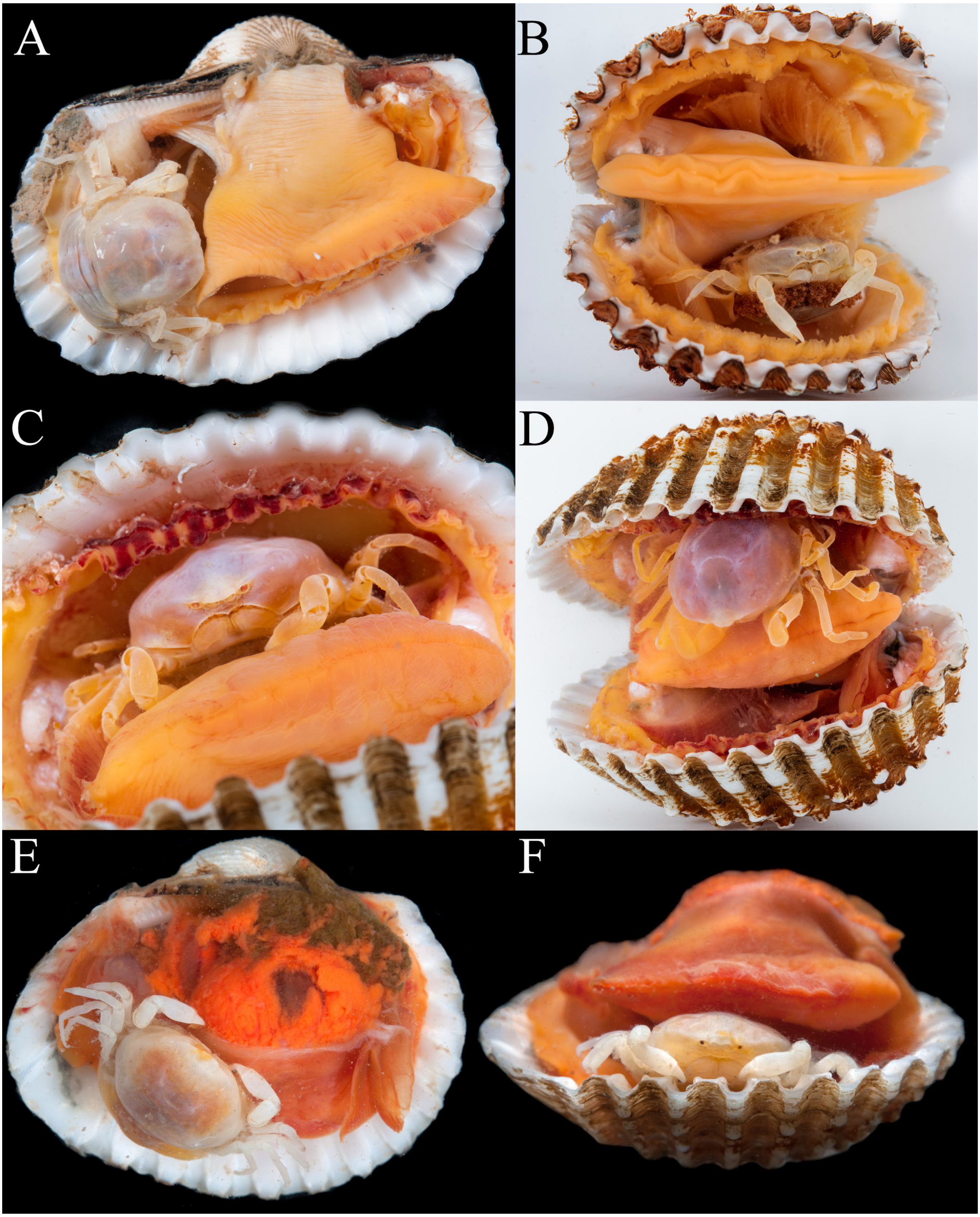

Fig. 2. *Arcotheres palaensis* (Bürger, 1895), colour in life, in situ in *Anadara* and *Tegillarca* (Arcidae). A, ovigerous female (13.3 × 11.2 mm) (ZRC 2017.1281), Peninsular Malaysia; B, ovigerous female (8.7 × 8.0 mm) (ZRC 2020.1), Peninsular Malaysia; C, D, ovigerous female (11.6 × 10.3 mm) (ZRC 2020.11), Peninsular Malaysia; E, F, female (7.9 × 6.6 mm) (ZRC 2018.255), Peninsular Malaysia. A, D, E, in situ; B, dorsal view; C, ventral view. A, host *A.* cf. *rhombea* (Born, 1778); B–F, host *T. granosa* (Linnaeus, 1758). Photographs: Paul Y. C. Ng.

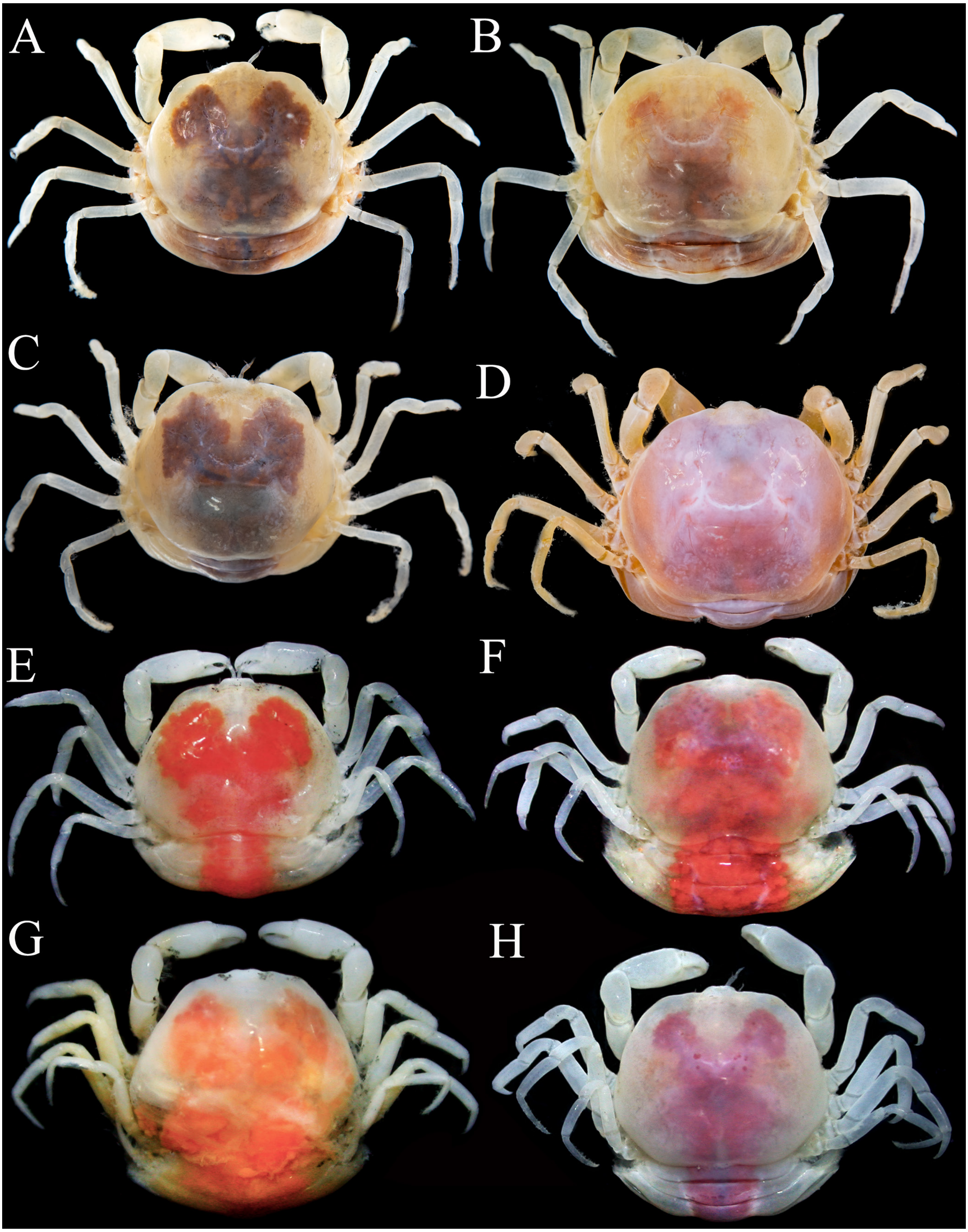

Fig. 3. *Arcotheres palaensis* (Bürger, 1895), colour in life, overall dorsal view. A, ovigerous female (8.7 × 8.0 mm) (ZRC 2020.1), Peninsular Malaysia; B, female (9.5 × 8.2 mm) (ZRC 2020.1), Peninsular Malaysia; C, female (9.3 × 8.3 mm) (ZRC 2020.1), Peninsular Malaysia; D, ovigerous female (11.6 × 10.3 mm) (ZRC 2020.11), Peninsular Malaysia; E, female (6.3 × 5.0 mm) (ZRC 2021.821), Peninsular Malaysia; F, ovigerous female (7.9 × 6.4 mm) (ZRC 2021.821), Peninsular Malaysia; G, female (6.4 × 4.8 mm) (ZRC 2021.821), Peninsular Malaysia; H, female (7.8 × 6.6 mm) (ZRC 2021.0801), Peninsular Malaysia. Photographs: Paul Y. C. Ng, P. K. L. Ng.

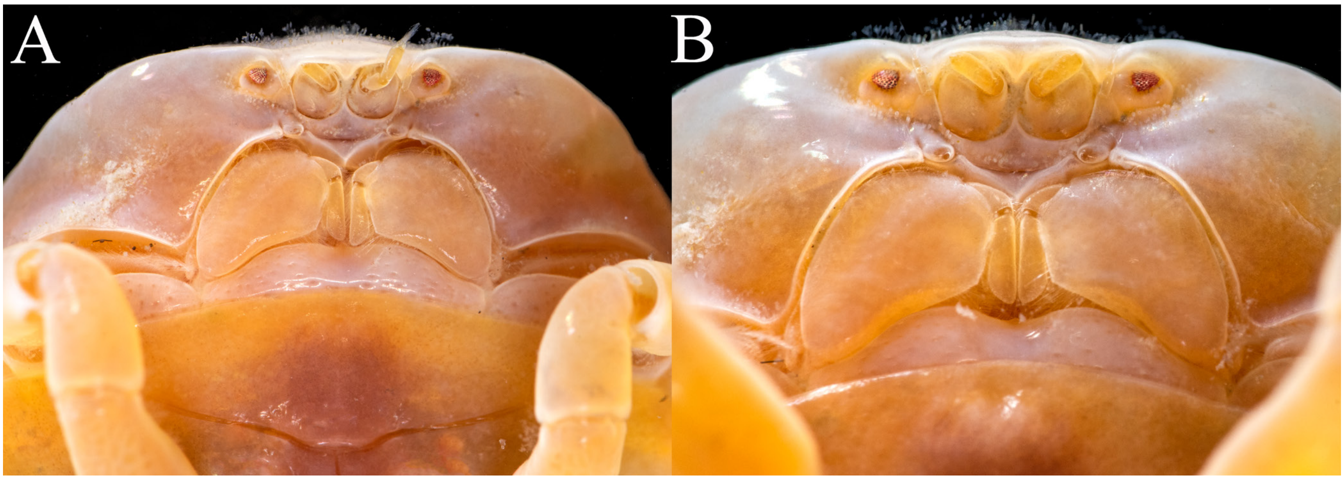

Fig. 4. *Arcotheres palaensis* (Bürger, 1895), ovigerous female (11.6 × 10.3 mm) (ZRC 2020.11), Peninsular Malaysia, colour in life. Two subventral views showing eyes, antennules, antennae, and MXP3.

in *Tegillarca granosa*, from markets, coll. P. K. L. Ng, November 1987; 1 ovigerous female (8.5 × 7.2 mm) (ZRC 1992.8378), in *Tegillarca granosa*, from markets in Singapore, coll. P. K. L. Ng, January 1992; 1 female (9.6 × 7.5 mm) (ZRC 1999.975), probably Peninsular Malaysia, from food with cockles (Clementi Town Centre, Singapore), coll. D. C. J. Yeo, 27 May 1999; 1 soft female (ca. 9.0 mm carapace width) (ZRC 2000.2613), Batu Pahat, Johor, in *Tegillarca granosa*, mangroves, coll. H. K. Tan, 16 August 1983; 1 ovigerous female (13.3 × 11.2 mm) (ZRC 2017.1281), probably Malaysia, in *Tegillarca* cf. *rhombea*, Chinatown market, Singapore, coll. 14 January 2018; 1 ovigerous female (7.9 × 6.6 mm) (ZRC 2018.255), 1 ovigerous female (8.6 × 6.5 mm) (AM P105905), probably Peninsular Malaysia, in *Tegillarca granosa*, from Chinatown market, Singapore, coll. P. K. L. Ng, 25 February 2018; 1 ovigerous female (7.5 × 5.8 mm) (ZRC 2018.770), from food, probably from *Tegillarca* sp., coll. B. Y. Lee, 6 May 2018; 1 ovigerous female (8.4 × 6.6 mm) (ZRC 2018.759), probably Peninsular Malaysia, in *Tegillarca granosa*, from Chinatown market, Singapore, coll. P. Y. C. Ng, 4 November 2018; 1 ovigerous female (ZRC 2019.1039), Johor, in *Tegillarca granosa*, from Chinatown market, Singapore, coll. P. K. L. Ng, 27 July 2019; 9 females (3 photographed live) (ZRC 2020.1), Kandang Kerbau market, Singapore, in *Tegillarca granosa*, coll. 5 January 2020; 1 ovigerous female (ZRC 2021.379), Kandang Kerbau market, Singapore, in *Tegillarca granosa*, coll. P. K. L. Ng, 12 January 2020; 1 ovigerous female (ZRC 2020.2), Kandang Kerbau market, Singapore, in *Tegillarca granosa*, coll. 12 January 2020; 10 females (smallest 4.1 × 4.1 mm) (ZRC 2020.9), Kandang Kerbau market, Singapore, in *Tegillarca granosa*, coll. P. K. L. Ng, 29 March 2020; 3 ovigerous females (10.2 × 7.8 mm, 10.3 × 7.9 mm, 11.6 × 10.3 mm) (ZRC 2020.11), in *Tegillarca granosa*, from Chinatown market, Singapore, coll. P. K. L. Ng, 16 April 2020; 1 female (7.8 × 6.6 mm) (ZRC 2021.0801), from Kandang Kerbau market, in *Tegillarca granosa*, coll. P. K. L. Ng, 5 December 2021; 1 ovigerous female (8.9 × 7.8 mm) (ZRC 2021.814), in *Tegillarca nodifera*, from Yew Tee Market, Singapore, coll. H. H. Tan, 12 December 2021; 1 ovigerous female (7.9 × 6.4 mm), 2 females (6.3 × 5.0 mm, 6.4 × 4.8 mm) (ZRC 2021.0821), in *Tegillarca granosa*, from Kandang Kerbau Market, Singapore, from Peninsular Malaysia, coll. P. K. L. Ng, 26 December 2021; 1 female (7.4 × 6.7 mm) (ZRC 2022.42), in *Tegillarca granosa*, from Yew Tee Market, Singapore, coll. H. H. Tan, 23 January 2022. **Indonesia:** 2 ovigerous females (ZRC 1999.2404), Indonesian markets, in *Tegillarca granosa*, coll. C. M. Yang, 3 August 1983; 1 ovigerous female (7.1 × 5.7 mm), 1 non-ovigerous female (7.7 × 6.2 mm), 1 ovigerous female (carapace length 7.1 mm; with bopyrid) (ZRC 1993.120–122), *Tegillarca granosa*, from markets, coll. P. K. L. Ng, 8 December 1987; 1 ovigerous female (5.1 × 4.3 mm) (ZRC 1999.1202), between Pulau Berang and Pulau Ileu, Pulau Lingga, Riau Islands, coll. J. B. Sigurdsson, 28 March 1993; 1 female (8.8 × 7.8 mm) (ZRC 2018.764), Teluk Kodek, Lombok, Indonesia, unknown host, coll. S. Dwiono, 2014; 1 female (carapace length 6.7 mm; with bopyrid) (ZRC 2018.762), Teluk Kodek, Lombok, Indonesia, in *Anadara antiquata*, coll. S. Dwiono, 12 November 2013; 1 male (3.6 × 3.6 mm) (ZRC 2019.1788), in *Tegillarca granosa*, from Kandang Kerbau market, Singapore, coll. P. K. L. Ng, 29 December 2019; 2 ovigerous females (ZRC 2021.355), from supermarket, in *Tegillarca granosa*, coll. P. Y. C. Ng, 26 March 2021. **Singapore:** 2 females (ZRC 2014.217), coll. P. K. L. Ng, 2005; 10 females (ZRC 1965.11.24.17–26), from market, probably from cockles, coll. August 1934; 1 female (6.7 × 5.0 mm) (ZRC 2017.1038), Tanah Merah Ferry Terminal Beach, near Changi Point, intertidal, in *Barbatia* sp., coll. S. K. Tan et al., 12–15 January 2017; 3 females (largest 9.5 × 7.7 mm) (ZRC 1965.11.24.30–32), Pulau Senang, in "*Barbatia* sp. J", coll. November 1934; 1 female (7.0 × 5.6 mm) (ZRC 1965.11.24.33), Raffles Lighthouse, inside *Barbatia decussata*, coll. 1930s. **Borneo:** 1 female (8.7 × 8.1 mm) (ZRC 2017.1260), off Kuching, Sarawak, from large *Tegillarca* sp. from mudflats, from seafood market, coll. P. K. L. Ng, June 2015. **Thailand:** 3 females (3.3 × 3.4 mm, 5.0 × 4.2 mm, 11.1 × 9.8 mm) (ZRC 2018.767), Bangkok market, from *Tegillarca granosa*, coll. P. Y. C. Ng, 8 April 2018. **Japan:** 17 females (2.3 × 2.0–9.6 × 6.5 mm), 1 male (4.2 × 3.7 mm) (NSMT-Cr 9363), Mukaishima, Hiroshima Prefecture, Seto Inland Sea, in *Barbatia virescens*, coll. K. Konishi, 18 June 1981; 6 females (4.5 × 3.8–8.6 × 6.1 mm) (ZRC 2019.1879), Kawachi, Kumamoto, Kyushu, in *Barbatia*

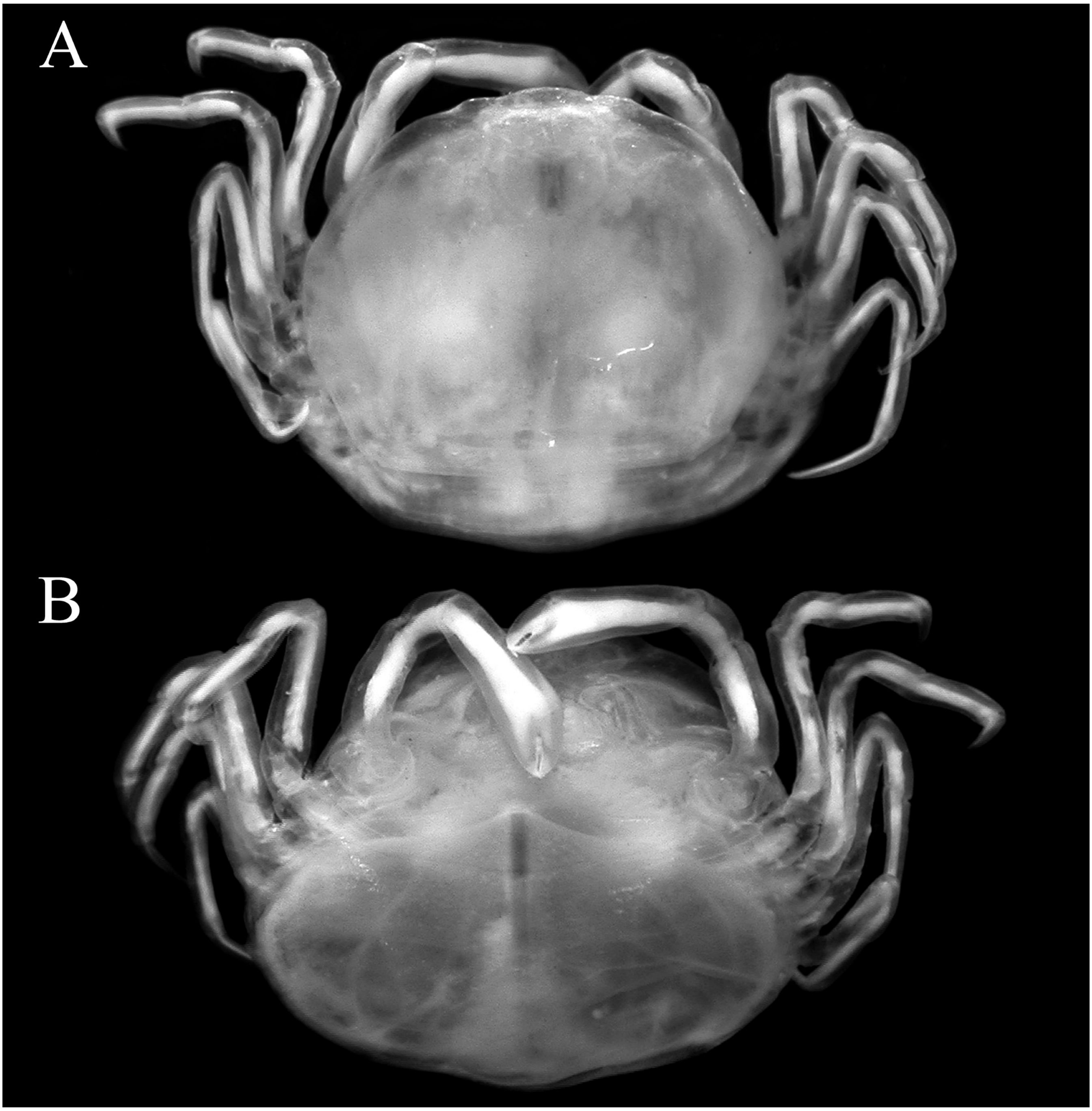

Fig. 5. *Arcotheres palaensis* (Bürger, 1895). A, B, lectotype female (10.2 × 8.4 mm) (SMF-ZMG 948a), Palau. A, overall dorsal view; B, ventral view of cephalothorax.

virescens, coll. T. Watanabe, 15 October 2007. **Others:** 1 spent female (9.6 × 7.9 mm), 1 ovigerous female (9.3 × 8.2 mm) (NHM 1860.6), "Indo-Malayan Seas".

Description. Carapace and pereopods well chitinised, usually firm in post-hard stage. Female: Carapace subovate to subhexagonal, wider than long; dorsal and lateral surfaces smooth, glabrous; appearing domed in frontal view; front sometimes projecting anteriorly beyond orbits, margin gently sinuous to gently convex; anterolateral margin thickened, blunt but defined, sometimes subparallel with frontal margin or sloping posteriorly to various degrees, forming rounded angle with posterolateral margin (Figs. 3, 5A, 8A, 9A, 11–14). Eyes small, not or slightly visible in dorsal view in adults; mobile, completely filling orbit (Figs. 3, 5A, 8A, C, 9A, C, 13, 14). Epistome with median part triangular, lateral margins gently concave (Figs. 8C, 9C, 17O, 18M).

MXP3 outer surface with scattered short setae; ischiomerus completely fused, subrhomboidal, maximum length 1.5–1.8 times maximum width, inner margin usually rounded, occasionally slightly angular at widest point; carpus short; propodus about 3 times as long as high, subspatulate, distinctly longer than carpus, tip rounded to subtruncate; dactylus slender, inserted at proximal one-third to near midlength of propodus, tip not reaching propodal apex; exopod relatively slender, about two-thirds length of ischiomerus, flagellum 2-segmented (Fig. 16).

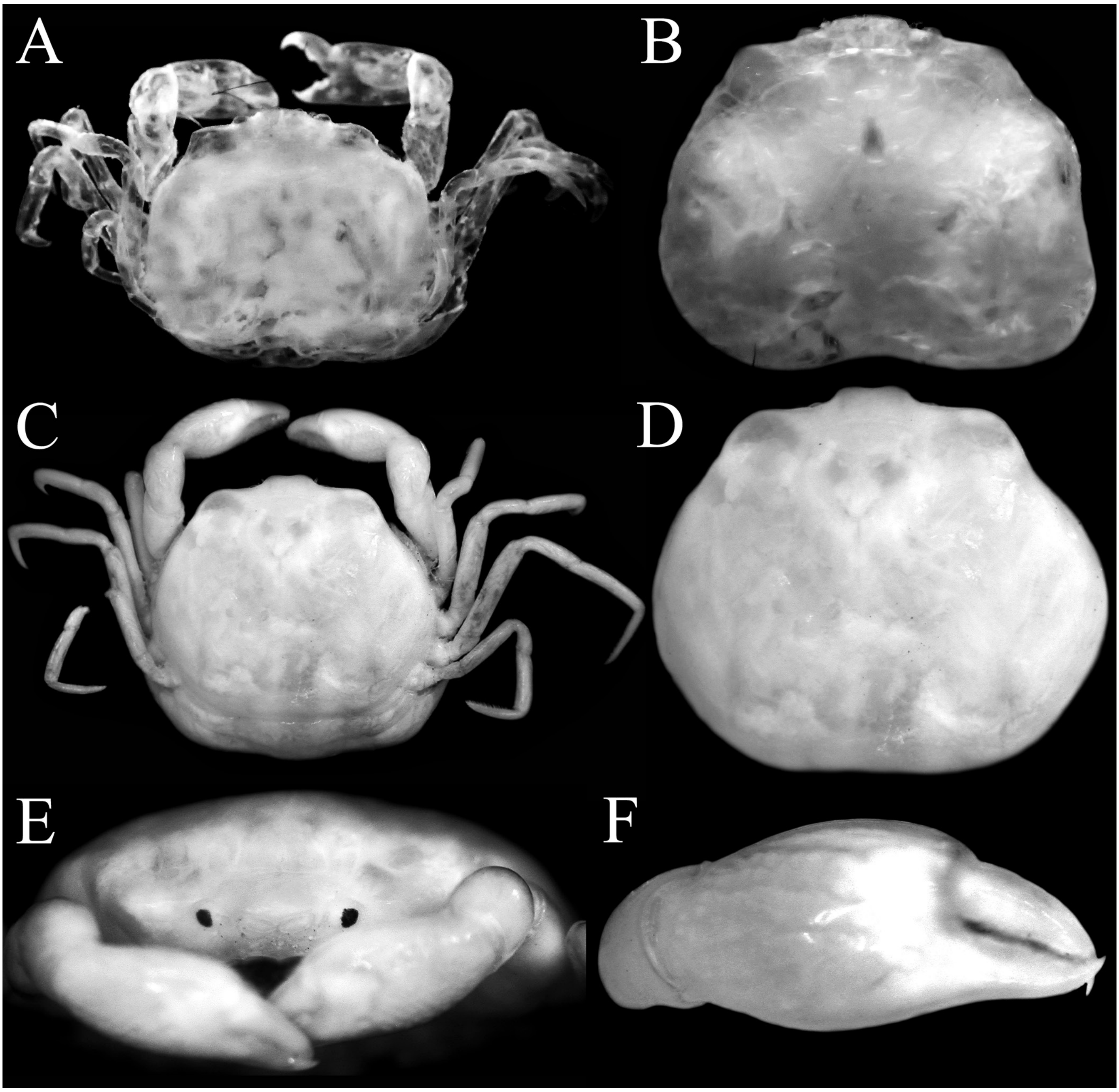

Fig. 6. *Arcotheres palaensis* (Bürger, 1895). A, B, female (5.3 × 4.7 mm) (SMF-ZMG 172a) (lectotype of *Pinnotheres arcophilus* Bürger, 1895), Philippines; C–F, ovigerous female (5.1 × 4.3 mm) (ZRC 1999.1202), Indonesia. A, C, overall dorsal view; B, D, dorsal view of carapace; E, frontal view of cephalothorax; F, outer view of right chela.

Chela not prominently elongate, dactylus about two-thirds palm length; palm relatively slender, narrower proximally than distally; outer surface of palm, fingers (except for distal part) almost glabrous, with only scattered short setae; ventral margin of palm gently convex to sinuous, sometimes with low bulge near midlength, extending onto mesial surface; dactylus occlusal margin with distinct subproximal tooth; pollex occlusal margin with 1 low proximal tooth, 1 submedian tooth, and minute denticles; tips of fingers sharp, hooked (Figs. 8D, 9D, 15B).

P2–P5 dorsally, ventrally unarmed; outer surface covered with scattered, very short setae or glabrous; ventral margins of propodus and dactylus slightly more setose; relative lengths of meri P4>P3>P2>P5; left (sometimes right) P4 distinctly the longer; P2 and P3 dactyli short, subequal, tip gently hooked, half propodus length or less; longer P4 dactylus elongate, slender, almost straight, sparsely setose distally; P5 merus 3.6–4.0 times longer than wide, P5 dactylus longest, margins lined with short and long setae, denser on ventral margin, distoflexor margin without rows of spinules, at most sometimes with 3–8 scattered low spinules (Figs. 17A–N, 18A–L).

Pleon extending to buccal region, covering bases of P2–P5; telson gently recessed into concave distal margin of somite 6 (Figs. 5B, 6B, 9B).

Male: Carapace almost circular, slightly wider than long; dorsal surface almost smooth, not prominently inflated,

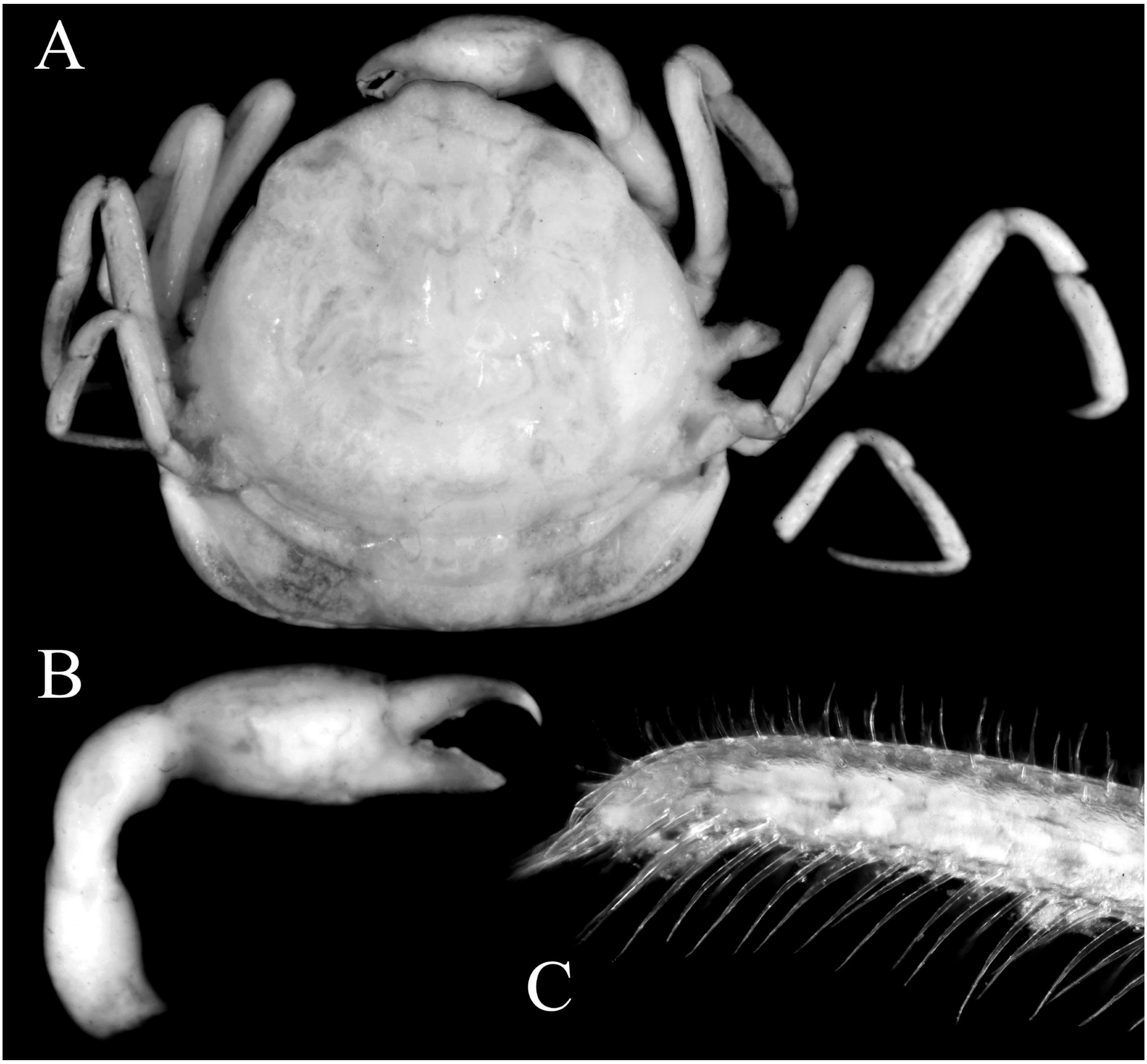

Fig. 7. *Arcotheres palaensis* (Bürger, 1895), female (6.4 × 5.8 mm) (MNHN-B9498), Thailand (holotype of *A. guinotae* Campos, 2001). A, overall dorsal view; B, left cheliped; C, ventral view of distal part of P5 dactylus. Photographs: A, B, Arthur Anker; C, Sébastien Soubzmaigne.

lateral surfaces with setae; front projecting anteriorly, margin sinuous to almost straight (Figs. 20A, B, 21A, B). Eyes distinctly visible in dorsal view (Figs. 20A, 21A). MXP3 as in female (Fig. 22A). Anterior thoracic sternum wide, sternites 1, 2 fused, partially sunken into buccal cavity; suture between sternites 2 and 3 shallow; sternites 3, 4 completely fused, separated only by shallow grooves. Chela relatively stout, shorter than in female (Figs. 20A, B, 21A, C); ventral margin of palm gently to distinctly sinuous, sometimes with low bulge near midlength. P2–P5 dorsally, ventrally unarmed; outer surface covered with short setae; P3 and P4 carpus and propodus with long natatory setae; left and right meri equal, relative lengths of meri P4>P3>P2>P5; dactyli of P2–P4 progressively longer; left P4 dactylus slightly longer, more slender than right side; P4 and P5 dactylus subequal to that of P3, covered with short setae (Fig. 22B–I). Pleon slender, triangular, widest at somite 3, lateral margins of somite 4 gently concave to almost straight; somite 6 trapezoidal or subquadrate; telson ovate to semicircular, slightly wider than long, widest near midlength (Fig. 22J, O). G1 relatively stout, arcuate, curved outwards, tip gently curved upwards or straight (Fig. 22K–M, O). G2 short, with spatuliform tip; exopod present as long curved structure (Fig. 22N).

Variation. Preservational effects notwithstanding, there is considerable variation in the shape of the carapace (Figs. 13, 14), from transversely ovate with the front barely protruding in dorsal view (Figs. 5A, 6A, 11A, D, 12F, 13A–C), to more rounded with a distinctly protruding frontal margin (Figs. 11E, G, H, 12A–C, E, G, H, 13E–H, 14); and in some, the carapace is almost subtrapezoid (Fig. 14E–H). The good series of specimens demonstrates that there are many intermediate conditions that make precise carapace shape unreliable as a diagnostic character in *A. palaensis*. There is some variation

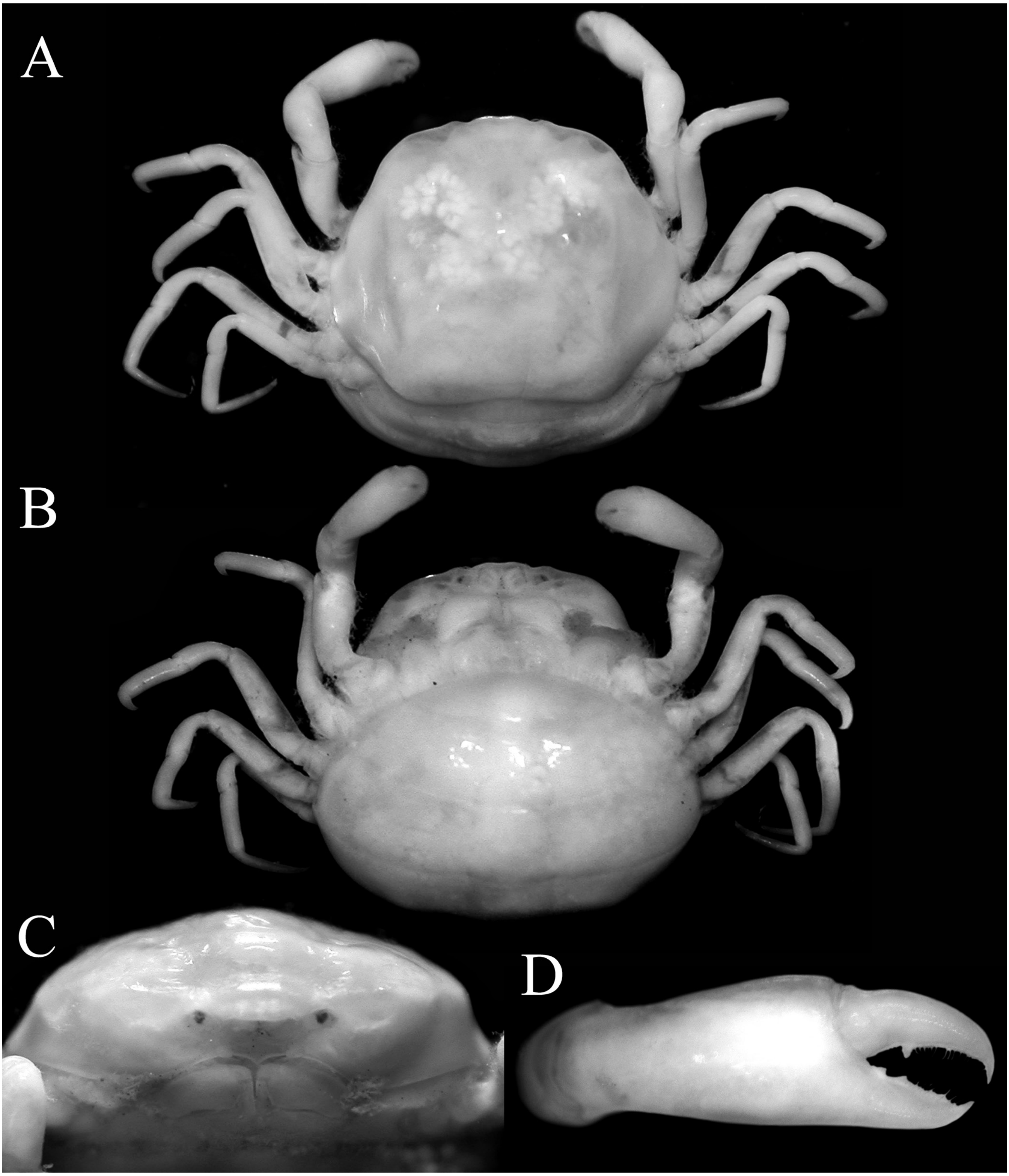

Fig. 8. *Arcotheres palaensis* (Bürger, 1895), ovigerous female (8.5 × 7.2 mm) (ZRC 1992.8378), Peninsular Malaysia. A, overall dorsal view; B, ventral view of cephalothorax; C, frontal view of cephalothorax; D, outer view of right chela.

in the length of the MXP3 dactylus, being relatively shorter in some specimens (e.g., Fig. 17D, G); in most specimens, however, the dactylus almost reaches the tip of the propodus (e.g., Fig. 17H), but never beyond. In most adult female *A. palaensis* examined (including small specimens of about 5 mm in carapace width), the distal margin of fused thoracic sternites 1–4 is proportionately narrower and the median part is deeply concave, appearing as a broad indentation. In the largest female of *A. palaensis* examined (13.3 × 11.2 mm; ZRC 2017.1281), however, the anterior thoracic sternum is also broad and medially shallow; and as such, this character may vary to some degree. In the smallest female examined (3.3 × 3.4 mm; ZRC 2018.767; Fig. 15A), the pleon resembles that of males, being elongate with a semicircular telson

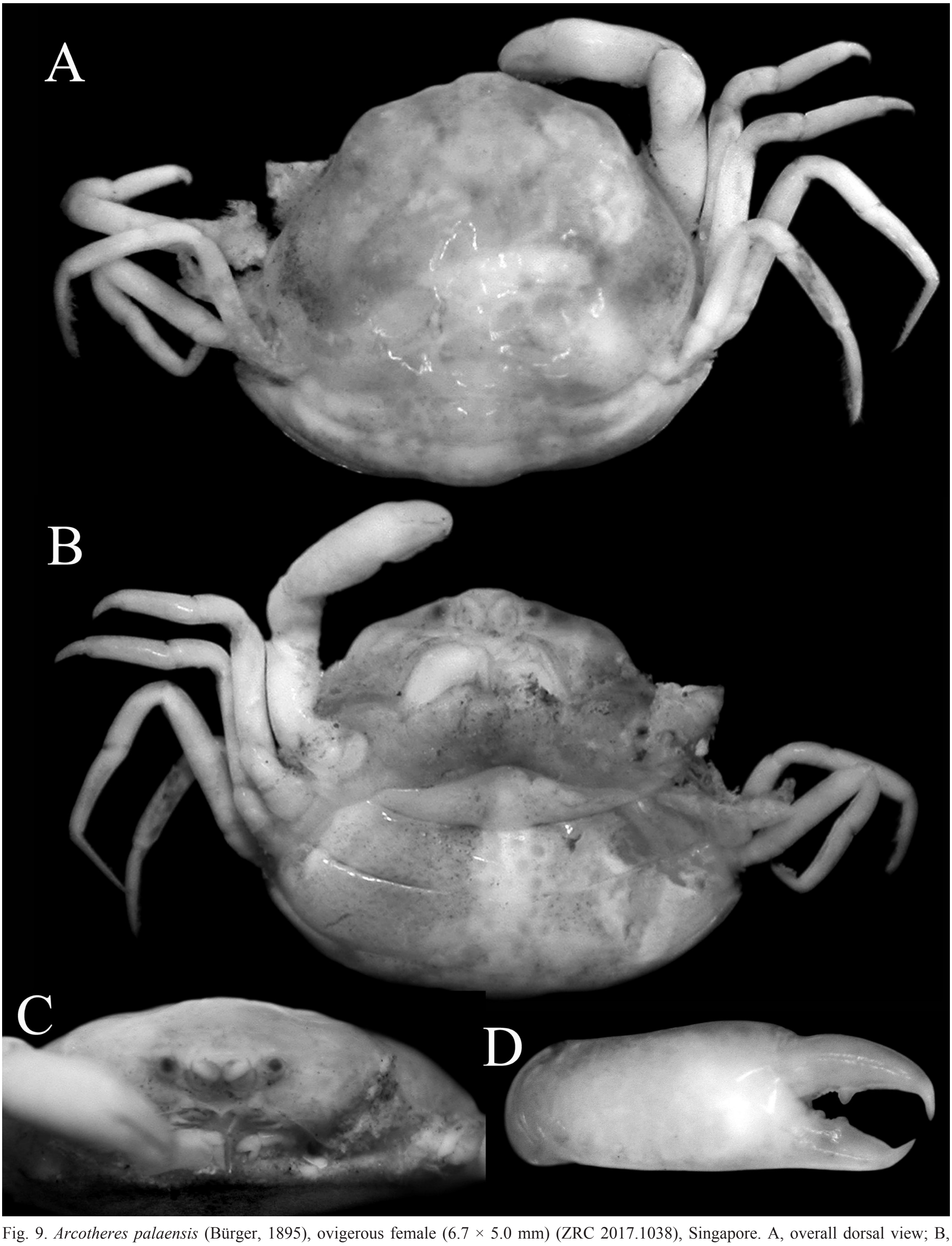

Fig. 9. *Arcotheres palaensis* (Bürger, 1895), ovigerous female (6.7 × 5.0 mm) (ZRC 2017.1038), Singapore. A, overall dorsal view; B, ventral view of cephalothorax; C, frontal view of cephalothorax; D, outer view of right chela.

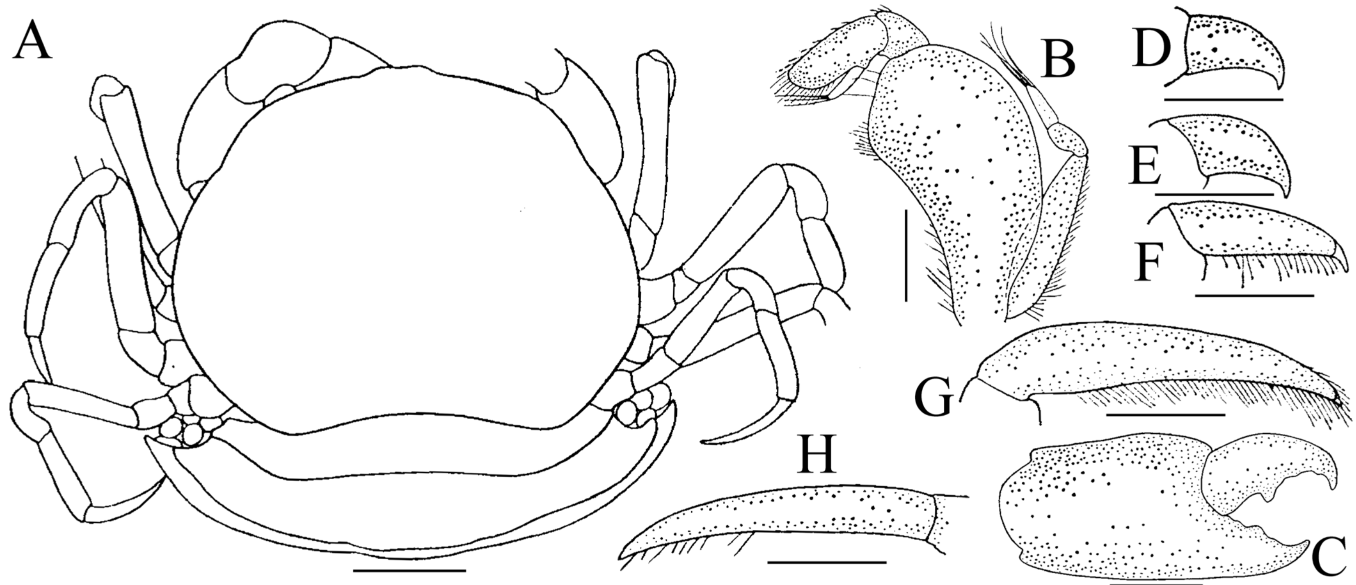

Fig. 10. *Arcotheres palaensis* (Bürger, 1895), female (7.3 × 5.2 mm) (CAS), China (holotype of *Pinnotheres paralatissimus* Dai & Song, 1986); after Dai & Song (1986: fig. 2(1–7)). A, overall dorsal view; B, left MXP3; C, outer view of right chela; D–G, right P2–P5 dactyli; H, left P4 dactylus. Scales = A, 2.0 mm; B, D–H, 0.5 mm; C, 1.0 mm.

(Fig. 15C). The male pleon varies slightly in shape, with the Philippine paralectotype male of *P. arcophilus* (2.8 × 2.5 mm; SMF-ZMG 172b) being slightly more hexagonal (Fig. 22O), whereas that of the Indonesian male is somewhat more rounded (Fig. 20J). Their G1 morphologies, however, agree in all key aspects (Fig. 22K, O).

Colour. The colour is variable, from pale to dirty white to pinkish or yellowish when alive, with the eyes pigmented red to black (Figs. 2–4). In the freshly collected male (ZRC 2019.1788), the carapace is dirty white with numerous small brown flecks and the ventral surfaces are white (Fig. 20).

Host. Known with certainty only from the Arcidae Lamarck, 1809. *Arcotheres palaensis* has been found in *Anadara antiquata* (Linnaeus, 1758), *Tegillarca granosa* (Linnaeus, 1758), *Tegillarca* cf. *rhombea* (Born, 1778), *Tegillarca nodifera* (Martens, 1860), *Barbatia decussata* (Lamarck, 1819), *Barbatia virescens* (Reeve, 1844), and *Barbatia* sp. The one record from *Tucitona aurifluus* (Reeve, 1843) (previously in *Pectunculus*) (Glycymerididae Dall, 1908) (supposedly for two synonyms, *Pinnotheres rhombifer* Bürger, 1895, and *Pinnotheres latissimus* Bürger, 1895) needs to be confirmed. Noteworthy, however, is that both Arcidae and Glycymerididae belong to the superfamily Arcoidea Lamarck, 1809. As discussed earlier, records of "*A. palaensis*" from *Placuna* Lightfoot, 1786 (Placunidae), and *Mactra* Linnaeus, 1767 (Mactridae) (cf. Schmitt et al., 1973: 65), almost certainly belong to other species.

Remarks. The large series of *A. palaensis* available for study, particularly from Singapore and Malaysia, has enabled documentation of the range of morphological variation in this species. The morphological range observed in the Singapore–Malaysia material alone fully encompasses that of the lectotype from Palau, giving confidence in species identification. Moreover, our observations based on the large sample size enabled reassessment of the taxonomy of nominal species of *Arcotheres* similar to *A. palaensis*, many of which are synonymised herein, as well as clarification of the identity of most published records in the region. Unfortunately, we have not been able to obtain additional specimens of *A. palaensis* from the type locality in Palau; despite a recent survey there to sample topotypic material of Brachyura (e.g., see Ng, 2019), the molluscs sampled did not yield any pinnotherids. *Arcotheres palaensis* is present in the adjacent Philippines (through the types and synonymisation of *Pinnotheres latissimus* and *Pinnotheres rhombifer* with it, their type localities being there; see later). We also have specimens from Borneo and Thailand, which connects the distribution of the species to Malaysia and Singapore. The records from Japan are also probably *A. palaensis*, though these may warrant further study (see later).

Ahyong & Ng (2007b: 205–206) synonymised *Pinnotheres latissimus* Bürger, 1895, under *Pinnotheres rhombifer* Bürger, 1895, commenting that there were no major characters separating them. The species had already been transferred to *Arcotheres* by Campos & Manning (2001). The good series of specimens of *A. palaensis* on hand now shows that both *P. rhombifer* and *P. latissimus* are its junior synonyms. No other characters apart from small differences in carapace proportions purportedly separate *A. palaensis* from *A. rhombifer* and *A. latissimus*, differences that are fully encompassed by the range in variation observed here. As all the synonymised species by Bürger were described in the same paper (Bürger, 1895), the names are considered as simultaneously published under the zoological Code (ICZN, 1999). Under Article 24 of the Code (ICZN, 1999), we here regard *Pinnotheres palaensis* Bürger, 1895, as having priority over *P. latissimus* Bürger, 1895, and *P. rhombifer* Bürger, 1895, when they are regarded as synonyms.

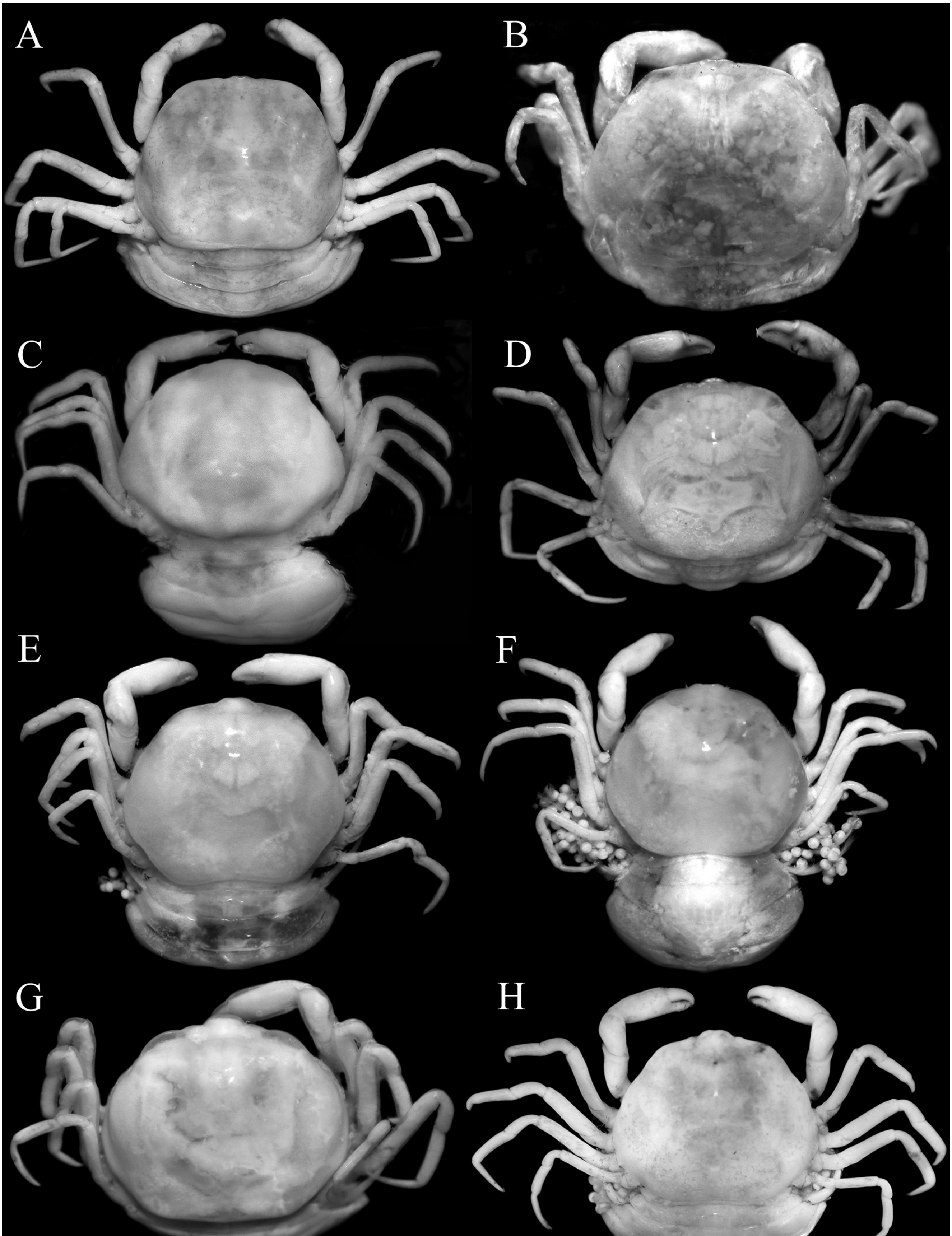

Fig. 11. *Arcotheres palaensis* (Bürger, 1895), overall dorsal view. A, ovigerous female (13.3 × 11.2 mm) (ZRC 2017.1281), Peninsular Malaysia; B, female (7.0 × 5.6 mm) (ZRC 1965.11.24.33), Singapore; C, female (9.6 × 7.5 mm) (ZRC 1999.975), Peninsular Malaysia; D, female (8.1 × 6.6 mm) (ZRC 2017.1252), Peninsular Malaysia; E, female (7.3 × 5.8 mm) (ZRC 1987.537), Peninsular Malaysia; F, ovigerous female (7.1 × 5.7 mm) (ZRC 1993.120), Peninsular Malaysia; G, female (8.4 × 7.3 mm) (ZRC 1965.11.24.17), Peninsular Malaysia; H, ovigerous female (7.9 × 6.6 mm) (ZRC 2018.0255), Peninsular Malaysia.

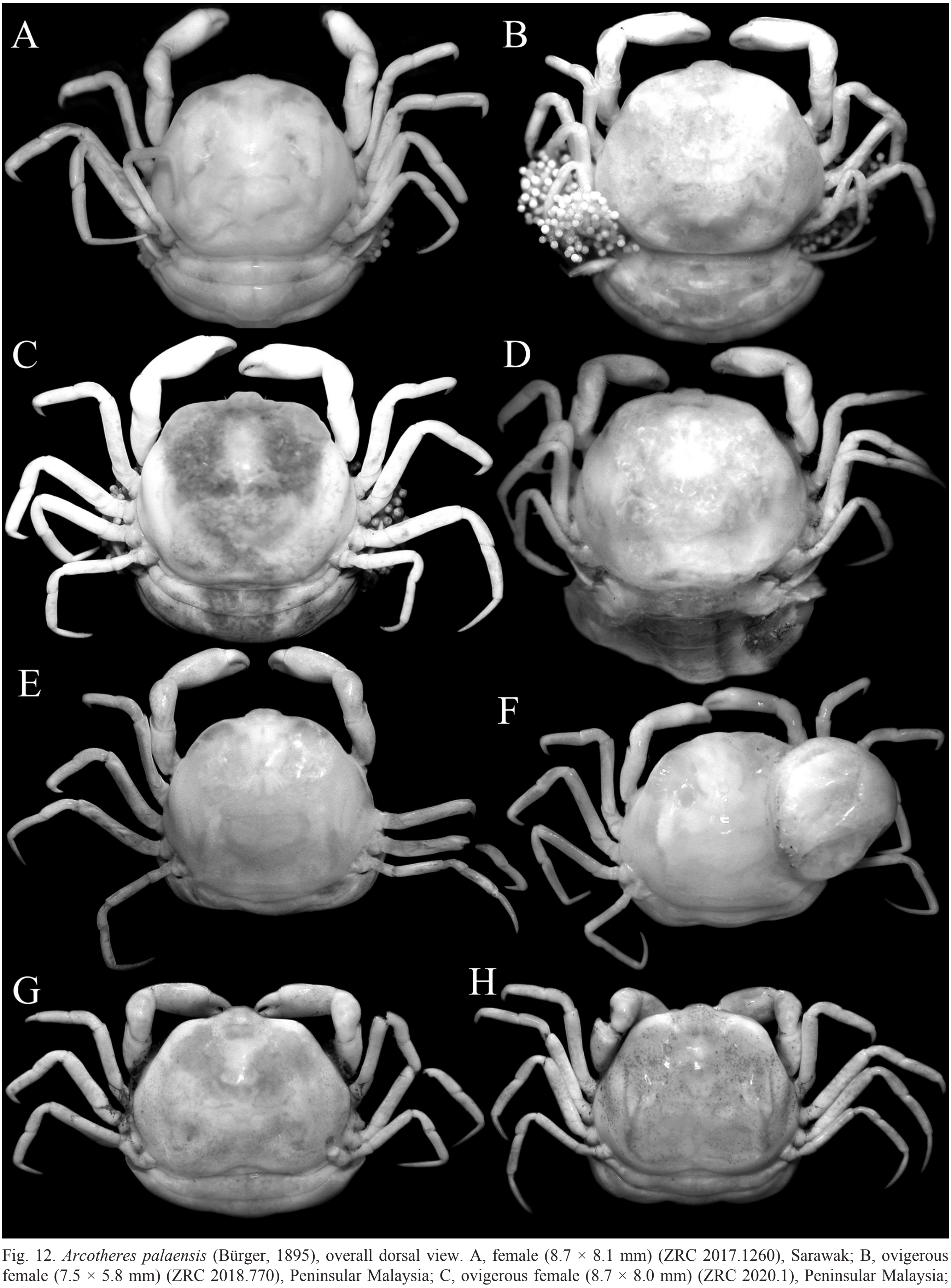

Fig. 12. *Arcotheres palaensis* (Bürger, 1895), overall dorsal view. A, female (8.7 × 8.1 mm) (ZRC 2017.1260), Sarawak; B, ovigerous female (7.5 × 5.8 mm) (ZRC 2018.770), Peninsular Malaysia; C, ovigerous female (8.7 × 8.0 mm) (ZRC 2020.1), Peninsular Malaysia; D, female (7.7 × 6.2 mm) (ZRC 1993.121), Indonesia; E, female (8.8 × 7.8 mm) (ZRC 2018.764), Lombok, Indonesia; F, female with bopyrid (carapace length 6.7 mm) (ZRC 2018.762), Lombok, Indonesia; G, female (8.0 × 5.8 mm) (ZRC 2019.1879), Japan; H, female (8.6 × 6.1 mm) (ZRC 2019.1879), Japan.

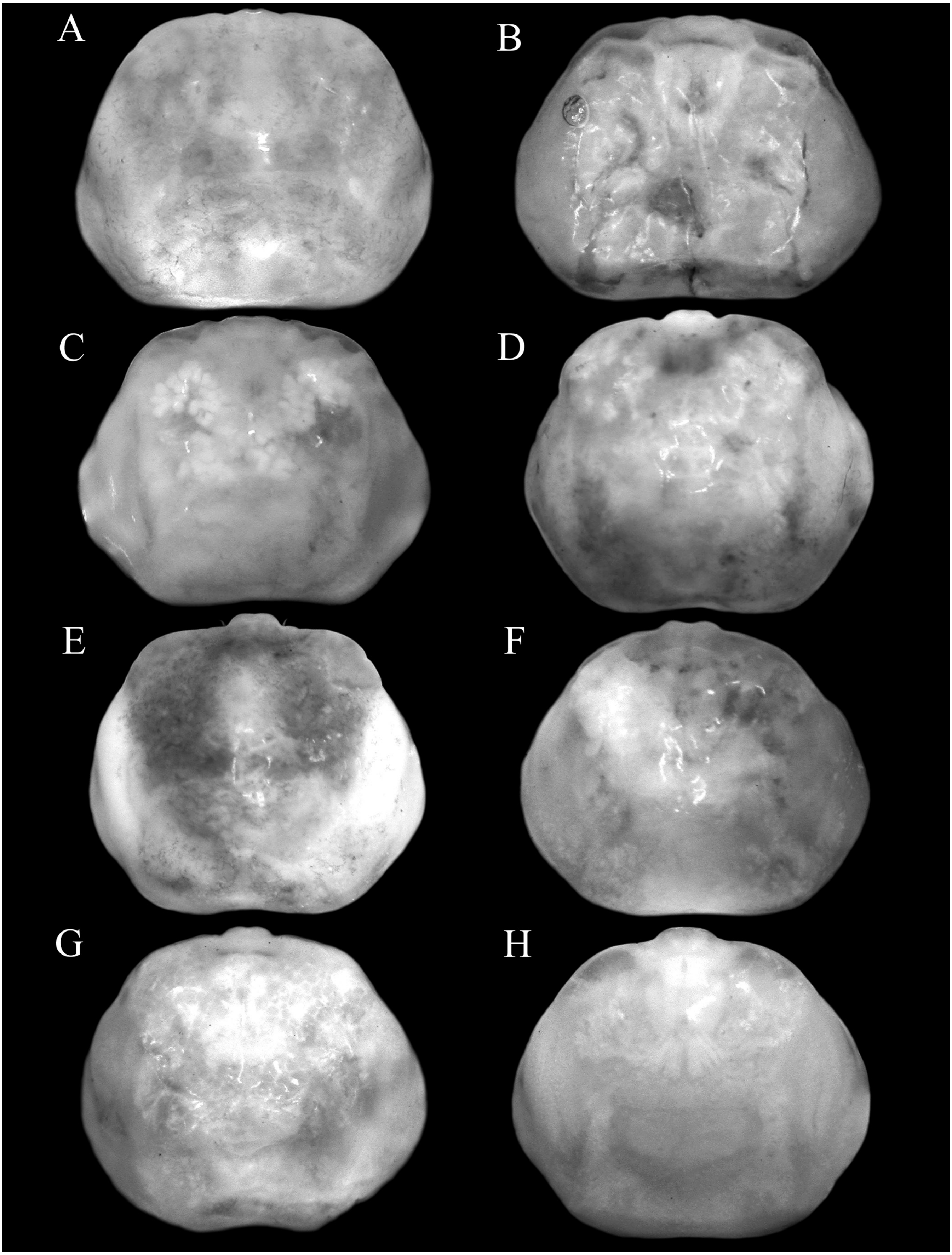

Fig. 13. *Arcotheres palaensis* (Bürger, 1895), dorsal view of carapace. A, ovigerous female (13.3 × 11.2 mm) (ZRC 2017.1281), Peninsular Malaysia; B, female (8.9 × 6.5 mm) (ZRC 1965.11.24.27), Singapore; C, ovigerous female (8.5 × 7.2 mm) (ZRC 1992.8378), Peninsular Malaysia; D, female (9.3 × 8.3 mm) (ZRC 2020.1), Peninsular Malaysia; E, ovigerous female (8.7 × 8.0 mm) (ZRC 2020.1), Peninsular Malaysia; F, ovigerous female (7.1 × 5.7 mm) (ZRC 1993.120), Peninsular Malaysia; G, female (7.7 × 6.2 mm) (ZRC 1993.121), Indonesia; H, female (8.8 × 7.8 mm) (ZRC 2018.764), Lombok, Indonesia.

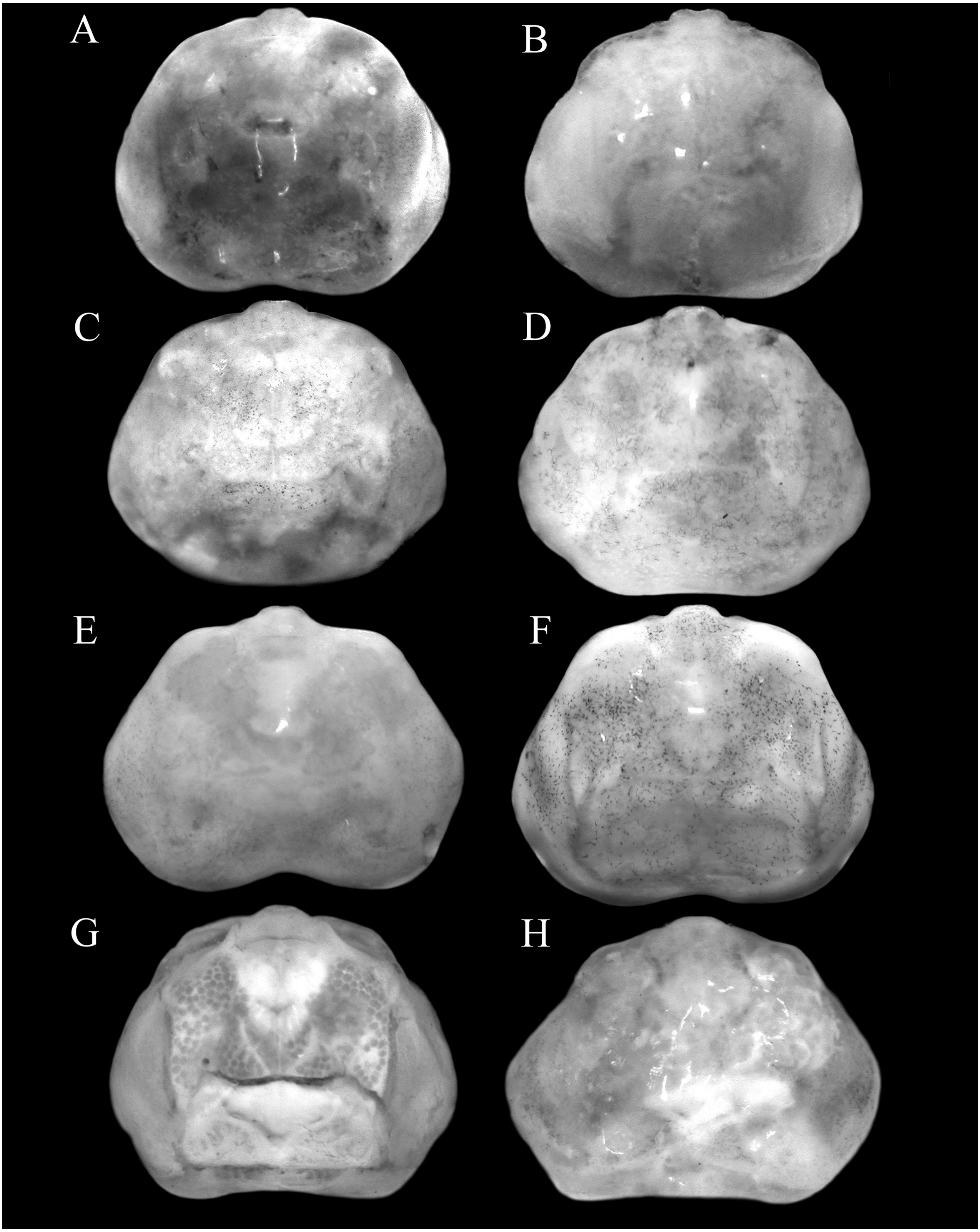

Fig. 14. *Arcotheres palaensis* (Bürger, 1895), dorsal view of carapace. A, female (9.5 × 8.2 mm) (ZRC 2020.1), Peninsular Malaysia; B, female (6.1 × 5.2 mm) (ZRC 1993.0119), Peninsular Malaysia; C, female (7.5 × 5.8 mm) (ZRC 2018.770), Peninsular Malaysia; D, ovigerous female (7.9 × 6.6 mm) (ZRC 2018.0255), Peninsular Malaysia; E, female (8.0 × 5.8 mm) (ZRC 2019.1879), Japan; F, female (8.6 × 6.1 mm) (ZRC 2019.1879), Japan; G, female (9.5 × 7.7 mm) (ZRC 1965.11.24.30), Singapore; H, ovigerous female (6.7 × 5.0 mm) (ZRC 2017.1038), Singapore.

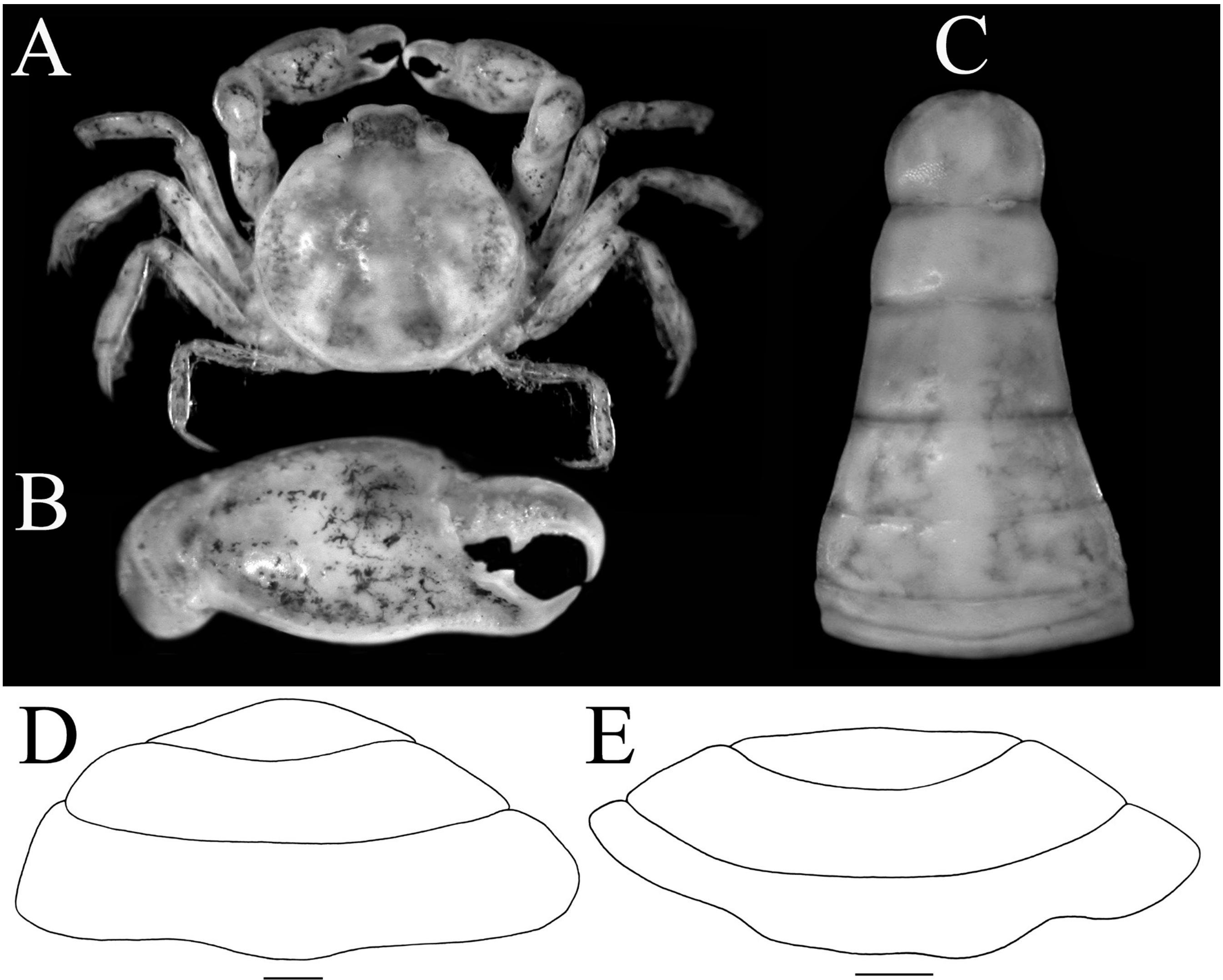

Fig. 15. *Arcotheres palaensis* (Bürger, 1895). A–C, juvenile female (3.3 × 3.4 mm) (ZRC 2018.767), Thailand; D, female (8.2 × 7.0 mm) (ZRC 2020.9), Singapore; E, ovigerous female (6.6 × 5.2 mm) (ZRC 1965.11.24.32), Singapore. A, overall dorsal view; B, outer view of left chela; C, juvenile female pleon; D, E, female pleonal somites 5 and 6 and telson. Scales = 1.0 mm.

Arcotheres arcophilus is also certainly a junior synonym of *A. palaensis*. The types of *A. arcophilus* (a female and a male) are in poor condition (Figs. 6A, B, 19A), and appear to differ from the lectotype of *A. palaensis* only in that: the female carapace is relatively more hexagonal in shape with a relatively more distinct front (Figs. 6A, B, 19A), the anterior carapace margins of females are relatively less divergent (Figs. 6A, B, 19A), the eyes (for both sexes) are clearly visible in dorsal view (Figs. 6A, B, 19A), and the female ambulatory meri are slightly more slender (Fig. 19A) (see also Ahyong & Ng, 2007b: fig. 2A, C). One small ovigerous female specimen (5.1 × 4.3 mm) from the Riau Islands in Indonesia (ZRC 1999.1202) closely resembles the lectotype female in these characters (Figs. 6C–E, 19D–M); while a recently collected male (3.6 × 3.6 mm; ZRC 2019.1788) agrees very well with the paralectotype male of *A. arcophilus* (SMF-ZMG 172b), notably in the structures of the ambulatory legs, pleon, and G1 (Figs. 20–22).

Carapace proportions and the anterior outline, however, have already been shown to be very variable in *A. palaensis*. Some specimens of *A. palaensis* superficially resemble *A. arcophilus* in possessing a more projecting frontal margin and in the less divergent anterior part of the lateral carapace margins. One female specimen (8.7 × 8.0 mm; ZRC 2020.1; Figs. 3A, 12C, 13E) of *A. palaensis* has a carapace closely resembling that of the type female *A. arcophilus* (Fig. 6A, B), but its eyes are completely hidden by the carapace rim in dorsal view, the ambulatory meri are slightly more slender, the longer P4 propodus is somewhat shorter, and the chela is relatively more elongate. Eight other female specimens of *A. palaensis* from that lot (ZRC 2020.1) show a range of carapace shape variation (Figs. 3B, C, 11D, 12D, 14A). Most specimens of *A. palaensis*, however, have the same eye, leg, and chela features. Another female *A. palaensis* from Malaysia (ZRC 2018.770) has a carapace shape that is superficially like that of the type and other female specimen of *A. arcophilus* (ZRC 1999.1202), but the anterior parts of the lateral margins diverge more strongly and the eyes are underneath the anterior margins, completely invisible in dorsal view (Figs. 11B, 14C). The differences in the ambulatory legs are not significant and can easily be accounted for by variation. In the lectotype female of *A. arcophilus*, the MXP3 dactylus does not reach the apex of

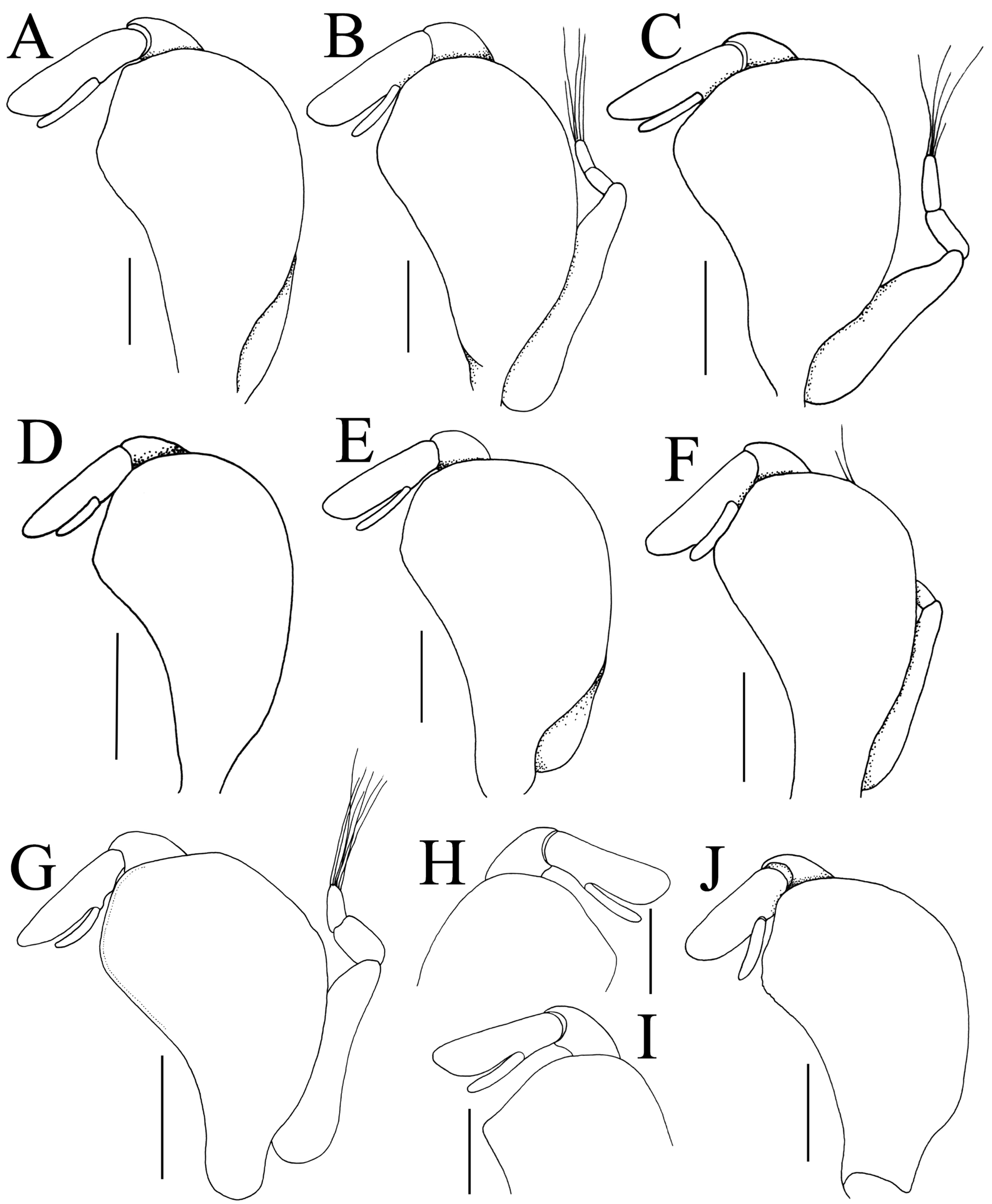

Fig. 16. *Arcotheres palaensis* (Bürger, 1895), outer view of left MXP3. A, female (9.6 × 7.5 mm) (ZRC 1999.975), Peninsular Malaysia; B, ovigerous female (8.5 × 7.2 mm) (ZRC 1992.8378), Peninsular Malaysia; C, female (7.3 × 5.8 mm) (ZRC 1987.537), Peninsular Malaysia; D, female (6.1 × 5.2 mm) (ZRC 1993.119), Peninsular Malaysia; E, female (8.1 × 6.6 mm) (ZRC 2017.1252), Peninsular Malaysia; F, female (7.7 × 6.2 mm) (ZRC 1993.121), Indonesia; G, ovigerous female (6.7 × 5.0 mm) (ZRC 2017.1038), Singapore; H, I, ovigerous female (10.3 × 7.9 mm) (ZRC 2020.11), Peninsular Malaysia; J, female (8.8 × 7.8 mm) (ZRC 2018.764), Lombok, Indonesia. Scales = 0.5 mm.

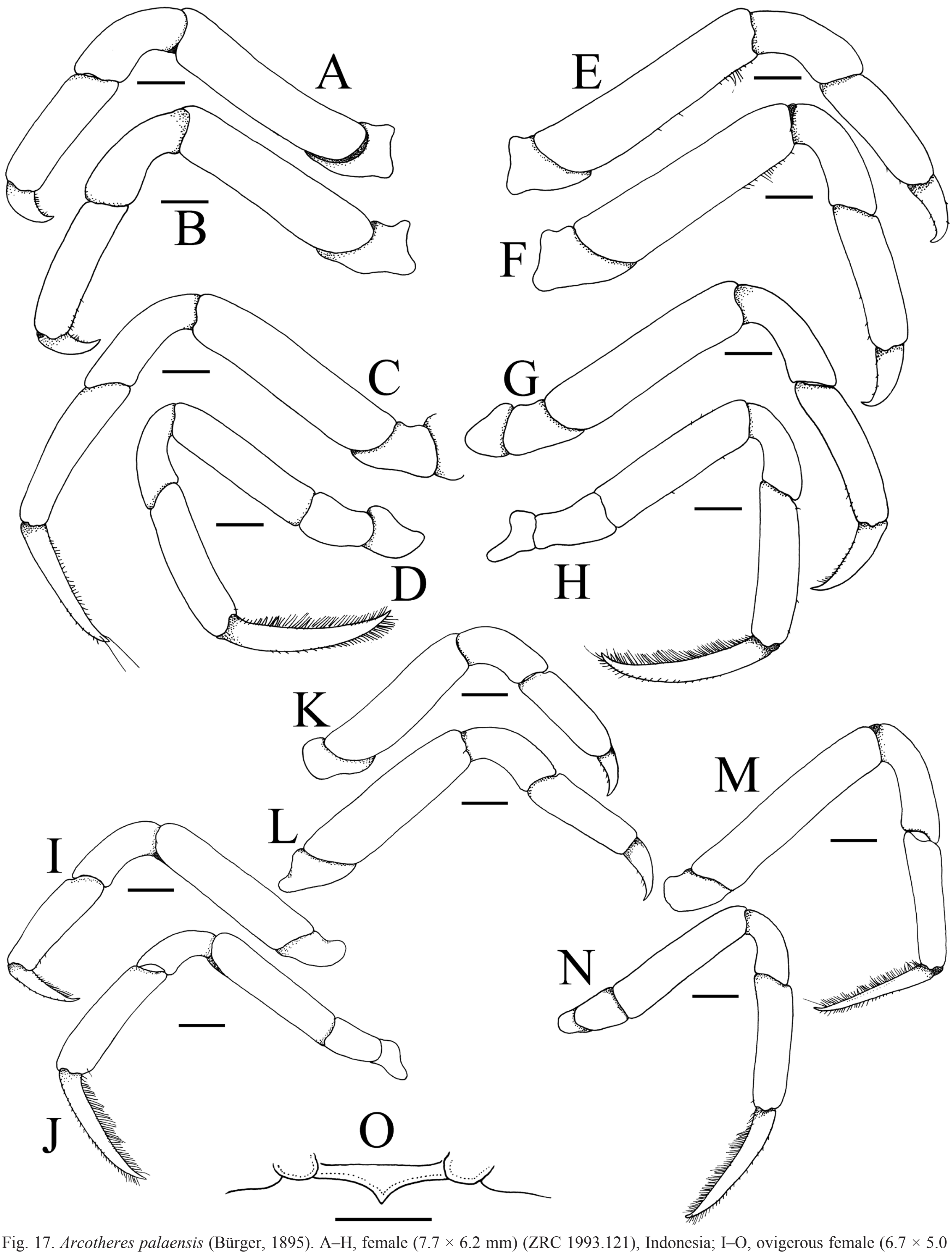

Fig. 17. *Arcotheres palaensis* (Bürger, 1895). A–H, female (7.7 × 6.2 mm) (ZRC 1993.121), Indonesia; I–O, ovigerous female (6.7 × 5.0 mm) (ZRC 2017.1038), Singapore. A–D, left P2–P5, respectively; E–H, right P2–P5, respectively; I, J, left P4 and P5, respectively; K–N, right P2–P5, respectively; O, posterior margin of epistome. Scales = 0.5 mm.

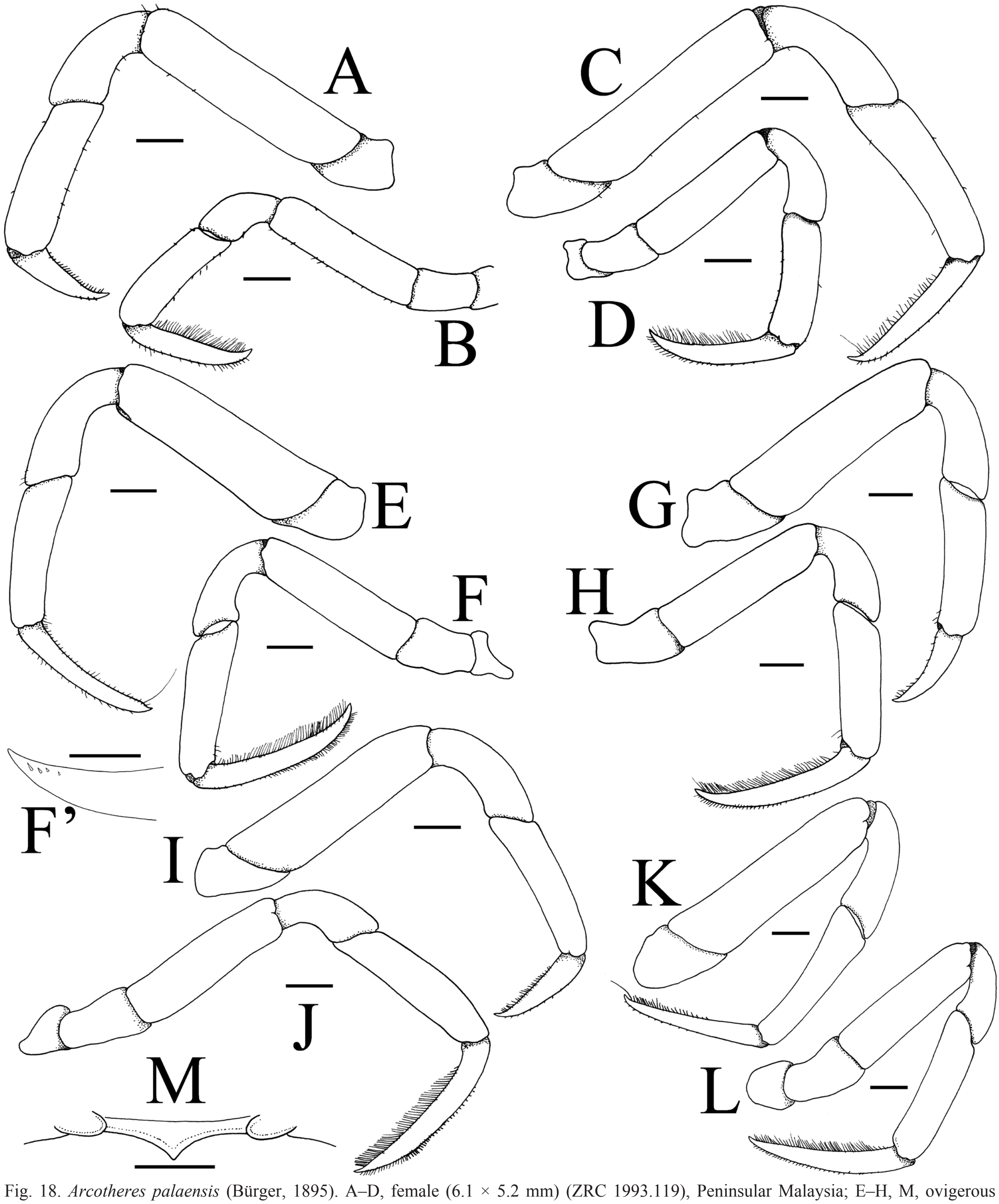

Fig. 18. *Arcotheres palaensis* (Bürger, 1895). A–D, female (6.1 × 5.2 mm) (ZRC 1993.119), Peninsular Malaysia; E–H, M, ovigerous female (8.5 × 7.2 mm) (ZRC 1992.8378), Peninsular Malaysia; I, J, soft female (ca. 9.0 mm carapace width) (ZRC 2000.2613), Peninsular Malaysia; K, L, female (9.5 × 7.7 mm) (ZRC 1965.11.24.30), Singapore. A, B, left P4 and P5, respectively; C, D, right P4 and P5, respectively; E, F, left P4 and P5, respectively; F', distal part of left P5 dactylus (subventral view, soft setae omitted); G, H, right P4 and P5, respectively; I, J, right P4 and P5, respectively; K, L, right P4 and P5, respectively; M, posterior margin of epistome. Scales = A–M, 0.5 mm; F', 0.25 mm.

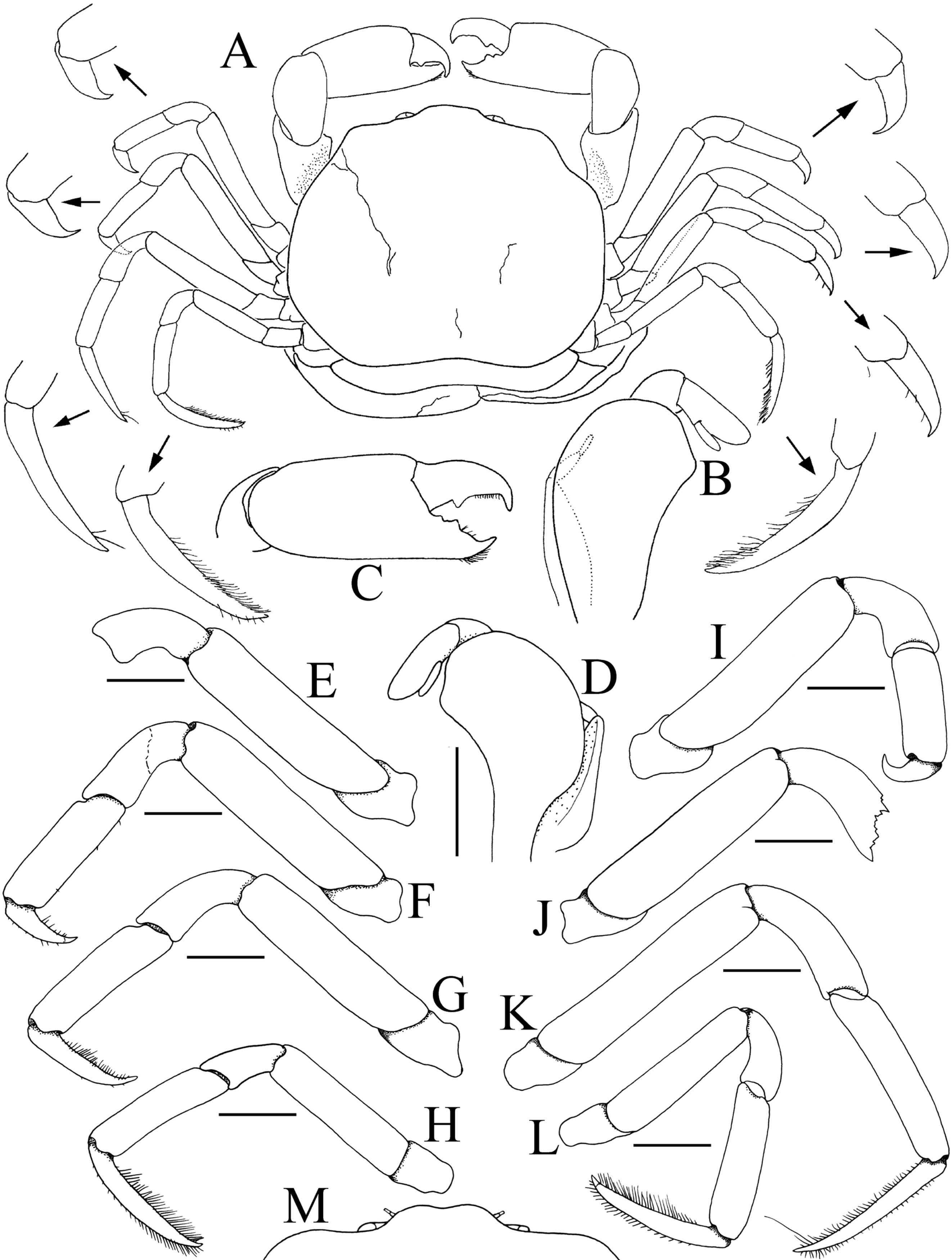

Fig. 19. *Arcotheres palaensis* (Bürger, 1895). A–C, female (5.3 × 4.7 mm) (SMF-ZMG 172a) (lectotype of *Pinnotheres arcophilus* Bürger, 1895), Ubay, Philippines; D–M ovigerous female (5.1 × 4.3 mm) (ZRC 1999.1202), Indonesia. A, overall dorsal view; B, right MXP3; C, right chela; D, left MXP3; E–H, left P2–P5, respectively; I–L, right P2–P5, respectively; M, frontal margin of carapace showing eyes in dorsal view. Scales = A–L, 0.5 mm; M, 1.0 mm.

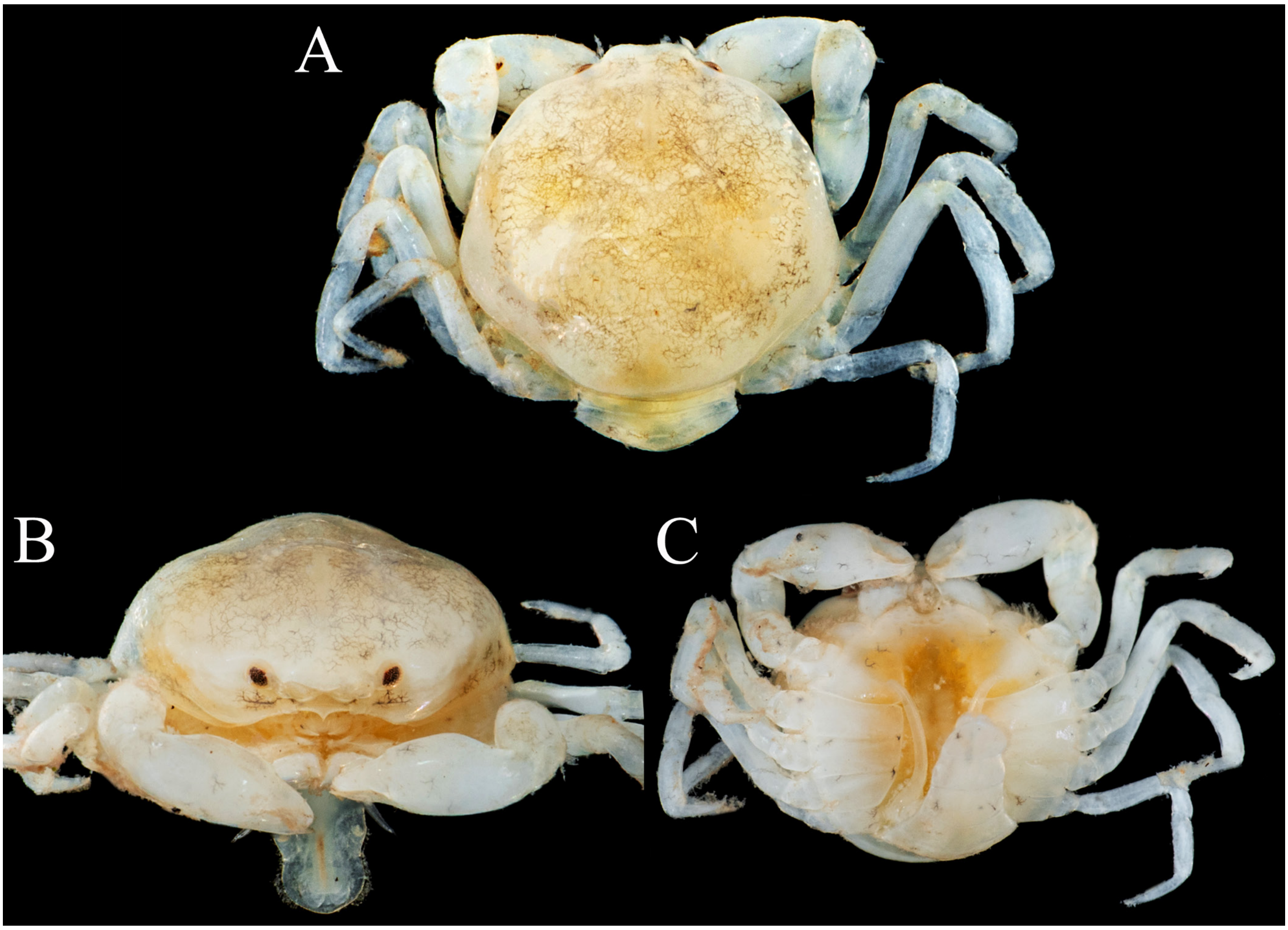

Fig. 20. *Arcotheres palaensis* (Bürger, 1895), male (3.6 × 3.6 mm) (ZRC 2019.1788), Indonesia, colour in life. A, overall dorsal view; B, frontal view; C, ventral view. Photographs: Paul Y. C. Ng.

the propodus (Fig. 19B), but this character varies substantially in *A. palaensis*, with the dactylus sometimes almost reaching the tip of the propodus (Fig. 16).

The one character of *A. arcophilus* that needs discussion is the visibility of the eyes of female specimens in dorsal view. The type specimens of *A. arcophilus* have part of the eyes visible in dorsal view (Figs. 6A, B, 19A), as does the more recent Indonesian female (ZRC 1999.1202; Figs. 6C, D, 19M). The eyes in all other females we referred to *A. palaensis* are concealed under the frontal margins or, at most, scarcely visible in dorsal view. Komai et al. (2020) had used the dorsally exposed eyes as one of the diagnostic features of *A. ocularius* from Fiji and Lombok, but this feature was consistent in a large series of specimens of various sizes. In the case of *A. arcophilus*, however, the types and recent specimen from Indonesia are all relatively small (and the types are poorly preserved), and it would be more parsimonious to consider the dorsally exposed eyes of *A. arcophilus* as being at one end of a continuum of variation within the species, present at smaller sizes prior to maximum swelling of the adult carapace. It is not uncommon, in smaller *A. palaensis*, for the carapace margins lateral to the front to be sufficiently recessed that the eyes lie at the edge of the carapace, albeit remaining concealed in dorsal view; more rarely, however, are the eyes just visible from above, approaching the condition in the type material of *A. arcophilus*. In any case, *A. ocularius* can be distinguished by other characters of the carapace, pleon, and MXP3 (Komai et al., 2020). Under Article 24 of the Code (ICZN, 1999), we here also regard *Pinnotheres palaensis* Bürger, 1895, as having priority over *P. arcophilus* Bürger, 1895, when they are regarded as synonyms.

Miers (1880) recorded *Pinnotheres obesus* with doubt from "Indo-Malayan Seas", but Gordon (1936: 176) re-examined and identified them as *P. latissimus* instead (see also Schmitt et al., 1973: 51). Komai et al. (2020: 230), in revising *P. obesa* s. str., commented that Miers' (1880) material was actually *A. exiguus* based on a personal communication by the present authors, but this is incorrect. Miers' (1880) poorly preserved specimens (NHM 1860.6), re-examined here, are actually referable to *A. palaensis*, the chelae and ambulatory legs agreeing well with this species.

Tesch (1918) described *Pinnotheres onychodactylus* from three females collected from an unspecified host on a reef at 18-m depth, from between Gisser and Ceram islands in the Moluccas, Indonesia, the largest female being 8.8 × 6.8 mm. Tesch (1918: 259) comments: "This species much resembles *P. rhombifer* Bürger, which, perhaps, is nothing but *P. palaensis* Bürger, from which *P. rhombifer* is only

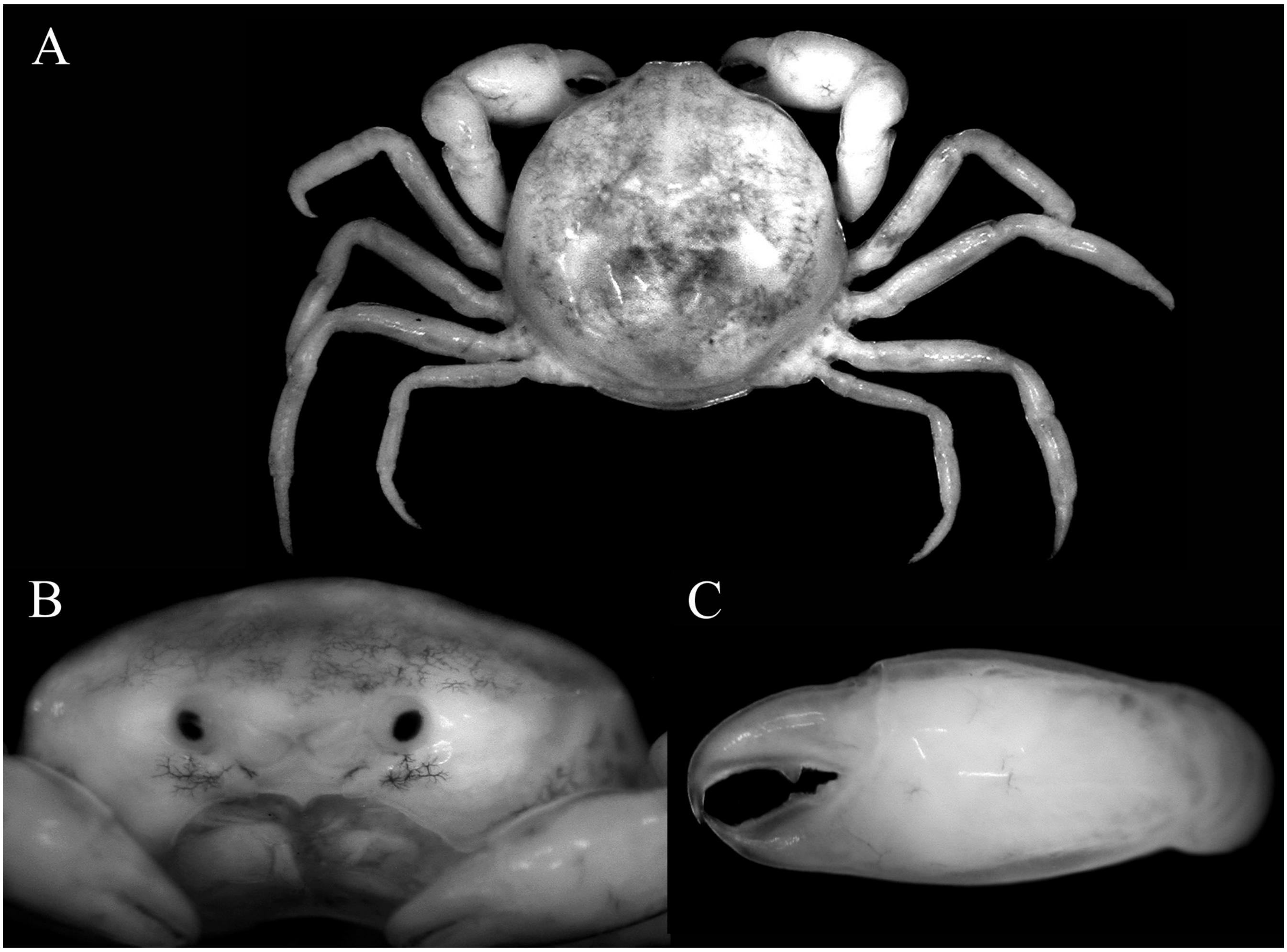

Fig. 21. *Arcotheres palaensis* (Bürger, 1895), male (3.6 × 3.6 mm) (ZRC 2019.1788), Indonesia. A, overall dorsal view; B, frontal view of cephalothorax; C, outer view of right chela.

distinguished by having the penultimate pair of legs shorter than the last pair. In the 'Siboga' specimens the carapace, the breadth of which is 1⅓ times its length, agrees with these of the two named species of Bürger; it is very much vaulted, with bulging hepatic and branchial regions, without sculpture, completely naked and very thin. The front is thickened, not prominent, and the eyes are not visible from above." His figures and description, which note the diagnostic ambulatory dactylar structures, strongly suggest that his species is *A. palaensis* s. str. Unfortunately, he figures the legs (especially the P4) as symmetrical (Tesch, 1918: pl. 17 fig. 5), with the left and right P4 dactyli the same size and form, and the MXP3 dactylus also exceeding the tip of the propodus (Tesch, 1918: pl. 17 fig. 5A). Until the types can be re-examined to ascertain the accuracy of the P4 and MXP3 characters, it may be better to treat it as a distinct species for the moment. In any case, as discussed earlier, we regard *A. rhombifer* as a subjective junior synonym of *A. palaensis*. As we do not know whether the P4 is asymmetrical, we leave the species in *Pinnotheres* s. lato for the time being, although it is likely to be an *Arcotheres*.

De Man's (1921) description and figure of a female specimen from Ambon, Indonesia, as well as his record of 11 females and two males from Java (De Man, 1929), from a species of "*Arca*", match those of *A. palaensis* very well and we have no doubt of his identification. De Man (1921) also figured a female *Arcotheres* specimen (as a *Pinnotheres*) from Ambon and another from Lombok, referring them to *A. palaensis* and *A. arcophilus*, respectively (they are regarded as synonyms here). De Man based this mainly on the structure propodus, MXP3 dactylus, and the form of the chela, following Bürger's (1895) original descriptions and figures. He noted that the carapace was in bad condition in both specimens and could not help the taxonomy. He discussed at length the asymmetry in the ambulatory legs and considered the possibility of it being anomalous or even the result of bopyrid infection. Ambulatory leg asymmetry was revisited in a later paper (De Man, 1929). Perez (1921: 61), following on his correspondence with De Man (1921), briefly commented on this problem and followed De Man's identifications of the Ambon and Lombok specimens. De Man's (1921) figures for the two species are excellent and his figures of the third maxillipeds and chelipeds in particular agree very well with those of *A. palaensis* (and *A. arcophilus*) here. The MXP3 dactylus of his "*A. arcophilus*" is short, terminating some distance from the tip of the propodus, and the chela is short and stout (De Man, 1921: pl. 8 figs. 1, 2), while in *A. palaensis*, the MXP3 dactylus is slightly longer, almost reaching the tip of the propodus, and the chela is relatively more elongate and slender (De Man, 1921: pl. 8 figs. 8, 9; cf. present Figs. 8D, 9D, 16). De Man's (1921)

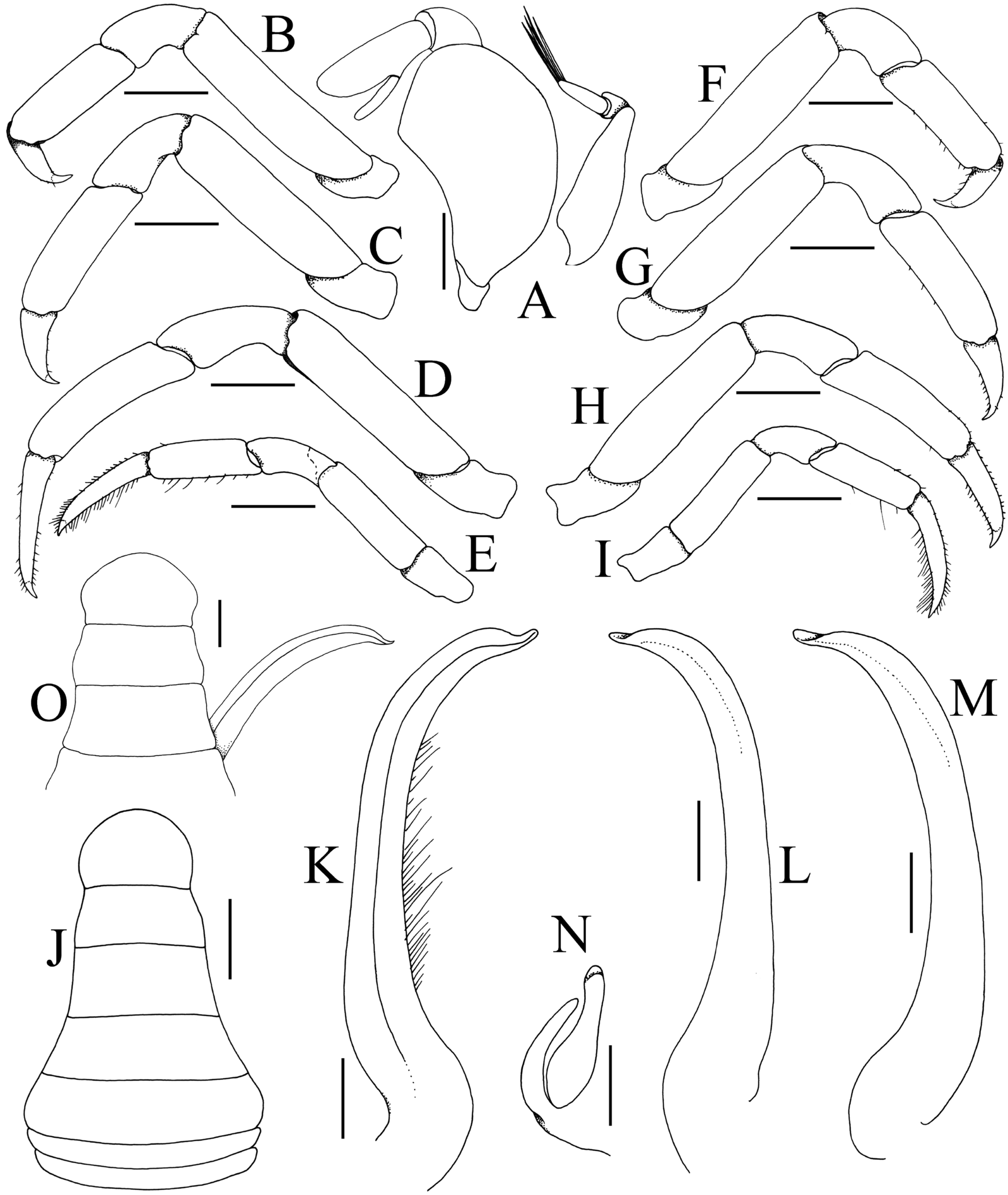

Fig. 22. *Arcotheres palaensis* (Bürger, 1895). A–N, male (3.6 × 3.6 mm) (ZRC 2019.1788), Indonesia; O, male (2.8 × 2.5 mm) (SMF-ZMG 172b) (paralectotype of *Pinnotheres arcophilus* Bürger, 1895), Philippines. A, left MXP3; B–E, left P2–P5, respectively; F–I, right P2–P5, respectively; J, pleon; K, left G1 (ventral view); L, M, left G1 (slightly different dorsal views); N, left G2; O, pleonal somites 3–5, telson, and left G1. Scales = A, K–N, 0.2 mm; B–J, 0.5 mm; O, 0.1 mm.

record of "*A. arcophilus*" is also almost certainly from an *Anadara* or *Tegillarca* (then known as *Arca*).

Pinnotheres paralatissimus Dai & Song, 1986, was described from two females collected from an unspecified host in Beihai, Guangxi, southern China (Dai & Song, 1986: 55, text-fig. 2; Fig. 10A–H). Despite two separate searches in 2018 and 2019, the types could not be found in the Institute of Zoology, Chinese Academy of Sciences (Academia Sinica), where they were stated to have been kept (Meng Kai, Ng Ngan Kee, Lee Bee Yan, pers. comm.). The description and figures, however, are identical with what is here recognised as *A. palaensis* s. str.

Campos (2001) described *A. guinotae* from one female (6.4 × 5.8 mm; MNHN-B9498), collected from somewhere in Thailand from an unidentified species of *Barbatia*. He compared it with *A. similis*, *A. spinidactylus*, *A. alcocki*, and *A. tivelae* (Gordon, 1936), noting that "the acute and sinuous anterolateral margin of the carapace in *A. guinotae* n. sp., is not observed in all other known congeners" (Campos, 2001: 497). We have examined photographs of the type specimen, courtesy of A. Anker (Fig. 7), who also kindly confirmed various key characters for us. The carapace shape of *A. guinotae* is somewhat unusual (Figs. 1B, 7A; Campos, 2001: fig. 1A), but we have on hand a female (6.7 × 5.0 mm; ZRC 2017.1038) collected from a *Barbatia* in Singapore, which is comparable in size to the holotype female of *A. guinotae* and agrees with it in all features, including the carapace shape (Figs. 9, 14H, 16G, 17K–O). Our comparisons of the large series of *A. palaensis*, including specimens collected from *Barbatia*, found that the carapace shape variation fully encompasses that reported for *A. guinotae*. We have specimens that have carapace shape of intermediate conditions that transition into the more ovate form, also found in *A. palaensis* (Figs. 11–14). The female telson of *A. guinotae* is proportionately narrower (Campos, 2001: fig. 1C) than those in most adult female specimens (e.g., Figs. 5B, 8B, 9B), which we consider intraspecific variation. We have a few specimens of *A. palaensis* in which the female telson (Fig. 15D, E) is similar to that of the holotype of *A. guinotae*. Other specimens from the same lot or site have the more typically wide female telsons. There are no other characters that can separate the two species and the excellent description and figures by Campos (2001) leave no doubt. As such, we synonymise *A. guinotae* under *A. palaensis*.

The Indian record of "*Arcotheres alcocki*" by Lalitha Devi (1981: 216, figs. 1 (right), 2, 3) from *Tegillarca granosa* in Kakinada Bay in the Bay of Bengal may be *A. palaensis* as well. The figures of the female specimen are not all given in sharp detail (Lalitha Devi, 1981: fig. 2), but nevertheless agree well with *A. palaensis*. The figured male agrees very well with male specimens examined here, including in the form of the pleon and G1 (Lalitha Devi, 1981: fig. 3). The available evidence of "*Arcotheres alcocki*" presented by Lalitha Devi (1981) points to *A. palaensis*, but her material should be re-examined to determine if this is indeed the case. Trivedi et al. (2018a) recently described a species from southern India, *A. shahi*, ostensibly from oysters, that closely resembles *A. palaensis*, and necessary comparisons should be made to determine if they are related.

The Japanese records of "*A. alcocki*" are not that species. Ahyong & Ng (2007b: 193–194) observed that the record of "*A. alcocki*" by Takeda & Konishi (1988) is a different species close to *A. sinensis* (Shen, 1932), or perhaps even undescribed. We have since examined their specimens from the Hiroshima area as well as a series of females from nearby Kumamoto (Figs. 12G, H, 14E, F), and they agree best with *A. palaensis* as recognised here. As such, the records by Watanabe & Henmi (2009) and Watanabe (2013) should now also be referred to *A. palaensis*. The male reported by Takeda & Konishi (1988) is not in good condition but agrees with the present male from Indonesia (Figs. 20–22) in most features. The carapace is slightly more rounded in the Japanese male (not evident from the figure) and its frontal margin is weakly emarginate (carapace wider with a straighter frontal margin in the Indonesian male; Figs. 20A, 21A). The male pleon of the Japanese male, however, is unusual in being proportionately wider, with strongly concave margins, and with the telson relatively broader and subcircular in shape (Takeda & Konishi, 1988: fig. 3c) (versus pleon less wide, margins weakly concave, and telson sub-hexagonal to semicircular in the Indonesian male; Fig. 22J, O). The differences in carapace and pleon features may be due to size-associated variation—the Japanese male, at 4.2 × 3.7 mm, is larger than the Indonesian specimen (3.6 × 3.6 mm). In *A. placunicola*, however, smaller males have a relatively wider pleonal somite 6 and a somewhat more rectangular telson, with somite 6 becoming proportionately longer and the telson semicircular in larger specimens (Ng, 2018a: 478, fig. 4B, C); their G1s, however, agree in relative stoutness. Takeda & Konishi (1988: fig. 3d, e) figured the tip of the G1 as having a small spine, but this proved to be an uneven evaginated fold caused by preservation; the gonopods are otherwise indistinguishable between Japanese and Malaysian specimens. The Japanese records, however, are the northernmost and only records of the species from temperate-subtropical waters, all others being from the tropics. It cannot be excluded that the morphological differences between the Japanese and Malaysian males possibly indicate more than one species; more work should be done to confirm this. The Japanese taxon, however, is certainly not *A. alcocki* s. str. (see later for this species).

We have on hand female specimens from Lombok, two of which were collected from specimens of *Anadara antiquata* (ZRC 2018.764, ZRC 2018.762) and belong to two separate species. Two specimens, one of which is infected by a bopyrid (carapace length 6.7 mm; ZRC 2018.762), match *A. palaensis* in all diagnostic features (Fig. 12F). The second specimen (9.4 × 8.4 mm; ZRC 2019.1025) is referable to *A. ocularius* Komai, Kawai & Ng, 2020 (Fig. 23B), as the MXP3 has a proportionately longer MXP3 dactylus, the front is more pronounced anteriorly, the eyes are clearly visible in dorsal view, and the female anterior thoracic sternum (fused sternites 1–4) is relatively broader with the median part shallow rather than deeper (Komai et al., 2020). Our morphological identification of *A. ocularius* is corroborated by unpublished molecular comparisons currently underway in collaboration with L. M. Tsang.

In the ZRC there is one lot with a male and a female specimen initially identified as *A. palaensis*, collected in 1983 from *Tegillarca* (as *Anadara*) in mangroves in Batu Pahat, Peninsular Malaysia (ZRC 2000.2613). These specimens had been loaned to Charles Pregenzer for his comparative studies (unpublished) and Gerhard Pohle for his phylogenetic work (see Pohle & Marques, 1998). The female specimen (ca. 9.0 mm carapace width) is in poor condition now, soft and with a deformed carapace, but is clearly *A. palaensis* as presently defined (Fig. 18I, J). The small male (3.7 × 3.3 mm), which is relatively hard and in good condition, however, cannot be this species even though it is labelled as being from the same host and location, because the P5 dactylus has a row of spinules (Fig. 60H) which *A. palaensis* lacks. In the shape and flatness of the carapace (when viewed frontally; Fig. 60D, E), it closely resembles *A. placunicola*. In addition, the G1 is more similar in shape and features to that of *A. placunicola*, including the obliquely directed distal tip (Figs. 60G, 62M, N). We are confident this small male is actually *A. placunicola* and is here referred to that species with a new catalogue number (ZRC 2021.802). Although it cannot be excluded that the small male entered a *Tegillarca* instead of *Placuna* host, we consider it more likely that the specimen was mislabelled or misplaced. If this is the case, we do not know how the specimens of the two species got mixed in one lot, nor whether it was collection error or otherwise. It is important to note, however, that the male *A. palaensis* obtained by the authors from *Tegillarca* and *Anadara* has a clearly more elongate carapace, with the dorsal surface prominently convex and the front clearly more projected anteriorly (Figs. 20A, B, 21A, B).

Distribution. Western Pacific to the eastern Indian Ocean, from Palau and Japan to the South China Sea including the Philippines, Indonesia, Borneo, Malaysia, Singapore, Thailand, and eastern India.

Arcotheres ocularius Komai, Kawai & Ng, 2020
(Figs. 23, 24)

Arcotheres ocularius Komai, Kawai & Ng, 2020: 232, figs. 7–17 [type locality: Fiji]; De Gier & Becker, 2020: tab. 1.

Type material. Holotype: ovigerous female (11.8 × 10.2 mm) (CBM-ZC 15952), Kumi Village, Viti Levu, Fiji, 17°53.21′S, 178°36.07′E, intertidal, with *Anadara* sp. (Bivalvia: Arcidae), 16 August 2010, coll. K. Kawai. Paratypes: 1 female (8.9 × 8.2 mm), 3 ovigerous females (9.6 × 8.4 mm, 10.9 × 9.7 mm, 12.3 × 11.9 mm) (ZRC 2019.1877), coll. 16 August 2010; 2 females (5.5 × 5.0 mm, 6.9 × 6.4 mm), 17 ovigerous females (8.5 × 7.4–13.4 × 9.6 mm) (CBM-ZC 15953), coll. 16 August 2010; 1 male (6.2 × 6.8 mm) (CBM-ZC 15954); 1 female (5.2 × 5.2 mm) (CBM-ZC 15956), coll. 16 August 2010; 1 male (4.6 × 5.0 mm) (CBM-ZC 15957), coll. 16 August 2010; 2 males (3.2 × 3.2 mm, 3.3 × 3.4 mm) (CBM-ZC 15958), coll. 16 August 2010; 1 male (5.8 × 5.8 mm) (CBM-ZC 15959); 1 male (4.8 × 5.4 mm) (ZRC 2020.7), coll. 16 August 2010; 1 ovigerous female (10.7 × 9.1 mm) (CBM-ZC 15960), coll. 6 September 2011; 7 ovigerous females (8.6 × 7.2–10.7 × 9.5 mm) (CBM-ZC 15961), August 2018; 5 ovigerous females (9.4 × 8.0–10.7 × 9.3 mm) (ZRC 2020.8), August 2018 (all from same locality as holotype); 1 ovigerous female (CBM-ZC 19562), Ucikumi, near Kumi Village, coll. 22 February 2019.

Other material examined. Fiji: 4 poorly preserved females (4.2 × 3.3–6.0 × 4.6 mm) (ZRC 2019.1878), intertidal, associated with *Anadara* sp., coll. K. Kawai, August 2018. **Indonesia:** 1 female (9.4 × 8.4 mm) (ZRC 2019.1025), Teluk Kodek, Lombok, intertidal, in *Anadara antiquata* (Linnaeus, 1758) (Arcidae), coll. S. Dwiono, 12 November 2013.

Description. Carapace and pereopods well chitinised. Female: Carapace subcircular, wider than long; dorsal and lateral surfaces smooth, glabrous; appearing domed in frontal view; front projecting anteriorly beyond orbits, margin gently convex to almost straight; anterolateral margin smooth, subparallel with frontal margin or gently sloping posteriorly, forming rounded angle with posterolateral margin (Fig. 23). Eyes clearly visible in dorsal view in adults; mobile, filling orbit (Fig. 23). Epistome with median part low, triangular, lateral margins wide, gently concave (Komai et al., 2020: figs. 7D, 8B).

MXP3 outer surface with scattered short setae; ischiomerus completely fused, subrhomboidal, inner margin rounded to gently angular at widest point; carpus short; propodus about 3 times as long as high, subspatulate, longer than carpus, tip rounded; dactylus digitiform, inserted submedially on flexor margin of propodus, tip reaching end of or slightly overreaching propodal apex; exopod relatively slender, about two-thirds length of ischiomerus, flagellum 2-segmented (Fig. 24A, B).

Chela short, stout, dactylus about two-thirds palm length; palm relatively slender, medially widest; outer surfaces of palm, fingers (except for distal part) almost glabrous, with only scattered short setae; ventral margin of palm gently convex, with low bulge near midlength; dactylus occlusal margin with 1 subproximal tooth; pollex occlusal margin with 1 low sharp proximal tooth and denticles; tips of fingers sharp, hooked (Fig. 24C).

P2–P5 dorsally, ventrally unarmed; outer surface covered with scattered, very short setae or glabrous; ventral margins of propodus and dactylus slightly more setose; merus relatively short, stout, relative lengths of meri P4>P3>P2>P5; left (sometimes right) P4 distinctly the longer; P2 and P3 dactyli short, subequal, tip gently hooked, half length of propodus; longer P4 dactylus elongate, almost straight, sparsely setose, longer than P5 dactylus; P5 merus 4.1–4.4 times longer than wide; P5 dactylus shorter than longer P5 dactylus, longer than shorter P4 dactylus, margins lined with short and long setae, denser on ventral margin, distoflexor margin without rows of spinules (Fig. 24D–K).

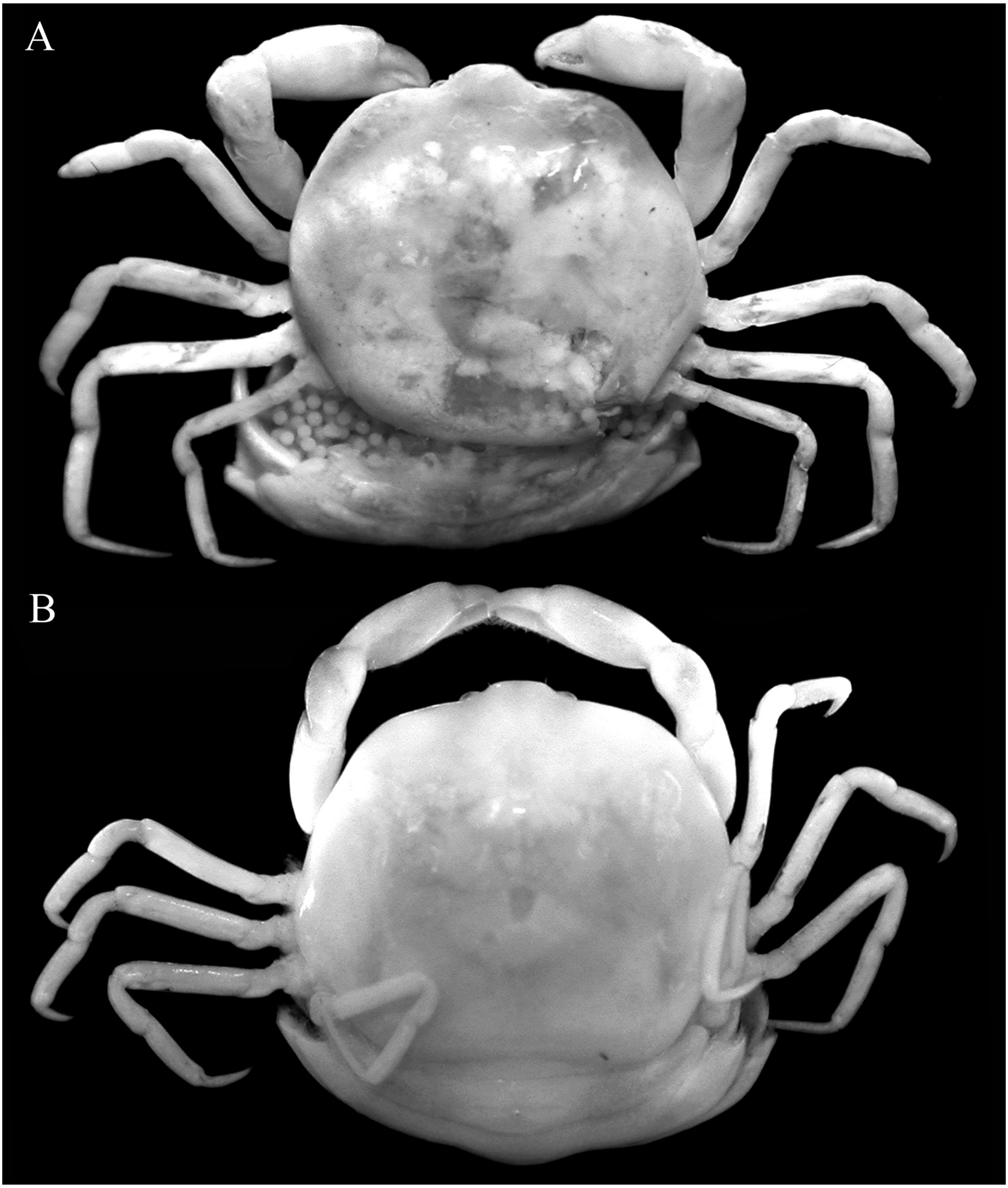

Fig. 23. *Arcotheres ocularius* Komai, Kawai & Ng, 2020, overall dorsal view. A, paratype ovigerous female (10.9 × 9.7 mm) (ZRC 2019.1877), Fiji; B, female (9.4 × 8.4 mm) (ZRC 2019.1025), Indonesia.

Pleon extending to buccal region, covering bases of P2–P5; telson gently recessed into concave distal margin of somite 6 (Komai et al., 2020: fig. 8D, E).

Male: Carapace almost circular, slightly longer than wide; dorsal surface almost smooth, gently inflated, lateral surfaces with setae; front projecting anteriorly, margin gently convex to sinuous (Komai et al., 2020: figs. 12, 13A, 15A). Eyes distinctly visible in dorsal view (Komai et al., 2020: figs. 12, 13A, 15A). MXP3 as in female except dactylus just reaching tip of propodus (Komai et al., 2020: figs. 13C, 16A). Anterior thoracic sternum wide, sternites 1, 2 fused, partially sunken into buccal cavity; suture between sternites 2 and 3 shallow; sternites 3, 4 completely fused, separated

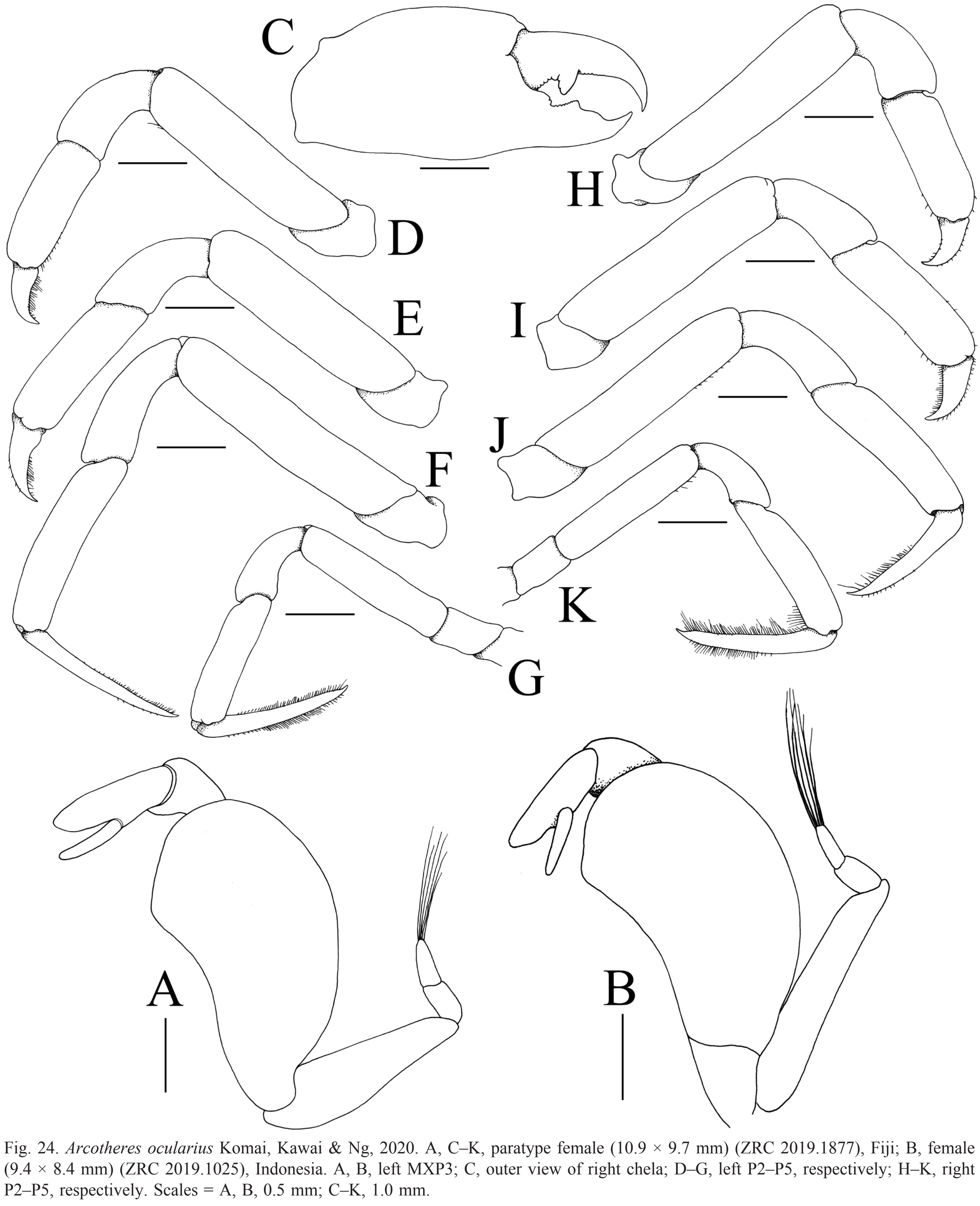

Fig. 24. *Arcotheres ocularius* Komai, Kawai & Ng, 2020. A, C–K, paratype female (10.9 × 9.7 mm) (ZRC 2019.1877), Fiji; B, female (9.4 × 8.4 mm) (ZRC 2019.1025), Indonesia. A, B, left MXP3; C, outer view of right chela; D–G, left P2–P5, respectively; H–K, right P2–P5, respectively. Scales = A, B, 0.5 mm; C–K, 1.0 mm.

only by shallow grooves (Komai et al., 2020: figs. 13D, 15B). Chela relatively stout, shorter than in female (Komai et al., 2020: figs. 14A, 16B). P2–P5 dorsally, ventrally unarmed; outer surface covered with short setae; P3 and P4 carpus and propodus with long natatory setae; left and right meri equal, relative lengths of meri P4>P3>P2>P5; dactyli of P2–P4 progressively longer; left P4 dactylus slightly longer, more slender than right side; P4 and P5 dactylus subequal to that of P3, covered with short setae (Komai et al., 2020: figs. 14C–G, 15A, 16D–H). Pleon slender, triangular, widest at somite 3, lateral margins of somite 4 gently sinuous to almost straight; somite 6 subtrapezoidal; telson subhexagonal, much wider than long (Komai et al., 2020: figs. 13D, H, 15F). G1 relatively stout, arcuate, curved outwards, tip subtruncate, without elongate process (Komai et al., 2020: figs. 13I, J, 15G, H). G2 short, with spatuliform tip; exopod slightly longer than endopod (Komai et al., 2020: figs. 13K, 15I).

Variation. Komai et al. (2020: 241) noted that the carapace shape varied from broadly ovate (Komai et al., 2020: fig. 7A) to almost circular (Komai et al., 2020: fig. 7B, C). The condition of the dorsally exposed eyes and dactylus reaching end of or slightly overreaching MXP3 propodus, however, were always reliable.

Colour. "Entirely whitish; female ovary, visible through integument, orange; cornea of eye red" (Komai et al., 2020: 241).

Host. Known from *Anadara* sp. in Fiji and *Anadara antiquata* (Linnaeus, 1758) in Lombok (Arcidae Lamarck, 1809).

Remarks. Komai et al. (2020) discussed the taxonomy of *A. ocularius* at length, differentiating it from the morphologically similar *A. palaensis* s. str. in the more strongly chitinised carapace and pereopods, eyes that are clearly visible in dorsal view in adult females, the prominently projecting front, the MXP3 dactylus being always long and reaching or overreaching the propodus apex, the male telson being subpentagonal or subhexagonal, and the G1 with a subtruncate tip (Figs. 23, 24A, B; Komai et al., 2020: figs. 7A–D, 8C, F, G, 10B, E, 13D, H–J, 15F–H, 16A). They also noted that unpublished genetic studies by Tsang Ling Ming from the Chinese University of Hong Kong show both species to be distinct. *Arcotheres ocularius* is known from Fiji and Lombok, Indonesia, but not recorded from the main Sunda Shelf where *A. palaensis* is common. Both species, however, are present in Lombok.

Komai et al. (2020: 244) observed that in the figure of the lectotype of *A. arcophilus* in Ahyong & Ng (2007b: fig. 2A) (present Figs. 6A, 19A), the "female P4 merus is proportionately longer in *A. ocularius*" than in *A. arcophilus*. We have re-examined the lectotype of *A. arcophilus* (at present synonymised under *A. palaensis*) and the P4 merus is actually similar to *A. ocularius* and more like the condition in a more recent female of *A. palaensis* from Indonesia (Figs. 6C, 19E–L). In the protruding front and dorsally visible eyes in adult females, *A. ocularius* resembles some specimens of *A. palaensis*, but the carapace of *A. ocularius* is always more strongly chitinised, the MXP3 dactylus always long and overreaching the propodus apex, the longer female P4 merus relatively longer, the male telson subpentagonal or subhexagonal, and the G1 with a subtruncate tip (Figs. 23, 24A, B; Komai et al., 2020: figs. 7A–D, 8C, F, G, 10B, E, 13D, H–J, 15F–H, 16A).

Distribution. Western Pacific, from Fiji to southeastern Indonesia.

Arcotheres similis (Bürger, 1895)
(Figs. 25–33)

Pinnotheres similis Bürger, 1895: 373, 374, pl. 9 fig. 14 [type locality: Ubay, Philippines]; Tesch, 1918: 250 (list); Silas & Alagarswami, 1967: 1210 (list); Serène, 1968: 94; Schmitt et al., 1973: 86.
Pinnotheres modiolicola Bürger, 1895: 370, pl. 9 fig. 9, pl. 10 fig. 9 [type locality: Philippines, from *Modiolus philippinarium*]; Lanchester, 1900: 761 (Singapore); Estampador, 1937: 5 (list). [New synonymy]
Pinnotheres kamensis Rathbun, 1909: 110; 1910: 335, figs. 18, 19; Tesch, 1918: 249, 252; Suvatti, 1938: 69; 1950: 159; Silas & Alagarswami, 1967: 1200, 1223, 1225; Schmitt et al., 1973: 50; Naiyanetr, 1980: 42; 1998: 104; 2007: 11; De Gier & Becker, 2020: tab. 1.
Pinnotheres modiolicolus — Tesch, 1918: 249 (list); Silas & Alagarswami, 1967: 1203 (list); Serène, 1968: 94; Schmitt et al., 1973: 57; Dev Roy, 2013: 156, 157.
Pinnotheres spinidactylus Gordon, 1936: 169, figs. 1, 2; Serène, 1968: 94; ?Griffin & Campbell, 1969: 157, figs. 7, 8; Stephenson et al., 1970: 492; Schmitt et al., 1973: 88; Jones, 1990: 202; Davie, 2002: 428, fig. a, b, 434.
Arcotheres spinidactylus — Campos, 2001: 494; Ahyong & Brown, 2003: 10; Ng et al., 2008: 248; Ng et al., 2017: 1094; Trivedi et al., 2018a: 197, 248; De Gier & Becker, 2020: tab. 1.
Arcotheres similis — Ahyong & Ng, 2007b: 207, fig. 14; Ng et al., 2008: 248; Ng et al., 2017: 1094; Trivedi et al., 2018a: 197; De Gier & Becker, 2020: fig. 8B, tab. 1.
Arcotheres modiolicola — Ahyong & Ng, 2007b: 199, fig. 7; Ng et al., 2008: 248; Ng et al., 2017: 1094; Trivedi et al., 2018a: 197; De Gier & Becker, 2020: tab. 1.

Type material. Holotype: female (8.3 × 6.4 mm) (SMF-ZMG 956), Ubay, Philippines, coll. C. Semper. **Philippines:** 1 damaged ovigerous female (8.0 × 6.5 mm) (SMF-ZMG 168), from *Modiolus philippinarum*, coll. C. Semper (holotype of *Pinnotheres modiolicola* Bürger, 1895). **Thailand:** 1 juvenile male (1.8 × 1.6 mm) (NHMD CR-9396), west of Koh Kam, Gulf of Thailand, 9.1 m, coll. Th. Mortensen, 6 February 1900 (holotype of *Pinnotheres kamensis* Rathbun, 1909). **Singapore:** 1 ovigerous female (6.7 × 5.5 mm) (NHM 1936.6.19.2), Siglap, from *Modiolus philippinarum*, coll. R. Winckworth (holotype of *P. spinidactylus* Gordon, 1936); 1 male (3.3 × 3.3 mm), 4 ovigerous females (5.8 × 4.7 mm, 6.7 × 5.8 mm, 5.7 × 4.9 mm, 6.3 × 5.3 mm) (NHM 1936.6.19.3–7), Siglap, from *Modiolus philippinarum*, coll. R. Winckworth (paratypes of *P. spinidactylus* Gordon, 1936).

Other material examined. Singapore: 2 males (4.0 × 4.3 mm, 4.8 × 5.0 mm) (NHM 1936.6.19.14–15), Siglap, coll. R. Winckworth; 1 female (9.3 × 7.8 mm) (ZRC 2017.1034), from *Modiolus philippinarum*, intertidal area, off Changi beach, next to Carpark 7, near ferry terminal, coll. S. K. Tan et al., 8 June 2016; 3 ovigerous females (7.1 × 5.9 mm, 7.6 × 6.4 mm, 8.3 × 6.7 mm) (ZRC 2017.1035), from *Modiolus philippinarum*, intertidal area, off Changi beach, next to Carpark 7, near ferry terminal, coll. S. K. Tan et al., 3 August 2012; 1 male (5.5 × 5.8 mm), 5 females, 1 juvenile female (ZRC 2017.1264), 1 female (AM P102287), from *Modiolus philippinarum*, intertidal area, off Changi

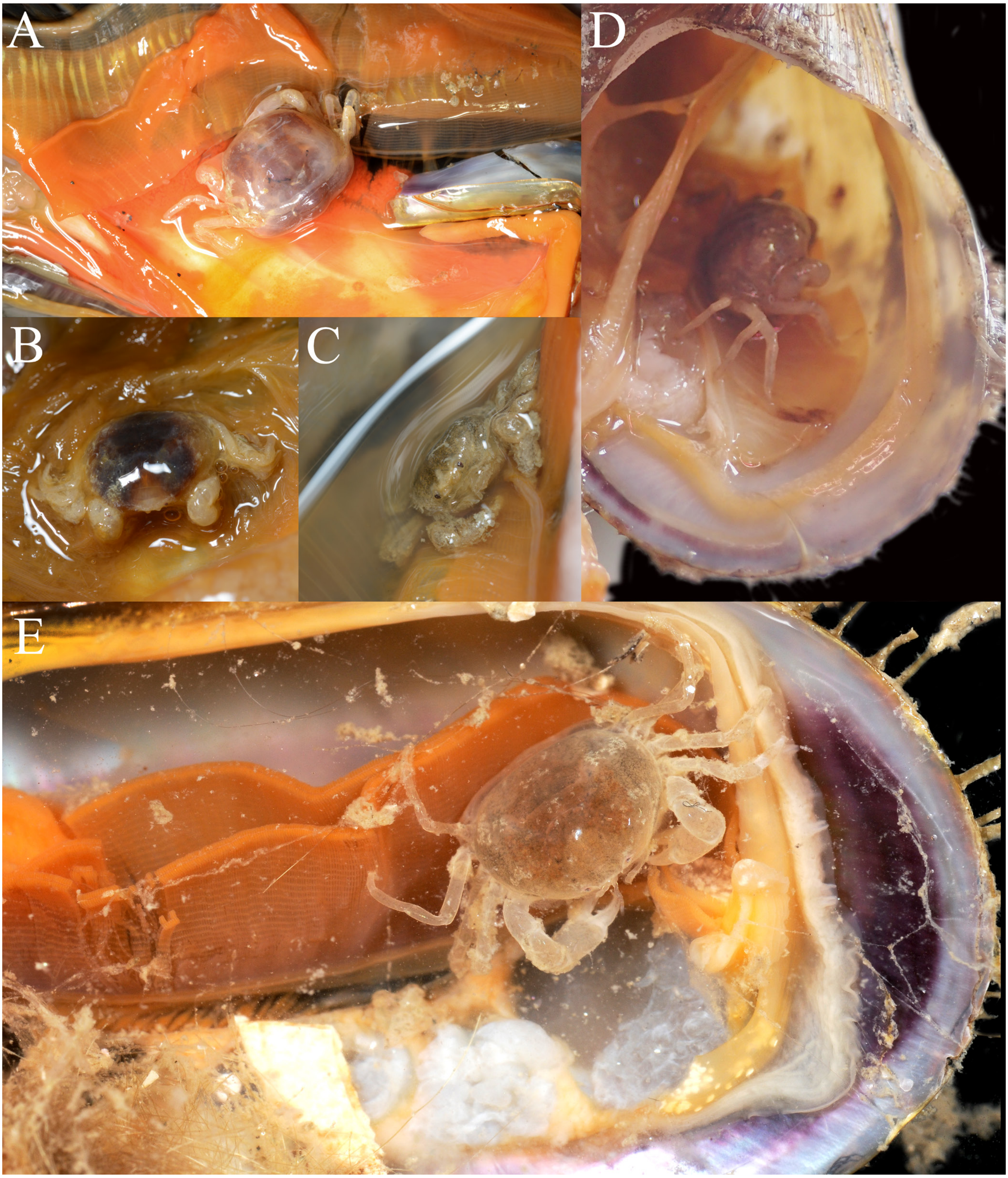

Fig. 25. *Arcotheres similis* (Bürger, 1895). A, ovigerous female (9.3 × 7.8 mm) (ZRC 2017.1034), Changi, Singapore; B, C, two females (ZRC 2017.1264) in situ on *Modiolus philippinarum* (Hanley, 1843) (Mytilidae); D, ovigerous female (7.9 × 6.3 mm) (ZRC 2017.1037), Tuticorin, India; E, female (6.5 × 5.2 mm) (ZRC 2013.1429), in situ on *Modiolus philippinarum* (Hanley, 1843) (Mytilidae), Pulau Ubin, Singapore. Photographs: A–C, E, Tan Heok Hui; D, R. Ravinesh.

beach, next to Carpark 7, near ferry terminal, coll. S. K. Tan et al., 26 June 2017; 1 female (6.5 × 5.2 mm) (ZRC 2013.1429), in *Modiolus philippinarum*, Pulau Ubin, coll. S. K. Tan et al., 6 March 2012; 1 female (8.6 × 6.8 mm) (ZRC 2017.1036), Tanah Merah Besar beach, coll. R. U. Gooding, 3 April 1966; 4 shrivelled females (largest ca. 7.6 × 6.3 mm) (ZRC 1965.11.24.42–45), from "*Pinna* sp.", coll. February 1938; 4 females (ZRC 1965.11.24.42–45), "in *Pinna*", Pulau Senang, Southern Islands, coll. 1930s; 2 females (8.8 × 8.1 mm, 5.8 × 5.1 mm) (ZRC 2018.785), 1 male (4.8 ×

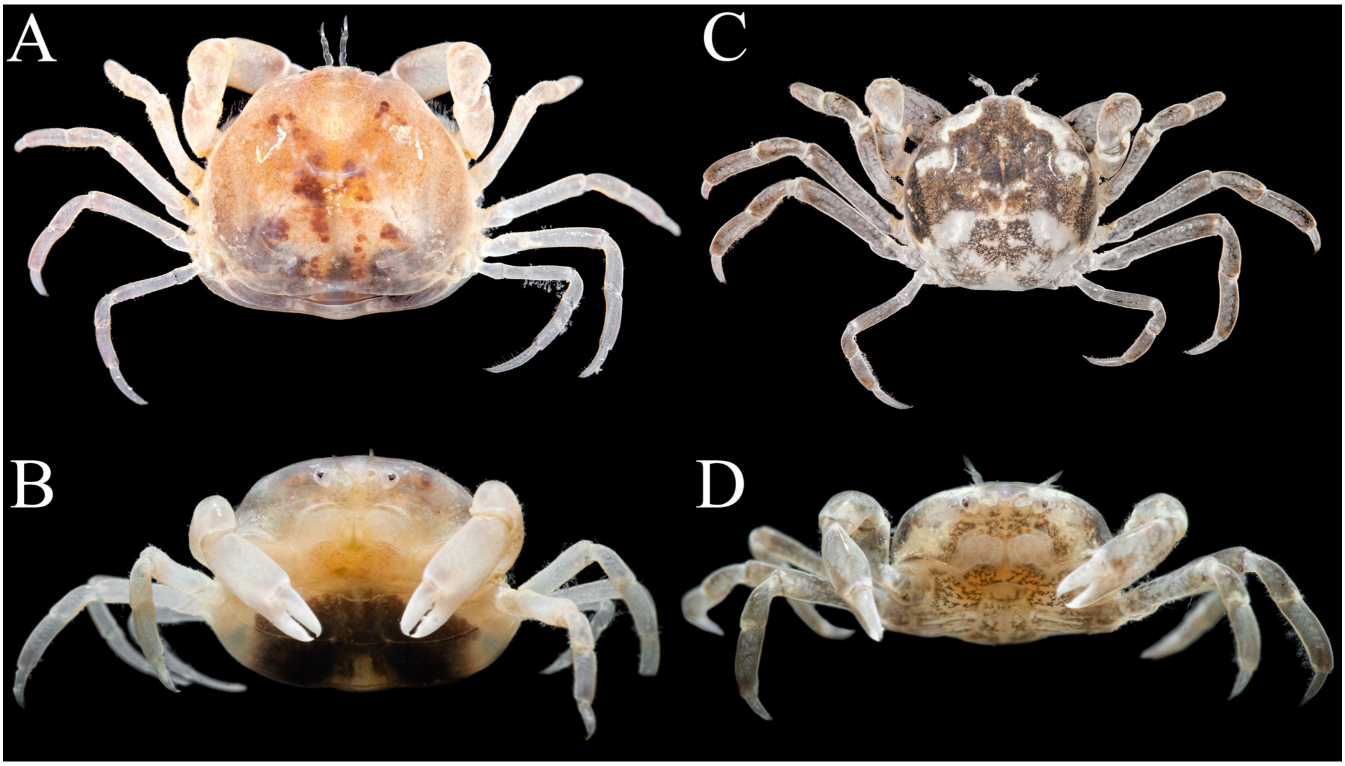

Fig. 26. *Arcotheres similis* (Bürger, 1895), colour in life. A, B, ovigerous female (8.4 × 7.1 mm) (ZRC 2021.79), Pulau Ubin, Singapore; C, D, male (5.5 × 5.5 mm) (ZRC 2021.79), Tuticorin, India. Photographs: Paul Y. C. Ng.

4.8 mm), 2 females (9.5 × 7.7 mm, 8.8 × 7.7 mm) (AM P105906), from *Modiolus philippinarum*, intertidal area, off Changi beach, next to Carpark 7, near ferry terminal, coll. S. K. Tan et al., 25 July 2018; 2 males (4.7 × 4.9 mm, 4.5 × 4.3 mm), 3 females (larger 9.2 × 7.7 mm, 6.3 × 4.7 mm), 1 ovigerous female (6.3 × 5.2 mm) (ZRC 2018.1369), from *Modiolus philippinarum*, intertidal area, off Changi beach, next to Carpark 7, near ferry terminal, coll. S. K. Tan et al., 25 December 2018 [largest pair male 4.7 × 4.9 mm, female 9.2 × 7.7 mm from 100.4 mm long *Modiolus*]; 5 males, 13 females (ZRC 2018.1389), from *Modiolus philippinarum*, intertidal area, off Changi beach, next to Carpark 7, near ferry terminal, coll. S. K. Tan et al., 25 December 2018; 9 males, 19 ovigerous females, 6 females (2 females with bopyrids under pleon) (ZRC 2019.534), from *Modiolus philippinarum*, intertidal area, off Changi beach, next to Carpark 7, near ferry terminal, coll. S. K. Tan et al., 22 April 2019; 6 males, 1 juvenile female, 25 ovigerous females (ZRC 2019.578), from *Modiolus philippinarum*, intertidal area, off Changi beach, next to Carpark 7, near ferry terminal, coll. S. K. Tan et al., 4 July 2019; 1 male, 22 females (ZRC 2019.579), from *Modiolus philippinarum*, intertidal area, off Changi beach, next to Carpark 7, near ferry terminal, coll. S. K. Tan et al., 5 July 2019; 1 ovigerous female (ZRC 2021.16), station DW57, probably from *Modiolus* sp., east of Pulau Tekong, 01°25.342′N, 104°04.775′E–01°24.949′N, 104°05.080′E, coll. Comprehensive Marine Biodiversity Survey, 22 October 2012; 1 male (5.5 × 5.5 mm), 10 females (1 photographed: 8.4 × 7.1 mm) (ZRC 2021.79), in *Modiolus philippinarum*, Changi Bay, ex Red Cliff Shoal area, Singapore, coll. S. K. Tan et al., 13 January 2021; 3 females (1 dismembered, poor condition) (ZRC 2013.574), no host record, East Coast Park, Bedok Jetty, Singapore, coll. S. Y. Chan, 31 July 2012. **Peninsular Malaysia:** 3 females (ZRC 2017.1282), no other data. **Borneo:** 1 female (7.3 × 6.0 mm; soft) (ZRC 1965.11.24.47), in *Vulsella vulsella*, on deep sea cable, 45 fathoms, South China Sea, near Sarawak, 4°26′42″N, 112°16′55″E, coll. 16 October 1933. **Indonesia:** 3 males (largest 5.7 × 5.6 mm), 16 females (largest 8.5 × 7.0 mm) (ZRC 2019.1026), in sand at Ekas, Lombok, probably discarded by artisanal shell collectors, Indonesia, coll. D. L. Rahayu, 14 May 2007. **India:** 5 females (7.1 × 5.8 mm, 7.3 × 6.0 mm, 7.9 × 6.3 mm, 8.0 × 6.7 mm, 8.1 × 6.7 mm) (ZRC 2017.1037), from *Modiolus philippinarum*, Tuticorin, Tamil Nadu, coll. R. Ravinesh, March 2017. **Uncertain locality:** 5 females (6.3 × 4.8 mm, 7.4 × 5.6 mm, 8.6 × 6.9 mm, 9.6 × 7.5 mm, 9.9 × 7.9 mm) (ZRC 1965.11.24.9–13), unidentified location, possibly from South Island, Cocos-Keeling Islands, Indian Ocean Territory, label badly damaged.

Description. Carapace and pereopods well chitinised. Female: Carapace subcircular, wider than long; dorsal and lateral surfaces smooth, glabrous; appearing domed in frontal view; front produced slightly anteriorly beyond orbits, margin gently concave to gently sinuous; anterolateral margin subparallel with frontal margin or gently sloping posteriorly to varying degrees, forming rounded angle with posterolateral margin (Figs. 27A, C, D, 28A, C, D, 29). Eyes usually just visible in dorsal view in adults; filling orbit (Figs. 27A, 29C, D). Epistome with median part triangular, lateral margins gently concave (Figs. 27D, 28D, 30K).

MXP3 outer surface with scattered short setae; ischiomerus completely fused, subovate, inner margin usually rounded

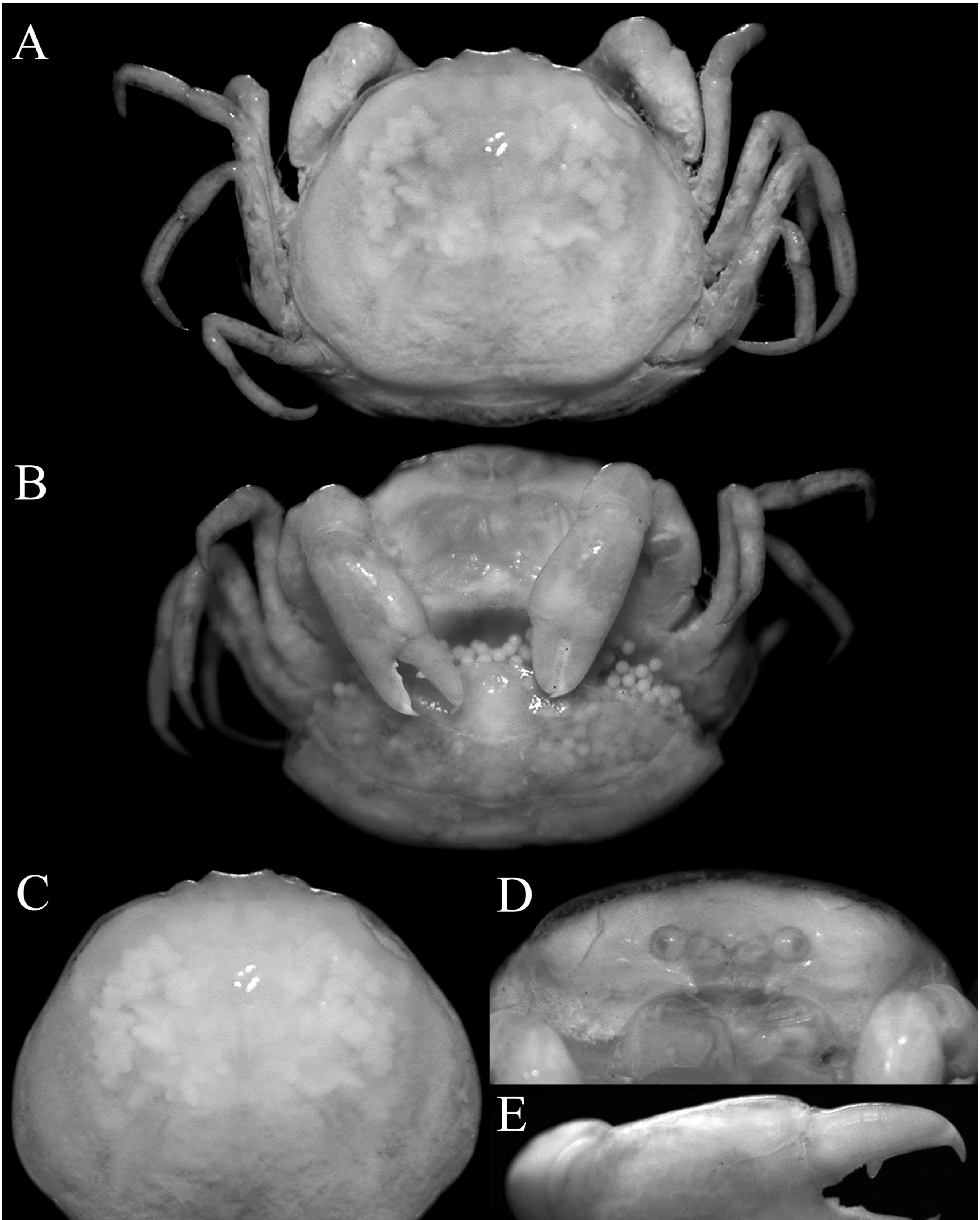

Fig. 27. *Arcotheres similis* (Bürger, 1895), female (6.7 × 5.5 mm) (NHM 1936.6.19.2), Singapore (holotype female of *Pinnotheres spinidactylus* Gordon, 1936). A, overall dorsal view; B, ventral view of cephalothorax; C, dorsal view of carapace; D, frontal view of cephalothorax; E, outer view of right chela.

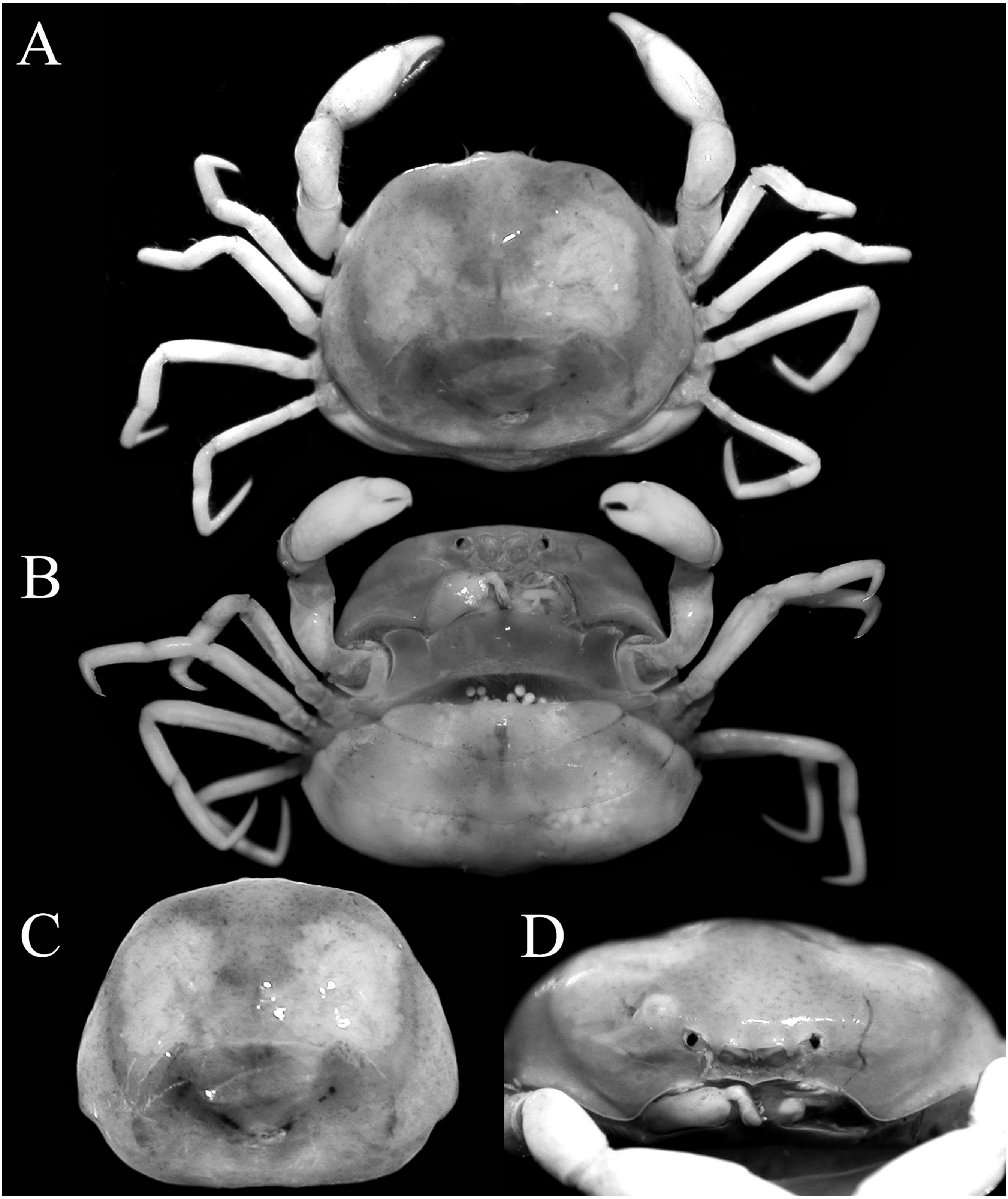

Fig. 28. *Arcotheres similis* (Bürger, 1895), ovigerous female (9.3 × 7.8 mm) (ZRC 2017.1034), Changi, Singapore. A, overall dorsal view; B, ventral view of cephalothorax; C, dorsal view of carapace; D, frontal view of cephalothorax.

even at widest point; carpus short; propodus about 3 times as long as high, subspatulate, distinctly longer than carpus, tip rounded to subtruncate; dactylus slender, inserted slightly proximal to midlength of propodus, tip not reaching propodal apex; exopod relatively slender, about two-thirds length of ischiomerus, flagellum 2-segmented (Figs. 30J, 33C, D).

Chela not prominently elongate, dactylus about two-thirds palm length; palm relatively slender, proximally narrower than distally or subequal; outer surfaces of palm, fingers (except for distal part) almost glabrous, with only scattered short setae; ventral margin of palm gently sinuous to almost straight; dactylus occlusal margin with distinct subproximal

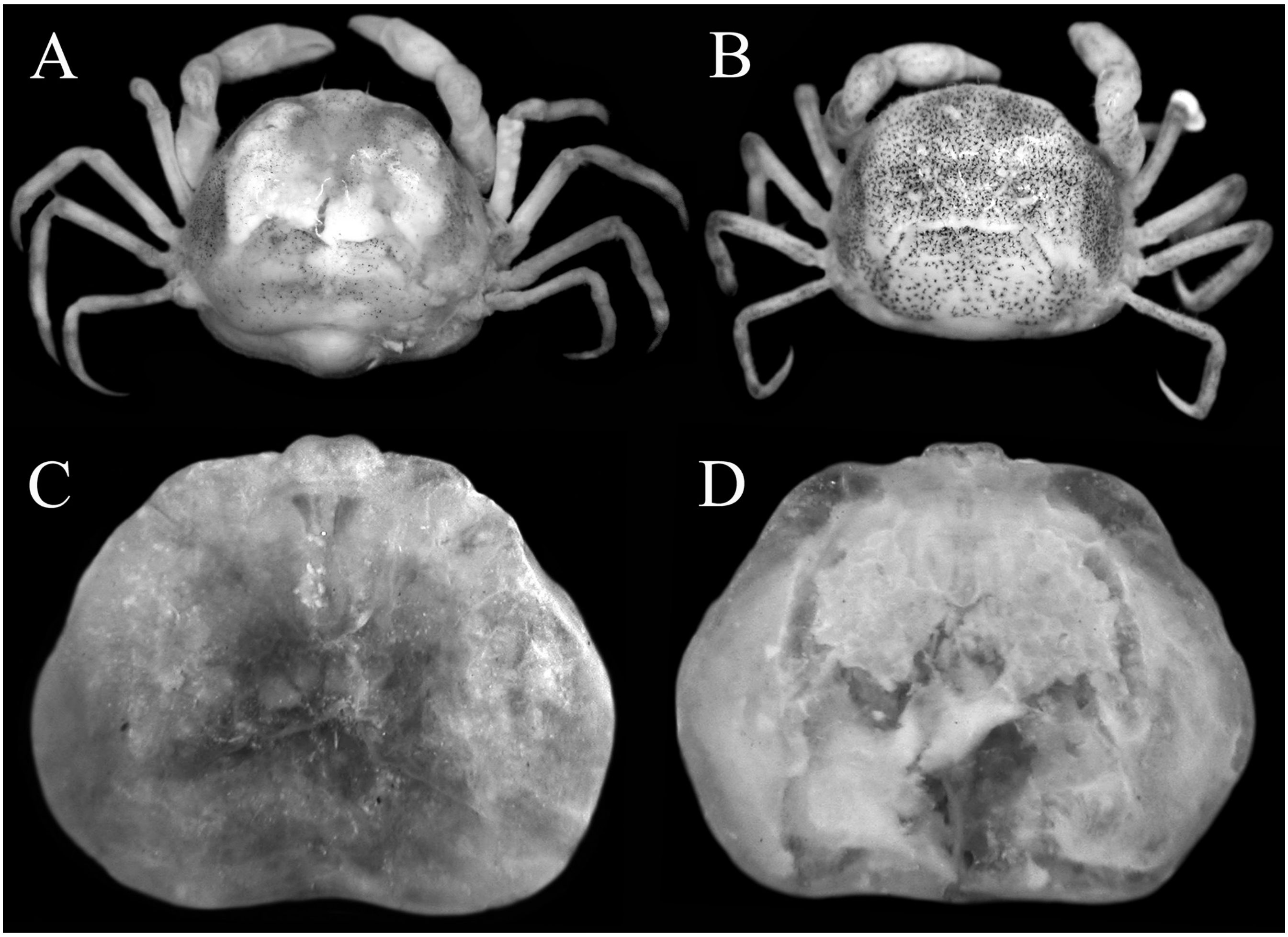

Fig. 29. *Arcotheres similis* (Bürger, 1895). A, female (8.1 × 6.7 mm) (ZRC 2017.1037), Tuticorin, India; B, female (8.0 × 6.7 mm) (ZRC 2017.1037), Tuticorin, India; C, female (7.4 × 5.6 mm) (ZRC 1965.11.24.10), Cocos-Keeling Islands (?); D, female (6.3 × 4.8 mm) (ZRC 1965.11.24.9), Cocos-Keeling Islands (?). A, B, overall view of carapace; C, D, dorsal view of carapace.

tooth; pollex occlusal margin with 1 low proximal tooth and denticles; tips of fingers sharp, hooked (Figs. 27E, 30I).

P2–P5 merus–propodus dorsally, ventrally unarmed; outer surface covered with scattered, very short setae or glabrous; ventral margins of propodus and dactylus slightly more setose; merus relatively longer, more slender, relative lengths of meri P4>P3=P2>P5; right (sometimes left) P4 distinctly the longer; P2 and P3 dactyli subequal, weakly curved, exceeding two-thirds length of propodi, with or without flexor row of spinules; longer P4 dactylus weakly falciform, slightly shorter than propodus, with or without flexor row of spinules; P5 merus 4.6–5.2 times longer than wide; P5 dactylus longer than longer P4 dactylus, longer than propodus, margins lined with short and long setae, denser on ventral margin, distal part lined with 2 distinct rows of distoflexor spinules, upper row with 5–10 spinules, lower row with 8–31 spinules, increasing in size distally, lower row always with distinctly more spinules than upper row in adults (Fig. 30A–H').

Pleon extending to buccal region, covering bases of P2–P5; telson gently recessed into concave distal margin of somite 6 (Figs. 27B, 28B).

Male: Carapace longitudinally ovate, slightly longer than wide; dorsal surface appears punctate to smooth, gently inflated, dorsal surfaces convex, lateral surfaces with setae; front projecting anteriorly, margin sinuous to almost straight (Figs. 31A, B, 32A). Eyes distinctly visible in dorsal view (Figs. 31A, 32A). MXP3 similar to that of female, although ischiomerus with slightly more angular inner distal margin (Fig. 32C). Anterior thoracic sternum wide, sternites 1, 2 fused, partially sunken into buccal cavity; suture between sternites 2 and 3 shallow; sternites 3, 4 completely fused, separated only by shallow grooves. Chela relatively stout, shorter than in female (Fig. 31C). P2–P5 legs dorsally, ventrally unarmed; outer surface covered with short setae; P3 and P4 carpus and propodus with long natatory setae; left and right meri equal, relative lengths of meri P4>P3>P2>P5; dactyli of P2–P4 progressively longer, flexor margin with setae and row of small spinules; right P4 dactylus slightly longer, more slender than left side; P4 and P5 dactylus subequal or longer to that of P3, covered with short setae; P5 dactylus with 2 rows of distoflexor spinules, one row sometimes low, indistinct (Fig. 32D–K'). Pleon slender, triangular, widest at somite 3 with distinctly convex lateral margins, lateral margins of somite 4 gently concave; somite 6 subtrapezoidal; telson semicircular with convex margins, wider than long (Fig. 32B). G1 relatively stout, arcuate,

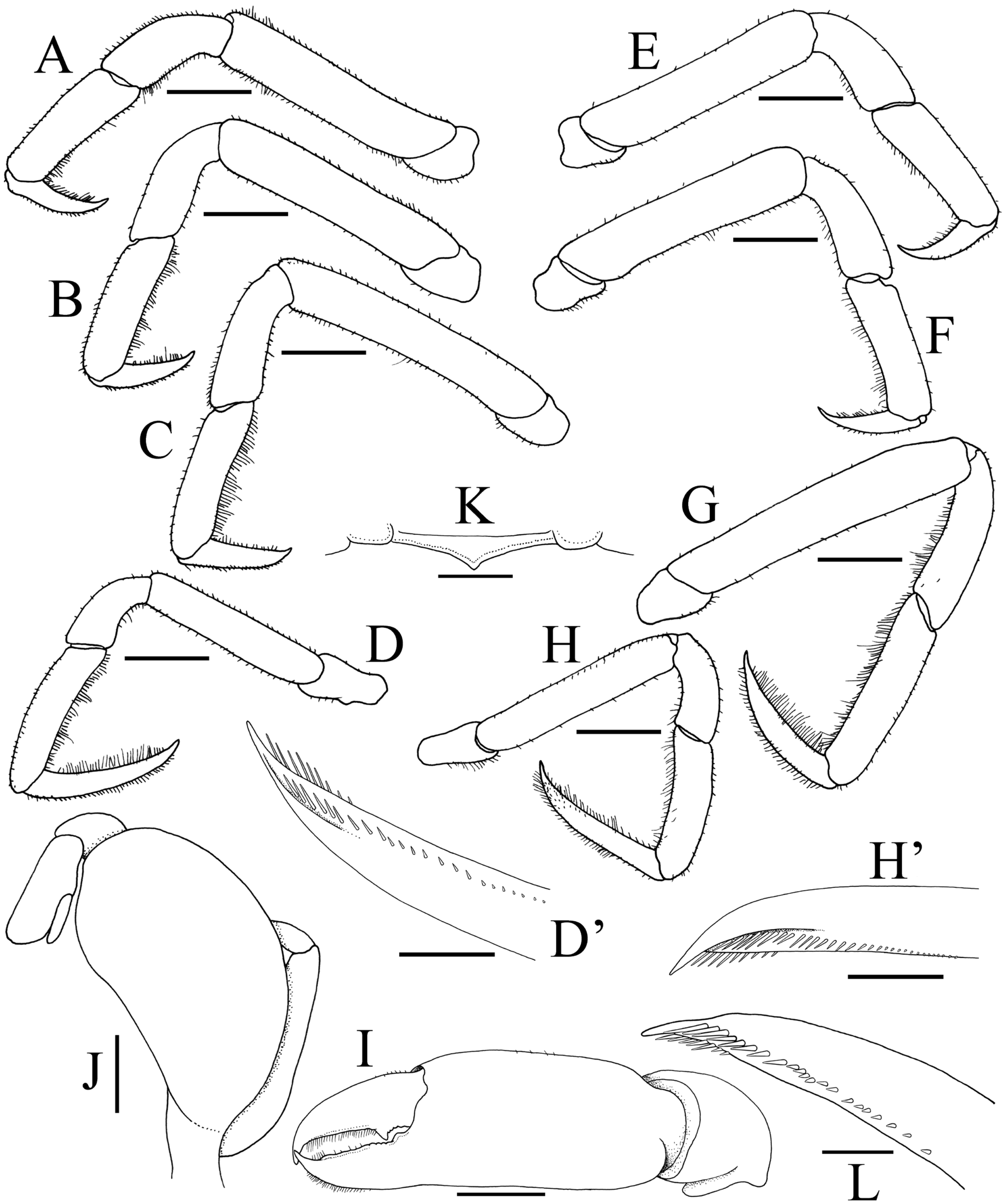

Fig. 30. *Arcotheres similis* (Bürger, 1895). A–K, ovigerous female (9.3 × 7.8 mm) (ZRC 2017.1034), Singapore; L, ovigerous female (6.7 × 5.5 mm) (NHM 1936.6.19.2), Singapore (holotype of *Pinnotheres spinidactylus* Gordon, 1936). A–D, left P2–P5, respectively; D', distal part of dactylus of left P5 showing stiff subdistal spinules (subventral view, soft setae omitted); E–H, right P2–P5, respectively; H', L, distal part of dactylus of right P5 showing stiff subdistal spinules (subventral view, soft setae omitted); I, outer view of left chela and carpus; J, outer view of left MXP3 (setae omitted); K, posterior margin of epistome. Scales = A–H, I, 1.0 mm; J, K, 0.5 mm; D', H' = 0.25 mm; L = 0.10 mm.

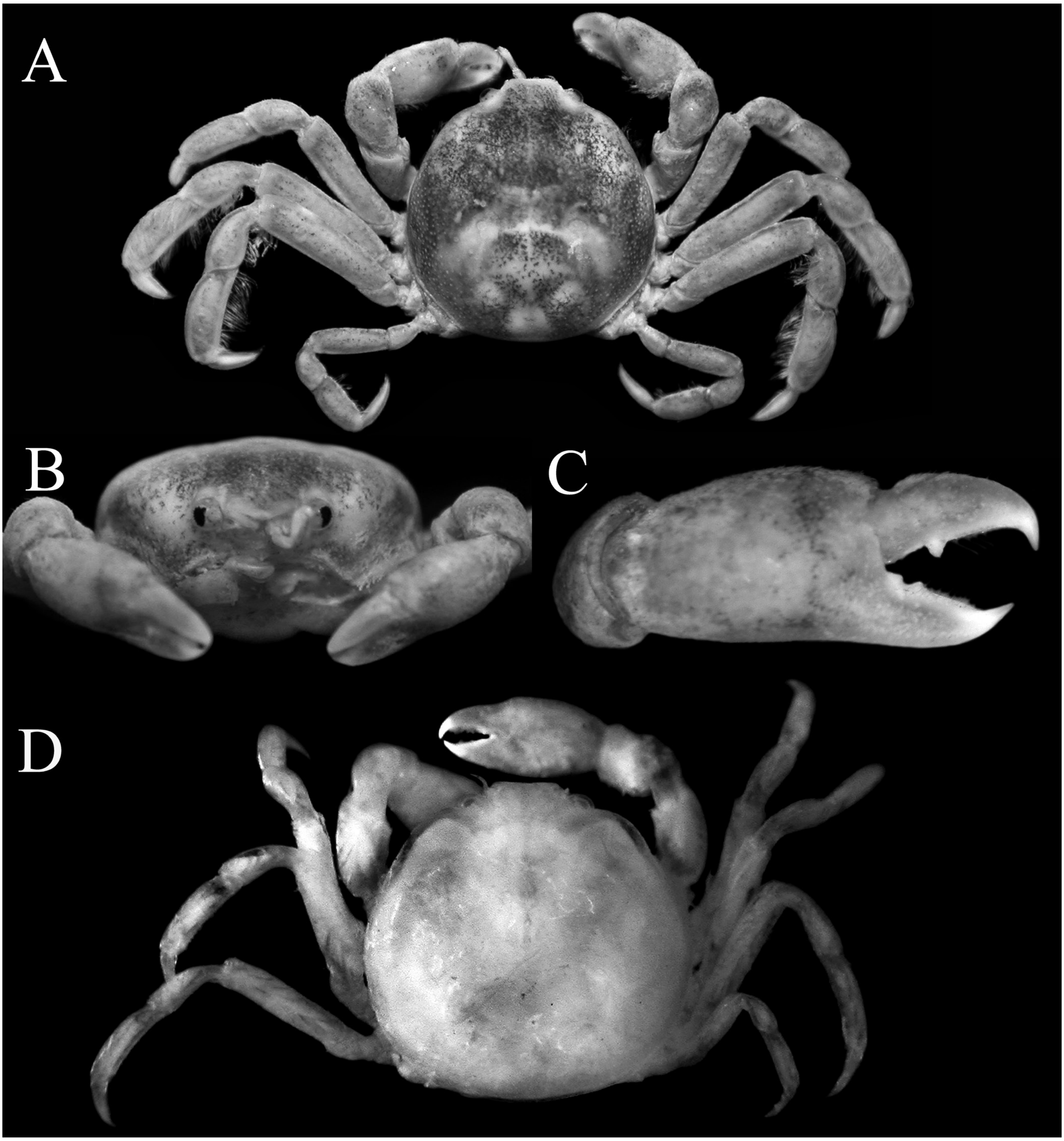

Fig. 31. *Arcotheres similis* (Bürger, 1895). A–C, male (5.5 × 5.8 mm) (ZRC 2017.1264), Singapore; D, male (3.3 × 3.3 mm) (NHM 1936.6.19.3), Singapore (paratype of *Pinnotheres spinidactylus* Gordon, 1936). A, D, overall dorsal view; B, frontal view of cephalothorax; C, outer view of right chela.

curved outwards, tip produced to differing lengths as short projection in line with main axis (Figs. 32L–N, 33E–H, J, K). G2 short, with spatuliform tip; exopod curved, two-thirds endopod length (Figs. 32O, 33I).

Variation. The eyes of *A. similis* are usually partially visible in dorsal view (Fig. 27A), although sometimes completely hidden (Figs. 28A, 29).

Colour. In life, the colour is light brown to whitish brown overall, with the pereopods relatively lighter in colour (Figs. 25, 26).

Host. Almost always from *Modiolus philippinarum* (Hanley, 1843) (Mytilidae Rafinesque, 1815). The one exception is a specimen (ZRC 1965.11.24.47) recorded from *Vulsella vulsella* (Linnaeus, 1758) (Pteriidae Gray, 1847). This record from *Vulsella*, however, is highly unusual not only because of the disparate taxonomic and phylogenetic position of the hosts (Combosch et al., 2017), but because it was taken at 45

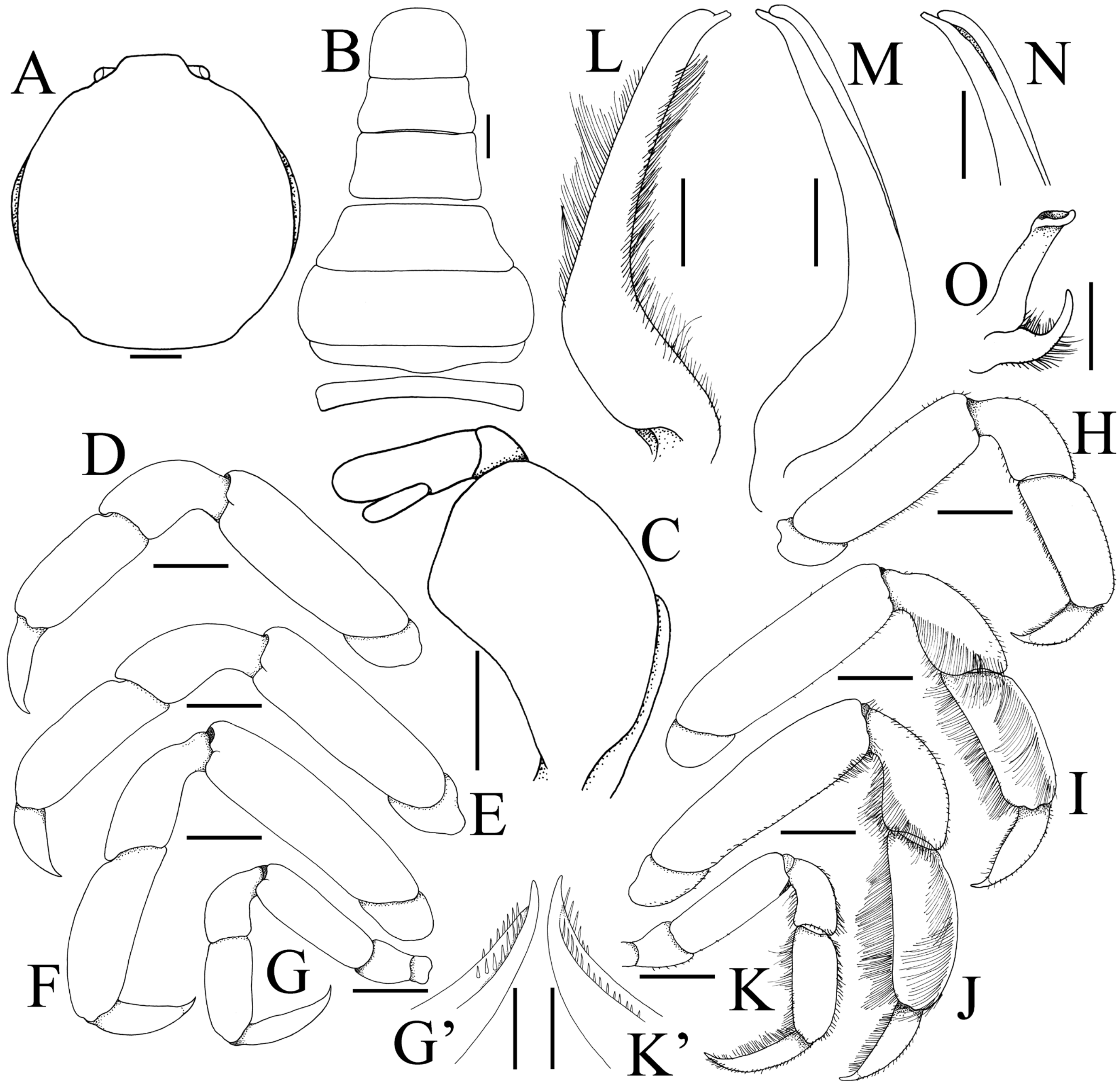

Fig. 32. *Arcotheres similis* (Bürger, 1895), male (5.5 × 5.8 mm) (ZRC 2017.1264), Singapore. A, dorsal view of carapace; B, pleon (setae omitted); C, left MXP3 (setae denuded); D–G, left P2–P5, respectively (setae omitted); H–K, right P2–P5, respectively; G', distal part of dactylus of left P5 showing stiff subdistal spinules (dorsal view, soft setae omitted); K', distal part of dactylus of right P5 showing stiff subdistal spinules (dorsal view, soft setae omitted); L, left G1 (ventral view); M, N, left G1 (dorsal view, setae omitted); O, left G2. Scales = A, D–K, 1.0 mm; B, C, L–O, 0.5 mm; G', K', 0.25 mm.

fm (82 m) depth on an undersea cable, significantly deeper than any known record of *A. similis*, which is otherwise known only from intertidal and shallow subtidal depths. The accuracy of the *Vulsella* host record requires corroboration; it may represent an atypical vagrant association given the unusual habitat.

Remarks. We consider *Pinnotheres similis* Bürger, 1895, *Pinnotheres modiolicola* Bürger, 1895, *Pinnotheres kamensis* Rathbun, 1909, and *Pinnotheres spinidactylus* Gordon, 1936, to all represent the same species, *Arcotheres similis*. The confusion has stemmed from the combination of incomplete descriptions by Bürger (1895), the badly damaged type female of *P. modiolicola*, the minimal original description of *P. kamensis*, and the confused identity and mixed material of *P. similis* reported by Gordon (1936) (see Ahyong & Ng, 2007b; Ng, 2018a). Griffin & Campbell (1969: 161) had already noted the strong similarities between *P. modiolicola* and *P. spinidactylus*, and Ahyong & Ng (2007b: 207), in redescribing *A. similis*, observed that it may be synonymous with *A. spinidactylus*, although the number of distoflexor rows of spinules on the P5 dactylus seemingly differed (one row, based on Gordon's 1936 account). Clarification of the identity of these four nominal species has only been possible following restudy of their respective type specimens. Re-examination of Gordon's (1936) material of *P. spinidactylus*

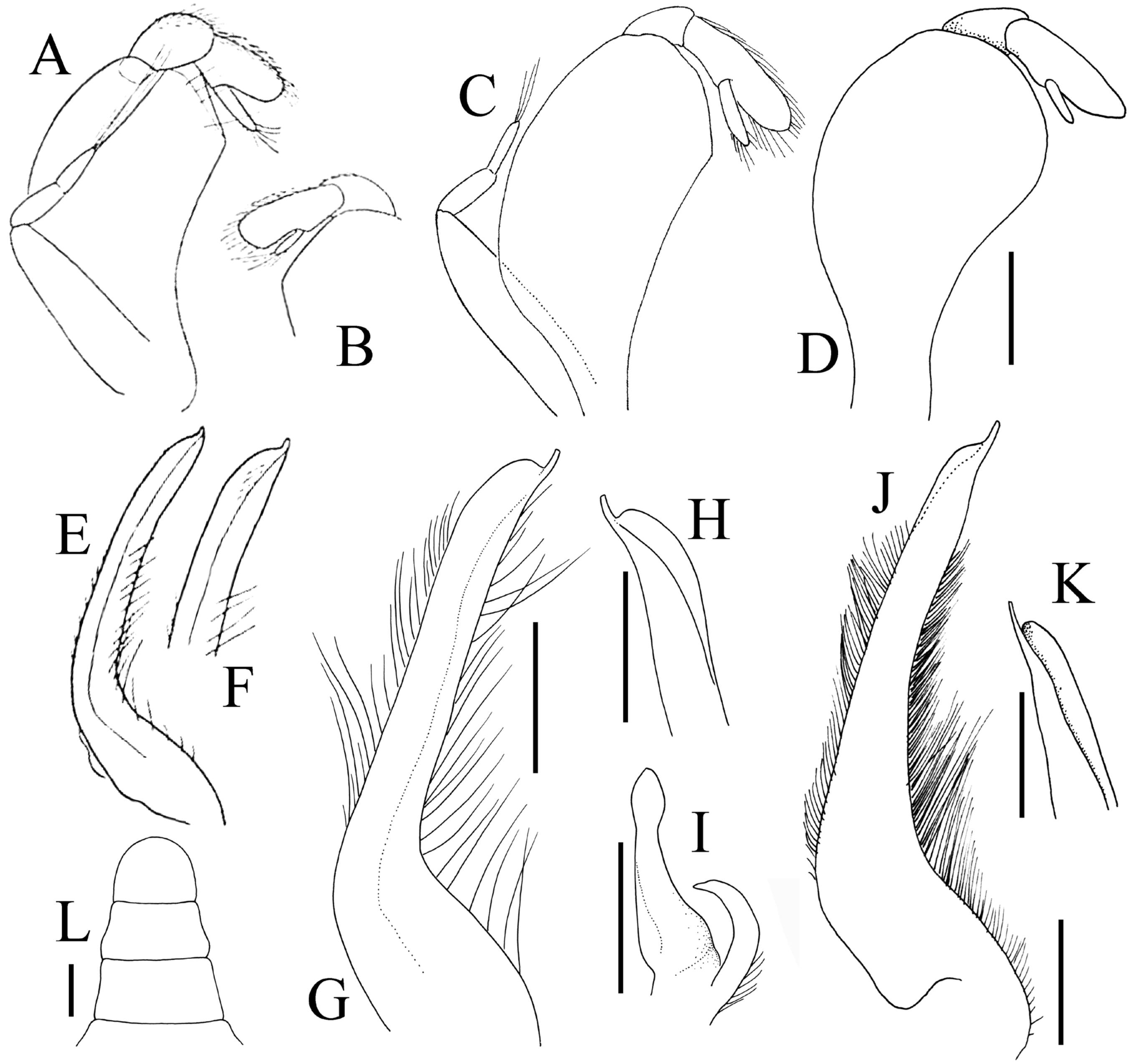

Fig. 33. *Arcotheres similis* (Bürger, 1895). A, B, ovigerous female (6.7 × 5.5 mm) (NHM 1936.6.19.2), Singapore (holotype of *Pinnotheres spinidactylus* Gordon, 1936); C, holotype female (8.3 × 6.4 mm) (SMF-ZMG 956 Go 950a), Philippines (holotype of *Pinnotheres similis* Bürger, 1895); D, female (7.3 × 6.0 mm; soft) (ZRC 1965.11.24.47), Sarawak; E, F, male (3.3 × 3.3 mm) (NHM 1936.6.19.3), Singapore; G–I, male (4.8 × 5.0 mm) (NHM 1936.6.19.14), Singapore; J, K, male (5.7 × 5.6 mm) (ZRC 2019.1026), Lombok, Indonesia; L, male (3.3 × 3.3 mm) (NHM 1936.6.19.3), Singapore (paratype of *P. spinidactylus* Gordon, 1936). A, left MXP3 (inner view); B, palp of left MXP3 (outer view); C, D, right MXP3 (outer view); E, G, J, left G1 (ventral view); F, distal part of left G1 (ventral view); H, K, distal part of left G1 (dorsal view); I, left G2; L, male pleonal somites 5, 6 and telson. A, B, E, F, after Gordon (1936: figs. 1c, 2a); C, after Ahyong & Ng (2007: fig. 14C). Scales = D, G–K, 0.5 mm; L, 0.2 mm.

revealed that two rows of distoflexor spinules are present on the P5 dactylus in both sexes (Fig. 30L), as in *A. similis* (Figs. 30D', H', 32G', K'). Ahyong & Ng (2021) showed that *A. similis* is a senior synonym of *A. spinidactylus* and *A. kamensis*. Likewise, our reassessment of *A. modiolicola* finds it to be indistinguishable from *A. similis*. Note that Ahyong & Ng (2007b) incorrectly indicated the presence of a single row of P5 dactylar spines, rather than two. The present reappraisal, which has examined types of all four nominal species, indicates they are conspecific.

Pinnotheres similis Bürger, 1895, and *Pinnotheres modiolicola* Bürger, 1895, were described in the same paper (Bürger, 1895) so both names must be considered as simultaneously published under Article 24 of the ICZN (1999). As first revisers, we here select *Pinnotheres similis* Bürger, 1895, to have priority over *P. modiolicola* Bürger, 1895, when they are regarded as synonyms. We select *P. similis* to have priority because it is the more widely cited species and because its holotype is still in good condition, whereas that of *P. modiolicola* is badly damaged (Ahyong & Ng, 2007b).

Gordon (1936: 169) described *Pinnotheres spinidactylus* on the basis of five females and one male from Siglap, Singapore, all from the mytilid *Modiolus philippinarum* (Hanley, 1843). She compared her new species with *Pinnotheres latus* Bürger, 1895 (now in *Magnotheres*, new genus), *Pinnotheres parvulus* Stimpson, 1858, the Chinese *Pinnotheres sinensis* Shen, 1932 (now in *Arcotheres*), *Pinnotheres tsingtaoensis* Shen, 1932 (now in *Nepinnotheres*, see Remarks for *Plenotheres*, new genus), and *Pinnotheres gordoni* Shen, 1932. The excellent series of specimens from Singapore agrees with the descriptions and figures of Gordon (1936) very well. The G1 figured by Gordon (1936: fig. 2c) agrees well in general shape with that of the present male except that the distal tip is straight (versus gently curved inwards; Fig. 33E, F). In any case, the distal tip varies in length as well, from typically short (Fig. 32L–N) to sometimes long (Fig. 33G, H, J, K). Gordon's (1936) *P. spinidactylus* is referable to *A. similis*, but her record of *P. similis* from Singapore is referable to *A. placunicola* (cf. Ng, 2018a).

Of the males available to Gordon (1936: 169), only the smallest male (3.3 × 3.3 mm; NHM 1936.6.19.3) was referred to the type series (Fig. 31D). She noted that the "two other [non-type] male specimens, measuring about 4.4 and 5.4 mm in length respectively [NHM 1936.6.19.14–15], have the second and third legs fringed with setae on the propodus and carpus much as in *P. tsingtaoensis* Shen (1932, p. 149). The abdomen, however, and the dactylus of the external maxillipede are more like those of *P. gordoni* Shen (p. 152), but the first pleopod is heavily setose on both sides and is straight, not curved, at the apex" (Gordon, 1936: 171). We examined all three males and they belong to the same species. The differences noted by Gordon (1936) can all be accounted for by size-associated change, the paratype male being smallest and yet to exhibit fully adult features. Fully adult male specimens have the G1 distinctly more setose (Figs. 32L, M, 33G, H), and ambulatory propodi and carpi that are also lined with long setae along the flexor margins (Fig. 31A). Gordon (1936: fig. 1c) did not remove the G1s from the males when she compared the G1, and their shape is actually very similar (Fig. 33E–H), except that the distal projection is relatively longer and the subdistal hump is relatively higher in the larger male (Fig. 33G, H; cf. Fig. 33E, F).

Griffin & Campbell (1969: 157, figs. 7, 8) recorded "*Pinnotheres spinidactylus*" from two females and one male collected from the mytilid, *Modiolus*, in Moreton Bay in Queensland, Australia, commenting that although the leg proportions appeared to differ slightly, the carapace shape, front, and presence of distoflexor rows of spinules on the P5 dactylus are diagnostic for the species. Their figures agree closely with *A. similis* as characterised here except for the pleon of a 3.1-mm cw male, figured with somite 6 proportionately broader and the lateral margins prominently convex rather than gently concave (compared to the mature 5.5-mm cw male) (Fig. 32B versus Griffin & Campbell, 1969: fig. 8B), and gonopods described as "immature, two pairs of biramous appendages" (Griffin & Campbell, 1969: 159). The Griffin & Campbell (1969) male is a juvenile and the difference in pleon shape may be a function of its immaturity, but we are of the opinion that it is actually an immature female, especially since the authors describe it as having "two pairs of biramous pleopods". The G1 of a 3.3 × 3.3-mm male (NHM 1936.6.19.3) from Singapore was already developed and clearly visible, so Griffin & Campbell's "male" specimen and its pleon is similar to that of larger males, except that somite 6 is relatively shorter with the lateral margins of somite 6 gently concave (Fig. 33L). We also note that in the immature female of *A. palaensis*, the lateral margins of pleonal somite 6 are prominently convex (Fig. 15C), unlike that of similarly sized males which have the margins gently convex to sinuous (Fig. 22J, O). These observations suggest that Griffin & Campbell's male of cw 3.1 mm is almost certainly a juvenile female instead. Without re-examination of the pleopods, however, we cannot be certain, but on the basis of the other female characters and its host, we provisionally include Griffin & Campbell's (1969) record in the synonymy of *P. similis*; this Australian record will need to be confirmed with fresh collections, especially since Queensland is some distance from the nearest confirmed records in Southeast Asia. Australian records of *A. similis* by Ward (1967) and Ahyong & Brown (2003) are actually referable to *M. globosus*, new combination (see account of *M. globosus* below; Ahyong, 2020b); that of Rathbun (1924) requires verification (Ahyong, 2020b).

George & Noble (1970: 392) recorded *Pinnotheres modiolicolus* from Karwar and Kodibag in southwestern India, but it is probably misidentified (see also Trivedi et al., 2018b: 61). They recorded the species from *Marcia opima* (Gmelin, 1791) (as a *Katelysia* Römer, 1857) (Veneridae) and *Mactra violacea* Gmelin, 1791 (Mactridae), both from the order Venerida. Although the MXP3 figured (George & Noble, 1970: fig. 1.4) agrees with that of *A. similis* as defined here (Figs. 30J, 32C, 33C, D), the G1 is different, with the tip truncated (George & Noble, 1970: fig. 1.5, 1.6) and without the recurved slender part as is typical for the species (Figs. 32L–N, 33G, H, J, K). The G1 differences, together with the fact that they were from venerid clams and not mytilids, indicates that their record is not correct. The Karwar and Kodibag specimens will need to be re-examined to determine their identity.

Dai et al. (1980: 131, fig. 3) reported "*Pinnotheres spinidactylus*" from the mytilid *Mytilus crassitesta* Lischke, 1868, from Hainan Island. The figures in her paper (see also Dai et al., 1986: 393, fig. 208 (1–7); Dai & Yang, 1991: 424, fig. 208 (1–7)) superficially agree with *A. similis*. We have, however, examined photographs of the Hainan specimens in CAS, and while the carapace and pereopod features seem to agree with *A. similis*, there are two problems: the male pleon and G1 (neither figured by the above authors) are very different from those of *A. similis* s. str., and indicate that it is a different species. The male pleon of the Hainan specimens has somite 6 and the telson proportionately more elongate, and most significantly, the G1 is much longer and less curved, with the distal part very elongate and gradually tapering to a subtruncate tip. They are also not referable to *Arcotheres boninensis* (Stimpson, 1858) or *A. purpureus*

(Alcock, 1900), which have a markedly wider, more rounded carapace and relatively shorter P2–P5 (Ahyong & Ng, 2021). Nevertheless, Dai et al. (1980, 1986) and Dai & Yang (1991) recorded *A. boninensis* from China, and their figures conform to what we know about the species. The Chinese specimens of "*Pinnotheres spinidactylus*" will need to be restudied to ascertain their true identity.

Distribution. Western Pacific to the central Indian Ocean, including Australia, the Philippines, Indonesia, Singapore, Malaysia, Thailand, eastern India, and possibly the Cocos-Keeling Islands.

Arcotheres exiguus (Bürger, 1895)
(Figs. 34–45, 50A–G)

Pinnotheres exiguus Bürger, 1895: 377, pl. 9 fig. 19, pl. 10 fig. 30 [type locality: Samar Island, Philippines]; Serène, 1968: 93.
Pinnotheres winckworthi Gordon, 1936: 177, fig. 7; Serène, 1968: 95. [New synonymy]
Pinnotheres vicajii Chhapgar, 1957: 505, 506, pl. 12 fig. n–q; Chhapgar, 1958: 253, fig. 2; Silas & Alagarswami, 1967: 1212; Schmitt et al., 1973: 81; Kumari & Rao, 1974: 165, figs. 1–19; Ng et al., 2008: 251; Pati et al., 2012: 384; Dev Roy, 2013: 156, 157. [New synonymy]
Pinnotheres sp. — Silas & Alagarswami, 1967: 1163, text-figs. 1, 2, pls. 1–3.
Pinnotheres gracilis — George & Noble, 1970: 392, fig. 1.1–1.3 [not *Pinnotheres gracilis* Bürger, 1895].
Pinnotheres casta Antony & Kutyamma, 1971: 60, figs. 1, 2; Schmitt et al., 1973: 81; Dev Roy, 2013: 156, 157. [New synonymy]
Pinnotheres obscuridentata Dai & Song, 1986: 56, 62, text-fig. 3 [type locality: Longmen, Guangxi, China]; De Gier & Becker, 2020: tab. 1. [New synonymy]
Arcotheres exiguus — Campos & Manning, 2001: 168; Ahyong & Ng, 2007b: 195, fig. 4; Ng et al., 2008: 248; Ng et al., 2017: 1093.
Arcotheres winckworthi — Ng et al., 2008: 248; Ng et al., 2017: 1093.
Arcotheres alcocki — Pati et al., 2015: 1067, fig. 1; Dev Roy & Rath, 2017: 103 (not *Pinnotheres alcocki* Rathbun, 1909).
Nepinnotheres vicajii — Ng & Kumar, 2015: 265; Trivedi et al., 2018b: 62.
Arcotheres casta — Ng & Kumar, 2015: 265; Ng et al., 2017: 1094; Kazmi et al., 2018: 136, fig. 5; Trivedi et al., 2018a: 197; Trivedi et al., 2018b: 61 (list); Trivedi et al., 2020: 505.
Viridotheres gracilis — Dev Roy, 2013: 156, 157; Trivedi et al., 2018b: 62 (not *Pinnotheres gracilis* Bürger, 1895).
Arcotheres vicajii — Trivedi et al., 2020: 497–507, figs. 1–8; De Gier & Becker, 2020: tab. 1.

Type material. Lectotype: female (5.6 × 4.6 mm), Samar Island, Philippines, coll. C. Semper, 1876. **Peninsular Malaysia:** 1 ovigerous female (9.3 × 7.6 mm) (NHM 1936.6.19.12), Penang, Malay Peninsula, from *Protapes gallus*, coll. R. Winckworth, March 1933 (holotype of *Pinnotheres winckworthi* Gordon, 1936); 1 ovigerous female (8.8 × 7.3 mm) (NHM 1936.6.19.13), Penang, Malay Peninsula, from *Protapes gallus*, coll. R. Winckworth, March 1933 (paratype of *Pinnotheres winckworthi* Gordon, 1936); 3 males (4.3 × 4.2–5.1 × 4.9 mm), 6 ovigerous females (6.3 × 5.4–7.7 × 6.7 mm). **India:** 1 ovigerous female (8.2 × 6.9 mm) (ZRC 2021.784) (neotype of *Pinnotheres casta* Antony & Kutyamma, 1971), in *Marcia* cf. *cordata*, west coast of Tamil Nadu, India, coll. R. Ravinesh, 2016.

Other material examined. Peninsular Malaysia: 6 spent females (4.6 × 4.2–7.0 × 6.3 mm), 1 juvenile female (3.8 × 3.6 mm) (ZRC 2018.772), Chinatown market, Singapore, from *Marcia recens*, coll. P. K. L. Ng, 25 February 2018; 1 male (4.9 × 4.8 mm) (ZRC 2018.773), from venerid bought from Sheng Siong Supermarket, Singapore, coll. 27 September 2018; 2 males (3.4 × 3.4 mm, 3.7 × 3.7 mm), 1 ovigerous female (4.8 × 3.9 mm), 1 spent female (4.5 × 4.1 mm), 1 ovigerous female (4.3 × 4.0 mm) (ZRC 2018.774), in *Dosinia* sp., from local market, Singapore, coll. S. K. Tan, 10 December 2013; 1 male (4.7 × 4.6 mm), 1 ovigerous female (6.9 × 5.6 mm), 3 spent females (5.4 × 4.6–8.2 × 7.4 mm), 1 ovigerous female (4.5 × 4.0 mm) (ZRC 2018.775), in *Marcia* sp., from market, Singapore, coll. S. K. Tan, 10 December 2013; 1 ovigerous female (ZRC 2018.1068), from clam, Yew Tee Market, Singapore, coll. H. H. Tan, 9 September 2018; 1 male (4.3 × 4.2 mm), 1 ovigerous female (6.9 × 6.1 mm) [photographed], 1 ovigerous female (7.9 × 7.3 mm) [photographed], 8 ovigerous females, 6 spent females, 2 juvenile females (2.1 × 1.6 mm, 1.6 × 1.5 mm) (ZRC 2019.516), from *Marcia recens*, from market, Singapore, coll. P. Y. C. Ng, March 2019; 1 ovigerous female (ZRC 2020.352), from *Marcia recens*, Yew Tee Market, Singapore, coll. H. H. Tan, 2 June 2019; 1 male (4.3 × 4.2 mm), 2 non-ovigerous females (5.7 × 4.9 mm, 5.7 × 5.1 mm), 2 ovigerous females (5.7 × 4.9 mm, 7.0 × 5.0 mm) (ZRC 2020.14), in *Marcia recens*, from Sheng Shiong Supermarket, Singapore, coll. S. K. Tan, 23 March 2020; 2 ovigerous females (ZRC 2020.66), in *Marcia recens*, from Chinatown market, Singapore, coll. P. K. L. Ng, 4 June 2020. **Singapore:** 4 ovigerous females (6.2 × 5.2–7.0 × 6.3 mm) (ZRC 2018.776), from kelong (artisanal fish traps), in "Lala clams" (probably *Marcia recens*), coll. B. Y. Lee, 25 March 2018; 2 ovigerous females (ZRC 2020.390), in "Lala clams" (*Marcia* sp.), in seafood dish, Ah Hua Kelong Restaurant, Singapore, coll. M. S. Foo, 1 November 2020; 2 males (5.6 × 5.4 mm, 5.4 × 5.2 mm) (ZRC 2020.419), from *Meretrix meretrix*, from Sheng Shiong Supermarket in Bukit Batok, Singapore, coll. W. Xu, 12 February 2017; 1 ovigerous female (ZRC 2021.10), from clam in seafood restaurant, Singapore, coll. students, 2005. **Philippines:** 1 female (ZRC 2021.17), in *Ruditapes philippinarum*, from plate of noodles at seafood restaurant, purportedly from Korea but probably from Philippines or adjacent area, coll. S. K. Tan, 16 December 2020. **India:** 3 males (4.3 × 4.1 mm, 4.5 × 4.2 mm, 4.7 × 4.4 mm), 1 non-ovigerous female (8.0 × 6.7 mm), in *Marcia* cf. *cordata*, Tamil Nadu, India, coll. R. Ravinesh, 2016 (ZRC 2018.768); 1 juvenile female (4.0 × 3.6 mm) (ZRC 2018.769), in *Protapes* cf. *rhamphodes*, Tamil Nadu, coll. R. Ravinesh, 2016; 1 female (ZRC 2018.498), male (8.3 × 5.5 mm), *Meretrix aurora*, Mumbai, Maharashtra state, India, coll. S. Gosavi, 27 September 2018.

Description. Female: Carapace and pereopods poorly chitinised, soft. Carapace subcircular to subhexagonal, wider than long; dorsal and lateral surfaces smooth, glabrous; appearing domed in frontal view; front slightly projecting

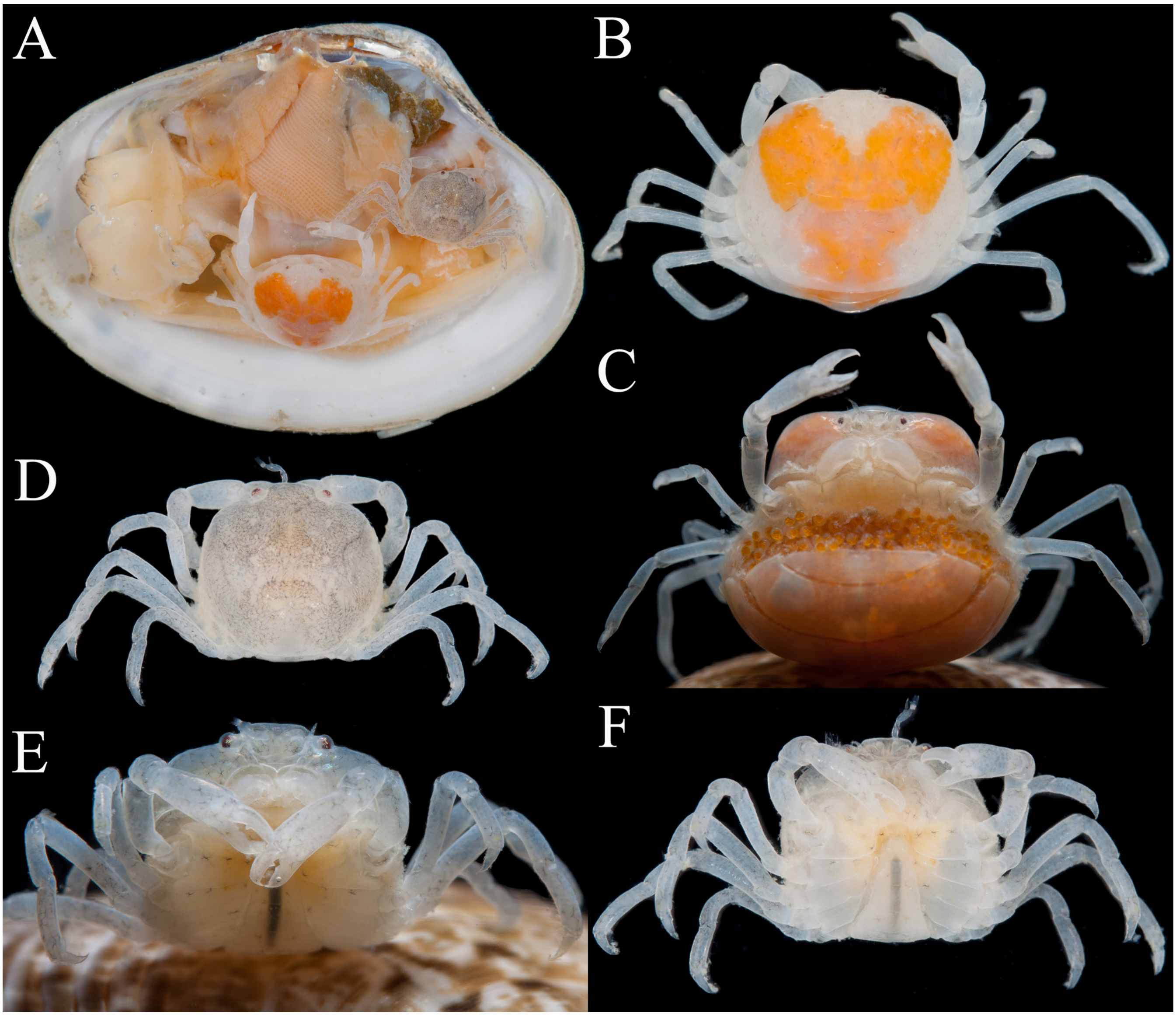

Fig. 34. *Arcotheres exiguus* (Bürger, 1895), colour in life and in situ in *Marcia recens* (Holten, 1802) (Veneridae), Peninsular Malaysia. A, male (4.3 × 4.2 mm) and ovigerous female (6.3 × 5.4 mm) (ZRC 2018.772) (placed together for photograph but originating from different shells); B, C, ovigerous female (6.3 × 5.4 mm) (ZRC 2018.772); D–F, male (4.3 × 4.2 mm) (ZRC 2018.772). Photographs: Paul Y. C. Ng.

anteriorly beyond orbits, margin gently sinuous to gently convex; anterolateral margin usually subparallel with frontal margin or sloping posteriorly to various degrees, forming rounded angle with posterolateral margin (Figs. 34B, 35B, E, 36C, 37A, C, D, 38A–C, 39A, C–E, 41A, N). Eyes small, not or just visible in dorsal view in adults; mobile, completely filling orbit (Fig. 41A, N). Epistome with median part triangular, lateral margins gently concave (Figs. 38C, 39C, 41C).

MXP3 outer surface with scattered short setae; ischiomerus completely fused, subrhomboidal, inner margin rounded to angular at widest point; carpus short; propodus about 3 times as long as high, subspatulate, distinctly longer than carpus, tip rounded to subtruncate; dactylus slender, varying lengths, inserted slightly proximal to midlength to near proximal one-third of propodus, tip not reaching or just reaching propodal apex; exopod relatively slender, about two-thirds length of ischiomerus, flagellum 2-segmented (Figs. 36E, 41B, Q, 42A, L).

Chela relatively short to not prominently elongate, dactylus half to two-thirds palm length; palm relatively slender, proximally narrower than distally; outer surfaces of palm, fingers (except for distal part) almost glabrous, with only scattered short setae; ventral margin of palm gently concave to sinuous; dactylus occlusal margin with distinct subproximal tooth; pollex occlusal margin with 1 low proximal tooth, 1 submedian tooth, and minute denticles; tips of fingers sharp, hooked (Figs. 36F, 37E, 38D, E, 41E, 42B).

P2–P5 dorsally, ventrally unarmed; outer surface covered with scattered, very short setae or glabrous; ventral margins of propodus and dactylus slightly more setose; merus relatively longer, more slender, relative lengths of meri P4>P3>P5>P2; left (sometimes right) P4 distinctly the longer; P2 and P3

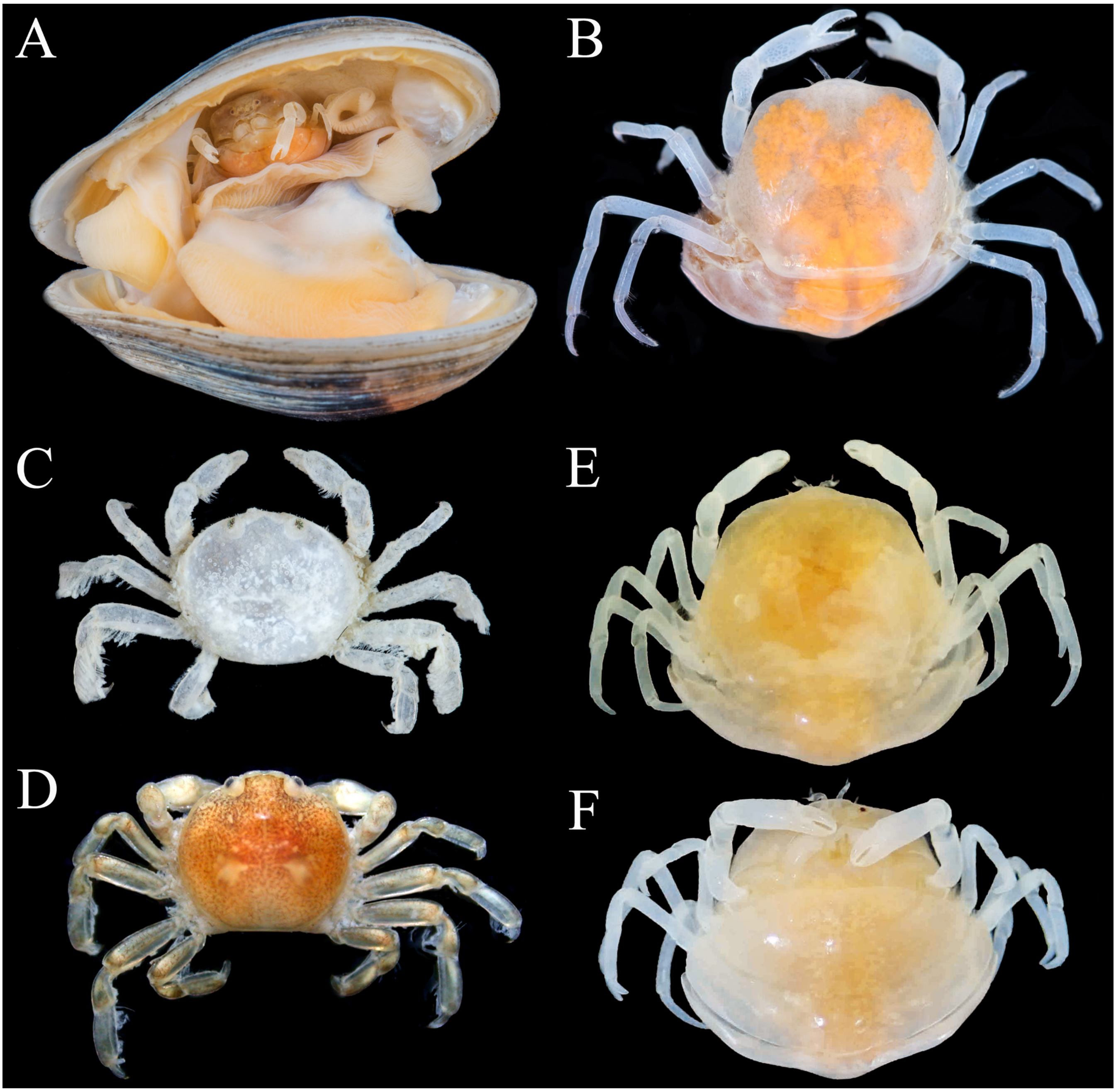

Fig. 35. *Arcotheres exiguus* (Bürger, 1895), colour in life. A, B, ovigerous female (7.9 × 7.3 mm) (ZRC 2019.516), in situ in *Marcia recens* (Holten, 1802) (Veneridae), Peninsular Malaysia; C, male (4.3 × 4.2 mm) (ZRC 2019.516), Peninsular Malaysia; D, male (4.5 × 4.2 mm) (ZRC 2018.768), India; E, F, ovigerous female, from *Meretrix aurora* Hornell, 1917 (Veneridae), India (specimens not examined). Photographs: A–C, Paul Y. C. Ng; D–F, R. Ravinesh.

dactyli short, subequal, tip gently hooked, half propodus length; longer P4 dactylus elongate, broadly falciform, distinctly longer than half propodus length, slightly longer than P5 dactylus; P5 merus 4.1–4.5 times longer than wide; P5 dactylus shorter to longer (in specimens > 6.5 mm cl) than propodus extensor margin, length/height > 5.0 in specimens > 6.0 mm cl, margins lined with short and long setae, denser on ventral margin, distoflexor margin without distinct rows of spinules, sometimes with a row or patches of very low, spinule-like structures which are all similarly sized (Figs. 36C, D, 41F–M, O, P, 42C–K, M, 50A–G). Pleon extending to buccal region, covering bases of P2–P5; telson gently recessed into concave distal margin of somite 6 (Figs. 34C, 35F, 37B, 39B, 41D).

Male: Carapace and pereopods well chitinised, firm. Carapace almost circular, slightly wider than long; dorsal surface almost smooth, not prominently inflated, lateral surfaces with setae; front projecting anteriorly, margin gently sinuous to almost straight (Figs. 34D, 35C, D, 43A, B, 44A). Eyes distinctly visible in dorsal view (Figs. 34D, 35C, D, 43A, B, 44A). MXP3 as in female (Figs. 44B, 45A). Anterior

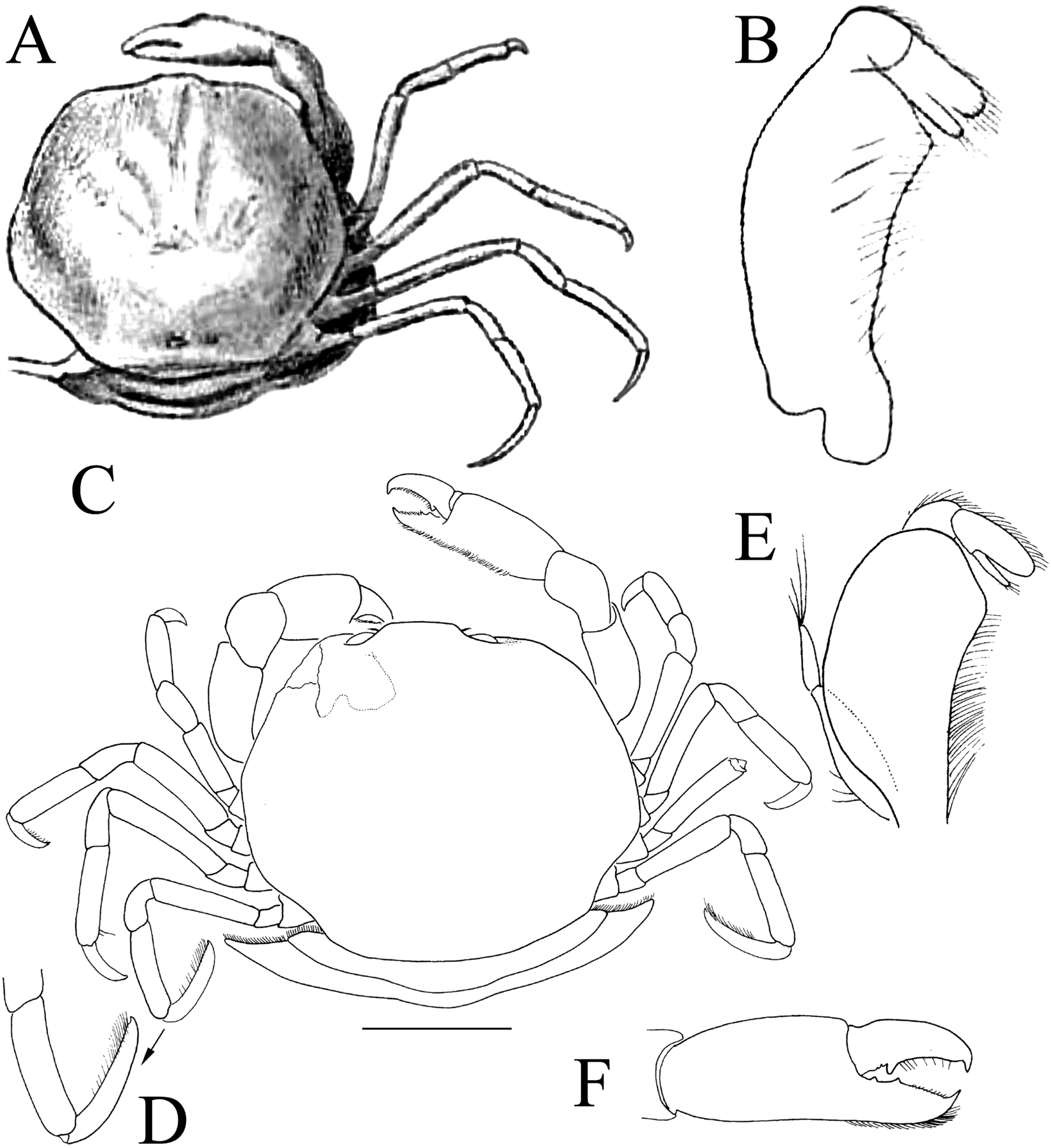

Fig. 36. *Arcotheres exiguus* (Bürger, 1895). A, B, after Bürger (1895: pl. 9 fig. 19, pl. 10 fig. 30); C–F, lectotype female (5.6 × 4.6 mm) (USNM 32432), Samar, Philippines, after Ahyong & Ng (2007: fig. 4). A, C, overall dorsal view; B, E, right MXP3; D, left P5 propodus and dactylus; F, right chela. Scale = B, 1.5 mm; C, 2.0 mm; E, 1.0 mm.

thoracic sternum wide, sternites 1, 2 fused, partially sunken into buccal cavity; suture between sternites 2 and 3 shallow; sternites 3, 4 completely fused, separated only by shallow grooves. Chela relatively stout, shorter than in female (Figs. 34F, 44D, 45B). P2–P5 dorsally, ventrally unarmed; outer surface covered with short setae; P3 and P4 carpus and propodus with long natatory setae; left and right meri equal, relative lengths of meri P4>P3>P2>P5; dactyli of P2–P4 progressively longer; P4 and P5 dactylus subequal to that of P3, covered with short setae (Figs. 44F–I, 45C–F). Pleon slender, triangular, widest at somite 3, lateral margins of somite 4 gently concave to almost straight; somite 6 trapezoidal; telson semicircular, wider than long (Figs. 44J, 45G). G1 relatively stout, arcuate, curved outwards, with distinct subdistal dorsal projection, tip rounded (Figs. 44K, L, 45H, I). G2 short, with spatuliform tip; exopod about half endopod length (Figs. 44M, N, 45J).

Variation. The length of the MXP3 dactylus varies somewhat, from falling short of (Fig. 42A, C) to reaching

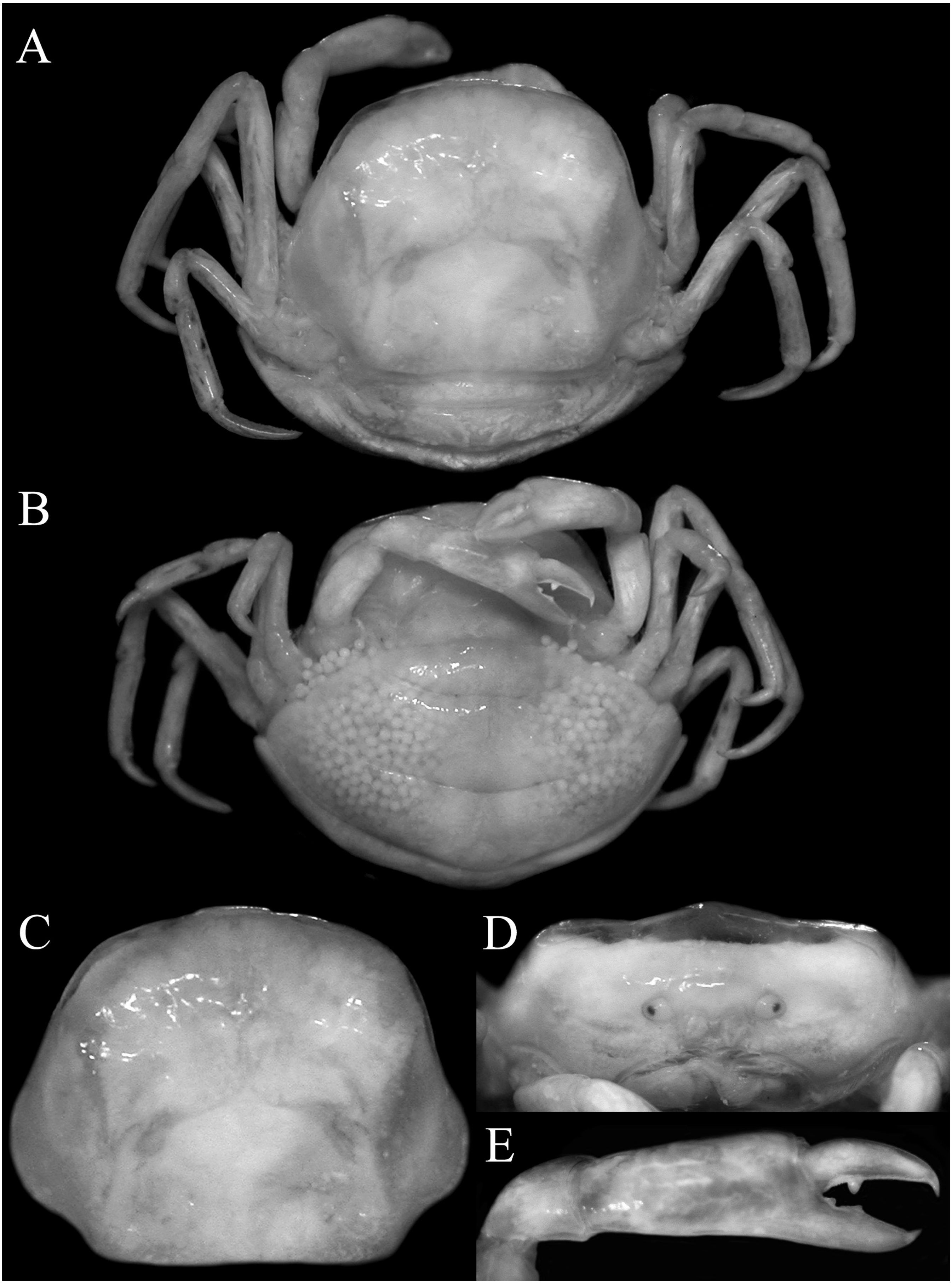

Fig. 37. *Arcotheres exiguus* (Bürger, 1895), ovigerous female (9.3 × 7.6 mm) (NHM 1936.6.19.12), Peninsular Malaysia (holotype of *Pinnotheres winckworthi* Gordon, 1936). A, overall dorsal view; B, ventral view of cephalothorax; C, dorsal view of carapace; D, frontal view of cephalothorax; E, outer view of right chela.

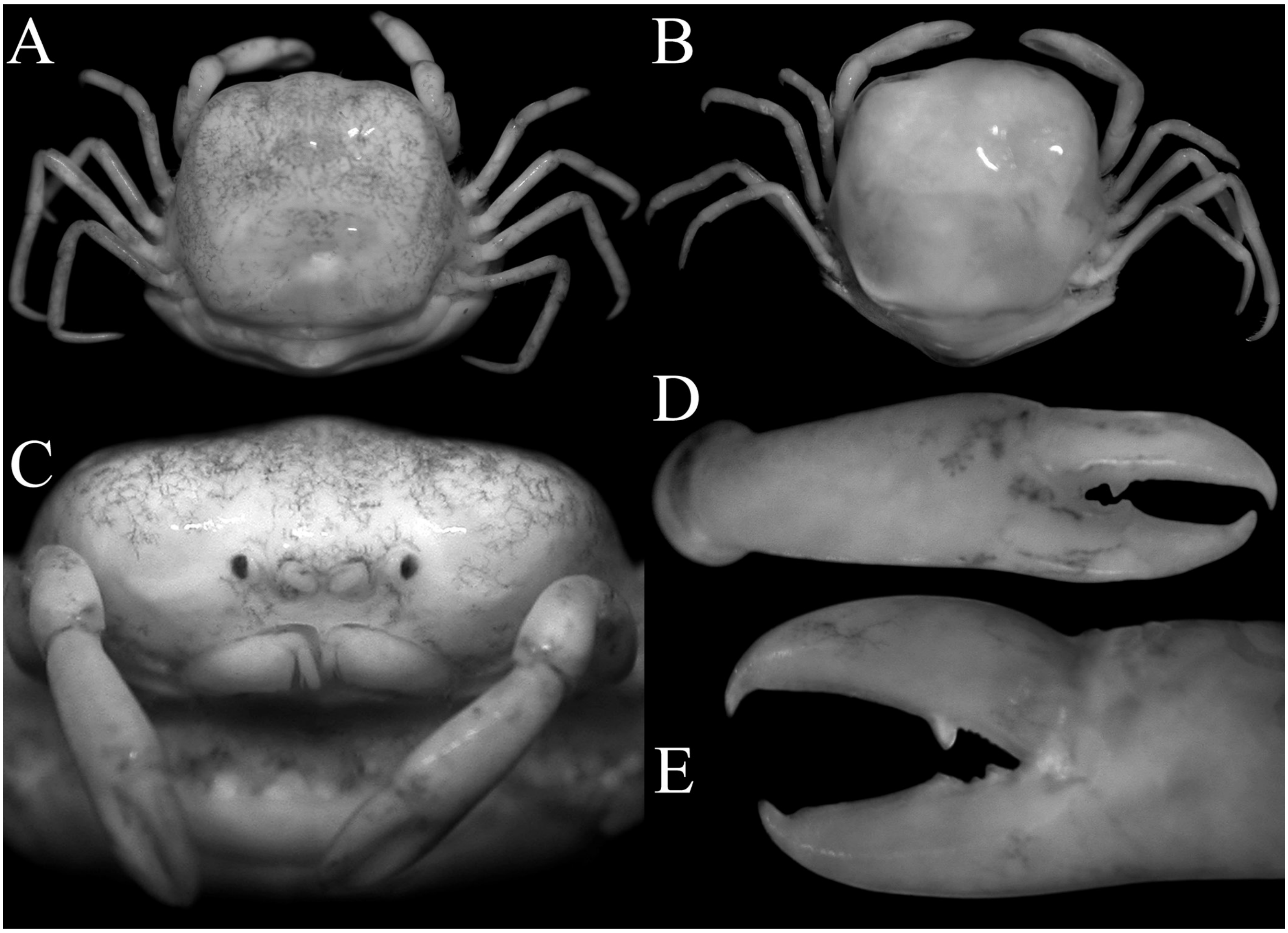

Fig. 38. *Arcotheres exiguus* (Bürger, 1895). A, C–E, ovigerous female (7.7 × 6.7 mm) (ZRC 2018.772), Peninsular Malaysia; B, female (8.2 × 7.4 mm) (ZRC 2018.775), Peninsular Malaysia. A, B, overall dorsal view; C, frontal view of cephalothorax; D, outer view of right chela; E, outer view of fingers of left chela.

as far as, but not beyond, the propodus (Figs. 36E, 41B). In the lectotype female of *A. exiguus*, the MXP3 dactylus is relatively long (Fig. 36E; Ahyong & Ng, 2007b: fig. 4C). The degree of variation highlights the importance of a large series of specimens for accurate morphological characterisation. The MXP3 dactylus figured by Trivedi et al. (2020: figs. 6L, 7A) for two Indian specimens is inaccurate as the structure is actually much shorter (present Figs. 42C, 45A), albeit still within the known variation in this species. The general features of adults vary little: the frontal margin is invariably slightly protruding in dorsal view, whereas the lateral margins are usually divergent but may be gently convex and subparallel (Figs. 36C, 37A, 38A, B, 39A, D, E, 41A, N). The P5 distoflexor margin is usually not armed with spinules, although it may be possible to sometimes discern a row of very low, spinule-like structures (e.g., Fig. 42M). These structures, however, are unlike those in *A. similis* or *A. placunicola* because they are much weaker and all similarly sized, with the distal ones not elongate. Trivedi et al. (2020: fig. 4I) figured a P5 distoflexor margin (as *A. vicajii*, here treated as a junior synonym of *A. exiguus*) that has several prominent spinules, but these are not arranged in a row and actually much smaller than drawn. As with *A. rayi*, the slenderness of the P5 dactylus on *A. exiguus* varies allometrically, becoming more slender with increasing body size. However, at any given size, the P5 dactylus is more slender in *A. exiguus* than in *A. rayi* (Table 2; Fig. 50).

Colour. The colour is rather variable, with females usually pale yellowish- to cream-white, but the gonads, when mature, are bright orange (Figs. 34A–C, 35A, B). In some specimens, however, the overall carapace and appendages are pale yellow as well (Fig. 35E, F), the colour possibly being a consequence of host metabolism or food. Males are white to orange, with numerous small black spots (Figs. 34D–F, 35C, D).

Host. Almost always from *Protapes gallus* (Gmelin, 1791), *Protapes* cf. *rhamphodes* (Oliver & Glover, 1996), *Marcia recens* (Holten, 1802), *Marcia* cf. *cordata* (Forskål, in Niebuhr, 1775), *Meretrix aurora* Hornell, 1917, *Meretrix meretrix* (Linnaeus, 1758), *Dosinia* sp., and *Ruditapes philippinarum* Adams & Reeve, 1850 (all Veneridae Rafinesque, 1815). Kazmi et al. (2018: 136) reported the Pakistani host as *Mercenaria* Schumacher, 1817, but this is a coldwater genus not known from Asia, so the authors were probably dealing with a different venerid.

Remarks. *Pinnotheres exiguus* Bürger, 1895, transferred to *Arcotheres* by Campos & Manning (2001), was described

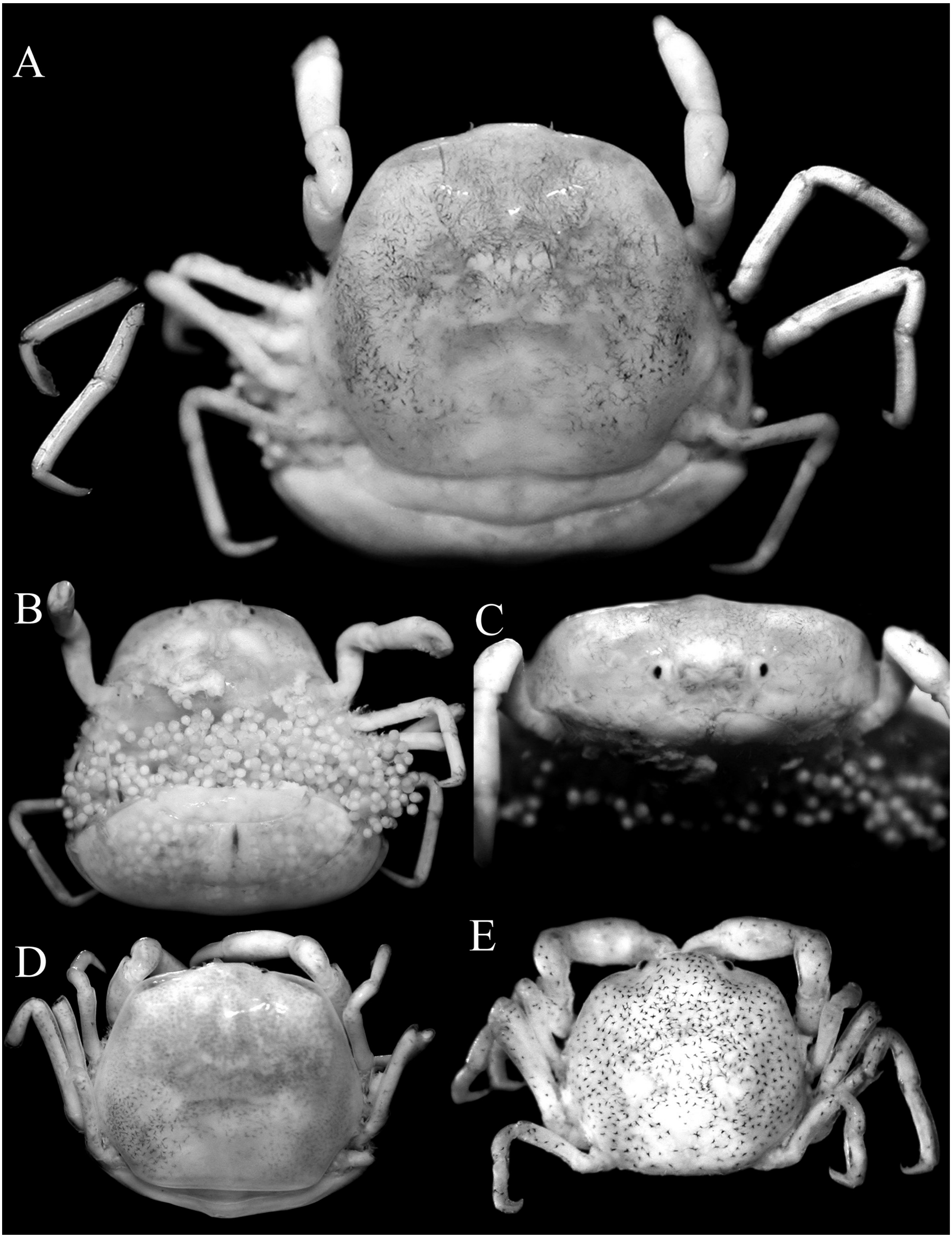

Fig. 39. *Arcotheres exiguus* (Bürger, 1895). A–C, ovigerous female (8.2 × 6.9 mm) (ZRC 2021.784), India (neotype of *Pinnotheres casta* Antony & Kutyamma, 1971); D, non-ovigerous female (8.0 × 6.7 mm) (ZRC 2017.1037), India; E, juvenile female (4.0 × 3.6 mm) (ZRC 2018.769), India. A, D, E, overall dorsal view; B, ventral view of cephalothorax; C, frontal view of cephalothorax.

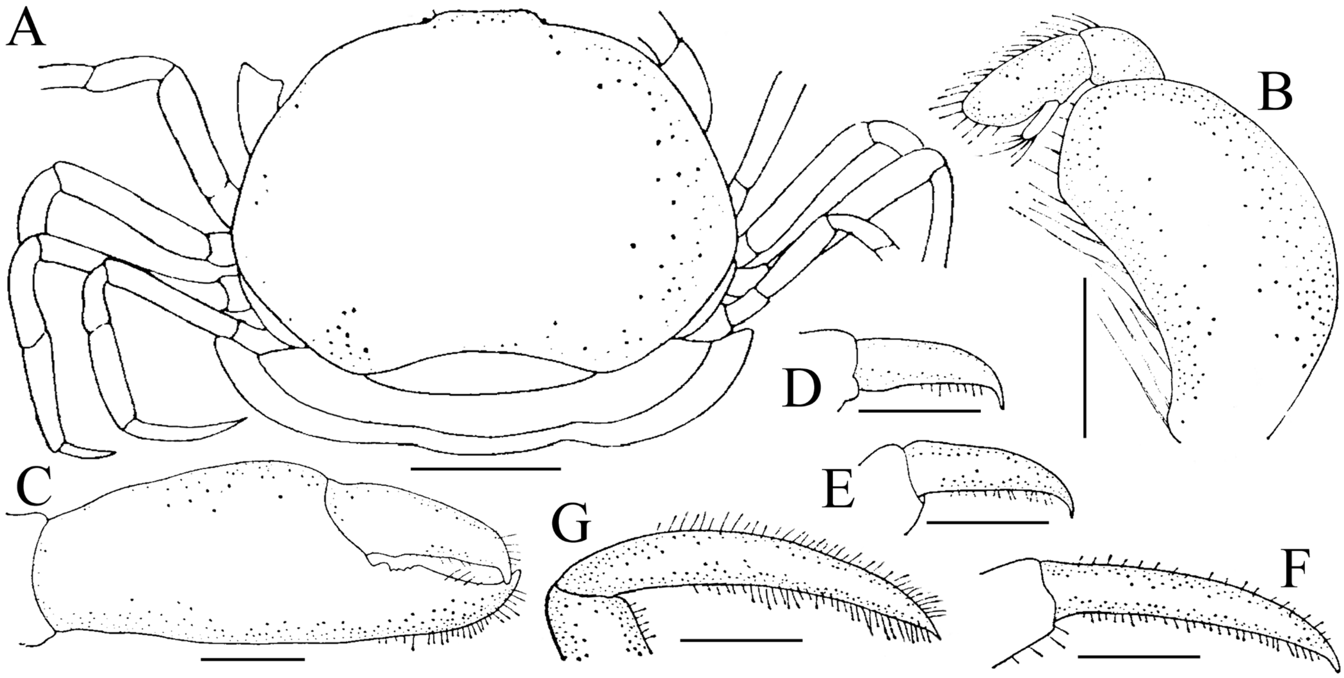

Fig. 40. *Arcotheres exiguus* (Bürger, 1895), female (6.8 × 4.8 mm) (CAS), China (holotype of *Pinnotheres obscuridentata* Dai & Song, 1986); after Dai & Song (1986: text-fig. 3). A, overall dorsal view; B, left MXP3; C, outer view of right chela; D–G, right P2–P5 dactyli. Scales = A, 2.0 mm; B–G, 0.5 mm.

from a small female (5.6 × 4.6 mm) from the Philippines, with the lectotype fixed by Ahyong & Ng (2007b: 195) (Fig. 36A, B). The lectotype (Fig. 36C–F) is now in poor condition, but agrees well, in all its MXP3 and ambulatory leg characters, with the type material of *A. winckworthi* (Gordon, 1936) and the series of specimens on hand; the two species are herein synonymised. *Arcotheres exiguus* is distinctive in the genus in its combination (in females) of the elongated P5 dactylus (as long as or longer than the propodus and twice as long as the dactyli of the P2, P3, and shorter P4), which lacks a row of distinct distoflexor spinules on the distal part and is strongly setose only on the flexor margins, being glabrous or sparsely setose on the other surfaces. As discussed earlier (under Characters), the setation of the P5 dactylus of *A. exiguus* (as well as *A. rayi*) contrasts with that of *A. palaensis*, *A. ocularius*, and *A. similis*, with the flexor margin distinctly more setose. Males of *A. exiguus* and *A. rayi* are unusual among congeners, of which males are known for having the articulation between the P5 ischium and merus diagonal rather than perpendicular to the segment axis, and a triangular subdistal lobe on the G1 (absent in others). In these respects, males of *A. exiguus* and *A. rayi* resemble male *Plenotheres coarctatus*. *Arcotheres exiguus* is most similar to *A. rayi*; distinguishing features are discussed under the account of the latter.

Females of *Arcotheres exiguus* are ovigerous by 4.1 mm cl (ZRC 2018.775). The smallest male examined (cl 3.4 mm; ZRC 2018.774) is already mature.

Silas & Alagarswami (1967) described and figured in detail an unidentified species of *Pinnotheres* obtained from the venerid clam *Meretrix casta* (Gmelin, 1791) from Cochin, western India. Antony & Kutyamma (1971) subsequently collected the same species from the same host in Cochin, formally naming it *Pinnotheres casta*. On the basis of the characters, this is clearly a species of *Arcotheres*. The present specimens from southern India (ZRC 2018.768, ZRC 2018.769, ZRC 2021.784) agree very well with the accounts by Silas & Alagarswami (1967) and Antony & Kutyamma (1971) of *P. casta*. The figure of the overall female habitus by Antony & Kutyamma (1971: fig. 1A) is schematic, but those of the MXP3 and ambulatory legs clearly show the asymmetry and leg proportions (Antony & Kutyamma, 1971: figs. 1B, 2) (see also Silas & Alagarswami, 1967: text-fig. 2). Silas & Alagarswami (1967) also had males of the species and figured their G1 and MXP3 (Silas & Alagarswami, 1967: text-fig. 1(4–6)). Interestingly, Chhapgar (1957) had described *Pinnotheres vicajii* from western India, but the identity of his species was always in doubt because the original description was very brief and the figures too schematic. Ng & Kumar (2015) transferred the species to *Nepinnotheres* on the basis of Chhapgar's (1957) figures of the ambulatory legs, which appeared to be symmetrical. Trivedi et al. (2020) re-examined the holotype male and fresh specimens of *P. vicajii* from the type locality and showed that *P. casta* was its junior subjective synonym.

Both sexes of *P. vicajii* (and *P. casta*) agree very well with *A. exiguus* (Fig. 42) and we regard them as conspecific. The structure of the G1, in particular, is diagnostic (Figs. 44K, L, 45H, I; cf. Trivedi et al., 2020: figs. 3D, 7H, I). As discussed by Trivedi et al. (2020), the types of *Pinnotheres casta* Antony & Kutyamma, 1971, are no longer extant. In view of the complex taxonomy of the various species now synonymised under *A. exiguus*, to stabilise the taxonomy of these taxa, we here select an ovigerous female (8.2 × 6.9 mm; ZRC 2021.784) from the western shore of Tamil Nadu, India (Fig. 39A–C), as the neotype of *P. casta*; it agrees with the type description and figures in almost all

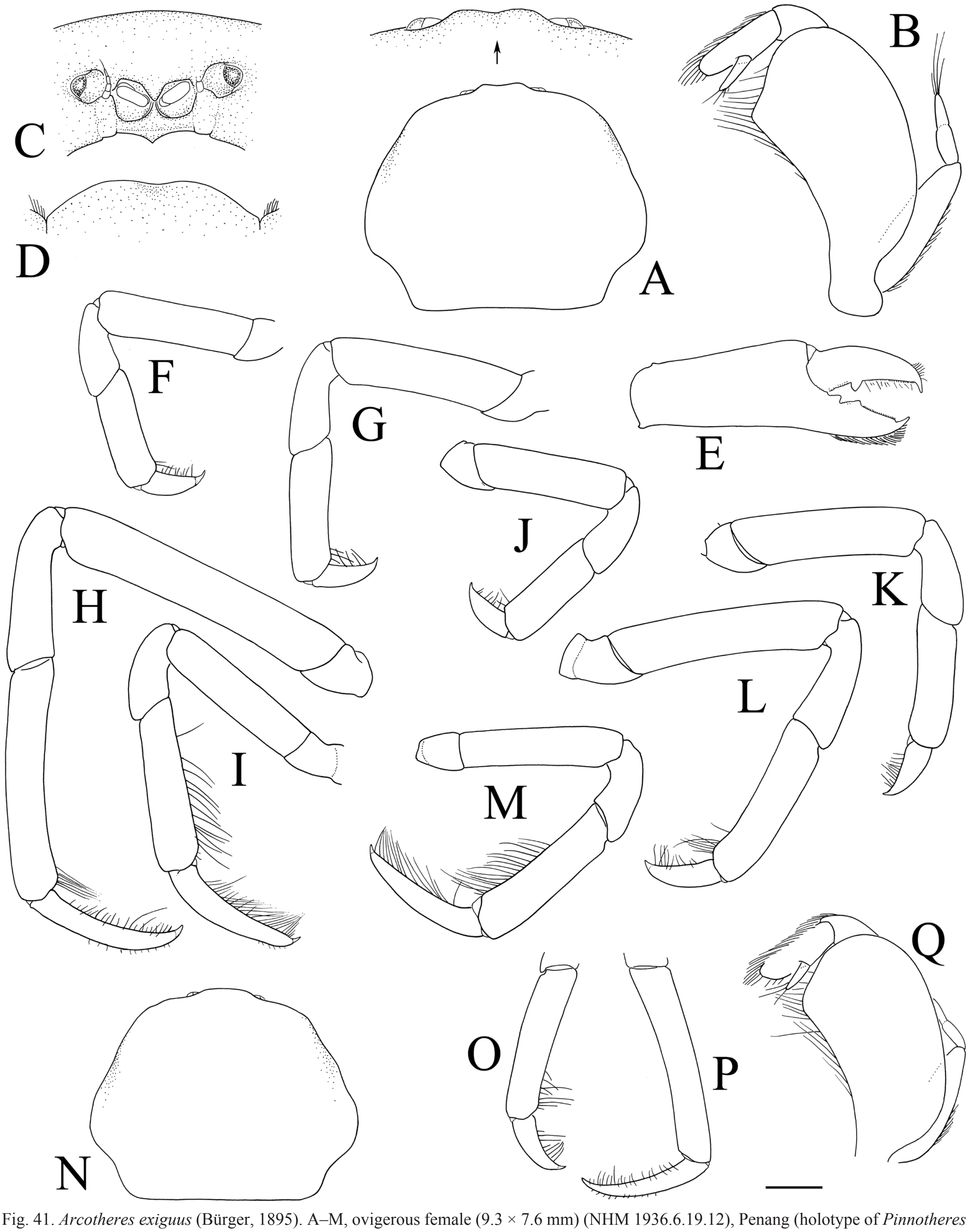

Fig. 41. *Arcotheres exiguus* (Bürger, 1895). A–M, ovigerous female (9.3 × 7.6 mm) (NHM 1936.6.19.12), Penang (holotype of *Pinnotheres winckworthi* Gordon, 1936); N–Q, ovigerous female (8.8 × 7.3 mm) (NHM 1936.6.19.13), Penang (paratype of *Pinnotheres winckworthi* Gordon, 1936). A, N, carapace; B, Q, left MXP3; C, frontal view of cephalothorax; D, anterior thoracic sternum; E, right chela; F–I, left P2–P5; J–M, right P2–P5; O, left P4, dactylus, and propodus; P, right P4, dactylus, and propodus. Scale = A, N, 2.5 mm; B, Q, 0.625 mm; C–M, O, P, 1.25 mm.

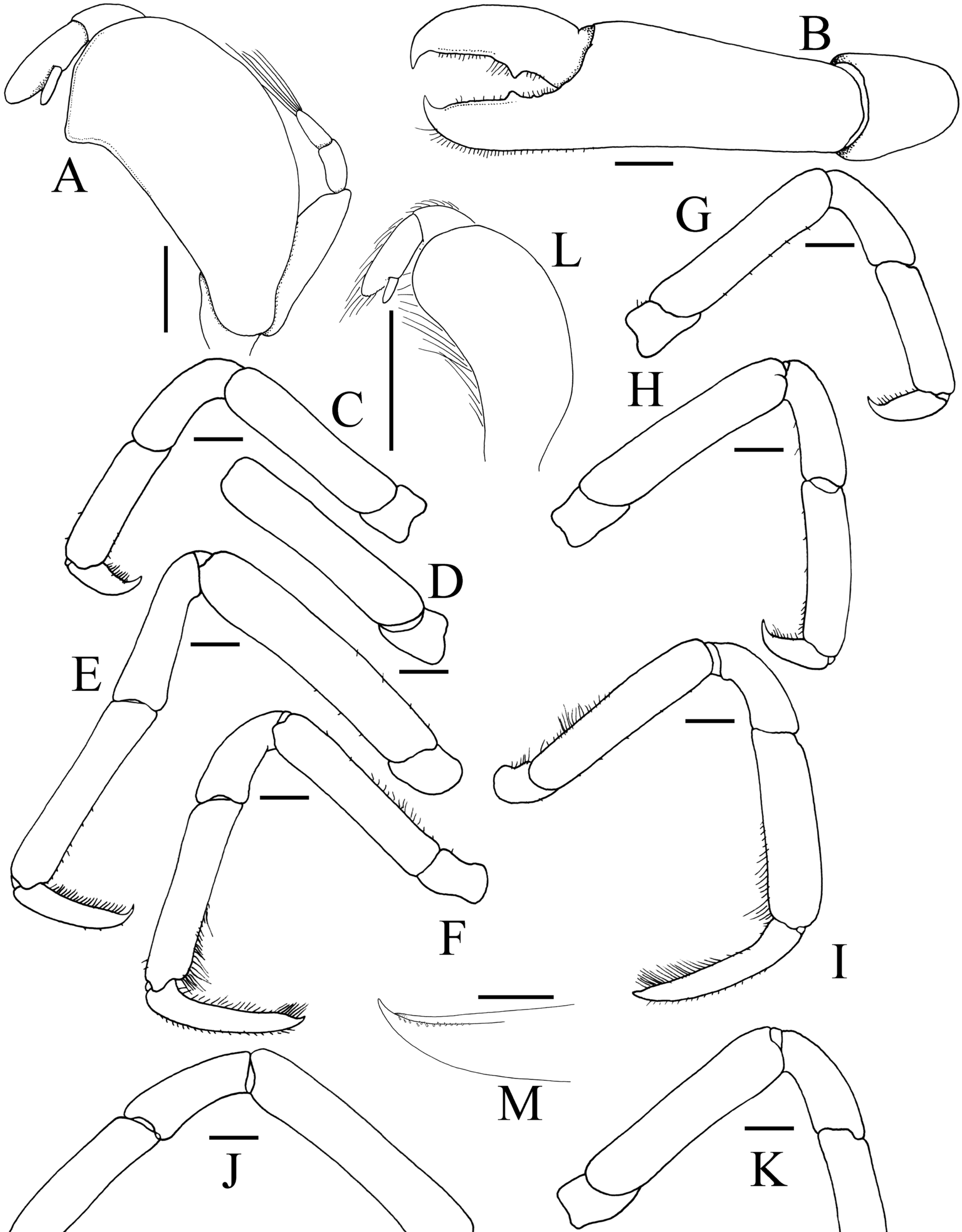

Fig. 42. *Arcotheres exiguus* (Bürger, 1895). A–I, ovigerous female (8.2 × 6.9 mm) (ZRC 2021.784), India (neotype of *Pinnotheres casta* Antony & Kutyamma, 1971); J, K, non-ovigerous female (8.0 × 6.7 mm) (ZRC 2018.768), India; L, juvenile female (4.0 × 3.6 mm) (ZRC 2018.769), India; M, ovigerous female (4.5 × 4.0 mm) (ZRC 2018.775), Peninsular Malaysia. A, L, left MXP3 (setae omitted); B, left chela and carpus; C–F, left P2–P5, respectively (P3 carpus, propodus, and dactylus missing); G–I, right P2, P4, and P5, respectively; J, K, left and right P4, respectively; M, distal part of right P5 dactylus (ventral view, soft setae omitted). Scales = A–L, 0.5 mm; M, 0.25 mm.

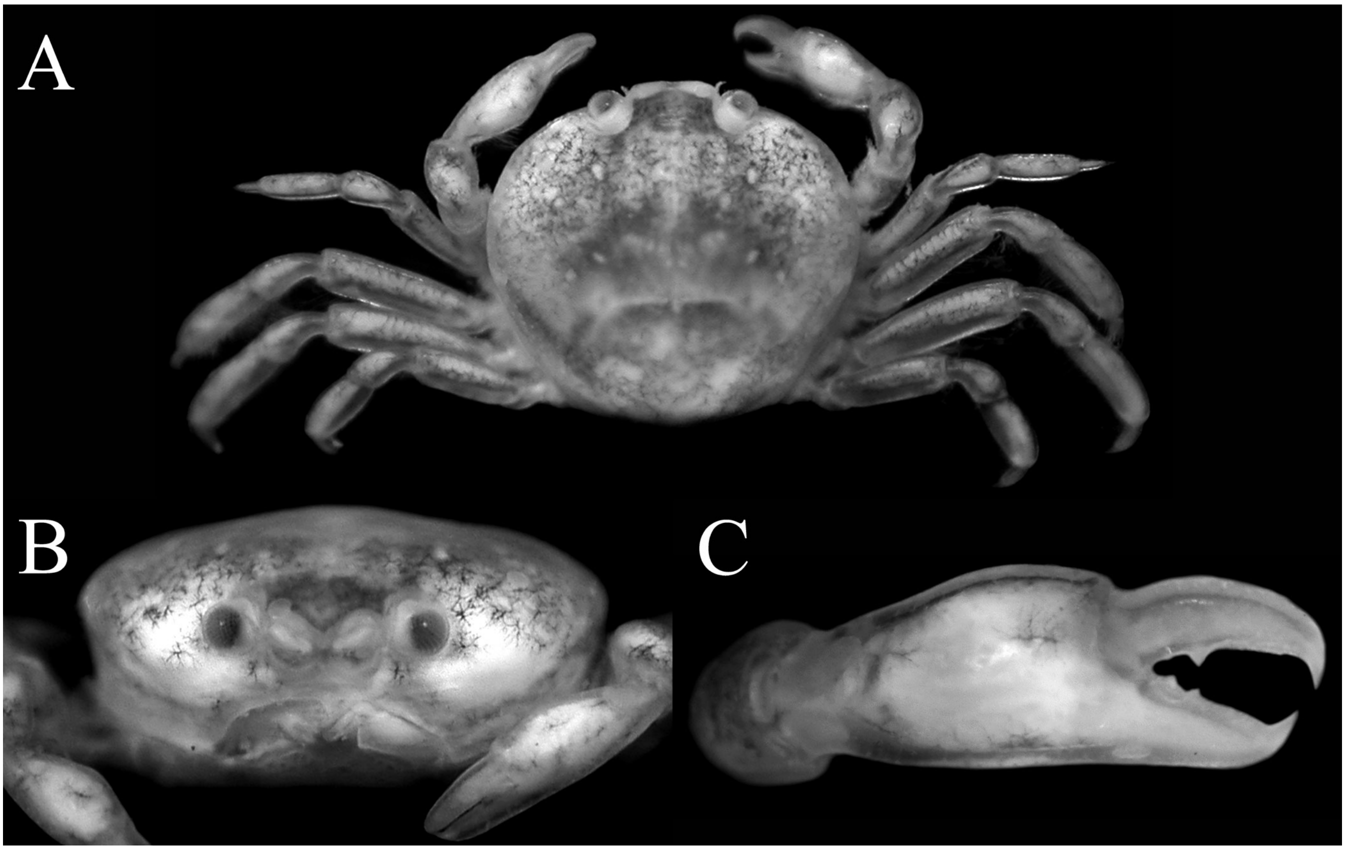

Fig. 43. *Arcotheres exiguus* (Bürger, 1895), male (5.1 × 4.9 mm) (ZRC 2018.772), Peninsular Malaysia. A, overall dorsal view; B, frontal view of cephalothorax; C, outer view of right chela.

aspects. The neotype is from a location south of Kochi in the Indian state of Kerala, the original type locality, but is still in the southwestern part of India. Trivedi et al. (2020) redescribed the species at length, as *A. vicajii*.

Pinnotheres obscuridentata Dai & Song, 1986, described from one female (no host recorded) collected in Longmen, Guangxi, southern China (Fig. 40), is here provisionally considered to be a junior synonym of *A. exiguus*. Dai & Song (1986: 56, 62) commented that a distinguishing feature was the absence of a sub-basal tooth on the dactylar finger of the chela, but it seems more likely that it is simply broken or eroded; all other species of *Arcotheres* possess the dactylar tooth. In almost all other features as understood at present, it agrees well with *A. exiguus*. The MXP3 has a relatively short propodus with a short dactylus, and the chela is short and stocky (Dai & Song, 1986: fig. 3-2, 3-3); all characters of *A. exiguus* and the proportions of the ambulatory legs also agree (Dai & Song, 1986: fig. 3-1, 3-4–3-7). The carapace of *P. obscuridentata* is proportionally slightly wider than typical *A. exiguus* (at least as figured by Dai & Song, 1986: fig. 3-1), but the carapace in this species is weakly chitinised and if poorly preserved can appear to vary substantially (Figs. 36A, 37A, 38A, B, 39A, D, E, 41A, N). The concave posterior margin of the carapace of *P. obscuridentata*, as figured by Dai & Song (1986), is a result of contraction of the soft carapace cuticle and slight anterior tilt of the specimen when figured, which in *A. exiguus*, is usually almost straight but occasionally concave (Fig. 39A). The holotype of *P. obscuridentata* could not be found in the type repository, Institute of Zoology in the Chinese Academy of Sciences (Academia Sinica) (Dai & Song, 1986), despite two separate searches in 2018 and 2019 (Meng Kai, Ng Ngan Kee, Lee Bee Yan, pers. comm.). The account by Dai & Song (1986: 56) is somewhat confusing, indicating that only the holotype female was available, yet providing two sets of carapace measurements, perhaps corresponding to more than one specimen or multiple points of measurement of the same specimen (carapace width 5.3–7.0 mm and length 3.9–4.8 mm). Their figured holotype specimen measures 6.8 × 4.8 mm according to the figure scale (Dai & Song, 1986: fig. 3-1; Fig. 40A).

The record of "*Pinnotheres gracilis*" by George & Noble (1970: 392) from Karwar in India is very likely *A. exiguus*. They did not illustrate the whole specimen, but the G1 figured (George & Noble, 1970: fig. 1.2, 1.3) agrees very well with that of *A. exiguus* (Figs. 44K, L, 45H, I). The MXP3 (figured from the inner view), however, depicts a relatively long dactylus that extends beyond the tip of the propodus (George & Noble, 1970: fig. 1.1); in *A. exiguus*, the dactylus is always shorter (Figs. 36E, 41B, 42A, C, 44B, 45A). The MXP3 figured shows its internal (rather than external) surface and does not appear to have been illustrated with the palp articles in the same plane, making the propodus appear shorter than it actually is. The G1 as figured is almost identical to that known for *A. exiguus.* Therefore, we provisionally refer their record to *A. exiguus*. It is noteworthy that George & Noble (1970) recorded the crab from the venerid clam *Marcia opima* (Gmelin, 1791) (as a

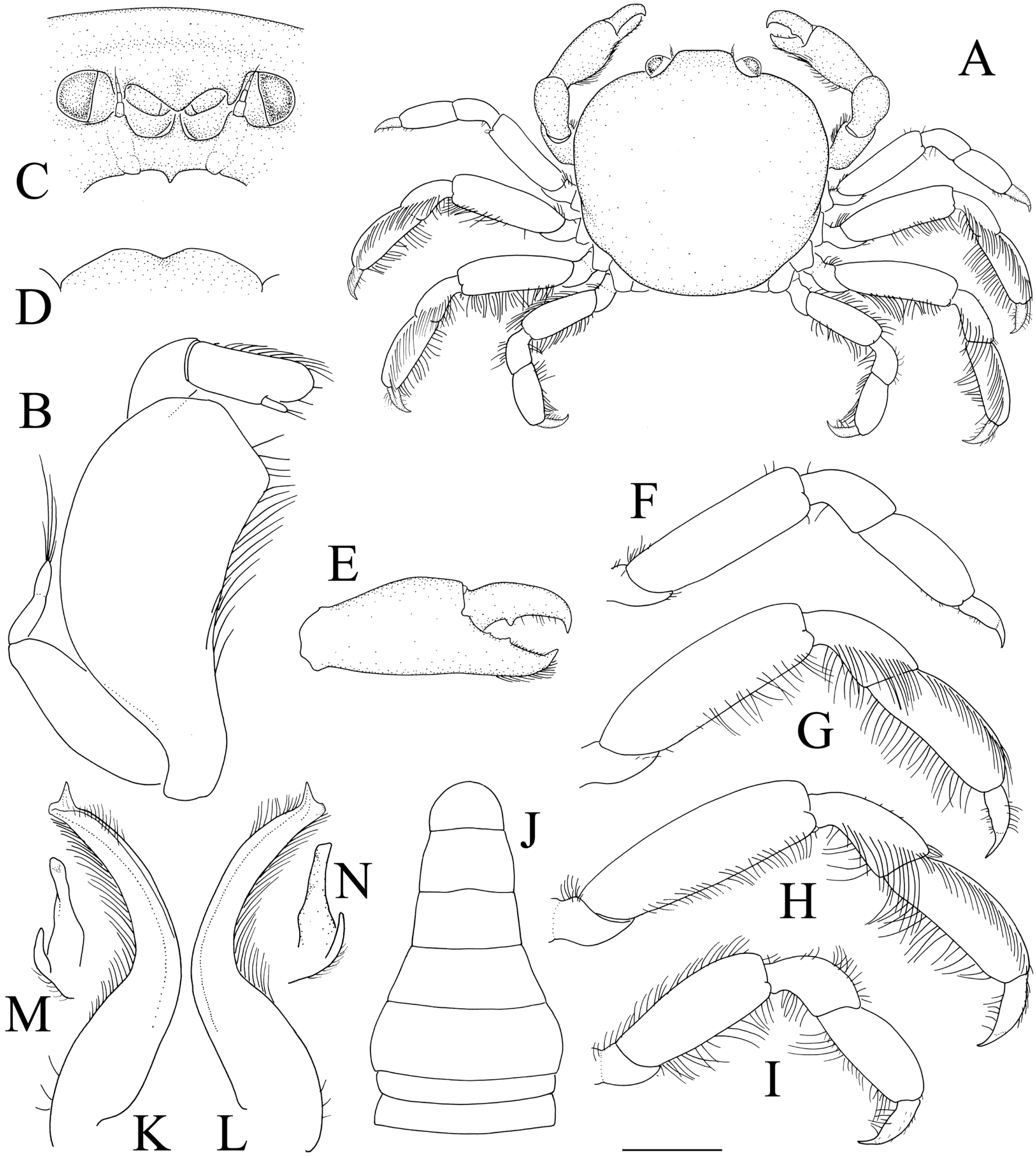

Fig. 44. *Arcotheres exiguus* (Bürger, 1895), male (5.1 × 4.9 mm) (ZRC 2018.772), Peninsular Malaysia. A, overall dorsal view; B, right MXP3; C, frontal view of cephalothorax; D, anterior thoracic sternum; E, right chela; F–I, right P2–P5; J, pleon; K, L, left G1 (ventral and dorsal views, respectively); M, N, left G2 (ventral and dorsal views, respectively). Scale = A, 2.0 mm; B, K–N, 0.5 mm; C–J, 1.0 mm.

Katelysia). *Pinnotheres gracilis* s. str. is now in *Viridotheres* Manning, 1996 (see Ahyong & Ng, 2007b: 220; Trivedi et al., 2018b: 62), and occupies *Solen* sp. (Adapedonta).

The record of "*Pinnotheres gracilis*" by Lalitha Devi (1981: fig. 1 (left)) from Kakinada Bay, Bay of Bengal, was from the pectenid scallop *Amusium pleuronectes* (Linnaeus, 1758) and is misidentified. The photograph of the specimen is not clear, but considering the host and pereopod proportions, it is almost certainly referable to *Amusiotheres hanumantharaoi* (Devi & Shyamasundari, 1989), known from the Bay of Bengal (see Devi & Shyamasundari, 1989; Ng & Ho, 2016a).

Arcotheres exiguus is superficially very close to *A. cyclinus* (Shen, 1932), especially in the form of the carapace, pereopods, and slender chelae (Shen, 1932: figs. 80, 81c). The species was described from China from the venerid clam *Cyclina sinensis* (Gmelin, 1791). The one major difference

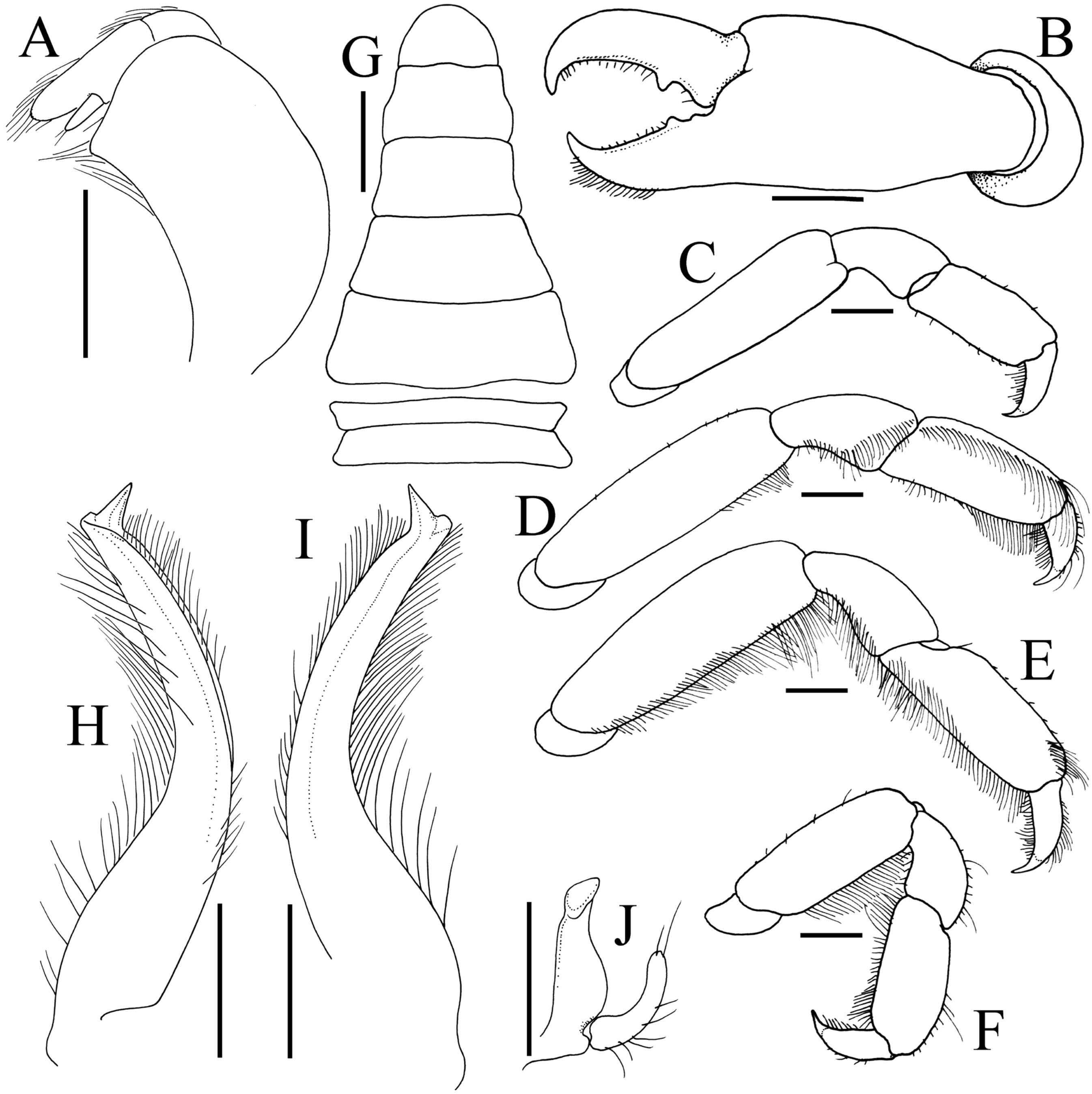

Fig. 45. *Arcotheres exiguus* (Bürger, 1895), male (4.5 × 4.2 mm) (ZRC 2018.768), India. A, left MXP3 (setae omitted); B, left chela and carpus; C–F, right P2–P5, respectively; G, male pleon; H, left G1 (dorsal view); I, left G1 (ventral view); J, left G2 with exopod. Scales = 0.5 mm.

is the proportionately longer MXP3 dactylus, which extends beyond the tip of the propodus (Shen, 1932: fig. 81a); the dactylus extends no further than the propodus tip in *A. exiguus* (Figs. 36E, 41B, 42A, C, 44B, 45A).

With clarification of the identity of *A. exiguus* and documentation of its geographic range, it is now evident that the species ranges widely from the South China Sea westwards to the northern Arabian Sea. Our scutiny of material from across the range has not revealed distinctions that would suggest that more than one species is present, as might be suspected on the basis of its wide distribution. Evidently, the distribution of *A. exiguus* appears to track that of its hosts. Nevertheless, should *A. exiguus* prove to be a composite taxon, four names are available that could be resurrected from synonymy.

Distribution. South China Sea, including the Philippines, to Singapore, Malaysia, India, and the northern Arabian Sea.

Arcotheres rayi Ahyong & Ng, 2007b
(Figs. 46–49, 50H–L, 51, 52)

Arcotheres rayi Ahyong & Ng, 2007b: 203, fig. 11 [type locality: Mariveles or Bohol, Philippines]; Ng et al., 2008: 248; Clark & Schram, 2009: 450; Ng et al., 2017: 1094; Trivedi et al., 2018a: 54, 56; Trivedi et al., 2019: 590, tab. 1; De Gier & Becker, 2020: tab. 1.

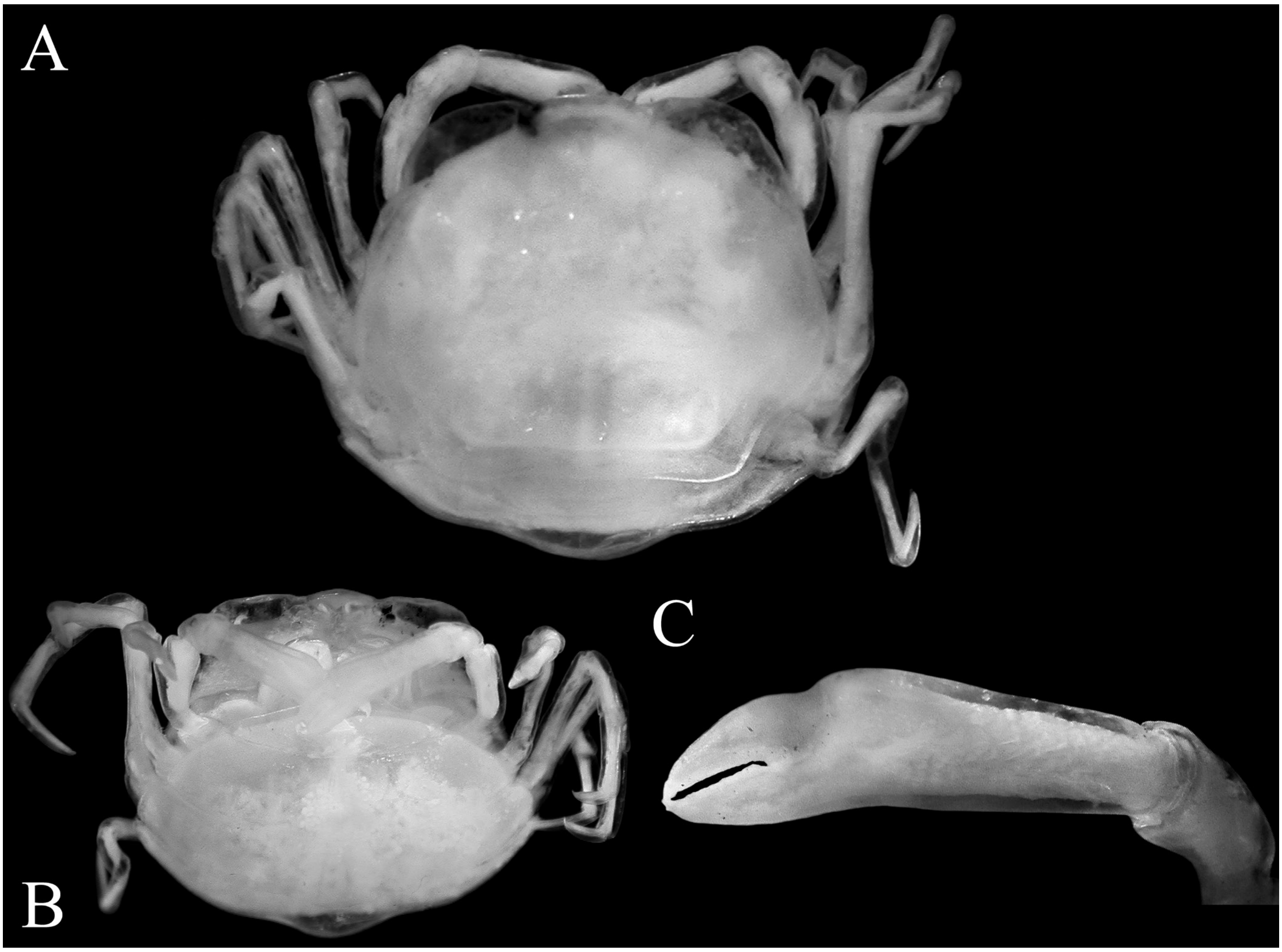

Fig. 46. *Arcotheres rayi* Ahyong & Ng, 2007, holotype female (11.3 × 8.7 mm) (SMF-ZMG 952), Philippines. A, overall dorsal view; B, ventral view of cephalothorax; C, outer view of left chela.

Type material. Holotype: female (11.3 × 8.7 mm) (SMF-ZMG952), Mariveles or Bohol, Philippines, coll. Semper (paralectotype of *Xenophthalmus latifrons* Bürger, 1895).

Other material examined. Peninsular Malaysia: 3 males (4.2 × 3.8–4.4 × 4.0 mm), 8 ovigerous females (5.4 × 5.1–8.4 × 7.0 mm), 5 spent females (5.6 × 4.0–6.9 × 5.2 mm), 10 females with bopyrids (5.4 × 3.8–10.4 × 6.2 mm) (ZRC 2013.1416), Bentong market, Pahang, in *Paphia* sp., coll. M. Low, 10 May 2010.

Description. Female: Carapace and pereopods poorly chitinised, soft. Carapace subcircular to subhexagonal, wider than long; dorsal and lateral surfaces smooth, glabrous; appearing domed in frontal view; front in line with (larger specimens) or slightly produced anteriorly (smaller specimens) beyond transverse anterolateral margins, margin gently convex; anterior margin with (larger specimens) or without (smaller specimens) shallow notch above orbit flanking front (Figs. 46A, 47A, C, D, 48A–C, 49A). Eyes small, not or just visible in dorsal view in adults; mobile, completely filling orbit (Figs. 46A, 47A, C, D, 48A–C, 49A, C). Epistome with median part triangular, lateral margins gently concave (Fig. 49C).

MXP3 outer surface with scattered short setae; ischiomerus completely fused, subrhomboidal, inner margin usually rounded, at widest point; carpus short; propodus about 3 times as long as high, subspatulate, distinctly longer than carpus, tip rounded to subtruncate; dactylus slender, inserted medially on propodus, tip underreaching or just reaching propodal apex; exopod relatively slender, about two-thirds length of ischiomerus, flagellum 2-segmented (Fig. 49B).

Chela not prominently elongate, dactylus half to two-thirds palm length; palm relatively slender, proximally narrower than distally; outer surfaces of palm, fingers (except for distal part) almost glabrous, with only scattered short setae; ventral margin of palm gently convex to sinuous; dactylus occlusal margin with distinct subproximal tooth; pollex occlusal margin usually with 1 low proximal tooth (sometimes obsolete), 1 submedian tooth, and minute denticles; tips of fingers sharp, hooked (Figs. 46C, 47E, 49E).

P2–P5 dorsally, ventrally unarmed; outer surface covered with scattered, very short setae or glabrous; ventral margins of propodus and dactylus slightly more setose; merus relatively longer, more slender, relative lengths of meri P4>P3>P5>P2; left (sometimes right) P4 distinctly the longer; P2 and P3 dactyli short, subequal, tip gently hooked; P4 longer

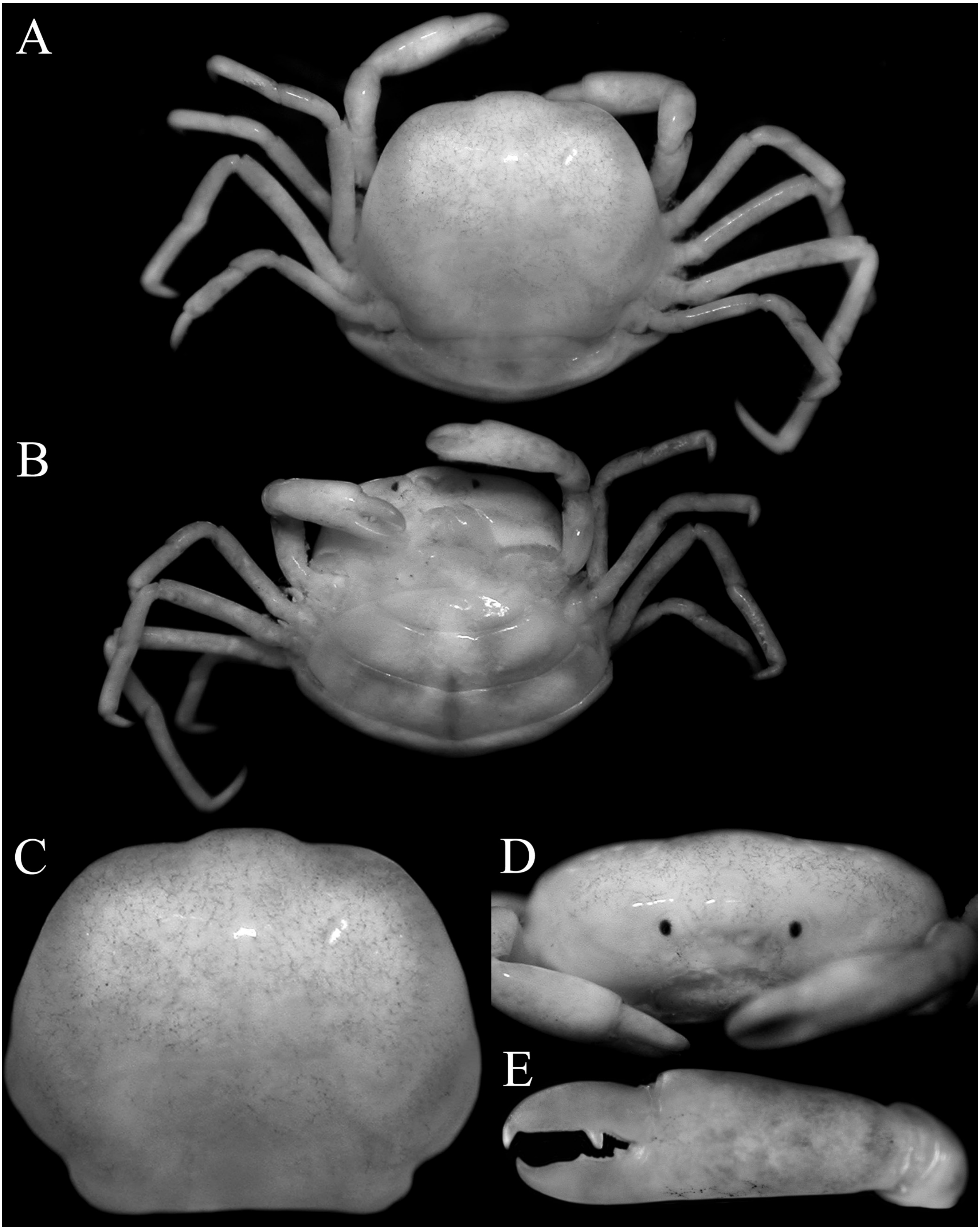

Fig. 47. *Arcotheres rayi* Ahyong & Ng, 2007, female (6.9 × 5.2 mm) (ZRC 2013.1416), Peninsular Malaysia. A, overall dorsal view; B, ventral view of cephalothorax; C, dorsal view of carapace; D, frontal view of cephalothorax; E, outer view of left chela.

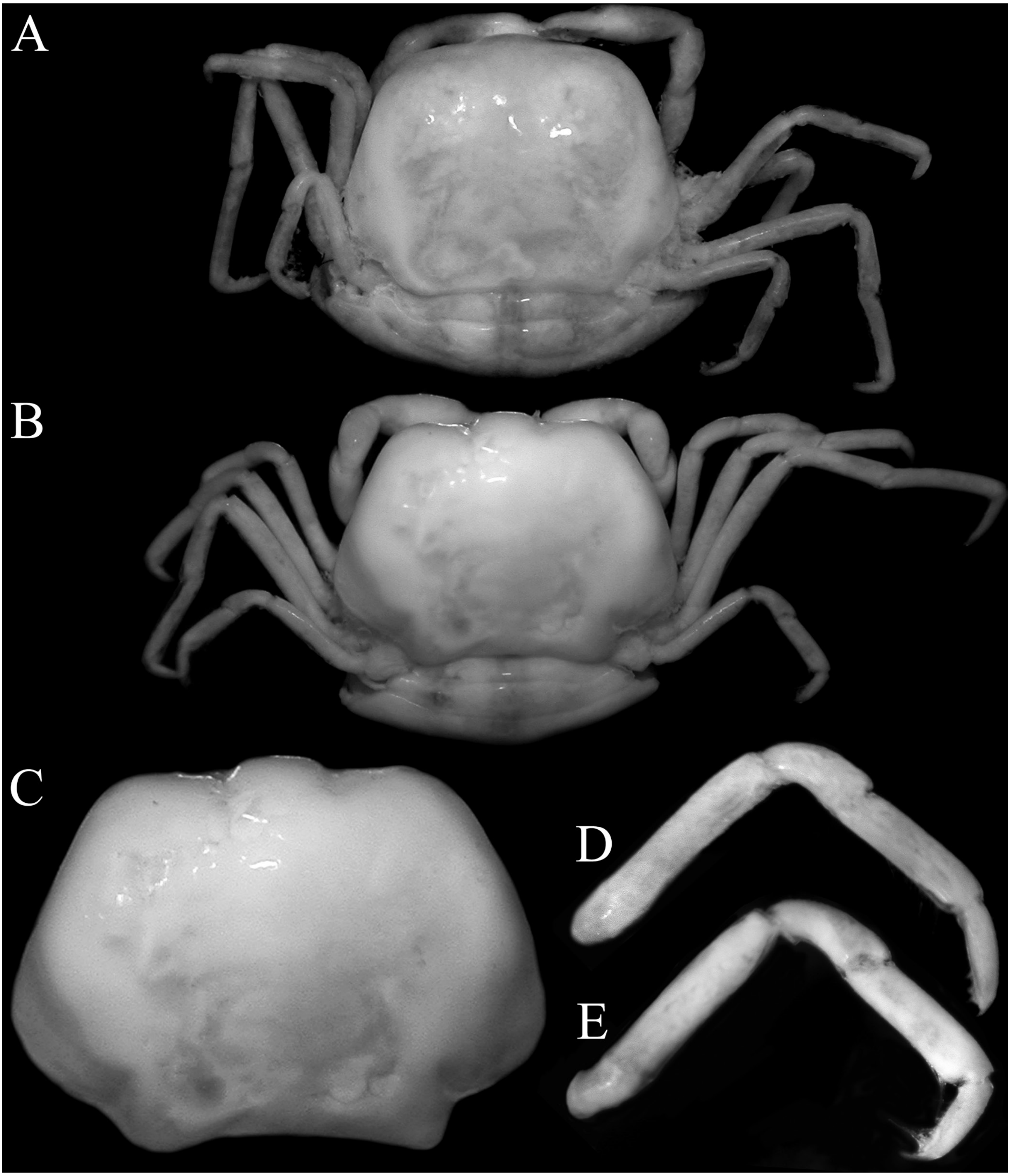

Fig. 48. *Arcotheres rayi* Ahyong & Ng, 2007. A, D, ovigerous female (7.6 × 5.8 mm) (ZRC 2013.1416), Peninsular Malaysia; B, C, E, female (6.2 × 4.4 mm) (ZRC 2013.1416), Peninsular Malaysia. A, B, overall dorsal view; C, dorsal view of carapace; D, E, right P5.

dactylus elongate, weakly falciform, distinctly longer than half propodus length, longer than P5 dactylus; P5 merus 3.9–4.5 times longer than wide; P5 dactylus shorter than propodus extensor margin, longer than P2 and P3 dactyli, length/height < 5.0, margins lined with short and long setae, denser on ventral margin, distoflexor margin without rows of spinules (Figs. 49F–M, 50H–L).

Pleon extending to buccal region, covering bases of P2–P5; telson gently recessed into concave distal margin of somite 6 (Figs. 46B, 47B, 49D).

Male: Carapace and pereopods well chitinised, firm. Carapace almost circular, slightly wider than long; dorsal surface almost smooth, not prominently inflated, lateral surfaces with

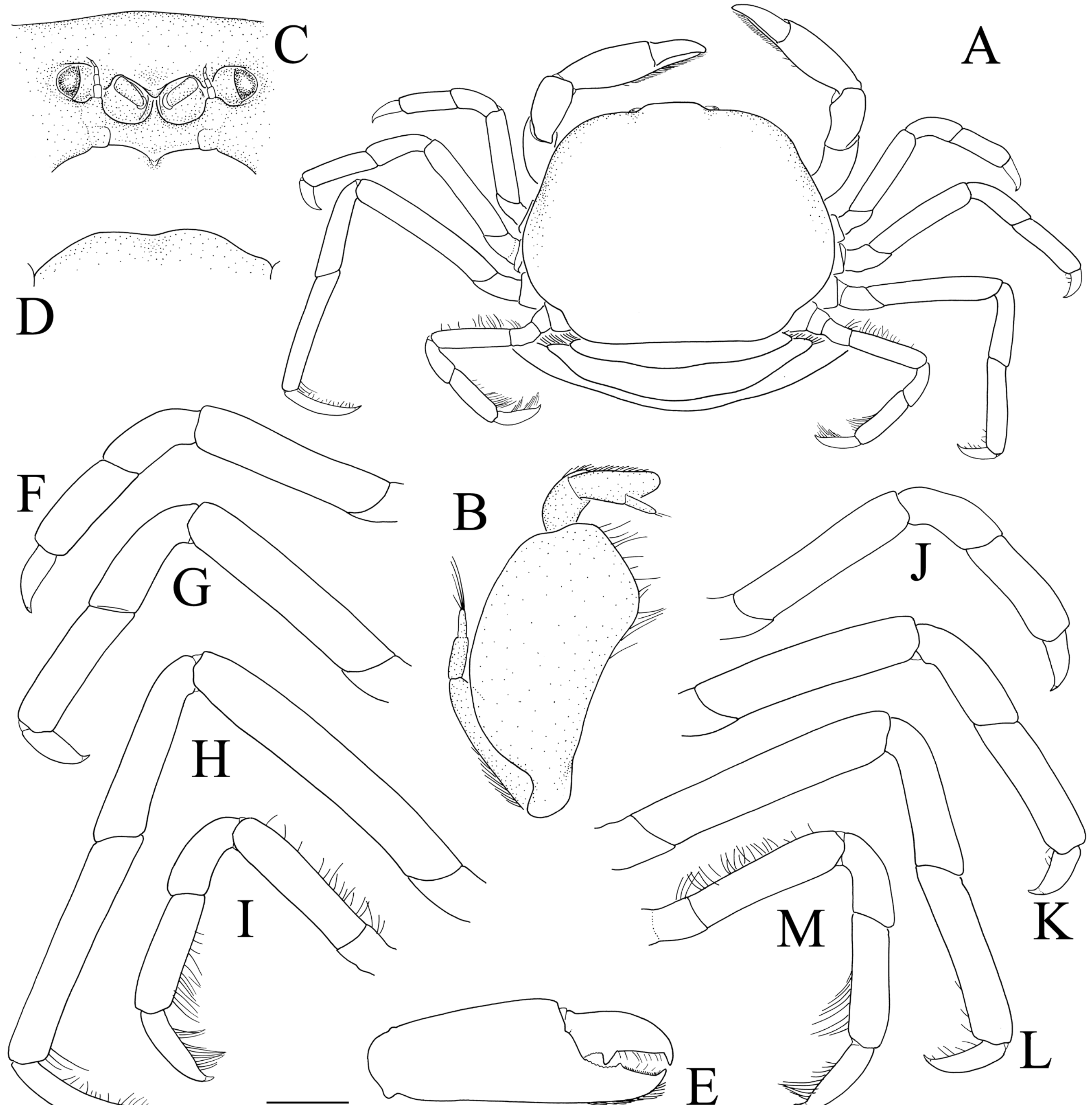

Fig. 49. *Arcotheres rayi* Ahyong & Ng, 2007, ovigerous female (7.6 × 5.8 mm) (ZRC 2013.1416), Peninsular Malaysia. A, overall dorsal view; B, right MXP3; C, frontal view of cephalothorax; D, anterior thoracic sternum; E, right chela; F–I, left P2–P5; J–M, right P2–P5. Scale = A, 2.0 mm; B, 0.5 mm; C–M, 1.0 mm.

setae; front projecting anteriorly, margin gently sinuous to almost straight (Figs. 51A, 52A). MXP3 as in female but dactylus shorter (Fig. 52B). Anterior thoracic sternum wide, sternites 1, 2 fused, partially sunken into buccal cavity; suture between sternites 2 and 3 shallow; sternites 3, 4 completely fused, separated only by shallow grooves. Chela relatively stout, shorter than in female (Figs. 51C, 52D). P2–P5 dorsally, ventrally unarmed; outer surface covered with short setae; P3 and P4 carpus and propodus with long natatory setae; left and right meri equal, relative lengths of meri P4>P3>P2>P5; dactyli of P2–P4 progressively longer; right P4 dactylus slightly longer, more slender than left side; P4 and P5 dactylus subequal to that of P3, covered with short setae (Fig. 52E–L). Pleon slender, triangular, widest at somite 3, lateral margins of somite 4 gently concave; somite 6 trapezoidal; telson semicircular, wider than long (Fig. 52M). G1 relatively stout, arcuate, curved outwards, with short triangular subdistal dorsal projection, tip rounded (Fig. 52N, O). G2 short, with spatuliform tip; exopod about two-thirds endopod length (Fig. 52P).

Variation. The carapace shape varies somewhat, the most important being the prominence of the front, whose variation is broadly size-related. In the holotype of *A. rayi*, the largest

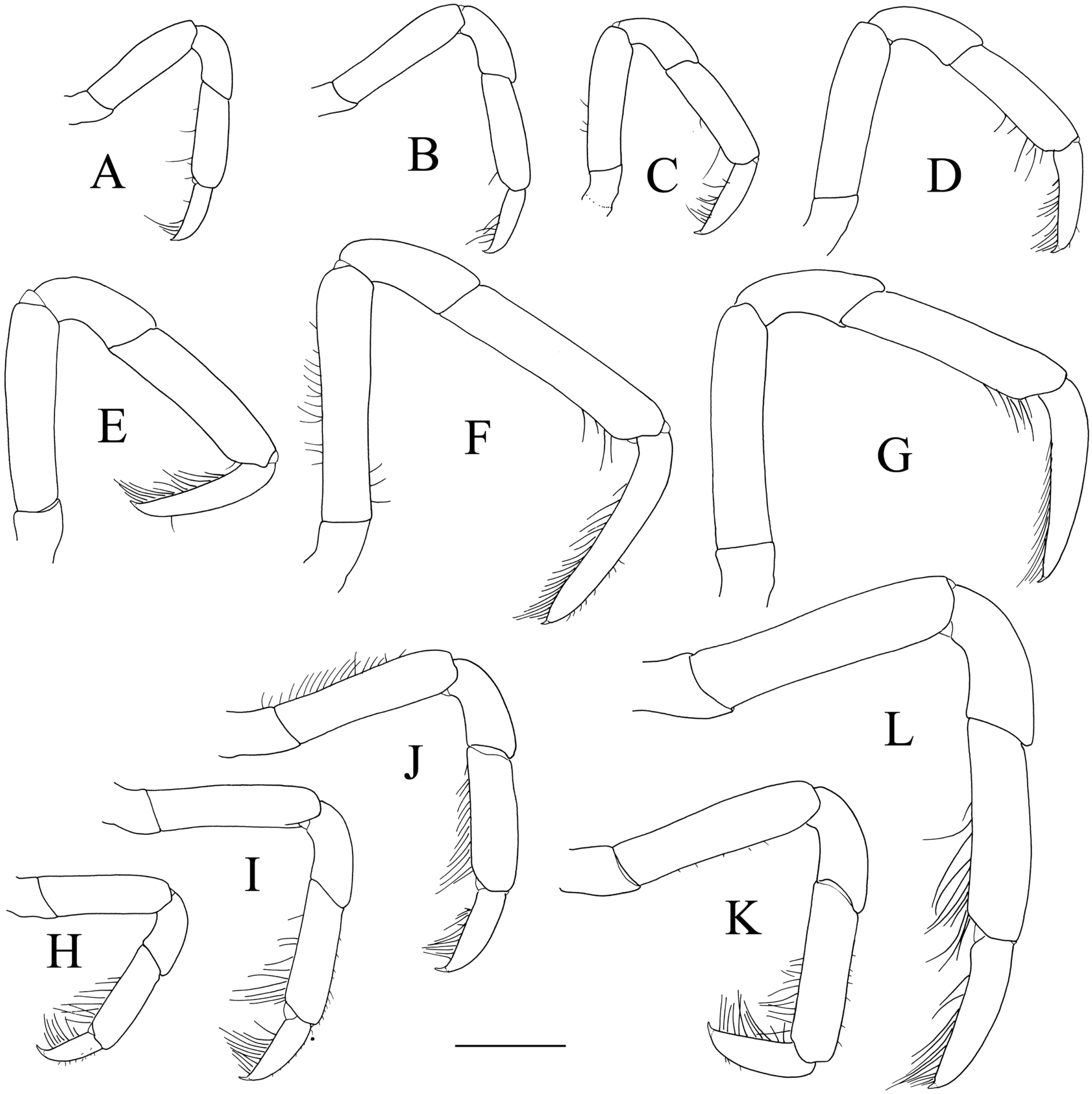

Fig. 50. Right female P5. A–G, *Arcotheres exiguus* (Bürger, 1895), Peninsular Malaysia: A, juvenile (3.8 × 3.6 mm) (ZRC 2018.772); B, ovigerous (4.5 × 4.1 mm) (ZRC 2018.775); C, non-ovigerous (4.6 × 4.2 mm) (ZRC 2018.772); D, spent (5.4 × 4.6 mm) (ZRC 2018.775); E, ovigerous (6.8 × 6.1 mm) (ZRC 2019.516); F, ovigerous (7.7 × 6.7 mm) (ZRC 2018.772); G, ovigerous (8.9 × 7.6 mm) (ZRC 2018.775). H–L, *A. rayi* Ahyong & Ng, 2007, Peninsular Malaysia: H, juvenile (5.4 × 5.8 mm) (ZRC 2013.1416); I, non-ovigerous (5.6 × 4.3 mm) (ZRC 2013.1416); J, non-ovigerous (8.1 × 5.2 mm) (ZRC 2013.1416); K, spent (6.9 × 5.2 mm) (ZRC 2013.1416); L, ovigerous (8.4 × 7.0 mm) (ZRC 2013.1416). Scale = 1.0 mm.

known specimen of the species, the front does not protrude in advance of the general anterior margin, but is demarcated on either side by a shallow notch above each orbit (Fig. 46). Other specimens, however, have a front that protrudes anteriorly beyond the general anterior margin, some retaining the notch on either side of the front (Fig. 48B, C), but most others without (Figs. 47, 48A, 49). The length of the longer P5 dactylus varies allometrically, being proportionately shorter in small specimens (Table 2; Fig. 50H–L).

Host. Known only from *Paphia* sp. (Veneridae Rafinesque, 1815).

Remarks. *Arcotheres rayi* is morphologically very close to *A. exiguus*, but the good series of specimens has permitted evaluation of intraspecific variability, enabling more reliable recognition of interspecific differences. Females of *A. rayi*, in which the carapace front is demarcated by a notch in the anterior margin above each orbit (Figs. 46, 48B, C, E), are readily distinguished from *A. exiguus*, which does not have the anterior carapace notches (Figs. 33B, C, 35B, E,

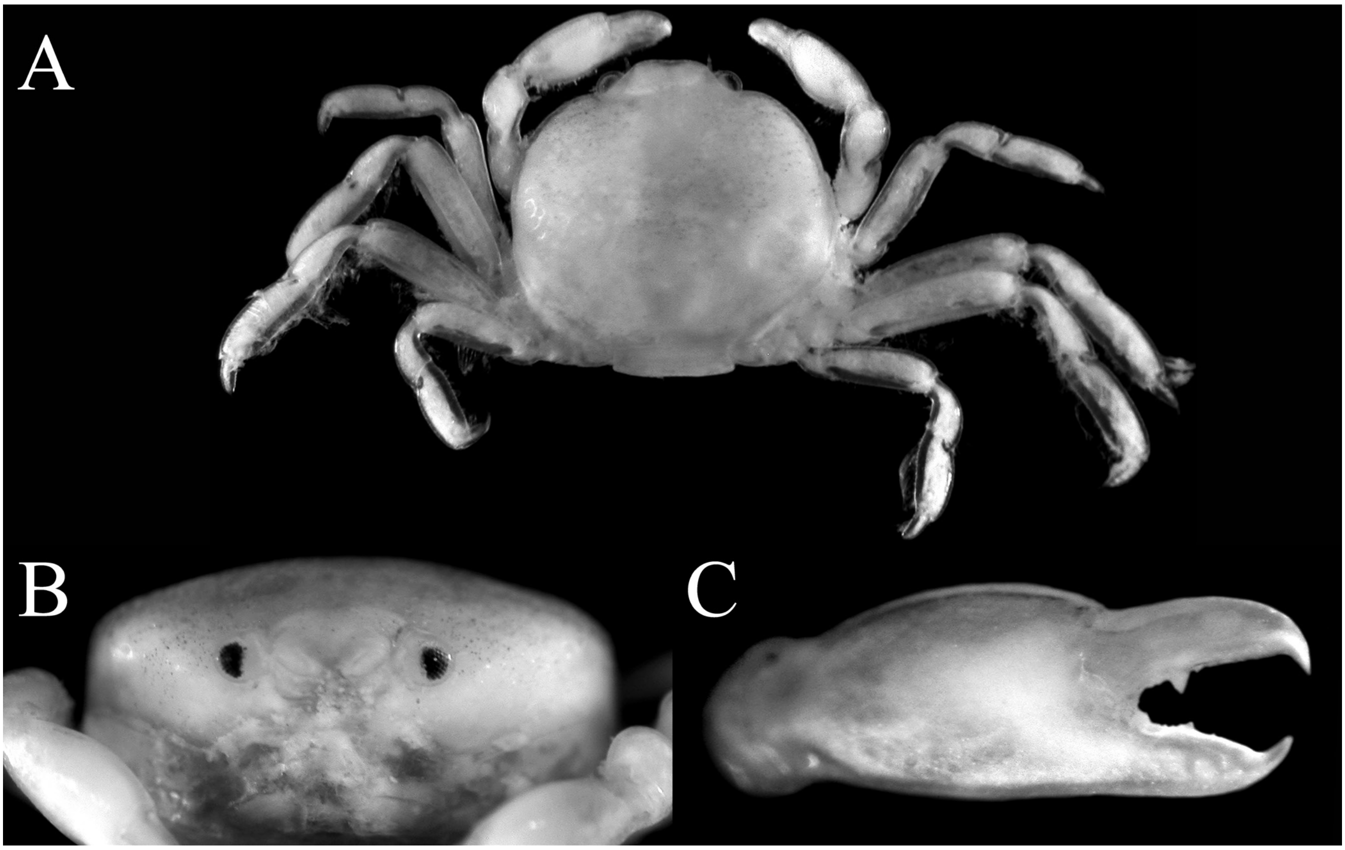

Fig. 51. *Arcotheres rayi* Ahyong & Ng, 2007, male (4.2 × 3.8 mm) (ZRC 2013.1416), Peninsular Malaysia. A, overall dorsal view; B, frontal view of cephalothorax; C, outer view of right chela.

36–41). Female *A. rayi*, however, with the anteriorly produced front but without the flanking notches (Figs. 47A, C, 48A), are indistinguishable from *A. exiguus* based on carapace features, although the two species can still be separated by the proportional differences in the P5 dactylus length and stoutness. The proportional length and stoutness of the P5 dactylus in *A. rayi* and *A. exiguus* increases allometrically, but when similarly sized females of *A. exiguus* and *A. rayi* are compared, the P5 dactylus is always proportionally shorter and stouter in *A. rayi* (see Figs. 48D, E, 50H–L versus Fig. 50A–G; Table 2). The length:height ratio of the female P5 dactylus is always less than 5.0 in *A. rayi*, but exceeds 5.0 in specimens of *A. exiguus* larger than 6.0 mm cl. Similarly, the female P5 dactylus in *A. rayi* is always shorter than the extensor margin of the corresponding propodus, but as long as or slightly longer in *A. exiguus* exceeding 6.5 mm cl, sometimes 5 mm. Males of *A. rayi* and *A. exiguus* are similar but easily distinguishable by the subdistal projection on the G1, which is always proportionately longer in *A. exiguus* (Figs. 44K, L, 45H, I) than in *A. rayi* (Fig. 52N, O).

Arcotheres rayi appears to mature at a similar size to *A. exiguus*. Females of *A. rayi* are mature by at least cl 4.0 mm (smallest ovigerous female 5.4 mm cl; ZRC 2013.1416). The smallest male examined (cl 3.8 mm; ZRC 2013.1416) is mature.

Table 2. Length/height proportions of P5 dactylus of *Arcotheres exiguus* and *A. rayi*.

cl (mm)	***A. exiguus***	***A. rayi***
	P5 length/height	**P5 length/height**
4.0–4.5	3.83–4.01	3.05
4.5–5.5	4.66–5.63	2.97–3.51
5.5–6.5	5.20	3.9
6.5–7.5	5.97–6.32	4.02
7.5–8.5	5.70–6.09	–
8.5–9.5	–	4.69

Distribution. Philippines and Peninsular Malaysia.

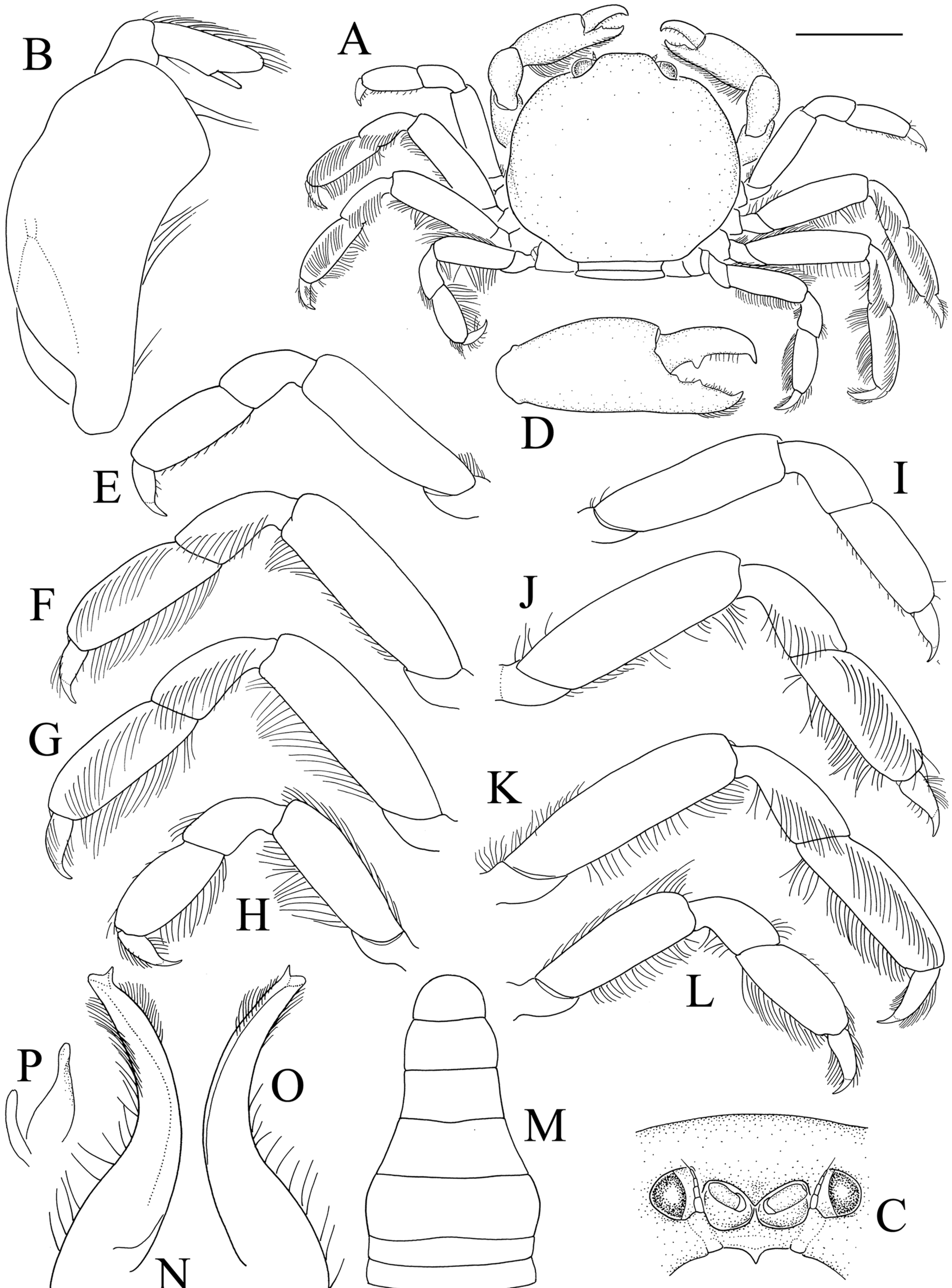

Fig. 52. *Arcotheres rayi* Ahyong & Ng, 2007, male (4.2 × 3.8 mm) (ZRC 2013.1416), Peninsular Malaysia. A, overall dorsal view; B, right MXP3; C, frontal view of cephalothorax; D, right chela; E–H, left P2–P5; I–L, right P2–P5; M, pleon; N, O, right G1 (dorsal and ventral views, respectively); P, right G2. Scale = A, 2.0 mm; B, N–P, 0.5 mm; C–M, 1.0 mm.

Arcotheres alcocki (Rathbun, 1909)
(Figs. 53, 54)

Pinnotheres parvulus — Bürger, 1895: 375, pl. 9 fig. 18, pl. 10 fig. 17 [not *P. parvulus* Stimpson, 1858].
Pinnotheres alcocki Rathbun, 1909: 114 (part; replacement name) [type locality: Burias, Philippines, by lectotype designation (Ahyong & Ng, 2007b)]; 1910: 304; Serène, 1968: 93.
Arcotheres alcocki — Ahyong & Ng, 2007b: 193, 194, fig. 1; Ng et al., 2008: 248; Ng et al., 2017: 1094; Trivedi et al., 2018a: 197; De Gier & Becker, 2020: tab. 1.

Material examined. 1 female (9.6 × 7.0 mm) (ZRC 2016.272), Pasir Panjang food terminal, Singapore, from *Marcia recens*, coll. J. C. Mendoza, 5 April 2016.

Description. Carapace and pereopods well chitinised. Female: Carapace transversely ovate-subhexagonal, wider than long; dorsal and lateral surfaces smooth, glabrous; appearing gently domed in frontal view; front barely projecting anteriorly beyond orbits, margin gently convex; anterolateral margin gently sloping posteriorly to various degrees, forming rounded angle with posterolateral margin (Figs. 53A, C, D, 54A). Eyes small, partially visible in dorsal view in adults; filling orbit (Figs. 53C, 54A). Epistome with median part triangular, lateral margins gently concave (Fig. 54C).

MXP3 outer surface with scattered short setae; ischiomerus completely fused, subrhomboidal, inner margin rounded, even at widest point; carpus short; propodus about 3 times as long as high, subspatulate, distinctly longer than carpus, tip rounded; dactylus slender, inserted at slightly proximal to midlength of propodus, tip not reaching propodal apex; exopod relatively slender, about two-thirds length of ischiomerus, flagellum 2-segmented (Fig. 54B).

Chela not prominently elongate, dactylus about two-thirds palm length; palm relatively slender, proximally narrower than distally; outer surfaces of palm, fingers (except for distal part) almost glabrous, with only scattered short setae; ventral margin of palm gently sinuous; dactylus occlusal margin with distinct subproximal tooth; pollex occlusal margin with 1 low proximal tooth, 1 submedian tooth, and minute denticles; tips of fingers sharp, hooked (Figs. 53E, 54E).

P2–P5 dorsally, ventrally unarmed; outer surface covered with scattered, very short setae or glabrous; ventral margins of propodus and dactylus slightly more setose; merus relatively short, stout, relative lengths of meri P4>P3>P2>P5; right P4 longer than left; P2 and P3 dactyli short, subequal, tip gently hooked, half propodus length; right P4 dactylus longer, weakly falciform, shorter than propodus, shorter than P5 dactylus; P5 merus 4.3–4.4 times longer than wide; P5 dactylus longest, longer than propodus, margins lined with short and long setae, denser on ventral margin, distoflexor margin with 2 rows of 7–12 spinules (Fig. 54F–M).

Pleon extending to buccal region, covering bases of P2–P5; telson gently recessed into concave distal margin of somite 6 (Figs. 53B, 54D).

Male: Not known.

Variation. Not known.

Colour. Not known.

Host. The lectotype female did not have any host record (Ahyong & Ng, 2007b: 193). The present specimen was from a clam, *Marcia* sp. (Veneridae).

Remarks. The taxonomy of this poorly known species was discussed at length by Ahyong & Ng (2007b). Rathbun (1909, 1910) argued that specimens identified as "*Pinnotheres parvulus*", recorded by Bürger (1895) from the Philippines, De Man (1887: 105; 1888: 383) from the Mergui Archipelago and Indonesia, and Alcock (1900), presumably from Indian waters, were not conspecific with *Pinnotheres parvulus* Stimpson, 1858, and as such, she proposed a new name for them, *Pinnotheres alcocki*. No types were selected, rendering all of the material referred by these authors to *P. parvulus* as syntypes of *P. alcocki* (see Schmitt et al., 1973). Ahyong & Ng (2007b) studied one of Bürger's (1895) "*P. parvulus*" specimens reported from Burias, Philippines, which they designated as the lectotype of *Pinnotheres alcocki* Rathbun, 1909. They redescribed and figured the specimen and transferred the species to *Arcotheres*. Ahyong & Ng (2007b) argued that the syntype specimens from Mergui (De Man, 1887) were not conspecific with the Philippine lectotype, but were uncertain of their correct identity. As a result of the present restudy of Mergui material, these records and those of Alcock (1900) and Gordon (1936) are clarified here as *Magnotheres globosus*. De Man's (1888) records of "*P. parvulus*" from Indonesia remain to be verified.

The present female specimen (ZRC 2016.272) of *A. alcocki* agrees very well with the lectotype in all key aspects. Ahyong & Ng (2007b: 194) indicated that *A. alcocki* s. str. was morphologically very close to *A. sinensis* (Shen, 1932) from Chinese waters, and that the two may be synonyms. Detailed comparison of these two species is being undertaken as part of a separate study. We note, however, that several reports of *Arcotheres sinensis* (as *Pinnotheres*) from Tamil Nadu, India (Sethuramalingam & Khan, 1991: pl. 24 fig. i; Ravichandran & Kannupandi, 2007: 334; Kannappan et al., 2012: 45; see also Trivedi et al., 2018b: 61), cannot presently be determined as the original descriptions and/or figures are not sufficiently informative. Sethuramalingam & Khan (1991) and Ravichandran & Kannupandi (2007) did not record hosts, whereas Kannappan et al.'s (2012) specimens came from a gastropod (*Turritella attenuata* Reeve, 1849, family Turritellidae Lovén, 1847), and from his figure (Kannappan et al., 2012: fig. 2) their species appears to be something quite different from *A. alcocki* or *A. sinensis*.

The precise provenance of the present specimen (ZRC 2016.272) is not known, as *Marcia* clams, although occurring in Singapore, are also imported as seafood; most imported stocks come from Peninsular Malaysia or Indonesia.

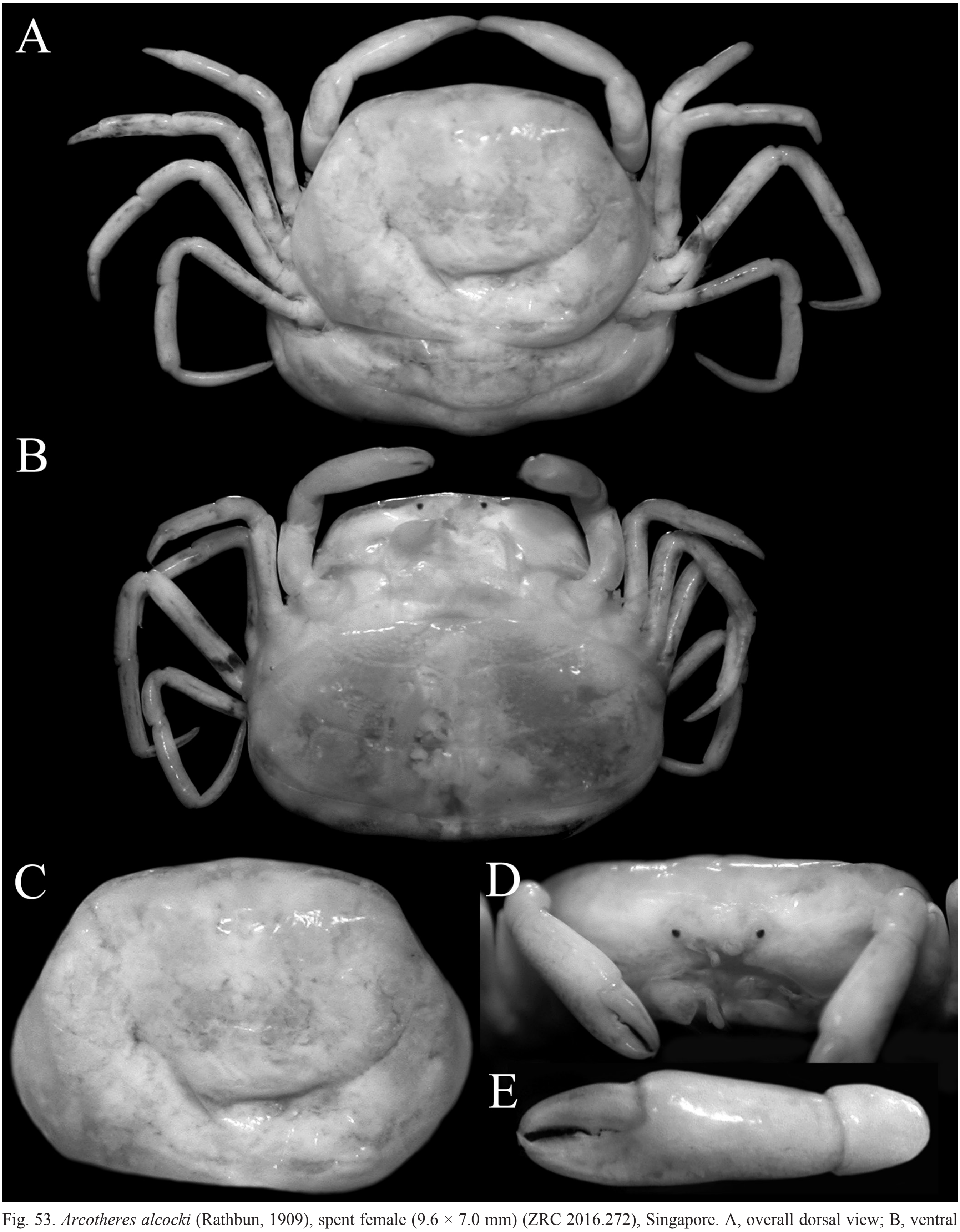

Fig. 53. *Arcotheres alcocki* (Rathbun, 1909), spent female (9.6 × 7.0 mm) (ZRC 2016.272), Singapore. A, overall dorsal view; B, ventral view of cephalothorax; C, dorsal view of carapace; D, frontal view of cephalothorax; E, outer view of left chela.

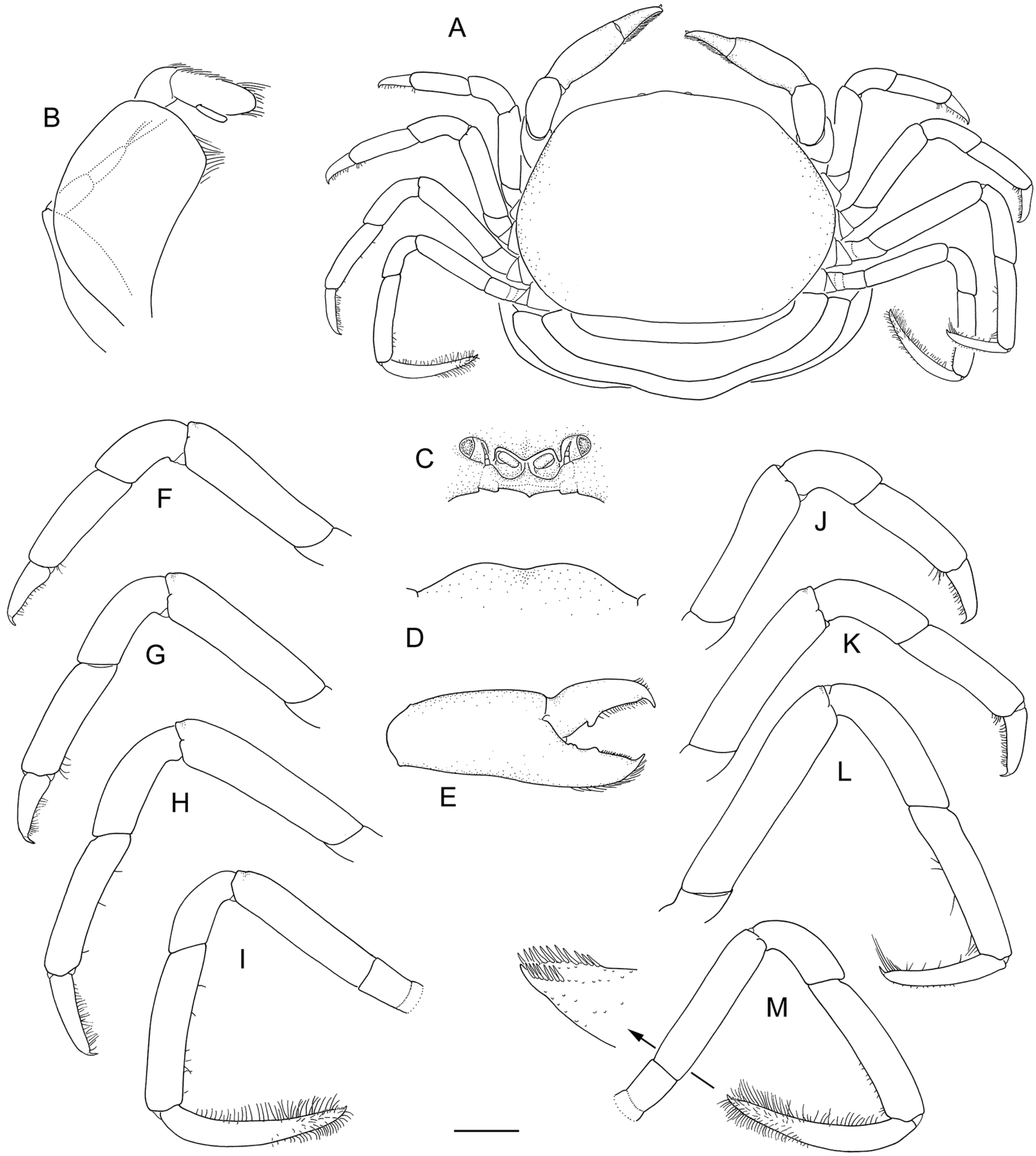

Fig. 54. *Arcotheres alcocki* (Rathbun, 1909), spent female (9.6 × 7.0 mm) (ZRC 2016.272), Singapore. A, overall dorsal view; B, right MXP3; C, front view of cephalothorax; D, anterior thoracic sternum; E, right chela; F–I, left P2–P5; J–M, right P2–P5. Scale = A, 2.0 mm; B, 0.5 mm; C–M, 1.0 mm.

Distribution. South China Sea, from the Philippines and probably to the vicinity of Peninsular Malaysia or Indonesia.

***Arcotheres obesus* (Dana, 1852)**
(Figs. 55, 56)

Pinnothera obesa Dana, 1852: 380 [type locality: Kumi Village, Viti Levu, Fiji, by neotype designation (Komai et al., 2020)]; 1855: pl. 24 fig. 3; Woodward, 1886: 177 (list).

Pinnotheres obesus — Silas & Alagarswami, 1967: 1204 (list); Serène, 1968: 94; Schmitt et al., 1973: 60 (part) (list and discussion).

Pinnotheres obesus — Ng et al., 2008: 250 (list).

Arcotheres obesus — Komai et al., 2020: 223, figs. 1–6; De Gier & Becker, 2020: tab. 1.

Type material. Neotype: female (5.5 × 4.4 mm) (CBM-ZC 15945), Kumi Village, Viti Levu, Fiji, intertidal, associated

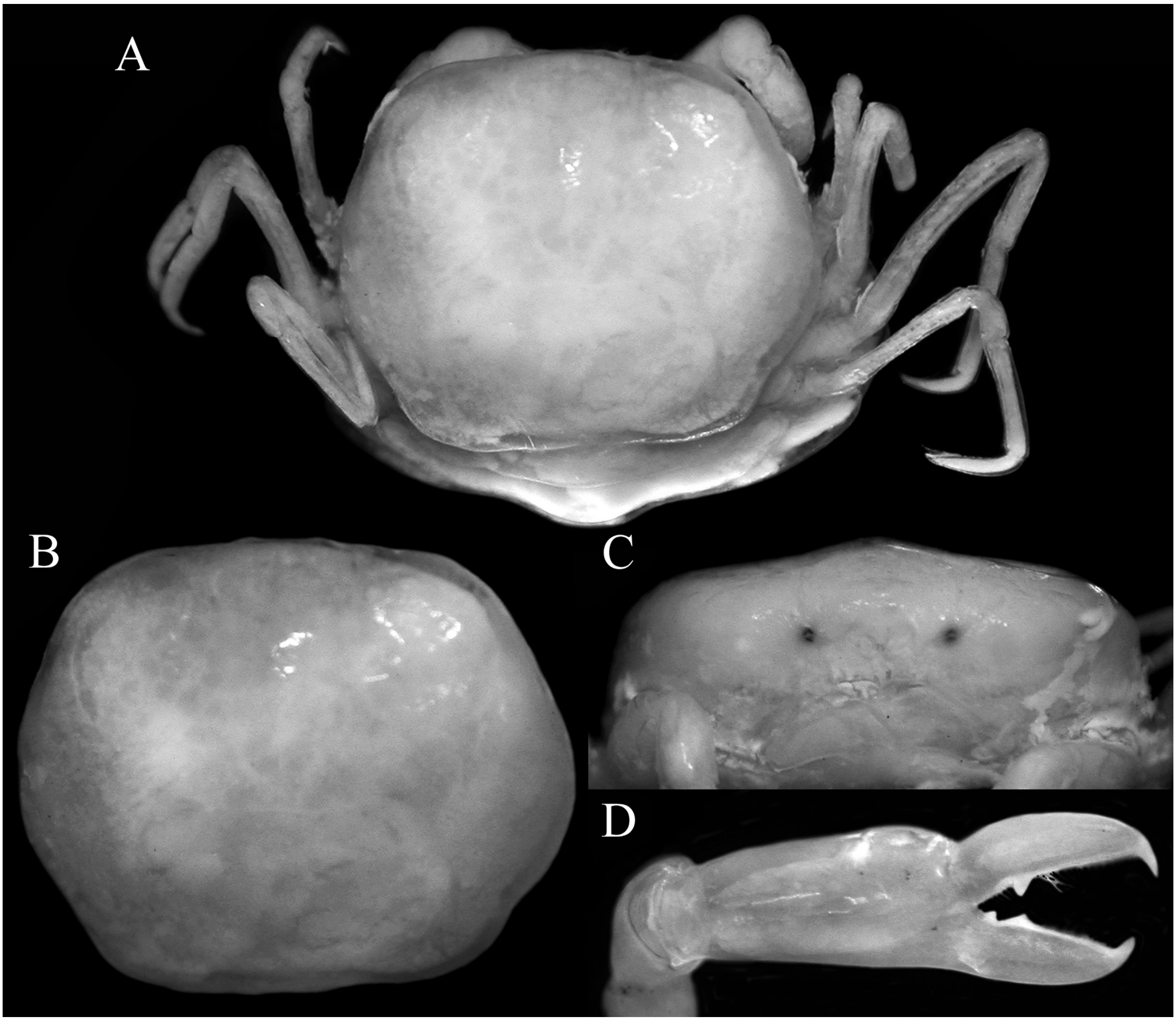

Fig. 55. *Arcotheres obesus* (Dana, 1852), female (8.9 × 6.9 mm) (ZRC 2019.1876), Fiji. A, overall dorsal view; B, dorsal view of carapace; C, frontal view of cephalothorax; D, outer view of right chela.

with *Gafrarium pectinatum*, coll. K. Kawai, 22 February 2019.

Other material examined. Fiji: 3 ovigerous females (6.7 × 5.4 mm, 6.6 × 5.6 mm, 5.9 × 4.6 mm) (CBM-ZC 15949–15951), same data as neotype, in *G. tumidum*; 3 females (5.3 × 4.2–6.1 × 5.1 mm), 1 ovigerous female (5.4 × 4.8 mm), 2 males (4.2 × 3.6 mm, one damaged) (CBM-ZC 15946), Kumi Village, Viti Levu, intertidal, in *Gafrarium pectinatum*, coll. K. Kawai, 16 August 2010; 2 females (5.3 × 4.0 mm, 9.2 × 7.2 mm) (CBM-ZC 15947, 15948), 2 soft females (8.8 × 6.2 mm, 8.9 × 6.9 mm), 2 males (1.9 × 1.7 mm, 2.6 × 2.2 mm) (ZRC 2019.1876), Waiganake, Viti Levu, intertidal, associated with *Gafrarium pectinatum* (Linnaeus, 1758), coll. K. Kawai, 22 August 2011; 1 ovigerous female (6.2 × 4.9 mm) (ZRC 2020.6), associated with *Gafrarium pectinatum*, Telau, Viti Levu, coll. K. Kawai, 22 February 2019. **Peninsular Malaysia:** 2 soft females (7.2 × 5.4 mm, 5.7 × 4.7 mm) (ZRC 2000.2281), Pulau Tinggi, Johor, in *Gafrarium dispar*, 7 May 1969.

Description. Carapace and pereopods very poorly chitinised. Female: Carapace subovate, wider than long; dorsal and lateral surfaces smooth, glabrous; appearing gently domed in frontal view; front not clearly projecting anteriorly beyond orbits, margin gently sinuous to gently convex, appearing almost contiguous with convex anterolateral margin, forming rounded angle with posterolateral margin (Komai et al., 2020: fig. 55A–C). Eyes small, not visible in dorsal view in adults; filling orbit (Komai et al., 2020: fig. 55A–C). Epistome with median part triangular, lateral margins concave (Komai et al., 2020: fig. 3B).

MXP3 outer surface with scattered short setae; ischiomerus completely fused, subrhomboidal, inner margin rounded at widest point; carpus short; propodus about 3 times as long as high, spatulate, distinctly longer than carpus, tip subtruncate; dactylus slender, inserted at midlength of propodus, tip not reaching propodal apex; exopod relatively slender, about two-thirds length of ischiomerus, flagellum 2-segmented (Fig. 56K, L).

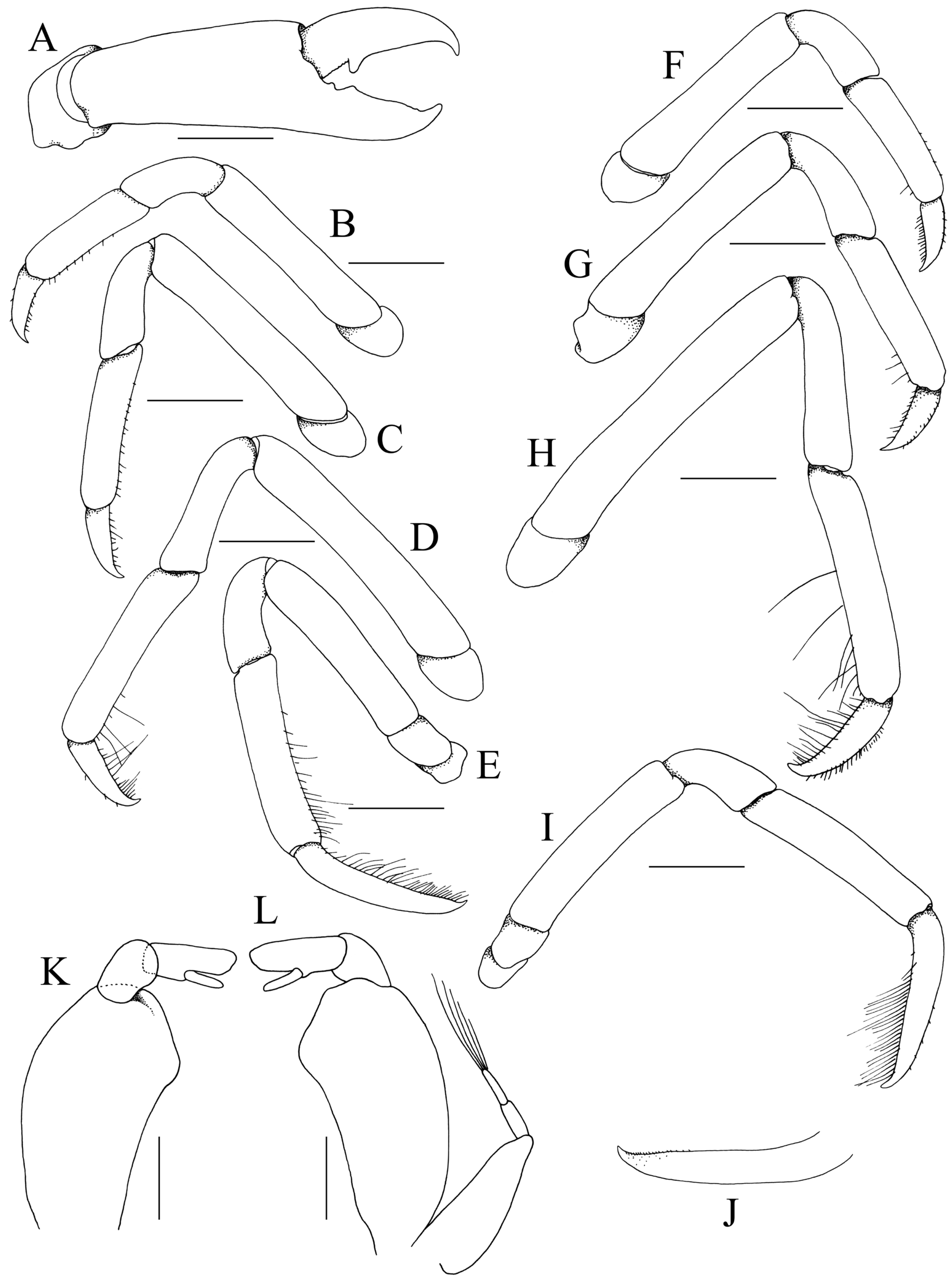

Fig. 56. *Arcotheres obesus* (Dana, 1852), female (8.3 × 5.9 mm) (ZRC 2019.1876), Fiji. A, outer view of right chela; B–E, left P2–P5, respectively; F–I, right P2–P5, respectively; J, right P5 dactylus (long setae omitted); K, inner view of left MXP3; L, outer view of left MXP3. Scales = A–I, 1.0 mm; J–L, 0.5 mm.

Chela not prominently elongate, dactylus about two-thirds palm length; palm relatively slender, proximally narrower than distally; outer surfaces of palm, fingers (except for distal part) almost glabrous, with only scattered short setae; ventral margin of palm gently concave; dactylus occlusal margin with distinct subproximal tooth; pollex occlusal margin with 1 low proximal tooth, 1 sharp submedian tooth, and denticles; tips of fingers sharp, hooked (Figs. 55D, 56A).

P2–P5 dorsally, ventrally unarmed; outer surface covered with scattered, very short setae or glabrous; ventral margins of propodus and dactylus more setose; merus long, slender, relative lengths of meri P4>P3>P2>P5; right (sometimes left) P4 distinctly longer; P2 and P3 dactyli relatively short, subequal, tip slightly hooked, half or slightly longer than half propodus length; P4 dactylus about half propodus length, longer than P2 and P3 dactyli, shorter than P5 dactylus; P5 merus 4.9–5.0 times longer than wide; P5 dactylus longest, margins lined with short and long setae, denser on ventral margin, distoflexor margin without rows of graded spinules, at most with scattered, very low, minute spinules or acute granules of similar size (Fig. 56B–J).

Pleon extending to buccal region, covering bases of P2–P5; telson gently recessed into concave distal margin of somite 6 (Komai et al., 2020: fig. 3D).

Male: Carapace almost circular, as wide as long; dorsal surface almost smooth, not prominently inflated, lateral surfaces with setae; front projecting anteriorly, margin gently sinuous (Komai et al., 2020: fig. 5A). Eyes distinctly visible in dorsal view (Komai et al., 2020: fig. 5A). MXP3 as in female (Komai et al., 2020: fig. 5B). Anterior thoracic sternum wide, sternites 1, 2 fused, partially sunken into buccal cavity; suture between sternites 2 and 3 shallow; sternites 3, 4 completely fused, separated only by shallow grooves (Komai et al., 2020: fig. 10B). Chela relatively stout, shorter than in female (Komai et al., 2020: fig. 6A, B). P2–P5 dorsally, ventrally unarmed; outer surface covered with short setae; P3 and P4 carpus and propodus without long natatory setae; left and right meri equal, relative lengths of meri P4>P3>P2>P5; dactyli of P2–P4 progressively longer; left P4 dactylus longer, more slender than right side; P4 and P5 dactylus longer to that of P3, covered with short setae (Komai et al., 2020: figs. 5A, 6E–N). Pleon slender, triangular, widest at somite 3, lateral margins of somite 4 gently concave; somite 6 trapezoidal or subquadrate; telson semicircular, slightly wider than long (Komai et al., 2020: fig. 5D). G1 relatively stout, arcuate, curved outwards, distal part subtruncate, without elongate tip (Komai et al., 2020: fig. 5E, F). G2 short, with spatuliform tip; exopod about half endopod length (Komai et al., 2020: fig. 5G).

Variation. This is the most poorly chitinised and calcified *Arcotheres* treated here, with the carapace appearing almost membranaceous, even in the relatively fresh specimens recently collected from Fiji (Komai et al., 2020). Nevertheless, the carapace shape is relatively invariate, being always transversely ovate (see Komai et al., 2020).

Colour. Not known.

Host. Known for certain from *Gafrarium pectinatum* (Linnaeus, 1758) and *G. dispar* (Holten, 1802) (Veneridae Rafinesque, 1815).

Remarks. The identity of *Pinnotheres obesus* was long uncertain until Komai et al. (2020) redescribed and transferred it to *Arcotheres* based on a neotype from Fiji (type locality). *Arcotheres obesus* appears to be an obligate commensal of clams of the genus *Gafrarium*. The specimens from Peninsular Malaysia, while soft and in poor condition, agree very well with the material from Fiji. A male specimen will need to be obtained to confirm the identity of these Malaysian specimens, especially considering the geographical distance separating the two locations.

Distribution. Western Pacific from Fiji and Peninsular Malaysia.

***Arcotheres placunicola* Ng, 2018a**
(Figs. 57–62)

Pinnotheres similis — Tesch, 1918: 254 (list); Gordon, 1936: 172, fig. 3 (Singapore); Silas & Alagarswami, 1967: 1210 (list) (not *Pinnotheres similis* Bürger, 1895).
Arcotheres palaensis — Pohle & Marques, 1998: 231 (part) (not *Pinnotheres palaensis* Bürger, 1895).
Arcotheres placunicola Ng, 2018a: 475, figs. 1–6 [type locality: Changi, Singapore]; De Gier & Becker, 2020: tab. 1.

Type material. Holotype: ovigerous female (11.2 × 8.6 mm) (ZRC 2017.1009), off Changi beach, next to Carpark 7, near ferry terminal, 1.374223°N, 104.006827°E, coll. S. K. Tan et al., 7 June 2016. Paratypes: 5 males (5.6 × 4.7 mm, 4.7 × 4.1 mm, 4.0 × 3.7 mm, 3.9 × 3.6 mm, 3.6 × 3.4 mm), 4 ovigerous females (10.4 × 8.3 mm, 8.7 × 7.5 mm, 7.5 × 6.1 mm, 7.0 × 5.5 mm), 1 female (8.8 × 6.9 mm), 3 females (with rhizocephalans) (8.6 × 6.3 mm, 8.6 × 7.1 mm, 9.0 × 6.9 mm), 2 juvenile females (3.6 × 2.9 mm, 6.2 × 5.1 mm) (ZRC 2017.1010), same data as holotype; 14 males (largest 5.1 × 4.4 mm, smallest 2.4 × 2.3 mm), 2 males (with rhizocephalans) (5.7 × 4.7 mm, 5.5 × 5.0 mm), 16 ovigerous females (largest 10 × 8.7 mm, smallest 7.7 × 6.3 mm), 1 ovigerous female (10.1 × 8.0 mm), 10 non-ovigerous females (largest 10.3 × 7.8 mm, smallest 5.4 × 4.5 mm), 2 females (with rhizocephalan) (6.3 × 4.9 mm, 7.8 × 5.8 mm), 1 juvenile female (3.8 × 3.7 mm) (ZRC 2017.1012), off Changi beach, next to Carpark 7, near ferry terminal, 1.374223°N, 104.006827°E, coll. S. K. Tan et al., 8 June 2016; 1 male (4.2 × 3.8 mm), 2 ovigerous females (7.2 × 6.1 mm, 7.5 × 6.2 mm) (ZRC 2012.432), off Changi beach, next to Carpark 7, near ferry terminal, 1.374223°N, 104.006827°E, coll. P. K. L. Ng et al., 5 July 2012; 4 ovigerous females (largest 9.1 × 7.4 mm, smallest 6.5 × 5.4 mm), 3 non-ovigerous females (largest 8.9 × 6.9 mm, smallest 8.1 × 6.7 mm), 2 females (with rhizocephalan) (8.2 × 7.3 mm, 11.2 × 9.1 mm) (ZRC 2017.1013), off Changi beach, next to Carpark 7, near ferry terminal, 1.374223°N, 104.006827°E, coll. P. K. L. Ng & P. Y. C. Ng, June 2016; 2 males (2.2 × 2.2 mm, 2.4 × 2.4 mm) (ZRC 2017.1014), Tanah Merah Ferry Terminal Beach,

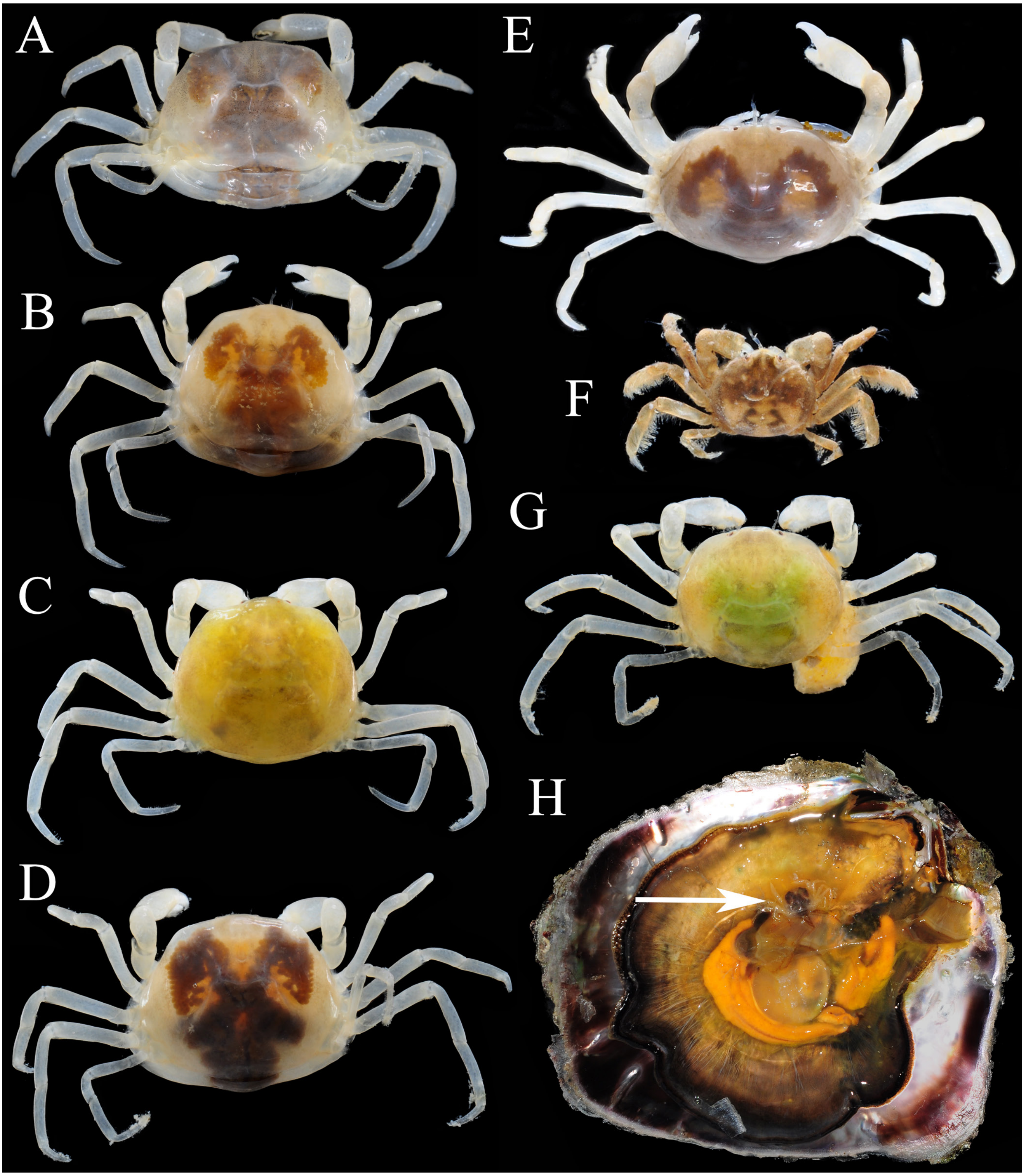

Fig. 57. *Arcotheres placunicola* Ng, 2018, colour in life, after Ng (2018a: figs. 5, 6). A, paratype female (size not known) (ZRC 2017.1010); B, paratype ovigerous female (8.0 × 6.1 mm) (ZRC 2017.1015); C, paratype non-ovigerous female with rhizocephalan (9.0 × 7.4 mm) (ZRC 2017.1015); D, paratype ovigerous female (7.3 × 5.9 mm) (ZRC 2017.1015); E, paratype female (8.8 × 6.9 mm) (ZRC 2017.1010), Changi, Singapore; F, paratype male (4.7 × 4.1 mm) (ZRC 2017.1010); G, paratype male with rhizocephalan (5.6 × 5.1 mm) (ZRC 2017.1015); H, paratype ovigerous female (7.3 × 5.9 mm) (ZRC 2017.1015), in situ on *Placuna* (crab indicated by arrow). All specimens from Singapore.

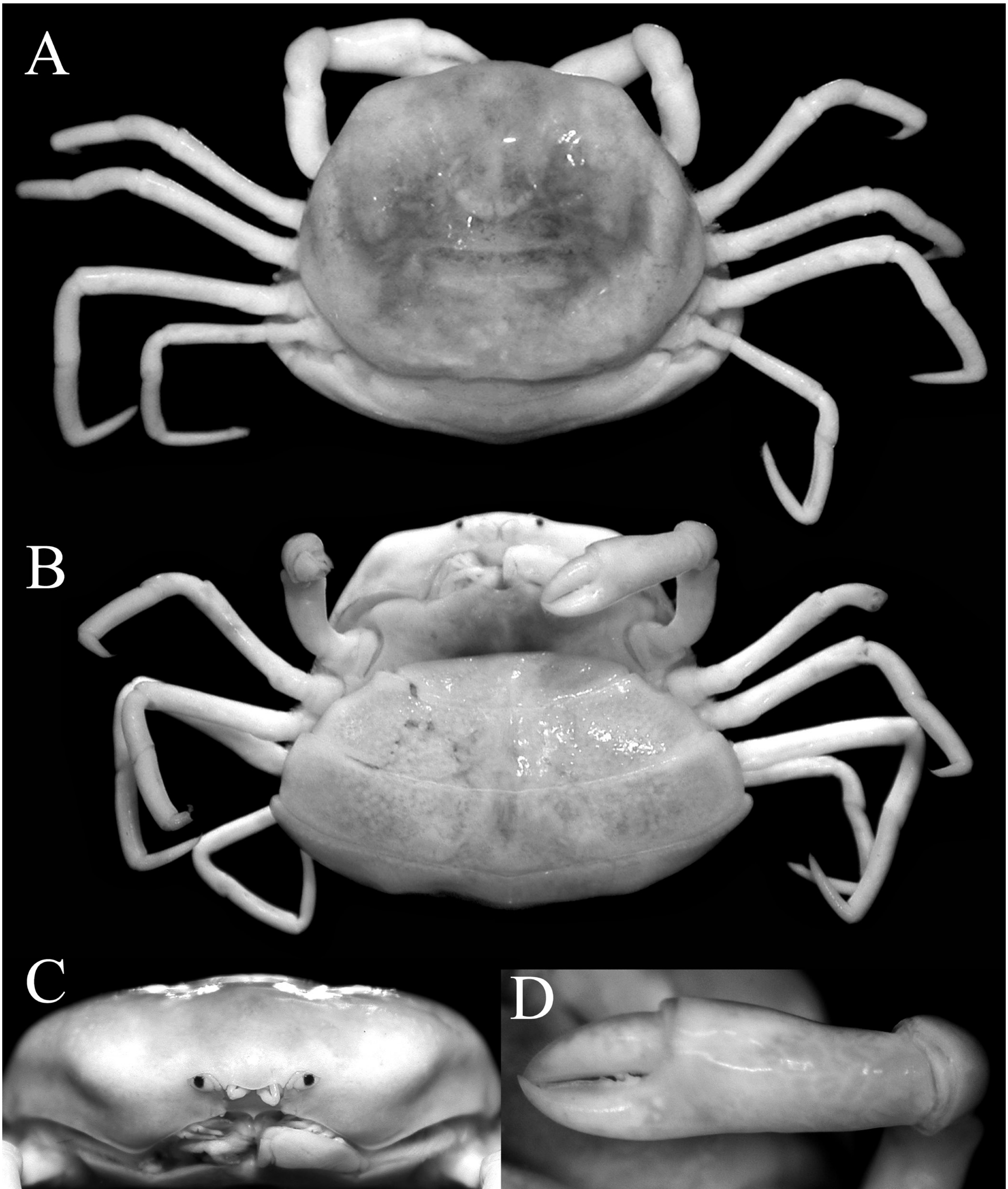

Fig. 58. *Arcotheres placunicola* Ng, 2018, holotype ovigerous female (11.2 × 8.6 mm) (ZRC 2017.1009), Changi, Singapore; after Ng (2018a: fig. 1). A, overall dorsal view; B, ventral view of cephalothorax; C, frontal view of cephalothorax; D, outer view of left chela.

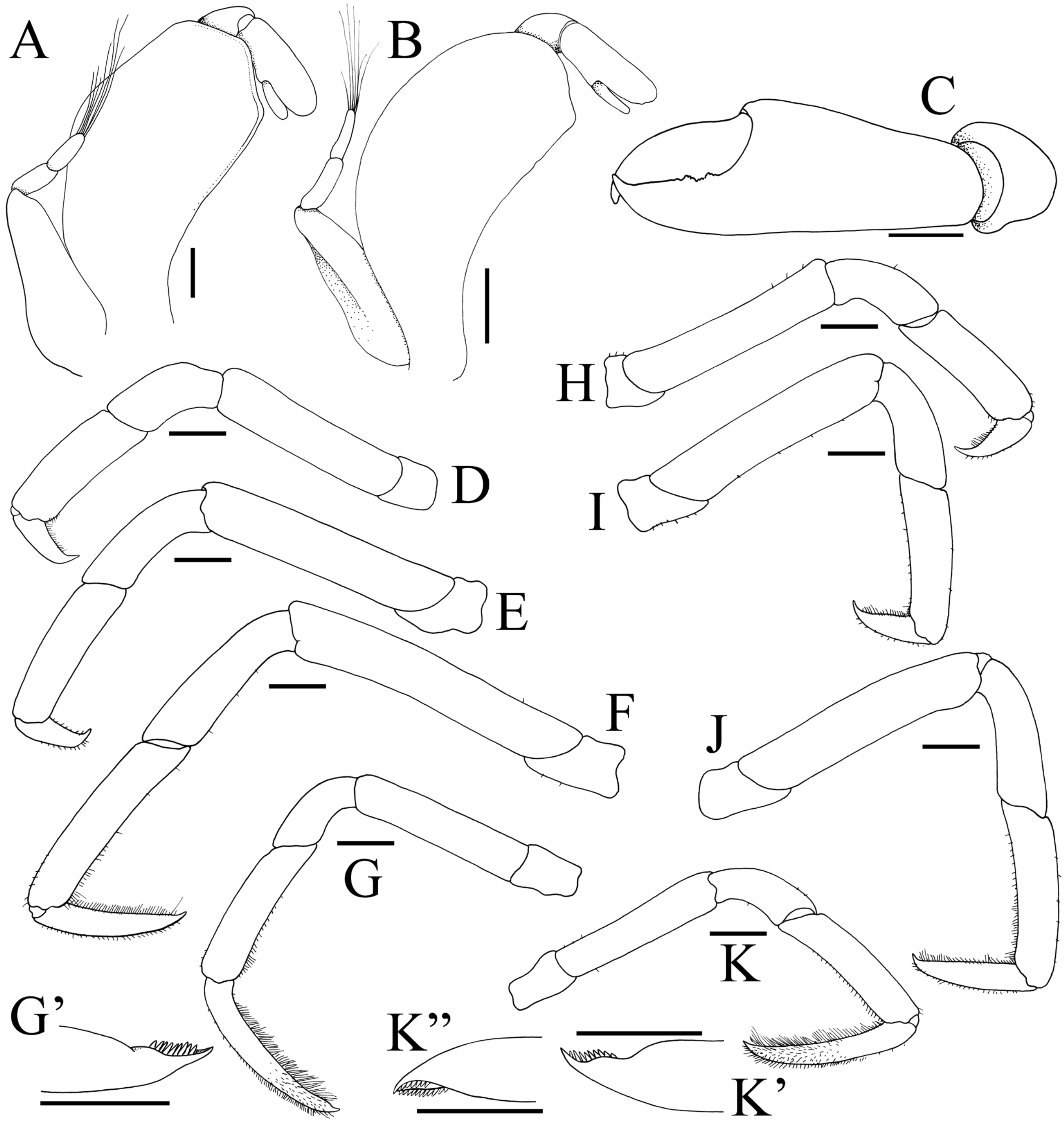

Fig. 59. *Arcotheres placunicola* Ng, 2018, after Ng (2018a: fig. 3). A, C, E–K, holotype ovigerous female (11.2 × 8.6 mm) (ZRC 2017.1009), Changi, Singapore; B, D, paratype ovigerous female (10.1 × 8.0 mm) (ZRC 2017.1012), Changi, Singapore. A, B, outer view of right MXP3; C, left chela and carpus; D–G, left P2–P5, respectively; G', distal part of dactylus of left P5 showing stiff subdistal spinules (dorsal view, soft setae omitted); H–K, right P2–P5, respectively; K', distal part of dactylus of right P5 showing stiff subdistal spinules (ventral view, soft setae omitted); K'', distal part of dactylus of left P5 showing stiff subdistal spinules (dorsal view, soft setae omitted). Scales = A, B, G', K', K'', 0.5 mm; C–K, 1.0 mm.

near Changi Point, coll. S. K. Tan et al., 17 November 2016; 1 male (with rhizocephalan) (5.6 × 5.1 mm), 3 ovigerous females (7.3 × 5.9 mm, 8.0 × 6.1 mm, 9.5 × 7.2 mm), 1 non-ovigerous female (with rhizocephalan) (9.0 × 7.4 mm) (ZRC 2017.1015), off Changi beach, next to Carpark 7, near ferry terminal, 1.374223°N, 104.006827°E, coll. P. K. L. Ng & P. Y. C. Ng, 31 March 2017; 1 male (with *Sacculina*) (4.8 × 4.5 mm) (ZRC 2017.1016), off Changi beach, adjacent to National Service Recreational Country Club, coll. H. H. Tan et al., 26 May 2017; 4 females, 1 juvenile female (ZRC 2017.1011), 1 male, 2 ovigerous females (AM P105907), off Changi beach, next to Carpark 7, near ferry terminal, 1.374223°N, 104.006827°E, coll. S. K. Tan et al., 5 July 2017; 1 male (with rhizocephalan), 3 females (AM P105908), intertidal area, off Changi beach, next to Carpark 7, near ferry terminal, 1.374223°N, 104.006827°E, coll. S. K. Tan et

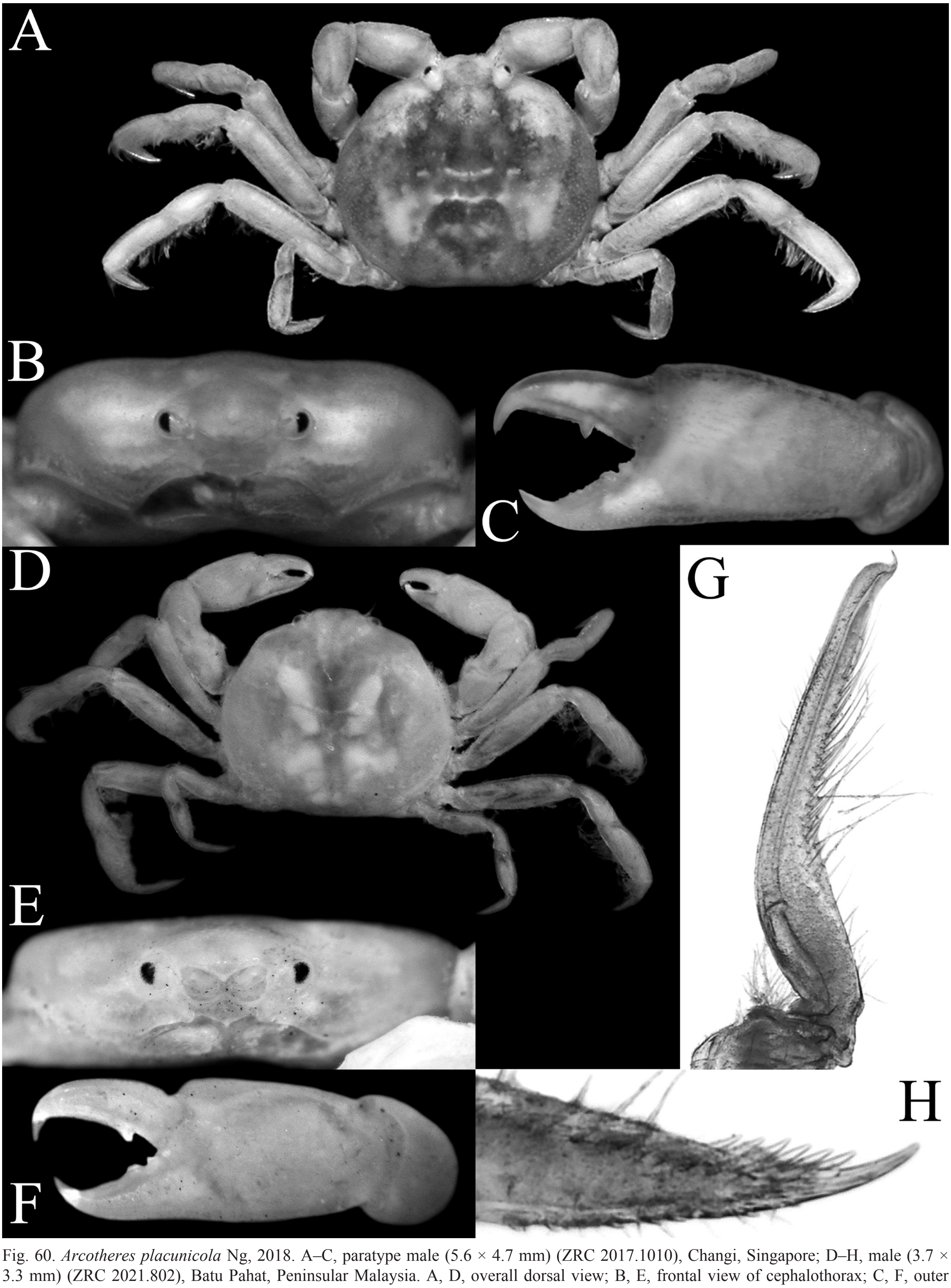

Fig. 60. *Arcotheres placunicola* Ng, 2018. A–C, paratype male (5.6 × 4.7 mm) (ZRC 2017.1010), Changi, Singapore; D–H, male (3.7 × 3.3 mm) (ZRC 2021.802), Batu Pahat, Peninsular Malaysia. A, D, overall dorsal view; B, E, frontal view of cephalothorax; C, F, outer view of left chela; G, left G1; H, distal part of P5 (ventral view). B after Ng (2018a: fig. 2B).

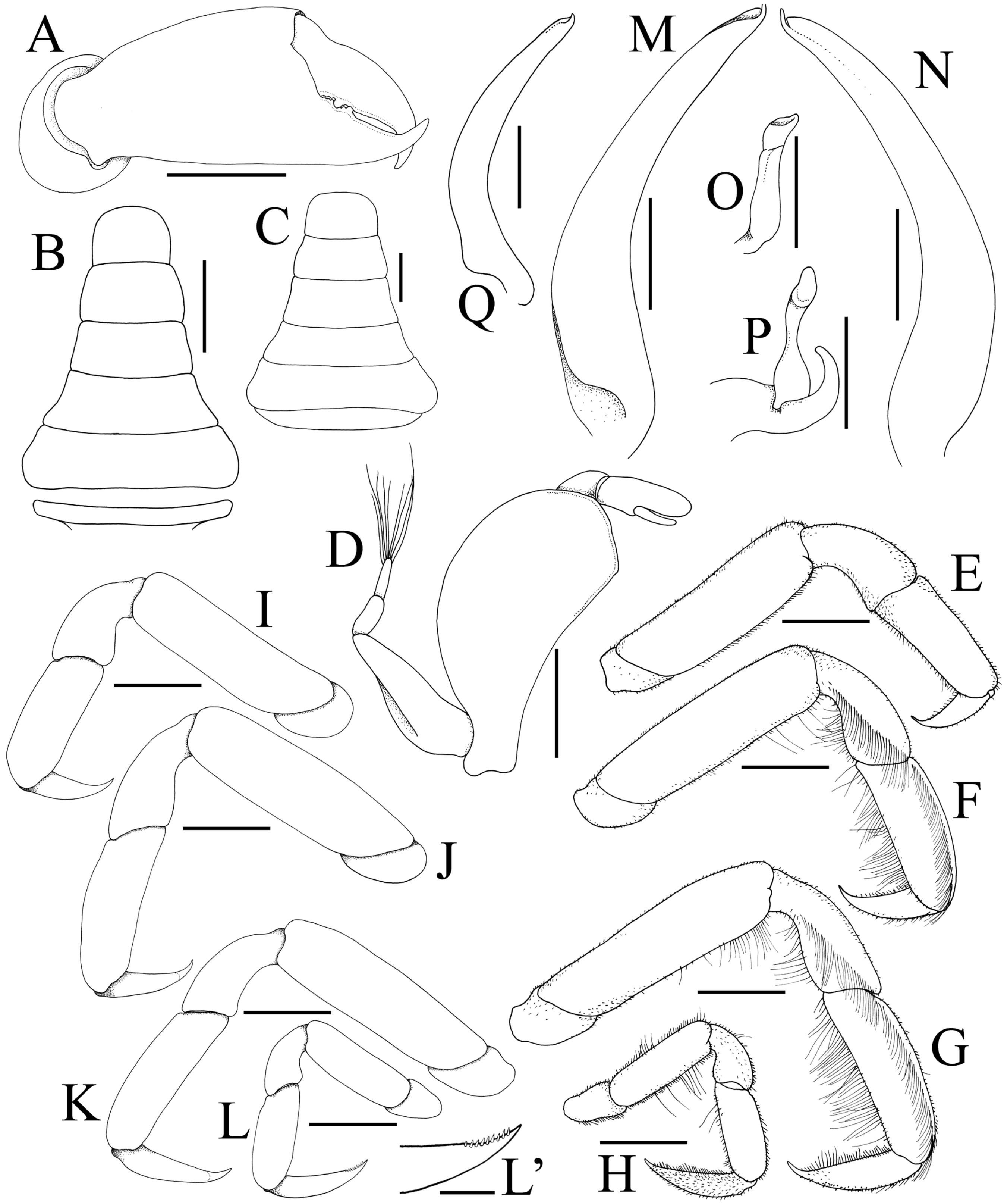

Fig. 61. *Arcotheres placunicola* Ng, 2018, after Ng (2018a: fig. 4). A, B, D–P, paratype male (5.6 × 4.7 mm) (ZRC 2017.1010); C, Q, paratype young male (2.4 × 2.4 mm) (ZRC 2017.1014). Both specimens from Changi, Singapore. A, right chela and carpus (setae omitted); B, C, male pleon; D, right MXP3 (setae omitted); E–H, right P2–P5, respectively; I–L, left P2–P5, respectively (setae omitted); L', distal part of P5 dactylus (dorsal view, soft setae omitted); M, Q, left G1 (ventral view, setae omitted); N, left G1 (dorsal view, setae omitted); O, left G2 (setae omitted); P, right G2 (mesial view showing exopod, setae omitted). Scales = A, B, E–L, 1.0 mm; D, M–P, 0.5 mm; C, L', Q, 0.25 mm.

al., 26 June 2017; 1 female (ZRC 2017.1265), Telok Paku, beach, in "*Placuna sella*", coll. 8 April 1965. All locations in Singapore.

Other material examined. Singapore: 3 males, 6 females (ZRC 2019.1113), probably in *Placuna ephippium*, intertidal area, off Changi beach, next to Carpark 7, near ferry terminal, 1.374223°N, 104.006827°E, Singapore, coll. P. K. L. Ng et al., 3 August 2012; 1 female (ZRC 2019.1021), intertidal area, off Changi beach, next to Carpark 6, Singapore, coll. H. H. Tan et al., 24 December 2018; 1 female (ZRC 2019.1037), intertidal area, off Changi beach, next to Carpark 7, near ferry terminal, 1.374223°N, 104.006827°E, Singapore, coll. H. H. Tan et al., 4 July 2019; 1 female (11.6 × 8.6 mm), 1 juvenile female (ZRC 2021.80), inside *Placuna ephippium*, Changi Bay, ex Red Cliff Shoal area, Singapore, coll. S. K. Tan et al., 13 January 2021. **Peninsular Malaysia:** 1 male (3.7 × 3.3 mm) (ZRC 2021.802, ex part ZRC 2000.2613), Batu Pahat, Johor, supposedly from *Tegillarca granosa*, mangroves, coll. H. K. Tan, 16 August 1983; 1 male, 3 females, 1 juvenile female (ZRC 2009.905), supposedly from *Tegillarca*, Pahang, coll. students, Universiti Teknologi Malaysia, 2006.

Description. Carapace and pereopods well chitinised. Female: Carapace subcircular to subhexagonal, distinctly wider than long; dorsal and lateral surfaces smooth, glabrous; front usually projecting anteriorly beyond orbits, entire, margin slightly convex; anterior quarter of anterolateral margin gently sloping posteriorly, forming angle with rest of convex margin (Fig. 58A). Eyes small, not visible in dorsal view; mobile, completely filling orbit (Fig. 58A–C). Epistome with median part triangular, lateral margins gently concave (Fig. 58C).

MXP3 outer surface with scattered short setae; ischiomerus completely fused, subrhomboidal, inner margin angular at widest point; carpus short; propodus about 3 times as long as high, subspatulate, distinctly longer than carpus; dactylus slender, inserted at midlength of propodus, tip not reaching propodal apex; exopod relatively slender, about one-third length of ischiomerus, flagellum 2-segmented (Fig. 59A, B).

Chela slender, dactylus almost two-thirds palm length; palm slender, proximally narrower than distally; outer surface of palm, fingers (except for distal part) almost glabrous, with only scattered short setae; dactylus occlusal margin with large subproximal tooth; pollex occlusal margin with 1 low proximal tooth, 1 submedian tooth; tips of fingers sharp, hooked (Figs. 58D, 59C).

P2–P5 dorsally, ventrally unarmed; outer surface covered with scattered, very short setae or glabrous; ventral margins of propodus and dactylus more setose; merus relatively longer, more slender, relative lengths of meri P4>P3>P5>P2; left (sometimes right) P4 distinctly the longer; P2 and P3 dactyli short, subequal, tip gently hooked, half propodus length; P4 dactylus elongate, weakly falciform, three-fourths propodus length, longer than P2 and P3 dactyli, shorter than P5 dactylus; P5 merus 4.3–4.4 times longer than wide; P5 dactylus longest, longer than propodus, distal half covered with short setae, ventral margin of distal part with 2 rows of up to 11 spinules each, lower row usually with few spinules, lower and upper rows with subequal number of spinules (Fig. 50D–K").

Pleon extending to buccal region, covering bases of P2–P5; telson recessed into distal margin of somite 6 (Fig. 58B).

Male: Carapace almost circular, slightly wider than long; dorsal surface covered with scattered short setae or smooth, slightly convex to almost flat; front distinctly projecting anteriorly, margin gently sinuous (Figs. 60A, D, 62A). Eyes distinctly visible in dorsal view (Figs. 60A, D, 62A). MXP3 as in female (Figs. 61D, 62C). Anterior thoracic sternum wide, sternites 1, 2 fused, partially sunken into buccal cavity; suture between sternites 2 and 3 shallow; sternites 3, 4 completely fused, separated only by shallow grooves; sternopleonal cavity reaching to junction between sternites 3 and 4. Chela relatively stouter, shorter than in female, tip of fingers longer (Figs. 60C, F, 61A, 62D). P2–P5 dorsally, ventrally unarmed; outer surface covered with short setae; carpus and propodus with long natatory setae; left and right meri equal, relative lengths of meri P4>P3>P2>P5; dactyli of P2–P4 progressively longer; left (sometimes right) P4 dactylus slightly longer, more slender than right side; P4 and P5 dactyli subequal to that of P3, completely covered with short setae (Figs. 61E–L, 62E–L'); P5 dactylus with 2 rows of up to 11 or 12 distoflexor spinules each (Figs. 60H, 61L). Pleon slender, triangular, widest at somite 3, lateral margins of somite 4 distinctly concave, tapering distally to telson; telson subquadrate-linguiform with convex lateral margins, wider than long (Figs. 61B, C, 62B). G1 relatively stout, arcuate, curved outwards, short extended tip gently curved upwards or straight (Figs. 60G, 61M, N, Q, 62M, N). G2 short, with spatuliform tip; exopod almost as long as endopod (Figs. 61O, P, 62O).

Variation. Several female specimens have the frontal margin weakly projecting, being almost level with the anterolateral margin, making the carapace appear more evenly ovate (Fig. 58A). Significantly, the male pleon changes shape (notably somite 6 and telson) with size, with somite 6 becoming proportionally narrower and the telson less tapering with increasing body size (Figs. 61B, C, 62B). The G1 in *A. placunicola* varies slightly, with the tapering tip generally longer in larger males (Fig. 61M, N) and relatively shorter in some smaller males (Fig. 61Q), but also sometimes long in small specimens (Figs. 60G, 62M, N).

Colour. Rather variable: females pale yellow to orange or dirty white with brown patterns; males more uniform brown to greenish brown (Fig. 57F).

Host. Known with certainty only from *Placuna ephippium* (Philipsson, 1788) (Placunidae Rafinesque, 1815). One lot (ZRC 2009.905) of *A. placunicola* collected in 2006 from Pahang, Malaysia, as part of aquaculture surveys by

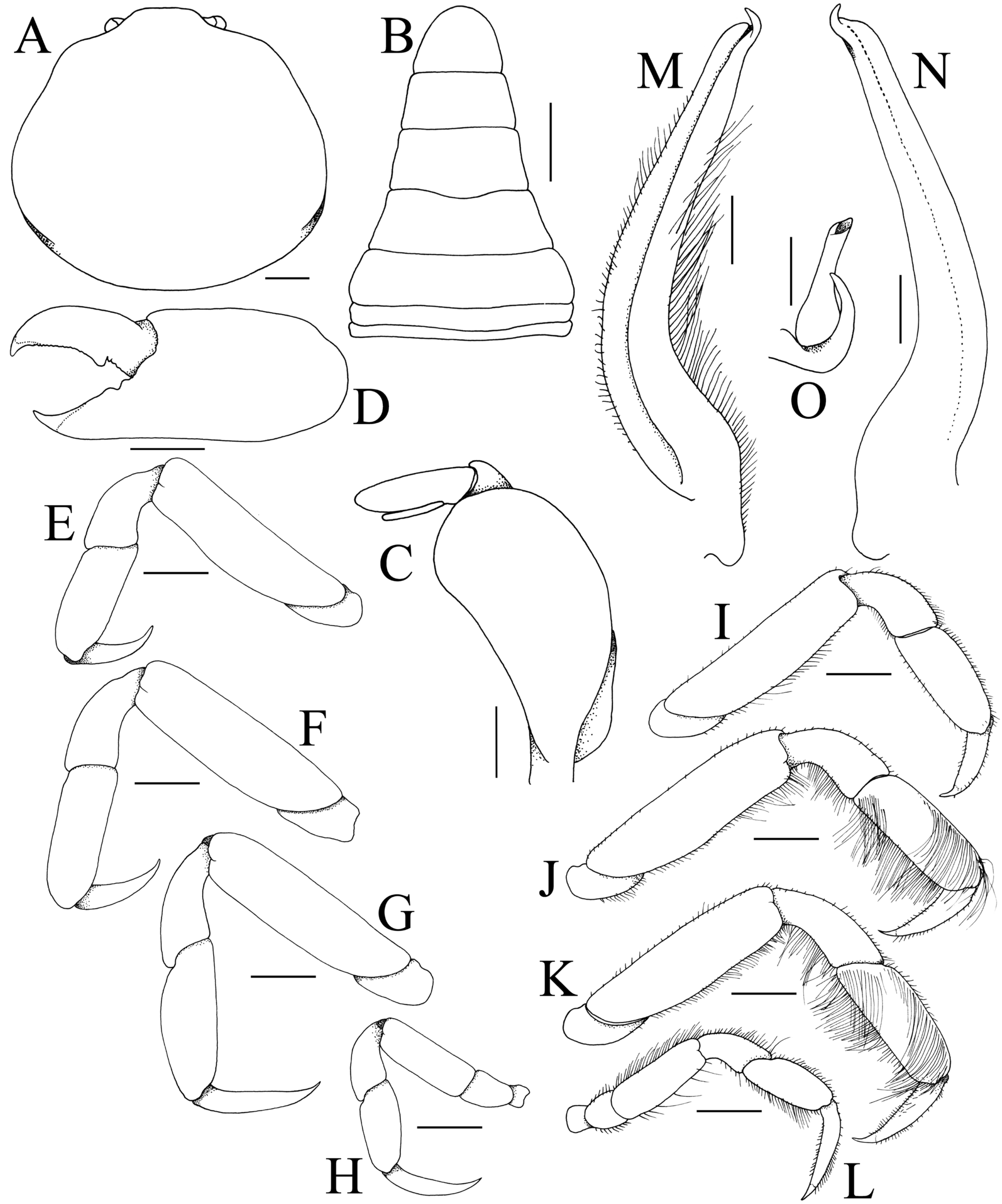

Fig. 62. *Arcotheres placunicola* Ng, 2018, male (3.7 × 3.3 mm) (ZRC 2021.802), Batu Pahat, Peninsular Malaysia. A, dorsal view of carapace; B, pleon (setae omitted); C, outer view of left MXP3 (setae denuded); D, outer view of left chela; E–H, left P2–P5, respectively (setae omitted); I–L, right P2–P5, respectively; M, left G1 (ventral view); N, left G1 (dorsal view, setae omitted); O, left G2. Scales = A, B, D–L, 0.5 mm; C, M–O, 0.2 mm.

students from the Universiti Teknologi Malaysia, were labelled as collected from "*Anadara*". We suspect the host was incorrectly recorded.

Remarks. *Arcotheres placunicola* most closely resembles *A. palaensis* and *A. similis*, with which it has been confused (see Ng, 2018a). *Arcotheres placunicola* and *A. similis* are superficially similar, with similar MXP3 and P5 morphology, so the two species can be easily mistaken if not examined carefully. The female carapaces of the two species are superficially similar but can usually be distinguished, especially with fresh material. In *A. placunicola* (Figs. 57A–D, 58A), the carapace shape is more polygonal, with the anterolateral corners of the carapace bluntly angular, contrasting with the more rounded carapace of *A. similis* (Figs. 27A, C, 28A, C), in which the anterolateral corners are evenly curved. As discussed earlier, carapace shape can change to varying degrees when preserved. That being said, there is some overlap in carapace shape between the two species, so other characters must also be checked to confirm identifications. The female P2 and P3 dactyli also differ in shape, being evenly curved in *A. similis* (Fig. 30A, B, E, F), and tightly curved distally with a more falcate apex in *A. placunicola* (Fig. 59D, E, H, I). While the P5 dactylus of both species possess two rows of distoflexor spinules, in *A. placunicola*, the lower row is shorter and usually has only a few more spinules than the upper row, the two rows often with subequal numbers of more closely packed spinules (Fig. 59G', K', K") (versus absent in *A. exiguus*...

Males of *A. placunicola* and *A. similis* are quite different. Compared to *A. similis*, the carapace of *A. placunicola* is distinctly more transversely ovate with the dorsal surface gently convex to almost flat (Figs. 60A, B, E, 62A) (versus carapace round or longitudinally ovate with the dorsal surface inflated and distinctly convex in *A. similis*; Figs. 31A, B, D, 32A). The G1 of *A. placunicola* and *A. similis* are superficially similar, but that of *A. placunicola* is more evenly curved with the slender apical projection directed oblique to the main axis (Figs. 60G, 61M, N, Q, 62M, N), while in *A. similis*, the median and subdistal parts are almost straight and the apical projection almost in line with the main axis (Figs. 32L–N, 33E–H, J, K). *Arcotheres placunicola* closely resembles *A. palaensis* in the structure of the carapace, P2 and P3 dactyli, MXP3, and G1, but adults can be distinguished by the relatively longer P2–P5 (P5 merus 4.3–4.4 times longer than wide, versus 3.6–4.0 times in *A. palaensis*) and by the P5 dactylus possessing two rows of distoflexor spinules (Fig. 59G', K', K") (versus absent in *A. palaensis*). The adult chela is also usually relatively longer and more slender in *A. placunicola*, with the proximal part more narrow than the distal section (Fig. 59C); it is often proportionately and evenly stouter in *A. palaensis* (Figs. 5D, 6D), although the palm may also be elongated (Fig. 4A, B; Ahyong & Ng, 2007b: fig. 9B). The MXP3 of *A. placunicola* usually has a proportionately shorter dactylus (Fig. 59A, B), but it varies too much in *A. palaensis* (Fig. 13) to reliably distinguish the two species. The G1 of *A. placunicola* and *A. palaensis* are also superficially similar, although that of *A. placunicola* is slightly more curved as well as relatively shorter and stouter (Figs. 60G, 61M, N, Q, 62M, N) (cf. Fig. 22K–M for *A. palaensis*).

Arcotheres exiguus also superficially resembles *A. placunicola*, especially with regards to the general carapace shape and relatively longer P2–P5. Female *A. placunicola*, however, can be reliably distinguished by the P5 dactylus possessing a double row of subdistal spinules on the ventral margin (Fig. 59G', K', K") (versus absent in *A. exiguus*; Fig. 40G); and the chela is often proportionately longer and more slender proximally than distally (Figs. 58D, 59C) (versus short and stout in *A. exiguus*; Fig. 40C). In addition, the frontal margin of *A. placunicola* is relatively wider and curves gently to join the anterolateral margin (Fig. 58A) (versus shorter frontal margin which joins lateral margins at a sharper angle in *A. exiguus*; Fig. 40A).

Distribution. South China Sea from Singapore and Peninsular Malaysia.

Plenotheres, new genus

Type species. *Pinnotheres coarctatus* Bürger, 1895, by present designation.

Diagnosis. Carapace dorsal surface smooth, with distinct, relatively deep, clearly incised gastric grooves. MXP3 dactylus slender, inserted near proximal one-third of ventral margin of propodus, exceeding tip of propodus; propodus conical; inner margin of widest part of ischiomerus prominently angular; proximal part of exopod very wide. Female P4 asymmetrical, with left or right side distinctly longer (merus and propodus); dactyli of P2–P4 relatively short, subequal; P5 dactylus long, weakly falciform, different in structure from those of P2–P4. Male pleon relatively broadly triangular, telson semicircular. G1 very stout, arcuate, with prominent subdistal projection, dorsal fold well developed; G2 exopod half length of endopod.

Etymology. From the Latin 'plenus' for plump and well built, alluding to the size and shape of the type species; in arbitrary combination with a typical ending '-*theres*' for pea crabs, from the genus name *Pinnotheres*. Gender masculine.

Comparative material. *Nepinnotheres corbiculae* (Sakai, 1939), new combination: 1 male (2.1 × 1.8 mm) (KPM-NH 106679), from *Corbicula japonica* (Prime, 1864) (Corbiculidae), Kumamoto Prefecture, Japan, coll. T. Sakai, 1963.

Remarks. *Pinnotheres coarctatus* Bürger, 1895, transferred to *Arcotheres* by Ahyong & Ng (2007b), is unusual in the genus in that the gastric grooves on the female carapace are relatively deep and clearly incised (Figs. 64A, 65), resembling some species of *Fabia* Dana, 1851; the MXP3 propodus is conical and stout with the dactylus digitiform and extending beyond the tip of the propodus (Figs. 66I, 68J–L); and the MXP3 exopod is relatively broader basally (Fig. 66I). In addition, males of *P. coarctatus*, together with *A. exiguus* and *A. rayi*, differ from other species of *Arcotheres* in the G1 having a prominent, triangular subdistal lobe (Fig. 68N–P) (absent in other species of *Arcotheres*), and in the articulation between the P5 ischium and merus being oblique rather than perpendicular to the segment axis (Figs. 67A, 68D, H). As such, a separate genus, *Plenotheres*, new genus, is here established for *A. coarctatus*.

The similarities between the G1 of *A. exiguus*, *A. rayi*, and *Pl. coarctatus*, new combination, are, at present, difficult to interpret; whether they are evidence of close phylogenetic proximity or convergence is unclear. All three species are currently subject of wider phylogenetic studies by us.

In the carapace shape, structure of the MXP3, and general P2–P4 leg proportions, *Plenotheres coarctatus* superficially resembles the ecologically similar species from Japan, *Pinnotheres corbiculae* Sakai, 1939 (Figs. 69–71). The hosts of *Pinnotheres corbiculae* are noteworthy, being freshwater and estuarine clams of the family Corbiculidae Gray, 1847. *Plenotheres coarctatus* is known from mangrove clams of the families Cyrenidae Gray, 1840, and Glauconomidae Gray, 1853, and all three bivalve families belong to the Cyrenoidea Gray, 1840, with most of the species inhabiting brackish or freshwater habitats.

Pinnotheres corbiculae was first referred to "*Pinnotheres pholadis*" by Urita (1926: 18), but Sakai (1939: 591, text-fig. 77a, b) described it as a new species from two female specimens (one measured, 5.5 × 4.5 mm) supposedly collected from Nagasaki from *Corbicula japonica* (Prime, 1864) (Corbiculidae), figuring only part of the MXP3 and chela (Fig. 69B, C). Sakai (1976: 572, pl. 200 fig. 4) figured the overall animal (Fig. 69A), corrected the type locality to "Sendai-gawa, Kagoshima", and also recorded additional specimens: five males and seven females from the same host, from Kikuchi-gawa in Kumamoto (see also Silas & Alagarswami, 1967: 1197, 1224; Schmitt et al., 1973: 42; Ng et al., 2008: 250). The whereabouts of the type material is uncertain; Muraoka (1998: 48) records one specimen from Kumamoto in the Kanagawa Museum, but this specimen, collected in 1963, is not a type. This specimen is examined and figured here. The whereabouts of the types is not known.

Sakai's (1939, 1976) description of *P. corbiculae* is relatively brief, but nevertheless useful to quote here as it is the only diagnosis of the species: "The carapace is broad and roundish, the lateral borders are subparallel but the shoulders are weakly angular and the posterior border slightly convex. The front is moderately produced, and the eyes may be observed in dorsal aspect. The external maxilliped has the dactylus slender and much exceeding the tip of propodus (in *tsingtaoensis*, this segment is distally broadened). The immovable finger has four or five denticles near the base, the movable finger has a stout tooth near the base and its apex is strongly curved inwards. The anterior three pairs of ambulatory legs are subequal in length, the last pair conspicuously smaller. The anterior and posterior borders of all pairs are fringed with longish hairs but the carpus is not crossed by an oblique row of hairs contrary to *P. pholadis*, which is also the nearest kin of this species. I could not examine the male specimen, but its seventh segment seems to be triangular according to Urita, who referred this species erroneously to *P. pholadis*" (Sakai, 1939: 591).

The only overall habitus figure of *P. corbiculae*, that of Sakai (1976: pl. 200 fig. 4) (present Fig. 69A), is rather schematic and does not clearly show the structure of the ambulatory dactyli, but the general appearance agrees well with *Pl. coarctatus*. The only figure of the MXP3 by Sakai (1939: fig. 77b) does not show the exopod (Fig. 69B).

The male specimen of *Pinnotheres corbiculae* examined (Figs. 70, 71) is relatively well preserved, and the general structure of the chela, MXP3, and P2–P5 are not very different from that of the male *Plenotheres coarctatus*. The MXP3 propodus is not as short or conical in shape, but the inner angle of the MXP3 ischiomerus is angular. The male pleon (Fig. 71K) is relatively more elongate than that in *Pl. coarctatus* (Fig. 68M). The G1 (Fig. 71L–O), however, is very different, being long and slender with the tip tapering to a sharp point, without any folds or projections (cf. *Pl. coarctatus*; Fig. 68N–P). The absence of a female specimen makes a decision on its genus affiliation more difficult, but based on Sakai's (1976: pl. 200 fig. 4) figure (present Fig. 69A), the P2–P5 on both sides appear to be symmetrical, with the dactylus of all legs relatively short with none prominently elongated. Significantly, Sakai (1939: 591) commented that *Pinnotheres corbiculae* was close to *Pinnotheres tsingtaoensis* Shen, 1932, and both species have relatively short ambulatory dactyli. Their G1s are also similar (Fig. 71L–O; Shen, 1932: text-fig. 94c). On the basis of the available data, both *Pinnotheres corbiculae* and *Pinnotheres tsingtaoensis* should now be referred to *Nepinnotheres*, as *N. corbiculae*, new combination, and *N. tsingtaoensis*, new combination: the MXP3 dactylus is slender in both species and inserts sub-basally (rather than basally), the female P2–P4 do not show any obvious asymmetry, and the ambulatory dactyli are all relatively short and not strongly dissimilar in length.

Plenotheres coarctatus (Bürger, 1895), new combination

(Figs. 63–68)

Pinnotheres coarctatus Bürger, 1895: 369, pl. 9 fig. 7, pl. 10 fig. 7 [type locality: Tipoeka, Timika, Indonesian Papua, Indonesia, by present neotype designation]; Tesch, 1918: 248 (list); Estampador, 1937: 546 (list); Silas & Alagarswami, 1967: 1197 (list); Serène, 1968: 93; Schmitt et al., 1973: 42.

Pinnoteres coarctatus — Balss, 1957: 1419 (list).

Arcotheres coarctatus — Ahyong & Ng, 2007b: 195, fig. 3A; Ng et al., 2008: 248; Ng et al., 2017: 1094; Trivedi et al., 2018a: 197; De Gier & Becker, 2020: tab. 1; Ahyong & Ng, 2021: 207–209, fig. 17.

Pinnotheres parvulus — Rathbun, 1910: 331, fig. 13, pl. 2 fig. 9; Naiyanetr, 1980: 42; 1998: 104; 2007: 118 (not *Pinnotheres parvulus* Stimpson, 1858).

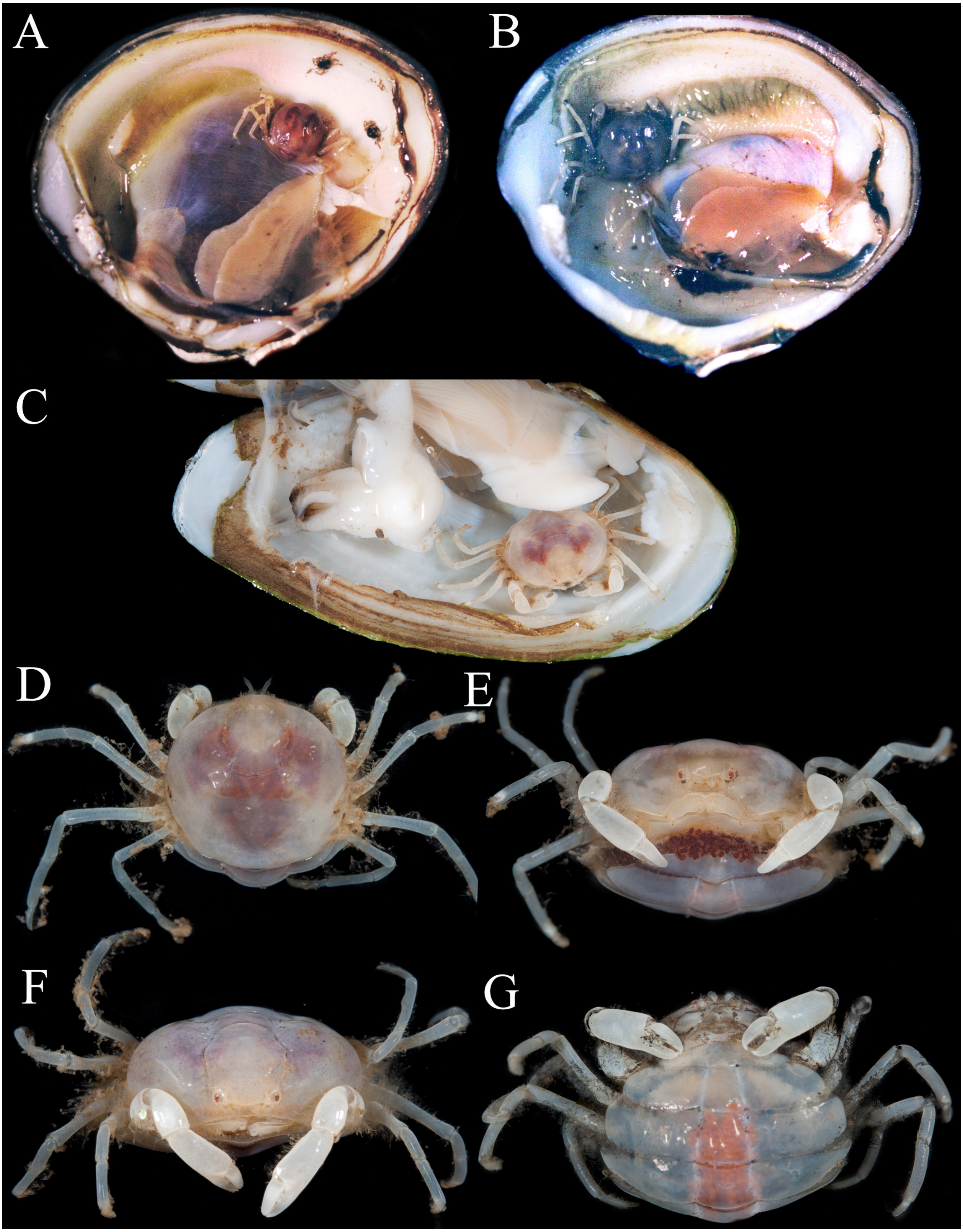

Fig. 63. *Plenotheres coarctatus* (Bürger, 1895). A, B, specimens in situ (ZRC 2018.765) in *Polymesoda expansa* (Mousson, 1849) (Cyrenidae Gray, 1840), Indonesian Papua; C–G, female (11.7 × 11.2 mm) (ZRC 2017.1283), Peninsular Malaysia. C, in situ in *Glauconome rugosa* Hanley, 1843 (Glauconomidae); D, overall habitus; E, F, frontal view; G, ventral view. Photographs: A, B, Sigit Dwiono; C–G, Paul Y. C. Ng.

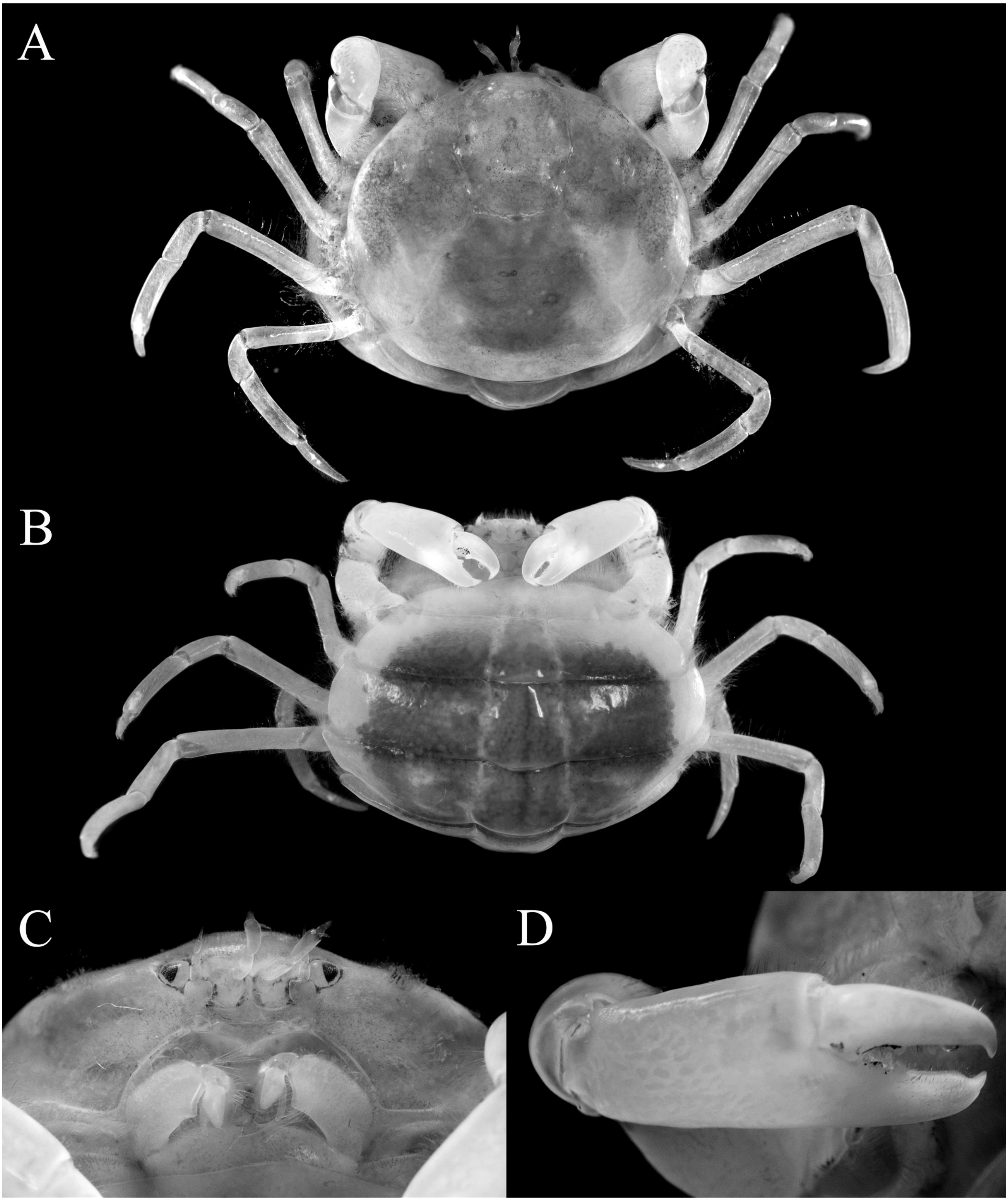

Fig. 64. *Plenotheres coarctatus* (Bürger, 1895), female (6.8 × 6.5 mm) (ZRC 2018.246), Peninsular Malaysia. A, overall dorsal view; B, ventral view of cephalothorax; C, frontal view of cephalothorax; D, outer view of right chela.

Type material. Neotype (here designated): female (13.1 × 11.4 mm) (ZRC 2020.13), Tipoeka, Timika, Indonesian Papua, Indonesia, in *Polymesoda expansa*, coll. D. L. Rahayu et al., 26 April 2000.

Other material examined. Indonesia: 2 males (2.7 × 2.8 mm, 3.3 × 3.4 mm), 1 female (11.9 × 10.8 mm), 2 juvenile females (3.4 × 3.3 mm, 3.2 × 3.2 mm) (ZRC 2018.765), same data as neotype; 1 female (7.9 × 7.2 mm) (ZRC 2019.1789), in *Glauconome rugosa*, from Kandang Kerbau market, Singapore, from Indonesia, coll. P. K. L. Ng, 29 December 2019; 2 females (11.3 × 10.7 mm, 10.2 × 9.5 mm) (ZRC 2017.1284), Ajkwa, Timika Province, Indonesian Papua, no host data, coll. D. L. Rahayu et al., 20 January 2000; 1

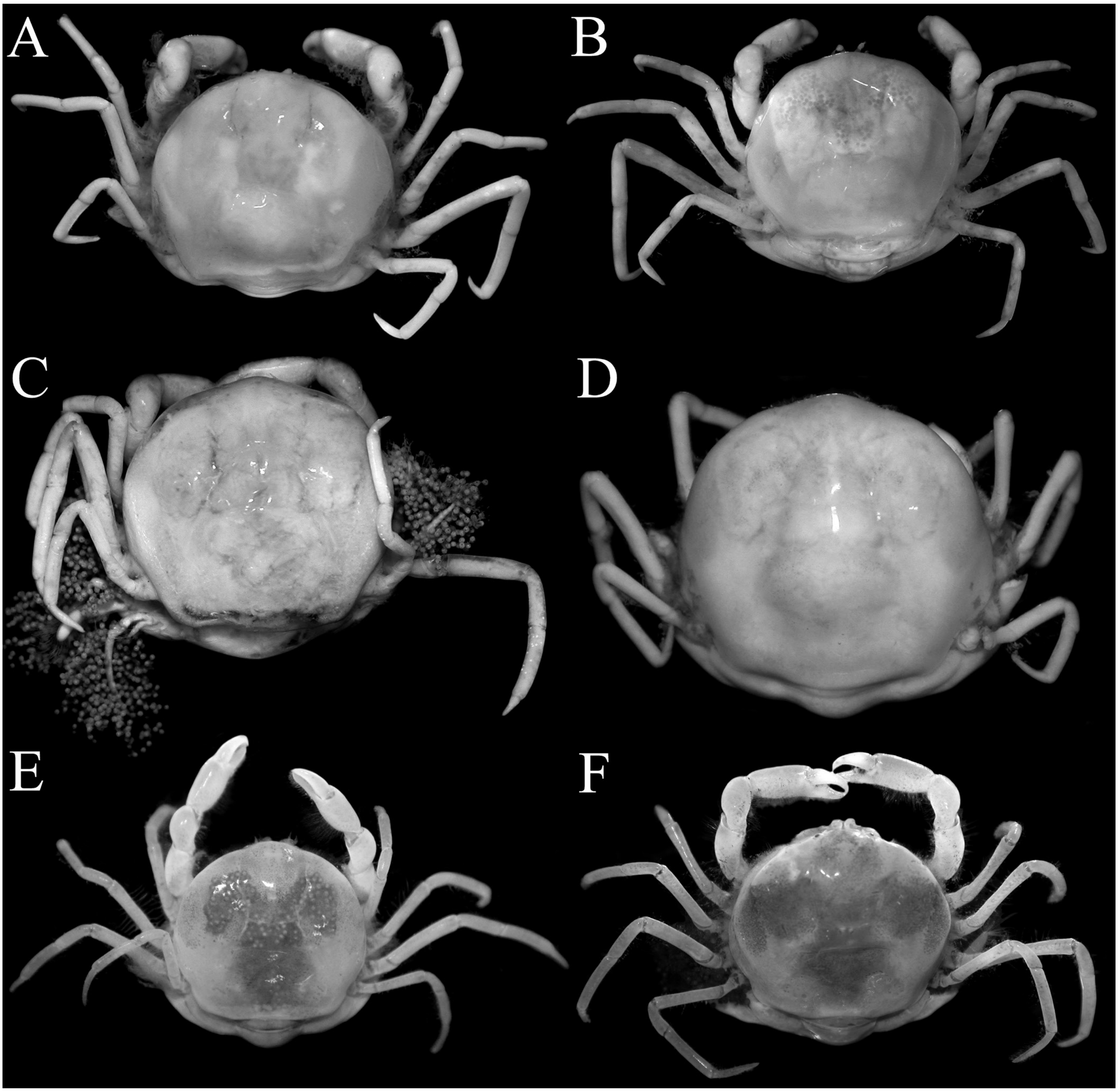

Fig. 65. *Plenotheres coarctatus* (Bürger, 1895), overall dorsal view. A, neotype female (13.1 × 11.4 mm) (ZRC 2020.13), Indonesian Papua; B, female (11.5 × 10.7 mm) (ZRC 2018.766), Indonesian Papua; C, female (13.9 × 12.4 mm) (ZRC 2003.681), Singapore; D, female (13.3 × 11.9 mm) (ZRC 2012.1223), Singapore; E, female (8.0 × 7.6 mm) (ZRC 2018.254), Peninsular Malaysia; F, female (11.9 × 10.6 mm) (ZRC 2018.254), Peninsular Malaysia.

female (11.3 × 10.2 mm) (ZRC 2017.1285), Ajkwa, Timika Province, Indonesian Papua, in *Geloina coaxans*, coll. D. L. Rahayu et al., 11 January 2000; 1 female (13.2 × 11.6 mm) (ZRC 2017.1286), Tipoeka, Timika Province, Indonesian Papua, in *Polymesoda expansa*, coll. D. L. Rahayu et al., 21 December 1999; 2 females (11.5 × 10.7 mm, 6.7 × 6.1 mm) (ZRC 2018.766), in *Batissa violacea*, peat site, Timika, Indonesian Papua, Indonesia, coll. D. L. Rahayu et al., 27 November 1999. **Singapore:** 1 female (14.1 × 13.1 mm) (ZRC 2001.2237), Loyang mangroves, off Loyang Avenue, in *Polymesoda expansa*, coll. N. Sivasothi, 17–18 July 2001; 3 females (16.5 × 14.4 mm, 15.5 × 13.2 mm, 13.9 × 12.4 mm) (ZRC 2003.681), in "*Geloina zeylanica* (Lamarck, 1806)" (= present *Geloina coaxans*), coll. A. Ibrahim, June 2003; 2 females (14.4 × 13.2 mm, 13.3 × 11.9 mm) (ZRC 2012.1223), in *Polymesoda expansa*, mudflats, Pulau Ubin, coll. G. Jahvel, 5 November 2012. **Peninsular Malaysia:** 1 female (10.1 × 9.1 mm) (ZRC 1995.438), in *Glauconome rugosa*, from market, coll. P. K. L. Ng, 21 December 1992; 5 females (11.7 × 11.2 mm, 9.5 × 8.8 mm, 9.4 × 9.0 mm, 8.7 × 8.2 mm, 6.6 × 6.3 mm) (ZRC 2017.1283), in *Glauconome rugosa*, from Chinatown market, Singapore, from Malaysia, coll. P. K. L. Ng, 21 January 2018; 9 ovigerous females (6.8 × 6.5 mm, 8.0 × 7.1 mm, 8.1 × 6.7 mm, 8.1 × 7.6 mm, 8.4 × 8.6 mm, 9.0 × 8.0 mm, 9.1 × 8.0 mm, 9.9 × 8.8 mm, 10.5 × 9.2 mm) (ZRC 2018.246), 2 ovigerous females (9.1 × 8.4 mm, 7.2 × 6.1 mm) (AM P105903), in *Glauconome rugosa*, Chinatown market, Singapore, from Malaysia, coll. P. K. L.

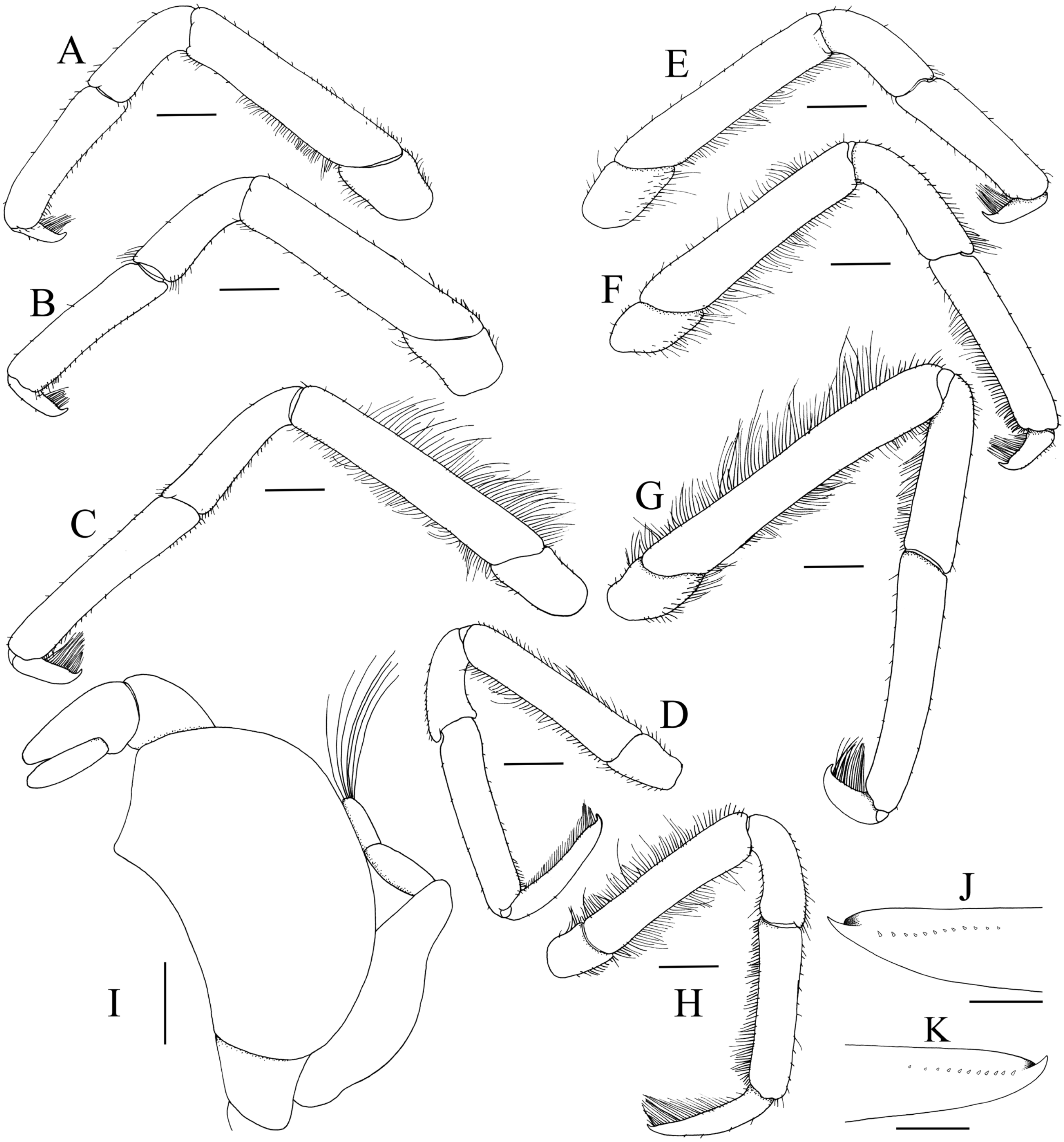

Fig. 66. *Plenotheres coarctatus* (Bürger, 1895). A–I, neotype female (13.1 × 11.4 mm) (ZRC 2020.13), Indonesian Papua; J, K, female (14.1 × 13.1 mm) (ZRC 2001.2237), Singapore. A–D, left P2–P5, respectively; E–H, right P2–P5, respectively; I, left MXP3; J, distal part of left P5 dactylus (ventral view, soft setae omitted); K, distal part of right P5 dactylus (ventral view, soft setae omitted). Scales = A–H, 1.0 mm; I, 0.5 mm; J, K, 0.25 mm.

Ng, 11 February 2018; 4 females (8.0 × 7.6 mm, 9.1 × 8.0 mm, 10.2 × 9.5 mm, 11.9 × 10.6 mm) (ZRC 2018.254), in *Glauconome rugosa*, Chinatown market, Singapore, from Malaysia, coll. P. K. L. Ng, 11 March 2018; 3 females (photographed 8.4 × 7.9 mm) (ZRC 2020.10), in *Glauconome rugosa*, from Kandang Kerbau market, Singapore, coll. P. K. L. Ng, 29 March 2020. **Thailand:** 1 ovigerous female (8.8 × 7.6 mm) (NHMD Cr-284250), Lem Ngob, Gulf of Thailand, mangrove swamp, coll. Th. Mortensen, 23–27 December 1900.

Description. Carapace and pereopods poorly chitinised. Female: Carapace subcircular, slightly wider than long; appearing domed in frontal view; dorsal and lateral surfaces smooth, glabrous; with pair of fine longitudinally arcuate grooves almost always well defined, extending from behind orbits to indistinct gastrocardiac groove; front slightly projecting anteriorly beyond anterolateral margins, margin straight to gently convex; anterolateral margin smooth, convex, gently curving to join rounded angle with posterolateral margin (Figs. 63D, 64A, 65). Eyes small, just

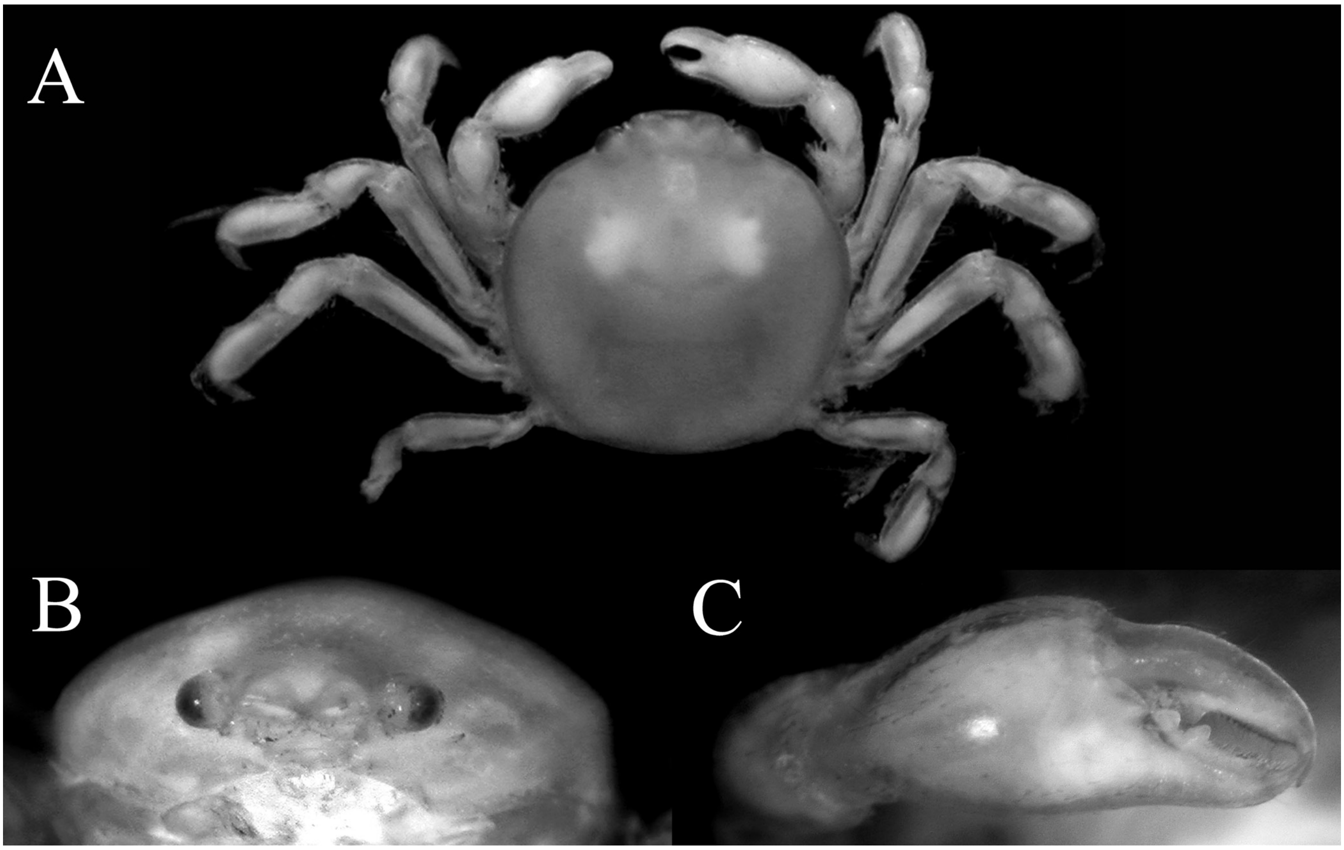

Fig. 67. *Plenotheres coarctatus* (Bürger, 1895), male (3.3 × 3.4 mm) (ZRC 2018.765), Indonesian Papua. A, overall dorsal view; B, frontal view of cephalothorax; C, outer view of right chela.

visible in dorsal view in adults; mobile, filling orbit (Figs. 63D–F, 64A, C). Epistome with median part triangular, lateral margins concave (Fig. 64C).

MXP3 outer surface with scattered short setae; ischiomerus completely fused, subrhomboidal, inner margin prominently angular (almost 90°) at widest point; carpus short; propodus conical, about 2.5 times as long as high, distinctly longer than carpus, tip rounded; dactylus slender, inserted at proximal one-third of propodus, tip slightly overreaching propodal apex; exopod relatively stout, with proximal part very wide, about two-thirds length of ischiomerus, flagellum 2-segmented (Figs. 64C, 66I).

Chela not prominently elongate, stout, dactylus exceeding two-thirds palm length; palm proximally narrower than distally; outer surfaces of palm, fingers (except for distal part) almost glabrous, with only scattered short setae; ventral margin of palm gently convex to almost straight; dactylus occlusal margin with blunt triangular tooth proximal to midlength, margin straight in distal half, finely denticulate, sparsely setose; pollex occlusal margin with 2 blunt triangular teeth proximal to midlength, straight margin in distal half, finely denticulate, sparsely setose, with fringe of short setae on inner ventral margin, extending to inner surface of palm (Fig. 64D).

P2–P5 dorsally, ventrally unarmed; margins of P2 and P3 covered with short setae; outer surface of P3 (especially merus) with dense long setae; ventral margins of dactylus with long dense setae; merus relatively longer, more slender, relative lengths of meri P4>P3>P2>P5; right (sometimes left) P4 merus and propodus distinctly the longer; P2–P4 dactyli relatively short, subequal, tip hooked, shorter than half propodus length; dactylus of longer P4 stout, weakly curved, longer than P2 and P3 dactylus, shorter than P5 dactylus; P5 merus 4.3–4.4 times longer than wide; P5 dactylus longest, gently falciform, ventral margin lined with short and long setae, distoflexor margin with relatively short row of 6–12 small spinules (Fig. 66A–K).

Pleon extending to buccal region, covering bases of P2–P5; telson slightly recessed into concave distal margin of somite 6 (Fig. 64B).

Male: Carapace almost circular, slightly longer than wide; dorsal surface smooth, inflated, lateral surfaces with setae; front projecting anteriorly, margin almost straight (Fig. 67A, B). Eyes distinctly visible in dorsal view (Fig. 67A, B). MXP3 as in female but dactylus shorter than propodus (Fig. 68J–L). Anterior thoracic sternum wide, sternites 1, 2 fused, partially sunken into buccal cavity; suture between sternites 2 and 3 shallow; sternites 3, 4 completely fused, separated only by shallow grooves. Chela relatively stout, shorter than in female (Figs. 67C, 68I). P2–P5 dorsally, ventrally unarmed; outer surface covered with short setae; P3 and P4 carpus and propodus with long natatory setae; left and right meri equal, relative lengths of meri P3=P4>P2>P5; dactyli of P2–P4 progressively longer; left P4 merus slightly longer than right side; P4 and P5 dactylus subequal to that of P3,

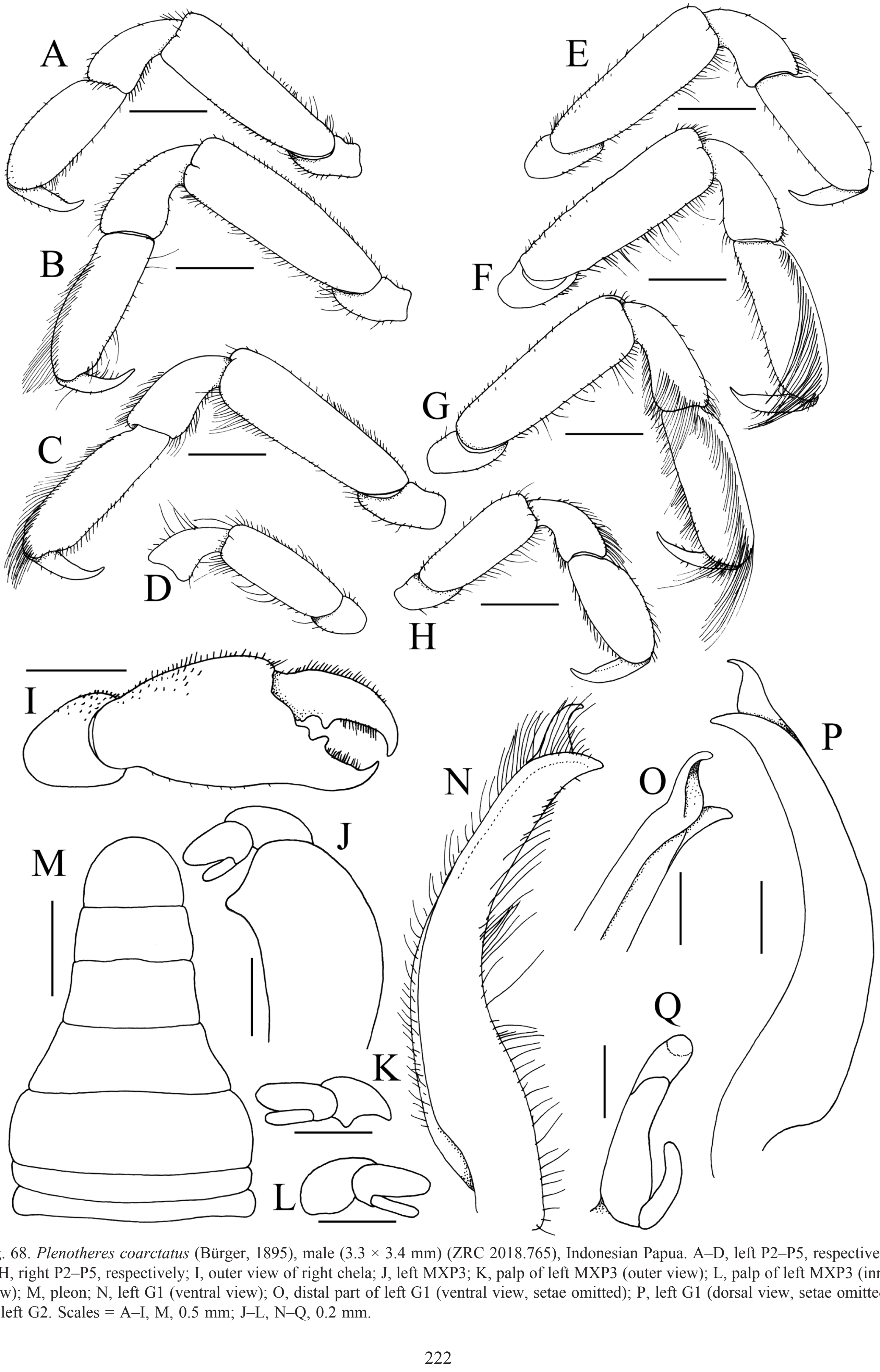

Fig. 68. *Plenotheres coarctatus* (Bürger, 1895), male (3.3 × 3.4 mm) (ZRC 2018.765), Indonesian Papua. A–D, left P2–P5, respectively; E–H, right P2–P5, respectively; I, outer view of right chela; J, left MXP3; K, palp of left MXP3 (outer view); L, palp of left MXP3 (inner view); M, pleon; N, left G1 (ventral view); O, distal part of left G1 (ventral view, setae omitted); P, left G1 (dorsal view, setae omitted); Q, left G2. Scales = A–I, M, 0.5 mm; J–L, N–Q, 0.2 mm.

Fig. 69. *Nepinnotheres corbiculae* (Sakai, 1939). A, female, overall dorsal view; B, left female MXP3; C, outer view of left female chela. A, after Sakai (1976: pl. 200 fig. 4); B, C, after Sakai (1939: text-fig. 77).

covered with short setae (Fig. 68A–H). Pleon triangular, widest at somite 3, lateral margins of somite 4 gently concave; somite 6 subrectangular; telson semicircular, slightly wider than long (Fig. 68M). G1 relatively stout, widely C-shaped, curved outwards, with elongate sharp subdistal dorsal flap at right angles to main structure (Fig. 68N–P). G2 short, with spatuliform tip; exopod long, curved (Fig. 68Q).

Variation. General setation is often less dense in larger specimens. The gastric grooves on the carapace are usually distinct, but less obvious in a few specimens, probably as a result of poor preservation. The single row of spinules on the ventral margin of the distal part of the P5 dactylus varies in number from 6 to 12, but the proximal ones are frequently very low and barely visible (Fig. 66J, K).

Colour. In life, the carapace varies from brown and grey to dirty white overall, with the ovaries appearing purplish and the eyes dull red (Fig. 63).

Host. Confirmed from *Geloina coaxans* (Gmelin, 1791), *Polymesoda expansa* (Mousson, 1849), and *Batissa violacea* (Lamarck, 1818) (Cyrenidae Gray, 1840); or *Glauconome rugosa* Hanley, 1843 (Glauconomidae Gray, 1853). Both families are in the superfamily Cyrenoidea Gray, 1840. Bürger (1895) recorded the host as “Cahebe” (= *Polymesoda* spp.) (Schmitt et al., 1973). Note that Bürger’s (1895) “Cahebe” is probably a misspelling of the local name for a commonly harvested brackish water clam (*Geloina* sp.), known as “kabibe” in Tagalog and other Philippine languages, or “cabebe” or “cabibe” under old Hispanised renderings (J. C. E. Mendoza, pers. comm.; Ahyong & Ng, 2021).

Remarks. Ahyong & Ng (2007b: 195) regarded *Plenotheres coarctatus*, new combination, originally described from Zamboanga, Philippines, and whose original types are lost, to be sufficiently recognisable as to not require a neotype designation at that time. Females of *Pl. coarctatus* as understood here are distinguishable from species of *Arcotheres* by the pair of anterior dorsal carapace grooves. Males of *Pl. coarctatus*, however, closely resemble male *A. exiguus* and *A. rayi* in most respects including the gonopod and P5 structure; they can be externally distinguished by the shape and elongation of the MXP3 propodus, which is shorter and conical in *Pl. coarctatus*, with the dactylus articulating slightly proximal to the midlength (Fig. 68J–L) (versus elongate and spatulate with the dactylus articulating slightly distal to the midlength in the two species of *Arcotheres*; Figs. 44A, 45A, 52B). In view of the strong similarities between males of *A. exiguus*, *A. rayi*, and what is here considered to be *Pl. coarctatus*; and because this species is herein made the type species of a new genus, a neotype selection is required to fix its identity. This will stabilise the taxonomy of *Pinnotheres coarctatus* and the genus. The neotype selected is a female (13.1 × 11.4 mm; ZRC 2020.13) collected from *Polymesoda expansa* in Indonesian Papua. This location is southeast of the original type locality in southern Philippines.

Ahyong & Ng (2021) showed that Rathbun’s (1910) record of *Pinnotheres parvulus* from the Gulf of Thailand is referable to *Pl. coarctatus*.

Distribution. South China Sea from the Philippines, Indonesia, Peninsular Malaysia, Singapore, and Thailand.

Magnotheres, new genus

Type species. *Pinnotheres globosum* Hombron & Jacquinot, 1846, by present designation.

Diagnosis. Carapace dorsal surface smooth, without obvious gastric grooves. MXP3 dactylus slender, inserted near or slightly proximal to ventral midlength of propodus, variable length; propodus spatuliform, about 3.0 times longer than wide; inner margin of widest part of ischiomerus rounded to angular; exopod relatively slender with proximal part of exopod not especially wide. Female P4 slightly asymmetrical, with merus on left or right side slightly longer; dactyli of P2 and P3 subequal, weakly curved, longer than half propodus length, P4 dactylus similar in shape but slightly longer than P2 and P3 dactyli; P5 dactylus elongate, weakly falciform, with 2 rows of distoflexor spinules. Male pleon relatively

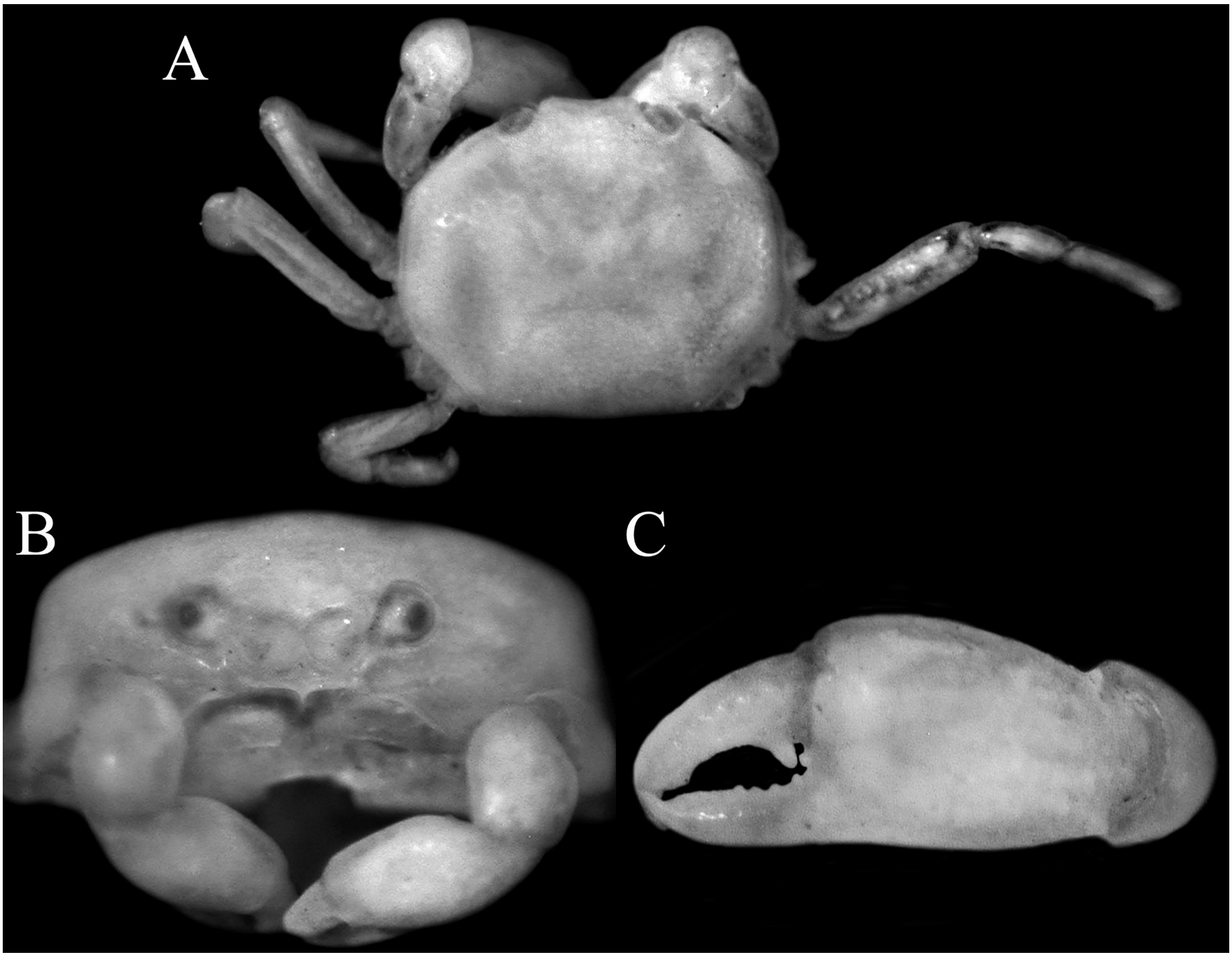

Fig. 70. *Nepinnotheres corbiculae* (Sakai, 1939), male (2.1 × 1.8 mm) (KPM-NH 106679), Japan. A, overall dorsal view; B, frontal view of cephalothorax; C, outer view of left chela.

narrowly triangular, telson broadly trapezoidal, widest distally, distal margin sinuous. G1 very slender, proximal two-thirds straight, broadly curved at distal one-third, with sharply tapering tip; G2 exopod as long as endopod.

Etymology. The name is derived from the Latin 'magnus' for big, alluding to the relatively large size of the type species; in combination with a typical ending for pinnotherid crabs. Gender masculine.

Remarks. Ng et al. (2017: 1081, 1092) alluded to the possible polyphyly of *Arcotheres* in treating the taxonomy of two nominal species from India, *Pinnoteres borradailei* Nobili, 1906a (replacement name for *Pinnotheres tenuipes* Borradaile, 1903), and *Pinnoteres ridgewayi* Southwell, 1911. Although they referred both species to *Arcotheres*, they recognised that the asymmetry of the female left and right P4 was slight at best, as in *Arcotheres latus* (Bürger, 1895).

As a result of the present review of all of these nominal species, *A. borradailei*, *A. ridgewayi*, and *A. latus* have been found indistinguishable and are synoynymised. Moreover, reassessment and revision of the poorly known *Pinnotheres globosum* Hombron & Jacquinot, 1846 (type locality: Singapore) have revealed that it is not only a senior synonym of *A. borradailei*, *A. ridgewayi*, and *A. latus*, but that it warrants transfer to a new genus, *Magnotheres*, new genus (see also Remarks for *M. globosus*).

The symmetry or near symmetry of the female P4 is diagnostic of *Magnotheres* (see Fig. 83A–H) relative to *Arcotheres* s. str. In all other species that have been referred to *Arcotheres*, the asymmetry in the female P4 is very distinct and can be discerned even in males (e.g., see Ng, 2018a). Females of *Magnotheres* also differ from most female *Arcotheres* by the gently curved P2 and P3 dactyli (Fig. 83A, B, E, F), in contast to the condition found in most species of *Arcotheres*, in which the apex of the P2 and P3 dactyli have a distinctly turned, gently hooked, spiniform tip (e.g., Figs. 14A, B, E, F, 54F, G, J, K). Males of *M. globosus*, new combination, are notable because the pleon is unlike that of known *Arcotheres*, with somites 5 and 6 narrow and the telson broadly trapezoidal, being widest across the distal margin (Figs. 85C, 86J); and with the G1 very long and slender (Fig. 86K). The unusual male telson of *M. globosus* is similar to that of *Fabia concharum* (Rathbun, 1893) (Campos, 1996: fig. 4A) from the Americas. In all other species of *Arcotheres*, male pleonites 5 and 6 are proportionally wider and the

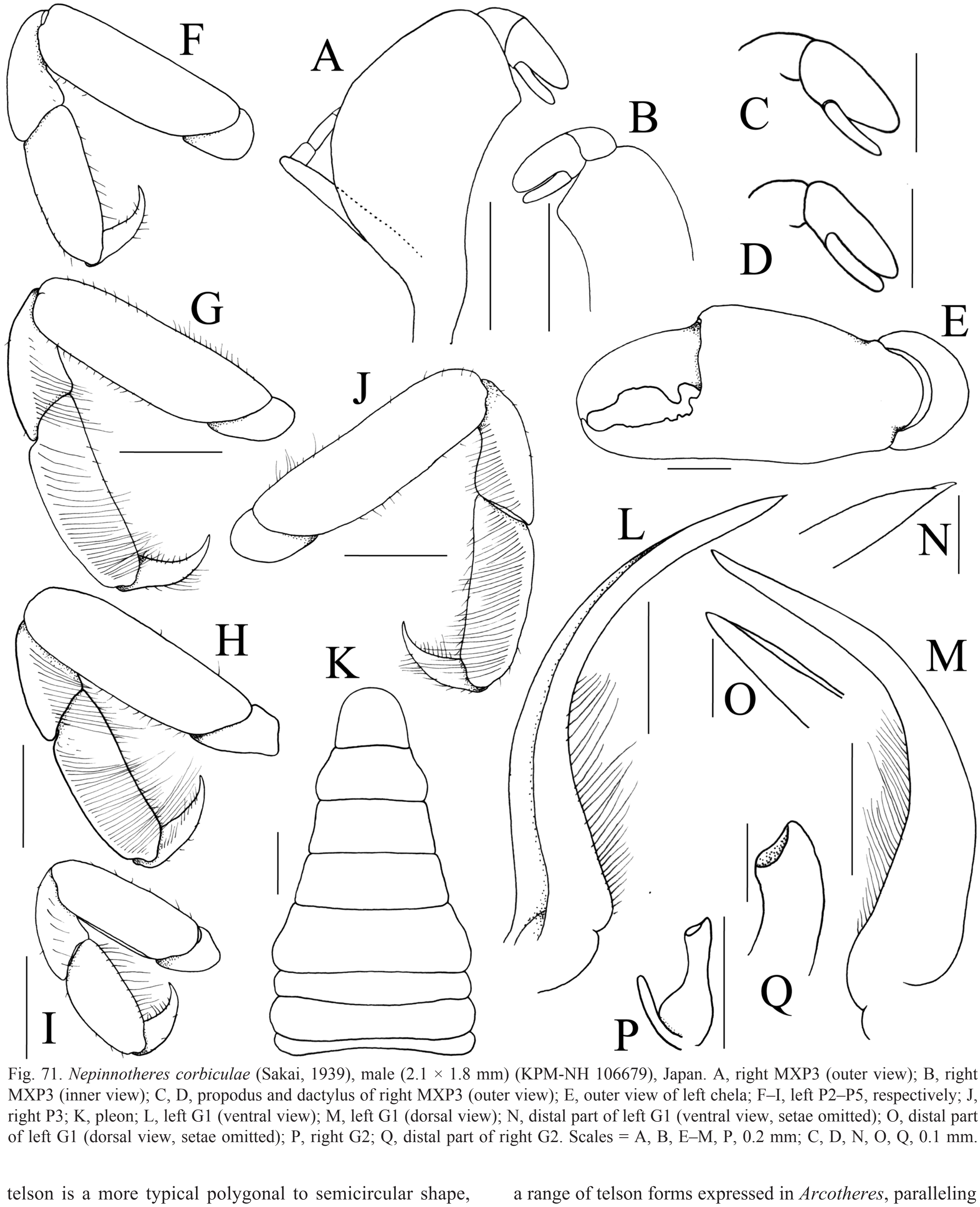

Fig. 71. *Nepinnotheres corbiculae* (Sakai, 1939), male (2.1 × 1.8 mm) (KPM-NH 106679), Japan. A, right MXP3 (outer view); B, right MXP3 (inner view); C, D, propodus and dactylus of right MXP3 (outer view); E, outer view of left chela; F–I, left P2–P5, respectively; J, right P3; K, pleon; L, left G1 (ventral view); M, left G1 (dorsal view); N, distal part of left G1 (ventral view, setae omitted); O, distal part of left G1 (dorsal view, setae omitted); P, right G2; Q, distal part of right G2. Scales = A, B, E–M, P, 0.2 mm; C, D, N, O, Q, 0.1 mm.

telson is a more typical polygonal to semicircular shape, being widest proximally (e.g., Fig. 62B). A few species of *Arcotheres* (e.g., *A. ocularius* Komai, Kawai & Ng, 2020), have the male telson trapezoidal or almost pentagonal in shape, but the widest point is near the midlength (Komai et al., 2020: figs. 10B, E, 13D, H, 15F), and somites 5 and 6 are still proportionally wider. It could be argued that the inverted trapezoidal male telson in *M. globosus* is simply an autapomorphy, being one mode of polymorphism within a range of telson forms expressed in *Arcotheres*, paralleling similar variations observed in *Fabia*, for instance (Campos, 1996). However, unlike *Fabia* in which the G1 follows a common pattern despite variation in telson shape, the G1 of *M. globosus* is also of a distinctly different form from all known species of *Arcotheres*, being proportionately more elongated, straighter, and more slender (Fig. 86K), approaching that seen in *Afropinnotheres* Manning, 1993 (Manning, 1993b: figs. 4i, 5c; Ahyong, 2019: fig. 2K). In all species of *Arcotheres*, however, where known, the G1 is much stouter and shorter than in *M. globosus*, even for species like *A. palaensis* (see Figs. 22K–M, 32L, M, 33G, J, 44K, L, 45H, I; Komai et al., 2020: figs. 5E, F, 13I, J, 15G, H). A preliminary genetic study by Tsang Ling Ming from the Chinese University of Hong Kong also recovers *Magnotheres globosus* in a separate clade from other species of *Arcotheres* from Southeast Asia, India, Japan, Hong Kong, and Fiji (L. M. Tsang, pers. comm.). As such, with the presence of correlated differences compared to all known male *Arcotheres*, we consider *Magnotheres* to be generically distinct.

Ng et al. (2017: 1081) noted that in *A. borradailei* and *A. ridgewayi*, the P5 basis-ischium appeared to be more elongated and cylindrical (Fig. 83D, H) than in most other pinnotherids, and that this may have diagnostic value among species of *Arcotheres* in the future. Indeed, females of *Magnotheres* and *Arcotheres* share the "bar-like" P5 merus and elongated ischium in which the articulation between the two articles is perpendicular to the segment axis, rather than diagnonal as seen in other pinnotherids. The condition of the P5 ischium-merus articulation in males of *Magnotheres* and most species of *Arcotheres* (where known) is similar to that of females. In males of *A. exiguus* and *A. rayi*, however, the ischium-merus articulation is diagonal, indicating possible heterogeneity in *Arcotheres*.

Sankarankutty (1966: text-figs. 23, 28) figured the distal half of the G1 and male pleon of a specimen from southern India (as *P. ridgewayi*), and his figures, although somewhat simple, show the same features as our male from Singapore. The slender G1 and trapezoidal male telson are diagnostic.

Magnotheres globosus (Hombron & Jacquinot, 1846), new combination

(Figs. 72–86)

Pinnotheres globosum Hombron & Jacquinot, 1846: pl. 5 figs. 21–26 [type locality: Changi, Singapore, by present neotype designation]; Jacquinot & Lucas, 1853: 58; Ng & Corbari, 2019: 245, fig. 6.10–6.13 (discussion).

Pinnotheres rouxi — ?Paulson, 1875: 70, pl. 9 fig. 2-2c (not *Pinnotheres rouxi* H. Milne Edwards, 1853).

Pinnotheres latus Bürger, 1895: 374, 375, pl. 9 fig. 16, pl. 10 fig. 15 [type locality: Ubay, Philippines, by present lectotype designation, from *Pinna* sp.]; Tesch, 1918: 249 (Sumba and Amboina, Indonesia); Gordon, 1936: 171 (discussion); Estampador, 1937: 547 (list); Miyake, 1939: 221 (list); Silas & Alagarswami, 1967: 1201 (list); Serène, 1968: 94; Schmitt et al., 1973: 52.

Pinnotheres parvulus — De Man, 1888: 105; Alcock, 1900: 339 [not *Pinnotheres parvulus* Stimpson, 1858].

Pinnoteres borradailei Nobili, 1906a: 410 (replacement name for *Pinnotheres tenuipes* Borradaile, 1903) [type locality: Minicoy, Lakshadweep Islands, India]; 1906b: 306 (part); Guinot, 1967: 279 (list).

Pinnotheres borradailei — ?Lenz, 1910: 558, 576; Laurie, 1915: 415 (list); Tesch, 1918: 248, 253, 287 (list and key); Silas & Alagarswami, 1967: 1197 (list); Schmitt et al., 1973: 40 (list); Ng et al., 2008: 250 (list); Ng et al., 2017: 1080.

Pinnoteres ridgewayi Southwell, 1911: 226, pl. 3 figs. 1, 2, 2a [type locality: Kondatchi Paar, Sri Lanka, by lectotype designation, Ng et al., 2017].

Pinnotheres ridgewayi — Tesch, 1918: 250, 251 (list); Gravely, 1927: 146, pl. 23 fig. 37; Prasad & Tampi, 1957: 22, fig. 1 (larvae); Sankarankutty, 1966: 349, 350, 358, 360, figs. 23, 28; Silas & Alagarswami, 1967: 1177, 1183, 1208, 1219, 1223, 1225, 1227 (discussion); Serène, 1968: 94; Schmitt et al., 1973: 84; Ng et al., 2008: 251 (list); Ng et al., 2017: 1080.

Pinnotheres similis — Rathbun, 1924: 15; Davie, 2002: 434 (not *Pinnotheres similis* Bürger, 1895).

Pinnotheres alcocki — Rathbun, 1909: 114 (part); Gordon, 1936: 176, fig. 5 [not *Pinnotheres alcocki* Rathbun, 1909].

Pinnotheres sp. — Ward, 1967: 62.

Pinnotheres globosa — Silas & Alagarswami, 1967: 1199, 1204; Schmitt et al., 1973: 46; Ng et al., 2008: 250.

Pinnotheres globosus — Serène, 1968: 93; Schmitt et al., 1973: 46 (part); De Gier & Becker, 2020: tab. 1.

Arcotheres similis — Ahyong & Brown, 2003: 9; De Gier & Becker, 2020: tab. 1 (part) [not *Pinnotheres similis* Bürger, 1895].

Arcotheres latus — Ahyong & Ng, 2007b: 198, fig. 6; Ng et al., 2008: 248; Ng et al., 2017: 1093; Trivedi et al., 2018a: 197; Ahyong, 2020b: 880; De Gier & Becker, 2020: tab. 1; Ahyong & Ng, 2021: 195, 207.

Nepinnotheres ridgewayi — Ng & Kumar, 2015: 265 (discussion).

Arcotheres borradailei — Ng & Kumar, 2015: 265; Ng et al., 2017: 1081, figs. 1–3, 8A; Trivedi et al., 2018a: 197; Trivedi et al., 2018b: 61; Trivedi et al., 2018c: 50; De Gier & Becker, 2020: tab. 1.

Arcotheres ridgewayi — Ng et al., 2017: 1085, figs. 4–7, 8B; Trivedi et al., 2018a: 197; Trivedi et al., 2018b: 61; Trivedi et al., 2018c: 50; De Gier & Becker, 2020: tab. 1.

Type material. Neotype (here designated): female (10.2 × 8.4 mm) (ZRC 2016.164), off Changi Beach, Singapore, adjacent to National Service Recreational Country Club, from *Pinna atropurpurea*, intertidal area, coll. S. K. Tan et al., 6 July 2016. **Myanmar:** 1 ovigerous female (ca. 8.3 × 6.7 mm, carapace soft) (NHM 1886.52), Mergui Archipelago, coll. J. Anderson (paralectotype of *Pinnotheres alcocki* Rathbun, 1909). **Philippines:** 1 female (10.6 × 8.7 mm) (SMF-ZMG 956a) (lectotype of *Pinnotheres latus* Bürger, 1895), from *Pinna* sp., Burias; 3 females (9.5 × 7.5–10.5 × 9.0 mm) (SMF-ZMG 956b) (paralectotypes of *Pinnotheres latus* Bürger, 1895), same data as lectotype. **India:** 1 ovigerous female (8.0 × 6.8 mm) (CUMZ I.63816) (holotype of *Pinnotheres borradailei* Nobili, 1906a, replacement name for *Pinnotheres tenuipes* Borradaile, 1903), Minikoi (present day = Minicoy), Lakshadweep Islands (previously known as the Laccadive, Minicoi, and Aminidivi Islands), India, previously part of Maldive and Laccadive Islands, supposedly from *Mya*, coll. J. S. Gardiner. **Sri Lanka:** 1 female (14.9 × 12.8 mm) (ZSI/WGRC/IRINV 8102/10) (lectotype of *Pinnotheres ridgewayi* Southwell, 1911) [photographs examined], from *Pinna bullata* Gmelin, 1791, pearl banks, Kondatchi Paar, Ceylon (= Sri Lanka), coll. T. Southwell, 1910; 2 females (14.4 × 11.9 mm, one with carapace in poor condition) [photographs examined], same data as lectotype (paralectotypes of *Pinnotheres ridgewayi* Southwell, 1911).

Other material examined. Singapore: 1 ovigerous female (13.2 × 9.9 mm), 1 non-ovigerous female (14.4 × 10.8 mm)

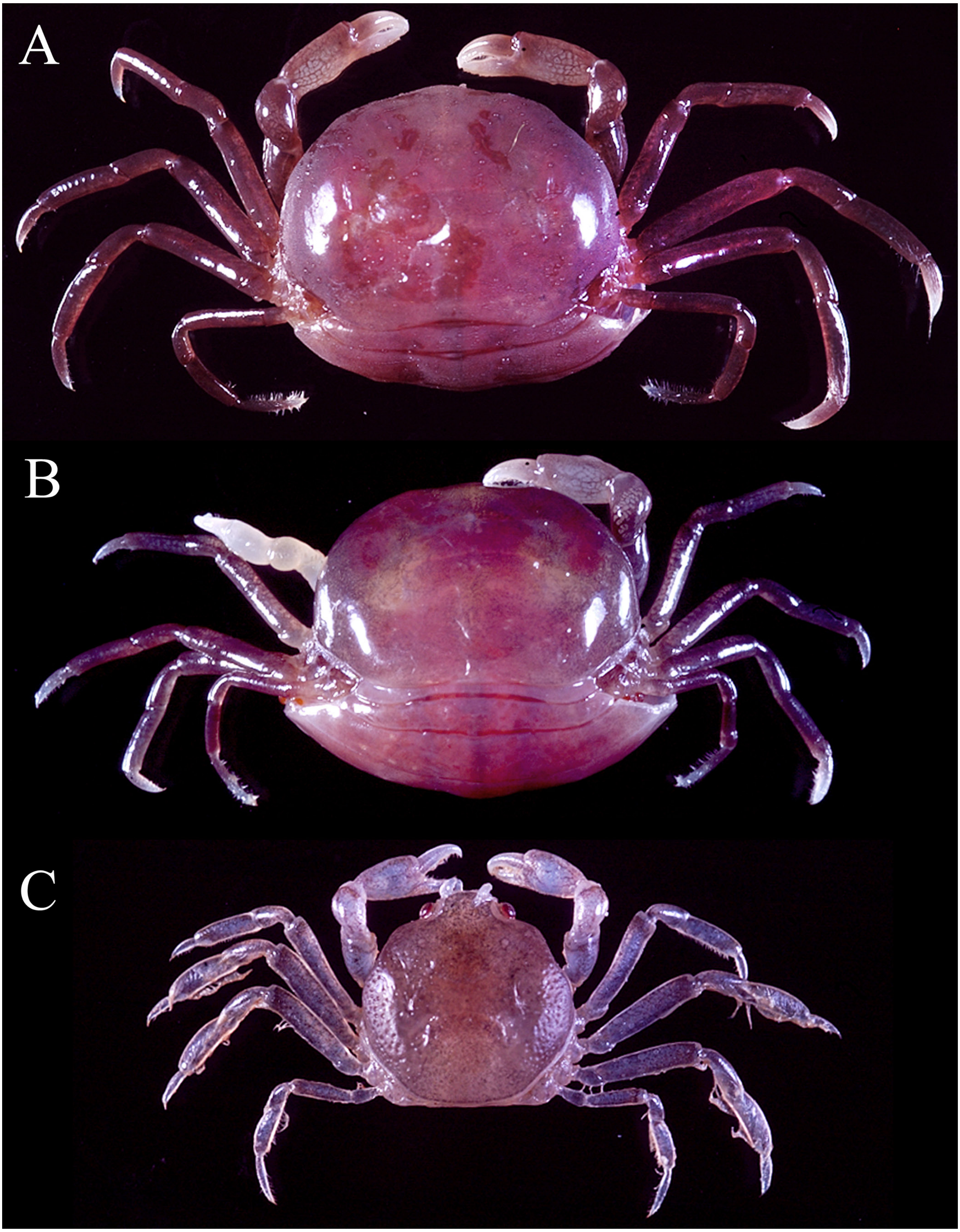

Fig. 72. *Magnotheres globosus* (Hombron & Jacquinot, 1846), colour in life. A, ovigerous female (13.0 × 10.0 mm) (ZRC 2018.782), Philippines; B, ovigerous female (9.0 × 6.8 mm) (ZRC 2018.781), Philippines; C, male (5.4 × 5.5 mm) (ZRC 2018.783), Philippines. Photographs: A, Chan Tin-Yam.

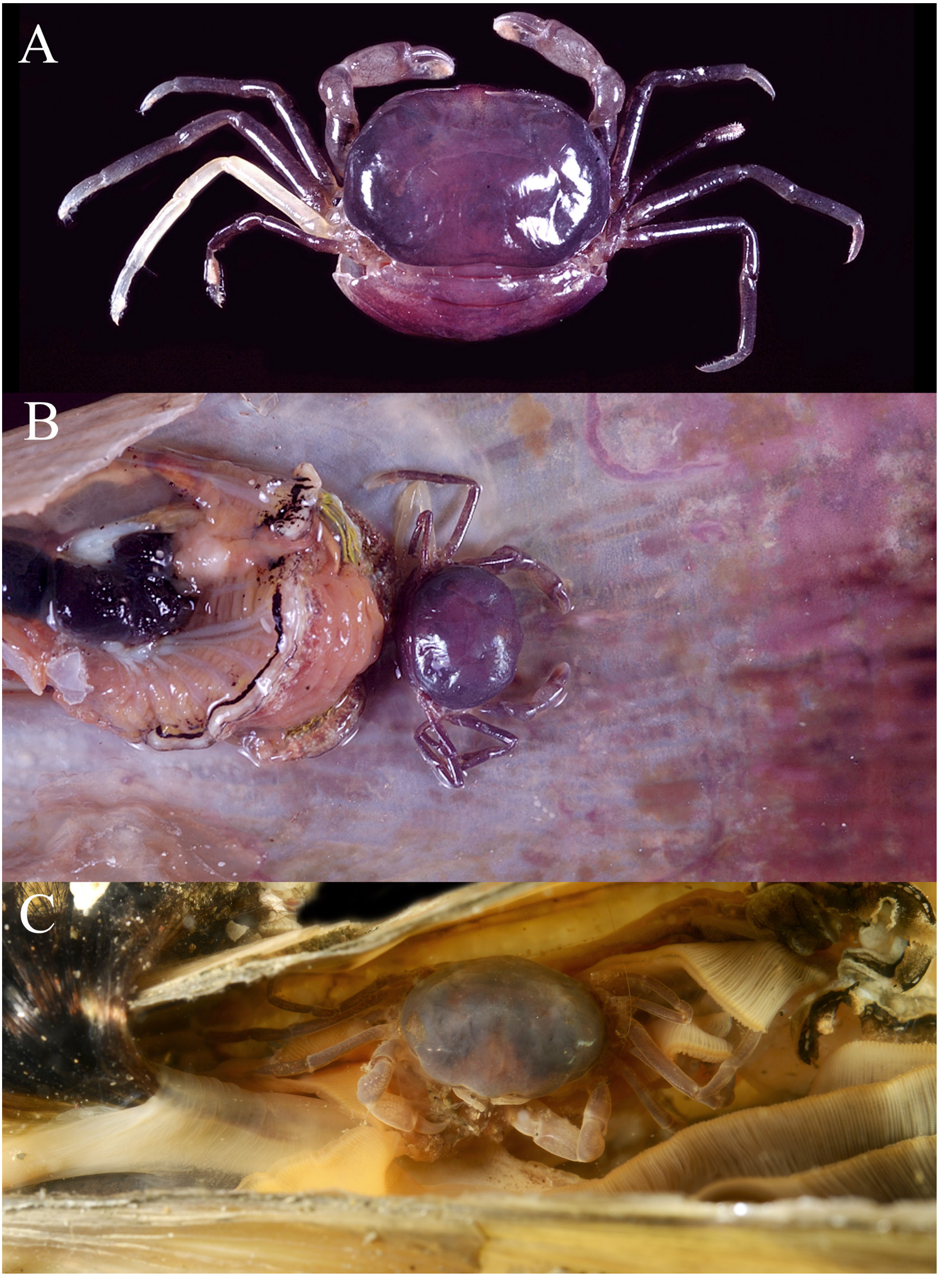

Fig. 73. *Magnotheres globosus* (Hombron & Jacquinot, 1846). A, B, colour in life and in situ in *Pinna* sp., ovigerous female (11.8 × 9.5 mm) (ZRC 2017.1017), Panglao, Philippines; C, female in situ in *Pinna atropurpurea*, Singapore, coll. 12 January 2017 (not collected). Photographs: A, Chan Tin-Yam; B, C, Tan Heok Hui.

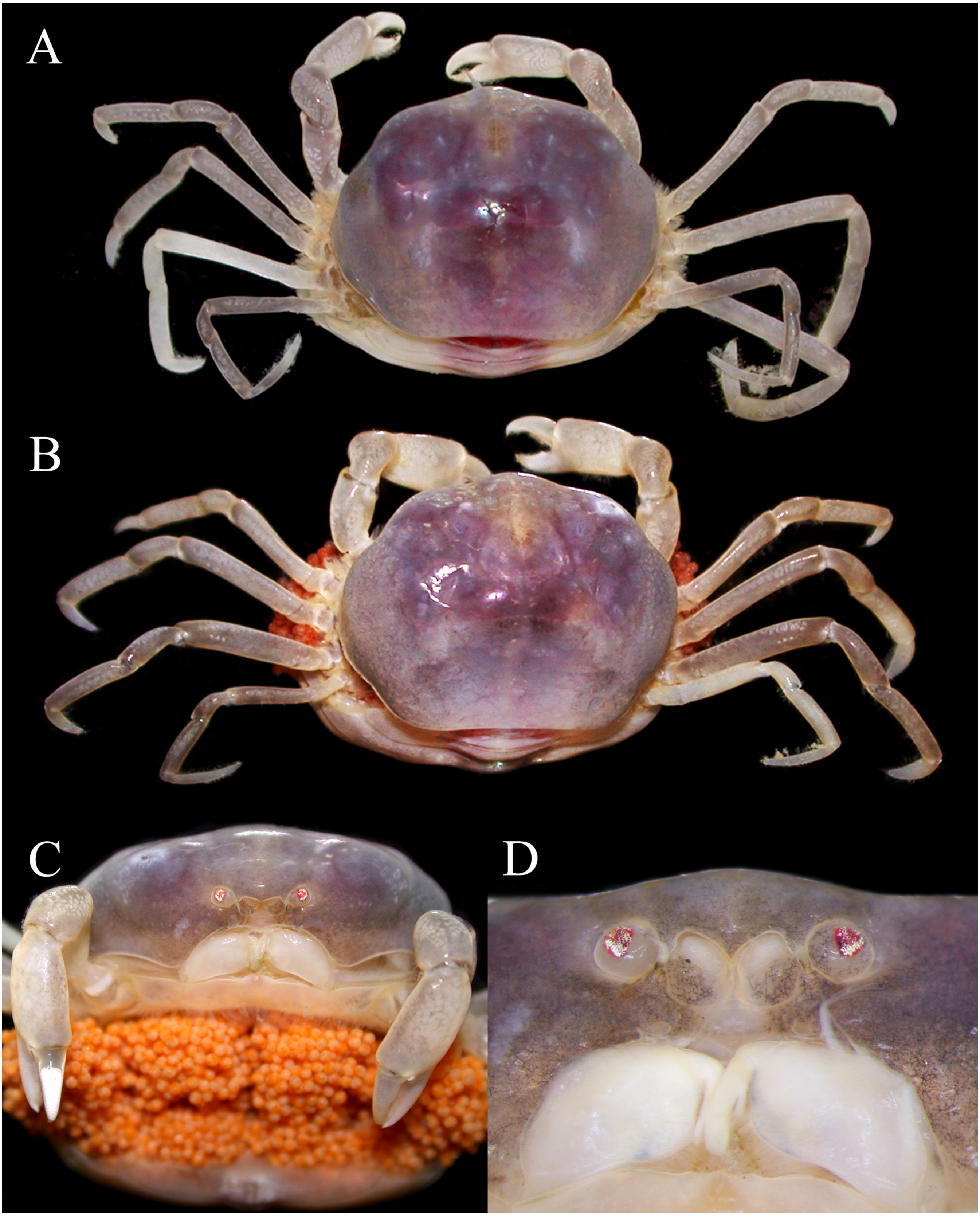

Fig. 74. *Magnotheres globosus* (Hombron & Jacquinot, 1846), colour in life. A, non-ovigerous female (14.4 × 10.8 mm) (ZRC 2017.1018), Changi, Singapore; B–D, ovigerous female (13.2 × 9.9 mm) (ZRC 2017.1018), Changi, Singapore. A, B, overall dorsal view; C, D, frontal view of cephalothorax. Photographs: Tan Heok Hui.

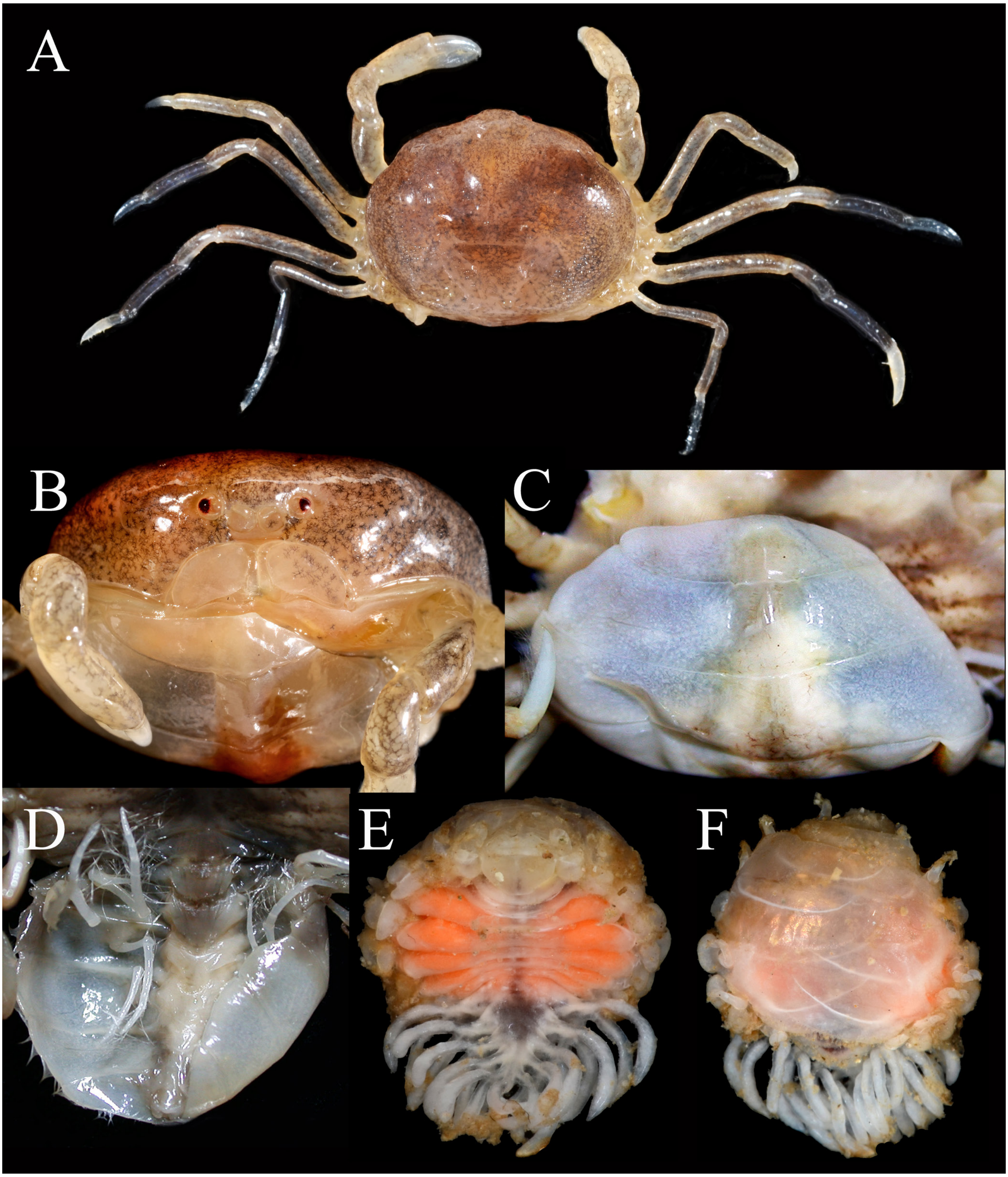

Fig. 75. *Magnotheres globosus* (Hombron & Jacquinot, 1846), colour in life, non-ovigerous female (14.6 × 10.7 mm) (ZRC 2017.1020), with bopyrid parasite (*Rhopalione* sp.), Changi, Singapore. A, overall habitus; B, frontal view of cephalothorax showing asymmetrical pleon; C, female pleon with left side folded inwards; D, ventral surface of pleon showing folding of left side; E, ventral view of *Rhopalione* sp.; F, dorsal view of *Rhopalione* sp. Photographs: Lee Bee Yan.

(ZRC 2017.1018), from *Pinna atropurpurea*, intertidal area, Tanah Merah Ferry Terminal Beach, near Changi Point, coll. S. K. Tan et al., 13 December 2016; 3 ovigerous females (11.9 × 9.3 mm, 13.1 × 11.0 mm, 13.6 × 10.5 mm) (ZRC 2017.1019), from *Pinna atropurpurea*, intertidal area, Changi East, east of Tanah Merah Ferry Terminal Beach, near Changi Point, coll. S. K. Tan et al., 14–16 December 2016; 1 non-ovigerous female (14.6 × 10.7 mm) (ZRC 2017.1020), with *Rhopalione* sp. bopyrid parasite, from *Pinna atropurpurea*, intertidal area, Changi East, east of Tanah Merah Ferry Terminal Beach, near Changi Point, coll. S. K. Tan et al., 14–16 December 2016; 2 ovigerous females (ZRC 2018.786),

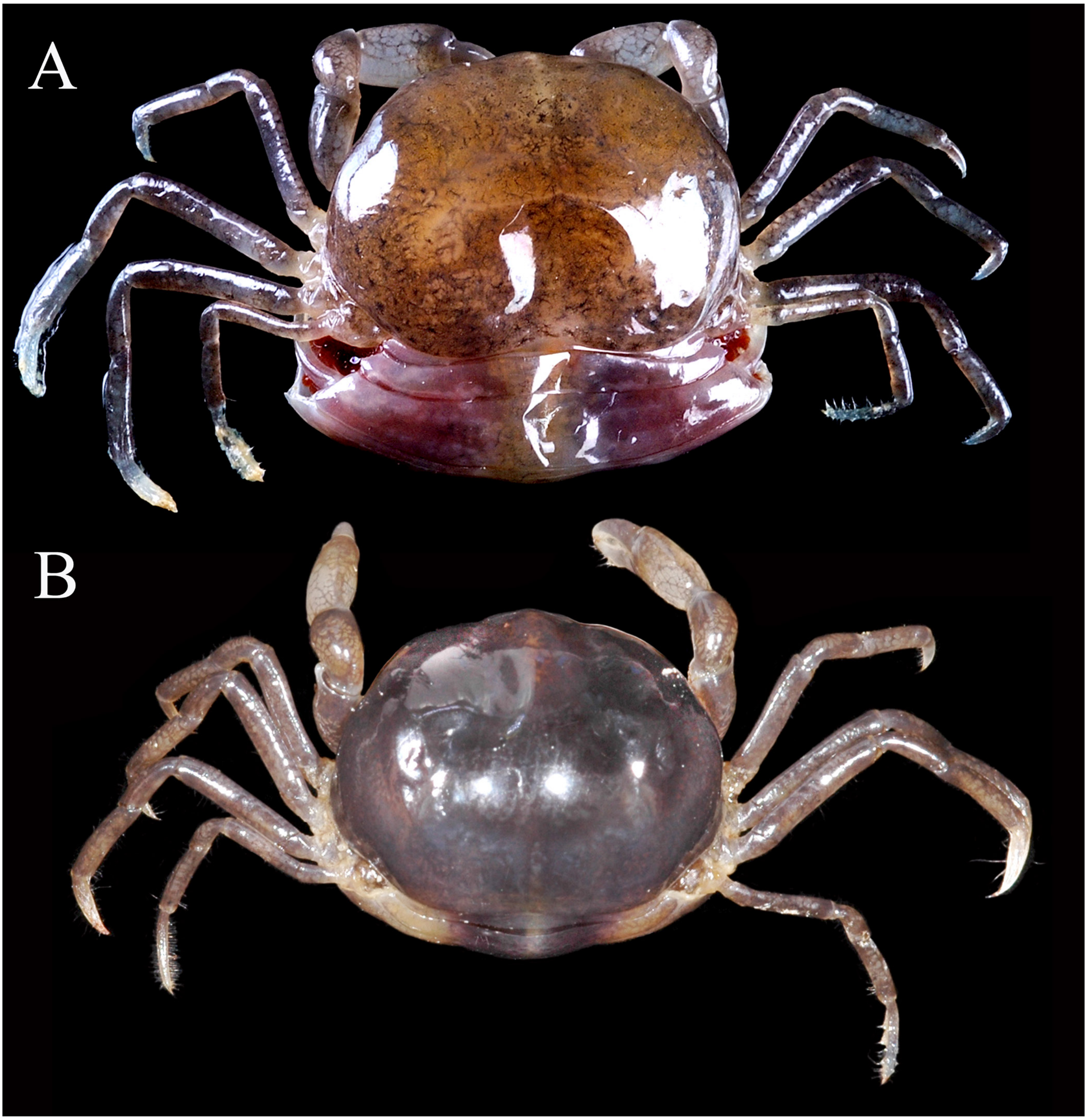

Fig. 76. *Magnotheres globosus* (Hombron & Jacquinot, 1846), colour in life. A, ovigerous female (12.1 × 9.4 mm) (ZRC 2016.166), Vanuatu; B, ovigerous female (13.5 × 10.7 mm) (ZRC 2016.165), Vanuatu. Photographs: Chan Tin-Yam.

from *Pinna atropurpurea*, intertidal area, Tanah Merah Ferry Terminal Beach, near Changi Point, coll. P. K. L. Ng & S. K. Tan, 12–15 January 2017; 1 ovigerous female (13.6 × 10.4 mm) (ZRC 2017.176), from *Pinna atropurpurea*, intertidal area, Tanah Merah Ferry Terminal Beach, near Changi Point, coll. P. K. L. Ng & S. K. Tan, 26 May 2017; 1 ovigerous female (13.2 × 10.1 mm) (AM P105903), from *Pinna atropurpurea*, intertidal area, Tanah Merah Ferry Terminal Beach, near Changi Point, coll. S. K. Tan et al., 27 May 2017; 3 females (ZRC 2018.786), from *Pinna atropurpurea*, intertidal area, Changi East, east of Tanah Merah Ferry Terminal Beach, near Changi Point, coll. S. K. Tan et al., 12 and 15 January 2017; 1 male (8.0 × 7.8 mm) (ZRC 2020.12), station IT140 (collection number station SS-4132), intertidal, from *Pinna atropurpurea*, Pulau Tekukor, Southern Islands, 01°13.899′N, 103°50.265′E, 0.4–0.8 m, coll. Comprehensive Marine Biodiversity Survey, 31 May 2013. **Philippines:** 3 ovigerous females (9.8 × 7.6 mm, 11.0 × 8.9 mm, 11.8 × 9.5 mm), 1 ovigerous female (carapace broken, carapace length 11.9 mm), 1 non-ovigerous female (7.2 × 6.2 mm) (ZRC 2017.1017), from *Pinna* sp., Panglao Island, Bohol, Visayas, coll. Panglao 2004 Expedition, 5 July 2004; 1 ovigerous female (9.0 × 6.8 mm) (ZRC 2018.781), station M11, host not recorded, rocky intertidal, fringe mangrove, and seagrass habitat, Sungcolan Bay, Panglao Island, Bohol, Visayas, 0–3 m, 9°38.3′N, 123°49.6′E, coll. Panglao 2004

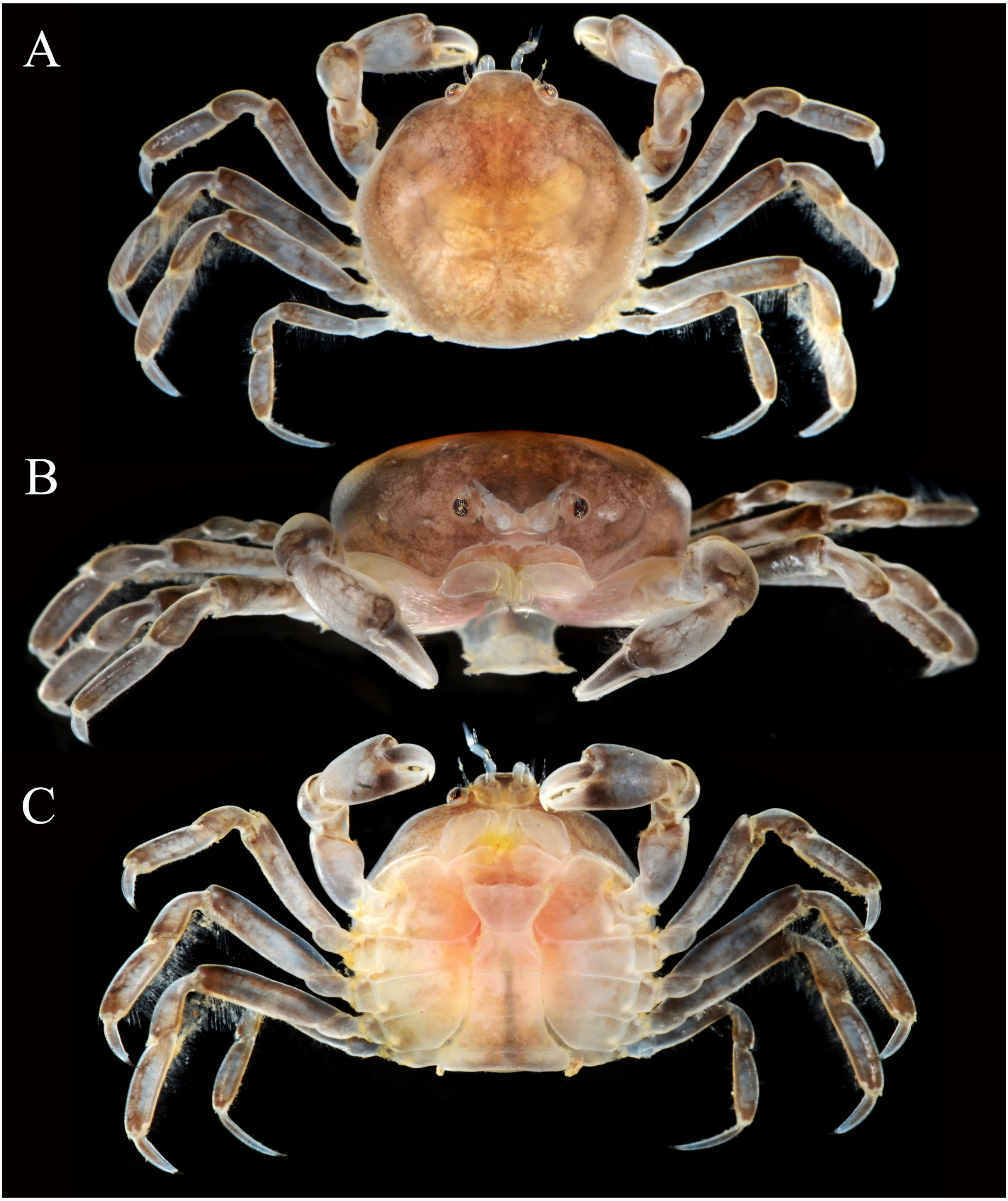

Fig. 77. *Magnotheres globosus* (Hombron & Jacquinot, 1846), male (8.0 × 7.8 mm) (ZRC 2020.12), Singapore. A, overall dorsal view; B, frontal view of cephalothorax; C, ventral view of cephalothorax. Photographs: Arthur Anker.

Expedition, 6 June 2004; 1 ovigerous female (13.0 × 10.0 mm) (ZRC 2018.782), station M18, in *Pinna muricata*, on sandy bottom and seagrass, Gak-Ang Islet, Panglao Island, Bohol, Visayas, 0–1 m, 9°33.0′N, 123°43.5′E, coll. Panglao 2004 Expedition, 10 June 2004; 1 male (5.4 × 5.5 mm) (ZRC 2018.783), station M18, in *Pinna muricata*, on sandy bottom and seagrass, Gak-Ang Islet, Panglao Island, Bohol, Visayas, 0–1 m, 9°33.0′N, 123°43.5′E, coll. Panglao 2004 Expedition, 10 June 2004. **Palau:** 2 females (8.7 × 7.2 mm, 7.3 × 6.3 mm) (SMF-ZMG 955), from *Pinna nigrina*, coll. Semper. **Vanuatu:** 1 female (13.5 × 10.7 mm) (ZRC 2016.165), from unknown host, intertidal area, sand and

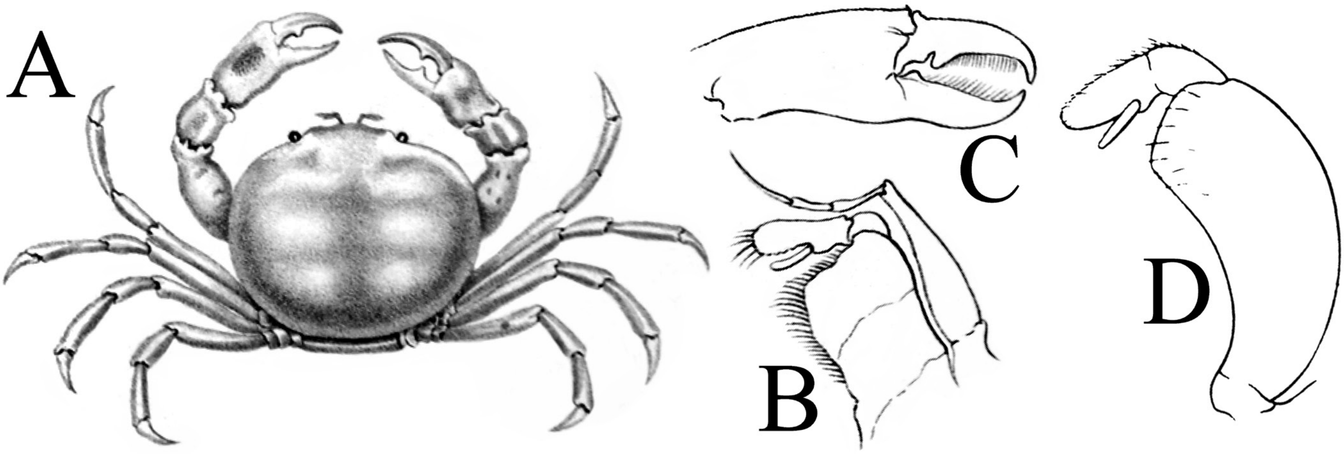

Fig. 78. *Magnotheres globosus* (Hombron & Jacquinot, 1846), type female (20.0 × 18.0 mm). A, overall dorsal view; B, D, left MXP3; C, outer view of right chela. A–C, after Hombron & Jacquinot (1846: pl. 5 figs. 21–23); D, after Milne Edwards (1853: pl. 11 fig. 6).

muddy rock substrate, Belmoul Lagoon, Santo, 15°35.8′S, 167°06.1′E, coll. SANTO Expedition, 13 September 2006; 1 female (12.1 × 9.4 mm) (ZRC 2016.166), specimen data BC 3888, from inside unidentified Pinnidae, Santo, coll. 9 October 2006. **Australia:** 2 males (5.1 × 5.1–6.8 × 6.8 mm), 7 females (4.0 × 4.3–9.0 × 11.7 mm) (AM P7067), Fields Reef, Port Denison, Queensland, 20°01′S, 148°15′E, from young *Pinna* sp. in shallow water, coll. E. Rainford, 1923; 1 female (8.9 × 7.1 mm) (AM P12173), Michelmas Cay, Great Barrier Reef, Queensland, 16°35′S, 146°02′E, from *Pinna* sp. on coral reef, coll. G. P. Whitley & T. Iredale, June 1926; 1 female (12.2 × 9.0 mm) (AM P64685), Lindeman Island, Queensland, dredged, coll. M. Ward, December 1928; 1 female (11.5 × 9.2 mm) (AM P20161), East Arm, Darwin Harbour, Northern Territory, in mytilid *Stavilla* [sic] *horrida* (= *Stavelia subdistorta* (Reclúz, 1852)), coll. O. Cameron, 19 December 1971. **India:** 1 female (17.7 × 13.6 mm) (ZSI/WGRC/IR-INV 8235), from *Pinna atropurpurea*, Kovalam, 8.3°N, 77.2°E, Thiruvananthapuram, Kerala, southwestern India, 5–10 m depth, coll. A. B. Kumar & R. Ravinesh, 2014; 1 ovigerous female (14.7 × 11.2 mm) (ZRC 2016.184), same locality and host as preceding, coll. R. Ravinesh, early 2016; 1 ovigerous female (16.6 × 12.3 mm) (ZRC 2016.185), same locality and host as preceding, coll. R. Ravinesh, June 2016.

Description. Carapace and pereopods well chitinised. Female: Carapace subcircular to transversely subhexagonal, wider than long; dorsal and lateral surfaces smooth, glabrous; appearing domed in frontal view; front occasionally projecting anteriorly beyond orbits, margin straight to gently convex; anterolateral margin gently convex (Figs. 72A, 73A, 74A–C, 75A, B, 76, 79A, C, 80A, C, 81A–E, 82). Eyes small, usually not clearly visible in dorsal view in adults, filling orbit (Figs. 72A, 73A, 74A, B, 75A, 76, 79A, 80A, 81A–D, 82, 84A). Epistome with median part triangular, lateral margins gently concave (Figs. 79C, 80C, 81E).

MXP3 outer surface with scattered short setae; ischiomerus completely fused, subrhomboidal, inner margin rounded to angular at widest point; carpus short; propodus about 3 times as long as high, spatuliform, distinctly longer than carpus, tip rounded to subtruncate; dactylus slender, inserted near or slightly proximal to ventral midlength of propodus, not or just reaching propodal apex; exopod relatively slender, about two-thirds length of ischiomerus, flagellum 2-segmented (Figs. 74D, 83I–K, 84B–G).

Chela not prominently elongate, dactylus about half to three-quarters palm length; palm relatively slender, proximally narrower than distally; outer surface of palm, fingers (except for distal part) almost glabrous, with only scattered short setae; ventral margin of palm gently concave to sinuous; dactylus occlusal margin with distinct subproximal tooth; pollex occlusal margin with 1 low proximal tooth, 1 submedian tooth, and denticles; tips of fingers sharp, hooked (Figs. 79D, 80D).

P2–P5 dorsally, ventrally unarmed; outer surface covered with scattered, very short setae or glabrous; ventral margins of propodus and dactylus slightly more setose; merus relatively slender, relative lengths of meri P4>P3>P2>P5; left or right P4 merus slightly longer than other side, propodus and dactylus not clearly bilaterally asymmetrical; P2–P4 dactyli relatively long, subequal, weakly curved, longer than half propodus length, P4 dactylus similar in shape but slightly longer than P2 and P3 dactyli; P5 merus 4.5–4.6 times longer than wide; P5 dactylus longest, margins lined with short and long setae, denser on ventral margin, with 2 rows of distoflexor spinules, upper row usually with 5–8 spinules, lower row with 12–18 small spinules, increasing in size distad (Figs. 81F, 83A–H).

Pleon extending to buccal region, covering bases of P2–P5; telson gently recessed into concave distal margin of somite 6 (Figs. 72B, 79B, 80B).

Male: Carapace almost circular, slightly wider than long; dorsal surface almost smooth, not prominently inflated, lateral surfaces with setae; front projecting anteriorly, margin almost straight (Figs. 72C, 77A, B, 85A, B, 86A). Eyes distinctly visible in dorsal view (Figs. 72C, 77A, 85A, B, 86A). MXP3 as in female (Fig. 86D). Anterior thoracic sternum wide, sternites 1, 2 fused, partially sunken into

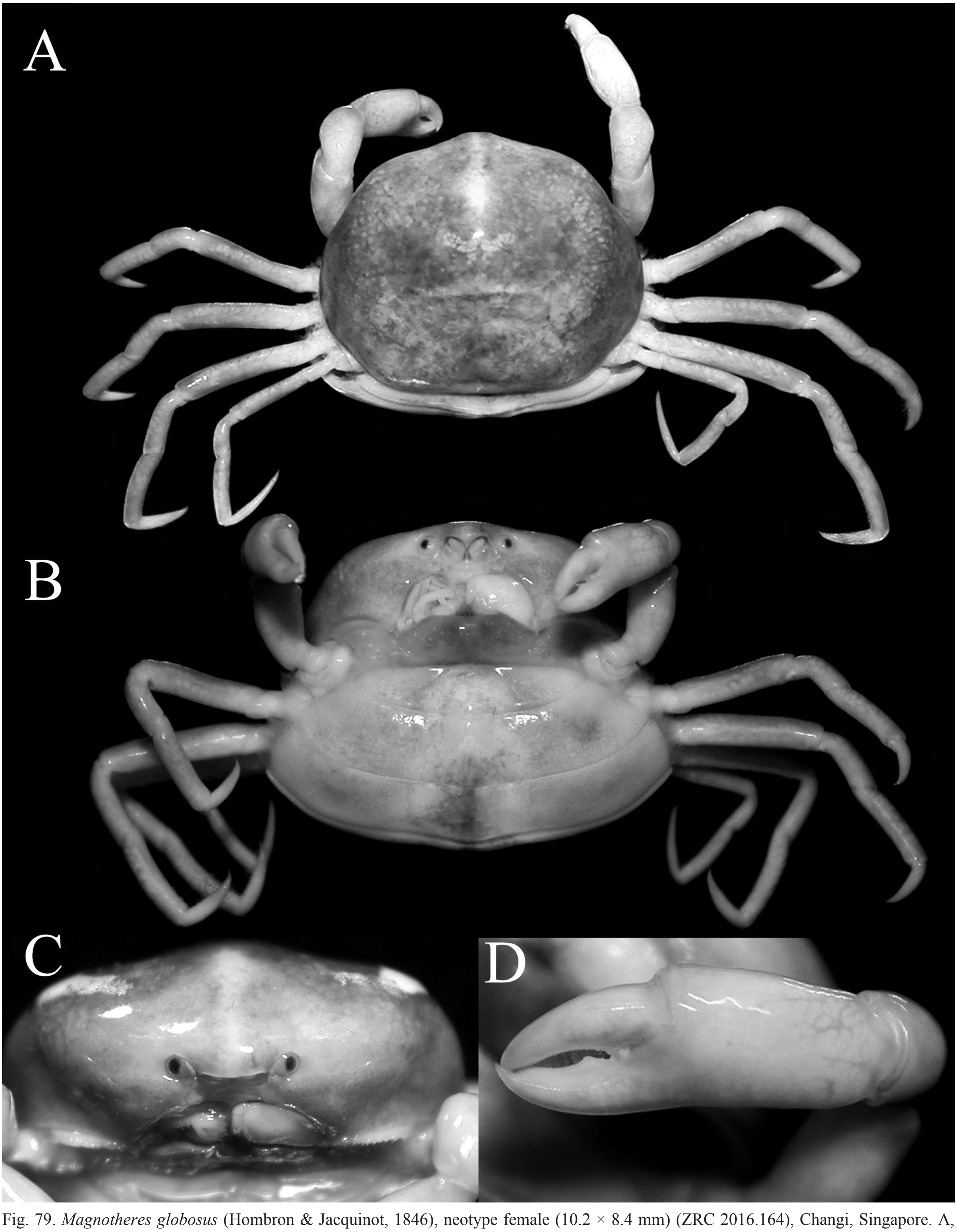

Fig. 79. *Magnotheres globosus* (Hombron & Jacquinot, 1846), neotype female (10.2 × 8.4 mm) (ZRC 2016.164), Changi, Singapore. A, overall dorsal view; B, ventral view of cephalothorax; C, frontal view of cephalothorax; D, outer view of left chela.

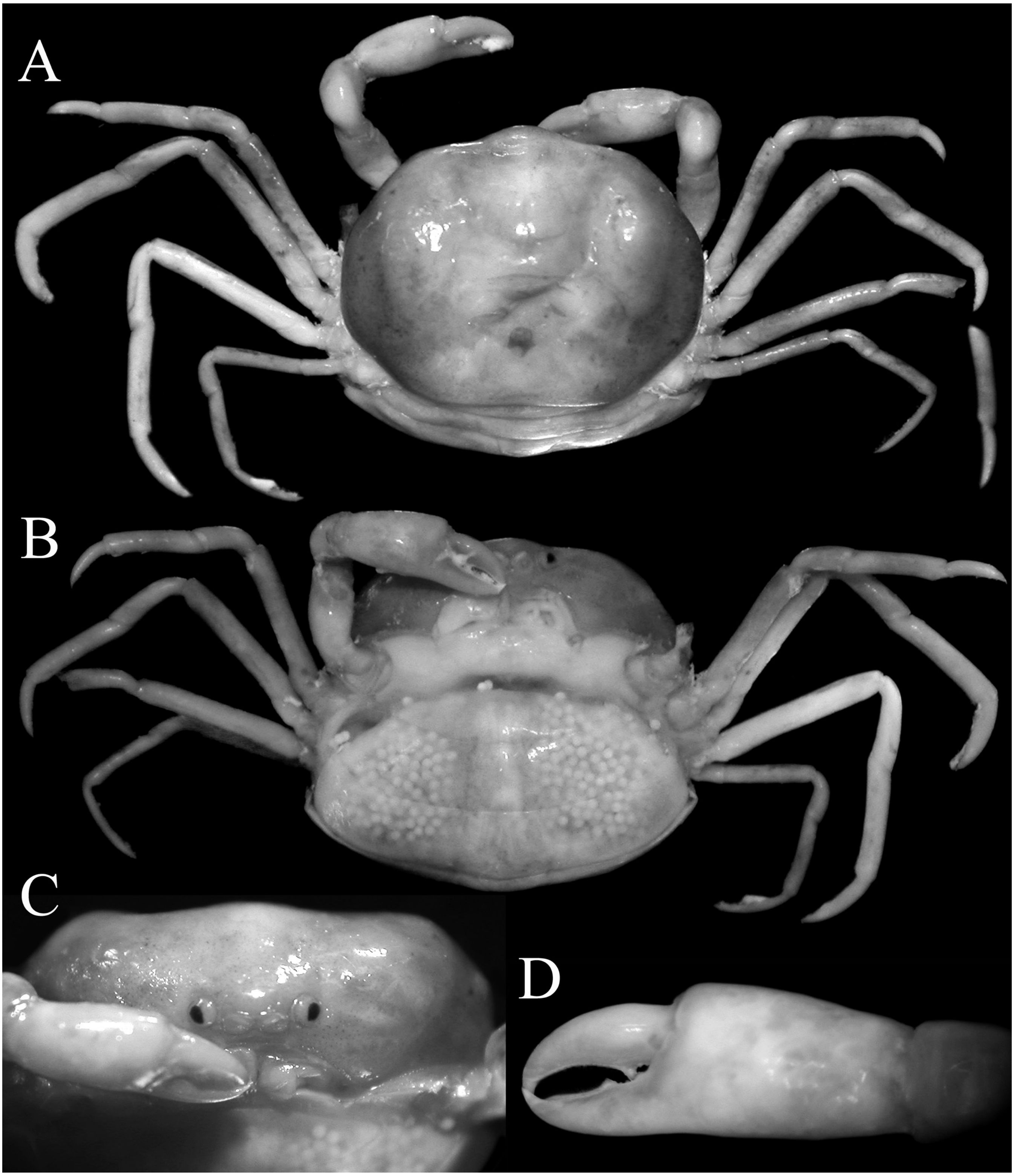

Fig. 80. *Magnotheres globosus* (Hombron & Jacquinot, 1846), ovigerous female (11.8 × 9.5 mm) (ZRC 2017.1017), Panglao, Philippines. A, overall dorsal view; B, ventral view of cephalothorax; C, frontal view of cephalothorax; D, outer view of left chela.

buccal cavity; suture between sternites 2 and 3 shallow; sternites 3, 4 completely fused, separated only by shallow grooves (Figs. 77C, 85C, 86C). Chela relatively stout, shorter than in female (Figs. 85D, 86E). P2–P5 dorsally, ventrally unarmed; outer surface covered with short setae; P3 and P4 carpus and propodus with long natatory setae; left and right meri equal, relative lengths of meri P4>P3>P2>P5; dactyli of P2–P4 progressively longer; P5 dactylus falciform, long, covered with short setae (Figs. 85A, 86F–I). Male pleon relatively narrowly triangular, widest at somite 3, lateral margins of somite 4 gently concave; somite 6 trapezoidal; telson broadly trapezoidal, distal margin sinuous, much wider than proximal one (Figs. 77C, 85C, 86J). G1 very slender, proximal two-thirds straight, broadly curved at distal one-third, with sharply tapering tip (Fig. 86K). G2 short, with spatuliform tip; exopod as long as endopod (Fig. 86L).

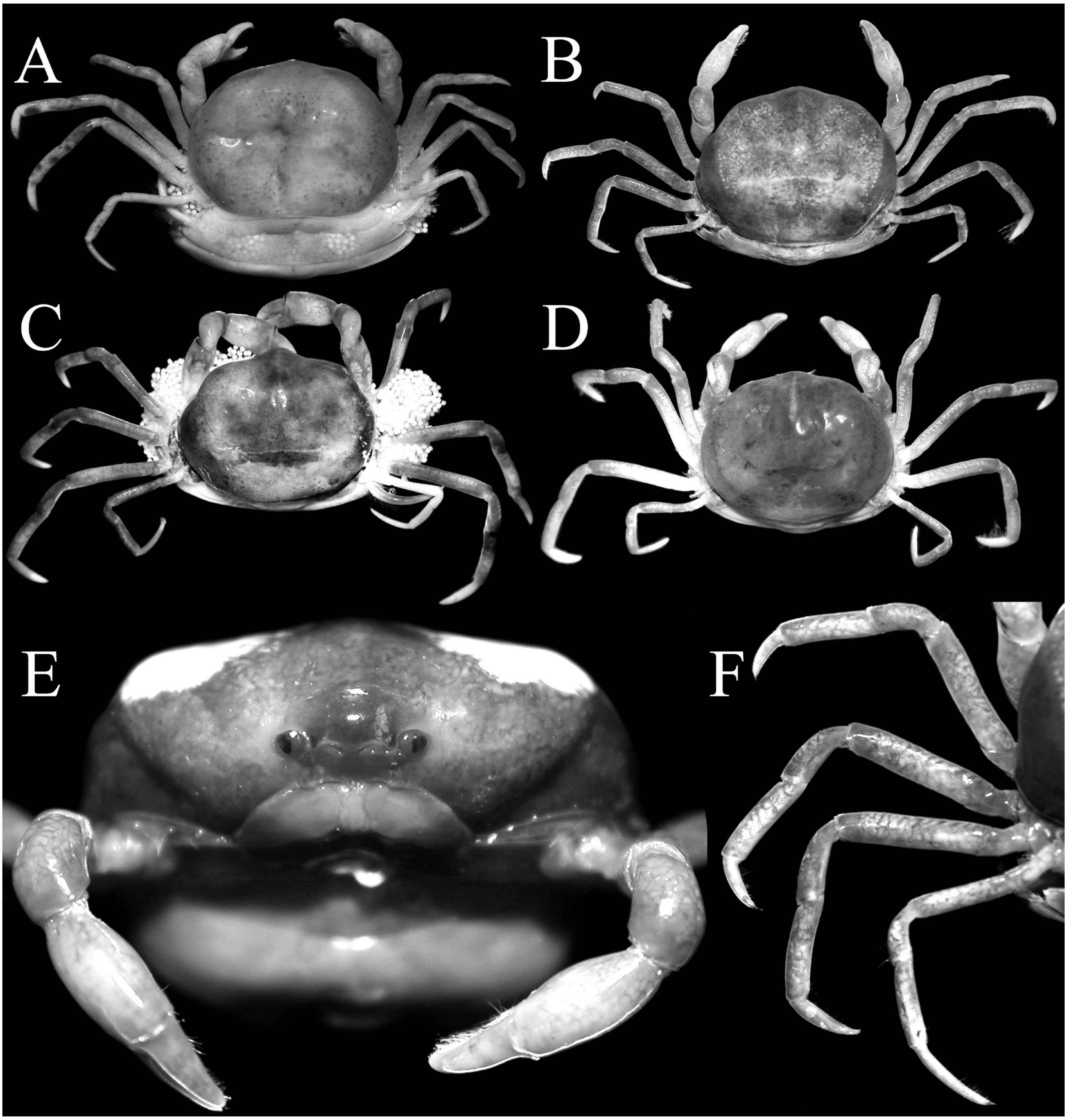

Fig. 81. *Magnotheres globosus* (Hombron & Jacquinot, 1846). A, ovigerous female (12.1 × 9.4 mm) (ZRC 2016.166), Vanuatu; B, E, F, ovigerous female (13.5 × 10.7 mm) (ZRC 2016.165), Vanuatu; C, ovigerous female (11.9 × 9.3 mm) (ZRC 2017.1019), Changi, Singapore; D, ovigerous female (13.6 × 10.5 mm) (ZRC 2017.1019), Changi, Singapore. A–D, overall dorsal view; E, frontal view of cephalothorax; F, left P2–P5.

Variation. The variation in carapace shape in this species is quite substantial, from transversely ovate with a low front (e.g., Fig. 82F) to more subhexagonal with a rounded, more produced front (e.g., Fig. 82D). The holotype of *Pinnotheres latus* has a relatively low truncate front (cf. Ahyong & Ng, 2007b: fig. 6A) as does another specimen from the Philippines (ZRC 2017.1017) (Fig. 84A), but in most specimens, the front is broadly convex (e.g., Fig. 82A, B). The shape of the MXP3 ischiomerus varies to some degree, with the inner angle at the widest point usually angular and relatively well defined (e.g., Figs. 83J, K, 84A, B), but in several specimens, it is more rounded (e.g., Fig. 84D, E) with one appearing almost broadly curved (Fig. 84F, G). The slender MXP3 dactylus varies slightly in length, usually not underreaching (Figs. 83I, 84B, E), but occasionally reaching the apex (Figs. 83J, K, 84C, D). The number of spinules on the two rows on the ventral distal part of P5 dactylus is quite variable. In the neotype female, there are only six spinules on the outer row (Fig. 83D') and 14 spinules on the inner row on the left side (Fig. 83D"), but on the right side, there are six

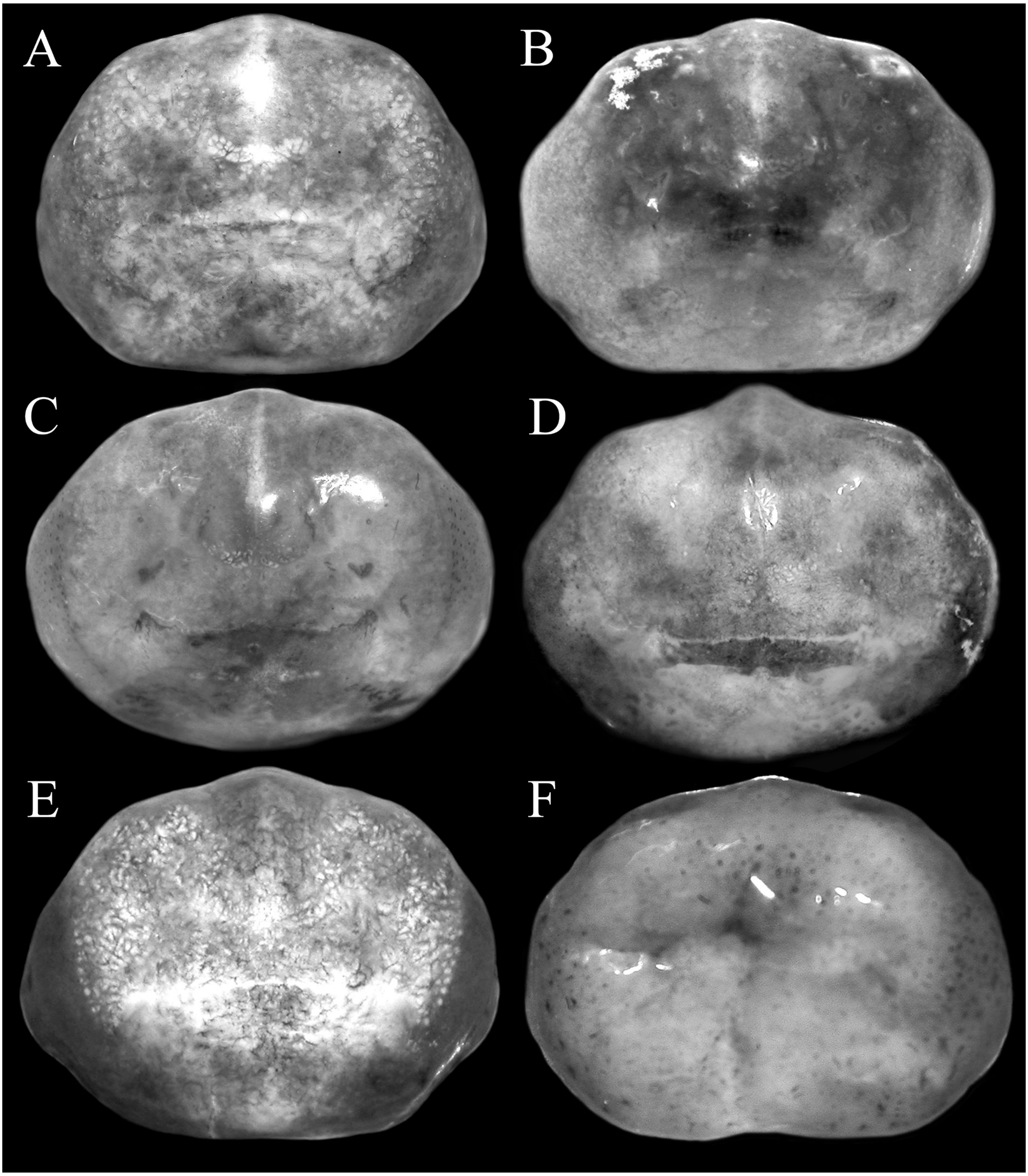

Fig. 82. *Magnotheres globosus* (Hombron & Jacquinot, 1846), dorsal view of female carapace. A, neotype ovigerous female (10.2 × 8.4 mm) (ZRC 2016.164), Singapore; B, ovigerous female (13.2 × 9.9 mm) (ZRC 2017.1018), Changi, Singapore; C, ovigerous female (13.6 × 10.5 mm) (ZRC 2017.1019), Changi, Singapore; D, ovigerous female (11.9 × 9.3 mm) (ZRC 2017.1019), Changi, Singapore; E, ovigerous female (13.5 × 10.7 mm) (ZRC 2016.165), Vanuatu; F, ovigerous female (12.1 × 9.4 mm) (ZRC 2016.166), Vanuatu.

spinules on the outer row (Fig. 83H') and only seven very short, barely visible spinules on the inner row (Fig. 83H"). The spinules on the inner row of the right side seem abraded, very short, and barely visible (Fig. 83H").

Colour. The colour of live females varies from pale brown, with numerous small, almost black flecks, to pale or bright purple (Figs. 72A, B, 73, 74, 75A, B, 76), with the eyes dark brown to red and white (Figs. 74C, D, 75B). In life, males are light brown with pale ventral surfaces (Fig. 77).

Host. Known with certainty from *Pinna* (*Subitopinna*) *atropurpurea* Sowerby, 1825, or *Pinna* (*Quantulopinna*) *muricata* Linnaeus, 1758 (Pinnidae Leach, 1819; Pinnoidea

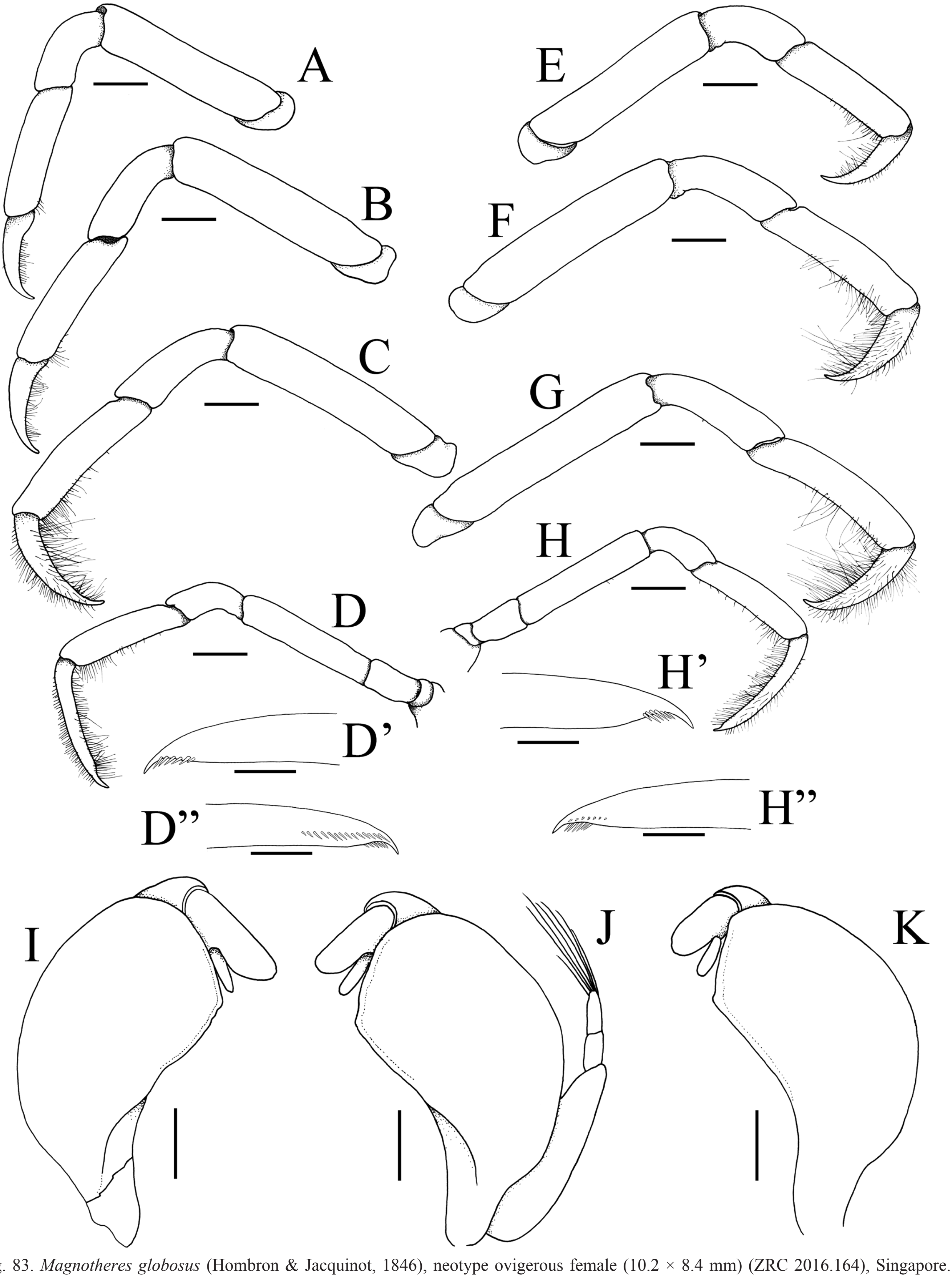

Fig. 83. *Magnotheres globosus* (Hombron & Jacquinot, 1846), neotype ovigerous female (10.2 × 8.4 mm) (ZRC 2016.164), Singapore. A–D, left P2–P5, respectively; D', distal part of dactylus of left P5 showing stiff subdistal spinules (dorsal view, soft setae omitted); D'', distal part of dactylus of left P5 showing stiff subdistal spinules (ventral view, soft setae omitted); E–H, right P2–P5, respectively; H', distal part of dactylus of right P5 showing stiff subdistal spinules (dorsal view, soft setae omitted); H'', distal part of dactylus of right P5 showing stiff subdistal spinules (ventral view, soft setae omitted); I, outer view of right MXP3 (basal part with breakage line, exopod, and setae omitted); J, left MXP3 (setae omitted); K, left MXP3 (slightly tilted, exopod and setae omitted). Scales = A–H, 2.0 mm; D', D'', H', H'', 0.2 mm; I–K, 1.0 mm.

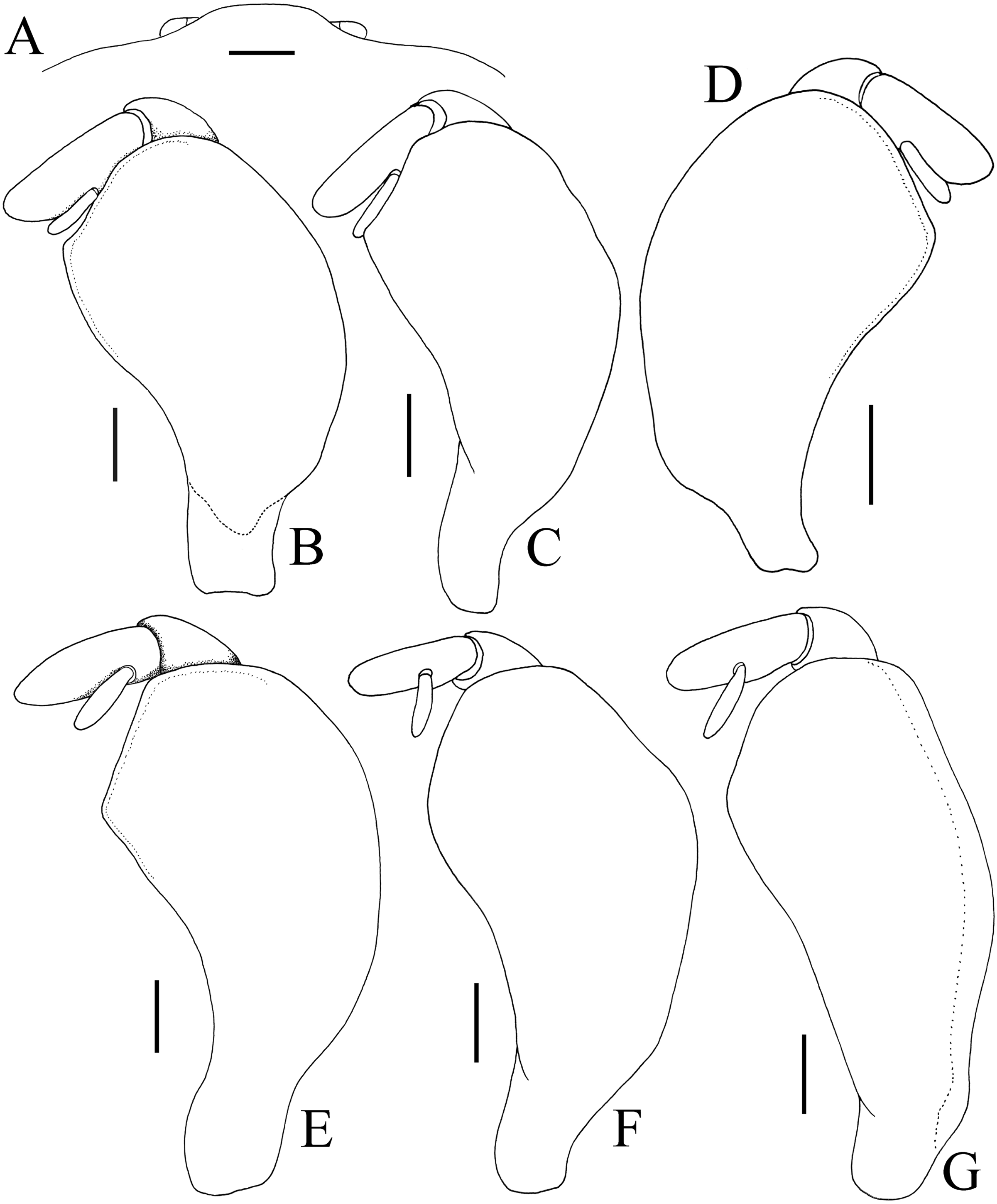

Fig. 84. *Magnotheres globosus* (Hombron & Jacquinot, 1846). A, ovigerous female (carapace width 11.9 mm, carapace broken) (ZRC 2017.1017), Panglao, Philippines; B, ovigerous female (13.6 × 10.5 mm) (ZRC 2017.1019), Changi, Singapore; C, ovigerous female (11.8 × 9.5 mm) (ZRC 2017.1017), Panglao, Philippines; D, ovigerous female (11.0 × 8.9 mm) (ZRC 2017.1017), Panglao, Philippines; E, ovigerous female (16.6 × 12.3 mm) (ZRC 2016.185), Kerala, India; F, G, ovigerous female (14.7 × 11.2 mm) (ZRC 2016.184), Kerala, India. A, frontal margin of carapace; B, C, E–G, left MXP3 (setae denuded); D, right MXP3 (setae denuded). F, G, drawn at different angles. Scales = A, 1.0 mm; B–G, 0.5 mm.

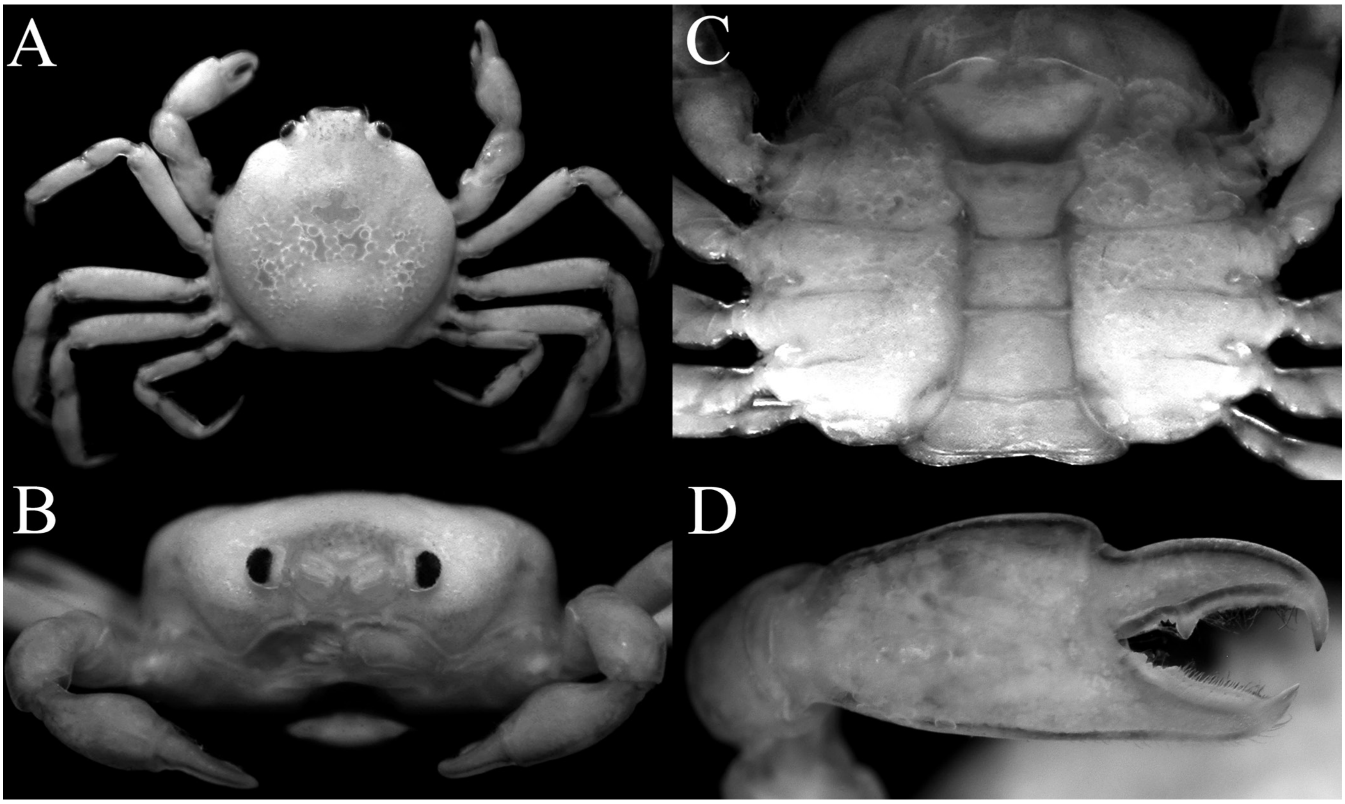

Fig. 85. *Magnotheres globosus* (Hombron & Jacquinot, 1846), male (5.4 × 5.5 mm) (ZRC 2018.783), Philippines. A, overall dorsal view; B, frontal view of cephalothorax; C, ventral view of sternum and pleon; D, outer view of right chela.

Leach, 1819). We have not found more than one specimen in any single *Pinna* collected. In Europe, another species, *Nepinnotheres pinnotheres* (Linnaeus, 1758), lives in *Pinna* (see Becker & Türkay, 2010; Trigos & Vicente, 2018; Acarli et al., 2019).

Remarks. The authorship and year of publication of *Pinnotheres globosum* was discussed by Clark & Crosnier (2000) and Holthuis (2002); we follow their recommendations to recognise the taxon as being validly published from the early published plate, i.e., the taxon should be cited as *Pinnotheres globosum* Hombron & Jacquinot, 1846. The text by Jacquinot & Lucas (1853) that actually described the species appeared later. Jacquinot & Lucas (1853: 59) apparently only had one 20 × 18-mm female, commenting that "Nous ne connaissons pas le mâle de ce *Pinnotheres*, qui a été pris dans une grosse Modiole à Singapour [We do not know the male of this *Pinnotheres*, who was caught in a big mussel in Singapore]" (Jacquinot & Lucas, 1853: 60). The French name for the host, "Modiole", is not a specific reference to *Modiolus*, but a vernacular reference to a mussel of some kind, which, at that time, would have included pinnids as well as mytilids. On the basis of the size and description of a "big mussel", it is almost certain that they obtained their specimen from a large species of *Pinna* (even today often called horse mussels), and that the crab species is what is currently known as *Arcotheres latus* (Bürger, 1895) (see Ng & Corbari, 2019). This is one of the two largest pinnotherids known from Singapore, with the largest known recent local specimen measuring 14.6 × 10.7 mm (ZRC 2017.1020), and the largest known specimen reaching 17.7 × 13.6 mm (from India). The carapace of this species is rather variable, with some almost circular in outline (Fig. 82).

Hombron & Jacquinot's (1846: pl. 5 fig. 21) figure of the species (present Fig. 78A–C) is very schematic, showing a round carapace with all the ambulatory legs symmetrical and the dactyli short and equal in length. Similarly, his figure of the MXP3 is inaccurate, with the presence of a faint suture between the ischium and merus, and the exopod long, exceeding the length of the ischiomerus (Hombron & Jacquinot, 1846: pl. 5 fig. 22). No species of pinnotherid from Singapore and Peninsular Malaysia has this kind of carapace, ambulatory legs, and MXP3. In fact, the MXP3 structure (shape as well as separation of the ischium and merus, and length of the exopod) is not found in any pinnotherid. Henri Milne Edwards (1853: pl. 11 fig. 6) depicted the MXP3 of a specimen from Vavao in the Solomon Islands more accurately, showing a long ischiomerus and relatively short dactylus which does not reach the tip of the propodus (Fig. 78D), features that agree very well with what is currently identified as *A. latus* (cf. Figs. 83I–K, 84B–G). Hombron & Jacquinot's (1846) figures are inaccurate and cannot be relied on.

The types of *Pinnotheres globosus* Hombron & Jacquinot, 1846, cannot be located in the MNHN and are almost certainly lost. In view of the complex and often confusing taxonomy of this species, uncertain identity, and the revised synonymy recognised here, a neotype should be selected. We here designate a recently collected female specimen (10.2

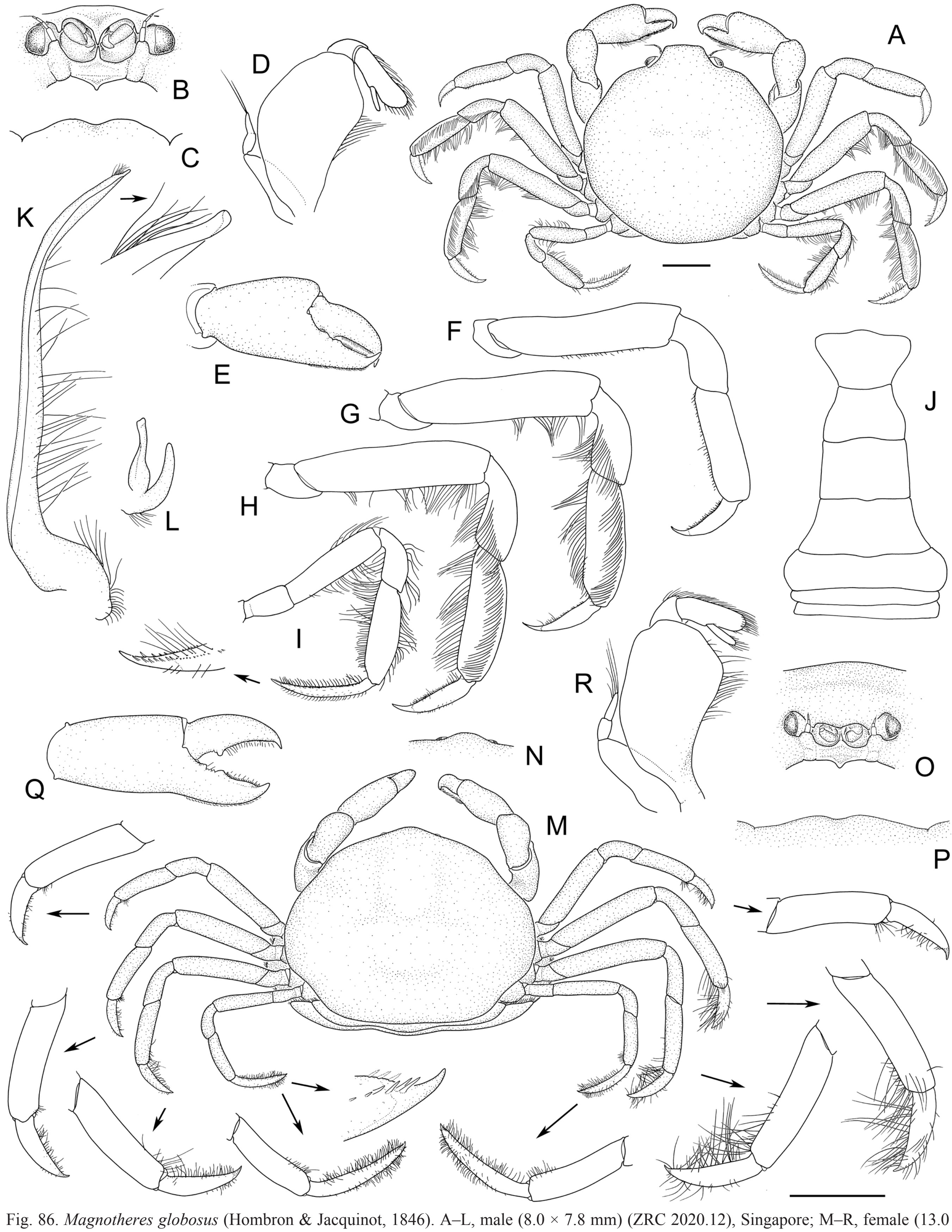

Fig. 86. *Magnotheres globosus* (Hombron & Jacquinot, 1846). A–L, male (8.0 × 7.8 mm) (ZRC 2020.12), Singapore; M–R, female (13.0 × 10.0 mm) (ZRC 2018.782), Philippines. A, M, overall dorsal view; B, O, frontal view of cephalothorax; C, P, anterior thoracic sternum; D, R, right MXP3; E, Q, right chela; F–I, right P2–P5; J, abdomen; K, left G1, abdominal view; L, left G2, abdominal view; N, carapace front, oblique dorsal view. Scales = A, 4.0 mm; B–J, 2.0 mm; K, L, 1.0 mm; M, N, 5.0 mm; O–Q, 2.5 mm; R, 1.25 mm.

× 8.4 mm; ZRC 2016.164) from Singapore as the neotype of *Pinnotheres globosus* Hombron & Jacquinot, 1846. This neotype is a recently collected, fully intact specimen from a known host and ethanol-preserved.

Comparisons of a large series of specimens of *M. globosus*, new combination, from many parts of the Indo-West Pacific, show that it is in fact a senior synonym of *Pinnotheres latus* Bürger, 1895 (type locality: Philippines), *Pinnoteres ridgewayi* Southwell, 1911 (type locality: Kondatchi Paar, Sri Lanka), and *P. borradailei* Nobili, 1906a (type locality: Lakshadweep, India). The lectotype of *P. latus* is relatively well preserved, but now relatively soft. Bürger (1895: pl. 9 fig. 16) figured the front as somewhat triangular, while Ahyong & Ng (2007b: fig. 6A) showed it to be truncate (see Variation). Ng et al. (2017: 1093) distinguished *A. ridgewayi* from *A. latus* by the proportionately longer MXP3 ischiomerus and differing proportions of the ambulatory dactyli, but the large series of specimens on hand now show that the differences are well within the range of variation for one species. Sankarankutty's (1966: text-figs. 23, 28) figures of the distal half of the G1 and male pleon of a specimen from southern India (as *P. ridgewayi*), although somewhat simple, show the characteristic slender G1 and trapezoidal male telson of *M. globosus*, new combination.

The taxonomy of *Arcotheres borradailei* (Nobili, 1906a) (a replacement name for *Pinnotheres tenuipes* Borradaile, 1903) from the Maldives was revised by Ng et al. (2017: 1093), who separated it from *A. ridgewayi* in possessing denser setation on the occlusal surfaces of the fingers of the chela, more rounded inner angle of the MXP3 ischiomerus, and proportionately shorter and stouter P3 and P4. Following our assessment of *M. globosus* based on the extensive series examined here, it is evident that the supposed distinguishing features of *A. borradailei* and *A. ridgewayi* are well within the range of variation of *M. globosus*, so the two species are herein synonymised. The original host record by Borradaile (1903: 432) is uncertain, said to be a "? *Mya*" (Myidae Lamarck, 1809), but this is probably a misidentification as the family is primarily a temperate one.

Rathbun (1909) proposed the name, *Pinnotheres alcocki*, for specimens reported as *P. parvulus* Stimpson, 1858, by De Man (1887, 1888) from Indonesia and the Mergui Archipelago, Bürger (1895) from the Philippines, and Alcock (1900) from an unspecified locality (presumably in Indian waters), rendering the "*P. parvulus*" material of all of these authors as syntypes. To fix the identity of the species, Ahyong & Ng (2007b) designated one of Bürger's (1895) Philippine specimens as the neotype of *Pinnotheres alcocki* and transferred it to *Arcotheres*. Gordon (1936: fig. 5) reported and partially figured one of the Mergui specimens of De Man (1887) as *Pinnotheres alcocki*, but after reexamination of the specimen (NHM 1886.52, a paralectotype of *P. alcocki*), we refer the specimen instead to *M. globosus*. Indeed, De Man (1887) had already noted the similarity of his material to *M. globosus* (as *Pinnotheres*) based on the limited type description and figures despite ultimately referring it to *P. parvulus*. The Mergui specimen, an ovigerous female, is in poor condition, appearing to have been fixed in formalin given the "stiffness" of the appendages and cuticle texture. The carapace is collapsed and the frontal margins sunken in, but the walking legs are intact with the right P4 only slightly longer than the left. De Man (1887) reported the host as *Pinna atropurpurea* Sowerby, 1825, and *Pinna vexilllum* Born, 1778 (now *Atrina*), consistent with what we know of *M. globosus*. The present record constitutes the first confirmation of *M. globosus* from the Andaman Sea.

Females of several species of *Arcotheres* superficially resemble *M. globosus* in sharing similar MXP3 form and a similarly elongated P5 dactylus with two distoflexor rows of spinules on the dactylus: *A. alcocki*, *A. similis*, and *A. placunicola*. Although the differences in P4 symmetry and carapace shape are distinctive in intact, well-preserved specimens, incomplete, poorly preserved specimens, or specimens with regenerating pereopods can be more difficult to separate generically. In such a situation, the distally hooked P2 and P3 dactyli will separate *A. alcocki* and *A. placunicola* from *M. globosus*, which has broadly curved dactyli. Both *A. similis* and *M. globosus* share similarly broadly curved P2 and P3 dactyli, and are difficult to separate without reference to the P4 and carapace. In female *M. globosus*, however, the buccal margin of the epistome is transverse with a narrowly triangular median point (Figs. 79C, 81E), rather than very broadly angular in *A. similis* (Figs. 28D, 30K).

The Australian specimens of "*A. similis*" reported by Ahyong & Brown (2003) and Ward (1967), mostly from *Pinna*, were restudied and referred to *A. globosus* by Ahyong (2020b). Among these is a large female (AM P20161) with the host recorded as the mytilid *Stavelia subdistorta* (Récluz, 1852); the host data for this specimen may be incorrect given that *M. globosus* is otherwise not known from the Mytilidae.

Distribution. Western Pacific to central Indian Ocean, including Palau, Vanuatu, Australia, Philippines, Singapore, Myanmar, Sri Lanka, and India.

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