ORIGINAL PAPER



A new genus and four new species of Cylindropsyllidae Sars, 1909 (Copepoda: Harpacticoida) from the Great Meteor Seamount plateau (North-East Atlantic Ocean), with remarks on the phylogeny and the geographical distribution of the taxon

Karin Richter¹

Received: 6 July 2018 / Revised: 7 March 2019 / Accepted: 18 March 2019 © Senckenberg Gesellschaft für Naturforschung 2019

Abstract

The Great Meteor Seamount plateau comprises three regions (north, middle, south), and sampling across the whole area, six species of Cylindropsyllidae Sars, 1909 were discovered. These species were homogenously distributed, indicating that the community of Cylindropsyllidae on the plateau was not zonated according to geographical features, but might be influenced by the presence of microhabitats. The new genus *Monsmeteoris* gen. nov. is characterized by the presence of two segments distally inserted to the swollen segment with aesthetasc on the male antennule, five elements on the antennal enp2, and completely reduced P4 endopod. Two new species, *M. wiesheuorum* sp. nov. and *M. reductus* sp. nov. are hereby described. Additionally, two closely related species belonging to *Cylindropsyllus* Brady, 1880 are described: *C. valentini* sp. nov. and *C. flexibilis* sp. nov., having at most two distal setae on the mandibular endopod, the inner seta of P4 enp2 lost, strongly pronounced styliform proximal part of seta V on the caudal rami, and an apical process on the female P3 enp2.

Keywords Biogeography · Cylindropsyllus · Meiofauna · Monsmeteoris · Seamounts · Systematics

Introduction

Owing to their small body size (< 1 mm), a lack of planktonic lifecycle stages and benthic life history traits (Giere 2009), meiofaunal species, including harpacticoid copepods, are expected to exhibit

This article is registered in ZooBank under urn:lsid:zoobank.org:pub: 0598E650-DE29-49EC-A22A-3FC1880A687.

Cylindropsyllus flexibilis sp. nov. is registered in ZooBank under urn:lsid: zoobank.org:act:1C9E4920-56BA-483B-8ADB-E8138056F3E0. *Cylindropsyllus valentini* sp. nov. is registered in ZooBank under urn:lsid: zoobank.org:act:46E5CF31-D064-4BAC-96F1-B1A905CD99BB. *Monsmeteoris reductus* sp. nov. is registered in ZooBank under urn:lsid: zoobank.org:act:9319D84F-C6FC-4C6C-8A43-7CBEBAAAE4F1. *Monsmeteoris wiesheuorum* sp. nov. is registered in ZooBank under urn: lsid:zoobank.org:act:B50573D0-A646-471A-AAF7-06E64BFADF19.

Communicated by L. Menzel

Karin Richter karin_richter@hotmail.com

restricted distribution patterns. Nevertheless, several species are known to have cosmopolitan distributions (Yeatman 1962; Higgins and Thiel 1988; Menzel et al. 2011; Pointner et al. 2013; Packmor et al. 2015; Packmor and Riedl 2016; George 2017). Many dispersal methods, such as drifting, emergence, and rafting have been proposed to explain species distributions over short distances (Gerlach 1977; Giere 2009), but it is unlikely these could account for the dispersal of shallow-water species on an oceanic scale. Seamounts and islands provide suitable habitats for shallow-water species crossing the deep sea, and, therefore, play a significant role in their distribution, as shown for harpacticoid copepods (George 2013; Packmor et al. 2015; Packmor and George 2018).

The Great Meteor Seamount (GMS) is of particular interest concerning its role in the dispersal of harpacticoid copepods, due to its isolated location in the north-eastern Atlantic Ocean (30.0° N, 28.5° W). The closest islands are the Azores, 834 km north of the GMS, and the closest mainland is the African coast, 1482 km to the west. The GMS rises from 4200 m depth up to 270 m below sea level (Hinz 1969) and is a typically "guyot"-shaped seamount. Its summit comprises a plateau with a surface area of 1465 km² (Fischer 2005) covered by a homogeneous coralline sediment (Hesemann 2013), with two 100-m-high mesoscale pinnacles,

¹ Senckenberg am Meer, Abt. Deutsches Zentrum für Marine Biodiversitätsforschung DZMB, Südstrand 44, 26382 Wilhelmshaven, Germany

one in the north and one in the south (Ulrich 1971; Mohn and Beckmann 2002), enclosing the central plateau region. Thus, these topographic characteristics of the plateau allow its division in three different regions (north, middle, south). Due to its geomorphology, it is surrounded by a complex hydrological current system with various instable current flows. The upper thermocline layer is connected to the seamount summit layer by upwellings above the slope and downwellings above the middle region of the plateau, creating a reservoir for drifting particles (Beckmann and Mohn 2002; Mohn and Beckmann 2002). The system is also strongly affected by tidal motions (Mouriño et al. 2001; van Haren 2005) and strong weather events (Beckmann and Mohn 2002).

The geomorphological conditions at the GMS might be expected to result in a zonation of the Harpacticoida community across the three regions, as suggested for Nematoda (Gad 2009). However, studies on the epibenthic Zosimeidae Seifried, 2003 (Pointner 2017) and Canuellidae Lang, 1944 (Pointner 2015) revealed no significant differences in their community structures across the plateau. This present contribution therefore focuses on the community structure of the interstitial Cylindropsyllidae, in a further effort to detect any influence of the geomorphological conditions on benthic Harpacticoida.

The phylogenetic position of the Cylindropsyllidae Sars, 1909 is controversial and has been reviewed a number of times. Martínez Arbizu and Moura (1994) considered Cylindropsyllidae to comprise of two monophyletic groups: Cylindropsyllinae Sars, 1909 and Leptopontiinae Lang, 1948 + Psammopsyllinae Krishnaswamy, 1956. They suggested that the Cylindropsyllinae shared the same synapomorphic transformation as species of Canthocamptidae Brady, 1880 and thus placed it within Canthocamptidae. However, Huys and Conroy-Dalton (2006a) reinstated Cylindropsyllidae, arguing that the synapomorphies are homologous with a number of taxa in addition to Canthocamptidae. They also rejected the pore pattern on the female genital somite as additional evidence for placing Cylindropsyllinae to Canthocamptidae (Moura and Pottek 1998). The Canthocamptidae is a heterogeneous group of fresh-water, brackish, and marine species (Huys and Conroy-Dalton 2006a; Wells 2007 and references therein), and a revision of this taxon might help to clarify the phylogenetic relationships within this group, and that of Cylindropsyllidae.

Cylindropsyllidae can be characterized by the apomorphic characters described by both Martínez Arbizu and Moura (1994) and Huys and Conroy-Dalton (2006a). Within the present contribution, four new species of Cylindropsyllidae are described, two of which belong to a new genus.

Material and methods

Sediment samples were collected during the RV "Poseidon" cruise POS397 (GroMet expedition, March 2010, see George 2010) to the GMS (30° 00.0 N, 28° 30.0 W). Two to four

replicates were taken with a Van Veen grab (surface area, 0.1 m^2) from each of 21 stations (Table 1) evenly distributed over the GMS plateau. The samples were centrifuged with a mixture of colloidal silica polymer and kaolin (for detailed information, see Pointner et al. 2013) to extract meiofaunal organisms, which were then fixed with 96% undenatured ethanol.

Harpacticoid copepods were identified as Cylindropsyllidae using Huys et al. (1996) and further to species-level with the help of Wells (2007) and original species descriptions, under a Leica DMR microscope. The total abundances of each species are given in Table 2.

The descriptive terminology is adopted from Huys et al. (1996). The setal formula of the species described here (Table 3) is given according to Sewell (1949). All drawings were made using a Leica DM 2500 microscope at \times 400 and \times 2000 magnification and processed with the software Adobe Photoshop CS6. The type material is stored in the collection of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt am Main (SMF), Germany.

Within the discussion of the systematics of the described taxa, autapomorphic characters (Tables 4 and 5) are given, whose plesiomorphic conditions are defined against a baseline morphology of Leptopontiidae Lang, 1948 (chosen as outgroup, as a sister taxon of Cylindropsyllidae) and Copepoda (Huys and Boxshall, 1991). Several different losses of setae are seen as apomorphies in the following discussion. Up to date, most setae cannot be homologized at certain. Thus, it cannot be stated in detail which exact seta is lost and only the total number of setae is given as apomorphic character.

Results

Systematics

Subphylum **Crustacea** Brünnich, 1772 Subclass **Copepoda** Milne Edwards, 1840 Order **Harpacticoida** Sars, 1903 Family **Cylindropsyllidae** Sars, 1909

Genus Monsmeteoris gen. nov.

Diagnosis: Body slender and vermiform. Rostrum triangular. No distinction between prosome and urosome. Female genital double-somite completely fused. Anal operculum present. Caudal rami longer than broad, with six setae; seta I absent, seta IV fused at base to seta V, seta V with styliform proximal quarter, distal part flexible. Sexual dimorphism in body size, genital segmentation, antennule, pereiopods 2 (P2), 3 (P3), 5 (P5), and 6 (P6). Antennule seven-segmented in both sexes, second segment longest, aesthetasc in female at fourth and seventh segment, in male at fifth and seventh segment, male antennule with small fourth segment, subchirocer. Antenna Table 1List of sampled stationsduring the R/V Poseidon expedi-
tion POS397 GroMet to the GreatMeteor Seamount (GMS) plateau
in 2010. Region, station, number
of replicates, sampling date, co-
ordinates, and depth (m) are given

Region	Station	Number of replicates	Sampling date	Coordinates	Depth (m)
North	#1	3	15 Mar 2010	30.0833° N, 28.6330° W	310
North	#2	3	15 Mar 2010	30.0841° N, 28.5661° W	301
North	#3	3	17 Mar 2010	30.0838° N, 28.5008° W	309
North	#4	3	17 Mar 2010	30.0168° N, 28.4667° W	302
North	#5	3	16 Mar 2010	30.0169° N, 28.5327° W	287
North	#6	3	17 Mar 2010	30.0168° N, 28.6003° W	290
Middle	#7	3	17 Mar 2010	29.9499° N, 28.6335° W	308
Middle	#8	3	19 Mar 2010	29.9526° N, 28.5663° W	288
Middle	#9	3	18 Mar 2010	29.9501° N, 28.5000° W	287
Middle	#10	3	18 Mar 2010	29.9502° N, 28.4333° W	308
Middle	#11	3	19 Mar 2010	29.8830° N, 28.3999° W	339
Middle	#12	3	19 Mar 2010	29.8830° N, 28.4659° W	299
Middle	#13	3	19 Mar 2010	29.8837° N, 28.5332° W	288
Middle	#14	2	14 Mar 2010	29.8849° N, 28.5998° W	296
South	#15	3	20 Mar 2010	29.8164° N, 28.5668° W	307
South	#16	3	21 Mar 2010	29.8173° N, 28.4999° W	298
South	#17	3	19 Mar 2010	29.8161° N, 28.4327° W	299
South	#18	4	21 Mar 2010	29.7510° N, 28.3997° W	292
South	#19	3	21 Mar 2010	29.7497° N, 28.4656° W	292
South	#20	2	14 Mar 2010	29.7499° N, 28.5332° W	316
South	#21	3	21 Mar 2010	29.6827° N, 28.4342° W	289

with basis and two-segmented endopod, exopod onesegmented with two setae. Mandibular palp uniramous, twosegmented, basis with one seta, endopod with one lateral seta and two groups of basally fused setae. Basis of maxillule elongated, exopod and endopod represented by setae. Proximal endite of maxilla reduced, endopod represented by three setae. Maxilliped well developed, prehensile. Pereiopods 1–4 (P1–P4) with three-segmented exopod, P1 with two-segmented endopod, with one-segmented endopod in P2 as well as in P3, endopod of P4 absent. P1 with inner seta on basis, expopod 3 (exp3) with four elements, proximal segment of endopod (enp1) with inner seta, middle segment of endopod (enp2) with two distal elements. Exp3 of P2 and P3 with at most four and exp3 of P4 with three elements. P2 endopod of female with at most two elements, and P2 and P3 with one element in male. P5 baseoendopod and exopod fused to single plates, female with at most five elements, male with at most four elements. Female P6 symmetrical plates, with at most two bare setae. Male P6 asymmetrical plates, with at most two setae.

Type species: *Monsmeteoris wiesheuorum* sp. nov. Additional species: *Monsmeteoris reductus* sp. nov.

Etymology: The genus name refers to the type locality, the Great Meteor Seamount in the north-east Atlantic Ocean.

 Table 2
 Species-Station matrix for all adult specimens of Cylindropsyllidae identified at each station and in each region of the plateau of the Great

 Meteor Seamount

No.	Cylindropsyllidae Sars, 1909	No	rth					Mi	ddle							Sout	h						SUM
		#1	#2	#3	#4	#5	#6	#7	#8	#9	#10	#11	#12	#13	#14	#15	#16	#17	#18	#19	#20	#21	
1 2	Boreopontia heipi Willems, 1981 Cylindropsyllus flexibilis sp. nov.	2	3	1	6		1		1	2	9	3	15	4		4		1	5		8	9 12	74 16
3	<i>Cylindropsyllus valentini</i> sp. nov.	13	10	13	9	7	5	10	13	8	12	13	16	12	13	19	2	2	10	6	14	20	227
4	Monsmeteoris wiesheuorum sp. nov.								1				2			1		2	7	4	3	6	26
5	Monsmeteoris reductus sp. nov.	4	4	5	3	4	1	5	1	8	1	2	32	4	12	10		9	3	7	9	11	135
6	Selenopsyllus dahmsi Moura & Pottek, 1998		2							3		1	3	2		2				1	1		15
SUM		19	19	19	18	11	7	15	16	21	22	19	68	22	25	36	2	14	25	18	39	58	493

Table 3Setal and spine formulae for Monsmeteoris wiesheuorum sp. nov., Monsmeteoris reductus sp. nov., Cylindropsyllus valentini sp. nov., and
Cylindropsyllus flexibilis sp. nov. given according to Sewell (1949)

Species		Coxa	Basis	Exopo	dal segmen	ts	Endopodal	l segments
				1	2	3	1	2
Monsmeteoris wiesheuorum sp. nov.	P1	0–0	1-0	I-0	I-0	I,3,0	0-1	0,2,0
	P2 female	0–0	0–0	I-0	I-0	I,3,0	0,2,0	_
	P2 male	0–0	0–0	I-0	I-0	I,3,0	0,1,0	_
	P3 female	0–0	1-0	I-0	I-0	I,2,1	0,1,0	_
	P3 male	0–0	1-0	I-0	I-0	I,2,1	0,1,0	_
	P4	0–0	1-0	I-0	I-0	I,2,0	-	_
Monsmeteoris reductus sp. nov.	P1	0–0	0–0	I-0	I-0	I,3,0	0-1	0,2,0
	P2	0–0	0–0	I-0	I-0	I,2,0	0,1,0	_
	P3 female	0–0	1-0	I-0	I-0	I,2,0	-	_
	P3 male	0–0	1-1	I-0	I-0	I,2,0	0,1,0	_
	P4	_	-	_	_	-	-	_
Cylindropsyllus valentini sp. nov.	P1	0–0	0–0	I-0	I-0	I,2,0	0-1	0,2,1
	P2 female	0–0	1-0	I-0	I-0	I,2,0	0-1	0,1,0
	P2 male	0–0	1-0	I-0	I-0	I,1C,0	0-1	0,1,0
	P3 female	0–0	1-0	I-0	I-0	I,2,1	0–0	0,1,0
	P3 male	0–0	1-0	I-0	I-0	I,2,1	0–0	0,2,0
	P4	0–0	1-0	I-0	I-0	I,2,1	0–0	0,1,0
Cylindropsyllus flexibilis sp. nov.	P1	0–0	0–0	I-0	I-0	I,2,0	0-1	0,2,1
	P2 female	0–0	1-0	I-0	I-0	I,2,0	0-1	0,1,0
	P2 male	0–0	1-0	I-0	I-0	I,1C,0	0-1	0,1,0
	P3 female	0–0	1-0	I-0	I-0	I,2,1	0–0	0,2,0
	P3 male	0–0	1-0	I-0	I-0	I,2,1	0–0	0,2,0
	P4	0–0	1-0	I-0	I-0	I,2,1	0–0	0,1,0

Roman numerals indicate spines, Arabic numerals setae: notation as "outer margin-inner margin." Setation of distal segment separated by commas: "outer, distal, inner" margins

C, claw; "-" segment not present

Monsmeteoris wiesheuorum sp. nov.

Type locality: Plateau of the Great Meteor Seamount, subtropical north-eastern Atlantic (30.0° N, 28.5° W), biogenic carbonate sediment, 284-339 m water depth.

Type material: Holotype, female, no. 21, undissected, 1 slide, coll. no. SMF 37160/1; paratype 1 (allotype), male, no. 19, undissected, 1 slide, coll. no. SMF 37161/1; paratype 2, female, no. 21, dissected, mounted on 9 slides, coll. no. SMF 37162/1–9; paratype 3, female, no. 21, dissected, mounted on 5 sides, coll. no. SMF 37163/1–5; paratype 4, male, no. 21, dissected, mounted on 8 slides, coll. no. SMF 37164/1–8.

Etymology: This species is dedicated to the author's grandparents Elisabeth and Joseph Wiesheu, Munich, Germany.

Description of the female:

Habitus (Fig. 1). Slender and vermiform, body length measured in lateral view, excluding rostrum and caudal rami, 482– 513 μ m (average: 495 μ m, n=3). P1-bearing somite fused with cephalosome to form cephalothorax, covered with several sensilla and pitted (see inset in Fig. 1a). Rostrum triangular, separated from cephalothorax, hardly seen in lateral view (Fig. 1b), not extending beyond first antennular segment, and with two sensilla. Postero-dorsal margins of all somites (except anal somite and cephalothorax) with short hyaline frill. Somites with sensilla and lateral and dorsal pores, penultimate somite without sensilla. Urosomites two and three fused to form genital double-somite. Anal operculum small, armed with minute setules (Fig. 2a).

Caudal ramus (Fig. 2a, b). $1.7 \times$ longer than proximal width, tapering distally, inner margin concave; laterally with two pores (Fig. 2b). Six setae, all in distal third: seta I absent; seta II and III located on outer margin, long and slender; seta IV apically located, short and slender, fused at basis with seta V; proximal quarter of apical seta V styliform, remainder long and flexible; seta VI apical, slender, not visible in lateral view; seta VII dorsal, plumose, biarticulated at base.

Antennule (Fig. 3). Seven-segmented; second segment longest, seventh segment as long as segments five and six combined.



Fig. 1 *Monsmeteoris wiesheuorum* sp. nov., female. **a** Habitus, dorsal, rectangular inset showing detailed surface structure (holotype); **b** habitus, lateral, * indicating corresponding seta (holotype); **c** P5, P6, and genital complex (paratype 2). Scale bar = $200 \mu m$ (**a**, **b**) and $50 \mu m$ (**c**)



Fig. 2 *Monsmeteoris wiesheuorum* sp. nov., caudal rami, female (paratype 2). **a** dorsal, caudal setae indicated by I–VII; **b** lateral; * and # indicating corresponding application points of setae. Scale bar = $50 \mu m$



Fig. 3 Monsmeteoris wiesheuorum sp. nov., antennule, female, ventral (paratype 2). Scale bar = $25 \ \mu m$

All setae slender and bare, except for a seta on first segment and lateral seta on third segment; second segment with nine setae, four anterior, five posterior; seventh segment with nine setae, four anterior, one inner, one outer, and three setae and one aesthetasc apically. Setal formula: 1-1; 2-9; 3-5; 4-1+(1+aesthetasc); 5-1; 6-2; 7-8+(1+aesthetasc).

Antenna (Fig. 4a). Coxa small. Basis almost square and bare. Exopod one-segmented: 2.8× longer than wide, with two slender and bare setae apically. Endopod two-segmented: enp1 with several spinules along abexopodal margin; enp2 with projection on outer apical edge, armed with small spinules, two pinnate spines and seven large spinules laterally, and with two spines, two long geniculate setae and an outermost seta bearing large spinules in middle, decreasing spinula row on distal half.

Mandible (Fig. 4b, b', b*). Gnathobase well developed with seven teeth, one with two tips, and one short, bare seta (Fig. 4b'). In ventral view (Fig. 4b*) largest tooth swollen. Basis about $3.3 \times$ as long as wide with one pinnate seta on inner apical edge. Endopod with one slender, bare inner seta, and two bare, apical setae, merged at basis and two bare sub-apical setae, merged at basis.

Maxillule (Fig. 4c). Praecoxa with two setae laterally, five spines and one plumose seta apically, and two long, slender anterior surface setae. Coxa with two long apical setae, one bare and one with spinules apically; coxal epipodite bare. Basis elongate, with three slender bare setae, one claw distally and two setae subdistally. Exopodite represented by two slender bare setae. Endopod represented by three slender bare setae.

Maxilla (Fig. 4d). Syncoxa with two cylindrical endites, proximal endite with two pinnate setae, distal endite with three setae, two bare and one pinnate. Basis with one claw and two setae, all bare and emerging close together. Endopod represented by three bare slender setae.

Maxilliped (Fig. 4e). Prehensile. Syncoxa with pinnate seta on outer apical corner. Basis with long spinules on both margins. Endopod comprising small segment with one long, bipinnate seta.

Swimming legs (Fig. 5a–d). Unless otherwise specified, outer spines of proximal, middle, and distal segment of exopod 1, 2, and 3 (exp1–3) pinnate, distal margin of exp1,2, and outer margin of exp1–3 with long spinules. For setal formula, see Table 3.

P1 (Fig. 5a). Coxa with row of small spinules. Basis with long, pinnate inner seta; outer setae absent. Exopod three-segmented: exp1 and exp2 with outer spine, distal margin of segments bare; exp3 with one outer spine and two apical and one subapical setae, outer two flexible and pinnate, inner seta flexible and plumose with longer setules on inner margin. Endopod two-segmented, as long as exopod: enp1 with apically serrated inner seta, located in distal third of segment; enp2 with long

spinules on both margins, and with two long, flexible and pinnate apical setae, innermost longest.

P2 (Fig. 5b). Coxa bare. Basis without outer seta. Exopod three-segmented: exp1 and exp2 with one outer spine; exp3 with one outer spine and three long, plumose distal setae. Endopod one-segmented, one third length of exp1, with two apical setae, both plumose, inner one shortest. Intercoxal sclerite small, $2 \times$ longer than wide.

P3 (Fig. 5c). Coxa bare. Basis with long and plumose outer seta. Exopod three-segmented: exp1 and exp2 with one outer spine; exp3 with one outer spine, two long, bipinnate apical setae and one long, apically serrated inner seta. Endopod one-segmented, one fifth length of exp1, with one long, bipinnate apical seta.

P4 (Fig. 5d). Coxa bare. Basis with long and bare outer seta. Exopod three-segmented: exp1 and exp2 with one outer spine; exp3 with spinules absent from outer margin but apically present, and with an outer spine and two apical setae, one long and plumose, one long and apically serrated. Endopod absent. Intercoxal sclerite small and square.

P5 (Fig. 1c). Left and right sides identified as single plates; inner margin with small process; lobe with two apical setae, inner seta with serrated end and unipinnate seta apically, outer seta slender and plumose; small outer lobe with two slender, bare setae, inner seta longest; outer basal seta long and slender.

P6 and genital field (Fig. 1c). Genital double-somite completely fused. P6 consisting of symmetrical plates which strongly narrow distally; two slender, bare distal setae, inner seta about five times longer than outer seta. Copulatory pore covered by a pair of flaps forming genital operculum, both flaps located in middle of P6.

Description of the male:

Habitus (Fig. 6a, b) and most features as in female. Sexual dimorphism observed in body length, antennule, P2, P3, P5, and P6. Body length measured in lateral view, excluding rostrum and caudal rami, 418–453 μ m (average, 439 μ m, *n* = 3).

Antennule (Fig. 7a, b). Subchirocer, seven-segmented: second segment longest, fourth segment very small, only visible in dorsal view (Fig. 7a), covered by swollen fifth segment in ventral view (Fig. 7b), sixth and seventh segments of equal length; all setae slender and bare, except for a plumose seta on first segment, a dorsal seta on second segment, and a seta on inner apical margin of third segment; third segment with five setae, all located on inner apical margin. Setal formula: 1-1; 2-9; 3-5; 4-1; 5-3+(1+ aesthetasc); 6-1; 7-8+(1+ aesthetasc).

P2 (Fig. 5e). Coxa and basis as in female. Exopodal segments shorter than in female, armed with fewer spinules on outer margin; setae of exp3 plumose only on outer side of setae. Endopodal segment smaller than in female, knob-like, with one long, plumose seta.

P3 (Fig. 5f). Coxa and basis as in female, but outer seta on basis bare. Exopod as in female. Endopodal segment of same size as female, but apical seta bare.



Fig. 4 *Monsmeteoris wiesheuorum* sp. nov., mouthparts, female. **a** Antenna (paratype 2); **b** mandibular palpus (paratype 2); **b** mandible, lateral (paratype 3); **b*** mandible, ventral (paratype 2); **c** maxillule,

anterior (paratype 3); **d** maxilla (paratype 3); **e** maxilliped (paratype 3). Scale bar = $25 \ \mu m$



Fig. 5 *Monsmeteoris wiesheuorum* sp. nov., swimming legs, anterior. **a** Female P1 (paratype 2); **b** female P2, with intercoxal sclerite (paratype 2); **c** female P3 (paratype 2); **d** female P4, with intercoxal sclerite (paratype 2); **e** male P2 (paratype 4); **f** male P3 (paratype 4). Scale bar = $50 \mu m$



Fig. 6 *Monsmeteoris wiesheuorum* sp. nov., male. **a** Habitus, dorsal, rectangular inset showing detailed surface structure, asterisk indicates corresponding seta (paratype 1); **b** habitus, lateral, number sign indicates corresponding seta (paratype 1); **c** P5 and P6 (paratype 4). Scale bar = $200 \mu m$ (**a**, **b**) and $50 \mu m$ (**c**)



Fig. 7 *Monsmeteoris wiesheuorum* sp. nov., antennule, male (paratype 4). **a** General shape, dorsal; **b** segments III to V, small segment IV not visible in ventral view. Scale bar = $25 \mu m$

P5 (Fig. 6c). Similar to female; process on inner margin weaker than in female, with one short, plumose inner seta and three slender, bare outer setae.

P6 (Fig. 6c). Two asymmetrical plates, left side more circular, right side broader than long; each with two setae, inner seta longest and plumose, outer seta bare.

Monsmeteoris reductus sp. nov.

Type locality: Plateau of the Great Meteor Seamount, subtropical north-eastern Atlantic (30.0°N, 28.5°W); biogenic carbonate sediment; 284–339 m water depth.

Type material: Holotype, female, no. 12, undissected, 1 slide, coll. no. SMF 37165/1; paratype 1 (allotype), male,

no. 12, undissected, 1 slide, coll. no. SMF 37166/1; paratype 2, female, no. 12, dissected, mounted on 8 slides, coll. no. SMF 37167/1–8; paratype 3, female, no. 13, dissected, mounted on 5 sides, coll. no. SMF 37168/1–5; paratype 4, male, no. 13, dissected, mounted on 6 slides, coll. no. SMF 37169/1–6; paratype 5, male, #13, dissected, mounted on 4 slides, coll. no. SMF 37170/1–4.

Etymology: The species name "reductus" refers to the strongly reduced swimming legs.

Description of the female:

Habitus (Fig. 8). Slender and vermiform, body length measured in lateral view, excluding rostrum and caudal rami, 487–567 μ m (average, 537 μ m, n = 6). P1-bearing somite fused with cephalosome to form cephalothorax, covered with several sensilla and pitted (see inset in Fig. 8a). Rostrum fused to cephalothorax, triangular, small and armed with two sensilla. Postero-dorsal margin of cephalothorax and following three somites with small hyaline frill. Somites with sensilla and one dorsal pore; pores absent from P2- and P3-bearing somites and anal somite, no sensilla on penultimate somite. First urosomite with two lateral pores. Urosomites two and three fused to form genital double-somite. Anal operculum small and bare (Fig. 9).

Caudal ramus (Fig. 9a, b). About $1.7 \times$ longer than proximal width, cylindrical. Six setae located in distal third: seta I absent, seta II and III located on outer margin, long and slender, seta III shorter than seta II, seta IV and V apical, fused at basis, seta IV small and slender, fused at basis with seta V; proximal fifth of apical seta V styliform, remaining seta long, flexible; seta VI apically located, slender, smaller than seta IV; seta VII dorsal, plumose, biarticulated at base.

Antennule (Fig. 10). Seven-segmented, first segment with row of long setules; second segment longest; seventh segment as long as segments five and six combined. All setae slender and bare, except for three dorsal plumose setae on second segment; second segment with nine setae, five dorsal, four ventral on apical margin; seventh segment with nine setae, five on outer margin, one lateral on inner margin, and three apical, one of which fused at basis with aesthetasc. Setal formula: 1-1; 2-9; 3-5; 4-1+ (1+ aesthetasc); 5-1; 6-2; 7-8+ (1+ aesthetasc).

Antenna (Fig. 11a). Coxa small. Basis bare, $1.4 \times$ longer than wide. Exopod one-segmented: $4.3 \times$ longer than wide, with two slender apical setae, inner one longest and plumose. Endopod two-segmented: enp1 with row of small spinules on abexopodal margin; enp2 with projection on outer apical edge, armed with small spinules laterally, two lateral pinnate spines and five large spinules, with five apical setae, innermost two setae spine-like and pinnate, central two setae long, slender and flexible, outer most seta long and flexible, with spines

enlarging centrally from proximal end of seta, distal half of seta flexible with distally decreasing small spines.

Mandible (Fig. 11b, b'). Gnathobase well developed with eight teeth, one with two tips and one short bare seta (Fig. 11b'). Basis about $3.4 \times$ longer than wide, with one plumose seta on inner apical margin (Fig. 11b). Endopod with one slender, bare inner seta, and two apical setae merged at basis and two subapical setae merged at basis.

Maxillule (Fig. 11c). Praecoxa with two lateral setae, five spines, each with one setule in distal part, and two long, slender setae on the anterior surface. Coxa apical with two long, bare setae; coxal epipodite bare. Basis elongate, with four distal setae including one pinnate, and two subdistal setae. Exopodite represented by one slender, bare seta. Endopod represented by three slender, bare setae.

Maxilla (Fig. 11d). Syncoxa with two cylindrical endites, proximal endite with three bare setae, distal endite with two bare and one pinnate setae. Basis with one claw and two setae, all bare and emerging close together. Endopod represented by three bare, slender setae.

Maxilliped (Fig. 11e). Prehensile. Syncoxa with pinnate subapical seta on outer edge. Basis with long spinules on distal half of segment. Endopod one-segmented, small with one long, pinnate claw, forming an apical hook.

Swimming legs (Fig. 12a–c). Unless otherwise specified, outer spines of exp1–3 pinnate, distal margin of exp1,2, and outer margin of exp1–3 with long spinules. For setal formula, see Table 3.

P1 (Fig. 12a). Coxa bare. Basis with long setules on distal margin, long, pinnate seta on inner edge, and outer seta absent. Exopod three-segmented: exp1 and exp2 with outer spine, distal margin bare; exp3 with one outer spine and two apical and one subapical setae, all flexible and pinnate, inner seta the longest. Endopod two-segmented: both segments subequal, slightly shorter than exopod: enp1 with three long inner spinules and pinnate inner seta centrally; enp2 with long spinules on inner and distal margin and two long, flexible, pinnate apical setae, innermost longest. Intercoxal sclerite 2.8× broader than long.

P2 (Fig. 12b). Coxa with two spinules on inner margin. Basis bare, outer seta absent. Exopod three-segmented: exp1 and exp2 with outer spine; exp3 without spinules, with one outer spine, one long bipinnate subapical seta, and one short bipinnate apical seta. Endopod one-segmented: small, length one quarter of exp1, with one long, pinnate seta reaching distal end of exp2.

P3 (Fig. 12c). Coxa bare. Basis bare, outer seta long and plumose. Exopod three-segmented: exp1 and exp2 with one outer spine; exp3 with one outer spine and two pinnate apical setae. Endopod absent.

P4. Absent.

P5. Absent.

P6 and genital field (Fig. 8c). Genital double-somite completely fused. P6 consisting of a pair of symmetrical plates



Fig. 8 *Monsmeteoris reductus* sp. nov., female. **a** Habitus, dorsal, rectangular inset showing detailed surface structure (holotype); **b** habitus, lateral (holotype); **c** P6 and genital complex (paratype 2). Scale bar = $200 \mu m (a, b)$ and $50 \mu m (c)$



Fig. 9 Monsmeteoris reductus sp. nov., caudal rami, female (paratype 2). a Dorsal, caudal setae indicated by I–VII; b lateral. Scale bar = 50 µm

which narrow slightly distally; without setae. Copulatory pore not covered by plates.

Description of the male:

Habitus (Fig. 13a, b) and most features as in female. Sexual dimorphism observed in body length, antennule, P3, P5, and P6. Body length measured in lateral view, excluding rostrum, and caudal rami, 445–543 μ m (average, 498 μ m, *n* = 6).

Antennule (Fig. 14a, b). Subchirocer (seven-segmented: second segment the longest, fourth segment very small, only visible in dorsal view (Fig. 14a), covered by swollen fifth segment in ventral view (Fig. 14b), sixth and seventh segment of same length; all setae slender and bare, except on third segment which has two plumose seta, one on dorsal inner margin and one on inner apical margin. Setal formula: 1-1; 2-9; 3-5; 4-1; 5-4+ (1+ aesthetasc); 6-2; 7-7+ (1+ aesthetasc).

P3 (Fig. 13c). Coxa and basis as in female. Exopod shorter than that of female, setation as in female. Endopod one-segmented: enp1 small, knob-like, with one long, bare apical seta.

P5 (Fig. 13d). Strongly reduced; four small setae on somite margin.

P6 (Fig. 13e). Two asymmetrical small plates, each with one small, bare seta.

Genus Cylindropsyllus Brady, 1880

Type species: Cylindropsyllus laevis Brady, 1880.

Additional species: Cylindropsyllus flexibilis sp. nov., Cylindropsyllus govaerei Huys & Willems, 1993, Cylindropsyllus ibericus Huys & Willems, 1993, Cylindropsyllus kunzi Huys, 1988, Cylindropsyllus remanei Kunz, 1949, Cylindropsyllus valentini sp. nov.

Cylindropsyllus valentini sp. nov.

Type locality: Plateau of the Great Meteor Seamount, subtropical north-eastern Atlantic (30.0°N, 28.5°W); biogenic carbonate sediment; 284–339 m water depth.

Type material: Holotype, female, no. 3, undissected, 1 slide, coll. no. SMF 37171/1; paratype 1 (allotype), male, no. 3, undissected, 1 slide, coll. no. SMF 37172/1; paratype 2, female, no. 3, dissected, mounted on 8 slides, coll. no. SMF 37173/1–8; paratype 3, female, no. 3, dissected, mounted on 5



Fig. 10 *Monsmeteoris reductus* sp. nov., antennule, female, ventral (paratype 3). Scale bar = $25 \mu m$



Fig. 11 *Monsmeteoris reductus* sp. nov., mouthparts, female. **a** Antenna (paratype 2); **b** mandibular palpus (paratype 2); **b** mandible, lateral (paratype 2); **c** maxillule (paratype 2); **d** maxilla (paratype 2); **e** maxilliped (paratype 3). Scale bar = $50 \mu m$



Fig. 12 *Monsmeteoris reductus* sp. nov., swimming legs, female, anterior. **a** P1, with intercoxal sclerite (paratype 3); **b** P2, (paratype 2); **c** P3 (paratype 2). Scale bar = $25 \ \mu m$



Fig. 13 *Monsmeteoris reductus* sp. nov., male. **a** habitus, dorsal, rectangular inset showing detailed surface structure (paratype 1); **b** habitus, lateral (paratype 1); **c** P3, anterior (paratype 4); **d** P5 (paratype 4); **e** P6 (paratype 4). Scale bar = 200 μ m (**a**, **b**) and 25 μ m (**c**-**e**)



Fig. 14 Monsmeteoris reductus sp. nov., antennule, male (paratype 5). a General shape, dorsal; b segments III to V, small segment IV not visible in ventral view. Scale bar = $25 \mu m$

sides, coll. no. SMF 37174/1–5; paratype 4, male, no. 3, dissected, mounted on 8 slides, coll. no. SMF 37175/1–8.

Etymology: This species is dedicated to Valentin Campano Pointner.

Description of the female:

Habitus (Fig. 15a, b). Slender and vermiform, body length measured in lateral view, excluding rostrum and caudal rami, 470–613 µm (average: 507 µm, n = 10). P1-bearing somite fused with cephalosome to form cephalothorax, pitted (see inset in Fig. 15a) and with several sensilla. Rostrum triangular with two sensilla, separate from cephalothorax, extending to

distal margin of first antennular segment. Postero-dorsal margins of all somites with hyaline frill, most visible in lateral view (Fig. 15b). Dorsal and lateral sensilla on all somites, except penultimate somite. Urosomites two and three fused to form genital double-somite (Fig. 15a). Anal operculum small, bare (Fig. 15c). Female with two separate eggs.

Caudal ramus (Fig. 15c, d). About $3.4 \times$ longer than proximal width, slight proximal narrowing. Six bare setae located in distal third: seta I absent, seta II lateral, slender; seta III dorsal, arising from small pedestal, long and slender; seta IV apical, small and slender, fused at basis with seta V; seta V



Fig. 15 *Cylindropsyllus valentini* sp. nov., female. **a** Habitus, dorsal, rectangular inset showing detailed surface structure (holotype); **b** habitus, lateral (holotype); **c** caudal rami, dorsal, caudal setae indicated by I–VII (paratype 2); **d** caudal ramus, lateral (paratype 2). Scale bar = 200 μ m (**a**, **b**) and 50 μ m (**c**, **d**)

apical, proximal part (about same length as caudal ramus) styliform, remainder long, flexible; seta VI apical, on inner margin, slender, smaller than seta IV; seta VII dorsal, on inner margin, slender and bare, biarticulated at base.

Antennule (Fig. 16a). Seven-segmented: first segment with row of long setules; second segment longest; seventh segment as long as fifth and sixth segments combined. All setae slender and bare; sixth segment with very slender seta on ventral side. Setal formula: 1-1; 2-6; 3-4; 4-1+(1+ aesthetasc); 5-1; 6-1; 7-7+(1+ aesthetasc).

Antenna (Fig. 17a). Coxa small. Allobasis 2.7× longer than wide, bare. Exopod one-segmented, located in proximal third of allobasis: elongate, 3.7× longer than wide, with two slender and bare apical setae, inner one longest. Endopod one-segmented: armed with spinules and two bare spines on inner margin; five apical elements, innermost two spine-like with hooked tip and bare, innermost smallest, two long, slender and flexible central setae, outermost seta with spinules on proximal half, distally enlarging, flexible and with minute spinules.

Mandible (Fig. 17b). Gnathobase well developed with four teeth, of which two with several tips, and one short, bare seta. Basis bare. Endopod with two slender, bare apical setae.

Maxillule (Fig. 17c). Praecoxa with five spines and two long, slender surface setae running parallel on anterior side. Coxa with one long, bare seta; coxal epipodite bare. Basis with three slender, bare setae. Exopodite and endopodite each represented by one slender, bare seta.

Maxilla (Fig. 17d). Syncoxa with two cylindrical endites, proximal endite with two setae, distal seta pinnate, distal endite with two setae, one pinnate and one bare. Basis with one pinnate claw, accompanied by two slender, bare setae, one dorsal and one ventral. Endopod represented by two slender, bare setae.

Maxilliped (Fig. 17e). Rudimentary. Single plate with two protrusions on distal end, connected to syncoxa of maxilla (Fig. 17d).

Swimming legs (Fig. 18a–d). Unless otherwise specified, exp1–3 with spinules on outer margins and pinnate outer spines. For setal formula see Table 3.

P1 (Fig. 18a). Coxa bare. Basis bare, without setae. Exopod three-segmented: exp1 and exp2 with one outer spine; exp3 with one outer spine and two pinnate apical setae. Endopod two-segmented, as long as exopod: enp1 with setules on inner margin and one long, slender inner seta with apical serration; enp2 with spinules on outer margin, two long, flexible pinnate apical setae and one minute, bare seta on inner margin.

P2 (Fig. 18b). Coxa bare. Basis bare, outer seta present, slender and bare. Exopod three-segmented: exp1 and exp2 with one outer spine; exp3 with one outer spine and two bipinnate, long apical setae. Endopod two-segmented, slightly longer than exp1: enp1 with long, slender inner seta with apical serration; enp2 with long, bipinnate apical seta. Intercoxal sclerite $3 \times$ wider than long.

P3 (Fig. 18c). Coxa bare. Basis bare, outer seta present, long, slender, and apically plumose. Exopod three-segmented: exp1 and exp2 with one outer spine; exp3 with one outer subdistal spine, two bipinnate apical setae, and one long, inner distal seta with distal serration. Endopod two-segmented, nearly as long as exp1 and exp2 combined: enp1 bare; enp2 with distal process, and one bipinnate apical setae. Intercoxal sclerite 3× broader than long.

P4 (Fig. 18d). Coxa bare. Basis bare, outer seta present, long, slender and bare. Exopod three-segmented: exp1 and exp2 with small number of spinules on outer margin and one outer spine, exp1 with row of small spinules on distal margin; exp3 about one-quarter as long as exp2, one outer spine, two bipinnate apical setae, and one subapical seta with distal serration on inner margin. Endopod two-segmented, longer than exp1: enp1 bare; enp2 with one bipinnate apical seta.

P5 (Fig. 18e). Pair of separate plates, each with one pore proximally. Seven setae present, all bare except outermost, plumose seta: innermost two setae small and slender; four distal setae bare, inner one longest, adjacent one spine-like, followed by two small, bare setae; outermost seta articulated at base and plumose at distal end.

P6 and genital field (Fig. 18e). Genital double-somite completely fused. P6 consisting of symmetrical plates, distally without setae and strongly narrowing. Copulatory pore uncovered, distal.

Description of the male:

Habitus (Fig. 19a, b) and most features as in female. Sexual dimorphism observed in body length, antennule, P2, P3, P5, P6 and anal operculum. Body length measured in lateral view, excluding rostrum and caudal rami, 483–517 μ m (average, 495 μ m, *n* = 10), anal operculum with pores (Fig. 20a).

Antennule (Fig. 16b, c). Haplocer, nine-segmented: first segment with three rows of spinules of different sizes; second segment longest, fourth segment very small, only visible in dorsal view (Fig. 16c, arrow), covered by swollen fifth segment in ventral view (Fig. 16b), sixth segment hardly visible in ventral view (Fig. 16b), large in dorsal view (Fig. 16c); all setae slender and bare, except for two plumose dorsal setae on second segment. Setal formula: 1-1; 2-8; 3-5; 4-2; 5-6+(1+ aesthetasc); 6-1; 7-1; 8-0; 9-7+(1+ aesthetasc).

P2 (Fig. 19c). Coxa bare. Basis with plumose outer setae and hook-shaped apophysis on inner edge. Exopod as in female but with fewer spinules: exp3 without inner seta, claw present, as long as whole exopod, heavily plumose. Endopod as in female.

P3 (Fig. 19d, e). Coxa, basis as in female. Exopod-like female: exp3 setae all pinnate, except long, plumose inner apical seta. Endopod segments partly fused, visible in lateral view (Fig. 19e): Enp1 inner margin with spiniform extension, nearly as long as exopodal segments, blunt tip; enp2 with two plumose, long setae.



Fig. 16 *Cylindropsyllus valentini* sp. nov., antennule. **a** Female, ventral (paratype 2); **b** male, ventral (paratype 4); C, male, segments III to VI, small segment IV marked by arrow, dorsal (paratype 4). Scale bar = $25 \mu m$



Fig. 17 *Cylindropsyllus valentini* sp. nov., mouthparts, female. **a** Antenna (paratype 2); **b** mandible (paratype 2); **c** maxillule (paratype 3); **d** maxilla with attached maxilliped (paratype 3); **e** maxilliped (paratype 3). Scale bar = $25 \mu m$

P5 (Fig. 18f). Similar to female P5. Surface with two additional pores. Innermost seta absent, remaining six setae similar to setae of female P5.

P6 (Fig. 18). Two asymmetrical plates, left side bigger than right. Each side with three setae, central seta longest with plumose distal half, other two setae slender and bare.

Cylindropsyllus flexibilis sp. nov.

Type locality: Plateau of the Great Meteor Seamount, subtropical north-eastern Atlantic (30.0° N, 28.5° W); biogenic carbonate sediment; 284-339 m water depth.

Type material: Holotype, female, no. 21, undissected, 1 slide, coll. no. SMF 37176/1; paratype 1 (allotype), male, no. 21, undissected, 1 slide, coll. no. SMF 37177/1; paratype 2, female, no. 20, dissected, mounted on 10 slides, coll. no.

SMF 37178/1–10; paratype 3, female, no. 21, dissected, mounted on 2 sides, coll. no. SMF 37179/1–2; paratype 4, female, no. 21, dissected, mounted on 8 slides, coll. no. SMF 37180/1–8; paratype 5, male, no. 21, dissected, mounted on 7 slides, coll. no. SMF 37181/1–7; paratype 6, male, no. 20, dissected, mounted on 3 slides, coll. no. SMF 37182/1–3.

Etymology: The species name "flexibilis" refers to the very flexible setae on the antennal endopod and the P4 exp3.

Description of the female:

Habitus (Fig. 20a, b). Slender and vermiform, body length measured in lateral view, excluding rostrum and caudal rami, 707–758 μ m (average, 731 μ m, *n* = 4). P1-bearing somite fused with cephalosome to form cephalothorax, covered with several sensilla and pitted (see inset in Fig. 20a). Rostrum triangular with two sensilla, separated from cephalothorax, visible in lateral view, extending to distal margin of first



Fig. 18 *Cylindropsyllus valentini* sp. nov., swimming legs, dashed setae added from other side of corresponding paratype. **a** Female P1, anterior (paratype 3); **b** female P2, posterior, with intercoxal sclerite, seta on basis broken (paratype 2); **c** female P3, posterior, with intercoxal sclerite, seta on

basis broken (paratype 3); **d** female P4, anterior, seta on basis broken (paratype 3); **e** female P5, P6, and genital complex (paratype 3); **f** male P5 and P6, setae on right P6 broken (paratype 4). Scale bar = $50 \ \mu m$



Fig. 19 *Cylindropsyllus valentini* sp. nov., male. **a** Habitus, dorsal, rectangular inset showing detailed surface structure (paratype 1); **b** habitus, lateral (paratype 1); **c** P2, anterior (paratype 4); **d** P3, anterior (paratype 4); **e** endopod of P4, lateral (paratype 4). Scale bar = $200 \mu m (a, b)$ and $25 \mu m (c-e)$



Fig. 20 *Cylindropsyllus flexibilis* sp. nov., female. **a** Habitus, dorsal, rectangular inset showing detailed surface structure (holotype); **b** habitus, lateral (holotype); **c** caudal rami, dorsal, caudal setae indicated by I–VII (paratype 2); **d** caudal ramus, lateral (paratype 2). Scale bar = $200 \mu m$ (**a**, **b**) and $25 \mu m$ (**c**, **d**)

antennular segment. Postero-dorsal margins of all somites with hyaline frill. Dorsal and lateral sensilla on each somite, except for penultimate somite. Urosomites two and three fused to form genital double-somite (Fig. 20b). Anal operculum small and bare (Fig. 20c).

Caudal ramus (Fig. 20c, d). About 2.7× longer than proximal width, cylindrical. Six bare setae in distal third: seta I absent, seta II lateral, slender; seta III dorsal, arising from small pedestal, long and slender; seta IV apical, small and slender, fused at basis with seta V; seta V apical, proximal quarter styliform, remainder long and flexible; seta VI apical on inner margin, slender, smaller than seta IV; seta VII dorsal, on inner margin, slender and bare, biarticulated at base.

Antennule (Fig. 21). Seven-segmented, second segment longest; seventh segment as long as fifth and sixth segments combined. All setae slender and bare, except for plumose outer dorsal seta on second segment. Setal formula: 1-1; 2-7; 3-4; 4-2+(1+ aesthetasc); 5-1; 6-2; 7-7+(1+ aesthetasc).

Antenna (Fig. 22a). Coxa small. Allobasis $2.3 \times$ longer than wide, bare. Exopod one-segmented, in proximal third of allobasis; elongated, $4.6 \times$ longer than wide, with two slender apical setae, inner one longest and plumose. Endopod one-segmented: armed with broad spinules and two bare, broad inner spines; five apical elements, innermost two spine-like and bipinnate, innermost one smallest, two central setae long, slender and flexible, outermost seta distally flexible, with broad spinules on proximal half.

Mandible (Fig. 22b, b'). Gnathobase well developed with four teeth, two with several tips, and one short, bare seta (Fig. 23b'). Basis bare. Endopod with one lateral seta close to basis on inner margin, and two apical setae, both slender and bare.

Maxillule (Fig. 22c). Praecoxa with five spines, each with several tips, one bare apical seta on posterior side and two long, slender surface setae on anterior side. Coxa with one long, bipinnate seta; coxal epipodite bare. Basis with three slender, bare setae. Exopodite and endopodite, each represented by one slender, bare seta.

Maxilla (Fig. 22d). Syncoxa with two cylindrical endites: proximal endite with two setae, proximal seta pinnate; distal endite with three setae, two pinnate, one bare. Basis with one pinnate claw, accompanied by two slender, bare setae, one dorsal and one ventral. Endopod represented by three slender, bare setae.

Maxilliped (Fig. 22d'). Rudimentary, comprising single plate with two protrusions on distal end; plate connected to syncoxa of maxilla.

Swimming legs (Fig. 23a–d). Unless otherwise specified, outer spines of exp1–3 pinnate. For setal formula see Table 3.

P1 (Fig. 23a). Coxa bare. Basis bare, without seta. Exopod three-segmented: exp1 and exp2 outer margin with setules, and each with outer spine; exp3 outer margin with setules,

one subapical and two pinnate outer spines, and flexible apical setae. Endopod two-segmented, slightly shorter than exopod: enp1 with small spinules across surface and distally serrated inner seta; enp2 with spinules on outer margin, two long, flexible apical setae and one small, bare subapical inner seta.

P2 (Fig. 23b). Coxa with two pores. Basis with slender and bare seta. Exopod three-segmented: exp1 with broad spinules on outer margin, exp2 with small spinules on outer margin, both with one outer spine; exp3 with small spinules on outer margin, one outer spine and two bipinnate, long apical setae. Endopod two-segmented, slightly longer than exp1: enp1 with distally serrated inner seta; enp2 with one long, bipinnate apical seta. Intercoxal sclerite $3 \times$ broader than long.

P3 (Fig. 23c, c'). Coxa bare. Basis with slender and bare seta. Exopod three-segmented: exp1 and exp2 with few spinules on outer margin and one outer spine; exp3 with several spinules on outer margin, one outer spine, two long, bipinnate apical setae and one long, distally serrated inner seta. Endopod two-segmented, nearly as long as exp1 and exp2 combined: enp1 bare; enp2 with process (Fig. 23c'), and two bare apical setae. Intercoxal sclerite $2 \times$ broader than long.

P4 (Fig. 23d). Coxa bare. Basis with one pore, and plumose outer seta. Exopod three-segmented: exp1 with several pores and broad spinules, exp2 with two pores, row of setules proximally and broad spinules distally, both with one outer spine; exp3 half as long as exp2, with row of setules proximally and small spinules distally, one outer spine, two bipinnate apical setae, inner one flexible, and one distally serrated subapical seta on inner margin. Endopod two-segmented, as long as exp1: enp1 bare; enp2 bare, one bipinnate apical seta.

P5 (Fig. 23e). Pair of separate plates, each with one pore and one spinule. Seven setae present: innermost seta pinnate, second inner seta slender and bare, two setae on distal end, both bare, inner one longest, three setae on outer margin, two small and slender, outermost articulated at base, plumose at distal end.

P6 and genital field (Fig. 23e). Genital double-somite completely fused. P6 consisting of symmetrical plates which strongly narrow distally; one slender, bare distal seta, broken on left side. Copulatory pore uncovered, distal, far from P6.

Description of the male:

Habitus (Fig. 24a, b) and most features as in female. Sexual dimorphism of body length, antennule, P2, P3, P5, and P6. Body length measured in lateral view, excluding rostrum and caudal rami, 680–731 μ m (average, 706 μ m, *n* = 2).

Antennule (Fig. 25a, b). Haplocer, nine-segmented: second segment the longest, fourth segment very small, only visible in dorsal view (Fig. 25b, arrow), covered by swollen fifth segment in ventral view (Fig. 25a), sixth segment hardly visible in ventral view (Fig. 25a), large in dorsal view (Fig. 25b); all setae slender and bare, except for plumose dorsal seta on second segment; second segment with eight setae, four on ventral



Fig. 21 *Cylindropsyllus flexibilis* sp. nov., antennule, female, dorsal (paratype 2). Scale bar = $25 \mu m$



Fig. 22 *Cylindropsyllus flexibilis* sp. nov., mouthparts, female. **a** Antenna (paratype 2); **b** mandible (paratype 3); **b** mandible, lateral (paratype 3); **c** maxillule (paratype 3); **d** maxilla (paratype 3); **d** maxilla (paratype 3), attached to maxilla. Scale bar = $25 \mu m$



Fig. 23 *Cylindropsyllus flexibilis* sp. nov., swimming legs, female. **a** P1, anterior (paratype 3); **b** P2, anterior, dashed seta added from other side of same paratype, with intercoxal sclerite (paratype 4); **c** P3, anterior, with

intercoxal sclerite (paratype 2); \mathbf{c} P3 enp2, lateral (paratype 2); \mathbf{d} P4, anterior (paratype 2), arrow indicates flexible seta; \mathbf{e} P5, P6 and genital complex, seta on left P6 broken (paratype 2). Scale bar = 50 μ m



Fig. 24 Cylindropsyllus flexibilis sp. nov., male. a Habitus, dorsal, rectangular inset showing detailed surface structure (paratype 1); b habitus, lateral (paratype 1); c P2, anterior (paratype 5); d P3,

 $\underline{\textcircled{O}}$ Springer

anterior (paratype 5); **e** P5 (paratype 5); **f** P6, outer seta of right P6 broken (paratype 5). Scale bar = 200 μ m (**a**, **b**) and 25 μ m (**c**–**f**)



Fig. 25 *Cylindropsyllus flexibilis* sp. nov., antennule, male (paratype 2). **a** General shape, ventral; **b** segments III to VI, small segment IV marked by arrow, dorsal. Scale bar = $25 \mu m$



◄ Fig. 26 Distribution of the recorded species of Cylindropsyllidae at the sampled locations (#1-#21) across the plateau of the Great Meteor Seamount during the expedition POS397 GroMet of the R/V "Poseidon" in 2010 (contour interval 50 m; R/V Meteor M42/3 Hydrosweep Survey, Mercator WGS84 1:550000 at 0°)

side, four on dorsal side, five in total on distal margin. Setal formula: 1-1; 2-8; 3-5; 4-2; 5-6+(1+ aesthetasc); 6-1; 7-1; 8-0; 9-7+(1+ aesthetasc).

P2 (Fig. 24c). Coxa bare. Basis with hook-shaped apophysis on inner edge. Exopod as in female: Exp3 inner seta absent, claw present, as long as whole exopod, heavily plumose, distal tip with minute spinules. Endopod as in female.

P3 (Fig. 24d). Coxa, basis and exopod as in female. Endopod two-segmented: enp1 inner margin with spiniform extension, longer than exopodal segments, blunt tip; enp2 with two long, pinnate setae.

P5 (Fig. 24e). Similar to female P5. Surface with tube-pore. Six setae present: innermost seta minute; two elements on distal end, one long, slender inner setae and one stout, bare outer spine; outer margin with three setae, inner two smaller than in female, outer one articulated at base and biplumose at distal end.

P6 (Fig. 24f). Two asymmetrical plates with pores, left side bigger than right. Each plate with three setae, central seta longest with plumose tip, other two setae slender and bare, inner one shortest.

Geographical distribution

In total 493 adult specimens were collected from the GMS plateau, 93 (19%) from the northern region, 208 (42%) from the middle region, and 192 (39%) from the southern region. Six species were identified, two (*Boreopontia heipi* Willems, 1981, *Selenopsyllus dahmsi* Moura & Pottek, 1998) were already known to science, and four are described as new species in the present contribution: *Cylindropsyllus valentini* sp. nov, *Cylindropsyllus flexibilis* sp. nov., *Monsmeteoris wiesheuorum* sp. nov., and *Monsmeteoris reductus* sp. nov. (Table 2).

Specimens of Cylindropsyllidae were found across the plateau (Fig. 26). *Cylindropsyllus valentini* sp. nov. was the most abundant species identified, being present at each station in every region. *Monsmeteoris reductus* sp. nov. and *B. heipi* were also recorded in every region, but not at every station: *M. reductus* sp. nov. was not found at southern station #16, and *B. heipi* was not found at northern station #5, middle stations #7 and #14 or southern stations #16 and #19. *Selenopsyllus dahmsi* was less abundant and was found in every region but only at single stations (northern region: #2; middle region: #9, #11, #12, #13; southern region: #15, #19, #20). *Cylindropsyllus flexibilis* sp. nov. and *M. wiesheuorum* sp. nov. were the rarest species on the plateau: *M. wiesheuorum* sp. nov. was only identified in the middle (#8, #12) and southern regions (#15, #17, #18, #19, #20, #21), whilst *C. flexibilis* sp. nov. was only recorded in the southern region (#20, #21).

Discussion

Systematics

The taxon Cylindropsyllidae comprises 13 genera: Bolbotelos Huys & Conroy-Dalton, 2006 (Huys and Conroy-Dalton 2006b), Boreopontia Willems, 1981, Boreovermis Huys & Conroy-Dalton, 2006 (Huys and Conroy-Dalton 2006b), Cylindropsyllus Brady, 1880, Cylinula Coull, 1971, Evansula Scott, 1906, Monsmeteoris gen. nov., Navalonia Huys & Conroy-Dalton, 1993, Selenopsyllus Moura & Pottek, 1998, Stenocaris Sars, 1909, Stenocaropsis Apostolov, 1982, Vermicaris Kornev & Chertoprud, 2008, and Willemsia Huys & Conroy-Dalton, 1993. It is monophyletic and can be characterized by several in detailed discussed apomorphic characters (Table 4, characters 1-3) given by Martínez Arbizu and Moura (1994) and expanded by Huys and Conroy-Dalton (2006a). However, the apomorphic (or possibly plesiomorphic) state of some characters (Table 4, no. 4-6) remains unclear in these studies, as they may be either original or secondary lost. Thus, a systematic revision, including also genetic analysis, is needed to update, by addition and refinement, the autapomorphies for Cylindropsyllidae.

Placement of Monsmeteoris gen. nov.

Given the list of apomorphies of Cylindropsyllidae (Table 4, nos. 1–3), the placement of the new genus *Monsmeteoris* gen. nov. within this family is without difficulty, all apomorphies being present in *Monsmeteoris* gen. nov.

Within the Cylindropsyllidae, genera can be identified by specific apomorphic characters, being discussed in detail in the corresponding articles (Table 4, nos. 8-38; genera Stenocaris and Vermicaris are excluded from Table 4 and any further discussion, as no apomorphic characters were mentioned in the associated study). As none of these characters applies to the species Monsmeteoris wiesheuorum sp. nov. and M. reductus sp. nov., they cannot be included within any of the genera proposed in previous studies. Moreover, the groundpattern of all genera reveal an antenna with allobasis (Table 4, no. 7), whereas the plesiomorphic condition is present in the outgroup Leptopontiidae as well as in *M. wiesheuorum* sp. nov. and *M. reductus* sp. nov., possibly indicating a basal position of Monsmeteoris gen. nov. within the Cylindropsyllidae. Additionally, the two cylindropsyllid species share two synapomorphic characters (Table 4, nos. 31, 32), which are based on the principle of oligomerization

Je	
iida	
ont	
otop	
Lep	
[dr	
grou	
outg	
Je C	
ig th	
din	
clu	
.E.	
dae	
ylli	
sdc	
Jdro	
ylii	
e C	
f th	
a ol	
tax	
he	
to t	
ant	
orta	
dur	
re i	
sh a	
/hic	
s, v	
cter	
arac	
ch	
l of	
tior	
ndi	
CO	
0	
hic	
orp	
om	
lesi	
d p	
an	
(1)	
hic	
orp	
un	
ap	
t of	
Lis	
le 4	
Lab	

No.		Leptopoi	ntiidae B	solbotelos	Boreovermis	Navalonia	Willemsia	Cylinula (Cylindropsyllus	Boreoponita	Evansula	Monsmeteoris gen. nov.	Selenopsyllus	Stenocaropsis	Reference
_	Female P3 enp1 without inner seta	0	-		1	1			_	1	_	-	-	-	Martínez Arbizu and
7	P5 forming a common plate not differentiated in exp. and enp in both sexes, male with 6 setae and female with 8 setae	0	-		1	1	1	1	_	1	1	-	1	1	Mattinez (1994) Mattinez Arbizu and Moura (1994)
ŝ	(P5 with distinct exopod) Caudal rami with seta V composite (not composite)	0	1		1	Т	_	1	_	Т	1	1	_	1	Huys and Conroy-Dalton
4	Male P2 exp3 with the apical seta modified (male and female	0	1		1	1	1	1	1	1	1	0	1	0	(2006a) Martínez Arbizu and Moura (1994)
Ś	With same structure) Male P2 with process at inner basis (without any small	0	ċ		1	1	-	1	I	Ц	0	0	-	ć	Martínez Arbizu and Moura (1994);
9	appearance of such process) A1 second segment longest (as long as first segment)	0	1		-	1	1	1	1	1	0	-	1	1	Huys (1988) Huys and Willems
8	A2 with allobasis (basis present) P1 enp2 with at most one claw distally (geniculate seta	0 0	10		- 0	0 1	0	1 1	- 0	- 0	0 1	0 0	- 0	- 0	Present contribution Huys and Willems (1993)
6	present) Outer distal spine of female P3 enp2 modified into anterior spinios process (not	0	0		0	0	0	1 (0	0	0	0	0	0	
10	P1 exp2 without outer spine	0	0		0	0	0	0	0	1	0	0	0	0	Huys and
П	(present) Innermost element of female P5	0	0		0	0	0	0	0	1	0	0	0	0	Conroy-Dalton (1993)
12	robust spine (clongated seta) Foot-shaped apophysis on P5 present (such apohpysis	0	0		0	0	1	0	0	0	0	0	0	0	Huys and Conroy-Dalton
13	absent) Male P2 exp1 with bulbiform, hyaline strucutre on inner	0	0		0	0	_	0	0	0	0	0	0	0	(1993)
14	margun (absent) Coxa of male P3 with large, conspicuous apophysis-like	0	0		0	0	_	0	0	0	0	0	0	0	
15	structure (aussent) Seta V of caudal ramus strongly sexually dimorphic (sexual dimorphism absent or only dished: conserved)	0	0		0	-	0	0	0	0	0	0	0	0	Huys and Conroy-Dalton (1993)
16	Male P4 enp with strong process on the inner margin (sexual dimorphism absent)	0	0		0	1	0	0	0	0	0	0	0	0	
17	Body extremely vermiform	0	1		0	0	0	0	0	0	0	0	0	0	Huys and Conrow Dalton
18	Caudal ramus bilateral compressed and bulbous (not	0	1		0	0	0	0	0	0	0	0	0	0	(2006b)
19	Corpulatory pore extremely wide	0	1		0	0	0	0	0	0	0	0	0	0	
20	Inner geniculate setae on P1 exp3 and enp2 very long and slender	0	1		0	0	0	0	0	0	0	0	0	0	
21	(short and not slender) Basis of male P2 with a double spinous process (at most one	0	0		1	0	0	0	0	0	0	0	0	0	Huys and Conroy-Dalton
22	process) Male P3 exp1 reduced in size (of	0	0		1	0	0	0	0	0	0	0	0	0	(2006b)
23	same size as exp2) Male P3 exp2 with reduced outer spine compared with outer	0	0		1	0	0	0	0	0	0	0	0	0	

Tab	le 4 (continued)													
No.		Leptopontiidae	Bolbotelos	Boreovermis	Navalonia	Willemsia	Cylimla	Cylindropsyllus	Boreoponita	Evansula	Monsmeteoris gen. nov.	Selenopsyllus	Stenocaropsis	Reference
24	spines of exp1 and exp3 (spine well developed) Very long setae on exopods and endopods present (of normal	0	0	0	0	0		0	0	0	0	_	0	Moura and Pottek (1998)
25	length) Apical element of female P5 robust spine (elongated seta)	0	0	0	0	0	0	0	0	0	0	0	_	Huys and Conroy-Dalton
26	Male P2 exp1 with apophysis on inner margin (sexual	0	ċ	0	0	0	0	0	0	0	0	0	_	(1993) Moura and Pottek (1998)
27	dimorphism absent) Caudal ramus seta V hook-like transformed (with styliform proximal and flagellate distal	0	0	0	0	0	0	0	0	0	0	0	1	Kunz (1949)
28	Parts) P1 enp1 inner seta plumose proximally and pinnate distally (serreated in distal half)	0	0	0	0	0	0	0	0	1	0	0	0	Huys and Conroy-Dalton
29	Outer apical element of female P5 modified into strong spine (not	0	0	0	0	0	0	0	0	1	0	0	0	
30	Male P5 with spinous process	0	i	0	0	0	0	0	0	1	0	0	0	
31	(without such process) Antennal endopod with at most 5 distal elements, outermost small seta absent (outermost	0	0	0	0	0	0	0	0	0	-	0	0	Present contribution
32	If P4 present, endopod completely	0	0	0	0	0	0	0	0	0	1	0	0	
33	nost (at reast 1-segmented) Maxilliped reduced (prehensile)	0	0	0	0	0	1	1	0	0	0	0	0	Huys (1988); Huys and
34	P2 enp1 inner serrate seta suppressed in female	0	1	-	1	1	0	0	0	0	0	0	0	Huys and Conroy-Dalton
35	(Rexpressed in Dout secks) (Rexpressed in Dout secks) provinal segment, in provinal segment, in conjunction with the excessive reduction of the basis (emp not displaced, basis of normal size and death and services.	0	_	_	-	-	0	0	0	0	o	0	0	(0000)
36	Seminal neceptacles forming paired elongate reservoirs which are compathmentalized in ventral and anteriorly directed dorsal chambers (oval/round sacs, not	0	-	_	-	-	0	0	0	0	0	0	0	
37	Male P2 exp1 and 2 fused	0	1	1	1	1	0	0	0	0	0	0	0	
38	Styliform and flagellate parts of seta V of caudal ramus secondarily lost (such seta present)	0	-	_	_	-	0	0	0	0	0	0	0	
Gen orde	era listed in the following o red as status of relationship unknown	order: <i>Bolbotelc</i> unknown. Ger	os, Boreover 1era Stenoca	mis, Navalon tris and Vermi	<i>iia</i> , and <i>Wil</i> <i>icaris</i> are ex	<i>lemsia</i> form kcluded, as	aing the <i>l</i> no apom	V <i>avalonia</i> -clad orphic charact	le; <i>Cylinula ɛ</i> ers were men	und <i>Cylina</i> ttioned du	ropsyllus bein ing their desc	ıg closely rela ription	tted; other gen	era: alphabetically

Mar Biodiv

(Huys and Boxshall 1991) and whose plesiomorphic conditions are defined against a baseline morphology of Leptopontiidae and Copepoda (Huys and Boxshall 1991), supporting the erection of the new genus *Monsmeteoris* gen. nov.:

Five distal elements on the antennal endopod, outermost small seta absent (character 31), the most derived condition, is recorded in both species of Monsmeteoris gen. nov. Even though this state of character is also present in single species of other Cylindropsyllidae genera (e.g., Cylindropsyllus valentini sp. nov., C. flexibilis sp. nov., Selenopsyllus profundus (Becker, 1979), Stenocaropsis pristina (Wells, 1968), the groundpattern of these genera reveals the plesiomorphic condition, six distal elements, with the small, outermost seta fused at the basis to the adjacent seta. Due to the principle of parsimony, it is more likely that the loss of the small, outermost seta may have occurred several times within the Cylindropsyllidae than the same secondary development of the outermost seta being fused at the basis of the adjacent one. Moreover, the taxa bearing the same apomorphic condition of this character as Monsmeteoris gen. nov. can be distinguished from the latter by other apomorphies, which are present in their plesiomorphic condition in Monsmeteoris gen. nov. (see Table 4, nos. 8-30 and 33-38). Thus, the loss of the minute, outermost seta of the antennal endopod is seen as an autapomorphy for the new genus.

The P4 endopod is absent (character 32) in *Monsmeteoris* gen. nov. This segmental loss is unique within the Cylindropsyllidae, the P4 endopod being at least one-segmented in the groundpattern of all other cylindropsyllid taxa, as well as in the outgroup Leptopontiidae. This reduced state is, therefore, seen as autapomorphy for *Monsmeteoris* gen. nov.

The taxon *Monsmeteoris* gen. nov. is a valid monophylum characterized by autapomorphies 31 and 32 (Table 4).

Additionally, the swollen segment bearing an aesthetasc of the male antennule is followed by two segments distally in *Monsmeteoris* gen. nov., which is unique within all genera of Cylindropsyllidae. The groundpattern of *Navalonia* indicates the presence of three distally located segments and each of the remaining genera (as well as in the outgroup Leptopontiidae) shows a total of four segments distally to the swollen (5th segment) with aesthetasc. Thus, the distal segments 6 and 7 of the adult (C VI) *Monsmeteoris* gen. nov. possibly consisted of two segments each in the C V-stage, which got fused in the last molt (Dahms 1989). This was already observed for male antennules in other Harpacticoida, e.g., in *Alteutha interrupta* (Goodsir, 1845) and *Drescheriella gracilis* Dahms & Dieckmann, 1987(Dahms 1989). However,

without information on the appearance of the antennule at the C V-stage, this remains uncertain and future investigation on the development of the antennule of all cylindropsyllid taxa will reveal, if this fusion can be designated as autapomorphy for *Monsmeteoris* gen. nov. Nevertheless, as the character "swollen segment bearing an aesthetasc of the male antennule followed by two segments distally" is only present in the species of *Monsmeteoris* gen. nov., it can be used for the typological classification of *Monsmeteoris* gen. nov.

However, the placement of *Monsmeteoris* gen. nov. within the Cylindropsyllidae and its relationship with other genera is difficult to evaluate. *Monsmeteoris* gen. nov. shares different apomorphies with taxa throughout Cylindropsyllidae (e.g., *Cylindropsyllus*, seta I of the caudal rami reduced; *Evansula*, female P2 endopod one-segmented), which indicate their close relationship. In contrast, Huys and Conroy-Dalton (2006b) revealed a well-supported clade within the Cylindropsyllidae, the *Navalonia*-clade, including the taxa *Navalonia*, *Willemsia*, *Boreovermis* and *Bolbotelos*. Basing on these characters (Table 4, nos. 34–38), the genus *Monsmeteoris* gen. nov. is not closely related to this clade. However, a detailed phylogenetic revision of this family including not only morphological but also genetic data is required to clarify the relationships within the taxon.

The placement of *Monsmeteoris wiesheuorum* sp. nov. and *Monsmeteoris reductus* sp. nov. within *Monsmeteoris* gen. nov.

Monsmeteoris wiesheuorum sp. nov. and *Monsmeteoris reductus* sp. nov. can be clearly assigned to *Monsmeteoris* gen. nov. due to apomorphies 31 and 32 (Table 4). They can be separated into distinct species based on specific autapomorphies (Table 5):

In *Monsmeteoris wiesheuorum* sp. nov., the genital pore is covered by a two-flapped genital operculum (character A), which is unique within the Cylindropsyllidae. The genital field of *M. reductus* sp. nov. is without this operculum and resembles that of other cylindropsyllid species (e.g., *Boreovermis bilobatus* Huys & Conroy-Dalton, 2006 (Huys and Conroy-Dalton 2006b)). Therefore, this character is autapomorphic for *Monsmeteoris wiesheuorum* sp. nov.

In *M. wiesheuorum* sp. nov., the first segment of the antennule is bare (character B), but armed with spinules in *M. reductus* sp. nov. and other species of Cylindropsyllidae (e.g., *Evansula incerta* (Scott, 1892), *Cylindropsyllus laevis*, *Cylinula arganoi* Cottarelli & Venanzetti, 1989). Following the principle of parsimony, it is more likely that the spinules were lost in *M. wiesheuorum* sp. nov. than evolved several times in different taxa. Hence, it is seen as autapomorphic for *M. wiesheuorum* sp. nov.

	No.	Apomorphic condition	Plesiomorphic condition
Apomorphic characters of	А	Genital pore covered by 2-flapped genital operculum	Without genital operculum
Monsmeteoris wiesheuorum sp. nov.	В	First segment of antennule without spinules	With spinules
	С	Proximal endite of maxilla with 2 elements, distal seta lost	With 3 elements, distal seta present
Apomorphic characters of	D	Rostrum fused to cephalothorax	Rostrum separated
Monsmeteoris reductus sp. nov.	Е	Maxillular exopod represented by 1 seta	Represented by 2 setae
	F	Female P3 endopod absent	At least 1-segmented
	G	P4 absent	Present
	Н	Female P5 absent	Present
	Ι	P2 exp3 with 3 distal elements, 1 of which apically located	4 distal elements, 2 of which apically located
	J	P3 exp3 with 3 distal elements, innermost serrated seta absent	4 distal elements, innermost serrated seta present
	Κ	P2 enp1 with 1 distal element, apically located	2 distal elements, apically located
	L	Male P5 with 2 pairs of 2 small setae, reminding 2 lost plates	With at least 3 setae on each plate
	М	Plates of male P5 lost	Present
	Na	Female P6 outer seta lost	Present
	Nb	Female P6 middle seta lost	Present
	Nc	Female P6 inner seta lost	Present
	0	Male P6 with 1 seta on each plate	With at least 2 setae on each plate
Apomorphic characters of <i>Cylindropsyllus valentini</i> sp. nov.	Р	Female P3 enp2 with at most 1 distal element, apically located	2 distal elements, apically located
	Q	Lateral seta of mandibular endopod lost	Present
	Ra	Female P6 outer seta lost	Present
	Rb	Female P6 middle seta lost	Present
	Rc	Female P6 inner seta lost	Present
	S	Inner margin of caudal rami concave	Straight
Apomorphic characters of	Т	Inner apical seta of P4 exp3 very flexible	Of normal shape
Cylindropsyllus flexibilis sp. nov.	U	Distal part of outermost seta of the antenna endopod very flexible	Of normal shape
	V	Antenna endopod with stout spines	Of normal shape
Synapomorphic characters of	W	Mandibular endopod with at most 2 distal setae	With at least 3 distal setae
Cylindropsyllus valentini sp. nov.	Х	Inner seta P4 enp2 absent	Present
and Cymaropsynus Jexions sp. 1100.	Y	Proximal styliform part of seta V of caudal rami strongly pronounced	Slightly pronounced

 Table 5
 List of apomorphic characters for the species Monsmeteoris wiesheuorum sp. nov., Monsmeteoris reductus sp. nov., Cylindropsyllus valentini sp. nov., and Cylindropsyllus flexibilis sp. nov., as well as of synapomorphic characters of the latter two species

In *M. wiesheuorum* sp. nov., the proximal endite of the maxilla is armed with only two elements, the distal seta is lost (character C), but three elements are present in *M. reductus* sp. nov. as well as in other species (e.g., *Boreopontia heipi*, *Willemsia calceola* Huys & Conroy-Dalton, 1993). Two elements are also present in species of *Cylindropsyllus*, but this taxon can be clearly distinguished from *Monsmeteoris* gen. nov. by the plesiomorphic states of apomorphies 31 and 32 (Table 4), and the apomorphic appearance of the reduced maxilliped (Table 4, character 33), which is prehensile in *Monsmeteoris* gen. nov. Thus, this reduction is seen as autapomorphy for *M. wiesheuorum* sp. nov.

The combined autapomorphies, A–C, clearly support the erection of *M. wiesheuorum* sp. nov. as a new species.

In *M. reductus* sp. nov., the rostrum is fused to the cephalothorax (character D), whereas it is separated in *M. wiesheuorum* sp. nov. and all other species of Cylindropsyllidae. Therefore, this unique character is seen as autapomorphy for *M. reductus* sp. nov.

In *M. reductus* sp. nov., the exopod of the maxillule is represented by one slender seta (character E), while in *M. wiesheuorum* sp. nov. two setae are present. The exopod of the maxillule represented by one seta is also seen in other species of Cylindropsyllidae (e.g., *Boreovermis bilobatus*,

Cylindropsyllus laevis, Cylinula proxima Coull, 1971), as is the two setae state (e.g., Bolbotelos longisetosus Huys & Conroy-Dalton, 2006 (Huys and Conroy-Dalton 2006b), Selenopsyllus dahmsi). However, all these species can be separated by other apomorphies (Boreovermis bilobatus: basis of male P2 with double spinous process (Huys and Conroy-Dalton 2006b); Cylindropsyllus laevis: unisetose antennal exopod (Huys 1988); Cylinula proxima: one-segmented mandibular palp; Bolbotelos longisetosus: caudal ramus bilaterally compressed and bulbous (Huys and Conroy-Dalton 2006b); Selenopsyllus dahmsi: nine-segmented male antennule), which are plesiomorphic in *M. reductus* sp. nov. Similarly, M. reductus sp. nov. can be clearly distinguished from M. wiesheuorum sp. nov., see above, and therefore the maxillular exopod represented by one seta is considered autapomorphic for M. reductus sp. nov.

Monsmeteoris reductus sp. nov. exhibits three different segmental losses which are not seen in *M. wiesheuorum* sp. nov., and these are, therefore, designated as autapomorphies for *M. reductus* sp. nov.: The female P3 enp (character F), the P4 (character G), and the female P5 (character H) of *M. reductus* sp. nov. are absent. These segmental losses are unique within the Cylindropsyllidae, and therefore account as autapomorphies for *M. reductus* sp. nov.

Monsmeteoris reductus sp. nov. exhibits three setal reductions: Only three distal elements are present on the P2 exp3, one of which being apically located (character I), three distal elements are present on the P3 exp3, with the innermost, serrated seta being absent (character J), and only one apically located distal element is present on the P2 enp1 (character K), whereas P2 exp3 of M. wiesheuorum sp. nov. is armed with four distal elements, two of which being apically located, P3 exp3 bears the innermost serrated seta, and P2 enp1 is armed with two apical elements. These setal reductions also occur in some cylipdropsyllid species (e.g., Boreovermis bilobata: P2 exp3 with three distal elements, one of which apically located; Evanusla incerta: innermost, serrated seta of P3 exp3 absent; Selenopsyllus dahmsi: P1 enp1 with one apical seta), whilst others retain these setae (e.g., Cylinula proxima: P2 exp3 with four distal elements, two of which apically located; Selenopsyllus dahmsi: innermost, serrated seta of P3 exp3 present; Evansula arenicola: P1 enp1 with two apical setae). Due to the apomorphic characters listed in Table 4, the species can clearly be separated and these setal reductions seem to have occurred several times. Therefore, these setal reductions can be designated as autapomorphies for *M. reductus* sp. nov.

In *M. reductus* sp. nov., the P5 has the most derived state known within the Cylindropsyllidae. The female P5 is lost (character H), while the male P5 is reduced to two pairs of two small setae each, reminding two lost plates, (character L) on the segment margin, thus the plates are lost (character M). In all other species, the P5 consists of distinct plates, each

armed with up to eight setae of different shapes in the female, and up to seven setae in the male. Thus, the loss of the P5 in the female and the reduction in the male are seen as two autapomorphies for *M. reductus* sp. nov.

In *M. reductus* sp. nov., the P6 is strongly reduced in both sexes. The female P6 consists of two symmetrical bare plates without setae (characters Na–Nc): This is known from three other species, *Cylindropsyllus valentini* sp. nov, *Willemsia calceola*, and *Bolbotelos longisetosus*, but these can be clearly separated from *M. reductus* sp. nov. by apomorphies 31 and 32 (Table 4). Therefore, it is assumed that this loss of setae occurred several times and is therefore autapomorphic for *M. reductus* sp. nov.

In contrast, the male P6 consists of asymmetrical plates as in all other species of Cylindropsyllidae, but they are much smaller in size and armed with only one seta on each side (character O). This is the most derived condition for this character and is unique within the Cylindropsyllidae and thus again represents an autapomorphy for *M. reductus* sp. nov. In most cylindropsyllid species, the male P6 is armed with three setae on each plate, whereas also two setae per plate are present (e.g., *Boreovermis bilobatus*).

Autapomorphies D–O clearly support the erection of *M. reductus* sp. nov. as a new species.

Placement of *Cylindropsyllus valentini* sp. nov. and *Cylindropsyllus flexibilis* sp. nov. within the genus *Cylindropsyllus*

In contrast with the typical prehensile maxilliped (Fig. 4e) of Cylindropsyllidae, all species of *Cylindropsyllus* share a reduced maxilliped (Table 4, no. 33), consisting of a single plate with two protrusions on the distal end (Fig. 17e). This apomorphic condition is only shared with the taxon *Cylinula* (Table 4, no. 33), indicating that *Cylinula* and *Cylindropsyllus* could be sister taxa (Huys 1988; Huys and Willems 1993). *Cylinula* can be distinguished from *Cylindropsyllus* by the apomorphic P1 endopod, being armed with claws on the distal segment and having a first segment that is longer than the exopod. Unfortunately, up to date no further autapomorphies are known to designate the taxon *Cylindropsyllus* as monophylum. To do so, a detailed revision on this genus is needed, which was not the scope of the present study.

Both *C. valentini* sp. nov. and *C. flexibilis* sp. nov. can be assigned to Cylindropsyllidae, as they share synapomorphies 1–6 (Table 4). Moreover, in both species the reduced maxilliped is present, indicating the affiliation to *Cylindropsyllus* or *Cylinula*. The two species *C. valentini* sp. nov. and *C. flexibilis* sp. nov. are typologically allocated to the taxon *Cylindropsyllus*, as the shape, segmentation and setation of the P1 indicates that they belong to *Cylindropsyllus* rather than to *Cylinula*.

Within the taxon *Cylindropsyllus* both *C. valentini* sp. nov. and *C. flexibilis* sp. nov. can be defined as distinct species owing to several apomorphies (Table 5):

In *C. valentini* sp. nov., five different setal reductions are considered to be autapomorphies following the principle of oligomerization (Huys and Boxshall 1991). Firstly, the female P3 enp2 is armed with only one apical seta (character P), whereas in all other species of Cylindropsyllidae more than one seta is present and is therefore unique within this taxon.

The second setal reduction considered to be autapomorphic in *C. valentini* sp. nov. is the absence of a lateral seta on the mandibular endopod (character Q), which is present in all other species of *Cylindropsyllus*. This seta is also absent in species of different taxa (e.g., *Willemsia calceola*), but these can be distinguished by the appearance of the maxilliped, which is reduced in *Cylindropsyllus* but prehensile in the other taxa.

The third to fifth setal reductions considered to be autapomorphic in *C. valentini* sp. nov. are the absence of all setae on the female P6 (character Ra–Rc), which has three setae in *C. remanei*, and one (presumably the remaining middle seta) in *C. flexibilis* sp. nov. It is not possible to compare this character in all species of Cylindropsyllidae, as either females are unknown (*C. govaerei*, *C. kunzi*, *C. ibericus*) or the female P6 is not described (e.g., Sars 1909; Huys 1988). A bare female P6 has been also described for *Bolbotelos longisetosus*, *Monsmeteoris reductus* sp. nov., and *Willemsia calceola*. These species belong to distinctive taxa, suggesting that this reduction took place convergently several times.

These five setal reductions (characters P–R) are also discernable in Leptopontiidae, but Leptopontiidae and Cylindropsyllidae can be clearly distinguished by apomorphies 1–6 (Table 4) for Cylindropsyllidae. Therefore, it is assumed these five setal reductions evolved convergently and are seen as apomorphies for *C. valentini* sp. nov.

In C. valentini sp. nov., an additional autapomorphy is the concave inner margin of the caudal ramus (character S), which is straight in all other species of Cylindropsyllus. A concave inner margin is also recorded for Evansula arenicola Nicholls, 1940 and E. spinosa Huys & Conroy-Dalton, 2006 (Huys and Conroy-Dalton 2006a). But both taxa can be clearly distinguished by the maxilliped (reduced in Cylindropsyllus, prehensile in Evansula) and the P1 enp1 (longer than exp1 in Cylindropsyllus, longer than whole exopod in Evansula). Following the principle of parsimony, a concave inner margin of the caudal ramus is most likely to have evolved convergently in C. valentini sp. nov. and the Evansula species mentioned above. Furthermore, the straight inner margin of the caudal ramus is suggested to be plesiomorphic since it is also recorded in Leptopontiidae, which can be separated from Cylindropsyllidae by the apomorphic characters listed in Table 4. Thus, the concave inner margin of the caudal ramus is considered to be an autapomorphy for *C. valentini* sp. nov.

These six apomorphies (characters P–S) clearly support the erection of *C. valentini* sp. nov. as a new species.

Cylindropsyllus flexibilis sp. nov. can be defined by three autapomorphies. Firstly, the inner apical seta of P4 exp3 is very flexible (character T, indicated by arrow in Fig. 23), a character state reported neither in Cylindropsyllidae nor in Leptopontiidae.

Cylindropsyllus flexibilis sp. nov. also exhibits an antennal endopod with an outermost seta that is distally very flexible (character U). Slightly flexible setae are present in all species of Cylindropsyllus (proximal half spine-like, with spinules, distal part slightly flexible with minute spinules; e.g., C. laevis, C. valentini sp. nov.). However, in Cylindropsyllus, this strongly pronounced flexibility is only recorded in C. flexibilis sp. nov. In Cylindropsyllidae, this kind of flexibility is only described in text for Selenopsyllus profundus: "Äußere Terminalborste des enp [A2] geißelartig, die übrigen gekniet. [Outermost apical seta of the endopod [of antenna] very flexible, remaining setae geniculated]" (Becker et al. 1979), but it is not discernable in the figure. Even though C. flexibilis sp. nov. and Selenopsyllus profundus both have this very flexible setae at the antennal endopod, they can clearly be distinguished by the maxilliped, which is reduced in C. flexibilis sp. nov. and prehensile in S. profundus.

It is most plausible that these flexible setae (characters T, U) evolved in *C. flexibilis* sp. nov. rather than them being simultaneously reduced in all other *Cylindropsyllus* species. Hence, they are defined as autapomorphies for *C. flexibilis* sp. nov.

Cylindropsyllus flexibilis sp. nov. can be also defined by stout and robust spines on the antennal endopod (character V), which is unique within Cylindropsyllidae and Leptopontiidae. This is therefore considered as autapomorphy for *C. flexibilis* sp. nov.

Autapomorphies T–V clearly support the erection of *C. flexibilis* sp. nov. as a new species.

Despite being distinct species, *C. valentini* sp. nov. and *C. flexibilis* sp. nov. share a number of synapomorphies, indicating a close relationship. For example, in both species the mandibular endopod is armed with at most two distal setae (character W), whereas all other species of Cylindropsyllidae bear more than two distal setae (e.g., *Cylindropsyllus laevis*: three setae; *Selenopsyllus dahmsi*: four setae). Additionally, the P4 enp2 inner seta is completely reduced (character X) in *C. valentini* sp. nov. and *C. flexibilis* sp. nov., but present in all other species of *Cylindropsyllus*. This setal loss is also present in species of *Stenocaropsis* (e.g., *S. pristina*), in *Boreovermis bilobatus* and in *Bolbotelos longisetosus*. Although these setae (characters W, X) are absent in the above mentioned species, these species also bear a prehensile maxilliped clearly differentiating them from C. valentini sp. nov. and C. flexibilis sp. nov. Therefore, the loss of the outer seta on the mandibular endopod and the loss of the inner seta of P4 enp2 are seen as synapomorphies for C. valentini sp. nov. and C. flexibilis sp. nov. Moreover, the hook-shape of the proximal styliform part of seta V of the caudal ramus is strongly pronounced (character Y) in C. valentini sp. nov. and C. flexibilis sp. nov., whereas it is only weakly present (e.g., Cylindropsyllus laevis, Evansula incerta) or absent (e.g., Boreopontia heipi) in other taxa of Cylindropsyllidae. The styliform proximal part of seta V is considered plesiomorphic due to its presence in basal taxa (Huys and Conroy-Dalton 2006a). However, its strongly pronounced appearance in C. valentini sp. nov. and C. flexibilis sp. nov. could indicate two different evolutionary lineages of seta V within Cylindropsyllidae: the secondary loss of this trait (Navalonia, Willemsia; Huys and Conroy-Dalton 1993) and the amplification of the hook-shaped structure. Nevertheless, as it is shaped in the same way in C. valentini sp. nov. and C. flexibilis sp. nov., it can be defined as a synapomorphy for these species and is a strong indicator of their close relationship.

Furthermore, a process is present on the female P3 enp2 in C. valentini sp. nov. and C. flexibilis sp. nov., possibly the transformation of the outer distal spine (Huys and Willems 1993), which is only also recorded in the two species of Cylinula. The differentiation between Cylindropsyllus and Cylinula is only based on two apomorphic characters of Cylinula (Table 4, nos. 8 and 9) as no autapomorphy of Cylindropsyllus is known up to date. Thus, the arrangement of these two taxa has to be conducted typologically. As a consequence of this unresolved relationship within Cylindropsyllus and Cylinula, and of the missing apomorphic characters of *Cylindropsyllus*, it is not possible to determine the apomorphic state of the process on the female P3 enp2. A future revision on Cylindropsyllus revealing unambiguous autapomorphies might identify the process on the female P3 enp2 as an synapomorphy only for C. valentini sp. nov., C. flexibilis sp. nov., or as a synapomorphy for C. valentini sp. nov., C. flexibilis sp. nov., and the species of Cylinula. Nevertheless, this character is one more strong indicator for the close relationship of C. valentini sp. nov. and C. flexibilis sp. nov.

Geographical distribution

Cylindropsyllidae occurred all over the plateau (Table 2), whereas *Cylindropsyllus valentini* sp. nov. was the most abundant species of Cylindropsyllidae on the plateau and occurred at every station. The species *Boreopontia heipi* and *Monsmeteoris reductus* sp. nov. were identified in every region, but were not identified at every station. However, this is likely to result from undersampling rather than their absence per se, since they are present across the plateau and where they are recorded they are in high abundance. Additionally, *Selenopsyllus dahmsi* and *M. wiesheuorum* sp. nov. occurred at single stations but across the plateau.

The distribution of these five species indicates that the geomorphology of the plateau does not affect their dispersal, as already suggested for Zosimeidae (Pointner 2017). Hence, the two pinnacles on the plateau seem not to act as barriers to dispersal. Additionally, the complex current system around the GMS seems not to zonate the community of Cylindropsyllidae, but possibly intermixes it. Strong currents could stir up specimens of Cylindropsyllidae and distribute them across the plateau, as already suggested for Zosimeidae (Pointner 2017). The elongated body shape of Cylindropsyllidae is typical of interstitial inhabitants of coarse sediments (Hicks and Coull 1983), and it is likely that when they re-enter the plateau sediment following dispersal they are able to inhabit this new area owing to the homogeneous biogenic carbonate sediment. Thus, the geographical features present at the GMS do not zonate the community of Cylindropsyllidae on the plateau, but support one heterogeneous assemblage.

The rare species, *Cylindropsyllus flexibilis* sp. nov., was only recorded at two stations in the southern region and seems to have a restricted distribution. This may indicate the presence of microhabitats on the plateau, but this will need to be confirmed by additional sampling at a smaller scale.

The two species identified on the plateau that were already known to science exhibit a wide distribution. *Boreopontia heipi* has been also recorded in the southern North Sea, the Kwinte Bank (Belgium; Willems 1981) and the Southern Bight (Belgium, Netherlands; 12.6–49.1 m; Huys and Conroy-Dalton 1993), and the Atlantic Ocean, Bay of Douarnenez (France; Bodin 1984). *Selenopsyllus dahmsi* has been recorded from the Antarctic Ocean (Weddell Sea, 2000 m; Moura and Pottek (1998)) and the southeast Atlantic Ocean (Angola Basin, 5389 m; George et al. 2014), and with the addition of the GMS plateau, is now known to be eurybathic, with a depth range from 5389 up to 287 m (GMS, station no. 9) below sea level.

The presence of the two known species on the plateau indicates that species reach this seamount by chance (via accidentally drifting in the water column or through the deep sea needs to be further investigated), as already suggested at the GMS for Harpacticoida in general (George and Schminke 2002) and for Zosimeidae (Pointner 2017) and Argestidae (George 2004) in particular. The GMS may, therefore, play an important role in species distribution and act as a "stepping stone," as it provides a suitable shallow-water habitat within the deep sea for harpacticoid species. In contrast, the four newly described species have several autapomorphies (Table 5, nos. W–Z). Additionally, *C. valentini* sp. nov. and *C. flexibilis* sp. nov. seem to be very closely related, and the presence of a new genus within the Cylindropsyllidae, which bears reduced features as well as very basal characters, might

point to radiation on the plateau, as already suggested for Argestidae (George 2004), Paramesochridae (Plum and George 2009), and Zosimeidae (Pointner 2017). The presence of these four species, therefore, might support a possible isolated ("trapping stone") character of the GMS for at least part of the Harpacticoida (George 2004; Plum and George 2009; Pointner 2015, 2017) compared with other seamounts and islands, which seem to act as stepping stone or even as "staging post" at least for Paramesochridae (Packmor et al. 2015) and Normanellidae (Packmor and Riedl 2016).

The presence of *B. heipi* and *S. dahmsi* indicating a possible stepping stone role of GMS, combined with the characteristics of the newly described species indicating the trapping stone potential of GMS, highlight the urgent need for continued investigation on more seamounts, islands and their surrounding deep sea in order to elucidate the role of these elevations in the oceanic distribution of Harpacticoida.

Acknowledgments The author is grateful to Dr. Kai Horst George (Senckenberg am Meer, DZMB, Wilhelmshaven) for the helpful discussions and comments on the manuscript. Additionally, the author acknowledges and thanks the support in centrifuging and sorting samples from the technical staff of the DZMB, Marco Bruhn, Annika Hellmann, Stefan Gogulla and Rebekka Schüller. The author is also grateful for the correction of the English text by Dr. Natalie Barnes (Hampshire, UK). Additionally, she thanks the three anonymous reviewers for their constructive remarks on the manuscript.

Funding This research was funded by the Deutsche Forschungsgemeinschaft (DFG-GZ: GE 1086/15-1).

Compliance with ethical standards

Conflict of interest The author declares that she has no conflict of interest.

Ethical approval All applicable international, national and institutional guidelines for the care and use of animals were followed by the author.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the author from the competent authorities and are mentioned in the acknowledgements, if applicable.

Data availability All data generated or analyzed during this study are included in this published article.

References

- Apostolov A (1982) Genres et sous-genres nouveaux de la famille Diosaccidae Sars et Cylindropsyllidae Sars, Lang (Copepoda, Harpacticoida). Acta zool bulg 19:37–42
- Becker KH, Noodt W, Schriever G (1979) Eidonomie und Taxonomie abyssaler Harpacticoidea (Crustacea, Copepoda). Teil II. Paramesochridae, Cylindropsyllidae und Cletodidae. Meteor Forsch-Ergebn D 31:1–37

- Beckmann A, Mohn C (2002) The upper ocean circulation at great meteor seamount, part II: retention potential of the seamount-induced circulation. Ocean Dynam 52:194–204. https://doi.org/10.1007/ s10236-002-0018-3
- Bodin P (1984) Densité de la meiofauna et peuplements de copépodes harpacticoïdes en Baie de Douarnenez (Finistère). Ann Inst Océanogr 60:5–17
- Brady GS (1880) A monograph of the free and semi-parasitic Copepoda of the British Islands, vol II. Ray Society, London
- Brünnich MT (1772) Zoologiae fundamenta praelectionibus academicis accomodata. Grunde i Dyrelaeren, Hafniae et Lipsidae
- Cottarelli V, Venanzetti F (1989) Richerche zoologiche della nave oceanografica 'Minerva' (C.N.R.) sulle isola circumsarde. II. Cylindropsyllidae del meiobenthos de Montecristo e della isola circumsarde (Crustacea, Copepoda, Harpacticoida). Ann Mus Civic Storia Nat Giacomo Doria 87:183–235
- Coull BC (1971) Meiobenthic Harpacticoida (Crustacea, Copepoda) from the North Carolina continental shelf. Cah Biol Mar 12:195–237
- Dahms HU (1989) Antennule development during copepodite phase of same representatives of Harpacticoida (Copepoda, Crustacea). Bijdr Dierk 59:159–189a
- Dahms HU, Dieckmann (1987) Drescheriella glacilis gen. nov., sp. nov. (Copepoda, Harpacticoida) from Antarctic sea ice. Pol Biol 7:329–337
- Fischer L (2005) Der Einfluss der Großen Meteorbank auf die Ernährungsbiologie und Verteilung dominanter Calanoida (Crustacea, Copepoda). Ber zur Polarforsch Meeresforsch 499:1– 202
- Gad G (2009) Colonization and speciation on seamounts, evidence from Draconematidae (Nematoda) of the Great Meteor Seamount. Mar Biodivers 39:57–69
- George KH (2004) Description of two new species of *Bodinia*, a new genus incertae sedis in Argestidae Por, 1986 (Copepoda, Harpacticoida), with reflections on argestid colonization of the Great Meteor Seamount plateau. Organ Div Evol 4:241–264
- George KH (2010) POS397 Abschlussbericht. Deutsches Zentrum für Marine Biodiversitätsforschung, Senckenberg am Meer, Wilhelmshaven
- George KH (2013) Faunistic research on metazoan meiofauna from seamounts—a review. Meiofauna Marina 20:1–32
- George KH (2017) Phylogeny of the taxon Paralaophontodes Lang (Copepoda, Harpacticoida, Laophontodinae), including species descriptions, chorological remarks, and a key to species. Zoosystematics Evol 93:211–241
- George KH, Schminke HK (2002) Harpacticoida (Crustacea, Copepoda) of the Great Meteor Seamount with first conclusions as to the origin of the plateau fauna. Mar Biol 144:887–895
- George KH, Veit-Köhler G, Martínez Arbizu P, Seifried S, Rose A, Willen E, Bröhldick K, Corgosinho PH, Drewes J, Menzel L, Moura G, Schminke KH (2014) Community structure and species diversity of Harpacticoida (Crustacea: Copepoda) at two sites in the deep sea of the Angola Basin (Southeast Atlantic). Organ Div Evol 14:57–73
- Gerlach SA (1977) Means of meiofauna dispersal. Mikrofauna Meeresboden 61:89–103
- Giere O (2009) Meiobenthology: the microscopic motile fauna of aquatic sediments, 2nd edn. Springer-Verlag, Berlin
- Goodsir HDS (1845) On several new species of crustaceans allied to Saphirina. Ann Mag Nat Hist 16:325–327
- Hesemann F (2013) Genese der bioklastischen Sedimente der Großen Meteorbank (Atlantik). Bachelor thesis, University of Bremen, Bremen
- Hicks GRF, Coull BC (1983) The ecology of marine meiobenthic harpacticoid copepod. Oceanogr Mar Biol Annu Rev 21:67–175
- Higgins RP, Thiel H (1988) Introduction to the study of meiofauna. Smithsonian Institution Press, Washington

- Hinz K (1969) The Great Meteor Seamount. Results of seismic reflection measurements with a pneumatic sound source, and their geological interpretation. Meteor Forsch-Ergebn C 2:63–77
- Huys R (1988) Studies on the Cylindropsyllidae (Copepoda, Harpacticoida). 2. A revision of the genus *Cylindropsyllus* Brady. Zool Scr 17:253–276
- Huys R, Boxshall GA (1991) Copepod evolution. The Ray Society, London
- Huys R, Conroy-Dalton S (1993) *Willemsia* gen. nov. and *Boreopontia* Willems, 1981 revisited (Harpacticoida: Cylindropsyllidae). Sarsia 78:237–300
- Huys R, Conroy-Dalton S (2006a) Revision of the genus *Evansula* T. Scott, 1906 (Copepoda, Harpacticoida, Cylindropsyllidae) with a description of three new species. Zool J Linnean Soc 147:419–472
- Huys R, Conroy-Dalton S (2006b) Comparative analysis of vermiform genera (Copepoda: Harpacticoida: Cylindropsyllidae), including descriptions of *Boreovermis*, new genus and *Bolbotelos*, new genus, from the southern North Sea. J Crust Biol 26:206–223
- Huys R, Willems KA (1993) A revision of *Cylinula* and two new species of *Cylindropsyllus* (Copepoda, Harpacticoida, Cylindropsyllidae). Zool Scr 22:347–362
- Huys R, Gee JM, Moore CG, Hamond R (1996) Synopses of the British Fauna (new series) no. 51: marine and brackish water harpacticoid copepods, part 1. Field Studies Council, Shrewsbury
- Kornev PN, Chertoprud EC (2008) Copepod crustaceans of the order Harpacticoida of the White Sea. Morphology, systematics, ecology. Biology faculty, Moscow State University. Tovarishchestvo Nauchmikh Izdanii, KMK, Moscow
- Krishnaswamy S (1956) Sewellina reducta gen. et sp. nov., a new sanddwelling copepod from Madras. Zool Anz 157:248–250
- Kunz H (1949) Die sandbewohnenden Copepoden von Helgoland, II Teil. Kiel Meeresforsch 6:51–58
- Lang K (1944) Monographie der Harpacticiden (Vorlaufige Mitteilung). Almqvist & Wiksells Boktryckeri Ab, Uppsala
- Lang K (1948) Monographie der Harpacticiden. Håkan Ohlsson, Lund
- Martínez Arbizu P, Moura G (1994) The phylogenetic position of the Cylindropsyllinae Sars (Copepoda, Harpacticoida) and the systematic status of the Leptopontiinae Lang. Zool Beitr 35:55–77
- Menzel L, George KH, Martínez Arbizu P (2011) Submarine ridges do not prevent large-scale dispersal of abyssal fauna: a case study of *Mesocletodes* (Crustacea, Copepoda, Harpacticoida). Deep Sea Res I 58:839–864
- Milne Edwards H (1840) Histoire naturelle des Crustaces, comprenant l'anatomie, la physiologie et la classification de ces animaux. Librairie encyclopédique de Roret, Paris
- Mohn C, Beckmann A (2002) The upper ocean circulation at great meteor seamount, part I: structure of density and flow fields. Ocean Dyn 52: 179–193
- Moura G, Pottek M (1998) *Selenopsyllus*, a new genus of Cylindropsyllinae (Copepoda, Harpacticoida) from Atlantic and Antarctic deep waters. Senckenberg Marit 28:185–209
- Mouriño B, Fernández E, Serret P, Harbour D, Sinha B, Pingree R (2001) Variability and seasonality of physical and biological fields at the Great Meteor Tablemount (subtropical NE Atlantic). Oceanol Acta 24:1–20
- Nicholls AG (1940). Marine harpacticoids and cyclopoids from the shores of the St. Lawrence (Vol. 2). Université Laval
- Packmor J, George KH (2018) Littoral harpacticoida (Crustacea: Copepoda) of Madeira and Porto Santo (Portugal). J Mar Biol Assoc UK 98(1):171–182

- Packmor J, Riedl T (2016) Records of Normanellidae Lang, 1944 (Copepoda, Harpacticoida) from Madeira island support the hypothetical role of seamounts and oceanic islands as "stepping stones" in the dispersal of marine meiofauna. Mar Biodivers 46:861–877
- Packmor J, Müller F, George KH (2015) Oceanic islands and seamounts as staging posts for Copepoda Harpacticoida (Crustacea)—shallowwater Paramesochridae Lang, 1944 from the North-East Atlantic Ocean, including the (re-) description of three species and one subspecies from the Madeiran archipelago. Prog Oceanogr 131:59–81
- Plum C, George KH (2009) The paramesochrid fauna of the Great Meteor Seamount (Northeast Atlantic) including the description of a new species of *Scottopsyllus* (*Intermedopsyllus*) Kunz (Copepoda: Harpacticoida: Paramesochridae). Mar Biodivers 39:265–289
- Pointner K (2015) Description of a new species of *Microcanuella* Mielke, 1994 (Copepoda: Polyarthra: Canuellidae) from the Great Meteor Seamount plateau (subtropical NE Atlantic Ocean), with remarks on the geographical distribution of the genus. Zool Anz 259:97–112
- Pointner K (2017) Description of two new species of *Zosime* (Copepoda: Harpacticoida: Zosimeidae), including remarks on its phylogeny and distribution on the Great Meteor Seamount plateau (NORTH-EAST Atlantic Ocean). J Nat Hist 51:2283–2330
- Pointner K, Kihara TC, Glatzel T, Veit-Köhler G (2013) Two new closely related deep-sea species of Paramesochridae (Copepoda, Harpacticoida) with extremely differing geographical range sizes. Mar Biodivers 43:293–319
- Sars GO (1903) An account of the Crustacea of Norway: volume V Copepoda Harpacticoida, parts 1–2. Bergen Museum, Bergen
- Sars GO (1909) Copepoda Harpacticoida. Parts XXVII & XXVIII. Cletodidae (concluded), Anchorabolidae, Cylindropsyllidae, Tachidiidae (part). An account of the Crustacea of Norway, with short descriptions and figures of all the species. Bergen Museum, Bergen
- Scott T (1892) Additions to the fauna of the Firth of Forth. Part IV. Rep Fish Board Scotl, Edinb 10:244–272
- Scott T (1906) A catalogue of the land, fresh-water and marine Crustacea found in the basin of the River Forth and its estuary. Copepoda. Proc Roy Phys Soc Edinb 16:296–375
- Seifried S (2003) Phylogeny of Harpacticoida (Copepoda): revision of 'Maxillipedasphalea' and Exanechentera. Cuvillier Verlag, Göttingen
- Sewell RBS (1949) The littoral and semi-parasitic Cyclopoida, the Monstrilloida and Notodelphyoida. Scient Rep John Murray Exped 9:17–199
- Ulrich J (1971) Zur Topographie und Morphologie der Großen Meteorbank. Meteor Forsch-Ergebn C 6:48–68
- van Haren H (2005) Details of stratification in a sloping bottom boundary layer of Great Meteor Seamount. Geophys Res Lett 32:L07606
- Wells JBJ (1968) New and rare Copepoda Harpacticoida from the Isles of Scilly. J Nat Hist 2:397–424
- Wells JBJ (2007) An annotated checklist and keys to the species of Copepoda Harpacticoida (Crustacea). Zootaxa 1568:1–872
- Willems KA (1981) *Boreopontia heipi* ng., n.sp. An insterstital harpacticoid (Copepoda) from the Southern Bight of the North Sea. Biol Jaarb Dodonaea 49:200–209
- Yeatman HC (1962) The problem of dispersal of marine littoral copepods in the Atlantic Ocean, including some redescriptions of species. Crustaceana 4:253–272

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.