Meiofauna Marina, Vol. 20, pp. 1–32, 6 figs., 4 tabs., February 2013

Faunistic research on metazoan meiofauna from seamounts – a review

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Abstract

Few biological studies at seamounts have focused on meiofauna in comparison to the relatively many studies dealing with plankton, fish, and benthic mega- and macrofauna. World-wide, just eight seamounts have been the object of meiobenthic investigation. The first taxonomic and biogeographic studies of the meiobenthos were conducted on the Great Meteor Seamount (northeast Atlantic) in the 1970's. A decade later, the focus turned towards ecology and switched to north-eastern Pacific seamounts. More recently, there has been a renewed interest in taxonomic as well as chorological, biogeographic, and other faunistic topics, particularly on the Atlantic seamounts. To date, 357 meiobenthic species from 26 major taxa have been reported from the eight seamounts studied, but only 48 species have been described so far. The Copepoda Harpacticoida are most frequently recorded ($S = 215$), followed by Tardigrada ($S = 35$), and Nematoda ($S = 32$). The majority of collected species (92.2 %) have not been reported from elsewhere, indicating a remarkable potential for endemism. The present contribution reviews the scientific research on seamount meiofauna over the past >40 years, including remarks on fundamental questions such as the potential role of seamounts as stepping stones/staging posts or "trapping stones" for meiofaunal species.

Key words: deep sea, biogeography, stepping stones, staging posts, meiobenthos, dispersal

Introduction

"There are no such things as mountains and valleys on the deep-sea bottom."
H. N. Moseley (1880, p. 543)

In contrast to Moseley's (1880) statement that there is a complete absence of submerged mountains on the deep-sea bottom, we now know that the world's oceans exhibit numerous undersea elevations of mostly volcanic origin. Following the classic geological definition, the term "seamount" is given to those elevations reaching at least 1000 m in height from the seabed, whilst elevations between 500 and 1000 m are classified as "knolls", and those not reaching 500 m as "hills" (Kitchingman et al. 2007, Yesson et al. 2011). Pitcher et al. (2007) estimated a global total of 10 000–100 000 seamounts: Kitchingman et al. (2007) listed 14 000 named seamounts and Yesson et al. (2011) identified 33 452 in total.

However, as noted by Wessel (2007, p. 3), there is no geological reason "to separate smaller seamounts from their taller counterparts using an

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arbitrary cut-off height". More recent estimates of seamount numbers are therefore considerably higher, varying from 200 000 (Schlacher et al. 2010a) to 1 000 000 (Pitcher et al. 2007) when considering elevations greater than 100 m (itself an "arbitrary cut-off height", Pitcher et al. 2007). According to Yesson et al. (2011), the comparatively high number of elevations between 500 and 1000 m in height (138 412 identified) points to an importance which may equal that of the higher seamounts, which have so far been the main object for biological studies.

Hubbs (1959) was the first to ask (among other questions) whether seamounts play an important role in (a) the dispersal of marine organisms; (b) speciation due to isolation, and; (c) the formation of relict faunas due to sinking or flooding processes during a seamount's "life". In the subsequent decades, an increasing number of papers focused on distinct ecological objectives (for reviews see Wilson & Kaufmann 1987, Rogers 1994, Mironov et al. 2006, Clark et al. 2010), leading to several more or less sophisticated hypotheses all aimed at developing a general theory of seamounts biology and ecology. These generalized paradigms have been recently re-evaluated by Rowden et al. (2010). Attempts to develop general theories regarding seamount biology and ecology have been criticised, however, for being based on too few data: McClain (2007, p. 5) notes that "an expansion of predominantly megafaunal (e. g. corals and fish) focus, to include more work on macro- and meiofauna" is needed.

A revision of the literature on seamount ecology finds that most concentrate on fish, plankton, or single sessile megabenthic taxa, and that these were chosen owing to their status as indicators in biological productivity, ecology, biogeography, fisheries, and conservation studies (cf. Hubbs 1959, Pitcher et al. 2007, Schlacher et al. 2010b). Numerous papers have been dedicated to specific questions and/or taxonomic groups. These were followed by several compilations and revisions (e. g. Boehlert & Genin 1987, Wilson & Kaufmann 1987, Rogers 1994, Richer de Forges et al. 2000), which summarized results and hypotheses, and lead, finally, to special issues, volumes and books that updated the seamount literature and collated generalized assumptions and hypotheses (e. g. Mironov et al. 2006, Pitcher et al. 2007, Christiansen & Wolff 2009, Schlacher et al. 2010b). In reviewing this literature, particularly the compilations and special editions, one may note that research on metazoan meiofauna is rarely included (see in Boehlert & Genin 1987, Wilson & Kaufmann 1987, Mironov & Krylova 2006) and is not used to inform the development of generalized "seamount paradigms" (Pitcher et al. 2007, Rowden et al. 2010, Schlacher et al. 2010a). Nonetheless, protozoan meiofauna (e. g. Heinz et al. [2004] for Foraminifera; Levin et al. [1986] and Levin [1991] for Xenophyophorea) and metazoan meiofauna have been investigated: It is the object of this present contribution to review these meiobenthic studies on seamounts and develop some initial conclusions.

Abbreviations used in the text are: FaB, Faroe Bank; FieG, Fieberling Guyot; GMS, Great Meteor Seamount; HorG, Horizon Guyot; JoB, Josephine Bank; MagR, Magellan Rise; *S*, number of species; SedS, Sedlo Seamount; SeiS, Seine Seamount.

Results and discussion

Meiofauna studies on seamounts. According to Samadi et al. (2007), 232 seamounts have been biologically sampled world-wide, but only 8 have been studied for the meiobenthos (Fig. 1: triangles)[1]. Thus compared with a large number of seamount-related studies on fish, plankton, and megabenthos, only 45 publications[2] have been dedicated to meiofauna since 1971. The earliest qualitative studies on seamount meiofauna were made in the late 1960's and early 1970's (Hempel 1968; Thiel 1970, 1972; Hempel & Nellen 1972). These focused on the Great Meteor Seamount (GMS) and Josephine Bank (JoB), and resulted in four taxonomic papers regarding distinct meiobenthic taxa (Emschermann 1971; Bartsch 1973a,b,c).

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[1] Levin & Thomas (1988) sampled/photographed 17 additional deep eastern Pacific seamounts, studying the ecology of xenophyophores. Although they observed (among others) meiobenthic Nematoda, Harpacticoida, and Ostracoda, no species list has been provided. Therefore, that publication is not considered here.

[2] Parker & Tunnicliffe (1994, p. 338; Table 1) mention "several species of nematodes" and a "harpacticoid copepod" from Cobb Seamount (NE Pacific), but without providing any detailed information. Therefore, that paper is not considered here.

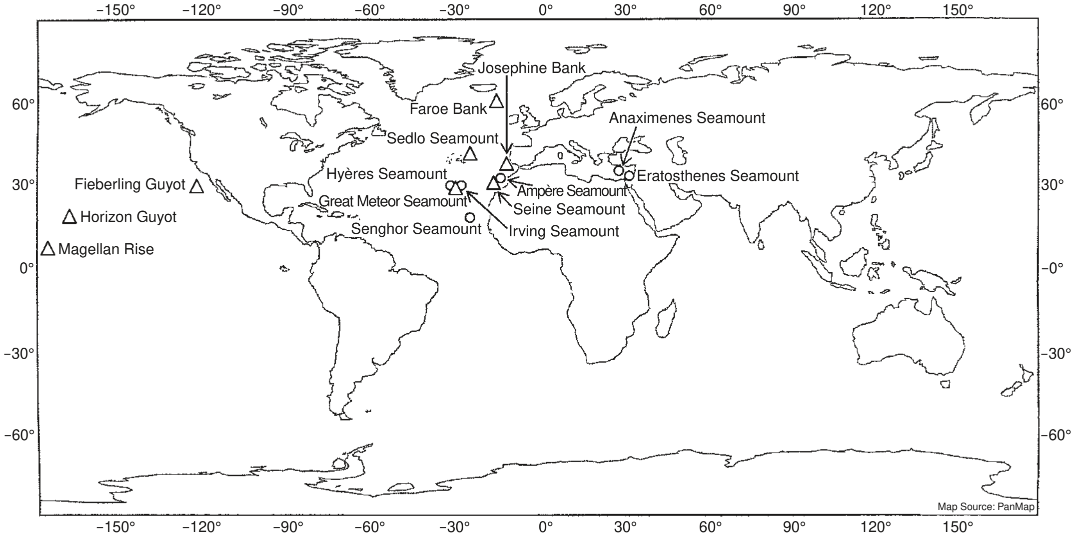


Fig. 1. The location of seamounts from which meiofauna have been studied (△) or sampled and currently under analysis (○).

Between 1974 and 1986 no seamount-related meiobenthic research was published. It was resumed by Levin et al. (1986), with the focus turned from taxonomic descriptions and inventorying of the seamount meiobenthos toward ecological questions. The relationships between large protozoans (Xenophyophorea) and macro- and metazoan meiofauna, and the possible role of the former as habitats for the latter (Levin et al. 1986, Levin & Thomas 1988, Levin 1991) was of particular interest, and it was found that some meiobenthic groups, namely Nematoda, Harpacticoida, and Ostracoda live as epibionts on Xenophyophorea (Levin & Thomas 1988; Levin 1991). Also of increasing interest was the effect and influence of near-bottom flow on seamount meiofauna; the main research locations were the Horizon Guyot, HorG and the Magellan Rise, MagR, (Levin & Thomas 1989), and Fieberling Guyot, FieG, (Thistle 1998, Thistle & Levin 1998, Thistle et al. 1999). It was not until the beginning of the 21st century that faunistic studies regarding seamount meiofauna, including taxa registration, taxonomical, chorological, biogeographic, and community analyses were purposefully resumed. Between 1974 and 2000 only two taxonomic papers were published, one describing a halacarid species from GMS (Bartsch 1991), and the other a new Tantulocarida from the Faroe Bank (FaB) (Huys et al. 1992). Meiofaunal community studies on seamount summits increased remarkably from 2001, resulting in a concomitant increased number of publications. Most papers focused on inventorying certain seamount meiofauna assemblages and the taxonomic description of collected species. These new data have finally allowed more informed discussion regarding the origin and colonization of seamount summits by meiobenthic taxa as first addressed by Thiel (1970) and Emschermann (1971).

Occurrence of meiofauna on seamounts. As meiofaunal sampling on seamounts is somewhat challenging owing to their bottom structure (even or uneven, slope gradient) and sediment type (hard and/or rocky, sandy or muddy), quantitative samples are rarely obtained: Often standard deep-sea sampling devices must be orientated and applied to the seamount surface intuitively based on the given conditions at the sampling site. Thus, faunistic studies of seamount meiofauna are rather qualitative and may include many different sampling devices (e. g. Multicorer, Box corer, Epibenthic sledges), inhibiting direct comparison of sampled materials (George & Schminke 2002).

Consequently, sophisticated analyses of meiobenthic productivity, application of statistical tests, or direct comparison of absolute abundances and densities are rarely possible. Instead, faunistic investigations of seamount meiofauna focus on qualitative comparisons and explorative statistics like similarity and diversity analyses within and between seamounts and adjacent areas (e. g. Hansen et al. 2001, George & Schminke 2002, Büntzow 2011). Qualitative data has been further used to address the origins of seamount summit meiobenthos (e. g. Emschermann 1971, Gad 2004a, Gad & Schminke 2004, George 2004a, Gad 2009, Plum & George 2009) and to assess geographic and/or bathymetric exchange of the summit fauna (cf. George & Schminke 2002, Bartsch 2003, Gad 2004b, George 2004a, Heiner & Kristensen 2005, Plum & George 2009, Büntzow 2011, Koller & George 2011). Efforts to elucidate these questions continue to increase and the inclusion of new material will be essential (Fig. 1, circles).

Twenty-six major meiobenthic taxa have been reported from the eight investigated seamounts (Table 1, Fig. 1). Despite sampling difficulties and the resulting difficulties of analyses, some conclusions can be made. Firstly, however, it should be noted that the scientific intentions of studies at the different seamounts varied. The fact that 25 of the 26 major meiofaunal taxa have been reported from GMS but only one from JoB does not reflect actual occurrence, but results from the scientific aims of each study. As mentioned above, the Pacific seamounts MagR, HorG, and FieG (Fig. 1) were subject to distinct ecological investigations (Levin & Thomas 1989, Thistle 1998, Thistle & Levin 1998, Thistle et al. 1999), for which the dominant Harpacticoida, Kinorhyncha, Loricifera, Nematoda, and Ostracoda provided the most relevant information, data on the remaining meiobenthic taxa either neglected or not published. Data limitations are greatest at JoB, where only the Halacarida were stud-

Tab. 1. List of the major meiobenthic taxa reported from the eight seamounts studied to date (cf. Fig. 1). See text for abbreviations.

No.	Major taxon	MagR	HorG	FieG	GMS	SedS	SeiS	JoB	FaB	Number of seamounts
1	Amphipoda*				+	+	+			3
2	Bivalvia				+	+	+			3
3	Bryozoa				+					1
4	Cnidaria				+		+		+	3
5	Cumacea				+					1
6	Entoprocta*				+					1
7	Gastropoda				+					1
8	Gastrotricha*				+	+	+		+	4
9	Halacarida*				+	+	+	+		4
10	Harpacticoida*	+	+	+	+	+	+			6
11	Isopoda				+	+	+			3
12	Kinorhyncha	+	+	+	+	+	+		+	7
13	Leptostraca				+					1
14	Loricifera	+			+	+	+		+	5
15	Nematoda	+	+	+	+	+	+		+	7
16	Oligochaeta				+					1
17	Ostracoda	+	+	+	+	+	+		+	6
18	Pantopoda				+	+				2
19	Polychaeta				+				+	2
20	Rotatoria				+		+		+	3
21	Sipuncula				+					1
22	Solenogastres					+				1
23	Tanaidacea				+	+	+			3
24	Tantulocarida				+		+		+	3
25	Tardigrada				+	+	+		+	4
26	Turbellaria				+				+	2
	Number of taxa	5	4	4	25	14	15	1	10	

* taxa which have been studied in more detail for both taxonomic and faunistic aspects.

ied taxonomically and chorologically (Bartsch 1973a,b,c). In contrast, investigations at the four Atlantic seamounts GMS, SedS, SeiS, and FaB (Fig. 1) included a taxonomical inventory from the beginning, including the description of new species, and other faunistic aspects. Meiobenthic material was sorted carefully and extensively, taking into account as many organisms as possible to maximise data for further research (George & Schminke 2002, Kristensen 2005, Büntzow 2011).

Kinorhyncha and Nematoda have been documented from seven of the eight studied seamounts, followed by Harpacticoida and Ostracoda (each recorded on six seamounts, Table 1). The low number of "worm-like" organisms recorded such as Oligochaeta, Sipuncula and Solenogastres across the studies may not necessarily reflect true distribution patterns but result from scientific objectives or possibly poor sample sorting, perhaps combined with damage to specimens hindering identification. Also, the small Entoprocta and Bryozoa were only documented at GMS, further implying that precise and careful examination of material occurred for this site only.

The meiobenthic Cumacea, Gastropoda, and Leptostraca, were apparently absence from almost all seamounts studied for meiofauna (except GMS), and since these taxa are represented by comparatively large organisms it seems unlikely they were overlooked. In the author's opinion their absence from published data simply indicates that they were neglected because they were not of scientific interest. One might suppose therefore that the composition of summit meiofauna, at major taxa level (as listed in Table 1) may be very similar across all seamounts. To avoid a biased dataset, future treatment of meiobenthic samples should include at least the recording of all major meiofaunal taxa to produce a semi-quantitative dataset for future potential analysis.

From the eight seamounts studied to date, 357 meiobenthic species have been reported (Table 2). Although most of them are listed as only "working species" by the respective authors, that species number may express the actual one. However, each major taxon has been studied by several or even solitary specialists (Tables 3 and 4), who predominantly worked on material from single seamounts. Only the Amphipoda, Halacarida, and Harpacticoida have been compared between seamounts. For instance, both George & Schminke (2002) and Büntzow (2011) listed "*Eurycletodes* sp. 2", "*Mesocletodes* sp. 2", and "*Mesocletodes* sp. 7"; but George & Schminke's (2002) material was examined by Büntzow (2011) who confirmed that the corresponding species where in fact different (Table 4). For this current review, only the Harpacticoida 'species' data collected from Fieberling Guyot (Thistle & Levin 1998), and kindly

Tab. 2. List of the nine meiobenthic major taxa which were subject to detailed taxonomic and/or faunistic investigation and the seamounts on which they were recorded. The additional columns list the following (from left to right): *S* = number of species reported per major taxon; *S* (known) = species that were scientifically known before; % (taxon) = percentage of previously known species in relation to *S*; % (total) = percentage of known species in relation to all 357 known meiobenthic seamount species; *S* (described) = number of species described from seamounts; % (taxon) = percentage of described seamount species in relation to *S*; % (described spp.) = percentage of described species in relation to all so far described seamount meiofauna; % (total) = percentage of described species in relation to all 357 known meiobenthic seamount species.

Taxon	Seamount	S	S (known)	% (taxon)	% (total)	S (described)	% (taxon)	% (described S)	% (total)
Harpacticoida	GMS, SeiS, SedS	215	4	1.9	1.1	9	4.2	19.1	2.5
Tardigrada	FaB	35	10	28.6	2.8	1	2.9	2.1	0.3
Nematoda	GMS	32	0	0.0	0.0	1	3.1	2.1	0.3
Halacarida	GMS, JoB	28	4	14.3	1.1	21	75.0	44.7	5.9
Loricifera	GMS, FaB	23	0	0.0	0.0	5	21.7	10.6	1.4
Gastrotricha	FaB	20	10	50.0	2.8	6	30.0	12.8	1.7
Amphipoda	GMS, SeiS	2	0	0.0	0.0	2	100.0	4.3	0.6
Entoprocta	GMS	1	0	0.0	0.0	1	100.0	2.1	0.3
Tantulocarida	FaB	1	0	0.0	0.0	1	100.0	2.1	0.3
	Total	357	28		7.8	47		100.0	13.2

Tab. 3. List of species currently known from seamounts. Species sorted by major taxa, except Harpacticoida which are distinguished from the other Copepoda. The seamounts on which they were recorded are indicated, with the citation for each record. Grey fields in the "taxa" column highlight species that were known from other habitats, whilst grey fields in the "seamount" columns highlight species recorded at multiple seamounts.

S cum.	*S*/ taxon	Taxa	GMS	SeiS	JoB	FaB	References
	I.	**Amphipoda**					
1	1	*Ingolfiella georgei* Andres, 2005*		+			Andres (2005)
2	2	*Ingolfiella sandroruffoi* Andres, 2004*	+				Andres (2004)
	II.	**Entoprocta**					
3	1	*Loxomespilon* cf. *perezi* var. *meteoris* Emschermann, 1971*	+				Emschermann (1971)
	III.	**Gastrotricha**					
4	1	*Dactylopodola cornuta* Swedmark, 1956				+	Clausen (2004)
5	2	*Dactylopodola typhle* Remane, 1927				+	Clausen (2004)
6	3	*Diplodasys ankeli* Wilke, 1954				+	Clausen (2004)
7	4	*Halichaetonotus* cf. *aculifer* Gerlach, 1953				+	Clausen (2004)
8	5	*Halichaetonotus* sp. 1				+	Clausen (2004)
9	6	*Lepidodasys arcolepis* Clausen, 2004*				+	Clausen (2004)
10	7	*Lepidodasys castoroides* Clausen, 2004*				+	Clausen (2004)
11	8	*Lepidodasys* cf. *martini* Remane, 1926				+	Clausen (2004)
12	9	*Platydasys mastigurus* Clausen, 1965				+	Clausen (2004)
13	10	*Platydasys maximus* Remane, 1926				+	Clausen (2004)
14	11	*Platydasys ocellatus* Clausen, 1965				+	Clausen (2004)
15	12	*Platydasys* sp. 1				+	Clausen (2004)
16	13	*Platydasys* sp. 2				+	Clausen (2004)
17	14	*Pseudostomella faroensis* Clausen, 2004*				+	Clausen (2004)
18	15	*Ptychostomella brachycephala* (Lévi, 1954)				+	Clausen (2004)
19	16	*Ptychostomella higginsi* Clausen, 2004*				+	Clausen (2004)
20	17	*Tetranchyroderma faroense* Clausen, 2004*				+	Clausen (2004)
21	18	*Thaumastoderma moebjergi* Clausen, 2004*				+	Clausen (2004)
22	19	*Thaumastoderma* cf. *renaudae* Kisielewski, 1987				+	Clausen (2004)
23	20	*Xenodasys sanctigoulveni* Swedmark, 1967				+	Clausen (2004)
	IV.	**Halacarida**					
24	1	*Acanthohalacarus reticulatus* Bartsch, 2001*	+				Bartsch (2001a)
25	2	*Acaromantis squilla* Trouessart & Neumann, 1893	+				Bartsch (1973b)
26	3	*Agauopsis tricuspidata* Bartsch, 2002*	+				Bartsch (2002b)
27	4	*Agauopsis valida* Bartsch, 2001*	+				Bartsch (2001b)
28	5	*Arhodeoporus brevocularis* Bartsch, 1973*			+		Bartsch (1973b)
29	6	*Arhodeoporus lineatus* Bartsch, 1973*	+				Bartsch (1973b)
30	7	*Atelopsalis meteorensis* Bartsch, 2002*	+				Bartsch (2002b)
31	8	*Atelopsalis newelli* Bartsch, 1973*			+		Bartsch (1973b)
32	9	*Atelopsalis tricuspis* Trouessart, 1896			+		Bartsch (1973b)
33	10	*Bradyagaue meteoris* (Bartsch, 1973)*	+				Bartsch (1973a,1991)
34	11	*Coloboceras karamani* Bartsch, 1973*	+				Bartsch, 1973b)
35	12	*Copidognathus leiodermus* Bartsch, 2004*	+				Bartsch (2004a)
36	13	*Copidognathus leptus* Bartsch, 2002*	+				Bartsch (2002a)
37	14	*Copidognathus longipes* Bartsch, 1973*	+		+		Bartsch (1973a,b, 2003)
38	15	*Copidognathus magniporus* Bartsch, 1973*	+				Bartsch (1973b)
39	16	*Copidognathus procerus* Bartsch, 2002*	+				Bartsch (2002a)
40	17	*Copidognathus raekor* Bartsch, 1973*	+				Bartsch (1973c)
41	18	*Copidognathus tricorneata* (Lohmann, 1938)	+		+		Bartsch (1973a,b)

Tab. 3. (continued)

S cum.	*S*/ taxon	Taxa	GMS	SeiS	JoB	FaB	References
42	19	*Halacarus leptopus* Bartsch, 2002*	+				Bartsch (1973a, 2002b)
43	20	*Halacarus spiniger* Bartsch, 1973*	+				Bartsch (1973b, 2002b)
44	21	*Lohmannella falcata* (Hodge, 1863)	+		+		Bartsch (1973a,b)
45	22	*Lohmannella subfalcata* Bartsch, 2003*	+				Bartsch (2003)
46	23	*Scaptognathus meteorensis* Bartsch, 2003*	+				Bartsch (2003)
47	24	*Scaptognathus minutus* Bartsch, 1973*	+		+		Bartsch (1973b)
48	25	*Scaptognathides* sp.	+				Bartsch (2003)
49	26	*Scaptognathus* sp. A (larva)	+				Bartsch (1973b)
50	27	*Scaptognathus* sp. B (larva)	+				Bartsch (1973b)
51	28	*Simognathus serratus* Bartsch, 2004*	+				Bartsch (2004b)
	V.	**Harpacticoida** (216 reported [working] species): cf. Table 3					
	VI.	**Loricifera**					
52	1	Loricifera gen. et sp. nov.				+	Heiner (2005)
53	2	Nanaloricidae gen. et sp. I	+				Gad (2004a)
54	3	Nanaloricidae gen. et sp. II	+				Gad (2004a)
55	4	Nanaloricidae nov. gen. et nov.sp. 1				+	Heiner (2005)
56	5	*Armorloricus kristenseni* Heiner, 2004*				+	Heiner (2004, 2005)
57	6	*Armorloricus* sp. 2				+	Heiner (2005)
58	7	*Nanaloricus* sp. 1				+	Heiner (2005)
59	8	*Nanaloricus* sp. 2				+	Heiner (2005)
60	9	Pliciloricidae sp. V	+				Gad (2004a)
61	10	*Pliciloricus* sp. III	+				Gad (2004a)
62	11	*Pliciloricus* sp. IV	+				Gad (2004a)
63	12	*Pliciloricus leocaudatus* Heiner & Kristensen, 2005*				+	Heiner (2005), Heiner & Kristensen (2005)
64	13	*Pliciloricus shukeri* Heiner & Kristensen, 2005*				+	Heiner (2005), Heiner & Kristensen (2005)
65	14	*Rugiloricus bacatus* Heiner, 2008*				+	Heiner (2008)
66	15	*Rugiloricus* sp. VI	+				Gad (2004a)
67	16	*Rugiloricus* sp. VII	+				Gad (2004a)
68	17	*Rugiloricus* sp. VIII	+				Gad (2004a)
69	18	*Rugiloricus* sp. IX	+				Gad (2004a)**
70	19	*Rugiloricus* nov. sp. 1				+	Heiner (2005)
71	20	*Rugiloricus* nov. sp. 2				+	Heiner (2005)
72	21	*Rugiloricus* nov. sp. 3 (= *R.* sp. nov. A)				+	Heiner (2005, 2008)
73	22	*Rugiloricus* nov. sp. 4 (= *R.* sp. nov. B)				+	Heiner (2005, 2008)
74	23	*Urnaloricus gadi* Heiner & Kristensen, 2009*				+	Heiner & Kristensen (2009)
	VII.	**Nematoda**					
75	1	Epsilonematinae sp. 1	+				Gad (2004b)
76	2	*Bathyepsilonema* sp. 2	+				Gad (2004b)
77	3	*Bathyepsilonema* sp. 3	+				Gad (2004b)
78	4	*Epsilonema* sp. 4	+				Gad (2004b)
79	5	*Epsilonema* sp. 5	+				Gad (2004b)
80	6	*Epsilonema* sp. 6	+				Gad (2004b)
81	7	*Epsilonema* sp. 7	+				Gad (2004b)
82	8	*Leptepsilonema* sp. 8	+				Gad (2004b)
83	9	*Leptepsilonema* sp. 9	+				Gad (2004b)
84	10	*Metepsilonema* sp. 10	+				Gad (2004b)

Tab. 3. (continued)

S cum.	*S*/ taxon	Taxa	GMS	SeiS	JoB	FaB	References
85	11	*Metepsilonema* sp. 11	+				Gad (2004b)
86	12	*Metepsilonema* sp. 12	+				Gad (2004b)
87	13	*Metepsilonema* sp. 13	+				Gad (2004b)
88	14	*Metepsilonema* sp. 14	+				Gad (2004b)
89	15	*Metepsilonema* sp. 15	+				Gad (2004b)
90	16	*Perepsilonema* sp. 16	+				Gad (2004b)
91	17	*Glochinema kentrosaurides* Gad, 2002*	+				Gad (2002, 2004b)
92	18	*Draconema* sp. 1	+				Gad (2009)
93	19	*Paradraconema* sp. 2	+				Gad (2009)
94	20	*Paradraconema* sp. 3	+				Gad (2009)
95	21	*Dracograllus* sp. 4	+				Gad (2009)
96	22	*Dracograllus* sp. 5	+				Gad (2009)
97	23	*Dracograllus* sp. 6	+				Gad (2009)
98	24	*Dracograllus* sp. 7	+				Gad (2009)
99	25	*Tenuidraconema* sp. 8	+				Gad (2009)
100	26	*Tenuidraconema* sp. 9	+				Gad (2009)
101	27	*Cephalochaetosoma* sp. 10	+				Gad (2009)
102	28	*Prochaetosoma* sp. 11	+				Gad (2009)
103	29	*Prochaetosoma* sp. 12	+				Gad (2009)
104	30	*Prochaetosoma* sp. 13	+				Gad (2009)
105	31	*Prochaetosoma* sp. 14	+				Gad (2009)
106	32	*Eudraconema* sp. 15	+				Gad (2009)
	VIII.	**Tantulocarida**					
107	1	*Tantulacus hoegi* Huys, Andersen & Kristensen, 1992*				+	Huys et al. (1992)
	IX.	**Tardigrada**					
108	1	*Batillipes similis* Schulz, 1955				+	Hansen et al. (2001)
109	2	*Batillipes* sp. 1				+	Hansen et al. (2001)
110	3	*Batillipes* sp. 2				+	Hansen et al. (2001)
111	4	*Coronarctus stylisetus* Renaud-Mornant, 1987				+	Hansen et al. (2001)
112	5	*Parmursa* sp. 1				+	Hansen et al. (2001)
113	6	*Angursa* sp. 1				+	Hansen et al. (2001)
114	7	*Tholoarctus natans* Kristensen & Renaud-Mornant, 1983				+	Hansen et al. (2001)
115	8	*Styraconyx nanoqsunguak* Kristensen & Higgins, 1984				+	Hansen et al. (2001)
116	9	*Styraconyx qivitoq* Kristensen & Higgins, 1984				+	Hansen et al. (2001)
117	10	*Styraconyx* cf. *kristenseni* Renaud-Mornant, 1981				+	Hansen et al. (2001)
118	11	*Styraconyx* sp. 1				+	Hansen et al. (2001)
119	12	*Styraconyx* sp. 2				+	Hansen et al. (2001)
120	13	*Raiarctus aureolatus* Renaud-Mornant, 1981				+	Hansen et al. (2001)
121	14	*Raiarctus colurus* Renaud-Mornant, 1982				+	Hansen et al. (2001)
122	15	*Raiarctus* sp. 1				+	Hansen et al. (2001)
123	16	*Rhomboarctus aslaki* Hansen, Gallo D'Addabbo & De Zio Grimaldi, 2003				+	Hansen et al. (2001), Hansen et al. (2003)
124	17	*Halechiniscus perfectus* Schulz, 1955				+	Hansen et al. (2001)
125	18	*Halechiniscus* sp. 1				+	Hansen et al. (2001)
126	19	*Paradoxipus* sp. 1				+	Hansen et al. (2001)
127	20	*Wingstrandarctus* sp. 1				+	Hansen et al. (2001)
128	21	Florarctinae nov. gen. 1 et nov. sp. 1				+	Hansen et al. (2001), Hansen (2005)

Tab. 3. (continued)

S cum.	*S*/ taxon	Taxa	GMS	SeiS	JoB	FaB	References
129	22	*Actinarctus* cf. *physophorus* Grimaldi De Zio et al., 1984				+	Hansen et al. (2001)
130	23	*Tanarctus bubulubus* Jørgensen & Kristensen, 2001*				+	Hansen et al. (2001), Jørgensen & Kristensen (2001)
131	24	*Tanarctus gracilis* Renaud-Mornant, 1980				+	Hansen et al. (2001)
132	25	*Tanarctus heterodactylus* Renaud-Mornant, 1981				+	Hansen et al. (2001)
133	26	*Tanarctus* sp. 1				+	Hansen et al. (2001)
134	27	*Tanarctus* sp. 2				+	Hansen et al. (2001)
135	28	*Tanarctus* sp. 3				+	Hansen et al. (2001)
136	29	*Tanarctus* sp. 4				+	Hansen et al. (2001)
137	30	*Tanarctus* sp. 5				+	Hansen et al. (2001)
138	31	*Tanarctus* sp. 6				+	Hansen et al. (2001)
139	32	*Tanarctus* sp. 7				+	Hansen et al. (2001)
140	33	*Tanarctus* sp. 8				+	Hansen et al. (2001)
141	34	*Dipodarctus* cf. *subterraneus* (Renaud-Debyser, 1959)				+	Hansen et al. (2001)
142	35	*Pseudostygarctus* sp. 1				+	Hansen et al. (2001)

given to the author by Dr D. Thistle (Tallahassee, U.S.A.), have to be treated with reservation: This material has not been directly compared with that from the Atlantic seamounts (see below). Across all eight seamounts, Harpacticoida had the highest species numbers ($S=215$), followed by Tardigrada ($S=35$), Nematoda ($S=32$), and Halacarida ($S=28$) (Table 2). Most of the reported seamount species are unknown to science; only 7.0 % ($S=25$) have been reported previously from other, non-seamount, localities. The highest number of known species belongs to Gastrotricha (40.0 % of seamount Gastrotricha), Tardigrada (28.6 %), and Halacarida (14.3 %) (Table 2). In contrast, all nematode and loriciferan species collected from seamounts are so far unique, whilst just four out of the 215 (1.9 %) recorded Harpacticoida species have been found elsewhere.

In total, 48 new seamount metazoan meiobenthic species have been described, only 13.4 % of those collected so far (Table 2). The Halacarida represent the highest number of species descriptions ($S=21$), nearly half of all descriptions. In contrast, the number of harpacticoid species described is comparably low ($S=9$), but combined with the Halacarida account for 62.6 % of all species described so far (Table 2).

Are seamounts stepping stones/staging.posts or trapping stones for meiofauna? The circumstances and mechanisms of meiofauna distribution have been discussed for many decades and several potential mechanisms of dispersal have been proposed (cf. Yeatman 1962, Sterrer 1973, Gerlach 1977, Hagerman & Rieger 1981, Hockin 1982, Westheide 1987, Stock 1994; see also Gad & Schminke 2004, Fontaneto 2011). The recently formulated "ubiquitous hypothesis" ("everything is everywhere") (e. g. Finlay 2002, Fenchel & Finlay 2004, Fontaneto 2011), supposing that species smaller than 1–2 mm show no biogeography but a ubiquitous distribution, must probably be restricted to unicellular organisms as many metazoan meiobenthic groups apparently do present variable distribution patterns, including regional restriction and even endemism (George & Schminke 2002; Gad 2004a,b; George 2004a; Artois et al. 2011). However, it must be admitted that the data available to undertake biogeographic analyses of meiobenthic distributions is quite fragmentary (George & Schminke 2002, Bartsch 2003, Artois et al. 2011).

Despite their (i) very small body sizes, (ii) lack of planktonic life stages, and (iii) solely benthic habit, shallow-water species may show an amphi-oceanic to cosmopolitan distribution (see Giere 2009 for review). In fact, it has been shown that many meiobenthic groups indeed enter the

Tab. 4. List of Harpacticoid species currently known from seamounts. Species are sorted alphabetically by families and the seamounts on which they were recorded are indicated, with the citation for each record. Grey fields in the “taxa” column highlight species that were known from other habitats, whilst grey fields in the “seamount” columns highlight species recorded at multiple seamounts.

S cum.	*S*/ taxon	Species Working species; no detailed species list.	FieG	GMS	SedS	SeiS	References
	I.	**Aegisthidae (Cerviniinae)**					
143	1	*Cerviniella* sp. 1				+	Büntzow (2011)
144	2	*Cerviniella* sp. 2			+		Büntzow (2011)
145	3	*Paracerviniella* sp. 1				+	Büntzow (2011)
	II.	**Ameiridae (Stenocopiinae)**					
146	4	*Stenocopia* sp. 1			+	+	Büntzow (2011)
	III.	**Ancorabolidae**					
147	5	*Laophontodes* aff. *bicornis* (= *Ancorabolina* sp.; George, pers. obs.)			+		Büntzow (2011)
148	6	*Dorsiceratus dinah* George & Plum, 2009*				+	George & Plum (2009), Büntzow (2011)
149	7	*Dorsiceratus wilhelminae* George & Plum, 2009*			+		George & Plum (2009), Büntzow (2011)
150	8	*Laophontodes* cf. *typicus* T. Scott, 1894		+			George & Schminke (2002)
151	9	*Laophontodes* sp.		+			George & Schminke (2002)
152	10	*Pseudechinopsyllus sindemarkae* George, 2006*		+			George & Schminke (2002), George (2006)
	IV.	**Argestidae**					
153	11	Argestidae sp. 1 (Ge & Sch)		+			George & Schminke (2002)
154	12	Argestidae sp. 1 (Bü)				+	Büntzow (2011)
155	13	Argestidae sp. 2		+			George & Schminke (2002)
156	14	Argestidae sp. 3		+			George & Schminke (2002)
157	15	Argestidae sp. 4		+			George & Schminke (2002)
158	16	Argestidae sp. 5		+			George & Schminke (2002)
159	17	*Argestes* sp. 1		+			George & Schminke (2002)
160	18	*Argestes* sp. 2		+			George & Schminke (2002)
161	19	*Parargestes* sp. 1 (= *Argestes*; cf. George 2011)		+			George & Schminke (2002)
162	20	*Parargestes* sp. 2 (= *Argestes*; cf. George 2011)		+			George & Schminke (2002)
163	21	*Parargestes* sp. 3 (= *Argestes*; cf. George 2011)		+			George & Schminke (2002)
164	22	*Argestigens* sp. 1		+			George & Schminke (2002)
165	23	*Argestigens* sp. 2		+			George & Schminke (2002)
166	24	*Bodinia meteorensis* George, 2004*		+			George & Schminke (2002), George (2004a)
167	25	*Bodinia peterrummi* George, 2004*		+			George & Schminke (2002), George (2004a)
168	26	*Bodinia* sp.		+			George & Schminke (2002)
169	27	*Dizahavia* sp. 1		+			George & Schminke (2002)
170	28	*Dizahavia* sp. 2		+			George & Schminke (2002)
171	29	*Dizahavia* sp. 3		+			George & Schminke (2002)
172	30	*Eurycletodes* sp. 1		+			George & Schminke (2002)
173	31	*Eurycletodes* sp. 2 (Ge & Sch)		+			George & Schminke (2002)
174	32	*Eurycletodes* sp. 3		+			George & Schminke (2002)
175	33	*Eurycletodes* sp. 4		+			George & Schminke (2002)
176	34	*Eurycletodes* sp. 5		+			George & Schminke (2002)
177	35	*Eurycletodes* sp. 6		+			George & Schminke (2002)
178	36	*Eurycletodes* sp. 7		+			George & Schminke (2002)

Tab. 4. (continued).

S cum.	*S*/ taxon	Species Working species; no detailed species list.	FieG	GMS	SedS	SeiS	References
179	37	*Eurycletodes* sp. 8		+			George & Schminke (2002)
180	38	*Eurycletodes* sp. 2 (Bü)				+	Büntzow (2011)
181	39	*Malacopsyllus* sp.		+			George & Schminke (2002)
182	40	*Malacopsyllus* sp. 1			+		Büntzow (2011)
183	41	*Malacopsyllus* sp. 2			+	+	Büntzow (2011)
184	42	*Malacopsyllus* sp. 3			+		Büntzow (2011)
185	43	*Malacopsyllus* sp. 4			+		Büntzow (2011)
186	44	*Mesocletodes* sp. 1		+			George & Schminke (2002)
187	45	*Mesocletodes* sp. 2 (Ge & Sch)		+			George & Schminke (2002)
188	46	*Mesocletodes* sp. 2 (Bü)				+	Büntzow (2011)
189	47	*Mesocletodes* sp. 3		+			George & Schminke (2002)
190	48	*Mesocletodes* sp. 4		+			George & Schminke (2002)
191	49	*Mesocletodes* sp. 5		+			George & Schminke (2002)
192	50	*Mesocletodes* sp. 6		+			George & Schminke (2002)
193	51	*Mesocletodes* sp. 7 (Ge & Sch)		+			George & Schminke (2002)
194	52	*Mesocletodes* sp. 7 (Bü)			+		Büntzow (2011)
195	53	*Mesocletodes* sp. 8		+			George & Schminke (2002)
196	54	*Mesocletodes* sp. 9		+			George & Schminke (2002)
	V.	**Canthocamptidae**					
197	55	*Bathycamptus* sp. 9				+	Büntzow (2011)
198	56	*Boreolimella* sp. 3				+	Büntzow (2011)
199	57	*Heteropsyllus* sp. 2			+		Büntzow (2011)
200	58	*Heteropsyllus* sp. 5				+	Büntzow (2011)
201	59	*Heteropsyllus* sp. 7				+	Büntzow (2011)
202	60	*Mesopsyllus* sp. 8			+		Büntzow (2011)
203	61	*Mesochra* sp. 4				+	Büntzow (2011)
204	62	*Mesochra* sp. 6				+	Büntzow (2011)
205	63	Cylindropsyllinae sp. 9				+	Büntzow (2011)
206	64	Cylindropsyllinae sp. 10				+	Büntzow (2011)
207	65	*Cylindropsyllus* sp. 5				+	Büntzow (2011)
208	66	*Cylindropsyllus* sp. 7				+	Büntzow (2011)
209	67	*Cylinula* sp. 6			+	+	Büntzow (2011)
210	68	*Stenocaris* sp. 3				+	Büntzow (2011)
211	69	*Stenocaropsis* sp. 4				+	Büntzow (2011)
212	70	*Stenocaropsis* sp. 8				+	Büntzow (2011)
	VI.	**Canuellidae**					
213	71	*Microcanuella* sp. 1			+		Büntzow (2011)
214	72	*Microcanuella* sp. 2				+	Büntzow (2011)
	VII.	**Cletodidae**					
215	73	*Cletodes* sp.		+			George & Schminke (2002)
216	74	*Cletodes* sp. 2			+	+	Büntzow (2011)
217	75	*Stylicletodes longicaudatus* (Brady & Robertson, 1880)			+	+	Büntzow (2011)
	VIII.	**Harpacticidae**					
218	76	*Harpacticus* sp.		+			George & Schminke (2002)
219	77	*Perissocope* sp. 1		+			George & Schminke (2002)
220	78	*Perissocope* sp. 2		+			George & Schminke (2002)
221	79	*Perissocope* sp. 3		+			George & Schminke (2002)

Tab. 4. (continued).

S cum.	*S*/ taxon	Species Working species; no detailed species list.	FieG	GMS	SedS	SeiS	References
	IX.	**Huntemanniidae**					
222	80	*Metahuntemannia* sp. 1			+		Büntzow (2011)
223	81	*Metahuntemannia* sp. 2				+	Büntzow (2011)
	X.	**Idyanthidae**					
224	82	*Meteorina magnifica* George, 2004*		+			George & Schminke (2002), George (2004b)
225	83	*Idyella* sp. 1			+	+	Büntzow (2011)
226	84	*Idyella* sp. 1				+	Büntzow (2011)
227	85	*Idyellopsis* sp. 1				+	Büntzow (2011)
228	86	*Tachidiella* sp. 1				+	Büntzow (2011)
229	87	*Tachidiella* sp. 2			+		Büntzow (2011)
	XI.	**Laophontidae**					
230	88	Laophontidae sp. 1		+			George & Schminke (2002)
231	89	Laophontidae sp. 2		+			George & Schminke (2002)
232	90	Laophontidae sp. 3 (Ge & Sch)		+			George & Schminke (2002)
233	91	Laophontidae sp. 3 (Bü)			+		Büntzow (2011)
234	92	*Paralaophonte* sp. 1				+	Büntzow (2011)
	XII.	**Latiremidae**					
235	93	*Latiremus* sp. 1				+	Büntzow (2011)
	XIII.	**Leptastacidae**					
236	94	Leptastacidae sp.		+			George & Schminke (2002)
237	95	*Leptastacus* sp. 1				+	Büntzow (2011)
	XIV.	**Leptopontiidae**					
238	96	Arenopontiinae sp. 1		+			George & Schminke (2002)
239	97	Arenopontiinae sp. 2		+			George & Schminke (2002)
240	98	Leptopontiidae sp. 1			+		Büntzow (2011)
241	99	Leptopontiidae sp. 2				+	Büntzow (2011)
242	100	Leptopontiidae sp. 3				+	Büntzow (2011)
243	101	Leptopontiidae sp. 4				+	Büntzow (2011)
244	102	Leptopontiidae sp. 5				+	Büntzow (2011)
245	103	*Syrticola* sp. 1				+	Büntzow (2011)
	XV.	**Miraciidae (Diosaccinae)**					
246	104	Miraciidae sp. 1			+		Büntzow (2011)
247	105	Miraciidae sp. 2			+		Büntzow (2011)
248	106	*Amphiascoides* sp. 1			+		Büntzow (2011)
249	107	*Amphiascus* sp. 1			+		Büntzow (2011)
250	108	*Amphiascus* sp. 2			+		Büntzow (2011)
251	109	*Amphiascus* sp. 3			+		Büntzow (2011)
252	110	*Amphiascus* sp. 4			+		Büntzow (2011)
253	111	*Amphiascus* sp. a				+	Büntzow (2011)
254	112	*Amphiascus* sp. b				+	Büntzow (2011)
255	113	*Amphiascus* sp. c				+	Büntzow (2011)
256	114	*Bulbamphiascus* sp. 1			+		Büntzow (2011)
257	115	*Bulbamphiascus* sp. a				+	Büntzow (2011)
258	116	*Haloschizopera* sp. 1			+		Büntzow (2011)
259	117	*Haloschizopera* sp. a				+	Büntzow (2011)
260	118	*Haloschizopera* sp. b				+	Büntzow (2011)
261	119	*Paramphiascella* sp. a				+	Büntzow (2011)

Tab. 4. (continued).

S cum.	*S*/ taxon	Species Working species; no detailed species list.	FieG	GMS	SedS	SeiS	References
262	120	*Paraschizopera* sp. 3				+	Büntzow (2011)
263	121	*Paramphiascopsis* sp. 1			+		Büntzow (2011)
264	122	*Paraschizopera* sp. 1			+		Büntzow (2011)
265	123	*Robertgurneya* sp. 1			+		Büntzow (2011)
266	124	*Robertgurneya* sp. 2			+		Büntzow (2011)
267	125	*Robertgurneya* sp. a				+	Büntzow (2011)
268	126	*Robertgurneya* sp. b				+	Büntzow (2011)
269	127	*Schizopera* sp. 1			+		Büntzow (2011)
270	128	*Schizopera* sp. a				+	Büntzow (2011)
271	129	*Schizopera* sp. b				+	Büntzow (2011)
272	130	*Schizopera* sp. c				+	Büntzow (2011)
	XVI.	**Neobradyidae**					
273	131	*Marsteinia* sp. 1			+	+	Büntzow (2011)
274	132	*Marsteinia* sp. 2				+	Büntzow (2011)
275	133	*Marsteinia* sp. 3			+	+	Büntzow (2011)
276	134	*Marsteinia* sp. 4				+	Büntzow (2011)
277	135	*Marsteinia* sp. 5				+	Büntzow (2011)
278	136	*Tachidiopsis* sp. 1			+		Büntzow (2011)
	XVII.	**Normanellidae**					
279	137	*Normanella* sp. 1				+	Büntzow (2011)
280	138	*Retrocalcar brattstroemi* (Geddes, 1981)		+			George & Schminke (2002)
	XVIII.	**Paramesochridae**					
281	139	*Apodopsyllus* sp. 1			+	+	Büntzow (2011)
282	140	*Apodopsyllus* sp. 3				+	Büntzow (2011)
283	141	*Biuncus* sp. 1			+		Büntzow (2011)
284	142	*Biuncus* sp. 2				+	Büntzow (2011)
285	143	*Biuncus* sp. 3				+	Büntzow (2011)
286	144	*Biuncus* sp. 4				+	Büntzow (2011)
287	145	*Biuncus* sp. 5				+	Büntzow (2011)
288	146	*Biuncus* sp. 6				+	Büntzow (2011)
289	147	*Diarthrodella* sp. 1				+	Büntzow (2011)
290	148	*Diarthrodella* sp. 2				+	Büntzow (2011)
291	149	*Emertonia* sp. 1 (listed as *Kliopsyllus* sp. 1)			+		Büntzow (2011)
292	150	*Emertonia* sp. 2 (listed as *Kliopsyllus* sp. 2)			+		Büntzow (2011)
293	151	*Emertonia* sp. 3 (listed as *Kliopsyllus* sp. 3)			+		Büntzow (2011)
294	152	*Emertonia* sp. 4 (listed as *Kliopsyllus* sp. 4)			+		Büntzow (2011)
295	153	*Emertonia* sp. 5 (listed as *Kliopsyllus* sp. 5)				+	Büntzow (2011)
296	154	*Emertonia* sp. 6 (listed as *Kliopsyllus* sp. 6)				+	Büntzow (2011)
297	155	*Emertonia* sp. 7 (listed as *Kliopsyllus* sp. 7)				+	Büntzow (2011)
298	156	*Emertonia* sp. 8 (listed as *Kliopsyllus* sp. 8)				+	Büntzow (2011)
299	157	*Emertonia* sp. 9 (listed as *Kliopsyllus* sp. 9)				+	Büntzow (2011)
300	158	*Paramesochra* sp. 1			+		Büntzow (2011)
301	159	*Paramesochra* sp. 3			+		Büntzow (2011)
302	160	*Paramesochra* sp. 4			+		Büntzow (2011)
303	161	*Paramesochra* sp. 5			+		Büntzow (2011)
304	162	*Paramesochra* sp. 6			+		Büntzow (2011)
305	163	*Paramesochra* sp. 7				+	Büntzow (2011)
306	164	*Paramesochra* sp. 8				+	Büntzow (2011)

Tab. 4. (continued).

S cum.	*S*/ taxon	Species Working species; no detailed species list.	FieG	GMS	SedS	SeiS	References
307	165	*Paramesochra* sp. 9				+	Büntzow (2011)
308	166	*Paramesochra* sp. 10				+	Büntzow (2011)
309	167	*Paramesochra* sp. 11				+	Büntzow (2011)
310	168	*Paramesochra* sp. 12				+	Büntzow (2011)
311	169	*Paramesochra* sp. 13				+	Büntzow (2011)
312	170	*Paramesochra* sp. 14				+	Büntzow (2011)
313	171	*Tisbisoma* sp. 1			+	+	Büntzow (2011)
314	172	*Tisbisoma* sp. 2			+		Büntzow (2011)
315	173	*Tisbisoma* sp. 3				+	Büntzow (2011)
316	174	*Wellsopsyllus (Intermediopsyllus) antoniae* (Plum & George, 2009)*		+	+		Plum & George (2009), Büntzow (2011)
317	175	*Wellsopsyllus (Intermediopsyllus) intermedius* (T. & A. Scott, 1895)		+			Plum & George (2009)
	XIX.	**Pseudotachidiidae**					
318	176	*Cylindronannopus* sp. 1			+		Büntzow (2011)
319	177	*Danielssenia* sp. 2			+		Büntzow (2011)
320	178	*Danielssenia* sp. 4				+	Büntzow (2011)
321	179	*Idomene* sp. 1			+		Büntzow (2011)
322	180	*Idomene* sp. 2				+	Büntzow (2011)
323	181	*Micropsammis* sp. 5				+	Büntzow (2011)
324	182	*Paradanielssenia* sp. 1			+		Büntzow (2011)
325	183	*Pseudomesochra* sp. 3				+	Büntzow (2011)
326	184	*Pseudomesochra* sp. 7			+		Büntzow (2011)
327	185	*Pseudomesochra* sp. 8			+		Büntzow (2011)
328	186	*Pseudotachidius* sp. 6				+	Büntzow (2011)
	XX.	**Rhizotrichidae**					
329	187	*Fiersiella* sp. 1			+		Büntzow (2011)
	XXI.	**Rometidae**					
330	188	*Romete bulbiseta* Seifried & Schminke, 2003*		+			Seifried & Schminke (2003)
	XXII.	**Superornatiremidae**					
331	189	Superornatiremidae sp. 1				+	George & Martínez Arbizu (2005), Büntzow (2011)
	XXIII.	**Tegastidae**					
332	190	Tegastidae sp.		+			George & Schminke (2002)
333	191	*Parategastes* sp. 1				+	Büntzow (2011)
334	192	*Tegastes sp.* 1		+			George & Schminke (2002)
335	193	*Tegastes sp.* 2		+			George & Schminke (2002)
	XXIV.	**Tetragonicipitidae**					
336	194	*Phyllopodopsyllus* sp. 2				+	Büntzow (2011)
337	195	*Pteropsyllus* sp. 4				+	Büntzow (2011)
338	196	*Tetragoniceps* sp. 1			+		Büntzow (2011)
	XXV.	**Tisbidae**					
339	197	*Tisbe* sp. 2				+	Büntzow (2011)
	XXVI.	**Zosimeidae**					
340	198	*Zosime anneae* Koller & George, 2011*		+			Koller & George (2011)
341	199	*Zosime bergensis* Drzycimski, 1967		+			Koller & George (2011)
342	200	*Zosime* sp. 1			+		Büntzow (2011)
343	201	*Zosime* sp. 2 (Bü)			+		Büntzow (2011)

Tab. 4. (continued).

S cum.	*S*/ taxon	Species Working species; no detailed species list.	FieG	GMS	SedS	SeiS	References
344	202	*Zosime* sp. 3 (Bü)				+	Büntzow (2011)
345	203	*Zosime* sp. 4 (Bü)				+	Büntzow (2011)
346	204	*Zosime* sp. 5 (Bü)				+	Büntzow (2011)
347	205	*Zosime* sp. 6 (Bü)				+	Büntzow (2011)
348	206	*Zosime* sp. 7 (Bü)				+	Büntzow (2011)
349	207	*Zosime* sp. 2 (Ko & Ge)		+			Koller & George (2011)
350	208	*Zosime* sp. 3 (Ko & Ge)		+			Koller & George (2011)
351	209	*Zosime* sp. 4 (Ko & Ge)		+			Koller & George (2011)
352	210	*Zosime* sp. 5 (Ko & Ge)		+			Koller & George (2011)
353	211	*Zosime* sp. 6 (Ko & Ge)		+			Koller & George (2011)
354	212	*Zosime* sp. 7 (Ko & Ge)		+			Koller & George (2011)
355	213	*Zosime* sp. 8		+			Koller & George (2011)
356	214	*Zosime* sp. 9		+			Koller & George (2011)
357	215	*Zosime* sp. 10		+			Koller & George (2011)

water column by either passive re-suspension or active emergence (Fleeger et al. 1984; Palmer & Gust 1985; Walters & Bell 1986; Armonies 1988; Fegley 1988; Palmer 1988; Armonies 1990, 1994; Thistle 2003; Thistle & Sedlacek 2004; Ullberg 2004; Sedlacek & Thistle 2006; Boeckner et al. 2009). Nonetheless, dispersal by horizontal drift following such emergence is likely to be limited in comparison to that of planktonic organisms. That may be particularly true for shallow-water meiofauna which must transverse hundreds of kilometres of deep-sea areas (with average depths of 4000–5000 m) before reaching new shallow-water areas.

Most of the proposed mechanisms of meiobenthic dispersal (with plate tectonics, on airborne animals, on drifting materials or in ship ballast water; see Sterrer 1973, Gerlach 1977, Giere 2009) are controversial. Another possible explanation for meiofaunal distributions includes "ostensive distance diminishment" between habitats suitable for colonization. As discussed by Hagerman & Rieger (1981), the drift of suspended organisms must not play a significant role in large-scale meiofauna distribution because shallow-water animals leaving the coastal shelf would sink too fast. However, rarely, that inevitable sinking must deposit organisms on to relatively shallow seamount summits, which may then provide suitable sublittoral conditions regarding depth, substrate and other abiotic variables. If sufficient members of a population reach such a "resting place", with environmental conditions corresponding to their coastal shelf origins (cf. Thiel 1970), new permanent sub-populations could be established. Where seamounts lie within the "critical dispersal distance" of species (Cecca 2002), and when such "favourable" dispersal conditions and mechanisms occur, they may potentially take on the role of "staging posts" (Rosen 1983, Cecca 2002) contributing to the maintenance of gene flow between several sub-populations. These sub-populations may be located on adjacent seamounts, islands, and/or mainland. Under such conditions, a seamount might also become a "stepping stone" – as per Hubbs (1959) and MacArthur & Wilson (1967) – an intermediate "submerged island" supporting meiofaunal transport towards previously uncolonized areas (Cecca 2002).

Equally, many seamounts stand alone, with no adjacent mainland, island, or seamount. The fauna on these seamounts may be isolated by topography (steep slopes resulting in rapid faunal turnover with depth), hydrographic conditions (particular current systems, e.g. taylor caps) and large distances. Such isolating conditions would result in only random exchange of meiobenthic species (George & Schminke 2002, Gad & Schminke 2004) preventing a staging post/stepping stone function and any meiobenthic organism reaching this type of seamount would be "trapped". Where trapped species survive, they have the potential to establish new populations and even new species – seamounts thus acting as "trapping stones" and potentially resulting in a highly diverse, endemic meiofauna (George & Schminke 2002, George 2004a).

To determine whether seamounts do or do not play a role as staging posts, stepping stones or trapping stones for meiobenthos requires sufficiently large data sets from the summits of multiple seamounts and their adjacent geographical areas. Similarly large datasets are needed to address questions regarding bathymetric exchange; here, material from the surrounding deep sea is also needed. There are, however, only a few such data sets available (Table 2) with only a few of the major meiobenthic taxa providing sufficient information (e. g. species known from other locations) to allow a meaningful comparison (Tables 3 and 4). Of the 26 major taxa recorded, nine (Fig. 2) have been studied at the more detailed species-level (taxonomic and/or faunistic). Their distributions are discussed below, following the numeration in Tables 3 and 4.

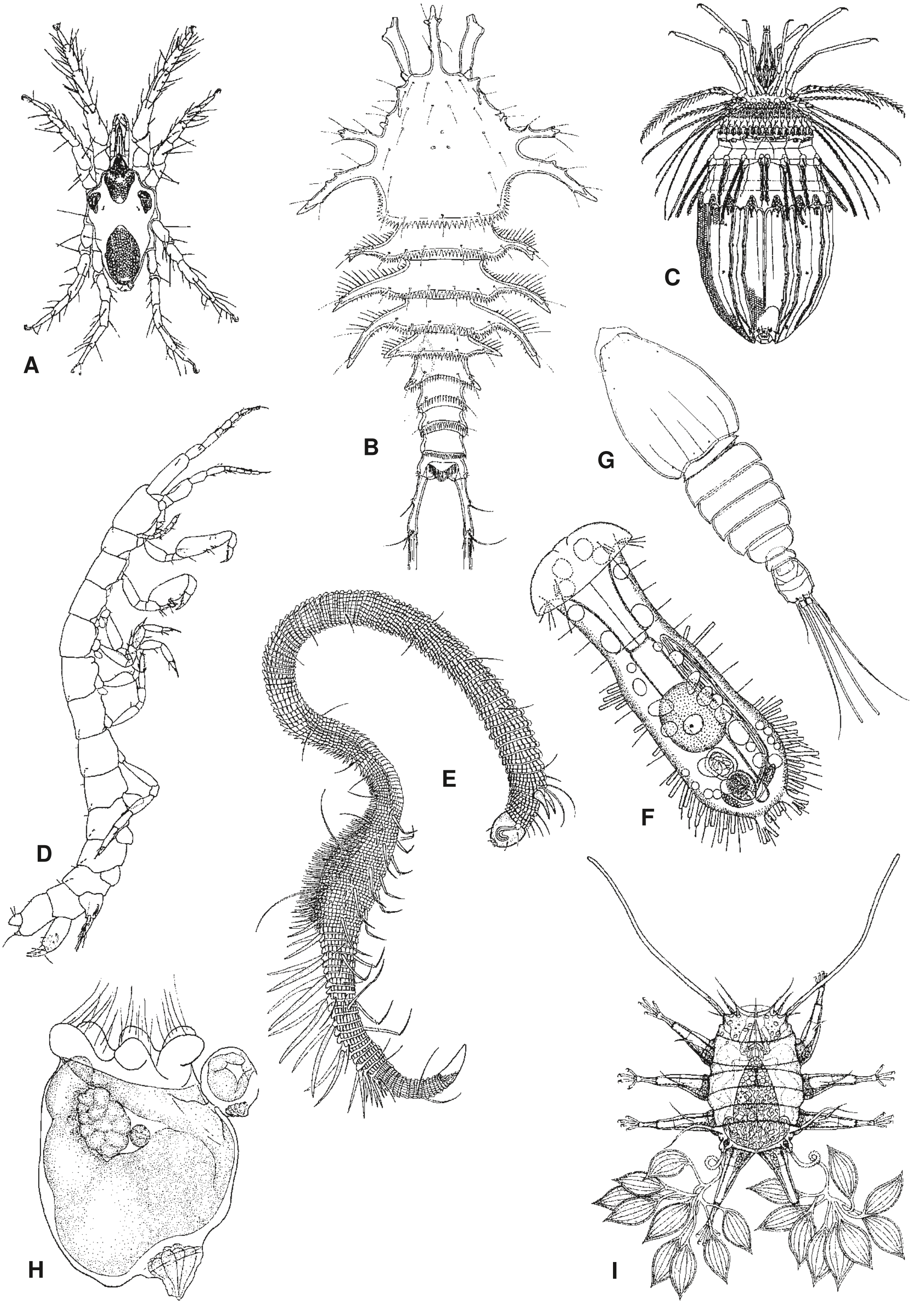
I. Amphipoda (Fig. 2D). Amphipoda have been recorded on only three seamounts (Table 1) and with only two species described, one from GMS and one from SeiS (Table 2), a comparison of seamount Amphipoda would be meaningless. Both described amphipods belong to the same genus, namely *Ingolfiella* Hansen, 1903 (Andres 2004, 2005). Atlantic ingolfiellids have been mostly reported from shallow waters or anchialine caves, while oceanic records are scarce (Andres 2004). *I. sandroruffoi* Andres, 2004 was the first ingolfiellid reported from a seamount (GMS); the second species *I. georgei* Andres, 2005 was collected during RV "Meteor" cruise M 60/1 (OASIS) (Christiansen & Wolff 2009) from SeiS (Table 3). Since ingolfiellids lack highly-developed pleopods that enable active forward movement and lack dispersal stages, Andres (2004) agreed with the assumption made by George & Schminke (2002) for Harpacticoida that seamount ingolfiellids are of deep-sea origin, descendant from ancestors that arose from the seabed with the seamount.

II. Entoprocta (Figs. 2H, 3). The first meiobenthic species reported from a seamount was the entoproct *Loxomespilon* cf. *perezi* var. *meteoris* Emschermann, 1971 (Entoprocta, Loxosomatidae), which was reported living epizoically on the polychaete *Sigalion squamatum* on GMS (Emschermann 1971). In addition to describing this new subspecies, Emschermann (1971) was the first to consider meiobenthic biogeography and possible sources of faunal colonization to the Great Meteor Seamount.

III. Gastrotricha (Figs. 2F, 3). Gastrotrichs have been documented from four Atlantic seamounts (Table 1), but only those from FaB have been studied in detail. Twenty species have been recorded from FaB (Tables 2, 3), half previously documented across a wide geographical range in the North Atlantic (from Tromsø, Norway and FaB in the north to the Mediterranean in the south), and the coast of North America in the west (Clausen 2004). Clausen (2004) described six new gastrotrich species from FaB and registered three further species that remain undescribed (Table 3). He also undertook a chorological study of the seamount gastrotrichs, including *Dactylopodola typhle* Remane, 1927, and *Diplodasys ankeli* Wilke, 1954, (Fig. 3) but excluding *Halichaetonotus* cf. *aculifer* Gerlach, 1953 because it could not be determined satisfactorily. In total, 16 of 20 gastrotrich species (80.0 %) recorded on seamounts have been described, six described from seamounts and 10 from other habitats, and are therefore available for further investigation.

IV. Halacarida (Figs. 2A, 4). Marine mites have been reported from four seamounts (Table 1). However, detailed taxonomic and faunistic analyses have been carried out for two Atlantic seamounts only, namely the Great Meteor Seamount and Josephine Bank (Table 3). Twenty four species were collected from GMS, which is the type locality for 21 of these species, only three species previously reported from other locations

Fig. 2. Representatives of the nine meiobenthic major taxa that have been investigated taxonomically and faunistically from seamounts: **A.** *Halacarus ctenopus* Gosse, 1855 (Halacarida; the species shown has not been found on seamounts, but is a close relative of *H. leptopus* Bartsch, 2002); **B.** *Meteorina magnifica* George, 2004 (Harpacticoida); **C.** Nanaloricidae gen. et sp. II (Loricifera); **D.** *Ingolfiella sandroruffoi* Andres, 2004 (Amphipoda); **E.** *Glochinema kentrosauroides* Gad, 2002 (Nematoda); **F.** *Tetranchyroderma faroenese* Clausen, 2004 (Gastrotricha); **G.** *Tantulacus hoegi* Huys, Andersen & Kristensen, 1992 (Tantulocarida); **H.** *Loxomespilon* cf. *perezi* var. *meteoris* Emschermann, 1971; **I.** *Tanarctus bubulubus* Jørgensen & Kristensen, 2001 (Tardigrada). Modified from the respective authors; not to scale. ▷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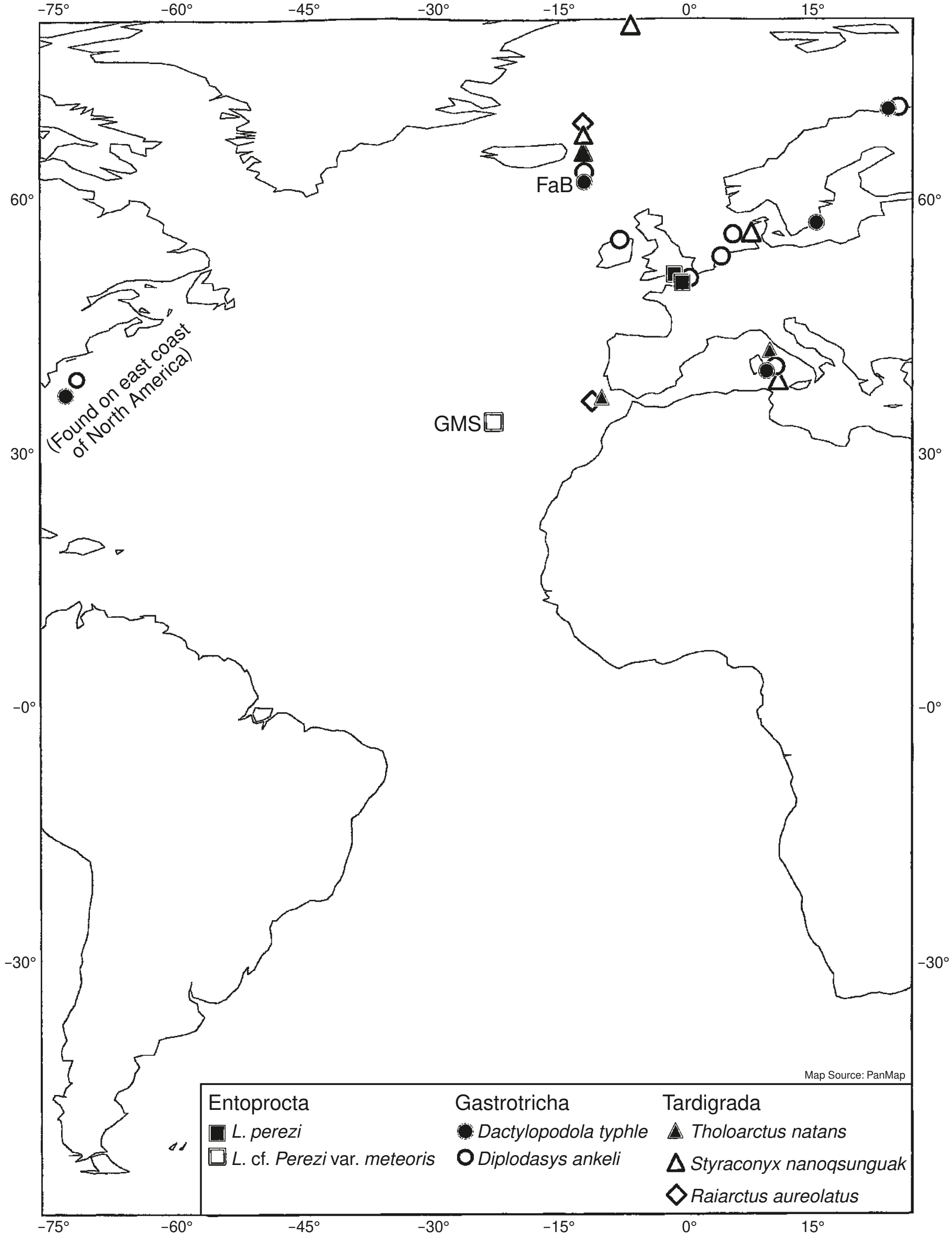

Fig. 3. Atlantic and Mediterranean distribution of some Entoprocta, Gastrotricha (two examples) and Tardigrada (three examples), including the respective seamounts (FaB, GMS).

(grey marked taxon fields in Table 3): Bartsch (1973a,b, 2003) noted *Acaromantis squilla* Trouessart & Neumann, 1893 in the North Atlantic and Mediterranean, *Copidognathus tricorneata* (Lohmann, 1938) in Australia (Bartsch 1973a,b), and presumes *Lohmannella falcata* (Hodge, 1863) to be cosmopolitan (Bartsch 1973b). Bartsch (2003) also noted that five halacarid species reported from GMS were subsequently collected from other, primarily North Atlantic locations (*Coloboceras karamani* Bartsch, 1973, *Copidognathus longipes* Bartsch, 1973, *Copidognathus trouessarti* Bartsch,

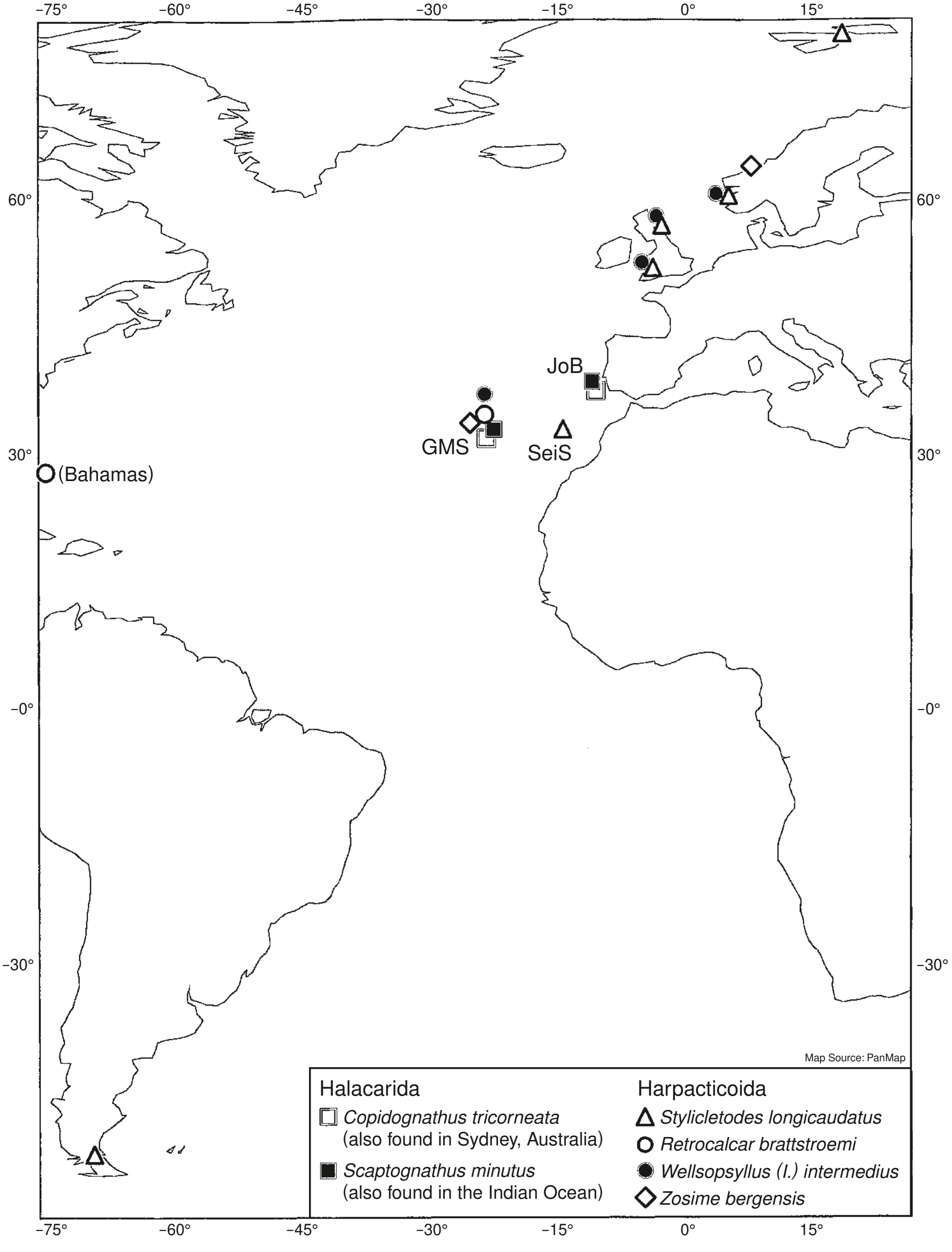

Fig. 4. Atlantic distribution of Halacarida (two examples) and Harpacticoida including the respective seamounts (GMS, JoB, SeiS).

1973, *Lohmannella subfalcata* Bartsch, 1973, and *Scaptognathus minutus* Bartsch, 1973 [also Indian Ocean]).

Seven halacarid species were collected from JoB, three of which have not been found elsewhere (Table 3). The remaining four species, *Atelopsalis tricuspis* Trouessart, 1896; (Gulf of Gascogne; cf. Bartsch 1973b), *Copidognathus longipes*, *C. tricorneata*, *Lohmannella falcata*, and *Scaptognathus minutus*, have an Atlantic-wide distribution, as exemplified by *Copidognathus tricorneata* (Lohmann, 1938) and *Scaptognathus minutus* Bartsch, 1973 (Fig. 4).

The halacarid fauna of the regions adjacent to these two Atlantic seamounts remains relatively unknown Bartsch (2003), but nine species are recorded on these seamounts and other Atlantic regions (single species even in the Mediterranean and the Indian Ocean) suggesting that seamounts play an important role in halacarid distribution. Thus, Bartsch (2003) suggests that, unlike the high level of endemism assumed for the Harpacticoida (George & Schminke 2002), GMS Halacarida will be found off the coasts of the Azores, Europe, and North Africa in the future.

V. Harpacticoida (Figs. 2B, 4). Harpacticoid copepods have been the subject of the most extensive seamount studies (Table 4) and have been collected from seven seamounts (Table 1). However, detailed taxonomic and faunistic investigations at the species-level are restricted to three Atlantic seamounts, GMS, SedS, and SeiS (Table 4). Samples from additional seamounts (circles in Fig. 1) are currently being sorted and processed by the author. Currently, only one species (*Ancorabolus chironi* Schulz & George, 2010) has been described, from the base of the Eastern Mediterranean Anaximenes Seamount (Schulz & George 2010).

Of the Pacific seamounts, only FieG (Fig. 1), has been studied in detail. Thistle & Levin (1998, Table 4) published a list of 54 Harpacticoida collected from the 0–2 cm sediment layer and Dr D. Thistle (Tallahassee, U.S.A.) has kindly provided to the author a list of tentative identifications. Nineteen species (35.2 %) could not be assigned to a known harpacticoid family, and identification to the genus-level was possible for only 14 species (25.9 %). However, the harpacticoid material from FieG has not been directly compared with that from the Atlantic seamounts, so it is not possible to combine or compare the datasets. Thus, the following discussion focuses on Harpacticoida from the Atlantic GMS, SedS, and SeiS only. From the three Atlantic seamounts 215[3] species, distributed over 26 families, have been reported (Table 4). Many more species are yet to be determined, however, since studies often focus on particular families. George & Schminke (2002) for example found 28 families, but studied only 11 families at species-level, with two others studied subsequently (Paramesochridae: Plum & George 2009; Zosimeidae: Koller & George 2011). Owing to the continual revision of Harpacticoida systematics and nomenclature, with groups (re-) combined and/or split, it is essential to identify specimens to the species-level for faunistic and biogeographic research. For instance, George & Schminke (2002) listed *Malacopsyllus* sp. as the single member of Stenocopiinae, but Corgosinho & Martínez Arbizu (2010) demonstrated that this genus in fact belongs to Argestidae. Also, Diosaccidae were determined to be a subfamily within Miraciidae (Willen 2000), but were still listed as a distinct family by George and Schminke (2002). Finally, Zosimeidae were moved from Tisbidae and elevated to family by Seifried (2003) having been listed as Tisbidae by George & Schminke (2002).

From the 215 species found at GMS, SedS, and SeiS, only four have been reported previously from regions other than seamounts (Table 4, Fig. 4).

The number of described species recorded on seamounts is relatively low, with 9 new descriptions (Table 4: species marked with *) and 4 species first recorded elsewhere (grey marked taxon fields in Table 4), totalling 6.5 % of all harpacticoid species listed in Table 4. Clearly there is an urgent need for more taxonomic species descriptions to enable further chorological, phylogenetic, and biogeographic investigation.

George & Schminke (2002) provided a faunistic analysis based on 56 harpacticoid species from the above mentioned 11 selected families (Table 4). Fifty-four species were previously unknown to science, only *Retrocalcar brattstroemi* (Geddes, 1981) (Cletopsyllidae) and *Laophontodes typicus* (Ancorabolidae) had been reported from other localities. *R. brattstroemi* was described from the littoral of a lagoon in the Bahamas (Geddes 1981). However, recent re-examination of the GMS *L. typicus* material in direct comparison with material kindly provided by Ms M. Lowe (Natural History Museum, London, UK) raised doubts as to its unequivocal designation. The GMS material is therefore named *L.* cf. *typicus* and treated as a new species. An additional species, *Dorsiceratus ursulae* George, 2006 was collected from the GMS slope (George & Schminke 2002, George 2006)

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[3] In the following, species that have been found at a seamount's base or slope only (i.e. *Ancorabolus chironi*, *Dorsiceratus ursulae* George, 2006, *Emertonia schminkei* [Veit-Köhler & Drewes, 2009], *E. diva* [Veit-Köhler, 2005]) are not considered in the chorological considerations, as they focus on the distribution of the summit fauna.

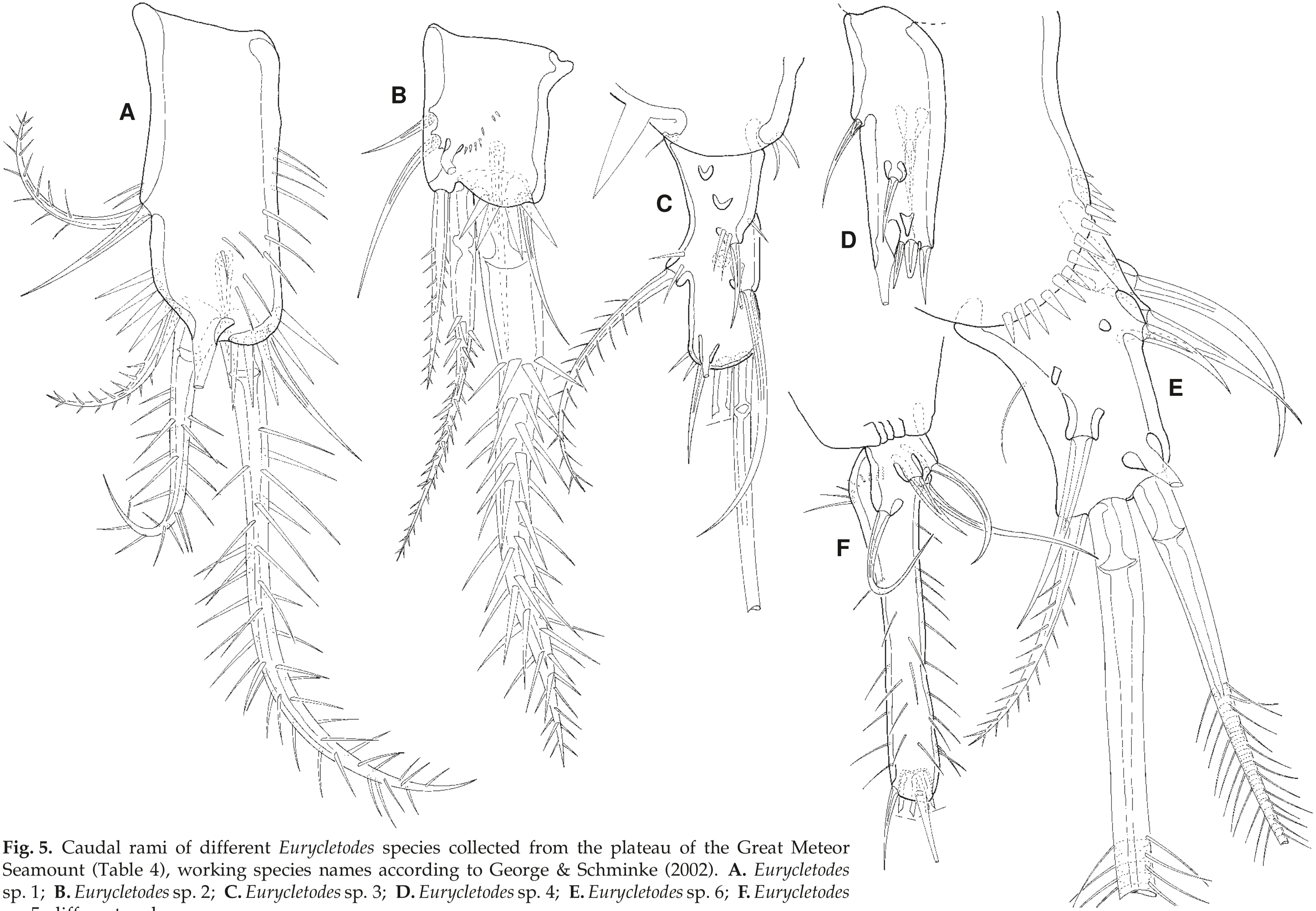

Fig. 5. Caudal rami of different *Eurycletodes* species collected from the plateau of the Great Meteor Seamount (Table 4), working species names according to George & Schminke (2002). **A.** *Eurycletodes* sp. 1; **B.** *Eurycletodes* sp. 2; **C.** *Eurycletodes* sp. 3; **D.** *Eurycletodes* sp. 4; **E.** *Eurycletodes* sp. 6; **F.** *Eurycletodes* sp. 5; different scales.

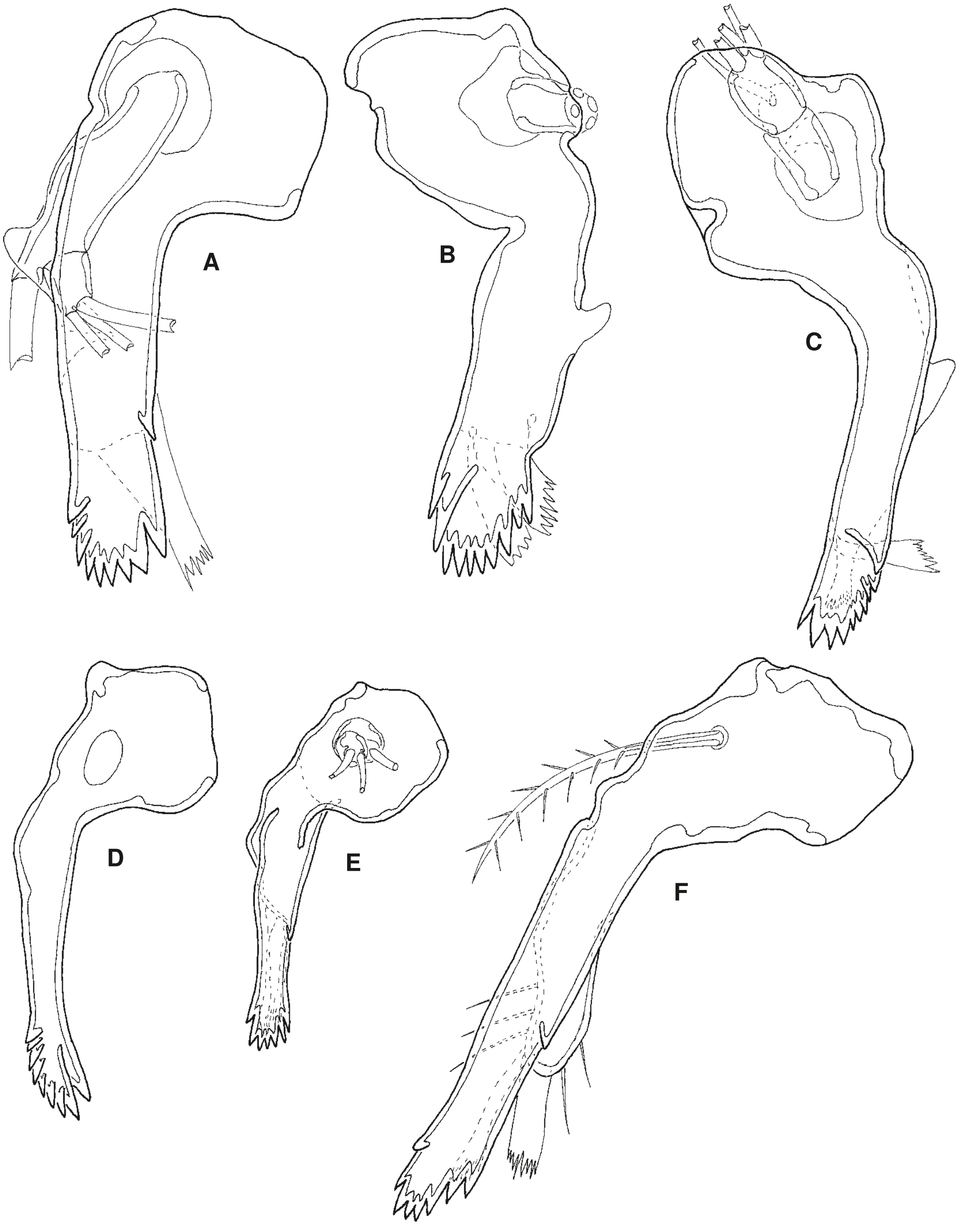

Fig. 6. Mandibles of different *Eurycletodes* species collected from the plateau of the Great Meteor Seamount (cf. Table 4), working species names according to George & Schminke (2002). **A.** *Eurycletodes*. sp. 1; **B.** *Eurycletodes*. sp. 2; **C.** *Eurycletodes*. sp. 3; **D.** *Eurycletodes* sp. 4; **E.** *Eurycletodes*. sp. 5; **F.** *Eurycletodes* sp. 6; different scales.

and was therefore excluded from the evaluation. George & Schminke (2002) concluded that a continuous exchange of harpacticoids did not occur at GMS, either with geography or bathymetry, and thus rejected a stepping stone or staging post function. The significantly low number of previously known species suggests instead that accidental arrivals to the seamount summit are more likely, with GMS acting as a "trapping stone": Equally, local hydrographical conditions and its geographic isolation, probably result in faunistic isolation and an endemic harpacticoid assemblage at the seamount (George & Schminke 2002). This conclusion is supported by the distribution of the highly diverse argestid fauna on the GMS plateau (George 2004a). Argestidae Por, 1986 are considered to be typical deep-sea harpacticoids inhabiting soft sediments (George 2004a, 2008). The sediments of the GMS plateau consist of biogenic calcareous sands, which support 35 different argestid species. Refining the hypothesis of George & Schminke (2002), George (2004a) suggested that seamount uplift, and the accompanying implementation of new ecological niches, enabled a remarkable radiation within the Argestidae family. For example, species of the argestid genus *Eurycletodes* Sars, 1910 (Table 4) found on the plateau show strong morphological similarities, but clearly differ with respect to furcal rami (Fig. 5) and mandibulae (Fig. 6), suggesting closely related but distinct species.

Data for Paramesochridae Lang, 1944 on GMS also support the "trapping stone" hypothesis (Plum and George 2009), with >90 % of the reported species ($S = 28$) unknown to science. Only one species on the GMS plateau was already known to science, namely *Wellsopsyllus (Intermedopsyllus) intermedius* (T. & A. Scott, 1895). A second species, *Emertonia schminkei* (Veit-Köhler & Drewes, 2009) was reported from the seamount's base in the deep sea (3009–4005 m depth), a species that was described from the Angola Basin, SE Atlantic) by Veit-Köhler & Drewes (2009).

Koller & George (2011) studied Zosimeidae on the GMS, a taxon considered to be eurybathyal and recorded from the littoral to a depth of 4015 m. It is perhaps not surprising, therefore, that of the 12 species they recorded 50 % showed a pronounced eurybathyal distribution, being present on the plateau, the slope and the base, contrary to the results of other harpacticoid studies (e.g. Argestidae: 6 %). One species, *Zosime bergensis* Drzycimski, 1967, was previously known from Norway (Drzycimski 1967) and the Porcupine Seabight, NE-Atlantic (Gheerardyn et al. 2009).

Büntzow (2011) analysed the harpacticoid fauna of the two other NE Atlantic seamounts for which species level data is available, Sedlo and Seine (Fig. 1). He recorded 262 species distributed over 26 families across the seamounts' summits (SedS: $S = 61$; SeiS: $S = 97$) and adjacent deep-sea stations ($S = 114$), it was by far the most extensive faunistic analysis of seamount meiofauna. One previously described species was detected on both seamounts: *Stylicletodes longicaudatus* (Brady & Robertson, 1880), reported from several NE Atlantic locations (see Lang 1948 and references therein), the Magellan Region (George 2005) and the Eastern Mediterranean (Büntzow 2011). Also, at one deep-sea station near SedS, *Emertonia diva* (Veit-Köhler, 2005) was found, a species described from the Angola Basin, SE Atlantic (Veit-Köhler 2005).

In contrast to the results from GMS, species on SedS and SeiS did not occur in both the deep-sea and the summit. Büntzow (2011) therefore concluded that there was no bathymetrical exchange between each seamount and its surrounding deep sea. However, he documented 10 species that were present at both seamounts and further comparison with data from GMS revealed 3 species in common, *Wellsopsyllus (Intermedopsyllus) antoniae* (Plum & George, 2009) (Table 4) and two undetermined *Emertonia* species (stated by Büntzow [2011] but not verified by that author and therefore not listed in Table 4). Thus, Büntzow (2011) concluded that, generally, seamounts act as stepping stones, in conflict with earlier harpacticoid seamount studies (George & Schminke 2002, George 2004a, Plum & George 2009).

VI. Loricifera (Fig. 2C). Members of the Loricifera have been reported from five seamounts (Table 1), but detailed studies (Tables 2 and 3) have been undertaken on only two, namely GMS and FaB. Nine Loricifera species were recorded from GMS (Gad 2004a)[4] and 14 from FaB (Heiner

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[4] Gad's (2004a) list of Loricifera is somewhat confusing. Firstly, he mentions 14 species (12 plateau plus 2 deep-sea species) (pp. 9, 14), but later names 2 nanaloricid, 3 *Pliciloricus*, and "five or six" *Rugiloricus* species, making that a total number of 10–11 species only. Thus, the list of Loricifera collected from GMS (Table 3) is restricted to those species that were explicitly named by Gad (2004a).

2004, 2008; Heiner & Kristensen 2009). FaB therefore presents a high lorifician species diversity, being comparable only with similar results found off Roscoff (France), off North Carolina (U.S.A.), and on GMS (Heiner 2005). Direct comparison of the species found on the different seamounts has not yet occurred and most species are still awaiting description. All species from GMS and FaB were new to science and five species from FaB have been described (Heiner 2004, 2008; Heiner & Kristensen 2009).

Gad (2004a), Gad & Schminke (2004), and Heiner & Kristensen (2005) discussed the origin of seamount Loricifera and the potential for radiation on seamount plateaus, while Heiner (2005) reflected on loriciferan diversity in the Atlantic Ocean. Gad (2004a) noted a remarkable loriciferan diversity on the plateau of GMS, coupled with an apparently accidental arrival of Loricifera on that seamount, and concluded that, like the harpacticoid Argestidae (George & Schminke 2002, George 2004a), Loricifera went through an "astonishing radiation" (Gad 2004a, p. 26). However, on FaB highest species numbers were counted on the slope and few species were found on the plateau (Heiner 2004, 2008; Heiner & Kristensen 2009).

VII. Nematoda (Fig. 2E). Despite being the dominant meiobenthic taxon in nearly all marine meiofauna samples, Nematoda from seamounts have not received a correspondingly high scientific attention. With the exception of JoB, nematodes have been documented from all investigated seamounts (Table 1). So far, 32 species have been reported (Epsilonematidae: $S = 17$; Draconematidae: $S = 15$; Table 2) but only from GMS (Gad 2002, 2004b, 2009). Gad (2002) described one new *Glochinema* species (Epsilonemtaidae) (Table 3), and dedicated faunistic analyses to that family (Gad 2004b) and the Draconematidae (Gad 2009), and provided lists of 'working species' without describing other new species.

Gad (2004b) showed high species diversity in the Epsilonematidae, similar to that noted for Harpacticoida (George & Schminke 2002) and Loricifera (Gad 2004a). He also found that although the generic composition of Epsilonematidae was similar at FaB and GMS, more species were observed at FaB. Interestingly, and contrary to the GMS material, nearly all epsilonematid species from FaB were already known to science, showing a polar to boreal Atlantic distribution. However, Gad (2004b) also noted that discussion of epsilonematid chorology and biogeography must be provisional, since most Epsilonematidae species have been recorded from only single locations, such limited and sporadic data restricting the value of general hypotheses.

With respect to Draconematidae, Gad (2009) proposed five different areas from which the GMS species might originate, (1) shallow-water North Atlantic habitats, (2) coastal and sublittoral Mediterranean habitats, (3) North Atlantic deep-sea cold-water coral reefs, (4) the surrounding deep sea, and (5) islands (Azores, Madeira, Canary Islands) and other neighbouring seamounts (up to 21). Gad (2009) rejected the hypothesis proposed by George (2004a) for deep-sea Argestidae that uplift of seamounts facilitated high diversity, favouring instead immigration to GMS from neighbouring geographic regions. He also applied that latter hypothesis to Epsilonematidae and Loricifera. However, like the Harpacticoida, Loricifera, and Epsilonematidae, some Draconematidae were also considered to exhibit ongoing speciation on the plateau of GMS, for example *Dracograllus* sp. 4 and *Prochaetosoma* species (Gad 2009).

VIII. Tantulocarida (Fig. 2G). With three free-living Tantulus-larvae, *Tantulacus hoegi* Huys, Andersen & Kristensen, 1992 was the first representative of the parasitic crustaceans Tantulocarida described from a seamount (FaB; Tabs. 2, 3). However, as shown in Table 1, Tantulocarida have only been sampled at GMS (George & Schminke 2002) and SeiS (Büntzow 2011) and species inventories and descriptions are urgently needed to enable faunistic analyses of their biogeography and chorology.

IX. Tardigrada (Figs. 2I, 3). After the Gastrotricha, Halacarida, and Harpacticoida, Tardigrada is the fourth meiobenthic taxon to receive relatively detailed treatment. Reported from four seamounts (GMS, SedS, SeiS, FaB; Table 1), Tardigrada were the subject of an extensive study on the Faroe Bank which included four research cruises (Hansen et al. 2001 and Hansen 2005). In the Faroe Bank study, Hansen et al. (2001) determined 35 tardigrade species (Table 2) distributed over 13 genera, but estimated that up to 60–70 species might be present there (Hansen et al. 2001). Hansen (2005) confirmed that 35 species had been found, but added one further genus, *Chrysoarctus*, without assigning a corresponding species, and changed the distribution of species between the genera. Whilst these changes were undoubtedly due to refined taxonomic determinations, Hansen (2005) did not provide an updated species list. Since only the number of taxa were provided, it is not possible to properly account for the tardigrade species in Table 3.

Only two tardigrade species have been described from seamounts (*Tanarctus bubulubus* Jørgensen & Kristensen, 2001; *Rhomboarctus aslaki* Hansen, D'Addabbo & De Zio Grimaldi, 2003), but the proportion of species known from other locations is comparatively high – 10 species plus 3 others of uncertain assignation (Table 3). As evident from Hansen's et al. (2001) publication, they were the first to undertake a detailed examination of Tardigrada on seamounts. Comparison of the FaB data with published data from other habitats revealed that the tardigrade assemblage at FaB seemed to include various components similar to those found at different latitudes (e. g. the Mediterranean, Roscoff [France], Helsingør [Denmark], Florida [U.S.A.], and the Arctic). Consequently, they concluded that substrate characteristics may be of greater importance than temperature for tardigrade assemblages (Hansen et al. 2001). This hypothesis is supported by the fact that, except for one scientifically known species, all known Tardigrada on FaB were previously found in the Mediterranean. Two of these species were originally described from the Arctic (Hansen et al. 2001). Also, one new but unpublished genus, namely Florarctinae nov. gen. 1 et nov. sp. 1 had been earlier found in deep-sea sediments off Chile (Hansen 2005).

It is noteworthy that, as with the Nematoda, seamounts appear to play an important role in the geographical distribution of Tardigrada, which combined with favourable conditions enabled certain taxa to radiate on them. Hansen et al. (2001) observed evident radiation in *Tanarctus* Renaud-Debyser, 1959, with eight new species recorded at FaB (plus one additional species that was not considered in further analyses). In contrast, the dominant genus *Actinarctus* Schulz, 1935, shows no morphological modifications which could point to speciation processes (Hansen et al. 2001).

Concluding remarks

The compilation of literature and data presented here emphasises the need for more studies on seamount meiofauna (McClain 2007). Taxonomic and faunistic aspects of metazoan seamount meiofauna have been addressed in 37 published papers (Tables 3, 4), or 45 papers if including contributions in which (selected) meiobenthic major taxa (mainly Nematoda, Harpacticoida, Kinorhyncha and Ostracoda) were studied as part of a larger investigation. Of the 232 biologically studied seamounts (Samadi et al. 2007), just eight investigations have been dedicated to metazoan meiobenthos. These have identified 357 meiobenthic species, 28 of which were previously known from other locations, corresponding to 92.2 % seamount-endemic meiobenthic species. Only 48 meiobenthic species have been described (13.4 % of those found) indicating the urgency for taxonomic contributions to marine biology. Any chorological, biogeographic, or faunistic study depends on clear taxonomic determinations and hypotheses (i. e., taxonomic species descriptions); without these faunistic comparison between assemblages are useless.

Rowden et al. (2010, pp. 228–229) listed 11 "paradigms in seamount ecology" and discussed their validity. However, it is not yet possible to assess the efficacy of these paradigms for seamount meiofauna, owing to the paucity of data. Nevertheless, at least five of the proposed paradigms are relevant to the faunistic discussion on seamount meiofauna and are discussed below.

1. Seamounts are submarine "islands"; larval dispersal between seamounts is limited by oceanographic retention processes. As meiobenthos in general lack planktonic life stages, this paradigm sounds plausible when substituting "larval" by "meiobenthic". It may be supported by the high number of scientifically unknown species found on seamount summits, and by the generally low number of species shared with adjacent geographical areas or the surrounding deep sea. Nevertheless, there are some species collected from seamounts that show a wide distribution (e. g. several Tardigrada, some Halacarida, and two Harpacticoida), demonstrating that meiobenthic species can be transported to high-sea shallow-water areas and therefore qualifying this first paradigm. So far, there is no evidence to confirm or refute the presence of meiobenthic relict species on seamounts.

2. Seamounts have high levels of endemism. It is not the aim of this contribution to discuss whether earlier assumptions that seamounts are areas of high endemism are or are not premature. In fact, such a claim cannot be made for meiofauna since only eight seamounts have been investigated for meiofauna. Nevertheless, so far most of the reported seamount meiobenthos has not been found elsewhere. The only way to prove or disprove that there are high levels of meiobenthic endemism on seamounts is to increase meiobenthic seamount research, including the sampling of adjacent regions and the deep sea immediately surrounding seamounts.

3. Seamounts are "stepping stones" for dispersal. Talking about seamounts as stepping stones for meiofauna may sound somewhat exaggerated, as the term "stepping stone" may suggest a somewhat "purposeful" act of dispersal in search of perhaps favourable environmental conditions or less competition, which is certainly not the case when talking about wide geographic dispersal of meiofauna. Nonetheless, meiobenthic organisms, particularly those from shallow waters, may disperse via different pathways or mechanisms. When this includes suspension in the water column or floating, the subsequent settlement to the seafloor may incidentally occur on to a seamount, and if meiobenthos subsequently drifted away from that seamount, then its role may be interpreted as that of a stepping stone.

4. Seamount communities are at risk from disturbance by bottom trawling. For many decades the GMS, as with other seamounts near the South Azores) has been the object of economically orientated exploitation by fishing and bottom trawling (Clark et al. 2007). The mega- and macrofauna of the GMS plateau has been impoverished drastically in the past >40 years by extensive trawling (Hempel & Nellen 1972, Brenke 2002, Piepenburg & Müller 2004, Brenke et al. 2010), therefore supporting Rowden's et al. (2010) paradigm. Meiofaunal diversity, however, shows no such decrease in abundance or diversity.

During cruise P397 of RV "POSEIDON" in March 2010 (George 2010), a grid of 21 stations on the plateau of GMS was sampled for meiofauna, using a van-Veen grab (0.1 m^2) to collect three to five samples per station. An initial analysis of the sorted material (George pers. obs.) suggests a relatively abundant and diverse meiofauna including most of the major taxa reported by George & Schminke (2002). This suggests that meiofauna are much more robust to the effects of bottom trawling. The observed decrease in macro- and megabenthos on the plateau may even enhance the formation of an abundant and diverse meiobenthic assemblage, as has been recorded and established as "general rule" for other habitats (Gad & Schminke 2004).

5. Seamounts are "hotspots" of species richness. The seamounts so far investigated support a diverse meiobenthic summit fauna. This diversity potentially indicates enhanced speciation by radiation as observed in some Harpacticoida (George 2004a), in Epsilonematidae (Gad 2004b), and in Tardigrada (Hansen et al. 2001). Future investigation of areas adjacent to seamounts will be needed to determine if the high number of closely related but distinct species found on seamount summits is a result of radiation on the summits or of immigration from other localities.

These comments on seamount meiofauna are only preliminary, because the available faunistic meiobenthic data is inadequate. Some species show a wide distribution whilst others are found only on seamounts and are potentially endemic. However, records are scarce, meiobenthic species often collected at single sites, and it is therefore not possible to reach conclusions regarding meiobenthic distributional patterns. To ascertain whether seamounts act as stepping stones, staging posts, or trapping stones for metazoan meiobenthos, chorological, faunistic, and biogeographic analyses are required. Such analyses will need comprehensive data on the meiobenthos from seamounts, adjacent islands, the surrounding deep sea, and from continental areas. Such an approach requires taxonomic expertise to be sustained, but it has shown an alarming decline in recent years.

Outlook

From a chorological, faunistic and biogeographic point of view, the main questions regarding the role of seamounts in the dispersal of meiobenthos still remain unanswered. They are:

1 Do some seamounts act as staging posts / stepping stones for shallow-water meiobenthos? If they did, would this contribute to an explanation of the "meiofauna paradox"?
2 Do some seamounts act as "trapping stones", confining meiobenthic organisms and preventing them from leaving the seamount?
3 What are the main reciprocal effects between seamounts and meiobenthic taxa that result in staging post/stepping stone/trapping stone effects?

One major conclusion from this review of the published literature is the necessity to increase the extent of meiofauna sampling on seamounts. Only comprehensive sampling, preferably including other nearby seamounts, islands, mainland subtidal, and the surrounding deep sea, will enable thorough faunistic and biogeographic understanding of meiofaunal assemblages, and thus help answer the above questions. Certainly, over the past 10 years the number of Atlantic seamounts which have been sampled for meiofauna has increased considerably. Whilst some of this material has been investigated (Fig. 1, triangles), more, both qualitative and quantitative, is awaiting examination (Fig. 1, circles). Cruise P397 of RV "POSEIDON" to GMS (George 2010) was the first to collect multiple meiobenthic samples from that seamount using a single sampling device. This finally enabled direct and quantitative analysis of meiofaunal communities across the 21 stations. Essentially, it will enable the completion of a meiobenthic inventory, thorough comparison with corresponding material from other NE Atlantic seamounts, and thus refine our knowledge of the GMS's role in meiofaunal distribution.

In the context of including islands in future faunistic analyses, an ongoing investigation also aims to thoroughly inventory the Harpacticoida of Madeira and Porto Santo islands (both Portugal). Additionally, comparisons of the harpacticoid assemblages on adjacent seamounts, in particular Seine and Ampère as well as GMS, and qualitative material from Hyères and Irving seamounts (Fig. 1), will be included. Furthermore, RV "METEOR" cruise M 79/3 to Senghor Seamount (eastern Atlantic, Fig. 1) provides meiobenthic material (Kieneke & Büntzow 2011). Finally, a third project will inventory and compare the Harpacticoida on two seamounts of the Eastern Mediterranean, namely Anaximenes and Eratosthenes seamounts (Fig. 1). A subsequent comparison of the Mediterranean and NE Atlantic seamount data will attempt to determine any differences or similarities between their meiofaunal assemblages, facilitating the creation of general conclusions regarding the above listed questions.

Acknowledgments

I am greatly indebted to Drs Iben Bang-Berthelsen (Søborg, Denmark), Reinhardt Møbjerg Kristensen (Copenhagen, Denmark), and David Thistle (Tallahassee, U.S.A.) for providing literature and reference support. Dr D. Thistle also kindly provided the author with a list of Harpacticoida sampled from Fieberling Guyot. Two anonymous reviewers provided helpful critics on the manuscript. I am particularly grateful to Dr Natalie Barnes (London, UK) for the enormous help with the English text.

References

Andres, H. G. (2004). *Ingolfiella sandroruffoi* sp. nov. (Crustacea: Amphipoda: Ingolfiellidae) from the Great Meteor Seamount (north-eastern Atlantic Ocean). Mitteilungen des hamburger zoologischen Museums und Instituts 101: 225–236.

— (2005). *Ingolfiella georgei* sp. nov. (Crustacea: Amphipoda: Ingolfiellidae) recorded from the Atlantic Seine Seamount northeast of Madeira Islands. Mitteilungen des hamburger zoologischen Museums und Instituts 102: 71–84.

Armonies, W. (1988). Active emergence of meiofauna from intertidal sediment. Marine Ecology Progress Series 43: 151–159.

— (1990). Short-term changes of meiofaunal abundance in intertidal sediments. Helgoländer Meeresuntersuchungen 44: 375–386.

— (1994). Drifting meio- and macrobenthic invertebrates on tidal flats in Königshafen: a review. Helgoländer Meeresuntersuchungen 48: 299–320.

Artois, T., D Fontaneto, W. D. Hummon, S. J. McInnes, M. A. Todaro, M. V. Sørensen & A. Zullini (2011). Ubiquity of microscopic animals? Evidence from the morphological approach in species identification. In: Biogeography of microscopic organisms. Is everything small everywhere? Fontaneto, D. (ed.), pp. 244–283. Cambridge University Press, Cambridge, UK.

Bartsch, I. (1973a). Halacaridae (Acari) von der Josephinebank und der Großen Meteorbank aus dem östlichen Nordatlantik. I. Die Halacaridae aus den Schleppnetzproben. "Meteor" Forschungs-Ergebnisse D 13: 37–46.

— (1973b). Halacaridae (Acari) von der Josephinebank und der Großen Meteorbank aus dem östlichen Nordatlantik. II. Die Halacaridae aus den Bodengreiferproben. "Meteor" Forschungs-Ergebnisse D 15: 51–78.

— (1973c). *Copidognathus raekor*, eine neue Halacaridae (Acari) von der Großen Meteorbank. “Meteor” Forschungs-Ergebnisse D 16: 65–68.

— (1991). On the identity of some North Atlantic halacarid species (Acari). Journal of Natural History 25: 1339–1353.

— (2001a). A new halacarid genus (Acari: Halacaridae: Halacarinae) from the Great Meteor Seamount, Eastern North Atlantic. Specis Diversity 6: 117–125.

— (2001b). *Agauopsis* (Arachnida: Acari: Halacaridae) from the Northeastern Atlantic, description of two new species, *A. minor* (Trouessart) and *Agauopsis valida* sp. nov. Mitteilungen des hamburger zoologischen Museums und Instituts 98: 63–75.

— (2002a). Halacaridae (Acari) from the Great Meteor Seamount (northeastern Atlantic): Description of two new *Copidognathus* species. Entomologische Mitteilungen des Museums Hamburg 14 (166): 71–82.

— (2002b). Halacarids from the Great Meteor Seamount (northeastern Atlantic). Description of new species of the genera *Agauopsis*, *Atelopsalis* and *Halacarus* and redescription of *H. spiniger* Bartsch (Arachnida: Acari: Halacaridae). Mitteilungen des hamburger zoologischen Museums und Instituts 99: 29–45.

— (2003). Lohmannellinae (Halacaridae: Acari) from the Great Meteor Seamount (northeastern Atlantic). Description of new species and reflections on the origin of the seamount fauna. Mitteilungen des hamburger zoologischen Museums und Instituts 100: 101–117.

— (2004a). *Copidognathus leiodermus* sp. n. (Copidognathinae: Halacaridae: Acari), eine neue Art von der Großen Meteor Bank (nordöstlicher Atlantik). Entomologische Mitteilungen des Museums Hamburg 14(169): 171–179.

— (2004b). Halacaridae (Acari) from the Great Meteor Seamount (Northeastern Atlantic). Description of *Simognathus* species. Mitteilungen des hamburger zoologischen Museums und Instituts 101: 185–196.

Boeckner, M. J., J. Sharma & H. C. Proctor (2009). Revisiting the meiofauna paradox: dispersal and colonization of nematodes and other meiofaunal organisms in low- and high-energy environments. Hydrobiologia 624: 91–106.

Boehlert, G. W. & A. Genin (1987). A review of the effects of seamounts on biological processes. In: Seamounts, islands, and atolls, Keating, B. H., P. Fryer, R. Batiza & G. W. Boehlert (eds.). Geophysical Monographs 43: 319–334.

Brenke, N. (2002). The benthic community of the Great Meteor Bank. ICES Annual Science Conference and ICES Centenary, 1.–5. October 2002, Copenhagen, Theme Session M, paper M30 (unpublished): 1–12.

Brenke, N., S. Keller, T. Molodtsova & K. H. George (2010). Macro- und Mega-Epifauna. In: George, K. H. Die Große Meteorbank (Nordost-Atlantik) – Trittstein oder Abstellgleis? Quantitative Untersuchungen zur Verbreitung, der Diversität und em Ursprung der benthonischen Kuppenfauna. Cruise P397 of RV “POSEIDON” from 10.03.–29.03.2010: 8–9.

Büntzow, M. (2011). Vergleichende gemeinschaftsanalytische und taxonomische Untersuchungen der Harpacticoidenfauna der Seeberge “Sedlo” und “Seine” (nördlicher Mittelatlantik). Doctoral thesis, pp. 1–128. Carl-von-Ossietzky-Universität, Oldenburg, Germany.

Cecca, F. (2002). Palaeobiogeography of marine fossil invertebrates – concepts and methods. Taylor and Francis, London, UK.

Christiansen, B. & G. Wolff (eds.) (2009). The oceanography, biogeochemistry and ecology of two NE Atlantic seamounts: OASIS. Deep-Sea Research II 56: 2579–2730.

Clark, M. R., V. I. Vinnichenko, J. D. M. Gordon, G. Z. Beck-Bulat, N. N. Kukharev & A. F. Kakora (2007). Large-scale distant-water trawl fisheries on seamounts. Pp. 361–399 in: Pitcher, T. J., T. Morato, P. J. B. Hart, M. R. Clark, N. Haggan & R. S. Santos (eds.): Seamounts: Ecology, fisheries and conservation. Blackwell Publishing Oxford, UK.

Clark, M. R., A. A. Rowden, T. A. Schlacher, A. Williams, M. Consalvey, K. I. Stocks, A. D. Rogers, T. D. O’Hara, M. White, T. M. Shank & J. M. Hall-Spencer (2010). The ecology of seamounts: structure, function, and human impacts. Annual Review of Marine Science 2: 253–278.

Clausen, C. (2004). Gastrotricha from the Faroe Bank. Sarsia 89: 423–458.

Corgosinho, P. H. C. & P. Martínez Arbizu (2010). Ameiridae Boeck and Argestidae Por revisited, with establishment of Parameiropsidae, a new family of Harpacticoida (Crustacea, Copepoda) from deep-sea sediments. Helgoland Marine Research 64: 223–255.

Drzycimski, I. (1967). Zwei neue Harpacticoida (Copepoda) aus dem westnorwegischen Küstengebiet. Sarsia 30: 75–82.

Emschermann, P. (1971). *Loxomespilon perezi* – ein Entoproctenfund im Mittelatlantik. Überlegungen zur Benthosbesiedlung der Großen Meteorbank. Marine Biology 9: 51–62.

Fegley, S. R. (1988). A comparison of meiofaunal settlement onto the sediment surface and recolonization of defaunated sandy sediment. Journal of Experimental Marine Biology and Ecology 123: 97–113.

Fenchel, T. & B. J. Finlay (2004). The ubiquity of small species: Patterns of local and global diversity. Bioscience 54 (8): 777–784.

Finlay, B. J. (2002). Global dispersal of free-living microbial eukaryote species. Science 296: 1061–1063.

Fleeger, J. W., G. T. Chandler, G. R. Fitzhugh & F. E. Phillips (1984). Effects of tidal currents on meiofauna densities in vegetated salt marsh sediments. Marine Ecology Progress Series 19: 49–53.

Fontaneto, D. (ed.) (2011). Biogeography of microscopic organisms. Is everything small everywhere? Cambridge University Press, Cambridge, UK.

Gad, G. (2002). The relation between habitus and habitat structure as evidenced by a new species of *Glochinema* (Nematoda, Epsilonematidae) from the plateau of the Great Meteor Seamount. Hydrobiologia 474: 171–182.

— (2004a). The Loricifera fauna of the plateau of the Great Meteor Seamount. Archive of Fishery and Marine Research 51 (1–3): 9–29.

— (2004b). Diversity and assumed origin of the Epsilonematidae (Nematoda) of the plateau of the Great Meteor Seamount. Archive of Fishery and Marine Research 51 (1–3): 30–42.

— (2009). Colonisation and specialisation on seamounts, evidence from Draconematidae (Nematoda) of the Great Meteor Seamount. Marine Biodiversity 39: 57–69.

Gad, G. & H. K. Schminke (2004). How important are seamounts for the dispersal of interstitial meiofauna? Archive of Fishery and Marine Research 51 (1–3): 43–54.

Geddes, D. C. (1981). Marine biological investigations in the Bahamas. 21. A new species of *Cletopsyllus* (Copepoda, Harpacticoida). Sarsia 66: 287–291.

George, K. H. (2004a). 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. Organisms, Diversity & Evolution 4: 241–264.

— (2004b). *Meteorina magnifica* gen. et sp. nov., a new Idyanthidae (Copepoda, Harpacticoida) from the plateau of the Great Meteor Seamount (Eastern North Atlantic). Meiofauna Marina 13: 95–112.

— (2005). Sublittoral and bathyal Harpacticoida (Crustacea: Copepoda) of the Magellan region. Composition, distribution and species diversity of selected major taxa. Scientia Marina 69 (2): 147–158.

— (2006). New Ancorabolinae Sars, 1909 (Copepoda, Harpacticoida, Ancorabolidae) of the Atlantic Ocean. Description of *Pseudechinopsyllus sindemarkae* gen. et sp. nov. and *Dorsiceratus ursulae* sp. nov. from the Great Meteor Seamount, and redescription of *D. octocornis* Drzycimski, 1967, and *D. triarticulatus* Coull, 1973 (part.). Meiofauna Marina 15: 123–156.

— (2008). *Argestes angolaensis* sp. nov. (Copepoda: Harpacticoida: Argestidae) from the Angola Basin (Southeast Atlantic), and the phylogenetic characterization of the taxon *Argestes* Sars, including the rediscription of *A. mollis* Sars, 1910, and *A. reductus* (Itô, 1983). Zootaxa 1866: 223–262.

— (2010). Die Große Meteorbank (Nordost-Atlantik) – Trittstein oder Abstellgleis? Quantitative Untersuchungen zur Verbreitung, der Diversität und em Ursprung der benthonischen Kuppenfauna. Cruise P397 of RV "POSEIDON" from 10.03.–29.03.2010, 11 pp. http://www.ifm-geomar.de/index.php?id=6231

George, K. H. & P. Martínez Arbizu (2005). Discovery of Superornatiremidae Huys (Copepoda, Harpacticoida) outside anchialine caves, with the description of *Gideonia noncavernicola* gen. et sp. nov. from the Patagonian continental slope (Chile). Meiofauna Marina 14: 75–89.

George, K. H. & C. Plum (2009). Description of two new species of *Dorsiceratus* Drzycimski, 1967 (Copepoda: Harpacticoida: Ancorabolidae) from Sedlo and Seine Seamounts (Northeastern Atlantic) and remarks on the phlogenetic status of the genus. Zootaxa 2096: 257–286.

George, K. H. & H. K. Schminke (2002). Harpacticoida (Crustace, Copepoda) of the Great Meteor Seamount, with first conclusions as to the origin of the plateau fauna. Marine Biology 144: 887–895.

Gerlach, S. A. (1977). Means of meiofauna dispersal. Mikrofauna Meeresboden 61: 89–103

Gheerardyn, H., M. De Troch, M. Vincx & A. Vanreusel (2009). Harpacticoida (Crustacea: Copepoda) associated with cold-water coral substrates in the Porcupine Seabight (NE Atlantic): species composition, diversity and reflections on the origin of the fauna. Scientia Marina 73 (4): 747–760.

Giere, O. (2009). Meiobenthology. The microscopic motile fauna of aquatic sediments. Springer Verlag Berlin, Germany.

Hagerman, G. M. & R. M. Rieger (1981). Dispersal of benthic meiofauna by wave and current action in Bogue Sound, Northa Carolina, USA. Marine Ecology 2 (3): 245–270.

Hansen, J. G. (2005). The ongoing investigation of the Faroe Bank tardigrade fauna. Biofar Proceedings 2005: 220–223.

Hansen, J. G., M. Gallo D'Addabbo & S. De Zio Grimaldi (2003). A comparison of morphological characters within the genus *Rhomboarctus* (Tardigrada: Heterotardigrada) with the description of two new species. Zoologischer Anzeiger 242: 83–96.

Hansen, J. G., A. Jørgensen & R. M. Kristensen (2001). Preliminary studies of the tardigrade fauna of Faroe Bank. Zoologischer Anzeiger 240: 385–393.

Heiner, I. (2004). *Armorloricus kristenseni* (Nanaloricidae, Loricifera), a new species from the Faroe Bank (North Atlantic). Helgoland Marine Research 58: 192–205.

— (2005). Preliminary account of the loriciferan fauna of the Faroe Bank (NE Atlantic). Biofar Proceedings 2005: 213–219.

— (2008). *Rugiloricus bacatus* sp. nov. (Loricifera – Pliciloricidae) and a ghost-larva with paedogenetic reproduction. Systematics and Biodiversity 6 (2): 225–247.

Heiner, I. & R. M. Kristensen (2005). Two new species of the genus *Pliciloricus* (Loricifera, Pliciloricidae) from the Faroe Bank, North Atlantic. Zoologischer Anzeiger 243: 121–138.

Heiner, I. & R. M. Kristensen (2009). *Urnaloricus gadi* nov. gen. et nov. sp. (Loricifera, Urnaloricidae nov. fam.), an aberrant Loricifera with a viviparous pedogenetic life cycle. Journal of Morphology 270: 129–153.

Heinz, P., D. Ruepp & C. Hemleben (2004). Benthic foraminifera assemblages at Great Meteor Seamount. Marine Biology 144: 985–998.

Hempel, G. (1968). Biologische Arbeiten auf den Atlantischen Kuppenfahrten von FS "Meteor". Naturwissenschaftliche Rundschau 21 (3): 108–113.

Hempel, G. & W. Nellen (1972). Bericht über den Verlauf der Rossbreiten-Expedition 1970. "Meteor" Forschungs-Ergebnisse A 10: 51–78.

Hockin, D. C. (1982). Experimental insular zoogeography: some tests of the equilibrium theory using meiobenthic harpacticoid copepods. Journal of Biogeography 9: 487–497.

Hubbs, C. L. (1959). Initial discoveries of fish faunas on seamounts and offshore banks in the eastern Pacific. Pacific Science 13: 311–316.

Huys, R., P. F. Andersen & R. M. Kristensen (1992). *Tantulacus hoegi* gen. et sp. nov. Tantulocarida: Deoterthridae) from the meiobenthos of the Faroe Bank, North Atlantic. Sarsia 76: 287–297.

Jørgensen, A. & R. M. Kristensen (2001). A new tanarctid arthrotardigrade with buoyant bodies. Zoologischer Anzeiger 240: 425–439.

Kieneke, A. & M. Büntzow (2011). Meiobenthos. In: Christiansen, B., T. Brand, M. Büntzow, J. Busecke, R. Coelho, S. Correia, A. Denda, T. Diniz, S. Jung, M. Kaufmann, A. Kieneke, K. Kiriakoulakis, R. Koppelmann, J. Kuhnert, T. Kwasnitschka, P. Lamont, B. Martin, J. Montgomery, F. Peine, A. Piedade, T. Reichelt, V. Rieger, A. Schmidt, H. Stahl, J. Tiedke, T. Truscheit, R. Turnewitsch, K. Unger, S. Vogel & C. Warneke-Cremer. Structure and Function of Seamount Ecosystems in the Cape Verde Region, Northeast Atlantic. Cruise No. M79, Leg 3. "Meteor"-Berichte 11-1: 27–30.

Kitchingman, A., S. Lai, T. Morato & D. Pauly (2007). How many seamounts are there and where are they located? Pp. 27–40 in: Pitcher, T. J., T. Morato, P. J. B. Hart, M. R. Clark, N. Haggan & R. S. Santos (eds.): Seamounts: Ecology, fisheries and conservation. Blackwell Publishing Oxford, UK.

Koller, S. & K. H. George (2011). Description of a new species of *Zosime* Boeck, 1872 (Copepoda: Harpacticoida: Zosimeidae) from the Great Meteor Seamount, representing one of the few eurybathic Harpacticoida among the distinct plateau and deep-sea assemblages. Meiofauna Marina 19: 109–126.

Kristensen, R. M. (2005). Fifteen years investigation of the meiofauna of the Faroe Bank (NE Atlantic). Biofar Proceedings 2005: 202–212.

Lang, K. (1948). Monographie der Harpacticiden I & II. Reprint 1975. Otto Koeltz Science Publishers, Königstein, Germany.

Levin, L. A. (1991). Interactions between metazoans and large, agglutinating protozoans: Implications for the community structure of deep-sea benthos. American Zoologist 31: 886–900.

Levin, L. A. & C. L. Thomas (1988). The ecology of xenophyophores (Protista) on eastern Pacific seamounts. Deep Sea Research 35 (12): 2003–2027.

Levin, L. A. & C. L. Thomas (1989). The influence of hydrodynamic regime on infaunal assemblages inhabiting carbonate sediments on central Pacific seamounts. Deep-Sea Research 36 (12): 1897–1915.

Levin, L. A. D. J. DeMaster, L. D. McCann & C. L. Thomas (1986). Effects of giant protozoans (class: Xenophyophorea) on deep-seamount benthos. Marine Ecology Progress Series 29: 99–104.

MacArthur, R. H. & E. O. Wilson (1967). The theory of island biogeography. Princeton University Press, Princeton (NJ).

McClain, C. R. (2007). Seamounts: identity crisis or split personality? Journal of Biogeography 34/12: 2001–2008.

Menzel, L., K. H. George & P. Martínez Arbizu (2011). Submarine ridges do not prevent large-scale dispersal of abyssal fauna: A case study of *Mesocletodes* (Crustacea, Copepoda, Harpacticoida). Deep-Sea Research I 58: 839–864.

Mironov, A. N. & E. M. Krylova (2006). Origin of the fauna of the Meteor Seamounts, north-eastern Atlantic. Pp. 22–57 in: Mironov, A. N., A. V. Gebruk & A. J. Southward (eds.): Biogeography of the North Atlantic seamounts. KMK Scientific Press, Moscow.

Mironov, A. N., A. V. Gebruk & A. J. Southward (eds.) (2006). Biogeography of the North Atlantic seamounts. KMK Scientific Press, Moscow.

Moseley, H. N. (1880). Deep-sea dredging and life in the deep sea I. Nature 21: 543–547.

Palmer, M. A. (1988). Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. Marine Ecology Progress Series 48: 81–91.

Palmer, M. A. & G. Gust (1985). Dispersal of meiofauna in a turbulent tidal creek. Journal of Marine Research 43: 179–210.

Parker, T. & V. Tunnicliffe (1994). Dispersal strategies of the biota on an oceanic seamount: Implications for ecology and Biogeography. Biological Bulletin 187: 336–345.

Piepenburg, D. & B. Müller (2004). Distribution of epibenthic communities on the Great Meteor Seamount (North-east Atlantic) mirrors pelagic processes. Archive of Fishery and Marine Research 51 (1–3): 55–70.

Pitcher, T. J., T. Morato, P. J. B. Hart, M. R. Clark, N. Haggan & R. S. Santos (eds.) (2007). Seamounts: Ecology, fisheries and conservation. Blackwell Publishing Oxford.

Plum, C. & K. H. George (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). Marine Biodiversity 39: 265–289.

Richer de Forges, B., J. A. Koslow & G. C. B. Poore (2000). Diversity and endemism of the benthic seamount fauna in the southwest Pacific. Nature 405: 944–947.

Rogers, A. D. (1994). The biology of seamounts. Advances in Marine Biology 30: 305–351.

Rosen, B. (1983). Reef island staging posts and Noah's arks. Reef encounter 1: 5–6.

Rowden, A. A., J. F. Dower, T. A. Schlacher, M. Consalvey & M. R. Clark (2010). Paradigms in seamount ecology: fact, fiction and future. Marine Ecology 31 (1): 226–241.

Samadi, S., T. Schlacher & B. Richer de Forges (2007). Seamount Benthos. Pp. 119–140 in: Pitcher, T. J., T. Morato, P. J. B. Hart, M. R. Clark, N. Haggan & R. S. Santos (eds.): Seamounts: Ecology, fisheries and conservation. Blackwell Publishing Oxford, UK.

Schlacher, T., A. A. Rowden, J. F. Dower & M. Consalvey (2010a). Seamount science scales undersea mountains: new research and outlook. Marine Ecology 31 (1): 1–13.

Schlacher, T., A. A. Rowden, J. F. Dower & M. Consalvey (eds.) (2010b). Recent advances in seamount ecology. Marine Ecology 31 (1): 1–241.

Schulz, M. & K. H. George (2010). *Ancorabolus chironi* sp. nov., the first record of a member of the *Ancorabolus*-group (Copepoda: Harpacticoida: Ancorabolidae) from the Mediterranean. Marine Biodiversity 40: 79–93.

Sedlacek, L. & D. Thistle (2006). Emergence on the continental shelf: differences among species and between microhabitats. Marine Ecology Progress Series 311: 29–36.

Seifried, S. (2003). Phylogeny of Harpacticoida (Copepoda): Revision of "Maxillipedasphalea" and Exanechentera. Cuivillier Verlag Göttingen.

Seifried, S. & H. K. Schminke (2003). Phylogenetic relationships at the base of Oligoarthra (Copepoda, Harpacticoida) with a new species as the cornerstone. Organisms, Diversity & Evolution 3 (1): 13–37.

Sterrer, W. (1973). Plate tectonics as a mechanism for dispersal and speciation in interstitial sand fauna. Netherlands Journal of Sea Research 7: 200–222.

Stock, J. H. (1994). Biogeographic synthesis of the insular groundwater faunas of the (sub)tropical Atlantic. Hydrobiologia 287: 105–117.

Thiel, H. (1970). Bericht über die Benthosuntersuchungen während der "Atlantischen Kuppenfahrten 1967" von F.S. "Meteor". "Meteor" Forschungs-Ergebnisse D 7: 23–42.

— (1972). Die Bedeutung der Meiofauna in küstenfernen benthischen Lebensgemeinschaften verschiedener geographischer Regionen. Verhandlungsbericht der Deutschen Zoologischen Gesellschaft, Gustav Fischer Verlag Berlin: 37–42.

Thistle, D. (1998). Harpacticoid copepod diversity at two physically reworked sites in the deep sea. Deep-Sea Research II 45: 13–24.

— (2003). Harpacticoid copepod emergence at a shelf site in summer and winter: implications for hydrodynamic and mating hypotheses. Marine Ecology Progress Series 248: 177–185.

Thistle, D. & L. A. Levin (1998). The effect of experimentally increased near-bottom flow on metazoan meiofauna at a deep-sea site, with comparison data on macrofauna. Deep-Sea Research I 45: 625–638.

Thistle, D. & L. Sedlacek (2004). Emergent and non-emergent species of harpacticoid copepods can be recognized morphologically. Marine Ecology Progress Series 266: 195–200.

Thistle, D., L. A. Levin, A. J. Gooday, O. Pfannkuche & P. J. D. Lambshead (1999). Physical reworking by near-bottom flow alters the metazoan meiofauna at Fieberling Gyot (northeast Pacific). Deep-Sea Research I 46: 2041–2052.

Ullberg, J. (2004). Dispersal in free-living, marine, benthic nematodes: Passive or active processes? Doctoral Dissertation, University of Stockholm.

Veit-Köhler, G. (2005). First deep-sea record of the genus *Kliopsyllus* Kunz, 1962 (Copepoda: Harpacticoida) with the description of *Kliopsyllus diva* sp. n. – the most abundant member of Paramesochridae at two different sites of the Angola Basin. Organisms, Diversity & Evolution 5 (1): 29–41.

Veit-Köhler, G. & J. Drewes (2009). *Kliopsyllus schminkei* sp. n. (Copepoda, Harpacticoida, Paramesochridae) – a new copepod from the southeast Atlantic deep sea (Angola Basin). Zootaxa 2096: 313–326.

Walters, K. & S. S. Bell (1986). Diel patterns of active vertical migration in seagrass meiofauna. Marine Ecology Progress Series 34: 95–103.

Wessel, P. (2007). Seamount characteristics. Pp. 3–25 in: Pitcher, T. J., T. Morato, P. J. B. Hart, M. R. Clark, N. Haggan & R. S. Santos (eds.): Seamounts: Ecology, fisheries and conservation. Blackwell Publishing Oxford.

Westheide, W. (1987). The interstitial polychaete *Hesionides pettiboneae* n. sp. (Hesionidae) from the U.S. East coast and its transatlantic relationships. Bulletin of the Biological Society of Washington 7: 131–139.

Willen, E. (2000). Phylogeny of the Thalestridimorpha Lang, 1944 (Crustacea, Copepoda). Cuvillier Verlag Göttingen.

Wilson, R. R. & R. S. Kaufmann (1987). Seamount biota and biogeography. Geophysical Monographs 43: 355–377.

Yeatman, H. C. (1962). The problem of dispersal of marine littoral copepods in the Atlantic Ocean, including some redescriptions of species. Crustaceana 4 (4): 253–272.

Yesson, C., M. R. Clark, M. L. Taylor & A. D. Rogers (2011). The global distribution of seamounts based on 30 arc seconds bathymetry data. Deep-Sea Research I 58: 442–453.