

A new species of *Eurycletodes* Sars, 1909 (Copepoda: Harpacticoida: Argestidae) from the southern hemisphere including remarks on the phylogeny of the genus and its subgenera

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Abstract This paper deals with taxonomy and phylogenetics of the genus *Eurycletodes* Sars, 1909 (Copepoda: Harpacticoida: Argestidae). Samples, collected from the southeast Atlantic on board RV “Meteor” during the cruises DIVA-1 (M48/1) and DIVA-2 (M63/2), contain specimens of *Eurycletodes*. *Eurycletodes* is characterized as a monophylum by A1 segments III + IV fused, basal seta of md palp lost, exp of md palp reduced to 1 seta or completely lost. Similarly, the subgenera *Eurycletodes* (*Eurycletodes*) and *Eurycletodes* (*Oligocletodes*) are characterized as monophyletic by the loss of the inner seta on P1 exp2 (apomorphic to *E. (E.)*) and the absence of the inner seta on P5 endopodal lobe (apomorphic to *E. (O.)*). *Eurycletodes profundus* is renamed as *E. (O.) profundus*. *Eurycletodes ephippiger* is the only species of the genus without subgeneric designation. *Eurycletodes (O.) diva* sp. nov. is described. The new species differs from described species of the genus by a larger body size, P5 endopodal lobe only slightly protruding, last segment of A1 with 2 outer setae, furcal rami elongated between setae VII and IV. The occurrence of 2 specimens of *Eurycletodes (O.) diva* sp. nov. at 2 sites separated by the Walvis Ridge supports the hypothesis that geographic obstacles do not prevent harpacticoid copepods from spreading in the deep sea.

Keywords Deep sea · DIVA · *Eurycletodes* (*Eurycletodes*) · *Eurycletodes* (*Oligocletodes*) · *Eurycletodes (O.) diva* sp. nov. · Phylogeny · South Atlantic · Taxonomy

Introduction

A number of specimens of *Eurycletodes* Sars, 1909 were found in sediment samples collected from the Cape Basin, Angola Basin, and Guinea Basin off the western coast of Africa during the DIVA-1 (M48/1) and DIVA-2 (M63/2) cruises in July 2000 and February 2005.

Generally in deep-sea samples, *Eurycletodes* represents about 25% of all Argestidae Por, 1986b, which is one of the most abundant taxa of Harpacticoida in these samples. Due to the high frequency and abundance in deep-sea samples, *Eurycletodes* is an interesting and informative taxon for chorological, faunistic, and biogeographical research. The number of species as well as species diversity in the deep sea is high, and the species are well discernible.

Within Argestidae, *Eurycletodes* is characterized by a relatively large body size (about 1 mm body length) and shows distinctive morphological features that allow rapid recognition in metazoan meiofauna samples: body of cylindrical shape, A1 6-segmented, P1 exp short in relation to the exps of P2–P4, P2–P4 enps at most 2-segmented, P5 foliaceous, telson square, furcal rami square to rectangular, at most 3 times as long as wide. *Eurycletodes* contains 26 species, 4 of which belong to the subgenus *Eurycletodes* (*Eurycletodes*) (*E. (E.)*) Lang, 1944, and 20 belong to *Eurycletodes* (*Oligocletodes*) (*E. (O.)*) Lang, 1944. Allocation of 2 species to one of the subgenera has not been possible to date (Wells 2007). The morphological features used to characterize *Eurycletodes* and to assign species to one of the subgenera are re-evaluated according to phylogenetic aspects. Furthermore, this publication contains the description of *Eurycletodes (O.) diva* sp. nov. from the Cape Basin and the Angola Basin.

The type locality of *Eurycletodes (O.) diva* sp. nov., the Cape Basin, was sampled during expedition DIVA-2, while

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the paratype was found in samples taken during the preceding expedition DIVA-1 in the Angola Basin. The 2 deep-sea basins are separated by the Walvis Ridge (Shannon and Nelson 1996).

Materials and methods

Sediment samples were taken with a multicorer during the cruises DIVA-1 (M48/1) from July 6 to August 2, 2000 (Martínez Arbizu and Schminke 2005) and DIVA-2 (M63/2) from February 25 to March 10, 2005 (Türkay et al. 2005) on board the RV “Meteor” to the Cape Basin, Angola Basin, and Guinea Basin (Fig. 1). For methodology and sample treatment, see Rose et al. (2005). The copepods were mounted on separate slides using glycerol as the embedding medium. Identification at species level and drawings were done using a DMR Leica microscope equipped with a camera lucida and interference contrast at a maximum magnification of 1600 \times .

The type material was deposited in the collection of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt (Germany). Abbreviations used in the text are: aes (aesthetasc), cphth (cephalothorax), enp (endopod), exp (exopod), benp (baseoendopod), A1 (antennula), A2 (antenna), md (mandibula), mxl (maxillula), mx (maxilla), mxp (maxilliped), P1–P6 (pereopods 1–6), GF (genital field), and FR (furcal rami). The type material of *E. (O.) denticulatus* Por, 1967 was kindly provided by Prof.

Francis Dov Por and Dr. Ariel Chipman from the Hebrew University of Jerusalem in Israel.

Taxonomy

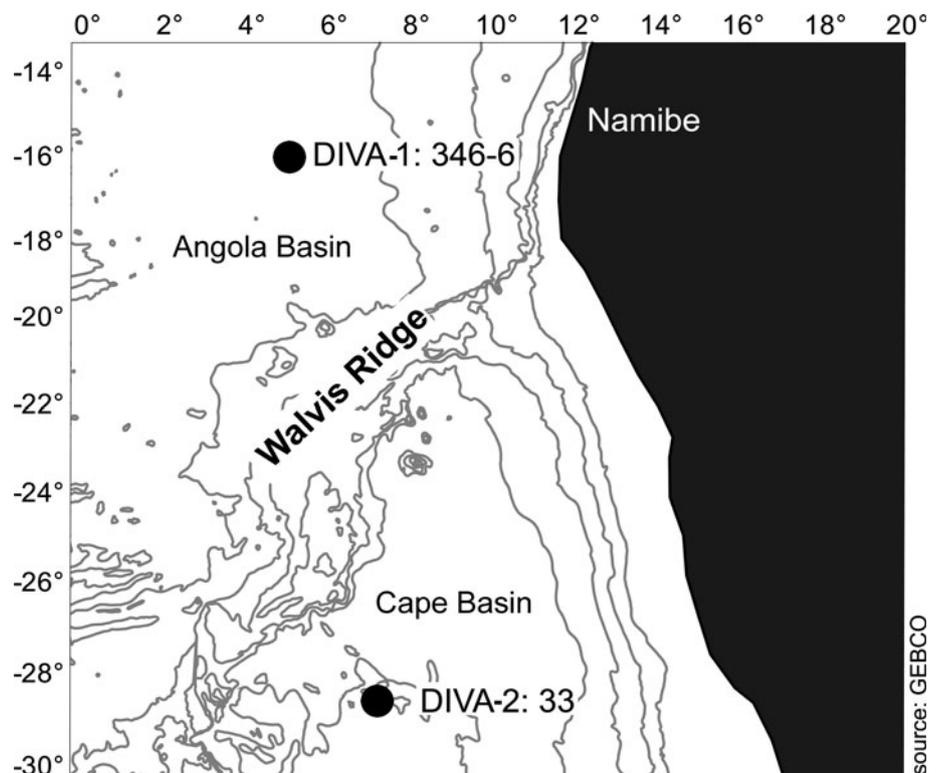
Argestidae Por, 1986b

Eurycletodes Sars, 1909

Type species: *Eurycletodes (E.) laticauda* (Boeck, 1872) (described as *Cletodes laticauda*).

Additional species: *Eurycletodes* contains 26 species (Boxshall and Halsey 2004; Wells 2007), including the new species described herein: *E. ephippiger* Por, 1964b; *E. (E.) gorbunovi* Smirnov, 1946; *E. (E.) rectangulatus* Lang, 1936; *E. (E.) serratus* Sars, 1921; *E. (O.) abyssii* Lang, 1936; *E. (O.) aculeatus* Sars, 1921; *E. (O.) arcticus* Lang, 1936; *E. (O.) denticulatus* Por, 1967; *E. (O.) echinatus* Lang, 1936; *E. (O.) hoplurus* Smirnov, 1946; *E. (O.) irelandica* Roe, 1959; *E. (O.) latus* (T. Scott, 1892); *E. (O.) major* Sars, 1909; *E. (O.) minutus* Sars, 1921; *E. (O.) monardi* Smirnov, 1946; *E. (O.) oblongus* Sars, 1921; *E. (O.) parasimilis* Por, 1959; *E. (O.) peruanus* Becker, Noodt and Schriever, 1979; *E. (O.) petiti* Soyer, 1964a; *E. (O.) profundus* Becker, Noodt and Schriever, 1979; *E. (O.) quadrispinosa* Schriever, 1986; *E. (O.) similis* (T. Scott, 1895); *E. (O.) uniarticulatus* Smirnov, 1946; *E. (O.) versimilis* Willey, 1935; *E. (O.) diva* sp. nov.

Fig. 1 Positions of the two stations at the DIVA-1 and DIVA-2 expeditions containing the species studied (station DIVA-1: 346-6 and DIVA-2: 33)



Diagnosis (amended from Sars (1909))

Body of cylindrical shape, integument soft and flexible. Cphth comparatively short (at most as long as first 3 free prosomites), rostrum small. Telson large, square, anal operculum broad, semicircular. Furcal rami square to rectangular, at most 3 times as long as wide at the base. A1: 6-segmented, third segment with aes accompanied by 1 seta, sixth segment with acrothek. A2: with allobasis, without abexopodal seta, exp absent or represented by a small bristle. Md: palp small, at most biarticulated, exp represented by at most 1 seta, basal armature absent, gnathobase with 3 elements. Mxl: praecoxal arthrite with several spines, at least 1 surface seta, coxa always expressed, basis with few setae or absent, exp and enp absent. Mx: proximal endite with 2, but mostly only 1 seta. Mxp: strong, prehensile, with strong claw distally. P1–P4: enp at most biarticulate, small, equal in armature at each leg, but decreasing in length from P1 to P4. Exp 3-segmented, of P1 fairly small, of P2–P4 long and slender. P5: endopodal lobe not to extremely protruding, fused in the middle, with at most 3 setae. P5 exp foliaceous, with at most 6 setae. Usually with 1 egg sack, but Lang (1948) observed 2 egg sacks for *Eurycletodes (O.) similis* and *Eurycletodes (O.) minutus*.

Eurycletodes (O.) diva sp. nov.

Figures 2, 3, 4, 5, 6, 7.

Etymology: The name is dedicated to the project DIVA, during which the samples containing the new species were taken.

Locus typicus: Cape Basin (off the West African coast), RV “Meteor”, Cruise M63/2 (DIVA-2), station 33 (28°6.7′S/7°20.8′E, 5035 m), March 3, 2005.

Type material: Holotype: 1 female, dissected, mounted on 16 slides, coll. no. SMF 37000/1–16, RV “Meteor”, Cruise M63/2 (DIVA-2) collected at station 33 (28°6.7′S/7°20.8′E, 5035 m), March 3, 2005.

Paratype: 1 female, dissected, mounted on 4 slides, coll. no. SMF 37001/1–4, RV “Meteor”, Cruise M48/1 (DIVA-1) collected at station 346-6 (16°17.0′S/05°27.0′E, 5389 m), July 27, 2000.

Description of female

Habitus (Fig. 2a, b, c) of cylindrical shape, no clear distinction between prosome and urosome. Body length including FR 0.73 mm. Distal margins of cphth and free thoracic somites with conspicuous, coarsely ornamented denticulated hyaline frill, denticles increasing in size

posteriorly. The hyaline frill of the last 2 urosomites bears a bifid denticle each. Body with several remarkably long sensilla arising from tubercles. Distal margins of second and fifth urosomite without sensilla. Cphth of shield-like appearance. Rostrum slightly protruding, with 2 sensilla. Telson (Figs. 2a, b, c; 3c, d) as large as 3 preceding urosomites together, almost square from lateral and dorsal view, dorsally and laterally covered with stout spinules. Ventrally with 4 rows of 4 long spinules each. Operculum with several denticles (Figs. 2a; 3e).

A1 (Fig. 3a) 6-segmented. All segments textured as shown for part of the first segment. Segment III with aes accompanied by 1 seta, segment VI with acrothek. Setal formula: I: 0; II: 3; III: 4 + aes; IV: 1; V: 1; VI: 9 + acrothek (=11 + aes).

A2 (Fig. 3b) with allobasis, without abexopodal seta. Exp reduced to an almost indiscernible bulb without armature (highlighted by arrow in Fig. 3b). Allobasis and enp covered with spinules. Enp2 with 2 bipinnate spines medially and 4 setal elements terminally, the two outermost fused at the base.

Md (Fig. 4a, b, c) with gnathobase formed by 3 tooth-like projections: ventrally 1 hand-shaped, followed by one medial and one dorsal projection, both terminally serrated. Md palp 1-segmented, with several spinules and 3 endopodal setal elements: 1 inner seta subterminally and 2 terminally. Exp not expressed, basal seta lost.

Paragnaths (Fig. 4d) with several rows of brush-like setae ventrally and several spinules dorsally.

Mxl (Fig. 4e) precoxal arthrite terminally with 6 strongly pinnate spines, subterminally with another bipinnate spine and 1 bare seta ventrally. Coxa with 2 bare apical setae. Basis, enp and exp reduced.

Mx (Fig. 4f) syncoxa with 2 endites. Proximal endite with 2 setae. Distal endite with 3 setae, the biggest one incompletely fused to segment, bipinnate. Basis with 2 strong setae fused to segment and 2 bare setae. Enp distinct, with 2 bipinnate setae.

Mxp (Fig. 4g) prehensile, conspicuously large, syncoxa slightly shorter than basis, with 1 seta and several setules. Basis of triangular shape with spinules of different sizes. Enp 1-segmented, fused to strongly pinnate claw.

P1 (Fig. 5b) with 3-segmented exp and 1-segmented enp. Coxa considerably bigger than basis, with several spinules. Intercoxal sclerite transversely elongated and bow-like. Basis with inner and outer spine, with several groups of spinules and long inner setules. Exp1 without, exp2 with inner seta. Exp3 with 4 elements. Enp with 1 terminal spine, 1 terminal seta and 1 inner seta (the 2 setae are lost during dissection, see arrows in Fig. 5b). For setal formula see Table 1.

P2–P4 (Figs. 5a; 6a, b) with 3-segmented exps and 1-segmented enps. Coxae approximately 2 times bigger

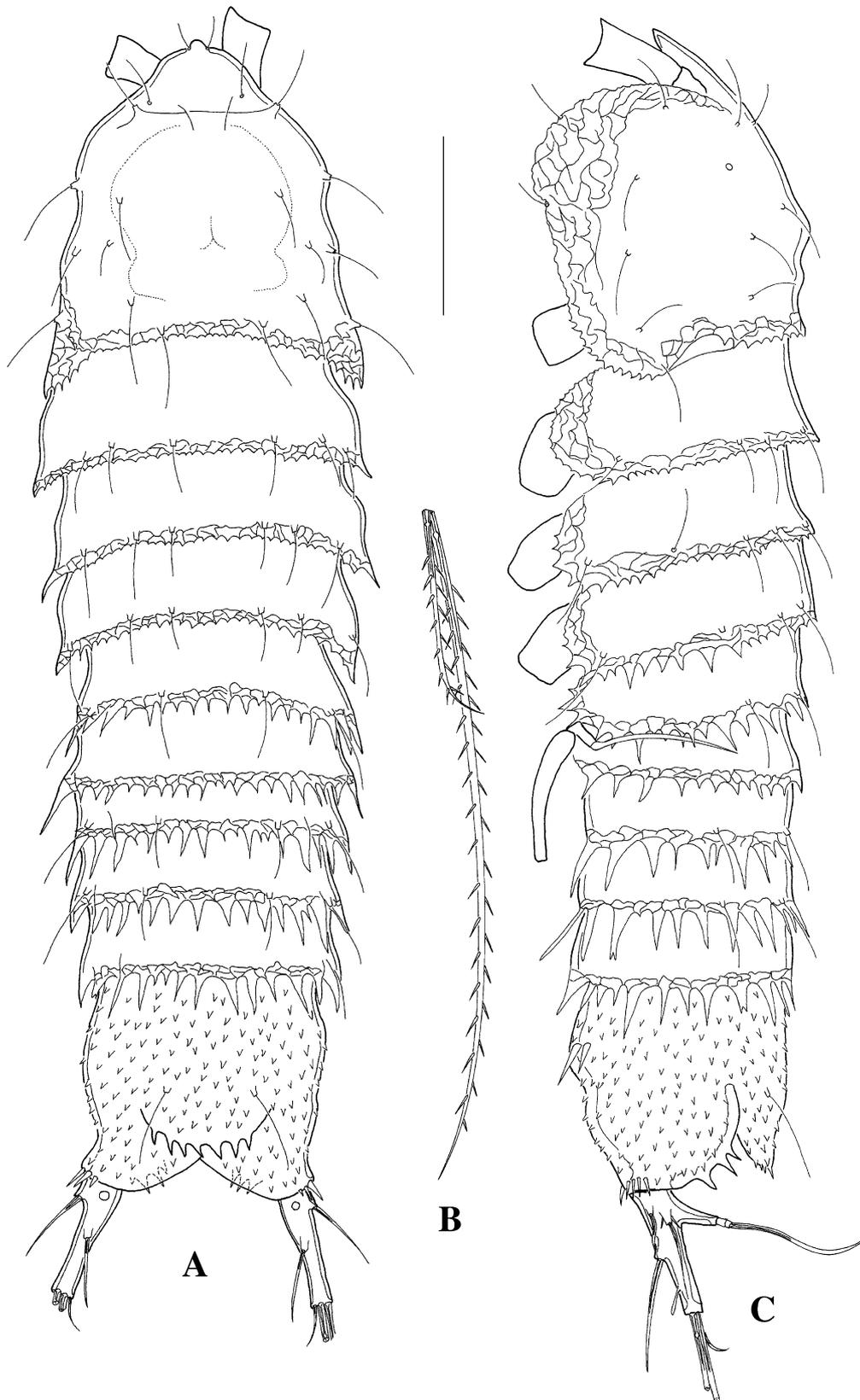


Fig. 2 *Eurycletodes (O.) diva* sp. nov., female (holotype). **a** habitus dorsal view; **b** terminal setae of furcal rami; **c** habitus lateral view. Scale bar 100 μ m

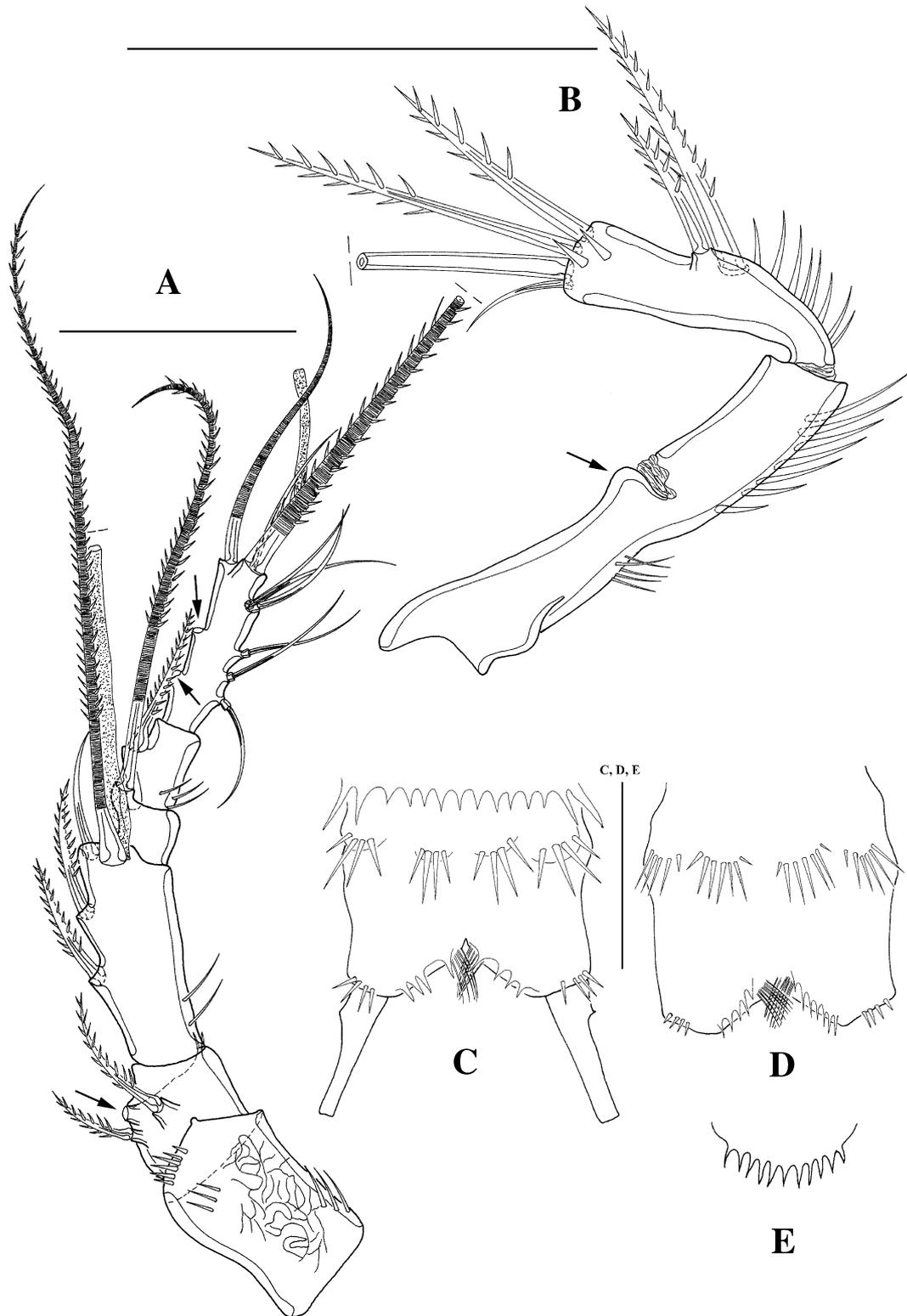


Fig. 3 *Eurycletodes (O.) diva* sp. nov., female. **a** A1 (holotype), inner spines in segments II and VI broken off, highlighted by arrows; **b** A2 (holotype), indiscernible bulb of exp highlighted by arrow;

c Telson ventral view (holotype); **d** Telson ventral view (paratype); **e** operculum dorsal view (paratype). Scale bars **a**, **b** 50 μm; **c**, **d**, **e** 100 μm

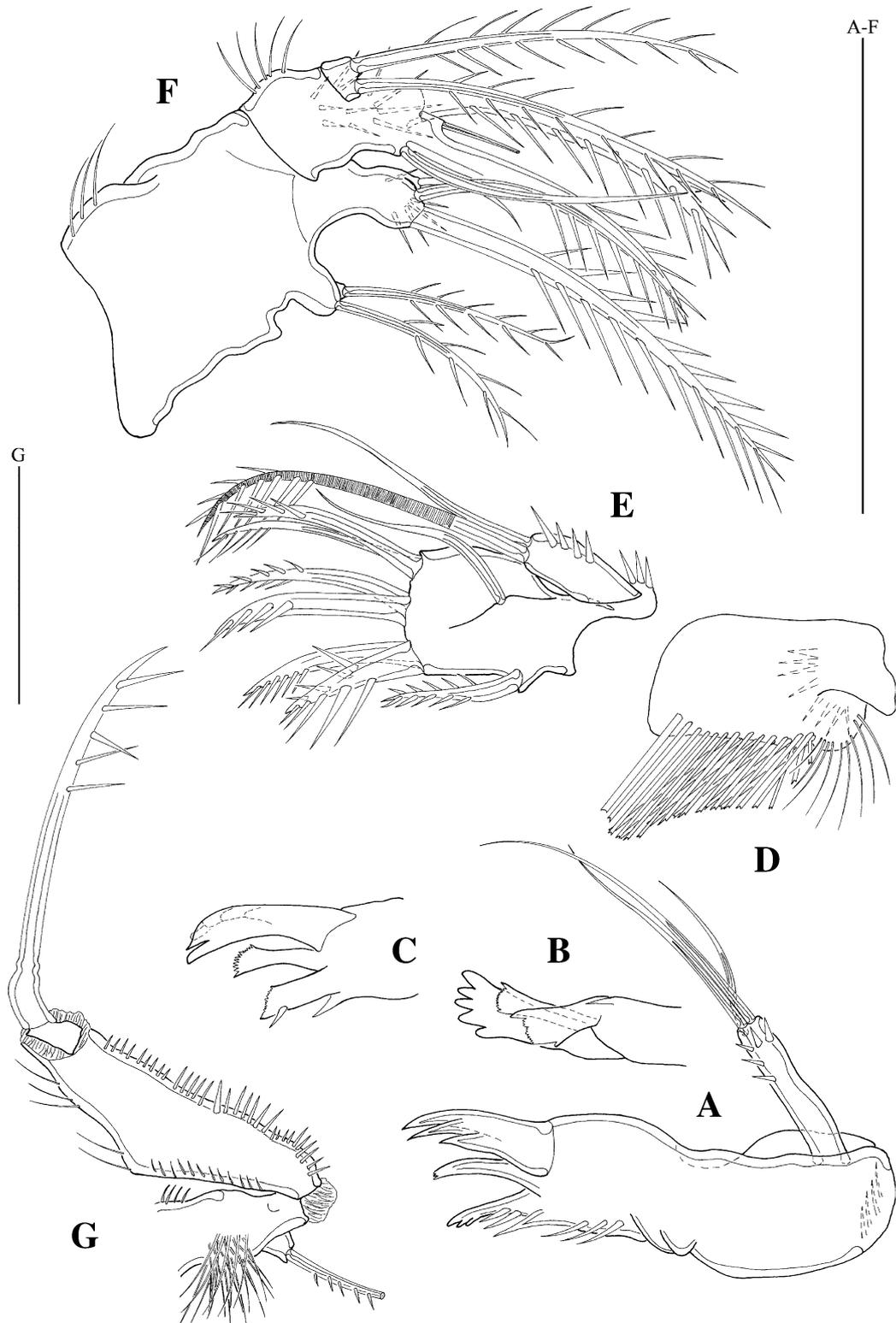


Fig. 4 *Eurycletodes (O.) diva* sp. nov., female. **a** Mandibula (holotype); **b** Mandibula gnathobase (holotype), ventral view; **c** Mandibula gnathobase (holotype), lateral view; **d** Paragnaths (paratype) ventral

view; **e** Maxillula (holotype) ventral view; **f** Maxilla (paratype); **g** Maxilliped (paratype) ventral view. Scale bars 50 μ m

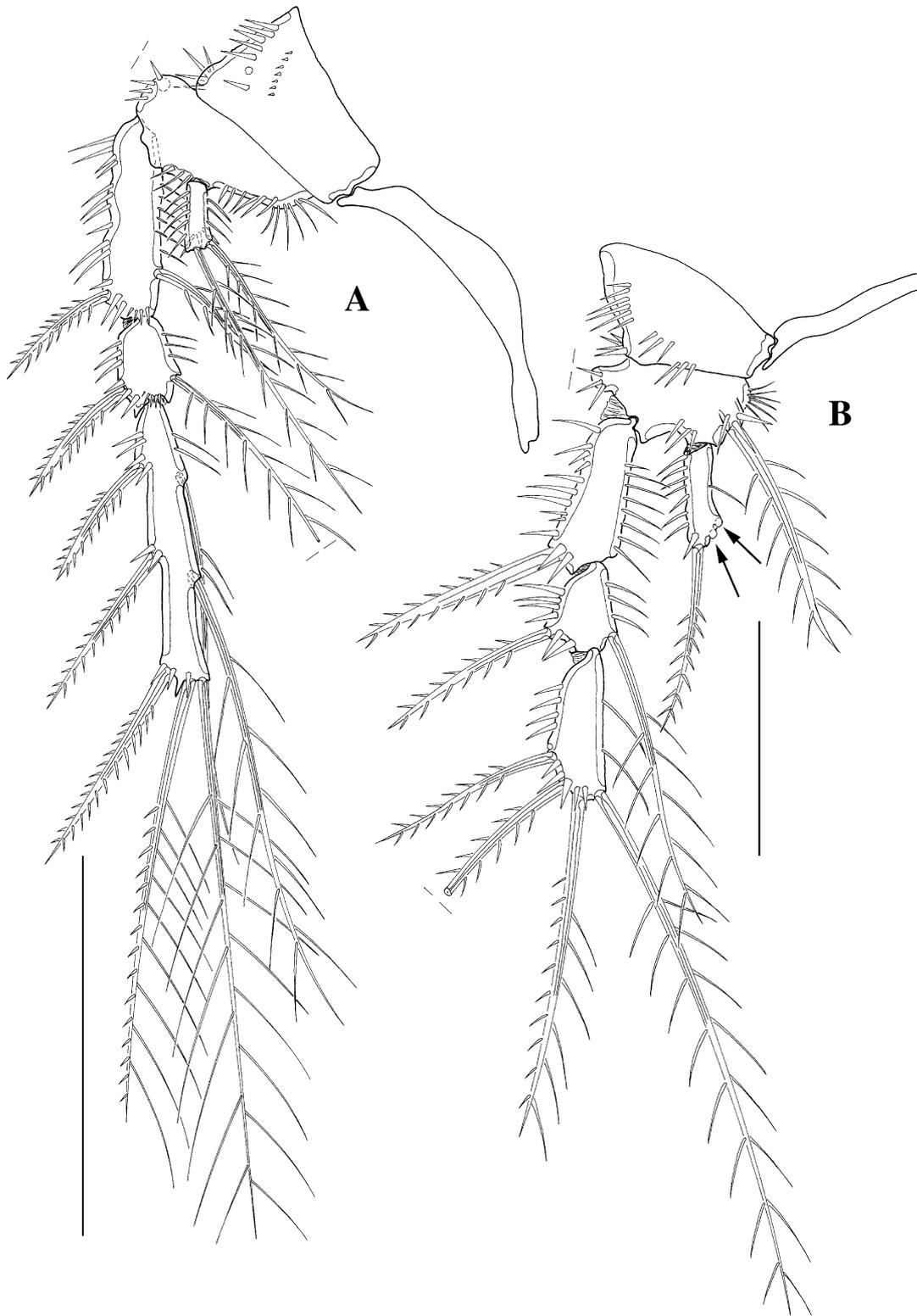


Fig. 5 *Eurycletodes (O.) diva* sp. nov., female (holotype). **a** P2 ventral view; **b** P1 ventral view, terminal and inner endopodal setae broken, highlighted by *arrows*. External basal setae broken. *Scale bars a* 100 μ m; *b* 50 μ m

than bases, with strong spinules at outer margins. Bases 2 times as broad as long, exps and enps translocated outwardly. Bases with outer spines, at inner margin with long

setules. Segments with strong, outer spinules and inner setules. Exp3 almost as long as exp1 and exp2 together. P3 exp1 inner seta lost during dissection of holotype (see arrow

Table 1 *Eurycletodes (O.) diva* sp. nov., setal formula of P1–P4

	Exp1	Exp2	Exp3	Enp
P1	I-0	I-1	2,1,1	0,11,1
P2	I-1	I-1	III,2,2	0,2,0
P3	I-1	I-1	III,2,2	0,2,0
P4	I-0	I-1	III,2,2	0,2,0

in Fig. 6b). P4 exp1 without inner seta, proximal inner seta of exp3 short and bare. P4 exopodal segments with several spinules dorsally. Setation of exp and enp as in Table 1.

P5 (Fig. 7a) with extended setophore, which bears several spinules and long bipinnate seta (lost during dissection, see arrow in Fig. 7a). Endopodal lobe barely protruding, with 2 setae (lost during dissection, see arrow in Fig. 7a). Exp broken during dissection, about 4 times as long as wide basally, with 3 outer and 1 terminal seta. Additionally with 1 short and 1 long tube pore subterminally.

P6 integrated into GF (Fig. 7c), reduced to small lateral bristle (see arrow in Fig. 7c). GF with single aperture.

FR (Fig. 7b) tapering distally. Approximately 3 times as long as wide (measured at its base), with conspicuous long dorsal process arising near the base, bearing the triarticulate seta VII. Seta I displaced ventrolaterally, close to seta II. Seta III medially ventrolaterally, setae IV–VI located terminally. FR ventrolaterally with subterminal tube pore (see arrow in Fig. 7b).

Remarks

Morphological differences between the two type specimens occurred only in the telson and are therefore considered as intraspecific variability: telson of the female paratype with more long spinules ventrally, with 7 denticles distally on each side and anal operculum with 11 denticles (Figs. 2a, b; 3c, d, e).

Male unknown.

Discussion

Historical background

Eurycletodes belongs to the Argestidae, which are large, free-living and typical deep-sea harpacticoid copepods. The first described species of *Eurycletodes* were originally attributed to the genus *Cletodes* Brady, 1872: *Cletodes laticauda* Boeck, 1872, *Cletodes latus* T. Scott, 1892, and *Cletodes similis* T. Scott, 1895. These species were transferred to *Eurycletodes* on its establishment (Sars 1909), which remained in Cletodidae T. Scott, 1904. Only several decades after the morphological characterization of

Eurycletodes Por (1986b) erected the Argestidae and transferred *Eurycletodes* to this new family, which nowadays includes 21 genera, 8 of which are considered to be *incertae sedis* (Bodin 1997; Corgosinho and Martínez Arbizu 2009; George 2004; George 2008).

In 1944, when *Eurycletodes* contained 13 species, Lang suggested two lineages within *Eurycletodes* and defined the subgenera *Eurycletodes (Eurycletodes)* and *Eurycletodes (Oligocletodes)*. *E. (E.)* is characterized by the loss of the inner setal element in P1 exp2 and the presence of 3 setae on P5 endopodal lobe, whereas *E. (O.)* possesses 1 inner seta in P1 exp2 and only 2 setae on P5 endopodal lobe. The type species *E. laticauda* as well as *E. latus* and *E. similis* were integrated into the subgenera as follows: *E. laticauda* was attributed to *E. (E.)* (Lang 1944) as *E. (E.) laticauda*, *E. latus* and *E. similis* became part of *E. (O.)* (Lang 1944; Lang 1948) as *E. (O.) latus* and *E. (O.) similis*. All species described subsequently were accommodated in one of the 2 subgenera, except *E. profundus* and *E. ephippiger* (Wells 2007).

Females are known for all 26 described species of *Eurycletodes*, but males have only been described for 7 species thus far (Griga 1964; Klie 1950; Kornev and Chertoprud 2008; Lang 1948; Por 1959; Por 1967; Schriever 1986; Smirnov 1946; Soyer 1964a; Willey 1935). Sexual dimorphism has been observed in the A1, the armature of P5, and the ornamentation of the urosome (Soyer 1964a). The morphology of the remaining characters, such as pereopods, mouthparts, general appearance and body shape, seems to be same in males and females. Thus, the males of *E. (O.) diva* sp. nov. should be recognizable if present in the samples.

Remarks on the phylogenetic status of *Eurycletodes* and its two subgenera *Eurycletodes (E.)* and *Eurycletodes (O.)*

Members of *Eurycletodes* conform with most of the morphological features of Argestidae as listed by Por (1986b) and George (2004), but the exact positioning inside Argestidae is still unclear. However, the highly derived character states (e.g. the loss of setae and fusion or loss of segments) suggest a rather derived position within Argestidae.

The generic diagnosis of *Eurycletodes* (Sars 1909) enabled many authors to assign new species to this genus. However, there has been no phylogenetic characterization of *Eurycletodes* to date, thus, the characters were merely diagnostic. Only recent investigations provide a first phylogenetic characterization of the genus *Eurycletodes*, based on three characters, which were revealed to be apomorphic for this genus [plesiomorphic states in brackets]:

- (1) A1 segments III + IV fused [segments clearly separated]

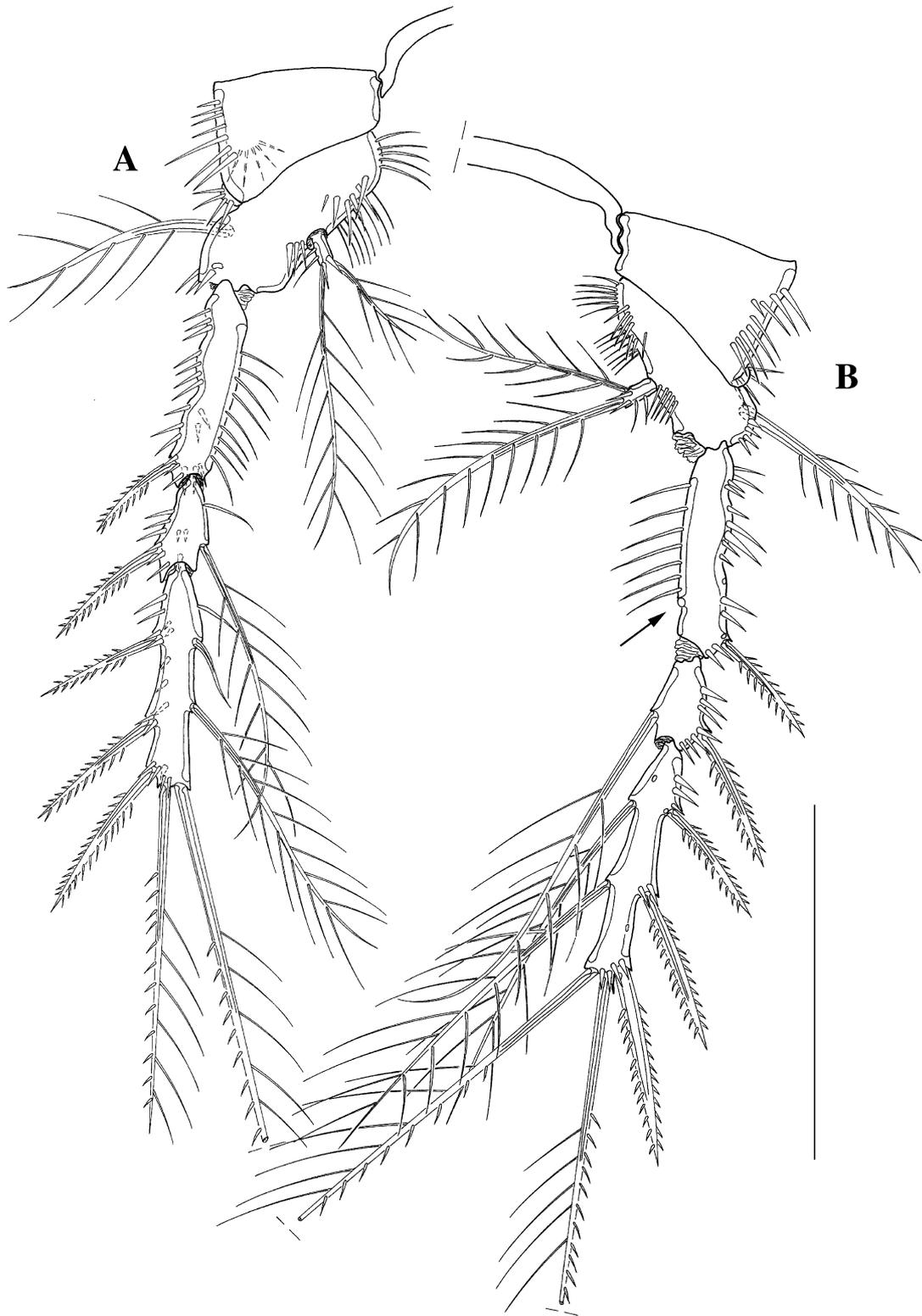


Fig. 6 *Eurycletodes (O.) diva* sp. nov., female (holotype). **a** P4 ventral view; **b** P3 ventral view, inner seta in exp1 broken, highlighted by arrow. Scale bar 100 μ m

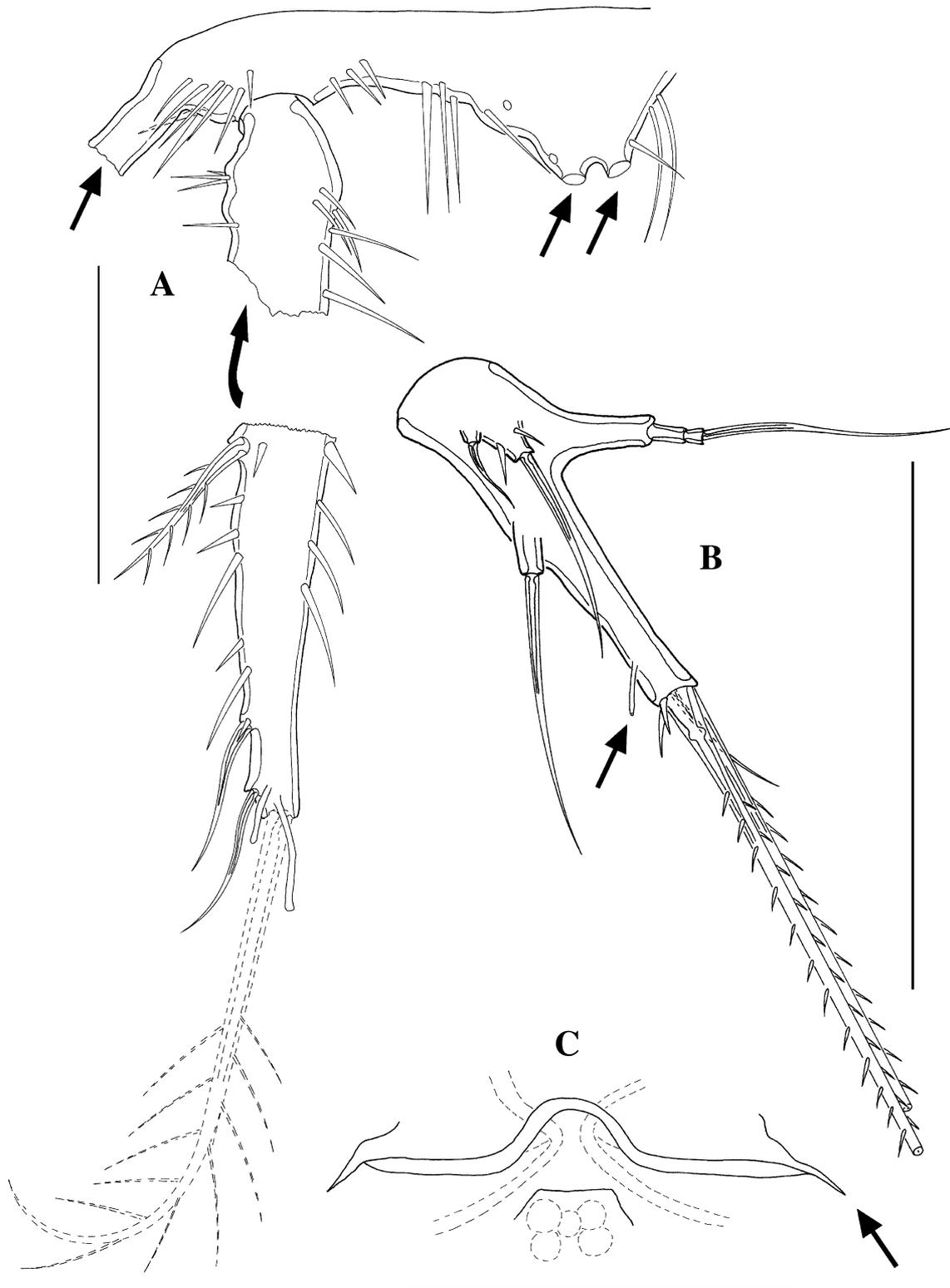


Fig. 7 *Eurycletodes (O.) diva* sp. nov., female (holotype). **a** P5, ventral view, exp broken into 2 parts, terminal seta of exp completed from counterpart, setae of endopodal lobe broken during dissection

(see arrows); **b** Furcal ramus, lateral view, arrow highlights subterminal tube pore; **c** Genital field, P6 highlighted by an arrow. Scale bars **a**, **c** 50 µm; **b** 100 µm

- (2) Md palp basal seta lost [present]
 (3) Md palp exp reduced to 1 seta [segment expressed]

Character (1) A1 segments III + IV fused [segments clearly separated]

In basal female Argestidae, the A1 consists of 8 distinct articles, segments IV and VIII possess aesthetascs. Segment III is provided with several inner spines and few inner and lateral setae. Segment IV (further named: proximal aes-bearing segment) bears at most 2 setae and 1 spine (George (2008); personal observations) plus an aes accompanied by 1 long seta. The exact number of setal elements is species specific.

In several species within Argestidae, the proximal aes-bearing segment is elongated in relation to the following segments and bears more setal elements than characteristic of this segment. Segment III is not separated from segment IV, but its setal elements occur in the aes-bearing segment. As follows, a fusion of original segments III + IV is obvious, even if homologization of all setae (mainly based on original descriptions) has not been possible to date. Besides all members of *Eurycletodes*, several species belonging to different genera show this characteristic fusion: 5 species out of 36 of *Mesocletodes* Sars, 1909 [*M. abyssicola* (T. and A. Scott, 1901), *M. bathybia* Por, 1964b, *M. bodini* Soyer, 1975, *M. opoteros* Por, 1986a and *M. parabodini* Schriever, 1983] and four monotypic or at most bitypic genera (*Dizahavia* Por, 1979, *Corallicletodes* Soyer, 1966, *Hemicletodes* Lang, 1936, and *Hypalocletodes* Por, 1967) show a fusion of these A1 segments. However, this fusion of A1 segments III + IV is regarded as apomorphic to *Eurycletodes*, a convergent development in the remaining species is considered plausible.

Mesocletodes was recently characterized as a monophylum (Menzel and George 2009): (a) second A1 segment with a strong protrusion bearing one strong, bipinnate seta, (b) proximal outer spine of P1 exp3 is reduced, (c) P1 exp3 spines are equipped with subapical tubulate extensions, and (d) md gnathobase forms a strong grinding face. Species in which the fusion of A1 segments III + IV occurs hold a derived position within *Mesocletodes*.

Dizahavia shows a series of morphological characters probably connecting it to basal Argestidae, such as *Argestes* Sars, 1910 and *Fultonia* T. Scott, 1902: the complete body is covered with small cuticular spinules (George 2008), the md palp bears 2 basal setae, P3 exp3 has 3 inner setae, P2 and P3 show 3 distinct endopodal segments, the setae of short furcal rami are inserted close to the posterior margin.

Assuming the fusion of A1 segments III + IV as a synapomorphy of *Eurycletodes*, *Mesocletodes*, and *Dizahavia* would imply a secondary separation of the corresponding A1 segments in most species of the monophyletic

Mesocletodes as well as in *Argestes* and *Fultonia*. Therefore, a convergent fusion of A1 segments III + IV in *Eurycletodes* and the 6 species is considered plausible.

The genera *Corallicletodes*, *Hemicletodes*, and *Hypalocletodes* were established in order to accommodate new species that could not be attributed to any genus known at that time: *Corallicletodes boutieri* Soyer, 1966, *Hemicletodes typicus* Lang, 1936, and *Hypalocletodes salomonis* Por, 1967. *Hypalocletodes aberrans* (Marinov, 1973) was added subsequently. With the establishment of the new genera, the 4 species are clearly excluded from *Eurycletodes*. However, the original descriptions are incomplete and poorly detailed. References on their phylogenetic positioning are very scarce and not helpful in resolving the question of whether the fusion of A1 segments III + IV is synapomorphic or convergent to *Eurycletodes*. At present, it is not possible to address this issue, but preliminary results of ongoing studies suggest a convergent fusion in *Eurycletodes* and the 3 genera in question.

Consequently, the fusion of A1 segments III + IV is considered to be apomorphic to *Eurycletodes*.

Character (2) Md palp basal seta lost [present] and Character (3) Md palp exp reduced to 1 seta [segment expressed]

The md palp of basal Argestidae (e.g. *Argestes*, *Fultonia*) possesses a clearly articulated basis, enp and exp and bears setae on all 3 segments. Species of *Eurycletodes* show a poorly developed md palp, at most biarticulate, but usually unarticulated and with none (*E. (O.) irelandica*) to 5 setae (*E. ephippiger*). Soyer (1964a) described the md palp of *E. ephippiger* with articulated enp equipped with 4 setae and 1 external basal seta, but without exp. Throughout Copepoda, external basal setae have not been observed thus far (e.g. Huys and Boxshall 1991; Seifried 2003). However, reduction of basal setae has been observed, for example in *Malacopsyllus* Sars, 1911 (e.g. Becker 1974; Itô 1983). Thus, it seems likely that the external basal seta described for *E. ephippiger* (Soyer 1964a) in fact represents an exp reduced to 1 seta. Accordingly, species possessing an enp (which is mostly fused to the basis) and external setae on the md palp are supposed to have lost the basal seta, but retained a (strongly reduced) exp. This condition is described for 4 species (*E. ephippiger*, *E. (O.) echinatus*, *E. (O.) minutus*, and *E. (O.) peruanus*). If only terminal (endopodal) setae are present, the exopodal armature should be missing too. A complete loss of the exp and basal setae is reported for 15 species of *Eurycletodes* (*E. (E.) laticauda*, *E. (E.) serratus*, *E. (O.) aculeatus*, *E. (O.) denticulatus*, *E. (O.) hoplurus*, *E. (O.) irelandica*, *E. (O.) latus*, *E. (O.) major*, *E. (O.) monardi*, *E. (O.) oblongus*, *E. (O.) petiti*, *E. (O.) profundus*, *E. (O.) quadrispinosa*, *E. (O.)*

similis, and *E. (O.) diva* sp. nov.). The original descriptions of the remaining 7 species of *Eurycletodes* (*E. (E.) gorbunovi*, *E. (E.) rectangulatus*, *E. (O.) abyssi*, *E. (O.) parasimilis*, *E. (O.) arcticus*, *E. (O.) uniarticulatus*, and *E. (O.) versimilis*) conceal information regarding the chaetotaxy of the palpus.

The loss of the basal seta and a strongly reduced exopod are discussed herein as apomorphic for *Eurycletodes*.

The following characters (4)–(6) provide information on the phylogeny within *Eurycletodes* [plesiomorphic states in brackets]:

- (4) P1 exp2 inner seta lost [present]
- (5) P4 exp1 inner seta lost [present]
- (6) P5 endopodal lobe inner seta lost [present]

Character (4) P1 exp2 inner seta lost [present]
and Character (5) P4 exp1 inner seta lost [present]

P1–P4 exps of Argestidae are, with exception of P4 exp in *Hemicletodes*, always 3-segmented (e.g. Por 1986b). While the outer exopodal setation is highly conservative, the inner exopodal armature appears to be more variable.

The loss of the inner seta in P1 exp2 has exclusively been observed in species belonging to *E. (E.)* and is therefore considered apomorphic to this subgenus.

In order to characterize *E. (O.)*, Soyer (1964a) suggested considering the loss of the inner seta in P4 exp1. However, recent observations do not support this view. In addition to all members of *E. (E.)*, *E. ephippiger*, *E. (O.) echinatus*, *E. (O.) profundus*, and *E. (O.) peruanus* bear an inner seta on this segment. Thus, the loss of the inner seta in P4 exp1 is not considered apomorphic to *E. (O.)*, but might prove to be informative to characterize a monophylum within this subgenus.

The absence of the inner setae in P1 exp2 and P4 exp1 has also been observed in *Hypalocletodes*, *Leptocletodes* Sars, 1921, *Megistocletodes* Por, 1986a, and *Mesocletodes*. It is noteworthy that these genera always show these characters combined, while species of *Eurycletodes* show either one or the other condition (see above). A close relationship based on the absence of the inner setae in P1 exp2 or P4 exp1 is not deemed plausible, since these features are not present in all species of *Eurycletodes* and thus would imply a secondary regain of the setae in question.

Therefore, the view of a convergent loss of setae of *Eurycletodes* and the 4 remaining genera is adopted here.

Character (6) P5 endopodal lobe inner seta lost [present]

To date, P5 morphology has only been used for species discrimination, but not for characterization of monophyla

within Argestidae. However, since a reduction in setae and the virtual absence of the lobe is considered to be a derived condition (e.g. Huys and Boxshall 1991), especially the chaetotaxy of the P5 endopodal lobe might prove to be phylogenetically informative. To what extent the shape and specifically the virtual absence of the endopodal lobe reflects convergent development or sexual dimorphism (c.f. Kornev and Chertoprud 2008; Por 1967) is not discussed herein, but is subject to ongoing and future studies.

Homologization of setae on P5 endopodal lobe of *Eurycletodes* reveals the outer and medial setae as being inserted terminally and near each other, whereas the inner seta is inserted subterminally into the inner edge. Similar morphology of the P5 endopodal lobe has been observed for several argestid genera (i.e. *Bodinia* George, 2004, *Dizahavia*, *Mesocletodes*, and *Odiliacletodes* Soyer, 1964a). Therefore, this condition is regarded as plesiomorphic to *Eurycletodes*. This character state with 3 setae on the P5 endopodal lobe is retained in all species of *E. (E.)* plus *E. ephippiger*. The derived character state of 2 setae (outer and medial) inserted terminally on the P5 endopodal lobe, while the subterminal (inner) seta is lost, was observed in all members of *E. (O.)* and is therefore considered apomorphic to this subgenus. The female of *E. profundus* shows only one terminal seta (Becker et al. 1979). The proceeded loss of the second terminal seta represents an even more derived character state. Therefore, *E. profundus* clearly belongs to *E. (O.)*.

In conclusion, the phylogenetic status of *Eurycletodes* and its two subgenera *E. (E.)* and *E. (O.)* is as follows: the characteristic fusion of segments in A1 (character 1) as well as the setation of the md palp (characters 2 and 3) clearly characterize and separate *Eurycletodes* from the remaining Argestidae. Becker et al. (1979) suggested including *Leptocletodes* as a subgenus in *Eurycletodes*. But apart from morphological discrepancies, *Leptocletodes* does not share the apomorphies of *Eurycletodes* [A1 segments III + IV are separated in *Leptocletodes* and the md palp bears a well-developed basal seta. The condition of the exp is not apparent from the corresponding species descriptions (Sars 1921; Smirnov 1946)].

For the first time, characters traditionally used for discrimination between the two subgenera *E. (E.)* and *E. (O.)* were interpreted phylogenetically and could be confirmed as apomorphies. The loss of the inner seta in P1 exp2 (character 4) is apomorphic to *E. (E.)*, the loss of the inner seta in P5 endopodal lobe (character 6) is an apomorphy for *E. (O.)*. Based on this reinterpretation, allocation of *E. profundus* is no longer problematic: the reduction to a single seta on P5 endopodal lobe is regarded as a derived state of the apomorphy of *E. (O.)*. Thus, it is necessary to include the subgeneric designation in the species name: *E. (O.) profundus*.

Conversely, the positioning of *E. ephippiger* remains unresolved, since this species does not show any apomorphy of either of the 2 subgenera: the presence of an inner seta on P1 exp2 (character 4) rejects its position within *E. (E.)*, the presence of three setae on P5 endopodal lobe (character 6) rejects its position within *E. (O.)*. Therefore, it seems reasonable to place *E. ephippiger* as the only species without a subgeneric designation at the most basal position of *Eurycletodes*. But doing so causes another difficulty: based on the available data, it is impossible to find synapomorphies for *E. (E.)* and *E. (O.)* and to exclude *E. ephippiger*. The position of *E. ephippiger* will be the subject of future research.

Allocation of *Eurycletodes (O.) diva* sp. nov. to *Eurycletodes*

The allocation of *E. (O.) diva* sp. nov. to the taxon *Eurycletodes* was indisputable. In addition to all generic characters of *Eurycletodes*, the two females of *E. (O.) diva* sp. nov. show the herein defined apomorphies of *Eurycletodes*: the fusion of A1 segments III + IV (character 1) and basal seta and exopodal element of md palp is completely reduced (characters 2 and 3). The loss of the inner seta of the P5 endopodal lobe (character 6) justifies the placement of the new species in *E. (O.)*.

E. (O.) diva sp. nov. seems to be closely related to *E. (O.) denticulatus*, which itself was described as very similar to *E. (O.) aculeatus* (Por 1967). These species share 1-segmented endopods of P1–P4, loss of the proximal outer spine in P1 exp3 and loss of the subterminal inner seta in P5 exp. The phylogenetic significance of these characters will be the subject of future studies.

Beyond that, *E. (O.) diva* sp. nov. is morphologically different from both species by virtue of the slightly protruding P5 endopodal lobe and the elongated furcal rami. Furthermore, it differs from *E. (O.) aculeatus* based on the absence of A2 exopodal seta, 2 setae in mx proximal endite instead of one and a short proximal inner seta in P4 exp3. In contrast to *E. (O.) denticulatus*, *E. (O.) diva* sp. nov. shows a larger body size and has 2 inner setae on the last segment of A1. Generally, the FR of *Eurycletodes* are not much longer than their width. But in some species (*E. (O.) similis*, *E. (O.) latus*, and *E. (O.) diva* sp. nov.), the distance between setae VII and IV is greater, resulting in an elongation. However, comparison of original descriptions revealed *E. (O.) similis* and *E. (O.) latus* possessing 2-segmented enps in P1–P4 and only 2 setae on the md palp. As a result, they are morphologically different from *E. (O.) diva* sp. nov., *E. (O.) denticulatus*, and *E. (O.) aculeatus*. Therefore, a convergent elongation of the FR in *E. (O.) diva* sp. nov. is considered plausible.

On the other hand, in all specimens of a yet undescribed species of *Mesocletodes*, collected from different regions in the deep sea, the FR are extremely elongated. However, the total length seems to be species specific as also is the length, setation, and spinulation of appendages (Menzel unpublished data). Thus, the deviating proportions in *E. (O.) diva* sp. nov. from *E. (O.) denticulatus* combined with a high resemblance in other characters could lead to the conclusion that the new species is a variant of *E. (O.) denticulatus*. Nevertheless, there is a series of *Eurycletodes* species in addition to *E. (O.) denticulatus*, and *E. (O.) aculeatus* with only small divergences in segmentation and setation of appendages and body proportions: *E. (O.) abyssi*, *E. (O.) hoplurus*, *E. (O.) major*, *E. (O.) minutus*, and *E. (O.) oblongus*. Intraspecific variability has not been subject to comprehensive studies yet, only the diverging ventral spinulation of the telson in the holotype and the paratype of *E. (O.) diva* sp. nov. is initial evidence for this (see Figs. 2a, b; 3c, d, e). Studies on the phylogeny within *Eurycletodes* are still in progress, but it appears that the morphological differences between species might be very small. In this respect, *E. (O.) diva* sp. nov. is clearly rated as a new species since there are minute, but sharp characters that separate it from closely related species: body size larger, FR elongated, A1 last segment with 2 inner setae, P5 endopodal lobe less protruding.

Brief remarks on the geographic distribution of *Eurycletodes (O.) diva* sp. nov.

Metazoan meiofauna is traditionally considered to be strongly bound to the sediment and without life stages that enter the water column, as for example, larvae of many sessile organisms do. Therefore, metazoan meiofauna is considered to show limited mobility (e.g. Hicks and Coull 1983; Higgins and Thiel 1988; Hulings 1971; Sterrer 1973). This implies that detection of the same species or even closely related species in remote regions of the oceans or on different sides of an obstacle should be quite improbable. However, Giere (2008), for example, rates metazoan meiofauna, and harpacticoid copepods among others, as highly motile with a high probability of emerging in the water column and being dispersed by water currents (see also Thistle and Sedlacek 2004 and Thistle et al. 2007). Therefore, detection of the same species in remote regions of the oceans is quite conceivable, especially since an exchange of vast water masses with possible transport of particles near the bottom occurs in the deep oceans. Recently, Gheerardyn and Veit-Köhler (2009) verified for certain congeners of Paramesochridae Lang, 1944 distribution ranges that span thousands of kilometers across the South Atlantic and Southern Ocean Abyssal Plains. This family of harpacticoid copepods has considerably reduced

pereiopods and is therefore dependent on other ways of dispersion than active swimming. Investigations into the effects of plate tectonics on the distribution of deep-sea Paramesochridae are outstanding.

The published records of *Eurycletodes* indicate a worldwide distribution at the genus level: the North Atlantic (Scandinavian coast (Lang 1948; Por 1964a, 1965; Sars 1909, 1921), Irish, English, and Scottish coasts (Roe 1958; Scott 1892, 1895), Spitzbergen coast (Lang 1936), Arctic Ocean (Smirnov 1946), Icelandic coast (Schriever 1986), off North Carolina (Coull 1973), French Atlantic coast (Bodin 1968), Iberian Basin (Becker et al. 1979), North Sea (Klie 1950), Great Meteor Bank (George and Schminke 2002), and near the Bermuda Islands (Roe 1959; Willey 1935)), the whole Mediterranean Sea (Pesta 1959; Por 1964b; Soyer 1964a, b) Black Sea (Apostolov and Marinov 1988; Griga 1964; Por 1959), Red Sea (Por 1967), equatorial Pacific (Peru Trench (Becker et al. 1979)), and Southwest Atlantic (George 2005). However, practically nothing is known regarding the distribution of *Eurycletodes* at the species level.

The description of *E. (O.) diva* sp. nov. represents the first record of a species of *Eurycletodes* in the Southeast Atlantic Ocean. Moreover, the geographic provenance of the 2 specimens provides information on the distribution of *Eurycletodes* at the species level. The holotype was found in the northern Cape Basin, the paratype in the southern Angola Basin, both at about 5000 m depth (see Fig. 1). These two localities in the different deep-sea basins are geographically very distant from each other (about 1000 km) and separated by the Walvis Ridge, which rises up to an average depth of about 3000 m (Shannon and Nelson 1996). Recent studies (e.g. Gheerardyn and Veit-Köhler 2009, Seifried and Martínez Arbizu 2008) and the present report of *E. (O.) diva* sp. nov. from these two deep-sea basins indicate that the Walvis Ridge does not interrupt the distribution of certain harpacticoid species.

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