



## Description of two new species of *Bodinia*, a new genus incertae sedis in Argestidae Por, 1986 (Copepoda, Harpacticoida), with reflections on argestid colonization of the Great Meteor Seamount plateau <sup>☆</sup>

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### Abstract

The present paper focuses on the results of taxonomic, faunistic and chorologic investigations on Argestidae Por, 1986 (Copepoda, Harpacticoida). All argestid species collected during the cruise M42/3 of RV “Meteor” (1998) are new to science. In the present contribution, two species are described and united within *Bodinia* gen. nov.: *Bodinia meteorensis* sp. nov. and *Bodinia peterrummi* sp. nov. The new genus is placed as incertae sedis in Argestidae in light of uncertainty concerning the phylogenetic relations within this group and even its status as a monophylum. The question is discussed how members of Argestidae, previously seen as a deep-sea taxon, may have colonized the shallow-water habitat of the Great Meteor Seamount plateau.

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**Keywords:** Copepoda; Argestidae; *Bodinia*; Great Meteor Seamount; Deep sea; Meiofauna.

### Introduction

An examination of material collected on the plateau of the Great Meteor Seamount (GMS) (southern North Atlantic) yielded representatives of 11 suprageneric harpacticoid taxa (traditionally treated as families). A

*Abbreviations:* A1, antennule; A2, antenna; aes, aesthetasc; benp, baseopod; cphth, cephalothorax; CR, caudal ramus/rami; enp, endopod; exp, exopod; GF, genital field; GMS, Great Meteor Seamount; md, mandible; mx, maxilla; Mxl, maxillule; mxp, maxilliped; P1–P6, pereopods 1–6.

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remarkable proportion of these were new species of Argestidae Por, 1986 (George and Schminke 2002). Previously, Argestidae had been considered a typical deep-sea taxon (Noodt 1971; Hicks and Coull 1983; Huys and Conroy-Dalton 1997) with members preferring muddy sediments to sandy ones (Noodt 1971; Hicks and Coull 1983). Therefore, the new material posed several questions: (1) Why does Argestidae show such a high species richness on the sandy Seamount plateau? (2) Should the new species be considered as endemic to the plateau, or do they show a wider distribution in the surrounding deep sea and/or the Atlantic Ocean? (3) Does the argestid plateau community indicate any geographic or bathymetric migration, or would an isolated evolution from deep-sea ancestors be more plausible?

To provide the taxonomic foundation for addressing these questions, and to contribute to further

phylogenetic analyses of Argestidae, the new genus *Bodinia* and two new species are here described. For the time being, the genus is placed as incertae sedis in Argestidae, a taxon whose monophyly and internal phylogenetic relations are uncertain on present evidence.

## Material and methods

The material was collected during Expedition M42/3 of the German RV “*Meteor*” in 1998, from 26 stations at the GMS (Table 1), a guyot located in the subtropical Atlantic Ocean south of the Azores and west of the Canary Islands (Pfannkuche et al. 2000; George and Schminke 2002). For sampling methods and treatment of samples see George and Schminke (2002).

## Results

### *Bodinia* gen. nov.

#### Etymology

The genus name is given in grateful dedication to Dr. Philippe Bodin (Brest, France), who has provided an extensive database on the Harpacticoida of the Atlantic Ocean, enormously facilitating chorologic and faunistic work on this group.

#### Species included

Type species: *Bodinia meteorensis* sp. nov., by present designation. Other included species: *Bodinia peterrummi* sp. nov.

#### Diagnosis

Representative of Argestidae Por, 1986. Habitus long and slender, almost cylindrical. Body length 240–300 µm. No clear distinction between prosome and urosome. Urosomites dorsolaterally with 1–2 rows of spinules at distal margin. Telson almost as long as two preceding somites combined, nearly square in shape. Anal operculum distally with spinules. Telson proximally on its ventral side with a strong, caudally directed cuticular structure here termed an apron (Fig. 1B: arrow). At the base of this apron, the female telson is laterally indented. Caudal ramus/rami (CR) 2–3 times longer than broad, with seven setae. Setae I and II standing close together, displaced distally. Antennule (A1) of female 7-, of male 10-segmented, haplocer. Aesthetasc (aes) in female at fourth, in male at sixth antennular segment. Antenna (A2) with allobasis, without abexopodal setation. Exopod (exp) 1-segmented, with one seta. Mandible (md) palp without exp and 1-segmented endopod (enp). Maxilliped (mxp) with 1–2 setae at the syncoxa. Pereiopod (P1) prehensile,

with 2-segmented enp and 3-segmented exp. Exp3 with 4–5 setae. P2–P4 with 3-segmented exps and 2–3-segmented enps, not sexually modified in male. Male P5 sexually modified, with baseoendopod (benp) and distinct, long exp.

### *Bodinia meteorensis* sp. nov.

#### Etymology

The species name refers to the type locality, the GMS.

#### Type material

North Atlantic Ocean, GMS, RV “*Meteor*” expedition M42/3, station 551, 29°53.4'N 28°19.5'W, 476 m depth, epibenthic sledge (EBS), 18 September 1998.

Holotype: male, mounted on eight slides, deposited in the collection of the AG Zoosystematik & Morphologie, Carl von Ossietzky Universität Oldenburg (UNIO), Germany (coll. Nos. UNIO 2001.001/1–8). Paratypes: female (allotype), mounted on eight slides (UNIO 2001.002/1–8); four males, each mounted on one slide (UNIO 2001.003 to 2001.006).

#### Description of male (holotype)

Habitus (Fig. 1A and B) long, slender, dorsoventrally slightly depressed. Body length 240–285 µm (average 262.5 µm). No clear distinction between prosome and urosome. Cephalothorax (cphth) and distal margins of free thoracic somites dorsally and laterally with fine sensilla. Urosomites dorsally and laterally with two rows of spinules at distal margin. First abdominal somite dorsally with two sensilla at distal margin. Telson as in generic diagnosis, with apron (Figs. 1B and 2A); apron distally with spinules.

CR (Fig. 2A and D) approximately 3 times as long as broad, with seven setae. Setae I and II in distal half of CR, standing close together, II slightly longer than I. Seta III displaced ventrally and proximally, arising from protrusion and accompanied by some spinules. Setae IV–VI in terminal positions, V being the longest, VI very small. Seta VII dorsally at inner margin, articulated.

A1 (Fig. 2B) 10-segmented, haplocer. First segment with one bare seta. Second segment slightly prolonged laterally on its distal part, on this prolongation with one bare seta. Third segment with seven, fourth segment with five bare setae. Fifth segment smallest, with one bare seta. Sixth segment with three small setae, one of them broad and bipinnate, and with aes and one very long bare seta. Seventh segment small, with one small and broad bipinnate seta. Eighth to tenth segments prolonged, showing a slight sexual modification (haplocerous geniculation). Eighth segment with one small, broad, bipinnate seta and one longer bare seta. Ninth segment distally with one bare seta. Tenth segment with

**Table 1.** List of data on samples taken at the Great Meteor Seamount during expedition M42/3 of RV “*Meteor*” in 1998

Sampling date	Station	Gear	Geographic locality	Depth (m)
01.09.2002	451	GKG	30°08.4'N, 28°34.8'W	455
02.09.2002	452	GKG	29°42.9'N, 28°22.7'W	297
02.09.1999	455	GKG	29°42.9'N, 28°22.7'W	297
03.09.2002	456	GKG	29°48.2'N, 28°29.7'W	303
04.09.2002	DS 459	MUC	29°45.7'N, 28°44.3'W	2722
06.09.2002	467	GKG	30°02.1'N, 28°32.6'W	292
08.09.2002	DS 484	MUC	29°25.5'N, 28°33.9'W	4015
09.09.2002	489	GKG	29°57.0'N, 28°23.1'W	323
09.09.2002	492	GKG	29°58.5'N, 28°29.7'W	294
11.09.2002	DS 505	GKG	30°18.3'N, 28.03.3'W	4005
12.09.2002	DS 506	MUC	30°12.2'N, 28°14.2'W	3009
13.09.2002	511	GKG	30°07.2'N, 28°22.8'W	597
13.09.2002	515	EBS	29°48.9'N, 28°29.0'W	302
14.09.2002	516	GKG	29°49.3'N, 28°37.1'W	325
14.09.2002	517	EBS	30°05.9'N, 28°32.2'W	312
14.09.2002	518	EBS	30°02.0'N, 28°32.0'W	293
14.09.2002	519	EBS	30°06.2'N, 28°24.5'W	416
14.09.2002	520	EBS	30°06.0'N, 28°24.3'W	422
14.09.2002	521	EBS	30°05.9'N, 28°23.2'W	511
14.09.2002	522	EBS	30°05.6'N, 28°23.0'W	518
17.09.2002	DS 548	MUC	29°52.8'N, 28°14.2'W	2320
18.09.2002	551	EBS	29°53.4'N, 28°19.5'W	476
18.09.2002	552	EBS	29°53.9'N, 28°22.0'W	322
19.09.2002	DS 558	MUC	30°32.1'N, 28°46.8'W	4111
20.09.2002	565	EBS	29°39.4'N, 28°22.9'W	403
20.09.2002	DS 566	MUC	29°32.7'N, 28°29.9'W	3077

11 bare setae, two of them articulated, and with one small aes.

Setal formula: I—1, II—1, III—7, IV—5, V—1, VI—4 + aes, VII—1, VIII—2, IX—1, X—11 + aes.

A2 (Fig. 2C) with allobasis lacking abexopodal seta. Exp small, 1-segmented, with one bare seta. Enp at inner margin with two bare setae, terminally with four geniculate and two small bare setae.

Mouthparts as in female, except mxp (see below). Fig. 1C' shows male md for better interpretation.

Mxp (Fig. 1F). Syncoxa smaller than basis, with spinules and one bipinnate seta. Basis without setation but distally with row of spinules. Enp represented by one spinulose claw.

P1 (Fig. 3A) prehensile. Coxa on its outer side with spinulose “outgrowths” resembling the “cristae” of Cristacoxidae Huys, 1990. Basis with bipinnate inner and outer seta, the inner one accompanied by a row of spinules. Exp 3-segmented, second segment with inner seta. Exp3 with three setae and one outer spine. Enp 2-segmented. Enp1 as long as exp, distally at inner margin with one bare seta. Enp2 approximately 1/4 of length of enp1, subterminally at inner margin with one bare seta; terminally with one long seta and one additional, unipinnate claw.

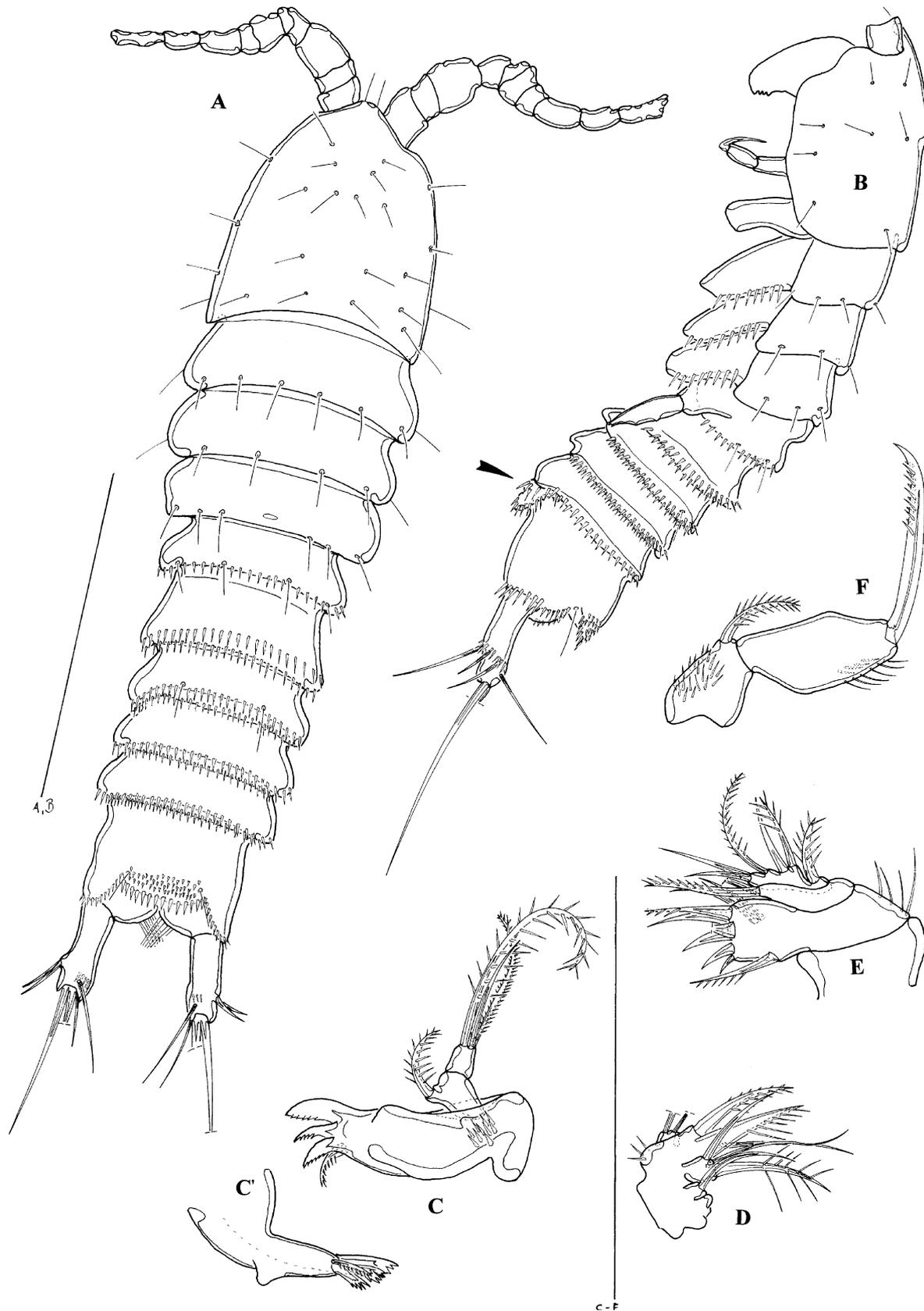
P2–P4 (Figs. 3B and 4). Bases with bipinnate outer seta. Exps 3-segmented, exp2 smallest segment. Exp1 without inner seta. Exp2 with one bipinnate inner seta. Exp3 of P2 and P3 each with two inner and two terminal setae, and with two outer spines; exp3 of P4 similar, but with only one inner seta. Enps 2-segmented, not reaching length of exps, and displaced outwardly. Enp1 smaller than enp2, with one bipinnate inner seta. Enp2 with one inner and two terminal setae, the latter accompanied by one terminal outer spine. Enp of P2 more slender than enps of P3 and P4.

Setal formulae:

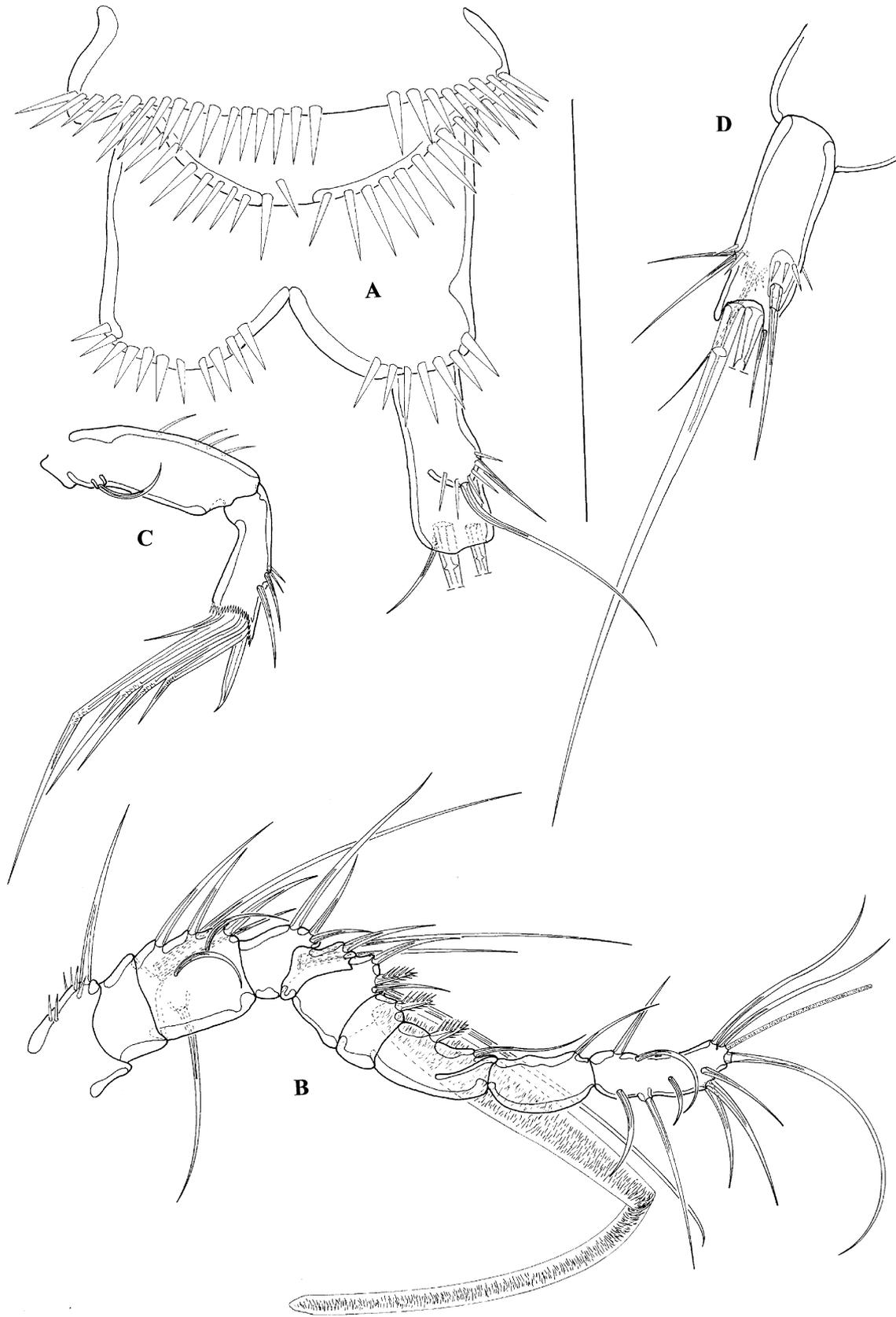
	Exp	Enp
P2	I—0, I—1, II—2—2	0—1, 1—2—1
P3	I—0, I—1, II—2—2	0—1, 1—2—1
P4	I—0, I—1, II—2—1	0—1, 1—2—1

P5 (Fig. 3C) with reduced benp, bearing one outer seta. Exp articulated, almost 3 times longer than broad, with four bare setae and one long bipinnate seta, and with one long tube pore.

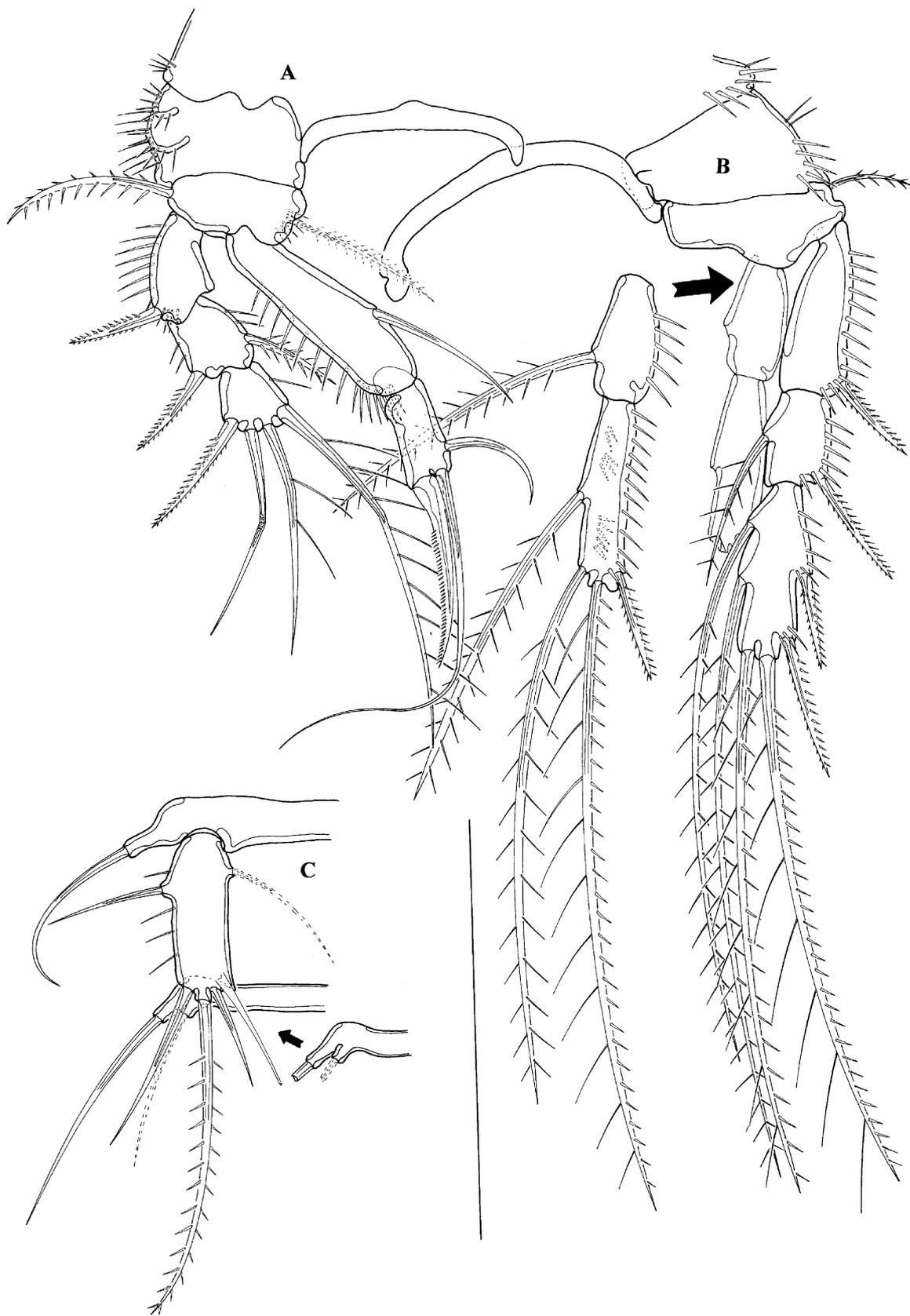
P6 (Fig. 3C) small, with two bare setae.



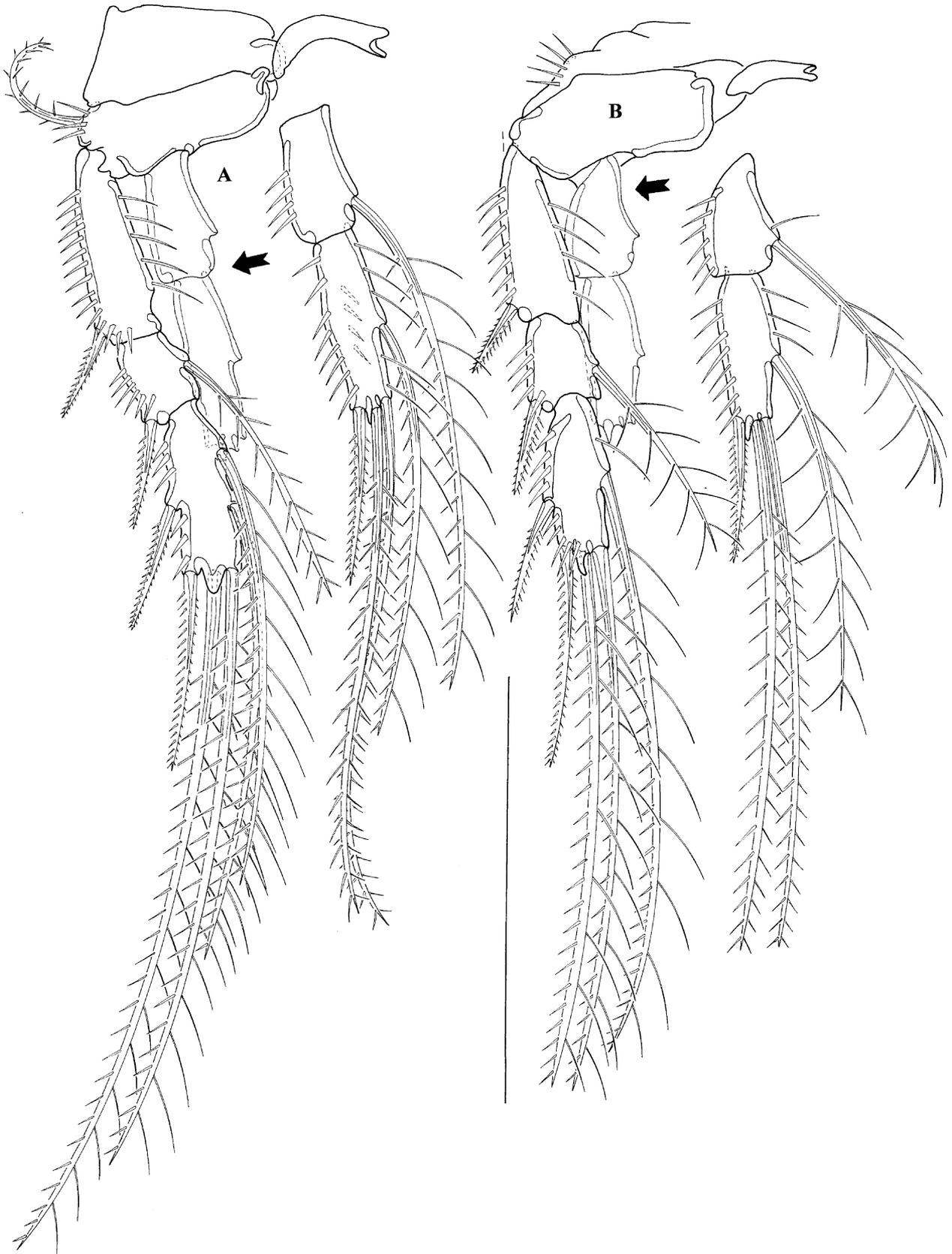
**Fig. 1.** *B. meteorensis* sp. nov. (A), (B) male habitus, dorsal and lateral view, arrow points to apron of telson; (C) female md; (C') male md; (D) female mx; (E) female mxl; and (F) male mxp. Scale bars (A,B) = 100  $\mu$ m, (C–F) = 50  $\mu$ m.



**Fig. 2.** *B. meteorensis* sp. nov., male. (A) telson with apron and CR, ventral view; (B) A1; (C) A2; and (D) CR, dorsal view. Scale bar = 50  $\mu$ m.



**Fig. 3.** *B. meteorensis* sp. nov., male pereiopods. (A) P1; (B) P2; and (C) P5 and P6. Scale bar = 50  $\mu$ m.



**Fig. 4.** *B. meteorensis* sp. nov., male pereiopods. (A) P3; and (B) P4. Scale bar = 50  $\mu$ m.

### Description of female

Habitus, size, and shapes of most appendages as in male. Sexual dimorphism is observed in the body parts described below. In addition, the md, maxillule (mxl) and maxilla (mx) are described.

A1 (Fig. 5A) 7-segmented. First segment with bipinnate seta, cuticula posteriorly very strong. Second segment biggest, with seven bare setae. Third segment with five bare setae. Fourth segment with strong protrusion which bears two long bare setae and one aes. Fifth segment as long as fourth, with one bare seta. Sixth segment with three bare setae. Seventh segment nearly as long as second, bearing 11 setae and terminally one small aes.

Setal formula: I—1, II—7, III—5, IV—2 + aes, V—1, VI—3, VII—11 + aes.

Md (Fig. 1C). Gnathobase strong, with one big serrated tooth and two smaller ones, and with one unipinnate seta. Md palp with exp represented by one bipinnate seta. Enp 1-segmented, with two bipinnate setae and one bare seta. Fig. 1C' shows md (of male) in another perspective.

Mxl (Fig. 1E). Precoxal arthrite with several long spinules, terminally with five bare setae and one unipinnate seta. Subterminally with one unipinnate seta, on the opposite side with two bare setae. Coxa with one unipinnate and one small bare seta. Basis, exp and enp fused, with three bipinnate, one bare, and two bare setae, respectively.

Mx (Fig. 1D) very small. Syncoxa with two endites, the proximal one small, with one bare seta. Second endite bigger, with three setae, the biggest one bipinnate, the remaining ones bare. Basis fused to syncoxa, with three setae, one of them unipinnate and fused to the segment. Enp small, fused to basis, with two setae.

P5 (Fig. 5D) benp small, with three long bipinnate setae. Exp articulated, slender, about 4.5 times longer than broad, with five setae, the terminal one bipinnate. Pore tubeless.

Genital field (GF) (Fig. 5B) small, sclerotized. No evidence of fusion of last thoracic somite with first abdominal somite, nor of P6.

Apron of telson (Fig. 5C) more strongly developed than in male. Telson laterally indented at its proximal margin.

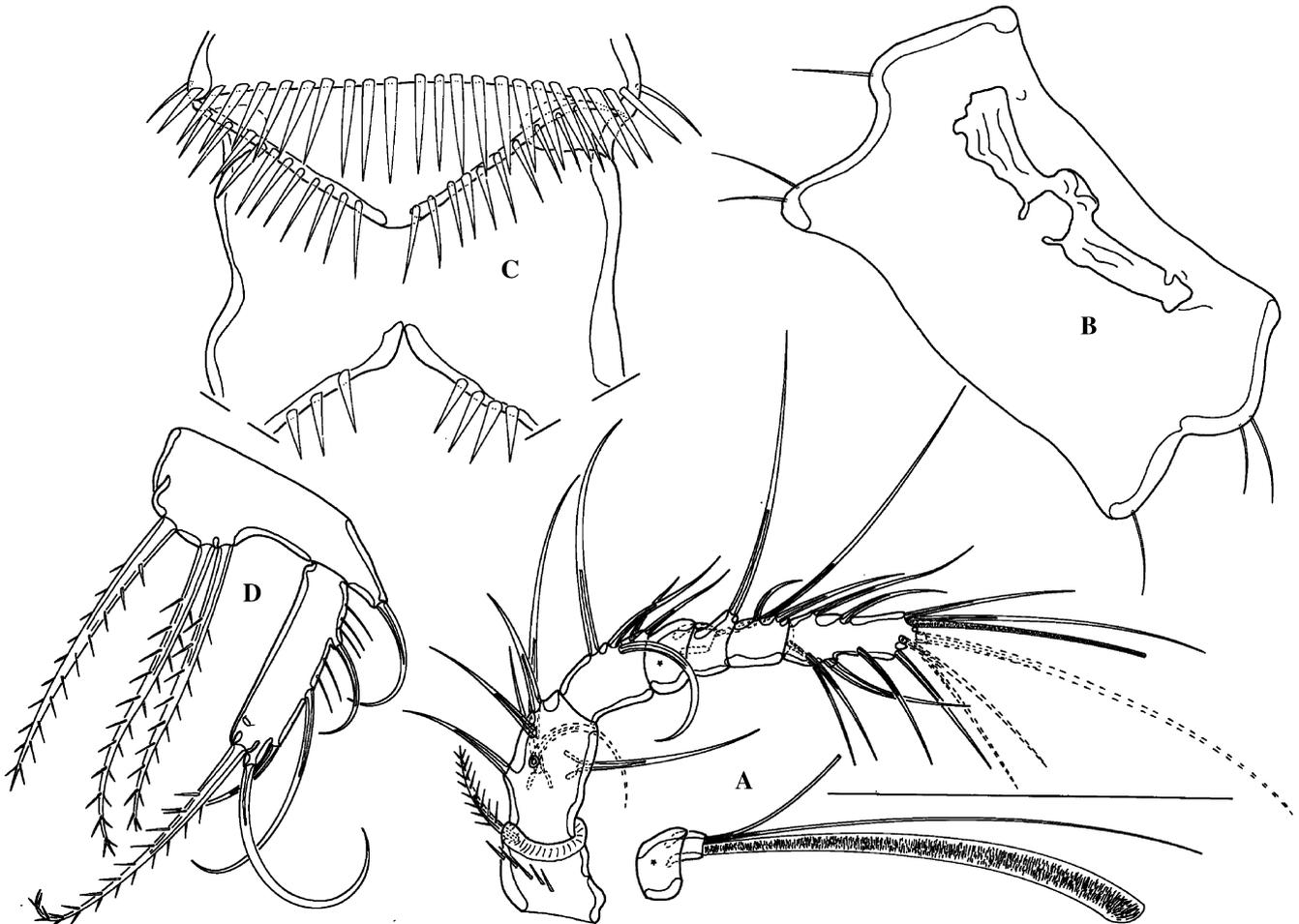


Fig. 5. *B. meteorensis* sp. nov., female. (A) A1; (B) GF; (C) telson with apron, ventral view; and (D) pereiopod 5. Scale bar = 50  $\mu$ m.

***Bodinia peterrummi* sp. nov.****Etymology**

The species name is given in friendly and grateful dedication to Dr. Peter Rumm (Munich, Germany).

**Type material**

North Atlantic Ocean, GMS, RV “*Meteor*” expedition M42/3, several stations sampled with EBS or giant boxcorer (GKG).

Holotype: female, mounted on nine slides, deposited in the collection of the AG Zoosystematik & Morphologie, Carl von Ossietzky UNIOL, Germany (coll. Nos. UNIOL 2001.007/1-9); station 516, 29°49.3'N 28°37.1'W, 325 m depth, GKG. Paratypes: described male, distributed on two slides (UNIOL 2001.008/1-2), station 518, 30°02.0'N 28°32.0'W, 293 m depth, EBS; male (UNIOL 2001.009), station 452, 29°42.9'N 28°22.7'W, 297 m depth, GKG; male (UNIOL 2001.010), station 552, 29°53.9'N 28°22.0'W, 322 m depth, EBS; female, distributed on four slides (UNIOL 2001.011/1-4), as holotype; male (UNIOL 2001.012), station 451, 30°08.4'N 28°34.8'W, 455 m depth, GKG; male (UNIOL 2001.013), as holotype.

**Description of female (holotype)**

Habitus as in male (see Fig. 6A and B). GF (Fig. 7C) small, sclerotized; P6 and GDS not discernible. Telson ventrally with modified apron (Fig. 7D), the latter with a broad distal part separated from the triangular base by a relatively narrow neck. At the base of the apron the somite is laterally indented. CR (Fig. 7D) about 2 times longer than broad, with seven setae. Setae I and II close together, displaced distally. Seta III displaced ventrally and accompanied by some spinules. Setae IV and V in terminal positions, IV smaller than V. Seta V longest. Seta VI small, terminally at inner margin. Seta VII dorsally at inner margin, arising from knob.

A1 (Fig. 7A) 7-segmented. First segment very small, neither a seta nor its base discernible. Second segment longest, with seven bare setae. Third segment also with seven setae. Fourth segment half as long as third, with three short bare setae and one longer bipinnate seta. Aes and one additional long and bipinnate seta arising from protrusion. Fifth segment smallest, with two small setae and one longer one. Sixth segment with three bare setae. Seventh segment with 11 bare setae and terminally with small aes, as revealed by comparison with female paratype.

Setal formula: I—0(?), II—7, III—7, IV—5 + aes, V—3, VI—3, VII—11 + aes.

A2 (Fig. 7B) with allobasis bearing a 1-segmented exp, lacking any abexopodal setae. At abexopodal margin with spinules. Exp small and knob-like, with one bipinnate seta. Enp 1-segmented, at inner margin

with row of spinules and two bipinnate setae; terminally with four geniculate and two additional, smaller bare setae.

Md and Mx as in male (Fig. 8B and C).

Mxl (Fig. 8A). Precoxal arthrite terminally with six strong setae and one unipinnate seta; laterally with one bipinnate seta; on the opposite side with two slender bare setae. Coxa (marked “\*” in Fig. 8A) with two bare setae and one strong unipinnate seta. Basis, exp, and enp fused to single lobe (marked “o” in Fig. 8A) which bears three bare and two bipinnate setae.

Mxp (Fig. 8D) prehensile. Syncoxa with row of spinules, one bipinnate and one unipinnate seta. Basis strong, 2 times longer than syncoxa, without setation, but with group of small spinules. Enp represented by spinulose claw which is longer than basis.

P1 (Fig. 9A) prehensile. Basis smaller than coxa, with bipinnate inner and outer seta, the inner one as long as enp1. Exp 3-segmented, all segments of almost the same size. Exp2 with bipinnate inner spine. Exp3 with two outer bipinnate spines, two terminal bare geniculate setae, and one inner subterminal seta. Enp 2-segmented. Enp1 slightly longer than enp2, reaching at most the end of exp, with one bipinnate seta at inner margin. Enp2 with two bipinnate spines at inner margin, terminally with one long unipinnate seta and one unipinnate claw.

P2–P4 (Figs. 9B and 10) with 3-segmented exps and enps. Basis transversely slightly prolonged, with bare outer seta. Exps inserting outermost, with one inner seta each on exp1 and exp2. Exp2 smallest segment. Exp3 with three outer spines and two terminal setae. Exp3 of P2 and P3 each with two inner setae, exp3 of P4 with one inner seta. Enps inserted in the middle of basis, standing close to exps. Enp1 with one inner seta. Enp2 of P2 and P3 with, enp2 of P4 without inner seta. Enp3 with one inner seta and one outer spine, as well as with two terminal setae.

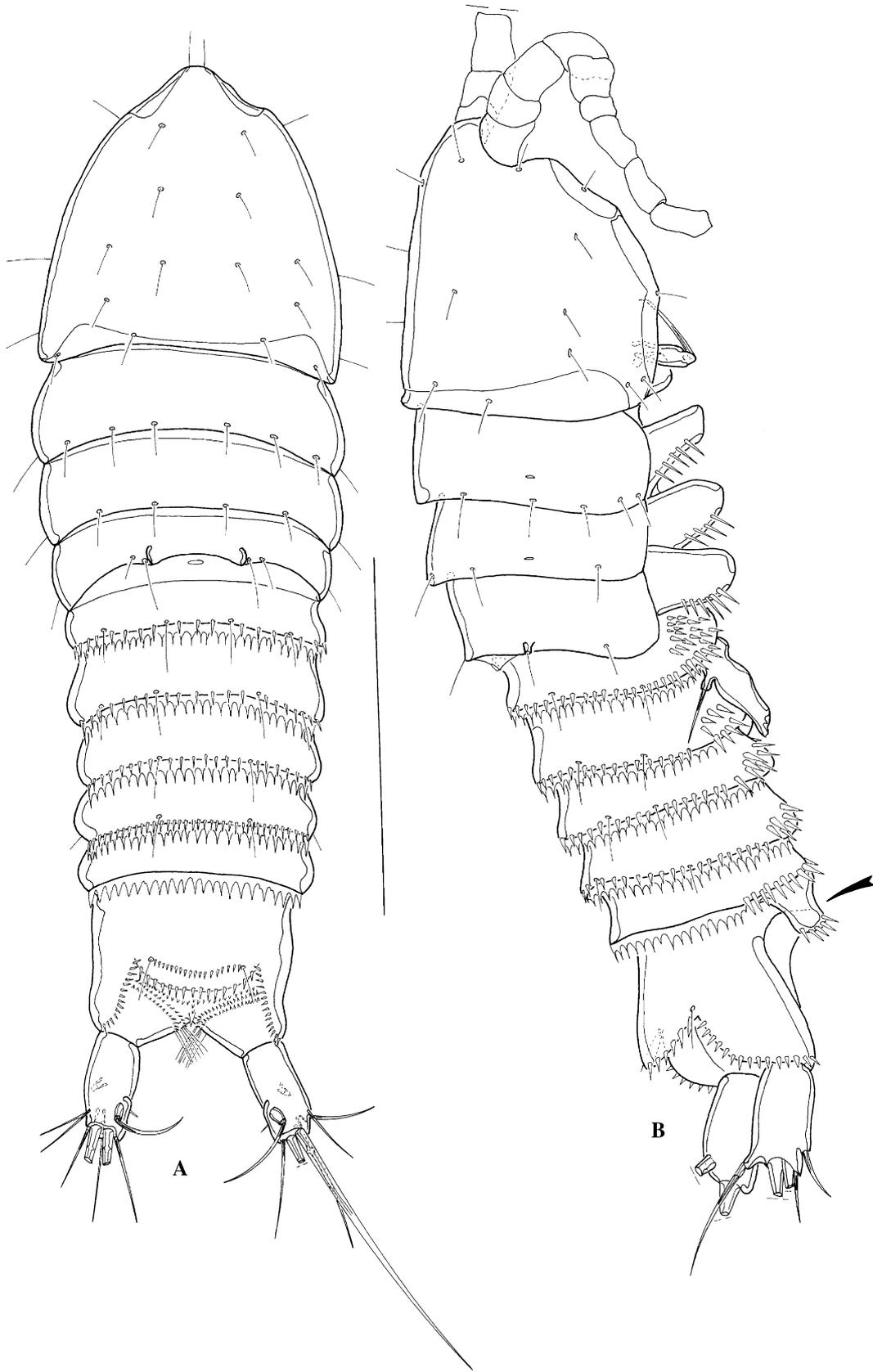
Setal formula:

	Exp	Enp
P2	I—1, I—1, III—2—2	0—1, 0—1, 1—2—1
P3	I—1, I—1, III—2—2	0—1, 0—1, 1—2—1
P4	I—1, I—1, III—2—1	0—1, 0—1, 1—2—1

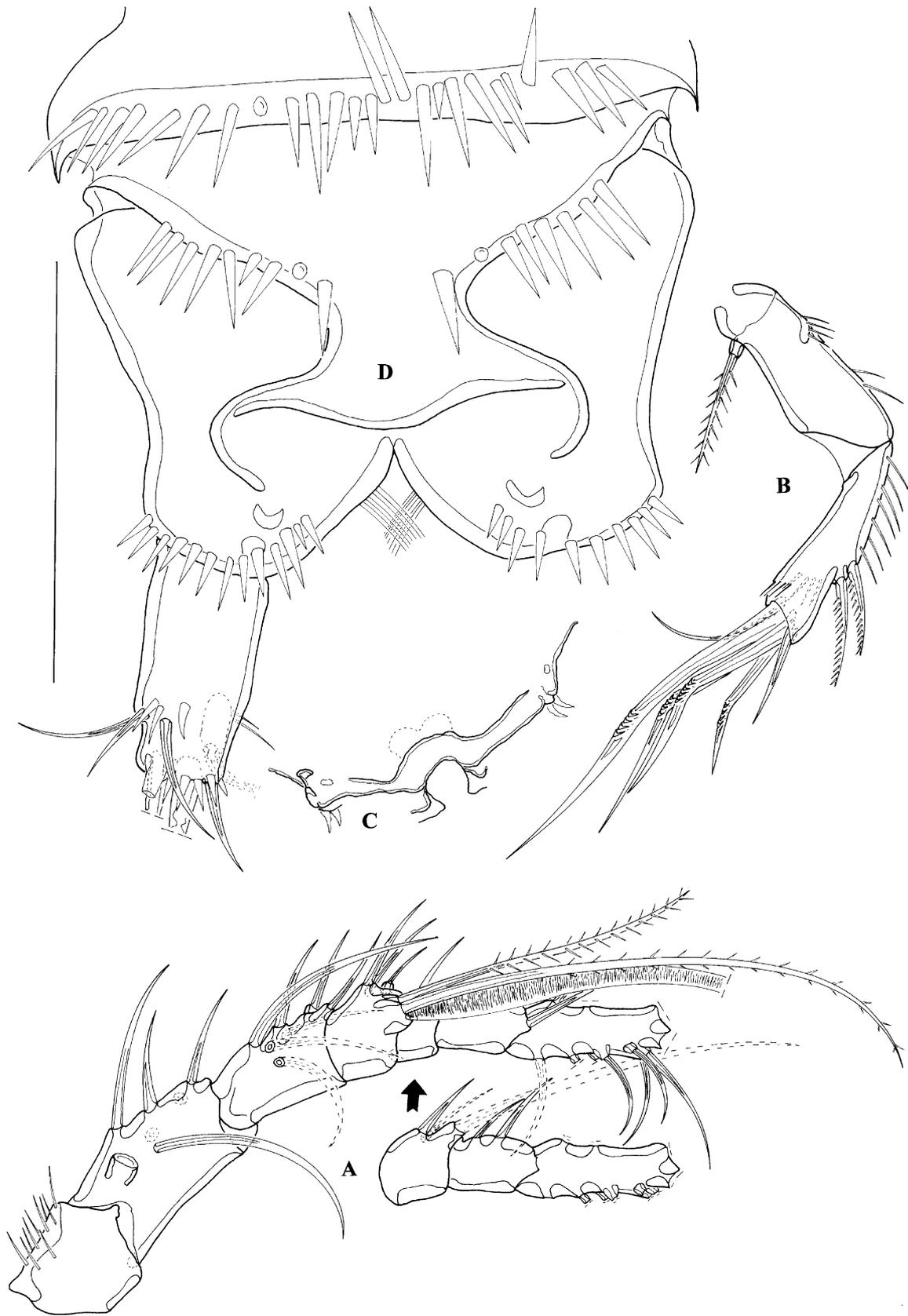
P5 (Fig. 8E) with articulated exp. Benp small, with three long bipinnate setae, at its inner margin with a group of long and soft spinules. Exp about 3.5 times longer than broad, with two bipinnate setae and one additional bare seta; terminally and subterminally with one bipinnate seta; at its inner margin with long tube pore.

**Description of male**

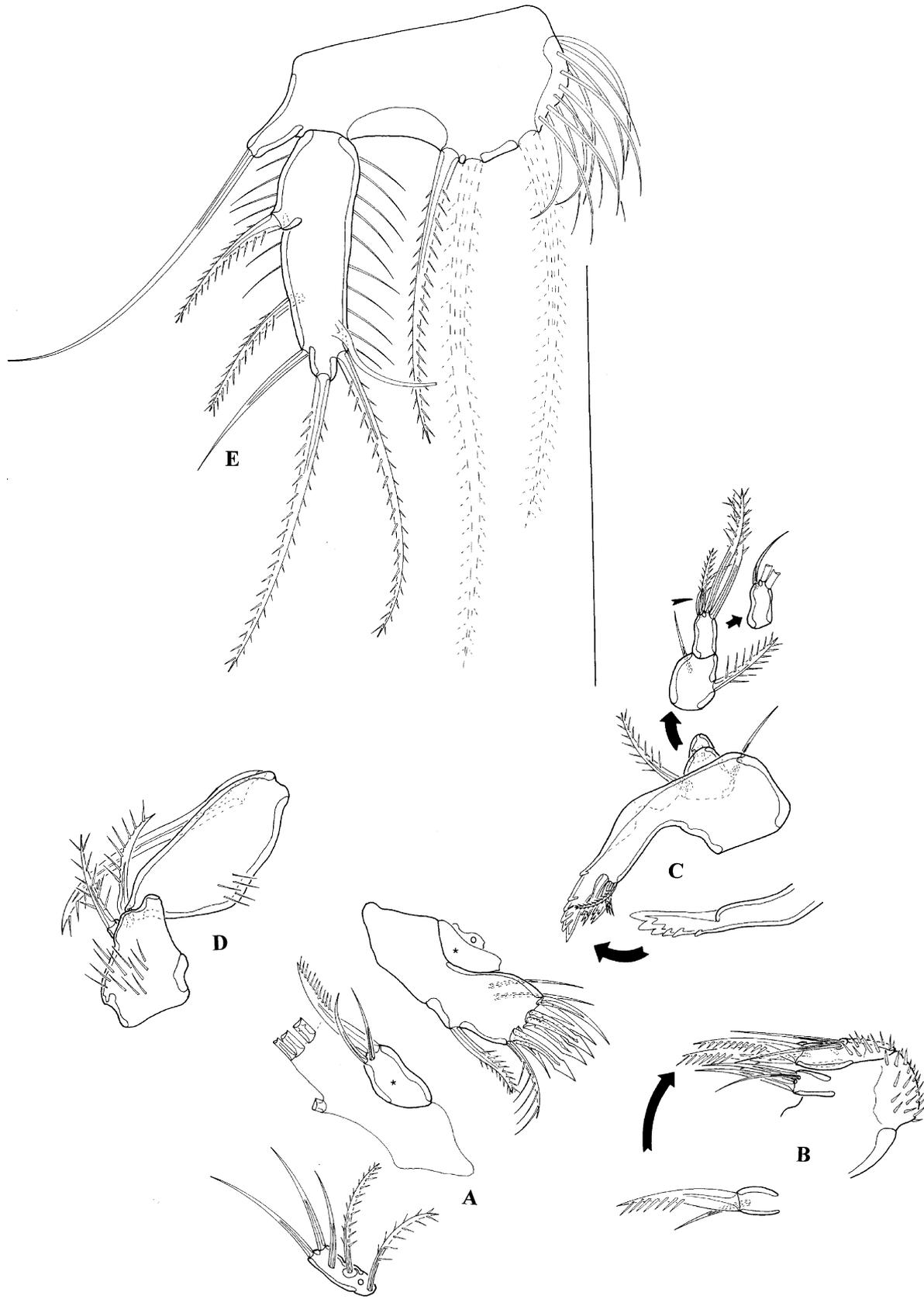
Based on specimen from station 518.



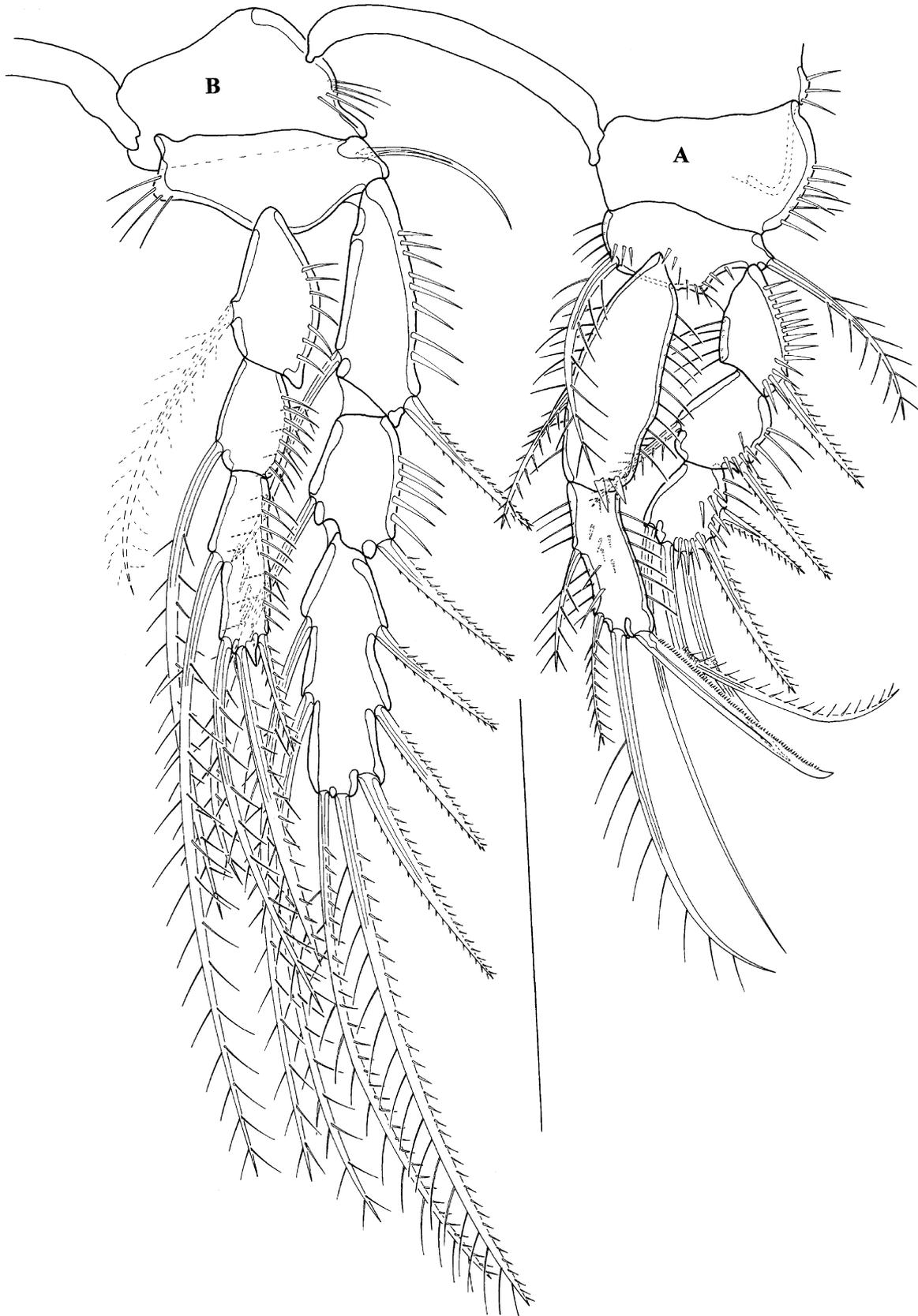
**Fig. 6.** *B. peterrummi* sp. nov., male habitus. (A) dorsal view; and (B) lateral view, arrow points to apron of telson. Scale bar = 100  $\mu$ m.



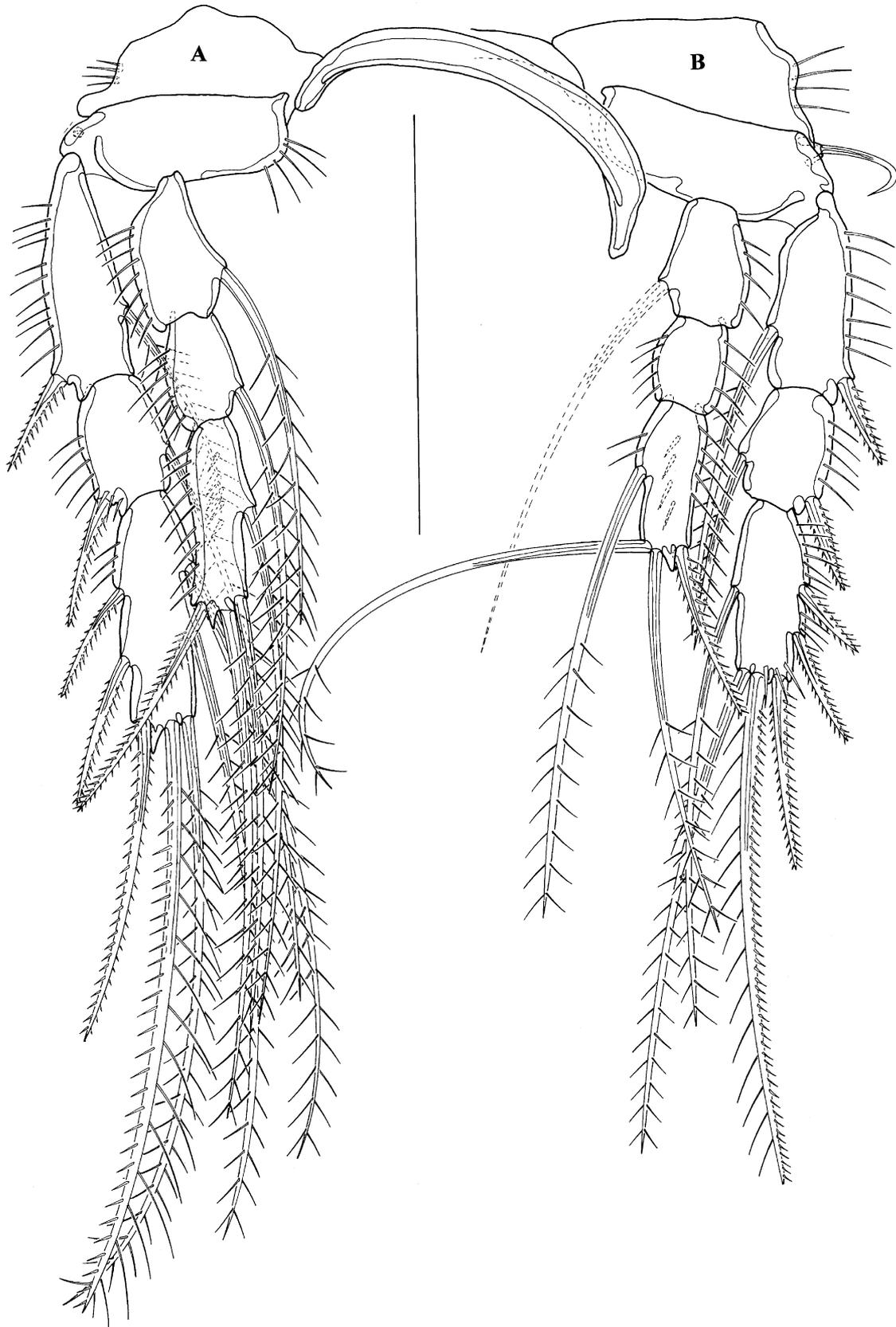
**Fig. 7.** *B. peterrummi* sp. nov., female. (A) A1; (B) A2; (C) GF; and (D) telson with apron and CR, ventral view. Scale bar = 50  $\mu$ m.



**Fig. 8.** *B. peterrummi* sp. nov. (A) female mxl; coxa marked “\*”, fused basis/enp/exp lobe marked “◊” (B) male mxl; (C) male md; (D) female mxp; and (E) female pereiopod 5. Scale bar = 50  $\mu$ m.



**Fig. 9.** *B. peterrummi* sp. nov., female pereopods. (A) P1; and (B) P2. Scale bar = 50  $\mu$ m.



**Fig. 10.** *B. peterrummi* sp. nov., female pereiopods. (A) P2; and (B) P3. Scale bar = 50  $\mu$ m.

Habitus (Fig. 6A, B) long and slender, almost cylindrical. Cphth and free thoracic somites 1–3 with sensilla and no ornamentation at distal margins. Cuticula of third free thoracic somite noticeably thicker, somite with big porus. Adjoining body somites distally with toothed hyaline frill accompanied subterminally by a row of small spinules; also with sensilla, except last somite. Telson nearly square, anal operculum with a terminal and a subterminal row of spinules, the subterminal one flanked by two sensilla. Apron (Fig. 11C) similar to that of female, but less developed. CR (Fig. 11C) as in female.

A1 (Fig. 11A) 10-segmented. In the first segment, as in female, seta not discernible. Second segment with one seta, third segment with six setae. Fourth to seventh segments distinctly smaller. Fourth segment with three, fifth segment with two setae. Sixth segment with one unipinnate, one bare, and one short but strong unipinnate seta. One seta and a mighty aes insert on a very strong protrusion which reaches up to the seventh segment. Seventh segment with one small, strong unipinnate and one bare seta. Eighth to tenth segments of nearly the same length, longer than preceding segments, and showing sexual dimorphism. Eighth segment distally modified, showing a longitudinal cuticular “ridge”, with one small unipinnate seta and one additional, longer bare seta. Ninth segment with one small and one longer bare seta. Tenth segment with 10 bare setae and one small aes.

Setal formula: I—0, II—1, III—6, IV—3, V—2, VI—4+ aes, VII—2, VIII—2, IX—2, X—10+ aes.

Md (Fig. 8C) resembling that in the type species, main tooth remarkably developed. Md palp with exp represented by one bipinnate and one smaller bare seta. Enp 1-segmented, terminally with two bipinnate and two bare setae.

Mx (Fig. 8B). Syncoxa distally with small spinules and two endites. Proximal endite with one small bare seta, and with one stronger unipinnate seta. Distal endite with three bare setae. Basis articulated, with one unipinnate seta. Enp represented by two bare setae.

P5 (Fig. 11B). Benp small, with one outer and one inner seta. Exp articulated, about 2 times longer than broad, with three bipinnate and two bare setae, as well as one long tube pore.

P6 (Fig. 11B) small, with one bare seta.

### Worldwide geographic and bathymetric distribution of Argestidae

Table 2 presents a list of all species so far recorded in Argestidae, including data on geographic and bathymetric distribution. Including recently discovered undescribed species from the Magellan Region and the GMS, 133 species have been recorded. Most of them

were collected in the Atlantic Ocean, but there are also some records from the Mediterranean (e.g. *Eurycletodes* (*Oligocletodes*) *denticulatus* Por, 1967; *E. (O.) petiti* Soyer, 1964; *Fultonia bougisi* Soyer, 1964), the Pacific and Indian oceans (e.g. *Argestes reductus* (Itô, 1983); *Argestoides prehensilis* Huys & Conroy-Dalton, 1997; *Megistocletodes translucens* Por, 1986; *Mesocletodes opotheros* Por, 1986), and even from the Red Sea (*Dizahavia halophila* Por, 1979) and the Black Sea (*Eurycletodes (O.) parasimilis* Por, 1959). This indicates a worldwide distribution of the group. Comparison of the corresponding depths (Table 2) reveals that Argestidae range from the sublittoral down to abyssal depths. However, Fig. 12 illustrates a preference for deep-sea habitats, where 57.74% of all species have been recorded, whereas only 14.8% inhabit littoral–sublittoral areas. About 1/4 of the records do not include data on bathymetric distribution.

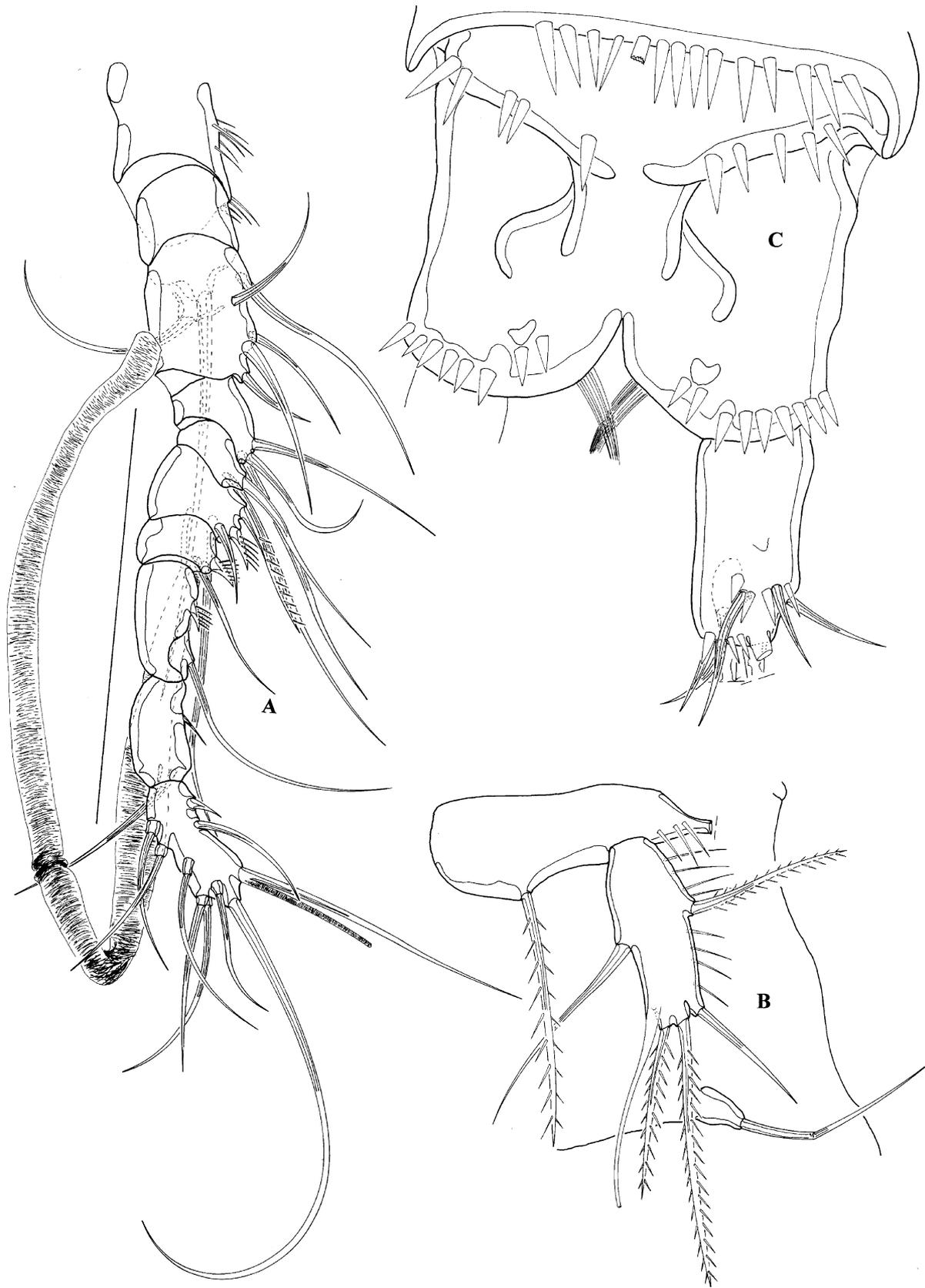
Table 3 summarizes the Argestidae so far recorded from the plateau of the GMS and the surrounding deep sea. Representatives have been found at almost all (six of seven) deep-sea stations, but only at eight of 19 plateau stations. Fig. 13 shows the bathymetric species distribution at the GMS: 65% seem to be restricted to the deep sea, 29% were collected only from the plateau, and 6% are present in both areas.

So far, seven argestid genera have been recorded in the sampling area: *Argestes* Sars, 1910; *Argestigenes* Willey, 1935; *Bodinia* gen. nov.; *Dizahavia* Por, 1979; *Eurycletodes* Sars, 1909; *Mesocletodes* Sars, 1909; and *Parargestes* Lang, 1948. Five species could not be assigned to any known genus and are therefore named “Argestidae GMS sp.1” to “Argestidae GMS sp.5”. The number of species recorded is highest in *Mesocletodes* (9) and *Eurycletodes* (8).

## Discussion

### Argestidae Por, 1986

In the context of splitting the Cletodidae, Por (1986) erected, among other taxa, the Argestidae. According to Bodin (1997), the family comprises 14 genera: *Argestes* Sars; *Argestigenes* Willey; *Corallicletodes* Soyer, 1966; *Dizahavia* Por; *Eurycletodes* Sars; *Fultonia* T. Scott, 1902; *Hemicletodes* Lang, 1936; *Hypalocletodes* Por, 1967; *Leptocletodes* Sars, 1920; *Megistocletodes* Por, 1986; *Mesocletodes* Sars; *Neoargestes* Drzycimski, 1967; *Odiliacletodes* Soyer, 1964; and *Parargestes* Lang. Although the family diagnosis by Por (1986) is relatively clear, Argestidae has not been demonstrated to be monophyletic. Previously, they had been subsumed under Cletodidae (e.g. Lang 1948; Wells 1976) or assigned to the Ameiridae Monard, 1927 (part.), Lang,



**Fig. 11.** *B. peterrummi* sp. nov., male. (A) A1; (B) pereopods 5 and 6; and (C) telson with apron and CR, ventral view. Scale bar = 50  $\mu$ m.

**Table 2.** Worldwide list of all species so far recorded in Argestidae, including data on geographic and bathymetric distribution

No.	Species	Authorship or reference	Geographic distribution	Depth (m)
1	<i>Argestes mollis</i>	Sars, 1910	Atlantic, Northern Subpolar Seas, King Karls Land, Scandinavia	100–385
2	<i>Argestes reductus</i>	(Ito, 1983)	Pacific (Mindanao)	?
3	<i>Argestes</i> GMS sp.1	Present study	Atlantic, Great Meteor Seamount	3009
4	<i>Argestes</i> GMS sp.2	Present study	Atlantic, Great Meteor Seamount	403–476
5	<i>Argestigens abyssalis</i>	Becker, Noodt & Schriever, 1979	Atlantic, Iberian Sea	?
6	<i>Argestigens glacialis</i>	Lang, 1936	Atlantic, Northern Subpolar Seas, Seven Islands (Spitzbergen)	150
7	<i>Argestigens uniremis</i>	Wiley, 1935	Atlantic, Bermuda	?
8	<i>Argestigens</i> GMS sp.1	Present study	Atlantic, Great Meteor Seamount	4005
9	<i>Argestigens</i> GMS sp.2	Present study	Atlantic, Great Meteor Seamount	4005
10	<i>Argestoides prehensilis</i>	Huys & Conroy-Dalton, 1997	Pacific, Galapagos Rift	2494
11	<i>Bodinia meteorensis</i>	gen. et sp.n., present study	Atlantic, Great Meteor Seamount	476
12	<i>Bodinia peterrummi</i>	gen. et sp.n., present study	Atlantic, Great Meteor Seamount	293–4111
13	<i>Bodinia</i> sp.	gen. n., present study	Atlantic, Great Meteor Seamount	2320
14	<i>Corallicletodes boutieri</i>	Soyer, 1966	Mediterranean, Cap l'Abeille	35
15	<i>Dizahavia halophila</i>	Por, 1979	Red Sea, Sinai	4.5
16	<i>Dizahavia</i> GMS sp.1	Present study	Atlantic, Great Meteor Seamount	476–4005
17	<i>Dizahavia</i> GMS sp.2	Present study	Atlantic, Great Meteor Seamount	4005
18	<i>Dizahavia</i> GMS sp.3	Present study	Atlantic, Great Meteor Seamount	293–2320
19	<i>Eurycletodes (O.) abyssi</i>	Lang, 1936	Atlantic, Northern Subpolar Seas, Hornsund; Magellan Region	100–1750
20	<i>Eurycletodes (O.) aculeatus</i>	Sars, 1920	Atlantic, Scandinavia; Mediterranean	50–?
21	<i>Eurycletodes (O.) arcticus</i>	Lang, 1936	Atlantic, Northern Subpolar Seas, King Karls Land	210
22	<i>Eurycletodes (O.) denticulatus</i>	Por, 1967	Mediterranean, Elat (Israel)	180
23	<i>Eurycletodes (O.) echinatus</i>	Lang, 1936	Atlantic, Northern Subpolar Seas, Hornsund	1750
24	<i>Eurycletodes (O.) ephippiger</i>	Por, 1964	Mediterranean, Israel	3950
25	<i>Eurycletodes (E.) gorbunovi</i>	Smirnov, 1946	Atlantic, Northern Subpolar Seas	?
26	<i>Eurycletodes (O.) hoplurus</i>	Smirnov, 1946	Atlantic, Northern Subpolar Seas	?
27	<i>Eurycletodes (O.) irelandica</i>	Roe, 1959	Atlantic, Irish Sea	?
28	<i>Eurycletodes (E.) laticauda</i>	(Boeck, 1872)	Atlantic, Scandinavia	60–120
29	<i>Eurycletodes (O.) latus</i>	T. Scott, 1892	Atlantic, Scandinavia	?
30	<i>Eurycletodes (O.) major</i>	Sars, 1909	Atlantic, Scandinavia	14,946
31	<i>Eurycletodes (O.) minutus</i>	Sars, 1920	Atlantic, Scandinavia	?
32	<i>Eurycletodes (O.) monardi</i>	Smirnov, 1946	Atlantic, Northern Subpolar Seas; Magellan Region	219–?
33	<i>Eurycletodes (O.) oblongus</i>	Sars, 1920	Atlantic, Northern Subpolar Seas; Mediterranean; Magellan Region	200–1540
34	<i>Eurycletodes (O.) parasimilis</i>	Por, 1959	Black Sea	20–100
35	<i>Eurycletodes (O.) peruanus</i>	Becker, Noodt & Schriever, 1979	Pacific, Peru Trench	6300
36	<i>Eurycletodes (O.) petiti</i>	Soyer, 1964	Mediterranean	?
37	<i>Eurycletodes (O.) profundus</i>	Becker, Noodt & Schriever, 1979	Atlantic, Iberian Sea	?
38	<i>Eurycletodes (O.) quadrispinosa</i>	Schriever, 1986	Atlantic, Northern Subpolar Seas, Faroe Ridge	2500
39	<i>Eurycletodes (E.) rectangulatus</i>	Lang, 1936	Atlantic, Northern Subpolar Seas, Hornsund	210
40	<i>Eurycletodes (E.) serratus</i>	Sars, 1920	Atlantic, Scandinavia	100–150
41	<i>Eurycletodes (O.) similis</i>	(T. Scott, 1895)	Atlantic, Northern Subpolar Seas, North Sea	?

Table 2. (continued)

No.	Species	Authorship or reference	Geographic distribution	Depth (m)
42	<i>Eurycletodes (O.) unarticulatus</i>	Smirnov, 1946	Atlantic, Northern Subpolar Seas	?
43	<i>Eurycletodes (O.) verisimilis</i>	Wiley, 1935	Atlantic, Bermuda	?
44	<i>Eurycletodes</i> GMS sp.1	Present study	Atlantic, Great Meteor Seamount	4005
45	<i>Eurycletodes</i> GMS sp.2	Present study	Atlantic, Great Meteor Seamount	4005
46	<i>Eurycletodes</i> GMS sp.3	Present study	Atlantic, Great Meteor Seamount	4005–4111
47	<i>Eurycletodes</i> GMS sp.4	Present study	Atlantic, Great Meteor Seamount	325
48	<i>Eurycletodes</i> GMS sp.5	Present study	Atlantic, Great Meteor Seamount	4005
49	<i>Eurycletodes</i> GMS sp.6	Present study	Atlantic, Great Meteor Seamount	3009
50	<i>Eurycletodes</i> GMS sp.7	Present study	Atlantic, Great Meteor Seamount	325
51	<i>Eurycletodes</i> GMS sp.8	Present study	Atlantic, Great Meteor Seamount	403
52	<i>Eurycletodes</i> MR sp.1	George (1999)	Magellan Region	110–459
53	<i>Eurycletodes</i> MR sp.2	George (1999)	Magellan Region	219
54	<i>Eurycletodes</i> MR sp.3	George (1999)	Magellan Region	219–351
55	<i>Fultonia bougisi</i>	Soyer, 1964	Mediterranean; Magellan Region	110–?
56	<i>Fultonia gascognensis</i>	Bodin, 1968	Atlantic, Gulf of Biscay	?
57	<i>Fultonia hirsuta</i>	T. Scott, 1902	Atlantic, Northern Subpolar Seas; North Sea	?
58	<i>Fultonia sarsi</i>	Smirnov, 1946	Atlantic, Northern Subpolar Seas; Magellan Region	219–?
59	<i>Fultonia</i> MR sp.1	George (1999)	Magellan Region	123
60	<i>Fultonia</i> MR sp.2	George (1999)	Magellan Region	123–320
61	<i>Fultonia</i> MR sp.3	George (1999)	Magellan Region	320–459
62	<i>Fultonia</i> MR sp.4	George (1999)	Magellan Region	309
63	<i>Fultonia</i> MR sp.5	George (1999)	Magellan Region	346
64	<i>Hemicletodes typicus</i>	Lang, 1936	Atlantic, Northern Subpolar Seas, Hornsund	1750
65	<i>Hyalocletodes aberrans</i>	Marinov, 1973	Atlantic, African West coast	?
66	<i>Hyalocletodes salomonis</i>	Por, 1967	Red Sea, Sinai	?
67	<i>Leptocletodes chaetophorus</i>	Smirnov, 1946	Atlantic, Northern Subpolar Seas	?
68	<i>Leptocletodes debilis</i>	Sars, 1920	Atlantic, Scandinavia	?
69	<i>Leptocletodes</i> sp.	Soyer (1964)	Mediterranean	?
70	<i>Megistocletodes translucens</i>	Por, 1986	Indic	?
71	<i>Mesocletodes abyssicola</i>	T. & A. Scott, 1901	Atlantic, Scandinavia; Magellan Region	50–459
72	<i>Mesocletodes ameliae</i>	Soyer, 1975	Western Mediterranean	100
73	<i>Mesocletodes arenicola</i>	Noodt, 1952	Atlantic, North Sea	
74	<i>Mesocletodes bathybia</i>	Por, 1964	Mediterranean	?
75	<i>Mesocletodes bodini</i>	Soyer, 1975	Westl. Mediterranean	88
76	<i>Mesocletodes brevifurca</i>	Lang, 1936	Atlantic, Northern Subpolar Seas, Seven Islands (Spitzbergen)	150
77	<i>Mesocletodes carpinei</i>	Soyer, 1975	Western Mediterranean	88
78	<i>Mesocletodes commixtus</i>	Coull, 1973	Atlantic, US East coast	500
79	<i>Mesocletodes dolichurus</i>	Smirnov, 1946	Atlantic, Northern Subpolar Seas	?
80	<i>Mesocletodes duosetosus</i>	Schriever, 1985	Atlantic, Island-Faroe Ridge	985
81	<i>Mesocletodes faraumi</i>	Por, 1967	Mediterranean, Israel	?
82	<i>Mesocletodes faroerensis</i>	Schriever, 1985	Atlantic, Island-Faroe Ridge	1540
83	<i>Mesocletodes fladensis</i>	Wells, 1965	Atlantic, North Sea	?
84	<i>Mesocletodes glaber</i>	Por, 1964	Skagerrak	?
85	<i>Mesocletodes guillei</i>	Soyer, 1964	Mediterranean	?
86	<i>Mesocletodes inermis</i>	Sars, 1920	Atlantic, Norway	50–100
87	<i>Mesocletodes irrasus</i>	(T. A. Scott, 1894)	Atlantic, Northern Subpolar Seas, Mediterranean	?
88	<i>Mesocletodes katharinae</i>	Soyer, 1964	Mediterranean	?
89	<i>Mesocletodes kunzi</i>	Schriever, 1985	Atlantic, Island-Faroe Ridge	1850
90	<i>Mesocletodes langi</i>	Smirnov, 1946	Atlantic, Northern Subpolar Seas	?
91	<i>Mesocletodes makarovi</i>	Smirnov, 1946	Atlantic, Northern Subpolar Seas	?

Table 2. (continued)

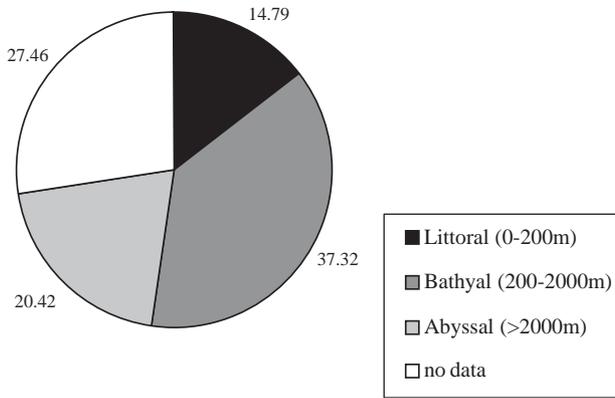
No.	Species	Authorship or reference	Geographic distribution	Depth (m)
92	<i>Mesocletodes monensis</i>	(I.C. Thompson, 1893)	Atlantic, North Sea, Mediterranean	?
93	<i>Mesocletodes ophotheros</i>	Por, 1986	Indic	?
94	<i>Mesocletodes parabodini</i>	Schriever, 1983	Atlantic, Island-Faroe Ridge	?
95	<i>Mesocletodes parirrasus</i>	Becker, Noodt & Schriever, 1979	Pacific, Peru Trench	500
96	<i>Mesocletodes quadrispinosa</i>	Schriever, 1985	Atlantic, Island-Faroe Ridge	505
97	<i>Mesocletodes robustus</i>	Por, 1965	Atlantic, Norway	?
98	<i>Mesocletodes sarsi</i>	Becker, Noodt & Schriever, 1979	Atlantic, Iberian Sea	?
99	<i>Mesocletodes soyeri</i>	Bodin, 1968	Atlantic, Biscaya; Magellan Region	219–?
100	<i>Mesocletodes thieli</i>	Schriever, 1985	Atlantic, Island-Faroe Ridge	500
101	<i>Mesocletodes trisetosa</i>	Schriever, 1983	Atlantic, Island-Faroe Ridge	500
102	<i>Mesocletodes variabilis</i>	Schriever, 1983	Atlantic, Island-Faroe Ridge	500
103	<i>Mesocletodes</i> GMS sp.1	Present study	Atlantic, Great Meteor Seamount	4005
104	<i>Mesocletodes</i> GMS sp.2	Present study	Atlantic, Great Meteor Seamount	4005
105	<i>Mesocletodes</i> GMS sp.3	Present study	Atlantic, Great Meteor Seamount	325
106	<i>Mesocletodes</i> GMS sp.4	Present study	Atlantic, Great Meteor Seamount	4005
107	<i>Mesocletodes</i> GMS sp.5	Present study	Atlantic, Great Meteor Seamount	4005
108	<i>Mesocletodes</i> GMS sp.6	Present study	Atlantic, Great Meteor Seamount	4005
109	<i>Mesocletodes</i> GMS sp.7	Present study	Atlantic, Great Meteor Seamount	4005
110	<i>Mesocletodes</i> GMS sp.8	Present study	Atlantic, Great Meteor Seamount	325
111	<i>Mesocletodes</i> GMS sp.9	Present study	Atlantic, Great Meteor Seamount	4005
112	<i>Mesocletodes</i> MR sp.1	George (1999)	Magellan Region	257–346
113	<i>Mesocletodes</i> MR sp.2	George (1999)	Magellan Region	257–459
114	<i>Neoargestes incertus</i>	Becker, Noodt & Schriever, 1979	Atlantic, Iberian Sea	?
115	<i>Neoargestes variabilis</i>	Drzycimski, 1967	Atlantic, Norway	520
116	<i>Odiliaclatodes gracilis</i>	Soyer, 1964	Mediterranean	?
117	<i>Parargestes tenuis</i>	(Sars, 1921)	Atlantic, Northern Subpolar Seas, Scandinavia	50–210
118	<i>Parargestes</i> GMS sp.1	Present study	Atlantic, Great Meteor Seamount	4,015
119	<i>Parargestes</i> GMS sp.2	Present study	Atlantic, Great Meteor Seamount	3009
120	<i>Parargestes</i> GMS sp.3	Present study	Atlantic, Great Meteor Seamount	325
121	Argestidae GMS sp.1	Present study	Atlantic, Great Meteor Seamount	325
122	Argestidae GMS sp.2	Present study	Atlantic, Great Meteor Seamount	293–312
123	Argestidae GMS sp.3	Present study	Atlantic, Great Meteor Seamount	3077
124	Argestidae GMS sp.4	Present study	Atlantic, Great Meteor Seamount	3077
125	Argestidae GMS sp.5	Present study	Atlantic, Great Meteor Seamount	3009
126	Argestidae MR sp.1	George (1999)	Magellan Region	200–440
127	Argestidae MR sp.2	George (1999)	Magellan Region	110–459
128	Argestidae MR sp.3	George (1999)	Magellan Region	320–459
129	Argestidae MR sp.4	George (1999)	Magellan Region	346
130	Argestidae MR sp.5	George (1999)	Magellan Region	320
131	Argestidae MR sp.6	George (1999)	Magellan Region	320–346
132	Argestidae MR sp.7	George (1999)	Magellan Region	336
133	Argestidae MR sp.8	George (1999)	Magellan Region	550

GMS—Great Meteor Seamount; MR—Magellan Region.

1936 (see Huys and Conroy-Dalton 1997 and references therein).

Not all of Por's (1986) diagnostic features are of phylogenetic value, but some characteristics have to be considered as derived and may therefore indicate the monophyletic status of this group: (1) integument

poorly chitinized; (2) telson nearly square, large; (3) anal operculum shifted posteriorly; (4) caudal rami (CR) set wide apart at corners of telson; (5) exp A2 1-segmented; (6) pereopods remarkably elongated, situated wide apart. Comparisons of material and literature reveal even more shared derived characteristics: (7) exp



**Fig. 12.** Vertical distribution (in % of species) of Argestidae recorded so far.

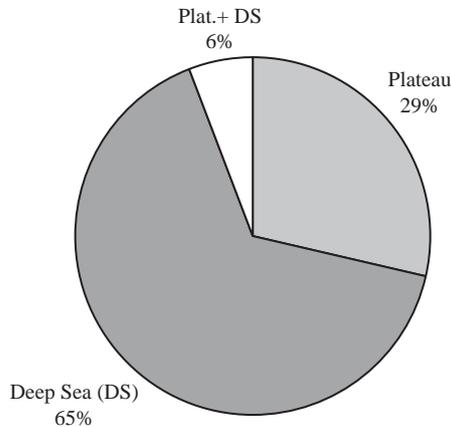
A2 with only one seta; (8) small seta on mxp enp completely lost; (9) bases of pereopods elongated transversely; (10) exp and enp of P2–P4 displaced to the outer margin of the basis. Although these 10 presumed synapomorphies still have to be tested for validity in every argestid taxon, they are here considered sufficient to work, for the time being, from the assumption that Argestidae is monophyletic.

**Placement of *Bodinia* gen. nov. incertae sedis**

The assignment of *Bodinia* gen. nov. to Argestidae is non-problematic. The new genus shows all of the 10 characteristics listed above. However, with the mono-

**Table 3.** List of Argestidae collected at the Great Meteor Seamount during M42/3 of RV “Meteor”

No.	Species	451	452	DS484	DS505	DS506	516	517	518	DS548	551	552	DS558	565	DS566	n/S
1	<i>Argestes</i> sp.1					1										1
2	<i>Argestes</i> sp.2										3			1		4
3	<i>Argestigens</i> sp.1			1												1
4	<i>Argestigens</i> sp.2			1												1
5	<i>Bodinia meteorensis</i> gen. et sp.n.					1					5					6
6	<i>Bodinia peterrummi</i> gen. et sp.n.	1	3			3		1		1	5	1				15
7	<i>Bodinia</i> gen.n. sp.								1							1
8	<i>Dizahavia</i> sp.1			1							1					2
9	<i>Dizahavia</i> sp.2			1												1
10	<i>Dizahavia</i> sp.3						2	1	1	10	1	1		1		11
11	<i>Eurycletodes</i> sp.1			1												1
12	<i>Eurycletodes</i> sp.2			1												1
13	<i>Eurycletodes</i> sp.3			2									1			3
14	<i>Eurycletodes</i> sp.4					1										1
15	<i>Eurycletodes</i> sp.5			1												1
16	<i>Eurycletodes</i> sp.6					1										1
17	<i>Eurycletodes</i> sp.7					1										1
18	<i>Eurycletodes</i> sp.8													1		1
19	<i>Mesocletodes</i> sp.1			2											1	3
20	<i>Mesocletodes</i> sp.2			1												1
21	<i>Mesocletodes</i> sp.3					1										1
22	<i>Mesocletodes</i> sp.4									1						1
23	<i>Mesocletodes</i> sp.5									1						1
24	<i>Mesocletodes</i> sp.6									1						1
25	<i>Mesocletodes</i> sp.7									1						1
26	<i>Mesocletodes</i> sp.8					1										1
27	<i>Mesocletodes</i> sp.9				1											1
28	<i>Parargestes</i> sp.1		2													2
29	<i>Parargestes</i> sp.2					1										1
30	<i>Parargestes</i> sp.3						1									1
31	Argestidae sp.1					1										1
32	Argestidae sp.2							1	2							3
33	Argestidae sp.3														1	1
34	Argestidae sp.4														1	1
35	Argestidae sp.5															2
n/station		1	3	2	13	5	12	2	4	9	11	6	2	3	3	76
S/station		1	1	1	11	4	9	2	3	6	5	2	2	3	3	



**Fig. 13.** Argestid distribution (in % of species) at the GMS. Plat. = plateau; DS = deep sea; Plat. + DS = occurring in both areas.

phyly of Argestidae still unproven, *Bodinia* gen. nov. is here classified as a genus incertae sedis within this group.

*B. meteorensis* sp. nov., *B. peterrummi* sp. nov. and a third species, *Bodinia* sp., from the GMS share the possession of a ventral apron at the proximal margin of the telson as a synapomorphy. Such a strongly developed cuticular structure, combining with the lateral indentation of the telson in the female, has not been detected in any other argestid, nor in any species of the presumably closely related Ameiridae (Huys and Conroy-Dalton 1997). The apron is therefore considered as autapomorphic for *Bodinia* gen. nov. and justifying its status as a monophylum. However, the relationships to other argestid genera are unclear. Shapes and setation of the swimming legs seem to place *Bodinia* gen. nov. near *Dizahavia*. Moreover, two of the three *Dizahavia* species collected at the GMS (*Dizahavia* sp.1 and sp.3; Table 2) show a slight modification of the telson, which may provide additional support for a stronger relationship to *Bodinia* gen. nov.

### Origin of the argestid GMS plateau fauna

The deep-sea floor, although comprising >50% of the earth's surface (Tyler 2003), has to be considered as terra incognita with respect to benthological research. According to Lambshead (1993), the worldwide deep-sea area sampled for meiofauna hardly reached 20 m<sup>2</sup> at that time. Thus, it is quite difficult and may be even futile to attempt any general conclusions on species distribution. On the other hand, it may be allowable to generalize that the Argestidae are commonly present in the deep sea and can therefore be considered as typical deep-sea inhabitants. As summarized in Table 2 and

Fig. 12, most argestid species have been collected at depths below 200 m (i.e. in the bathyal), a considerable proportion even below 2000 m (abyssal). Although there is proof for the presence of eurybathic species ranging from the littoral down to deepest bathyal areas (*Argestes mollis* Sars, 1910; *Eurycletodes (O.) abyssii* Lang, 1936; *Parargestes tenuis* (Sars, 1921); an undescribed Magellanic species), their number is very low compared to that of species restricted to the deep sea. The characterization of Argestidae as typical deep-sea organisms has been generally accepted for many decades (Noodt 1971; Hicks and Coull 1983; Huys and Conroy-Dalton 1997) and is justified not only because of frequent records in deep-sea samples, but also because they are always one of the clearly dominating harpacticoid taxa there (Hicks and Coull 1983; Rose et al. 2005). The material obtained from the GMS may serve as an additional example: although the GMS plateau was sampled nearly 3 times as much as the surrounding deep sea (19 vs. 7 stations), 65% of the collected species of Argestidae occurred at deep-sea stations (Fig. 13). The deep-sea preference may also include a sedimentological component: as shown by Noodt (1971), Argestidae belong to the so-called “*Cervinia* Norman—*Laophontodes* T. Scott type” characterized by the presence of several special morphological structures, and by preferring “soft bottoms, particularly in greater depths” (Noodt 1971, p. 99). On the other hand, Hicks and Coull (1983) do not mention any argestid genus in their list of Harpacticoida inhabiting shallow muddy substrata, nor do other investigations of littoral and sublittoral soft bottoms report any argestid taxon (e.g. Soyer 1977; Sach 1984; Bodin and Le Guellec 1994; Sach and van Bernem 1996). It can, therefore, be concluded that Argestidae generally prefer soft instead of sandy substrata, and deep-sea areas rather than littoral–sublittoral ones.

In this context, it is quite surprising that Argestidae form the most species-rich harpacticoid taxon on GMS plateau. The average depth of the latter corresponds to the sublittoral–bathyal frontier, the substrate is formed by calcareous sands (Ulrich 1971).

As shown by George and Schminke (2002), on the GMS plateau Argestidae make up 45% of all investigated Harpacticoida species. This leads to the question of how and why this deep-sea- and mud-adapted taxon has been so successful in the colonization of the GMS plateau. In order to discuss various possible explanations, it is necessary first to briefly summarize the evolution of the GMS.

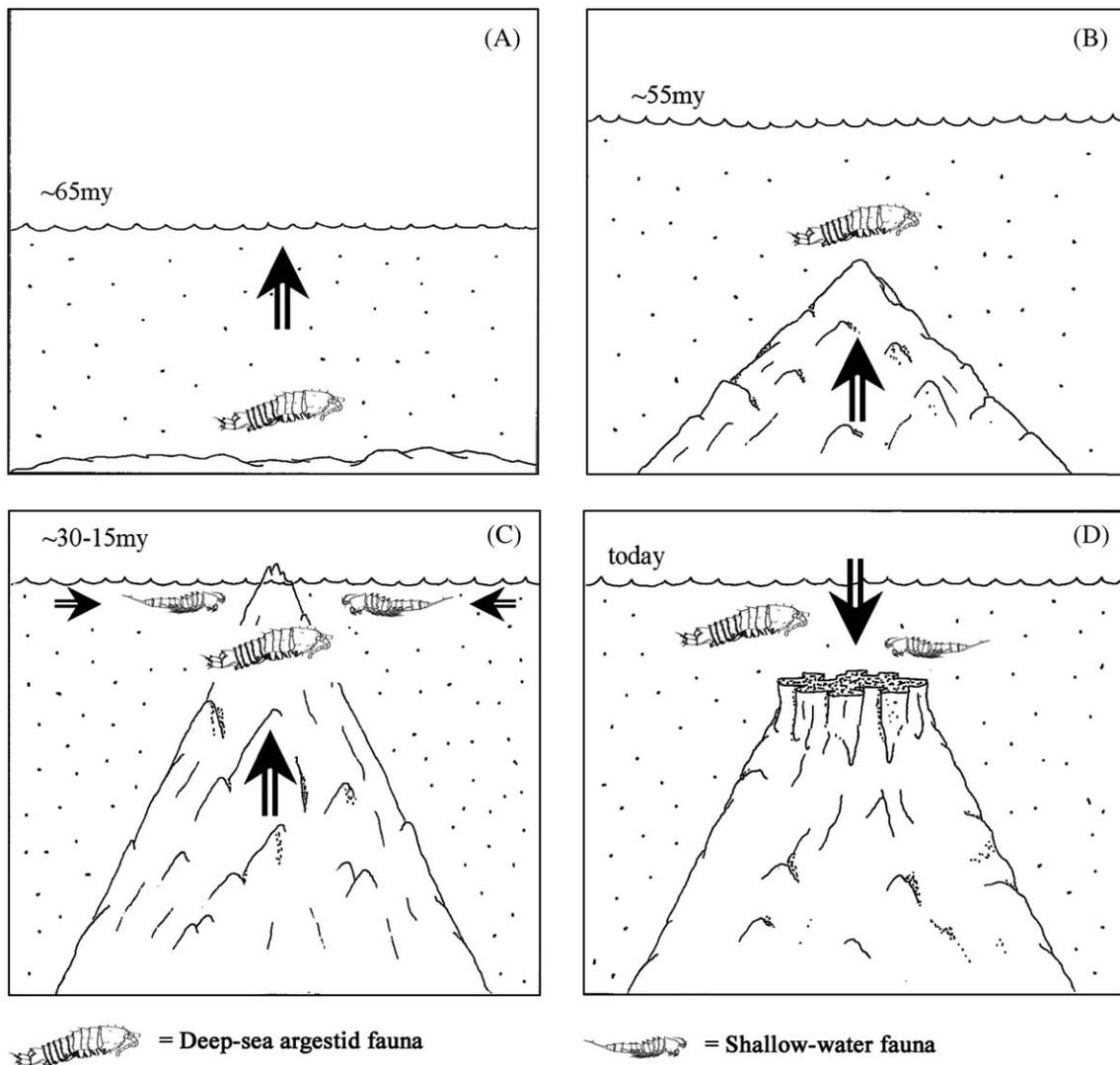
The seamount rises from about 5000 m depth to 450–270 m. It is of volcanic origin. Its age is estimated at between >51 and 11 million years (see Grevemeyer 1994 and references therein). Generally, it is assumed that the development of the GMS started around the end of the Cretaceous and the beginning of the Tertiary (approx. 70–55 million years ago) (Hinz 1969; Dietrich et al.

1975; see also Grevenmeyer 1994). The shape of the seamount, called a “guyot” because its summit is flattened and forms a plateau, leads to the conclusion that it rose above sea level and formed an island several million years ago (Hinze 1969; Dietrich et al. 1975). When volcanic activity diminished, the island sank into the sea again, due to changing geological conditions (Dietrich et al. 1975). Water energy eroded the sinking summit and formed the plateau.

**Scenario 1: geographical immigration**

One possibility for plateau colonization is by immigration. It is conceivable that species reach the seamount plateau from other shallow-water areas. This happens at least sporadically, as is confirmed by the presence of a few shallow-water species that were previously recorded

from other localities (George and Schminke 2002). Nevertheless, geographical immigration of meiofauna via the water column generally seems rather improbable, due to the lack of planktonic larvae or juveniles within this group (Dahms 1992), that would be required to enter the water column. Thus, the traversing of hundreds of nautical miles from the nearest shallow-water areas within the water column would occur rather accidentally, which is confirmed by the remarkably low number of scientifically known species reported from the GMS plateau (George and Schminke 2002). Moreover, the problem arises that, as shown above, Argostidae primarily inhabit deep-sea habitats. It is, therefore, rather unlikely that the argostid assemblage of the GMS descends from shallow-water ancestors who had immigrated geographically from other shallow-water areas.



**Fig. 14.** Hypothetical evolution of the plateau-living harpacticoid fauna of the GMS (schematic) according to the elevation scenario (see text: Discussion); my = million years ago. (A) argostid ancestors lived in the deep sea; (B) they were elevated with the rising of the seamount; (C) a shallow-water (littoral/sublittoral) community was formed, comprising descendants of the former deep-sea taxa as well as of shallow-water immigrants from adjacent geographic regions; and (D) subsequent sinking of the seamount and forming of the guyot resulted in establishment of a unique, isolated plateau fauna comprising former deep-sea and shallow-water taxa.

### Scenario 2: bathymetrical immigration

A second possibility is immigration from the deep sea. This seems conceivable, as it would explain the presence of the deep-sea taxon Argestidae on the plateau. However, two problems arise: (1) The GMS is characterized by a quite complicated hydrographical current system (Horn et al. 1971) that separates the inner from the outer seamount regime almost permanently (Beckmann and Mohn 2002), a circumstance that certainly hinders the colonization of the plateau, in particular by meiobenthic deep-sea species. Thus, although perhaps possible for representatives of the macro- and megafauna, an active migration from the deep-sea bottom up to the plateau seems rather unlikely for meiobenthic organisms. (2) The plateau is characterized by sandy sediments (Ulrich 1971), whereas Argestidae prefer muddy bottoms (Noodt 1971; Hicks and Coull 1983). This circumstance leads to the question, how species of Argestidae were able to disperse or evolve to this remarkably high species number on the GMS plateau, while other taxa, such as Laophontidae, Harpacticidae, Cletodidae (George and Schminke 2002: Table 4), whose members are normally much better adapted to sandy and shallow habitats (Hicks and Coull 1983), are present on the plateau in considerably lower species numbers.

### Scenario 3: elevation with the seamount

A third possibility is gradual elevation of deep-sea organisms along with the rising of the seamount during its millions of years of continuous growth (Fig. 14A). In the process, argestids would have been able to realize several ecological niches resulting from the developing new conditions (Fig. 14B). The evolving species were even able to adapt to shallow-water conditions, when the GMS became an island millions of years ago (Fig. 14C), as well as to the change of substrate composition and the increase of sandy components when the island sank again and turned into the Recent guyot (Fig. 14D). This hypothesis, which is favoured by the author, explains the Argestidae found today on the GMS plateau as being the descendants of an old deep-sea assemblage which was lifted up and later sank again with the seamount. A similar hypothesis was presented years ago already, trying to explain the high endemism in marine caves of Bermuda and other Atlantic islands (Iliffe et al. 1983, 1984). The scenario presented here is also able to explain the low species numbers of non-argestid shallow-water Harpacticoida. Being able to reach the seamount only after it had become an island (Fig. 14C), these “secondary” colonists found several niches already occupied by Argestidae. When the island started sinking again, those shallow-water species that still had been able to colonize its littoral and sublittoral sank along with the Argestidae. The non-argestid shallow-water species now recorded on

the plateau are the descendants of these “secondary” colonists (Fig. 14D).

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