RAFFLES BULLETIN OF ZOOLOGY **68**: 267–307
Date of publication: 29 April 2020
DOI: 10.26107/RBZ-2020-0023
http://zoobank.org/urn:lsid:zoobank.org:pub:057B08EE-1006-43E8-AE20-0AF8F224BA2D

A revision of the deep-sea porter crabs of the genus *Gordonopsis* Guinot & Richer de Forges, 1995 (Crustacea, Decapoda, Brachyura, Homolidae), with descriptions of five new species

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Abstract. For the century to 2018, only one species of the deep-water porter crab *Gordonopsis* Guinot & Richer de Forges, 1995 (Brachyura, Homolidae), the type species, *G. profundorum* (Alcock & Anderson, 1899), was known, and only from a handful of specimens from the Indian Ocean. In 2019, two species were described from the eastern Indian and western Pacific Oceans. The present revision of available material, most of which was only collected in the last decade, adds five new species to the genus. This explosion in species numbers demonstrates just how poor our understanding is of deep-sea habitats and their constituent fauna.

Key words. taxonomy, world revision, Homoloidea, new species, rarity

INTRODUCTION

The many deep-sea surveys in the Indo-West Pacific between 1986 and 2013 by French vessels have collected large numbers of porter crabs of the family Homolidae De Haan, 1839 (see Guinot & Richer de Forges, 1995; Richer de Forges & Ng, 2007, 2008, 2020; Naruse & Richer de Forges, 2010; Richer de Forges et al., 2013; Ng & Richer de Forges, 2017), and numerous new taxa have been reported over the years. One genus, however, that has remained relatively unchanged is *Gordonopsis* Guinot & Richer de Forges, 1995, established for one species, *Homola profundorum* Alcock & Anderson, 1899, from the Indian Ocean and known only from a handful of specimens.

Over the last five years, various French and other expeditions have collected a number of specimens of *Gordonopsis* from both the Indian and Pacific Oceans. The authors have been progressively examining these as well as old material in an attempt to revise the genus, but this work was constrained by their inability to find the type specimens. Recently, Ng et al. (2019) described a new species, *G. robusta*, from the eastern Indian Ocean, while Takeda & Suyama (2019) described *G. pacifica*, from southernmost Japan. The present study revises *Gordonopsis*. The poorly known *Gordonopsis profundorum* s. str. is rediagnosed based on a neotype selection. Five species of *Gordonopsis* from the Indian and Pacific Oceans are here described as new: *G. alaini* (Madagascar), *G. hera* (Papua New Guinea), *G. velutina* (Admiralty Islands), *G. phorcys* (Solomon Islands), and *G. ceto* (South China Sea).

MATERIAL AND METHODS

The abbreviations G1 and G2 are used for male first and second gonopods, respectively. The terminology follows Guinot & Richer de Forges (1995), Guinot & Bouchard (1998), and Davie et al. (2015). Measurements provided (in millimetres) are of the maximum carapace width and length (including spines and rostrum), respectively. The term spine is used when the structure is prominent and long; when small (e.g., resembling a sharp and elongate granule), the term spinule is used instead.

The material examined is deposited in the Muséum National d'Histoire Naturelle, Paris, France (MNHN); The Natural History Museum, London, U.K. (NHM); Museum für Naturkunde, Berlin, Germany (ZMB); Centre for Marine Living Resources and Ecology, Kochi, Kerala, India (CMLRE); National Science Museum, Tokyo, Japan (NSMT); Crustacean Collections of the National Taiwan Ocean University, Taiwan (NTOU); and the Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore (ZRC).

Accepted by: Jose Christopher E. Mendoza

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

SYSTEMATICS

Family Homolidae De Haan, 1839

Gordonopsis Guinot & Richer de Forges, 1995

Type species. *Homola profundorum* Alcock & Anderson, 1899, by original designation and monotypy.

Diagnosis. Carapace longitudinally ovate to subpyriform, anterior half of carapace narrower than posterior half; dorsal surface not ornamented but with scattered to dense setae; gastric fossa distinct; cervical groove pronounced; homolian line (linea homolica) on each side prominent; subhepatic region gently convex but not swollen, with short spine; rostral spine long, thick, pseudorostral spines well developed, directed anterolaterally; no teeth or latero-anterior spines, gastric and cardiac regions gently convex; latero-posterior edge with low prominence or distinct tooth or spine; orbit absent; ocular peduncle short, stout; infra-orbital spine absent; acute antennal spine, visible dorsally; antennal articles 2 and 3 very wide, with strong external distal spine, article 4 relatively short, broad; proepistome weakly developed; epistome very reduced; third maxilliped pediform, narrow, covering only part of buccal frame, anterior margin of merus exceeding endostomial crest; chelipeds not prominently elongate, fingers relatively long, thin, without pigmented spot at base of pollex; P2–P4 relatively long; merus long, dorsal margins armed with spines, ventral margin with short spines or unarmed; proximal part of outer surface of P4 may have tubercle or short spine on outer surface or unarmed; P5 short, total length less than length of P4 merus; merus slender, unarmed on all surfaces, reaching to gastric groove or mesogastric region on the carapace above gastric fossae, propodus and dactylus subchelate, occluding margins with long spines; male pleon locked between coxae of P1–P4: spinule present on inner margin of each coxa of P1–P3 that locks pleon to appress it to sternum; anterior tip of telson positioned between basis and coxa of third maxillipeds; lock present as "homolid press button" mechanism (sternal prominence on outer edge of sternite 4 above articular condyle of P1 coxa, socket in inner surface of pleonal somite 6); male and female pleon with 6 free somites and telson; G1 stout, short with distal part tapering; G2 short, as long as G1, distal part spatuliform. (Modified from Guinot & Richer de Forges, 1995: 463)

Remarks. *Gordonopsis* Guinot & Richer de Forges, 1995, was established for a rare species formerly placed in *Paromola* Wood-Mason in Wood-Mason & Alcock, 1891 (Alcock, 1901; Doflein, 1904; Ihle, 1913). Only one species was known at that time, *G. profundorum* (Alcock & Anderson, 1899), described from three young female specimens (ca. 13.0 × 9.0 mm) collected in the western Indian Ocean off the Travancore coast, India (7°17′30″N, 76°54′30″E) at a depth of 796 m (Alcock & Anderson, 1899: 5; Alcock, 1901: 65) (Fig. 1). The species was subsequently reported from the east coast of Africa by Doflein (1904: 16) from a male 24 mm in carapace length, with Gordon (1950: 220) recording a male 16.0 × 11.0 mm from the Maldives. Guinot & Richer de Forges (1981: 536) later examined a male 15.4 × 10.0 mm from Madagascar.

Guinot & Richer de Forges (1995) studied the material from the Maldives and Madagascar as well as one broken specimen from the Seychelles and observed differences between the description of *G. profundorum* as described and figured by Alcock & Anderson (1899) and Alcock (1901). As such, they were uncertain if all the specimens were conspecific. The Seychelles specimen was too damaged to be useful. Guinot & Richer de Forges (1995) identified their material as "*Gordonopsis* aff. *profundorum*", particularly for the specimen from the Maldives, which according to them, had a more bulging carapace as well the possession of a distinct short spine on the latero-posterior part of the carapace, just behind the branchio-hepatic groove (Fig. 2B). The specimen from Madagascar (Fig. 9B) agrees with the type description and figures of *G. profundorum* in possessing a short spine on the latero-posterior part of the carapace (Fig. 9B). Alcock & Anderson (1899: 10, pl. 1 fig. 2) noted that there was a "blunt denticle near the middle of the ill-defined lateral border" of the carapace and their figures actually show this (Fig. 1B). The excellent figure of the East African specimen by Doflein (1904) also shows a latero-posterior tubercle on the carapace (Fig. 6B). The specimen from the Maldives has the lateral sides of the carapace slightly more bulging, giving the carapace a less pyriform and more ovate shape and the latero-posterior carapace tubercle is a distinct short spine (Fig. 2B). Guinot & Richer de Forges (1995: 467) also commented that the ambulatory legs of the specimens from Madagascar and Maldives appeared to be longer and slenderer than the Indian ones, but the accuracy of Alcock's (1901) figures cannot be ascertained.

The uncertainty over the identity of *G. profundorum* has been a major problem, and a revision of the genus is only possible once this has been resolved. In this revision, we select a neotype for the species (see discussion for type species below). We also rediagnose *G. robusta* and *G. pacifica* based on the type material and describe five new species from Madagascar, Papua New Guinea, Admiralty Islands, Solomon Islands, and the South China Sea.

Gordonopsis profundarum (Alcock & Anderson, 1899)

(Figs. 1–8)

Homola profundorum Alcock & Anderson, 1899: 5; Alcock, 1899: 10, pl. 1 fig. 2.

Homola (*Paromola*) *profundorum* – Alcock, 1901: 64, pl. 5 fig. 22; Doflein, 1904: 16, pl. 7 figs. 1, 2.

Paromola profundorum – Ihle, 1913: 57; Serène & Lohavanijaya, 1973: 27.

Paromola profundarum – Gordon, 1950: 223; Griffin, 1965: 87.

Gordonopsis profundorum – Guinot & Richer de Forges, 1995: 463, figs. 63d–h, 64A, B.

Gordonopsis aff. *profundorum* – Guinot & Richer de Forges, 1995: 467 (in part).

Gordonopsis profundorum – Ng et al., 2008: 40.

Material examined. Neotype: male (11.0 × 16.0 mm) (here designated) (NHM 1948.9.7.28), stn 153, 4°42′36″N,

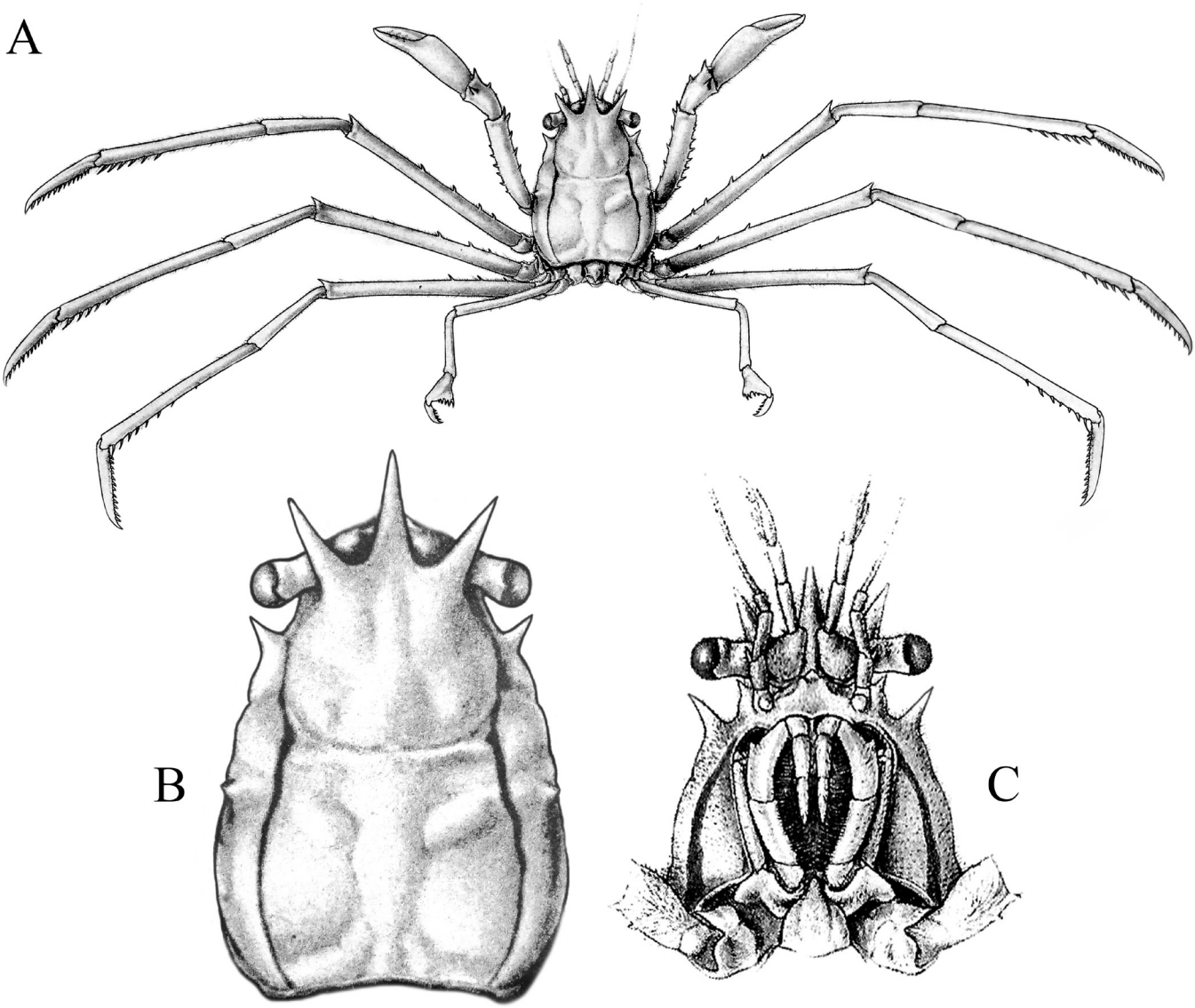

Fig. 1. *Gordonopsis profundarum* (Alcock & Anderson, 1899), syntype female (ca. 13.0 × 9.0 mm), Travancore, India. A, overall habitus; B, dorsal view of carapace; C, frontal view of cephalothorax showing buccal cavity, epistome, antennae, antennules, and third maxillipeds. After Alcock (1901: pl. 5 fig. 22).

72°50′24″E – 4°45′36″N, 72°52′12″E, Maldives, 256–293 m, dredge, coll. John Murray Expedition, 4 April 1934. – 1 male (16.3 × 24.1 mm) (ZMB 13645), stn 258, 2°58.5′N, 46°50.8′E, off Somalia, East Africa, 1,362 m, coll. Deutsche Tiefsee Expedition, coll. Valdivia, 1898–1899.

Diagnosis. Male: carapace longitudinally ovate, width to length ratio 0.68–0.69, distinctly wider posteriorly than anteriorly; dorsal carapace surface with well-defined regions, separated by broad, deep grooves; lateral margin distinctly convex; dorsal parts with numerous scattered soft setae, not obscuring surface; lateral parts with denser setae, partially obscuring surface, relatively denser on hepatic, pterygostomial, and suborbital regions (Figs. 1A–C, 2A–C, 3A, B, 6A–C, 7A, B). Rostrum relatively long, sharp, with 2 long, obliquely directed pseudorostral spines, just shorter than rostrum (Figs. 1B, 2B, 6B). Supraorbital margin relatively narrow, C-shaped; pseudorostral spines directed obliquely laterally at angle of about 45° to median axis (Figs. 1B, 2B, 6B). Eyes with short ocular peduncle, cornea prominent; no discernible orbit (Figs. 1B, 2B, 6B). Hepatic region gently inflated, with short obliquely directed spine (Figs. 1B, 2B, 6B). Gastric region without spines (Figs. 1B, 2B, 6B). Gastric groove well marked, with distinct ovate gastric fossae just above (Figs. 1B, 2B, 6B). Cardiac region swollen; branchial region inflated, with distinct branchio-cardiac grooves (Figs. 1B, 2B, 6B). Latero-posterior tubercle on carapace large, prominent, sharp (Figs. 1B, 2B, 6B). Base of antenna with strong spine (Figs. 1C, 3D, 7D). Antennal flagellum short, second and third articles thick, setose. Epistome triangular (Figs. 1C, 3D, 7D). Third maxilliped pediform, merus elongate with angular external angle (Figs. 1C, 3C, 7C). Chelipeds long; fingers long, about half length of palm; surface gently rugose with scattered small granules; carpus longitudinally ovate, outer margin with 3 spines and 2 or 3 spinules, distal edge with 1 spine, inner margin with 2 or 3 spines and 2 or 3 spinules, dorsal surface with low ridge lined with 6–9 low or sharp granules, never spines; merus triangular in cross-section, relatively long, curved, dorsal margin with 5 or 6 spines and distal 2 spines bracketing

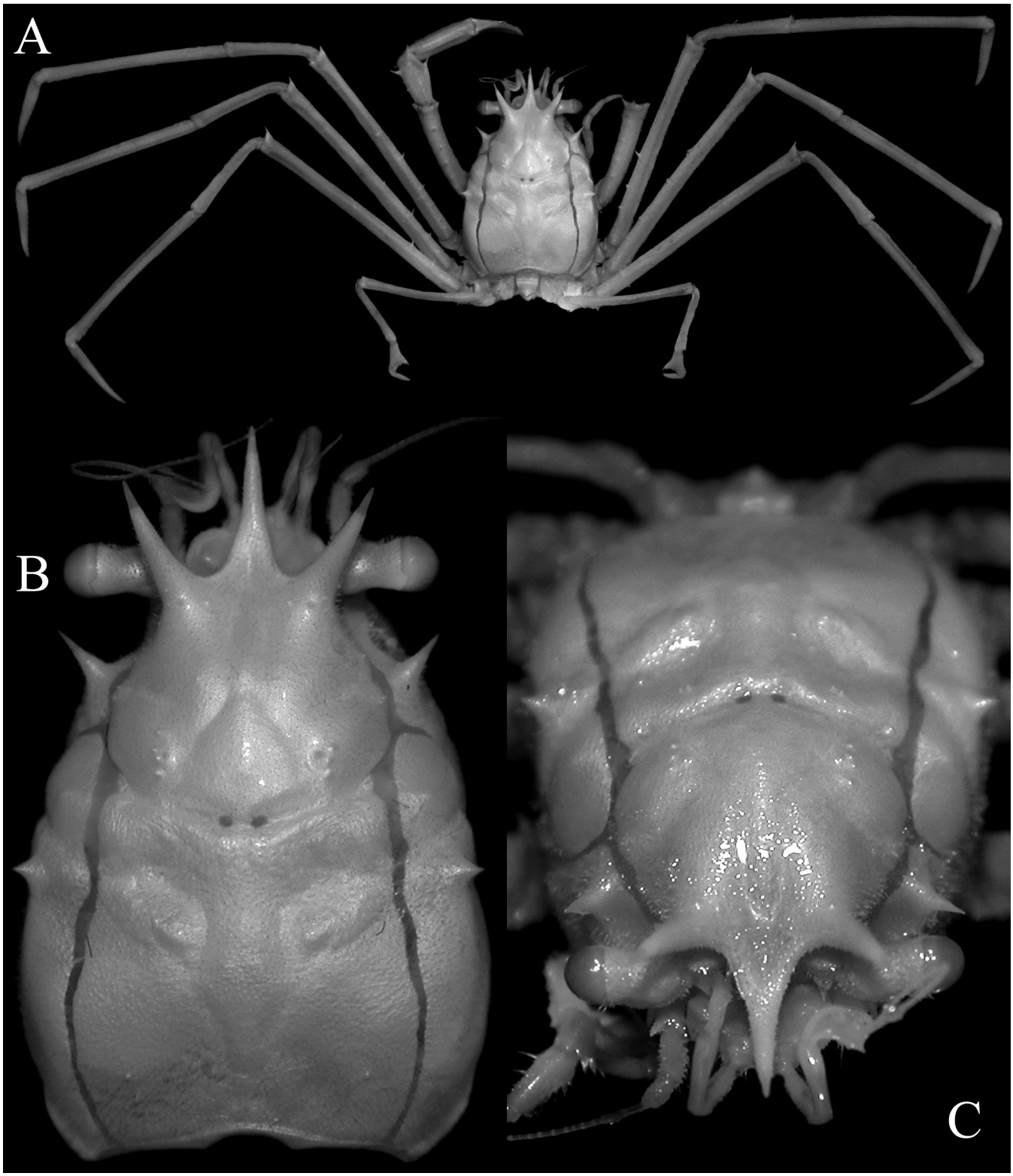

Fig. 2. *Gordonopsis profundarum* (Alcock & Anderson, 1899), neotype male (16.0 × 11.0 mm) (NHM 1948.9.7.28), Maldives. A, overall habitus; B, dorsal view of carapace; C, dorso-frontal view of carapace.

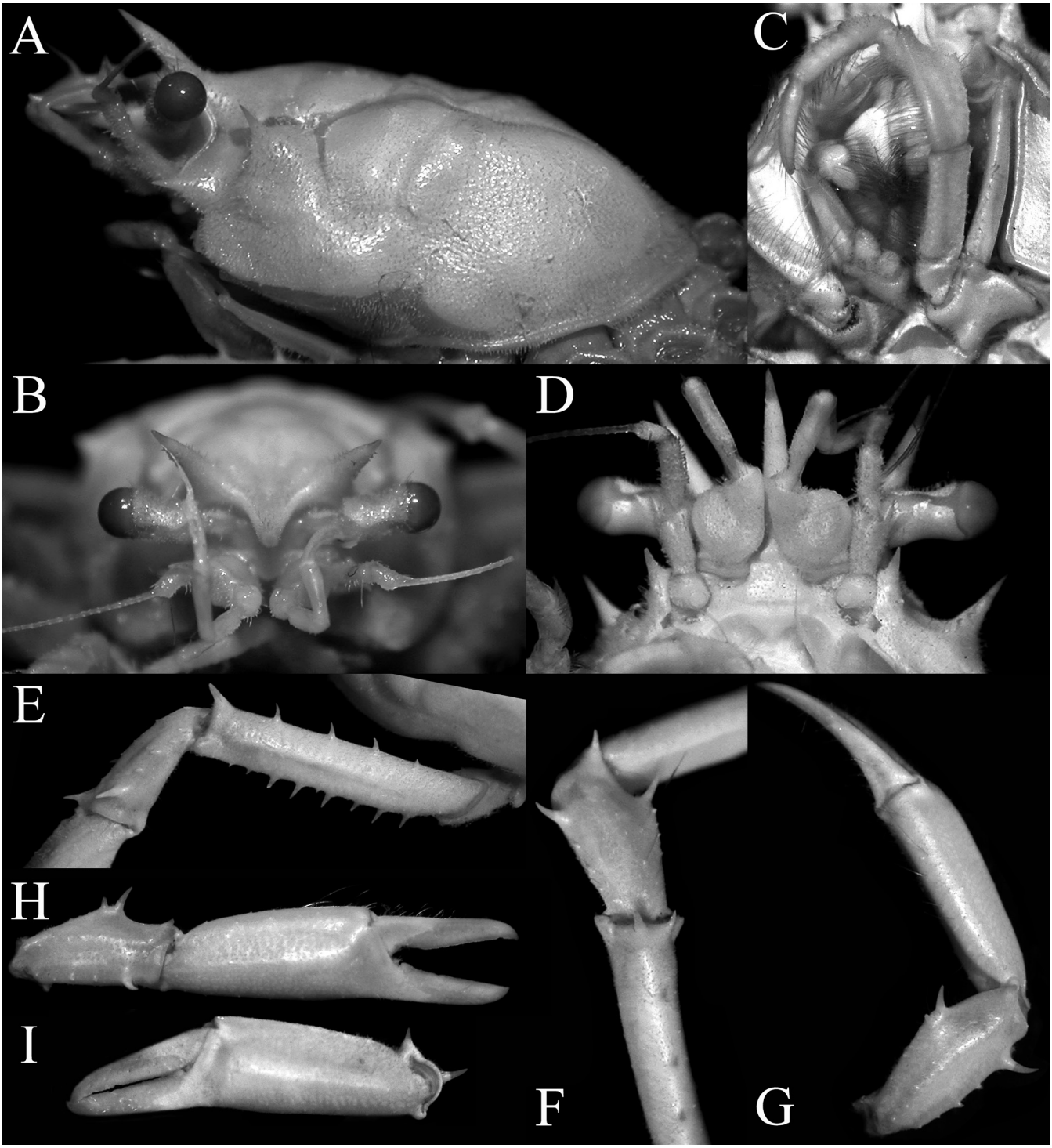

Fig. 3. *Gordonopsis profundarum* (Alcock & Anderson, 1899), neotype male (16.0 × 11.0 mm) (NHM 1948.9.7.28), Maldives. A, lateral view of cephalothorax; B, frontal view of cephalothorax; C, left third maxilliped; D, ventral view showing buccal cavity, epistome, antennae, and antennules; E, outer view of merus and carpus of left cheliped; F, dorsal view of left merus, carpus, and chela; G, dorsal view of right carpus and chela; H, outer view of right chela; I, outer view of left chela.

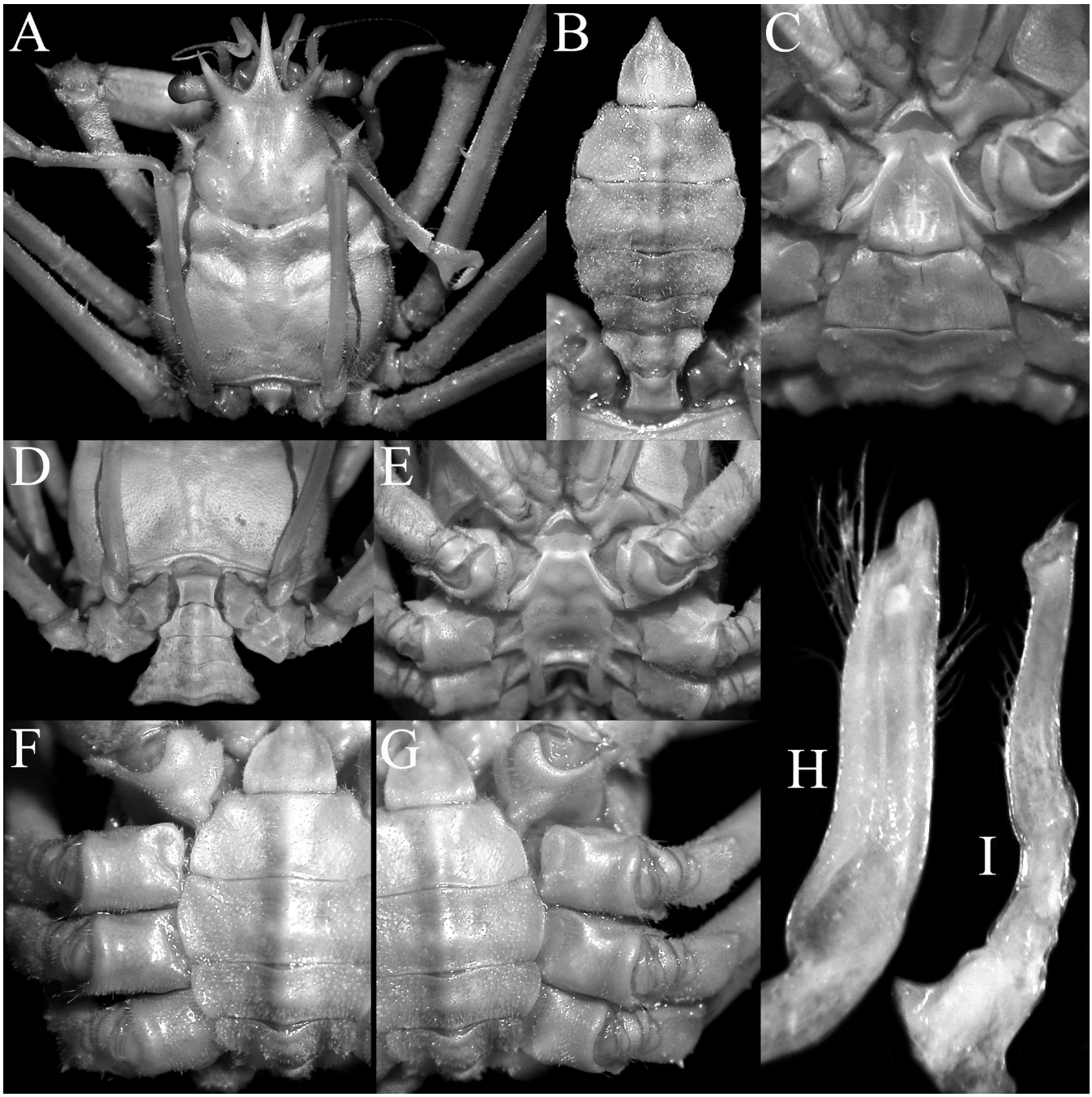

Fig. 4. *Gordonopsis profundarum* (Alcock & Anderson, 1899), neotype male (16.0 × 11.0 mm) (NHM 1948.9.7.28), Maldives. A, dorsal view of carapace showing relative P5 length; B, pleon; C, telson and pleonal somite 6; D, posterior part of carapace and pleon; E, sternopleonal cavity; F, right P2–P4 coxae and basis-ischia (denuded); G, left P2–P4 coxae and basis-ischia (denuded); H, ventral view of left G1; I, ventral view of left G2.

chela, outer ventral margin with 7–9 spines or spinules, inner ventral margin with 5 or 6 spines or spinules (Figs. 1A, 2A, 3E–I, 6A, 7E–G). Ambulatory legs long; basis-ischium with small granules, not spines; P2 merus with 5 spines or spinules on dorsal margin (excluding 1 distal spine), ventral and subventral margins with 1–4 spinules; P3 merus with 5 or 6 spines or spinules on dorsal margin (excluding 1 distal spine), ventral and subventral margins with 0–3 spinules; P4 merus with 3 or 4 spines or spinules on dorsal margin (excluding 1 distal spine), ventral margin with 1 spine or spinule, outer surface with 1 strong proximal spine or spinule (Figs. 1A, 2A, 5A–C, 6A, 8F–H). P5 merus slender, unarmed on all margins, reaching beyond gastric groove when folded anteriorly; carpus long, propodus short, enlarged, forming prominent pseudochela with stout, gently curved dactylus; occlusal margin of fixed finger with 7–9 spines, that of dactylus with 7 or 8 spines (Figs. 4A, 5D–F, 8A, I, J). Outer margins of P2–P4 coxae smooth, unarmed (Figs. 4E–G, 8D, E). Telson triangular, with convex lateral margins, distal part distinctly narrowing (Figs. 4B–D, 8B, C). G1 short, stout, distal part subconical with convex tip (Figs. 4H, 8K). G2 stout, tubular, subequal to G1 length, distal portion cup-shaped (Figs. 4I, 8L).

Description of male neotype. Male: carapace longitudinally ovate, width to length ratio 0.69, distinctly wider posteriorly

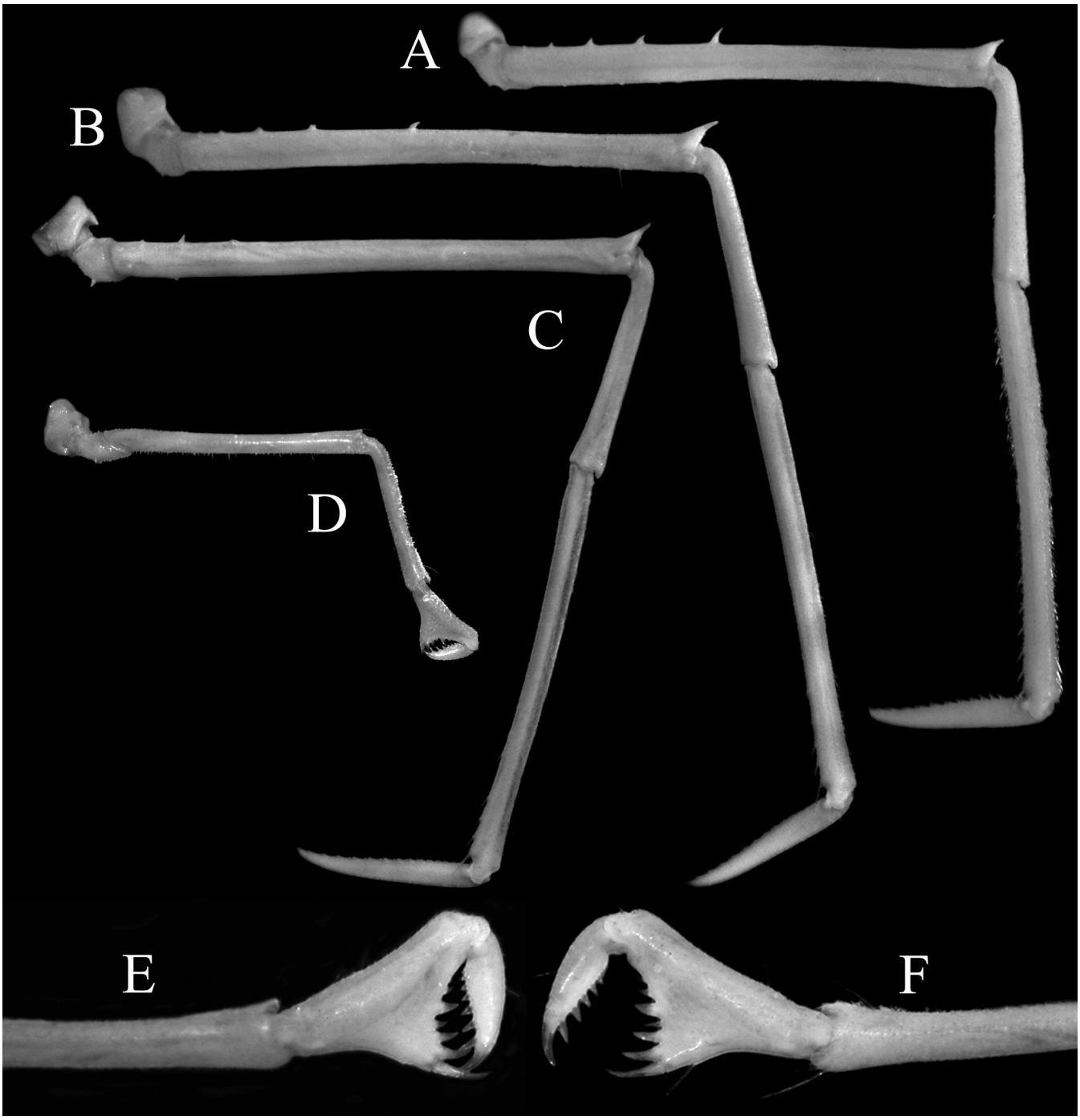

Fig. 5. *Gordonopsis profundarum* (Alcock & Anderson, 1899), neotype male (16.0 × 11.0 mm) (NHM 1948.9.7.28), Maldives. A–D, right P2–P5, respectively (all to same scale); E, right P5 pseudochela; F, left P5 pseudochela.

than anteriorly; dorsal carapace surface with well-defined regions, separated by broad, deep grooves; lateral margin distinctly convex; dorsal parts with numerous scattered soft setae, not obscuring surface; lateral parts with denser setae, partially obscuring surface, relatively denser on hepatic, pterygostomial, and suborbital regions (Figs. 1A–C, 2A–C, 3A, B, 6A–C, 7A, B). Rostrum relatively long, sharp, with 2 long, obliquely directed pseudorostral spines, shorter than rostrum (Figs. 1B, 2B, 6B). Supraorbital margin relatively narrow, C-shaped; pseudorostral spines directed antero-laterally at angle of about 45° to median axis (Figs. 1B, 2B, 6B). Eyes with short ocular peduncle, cornea prominent; no discernible orbit (Figs. 1B, 2B, 6B). Hepatic region gently inflated, with short obliquely directed spine (Figs. 1B, 2B, 6B). Gastric region without spines, each mesogastric region with median patch of small granules (Figs. 1B, 2B, 6B). Gastric groove well marked, with distinct ovate gastric fossae just above (Figs. 1B, 2B, 6B). Cardiac region swollen; branchial region inflated, with distinct branchio-cardiac grooves (Figs. 1B, 2B, 6B). Latero-posterior tubercle on carapace distinct, prominent (Figs. 1B, 2B, 6B). Base of antenna with strong spine (Figs. 1C, 3D, 7D). Antennal flagellum short, second and third articles thick, setose. Epistome triangular (Figs. 1C, 3D, 7D). Third maxilliped pediform, merus elongate with angular external angle (Figs. 1C, 3C, 7C). Chelipeds long; fingers long, about half length of palm; surface gently

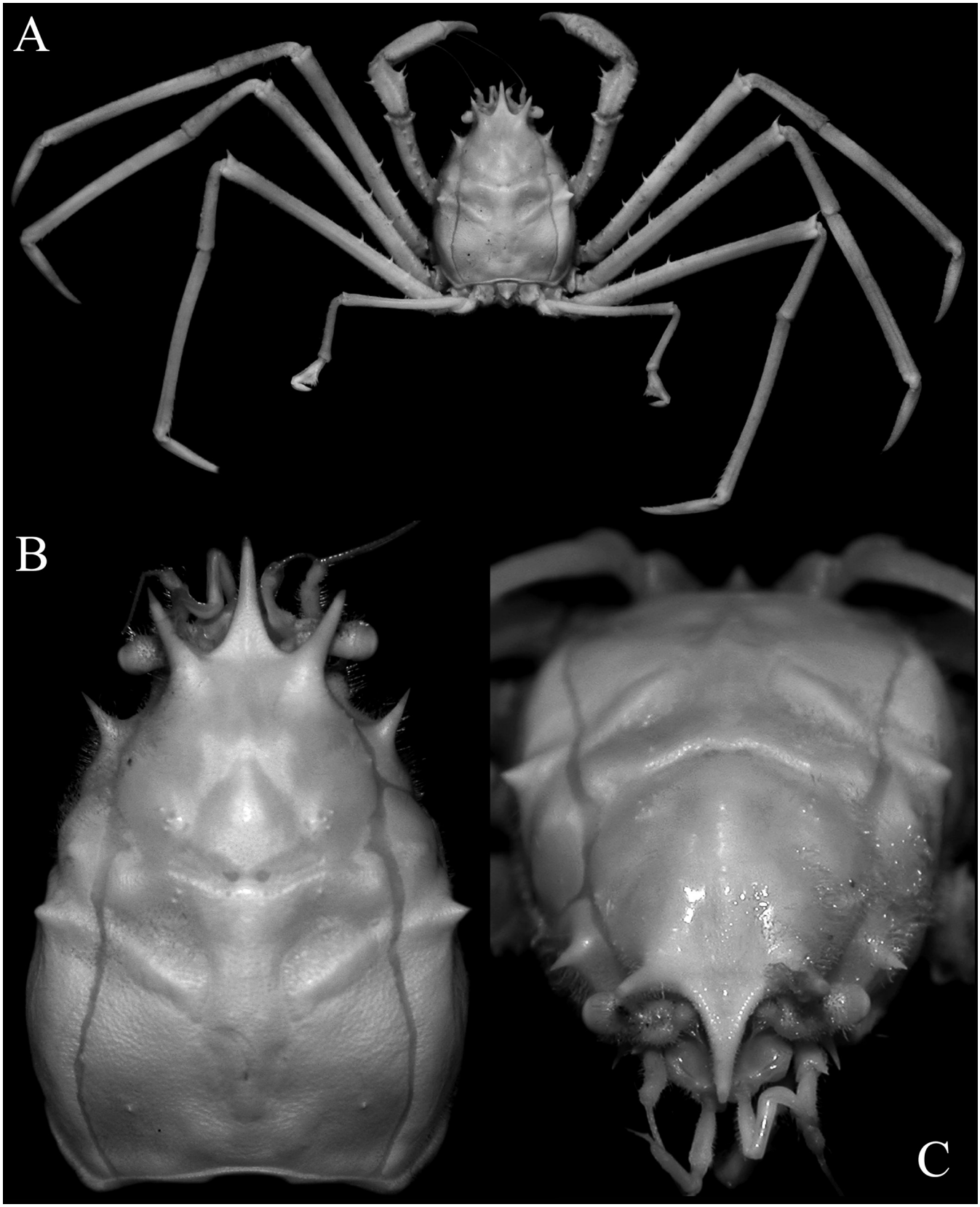

Fig. 6. *Gordonopsis profundarum* (Alcock & Anderson, 1899), male (16.3 × 24.1 mm) (ZMB 13645), East Africa. A, overall habitus; B, dorsal view of carapace; C, dorso-frontal view of carapace.

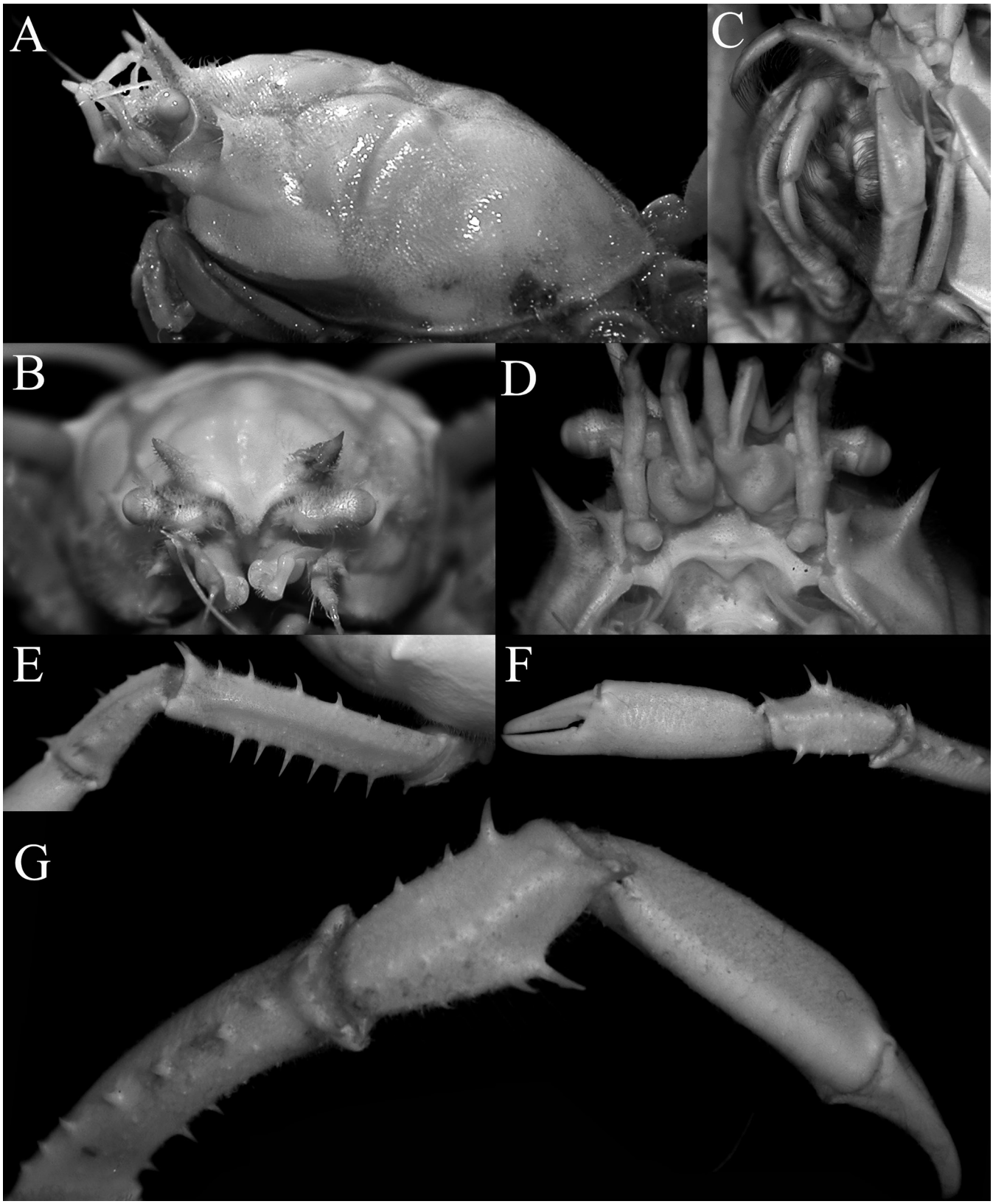

Fig. 7. *Gordonopsis profundarum* (Alcock & Anderson, 1899), male (16.3 × 24.1 mm) (ZMB 13645), East Africa. A, lateral view of cephalothorax; B, frontal view of cephalothorax; C, left third maxilliped; D, ventral view showing buccal cavity, epistome, antennae, and antennules; E, outer view of merus and carpus of left cheliped; F, outer view of left carpus and chela; G, dorsal view of left cheliped.

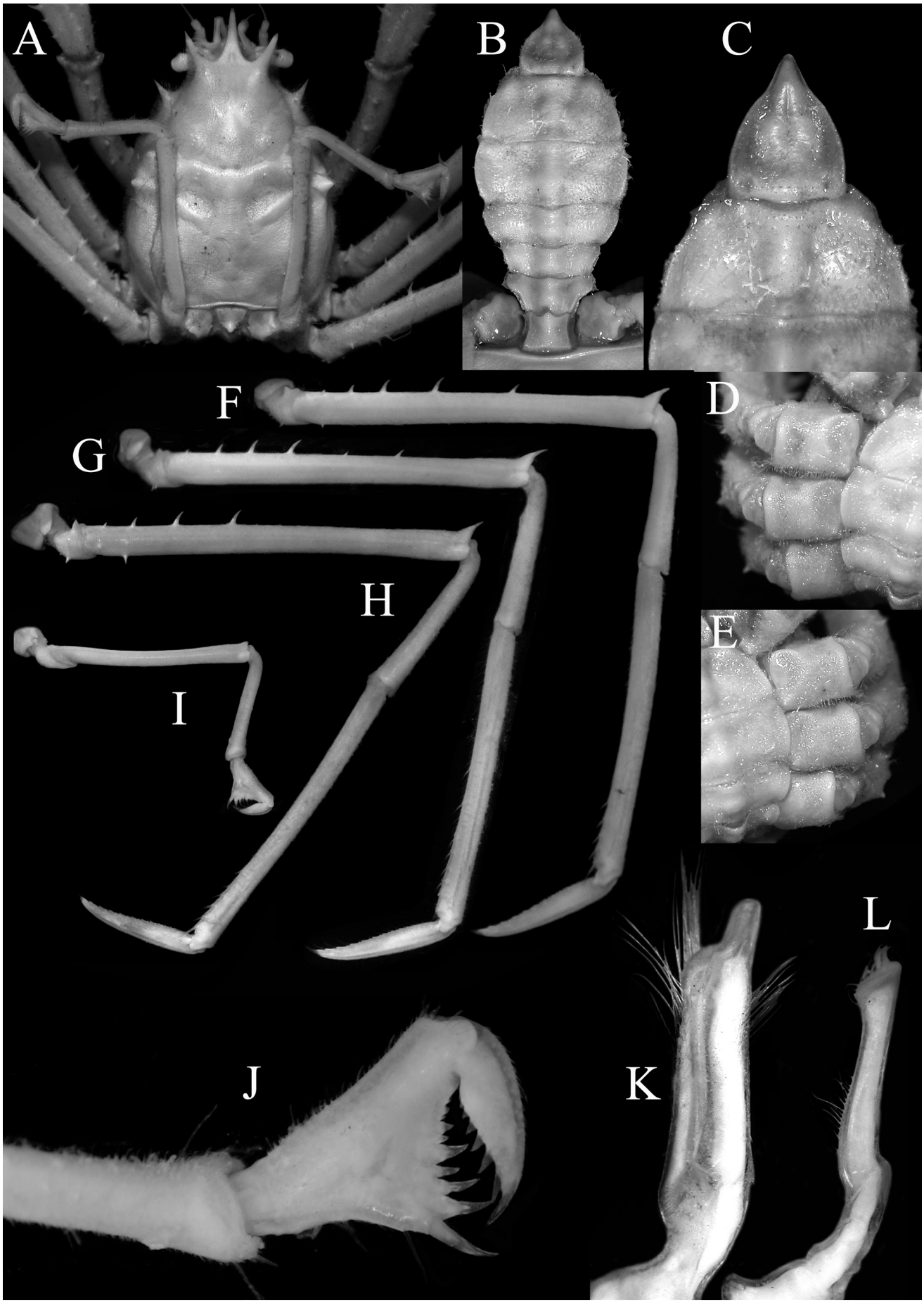

Fig. 8. *Gordonopsis profundarum* (Alcock & Anderson, 1899), male (16.3 × 24.1 mm) (ZMB 13645), East Africa. A, dorsal view of carapace showing relative P5 length; B, pleon; C, telson and pleonal somite 6; D, right P2–P4 coxae and basis-ischia (denuded); E, left P2–P4 coxae and basis-ischia (denuded); F–I, right P2–P5, respectively (all to same scale); J, right P5 pseudochela; K, ventral view of left G1; L, ventral view of left G2.

rugose with scattered small granules; carpus longitudinally ovate, outer margin with 3 spines and 2 spinules, distal edge with 1 spine, inner margin with 2 spines and 3 spinules, dorsal surface with low, uneven ridge lined with 6–8 very low granules; merus triangular in cross-section, relatively long, curved, dorsal margin with 4 spines and 2 spinules, with distal 2 spines bracketing chela, outer ventral margin with 8 or 9 spines or spinules, inner ventral margin with 6 spinules (Figs. 1A, 2A, 3E–I, 6A, 7E–G); basis-ischium quadrate, outer margin with 2 spinules, inner margin with 3 spinules, dorsal margin with prominent spine. Ambulatory legs long; basis-ischium with 4 small granules (sometimes very small and almost undiscernible), never with spines; P2 merus with 5 spines or spinules on dorsal margin (excluding 1 distal spine), subventral margin with 4 spinules; P3 merus with 5 spines or spinules on dorsal margin (excluding 1 distal spine), subventral margin with 3 spinules; P4 merus with 3 spines on dorsal margin (excluding 1 distal spine), ventral margin with 1 spinule, outer surface with 1 strong proximal spinule (Figs. 1A, 2A, 5A–C, 6A, 8F–H). P5 merus slender, unarmed on all margins, reaching beyond gastric groove when folded anteriorly; carpus long, propodus short, enlarged, forming prominent pseudochela with stout, gently curved dactylus; occlusal margin of fixed finger with 7 spines, that of dactylus with 7 or 8 spines (Figs. 4A, 5D–F, 8A, I, J). Outer margins of P2–P4 coxae smooth, unarmed (Figs. 4E–G, 8D, E). Telson triangular, with gently convex lateral margins, distal part distinctly narrowing (Figs. 4B–D, 8B, C). G1 short, stout, distal part subconical with gently convex tip (Figs. 4H, 8K). G2 stout, tubular, subequal to G1 length, distal portion cup-shaped (Figs. 4I, 8L).

Variation. The latero-posterior carapace tubercles do not appear to vary—both the small female from Maldives and the large East African specimens have similarly sized large ones (Figs. 2B, 6B); and both have the same carapace shape as well as long ambulatory legs of similar proportions.

Colour. Not known.

Remarks. Alcock & Anderson (1899) named the species "*Homola profundorum*" and also used this spelling in another paper (Alcock, 1901). Gordon (1950) used the spelling "*profundarum*" for the species but she did not explain why, and other authors have continued to use "*profundorum*" (cf. Ihle, 1918; Guinot & Richer de Forges, 1995; Ng et al., 2008). If the gender of the genus name is masculine or neuter, the species name should be spelled, "*profundorum*". *Gordonopsis*, however, is feminine (all names ending in -*opsis* are feminine under Article 30.1.2 of the zoological code; ICZN, 1999) and so, the correct spelling for the species name is "*profundarum*".

Alcock & Anderson (1899: 5) described the species on the basis of three young females (size given as about 13.0 × 9.0 mm) collected by the "Investigator" from the Travancore coast (7°17′30″N, 76°54′30″E), from a depth of 430 fathoms (= 796 m). One of these syntype specimens was figured by Alcock (1899: 10, pl. 1 fig. 2; 1901: 64, pl. 5 fig. 22). In the structure of the carapace and chelipeds, the original description and figures agree very well with the two males examined in this study from the Maldives and East Africa. While the armature on the meri of P2–P4 of the type figure agree with the present specimens, the meri and propodi are significantly shorter (Fig. 1A). This discrepancy in proportions cannot be explained by size alone even though the syntypes are smaller in size than the present material. Specimens of other species in which large and small specimens are known (e.g., *G. robusta*, Fig. 12) do not show such a substantial difference in proportions. We tried to examine the type material of *G. profundarum*, all supposedly still in the present Zoological Survey of India (Calcutta) but the material could not be located despite several searches over two years (S. Mitra, personal communication). They are also not in the NHM. The syntypes are thus almost certainly lost.

The only species that has ambulatory meri as short as those figured by Alcock (1899, 1901) (present Fig. 1A) is *G. robusta* from the Andamans in the eastern Indian Ocean (Figs. 12A, B, 13G, H); but in this species, the carapace and P2–P5 are prominently more setose (Fig. 12A–D) (versus less setose in *G. profundarum*; Figs. 1A–C, 6A–C); the surfaces of the chela are prominently granulated (Fig. 12E) (versus smooth in *G. profundarum*; Figs. 3H, I, 7F); the carpus of the cheliped has more spines (Fig. 13F) (versus carpus less prominently spinose in *G. profundarum*; Figs. 3F, G, 7F, G); the lateral margins of the male telson are uniformly convex (Fig. 13D) (versus with the proximal part convex but tapering more sharply to the tip in *G. profundarum*; Figs. 4B, 8C); and the distal part of the G1 is more elongate with a bifurcate tip (Fig. 13K) (versus the distal part being shorter with a convex tip in *G. profundarum*; Figs. 4H, 8K).

As discussed earlier, the specimens here, referring to *G. profundarum* s. str. from the Maldives and East Africa, differ from those figured by Alcock (1899, 1901) (present Fig. 1A) only in possessing proportionately longer P2–P5. We are of the opinion that Alcock's (1899, 1901) figures of the P2–P4 are inaccurate, with the legs probably originally drawn at an angle. In view of the uncertainty of the identity of what is *G. profundarum* s. str., the loss of the types, and that it is the type species of the genus, there is now a clear need to designate a neotype for the species. To stabilise the taxonomy of the species and genus, we here select a male (11.0 × 16.0 mm, NHM 1948.9.7.28) as the neotype of *Homola profundorum* Alcock & Anderson, 1899. This specimen was collected from the Maldives at 4°42′36″N, 72°50′24″E – 4°45′36″N, 72°52′12″E (cf. Sewell, 1935), a site approximately 500 km southwest of the type locality of the original *H. profundorum* off Travancore. Both sites are in the same basin.

The waters off Travancore and western Indian Ocean are home to two species of *Gordonopsis*. *Gordonopsis alaini*, new species, from off Madagascar, has P2–P5 meri and propodi proportions that agree better with those of *G. profundarum* figured by Alcock (1899, 1901) (present Fig. 1A) but can easily be distinguished by its more triangular carapace shape (Fig. 9B) (versus more ovate in *G. profundarum*; Figs. 2B,

6B); the latero-posterior carapace tubercle is visible only as a low swelling (Fig. 9B) (versus present as a distinct tubercle in *G. profundarum*; Figs. 2B, 6B); the carpus of the cheliped has fewer spines (Fig. 10E–G) (versus with numerous spines in *G. profundarum*; Figs. 3F, G, 7F, G); and the distal part of the G1 is very broad (Fig. 10H) (versus G1 distal part narrow in *G. profundarum*; Figs. 4H, 8K). See general discussion for comparisons with other congeners.

Gordonopsis alaini, new species
(Figs. 9–11)

Paromola profundorum – Guinot & Richer de Forges, 1981: 536, figs. 3A, 4F, 5A, A1, pl. 3 fig. 1, 1a.
Gordonopsis aff. *profundorum* – Guinot & Richer de Forges, 1995: 467, figs. 63d–h, 64A, B.
Gordonopsis profundorum – Garassino, 2009: 11, pl. 2.

Material examined. Holotype: male (10.9 × 16.8 mm) (MNHN-IU-2017-9049 = MNHN B-7026), station CH38 P3 trawl 38, 12°50.0′S, 48°09.1′E, northwest coast, Madagascar, 580–585 m, coll. CREVETTIERE 1972, A. Crosnier, 14 September 1972.

Diagnosis. Male: carapace longitudinally pyriform, width to length ratio 0.65, distinctly wider posteriorly than anteriorly; dorsal carapace surface with well-defined regions, separated by broad, deep grooves; lateral margin sinuous, almost straight; dorsal parts with scattered soft setae, not obscuring surface; lateral parts more setose but not obscuring surface (Figs. 9A–C, 10A, B). Rostrum relatively long, sharp, with 2 long, obliquely directed pseudorostral spines, just shorter than rostrum (Fig. 9B). Supraorbital margin relatively narrow, C-shaped; pseudorostral spines directed obliquely laterally at angle of about 45° (Fig. 9B). Eyes with short ocular peduncle, cornea prominent; no discernible orbit (Fig. 9B). Hepatic region not inflated, with short obliquely directed spine (Fig. 9B). Gastric region without spines (Fig. 9B). Gastric groove well marked, with distinct ovate gastric fossae just above (Fig. 9B). Cardiac region swollen; branchial region inflated, with distinct branchio-cardiac grooves (Fig. 9B). Latero-posterior tubercle on carapace very low, barely discernible (Fig. 9B). Base of antenna with short spine (Fig. 10D). Antennal flagellum short, second and third articles thick, setose. Epistome triangular (Fig. 10D). Third maxilliped pediform, merus elongate with spiniform external angle (Fig. 10C). Chelipeds long; fingers stouter, about two-thirds length of palm; surface gently rugose to smooth; carpus longitudinally ovate, outer, distal, and inner margins with 1 long spine each, dorsal surface with low ridge but unarmed; merus triangular in cross-section, relatively long, curved, dorsal margin with 7 spines and distal 2 spines bracketing chela, outer ventral margin with 7 spines, inner ventral margin with 6 spinules (Figs. 9A, 10E–G). Ambulatory legs relatively long; basis-ischium with small granules, not spines; P2 merus with 3 spines on dorsal margin (excluding 1 distal spine), ventral margin with 2 spinules; P3 merus with 3 spines on dorsal margin (excluding 1 distal spine), ventral margin unarmed; P4 merus with 2 spines on dorsal margin (excluding 1 distal spine), ventral margin unarmed, outer surface with 1 strong proximal spine (Figs. 9A, 11A, E–G). P5 merus slender, unarmed on all margins, reaching beyond gastric groove when folded anteriorly; carpus long, propodus short, enlarged, forming prominent pseudochela with stout, gently curved dactylus; occlusal margin of fixed finger with 5 or 6 spines, that of dactylus with 5 or 6 spines (Fig. 11H–K). Outer margins of P2–P4 coxae smooth, unarmed (Fig. 11C). Telson triangular, with convex lateral margins, distal part distinctly narrowing (Fig. 11B, D). G1 short, stout, distal part prominently narrowed with subtruncate tip (Fig. 10H). G2 stout, tubular, length subequal to G1, basal portion slightly dilated, covered with long setae, distal portion cup-shaped (Fig. 10I).

Colour. Not known.

Etymology. The species is named after our good friend Alain Crosnier, who first collected this species. Alain has changed the face of modern carcinology through his many decades of work, for which we are most grateful.

Remarks. See general discussion for comparisons with congeners.

Gordonopsis robusta Ng, Padate & Saravanane, 2019
(Figs. 12, 13)

Gordonopsis robusta Ng, Padate & Saravanane, 2019: 511, figs. 1–4.

Material examined. Holotype: male (33.5 × 44.9 mm) (CMLRE IO/SS/BRC/00082), Andaman Sea, FORVSS station 36708, 13.27°N, 93.26°E, 635 m, HSDT (CV), coll. S. S. Cubelio, 26 November 2017. Paratype: 1 young female (15.6 × 20.8 mm) (CMLRE IO/SS/BRC/00083), same data as holotype.

Diagnosis. Male: carapace longitudinally ovate, width to length ratio 0.75, distinctly wider posteriorly than anteriorly; dorsal carapace surface with well-defined regions, separated by broad, deep grooves; lateral margin distinctly convex; dorsal parts with dense soft setae partially obscuring surface; lateral parts densely setose, completely obscuring surface (Figs. 12A–D, 13A, B). Rostrum relatively long, sharp, with 2 relatively long, obliquely directed pseudorostral spines, just shorter than rostrum (Fig. 12C). Supraorbital margin relatively narrow, C-shaped; pseudorostral spines directed obliquely laterally at angle of about 45° (Fig. 12C). Supraorbital margin relatively narrow, C-shaped; pseudorostral spines directed obliquely laterally at angle of about 45° (Fig. 12C). Eyes with short ocular peduncle, cornea prominent; no discernible orbit (Fig. 12C). Hepatic region gently inflated, with short obliquely directed spine (Fig. 12C). Gastric region without spines (Fig. 12C). Gastric groove well marked, with distinct ovate gastric fossae just above (Fig. 12C). Cardiac region swollen; branchial region inflated, with distinct branchio-cardiac grooves (Fig. 12C). Latero-posterior tubercle strong, sharp (Fig. 12C). Base of antenna with short spine. Antennal flagellum short, second and third articles thick, setose. Epistome triangular. Third maxilliped pediform, merus elongate with dentiform external angle (Fig. 13C). Chelipeds long; fingers short, less than half

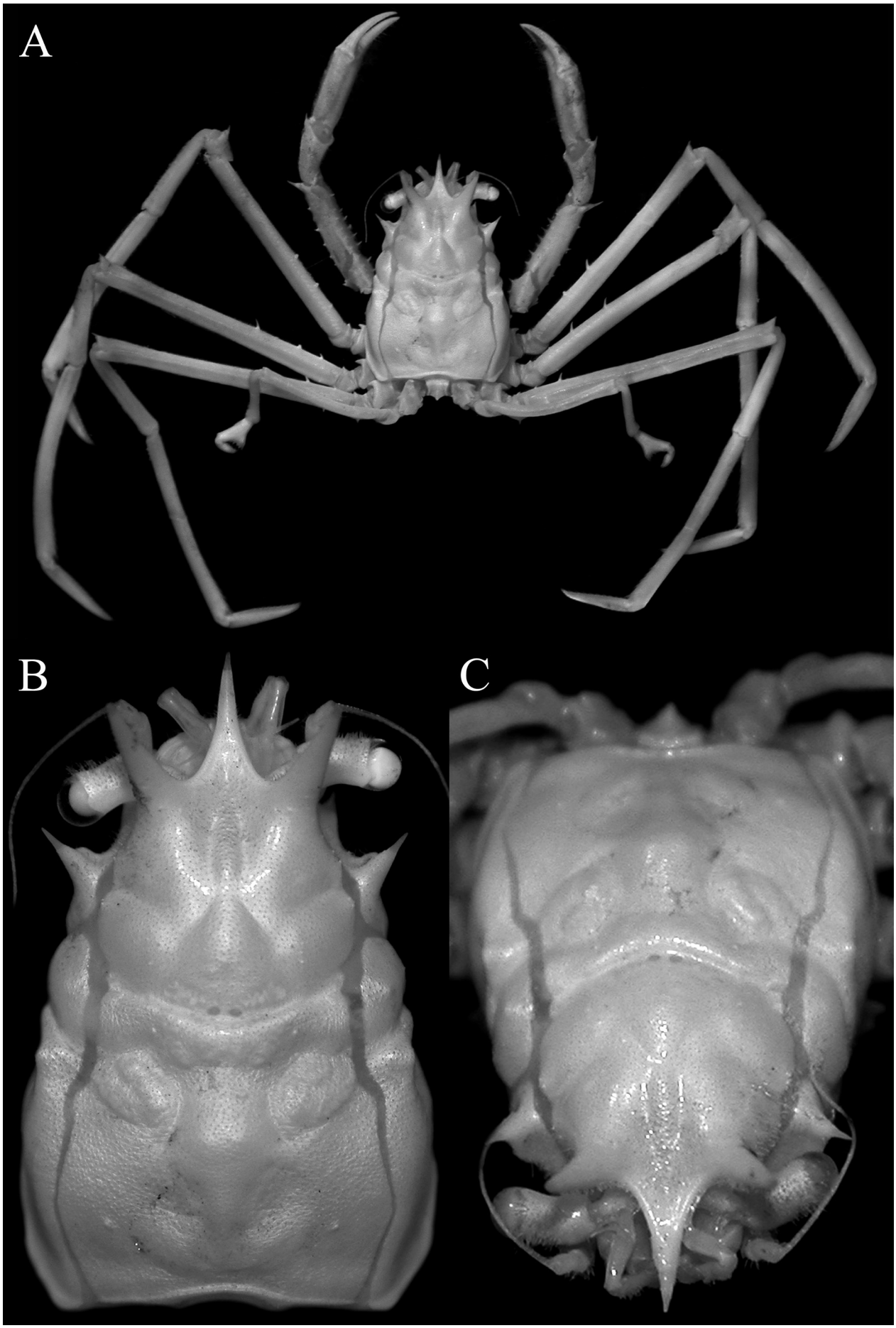

Fig. 9. *Gordonopsis alaini*, new species, holotype male (15.4 × 10.0 mm) (MNHN-IU-2017-9049), Madagascar. A, overall habitus; B, dorsal view of carapace; C, dorso-frontal view of carapace.

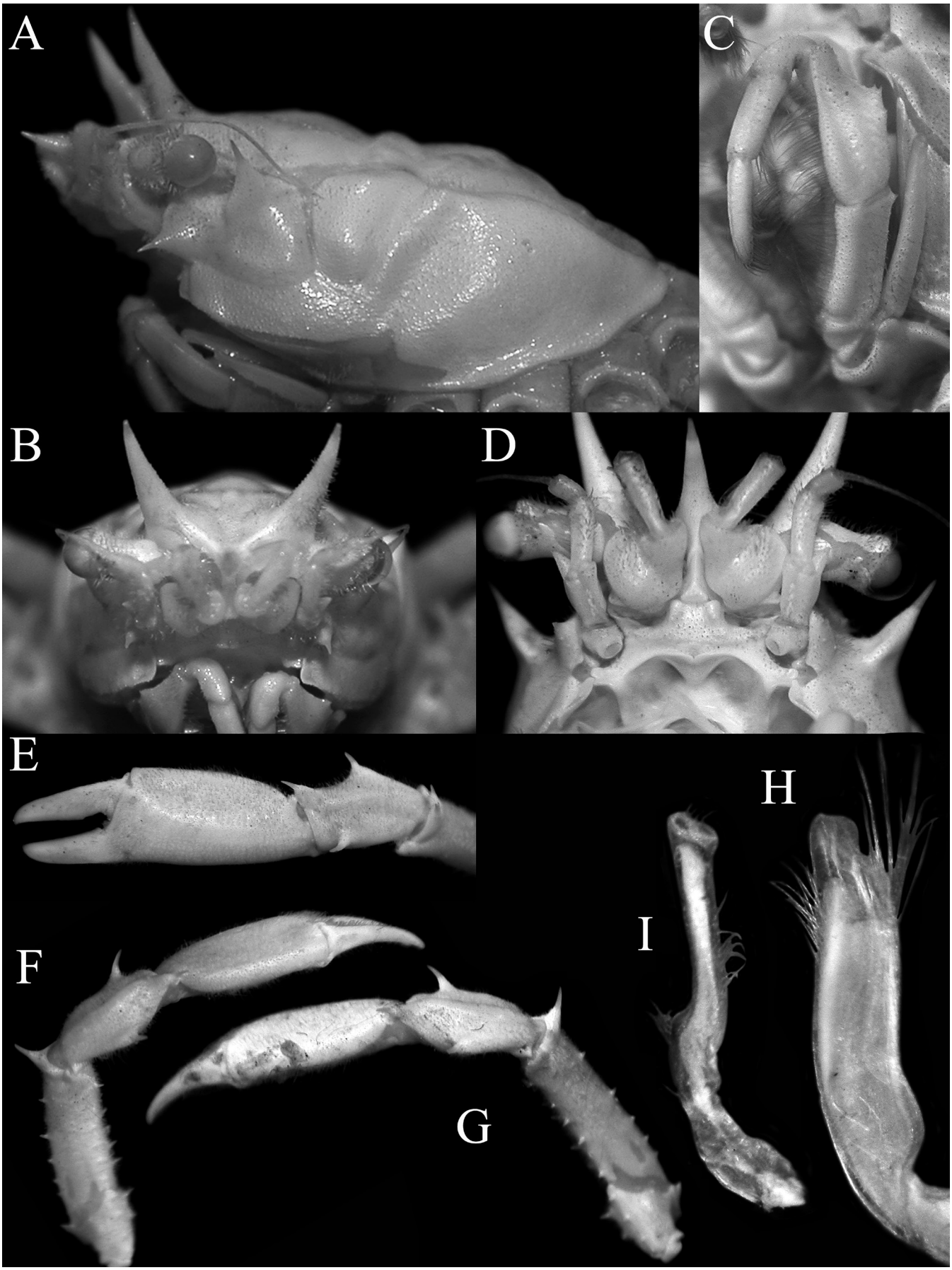

Fig. 10. *Gordonopsis alaini*, new species, holotype male (15.4 × 10.0 mm) (MNHN-IU-2017-9049), Madagascar. A, lateral view of cephalothorax; B, frontal view of cephalothorax; C, left third maxilliped; D, ventral view showing buccal cavity, epistome, antennae, and antennules; E, outer view of right carpus and chela; F, dorsal view of left cheliped; G, dorsal view of right cheliped; H, ventral view of right G1; I, ventral view of right G2.

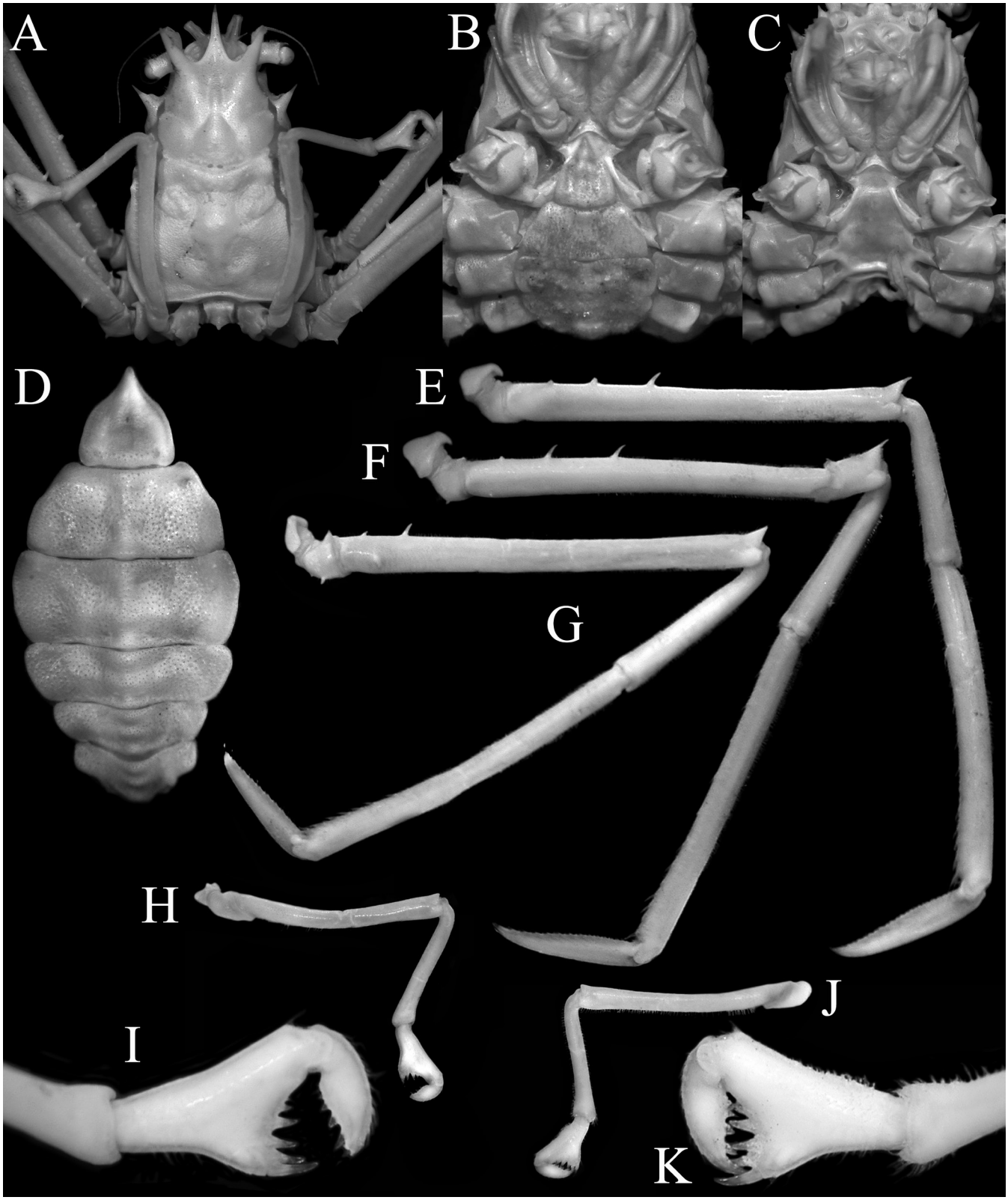

Fig. 11. *Gordonopsis alaini*, new species, holotype male (15.4 × 10.0 mm) (MNHN-IU-2017-9049), Madagascar. A, dorsal view of carapace showing relative P5 length; B, ventral view of cephalothorax showing pleon and unarmed P2–P4 coxae; C, ventral view of cephalothorax showing sternopleonal cavity and unarmed P2–P4 coxae; D, pleon; E–H, right P2–P5, respectively (all to same scale); I, right P5 pseudochela (same scale as E–H); J, left P5; K, left P5 pseudochela.

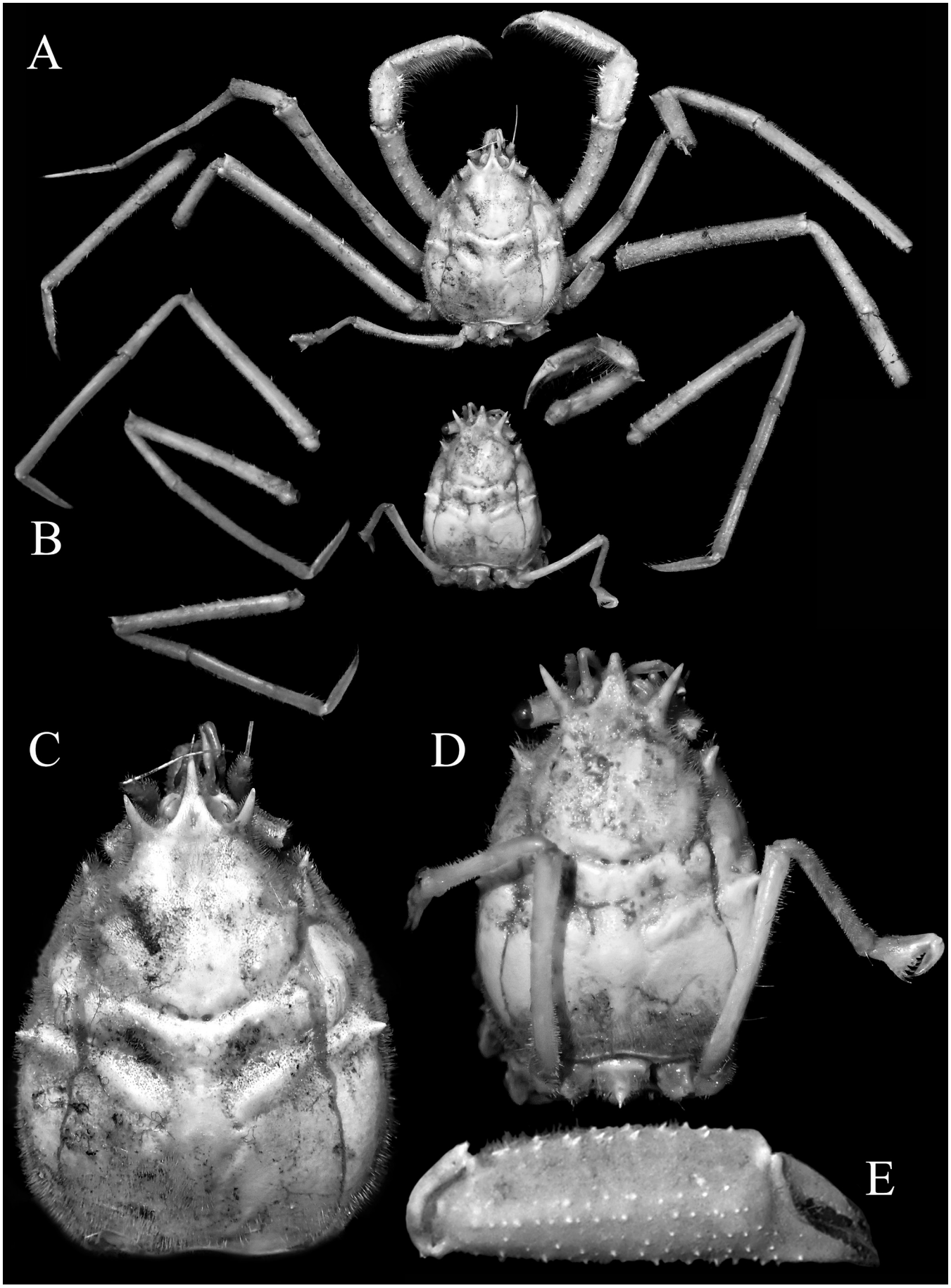

Fig. 12. *Gordonopsis robusta* Ng, Padate & Saravanane, 2019. A, C, E, holotype male (33.5 × 44.9 mm) (CMLRE), Andaman Sea; B, D, paratype female (15.6 × 20.8 mm) (CMLRE), Andaman Sea. A, B, overall habitus; C, dorsal view of carapace; D, dorsal view of carapace showing relative P5 length; E, outer view of right chela.

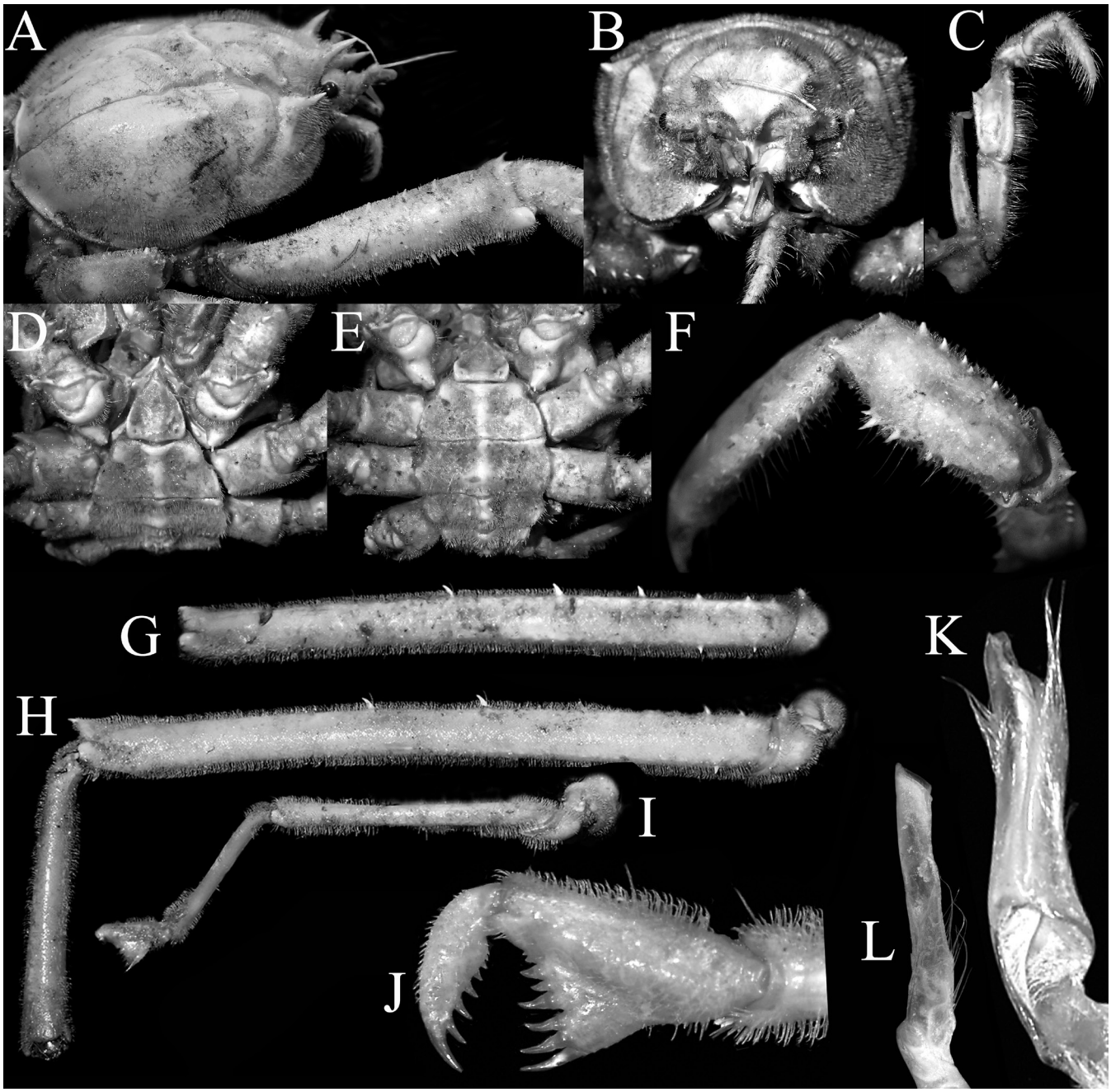

Fig. 13. *Gordonopsis robusta* Ng, Padate & Saravanane, 2019, holotype male (33.5 × 44.9 mm) (CMLRE), Andaman Sea. A, dorso-lateral view of cephalothorax; B, frontal view of cephalothorax; C, right third maxilliped; D, E, ventral view of cephalothorax showing pleon and coxae; F, dorsal view of carpus of right cheliped; G–I, left P3–P5 meri and leg, respectively (all to same scale); J, left P5 pseudochela; K, ventral view of right G1; L, ventral view of right G2.

length of palm; surface gently rugose with 4 or 5 longitudinal rows of small granules, margins with sharp granules and short spines; carpus longitudinally ovate, outer margin with 8–10 short spines, distal edge with short spine, inner margin with 5 or 6 spines, dorsal surface with ridge lined with 3–5 short sharp tubercles or granules; merus triangular in cross-section, relatively long, curved, dorsal margin with 5 short spines and distal 2 spines bracketing chela, outer ventral margin with 16–18 spines and spinules, inner ventral margin with 6–8 spines or spinules (Figs. 12A, E, 13F). Ambulatory legs relatively long; basis-ischium with small granules, not spines; P2 merus with 6 spines or sharp tubercles on dorsal margin (excluding 1 distal spine), ventral margin with 3–5 spinules or tubercles; P3 merus with 5 spines on dorsal margin (excluding 1 distal spine), ventral margin with 1 or 2 sharp tubercles; P4 merus not known (Figs. 12A, B, 13G, H). P5 merus slender, unarmed on all margins, just reaching gastric groove when folded anteriorly; carpus long, propodus short, enlarged, forming prominent pseudochela with stout, gently curved dactylus; occlusal margin of fixed finger with 8 spines, that of dactylus with 8 spines (Figs. 12D, 13I, J). Outer margins of P2–P4 coxae smooth, unarmed (Fig. 13D, E). Telson triangular, with gently convex lateral margins and sharp tip (Fig. 13D, E). G1 short, stout, distal part gently upcurved, tip concave (Fig. 13K). G2 stout, tubular, length subequal to G1, distal portion cup-shaped (Fig. 13L). Female:

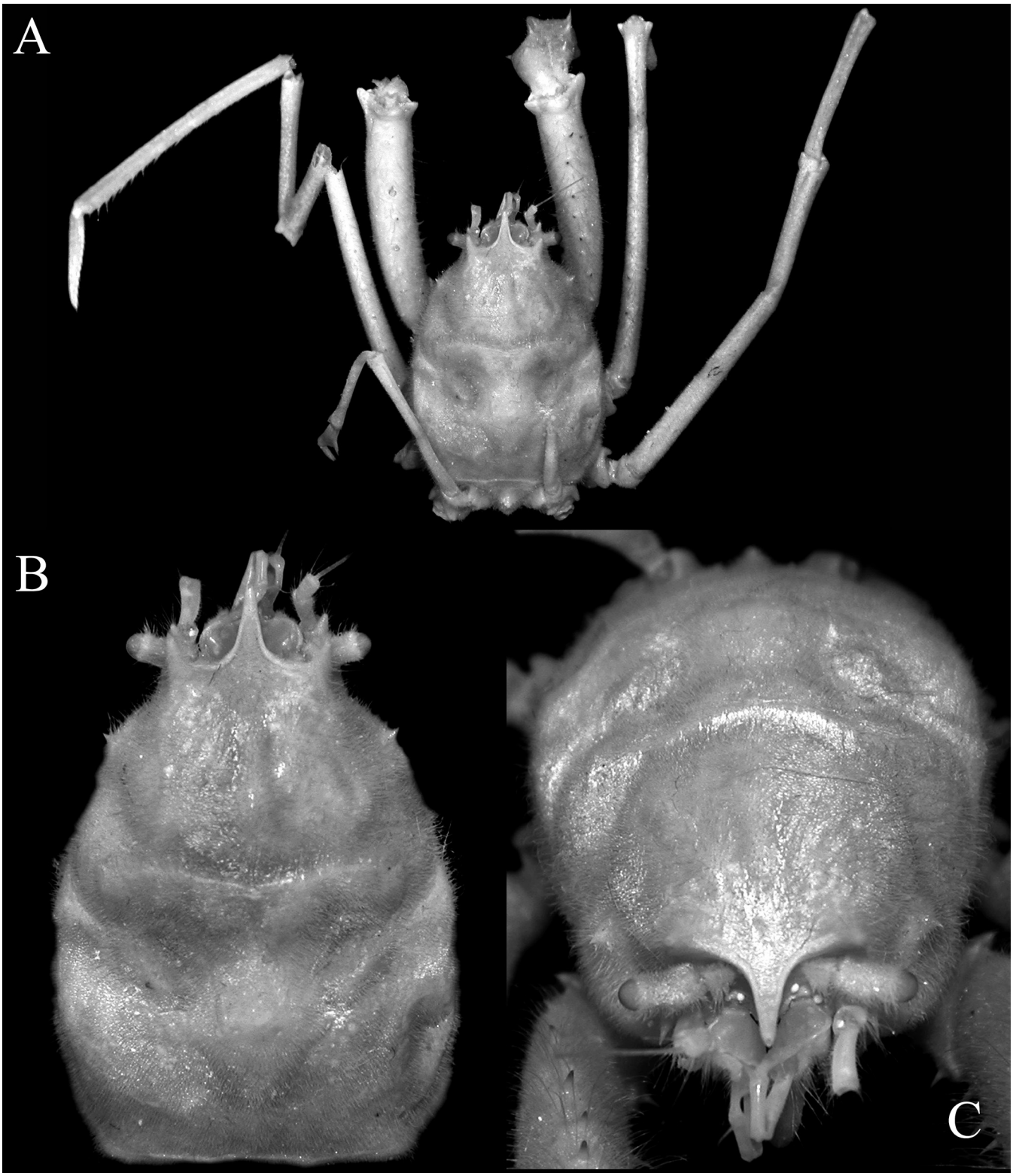

Fig. 14. *Gordonopsis pacifica* Takeda & Suyama, 2019, holotype male (31.0 × 43.0 mm) (NSMT-Cr 26053), Okino-Torishima Island, Japan. A, overall habitus; B, dorsal view of carapace; C, dorso-frontal view of carapace.

non-sexual characters similar to male except cheliped merus with 6 spines on upper margin, 8 short spines and tubercles on outer ventral margin, 5 or 6 sharp tubercles on inner ventral margin; P2 merus with 5 spines on dorsal margin, ventral margin with 1 sharp tubercle; P3 merus with 5 spines on dorsal margin, ventral margin with 1 sharp tubercle; P4 with 3 spines on dorsal margin, ventral margin unarmed; telson broadly triangular with convex lateral margins.

Colour. Not known.

Remarks. See general discussion for comparisons with congeners.

Gordonopsis pacifica Takeda & Suyama, 2019
(Figs. 14–16)

Gordonopis pacifica Takeda & Suyama, 2019: 46, figs. 1B, 2–4.

Material examined. Holotype: male (31.0 × 43.0 mm) (NSMT-Cr 26053), south of Okinotorishima (= Okinotori Island), 20°25′31″N, 136°04′52″E, southern Japan, 300–600 m deep, coll. 13 January 2006.

Diagnosis. Male: carapace longitudinally ovate, width to length ratio 0.72, distinctly wider posteriorly than anteriorly; dorsal carapace surface with well-defined regions, separated by broad, deep grooves; lateral margin gently convex; dorsal parts with numerous setae that partially obscure surface; lateral parts with soft setae that almost obscure surface, denser on hepatic, pterygostomial and suborbital regions (Figs. 14A–C, 15A, B). Rostrum long, sharp, with 2 relatively short, obliquely directed pseudorostral spines, just shorter than rostrum (Fig. 14B). Supraorbital margin relatively wide; pseudorostral spines directed obliquely laterally at angle of about 20° (Fig. 14B). Eyes with short ocular peduncle, cornea prominent; no discernible orbit (Fig. 14B). Hepatic region gently inflated, with short obliquely directed spine (Fig. 14B). Gastric region without spines (Fig. 14B). Gastric groove well marked, with distinct ovate gastric fossae just above (Fig. 14B). Cardiac region swollen; branchial region inflated, with distinct branchio-cardiac grooves (Fig. 14B). Latero-posterior tubercle on carapace not distinct, just discernible as low tubercle (Fig. 14B). Base of antenna with short spine. Antennal flagellum short, second and third articles thick, setose. Epistome triangular. Third maxilliped pediform, merus elongate with dentiform external angle (Fig. 15C). Chelipeds long; fingers long, greater than half length of palm; surface almost smooth with low slightly oblique longitudinal ridge; carpus longitudinally ovate, outer margin with 3 long spines, distal edge with 1 long spine, inner margin with 1 long spine, dorsal surface with longitudinal row of 3 short spines; merus triangular in cross-section, relatively long, curved, dorsal margin with 7 or 8 spines and distal 2 short spines bracketing chela, outer ventral margin with 7 or 8 spines, inner ventral margin with 6 short spines (Figs. 14A, 15E–G). Ambulatory legs long; basis-ischium with 4 spines on each margin; P2 merus with 3 or 4 spines on dorsal margin (excluding 1 distal spine), ventral margin with 1 or 2 spines; P3 merus with 2 spines on dorsal margin (excluding 1 distal spine), ventral margin with 1 spine; P4 merus with 2 spines on dorsal margin (excluding 1 distal spine), ventral margin with 1 spine, outer surface with 1 proximal tubercle (Figs. 14A, 16E–G, I, K, L). P5 merus slender, unarmed on all margins, reaching just beyond gastric groove when folded anteriorly; carpus long, propodus short, enlarged, forming prominent pseudochela with stout, gently curved dactylus; occlusal margin of fixed finger with 7 spines, that of dactylus with 8 spines (Fig. 16A, H, J). Outer margin of P2 coxa with l short, stout spine on distal edge; outer margin of P3 coxa with 1 short, stout spine on proximal edge, outer margin of P4 coxa with 1 or 2 short, stout spines on proximal edge (Fig. 16C, D). Pleon missing from holotype.

Colour. The freshly collected specimen has a yellowish-brown carapace with the chelipeds and ambulatory leg bright red (Takeda & Suyama, 2019: fig. 1B).

Remarks. The holotype specimen is in poor condition with several parts of the carapace damaged, pereiopod missing and most of the pleon absent. It appears to have recently moulted given that the cuticle is not completely hardened and still quite brittle. Some of the spines on the pereiopods are broken off but their bases can still be discerned.

See general discussion for comparisons with congeners.

Gordonopsis hera, new species
(Figs. 17–20)

Material examined. Holotype: ovigerous female (21.8 × 31.2 mm) (MNHN-IU-2013-2245), station CP 4246, northwest of Vitu Island, Bismarck Sea, 04°07′S, 148°09′E, Papua New Guinea, 695–899 m, coll. MADEEP Expedition, 22 April 2014.

Diagnosis. Female: carapace longitudinally pyriform, width to length ratio 0.70, distinctly wider posteriorly than anteriorly; dorsal carapace surface with well-defined regions, separated by broad, deep grooves; lateral margin gently convex to almost straight; dorsal parts with numerous stiff setae that do not obscure surface; lateral parts with denser soft and stiff setae that partially obscure surface, denser on hepatic, pterygostomial and suborbital regions (Figs. 17A–C, 18A, B). Rostrum long, sharp, with 2 relatively short, obliquely directed pseudorostral spines, just shorter than rostrum (Fig. 17B). Supraorbital margin relatively wide; pseudorostral spines directed obliquely laterally at angle of about 30° (Fig. 17B). Eyes with short ocular peduncle, cornea prominent; no discernible orbit (Fig. 17B). Hepatic region gently inflated, with short obliquely directed spine (Fig. 17B). Gastric region without spines (Fig. 17B). Gastric groove well marked, with distinct ovate gastric fossae just above (Fig. 17B). Cardiac region swollen; branchial region inflated, with distinct branchio-cardiac grooves (Fig. 17B). Latero-posterior tubercle on carapace low, just discernible as granule (Fig. 17B). Base of antenna with short spine (Fig. 18D). Antennal flagellum short, second and third articles thick, setose. Epistome triangular (Fig. 18D). Third maxilliped pediform, merus elongate with dentiform external angle (Fig. 18C). Chelipeds long; fingers long, greater than half length of palm; surface gently rugose with scattered small granules; carpus longitudinally ovate, outer margin with 3 or 4 long spines, distal edge with 1 long spine, inner margin with 1 long spine, dorsal surface with longitudinal row of 3 spines; merus triangular in cross-section, relatively long, curved, dorsal margin with 8 spines and distal 2 spines bracketing chela, outer ventral margin with 6 spines, inner ventral margin with 4 or 5 spinules (Fig. 18E–I). Ambulatory legs very long; basis-ischium with 4 spines on each margin; P2 merus with 3 spines on dorsal margin (excluding 1 distal spine), ventral margin with 1 spine; P3 merus with 2 spines on dorsal margin (excluding 1 distal spine), ventral margin unarmed; P4 merus with 1 spine on dorsal margin (excluding

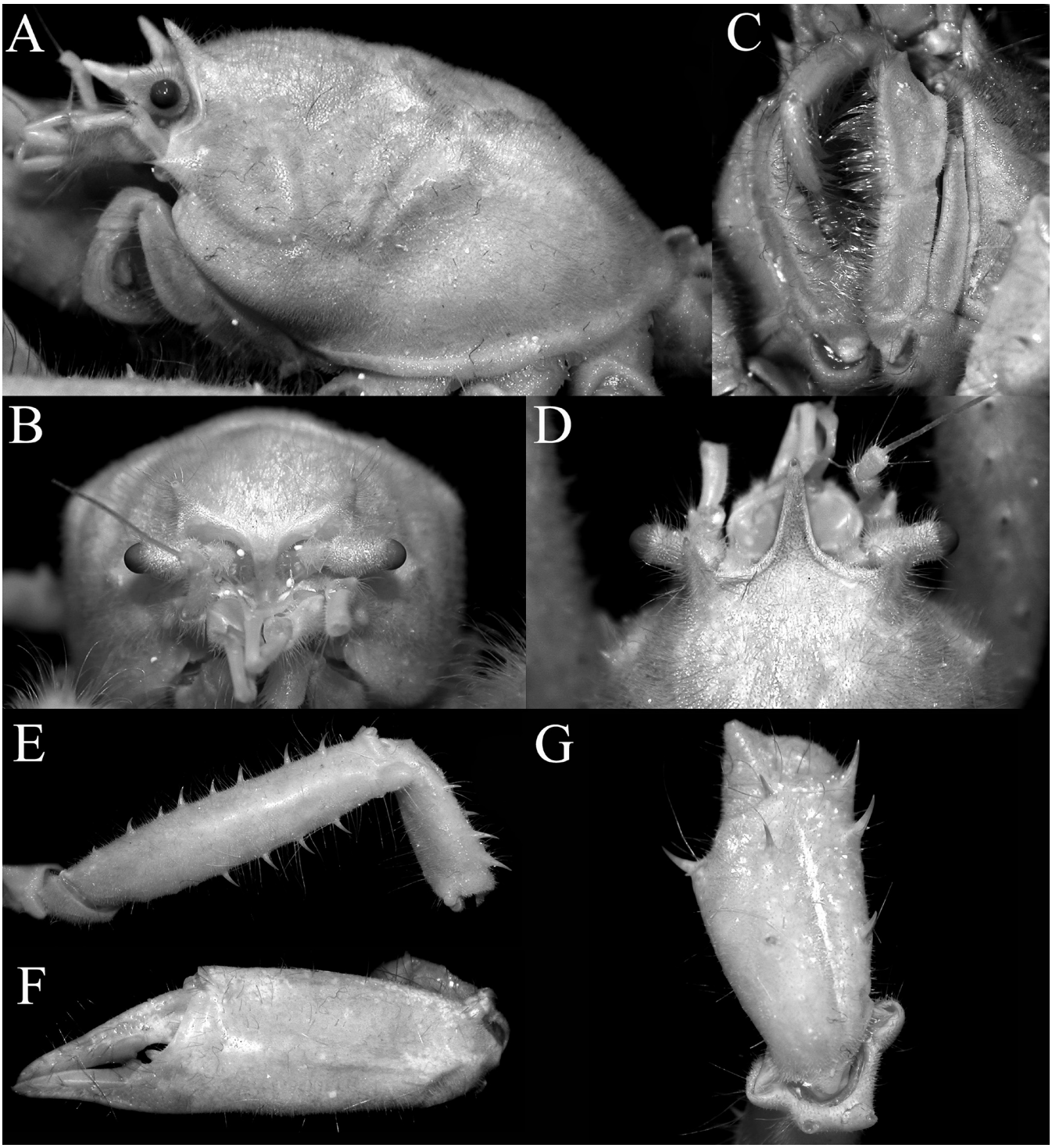

Fig. 15. *Gordonopsis pacifica* Takeda & Suyama, 2019, holotype male (31.0 × 43.0 mm) (NSMT-Cr 26053), Okino-Torishima Island, Japan. A, lateral view of cephalothorax; B, frontal view of cephalothorax; C, left third maxilliped; D, dorsal view of front; E, outer view of merus and carpus of right cheloped; F, outer view of right chela; G, dorsal view of carpus of right cheliped.

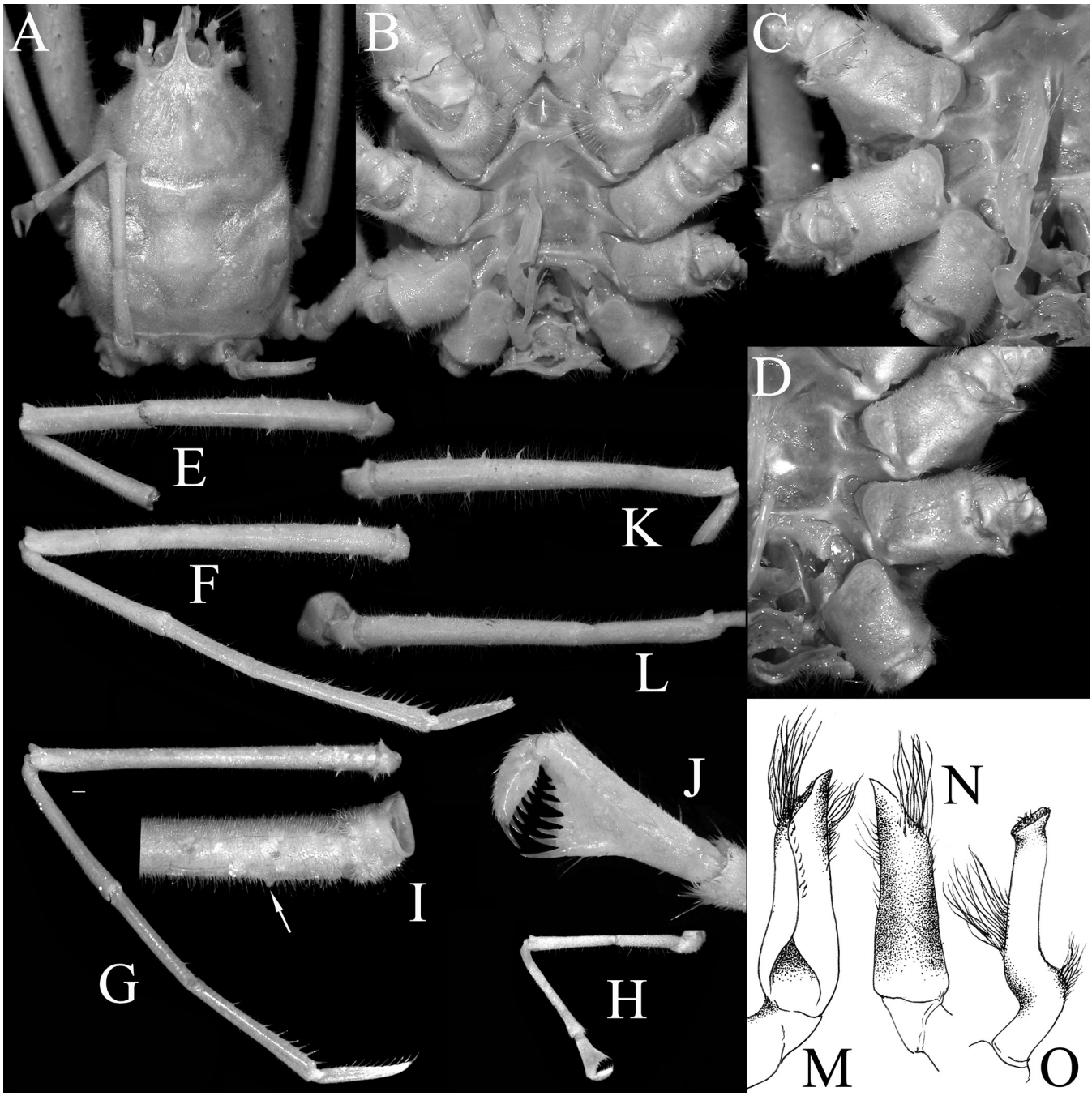

Fig. 16. *Gordonopsis pacifica* Takeda & Suyama, 2019, holotype male (31.0 × 43.0 mm) (NSMT-Cr 26053), Okino-Torishima Island, Japan. A, dorsal view of carapace showing relative P5 length; B, sternopleonal cavity; C, right P2–P4 coxae and basis-ischia; D, left P2–P4 coxae; E–H, left P2–P5, respectively; I, dorsomesial view of proximal part of merus of P4 showing tubercle on outer surface (arrow); J, left P5 pseudochela; K, L, right P2 and P3, respectively; M, N, left G1; O, left G2. All ambulatory legs shown to same scale. M–O after Takeda & Suyama (2019: fig. 4B–D).

1 distal spine), ventral margin unarmed, outer surface smooth, without trace of spinule or granule (Figs. 17A, 19D–F). P5 merus slender, unarmed on all margins, reaching beyond gastric groove when folded anteriorly; carpus long, propodus short, enlarged, forming prominent pseudochela with stout, gently curved dactylus; occlusal margin of fixed finger with 7 spines, that of dactylus with 7 spines (Fig. 19A, G, H). Outer margin of P2 coxa with l short, stout spine on distal edge; outer margin of P3 coxa with 1 short, stout spine on proximal edge, outer margin of P4 coxa with 0 or 1 short, stout spine on proximal edge (Fig. 18J, K). Proximal part of telson subtruncate, with distal half triangular (Fig. 19B).

Variation. The photographs from the Tokelau Seamount (Fig. 20) appear to show large specimens of *G. hera*, which agree very well with the holotype female, including in the pereiopod proportions and armature.

Colour. In life, the carapace is whitish to brown; with the ambulatory legs clear or pale orange with white spines (Figs. 20, 30A).

Etymology. Hera is a Greek goddess, sister and wife of Zeus who was educated by Okeanos and Tethys; she was the one who placed Karkinos in the stars forming the constellation

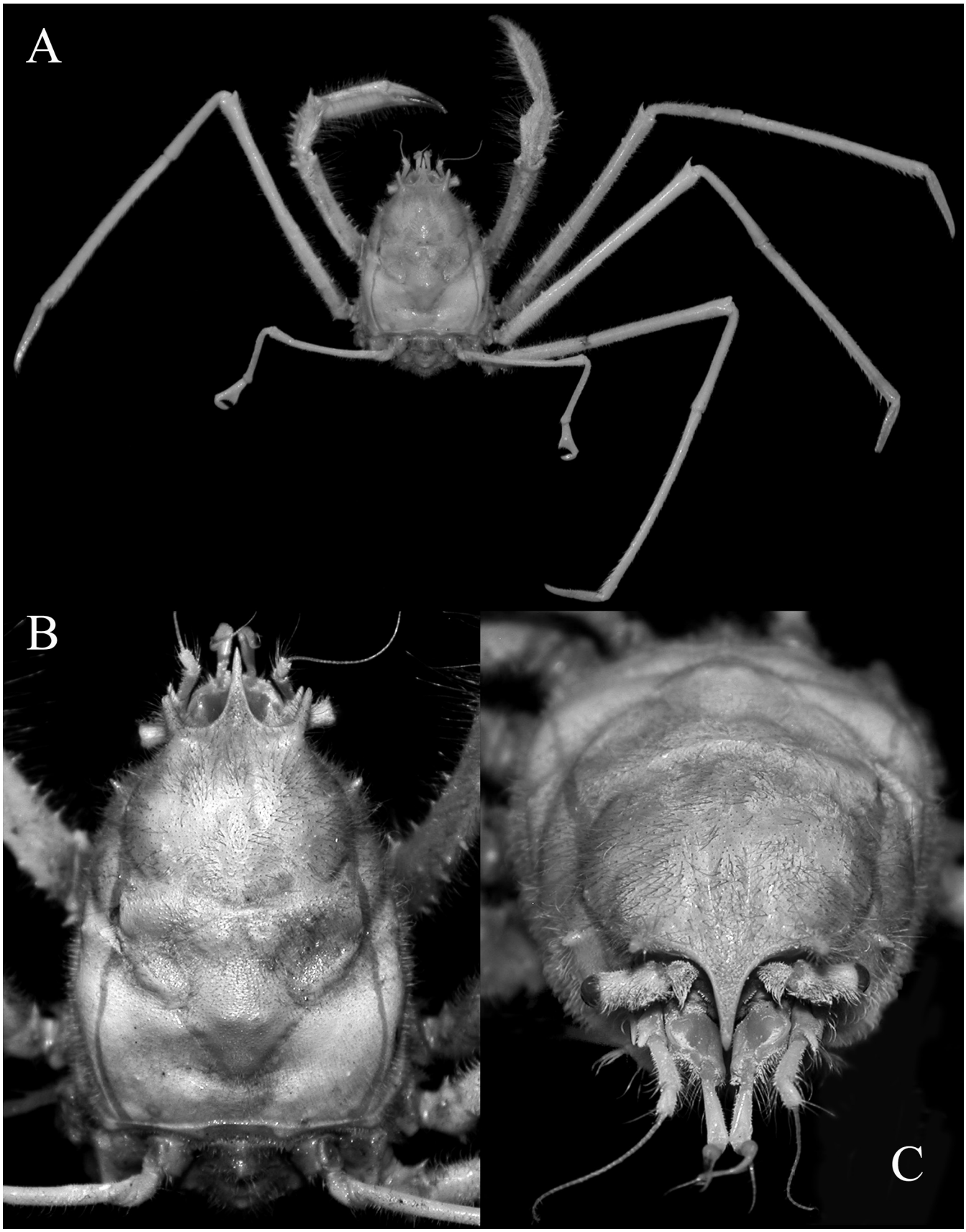

Fig. 17. *Gordonopsis hera*, new species, holotype ovigerous female (21.8 × 31.2 mm) (MNHN-IU-2013-2245), Papua New Guinea. A, overall habitus; B, dorsal view of carapace; C, dorso-frontal view of carapace.

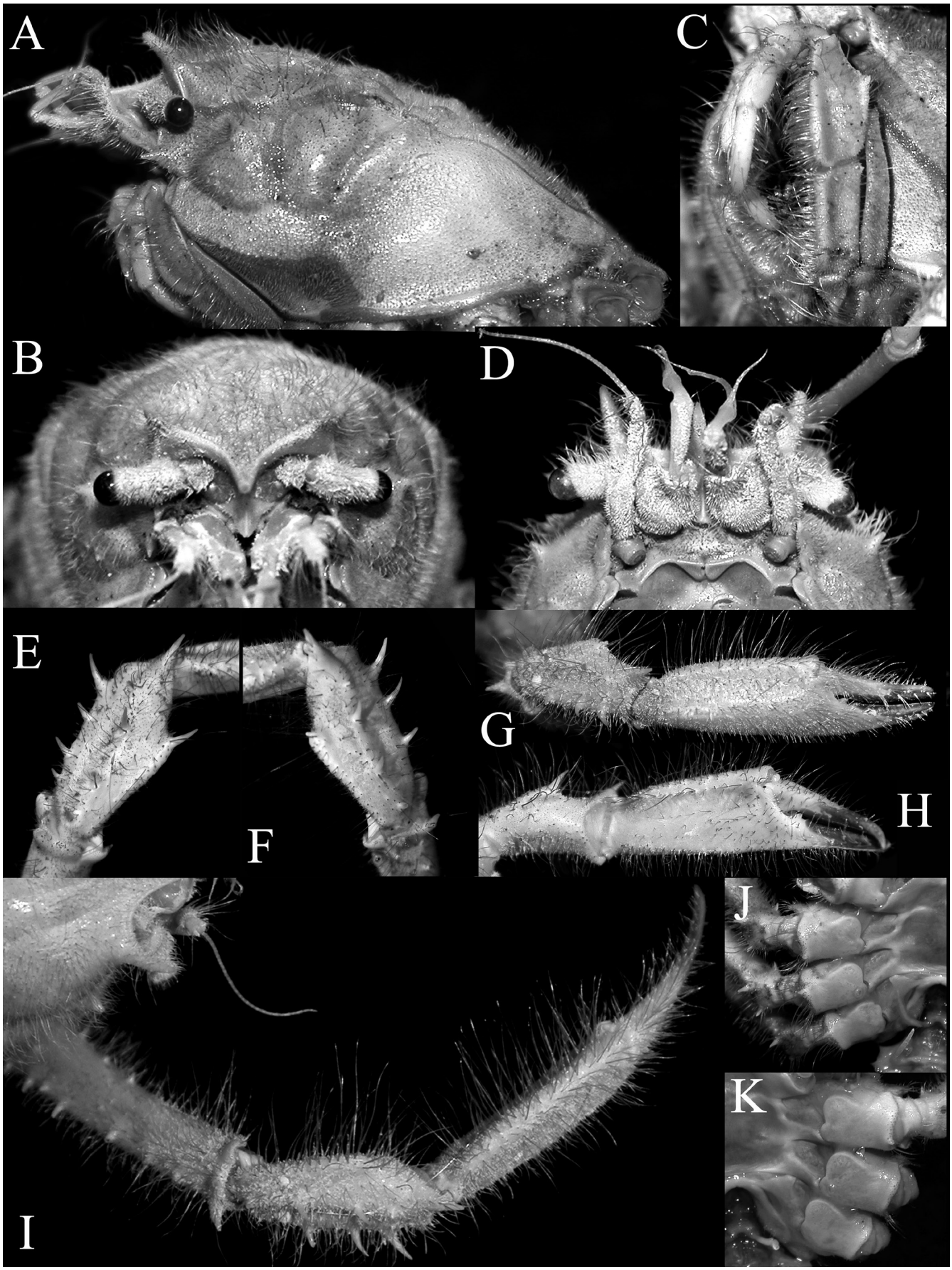

Fig. 18. *Gordonopsis hera*, new species, holotype ovigerous female (21.8 × 31.2 mm) (MNHN-IU-2013-2245), Papua New Guinea. A, lateral view of cephalothorax; B, frontal view of cephalothorax; C, left third maxilliped; D, ventral view showing buccal cavity, epistome, antennae, and antennules; E, dorsal view of carpus of left cheliped (denuded); F, dorsal view of carpus of right cheliped (denuded); G, outer view of right chela; H, inner view of right chela; I, dorsal view of right cheliped; J, right P2–P4 coxae and basis-ischia (denuded); K, left P2–P4 coxae (denuded).

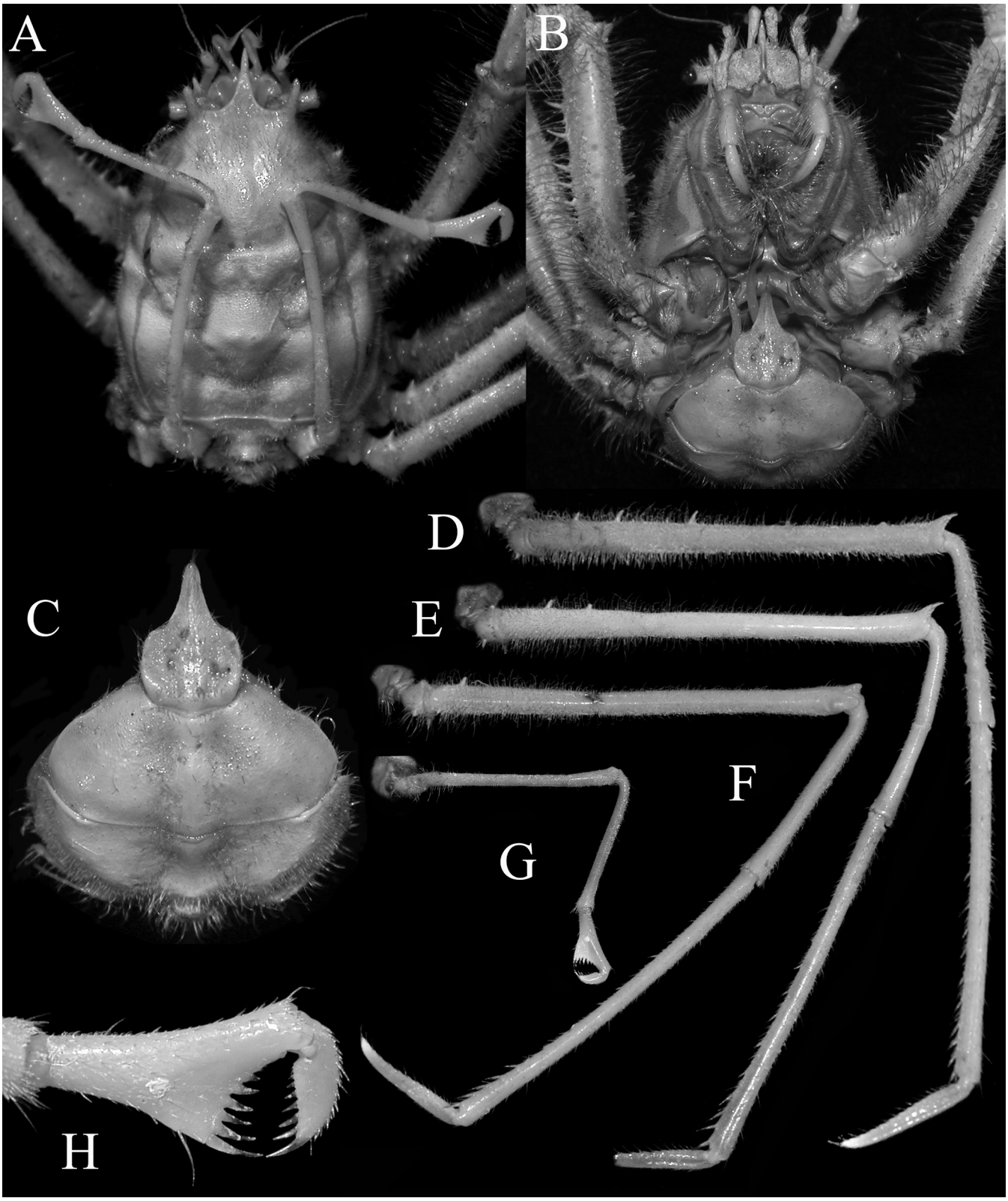

Fig. 19. *Gordonopsis hera*, new species, holotype ovigerous female (21.8 × 31.2 mm) (MNHN-IU-2013-2245), Papua New Guinea. A, dorsal view of carapace showing relative P5 length; B, ventral view of cephalothorax showing pleon; C, telson and pleon somites 5 and 6; D–G, right P2–P5, respectively (all to same scale); H, right P5 pseudochela.

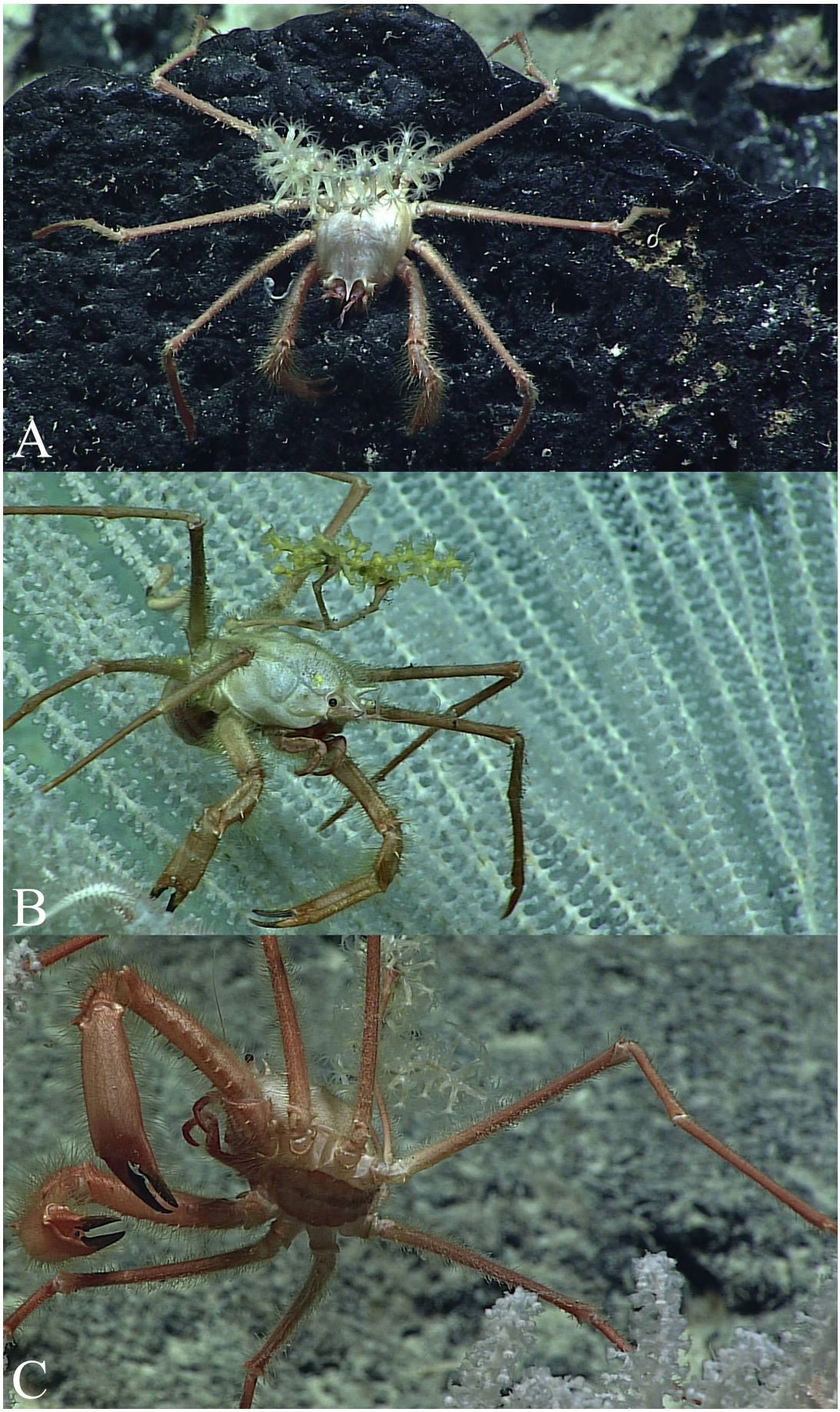

Fig. 20. *Gordonopsis hera*, new species, photographed in situ, specimens not collected. Ufiata Seamount, Tokelau Seamounts, 8°09.50′S, 172°54.08′W, 755–995 m, March 2017. Photographs courtesy of the U.S. National Oceanographic and Atmospheric Administration Office of Ocean Exploration and Research.

Cancer. It alludes to, and honours, our friend and respected colleague, Danièle Guinot, for her stellar work on marine Brachyura over the years. The name is used as a noun.

Remarks. Specimens were observed by a submersible, in March 2017, at Ufiata Seamount in the Tokelau Seamounts in the central Pacific (8°09.50′S, 172°54.08′W), at depths of 755–995 m (Fig. 20). Although no specimens were collected, the photographs agree very well with what is here described for *G. hera* and we believe they are conspecific. These seamounts are some 4,000 km east of the type locality of *G. hera* in the Bismarck Sea.

See general discussion for comparisons with congeners.

Carrying behaviour. The specimens from the Tokelau Seamounts in the central Pacific were all observed carrying an unidentified hydroid colony (Fig. 20). This is the first record of carrying behaviour in this genus (see Guinot et al., 1995; Guinot & Wicksten, 2015).

Gordonopsis phorcys, new species
(Figs. 21–23)

Material examined. Holotype: female (10.9 × 16.8 mm) (MNHN-IU-2008-12211 = MNHN B30261), station CP2197, southwest of Santa Isabel, 8°24.4′N, 159°22.5′E, Solomon Islands, 897–1,057 m, coll. Expedition SALOMON 2, N.O. Alis, November 2004.

Diagnosis. Female: carapace longitudinally ovate, width to length ratio 0.65, distinctly wider posteriorly than anteriorly; dorsal carapace surface with well-defined regions, separated by broad, deep grooves; lateral margin gently convex; dorsal parts with scattered soft setae that do not obscure surface; lateral parts with setae that do not obscure surface (Figs. 21A–C, 22A, B). Rostrum long, sharp, with 2 long, obliquely directed pseudorostral spines, just shorter than rostrum (Fig. 21B). Supraorbital margin relatively narrow, C-shaped; pseudorostral spines directed obliquely laterally at angle of about 45° (Fig. 21B). Eyes with short ocular peduncle, cornea prominent; no discernible orbit (Fig. 21B). Hepatic region gently inflated, with short obliquely directed spine (Fig. 21B). Gastric region without spines (Fig. 21B). Gastric groove well marked, with distinct ovate gastric fossae just above (Fig. 21B). Cardiac region swollen; branchial region inflated, with distinct branchio-cardiac grooves (Fig. 21B). Latero-posterior tubercle on carapace low, just discernible as granule (Fig. 21B). Base of antenna with distinct spine (Fig. 22D). Antennal flagellum short, second and third articles thick, setose. Epistome triangular (Fig. 22D). Third maxilliped pediform, merus elongate with angular external angle (Fig. 22C). Chelipeds long; fingers long, greater than half length of palm; surface gently rugose with scattered small granules; carpus longitudinally ovate, outer margin with 1 or 2 long spines and sometimes a third spinule, distal edge with 1 long spine, inner margin with 1 long spine, sometimes with 1 more spinule, dorsal surface with longitudinal row of 3 short spines; merus triangular in cross-section, relatively long, curved, dorsal margin with 8 spines and distal 2 spines bracketing chela, outer ventral margin with 7 or 8 spines, inner ventral margin with 5 or 6 spinules (Fig. 22E–H). Ambulatory legs very long; basis-ischium with 4 distinct curved spines on each margin, that on P4 sometimes with additional ventral spine; P2 merus with 4 spines on dorsal margin (excluding 1 distal spine), ventral margin with 1 or 2 spinules or sharp granules; P3 merus with 3 spines on dorsal margin (excluding 1 distal spine), ventral margin with 1 spinule; P4 merus with 2 spines on dorsal margin (excluding 1 distal spine), ventral margin unarmed, outer surface with 1 strong proximal spine (Figs. 21A, 23C–E). P5 merus slender, unarmed on all margins, reaching beyond gastric groove when folded anteriorly; carpus long, propodus short, enlarged, forming prominent pseudochela with stout, gently curved dactylus; occlusal margin of fixed finger with 8 spines, that of dactylus with 8 spines (Fig. 23A, F, G). Outer margin of P2 coxa with 1 short, stout spine on distal edge; outer margin of P3 coxa with 1 or 2 strong curved spines on each edge, outer margin of P4 coxa with 2 strong curved spines on each edge (Figs. 22I, J, 23B, H). Proximal part of telson subtruncate, with distal half triangular (Fig. 23B).

Colour. Not known.

Etymology. The species is named after Phorcys, a primordial Greek sea god, son of Gaia, brother and husband of Ceto. The name is used as a noun.

Remarks. See general discussion for comparisons with congeners.

Gordonopsis ceto, new species
(Figs. 24–26)

Material examined. Holotype: female (9.3 × 13.6 mm) (NTOU), station CST 12, Horse Shoe Ridge, hard bottom without mud, with many white dead bivalves and one *Bathymodiolus* shell, many soft corals and squat lobsters, 22°0.953′N, 118°53.955′E – 22°4.864′N, 118°52.785′E, 758–1,346 m, South China Sea, Taiwan, coll. T.-Y. Chan, 29 April 2016.

Diagnosis. Female: carapace longitudinally ovate, width to length ratio 0.68, distinctly wider posteriorly than anteriorly; dorsal carapace surface with well-defined regions, separated by broad, deep grooves; lateral margin convex; dorsal parts with scattered soft setae that do not obscure surface; lateral parts with setae that do not obscure surface (Figs. 24A–C, 25A, B). Rostrum long, sharp, with 2 long, obliquely directed pseudorostral spines, just shorter than rostrum (Fig. 24A). Supraorbital margin relatively narrow, C-shaped; pseudorostral spines directed obliquely laterally at angle of about 45° (Fig. 24A). Eyes with short ocular peduncle, cornea prominent; no discernible orbit (Fig. 24A). Hepatic region gently inflated, with short obliquely directed spine (Fig. 24A). Gastric region without spines (Fig. 24A). Gastric groove well marked, with distinct ovate gastric fossae just above (Fig. 24A). Cardiac region swollen; branchial region inflated, with distinct branchio-cardiac grooves (Fig. 24A).

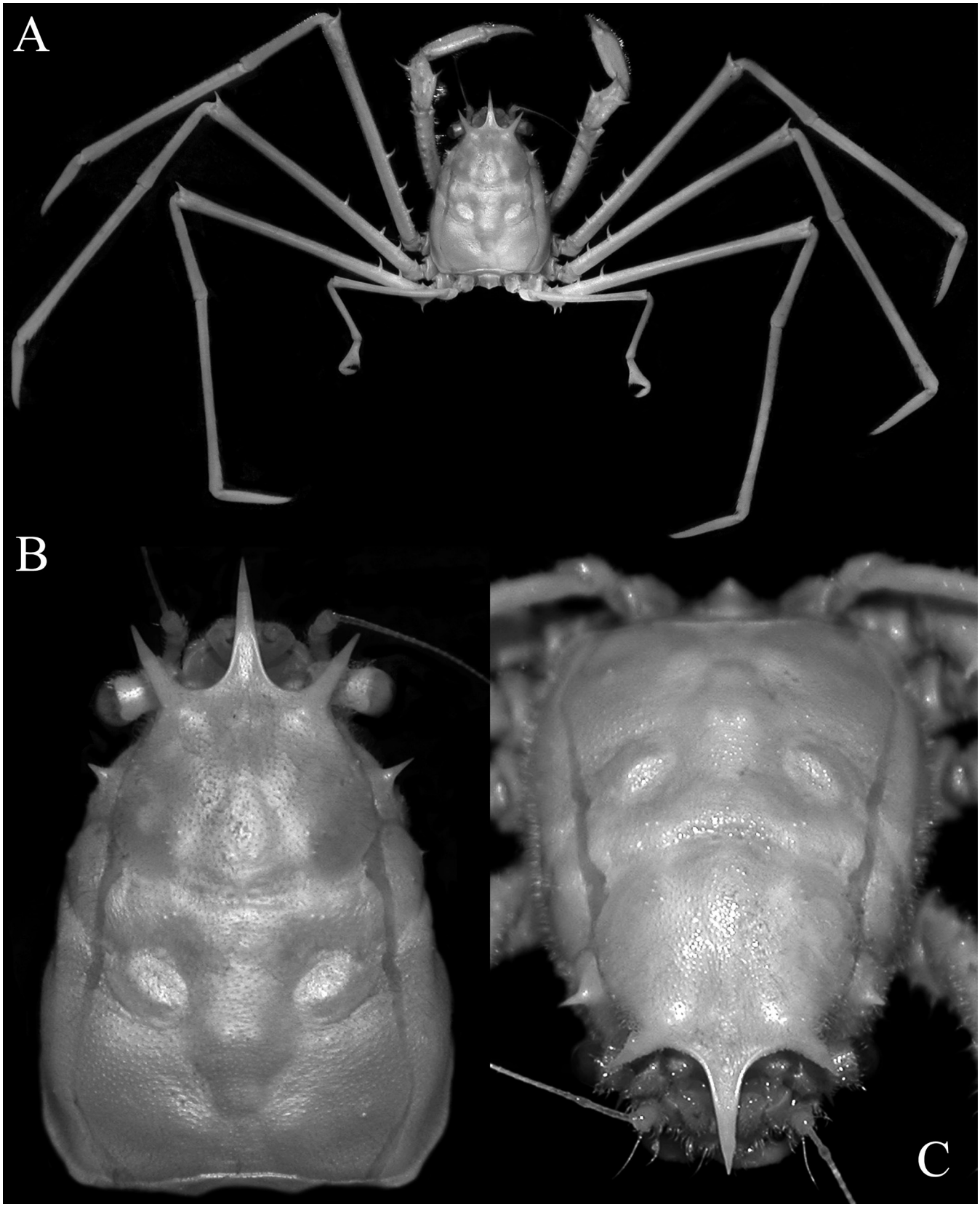

Fig. 21. *Gordonopsis phorcys*, new species, holotype female (10.9 × 16.8 mm) (MNHN-IU-2008-12211), Solomon Islands. A, overall habitus; B, dorsal view of carapace; C, dorso-frontal view of carapace.

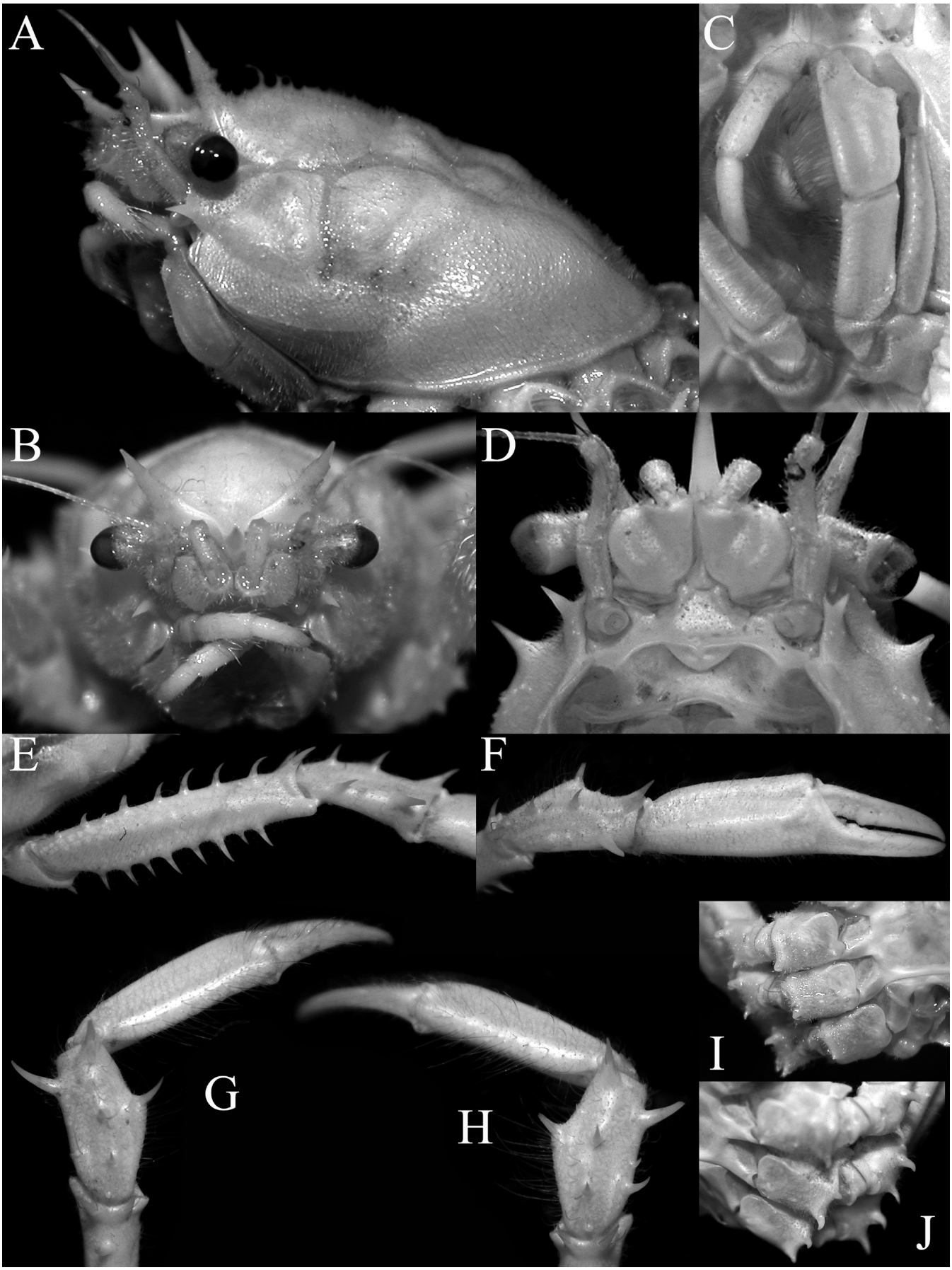

Fig. 22. *Gordonopsis phorcys*, new species, holotype female (10.9 × 16.8 mm) (MNHN-IU-2008-12211), Solomon Islands. A, lateral view of cephalothorax; B, frontal view of cephalothorax; C, left third maxilliped; D, ventral view showing buccal cavity, epistome, antennae, and antennules; E, outer view of merus and carpus of right cheliped; F, outer view of right carpus and chela; G, dorsal view of left cheliped; H, dorsal view of right cheliped; I, right P2–P4 coxae and basis-ischia (denuded); J, left P2–P4 coxae and basis-ischia (denuded).

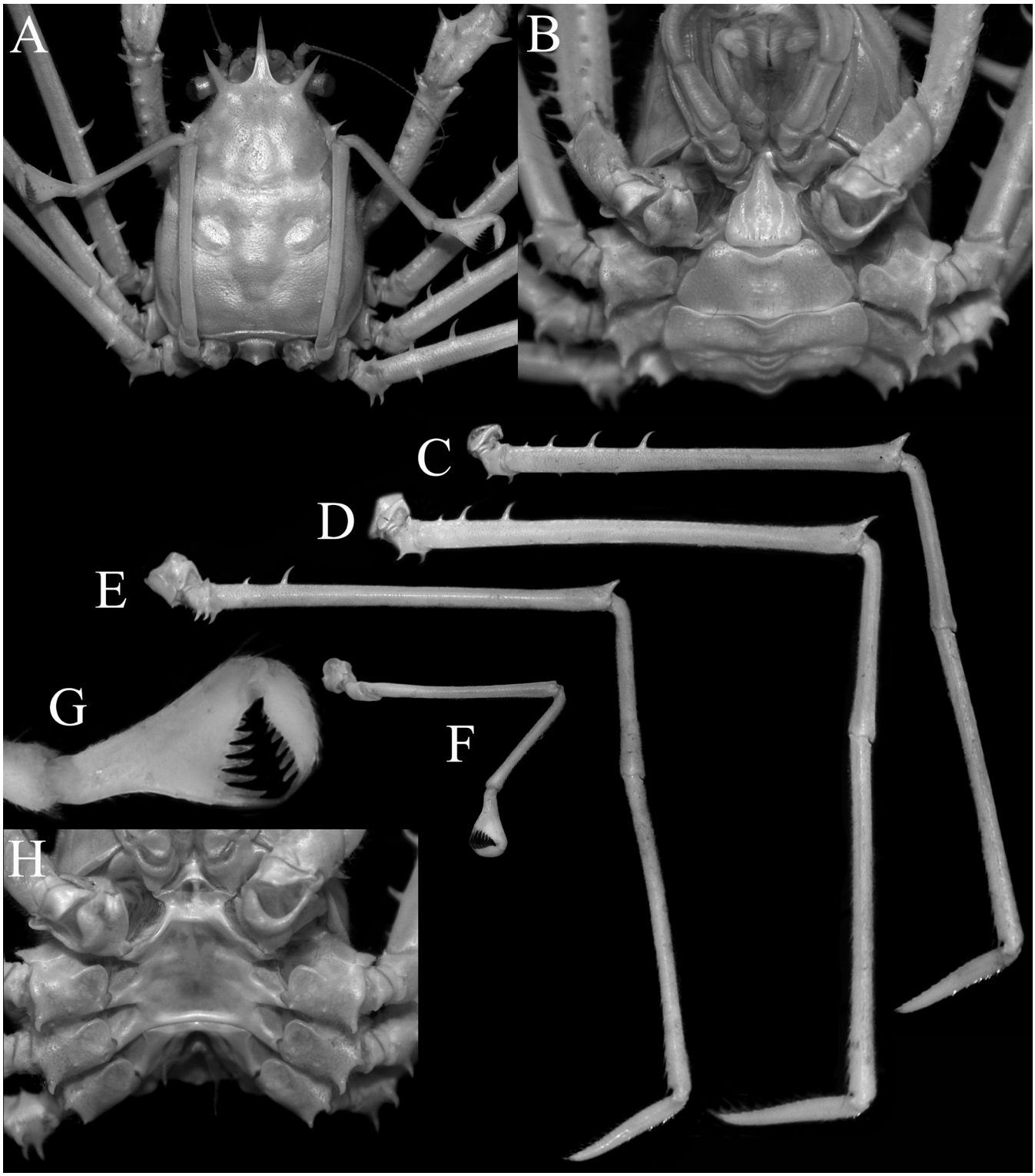

Fig. 23. *Gordonopsis phorcys*, new species, holotype female (10.9 × 16.8 mm) (MNHN-IU-2008-12211), Solomon Islands. A, dorsal view of carapace showing relative P5 length; B, ventral view of cephalothorax showing coxae, basis-ischia, and pleon; C–F, right P2–P5, respectively (all to same scale); G, right P5 pseudochela; H, ventral view of cephalothorax showing sternopleonal cavity, coxae, and basis-ischia.

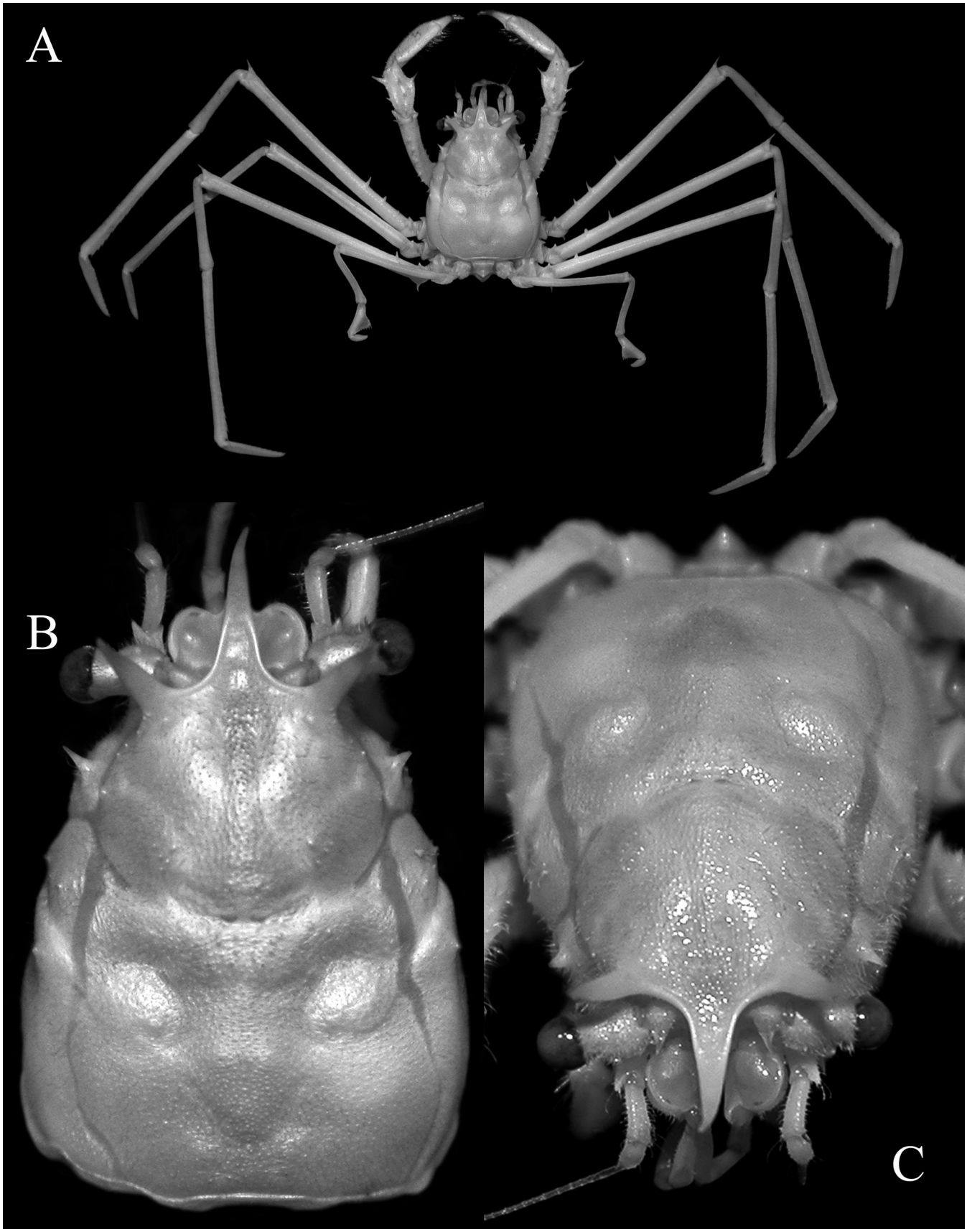

Fig. 24. *Gordonopsis ceto*, new species, holotype female (9.3 × 13.6 mm) (NTOU), South China Sea. A, overall habitus; B, dorsal view of carapace; C, dorso-frontal view of carapace.

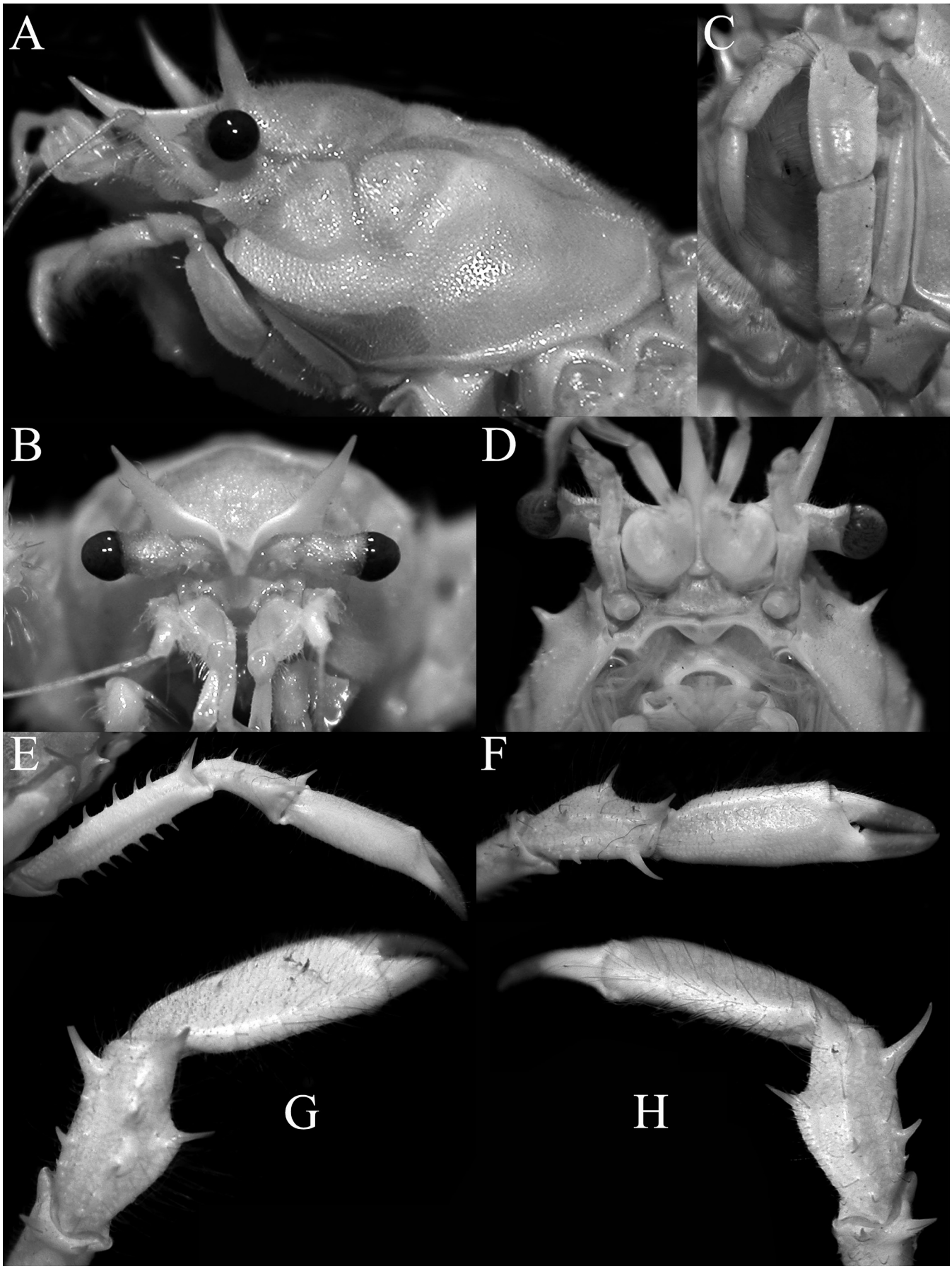

Fig. 25. *Gordonopsis ceto*, new species, holotype female (9.3 × 13.6 mm) (NTOU), South China Sea. A, lateral view of cephalothorax; B, frontal view of cephalothorax; C, left third maxilliped; D, ventral view showing buccal cavity, epistome, antennae, and antennules; E, outer view of merus and carpus of right cheliped; F, outer view of right carpus and chela; G, dorsal view of left cheliped; H, dorsal view of right cheliped.

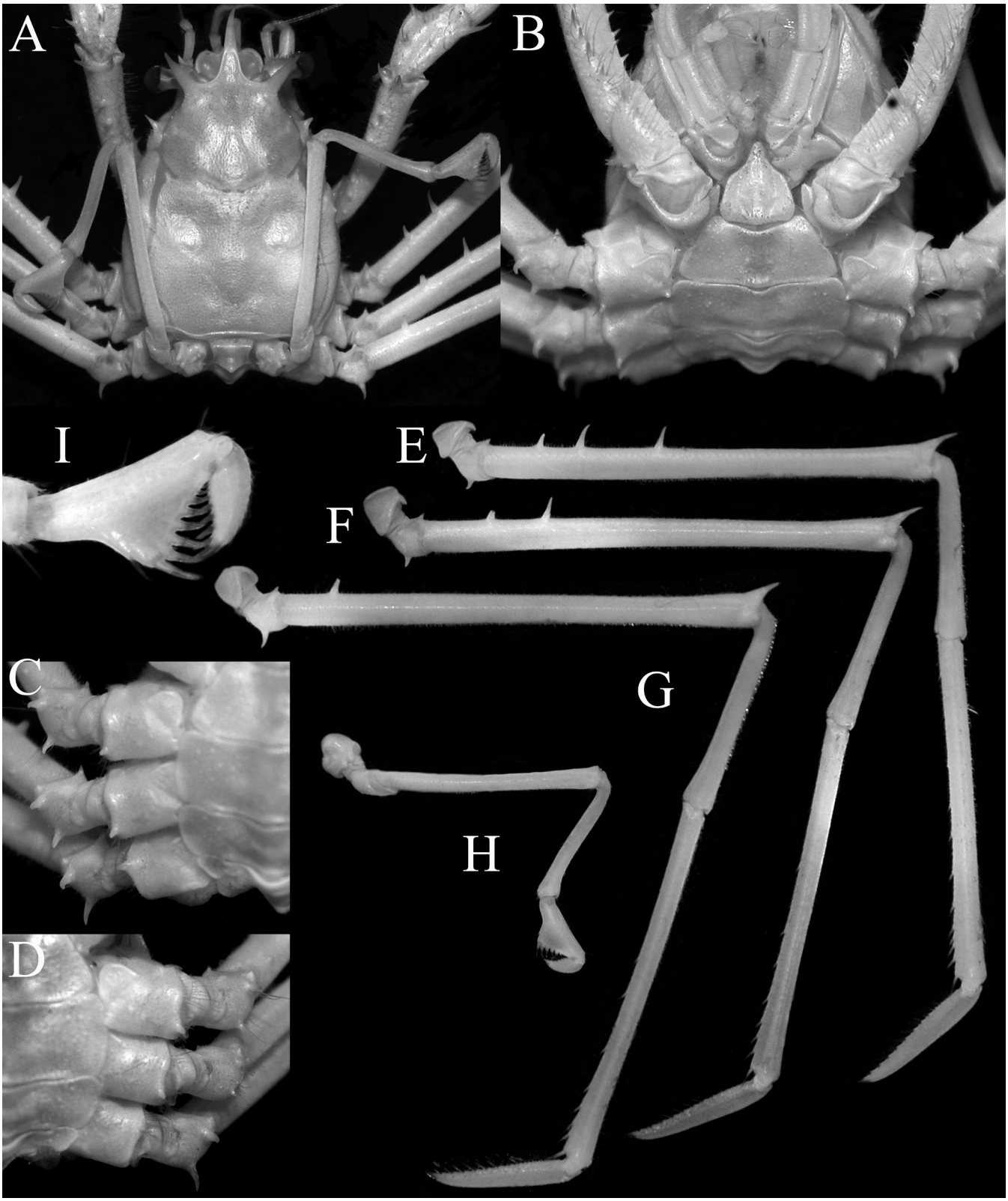

Fig. 26. *Gordonopsis ceto*, new species, holotype female (9.3 × 13.6 mm) (NTOU), South China Sea. A, dorsal view of carapace showing relative P5 length; B, ventral view of cephalothorax showing coxae, basis-ischia, and pleon; C, right P2–P4 coxae and basis-ischia (denuded); D, left P2–P4 coxae and basis-ischia (denuded); E–H, right P2–P5, respectively (all to same scale); I, right P5 pseudochela.

Latero-posterior tubercle on carapace low, just discernible as granule (Fig. 24A). Base of antenna with distinct spine (Fig. 25D). Antennal flagellum short, second and third articles thick, setose. Epistome triangular (Fig. 25D). Third maxilliped pediform, merus elongate with angular external angle (Fig. 25C). Chelipeds long; fingers long, greater than half length of palm; surface gently rugose with scattered small granules; carpus longitudinally ovate, outer margin with 2 or 3 long spines, distal edge with 1 long spine, inner margin with 1 long spine, sometimes with additional spinule, dorsal surface with longitudinal row of 2 or 3 spinules; merus triangular in cross-section, relatively long, curved, dorsal margin with 7 spines and distal 2 spines bracketing chela, outer ventral margin with 7 spines, inner ventral margin with 3–5 spinules (Fig. 25E–H). Ambulatory legs very long; basis-ischium with 4 spines on each margin; P2 merus with 3 spines on dorsal margin (excluding 1 distal spine), ventral margin with 1 or 2 spinules or sharp granules; P3 merus with 2 spines on dorsal margin (excluding 1 distal spine), ventral margin with 1 spinule; P4 merus with 1 spine on dorsal margin (excluding 1 distal spine), ventral margin unarmed, outer surface smooth, without trace of spinule or granule (Figs. 24A, 26A, E–G). P5 merus slender, unarmed on all margins, reaching beyond gastric groove when folded anteriorly; carpus long, propodus short, enlarged, forming prominent pseudochela with stout, gently curved dactylus; occlusal margin of fixed finger with 8 spines, that of dactylus with 7 or 8 spines (Fig. 26H, I). Outer margin of P2 coxa with 1 short, stout spine on proximal edge, outer margin of P4 coxa with 1 or 2 short, stout spines on each edge (Fig. 26B–D). Proximal part of telson subtrapezoidal, with distal half triangular (Fig. 26B).

Colour. In life, the carapace is greyish-brown, and the chelipeds and ambulatory legs are orange (Fig. 30B).

Etymology. The species is named after Ceto, a Greek sea goddess, sister and wife of Phorcys. The name is used as a noun.

Remarks. See general discussion for comparisons with congeners.

Gordonopsis velutina, new species
(Figs. 27–29)

Material examined. Holotype: female (20.8 × 27.8 mm) (MNHN-IU-2013-2269), station CP4249, southeast of Sherburne reefs, southeast Admiralty Islands, Bismark Sea, 3°31′S, 148°05′E, 598–650 m, coll. Expedition MADEEP, N.O. Alis, 23 April 2014.

Diagnosis. Female: carapace longitudinally ovate, width to length ratio 0.75, distinctly wider posteriorly than anteriorly; dorsal carapace surface with well-defined regions, separated by broad, deep grooves; lateral margin distinctly convex; dorsal parts with numerous soft and stiff setae that almost completely obscure surface; lateral parts with denser setae that obscure surface, relatively denser on hepatic, pterygostomial and suborbital regions (Figs. 27A–C, 28A, B, 30C). Rostrum relatively long, sharp, with 2 long, obliquely directed pseudorostral spines, just shorter than rostrum (Fig. 27B). Supraorbital margin relatively narrow, C-shaped; pseudorostral spines directed obliquely laterally at angle of about 45° (Fig. 27B). Eyes with short ocular peduncle, cornea prominent; no discernible orbit (Fig. 27B). Hepatic region gently inflated, with short obliquely directed spine (Fig. 27B). Gastric region without spines (Fig. 27B). Gastric groove well marked, with distinct ovate gastric fossae just above (Fig. 27B). Cardiac region swollen; branchial region inflated, with distinct branchio-cardiac grooves (Fig. 27B). Latero-posterior tubercle on carapace barely visible only as slight swelling (Fig. 27B). Base of antenna with distinct spine (Fig. 28D). Antennal flagellum short, second and third articles thick, setose. Epistome triangular (Fig. 28D). Third maxilliped pediform, merus elongate with slightly rounded external angle (Fig. 28C). Chelipeds long; fingers long, slightly greater than half length of palm; surface gently rugose with scattered small granules; carpus longitudinally ovate, outer, distal and inner margins with 1 long spine each, dorsal surface with low ridge, unarmed; merus triangular in cross-section, relatively long, curved, dorsal margin with 6 or 7 spines and 1 distal spine adjacent to chela, outer ventral margin with 6 or 7 spines, inner ventral margin with 5 or 6 spinules (Figs. 27A, 28E–H). Ambulatory legs long; basis-ischium with small granules, not spines; P2 merus with 3 spines on dorsal margin (excluding 1 distal spine), ventral margin unarmed; P3 merus with 2 or 4 spinules on dorsal and subdorsal margins (excluding 1 distal spine), ventral margin unarmed; P4 merus with 0 or 4 spinules on dorsal and subdorsal margins (excluding 1 distal spine), ventral margin unarmed, outer surface with 1 distinct granule (Figs. 27A, 29A, F–H). P5 merus slender, unarmed on all margins, reaching beyond gastric groove when folded anteriorly; carpus long, propodus short, enlarged, forming prominent pseudochela with stout, gently curved dactylus; occlusal margin of fixed finger with 7 spines, that of dactylus with 7 spines (Fig. 29A, I, J). Outer margins of P2–P4 coxae smooth, unarmed (Fig. 29C–E). Proximal part of telson subcircular with strongly convex lateral margins, distal part triangular (Fig. 29B).

Colour. The carapace and appendages are dirty white, with the setae yellowish-brown (Fig. 30C).

Etymology. The name is derived from the Latin word for velvety, alluding to the dense setae all over the body of the species.

Remarks. See general discussion for comparisons with congeners.

GENERAL DISCUSSION

Gordonopsis, as diagnosed in this revision, can be divided into two groups of species based on whether the outer margins of P2–P4 coxae possesses a spine. In one group of species, comprising *G. profundarum* s. str., *G. alaini*, *G. robusta*, and *G. velutina*, the outer margin of the P2–P4 coxae is

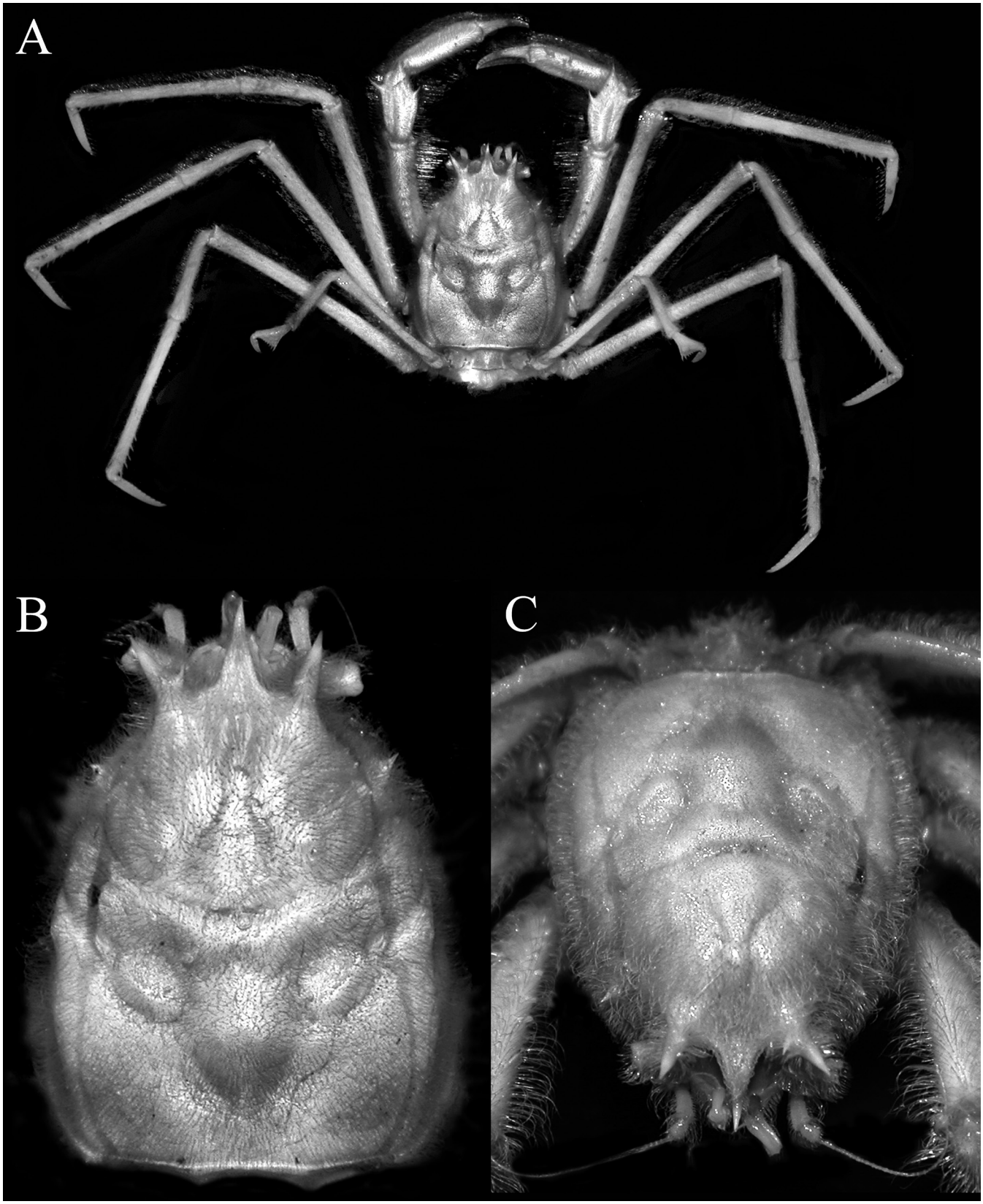

Fig. 27. *Gordonopsis velutina*, new species, holotype female (20.8 × 27.8 mm) (MNHN-IU-2013-2269), Admiralty Islands. A, overall habitus; B, dorsal view of carapace; C, dorso-frontal view of carapace.

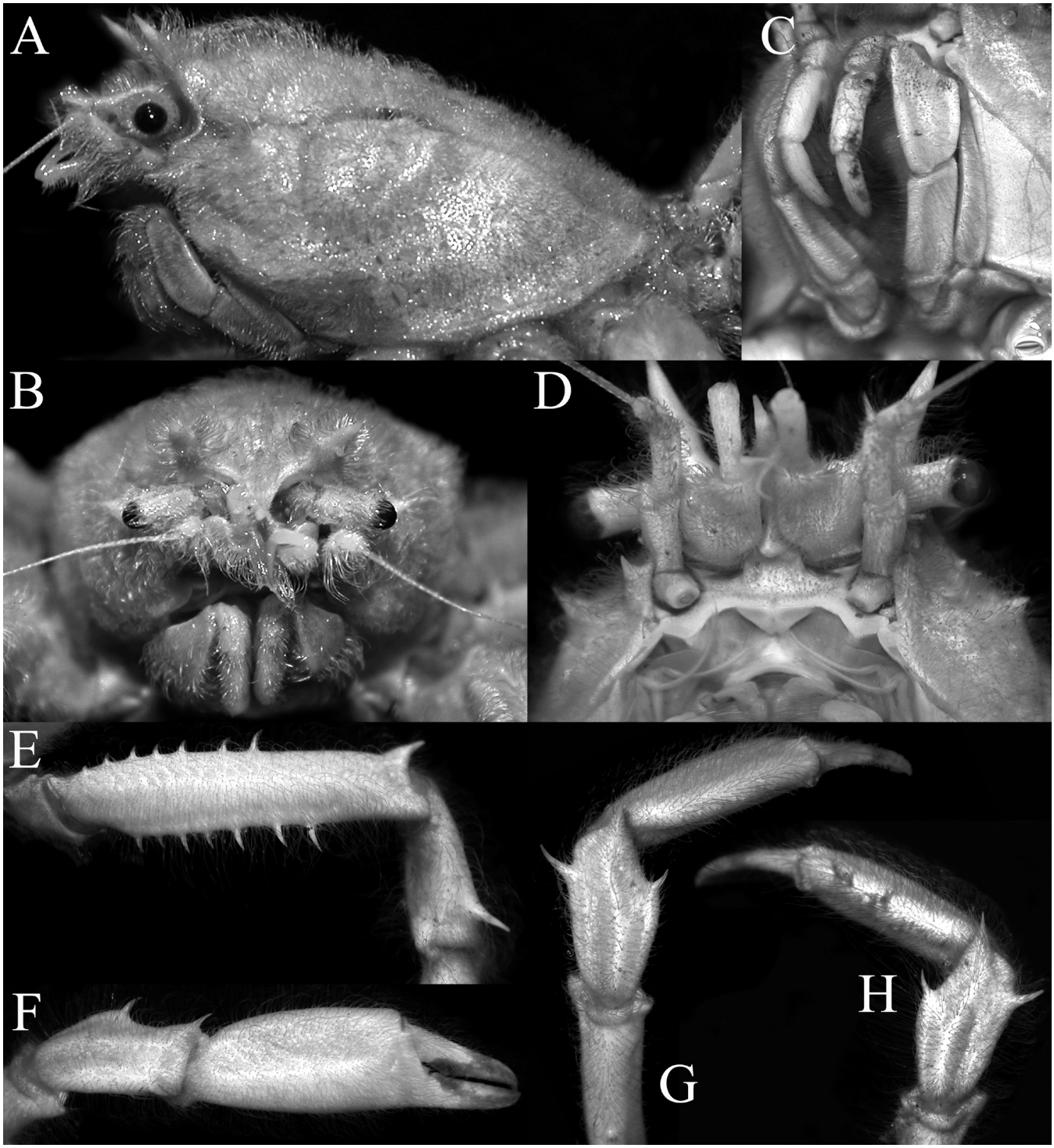

Fig. 28. *Gordonopsis velutina*, new species, holotype female (20.8 × 27.8 mm) (MNHN-IU-2013-2269), Admiralty Islands. A, lateral view of cephalothorax; B, frontal view of cephalothorax; C, left third maxilliped; D, ventral view showing buccal cavity, epistome, antennae, and antennules; E, outer view of merus and carpus of right cheliped; F, outer view of right carpus and chela; G, dorsal view of left cheliped; H, dorsal view of right cheliped.

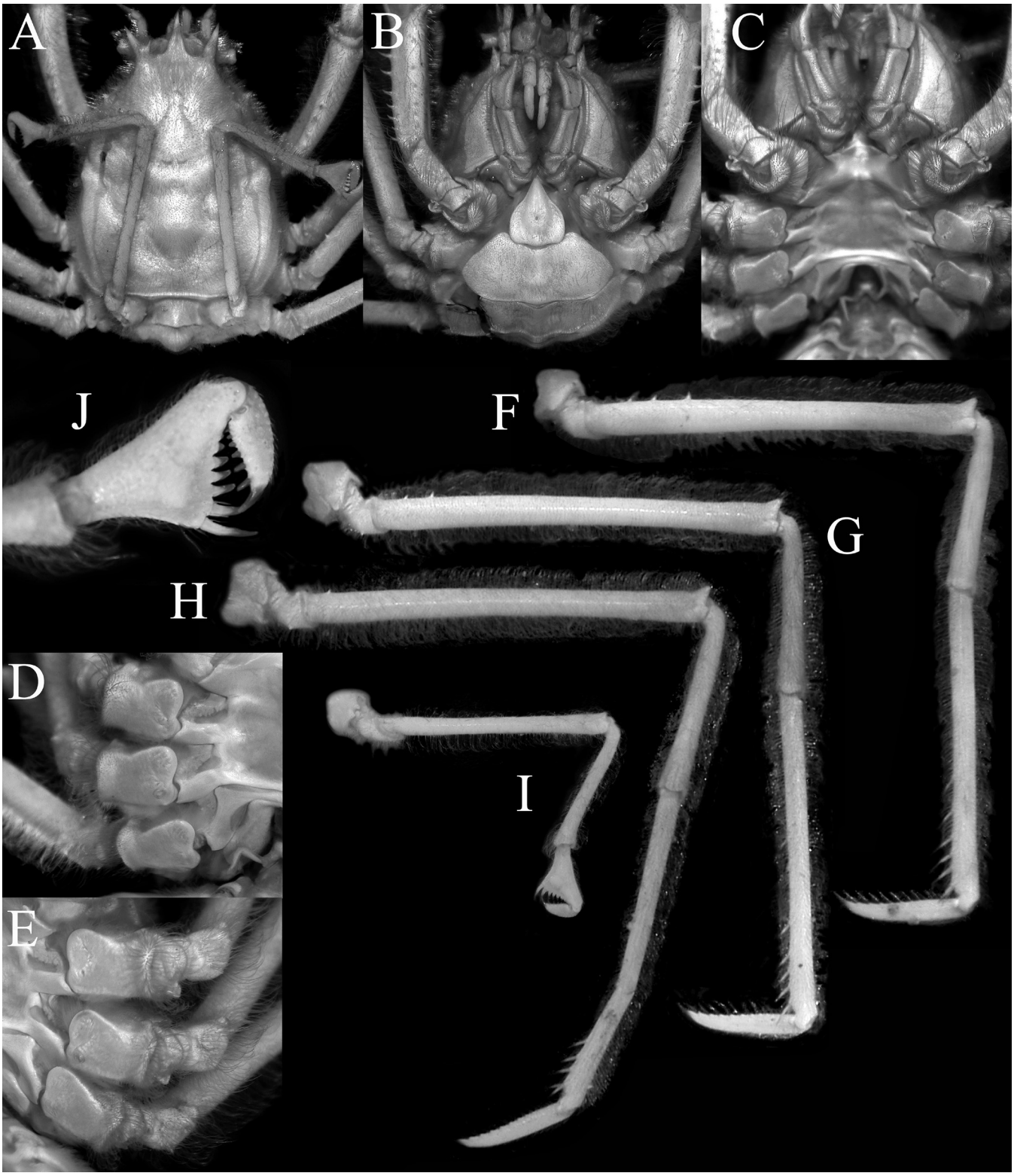

Fig. 29. *Gordonopsis velutina*, new species, holotype female (20.8 × 27.8 mm) (MNHN-IU-2013-2269), Admiralty Islands. A, dorsal view of carapace showing relative P5 length; B, ventral view of cephalothorax showing coxae, basis-ischia, and pleon; C, ventral view of cephalothorax showing sternopleonal cavity and coxae; D, right P2–P4 coxae and basis-ischia; E, left P2–P4 coxae and basis-ischia; F–I, right P2–P5, respectively (all to same scale); J, right P5 pseudochela.

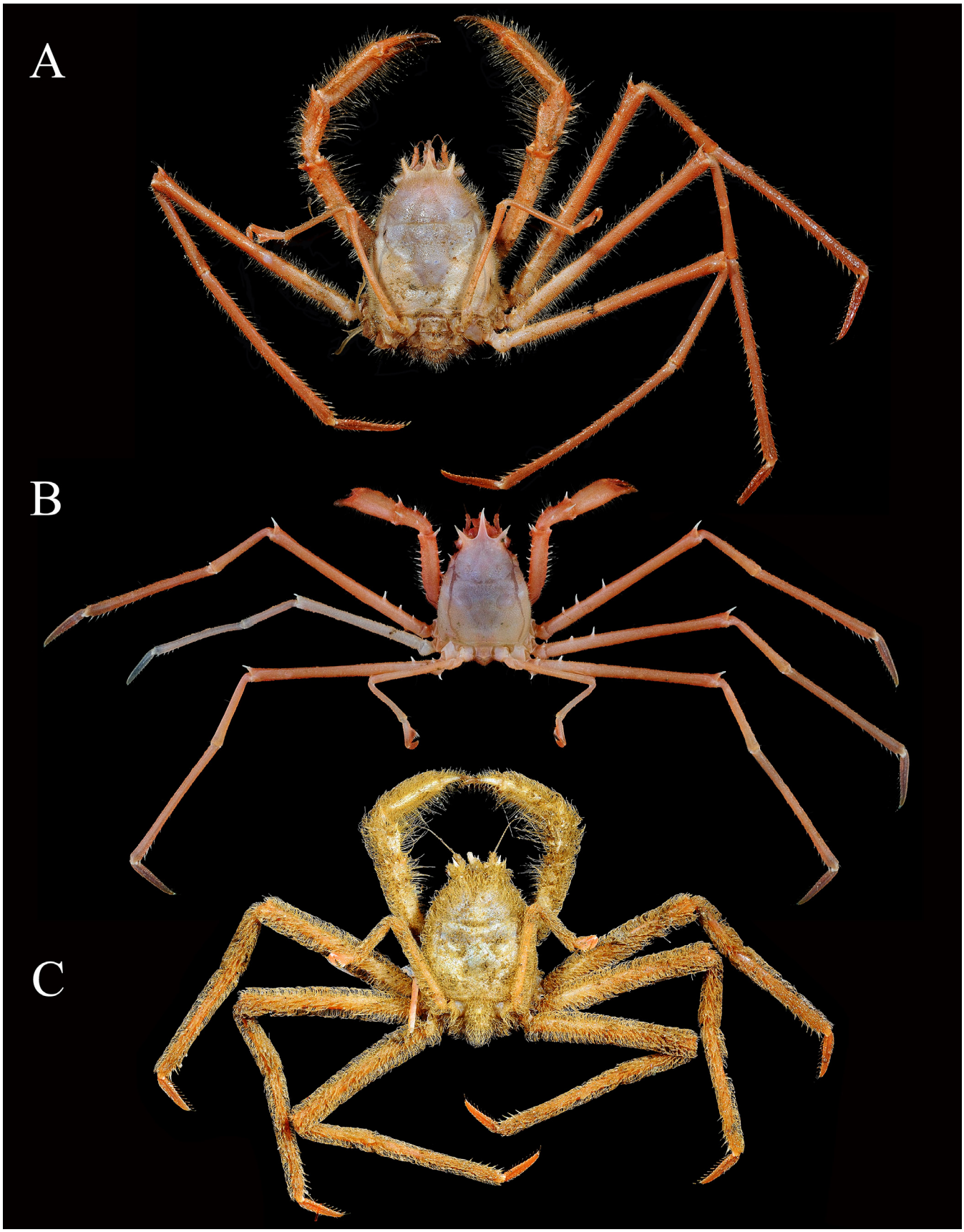

Fig. 30. Colour in life. A, *Gordonopsis hera*, new species, holotype ovigerous female (21.8 × 31.2 mm) (MNHN-IU-2013-2245), Papua New Guinea; B, *G. ceto*, new species, holotype female (9.3 × 13.6 mm) (NTOU), South China Sea; C, *G. velutina*, new species, holotype female (20.8 × 27.8 mm) (MNHN-IU-2013-2269), Admiralty Islands. Photographs: A, C, Laure Corbari (MNHN); B, Chan Tin-Yam (NTOU).

smooth and entire. With the exception of *G. velutina* from the western Pacific, these species are from the Indian Ocean. In the second group of species, comprising *G. pacifica*, *G. hera*, *G. phorcys*, and *G. ceto*, the outer margin of P2–P4 coxae has one or two spines that may be low but are always visible, at least as a tubercle (although some of the coxae on individual specimens may appear smooth); all are western Pacific in distribution. In these species, the spines on the dorsal margin of the P2–P4 basis-ischium and merus are also proportionately longer and more prominent (e.g., Figs. 18J, K, 19B, 22I, J, 23B, H, 26B–D).

Gordonopsis velutina is the most distinctive species of the genus; it uniquely has the distal edge of the dorsal margin of the cheliped merus armed with only one spine (Fig. 28G) (versus with two distinct spines at this position in all other congeners, e.g., Figs. 3F, 7G, 13F, 15G, 22E, 25G, H); and the carapace and pereiopods are covered with long dense setae, which hide the surfaces and margins and are difficult to brush off (Fig. 27A–C) (versus less dense setae covering or with soft setae that can be brushed off easily; Figs. 2A–C, 6A–C, 9A–C, 21A–C, 24A–C). Species like *G. robusta*, *G. pacifica*, and *G. hera* are setose (Fig. 12A–D, 14A–C, 17A–C) but none to the extent observed in *G. velutina*.

The armature on the cheliped carpus appears to be independent of sex and separates the species into three forms. One form (*G. alaini* and *G. velutina*) has only one spine on each of the outer and inner margins and the dorsal ridge is smooth and unarmed (e.g., Figs. 10E–G, 28G, H). The second form (*G. pacifica*, *G. hera*, *G. phorcys*, and *G. ceto*) has two or more spines and spinules on the outer margin and one spine on the inner margin, with three spines or spinules on the dorsal ridge (e.g., Figs. 18E, F, I, 22G, H, 25G, H). The third form (*G. profundarum* and *G. robusta*) has three or more spines and spinules on each of the outer and inner margins and the dorsal ridge is not armed with spines or spinules (e.g., Figs. 3F, G, 7G, 13F). In *G. profundarum*, however, the dorsal ridge has a row of low granules, while in *G. robusta*, the ridge has a row of low sharp tubercles.

Gordonopis pacifica and *G. hera* share several characters: the supraorbital margin is proportionately wider and the pseudorostral spines are relatively shorter and directed only slightly obliquely laterally at an angle of 20–30° (Figs. 14B, 15D, 17B). In all other species of *Gordonopsis*, the supraorbital margin is C-shaped, narrower, and the pseudorostral spines are longer and directed almost 45° obliquely laterally (e.g., Fig. 6B). *Gordonopis pacifica* can easily be separated from *G. hera* by the distinctly higher and more inflated carapace when viewed laterally and frontally (Fig. 15A, B) (versus carapace distinctly lower in *G. hera*; Fig. 18A, B); P2–P4, particularly the meri, are proportionately shorter (Fig. 16E–G, K, L) (versus meri of P2–P5 proportionally longer in *G. hera*; Fig. 19D–F); the P5 is proportionally shorter, reaching just beyond the gastric groove (Fig. 16A) (versus longer P5 extending well beyond gastric groove in *G. hera*; Fig. 19A); and the outer surface of the proximal part of the merus of P4 is armed with a distinct tubercle (Fig. 16G, I) (versus outer surface of the proximal part of the merus of P4 is smooth in *G. hera*; Fig. 19F).

Gordonopsis phorcys and *G. ceto* appear to be closely related, with a similar carapace and elongate ambulatory legs. The main difference is that in *G. phorcys*, the outer margin of each P3 and P4 coxa has two long spines (Figs. 22I, J, 23B, H) (versus with only one spine on each P3 and P4 coxa in *G. ceto*; Fig. 26B–D); and the outer surface of the P4 merus has one perpendicular spine on the proximal part (versus outer surface of the P4 merus is completely smooth in *G. ceto*). *Gordonopsis hera* is the only other species with the outer surface of the P4 merus smooth and unarmed.

The carapace shape is useful for separating several species. The carapace is distinctly ovate, with the posterior part more globose and lateral margins distinctly convex in *G. profundarum*, *G. robusta*, *G. pacifica*, *G. phorcys*, *G. ceto*, and *G. velutina* (Figs. 2B, 6B, 12C, D, 14B, 21B, 24B, 27B). The carapace is narrower, with the lateral margins straighter and less convex in *G. alaini* and *G. hera* (Figs. 9B, 17B). The carapace of the four western Pacific species, as well as the Indian Ocean *G. alaini*, has only a small latero-posterior carapace tubercle or granule (e.g., Figs. 9B, 17B). This is in sharp contrast to the condition in *G. profundarum* s. str. and *G. robusta*, in which the latero-posterior tubercle is large and prominent (e.g., Figs. 2B, 6B, 12B).

The G1 of the three species for which this structure is known differs significantly, but it is difficult to evaluate the significance of differences as all are singletons. That of *G. profundarum* has the distal part subconical in shape with the tip rounded (Figs. 4H, 8H). In *G. alaini*, the G1 distal part is proportionately broader, more truncate with the tip gently concave with a sharper tip (Fig. 10H). The distal part of the G1 tip in *G. robusta* is gently curved upwards with the tip concave, appearing almost bifurcate (Fig. 13K). In *G. pacifica*, the tip of the G1 is acute and sharp (Fig. 16M, N).

The material on hand is too limited to determine the possible degree of variation in the various characters observed, notably in the shape of the carapace, strength of the latero-posterior carapace tubercle, and ambulatory leg proportions. In *G. profundarum* and *G. robusta* at least, which are each represented by a large adult male and a young female, these characters certainly do not vary between sex and size, suggesting they may be taxonomically reliable. This also appears to be the case for the cheliped carpus and merus, as well as armature on P4 (notably the presence or absence of a median granule or spine on the outer proximal surface).

The recognition of a second species, *G. alaini*, in the western Indian Ocean is notable. Despite the proximity of the Maldives to India and Madagascar, the deep waters in that part of the Indian Ocean have a complex geological history which appears to have affected the species composition and biogeography of the region. The recognition of *G. alaini* from Madagascar, distinct from the Maldives and Somalia (*G. profundarum* s. str.) is not surprising. Guinot & Richer de

Forges (1995) recognised three species of *Moloha* Barnard, 1946, from that part of the Indian Ocean, *M. alisae* Guinot & Richer de Forges, 1995 (Seychelles), *M. grandperrini* Guinot & Richer de Forges, 1995 (Maldives), and *M. alcocki* (Stebbing, 1920) (South Africa and Mozambique). Ng & Kumar (2015) added one more species, *M. tumida* Ng & Kumar, 2015, from the west coast of India; and showed all four were distinct taxa. Similar patterns have also been observed in some deep water oregoniids (*Pleistacantha* Miers, 1879, cf. Ahyong & Ng, 2007; Ng et al., 2017) and mathildellids (*Neopilumnoplax* Serène in Guinot, 1969, cf. Ahyong & Ng, 2016), and even in munidopsid squat lobsters (*Munidopsis* Whiteaves, 1874, cf. Ahyong, 2014).

The apparent rarity of *Gordonopsis* is almost certainly an artefact of collecting—their preferred habitat is probably too difficult to sample using standard collecting methods (see Ng et al., 2009; Mendoza et al., 2010). The in situ photographs taken of *G. hera* (Fig. 20) suggest its preferred habitat is uneven, hard rocky substrates. The same observation was made for *G. ceto*, with the collector noting that the ecosystem was extremely difficult to sample using dredges and trawls due to the very rough terrain. That being said, the present recognition of eight species in a genus that has been monotypic since 1995 is indicative of just how poor our knowledge of the deep-sea fauna is. In fact, until 2019, the genus was not even known from the western Indian Ocean and Pacific Ocean!

Key to species of *Gordonopsis*

1. Carapace and pereiopods covered with long dense setae which obscures surfaces and margins (Fig. 27A–C); distal edge of dorsal margin of cheliped merus with 1 spine (Fig. 28E, G, H) ..... *Gordonopsis velutina*, new species (Admiralty Islands)
– Carapace and pereiopods glabrous, covered with short setae that may obscure surface or longer sparser setae that does not obscure surface (e.g., Figs. 2A–C, 14A–C, 17A–C); distal edge of dorsal margin of cheliped merus with 2 spines (e.g., Figs. 3F, G, 15G) 2
2. Latero-posterior margin of carapace with distinct tubercle or spine (e.g., Fig. 2A); outer margin of P2–P4 coxae unarmed, smooth 3
– Latero-posterior margin of carapace with very low tubercle, barely visible (e.g., Fig. 17A); outer margin of P2–P4 coxae with a spine or tubercle (may be reduced or absent on some of articles) (e.g., Figs. 18J, K, 22I, J) 5
3. Carapace relatively narrower with lateral margins straighter, less convex (Fig. 9B); carpus of cheliped with 1 spine on each of outer and inner margins, dorsal ridge smooth, unarmed (Fig. 10F, G) ..... *Gordonopsis alaini*, new species (Madagascar)
– Carapace longitudinally ovate, with posterior part more globose, lateral margins distinctly convex (e.g., Fig. 2A); carpus of cheliped with 3 or more spines and spinules on each of outer and inner margins, dorsal ridge not armed with spines or spinules (e.g., Fig. 3F, G) 4
4. Ambulatory legs long (Figs. 2A, 6A); distal part of P5 merus extending beyond gastric groove when folded anteriorly (Figs. 4A, 8A); dorsal ridge of carpus of cheliped with row of low granules (Figs. 3F, G, 7G); tip of G1 subtruncate (Figs. 4H, 8K) ... *Gordonopsis profundarum* (Alcock & Anderson, 1899) (western Indian Ocean)
– Ambulatory legs short (Fig. 12A, B); distal part of P5 merus just reaching gastric groove when folded anteriorly (Fig. 12D); dorsal ridge of carpus of cheliped with row of low sharp tubercles (Fig. 13F); tip of G1 appears bifurcated (Fig. 13K) ... *Gordonopsis robusta* Ng, Padate & Saravanane, 2019 (Andaman Sea)
5. Supraorbital margin proportionately wider, pseudorostral spines relatively short, directed slightly obliquely laterally at angle of 20–30° (Figs. 14B, 15D, 17B) 6
– Supraorbital margin C-shaped, less wide, pseudorostral spines long, directed almost 45° obliquely laterally (Figs. 21B, 24B) 7
6. Carapace appears inflated when viewed laterally and frontally (Fig. 15A, B); P2–P4, particularly merus, proportionately shorter (Fig. 16E–G, K, L); outer surface of P4 merus with 1 tubercle on proximal part (Fig. 16G, I) ..... *Gordonopsis pacifica* Takeda & Suyama, 2019 (southern Japan)
– Carapace appears inflated when viewed laterally and frontally (Fig. 18A, B); P2–P4, particularly merus, proportionately longer (Fig. 19D–F); outer surface of P4 merus unarmed, completely smooth (Fig. 19F) ..... *Gordonopsis hera*, new species (Papua New Guinea)
7. Outer margin of each P3 and P4 coxa with 2 long spines each (Figs. 22I, J, 23B, H); outer surface of P4 merus with 1 perpendicular spine on proximal part ... *Gordonopsis phorcys*, new species (Solomon Islands)
– Outer margin of each P3 and P4 coxa with 1 spine each (Fig. 26B–D); outer surface of P4 merus unarmed, completely smooth ..... *Gordonopsis ceto*, new species (South China Sea)

ACKNOWLEDGEMENTS

The specimens from Papua New Guinea were collected by R.V. Alis during the following deep-sea cruises: MADEEP (https://doi.org/10.17600/14004000) and SALOMON 2 (https://doi.org/10.17600/4100090). These cruises, PIs Sarah Samadi, Laure Corbari, and Philippe Bouchet, were operated by MNHN and Institut de Recherche pour le Développement (IRD) as part of the research programme "Tropical Deep Sea Benthos". The exploration of the Papua New Guinea waters in the programme "La Planete Revisitee" was organised jointly by MNHN, Pro-Natura International, and IRD, with support from the National Fisheries Authority of Papua New Guinea. The organisers acknowledge supporting funding from the Total Foundation, the Laboratoire d'Excellence Diversités Biologiques et Culturelles (LabEx BCDiv, ANR-10-LABX-0003-BCDiv), and the expedition was endorsed by the New Ireland Provincial Administration and operated under a Memorandum of Understanding with University of Papua New Guinea (UPNG). We are also grateful to Chan Tin-Yam (NTOU) and Laure Corbari (MNHN) for their photographs of fresh *Gordonopsis*. Paul Clark helped us check material in the NHM and Harry Taylor from its Photographic Unit kindly took some of the photographs needed. We thank Santanu Mitra (Zoological Survey of India) for trying to help us locate the type material of Alcock. Masatsune Takeda and Hironori Komatsu (NSMT) kindly allowed the first author access to the type of *G. pacifica*. Laure Corbari and Paula Martin-Lefevre (MNHN) kindly helped with the data for the French material. Thanks are due to the U.S. National Oceanographic and Atmospheric Administration Office of Ocean Exploration and Research for photographs

of *Gordonopsis hera* taken in situ in the Tokelau Seamounts; and to Mary Wicksten for bringing them to our attention. We are most grateful to Danièle Guinot and Shane Ahyong for their many important recommendations and suggestions which have helped the manuscript.

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