Revision of the *hirsuticornis*-like species of *Macrothrix* Baird, 1843 (Cladocera: Anomopoda: Macrothricidae) from Subantarctic and temperate regions of the southern hemisphere

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Abstract
The aim of this paper is to revise populations of *Macrothrix cf. hirsuticornis* (Cladocera: Anomopoda: Macrothricidae) from different regions of the southern hemisphere. It is demonstrated that *M. hirsuticornis* Norman and Brady, 1867 s. str. is absent there, and five related species occupy different Subantarctic islands and the southernmost portions of South America, and Africa. *Macrothrix boergeni* Studer, 1878 from the Kerguelen Archipelago is redescribed and a neotype is selected. All populations in the southernmost portion of continental South America, Tierra del Fuego, Falklands, South Georgia, South Orkney Islands, and on the Antarctic Peninsula belong to *M. oviformis* Ekman, 1900. All the taxa described from this region—*M. ciliata* Vávra, 1900, *M. odontocephala* Daday, 1902, *M. propinqua* Sars, 1909, and, probably, *M. inflata* Daday, 1902—are junior synonyms of *M. oviformis*. Two new species are established: *M. sarsi* sp. nov. from the Cape region of South Africa and *M. ruehei* sp. nov. from Crozet, Marion islands, and Île Amsterdam. *Macrothrix cf. flagellata* Smirnov and Timms, 1983, previously known only from Tasmania, is found on Macquarie Island too. Differences between species from the southern hemisphere and Palaeartic *M. hirsuticornis* are summarized. It is demonstrated that characters of the general body shape (i.e. presence of a hood or a tooth on posterior head border) have a limited value for the systematics of *Macrothrix*. In contrast, some fine details, mostly missed by previous authors, are valuable for species discrimination. The present study increases the number of species recorded from the Antarctic-Subantarctic region. Probably, the current pattern of *Macrothrix* distribution results from a disruption of a pan-continental (early Mesozoic?) species complex.

Keywords: Africa, Cladocera, Macrothrix, morphology, South America, Subantarctic, systematics

Introduction
A decade ago Korovchinsky (1996) pointed out the poor state of systematics for the Macrothricidae (Cladocera: Anomopoda). Fortunately the situation has significantly improved, especially for *Macrothrix* Baird, 1843, which was previously regarded as a “hopeless” genus (Smirnov 1976). Several species groups have been revised (Silva-Briano...
et al. 1999; Dumont et al. 2002; Kotov and Hollwedel 2004; Kotov et al. 2004, 2005) and several remarkable new representatives have been found (Ciros-Pérez et al. 1996; Elias-Gutiérrez and Smirnov 2000). The dissertation of Silva-Briano (1998) was a significant contribution to the morphology and systematics of the genus, but, unfortunately, only some of its chapters have been published (Silva-Briano et al. 1999; Dumont et al. 2002). It is necessary to note that most of the aforementioned efforts were concentrated on tropical and subtropical regions.

Investigations on the Cladocera of the Subantarctic were started by Studer (1878), who described a series of species from the Kerguelen Archipelago including *Macrothrix boergeni* Studer, 1878. Subsequently, a series of new species and varieties was found in the southernmost portions of South America and Africa (Ekman 1900; Daday 1902; Sars 1916). Populations of *Macrothrix* sp. have also been reported from many Subantarctic localities (Pugh et al. 2002; Dartnall et al. 2005), and from the Antarctic Peninsula (Harding 1941).

While Smirnov (1976, 1992) regarded all species of *Macrothrix* from the Subantarctic islands, southern areas of South America and Africa, as well as many other taxa from different regions of the planet, as junior synonyms of a widely distributed species *M. hirsuticornis* Norman and Brady, 1867. David G. Frey in a personal communication to Dartnall (1995) doubted the conspecifity of the Palaearctic and Subantarctic populations. Examination of populations from different regions of the southern hemisphere revealed substantial differences between them, sufficient to consider them to be a series of separate species, and also different from Palaearctic *M. hirsuticornis* s. str.

### Material and methods

Samples of *Macrothrix* preserved in formalin or alcohol were obtained from different museums and colleagues. Animals were selected from preserved samples under a binocular stereoscopic microscope, placed on slides (in a drop of a glycerol–formaldehyde mixture) and studied under an optical microscope in toto. At least five parthenogenetic females from each locality (with the exception of the museum loans) were dissected under a stereoscopic microscope for the study of appendages and postabdomen. A single female was dissected from Sars’s type material, with the permission of the Collection Manager. The dissected parts were kept on a series of slides, like a single paralectotype. Drawings were prepared using a camera lucida attached to an Alphaphot compound microscope.

A system of numeration for different setae on thoracic limbs proposed by Kotov (2000) for chydorids was used here, on the basis of similarity of limbs in Chydoridae and Macrothricidae (Smirnov 1971, 1976; Dumont and Silva-Briano 1998). All operations with SEM have been described previously (Kotov 1999; Kotov and Štifter 2006).

The cladistic analysis was performed using PAUP program version 4.0b10 for 32 bit Microsoft Windows (Swofford 2000), using branch-and-bond search with an aim to elucidate the possible phylogeny of the *hirsuticornis*-like species, with the well-studied *M. tripectinata* as an outgroup. A bootstrap simulation of 100 replications was performed as a test of robustness of this analysis.

The following abbreviations are used for the collections: AM, Australian Museum, Sydney, Australia; AAK, personal collection of A. A. Kotov, Moscow, Russia; BAS, British Antarctic Survey, Cambridge, UK; DAD, Collectio Dadayana, the Hungarian Natural History Museum, Budapest, Hungary; DGF, Collection of D. G. Frey, Support Center of the Smithsonian Institution Museum of Natural History in Suitland, MD, USA; GOS,
Collection of G. O. Sars, Zoological Museum of the Oslo University, Norway; NHM, Natural History Museum, London, UK; NMK, personal collection of Dr N. M. Korovchinsky, Moscow, Russia; NNS, personal collection of Prof. N. N. Smirnov, Moscow, Russia; NNS MGU, slides of Prof. N. N. Smirnov, deposited in the Zoological Museum of Moscow State University ("Moskovskij Gosudarstvennij Universitet"), Russia (with a special enumeration); SMNH, Swedish Museum of Natural History, Stockholm, Sweden; ZIN, Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia; ZMHU, Zoologisches Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.

Results

*Macrothrix boergeni* Studer, 1878

(Figures 1–5, 6A–C)

*Macrothrix Börgeni* Studer 1878, p 108, Plate 3, Figure 2.

*Macrothrix hirsuticornis* Norman and Brady in Rühe 1914, p 55–56, Figures 6b, 19 (only specimens from Kerguelen!); Brehm 1954, p 41; Gay 1981, p 51, Figures 21–24.

*Macrothrix cf. hirsuticornis* in De Smet 2001, p 263.

All records of *Macrothrix* from Kerguelen listed by Pugh et al. (2002) probably present *M. boergeni*.

Type locality (according to neotype selected here)

An un-named pond near Port-aux-Franc¸ais, Îles Kerguelen, French Subantarctic Territories (approximately 49°21′S, 70°13′E). The sample was collected 5 February 1988 by W. H. De Smet.

Type material

Neotype (selected here): a parthenogenetic female in 90% alcohol, NHM 2004.2092. Author’s type material is apparently lost.

Label of the neotype: “*Macrothrix boergeni* Studer, 1878; 1 parth. ♃, A pond near Port-aux-Français, Îles Kerguelen, collected 5 February 1988 by W. H. De Smet, NEOTYPE”.

Other material examined

Kerguelen Archipelago: many parthenogenetic (parth.) ♀♀ taken from the sample, from which the neotype was selected, AAK 2002-027 (tube); 35 parth. ♀♀ taken from the same sample, NHM 2004.2093–2102 (tube).

Amended diagnosis

Parthenogenetic female. In lateral view body subovoid, cervical depression absent, dorsal margin breached by a “step” in posterior boundary of head, dorsal margin of valves without any serration. Postero-dorsal angle as rounded triangle, lies in level of middle of body height. No dome above eye. Ocellus large. Dorsal organ ovoid, small. Labrum with moderately projected apex bearing several small tubercles.
Postabdomen subovoid, with rounded distal extremity, without a “heel” basally, and without a reticulation on sides. Ventral margin straight, with a few series of small, robust denticles. Dorsal margin distinctly bilobed; preanal margin with transversal series of minute denticles.

Figure 1. *Macrotich boergeni*, parthenogenetic female from an unnamed pond near Port-aux-Français, Îles Kerguelen. (A) Large adult; (B, C) head; (D) setae in anterior portion of valve ventral margin; (E) middle of ventral margin; (F, G) posterior portion of ventral margin; (H) postabdomen; (I, J) postabdominal claw, outer view; (K) postabdominal claw, inner view; (L, M) antenna I in lateral and anterior view; (N) its distal end; (O) aesthetasc; (P) juvenile. Scale bars: 0.1 mm.
Figure 2. *Macrothric borrerii*, adult parthenogenetic female from an unnamed pond near Port-aux-Français, Îles Kerguelen. (A) Lateral view; (B) latero-ventral view; (C) anterior view; (D) setae at ventral margin of valve; (E) dorsal head pore; (F) mandibular articulation; (G, H) postabdomen, lateral and dorsal view. Scale bars: 0.1 mm (A–D, G, H); 0.01 (E, F).
Figure 3. *Macrothric boergeni*, adult parthenogenetic female from an unnamed pond near Port-aux-Français, Îles Kerguelen. (A, B) Postabdominal claw; (C) antennae I; (D) antenna II; (E) its basal segment and basal portion of branches; (F) setae of antenna II; (G) limb I, inner view; (H) its distal portion; (I) distal portion of limb II. Scale bars: 0.1 (C–E, G); 0.01 mm (A, B, F, H, I).
setules, anal margin with groups of thicker setules. Postabdominal seta with short distal segment, densely armed with relatively short setules; basal segment with very few (two to three) short, sparsely located setules. On external side of postabdominal claw, a series of

Figure 4. *Macrothrix boergeni*, head and thoracic appendages of adult parthenogenetic female from an unnamed pond near Port-aux-Français, Iles Kerguelen. (A) Antenna II; (B–M) its setae; (N) limb I; (O) its distal portion in anterior view; (P) its inner portion; (Q–S) stiff (anterior setae); (T–V) ejector hooks of different individuals. Scale bars: 0.1 mm.
three to five robust denticles; medial row (on ventral margin) of about seven to nine denticles; inner row with numerous denticles, organized in three successive series.

Antenna I widened distally, straight, without a subapical external angulation; sensory seta at distance of about two antennular diameters (at base) from antenna I joint; on
anterior face about six to eight transverse rows of spinules, associated with distinct
reticulation. Nine short aesthetascs, three of them slightly larger than the rest. Antenna II
with distal burrowing spine on basal segment somewhat shorter than proximal segment of
exopod. Length of all apical swimming setae subequal. Lateral seta on proximal endopod
segment larger than other setae, lacking robust denticles in middle. A spine on second
segment of exopod half as long as the next (second) segment. On posterior side of segments
1–3 of exopod there are a series of small additional denticles.

Limb I with outer distal lobe supplied with longest apical seta having distal segment
unilaterally armed with relatively robust setules, located more rarely on proximal portion of
seta distal segment; inner-distal lobe with three bisegmented setae of different size, unilaterally
setulated in distal part, robustness of armature different in different setae, smallest one with
numerous fine setules; two ejector hooks of different size, sometimes one of them
rudimentary; a remainder of gnathobase I with single fully setulated setae. On limb II,
scrapers 1–2 with delicate feathering, but scrapers 3–7 with denticles specially massive; a
solitary posterior seta near gnathobase present; filter plate II with four setae, without a
rudiment of fifth seta. On limb III epipodite with five setae; a distal group of three long setae,
seta 1 shortest, armed with robust denticles; setulated projections proximally to seta 3 and
between setae 2 and 3; on inner-distal portion, seta 1 with specially short and robust denticles;
seta \(a\) with fine setules basally and robust spinules distally, seta \(b\) characteristically long; basal
endite posteriorly with four soft setae. Limb IV with exopodite small, bearing only a distal
group of three bilaterally feathered setae of subequal size; on inner-distal portion of this limb
seta 1 with strong setules basally and two to three robust denticles distally; posteriorly a row of
five long setae. On limb V there are three setae at inner margin, sometimes seta 3 reduced.

\textit{Ephippial female, male.} Not adequately described.

\textit{Size.} Up to 1.06 mm.

\textit{Full redescription}

\textit{Adult parthenogenetic female.} Body of large female subovoid in lateral view (Figures 1A, 2A,
B, 6A), with maximum height in the middle, height/length = 0.66–0.70. Dorsal margin in
general as a regular arch from tip of rostrum to posteriormost point, without traces of
cervical depression or with a slight depression, mostly breached by a “step” in posterior
boundary of head, sometimes forming a blunt tooth (Figure 1A). Dorsal margin of valves
not elevated, or slightly elevated above dorsal margin of head. Postero-dorsal angle as a
rounded triangle, lies in level of middle of body height. Whole surface of valves with fine
reticulation, while head without it. No remarkable structures on valves or head. In anterior
view body moderately compressed laterally (Figure 2C).

Head large, length/body length up to 0.4. In lateral view, dorsal margin in general evenly
convex, no dome above eye; ventral margin almost straight, with minute crossing ridges, no
projection at base of labrum (Figure 1B, C). A special line (fold) goes from mandibular
joint anteriorly, it corresponds to a poorly expressed fornix. Compound eye large, ocellus
also large (its size more than half of eye diameter), located approximately in middle of
distance between tip of rostrum and eye.

“Dorsal head pore” (“dorsal organ” or “window” are more correct names, because no
pore is really present here, only a window of specialized cuticle) ovoid, small, located on
posterior part of head (Figure 2E).
Labrum wide, in lateral view approximately triangular, with a moderately projected apex bearing several small tubercles, and setulated distal labral plate (term according to Kotov 1999, or anterior plug according to Dumont and Silva-Briano (2000)).

Valve surface with a distinct reticulation. Dorsal margin without any serration, but ventral margin denticulated. Marginal setae jointed to posterior sides of these denticles (Figures 1D, G, 2D, 6B). These setae variable in length and size in different individuals, but there is a general order to their sequence: there are two ventrally directed setae between each larger, laterally oriented one, characteristic also of the majority of other species (Kotov 1999; Kotov and Hollwedel 2004; Kotov et al. 2004). In anterior and posterior portion of ventral margin the order of seta alternation is not too precise.

Thorax long, while abdomen short, without projections. Intestine without convolutions.

Postabdomen subovoid in lateral view, with a rounded distal extremity, without “heel” (inflated base of postabdominal setae) basally (Figures 1H, 2H). Ventral margin straight, with few series of small, robust denticles. Dorsal margin distinctly bilobed, and the incision, which bilobes the margin, located at the level of proximal border of anus, separating anal and preanal margin. The latter long, slightly and regularly convex, with short transversal series of minute setules. On anal margin groups of setules with size significantly larger than those on postanal margin, laterally to them there are series of finer setules (Figure 2G). Small postanal margin also with series of minute setules. A reticulation on sides of postabdomen fully absent.

Postabdominal seta approximately as long as postabdomen, with short distal segment, densely armed with relatively short setules; basal segment with a very few (two to three) short, sparsely located setules.

Postabdominal claw small, directed distally, slightly and regularly bent dorsally, with pointed tip and wide base in lateral view. On claw, a series of few (three to five) robust denticles on external side, medial row (immediately on ventral margin as seen laterally) of about seven to nine denticles (Figures 1I, J, 3A, B), and inner dorsal row with numerous denticles, organized in three successive series (Figure 1K).

Antenna I widened distally, straight, without subapical external angulation (“subapical ventral angulation” sensu of Silva-Briano (1998)); sensory seta located externally at distance of about two antennular diameters (at base) from antenna I joint (Figures 1L, M, 3C). About six to eight transverse rows of spinules, associated with a distinct reticulation on anterior surface of antenna I, series of fine spinules at its end. Nine relatively short terminal aesthetascs (longest about one-quarter of antenna I length), each with two minute “claws” at the apex (Figure 1N, O). Three aesthetascs slightly larger than the rest, bearing unknown thin-walled, delicate structures, which could be additional sensory elements, but there is a chance that these are only epibiotic bacteria.

Antenna II large, coxal region folded, with two small basal sensory setae of slightly different size in middle part and rows of small setules on each fold (Figures 3D, 4A, 6C). Basal segment robust, bearing numerous transverse series of spinules, and long, bisegmented distal sensory seta at inner (posterior) margin. Distal burrowing spine somewhat shorter than proximal segment of exopod, located on outer (anterior) surface, close to end of the basal segment (Figure 3E).

Antennal branches long (about two times longer than basal segment), only proximal member of exopod shortened, all other segments elongated. Segments 2–3 of exopod subequal in size, while terminal segment as long as these two. Endopod apical segment longer than each of the other segments of this branch. All segments with transverse rows of setules. Swimming setae 0-0-1-3/1-1-3, spines 0-1-0-1/0-0-1. Length of all apical
swimming setae subequal, approximately equal to length of basal segment plus length of branch. Each seta is marked with an individual number in Figure 4A, armature of each seta is illustrated in Figure 4B–I. Lateral seta on proximal endopod segment larger than other setae, lacking robust denticles in middle (Figures 3F, 4J–M). Apical spines short, from slightly curved to straight. A single spine on second segment of exopod, this spine half as long as next segment. On posterior side of exopod segments 1–3 there are a short series of small additional denticles (see discussion in Kotov et al. (2004)).

Mandible small, elongated, evenly dilated distally. Mandibular articulation located externally at point where valve and head come together (Figure 2F).

Limb I large, without accessory seta; outer distal lobe cylindrical (Figures 3H, 4N, O), supplied with a long apical seta with distal segment unilaterally armed with relatively robust setules, located more rarely in proximal portion of seta distal segment, and a small lateral seta with bilaterally setulated distal segment. Inner-distal lobe massive, with median series of setules, few groups of minute setules, and three bisegmented setae of different size, unilaterally setulated in distal part, robustness of armature different in different setae, smallest one bears numerous fine setules. Endite III with a long, slightly curved, distally setulated seta a, while setae b–c short, clearly bisegmented, setulated bilaterally in middle (Figures 3G, 4N, P); anteriorly on this endite there is a short bisegmented seta 1, bearing sparse, long setules distally (Figure 4Q). Endite II with three long bisegmented setae of subequal size (Figure 4P: d–f), each with distal segment bearing fine setules on distal parts, and more robust setules basally, and with fully setulated basal segment, and a fork-like seta 2 (Figure 4R) anteriorly. Endite I with two bisegmented setae (Figure 4P: g–h) naked basally and supplied with long, dense setules distally; a fork-like seta 3 (Figure 4S) anteriorly. Ejector hooks of different size, bilaterally setulated, in some specimens second hook significantly reduced in size and naked (Figures 4T–V). A fully setulated seta at inner side of limb base, so-called maxillar process, represents a remnant of gnathobase I (Kotov 1999).

Limb II: epipodite subglobular, exopodite as a subovoid lobe with three transverse rows of small setules and a short, bilaterally setulated seta distally (Figure 5A, B). At inner margin of limb, eight robust scrapers, scrapers 1–2 with delicate feathering, but scrapers 3–8 with denticles specially massive for the genus (Figures 3I, 5B), a small sensillum near each scraper 1 and 4. Posteriorly to marginal scrapers, a system of low hillocks in distal limb portion, a setulated hillock near seta 4, and a solitary “soft” seta near gnathobase (Figure 5C). Distal armature of gnathobase with four setae (Figure 5C: 1–4). Filter plate with four long setae, with size slightly decreasing distally.

Limb III: epipodite very small, globular, exopodite large and flat, with a distal group of three long setae (Figure 5D: 1–3), seta 1 shortest and armed with robust denticles, setae 2–3 with fine setules; there are setulated projections proximally to seta 3 and between setae 2 and 3; lateral group consists of two setae (4 and 5), similar in armature to 2 and 3. Distal endite (see discussion of its homology in Kotov (1999)) anteriorly with three bisegmented setae (Figure 5E: 1–3), unilaterally armed in distal part, seta 1 with specially short and robust denticles; small sensillum near each base of seta 1 and 3. Posteriorly, there are three soft setae: seta a with fine setules basally and robust spinules distally, setae b and c with fine setules distally, seta b characteristically long. Basal endite approximately equal in size to distal one. Anteriorly, a bottle-shaped sensillum and four setae with size increasing basally (4–7), each fully setulated distally, with distal segment longer than basal one. Posteriorly, four thick, soft setae (d–g) subequal in size, each armed with fine setules, each has an inflated basal portion and a blunt tip. Gnathobase unclearly demarcated from basal endite, with four elements of
distal armature: a large, bottle-shaped sensillum near border with basal endite, and two hooks plus a short bisegmented seta distally (Figure 5E: 1–4).

Limb IV: pre-epipodite small, with few setules, epipodite small and globular, exopodite small, with only a distal group of three bilaterally feathered setae of subequal size (Figure 5F: 1–3). Inner margin of limb with four setae (Figure 5G: 1–4), seta 1 with strong setules basally and two to three robust denticles distally (Figure 5H), while setae 2–4 each with an inflated basal and elongated distal part, the latter pointed at the tip, fully feathered. A small sensillum near each base of seta 2 and 3. Posteriorly, a row of five long, erect, soft setae, similar in size, bilaterally setulated from base to tip (Figure 5G: a–e). Distal armature of gnathobase with four elements: a thick, bottle-shaped sensillum near border with basal endite; a large seta with inflated basal segment and elongated, fully setulated distal segment; a heavy hook; and a small, naked, bisegmented and curved seta bearing minute setules distally. Posteriorly on gnathobase, a single small seta continues the posterior row of setae of the inner limb face, the sole vestige of a filter plate IV.

Limb V: pre-epipodite relatively small, flat, its margin setulated; epipodite large, subglobular. Only a small lobe with single seta represents a vestige of the exopodite. Inner-distal portion as a large flap, fringed by fine setules, on inner margin three setae with size significantly increasing distally (Figure 5J: 1–3), in some specimens seta 3 almost reduced (Figure 5I).

Differences of juvenile female. In contrast to adult, body somewhat lower (height/length = 0.63–0.67), subquadrangular, without a tooth on posterior border of head, with valve dorsal margin straight, significantly elevating beneath head (Figure 1P), with postero-ventral angle oblique, located above middle axis of body, with antennae II and swimming antennal setae longer, rows of setules on antenna I and II weakly developed.

Ephippial female, male. Unknown. Gay (1981) attempted to described some peculiarities of the adult male, but no valuable information was presented.

Size. Neotype 1.04 mm, juvenile and adult parthenogenetic females 0.41–1.06 mm.

Taxonomic comment. The only character of *M. boergeni* important for the differentiation from some other *hirsuticornis*-like species, reported by Studer (1878), is the finely setulated distal segment of the seta on the proximal segment of antenna II. During the whole of the 20th century (Rühe 1914; Smirnov 1976, 1992), *M. boergeni* was regarded as a junior synonym of *M. hirsuticornis*; the former is shown to be a well-differentiated valid species (see Table I), the second *hirsuticornis*-like taxon described for the World’s fauna.

Distribution. Endemic to the Kerguelen Archipelago.
Revision of the hirsuticornis-like species of Macrothrix

Macrothrix propinquua Sars 1909, p 5–15, Plate 1; Pesta 1928, p 80; Olivier 1962, p 230, Plate 19, Figures 6, 7, Plate 20, Figure 1.

Macrothrix hirsuticornis Norman and Brady in Ekman 1905, p 7–8; Harding 1941, p 319; Olivier 1962, p 225–226, Plate 17, Figures 1–3; Dartnall and Hollwedel 2007, p 1273–1274, Figures 18, 19.

? Macrothrix inflata Daday 1902, p 271–272, Plate 10, Figures 13–16, Plate 11, Figure 1; Olivier 1962, p 226, Plate 17, Figures 4–6; Smirnov 1976, p 89, Figure 60.

not Macrothrix odontocephala Daday 1902 in Daday 1906, p 39; Daday 1913, p 321, 345, 347, 348, 351, 352, 356.

Type locality
“...einer Lagune in der Nähe von Rio Turbio” (Ekman 1900) in Santa Cruz, Argentina.

Type material
Most probably lost. Absent from Ekman’s Collection in SMNH (Kotov and Gololobova 2005).

Type series of junior synonyms examined here

Macrothrix ciliata Vávra, 1900—neotype (selected here): juvenile female 0.53 mm from Port Stanley, Falkland Islands, coll. 18 August 1902 by South Polar Expedition of 1901–1903, collection of S. Ekman, tube SMNH 5874. Neotype label: “Macrothrix ciliata Vávra, 1900, 1 juv. ♀ from Port Stanley, Falkland Islands, NEOTYPE”.

Macrothrix inflata Daday, 1902—syntypes: four females from unknown locality in Santa Cruz, Argentina, coll. by F. Sylvestri, slide DAD II/P-418. We found that Smirnov (1992) was correct when he said that the slide is dried, and the specimens are in a bad state.

Macrothrix odontocephala Daday, 1902—type material: lost. Specimens in slide DAD D V-96; II/P-420 and tube DAD D 1917-142; II-457 (see Forró and Frey 1982), misidentified as “M. odontocephala” by Daday (1906), contain material from Mongolia, apparently belonging to Palaeartic M. hirsuticornis.

Macrothrix propinquua Sars, 1909—lectotype (selected here): parthenogenetic female 1.05 mm from unknown locality in South Georgia, GOS F 12298a. Paralectotypes (selected here): 127 parthenogenetic, ehippial females and males, the same locality with the lectotype, GOS F 12298b; one dissected parthenogenetic female on eight slides, GOS F 12298c-j; one dissected male on five slides, GOS F 12298k-o.

Other material examined

Continental South America. Argentina (Santa Cruz): a pond (or an old river channel) at Mission Salesiana, Highway 3, 12 km north of Rio Gallegos, coll. 19 January 1989 by D. G. Frey, DGF 8713; drainage channel, Highway 3, 2 km north of P. Maria, coll. 20 January 1989 by D. G. Frey, DGF 8714; seepage pools in dry bottom of Brazo Rico of Lago Argentino, coll. 25 January 1989 by D. G. Frey, DGF 8745; Altwässer, Rio Coig, 19 km west of Estancia La Vanguardia, coll. 26 January 1989 by D. G. Frey, DGF 8748; a small creek, tributary of Rio Coig, west of Esperanza, coll. in 26 January 1989 by D. G. Frey, DGF 8749; Lago Largo, on road from Rio Turbio to Rio Gallegos, coll. 27 January 1989
Figure 6. Different species of *Macrothrix* from the southern hemisphere. (A) *M. boergeni*, large adult parthenogenetic female, neotype, lateral view; (B, C) its valve margin and antenna II; (D) *M. inflata*, female in bad state, syntype; (E) *M. ciliata*, juvenile female, neotype; (F, G) its postero-dorsal angle and antenna II; (H) adult parthenogenetic female from the same locality. No scale bars were taken during photographing.
by D. G. Frey, DGF 8755; pools near crossing of Rio el Zorro on road from Rio Turbio to
Rio Gallegos, coll. 27 January 1989 by D. G. Frey, DGF 8757; valley pond dammed by
road, 13 km north of Estancia Monte Dinero on road from C. Virgenes to Rio Gallegos,
coll. 28 January 1989 by D. G. Frey, DGF 8759. Chile (Magallanes): Laguna Melliza,
Parque Nacional de los Torres del Paine, coll. 14 January 1989 by D. G. Frey, DGF 8764;

Table I. Peculiarities of studied *Macrothrix* species: autapomorphic characters are marked by bold type.

| Species                        | *triplctinata* | *flagellata* | *boergeni* | *ruehei* | *sarsi* | *oviformis* | *hirsuticornis* str. |
|-------------------------------|---------------|-----------|--------|---------|---------|----------|---------------------|
| Cervical depression well-expressed (1—yes) | 0 | 0 | 0 | 0 | 1 | 0–1 | 0–1 |
| **Labrum apex strongly projected and remarkably narrowing distally (1—yes)** | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| On labral apex tubercles reduced (1—yes) | 0 | 0 | 0 | 1 | 0 | 0–1 | 1 |
| **Setules on ventral margin of postabdomen fine, long** | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Setules on basal segment of postabdominal setae absent or very reduced (1—yes) | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| Setules on distal segment of postabdominal setae long (1—yes) | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| On external side of postabdominal claw a series of robust denticles | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| Antenna I remarkably widened distally (1—yes) | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| Number of rows of crossing setules of antenna I reduced (1—yes) | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| **Reticulation on antenna I well-expressed (1—yes)** | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| Difference between largest and smallest aesthetascs in size strong (1—yes) | 0 | 1 | 0 | 1 | 1 | 1 | 1 |
| On basal segment of antenna II distal spine longer that proximal segment of exopod | 0–1 | 0 | 0 | 0–1 | 1 | 1 | 1 |
| **Antenna II: largest seta with specially rare and robust denticles in middle** | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Limb I: few setules on smallest seta of inner-distal lobe | 0 | 0 | 0 | 0–1 | 1 | 1 | 1 |
| **Maxillar process (gnathobase) I, number of setae** | 1 | 2 | 1 | 1 | 1 | 1 | 1 |
| **Limb II: scrapers 3–7 with specially massive denticles (1—yes)** | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| Limb III: on distal endite soft seta very short (1—yes) | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| Limb IV: short, robust denticles on distal portion of scraper 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| **Limb V seta on inner margin with a terminal whip** | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
Figure 7. *Macrothrix oviformis* from seepage pools in dry bottom of Lago Argentino, Santa Cruz, Argentina (A–G), Lago Largo, Santa Cruz, Argentina (H, I), ponds a few kilometres south of Rt. E crossing of Rio Mac Lennan, Tierra del Fuego (J–P), and Heywood Lake, Signy Island (Q–V). (A, B) Large parthenogenetic female and its head; (C, D) postabdominal claw in outer and ventral view; (E) postabdominal seta; (F, G) seta on proximal segment of endopod; (H, I) adult parthenogenetic female and its seta on proximal segment of endopod; (J, K) large parthenogenetic female and dorsal margin of other female; (L–N) smaller adult parthenogenetic female, its dorsal margin and seta on proximal segment of endopod; (O, P) juvenile female and its seta on proximal segment of endopod; (Q) juvenile male of prereproductive instar; (R, S) its postabdomen and postabdominal claw; (T, U) antenna I in outer and anterior view; (V) inner-distal lobe of limb I. Scale bars: 0.1 mm.
Revised of the hirsuticornis-like species of Macrothrix

Figure 8. *Macrothrix oviformis*, parthenogenetic females from unknown water body near Port Stanley, Falklands (neotype locality of *M. ciliata*). (A) Large adult; (B) head; (C, D) setae at middle and posterior portion of ventral margin; (E, F) postabdomen and postabdominal claw; (G) antenna I; (H) proximal portion of branches of antenna II; (I–K) seta on proximal segment of endopod in its proximal, medium, and distal portion, respectively; (L) small adult; (M) juvenile (neotype of *M. ciliata*). Scale bars: 0.1 mm.

Grassy meadow, 8 km north of turnoff to Monte Aymond, coll. 15 January 1989 by D. G. Frey, DGF 8780.

*Tierra del Fuego (Argentinian part).* Freshwater lake near ocean, on Pt. Almte Broun Road, coll. 14 January 1989 by D. G. Frey, DGF 8666; Lago Fagnano, coll. 15 January 1989 by
Figure 9. *Macrothrix oviformis*, parthenogenetic females from unknown locality in South Georgia (lectotype and paralectotypes of *M. propinqua*). (A, B) Large adult, lectotype of *M. propinqua*, in lateral and anterior view; (C) head; (D) reticulation of valve; (E) setae at anterior portion of ventral margin; (F, G) setae in medium portion of ventral margin; (H) setae at posterior portion of ventral margin; (I) postabdomen; (J, K) postabdominal claw; outer and inner view; (L) distal portion of postabdomen, ventral view; (M) postabdominal seta; (N, O) antenna I, posterior and outer view. Scale bars: 0.1 mm.
Figure 10. *Macrothrix oviformis* from unknown locality in South Georgia (paralectotypes of *M. propinqua*). (A) Antenna II of adult female; (B–H) setae of antenna II; (J) seta on proximal segment of its endopod; (K–N) proximal, medium, distal portion, and tip of this seta, respectively; (O) antenna II of adult male. Scale bars: 0.1 mm.
Figure 11. *Macrothrix oviformis*, limbs of parthenogenetic female from unknown locality in South Georgia (paralectotype of *M. propinqua*). (A) Limb I; (B, C) its distal portion and smallest seta of inner-distal lobe; (D, E) limb II and its proximal portion; (F, G) limb III and its inner part; (H, I) limb IV and its inner part; (J) limb V. Scale bars: 0.1 mm.
Figure 12. *Macrothrix oviformis* from unknown locality in South Georgia (paralectotypes of *M. propinqua*). (A, B) Ephippial female, lateral and anterior view; (C) adult male; (D) its head; (E, F) setae at anterior and posterior portion of ventral margin; (G, H) postabdomen and postabdominal claw; (I, J) antenna I, outer and anterior view; (K) its tip; (L) tip of aesthetasc (schematic drawing, without scale bar); (M) distal portion of limb I. Scale bars: 0.1 mm.
D. G. Frey, DGF 8679; a lagoon along Highway 3, 8 km north of Hosteria Kaiken, coll. 15 January 1989 by D. G. Frey, DGF 8689; northern and middle pond of three ponds, a few km south of Rt. E crossing of Rio Mac Lennan, coll. 17 January 1989 by D. G. Frey, DGF 8701 and 8702; flooded grassland near where Rt. B takes off from Highway 3, coll. 18 January 1989 by D. G. Frey, DGF 8703.

Falkland Islands. Unknown water body near Port Stanley, coll. 18 August 1902 by South Polar Expedition of 1901–1902, SMNH 5875 and 32918 (neotype locality).

South Georgia. Unknown locality, NHM 1962.4.3.2.

Signy Island (South Orkney Island group). Heywood Lake, coll. March 1964 by R. B. Heywood, BAS 64/257; Pumphouse Lake, coll. February 1964 by R. B. Heywood, BAS 64/260; unknown locality, coll. 1964 by R. B. Heywood, BAS no number.

Antarctic Peninsula. Horseshoe harbour (“Penola”?), Graham Land, coll. 19 February 1937 by British Graham Land Expedition 1934–1937, NHM 1940.3.5.41–42.

Amended diagnosis

Parthenogenetic female. In lateral view body subovoid (height/length = 0.71–0.78 in largest adults), cervical depression expressed (although shallow), posterior boundary of head forming or not forming a “step” on dorsum, dorsal margin of valves without any serration or with minute serration (Figures 6H, 7A, H, J–L, 8A, 9A, 13A). Postero-dorsal angle obtuse, lies in large adults ventral to middle of body height. Ventral margin (Figures 8C, D, 9E–H) with setae as in M. boergeni. In anterior view, body compressed laterally, with a distinct dorsal keel (Figure 9B). No dome above eye. Ocellus small (Figure 13C). Dorsal organ small or of moderate size. Labrum with a thick, rounded, moderately projected apex, supplied with few low tubercles, which may be absent (Figures 7B, 8B, 9C).

Abdomen with a distinct, setulated dorsal projection (Figures 8E, 9I). Postabdomen subovoid, with rounded distal extremity, without a “heel” basally, with ill-defined reticulation on sides, or without it (Figures 8E, 9I). Ventral margin slightly convex, with few series of short denticles (Figures 8F, 9L). Dorsal margin distinctly bilobed; preanal margin with transversal series of minute setules, anal margin with groups of thicker setules (Figure 13E). Postabdominal seta with distal segment densely armed with long setules; proximal segment with numerous, relatively long setules (although shorter than on distal one) (Figures 7E, 8E, 9M, 13F). On outer side of postabdominal claw, a series of 7–14 fine spinules, with size increasing distally; medial row of about six to eight denticles; inner row with numerous denticles, organized in two successive series, subdivided by a specially large denticle (Figures 7C, D, 8F, 9J–L).

Antenna I widened distally, slightly curved, without a subapical external angulation; sensory seta at distance of about 2–2.5 antennular diameters (at base) from antenna I joint; on anterior face about five to six transverse rows of strong spinules, and rows of finer setules, but no reticulation (Figures 7B, 8B, G, 9N, O, 13B). Nine short aesthetasc (longest shorter than half of antenna I length), two of them significantly larger than the rest. On the latter, sometimes there are some thin-walled, delicate
structures (Figure 9O), which could be additional sensory elements, but there is a chance that these are only epibiotic bacteria, as in the case of M. boergeni. Antenna II with distal burrowing spine on basal segment longer than proximal segment of exopod (Figures 10A, 13D). Length of all apical swimming setae subequal, their armature represented in Figure 10B–I. Lateral seta on proximal endopod segment larger than other setae, with robust denticles in the middle (Figures 7F–G, I, N, P, 8I–K, 10F–N). A spine on second segment of exopod approximately half as long as next segment. On posterior side of segments 1–3 of exopod there are minute additional denticles.

Limb I with longest apical seta of outer distal lobe (Figure 11A, B) having distal segment unilaterally armed with relatively fine, spaced setules; inner-distal lobe with three bisegmented setae of different size, unilaterally setulated in distal part, robustness of armature different in different setae, smallest one with whole distal segment setulated (Figure 11C), or these setules present only in proximal portion of distal segment (Figure 11B); two ejector hooks of similar size; a remainder of gnathobase I with single fully setulated setae. On limb II (Figure 11D, E), scrapers 1–2 with delicate feathering, scrapers 3–7 with robust denticles of size characteristic for the genus; a solitary posterior seta near gnathobase present; filter plate II with four setae, without a rudiment of fifth seta. On limb III (Figure 11F) epipodite small, exopod with a distal group of three long setae, seta 1 shortest, armed with short setules; setulated projections proximally to seta 3 and between setae 2 and 3; inner-distal limb portion (Figure 11G) with seta 1 with short and robust denticles; seta a with fine setules basally and robust spinules distally, seta b longer than c; basal endite posteriorly with four soft setae. Limb IV (Figure 11H) with exopodite small, bearing only a distal group of three bilaterally feathered setae of subequal size; on inner-distal portion of this limb (Figure 11I) seta 1 with strong setules basally and two to five robust denticles distally; posteriorly row of five long setae. On limb V there are three setae on inner margin (Figure 11J).

**Juvenile female.** Body less high (height/length = 0.64–0.68), subquadrangular, with almost straight dorsal margin (Figures 6E–G, 7O, 8L, M).

**Ephippial female.** In contrast to adult parthenogenetic female, body less high (height/length = 0.65–0.72), postero-dorsal angle more prominent and lies in level of middle of body height (Figure 12A). Body less compressed laterally and lacking a dorsal keel (Figure 12B). Dorsal portion of valves forming an ephippium, slightly pigmented in brownish colour, without clear border between it and rest of valves. Dorsal wall of carapace forms a special dark, chitinized plate. Two eggs in ephippium.

**Male.** Body subquadrangular in lateral view. Apex of labrum with a series of tubercles; a reticulation on sides of postabdomen fully absent, gonopores open on its distal margin, distalmost denticle in median series on postabdomen claw significantly larger than the rest. Antennular sensory seta located there at distance of about 1.5 antennular diameters (at base) from antenna I joint; at the same level, a large male seta, with length of half of antenna I length, bisegmented, with basal segment short and naked, and distal segment fully setulated; 14 relatively short terminal aesthetascs, two aesthetascs slightly larger than the rest. Limb I with inner-distal lobe bearing four setae, additional male seta large;
copulatory hook large, with three ridges distally, copulatory brush seta on a low pedestal, bisegmented, with blunt tip to distal segment.

**Size.** Females up to 1.14 mm, males up to 0.56 mm.

**Redescription of adult male**

Body subquadriangular in lateral view, height/length = 0.63–0.69, dorsal margin without a distinct cervical depression, no “step” in posterior boundary of head (Figure 12C). Dorsal margin of valves not elevated significantly above dorsal margin of head. Postero-dorsal angle obtuse, rounded, lies dorsal to middle of body height.

Head with dorsal margin evenly convex, no dome above eye; ventral margin slightly concave to straight, without ridges, no projection at base of labrum (Figure 12D). Compound eye large, ocellus even smaller than in female (its size about one-third of eye diameter), located closely to tip of rostrum. Dorsal organ small, located on posterior part of head.

Labrum in lateral view approximately triangular, with a moderately projected apex bearing several small tubercles, and setulated distal labral plate.

Valve surface with a delicate reticulation. Dorsal margin without any serration, ventral margin as in female, but marginal setae relatively longer (Figure 12E, F).

Postabdomen in lateral view (Figure 12G) with subquadriangular distal portion and without a “heel” basally. Ventral margin inflated, without series of denticles. Dorsal margin distinctly bilobed, preanal margin regularly convex, with short transversal series of minute setules. On anal margin groups of setules with size significantly larger than those on postanal margin, laterally to them there are series of finer setules. A reticulation on sides of postabdomen fully absent. Gonopores open on distal margin, ventrally to postabdominal claws.

Postabdominal seta longer than postabdomen, with short distal segment, densely armed with long setules; basal segment with numerous, shorter setules.

Postabdominal claw small, directed distally, less elongated than in female, slightly and regularly bent dorsally, with pointed tip and wide base in lateral view (Figure 12H). On claw, a series of seven to ten fine denticles on external side; medial row with about five to six denticles, distalmost one significantly larger than the rest.

Antenna I almost straight, with maximum width in basal portion, this part a homologue of subapical external angulation; antennular sensory seta located at distance of about 1.5 antennular diameters (at base) from antenna I joint (Figure 12IJ). On anterior surface of antenna I, at level of sensory seta, a large male seta, half length of antenna I, bisegmented, with basal segment short and naked, and distal segment fully setulated. About six to seven transverse rows of spinules on anterior surface of antenna I, but no reticulation. Fourteen relatively short terminal aesthetascs (longest one-quarter length of antenna or even shorter), apex of each with a conical depression on distal side (Figure 12K, L), two aesthetascs slightly larger than the rest.

Antenna II with relative size larger than in female; basal segment of exopod relatively shorter than in female; distal burrowing spine on basal segment and a spine on the second segment of exopod significantly longer than in female (Figure 10O).

Limb I with outer distal lobe as in female; inner-distal lobe with four setae, additional male seta large; copulatory hook large, with three ridges distally
Copulatory brush seta on a low pedestal, bisegmented, with blunt tip to distal segment.

**Juvenile (pre-reproductive) male.** Body shape (Figure 7Q) similar to adult; height as in adult male (height/length = 0.61–0.66), postabdomen (Figure 7R) as in female, distal denticle of median row on postabdominal claw (Figure 7S) not as large as in adult male; antenna I with nine aesthetascs and shorter male seta (Figure 7T, U); male seta on inner-distal lobe of limb I smaller and located at a distance from other setae, copulatory hook shorter than in adult (Figure 7V).

**Size.** Parthenogenetic females from Lago Largo, on road from Rio Turbio to Rio Gallegos, Santa Cruz (DGF 8755) 0.37–0.71 mm; from ponds a few km south of Rt. E crossing of Rio Mac Lennan, Tierra del Fuego (DGF 8701) 0.43–0.90 mm; from Port Stanley, Falkland Islands (SMNH 32918) 0.50–1.06 mm; parthenogenetic females from unknown locality in South Georgia (GOS F 12298b) 0.36–1.05 mm, ephippial females 0.67–0.79 mm, juvenile males 0.42–0.49 mm, adult males 0.47–0.56 mm. According to Sars (1909), female length reaches 1.14 mm.

**Taxonomic notes.** The southernmost portion of the South American continent, South Atlantic (Subantarctic) islands and Antarctic Peninsula are inhabited by only a single hirsuticornis-like species, for which several formal names were suggested: *M. oviformis* Ekman, 1900, *M. ciliata* Vávra, 1900, *M. inflata* Daday, 1902, *M. odontocephala* Daday, 1902, and *M. propinqua* Sars, 1909.

Two species (*M. oviformis* Ekman and *M. ciliata* Vávra) were published within the same year; the article of Ekman (1900) appeared on 22 October 1900 (this information present on the title page of the issue where it was published). Attempts to establish when Vávra’s (1900) paper appeared, including special requests to several libraries in Germany (including Hamburg, where it was published), were unsuccessful. According to case 21.3.2 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 2000), the latter article must be regarded as published on “the last day of the year”, namely on 31 December 1900. So, *M. oviformis* Ekman, 1900 has priority, and *M. ciliata* is its junior synonym.

First description of *M. oviformis* Ekman, 1900 was relatively detailed for that time. The distinctive characters listed by Ekman (1900, p 71–73) are now considered of dubious value. The first description contains some important characters such as (1) a depression bordering dorsal margin of head and valves; (2) nine aesthetascs of different size; (3) two dorsal projections on abdomen, and his illustrations adequately represent others such as (1) shallow cervical depression; (2) presence of numerous setules on proximal segment of postabdominal seta; (3) long setules on distal segment of postabdominal seta. Specimens very similar to that illustrated by Ekman (1900) were found at localities close to the type locality (Rio Turbio), as well as at other localities in continental South America.

*Macrothrix ciliata* Vávra, 1900 was described from the Falkland Islands. Most of the characters listed by Vávra (1900, p 18–19) are characters of a juvenile hirsuticornis-like species. A neotype of this taxon is here selected from Ekman’s (1905) sample collected in the vicinity of the type locality; a juvenile female is selected, confirming Vávra’s ideas.
on this species. There is no doubt that *Macrothrix ciliata* is a junior synonym of *M. oviformis*.

*Macrothrix odontocephala* Daday, 1902 is an apparent junior synonym of *M. oviformis*. Similar morphotypes with a tooth-like projection, or with a “monk’s hood” (in terminology of Fox 1962) on posterior portion of head (“var. groenlandica Lilljeborg, 1901”) are known also for Palaearctic *M. hirsuticornis* (Fox 1962; Flössner 1967, 1972, 2000). Several samples have been examined from Santa Cruz, from where the taxon was described, revealing several “odontocephala”-like populations (with a tooth at posterior border of head) of *M. oviformis*. In contrast, Daday’s (1906) “*M. odontocephala*” from Mongolia is a “toothed” morphotype of *M. hirsuticornis*.

*Macrothrix inflata* Daday, 1902 is more problematic. Females from a single population from continental South America (DGF 8780, unfortunately, with few specimens), lacking a depression between head and valves, also have some other specific traits (Figure 7A–G): (1) setules on seta on proximal segment of antennal endopod are relatively small, and (2) the dorsal organ is very large as compared with populations with clear border between head and valves. This may indicate that *M. inflata* is a valid species, but this conclusion must be confirmed by examination of better material; however, there is a high probability that the *inflata*-like morphotype is only an extreme example of the *oviformis* variability. Ekman (1900) clearly stated that *M. oviformis* has a distinct border between head and valves, so in the case that two taxa are recognized in South America, *M. oviformis* is widely distributed and *M. inflata* rare.

*Macrothrix propinqua* Sars, 1909 was described in detail, but no real differences from other species described from the South Atlantic region were reported. Re-examination of Sars’ (1909) type material led to the conclusion that his taxon is an apparent synonym of *M. oviformis*.

Two other species described from the southern part of South America, *M. goeldi* Richard, 1897 and *M. magna* Daday, 1902, are not members of the *hirsuticornis*-group. *Macrothrix goeldi* Richard, 1897 is a member of the *laticornis*- or *spinosa*-group, because the first description (Richard 1897, p 287–289) contains a clear reference to distinct denticulation at the dorsal margin of the valves. *Macrothrix magna* Daday, 1902 was regarded by Smirnov (1992) as a junior synonym of *M. hirsuticornis*, but this is incorrect. The male of *M. magna* has a very thin antenna I with a great distance between male seta and antennular sensory seta. This is apparently a relative of the *triserialis-rosea* group, sensu Dumont et al. (2002). At the same time, *M. magna* has postabdominal seta with a long distal segment, so the former is not a junior synonym of *M. triserialis* s. str. or *M. elegans* Sars, 1901 (the latter is one of the most common species in the more southern portion of South America; Kotov et al. 2004). *Macrothrix magna* needs to be revised, as a species outside of the *hirsuticornis*-like group. Olivier (1962) listed differences between all species described by previous authors, but these differences are dubious.

**Distribution.** Southernmost portion of continental South America, Tierra del Fuego, Falkland Islands, South Georgia, South Orkney Islands, and the Antarctic Peninsula. All records from the South Atlantic listed by Pugh et al. (2002) refer to this species. It is necessary to note that in these localities *M. oviformis* is a quite common species. Most probably *Macrothrix* from the South Shetland Islands (Toro et al. 2007) and Palmer Land (Pugh et al. 2002) also belong to this species.
Figure 13. Optical micrographs of different species of *Macrothrix*. (A) *M. propinqua*, lectotype in lateral view; (B) tip of antenna I; (C) head; (D) antenna II; (E) postabdomen; (F) postabdominal seta; (G, H) *M. sarsi*, holotype in lateral view and its head. No scale bars were taken during photographing.
Figure 14. *Macrothrix sarsi* sp. nov., parthenogenetic female from a water body “Cape of Good Hope V”, Western Cape Province, Republic of South Africa. (A, B) Large adult, lateral and anterior view; (C) ventral margin of head and labrum; (D) dorsal margin of valves; (E–G) setae at anterior, medium, and posterior portion of ventral margin, respectively; (H) postabdomen; (I, J) distal end of postabdomen in lateral and ventral view; (K, L) antenna I; (M) juvenile. Scale bars: 0.1 mm.
Macrothrix sarsi

(Figures 13G, H, 14–16)

Macrothrix propinqua Sars 1909 in Sars 1916, p 325–326, Plate 36, Figures 2, 2a–c; Seaman et al. 1999, p 104.
Not Macrothrix propinqua Sars 1909, p 5–15, Plate 1.

**Etymology**

The species is named after George Ossian Sars, a famous Norwegian carcinologist and one of the greatest investigators of the Cladocera, whose material is used for the species description.

**Type locality**

A water body “Cape of Good Hope V”, Western Cape Province, Republic of South Africa. Sars (1916) wrote that the sample was taken “in the neighbourhood of Bergvliet”.

**Type material**

Holotype: a parthenogenetic female in 90% alcohol, tube GOS F18493a. Label of holotype: “Macrothrix sarsi n.sp., Cape of Good Hope, parth. fem., HOLOTYPE”.

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Figure 15. *Macrothrix sarsi* sp. nov., antenna II of female from a water body “Cape of Good Hope V”, Republic of South Africa. (A) Antenna II; (B, C) seta at proximal segment of endopod; (D) seta on second segment of endopod; (E–G) apical setae of endopod. Scale bars: 0.1 mm.
Figure 16. *Macrothrix sarsi* sp. nov., thoracic limbs of female from a water body “Cape of Good Hope V”, Republic of South Africa. (A) Limb I; (B) its distal portion; (C-E) anterior setae 1–3; (F) tip of seta d; (G, H) ejector hooks; (I) limb II; (J) exopodite II of atypical female; (K) inner portion of limb II of typical female; (L) limb III of typical female; (M) inner limb part of atypical specimen with five anterior setae on basal endite; (N) limb III; (O) its inner portion; (P) limb V. Scale bars: 0.1 mm.
Paratypes: 78 parth. ♀ ♀ from type locality, GOS F18493b (tube); one dissected parth. ♀ ♀ from type locality, GOS F18493c–h (six slides); nine parth. ♂ ♀ from type locality, GOS F9304 (slide); eight parth. ♂ ♀ from “Cape of Good Hope II”, GOS F9303 (slide); 11 parth. ♂ ♀ from “Cape of Good Hope”, GOS F11171 (slide).

Diagnosis

**Adult parthenogenetic female.** In lateral view body subovoid, cervical depression very shallow, dorsal margin not breached by a “step” in posterior boundary of head (Figure 14A), dorsal margin of valves with a minute serration (Figure 14D), postero-dorsal angle as rounded triangle, lies somewhat ventrally to middle of body height. In anterior view, body compressed laterally and supplied with a sharp dorsal keel. No dome above eye. Ocellus small. Dorsal organ small. Labrum with a slightly projected apex bearing two tubercles. Setae on ventral margin of valve as in other species (Figures 14E–G).

Postabdomen subovoid, with rounded distal extremity, without “heel” basally, distinct reticulation on sides (Figure 14H), its ventral margin straight, with few series of fine spinules; first series consists of specially long elements (Figure 14I, J). Dorsal margin distinctly bilobed; preanal margin with transversal series of minute setules, anal margin with groups of thicker setules. Postabdominal seta longer than postabdomen, with distal segment somewhat shorter than basal one and densely armed with long setules; basal segment with numerous, short setules. On external side of postabdominal claw, a series of three to four thin denticles.

Antenna I markedly widened distally, slightly curved, without a subapical external angulation; sensory seta located externally very far (three or even more antennular diameters at base) from antenna I joint; on anterior face five transverse rows of spinules, but no reticulation (Figure 14K, L). Nine relatively long aesthetascs, two of them significantly larger than the rest. Antenna II with distal burrowing spine on basal segment markedly longer than proximal segment of exopod (Figure 15A). Length of all apical swimming setae subequal, armature as in other species (Figure 15D–G). Lateral seta on proximal endopod segment larger than other setae, lacking robust denticles in middle (Figure 15B, C). A spine on second segment of exopod short, less than half length of next segment. On posterior side of segments 1–3 of exopod there are no additional denticles, but sometimes there are several small spinules.

Limb I with apical seta of outer distal lobe having distal segment unilaterally armed with robust setules (Figure 16A, B), inner-distal lobe with three bisegmented setae of different size, smallest seta setulated only on its middle portion, anterior setae as represented in Figure 16CE, posterior setae d–e with bulbs at tips (Figure 16F), ejector hooks of subequal size (Figure 16G, H). On limb II, scrapers 1–2 with delicate feathering, scrapers 3–7 with thicker denticles of size characteristic for the genus; a solitary posterior seta present near gnathobase (Figure 16J, K), filter plate II with four setae, without a small rudiment of fifth seta. On limb III epipodite with five setae; seta 1 as long as 3, armed with fine setules distally; smooth setulated projections proximally to seta 3 and between setae 2 and 3 (Figure 16L), on inner-distal limb portion, seta 1 with fine setules distally, seta a with fine setules basally and strong spinules distally, seta b slightly longer than a, but markedly longer than e (Figure 16M), basal endite normally with four soft setae (Figure 16L). Limb IV with exopodite bearing a distal group of three bilaterally feathered setae of somewhat different size (Figure 16N); on inner-distal portion of the limb seta 1 with strong setules basally and five to six denticles distally; posteriorly on limb inner margin a row of five long setae...
(Figure 16O). On limb V there are three setae at inner margin, seta 1 with distalmost extremity as a naked whip (Figure 16P).

*Atypical adult.* A single atypical adult had two setae on exopodite II (Figure 16J) and five setae on basal endite III (Figure 16M).

*Juvenile female.* In contrast to adult, body more elongated and quadrangular (Figure 14M), with posterior border of dorsal head margin elevated above valves; posterior margin of valve almost straight, postero-dorsal angle at level of dorsal margin, ventral margin of valve strongly convex; antenna I relatively longer; antennae II and swimming antennal setae longer, rows of setules on antenna I and II weakly developed.

*Ephippial female, male.* Unknown.

**Size.** Parthenogenetic females 0.45–0.86 mm; up to 0.93 mm according to Sars (1916).

**Taxonomic notes.** Sars (1916) determined this population from the Cape of Good Hope as belonging to his species *M. propinqua* Sars, 1909. The latter is here considered as a junior synonym of *M. oviformis*. At the same time, the South African populations, misidentified as “*M. propinqua*” by Sars (1916), belong to another species, named here *M. sarsi* sp. nov.

The description of Sars (1916) contains few characters helpful for distinguishing the species of *hirsuticornis*-like forms as some of the “differences” are doubtful in terms of recent understanding of *Macrothrix* systematics. For example, Sars (1916) mentioned a large epipodite on limb V, but its size is too variable in other species of *Macrothrix* (Kotov et al. 2004) to be a good taxonomic character. The present opinion is based predominantly on a study of Sars’ material instead of his description.

**Distribution.** *Macrothrix sarsi* sp. nov. is present only in the Cape of Good Hope region of the Republic of South Africa. Some species of *Macrothrix* (i.e. *M. spinosa*, *M. odiosa*, and *M. capensis*) are common in South African water bodies. In contrast, *M. sarsi* is apparently a rare species, it was not found by Smirnov (2007a), who examined in detail some 290 samples from South Africa. Clarke and Rayner’s (1999) report of “*M. propinqua*” from Namibia must be confirmed.

*Macrothrix ruehei* sp. nov.
(Figures 17, 18)

*Macrothrix hirsuticornis* Norman and Brady in Rühe 1914, p 55–56 (only populations from Île Amsterdam); Brehm 1958, p 29, Figure 6.

**Etymology**

The species is named after Friedrich Eduard Rühe, well-known German investigator of Cladocera, who identified this species as *M. hirsuticornis* from Île Amsterdam (Rühe 1914).

**Type locality**

A pond at Baie Americaine, Île de la Possession, Crozet Islands, French Subantarctic Territories. The type series was collected 24 February 1968 by L. Davies.
Figure 17. *Macrothrix ruehei* sp. nov., parthenogenetic female from a pond in Baie Americaine, Île de la Possession, Crozet Islands (A–I, L–N) and unknown locality in Île Amsterdam (J, K, O). (A, B) Large adult, holotype in lateral and anterior view; (C) paratype; (D) head; (E) labrum; (F, G) setae on anterior and posterior portion of ventral valve margin; (H–J) postabdominal claw, outer view; (K) its inner view; (L, M) proximal and distal segment of postabdominal seta; (N, O) antenna I. Scale bars: 0.1 mm.
Figure 18. *Macrothrix ruehei* sp. nov., head and thoracic appendages of parthenogenetic female from a pond in Baie Americaine, Ile de la Possession, Crozet Islands (A–C, G–L, N–Q) and unknown locality in Ile Amsterdam (D–F, M, R). (A) Antenna II; (B, C) its exopod; (D, E) distal portion of basal segment and proximal portion of exopod; (F, G) lateral seta on proximal endopod segment; (H) inner-distal lobe of limb I; (I) ejector hooks of limb I; (J, K) distal portion of limb II; (L, M) exopod III; (N) inner-distal portion of limb III; (O) exopod IV; (P–R) distalmost seta on inner portion of limb IV. Scale bars: 0.1 mm.
Type material

Holotype: a parthenogenetic ♀ in 90% alcohol, NHM 2004.2309. Label of holotype: “*Macrothrix ruehei* n.sp.; pond, Baie Americaine, Possession Is., Crozet Islands, coll. 24.02.1968 by L. Davies, I parth. fem., HOLOTYPE”. Paratypes (all from Crozet): 151 parth. ♀♀ from the type locality, coll. 24 February 1968 by L. Davies, NHM 1968.7.10.2 (tube); one parth. ♂ from the type locality, coll. 24 February 1968 by L. Davies, NHM 1968.7.10.2.b (slide); one dissected parth. ♀ from the type locality, coll. 24 February 1968 by L. Davies, NHM 2004.2310 (six slides); one parth. ♀ from locality “Net. Riv. du camp”, Île de la Possession, coll. 16 January 1968 by L. Davies, NHM 1968.7.10.3 (tube); 20 parth. ♀♀ from unknown locality in Île de l’Est, coll. 28 February 1969, NHM 1970.4.30.1 (tube).

Other material studied

Marion Island: six parthenogenetic females from loc. 2494, coll. 1965 by B. J. Huntley (Marion Island Expedition 1965–1966), tube NHM 1971.6.8.96–103.; one parth. ♀ from loc. 3345, coll by E. Z. Bakker, slide NHM 1971.6.8.85.; 16 parth. ♀♀ from loc. 3346, coll. by Marion Island Expedition 1965–1966, tube NHM 1971.6.8.55–95.

New Amsterdam Island (Île Amsterdam): 119 parthenogenetic females from unknown locality, coll. 27 March 1903 by Deutch Südpolar-Expedition, tube ZMHU 17465; one parth. ♀ from unknown locality, coll. 27 March 1903 by Deutch Südpolar-Expedition, slide in ZMHU, no number accessed.

Diagnosis (based exclusively on Crozet specimens)

Parthenogenetic female. In lateral view body subovoid (height/length = 0.62–0.67 in large adults), cervical depression present, dorsal margin breached by a “step” in posterior boundary of head, forming a blunt tooth, dorsal margin of valves not elevated under dorsal margin of head, without any serration (Figure 17A). Postero-dorsal angle as rounded triangle, lies in level of middle of body height. Body compressed laterally, with a low, but sharp dorsal keel (Figure 17B). No dome above eye; ocellus small (Figure 17D). Dorsal organ ovoid, small. Labrum with a thick, rounded, moderately projected apex lacking any tubercles (Figure 17D, E). Armature of ventral margin as in other species (Figure 17F, G).

Postabdomen without “heel” basally, and without a reticulation on sides. Ventral margin straight, with few series of small denticles. Postabdominal seta with a short distal segment, armed with relatively short setules; basal segment without any setules (Figure 17L, M). On external side of postabdominal claw, a series of six to nine moderately robust denticles; medial row of about seven to nine denticles; inner row with numerous denticles, organized in two successive series (Figure 17H, I), on inner side two pectens of denticles (Figure 17K).

Antenna I widened distally, straight or slightly curved, without a subapical external angulation; sensory seta at distance of about 1.5–2 antennular diameters (at base) from antenna I joint; on anterior face about five to seven transverse rows of spinules, but no reticulation (Figure 17N, O). Nine short aesthetascs, two or three of them significantly larger than the rest. Antenna II with distal burrowing spine on basal segment as long as or longer than proximal segment of exopod (Figure 18A). Length of all apical swimming setae subequal, their armature as in *M. boergeni*. Lateral seta on proximal endopod segment larger than other setae, lacking robust denticles in middle (Figure 18G). A spine on second segment of exopod half as long as next segment (Figure 18B, C), on posterior side of segments 1–3 of exopod there are series of relatively large additional denticles.
Limb I outer distal lobe with longest apical seta having distal segment unilaterally armed with robust setules; inner-distal lobe with three bisegmented setae of different size, unilaterally setulated in distal part, smallest one with whole distal segment setulated, or these setules present only in proximal portion of distal segment (Figure 18H); two ejector hooks of similar size (Figure 18I). On limb II, scrapers 1–2 with delicate feathering, scrapers 3–7 with robust denticles of size characteristic for the genus (Figure 18J, K); a solitary posterior seta present near gnathobase; filter plate II with four setae, without a rudiment of fifth seta. On limb III epipodite with five setae; a distal group of three long setae, seta 1 armed with robust denticles (Figure 18L); setulated projections proximally to seta 3 and between setae 2 and 3; on inner-distal limb portion, seta 1 with short and robust denticles; seta a with fine setules basally and robust spinules distally, seta b only somewhat longer than c (Figure 18N); basal endite posteriorly with four soft setae. Limb IV with exopodite small, bearing only a distal group of three bilaterally feathered setae of different size (Figure 18O); on inner-distal portion of this limb seta 1 with strong setules basally and two to six robust denticles distally (Figure 18P, Q); posteriorly, row of five long setae. On limb V there are three setae at inner margin.

Differences of juvenile female. In contrast to adult, body more elongated, with less-developed tooth on posterior border of head, with valve dorsal margin less convex, with antennae II and swimming antennal setae longer, rows of setules on antenna I and II weakly developed (Figure 17C).

Ephippial female, male. Unknown.

Differences of Île Amsterdam populations. Île Amsterdam females (Figures 17J, K, O; 18D–F, M, R) have (1) smaller, more numerous (up to 10), denticles projected exactly dorsally on outer surface of postabdominal claw; (2) antenna I somewhat more widened distally; (3) shorter aesthetascs of antenna I with smaller differences between smallest and largest members; (4) very small additional denticles on segments 1–3 of antenna II; (5) more prominent projections between setae 2 and 3 and distally to seta 3 on exopodite III; (6) more numerous denticles (up to six) on seta 1 of inner margin of limb III. Except for difference 1, the rest of the specific traits of Île Amsterdam populations seem to be subject to strong variability among Macrothrix populations. Populations from all three groups of islands examined here are considered conspecific.

Size. Holotype 0.84 mm, juvenile and adult parthenogenetic females from the type series, Crozet 0.44–0.97 mm, from Île Amsterdam 0.65–1.00 mm.

Taxonomic notes. Rühe (1914) was the first to observe M. ruehei sp. nov., which he identified as “M. hirsuticornis”, although he mixed in the description populations from Île Amsterdam and Kerguelen, belonging to different species in present understanding. Brehm (1958) made a drawing of the head of “M. hirsuricornis” from Île Amsterdam with widely rounded labral apex. This is undoubtedly M. ruehei sp. nov. There is no doubt about the conspecificity of populations from Crozet, Marion, and Île Amsterdam, but due to small differences between them, all material not from Crozet is “expressly excluded from the type series” (case 72.4.1 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 2000)).
Distribution. French Southern Territories: Crozet, Marion, Île Amsterdam, but not Kerguelen, where its congener, *M. boergeni*, occurs. Apparently, *M. ruehei* sp. nov. is a very common species in small water bodies on the aforementioned islands. Note that it is not clear which species of *Macrothrix* (recorded by Dartnall (1995)) inhabits Heard Island.

**Macrothrix cf. flagellata** (Smirnov and Timms, 1983)
(Figures 19, 20)

? *Echinisca flagellata* Smirnov and Timms 1983, p 80–81, Figure 93.
? *Macrothrix flagellata* (Smirnov and Timms) in Smirnov 1992, p 62, Figures 252–259.

Figure 19. *Macrothrix cf. flagellata*, parthenogenetic female from Langdon Point, Macquarie Island. (A) Lateral view; (B) head; (C) reticulation of valves; (D) marginal setae; (E) postabdomen; (F) postabdominal claw; (G) antenna I; (H) its tip. Scale bars: 0.1 mm.
Figure 20. *Macrothrix cf. flagellata*, head and thoracic appendages of parthenogenetic female from Langdon Point, Macquarie Island. (A) Antenna II; (B) distal sensory seta; (C–E) seta on proximal segment of endopod of an adult female, proximal, medium, and distal portion, respectively; (F, G) the same seta in two other females, medium portion; (H) limb I; (I–K) anterior setae 1–3; (L) limb II; (M) limb III; (N, O) limb IV and its gnathobase; (P) limb V. Scale bars: 0.1 mm.
Material examined here

Macquarie Island: Langdon Point, collected by H. J. G. Dartnall, AAK 1999-012; unknown locality “Ros 204”, coll. by B. A. N. Z. A. R. Expedition, NHM 1966.7.20.3. and NHM 1966.7.20.4.

Diagnosis (based exclusively on population from Macquarie)

Parthenogenetic female. In lateral view body subovoid, relatively high (height/length = 0.65–0.70), cervical depression absent, dorsal margin not interrupted by a “step” in posterior boundary of head, dorsal margin of valves without any serration, postero-dorsal as rounded angle, lies in level of middle of body height (Figure 19A). No dome above eye. Ocellus small, less than half of eye diameter. Dorsal organ ovoid, small. Labrum with a strongly projected triangular apex bearing few tubercles (Figure 19B). Valves with fine reticulation (Figure 19C) and marginal setae as in previously described congeners (Figure 19D).

Postabdomen subovoid, with rounded distal extremity, without “heel” basally, with a reticulation on sides (Figure 19E). Ventral margin straight, with four to five series of moderately long, thin spinules. Dorsal margin distinctly bilobed; preanal margin with transversal series of minute setules, anal margin with groups of thicker setules. Postabdominal seta distal segment slightly shorter than basal one, densely armed with relatively short setules; basal segment with numerous, short setules. On external side of postabdominal claw, a series of 10–12 fine spinules; medial row of about six to eight denticles (Figure 19F).

Antenna I very slightly widened distally, straight to slightly curved, without any traces of subapical external angulation; sensory seta at distance of about 1.5–2 antennular diameters (at base) from antenna I joint; on anterior face about seven to ten transverse rows of spinules, but no reticulation (Figure 19G). Nine short aesthetascs, three of them significantly larger than the rest (Figure 19H). Antenna II with distal burrowing spine on basal segment slightly shorter than proximal segment of exopod (Figure 20A), distal sensory seta (Figure 20B) somewhat longer than distal burrowing spine. Length of all apical swimming setae subequal. Lateral seta on proximal endopod segment larger than other setae, lacking robust denticles in middle (Figure 20C–G). A spine on second segment of exopod longer than half of next segment. On posterior side of segments 1–3 of exopod there are a series of small, thin additional denticles.

Limb I outer distal lobe with longest apical seta having distal segment unilaterally armed with robust setules, inner-distal lobe with three bisegmented setae of different size, unilaterally setulated in distal part, smallest one with whole distal segment and distal portion of basal segment setulated; two ejector hooks of different size; maxillar process with two setae (Figure 20H), anterior setae as represented in Figure 20I–K. On limb II, scrapers 1–2 with delicate feathering, scrapers 3–7 with robust denticles of size characteristic for the genus; a solitary posterior seta near gnathobase; filter plate II with four setae, without a small hillock in position of rudiment of fifth seta (Figure 20L). On limb III epipodite with a distal group of three long setae, seta 1 shortest, armed with robust denticles; setulated projections proximally to seta 3 and between setae 2 and 3 (Figure 20M); on inner-distal limb portion, seta 1 with short and robust denticles; seta a with fine setules basally and robust spinules distally, seta b markedly longer than c; basal endite posteriorly with four soft setae. Limb IV (Figure 20N, O) with exopodite small, bearing only a distal group of three bilaterally feathered setae of different size; on inner-distal portion of this limb seta 1
without setules basally and few denticles distally; posteriorly row of five long soft setae. On limb V there are three setae at inner margin (Figure 20P).

**Ephippial female, male.** Unknown.

**Size.** In our samples 0.62–1.22 mm. In Tasmania, *M. flagellata* specimens up to 1.39 mm are found (Smirnov and Timms 1983).

**Taxonomic notes.** At this level of morphological description of *M. flagellata*, it is impossible to conclude that I found just *M. flagellata* s. str. An accurate comparison with the original type material should be made and the Australian macrothricids need to be reassessed.

Smirnov and Timms (1983) initially placed *M. flagellata* in the genus *Echinisca* because of the undilated antenna I; however, this genus was subsequently synonymized with *Macrothrix* (Smirnov 1992). Serious doubts were expressed regarding the subjective status of the character “dilated—undilated antenna I” (Kotov 1999). This character is applicable only in extreme states. In the intermediate state it is not possible to conclude whether antenna I of this species (or even specimen) is dilated or not. In the case of *M. flagellata*, a completely undilated antenna I is the only character distinguishing this species from others listed above. At the same time, *M. flagellata* and other aforementioned species have a set of similar characters, possible synapomorphies. In other *hirsuticornis*-like species the level of dilation is different, and variable. Consequently, I believe that *M. flagellata* is a *hirsuticornis*-like species.

**Distribution.** Tasmania and Macquarie Island. Dartnall et al. (2005) recorded *M. hirsuticornis* from Macquarie; their material may belong to *M. flagellata*, or to another species from this genus.

**Macrothrix hirsuticornis** Norman and Brady, 1867 s. str.  
(Figures 21, 22)  
*Macrothrix hirsuticornis* Norman and Brady 1867, p 10–11, Plate 23, Figures 6, 7.

See references to many other descriptions from the Palaeartic in Smirnov (1976, 1992) and Flössner (1972, 2000).

**Type locality**  
“A slowly-running stream at Ashburn, Sunderland”, England, UK.

**Type material**  
Lectotype: a female in bad condition from “Ashborne, Sunderland”, Norman’s Collection, NHM 1911.11.8.M.4038.

**Material examined**  
Germany: a temporary water pool, Juist Island, East Frisian Islands, Lower Saxony, coll. 26 June 1987 by W. Hollwedel, AAK 1999-011. Iceland: locality #27, coll. 16 July 1996 by A. Thiery, NMK 1873; locality #7, 30 km from Stadur, coll. 28 June 1996 by A. Thiery, NMK 1875. Italy: Lake Campo Felice, Abruzzi, coll. 1982 by F. Margaritora, AAK
1999-084. Israel: a pool in Dor, coll. 23 January 1967 by N. N. Smirnov, NNS 1997-045.
Iraq: a channel, Euphrates at Chybayish, coll. 18 November 1974 by N. N. Smirnov, NNS 1998-196.
Russia: Farm Urozhayniy, near Lake Svetloe, Altai Territory, coll. 18 August 1967, NNS 1997-246; Teletskoe Lake, Altai Territory, coll. 12 August 2002 by O. S. Burmistrova, NMK 2514; Irkutsk water Reservoir, Irkutsk Area, coll. 24 June 1968, NNS

Figure 21. *Macrothrix hirsuticornis*, parthenogenetic female from Lake Solongul-Kul, Central Pamirs, Tajikistan, sample NNS-1997-036. (A) Large adult, lateral view; (B) dorsum of different individuals; (C) labrum; (D, E) setae at medium portion of ventral margin; (F–H) setae at postero-ventral portion of valve; (I, J) postabdomen and its distal portion; (K, L) postabdominal claw in outer and inner view; (M, N) juvenile and its postabdomen; (O) seta on proximal segment of endopod of antenna II of adult. Scale bars: 0.1 mm.
Figure 22. *Macrothrix hirsuticornis*, appendages of parthenogenetic female from Lake Solongul-Kul, Central Pamirs. (A, B) Antenna I of adult; (C) antenna I of juvenile; (D) antenna II of adult; (E) the same of juvenile; (F) limb I; (G) its distal portion; (H, I) fork-like setae 2 and 3; (J, K) limb II and distal armature of its gnathobase; (L–N) limb III, its inner-distal portion and gnathobase, respectively; (O, P) limb IV and large sensillum on its gnathobase; (Q) limb V. Scale bars: 0.1 mm.
Short diagnosis

Parthenogenetic female. In lateral view body subovoid, cervical depression absent, dorsal margin breached by a “step” in posterior boundary of head, or not breached; postero-dorsal angle as rounded triangle, lies in level of middle of body height or ventrally to it (Figure 21A, B). No dome above eye. Ocellus small. Dorsal organ ovoid, small. Labrum with a moderately projected apex, with or without ill-defined tubercles (Figure 21C). Armature of valve margin as in previously described species (Figure 21D–H).

Postabdomen subovoid, with rounded distal extremity, without “heel” basally, and without a reticulation on sides or with poorly observable reticulation (Figure 21I). Ventral margin straight, with series of fine setules (Figure 21J). Dorsal margin distinctly bilobed; preanal margin with transversal series of minute setules, anal margin with groups of thicker setules. Postabdominal seta with distal segment densely armed with relatively long setules; basal segment with numerous, shorter setules (Figure 21I). On external side of postabdominal claw, a series of 8–12 thin spinules (Figure 21K); medial row of about seven to ten denticles; inner row with numerous denticles, organized in two successive series, subdivided by a larger denticle (Figure 21L).

Antenna I widened distally, straight or slightly curved, without a subapical external angulation; sensory seta at distance of about two antennular diameters (at base) from antenna I joint; on anterior face about six to eight transverse rows of spinules, but no reticulation (Figure 22A, B). Nine short aesthetascs, three of them significantly larger than the rest. Antenna II with distal spine on basal segment longer than proximal segment of exopod (Figure 22D). Lateral seta on proximal endopod segment larger than other setae, lacking robust denticles in middle (Figure 21O). A spine on second segment of exopod longer than half next segment. On posterior side of segments 1–3 of exopod there are series of small to large additional denticles.

Limb I with longest apical seta of outer distal lobe having distal segment unilaterally armed with robust setules, inner-distal lobe with three bisegmented setae of different size, unilaterally setulated in distal part, smallest one with whole distal segment setulated; two ejector hooks of similar size, a vestige of gnathobase I with a single fully setulated seta (Figure 22F), anterior setae as represented in Figure 22H, I. On limb II, scrapers 1–2 with delicate feathering, scrapers 3–7 with robust denticles of size characteristic for the genus; a solitary posterior seta near gnathobase; filter plate II with four setae, without a small hillock, a rudiment of fifth seta (Figure 22J, K). On limb III epipodite with a distal group of three long setae, seta 1 shortest, distally armed with relatively fine setules (Figure 22L); setulated projection proximally to seta 3; on inner-distal limb portion, seta 1 distally with short and robust denticles; seta a with fine setules basally and robust spinules distally, seta b long, seta c short (Figure 22M); basal endite posteriorly with four soft posterior setae, gnathobase as in other species (Figure 22N). Limb IV with exopodite small, bearing only a distal group of three bilaterally feathered setae of subequal size; on inner-distal portion of this limb, seta 1 without strong denticles distally; posteriorly row of five long setae (Figure 22O), seta 1 on gnathobase as a bottle-shaped sensillum (Figure 22P). On limb V there are three setae at inner margin (Figure 22Q).

Juvenile female. Subquadrangular in shape, with relatively longer antenna I and II (Figures 21M, N, 22C, E).

Revision of the hirsuticornis-like species of Macrothrix
**Ephippial female.** Similar to parthenogenetic female, with slightly pigmented ephippium bearing a slight additional sculpture of fine polygonal reticulation, no clear border between ephippium and rest of valve, dorsal wall of carapace forms a special dark, chitinized plate; normally two eggs, sometimes three in ephippium (Berg 1933; Hudec 1983).

**Male.** Previous descriptions (Smirnov 1976; Hudec 1983; Alonso 1996; Silva-Briano 1998) insufficiently accurate in fine details to discuss differences from congeners.

**Size.** Parthenogenetic females 0.5–2 mm, ephippial females 0.5–0.65 mm, males 0.4–0.65 mm (Flössner 2000).

**Taxonomic notes.** Initial examination of a relatively limited set of samples with *Macrothrix* from the Palaearctic (A. A. Kotov, unpublished) revealed three *hirsuticornis*-like taxa: *M. hirsuticornis* Norman and Brady, 1867, *M. tripectinata* Weisig, 1934, and *M. dadayi* Behning, 1941. Silva-Briano (1998) redescribed *M. hirsuticornis* s. str. in his PhD thesis, but these results are not published. It is necessary to note that although Silva-Briano (1998) concluded that *M. cornuta* is a “horned” morphotype of *M. hirsuticornis*, the female of the former species from Turkey (whose identity with Daday’s (1903) species from Mongolia must be checked!) has strong spines on the seta on the proximal segment of the endopod of antenna II. Most probably the *M. cornuta* of Silva-Briano (1998) is another Palaearctic *hirsuticornis*-like species, but it is clear that the revision of *M. hirsuticornis* in the Palaearctic still has some way to go and must be done using better material.

Previous efforts by taxonomists examining the *M. hirsuticornis* group have predominantly concentrated on the variability of characters regarded as helpful for systematics by cladocerologists of the 19th century (Sars 1890; Lilljeborg 1901). These include the expression of a tooth or hood on posterior border of head, or additional spines on antennal branches (Fox 1962; Flössner 1967, 1972; Hudec 1983; Margaritora and Usai 1983; Silva-Briano 1998; Flössner 2000). All of these publications, dealing with external shape of body, lacked a detailed analysis of other, “finer”, traits of different populations. Only after such accurate examination of many populations may a conclusion be made on the number of *hirsuticornis*-like species in the Palaearctic.

In any case, all southern hemisphere species described above differ from Palaearctic *M. hirsuticornis* s. str. (Table I).

**Distribution.** Widely distributed in the Palaearctic. Status of Nearctic and all southern hemisphere populations must be checked.

**Phylogeny**

A list of characters analysed is given in Table I. Autapomorphies, marked by bold type, were excluded from the analysis; each variable character is marked as data missing. A cladistic search using 12 characters reveals three equally short trees (TL=16; CI=0.75; RI=0.71); a strict consensus tree is represented in Figure 23. The 50% majority rule bootstrap simulation led to a tree of similar topology with the consensus tree. Due to this fact, branch probabilities were assigned to the aforementioned consensus tree.

Two well-supported clades are found: *boergeni–ruhei* and *sarsi–oviformis–hirsuticornis*; these are grouped together, but this grouping has a moderate support (66%). *Macrothrix flagellata* is not grouped with any other taxa; this species as well as *M. tripectinata* (the outgroup) are basal members of the studied group.
Discussion

Morphology and systematics

Characters such as general body shape (the presence of a hood or tooth on the posterior head border) have a limited application for *Macrothrix* systematics (Fox 1962; Silva-Briano 1998). The aforementioned tooth is, probably, an element of antipredator morphology (Kotov 1999) in addition to spines on the branches of antenna II. Also, the general body shape in this genus is the subject of strong instar variability (Smirnov 1992). In contrast, some fine details, often neglected by previous investigators, are valuable for species determination (see Table I). These characters have been discussed by Kotov (1999).

The value of a general body shape is similarly compromised in the genera of other families such as *Bosmina* (Haney and Taylor 2003), where male sexual characters are found to be significantly more valuable (Kotov 1996; Kim et al. 2006). Many species of *Daphnia* have been established based on inapplicable characters that are too variable within populations and too ecologically plastic to be used (Glagolev 1986a, 1986b). Illusory “differences” such as those between females with an empty or full brood pouch in the same species of *Moina* were specially discussed by Fryer (1991). Only relatively recently have the more applicable “fine” characters of appendages armature and secondary male characters been applied to anomopod systematics.

While the antenna I is a good diagnostic character when it is widened distally in maximum expression, it is almost impossible to distinguish “slightly dilated” from “undilated” (Kotov 1999). All species with a more dilated antenna have been grouped together in the consensus tree, but the probability of this grouping is only 66%. This cannot be regarded as evidence that it appeared only once in the evolution of *hirsuticornis*-like species. A dilated antenna is characteristic of some other groups of *Macrothrix*, i.e. *M. spinosa* and *M. laticornis* (Smirnov 1976, 1992). It is likely that dilation of antenna II took place independently within different species groups (Kotov 1999). Further, this process is associated with increasing size of some aesthetascs on the tip on antenna I. Indeed, in *M. tripectinata* and *M. flagellata* which have a slightly widened antenna, the difference in size between aesthetascs is less than in species with a strongly widened antenna I.

The armature of the largest seta on antenna II (seta on proximal segment of endopod) has traditionally been regarded as helpful for macrothricid systematics (Smirnov 1976, 1992), ever since the first description of *Macrothrix triserialis* Brady, 1886. Similarly, the armature of lateral setae on segments 1–2 of endopod of antenna II has been found to be very useful for *Ilyocryptus* (Kotov and Štifter 2006).
A remarkable hypertrophy of scrapers on limb II of *M. boergeni* is analogous to that of the distal-most seta on the inner portion of limb III in tropical *M. marthae* (Elias-Gutiérrez and Smirnov 2000). In both cases, the unusual specialization of the setae, to enable dragging of particles from a substratum, is a reflection of an unusual feeding specialization. Unfortunately, feeding behaviour and other aspects of biology have been investigated only in a few species (Fryer 1974) and remain unknown for most species of *Macrothrix*.

Unfortunately, ephippial females and males were found only in *M. oviformis*, so the importance of their characters for species discrimination within the *M. hirsuticornis* group has not been investigated yet.
Biogeography

*Macrothrix hirsuticornis* Norman and Brady, 1867 s. str. is absent from the southern hemisphere, where five other, related species occupy different Subantarctic islands and archipelagos, and the southernmost portions of South America and Africa (Figure 24).

*M. sarsi* sp. nov. is endemic to the Cape region of South Africa, which is regarded as a specific biogeographic zone. Many endemics are confined to the Cape Floral Kingdom (Wishart and Day 2002). The level of endemism in the freshwater fauna of South Africa has been discussed previously (Wishart and Day 2002; Smirnov 2007a). Recent additions (Kotov and Štifter 2006; Smirnov 2007b) and revised descriptions (Smirnov et al. 2006) may cause our ideas on endemism in South Africa to be reviewed. For example, *Lathonura* sp., regarded as a Holarctic taxon, was recently recorded in Botswana (Hart and Dumont 2005).

This study increases the number of species recorded from the Antarctic-Subantarctic region (these data have already been incorporated in Table 1 of Forró et al. 2007). It is significant that *Macrothrix oviformis* together with *Daphnia studeri* are the only two species of the Cladocera present in continental Antarctica (the former is found only on the Antarctic Peninsula). Even during the Last Glacial Maximum, some refugia of the freshwater fauna existed on the Antarctic continent (Cromer et al. 2006; Gibson and Bayly 2007), so we can assume that these continental populations of *Daphnia* and *Macrothrix* were not recently introduced, but existed from a pre-glacial time. At the same time, some other territories, i.e. South Georgia and the South Orkneys, were completely covered with ice and “must have lost their cladocera completely during the last glacial age” (Frey 1988). This means that these islands were apparently re-colonized through the agency of migratory birds, or as a result of a passive dispersal of ephippia attached to kelps drifting through sea currents (Akatova 1964). Currently, the main factor in cladoceran dispersal has been human activity; for example, *Alona weinecki* was introduced to Easter Island (Dumont and Martens 1996), where freshwater cladocerans have been long absent.

Only two species of Cladocera can be definitively regarded as widely distributed in the Subantarctic, *Alona weinecki* and *Daphnia studeri* (Frey 1988; Pugh et al. 2002; Benzie 2005; Gibson and Bayly 2007). The status of populations of *Chydorus* cf. *sphaericus* and *Chydorus* cf. *patagonicus*, appearing also to be circum-Subantarctic, must be checked in the future.

Other cladocerans demonstrate other patterns of distribution. *Ilyocryptus brevidentatus* Ekman, 1905, originally described from the Falklands and South Georgia, and then discovered at Signy Island (Heywood, 1967), was also found in Tierra del Fuego and continental South America (Kotov et al. 2002). *Macrothrix oviformis* demonstrates a similar distributional pattern, but its range is somewhat wider, and includes also the South Shetland Islands and the Antarctic Peninsula. At present, we can conclude that the Falkland Islands have no known endemic cladocerans (see also Dartnall and Hollwedel 2007).

Frey (1993) analysed the distribution of *Pleuroxus* cf. *aduncus* in the Subantarctic and the southernmost portion of South America, and found several isolated species. This study also demonstrates that different Subantarctic islands are inhabited by different species of *Macrothrix*. There is a partial similarity in the distribution of *Pleuroxus* and *Macrothrix* species in the Subantarctic, which may reflect the geological and climatic history of this region. Macquarie Island seems to be a most unusual Subantarctic territory. In addition to *M. cf. flagellata*, absent from all other localities of the South Polar Ocean, the endemic *Pleuroxus macquariensis* and *Daphnia gelida* occur there (Dartnall et al. 2005). It is necessary to note that the pattern of global distribution of *Macrothrix* species, where the number of
known taxa in the southern hemisphere is significantly greater than in the northern hemisphere (especially when including the Australian endemics) agrees with the distribution pattern of *Pleuroxus* species.

There was no evidence of a Gondwanian heritage (Bayly 1995; Pugh et al. 2002; Benzie 2005) in the distribution of *Macrothrix*. In contrast, South African and South American species are apparently the closest relatives of Laurasian (Palaearctic and, perhaps, Nearctic) *M. hirsuticornis* s. str. At the same time, *M. tripectinata* and *M. flagellata*, two taxa with a more basal position on the phylogenetic tree, are distantly isolated from each other. Most probably, this pattern of distribution appeared as a result of the disruption of a pancontinental (early Mesozoic?) species complex. Locally distributed species from the southern hemisphere can be regarded as relicts of this large Pangaea group, which is in accordance with the recent concept of the cladoceran biogeography proposed by Korovchinsky (2006) and ideas on earlier (Palaeozoic) differentiation of the cladoceran taxa (Sacherova and Hebert 2003; Kotov 2007). In this case, *M. sarsi* sp. nov. from the Cape region must be regarded as a palaeo-endemic form *sensu* Harrison (1965).

Only a preliminary revision of the *Macrothrix hirsuticornis* group was conducted in this study. *Macrothrix hirsuticornis* s. lat. has been found in other non-Palaearctic localities. The findings from the southern hemisphere are intriguing, especially those from tropical Argentina (Vavra 1900), the Columbian Andes (Stingelin, 1913), and Australia (Smirnov and Timms, 1983). It is likely that the number of *hirsuticornis*-like species is still underestimated.

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