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Article



# Two new *Pseudorchomene* species from the Southern Ocean, with phylogenetic remarks on the genus and related species (Crustacea: Amphipoda: Lysianassoidea: Lysianassidae: Tryphosinae)

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#### Abstract

Two new lysianassoid amphipods of the genus *Pseudorchomene* Schellenberg, 1926 from the Southern Ocean are described: *P. debroyeri* **sp. n.** collected in baited traps deployed around the Falkland Islands, Burdwood Bank and Îles Kerguelen between 55 and 470 m, and *P. lophorachis* **sp. n.** collected in baited traps and Agassiz trawls deployed in the Scotia and Weddell Seas at depths between 847 and 1943 m. *P. lophorachis* **sp. n.** is characterized by an strongly elongated first gnathopod and by the occurrence of low posterodorsal humps on the body segments. *P. debroyeri* **sp. n.** is very similar to *P. coatsi* (Chilton, 1912) but exhibits slight differences of proportions in the articles of gnathopods 1 and 2, more spines on pereopods and more acute spines on the propodus of pereopods 3–7. Molecular data indicate the existence of a well-defined clade comprising *P. lophorachis* **sp. n.**, *P. debroyeri* **sp. n.**, *P. coatsi* (Chilton, 1912), *Abyssorchomene plebs* (Hurley, 1965) and *A. rossi* (Walker, 1903). On the other hand, *A. plebs* and *A. rossi* do not form a clade with *A. chevreuxi* (Stebbing, 1906), which is the type species of the genus *Abyssorchomene* De Broyer, 1984. The definition of *Pseudorchomene* is amended, so that it now includes *P. coatsi*, *P. debroyeri*, *P. lophorachis*, *P. plebs* and *P. rossi*. The triangular coxa 1 in these 5 species is unique for 'orchomenid' lysianassoids, thus considered as a putative synapomorphy. *P. coatsi* (Antarctic species) is morphologically extremely similar to *P. debroyeri* (sub-Antarctic species) but it is genetically closer to the morphologically distinct *P. lophorachis* (Antarctic species). Hypotheses for these recent speciations and the mor-

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phological evolution within *Pseudorchomene* are discussed. The type species and the nomenclatural history of the genus *Tryphosa* Boeck, 1871, which is the type genus of the subfamily Tryphosinae, are discussed.

Key words: Amphipoda, Lysianassoidea, Pseudorchomene, Abyssorchomene, Tryphosa, Southern Ocean, systematics, new species

#### Introduction

The genus Pseudorchomene Schellenberg, 1926 belongs to the so-called 'Orchomene complex' (De Broyer 1984), which also includes the genera Abyssorchomene De Broyer, 1984, Allogaussia Schellenberg, 1926, Falklandia De Broyer, 1985, Orchomene Boeck, 1871, Orchomenella G.O. Sars, 1890, Orchomenopsis G.O. Sars, 1891, Orchomenyx De Broyer, 1984 and Tryphosa Boeck, 1871. This complex is here designed as 'orchomenids', as a shorthand reference device that has no implicit systematic connotations. The generic subdivision of this group has been the object of long debates between splitters and lumpers (Stebbing 1906; K.H. Barnard 1932; Gurjanova 1962; Barnard 1964, 1967, 1969; Bellan-Santini 1972a, 1972b; Bousfield 1973; Oleröd 1975; Shulenberger & Barnard 1976; De Broyer 1983, 1984, 1985; Barnard & Karaman 1991; Lowry & Stoddart 1997, 2003), but today the point of view of the splitters prevails. Following Barnard & Karaman (1991), the 'orchomenids' include the following genera: Abyssorchomene, Allogaussia, Orchomene, Orchomenella, Orchomenopsis, Orchomenyx and Tryphosa, but excludes Falklandia and Pseudorchomene. Lowry & Stoddart (1997) included Allogaussia, Orchomene, Orchomenella, Orchomenyx and Tryphosa in their newly-created sub-family Tryphosinae within the Lysianassidae Dana, 1849, but omitted Abyssorchomene. More recently, De Broyer et al. (2007), who treated only Antarctic and sub-Antarctic taxa, placed the genera Falklandia, Orchomene, Orchomenella (subdivided into the subgenera Orchomenella and Orchomenopsis), Orchomenyx and Pseudorchomene in the Tryphosinae and Abyssorchomene in the Uristidae Hurley, 1963, which suggests that these authors no longer consider 'orchomenids' as a clade. A review of the successive generic and familial assignation for Antarctic 'orchomenids' has been compiled in Table 1 of Havermans et al. (2010).

Until recently, all statements were based on morphological arguments, and the question on the subdivisions of 'orchomenids' and on the monophyly of this group remained entirely open. A recent molecular study on 'orchomenids' of the Southern Ocean (Havermans *et al.* 2010) rejected several generic subdivisions of this group proposed by authors like De Broyer (1983, 1984). The genera *Abyssorchomene* and *Orchomenella*, as well as the subgenus *Orchomenopsis*, appeared to be non-monophyletic. Furthermore, the phylogenetic results also indicated the need for a revision of the family-level systematics and do not support the scattering of these genera across the families Lysianassidae (subfamily Tryphosinae) and Uristidae but showed that all the 'orchomenid' genera from the Southern Ocean belong to a large and well-supported clade. However, Havermans *et al.* (2010) did not include lysianassids from the northern hemisphere. Hence, the monophyly of 'orchomenids' at the global scale remains an unresolved question.

Havermans et al. (2010) also identified a monophyletic clade comprising Pseudorchomene coatsi (Chilton, 1912), Pseudorchomene sp. (here described as P. lophorachis n. sp.) and Abyssorchomene plebs (Hurley, 1965). The same cluster, now also including Abyssorchomene rossi (Walker, 1903), was revealed by the genetic barcoding study of Havermans et al. (2011). Further studies of partial mitochondrial COI sequences detected another undescribed species of the genus Pseudorchomene. The aim of the present paper is to define this newly detected clade nested among southern 'orchomenids'. The definition of the initially monotypic genus Pseudorchomene (type species P coatsi) is expanded to encompass all five species of this clade. It can be separated morphologically from other 'orchomenids' by the triangular or adz-shaped coxa 1, this character state being considered as a putative synapomorphy. The genus now includes the following five species: P. coatsi, P. debroyeri sp. n., P. lophorachis sp. n., P. plebs (Hurley, 1965) and P rossi (Walker, 1903). The first three species, which have an elongate gnathopod 1, are described fully and illustrated, whilst the other two species, which have a stocky gnathopod 1, are treated more succinctly because they have been described in detail by Hurley (1965a, 1965b). An identification key and illustrations are given for these five species. Finally, the generic assignation of some other Antarctic and sub-Antarctic 'orchomenids' and hypotheses for speciation are considered briefly.

#### Material and methods

Amphipod specimens used for molecular studies were collected mostly in 2003-2004 during the cruise ANT-XXI/2 (BENDEX) of the R/V Polarstern (Arntz & Brey 2005) and in early 2005 during the cruise ANT-XXII/3 (ANDEEP III) of the R/V Polarstern (Fahrbach 2006). This collection was augmented with other samples collected during various expeditions. Specimens were collected using baited traps and Agassiz trawls. Material used for DNA studies was fixed initially in 96% pre-cooled ethanol, kept at -30°C. Other specimens were fixed in 10% formalin and afterwards transferred to 70% ethanol. Complete specimens and appendages were examined with a WILD M5A dissecting microscope and a DML Leica compound microscope, both equipped with a drawing tube. They were afterwards permanently mounted in Euparal or conserved in alcohol. Pencil drawings were scanned and inked with the software Adobe Illustrator 11.0.0 on an A3 drawing table (Wacom Intuos3 12 x 19), using the methods described by Coleman (2003, 2009). Photographs were made with a Canon Powershot S3 IS digital camera. The following abbreviations are used in figure captions: A1-2, antennae 1-2; Ep1-3, epimeral plates 1-3; Gn1-2, gnathopods 1-2; Md, mandible; Mx1-2, maxillae 1-2; Mxp, maxilliped; P3-7, percopods 3-7; U1-3, uropods 1-3. Nomenclature of the setae of the mandibular palp follows Lowry and Stoddart (1993). In the description, the traditional definition of the terms 'tooth', 'spine' and 'seta' (e.g. Barnard & Karaman 1991) is applied. The term 'tooth' is used for non-articulated, pointed ectodermic structures, 'spine' for stout, inflexible articulated structures, and the term 'seta' for slender, flexible articulated structures. For a discussion of the validity of this terminology, see d'Udekem d'Acoz (2010) and Krapp-Schickel (2011).

Type material is housed in the Royal Belgian Institute of Natural Sciences, Brussels (Belgium) [RBINS], the Zoological Museum of Hamburg (Germany) [ZMH] (material of the ANDEEP cruises) and the Smithsonian Institute, Washington D.C. (U.S.A.) [USNM] (material of the ICEFISH cruise).

The molecular analysis included 32 specimens, including one specimen of Abyssorchomene scotianensis used as outgroup (GenBank accession number GU109242). Sequences from *Pseudorchomene coatsi*, *P. plebs*, *P. rossi*, and *Pseudorchomene* sp. (corresponding to *P. lophorachis* sp. n.) of Havermans *et al.* (2011) were used for the analyses. One sequence of *P. coatsi* was obtained by the CAML barcode project "Amphipods of the Southern Ocean". For specimens of *P. debroyeri* and supplementary specimens of *P. coatsi and P. plebs*, genomic DNA was isolated using the QIAamp DNA Mini Kit (Qiagen) and the amplification of the COI marker was carried out by polymerase chain reaction using the universal primers LCO1490 and HCO2198 (Folmer *et al.* 1994). Purified PCR products were sequenced bidirectionally using an ABI 3130xl capillary DNA sequencer (Applied Biosystems). The newly obtained sequences of *P. coatsi*, *P. debroyeri* and *P. plebs* have been deposited in GenBank.

Alignments were made manually. A neighbour-joining tree (Saitou & Nei 1987) was estimated using MEGA 5 (Tamura *et al.* 2011) and sequence divergences were calculated using the Kimura 2-parameter (K2P) distance model (Kimura 1980), the best metric system when distances are low, according to Nei and Kumar (2000). Branch support was evaluated using non-parametric bootstrapping (number of replicates was 5000).

#### **Morphological** Systematics

**Order Amphipoda Latreille, 1816** 

Superfamily Lysianassoidea Dana, 1849

Family Lysianassidae Dana, 1849

#### Subfamily Tryphosinae Lowry and Stoddart, 1997

Type genus. Tryphosa Boeck, 1871; see Lowry & Stoddart, 1997. Type species. Anonyx nanus Krøyer, 1846; designation by Boeck (1876: 180).

**Remarks.** Lowry & Stoddart (1997) designated *Tryphosa* as the type genus of their subfamily Tryphosinae, which includes the genus *Pseudorchomene*. However, for 140 years there was endless controversy concerning the type species of *Tryphosa*, and the validity and definition of that genus, resulting in extreme confusion. Since the identity

of the subfamily Tryphosinae is based on its type genus (*Tryphosa*) and the type species of its type genus, a reconstruction of the '*Tryphosa* saga' is given herein, in order to solve this thorny problem.

Krøyer (1846) described Anonyx nanus in a long and precise description devoid of illustrations. When creating the genus Tryphosa Boeck, 1871 (the type genus of the subfamily Tryphosinae), Boeck (1871) described four species without designating a type species, in the following order: T. nanus (Krøyer, 1846) (original combination: Anonyx nanus), T. Høringii Boeck, 1871, T. nanoides (Lilljeborg, 1865) (original combination: Anonyx nanoides) and T. longipes (Spence Bate' & Westwood, 1861) (original combination: Anonyx longipes). Five years later, Boeck (1876) formally designated Anonyx nanus Krøyer, 1846 as the type species of Tryphosa in repeating and expanding his earlier description. G.O. Sars (1883) redescribed Krøyer's (1846) and Boeck's (1871, 1876) species under the name Tryphosa ciliata G.O. Sars, 1883, not realizing that his species had already been named earlier. G.O. Sars (1890) created the genus Orchomenella (with O. minuta as type genus) and described again Tryphosa nana sensu Krøyer & Boeck, this time as Orchomenella ciliata (G.O. Sars, 1883). G.O. Sars (1891) described as Tryphosa nana, a species which is not that of Krøyer (1846) and Boeck (1871, 1876), and which was still devoid of valid name at that time. Bonnier (1893) pointed out the mistakes of G.O. Sars (1890, 1891) and created the genus Tryphosella Bonnier, 1893 for the species fitting the definition of Tryphosa proposed by G.O. Sars (1891). He did not suggest a type species for Tryphosella but listed seven species, in the following order: T. sarsi Bonnier, 1893 (= Tryphosa nana sensu G.O. Sars, 1891), T. compressa (G.O. Sars, 1891) (original combination: Tryphosa compressa), T. Hörringi (Boeck, 1871), T. angulata (G.O. Sars, 1891) (original combination: Tryphosa angulata), T. nanoïdes (Lilljeborg, 1865) (original combination: Anonyx nanoides), T. antennipotens (Stebbing, 1888) (original combination: Tryphosa antennipotens) and T. barbatipes (Stebbing, 1888) (original combination: Tryphosa barbatipes). Bonnier (1893) restricted the genus Tryphosa to T. nana (Krøyer, 1846) and T. pinguis (Boeck, 1861) (original combination: Anonyx pinguis). G.O. Sars (1895) accepted the conclusions of Bonnier (1893) concerning G.O. Sars' (1891) misidentification of T. nana (thus accepting the specific epithet sarsi Bonnier, 1893) but rejected Bonnier's (1893) generic changes, transferring Tryphosella sarsi to Tryphosa and transferring the true Tryphosa nana to Orchomenella. The resulting nomenclaturally invalid binomen Orchomenella nana (Krøyer, 1846) has been accepted in all subsequent literature. Stebbing (1906) restricted Tryphosella to T. barbatipes and put T. sarsi and its satellite species in Tryphosa. On the other hand, Stephensen (1921, 1925 and 1935) accepted the definition of Tryphosa proposed by G.O. Sars (1891–95). Under the genus Tryphosa, Chevreux & Fage (1925) wrote without further comment: "Type: Tr. hörringi, Boeck, 1871". This statement is repeated by Gurjanova (1951). Barnard (1962) accepted Tryphosa horringi Boeck as the type species of the genus Tryphosa, without citing his sources, but probably referring to Chevreux & Fage (1925) and/or Gurjanova (1951). As far we know, there is no other reference to the action of Chevreux & Fage (1925) in more recent literature. Barnard (1967) considered 'Tryphosa' both as a useful concept and as an invalid synonym of Tryphosella. Barnard (1967) also designated T. sarsi as the type species of Tryphosella and Barnard (1969) reiterated this type designation. In recent literature, Tryphosa is implicitly considered as invalid (Lincoln 1979; Ruffo 1985; Oleröd, 1987; Diviacco & Ruffo 1989; Palerud & Vader 1991; Kilgallen et al. 2006a; Lowry & Stoddart 2011b) or rejected on the basis of practical but nomenclaturally unsupported arguments (Thurston 1974a), and its former components are assigned to the genera Orchomenella and Tryphosella, which have been created later than Tryphosa. Only Lowry & Stoddart (1995, 1997) recognized Tryphosa as valid and distinct from Tryphosella, although they did not indicate which species they considered as belonging to Tryphosa.

Finally, Lowry & Stoddart (1997) created the family Tryphosinae Lowry & Stoddart, 1997 with *Tryphosa* as type genus, without indicating the type species of that genus.

The conclusions of this account are that *Tryphosa* Boeck, 1871 is a nomenclaturally valid genus with *Tryphosa* nana (Krøyer, 1846) as type species and that all subsequent alternative proposals concerning the type species of *Tryphosa* are irrelevant.

Whether the genus Orchomenella G.O. Sars, 1890 (type species: O. minuta G.O. Sars, 1890) is distinct from Tryphosa Boeck, 1871 (type species: T. nana (Krøyer, 1846)) or not, is a question, which falls out of the scope of the present paper.

<sup>1.</sup> See De Grave & Fransen (2011) for a discussion on the spelling of the name of that author.

#### Genus Pseudorchomene Schellenberg, 1926

Pseudorchomene Schellenberg, 1926: 295. - Lowry & Stoddart, 1983: 381.

Description. Body shape: typical lysianassoid facies.

*Head*: anterior lobe of head moderately produced and broadly rounded; eye large, pyriform, dark, with fully developed ommatidia.

Antenna 1: major flagellum with article 1 very elongate; accessory flagellum with 5–7 articles, of which the first is very elongate.

Mouthparts forming quadrate bundle.

Upper lip and epistome differentially produced, prominent, separate; upper lip distinctly overreaching epistome.

*Mandible*: elongate, with posteriorly directed opening; margins of this posterior opening prolonged by 3 processes or lobes: 1 upper and 2 lower ones; incisor process with smooth cutting edge; lacinia mobilis present on left side only, narrowly cylindrical (finger-like), slightly curved, distally slightly dilated and with dentiform processes; longitudinal group of 3 small raker spines and an elongated patch of short fine setae present between incisor and molar processes; molar process elliptic, broad to moderately narrow, triturative; molar process not distally followed by row of spines; lateral setigerous crest arising from proximal 0.2 or 0.3 of molar process; palp 3-articulate, attached midway, proximal to molar process (anteroproximal corner of article 1 of palp not reaching or just reaching proximal border of molar process); article 1 without setae, article 2 longest with row of strong distal and subdistal A2-setae, article 3 of palp about 4 x as long as wide, with 1–2 proximal A3-setae, a row of D3-setae on distal 0.7, with 2–4 E3-setae.

*Maxilla 1*: inner plate very elongate, distally very narrow, with 2–3 setae in truly distal position; outer plate with 11 blade-shaped denticulate spines ('spine teeth'); palp 2-articulate, broad with distal row of 8–13 spines anteriorly followed by stout antero-distal seta; left and right palps similar but not identical.

Maxilla 2: plates very narrow, tapering towards tip; inner plate much shorter than outer plate.

*Maxilliped*: inner and outer plates well developed; inner plate narrow, reaching about half of outer plate, with well-developed posteromedial row of strong setae, with 3 nodular apical spines and 1 anterodistal stout seta; outer plate reaching or overreaching tip of article 2 of palp, with double row of anterior setae, with 2 large anterodistal elongated stout spines, with posterior row of much smaller low nodular spines, with small narrow posterofacial spines; dactylus well developed.

Coxae 1-4 longer than the depth of their corresponding perconites, their lower profile forming a very even line.

Gnathopod 1: coxa large, visible, triangular, with anterior and posterior margin nearly straight and strongly divergent, with ventral margin broad and weakly convex; leg subchelate, palm oblique to transverse; proportions of ischium, merus, carpus and propodus very variable.

Gnathopod 2: propodus much shorter than carpus with anterior border strongly convex, with posterior border straight to slightly concave; minutely chelate.

Pereopod 4: coxa with well-developed and fairly broad posterior lobe.

Pereopod 5: coxa without umbo or carina, with posteroventral lobe very blunt; basis as broad as long, or broader than long, distinctly shorter than coxa.

Gills: long accessory process on gill of percopods 5-6; gill of percopod 7 well-developed and posteriorly pointed.

Oostegites: linear, from gnathopod 2 to pereopod 5.

Epimeron 1: anteroventrally angular or produced.

Epimeron 3: posteroventrally rounded or weakly produced.

Urosomite 1: dorsal process rounded, anteriorly preceded on each side by dorsolateral carina.

Urosomite 3: sharp dorsolateral carina on each side.

Uropod 1: inner ramus about 0.6 x as long as peduncle.

Uropod 2: inner ramus not constricted.

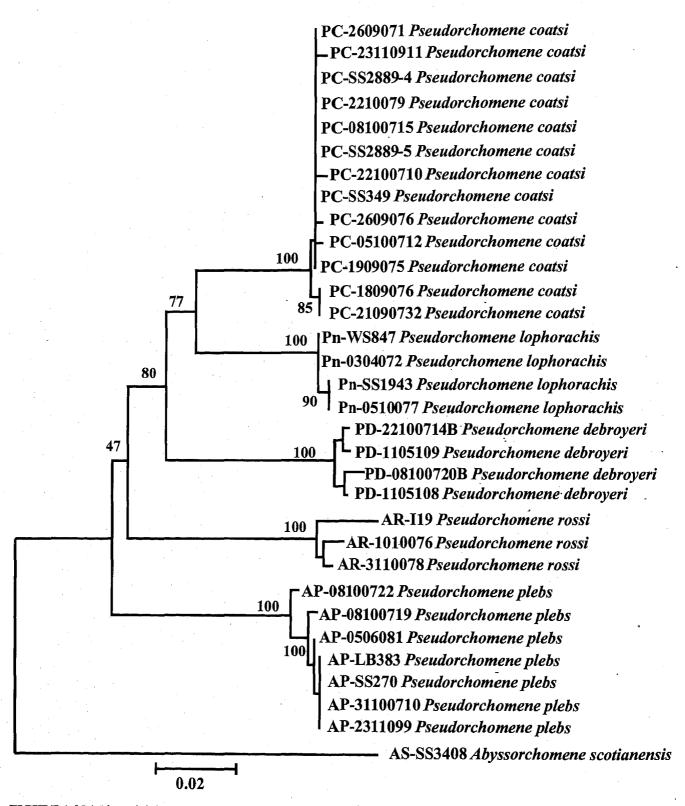
Uropod 3: ordinary, with rami well developed, with outer ramus 2-articulate and longer than peduncle. *Telson*: longer than broad, cleft more than half its length, with dorsolateral spines.

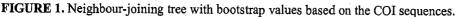
Type species. Orchomenopsis coatsi Chilton, 1912.

**Composition.** Pseudorchomene coatsi (Chilton, 1912); Pseudorchomene debroyeri **sp. n.**; Pseudorchomene lophorachis **sp. n.**; Pseudorchomene plebs (Hurley, 1965); Pseudorchomene rossi (Walker, 1903).

Putative synapomorphy. Coxa 1 triangular or adz-shaped.

**Distribution.** Circum-Antarctic and circum-sub-Antarctic. **Depth range.** 0–2889 m.





**Biology.** Opportunistic or exclusive scavengers (Dauby *et al.* 2001). All species enter baited traps, which can capture up to thousands of specimens. They have been observed in benthic (Rakusa-Suszczewski 1982), pelagic (Hopkins 1987) and sympagic conditions (Kaufmann *et al.* 1993, 1995). Females are iteroparous, at least *P. debroy-eri* (present data).

**Remarks.** Molecular analyses recovered the species *P. coatsi, P. lophorachis, P. debroyeri, P. rossi* and *P. plebs* as a monophyletic group, which is separated by a minimum genetic distance of 15.6 % from the specimen of *Abyssorchomene scotianensis* (Fig. 1). This species indeed belongs to a distinct clade, identified by Havermans *et al.* (2010), comprising the abyssal *Abyssorchomene* species. The monophyly of each species was confirmed and bootstrap values gave significant support to each species cluster. Specimens of *P. lophorachis* and *P. debroyeri* were separated from *P. coatsi* by a minimum divergence of 5.7 % and 7.9 %, respectively. Both newly described species were separated by a minimum 7.8 % sequence divergence. The intraspecific variation did not exceed 1.1 % for *P. debroyeri* and 0.3 % for *P. lophorachis*. These aspects are treated more extensively in the discussion.

# Key to Pseudorchomene species (i.e. 'orchomenids' with triangular coxa 1)

1.	Gnathopod 1 with anterior margin of basis straight, with carpus about as long as wide, with propodus about 1.5 x as long as wide
-	Gnathopod 1 with anterior margin of basis convex, with carpus at least 3 x as long as wide, with propodus at least 3.5 x as long as wide
2.	Eye dark brown in life; merus of percopod 5 1.5 x as long as wide, with setae followed by normally developed spines on
2.	posterior border; inner ramus of uropod 3 shorter than article 1 of outer ramus and medial border of outer ramus with plumose
	setae
-	Eye deep black in life; merus of percopod 5 1.2 x as long as wide, without setae and with very short stout spines on posterior
	border; inner ramus of uropod 3 reaching at least to the base of article 2 of outer ramus and medial border of outer ramus
	without setae (but spines may be present) Pseudorchomene rossi (Walker, 1903)
3.	Somites of pereon and pleosome without small posterior humps; gnathopod 1 with ischium 4.5 x, merus 3 x, carpus 5 x,
	propodus 5.5 x as long as wide or broader
-	Somites of pereon and pleosome with small posterior humps; gnathopod 1 with ischium 9 x, merus 7 x, carpus 7.5 x, propodus
	8.5 x as long as wide Pseudorchomene lophorachis sp. n.
4.	Coxa 5 as long as broad; gnathopod 1 with palm oblique, with ischium 4.5 x, carpus 5 x, propodus 5.5 x as long as wide;
	gnathopod 2 with carpus 2.3 x as long as wide; percopods 3-7, propodus with stoutest spine of each pair or triplet very blunt;
	percopod 7 carpus, anterior margin normally spinose, posterior margin with posterodistal spines only
-	Coxa 5 broader than long; gnathopod 1 with palm transverse, with ischium 3.5 x, carpus 3 x, propodus 3.5 x as long as wide;
	gnathopod 2 with carpus 3.0 x as long as wide; percopods 3-7, propodus with stoutest spine of each pair or triplet sharp;
	percopod 7 carpus, anterior margin very spinose, posterior margin with posterior and posterodistal spines
	Preudorchomene debroyeri sp. n.

# Pseudorchomene coatsi (Chilton, 1912)

(Figs 2–9)

Orchomenopsis coatsi Chilton, 1912: 477, pl. 1 figs. 8-9.

Pseudorchomene coatsi. — Schellenberg, 1926: 295. — Lowry & Stoddart, 1983: 381–385, figs. 72–74 (possibly excluding the specimens from Macquarie Island). — De Broyer et al., 2007: 150, in part (ubi syn.).

Not Pseudorchomene coatsi. — De Broyer, 1983: 193-195, figs. 72-74 (= P. debroyeri sp. n.).

**Type material.** Not seen. A male, 17.9 mm, was selected by Lowry and Stoddart (1983) as LECTOTYPE from the syntype series, Royal Scottish Museum 1921.143.938, station 411, off Coats Land, Weddell Sea, 71°01 'S 22°00'W, from baited trap, 290 m, "Scotia", 12 March 1904.

Material examined. Expedition ARC94, sta. NA62, King George Island, Admiralty Bay, 62°08'S 58°27'W, 470 m, 29.xii.1963–02.i.1964: about 25 specimens, RBINS, INV. 100969 (2 tubes). — R/V "Polarstern" cruise ANT-XIX/3-4 (ANDEEP I & II), West of Elephant Island, sta. 083, 61°07.18'S 56°08.84'W-61°07.09'S 56°08.41'W, 340–350 m, baited trap, 07.ii.2002: 15 specimens, Specimen Ids with corresponding GenBank accession numbers: PC-2609071 (HM054048) [ZMH-43135] (specimen used for illustrations), PC-05100712 (HM054047) [ZMH-43136], PC-SS349 (GU109245) [ZMH-43137], PC-1809076 (HM054046) [ZMH-43138].

- R/V "Polarstern" cruise ANT-XIX/3-4 (ANDEEP I & II), North of Livingstone Island, sta. 114, 61°45'43"S 60°45'28"W-61°45'31"S 60°45'08"W, 2743-2754 m, baited trap, 17.ii.2002: 2 specimens, Specimen Ids with corresponding GenBank accession numbers: PC-SS2889-4 (GU109232) [ZMH-43139], PC-SS2889-5 (GU109234) [ZMH-43140]. - R/V "Polarstern" cruise ANT-XV/3 (EASIZ II), Atka Bay, sta. 280/284, Trap 13, 70°27.4'S 07°55.9'W, 550 m, baited trap, 29.ii.1998: 4 specimens, Specimen Ids with corresponding GenBank accession numbers: PC-2210079 (HM054049), PC22100710 (HM054050), RBINS, INV. 100965 (3 tubes). - R/V "Polarstern" cruise ANT-XIX/5 (LAMPOS), South of King George Island, sta. 261, 62°16.44' S 58°15.45' W, 723 m, baited trap, 27.iv.2002: 16 specimens, Specimen Id with corresponding GenBank accession number: PC-1909075 (HM054053), PC-21090732 (HQ546593), RBINS, INV. 100961. (2 tubes). - R/V "Polarstern" cruise ANT-XXI/2 (BENDEX), Eastern Weddell Sea, sta. 103-104, 70°49'03"S 10°39'47"W-70°49'10"S 10°39'47"W, 387 m, Fish Trap, 14.xii.2003: 1 specimen, Specimen Id with corresponding GenBank accession number: PC-08100715 (HM054052), RBINS, INV. 100963. - R/V "Polarstern" cruise ANT-XXI/2 (BENDEX), Eastern Weddell Sea, sta. 240, 70°48'58"S 10°39'55"W-70°49'03"S 10°40'15"W, 406 m, Lander, 22.xii.2003: 5 specimens. Specimen Id with corresponding GenBank accession number: PC-2609076 (HM054051), RBINS, INV. 100964. - R/V "Polarstern" cruise ANT XXI-2 (BENDEX), Eastern Weddell Sea, sta. 288-1, 72°47.58'S 19°29.86'W. 847 m, Fish Trap, 31.xii.2003-03.i.2004: 1 specimen, stored in 96% ethanol, RBINS, INV. 100987. - R/V "Ivan Papanin" cruise BELARE, 70°S 23°E, 230 m, Crown Bay, Baited Trap, 23.xii.2008: 10 specimens, Specimen Id with corresponding GenBank accession number: PC-231109112 (JQ423240), RBINS, INV. 100962.

Type locality. Antarctica, off Coats Land, Weddell Sea, 71°01'S 22°00'W, 290 m depth (Lowry & Stoddart 1983).

**Diagnosis**. Somites of pereon and pleosome without posterior humps. Mandibular palp inserted well proximal to molar process. Molar process broad. Gnathopod 1: anterior margin of basis convex, palm oblique, basis 3.0 x as long as wide, ischium 6 x, merus 3 x as long as wide, carpus 5 x, propodus 5.5 x as long as wide. Gnathopod 2: carpus 2.3 x as long as wide. Pereopod 3: propodus with about 9–10 spines or pairs of spines (which are well developed). Pereopod 3–7: on propodus, broadest spine of each pair or triplet with tip blunt to very blunt. Coxa 4: rounded posteroventrally. Pereopod 5: coxa slightly longer than broad; basis strongly expanded; merus with setae posteriorly and one fairly slender posterodistal spine. Ratio length/width of merus of pereopod 5–7: 1.3; 1.9; 1.9. Ratio length/width of carpus of pereopods 5–7: 2.0; 2.6; 2.7. Posterodistal angle of carpus of pereopods 5–7 with spines of normal length and stoutness. Pereopod 7: anterior margin of carpus normally spinose, posterior margin of carpus and propodus with posterodistal spines only. Epimeron 3: regularly rounded posteriorly or rounded with trace of angularity. Uropod 3: medial margin of both rami with many long setae, inner ramus reaching or not reaching tip of article 1 of outer ramus.

**Description.** Based on a female, 19 mm, ANT-XIX/3-4 (ANDEEP I & II), sta. 083, West of Elephant Island, 61°07.18'S 56°08.84'W-61°07.09'S 56°08.41'W, 340-350 m.

*Body* without dorsal carina; somites of pereon and pleosome without small posterior bumps. *Head* with lateral cephalic lobes broadly rounded.

*Eyes* occupying the most of anterior part of head, much longer than broad, lower part much broader than upper part, anteriorly distinctly concave, posteriorly nearly straight, dark, with fully developed ommatidia.

Antenna 1 distinctly shorter than antenna 2; major flagellum, first article very elongate; accessory flagellum, first article very elongated; calceoli present in males, absent in females.

Antenna 2 about 0.15 x as long as body; peduncular articles 3 to 5 not enlarged, with brush of setae; flagellum 31-articulate, calceoli present in males, absent in females.

*Mouthparts* forming a quadrate bundle. Epistome carinate, scarcely produced, terminating in small blunt tooth; upper lip broadly rounded, slightly overreaching epistome.

*Mandible*: incisor process, cutting edge smooth except for small blunt denticle on each side, lateral and medial borders parallel; lacinia mobilis present on left side only, narrowly cylindrical (finger-like), slightly curved, distally slightly dilated with 5 medium-sized dentiform processes; 3 small raker spines and a dense patch of short setules present between incisor and molar processes; molar process broad, elliptic to subovate, transversally ridged and triturative; lateral setigerous crest arising from proximal 0.3 of molar process; palp 3-articulate, attached midway, well proximal to molar process; article 1 without setae, article 2 longest with row of 21–22 strong distal and subdistal A2-setae, article 3 of palp 0.60 x as long as article 2, 3.5 x as long as wide, with 1 proximal A3-seta, a row of 21–23 D3-setae on distal 0.7 (these setae are slightly shorter than width of article 3), and 3 E3-setae.

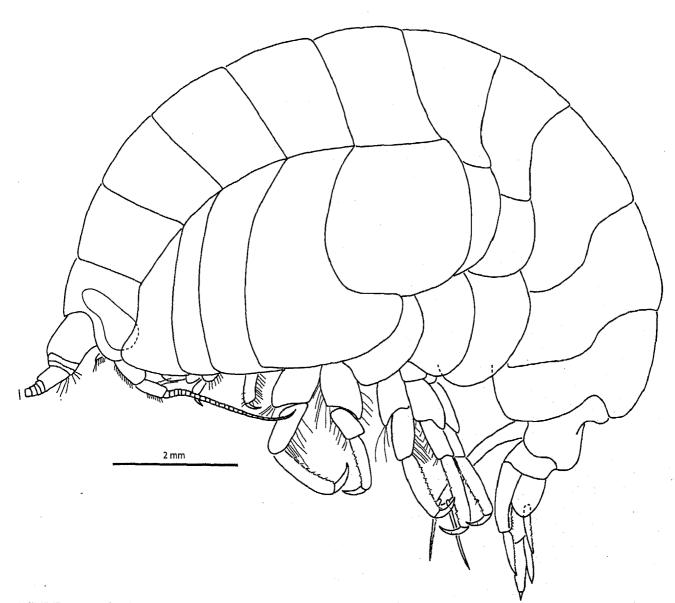


FIGURE 2. Pseudorchomene coatsi (Chilton, 1912), female, 19 mm, habitus, ANT-XIX/3-4 (ANDEEP I & II), sta. 083, West of Elephant Island.

Maxilla 1: inner plate very elongate, distally very narrow, with 2 stout setae in truly distal position; outer plate with 11 blade-shaped spines (in 7/4 arrangement), which are denticulate on one side; palp 2-articulate, broad with distal row of 12 cuspidate spines anteriorly followed by a stout antero-distal flag seta.

Maxilla 2: plates very narrow, tapering towards tip; inner plate much shorter and slightly narrower than outer plate.

*Maxilliped*: inner and outer plates well developed; inner plate narrow, about half the length of outer plate, with well-developed posteromedial row of strong setae, 3 apical nodular spines and 1 anterodistal stout seta; outer plate reaching tip of article 2 of palp, with lateral double row of long setae, 2 distal large stout blunt spines, a medial row of 22 much smaller low nodular spines, and 7 small slender isolated facial spines; dactylus well developed.

Gills: long accessory process on gill of percopods 5-6; gill of percopod 7 well developed and posteriorly pointed.

Oostegites: linear, from gnathopod 2 to percopod 5.

Gnathopod 1: subchelate; coxa large but slightly shorter than coxa 2, externally visible, triangular, anterior and posterior margins nearly straight and strongly divergent, ventral margin broad and distinctly convex; all articles except merus and dactylus elongate; basis strongly convex anteriorly, weakly convex posteriorly, with many long setae along anterior margin, 3.0 x as long as wide; ischium linear, 6 x as long as wide; merus triangular, 3 x as long as wide, much shorter than ischium and carpus; carpus linear, 5 x as long as wide; propodus linear, 5.5 x as long as wide and as long as carpus, palm oblique and minutely denticulate; dactylus well developed.

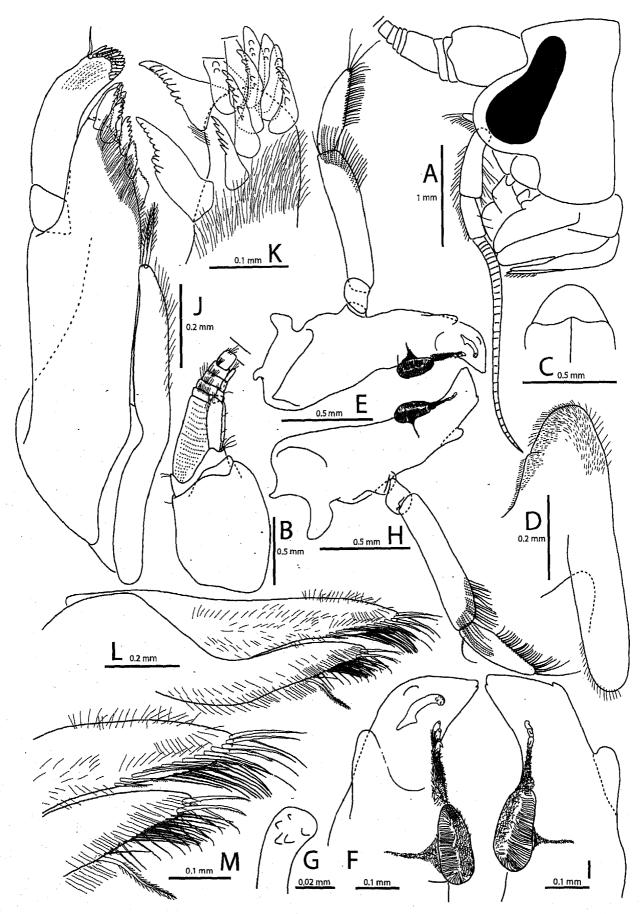


FIGURE 3. Pseudorchomene coatsi (Chilton, 1912), female, 19 mm, ANT-XIX/3-4 (ANDEEP I & II), sta. 083, West of Elephant Island. A, head with appendages; B, right A1 in medial view; C, upper lip and epistome in frontal view; D, left half of lower lip; E, left Md; F, tip of left Md; G, tip of lacinia mobilis; H, right Md; I, tip of right Md; J, right Mx1; K, tip of outer plate of right Mx1 in medial view; L, right Mx2; M, tip of right Mx2.

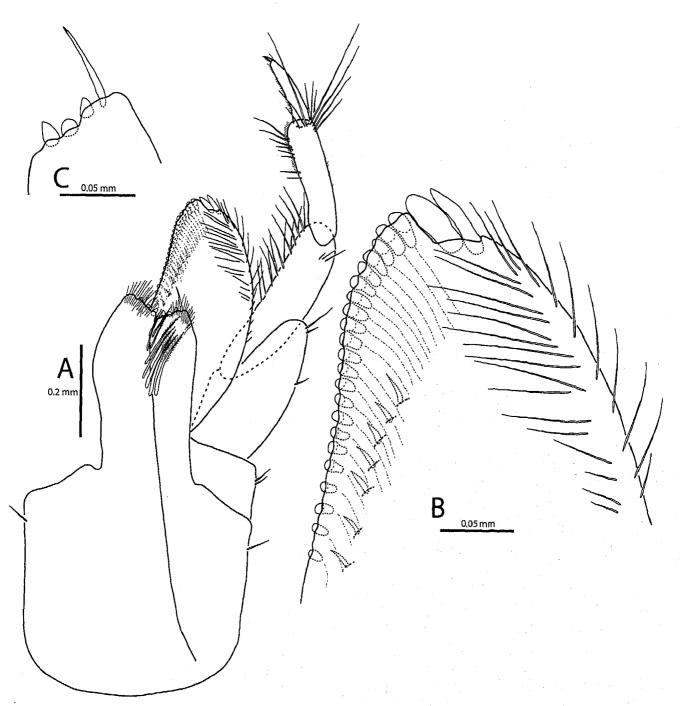


FIGURE 4. Pseudorchomene coatsi (Chilton, 1912), female, 19 mm, ANT-XIX/3-4 (ANDEEP I & II), sta. 083, West of Elephant Island. A, Mxp; B, distal half of right outer plate; C, tip of right inner plate.

Gnathopod 2: minutely chelate; coxa large but slightly shorter than coxa 3, subrectangular; ischium 3.4. x as long as wide; carpus 2.3 x as long as wide, 2.0 x as long as propodus, anterior margin with dense row of very short setae beyond midlength and many long setae distally; propodus strongly convex, anteriorly with many long setae, weakly concave posteriorly with many very short setae, palm with a cavity and an extended inner dentate basket; dactylus very short, denticulate, reaching corner of palm.

*Pereopod 3*: coxa large, about as long as coxa 4, subrectangular, with posterior margin slightly concave; ischium, merus and carpus with many long setae posteriorly; merus slightly expanded anteriorly, 2.8 x as long as wide; carpus 3.1 x as long as wide and 0.73 x as long as merus; propodus 5.4 x as long as wide, 1.3 x as long as carpus, with 10 well-developed spines (or pairs of spines), posteriorly, the largest spines of each group blunt-tipped and with accessory branch; dactylus normally developed, curved, with long unguis, 0.39 x as long as propodus.

Pereopod 4: coxa deeper than wide, posteroventral lobe large, posteroventral corner of lobe more or less rounded (with scarcely distinct angular discontinuity); ischium, merus and carpus with many long setae posteriorly;

merus slightly expanded anteriorly, 2.6 x as long as wide; carpus 2.6 x as long as wide and 0.62 x as long as merus; propodus 4.7 x as long as wide, 1.3 x as long as carpus, with 10 well-developed spines (or pairs of spines) posteriorly, the largest spines of each group blunt-tipped and with accessory branch; dactylus normally developed, curved, with long unguis, 0.41 x as long as propodus.

*Pereopod 5*: coxa very slightly longer than broad, weakly bilobate, posterior lobe slightly produced ventrally, 1.6 x as long as basis; basis strongly expanded posteriorly, about as long as broad, with 14 short spines or groups of spines anteriorly, 7 very weak crenellations posteriorly, and well-developed broadly rounded posteroventral lobe; ischium with 4 groups of short spines anteriorly, the distal one associated with a long seta; merus expanded, 1.3 x as long as broad, anterior margin straight, posterior margin convex bearing 4 long setae and 1 distal medium-sized spine; carpus 2.0 x as long as broad, with 1 posterodistal short seta and 1 posterodistal spine of normal length and stoutness; propodus 4.8 x as long as broad, 1.5 x as long as carpus, with 7 blunt-tipped spines (or pairs of spines in which one is blunt-tipped) anteriorly, each spine with accessory branch (except those of distal pair); dactylus normally developed, curved, with long unguis, 0.40 x as long as propodus.

*Pereopod 6*: coxa slightly concave anteriorly, convex posteriorly, distinctly bilobed, shorter than coxa 5, 1.4 x as long as broad, 0.96 x as long as basis; basis longer than basis of pereopod 5, expanded posteriorly, 1.3 x as long as broad, with 11 short spines or groups of spines anteriorly, 11 very weak crenellations posteriorly, posteroventral lobe well-developed and broadly rounded; ischium-dactylus combined slightly longer than in pereopod 5 and as long as in pereopod 7; ischium with 4 short spines and 3 long setae on anterior margin; merus weakly expanded, 1.9 x as long as broad, anterior margin nearly straight, posterior margin weakly convex, bearing 4 isolated small spines of normal stoutness; carpus 2.6 x as long as broad, 1.5 x as long as carpus, with 9 blunt-tipped spines (or pairs of spines in which one is blunt-tipped) anteriorly, each spine with an accessory branch (except those of distal pair); dactylus normally developed, curved, with long unguis, 0.39 x as long as propodus.

*Pereopod 7*: coxa regularly rounded, shorter than coxa 6, slightly longer than broad, 0.5 x as long as basis; basis longer than basis of pereopod 6, expanded posteriorly, 1.4 x as long as broad, with 11 short spines or groups of spines anteriorly, 11 very weak crenellations posteriorly, posteroventral lobe low and broadly rounded; ischium with 4 groups of 1 or 2 short spines on anterior margin, without long setae; merus weakly expanded, 1.9 x as long as broad, anterior margin straight, posterior margin weakly convex, bearing 4 isolated small spines of normal stoutness; carpus 2.7 x as long as broad, with number and strength of anterior spines normal, with 1 short seta and 2 spines of normal length and stoutness on posterodistal corner and no other posterior spines; propodus 5.2 x as long as broad, 1.4 x as long as carpus, with 9 blunt-tipped spines (or pairs of spines in which one is blunt-tipped) anteriorly, each spine with an accessory branch (except those of distal pair); dactylus normally developed, curved, with long unguis, about 0.35 x as long as propodus (not perfectly levelled on illustration).

*Epimeron 1*: anteroventral corner subquadrate, not produced; posteroventral corner regularly rounded; ventral margin nearly straight; posterior margin strongly convex.

*Epimeron 2*: anteroventral corner rounded, posteroventral corner bluntly subquadrate; ventral margin straight [to slightly concave]; posterior margin straight.

Epimeron 3: posteroventral corner regularly rounded; ventral and posterior margins slightly convex.

Urosomite 1 with a deep dorsal depression flanked on each side by lateral carina and followed by a prominent dorsal hump which is bluntly angular posteriorly.

Uropod 1: peduncle 1.6 x as long as inner ramus, with 15 very small stout lateral spines and 23 medium-sized slender spines; outer ramus slightly longer than inner ramus, with 7 small lateral spines and no medial spines; inner ramus with 4 medium-sized lateral spines and 9 well-developed medial spines.

Uropod 2 [abnormal in specimen used for description and illustration: inner ramus unusually short, possibly broken and regenerated]: peduncle 1.5 x as long as inner ramus, with 8 small to very small stout lateral spines and 9 medium-sized slender spines (all spines on distal 0.4); outer ramus much longer than inner ramus, with 12 stout medium-sized lateral spines and no medial spines; inner ramus without notch, with 4 lateral spines and 8 medial spines, all medium-sized.

Uropod 3: peduncle ordinary, about 0.85 x as long as outer ramus; outer ramus article 1 with 6 lateral spines, 11 medial long plumose setae and 1 long slender distormedial spine, article 2 at least 0.21 x as long as article 1; inner ramus reaching about 0.9 of article 1 of outer ramus, with 3 lateral spines and long plumose setae all along medial margin, without apical setae.

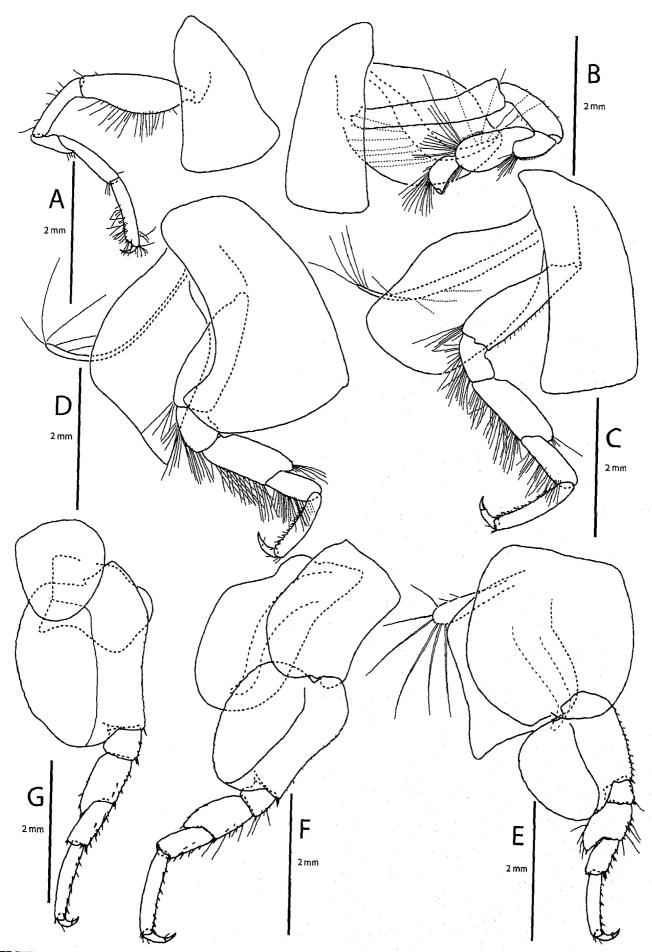


FIGURE 5. Pseudorchomene coatsi (Chilton, 1912), female, 19 mm, ANT-XIX/3-4 (ANDEEP I & II), sta. 083, West of Elephant Island. A, right Gn1; B, left Gn2; C, right P3; D, right P4; E, right P5; F, right P6; G, right P7.

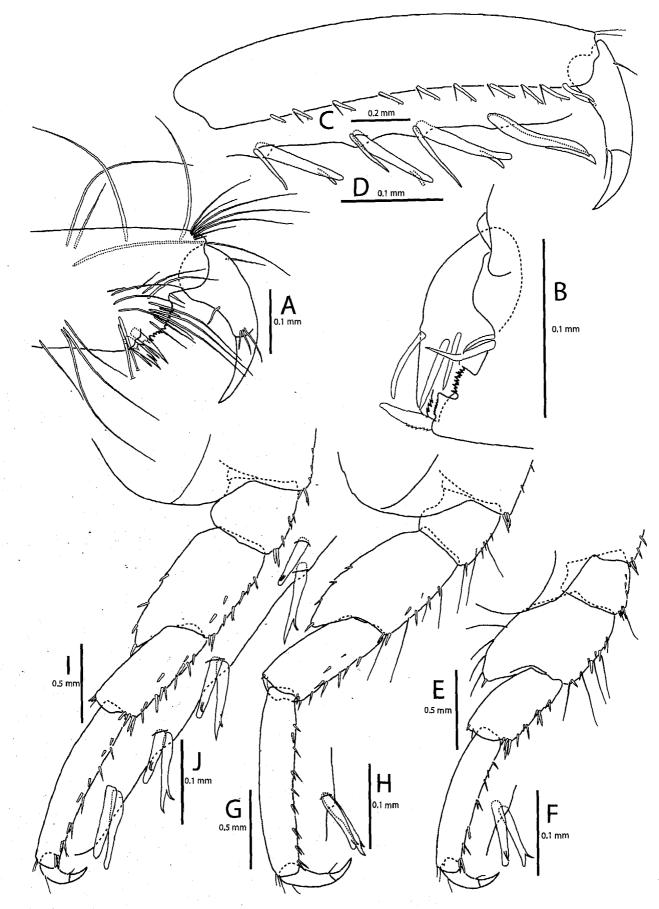


FIGURE 6. Pseudorchomene coatsi (Chilton, 1912), female, 19 mm, ANT-XIX/3-4 (ANDEEP I & II), sta. 083, West of Elephant Island. A, tip of chela of right Gn1; B, tip of chela of left Gn2; C, propodus and dactylus of right P3; distal spines of propodus of right P3; E, distal half of right P5; F, penultimate pair of spines of propodus of right P5; G, distal half of right P6; H, penultimate pair of pines of propodus of right P6; I, P7 distal half of right P7; J, distal spines of propodus of right P7.

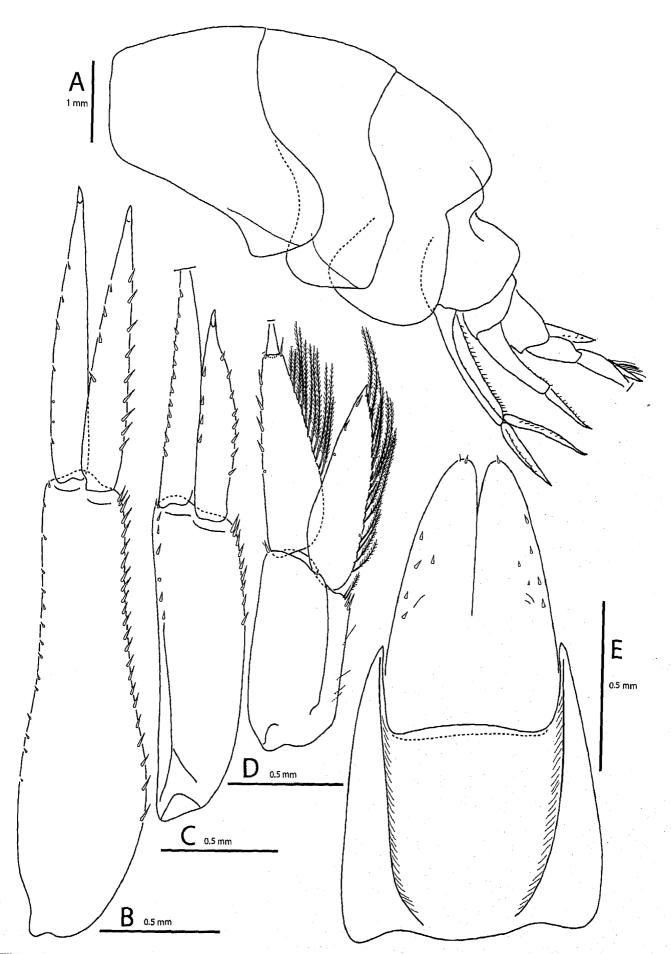


FIGURE 7. Pseudorchomene coatsi (Chilton, 1912), female, 19 mm, ANT-XIX/3-4 (ANDEEP I & II), sta. 083, West of Elephant Island. A, pleon; B, right U1; C, right U2; D, right U3; E, telson and urosomite 3.

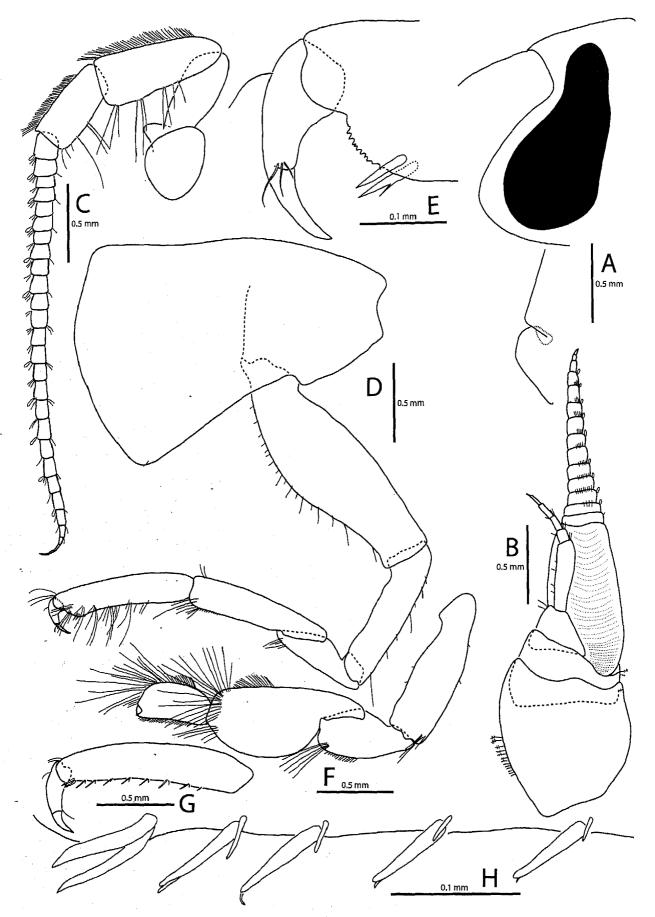


FIGURE 8. Pseudorchomene coatsi (Chilton, 1912), male, 16 mm ARC94, NA62, Admiralty Bay. A, anterior part of head, epistome and upper lip; B, left A1 in medial view; C, left A2 in lateral view; D, left Gn1; E, tip of chela of left Gn1 (setae of propodus not shown); F, 5 distal articles of left Gn2; G, propodus and dactylus of left P3; H, posterodistal spines of propodus of left P3.

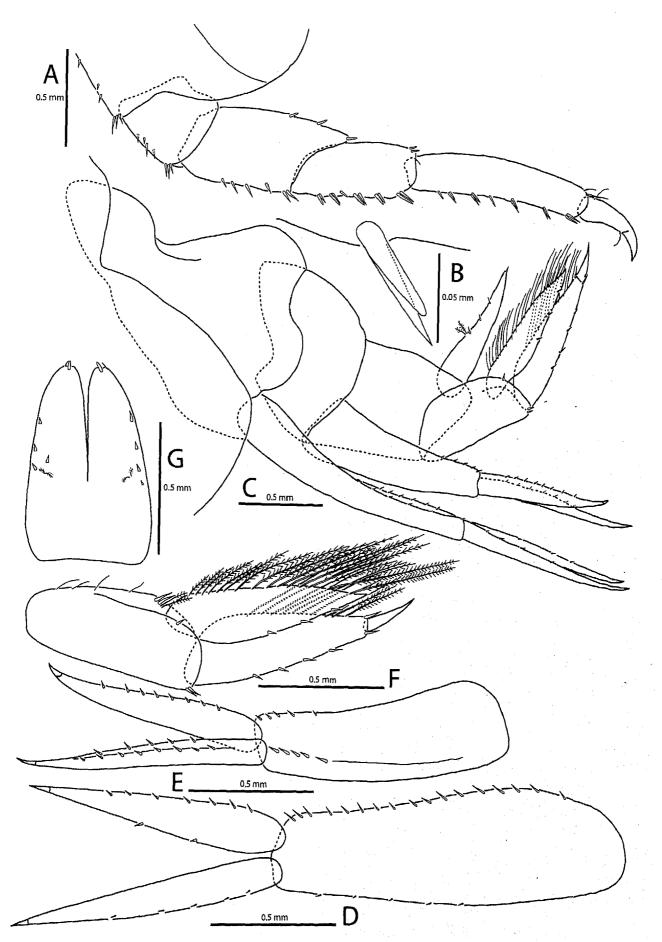


FIGURE 9. Pseudorchomene coatsi (Chilton, 1912), male, 16 mm ARC94, NA62, Admiralty Bay. A, distal half of left P7; B, antepenultimate pair of spines of anterior border of propodus of left P7; C, urosome and posterior part of pleonite 3; D, right U1; E, left U2; F, left U3; G, telson.

*Telson* elongate, cleft 0.57 of length, each lobe with 1 apical spine paired or not with 1 small seta, and 5–6 dor-solateral spines which are not all in a row.

**Complementary description**. The female described above has the flagellum of antenna 1 incomplete and the rami of uropod 2 with abnormal relative proportions (they were possibly broken and regenerated). A complementary account is given of a male from the expedition ARC94, sta. NA62, King George Island, Admiralty Bay, 62°08'S 58°27'W, 470 m, RBINS, INV. 100969.

Antenna 1 a bit shorter than antenna 2; major flagellum 15-articulate, with calceoli, first article nearly 0.5 x as long as entire flagellum; accessory flagellum 6-articulate, article 1 elongate, slightly longer than 5 distal articles combined.

Antenna 2 about  $0.2 \times as$  long as body; peduncular articles 3 to 5 not enlarged, with brush of setae; flagellum with 29 articles, calceoli present.

Gnathopods similar to those of female, but setae of anterior border of basis of gnathopod 1 shorter.

Pereopods 3-7 very similar to females but number of spines slightly lower.

Epimeron 3 with posteroventral margin not perfectly rounded, with trace of angularity.

Uropod 1: peduncle 1.4 x as long as inner ramus, with 5 very small lateral spines and 17 medium-sized slender medial spines; outer ramus slightly longer than inner ramus, with 5 small lateral spines and no medial spines; inner ramus with 2 medium-sized lateral spines and 7 medium-sized medial spines.

Uropod 2: peduncle as long as inner ramus, with 5 small lateral spines and 5 medium-sized medial spines (all spines on distal 0.25); outer ramus 0.9 x as long as inner ramus, with 8 medium-sized lateral spines and no medial spines; inner ramus without notch, with 5 lateral spines and 8 medial spines, all medium-sized.

Uropod 3: peduncle ordinary, about 0.74 x as long as outer ramus; outer ramus article 1 with 5 lateral spines, 10 medial long plumose setae and 1 long slender distomedial spine, with article 2 distally very narrow, about 0.31 x as long as article 1; inner ramus reaching tip of article 1 of outer ramus, with 3 lateral spines and with long plumose setae all along its medial margin, without apical setae.

*Telson:* elongate, cleft for 0.58 of its length, each lobe with 1 apical spine paired with 1 small seta, and 4 dor-solateral spines which are all in a row or not.

**Colour pattern.** An unpublished photograph made by M. Rauschert and identified by him as *P. coatsi* was examined. It shows an amphipod with red eyes, but otherwise almost colourless except a trace of reddish pigmentation.

#### Size. 19 mm.

**Distribution and depth range.** Davis Sea, Enderby Land, South Georgia, South Shetland Islands, Weddell Sea, 50–2889 m (De Broyer *et al.* 2007; Havermans *et al.* 2011). The records from Îles Kerguelen (De Broyer 1983) are based on *P. debroyeri* and this might also be the case of those from Macquarie Island and Prince Edward Islands.

**Biology.** "The species was captured mainly in baited traps, wherein it can represent up to 96% of total number of amphipods, with a record of 24 560 specimens in one trap. The digestive tract content of all individuals analyzed (collected either by trawl or by trap) revealed only fragments of carrion, indicating that *P. coatsi* is a true necrophage" (Dauby *et al.* 2001). The specimen dissected for study, which was a well-calcified female, had fully developed oostegites with setae and, at the same time, ovaries full of eggs. Female amphipods lay their eggs shortly after moulting and since the occurrence of setae on oostegites is a sign of fertile intermoult (Bellan-Santini 1999). This suggests that the dissected specimen had previously laid a batch of eggs, which hatched before capture, and that a further batch of eggs was developing. If this assumption is correct, this would mean that *P. coatsi* is iteroparous, as it is the case for other 'orchomenids' (see e.g. Thurston 1979; Stockton 1982; Moore & Wong 1996).

### Pseudorchomene debroyeri sp. n.

(Figs 10–16)

Pseudorchomene coatsi. — De Broyer, 1983: 193–195, figs. 72–74. Not Orchomenopsis coatsi Chilton, 1912: 477, pl. 1, fig. 8–9.

Type material specimens. "ICEFISH" cruise, Falkland Islands, S of Beauchene Island, sta. 14, trap 3, 53°02'32"S 59°08'03"W-53°26'24"S 59°08'39"W, 470 m, 26.v.2004: 1 HOLOTYPE female, USNM 1156918, dissected and

mounted on 20 slides in Euparal, and 18 PARATYPES in alcohol, USNM 1156919, Specimen Ids with corresponding GenBank accession numbers: PD-1105108 (JQ423241), PD-1105109 (JQ423242). — R/V "Polarstern" cruise ANT-XIX/5 (LAMPOS), Burdwood Bank, sta. 147-1, 54°32'S 55°55'W, 413 m, baited traps, 06.iv.2002: 30 PARATYPES, Specimen Ids with corresponding GenBank accession numbers: PD-081007202B (JQ423244), PD-221007142B (JQ423243), RBINS, INV. 100955.(2 tubes).

Additional material. Expedition KER 82, sta. N4, Fosse de l'Hydrographie, between île Suhm and Port Douzième, 49°30'00"S 70°10'00"E, 90 m, 18–29.i.1982: 1 female, leg. C. De Broyer, RBINS, INV. 100968 (2 tubes). — Expedition KER 82, sta. N6, between île Heugh and îles Gibson, label inside vial indicating 'Narres', 49°00'00"S 69°00'00"E, 140 m, 08–09.ii.1982: about 100 specimens (one female partly dissected but not permanently mounted), leg. C. De Broyer, RBINS, INV. 100972. — Expedition KER 82, sta. N8, 'near Port Bizet, fosse de Green', 49°31'00"S 69°54'00"E, 100 m, 08–09.ii.1982, about 30 specimens, leg. C. De Broyer, RBINS, INV. 100967. — Expedition KER 82, sta. N10, 'along Fosse de Channer', 49°S 69°E, 55 m, 23–24.ii.1982: 10 specimens, leg. C. De Broyer, RBINS, INV. 100971. — Expedition KER 82, sta. N10, 'along Fosse de Channer', 49°S 69°E, 55 m, 23–24.ii.1982: 3 specimens, leg. C. De Broyer, RBINS, INV. 100966.

Type locality. Falkland Islands, south of Beauchene Island, 53°02'32"S 59°08'03"W-53°26'24"S 59°08'39"W, 470 m.

Etymology. The species is dedicated to Claude De Broyer, who provided good illustrations of the species under the name *P. coatsi*; see De Broyer (1983). The name is a genitive.

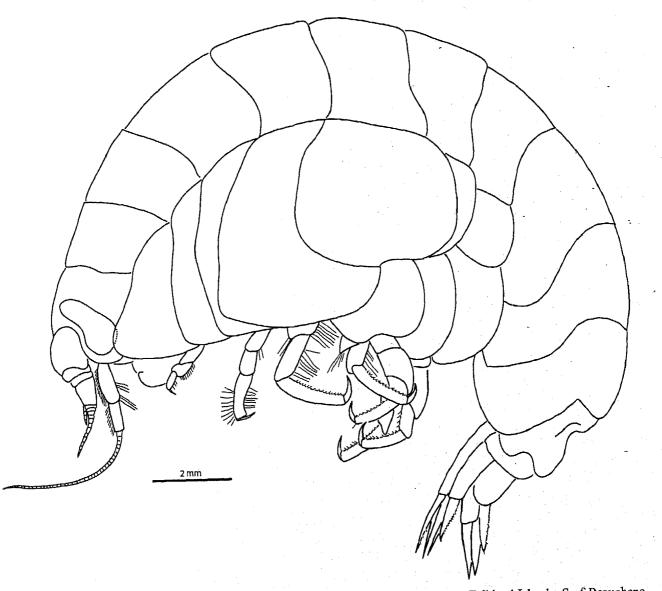
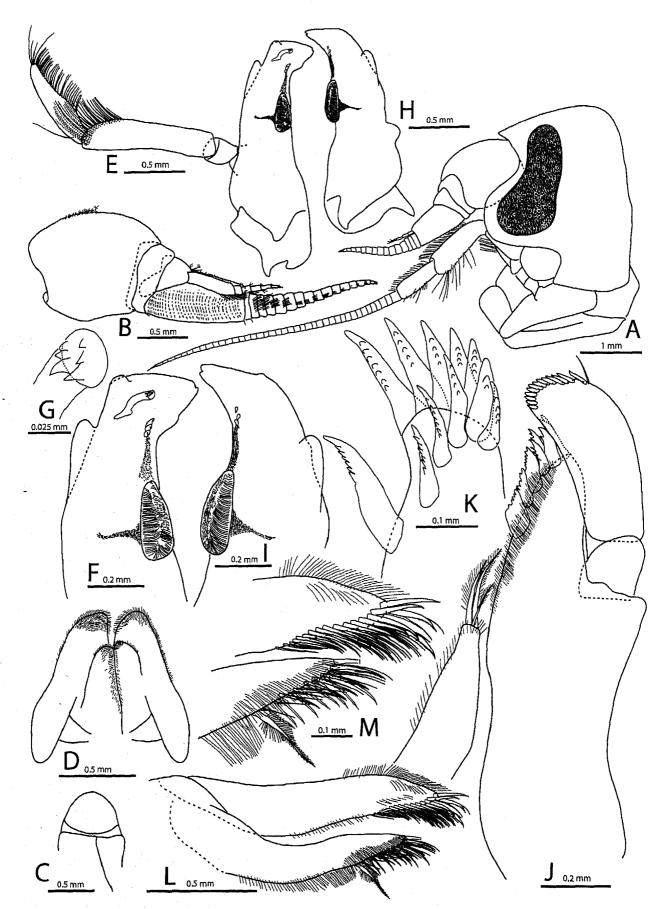


FIGURE 10. Pseudorchomene debroyeri sp. n., female, 31 mm habitus, ICEFISH cruise, Falkland Islands, S of Beauchene Island, station 14.



**FIGURE 11.** *Pseudorchomene debroyeri* **sp. n.**, female holotype, 31 mm, ICEFISH cruise, Falkland Islands, S of Beauchene Island, station 14. A, head with appendages; B, left A1 in medial view; C, upper lip and epistome in frontal view; D, lower lip; E, left Md; F, tip of left Md; G, tip of lacinia mobilis; H, right Md; I, tip of right Md; J, left Mx1; K, tip of outer plate of left Mx1 in medial view; L, right Mx2; M, tip of right Mx2.

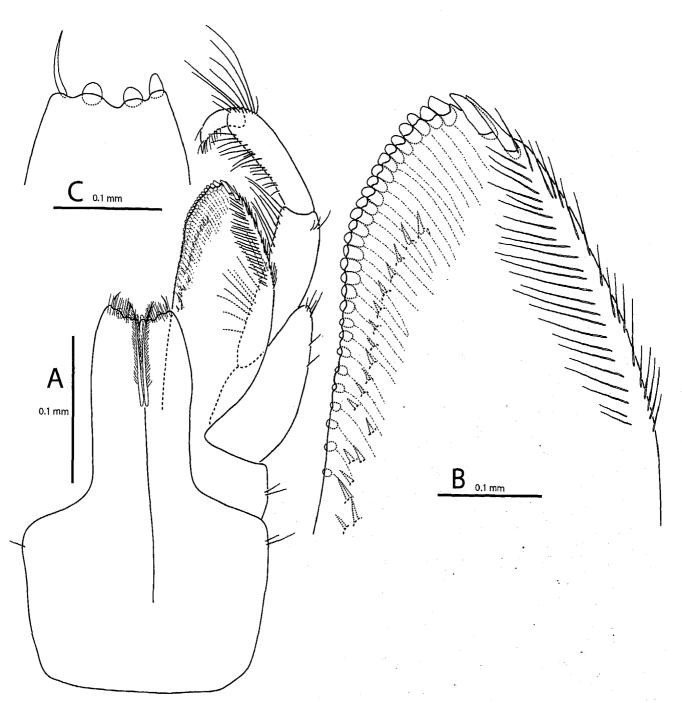


FIGURE 12. Pseudorchomene debroyeri sp. n., female holotype, 31 mm, ICEFISH cruise, Falkland Islands, S of Beauchene Island, station 14. A, Mxp; B, distal half of right outer plate; C, tip of left inner plate.

**Diagnosis.** Somites of pereon and pleosome without posterior humps. Mandibular palp inserted well proximal to molar process. Molar process broad. Gnathopod 1: anterior margin of basis convex, palm transverse, basis 2.4 x, ischium 3.5 x, carpus 3 x, propodus 3.5 x as long as wide. Gnathopod 2: carpus 3.0 x as long as wide. Pereopod 3: propodus with about 16–18 spines or pairs of spines (which are well developed). Pereopod 3–7: on propodus, broadest spine of each pair or triplet with tip pointed. Coxa 4 posteroventrally rounded. Pereopod 5: coxa distinctly broader than long; basis strongly expanded; merus with setae posteriorly and one distal fairly slender posterodistal spine. Ratio length/width of merus of pereopods 5–7: 1.8; 2.3; 2.6. Ratio length/width of carpus of pereopods 5–7: 1.7; 2.6; 2.4. Posterodistal angle of carpus of pereopods 5–7 with spines of normal length and stoutness. Pereopod 7: anterior margin of carpus with spines longer and more numerous than in other species, posterior margin of carpus and often of propodus with non-distal spine(s). Epimeron 3 regularly rounded posteriorly. Uropod 3: medial margin of both rami with many long setae, inner ramus not reaching tip of article 1 of outer ramus.

Description. Based on HOLOTYPE female, "ICEFISH" cruise, Falkland Islands, S of Beauchene Island, station 14, trap 3, 53°02'32"S 59°08'03"W-53°26'24"S 59°08'39"W, 470 m, USNM 1156918.

*Body* without dorsal carina; somites of pereon and pleosome without small posterior humps. *Head*: lateral cephalic lobes broadly rounded.

*Eyes* occupying the most of anterior part of head, much longer than broad, lower part much broader than upper part, distinctly concave anteriorly, nearly straight posteriorly, dark, with fully developed ommatidia.

Antenna 1 distinctly shorter than antenna 2; major flagellum 18-articulate, first article 0.4 x as long as entire flagellum; accessory flagellum 7-articulate, article 1 elongate, slightly longer than 6 distal articles combined; calceoli absent.

Antenna 2 about 0.2 x as long as body; peduncular articles 3 to 5 not enlarged, with brush of setae; flagellum 42-articlulate; calceoli absent.

*Mouthparts* forming a quadrate bundle. Epistome carinate, scarcely produced, terminating in small blunt tooth; upper lip broadly rounded, distinctly overreaching epistome.

*Mandible*: incisor process, cutting edge smooth, except for small blunt denticle on each side, lateral and medial borders parallel; lacinia mobilis present on left side only, narrowly cylindrical (finger-like), slightly curved, distally slightly dilated with 6 well-developed dentiform processes; 3 small raker spines and a dense patch of short setules present between incisor and molar processes; molar process broad, elliptic to subovate, transversally ridged and triturative; lateral setigerous crest arising from proximal 0.3 of molar process; palp 3-articulate, attached midway, well proximal to molar process; article 1 without setae, article 2 longest with row of 25 strong distal and subdistal A2-setae, article 3 of palp 0.70 x as long as article 2, 4.1 x as long as wide, with 1 proximal A3-seta, a row of 29 D3-setae on distal 0.7 (these setae are slightly shorter than width of article 3), and 4 E3-setae.

*Maxilla 1*: inner plate very elongate, distally very narrow, with 3 stout setae [one is much more slender than the others] in truly distal position; outer plate with 11 blade-shaped spines (in 7/4 arrangement), which are denticulate on one side; palp 2-articulate, broad with distal row of 13 cuspidate spines anteriorly and a stout antero-distal flag seta.

Maxilla 2: plates very narrow, tapering; inner plate much shorter and slightly narrower than outer plate.

*Maxilliped*: inner and outer plates well developed; inner plate narrow, about half the length of outer plate, with well-developed posteromedial row of strong setae, 3 apical nodular spines and 1 anterodistal stout seta; outer plate overreaching tip of article 2 of palp, with lateral double row of long setae, 2 distal large stout blunt spines, a medial row of 28 much smaller low nodular spines, and 19 small slender facial (isolated or paired) spines; dactylus well developed.

Gills: long accessory process on gill of pereopods 5-6; gill of pereopod 7 well developed and posteriorly pointed.

Oostegites: linear, from gnathopod 2 to percopod 5.

Gnathopod 1: subchelate; coxa large but slightly shorter than coxa 2, externally visible, triangular, anterior and posterior margins nearly straight and strongly divergent, ventral margin broad and distinctly convex; all articles except merus and dactylus elongate; basis strongly convex anteriorly and weakly convex posteriorly, with many long setae along anterior margin, 2.4 x as long as wide; ischium moderately elongate, 3.5 x as long as wide; merus triangular, 2.5 x as long as wide, a bit shorter than ischium and carpus; carpus moderately elongate, 3 x as long as wide; propodus linear, 3.5 x as long as wide and slightly longer than carpus, palm transverse and minutely denticulate; dactylus well developed.

Gnathopod 2: minutely chelate; coxa large but slightly shorter than coxa 3, subrectangular; ischium 3.4. x as long as wide; carpus 3.0 x as long as wide, 2.2 x as long as propodus, anterior margin with dense row of very short setae beyond midlength, and many long setae distally; propodus strongly convex anteriorly with many long setae, weakly concave posteriorly with many very short setae, palm with a cavity and an extended inner dentate basket; dactylus very short, denticulate, reaching corner of palm.

Percopod 3: coxa large, about as long as coxa 4, subrectangular, posterior margin slightly concave; ischium, merus and carpus with many long setae posteriorly; merus slightly expanded anteriorly,  $2.8 \times as$  long as wide; carpus 3.7 x as long as wide and 0.73 x as long as merus; propodus 6.3 x as long as wide,  $1.4 \times as$  long as carpus, with 18 well-developed spines (or pairs of spines) posteriorly, the largest spines of each group acute-tipped and with accessory branch; dactylus normally developed, curved, with long unguis,  $0.31 \times as$  long as propodus.

*Pereopod 4*: coxa deeper than wide, posteroventral lobe large, posteroventral corner of lobe more or less rounded (with slight angular discontinuity); ischium, merus and carpus with many long setae posteriorly; merus slightly expanded anteriorly, 2.8 x as long as wide; carpus 3.6 x as long as wide and 0.53 x as long as merus; propo-

dus 4.7 x as long as wide, 1.4 x as long as carpus, with about 16 well-developed spines (or pairs of spines) posteriorly, the largest spines of each group acute-tipped and with accessory branch; dactylus normally developed, curved, with long unguis, 0.35 x as long as propodus.

*Pereopod 5*: coxa broader than long, weakly bilobate, posterior lobe not produced ventrally, 1.3 x as long as basis; basis strongly expanded posteriorly, about as long as broad, with 26 short spines anteriorly, 16 weak but distinct crenellations posteriorly, posteroventral lobe well developed and broadly rounded; ischium with 2 groups of short spines anteriorly, the distal one associated with a long seta; merus expanded, 1.8 x as long as broad, anterior margin straight, posterior margin convex, bearing 6 long setae and 1 distal medium-sized spine; carpus 1.7 x as long as broad, with 3 posterodistal slender spines of normal length; propodus 5.9 x as long as broad, 1.9 x as long as carpus, with 11 acute spines (or pair of spines) anteriorly, each spine with accessory branch (except those of distal pair); dactylus normally developed, curved, with long unguis, 0.38 x as long as propodus.

Percopod 6: coxa slightly concave anteriorly, convex posteriorly, distinctly bilobed, shorter than coxa 5, 1.4 x as long as broad, 0.88 x as long as basis; basis longer than basis of percopod 5, expanded posteriorly, 1.5 x as long as broad, with 10 short marginal spines or groups of spines (and some submarginal spines) anteriorly, 20 weak but distinct crenellations posteriorly, posteroventral lobe well-developed and broadly rounded; ischium-dactylus combined slightly longer than in percopod 5 and as long as in percopod 7; ischium with 7 spines and 3 long setae on anterior margin; merus weakly expanded, 2.3 x as long as broad, anterior margin nearly straight, posterior margin weakly convex bearing 6 isolated small spines of normal stoutness; carpus 2.6 x as long as broad, 1.5 x as long as carpus, with 14 acute spines (or pairs of spines in which one is acute) anteriorly, each spine with an accessory branch (except those of distal pair); dactylus normally developed, curved, with long unguis, about 0.32 x as long as propodus.

*Pereopod 7*: coxa rounded, shorter than coxa 6, slightly broader than long, 0.5 x as long as basis; basis longer than basis of pereopod 6, expanded posteriorly, 1.4 x as long as broad, with 9 short spines or groups of spines (and some submarginal spines) anteriorly, 18 very weak crenellations posteriorly, posteroventral lobe low and broadly rounded; ischium with 5 anterior groups of 1 to 5 short spines, without long setae; merus weakly expanded, 2.6 x as long as broad, anterior margin straight, posterior margin weakly convex, bearing 6 groups of 1–2 small spines of normal stoutness; carpus 2.6 x as long as broad, with spines unusually strong and numerous, with 3 spines of normal length and stoutness on posterodistal corner and two other spines on the posterior margin; propodus 5.8 x as long as broad, 1.6 x as long as carpus, with 11 acute spines (or pairs or triplets of acute spines) anteriorly, each spine with an accessory branch (except those of distal pair); dactylus normally developed, curved, with long unguis, about 0.34 x as long as propodus.

*Epimeron 1*: anteroventral corner subquadrate, slightly produced; posteroventral corner regularly rounded; ventral margin very slightly concave; posterior margin strongly convex.

*Epimeron 2*: anteroventral corner rounded, posteroventral corner acutely quadrate; ventral margin very slightly concave; posterior margin straight.

Epimeron 3: posteroventral corner regularly rounded; ventral and posterior margins slightly convex.

Urosomite 1 with a deep dorsal depression flanked on each side by lateral carina and followed by a prominent dorsal hump which is bluntly angular posteriorly.

Uropod 1: peduncle 1.6 x as long as inner ramus, with 10 very small stout lateral spines and 33 medial medium-sized slender spines; outer ramus slightly shorter than inner ramus, with 13 small lateral spines and 1 small medial spine; inner ramus with 5 medium-sized lateral spines and 15 well-developed medial spines.

Uropod 2: peduncle 1.2 x as long as inner ramus, with 7 very small stout lateral spines and 10 medium-sized narrow spines (all spines on distal 0.4); outer ramus 0.9 x as long as inner ramus, with 15 stout and medium-sized lateral spines and no medial spines; inner ramus without notch, with 8 lateral spines and 19 medial spines, all medium-sized.

Uropod 3: peduncle ordinary, about 0.80 x as long as outer ramus; outer ramus with article 1 with 10 lateral spines, 17 medial long plumose setae and 1 normally developed distomedial spine, with article 2 about 0.15 x as long as article 1; inner ramus reaching about 0.85 of article 1 of outer ramus, with 6 lateral spines and long plumose setae all along medial margin.

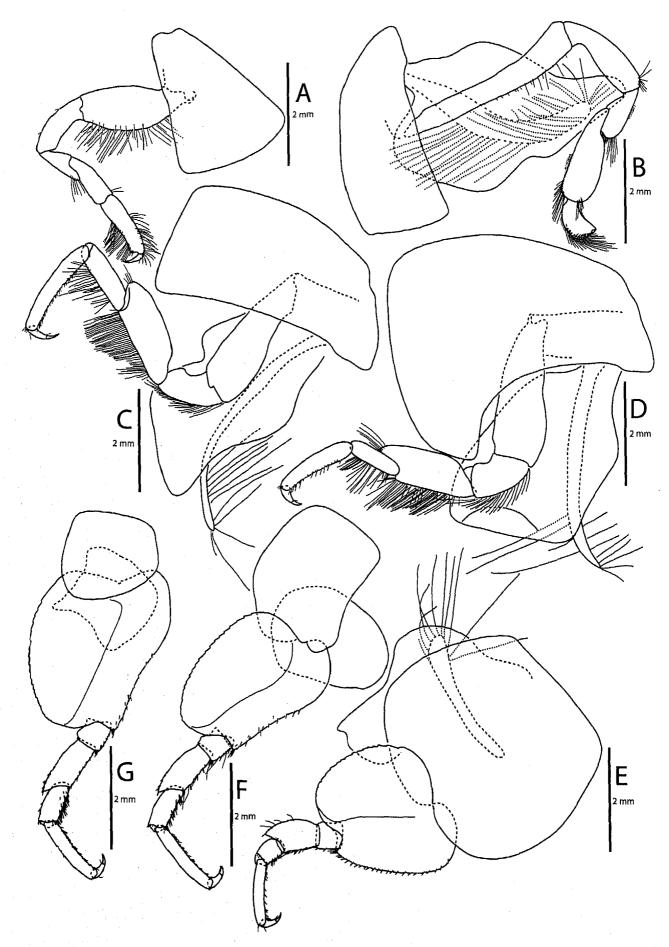


FIGURE 13. Pseudorchomene debroyeri sp. n., female holotype, 31 mm, ICEFISH cruise, Falkland Islands, S of Beauchene Island, station 14. A, right Gn1; B, left Gn2; C, left P3; D, left P4; E, right P5; F, left P6 (drawing inverted); G, right P7.

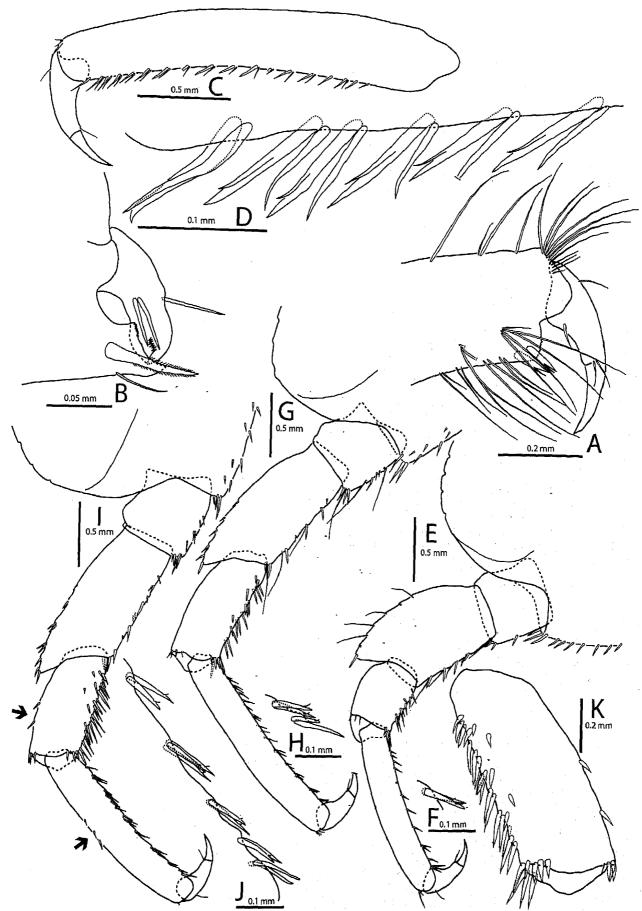


FIGURE 14. Pseudorchomene debroyeri sp. n., female holotype, 31 mm, ICEFISH cruise, Falkland Islands, S of Beauchene Island, station 14. A, tip of chela of right Gn1; B, tip of chela of right Gn2; C, propodus and dactylus of left P3; D, distal spines of propodus of left P3; E, distal half of right P5; F, antepenultimate pair of spines of propodus of right P5; G, distal half of left P6 (drawing inverted); H, antepenultimate and penultimate pairs of spines of propodus of left P6; I, distal half of right P7; J, distal pairs of spines of propodus of right P7; K, carpus of left P7.

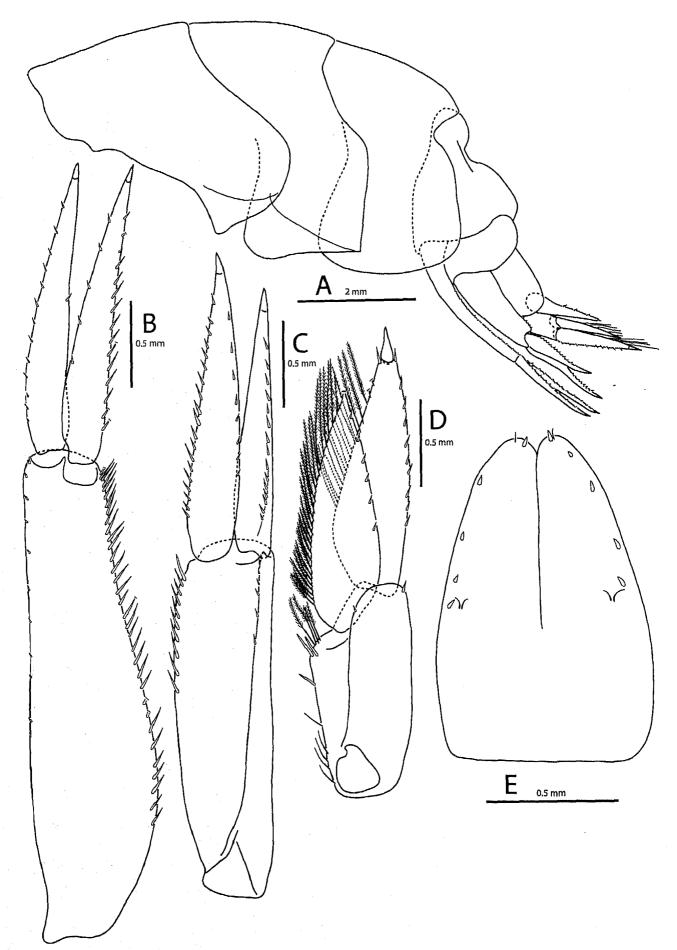


FIGURE 15. Pseudorchomene debroyeri sp. n., female holotype, 31 mm, ICEFISH cruise, Falkland Islands, S of Beauchene Island, station 14. A, pleon; B, right U1; C, left U2; D, left U3; E, telson.

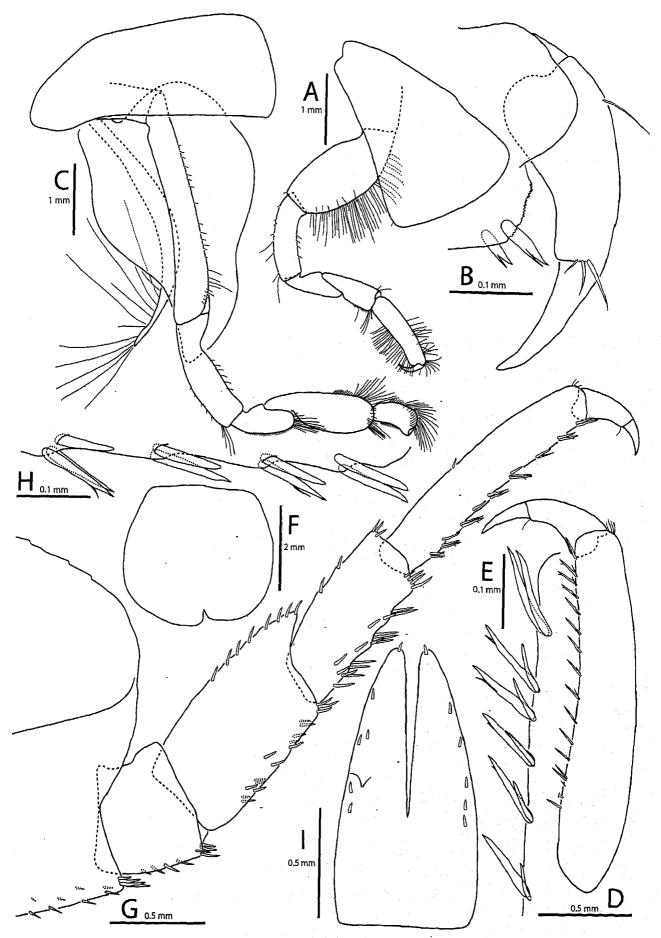


FIGURE 16. Pseudorchomene debroyeri sp. n., female, 23 mm, Kerguelen, Narres, sta. KER 82 – N6. A, right Gn1; B, tip of chela of right Gn1; C, right Gn2; D, propodus and dactylus of left P3; E, distal spines of propodus of left P3; F, coxa 5; G, distal half of left P7; H, distal spines of propodus of left P7.

*Telson*: elongate, cleft for 0.60 of its length, each lobe with 1 apical spine paired with 1 small seta, and 4 dorsolateral spines which are all in a row.

Variations in type material. The propodus of pereopod 7 was sometimes devoid of posterior spines in paratypes (from the Falkland Islands) smaller in body size than the holotype.

Colour pattern. unknown.

Size. Up to 31 mm.

**Distribution and depth range.** Falkland Islands, Burdwood Bank (present material), Îles Kerguelen (De Broyer 1983, as *P. coatsi*), 55–470 m.

Biology. This species is at least a facultative scavenger, as it enters baited traps in large swarms.

**Remarks.** The specimens of *Pseudorchomene coatsi* from Îles Kerguelen illustrated by De Broyer (1983) are identified as *P. debroyeri* **sp. n.** based on their morphological similarity. However, this would require genetic confirmation, by comparing DNA sequences with the type specimens from the distant Magellan region.

#### Pseudorchomene lophorachis sp. n.

(Figs 17-22)

**Type material.** R/V "Polarstern" cruise ANT XXI-2 (BENDEX), Eastern Weddell Sea, sta. 288–1, 72°47.58'S 19°29.86'W, 847 m, Fish Trap, 31.xii.2003–03.i.2004: 1 HOLOTYPE [sex undetermined (sex determination impossible without full dissection); no oostegites observed, 14.5 mm, right gnathopod 1 and left uropod 1 dissected but not mounted] stored in 96% ethanol, RBINS, INV. 100954, Specimen (HOLOTYPE) Id with corresponding Gen-Bank Accession number: Pn–WS847 (GU109238) — R/V "Polarstern" cruise ANT XXI-2 (BENDEX), Eastern Weddell Sea, sta. 288–1, 72°47.58'S 19°29.86'W, 847 m, Fish Trap, 31.xii.2003–03.i.2004: 1 PARATYPE [sex undetermined (sex determination impossible without full dissection); no oostegites observed, stored in 96% ethanol, RBINS, INV. 10954. — R/V "Polarstern" cruise ANT–XXII/3 (ANDEEP III), South of South Orkney Islands, sta. 150–7, 61°48'S 47°27'W, 1943 m, Agassiz trawl, 20.iii.2005: 1 female PARATYPE, 18 mm, stored in 96% ethanol, Specimen Id with corresponding GenBank accession number: Pn–0304072 (HM054054) [ZMH-43141]. — R/V "Polarstern" cruise ANT–XXII/3 (ANDEEP III), South of South Orkney Islands, sta. 150–7, 61°48'S 47°27'W, 1943 m, Agassiz trawl, 20.iii.2005: 4 PARATYPES stored in 96% ethanol and 1 PARATYPE dissected and mounted on 15 slides in Euparal [ZMH-43142], 10 PARATYPES, Specimen Ids with corresponding GenBank accession numbers: Pn–0510077 (HM054055), Pn–SS1943 (GU109253) [ZMH-43143].

Type locality. South of South Orkney Islands, 61°48'S 47°27'W, 1943 m.

Etymology. Lophorachis is a noun in apposition formed by combining the Greek nouns  $\lambda \delta \varphi \circ \zeta$ , hill, and  $\varphi \alpha \chi \circ \zeta$ , backspine. The name refers to the low posterodorsal protuberances of the body segments.

**Diagnosis.** Somites of pereon and pleosome with small posterior humps. Mandibular palp inserted well proximal to molar process. Molar process broad. Gnathopod 1: basis anterior margin convex, palm oblique, basis  $3.5 \times 1$ , ischium 9 x, merus 7 x, carpus 7.5 x, propodus  $8.5 \times as$  long as wide. Gnathopod 2: carpus 2.3 x as long as wide. Pereopod 3: propodus with about 11 spines or pairs of spines (which are well developed). Pereopod 3-7: on propodus, broadest spine of each pair or triplet acute. Coxa 4 rounded posteroventrally. Pereopod 5: coxa very slightly longer than broad; basis strongly expanded; merus with setae posteriorly and one fairly slender posterodistal spine. Ratio length/width of merus of pereopod 5-7: 1.3; 1.8; 1.9. Ratio length/width of carpus of pereopod 5-7: 1.8; 2.4; 2.3. Posterodistal angle of carpus of pereopod 5-7 with spines of normal length and stoutness. Pereopod 7: anterior margin of carpus normally spinose, posterior margin of carpus and propodus with posterodistal spines only. Epimeron 3 posteriorly regularly rounded. Uropod 3 with medial margin of both rami with many long setae, with inner ramus not reaching tip of article 1 of outer ramus.

Description. Based on PARATYPES from R/V "Polarstern" cruise ANT-XXII/3 (ANDEEP III), South of South Orkney Islands, sta. 150-7, 61°48'S 47°27'W, 1943 m.

*Body* without dorsal carina; somites of pereon and pleosome with small posterior humps. *Head* with lateral cephalic lobes broadly rounded.

Eyes occupying the most of anterior part of head, much longer than broad, lower part much broader than upper part, distinctly concave anteriorly, nearly straight posteriorly, dark, with fully developed ommatidia.

Antenna 1 slightly shorter than antenna 2; major flagellum 13-articulate, with first article 0.4 x as long as entire

flagellum; accessory flagellum 5-articulate, with article 1 elongate, slightly longer than sum of 4 distal articles combined.

Antenna 2 about 0.1 x as long as body; peduncular articles 3 to 5 not enlarged, with brush of setae; flagellum 27-articlulate; calceoli absent.

*Mouthparts* forming a quadrate bundle. Epistome carinate, scarcely produced, terminating in small blunt tooth; upper lip broadly rounded. slightly overreaching epistome.

*Mandible*: incisor process, cutting edge smooth except for small blunt denticle on each side, lateral and medial borders parallel; lacinia mobilis present on left side only, narrowly cylindrical (finger-like), slightly curved, slightly dilated distally with 3 dentiform processes (1 strong and 2 weak); 3 small raker spines and a elongate patch of short setules present between incisor and molar processes; molar process broad, elliptic to subovate, transversally ridged and triturative; lateral setigerous crest arising from proximal 0.3 of molar process; palp 3-articulate, attached mid-way, well proximal to molar process; article 1 without setae, article 2 longest with row of 12 strong distal and sub-distal A2-setae, article 3 of palp 0.65 x as long as article 2, 4.2 x as long as wide, with 2 proximal A3-setae, a row of 22 D3-setae on distal 0.6 (these setae are shorter than width of article 3), and 2 E3-setae.

*Maxilla 1*: inner plate very elongate, very narrow distally, with 2 stout setae in truly distal position; outer plate with 11 blade-shaped spines (in 7/4 arrangement), which are denticulate on one side; palp 2-articulate, broad with distal row of 9 cuspidate spines anteriorly followed by a stout antero-distal flag seta.

Maxilla 2: plates very narrow, tapering; inner plate much shorter and slightly narrower than outer plate.

*Maxilliped*: inner and outer plates well developed; inner plate narrow, about half the length of outer plate, with well-developed posteromedial row of strong setae, with 3 apical nodular spines and 1 anterodistal stout seta; outer plate reaching tip of article 2 of palp, with lateral double row of medium setae, 2 distal large stout blunt spines, a medial row of 19 much smaller low nodular spines, and 8 small slender isolated facial spines; dactylus well developed.

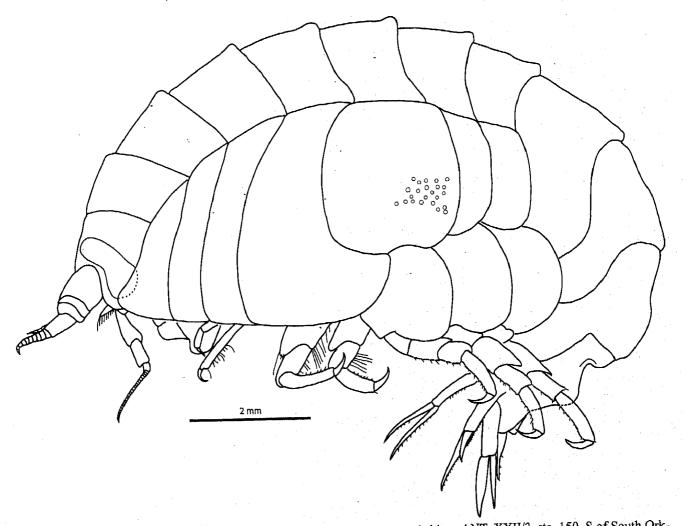


FIGURE 17. Pseudorchomene lophorachis sp. n., paratype, female, 18 mm, habitus, ANT-XXII/3, sta. 150, S of South Orkney Islands.

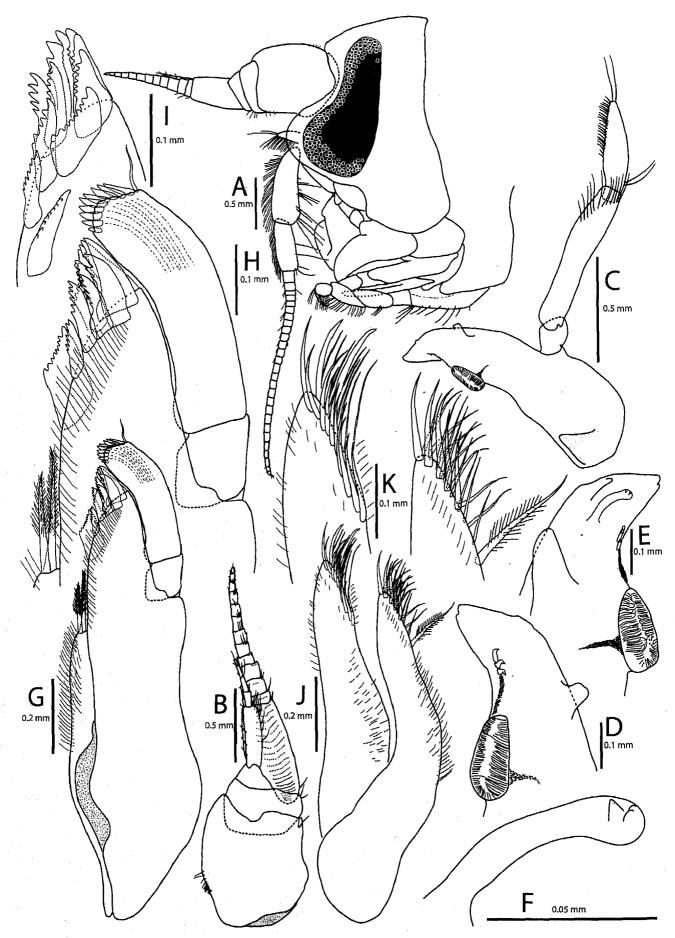


FIGURE 18. Pseudorchomene lophorachis sp. n., paratype, female, 18 mm, ANT-XXII/3, sta. 150, S of South Orkney Islands. A, head with appendages; B, left antenna in medial view; C, right Md; D, tip of right Md; E, tip of left Md; F, lacinia mobilis; G, left Mx1; H, tip of left Mx1; I, tip of right Mx1; J, right Mx2; K, tip of right Mx2.

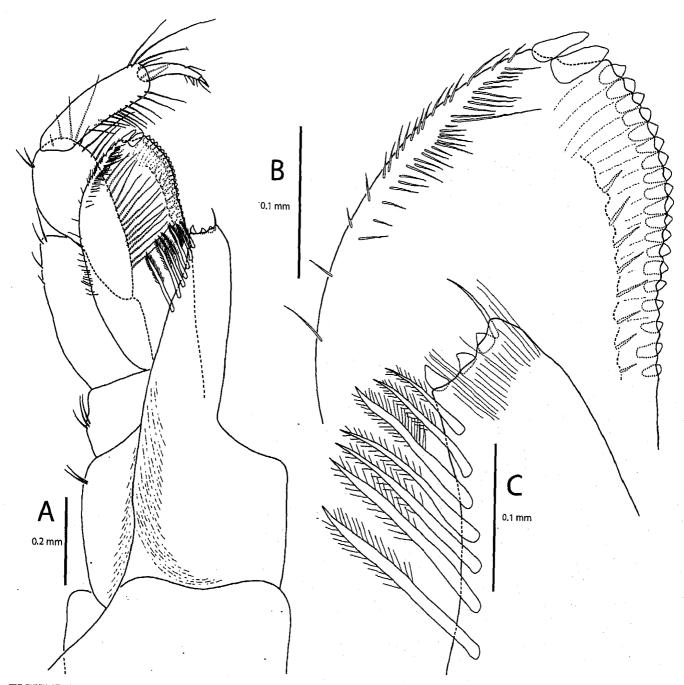


FIGURE 19. Pseudorchomene lophorachis sp. n., paratype, female, 18 mm, ANT-XXII/3, sta. 150, S of South Orkney Islands. A, Mxp (left inner plate not shown); B, left outer plate; C, right inner plate.

Gills: long accessory process on gill of percopods 5-6; gill of percopod 7 well developed and posteriorly pointed.

Oostegites: linear, from gnathopod 2 to percopod 5.

Gnathopod 1: subchelate; coxa large but slightly shorter than coxa 2, externally visible, triangular, with anterior and posterior margins weakly concave and strongly divergent, ventral border broad and weakly convex; all articles except dactylus extremely elongate; basis anteriorly strongly convex and posteriorly straight, with many long setae along anterior margin, about  $3.5 \times as$  long as wide; ischium linear,  $9 \times as$  long as wide; merus linear,  $7 \times as$  long as wide, slightly shorter than ischium and as long as carpus; carpus linear,  $7.5 \times as$  long as wide; propodus linear,  $8.5 \times as$  long as wide and slightly shorter than carpus, palm oblique and minutely denticulate; dactylus well developed.

Gnathopod 2: minutely chelate coxa large but slightly shorter than coxa 3, subrectangular; ischium 3.7 x as long as wide; carpus 2.3 x as long as wide, 2.2 x as long as propodus, anterior margin with dense row of very short setae beyond midlength, and many long setae distally; propodus strongly convex anteriorly with many long setae, straight posteriorly with many very short setae, palm with a cavity and an extended inner dentate basket; dactylus very short, denticulate, reaching corner of palm.

*Pereopod 3*: coxa large, about as long as coxa 4, subrectangular, posterior margin slightly concave; ischium, merus and carpus with many long setae posteriorly; merus slightly expanded anteriorly, 2.6 x as long as wide; carpus 2.6 x as long as wide and 0.67 x as long as merus; propodus 4.9 x as long as wide, 1.4 x as long as carpus, with 11 well-developed spines (or pairs of spines) posteriorly, the largest spines of each group acute and with accessory branch; dactylus normally developed, curved, with long unguis, 0.41 x as long as propodus.

*Pereopod 4*: coxa deeper than wide, posteroventral lobe large, posteroventral corner of lobe regularly rounded (without angular discontinuity); ischium, merus and carpus with many long setae posteriorly; merus slightly expanded anteriorly, 2.4 x as long as wide; carpus 2.0 x as long as wide and 0.56 x as long as merus; propodus 4.6 x as long as wide, 1.4 x as long as carpus, with 11 well-developed spines (or pairs of spines) posteriorly, the largest spines of each group acute and with accessory branch; dactylus normally developed, curved, with long unguis, 0.39 x as long as propodus.

*Pereopod 5*: coxa very slightly longer than broad, weakly bilobate, posterior lobe slightly produced ventrally, 1.5 x as long as basis; basis strongly expanded posteriorly, about as long as broad, with 10 short spines or groups of short spines anteriorly, 6 very weak crenellations posteriorly, each associated with tiny setule, posteroventral lobe well developed and broadly rounded; ischium with 3 anterior groups of short spines, the distal one associated with long seta; merus expanded, 1.3 x as long as broad, anterior margin straight, posterior margin rounded, bearing 5 long setae and 1 distal medium-sized spine; carpus 1.8 x as long as broad, with 2 posterodistal spines of normal length and stoutness; propodus 4.2 x as long as broad, 1.4 x as long as carpus, with 6 pairs of acute spines anteriorly, each spine with an accessory branch (except those of distal pair); dactylus normally developed, curved, with long unguis, 0.42 x as long as propodus.

*Pereopod 6*: coxa anterior margin slightly concave, posterior margin convex, weakly bilobed, shorter than coxa 5, 1.6 x as long as broad, 0.9 x as long as basis; basis longer than basis of pereopod 5, expanded posteriorly, 1.4 x as long as broad, with 9 short spines or groups of short spines anteriorly, 8 very weak crenellations posteriorly, each associated with tiny setule, posteroventral lobe well-developed, broadly rounded; ischium-dactylus combined slightly longer than in pereopod 5 and as long as in pereopod 7; ischium with 4 anterior groups of articulated structures including a short spine and/or a long seta; merus weakly expanded, 1.8 x as long as broad, anterior margin straight, posterior margin weakly curved, bearing 6 isolated small spines of normal stoutness; carpus 2.4 x as long as broad, with 1 short seta and 2 spines of normal length and stoutness on posterodistal corner; propodus 4.8 x as long as broad, 1.4 x as long as carpus, with 9 acute spines (or pairs of spines) anteriorly, each spine with an accessory branch (except those of distal pair); dactylus normally developed, curved, with long unguis, 0.39 x as long as propodus.

Percopod 7: coxa regularly rounded, shorter than coxa 6, as long as broad, 0.5 x as long as basis; basis longer than basis of percopod 6, expanded posteriorly, 1.4 x as long as broad, with 14 short spines or groups of short spines anteriorly, 10 very weak crenellations posteriorly, most associated with tiny setule, posteroventral lobe low and broadly rounded; ischium with 4 groups of 1 or 2 short spines on anterior margin, without long setae; merus weakly expanded, 1.9 x as long as broad, anterior margin straight, posterior margin weakly convex bearing 7 isolated small spines of normal stoutness; carpus 2.3 x as long as broad, with number and strength of anterior spines normal, with 3 posterodistal spines of normal length and stoutness and no other posterior spines; propodus 4.6 x as long as broad, 1.4 x as long as carpus, with 9 acute spines (or pairs of spines) anteriorly, each spine with an accessory branch (except those of distal pair), without posterior spines; dactylus normally developed, curved, with long unguis, 0.36 x as long as propodus.

*Epimeron 1*: anteroventral corner subquadrate, slightly produced; posteroventral corner regularly rounded; ventral margin straight; posterior margin slightly convex.

*Epimeron 2*: anteroventral corner very broadly angular, posteroventral corner bluntly subquadrate; ventral margin slightly concave; posterior margin straight.

Epimeron 3: posteroventral corner regularly rounded; ventral and posterior margins slightly convex.

Urosomite 1 with a deep dorsal depression flanked on each side by lateral carina and followed by a prominent regularly rounded dorsal hump.

Uropod 1: peduncle 1.5 x as long as inner ramus, with 12 small stout lateral spines and 16 medium-sized slender spines; outer ramus almost as long as inner ramus, with 7 stout and medium-sized lateral spines and no medial spines; inner ramus with 3 lateral spines and 9 medial spines, all medium-sized.

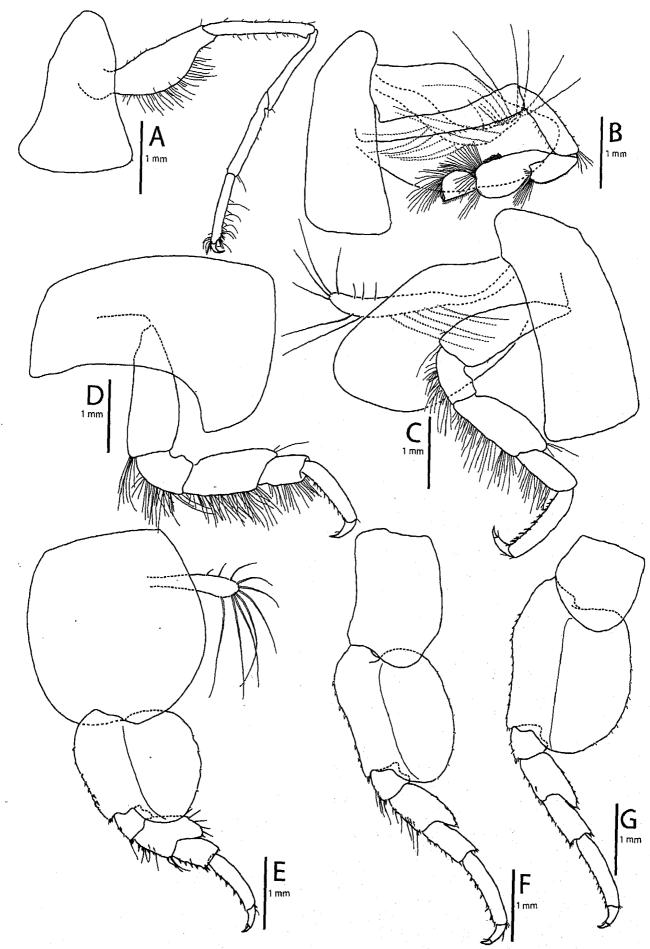
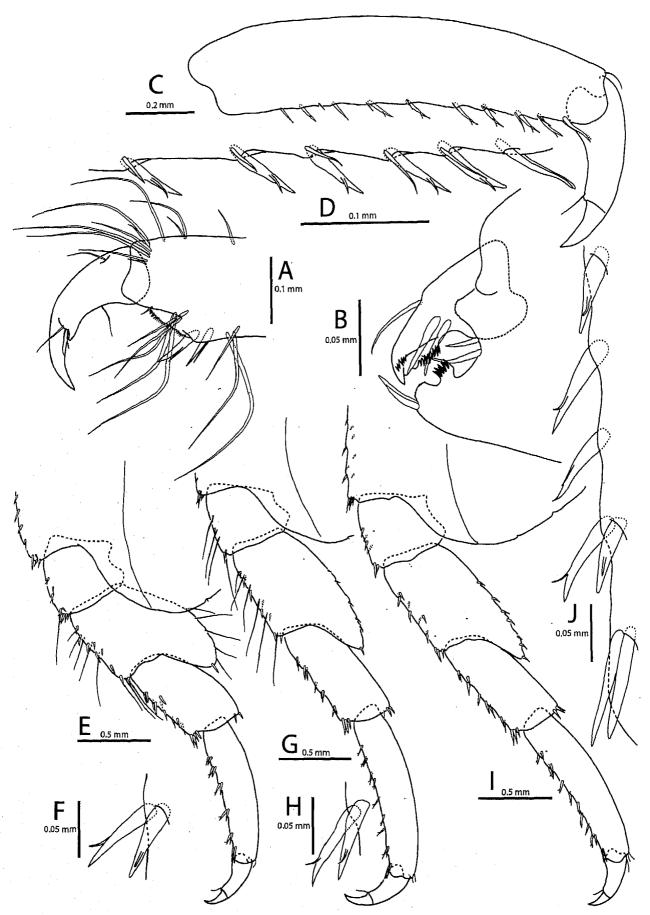


FIGURE 20. Pseudorchomene lophorachis sp. n., paratype, female, 18 mm, ANT-XXII/3, sta. 150, S of South Orkney Islands. A, left Gn1; B, left Gn2; C, right P3; D, right P4; E, left P5; F, left P6; G, left P7.



**FIGURE 21.** Pseudorchomene lophorachis **sp. n.**, paratype, female, 18 mm, ANT-XXII/3, sta. 150, S of South Orkney Islands. A, tip of chela of left Gn1; B, tip of chela of left Gn2; C, propodus and dactylus of right P3; D, distal spines of propodus of right P3; E, distal half of left P5; F, penultimate pair of spines of propodus of left P5; G, distal half of left P6; H, penultimate pair of spines of propodus of left P7.

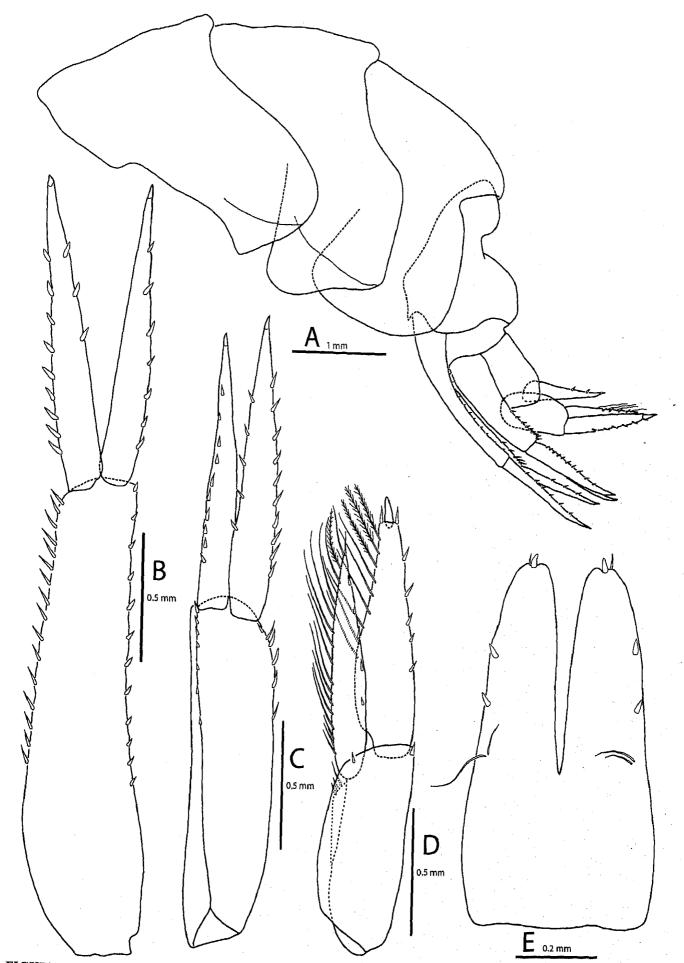


FIGURE 22. Pseudorchomene lophorachis sp. n., paratype, female, 18 mm, ANT-XXII/3, sta. 150, S of South Orkney Islands. A, pleon; B, left U1; C, right U2; D, left U3; E, telson.

Uropod 2: peduncle 1.2 x as long as inner ramus, with 7 small to very small stout lateral spines and 6 mediumsized slender spines (all spines on distal 0.3); outer ramus 0.9 x as long as inner ramus, with 10 stout and mediumsized lateral spines and no medial spines; inner ramus without notch, with 5 lateral spines and 10 medial spines, all medium-sized.

Uropod 3: peduncle ordinary,  $0.78 \times as$  long as outer ramus; outer ramus with article 1 with 6 lateral spines, 9 medial long plumose setae and distomedial spine, with article 2 0.13 x as long as article 1; inner ramus reaching 0.85 of article 1 of outer ramus, with 5 lateral spines, long plumose setae all along medial margin and 2 apical setae.

*Telson*: elongate, cleft for 0.57 of its length, each lobe with 1 apical spine paired with 1 small seta, dorsolateral spines.

Colour pattern. Unknown.

Size. 18 mm.

Distribution and depth range. Scotia Sea and Weddell Sea, 847-1943 m.

**Biology.** Carrion is part of the diet of the species since specimens were captured occasionally by means of fish traps, but it is not known if it is an obligatory or a facultative scavenger. The remarkably elongated gnathopod 1 (even more elongated than in *P. coatsi* and *P. debroyeri*) might suggest a specialized feeding behaviour.

**Remarks.** *Pseudorchomene lophorachis* is similar to *P. coatsi* and *P. debroyeri* but has the first gnathopod characterized by an elongated and slender ischium, merus and carpus, while only the ischium and carpus are elongate in the two other species. *P. lophorachis* bears rounded dorsal humps, which are absent in *P. coatsi* and *P. debroyeri*.

The holotype deposited at the Royal Belgian Institute of Natural Sciences is identical to the illustrated specimens: it has small posterodorsal humps on body segments, coxa 1 is adz-shaped, and gnathopod 1 is immensely elongated.

## Pseudorchomene plebs (Hurley, 1965)

(Figs. 23-26)

Orchomenella plebs Hurley, 1965a: 109, figs. 1-2.

Orchomene plebs. — Thurston, 1974b: 59. — Andres, 1979: 96. — Andres, 1983: 203-204.

Abyssorchomene plebs. — De Broyer, 1983: 146–149, fig. 12a. — Andres, 1990: 135, 137, fig. 267 — De Broyer et al., 2007: 161 (ubi syn.).

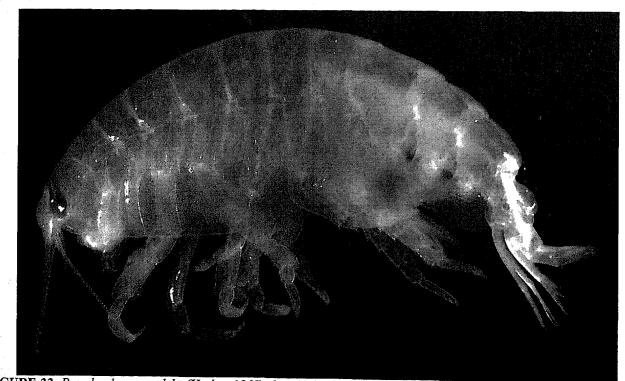


FIGURE 23. Pseudorchomene plebs (Hurley, 1965), female, habitus, size unrecorded. ANT-XXIII/8 sta. 625-1/625-2, Elephant, 60°59'S 055°57'W, 280-322 m, 23-25.xii.2006, (specimen not preserved). Note the reddish/brownish colour of the eye.

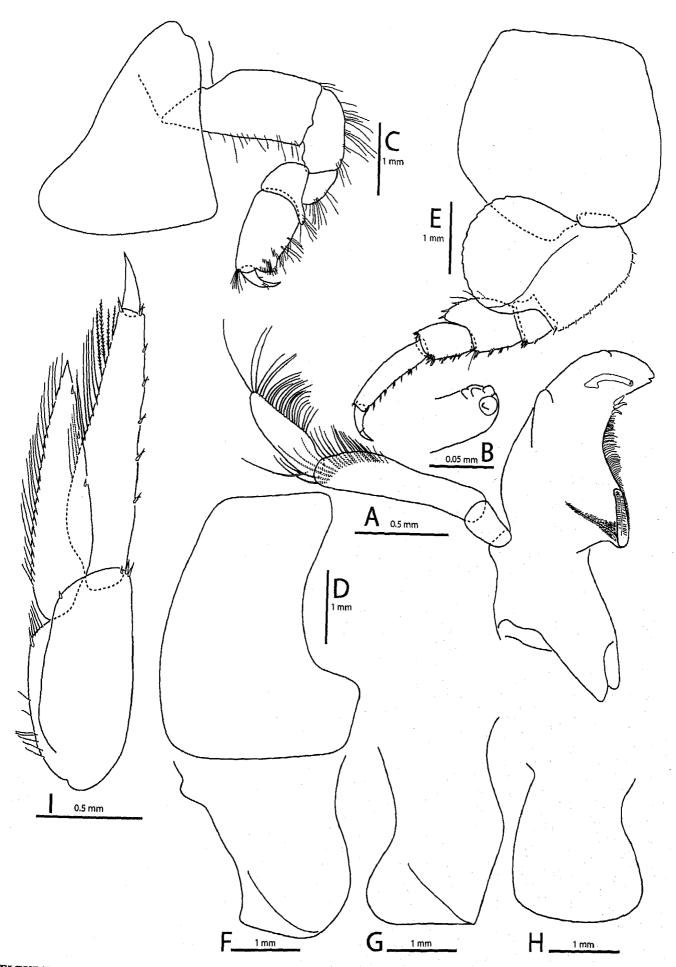


FIGURE 24. Pseudorchomene plebs (Hurley, 1965), female. 24 mm, ANT-XXIII/8 sta. 713-1, Larsen B. A, left Md; B, tip of lacinia mobilis; C, left Gn1; D, left coxa 4; E, right P5; F, left Ep1; G, left Ep2; H, left Ep3; I, left U3.

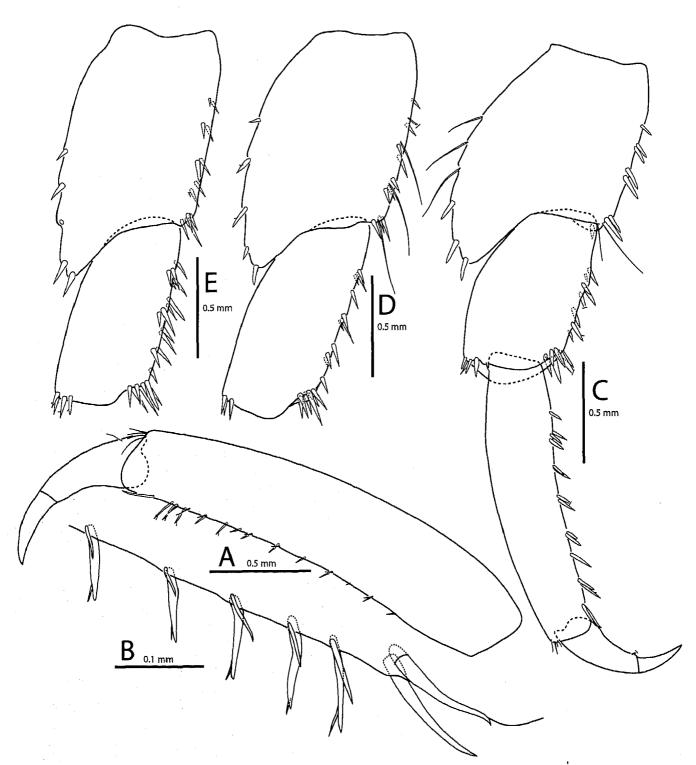


FIGURE 25. Pseudorchomene plebs (Hurley, 1965), female. 24 mm, ANT-XXIII/8 sta. 713-1, Larsen B. A, propodus and dactylus of left P3; B, distal spines of propodus of right P3; C, distal half of right P5; D, merus and carpus of right P6; E, merus and carpus of right P7.

**Type material.** Not seen. "HOLOTYPE No. 112416 deposited in the U.S. National Museum, length 20 mm; also PARATYPES. PARATYPES also deposited in N.Z. Oceanographic Institute, Dominion Museum, and British Museum (Nat. Hist.). The material described is from Station A.32, "White Island, 15 Nov. 1961." (Hurley 1965a).

Material examined. Expedition ARC94, sta. NA62, King George Island, Admiralty Bay, 62°08'S 58°27'W, 470 m, 29.xii.1963–02.i.1964: about 35 specimens, RBINS, INV. 100980 (2 tubes) — R/V "Polarstern" cruise ANT-XV/3 (EASIZ II), Atka Bay, sta. 280/284, Trap 13, 70°27.4'S 07°55.9'W, 550 m, baited trap, 28–29.ii.1998: 5 specimens, Specimen Id with corresponding GenBank accession number: AP-31100710 (HM054000), RBINS, INV. 100956. — R/V "Polarstern" cruise ANT-XIX-5 (LAMPOS), sta. 191–1, Saunders Island, 57°41'S 26°24'W,

270 m, baited trap, 15.iv.2002: 29 specimens, Specimen Ids with corresponding GenBank accession numbers: AP-SS270 (GU109258), AP-08100719 (HM053987), AP-08100722 (HM053988), AP-0506081 (HM053989), RBINS, INV. 100958 (5 tubes). — R/V "Ivan Papanin" cruise BELARE, Crown Bay, 70°S 23°E, 230 m, baited trap, December 2008, 10 specimens, Specimen Id with corresponding GenBank accession number: AP-23110992 (JQ423245), RBINS, INV. 100960. — R/V "Polarstern" cruise ANT-XXIII/8, Larsen B, sta. 698-1, 65°59'S 60°24'W, 383 m, Amphipod Trap, 11-12.i.2007: 1 specimen, Specimen Id with corresponding GenBank accession number: AP-LB383 (GU109233), RBINS, INV. 100959. — R/V "Polarstern" cruise ANT-XXIII/8, Larsen B, sta. 713-1, 65°06'S 60°46'W, 299 m, amphipod trap, 18-19.i.2007. 1 female, dissected and mounted on 12 slides in Euparal, RBINS, INV.100989/1-12.

**Diagnosis.** Eye dark brownish/reddish when alive. Somites of pereon and pleosome without posterior humps. Mandibular palp inserted just proximal to molar process. Molar process narrow. Gnathopod 1: basis, anterior margin straight, palm transverse, with basis 2.2 x, ischium 1.9 x, merus 1.5 x, carpus 0.8 x, propodus 1.8 x as long as wide. Gnathopod 2: carpus 2.6 x as long as wide. Pereopod 3: propodus with about 14 spines or pairs of spines (which are small). Pereopod 3–7: on propodus, broadest spine of each pair or triplet with tip acute to subacute. Coxa 4 angular posteroventrally. Pereopod 5: coxa as long as broad; posterior half of basis extremely expanded; merus with setae posteriorly and a few posterodistal fairly slender spines. Ratio length/width of merus of pereopods 5–7: 1.4; 1.7; 1.8. Ratio length/width of carpus of pereopods 5–7: 1.8; 2.3; 2.1. Posterodistal angle of carpus of pereopods 5–7 with spines of normal length and stoutness. Pereopod 7: carpus anterior margin normally spinose, posterior border of carpus and propodus with posterodistal spines only. Epimeron 3 posterior margin regularly rounded. Uropod 3 with medial margin of both rami with many long setae, inner ramus not reaching tip of article 1 of outer ramus.



FIGURE 26. Swarms of *Pseudorchomene plebs* (Hurley, 1965) and one *Natatolana* sp., scavenging on dead fish in baited trap, ANT-XXIII/8 sta. 625-1/625-2, Elephant Island, trap deployed on 23.xii.2006 and hauled up on 25.xii.2006.

Maximal length. Up to 25 mm (Dauby et al. 2001).

Distribution. Circum-Antarctic, as far north as South Orkneys and Macquarie, 0–2889 m (De Broyer et al. 2007; Havermans et al. 2011), mostly between 400–800 m (De Broyer et al. 2004).

**Biology.** "... collected by midwater trawls, indicating a bentho-pelagic way of life. Stomach and gut contents varied from one individual to another. Crustacean parts (eyes or ommatidia, appendages and chitinous plates) were frequent. Some individuals contained fragments of carrion (muscles), while others had ingested diatoms. It is worth noting that *A. plebs* is more commonly found in baited traps (from 1 to 98% of attracted amphipods) than *A. rossi* (only few specimens), which could indicate a preference for scavenging" (Dauby *et al.* 2001). While it is not an obligatory scavenger, *P. plebs* often enters baited traps in considerable swarms (hence the name of the species) (Fig. 26), sometimes of thousands of specimens (Rakusa-Suszczewski 1982; De Broyer & Klages 1990; d'Udekem d'Acoz & Robert 2008, Havermans & Robert *in press*). Such swarms are able to devour fish carcasses in three days, leaving perfectly clean skeletons (Fig. 27).

**Remarks.** In Figure 2 of Hurley (1965a), the illustration labelled 'epimeron 3' is actually (left) epimeron 2 and that labelled 'epimera 1–2' shows (left) epimera 1 and 3. Coxa 4 of the same Hurley's illustration does not look as angular posteriorly as in specimens studied herein.

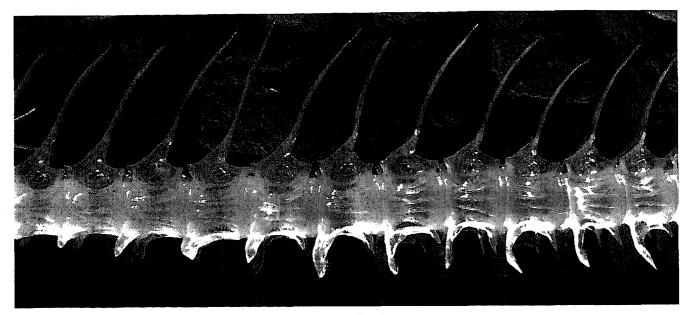


FIGURE 27. Fish skeleton from a baited trap, cleaned up by swarms of *Pseudorchomene plebs* (Hurley, 1965) (and by a few *Natatolana* spp.); ANT-XXIII/8 sta. 625-1/625-2, Elephant Island, trap deployed on 23.xii.2006 and hauled up on 25.xii.2006.

**Pseudorchomene rossi (Walker, 1903)** (Figs. 28–30)

Orchomenopsis rossi Walker, 1903: 45, pl. 18-23.
Orchomenopsis chilensis f. rossi. — Schellenberg, 1926: 287-290, fig. 26.
Orchomenella rossi. — Hurley, 1965b: 15, figs. 1-2.
Orchomene rossi. — Thurston, 1974b: 59-60. — Andres, 1979: 96-97. — Andres, 1983: 204-205.
Abyssorchomene rossi. — De Broyer, 1983: 150-152, fig. 12a, photos 4-9, 15-16. — Andres, 1990: 135, 137, fig. 266 — De Broyer et al., 2007: 162 (ubi syn.).

**Type material.** Not seen. "Cape Adare. Lat. 78°35'S; Feb. 18, 1900; near surface. Many specimens" (Walker 1903). According to Hurley (1965b), the SYNTYPES are deposited in the British Museum (current name: Natural History Museum, London).

Material examined. Expedition ARC94, sta. NA62, King George Island, Admiralty Bay, 62°08'S 58°27'W, 470 m, 29.xii.1963–02.i.1964: 3 small (about 10 mm) specimens, RBINS, INV. 100983. — R/V "Polarstern" cruise ANT-XXIII/8, Larsen B, sta. 698–1, 65°59.99'S 60°24.90'W, 383–390 m, baited trap, 11–12.i.2007: 1 male dissected and 4 other specimens, RBINS, INV. 100981. — R/V "Polarstern" cruise ANT-XV/3 (EASIZ II), Atka Bay,

sta. 280/284, Trap 13, 70°27.4'S 07°55.9'W, 550 m, baited trap, 29.ii.1998: 1 specimen, Specimen Id with corresponding GenBank accession number: AR-3110078 (HM054002), RBINS, INV. 100957. — R/V "Polarstern" 31.xii.2003-03.i.2004: 1 specimen, Specimen Id with corresponding GenBank Accession number: AR-1010076 (HM054001), RBINS, INV. 100973. — R/V "Polarstern" cruise ANT-XXIII/8, sta. 698-1, 65°59'S 60°24'W, 383 number: AR-I19 (HM054003), RBINS, INV. 100982.

Type locality. Antarctica, Cape Adare, 78°35'S, no longitude given, near surface (Walker 1903).



FIGURE 28. Pseudorchomene rossi (Walker, 1903), female, habitus, size unrecorded. ANT-XXIII/8 sta. 698-1, Larsen B. Note the black colour of the eye.

**Diagnosis.** Eye black when alive. Somites of pereon and pleosome without posterior bumps. Mandibular palp inserted just proximal to molar process. Molar process narrow. Gnathopod 1: basis, anterior margin straight, palm transverse, basis 2.3 x, ischium 1.4 x, merus 1.4 x, carpus 0.9 x, propodus 1.8 x as long as wide. Gnathopod 2: carpus 3.8 x as long as wide. Pereopod 3: propodus with about 12 spines or pairs of small spines. Pereopod 3-7: on propodus, broadest spine of each pair or triplet with tip very blunt. Coxa 4 angular posteroventrally. Pereopod 5: coxa as long as broad; basis strongly expanded; merus posteriorly with short and stout spines only. Ratio length/ width of merus of pereopods 5-7: 1.2; 1.3; 1.3. Ratio length/width of carpus of pereopod 7: carpus, anterior margin normally spinose, posterior margin of carpus and propodus with postero-distal spines only. Epimeron 3 with large and very blunt tooth posterioventrally. Uropod 3: outer ramus medial margin without setae, inner ramus, medial margin with a few short setae, inner ramus reaching or overreaching tip of article 1 of outer ramus.

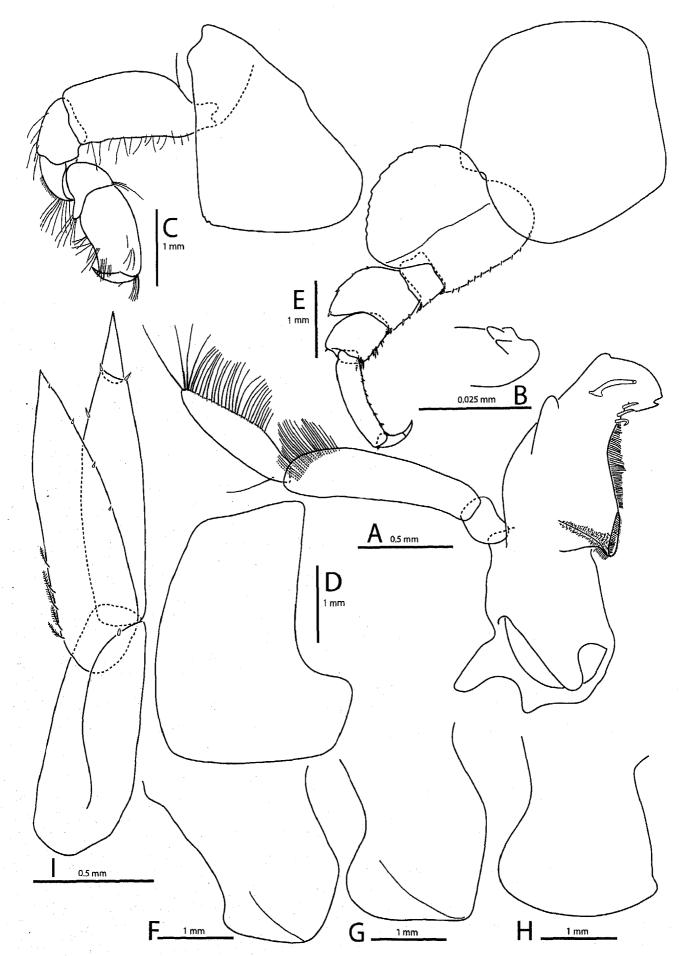


FIGURE 29. Pseudorchomene rossi (Walker, 1903), male, 24 mm, ANT-XXIII/8 sta. 698-1, Larsen B. A, left Md; B, tip of lacinia mobilis; C, right Gn1; D, left coxa 4; E, right P5; F, left Ep1; G, left Ep2; H, left Ep3; I, left U3.

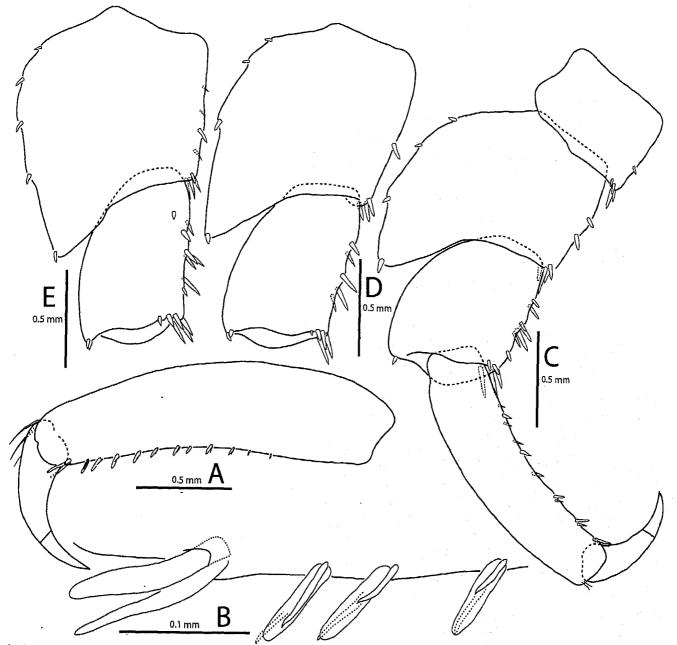


FIGURE 30. Pseudorchomene rossi (Walker, 1903), male, 24 mm, ANT-XXIII/8 sta. 698-1, Larsen B. A, propodus and dactylus of left P3; B, distal spines of propodus of left P3; C, distal half of right P5; D, merus and carpus of right P6; E, merus and carpus of right P7.

Maximal length. Up to 40 mm (Schellenberg 1926; Dauby et al. 2001).

**Distribution.** Circum-Antarctic, as far north as South Georgia (De Broyer *et al.* 2007), 7–1453 m (De Broyer *et al.* 2007) but mostly 200–600 m (De Broyer *et al.* 2004).

**Biology.** Occurs in water column as well as on benthic substrates (Dauby *et al.* 2001). Sometimes in large number under pack ice (Kaufmann *et al.* 1993, 1995). "Stomachs of benthic specimens were dominated by fluidish organic matter spotted with oily droplets, likely to be flesh at various stages of digestion; some other items are found, but in small quantity: sponge spicules, crustacean appendages and diatoms. Stomachs of pelagic individuals have a totally different content. While flesh was still present (about 25%), copepod remains formed the bulk (55%) of the diet; polychaete setae constitute a third, less common, item. The exact trophic position of *A. rossi* is unclear. Although an apparently selective copepod predator within the water column, it appears to be able to migrate down to the bottom to scavenge on different materials" (Dauby *et al.* 2001).

**Remarks.** In baited traps, *P. rossi* is sometimes found mixed with *P. plebs*, although this co-occurrence is rather infrequent (Thurston 1974b). The two species have the same general appearance, which can make their separation very time consuming in preserved samples. However, when live sorting, the species can be separated easily by eye colour: black in *P. rossi*, dark brown/reddish in *P. plebs*.

## Discussion

Familial and subfamilial assignation of Antarctic and sub-Antarctic 'orchomenids'. In the past, 'orchomenids' have been divided in several genera (e.g. De Broyer 1984) or merged together in the supergenus Orchomene (e.g. Barnard & Karaman 1991), but until recently have always been considered informally as forming a clade. In a process initiated by Hurley (1963), starting slowly but accelerating dramatically during the last two decades (Lowry & Stoddart 1992, 1997, ..., 2011a), the family Lysianassidae (now elevated to the rank of superfamily: Lysianassoidea) has been split into more than twenty families and subfamilies. As a result, 'orchomenids' are now scattered across different taxa of familial rank. De Broyer et al. (2007) placed Abyssorchomene in Uristidae Hurley, 1963 and the remaining genera, Allogaussia, Falklandia, Orchomene, Orchomenella, Orchomenopsis, Orchomenyx, Pseudorchomene in Lysianassidae Dana, 1849 (subfamily Tryphosinae Lowry & Stoddart 1997). The arguments invoked for this fragmentation of the Lysianassidae, were purely pheno-morphological and not always very consistent, often being based on insufficiently discriminating character states as the disposition of spines on the outer plate of maxilla 1. Lowry and Stoddart (2003) admitted that "until the polyphyly of the Lysianassidae is resolved it is not possible to diagnose the family Uristidae". In their recent molecular studies, Havermans et al. (2010, 2011) have challenged the conclusions of these typological classifications. In addition, they have shown that all Antarctic/sub-Antarctic 'orchomenids' and some deep-sea 'orchomenids' from other oceans belong to the same clade. Since the type genus of the subfamily Tryphosinae (Tryphosa) is traditionally considered as an 'orchomenid' (Barnard & Karaman 1991) and since the type genus of the family Uristidae (Uristes) has never been associated with Orchomene, it is proposed herein to transfer Pseudorchomene to the Tryphosinae, where it joins other 'orchomenids'. However, the molecular analysis of Tryphosa and Orchomene sensu stricto will be necessary to confirm the relative position of the (sub-)Antarctic 'orchomenid' clade and its alleged related species.

Generic arrangement and phylogenetic relationships of some Antarctic and sub-Antarctic 'orchomenids'. Chilton (1912) described Orchomenopsis coatsi from Coats Land, Weddell Sea, 290 m. He considered that gnathopod 1 of O. coatsi was so different from other species of Orchomenopsis G.O. Sars, 1891 that it should be transferred to another genus. However he refrained to take any formal action. It is Schellenberg (1926), who followed Chilton's (1912) suggestion, and erected Pseudorchomene for O. coatsi on the basis of specimens from Gauss Station, Davis Sea, from 385 m depth. Walker (1903) described Orchomenopsis rossi from the Ross Sea and K.H. Barnard (1932) transferred this species to the genus Orchomenella G.O. Sars, 1890. Hurley (1965a) described Orchomenella plebs from the Ross Sea. Lowry and Stoddart (1983) redescribed the genus Pseudorchomene and P. coatsi on the basis of the syntypes. De Broyer (1983) accurately described and illustrated a species from the sub-Antarctic Îles Kerguelen, which he believed to be P. coatsi. Finally, De Broyer (1984) transferred Orchomenella plebs and O. rossi to the genus Abyssorchomene De Broyer, 1984.

Molecular data by Havermans *et al.* (2010, 2011) showed the existence of an undescribed Antarctic *Pseudorchomene* (described herein as *P. lophorachis* **sp. n.**). Havermans *et al.* (2010, 2011) demonstrated that *P. coatsi* and *Pseudorchomene* sp. (described herein as *P. lophorachis* **n. sp.**) form a highly supported clade with the species named as *Abyssorchomene plebs* and *A. rossi*. Havermans *et al.* (2010, 2011) further demonstrated that *A. plebs* and *A. rossi* do not form a clade with the type species of the genus *Abyssorchomene* De Broyer, 1984: *Orchomenopsis chevreuxi* Stebbing, 1906. As such, *A. plebs* and *A. rossi* cannot remain in the genus *Abyssorchomene* and we herein transfer these species to the same genus as their sister group (sensu Havermans *et al.* 2010, 2011), the pair *P. coatsi* + *P. lophorachis*, rather than creating one more genus within the 'orchomenid' group. *P. debroyeri*, which was not included in previous genetic analyses, also proves to be nested within the *Pseudorchomene* cluster (Figure 1), confirming the validity of the previously assumed pattern of phylogenetic relationships within the 'orchomenid' clade.

A detailed redescription of *Abyssorchomene* falls out of the scope of the present paper. However, it must be pointed out that true *Abyssorchomene*, i.e. species belonging to the same clade as *A. chevreuxi* recognized by Havermans *et al.* (2010) do not have the dark pyriform eyes with fully developed ommatidia like *Pseudorchomene* spp., but instead have pale eyes without distinct ommatidia (fading in alcohol), which at least in one case are L-shaped. This difference can be observed in comparing the photographs of living individuals of *P. plebs* and *P. rossi* (Figs. 23, 28) with that of an undescribed *Abyssorchomene* species close to *A. scotianensis* (Fig. 31). On the other hand, *Abyssorchomene nodimanus* (Walker, 1903), which is an Antarctic shelf species with pyriform eyes and fully developed ommatidia, is genetically and morphologically excluded from *Pseudorchomene* and *Abyssorchomene* 

(Havermans et al. 2010). The remaining Antarctic and sub-Antarctic 'orchomenids' are currently scattered across the genera Allogaussia Schellenberg, 1926 (type species: Allogaussia paradoxa Schellenberg, 1926, Antarctic species), Falklandia De Broyer, 1985 (type species Orchomenopsis reducta Schellenberg, 1931, sub-Antarctic species), Orchomenella G.O. Sars, 1890 (type species = Anonyx minutus Krøyer, 1846, European species), Orchomenopsis, G.O. Sars, 1891 (type species = Orchomenopsis obtusa G.O. Sars, 1891, European species) and Orchomenyx De Broyer, 1984 (type species = Orchomenella macronyx Chevreux, 1905, Antarctic species). The molecular study of Havermans et al. (2010) has demonstrated that this generic arrangement is largely untenable, but at the same time, the data in hand are insufficient to allow reconstructing a satisfactory alternative. A stable and rational generic arrangement will require further molecular and morphological studies.



FIGURE 31. Abyssorchomene sp. n. aff. scotianensis (Andres, 1983), sex unknown, size unrecorded (specimen not isolated), habitus, ANT-XXIII/8, sta.706-7/706-8, Larsen B, 65°27'S 61°27'W, 828-833 m, 15-17.i.2007, RBINS, I.G. 31.070.

**Hypotheses on the evolution of the genus** *Pseudorchomene*. Molecular data clearly support *P. lophorachis* **sp. n.** and *P. debroyeri* **sp. n.** as new and distinct species, represented by monophyletic clusters, separated by genetic distances greater than 5% from their nearest congeners, *P. coatsi*, *P. plebs* and *P. rossi* (Fig. 1). Moreover, as discussed in the previous section, two species usually assigned to the polyphyletic short-handed genus *Abyssorchomene* (*P. rossi* and *P. plebs*) appeared to be genetically closely related to the *Pseudorchomene* group, with these five species clustering together. Specimens of *P. debroyeri* were separated by 7.8–9.0 % sequence divergence from *P. lophorachis* and by 7.9–9.6 % sequence divergence from *P. coatsi*, which is within the range of that previously documented for 'orchomenid' species (6.3–20.1 %, with a mean of 14.5 %; Havermans *et al.* 2011). Specimens of *P. lophorachis* were separated from *P. coatsi* with a minimum divergence of 5.7 %, the lowest value observed for any 'orchomenid' species. In contrast, the intraspecific variation did not exceed 1.1 % for *P. debroyeri* and 0.3 % for *P. lophorachis*, confirming the validity of both species despite the morphological variations observed in *P. debroyeri* concerning the spines on the propodus of P7.

Using a phenetic approach, *P. lophorachis* could have been classified in a new genus, as the elongation of one article of gnathopod 1 could be considered as sufficient to create a new genus. Nevertheless, this has to be rejected due to the low genetic divergence between pairs of *Pseudorchomene* species, which are clearly congeneric on this basis. Indeed, the distances are even lower than the average intrageneric interspecific distances amongst 'orchomenids'. The case of *P. lophorachis* is very similar to the one of *Falklandia reducta* (Schellenberg, 1931), as discussed by Havermans *et al.* (2010).

*P. coatsi* (Antarctic species) is morphologically extremely similar to *P. debroyeri* (sub-Antarctic species) but genetically closer to the morphologically distinct *P. lophorachis* (Antarctic species). This decoupling between morphological and genetic evolution might be explained by intense evolutionary pressure on *P. lophorachis* (possibly linked to trophic specialisation) in contrast with the other two species, which retained their plesiomorphic conditions (see below). The low genetic divergences between the Antarctic species *P. coatsi* and sub-Antarctic *P*.

debroyeri (7.8–9.6 %), might suggest a fairly recent speciation. Considering the rate of 1.5 % per million years of Quek et al. (2004), these two species may have speciated around 6 Myr ago, well after the onset of the Antarctic Circumpolar current (around 24 Myr ago) (Pfuhl & McCave 2005). Hence, the fragmentation of populations north and south of the Polar Front might have favoured speciation, leading to two morphologically similar species *P. debroyeri*, and the common ancestor of *P. coatsi* and *P. lophorachis*. *P. coatsi* and *P. lophorachis* could have speciated afterwards, in an environment with only loose and/or short-term barriers (e.g. isolation of populations in refuges during glacial maxima). During interglacial cycles and when occurring in sympatry again, *P. coatsi* could have retained its original trophic niche and plesiomorphic character states, whilst *P. lophorachis* may have adopted a new trophic specialisation inducing intense morphological changes. *P. plebs* and *P. rossi* exhibit profound differences in the shape of gnathopod 1 with other *Pseudorchomene*. Yet, there is a morphological line of evidence that all these species form a clade, supporting the molecular data. Indeed, they all exhibit a triangular or adz-shaped coxa 1, i.e. a character state unique among 'orchomenids'. This character state is herein considered as a probable synapomorphy, uniting long-handed and short-handed *Pseudorchomene* species.

Ecological and phylogenetic significance of morphological innovation in Pseudorchomene. In many non-Pseudorchomene lysianassoids recorded as feeding on carrion, there is either no elongation of gnathopod 1: e.g. Anonyx sarsi Steele, 1968 (see Steele 1968); Eurythenes gryllus (Lichtenstein, 1822) (see G.O. Sars, 1890-1895), Onisimus spp. (see G.O. Sars, 1890-1895), various Antarctic 'orchomenids', Tryphosa nana (Krøyer, 1846) (see Kilgallen et al. 2006b, as Orchomenella nana) and Tryphosella murrayi (Walker, 1903) (see Walker 1903 as Tryphosa m.), or only a slight elongation of this appendage: e.g. Tmetonyx cicada (O. Fabricius, 1780) (see G.O. Sars, 1890-1895 as Hoplonyx c.) and Waldeckia obesa (Chevreux, 1905) (see Chevreux 1905 as Charcotia o.). However, in other scavenger genera like Stephonyx Lowry & Stoddart, 1989, gnathopod 1 is elongate. Furthermore, there is appreciable elongation of the propodus of gnathopod 1 in Cyclocaris tahitensis Stebbing, 1888 and C. guilelmi Chevreux, 1899 although here the gnathopod is simple. Observations on undescribed species from the Atlantic abyss suggest that entities in this genus are very likely to be obligate necrophages based on mandibular structure and an ability to ingest huge quantities of food (Thurston, pers. comm.). On the other hand, in the genus Pseudorchomene there is an evolutionary progression going from plebs/rossi (stocky gnathopod 1), to debroyeri (slender gnathopod 1), coatsi (very slender gnathopod 1), and to lophorachis (extremely slender gnathopod 1). A more or less extreme trophic specialisation could possibly explain this gradation. Carrion is indeed consumed by amphipods with a wide range of diets, from occasional scavengers, e.g. Waldeckia obesa, to exclusive necrophagous species, e.g. Eurythenes gryllus (see Dauby et al. 2001). Therefore it could be hypothesised that an increasing trophic specialisation creating an intense evolutionary pressure could be responsible for the morphological gradation observed in *Pseudorchomene*. Dauby et al. (2001) considered the short-handed P. plebs and P. rossi as opportunistic feeders and *P. coatsi* (the only long-handed species known at the time) as an obligate scavenger, since they only found muscular tissues of fish in the stomach of *P. coatsi*. The significant elongation of gnathopod 1 in the more specialized *P. coatsi* could be an advantage for digging out the last pieces of flesh from fissures of fish skeletons. The far more remarkable elongation of gnathopod 1 of *P. lophorachis* could indicate a further shift in trophic niche of unknown nature. A possible hypothesis is the feeding on very bony food items such as dead ophiurids, requiring the excision of very small pieces of flesh from a complex skeletal architecture. In this context, it must be noticed that specialized scavenging has already been recorded amongst lysianassoid amphipods, as exemplified by Tryphosa nana, which is almost exclusively feeding on dead crabs (Moore & Wong 1995 as Orchomene nanus). One might expect some similar scavenging specialisation in *Stephonyx* Lowry and Stoddart, 1989 where the propodus of gnathopod 1 is slender, elongate and chelate, and which is similar and presumably related to the genus *Euonyx* Norman, 1867, which includes commensal species of sea urchins (Lowry & Stoddart 1989).

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