

Three bathypelagic scolecitrichids new to the North Pacific, with comments on diagnostic features of Scolecitrichidae and Tharybidae and on the positions of *Heteramalla*, *Rythabis* and *Parkius* (Copepoda: Calanoida)

N.V. Vyshkvartzeva

Vyshkvartzeva, N.V. 2005. Three bathypelagic scolecitrichids new to the North Pacific, with comments on diagnostic features of Scolecitrichidae and Tharybidae and on the positions of *Heteramalla*, *Rythabis* and *Parkius* (Copepoda: Calanoida). *Zoosystematica Rossica*, **13**(2), 2004: 157-180.

Additional descriptions and illustrations of the females of *Heteramalla sarsi* Roe, 1975, *Amalothrix aspinosa* Roe, 1975 and *Landrumius gigas* (A. Scott, 1909), collected in the central and northwestern Pacific for the first time, are presented. The diagnostic significance of the setation of the maxillules, maxillae and maxillipeds in Scolecitrichidae, Tharybidae and Diaixidae is analyzed. The proportions of maxillule expressed as indices showing length or width of its different parts in relation to the width of the first inner lobe are proposed here as the main distinguishing characters separating Scolecitrichidae and Tharybidae, more informative than some diagnostic features of its setation. The relationships between the Bradfordian families and between sections of the family Scolecitrichidae are discussed, mainly on the basis of setation of the maxilla and maxilliped. The systematic positions of *A. aspinosa* and the genera *Heteramalla*, *Puchinta*, *Cenognatha*, *Plesioscolecithrix*, *Rythabis* and *Parkius* are discussed. A detailed comparative analysis of characters of the genus *Heteramalla* is provided. *Heteramalla* and *Puchinia* belong to the group of early offshoots of the family Scolecitrichidae, not to the central core, where they were placed by Ohtsuka with coauthors (2003) and by Boxshall & Hulsey (2004). *Rythabis* has the setation of maxillule closer to the ancestral type common to all Bradfordian families, but the proportions of maxillule typical to Tharybidae. Since the indices of maxillule do not overlap in Scolecitrichidae and Tharybidae, and the maxillule and other mouthparts show different evolutionary trends of specialization, *Rythabis* is considered as a member of the Tharybidae, where it was placed by Schulz (in Schulz & Beckmann, 1995). *Parkius* has the proportions of the maxillule intermediate between those in Scolecitrichidae and Tharybidae and unique apomorphic features recorded earlier by Ferrari & Markhaseva (1996). These unique progressive features of *Parkius* can be a result of important biological transformations, compared with the other Bradfordian families; therefore the status of the separate family Parkiidae, **fam. dist.**, is restored. The male considered as *Racovitzanus* sp. (Grice & Hulsemann, 1967) actually belongs to *Parkius*. Swimming legs 5 of this male are peculiar, fitting those neither of Scolecitrichidae nor of Tharybidae. Their structure shows a separate evolutionary trend and also justifies the family status of Parkiidae.

N.V. Vyshkvartzeva, Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St.Petersburg 199034, Russia.

Material and methods

The examined specimens were taken from plankton samples obtained during the 19th and 39th cruises of R/V "Vityaz" and the 40th cruise of R/V "Akademik Korolev" with use of big Judey net, mesh size 0.33 mm, and preserved in 4% formaldehyde. The examined specimens are kept at the Zoological Institute, St.Petersburg. The techniques of measurements, preparation of slides and drawings are described by Vyshkvartzeva (2000).

The abbreviations used in this paper are as follows: Ce – cephalosome, Pr – prosome, SmP1-SmP5 – somites bearing 1st-5th swimming legs, Ur – urosome, Ur1-Ur5 – 1st-5th urosomal somites, A1 – antennule, A2 – antenna, Md – mandible, Mx1 – maxillule (Li1 – praecoxal arthrite or gnathobase, Li2 – coxal endite, Li3 and Li4 – basal endites, Le1 – coxal epipodite), Mx2 – maxilla (Li1 and Li2 – praecoxal endites, Li3 and Li4 – coxal endites, Li5 – basal endite, Wo – worm-like seta, Br – brush-like seta), Mxp – maxilliped (Li1-Li4 – 1st-4th endites of syncoxa),

P1-P4 – 1st-4th pairs of swimming legs, P5 – 5th pair of legs, Re1-Re7 – 1st-7th segments of exopod, Ri1-Ri3 – 1st-3rd segments of endopod.

The measurements of different parts of Mx1 were made using the author's original illustrations, both published or unpublished, and employing the works of previous investigators (see references in the text). The length of Mx1 Li1 was measured along the distal margin, from distal marginal seta to the point of attachment of Li2. The width of Li1 and Le1 was measured from the proximal marginal seta to the distal marginal seta. The length of Li2+Li3+Li4+Ri was measured from the point of attachment of Li2 to the distal margin of Ri. Additionally, the length of the longest distal marginal seta of Li1 was measured. The indices representing the ratios of the following distances to the width of Mx1 Li1: (A) the length of Li1, (B) the length of the longest distal marginal seta of Li1, (C) the width of Le1, (D) the length of Li2+Li3+Li4+Ri, are calculated for the taxonomic groups under discussion.

TAXONOMIC ACCOUNT

Heteramalla sarsi Roe, 1975 (Figs 1-19)

Heteramalla sarsi Roe, 1975: 342 (341: remark); Bradford et al., 1983: 87 (88: remark); Razouls, 1995: 346.
Heteramalla dubia: Sars, 1907: 17 (part); A. Scott, 1909: 86-87 (part), pl. 33, figs 1-9; Sars, 1924: pl. 39, figs 1-16; 1925: 142-144 (part); Rose, 1933: 135 (part), fig. 130 (after Sars, 1924); ?Wilson, 1942: 69, 161, 189 (part); ?Wilson, 1950: 238, 368 (sex not indicated); Grice & Hulsemann, 1965: 221, 223, 235; Vervoort, 1965: 28-30 (part); ?Grice & Hulsemann, 1967: 16 (sex not indicated).

Material. 1 ♀, 14°00'N 133°00'W, R/V "Akademik Korolev", cruise 40, depth 2610-3920 m, XI.1985; 1 ♀, 14°00'N 132°30'W, R/V "Akademik Korolev", cruise 40, depth 1395-2610 m, 28.X.1985; 1 ♀, 45°20'N 153°54'E, R/V "Vitjaz", cruise 39, depth 0-4000 m, 19.VIII.1966.

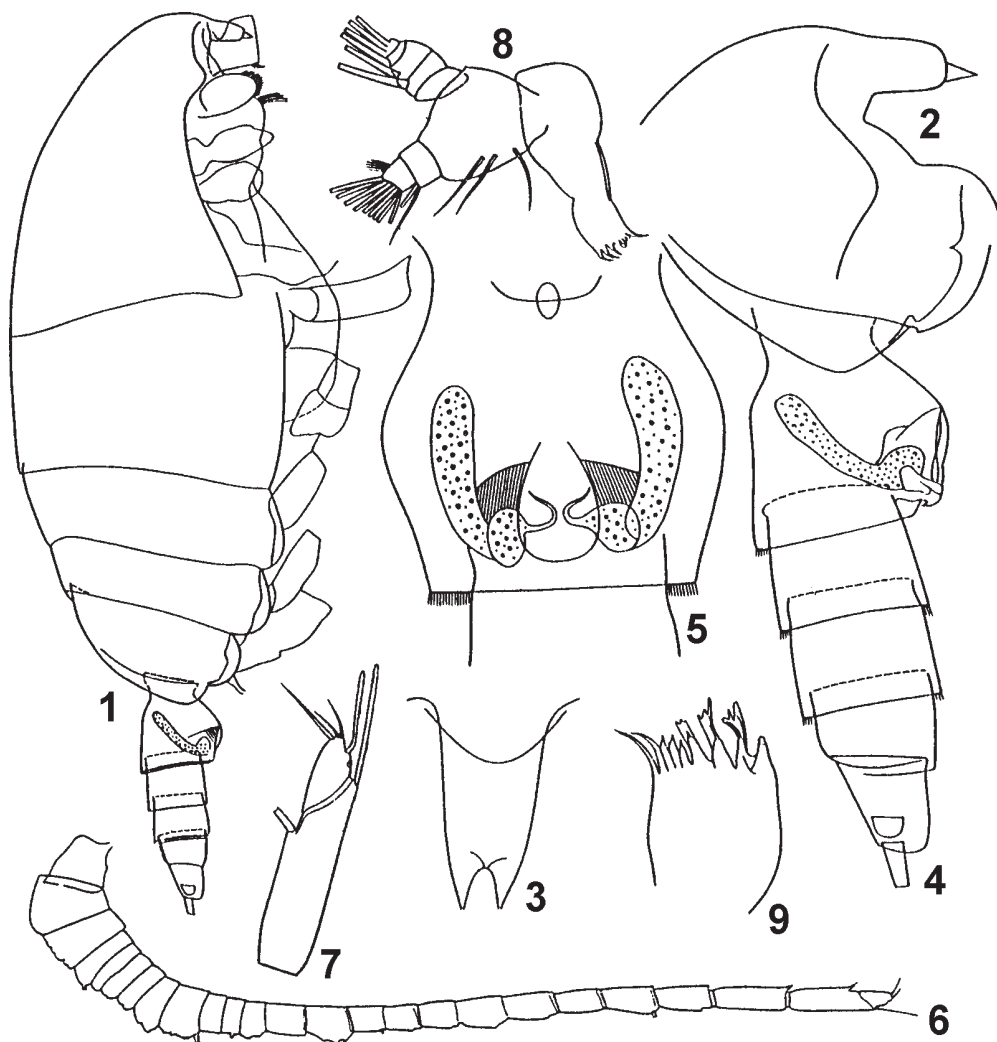
Description of female. Body length 3.41-3.78 mm (n = 3). Prosome elliptical in lateral (Fig. 1) and dorsal views. Forehead low, not produced compared with base of rostrum, broadly rounded in lateral (Fig. 2) and dorsal views. Rostrum (Fig. 3) directed ventrally, large, single, distally divided into two strong conical processes. Ce and Smp1 separated by a thin suture, as well as Smp4 and Smp5. Posterolateral corners of Smp5 not produced, laterally rounded, dorsally triangular, reaching the proximal part of genital double-somite (Fig. 4).

Urosome (Fig. 4) about 0.3 times as long as prosome. Urosomites and caudal rami with following relative lengths: 29:20:19:16:16=100. Posterior margins of Ur1-Ur3 with short spinules. Genital double-somite in dorsal view distinctly

wider than long, with highly convex sides; in lateral view, it slightly deeper than long, with a large genital prominence; spermatheca very long, finger-like, directed anterodorsally and reaching anterodorsal angle of genital double-somite (Fig. 4). Genital field in ventral view (Fig. 5) with ovoid operculum widened distally; long vesicles directed anteriorly, lateral skeletal plates not visible. Ur2-Ur4 wider than long. Caudal rami about as long as wide. Dorsal seta II shorter than caudal ramus; ventral seta VII slightly longer than caudal ramus; proximal part of apical seta VI thicker than that of apical setae III-V.

A1 (Figs 6, 7) with 24 free segments, reaching Smp5. Md and A2 in Figs 8, 9 and 10, respectively. Mx1 (Fig. 11): Li1 with 7 marginal and 1 posterior setae, Li2-Li4 with 0, 3 and 4 setae, respectively, endopod two-segmented with 3 and 4 setae, exopod with 10 setae, Le1 with 7 long and 2 shorter setae. Mx2 (Fig. 12) with 5 setae on Li1, 3 setae on each of Li2-Li4 and 4 setae on Li5 (all setae tapering and plumose). Endopod of Mx2 with 3 long worm-like sensory setae distally, 3 long brush-like setae with small apical brushes and two shorter but strongly thickened setae each with large globular apical brush; central part of each brush with numerous thin setules, surrounded on periphery by longer flattened setules with fused proximal parts. Syncoxa of Mxp (Fig. 13) with 4 inner lobes bearing, respectively: 1 seta; 1 aesthetasc-like thin-walled seta (similar to worm-like but with pointed tip); 1 short plumose + 1 long aesthetasc-like setae, similar to that of Li2; 3 plumose distal setae. Basis of Mxp with 2 medial and 1 distal setae and a row of spinules reaching proximal medial seta. Ri1-Ri6 with 2, 4, 4, 3, 3, and 2 setae, respectively; Ri1 fused with Ri2; outer setae of Ri5 and Ri6 absent.

P1 as in Fig. 14; its basis without inner seta; exopod two-segmented, endopod one-segmented. Re1 without outer spine and inner seta; Re2 and Re3 completely fused, compound segment with 2 outer spines, 4 inner and 1 apical setae (i.e., outer spine and inner seta of former Re2 retained, as well as armament of Re3 typical to scolecitrichids). Endopod one-segmented, with 3 inner and 2 apical setae and a group of spinules on posterior surface; outer lobe of endopod lacking. P2 and P4 as in Figs 15 and 18, respectively, with segmentation and setation typical to scolecitrichids. P3 (Figs 16, 17) with three-segmented exopod and two-segmented endopod (two distal segments fused; a thin suture visible on anterior surface); outer setae of Re1-Re3 rudimentary, small; apical spine of Re3 1.3 times as long as segment, finely serrated. P5 (Fig. 19) minute, slightly asymmetrical, coxa fused with intercoxal sclerite, basis longer than wide; basis of right leg



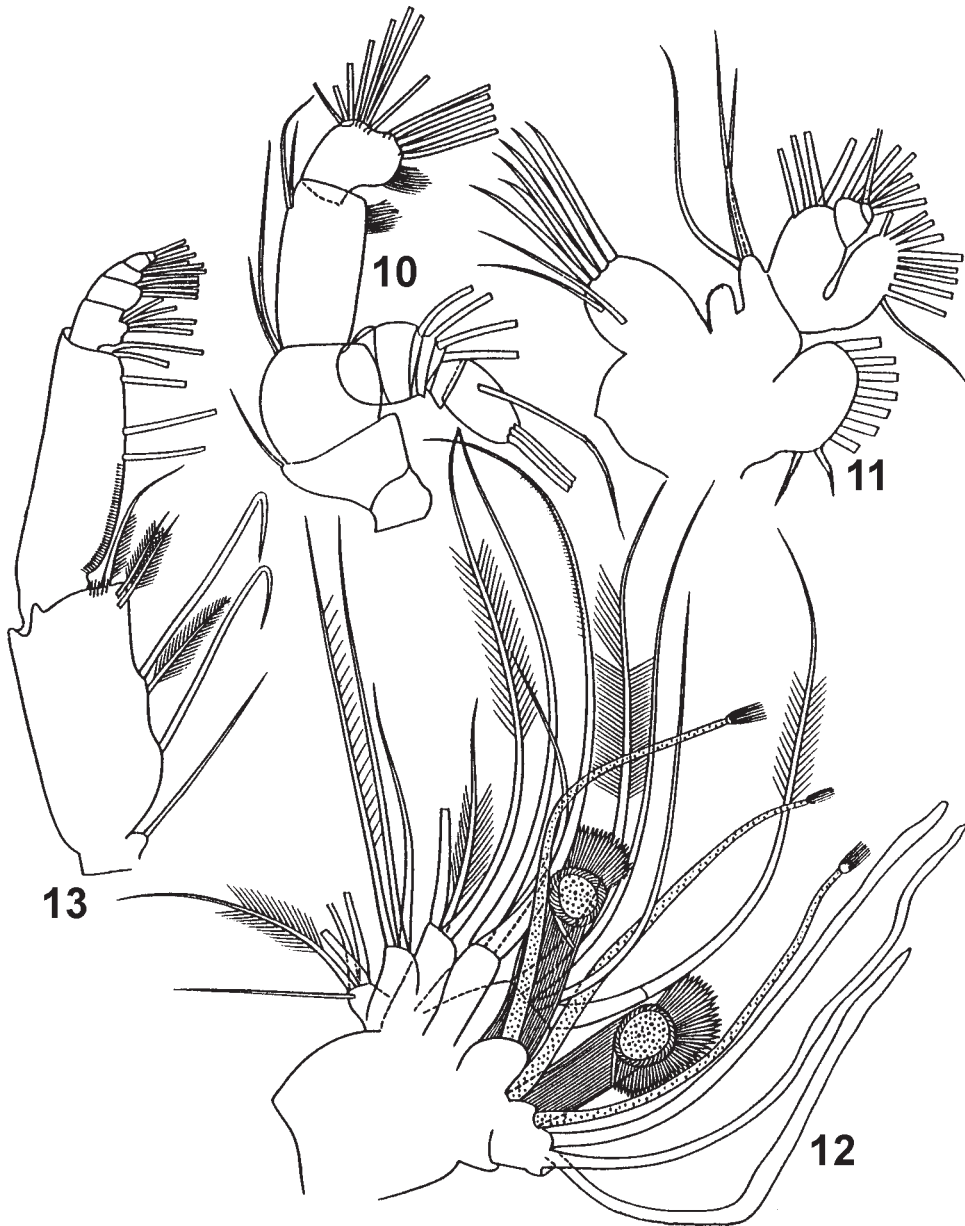
Figs 1-9. *Heteramalla sarsi* Roe, 1975, female. 1, body, right lateral view; 2, forehead, right lateral view; 3, rostrum; 4, SmP5 and Ur, right lateral view; 5, genital double-somite, ventral view; 6, A1; 7, distal segments of A1; 8, Md; 9, gnathobase of Md.

slightly longer than left; terminal segment of right leg small, with an apical spine; spine of right leg slightly shorter than left one.

Male unknown.

Remarks. Sars (1907) erected the genus *Heteramalla* for a female which he believed, with some doubts, to be conspecific with T. Scott's (1894) *Amalophora dubia* described from male, as both have two much enlarged brush-like sensory setae on the endopod of Mx2. At the moment, such setae were known only in the males of the genus *Xanthocalanus* (Phaennidae). Roe (1975) examined females and males of *Heteramalla dubia*

(T. Scott, 1894), collected in the northeastern Atlantic close to the type locality, where female specimens had been collected, according to Sars (1907, 1924-1925). Roe compared Atlantic females with Sars' description and Atlantic males with T. Scott's type specimens collected in the Gulf of Guinea and found that females and males previously considered as conspecific, apart from the normal sexual differences, clearly differ in several (five) features, and thus belong not only to different species but also to different genera. Therefore, the species described from female by Sars (1907) was given a new name, *Heteramalla*

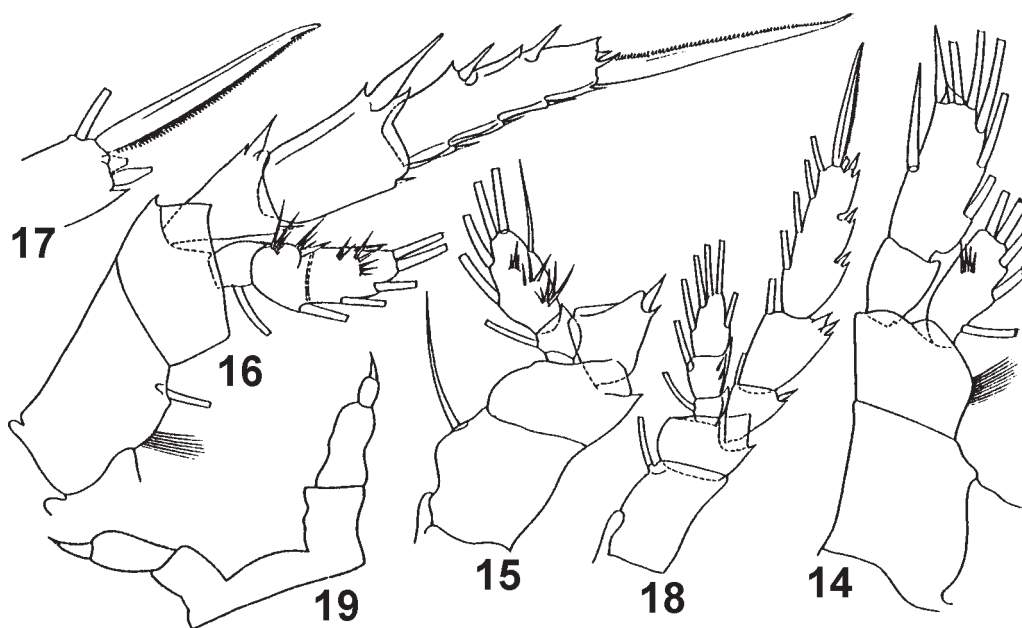


Figs 10-13. *Heteramalla sarsi* Roe, 1975, female. 10, A2; 11, Mx1; 12, Mx2; 13, Mxp.

sarsi Roe, 1975. At the same time, *A. dubia* T. Scott, 1894 has been placed to a new genus, *Scopalatum* Roe, 1975, because the genus *Amalophora* was not valid, as based on a male specimen which actually belongs to the genus *Xanthocalanus* Giesbrecht, 1892. All remaining *Amalophora* spp. were recognized as belonging to other new or rediagnosed genera of the family

Scolecitrichidae (Bradford et al., 1983; Roe, 1975; Vyshkvartzeva, 2003).

Female specimens of *Heteramalla sarsi*, described above from the North Pacific, generally agree well with Sars' (1924-1925) description of his Atlantic specimens, except that they lack a seta on Li2 of Mx1 (this feature conforms with Roe's (1975) Atlantic specimens, but possibly it



Figs 14-19. *Heteramalla sarsi* Roe, 1975, female. **14,** P1; **15,** P2 (Re2-3 detached); **16,** P3; **17,** apical spine of P3; **18,** P4; **19,** P5.

is a variable feature in this species) and bear one plumose and one aesthetasc-like seta on Li3 of Mxp syncoxa (this feature is described here for the first time). Sars (1924: Pl. 39, Fig. 11) did not describe Mxp, but in his illustration of Mxp only one seta with a tapering tip, which is treated here as a transformed, aesthetasc-like seta, is shown on Li3. The other authors dealing with this species (A. Scott, 1909; Rose, 1933; Roe, 1975; etc.: see Table 1) gave no information on the morphology of Mxp.

There are some other discrepancies in the descriptions of *H. sarsi* (Table 1). Sars (1907, 1924-1925), Rose (1933) and Roe (1975) noted that the endopod of P3 is two-segmented. A. Scott (1909) described the endopod of P3 as three-segmented but gave no illustration. In our specimens from the North Pacific there is a thin suture visible on the ventral side of endopod just distal to the proximal inner seta, but the outer margin of segment opposite to the inner seta in our specimens is not pointed but straight. The proximal endopodal segments of swimming legs in Scolecitrichidae usually have the outer distal corner produced, as on Ri1 of P2 and P3 and on Ri1-2 of P4 in *H. sarsi* (Figs 14-18). The 2nd and 3rd endopodal segments of P3 in this species are completely fused and this compound segment has 3 inner setae, 2 apical setae and 4 rows of spines; the second row in our specimens consists of 4 spines and is situated on a raised lobe. In con-

trast to this, no lobe was pictured by Sars (1924: Fig. 14). At last, Grice & Hulsemann (1965) and Roe (1975) reported that females of *H. sarsi* were lacking P5. In our specimens, P5 is small and rudimentary, as described by Sars (1924-1925), A. Scott (1909) and Rose (1933), but slightly asymmetrical. In some other species of Scolecitrichidae, P5 is sometimes not observed (i.e., *Scolecithricella tenuiserrata* Giesbrecht, 1892 and *Scolecithrix bradyi* Giesbrecht, 1888). It is not clear if the above-mentioned absence of P5 is a variability of the species or P5 has been broken during preparation of these minute legs. However, at present the conclusion should be made that *H. sarsi* is a variable species.

Up to now, the females of *Heteramalla sarsi* were known only from the Atlantic Ocean (Sars, 1907, 1924-1925; Grice & Hulsemann, 1965; Vervoort, 1965), the Gulf of Lions in the Mediterranean Sea (Rose, 1933) and in the Obi Strait of Indo-Malayan waters (A. Scott, 1909) (Table 1). *Heteramalla dubia* was recorded from the Indian Ocean (Grice & Hulsemann, 1967) and the Pacific Ocean: in the Hawaiian Islands region and in the central and southeastern Pacific (Wilson, 1942, 1950). However, it is not clear which species, *Heteramalla sarsi* or *Scopalatum dubium*, were encountered here since the sex of collected specimens was not indicated. So, the above-described females are the first reliable and the northernmost record of *H. sarsi* in the Pacific.

Table 1. Sampling localities, size and morphological variation of *Heteramalla sarsi* Roe, 1975.

Author	Locality	Depth (m)	Body length (mm)	P5	Endopod of P3 (number of segments)	Mx1 Li2 (number of setae)	Mx2 Li1 (number of setae)	Mxp Li1, Li2, Li3 (number of setae)
Sars, 1907	31°41'N 42°40'W	0-3000	3.5	present	2	?	?	?
Sars, 1924-25	30°04'N 42°29'W; 31°06'N 24°07'W	0-5000	3.7	present	2	1	?	1, 1ae, 1ae
A. Scott, 1909	1°05'S 127°52'E	0-1000	3.78	present	3	?	?	?
Rose, 1933	Western Mediterranean Sea (Gulf of Lions)	near surface (at night)	3.7	present	2	?	?	?
Wilson, 1942	31°49'S 109°04'W; 7°45'N 141°24'W	100	?	?	?	?	?	?
Wilson, 1950	29°22'N 139°31'W	0-100	?	?	?	?	?	?
Vervoort, 1965	1°30'N 10°10'W	about 600	3.41-3.65			?	?	?
Grice & Hulse-mann, 1965	29°57'N 22°58'W	2000-3000	—	absent	?	?	?	?
?Grice & Hulse-mann, 1967	6°00'S 65°10'E	1015-1950	—	?	?	?	?	?
Roe, 1975	18°N 25°W	800-1020	?	absent	2	0	?	?
Present records	Central and north Pacific	1395-3920	3.68-3.7	present	2	0	5	1, 1ae, 2(1ae)

Note. “?” means absence of data.

In addition, it should be mentioned that Alzamora (1940: 6) misidentified another species as “*Heteramalla dubia*”. Actually, his material fits neither *Heteramalla sarsi* nor *Scopalatum dubium*.

***Amalothrix aspinosa* (Roe, 1975)** (Figs 20-36)

Scolecithricella aspinosa Roe, 1975: 321, Fig. 13.
Amalothrix aspinosa: Vyshkvartzeva, 2000: 236 (remark).

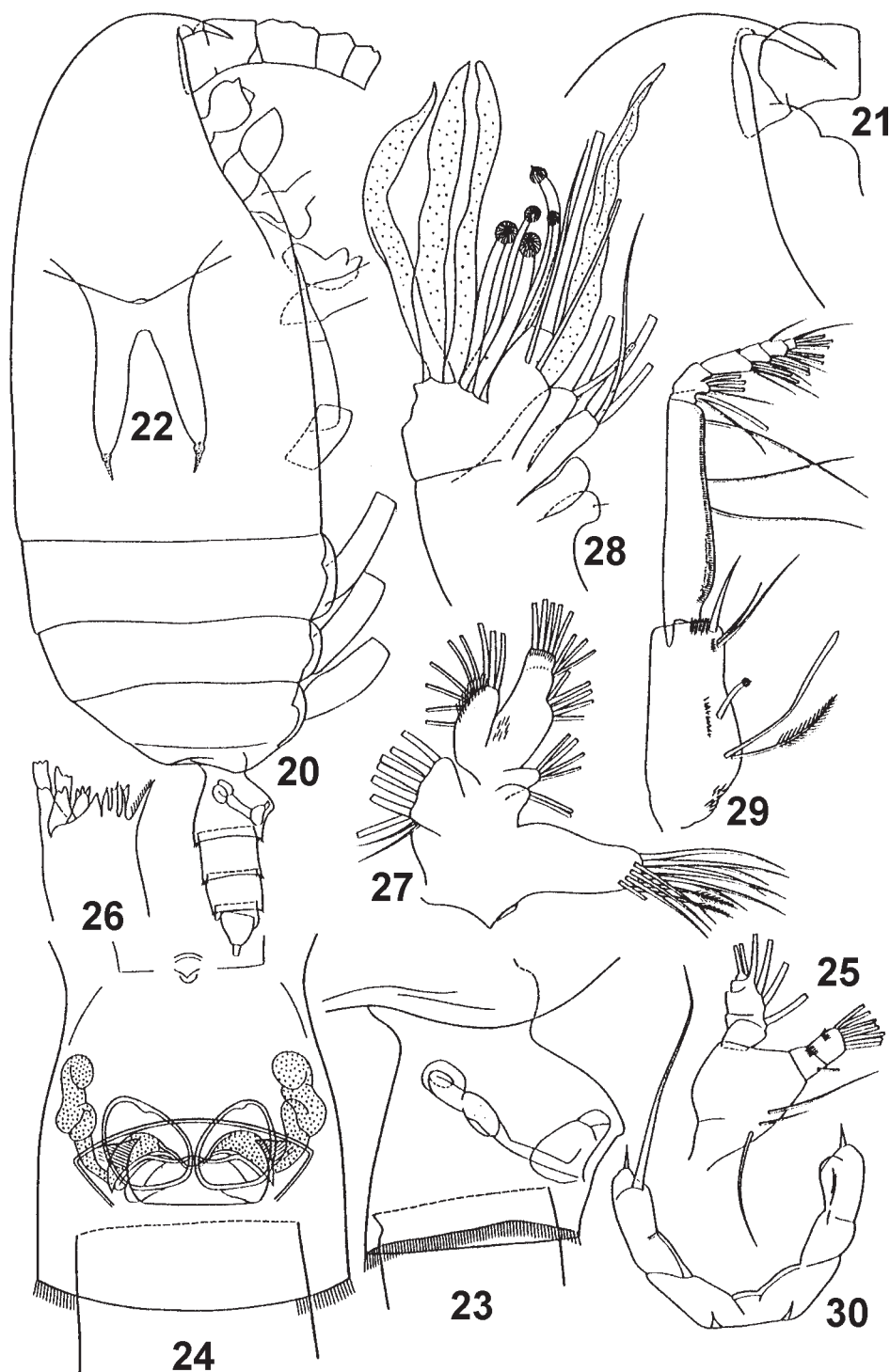
Material. 2 ♀, 14°00'N 132°30'W, R/V “Akademik Korolev”, cruise 40, depth 1395-2610 m, 28.X.1985.

Description of female. Body length 3.88 mm (n = 2). Prosoma oval and robust in lateral (Fig. 20) and dorsal views. Forehead low, not produced anteriorly as compared with base of rostrum, broadly rounded in lateral (Fig. 21) and dorsal views. Rostrum (Fig. 22) consisting of two long, strong, sausage-shaped processes, distally continuing into two short conical processes. Ce and Smp1 fused; Smp4 and Smp5 separated by a thin suture. Posterolateral corners of Smp5 in lateral view not produced, broadly rounded, with a shallow excision, reaching proximal part of genital

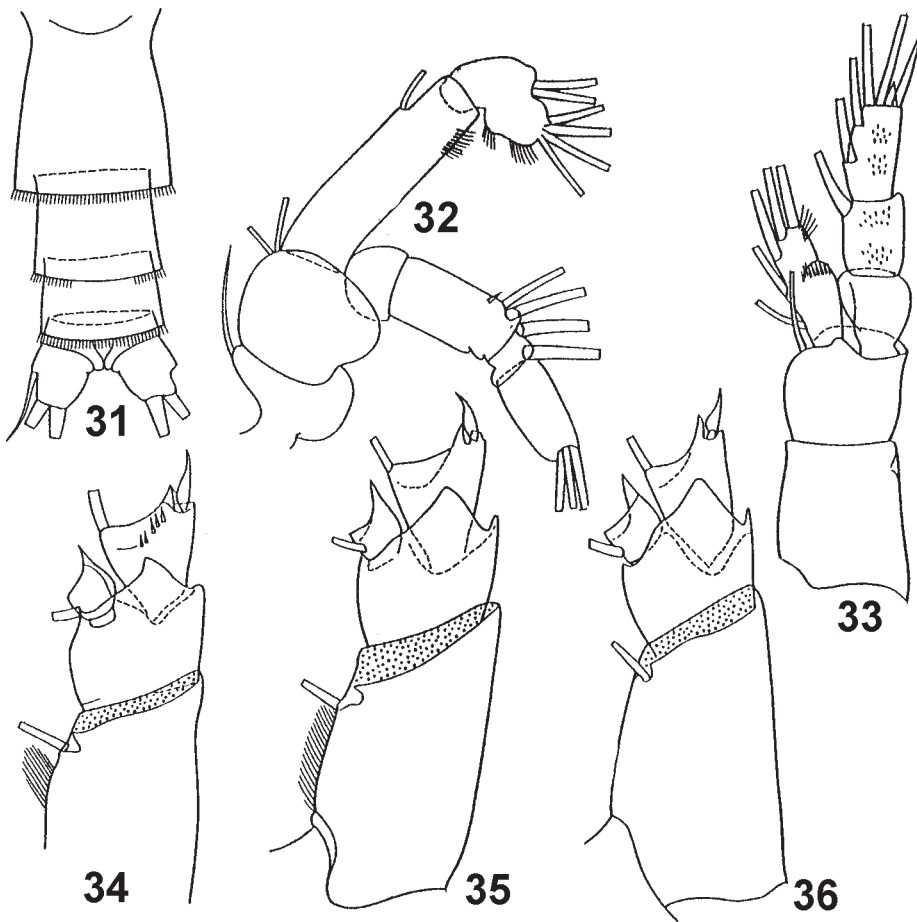
double-somite (Fig. 20), in dorsal view narrowly rounded.

Urosome (Figs 20, 31) about 0.2 times as long as prosoma. Urosomites and caudal rami with following relative lengths: 33:23:18:12:14 = 100. Posterior margins of Ur1-Ur3 with short spinules. Genital double-somite in dorsal view (Fig. 31) distinctly longer than wide, parallel-sided; in lateral view (Fig. 23), it slightly deeper than long, with genital prominence anteriorly and with concave posteroventral margin; spermatheca very long, directed anterodorsally and reaching anterodorsal angle of genital double-somite. Genital field ventrally (Fig. 24) with rectangular operculum, large rounded skeletal plates and long vesicles; vesicles directed anteriorly, with 2-3 bendings in distal half. Genital field with a cuticular structure looking as a thin line in shape of large shallow arc, curving on both sides and continued in short posteromedial shoulders; probably, this structure outlines an invagination of cuticle. Ur2 as wide as long; Ur3-Ur4 wider than long. Caudal rami about as long as wide.

Both A1 broken. A2 as in Fig. 32; Md as in Figs 25, 26; Mx1 as in Fig. 27; Mx2 as in Fig. 28; Mxp as in Fig. 29. P1 as in Fig. 33; Re1 and



Figs 20-30. *Amalothrix aspinosa* Roe, 1975, female. 20, habitus, right lateral view; 21, forehead; 22, rostrum; 23, SmP5 and Ur, right lateral view; 24, genital double-somite, ventral view; 25, palp of Md; 26, gnathobase of Md; 27, Mx1; 28, Mx2; 29, Mxp; 30, P5.



Figs 31-36. *Amallothrix aspinosa* Roe, 1975, female. **31**, Ur; **32**, A2; **33**, P1; **34**, P2; **35**, P3; **36**, P4 (34-36: two distal segments of Re and Ri of P2-P4 detached).

Re2 without outer spine, posterior surface of Re2 and Re3 with minute spinules. P2, P3 and P4 as in Figs 34, 35 and 36, respectively; distal segments of both rami broken, cuticle in distal part of coxa of P2-P4 thin. P5 (Fig. 30) apparently symmetrical, three-segmented; 2nd and 3rd segments partially fused, 3rd segment with a small terminal spine and a long, thin inner seta (apparently, in this specimen broken on one of P5).

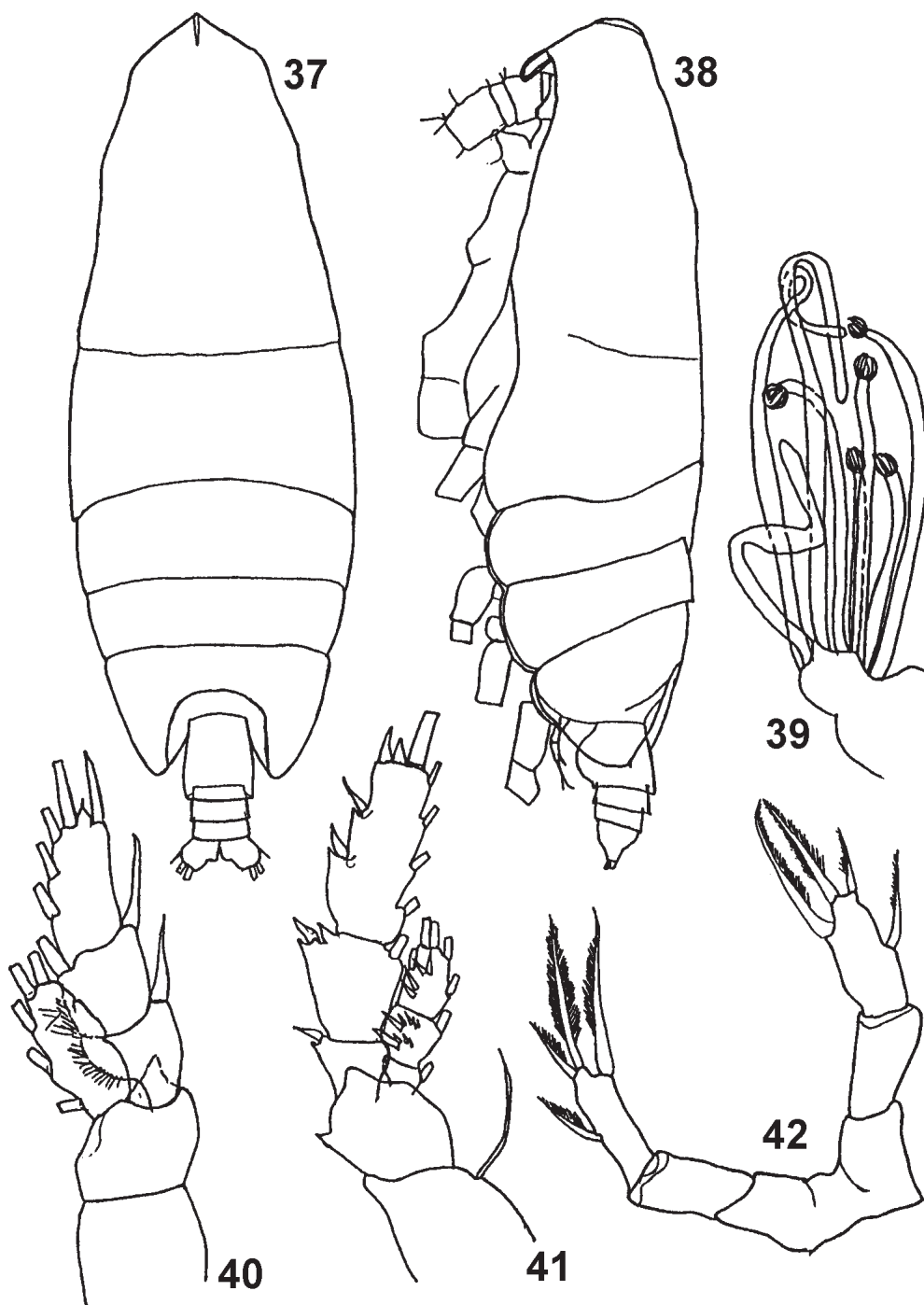
Male unknown.

Remarks. Females from the northwestern Pacific agree with the description of *Scolecithriella aspinosa* Roe, 1975 from the northeastern Atlantic, apart from the following features: the body is slightly larger; A2 has a short seta on Re2 (ancestral segment Re IV) and no medial seta on the terminal segment; the basis of Md bears three inner setae; the syncoxa of Mxp lacks a seta on the first inner lobe (this seta is present in Roe's specimen); Mx1 has a group of spinules on the

exopod and also on the basis and endopod; Mx2 has three wide, flattened worm-like setae on the endopod and one worm-like seta on Li5. The latter worm-like seta is not mentioned by Roe (1975: Fig. 13h), while other three ones are different from those figured by Roe, not wrinkled and not as long as shown by him. However, this author noted that one of the paratypes had simple, flattened worm-like setae on the endopod of Mx2. Thus, there are no significant differences between the Atlantic and Pacific specimens.

Landrumius gigas (A. Scott, 1909)
(Figs 37-42)

- Brachycalanus gigas* A. Scott, 1909: 81, Pl. 35, Figs 10-18.
Lophothrix gigas: Vervoort, 1965: 58; Grice & Hulsemann, 1968: 332, Figs 63-74.
Lophothrix thorsoni Björnberg, 1975: 178, Figs 15-30.
Landrumius gigas: Park, 1983: 195, Figs 17-18.



Figs 37-42. *Landrumius gigas* (A. Scott, 1909), female. 37, body, dorsal view; 38, body, left lateral view; 39, distal endopodal complex of Mx2; 40, P1; 41, P3; 42, P5.

Material. 1 ♀, 30°48'N 155°02'E, R/V "Vitjaz", cruise 19, St. 3206, depth 0-5000 m, 19.X.1954.

Description of female. Body length 7.8 mm (n = 1). Prosome elongate, strongly built. Forehead with a short, low and somewhat flattened crest clearly visible dorsally (Fig. 37), ventrally and laterally (Fig. 38). Head produced anterior to base of rostrum, in lateral view broadly rounded, in dorsal view triangular. Rostrum (Fig. 38) strongly developed, somewhat plate or sausage-like, with rounded tip. Line of fusion between Ce and SmP1 very faint, like that between SmP4 and SmP5; both visible mainly laterally. Posterolateral corner of SmP5 produced posteriorly as a rounded lobe, covering anterior half of genital double-somite, and having a small distal knob on dorsal side.

Urosome about 0.19 times the length of prosome, consisting of 4 somites. Genital double-somite in lateral view as long as remaining somites including caudal ramus, distinctly wider than long, with a large and high genital prominence, in dorsal view longer than wide, with parallel lateral margins. Spermatheca elongate, finger-like. Ur2-Ur4 each distinctly wider than long. Caudal rami about as long as wide, divergent.

A1 broken. Mouthparts as in *L. antarcticus* Park, 1983, except that in our specimen 6th short brush-like sensory seta on endopod of Mx2 (Fig. 39) not visible, possibly due to the fact that on permanent slide it is masked by proximal parts of other five brush-like sensory setae. P1, P3 and P5 as in Figs 40, 41 and 42, respectively.

Male unknown.

Remarks. The female of *Landrumius gigas* collected in the North Pacific is similar to that described and illustrated by Park (1983) from the southeastern Pacific. It differs from the latter in the shape of the forehead having a somewhat flattened crest in lateral view, the posterolateral corners of SmP5 bearing a small distal knob, the rostrum devoid of distal points (which corresponds to the rostrum, described by Björnberg (1975)), and the absence of distal vesicle of the spermatheca. Specimens from the southeastern Pacific reported by Grice & Hulsemann (1968) and Björnberg (1975) also slightly differ from those illustrated by Park (1983) in the shape of the forehead (the head is very slightly produced anteriorly in Fig. 66 in Grice & Hulsemann (1968); the crest is not indicated by Björnberg (1975)), in the rostrum (devoid of distal points in Björnberg's description) and in the longer and pointed posterolateral corners of SmP5, almost reaching the distal margin of genital double-somite. P5 of specimens illustrated by Grice & Hulsemann (1968) differs from that of our and Park's specimens in having the inner apical spine much longer than the other three spines. Park

(1983) noted individual variations in both the distal end of SmP5 and the rostrum among his six specimens. The differences observed in the present specimen also appear to be attributable to individual variations within this variable species.

In addition to the southeastern (Grice & Hulsemann, 1968; Björnberg, 1975; Park, 1983) and northern Pacific records, the species was collected also in the waters of the Malay Archipelago (A. Scott, 1909) and in Antarctic waters (Park, 1983).

DISCUSSION

The phylogenetic relationships of the five Bradfordian families, i.e., Phaennidae, Scolecitrichidae, Tharybidae, Diaixidae and Parkiidae (the latter family is not accepted by Boxshall & Halsey, 2004) need a special comprehensive analysis. Such a study is impossible until the boundaries, composition of genera included and diagnostic characters of these families are clarified. Below, the positions of *Amallothrix aspinosa* (Roe, 1975), *Heteramalla* Sars, 1907, *Puchinia* Vyshkvartzeva, 1989, *Cenognatha* Bradford-Grieve, 2001, *Plesioscolecithrix* Markhaseva & Dahms, 2004, *Rythabis* Schulz, 1995 and *Parkius* Ferrari & Markhaseva, 1996 will be discussed, and comments on the relationships and on the diagnostic significance of some characters in the families Scolecitrichidae, Tharybidae and, briefly, in Diaixidae, will be given.

The five Bradfordian families are characterized by the possession of sensory setae on the endopod and some lobes of Mx2 and on the syncoxa of Mxp, which is a unique character state among the monophyletic superfamily Clausocalanoidea. These families together comprise a monophyletic group (Fleminger, 1957; Ferrari & Markhaseva, 1996). The ancient ancestor of the Bradfordian families is supposed to have all setae of Mx2 and Mxp as normal, sclerotized setae. Nine setae on the endopod of Mx2 and three setae on Li3 of the syncoxa of Mxp are symplesiomorphies of Scolecitrichidae (Vyshkvartzeva, 1989a, 1989b, 2001) and the other Bradfordian families (Ferrari & Markhaseva, 2000; Ohtsuka et al., 2003; Boxshall & Halsey, 2004). After separation of the Phaennidae lineage, the ancestor common for the remaining Bradfordian families seems to retain these plesiomorphic states of Mx2 and Mxp.

The diagnostic significance of the composition of sensory setae on the endopod of Mx2 in four Bradfordian families (Scolecitrichidae, Tharybidae, Parkiidae and Diaixidae) is controversially discussed presently. Some other authors also consider that (1) the "ninth element may be modified into a small sensoriform seta or can remain

unmodified, but most commonly it is lost” and (2) evolution of the 9th endopodal seta was independent. At the same time, they suppose the presence of 3 worm-like plus 5 brush-like sensory setae on the endopod of Mx2 to be a symplesiomorphic feature for Scolecitrichidae, Tharybidae, Parkiidae and Diaixidae (Ohtsuka et al., 2003: 62; Boxshall & Halsey, 2004). These authors consider that the 3+5 sensory setae have transformed in the common ancestor of above-listed families, and thus are of no value in distinguishing between these four families. I cannot agree with this interpretation.

Contrary to this supposition I assume that after separation of the Phaennidae lineage with the widely accepted apomorphy of 1 worm-like + 7 brush-like setae on Mx2 endopod (Bradford, 1973; Bradford et al., 1983; Ohtsuka et al., 2003; Boxshall & Halsey, 2004; etc.), 9 normal, sclerotized setae on the endopod of Mx2 and 3 setae on Li3 of the syncoxa of Mxp remain as a symplesiomorphic feature for the common ancestor of Scolecitrichidae, Tharybidae, Parkiidae and Diaixidae.

The position of the genus *Heteramalla*, comparative analysis of its characters, and comments on the diagnostic value of Mx1 setation and proportions in Scolecitrichidae

The monotypic genus *Heteramalla* Sars, 1907 was originally placed in the family Phaennidae, considering that such a peculiar enlarged sensory seta on Mx2 that far was described only in the male of *Xanthocalanus* Giesbrecht, 1892. Bradford (1973) transferred *Heteramalla* from the Phaennidae to the Scolecitrichidae primarily on account of the presence of 3 worm-like and 5 brush-like sensory setae on the endopod of Mx2 in contrast to 1-2 worm-like and usually 7 brush-like setae in Phaennidae. This opinion has been widely accepted (Roe, 1975; Bradford et al., 1983; Vyshkvartzeva, 2001; Ohtsuka et al., 2003; Boxshall & Halsey, 2004) and seems to be justified by the analysis presented below.

Heteramalla shares the composition of 8 sensory setae on the endopod of Mx2, i.e. 3 long identical worm-like and 5 brush-like sensory setae, with 20 other genera of Scolecitrichidae (see Table 5), except *Racovitzanus* Giesbrecht, 1902, *Cenognatha* Bradford-Grieve, 2001 and *Plesioscolecithrix* Markhaseva & Dahms, 2004. In the latter three genera, the endopodal setae of Mx2 seem to have been transformed independently, as these genera probably separated independently from the common ancestor of scolecitrichids (see below). This permanent composition (3+5 sensory setae) is a synapomorphic character state of these 21 scolecitrichid genera (Vyshkvartzeva,

2001). The ninth setal element of the common ancestor has been lost in *Heteramalla* and also in most of scolecitrichid genera, but is retained as a rudimentary seta in *Xantharus renatehaassae* Schulz, 1998 or was transformed independently in *Landrumius* Park, 1983, *Grievella* Ferrari & Markhaseva, 2000 and *Falsilandrumius* Vyshkvartzeva, 2001, as supposed by Vyshkvartzeva (2001). For this reason, in these three genera it differs from the other 5 brush-like setae: it is much smaller (in *Landrumius* and *Falsilandrumius*) or slenderer than these brush-like setae and bears a peculiar apical part (in *Grievella*). The enlargement of one or two brush-like setae in *Heteramalla* and some other genera (see below) is a result of their further specialization that has independently evolved in scolecitrichids, and also in the genus *Xanthocalanus* (Phaennidae).

Heteramalla has scolecitrichid-like mouthparts: the masticatory blade of Md is not enlarged and bears 4 large widely-spaced ventral teeth (as usual in scolecitrichids and aetideids). This seems to be a primitive state of ventral teeth location on mandibular gnathobase in the superfamily Clausocalanoidea (personal observations). At the same time, *Heteramalla* has scolecitrichid proportions of different parts of Mx1, which are in the limits characteristic to those in the other scolecitrichid genera (Table 2): 1) Li1 of Mx1 1.55-2.42 times as long as wide; 2) well-developed epipod (Le1) 1.08-2.14 times as wide as Li1; 3) well-developed distal part of Mx1, comprising Li2+Li3+Li4+Ri, is 2.27-3.5 times the width of Li1; 4) well-developed exopod in the shape of oval plate subequal to the basis (Table 2). *Archeoscolecithrix auropecten* (Giesbrecht, 1892) (Table 2) and *Amallothrix aspinosa* (Roe, 1975) have about the same indices of Mx1. The latter species has accordingly: 1) Li1 of Mx1 3 times as long as wide; 2) well-developed epipod (Le1) 1.66 times as wide as Li1; 3) well-developed distal part of Mx1, comprising Li2+Li3+Li4+Ri, is 4 times as long as Li1; 4) well-developed exopod in the shape of oval plate subequal to basis. About the same limits of indices are characteristic to the family Scolecitrichidae, s.l. in general (Table 4). These proportions clearly distinguish scolecitrichids from tharybids (see below).

The genus *Heteramalla* is characterized by a number of derived (apomorphic) characters: 1) rostrum large, uniramous (ancestral state: rostrum bifid); 2) Re1 of A2 (ancestral segment I) and Re2 (fused ancestral segments II-IV) without setae (4 setae lost); 3) Li1 of Mx1 with 7 marginal and 1 posterior seta (2 proximal marginal and 3 posterior setae lost); 4) Li2 of Mx1 without setae (5 setae of ancestral Mx1 lost); 5) Li3 of Mx1 with 3 setae (one seta lost); 6) Li4 of Mx1 with 4 setae (one seta lost); 7) Ri of Mx1

Table 2. Summary of selected morphological characters in some scolecitrichid genera.

Character	<i>Archescole- cithrix</i>	<i>Cenognatha</i>	<i>Falsiland- rumius</i>	<i>Grievella</i>	<i>Heteramalla</i>	<i>Landrumius</i>	<i>Plesioscole- cithrix</i>	<i>Puchinia</i>	<i>Xantharus</i>	Ancestral for Bradfordian families
Female body length (mm)	about 2	1.75-2.37	> 3.5	2.15	3.4-3.8	7.0-8.6	1.7-1.74	2.95	< 1.5	
Habitat	epipelagic- mesopelagic	benthopelagic	abyssopelagic	benthopelagic	mesopelagic- bathypelagic	?bathypelagic	benthopelagic	abyssopelagic (?benthopelagic)	epipelagic- mesopelagic	
Rostrum	2 long filaments	2 long filaments	2 long filaments	2 filaments, proximal part robust	thick long ramus, tip bifid, spine-like	thick long ramus, tip bifid	bifurcate plate, rami thick with filaments	short ramus, 2 short widely-spaced processes	thick long ramus, tip bifid, with or without filaments	2 rami
A2 Re, segment number	7	<u>6</u>	<u>6</u>	7	7	<u>6</u>	7	7	7	7
A2 setae number: ReI-ReIV	0, 0+0+1	1+1, 1+1	0, 0+0+1	?0, 0+1+1	0, 0+0+0	0, 0+0+0	0, 0+0+0	1, 1+1+1	0, 0+0+1	1, 1, 1, 1
A2 terminal segment setae number	1+3	1+3	1+3	1+3	1+3	1+3	1+3	0+3	1+3	1+3
Mx1 Li1 setae number	<u>12</u>	14	<u>12</u>	<u>12</u>	<u>8</u>	14	14	<u>12</u>	<u>12</u>	14
Mx1 posterior setae number	<u>2</u>	4	<u>2</u>	<u>3</u>	<u>1</u>	4	4	<u>2</u>	<u>3</u>	4
Mx1 Li2 setae number	<u>2</u>	<u>3</u>	4	2	<u>0</u>	<u>3</u>	2	5	2	5 (*6)
Mx1 Li3 setae number	4	4	4	4	<u>3</u>	4	4	4	4	4
Mx1 Li4 setae number	<u>6</u>	5	5	<u>4</u>	<u>4</u>	5	<u>4</u>	<u>4</u>	<u>4</u>	5
Mx1 Ri segment number	<u>1 (fused with basis)</u>	<u>1</u>	2	2	2	2	<u>1</u>	3	<u>1 (fused with basis)</u>	3
Mx1 Ri setae number	9: 3+6	11: 3+3+5	11: 3+3, 5	10: 3, 7	7: 2, 5	9: 2+2, 5	7: 3+4	11: 3, 3, 5	10-11: 3+3+4-5	13: 3, 3, 7 (*16: 4, 5, 7)
Mx1 Re setae number	<u>10</u>	9	10-11	<u>6</u>	<u>10</u>	<u>10</u>	<u>6</u>	<u>8-9</u>	<u>8</u>	11
Mx1 Le1 setae number	9	9	9	9	9	9	9	9	9	9
Mx1 ratio L(Li1) : W(Li1)	2.7	1.55	1.73	2.42	1.85	2.13	2.23	1.75	1.88	?

Character	<i>Archescolecithrix</i>	<i>Cenognatha</i>	<i>Falsilandrums</i>	<i>Grievella</i>	<i>Heteramalla</i>	<i>Landrumius</i>	<i>Plestoscolecithrix</i>	<i>Puchimia</i>	<i>Xantharus</i>	Ancestral for Bradfordian families
Mx1 ratio L (marginal seta of Li1) : W(Li1)	2.4	1.54	1.83	1.78	2.85	1.45	1.85	3.12	2.0	?
Mx1 ratio W(Le1) : W(Li1)	1.49	1.18	1.17	1.15	2.14	1.08	<u>0.85</u>	1.25	1.2	?
Mx1 ratio L(Li2+Li3+Li4+Ri) : W(Li1)	3.2	2.71	2.27	3.36	3.7	2.63	2.46	3.5	3.02	?
Mx1 ratio L(Re) : L(basis)	1	<u>1.2</u>	<u>1.2</u>	1	<u>1.2</u>	<u>1.2</u>	<u>1.2</u>	1	<u>1.1</u>	1
Mx2 Li1 setae number	<u>3</u>	5	5	5 + 1 spine	5	5	5	<u>4</u>	4-5	5 (*6)

Notes. Data marked with asterisk refer to the primitive state for Spinocalanidae. Apomorphic state is marked by underlining and bold type. [Spinocalanidae is the most suitable antecedent group for Clausocalanoidea (according to Schulz, 1989). Fleminger (1983) considered that ancestral spinocalanid setation of the endopod of Mx1 consisted of 25 setae, as that found on Ri of Mx1 in *Mimocalanus crassus* Park, 1970. However, this extraordinary high number of setae is found only in this species and appears to be a matter of the secondary increase-hypersetation (unique autapomorphy), since all remaining spinocalanid taxa have a maximum of 16 setae on Ri; Mx1 (Vyshkvartzeva, 1983, 1989b; Schulz, 1989)].
Abbreviations: L – length; W – width; A2 Re1-ReIV – first-fourth ancestral exopodal segments of A2.

two-segmented (two distal segments fused); 8) Ri of Mx1 with 7 setae on two segments: 2 and 5, respectively (4 or 6 setae lost); 9) Re of Mx1 with 10 setae (one seta lost); 10) endopod of Mx2 with 2 brush-like setae much stronger than 3 others; 11) Li3 of Mxp syncoxa with 2 setae (one seta lost; one of two retaining setae transformed, aestethasc-like); 12) basis of P1 with inner seta lost; 13) Ri of P1 with outer lobe lost; 14) Re1 of P1 with outer spine lost; 15) Re2-Re3 of P1 fused; 16) Ri2 and Ri3 of P3 completely fused; 17) the second row of spines on fused Ri2-Ri3 of P3 consisting of 4 spines, situated on raised lobe; 18) outer setae of Re1-Re3 of P3 short and thin, rudimentary as compared with the typical scolecitrichid pattern; 19) P5 with one apical spine (3 spines lost).

If we compare the above-listed apomorphies with those of the other scolecitrichid genera, we obtain the following results:

1) The large uniramous rostrum similar to that of *Heteramalla* occurs among Scolecitrichidae in the genera *Landrumius* and *Xantharus* Andronov, 1981 (Table 2), and also in *Mixtocalanus* Brodsky, 1950, *Scottocalanus* Sars, 1905 and *Scolecocalanus* Farran, 1936, but it is worth to note that the rostrum in all above-mentioned genera differs by its apical part, notched more or less deeply and continuing or not into spine-like processes or filaments; this type of single derived rostrum seems to appear several times, independently in parallel way amongst scolecitrichids.

2) Re1 and Re2 of A2 without setae (loss of 4 setae) occur in *Landrumius* and in some other genera. The apomorphic state with 3 setae lost on Re1-2 of A2 is the most frequent in scolecitrichids. It is known in *Falsilandrums*, *Xantharus* and *Archescolecithrix* Vyshkvartzeva, 1989 (Table 2), and also in *Scolecithricella* Sars, 1902, *Scolecithrix* Brady, 1883 and *Scopalatum*.

3) Li1 of Mx1 with three posterior and two proximal marginal setae lost occurs only in *Heteramalla*, *Scolecithricella minor* (Brady, 1883), *S. marginata* Giesbrecht, 1888 and *S. paramarginata* Schulz, 1991.

4) Li2 of Mx1 with one seta or without setae (4-5 setae of ancestral Mx1 lost): the loss of five setae is the most advanced state that occurs only in *Heteramalla*, but the loss of four setae is known in *Mixtocalanus alter* (Farran, 1929) re-described by Park (1980).

5) Li3 of Mx1 with 3 setae (one seta lost) occurs among scolecitrichids not rarely, for example, in *Scolecithricella*, *Scolecithrix*, *Scottocalanus*, *Scaphocalanus vervoorti* Park, 1982, *S. insignis* Brodsky, 1950, *S. difficilis* Roe, 1975, and *Amalothrix obscura* (Roe, 1975).

6) Li4 of Mx1 with 4 setae (one seta lost) occurs in scolecitrichids not frequently, for exam-

ple, in *Amalothrix obscura* (Roe, 1975), *Scaphocalanus difficilis* Roe, 1975 and *Pseudoamalothrix emarginata* (Farran, 1905).

7) Two-segmented Ri of Mx1 (two distal segments fused) occurs in *Falsilandrumius*, *Grievella* and *Landrumius*.

8) Ri of Mx1 with 7 setae on two segments occurs among scolecitrichids rarely, for example, in *Scolecithricella dentata* (Giesbrecht, 1892), *S. globulosa* Brodsky, 1950, *S. orientalis* Mori, 1937, *Scaphocalanus difficilis* Roe, 1975, and *Scottocalanus rotundatus* Tanaka, 1961.

9) Re of Mx1 with 10 setae occurs in several genera (Table 2).

10) Endopod of Mx2 with two brush-like setae enlarged, much stronger than three others, occurs also in *Puchinia* (female) and *Scopalatum*. In the latter genus, the males have two setae enlarged, while the females, one seta enlarged. The appearance of these two enlarged brush-like setae with the retaining scolecitrichid pattern of 3+5 transformed setae seems to be a result of subsequent differentiation of brush-like setae, i.e., of their specialization, which was independent but parallel in allied genera.

11) Li1-Li3 of Mxp syncoxa with one normal, one thin-walled aesthetasc-like sensory seta (one seta is lost) and two setae (one seta is lost and one of the remaining is a thin-walled aesthetasc-like sensory seta), respectively; this pattern was not described in scolecitrichids earlier. The same setal pattern (1, 1 and 2 setae on Li1-Li3 of Mxp) possibly occurs also in *Puchinia*. In this monotypic genus known only from a female specimen, there are 4 setae on Li1-Li3 of Mxp syncoxa: one (worm-like) seta on each Li1 and Li2, and two closely-spaced setae on Li3 (a short normal plumose seta and a long brush-like seta). (Usually in scolecitrichid genera, not in *Puchinia*, setae of Li1, Li2 and Li3 are widely spaced and can be easily attributed to the lobe, but in *Puchinia* three setae in the middle part of Mxp syncoxa are closely spaced, that was why Vyshkvartzeva (1989b) considered these three setae as belonging to Li3). Recently two setae in the middle part of Mxp syncoxa were recorded also in *Plesioscolecithrix juhlae* Markhaseva & Dahms, 2004. All other 15 genera of the family Scolecitrichidae except *Cenognatha*, *Falsilandrumius*, *Grievella*, *Heteramalla*, *Landrumius*, *Plesioscolecithrix*, *Xantharus* and *Puchinia* (see Table 2) have one moderately long (usually about 0.3 times as long as syncoxa) brush-like seta on Li3 of Mxp syncoxa (two setae lost). In the genera of early offshoots a variable setal pattern of Mxp syncoxa seems to be a result of independent evolution and hence of the independent transformation of some setae in the genera (Vyshkvartzeva, 1989a, 1989b; Ohtsuka et al., 1998). On the contrary, the presence of one

brush-like seta on Li3 of Mxp syncoxa in 15 genera of the crown group seems to be a synapomorphic feature. (The composition of the crown group and early offshoots as well as the position of *Heteramalla* regarding these groups of genera are considered below).

12) Basis of P1 with distal inner seta lost is found also in *Falsilandrumius* and *Landrumius*.

13) Ri of P1 without outer lobe occurs in *Archescocleithrix*, *Falsilandrumius*, *Heteramalla*, *Landrumius*, *Mixtocalanus*, *Parascaphocalanus* Brodsky, 1955, and in some species of *Scaphocalanus* Sars, 1900.

14) Re1 of P1 without outer spine occurs in *Parascaphocalanus*, some species of *Scaphocalanus* and *Scolecithricella*, *Scolecithrichopsis ctenopus* (Giesbrecht, 1888), *Scolecithrix bradyi* and others.

15) Fused Re2-Re3 of P1 is apparently a unique apomorphy. A similar fusion is recorded only in some specimens of *Falsilandrumius bogorovi* (Brodsky, 1955: fig. 6).

16) Completely fused Ri2 and Ri3 of P3 is a unique apomorphy.

17) The second row of spines on fused Ri2-Ri3 of P3, situated on raised lobe, is a unique apomorphy. However, Roe (1975) described an analogous raised lobe bearing spinules on Ri2 of P2 in *Amalothrix aspinosa* (Roe, 1975) and *Pseudoamalothrix canariensis* (Roe, 1975).

18) Inner setae on Re1-Re3 of P3 short, rudimentary, compared with those typical of scolecitrichids, represent a unique among scolecitrichids apomorphy.

19) Female P5 with one apical spine (three spines lost) is described for *Mixtocalanus robustus* Brodsky, 1950.

Thus a greater part (14 of 19) of derived characters of *Heteramalla* evolved convergently, in parallel with some other scolecitrichid genera. Moreover, apomorphies 2, 3, 4, 5, 6, 8, 9, 12, 14, 18, and 19 represent reduction in setation elements without any cardinal changes in the type of the appendages. For example, the setation of Mx1 in *Heteramalla* differs from those of the other scolecitrichids and in this genus is more advanced, unique on Li1 and Li2 of Mx1 (Table 2). The peculiar setation, however, does not prevent us to place the genus in the family Scolecitrichidae, as Mx1 retains the scolecitrichid type with proportions typical of Scolecitrichidae (Table 2). In Scolecitrichidae, the setation varies significantly on all parts of Mx1, except Li3 and Le1 (Table 3). Furthermore, the number of setae on homologous parts of Mx1 is similar or overlaps in different genera (Table 2). It also overlaps in the families under consideration (Table 3). Thus, the setal formula of Mx1 is not always a good diagnostic feature. It may be used as a distinguishing

Table 3. Characteristics of Mx1 armature in some Bradfordian families and genera.

Family/Genus	Literature source	Number of setae							Re : basis (lengths ratio)
		Li1	Li2	Li3	Li4	Ri	Le1	Re	
Scolecitrichidae	*	<u>8, 12,</u> <u>13, 14</u>	<u>0, 1, 2,</u> <u>3, 4, 5</u>	<u>3, 4</u>	<u>3, 4,</u> <u>5, 6</u>	<u>5, 7, 8,</u> <u>9, 10, 11</u>	9	<u>4, 5, 6, 7,</u> <u>8, 9, 10, 11</u>	<u>1/2, 4/5,</u> <u>1, 5/4</u>
Parkiidae	Ferrari & Markhaseva, 1996	11	4	4	4	10	9	8	1
Tharybidae	Andronov, 2002; Schulz, 1981	<u>11, 13, 14</u>	<u>2, 3</u>	<u>3, 4</u>	<u>2, 3, 5</u>	<u>5, 6, 7, 8</u>	<u>6, 7, 8, 9</u>	2-5	<u>1/2, 3/5,</u> <u>4/5</u>
<i>Undinella</i>	Andronov, 2002; Vaupel-Klein, 1970	<u>10, 11-13</u>	<u>2</u>	<u>3, 4</u>	<u>4, 5</u>	<u>4, 5, 6</u>	<u>5, 6</u>	<u>2, 3</u>	<u>1/2, 3/5</u>
<i>Rythabis</i>	Schulz & Beckmann, 1995	14	5	4	5	12	9	4	1
<i>Parundinella</i>	Fleminger, 1957; Andronov, 2002;	11, 12	2, 3	4	4	7	7	5-7	2/3
<i>Diaixis</i>	Andronov, 2002	?7	1, 2	2	2, 3, 4	6, 8, 9, 10	6, 7, 8	6, 7, 8, 9	5/4
<i>Anawekia</i>	Othman & Greenwood, 1994	8	2	?2	3	7	8	8	1
Ancestral for Bradfordian families	author's data	14 (15)	5 (6)	4	5	13 (16)	9	11	1
Ancestral for Calanoida	Huys & Boxshall, 1991	16	5	4	5	17	9	11	?1

Notes. The variations in setation occurring most frequently are underlined. The supposed plesiomorphic setation state of Spinocalanidae is given in parentheses as that of the most probable antecedent group of the superfamily Clausocalanoida (according to Schulz, 1989).

* Setation of Mx1 in species of the family Scolecitrichidae is given according to the descriptions in the following papers: Andronov, 1981; Bradford, 1973; Bradford et al., 1983; Campaner, 1984; Farran, 1905, 1936; Ferrari & Markhaseva, 2000; Fosshagen, 1972; Giesbrecht, 1892; Grice, 1962, 1972; Halsemann, 1985; Mori, 1937; Park, 1970, 1980, 1982, 1983; Roe, 1975; Rose, 1942; Sars, 1903, 1924; Schulz, 1991, 1998; Shich & Stallard, 1982; Tanaka, 1961; Vervoort, 1990; Vyshkvartzeva, 1987, 1989a, 1989b, 1993, 2000, 2001, 2003; Vyshkvartzeva & Prusova, 1997; and author's unpublished data.

feature mainly between genera, and only sometimes, in the case when the number of setae on some parts is stabilized. Apomorphies 7, 15 and 16 represent reduction in the segment number by fusion of segments of appendages without changes in the typical scolecitrichid spine and setal formula. The progressive reduction in the segment number and armature of the appendages is a general way of evolutionary changes in Calanoida. Moreover, it is, as noted Huys & Boxshall (1991), a common evolutionary process in the Copepoda. Transformations in the shape and proportions of parts of Mx1 or Mxp, or those of some other appendages and cardinal transformation of the armature seem to offer much more information for treatment of phylogenetic relationships and evolutionary interpretations of the Bradfordian families (see other parts of Discussion).

The position of *Amallothrix aspinosa* (Roe, 1975)

Amallothrix aspinosa was originally described in the genus *Scolecithricella*. However, it does not fit the diagnosis of *Scolecithricella* given by Vyshkvartzeva (2000, 2001), as it has no key features of this genus (in *A. aspinosa*, no outer distal knob-like process is developed on the coxa of P4, and P5 is not a one-segmented flat appendage attached to short coupler, but three-segmented, subcylindrical, and has a long basal segment).

At the same time, the species quite agrees with the characters of the genus *Amallothrix* except the following ones: 1) some details of the genital field, i.e., the shape of the spermatheca with distal loops and, probably, the presence of cuticular invagination; 2) Li1 of Mx2 with 4 setae, according to Roe (1975); in our specimens these setae are broken (in *Amallothrix*, three setae are

usually developed); 3) wide, flattened shape of all worm-like setae of Mx2 (in *Amallothrix*, worm-like setae are usually not flattened but circular in section); 4) P1 without outer spines on Re1-Re2; 5) female P5 with two setae, inner seta is slender and longer than the entire leg (in *Amallothrix*, P5 usually bears three spines, inner spine is stout).

P1 without outer spines on Re1-Re2 is a strongly advanced feature; similar features occur in some species of other scolecitrichid genera: *Scaphocalanus invalidus* Hure & Scotto di Carlo, 1968, *S. subcurtus* Park, 1970, *Falsilandrumius bogorovi* (Brodsky, 1955), *Pseudoamallothrix canariensis* (Roe, 1975), *Grievella shan-ki* (Ferrari & Markhaseva, 2000). Derived characters 2, 4 and 5 appear to be a result of convergent, parallel evolution in allied genera and by themselves provide no information about the taxonomic position of species (Ferrari & Markhaseva, 2000; Vyshkvartzeva, 2000), but do not prevent one to place this species in the genus *Amallothrix*. The peculiar shapes of the spermatheca, inner spine of P5 and, possibly, worm-like setae of Mx2 may indicate the appearance of a new lineage in the genus *Amallothrix*. However, additional material and the description of the male are necessary to analyze whether this species may belong to a new genus.

Comments on the relationships in Scolecitrichidae, based mainly on setation of Mx2 and Mxp

The endopod of Mx2 with the sensory setae pattern 3 Wo + 5 Br is a permanent feature in 22 genera of Scolecitrichidae. It is different only in *Racovitzanus* and *Plesioscolecithrix*, which seem to deviate from the common ancestor earlier (*Racovitzanus* will be discussed in the next paper). For 21 genera, this pattern is a synapomorphic feature. *Cenognatha* has the same pattern of endopodal sensory setae (3+5), but it seems to be a result of independent and convergent transformation. The setal pattern of *Plesioscolecithrix* (3+4) is probably also the result of independent transformation. However, these three genera share a number of features with scolecitrichids, including the shape of Mx1, which is a distinguishing scolecitrichid feature (Table 2). That is why species presently considered in the genera *Cenognatha* and *Plesioscolecithrix* were included in the family Scolecitrichidae by Vyshkvartzeva (1989b, 2001), Ohtsuka et al. (2003), Boxshall & Halsey (2004), and Markhaseva & Dahms (2004); see also Table 5. Undoubtedly, only the ninth ancestral seta has transformed in some genera of Scolecitrichidae independently, and for this reason it differs strongly from the

other sensory setae, but in most taxa this seta was lost (Vyshkvartzeva, 2001; Ohtsuka et al., 2003; Boxshall & Halsey, 2004). This constant pattern of sensory setae implies that eight normal endopodal Mx2 setae of the common ancestor transformed into sensory setae once, in the ancestor of 21 above genera. Based on this supposition, Vyshkvartzeva (2001) considered this character state to be a synapomorphic character in the Scolecitrichidae. Thus, the 3+5 pattern of sensory setae on the Mx2 endopod is a good diagnostic criterion of the family, in combination with the trend to specialization in the male Mxp of scolecitrichids (Vyshkvartzeva, 2003), proportions of different parts of Mx1 in relation to the width of the praecoxal arthrite Li1 (Tables 2 and 4) and some other differing characters of mouthparts (unpublished data).

Ohtsuka et al. (2003) and Boxshall & Halsey (2004) outline two groups of species within the family Scolecitrichidae: a central core or crown group, of eighteen genera, and a group of seven genera, representing early offshoots and leading to the crown group of the paraphyletic (Ohtsuka et al., 2003; Boxshall & Halsey, 2004) family Scolecitrichidae. According to these authors, Scolecitrichidae includes *Neoscolecithrix* s. str. Canu, 1896 (Tharybidae according to Bradford et al., 1983, Ferrari & Markhaseva, 1996, and Bradford-Grieve, 2001), *Parkius* Ferrari & Markhaseva, 1996 (Parkiidae according to Ferrari & Markhaseva, 1996) and *Rythabis* Schulz, 1995 (Tharybidae in Schulz & Beckmann, 1995), along with 23 genera listed by Vyshkvartzeva (2001) and the recently described genus *Plesioscolecithrix* Markhaseva & Dahms, 2004 (Table 5).

The crown group was defined by two synapomorphies: (1) "a maximum of 4 setae on proximal praecoxal endite [Li1] of maxilla (apomorphic state = fifth seta lost), (2) third syncoxal endite of maxilliped [Li3] represented by a single setal element, usually a brush-like sensoriform seta (apomorphic state = loss of other 2 setae)" (Ohtsuka et al., 2003: 62; Boxshall & Halsey, 2004).

The group of early offshoots for the most part retains the primitive number of 3 setae on Li3 of Mxp, except *Heteramalla* and *Puchinia* having two setae. In Scolecitrichidae, the latter state also occurs only in the independently arising genus *Plesioscolecithrix*. One seta is usually transformed into a long (more than 0.3 times as long as the syncoxa) thin brush-like seta, except *Heteramalla*, which has the transformed seta similar to worm-like ones and except *Grievella*, which retains all three setae sclerotized. The variable composition of sensory setae (variable setae number: 1, 1-2, 2-3, and variable setae structure) on Li1-Li3 of Mxp in the scolecitrichid genera supposes its independent transformation.

Table 4. Indices showing ratios of different Mx1 parts to Mx1 Li1 width in Scolecitrichidae (20 genera, excepting *Macandrewella*, *Plesioscolecithrix*, *Scopalatum* and *Racovitzanus*), Tharybidae (*Tharybis*, *Undinella* and *Rythabis*), *Parundinella* and *Parkius*.

Family/Genus	Literature source	Index A	Index B	Index C	Index D
Scolecitrichidae					
	*				
Limits		1.55-3.39	1.54-3.33	1.08-1.53	2.25-4.16
Range		1.78	1.79	0.49	1.91
Average (n = 89)		2.37	2.25	1.36	2.87
S.D.		0.64	0.54	0.32	0.39
Tharybidae					
<i>Tharybis</i>	Andronov, 2002; Schulz, 1981				
Limits		0.8-1.62	1.15-1.54	0.5-0.87	0.8-1.4
Range		0.82	0.39	0.37	0.6
Average (n = 14)		1.17	1.42	0.67	1.13
S.D.		0.21	0.16	0.09	0.19
<i>Undinella</i>	Andronov, 2002; Vaupel-Klein, 1970				
Limits		1.0-1.55	1.16-1.66	0.3-0.58	1.13-2.0
Range		0.55	0.5	0.28	0.87
Average (n = 7)		1.28	1.48	0.42	1.52
S.D.		0.19	0.18	0.09	0.29
<i>Rythabis</i> (<i>R. atlantica</i> , n = 1)	Schulz & Beckmann, 1995	1.2	1.6	0.9	1.4
Parundinella					
	Fleminger, 1957; Andronov, 2002				
Limits		1.6-1.8	3.4	0.9-1.3	2.75-3.7
Range		0.2		0.4	0.95
Average (n = 3)		1.73	3.4	1.1	3.28
S.D.		0.12			0.49
<i>Parkius</i> (<i>P. karenwishnerae</i> , n = 1)	Ferrari & Markhaseva, 1996	1.2	1.7	0.8	2.3

Index A = length of Li1 : width of Mx1Li1.

Index B = length of the longest distal marginal seta of Li1 : width of Mx1Li1.

Index C = width of Li1: width Mx1Li1.

Index D = length of Li2+Li3+Li4+Ri : width of Mx1Li1.

Abbreviations: n – number of specimens measured; S.D. – standard deviation.

* For the literature employed for Mx1 characteristics of scolecitrichid species, see Table 3.

Li1 of Mx2 in the genera of early offshoots usually retains 5 setae (an ancestral character state), but *Puchinia* and some *Xantharus* (*X. formosus* Andronov, 1981 and *X. siedleckii* Schulz & Kwasnewski, 2004) have 4 setae on Li1 of Mx2. The same number of setae occurs among species of the crown group: *Amallothrix aspino-*

sa (Roe, 1975), *Pseudoamallothrix profunda* (Brodsky, 1950), *P. laminata* (Farran, 1926), *P. paralaminata* Vyshkvartzeva, 2003 and all species of the genus *Lophothrix* Giesbrecht, 1895. However, the typical state in species of the crown group is 3 setae on Li1 of Mx2 (2 setae lost). In consequence, the number of setae on Li1 of Mx2

is not a good distinguishing feature among both the groups of scolecitrichids. Seemingly, the crown group can be distinguished from the group of early offshoots by the only one apomorphy: the third syncoxal endite of Mxp (Li3) with a single short (about 0.3 times as long as the syncoxa) brush-like sensoriform seta (apomorphic state = loss of other 2 setae, the remaining seta transformed).

Ohtsuka with coauthors (2003) and also Boxshall & Halsey (2004) did not include into the group of early offshoots *Heteramalla* and *Puchinia*, but included *Neoscolecithrix* s. str. (Tharybidae according to Bradford et al., 1983 and Bradford-Grieve, 2001), *Rythabis* (Tharybidae according to Schulz, in Schulz & Beckmann, 1995) and *Parkius* (Parkiidae, according to Ferrari & Markhaseva, 1996). The systematic positions of the latter two genera are discussed below.

These authors placed the genus *Heteramalla*, as also *Puchinia*, in the crown group. However, *Heteramalla* does not share both the distinguishing characters as it has 5 setae on Li1 of Mx2 and 2 setae on Li3 of Mxp syncoxa; at the same time, *Puchinia* has 2 setae, not one, on Li3 of Mxp syncoxa (for details, see the description of *H. sarsi* and the above part of Discussion on *Heteramalla*). *Heteramalla* and *Puchinia* (2 setae on Li3 of Mxp and 4-5 setae on Li1 of Mx2) probably occupy a position among early offshoots of the family Scolecitrichidae. These two genera have proportions of Mx1 similar to those of the other genera in early offshoots (Table 2). The group of early offshoots includes also the genera *Falsilandrumius*, *Grievella*, *Landrumius* and *Xantharus* (Tables 2 and 5).

The genus *Cenognatha* has some features similar to those in genera of early offshoots: setal pattern on Li1 of Mx2 and on Li3 of Mxp, as also some other characters (Table 2). I suppose this genus has deviated from the common ancestor independently, with two unique apomorphies: 1) posterolateral corners of the prosome with two spine-like processes; 2) unique pattern of fusion of ancestral exopodal free segments Re1 (Re1 + ReII) and Re2 (ReIII + ReIV) of A2 (see Bradford-Grieve, 2001) in contrast to the pattern of scolecitrichids (Re1 = ReI; Re2 = ReII + ReIII + ReIV). However, most characters in *Cenognatha* correspond to those of Scolecitrichidae, although they evolved in parallel with other scolecitrichids (Table 5). Thus, *Cenognatha* is included in this paraphyletic family.

The genus *Plesioscolecithrix* which has the setal pattern of Mx2 endopod 3 Wo + 4 Br, a very low index showing the Mx1 ratio [W(Le1):W(Li1) = 0.85], and also some other unique autapomorphies (Markhaseva & Dahms, 2004), seems to separate earlier than the synapo-

morphic scolecitrichid pattern 3 Wo + 5 Br arose. This genus evolved independently but convergently with most scolecitrichids, as well as *Cenognatha* (Table 2). *Plesioscolecithrix* is also placed in the paraphyletic family Scolecitrichidae as its independently arising branch (Table 5).

The setation of Mx1, Mx2 and Mxp in Tharybidae and Diaixidae and its diagnostic significance

The composition of endopodal sensory setae of Mx2 in Tharybidae and Diaixidae is variable between genera and species in contrast to that in Scolecitrichidae. This variability is noted also by Boxshall & Halsey (2004). The following setal patterns of Mx2 endopod occur in tharybids: *Tharybis* Sars, 1902: 3 long Wo + 4 shorter Br + 1 long normal seta (type species), or 3 long Wo + 5 shorter Br, or 3 long Wo + 6 shorter Br, or 4 long Wo + 4 shorter Br; *Undinella* Sars, 1900: 5 very thin and short Br (Wo absent); *Rythabis* Schulz, 1995: 6 long Wo + 2 much shorter Br, with external structure different from that in scolecitrichids and tharybids; *Parundinella* Fleminger, 1957: 5-6 transformed setae, all worm-like, or composition of setae is variable in the same species, with 1 or 3 brush-like setae among transformed ones. In Diaixidae, the composition of endopodal sensory setae on Mx2 is as follows: *Diaixis* Sars, 1902: 3-4 long Wo + 4-5 shorter Br; *Anawekia* Othman & Greenwood, 1994: 4 long Wo, Br absent.

If we accept the hypothesis of Ohtsuka with coauthors (1998) and Boxshall & Halsey (2004) which states that the sensory setae pattern 3 Wo + 5 Br is a symplesiomorphy appeared in the common ancestor of four families (Scolecitrichidae, Tharybidae, Diaixidae and Parkiidae), one should accept (1) the secondary loss of all worm-like setae in *Undinella*, or of all brush-like setae in *Anawekia*, and (2) the secondary transformation of some brush-like setae into worm-like ones in *Anawekia*, *Parundinella*, *Rythabis*, as also in some species of *Tharybis*. (The above loss is not a character reversal, which, as noted Huys & Boxshall (1991), sometimes occur in Copepoda, because it does not represent a return to the original state). However, the secondary loss of sensory setae in mesopelagic actively-feeding *Undinella* seems to be improbable, but the loss of some normal ancestral setae accompanying the transformation of the other ancestral setae is in accordance with the principle of oligomerization, as it was formulated by Dogiel (1954). The secondary transformation of some brush-like setae to worm-like ones is hardly reasonable as well, because, as Nishida & Ohtsuka (1997) have shown, these setae differ in external and internal struc-

Table 5. Generic composition of the paraphyletic family Scolecitrichidae.

Genera with synapomorphic arrangement: 3+5 sensory setae on Mx2 endopod		Genera independently arising from the common ancestor of the family Scolecitrichidae
Genera of the crown group: Li3 of Mxp syncoxa with 1 brush-like seta	Early offshoots: Li3 of Mxp syncoxa with 2-3 setae, one of them is usually the transformed sensory seta	
<i>Amallothrix</i> Sars, 1925	<i>Falsilandrumius</i> Vyshkvartzeva, 2001	<i>Racovitzanus</i> Giesbrecht, 1902
<i>Archescolecithrix</i> Vyshkvartzeva, 1989	<i>Grievella</i> Ferrari & Markhaseva, 2000	<i>Cenognatha</i> Bradford-Grieve, 2001
<i>Lophothrix</i> Giesbrecht, 1895	<i>Heteramalla</i> Sars, 1907	<i>Plesioscolecithrix</i> Markhaseva & Dahms, 2004
<i>Macandrewella</i> A. Scott, 1909	<i>Landrumius</i> Park, 1983	?? <i>Neoscolecithrix</i> Canu, 1896
<i>Mixtocalanus</i> Brodsky, 1950	<i>Puchinia</i> Vyshkvartzeva, 1989	
<i>Parascaphocalanus</i> Brodsky, 1955	<i>Xantharus</i> Andronov, 1981	
<i>Pseudoamallothrix</i> Vyshkvartzeva, 2000		
<i>Scaphocalanus</i> Sars, 1900		
<i>Scolecithricella</i> Sars, 1902		
<i>Scolecithrix</i> Brady, 1883		
<i>Scolecithrichopsis</i> Vyshkvartzeva, 2000		
<i>Scolecocalanus</i> Farran, 1936		
<i>Scopalatum</i> Roe, 1975		
<i>Scottocalanus</i> Sars, 1905		
<i>Undinothrix</i> Tanaka, 1961		
Genera additionally included by Ohtsuka et al., 1998, and Boxshall & Halsey, 2004		
In crown group	In early offshoots	
<i>Heteramalla</i> Sars, 1907	<i>Cenognatha</i> Bradford-Grieve, 2001	
<i>Puchinia</i> Vyshkvartzeva, 1989b	? <i>Neoscolecithrix</i> Canu, 1896	
<i>Racovitzanus</i> Giesbrecht, 1902	? <i>Parkius</i> Ferrari & Markhaseva, 1996	
	? <i>Rythabis</i> Schulz, in Schulz & Beckmann, 1995	

ture, the structure of the former being more complex than of the latter; in addition, they have a different functional specialization.

In contrast to the suppositions of Ohtsuka with coauthors (2003) and Boxshall & Halsey (2004), I assume that the transformations of endopodal setae of Mx2 in genera of the family Tharybidae from the plesiomorphic state of the common ancestor have occurred independently, alike those of the setae on Li1-Li3 of Mxp syncoxa and Li5 of Mx2. A similar situation probably takes place in Diaixidae (the latter family is not a subject of special analysis in the present paper). The supposition about the independent transformation of the latter setae variable in genera or some species of Bradfordian families (Vyshkvartzeva, 1989a,

1989b, 2000, 2001; Ohtsuka et al., 1998) is quite accepted and did not meet any objections. Concerning the latter, an assumption about the variable in number and structure endopodal setae of Mx2 which could transform independently also in the genera of Tharybidae is very reasonable. Possibly, even in species or in species groups of *Tharybis*, the transformation of setae also occurred independently. Thus, the sensory setae pattern within the family Tharybidae, contrary to Scolecitrichidae, is of no diagnostic value.

The genera of Tharybidae show a similar trend in transformation (specialization) of mouthparts. Boxshall & Halsey (2004) adopt as “a rigid definition of the family [Tharybidae] ... form of the maxillule with broad praecoxal arthrite [Li1] and

reduced palp setation and the form of the swimming legs 2 to 4..." and included the genera *Parundinella*, *Tharybis* and *Undinella* in this family (Boxshall & Halsey, 2004: 210). The family position of *Parundinella*, which has the indices of Mx1 closer to those of the family Scolecitrichidae (Table 4), however, is unclear to me and needs a special discussion.

Evidently, palp setation of Mx1 cannot serve as a good distinguishing feature of Tharybidae, especially if *Parundinella* is included in this family. The number of setae on homologous parts of Mx1 is similar or overlaps in different Bradfordian families (Table 3). Therefore, setal formula of Mx1 is not always a good diagnostic feature, as the progressive reduction in the segmentation of endopod and in the armature of Mx1, which is recorded in all genera of Bradfordian families (Table 3), is a general way of evolutionary changes of the appendages in Calanoida. The differences in the shape of Mx1, which may be characterized by the indices showing the ratio of different parts of Mx1 to the width of Li1, distinguish the families Scolecitrichidae and Tharybidae much better (the latter family including *Tharybis*, *Undinella* and *Rythabis*; see Table 4). The tharybid genera *Tharybis*, *Undinella* and *Rythabis* have the following indices of Mx1, respectively (indices of Scolecitrichidae are given in parentheses): index A = 1.17-1.28 (1.55-3.39); index B = 1.42-1.6 (1.54-3.33); index C = 0.42-0.9 (1.08-1.53, except 0.85 in *Plesioscolecithrix*); index D = 1.13-1.52 (2.25-4.16). Thus, indices A, C and D do not overlap in two families under discussion and may serve as good distinguishing characters. Moreover, between the two families there are some differences in Mx2 other than its armature. Tharybids are characterized by the long setae on Li1-Li4 of Mx2 which are no more than 1.5 times as long as Mx2 and have spine-like tips. In scolecitrichids these setae are twice as long as Mx2, whip-like, with slender tips. Some cryptic changes in the generotype of the ancestor of the Tharybidae lineage are possible, which resulted in similar modifications of mouthparts in tharybids. Thus, the shape of Mx1 characterized by the indices proposed here (Table 4) and the above-mentioned details of Mx2 in combination with the features noted by Fleminger (1957), Bradford et al. (1983) and Boxshall & Halsey (2004): a similarly organized P5 of female and male and the shape of P2-P4, could be a good differential characteristic of the family Tharybidae.

The position of the genus *Rythabis*

Ohtsuka with coauthors (2003) placed the genus *Rythabis* Schulz, 1995 in the same group with the early offshoots of scolecitrichids. However,

the representatives of *Rythabis* have the proportions of Mx1 closer to those of Tharybidae (Table 4). By this means, the genus has a similar with tharybids trend of Mx1 specialization, though the setation of all parts of Mx1 excepting the exopod is closer to the ancestral pattern than in the other genera of tharybids. At the same time, *Rythabis* has the exopod of Mx1 with 4 setae (7 setae lost) and one-segmented short endopod. These are strongly advanced features more characteristic of Tharybidae. Moreover, the elements of ancestral setation in combination with advanced states of setation occur frequently in different parts of Mx1 also in *Tharybis* (Table 3). A combination of primitive characters with strongly advanced features (heterobaty according to Takhtajan, 1966, 1980) is typical of the other genera of Bradfordian families (Tables 2 and 3) and was earlier described in other Calanoida, mainly in benthopelagic genera (Vyshkvartzeva, 1989b; Markhaseva, 1993). Considering that the reduction in setal number (according to the principle of oligomerization) is a common way of specialization in genera of Bradfordian families and, as noted Huys & Boxshall (1991), in Calanoida on the whole, the setal numbers of Mx1 seem to be less important for a study of relationships than the trend to the shape modification of Mx1 observed in tharybids, and also the specialization of Mx2 shape. According to Schulz & Beckmann (1995), *Rythabis* also has a number of features similar to *Tharybis*: compact ovate body, similar rostrum and A1, identical numbers of large and massive spines on Li1 of Mx1, Li1 of Mx2 with 4 setae, and also similarly organized female P5. Thus, I follow the opinion of Schulz (in Schulz & Beckmann, 1995) and place *Rythabis* in the family Tharybidae.

The position of the genus *Parkius*

The monotypic genus *Parkius* Ferrari & Markhaseva, 1996 is very close to scolecitrichids. It shares a pattern of 3 Wo + 5 Br sensory setae on Mx2 endopod with 22 scolecitrichid genera and also has the armature of Li3 of Mxp syncoxa (1 normal and 1 brush-like setae; one seta lost) as in *Heteramalla*, *Plesioscolecithrix* and *Puchinia*. That is why Boxshall & Halsey (2004) supposed that *Parkius* derived within the Scolecitrichidae as its early offshoot and therefore they consider Parkiidae as a synonym of Scolecitrichidae.

However, *Parkius* represents a strongly specialized branch with a unique among Bradfordian families modification of Mxp and a unique apomorphy, an area of denticles of Vaupel-Klein's organ in proximal position on the endopod of leg 1. The basis of Mxp is strongly elongate distal to its proximal medial denticle row and two

Table 6. Comparison of the female of *Parkius karenwishnerae* Ferrari & Markhaseva, 1996 with the male of “*Racovitzanus* sp.” (after Grice & Hulsemann, 1967).

Character	Female of <i>Parkius karenwishnerae</i> Ferrari & Markhaseva, 1996	Male of “ <i>Racovitzanus</i> sp.” (after Grice & Hulsemann, 1967)
Body length (mm)	1.8-2.15	1.92
Habitat	1-5 m above the bottom	?
Locality	13°23'N 102°27'W	18°02'N 65°08'E
Depth (m)	2945-3010	2000-3000
Posterolateral corner of SmP5	rounded, indented	rounded, indented
Rostrum	simple plate with filaments	large plate without filaments
A1 length	reaching Ur2	almost reaching furca
A1 segments (number)	24	23
Md: teeth of gnathobase (number)	3 high V + 4 small D	3 high V + 5 small D
Md: dorsal seta of gnathobase	thin, as long as V teeth	thin, as long as V teeth
Mx1: setae of Li1 (number)	9	9
Mx1: posterior setae (number)	2	2
Mx1: setae of Li2 (number)	4	3
Mx1: setae of Li3 (number)	4	4
Mx1: setae of Li4 (number)	4	3
Mx1: segments of Ri (number)	1	1
Mx1: setae of Ri (number)	10	8
Mx1: setae of Re (number)	8	8
Mx1: ratio L(Li1):W(Li1)	1.2	1.66
Mx1: ratio L(marginal setae of Li1):W(Li1)	1.7	1.77
Mx1: ratio W(Le1):W(Li1)	0.8	?
Mx1: ratio L(Li2+Li3+Li4+Ri):W(Li1)	2.1	2.55
Mx1: ratio L(Re):L(basis)	1.0	1.2
Mx2: setae of Li1 (number)	4	4
Mx2: sensory setae of Ri (number)	3 Wo + 5 Br	3 Wo + ?2 Br
Mxp: setae of Li1-Li3 (number)	1, 2, 2	1, 2, 2
Mxp: shape of basis	proximal 0.35 of the length thickened; the part distal to inner setae narrow, elongate	proximal 0.3 of the length thickened; the part distal to inner seta narrow, elongate
Mxp: medial setae of basis (number)	2 (1 long, 1 short)	1 long
Mxp: shape of endopodal segments	3 proximal elongate, terminal very small	3 proximal elongate, terminal very small
Mxp: armament of endopodal segments	2, 2, 2, 1, 4	2, 1, 2, 2, 2

Note. The characters considered as the most significant for identification are given in bold.

Abbreviations: L – length; W – width; V – teeth of ventral part of gnathobase; D – teeth of dorsal part of gnathobase; Wo – worm-like seta; Br – brush-like seta.

medial setae (unique apomorphy: loss of the third seta combined with a unique elongation of distal part of the basis). Furthermore, the endopod of Mxp has segments 2-5 attenuate, bearing a re-

duced armament of 2+2, 2, 2, 1 and 4 setae, respectively; one endopodal seta on each of Ri1-Ri4 is not articulated but fused with the segment and is transformed, hook-like (Ferrari & Markha-

seva, 1996). In *Parkius*, the proportions of Mx1 are intermediate between scolecitrichids and tharybids: the indices A, B and C are as in tharybids, D, as in scolecitrichids (Table 4). The unique among Bradfordian families Mxp shape together with a unique position of the area of denticles of Vaupel-Klein's organ and Mx1 indices intermediate between those in scolecitrichids and tharybids can result from some important differences in the biology of the species/genus compared with the other scolecitrichids. Therefore, the other possibility, that *Parkius* is a branch separate from Scolecitrichidae, and 3+5 sensory setae on Mx2 and 2 setae on Li3 of Mxp evolved from the common ancestor independently and convergently with scolecitrichids, is quite probable. In any case, the unique apomorphies listed above and marking important changes in the biology of the species/genus enable one to separate this genus in a distinct family, Parkiidae, **fam. dist.**

The morphology of male could clarify the family position of *Parkius*. It seems to me that the male of *Parkius* considered till nowadays as unknown, was described by Grice & Hulsemann (1967) as "*Racovitzanus* sp.". The recorded male does not fit the latter genus in the following characters (features of *Racovitzanus* in parentheses): Ur5 as long as half-length of Ur4 (Ur5 about 1.4 times as long as Ur4, that is a unique feature among the Bradfordian families), the rostrum in the shape of a large plate (rostrum single, finger-like), different setation of Mx1 (see Table 6, in contrast to Li1 with 2 proximal marginal setae short and Re with 5 setae), Li1 of Mx2 with 4 setae (with 3 setae), the syncoxa of Mxp with two setae on Li3 (one brush-like setae), the basis of Mxp distal to medial seta about twice as long as proximal part (about 0.5 times as long as proximal part), the shape and setation of endopodal segments of Mxp significantly different, and the male mouthparts well-developed (significantly reduced compared with female). On the contrary, a comparison between the descriptions of the female of *Parkius* (Ferrari & Markhaseva, 1996) and the male of "*Racovitzanus* sp." (Grice & Hulsemann, 1967) shows that they share the unique shape and setation of Mxp as also almost all other described features which are presented in Table 6. Therefore the male of "*Racovitzanus* sp." (Grice & Hulsemann, 1967) is treated here as *Parkius* sp. P5 of this male is biramous, with protopods (coxa and basis) of both legs equal in length (almost as in some species of the scolecitrichid genus *Xantharus*), but the basis of both legs is swollen. The latter does fit neither Scolecitrichidae nor Tharybidae. The structure of P5 represents a separate evolutionary morphological trend and thus, it also justifies a distinct family position of Parkiidae.

Acknowledgements

The collection of the Zoological Institute, Russian Academy of Sciences, which is supported by the Russian Federation Ministry of Science and Technology (grant no. 2002-03-16), was used in this study. I am very grateful to Dr. Knud Schulz for a critical review and huge work for correction of my English. I am very thankful to A.A. Przhiboro for careful editing of my paper.

References

- Alzamora, M.M.** 1940. Los copépodos pelágicos del mar de Baleares. *Notas Resúm. Inst. Espan. Oceanogr.*, ser. 2, **99**: 1-15.
- Andronov, V.N.** 1981. *Xantharus formosus* gen. et sp. n. (Copepoda, Calanoida) from the north-western Atlantic. *Zool. Zh.*, **60**(11): 1719-1721. (In Russian).
- Andronov, V.N.** 2002. The calanoid copepods (Crustacea) of the genera *Diaixis* Sars, 1902, *Parundinella* Fleminger, 1957, *Undinella* Sars, 1900 and *Tharybis* Sars, 1902. *Arthropoda Selecta*, **11**: 1-80.
- Björnberg, T.K.S.** 1975. New species of marine bathypelagic copepods collected off South America. *Ciênciã e Cultura*, **27**: 175-188.
- Boxshall, G.A. & Halsey, S.H.** 2004. *An introduction to copepod diversity*. London: The Ray Society. 966 p.
- Bradford, J.** 1973. Revision of family and some generic definitions in the Phaennidae and Scolecitrichidae (Copepoda: Calanoida). *N. Z. J. mar. freshw. Res.*, **7**: 133-152.
- Bradford, J.M., Haakonssen, L. & Jillett, J.B.** 1983. The marine fauna of New Zealand: pelagic calanoid copepods: families Euchaetidae, Phaennidae, Scolecitrichidae, Diaixidae, and Tharybidae. *N. Z. oceanogr. Inst. Mem.*, **90**: 1-150.
- Bradford-Grieve, J.M.** 2001. Two species of benthopelagic calanoid copepods of the genus *Neoscolecithrix* Canu, 1896 s. str. from New Zealand and the segregation of *Cenognatha* n. gen. *N. Z. J. mar. freshw. Res.*, **35**: 781-793.
- Campaner, A.F.** 1984. *Scaphocalanus* and *Scolecithriella* (Copepoda, Calanoida, Scolecitrichidae) from the epipelagial off Southern Brazil: a taxonomic and distributional survey. *Bol. Zool.*, **8**: 165-187.
- Dogiel, V.A.** 1954. *Oligomerizatsiya gomologichnykh organov kak odin iz glavnykh putey evolyutsii zhivotnykh* [Oligomerization of the homologous organs as one of the main pathways in animal evolution]. Leningrad: Izd. Leningr. Univ. 368 p. (In Russian).
- Farran, G.P.** 1905. Report on the Copepoda of the Atlantic slope off counties Mayo and Galway. *Ann. Rep. Fish. Ireland*, 1902-1903, **2**, App. 2, sci. Invest.: 23-52.
- Farran, G.P.** 1936. Copepoda. *Sci. Rep. of the Great Barrier Reef Exped. 1928-1929*, **5**(3): 73-142. London: British Mus. (Natur. Hist.).
- Ferrari, F.D. & Markhaseva, E.L.** 1996. *Parkius karenishnerae*, a new genus and species of calanoid copepod (Parkiidae, new family) from benthopelagic waters of the eastern tropical Pacific Ocean. *Proc. biol. Soc. Wash.*, **190**: 262-285.
- Ferrari, F.D. & Markhaseva, E.L.** 2000. *Grievella shanki*, a new genus and species of scolecitrichid calanoid copepod (Crustacea) from a hydrothermal vent along the southern East Pacific Rise. *Proc. biol. Soc. Wash.*, **113**: 1079-1088.
- Fleminger, A.** 1957. New genus and two species of Tharybidae (Copepoda: Calanoida) from the Gulf of Mexico with remarks on the status of the family. *Fish. Wildlife Serv. U. S.*, **57**(116): 347-354.

- Fleminger, A.** 1983. Description and phylogeny of *Isaacsicalanus paucisetus*, n. gen., n. sp. (Copepoda: Calanoida: Spinocalanidae) from an East Pacific hydrothermal vent site (21°N). *Proc. Biol. Soc. Wash.*, **96**: 605-622.
- Fosshagen, A.** 1972. *Neoscolecithrix farrani* Smirnov (Copepoda, Calanoida) from North Norway. *Astarte*, **5**: 1-6.
- Giesbrecht, W.** 1892. Systematik und Faunistik der pelagischen Copepoden des Golfs von Neapel und der angrenzenden Meeresabschnitte. *Fauna und Flora des Golfes von Neapel*, **19**: 1-831.
- Grice, G.D.** 1962. Calanoid copepods from equatorial waters of the Pacific Ocean. *Fish. Bull.*, **61**(186): 171-246.
- Grice, G.D.** 1972. The existence of a bottom-living calanoid copepod fauna in deep water with description of five species. *Crustaceana*, **23**: 219-242.
- Grice, G.D. & Hulsemann, K.** 1965. Abundance, vertical distribution and taxonomy of calanoid copepods at selected stations in the north-east Atlantic. *J. Zool.* (London), **146**: 213-262.
- Grice, G.D. & Hulsemann, K.** 1967. Bathypelagic calanoid copepods of the western Indian Ocean. *Proc. U. S. Nat. Mus.*, **122**(3583): 1-67.
- Grice, G.D. & Hulsemann, K.** 1968. Calanoid copepods from midwater trawl collections made in the south-eastern Pacific Ocean. *Pacif. Sci.*, **22**: 322-335.
- Hulsemann, K.** 1985. A new species of *Neoscolecithrix* Canu (Copepoda Calanoida) in Antarctic waters with remarks on the genus. *Polar Biol.*, **5**: 55-62.
- Huys, R. & Boxshall, G.A.** 1991. *Copepod evolution*. London: The Ray Society. 468 p.
- Markhaseva, E.L.** 1993. Phylogenetic trends within Aetideidae (Copepoda, Calanoida). *Issled. Fauny Morya*, **45**(53): 51-69. (In Russian).
- Markhaseva, E.L. & Dahms, H.-U.** 2004. *Plesioscolecithrix* (Copepoda, Calanoida, Scolecitrichidae): a new genus and a new species from the high Antarctic Weddell Sea (Southern Ocean). *Sarsia*, **89**: 326-337.
- Mori, T.** 1937. *The pelagic Copepoda from the neighbouring waters of Japan*. Tokyo. 150 p.
- Nishida, S. & Ohtsuka, S.** 1997. Ultrastructure of the mouthpart sensory setae in mesopelagic copepods of the family Scolecitrichidae. *Plankton Biol. Ecol.*, **44**(1-2): 81-90.
- Ohtsuka S., Boxshall, J. & Fosshagen, A.** 2003. A new species of *Neoscolecithrix* (Crustacea: Copepoda; Calanoida) from off Okinawa, Southwestern Japan, with comments on the generic position in the superfamily Clausocalanoidea. *Bull. Nat. Sci. Mus., Tokyo*, Ser. A, **29**: 53-63.
- Ohtsuka, S., Takeuchi, I. & Tanimura, A.** 1998. *Xanthocalanus gracilis* and *Tharybis magna* (Copepoda: Calanoida) rediscovered from the Antarctic Ocean with baited traps. *J. Natur. Hist.*, **32**: 785-804.
- Othman, B.H.R. & Greenwood, G.J.** 1994. A new genus with three new species of copepods from the family Diaixidae (Crustacea: Calanoida) and a redefinition of the family. *J. Natur. Hist.*, **28**: 987-1005.
- Park, T.S.** 1970. Calanoid copepods from the Caribbean Sea and Gulf of Mexico. 2. New species and new records from plankton samples. *Bull. Mar. Sci.*, **27**: 272-546.
- Park, T.S.** 1980. Calanoid copepods of the genus *Scolecithricella* from Antarctic and Subantarctic waters. Paper 2. Biology of the Antarctic Seas IX. *Antarctic Res. Ser.*, **31**: 1-79.
- Park, T.S.** 1982. Calanoid copepods of the genus *Scaphocalanus* from Antarctic and Subantarctic waters. Paper 2. Biology of the Antarctic Seas XI. *Antarctic Res. Ser.*, **34**: 1-127.
- Park, T.S.** 1983. Calanoid copepods of some scolecitrichid genera from Antarctic and Subantarctic waters. *Antarctic Res. Ser.*, **38**: 165-213.
- Razouls, C.** 1995. Diversité et répartition géographique chez les copepods pélagiques. 1. Calanoida. *Ann. Inst. Océanogr.*, **71**: 81-401.
- Roe, H.S.J.** 1975. Some new and rare species of calanoid copepods from the northeastern Atlantic. *Bull. Brit. Mus. Natur. Hist. Zool.*, **28**(7): 295-372.
- Rose, M.** 1933. Copépodes pélagiques. *Faune de France*, **26**. Paris. 374 p.
- Rose, M.** 1942. Les Scolecitrichidae (Copépodes pélagiques) de la Baie d'Alger. *Ann. Inst. Océanogr.*, **21**: 113-170.
- Sars, G.O.** 1903. Copepoda: Calanoida. *An account of the Crustacea of Norway*, **4**. Bergen. 171 p.
- Sars, G.O.** 1907. Notes supplémentaires sur les Calanoides de la Princess-Alice (corrections et additions). *Bull. Inst. Océanogr. Monaco*, **101**: 1-27.
- Sars, G.O.** 1924-1925. Copépodes particulièrement bathypélagiques provenant des campagnes scientifiques du Prince Albert 1-er de Monaco. *Résult. Camp. Sci. Prince Albert 1-er*, **69**: 1-408. (1924 – atlas, 1925 – text).
- Schulz, K.** 1981. *Tharybis minor* sp. n. (Copepoda: Calanoida: Tharybidae) aus dem nordwestafrikanischen Auftriebsgebiet mit Anmerkungen zur Gattung *Tharybis* Sars. *Mitt. Hamburg zool. Mus. Inst.*, **86**: 169-177.
- Schulz, K.** 1989. Notes on rare spinocalanid copepods from the eastern North Atlantic, with descriptions of new species of the genera *Spinocalanus* and *Teneriforma* (Copepoda: Calanoida). *Mitt. Hamburg zool. Mus. Inst.*, **86**: 185-208.
- Schulz, K.** 1991. New species of the family Scolecitrichidae (Copepoda: Calanoida) from the Arabian Sea. *Mitt. Hamburg zool. Mus. Inst.*, **88**: 197-209.
- Schulz, K.** 1998. A new species of *Xantharus* Andronov, 1981 (Copepoda: Calanoida) from the mesopelagic zone of the Antarctic Ocean. *Helgoländer Meeresuntersuch.*, **52**: 41-49.
- Schulz, K. & Beckmann, W.** 1995. New benthopelagic tharybids (Copepoda, Calanoida) from the deep North Atlantic. *Sarsia*, **80**: 199-211.
- Scott, A.** 1909. The Copepoda of the Siboga expeditions. Part 1. Free-swimming, littoral and semi-parasitic Copepoda. *Siboga Exped.*, **29a**. Leyden. 323 p.
- Scott, T.** 1894. Report on Entomostraca from the Gulf of Guinea collected by John Rattra. *Trans. Linn. Soc., Zool.*, **6**(1): 1-161.
- Shich, C.-T. & Stallard, N.** 1982. Notes on two deep-water calanoids (*Aetideopsis rostrata* and *Neoscolecithrix farrani*) from Lancaster Sound. *Arctic*, **35**: 56-60.
- Takhtajan, A.L.** 1966. *Klassifikatsiya i filogeniya tsvetkovykh rasteniy* [Classification and phylogeny of flowering plants]. Moscow-Leningrad: Nauka. 610 p. (In Russian).
- Takhtajan, A.L.** 1980. Outline of the classification of flowering plants (Magnoliophyta). *Bot. Rev.*, **46**(3): 1-359.
- Tanaka, O.** 1961. The pelagic copepods of the Izu Region, middle Japan. Systematic account. VII. Family Scolecitrichidae (Part 1). *Publ. Seto mar. biol. Lab.*, **9**: 139-190.
- Vaupel-Klein, J.C. von.** 1970. Notes on a small collection of calanoid copepods from the northeastern Pacific, including the description of a new species of *Undinella* (Fam. Tharybidae). *Zool. Verhandl.*, **110**: 1-43.

- Vervoort, W.** 1965. Pelagic Copepoda. Part II. Copepoda Calanoida of the families Phaennidae up to and including Acartiidae, containing the description of a new species of Aetideidae. *Atlantide Rep.*, **8**: 9-216.
- Vervoort, W.** 1990. *Scolecocalanus stocki* sp. nov., a new calanoid copepod from Indonesian waters. *Beaufortia*, **41**: 177-184.
- Vyshkvartzeva, N.V.** 1983. Spinocalanidae. In: Brodsky, K.A., Vyshkvartzeva, N.V., Kos, M.S. & Markhaseva, E.L. *Veslonogie rakoobraznye morey SSSR i sopredel'nykh vod* [Oar-footed crustaceans (Copepoda: Calanoida) of the USSR seas and adjacent waters]. *Opred. Faune SSSR*, **135**: 250-338. Leningrad: Nauka. (In Russian).
- Vyshkvartzeva, N.V.** 1987. *Scaphocalanus acutocornis* sp. n. (Copepoda, Scolecithricidae) from the abyssopelagial Kuril-Kamchatka Trench. *Zool. Zh.*, **66**: 1573-1576. (In Russian).
- Vyshkvartzeva, N.V.** 1989a. On the systematics of the family Scolecithricidae (Copepoda, Calanoida). New genus *Archescolecithrix* and redescription of the genus *Mixtocalanus* Brodsky, 1950. *Issled. Fauny Morey*, **41**(49): 5-23. (In Russian).
- Vyshkvartzeva, N.V.** 1989b. *Puchinia obtusa* gen. et sp. n. (Copepoda, Calanoida) from the ultraabyssal of the Kuril-Kamchatsk trench and the place of the genus in the family Scolecithricidae. *Zool. Zh.*, **68**: 29-38. (In Russian).
- Vyshkvartzeva, N.V.** 1993. To the systematics of *Scaphocalanus* species (Copepoda Calanoida Scolecithricidae) females of which have no fifth leg. *Issled. Fauny Morey*, **45**(53): 7-29. (In Russian).
- Vyshkvartzeva, N.V.** 2000. Two new genera of Scolecithricidae and redefinition of *Scolecithricella* Sars and *Amallothrix* Sars (Copepoda, Calanoida). *Zoosyst. Ross.*, **8**(2): 217-241.
- Vyshkvartzeva, N.V.** 2001. A key to the genera Scolecithricidae, with description of a new genus and redescription of two species (Crustacea, Calanoida). *Zoosyst. Ross.*, **9**(1): 77-98.
- Vyshkvartzeva, N.V.** 2003. A new bathypelagic copepod *Pseudoamallothrix paralaminata* sp. n. from the Arctic Basin and arguments for the transfer of *Xanthocalanus soaresmoreirai* Björnberg, 1975 to the genus *Pseudoamallothrix* (Calanoida: Scolecithricidae). *Zoosyst. Ross.*, **12**(1): 39-47.
- Vyshkvartzeva, N.V. & Prusova, I.J.** 1997. A new calanoid copepod, *Scaphocalanus somaliensis* from the western Arabian Sea (Copepoda: Scolecithricidae). *Zoosyst. Ross.*, **6**(1): 33-36.
- Wilson, C.B.** 1942. The copepods of the plankton gathered during the last cruise of the Carnegie. *Carnegie Inst. Wash.*, Publ. **536**: 1-237.
- Wilson, C.B.** 1950. Copepods gathered by the United States Fisheries Steamer "Albatross" from 1887 to 1909, chiefly in the Pacific Ocean. *U. S. nat. Mus. Bull.* 100, **14**(4): 141-441.

Received 2 July 2004