ZooKeys 752: 1–15 (2018)
doi: 10.3897/zookeys.752.24615
http://zookeys.pensoft.net

RESEARCH ARTICLE

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A new species of the land planarian *Issoca* sheds light on the polyphyletic status of the genus (Platyhelminthes, Tricladida, Geoplaninae)

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Academic editor: *D. Gibson* | Received 22 February 2018 | Accepted 4 April 2018 | Published 23 April 2018

http://zoobank.org/780F7546-CD36-4BAE-A0A4-F9B97D019AB5

Citation: Araujo APG, Carbayo F (2018) A new species of the land planarian *Issoca* sheds light on the polyphyletic status of the genus (Platyhelminthes, Tricladida, Geoplaninae). ZooKeys 752: 1–15. https://doi.org/10.3897/zookeys.752.24615

Abstract

A new species of the genus *Issoca* (Platyhelminthes, Tricladida, Geoplaninae) is described. *Issoca assanga* sp. n. presents the diagnostic features of the genus, with the exception of the relative position of the subneural parenchymal muscle layer with the cephalic retractor muscle, which are overlapped in the type species of the genus but are intersected in the new species. Rather than a polymorphic character, the relative position of these muscle layers might reflect the polyphyletic status of the genus.

Keywords

Brazil, Continenticola, flatworm, histology, morphology, Neotropical region, taxonomy

Introduction

Most Neotropical land planarians are grouped in the subfamily Geoplaninae (Platyhelminthes, Tricladida, Geoplaninae). The number of known species of this group exceeds 290 species (http://planarias.each.usp.br; accessed in 2. Apr. 2018). The genus *Issoca* Froehlich, 1955 (Geoplaninae) comprises five species, namely *I. spatulata*

(Graff, 1899), *I. rezendei* (Schirch, 1929, type species of the genus), *I. jandaia* Froehlich, 1955, *I. piranga* Froehlich, 1955, and *I. potyra* Froehlich, 1958. The most notable morphological feature of *Issoca* is a cephalic glandulo-muscular organ. This organ consists of a cephalic retractor muscle derived from the ventral longitudinal cutaneous musculature, and a set of adhesive glands piercing the ventral surface of the cephalic region (Froehlich 1955). In contrast to other representatives of Geoplaninae (namely, *Choeradoplana* Graff, 1899, *Cephaloflexa* Carbayo & Leal-Zanchet, 2003, *Supramontana* Carbayo & Leal-Zanchet, 2003, and *Luteostriata* Carbayo, 2010), the cephalic retractor muscle in *Issoca* is typically circular in cross-section and is traversed by muscle fibers of the parenchymal subneural musculature (Froehlich 1955, Carbayo and Leal-Zanchet 2003). The retractor muscle is externally imperceptible, but the spoon-shaped cephalic region of the body helps recognize representatives of the genus. This latter feature was noted in *Choeradoplana spatulata* Graff, 1899 by Froehlich (1955), who transferred the species to *Issoca* (Froehlich, 1955). Yet the internal organs of *I. spatulata* remain unstudied.

The phyletic status of *Issoca* was briefly discussed by Carbayo et al. (2013) in a paper focused on the molecular phylogeny of Geoplaninae. In that work, the genera *Issoca* (represented by three species), *Luteostriata* Carbayo, 2010 (10 species, including some polyphyletic species), and *Supramontana* Carbayo & Leal-Zanchet, 2003 (1 species), constituted the so-called clade LIS (Fig. 1). In this clade, *Issoca* turned out to be polyphyletic, with *I. rezendei* being the sister-species of all other members of the clade. Furthermore, *Luteostriata* was shown to be paraphyletic, and *Supramontana* was revealed as the sister species of a group constituted by *I. jandaia* and the undescribed species *Issoca* sp. 1. All species in the clade LIS have a cephalic retractor muscle (Froehlich 1955, 1958, Carbayo and Leal-Zanchet 2003, Carbayo 2010). No further taxonomic works were published on this genus. Herein we describe *Issoca* sp. 1 (Carbayo et al. 2013) and discuss the phyletic status of the genus from a morphological perspective.

Materials and methods

The specimens were collected in the Atlantic Forest in the States of Espírito Santo and Rio de Janeiro, Brazil. We conducted searches on soil litter and trails during the day and night, with the light of a flashlight. Geographic coordinates of collecting sites were recorded either with Garmin eTrex GPS device (Espírito Santo) or with Googlemaps (Rio de Janeiro). Specimens were photographed, then killed with boiling water and subsequently fixed in 10% formalin. In the laboratory, the specimens were cut into pieces, dehydrated in a graded ethanol series, cleared in clove oil, then infiltrated and embedded in Paraplast® Tissue Embedding Medium. Tissue blocks were sectioned at 7 µm intervals using a microtome and affixed the sections with albumin-glycerol (1:1) onto glass slides placed on a hot plate, and stained them according to Cason (1950). The sections were dehydrated in a graded ethanol series, cleared in xylene, and mounted in synthetic balsam. The slides were examined with an optical microscope,

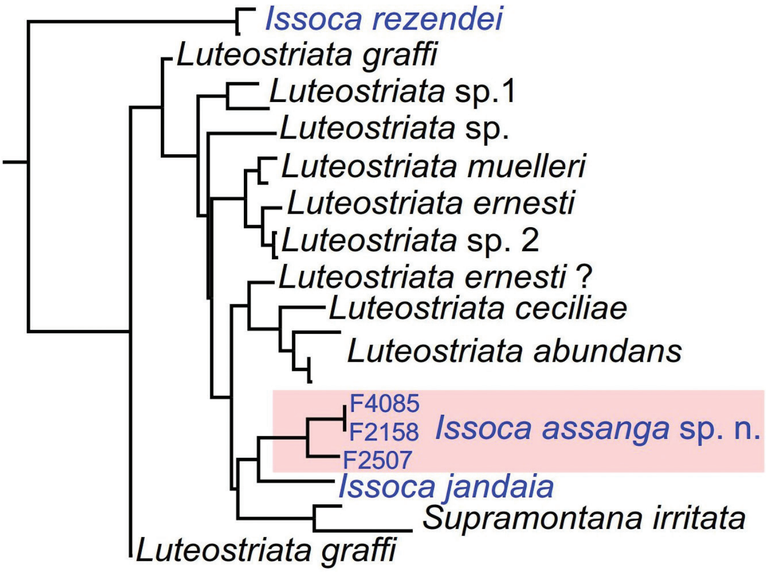

Figure 1. Molecular phylogenetic relationships of species of the so-called clade LIS (modified from Carbayo et al. 2013). *Issoca assanga* sp. n. was named as *Issoca* sp. 1 in Carbayo et al. (2013).

and drawings of the copulatory apparatus were made with the aid of a camera lucida attached to the microscope. Photomicrographs were taken with a digital camera attached to the microscope and edited with GIMP (GNU Image Manipulation Program 2.8.16; The GIMP team www.gimp.org, 1995–2016). Figures of sagittal and horizontal views are orientated with anterior to the left. The type material is deposited at the *Museu de Zoologia da Universidade de São Paulo* (*MZUSP*).

Abbreviations of figures

af	annular-shaped fold of male atrium
cb	cerebral ganglion
co	common glandular ovovitelline duct
dc	parenchymal layer of deccussate fibres
di	diagonal parenchymal muscle
dv	dorso-ventral parenchymal muscle
e	eye
ej	ejaculatory duct
ep	esophagus
f	fold
fa	female atrium
fd	female genital canal
g	gonopore
gl	glands
gs	ventral glandular surface of the cephalic region
i	intestine
ln	normal longitudinal cutaneous muscles
m	muscle
ma	male genital atrium
mc	common muscle coat
mo	mouth
o	ovary
ov	ovovitelline duct
pb	penis bulb
po	pharyngeal pouch
pp	penis papilla

pv	prostatic vesicle
r	cephalic retractor muscle
sb	subintestinal transverse muscles
sc	subcutaneous nerve net
sd	sperm duct
se	necks of secretory cells
sg	shell glands
sk	sunken longitudinal cutaneous muscles
sn	subneural transverse muscles
sp	supraintestinal transverse muscles
t	testis
vi	vitellaria
vn	ventral nerve plate

Results

Taxonomic section
Family Geoplanidae Stimpson, 1857
Subfamily Geoplaninae Stimpson, 1857
Genus *Issoca* Froehlich, 1955

Issoca assanga sp. n.
http://zoobank.org/FD7F2CF1-B799-4215-B75C-80E16FA90B1D

Synonymy. *Issoca* sp. 1; Carbayo et al. (2013).

Type material. Parque Estadual do Desengano (-21.87; -41.91), Santa Maria Madalena, Rio de Janeiro State, Brazil: **Holotype F4085** (MZUSP PL. 1085): J. Pedroni et al. col., 13 August 2009: sagittal sections of copulatory apparatus on 28 slides. **Paratype F4057** (MZUSP PL. 1082): J. Pedroni et al. col., 12 August 2009: sagittal sections of copulatory apparatus on 29 slides.

Reserva Biológica Augusto Ruschi (-19.88; -40.54), Santa Teresa, Espírito Santo State, Brazil: **Paratype F2158** (MZUSP PL 1020): F. Carbayo et al. col., 26 March 2008: fixed in 80% ethanol. **Paratype F2250** (MZUSP PL. 1023): F. Carbayo et al. col., 24 May 2008: fixed in 80% ethanol. **Paratype F2266** (MZUSP PL. 1024): F. Carbayo et al. col., 24 May 2008: fixed in 80% ethanol. **Paratype F2274** (MZUSP PL. 1025): F. Carbayo et al. col., 24 May 2008: sagittal sections of copulatory apparatus on 33 slides; transverse sections of cephalic region on 7 slides; horizontal sections of portion containing ovaries on 22 slides; sagittal sections of pharynx region on 34 slides; transverse sections of pre-pharyngeal region on 8 slides. **Paratype F2309** (MZUSP PL. 1032): F. Carbayo et al. col., 24 May 2008: fixed in 80% ethanol. **Paratype F2394** (MZUSP PL. 1037): F. Carbayo et al. col., 27 May 2008: sagittal sections of copulatory apparatus on 18 slides; sagittal sections of pharynx region on 20 slides; transverse sections of cephalic region on 4 slides; horizontal sections of portion containing ovaries on 8 slides; and transverse sections of pre-pharyngeal region on 6 slides. **Paratype F2470** (MZUSP PL. 1042): F. Carbayo et al. col., 29 May 2008: transverse sections of cephalic region on 14 slides; horizontal sections of portion containing ovaries on 48 slides; sagittal sections of a portion posterior to ovaries on 23 slides; sections immediately before pre-pharyngeal region on 33 slides; transverse sections of pre-pharyngeal region on 16 slides; sagittal sections of pharynx region on 41 slides; sagittal sections of copulatory apparatus on 61 slides. **Paratype F2507** (MZUSP PL. 1045): F. Carbayo et al. col., 29 May 2008: preserved in 80% ethanol.

Type locality. Parque Estadual do Desengano, Santa Maria Madalena, Rio de Janeiro State, Brazil.

Diagnosis. Species of *Issoca* up to 97 mm in length. Widest dorsal pigment bands with 33–40% of body width. A few cutaneous muscle bundles in-sunk in the prepharyngeal region. Cephalic retractor muscle and the sub-neural parenchymal muscle not intersecting with each other. Copulatory apparatus relatively long. Prostatic vesicle extrabulbar, proximally dilated, and non-anastomosed. Ejaculatory duct thin, with its opening at the tip of the penis papilla; this papilla is conical with dorsal insertion posterior to the ventral one. Female atrium spacious with some lateral folds. Common glandular duct almost as long as the female atrium. Common muscle coat envelops male and female atria.

External morphology. The body is elongated with nearly parallel margins (Fig. 2A–B). Its cephalic region (5% of the body length) is sometimes slightly laterally dilated before converging to the rounded anterior extremity of the body, which is slightly concave ventrally (Fig. 2C). The posterior extremity is pointed. The dorsum is slightly convex, the ventral side is flattened, and the body margins are rounded so that the section of the body is elliptic. Six mature, fixed specimens measured 48–97 mm in length. Fixed, paratype F2470 is 71 mm in length, 7 mm in width and 1.7 mm in height. The creeping sole is as wide as 74–84% of body width at the pre-pharyngeal region (paratypes F2470 and F2394, respectively). The mouth lies at a distance from the anterior extremity equal to 55% of body length; the gonopore is at 80% (paratype F2274).

The dorsal color consists of a cream-colored (specimens from Ruschi, Fig. 2A–B) or yellowish (specimens from Desengano, Fig. 2D) median stripe (6.7% of body width). This stripe is longitudinally divided by a very thin black median line (2.2%), which can be very tenuous and discontinuous (Fig. 2B). The .median stripe is bordered on either side by a wide black band (33–40%). This wide band is externally bordered by a whitish stripe (4–6.7%). The median and the lateral stripes gradually pass into orange of cephalic region (Fig. 2C). A marginal zone is either pigmented with a black stripe (5%, specimens from Ruschi, Fig. 2A–C) or mottled with black pigment spots (8.3%; Desengano, Fig. 2D). The ventral side is whitish, passing into orange of the cephalic surface. This surface (5% of body length) extends along the margins of the body progressively occupying a wider surface towards the anterior extremity until they fuse at 1 millimeter from the anterior extremity of the body (Fig. 3A).

The eyes are formed by one pigmented cup 50 µm in diameter. They contour the anterior extremity in a row of 2–3 eyes along the first 2 millimeters (Fig. 2C); going backwards, they spread progressively on each side of the dorsum in a band with 33% of the body width until the end of anterior half of the body. Posterior to this region they are scarcer and the band narrows until posterior extremity of the body.

Internal morphology. The sensory pits are 30 µm deep and are distributed in a simple ventro-lateral row, from the very anterior extremity up to at least 38% of body length. In the prepharyngeal region (Fig. 3B), rhabditogen cells and cell glands producing eryth-

Figure 2. *Issoca assanga* sp. n. Living specimens. Cephalic region is orangish. **A** paratype F2266 **B** paratype F2309 **C** Cephalic region of paratype F2250 **D** paratype F4085. Scale bars not available.

rophil granules open through the dorsal epithelium (Fig. 3B); necks of these glands are thick - 20 µm in width. Three additional gland types discharge their content through dorsal and marginal epidermis. They become progressively more abundant from the midbody towards the body margins. These gland cells are as follows: one type of cell with cell neck 20 µm in diameter produces xanthophilic granules; the second type produces xanthophilic granules, and its neck is 8–10 µm in diameter; the third type produces cyanophilic granules and its neck is 8–10 µm thick. The ventral epidermis is pierced by two types of scarce cell glands, each of them secreting either erythrophilic or xanthophilic granules.

The cutaneous musculature comprises the three typical layers of Geoplaninae, i.e., a subepithelial circular layer followed by a double diagonal layer with decussate fibers, and a strongly developed longitudinal layer, 60–125 µm thick. The fibers of the latter muscle layer are gathered into compact bundles (Fig. 3B–D). A few small muscle bundles of the cutaneous longitudinal muscle are sunken in the pre-pharyngeal region (Fig. 3C–D). The number of these sunken muscle fibers increases towards the cephalic region. The cutaneous musculature thickness relative to body height at the pre-pharyngeal region is 16–18%.

The three usual parenchymal muscle layers are present throughout the body: a dorsal layer of diagonal decussate fibers (50 µm thick, or 5% of the body height,

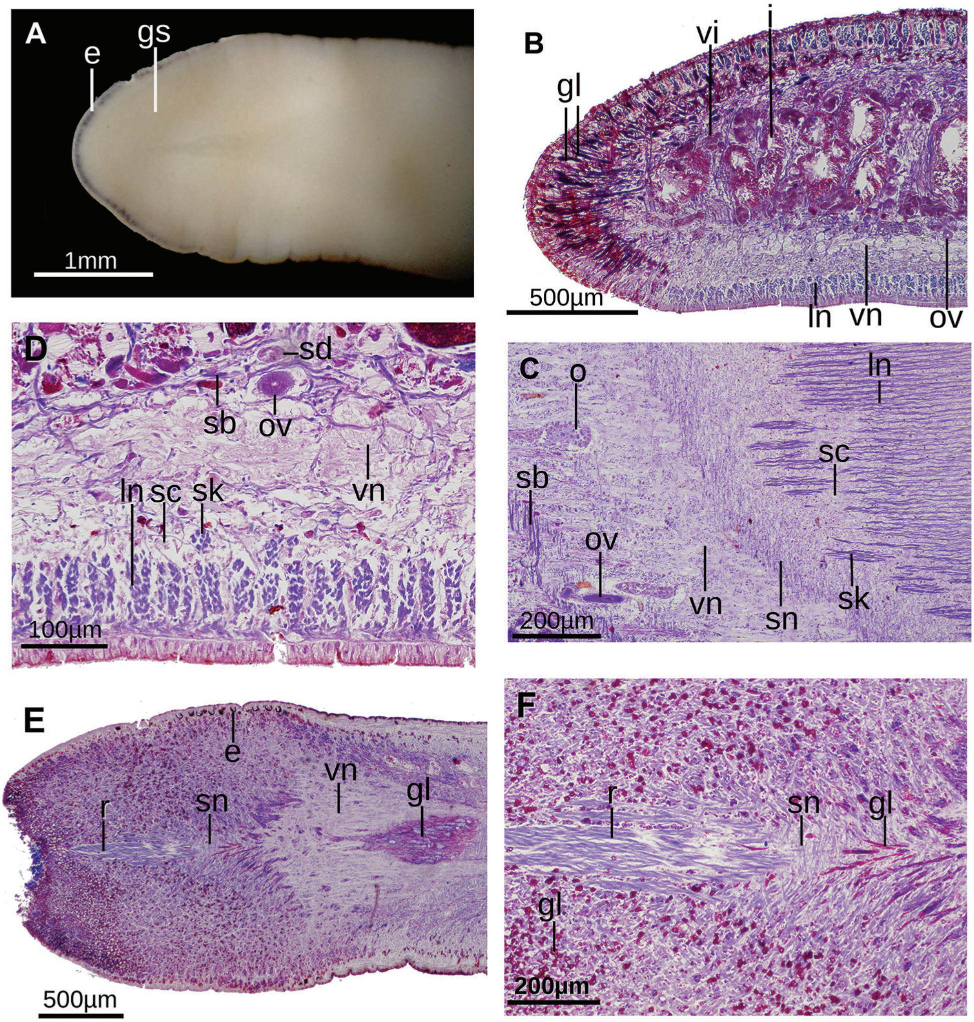

Figure 3. *Issoca assanga* sp. n. **A** Ventral view of cephalic region of fixed paratype F2274. (B-L): Photomicrograph of histological sections **B** transverse section of left side of pre-pharyngeal region of paratype F2394 **C** Horizontal section of paratype F2394 at the level of the ovaries **D** transverse section of pre-pharyngeal region of paratype F2394 **E, F** horizontal section of cephalic region of paratype F2394.

paratype F2470), a transverse supraintestinal layer (40 µm, or 4%), and a transverse subintestinal layer (50 µm, or 5%). Additionally, there is a subneural layer (40 µm, or 4%) of transverse muscles. Dorso-ventrally oriented parenchymal fibers are abundant in the pre-pharyngeal region.

The muscular organization changes (Fig. 4) in the anterior region of the body with respect to that of the pre-pharyngeal region. The number of sunken ventral longitudinal cutaneous fibers increases at 5 millimeters from the anterior extremity of the body (equal to 10% of body length in paratype F2394), and bundles of both normal and

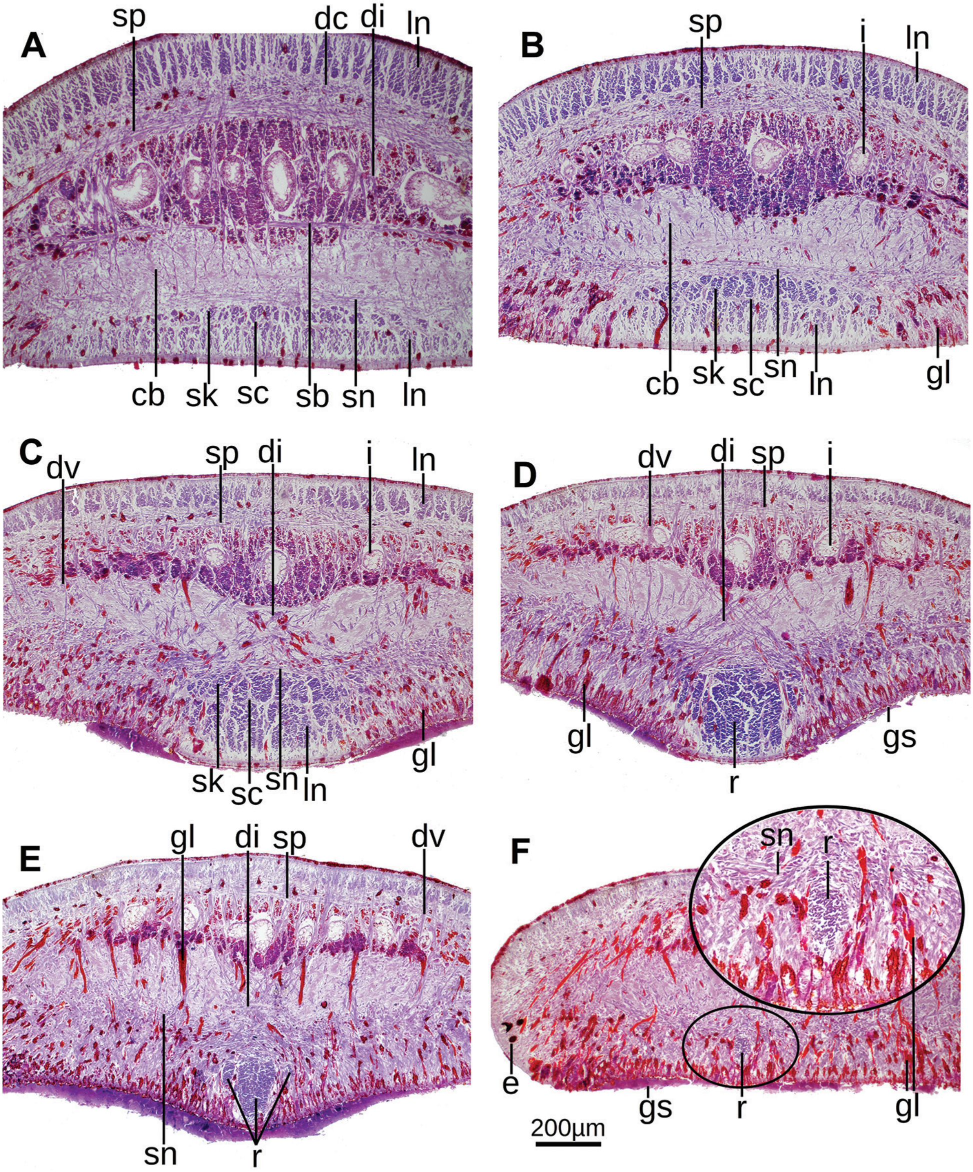

Figure 4. Serial transverse sections of the cephalic region of paratype F2470 at 4.0, 2.6, 2.0, 1.6, 1.3, and 1.0 mm from anterior extremity, respectively. Encircled region in **F** is enlarged in the inset. **A–E** at the same magnification as **F**.

sunken ventral cutaneous muscles concentrate medially to give rise to the cephalic retractor muscle. The retractor is lens-shaped in cross-section at 4–2.6 mm from anterior extremity (Fig. 4A–B). It becomes elliptic at 2.0 mm (Fig. 4C) and roughly quadrangular (Fig. 4D) at 1.6 mm from anterior extremity. Muscle fibers of the retractor muscle are gathered in few but thick bundles. From this region towards anterior extremity, fibers of the retractor muscle progressively detach in bundles that run to the body sides (Fig. 4D–F). As they detach, the retractor muscle becomes less apparent until it disappears close to the anteriormost extremity of the body. It could not be determined whether other fibers from this muscle run dorsally. Before disappearing the retractor muscle is elliptic in cross section (Fig. 4E–F).

In the cephalic region, diagonal, supraintestinal, and subneural parenchymal muscle layers are apparent and placed in the same position relative to the cutaneous longitudinal muscles. Even the subneural muscle and its fibers continue running over the retractor muscle (Fig. 4). The subintestinal parenchymal muscle layer is less apparent, and this layer is the first to disappear as it approaches the anterior extremity of the body. All parenchymal muscles fade out at the anteriormost body portion.

Dorso-ventral parenchymal muscle fibers are more abundant in the cephalic region than on the rest of the body, and they are frequently gathered in bundles of 3–10 fibers each. These fibers run approximately dorso-ventrally, connecting dorsal epidermis with the ventral glandular epidermis. Medially, these fibers run obliquely from the dorsal epidermis of one side of the body to anchor to the ventral glandular epidermis of the other body side, thereby rimming the retractor muscle (Fig. 4C–E).

The glandular surface of the ventral epidermis, orangish in color in living animals, widens towards anterior extremity of the body as the muscle fibers of the retractor concentrate medially. This surface is incompletely bipartite (Fig. 3A) and is richly pierced by gland cells (with 10–12 µm thick necks) producing erythrophilic granules, and by scarce glands (with 12–18 µm thick necks) producing cyanophilic granules.

The mouth is situated at a distance from the root of the pharynx equivalent to 25% of pharyngeal pocket length (Fig. 5). An esophagus is present with 13–20% of pharynx length. The pharynx is cylindrical, with dorsal insertion posterior to the ventral and located at mouth level. The lining epithelium of the pharyngeal pouch is squamous, non-ciliated, surrounded by a simple layer of circular fibers, followed by a layer of diagonal fibers (10 µm thick). The outer and inner pharyngeal epithelia are flat and ciliated. The outer epithelium is underlain by a longitudinal muscle (2.5 µm thick) followed by a circular muscle (17–75 µm), the latter with some longitudinal fibers interspersed. The inner epithelium is surrounded by a circular muscle (45–90 µm), followed by a longitudinal muscle (25 µm).

The central nervous system mainly consists of a ventral nerve plate. Cerebral ganglia (Fig. 4B) extend along the body from 1 millimeter to 4 millimeters behind the anterior tip (2% and 8%, respectively, paratype F2394).

The testes are located under the supraintestinal transverse muscle layer, partially between the intestinal diverticula. They extend from the level of the ovaries to nearly the root of the pharynx. The sperm ducts run between the subintestinal parenchymal muscle layer, dorsally to the ovovitelline ducts. They open into the antero-lateral portion of the prostatic vesicle. This vesicle is extrabulbar and proximally dilated, curves dorsally and penetrates the dorso-anterior aspect of the penis bulb. This vesicle is lined with a ciliated, columnar epithelium, showing an irregular free surface in its anterior portion. The prostatic vesicle receives fine erythrophilic granular secretions derived from glands

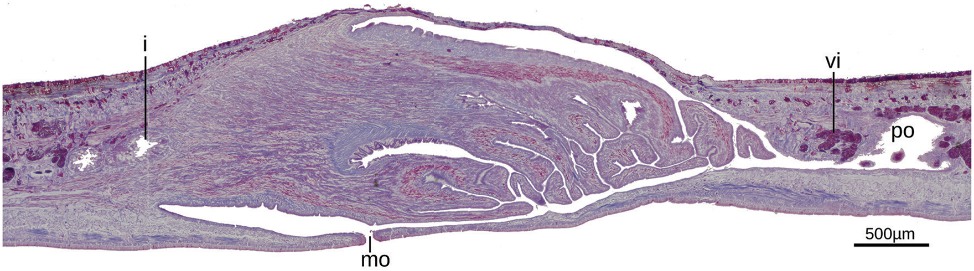

Figure 5. *Issoca assanga* sp. n. Photomicrograph a sagittal section of the pharynx of paratype F2394.

in the parenchyma. These penetrate the ciliated, columnar epithelium lining of the vesicle to discharge into the lumen. The vesicle is surrounded by intermingled decussate, circular, and longitudinal fibers. The prostatic vesicle passes into the relatively thin ejaculatory duct that is lined by a ciliated cuboidal epithelium surrounded by circular muscle. The ejaculatory duct is proximally sinuous and distally straight through the mid penis bulb, terminating at the tip of the penis papilla. The ejaculatory duct is lined with a cuboidal, ciliated epithelium and is surrounded by a circular muscle. The protrusible penis papilla is conical, slightly inclined ventrally, and with its dorsal insertion posterior to the ventral insertion (Fig. 6A–D). The penis papilla is as long as the male atrium, and is lined with a cuboidal, non-ciliated epithelium, and is surrounded by a circular muscle followed by a longitudinal muscle; some fibers of both muscles are intermingled. Numerous secretory cells located in the adjacent parenchyma produce erythrophilic granules (Fig. 6B) that are discharged along the length of the papilla.

The male atrium is mostly occupied by the penis papilla. It is more spacious in its anterior portion than in the posterior, and shows folded walls. One of these folds is a transverse, annular-shaped fold located halfway of the atrial length. From the roof of the distal portion of the male atrium, a large fold projects laterally and continues along the female atrium. The male atrium is lined with a columnar, non-ciliated epithelium, and is pierced by gland cells producing erythrophilic granules. A circular muscularis (5 µm thick) encircles the male atrium.

The ovaries are 500 µm long in the antero-posterior body axis and 200 µm wide. They are located immediately above the ventral nerve plate, at a distance from anterior tip equivalent to 26% of body length (Fig. 3D). The ovovitelline ducts arise from the dorso-external surface of the anterior portion of the ovaries, and run backwards above the ventral nerve plate. They ascend laterally to the gonopore region, and subsequently unite dorsally to form a common ovovitelline duct just dorsal to the anterior section of the female atrium (Fig. 6D). The distal third of the ascending portion of these paired ducts receives shell glands. The ovovitelline ducts unite to form the common glandular ovovitelline duct, which runs caudally and progressively curving to the ventral side to communicate with the female genital canal. This canal is a projection of the postero-dorsal portion of the female atrium that runs dorsally and slightly anteriorly. The female atrium is an irregular, spacious cavity. Its walls are partially projected into

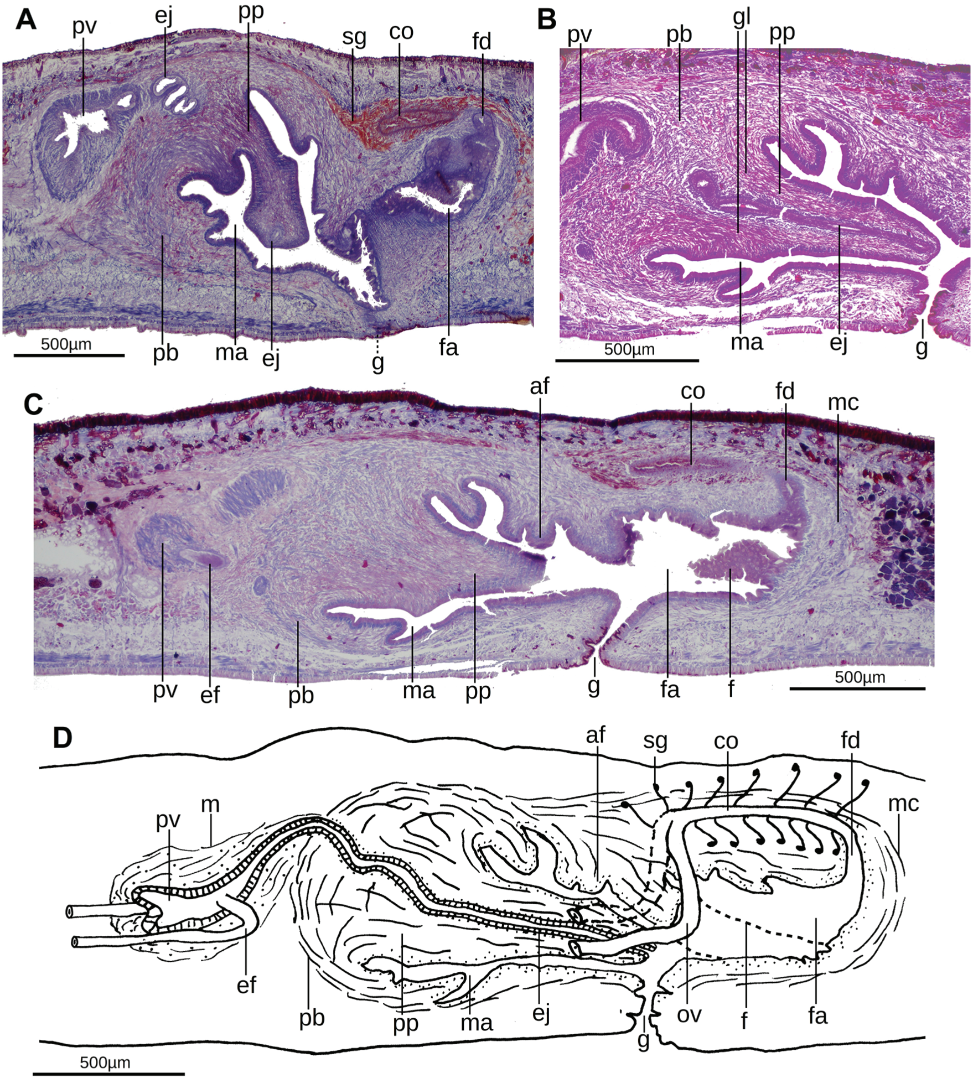

Figure 6. *Issoca assanga* sp. n. **A** photomicrograph of a sagittal section of the copulatory apparatus of paratype F2470 **B** photomicrograph of a sagittal section of the penis papilla of paratype F2394 **C** photomicrograph of a sagittal section of the copulatory apparatus of paratype F2394 **D** diagrammatic representation of the copulatory apparatus of paratype F2394 from sagittal sections.

its lumen. One of these folds is continuous with a fold coming from the male atrium (Fig. 6D).

The female atrium is lined with a columnar epithelium, which is lacunar in aspect in some parts. In the anterior portion of the female atrium, the simple columnar epithelium is 25 µm high; whereas the posterior portion is lined by a pseudostratified columnar epithelium (Fig. 7). The muscularis of the female atrium consists of two muscle layers; a simple (2.5 µm thick) longitudinal muscle followed by a circular muscle

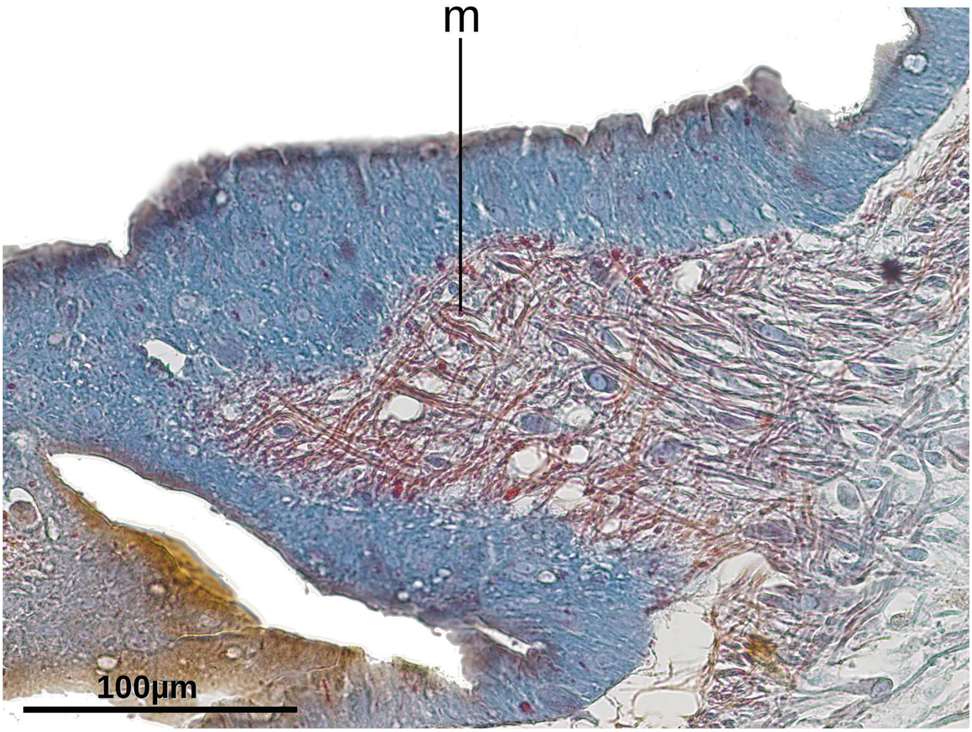

Figure 7. *Issoca assanga* sp. n. Photomicrograph of a sagittal section of the lining epithelium of the posterior section of the female atrium of the holotype.

(10 µm), both partially intermingled. The female atrium receives gland cells producing erythrophilic granules. The male atrium is 1.2 times longer than the female. The common muscle coat is well-developed, and wraps the male and female atria.

Etymology. The specific epithet refers to the Tupi (indigenous Brazilian tribe) name *assanga*, meaning dense, thick (Tibiriçá 1984). It refers to the apparent cephalic glandulo-muscular organ of the new species.

Distribution. Parque Estadual do Desengano (Municipality of Santa Maria Madalena, Rio de Janeiro State) and Reserva Biológica Augusto Ruschi (Municipality of Santa Teresa, Espírito Santo State), Brazil.

Discussion. The external aspect of *I. assanga* allows one to readily distinguish it from the remaining species of the genus by being considerably larger (97 mm in length after fixation) than the largest previously described species, i.e. *I. jandaia*, which is 50 mm in length alive, and 32 mm after fixation. Although the chromatic pattern of all species of the genus is striped, the stripes are as wide as 33–40% of the body width only in *I. assanga* sp. n. The widest colored stripe in other species of the genus is found in *I. potyra*, with a pair or paramedian bands with 17% of the body width each (Froehlich 1955, 1958; Graff 1899; Marcus 1951).

Regarding the digestive system anatomy, the new species can be distinguished from the other species because the mouth is situated at a distance from the root of the pharynx equivalent to 25% of pharyngeal pocket, whereas the mouth in the other species is at a distance equal to 33% (*I. jandaia*) or >30% (*I. rezendei* and *I. piranga*, 50%; *I. potyra*, 67%; Froehlich 1955, 1958; Marcus 1951).

The new species can also be readily distinguished from *I. rezendei* by the general shape of the copulatory apparatus. Unlike the new species (with a relatively long copulatory apparatus, an extrabulbar prostatic vesicle, a horizontal penis papilla and a conspicuous female atrium), the copulatory apparatus in *I. rezendei* is relatively compact, the prostatic vesicle is intrabulbar, the penis papilla is vertical, and the female atrium is absent (Marcus 1951). The outlines of the copulatory apparatuses of the remaining species of *Issoca* are comparable to that of the new species: those being a relatively long and extrabulbar prostatic vesicle; and a penis papilla, or a papilla-like fold horizontal or moderately inclined (Froehlich 1955, 1958). However, the three species *I. jandaia*, *I. piranga* and *I. potyra* (*I. spatulata* is not in this comparison because its copulatory apparatus is yet unknown), differ from the new species in the following details. In contrast to *I. assanga* sp. n., the ejaculatory duct of *I. jandaia* opens into a cavity inside a penis papilla-like fold of the male atrium, the common glandular duct is relatively long, and the female atrium is intensely folded. The penis papilla of *Issoca piranga* occupies only the anterior half of the male atrium, and the muscle coat enveloping the male atrium is separated from that wrapping the female one (Froehlich 1955), whereas in the new species the penis papilla is as long as the male atrium, and there is a common muscle coat wrapping male and female atria. Finally, *I. potyra* differs from the new species in that the wall of the prostatic vesicle is anastomosed, the ejaculatory duct is wide and irregular and it opens into the ventral side of the penis papilla, the male atrium is separated from the female one by a fold which is richly pierced by cyanophilic glands, the common glandular oviduct is relatively short, and the muscle coat enveloping the male atrium is separated from that of the female one (Froehlich 1958), whereas in *I. assanga* sp. n., there are no anastomoses in the prostatic vesicle, the ejaculatory duct is relatively thin, and terminates at the tip of the penis papilla, the male atrial fold is not pierced by cyanophilic glands, the common glandular oviduct is relatively long, and the muscle coat wraps both male and female atria.

One diagnostic feature of the genus is that the cephalic retractor muscle and the subneural parenchymal muscle are intersected, a condition present in the type species of the genus *Issoca rezendei* (see diagnosis in Carbayo and Leal-Zanchet 2003). This feature is the only mismatching diagnostic trait of *I. assanga* sp. n. This condition could be polymorphic within the genus. However, two aspects support a different interpretation: (a) the polyphyly of *Issoca* has been highlighted (Carbayo et al. 2013); and (b) the general anatomy of the copulatory apparatus of *I. rezendei* is very different from that of the remaining species of the genus. These points suggest that rather than an interspecifically polymorphic character, the muscle intersection might reflect the polyphyletic status of the genus (see Fig. 1). Description of the muscular cephalic retractor muscle in the other species of *Issoca* is limited. The muscular organization of the glandulo-muscular organ in *I. jandaia* was reported by Froehlich (1955) as following the same structure as *I. rezendei*. The glandulo-muscular organ in *I. piranga* was described as being very similar to that of *I. jandaia* (see Froehlich 1955). Froehlich (1958) mentioned that the glandulo-muscular organ (i.e., the cephalic retractor muscle plus associated viscid glands) in *I. potyra* "is similar to that of the other species of the genus". However, his diagrammatic reconstruction of the organ shows the cephalic retractor muscle underneath the subneural muscle layer, not intersected. Moreover, the retractor in *I. rezendei* diminishes by means of separating its fibers towards the body margins and the back (Carbayo and Leal-Zanchet 2003), whereas the fibers in *I. assanga* were observed only running to the body margins. This lack of morphological details reinforces the need of a taxonomic revision of the clade LIS, as already suggested by Carbayo et al. (2013).

Acknowledgements

We thank the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) and the Instituto Estadual do Ambiente do Governo do Rio de Janeiro (INEA) for the sampling license in the Reserva Biológica Augusto Ruschi and Parque Estadual do Desengano, respectively. We are indebted to Andrea Souza Aguiar, José Grau, Júlio Hisada Pedroni, Cláudia Tangerino Olivares, Débora Redivo, Marília Jucá, Leonardo Zerbone, and Welton Araujo for sampling help, and also Ítalo Silva de Oliveira Sousa, Geison Castro da Silveira, and Lucas Beltrami for the histological work. Lisandro Negrete (Museo de La Plata) and Marcos Ryotaro Hara (EACH, USP) are acknowledged for their critical reading of a previous version of the manuscript. Hugh David Jones (National History Museum London), Leigh Winsor (University of Townsville), and Ana Maria Leal-Zanchet (Unisinos) are sincerely thanked for their comments on a draft of this article. APGA thanks USP for an undergraduate fellowship. FC has financial support from FAPESP (Proc. 2016/18295-5).

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ZooKeys 752: 17–97 (2018)
doi: 10.3897/zookeys.752.23712
http://zookeys.pensoft.net

RESEARCH ARTICLE

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A revision of "blanket-hermit crabs" of the genus *Paguropsis* Henderson, 1888, with the description of a new genus and five new species (Crustacea, Anomura, Diogenidae)

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Academic editor: *S. De Grave* | Received 18 January 2018 | Accepted 19 February 2018 | Published 23 April 2018

http://zoobank.org/CCE50CBC-D7DC-44C0-B7A9-57F829813A83

Citation: Lemaitre R, Rahayu DL, Komai T (2018) A revision of "blanket-hermit crabs" of the genus *Paguropsis* Henderson, 1888, with the description of a new genus and five new species (Crustacea, Anomura, Diogenidae). ZooKeys 752: 17–97. https://doi.org/10.3897/zookeys.752.23712

Abstract

For 130 years the diogenid genus *Paguropsis* Henderson, 1888 was considered monotypic for an unusual species, *P. typica* Henderson, 1888, described from the Philippines and seldom reported since. Although scantly studied, this species is known to live in striking symbiosis with a colonial sea anemone that the hermit can stretch back and forth like a blanket over its cephalic shield and part of cephalothoracic appendages, and thus the common name "blanket-crab". During a study of paguroid collections obtained during recent French-sponsored biodiversity campaigns in the Indo-West Pacific, numerous specimens assignable to *Paguropsis* were encountered. Analysis and comparison with types and other historical specimens deposited in various museums revealed the existence of five undescribed species. Discovery of these new species, together with the observation of anatomical characters previously undocumented or poorly described, including coloration, required a revision of the genus *Paguropsis*. The name *Chlaenopagurus andersoni* Alcock & McArdle, 1901, considered by Alcock (1905) a junior synonym of *P. typica*, proved to be a valid species and is resurrected as *P. andersoni* (Alcock, 1899). In two of the new species, the shape of the gills, length/width of exopod of maxilliped 3, width and shape of sternite XI (of pereopods 3), and armature of the dactyls and fixed fingers of the chelate pereopods 4, were found to be characters so markedly different from *P. typica* and other species discovered that a new genus for them, *Paguropsina* **gen. n.**, is justified. As result, the genus *Paguropsis* is found to contain five species: *P. typica*, *P. andersoni*, *P. confusa* **sp. n.**, *P. gigas* **sp. n.**, and *P. lacinia* **sp. n.** Herein, *Paguropsina* **gen. n.**, is proposed and diagnosed for two new species, *P. pistillata* **gen. et sp. n.**, and *P. inermis* **gen. et sp. n.**; *Paguropsis* is redefined, *P. typica* and its previously believed junior synonym, *P. andersoni*, are redescribed. All species are illustrated, and color photographs provided. Also included are a summary of the biogeography of the two genera and all species; remarks on the significance of the unusual morphology; and remarks on knowledge of the symbiotic anemones used by the species. To complement the morphological descriptions and assist in future population and phylogenetic investigations, molecular data for mitochondrial COI barcode region and partial sequences of 12S and 16S rRNA are reported. A preliminary phylogenetic analysis using molecular data distinctly shows support for the separation of the species into two clades, one with all five species of *Paguropsis*, and another with the two species *Paguropsina* **gen. n.**

Keywords

Diogenidae, hermit crab, new species, *Paguropsina* gen n. *Paguropsis*, symbiotic anemone

> *"In the case of Paguropsis typica the association with a colonial sea-anemone of a genus related to Mamillifera is even more remarkable. Here there is no shell to play the part of "Sir Pandarus of Troy," but the sea-anemone settles upon the hinder part of the young hermit-crab's tail, and the two animals grow up together, in such a way that the spreading zoophytes form a blanket which the hermit can either draw completely forwards over its head or throw half-back, as it pleases."*
>
> (Alcock 1905: 7)

Introduction

Two unusual hermit crab specimens collected in the Sibuyan Sea, the Philippines, on board the HMS *Challenger* Expedition in 1874, were considered so unique by Henderson (1888) that he named a new genus and new species for them, *Paguropsis typicus* Henderson, 1888 [the spelling of the specific epithet was subsequently corrected by Alcock (1905) to *P. typica*, for gender agreement]. Henderson found the morphology of the specimens, a male and a female, to be peculiar among hermit crabs, in particular the subdorsal position of pereopods 4 and 5, the presence of unpaired pleopods on the right side rather than on the left, and the membranous pleon bent on itself rather than spirally curved. He was intrigued by the lack of pleonal curvature, and that no trace of habitation or pleonal protection was found with the specimens. Apparently unaware of Henderson's (1888) taxon, Alcock (1899) described, and Alcock and McArdle (1901) later illustrated, a new genus and species of a hermit crab based on hundreds of specimens collected off southern India, which he named *Chlaenopagurus andersoni* Alcock, 1899. Alcock also noted various unusual characters such as the puzzling general symmetry, despite the variability of pleopods 3-5 which in his specimens could be present on either the left or right sides in either sex, and devoted considerable discussion to the commensalism he observed. He was able to determine that his species did not use a shell for housing but instead was adapted to live with a colonial sea anemone with a sheet-like coenosarc that the hermit crab tucked under its telson and could stretch over its back like a blanket, thus the common name "blanket-crab" he used in the narratives while on board the "*Investigator*" expeditions (Alcock 1902). Subsequently, Alcock (1905) considered his taxon to be the same as Henderson's, and formally placed his *C. andersoni* as a junior synonym of *P. typica*.

Paguropsis Henderson, 1888 has remained a monotypic genus since its original description. The single representative of this genus, *P. typica*, has been presumed to have a broad distribution across the tropical Indo-West-Pacific, from the Philippines, Japan, and Indonesia, to off eastern Africa, where adults have been reported in depths ranging from 110 to 350 m (Henderson 1888, Alcock 1899, Thompson 1943, Kamalaveni 1950, Barnard 1962, Miyake 1982, Baba et al. 1986, Thomas 1989). *Paguropsis typica* has often been used as an example of a remarkable adaptive specialization and diversity in the Anomura (Stebbing 1893, Boas 1926, Russell 1962, Nicol 1967, Kaestner 1970, Schäfer et al. 1983, McLaughlin 2015) and considerable attention has been given to the curious symbiotic association of this hermit crab with its cnidarian symbiont. However, much confusion exists on the identity of the symbiont as various names and misspellings have been used, such as *Epizoanthus paguropsidis* or *E. paguropsides*, by Boas (1926), Schäfer et al. (1983), Ates (2003), and Williams and McDermott (2004); *Mammillifera* sp. or *Mammillifera* sp., by Balss (1924, 1927), and Kaestner (1970); *Anemonia mammifera*, by Nicol (1967); and *Actinia equina*, by Williams and McDermott (2004). Thus, the true identity of the cnidarian living with *P. typica* still remains uncertain.

Despite the uniqueness of *Paguropsis* among the Diogenidae and even Paguroidea as a whole, the morphology of *P. typica* has not been studied in sufficient detail in light of the modern concept of paguroids. Furthermore, aside from the inclusion of this genus and species in phylogenetic studies related to the origin of lithodids and the phenomenon of carcinization (Richter and Scholtz 1994, McLaughlin and Lemaitre 1997), the evolutionary significance and position of *Paguropsis* among paguroids has remained unexplored. This knowledge deficiency can be attributed, in part, to the fact that the material of *P. typica* reported in the literature is scattered in a few museums, with the majority of specimens originally deposited and largely unavailable, in the Indian Museum, Kolkata. The opportunity to examine new material of *Paguropsis* came when fresh specimens assignable to this genus were found while studying the rich paguroid collections obtained during various collaborative French deep-water faunistic expeditions to the tropical western Pacific. The detailed examination of this new material, and comparison with the types and other previously unreported specimens identified under *P. typica* and deposited in various museums, revealed that *Paguropsis* is not monotypic or even monophyletic, and that in addition to *P. typica*, there are six more species, five of them new to science, all confounded under what was previously believed to be a single species. Altogether, 1042 specimens were examined. Here it is shown that Alcock's (1899) name *P. andersoni* needs to be resurrected from the synonymy of *P. typica* as a valid species. Furthermore, a detailed comparative morphological

Table 1. List of species, collection site, museum catalog number of vouchers, and GenBank accession numbers for which mitochondrial COI barcode region and partial sequences of 12S and 16S rRNA were obtained in this report.

Species	Locality	Voucher deposition	COI GenBank no.	16S GenBank no.	12S GenBank no.
Paguropsis typica	Philippines	MNHN-IU-2014-9399	MG759674	MG759703	MG773703
	Philippines	MNHN-IU-2014-9427	–	MG759705	–
	Philippines	MNHN-IU-2014-9411	MG759677	MG759704	MG773704
Paguropsis andersoni	Indian Ocean	USNM 42719	–	MG950177	MG950176
	Madagascar	MNHN-IU-2014-9393	MG759673	MG759692	MG773702
Paguropsis confusa	Philippines	NMCR 50015	MG759683	MG759696	MG773707
	Locality uncertain	MNHN-IU-2014-9420	–	MG759695	MG773705
	Philippines	USNM 1441901	MG759682	MG759694	MG773706
Paguropsis gigas	South China Sea	NTOU A01445	MG759678	MG759697	MG773709
	South China Sea	NTOU A01446	MG759679	MG759698	MG773710
Paguropsis lacinia	Papua New Guinea	MNHN-IU-2013-2288	MG759665	MG759699	MG773711
	New Caledonia	MNHN-IU-2014-9360	MG759666	MG759700	MG773712
	Solomon Islands	MNHN-IU-2014-9367	MG759668	MG759701	MG773713
Paguropsina pistillata	New Caledonia	MNHN-IU-2014-9391	MG759672	MG759689	MG773695
	New Caledonia	MNHN-IU-2014-9401	MG759675	MG759690	MG773696
	New Caledonia	MNHN-IU-2014-9402	MG759676	MG759691	MG773699
Paguropsina inermis	Philippines	MNHN-IU-2014-9372	MG759669	MG759686	MG773700
	New Caledonia	USNM 1441892	MG759681	MG759684	MG773701
	New Caledonia	MNHN-IU-2014-9383	MG759670	MG759687	MG773698
	New Caledonia	MNHN-IU-2014-9362	MG759667	MG759685	MG773697
	South China Sea	NTOU A01447	MG759680	MG759688	MG773693

analysis has shown that two of the five new species discovered, although closely related to *P. typica*, are morphologically so fundamentally different in characters of the mouthparts, cephalothoracic sternite, chela of pereopods 4, and position of pleopods that they require placement in a new genus, *Paguropsina* gen. n. Thus, the genus *Paguropsis* is rediagnosed, and the new genus diagnosed. Both *P. typica* and *P. andersoni* are redescribed and illustrated, and all new species fully described and illustrated. Information on coloration is presented for all seven species with newly obtained color photographs. A key to the species of *Paguropsis* and *Paguropsina* gen. n. is provided, along with a brief discussion of the biogeography and significance of the morphology of the two genera among the Paguroidea. To assist in future phylogenetic studies, genetic data for each of the seven species is reported for the mitochondrial COI barcode region and partial sequences of 12S and 16S rRNA (Table 1).

Materials and methods

Specimens used for this study remain deposited in the following museums: The Natural History Museum, London, UK (formerly British Museum) (**BMNH**); Natural History Museum and Institute, Chiba, Japan (**CBM**); Lee Kong Chian Natural History Museum, Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore (**LKCNHM ZRC**); Muséum national d'Histoire naturelle, Paris, France (**MNHN**); National Museum of the Philippines, Manila (**NMCR**); National Taiwan Ocean University, Keelung, Taiwan, ROC (**NTOU**); National Natuurhistorisch Museum, Naturalis Biodiversity Center, Leiden (formerly Rijksmuseum van Natuurlijke Histoire), the Netherlands (**RMNH**); Iziko South African Museum, Cape Town, South Africa (**SAMC**); National Museum of Natural History, Smithsonian Institution, Washington DC USA (**USNM**); and the Zoological Museum, University of Copenhagen, Denmark (**ZMUC**).

General morphological terminology follows that of McLaughlin (2003) and Tudge et al. (2012), except for the use of "pleon" instead of "abdomen" used according to Schram and Koenemann (2004). The term "chelipeds" applies to pereopod 1, and "ambulatory legs" to pereopods 2 and 3. Paired pleopods 1 and 2 in males, and paired pleopod 1 in females, are referred to as gonopods. Cephalothoracic somites and their sternites, are numbered I–XIII (five cephalic and eight thoracic), and thoracomeres are I–VIII (three maxillipeds and five pereopods). The measurements indicated for the specimens refer to shield length (SL) in millimeters (mm), measured to the nearest 0.01 from the midpoint of the rostral lobe to the midpoint of the posterior margin of the shield. Miscellaneous abbreviations used are:

CC	otter trawl;
CP	beam trawl;
DW	Warén dredge;
FB	fishing boat;
INVMAR	Invertébrés Marins (for collections of MNHN);
NO	navire océanographique;
ovig	ovigerous female(s);
sta	station;
RV	research vessel;
ROV	remotely operated vehicle;
TRV	trawling vessel;
USFC	United States Fish Commission.

The station data for the following French collaborative campaigns have been obtained from the MNHN website (https://expeditions.mnhn.fr/), published reports (Richer de Forges 1990), or supplied by MNHN staff (P Bouchet, L Corbari, P Martin-Lefèvre, or P Maestrati): BIOPAPUA; BORDAU 1, 2; BATHUS 3; CREVETTIERE; EBISCO; KARUBAR; LITHIST; LUMIWAN; MADEEP; MAINBAZA; MUSORSTOM 1–3, 5, 6; NANHAI; NORFOLK 1, 2; PANGLAO; SALOMON 1, 2; ZHONGSHA. Other expedition or research program abbreviations: DST/NRF ACEP, Department of Science and Technology/National Research Foundation and African Coelacanth Ecosystem Programme or "Spatial Solutions Project". The original, official format (DDM or DDS) for reporting latitude and longitude for these expeditions has been retained in order to avoid confusion. Months are indicated using the first three letters.

Vouchers, tissue samples, and sequence data of specimens for DNA Barcoding or other genetic analysis were deposited in the MNHN or USNM. All PCR, sequencing, and analytics were carried out at the Laboratories of Analytical Biology at the National Museum of Natural History, Smithsonian Institution. Mitochondrial COI barcode region and partial sequences of 12S and 16S rRNA were obtained by standard protocols (see Evans and Paulay 2012). Unaligned sequences for at least one type specimen of each new species were accessioned to GenBank along with archival data for the respective voucher specimens listed in Table 1. Although this data is included as diagnostic identifiers for the species, and for future phylogenetic studies, a preliminary analysis was performed to generate a tree. Alignments for each locus were obtained using the L-INS-i alignment strategy in MAFFT version 7 (Katoh and Standley 2013). The aligned sequences were concatenated using Sequence Matrix (Vaidya et al. 2011). Phylogenetic analyses were performed on a concatenated dataset (12S + 16S + COI) using Maximum Likelihood (ML) with RAxML (Stamatakis 2006). ML options for RAxML included the GTRCAT model of nucleotide evolution (-m), rapid bootstrap analysis, and search for best-scoring ML tree (-f a), and 1000 bootstrap replicates.

Systematic account

Family Diogenidae Ortmann, 1892

Genus *Paguropsis* Henderson, 1888

Paguropsis Henderson, 1888: 98 (type species by monotypy: *Paguropsis typica* Henderson, 1888, gender feminine); Stebbing, 1893: 169; Alcock, 1905: 27; Gordan, 1956: 325; McLaughlin and Lemaitre, 1997: 112 (phylogeny); McLaughlin, 2003: 114 (key); McLaughlin et al., 2010: 23; McLaughlin, 2015: 153, fig. 6.3D.

Chlaenopagurus Alcock, 1899: 113 (type species by monotypy: *Chlaenopagurus andersoni* Alcock, 1899, gender masculine).

Diagnosis. Thirteen pairs of quadriserial gills [no pleurobranchs on thoracomere VIII (last)], gills consisting of series of twin lamellae each ending on distolateral and distomesial angles in filamentous or stub-like extensions (e.g., Fig. 3A). Shield well calcified, subtriangular or subrectangular; dorsal surface somewhat vaulted; lateral projections broadly triangular, each terminating in small spine. Rostrum prominent and projecting anteriorly, subtriangular, arched and dorsally ridged. Branchiostegite with dorsal margin (e.g., Fig. 2B, D) divided into two calcified plates: one anterodorsal plate poorly delimited ventrally, and one small, subtriangular median plate with distinct central pit. Posterior carapace (e.g., Fig. 2A, C) with well calcified posteromedian plate, and well calcified lateral lobe on each side adjacent to shield. Ocular peduncles short, approx. half as long as shield; corneas dilated (diameter typically half or slightly more than length of ocular peduncle, including cornea); ocular acicles relatively small, subtriangular, armed with small dorsodistal spine. Antennal peduncles distinctly exceeding distal margins of corneas; acicles long, reaching to level of corneas. Mouthparts: maxillule with well-developed and strongly recurved external lobe of endopod; maxilliped 1 with exopodal flagellum, endopodite medially bent at nearly right angle, with distinctly developed epipod; maxilliped 3 ischium with well-developed crista dentata, lacking accessory tooth, exopod slender, 4 or more times as long as broad. Epistome unarmed. Chelipeds symmetrical or nearly so, subequal in size, armed with moderately dense to dense setation and numerous well-spaced small spines or tubercles; coxae each with ventral surface having an uncalcified median longitudinal fissure starting on distal margin and incompletely covering length of ventral surface. Pereopods 2 and 3 long; dactyl of pereopods 3 distinctly longer than dactyl of pereopod 2. Sternite XI (between pereopods 3; e.g., Fig. 5B, D) narrow, separating coxae of pereopods 3 by distinctly less than half length of one coxa (typically 0.2 to 0.3 length of one coxa); anterior lobe flat or slightly concave, posterior lobes broad, arched and forming arrowhead shape with apex directed anteriorly. Pereopod 4 chelate, extending to subdorsal position to manipulate carcinoecium (e.g., Fig. 1A, 2A, C), lacking rasp-like surfaces; dactyl with cutting edge armed with row of small corneous spines; fixed finger with sharp spines on cutting edge arranged like bear claw; coxae (e.g., Fig. 5B, D) with anteroventral margin sharply delimited, keel-like. Sternite XII (between pereopods 4; e.g., Fig. 5B, D) broad, ridge-like, weakly divided medially, with fringe of setae. Pereopod 5 chelate, with weakly-developed propodal rasp. Pleon curling under but not dextrally or sinistrally twisted; pleonal somite 1 not fused to last thoracic somite, with partly calcified tergite and pleura. Male with well-developed paired gonopods 1 and 2, and reduced (uniramous or biramous) pleopod 3–5 on left or right side (occasionally lacking pleopod 5), or altogether lacking pleopods 3–5. Female with paired gonopores; with paired uniramous pleopods 1 modified as gonopods (Fig. 7D); left or right side of pleon with well-developed biramous unpaired pleopods 2–4 (ovigerous) and reduced biramous or uniramous unpaired pleopod 5 (not ovigerous, occasionally absent); brood pouch large (e.g., Figs 1C, 3C), covering pleopods 2–4 and entire egg mass. Uropods and telson symmetrical; exopods long, slender; endopod small, curved. Telson subquadrate or subrectangular, lacking or with obscure lateral indentations; posterior margin weakly divided into broadly rounded lobes.

Distribution. Subtropical to tropical Indo-West Pacific. Depth: 30 to 1125 m.

Habitat and symbionts. Several cnidarian names have been reported in the literature as symbionts of what has been presumed to be *P. typica*, including: *Epizoanthus paguropsidis* [e.g., Boas (1926), Schäfer et al. (1983, as *E. paguropsides*), Ates (2003), Williams and McDermott (2004)]; *Mammillifera* sp. [e.g., Alcock (1905), Balss (1924, 1927), Ross (1983)]; *Actinia equina* [e.g., Williams and McDermott (2004)]. There is considerable taxonomic confusion on these cnidarian names. The name *E. paguropsidis* is considered a nomen nudum apparently introduced by Boas (1926), and attributed to Ates (2003, as per WoRMS Editorial Board 2018). Schäfer et al.'s (1983) study identified the host of the cnidarian as *P. typica*, but that host is shown herein to actually apply to a species of Parapaguridae. *Mammillifera* is currently a subjective junior synonym of *Zoanthus*. Given the discovery of several species previously confounded under *P. typica* as well several new species, and the general unavailability of hermit crab materials that go along with reports of cnidarian symbionts, it is impossible to ascertain the identity of the cnidarian as well as to which species of *Paguropsis* or the new genus described herein. Those symbiont names apply to the Zoanthidea (often called Zoantharia), and those associated with hermit crabs that are typically assigned in the literature to colonial species of the genus *Epizoanthus*, (JD Reimer, pers. comm.; see Fig. 1D). However, the symbionts found with species of *Paguropsis* are actually indeterminate species of acontiate anemones which belong to the Actiniaria (DG Fautin, pers. comm.), and are herein reported as such.

Type species. *Paguropsis typica* Henderson, 1888, by monotypy. Gender: feminine.

Species included. In addition to the type species, *P. typica*, the genus includes: *P. andersoni* (Alcock, 1899), and three new species described herein.

Remarks. Henderson (1888) considered *Paguropsis* and its only species at that time, *P. typica*, to be unique among hermit crabs based on the peculiar subdorsal position of pereopods 4 and 5 adapted to manipulate the symbiont zoanthid, the presence on the left or right side of the pleopods, and the straight pleon. Alcock (1905) considered his monotypic genus *Chlaenopagurus* Alcock, 1899 to be a junior synonym of *Paguropsis*, although he provided no explanation for that taxonomic action. Alcock (1905) suggested that *Paguropsis* was closely related to *Paguristes* Dana, 1851, but differed in the former having stout eyestalk, a non-coiled pleon, symmetrical tail fan (uropods and telson), chelate pereopod 4, and indifferent position (left or right side) of the pleopods. The taxonomy or morphology of *Paguropsis* has not been discussed or revised since that early time, although Boas (1926) did study in detail the morphology of *P. typica* relative to its symbiotic zoanthid.

During this study, several important characters previously overlooked or not sufficiently discussed have been added to the diagnosis of *Paguropsis*. Among these are the shapes of mouthparts (maxillule external lobe of endopod, and maxilliped 3 exopod); presence on posterior carapace of a well delimited calcified lateral lobe (e.g., Fig. 2A) fused to shield; on the branchiostegite (e.g., Fig. 2B, D), presence of a well calcified median plate with a central pit adjacent to the cervical groove, and an anterodorsal plate; presence on ventral surface of coxae of chelipeds of a longitudinal, uncalcified fissure (e.g., Fig. 5B, D); shape of thoracic sternites XI and XII (between pereopods 3 and 4 respectively; e.g., Fig. 5B, D); development of a full chela lacking rasp on pereopod 4, and distinct, bear-like claw armature of fixed finger; and sharply delimited anteroventral margin of coxae of pereopods 4 (e.g., Fig. 5B, D). Furthermore, coloration has been found to be unique for each of the species (Figs 8, 18A, B, 28A–D).

Paguropsis typica Henderson, 1888

Figs 1A–C, 2A, B, 3, 4, 5A, B, 6, 7, 8A, B, 14A, 28A, Table 1

Paguropsis typicus Henderson, 1888: 99, pl. 10, fig. 4 (type locality: HMS *Challenger* sta 204A or B, off Tablas Island, Philippines); Murray, 1895: 789.

Paguropsis typicus: Pzibram, 1905: 199; Boas, 1926: 1, figs 1, 7, 8–11; Rabaud, 1941: 263; Gordan, 1956: 325 (in part). (See "Remarks").

Paguropsis typica: Estampador, 1937: 55; Balss, 1924: 775, figs 31, tbl. 2 (see "Remarks"); Balss, 1956: 1429 (in part); Nicol, 1967: 583; Kaestner, 1970: 299; Miyake, 1982: 98, pl. 33, fig. 6 (color photo); Schäfer et al., 1983: figs 12 (in part, see "Remarks"); Ross, 1983: 171; Baba et al., 1986: 192 (fig. 141, color photo), 193 (Japanese text), 299 (English text); Richter and Scholtz, 1994: 189 (phylogeny); Ates, 2003: 42, tbl. 1; Williams and McDermott, 2004: 16, tbl. 1; McLaughlin et al., 2010: 23; McLaughlin, 2015: 152, fig. 6.3D; Malay et al., 2018: 55.

Paguropsis tyica (misspelling): Schäfer et al., 1983, fig. 12 (in part, see "Remarks")

Not *Paguropsis typica*: Schäfer et al., 1983: 229, figs 1, 2; Williams and McDermott, 2004: 12, 66, tbl. 1 (= glaucothoë stage of Parapaguridae, see "Remarks")

Type material. Lectotype (herein selected), male 6.0 mm, Tablas Island, Philippines, HMS *Challenger*, sta 204A to 204B, 12°43' to 12°46'N, 122°09' to 122°10'E, 182.9–210.3 m, 2 Nov 1874 (BMNH 1888.33). Paralectotype: 1 female 7.1 mm, same data as lectotype (BMNH 1888.33).

Other material. *Japan*: Intensive Research of Unexploited Fisheries Resource on Continental Slopes, Japan Fisheries Resources Conservation Association, FB *Shin'ei-maru No. 53*, Kita-Koho Seamount, Kyushu-Palau Ridge, 26°46'09"N, 135°20'03"E, 360 m, 17 Nov 1978, trawl: 4 males 10.2–16.4 mm (CBM-ZC 4898); same data, 4 females 10.3–13.2 mm (CBM-ZC 4899).

South China Sea: NANHAI 2014, cruise OR5: sta DW 4105, 13°57.8902'N, 115°25.5073'E, 297–565 m, 3 Jan 2014: 1 male 3.6 mm (NTOU A01442). ZHONGSHA 2015, cruise ORI 1113: sta CP 4149, 16°06.54'N, 114°20.05'E, 165 m, 26 Jul 2015: 1 male 5.8 mm, 1 female 6.6 mm (NTOU A01443); sta CP 4150, 16°06.602'N, 114°21.45'E, 162 m, 26 Jul 2015: 1 male 6.0 mm (NTOU A01444). Hong Kong: Cruise 4/63, sta 66, Transect 56, [no locality, coordinates, depth, or date], coll. Fisheries Research Station: 1 female 5.8 mm (MNHN-IU-2014–9438).

Philippines: USFC *Albatross*, Philippines Expedition: Quezon, Luzon Island, Tayabas Bay, Lucena City, sta 5369, 13°48'00"N, 121°43'00"E, 193.8 m, 24 Feb 1909: 1 male 10.7 mm, 1 female 5.7 mm (USNM 1107610); Quezon, Luzon Island, Tayabas Bay, Lucena City, sta 5371, 13°49'40"N, 121°40'15"E, 151.8 m, 24 Feb 1909: 1 male 10.4 mm, 1 female 6.2 (molted, parasitized) (USNM 1107593); Quezon, Luzon Island, Tayabas Bay, Unisan, sta 5375, 13°42'15"N, 121°50'15"E, 195.7 m, 2 Mar 1909: 1 male 12.6 mm (USNM 1107608); Visayan Sea, Leyte Island, Villaba, near Capitancillo Island, sta 5403, 11°10'00"N, 124°17'15"E, 332.8 m, 16 Mar 1909: 1 male 11.0 mm (USNM 1107573); Camotes Sea, Cebu, Camotes Islands, NW of Pacijan Island, sta 5408, 10°40'15"N, 124°15'00"E, 290.8 m, 18 Mar 1909: 2 males 11.8, 12.8 mm, 1 female 11.7 mm, 1 ovig female 11.4 mm (USNM 1107590); Camotes Sea, Cebu, Camotes Islands, W of Pacijan Island, sta 5409, 345.6 m, 18 Mar 1909: 2 males 10.9, 14.6 mm, 1 female 8.5 mm (USNM 1107574); Cebu Island, Bohol Strait, SW of Lauis Point, sta 5411, 265.2 m, 23 Mar 1909: 2 males 8.6 mm, 13.3 mm, 2 females 11.2, 11.9 mm (USNM 1107594); Bohol Strait, Between Bohol and Cebu Islands, sta 5412, 10°09'00"N, 123°52'00"E, 296.3 m, 23 Mar 1909: 1 female 9.1 mm, 3 ovig females 10.9–11.8 mm (USNM 1107599); Cebu Island, Naga, Bohol Strait, sta 5417, 301.7 m, 25 Mar 1909: 4 males 7.9–13.2 mm, 2 females 7.1, 10.0 mm (USNM 1107584); Gulf of Albay, Albay, Luzon Island, E of S Luzon, sta 5454, 13°12'00"N, 123°50'30"E, 279.8 m, 7 Jun 1909: 1 female 7.8 mm (USNM 1107578); northern Mindanao, sta 5519, 8°47'00"N, 123°31'15"E, 332.8 m, 9 Aug 1909: 1 female 6.4 mm (USNM 1107588); Zamboanga del Norte, Mindanao Island, sta 5520, 10 Aug 1909, 186.5 m: 1 female 5.7 mm (USNM 1100423). MUSORSTOM 1, NO *Vauban*: N of Lubang, sta CC 12, 14°00'N, 120°17'E, 187–210 m, 20 Mar1976: 1 male 7.0 mm, 3 females 6.4–6.8 mm (USNM 1441983); N of Lubang, sta CP 18, 13°57'N, 120°17'E, 150–159 m, 21 Mar 1976: 1 ovig 7.5 mm (MNHN-IU-2014–9374); N of Lubang, sta CP 25, 14°02'N, 120°18'E, 191–200 m, 22 Mar 1976: 1 male 10.5 mm (MNHN-IU-2014–9373); N of Lubang, sta CP 27, 14°00'N, 120°16'E, 188–192 m, 22 Mar 1976: 22 males 4.6–4.8 mm, 25 females 3.9–9.0 mm (MNHN-IU-2014–9399); NW of Lubang, sta CP 54, 13°56'N, 119°58'E, 975–1125 m, 26 Mar 1976: 37 males 5.1–10.4 mm, 26 females 5.5–9.7 mm, 11 ovig females 6.7–8.3 mm (MNHN-IU-2014–9395); N of Lubang, sta CP 64, 14°00'N, 120°19'E, 194–195 m, 27 Mar 1976: 16 males 4.2–8.1 mm, 19 females 4.3–6.7 mm, 1 ovig female 7.0 mm (MNHN-IU-2014–9371). MUSORSTOM 2, NO *Coriolis*: N of Lubang, sta CP 01, 14°00'N, 120°18'E, 188–198 m, 20 Nov 1980: 5 males 5.8–11.0 mm, 2 females 6.0, 6.1 mm, 1 ovig female 9.6 mm (MNHN-IU-2014–9425); N of Lubang, sta CP 02, 14°00'N, 120°17'E, 184–186 m, 20 Nov 1980: 2 males 7.1, 9.4 mm, 1 female 6.7 mm, 2 ovig females 7.0, 7.8 mm (MNHN-IU-2014–9426), 1 ovig female 8.8 mm (MNHN-IU-2014–9431); between Luçon and Lubang, sta CP 06, 13°56'N, 120°22'E, 136–152 m, 20 Nov 1980: 1 female 6.7 mm (MNHN-IU-2014–9432); N of Lubang, sta CP 10, 14°01'N, 120°18'E, 188–195 m, 21 Nov 1980: 1 male 5.7 mm (MNHN-IU-2014–9429); N of Lubang, sta CP 11, 14°00'N, 120°19'E, 194–196 m, 21 Nov 1980: 2 males 6.1, 7.3 mm (MNHN-IU-2014–9427), 1 male 9.5 mm (MNHN-IU-2014–9428); N of Lubang, sta CP 18, 14°00'N, 120°17'E, 188–195 m, 22 Nov 1980: 1 female 6.4 mm (MNHN-IU-2014–9430); N of Lubang, sta CP 19, 14°01'N, 120°18'E, 189–192 m, 22 Nov 1980: 3 males 4.8–7.5 mm, 2 females 5.7, 5.8 mm, 1 ovig 6.0 mm (MNHN-IU-2014–9404); N Lubang, sta CP 53, 14°01'N, 120°17'E, 215–216 m, 27 Nov 1980: 1 male 7.2 mm (MNHN-IU-2014–9433); N of Lubang, sta CP 68, 14°00'N, 120°17'E, 195–199 m, 29 Nov 1980: 1 male 5.2 mm (MNHN-IU-2014–9434); N of Lubang, sta CP 71, 14°01'N, 120°19'E, 189–197 m, 30 Nov 1980: 1 female 6.0 mm (MNHN-IU-2014–9435); between Luçon and Lubang, sta CP 80, 13°45'N, 120°37'E, 178–205 m, 1 Dec 1980: 1 female 5.1 mm (MNHN-IU-2014–9436). MUSORSTOM 3, NO *Coriolis*: W of Luçon, sta CP 90, 14°00'N, 120°19'E, 195 m, 31 May 1985: 134 males 5.1–9.4 mm, 108 females 4.6–8.7 mm, 8 ovig females 6.4–7.8 mm (MNHN-IU-2014–9411), 16 males 5.1–9.7 mm, 11 females 4.9–7.5 mm, 9 ovig females 6.1–7.5 mm (MNHN-IU-2014–9413). PANGLAO 2004: sta T2, Bolod, Panglao Island, 9°32.4'N, 123°47.8'E, 152 m, coarse sand, 31 May 2004: not examined, color photos (#48, 54), Fig. 8A, B (ZRC or NTOU); Balicasag, [sta number unknown], May 2004: 1 male 12.1 mm (USNM 1441800). LUMIWAN 2008: NO *DA-BFAR*, sta CP 2870, 14°02'N, 120°17'E, 183–188m, 24 Mar 2008: 1 male, not examined (NMCR); [station unknown]: specimen not examined, color photograph, Fig. 28A.

Papua New Guinea: BIOPAPUA, NO *Alis*: Manus Island SE point, sta CP 3693, 02°10'S, 147°17'E, 300 m, 29 Sep 2010: 2 males 5.2, 6.7 mm (MNHN-IU-2014–2447), 10 males 4.3–6.7 mm, 6 females 4.2–5.3 mm, 4 ovig females 5.8–6.4 mm (MNHN-IU-2014–2653).

Indonesia: Danish Kai Islands Expedition: sta 44, 05°39'S, 132°23'E, 268 m, 30 Apr 1922: 1 female 12.2 mm (ZMUC-CRU–006723), 1 female 6.3 mm (ZMUC-CRU–006724); sta 49, 05°37'10"S, 132°24'E, 245 m, 3 May 1922: 1 female 8.7 mm (ZMUC-CRU 007031); sta 50, 05°34'S, 132°25'4"E, 233 m, 4 May 1922: 1 male 9.2 mm (ZMUC-CRU–006725). Dr. Th. Mortensen's Expedition: Java, sta 2, 07°33'S, 114°36'E, 200 m, 3 April 1929: 1 male 8.6 mm (ZMUC-CRU–006987). KARUBAR, RV *Baruna Jaya 1*: Kai Islands, sta CP 35, 06°08'S, 132°45'E, 390–502 m, 27 Oct 1991: 1 female 6.9 mm (USNM 1441994); Tanimbar Islands, sta DW 49, 08°00'S, 132°59'E, 206–210 m, 29 Oct 1991: 1 male 3.6 mm (USNM 1441991).

Fiji: BORDAU 1, NO *Alis*: Lau Ridge, Lakeba, sta DW 1463, 18°10'S, 178°44'W, 300–400 m, 6 Mar 1999: 1 male 10.7 mm (MNHN-IU-2014–9364); Lau Lakeba Ridge, sta DW 1507, 18°09'S, 178°38'W, 255–290 m, 13 Mar 1999: 1 male 5.1 mm (MNHN-IU-2014–9365).

New Caledonia: MUSORSTOM 5, NO *Coriolis*: Coral Sea, Lord Howe Ridge, Capel Bank, sta CP 275, 24°46.60'S, 150°40.30'E, 285 m, 9 Oct 1986: 1 male 4.3 mm (USNM 1441993); Coral Sea, Lord Howe Ridge, Argosta Bank, sta DC 291, 23°07.70'S, 159°28.40'E, 300 m, 11 Oct 1986: 3 females 4.8–5.7 mm (USNM 1441992). MUSORSTOM 6, NO *Alis*: NW of Lifou, sta CP 419, 20°42'S, 167°04'E, 283 m, 16 Feb 1989: 2 males 5.7, 5.8 mm, 2 females 5.7, 6.0 mm (USNM 1441990). LIFOU 2000, NO *Alis*: Santal Bay, in front of Hacu Hutighé islet, sta DW 1647, 20°42'S, 167°08'E, 150–200 m, 6 Nov 2000: 1 female 11.4 mm (MNHN-IU-2014–9376). NORFOLK 1, NO *Alis*: Norfolk Ridge, Kaimon-Maru Bank, sta CP 1676, 24°44'S, 168°09'E, 227–232 m, 22 Jun 2001: 1 female 8.5 mm (MNHN-IU-2014–9356); Norfolk Ridge, Kaimon-Maru Bank, sta CP 1683, 24°44'S, 168°07'E, 248–272 m, 22 Jun 2001: 1 male 7.8 mm (MNHN-IU-2014–9361). NORFOLK 2, NO *Alis*: Kaimon-Maru Bank, sta DW 2093, 24°44'S, 168°09'E, 230 m, 29 Oct 2003: 1 female 10.3 mm (MNHN-IU-2014–9387); Kaimon-Maru Bank, sta CP 2095, 24°46'S, 168°10'E, 283–310 m, 29 Oct 2003: 1 female 12.5 mm (MNHN-IU-2014–9384). EBISCO, NO *Alis*: Capel Bank, sta CP 2492, 24°44'S, 159°41'E, 285 m, 6 Oct 2005: 1 male 4.3 mm (ex MNHN-IU–2014–9401, USNM 1441984); N of Bellona, sta DW 2578, 20°21'S 158°40'E, 440–505 m, 14 Oct 2005: 1 female 3.0 mm (USNM 1441995).

Eastern Australia: Queensland, *Nimbus* 1/68, sta 29, 26°30'S, 153°44'E, 184 m, 29 Jul 1968, coll. AJ Bruce: 1 male 7.0 mm (MNHN-IU-2014–9403, = MNHN-Pg 3670); sta 39, [same coordinates, depth as sta 29], 30 Jul 1968: 1 male 8.0 mm (MNHN-IU-2014–9410).

[*Locality uncertain*]: INVMAR: sta 15, [coordinates on label in error], 240 m, [no day] April 1929: 1 male 10.3 mm, 1 female 3.9 mm (MNHN-IU-2014–9416); sta 50, 233 m, [no other data]: 1 ovig female 8.1 mm (MNHN-IU-2014–9414); sta 52, [no other data]: 2 males 8.6, 12.7 mm (MNHN-IU-2014–9418, = MNHN-Pg 2313); sta 66, [no other data]: 2 females 5.4, 7.8 mm (MNHN-IU-2014–9422, = MNHN-Pg 2316); sta 125, 200 m, 4 Mar 1977 [no other data]: 1 female 10.9 mm (MNHN-IU-2014–9405); [no data]: 5 males 6.6–7.6 mm (MNHN-IU-2014 9415), 1 ovig female 7.1 mm (MNHN-IU–2014–9423, = MNHN-Pg 2315).

Redescription. *Shield* (Figs 1A, 2A, 3B) subtriangular, ca. 1.2 times as long as broad; dorsal surface glabrous except for scattered setae and transverse fringe of short setae on sloping anterior margins of gastric region; anterior margin between rostrum and lateral projections concave; lateral projections broadly triangular, each terminating in small spine; posterior margin roundly truncate; lateroventral distal angle produced into strong spine adjacent to proximal margin of first segment of antennal segment, usually with 1 small sharp or blunt spine dorsally. Rostrum (Figs 2A, B, 3B) bluntly subtriangular, arched dorsally, strongly produced and extending slightly beyond distal margin of ocular acicles; with distinct rounded dorsal longitudinal ridge having few short setae laterally, ending smoothly or with 1 or 2 minute subterminal spines. Branchiostegites (Fig. 2B) unarmed except for 1 or 2 spines on dorsodistal angle of anterodorsal plate, and setose distal margin.

Ocular peduncles ca. 0.5 length of shield, constricted medially and noticeably broadened distally, glabrous or at most with row of short dorsomedian row of short setae; corneas strongly dilated, diameter 0.5–0.6 total peduncular length (including the cornea). Ocular acicles small, triangular, each armed with distal or dorsodistal spine often directed anterodorsally.

Antennular peduncles when fully extended overreaching distal margins of corneas by full length of ultimate peduncular segments. Ultimate and penultimate segments glabrous or at most with scattered short setae. Basal segment with ventromesial tuft of setae distally; lateral face with distal subrectangular lobe, small medial spine, and setose lobe proximally.

Antennal peduncles overreaching distal corneal margins by 0.3–0.4 lengths of ultimate segments. Fifth and fourth segments unarmed except for scattered setae. Third segment with spine at ventrodistal angle. Second segment with dorsolateral distal angle produced, terminating in small, usually bifid spine; mesial margin rounded, setose, dorsomesial distal angle with small, usually blunt spine. First segment unarmed. Antennal acicle reaching level of distal portion of optic calathus, slender, terminating in sharp spine, with long setae mostly distally; usually armed with row of 2 or 3 minute spines lateroproximally. Antennal flagellum long, reaching to distal end of cheliped fingers, articles with scattered short setae (< 1 flagellar article in length) and 1 or 2 longer setae (ca. 2 flagellar articles in length) every 12 articles or so.

Mandible (Fig. 4A) with stout palp. Maxillule (Fig. 4B) with recurved external lobe of endopod nearly as long as endopod. Maxilla (Fig. 4C) with endopod not exceeding distal end of scaphognathite. Maxilliped 1 (Fig. 4D) with endopodite bent medially nearly at right angle, reaching distal end of exopod; with oval-shaped epipod. Maxilliped 2 (Fig. 4E) without distinguishing characters. Maxilliped 3 (Fig. 4F) exopod 4.5 times as long as broad; ischium having crista dentata armed with 15–17 small subequal

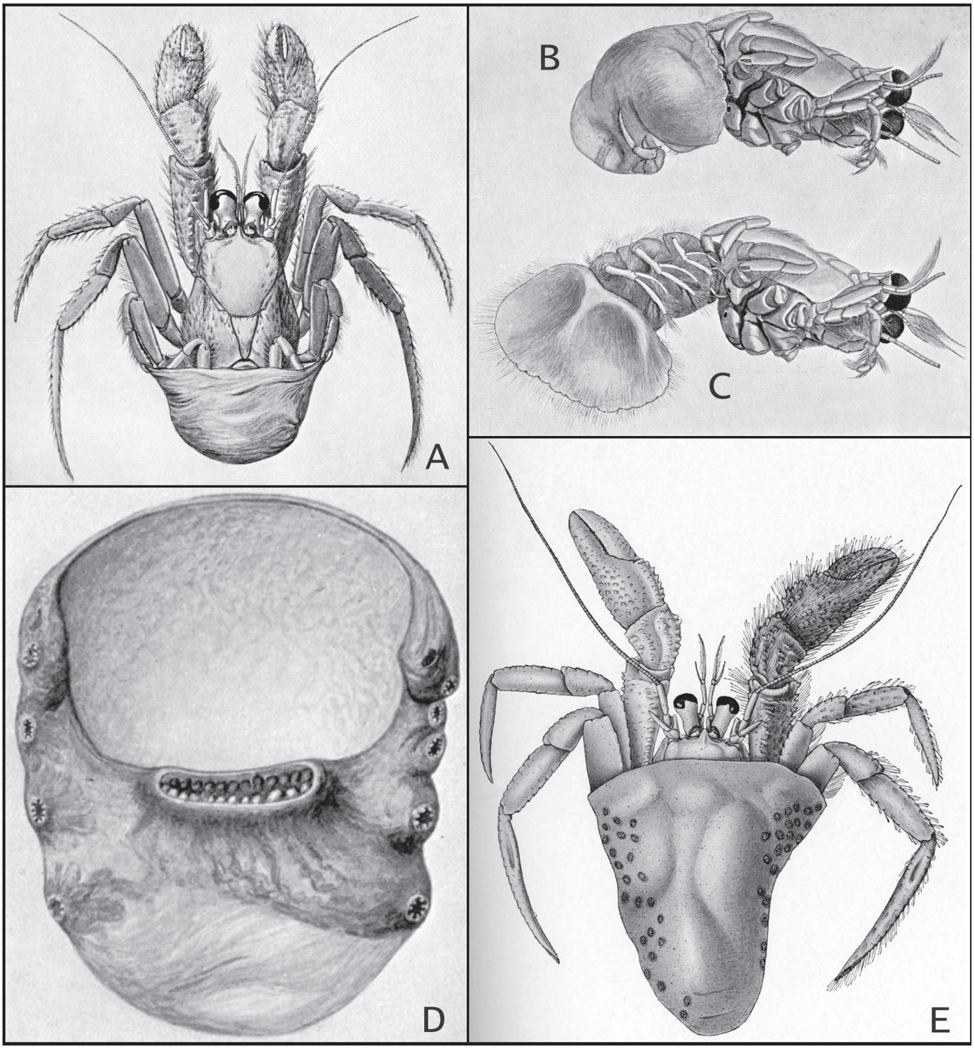

Figure 1.A–C *Paguropsis typica* Henderson, 1888, after Boas (1926: figs 1, 11A, B): **A** habitus **B, C** female right side with carcinoecium and pereopods 1–3 removed, with brood pouch (**B**) and with brood pouch folded posteriorly (**C**) showing pleopods **D** carcinoecium: *Epizoanthus paguropsidis* Ates, 2003 [nomen nudum], after Boas (1926: fig. 2) **E** *Paguropsis andersoni* (Alcock, 1899), after Alcock (1902: fig. 2), habitus.

(except for larger distal and proximal) corneous-tipped teeth; merus with 3–5 small spines on ventral margin, and usually two small spines on ventromesial distal angle; basis with row of small spines on mesial margin; coxa with ventromesial angle strongly produced ventrally, with 2–4 small spines and fringe of setae; sternite VIII narrow, with setose lobe on each side of midline.

Chelipeds (Figs 1A, 2A, 5A) subequal, similar in armature and setation; dorsal surfaces of chelae and carpi covered with moderately dense tufts or short rows of bristle-like setae not hiding ornamentation beneath; ventral surfaces of palms smooth ex-

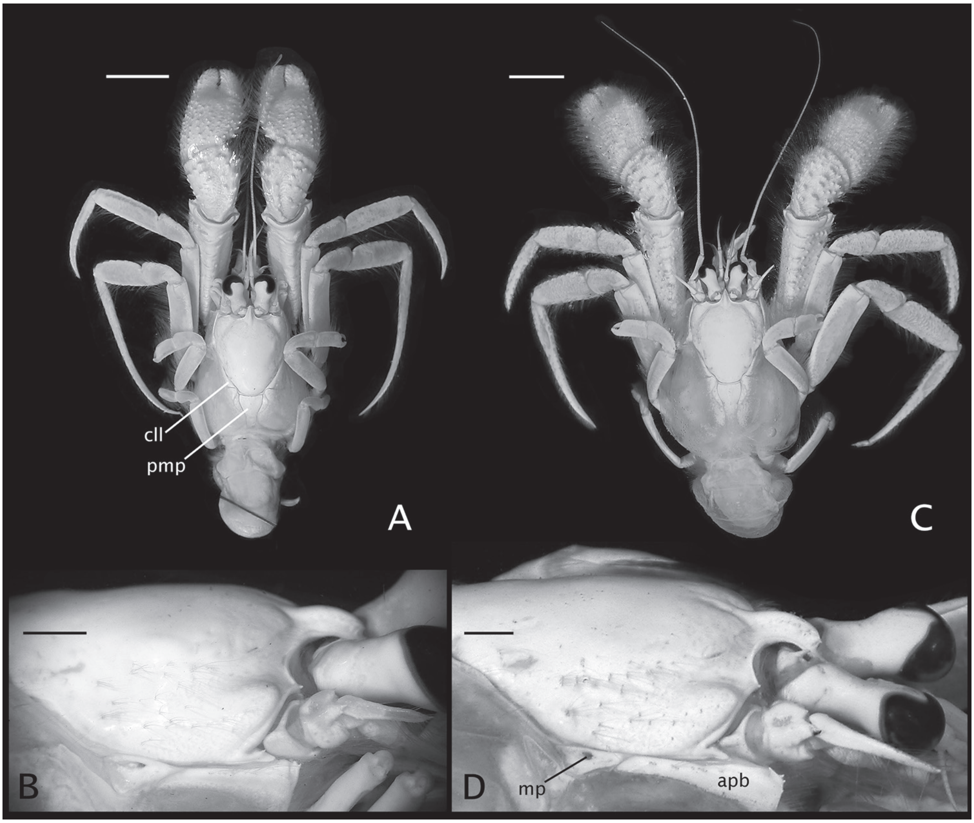

Figure 2. A, B *Paguropsis typica* Henderson, 1888 male, 14.6 mm, Philippines, USFC *Albatross*, sta 5409 (USNM 1107574) **C, D** *Paguropsis andersoni* (Alcock, 1899) lectotype male, 18.3 mm, Laccadive Sea, Indian Ocean, HM Indian Marine Survey Steamer *Investigator* (USNM 42719). **A, C** dorsal view **B, D** right side of shield and rostrum, branchiostegite, and anterodorsal portion of posterior carapace. Abbreviations: apb, anterodorsal plate of branchiostegite; mp, median plate; cll, carapace lateral lobe; pmp, posteromedian plate. Scale bars: 10 mm (**A, C**), 2 mm (**B, D**).

cept for two submedian longitudinal rows of well-spaced low tubercles each with tuft of long bristle-like setae. Fingers with narrow hiatus proximally, forming spoon-like shape in ventral view when closed; each finger terminating in small curved corneous claw and subdistal blunt calcareous tooth ventral to claw, both claws and teeth interlocking when fingers closed; cutting edge of dactyl with row of small, fused corneous teeth on distal one-third, and row of unequal calcareous teeth on proximal two-thirds; cutting edge of fixed finger with row of blunt calcareous teeth decreasing in size distally. Dactyl ca. 1.2 times as long as palm; dorsal surface somewhat convex, armed with small spines proximally, dorsomesial margin rounded; ventral face with well-spaced tufts of long bristle-like setae, lacking spines. Fixed finger with dorsal, lateral, and ventral surfaces similar to dactyl in armature. Palm slightly shorter than carpus; dorsal surface covered with moderately dense, well-spaced small spines, accompanied by tufts

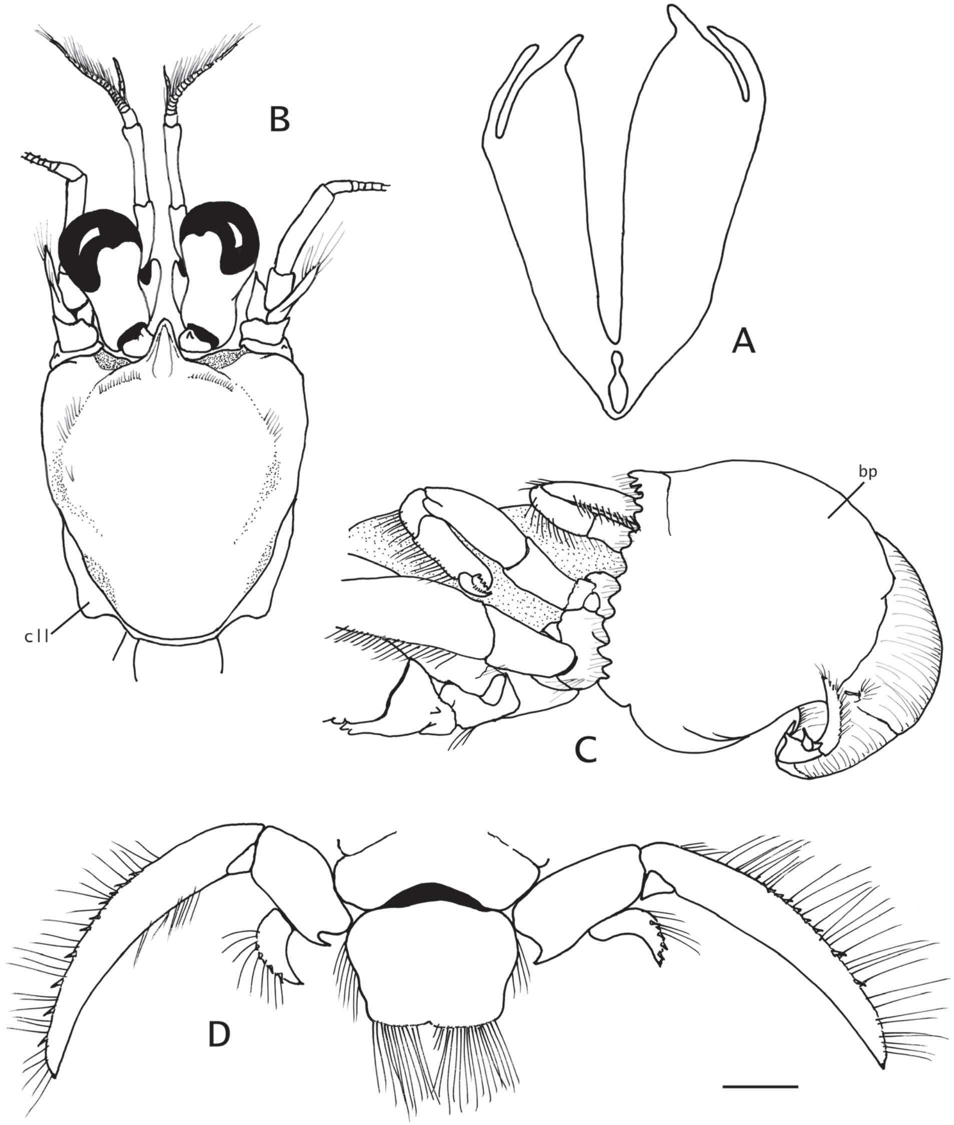

Figure 3. *Paguropsis typica* Henderson, 1888, Philippines, USFC *Albatross*, sta 5409: **A, B, D** male, 14.6 mm, **C** female, 7.1 mm (USNM 1107574). **A** gill lamella **B** shield and cephalic appendages, dorsal **C** left side of posterior thorax and pleon showing brood pouch (bp), lateral **D** uropods and telson, dorsal. Abbreviations: cll, carapace lateral lobe; bp, brood pouch. Scale bar: 0.5 mm (**A**), 4 mm (**B**), 2 mm (**C, D**).

of setae, arranged mostly in longitudinal rows (some extending to bases of fingers), and dense patch of plumose setae medially near base of fingers; dorsomesial margin with double row of well-spaced spines and tufts of long setae; dorsolateral margin rounded, not delimited, with irregular rows of small tubercles or spines, each accompanied by long setae. Carpus ca. 0.5 length of merus; dorsal surface with scattered simple spines

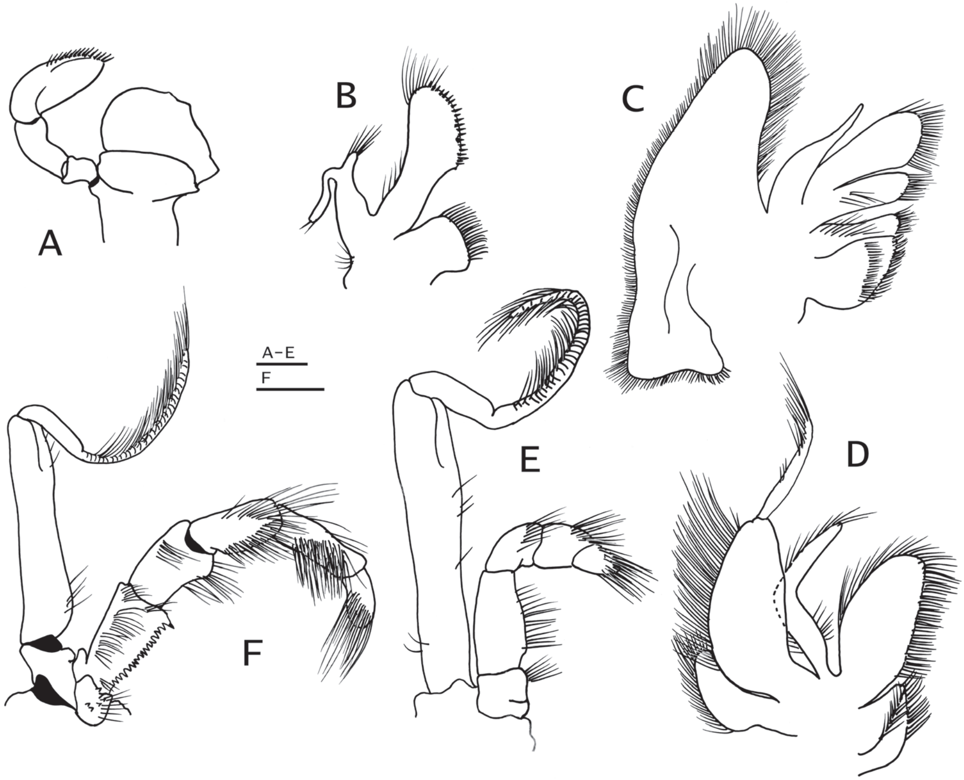

Figure 4. *Paguropsis typica* Henderson, 1888, female, 8.5 mm, Philippines, USFC *Albatross*, sta 5409 (USNM 1107574), left mouthparts, internal view: **A** mandible **B** maxillule **C** maxilla **D** maxilliped 1 **E** maxilliped 2 **F** maxilliped 3. Scale bars: 1 mm (**A–E**), 2 mm (**F**).

or short transverse rows of 2 or 3 small spines accompanied by tufts of setae; dorsomesial margin with row of spines accompanied by tufts of setae, and dorsodistal spine; dorsolateral margin rounded; ventral surface smooth, with fringe of long setae on ventrodistal margin. Merus nearly as long as chela, subtriangular in cross-section; dorsal margin with row of protuberances each bearing transverse row of setae, ventromesial and ventrolateral margins each with row of spines with tufts of long setae; lateral and mesial surfaces with tufts of long and short setae mostly on ventral half. Ischium with row of small spines on ventrolateral margin. Basis with ventromesial row of long setae. Coxa with well-marked longitudinal fissure (Fig. 5B) on ventral surface.

Pereopods 2 and 3 (Figs 1A, 2A, 6A–D, 8A) similar in armature and setation, distinctly dissimilar in length, with pereopod 2 shorter than pereopod 3. Dactyls 1.5 (pereopod 2) or 2.5 (pereopod 3) times as long as propodi, each terminating in sharp corneous claw, lateral and mesial surfaces flat or very weakly convex; dactyl of pereopod 2 broadly curved on distal half; dactyl of pereopod 3 slender, nearly straight except for broadly curved distally near claw, from 1.6–1.8 times as long as dactyl of pereopod 2; dorsal margins with tufts of long setae, ventral margins with row of usually 14 short, mi-

Figure 5. A, B *Paguropsis typica* Henderson, 1888 male, 14.6 mm, Philippines, USFC *Albatross*, sta 5409 (USNM 1107574); **C, D** *Paguropsis andersoni* (Alcock, 1899) lectotype male, 18.3 mm, Laccadive Sea, Indian Ocean, HM Indian Marine Survey Steamer *Investigator* (USNM 42719). **A, C** chelipeds, dorsal **B, D** coxae of pereopods 1–5, sternites IX–XIII, and anterior portion of pleon with gonopods 1 and 2 (arrow in B indicates keel-like anteroventral margin of coxa). Abbreviations: roman numerals refer to sternites; C1–5, coxae of pereopods 1–5; G1, G2, gonopods 1 and 2; lf, longitudinal fissure. Scale bars: 5 mm (**A, C**), 2 mm (**B**), 4 mm (**D**).

nutely obscure corneous spinules (pereopod 2) or lacking spines or spinules (pereopod 3). Propodi 1.2 length of carpi; surfaces unarmed except for tufts of long setae on dorsal and ventral margins. Carpi unarmed except for tufts of setae dorsally and ventrodistally.

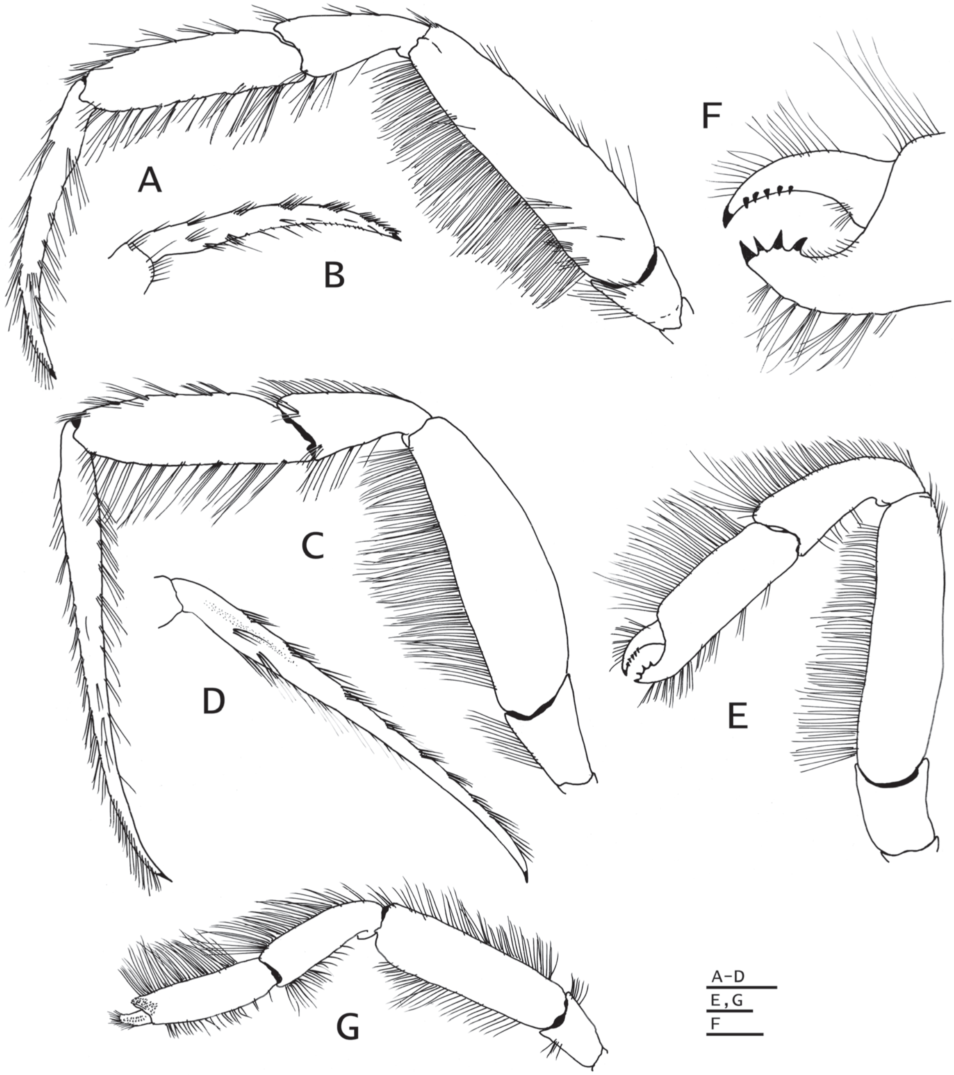

Figure 6. *Paguropsis typica* Henderson, 1888, male, 14.6 mm, Philippines, USFC *Albatross*, sta 5409 (USNM 1107574). **A** left pereopod 2, lateral **B** dactyl of same, mesial **C** left pereopod 3, lateral **D** dactyl of same, mesial **E** left pereopod 4, lateral **F** dactyl and fixed finger of same, lateral **G** left pereopod 5, lateral. Scale bars: 5 mm (**A–D**), 2 mm (**E, G**), 1 mm (**F**).

Meri with fringe of long setae on ventral margins; ventral margin of pereopod 2 with row of few small, well-spaced blunt spines hidden by setae. Ischia unarmed except for scattered setae or tufts of setae (pereopod 2) or with ventral row of small spines (pereopod 3). Coxae of pereopods 3 (Fig. 5B) separated by 0.3 ventral length of 1 coxa. Sternite XI (between pereopods 3; Fig. 5B) having anterior lobe slightly concave and short setae on distal margin; posterior lobes each with transverse fringe of setae.

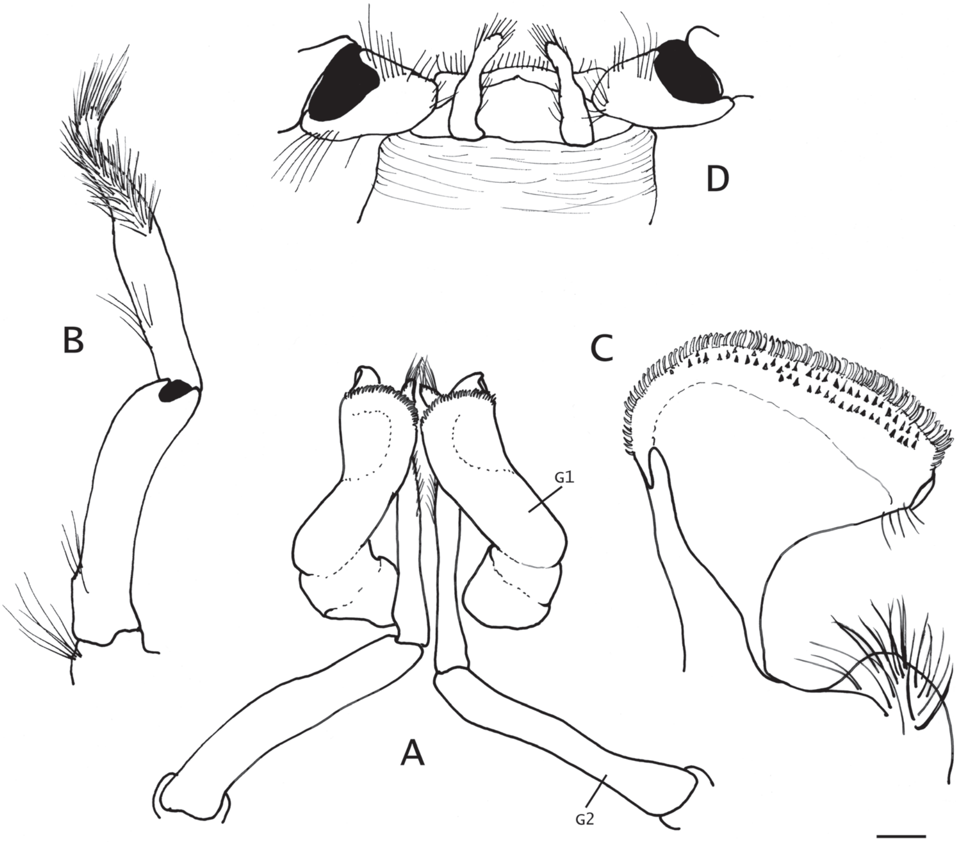

Figure 7. *Paguropsis typica* Henderson, 1888, Philippines, USFC *Albatross*, sta 5409 (USNM 1107574): **A–C** male, 14.6 mm, **D** female, 7.1 mm. **A** gonopods 1 and 2 *in situ*, ventroposterior **B** left gonopod 2, lateral, **C** distal portion of left gonopod 1, anterior **D** female gonopods 1 *in situ*, sternite XIII and coxae of pereopods 5. Abbreviations: G1, G2, gonopods 1 and 2. Scale bar: 1 mm (**A, B**), 0.25 mm (**C**), 0.5 mm (**D**).

Pereopod 4 (Fig. 6E, F) with chela 1.2 times as long as carpus and 3 times as long as high, palm 2.3 times as long as high. Dactyl and fixed finger widely gaping, each terminating in sharp, inwardly curved corneous claw crossing at tips when closed. Dactyl strongly curved inward, dorsal margin with row of short, sparse setae; cutting edge with ventrolateral row of 5–7 small corneous-tipped spines (in addition to corneous claw). Fixed finger curving inward, cutting edge of fixed finger with 3–5 corneous-tipped spines (in addition to corneous claw) arranged like bear claw; lateral face usually with one or two minute scale-like corneous spines near base of finger. Palm straight, dorsal margin with dense fringe of long setae often interspersed with fringe of shorter setae (occasionally slightly thickening distally), and few tufts of setae on ventral margin continued on fixed finger. Carpus unarmed except for fringe of long setae dorsally and scarce, moderately long setae ventrally. Merus long, 0.6 times as long as meri of pereo-

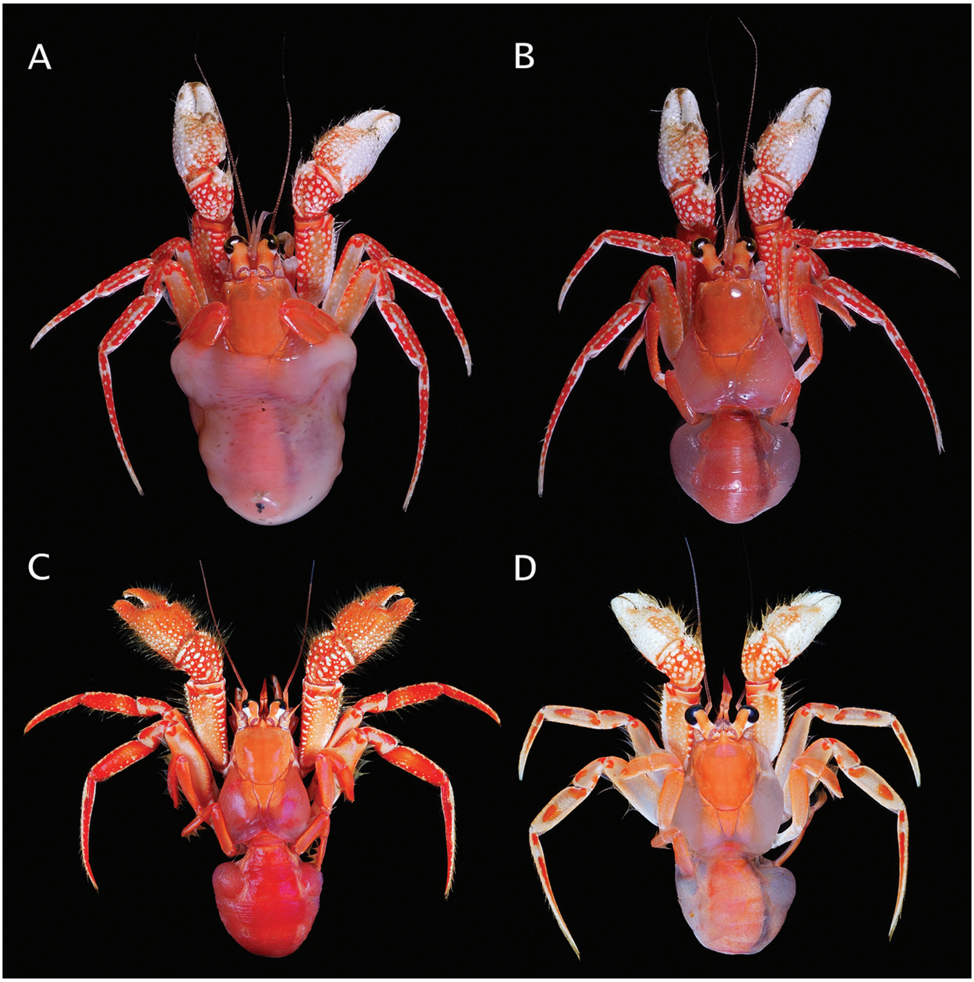

Figure 8. A, B *Paguropsis typica* Henderson, 1888, Philippines, PANGLAO 2004, sta T2 [#48] (**A**) and T2 [#54] (B) (photographs: T-Y Chan): **A** habitus, with carcinoecium **B** habitus, with carcinoecium removed **C** *Paguropsis andersoni* (Alcock, 1899), habitus, MAINBAZA sta CC 3159 (#29) (MNHN) (photograph: T-Y Chan) **D** *Paguropsis confusa* sp. n., MAINBAZA, sta CP 3134 (#23) (MNHN) (photograph: T-Y Chan).

pods 2 and 3. Sternite XII (between pereopods 4; Fig. 5B) broad, with fringe of long dense setae.

Pereopod 5 (Fig. 6G) with chela 0.7 times as long as merus, with long, brush-like setae on dorsomesial and ventromesial faces; merus and carpus each with dorsal and ventral row of long setae. Dactyl with rasp on ventral face. Propodal rasp consisting of minute, ovate scales, occupying 0.1 length of propodus. Ischium with setae dorsally and ventrally. Coxa with fringe of long setae on ventrodistal margin.

Male gonopod 1 (Fig. 7A, C) with inferior lamella armed on distal margin with posterior row of slender, semitransparent hook-like spines, and 2 anterior rows of short straight or slightly curved corneous spines. Gonopod 2 (Fig. 7A, B) with distal segment strongly twisted distally, densely setose. Usually with unpaired, reduced pleopods 3–5 on left side or less frequently on right side, as follows: biramous or uniramous pleopod 3 and 4, and lacking or rarely with uniramous pleopod 5 (see "Variations").

Female with unpaired pleopods 2–5 usually on left side or less frequently on right side, as follows: pleopods 2–4 biramous, well developed, and reduced biramous or uniramous vestigial pleopod 5. Brood pouch (Fig. 3C) large, subquadrate, distal margin scalloped and fringed with setae (see "Variations").

Uropodal exopods (Fig. 3D) slender, broadly curved, terminating in strong spine, anterior margin with fringe of long setae and row of well-spaced corneous-tipped spines; endopods short, strongly curved, anterior margin with long setae and row of corneous-tipped spines; protopods with strong, curved proximal spine.

Telson (Fig. 3D) subrectangular, wider than long; posterior lobes separated by shallow median cleft, terminal margins unarmed except for fringe of long setae.

Genetic data. See Table 1.

Color (Figs 8A, B, 28A). Shield evenly orange. Ocular peduncles orange except for white along proximal and proximomesial margins of black corneas, orange tone darker medially; ocular acicles light orange fading to weak orange distally. Antennules light orange, flagella of similar color except for transparent bluish color distally. Antennal peduncles light orange, and similar but lighter toned and somewhat transparent flagella. Chelipeds with dactyl and fixed finger white; palms mostly white except for light orange distally and reddish proximally with white spines or tubercles; carpi red with white spines or tubercles; meri red except for orange on lateral and mesial surfaces, and white spines or tubercles. Pereopods 2 and 3 red with white spots on lateral faces of dactyls, carpi and propodi; dactyls each with uneven or interrupted white band proximally; meri with orange lateral and mesial faces; ischium with orange.

Distribution. Western Pacific: from Japan, off Daito Islands, Ryukyu Islands (Miyake 1982), and Kyushu-Palau Ridge (Baba et al. 1986, this study); South China Sea; Philippines; New Guinea; Indonesia (Java and Arafura Seas); Fiji Islands; New Caledonia; and eastern Australia. Depth: 136 to 1125 m.

Habitat and symbiont. Found with indeterminate species of acontiate anemone (see "Remarks" under genus).

Variations. Aside from the meristics accounted for in the above redescription, this species is relatively constant in morphology. The only remarkable variation is in the position of unpaired pleopods 2–5 in females, and presence and degree of development of pleopods 3–5 in males. Females of *Paguropsis typica* have unpaired pleopods 2–5 on either side, with pleopods 2–4 well developed, biramous and ovigerous, whereas pleopod 5 is considerably reduced or absent. Males have unpaired pleopods 3–5 on either side, all considerably reduced, uni- or biramous, although pleopod 5 or occasionally all pleopods 3–5, can be absent. McLaughlin and Lemaitre (1997: 111) erroneously stated that males of *Paguropsis* lacked unpaired pleopods. Based on the specimens examined with complete pleons (n = 45), we observed that in females, 65.5% had pleopods 2–5 on the left side, 24.2% on the right side (often pleopod 5 is absent), and

10.3% did not have any unpaired pleopods on either side. In males, 75.1% had one or more of pleopods 3–5 on the left side, 18.7% on the right side, and 6.2% did not have any unpaired pleopods on either side.

Affinities. Except for the drastic difference in coloration, *Paguropsis typica* and *P. confusa* sp. n. are remarkably similar in morphology, and can thus be easily confused unless fresh specimens that still retain their color patterns are available (Figs 8A, B, D, 28A, C, D). In the absence of color information, the two can be separated with difficulty using only subtle characters, such as the degree of setation and strength of armature of chelipeds and pereopods 2 and 3 (less dense setation and spination in *P. typica* than in *P. confusa* sp. n.), and minor differences on the lateroproximal surface of the dactyl of pereopod 3 (convex in *P. typica* vs. slightly concave in *P. confusa* sp. n.).

General similarities exist between *Paguropsis typica* and *P. andersoni*, in particular the cephalic appendages (i.e., dilation of corneas, development of antennular and antennal peduncles), and shape of shield (i.e., posterior half of shield narrowly subtriangular). However, the two species can immediately be differentiated by the shape of the dactyls of pereopods 2 and 3 (Figs 1A, E, 2A, C, 6A–D, 8A–C, 10A–D), which are distinctly more slender and narrower in *P. typica* than in *P. andersoni*; and more clearly, the lateral face of the dactyl of pereopod 3 is evenly flat or convex throughout in *P. typica*, whereas the surface is distinctly concave (and often weakly calcified) on the proximal one-third in *P. andersoni*. Both species have numerous tufts of long setae on chelipeds and ambulatory legs, but in *P. typica* these are not as dense or as stiff and bristle-like as in *P. andersoni*. The antennal acicles are shorter, reaching approx. to the level of distal portion of optic calathus, and the chela of each pereopod 4 is more elongate (1.2 times as long as carpus), in *P. typica*; whereas the acicles slightly exceed the distal margins of corneas, and the palm of each chelate pereopod 4 is shorter (0.6 times as long as carpus), in *P. andersoni*. Color differences also exist between these two species, and these are discussed under "Remarks" for *P. andersoni*.

Remarks. Alcock (1905) corrected the spelling of Henderson's (1888) species for gender agreement, from *typicus* to *typica*, although as shown here, his specimens actually represent *Paguropsis andersoni*. Nevertheless, various carcinologists (Pzibram 1905, Boas 1926, Rabaud 1941, Thompson 1943, Kamalaveni 1950, Gordan 1956) continued to use the original spelling *P. typicus*.

Since Henderson's (1888) description of *Paguropsis typica* a good number of biologists have used Henderson's taxon name in faunal inventories or checklists (e.g., Estampador 1937, Miyake 1982, Baba et al. 1986, McLaughlin et al. 2010, Malay et al. 2018), as example of symbiosis (Balss 1924, 1956, Ross 1983, Ates 2003, Williams and McDermott 2004), in textbooks on biology or anatomy of invertebrates (Nicol 1967, Kaestner 1970), in phylogenetic analyses (Richter and Scholtz 1994), and reviews of hermit crab housing (McLaughlin 2015). Of these, records from the Indian Ocean are referred to *P. andersoni* (see "Remarks" under *P. andersoni*). Gordan (1956), in her bibliography of pagurids, did include under *Paguropsis typica* (using the spelling *P. typicus*), references to both Henderson's (1888) original description and Alcock's (1899) *Chlaenopagurus andersoni* (= *Paguropsis andersoni*); thus, her taxon concept included both *P. typica* and the herein resurrected *P. andersoni*. The studies by Balss (1924, 1956) did include figures or information that clearly are referable to *P. typica* or *P. andersoni*, and thus are herein listed accordingly in the synonymy for each of these two taxa as "in part". Miyake (1982) and Baba et al. (1986) reported on new specimens from Japanese waters. The specimen from off Daito Islands, shown in Miyake's (1982) book, has an abnormally small left cheliped perhaps in the process of regeneration, but agrees well with *P. typica* in the general coloration, confirming its identity. The specimens from the Kyushu-Palau Ridge examined in this study (CBM-ZC 4898, 4899) originated from the same source as the material studied by Baba et al. (1986).

Schäfer et al. (1983) studied the morphology of an aberrant actinian which they found attached to the underside of the thorax of planktonic glaucothoe larvae they identified as *Paguropsis typica*. However, in a worldwide review of hermit crab biocoenoses Williams and McDermott (2004, based on pers. comm. from PA McLaughlin), questioned the identity of the hermit crab host name used by Schäfer et al. (1983). We have examined the glaucothoe larval specimens used by Schäfer et al. deposited in ZMUC, and found the larvae to actually belong to one or more indeterminate species of the family Parapaguridae. These larvae are of the type similar to "*Glaucothoe peronii*", which were shown to represent parapagurids by de Saint Laurent-Dechancé (1964). Glaucothoe stages of several species of parapagurids have been described by Lemaitre and McLaughlin (1992) and Lemaitre (1997). Our assignment of Schäfer et al.'s (1983) glaucothoe to parapagurids is made based on the following characters present in those larvae: 1) maxilliped 1 lacking flagellum (a major parapagurid character); 2) pereopod 4 semi-chelate and with a propodal rasp (it is uniquely chelate and lacking a propodal rasp in *P. typica*); 3) pleonal pleura terminating ventrally in anteriorly directed hook-like process; 4) telson anterior half broad and rounded laterally, and narrow posterior half with long setae on terminal margin. Schäfer et al. (1983: fig. 12), however, based on the literature presented a map showing the known distribution of adult specimens of *P. typica* (misspelled therein also "*P. tyica*"), which includes historical records of both *P. typica* and the herein resurrected *P. andersoni*.

Paguropsis andersoni **(Alcock, 1899), resurrected**

Figs 1E, 2C, D, 5C, D, 8C, 9, 10, 14B, 28B, Table 1

Chlaenopagurus Andersoni Alcock, 1899: 115, pl. 1 (type locality: Indian Marine Survey *Investigator*, off Comorin).

Chlaenopagurus andersoni Alcock & McArdle, 1901: pl. 53, figs 1, 1a, 2, pl. 54, figs 1, 1a; Alcock, 1901: 229; Alcock, 1902: 67, fig. 2.

Paguropsis typica: Alcock, 1905: 28, pl. 2; Balss, 1924: 775, figs 30, 32 (see "Remarks" under *P. typica*); Balss, 1927: 963, fig. 1059; Thompson, 1943: 414 (see "Remarks"); Balss, 1956: 1429 (in part); Barnard, 1962: 240; Russell, 1962: 19, fig. 12; Sarojini and Nagabhushanam, 1972: 250, fig. I, fig. A, B, C; Kensley, 1981: 33 (list); Thomas, 1989: 59; Schäfer et al., 1983: figs 12 (in part, see "Remarks" under *P. typica*); Emmerson, 2016: 449 (list).

Paguropsis typicus: Thompson, 1943: 413 (see "Remarks"); Kamalaveni, 1950: 77, fig. 1 (see "Remarks"); Gordan, 1956: 325 (in part, see "Remarks" under *P. typica*).
P. tyica (misspelling): Schäfer et al., 1983, fig. 12 (in part, see "Remarks")

Type material. Lectotype herein selected: off Cape Comorin (Kanyakumari), Laccadive Sea, Indian Ocean, HM Indian Marine Survey Steamer *Investigator*, [probably sta 258, see "Remarks"], 23 Apr 1899, 08°23'N, 76°28'E, 186.5 m (102 fm): male 18.3 mm (USNM 42719, ex Indian Museum reg. no. 3173–5). Paralectotypes, [same sta data as lectotype]: 2 males 11.7, 17.6 mm (USNM 1441996, ex Indian Museum reg. no. 3173–5); 2 males 7.8, 8.2 mm (ZMUC-CRU–006727); 1 ovig female 8.1 mm (BMNH 1899.11.30.3).

Other material. *Philippines*: NW coast of Panglao Island, 146.3–548.6 m, [no day] Jan-Mar 2011, coll. J Arbasto: 4 males 14.2–16.3 mm (LKCNHM ZRC 2011.0067). PANGLAO 2004: Balicasag Island, sta PN 1, 09°31'N, 123°41'E, 50–500 m, Apr-Jul 2004, from local fisherman: 1 male 16.6 mm (LKCNHM ZRC 2018.0171).

Indonesia: KARUBAR, RV *Baruna Jaya 1*: off Tanimbar Island (Arafura Sea), sta CP 46, 08°01'S, 132°51'E, 271–273 m, 29 Oct 1991: 7 males 9.3–16.1 mm (USNM 1442005).

Indian Ocean: southwestern India: off Neendakara, Munambam, Kerala State, 30 m, 2006, commercial trawler, coll. A Biju Kumar: 4 males 14.1–18.2 mm (CBM-ZC 10006). Kenya: off Mombasa, RV *Ujizi*, 03°09'S, 40°29'E, [no depth], 24 Mar 1980, coll. WJ Scheffers: 1 male 19.9 mm (RMNH.CRUS.D.34951). Seychelles Islands: CEPROS, traps, Radiale 2, Ech. 34, 04°22.5'S, 56°19.1'E, 200–190 m, 21–22 Oct 1987, coll. A Intes: 1 male 17.3 mm (MNHN-IU-2014–9400). Madagascar: CREVETTIERE 1971, N Madagascar, [Mozambique Channel], sta CH 11, 12°40'S, 48°15'E, 375–385 m, 14 Apr 1971: 2 males 12.4, 20.6 mm, 1 female 17.2 mm (MNHN-IU-2014–9394, = MNHN-Pg 1865); CREVETTIERE 1972, sta CH 32, 12°34'S, 48°18'E, 310–320 m, 13 Sep 1972: 2 males 17.1, 19.6 mm (MNHN-IU-2014–9393, = MNHN-Pg 1864). Mozambique Channel: Mozambique: RV *Algoa*, Mozambique Scad Survey SFRI, sta C00815–014–012–2144, 23°07.98'S, 35°42.00'E, 180 m, trawl, 12 Dec 1994: 1 male 16.8 mm (SAMC MB-A041691); MAINBAZA, NO *Vizconde de Eza*: Inhambane transect, sta CC 3159, 23°55'S, 35°37'E, 148–152 m, 15 Apr 2009, colls. P Bouchet, J Rosado & E Strong: not examined, color photograph (Fig. 8C) (MNHN). KwaZulu-Natal, South Africa: sta NAD11H, 29°46.02'S, 31°16.98'E, 110–130 m, 23 Apr 1958, coll. University of Cape Town Ecological Survey: 1 male 15.0 mm [det. KH Barnard] (SAMC MB-A019489); off Durban, KwaZulu-Natal, Oceanographic Research Institute ORI 68, sta ACEP 1–4, 29°58.56'S, 31°04.98'E, 119 m, trawl, 18 Feb 2010: 1 ovig female 14.4 mm (ZRC 2013.0535); off Durban, KwaZulu-Natal, Oceanographic Research Institute ORI 17, sta ACEP 4–1, 29°06.60'S, 32°07.32'E, 128 m, trawl, 20 Feb 2010: 1 male 14.2 mm (ZRC 2013.0537); Aliwal outer reef, off KwaZulu-Natal, DST/NRF ACEP, RY *Angra Pequena*, sta R50, 30°12.36'S, 30°59.16'E, 106–149 m, 5 Jun 2017, ROV: specimen not collected, color photograph *in situ* (Fig. 28B); Coffee Bay (Eastern Cape), 31°59.34'S, 29°09.96'E, 100 m, dredge, 10 Sep 2016: 1 male 24.1 mm (SAMC MB-A066723).

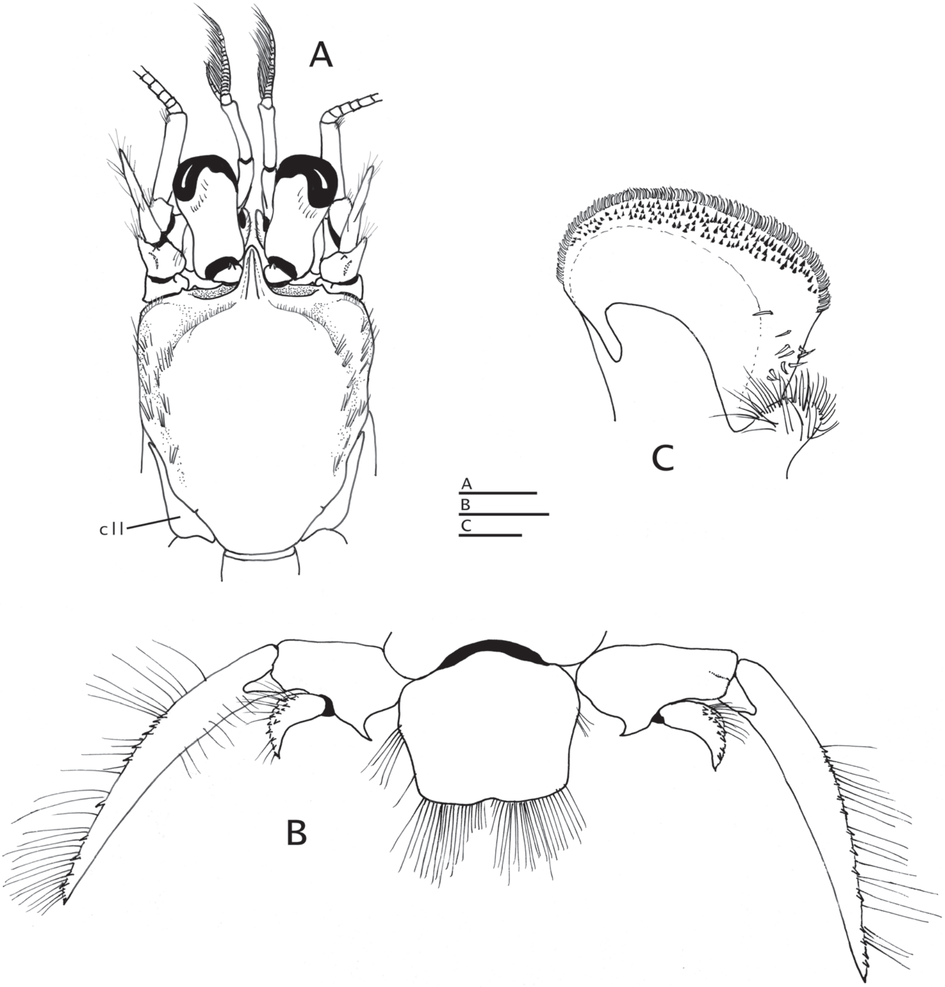

Figure 9. *Paguropsis andersoni* (Alcock, 1899) lectotype male, 18.3 mm, Laccadive Sea, Indian Ocean, HM Indian Marine Survey Steamer *Investigator* (USNM 42719). **A** shield and cephalic appendages, dorsal **B** uropods and telson, dorsal **C** distal portion of left gonopod 2, anterior. Abbreviations: cll, carapace lateral lobe. Scale bars: 5 mm (**A**), 3 mm (**B**), 0.5 mm (**C**).

[*Locality uncertain*]: INVMAR: sta 17, 155–165 m, 3 Aug 1964, coll. OT Chan: 1 ovig female 11.2 mm (MNHN-IU-2014–9412, = MNHN-Pg 1828).

Redescription. *Shield* (Figs 2C, 8C, 9A) subtriangular, ca. 1.3 times as long as broad; dorsal surface distinctly rounded, somewhat vaulted, glabrous except for tufts of setae anterolaterally and transverse fringe of short setae on sloping anterior margins of gastric region; anterior margin between rostrum and lateral projections concave; lateral projections broadly triangular, each terminating in small spine; posterior margin roundly truncate; lateroventral distal angle with strong blunt spine near proximal margin of first antennal segment. Rostrum (Fig. 9A) bluntly or sharply triangular, dorsally arched, strongly produced, extending beyond distal margin of ocular acicles, fringed by short marginal setae; with distinct rounded dorsal longitudinal ridge having row of short setae laterally, ending smoothly or in 1 minute subterminal spine. Branchiostegites (Fig. 2D) unarmed except for 1–3 spines on dorsodistal angle, distal margin setose; anterodorsal plate calcified, narrow.

Ocular peduncles ca. 0.4 length of shield, constricted medially and noticeably broadened distally, glabrous except for scattered short dorsodistal setae; corneas strongly dilated, diameter 0.5–0.6 total peduncular length (including the cornea). Ocular acicles small, triangular, each armed with distal or dorsodistal spine often directed anterodorsally.

Antennular peduncles when fully extended overreaching distal margins of corneas by 0.2 length of penultimate peduncular segments. Ultimate and penultimate segments glabrous or at most with scattered short setae. Basal segment with ventromesial tuft of setae distally; lateral face with distal subrectangular lobe, small medial spine, and setose lobe proximally.

Antennal peduncles overreaching distal corneal margins by ca. 0.5 length of fifth segment. Fifth and fourth segments unarmed except for scattered short setae and laterodistal tuft of long setae. Third segment with spine at ventrodistal angle. Second segment with dorsolateral distal angle produced, terminating in small simple or less frequently, bifid spine; mesial margin rounded, setose, and small spine on dorsomesial angle. First segment unarmed except for moderately long setae on lateral face. Antennal acicle length variable with growth, reaching from distal margin of optic calathus to slightly exceeding distal margin of cornea, slender, terminating in sharp spine, with long setae distally, at most with 1 or 2 minute proximal tubercles on mesial margin. Antennal flagellum long, reaching to distal end of cheliped fingers, articles with 1 or 2 short setae (< 1 article in length) and usually with 1 or 2 long setae every 12 articles or so.

Mouthparts not markedly different from those described for *Paguropsis typica* (e.g., Fig. 4A–F). Maxilliped 3 with exopod ca. 4.2 times as long as broad.

Chelipeds (Figs 1E, 2C, 5C, 8C) subequal, similar in armature and setation; dorsal surfaces of chelae and carpi densely covered with tufts of long, bristle-like setae obscuring spination below, often with areas of short dense plumose setae on dorsal faces of dactyl, fixed finger, and palm; ventral surfaces of palms smooth except for 2 submedian longitudinal rows of well-spaced low tubercles each with tuft of long bristle-like setae. Dactyl and fixed finger with narrow hiatus proximally, forming spoon-like shape in ventral view when closed; each finger terminating in small curved corneous claw and subdistal blunt calcareous tooth ventral to claw, both claws and teeth interlocking when fingers closed; cutting edge of dactyl with terminal row of small, fused corneous teeth on distal one-third, and row of unequal calcareous teeth on proximal two-thirds; cutting edge of fixed finger with row of blunt calcareous teeth decreasing in size distally. Dactyl ca. 1.4 times as long as palm; dorsal surface somewhat convex, armed with small spines proximally and patch of dense, short plumose setae proximally and extending to mesial face; dorsomesial margin rounded; ventral face with well-spaced tufts of long bristle-like setae, lacking spines. Fixed finger with dorsal, lateral, and ventral surfaces similar to dactyl in armature. Palm ca. 0.6 times as long as carpus, dorsal surface covered with numerous small spines arranged in irregular longitudinal rows and accompanied by tufts of long, setae, strength and number of spines increasing with growth; dorsomesial margin with 2 or 3 rows of strong, well-spaced spines and tufts of long setae; dorsolateral margin rounded, not delimited, with irregular rows of small tubercles or spines, each accompanied by tuft of long setae. Carpus ca. 0.6 times length of merus; dorsal and dorsolateral surfaces with well-spaced spines often bifid or trifid and accompanied by tufts of long bristle-like setae; dorsomesial margin with row of strong spines accompanied by tufts of bristle-like setae, and dorsodistal spine; dorsolateral margin rounded; mesial surface with short transverse rows of bristle-like setae, otherwise smooth; ventral surface smooth except for fringe of long setae on ventrodistal margin extending onto mesial surface. Merus nearly as long as chela, subtriangular in cross-section; dorsal margin with row of protuberances accompanied by tufts of long setae, ventromesial and ventrolateral margins each with irregular row of strong spines with tufts of long setae; lateral and mesial surfaces with tufts of long and short setae. Ischium with row of small spines on ventrolateral margin. Basis with ventromesial row of long setae.

Pereopods 2 and 3 (Fig. 10A–D) similar in armature and setation, distinctly dissimilar in length, with pereopod 2 shorter than pereopod 3. Dactyls ca. 1.5 (pereopod 2) or 2.2 (pereopod 3) times as long as propodi; with dorsal and ventral margins, lateral and mesial surfaces, with numerous tufts of long, bristle-like setae; dactyl of pereopod 2 weakly curved, lateral surface convex, ventromesial distal margin armed with 10–19 minute corneous spinules; dactyl of pereopod 3 relatively broad on proximal one-third, becoming slender distally, terminating in sharp corneous claw, 1.5–1.6 times as long as dactyl of pereopod 2, lateral and mesial surfaces with shallow but distinct concavity (often weakly calcified) on proximal one-third, ventral margin lacking spines or spinules. Propodi ca. 1.2 times as long as carpi; dorsal and ventral surfaces with tufts of long setae. Carpi unarmed except for tufts of setae dorsally and distolateral fringe of long setae. Meri unarmed except for fringe of long setae ventrally and ventrolaterally (pereopod 2) or ventrally (pereopod 3). Ischia armed with row of small spines and setae (pereopod 2) or unarmed except for row of setae (pereopod 3). Coxae with ventromesial row of setae; coxae of pereopods 3 narrowly separated by ca. 0.2 ventral length of 1 coxa. Sternite XI (of pereopods 3; Fig. 5D) having anterior lobe flat to slightly concave, glabrous or with scattered short setae distally; posterior lobes strongly compressed laterally, each with transverse fringe of setae.

Pereopod 4 (Fig. 10E, F) with chela short, 1.1 times as long as carpus and 2.5 times as long as high. Dactyl and fixed finger leaving wide gap when closed, each terminating in sharp, inwardly curved corneous claw crossing at tips when closed. Dactyl curved inwardly, dorsal margin with row of setae; cutting edge of dactyl with ventrolateral distal row of 6–8 small corneous-tipped spines (in addition to corneous claw). Fixed finger curving inward, cutting edge with 4 or 5 strong corneous-tipped spines (in addition to corneous claw) arranged like bear claw; lateral face usually with 1–4 minute scale-like corneous spines basally. Palm straight or slightly curved, 1.6–1.8 times as long as high;

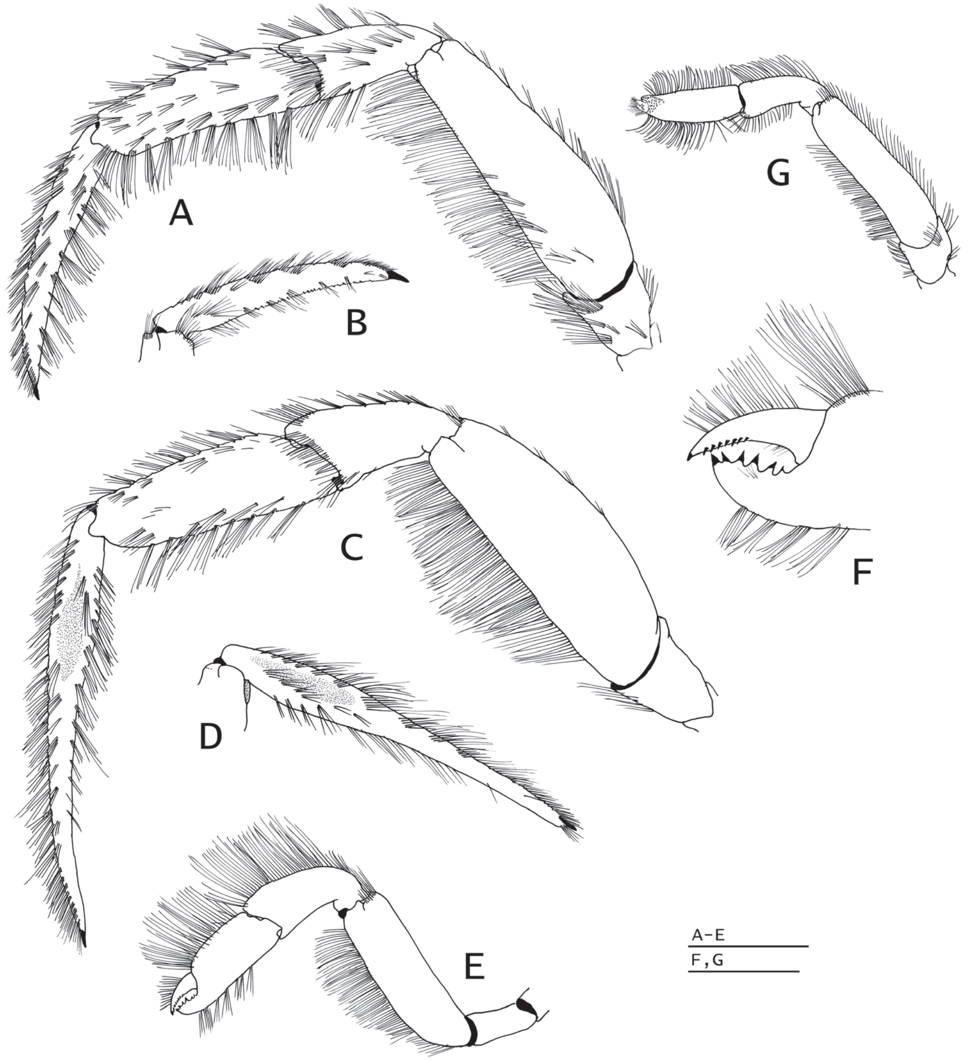

Figure 10. *Paguropsis andersoni* (Alcock, 1899), lectotype male, 18.3 mm, Laccadive Sea, Indian Ocean, HM Indian Marine Survey Steamer *Investigator* (USNM 42719). **A** left pereopod 2, lateral **B** dactyl of same, mesial **C** left pereopod 3, lateral **D** dactyl of same, mesial **E** left pereopod 4, lateral **F** dactyl and fixed finger of same, lateral **G** left pereopod 5, lateral. Scale bars: 10 mm (**A–E, G**), 3 mm (**F**).

with dense fringe of long setae on dorsal margin, and tufts of setae on ventral margin continued on fixed finger; carpus unarmed except for fringe of long setae dorsally and scarce setae ventrally; merus long, ca. 0.6 times as long as meri of pereopods 2 and 3. Sternite XII broad, with dense fringe of long dense setae (Fig. 5D).

Pereopod 5 (Fig. 10G) with chela ca. 0.6 times as long as merus, with long, brush-like setae on dorsomesial and ventromesial surfaces; merus and carpus each with dorsal and ventral row of long setae. Dactyl with rasp on ventral face. Propodal rasp consisting of minute, ovate scales, occupying 0.2 length of propodus. Ischium with setae dorsally and ventrally. Coxa with fringe of long bristle-like setae on rounded ventromesial distal angle.

Male gonopod 1 (Fig. 9C) with inferior lamella armed on distal margin with posterior row of slender, semitransparent hook-like spines, and up to 4 or 5 anterior irregular rows of small, straight or slightly curved corneous spines. Gonopod 2 with distal segment strongly twisted distally, densely setose; usually with unpaired, biramous or uniramous, reduced pleopods 3–5 on left side or less frequently on right side; often lacking pleopods 4 or 5 or lacking altogether pleopods 3–5 (see "Variations").

Female usually with pleopods 2–5 on left side or less frequently on right side, as follows: pleopods 2–4 biramous, well developed, and reduced biramous or uniramous and vestigial pleopod 5 (see "Variations"). Brood pouch large, subquadrate, distal margin scalloped and fringed with setae.

Uropodal exopods (Fig. 9B) slender, broadly curved, terminating in strong spine, anterior margin with fringe of long setae and row of well-spaced corneous-tipped spines; endopods short, strongly curved, anterior margin with long setae and 1 or 2 irregular rows of corneous-tipped spines; protopods with strong, curved proximal spine.

Telson (Fig. 9B) subrectangular, wider than long; posterior lobes separated by shallow median cleft, terminal margins unarmed except for fringe of long setae.

Genetic data. See Table 1.

Color (Fig. 8C, 28B). Shield and calcified dorsal portions of posterior carapace orange. Ocular peduncles orange dorsally, white otherwise; corneas black. Ocular acicles light orange. Antennular peduncles and flagella light orange. Antennal peduncles light orange, with color fading to cream or whitish proximally on first to fourth segments. Chelipeds red or orange with white spines and tubercles and yellow bristle-like setae; chelae orange; carpi red; meri dorsal margin red extending to lateral and mesial faces subdistally, dorsodistal margin and most of lateral and mesial surfaces light orange. Pereopods 2 and 3 as follows: dactyl red with white dorsal margin; propodi red with white dorsal margin and scattered small white spots ventrolaterally; carpi red with large white portions on lateral face medially and distally; meri mostly white with reddish dorsal and ventral margins and on lateral face distally; ischium reddish. Pereopods 4 and 5 red or orange.

In explaining the etymology of his genus name *Chlaenopagurus* where this species was originally placed, Alcock (1899) mentioned that the purple coloration of the polyps that he interpreted to be a colonial zoanthid used by this species, was similar to the *chlaina* (Gr.), a mantle used in Homeric times for protection against the weather.

Distribution. Western Pacific: from Philippines and Indonesia (Arafura Sea). Indian Ocean: from Gulf of Martaban, Andaman Sea (Alcock 1905); India, including eastern (Sarojini and Nagabhushanam 1972) and western (Thomas 1989) coasts; Seychelles Islands; eastern Africa, off Kenya; off Madagascar on Mozambique Channel; and eastern coast of South Africa. Depth: 30 to 548.6 m.

Habitat and symbiont. Found with indeterminate species of acontiate anemone (see "Remarks" under genus).

Variations. The following morphological features increase with size: length of antennal acicle; density and strength of spines on chelipeds; and density of tufts of setae on chelipeds and ambulatory legs. Larger males have more numerous subdistal spines or rows of spines on the distal margin of gonopod 1 (Fig. 9C).

Of the four females examined, one has pleopods 2–5 on the left side, and the other on the right side; both have pleopod 5 reduced. Of the 29 males examined, 53.8% had one or more unpaired pleopods 3–5 on the left side, 15.4% on the right side, 7.7% did not have any unpaired pleopods on either side, and 23.1% had paired pleopods 3–5. As in males of *P. typica*, the male pleopods 3–5 are reduced, uni- or biramous.

Affinities. As previously mentioned under the "Remarks" of *Paguropsis typica*, *P. andersoni* can be distinguished primarily from that species and other congenerics by the distinct longitudinal concavity present on the lateroproximal surface of the dactyls of pereopods 3 (second ambulatory legs). In addition, the coxae of pereopods 3 (Fig. 5D) are noticeably more narrowly separated (by ca. 0.2 ventral length of 1 coxa) from each other than in other congeners, and the posterior lobes of sternite XI are noticeably compressed. Other characters setting *P. andersoni* apart, albeit subject to some variability related to size, include the more numerous and stronger spination of the chelipeds, particularly on the dorsal surface of carpus, chela, ventromesial and ventrolateral margins of merus; the dense tufts of setae on chelipeds and meri to dactyls of ambulatory legs; and pereopod 4 with a shorter chela relative to the carpus length.

Coloration is clearly distinct in *Paguropsis andersoni* when compared to other congeners as well as with all other species discussed herein (see Figs 8, 18, 28). The overall color of *P. andersoni* (Figs 8C, 28B) does bear some general similarity with that of *P. typica* (Figs 8A, B, 28A); however, the ocular peduncles, chelae, and ambulatory legs in each of these two species have a different pattern. In *P. andersoni* the ocular peduncles are light orange dorsally, and white otherwise (vs. light orange overall with a darker orange band in *P. typica*), the chelae are mostly orange (vs. mostly whitish in *P. typica*), and the propodus and dactyl of pereopods 2 and 3 are mostly solid red except for white dorsal margins of dactyls (vs. reddish mottled with white spots, and a median longitudinal white line on the lateral surface of the propodus, in *P. typica*).

Remarks. Alcock (1905) concluded, without providing any explanation, that his genus and species described earlier as *Chlaenopagurus andersoni* Alcock, 1899, were the same as Henderson's (1888) genus and species *Paguropsis typica*, and thus placed his name in the synonymy of the latter. Alcock's synonymy has stood since that time. However, detailed study of types and specimens deposited in various museums, as well as recently collected material of *Paguropsis*, has shown that Alcock's name actually represents a valid and morphologically distinct species, and as such is resurrected herein with a lectotype selected from the syntype series. Alcock (1905: 30) described the coloration of *P. typica* and its cnidarian symbiont, as follows "The colour of the crab is red: the coenosarc of the polyp-colony is bluish, the polyps themselves are dark purple", actually is applicable as well to *P. andersoni*.

When Alcock (1899) described *Chlaenopagurus andersoni* he did not designate a holotype among his numerous specimens, and thus all are syntypes, several of which were distributed to major museums such as the USNM, BMNH, and ZMUC. A lectotype is herein selected for Alcock's taxon from the syntypes exchanged with the USNM. The labels with the syntype specimens sent to USNM lacked a station number, but based on all other information accompanying these syntypes and comparing them with Alcock's (1902) detailed station data, it seems clear that they came from *Investigator* Survey station 258.

Several studies have reported new specimens collected since Henderson's (1888) description, as *Paguropsis typica*. These are as follows: Alcock (1905), from the Gulf of Martaban (Andaman Sea); Balss (1927), from the "Indian Ocean"; Thompson (1943, spelled both *P. typicus* and *P. typica*), from Zanzibar; Barnard (1962), from East Africa (Natal); and Sarojini and Nagabhushanam (1972), from Waltair (eastern India, Bay of Bengal). Based on information therein, and in light of the finding during this study that Henderson's (1888) *P. typica* has not been found outside the western Pacific, these reports are herein referred to *P. andersoni*. The lists or catalogues of hermit crabs from southern Africa by Kensley (1981) and Emmerson (2016) that have included *P. typica* in the fauna from that region have been based on Barnard's (1962) original male specimen (SAMC MB-A019489) which is shown here to actually be *P. andersoni*.

As mentioned under the "Remarks" for *Paguropsis typica,* a number of reports (Balss 1924, 1956, Gordan 1956) that have used that name actually represent, in part, *P. andersoni*, as does the distribution map used by Schäfer et al. (1983).

In a summary of the hermit crabs from the Indian Museum, Kamalaveni (1950) based his discussion of *Paguropsis typica* (spelled *P. typicus*) exclusively on the material used by Alcock (1899) in his description of *Chlaenopagurus andersoni*, a taxon shown here to be a valid species of *Paguropsis*. Thus, Kamalaveni's report pertains entirely to *P. andersoni*.

Paguropsis confusa **sp. n.**

http://zoobank.org/D5200836-E6C3-4033-A9FB-680981F9D5FC
Figs 8D, 11–13, 14D, 28C, D, Table 1

Type material. Holotype, male 13.6 mm, Philippines, Bohol Sea, Maribojoc Bay, PANGLAO 2005, NO *DA-BFAR*, sta CP 2331, 09°39'N, 123°48'E, 256–268 m, 22 May 2005 (NMCR 50015).

Paratypes. *Philippines*: MUSORSTOM 1, NO *Vauban*: N of Lubang, sta CC 12, 14°00'N, 120°17'E, 187–210 m, 20 Mar 1976: 5 males 9.7–11.2 mm, 3 females 7.9–9.7 mm, 2 ovig females 9.2, 10.4 mm (MNHN-IU-2014–9397). MUSORSTOM 3, NO *Coriolis*: W of Luçon, sta CP 90, 14°00'N, 120°19'E, 195 m, 31 May 1985: 9 males 6.9–10.3 mm, 1 female 9.7 mm (USNM 1441901); N Cebu Island, sta CP 143, 11°29'N, 124°11'E, 205–214 m, 7 Jun 1985: 1 male 20.9 mm (MNHN-IU-2014–9396); NE of Cebu Island, sta CP 145, 11°01'N, 124°04'E, 214–246 m, 7 Jun 1985: 4 males 9.8–13.5 mm, 2 ovig females 11.0, 11.7 mm (MNHN-IU-2014–9398). LUMIWAN 2008, NO *DA-BFAR*: N of Lubang, sta CP 2867, 14°02'N, 120°12'E, 189–93 m, 23 Mar 2008: sex indet, not examined, color photograph (Fig. 28D) (NMCR).

South China Sea: INVMAR, [off Vietnam], sta 69, Cr. 4/63, 15°55'44"N, 15°57'54"N, 109°8'30"E –109°36'30"E, 260–315 m, 16 Sep 1963: 3 males 7.6–11.8 mm (MNHN-IU–2014–9419, = MNHN Pg 2314). Hong Kong: Cr. 4163, sta 66, Tr. 56, coll. Hong Kong Fisheries Research Station, [no other data]: 1 female 6.4 mm (MNHN-IU-2013–5658).

Indonesia: CORINDON 2, NO *Coriolis*: Kalimantan, Makassar Straits, sta CH 208, 00°15'S, 117°52'E, 150 m, 31 Oct 1980: 1 male 10.3 mm (MNHN-IU-2014–9377).

Western Indian Ocean: MIRIKY: Madagascar, between Nosy-bé and Banc du Leven, sta CP 3188, 12°31'S, 48°22'E, 298–301 m, 27 Jun 2009, colls. P Bouchet, N Puillandre & B Richer de Forges: 2 specimens not examined, identified and sexed from color photographs, 1 female (#50), 1 ovig female (#51) (MNHN). MAINBAZA, NO *Vizconde de Eza*: Mozambique Channel, Maputo transect, sta CP 3134, 25°11'S, 35°14'E, 303–403 m, 10 Apr 2009, colls. P Bouchet, J Rosado & E Strong: sex indet. (specimen #23), not examined, color photograph (Fig. 8D) (MNHN). DST/NRF ACEP: off Durban, KwaZulu-Natal, South Africa, RY *Angra Pequena*, sta R45 Echinoderm Extravaganza, 29°52.80'S, 31°11.76'E, 215 m, 23 Jun 2016, ROV: specimen not collected, color photograph *in situ* (Fig. 28C).

[Locality uncertain]: INVMAR: sta 8, 5 Dec 1963 [no other data]: 1 male 10.3 mm (MNHN-IU-2014–9424, = MNHN-Pg 2312); sta 26, [no other data]: 4 males 5.5–11.8 mm, 1 female 7.1 mm (MNHN-IU-2014–9421, = MNHN Pg 2319); sta 28, [no other data]: 3 ovig females 8.1–11.3 mm (MNHN-IU-2014–9420, = MNHN Pg 2318); sta 64, 16 Sep 1963: 3 males 6.2–9.7 mm, 2 females 5.2, 7.3 mm (MNHN-IU-2014–9417, = MNHN Pg 2317).

Description. *Shield* (Figs 8D, 11A, 12A) subtriangular, ca. 1.3 times as long as broad; dorsal surface glabrous except for anterolateral setae and transverse fringe of short setae on sloping anterior margins of gastric region; anterior margin between rostrum and lateral projections concave; lateral projections broadly triangular, each terminating in small spine; posterior margin roundly truncate; lateroventral distal angle produced into strong blunt spine adjacent to proximal margin of first antennal segment. Rostrum (Figs 8D, 11A, 12A) acutely subtriangular, arched dorsally, strongly produced and extending to distal margin of ocular acicles; with distinct rounded dorsal longitudinal ridge having few short setae laterally, and 1 minute subterminal spine. Branchiostegite with 1 spine on dorsodistal angle of anterodorsal plate, and setose distal margin.

Ocular peduncles ca. 0.4 length of shield, constricted medially and broadening distally, glabrous except for dorsal longitudinal row of short setae; corneas strongly dilated, diameter 0.5–0.6 total peduncular length (including the cornea). Ocular acicles small, triangular, each armed with distal spine directed anteriorly.

Antennular peduncles when fully extended overreaching distal margins of corneas by full length of ultimate peduncular segment; ultimate and penultimate segments

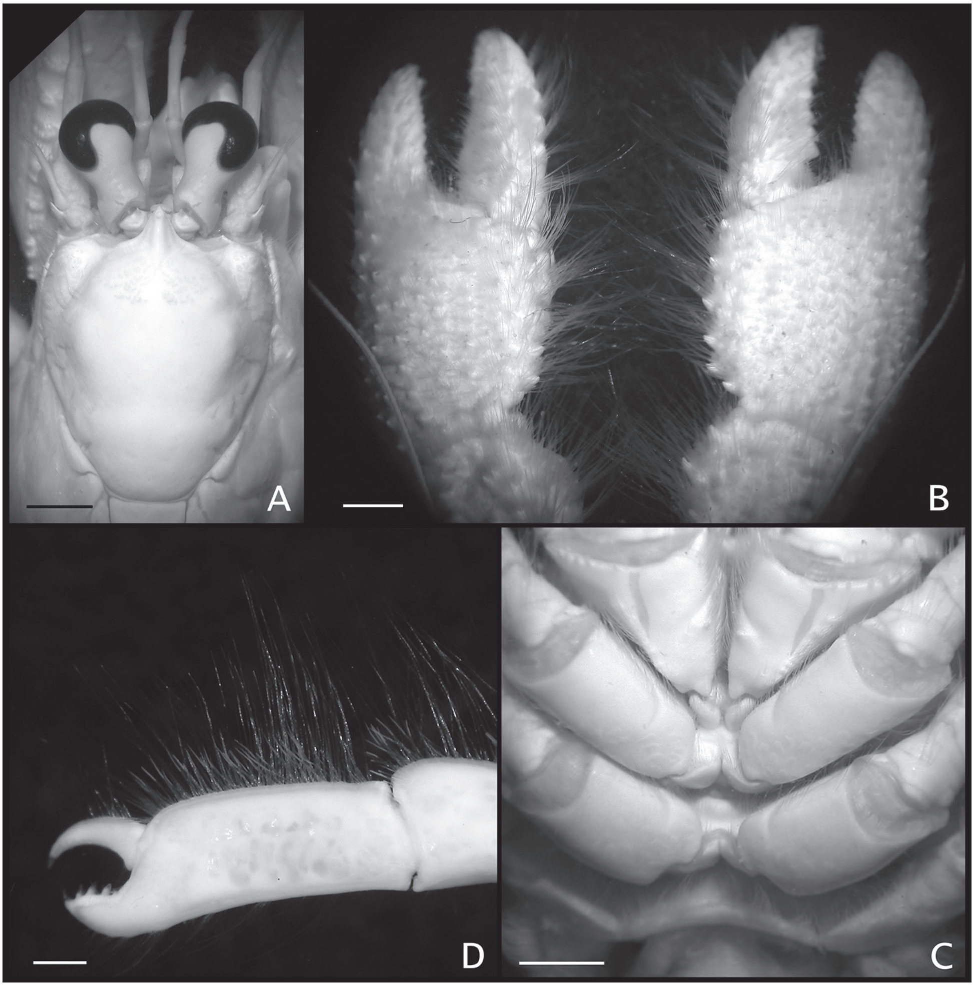

Figure 11. *Paguropsis confusa* sp. n., holotype male, 13.6 mm, Philippines, PANGLAO 2005, sta CP 2331 (NMCR 50015). **A** shield, cephalic appendages, and anterior portion of posterior carapace, dorsal **B** chelae, dorsal **C** coxae of pereopods 1–3, and sternites IX–XI, ventral **D** chela of left pereopod 4, lateral. Scale bars: 3 mm (**A–C**), 1 mm (**D**).

glabrous or at most with scattered short setae; basal segment with ventromesial tuft of setae distally; lateral face with distal subrectangular lobe, small medial spine, and setose lobe proximally.

Antennal peduncles overreaching distal corneal margins by ca. 0.3 length of ultimate segments. Fifth and fourth segments unarmed, nearly glabrous except for scattered short setae. Third segment with setose spine at ventrodistal angle. Second segment with dorsolateral distal angle produced, terminating in small simple or bifid spine; mesial margin rounded, setose, dorsomesial distal angle with small spine. First segment unarmed except for setae on lateral face. Antennal acicle relatively short, reaching at most

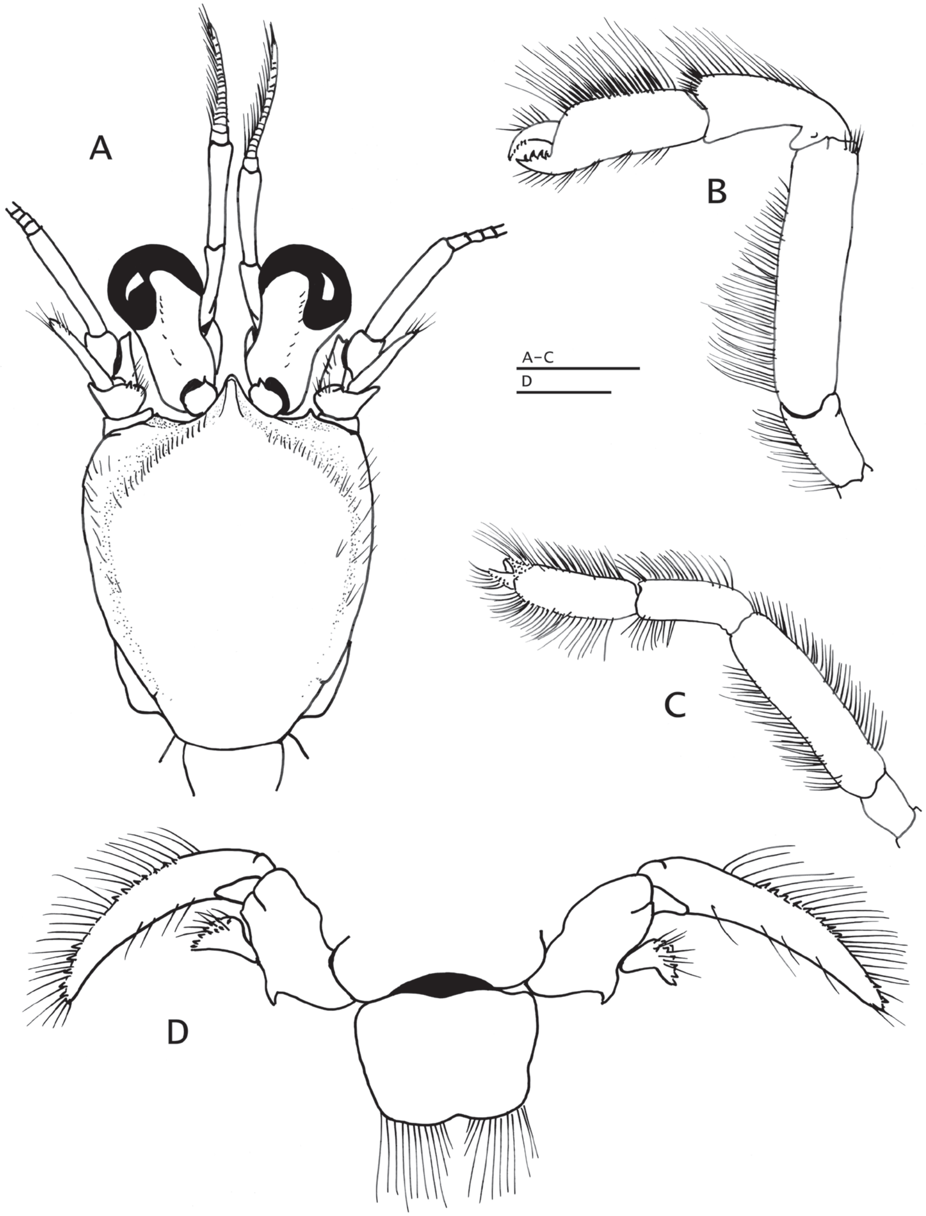

Figure 12. *Paguropsis confusa* sp. n., holotype male, 13.6 mm, Philippines, PANGLAO 2005, sta CP 2331 (NMCR 50015). **A** shield and cephalic appendages, dorsal **B** left pereopod 4, lateral **C** left pereopod 5, lateral **D** uropods and telson, dorsal. Scale bars: 5 mm (**A–C**), 2 mm (**D**).

to distal margin of optic calathus, slender, nearly straight and terminating in sharp spine, with few long setae distally. Antennal flagellum long, reaching to distal end of cheliped fingers, with few, scattered short setae less than 1 flagellar article in length.

Mouthparts not markedly different from those described for *Paguropsis typica* (see Fig. 4A–F). Maxilliped 3 with exopod ca. 4.1 times as long as broad.

Chelipeds (Figs 8D, 11B) subequal, similar in armature and setation; dorsal surfaces of chelae and carpi covered with moderately dense tufts or short rows of long, bristle-like setae not hiding ornamentation beneath; ventral surfaces of palms smooth except for 2 submedian longitudinal rows of well-spaced low tubercles each with tuft of long bristle-like setae. Dactyl and fixed finger with narrow hiatus proximally when closed, forming spoon-like shape in ventral view when closed; each terminating in small curved corneous claw and subdistal blunt calcareous tooth ventral to claw, both claws and teeth interlocking when fingers closed; cutting edge of dactyl with terminal row of small, fused corneous teeth on distal one-third, and row of unequal calcareous teeth on proximal two-thirds; cutting edge of fixed finger with row of blunt calcareous teeth decreasing in size distally. Dactyl ca. 1.2 times as long as palm; dorsal surface convex, with numerous tufts of long bristle-like setae, and few small blunt spines proximally; dorsomesial margin rounded, usually with patch of short dense plumose setae medially; ventral face with well-spaced tufts of long bristle-like setae inserted at bases of small tubercles, lacking spines. Fixed finger with dorsal, lateral, and ventral surfaces similar to dactyl in armature. Palm as long as carpus, dorsal surface covered with numerous small spines arranged in more or less irregular longitudinal rows of spines with tufts of long setae; dorsomesial margin with row of 6–8 spines with tufts of long setae; dorsolateral margin rounded, not delimited, with irregular rows of small tubercles or spines, each accompanied by long setae. Carpus 0.5–0.6 times length of merus; dorsal and dorsolateral surfaces with well-spaced spines or short transverse rows of 2 or 3 small spines each bearing tufts of long setae; dorsolateral margin rounded; dorsomesial margin with row of strong spines each bearing tufts of long setae; mesial surface with short transverse rows of bristle-like setae, otherwise smooth; ventral surface smooth except for fringe of long setae on ventrodistal margin extending on to mesial surface. Merus nearly as long as chela, subtriangular in cross-section; dorsal margin with row of low protuberances each bearing transverse row of 2 or 3 small tubercles and bearing tuft of long setae; ventromesial and ventrolateral margins each with irregular row of spines with tufts of long setae; lateral and mesial surfaces with tufts of long and short setae. Ischium with row of small spines on ventrolateral margin. Basis with ventromesial row of long setae. Coxa with well-marked longitudinal fissure (Fig. 11C) on ventral surface.

Pereopods 2 and 3 (Figs 8D, 13A–D) similar in armature and setation, distinctly dissimilar in length, with pereopod 2 distinctly shorter than pereopod 3. Dactyls ca. 1.4 (pereopod 2) or 2.3 (pereopod 3) times as long as propodi, broadly curved, each terminating in sharp corneous claw; dorsolateral and dorsomesial margins with short oblique rows of bristle-like setae; dactyl of pereopod 3 becoming slender distally, ca. 1.4 times as long as dactyl of pereopod 2; lateral surface with proximal third having shallow or weakly distinct longitudinal concavity; ventromesial margin armed with 10–15 minute corneous spinules (pereopod 2) or unarmed (pereopod 3), and with tufts of long bristle-like setae. Propodi ca. 1.4 (pereopod 2) or 1.1 (pereopod 3) times as long as carpi; dorsal surfaces with short tufts of setae, ventral surfaces with tufts of

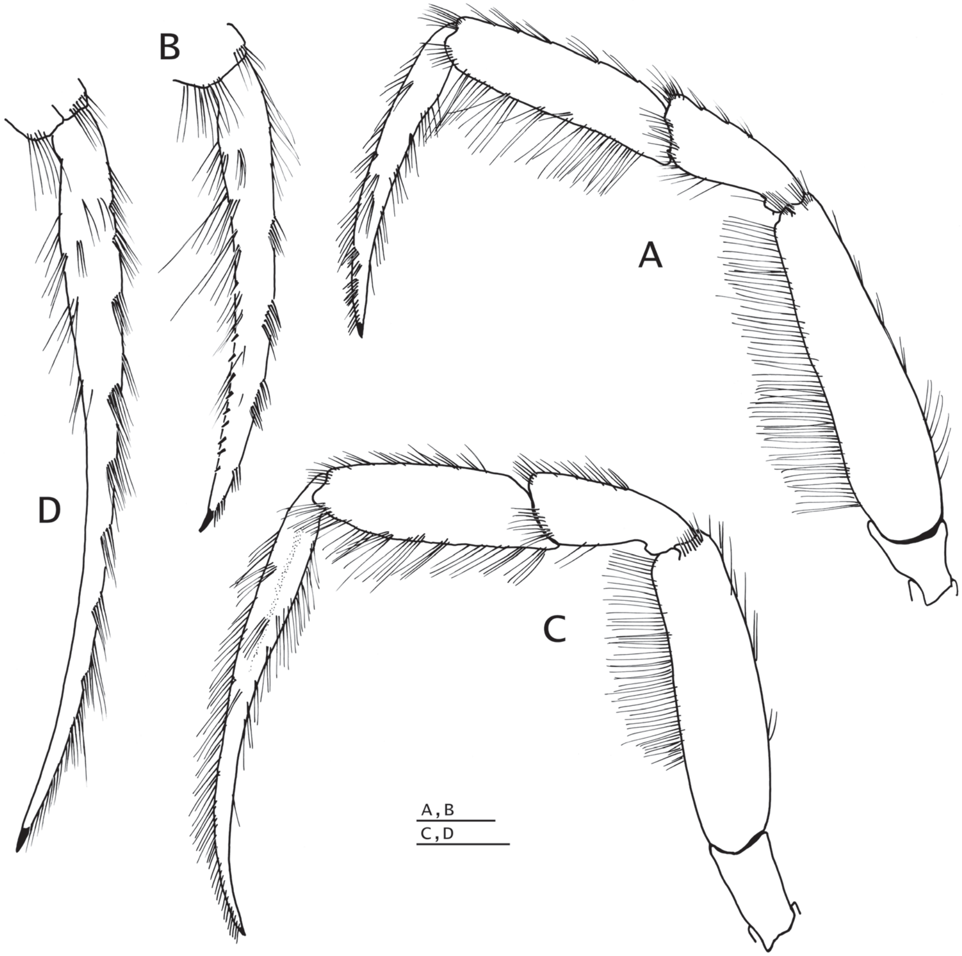

Figure 13. *Paguropsis confusa* sp. n., Philippines, holotype male 13.6 mm, PANGLAO 2005, sta CP 2331 (NMCR 50015). **A** left pereopod 2, lateral **B** dactyl of same, mesial **C** left pereopod 3, lateral **D** dactyl of same, mesial. Scale bars: 5 mm (**A, B**), 3 mm (**C, B**).

long setae. Carpi unarmed except for tufts of setae dorsally and distolateral fringe of long setae. Meri with fringe of long setae on ventral margins; ventral margin of merus of pereopod 2 with or without row of small blunt spines (frequently lacking or fewer spines in specimens SL ≤ 11.0 mm) hidden by setae. Ischia armed with row of few small spines and long setae (pereopod 2) or unarmed and scattered setae (pereopod 3). Coxae with ventromesial margin sparsely setose; coxae of pereopods 3 (Fig. 11C) narrowly separated by 0.2 ventral length of 1 coxa. Sternite XI (Fig. 11C) having anterior lobe flat or weakly concave medially, glabrous; posterior lobes compressed, each with transverse fringe of setae.

Pereopod 4 (Figs 12B, 14D) with chela as long as carpus and 3.2–3.6 times as long as high, palm 1.8–2.0 times as long as high. Dactyl and fixed finger leaving wide gap when

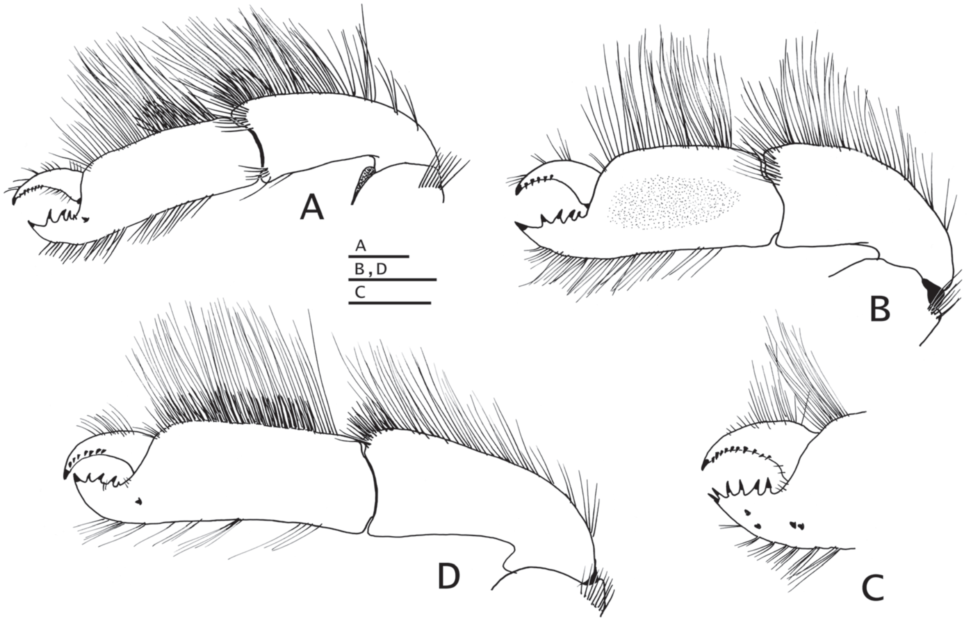

Figure 14. A *Paguropsis typica* Henderson, 1888, male, 7.9 mm, MUSORSTOM 3, sta CP 90 (MNHN-IU-2014–9411) **B, C** *P. andersoni* (Alcock, 1899): B ovig female, 11.2 mm, [Locality uncertain], INVMAR, sta 17 (MNHN-IU-2014–9412), C male, 15.2 mm, Indonesia, KARUBAR, sta CP 46 (USNM 1442005) **D** *P. confusa* sp. n., holotype male, 13.6 mm, Philippines, PANGLAO 2005, sta CP 2331 (NMCR 50015). **A, B, D** Left chela and carpus of pereopod 4, lateral **C** dactyl and fixed finger. Scale bars: 1 mm (**A**), 2 mm (**B, D, C**).

closed, each terminating in sharp, inwardly curved corneous claw crossing when closed. Dactyl strongly curved inward, dorsal margin with row of short setae; cutting edge with ventrolateral distal row of up to 8 small corneous-tipped spines (in addition to corneous claw). Fixed finger curving inward, cutting edge with 3 or 4 strong corneous-tipped spines (in addition to corneous claw) arranged like bear claw; lateral face usually with 1–4 minute scale-like corneous spines near base of finger. Palm straight, ca. 2.1 as long as high; dorsal margin with 2 interspersed fringes of setae, 1 of short thick setae and 1 of long thin setae; ventral margin with tufts of setae continued sparsely on fixed finger. Carpus unarmed except for fringe of long setae on dorsal margin, and fringe of short thick setae on dorsodistal angle of lateral face; with scattered short setae ventrally. Merus 0.5–0.6 times as long as meri of pereopod 2 and pereopod 3, respectively. Sternite XII (Fig. 11C) weakly divided medially, each side with fringe of long dense setae.

Pereopod 5 (Fig. 12C) with chela ca. 0.6 times as long as merus, with long, brush-like setae on dorsal and ventral surfaces; merus and carpus each with dorsal and ventral row of long setae. Dactyl with propodal rasp on ventral face. Propodal rasp consisting of minute, ovate scales, occupying 0.2 length of propodus. Ischium with setae dorsally and ventrally. Coxa with fringe of long bristle-like setae on rounded ventromesial distal angle.

Male gonopod 1 with inferior lamella armed on distal margin with posterior row of slender, semitransparent hook-like spines, and 2–4 anterior irregular rows of small, straight or slightly curved corneous spines. Gonopod 2 with distal segment strongly twisted distally, densely setose; usually with unpaired, reduced pleopods 3–5 on left side or less frequently on right side, as follows: biramous pleopods 3 and 4, and uniramous, vestigial pleopod 5 (see "Variations").

Female with unpaired pleopods 2–5 on left side or less frequently on right side, as follows: pleopods 2–4 biramous, well developed, and reduced biramous or uniramous and vestigial pleopod 5 (see "Variations"). Brood pouch large, subquadrate, distal margin scalloped and fringed with setae.

Uropodal exopods (Fig. 12D) slender, broadly curved, terminating in strong spine, anterior margin with fringe of long setae and row of well-spaced corneous-tipped spines; endopods short, strongly curved, anterior margin with long setae and 1 or 2 irregular rows of corneous-tipped spines; protopods with strong, ventrally curved proximal spine.

Telson (Fig. 12D) subrectangular, wider than long; posterior lobes separated by weak shallow median cleft, terminal margins unarmed except for fringe of long setae.

Genetic data. See Table 1.

Color (Figs 8D, 28C, D). Shield light orange except for pink medial area just posterior to rostrum. Ocular peduncles light orange except for white proximal margins and white distal margins bordering black corneas; ocular acicles mostly light orange except for white distal margins and white distal spine. Antennules light orange, flagella of similar but darker color than peduncle. Antennal peduncles light orange, and similar but lighter toned and somewhat transparent flagella. Chelipeds with white spines and tubercles; chelae white except for light orange proximally on dorsal surface of palms and near bases of dactyls and fixed fingers; carpi orange; meri with reddish dorsal margins, and two short dark red stripes on distolateral and distomesial margins. Pereopods 2 and 3 with white except as follows: dactyls each with orange stripe on lateral face interrupted at proximal one-fifth; propodi each with two broad orange bands (fading dorsally and ventrally), one band on lateral face proximally and another distally; carpi each with orange portion dorsodistally, ventrally, and proximally; meri each with light orange dorsal and ventral margins, and short orange band laterodistally; ischium with light orange dorsal margin.

Etymology. The specific name is derived from the Latin feminine singular of *confuso,* meaning confusion or disorder, and in reference to the state of morphological confusion that had prevented the unmasking of this and other new species under the name *P. typica*.

Distribution. Western Pacific: from Philippines, South China Sea, and Indonesia (Kalimantan) on the Macassar Strait. Western Indian Ocean: Mozambique Channel to off Durban, South Africa. Depth: 150 to 403 m.

Habitat and symbiont. Found with indeterminate species of acontiate anemone (see "Remarks" under genus).

Variations. Among the 31 males and 16 females examined, 99% of males had pleopods 3–5 on the left side, and 37.5% of females had pleopods 2–5 on the left side. There is no other appreciable morphological variation other than that incorporated in the description.

Affinities. This new species is superficially similar to *P. andersoni*, from which it differs drastically in coloration and several other characters. Generally, *P. confusa* sp. n. has a delicate morphology, in particular the less strongly armed chelipeds and slenderer pereopods 2 and 3 than in *P. andersoni* (see Figs 10A–D, 13A–D). The proximal one-third of the lateroproximal surface of the dactyl of pereopod 3 is weakly or indistinctly concave, whereas the lateroproximal surface is has a distinctly marked concavity in *P. andersoni*. The coxae of pereopods 3 are narrowly separated from each other in both species (by 0.2 ventral length of 1 coxa), but the posterior lobes of sternite XI (Figs 5D, 11C) are noticeably less compressed in *P. confusa* sp. n. than in *P. andersoni*. The discovery of the drastically different coloration patterns of these two species made possible, in part, the morphological separation of the two (compare Figs 8C, D, 28C, D).

Paguropsis gigas **sp. n.**

http://zoobank.org/81B16E94-F229-40C9-93AE-4CBA72D252C7
Figs 15–17, 18A, Table 1

Type material. Holotype: male 23.0 mm, South China Sea, NANHAI 2014, cruise OR 5, sta DW 4105, 13°57.8902'N, 115°25.5073'E, 297–565 m, 3 Jan 2014 (NTOU A01445).

Paratype. 1 ovig female 20.5 mm, same sta data as holotype (NTOU A01446).

Description. *Shield* (Figs 15A, 18A) subtriangular, ca. 1.3 times as long as broad; dorsal surface glabrous except for setae anterolaterally and transverse fringe of short setae on sloping anterior margins of gastric region; anterior margin between rostrum and lateral projections concave; lateral projections broadly triangular, each terminating in small spine; posterior margin roundly truncate; lateroventral distal angle produced into strong blunt spine adjacent to proximal margin of first antennal segment. Rostrum (Fig. 15A) acutely triangular, arched dorsally, strongly produced and extending to distal margin of ocular acicles; with distinct rounded dorsal longitudinal ridge having few short setae laterally, and ending in blunt subterminal spine. Branchiostegite unarmed except for 1 spine on dorsodistal angle of anterodorsal plate, and setose distal margin.

Ocular peduncles ca. 0.4 length of shield, constricted medially, glabrous except for dorsal longitudinal row of short setae; corneas strongly dilated, diameter 0.5 total peduncular length (including the cornea). Ocular acicles small, triangular, each terminating in blunt, setose distal spine directed anteriorly.

Antennular peduncles when fully extended overreaching distal margins of corneas by nearly full length of ultimate peduncular segment; ultimate and penultimate segments glabrous or at most with scattered short setae; basal segment with ventromesial tuft of setae distally; lateral face with distal subrectangular lobe, and setose lobe proximally.

Antennal peduncles overreaching distal corneal margins by ca. 0.2 length of ultimate segments. Fifth and fourth segments unarmed, nearly glabrous except for scattered

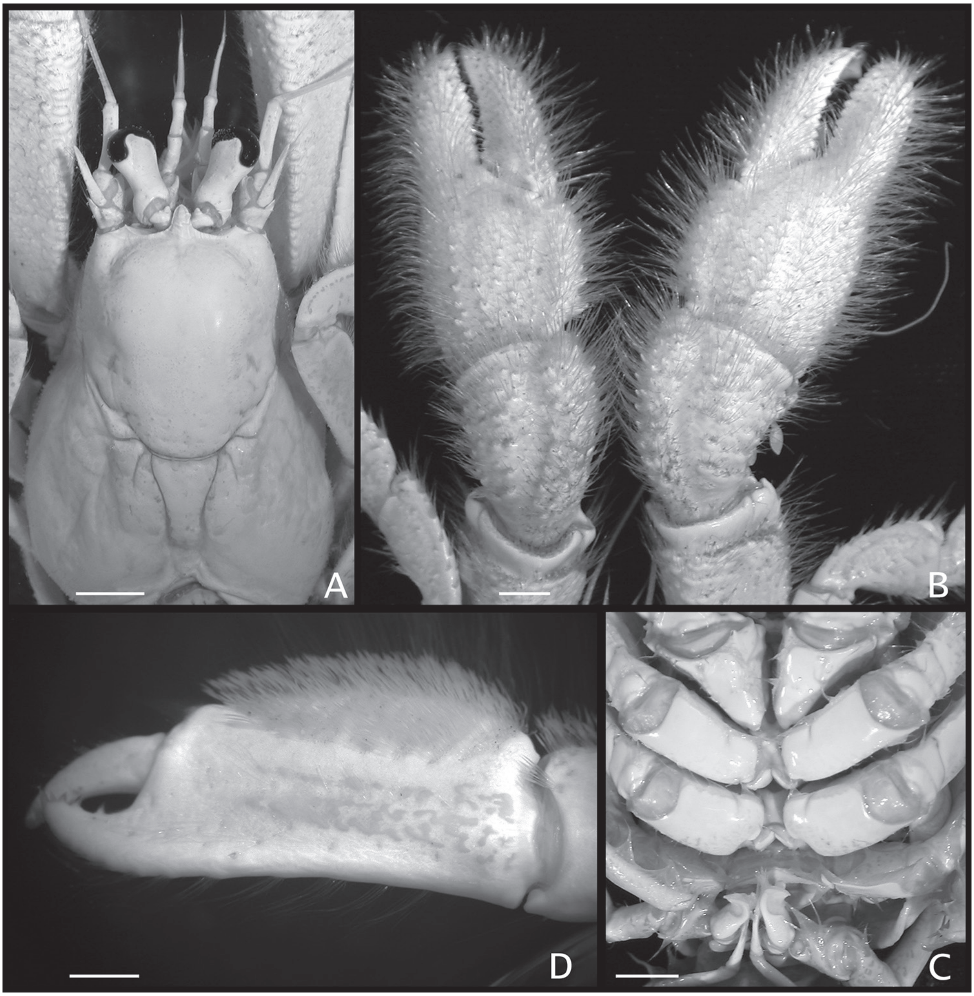

Figure 15. *Paguropsis gigas* sp. n., holotype male, 23.0 mm, South China Sea, TAIWAN, sta DW 4105 (NTOU A01445). **A** shield, cephalic appendages, and posterior carapace, dorsal **B** chelae and carpi of chelipeds, dorsal **C** coxae of pereopods 1–5, and sternites IX–XIII, ventral **D** chela of left pereopod 4, lateral. Scale bars: 6 mm (**A–C**), 2 mm (**D**).

short setae. Third segment with setose spine at ventrodistal angle. Second segment with dorsolateral distal angle produced, terminating in small simple or bifid spine; mesial margin rounded, setose, and small spine on dorsomesial angle. First segment unarmed except for moderately long setae on lateral face. Antennal acicle almost reaching distal margin of cornea, slender, nearly straight and terminating in sharp spine, with long setae dorsomesially and distally. Antennal flagellum reaching to midpoint of chelae, with few short setae less than one article in length.

Mouthparts not markedly different from those described for *Paguropsis typica* (see Fig. 4A–F). Maxilliped 3 with exopod 4.0 times as long as broad.

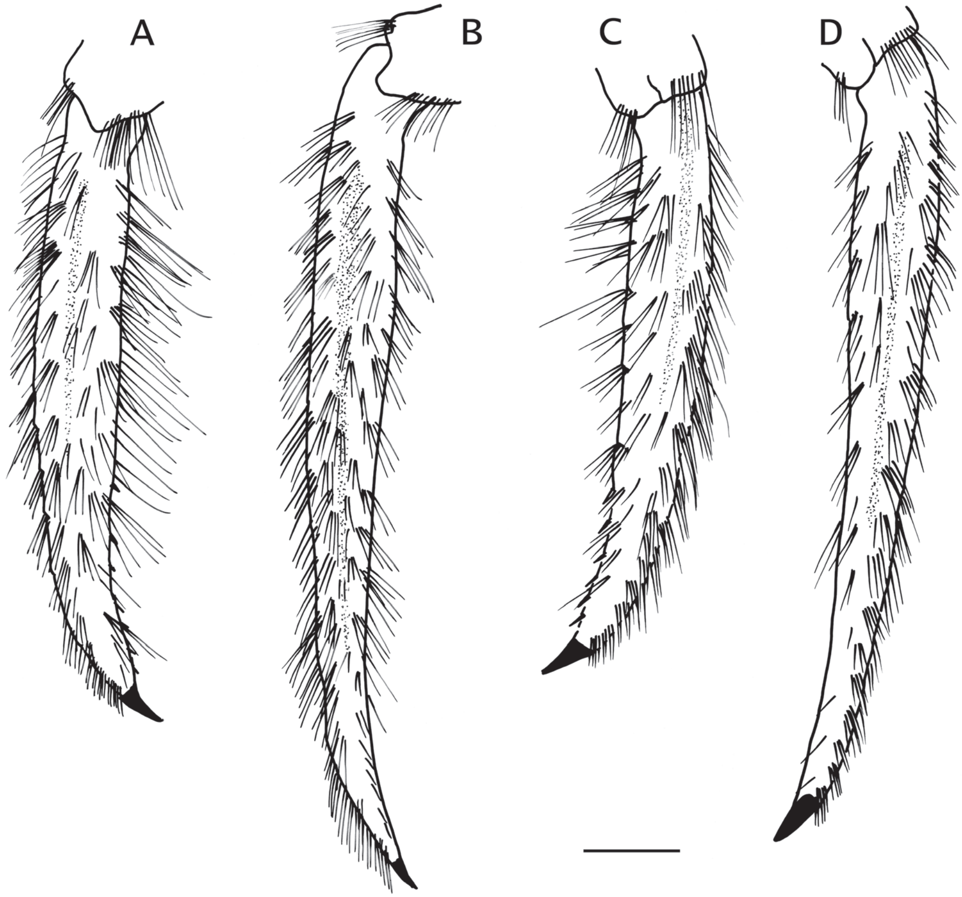

Figure 16. *Paguropsis gigas* sp. n., holotype male, 23.0 mm, South China Sea, TAIWAN, sta DW 4105 (NTOU A01445). **A, B** dactyl of right pereopod 2 (**A**) and pereopod 3, mesial (**B**) **C, D** dactyl of left pereopod 2 (**C**) and pereopod 3 (**D**), mesial. Scale bar: 5 mm.

Chelipeds (Figs 15B, 18A) subequal, similar in armature and setation; dorsal surfaces of chelae and carpi covered with dense tufts or short rows of long, bristle-like setae nearly obscuring armature below; ventral surfaces of palms with well-spaced tufts of long bristle-like setae, otherwise smooth except for few low tubercles or blunt spines ventrolaterally and ventromesially. Fingers with narrow hiatus proximally, forming spoon-like shape in ventral view when closed; each finger terminating in small curved corneous claw and subdistal blunt calcareous tooth ventral to claw, both claws and teeth interlocking when fingers closed; cutting edge of dactyl with terminal row of small, fused corneous teeth on distal one-third, and row of blunt calcareous teeth on proximal two-thirds and decreasing in size distally; cutting edge of fixed finger with row of blunt calcareous teeth decreasing in size distally. Dactyl 1.4–1.7 times as long as palm; dorsal surface convex, with numerous tufts of long bristle-like setae, and few small blunt spines or tubercles on rounded mesial surface; ventral surface with less dense tufts of bristle-like setae, lacking spines. Fixed finger with dorsal, lateral, and ventral surfaces similar to dactyl in armature. Palm ca. 0.7 times as long as carpus, dorsal surface convex, covered with numerous small blunt to sharp spines arranged in more or less longitudinal rows each with tufts of long setae; dorsomesial margin with 2–4 irregular rows of spines each with tufts of long setae; dorsolateral margin rounded, not delimited, with irregular rows of small tubercles or spines each with long setae. Carpus 0.5–0.6 times length of merus; dorsal and dorsolateral surfaces with well-spaced spines or short transverse rows of 2 or 3 small spines each bearing tufts of long setae, with longitudinal smooth area medially; dorsolateral margin rounded; dorsomesial margin with irregular rows of spines each bearing tufts of long setae; mesial surface with short transverse rows of bristle-like setae on dorsal half, otherwise smooth; ventral surface smooth, with fringe of long setae on ventrodistal margin. Merus subtriangular in cross-section, nearly as long as chela; dorsal margin with row of low protuberances each bearing transverse row of 2 or 3 small tubercles and bearing tuft of long setae; ventromesial and ventrolateral margins each with irregular row of spines with tufts of long setae; lateral and mesial surfaces with tufts of long and short setae; ventral margin smooth except for moderately dense bristle-like setae. Ischium with row of small spines on ventrolateral margin. Basis with ventromesial row of long setae. Coxa with short, weakly marked longitudinal fissure (Fig. 15C) near distal margin.

Pereopods 2 and 3 (Fig. 16A–D) similar in armature and setation, distinctly dissimilar in length, with pereopod 2 shorter than pereopod 3 (particularly dactyls). Dactyls ca. 1.4 (pereopod 2) or 1.8 (pereopod 3) times as long as propodi; nearly straight except for slightly incurved distal portion, terminating in sharp corneous claw; lateral and mesial faces with shallow longitudinal concavity; all surfaces covered with tufts of bristle-like setae often arranged in oblique rows; ventromesial margin with distal row of minute corneous spinules (pereopod 2) or lacking armature (pereopod 3) except for setae. Propodi 1.4 (pereopod 2) or 1.2 (pereopod 3) times as long as carpi; dorsolateral and ventrolateral surfaces with tufts or rows of tufts of long bristle-like setae; mesial face with scattered setae. Carpi unarmed except for scattered setae laterally and mesially, tufts of short setae dorsally, and distolateral fringe of long setae. Meri with fringe of long setae on ventral margins; ventral margin of merus of pereopod 2 with row of small blunt spines hidden by setae. Ischia unarmed except scattered setae on lateral face of pereopod 2. Coxae with ventromesial margin sparsely setose; coxae of pereopods 3 (Fig. 15C) narrowly separated by 0.2 ventral length of 1 coxa. Sternite XI (Fig. 15C) having anterior lobe flat or weakly concave; posterior lobes each with transverse fringe of setae.

Pereopod 4 (Figs 15D, 17A) with chela as long as or slightly shorter than carpus, ca. 2.2 times as long as high. Dactyl and fixed finger leaving wide gap when closed, each terminating in sharp, inwardly curved corneous claws crossing when closed. Dactyl strongly curved, dorsal margin with row of short setae; cutting edge with ventrolateral distal row of 4 or 5 small corneous-tipped spines (in addition to corneous claw). Fixed finger curving inward, cutting edge with 4 strong corneous-tipped spines (in addition to corneous

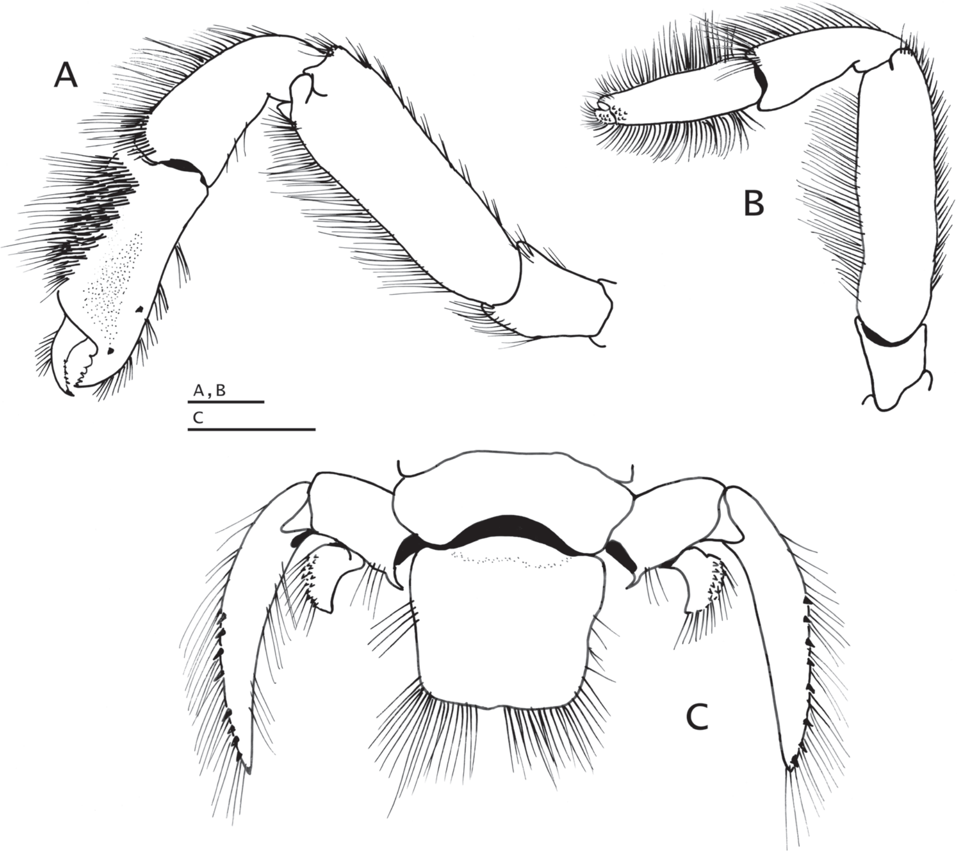

Figure 17. *Paguropsis gigas* sp. n., holotype male, 23.0 mm, South China Sea, TAIWAN, sta DW 4105 (NTOU A01445). **A** left pereopod 4, lateral **B** left pereopod 5, lateral **C** uropods and telson, dorsal. Scale bars: 1 mm (**A, B**), 3 mm (**C**).

claw) arranged like bear claw; lateral face usually with 1–4 minute scale-like corneous spines near base of finger. Palm straight, broad, ca. 1.6 times as long as high, lateral face weakly concave medially; dorsal face with long simple setae in addition to prominent dense patch of thin capsulate setae arranged in oblique fringes and occupying oval area from dorsal margin to midlength of lateral face; ventral margin with sparse tufts of short setae continuing on fixed finger. Carpus unarmed except for long setae on dorsal margin, and short oblique fringes of thin capsulate setae on dorsodistal angle of lateral face, and scattered short setae ventrally. Merus 0.5 or 0.6 times as long as meri of pereopod 2 and pereopod 3, respectively. Sternite XII with fringe of long dense setae (Fig. 15C).

Pereopod 5 (Fig. 17B) with chela as long as carpus and 0.7 times as long as merus, with long, brush-like setae on dorsal and ventral surfaces; merus and carpus each with dorsal and ventral row of long setae. Dactyl with rasp on ventral face. Propodal rasp consisting of minute, ovate scales, occupying 0.2 length of propodus. Ischium with setae dorsally and ventrally. Coxa with fringe of long bristle-like setae on rounded ventromesial distal angle.

Male gonopod 1 with inferior lamella armed on distal margin with posterior row of slender, semitransparent hook-like spines, and 2–4 anterior irregular rows of small, straight or slightly curved corneous spines. Gonopod 2 with distal segment strongly twisted distally, densely setose. In only known male, left side with biramous, reduced pleopods 3 and 4, and uniramous vestigial pleopod 5; right side with uniramous vestigial pleopod 3 and lacking pleopods 4 and 5.

Female (only one specimen known) with unpaired left pleopods 2–4 well developed, lacking pleopod 5. Brood pouch large, subquadrate, distal margin strongly scalloped and fringed with setae.

Uropodal exopods (Fig. 17C) slender, broadly curved, terminating in strong spine, anterior margin with fringe of long setae and row of well-spaced corneous-tipped spines; endopods short, strongly curved, anterior margin with long setae and 1 or 2 irregular rows of corneous-tipped spines; protopods with strong, ventrally curved proximal spine.

Telson (Fig. 17C) slightly subrectangular, broader than long; posterior lobes obscurely divided medially, terminal margins unarmed except for fringe of long setae.

Genetic data. See Table 1.

Color (Fig. 18A). Shield light orange except for white anterior margins. Ocular peduncles orange dorsally except for white near cornea and proximally, otherwise white; corneas black; ocular acicles light orange except for white distal spine and margins. Antennules orange, flagella of similar but darker color than peduncle. Antennal peduncles with fifth segment light orange on dorsal and lateral surfaces, otherwise white; acicle with tinge of light orange distally; flagella light orange. Chelipeds with yellow bristle-like setae; chelae very light orange to cream; meri and carpi orange except for white spines and tubercles, and white portion of ventrolateral and ventromesial distal margins of meri. Pereopods 2 and 3 generally orange except for white on proximal margins of ischia, distal margins of meri, carpi and propodi, and distal 0.3 of dactyls; meri each also with small white patch proximally on lateral faces. Pereopods 4 and 5 orange.

Etymology. The specific epithet is from the Latin *gigas*, meaning giant, used as a noun in apposition, and in reference to the large size attained by individuals of this new species.

Distribution. Western Pacific: known so far only from the South China Sea. Depth: 297 to 565 m.

Habitat and symbiont. Found with indeterminate species of acontiate anemone (see “Remarks” under genus).

Variations. With only two specimens known, no variations can be evaluated.

Affinities. *Paguropsis gigas* sp. n. shares with *P. lacinia* sp. n. the presence of a prominent patch of dense, capsulate setae on the dorsolateral face and dorsal margin of the palm of the chelae of pereopod 4. The shape and arrangement of the setae on the patch, however, is quite different in both species. In *P. gigas* sp. n., the capsulate setae are relatively short and arranged in a series of oblique fringes that occupy and oval area from the dorsal margin to midlength of the lateral face of the palm (Figs 15D, 17A). In *P. lacinia* sp. n., the capsulate setae are narrow and long, not arranged in rows, and occupy only one-third of the lateral surface of the palm (Figs 21B, C, 22F). The ultrastructure of these setae has not been studied, but they appear to be hollow and filled with a light

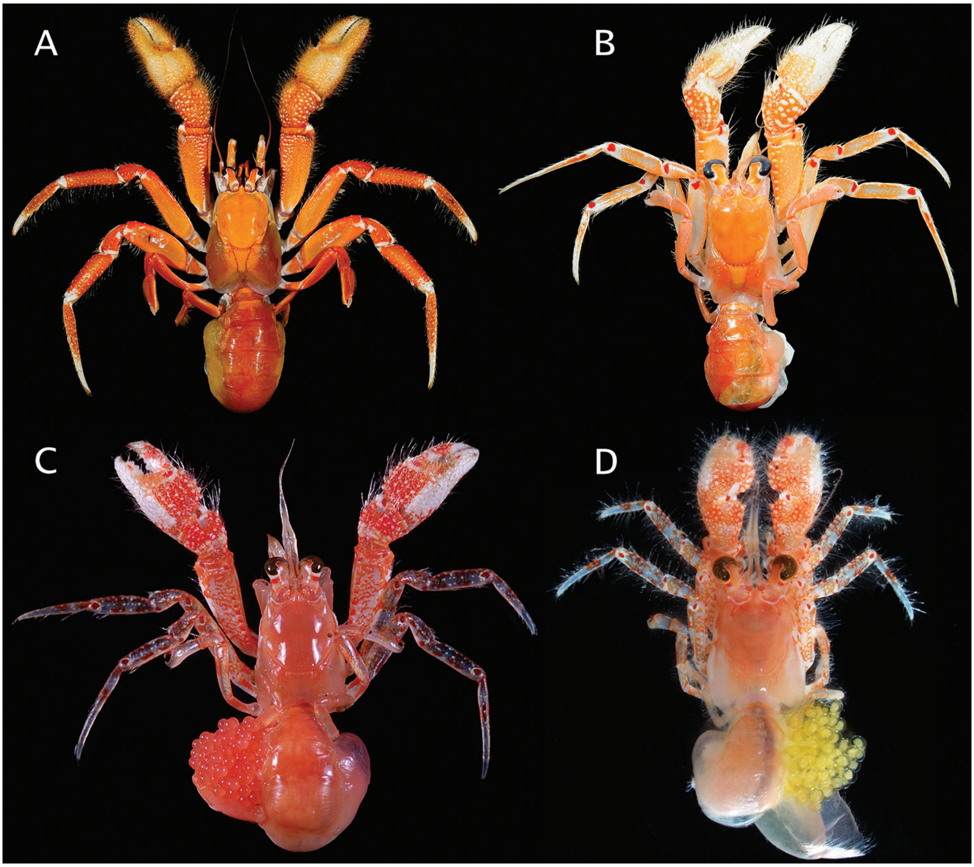

Figure 18. Habitus: **A** *Paguropsis gigas* sp. n., holotype male, 23.0 mm, South China Sea, NANHAI 2014, sta DW 4105 (NTOU A01445) **B** *Paguropsis lacinia* sp. n., paratype female, 9.8 mm, Papua New Guinea, PNG, sta CP 4254 (MNHN-IU-2013-2288) **C** *Paguropsina pistillata* gen et sp. n., ovig female, 4.2 mm, Philippines, PANGLAO, sta T37 [#08] (LKCNHM ZRC) (photograph: T-Y Chan) **D** *Paguropsina inermis* gen et sp. n., female, 2.5 mm, Japan, Ogasawara Islands, (CBM-ZC 14206) (photograph: T Komai).

brown fluid (at least in preserved specimens). The function, if any, of these setae is unknown, although conceivably they could be used for feeding or grooming. The presence of this unusual patch in these two species might suggest a close phylogenetic relationship. However, in other morphological characters these two species differ substantially, and thus the presence in both of a patch appears to reflect homoplasy. The two species differ also as follows: growth patterns, with specimens of *P. gigas* sp. n. reaching a much larger size than those of *P. lacinia* sp. n.; stronger spination of chelipeds, and denser setation of chelipeds and pereopods 2 and 3 in *P. gigas* sp. n. than in *P. lacinia* sp. n.; dactyls more robust and wider in *P. gigas* sp. n. than in *P. lacinia* sp. n., 7–9 times as long as broad in the former vs. 10–16 times as long as broad in the latter; and once again, as in other species of *Paguropsis*, drastically different coloration patterns (Fig. 18A, B).

Remarks. Among the species discussed in this revision, *Paguropsis gigas* sp. n. and *P. andersoni* are similar in that they grow to the largest size, the former reaching a shield length of 23.0 mm, the latter to a shield length of 20.6 mm. Morphologically they are also generally similar, both having strong, dense spination and bristle-like setation on the chelipeds, and numerous tufts of bristle-like setae on pereopods 2 and 3. The lateral surfaces of the dactyls of pereopods 2 and 3 are concave in both species, although only moderately so and along the proximal half or more of the segment in *P. gigas* sp. n., whereas the concavity is strongly marked along the proximal one-third in *P. andersoni*. Despite these similarities, *P. gigas* sp. n. differs markedly from *P. andersoni*, the former having a prominent dense patch of thin capsulate setae arranged in oblique fringes on the dorsal margin and dorsolateral face of the palm of the chelate pereopod 4, whereas in the latter there is no patch of setae and only a fringe of long setae on the dorsal margin of the palm. Furthermore, in *P. gigas* sp. n. the palm of pereopod 4 is often more noticeably lateromesially flattened than in *P. andersoni*, although there is some variation in this character in both species. The coloration of the ocular peduncles, chelipeds, and pereopods is also clearly different in these two species (compare Figs 8C, 18A).

***Paguropsis lacinia* sp. n.**

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Figs 18B, 19, 20, 21A–C, 22, Table 1

Type material. Holotype: female 8.4 mm, Solomon Islands, SALOMON 2, NO *Alis*, NW of Isabel Island, sta CP 2201, 07°43.5'S, 158°29.9'E, 307–310 m, 25 Oct 2004 (USNM 1442006).

Paratypes. *Papua New Guinea*: MADEEP, NO *Alis*: NW of Kavieng, sta CP 4254, 02°28'S, 150°42'E, 273–324 m, 24 Apr 2014: 1 female 9.8 mm, color photograph (Fig. 18B) (MNHN-IU-2013–2288).

Salomon Islands: SALOMON 1, NO *Alis*: N Buena Vista Island, sta DW 1765, 08°43'S, 160°07'E, 325–380 m, 27 Sep 2001: 1 female 6.1 mm (MNHN-IU-2014–9370); NW of San Cristobal, sta CP 1831, 10°12'S, 161°19'E, 135–325 m, 5 Oct 2001: 1 ovig female 10.3 mm (MNHN-IU-2014–9367).

Tonga Islands: BORDAU 2, NO *Alis*: NW of Tongatapu, sta CP 1643, 21°05'S, 175°22'W, 487 m, 22 Jun 2000: 1 male 7.3 mm, 1 female 7.2 mm (MNHN-IU-2014–9366).

New Caledonia: NORFOLK 1, NO *Alis*: Norfolk Ridge, Crypthelia Bank, sta CP 1731, 23°21'S, 168°16'E, 310–788 m, 27 Jun 2001: 1 male 8.5 mm (MNHN-IU-2014–9360). NORFOLK 2, NO *Alis*: Munida Bank, sta DW 2142, 23°01'S, 168°17'E, 550 m, 3 Nov 2003: 2 males 6.7, 6.8 mm (MNHN-IU-2014–9389). EBISCO, NO *Alis*: W of Bellona, sta CP 2551, 21°06'S, 158°35'E, 637–650 m, 11 Oct 2005: 1 male 7.8 mm (USNM 1442007).

Description. *Shield* (Figs 18B, 19A) weakly subtriangular (lateral margins subparallel on anterior two-thirds), 1.2 times as long as broad; dorsal surface glabrous except

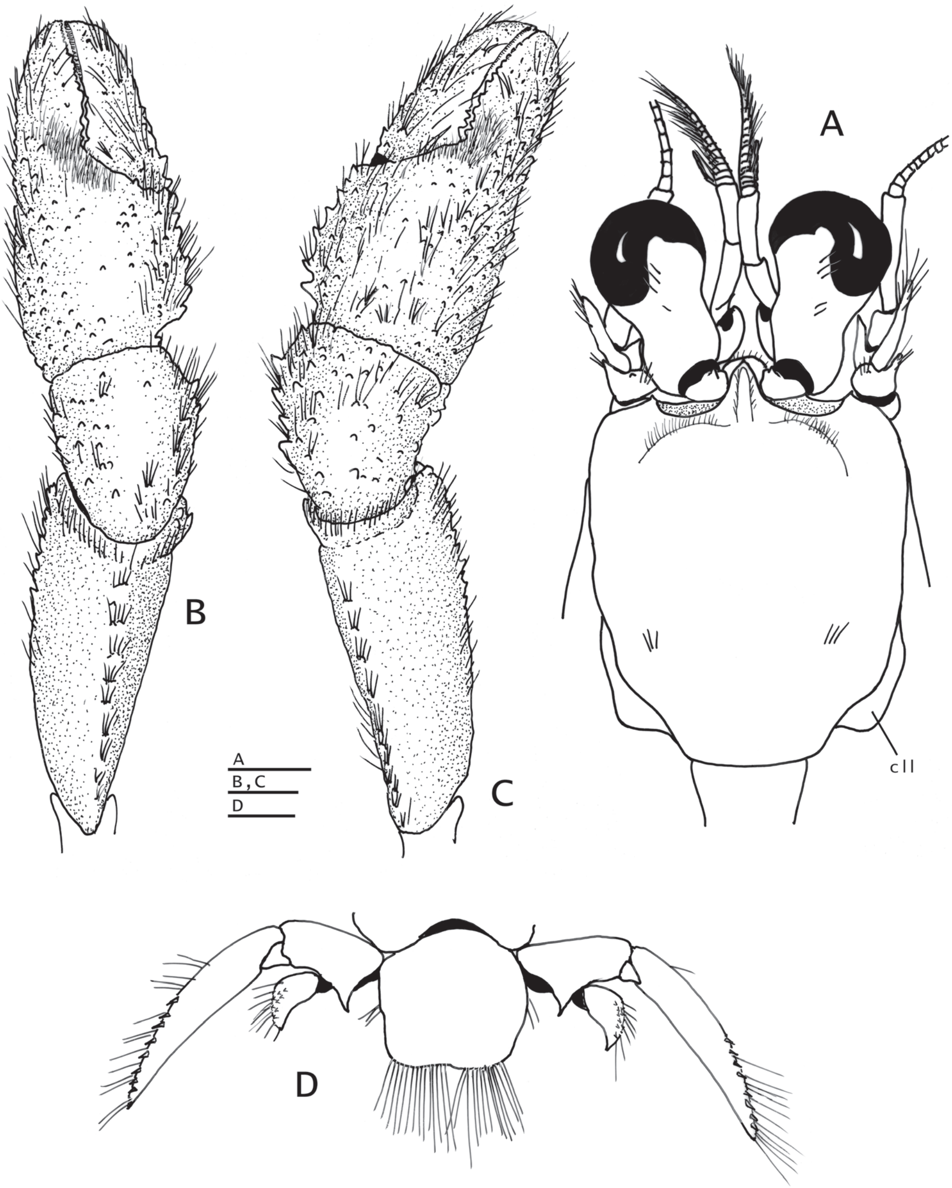

Figure 19. *Paguropsis lacinia* sp. n., holotype female, 8.4 mm, Solomon Islands, SALOMON 2, sta CP 2201 (USNM 1442006): **A** shield and cephalic appendages, dorsal **B** left cheliped, dorsal **C** right cheliped, dorsal **D** uropods and telson, dorsal. Abbreviations: cll, carapace lateral lobe. Scale bars: 2 mm (**A**), 2 mm (**B, C**), 1 mm (**D**).

for tufts of setae anterolaterally and transverse fringe of short setae on sloping anterior margins of gastric region; anterior margin between rostrum and lateral projections concave; lateral projections broadly triangular, each terminating in small spine; pos-

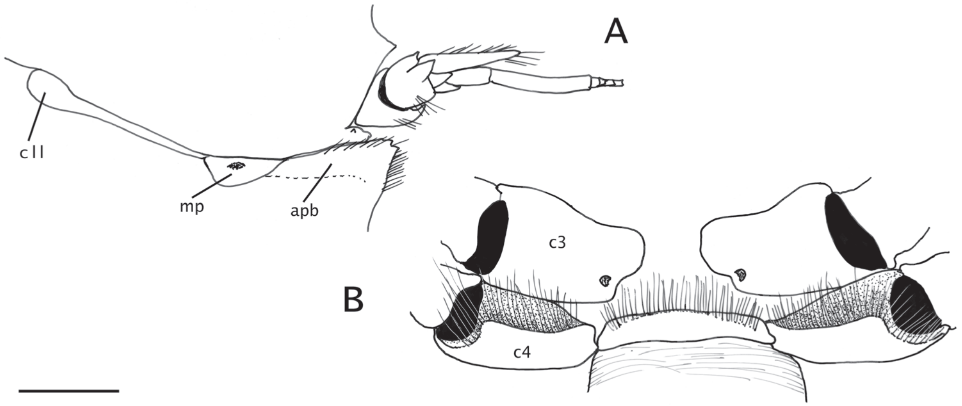

Figure 20. *Paguropsis lacinia* sp. n. holotype female, 8.4 mm, Solomon Islands, SALOMON 2, sta CP 2201 (USNM 1442006). **A** right antennal peduncle, branchiostegite, and anterodorsal portion of posterior carapace, lateral **B** coxae of pereopods 3 and 4 and sternites XI and XII. Abbreviations: apb, anterodorsal plate of branchiostegite; cll, carapace lateral lobe; mp, median plate; C3, C4, coxae of pereopods 3 and 4. Scale bar: 2 mm.

terior margin relatively wide, roundly truncate; lateroventral distal angle with strong spine adjacent to proximal margin of first antennal segment. Rostrum acutely triangular, arched, and curving ventrally, extending nearly to distal margin of ocular acicles, terminating in small spine; with distinct rounded dorsal longitudinal ridge with fringe of short setae laterally, and terminating subdistally in rounded tip. Branchiostegite (Fig. 20A) unarmed except for 1 or 2 minute tubercles on dorsodistal angle of anterodorsal plate, and setose distal margin.

Ocular peduncles stout, constricted medially and broadening distally, ca. 0.5 length of shield, glabrous except for row of few short dorsodistal setae; corneas strongly dilated, diameter 0.5–0.6 total peduncular length (including the cornea). Ocular acicles small, triangular, armed with distal or dorsodistal spine often directed anteriorly or anterodorsally.

Antennular peduncles when fully extended overreaching distal margins of corneas by nearly full length of ultimate peduncular segments. Ultimate and penultimate segments glabrous or at most with scattered short setae. Basal segment with ventromesial setae distally; lateral face with distal subrectangular lobe with or without small tubercles, small medial spine, and setose lobe proximally.

Antennal peduncles reaching or at most slightly exceeding distal margin of corneas. Fifth and fourth segments unarmed except for scattered short setae and laterodistal tuft of long setae. Third segment with strong spine at ventrodistal angle. Second segment with dorsolateral distal angle produced, terminating in small simple spine; mesial margin rounded, setose, and small spine on dorsomesial angle. First segment unarmed. Antennal acicle reaching to proximal margin of cornea, slender, terminating in sharp spine, with long setae distally, at most with 1 or 2 minute proximal tubercles on mesial margin. Antennal flagellum long, reaching to distal end of cheliped fingers, articles with 1 or 2 short setae (< 1 article in length) and usually with 1 or 2 long setae every 12 articles or so.

Mouthparts not markedly different from those described for *Paguropsis typica* (see Fig. 4A–F). Maxilliped 3 with exopod ca. 4.2 times as long as broad.

Chelipeds (Figs 18B, 19B, C) subequal, similar in armature and setation; dorsal surfaces of chelae and carpi moderately covered with short bristle-like setae not obscuring armature below, setation somewhat denser near base of fixed finger and distal portion of palm; ventral surfaces of chelae and carpi with scant setae or tufts of setae, and scattered small tubercles. Dactyl and fixed finger with narrow hiatus proximally when closed, forming spoon-like shape in ventral view when closed; each terminating in small curved corneous claw and subdistal blunt calcareous tooth ventral to claw, both claws and teeth interlocking when fingers closed; cutting edge of dactyl with terminal row of small, fused corneous teeth on distal one-third, and row of unequal calcareous teeth on proximal two-thirds; cutting edge of fixed finger with row of blunt calcareous teeth decreasing in size distally. Dactyl 1.4 times as long as palm; dorsal surface convex, armed with small spines or tubercles; dorsomesial margin rounded, armed with small spines or tubercles; ventral face with well-spaced tufts of long bristle-like setae, lacking spines. Fixed finger with dorsal, lateral and ventral surfaces similar to dactyl in armature. Palm slightly shorter than carpus, dorsal surface with scattered small tubercles medially, dorsolateral margin rounded, not delimited, with irregular rows of small spines or tubercles, dorsomesial margin with row of strong spines. Carpus ca. 0.6 times length of merus; dorsal and dorsolateral surfaces with well-spaced small spines or tubercles; dorsomesial margin with row of strong spines or tubercles, and small dorsodistal spine; dorsolateral margin rounded, not delimited; mesial surface smooth, unarmed except for setae on distal margin; ventral surface unarmed, ventrodistal margin with fringe of sparse long setae. Merus nearly as long as chela, subtriangular in cross-section; dorsal margin with row of protuberances accompanied by tufts of short setae, ventromesial and ventrolateral margins each with irregular row of spines with setae; lateral and mesial surfaces unarmed except for scattered short setae. Ischium with row of small spines on ventrolateral margin. Basis with ventromesial row of setae. Coxa with well-marked longitudinal fissure (Fig. 21A) on ventral surface.

Pereopods 2 and 3 (Figs 18B, 22A–D) similar in armature and setation, distinctly dissimilar in length, with pereopod 2 shorter than 3. Dactyls ca. 1.7 (pereopod 2) or 2.4 (pereopod 3) times as long as propodi; dactyl of pereopod 2 broadly curved, terminating in sharp corneous claw, with ventromesial distal row of usually ten minute short spinules; dactyl of pereopod 3 slender, nearly straight in lateral view, 1.5–1.6 times as long as dactyl of pereopod 2, ventromesial margin unarmed; dorsal and ventral margins with tufts of moderately long setae. Propodi 1.3–1.4 times as long as carpi; dorsal and ventral surfaces with tufts of long setae. Carpi unarmed except for tufts of setae dorsally, dorsodistal angle blunt or with obscure small tubercle. Meri unarmed except for fringe of long setae ventrally. Ischia unarmed except for scattered short setae. Coxae with ventromesial row of setae. Coxae of pereopods 3 (Figs 20B, 21A) separated by ca. 0.3 ventral length of 1 coxa. Anterior lobe of sternite XI (between pereopods 3;

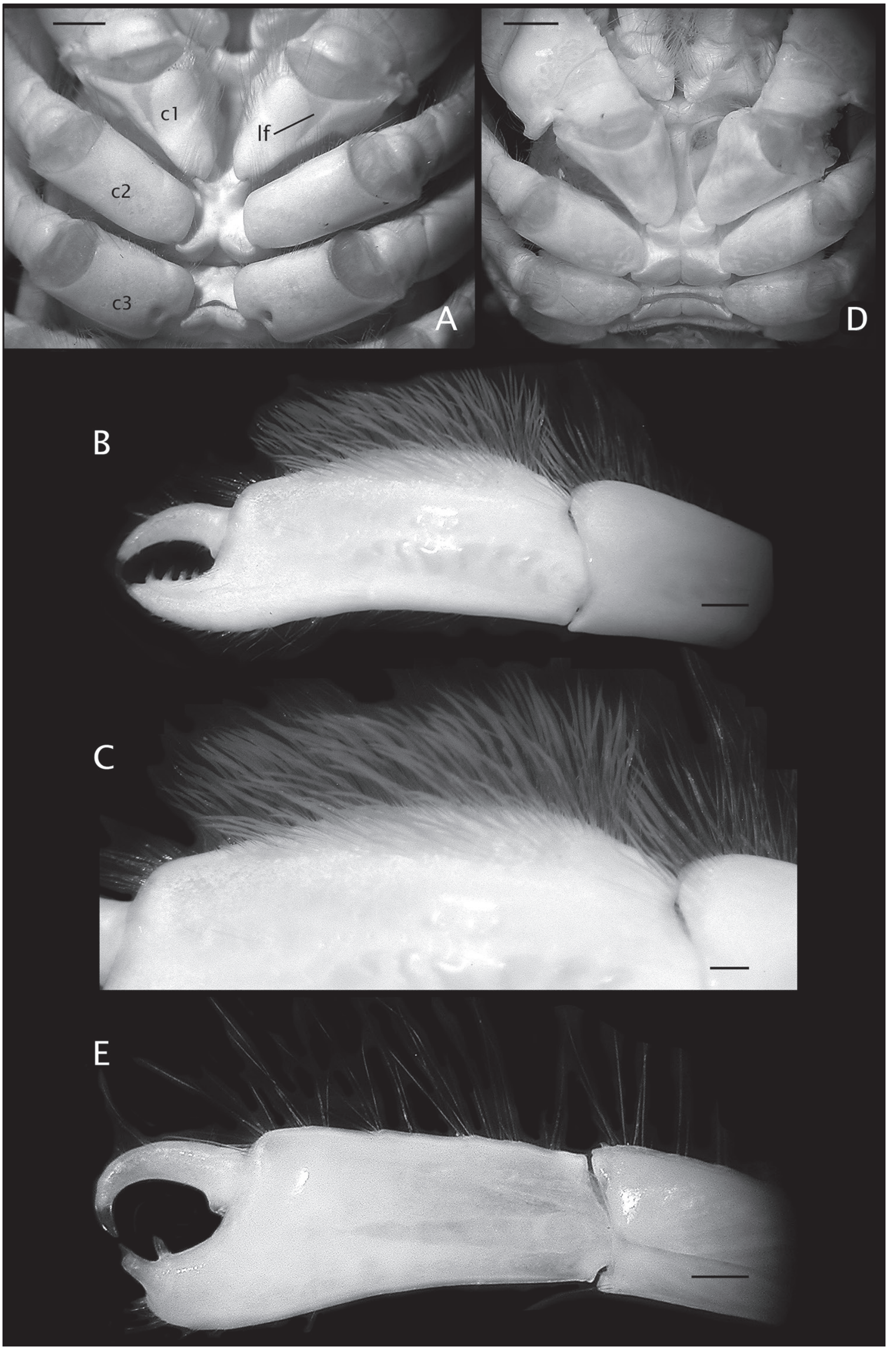

Figure 21. A–C *Paguropsis lacinia* sp. n., holotype female, 8.4 mm SALOMON 2, CP 2201 (USNM 1442006) **D, E** *Paguropsina pistillata* gen. et sp. n., holotype male, 4.4 mm New Caledonia, EBISCO, CP 2499 (USNM 1442008). **A, D** coxae of pereopods 1–3, and sternites IX–XI **B, E** chela of pereopod 4 **C** fringe of capsulate setae on dorsal surface of palm of pereopod 4. Abbreviations: C1–3, coxae of pereopods 1–3; lf, longitudinal fissure. Scale bars: 2 mm (**A**), 0.25 mm (**B, D**), 0.5 mm (**C**), 2 mm (**D**).

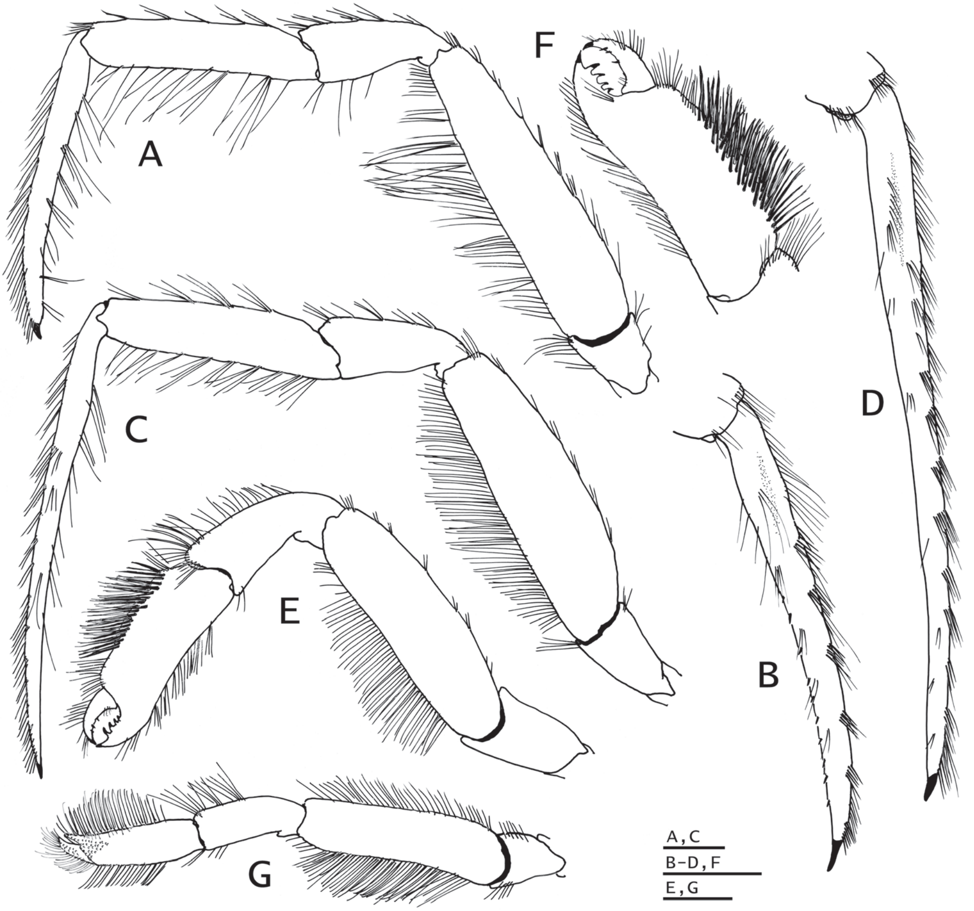

Figure 22. *Paguropsis lacinia* sp. n. holotype female, 8.4 mm, Solomon Islands, SALOMON 2, sta CP 2201 (USNM 1442006). **A** left pereopod 2, lateral **B** dactyl of same, mesial **C** left pereopod 3, lateral **D** dactyl of same, mesial **E** left pereopod 4, lateral **F** chela of same, lateral **G** left pereopod 5, lateral. Scale bars: 2 mm.

Fig. 21A) flat or slightly concave, unarmed, posterior lobes weakly arched, sloping, each with transverse fringe of sparse setae.

Pereopod 4 with chela (Fig. 21B) ca. 1.2 times as long as carpus and 1.7 times as long as high, palm 1.8–1.9 as long as high. Dactyl and fixed finger leaving wide gap when closed, each terminating in sharp, inwardly curved corneous claw crossing at tips when closed. Dactyl strongly curved inward, dorsal margin sparsely setose; cutting edge with ventrolateral row of usually 3 small corneous-tipped spines (in addition to corneous claw). Fixed finger curving inward, cutting edge with 4 strong corneous-tipped spines (in addition to corneous claw) arranged like bear claw; lateral face usually with 1 or 2 minute scale-like corneous spines near base of finger. Palm straight or slightly curved, dorsal face with prominent patch (Fig. 21B, C) of dense long, narrow capsulate setae extending for one-third of lateral surface. Carpus unarmed except for fringe of long setae dorsally and scattered setae ventrally. Merus ca. 0.7 times as long as meri of pereopods 2 and 3. Sternite XII (Fig. 20B) narrow, undivided or obscurely divided medially, with transverse fringe of long setae.

Pereopod 5 (Fig. 22G) with chela as long or slightly longer than carpus, and 0.7 times as long as merus. Chela with long, brush-like setae on dorsomesial and ventromesial face, Carpus with sparse tufts of setae on dorsal and ventral margins. Dactyl with rasp on ventral face. Propodal rasp weakly developed and consisting of minute, ovate scales, occupying 0.3 length of propodus. Ischium with setae dorsally and ventrally. Coxa with ventrodistal setae.

Male gonopod 1 with inferior lamella armed on distal margin with posterior row of slender, semitransparent hook-like spines, and 1 or 2 irregular rows of small straight or slightly curved corneous spines. Gonopod 2 with distal segment strongly twisted distally, densely setose. Pleon with left unpaired, reduced, biramous pleopods 3 and 4, lacking pleopod 5.

Female with left side having unpaired pleopods 2–4, and reduced biramous pleopod 5 (no unpaired pleopods 2–5 on right side). Brood pouch large, subquadrate, distal margin scalloped and fringed with setae.

Uropodal exopods (Fig. 19D) slender, nearly straight or broadly rounded, terminating in strong spine, anterior margin with fringe of long well-spaced setae and row of well-spaced corneous-tipped spines; endopods short, strongly curved, anterior margin with long setae and 1 or 2 irregular rows of corneous-tipped spines; protopods with strong, curved proximal spine.

Telson (Fig. 19D) subquadrate; posterior lobes separated by obsolete median cleft, terminal margins unarmed except for fringe of long setae.

Genetic data. See Table 1.

Color (Fig. 18B). Shield and calcified portion of posteromedian carapace evenly yellowish orange. Ocular peduncles yellowish orange except for white portions adjacent to corneas; corneas black; ocular acicles yellowish orange. Antennules and antennae light orange or pink, flagella of similar but darker color than peduncle but lighter. Chelipeds generally yellowish orange with white spines or tubercles; chelae proximally of lighter tone than rest of chelipeds, fading to nearly white or cream on dactyls and fixed fingers; carpi of darkest orange tone, ventromesial angle with reddish portion; meri light orange, with very short reddish stripe on distolateral and distomesial margin. Pereopods 2 and 3 with meri, carpi and propodi each with red spot distally on lateral face; dactyl light orange fading to white distally, and white dorsal margin; propodi and carpi light orange except for white distally around red spot; meri with light orange dorsal and ventral margins, otherwise white to cream except for red spot. Pereopod 4 more or less evenly orange except for white dactyl and fixed finger of chelae.

Etymology. The species name is from the Latin *lacinia*, a fringe, and refers to the characteristic setae of this new species on the dorsal margin of the palm of the chelate pereopod 4.

Distribution. Western Pacific: from off northern Papua New Guinea, Solomon Islands, Tonga Islands, and New Caledonia. Depth: 135 to 788 m.

Habitat and symbiont. Found with indeterminate species of acontiate anemone (see "Remarks" under genus).

Variations. No appreciable morphological variations were observed other than those incorporated in the description.

Affinities. See "Affinities" under *Paguropsis gigas* sp. n.

Remarks. The most prominent, distinctive morphological character of this species is the presence of a dense patch of capsulate, simple setae on the dorsal margin of the palms of pereopods 4 (Figs 21B, C, 22F), although a patch of capsulate setae is also present on the palm of pereopod 4 in *Paguropsis gigas* sp. n.. As noted under *P. gigas* sp. n., the extent and arrangement of the setae is different in these two species. The function, if any, of the patch is unknown. Furthermore, the unique coloration of *P. lacinia* sp. n., with pereopods 2 and 3 having meri, carpi and propodi each with a red spot distally on the lateral face (Fig. 18B), clearly distinguishes this species from other congeners.

Genus *Paguropsina* gen. n.

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Diagnosis. Thirteen pairs of quadriserial gills [no pleurobranchs on thoracomere VIII (last)], gills consisting of series of twin lamellae each deeply divided distally into finger-like extensions (e.g., Fig. 25E). Shield well calcified, subovate; dorsal surface somewhat vaulted. Rostrum prominent, subtriangular, arched, and dorsally ridged. Lateral projections of shield each terminating in short vertical keel-like ridge usually armed with few small spines. Branchiostegite with dorsal margin (e.g., Fig. 23B) divided into two calcified plates: one anterodorsal plate poorly delimited ventrally, followed by small, subtriangular plate with distinct central pit. Posterior carapace with well calcified posteromedian plate, and well calcified lateral lobe on each side adjacent to shield. Ocular peduncles stout, half length of shield; corneas strongly dilated (diameter typically ca. 0.8 times length of ocular peduncle, including cornea); ocular acicles relatively small, subtriangular, armed with small or often minuscule dorsodistal spine. Antennal peduncles slender, delicate, not exceeding distal margins of corneas; acicles short, not reaching level of cornea. Mouthparts: maxillule with well-developed and strongly recurved external lobe of endopod; maxilliped 1 with exopodal flagellum, endopod medially bent at nearly right angle, with distinctly developed epipod; maxilliped 3 ischium with well-developed crista dentata, lacking accessory tooth, exopod broad, ca. 2.4 times as long as broad. Epistome unarmed. Chelipeds symmetrical or nearly so, subequal in size, armed with scarce to moderately dense setation and numerous well-spaced small spines or tubercles; coxae each with ventral surface having uncalcified median longitudinal fissure starting on distal margin and incompletely covering length of ventral surface. Pereopods 2 and 3 long and slender; dactyl of pereopod 3 distinctly longer than dactyl of pereopod 2. Sternite XI (between pereopods 3; e.g., Fig. 21D) wide, separating coxae of pereopods 3 by length of 1 coxa; anterior lobe flat, consisting of narrow rod-like plate (typically 8–10 times as broad as long), posterior lobes weakly divided medially by shallow groove into two subrectangular (wider than long), glabrous lobes. Pereopod 4 chelate, extending to subdorsal position to manipulate carcinoecium, lacking rasp-like surfaces; dactyl with cutting edge unarmed; fixed finger with cutting edge unarmed or with 1 corneous spinules; coxae (e.g., Fig. 27B) with anteroventral margin sharply delimited, keel-like. Sternite XII (between pereopods 4; e.g., Fig. 21D, 27B) broad, ridge-like, weakly divided medially, with fringe of setae. Pereopod 5 chelate, with weakly developed propodal rasp. Pleon curling under but not dextrally or sinistrally twisted; pleonal somite 1 not fused to last thoracic somite, with partly calcified tergite and pleura. Male with well-developed paired gonopods 1 and 2, and reduced (uniramous or biramous) pleopod 3–5 on left side only, when present. Female with paired gonopores; with paired uniramous pleopods 1 modified as gonopods; left side with unpaired, well developed, biramous pleopods 2–4 (ovigerous), rarely with vestigial pleopod 5; right side with no unpaired pleopods 2–5; brood pouch large, covering pleopods 2–4 and entire egg mass. Uropods and telson symmetrical; exopods long, slender; endopod small, curved. Telson subrectangular, lacking or with obscure lateral indentations; posterior margin weakly divided into nearly straight or very broadly rounded lobes.

Type species. *Paguropsina pistillata* gen. et sp. n. Gender: feminine.

Species included. In addition to the type species, the genus includes *P. inermis* gen. et sp. n.

Etymology. The generic name is derived from the genus name *Paguropsis*, and using the Latin feminine suffix *–ina*, in reference to the relatively small size of individuals of the two species of this new genus.

Distribution. Subtropical to tropical western Pacific. Depth: 52 to 849 m.

Remarks. The two new species included in this genus have relatively small specimens ranging in shield length from 1.8 to 6.1 mm, with subovate shields, and a general delicate morphology with slender antennal peduncles and pereopods 2 and 3, weakly armed chelipeds having short, simple setation not obscuring the surface features of the segments, stout ocular peduncles, and wide corneas. Aside from the general, subtle appearance, species of *Paguropsina* gen. n. can be separated from those of *Paguropsis* primarily by four characters that are drastically different from those in species of *Paguropsis*. These are: the shape of the gills (lamellae deeply divided distally into finger-like extensions vs. distally divided into filamentous or stub-like extensions in *Paguropsis*); the shape of the exopod of the maxilliped 3 (broad, 2.4 times as long as broad vs. slender, 4 or more times as long as broad in *Paguropsis*); the width of sternite XI (ca. length of one coxa of pereopods 3 vs. less than half length of one coxa in *Paguropsis*); and armature of the cutting edges of dactyl and fixed finger of chela of pereopod 4 (cutting edges of dactyl and fixed finger unarmed or with one distinct corneous spinule vs. cutting edge of dactyl with row of small corneous spines and cutting edge of fixed finger with sharp spines arranged like bear claw in *Paguropsis*). In several other respects species of *Paguropsina* gen. n. and *Paguropsis* also differ albeit the differences are more subtle. The lateral projections of the shield each terminate in a short vertical keel-like ridge in species of *Paguropsina* gen. n., whereas the lateral projections terminate in a small spines without a keel in *Paguropsis* species. Additionally, it appears based on the material examined of both new species herein described under this new genus, that the location of pleopods tends to be fixed on the left side [see "Variations" under each species), whereas in species of *Paguropsis* the pleopods can frequently be present on either side.

Paguropsina pistillata **gen. et sp. n.**

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Figs 18C, 21D, E, 23, 24, Table 1

Type material. Holotype: 1 male 4.4 mm, New Caledonia, EBISCO, NO *Alis*, sta CP 2499, Capel Bank, 24°53'0"S, 159°52'0"E, 286–529 m, 7 Oct 2005 (USNM 1442008).

Paratypes. *Philippines*: PANGLAO 2004, W Pamilacan I. Cervera shoal, sta T37, 09°28'N, 123°51'E, 134–190 m, 4 Jul 2004: ovig female 4.2 mm, color photograph (Fig. 18C) (LKCNHM ZRC).

Indonesia: Danish Kei Islands Expedition: sta 49, 05°37'10"S, 132°24'E, 245 m, 3 May 1922: 1 ovig female 4.4 mm (ZMUC-CRU–007046).

Salomon Islands: SALOMON 1, NO *Alis*: N Malaita, sta DW 1778, 08°19'S, 160°34'E, 157–253 m, 29 Sep 2001: 1 male 2.7 mm (MNHN-IU-2014–9368); NW San Cristobal, sta CP 1831, 10°12'S, 161°19'E, 135–325 m, 5 Oct 2001: 1 male 4.0 mm, 1 ovig female 3.1 mm (ex MNHN-IU-2013–5582, USNM 1441980); E of Guadalcanal, sta CP 1857, 09°40'S, 160°49'E, 720–849 m, 7 Oct 2001: 1 female 3.4 mm (MNHN-IU-2014–9369).

New Caledonia: MUSORSTOM 6, NO *Alis*: Loyalty Islands, [sta number lost]: 1 male 3.1 mm (USNM 1441979). LIFOU, NO *Alis*: Lifou, Santal Bay, SE of Récif Shelter, sta DW 1648, 20°54'S, 167°03'E, 150–200 m, 7/19 Nov 2000: 2 ovig females 3.1, 3.4 mm (MNHN-IU-20149375). NORFOLK 1, NO *Alis*: Norfolk Ridge, Brachiopode Bank, sta DW 1657, 23°26'S, 167°50'E, 305–332 m, 19 Jun 2001: 1 female 3.7 mm (MNHN-IU-2014–9363); Norfolk Ridge, Kaimon-Maru Bank, sta DW 1679, 24°45'S, 168°10'E, 298–324 m, 22 Jun 2001: 1 female 4.0 mm (MNHN-IU-2014–9354). EBISCO, NO *Alis*: Capel Bank, sta CP 2492, 24°44'S, 159°41'E, 285 m, 6 Oct 2005: 74 males 1.8–2.3 mm, 65 females 1.9–3.4 mm, 23 ovig females 3.0–4.0 mm (MNHN-IU-2014–9401); Capel Bank, sta CP 2493, 24°44'0"S, 159°43'0"E, 285–545 m, 6 Oct 2005: 1 male 4.1 mm (USNM 1442021), 56 males 2.5–4.3 mm, 15 females 1.9–3.7 mm, 48 ovig females 1.9–3.4 mm (MNHN-IU-2014–9402); Capel Bank, sta CP 2499, 24°53'S, 159°52'E, 286–529 m, 07 Oct 2005: 2 males 2.4, 3.3 mm (MNHN-IU-2013–5659); Capel Bank, sta CP 2505, 24°45'S, 159°43'E, 328–463 m, 7 Oct 2005: 1 male 4.0 mm, 1 ovig female 3.6 mm (MNHN-IU-2014–9391); Capel Bank, sta CP 2507, 24°43'0"S, 159°43'0"E, 286 m, 7 Oct 2005: 1 male 4. 0 mm (USNM 1442011); Capel Bank, sta DW 2508, 24°41'0"S, 159°43'0"E, 304–350 m, 7 Oct 2005: 1 male, 3.2 mm (USNM 1442012); Kelso Bank, sta DW 2513 24°6'0"S, 159°42'0"E, 280–500 m, 8 Oct 2005: 1 female 3.0 mm (USNM 1442025); Kelso Bank, sta CP 2519, 24°8'0"S, 159°42'0"E, 310–463 m, 8 Oct 2005: 2 males 3.0, 3.1 mm (USNM 1442023); Nova Sud Bank, sta CP 2524, 24°6'0"S, 159°42'0"E, 315–325 m, 9 Oct 2005: 1 ovig female 3.0 mm (USNM 1441985); N of Nova Bank, sta DW 2538, 22°20'S, 159°25'E, 318–323 m, 10 Oct 2005: 1 ovig female 3.3 mm (MNHN-IU-2014–9392); Chesterfield Plateau, sta CP 2591, 19°4'0"S, 158°28'0"E, 244–258 m. 17 Oct 2005: 1 female ovig 3.7 mm (USNM 1442010); Chesterfield Plateau, sta CP 2592, 19°42'0"S, 158°30'0"E, 273–281 m, 17 Oct 2005: 1 male 4.1 mm (USNM 1442024); Chesterfield Plateau, sta CP 2593, 19°43'0"S, 158°32'0"E, 300–323 m, 17 Oct 2005: 1 male 6.0 mm (USNM 1442022).

Chesterfield Islands, Coral Sea: MUSORSTOM 5, NO *Coriolis*: Lord Howe Ridge, Capel Bank, sta CP 269, 24°47'S, 159°37'E, 250–270 m, 9 Oct 1986: 4 males 2.5–3.3 mm, 1 ovig female 3.1 mm (MNHN-IU-2014–9409); Lord Howe Ridge, Capel Bank, sta DW 260, 25°29'S, 159°44'E, 285 m, 8 Oct 1986: 1 male 3.6 mm (MNHN-IU-2014–9407); Lord Howe Ridge, Capel Bank, sta DW 274, 24°45'S, 159°41'E, 285 m, 9 Oct 1986: 1 female 2.2 mm (MNHN-IU-2014–9408); Lord Howe Ridge, Capel Bank, sta CP 275, 24°46.60'S, 150°40.30'E, 285 m, 9 Oct 1986: 1 male 3.7 mm (USNM 1441989); Lord Howe Ridge, Argo Bank, sta DC 291, 23°07.70'S, 159°28.40'E, 300 m, 11 Oct 1986:1 male 3.9 mm (USNM 1442009); Lord Howe Ridge, Nova Bank, sta CP 312, 22°17'S, 159°25'E, 315–320 m, 12 Oct 1986: 1 male 2.8 mm (MNHN-IU-2014–9406).

Description. *Shield* (Figs 18C, 23A) 0.9 to 1.1 longer than broad; dorsal surface glabrous or with scattered setae on sloping lateral surfaces; anterior margins between rostrum and lateral projections concave; posterior margin broadly rounded; lateroventral distal angle produced into small blunt spine-like projection (often with 2 minute terminal tubercles) adjacent to proximal margin of first antennal segment. Rostrum roundly subtriangular, relatively broad, weakly arched and curved ventrally, reaching to distal margin of ocular acicles; with rounded and glabrous dorsal longitudinal ridge. Lateral projections each terminating in short vertical keel-like ridge with 2 or 3 small blunt spines. Gastric region weakly elevated anteriorly. Branchiostegite (Fig. 23B) with anterodorsal plate unarmed or with small blunt distal spine; distal margin setose.

Ocular peduncles strongly broadened distally, ca. 0.5 length of shield; corneas strongly dilated, diameter ca. 0.8 of total peduncular length (including the cornea). Ocular acicles small, obtusely triangular, armed with minute subterminal blunt spine directed anterodorsally.

Antennular peduncles when fully extended overreaching distal margins of corneas by entire or nearly entire length of ultimate peduncular segments. Ultimate and penultimate segments glabrous or at most with scattered short setae. Basal segment with lateral face having distal subrectangular lobe, minute medial spine, and setose lobe proximally.

Antennal peduncles reaching nearly to distal corneal margins. Fifth segment slender, glabrous or with scattered setae. Fourth segment with scattered setae. Third segment with short ventrodistal spine. Second segment with dorsolateral distal angle not noticeably produced, terminating in short spine; mesial margin rounded, setose, dorsomesial distal angle blunt, unarmed. First segment (Fig. 23A) hardly visible in dorsal view or hidden by

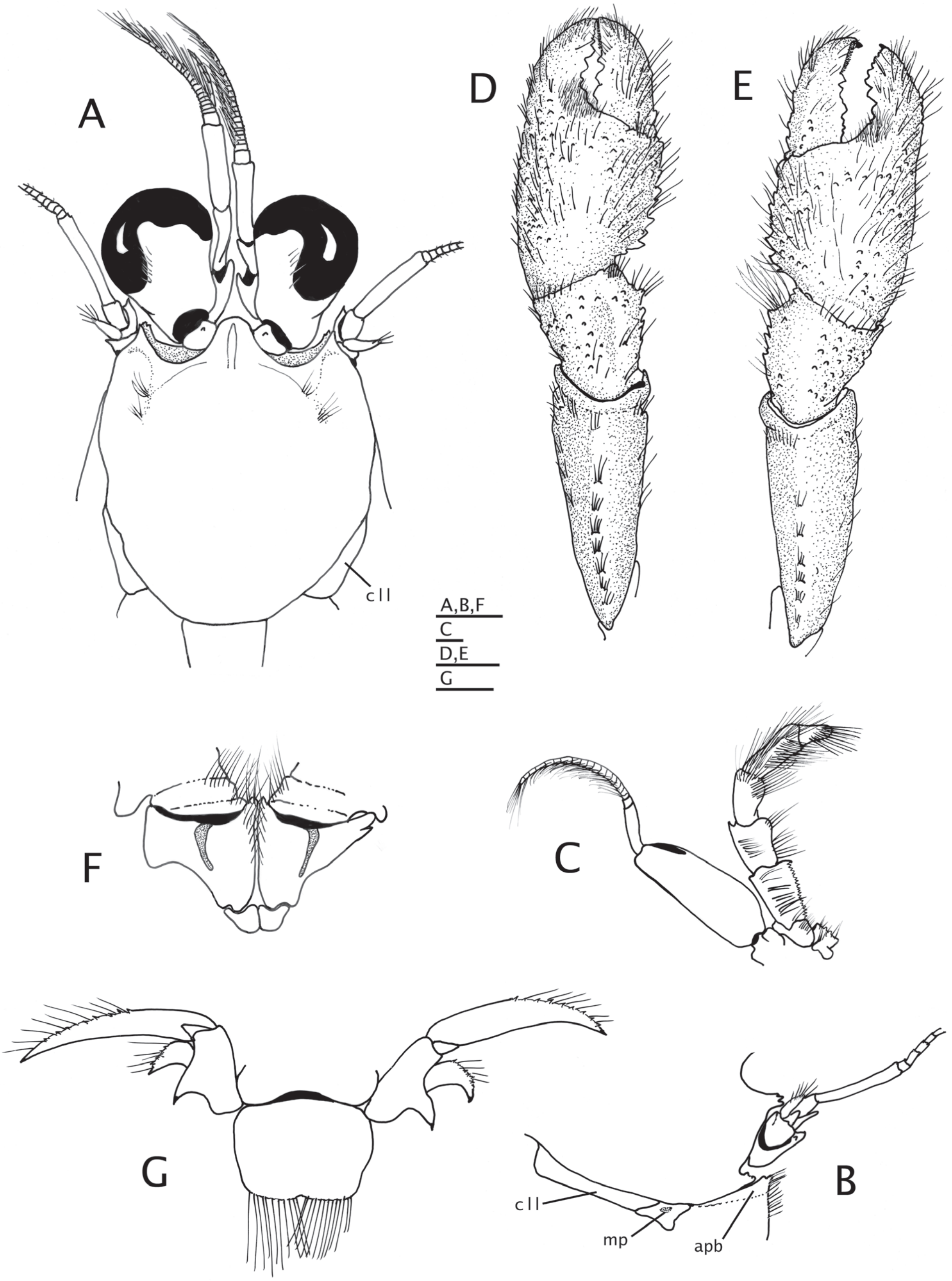

Figure 23. *Paguropsina pistillata* gen. et sp. n., holotype male, 4.4 mm New Caledonia, EBISCO, CP 2499 (USNM 1442008). **A** shield and cephalic appendages, dorsal **B** right antennal peduncle, branchiostegite, and anterodorsal portion of posterior carapace, lateral **C** left maxilliped 3, internal **D** left cheliped, dorsal **E** right cheliped, dorsal **F** coxae of chelipeds, ventral **G** uropods and telson, dorsal. Abbreviations: apb, anterodorsal plate of branchiostegite; cll, carapace lateral lobe; mp, median plate. Scale bars: 1 mm (**A, B**), 2 mm (**D, E, G**), 0.5 mm (**C, F**).

shield, unarmed. Antennal acicle short, only reaching to distal margin of fourth peduncular segment or mid-point of ocular peduncle, unarmed, terminating bluntly and with few short distal setae. Antennal flagellum short, delicate, not exceeding distal margin of chelae, with few short setae and 1 or 2 long setae every 4–6 flagellar articles.

Mouthparts. Mandible with stout palp. Maxillule with recurved external lobe of endopod nearly as long as entire endopod. Maxilla with endopod not exceeding distal end of scaphognathite. Maxilliped 1 with endopod bent medially nearly at right angle, reaching distal end of exopod; epipod elongated. Maxilliped 2 without distinguishing characters. Maxilliped 3 (Fig. 23C) with exopod ca. 2.4 times as long as broad; merus with 3–5 small spines on ventral margin, and usually 2 small spines on ventromesial distal angle; ischium having crista dentata armed with 15–18 small subequal (except for larger distal and proximal) corneous-tipped teeth; basis with row of small spines on mesial margin; coxa with ventromesial angle strongly produced ventrally, with 2–4 small spines and fringe of setae. Sternite VIII narrow, with small setose lobe on each side of midline.

Chelipeds (Figs 18C, 23D, E) subequal, similar in armament and setation; dorsal surfaces of chelae and carpi with weakly dense short setation mostly arranged in tufts; ventral surfaces of palms smooth except for scattered setae or tufts of setae. Dactyl and fixed finger with narrow hiatus proximally when closed, forming spoon-like shape in ventral view when closed; each terminating in small curved corneous claw and subdistal blunt calcareous tooth ventral to claw, both claws and teeth interlocking when fingers closed; cutting edge of dactyl with terminal row of small, fused corneous teeth on distal one-third, and row of unequal calcareous teeth on proximal two-thirds; cutting edge of fixed finger with row of blunt calcareous teeth decreasing in size distally. Dactyl as long as palm; dorsal surface convex, weakly pitted and mostly unarmed except for short setae; mesial margin rounded, with few small tubercles; ventromesial face concave. Palm as long as carpus, dorsal surface with scattered small tubercles on dorsolateral and dorsomesial margins, mostly unarmed medially, usually with dense patch of short plumose setae medially near base of fixed finger; dorsolateral margin rounded, not delimited, dorsomesial margin with row of strong spines. Carpus ca. 0.6 times length of merus; dorsal and dorsolateral surfaces with scattered small spines or tubercles; dorsomesial margin with row of weak to moderately strong spines or tubercles, and small blunt distal spine; dorsolateral margin rounded; mesial surface smooth, unarmed except for setae on distal margin; ventral surface smooth except for row of setae on distal margin. Merus nearly as long as chela, subtriangular in cross-section; dorsal margin with row of low protuberances accompanied by tufts of short setae, ventromesial and ventrolateral margins each with irregular row of weak spines or tubercles with setae; lateral and mesial surfaces unarmed except for scattered short setae. Ischium with lateral surface rounded, unarmed, ventromesial margin with row of small spines. Basis with ventromesial row of setae. Coxa with well-marked longitudinal fissure (Fig. 23F) on ventral surface.

Pereopods 2 and 3 (Fig. 24A–D) slender, similar in armature and setation, slightly dissimilar in length, with pereopod 2 shorter than pereopod 3. Dactyls ca. 1.4 (pereo-

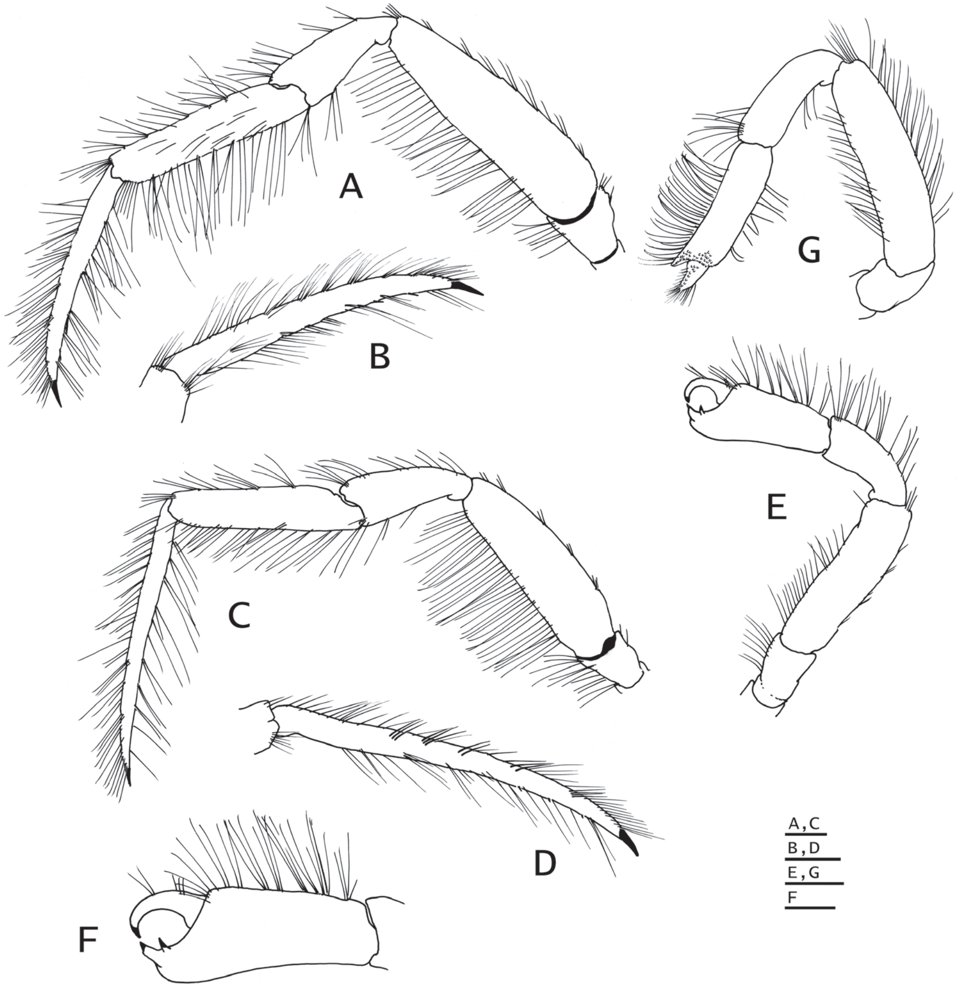

Figure 24. *Paguropsina pistillata* gen. et sp. n., holotype male, 4.4 mm New Caledonia, EBISCO, CP 2499 (USNM 1442008). **A** left pereopod 2, lateral **B** dactyl of same, mesial **C** left pereopod 3, lateral **D** dactyl of same, mesial **E** left pereopod 4, lateral **F** chela of same, lateral **G** left pereopod 5, lateral. Scale bars: 1 mm (**A–E, G**), 0.5 mm (**F**).

pod 2) or 1.7 (pereopod 3) times as long as propodi, mostly straight in lateral view except for weak distal curvature, terminating in sharp corneous claw; dorsal and ventral margins each with moderately dense simple setae or tufts of setae (some on dorsal margin occasionally bristle-like); ventromesial margins each with 2 or 3 obscure, minute corneous spinules distally; dactyl of pereopod 3 slender, nearly straight in lateral view, 1.1 times as long as dactyl of second pereopod. Propodi ca. 1.2 times as long as carpi; dorsal margin mostly with tufts of long setae, ventral margin with long simple setae or tufts of setae, lateral and mesial faces with scattered short setae. Carpi unarmed except for tufts of setae dorsally and scattered setae ventrally, dorsodistal angle blunt or with obscure small tubercle. Meri unarmed except for fringe of long setae ventrally. Ischia unarmed except for scattered short setae. Coxae of pereopods 3 (Fig. 21D) widely separated by full ventral length of 1 coxa, with few ventromesial setae. Sternite XI (between pereopods 3; Fig. 21D) with undivided anterior lobe consisting of narrow rod-like plate 8 times as broad as long; posterior lobes wider than long, glabrous.

Pereopod 4 (Figs 21E, 24E, F) with chela club-like, almost 1.1 times as long as carpus and 2.4–3.1 as long as high; palm 1.7–2.2 as long as high. Dactyl strongly curved, hook-like, crossing fixed finger at tip when fingers closed, terminating in distal or subdistal sharp corneous claw; cutting edge unarmed or rarely with few minutely obscure corneous spinules. Fixed finger broad, bulging ventrally at base, glabrous, terminating in sharp corneous claw; cutting edge with 1 distinct sharp corneous-tipped spine (often slightly offset laterally from cutting edge). Palm and carpus with long simple setae or tufts of setae on dorsal margins. Sternite XII (between pereopods 4; Fig. 21D) with fringe of setae more dense laterally than medially.

Pereopod 5 (Fig. 24G) with chela nearly 0.7 times as long as merus, with long, brush-like setae on dorsal and ventral surfaces. Dactyl with propodal rasp on ventral face. Propodal rasp consisting of minute ovate scales extending for ca. 0.1 length of propodus. Ischium with setae dorsally and ventrally. Coxa with ventrodistal setae.

Male gonopod 1 with inferior lamella armed on distal margin with posterior row of slender, semitransparent hook-like spines, and 1 or 2 irregular rows of small straight or slightly curved corneous spines. Gonopod 2 with distal segment strongly twisted distally, densely setose. Left unpaired pleopods 3–5 reduced when present, pleopod 3 biramous, pleopods 4 and 5 uniramous; no pleopods 3–5 on right side (see "Variations").

Female with left unpaired, well-developed, biramous pleopods 2–4 (ovigerous), rarely with vestigial pleopod 5; lacking or rarely having unpaired pleopods 2–5 on right side (see "Variations"). Brood pouch large, oblong, distal margin weakly scalloped and fringed with sparse short setae.

Uropodal exopods (Fig. 23G) slender, broadly curved, terminating in strong, usually corneous-tipped spine, anterior margin with fringe of long well-spaced setae and row of well- spaced corneous-tipped spines; endopods relatively short, curved, anterior margin with long setae and 1 or 2 irregular rows of corneous-tipped spines; protopods with strong, curved proximal spine.

Telson (Fig. 23G) subrectangular, broader than long; posterior lobes separated by shallow median cleft, terminal margins unarmed except for fringe of long setae.

Genetic data. See Table 1.

Color (Fig. 18C). Shield light orange-red except for white anterior margins. Ocular acicles light orange with white-tipped distal spine and small reddish spot mesially. Antennular and antennal peduncles light orange fading to transparent on distal segments. Ocular peduncles light orange proximally, whitish distally except for orange-red median portion of optic calathus; with dark orange-red band medially; corneas black except for somewhat yellowish external membrane. Chelipeds with carpus and chela with mostly light orange to red background, and white spines or tubercles; dactyl white except for light red portion medially, and small orange spot basally; fixed finger white except for small orange spot mesially at base of larger teeth of cutting edge, and orange portion basally, white coloration continued posteriorly on most of lateral face of palm; carpus with small white portion basally and distally; merus orange mottled with white, with small dorsodistal, laterodistal and mesiodistal dark orange or reddish spot. Pereopods 2 and 3 with dactyls semi-transparent except for median and basal red bands; carpi and meri mottled with semi-transparent white and light orange-red spots or blotches; meri with light orange background and mottled with white and red spots. Pereopod 4 light with dactyl light orange with white tip; chela mostly white except for light orange dorsal margin; carpus mostly white with light orange distal, ventral and proximal margins; merus white with light orange band medially. Pereopod 5 light orange.

Etymology. The species name derives from the Latin *pistillum*, a club-shaped pounder used in a mortar, and refers to the characteristic shape of the chela of pereopod 4.

Distribution. Western Pacific: from the Philippines, Indonesia (Arafura Sea), Solomon Islands, and New Caledonia. Depth: 135 to 849 m.

Habitat and symbiont. Found with undetermined species of acontiate anemone (see "Remarks" under genus *Paguropsis*).

Variations. Of the 152 males examined, 133 (87.5%) have unpaired pleopods 3–5 (reduced, uni- or biramous) on the left side, and the remaining lack unpaired pleopods on either side. Of the 166 females examined, 99% have unpaired pleopods 3–5 on the left side.

Remarks. This new species and *Paguropsina inermis* gen. et sp. n. are very similar. However, the two can be immediately separated by the difference in armature of the cutting edge of the fixed finger on the chela of pereopod 4. In *P. pistillata* gen. et sp. n. the cutting edge is armed with one distinct, sharp corneous-tipped spine that is often slightly offset laterally from the cutting edge, whereas the cutting edge in *P. inermis* gen. et sp. n. is unarmed. Coloration also differs in these two congeners (Fig. 18C, D), primarily on the pattern of the chelipeds (pereopod 1) and pereopods 2 and 3. The chela is orange to red with white spines, and the fixed finger and distolateral half of the palm are white in *P. pistillata* gen. et sp. n., whereas the chela is orange with irregular pattern and shapes of small white spots and white spines in *P. inermis* gen. et sp. n. Pereopods 2 and 3 have dactyls that are semi-transparent except for median and basal red bands, and the propodi, carpi and meri are mottled with semi-transparent white and light orange-red spots or blotches in *P. pistillata* gen. et sp. n., whereas pereopods 2 and 3 are light to dark orange or reddish mixed with irregularly-shaped white areas, the dactyls are white distally and proximally, and red medially, and propodi, carpi and meri are white distally with a small red spot distolaterally in *P. inermis* gen. et sp. n.

Paguropsina inermis gen. et sp. n.

http://zoobank.org/9DCB897F-C251-448D-9528-A9559F88AE08
Figs 18D, 25–27, Table 1

Type material. Holotype: male 3.7 mm, New Caledonia, NORFOLK 2, Antigonia Bank, sta CP 2119, 23°23'S, 168°02'E, 300 m, 1 Nov 2003 (MNHN-IU-2014–9386).

Paratypes. *Japan*: Ogasawara Islands: TRV *Shin'yo-maru* 1997 research cruise, sta 17: off Chichi-jima Island, 27°24.58'N, 142°10.21'E, 210–212 m, 16 Oct 1997, coll. T Komai: 1 ovig female 2.9 mm (CBM-ZC 14204). RV *Koyo*, 2009 research cruise, sta 21: NW of Otouto-jima Island, 27°13.09'N, 142°09.19'E, 136 m, 15 Jul 2009, coll. T Komai: 1 ovig female 3.8 mm (CBM-ZC 14205); sta 28, E of Nishi-jima Island, 27°07.05'N, 142°10.68'E, 52 m, 15 Jul 2009, coll. T Komai: 1 female 2.5 mm, color photograph (Fig. 18D) (CBM-ZC 14206); sta 34, W of Minami-jima Island, 27°02.34'N, 142°07.52'E, 139–140 m, coll. T Komai: 1 female 2.6 mm (CBM-ZC 14207).

South China Sea: ZHONGSHA 2015, ORI cruise 1113: sta CP 4160, 20°48.88'N, 116°43.153'E, 251 m, 30 Jul 2015: 1 ovig female 4.5 mm (NTOU A01447).

Philippines: MUSORSTOM 1, NO *Vauban*: N Lubang, sta CP63, 14°00'N, 120°16'E, 191–195 m, 27 Mar 1976: 1 female 6.1 mm (MNHN-IU-2014–9372). PANGLAO 2004: W of Pamilacan Island, Cervera shoal, sand on echinoderms bed, sta T37, 09°28'N, 123°51'E, 134–190 m, 4 Jul 2004: 1 ovig female 4.2 mm (LKCNHM ZRC 2018.0172). PANGLAO 2005, NO "*DA-BFAR*": Bohol Sea, off Balicasag Island, sta DW 2402, 09°31'N, 123°42'E, 101–118 m, rock/sand/corals, 31 May 2005: 3 males 2.7–3.9 mm (LKCNHM ZRC 2018.0173).

Indonesia: KARUBAR, NO *Baruna Jaya 1*: Kai Islands, sta DW18, 05°18'S, 133°01'E, 205–212 m, 24 Oct 1991: 2 males 3.1, 3.2 mm, 1 female 3.5 mm (MNHN-IU-2014–9380).

Fiji Islands: BORDAU 1, NO *Alis*: Lau Ridge, Yangasa Cluster, sta DW1497, 18°44'S, 178°25'W, 335–350 m, 12 Mar 1999: 1 male 2.5 mm, 1 female 3.0 mm (MNHN-IU-2013–19456).

Tonga Islands: BORDAU 2, NO *Alis*: Vava'u group, sta DW1583, 18°37'S, 174°03'W, 327–360 m, 13 Jun 2000: 1 female 3.0 mm (MNHN-IU-2013–19457).

New Caledonia: BATHUS 3, NO *Alis*: Norfolk Ridge, W of Mont Jumeau, sta CP 805, 23°41'S, 168°01'E, 278–310 m, 27 Nov 1993: 1 male 3.4 mm (MNHN-IU-2014–9378). LITHIST, NO *Alis*: Norfolk Ridge, W of Jumeau Bank, sta CP 17, 23°41'S, 168°01'E, 247–281 m, 12 Aug 1999: 1 male 5.7 mm (MNHN-IU-2014–9379). NORFOLK 1, NO *Alis*: Norfolk Ridge, Brachiopode Bank, sta DW 1651, 23°26'S, 167°50'E, 276–350 m, 19 Jun 2001: 4 males 3.1–4.6 mm (MNHN-IU-2014–9352), 2 females 2.8, 3.6 mm (MNHN-IU-2014–9362); Norfolk Ridge, Brachiopode Bank, sta DW 1652, 23°27'S, 167°51'E, 290–378 m, 19 Jun 2001: 1 male 4.6 mm (MNHN-IU-2014–9353); Norfolk Ridge, Brachiopode Bank, sta DW1653, 23°26'S, 167°51'E, 328–340 m, 19 Jun 2001: 4 males 3.6–4.8 mm, 1 female 3.7 mm (MNHN-IU-2014–9355), 1 male 4.2 mm, 1 3.6 mm (MNHN-IU-2014–9381); Norfolk Ridge, Brachiopode Bank, sta DW 1657, 23°26'S, 167°50'E, 305–332 m, 19 Jun 2001: 1 female 4.8 mm (USNM 1441977); Norfolk Ridge, Brachiopode Bank, sta DW 1658, 23°27'S, 167°50'E, 320–336 m, 19 Jun 200: 1 female 3.4 mm (MNHN-IU-2013–19455); Norfolk Ridge, W of Jumeau Bank, sta CP 1669, 23°41'S, 168°01'E, 302–325 m, 21 Jun 2001: 1 male 4.3 mm, 1 female 3.9 mm (MNHN-IU-2014–9351); Norfolk Ridge, W of Jumeau Bank, sta CP1671, 23°42'S, 168°01'E, 320–397 m, 21 Jun 2001: 1 male 5.1 mm (MNHN-IU-2014–9359);

Norfolk Ridge, Kaimon-Maru Bank, sta CP 1682, 24°42'S, 168°09'E, 331–379 m, 22 Jun 2001: 1 male 4.5 mm (MNHN-IU-2014–9357); Norfolk Ridge, Kaimon-Maru Bank, sta CP1683, 24°44'S, 168°07'E, 248–272 m, 22 Jun 2001: 1 male 4.5 mm (USNM 1441892); Norfolk Ridge, Crypthelia Bank, sta DW 1724, 23°19'S, 168°15'E, 200–291 m, 27 Jun 2001: 1 female 3.0 mm (MNHN-IU-2014–9358). NORFOLK 2, NO *Alis*: Brachiopode Bank, sta DW 2023, 23°27'S, 167°51'E, 282–297 m, 21 Oct 2003: 1 male 4.3 mm (MNHN-IU-2014–9388); Brachiopode Bank, sta DW 2024, 23°28'S, 167°51'E, 370–371 m, 21 Oct 2003: 1 ovig female 4.5 mm (MNHN-IU-2014–9383); Kaimon-Maru Bank, sta CP 2094, 24°44'S, 168°10'E, 286–300 m, 29 Oct 2003: 1 ovig female 3.9 mm (MNHN-IU-2014–9382), 1 male 4.3 mm (MNHN-IU-2014–9385); Antigonia Bank, sta CP 2119, 23°23'S, 168°02'E, 300 m, 1 Nov 2003: 2 ovig females 3.7, 3.8 mm (USNM 1441978); Crypthelia Bank, sta DW 2124, 23°18'S, 168°15'E, 260–270 m, 2 Nov 2003: 1 ovig female 3.6 mm (MNHN-IU-2014–9390).

Description. *Shield* (Figs 18D, 25A) subovate, about as long as broad; dorsal surface glabrous except for scattered setae on sloping lateral surfaces; anterior margins between rostrum and lateral projections concave; posterior margin broadly rounded; lateroventral distal angle produced into small blunt spine (often with 2 minute terminal tubercles) adjacent to proximal margin of first antennal segment. Rostrum roundly subtriangular, relatively broad, weakly arched and curved ventrally, reaching to distal margin of ocular acicles; with rounded, glabrous dorsomedian longitudinal ridge. Lateral projections each terminating in short vertical keel-like ridge with 2 or 3 small blunt spines distally. Gastric region weakly elevated anteriorly. Branchiostegite (Fig. 25B) with anterodorsal plate unarmed except for 1–3 small blunt distal spines, and setose distal margin.

Ocular peduncles strongly broadened distally, ca. 0.5 length of shield; corneas strongly dilated, diameter ca. 0.7 of total peduncular length (including the cornea). Ocular acicles small, obtusely triangular, armed with minute subterminal blunt spine directed anterodorsally.

Antennular peduncles when fully extended overreaching distal margins of corneas by entire or nearly entire length of ultimate peduncular segments; ultimate and penultimate segments glabrous or at most with scattered short setae; basal segment with lateral face having distal subrectangular lobe, minute medial spine, and setose lobe proximally.

Antennal peduncles reaching nearly to distal margin of corneas. Fifth segment slender, glabrous or with scattered setae. Fourth segment with few scattered setae. Third segment with short ventrodistal spine. Second segment with dorsolateral distal angle not noticeably produced, terminating in short spine; mesial margin rounded, setose, dorsomesial distal angle blunt, unarmed. First segment (Fig. 25A) hardly visible in dorsal view or hidden by shield, unarmed. Antennal acicle short, only reaching to distal margin of fourth peduncular segment or mid-point of ocular peduncle, unarmed, terminating bluntly and with few short distal setae. Antennal flagellum short, delicate, not exceeding distal margin of chelae, with few setae 1 to 2 flagellar articles in length.

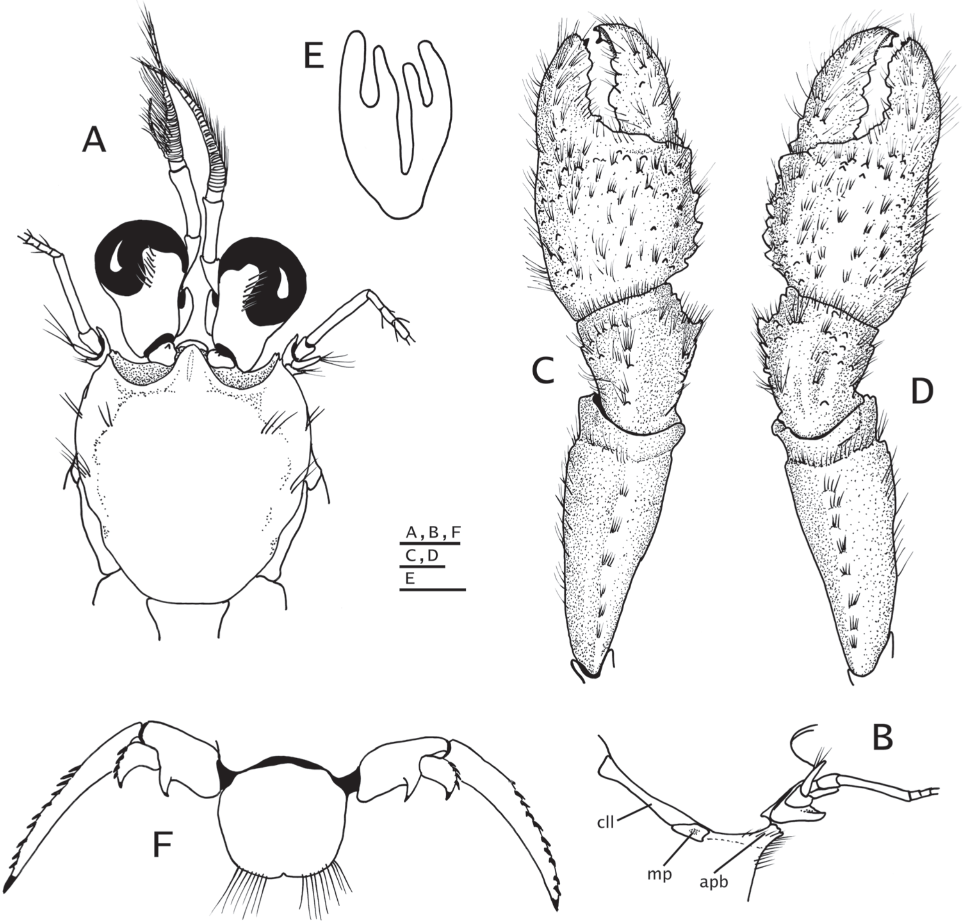

Figure 25. *Paguropsina inermis* gen. et sp. n., holotype male 3.7 mm, New Caledonia, NORFOLK 2, sta CP2119, (MNHN-IU-2014–9386): **A** shield and cephalic appendages **B** right antennal peduncle, branchiostegite, and anterodorsal portion of posterior carapace, lateral **C** left cheliped, dorsal **D** right cheliped, dorsal **E** gill lamella **F** uropods and telson, dorsal. Abbreviations as in Fig. 20. Scale bars: 1 mm (**A–D**), 0.2 mm (**E**), 0.5 mm (**F**).

Mouthparts similar to those described for the type species *Paguropsis pistillata* sp. n. Maxilliped 3 (Fig. 27A) with exopod 2.7 times as long as broad.

Chelipeds (Figs 18D, 25C, D) subequal, similar in armament and setation; dorsal surfaces of chelae and carpi with weakly dense short setation mostly arranged in tufts; ventral surfaces of palms smooth except for scattered setae or tufts of setae. Dactyl and fixed finger with narrow hiatus proximally when closed, forming spoon-like shape in ventral view when closed; each terminating in small curved corneous claw and subdistal blunt calcareous tooth ventral to claw, both claws and teeth interlocking when fingers closed; cutting edge of dactyl with terminal row of small, fused corneous teeth on distal one-third, and row of unequal, strong calcareous teeth on proximal two-thirds;

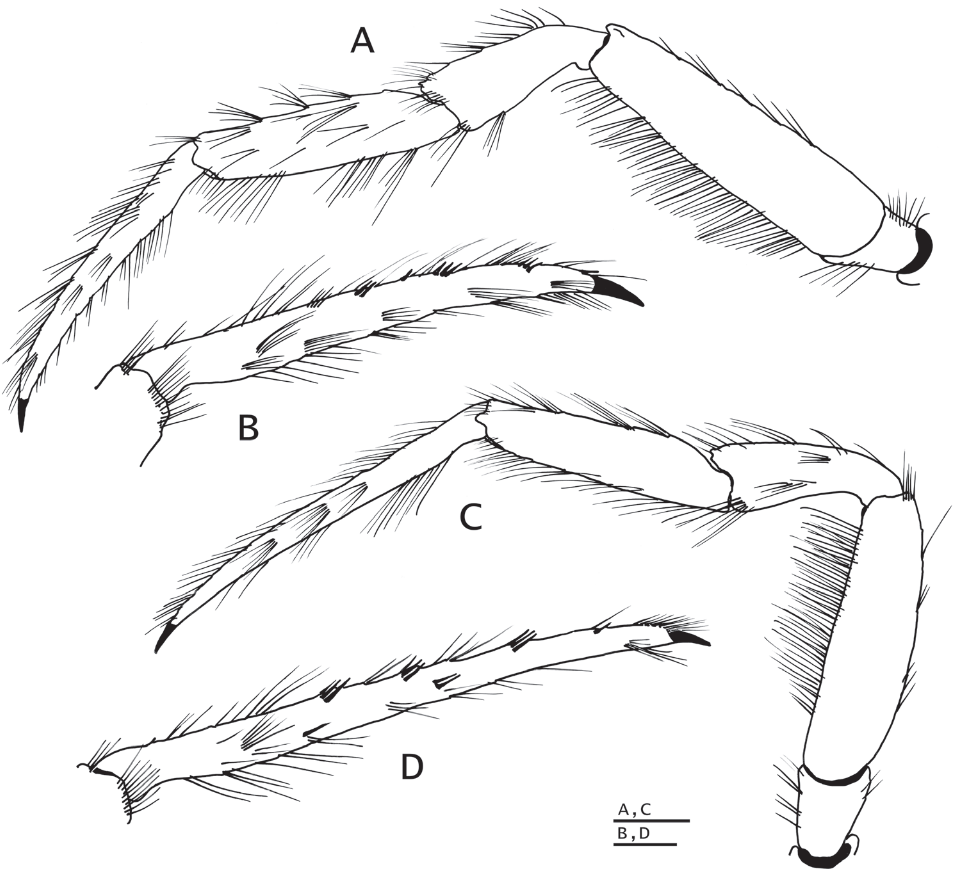

Figure 26. *Paguropsina inermis* gen. et sp. n., holotype male 3.7 mm, New Caledonia, NORFOLK 2, sta CP2119, (MNHN-IU-2014–9386): **A** left pereopod 2, lateral **B** dactyl of same, mesial **C** left pereopod 3, lateral **D** dactyl of same, mesial. Scale bars: 1 mm (**A, C**), 0.5 mm (**B, D**).

cutting edge of fixed finger with row of blunt, irregular calcareous teeth on proximal two-thirds, and row of partially fused, subequal, small calcareous teeth on distal third. Dactyl as long as palm; dorsal surface convex, weakly pitted and mostly unarmed except for scattered low tubercles with short setae; mesial margin rounded, with few small tubercles; ventromesial face concave. Palm as long as carpus, dorsal surface with scattered small tubercles on dorsolateral and dorsomesial margins, mostly unarmed medially except for well-spaced tufts of short to moderately long setae; dorsolateral margin rounded, not delimited, dorsomesial margin with row of strong spines. Carpus ca. 0.6 times length of merus; dorsal and dorsolateral surfaces with scattered small spines or tubercles; dorsomesial margin with row of weak to moderately strong spines or tubercles, and small blunt distal spine; dorsolateral margin rounded; mesial surface smooth, unarmed except for setae on distal margin; ventral surface smooth except for few long setae on distal margin. Merus slightly shorter to nearly as long as chela, sub-

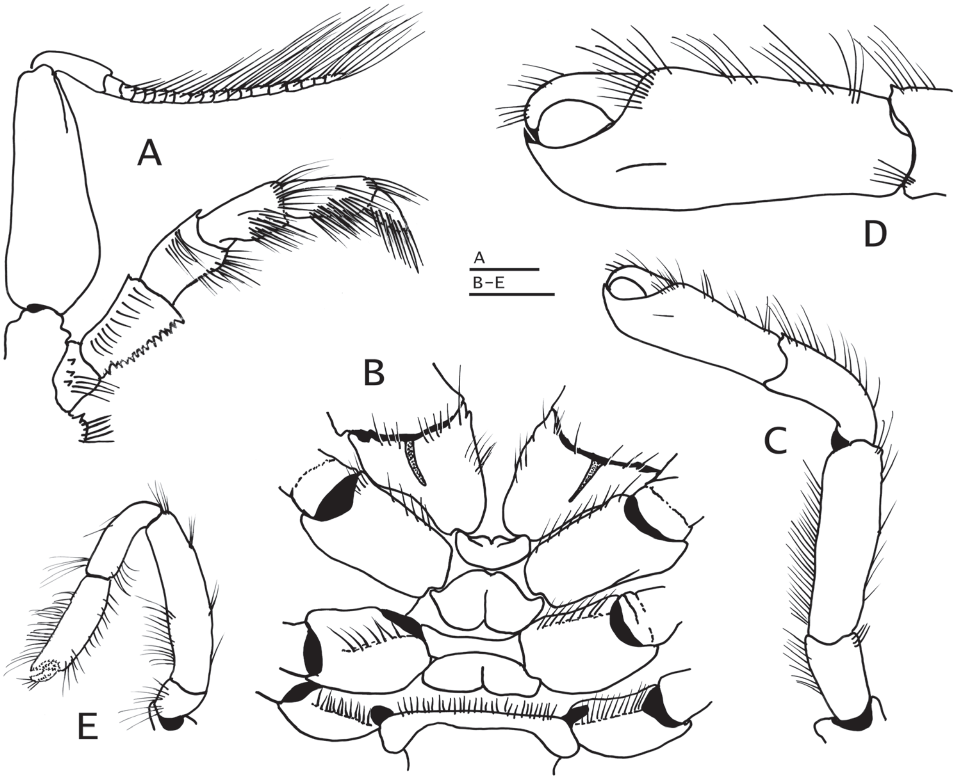

Figure 27. *Paguropsina inermis* gen. et sp. n., holotype male 3.7 mm, New Caledonia, NORFOLK 2, sta CP2119, (MNHN-IU-2014–9386): **A** left maxilliped 3, internal **B** coxae of pereopods 1–4, and sternites IX–XII **C** left pereopod 4, lateral **D** chela of same, lateral **E** left pereopod 5, lateral. Scale bars: 0.5 mm (**A, D**), 1 mm (**B, C, E**).

triangular in cross-section; dorsal margin with row of low protuberances accompanied by tufts of short setae, ventromesial and ventrolateral margins each with irregular row of weak spines or tubercles with setae; lateral and mesial surfaces unarmed except for scattered short setae. Ischium with lateral surface rounded, unarmed, and row of small spines on ventromesial margin. Basis with ventromesial row of setae. Coxa with well-marked longitudinal fissure (Fig. 27B) on ventral surface.

Pereopods 2 and 3 (Fig. 26A–D) similar in armature and setation, slightly dissimilar in length, with pereopod 2 shorter than pereopod 3. Dactyls ca. 1.5 (pereopod 2) or 1.8 (pereopod 3) times as long as propodi, mostly straight in lateral view except for weak distal curvature, terminating in sharp corneous claw; dorsal margins each with moderately dense, long simple setae; ventral margins each variably armed, with row of short or obscure spines, or with row of long, slender corneous spines; dorsomesial margins and mesial faces each usually with several tufts or short transverse rows of long, slender corneous spines (more numerous on pereopod 3); dactyl of pereopod 3 slender, ca. 1.2 times as long as dactyl of second pereopod. Propodi ca. 1.1 times as long as carpi; dorsal margin with few tufts of long setae, ventral margin with long simple setae or tufts of setae, lateral and mesial faces with scattered short setae. Carpi unarmed except for tufts of setae dorsally and scattered setae ventrally, dorsodistal angle with small blunt spine or obscure small tubercle. Meri unarmed except for few long setae dorsally and fringe of long setae ventrally. Ischia unarmed except for scattered short setae. Coxae of pereopods 3 (Fig. 27B) widely separated by ventral length of 1 coxa, with few ventromesial setae. Sternite XI (between pereopods 3; Fig. 27B) with undivided anterior lobe consisting of narrow rod-like plate 8–10 times as broad as long.

Pereopod 4 (Fig. 27C, D) with chela club-like, ca. 1.3 times as long as carpus and ca. 2.5 times as long as high; palm ca. 1.7 times as long as high. Dactyl strongly curved, hook-like, crossing fixed finger at tip when fingers closed, terminating in distal or subdistal sharp corneous claw; dorsal margin with scattered setae distally; cutting edge unarmed. Fixed finger broad basally, slightly bulging at base, glabrous, terminating in sharp corneous claw; cutting edge unarmed. Palm smooth, unarmed except for few setae on dorsal margin and distolateral margin next to base of dactyl. Sternite XII (between pereopods 4; Fig. 27B) with transverse fringe of setae all across.

Pereopod 5 (Fig. 27E) with chela 0.7 times as long as merus, with long, brush-like setae on dorsal and ventral surfaces. Dactyl with propodal rasp on ventral face. Propodal rasp consisting of minute ovate scales extending for 0.1 length of propodus. Ischium with setae dorsally and ventrally. Coxa with ventrodistal setae.

Male gonopod 1 with inferior lamella armed on distal margin with posterior row of slender, semitransparent hook-like, corneous spines. Gonopod 2 with distal segment strongly twisted distally, densely setose. Left unpaired pleopods 3–5 reduced when present (see Variations); when present, pleopod 3 biramous, pleopods 4 and 5 uniramous; no pleopods 3–5 on right side.

Female with left unpaired, well-developed, biramous pleopods 2–4 (ovigerous), rarely with vestigial pleopod 5; usually without unpaired pleopods 2–5 on right side (see "Variations"). Brood pouch large, oblong, distal margin weakly scalloped and fringed with sparse short setae.

Uropodal exopods (Fig. 25F) slender, broadly curved, terminating in strong, usually corneous-tipped spine, anterior margin with fringe of long, well-spaced setae and row of well-spaced corneous-tipped spines; endopods relatively short, curved, anterior margin with long setae and 1 or 2 irregular rows of corneous-tipped spines; protopods with strong, curved proximal spine.

Telson (Fig. 25F) subrectangular, slightly broader than long; posterior lobes usually broadly rounded, separated by shallow median cleft, terminal margins unarmed except for fringe of long setae.

Genetic data. See Table 1.

Color (Fig. 18D). Shield overall light orange overall, with darker orange and pair of white spots marking anterior margin of gastric region. Ocular acicles white. Ocular peduncles whitish basally, light orange distally, and with dark orange portion distolaterally and on optic calathus; corneas black except for somewhat yellowish external membrane. Antennular and antennal peduncles white to light orange. Chelipeds with meri, carpi, and chelae orange with irregular pattern and shapes of small white spots, and white spines; dactyls each with red spot basally; carpi each with red spot distodorsally; meri each with small red spots, one on dorsal margin distally, and three on distal margin. Pereopods 2 and 3 light to dark orange or reddish mixed with irregularly shaped white areas; dactyls white on distal one-third; carpi and meri each white distally and with small red spot distolaterally. Pereopod 4 with dactyl light orange dorsally, white distally and along cutting edge; palm and fixed finger mostly white except for orange medially on ventral and dorsal margins; carpus white to light orange, with darker orange on dorsal margin; merus distally light orange with darker orange on ventral margin, and white ventroproximally. Pereopod 5 mostly white with some light orange around margins of segments.

Etymology. The species name derives from the Latin *inermis*, meaning unarmed, and refers to the lack of armature on the cutting edge and lateral face of the fixed finger of pereopod 4, the main characteristic setting of this species.

Distribution. Western Pacific: Japan (Ogasawara Islands), South China Sea, Philippines, Indonesia (Banda Sea), Fiji Islands, Tonga Islands, and New Caledonia. Depth: 101 to 397 m.

Habitat and symbiont. Found with indeterminate species of acontiate anemone (see "Remarks" under genus *Paguropsis*).

Variations. As noted above, the armature of the dactyls of pereopods 2 and 3 is noticeably variable among the numerous specimens examined of this new species. The dorsomesial and ventromesial margins vary in armature from having bristle-like setae and obscure or altogether lacking any clearly visible corneous spines (e.g., in the holotype, Fig. 26B, D) to the margins armed with long, slender, corneous spines. When corneous spines are present, they can be arranged in dorsomesial and ventromesial rows of single spines (pereopod 2), or in rows of 1–3 clustered spines (pereopod 3). The presence or strength of the armature of the dactyls do not appear to be related to size of the specimens.

In the 25 males examined, the presence of left unpaired pleopods 3–5 is variable, as follows: 77% have reduced, biramous left pleopod 3; 55% have a reduced, uniramous pleopod 4; and 11% have a reduced, uniramous pleopod 5; 22% lack pleopods 3–5 altogether; no male specimens were found to have pleopods 3–5 on right side. Virtually all 22 females examined had pleopods 2–4 only on the left side and lacked pleopod 5. However, 10% of the females had a uniramous, vestigial pleopod 5. Only one ovigerous female (3.8 mm, CBM-ZC 14205) from Ogasawara Islands, Japan, was found to have right unpaired pleopods 2–4.

Remarks. See *Paguropsina pistillata* gen. et sp. n.

Key to species of *Paguropsis* and *Paguropsina* gen. n.

1 Exopod of maxilliped 3 slender, 4 or more times as long as broad (e.g., Fig. 4F); width of sternite XI less than 0.5 length of 1 coxa of pereopod 3 (e.g., Fig. 5B); cutting edge of fixed finger of chela of pereopod 4 armed with sharp spines arranged like bear claw (e.g., Fig. 14); gills with lamellae distally di-

vided into filamentous or stub-like extensions (e.g., Fig. 3A) .... ***Paguropsis*** **Henderson, 1888)**...**2**

– Exopod of maxilliped 3 broad, 2.4 times as long as broad (e.g., Fig. 23C); width of sternite XI same as length of 1 coxa 1 of pereopods 3 (e.g., Fig. 21D); cutting edge of fixed finger of chela of pereopod 4 unarmed or at most with 1 distinct corneous spinule (often slightly offset laterally from cutting edge; Figs 24F, 27D); gills with lamellae deeply divided distally into finger-like extensions (e.g., Fig. 25E) ....***Paguropsina*** **gen. n.**...**6**

2 Lateroproximal surface of dactyl of pereopod 3 with longitudinal concavity; sternite XI separating coxae of pereopods 3 by ca. 0.2 length of 1 coxa, posterior lobes of sternite XI strongly compressed...**3**

– Lateroproximal surface of dactyl of pereopod 3 convex, without longitudinal concavity; sternite XI separating coxae of pereopods 3 by distinctly more than 0.2 length of 1 coxa, posterior lobes of sternite XI not compressed **4**

3 Lateroproximal surface of dactyl of pereopod 3 with distinct and usually weakly calcified longitudinal concavity (Figs 1E, 10C); background coloration mostly orange-red (Figs 8C, 28B) ....***Paguropsis andersoni*** **(Alcock, 1899)**

– Lateroproximal surface of dactyl of pereopod 3 with weak, calcified longitudinal concavity; background coloration mostly white with orange patches on pereopods 2 and 3 (Figs 8D, 28C, D)..................***Paguropsis confusa*** **sp. n.**

4 Chela of pereopod 4 lacking dense patch of capsulate setae on dorsal margin of palm (only with fringe of long setae); coloration as in Figs 8A, B, 28A ....***Paguropsis typica*** **Henderson, 1888**

– Chela of pereopod 4 with dense patch of capsulate setae on dorsal margin of the palm; coloration not as above...**5**

5 Patch of capsulate setae on dorsal margin of palm of chela of pereopod 4 arranged in a series of oblique rows or fringes of setae, patch occupying area from dorsal margin to nearly midlength of lateral face of palm (Fig. 15D); dorsal surfaces of chelae and carpi covered with dense tufts or short rows of long, bristle-like setae nearly obscuring armature below; dactyls of pereopods 2 and 3 relatively wide (7–9 times as long as broad); coloration: Fig. 18A..... ....***Paguropsis gigas*** **sp. n.**

– Patch of capsulate setae on dorsal margin of palm of chela of pereopod 4 not arranged in rows or fringes of setae, patch occupying area from dorsal margin to nearly one-fourth of lateral surface of the palm (Fig. 21B, C); dorsal surfaces of chelae and carpi moderately covered with short bristle-like setae not obscuring armature below; dactyls of pereopods 2 and 3 relatively narrow (10–16 times as long as broad); coloration: Fig. 18B......................... ***Paguropsis lacinia*** **sp. n.**

6 Cutting edge of fixed finger of chela of pereopod 4 armed with 1 distinct corneous-tipped spine often slightly offset laterally from cutting edge (Fig. 24F); coloration: Fig. 18C ....***Paguropsina pistillata*** **gen. et sp. n**

– Cutting edge of fixed finger of chela of pereopod 4 unarmed (Fig. 27D); coloration: Fig. 18D...................................***Paguropsina inermis*** **gen. et sp. n**

Discussion

Biogeographic summary

The results of this revision provide a vision of the overall biogeographic distribution of the seven species herein discussed of *Paguropsis* and *Paguropsina* gen. n. This vision, however, is preliminary as it is evident that many of the vast marine shelf areas and deep-sea habitats of the Indo-West Pacific where species of these two genera live, still remain to be sampled. Species of *Paguropsis* are distributed in the tropical and subtropical regions of the Indo-West Pacific, in continental shelf to upper slope depths of 30 to 1125 m. Of the five species of *Paguropsis*, only two have been found to occur outside the western Pacific: *P. andersoni*, distributed widely across the Indian Ocean, from off southeastern Africa, both coasts of India, Andaman Sea, to the extreme southeastern coast of Indonesia in the Arafura Sea; and *P. confusa* gen. et sp. n., found from the southwestern Indian Ocean and the western Pacific from the Philippines and Makassar Straits, Indonesia (Kalimantan). The other three species of *Paguropsis*, *P. typica*, *P. gigas* sp. n., and *P. lacinia* sp. n., have been found to be distributed exclusively in the western Pacific region. Of these, *P. typica* occurs the farthest north (off Daito Islands, Ryukyu Islands, Japan) and the farthest south (off eastern Australia), and reaches the Fiji Islands to the east; *P. gigas* sp. n. is so far known only from the South China Sea; and *P. lacinia* sp. n. has the easternmost distribution in the South Pacific, distributed from the Solomon Islands to the Tonga Islands. The two species of *Paguropsina* gen. n. are exclusively distributed in the western Pacific, in depths ranging from 52 to 849 m. Of these, *P. pistillata* gen. et sp. n. occurs from the Philippines to the New Caledonia region; and *P. inermis* gen. et sp. n. from Ogasawara Islands, Japan and off Taiwan in the South China Sea, to the Tonga Islands. It is noteworthy that despite extensive sampling during the last three decades in French Polynesia (Tuamotu Archipelago), Marquesas, Society and Austral Islands (e.g., Bouchet 2009; Poupin 1991, 1998, 2010; Richer de Forges 2002; Richer de Forges et al. 1999), no species of *Paguropsis* or *Paguropsina* gen. n. have yet been found there.

Morphology and evolution

The unusual body symmetry and variable presence and position of unpaired pleopods 3–5 in males and unpaired pleopods 2–5 in females, and in the case of females also a brood pouch, indistinctly on the left or right side of *Paguropsis typica*, has been highlighted by various carcinologists since the time of Henderson's (1888) description of his remarkable species (e.g., Stebbing 1893, Alcock 1905, Boas 1926, Russell 1962). Indeed the striking symmetry of cephalothorax, pereopods (including chelipeds), membranous pleon (unpaired pleopods 2–5 excepted), uropods and telson, is unique among the so-called "asymmetrical" paguroids (i.e., all families except Pylochelidae). The pleonal symmetry and variability of pleopods of *P. typica* was compared by Mayo

(1973) with a similar condition found, at least in females, in species of the diogenid *Cancellus* H. Milne Edwards, 1836, which live in pieces of rock, sponge, coral or other firm substrates. As in the species discussed herein of *Paguropsis* and *Paguropsina* gen. n., those of *Cancellus* also have symmetrical pereopods (including chelipeds) uropods and telson. In several important respects, however, species of *Paguropsis* and *Paguropsina* gen. n. differ drastically from *Cancellus,* and it is probable that the symmetry exhibited by species of these genera is not indicative of a close phylogenetic relationship and instead is attributable to parallel evolution. In *Cancellus*, pereopods 4 and 5, and uropods, have strongly developed rasps as in many typical "asymmetrical" paguroids, and pereopod 4 is only semichelate (McLaughlin 2003), whereas in *Paguropsis* and *Paguropsina* gen. n. there are no rasps, and pereopod 4 is fully chelate. Furthermore, males of species of *Cancellus* lack all pleopods, whereas males of species of *Paguropsis* and *Paguropsina* gen. n. have paired pleopods 1 and 2 modified as gonopods, normally have unpaired pleopods 3 and 4, and often also pleopod 5 as well albeit reduced.

Previous to this study, the development of a fully chelate pereopod 4, without a propodal rasp, has been less noted in *Paguropsis*. This condition is only present in one other paguroid, the semi-terrestrial coenobitid *Birgus latro* (Linnaeus, 1767) where the abandonment of housing for protection by adults and the non-aquatic life has led to various unusual morphological feeding and respiratory specializations (Drew et al. 2010). It seems evident that convergence has taken place and thus the development of chelate pereopods 4 is for very different purposes, and has occurred independently in these two genera classified in different families, specifically for handling the carcinoecia (acontiate anemone) in *Paguropsis* and *Paguropsina* gen. n., or as a general prehensile mechanism in *B. latro*. Regrettably, the behavior of species of *Paguropsis* and *Paguropsina* gen. n. has not been studied other than the basic observation at the time of the discovery of *P. typica*, that individuals use the specialized chelae of pereopods 4 to grasp and pull the blanket-like coenosarc of their acontiate anemone symbiont to cover or uncover their bodies (Alcock, 1905).

The evolution of the specialized morphology of species of *Paguropsis* and *Paguropsina* gen. n. can be attributed to the symbiosis with anemones as mode of housing, without the intervention of mollusk shells or other hard habitat at any time during the life of the hermit crab. Aside from symmetry, species of *Paguropsis* and *Paguropsina* gen. n. are unique in lacking rasp structures on pereopods and uropods, a character that is a *sine qua non* for all five families of "asymmetrical" Paguroidea. Only two other species among the "asymmetrical" hermit crabs are known, or at least suspected, to use exclusively a cnidarian as carcinoecia, the Parapaguridae *Tylaspis anomala* Henderson, 1885 and *Sympagurus poupini* Lemaitre, 1994 (Lemaitre 1994 1998). However, except for the shape of the uropods and telson, these two parapagurids do have at least vestiges of rasps, are not strictly symmetrical as they have a right cheliped larger than the left. Although paired pleopods are present in *T. anomala*, these are asymmetrical and differ in degree of development from one side to the other.

Aside from the generic characters that differentiate species of *Paguropsis* and *Paguropsina* gen. n., the morphology of the species in these two genera is remarkably homogenous, with species differing only in relatively minor details. This homogeneity can be attributed, at least in part, of the adaptation to a similar symbiotic mode of life with an acontiate anemone as means of protection for the membranous pleon. All species in the two genera live symbiotically with indeterminate species of anemones. The need to manipulate their cnidarian symbiont has evidently led species of *Paguropsis* and *Paguropsina* gen. n. to develop fully chelate pereopods 4, the appendage used to grasp and move back and forth the sheet-like coenosarc of the symbiont. It is striking, however, that two species of *Paguropsis* (*P. gigas* sp. n. and *P. lacinia* sp. n.), and both known species of *Paguropsina* gen. n. (*P. pistillata* gen. et sp. n. and *P. inermis* gen. et sp. n.), have developed specialized morphological features on the chela of this appendage, those of the former genus as setal patches (Figs 15D, 17A, 21B, C, 22E), and those of the latter genus by the presence or absence of a conspicuous spine on the fixed finger (Figs 21E, 24F, 26D).

There is one unusual character discovered during this study that had not been documented before in the single previously known species of *Paguropsis*, *P. typica*: the presence on the ventral face of the coxae of the chelipeds of a decalcified longitudinal fissure (e.g., Fig. 5B, D). The fissure is present in all species of *Paguropsis* and *Paguropsina* gen. n. Although rare in paguroids, a similar and presumably homologous fissure on the coxae of the chelipeds has been documented by Forest (1989, 1993) in species of two other diogenid genera, *Paguristes* Dana, 1851 and *Bathynarius* Forest, 1989, and by Komai & Takeda (2004) in yet another species of the latter genus, *B. izuensis* Komai & Takeda, 2004. The function of this fissure is unknown, although as surmised by Forest (1989, 1993), it most likely plays a role during the molting period.

Modern studies that have focused on details of anomuran evolution (e.g., Tsang et al. 2011, Bracken-Grissom et al. 2013) have reaffirmed the virtually unanimous long held view that asymmetrical paguroids evolved from symmetrical ancestors similar to the “symmetrical” hermit crabs of the family Pylochelidae, and that the asymmetrical features exhibited by most paguroids originated as result of habitation in gastropod shells (particularly dextrally coiled shells). Although these modern studies have not been explicit in defining “asymmetry”, it is understood that the asymmetry refers to the most prominent external asymmetrical paguroid features, i.e., the right or left handedness, coiled pleon with unpaired pleopods, and various degrees of asymmetrical development of uropods and telson. One other external feature unique to all hermit crabs, whether they are symmetrical or asymmetrical, is the presence of rasp structures for better gripping their hard housing, on the propodi of pereopods 4 and 5 and anterior margins of uropods. These rasps structures consist of surfaces typically densely covered by modified setae that are scale-like or conical in shape (Keiler and Richter 2011). However, none of these modern studies have incorporated the previously monotypic *Paguropsis* in their data. That species of *Paguropsis* and *Paguropsina* gen. n. are symmetrical and lack any vestige of rasps in any appendage, seems to indicate three possible evolutionary scenarios: 1) the ancestor of these species did not use shells or for that matter any other form of hard type of housing for pleonal protection, and thus the asymmetry of pleopods requires a different explanation than the use of gastropod shells; 2) use of gastropod shell by the ancestor of these species occurred for a period not long enough to cause or fix any development of paguroid features except for beginnings of asymmetry in pleopods; or 3) the ancestor of these species was asymmetrical in all paguroid features but they secondarily regained their ancestral symmetry in all features except the pleopods. Regardless of which scenario is more plausible, species of *Paguropsis* and *Paguropsina* gen n. appear to represent a clade of key importance in paguroid evolution.

Preliminary remarks on molecular genetics

The molecular data herein included (Table 1) complements the morphological descriptions or redescriptions of all seven species of *Paguropsis* and *Paguropsina* gen. n. This data is intended for future studies of genetic relationships among populations of the different species or in comprehensive phylogenetic studies of diogenids in particular and paguroids in general. A preliminary maximum likelihood tree generated from a concatenated analysis of three mitochondrial genes (12S, 16S, COI), and using the pagurid *Phimochirus operculatus* (Stimpson, 1859) as outgroup, reveals that all the species herein discussed separate into two highly supported clades, matching the proposed morphologically-based separation into two genera, i.e., *Paguropsis*, with the five species, and *Paguropsina* gen. n., with two species. Thus it seems evident that at least the main morphological characters used to differentiate the two genera, i.e., the shape of gills, shape of exopod of the third maxilliped, width of sternite XI, and armature of the fingers of pereopod 4, are of significant evolutionary value. Within each clade or genus, the species can be distinguished as well, although in some phenotypically similar species-pairs, i.e., *Paguropsis typica-P. confusa*, and *Paguropsina pistillata-P. inermis*, the separation is minimal or obscure based on our mitochondrial gene dataset. The minimal genetic separation of these species-pairs is not unexpected, given that the morphological differences between them are minimal. A wide character analysis combining morphology and genetic data of *Paguropsis* and *Paguropsina* gen. n., and incorporating other diogenid genera, is needed to better understand the evolution and origin of the family Diogenidae.

Symbiotic association

The most remarkable biological feature of species of *Paguropsis* and *Paguropsina* gen. n. is their intriguing symbiotic association with acontiate anemones, without the intervention of snail shells or other hard type of housing. Regrettably, virtually no information exists on the nature and origin of the association except for the brief comments in reports of earlier naturalists (e.g., Alcock 1899, 1905, Boas 1926). Even the identity of the symbiont remains unclear, with earlier authors such as Boas (1926) reporting the cnidarian symbiont used by *Paguropsis typica* to be *Epizoanthus paguropsidis* (see

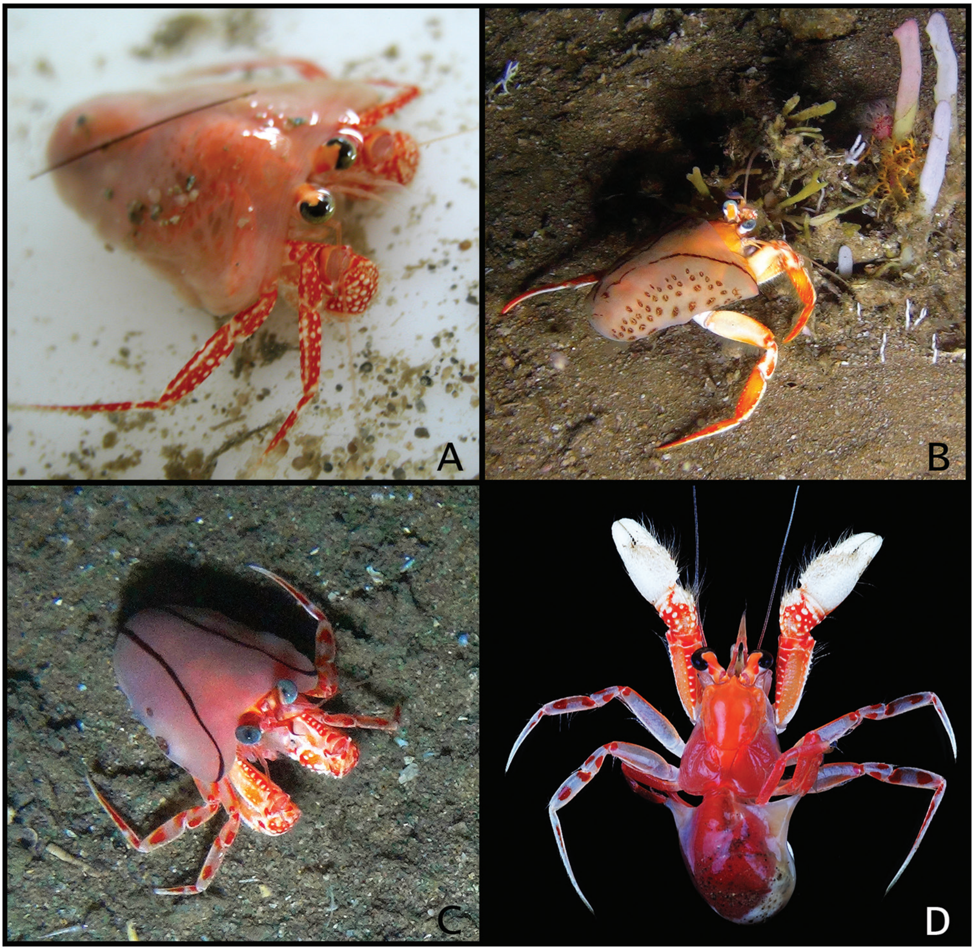

Figure 28. A *Paguropsis typica* Henderson, 1888: live specimen in sorting tray on board ship (photograph: B Richer de Forges) **B** *Paguropsis andersoni* (Alcock, 1899), not collected, ROV, KwaZulu-Natal, South Africa, DST/NRF ACEP Spatial Solutions cruise, Aliwal outer reef, off KwaZulu-Natal, RY *Angra Pequena*, sta R50: specimen photographed *in situ* with ROV, not collected (photograph: DST/NRF ACEP – Spatial Solutions project team) **C, D** *Paguropsis confusa* sp. n.: **C** specimen photographed *in situ* with ROV, not collected, off Durban, KwaZulu-Natal, South Africa, DST/NRF ACEP Spatial Solutions Project cruise, sta R45 Echinoderm Extravaganza (photograph: DST/NRF ACEP – Spatial Solutions project team) **D** not examined, Philippines, LUMIWAN CP 2867–16 (photograph: T-Y Chan).

Fig. 1D). However, recent photographs (Fig. 28A–D) of live specimens of *Paguropsis typica, P. andersoni*, and *P. confusa* (of the former species taken on board during an expedition in the Philippines, and of the latter two species taken *in situ* with ROV off South Africa, western Indian Ocean), reveal that the symbionts are undetermined species of acontiate anemones that have puzzling dark spots and lines on their body wall. Whether each species of *Paguropsis* or *Paguropsina* gen n. associate with a particular species of anemone remains unknown. In the interest of documenting additional information on the symbionts, we shared these photographs with anemone expert Dr. DG Fautin (Professor Emerita, University of Kansas), who kindly provided the following explanation (in litt.): "Many acontiate anemones that live on hermit crabs have cinclides (pores; singular cinclis) through which the acontia can be emitted. When the anemone contracts with the mouth tightly closed, the acontia are carried out through the cinclides with the water. Cinclides are typically in a ring distal to ("above") the base of the anemone but they otherwise resemble these spots in being darker around the edge (which may be raised) than in the middle (through which acontia are emitted). In some anemones the pore is patent; in others, there appears to be no actual pore but the body wall is much thinner in that part than elsewhere – so the wall ruptures when pressure rises, thus acting like safety valves." Various carcinologists (e.g., Alcock 1905; Boas 1926), based on preserved specimens, have documented and illustrated how *Paguropsis typica* presumably utilizes the prehensile chelae of pereopods 4 to move back and forth the coenosarc of the anemone to cover their bodies up to the shield and partially the meri of pereopods 3 (Figs 1A, E, 28A–C). A photograph of a freshly caught specimen of *P. confusa* sp. n. (Fig. 28D) obtained during this study, provides an indication of how effectively this species can grab onto the thin-walled body of the anemone using the dactyl and bear claw-like spination of the fixed finger of the chelae of pereopods 4. However, the two species of *Paguropsina* gen. n. have developed a slightly different and more simplified grasping morphology on the dactyl and fixed finger of pereopod 4 that resembles ice-block tongs. In these two species, the dactyl and fixed finger are strongly curved distally forming a near circle so that the claws directly face each other, and lack the bear claw-like spination on the fixed finger. In *P. pistillata* gen. et sp. n., the fixed finger is armed with a single spine (Figs 21B, 24F), and in *P. inermis* gen. et sp. n., the fixed finger is unarmed.

Acknowledgements

This study was conceived during team visits to the MNHN nearly two decades ago, by the late Dr. Patsy A. McLaughlin, DLR and RL, in order to study the extensive collections of paguroids obtained during French-sponsored campaigns to the Indo-West Pacific. After examining numerous samples we realized that the genus *Paguropsis*, long assumed to be monotypic, was in need of revision. Regrettably, our senior colleague, PA McLaughlin, passed away in 2011, when the project was just beginning to take shape. To her we are deeply grateful for advice, sharing of notes, archival information left to RL after her death, and especially for inspiration in so many ways. To the following at the MNHN we must extend our sincere thanks for making available for study the many specimens obtained during the extraordinary French-sponsored expeditions, and providing much information: A Crosnier, P Bouchet, L Corbari, P Maestrati, and P Martin-Lefèvre. Thanks are given to a number of colleagues at various other institutions and museums that loaned us type or other key specimens, or provided various kinds of data and information that greatly assisted us; these are: T-Y Chan, P Clark, CHJM Fransen, J Høeg, J Landschoff, M Lowe, PKL Ng, J Oleson, J Poupin, B Richer de Forges, M Thiel, and L Watling. We are greatly indebted to T-Y Chan and B Richer de Forges for permission to use their outstanding color photographs of freshly caught specimens. In South Africa, special thanks are due to: J Landschoff for his alert, enthusiastic field work, and kindly sharing data on specimens he collected and/or deposited at the SAMC, and for linking us to South African sampling programs; K Sink, Department of Science and Technology/National Research Foundation and African Coelacanth Ecosystem Programme in South Africa, and R Palmer, National Research Foundation, South African Institute for Aquatic Biodiversity, for station data and allowing us to use specimens and *in situ* ROV color photographs taken by the team of the DST/NRF ACEP – Spatial Solutions Project. In Japan, our colleague K Baba helped us to obtain various published information in Japanese. Critical explanations and opinion on the cnidarian symbionts were generously offered by JD Reimer and DG Fautin. We are extremely grateful to our colleague A Windsor, for kindly performing the DNA laboratory analyses included as "Genetic data" for each species and adding the data to GenBank (Table 1) as well as advice and comments on the preliminary tree generated. RA Gulledge prepared the digital versions of the illustrations and photographic plates. TK thanks scientists and personnel on board TRV *Shin'yo-maru* (Tokyo University of Marine Science and Technology) and RV *Koyo* (Ogasawara Fishery Center, Tokyo Metropolitan Government) for their generous help in sampling. The detailed comments and suggestions provided by two reviewers are greatly appreciated, and considerably improved the final product.

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ZooKeys 752: 99–123 (2018)
doi: 10.3897/zookeys.752.24440
http://zookeys.pensoft.net

RESEARCH ARTICLE

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First description of the larva of *Dinaraea* Thomson, 1858, with comments on chaetotaxy, pupa, and life history based on two saproxylic species from Europe (Staphylinidae, Aleocharinae, Athetini)

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Academic editor: *J. Klimaszewski* | Received 13 February 2018 | Accepted 23 March 2018 | Published 23 April 2018

http://zoobank.org/D7736703-68C6-4521-AC43-AA6AF774960F

Citation: Staniec B, Pietrykowska-Tudruj E, Pawlęga K (2018) First description of the larva of *Dinaraea* Thomson, 1858, with comments on chaetotaxy, pupa, and life history based on two saproxylic species from Europe (Staphylinidae, Aleocharinae, Athetini). ZooKeys 752: 99–123. https://doi.org/10.3897/zookeys.752.24440

Abstract

The paper describes the morphological ultrastructure of the previously unknown early (L1) and late larval instars (L2–3) of *Dinaraea*, including chaetotaxy, pupal cocoon, prepupa, and pupa, based on the saproxylic species *D. aequata* Erichson and *D. linearis* Gravenhorst. Diagnostic larval characters for the genus *Dinaraea* are given for the first time. Morphological differences between mature larvae of these two species relate to the colouration and degree of flattening of the body, details of antennal structure, anterior margin of the labrum, mandibles, and mala. The differences are relatively small, probably because of the similar ecological preferences of both species. As in the case of other aleocharine larvae, L1 in *Dinaraea* differs from L2–3 in the lack of some setae on the dorsal surface of the head and thorax, and on the abdominal tergites and sternites; the presence of a subapical seta on the urogomphi; egg bursters on some thoracic and abdominal tergites; a darker antennal segment III; and the relatively longer urogomphi and their apical setae. The differences established in the features of the chaetotaxy of L1 and L2–3 between Athetini (*Dinaraea*), Oxypodini (*Thiasophila*) and Homalotini (*Gyrophaena*) correspond with the molecular marker-based relationships of these taxa.

Keywords

aequata, aleocharines, Coleoptera, developmental stages, early and late larval instars, ecological preferences, *linearis*, morphology, pupal stage, rove beetles, staphylinids, subcortical, ultrastructure

Introduction

The genus *Dinaraea* Thomson, 1858 (Staphylinidae, Aleocharinae, Athetini) includes 21 species worldwide, 12 of which are known from the Nearctic and nine from the Palaearctic; five of the latter (*D. aequata* Erichson, *D. angustula* Gyllenhal, *D. arcana* Erichson, *D. hungarica* Ádám, *D. linearis* Gravenhorst) occur in Europe. They are small insects (the lengths of the European species are 2.5–3.7 mm) with a subparallel, flattened body, and the integument has a distinct meshed microsculpture and distinct punctation. The head is large, subquadrate to slightly elongate, and the genae are usually longer than the eyes. Mainly saproxylic, *Dinaraea* species inhabit the subcortical galleries of other insects. They are also found in rotting tree trunks and in the fruiting bodies of various polypores. Because of their environmental preferences and their probably predatory mode of life, most species of this genus are potentially important as enemies of economically significant forest pests. To date, however, the diet of these rove beetles remains unknown, as do other aspects of their biology (Benick and Lohse 1974, Nikitsky and Schigel 2004, Klimaszewski et al. 2013, Löbl and Löbl 2015).

Nothing is known of the morphology of the preimaginal stages of *Dinaraea*. This is not particularly surprising, since very little information is available on the external structure of other Athetini taxa, just as is the case with most Aleocharinae. The larvae of only a few of the more than 170 genera classified among Athetini are known (Paulian 1941, Pototskaya 1967, Topp 1978, Ashe and Watrous 1984, Ashe 1985, Newton et al. 2000, Ashe 2005). What is more, such descriptions as do exist are usually fragmentary and relate to just a few features illustrated in diagrams. The very poor state of knowledge regarding the larvae of these staphylinids makes it almost impossible to make use of their morphologies in phylogenetic analyses. Only Ashe (2005), in a work on the phylogeny of the tachyporine group subfamilies and 'basal' lineages of the Aleocharinae, took into account features of both imagines and larvae, including three genera of Athetini. It turns out that the larval characters to a large extent stabilise the phylogenetic tree covering the taxa under consideration in the present work. In the case of other aleocharines, this same author also used larval morphologies to examine phylogenetic relationships within the subtribe Gyrophaenina (Ashe 1986). The results turned out to be confluent with the morphological analysis of the imagines of these Staphylinidae. They point to the distinct monophyletic origin of that subtribe and are strongly underpinned especially by the external features of these Aleocharinae. The greater usefulness of larval than imaginal stages in phylogenetic analyses was also demonstrated by Grebennikov and Newton (2009) in the case of ten subfamilies in the Staphylininae group. Again, Pietrykowska-Tudruj et al. (2011, 2014) highlighted the great importance of larval features in establishing the systematic membership of *Quedius antipodum* Sharp and the genus *Astrapaeus* Gravenhorst. The results substantiate data obtained from analyses of adult morphology and/or DNA sequences, and suggest the separate position of *Q. antipodum* in relation to the north temperate genus *Quedius* and the genus *Astrapaeus* within the tribe Quediini.

The necessity to take larval morphological features into consideration in future phylogenetic analyses and assessments of the systematic membership of Staphylinidae thus seems wholly logical. Unfortunately, a major obstacle to doing so is the insufficient and often extremely fragmentary nature of the relevant data, as mentioned above, which applies in particular to the subfamily Aleocharinae, including the tribe Athetini.

The main aim of this study is to describe in detail the external morphology, including the chaetotaxy and ultrastructure, of the early (L1) and late (L2–3) larval instars of *Dinaraea* based on *D. aequata* and *D. linearis*. The paper also includes data on the external appearance of the hitherto unknown pupa of this genus, as well as the feeding preferences and the life histories of both species.

Materials and methods

Larval and pupal stages of the two species were obtained by rearing five adults of *D. aequata* and four adults of *D. linearis*. Specimens of *D. aequata* were collected at Parchatka near Kazimierz Dolny (51°22'54.55"N, 21°59'51.53"E, SE Poland) on 11 November 2004. The insects were sifted from the remains of birch bark, in deciduous woodland growing in a shady, damp loess gully. Individuals of *D. linearis* were collected at Łańcuchów near Lublin (51°16'15.33"N, 22°55'20.35"E, SE Poland) on 3rd December 2004. These beetles were sifted from pieces of bark torn off a wind-thrown ash (*Fraxinus excelsior* L.) in an old riparian wood of ash and alder (Circaeo-Alnetum) in the valley of the River Wieprz, a dozen or so metres from the river bank. *D. aequata* and *D. linearis* were reared from 19 November 2004 to 20 January 2005 and from 6 December 2004 to 21 February 2005, respectively, at room temperature (20 °C ± 3). Adults and larvae of both species were kept separately in plastic containers (diameter 10 cm, height 2 cm) filled with moist soil. Larvae were fed various sizes of small springtails of the family *Onychiuridae*. The immature stages (larvae and pupae) were killed in boiling water and preserved in ethanol (75%). The adults were identified by the first author.

Morphometry and morphology: specimens were measured using an Olympus BX63 compound microscope. Measurements were made in cellSens Dimension v1.9 software and are given in millimetres. Photographs showing total aspects of the mature (L3) larvae of both species, as well as the prepupa and pupal cocoon of *D. linearis* were taken with an Olympus DP72 digital camera mounted on an Olympus SZX16 compound microscope (Figs 1–6, 61–64). To prepare microscope slides for the morphological analyses, the preserved larvae were treated with 10% KOH for approximately twelve hours, rinsed in distilled water, then immersed in lactic acid. Photographs showing various details of the external structure of larva and the total aspect of larva and pupa were taken using an Olympus DP21 digital camera mounted on an Olympus BX63 compound microscope (Figs 14, 15c, 18–21, 24–26, 28–31, 33–35, 41, 43–60) or with a VEGA3 TESCAN SEM (Figs 7–11, 12, 13a, b, 15a, b, 16, 22, 23, 27a, 32, 34a, 36–40, 42, 47a, 54a, 65–68), and subsequently corrected using CorelDRAW Graphics Suite X6.

The material examined for morphological study and measurements is listed in Tables 1 and 3. Chaetotaxy nomenclature, symbols, and abbreviations follow Ashe and Watrous (1984), and the morphological description style is according to Staniec et al. (2016). The voucher specimens are deposited in the collection of the Department of Zoology, Marie Curie-Sklodowska University, Lublin.

Results

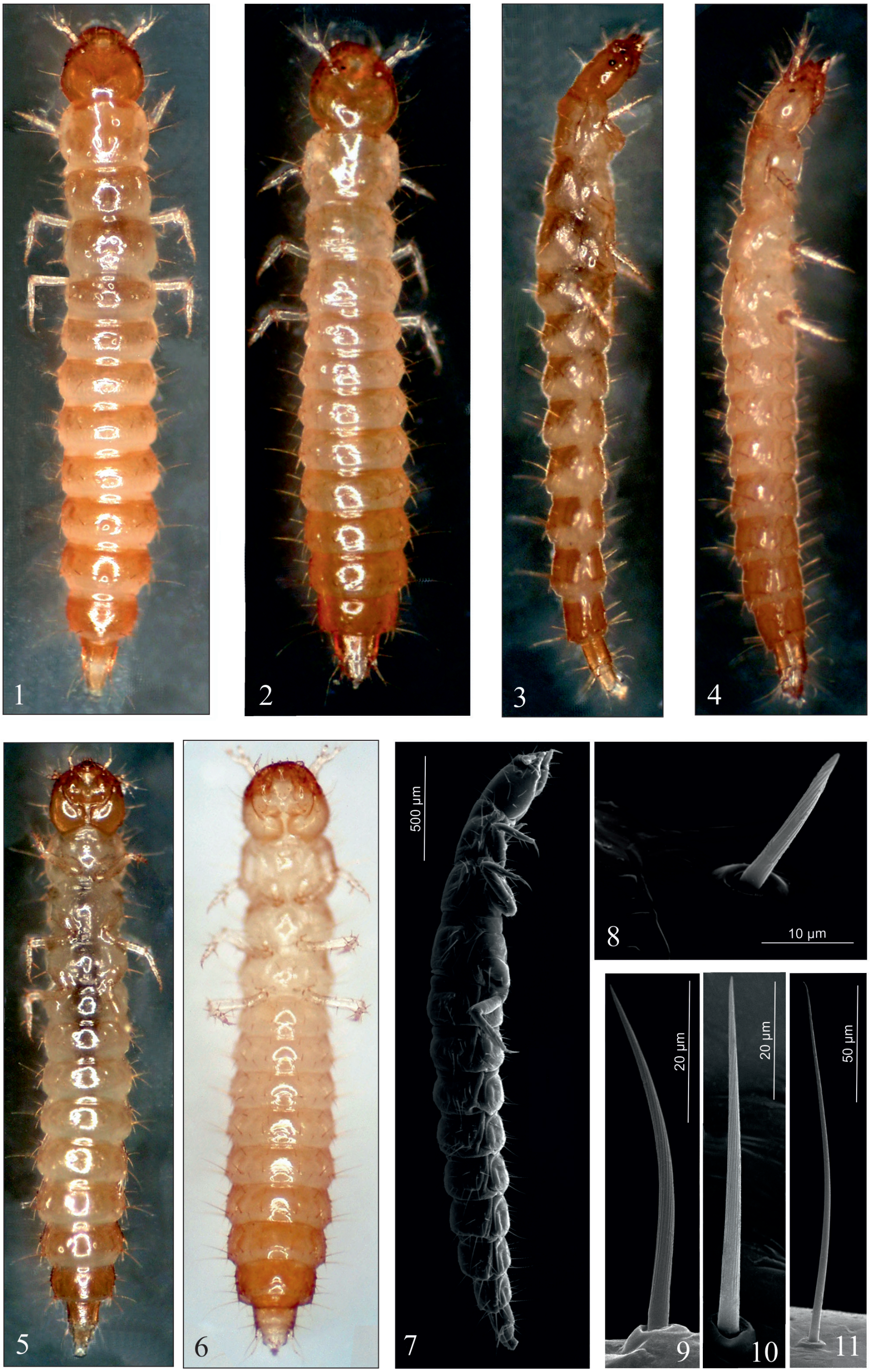
Generic diagnosis of the mature larvae

The combination of characteristics that enable mature larvae of *Dinaraea* to be distinguished from known larvae of other genera within the subfamily Aleocharinae are as follows (Paulian 1941, Pototskaya 1967, Topp 1975, Ashe 1981, 1985, Ashe and Watrous 1984, Ahn 1997, Jeon and Ahn 2009, Staniec et al. 2009, 2010, 2016, Zagaja et al. 2014, the present study): (1) body narrow, elongate, dorso-ventrally flattened, sides almost parallel; (2) pronotum slightly wider than (at most 1.1 as wide as) head; (3) antennal article I longer than wide; (4) sensory appendage (Sa) of antennal article II acorn-shaped, longer than antennal article III; (5) length ratio of antennal articles I and II – 1:1.6; (6) central region of anterior margin of labrum protruding and crenate; (7) mandibles with one large and two-five small subapical teeth; (8) mala at least slightly widened at adoral margin; (9) adoral margin of mala with eight large and approx. 15 small teeth; (10) length ratio of article I and III of maxillary palp – 1:1.5; (11) ligula finger-like, 2.5 × as long as wide; (12) hypopharynx with approx. 60 triangular microtrichia directed towards the central area without microtrichia; (13) length ratio of articles I and II of labial palp – 1:2.1; (14) pronotum without seta Da1; (15) on abdominal sternite I seta P5 present, seta D3 absent; (16) abdominal segment X approx. 2.5 × as long as urogomphus (without apical seta); (17) length ratio of urogomphus to its apical seta – 1:1.6.

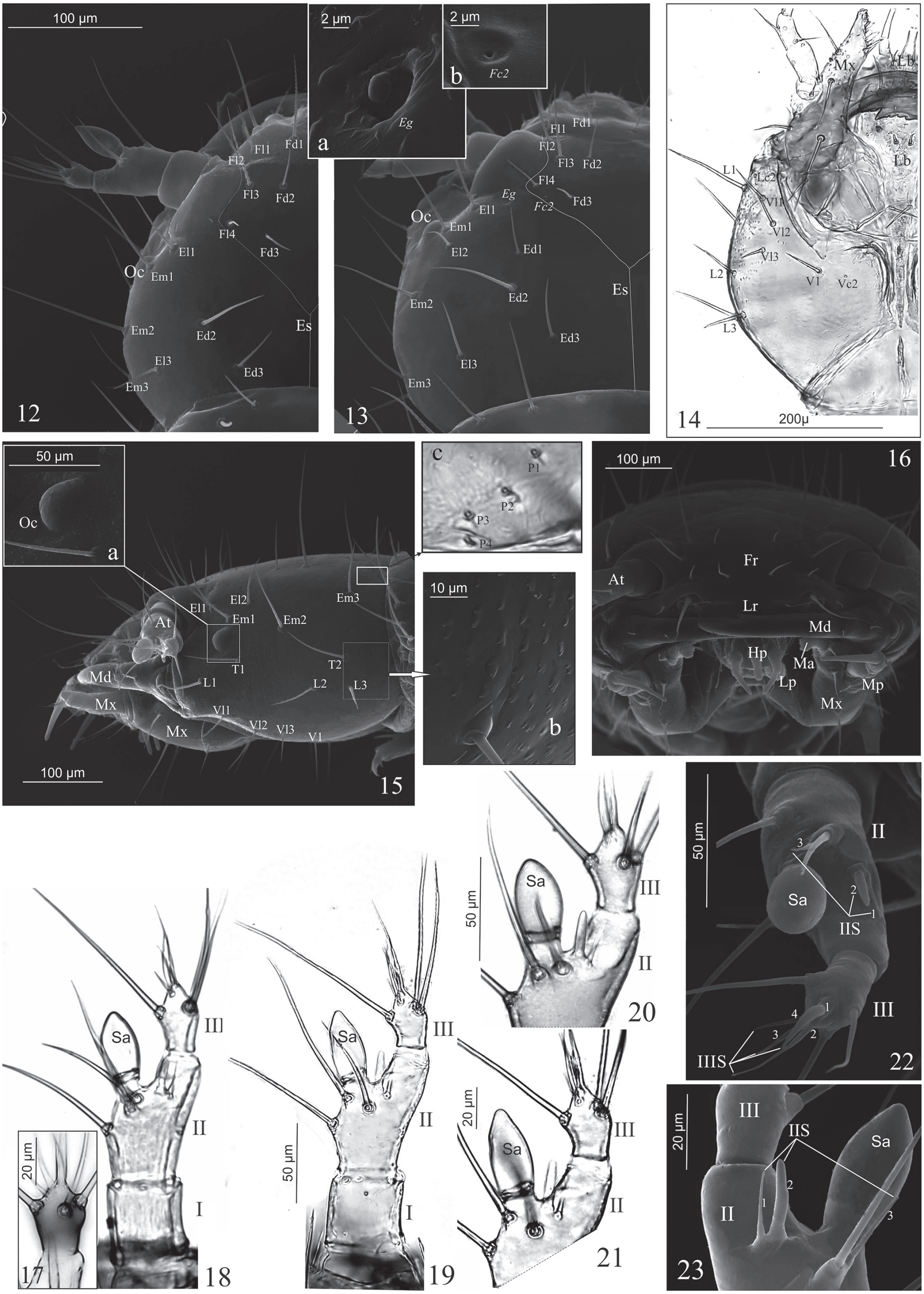
Description of larval stages (*D. aequata-D.a.*; *D. linearis-D.l.*)

Late larval instars (L2–3) (Figs 1–7)

Body narrow, elongate, semi-cylindrical, distinctly (*D.a.*) or moderately (*D.l.*) dorso-ventrally flattened, sides almost parallel, head slightly narrower than prothorax and as wide as mesothorax, pro- and metathorax almost equal in width, abdomen gradually widening to segments IV or V, then tapering to terminal segment of body; segments IX and X distinctly narrower than the others. Colour: whole head reddish brown (*D.a.*) or anterior area of head reddish brown, but posterior distinctly paler (*D.l.*), ocellus dark; all tergites yellowish brown (*D.a.*) or all thoracic and abdominal tergites I–V almost colourless, then tergites gradually darkening from yellow (VI) to yellowish brown (VII) and reddish brown (VIII, IX) *(D.l.)*; abdominal sternites gradually darkening from yellowish brown (I) to brown (VIII and IX) (*D.a.*) or abdominal sternites I–V almost



Figures 1–11. *D. aequata* (**1**, **3**, **5**, **7**–**11**), *D. linearis* (**2**, **4**, **6**), mature larva. **1–7** habitus in dorsal (**1**, **2**), lateral (**3**, **4**, **7**) and ventral (**5**, **6**) aspect, **8–11** setae near epicranial suture (**8**) of abdominal tergites (**9–11**).



Figures 12–23. *D. aequata* (**12**, **13**, **15**, **16–18**, **20**, **22**, **23**) *D. linearis* (**14**, **19**, **21**). First larval instar (**12**, **17**), mature larva (**13–16**, **18–23**), **12–16** head in dorsal (**12**, **13**), ventral (**14**), lateral (**15**) and frontal (**16**) aspect with glands (**13**a, **13**b), ocellus (**15a**), microstructure (**15b**) and posterior setae (**15c**), **17–23** right antenna, article III in dorsal aspect (**17**), entire in dorsal aspect (**18**, **19**), anterior region in dorsal aspect (**20**, **21**), entire in apical aspect (**22**), anterior region of article II in ventral aspect (**23**)..

colourless but the others somewhat darker (*D.l.*); legs and abdominal segment X colourless. Setae of different length, light brown, simple with longitudinal grooves (Figs 8–11). Microstructure of head and tergites as in Figs 15b, 54a.

Head (Figs 13–16): almost as long as wide, widest at level of setae Ed3, lateral margins distinctly rounded; dorsal ecdysial lines (Es) bifurcate at approx. half the head length; each side of head with one oval, weakly convex, black ocellus (Oc) (Figs 3, 4, 12, 13, 15, 15a). Chaetotaxy of dorsal side with 40 setae – 14 frontal [2(Fd1–3, Fl1–4)], 18 epicranial [2(Ed1–3, Ell-3, Em1-3)], eight posterior micro setae (2P1–4); a pair of frontal campaniform sensillae (Fc2) and epicranial glands (Eg) (Figs 13, 13a, 13b, 15c). Lateral margins with ten setae [2(T1–2, L1–3)] (Fig. 15). Ventral side with eight setae [2(Vl1–3, V1)], and a pair of ventral (Vc2) and lateral (Lc2) campaniform sensillae. Functional position of antennae (At), labrum (Lr), mandibles (Md), maxillae (Mx), hypopharynx (Hp), and labium (Lb) as in Figs 14–16.

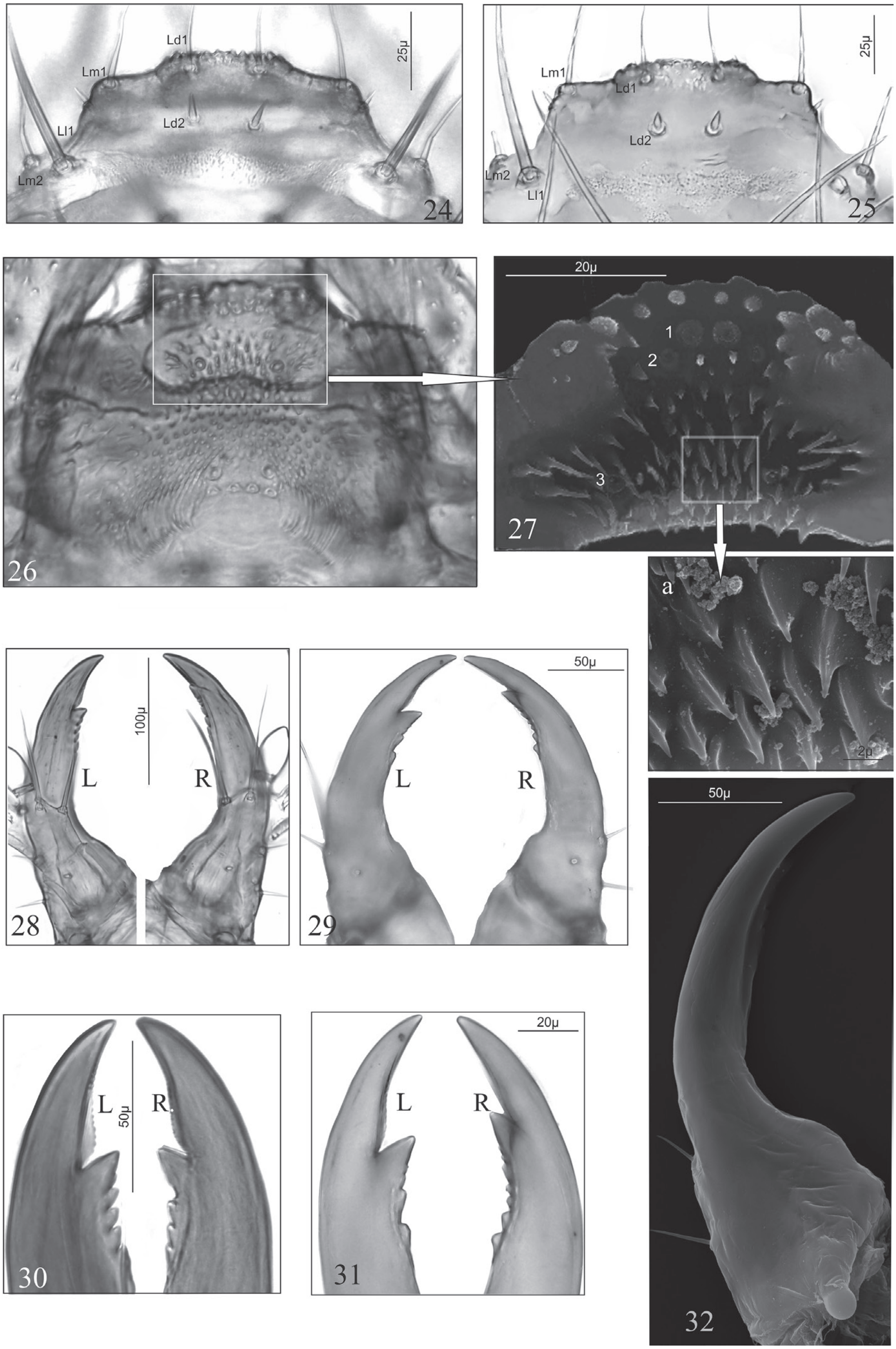
Antenna (Figs 18–21): three-articled, length ratio of articles I–III: 1.0:1.9:1.2 (*D.a.*) or 1.0:2.4:1.4 (*D.l.*). Article I almost 1.0–1.1 × as long as wide, with four pores; article II 1.8 × as long as wide, with three macro setae, one acorn-shaped sensory appendage (Sa), 1.8 (*D.a.*) or 2.1 (*D.l.*) × as long as wide (Figs 20, 21), and three solenidia ventrally of different size (IIS1–3) (Figs 22, 23); Sa longer than article III; article III 1.3–1.4 × as long as wide, with three macro setae and four solenidia apically (IIIS1–4) of different length (Fig. 22).

Labrum (Figs 24, 25): trapeziform in outline, central region of anterior margin protruding and crenate, length ratio of protruding region and whole anterior margin 1:2 (*D.a.*) or 1:1.7 (*D.l.*); with eight macro [2(Ld1, Lm1, Lm2, Ll1)] and two micro, spine-shaped (Ld2) setae; separated from clypeal region by membranous area. Adoral surface of labrum (epipharynx) (Figs 26, 27): membranous with numerous, pointed cuticular processes directed to central area of epipharynx (Fig. 27a) and three pairs of pores (coded: 1–3; Fig. 27).

Mandibles (Md) (Figs 28, 29, 32): elongate, strongly bent, moderately widened basally, with two macro setae near the outer margin and a pore; incisor lobe with one large and a different number (from two to five) of small subapical teeth: four teeth in left (L) and three teeth in right (R) mandible (*D.a.*) or two teeth in left (L) and five teeth in right (R) mandible (*D.l.*) (Figs 30, 31).

Maxilla (Mx) (Fig. 33): consisting of triangular cardo (Cd) divided by sclerotised ridge into two unequal parts, shorted stipes (Stp), slender, obliquely truncate mala (Ma) distinctly (*D.a.*) or slightly (*D.l.*) widened at adoral margin (Figs 34, 35), palpifer (Pf) and three articled maxillary palp (Pm); cardo with one ventral seta; stipes with

Figures 12–23. Continued. Abbreviations: **I–III** antennal articles, **IIS IIIS** solenidia of antennal article II or III, **At** antenna, **Ed** epicranial dorsal setae, **Eg** epicranial gland, **El** epicranial lateral setae, **Em** epicranial marginal setae, **Es** epicranial suture, **Fc** frontal campaniform sensilla, **Fd** frontal dorsal setae, **Fl** frontal lateral setae, **F** frons, **Hp** hypopharynx, **L** lateral setae, **Lb** labium, **Lc** lateral campaniform sensilla, **Lp** labial palp, **Lr** labrum, **Ma** mala, **Md** mandible, **Mx** maxilla, **Mp** maxillary palp, **Oc** ocellus, **P** posterior setae, **Pl** labial palp, **Pm** maxillary palp, **Sa** sensory appendage, **T** temporal setae, **V** ventral setae, **Vc** ventral campaniform sensilla, **Vl** ventral lateral setae.



Figures 24–32. *D. aequata* (**24**, **26**, **27**, **28**, **30**, **32**) *D. linearis* (**25**, **29**, **31**), mature larva. **24**, **25** labrum **26**, **27**, **27a** epipharynx, **28**, **29** left (**L**) and right (**R**) mandible in dorsal aspect **30**, **31** anterior region of left (**L**) and right (**R**) mandible in dorsal aspect **32** right mandible in ventral aspect. Abbreviations: **Ld** labral dorsal setae, **Lm** labral marginal setae, **Ll** labral lateral setae.

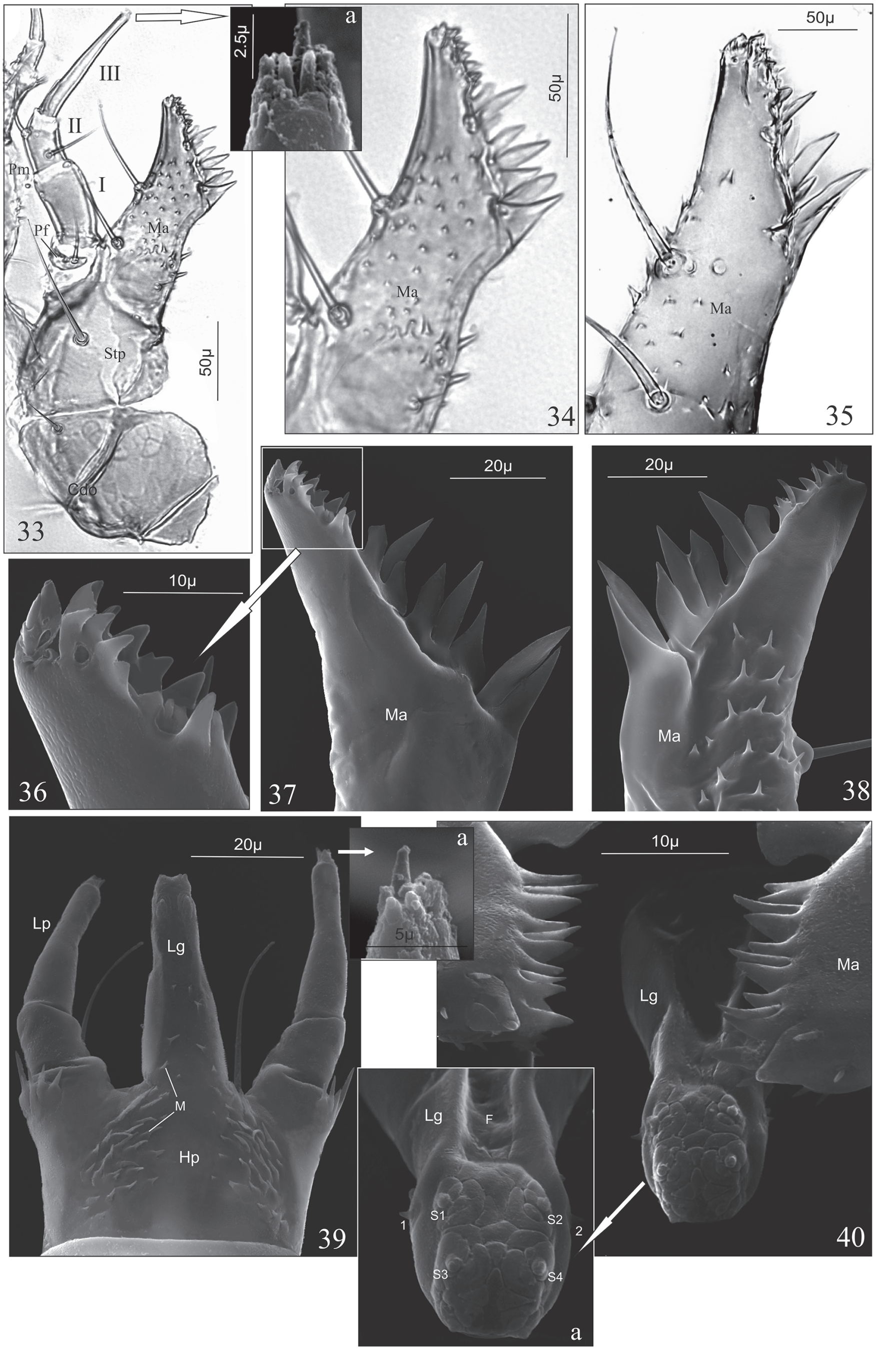
two setae; palpifer with one seta; mala separated from stipes by clearly visible line, with two setae, one pore and approx. 40 (*D.a.*) or 25 (*D.l.*) triangular cuticular processes ventrally; adoral margin of mala (functional positions in Fig. 40) with group of approx. 15 micro teeth apically (Fig. 36) and ctenidium of eight macro teeth, dagger-shaped, different sizes (Figs 37, 38).

Maxillary palp (Pm) (Fig. 33): length ratio of articles I–III: 1.6:1:2.2; article I wider than second, 1.8 × as long as wide with two pores; article II 1.5 × as long as wide with two setae; article III narrower than I and II, tapering slightly to apex, 6.8 × as long as wide, with one digitiform sensory appendage basally 0.3 × as long as article, one pore and a few tiny sensory appendages apically, among them the central one higher than the others (Fig. 33a).

Hypopharynx (Hp) (Fig. 39): membranous, surface (except central area) with approx. 60 triangular microtrichiae (M) directed to the central area without microtrichiae. Ligula (Lg) (Figs 39, 40): elongate, finger-like, gradually tapering to the top, approx. 2.5 × as long as wide at the base, with deep longitudinal furrow (F) and a few microtrichia laterodorsally; distal part with two spinose (coded: 1–2) and four button-like (coded: S1–4) sensilla, surface of apex with microsculpture resembling dermatoglyphics (Fig. 40a). Prementum (Pmnt) trapeziform, 1.4 × as wide at the base as long, with two long setae and four cuticular processes at the base of each labial palp (Lp) (Figs 14, 39). Labial palp two-articled, length ratio of articles I and II: 1:2.1, article I 1.1 × as long as wide, article II 3.5 × as long as wide with a few sensory appendages apically, among them the central one higher than the others (Fig. 39a).

Thorax. Foreleg (Fig. 41): consists of stocky coxa (Cx), short trochanter (Tr), elongated femur (Fe) 3 × as long as wide, slim tibia (Tb) 5.3 × as long as wide and tarsungulus (Ts) slightly curving inwards, 7.1 × as long as wide; Cx with 13 setae (Ad1–3, Al1–4, Bs, D1, Pd1–2, V1–2) and two pores (C1–2); Tr with 10 setae (Al1–5, Pl1v2, V1v3) and 5 pores (C1–5); Fe with 7 setae (Ad1, Av1, Al1, D1, Pd1, Pv1, V1) and two pores (C1–2); Tb with nine spine-shaped setae (Ad1–3, Av1–2, Pd1–2, Pl1, V1); Ts with two spine-shaped setae and one appendage (Ap) (Figs 41, 42). Length ratio of Fe, Tb and Ts: 1.9:2.2:1. Length ratio of pronotum (Pnt), mesonotum (Msn) and metanotum (Mtn): 1.4:1:1.3. Pnt with 50 setae [2(A1–6, Da2–3, Db1–3, Dc2–3, Dd1–2, L1–5, P1–4)] and 12 pores (2[C1–6]) (Fig. 43); Msn with 38 setae [2(A1–5, Da2–3, Db2, Dc2–3, Dd1–2, L3–4, P1–5)] and eight pores [(2C1, C2, C3, C6)]; chaetotaxy of metanotum identical with that of mesonotum; lateral area between pro- and mesothorax with a pair of functional spiracles (Sp), and between meso- and metathorax with a pair of atrophied spiracles (Asp) and one micro seta (Fig. 45). Prosternum (Fig. 47) with 22 setae [2(Eu1–2, Ls1–2, Pr1–3, Prehy1–2, St1–2)] and microstructure laterally (Fig. 47a).

Abdomen. Chaetotaxy of tergites: I–VII with 32 setae [2(A1–2, A4–5, Da2–3, Db2, Dc2–3, L1, L4, P1–5), six pores [2(C3, C5, C6)] and a pair of glands (Pg) (Fig. 49); VIII with 30 setae [2(A1–2, Da2–3, Db2, Dc2–3, L1, L3–4, P1–5)], two pores (C5) and a pair of glands (Pg) (Figs 54, 55). Tergal gland reservoir (R) clearly developed with split opening (Op) at the posterior margin of abdominal tergite VIII



Figures 33–40. *D. aequata* (**33**, **34**, **36–40**) *D. linearis* (**35**), mature larva. **33** right maxilla in ventral aspect and apex of maxillary palp (**33a**), **34**, **35** right mala in ventral aspect **36–38** adoral margin of left mala in dorsal (**36**, **37**) and ventral (**38**) aspect **39**, **39a** labium and apex of labial palp, view from hypopharynx, **40** functional position of hypopharynx and adoral margins of malae and apex of ligula (**40a**). Abbreviations: **I–III** articles of maxillary palp, **Cd** cardo, **F** furrow, **Hp** hypopharynx, **Lg** ligula, **Lp** labial palp, **M** microtrichia, **Ma** mala, **Pf** palpifer, **Pm** maxillary palp, **1–2** and **S1–4** sensilla, **Stp** stipes.

(Figs 54–56). Chaetotaxy of sternites: I (Fig. 51) with 16 setae (2[D1–2, Ps1, P1–5]); II–VIII (Fig. 51) with 20 setae (2[D1–3, Ps1, P1–6]). Segment IX and X with tergites and sternites fused in uniform ring; segment IX with 28 setae (six micro) (Figs 54, 55). Urogomphi (Ug) of segment IX (Figs 54, 55): two-articled, article I fused to tergum IX; article II slender, finger-shaped, moderately tapering apically, 1.5 × as long as basal article, 4.1 × as long as wide, with one short seta subapically, one macro seta apically and a pore basally; length ratio of Ug and apical seta: 1:1; length ratio of urogomphus (without apical seta) and segment X (pygopod): 1:1.5. Segment X with 16 setae and four anal hooks (Ah) (Fig. 58).

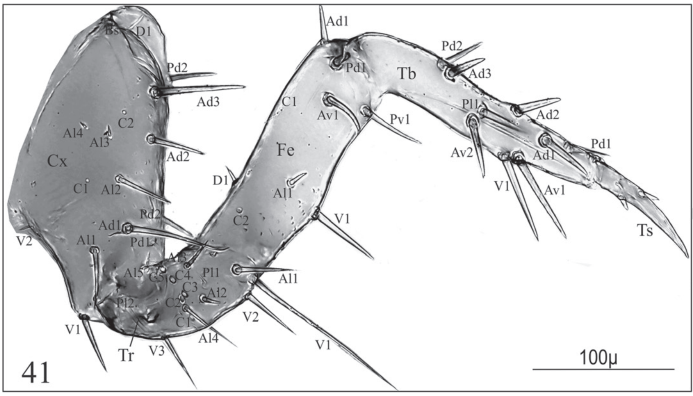
***First larval instar* (*L_1*) (Figs 13, 17, 44, 46, 48, 48a, 50, 52, 53, 57, 59, 60)**
The main differences between L1 and L2–L3 of *Dinaraea* involve: (1) colouration of last (III) antennal article: brown in L1, almost colourless in L2–L3; (2) chaetotaxy of head, pro-, meso-, metanotum, abdominal tergites and sternites I–VII: fewer setae in L1 than in L2–3; (3) egg bursters on metanotum (a pair of large ones) and abdominal segments I–III: present in L1, absent in L2–L3; (4) size of gland reservoir of segment VIII; (5) shape of urogomphi: slightly inward-curving in L1, straight in L2–L3; (10) number and length of subapical and apical setae of urogomphi. Some differences in measurements of all larval instars are shown in Table 1. For more details regarding the differences between L1 and L2–L3, see Table 2.

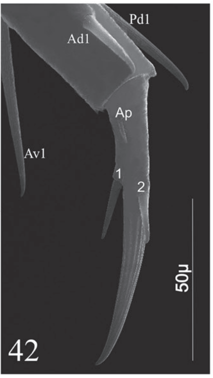
Pupal cocoon (Figs 61, 61a, 62, 64); before pupation, the mature larva (L3) spins a silken cocoon into which it weaves particles of the surrounding substrate; length 3.0 mm, width 1.8 mm. Prepupa as in Fig. 63.

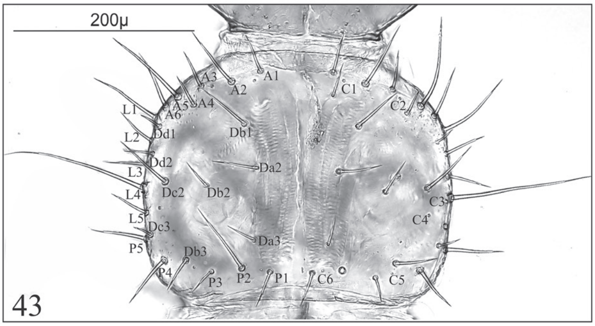
Morphological comments on the *Dinaraea pupa* (based on *D. aequata*)

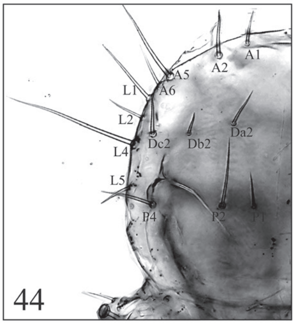
Because of the poor state of preservation of most of the reared research material, this description covers only the ventral part of the female pupa.

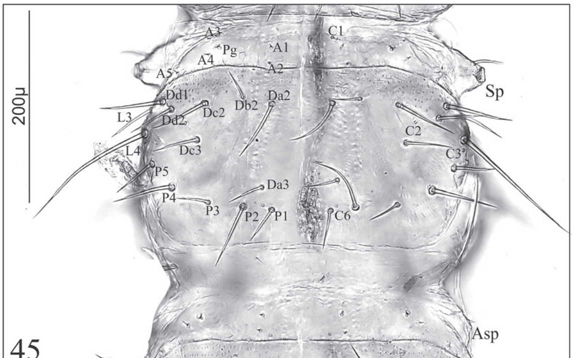
Pupa (Figs 64–68). Some measurements of pupae of both species are listed in Table 3. Pupa exarate, body moderately flattened dorso-ventrally, slightly sclerotised, with numerous setae growing from basal, cuticular protuberances (Fig. 66); colour white, long setae pale brown, short setae almost colourless. Head: directed downwards with 24 setae (among them two very short ones on labrum, four small ones at base of labrum) (Fig. 65). Labrum: anterior margin with deep incision dividing labrum into two parts and a pair of finger-like protuberances. Maxillary palp long, protruding beyond half-length of fore tarsi. Antennae: curved, lying on the fore and middle knees, protruding distinctly beyond apex of middle of knees (Fig. 65). Hind tarsi almost reaching middle of visible abdominal sternite III (actually V). Setae of abdominal sternites relatively short, numbers of setae on sternites: IV – 8, V–VII – each with 14, VIII, IX – each with eight setae (Figs 65, 67). Last tergite IX extended into two abdominal processes, each with one relatively long terminal prolongation (Tp) (Fig. 67). Terminal segments (IX) in female with double gonotheca as in Fig. 67. Microstructure of abdominal sclerites as in Fig. 68.

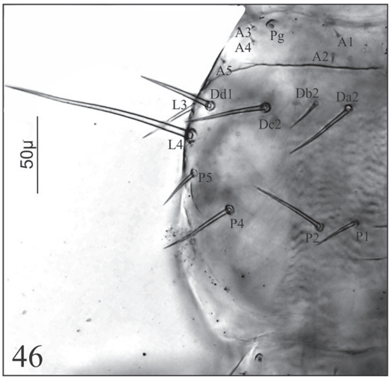

41
Bs
D1
Pd2
Ad3
C2
Al4
Al3
Cx
Ad2
C1
Al2
Pd2
Ad1
Pd1
V2
Al1
Al5
C4
C3
C2
C1
Pl1
Al2
Pl2
V1
Tr
V3
Al4
Ad1
Pd1
C1
Av1
Pv1
Fe
D1
Al1
C2
V1
Al1
V2
V1
Tb
Pd2
Ad3
Pl1
Ad2
Av2
Ad1
Pd1
V1
Av1
Ts
100µ

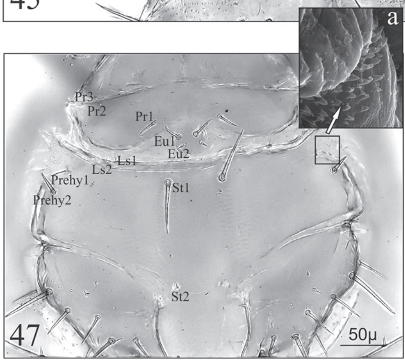

42
Pd1
Ad1
Ap
Av1
1
2
50µ


43
200µ
A3
A2
A1
A5
A4
A6
L1
Dd1
Db1
C1
C2
L2
Dd2
Da2
L3
Dc2
Db2
C3
L4
C4
L5
Dc3
Da3
P5
Db3
P4
P3
P2
P1
C6
C5


44
A5
A2
A1
L1
A6
L2
Dc2
Db2
Da2
L4
L5
P4
P2
P1


45
A3
Pg
A1
C1
A4
A2
A5
Sp
Dd1
Dc2
Db2
Da2
L3
Dd2
C2
L4
Dc3
C3
P5
P4
Da3
P3
P2
P1
C6
Asp
200µ


46
A3
Pg
A4
A1
A2
A5
Dd1
Db2
Da2
L3
Dc2
L4
P5
P4
P2
P1
50µ


47
a
Pr3
Pr2
Pr1
Eu1
Eu2
Ls1
Ls2
Prehy1
Prehy2
St1
St2
50µ

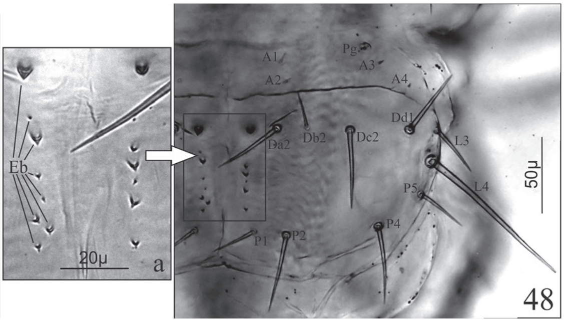

Eb
20µ
a
48
Pg
A1
A3
A2
A4
Dd1
Da2
Db2
Dc2
L3
L4
P5
P4
P1
P2
50µ

Table 1. Some measurements of larval instars of *Dinaraea aequata* and *D. linearis*. Symbols and abbreviations: L1–L3 larval instars, A average, N number of specimens, R range, SV standard variation.

Character	Species	L1		L2		L3	
		A/R	N/SV	A/R	N/SV	A/R	N/SV
Body length	*D. aequata*	1.93/1.61–2.21	7/0.21	2.31/1.61–2.83	5/0.46	3.42/3.01–3.78	11/0.24
	D. linearis	1.6/1.41–1.89	6/0.18	2.23/1.92–2.48	5/0.27	2.79/2.23–3.12	12/0.25
Epicranium length	*D. aequata*	0.26/0.24–0.28	7/0.01	0.34/0.34–0.35	5/0.01	0.43/0.42–0.46	11/0.01
	D. linearis	0.24/0.22–0.27	6/0.01	0.31/0.28–0.34	5/0.02	0.36/0.34–0.39	11/0.02
Epicranium width	*D. aequata*	0.28/0.28–0.28	7/0.00	0.35/0.34–0.35	5/0.01	0.43/0.42–0.45	11/0.01
	D. linearis	0.25/0.25–0.25	6/0.00	0.31/0.29–0.32	5/0.01	0.37/0.35–0.38	12/0.01
Pronotum width	*D. aequata*	0.29/0.28–0.29	7/0.01	0.36/0.34–0.36	5/0.01	0.49/0.46–0.50	11/0.01
	D. linearis	0.27/0.25–0.28	6/0.01	0.34/0.32–0.36	5/0.02	0.43/0.41–0.52	12/0.03

Notes on distribution, ecological preferences, and life history of *D. aequata* and *D. linearis*

Distribution

The geographical distributions of *D. aequata* and *D. linearis* are very similar. Both species are known from the majority of European countries, the Asian part of Russia (Siberia, Far East) and northern China. In Poland, they probably occur all over the country, although the former is usually come across more often than the latter (Burakowski et al. 1981, Löbl and Löbl 2015, unpublished data).

Ecological preferences

Dinaraea aequata and *D. linearis* have similar ecological preferences. Being saproxylic species, they are associated with damp, rotting tree trunks and stumps, mainly of deciduous trees, including *Acer*, *Alnus*, *Betula*, *Fagus*, *Fraxinus*, *Populus*, and *Quercus*. Koch (1989) has described them as eurytopic and corticolous species. They can be found in various types of woodland and other groups of trees, under loose bark, in the corridors of bark beetle larvae, in the rotten wood itself, or, especially the former species, in various polypore species (from the genera *Bjerkandera*, *Fomitopsis*, *Fomes*, *Funalia*, *Ganoderma*, *Inonotus*, *Piptoporus*, *Polyporus*, *Trametes,* etc.) (Nikitsky and Schigel 2004, authors' observations).

Recent research into saproxylic beetles in several regions of Poland (the Wielkopolska Plain, the Bieszczady Mts., the Eastern and Western Beskid Mts., the Pieniny

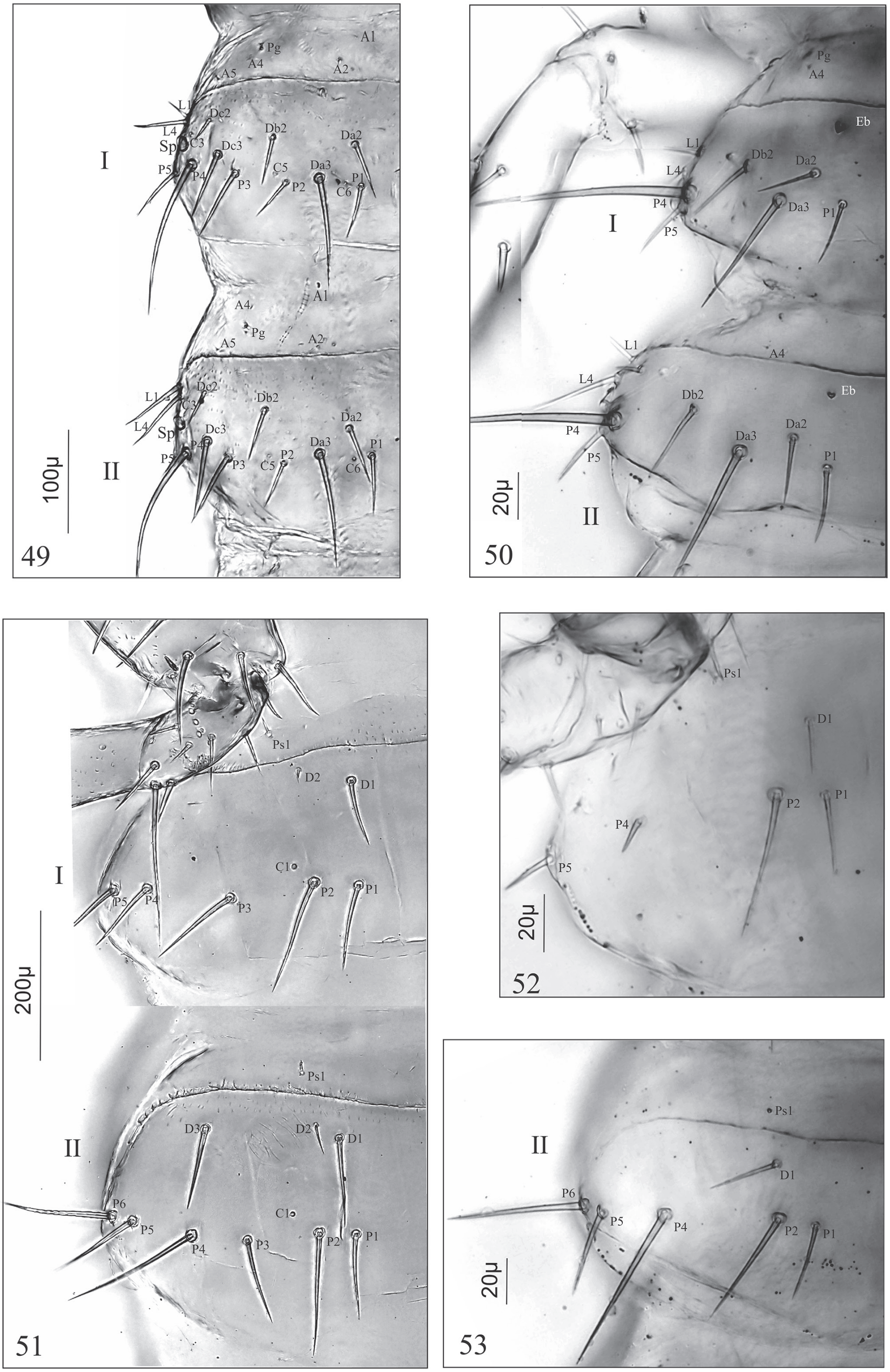
Figures 41–48. *D. linearis*, mature larva (**41**, **42**, **43**, **45**, **47**, **47a**), first larval instar (**44**, **46**, **48**, **48a**). **41**, **42** fore right leg in anterior aspect and tarsungulus (**42**), **43**, **44** pronotum, **45**, **46** mesonotum, **47** prosternum with microstructure (**47a**), **48** metanotum with egg-bursters (**48a**). Abbreviations: **A** anterior setae, **Ad** anterodorsal setae, **Al** anterolateral setae, **Ap** appendage, **Asp** atrophied spiracles, **Av** anteroventral setae, **Bs** basal setae, **C** campaniform sensilla, **Cx** coxa, **Eb** egg-bursters, **Eu** eusternum, **Fe** femur, **Da–d** dorsal setae, **L** lateral setae, **Ls** laterosternum, **P** posterior setae, **Pd** posterodorsal setae, **Pg** pretergal gland, **Pr** presternum, **Prehy** prehypopleuron, **Pv** posteroventral setae, **Sp** spiracle, **St** sternellum, **Tb** tibia, **Tr** trochanter, **Ts** tarsungulus, **V** ventral setae.

Table 2. Some differences in chaetotaxy between early (L1) and late (L2–3) larval instars of *Dinaraea*, *Thiasophila*, and *Gyrophaena*. Abbreviations: Ar article, As apical seta of urogomphus, At antenna, D dorsal, Ep epicranial part, l long, Ls lateral margin, Lr length ratio, Msn mesonotum, Mtn metanotum, NrS number of setae, NrEb number of egg bursters, Pnt pronotum, S segment, s short, Sas subapical setae of urogomphus, St sternite, Te tergite, Ug urogomphus, (…) new setae, ? no data available. Data based on Zagaja et al. (2014), Staniec et al. (2016), and present study.

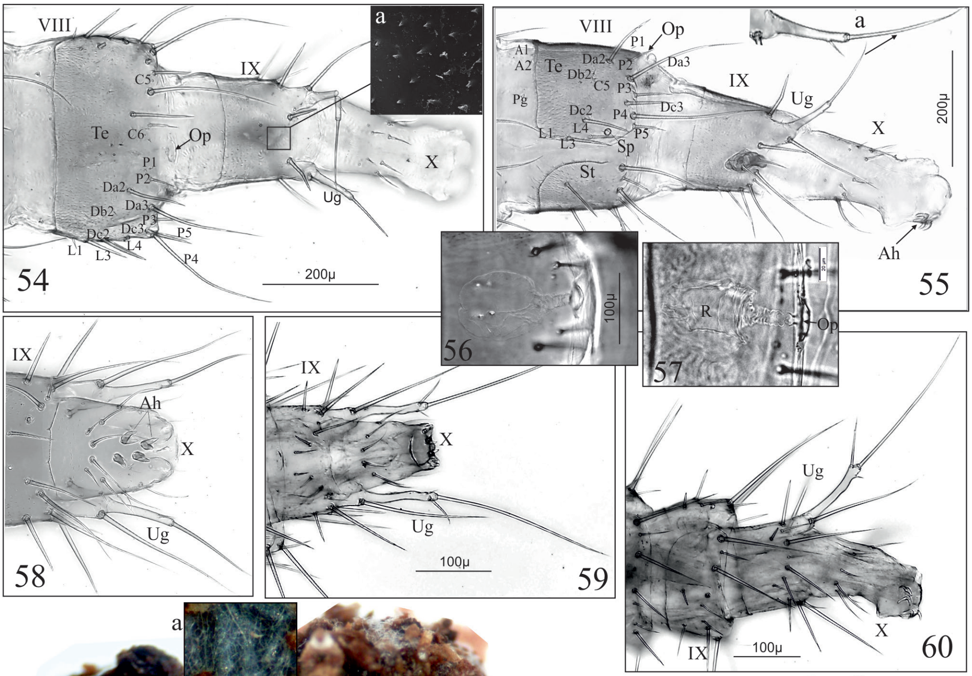
Characters	**Athetini**		**Oxypodini**		**Homalotini**	
	***Dinaraea* (*D. aequata, D. linearis*)**		***Thiasophila* (*T. angulata*)**		***Gyrophaena* (*G. boleti*)**	
Head						
	L1	L2–3	L1	L2–3	L1	L2–3
NrS: Ep	14	18 (Ed1, El2)	14	18 (Ea1, Ed1)	12	12
At: Ar III	dark	light	dark	light	dark	light
Thorax						
NrS: Pnt	28	50 2(A3, A4, Da3, Db2, Db3, Dc3, Dd1, Dd1, L3, P3, P5)	28	52 2(A3, Da1, Da3, Db1, Db3, Dc1, Dc3, Dd1, L2–3, L5, P3)	22	30 2(A3, A5, P3, L5)
NrS: Msn, Mtn, each	30	38 2(Da3, Dc3, Dd2, P3)	30	38 2(Da3, Db3, Dc2, P3)	16	18 2P3
NrEb: Msn	lack	lack	lack	lack	two	lack
NrEb: Mtn	14 (2big)	lack	approx. ten	lack (six big)	nine	lack
Abdomen						
NrEb: Te I–II/each	two	lack	two	lack	two	lack
NrEb: Te III–IV/each	lack	lack	lack	lack	two	lack
NrS: Te I–VIII	18	32 2(A1, A2, A5, P2, P3, Dc3, Dc2)	24	30 2(Db3, Dc2, P3)	14	18 2(Db3, P3)
NrS: St I	12	16 2(D2, P3)	ten	14 2(D2, Ps1)	ten	ten
NrS: St II–VII	14	20 2(D2, D3, P3)	14	20 2(D2, D3, P3)	12	16 2(D2, P3)
NrS: St VIII	14	20 2(D2, D3, P3)	14	20 2(D2, D3, P3)	12	14 2(D2)
Ug: Sas	2 /s and l/	1 s	2 /s and l/	1 s	2 /s and l/	1 s
Lr Ug to As	1:1.6	1:1	1:2.3	1.1:1	1:2.2	1:1.1
Lr Ug to S X	1:1.1	1:1.5	1.1:1	1:1.5	1.2:1	1:1

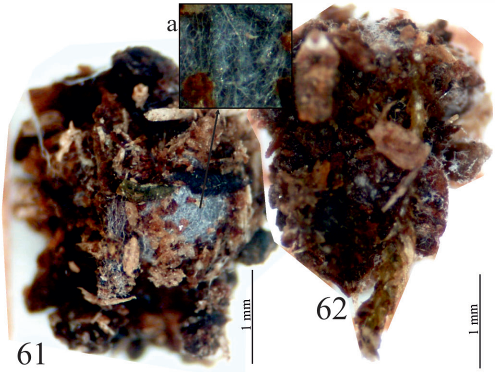
Table 3. Some measurements of pupae of *Dinaraea aequata* and *D. linearis*. Abbreviations: A average, N number of specimens, R range, SV standard variation.

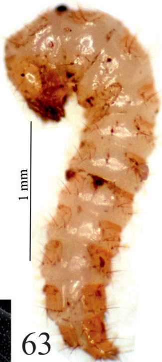
Species	**Body length**		**Body width**		**Epicranium width**		**Pronotum width**	
	A/R	N/SV	A/R	N/SV	A/R	N/SV	A/R	N/SV
D. aequata	2.48/2.42–2.53	3/0.08	1.12/1.08–1.15	3/0.05	0.53/0.52–0.54	3/0.01	0.63/0.62–0.64	3/0,01
D. linearis	2.16/2.13–2.20	4/0.03	0.87/0.7–1.0	4/0.26	0.49/0.49–0.49	4/0.0	0.57/0.54–0.59	4/0.02



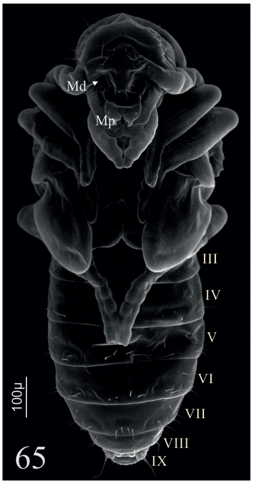
Figures 49–53. *D. aequata*, mature larva (**49**, **51**), first larval instar (**50**, **52**, **53**). **49**, **50** abdominal tergites I and II **51** abdominal sternites I and II **52** abdominal sternites I **53** abdominal sternites II. Abbreviations: **A** anterior setae, **C** campaniform sensilla, **D**, **Da–c** discal setae, **Eb** egg-bursters, **L** lateral setae, **P** posterior setae, **Pg** pretergal gland, **Ps** presternal setae, **Sp** spiracle.

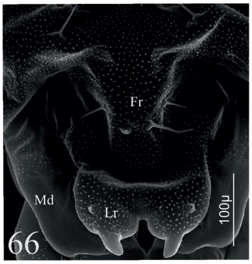

54
VIII
IX
X
a
C5
C6
Te
Op
P1
P2
P3
P4
P5
Da2
Da3
Db2
Dc2
Dc3
L1
L3
L4
Ug
200µ
55
VIII
Op
P1
P2
P3
P4
P5
A1
A2
Te
Pg
Da2
Da3
Db2
C5
Dc2
Dc3
L1
L3
L4
Sp
St
IX
Ug
X
a
Ah
200µ
56
100µ
57
R
Op
20 µm
58
IX
Ah
X
Ug
59
IX
X
Ug
100µ
60
Ug
X
IX
100µ

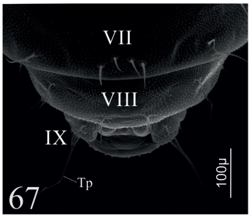

a
61
1 mm
62
1 mm


1 mm
63


1 mm
64


Md
Mp
III
IV
V
VI
VII
VIII
IX
100µ
65


Fr
Md
Lr
100µ
66


VII
VIII
IX
Tp
100µ
67

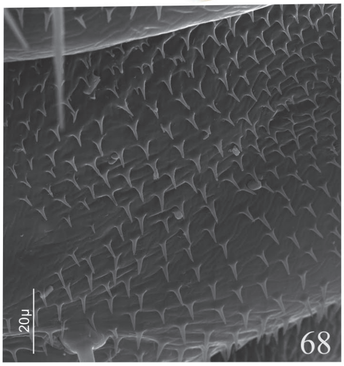

20µ
68

Table 4. Morphological differences between mature larva (L3) of *Dinaraea aequata* and *D. linearis*. Abbreviations: Lb labrum, Lr length ratio, LWr length to width ratio, MdL MdR left (L) and right (R) mandible, Nr number, Sa sensory appendage of antennal article II, NrSt number of subapical teeth.

Character	*D. aequata*	*D. linearis*	Figures
Body – colour/appearance			
Head: reddish brown	whole	posterior area distinctly lighter	1–6
Tergites	all yellowish brown	thoracic and abdominal I–V colourless	1–4
Abdominal sternites I–V	yellowish brown	almost colourless	5, 6
Dorso-ventrally flattened	distinctly	moderately	3, 4
Antenna			
Lr of articles I–III	1.0:1.9:1.2, respectively	1.0:2.4:1.4, respectively	18, 19
Sa: LWr	1.8:1	2.1:1	20,21
Mouthparts			
Lb: Lr of protruding region and whole anterior margin	1:2	1:1.7	24, 25
Lb: setae of Ld2	moderately elongate	extremely shortened	24, 25
Left mandible: NrSt	one big + four small	one big + two small well visible	30, 31
Right mandible: NrSt	one big + three small	one big + five small well visible	30, 31
Ma: widened at adoral margin	distinctly	slightly	34, 35
Ma: Nr of cuticular processes	approx. 40	approx. 25	34, 35

Mts., the Lublin Upland), has yielded a range of fresh information regarding the environmental preferences of these two *Dinaraea* species. In the lowlands, *D. aequata* was found in May and December under the bark of a standing birch (*Betula* L.) and the wet bark of a wind-thrown aspen trunk (*Populus tremula* L.), together with the following other species of beetles: *Anomognathus cuspidatus*, *Batrisodes venustus*, *Bolitochara obliqua*, *Dinaraea angustula*, *Hololepta plana*, and *Siagonium quadricorne*. In mountain and piedmont regions this species was captured from June to July and in November–December under the bark of the following broad-leaved tree species: beech (*Fagus sylvatica* L.), sycamore (*Acer pseudoplatanus* L.), field maple (*Acer campestre* L.), a burnt bird cherry (*Padus avium* Mill.), and the remains of firs (*Abies alba* Mill.), together with *Bolitochara obliqua*, *Corticeus unicolor*, *Homalota plana*, *Ipidia binotata*, *Phloeocharis subtilissima*, *Pissodes piceae*, *Xylostiba monilicornis*, and *Ropalopus macropus*. Some of *D. aequata* beetles have also been recorded on fungi *Auricularia auricula-judae* (Bull.) Quél. and *Sarcodontia crocea* (Schwein.) Kotl., along with *Acrulia inflata*, *Atheta crassicornis*, *Atheta ravilla*, *Autalia longicornis*, *Bolitochara obliqua*, *Gyrophaena manca*,

Figures 54–68. *D. linearis* (**54–57, 60–64**), *D. aequata* (**58, 59, 65–68**), mature larva (**54–56, 58**), first larval instar (**57, 59, 60**), prepupa (**61**), cocoon (**62**, **63**), cocoon and pupa (**64**), pupa (**65–68**). **54, 55** abdominal segments VIII-X in dorsal (**54**) and lateral (**55**) aspect **56**, **57** tergal gland reservoir of segment VIII **58–60** abdominal segments IX and X in ventral (**58, 59**) and lateral (**60**) aspect **61, 62** pupal cocoon **63** prepupa in lateral aspect **64** ripped cocoon with pupa inside in lateral aspect **65–68** pupa in ventral aspect (**65**), front of head (**66**), terminal abdominal sternites VII–IX (**67**) and microstructure of abdominal sternite VIII (**68**). Abbreviations: **Ah** anal hooks, **Fr** frons, **Lr** labrum, **Md** mandible, **Mp** maxillary palp, **Op** opening of gland reservoir, **Pg** pretergal gland, **R** tergal gland reservoir, **Sp** spiracle, **St** sternite, **Te** tergite, **Tp** terminal prolongation, **Ug** urogomphus.

Oxypoda alternans, and *Scaphisoma boleti.* In Poland *D. linearis* appears to be rarer than *D. aequata*. It has been recorded in January, March, July, and August, exclusively under the bark of various trees. In the lowlands these were larch (*Larix* Mill.), pine (*Pinus* L.), oak (*Quercus* L.), a wind-thrown ash (*Fraxinus* L.), the mountains lime (*Tilia* L.), and fir. Accompanying beetles included *Corticeus unicolor*, *Gasterocercus depressirostris*, *Paromalus parallelepipedus*, *Phloeostiba lapponica*, *Rhyncolus elongatus*, *Scaphisoma agaricinum*, *Silvanus bidentatus*, and *Tetropium gabrieli* (Melke, oral information).

Notes on the life history in the laboratory

In the rearing of adults of *D. aequata* (temp. 20 °C±3), started on 19 November 2004, the first larvae (L1 and L2) were observed just six days later (25 November), and eight and ten days later the first prepupae and pupae respectively appeared. Various late developmental stages (mostly L3 and pupae) were observed until 20 January 2005. Larval development in the rearing of adults of *D. linearis*, started on 6 December 2004, was observed from 1 January to 11 February, and pupation from 19 to 21 February 2005. The larval and imaginal forms of both species were fed exclusively with springtails from the family *Onychiuridae*. On several occasions foraging larvae of *D. aequata* were observed as they caught their victims of various sizes in their mandibles. Within the following 5 to 10 minutes they consumed most of the springtail bodies, but always rejected fragments of the carapace.

Discussion and summary

This paper describes in detail the external morphology of the hitherto unknown larval stage of the genus *Dinaraea*, including the chaetotaxy, using the terminology proposed for the subfamily Aleocharinae by Ashe and Watrous (1984). The description is based on individuals from European populations of *D. aequata* and *D. linearis*, the larvae of which were bred in the laboratory from imagines. The morphological differences between the mature larvae of the two species relate to: (a) the dimensions of various body parts, they are larger in *D. aequata* (Table 1); (b) colour of head, thoracic tergites and anterior abdominal tergites and sternites, generally darker in *D. aequata*; (c) degree of body flattening, somewhat more flattened in *D. aequata*; (d) shape of article II of antenna and Sa of article III, slightly more elongate in *D. linearis*; (e) structural details of the anterior margin of the labrum and the length of its setae Ld2; (f) number of subapical teeth on both mandibles, more on the left-hand one in *D. aequata*, more on the right-hand one in *D. linearis*; (g) shape of mala, more protracted at adoral margin in *D. aequata*; (h) number of cuticular processes on mala, more in *D. aequata* (Table 4). These diagnostic features distinguish the larvae of these two species, which may co-occur under natural conditions. Particularly useful in this respect are features a–c, relating to the dimensions of the body and its general appearance. Very many more features distinguishing aleocharine larvae belonging to the same genus were established for *Haploglossa* Kraatz, 1865 (Staniec et al. 2010). A comparative analysis of

H. picipennis (Gyllenhal, 1827) and *H. nidicola* (Fairmaire, 1852) revealed differences not only in larval size and colouration, but also in the chaetotaxy of abdominal segment X and epicranium (presence or absence of seta Ea1), structural details of all the mouthparts, lengths of the several leg parts, and urogomphi. It is likely that the scale of the morphological differences between the larvae of species from one genus depends largely on their different ecological preferences. The above-mentioned *Haploglossa* species inhabit micro-environments (*H. picipennis* – nests of raptors, *H. nidicola* – nest holes of sand martins) that are very different from those of *Dinaraea* species, which are usually found under bark, mainly of broad-leaved trees.

Measurements of the head and pronotum of the two *Dinaraea* species indicate that their larval development involves three stages (Table 1): this is typical of most known aleocharines (White 1977, Ashe and Watrous 1984, Ashe 1985, Ashe 1986, Zagaja et al. 2014, Staniec et al. 2016). Only in the case of *Pella* species (*P. laticollis*) (Lomechusini), inhabiting ants' nests, were just two larval stages found; this is due to the faster rate of development of these rove-beetles (Hölldobler et al. 1981, Staniec et al. 2009). This feature is probably an adaptation to the myrmecophilous lifestyle that aims to minimise the period during which staphylinid larvae are potentially endangered by their hosts in the anthill.

Morphological analysis of a *Dinaraea* larva revealed a series of differences between its first (L1), and its second (L2) and third (L3) instars, whose external structures are identical to that of L1. Apart from the clearly smaller body size (see Table 1), features exclusive to L1 include: (1) the absence of some setae on the dorsal surface of the head and thorax, and on the dorsal and ventral surfaces of the abdomen, (2) the presence of short subapical setae on the urogomphi, (3) egg bursters on some thoracic and abdominal tergites, (4) a darker terminal antennal segment than in L2–3, and (5) markedly longer urogomphi and their apical setae than in later stages. These morphological differences between the younger and older larval instars in *Dinaraea* are of a similar nature to those in other tribes of Aleocharinae (Table 2) (Ashe and Watrous 1984, Ashe 1986, Zagaja et al. 2014, Staniec et al. 2016). They enable one to easily distinguish L1 from the older larval stages without recourse to metric analysis. In view of the fragmentary nature of the available information on this subject, it is not possible to state definitively whether and to what extent these differences extend across the whole subfamily.

A combination of 17 diagnostic features (see "Generic diagnosis…") have been proposed for the mature larva of *Dinaraea*, described above, which enable it to be distinguished from other known older larval stages of Aleocharinae (Paulian 1941, Pototskaya 1967, Topp 1975, Ashe 1981, Ashe and Watrous 1984, Ashe 1985, Ahn 1997, Jeon and Ahn 2009, Staniec et al. 2009, 2010, 2016, Zagaja et al. 2014). In this respect the genus *Dalotia* (*Da*) Casey, (Athetini) most closely resembles the genus *Dinaraea* (*Di*) (Ashe and Watrous 1984), and the small differences relate solely to: (i) body habitus – moderately dorso-ventrally flattened in *Di* or cylindrical in *Da*; (ii) shape of antennal article I longer than wide in *Di* or wider than long in *Da*; (iii) structure of anterior margin of labrum central region protruding and crenate in *Di* or wholly rounded and smooth in *Da*; (iv) seta Da1 on pronotum absent in *Di* or present in *Da*; (v) setae D3 and P5 on abdominal sternite I absent and present respectively in *Di*, or present and absent in *Da*. It should be added that the dorso-ventrally flattened body and moderately elongated antennal segment I are most probably adaptations to the under-bark lifestyle of this larva, as in the case of the mature form of *Dinaraea*. On the other hand, the structure of the anterior margin of the labrum, and particularly the specific features of the body chaetotaxy, may be of phylogenetic significance. That is why these structures have been included in the morphological descriptions of other Aleocharinae larvae (Ashe and Watrous 1984, Ashe 1985, 1986, Ahn 1997, Jeon and Ahn 2009, Staniec et al. 2009, 2010, 2017). Only a few of these species has the chaetotaxy not only of older but also of younger larval forms been described (Zagaja et al. 2014, Staniec 2016, the present study).

A preliminary comparative analysis of the features of the chaetotaxy was carried out on the basis of well-researched larvae of three different tribes of Aleocharinae. This revealed that all the larval stages of Athetini (*Dinaraea*) and Oxypodini (*Thiasophila*) are much more similar to one another than to the larvae of Homalotini (*Gyrophaena*) (Table 2). In the first two taxa the slight differences in chaetotaxy of L1–3 concern only the number and homology of the setae on the tergites and first sternite of the abdomen. By contrast, a distinctly smaller number of setae develop on all body tagmata of L1–3, especially the thoracic ones, in Homalotini than in the other two tribes. These data indicate the distinctly closer relationship of *Dinaraea* (Athetini) with *Thiasophila* (Oxypodini) than with *Gyrophaena* (Homalotini). This state is partially corroborated by Thomas (2009), whose research was based on the molecular analysis of two mitochondrial DNA markers. This author showed that Homalotini are a group separate from the other taxa he/she analysed. The taxa from Athetini and Oxypodini belong to sister groups, at least in some of the trees generated.

Another question relates to the significance of the features of chaetotaxy for phylogenesis depending on the larval stage. Ashe (1986) suggested that later developmental stages would be more useful at lower taxonomic levels (e.g. genus), as they exhibit more features associated with a better-developed chaetotaxy. In contrast, the first larval stages, with their smaller numbers of setae, could be phylogenetically significant in the analysis of higher systematic units. This hypothesis is convergent with that underlying our preliminary studies. These have shown that at the tribal level of Aleocharinae, distinct differences may occur in the chaetotaxy (e.g. between Athetini and Homalotini), between not only the late larval stages but also the early ones. Interestingly, in L1 of some species these differences may be even greater than in the older larval stages, e.g. the chaetotaxy of abdominal tergites I–VIII of *Dinaraea* and *Thiasophila* (Table 2).

It should also be borne in mind that the development of setae on the different body parts of the larvae during ontogenesis is uneven. In the taxa we are analysing here, the fewest setae appear on the head – two pairs at most, if any at all (*Gyrophaena*). In contrast, the changes in the chaetotaxy are the greatest on the pronotum, and somewhat less so on the abdominal tergites and sternites (Table 2). A homologous series of setae that appear in the older larval stages (L2–3) of species from the tribes Athetini [A], Oxypodini [O] and Homalotini [H]) has been established. On the thoracic tergites they are the following setae: A3, P3 (A, O, H) and Da3, Db3, Dc3, Dd1, L3 (A, O); on abdominal tergites I–VIII: P3 (O, A, H), Dc2 (O, A) and Db3 (O, H); on abdominal sternite I: D2 (A, O); on abdominal sternites II–VII: D2, P3 (A, O, H) and D3 (A, O); on abdominal sternite VIII: D2 (A, O, H) and D3, P3 (A, O). Being homologous aspects of the chaetotaxy, they could be of phylogenetic importance, especially at lower systematic levels, e.g. subtribe or genus, but this would have to be confirmed by further research.

As a representative of Athetini, the pupa of *Dinaraea* possesses general structural features, such as an exarate body type, lightly sclerotised, with numerous setae growing from basal, cuticular protuberances and double gonotheca on the ventral surface of the final segment in the female, characteristic of the pupal stages of other aleocharines from Homalotini, Lomechusinii, and Oxypodini (Ashe 1981, Staniec et al. 2009, 2010, Zagaja et al. 2014). Its specific appearance relating to the body outline, width of head, shape of pronotum, length of legs and antennae, shape, and length of mouthparts, resembles the features of the adult form.

As in *Dinaraea*, the production of a pupal, silken cocoon, into which particles of the surrounding substrate are often woven, has been observed in numerous tribes of Aleocharinae, such as Athetini, Aleocharini, Corotocini, Falagriini, Homalotini (including members of subtribes Bolitocharina, Gyrophaenina and Homalotina), Hypocyphtini, Liparocephalini, Lomechusini, Oxypodini, and Placusini (Ashe 1982, Frank and Thomas 1984, Thayer et al. 2004, Staniec et al. 2010, Zagaja et al. 2014). Some authors assume that this behaviour may be at least a basal condition of the higher classification of Aleocharinae. Topp (1975) even suggested that this feature occurs exclusively in this subfamily of Staphylinidae. However, this statement seems controversial in the light of reports from other researchers, who described a similar structure in taxa from the subfamilies Steninae and Staphylininae, although in the latter case, it is made mostly from soil (Weinreich 1968, Staniec 2004, Pietrykowska-Tudruj and Staniec 2007, Staniec et al. 2008).

The pupal cocoon undoubtedly plays a protective role. That is why it is probably so common in the Aleocharinae, including *Dinaraea*, in which the delicate exarate pupae are enclosed in a weakly sclerotised cuticle (Staniec et al. 2010, Zagaja et al. 2014, the present study). Likewise, in the case of some Staphylininae, whose larvae spin cocoons (e.g. *Gabrius splendidulus*, *Rabigus tenuis*), their pupae are covered by an exceptionally thin cuticle compared with other members of this subfamily (Pietrykowska-Tudruj and Staniec 2007, Staniec et al. 2008). Presumably, then, pupation within a cocoon could have evolved independently in members of many different subfamilies of a range of rove-beetles, as an adaptation associated with the pupal structure and/or the biotic conditions of the environment, e.g. pressure on the part of predators. Nevertheless, knowledge of the life history of Staphylinidae, including the occurrence of a pupal cocoon in this, the largest family of beetles, remains fragmentary and is restricted to a very small number of taxa summarised for Staphylinidae by Frank and Thomas (1984). Thus, more data are required before more binding conclusions regarding this structure can be drawn.

In Europe, both *Dinaraea* species are quite widespread saproxylic rove-beetles, although both in Poland and some other countries *D. linearis* appears to be far less common than *D. aequata*. The flattened and parallel-sided body of adults and larvae (the present study) of these staphylinids are probably a consequence of their mode of life under tree bark; they do not display any particular preferences as regards the species of tree they colonise. *D. aequata* is also encountered in various arboreal fungi. In Poland both these rove-beetle species can be observed in nature all the year round, along with some 30 other species of saproxylic Coleoptera, from six families (Nikitsky and Schigel 2004, Alexander and Anderson 2012, Melke, oral information; authors' unpublished data).

In the rearing, the development of *D. aequata* and *D. linearis* took place in the autumn and winter months (November–February), as in the case of *Phloeonomus punctipennis* Thomson (Omaliinae) – another saproxylic staphylinid, whose larval stages were caught in the field in the second half of November (Staniec et al. 2016). It is not exactly known, however, whether the above-mentioned reproductive period of *Dinaraea* in the laboratory coincided in time with its reproduction in nature, or whether it was more the effect of the suitable ambient temperature at which the rearings were performed. Certain information was also obtained as regards the diet of these rove beetles, which was hitherto completely unknown (Klimaszewski et al. 2013). On the basis of laboratory observations, these rove beetles are presumably predators, which in natural conditions hunt for various tiny arthropods with delicate cuticles and consume their soft tissues.

Acknowledgements

The authors would like to thank their colleague Andrzej Melke for information on the ecological preferences of *D. aequata* and *D. linearis*. They also extent their gratitude to the anonymous reviewer for the useful comments that helped to improve the manuscript.

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ZooKeys 752: 125–136 (2018)
doi: 10.3897/zookeys.752.23884
http://zookeys.pensoft.net

RESEARCH ARTICLE

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The genus *Rhynchobanchus* Kriechbaumer in China, with descriptions of a new species and first record of the genus from Oriental region (Hymenoptera, Ichneumonidae, Banchinae)

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Academic editor: *J. Fernandez-Triana* | Received 25 January 2018 | Accepted 2 April 2018 | Published 23 April 2018

http://zoobank.org/B9EECF29-3310-4E97-A97F-1202486A58EA

Citation: Li Z-J, Li T, Yan J, Sheng M-L (2018) The genus *Rhynchobanchus* Kriechbaumer in China, with descriptions of a new species and first record of the genus from Oriental region (Hymenoptera, Ichneumonidae, Banchinae). ZooKeys 752: 125–136. https://doi.org/10.3897/zookeys.752.23884

Abstract

Six species and two subspecies of the genus *Rhynchobanchus* Kriechbaumer, 1894 are reported from China, of which one, *Rh. flavomaculatus* Sheng, **sp. n.**, is a new species and the first record of the genus from the Oriental Region. *Rhynchobanchus flavopictus orientalis* Kuslitzky, 2007 is a new Chinese record. A key to the species of *Rhynchobanchus* occurring in China is provided.

Keywords

Banchini, China, key, new species, Oriental Region, Palaearctic Region, *Rhynchobanchus*

Introduction

Rhynchobanchus Kriechbaumer, 1894, belonging to the tribe Banchini of the subfamily Banchinae (Hymenoptera: Ichneumonidae) and comprising seven species (Yu et al. 2016), is only known from the Palaearctic Region (Kriechbaumer 1894; Meyer 1927; Sheng et al. 1995, 1997; Kuslitzky 2007; Kim et al. 2012; Sheng and Sun 2014, Watanabe 2016). Four species restricted to the Eastern Palaearctic Region, one to the Western Palaearctic Region, and two species are trans-Palaearctic. The diagnostic characters of the genus were most recently revised by Sheng et al. (2014).

The aim of this study is to revise all available materials of *Rhynchobanchus* from China, describe one new species from the Oriental part of China, and provide an identification key to species occurring in China.

Materials and methods

Type specimens were collected using entomological sweep nets in the forest of Tianmu Mt., Lin'an, Zhejiang Province and Shaoyang, Hunan Province (China). Other Chinese specimens from the collections in the Insect Museum, General Station of Forest Pest Management, State Forestry Administration, People's Republic of China (GSFPM) were checked.

The holotype locality is a forest comprised of mixed deciduous angiosperms and evergreen conifers, mainly including *Liquidambar formosana* Hance, *Aphananthe aspera* (Thunb.), *Acer* spp., *Quercus* sp., *Castanea* spp., *Elaeagnus pungens* Thunb., *Rosa multiflora* Thunb., *Euscaphis japonica* (Thunb.) Dipppel, *Lindera glauca* (Sieb. et Zucc.) Bl., *Pinus massoniana* Lambert, *Cryptomeria japonica* (Linn.f.) D. Don, and *Metasequoia glyptostroboides* Hu et Cheng.

The photos of *Rh. flavopictus orientalis* Kuslitzky, 2007 (holotype), *Rh. bicolor* Kriechbaumer, 1894 identified by Townes, and *Rh. flavopictus* Heinrich, 1937 identified by Kuslitzky, deposited in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (ZISP), were compared to the new species.

Images were taken using a stereomicroscope Leica M205A with a LAS Montage MultiFocus. Morphological terminology is mostly based on Gauld (1991).

All examined material, including type specimens of the new species, is deposited in **GSFPM**.

Taxonomy

Rhynchobanchus Kriechbaumer, 1894

Type-species. *Rhynchobanchus bicolor* Kriechbaumer.

Diagnosis. *Rhynchobanchus* can be distinguished from all other genera of Banchini by a combination of the following characters: Antennae long and slender; apical margin of clypeus with a median notch (Fig. 2); upper tooth of mandible very wide, its apex oblique and concave, subdivided into two teeth (Fig. 2); lower tooth of mandible pointed; epicnemial carina absent (Fig. 5); propodeum short, without carinae (Fig. 6); fore wing with areolet receiving 2m-cu near center (Figs 7, 15); nervulus distal of 1/M by at least 0.5 its length; tarsal claws strongly pectinate; ovipositor sheath very short, slightly projecting beyond apex of metasoma (Fig. 9).

Host. Unknown.

Key to females of species of *Rhynchobanchus* known in China

1 Hindwing vein 1-cu almost disappeared (basal end of 2-Cu almost touching M+Cu). Areolet pentagonal (Fig. 15). Facial orbits with yellow longitudinal streak. Tergites black; posterior three sternites red to reddish brown. Scutellum yellow .... ***Rh. rufus*** **Sheng & Sun**

– Hindwing vein 1-cu distinct, approximately 0.2 as long as cu-a. Areolet quadrangular, if pentagonal, at least median tergites red. Others not entirely as above ... **2**

2 Propodeum very rough. Ovipositor sheath evidently reaching past tip of metasoma. Antenna black, or slightly brown ventrally. Mesosoma black, or at most anterolateral portion of mesoscutum with small yellow spots. Tergites black, or at most posterolateral portion of tergites 1 to 4 with small yellow spots .... ***Rh. niger*** **Sheng**

– Propodeum smooth or slightly rough, with distinct punctures or winkles. Ovipositor sheath at most reaching tip of metasoma. Antennae light in color, at least ventral profile red or reddish brown. Mesosoma with yellow spots. Scutellum yellow. Median portion of metasoma reddish brown, or at least apical lateral portion light in color **3**

3 Longest spur of mid tibia approximately 0.8 times as long as first tarsomere. Body predominantly yellow with brown markings (Fig. 1); median portion of frons, inverted triangular median stripe of mesoscutum, transverse groove in front of propodeum, median spots of first tergite black............................ .... ***Rh. flavomaculatus*** **sp.n.**

– Longest spur of mid tibia at most 0.7 times as long as first tarsomere. Body predominantly black with many yellow or brown spots............................... **4**

4 Flagellum reddish brown, its ventral profile slightly dark-reddish brown. Face reddish brown, or with small black spot. Basal portions of tergites 1 to 5 black, apical portions reddish brown; remainder of tergites almost entirely reddish brown. Hind tarsus dark reddish brown................ ***Rh. flavopictus flavopictus*** **Heinrich**

– Flagellum black, or dorsal profile black, ventral red. Face black. Tergites black, or median tergites red **5**

5 Tergite 2 as long as apical width. Propodeum and hind tarsus entirely black. Tergites black, at most lateral portions of median tergites with small yellow spots .... ***Rh. flavopictus orientalis*** **Kuslitzky**

– Tergite 2 longer or shorter than apical width. Apical portion of propodeum yellowish brown. Hind tarsus brown or darkish brown. Tergites 2 to 4 reddish brown **6**

6 Areolet pentagonal. Spiracle of first tergite strongly convex. First tergite 2.4 times as long as apical width, spiracle strongly convex (Fig. 12). Mediolateral portions of median tergites with yellow spots........***Rh. maculicornis*** **Sheng, Liu & Wang**

– Areolet quadrangular. First tergite 2.2 times as long as apical width, spiracle almost not convex (Fig. 13). Median tergites without yellow spot................ .... ***Rh. minomensis*** **(Uchida)**

Rhynchobanchus flavomaculatus **Sheng, sp.n.**

http://zoobank.org/87F55DB7-362C-4FE9-B7C6-25DA7EFA2E55
Figures 1–9

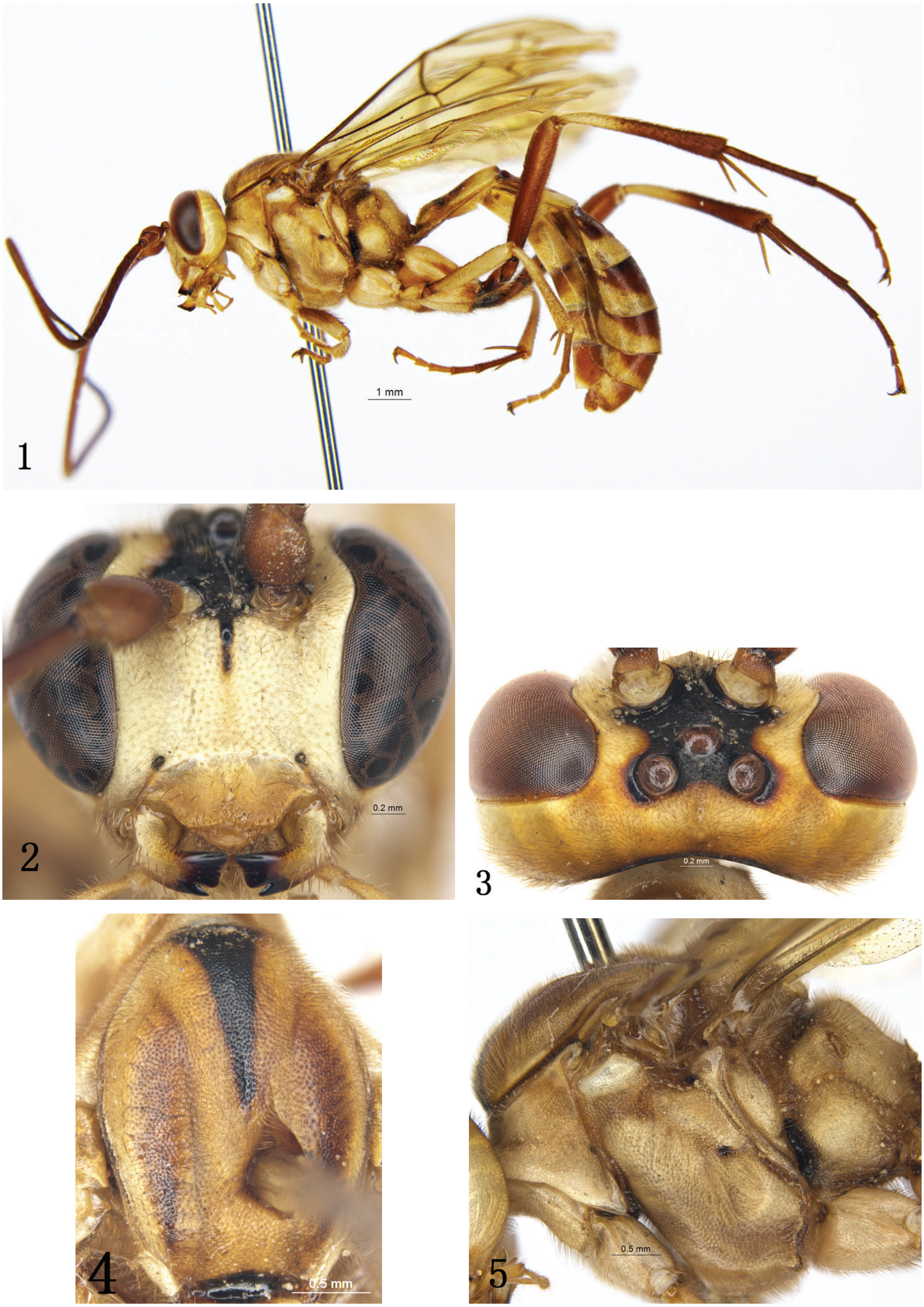
Material. Holotype, Female, **CHINA**: Kaishanlaodian, 1106 m, 30°32'N, 119°43'E, West Tianmu Mt., Lin'an, Zhejiang Province, 28 April 2017, leg. Ze-Jian Li, Meng-Meng Liu & Kai-Wen Gao. Paratypes: 1 female, Yun Mt., 1380m, 26°38'N, 110°37'E, Wugang, Shaoyang, Hunan Province, 18 April 2011, leg. Ze-Jian Li. 1 female, same data as holotype, but 8 April 2013, leg. Li-Wei Qi & Biao Chu. 1 male, same data as holotype, but 14 April 2014, leg. Hai-Yan Nie & Ping Hu. 2 females, same data as holotype, but 23/24 April 2014, leg. Ting-Ting Ji.

Diagnosis. Body yellowish brown with large irregular yellowish white spots (Fig. 1). Face (Fig. 2) finely granulose, with sparse fine punctures and yellowish brown setae, near upper margin with a small median tubercle. Inner orbits of compound eyes distinctly emarginate opposite antennal sockets, with regular yellowish brown setae. Posteromedian portion of vertex (behind ocellar triangle) with weak longitudinal groove (Fig. 3). Lower-posterior corner of mesopleuron with strong swelling (Fig. 5). Wings (Fig. 7) yellowish brown, semi-hyaline. Longer spur of mid tibia approximately 0.8 times as long as first tarsomere. Tergite 1 about 2.3 times as long as apical width, distinctly convex basal of spiracle.

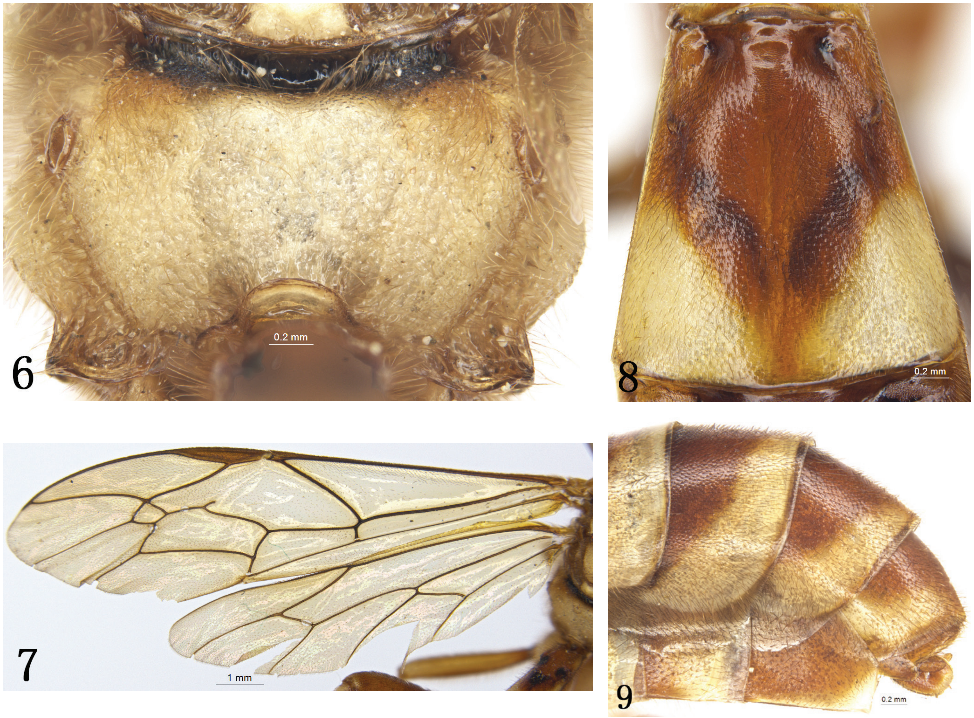
Description. Female (Fig. 1). Body length 15.6 to 17.1 mm. Forewing length 11.3 to 12.9 mm.

Head. Face (Fig. 2) approximately 1.7 times as wide as long, finely granulose, with sparse fine punctures and yellowish brown setae, median portion longitudinally convex; near upper margin with a small median tubercle. Clypeus approximately 2.5 times as wide as long, finely granulose, with indistinct, sparse brown setae; apical margin with distinct median emarginate. Mandible particularly strong, basal portion with sparse brown setae. Malar area finely granulose, approximately 0.5 times as long as basal width of mandible. Inner orbits of compound eyes distinctly emarginate opposite antennal sockets. Gena broad, evenly convergent backwardly, with dense, fine punctures and yellowish brown setae. Vertex (Fig. 3) with yellowish brown setae and weak median longitudinal groove. Ocellar triangle with distinct punctures. Postocellar line approximately 1.3 times as long as oculo-ocellar line. Lower median portion of frons slightly concave, with fine arched wrinkles; lateral portion with dense yellowish brown setae. Lateral margin of antennal socket with small tubercle. Antenna with 55 to 58 flagellomeres, ratio of length from first to fifth flagellomeres: 2.1:1.1:1.0:1.0:1.0. Occipital carina complete.

Mesosoma. Pronotum (Fig. 5) with granulose texture and dense yellowish brown setae; Epomia absent. Mesoscutum (Fig. 4) evenly convex, anterior and lateral portions with distinct dense punctures and brown setae, posteromedian portion with fine, indistinct punctures. Notaulus weak. Scutoscutellar groove smooth, shiny. Scutellum almost rounded convex, with fine dense punctures and long brown setae. Postscutel-



Figures 1–5. *Rhynchobanchus flavomaculatus* sp. n. Holotype. Female. **1** Habitus, lateral view **2** Head, anterior view **3** Head, dorsal view **4** Mesoscutum **5** Mesosoma, lateral view.



Figures 6–9. *Rhynchobanchus flavomaculatus* sp. n. Holotype. Female. **6** Propodeum **7** Wings **8** Tergite 2, dorsal view **9** Apical portion of metasoma, lateral view.

lum evenly convex, with fine punctures. Mesopleuron (Fig. 5) granulose with even fine punctures and brown setae; speculum very small, with fine punctures; mesopleural fovea small, shallow, smooth. Lower-posterior corner of mesopleuron strongly convex. Metapleuron evenly convex, with texture as that of mesopleuron; lower posterior portion with indistinct oblique wrinkles. Submetalpeural carina complete, strong, anterior portion strongly raised. Sulcus between postscutellum and propodeum deep, shiny, with short longitudinal wrinkles. Propodeum (Fig. 6) short, slightly oblique; weakly, finely reticulate, with dense yellowish brown setae; spiracle convex, oblique elongate, 3.0 times as long as width, located at basal 0.3.

Wings (Fig. 7). Yellowish brown, semi-hyaline. Forewing with vein 1cu-a distal of 1/M, distance between them approximately 0.5 times as long as 1cu-a. Ramulus long. Areolet pentangle, receiving 2m-cu approximately at basal 0.4, vein 3rs-m slightly longer than vein 2rs-m. 2-Cu 1.5 times as long as 2cu-a. Hindwing vein cu-a strongly reclivous, 1-cu 0.15 times as long as cu-a.

Legs. Dorsal profile and apical portion of tibia with uneven thorns. Longer spur of mid tibia 0.8 times as long as first tarsomere. Ratio of length of hind first to fifth tarsomeres 5.8:2.5:2.0:1.0:1.5.

Metasoma. Tergite 1 about 2.3 times as long as apical width, distinctly convex basal of spiracle, with fine punctures and yellowish brown short setae, apical margin smooth;

glymma deep, small; spiracle small, convex, almost circular, located at basal 0.3. Tergite 2 (Fig. 8) approximately as long as apical width, indistinctly reticular, with dense punctures and yellowish brown short setae; basal median portion transversely convex, smooth; thyridium distinct, almost smooth. Tergite 3 weakly shining, with dense fine punctures and yellowish brown setae, apical portion slightly compressed. Fourth and subsequent tergites compressed, with fine punctures and yellowish brown setae. Ovipositor sheath broad, not reaching to apex of metasoma.

Colour pattern (Fig. 1). Yellowish brown with large irregular yellowish white spots, except following: mandibular teeth, median portion of frons, ocellar triangle, line along occipital carina, anteromedian narrow reversed triangular spot, scutoscutellar groove, anterior portion of mesosternum, anterior margin of metapleuron, anterior transverse groove of propodeum, front and inner profiles of hind coxa, trochanter (dorsal and apical portions reddish brown), median portion of tergite 1 irregularly dark brown to black. Antenna except apical portion brown to dark brown, main portion of front femur, ventral profile of mid femur slightly; apical margin of hind coxa, hind trochantellus, hind femur, hind tibia except basal half yellowish brown, hind tarsus; tergites 2 and 3 except apical triangular spots yellow to brown, tergites 3 to 7 except lateral and apical margin yellow to yellowish brown; tergite 8, ovipositor sheath reddish brown to dark reddish brown. Pterostigma brown. Veins brown to dark brown.

Male. Body length approximately 13.1 mm. Forewing length approximately 10.0 mm. Antenna with 55 flagellomeres. Lateral longitudinal stripes of mesoscutum, transverse stripe beneath subalar ridge black brown to brown. Pterostigma yellowish brown. Otherwise similar to female.

Distribution. CHINA: Hunan, Zhejiang.

Remarks. This new species is similar to *Rh. maculicornis* Sheng et al., 1995, but can be distinguished from the latter by the following combination of characters: lower-posterior corner of mesopleuron with strong convexity; gena, vertex, mesopleuron and mesosternum yellow; and propodeum yellowish white. *Rhynchobanchus maculicornis* has lower-posterior corner of mesopleuron slightly convex; gena, vertex, mesopleuron and mesosternum black; basal portion of propodeum black, median reddish brown and apical yellow.

Etymology. The name of the new species is derived from Latin words “flavi” (yellow) and “maculatus” (macula) after its body with large irregular yellowish spots.

Additional records for Chinese species of *Rhynchobanchus*

Rhynchobanchus flavopictus flavopictus Heinrich, 1937

Figure 10

Specimen examined. 1 female, CHINA: Xinbin, Liaoning Province, 28 May 1994, leg. Mao-Ling Sheng (GSFPM).

Distribution. China, Germany, Italy, Italy, Poland, Russia, United Kingdom.

Figure 10. *Rhynchobanchus flavopictus flavopictus* Heinrich, 1937. Female. Metasoma, dorsal view.

Rhynchobanchus flavopictus orientalis Kuslitzky, 2007

Figure 11

Specimen examined. 1 female, CHINA: Benxi, Liaoning Province, 6 June 2007, leg. Mao-Ling Sheng (GSFPM). **New record for China**.

Distribution. China, Russia.

Rhynchobanchus maculicornis Sheng, Liu & Wang, 1995

Figure 12

Specimens examined. 1 male (holotype), CHINA: Benxi, Liaoning Province, 12 May 1985, leg. Shou-Lin Liu (GSFPM). 3 males (paratypes), same data as holotype (GSFPM). 1 male: Laotudingzi, Huanren, Liaoning Province, 25 May to 9 June 2011, IT (GSFPM). 1 male: Chagou, Haicheng, Liaoning Province, 15 May 2015, leg. Tao Li (GSFPM). 2 females, 2 males: Benxi, Liaoning Province, 30 May 2016, leg. Shu-Ping Sun (GSFPM). 5 males: Benxi, Liaoning Province, 16 May 2017, leg. Mao-Ling Sheng (GSFPM). 1 male: Kuandian, Liaoning Province, 18 May 2017, leg. Tao Li (GSFPM).

Distribution. China (Liaoning Province).

Rhynchobanchus minomensis (Uchida, 1933)

Figure 13

Specimens examined. 1 female, CHINA: Xinbin, Liaoning Province, 29 May 1994, leg. Mao-Ling Sheng (GSFPM). 2 females: Baishilazi, Kuandian, Liaoning Province, 26 May to 9 June 2011, IT (GSFPM).

Distribution. China, Japan, Korea, Russia.

Figure 11. *Rhynchobanchus flavopictus orientalis* Kuslitzky, 2007. Female. Habitus, lateral view.

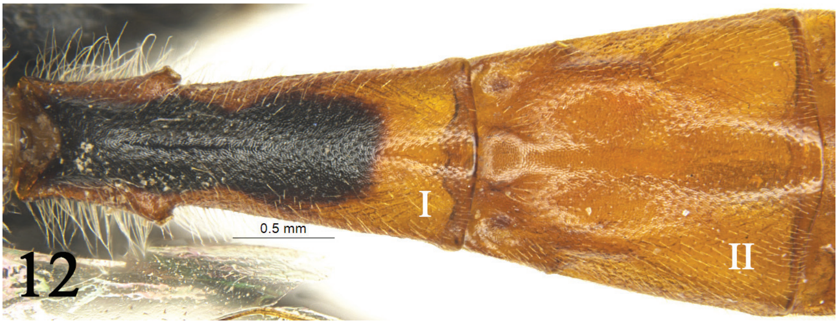


Figure 12. *Rhynchobanchus maculicornis* Sheng, Liu & Wang, 1995. Female. Tergites I–II, dorsal view.

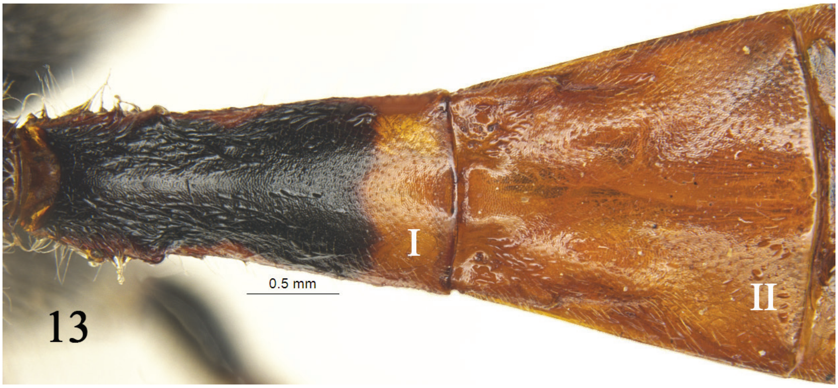


Figure 13. *Rhynchobanchus minomensis* (Uchida, 1933). Female. Tergites I–II, dorsal view.

Rhynchobanchus niger Sheng, Li & Pang, 1997
Figure 14

Specimens examined. 1 female (holotype), CHINA: Xinbin, Liaoning Province, 28 May 1994, leg. Mao-Ling Sheng (GSFPM). 28 males (paratypes), id., but 28/ 29 May, 1994. 2 males (paratypes), CHINA, Shenyang, Liaoning Province, 8 May, 1994. 1 female: Kuandian, Liaoning Province, 4 June 2001, leg. Shu-Ping Sun (GSFPM). 1 female: Shenyang, Liaoning Province, 6 May 2002, leg. Mao-Ling Sheng (GSFPM). 1 female: Benxi, Liaoning Province, 27 May 2006, leg. Chun-Tian Zhang (GSFPM). 1 female: Kuandian, Liaoning Province, 7 June 2007, leg. Shu-Ping Sun (GSFPM). 1 female: Laotudingzi, Huanren, Liaoning Province, 25 May 2011, Mao-Ling Sheng (GSFPM).

Distribution. China (Liaoning Province).

Rhynchobanchus rufus Sheng & Sun, 2014
Figure 15

Specimens examined. 1 female, CHINA: Shenyang, Liaoning Province, 3 May 2003, leg. Mao-Ling Sheng (GSFPM). 1 female (holotype): Kuandian, Liaoning Province, 6 June 2007, leg. Shu-Ping Sun (GSFPM). 1 female (paratype): Xinbin, Liaoning Province, 28 May, 1994, leg. Mao-Ling Sheng (GSFPM). 1 female (paratype): Huanren, Liaoning Province, June, 1996 (GSFPM). 3 females (paratypes): Kuandian, Liaoning Province, 6 to 8 June 2007, leg. Shu-Ping Sun & Mao-Ling Sheng (GSFPM). 1 female

Figure 14. *Rhynchobanchus niger* Sheng, Li & Pang, 1997. Holotype. Female. Apical portion of metasoma, lateral view.

Figure 15. *Rhynchobanchus rufus* Sheng & Sun, 2014. Holotype. Female. Apical portion of forewing.

(paratype): Tieshashan, 900m, Benxi, Liaoning Province, 12 June 2011, leg. Ya-Nan Tang & Ying Zhang (GSFPM). 1 female (paratype), id., 19 June 2011, Tie-Fei Zhao & Ying Yang. 1 female (paratype): Benxi, Liaoning Province, 19 June 2013, IT (GSFPM). 1 female: Benxi, Liaoning Province, 12 June 2015, leg. Mao-Ling Sheng (GSFPM).

Distribution. China (Liaoning Province).

Conclusions

There are now eight known species of *Rhynchobanchus* Kriechbaumer in the world, of which one is only known from the Oriental Region, and seven species are known from the Palaearctic Region. Six species have been known from China. Hitherto, there are no host records.

Acknowledgements

The authors are deeply grateful to Dr Masahiro Ohara (Hokkaido University Museum, Hokkaido University, Japan) for his help while the corresponding author was working in the museum, and Dr Kyohei Watanabe (Kanagawa Prefectural Museum of Natural History, Odawara, Kanagawa, Japan) for providing the photos of *Rh. flavopictus orientalis*, *Rh. bicolor*, and *Rh. flavopictus*. The authors also wish to thank Dr Dicky S.K. Yu (Canadian National Collection, Ottawa, Canada) for presenting valuable materials for this work. This research was supported by the National Natural Science Foundation of China (NSFC, No.31070585, No. 31372246, No. 31501887) and Natural Science Foundation of Zhejiang Province (LY18C040001).

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ZooKeys 752: 137–148 (2018)
doi: 10.3897/zookeys.752.20086
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DATA PAPER

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Ichthyological collection of the Museu Oceanográfico D. Carlos I

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Academic editor: *M.E. Bichuette* | Received 7 August 2017 | Accepted 31 March 2018 | Published 23 April 2018

http://zoobank.org/FA7DBFC6-21ED-4546-AEB1-1508E4351EA3

Citation: Silva AS, Pitta Groz M, Leandro P, Assis CA, Figueira R (2018) Ichthyological collection of the Museu Oceanográfico D. Carlos I. ZooKeys 752: 137–148. https://doi.org/10.3897/zookeys.752.20086

Resource citation: Silva AS, Pitta Groz M, Leandro P, Assis CA, Figueira R (2017) Ichthyological collection of the Museu Oceanográfico D. Carlos I. 675 records, published online, http://ipt.gbif.pt/ipt/resource?r=codc&v=1.0, released on 18 May 2017. GBIF Key of collection: https://gbif.org/dataset/6005f3b4-da6a-4d88-ac92-81f2e950eb24, Data Paper https://doi.org/10.3897/zookeys.752.20086

Abstract

The collection of the Museu Oceanográfico D. Carlos I is a historical specimen, instrument, and document collection that has been housed at the Aquário Vasco da Gama since 1935. The collection is largely the result of several scientific campaigns conducted by Dom Carlos de Bragança between 1896 and 1907. Specifically, the ichthyological collection consists of 675 surviving catalogue records of specimens caught, acquired or offered to D. Carlos I between 1892 to 1907, and includes the type specimen for *Odontaspis nasutus* Bragança, 1904 (junior synonym of *Mitsukurina owstoni* Jordan, 1898), along with several specimens of deep sea species. All specimens were captured in coastal Portuguese waters, and were preserved in alcohol, formalin, or mounted.

Keywords
Natural History collection, D. Carlos I, Animalia, Myxini, Petromyzonti, Elasmobranchii, Holocephali, Actinopterygii, Occurrence, Portugal

Introduction

Dom Carlos I, king of Portugal and the father of Portuguese oceanography (Saldanha 1997, 2002), was an avid naturalist. He was heavily influenced by his love of the sea, a love imparted by his father, D. Luis I, and also by the scientific explorations of his friend Prince Albert I of Monaco (Carpine-Lancre and Saldanha 1992, Ceríaco 2014). These influences, along with the many foreign scientific campaigns that crossed Portuguese waters and the impact that greater oceanographic knowledge could have on Portuguese fisheries, inspired D. Carlos I to organise a series of oceanographic campaigns to study the bathymetry and fauna of the Portuguese coast (Bragança, 1897b). These campaigns, undertaken between 1896 and 1907, resulted in many manuscripts, but only four formal publications (Bragança 1897b, 1899b, 1902b, 1904b), and a magnificent collection of marine animal specimens, some of which were displayed in national and international exhibitions (Saldanha 1997).

The writings of D. Carlos I include eleven detailed annual reports of his oceanographic campaigns (Bragança 1896, 1897a, 1898, 1899a, 1900, 1901, 1902a, 1903, 1904a, 1905, 1907), formally published in 1897 and 1902 (Bragança 1897b, 1902b), one publication on the tuna fisheries in the Algarve (Bragança 1899b), and one on the shark species captured along the Portuguese coast during the 1896-1903 campaigns (Bragança 1904b).

In his reports, D. Carlos I described, in great detail, the programme and objectives of each campaign, the sampling stations and materials used in each, their depth and benthic characteristics, and listed the specimens collected (Bragança 1896, 1897a, 1898, 1899a, 1900, 1901, 1902a, 1903, 1904a, 1905, 1907). In his "Esqualos obtidos nas costas de Portugal durante as campanhas de 1896 a 1903" (Bragança 1904b), D. Carlos I catalogued all the shark species captured, their geographical and bathymetric distribution, their systematic position, with the accepted scientific name and synonyms, and their vernacular names (in both Portuguese and French). D. Carlos I also described the morphological characteristics, length and coloration, stomach contents, and the economic uses for each species. In addition, D. Carlos also provided identification keys and an ecological classification for the collected species. As well as this published work, D. Carlos I also left many manuscript notes with similar information on other fish groups, possibly intended to serve as basis for other publications (Saldanha 1997).

The collection of the Museu Oceanográfico D. Carlos I has been housed at the Aquário Vasco da Gama (AVG) since 1935, but it comprises only a small fraction of the material collected by D. Carlos, as many specimens were lost between the king's assassination, in 1908, and the collection's transfer to the AVG (Nobre 1935, Carpine-Lancre and Saldanha 1992). The collection is a result of the king's fastidious work, and exploration of Portugal's distinctive underwater geography. Underwater canyons over 1000 m deep are as close as 5 nautical miles (9.26 Km) from the coast (Instituto Hidrográfico 2008), resulting in the occurrence of bathypelagic faunal assemblages close to shore. These geographical conditions facilitated the capture of a large number of deep-sea species, including the holotype of *Odontaspis nasutus* Bragança, 1904 (junior synonym of *Mitsukurina owstoni* Jordan, 1898).

The wider collection of the Museu Oceanográfico D. Carlos I is made up of ichthyological, mammalian, ornithological, reptilian and a wide variety of invertebrate specimens, along with scientific instruments, and a rich scientific library that includes the king's manuscripts and copies of his published works. This collection is of incalculable historical and scientific value as it is one of the few surviving royal Natural History collections in Portugal, most of which were destroyed in a fire at the Museu Bocage in 1978 (Alves et al. 2014, Ceríaco 2014). Of this material, ichthyological specimens are the most numerous (675 records), and have the most data associated with them, while also being extremely diverse and rich in rare deep-sea specimens.

Given the historical value of the collection and its wide faunal assemblage, a dataset of the ichthyological specimens housed at the Museu Oceanográfico D. Carlos I was made available on the Global Biodiversity Information Facility (GBIF) data portal. This dataset established the first records of at least 184 species in Portuguese waters as far back as the period between 1892 and 1907.

The objectives of the present paper are: (1) to present the existence and the composition of the ichthyological collection of the Museu Oceanográfico D. Carlos I, which comprises 675 records, captured between 1892 and 1907; and (2) to emphasise its importance, not only because of its historical value, but also due to its diversity and the rarity of some of the specimens within it. We also provide the historical context, and a summary catalogue of the taxa in the collection, and highlight some notable specimens.

General description

The dataset is comprised of the ichthyological specimens from the collection of the Museu Oceanográfico D. Carlos I. These specimens consist of 675 catalogued records, composed of 5 classes, 35 orders, 119 families, 196 genera, and 236 species. There are between 590 and 600 specimens preserved in alcohol and formalin, and between 75 and 90 mounted specimens, collected between 1892 and 1907. Many specimens have accompanying collection data in the king's manuscripts. The records include the holotype of *Odontaspis nasutus* Bragança, 1904 (junior synonym of *Mitsukurina owstoni* Jordan, 1898), an exquisitely preserved *Nemichthys scolopaceus* Richardson, 1848, and a mounted specimen of *Centrophorus lusitanicus* Barbosa du Bocage & de Brito Capello, 1864.

Project details

Project title: Revisão Taxonómica e Consolidação dos Catálogos das Coleções Ictiológicas do Aquário Vasco da Gama

Funding: No funding was required or used for this study.

Taxonomic coverage

General taxonomic coverage description: The collection comprises representatives of the classes Myxini, Petromyzonti, Elasmobranchii, Holocephali and Actinopterygii, with actinopterygians representing over 80% of all specimens (Figure 1). The classes Myxini, Petromyzonti, and Holocephali are each represented by a single species, with a varying number of specimens for each species. There are 30 genera and 38 species of elasmobranchs, from eight orders and 23 families. There are 163 genera and 192 species of actinopterygians, from 24 orders and 94 families, including Perciformes, which corresponds to 41% of the entire dataset (Figure 2). Figure 3 shows the temporal sampling profile of the specimens, and the number of specimens per order. Of 675 records, 652 are identified to the species or subspecies level, representing a total of 196 genera and 236 species.

Taxonomic ranks

Kingdom: Animalia
Phylum: Chordata
Class: Actinopterygii, Elasmobranchii, Holocephali, Myxini, Petromyzonti

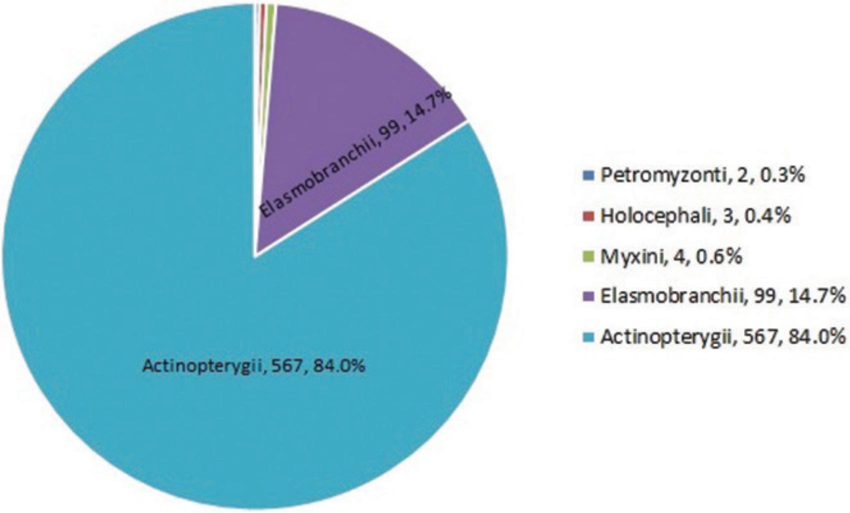

Figure 1. Number and percentage of the classes represented in the dataset.

Order: Anguilliformes, Atheriniformes, Aulopiformes, Batrachoidiformes, Beloniformes, Beryciformes, Carcharhiniformes, Chimaeriformes, Clupeiformes, Gadiformes, Gobiesociformes, Hexanchiformes, Lamniformes, Lampriformes, Lophiiformes, Myctophiformes, Myliobatiformes, Myxiniformes, Notacanthiformes, Ophidiiformes, Osmeriformes, Perciformes, Petromyzontiformes, Pleuronectiformes, Rajiformes, Saccopharyngiformes, Scorpaeniformes, Squaliformes, Squatiniformes, Stephanoberyciformes, Stomiiformes, Syngnathiformes, Tetraodontiformes, Torpediniformes, Zeiformes

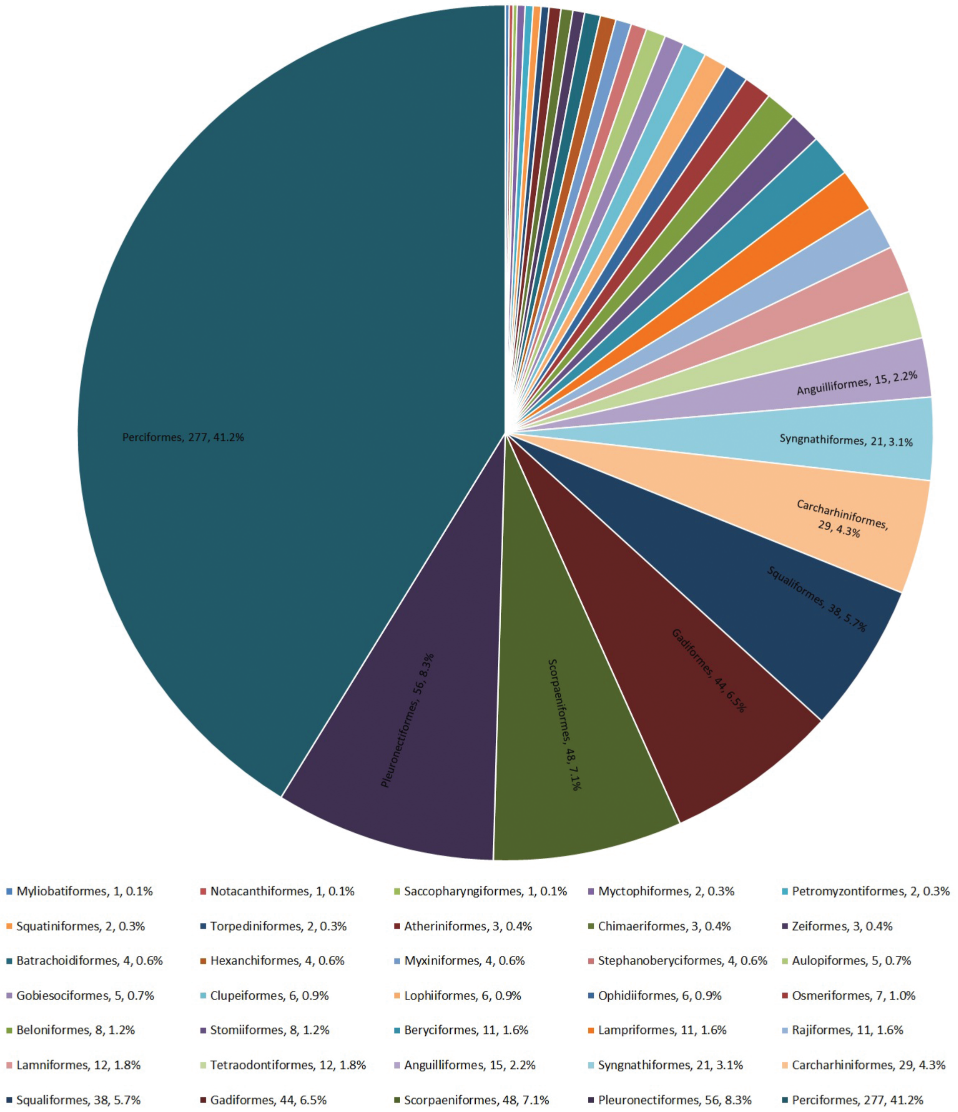

Figure 2. Number and percentage of the orders represented in the dataset. Only the orders with at least 15 specimens are labelled.

Family: Alepisauridae, Alepocephalidae, Alopiidae, Ammodytidae, Anguillidae, Antennariidae, Argentinidae, Atherinidae, Aulopidae, Balistidae, Batrachoididae, Belonidae, Berycidae, Blenniidae, Bothidae, Bramidae, Callionymidae, Caproidae, Carangidae, Carapidae, Carcharhinidae, Caristiidae, Centracanthidae, Centriscidae, Centrolophidae, Centrophoridae, Cepolidae, Cetorhinidae, Chaunacidae, Chiasmodontidae, Chimaeridae, Chlamydoselachidae, Citharidae, Clinidae, Clupeidae, Congridae, Cottidae, Cynoglossidae, Dalatiidae, Diodontidae, Echeneidae, Echinorhinidae, Epigonidae, Etmopteridae, Gadidae, Gempylidae, Gobiesocidae, Gobiidae, Gonostomatidae, Haemulidae, Hexanchidae, Himantolophidae, Labridae, Lamnidae, Lampridae, Lophiidae, Lotidae, Macrouridae, Melamphaidae, Merlucciidae, Mitsukurinidae, Molidae, Moridae, Moronidae, Mugilidae, Mullidae, Muraenidae, Myctophidae, Myliobatidae, Myxinidae, Nemichthyidae, Nomeidae, Notacanthidae,

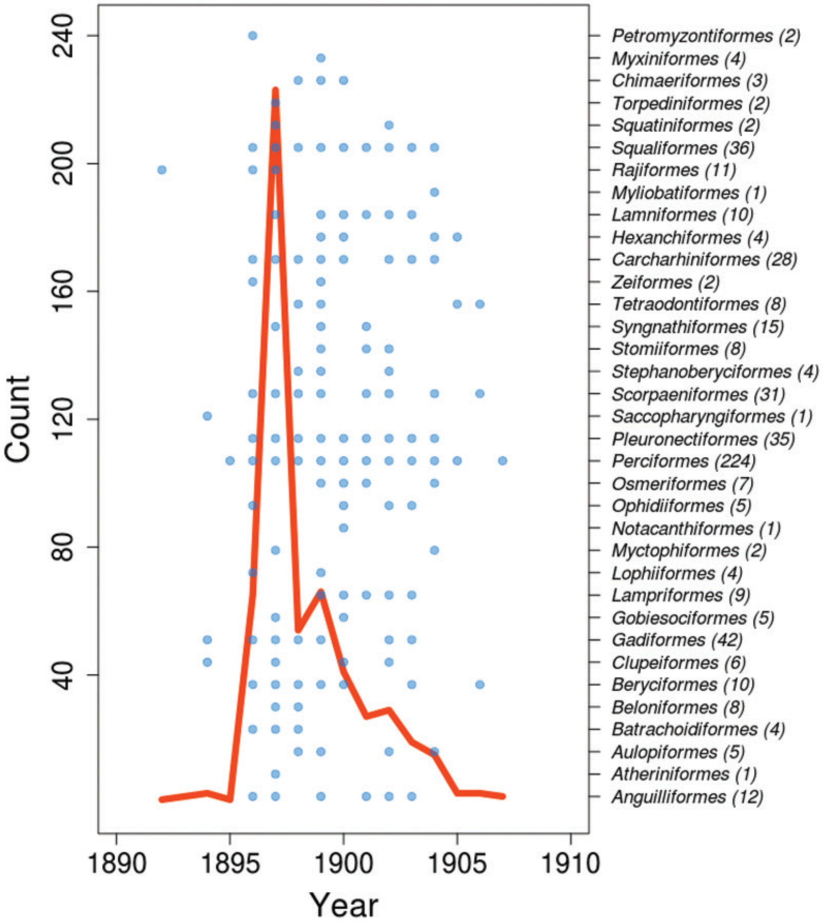

Figure 3. Temporal profile of the sampling years of the specimens held in the ichthyological collection. Blue dots represent sampling years for each order, for which, in parentheses, the number of specimens is provided. The red curve shows the number of specimens collected per year.

Ophichthidae, Ophidiidae, Oxynotidae, Peristediidae, Petromyzontidae, Phycidae, Polyprionidae, Pomacanthidae, Pomacentridae, Pomatomidae, Pseudotriakidae, Rajidae, Regalecidae, Rhinobatidae, Saccopharyngidae, Sciaenidae, Scomberesocidae, Scombridae, Scophthalmidae, Scorpaenidae, Scyliorhinidae, Sebastidae, Serranidae, Soleidae, Somniosidae, Sparidae, Sphyraenidae, Sphyrnidae, Squalidae, Squatinidae, Sternoptychidae, Stomiidae, Stromateidae, Synaphobranchidae, Syngnathidae, Tetraodontidae, Torpedinidae, Trachichthyidae, Trachinidae, Trachipteridae, Triakidae, Trichiuridae, Triglidae, Uranoscopidae, Xiphiidae, Zeidae

Spatial coverage

General spatial coverage: The bulk of the specimens were collected at the mouth of the rivers Tagus and Sado, and in the bays of Cascais and Sesimbra, usually within 50 nautical miles of the coast. The collection also features several specimens caught on the Algarve coast, a handful of specimens from the coast north of the Cabo da Roca, and one specimen tentatively identified as being from the Azores. The sampling depths range from surface level to 1875 m deep. Most specimens were captured within the polygon defined by the following coordinates: 36°42'14"N and 42°17'38"N latitude; 10°43'22"W and 6°11'45"W longitude (Figure 4).

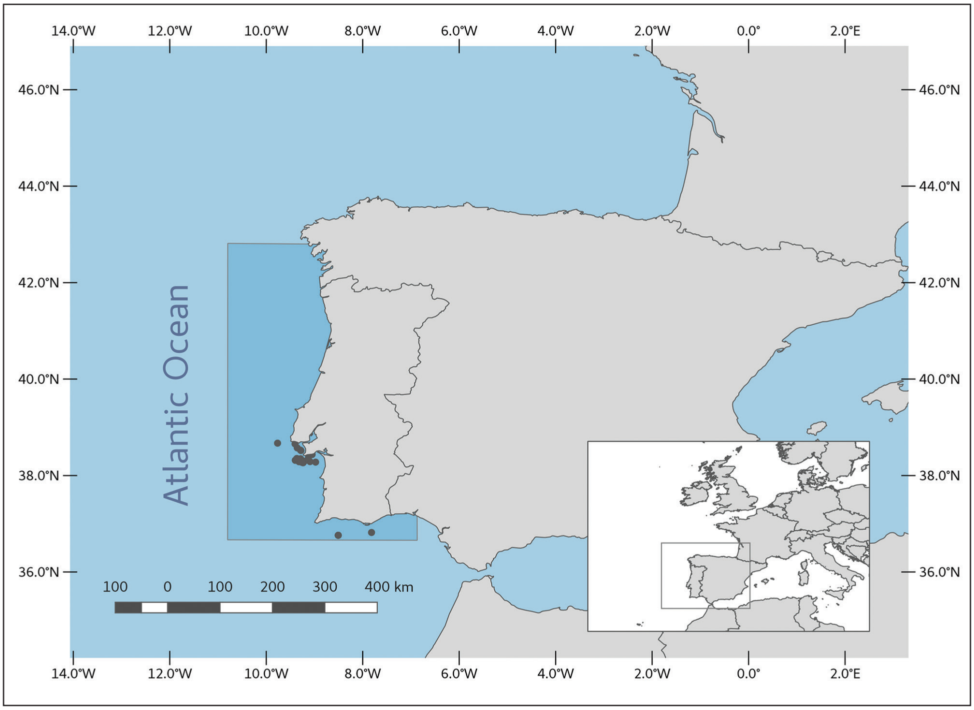

Figure 4. Geographic area covered by the collection (in darker blue). Plots indicate sites for the 29 georeferenced records.

Temporal coverage

July 18, 1892–June 8, 1907

Natural collections description

Collection name: Coleção do Museu Oceanográfico D. Carlos I

Collection identifier: bf52e001-eb74-421e-9d51-157d6eb5a358

Specimen preservation method: Alcohol, Formalin, Mounted

Curatorial unit: Between 590 and 600 jars, between 60 and 70 mounted specimens, and 16 jaws

Methods

Method step description: The ichthyological collection of the Museu Oceanográfico D. Carlos I was first catalogued for publication by Gonçalves (1942). That publication consisted of the first taxonomic check list since the collection moved to the AVG (Gonçalves 1942). Between 1942 and the present day only minor synonymic revisions have been made and noted in the card catalogue, with the exception of the Blenniidae, which were re-identified and described by Almeida (1981). More recently, an electronic catalogue was created as an Excel (Microsoft, Washington, USA, 2010) spread sheet, without systematic synonymy revision as it encompassed all the collections and taxa housed in the AVG.

The first step of the current revision project was to isolate ichthyological records from the electronic catalogue, and check them for synonymy using both FishBase (Froese and Pauly 2017) and the Catalogue of Fishes (Eschmeyer et al. 2017). The revised electronic catalogue was then cross-checked with the card catalogue and Gonçalves (1942) for collection date and location, depth of collection, and species name. If species names did not match the currently accepted name or the synonym used in the first electronic catalogue, they were re-checked for synonymy. When the card and electronic catalogue both had accepted, but different, species names, or the synonyms did not belong to the same valid taxon, the records were flagged for further identification.

Once catalogue crosschecking was complete, specimen labels were compared to the final electronic catalogue, both to confirm the information and to check the location of the specimens. The crosschecking process also identified two mislabelled elasmobranch specimens, which were identified using Compagno's Sharks of the World (1984). When mismatches were found, the information in the catalogue was substituted with the information from the specimen labels, including species names.

The last step in the creation of the electronic catalogue was to resolve naming inconsistencies. First, the species identification present on labels was checked for synonymy. Once valid names had been identified, the species range for each valid taxon was ascertained using FishBase (Froese and Pauly 2017). If one of the ranges was incongruent with the collection locality, the concordant species name was chosen for each record. If both ranges were congruent with the collection locality, the specimens were re-identified by the authors.

For publication purposes, the records pertaining to the collection of the Museu Oceanográfico D. Carlos I were extracted from the electronic catalogue and transformed into a DarwinCore compatible Excel (Microsoft, Washington, 2016) spread sheet. The dataset was enriched with collection data taken from the king's records of his oceanographic campaigns (Bragança 1896, 1897a, 1898, 1899a, 1900, 1901, 1902a, 1903, 1904a, 1905, 1907). The additional data included navigational bearings, depth ranges, and sampling methods.

Study extent description: The specimens belonging to D. Carlos's ichthyological collection can be divided in three non-taxonomical groups: specimens caught during the king's oceanographic campaigns, specimens caught by the king outside the campaigns, and those offered to the king. These groups vary in collection data completeness, with the specimens captured during oceanographic campaigns generally having the most information, including navigational bearings and collection depths, and those offered to D. Carlos having the least information attached to them, some have only the collection locality or purchase location. However, all specimens were captured in Portuguese coastal waters, and those caught by the king were captured mostly in the area between the Cabo da Roca and Setúbal, and some in the Algarve. The specimens were captured year-round, between 1892 and 1907, but the oceanographic campaigns were usually held in the spring and summer months, from 1896 to 1907.

Sampling description: The specimens were caught using a variety of fishing nets, lines and traps (côvo). The line fishing methods included longline fishing (espinhel) and angling. The fishing nets used range from bottom and midwater trawls to dragnets. Traditional fishing techniques may also have been used, as some specimens were bought in markets or offered by fishermen, but there is no specific additional information in these cases. Nonetheless, there is record of at least one specimen being harpooned.

Quality control description: The validity of species' names was checked using both FishBase (Froese and Pauly 2017) and the Catalogue of Fishes (Eschmeyer et al. 2017). Synonymy was checked across all three catalogues, if incongruences were found between catalogues the earliest name on record was used for disambiguation. If the names used in the earliest catalogue did not resolve the nomenclatural inconsistency, geographical ranges of the species were checked and used to assign the currently accepted species name. When these steps were insufficient to identify the correct species, the authors proceeded to a more thorough re-identification of the specimens. Lastly, for mislabelled elasmobranch specimens, the identification keys in Sharks of the World (Compagno 1984) were used.

Datasets

Dataset description

Object name: Darwin Core Archive Ichthyological Collection of the Museu Oceanográfico do Rei D. Carlos I
Character encoding: UTF-8
Format name: Darwin Core Archive format
Format version: 1.0
Distribution: http://ipt.gbif.pt/ipt/archive.do?r=codc
Publication date of data: 2017-05-22
Language: Portuguese
Licences of use: Creative Commons Attribution (CC-BY) 4.0 License
Metadata language: English
Date of metadata creation: 2017-04-11
Hierarchy level: Dataset

Acknowledgements

We would like to thank Paula Sousa from the Aquário Vasco da Gama for helping with the specimens' label verification and location. We also thank Patrick Reis Santos, from MARE - Marine and Environmental Sciences Centre, Faculdade de Ciências, Universidade de Lisboa, Portugal and School of Biological Sciences, University of Adelaide, Australia, and Nathan Kenny, from the Natural History Museum, London, United Kingdom, for proof-reading our manuscript. Lastly, we would like to thank André Esguícero, whose comments contributed to the improvement of the manuscript originally submitted.

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ZooKeys 752: 149–161 (2018)
doi: 10.3897/zookeys.752.24231
http://zookeys.pensoft.net

RESEARCH ARTICLE

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New identification of the moray eel *Gymnothorax minor* (Temminck & Schlegel, 1846) in China (Anguilliformes, Muraenidae)

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Academic editor: *N. Bogutskaya* | Received 5 February 2018 | Accepted 5 April 2018 | Published 23 April 2018

http://zoobank.org/C64D6428-1633-4414-8FAD-50EDA77AB45A

Citation: Li Y, Zhang L, Zhao L, Feng J, Loh KH, Zheng X, Lin L (2018) New identification of the moray eel *Gymnothorax minor* (Temminck & Schlegel, 1846) in China (Anguilliformes, Muraenidae). ZooKeys 752: 149–161. https://doi.org/10.3897/zookeys.752.24231

Abstract

A new identification of *Gymnothorax minor* (Temminck & Schlegel, 1846) is documented based on morphological characteristics and DNA barcoding. Sixty-one individuals of *G. minor* were collected from the East China Sea and the South China Sea. This species was previously reported as *Gymnothorax reticularis* Bloch, 1795 in China because of the similarity in external shape and color. *Gymnothorax minor* can be easily distinguished from *G. reticularis* by its color pattern of 18–20 irregular dark brown vertical bars and the body having scattered small brown spots. Additionally, the teeth are uniserial on both jaws, and the vertebrae number 137–139. By combining congener sequences of the cytochrome oxidase I (COI) gene from GenBank, two groups were detected among all the COI sequences of the currently named *G. minor*, which further indicated that two valid species were present based on genetic distance. A divergence also occurred on the number of vertebrae between the northern and southern populations. The phylogenetic and morphological analysis strongly supports that the northern and southern populations of *G. minor* are two different species. Furthermore, the distribution area of the northern *G. minor* has expanded southward to 5°15'N in the South China Sea. More specimens of *G. minor* and *G. reticularis* are crucial in order to define their geographical distribution boundaries and provide the correct DNA barcoding.

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[*] The authors contributed equally to this paper.

Keywords
DNA barcoding; geographical distribution; *Gymnothorax reticularis*; morphological characteristics; species taxonomy

Introduction

Moray eels are distributed in the subtropical and tropical seas, which are not well studied because of their cryptic habitats and occasionally aggressive behaviors. The genus *Gymnothorax* is regarded as a polyphyletic assemblage of ungrouped moray eels and can be easily distinguished from homologous species with irregular vertical bars along the dorsal midline before the dorsal fin origin (Smith 2012). However, *Gymnothorax minor* (Temminck & Schlegel, 1846) has been often confused with *Gymnothorax reticularis* Bloch, 1795 because of the similar morphological characteristics. More regional taxonomic reviews of *G. minor* can be found from Japan (Tawa and Mochioka 2009, Yamada et al. 2009, Nakabo 2013), Korea (Kim et al. 2012), Vietnam (Hibino et al. 2016), the Philippines (Bucol and Alcala 2015, Wagey et al. 2015), Australia, and New Zealand (Böhlke and McCosker 2001). A total of 37 species of the genus *Gymnothorax* exist, but *G. minor* has been reported rarely in China (Chen and Zhang 2015), while *G. reticularis* is the widely used identification by Chinese ichthyologist. The Chinese name "Wang Wen Luo Xiong Shan" was assigned to the species "*Gymnothorax reticularis*", which has been persistently confused with *G. minor* (Zhu et al. 1962, 1985, Cheng and Zheng 1987, Zhang et al. 2010, Chen and Zhang 2015). In fact, both species can be easily distinguished by the number of vertebrae and their differing distribution ranges: the vertebrae number 129–143 in *G. minor* vs. 114–126 in *G. reticularis*; *G. minor* is found from the northwestern to the southwestern Pacific vs. *G. reticularis* from the Indian Ocean to the Red Sea (Smith and Böhlke 1997, Kim et al. 2012). Therefore, the identification of these species in Chinese waters must be clarified based on actual specimens. During our ichthyofaunal surveys, we initially identified the moray eels as "*Gymnothorax reticularis*" by mistakes in 2012 and 2013. With our further research, we were fortunate to find this wrong identification and correct it. By now we have 61 individuals of *G. minor* found from the East China Sea and the South China Sea.

DNA barcoding, the mtDNA gene cytochrome c oxidase subunit I (COI) used in molecular taxonomy can help expand our knowledge by discriminating among species (Domingues et al. 2013, Puckridge et al. 2013), discovering newly recorded and new species (Xiao et al. 2016), revealing cryptic species (Hajibabaei et al. 2007, Zemlak et al. 2009), and identifying ichthyoplankton (Ko et al. 2013, Hubert et al. 2015, Li et al. 2017), which can also be sequenced with universal primers (Hebert et al. 2003). In the present study, DNA barcoding was employed to better solve the taxonomic problems of *Gymnothorax* at species level. Not surprisingly, misidentified DNA barcoding of these species has been found in GenBank, calling for correct identifications.

One objective of this study is to report the species of *G. minor* as the new identification with its new distribution in China; the other is to describe this species based on morphological characteristics and DNA barcoding, and to correct the current COI sequences of this species released in GenBank. The results will highlight the need for caution when identifying moray eels and will facilitate the fishery management, biodiversity conservation, and sustainable exploitation of this species.

Materials and methods

Specimen collection

A total of 61 individuals of *G. minor* was collected from the East China Sea and the South China Sea from September 2012 to November 2017 (Figure 1, Table 1). All specimens were identified based on morphological characteristics as defined by Nakabo (2013) and Yamada et al. (2009). For genetic studies, a piece of muscle tissue was obtained from randomly selected individuals and preserved in 95% ethanol. All examined specimens were preserved at the Third Institute of Oceanography, State Oceanic Administration.

Morphological analysis

Counting and measurement methods were performed as described by Böhlke (1989). The counts included the following characteristics: bars behind gill opening, teeth, dentition, median intermaxillary teeth, dorsal fin origin, and vertebrae (counted from X-ray photos). The measurements included the following traits: total length, pre-anal length, depth at gill-opening, depth at anus, width at gill-opening, width at anus, head length, snout length, eye diameter, and interorbital width. All measurements were performed to the nearest 0.1 mm using calipers. Color and brown brands/spots were documented in fresh fish, and all remaining measurements were implemented on preserved specimens.

Molecular analyses

Five individuals were randomly chosen from each survey for genetic analysis. Genomic DNA was isolated from muscle tissue by proteinase K digestion and extracted with Qiagen DNeasy kit. The fragment of mitochondrial DNA COI was amplified using the primers F1: 5'-TCAACCAACCACAAAGACATTGGCAC-3'; and R1: 5'-TAGACTTCTGGGTGGCCAAAGAATCA-3' (Ward et al. 2005). Each polymerase chain reaction (PCR) was performed in a 25 μL reaction mixture containing

17.5 μL of ultrapure water, 2.5 μL of 10×PCR buffer, 2 μL of dNTPs, 1 μL of each primer (5 μM), 0.15 μL of Taq polymerase, and 1 μL of DNA template. PCR amplification was performed in a Biometra thermal cycler under the following conditions: 5 min of initial denaturation at 95 °C; 30 cycles of 45 s at 94 °C for denaturation, 45 s at 52 °C for annealing, and 45 s at 72 °C for extension; and a final extension at 72 °C for 10 min. The PCR products were purified and sequenced by Personal Biotechnology Co., Ltd.

To determine the right DNA barcoding of *G. minor*, homologous COI sequences were downloaded from GenBank for comparative analysis (Table 1). The sequences were aligned using DNASTAR software (Madison, WI, USA). A neighbor-joining (NJ) tree was built and the distances between and within species were calculated using MEGA 5.0 (Tamura et al. 2011) with 1,000 bootstrapping replications under the best selected K2P model. The DNA barcoding gap was calculated for all species, which is the maximum intraspecific distance of each species against its minimum distance to the nearest neighbor (Ward et al. 2005). *Uropterygius fuscoguttatus* and *Muraenesox cinereus* were chosen as outgroup.

Results

Morphological analysis

Counts and measurements from 61 individuals of *G. minor* were conducted and the generally morphological characteristics of this species are presented in Figure 1 and Table 1. The total length ranged from 266.3 to 552.5 mm, and the range of weight was from 42.1 to 196.5 g. This species can be described as the following combination of characteristics referred to Kim et al. (2012):

Measurements presented as percentages of total length (%): head length 13.5–15.3, pre-anal length 45.1–52.1, depth at gill-opening 4.5–5.2, depth at anus 4.4–5.0, width at gill-opening 2.6–3.9, width at anus 3.4–3.8. Measurements presented as percentages of head length (%): snout length 13.4–15.2, eye diameter 9.2–10.2, interorbital width 12.1–14.8.

Body naked, elongate, slightly compressed, tapering toward the tail. Head with many wrinkles, mouth terminal, snout blunt and rounded. Gill opening a small slit. Nostrils two pairs, posterior nostrils small and oval, while anterior nostrils narrow and tubular. Cephalic pores minute; supraorbital pores three; four infraorbital pores along the upper jaw; six mandibular pores along the lower jaw; two branchial pores. Both sets of jaw teeth serrated. Mandibular teeth 14 in a single row, tapering in size posteriorly. One median intermaxillary tooth; vomerine teeth small blunt, 12 in a single row. Maxillary teeth 15 in a single row, tapering in size posteriorly. Dorsal fin origin slightly before the gill opening. Pectoral fin absent. Caudal fin small, confluent with dorsal and anal fins. Lateral line greatly reduced, pores inconspicuous. Anus located almost in the middle of the body. Vertebrae 137–139.

Figure 1. *Gymnothorax minor* (**A**) and X-ray photo (**B**), *Gymnothorax reticularis* (**C**). Photograph of *G. reticularis* is from Stern and Goren (2013).

Head and body pale yellowish, head with dark markings, body with scattered small brown spots, 18–20 irregular dark brown vertical bars from behind the gill opening to the caudal fin margin, and the bars may be diffuse and often indistinct.

Molecular analyses

The COI gene fragments of five *G. minor* individuals randomly chosen from each survey were sequenced and edited. All newly amplified sequences were submitted to GenBank with the accession numbers MG755735-MG755744. A set of homologous sequences were downloaded from GenBank and 36 sequences in total were used for analysis with 553 bp in length. Within all sequences, 196 variable sites, 187 parsimony-informative sites, and nine singleton sites were detected, and four deletions/insertions were observed. The A+T content (55.7%) was higher than that of G+C (44.3%), revealing a slight base against G+C.

An NJ tree of the *Gymnothorax* species group was constructed based on the K2P model (Figure 2). *U. fuscoguttatus* and *M. cinereus* were chosen as outgroups. The results showed that five groups were found in the NJ tree with high bootstrap values, supporting the existence of division. *Gymnothorax buroensis*, *G. reevesii*, and *G. fimbriatus* were clearly clustered together, while *G. minor* and *G. reticularis* were mixed together and formed two groups. Except for HM461876, the remaining *G. reticularis* sequences and KF681855 named *G. minor* clustered with our *G. minor* to form Group 1, suggesting that the specimens currently named *G. reticularis* should actually be identified as *G. minor*. HM461876 was submitted under the name "*Gymnothorax*

Table 1. Information on the moray eel specimens and sequences in this study.

Species	This study							Cited accession no.
	Sea	Number	Longitude (E)	Latitude (N)	Range of total length (mm)	Range of weight (g)	Accession no.	
Gymnothorax minor	South China Sea (2012)	12	110°	18°	347.4–481.9	42.1–180.2	MG755739-MG755740	HQ122466, KF681855
		1	110°	17°30'	396.9	74.3		
		1	110°	5°15'	362.2	190.2		
	South China Sea (2013)	3	109°	18°	266.3–299.6	81.1–134.0		
		5	109°	17°30'	306.9–495.6	46.2–195.1		
		1	109°	17°	404.3	154.2		
		23	110°	18°	300.9–526.5	48.5–196.5		
		2	109°	8°30'	332.3–432.0	71.6–94.4		
		1	109°30'	5°30'	447.8	145.1		
		7	109°	6°	375.2–453.1	94.3–142.8		
	East China Sea (2017)	5	118°05'	24°26'	406.2–552.5	97.3–180.1	MG755735-MG755738, MG755744	
G. reticularis	–							HM461876, KU942701, KU942736, KU942739, KU942760-KU942762, KX215183, KX215184, MG220570
G. buroensis	–							JQ350022, JQ431789, KF929925
G. reevesii	–							EF607396, EU595145, FJ237992
G. fimbriatus	–							KF929928
Muraenesox cinereus	–							HM068292, KU942795, KX215196
Uropterygius fuscoguttatus	–							HQ122477, JQ350410, JQ432206

reticularis", but it clustered with *G. fimbriatus.* HQ122466 formed Group 2 and was identified as *G. minor* collected from Australian.

Based on the K2P model, the genetic distances of COI within and between groups were computed (Table 2). The mean genetic distance within each group ranged from 0 to 0.6%, while the genetic distance between Group 1 and Group 2 was 3.8%, exceeding the threshold of species delimitation (approximately 2%) (Hebert et al. 2003), suggesting they were different valid species. Therefore, these five groups in the NJ tree should be five different and valid species.

The maximum intraspecific distance of each species ranged from 0–1.3%, while the minimum interspecific distances of all species were higher than 2%. The species discrimination power of DNA barcoding was demonstrated by the barcoding gaps that were drawn for all species on the basis of the K2P distances shown in Figure 3. Because the latter value was always higher than the former one, overlaps were not detected in all species.

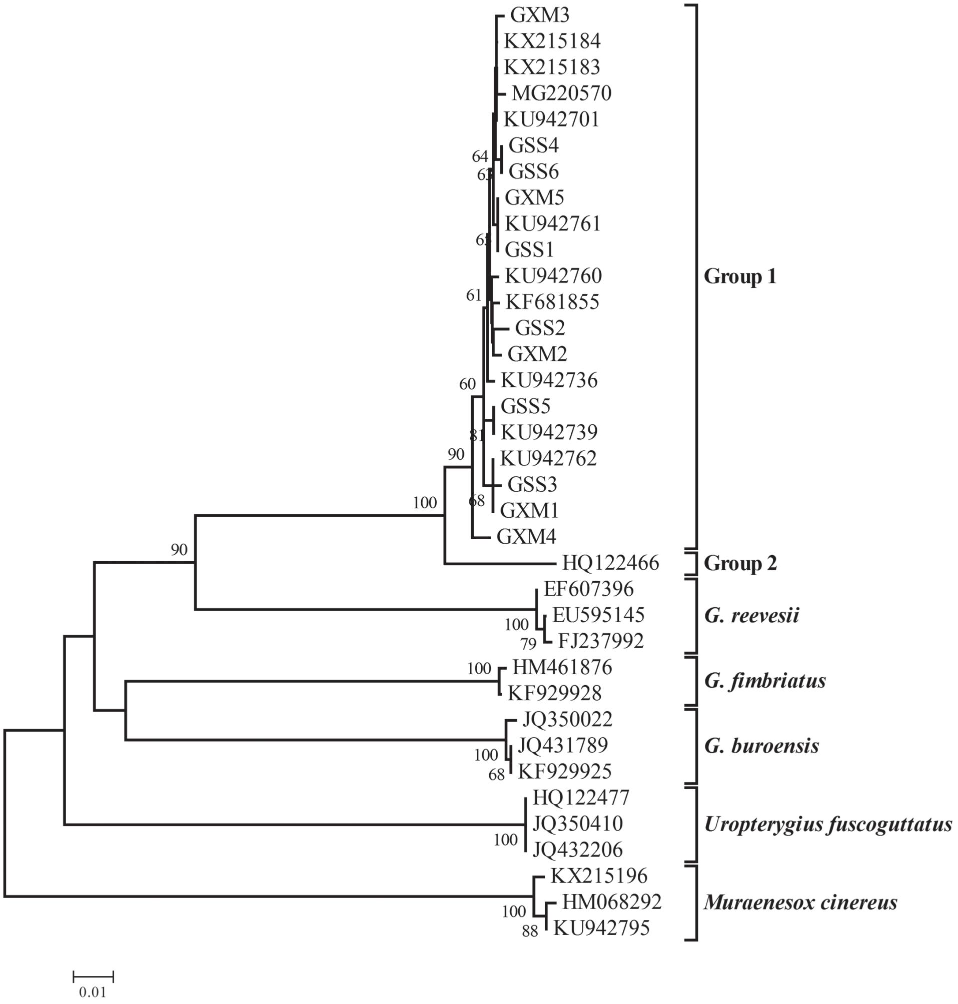

Figure 2. NJ tree of moray eels constructed with MEGA based on the K2P model. Bootstrap values of > 50% from 1,000 replications are shown.

Table 2. Genetic distances of COI within (on the diagonal in bold) and between (below the diagonal) groups.

	Group 1	Group 2	*G. reevesii*	*G. fimbriatus*	*G. buroensis*	*U. fuscoguttatus*	*M. cinereus*
Group 1	**0.006**						
Group 2	0.038	–					
G. reevesii	0.160	0.178	**0.002**				
G. fimbriatus	0.202	0.222	0.197	**0.002**			
G. buroensis	0.203	0.219	0.219	0.190	**0.002**		
U. fuscoguttatus	0.217	0.238	0.256	0.245	0.231	**0**	
M. cinereus	0.260	0.272	0.257	0.249	0.252	0.265	**0.005**

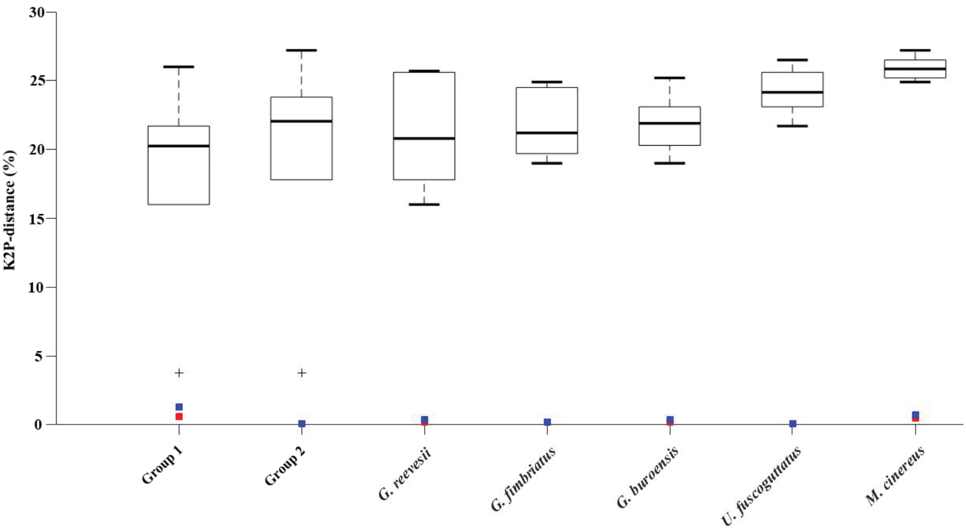

Figure 3. DNA barcoding gaps for all of the species based on the K2P model. Median interspecific distances with maximum and minimum values are represented by the upper and lower bars, respectively. Blue square: maximum intraspecific distance; Red square: mean intraspecific distance.

Discussion

The moray eels with irregular dark vertical bars on the body and serrated teeth on jaws and the intermaxillary region are defined as *Gymnothorax reticularis* species group. *Gymnothorax minor* and *G. reticularis* are common species in the assembled species group, and have usually been confused by many ichthyologists because of the similarity of external shape and color. However, the two species can be easily distinguished by their numbers of vertebrae and distribution range.

The moray eel collected from Chinese waters were initially identified as *G. reticularis* according to the descriptions of previous reports (Zhu et al. 1962, 1985, Cheng and Zheng 1987, Zhang et al. 2010, Chen and Zhang 2015), which included only simple external descriptions without vertebra number. The morphological analysis based on newly collected specimens in this study showed that the vertebra number ranged from 137 to 139, similar to that of *G. minor* (129–143) but obviously different from *G. reticularis* (114–126) (Smith and Böhlke 1997). Other morphological characteristics of *G. minor* collected from Chinese waters were highly consistent with the original morphological description (Temminck and Schlegel 1846) and the subsequent report of the lectotype of *G. minor* (Boeseman 1947). Considering the geographical distribution, the moray eel in Chinese waters was further shown to be *G. minor*.

By molecular analysis, it is shown that DNA barcoding is effective and reliable to identify the *Gymnothorax* species. Furthermore, a ten-fold sequence divergence between the average interspecific and the average intraspecific difference was detected because of the existence of barcoding gap, and this divergence has been suggested to be the standard COI threshold for species identification (Hebert et al. 2003). From the NJ tree, all COI sequences of *G. minor* in GenBank are now correctly identified; HM461876 as *G. reticularis* is in fact *G. fimbriatus*, while the other COI sequences of *G. reticularis* are clearly attributable to *G. minor*. The specimen (HQ122466) is acquired from Australian Museum (specimen voucher 35980) and identified as *G. minor.* Considering the collected geographical location, we can confirm the moray eel is unquestionably *G. minor* instead of *G. reticularis*. Unfortunately, the correct COI sequences of *G. reticularis* is absent in GenBank and the genetic relationship between *G. minor* and *G. reticularis* has not been evaluated.

The moray eel *G. minor* has been known as an anti-tropical species and initial geographical distribution was reported in northwestern Pacific from southern Honshu (Japan) to southern China, and coastal Australia from Western Australia to New South Wales (Smith and Böhlke 1997). With more attention to this species, new records have been occurred in different regions, such as Korea (Kim et al. 2012), Vietnam (nearly 12° N, Hibino et al. 2016), the central Philippines (Tañon Strait, Bucol and Alcala 2015, Wagey et al. 2015) and New Zealand (Böhlke and McCosker 2001). Therefore, the present report represents the new identification of the species in Chinese waters and expands its distributional area southward to 5°15'N into South China Sea (Table 3). Meanwhile, Smith and Böhlke (1997) mentioned that the two populations of *G. minor* (the northern and southern populations) are intraspecifically distinguishable by their number of total vertebrae (135–143 in the northern population and 129–135 in the southern population), although there is a slight overlap. The vertebral number of the present specimens agrees well with those of the northern population and do not overlap with the southern population, and similar results are described in other northern populations (Kim et al. 2012, Nakabo 2013, Wagey et al. 2015, Hibino et al. 2016). Hibino et al. (2016) also suggested the two populations of *G. minor* should be regarded as different species. From the NJ tree, two groups were detected among all COI sequences of *G. minor*, of which Group 1 collected from the northern hemisphere matched the northern population and Group 2 collected from Australia matched the southern population. Meanwhile, the genetic distance between both populations has exceeded the threshold of species delimitation. Therefore, we confirm the suggested classification of Hibino et al. (2016). In other case, *Gymnothorax mccoskeri* Smith & Böhlke, 1997 is also an anti-tropical species and distributed in both the northern and the southern hemispheres, but there are no morphological differences between both populations except for a minor variation in head length (Stern and Goren 2013, Hibino et al. 2015). Therefore, related species of *Gymnothorax* with similar distribution show different evolutionary strategy to adapt diverse local habitats, which can drive the formation of new species.

Our study further demonstrate that *G. minor* is distributed in the western Pacific but *G. reticularis* is absent in this region. More specimen collection is necessary in order to define clearly the geographical limits of *G. minor*, especially from Malaysia, Indonesia, or anywhere between 5°15'N and 10° S. Sightings of species differentiation in *G. minor* will be further validated from detailed morphological characteristics and nuclear gene. Specimens of *G. reticularis* are also needed to provide the DNA barcoding based on the correct morphological characteristics.

Table 3. Comparative count and measurement characteristics of *G. minor* and *G. reticularis* in different studies.

Source	*G. minor*					*G. reticularis*	
	This study	**Hibino et al. (2016)**	**Kim et al. (2012)**	**Smith and Böhlke (1997)**	**Boeseman (1947)**	**Stern and Goren (2013)**	**Smith and Böhlke (1997)**
Total length (mm)	266.3–552.5	270.5–363.0	469.0	245.0–508.0	450–463.0	460.0	207.0–256.0
Counts							
Total vertebrae	137–139	136–139	139	129–143	135–140	123	114–126
Dorsal fin origin	Before of gill opening	Before of gill opening	Before of gill opening	Before of gill opening	Before of gill opening	Before of gill opening	Before of gill opening
Teeth	Serrate	Serrate	Stout serrate	Stout serrate	Stout serrate	Fine serrate	Serrate
Dentition	Uniserial	Uniserial	Uniserial	Uniserial	Uniserial	Uniserial	Uniserial
Median intermaxillary teeth	0–1	0–1	1	0–2	1	1	0
Bars behind gill opening	18–20	19	19	15–22	18–20	18	16–20
Measurements							
In % of total length							
Head length	13.5–15.3	12.3–14.6	12.6	10.0–15.2	11.6–11.9	13.1	12.2–15.4
Pre-anal length	45.1–52.1	44.5–44.9	46.7	41.7–47.6	44.8–45.5	46.5	45.5–50.0
Depth at gill-opening	4.5–5.2	4.6–4.7	6.4	4.6–6.3	4.9–5.0	6.4	5.6–6.3
Depth at anus	4.4–5.0	3.6–4.2	5.0	–	–	–	–
Width at gill-opening	2.6–3.9	2.6–3.6	–	–	–	–	–
Width at anus	3.4–3.8	3.2–3.5	–	–	–	–	–
In % of head length							
Snout length	13.4–15.2	13.2–16.4	12.6	12.1–20.0	14.4–15.0	14.4	12.8–17.9
Eye diameter	9.2–10.2	8.9–9.9	10.2	7.7–14.9	7.1–8.9	6.8	10.0–12.8
Interorbital width	12.1–14.8	10.5–13.4	12.1	–	–	–	–

Acknowledgments

The present study could not have been performed without assistance from Mr. Zhihui Zhong in the collection of *G. minor* specimens. The research was funded by the the Bilateral Cooperation of Maritime Affairs (2200207), National Programme on Global Change and Air-Sea Interaction (GASI-02-SCS-YSWspr/aut), the China-ASEAN Maritime Cooperation Fund Project (HX150702, HX161101), the Provincial Research Institutes of Basic Research and Public Service Special Operations (2017R1006–5), and the University of Malaya research grants (RP018B-16SUS). The authors declare no conflicts of interest including the implementation of research experiments and the writing of this manuscript.

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