



Establishment of a new subfamily of Idyanthidae Lang, 1944 with the description of a new species of *Pseudometeorina* George & Wiest, 2015 (Copepoda, Harpacticoida) from the Eratosthenes Seamount (eastern Mediterranean Sea)

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Abstract

The description of *Pseudometeorina eratosthenica* sp. nov. from the eastern Mediterranean Eratosthenes Seamount was the release for a detailed phylogenetic comparison of a group of derived representatives of the family Idyanthidae Lang, 1944, namely *Aspinothorax* Moura & Martínez Arbizu, 2003, *Meteorina* George, 2004, *Pseudometeorina* George & Wiest, 2015, and *Styracothorax* Huys, 1993. The named genera share the derived presence of a 2-segmented P1 exopod as well as the transverse elongation of the bases of the swimming legs P1–P4, being these five deviations unique for Idyanthidae and therefore hypothesized here as synapomorphic for the above-named taxa. Consequently, they are pooled in the newly established Aspinothoracinae Moura & Martínez Arbizu, 2003 subfam. nov. The new species described from Eratosthenes Seamount doubtlessly belongs to *Pseudometeorina*, sharing with *P. mystica* George & Wiest, 2015, a set of 24 synapomorphies. Otherwise, *P. eratosthenica* sp. nov. provides nine autapomorphies that justify its establishment as distinct species. A detailed phylogenetic analysis, based on 131 morphological characters, is presented. Moreover, a key to the species of Aspinothoracinae subfam. nov. is provided.

Keywords Aspinothoracinae subfam. nov. · Crustacea · Meiofauna · Taxonomy · Systematics

Introduction

According to the exhaustive compilation of Harpacticoida undertaken by Wells (2007), the taxon Idyanthidae Lang, 1944 encloses nine genera, namely *Aspinothorax* Moura & Martínez Arbizu, 2003 (monotypic), *Dactylopiia* Becker, 1974 (monotypic), *Idyanthe* Sars, 1909 (four

species), *Idyella* Sars, 1905 (seven species), *Idyellopsis* Lang, 1944 (monotypic), *Meteorina* George, 2004 (monotypic), *Nematovorax* Bröhdick, 2005 (monotypic), *Styracothorax* Huys, 1993 (monotypic), and *Tachidiella* Sars, 1909 (six species). That list is also to be found in the WoRMS database (Walter and Boxshall 2022a), with two discrepancies: (a) these authors do not include *Aspinothorax*, which is instead placed in Tisbidae Stebbing, 1910 (Walter and Boxshall 2022b), however, without providing a phylogenetic justification or reference for that act; (b) the WoRMS database includes *Pseudometeorina* George & Wiest, 2015 (monotypic), which was described years after Wells' (2007) compilation. Thus, following Wells (2007) and including *Pseudometeorina*, the here undertaken analysis refers to the Idyanthidae as comprising 24 species in ten genera, seven of which are monotypic.

George and Wiest (2015) established the taxon *Pseudometeorina* George & Wiest, 2015 to allocate a species that was reported at > 5000 m water depth from the Guinea deep-sea basin (eastern tropical Atlantic Ocean). According to

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This article is a contribution to the Topical Collection *Seamounts and oceanic archipelagos and their role for the biodiversity, biogeography, and dispersal of marine organisms*

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these authors, the systematic position of *P. mystica* George & Wiest, 2015 is unclear; as on the one hand, it resembles the species *Styracothorax gladiator* Huys, 1993, *Aspinothorax insolentis* Moura & Martínez Arbizu, 2003, and in particular *Meteorina magnifica* George, 2004, all assigned to the Idyanthidae Lang, 1944 (Moura and Martínez Arbizu 2003; Seifried 2003; George 2004). On the other hand, *P. mystica* does not present any idyanthid autapomorphy, lacking especially the sexually dimorphic male P2 (George and Wiest 2015), which is a characteristic apomorphy of the Idyanthidae (Seifried 2003). Therefore, the assignment of *P. mystica* to Idyanthidae was done as species *incertae sedis* into that family (George and Wiest 2015).

During the research cruise MSM 14/1 of the RV MARIA S. MERIAN (December 2009–January 2010) to the Eratosthenes Seamount, a non-volcanic, isolated continental submarine elevation located south of Cyprus (Fig. 1), meiofauna samples were taken along two transects crossing the top of the seamount using a multiple corer (Christiansen et al. 2012; George 2022). Sampling

material from one station yielded, among others, a single male specimen of a harpacticoid copepod that strongly resembles *P. mystica*. The careful comparison showed, however, that it presents several morphological differences, so it is described here as *Pseudometeorina erasthenica* sp. nov. Besides the species description, the systematics of and within *Pseudometeorina*, as well as its relationship with the above-mentioned idyanthid species, is discussed in detail, based on 131 morphological characters. Moreover, a key to the species of the newly established taxon Aspinothoracinae Moura & Martínez Arbizu, 2003 subfam. nov. is provided.

Material and methods

The meiobenthic material from Eratosthenes Seamount was sampled during the research cruise MSM 14/1 of RV MARIA S. MERIAN to the eastern Mediterranean Sea (December 17, 2009–January 14, 2010; Christiansen et al.

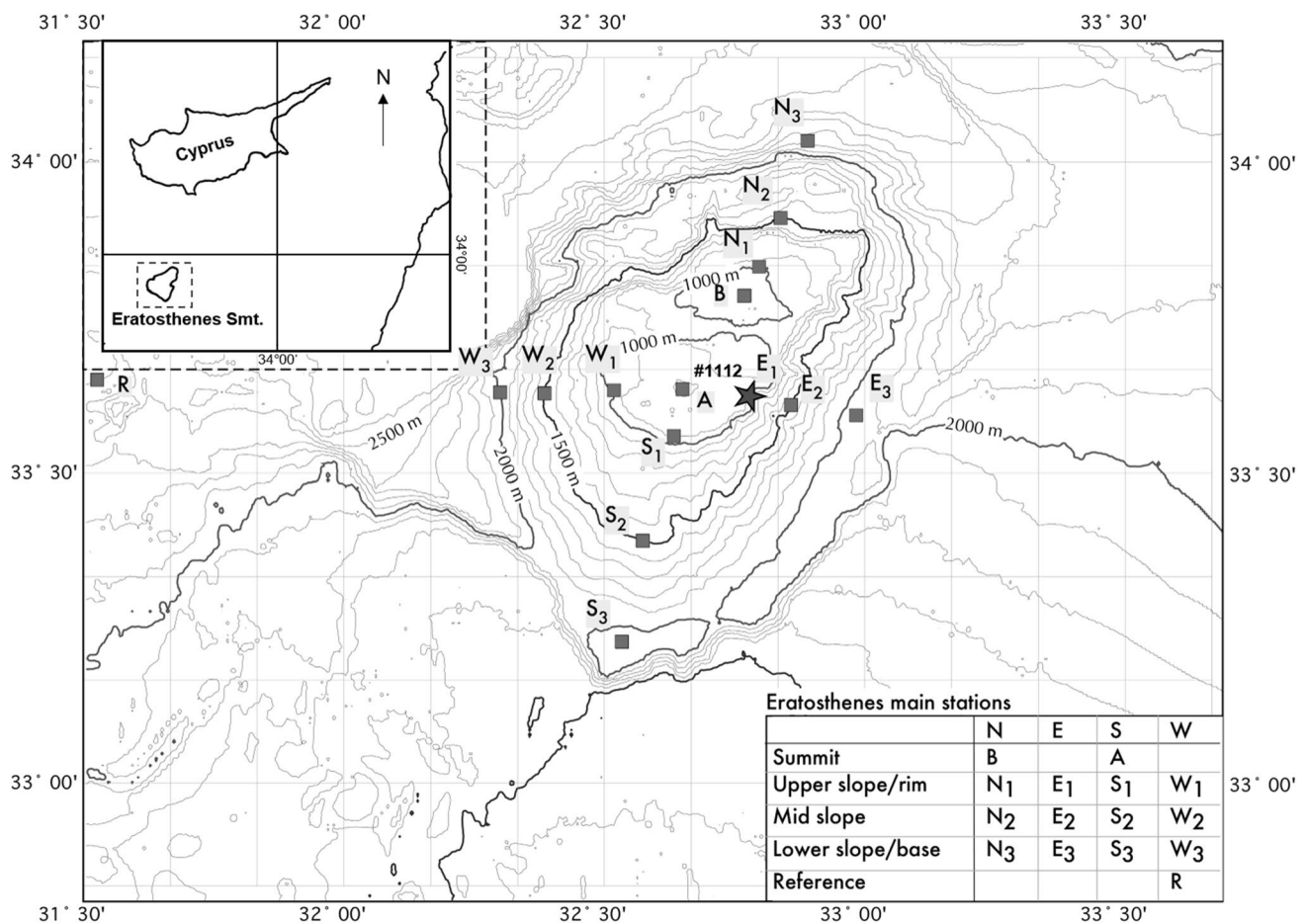


Fig. 1 Map showing the geographic position of the Eratosthenes Seamount (small cut-out on the upper left) and the areas sampled with the multicorer during research cruise MSM 14–1 of RV M.S. Merian

in 2009/2010. The grey star shows station #1112 as type locality of *Pseudometeorina erasthenica* sp. nov. Source: B. Christiansen, Hamburg

2012). Sampling and sample treatment are described in detail by Sevastou et al. (2012) and George (2022). The single male specimen of *Pseudometeorina eratosthenica* sp. nov. was collected on 29.12.2009 with a multiple corer at the eastern transect area E1, station #1112–7 (Fig. 1, grey star).

For the identification of the species, the individual was embedded in glycerol. The dissection was made using a Leica MZ 12–5 stereo microscope; the species identification and drawings were made by means of a camera lucida on a Leica DMR compound microscope equipped with differential interference contrast.

The type specimen is deposited in the collection of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt/Main, Germany.

For the phylogenetic evaluation, the morphological comparison was based on the respective original species descriptions and on the type material of *P. mystica* and *Meteorina magnifica*.

The phylogenetic analysis strictly adopts the concept of “consequent phylogenetics” (Hennig 1982; Ax 1984, 1988, 1995; Sudhaus and Rehfeld 1992; Wägele 2001). It consists of a detailed and comparative character discussion that enables the formulation of an intersubjective hypothesis (Ax 1984). The characterization of monophyla respectively sister groups results from the recognition of exclusive (autapomorphies) or shared deviations (synapomorphies), whilst ancestral (shared) characters ([sym]plesiomorphies) are irrelevant. Computer programs were used neither for the phylogenetic analysis nor for the generation of the presented cladogram (Fig. 8). The latter simply presents the graphic and condensed result of the phylogenetic analysis.

Concerning the number of segments and setae/spines, the generally accepted principle of oligomerization (Huys and Boxshall 1991; Seifried 2003), which postulates that the reduction of segments/elements constitutes the relatively more derived state, was adopted here.

General scientific terminology follows a literal translation of Lang (1948), with additional terms from Huys and Boxshall (1991). Phylogenetic terminology is translated from Ax (1984). The terms “telson” and “furca” are adopted from Schminke (1976).

Abbreviations used in the text:

A1: antennule; A2: antenna; aes: aesthetasc; cphth: cephalothorax; enp-1–enp-3: endopodal segments 1–3; exp-1–exp-3: exopodal segments 1–3; FR: furcal ramus/rami; md: mandible; mx: maxilla; mx1: maxillula; mxp: maxilliped; P1–P6: swimming legs 1–6.

Results

Taxonomy:

Phylum: Arthropoda von Siebold, 1848

Subphylum: Crustacea Brünnich, 1772

Superclass: Multicrustacea Regier et al., 2010

Subclass: Copepoda Milne-Edwards, 1840

Order: Harpacticoida Sars, 1903

Family: Idyanthidae Lang, 1944

Subfamily: Aspinothoracinae Moura & Martínez Arbizu, 2003, subfam. nov.

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Aspinothoracinae subfam. nov.

Idyanthidae Lang, 1944. Body elongate, cylindrical, and tapering posteriorly; podoplean boundary between pro- and urosoma somewhat inconspicuous. Sexual dimorphism in the A1, A2 (*Pseudometeorina*), P2 (not in *Pseudometeorina*), P4(?), P5, P6, and in the fusion of the last thoracic and the first abdominal somite to a genital double somite in the female (not in *Aspinothorax*). Rostrum fused to cphth, small, or prominent. Cephalothorax and free thoracic body somites with or without (*Aspinothorax*) dorsal and/or lateral well-developed cuticular processes that present highly variable ornamentation with spinules or setules; moreover, cphth and body somites smooth or densely covered with fine cuticular denticles (*Styracothorax*). Furcal rami are short (*Styracothorax*) or elongated, with 7 setae. Female antennule 6–7-segmented, in the male 8–10-segmented, haplocer (*Aspinothorax*) or weakly subchirocer (*Meteorina*, *Pseudometeorina*; unknown for *Styracothorax*). Antenna with a basis that bears 1 or lacks an abexopodal seta; endopod 2-segmented, enp-1 with or without an abexopodal seta; enp-2 with 3 lateral and 6–7 apical setae. Exopod of variable shape, size, and setation, generally 1-segmented in males and females, but in *Pseudometeorina* 1-segmented in the female but 3-segmented in the male. Mouthparts are well-developed or considerably atrophied (*Pseudometeorina*). Mandibular palp is rather short or remarkably elongated and slender (*Pseudometeorina*), with 1–2-segmented exopod and 1-segmented endopod. Mxp is well-developed, prehensile, with syncoxa, basis, and 1–2-segmented endopod carrying 1 claw-like apical seta and 2–3 small elements. P1–P4 with considerably transverse elongated bases that clearly surpass the outer lateral margin of the coxae; P1 with 2-segmented exopod; endopod prehensile, longer than exopod and 3-segmented, with strongly elongated enp-1 and apical claw on enp-3 (*Meteorina*), or non-prehensile, shorter than exopod, 1–2-segmented; enp-2 with or without inner and outer setae, and with 1–2 apical setae. P2–P4 with 3-segmented endo- and exopods; P2 with or without sexual dimorphism; if sexual dimorphism is present, then of characteristic idyanthidimorph shape. P5 with reduced or completely lost baseoendopod, bearing or being represented by 0–3 setae; exopod longer than broad, with 3–5 setae; sexual dimorphism observable but highly variable between the species. Female P6 and genital pore small (not discernible

in *Aspinothorax*), P6 bearing 1–3 tiny setae. Where known (*Aspinothorax*, *Meteorina*), the male P6 is rudimentary and forms 2 asetose plates.

Type genus: *Aspinothorax* Moura & Martínez Arbizu, 2003 (by designation). The monotypic *Aspinothorax* was selected, because according to the hypothesis resulting from the here provided phylogenetic analysis it represents the most ancestral of the taxa allocated to the Aspinothoracinae subfam. nov. Additional taxa: *Meteorina* George, 2004 (monotypic), *Pseudometeorina* George & Wiest, 2015 (two species, including the here presented *P. eratothenica* sp. nov.), *Styracothorax* Huys, 1993 (monotypic).

Genus: *Pseudometeorina* George & Wiest, 2015

Generic diagnosis

Idyanthidae, Aspinothoracinae Moura & Martínez Arbizu, 2003. Habitus long, tapering posteriorly, with conspicuous podoplean boundary between pro- and urosoma. Sexual dimorphism in A1, A2, and P5; uncertain for P4; female with genital double somite resulting from the fusion of last thoracic (P6-bearing) and first abdominal somite. Cphth massive, reaching more than 1/3 of total body length, dorsally with a row of spinules along the posterior margin and 3 pairs of lateral processes, the first and second ones smaller than the third pair, located in anterior half; the third pair on lateral half of cphth, long and distally curved, with some sensilla arising from small socles, and with fine setules or long spinules along anterior and posterior margin. Rostrum fused to cphth, elongate, with a rounded tip that bears a tube pore; frontally and/or laterally with fine setules and a pair of sensilla. Free thoracic somites carrying P2–P4 each with a pair of pronounced, backwardly curved lateral processes that bear long setules/spinules on their posterior and/or anterior margins; in addition, P2- and P3-bearing somites with a row of spinules on their posterior margins, P4-bearing somite posteriorly also with the spinulose row or with dentate frill. P5-bearing somite until penultimate abdominal somite laterally with setulose tufts; posterior margins of first four urosomal somites dorsally bare or with dentate frills; preanal somite dorsally with peculiar frill that consists of finger-shaped or smooth triangular appendages that are variable in appearance. Telson is small, broader than long, with an anal operculum that lacks accompanying sensilla. FR long and slender, of peculiar shape, about three times longer than broadest width, with 7 setae: I and II located closely together, arising from the laterally produced pedestal, being I smaller than II; III as long as II, also arising from laterally extended outgrowth, resulting in

a concave shape of the outer furcal margin between Setae I/II and III. IV as long as III, on the outer apical margin; V longest seta, on the apical edge; VI at the most as long as I, on the inner apical margin. Setae I–VI bipinnate. VII inserting subapically from the small pedestal on the dorsal surface, tri-articulate and bare. Antennule 6-segmented in the female, 8-segmented and subchirocer in the male, with weak geniculation between the sixth and seventh segment. Antenna with basis, 2-segmented endopod and 1-segmented female exopod (unknown for *P. eratothenica*) but 3-segmented male exopod. Basis and enp-1 lacking abexopodal seta. Enp-1 as long as the basis, enp-2 is longer than enp-1, with 3 bipinnate spines on the inner margin; apically with 4 long setae, 3 of which geniculate; additionally, with 1 small seta on each the inner and outer apical edge. Mouthparts except mxp atrophied; gnathobase of md unknown, md palp with slender but remarkably elongated basis, endo- and exopod. Mx1 minute, with 2 setae at most; mx small, with 2 or 3 endites. Mxp slender, prehensile, consisting of syncoxa, basis, and 1–2-segmented endopod that carries 1 long curved claw and 2 setae. Swimming legs 1–4 with transversely elongated bases. P1 not prehensile, with 2-segmented exopod and 1–2-segmented endopod. P2–P4 with 3-segmented exo- and endopods, no sexual dimorphism in the male P2. P5 with small baseoendopod; endopodal lobe completely reduced, represented by 2 setae, which are very small in the male. Exopod distinct or fused to baseoendopod, long and slender, with 2 outer, 1 inner and 3 apical setae in the female, and with 1 inner and 3 apical setae in the male. Female genital field small, partly covered by sclerotized plate; the female P6 forming a single plate situated in front of the genital field. Male P6 of *P. mystica* unknown, in *P. eratothenica* sp. nov. small, both limbs fused medially and bearing 1 long biplumose seta each.

Type species: *Pseudometeorina mystica* George & Wiest, 2015 (by designation); additional species: *P. eratothenica* sp. nov. (present contribution).

Pseudometeorina eratothenica sp. nov.

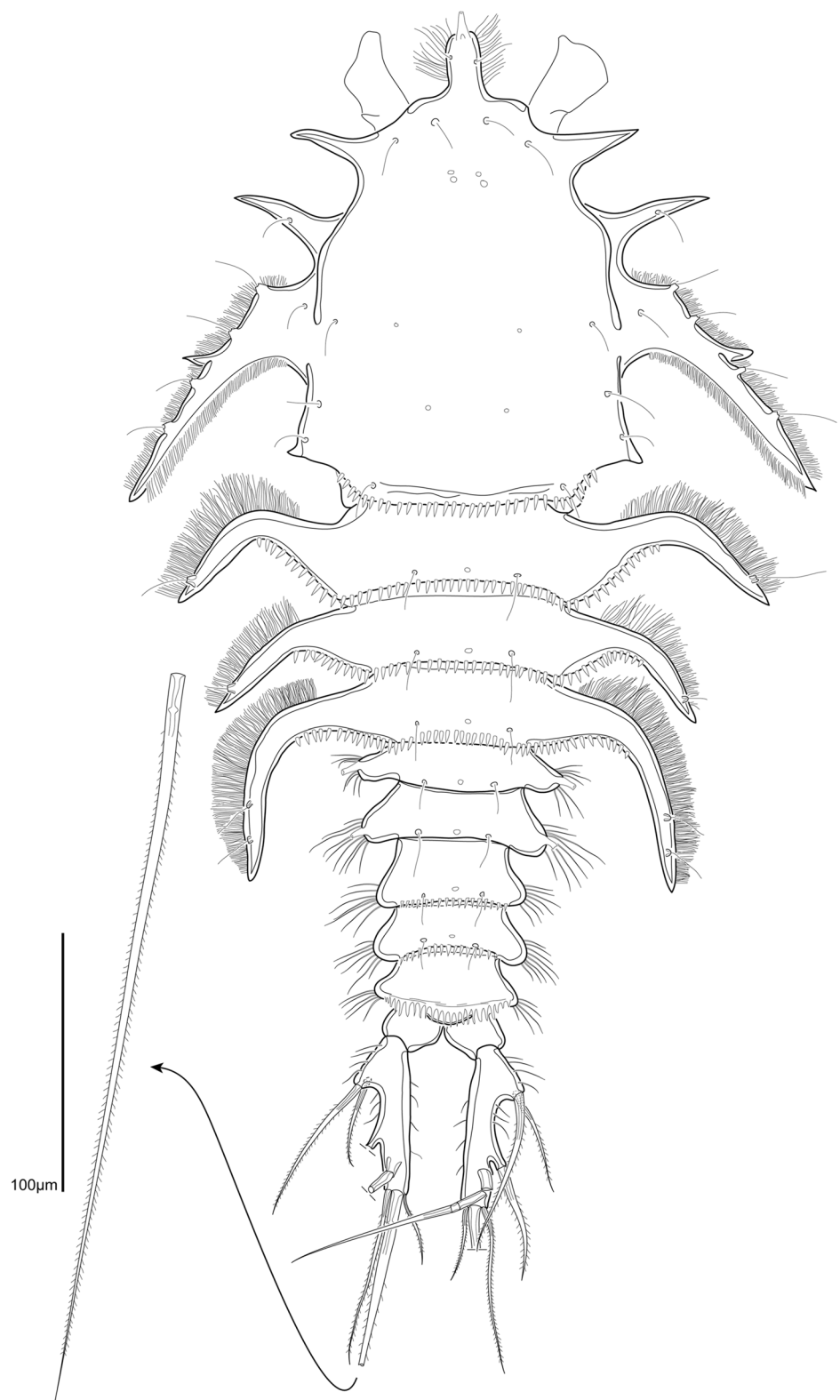
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Type locality: Eratosthenes Seamount (eastern Mediterranean Sea), station #1112–7 of cruise MSM 14/1 of German RV MARIA S. MERIAN, geographical location 33°37.48'N, 32°46.53'E (Fig. 1), water depth 874.8 m.

Type material: 1 adult male designated as holotype, dissected and mounted on 8 slides, collection number SMF 37,256/1–8.

Etymology: the specific epitheton *eratothenica* refers to the *locus typicus*, the Eratosthenes Seamount. Gender: feminine.

Fig. 2 *Pseudometeorina erato-*
sthenica sp. nov., male habitus,
dorsal view

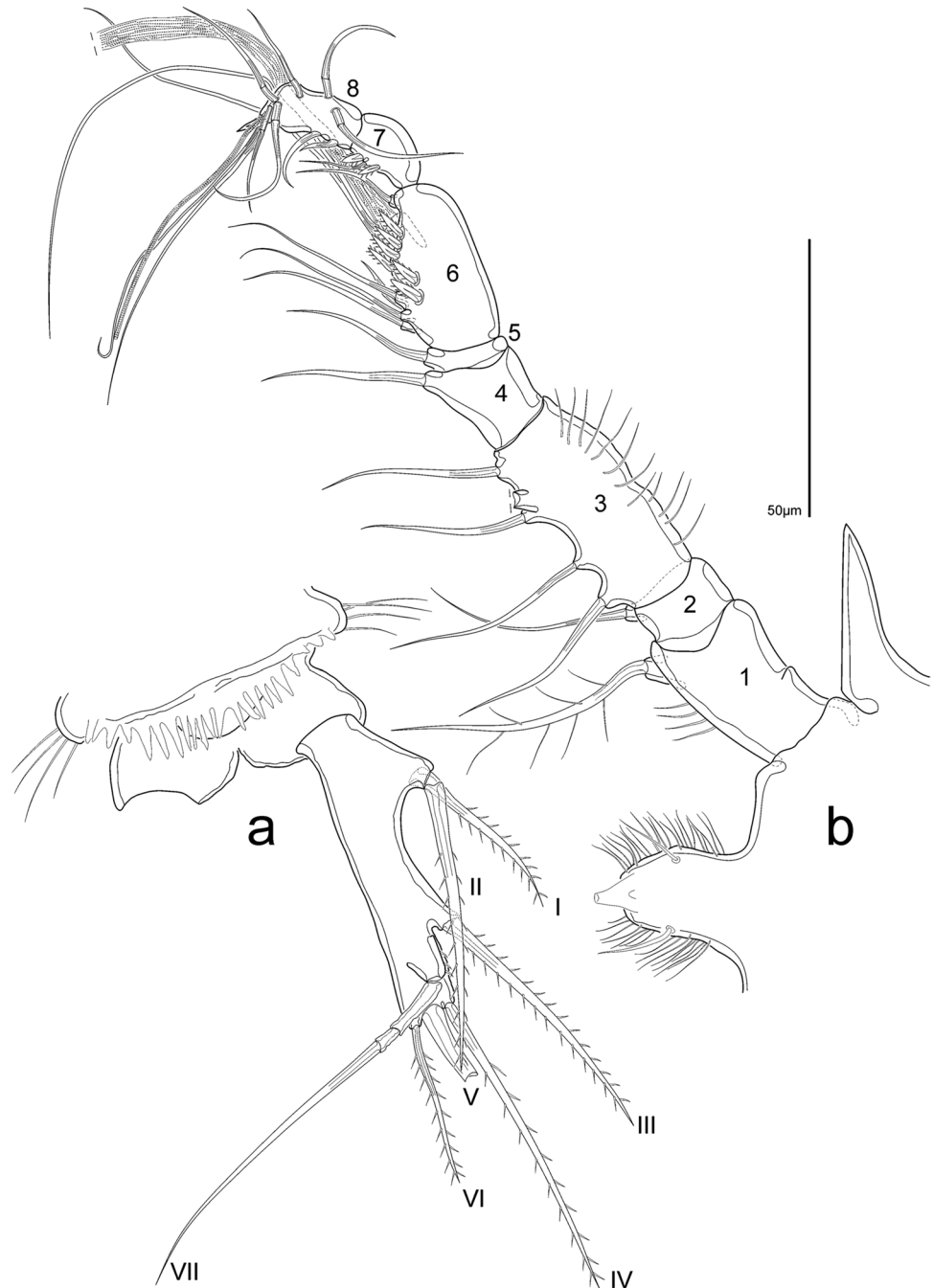


Male description

Habitus (Fig. 2) long, tapering posteriorly, body length from the rostrum to the end of FR about 446 μm . Cphth massive, reaching more than 1/3 of total body length, dorsally with a row of spinules along the posterior margin and 3 pairs of lateral processes, the first and second ones small, located in the anterior half; third pair on lateral half of cphth, long and distally curved, with some sensilla arising from small socles, and with fine setules along anterior and posterior margin. Rostrum (Figs. 2, 3b) fused to cphth,

elongate, with a rounded tip that bears a tube pore; laterally with fine setules and a pair of sensilla. Free thoracic somites carrying P2–P4 each with a pair of pronounced, backwardly curved lateral processes that bear long setules on their proximal margins; in addition, each somite with a row of spinules on its posterior margin. All free thoracic somites except penultimate somite and telson with a single pore on the posterior margin. P5-bearing somite until penultimate abdominal somite laterally with setulose tufts; P5- and P6-bearing somites additionally with tube pore but lacking spinules on posterior margins, which are present

Fig. 3 *Pseudometeorina eratosthenica* sp. nov., male, **a** Telson and right furcal ramus, dorsal view; **b** Rostrum and right antennule, dorsal view



on the first two abdominal somites. The frill on the penultimate abdominal somite is formed by smooth triangular appendages that are variable in appearance (Figs. 2, 3a). Telson is small, broader than long, with an anal operculum that lacks accompanying sensilla (Fig. 3a).

FR (Figs. 2, 3a) long and slender, of peculiar shape, about three times longer than broadest width, with 7 setae: I and II located closely together, arising from the laterally produced pedestal, being I smaller than II; III as long as II, also extended laterally, resulting in a concave shape of the FR between Setae I/II and III. IV apically on the outer margin, as long as III; V longest seta, on the apical margin; VI shortest seta, on the inner apical margin. Setae I–VI bipinnate. VII inserting subapically from the small pedestal on the dorsal side, tri-articulate and bare.

A1 (Fig. 3b) 8-segmented, subchirocer, with weak geniculation between the sixth and seventh segment; segments of different lengths. First segment with few spinules on the anterior margin and with 1 biplumose seta on the apical anterior margin. Second segment is small, with 1 bare seta; the third segment is longest, with fine, long spinules along the posterior margin, and with 5 bare setae (1 seta broken in Fig. 3b) on the anterior margin. Fourth segment trapezoid in lateral view, with 1 apical bare seta on anterior margin; fifth segment minute, discoid, also with 1 apical bare seta. Sixth segment slightly swollen, with 5 bare setae on the anterior margin, one of which inserted apically on a small socle; additionally, with 2 long bare setae arising together with an aes from a strong pedestal, and with 6 short bipinnate spines. Seventh segment small, with 2 short bipinnate spines and 1 tiny bare seta; eighth segment slightly longer than seventh one, with cuticular tooth apically, and with 2 small setae on anterior margin, setae, 6 bi-articulate setae, and 2 long setae forming an apical acrothek with a small aes.

Setal formula: 1–1; 2–1; 3–5; 4–1; 5–1; 6–11(+2 + aes); 7–3; 8–8(+2 + aes).

A2 (Fig. 4a) comprising coxa, basis, 2-segmented endopod, and 3-segmented exopod. Coxa squarish, with few slender spinules along the posterior margin; basis elongate, with few long spinules along the anterior margin; enp-1 as long as the basis, with few spinules on the anterior margin. Enp-2 is longer than enp-1, with a row of spinules and 3 bipinnate spines on the inner margin; apically with 4 long setae, 3 of which geniculate; additionally, with 1 small seta on each the inner and outer apical edge. Subapically with few spinules on the outer margin.

The apparently atrophied area of the mouthparts is shown in the semi-schematic Fig. 4b. It is notable that the former three pairs of mouthparts are very small, and the mx1 and part of the mx are overlapped by the supposed labrum. Moreover, the md gnathobase(?) seems to be strongly atrophied, reduced to 1 weak tooth, and seemingly fused to the body. Due to that condition, it was foreseen

from further dissection in order to avoid the destruction of the limbs. Thus, neither the md gnathobase nor the mx1 were recognized unambiguously and thus not drawn in detail. The md palp (Fig. 4c; both palps broken) is comparatively massive; it consists of an unarmed, elongate basis that carries each a 1-segmented elongated exo- and endopod. The endopod bears 1 lateral and 4 apical setae, all of which bipinnate; the exopod is equipped with 1 lateral bipinnate seta; apically it bears 2 setae, the innermost being biplumose, the outermost bare.

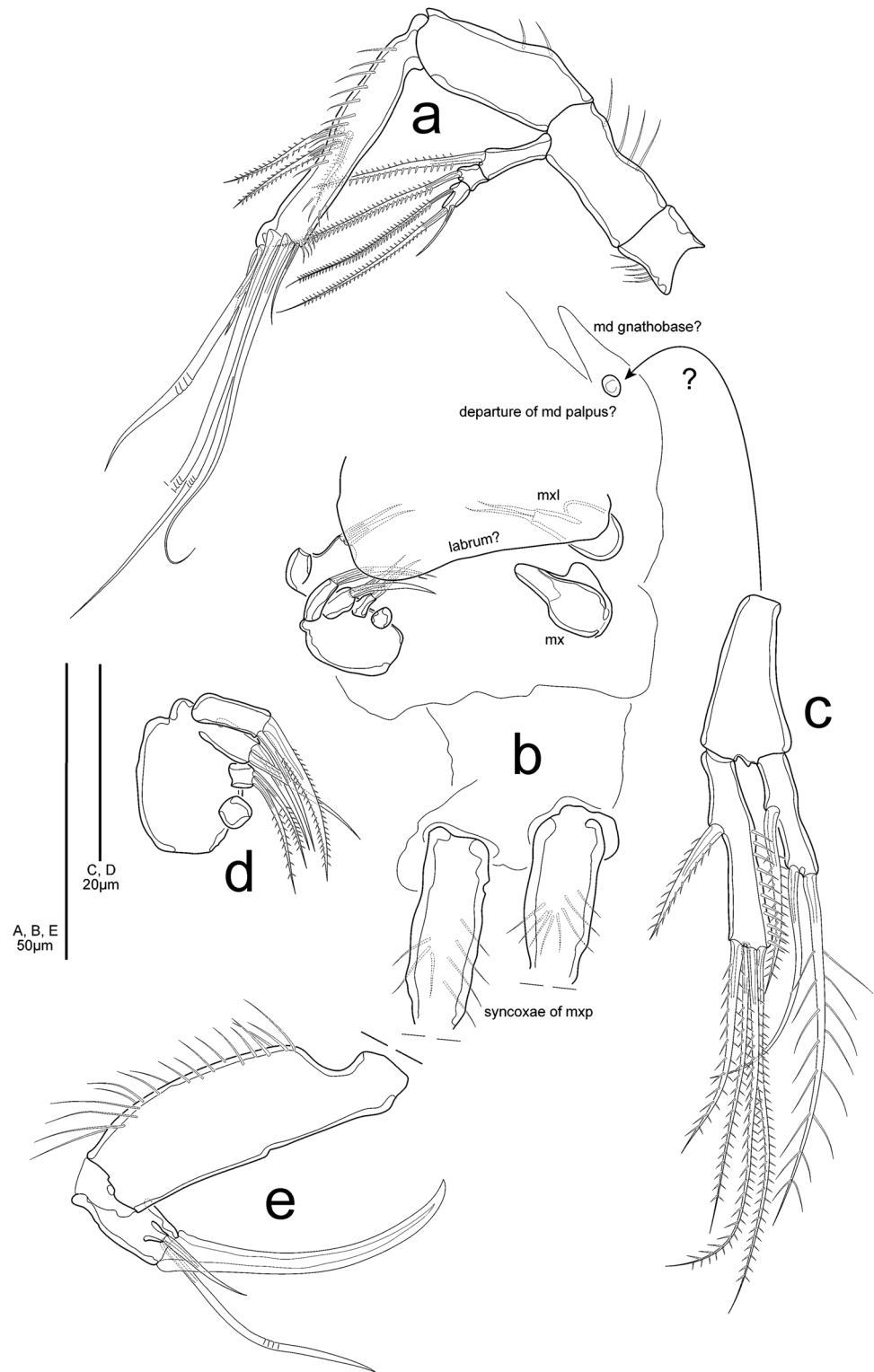
Mx (Fig. 4d) is very small, about 20 μm long; syncoxa with 3 endites, the proximal one knob-like, without setae; the middle endite as long as the proximal one, with 2 apical bipinnate setae; the distal endite largest, apically with 2 bare setae. Basis slightly longer than distal endite, apically with 1 strong bipinnate spine and a bare seta. Endopod lost.

Mxp (Fig. 4e) strong, prehensile. Syncoxa (Fig. 4b) and allobasis elongate, of nearly the same length. Syncoxa with several slender spinules, lacking apical seta; allobasis with a row of long spinules along the anterior margin. Endopod slightly elongate, armed with a long rounded apical claw, 1 small bare outer seta arising from projection, and 1 long and geniculate bare inner seta.

P1 (Fig. 5a) with small coxa, transversely elongated basis, 2-segmented exopod, and 1-segmented endopod. Intercostal sclerite is narrow and broader than long. Basis with 1 outer biplumose and 1 inner bare seta; endopod nearly as long as exp-1, with 1 bare biplumose seta apically. Exp-1 with few outer spinules and 1 biplumose outer seta; exp-2 is almost twice as long as exp-1, with 1 biplumose outer seta at the half length of the segment, and with 4 bare geniculate setae apically, additionally with 1 biplumose inner seta adverse of the outer one.

P2–P4 (Fig. 6a–c) with coxae carrying fine spinules on the outer margin; bases transversely elongated, with 1 outer bipinnate seta arising from the small pedestal (exemplary shown in Fig. 6a). Exo- and endopods 3-segmented; as the female remains unknown, sexual dimorphism cannot yet be detected. Nonetheless, the male P2 endopod does not show the “typical” idyanthid transformation; it deviates, however, somewhat from the P3 and P4 endopods in the shape of its third segment (Fig. 6a). Exps-1 and exps-2 with few inner and/or outer spinules as depicted, and with 1 inner and 1 outer seta; P2 exp-3 with 3 outer, 2 apical, and 2 inner setae; P3 exp-3 with 3 outer, 2 apical, and 3 inner setae; P4 exp-3 with 2 outer, 2 apical, and 3 inner setae. As exemplary shown in Fig. 6a for the P2, all outer exopodal setae are biplumose in their proximal, but bipinnate in their distal half. The outermost apical seta shows an outer bipinnate ornamentation but is biplumose on its inner margin; all remaining setae are biplumose. The endopods lack any spinules; all setae are biplumose. The enps-1 bear 1 subapical inner seta; the enps-2 of P3 and P4 also carry 1 inner seta, whilst the P2 enp-2 is equipped

Fig. 4 *Pseudometeorina eratothenica* sp. nov., male, **a** Antenna; **b** Semi-schematic illustration of the area of mouthparts, including the syncoxae of the maxilliped; **c** mandibular palp with basis, exopod (right-hand) and endopod (left-hand); **d** Maxilla; **e** Maxilliped, syncoxa broken



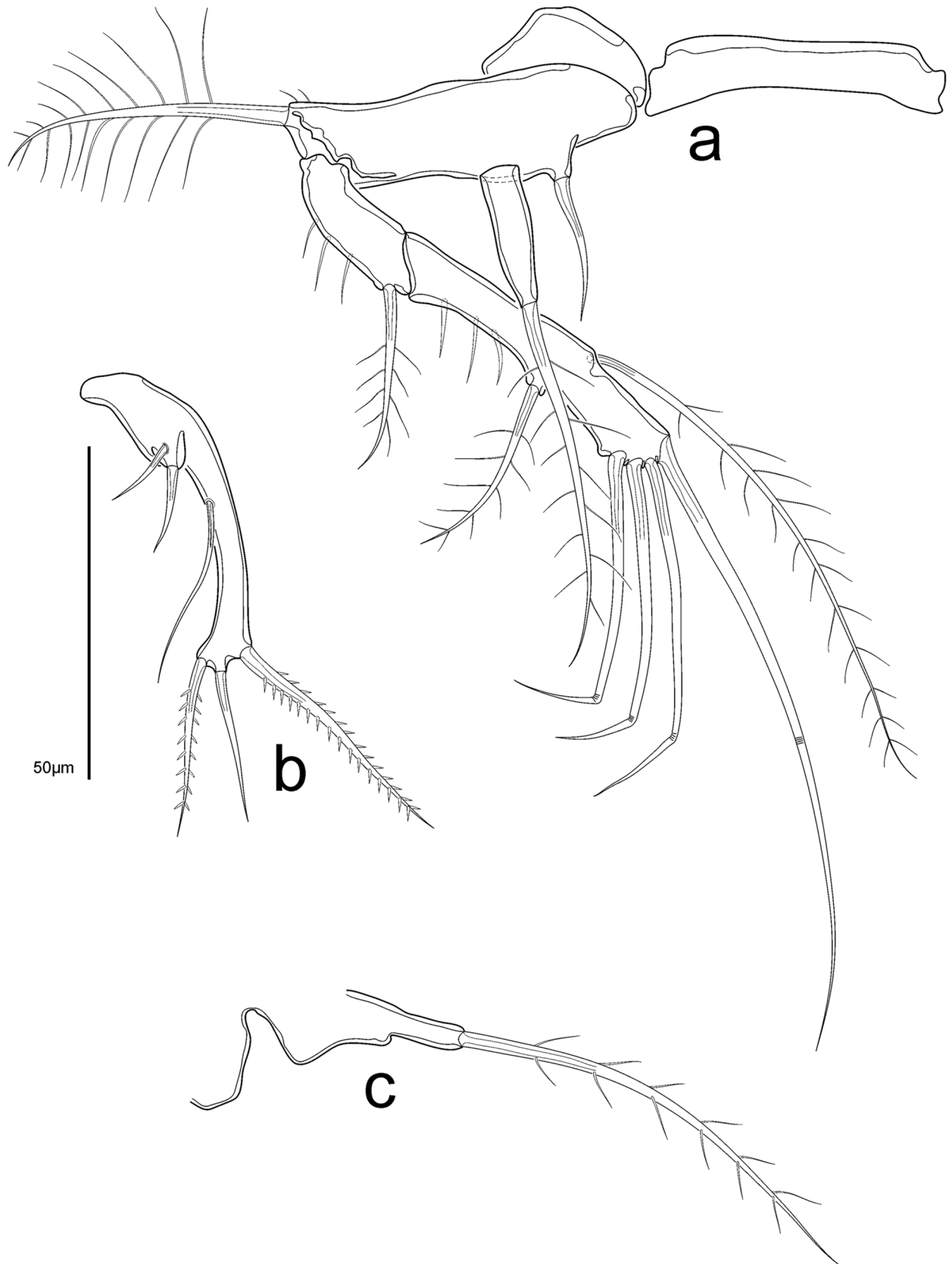


Fig. 5 *Pseudometeorina eratothenica* sp. nov., male, **a** Right P1; **b** Left P5; **c** Left P6

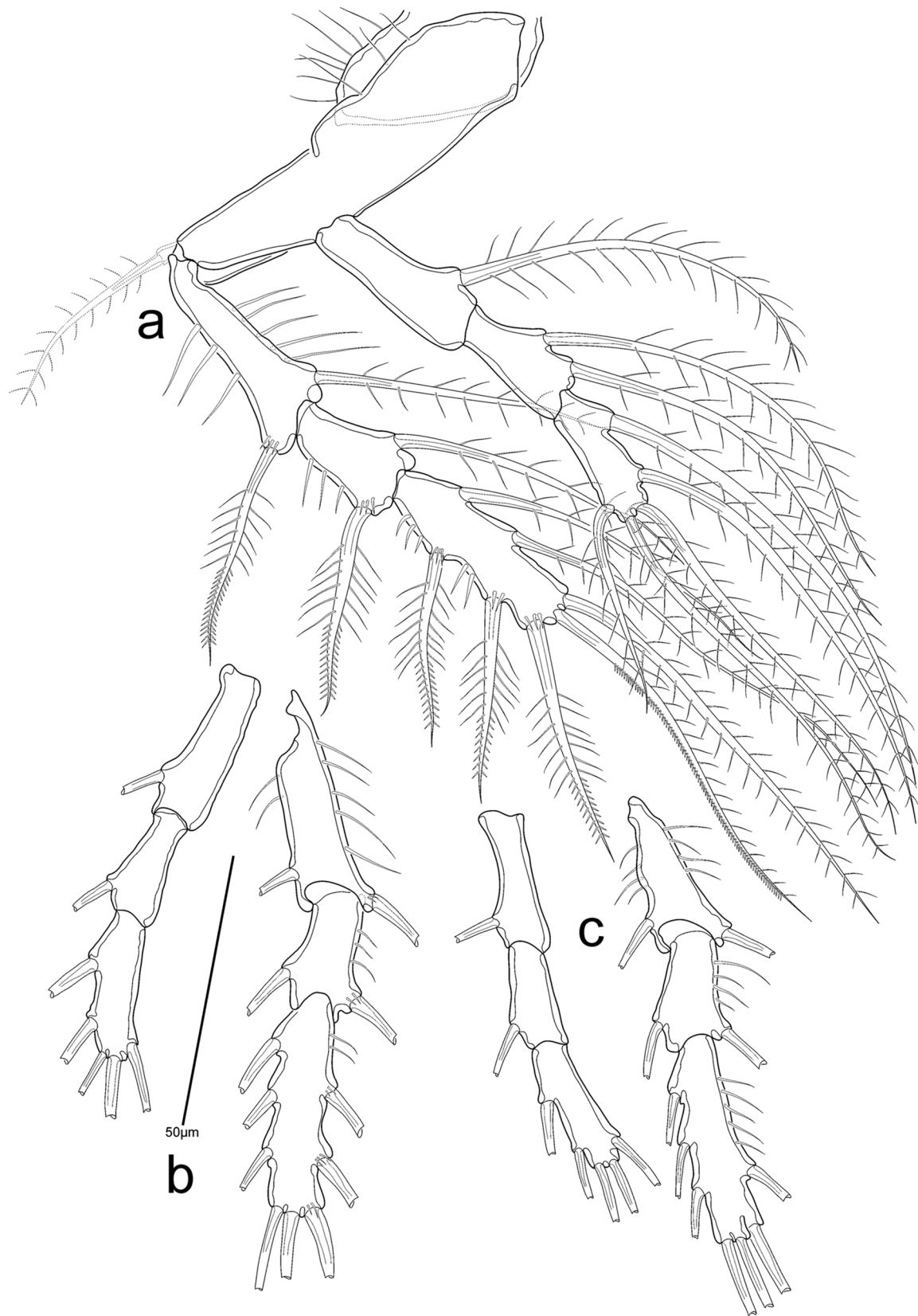


Fig. 6 *Pseudometeorina eratothenica* sp. nov., male, **a** Right P2; **b** Left P3 endo- and exopod (basis and setation omitted); **c** Left P4 endo- and exopod (basis and setation omitted)

with 2 inner setae. The enps-3 bear 1 outer, 2 apical, and 2 inner setae. The setal formula of P2–P4 is given in Table 1.

P5 (Fig. 5b) is small and elongate, baseoendopod and exopod fused. Baseoendopod without outer seta; endopodal lobe strongly reduced, with 2 small bare setae. Exopodal lobe with 1 inner bare seta on its proximal half, and with 3 apical setae, the outer and inner ones bipinnate.

P6 (Fig. 5c) is small, both limbs fused medially and bearing 1 long biplumose seta each.

Female unknown

Diagnostic key to the species of *Aspinothoracinae*:

1. Cphth and body somites laterally with well-developed cuticular processes, mxl endopod distinct, P1 endopod at least 2-segmented, P2–P4 endopods 3-segmented.....2
- Cphth and body somites lacking cuticular processes, mxl endopod fused with basis, P1 endopod 1-segmented, P2–P4 endopods 2-segmented.....*Aspinothorax insolentis*
2. Surface of cphth and body somites densely covered with cuticular minute denticles, preanal somite with strong spinules dorsally on posterior margin, FR short, not surpassing the length of the telson.....*Styracothorax gladiator*
- Surface of cphth and body somites smooth, preanal somite with comb-like or hyaline frill, FR remarkably elongated, at least more than twice as long as the telson.....3
3. FR slender, outer margin straight, P1 prehensile, endopod 3-segmented, enp-1 longer than the whole exopod, enp-3 with strong claw and tiny seta.....*Meteorina magnifica*
- Outer margin of FR with 2 pronounced outgrowths forming the bases of setae I/II and III, respectively; P1 non-prehensile, endopod 2-segmented, shorter than exopod.....4
4. Lateral processes of P2–P4-bearing somites with spinules on anterior and posterior margins, mxp syncoxa with 1 apical seta, P1 enp-2 with 2 apical setae.....*Pseudometeorina mystica*
- Lateral processes of P2–P4-bearing somites densely equipped with “hairy” setules on anterior margin, posterior margin bare, mxp syncoxa without apical seta, P1 enp-2 with 1 apical seta.....*Pseudometeorina eratosthenica* sp. nov.

Discussion

Background

Moura and Martínez Arbizu (2003) discussed and substantiated a close phylogenetic relationship of *Aspinothorax insolentis* and *Styracothorax gladiator*, concluding that both species belong to the Idyanthinae Lang, 1944, which at that time was placed in the Tisbidae Stebbing, 1910. *A. insolentis* was collected in the Laptev Sea (Arctic Ocean) at approximately 3000 m water depth (Moura and Martínez Arbizu 2003), whilst *S. gladiator* was first reported from 2050 m water depth in the Philippine deep sea, northwest of Manila (Pacific Ocean) (Huys 1993).

Seifried (2003) extracted the Idyanthinae Lang, 1944 from the Tisbidae, elevating it to family rank (= Idyanthidae)

Table 1 Setal formula of the P2–P4 swimming legs of *Pseudometeorina eratosthenica* sp. nov. (Roman numerals indicate outer elements)

	Exopod	Endopod
P2	I-1; I-1; III-2-2	0-1; 0-2; I-2-2
P3	I-1; I-1; III-2-3	0-1; 0-1; I-2-2
P4	I-1; I-1; II-2-3	0-1; 0-1; I-2-2

and characterizing it as monophylum by means of five autapomorphies [plesiomorphic states in square brackets]:

1. The md exp-1 (with 4 lateral setae) is remarkable elongated, much longer than exp-2 (with two apical setae) [md exp-1 not elongated];
2. Mxl exopod elongated [mxl exopod not longer than endopod];
3. P1 enp-1 elongated and broadened on the level of the inner seta; enps-2 and -3 shortened [all three endopodal segments of approximately the same length; enp-1 not broadened];
4. Outer spines of the female P5 exopod arising close to the basis and close to the apical edge of the exopod, respectively [spines located rather laterally on female P5];
5. Male P2 enp-3 showing the derived sexually dimorphic state of the Idyanthidimorpha Lang, 1944 (the outer ele-

ment transformed into a big bare spine that is fused to the segment and accompanied by one middle hyaline and one apical inner seta) but additionally having lost the inner setae [inner setae still present].

Seifried (2003) adopted Moura and Martínez Arbizu's (2003) hypothesis and added *Styracothorax* to the Idyanthidae (ignoring, for whatever reason, *Aspinothorax*). Subsequently, George (2004) described *Meteorina magnifica* from the Great Meteor Seamount plateau (302 m water depth). He assigned the species to the Idyanthidae, noting remarkable similarities between *S. gladiator* and *M. marina* and thus indicating a potentially close relationship of these species.

Subsequently, Bröhdick (2005) described *Nematovorax gebkelinae* Bröhdick, 2005 from the south-eastern Angola deep-sea basin (5389–5427 m water depth). She allocated *N. gebkelinae* to the Idyanthidae because of the above-listed family autapomorphies 3–5. Furthermore, Bröhdick (2005) assumed that *N. gebkelinae* might take a basal position within that family, because compared with other idyanthid taxa, it presents several features that correspond to the supposed idyanthid ground pattern (cf. Seifried 2003), which on its part had to be partially upgraded to accommodate the species (Bröhdick 2005). In contrast, the assignment of *S. gladiator*, *A. insolentis*, and *M. magnifica* to the Idyanthidae caused certain difficulties, because these species show further deviations especially in characters 1, 2, 3, and/or 4 (Moura and Martínez Arbizu 2003; Seifried 2003; George 2004). Thus, Seifried's (2003: 98) statement "...it is not possible to confirm the derived morphology of Idyanthidae.", which was referenced to *Styracothorax*, has to be extended to all three species. Nevertheless, despite the impossibility to confirm all idyanthid autapomorphies for *S. gladiator*, *A. insolentis*, and *M. marina* due to their further deviation, all three species do share character 5 (a sexually dimorphic male P2), i.e., the main and quite characteristic autapomorphy of the Idyanthidimorpha Seifried, 2003 (= Idyanthidae + Zosimeidae Seifried, 2003) combined with the additional idyanthid autapomorphy of the loss of the inner setae in the male P2 enp-3. Thus, their affiliation to the Idyanthidae remains unquestioned (Moura and Martínez Arbizu 2003; Seifried 2003; George 2004; Wells 2007).

With respect to *Pseudometeorina*, the circumstances become more complicated, because neither *P. mystica* nor the here-described *P. eratosthenica* sp. nov. share any of the above-listed five idyanthid autapomorphies. Both species present a strongly derived md, mx1, and mx, which are remarkably atrophied. That condition inhibits the confirmation of characters 1 and 2. Besides, like in *A. insolentis* and *S. gladiator*, the P1 is considerably derived, bearing 2-segmented limbs that differ remarkably from the characteristic idyanthidimorph/idyanthid shape, leading to a disutility also of character 3. Moreover, and like in *M.*

marina, the proximal outer spine in the female P5 exopod is not displaced towards the basis; additionally, also the distal outer spine did not shift towards the subapical edge of the exopod, so character 4 can neither be used for the allocation of *Pseudometeorina* to Idyanthidae. The main discrepancy is, however, the shape of the male P2 enp-3 (character 5). It lacks the characteristic idyanthidimorph apomorphic transformation of the apical elements but still retains the two inner setae that are lost in idyanthid males. So, the male P2 is identical with that of the female—*Pseudometeorina* shows no sexual dimorphism in the P2, and it was mainly this discrepancy that forced George and Wiest (2015) to assign *P. mystica* as *species incertae sedis* to the Idyanthidae. Though, in the following, it shall be proven that despite the missing idyanthid autapomorphies, *Pseudometeorina* in fact belongs to Idyanthidae. Within that taxon, it is most closely related with *Meteorina*, with which it shares a series of deviations, i.e., synapomorphies.

The most peculiar feature of *M. magnifica* is, without doubt, its general body shape (Fig. 7a). The large cphth, the remarkable long rostrum, and the shape and ornamentation of very characteristic lateral cuticular processes on the cphth and the prosomal body somites are noteworthy. Thus, the detection of a few specimens presenting an almost identical body shape (Fig. 7b) in a station of the Guinea deep-sea basin (George and Wiest 2015) led to the initial assumption of a new record of *M. meteorina* in that region. Subsequent detailed examination of the material revealed, however, several remarkable differences between the deep-sea and the seamount specimens, despite the impressive similarity of the general appearance. These differences prompted George and Wiest (2015) to assign the species name *Pseudometeorina mystica* for the Guinean deep-sea specimens.

The record of the here presented *Pseudometeorina eratosthenica* sp. nov. from Eratosthenes Seamount provides a third species of Idyanthidae showing a body shape (Figs. 2, 7c) that is—apart from marginal differences in size and ornamentation—nearly equal to that of *M. magnifica* and *P. mystica*, in particular with respect to the cphth and the body processes. These morphological features are not only unique within the Idyanthidae but in all Harpacticoida and are thus seen here as derived characters. Their similarity is such that a convergent development is regarded as quite improbable. Consequently, it is hypothesized that the development of these deviations reflects a close phylogenetic relationship of *M. magnifica*, *P. mystica*, and *P. eratosthenica* sp. nov.

Phylogenetic analysis

The given circumstances—(a) the assignment of *A. insolentis*, *S. gladiator*, and *M. marina* to the Idyanthidae, (b) their

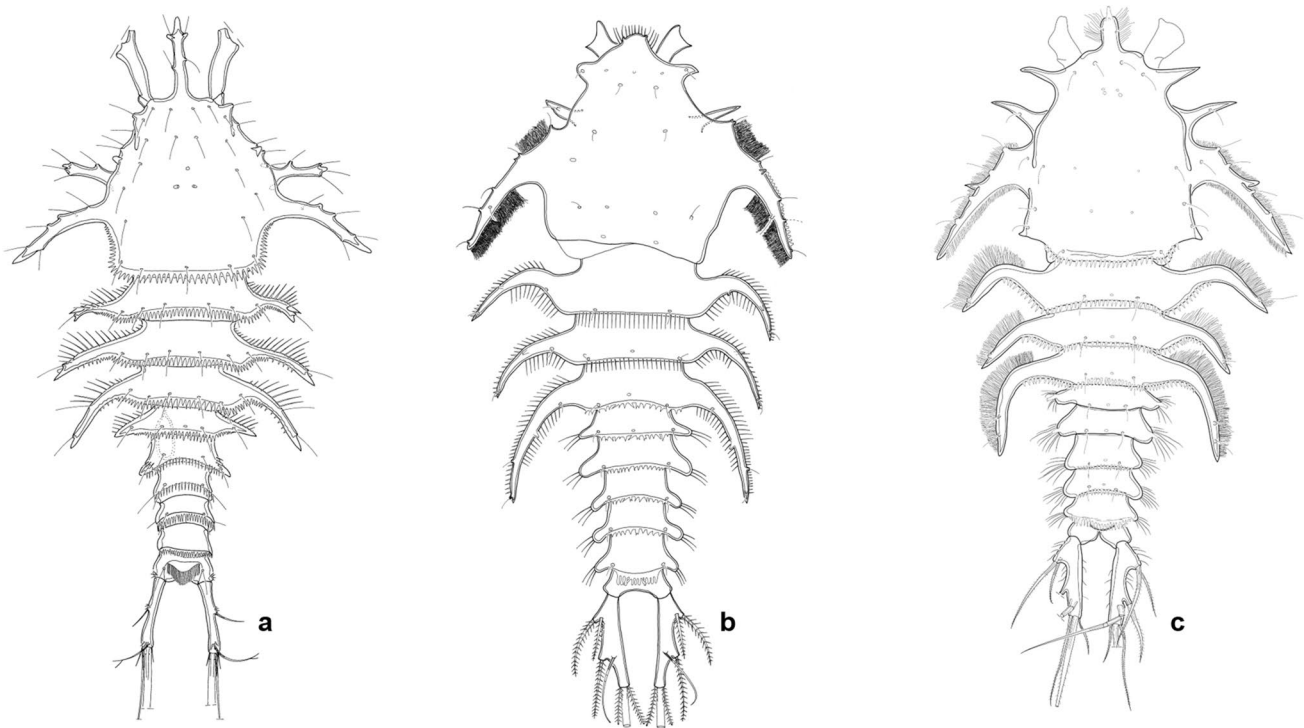


Fig. 7 Dorsal habitus of the males of **a** *Meteorina magnifica* George, 2004; **b** *Pseudometeorina mystica* George & Wiest, 2015; **c** *P. eratosthenica* sp. nov. **a** and **b** modified from George (2004) and George and Wiest (2015), respectively. No scales

presumed close relationship, (c) the striking morphological similarity of *M. marina*, *P. mystica*, and *P. eratosthenica* sp. nov., and (d) the ambiguous assignment of *Pseudometeorina* to the Idyanthidae—induced the here presented phylogenetic attempt. Although a detailed phylogenetic analysis of the Idyanthidae would go beyond the scope of the present contribution, in the following, a detailed comparative evaluation of the phylogenetic relationship between the above-named species is provided, based on 131 morphological characters (Table 2). As a premise, the phylogenetic characterization of the Idyanthidae as a monophylum provided by Seifried (2003) as well as the affiliation of the further derived *A. insolentis*, *S. gladiator*, and *M. magnifica* to that taxon and their supposed close relationship as discussed by Moura and Martínez Arbizu (2003), Seifried (2003) and George (2004) formed the base for the here presented argumentation. Consequently, the following hypothesis is formulated:

Aspinothorax, *Meteorina*, *Pseudometeorina*, and *Styracothorax* form a monophyletic group of quite derived Idyanthidae; the deviations are such, that they often go beyond the recognized family autapomorphies. Moreover, the deviations may include secondary transformations into states that resemble ancestral ones.

The out-group comparison was done with *Idyella nilmaensis* Kornev & Chertoprud, 2008 and *Tachidiella kimi*

Lee & Huys, 1999 (Lee and Huys 1999; Kornev and Chertoprud 2008). The former was selected since Seifried (2003) pointed towards a possible phylogenetic vicinity of *S. gladiator* to *Idyella*, whilst *T. kimi* represents a rather basal representative of Idyanthidae.

In the following, to avoid an exceeding character discussion, only those presumed apomorphies are discussed in detail that seems to be ambiguous or shall be justified as synapomorphies. Instead, the presumed autapomorphies of single taxa, particularly of *Aspinothorax*, *Styracothorax*, *Meteorina*, and *Pseudometeorina*, are so extraordinary and exclusively linked to the respective taxa that a brief argumentation is considered sufficient to confirm their autapomorphic state.

The result of the phylogenetic analysis is presented in Fig. 8. It shows that—based on the above-mentioned premise of a monophylum Idyanthidae (Table 2, Fig. 8: character 1)—*Tachidiella kimi* can be characterized by four derived characters (Table 2, Fig. 8: characters 2–5) that are absent in all remaining studied species and described in detail by Lee and Huys (1999). To clear the potential state of characters 2–5 as aut- or synapomorphies of the remaining idyanthid species is not the aim of the contribution on hand; here, they simply serve to unambiguously characterize *T. kimi* and to distinguish that species from the other species under study.

Table 2 List of the 131 morphological characters used for the presented phylogenetic analysis. Empty fields: plesiomorphic states; 1: apomorphic states; →: further deviation; **I**: presumed convergences

No	Character/species	<i>Tachidiella kimi</i>	<i>Idyella nilmaensis</i>	<i>Aspinothorax insolentis</i>	<i>Syracothorax gladiator</i>	<i>Meteorina magnifica</i>	<i>Pseudometeorina mystica</i>	<i>Pseudometeorina eratosthenica</i> sp. nov
1	→ Autapomorphies of Idyanthidae according to Seifried (2003)	1	1	→	→	→	→	→
2	Cphth with "irregularly crenulated internal pattern" on posterior margin	1						
3	P2-bearing somite with "irregularly crenulated internal pattern" on posterior margin	1						
4	P3-bearing somite with "irregularly crenulated internal pattern" on posterior margin	1						
5	P1 enp-3 elongated, longer than enp-2	1						
6	Rostrum fused with cphth		1	1	1	1	1	1
7	Md endopod with at most 2 lateral setae		1	1	1	1	1	1
8	→ P1 endopod at most 2-segmented		1	1	1	→	1	1
9	P5 baseoendopod completely reduced [baseoendopod developed]		1	1	1	1	1	1
10	Md exopod bent by 90° towards gnathobase		1					
11	Mx1 basis with at most 5 setae		1					
12	P1 basis with at least slight transverse elongation, broader than coxa			1	1	1	1	1
13	P1 exopod 2-segmented			1	1	1	1	1
14	P2 basis transversely elongated, broader than coxa			1	1	1	1	1
15	P3 basis transversely elongated, broader than coxa			1	1	1	1	1
16	P4 basis transversely elongated, broader than coxa			1	1	1	1	1
17	Cephalothoracic shield small, rounded		1					
18	P2-bearing somite: tergite reduced in size		1					
19	P3-bearing somite: tergite reduced in size		1					
20	P4-bearing somite: tergite reduced in size		1					
21	→ Mx1 endopod fused to basis		1				→	→
22	I P1 endopod 1-segmented		1				→	I

Table 2 (continued)

No	No. of convergences/further deviations	Character/species	<i>Tachidiella kimi</i>	<i>Idyella nilmaensis</i>	<i>Aspinothorax insolentis</i>	<i>Syracothorax gladiator</i>	<i>Meteorina magnifica</i>	<i>Pseudometeorina mystica</i>	<i>Pseudometeorina eratosthenica</i> sp. nov
23		P2 endopod 2-segmented			1				
24		P3 endopod 2-segmented			1				
25		P4 endopod 2-segmented			1				
26		P4 exopod 2-segmented			1				
27	2	P6 male forming asetose plate			1				
28		FR as long as all 4 abdominal somites together			1				
29		Cphth with median pair of lateral cuticular processes			1	1	1	1	1
30		Cphth with posterior pair of lateral cuticular processes			1	1	1	1	1
31		P2-bearing somite laterally extended, forming cuticular processes			1	1	1	1	1
32		P3-bearing somite laterally extended, forming cuticular processes			1	1	1	1	1
33		P4-bearing somite laterally extended, forming cuticular processes			1	1	1	1	1
34		Rostrum elongated			1	1	1	1	1
35	→	Mx1 exopod reduced in size, at most as long as endopod			1	1	1	→	→
36	→	Mx1 exopod with at most 2 setae		→	1	1	1	→	→
37		Cphth with posterior pair of dorsal cuticular processes			1	1	1	1	1
38		Cphth median pair of lateral processes irregularly structured by cuticular denticles and sensilla			1	1	1	1	1
39		P2-bearing somite: pair of lateral processes irregularly structured by cuticular denticles and sensilla			1	1	1	1	1
40		P3-bearing somite: pair of lateral processes irregularly structured by cuticular denticles and sensilla			1	1	1	1	1
41		P4-bearing somite: pair of lateral processes irregularly structured by cuticular denticles and sensilla			1	1	1	1	1
42		Cphth and body somites except telson covered with minute denticles dorsally and laterally			1	1	1	1	1

Table 2 (continued)

No	No. of convergences/further deviations	Character/species	<i>Tachidiella kimi</i>	<i>Idyella nilmaensis</i>	<i>Aspinothorax insolentis</i>	<i>Syracothorax gladiator</i>	<i>Meteorina magnifica</i>	<i>Pseudometeorina mystica</i>	<i>Pseudometeorina eratosthenica</i> sp. nov
43		Cphth with tricuspidate processes on posterior margin				1			
44		P2-bearing somite with pair of dorsal cuticular processes				1			
45		P3-bearing somite with pair of dorsal cuticular processes				1			
46		P4-bearing somite with pair of dorsal cuticular processes				1			
47		P2-bearing somite with tricuspidate processes on posterior margin				1			
48		P3-bearing somite with tricuspidate processes on posterior margin				1			
49		P4-bearing somite with tricuspidate processes on posterior margin				1			
50		P5-bearing somite with tricuspidate processes on posterior margin				1			
51		P5-bearing somite dorsally and dorsolaterally with strong spinules				1			
52		P6-bearing somite dorsally and dorsolaterally with strong spinules				1			
53		First abdominal somite dorsally and dorsolaterally with strong spinules				1			
54		Second abdominal somite dorsally and dorsolaterally with strong spinules				1			
55		Third abdominal somite dorsally and dorsolaterally with strong spinules				1			
56		Penultimate abdominal somite with strong spinules on posterior margin				1			
57	→	Mx endopod at most 2-segmented				1		→	↑
58		Cphth: posterior lateral processes long, backwardly directed, with several sensilla					1	1	1
59		Cphth: frontal edges extended laterally					1	1	1
60	3	FR elongate; at least as long as last three abdominal somites together		1			1	1	1
61		P2-bearing somite: pair of lateral processes falciform					1	1	1

Table 2 (continued)

No	No. of convergences/further deviations	Character/species	<i>Tachidiella kimi</i>	<i>Idyella nilmaensis</i>	<i>Aspinothorax insolentis</i>	<i>Syracothorax gladiator</i>	<i>Meteorina magnifica</i>	<i>Pseudometeorina mystica</i>	<i>Pseudometeorina eratosthenica</i> sp. nov
62		P3-bearing somite: pair of lateral processes falciform					1	1	1
63		P4-bearing somite: pair of lateral processes falciform					1	1	1
64		P5-bearing somite laterally extended					1	1	1
65		P6-bearing somite (anterior half of female GDS) laterally extended					1	1	1
66		Md basis at least twice as long as broadest width					1	1	1
67	4	Md exopod at most 1-segmented			1		1	1	1
68	5	Md exopod(-1) with at most 3 lateral setae			1		1	1	1
69		Mx middle endite at least reduced in size, with at most 2 apical setae					1	1	1
70		Mx distal endite with at most 2 setae					1	1	1
71		Cphth with comb-like cuticular frill on posterior margin					1	1	1
72		Cphth: median lateral processes elongate, not tapering distally					1	1	1
73		P2-bearing somite: lateral processes with long spinules along anterior margin					1	1	1
74		P3-bearing somite: lateral processes with long spinules along anterior margin					1	1	1
75		P4-bearing somite: lateral processes with long spinules along anterior margin					1	1	1
76		P2-bearing somite with comb-like cuticular frill on posterior margin					1	1	1
77		P3-bearing somite with comb-like cuticular frill on posterior margin					1	1	1
78		P4-bearing somite with comb-like cuticular frill on posterior margin					1	1	1
79		P5-bearing somite with comb-like cuticular frill on posterior margin					1	1	1
80		Second abdominal somite with comb-like cuticular frill on posterior margin					1	1	1
81		Penultimate abdominal somite with comb-like cuticular frill on posterior margin					1	1	1

Table 2 (continued)

No	No. of convergences/further deviations	Character/species	<i>Tachidiella kimi</i>	<i>Idyella nilmaensis</i>	<i>Aspinothorax insolentis</i>	<i>Syracothorax gladiator</i>	<i>Meteorina magnifica</i>	<i>Pseudometeorina mystica</i>	<i>Pseudometeorina eratosthenica</i> sp. nov
82		FR: seta VII with bifid tip					1		
83		Md exopod very small					1		
84		Md exopod(-1) without lateral setae					1		
85		Md exopod(-2) with at most 1 apical seta					1		
86	→	Mx1 endopod with at most 3 setae					1	→	
87		P1 prehensile, enp-3 with strongly developed claw					1		
88		P1 enp-1 longer than exopod					1		
89		Cphth: frontal extensions developed into anterior pair of lateral, cuspidal cuticular processes					1		1
90		Cphth median pair of lateral processes triangular, cuspidal, with sensillum					1		1
91		Cphth: posterior lateral processes with dense row of fine setules along anterior margin					1		1
92		Cphth: posterior lateral processes with dense row of fine setules along posterior margin					1		1
93		Urosomal somites except telson laterally with setular tufts					1		1
94		First abdominal somite (posterior half of female GDS) laterally extended					1		1
95		Second abdominal somite laterally extended					1		1
96		Third abdominal somite laterally extended					1		1
97		P2-bearing somite with spinulose row on posterior margin					1		1
98		P3-bearing somite with spinulose row on posterior margin					1		1
99		FR with concave sector between setae I/II and III					1		1
100		FR: setae I and II arising from laterally pronounced pedestal					1		1
101		FR: seta III arising from laterally pronounced projection					1		1
102	6	A2: basis without abexopodal seta					1		1

Table 2 (continued)

No	No. of convergences/further deviations	Character/species	<i>Tachidiella kimi</i>	<i>Idyella nilmaensis</i>	<i>Aspinothorax insolentis</i>	<i>Syracothorax gladiator</i>	<i>Meteorina magnifica</i>	<i>Pseudometeorina mystica</i>	<i>Pseudometeorina eratosthenica</i> sp. nov
103	7	A2: enp-1 without abexopodal seta	1						1
104	8	Md basis without setae			1				1
105		Md endopod with at most 4 apical setae					1		1
106		Md exopod strongly elongated, slender					1		1
107		Md endopod strongly elongated, slender					1		1
108		Mx1 minute, strongly atrophied					1		1
109		Mx without endopod					1		1
110		Mxp syncoxa: loss of at least 1 seta					1		1
111		Mxp endopod with 1 claw and 2 setae					1		1
112		P2 male lost sexual dimorphism					1		1
113		P2-bearing somite: lateral processes with moderate spinules along anterior and posterior margins					1		1
114		P3-bearing somite: lateral processes with moderate spinules along anterior and posterior margins					1		1
115		P4-bearing somite: lateral processes with moderate spinules along anterior and posterior margins					1		1
116		P4-bearing somite with irregularly serrated hyaline frill					1		1
117		P5-bearing somite with irregularly serrated hyaline frill					1		1
118		P6-bearing somite with irregularly serrated hyaline frill					1		1
119		Second abdominal somite (posterior half of female GDS) with irregularly serrated hyaline frill					1		1
120		Penultimate abdominal somite with hyaline frill formed by finger-shaped appendages					1		1
121		Md endopod with at most 3 apical setae					1		1
122		Mx middle endite lost					1		1
123		Cphth with spinulose row on posterior margin							1

Table 2 (continued)

No	No. of convergences/further deviations	Character/species	<i>Tachidiella kimi</i>	<i>Idyella nilmaensis</i>	<i>Aspinothorax insolentis</i>	<i>Syracothorax gladiator</i>	<i>Meteorina magnifica</i>	<i>Pseudometeorina mystica</i>	<i>Pseudometeorina eratosthenica</i> sp. nov
124		P2-bearing somite: lateral processes with dense row of fine setules along anterior margin							1
125		P3-bearing somite: lateral processes with dense row of fine setules along anterior margin							1
126		P4-bearing somite: lateral processes with dense row of fine setules along anterior margin							1
127		Penultimate abdominal somite with hyaline frill formed by variable triangular appendages							1
128		Md exopod(-1) with at most 1 lateral seta							1
129		Mx proximal endite small, knob-like, unarmed							1
130		Mxp syncoxa: without setae							1
131		P1 endopod 1-segmented, with 1 apical seta							1

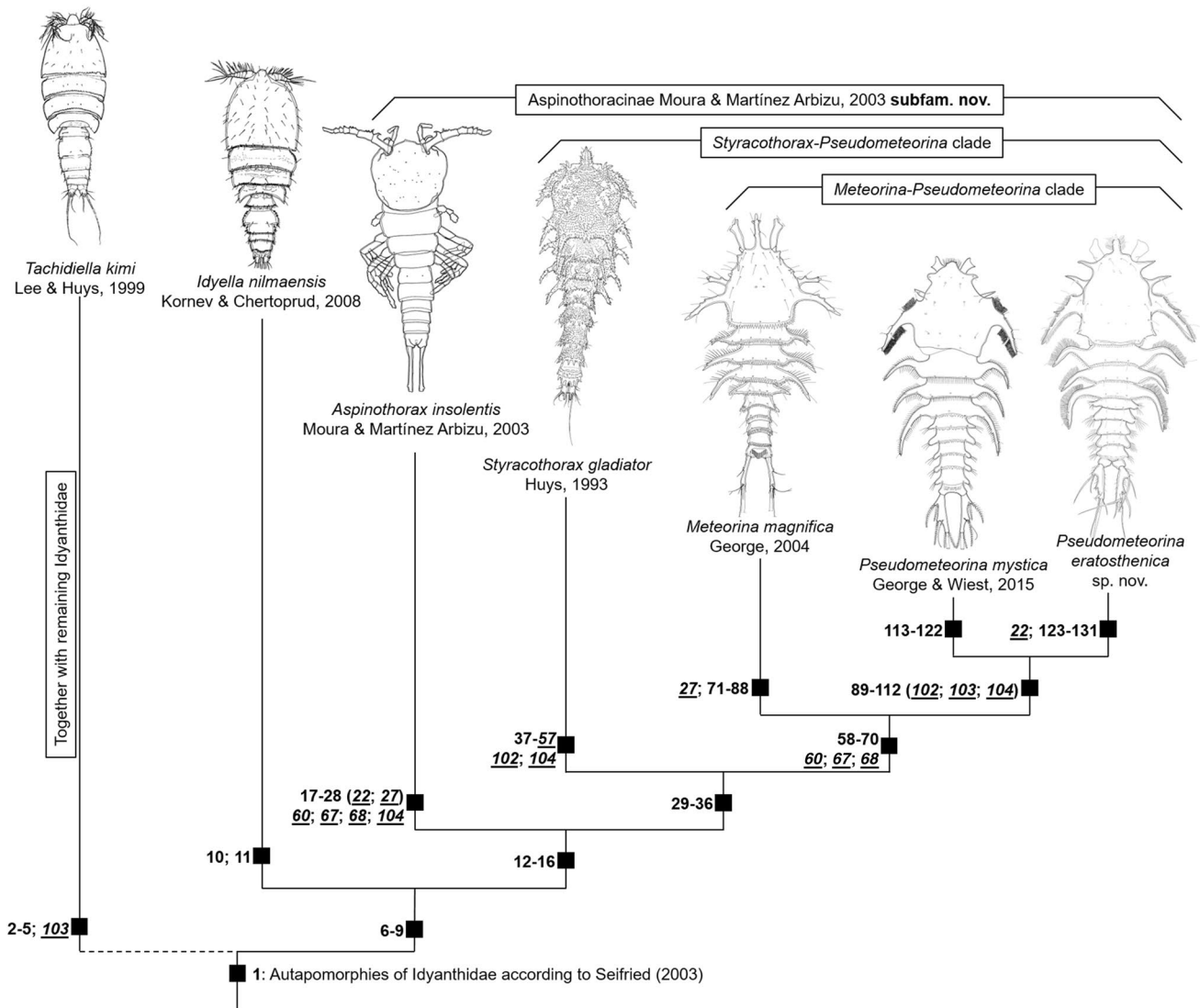


Fig. 8 Cladogram showing the phylogenetic relationships of and within the Aspinothoracinae subfam. nov. based on 131 morphological characters. The relationship of the new subfamily with the remain-

ing Idyanthidae is exemplified by the two outgroups *Tachidiella kimi* and *Idyella nilmaensis*. Bold underlined italics numerals = supposed convergences (cf. Table 2)

The *Idyella*—Aspinothoracinae subfam. nov. clade

Characters 6–9 (Table 2, Fig. 8) support the monophyletic status of *I. nilmaensis*, *A. insolentis*, *S. gladiator*, *M. magnifica*, and *Pseudometeorina* spp. These species share the fused rostrum (character 6) [distinct in *T. kimi*], the presence of two lateral setae on the md endopod (character 7) [*T. kimi* retains the plesiomorphic state of three lateral setae], a 2-segmented P1 endopod (character 8; but see discussion on *M. magnifica* below) [P1 endopod in *T. kimi* still 3-segmented], and a P5 baseoendopod whose endopodal lobe is completely reduced (character 9) [*T. kimi* retains a well-developed endopodal lobe].

Idyella nilmaensis can be characterized by two autapomorphies, i.e., the nearly 90° bent of the mandibular exopod (character 10; cf. Kornev and Chertoprud 2008) [md exopod rising almost parallel to the endopod], and the mx1 basis bearing only five setae (character 11; cf. Kornev and Chertoprud 2008) [mx1 basis with six setae].

The Aspinothoracinae Moura & Martínez Arbizu, 2003 subfam. nov.

The here newly established Aspinothoracinae subfam. nov. (Fig. 8) shows five derived characters (Table 2, Fig. 8: characters 12–16): the bases of P1 (character 12) and P2–P4

(characters 14–16) are transversely elongated and surpass the width of the respective coxae. That elongation, which can be observed in other Harpacticoida, too (e.g., Ancorabolidae Sars, 1909, Argestidae Por, 1986 [part.], Cletodidae T. Scott, 1904 [part.]), constitutes an exclusive development within Idyanthidae. The remaining taxa of that family present a P1–P4 basis that is connected with the coxa along its whole proximal margin; moreover, the basis is much smaller than the broad and large coxa. Additionally, all five genera are characterized by a 2-segmented P1 exopod (character 13), which shows three segments in all remaining Idyanthidae.

Characters 12–16 are considered as clearly autapomorphic for the Aspinothoracinae subfam. nov.

Aspinothorax Moura & Martínez Arbizu, 2003

Aspinothorax presents a set of 12 autapomorphies (Table 2, Fig. 8: characters 17–28). These refer to the ovoid shape of the cephalothoracic shield (character 17), the remarkably diminished size of the tergites on the pedigerous somites P2–P4 (characters 18–20), the fusion of the maxillular endopod with the basis (character 21), the only 1-segmented P1 (character 22), only 2-segmented P2–P4 endopods (characters 23–25), the only 1-segmented P4 exopod (character 26), the transformation of the male P6 into an asetose single plate (character 27), and the shape and length of the FR (character 28). All 12 characters are clearly derived in comparison with the remaining Idyanthidae and exclusively present in *Aspinothorax*; only characters 22 and 27 are also present in *P. erathostenica* sp. nov. and *M. magnifica*, respectively. As these species are, however, characterized by their own autapomorphies that are missing in *Aspinothorax*, the simultaneous development of characters 22 and 27 in the different species is regarded here as convergence.

The Styrauthorax—Pseudometeorina clade

The *Styrauthorax*—*Pseudometeorina* clade is characterized by eight unambiguous autapomorphies (Table 2, Fig. 8, characters 29–36). Characters 29–33 refer to the development of lateral cuticular processes on the cphth and the pedigerous body somites. The evolution of cuticular processes on the cphth and body somites took place in several harpacticoid major taxa (e.g., in Aegisthidae Giesbrecht, 1893 [part.], Ancorabolidae [part.], Argestidae [part.], Cletodidae [part.], Laophontidae T. Scott, 1904 [part.]). Their distribution along many different Harpacticoida, in combination with the restriction of their development to certain groups within the respective major taxa, doubtlessly points towards a multiple and independent evolution of cuticular processes in Harpacticoida. In Idyanthidae, only *Meteorina*, *Pseudometeorina*, and *Styrauthorax* have evolved lateral cuticular processes, which is therefore interpreted here as a synapomorphic state.

Further supposed autapomorphies of the *Styrauthorax*—*Pseudometeorina* clade are:

- the remarkably elongated and narrowed rostrum (character 34); the rostrum of the remaining Idyanthidae remains rather short and triangular in shape, as observable in *Aspinothorax*, *Dactylophia*, *Idyanthe*, *Idyella*, *Idyellopsis*, and *Nematovorax* (cf. Sars 1909; Becker 1974; Moura and Martínez Arbizu 2003; Bröhdick 2005; Kornev and Chertoprud 2008);
- the secondary diminution of the former elongated exopod of the mx1 (character 35); according to Seifried (2003; see above character 2), one autapomorphy of the Idyanthidae is the elongation of the maxillular exopod. In the derived *Styrauthorax*—*Pseudometeorina* clade the mx1 exopod is, however, small and does not surpass the length of the endopod. That reduction of the exopodal size is hypothesized here as a further deviation that resembles an ancestral, pre-idyanthid state. Such reduction is also notable in *Nematovorax* but considered here as convergent development, as *Nematovorax* lacks at least characters 12–16 (cf. Bröhdick 2005) and thus cannot be assigned even to the higher-levelled Aspinothoracinae.
- the presence of at most two setae on the mx1 exopod (character 36); the ground pattern of Idyanthidae encloses a mx1 exopod bearing three setae; this plesiomorphic state is retained in *Aspinothorax*, *Idyanthe*, *Idyellopsis*, *Nematovorax*, and *Tachidiella* (e.g., Sars 1909; Brady 1910; Lee and Huys 1999; Moura and Martínez Arbizu 2003; Bröhdick 2005; Kornev and Chertoprud 2008). Instead, the *Styrauthorax*—*Pseudometeorina* clade lost one seta, which is considered here as a shared deviation. Admittedly, however, also certain *Idyella* species (not confirmed for all species) show a mx1 endopod that bears two setae (cf. Sars 1905, 1920), whilst *I. nilmaensis* retains only one seta (Kornev and Chertoprud 2008). That circumstance might suggest a close relationship of *Idyella* and the *Styrauthorax*—*Pseudometeorina* clade. Nevertheless, this was the one and only apomorphy shared by these taxa, which would simultaneously exclude *Aspinothorax* (three setae on mx1 exopod) that on its part shares a series of deviations (Table 2, Fig. 8: characters 12–16) with the *Styrauthorax*—*Pseudometeorina* clade. Thus, it is concluded that character 36 evolved as a convergence in *Idyella* and the *Styrauthorax*—*Pseudometeorina* clade, whose closest congener remains *Aspinothorax*.

Styrauthorax Huys, 1993

Styrauthorax can unambiguously be characterized by 21 exclusive characters. Most of them (Table 2, Fig. 8: characters 37–56) focus on the presence and development of peculiar denticles, dorsal cuticular processes, tri-cuspidate processes, and/or strong spinules on the cphth and the body

somites. These striking structures are exclusively found in *Styracothorax* and therefore interpreted as autapomorphic characters of that taxon. Additionally, *Styracothorax* is the only idyanthid taxon presenting a 2-segmented maxillar exopod (character 57) (Huys 1993), which is 3-segmented in the remaining Idyanthidae (e.g., Lee and Huys 1999; Moura and Martínez Arbizu 2003; George 2004; Bröhdick 2005), with exception of *Pseudometeorina*, whose mouthparts are strongly atrophied (see below). Thus, that deviation is also assumed to be autapomorphic for *Styracothorax*.

The *Meteorina*—*Pseudometeorina* clade

The *Meteorina*—*Pseudometeorina* clade presents a set of 13 autapomorphies (Table 2, Fig. 8: characters 58–70), most of which (characters 58, 59, 61–65) are related to the further development of the lateral cuticular processes on the cphth and the body somites that have been discussed briefly in the first part of the discussion. As shown in Fig. 7, *Meteorina* and both *Pseudometeorina* species show an almost identical pattern of cuticular processes; moreover, these processes strongly resemble each other with respect to the size, shape, and even the ornamentation. In contrast, they differ remarkably from the processes exhibited in the supposed sister group *Styracothorax*. As such characteristic features have solely been found in *Meteorina* and *Pseudometeorina* (not even in any other Harpacticoida), it is concluded here that they originate from the last common ancestor of the *Meteorina*—*Pseudometeorina* clade, thus constituting an unequivocal complex of synapomorphies for *Meteorina* and *Pseudometeorina*. That assumption is supported by further derived characters:

- FR elongate; at least as long as the last three abdominal somites together (character 60): most Idyanthidae present short furcal rami, being only slightly longer than broad (e.g., *Tachidiella*, *Idyella*, *Nematovorax*, *Styracothorax*) (cf. Huys 1993; Lee and Huys 1999; Bröhdick 2005; Kornev and Chertoprud 2008), which is considered as part of the idyanthid ground pattern. Instead, the *Meteorina*—*Pseudometeorina* clade is characterized by considerably elongated FR. This is hypothesized here as synapomorphic for *Meteorina* and *Pseudometeorina*. The concurrent elongation of the FR in *Aspinothorax* is regarded as convergent development;
- Mandibular basis remarkably elongated, more than twice of its maximal width (character 66): Idyanthidae bear a rather compact md basis (e.g., *Aspinothorax*, *Nematovorax*, and *Tachidiella*) (cf. Lee and Huys 1999; Moura and Martínez Arbizu 2003; Bröhdick 2005). A certain elongation is already noticeable in some *Idyella* species and in *Styracothorax* (Sars 1920; Huys 1993; Kornev and Chertoprud 2008); however, only *Meteorina* and the

Pseudometeorina species present a md basis that is more than two times longer than its broadest width. This is considered as autapomorphic for the *Meteorina*—*Pseudometeorina* clade;

- Mandibular exopod 1-segmented (character 67): Idyanthidae are characterized by a 2-segmented md exopod. Instead, the *Meteorina*—*Pseudometeorina* clade presents a 1-segmented md exopod, which is regarded here as autapomorphy. Likewise, *Aspinothorax* shows a 1-segmented exopod on the md, but as shown above, that taxon branches off more basally, presenting several autapomorphies but lacking the apomorphies of the further derived taxa. Therefore, it is assumed that the loss of 1 exopodal segment occurred independently in *Aspinothorax* and the *Meteorina*—*Pseudometeorina* clade;
- Mandibular exopod(-1) with at most three lateral setae (character 68): the idyanthid ground pattern encloses a mandibular exopod(-1) equipped with four lateral setae (Seifried 2003). That condition is retained by most Idyanthidae, except for *Aspinothorax*, *Nematovorax*, and the *Meteorina*—*Pseudometeorina* clade; in the latter, only *P. mystica* bears three lateral setae, whilst *P. eratosthenica* sp. nov. carries only one lateral seta and *M. magnifica* lost all lateral setae. In combination with the remaining 14 apomorphies, the loss of (at least) one lateral seta is regarded as an additional autapomorphy for the *Meteorina*—*Pseudometeorina* clade. However, reduction of setal elements occurs often in Harpacticoida, so it is assumed here that like for other characters, the simultaneous reduction of one exopodal lateral seta in both *Aspinothorax* (and *Nematovorax*) is due to convergence;
- Maxillar middle endite reduced in size, with at most two apical setae (character 69): the ground pattern of Idyanthidae encloses a middle maxillar endite that bears three setae (Seifried 2003). That condition is retained in all here studied taxa (cf. Lee and Huys 1999; Moura and Martínez Arbizu 2003; Bröhdick 2005; Kornev and Chertoprud 2008) except *Meteorina* and *Pseudometeorina*, which lost one seta (cf. George 2004; George and Wiest 2015; present contribution). That reduction is hypothesized as synapomorphic for both genera;
- Maxillar distal endite with at most two setae (character 70): like for character 69, also the loss of one seta on the distal maxillar endite (= two setae present) is seen here as deviation shared by *Meteorina* and *Pseudometeorina*, whilst all other studied species still retain the ancestral condition of three setae.

Meteorina George, 2004

The *Meteorina*—*Pseudometeorina* clade splits into the remaining two genera. *Meteorina* presents a set of 18 unambiguous autapomorphies (Table 2, Fig. 8, characters 71–88),

most of which (characters 71–81) referring to the exclusive ornamentation of the cphth and body somites. The remaining characters relate to the FR seta VII showing a bifid tip (character 82), the strong diminution of the mandibular exopod (character 83), combined with the loss of lateral setae (character 84), and the retention of only one apical seta (character 85), the loss of three setae on the maxillular endopod (= three setae present) (character 86), the development of an elongated prehensile P1 endopod that carries a well-developed claw on the enp-3 (character 87), combined with a remarkable elongation of the P1 enp-1 that surpasses the length of the whole exopod (character 88). Admittedly, a 3-segmented P1 endopod (likewise the exopod) forms part of the idyanthid ground pattern. Nevertheless, the development of a 3-segmented endopod in *Meteorina* is interpreted here as a secondary evolution into a derived state that only resembles the ancestral one. This assumption is substantiated by the special shape of the endopod: *Meteorina* lacks the characteristic idyanthid P1 with a 3-segmented exopod and the first endopodal segment being clearly broadened on the level of the inner seta in the middle of the segment; in contrast, in *Meteorina*, the exopod is 2-segmented (see Table 2, character 13), and the enp-1 is remarkably elongated, becoming a long and slender segment that surpasses the length of the exopod and carries its inner seta in its distal quarter; the enp-3 bears just two elements, one of which tiny and the other produced into a strong serrated claw. Thus, as *Meteorina* is clearly embedded in the group of derived Idyanthidae due to the arguments presented in the contribution on hand, its P1 is seen here as the exclusive deviation of *Meteorina*.

Characters 71–88 evolved exclusively in *Meteorina*, whereas the remainder of the Idyanthidae presents comparatively ancestral conditions, with the exception of characters related to the mouthparts that are even further derived in *Pseudometeorina* (see below).

***Pseudometeorina* George & Wiest, 2015**

As stated above, seven out of the ten genera currently assigned to the Idyanthidae are monotypic. With respect to the here studied taxa, this applies to *Aspinothorax*, *Meteorina*, and *Styracothorax*. The finding of *P. eratothenica* sp. nov., however, now allows the phylogenetic characterization of the formerly also monotypic taxon *Pseudometeorina*. That genus presents a large set of 24 autapomorphies (Table 2, Fig. 8, characters 89–112), of which only three (characters 102–104) show a perhaps convergent development in single other species. Characters 89–101 relate to the shape and ornamentation of the cphth, the body somites and their respective cuticular processes, and to the shape of the FR. These features deviate remarkably from those of representatives that are considered as rather original ones like e.g., *Idyanthe*, *Nematovorax*, and

Tachidiella, because their morphology resembles that of the supposed idyanthid ground pattern as proposed by Seifried (2003). Furthermore, compared with *Aspinothorax*, *Meteorina*, and *Styracothorax*, characters 89–101 are observable only in the *Pseudometeorina* species. Their morphology eminently suggests a further deviation instead of the retention of ancestral conditions, so they are hypothesized here as unambiguous autapomorphies of *Pseudometeorina*.

Further deviations regard the loss of an abexopodal seta on the A2 basis (character 102) and on the enp-1 (character 103), the loss of setae on the mandibular basis (character 104), the loss of one apical seta on the mandibular endopod (character 105), the remarkable elongation of the mandibular endo- and exopod (characters 106, 107), the strong atrophy of the mxl (character 108), resulting in a minute lobe that apparently carries just two short setae (cf. Figure 4b), the complete loss of an endopod in the atrophied mx (character 109), the loss of one syncoxal seta in the mxp (character 110), the retention of only two setae and a claw in the maxillipedal endopod (character 111), and the loss of the sexual dimorphism in the male P2 (character 112).

Characters 102, 103: Idyanthidae retain an abexopodal seta on both the A2 basis and the enp-1 (Seifried 2003). This is still observable in the here studied species, with exception of *Pseudometeorina*. Nonetheless, also *Aspinothorax*, and *Styracothorax* lost the basal abexopodal seta (character 102) (Huys 1993; Moura and Martínez Arbizu 2003), whilst *Tachidiella* reduced the respective seta in the enp-1 (character 103) (Lee and Huys 1999). Nevertheless, as stated above, single setae are often and independently reduced in Harpacticoida, and as demonstrated in the discussion above, the named species are clearly separated from *Pseudometeorina* and characterized by own apomorphic characters. Therefore, the simultaneous loss of the abexopodal setae is interpreted here as synapomorphic for both *Pseudometeorina* species but as convergent development in *Tachidiella*, *Aspinothorax*, and *Styracothorax*.

Characters 104–111 refer to the mouthparts, which show deviations in *Pseudometeorina* in comparison with most remaining Idyanthidae. The genus presents a mandibular basis lacking any setation (character 104), whilst the remaining Idyanthidae bear three basal setae. This derived setal lack is also noticeable in *Styracothorax*. Though, as that genus lacks the 13 synapomorphies of *Pseudometeorina* and *Meteorina* (Table 2, characters 58–70), the loss of setae in the mandibular basis is considered here as convergent development in *Pseudometeorina* and *Styracothorax*. Moreover, the former presents a mandibular endopod that bears four apical setae (character 105) instead of five; likewise, its mandibular endo- and exopod are long and slender (characters 106, 107), giving to the mandibular palp an elongated and remarkable stretched aspect, whilst in the remaining Idyanthidae it retains a rather compact and short shape, and also characters 108–111 clearly reflect the atrophy of the

mx1, the mx, and the mxp in *Pseudometeorina*, which in the remaining here studied species are developed according to the idyanthid ground pattern as proposed by Seifried (2003).

Character 112, i.e., the here assumed complete loss of a sexually dimorphic male P2, may constitute the most striking characteristic of *Pseudometeorina*. One might assume that the absence of a sexually modified male P2 endopod represented a rather ancestral condition. But as the expression of the typical idyanthid sexual dimorphism is explicitly interpreted as one main autapomorphy of the family (Seifried 2003), its absence in *Pseudometeorina* demanded the exclusion of that genus from the Idyanthidae, despite the here discussed deviations shared with *Aspinothorax*, *Styracothorax*, and especially with *Meteorina*. The alternative, here adopted assumption is that *Pseudometeorina* in a secondary step lost the male sexual dimorphism in the P2. Such a loss definitely occurs in Harpacticoida and has been documented in some representatives, e.g., of Laophontidae T. Scott, 1904 (e.g. Lang 1965; Mielke 1981; Wells and Rao 1987; Fuentes-Reinés and Suárez-Morales 2017). In the present context, it is therefore regarded as an unambiguous autapomorphy of *Pseudometeorina*.

Establishment of *Pseudometeorina eratothenica* sp. nov.

The specimen collected from Eratosthenes Seamount shares the derived characters 89–112 (except characters 102–104) exclusively with *Pseudometeorina mystica*. Its allocation into *Pseudometeorina* is hence well-justified. However, both species differ from each other by means of several distinct deviations, here considered as respective autapomorphies. These relate to the shape and ornamentation of the posterior margins of the cphth and the body somites (characters 113–120: apomorphies corresponding to *P. mystica*; characters 123–127: apomorphies corresponding to *P. eratothenica* sp. nov.) (cf. Table 2), the setation of the mandibular endo- and exopod (character 121: md endopod with three apical setae in *P. mystica* but with four setae in *P. eratothenica* sp. nov.; character 128: md exopod with one lateral seta in *P. eratothenica* sp. nov. but with three lateral setae in *P. mystica*), the composition and/or ornamentation of the maxillar endites (character 122: middle maxillar endite lost in *P. mystica*, 1-segmented in *P. eratothenica* sp. nov.; character 129: proximal maxillar endite minute, knob-like, without setae in *P. eratothenica* sp. nov. but of regular size and bilobed, with two setae in *P. mystica*), and the maxillipedal syncoxa lacking any setae in *P. eratothenica* sp. nov. These morphological differences between the deep-sea and the seamount specimens, which furthermore constitute autapomorphies of each of them, clearly support the hypothesis of the Eratosthenes specimen belonging to a distinct species: *Pseudometeorina eratothenica* sp. nov.

Conclusion

The results of the exhaustive phylogenetic analysis as summarized and depicted in Fig. 8 support the above-formulated hypothesis: *Aspinothorax*, *Meteorina*, *Pseudometeorina*, and *Styracothorax* in fact form a monophylum within the Idyanthidae that can be verified by five unambiguous autapomorphies. The establishment of the Aspinothoracinae Moura & Martínez Arbizu, 2003 subfam. nov. for the unification of the above-named four genera is therefore well-justified. Moreover, each genus is characterized by exclusive autapomorphies. In the monotypic taxa, *Aspinothorax*, *Meteorina*, and *Styracothorax*, these exclusive deviations are identical with those of the assigned species. In contrast, the detection of *Pseudometeorina eratothenica* sp. nov. enables the characterization of *Pseudometeorina* as a monophylum, which is verified by means of 24 derived characters considered here as synapomorphies of the two enclosed species *P. mystica* and *P. eratothenica* sp. nov.

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Declarations

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Ethics approval No animal testing was performed during this study.

Sampling and field studies No special permits were needed at the time of sampling.

Data Availability All data generated or analysed during this study are included in this published article.

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