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# The paramesochrid fauna of the Great Meteor Seamount (Northeast Atlantic) including the description of a new species of *Scottopsyllus (Intermedopsyllus)* Kunz (Copepoda: Harpacticoida: Paramesochridae)

Christoph Plum · Kai-Horst George

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**Abstract** Because of their potentially important role for the distribution of marine benthic organisms, seamounts have been the subject of focused interest on the part of marine biologists particularly during the past decade. One of the largest seamounts sampled so far is the Great Meteor Seamount (GMS), which is located in the North Atlantic. Although some of the most detailed investigations have been carried out on this particular seamount, it is still a little-known environment regarding benthic copepod diversity and ecology. Therefore, material from 14 stations collected in 1998 was investigated to address the following aspects: (1) species composition and diversity of the harpacticoid family Paramesochrididae at the GMS; (2) faunistic comparison with other localities and *Intermedopsyllus*; and (3) revision of the worldwide distribution of known Paramesochrididae. Of the 28 paramesochrid species determined from the GMS, 26 are new to science. The vast majority were found on the plateau; only two species were detected in the deep-sea stations. Other species found at the GMS are already known from East Atlantic deep-sea areas. In the frame of providing new taxonomical information for future research, *Scottopsyllus (Intermedopsyllus) antoniae* sp. nov. from the plateau of the GMS is described here. The new species can without any doubt be allocated to *Scottopsyllus* because of the 1-segmented endopods but 3-segmented exopods in P2–P3, the “paramecium”-like shape of P2–P3 endopods, and the 1-segmented exopods in the antenna and the mandible. The new species differs from its congeners mainly by retention of

setae on the antennule, the reduced size of furcal seta VI, the fact that the proximal maxillar endite bears only 1 seta, and the loss of the maxillar endopod.

**Keywords** Biodiversity · Taxonomy · Seamounts · Deep sea · Meiofauna · Distribution patterns · *Scottopsyllus (Intermedius) antoniae*

## Introduction

Although it has been estimated that there may be as many as 100,000–200,000 seamounts spread throughout the world’s oceans (Wessel 2007), these undersea features are still little-known environments regarding their biodiversity and ecology. This is partly because of the complex conditions associated with seamounts, such as large depth ranges, cryptic topography, hard substrata, fast currents, and geographic isolation, which make them difficult to sample (Rogers 1994). However, at the same time, these specific conditions render seamounts unique habitats for deep-sea and shallow-water organisms (Rogers 1994; Richer de Forges et al. 2000).

The first scattered investigations on seamounts took place in the late nineteenth and early twentieth centuries (Brewin 2007), but only during recent decades have deep-water sampling gear and underwater vehicles allowed detailed sampling of the deep sea. Fundamental questions on species composition, diversity, community structure, and possible endemism at seamounts were first addressed by Hubbs (1959).

Because of their potentially important role for the distribution of marine benthic organisms (Hubbs 1959; Gad and Schminke 2004), there has been focused interest

C. Plum (✉) · K.-H. George  
Deutsches Zentrum für Marine Biodiversitätsforschung (DZMB),  
Senckenberg am Meer Wilhelmshaven,  
Südstrand 44,  
26382 Wilhelmshaven, Germany  
e-mail: cplum@senckenberg.de

on seamounts by marine biologists during the past decade (e.g., Thistle 1998; Richer de Forges et al. 2000; George and Schminke 2002; Mohn and Beckmann 2002; Bartsch 2003; George 2004a, b; Mironov and Krylova 2006; Samadi et al. 2006). The most detailed investigations on biodiversity, composition and distribution of the seamount benthic macrofauna and meiofauna have been carried out in the North Atlantic, particularly at the Great Meteor Seamount (Emschermann 1971; Grasshoff 1972, 1973, 1977; Bartsch 1973a, b, 1983, 2001a, b, 2003, 2004, 2008; Hartmann-Schröder 1979; George and Schminke 2002; George 2004a, b, 2006; Gad 2004a, b, 2008; Gad and Schminke 2004; Piepenburg and Müller 2004; Mironov and Krylova 2006). The Great Meteor Seamount (GMS) is one of the largest seamounts in the North Atlantic, rising from a depth of 4,200 m up to 275 m below sea level (Ulrich 1971). It is located in the subtropical Northeast Atlantic, west of the Canary Islands and south of the Azores. The distance to the African coast is about 1,600 km. Due to its shape and the large summit plateau, the GMS resembles a giant table mountain and is therefore characterized as a guyot. The plateau is covered by coarse biogenic sediment composed of fragments of mollusc shells and corals (Gad and Schminke 2004). Estimates of the age of the GMS range from 10 m.y. (Wendt et al. 1976) to 35 m.y. (Hinz 1969) and more than 50 m.y. (Grevemeyer 1994) to 82–86 m.y. (Verhoef 1984).

The present study is the result of the expedition M42/3 with the German RV “Meteor” to the Great Meteor Seamount in 1998, as part of the interdisciplinary SEAMEC (Seamount Ecology) project. A first detailed examination of the meiofauna material collected during M42/3 yielded a large number of Harpacticoida (Copepoda), including specimens of the family Paramesochridae Lang 1944 (George and Schminke 2002). They were one of the most abundant taxa found on the plateau of the GMS and presumably represent an important constituent of the harpacticoid fauna. To date, the Paramesochridae contain 125 species belonging to 13 genera and 4 subgenera (Bodin 1997; Boxshall and Halsey 2004; Wells 2007). Members of this family show a wide geographical distribution and are typically small, interstitial animals that inhabit intertidal and shallow-water sandy sediments. Only a few species have been recorded at depths greater than 300 m (Lang 1936; Drzycimski 1967; Becker 1972; Becker et al. 1979; Veit-Köhler 2004, 2005; Veit-Köhler and Drewes 2009; Vasconcelos et al. 2009). This leads to the essential question of how species of a typically interstitial taxon could settle on the Great Meteor Seamount, considering the large distance to the nearest coast and the assumption that fine-grained clayish bottoms in the deep sea may preclude dispersal of interstitial meiofauna adapted to coarse sand (Westheide 1991; Gad and Schminke 2004).

To increase our knowledge about harpacticoid species biodiversity, this study focuses on the Paramesochridae from the Great Meteor Seamount. The investigation includes: (1) a qualitative analysis of the species composition and diversity at the GMS, including distribution patterns on the seamount; (2) a faunistic comparison of the paramesochrid taxa of the GMS with associations from other localities; (3) a summarizing review of the geographical and bathymetric distribution of paramesochrid species; and (4) a description of *Scottopslus (Intermedopsyllus) antoniae* sp. nov. from GMS.

## Material and methods

Qualitative samples were collected from the GMS during expedition M42/3 of the German RV “Meteor” in 1998 (Pfannkuche et al. 2000). The GMS covers a total area of 1,465 km<sup>2</sup> and rises from a depth of approximately 4,200 m to a minimum of 275 m below the water surface. Its summit is represented by a plateau with a maximum length of 54 km, a maximum width of 31 km, and a surface area of about 1,200 km<sup>2</sup> (Ulrich 1971; Hinz 1969). The volcanic bedrock of the plateau is covered with a 150- to 400-m-thick cap of biogenic carbonates constituting the seabed of the summit (Piepenburg and Müller 2004). During expedition M42/3, 26 stations were sampled (Table 1), of which 14 stations contained specimens of Paramesochridae (Table 2). Two of them were located in the deep sea at the northeastern slope, while the rest were located on the plateau (Table 1, Fig. 1). The material was collected with a multicorer (MUC, after Barnett et al. 1984), epibenthic sledge (EBS, after Brandt and Barthelnt 1995) and giant boxcorer (GKG, after Hessler and Jumars 1974; see George and Schminke 2002).

Sample treatment is described by George and Schminke (2002). For determination of the paramesochrid species, the specimens were transferred on slides using glycerine as embedding medium (Pfannkuche and Thiel 1988). Sorting was done in the laboratory at Senckenberg am Meer, Department DZMB (German Centre of Marine Biodiversity Research) in Wilhelmshaven, Germany.

Before dissection, the holotype of *Sc. (I.) antoniae* sp. nov. was drawn from the dorsal and lateral side. Detailed drawings of the lateral and ventral view of the abdomen were also made. Dissected parts of the holotype and the paratypes were placed in glycerin drops, mounted on several slides. All drawings were made of female holotype except the maxillule (Fig. 3 from paratype 1). The paratype parts were drawn without dissection. Drawings were made with the aid of a drawing tube on a Leica differential interference contrast microscope (DMR with UCA condenser, IC prism and doubler  $\times 1.25$  and  $\times 1.6$ ). All specimens were deposited in the collection of the Senckenberg

**Table 1** Date, gear, geographical position, depth and numbers of sampled stations during the expedition M42/3 with the German RV “Meteor”

| Sampling date | Station | Gear | Geographic locality  | Depth (m) |
|---------------|---------|------|----------------------|-----------|
| 01.09.1998    | 451     | GKG  | 30°08.4'N, 28°34.8'W | 455       |
| 02.09.1998    | 452     | GKG  | 29°42.9'N, 28°22.7'W | 297       |
| 02.09.1998    | 455     | GKG  | 29°42.9'N, 28°22.7'W | 297       |
| 03.09.1998    | 456     | GKG  | 29°48.2'N, 28°29.7'W | 303       |
| 04.09.1998    | DS 459  | MUC  | 29°45.7'N, 28°44.3'W | 2,722     |
| 06.09.1998    | 467     | GKG  | 30°02.1'N, 28°32.6'W | 292       |
| 08.09.1998    | DS 484  | MUC  | 29°25.5'N, 28°33.9'W | 4,015     |
| 09.09.1998    | 489     | GKG  | 29°57.0'N, 28°23.1'W | 323       |
| 09.09.1998    | 492     | GKG  | 29°58.5'N, 28°29.7'W | 294       |
| 11.09.1998    | DS 505  | GKG  | 30°18.3'N, 28.03.3'W | 4,005     |
| 12.09.1998    | DS 506  | MUC  | 30°12.2'N, 28°14.2'W | 3,009     |
| 13.09.1998    | 511     | GKG  | 30°07.2'N, 28°22.8'W | 597       |
| 13.09.1998    | 515     | EBS  | 29°48.9'N, 28°29.0'W | 302       |
| 14.09.1998    | 516     | GKG  | 29°49.3'N, 28°37.1'W | 325       |
| 14.09.1998    | 517     | EBS  | 30°05.9'N, 28°32.2'W | 312       |
| 14.09.1998    | 518     | EBS  | 30°02.0'N, 28°32.0'W | 293       |
| 14.09.1998    | 519     | EBS  | 30°06.2'N, 28°24.5'W | 416       |
| 14.09.1998    | 520     | EBS  | 30°06.0'N, 28°24.3'W | 422       |
| 14.09.1998    | 521     | EBS  | 30°05.9'N, 28°23.2'W | 511       |
| 14.09.1998    | 522     | EBS  | 30°05.6'N, 28°23.0'W | 518       |
| 17.09.1998    | DS 548  | MUC  | 29°52.8'N, 28°14.2'W | 2,320     |
| 18.09.1998    | 551     | EBS  | 29°53.4'N, 28°19.5'W | 476       |
| 18.09.1998    | 552     | EBS  | 29°53.9'N, 28°22.0'W | 322       |
| 19.09.1998    | DS 558  | MUC  | 30°32.1'N, 28°46.8'W | 4,111     |
| 20.09.1998    | 565     | EBS  | 29°39.4'N, 28°22.9'W | 403       |
| 20.09.1998    | DS 566  | MUC  | 29°32.7'N, 28°29.9'W | 3,077     |

MUC Multicorer, EBS epibenthic sledge, GKG giant boxcorer

Forschungsinstitut und Naturmuseum Frankfurt am Main (SMF), Germany.

Abbreviations used in the text: A1 = antennula; A2 = antenna; aes = aesthetasc; benp = baseoendopod; Cphth = cephalothorax; enp = endopod; exp = exopod; enp-1 (2,3) = proximal (middle, distal) segment of endopod; exp-1 (2,3) = proximal (middle, distal) segment of exopod; FR = furcal ramus/rami; GF = genital field; GMS = Great Meteor Seamount; Md = mandibula; Mxl = maxillula; Mx = maxilla; Mxp = maxilliped; P1–P6 = first to sixth swimming leg.

## Results

### Taxonomy

Harpacticoida Sars 1903

Paramesochidae Lang 1944

Subfam. Paramesochrinae Huys 1987

*Scottopsyllus (Intermedopsyllus)* Kunz 1962 sensu Kunz 1981

*Scottopsyllus (I.) antoniae* sp. nov.

### Type material

*Holotype*: Female, dissected and mounted on 10 slides (Coll. No. SMF 33623). Paratype 1: non-dissected female, mounted on 1 slide (Coll. No. SMF 33624). Paratype 2: non-dissected male, mounted on 1 slide (Coll. No. SMF 33625). Additional material: 4 females and 6 males from station 516 (Coll. No. SMF 33626), 5 females and 3 males from station 451 (Coll. No. SMF 33627), 1 female and 2 males from station 455 (Coll. No. SMF 33628), all preserved in glycerine slides.

### Type locality

Northeast Atlantic, Great Meteor Seamount, 29°49.3'N, 28°37.1'W, southwest plateau, station 516, 325 m depth (Fig. 1).

### Etymology

The species name is given in dedication to the first author's grandmother, Antonie Behrends, and his newborn niece, Antonia Plum.

**Table 2** Paramesochrid species collected from the Great Meteor Seamount in 1998

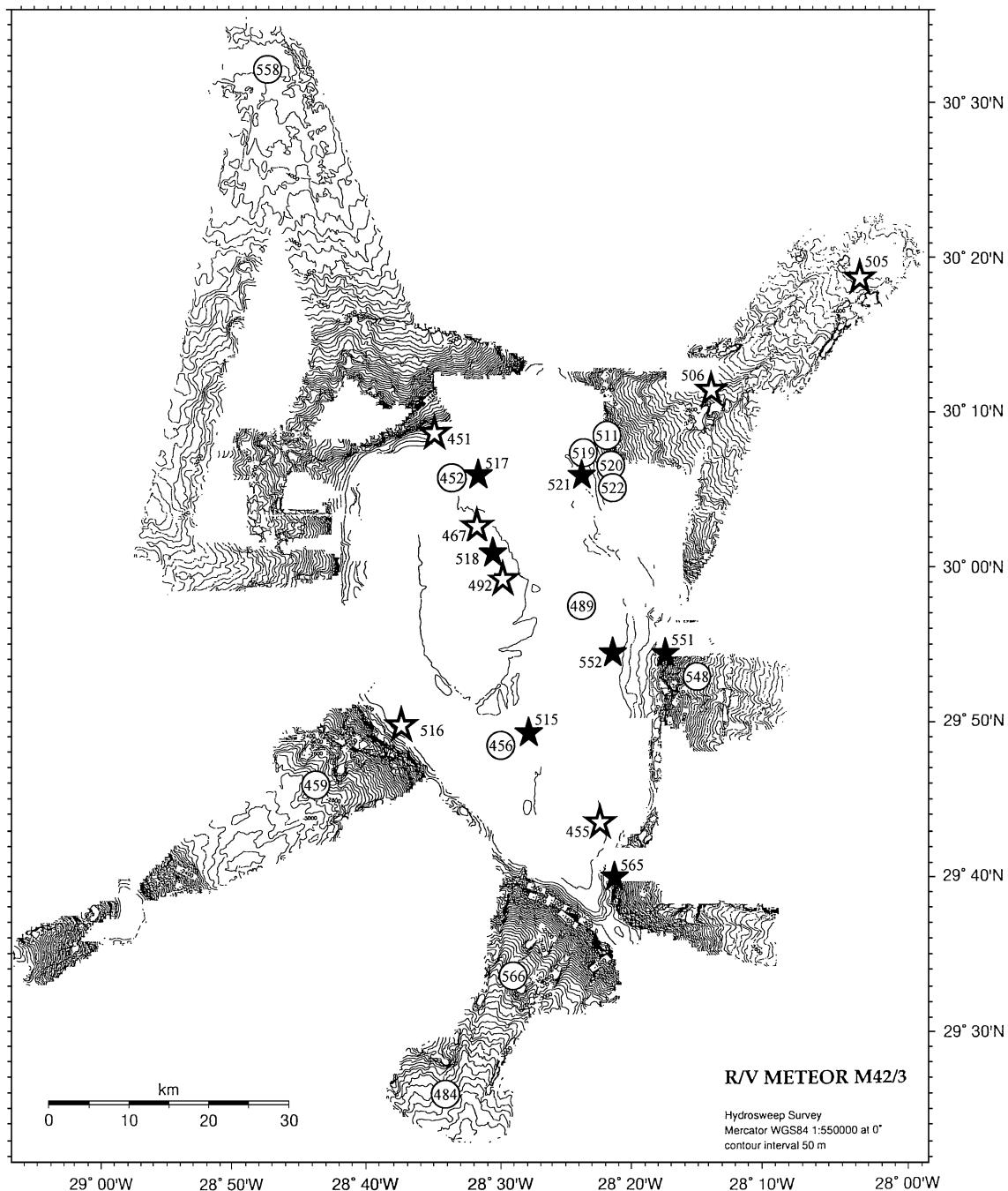
| Stations |  |     |     |     |     |     |     |     |      |     |     |     |      |     |     |
|----------|--|-----|-----|-----|-----|-----|-----|-----|------|-----|-----|-----|------|-----|-----|
| No.      | Species                                      | 467 | 492 | 451 | 455 | 505 | 506 | 515 | 516  | 517 | 518 | 521 | 551  | 552 | 565 |
| 1        | <i>Apodopsyllus</i> spec.                    | 2   | 1   | -   | 5   | -   | -   | -   | 4    | -   | -   | -   | 1    | -   | 1   |
| 2        | <i>Diarthrodelta</i> spec.                   | 1   | -   | -   | 1   | -   | -   | -   | -    | -   | -   | -   | 1    | -   | -   |
| 3        | <i>Kliopsyllus schminkei</i>                 | -   | -   | -   | -   | 1   | 1   | -   | -    | -   | -   | -   | -    | -   | -   |
| 4        | <i>Kliopsyllus</i> spec. 1                   | 8   | 7   | 7   | 2   | -   | -   | 1   | 1    | -   | 10  | 5   | 109  | 10  | 3   |
| 5        | <i>Kliopsyllus</i> spec. 2                   | 1   | -   | -   | -   | -   | -   | 1   | 2    | -   | -   | 1   | -    | -   | 1   |
| 6        | <i>Kliopsyllus</i> spec. 3                   | 20  | 9   | 1   | 14  | -   | -   | -   | 9    | -   | -   | -   | 1    | -   | -   |
| 7        | <i>Kliopsyllus</i> spec. 5                   | 5   | 2   | -   | -   | -   | -   | -   | -    | -   | -   | -   | -    | -   | -   |
| 8        | <i>Kliopsyllus</i> spec. 6                   | -   | -   | 7   | -   | -   | -   | -   | 6    | -   | -   | -   | 1    | -   | -   |
| 9        | <i>Kliopsyllus</i> spec. 7                   | -   | -   | 2   | -   | -   | -   | -   | -    | -   | -   | -   | 7    | 1   | -   |
| 10       | <i>Kliopsyllus</i> spec. 8                   | -   | -   | -   | -   | -   | -   | -   | -    | -   | -   | -   | -    | 1   | -   |
| 11       | <i>Kliopsyllus</i> spec. 9                   | -   | -   | -   | -   | 1   | -   | -   | -    | -   | -   | -   | 1    | -   | -   |
| 12       | <i>Kliopsyllus</i> spec. 10                  | -   | 1   | -   | 1   | -   | -   | -   | -    | -   | -   | -   | 4    | -   | -   |
| 13       | <i>Leptopsyllus</i> spec. 1                  | 1   | -   | -   | -   | -   | -   | -   | 11   | -   | 1   | -   | -    | -   | -   |
| 14       | <i>Leptopsyllus</i> spec. 2                  | 1   | 1   | 11  | 5   | -   | -   | -   | 46   | -   | 4   | -   | 10   | 1   | -   |
| 15       | <i>Paramesochra</i> spec. 1                  | 5   | 3   | 2   | 7   | -   | -   | 2   | 10   | -   | 1   | -   | 3    | -   | -   |
| 16       | <i>Paramesochra</i> spec. 2                  | 2   | -   | 7   | 2   | -   | -   | 1   | 6    | 1   | -   | -   | 3    | -   | 1   |
| 17       | <i>Paramesochra</i> spec. 3                  | -   | -   | 2   | -   | -   | -   | -   | -    | -   | -   | -   | 24   | -   | 1   |
| 18       | <i>Paramesochra</i> spec. 4                  | -   | -   | -   | -   | -   | -   | -   | -    | -   | -   | 7   | 2    | 1   | 2   |
| 19       | <i>Paramesochra</i> spec. 5                  | -   | -   | 2   | -   | -   | -   | -   | 2    | -   | -   | -   | -    | -   | -   |
| 20       | <i>Paramesochra</i> spec. 6                  | 1   | 7   | 6   | 12  | -   | -   | 3   | 10   | -   | 6   | -   | 5    | 4   | -   |
| 21       | <i>Paramesochra</i> spec. 7                  | -   | -   | 5   | -   | -   | -   | -   | -    | -   | -   | 3   | -    | 5   | -   |
| 22       | <i>Paramesochra</i> spec. 8                  | -   | -   | -   | -   | -   | -   | -   | -    | -   | -   | -   | 2    | -   | -   |
| 23       | <i>Paramesochra</i> spec. 9                  | -   | -   | 2   | -   | -   | -   | -   | 5    | -   | -   | -   | -    | -   | -   |
| 24       | <i>Paramesochra</i> spec. 10                 | -   | -   | -   | -   | -   | -   | -   | -    | -   | -   | 1   | -    | -   | -   |
| 25       | <i>Paramesochra</i> sp. 11                   | -   | -   | 1   | -   | -   | -   | -   | -    | -   | -   | -   | -    | -   | -   |
| 26       | <i>Scottopsyllus</i> (I.) <i>intermedius</i> | 3   | 17  | 4   | 8   | 1   | -   | -   | 13   | -   | 1   | -   | 1    | -   | -   |
| 27       | <i>Sc.</i> (I) <i>antoniae</i> sp.n.         | -   | -   | 8   | 3   | -   | -   | -   | 15   | -   | -   | -   | -    | -   | -   |
| 28       | Paramesochridae spec.                        | -   | -   | 1   | -   | -   | -   | -   | -    | -   | -   | -   | -    | -   | -   |
|          | N/station                                    | 50  | 48  | 68  | 60  | 3   | 1   | 8   | 140  | 1   | 23  | 17  | 175  | 23  | 9   |
|          | S/station                                    | 12  | 9   | 16  | 11  | 3   | 1   | 5   | 14   | 1   | 6   | 5   | 16   | 7   | 6   |
|          | N/S ratio                                    | 4.2 | 5.3 | 4.3 | 5.1 | 1.0 | 1.0 | 1.6 | 10.0 | 1.0 | 3.8 | 3.4 | 10.9 | 3.3 | 1.5 |

#### Description of the female

Body (Fig. 2a, b) elongate, cylindrical and slightly depressed dorsoventrally. Body length (including FR) 426 µm. Last abdominal segment and telson tapering posteriorly. Surface of the body covered with small rounded depressions resembling the surface of a golf ball (Fig. 6b). Rostrum nearly indiscernible. First pedigerous somite completely fused to dorsal cephalic shield forming the cphth. Cphth and thoracic somites bearing P2–P4 with sensilla laterally and dorsally. Last thoracic body somite (P5 bearing somite) without sensilla. First abdominal somite completely fused with last thoracic body somite, forming the genital double somite, with 6 sensilla and 2 pores dorsally, 1 sensillum and 3 pores on each lateral side. Following abdominal somite dorsally with 2 sensilla and 1

lateral pore. Penultimate body somite without sensilla, carrying a fine, well developed pseudoperculum. Telson short, tapering posteriorly. FR (Fig. 6a–c) short, about twice as long as wide, with 6 setae: I absent; II long, inserted dorsolaterally in proximal half; III slightly shorter than II, bipinnate in distal part, inserted subdistally; IV slightly longer than III, terminally; V longest seta, terminally; VI shortest seta, inserted terminally at inner side of ramus; VII longer than setae II and III, inserted dorsally on distal half of ramus, slightly displaced inwards. Length/width ratio: 2:1.

A1 (Fig. 3a) 8-segmented; armature formula: I–1, II–9, III–7, IV–3 + aes, V–1, VI–2, VII–3, VIII–6 + aes. Both aes basally fused with 1 seta. First two segments largest, following segments decreasing in size.



**Fig. 1** Location of the stations sampled during RV “Meteor” cruise M 42/3 (1998) at the Great Meteor Seamount (Northeast Atlantic Ocean). Stars Stations where Paramesochridae have been found: black stars sampled with EBS; white stars sampled with MUC and GKS

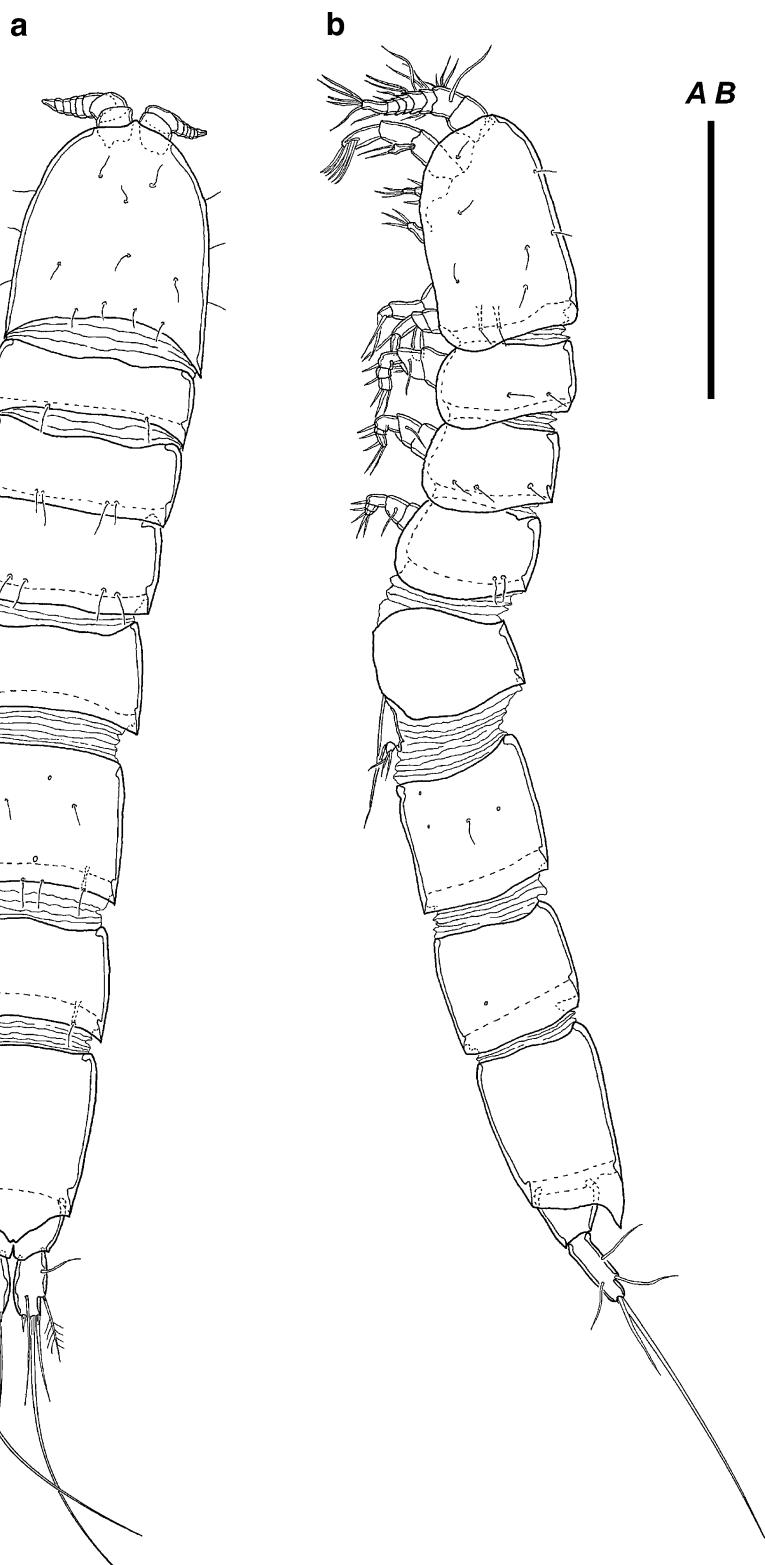
*A2* (Fig. 3b) Basis short and strong. Enp 2-segmented; enp-1 with 1 bare and slender abexopodal seta; enp-2 with 2 bare setae laterally and a group of 6 strong geniculate setae apically. Exp 1-segmented with 1 bare lateral seta and 2 apical setae (1 seta broken).

*Md* (Fig. 4a) Cutting edge lost during dissection. Md palp biramous, with basis, enp and exp. Basis with 1 unipinnate seta. Enp 1-segmented with 1 lateral seta and 4 apical

setae; all setae bare. Exp fused to basis, very small and cone-shaped, with 2 apical bare setae, 1 of which short and thin.

*Mxl* (Fig. 4b) Arthrite of praecoxa with 6 strong, stout spines terminally and 1 strong seta at the distal inner corner. Coxal endite with 1 slender naked seta apically. Basis with 5 apical setae and 1 slender naked seta laterally, representing enp. Exp very small, 1-segmented, with 2 bare apical setae.

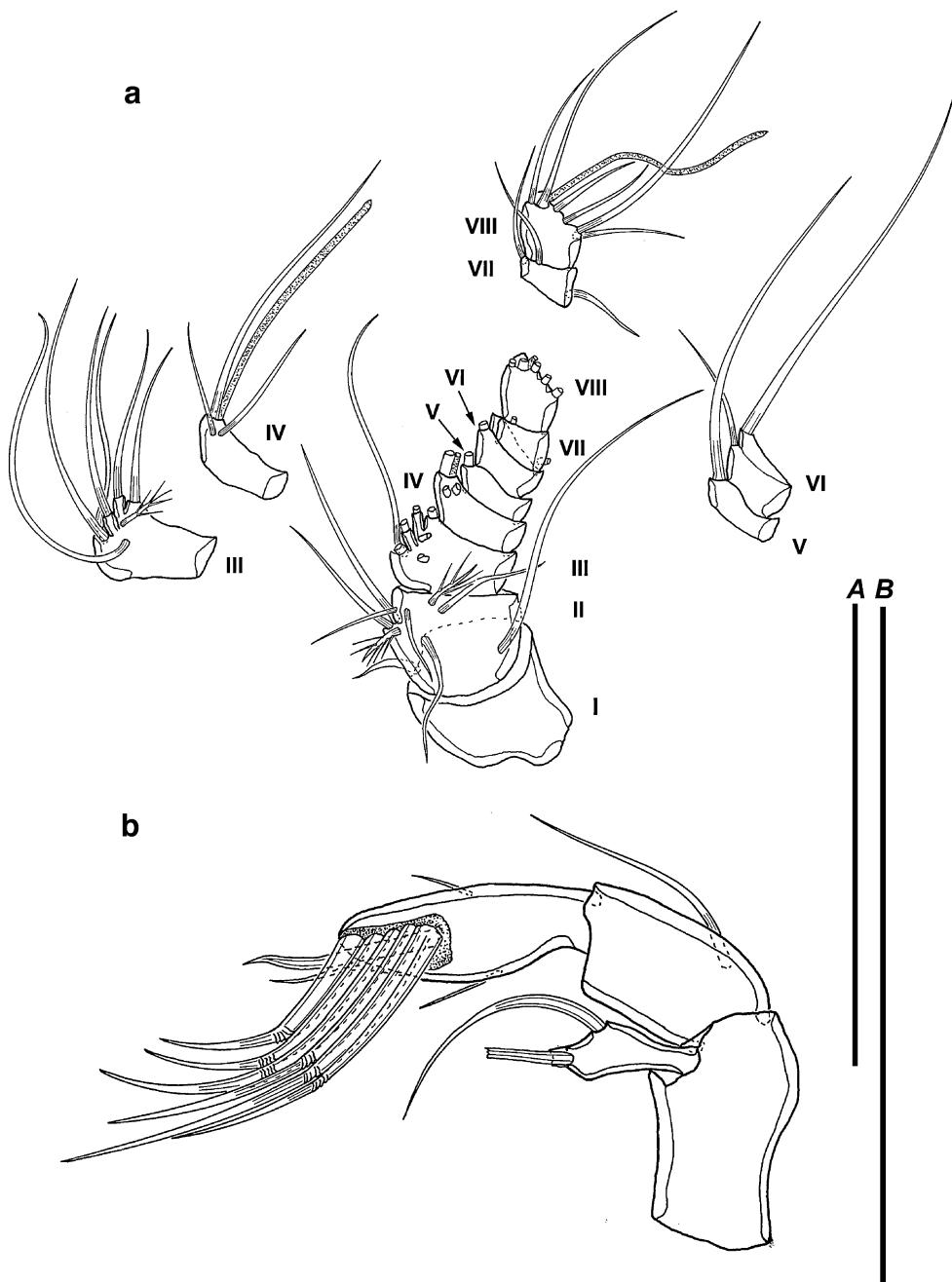
**Fig. 2** *Scottopsyllus*  
*(Intermedopsyllus) antoniae* sp.  
 nov., holotype female:  
 (a) habitus dorsal; (b) habitus  
 lateral. Scale bar: 100 µm



*Mx* (Fig. 4c) Syncoxa with 2 endites, proximal endite bearing 1 seta; distal endite with 2 setae; allobasis drawn out to form 1 strong unipinnate claw bearing 2 additional setae, one of which unipinnate. Enp represented by 4 setae.

*Mxp* (Fig. 4d) subchelate, comprising syncoxa, basis and 1-segmented enp. Syncoxa short and bare, without any ornamentation. Basis slightly elongate and swollen, with short row of strong spinules. Enp 1-segmented, with claw-

**Fig. 3** *Scottopsyllus (Intermedopsyllus) antoniae* sp. nov., holotype female: **a** antenull, **b** antenna. Scale bars: 50 µm



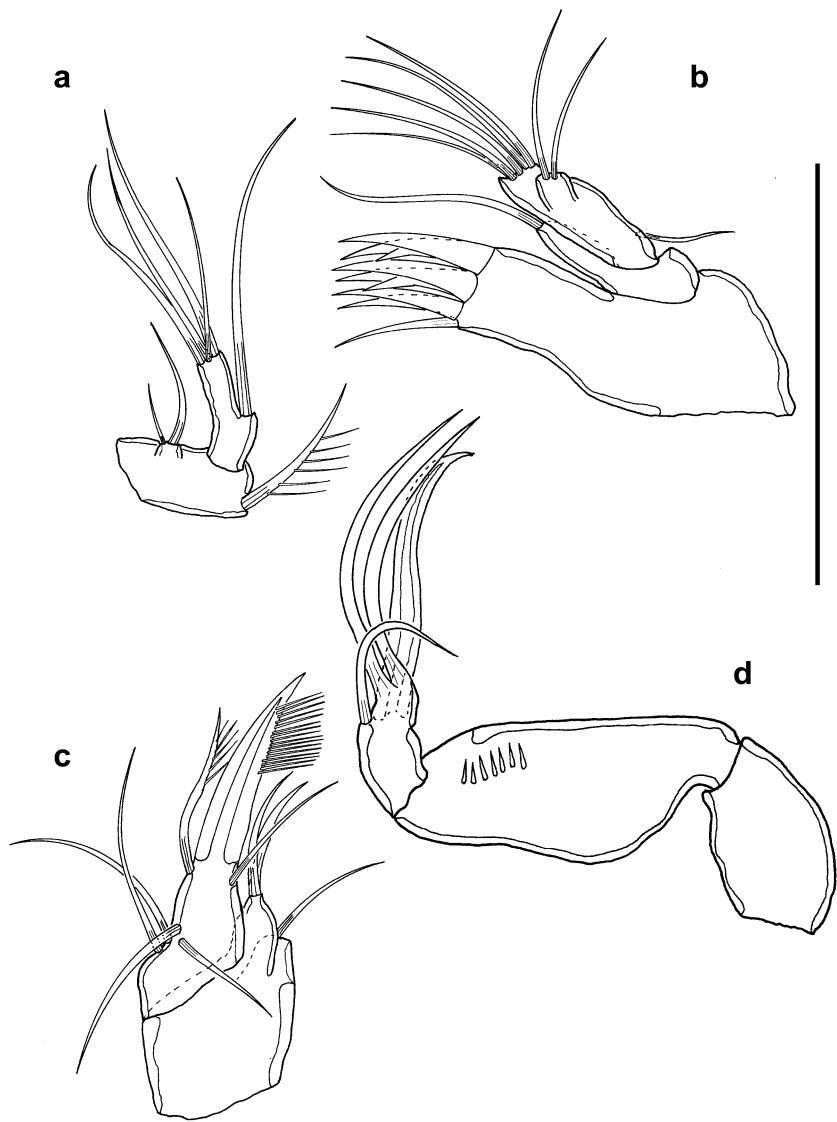
like seta accompanied by 1 small outer seta and 2 apical setae.

*P1* (Fig. 5a, Table 3) Coxa without setae. Basis with 1 inner seta, outer seta absent. Enp and exp 2-segmented. Exp-1 almost twice as long as exp-2, with 1 outer seta; exp-2 with 2 outer and 2 apical setae; both segments with outer row of strong spinules. Enp-1 without seta, but with outer row of long spinules. Enp-2 with 1 long, apical seta and 1 shorter, outer seta, both setae bare and geniculate.

*P2–P3* (Fig. 5b, c) Basis with 1 outer, bare seta. Enp 1-segmented, with long spinules along the margin and without seta. Exp 3-segmented, longer than enp, exp-2 shortest segment. Exp-1, exp-2 and exp-3 with stout outer spine and outer row of strong spinules; exp-3 with 2 apical setae, the inner of which unipinnate.

*P4* (Fig. 5d) Basis without outer seta. Enp as in P2 and P3 but smaller. Exp longer than enp. Exp 2-segmented due to fusion of exp-1 and exp-2. Exp-1 with 2 strong outer spines and outer row of strong spinules, exp-2 with 1 strong outer

**Fig. 4** *Scottopsyllus (Intermedopsyllus) antoniae* sp. nov.: **a** mandibular palp, **b** maxillule, **c** maxilla, **d** mandible. Scale bar: 25  $\mu\text{m}$



spine and 1 apical, bare seta; apically with row of strong spinules.

P5 (Fig. 6d) benps fused to single, broad and large lamelliform plate. Outer basal seta on short setophore. Each endopodal part of P5 with 1 seta. Exps distinct, not fused, and very small, with 3 slender, bare setae apically.

*GF and P6* (Fig. 6e) Gonopore not covered, almost triangular in ventral view. P6 represented by 2 medially fused plates, each bearing two minute spinules placed on small protrusions.

*Male differs from female as follows*

*A1* (Fig. 7b) 6-segmented, chirocer. Segment II with 1 bipinnate seta, other setae bare; segment V rounded and

bulbous; segment VI sharpened. Armature formula: I–1, II–9, III–7 + aes, IV–1, V–10 + aes, VI–11.

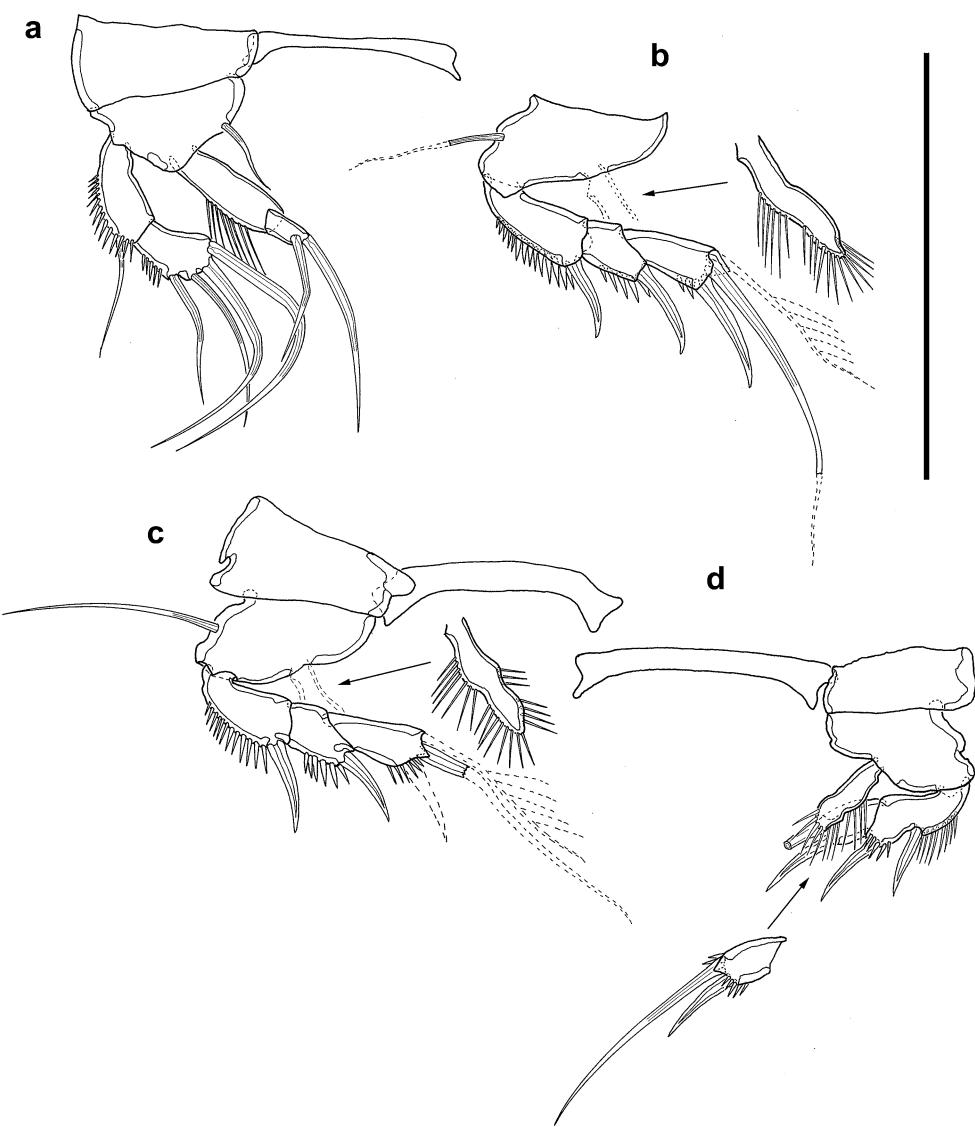
P5 (Fig. 7a) strongly resembling that of female, but without such a pronounced endopodal plate and without endopodal seta

*P6* (Fig. 7a) Represented by medially fused plates furnished each with 1 outer and 2 inner bare setae.

#### Paramesochridae of the Great Meteor Seamount

Paramesochridae were one of the most abundant harpacticoid taxa at the GMS, making up 20.4% of total harpacticoid number of individuals (George and Schminke 2002). Of the 1,249 collected specimens, 623 individuals (49.9%) were copepodids, and 626 (50.1%) adults. More than half of the adults (626 specimens or 65.0%) were

**Fig. 5** *Scottopsyllus (Intermedopsyllus) antoniae* sp. nov., holotype female: **a** swimming leg 1, **b** swimming leg 2, **c** swimming leg 3, **d** swimming leg 4. Scale bar: 50  $\mu$ m



found on the southern part of the plateau. The highest absolute individual number  $N$  was recorded at station 551 ( $N=175$ , i.e., 28.1%), followed by station 516 ( $N=140$ , 11.2%) and station 451 ( $N=68$ , 5.4%). Only one specimen was found at stations 506 and 517, respectively (Table 3). Median value  $Z$  for all stations:  $Z_N=23$ .

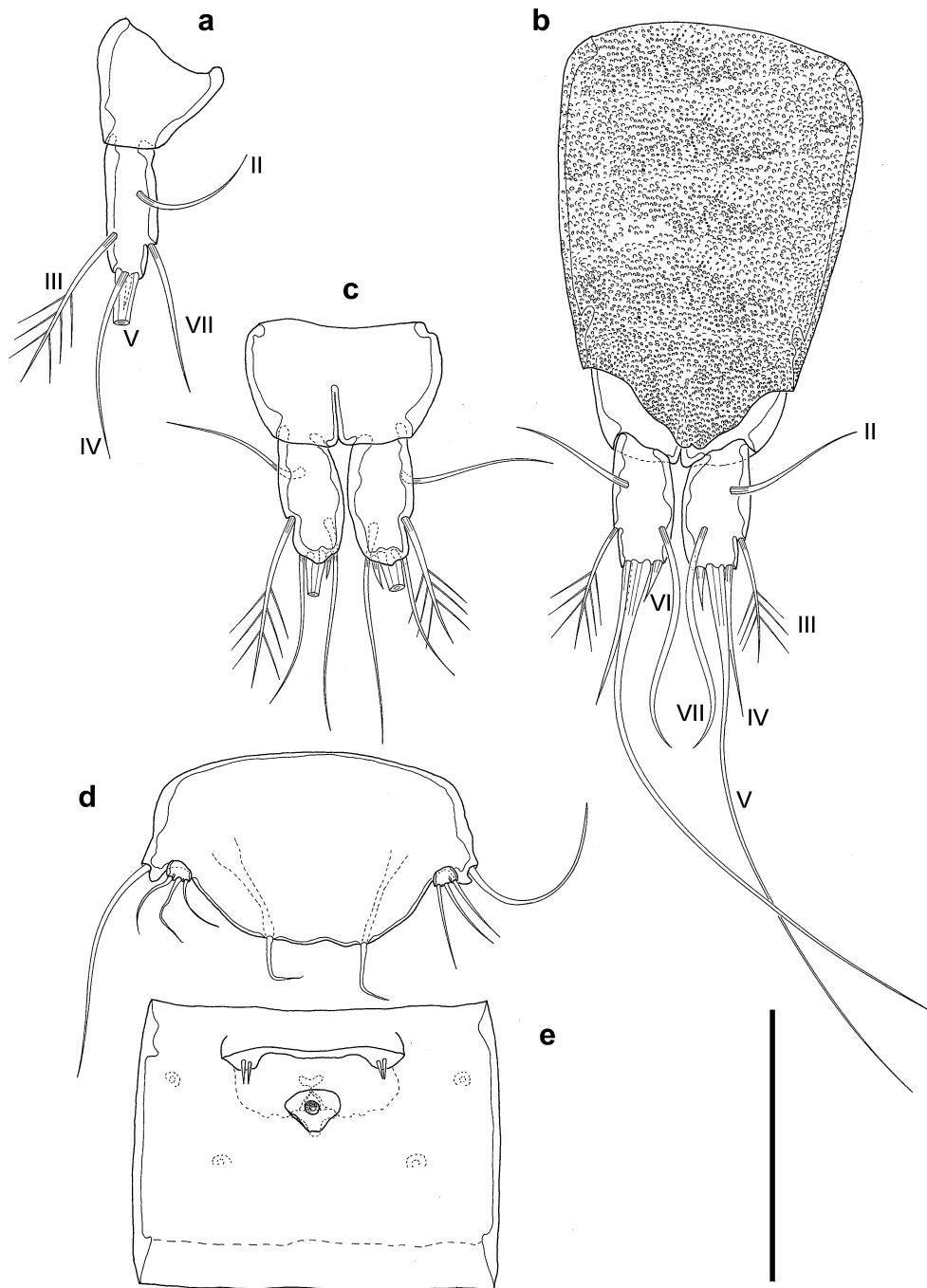
The obtained adults were assigned to six genera (*Apodopsyllus* Kunz 1962; *Diarthrodella* Klie 1949; *Kliop-*

*syllus* Kunz 1962; *Leptopsyllus* T. Scott 1894; *Paramesochra* T. Scott 1892 and *Scottopsyllus* Kunz 1962) and 28 species (Table 2). The number of species within the stations ranges from  $S=1$  (stations 506, 517) up to  $S=16$  (stations 451, 551; Table 3) (i.e., the latter two stations contain 57.1% of the total number of paramesochrid species at the GMS). Stations 451 and 551 show the highest species richness ( $S$ ). However, for a more objective impression,  $S$  should be standardized, and in our case,  $S$  can be related to the number of specimens,  $N$ , representing a simple measure of  $N/S$  (cf. Rose et al. 2005). The  $N/S$  ratio (Table 3) indicates how many individuals are needed to encounter a new species (cf. George 2004a). Not taking into account stations with  $<5$  specimens (i.e., st. 505, 506, 517), the highest evenness is observed at station 565 ( $N/S=1.5$ ), followed by st. 515 ( $N/S=1.6$ ), st. 552 ( $N/S=3.3$ ), and st. 521 ( $N/S=3.4$ ). The above mentioned stations 451 and 551 show much higher  $N/S$  ratios (4.3 and 10.9, respectively).

**Table 3** Setal formula of swimming legs of *Scottopsyllus (Intermedopsyllus) antoniae* sp. nov

| Leg | Coxa | Basis | Exopod            | Endopod |
|-----|------|-------|-------------------|---------|
| P1  | 0–0  | 0–1   | I–0; I,I,2        | 0–0,I,I |
| P2  | 0–0  | 1–0   | I–0; I–0; I,I + 1 | 0       |
| P3  | 0–0  | 1–0   | I–0; I–0; I,I + 1 | 0       |
| P4  | 0–0  | 0–0   | II–0; I,I         | 0       |

**Fig. 6** *Scotopsyllus (Intermedopsyllus) antoniae* sp. nov., holotype female: **a** furcal ramus, lateral, **b** furcal rami, telson and pseudoperculum, dorsal, **c** furcal rami, ventral, **d** P5, **(e)** GF with P6. Scale bar: 50 µm

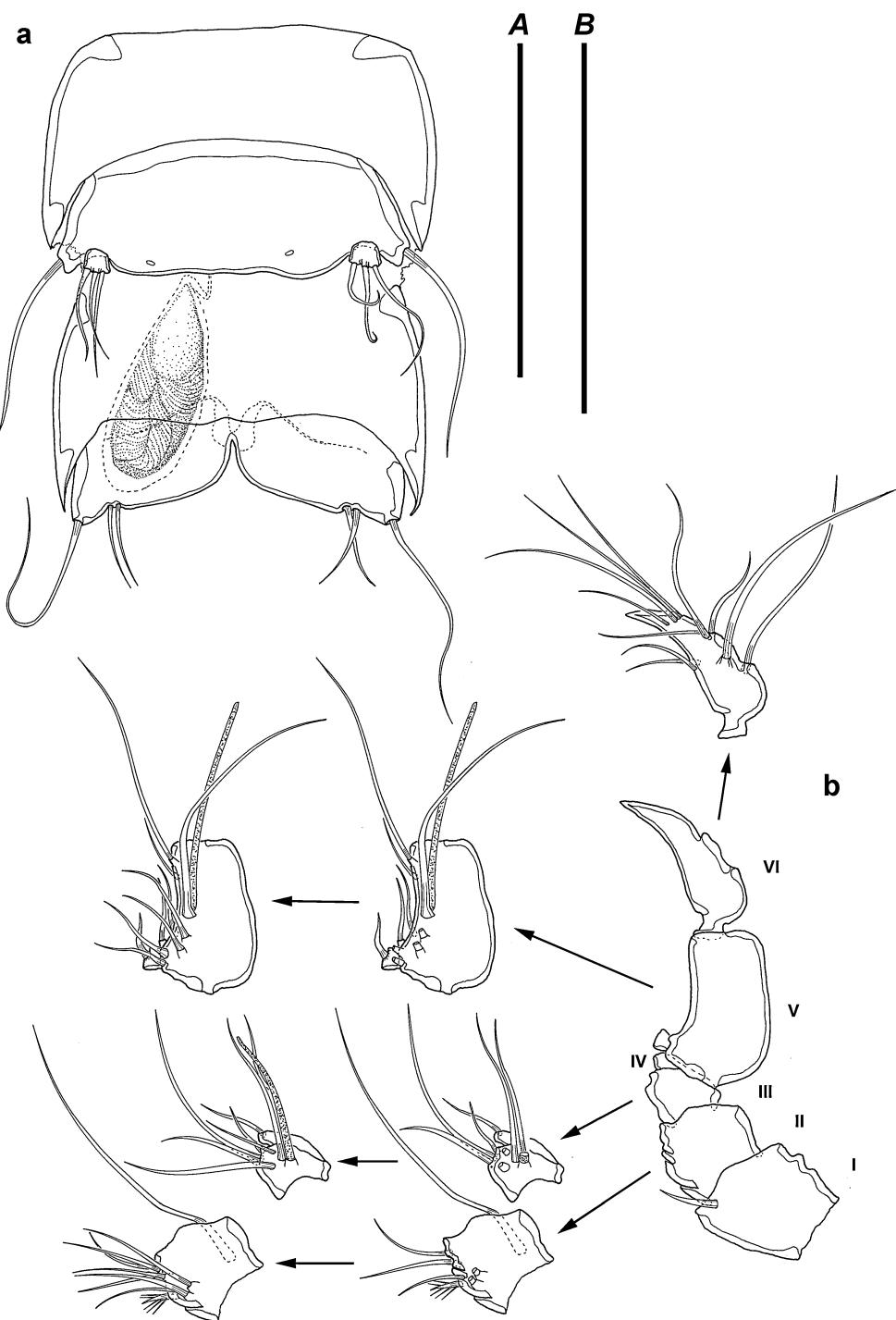


*Paramesochra* and *Kliopsyllus* were the most species-rich genera on the GMS plateau (Table 2) with 11 species for both genera, together comprising 78.6% of all paramesochrid species found. Two species have been recognized within *Leptopsyllus*, two within *Scotopsyllus*, one species within *Apodopsyllus* and one within *Diarthrorella*. Most of the paramesochrid species at the GMS ( $S=26$ , i.e., 92.9%) have not yet been reported from anywhere else. Only *Scotopsyllus (I.) intermedius* T. and A. Scott 1895 and *Kliopsyllus schminkei* Veit Köhler and Drewes 2009 were already known to science.

#### Bathymetric and geographical distribution of paramesochrid species from the GMS

Most of the 28 species ( $S=25$  or 89.3%) were found exclusively on the plateau (292–511 m) of the GMS (Fig. 8), while only one species, *Kliopsyllus schminkei*, was confined to the adjacent deep sea. This species has hitherto been reported from three abyssal plains of the southeast Atlantic Ocean, namely the Guinea, the Angola and the Cape Basins (Veit Köhler and Drewes 2009; Gheerardyn and Veit-Köhler 2009). The records of *K.*

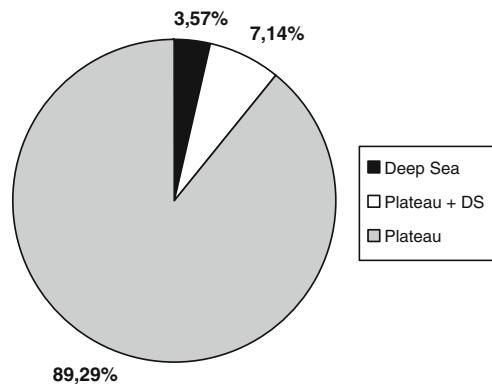
**Fig. 7** *Scottopsyllus (Intermedopsyllus) antoniae* sp. nov., paratype male: **a** P5 and P6, **b** antennula, ventral view. Scale bar: 50  $\mu$ m



*schmikei* from the GMS are from a similar depth, namely from the deep-sea stations 505 (4005 m) and 506 (3009 m).

*Kliopsyllus* sp. 3 and *Kliopsyllus* sp. 10 have been found at Seine seamount (Büntzow, personal communication), which is also located in the Northeast Atlantic Ocean, approximately 750 nm north-east of the GMS. Another species, *Kliopsyllus* sp. 7, found between 322 and 476 m depth at the GMS, was also found in the Guinea Basin during the DIVA-2 expedition (2005) (Gheerardyn and Veit-Köhler 2009).

*Scottopsyllus (I.) intermedius* and *Kliopsyllus* sp. 10 were found in the deep sea as well as on top of the seamount (Fig. 8). *Sc. (I.) intermedius* actually occurs in coastal waters of the East Atlantic, the North Sea, the Black Sea and the White Sea (Kornev and Chertoprud 2008). Its geographical distribution in the East Atlantic ranges from the Firth of Forth (Scotland) in the north to the Lüderitz Bay of Namibia in the south. This species could be characterized as a typical interstitial species of shallow-



**Fig. 8** Bathymetric distribution pattern (%) of paramesochrid species at the GMS (DS deep sea)

water habitats. Findings at the GMS were almost restricted to the shallow plateau, but one specimen was found at the deep-sea station 505 at 4,005 m depth. This is the first record of a *Scottopsylus* species from the deep Atlantic Ocean.

The species *Scottopsylus (I.) antoniae* sp. nov. described here is new to science, but was also recorded during the OASIS expedition (2003) (<http://www1.uni-hamburg.de/OASIS/>) on Sedlo Seamount (Büntzow, personal communication), approximately 630 nautical miles (nm) north of the GMS.

#### Review of the worldwide geographic and bathymetric distribution of Paramesochridae

Members of the harpacticoid family Paramesochridae have been reported from various parts of the world's oceans. They are typically small, interstitial animals that mostly inhabit sandy beaches as well as intertidal and shallow-water sandy sediments. Nevertheless, some species have also been recorded repeatedly in deep-sea sediments (e.g., Becker et al. 1979; Thistle 1982; Veit-Köhler 2004, 2005; Rose et al. 2005; Baguley et al. 2006) and were recently also discovered on the Seine and Sedlo seamounts in the Northeast Atlantic (Büntzow, personal communication) and on the Anaximenes seamount in the eastern Mediterranean Sea (George, personal observation).

Table 4 presents a list of all paramesochrid species described so far, with notes on their geographic and bathymetric distribution. Including the newly described species *Scottopsylus (I.) antoniae* sp. nov., 126 paramesochrid species with 15 subspecies, belonging to 13 genera and 4 subgenera, have been described thus far.

The majority of Paramesochridae (35 species or 29%) have been found in the Atlantic Ocean, but there are also many records from the Pacific Ocean (26 species or 21%), the Indian Ocean (26 species, 21%), the Mediterranean Sea (8 species or 7%), and even from Antarctic waters (*Kliopsyllus andeep* Veit-Köhler 2004; *Scottopsylus (Sc.)*

*praecipuus* Veit-Köhler 2000) or inland seas like the Black Sea and the Baltic Sea (e.g., *Kliopsyllus holsaticus* Klie 1929) (Fig. 9).

The bathymetric distribution of Paramesochridae ranges from the littoral down to abyssal depths (see Table 4 and Fig. 10). The vast majority of them occur in (sub-)littoral zones with records generally ranging from beaches down to coastal waters of 146 m depth [*Scottopsylus (Wellsopsyllus) gigas* Wells 1965]. Only nine species have been recorded at depths deeper than 300 m, including *Scottopsylus (I.) antoniae* sp. nov. (325 m), *Kliopsyllus minor* Vasconcelos et al. 2009. (492 m), *Leptopsyllus elongatus* Drzycimski 1967 (515 m), *Leptopsyllus (Paraleptopsyllus) articus* Lang 1936 (1,750 m), *Scottopsylus (Wellsopsyllus) abyssalis* Becker et al. 1979 (2,000 m), *Leptopsyllus abyssalis* Becker 1972 (3,820 m), *Kliopsyllus andeep* Veit-Köhler 2004 (4,541 m), *Kliopsyllus diva* Veit-Köhler 2005 (5,389 m), and *Kliopsyllus schminkei* Veit-Köhler and Drewes 2009 (5,389 m). Figure 10 shows the bathymetric distribution patterns based on the available record data and indicates that 77% of all species have been found in shallow waters. Only 7% of the species have been recorded at depths below 200 m.

The most species-rich genera of the Paramesochridae are *Kliopsyllus* (38 species) and *Apodopsyllus* (25 species) followed by *Paramesochra* (14 species) and *Scottopsylus* (13 species) (Table 4). As mentioned above, the genera *Kliopsyllus* and *Paramesochra* are found to be the most diverse paramesochrid taxa at the GMS. The majority of the described species of *Kliopsyllus* and *Paramesochra* have been reported from coastal waters, but recent studies extended the depth range of *Kliopsyllus* down to >4,000 m (Veit-Köhler 2004, 2005; Veit-Köhler and Drewes 2009). Geographically, most species are restricted to regional areas, but certain species can be considered as "cosmopolitans". For example, *Kliopsyllus holsaticus* has been recorded from the Northeast Atlantic, the North Sea, the Baltic, and the Black Sea. The reports of *Kliopsyllus andeep* by Veit-Köhler 2004 have expanded the distribution range of *Kliopsyllus* to Antarctic waters. Species of *Paramesochra* show a similar broad distribution range with records from the North Sea and the Northeast Atlantic (*Paramesochra dubia* T. Scott 1892; *Paramesochra borealis* Geddes 1981), the Baltic Sea, Hawaii (*Paramesochra acutata hawaiensis* Kunz 1981), the Mediterranean Sea (*Paramesochra brevifurca* Galhano 1970), the Indian Ocean (*Paramesochra denticulata* Rao and Ganapati 1969), Galapagos Islands (*Paramesochra helgolandica galapagoensis* Mielke 1984a, b), Panama (*Paramesochra kunzi* Mielke 1984a, b) and Perth in western Australia (*Paramesochra longicaudata* Nicholls 1945).

The genus *Scottopsylus*, in turn, encompasses 13 species (and 1 subspecies), including the *Scottopsylus (I.)*

**Table 4** List of all paramesochrid species recorded so far, including data on geographic and bathymetric distribution. Information are taken from original descriptions and references provided by Bodin 1997 and Wells 2007

| No. | Species and authorship                                     | References                               | Location/Records  | Depth/Habitat                       | Geogr. Region  |
|-----|--|--|---|-------------------------------------|----------------|
| I.  | <i>Apodopsyllus</i> Kunz 1962                              |  |   |                                     |                |
| 1   | <i>A. aberrans</i> Mielke 1984a, b                         | Mielke 1984a                             | Panama, Isla Naos, Isla Melones                                       | Beach                               | Pacific Ocean  |
| 2   | <i>A. adaptatus</i> Krishnaswamy 1957; Krishnaswamy 1957   | Krishnaswamy 1957; Rao and Ganapati 1969 | India, Lawsons Bay, Waltair, Madras                                   | Beach, sand, detritus               | Indian Ocean   |
| 3   | <i>A. africanus</i> Kunz 1962                              | Kunz 1962                                | Lüderitz-Bay, Namibia, SW Africa,                                     | Tidal, sand                         | Atlantic Ocean |
|     | <i>A. africanus listensis</i> Mielke 1975                  | Mielke 1975                              | Gemany, Sylt  | Wadden, tidal                       | North Sea      |
| 4   | <i>A. alejandrovillabosi</i> Gómez 2002                    | Gómez 2002                               | Mexico, Sinaloa   | Lagune                              | Pacific Ocean  |
| 5   | <i>A. arcuatus</i> Mielke 1984a, b                         | Mielke 1984b                             | Galapagos Islands, Santa Cruz   | Beach                               | Pacific Ocean  |
| 6   | <i>A. arenicolus</i> Chappuis 1954                         | Chappuis 1954; Kunz 1962; Bodin 1979     | Spain; Algiria, La Calle, Philippewille; France, Ile de Re            | Sandy beaches                       | “Cosmopolitan” |
| 7   | <i>A. bermudensis</i> Coull and Hogue 1978                 | Coull and Hogue 1978                     | Bermuda, Base of Castle Island  | Subtidal sand flat 1-2 m            | Atlantic Ocean |
| 8   | <i>A. biarticulatus</i> Cottarelli and Altamura 1986       | Cottarelli and Altamura 1986             | Philippines, Palawan Island   | Coastal waters                      | Pacific Ocean  |
| 9   | <i>A. camptus</i> Wells 1971                               | Wells 1971; Wells and Rao 1987           | South India   | ?                                   | Indian Ocean   |
| 10  | <i>A. chilensis</i> Mielke 1987                            | Mielke 1987                              | Chile, Coquimbo   | ?                                   | Pacific Ocean  |
| 11  | <i>A. cubensis</i> Mielke 1988                             | Mielke 1988                              | Caribbean, Cuba, Playa Larga  | Interstitial, beach                 | Atlantic Ocean |
| 12  | <i>A. depressus</i> Krishnaswamy 1957                      | Krishnaswamy 1957                        | Lawsons Bay, Waltair; India, Madras                                   | Beach, sand, detritus               | Indian Ocean   |
| 13  | <i>A. littoralis</i> Nicholls 1939                         | Nicholls 1939; Wells 1961                | Atlantic, Scotland  | 7–10 cm                             | Atlantic Ocean |
| 14  | <i>A. lynceorum</i> Cottarelli 1971                        | Cottarelli 1971                          | Mediterranean, Porto S. Stefano                                       | Sandy beach                         | Mediterranean  |
| 15  | <i>A. madrasensis</i> Krishnaswamy 1951; Krishnaswamy 1951 | Krishnaswamy 1951; Wells and Rao 1987    | Indian Ocean, Coast of Madras   | 9.15 m                              | Indian Ocean   |
| 16  | <i>A. melitae</i> Kunz 1992                                | Kunz 1992                                | Mediterranean, Mljet Island   | 30 cm depth                         | Mediterranean  |
| 17  | <i>A. perplexus</i> Wells 1963b                            | Wells 1963a, b                           | England   | Litoral                             | Atlantic Ocean |
| 18  | <i>A. panamensis</i> Mielke 1984a, b                       | Mielke 1984a                             | Panama, Pacific coast, Isla Culebra                                   | Beach                               | Pacific Ocean  |
| 19  | <i>A. pseudocubensis</i> Gómez 2002                        | Gómez 2002                               | Mexico, Sinaloa   | Lagune                              | Pacific Ocean  |
| 20  | <i>A. reductus</i> Petkovski 1955                          | Petkovski 1955; Kunz 1962                | Croatia, Split Zvan   | Littoral                            | Mediterranean  |
| 21  | <i>A. samubelgomezi</i> Gómez 2002                         | Gómez 2002                               | Mexico, Sinaloa   | Lagune                              | Pacific Ocean  |
| 22  | <i>A. schulzi</i> Noodt 1964                               | Noodt 1964                               | Red Sea   | Corral sand                         | Indian Ocean   |
| 23  | <i>A. spinipes</i> Nicholls 1939                           | Nicholls 1939                            | Atlantic, Scotland  | Intertidal zone, 7–10 cm            | Atlantic Ocean |
| 24  | <i>A. unguiformis</i> Coull and Hogue 1978                 | Coull and Hogue 1978                     | USA, Georgetown, South Carolina                                       | Sand, 1 m depth                     | Atlantic Ocean |
| 25  | <i>A. vermiculiformis</i> Lang 1965                        | Lang 1965; Coull and Hogue 1978          | USA, Monterey Bay, California, USA; Canada, Nanaimo, British Columbia | Intertidal pools, fine sand         | Atlantic Ocean |
| II  | <i>Biuncus</i> Huys 1996                                   |  |   |                                     |                |
| 26  | <i>B. ingens</i> Huys 1996                                 | Huys 1996                                | Collected by Karaman-Chappuis methode, Elat, Israel                   | Low-water line, amphioxus sand      | Mediterranean  |
| III | <i>Caligopsyllus</i> Kunz 1975                             |  |   |                                     |                |
| 27  | <i>C. primus</i> Kunz 1975                                 | Kunz 1975; Huys 1988                     | South Afrca, East London  | Tidal pools of a reef, shell gravel | Indian Ocean   |
| IV  | <i>Diarthrorella</i> Klie 1949                             |  |   |                                     |                |
| 28  | <i>D. chilensis</i> Mielke 1985a, b                        | Mielke 1985b                             | Niebla, Isla Maiquillahue, Quellon, Viña del Mar                      | Beach, sand                         | Pacific Ocean  |

**Table 4** (continued)

| No. | Species and authorship                                   | References   | Location/Records   | Depth/Habitat                             | Geogr. Region  |
|-----|--|--|--|---|----------------|
| 29  | <i>D. convexa</i> Kunz 1983                              | Kunz 1983  | Azores   | Littoral                                  | Atlantic Ocean |
| 30  | <i>D. galapagoensis</i> Mielke 1984a, b                  | Mielke 1984b   | Galapagos, Fernandina, Cabo Gougl; James, Bahia James; Santa Cruz, Bahia; Academy; Barrington; Floreana; San Christobal; | Beach                                     | Pacific Ocean  |
| 31  | <i>D. lancifera</i> Kunz 1983                            | Kunz 1983  | Azores   | Littoral                                  | Atlantic Ocean |
| 32  | <i>D. neotropica</i> Mielke 1984a, b                     | Mielke 1984b   | Galapagos, Santa Cruz, Playa Borrero; Hood, Bahia Gardner  | Beach, low water level; Groundwater level | Pacific Ocean  |
| 33  | <i>D. orbiculata</i> Klie 1949                           | Klie 1949  | Helgoland, North Sea   | Littoral                                  | North Sea      |
| 34  | <i>D. parorbiculata</i> Wells 1963a, b                   | Wells 1963b  | Northern Ireland   | ?   | Atlantic Ocean |
|     | <i>D. parorbiculata pacifica</i> Mielke 1984a, b         | Mielke 1984b   | Galapagos, Tower, Bahia Darwin; Santa Cruz, Bahia Academy  | Beach                                     | Pacific Ocean  |
| 35  | <i>D. psammophila</i> Bocquet and Bozic 1955             | Bocquet and Bozic 1955   | France, Roscoff  | Sand                                      | Atlantic Ocean |
| 36  | <i>D. secunda</i> Kunz 1954                              | Kunz 1954; Mielke 1975   | Germany, Island of Sylt  | Beach, low water level                    | North Sea      |
|     | <i>D. secunda pacifica</i> Kunz 1981                     | Kunz 1981  | Hawaii, Anaeho'omalu Bay   | Beach, sand, low water level              | Pacific Ocean  |
| V   | <i>Kunzia</i> Wells 1967                                 |  |  |   |                |
| 37  | <i>K. bispinosa</i> Kunz 1974                            | Kunz 1974  | Africa   | Coastal interstitial                      | Indian Ocean   |
| 38  | <i>K. epacra</i> Wells 1967                              | Wells 1967   | Indian Ocean, Ilha dos Portuguesos, Mozambique   | Beach, clean sand                         | Indian Ocean   |
| 39  | <i>K. minutissima</i> Wells 1967                         | Wells 1967   | Indian Ocean, Ilha dos Portuguesos, Mozambique   | Beach, clean sand                         | Indian Ocean   |
| VI  | <i>Kliopsyllus</i> Kunz 1962                             |  |  |   |                |
| 40  | <i>K. acutifurcatus</i> Mielke 1985a, b                  | Mielke 1985a, b  | Chile, Mehui   | Beach                                     | Pacific Ocean  |
| 41  | <i>K. andeep</i> Veit-Köhler 2004                        | Veit-Köhler 2004   | Antarctica, Weddell Sea  | Muddy sediment, 4,541 m                   | Antarctica     |
| 42  | <i>K. arenicolus</i> Krishnaswamy 1957                   | Krishnaswamy 1957  | India, Madras  | ?   | Indian Ocean   |
| 43  | <i>K. atlanticus</i> Kunz 1983                           | Kunz 1983  | Azore Islands  | Interstitial                              | Atlantic Ocean |
| 44  | <i>K. californicus</i> Kunz 1981                         | Kunz 1981  | Pacific, San Francisco, USA  | Tidal pools of a reef                     | Pacific Ocean  |
| 45  | <i>K. capensis</i> Krishnaswamy 1957                     | Krishnaswamy 1957; Rao Ganapati 1969                             | India, Cape Comorin; Waltair   | Beach                                     | Indian Ocean   |
| 46  | <i>K. chilensis</i> Mielke 1985a, b                      | Mielke 1985a   | Chile, Quellon, Viña del Mar, Reñaca   | Coastal waters                            | Pacific Ocean  |
| 47  | <i>K. coelebs</i> Monard 1935                            | Monard 1935; Pesta 1959; Kunz 1962; Wells 1963a, b; Marinov 1977 | France, Roscoff; Las Palmas; Mauritania  | Coarse sand, interstitial                 | Atlantic Ocean |
| 48  | <i>K. constrictus</i> Nicholls 1935                      | Nicholls 1935; Marinov 1971; Apostolov and Marinov 1988          | Helgoland; north-east Atlantic; Scotland; Mediterranean Sea; Marmara Sea; Black Sea; White Sea                           | Littoral, coarse sand                     | North-Europe   |
|     | <i>K. constrictus egyptus</i> Mitwally and Montagna 2001 | Mitwally and Montagna 2001                                       | Egypt, Alexandria, diterranean   | Sandy beach                               | Mediterranean  |
|     | <i>K. constrictus orotavae</i> Noodt 1958                | Noodt 1958; Rao and Ganapati 1969                                | Israel, Nahariyya, Mediterranean; Azores, Atlantic; Waltair, India, Indian Ocean   | Coarse sand                               | "Cosmopolitan" |
|     | <i>K. constrictus pacificus</i> Mielke 1984a, b          | Mielke 1984a, b, 1987  | Pacific, Isla Flamenco, Isla Melones; Chile, Coquimbo, Iquique   | Beach                                     | Pacific Ocean  |

**Table 4** (continued)

| No. | Species and authorship                                      | References   | Location/Records  | Depth/Habitat           | Geogr. Region  |
|-----|---|--|---|-------------------------|----------------|
| 49  | <i>K. debilis</i> Kunz 1981                                 | Kunz 1981  | Hawaii, Coconut Island, Ohau  | Fine sand, 20 cm        | Pacific Ocean  |
| 50  | <i>K. diva</i> Veit-Köhler 2005                             | Veit-Köhler 2005   | East Atlantic, Angola Basin   | Muddy sediment, 5,389 m | Atlantic Ocean |
| 51  | <i>K. enalius</i> Krishnaswamy 1957                         | Krishnaswamy 1957  | India, Madras   | ?                       | Indian Ocean   |
| 52  | <i>K. furcavariatus</i> Kunz 1974                           | Kunz 1974  | East Africa; Tanzania; West Indies  | Coral sand 3 m          | Indian Ocean   |
| 53  | <i>K. gracilis</i> Wilson 1932 (uncertain Bodin 1997)       | Wilson 1932  | ?   | ?                       | ?              |
| 54  | <i>K. holsaticus</i> Klie 1929                              | Klie 1929; Scheibel 1972; Mielke 1975; Wells and Rao 1987; Apostolov and Marinov 1988; Kunz 1981 | North-east Atlantic; Baltic Sea, Bay of Kiel; North Sea, Helgoland; Black Sea | Sand                    | “Cosmopolitan” |
|     | <i>K. holsaticus varians</i> Kunz 1951                      | Kunz 1951  | South West Africa   | Sand                    | Atlantic Ocean |
|     | <i>K. holsaticus longicaudatus</i> Galhano 1970             | Galhano 1970   | Portugal  | Interstitial            | Atlantic Ocean |
|     | <i>K. holsaticus listensis</i> Mielke 1984a, b              | Mielke 1984a, b  | ?   | ?                       | ?              |
| 55  | <i>K. idiotes</i> Wells 1967                                | Wells 1967   | Africa, Mozambique  | Coastal waters          | Indian Ocean   |
| 56  | <i>K. insularis</i> Kunz 1981                               | Kunz 1981  | Hawaii, Coconut Island  | Fine sand 20 cm         | Pacific Ocean  |
| 57  | <i>K. laurenticus</i> Nicholls, 1939 (uncertain Bodin 1997) | Nicholls 1939; Wells 1963a, b  | Canada, St. Lawrence River; USA, Woods Hole                                   | Sandy beach             | Atlantic Ocean |
| 58  | <i>K. longifurcatus</i> Scheibel 1975                       | Scheibel 1975  | Baltic Sea, Bay of Kiel   | Sand flat               | North Europe   |
| 59  | <i>K. longisetosus</i> Krishnaswamy 1951, 1957              | Krishnaswamy 1951, 1957  | India, Madras   | Coastal waters          | Indian Ocean   |
| 60  | <i>K. major</i> Nicholls 1939                               | Nicholls 1939  | Canada, St. Lawrence River  | Coarse sand 8 m         | Atlantic Ocean |
| 61  | <i>K. masryi</i> Masry 1970                                 | Masry 1970   | Israel, Shiqmona, Nahariyya; Italy; France                                    | Beach                   | Mediterranean  |
| 62  | <i>K. miguelensis</i> Kunz 1983                             | Kunz 1983  | Azores  | Interstitial            | Atlantic Ocean |
| 63  | <i>K. minutus</i> Krishnaswamy 1957                         | Krishnaswamy 1957  | India   | Coastal waters          | Indian Ocean   |
| 64  | <i>K. minor</i> Vasconcelos et al. 2009                     | Vasconcelos et al. 2009  | Northeastern Brazil   | 492 m                   | Atlantic Ocean |
| 65  | <i>K. panamensis</i> Mielke 1984a, b                        | Mielke 1984a, b  | Panama, Isla Melones  | ?                       | Pacific Ocean  |
| 66  | <i>K. paraholsaticus</i> Mielke 1975                        | Mielke 1975  | ?   | Sand, wadden            | North Sea      |
| 67  | <i>K. perhardiensis</i> Wells 1963a, b                      | Wells 1963b  | Atlantic; France, Roscoff; Ireland; England                                   | Beach, brackish waters  | Atlantic Ocean |
| 68  | <i>K. ponticus</i> Serban 1959                              | Serban 1959, 1968  | Black Sea   | Beach                   | North-Europe   |
| 69  | <i>K. psammobionta</i> Noodt 1964                           | Noodt 1964   | Cosmopolitan  | Coastal waters          | “cosmopolitan” |
| 70  | <i>K. psammophilus</i> Noodt 1964                           | Noodt 1964   | Red Sea   | ?                       | Indian Ocean   |
| 71  | <i>K. pseudogracilis</i> Krishnaswamy 1951                  | Krishnaswamy 1951; Rao and Ganapati 1969   | India, Waltair Sand   | Coastal waters          | Indian Ocean   |
| 72  | <i>K. pygmaeus</i> Nicholls 1939b                           | Nicholls 1939b   | Scotland, Balloch Bay, Firth of Clyde; Canada, St Lawrence                    | Sand, low water         | Atlantic Ocean |
| 73  | <i>K. regulexstans</i> Mielke 1984a, b                      | Mielke 1984a, b  | Galapagos Islands; Atlantic, Caribbean, Isla Mosquito                         | Coastal waters          | “Cosmopolitan” |
| 74  | <i>K. schminkei</i> Veit-Köhler and Drewes 2009             | Veit-Köhler and Drewes 2009  | South-east Atlantic, Angola Basin   | 5,389 m                 | Atlantic Ocean |
| 75  | <i>K. similis</i> Mielke 1984a, b                           | Mielke 1984a, b  | Galapagos Islands; Atlantic, Caribbean, Isla Mosquito                         | Beach                   | “Cosmopolitan” |

**Table 4** (continued)

| No.  | Species and authorship  | References                                     | Location/Records  | Depth/Habitat                            | Geogr. Region                   |
|------|---|--|---|--|---------------------------------|
| 76   | <i>K. spiniger</i> Wells et al. 1975<br><i>K. spiniger ornatus</i> Kunz 1981          | Wells et al. 1975; Mielke 1984b<br>Kunz 1981   | Indian Ocean, North Andaman, India; Galapagos Islands<br>Hawaii, Maui   | 10–30 cm<br>Coastal groundwater          | “Cosmopolitan”<br>Pacific Ocean |
| 77   | <i>K. unguiseta</i> Mielke 1984a, b   | Mielke 1984a, b                                | Galapagos Islands, Santa Cruz   | Beach                                    | Pacific Ocean                   |
| 78   | <i>K. wilsoni</i> Krishnaswamy 1957   | Krishnaswamy 1957; Rao and Ganapati 1969       | India, Waltair  | Sand                                     | Indian Ocean                    |
| 79   | <i>Kliopsyllus</i> sp. (sp. i.) Apostolov 1973b                                       | Apostolov 1973b                                | Black Sea   | ?  | Black Sea                       |
| VII  | <i>Leptopsyllus</i> T. Scott 1894   |  |   |  |                                 |
| 80   | <i>L. abyssalis</i> Becker et al. 1979  | Becker et al. 1979                             | Iberian Basin   | 3,820 m                                  | Atlantic Ocean                  |
| 81   | <i>L. celticus</i> Bodin and Jackson 1987   | Bodin and Jackson 1987                         | Ireland, An Poll Brean beach, Mweenish Island; France, Kersaint beach, Brittany   | Intertidal sand                          | Atlantic Ocean                  |
| 82   | <i>L. dubatyi</i> Soyer 1975  | Soyer 1975                                     | Kerguelen   | Mesopsammon                              | Antarctica                      |
| 83   | <i>L. elongatus</i> Drzycimski 1967   | Drzycimski 1967                                | Norway, Korsfjorden   | Mud, 515 m                               | Atlantic Ocean                  |
| 84   | <i>L. harveyi</i> Wells 1963a, b  | Wells 1963a, b, 1967                           | Indian Ocean, Ilha dos Portuguesos  | Beach, clean sand                        | Indian Ocean                    |
| 85   | <i>L. paratypicus</i> Nicholls 1939   | Nicholls 1939                                  | Scotland, Balloch Bay, Firth of Clyde   | Sand                                     | Atlantic Ocean                  |
| 86   | <i>L. platyspinosus</i> Mielke 1984a, b   | Mielke 1984a, b                                | Galapagos Islands   | Beach                                    | Pacific Ocean                   |
| 87   | <i>L. punctatus</i> Mielke 1984a, b   | Mielke 1984a, b                                | Galapagos, Marchena, Southwest beach, Santa Cruz, Playa Borrero, Bahia Academy, Bartholome Nord, Cop. Floreana, Punta Cormorant | Beach                                    | Pacific Ocean                   |
| 88   | <i>L. reductus</i> Lang 1948  | Lang 1948; Por 1964                            | Sweden, Gullmarsfjord   | 70–80 m, mud                             | North Europe                    |
| 89   | <i>L. typicus</i> Lang 1948   | Lang 1948                                      | Scotland, Queensferry, Firth of Forth   | ?  | Atlantic Ocean                  |
| 90   | <i>Leptopsyllus</i> ( <i>Paraleptopsyllus</i> )<br><i>L. (Par:) articus</i> Lang 1936 | Lang 1936; Lang 1948                           | Spitzbergen   | Clay 1,750 m                             | Atlantic Ocean                  |
| VIII | <i>Meiopsyllus</i> Cottarelli and Forniz 1994   |  |   |  |                                 |
| 91   | <i>M. marinae</i> Cottarelli and Forniz 1994  | Cottarelli and Forniz 1994                     | Sardinia, Asinara island, Cala Arena  | Seashore                                 | Mediterranean                   |
| IX   | <i>Paramesochra</i> T. Scott 1892   |  |   |  |                                 |
| 92   | <i>P. acutata</i> Klie 1935<br><i>P. acutata hawaiensis</i> Kunz 1981                 | Klie 1935; Lang 1948; Mielke 1975<br>Kunz 1981 | Germany, Baltic Sea, Courland Spit, Bay of Kiel<br>Hawaii, Kauai island, Maui Island, Beach                                     | Coastal groundwater<br>Beach, tidal pool | North Europe<br>Pacific Ocean   |
| 93   | <i>P. australis</i> Mielke 1994   | Mielke 1994                                    | Chile   | ?  | Pacific Ocean                   |
| 94   | <i>P. borealis</i> Geddes 1981  | Geddes 1981                                    | Norway, Tromsö  | Intertidal sand                          | Atlantic Ocean                  |
| 95   | <i>P. brevifurca</i> Galhano 1970<br><i>P. brevifurca mediterranea</i> Huys 1987      | Galhano 1970<br>Huys 1987; Cottarelli 1971     | Atlantic, Portugal<br>Mediterranean, Italy, Sardinia  | Interstitial sand<br>Interstitial sand   | Atlantic Ocean<br>Mediterranean |
| 96   | <i>P. denticulata</i> Rao and Ganapati 1969   | Rao and Ganapati 1969                          | India, Waltair, Palm Beach  | Medium sand, half-tide level             | Indian Ocean                    |
| 97   | <i>P. dubia</i> T. Scott 1892   | T. Scott 1892; Lang 1948                       | Norway, Korshavn; Germany, Helgoland;   | 12–43 m; mud, sand                       | North Europe                    |

**Table 4** (continued)

| No. | Species and authorship                               | References   | Location/Records   | Depth/Habitat                              | Geogr. Region             |                |
|-----|--|--|--|--|---------------------------|----------------|
| 98  | <i>P. helgolandica</i> Kunz 1936                     | Kunz 1936; Marinov 1971; Apostolov 1972, 1973b; Apostolov and Marinov 1988                                     | Scotland, Firth of Forth, St. Monas; England, Cornwell, St. Mary's Sound of Scilly Island, Liverpool Bay, Port Erin; Ireland, Killary Harbour; France, Roscoff | North Sea, Helgoland; Black Sea, White Sea | Amphioxus sand and gravel | North Europe   |
|     | <i>P. helgolandica galapagoensis</i> Mielke 1984a, b | Mielke 1984b   | Galapagos, Santa Cruz, Playa Borrero   | Sand                                       |                           | Pacific Ocean  |
| 99  | <i>P. kunzi</i> Mielke 1984a, b                      | Mielke 1984a   | Panama, Pacific, Isla Naos, Isla Melones; Isla Flamenco  | Sand                                       |                           | Pacific Ocean  |
| 100 | <i>P. longicaudata</i> Nicholls, 1945                | Nicholls, 1945; Noodt 1964   | Australia, Perth, Cottesloe Beach; Red Sea   | Sand, corral sand                          |                           | "Cosmopolitan" |
| 101 | <i>P. marisalbi</i> Kornev and Chertoprud 2008       | Kornev and Chertoprud 2008   | Russia, White Sea  | 12 m depth, sandy ground                   |                           | North Europe   |
| 102 | <i>P. mielkei</i> Huys 1987                          | Huys 1987  | North Sea, Southern Bay, Dutch coast   | Medium sand, 12 m                          |                           | North Sea      |
| 103 | <i>P. ornata</i> Krishnaswamy 1957                   | Krishnaswamy 1957  | India  | Brackish interstitial                      |                           | Indian Ocean   |
| 104 | <i>P. pterocaudata</i> Kunz 1936                     | Kunz 1936  | North Sea, Helgoland   | Amphioxus sand                             |                           | North Sea      |
| 105 | <i>P. similis</i> Kunz 1936                          | Kunz 1936; Apostolov and Marinov 1988  | Helgoland, Greatbritain, Black-Sea   | Amphioxus sand                             |                           | "Cosmopolitan" |
| 106 | <i>P. unaspina</i> Mielke 1984a, b                   | Mielke 1984a, b  | Galapagos, Isabey, Caleta  | Interstitial                               |                           | Pacific Ocean  |
| X   | <i>Remanea</i> Klie 1929                             |  |  |  |                           |                |
| 107 | <i>R. arenicola</i> Klie 1929                        | Klie 1929; Nicholls 1945; Bozic 1955; Mielke 1975; Arlt 1983   | Scotland, Fintry Bay, Isle of Cumbrae, Firth of Clyde; Germany, Bay of Kiel, Island Sylt France, Roscoff; Australia  | Coarse sand, low-water mark                |                           | "Cosmopolitan" |
| 108 | <i>R. plumosa</i> Pennak 1942                        | Pennak 1942  | USA, Woods Hole  | ?  |                           | Pacific Ocean  |
| XI  | <i>Rossopsyllus</i> Soyer 1975                       |  |  |  |                           |                |
| 109 | <i>R. kerguelensis</i> Soyer 1975                    | Soyer 1975   | Kerguelen  | Littoral                                   |                           | Antarctica     |
|     | <i>R. kerguelensis quellonensis</i> Mielke 1985a, b  | Mielke 1985a, b  | Chile, Quellón   | Beach                                      |                           | Pacific Ocean  |
| 110 | <i>R. obscurus</i> Cottarelli and Baldari 1987       | Cottarelli and Baldari 1987  | Macquarie Island   | Interstitial                               |                           | Pacific Ocean  |
| XII | <i>Scottopsyllus</i>                                 |  |  |  |                           |                |
| 111 | <i>S. (Sc.) depressus</i> Kornev and Chertoprud 2008 | Kornev and Chertoprud 2008   | Russia, White Sea  | 10 m depth, sandy ground                   |                           | North Europe   |
| 112 | <i>S. (Sc.) herdmani</i> Thompson and A. Scott 1900  | Thompson and A. Scott 1900; Marinov 1971; Apostolov 1972; Mielke 1975; Letova 1982; Apostolov and Marinov 1988 | U.K., Isle of Man, Port Erin; Scotland, Clyde; Bay of Kiel, Baltic Sea; White Sea; Black Sea   | Beach, sand                                |                           | "Cosmopolitan" |
| 113 | <i>S. (Sc.) langi</i> Mielke 1984a, b                | Mielke 1984a, b  | Galapagos, Tower, Bahia Darwin, Santa Cruz, Puerto Nunez, Bahia Academy  | Sand                                       |                           | Pacific Ocean  |
|     | <i>S. (Sc.) langi continentalis</i> Kunz 1992        | Kunz 1992  | Croatia, Mediterranean Sea, Korcula Island Lumbarda south beach  | Fine sand, sea level                       |                           | Mediterranean  |

**Table 4** (continued)

| No.  | Species and authorship  | References   | Location/Records   | Depth/Habitat   | Geogr. Region  |
|------|---|--|--|---|----------------|
| 114  | <i>S. (Sc.) minor</i> T. and A. Scott 1895                    | T. and A. Scott 1895; Mielke 1975; Apostolov and Marinov 1988            | Scotland, Firth of Forth, Musselburgh; Canada, St. Lawrence, Trois Pistoles; Germany, North Sea, Island of Sylt; Bulgaria, Black Sea, Mitschurin   | Near shore, Pools near low water, coarse sand, supratidal, breakwater, Sandwatt Coast | "Cosmopolitan" |
| 115  | <i>S. (Sc.) pararobertsoni</i> Lang 1965                      | Lang 1965  | California, Monterey Bay off Hopkins   | Tidal pool, shell sand  | Pacific Ocean  |
| 116  | <i>S. (Sc.) praecipuus</i> Veit-Köhler 2000                   | Veit-Köhler 2000   | Antarctica, South Shetland Islands, King George Island, Potter Cove  | Muddy sediments, 20–30 m depth  | Antarctica     |
| 117  | <i>S. (Sc.) robertsoni</i> T. and A. Scott 1895               | T. and A. Scott 1895; Apostolov 1972; Apostolov and Marinov 1988         | Scotland, Firth of Forth, Musselburgh; Bulgaria, Black Sea, Nessebar   | Shore near pools near low water, Clean sand, 10 m                                     | North Europe   |
| 118  | <i>S. (I.) antoniae</i> sp.nov<br>Plum and George, this paper | Plum and George, this paper  | Northeast Atlantic, Great Meteor seamount  | Coarse sand, 325 m depth  | Atlantic Ocean |
| 119  | <i>S. (I.) intermedius</i> T. and A. Scott 1895               | T. and A. Scott 1895; Kunz 1962; Mielke 1975; Apostolov and Marinov 1988 | Scotland, Firth of Forth, U.K., Isle of Man, Port Erin; Germany, North Sea, Island of Sylt; Africa, Namibia, Lüderitz-Bay; Bulgaria, Black Sea, Warna; Northeast Atlantic, Great Meteor seamount | Pools near low water, sand; sandwatt, supratidal groundwater; amphioxus sand          | "Cosmopolitan" |
| 120  | <i>S. I.) minutus</i> Nicholls 1939                           | Nicholls 1939  | Scotland, Firth of Forth   | Muddy sand  | Atlantic Ocean |
| 121  | <i>S. (I.) smirnovi</i> Kunz 1992                             | Kunz 1992  | Croatia, Mediterranean Sea, Mijet island   | Shell-sand  | Mediterranean  |
| 122  | <i>S. (W.) abyssalis</i> Becker et al. 1979                   | Becker et al. 1979   | Peru Trench, "Anton Bruun"   | 2,000 m depth   | Pacific Ocean  |
| 123  | <i>S. (W.) gigas</i> Wells 1965                               | Wells 1965   | Scotland, Fladen   | Mud, 146 m depth  | Atlantic Ocean |
| 124  | <i>S. (W.) runtzi</i> Soyer 1975                              | Soyer 1975   | Kerguelen, Port Kirk, Anse du Tranchant, Baie Charrier   | Littoral sands near estuaries   | Indian Ocean   |
| XIII | <i>Tisbisoma</i> Bozic 1964                                   |  |  |   |                |
| 125  | <i>T. spinisetum</i> Bozic 1964                               | Bozic 1964   | Reunion Island   | ?   | Indian Ocean   |
| 126  | <i>T. triarticulatum</i> Wells 1967                           | Wells 1967; Wells and Rao 1987   | Mozambique, Ponta Torres   | Clean sand  | Indian Ocean   |

*antoniae* sp. nov. (cf. Veit-Köhler 2000) described here. Most species were found in coastal waters of northern Europe, but there are also records from King George island [*Sc. (Sc.) praecipuus* Veit-Köhler 2000], the Lüderitz Bay, Namibia [*Sc. (I.) intermedius*], the Peru Trench [*Sc. (W.) abyssalis*], the Galapagos Islands [*Sc. (Sc.) langi* Mielke 1984a, b] and recently the Great Meteor Seamount [*Sc. (I.) antoniae* sp. nov., this study].

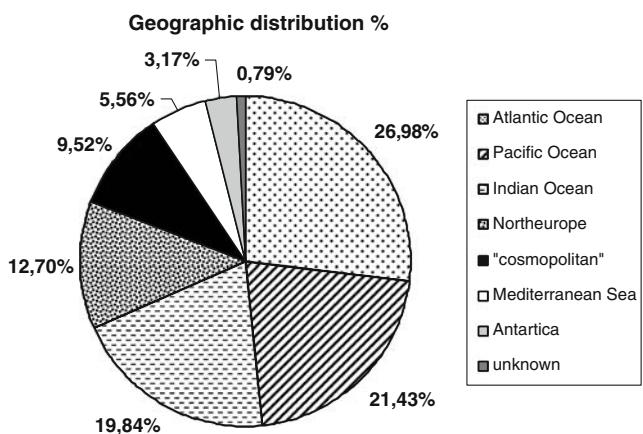
## Discussion

### Taxonomy

*Scotopsyllus (Intermedopsyllus) antoniae* sp. nov. is attributed to the genus *Scotopsyllus* Kunz 1962 mainly because of

the 1-segmented, "paramecium"-shaped endopods of P2 and P3. Besides these conspicuous features, the 1-segmented exp of the antenna, the 1-segmented exp of the mandible and the 3-segmented exopods of P2 and P3 characterize the new species as a member of *Scotopsyllus*.

In 1962, Kunz established the genera *Scotopsyllus* and *Intermedopsyllus* as part of a revision of the Paramesochridae (Kunz 1962). Later on, he relegated these genera to subgeneric status, placing them together with another new subgenus *Sc. (Wellsopsyllus)* in the genus *Scotopsyllus* (Kunz 1981). The three subgenera can be distinguished mainly by the segmentation of the endopods and exopods of P4. *Sc. (Wellsopsyllus)* exhibits a 3-segmented exp and a 1-segmented exp in P4, while in *Sc. (Scotopsyllus)* the P4 exp is 3-segmented and the exp 2-segmented. *Sc. (Intermedopsyllus)*,



**Fig. 9** Global geographic distribution of paramesochrid species

in turn, has a 2-segmented exp in P4 due to a fusion of the 2 proximal segments (and a 1-segmented enp). The new species *Scottopsylus (Intermedopsyllus) antoniae* sp. nov. is placed in the subgenus *Sc. (Intermedopsyllus)*, as it has this derived character in the exp of P4.

Within *Sc. (Intermedopsyllus)*, the new species can be distinguished from its congeners by virtue of the following characteristics:

#### Female A1

*Sc. (I.) antoniae* sp. nov. bears 1 seta on segment 1, 9 setae on segment 2 and 7 setae on segment 3. According to the original descriptions, the three other species of *Sc. (Intermedopsyllus)* lack a seta on the first segment and bear less setae in the following two segments [4 setae at both segments 2 and 3 in *Sc. (I.) intermedius*, 5 and 6 setae, respectively in *Sc. (I.) minutus* Nicholls 1939, 4 and 5 setae, respectively in *Sc. (I.) smirnovi* Kunz 1992].

#### Mandibular palp

*Sc. (I.) antoniae* shows a 1-segmented enp with 5 setae and a 1-segmented, small exp with 2 setae. In contrast, the palpus of *Sc. (I.) intermedius* possesses a 2-segmented enp with 8 setae in total and an exp with 4 setae, whereas that of *Sc. (I.) smirnovi* has a 1-segmented enp with 3 setae, while the exp is lacking. Furthermore, the basis lacks the terminal setae in *Sc. (I.) smirnovi*. The md palpus of *Sc. (I.) minutus* was not described by Nicholls (1939).

#### Maxilla

The mx of *Sc. (I.) antoniae* resembles that of *Sc. (I.) minutus*. Both species have 2 endites on the syncoxa but can be distinguished by the number of setae. The proximal endite in

*Sc. (I.) antoniae* sp. nov. exhibits only 1 seta, while that of *Sc. (I.) minutus* bears 2 setae. *Sc. (I.) intermedius* (after Kunz 1992) possess 3 endites on the syncoxa, while in *Sc. (I.) smirnovi* the two proximal of the three endites are each represented by a single seta. Furthermore, in *Sc. (I.) antoniae* sp. nov. the maxillary enp is absent and represented by 4 setae, while it is present but fused to the allobasis in *Sc. (I.) minutus* and *Sc. (I.) intermedius*. In *Sc. (I.) smirnovi* the enp seems to be separated and assembled with 3 setae. Additionally, *Sc. (I.) antoniae* sp. nov. and *Sc. (I.) intermedius* share the well developed claw of the allobasis, but in the latter the claw is not accompanied by additional setae.

#### P2 and P3 exp

The most outstanding feature of *Sc. (I.) antoniae* sp. nov. is the third seta on the terminal segment of P2 and P3 exp. This seta has never been described in any other species of the genus *Scottopsylus (Intermedopsyllus)*.

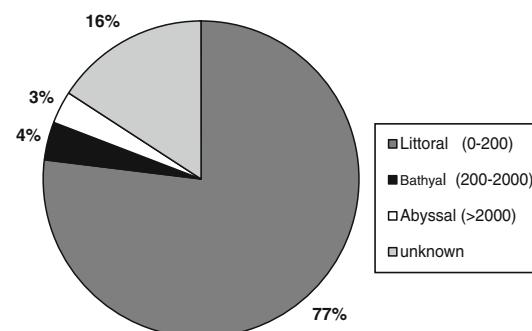
#### Furca

*Sc. (I.) antoniae* sp. nov. lacks furcal seta I, retaining only six furcal setae. Also, *Sc. (I.) minutus* and *Sc. (I.) smirnovi* lost furcal seta I. However, these species additionally lost seta IV, which is well developed in *Sc. (I.) antoniae* sp. nov.. The only species retaining all seven furcal setae is *Sc. (I.) intermedius*.

#### Ecological remarks

##### *Paramesochridae of the Great Meteor Seamount - distribution and endemism*

Due to sedimentological and topographical conditions, the plateau of GMS has been sampled quite pragmatically, using gear that was able to provide sampling material in these circumstances (cf. Martínez Arbizu and Schminke

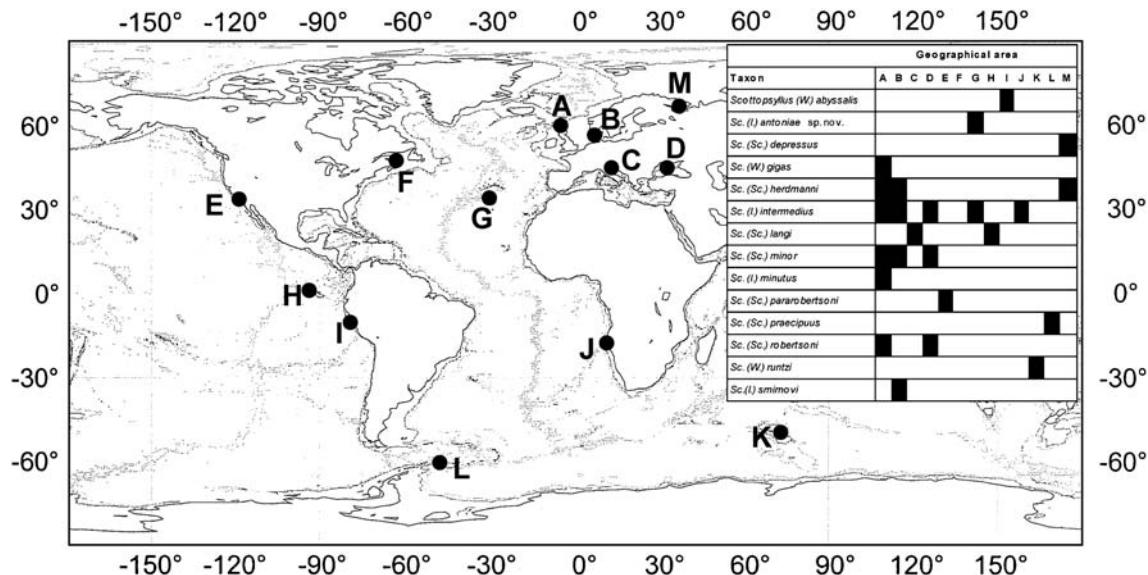


**Fig. 10** Global bathymetric distribution pattern (%) of paramesochrid species

2000; George and Schminke 2002). Consequently, the sampling was not standardized, and quantitative analysis is therefore impossible. However, regarding the distribution of Paramesochridae at GMS, no homogeneous distribution pattern can be detected. As shown in Table 2, even stations of the same plateau area may differ remarkably with respect to their number of individuals. For instance, eastern stations 551 and 552 were both sampled with the epibenthic sledge (EBS, cf. Table 1). However, station 552 yielded  $N=23$ , whereas neighboring station 551 provided  $N=175$  (Table 2). Interestingly, samples taken with the box corer (BC) produced almost the same number of specimens (stations 451, 455, 467, 492, cf. Table 2), ranging between 48 and 68 specimens, with the exception of stations 505 (deep sea:  $N=3$ ) and station 516 (western plateau:  $N=140$ ), and a mean value of  $Z=55$  individuals. This might be an indication for a non-patchy distribution, although a real quantitative sampling is needed to address that question. In contrast, the EBS demonstrates a large variation in specimen numbers, from 1 to 175, with a mean value of  $Z=17$  individuals. Evidently, this is due to the specific gear characteristics, as it is designed to catch bigger animals than Paramesochridae (Brandt and Barthelnt 1995).

The high degree of scientifically new species at GMS (>90%) was not surprising, as in many other recently extensive investigated marine environments most of the sampled harpacticoid species are considered to be new to science (e.g., George and Schminke 2002; George 2004a, b, 2005; Rose et al. 2005; Baguley et al. 2006; Gheerardyn and Veit-Köhler 2009). Contrary to Emschermann (1971), who suggested that the deep sea might act as a kind of

“faunal reservoir” for the GMS and that its faunal assemblages may mainly consist of deep-sea “resistant” species, George and Schminke (2002) came to the conclusion that the GMS plateau represents an isolated area with only occasional bathymetric and geographic exchange. They base their assumption on the large number of new species found on GMS plateau. Mironov and Krylova (2006) also mention a high degree of endemism (91%) on the GMS for meiofauna organisms. As shown by the results presented here, this hypothesis is supported with respect to Paramesochridae. Nevertheless, many isolated islands and seamounts show a lower endemism than less isolated islands and seamounts (Mironov and Krylova 2006). A differentiation has yet to be made between the taxa or major groups under study, a fact that is often not taken into account in such a comparison. Although a high number of new species does not necessarily mean a high degree of endemism, it certainly may be an indication for a significant to high isolation of the corresponding habitat. With respect to the GMS and to Harpacticoida, it means that the very high percentage of unknown species on the plateau supports the hypothesis of the seamount’s role as a “trapping stone” (Hubbs 1959) for at least that taxon. Quite opposite to that hypothesis, studies on other meiobenthic taxa and on megabenthic and macrobenthic groups from GMS suggest that most species are widespread elements of the North Atlantic fauna, indicating that the GMS area is not isolated. Bartsch (2003) criticizes the hypothesis of George and Schminke (2002), stating that marine mites (Halacarida), as well as several other macrobenthic and megabenthic taxa (including fish) certainly do present a



**Fig. 11** Geographic distribution patterns of the genus *Scottopsyllus*. Capital letters (A–L) indicate geographic areas where the known species were recorded. The small table assigns the species to the corresponding area(s). For detailed information cf. Table 4

widespread distribution, even though found solely on GMS so far. However, Bartsch's (2003) argumentation is inconsistent in our opinion. Especially with regard to the meiobenthic Halacarida, she turns from species to genus level, which is meaningless in connection with endemic species. The paramesochrid genera from GMS are widespread in the world's oceans (Table 4, Fig. 9), but it is a species that provides valuable information on endemism. Bartsch (2003, p. 114 and Table 1) shows that 17 of the 24 halacarid species (>70%) were new to science and exclusively found at GMS. When Bartsch (2003, p. 113) states that "Certainly more species will be found in future investigations", it is not less speculative than the contrary assumption of the species possibly being endemic ones.

Regarding macrofauna and megafauna, a direct comparison with meiobenthic data, as realized by several authors, is questionable. Percentages of endemism for macrobenthic and megabenthic species on the GMS (Piepenburg and Müller 2004) conform with values from studies of different seamounts (e.g., Rogers 1994; Richer de Forges et al. 2000; Gillet and Dauvin 2003; Ávila and Malaquias 2003) that presented much lower exclusive macrobenthic and megabenthic species than reported by George and Schminke (2002) for meiobenthic Harpacticoida. However, this is not surprising as the lifecycle of macrobenthic and megabenthic organisms includes life stages living in the water column, which is an important prerequisite for wide geographic dispersal. Nevertheless, results obtained by investigations on megafauna and macrofauna must not be extended to meiofauna, which does not meet the mentioned prerequisite. The antithesis presented by Bartsch (2003), and apparently supported by results obtained for macrofauna and megafauna, shows impressively that seamounts do not correspond to generalizing assumptions that attempt to assign single functions to them. A seamount should not be regarded as solely a staging post supporting geographical dispersal of benthic organisms, or only an isolated object retaining "trapped" organisms. The same seamount may play several roles at the same time, depending, among other things, on the taxon referred to. This assessment is not as trivial as one might believe, as demonstrated impressively by McClain (2007) in his criticism of seamount research.

In a study on the typical deep-sea family Argidae on the GMS, George (2004a) presumed that the relatively high percentage of closely related species on the plateau was due to radiation in that area rather than a successive colonization from other localities. Contrary to the Argidae, Paramesochridae are considered to be shallow-water rather than deep-sea organisms. In this context, it is remarkable that the paramesochrid community at GMS seems to be dominated by species of the taxa *Kliopsyllus* and *Paramesochra*. Species of these genera are typically found in coastal waters. Thus, the assumption by George (2004a, b) of an elevation of the

argestid fauna over millions of years together with the growing seamount itself appears unlikely for Paramesochridae. This is supported, for example, by *Scottopsylus (Intermedopsyllus) antoniae* sp. nov., which was also sampled on the summits of Sedlo and Seine seamounts. The same applies to *Sc. (I.) intermedius*, which has only been recorded in intertidal habitats so far (Table 4). Consequently, one might conclude that most of the Paramesochridae at GMS possibly originate from geographically adjacent regions rather than from the surrounding deep sea. It is plausible that "Scenario I: geographical immigration" as described by George (2004a, b, p. 262) applies to the Paramesochridae of the GMS, i.e., most Paramesochridae originate from shallow-water localities and reach the GMS by overcoming the vast deep-sea areas. However, we still have no information or even plausible ideas to explain how meiobenthic organisms surmount both the depth and deep-sea sediments, both of which are considered to be significant barriers for certain interstitial meiofauna species (Gerlach 1977; Westheide 1991; Gad and Schminke 2004). A bathymetrical migration obviously does occur, as demonstrated by the presence of *Scottopsylus (I.) intermedius* and *Kliopsyllus* sp. 10 on both the plateau and in the deep sea (cf. George and Schminke 2002 and George 2004a, b for other examples). Their presence in the deep sea may point to a much higher range of depth and sediment tolerance than presumed so far (but supporting Emschermann's 1971 hypothesis of deep-sea "resistant" species), and this may also be true for other Paramesochridae found exclusively on the plateau thus far.

#### *Bathymetrical and geographical distribution of the genus *Scottopsylus**

The reports of most paramesochrid species from only shallow waters so far may be the result of scientific history rather than real geographical distribution. Especially along European shorelines, many samples have been taken from littoral zones since the end of the nineteenth century. Consequently, species distribution ranges are concentrated in European waters and also in other regions, mainly confined to littoral zones. During the last decades, new paramesochrid taxa have increasingly been reported in different oceans and depths around the world, indicating a worldwide geographical and a broad bathymetrical distribution for this family. *Scottopsylus* may serve as an example to illustrate paramesochrid distribution patterns. Figure 11 shows the geographical distribution of all known *Scottopsylus* species (according to Veit-Köhler 2000) and includes the *Sc. (I.) antoniae* sp. nov. described here. None of the *Scottopsylus* species reported in the Atlantic has been found at depths greater than 400 m. Gheerardyn and Veit-Köhler (2009) found two new species of the genus

*Scottopsylus* at depths between 2,274 m and 5,194 m, but they were restricted to the Scotia Sea (Antarctica). *Scottopsylus (W.) abyssalis* was found at 2,000 m depth, but has only been reported in the Peru Trench (Pacific Ocean). In this context, it is remarkable that the finding of *Scottopsylus (I.) intermedius* at a GMS deep-sea station is the first record of *Scottopsylus* in the Atlantic deep sea. This species occurs in shallow waters from the Firth of Forth (Scotland) to Lüderitz Bay in Namibia, but has never been recorded in the East Atlantic deep sea before.

The study by Gheerardyn and Veit-Köhler (2009) already indicated that ranges of certain species might span thousands of kilometres across the East Atlantic (or also the northern European seas in the present study). The large distribution ranges of certain paramesochrid species found at the GMS are comparable to the distribution patterns of deep-sea Paramesochridae in the Southeast Atlantic and Antarctic abyssal plains (Gheerardyn and Veit-Köhler 2009). These findings support what Giere (1993) called the “meiofauna paradoxon”: small-sized marine animals (even from shallow-water areas), lacking planktonic life stages and strictly bound to marine sediments, show a widespread, often cosmopolitan distribution even at species level. Our findings provide further evidence that there are no real barriers that might hinder the dispersal of copepods in the Atlantic (Gheerardyn and Veit-Köhler 2009). Vermeij (2004) mentioned that the deep sea in itself is not an obstruction to dispersal for seamount organisms. He pointed out that, even for shallow-water organisms, deep-sea basins and sediments offer at most a porous barrier. Several factors, such as suspension and rafting with floating material (Gerlach 1977), plate tectonics and continental drift (Rao 1972; Sterrer 1973; Westheide 1977), or long generation times (Gheerardyn and Veit-Köhler 2009) are proposed in relevant literature as explanations for the large dispersal ranges of meiofauna organisms. Connections via currents between seamounts may also increase the dispersal potential. Regarding the GMS and following Emschermann (1971), a drift of meiofauna organisms and their larvae across large distances is unlikely due to the discontinuous peripheral currents of the Canary Current. To date, such hypotheses are still speculative and seem to be inadequate to explain distribution patterns of small benthic organisms because most of these hypotheses seek an explanation for dispersal near the ocean’s surface.

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