A cladistic analysis of the genera of Macrothricidae Norman & Brady (Crustacea, Cladocera, Radopoda)

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ABSTRACT. A cladistic analysis of the genera of the Macrothricidae (Crustacea, Cladocera, Radopoda) was performed based on 36 morphological characters, and including 15 terminal taxa (three as outgroups). The single tree obtained from this analysis supported the monophyly of Macrothricidae and Macrothricinae. The group called as "non-Macrothricinae" was indicated as paraphyletic. Neothricidae was also not supported.
KEY WORDS. Anomopoda, Macrothricinae, Macrothricoidea, phylogeny.

RESUMO. **Análise cladística dos gêneros de Macrothticidae Norman & Brady (Crustacea, Cladocera, Radopoda).** Foi conduzida uma análise cladística dos gêneros sul-americanos de Macrothricidae (Crustacea, Cladocera, Radopoda) com base em 36 caracteres morfológicos e incluindo 15 taxa terminais (três como grupos externos). Uma única árvore foi obtida pela análise, a qual suporta o monofiletismo de Macrothricidae e de Macrothricinae. O grupo chamado de "não-Macrothricinae" é indicado como parafilético. Neothricidae também não encontrou suporte.
PALAVRAS CHAVE. Anomopoda, filogenia, Macrothricinae, Macrothricoidea.

In its original definition, the family Macrothricidae Norman & Brady, 1867 (Branchiopoda, Anomopoda) embraced all littoral cladoceran genera with antennules long and attached near the tip of head, without rostrum, antenna with three endopodite and four expedite segments, and postabdomen with strong and numerous marginal dentils (for a detailed description, see Alonso 1996). According to Fryer (1974, 1995), most of the primitive anomopod characteristics were retained in this family.

In the last decade, Macrothricidae was redefined. At first, Smirnov (1992) transferred the genus *Ilyocryptus* Sars, 1892 to a new family, and more recently Dumont & Silva-Briano (1998) elevated the remaining group to superfamily status (Macrothricoidea). The Macrothricoidea embraces the families Macrothricidae *strictu sensu*, Acantholeberidae Smirnov, 1976, Neothricidae Dumont & Silva-Briano, 1997, and Ophryoxidae Smirnov, 1976. According to Dumont & Silva-Briano (1998), the Macrothricidae *strictu sensu* includes 11 genera, characterized by fork setae on trunk limb I and reduction of the number of trunk limb setae, if compared with more "primitive" macrothricid-like families. For example, the Acantholeberidae possess 8, 8, and 7 setae on exopodites of the trunk limbs III, IV, and V respectively, while the Macrothricidae have the maximum of 6, 6, and 3 setae on the same exopodites.

Although Dumont & Silva-Briano (1998) suggested a hypothetical evolutionary tree for the families of Macrothricoidea (and other Radopoda Dumont & Silva-Briano, 1997), the phylogenetic relationships within the Macrothricoidea have not yet been submitted to a cladistic analysis. As a starting point, the present study aims to investigate the phylogenetic relationships among the genera of the Family Macrothricidae, based on a formal cladistic analysis of 36 morphological characters.

MATERIAL AND METHODS

The ingroup taxa set consisted of 12 species representing the genera of Macrothricidae. The genus *Cactus* Vávra, 1900 was not included in the analysis because only a single specimen is known and its description is very vague. Three species of *Macrothrix* Baird, 1843 were included in the analysis in order to represent the synonymous genera *Iheringula* Sars, 1900 and *Echinisca* Liévin,1848. *Streblocerus* Sars, 1862 was represented by two terminal taxa because differences among species were observed. As outgroup, three genera of Macrothricoidea were included: two considered as "primitive" (*Acantholeberis* Lilljeborg,1846 and *Ophryoxus* Sars, 1862) and one considered as advanced (*Neothrix* Gurney, 1927) (Dumont & Silva-Briano 1998). The list of terminal taxa, the material examined, and the literature source are presented in table I.

The 36 selected morphological characters and the character states are summarized in table II. Most of these characters is traditionally used in cladoceran taxonomy and is well described in Alonso (1996) and Dumont & Negrea (2002). The

Table I. List of terminal taxa, localities from which specimens were examined in present study (all localities in Brazil), and literature sources.

	Species	Localities or literature source
Outgroup	*Acantholeberis curvirostris* (Müller, 1776)	Fryer (1974), Dumont & Silva-Briano (1998)
	Neothrix armata Gurney, 1927	Smirnov (1992), Dumont & Silva-Briano (1998)
	Ophryoxus gracilis Sars, 1862	Smirnov (1992), Dumont & Silva-Briano (1998)
Ingroup	*Bunops tuberculata* (Fryer & Paggi, 1972)	Fryer & Paggi (1972), Silva-Briano & Dumont (2001)
	Drepanothrix dentata (Eurén, 1861)	Smirnov (1992), Dumont & Silva-Briano (1998)
	Grimaldina brazzai Richard, 1892	Bahia (12°34'40.9"S, 38°00'47.4"W)
	Guernella raphaelis Richard, 1892	Paggi (1976), Fryer (1974), Dumont & Silva-Briano (1998)
	Lathonura rectirostris (O.F. Muller, 1785)	Smirnov (1992), Dumont & Silva-Briano (1998)
	Macrothrix elegans Sars, 1901	Bahia (12°35'43.0"S, 39°00'22.9"W)
		Distrito Federal (15°50'29.7"S, 47°53'55.1"W)
	Macrothrix laticornis group	Goiás (14°27'42.9"S, 47°00'15.2"W)
	Macrothrix paulensis (Sars, 1888)	Distrito Federal (15°41'16.5"S, 47°56'22.2"W)
		Bahia (12°45'42.2"S, 38°10'07.7 W)
	Paraphryoxus tubulatus Doolittle, 1909	Smirnov (1992), Dumont & Silva-Briano (1998)
	Pseudomoina lemnae (King, 1853)	Petkovski (1973), Dumont & Silva-Briano (1998)
	Streblocerus pygmaeus Sars, 1901	Distrito Federal (15°41'16.5"S, 47°56'22.2 W)
		Goiás (15°09'15.8"S, 47°28'04.7"W)
	Streblocerus serricaudatus (Fischer, 1847)	Fryer (1974), Dumont & Silva-Briano (1998)
	Wlassicsia pannonica Daday, 1904	Smirnov (1992), Dumont & Silva-Briano (1998)

terminology used to describe the trunk limbs follows Dumont & Silva-Briano (1998) and Dumont & Negrea (2002). The abbreviation TL*i* is used to indicate the trunk limbs I to V, and endite *i* - TL*i* to indicate the endite 1 to 4 of the corresponding trunk limb. When samples were available, the character states were confirmed by direct observation of the specimens. Character 23 followed Fryer (1974). Some discrepancies were detected among *Guernella* Richard,1892 data from Fryer (1974), Paggi (1976), and Dumont & Silva-Briano (1998), so in characters 10, 16, 20, and 27 the option was for the description of South American specimens (Paggi 1976). The data matrix is presented in the table III.

Parsimony analysis was performed with PAUP 4 (Swofford 1999), using the exhaustive search option. All characters were considered unordered and unweighted. ACCTRAN optimization was used and the tree was rooted using the outgroup method. The distribution of the characters states was further investigated using MacClade 3.04 (Maddison & Maddison 1992).

RESULTS AND DISCUSSION

The analysis produced a single most parsimonious tree (*l* = 79 steps; CI = 0.5696; RI = 0.6991; RCI = 0.3982), shown in figure 1. The apomorphy list is presented in table IV.

The monophyly of Macrothricidae is supported by 9 characters (Tab. IV). The presence of five pairs of trunk limbs, TL I without seta at exopodite base, TL II with duplication setae reduced and modified (Fig. 2), TL IV without pre-epipodite, and TL V with 1 or 2 setae on exopodite are constant characters within

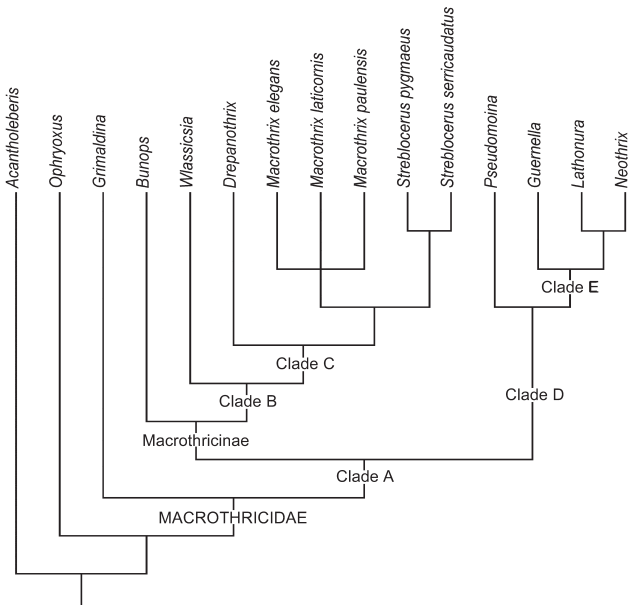


Figure 1. Phylogenetic topology for the genera of Macrothricidae. Single tree of minimum length (*l* = 79 steps; CI = 0.5696; RI = 0.6991; RCI = 0.3982).

Table II. List of characters and character states.

Number	Character	State
1	Antennule, curved outward:	(0) absent; (1) present
2	Antennule, thick and flat:	(0) absent; (1) present
3	Antenna, seta on second exopodite segment:	(0) absent; (1) present
4	Antenna, seta on third exopodite segment:	(0) absent; (1) present
5	Number of trunk limbs:	(0) 6; (1) 5
6	Trunk limb I, ejector hooks:	(0) 2; (1) 1; (2) none
7	Trunk limb I, plumose setae on the first endite:	(0) 4; (1) 3; (2) 2
8	Trunk limb I, fork-like seta:	(0) absent; (1) present
9	Trunk limb I, fork-like seta on endite 1:	(0) absent; (1) present
10	Trunk limb I, fork-like seta on endite 2:	(0) absent; (1) present
11	Trunk limb I, setae on endite 3 sclerotized:	(0) absent; (1) present
12	Trunk limb I, scrapers on endite 3:	(0) absent; (1) present
13	Trunk limb I, distalmost seta on endite 3 apart from the others:	(0) absent; (1) present
14	Trunk limb I, setae on IDL:	(0) 3; (1) 4
15	Trunk limb I, setae on exopodite (ODL):	(0) 2; (1) 1
16	Trunk limb I, seta at exopodite (ODL) base:	(0) present; (1) absent
17	Trunk limb I, gnathobasic setae:	(0) 2 or more; (1) 1 or none
18	Trunk limb II, number of scrapers:	(0) 8; (1) 7; (2) 9
19	Trunk limb II, duplication of the row of scrapers *	(0) present; (1) absent
20	Trunk limb II, duplication of the row of scrapers	(0) plumose setae; (1) reduced and modified
21	Trunk limb II, setae on exopodite	(0) 2-3; (1) 1; (2) none
22	Trunk limb II, gnathobasic filter comb	(0) 8 or more; (1) 6 or 7; (2) 4 or 5
23	Trunk limb III, setae on endite external lobe **	(0) filtratory; (1) not filtratory
24	Trunk limb III, distal seta modified as a thick spine:	(0) absent; (1) present
25	Trunk limb III, gnathobasic filter comb setae:	(0) 6 or 7; (1) 8 or more; (2) none
26	Trunk limb III, setae on exopodite:	(0) 8 or more; (1) 5 or 6; (2) 4 or 3
27	Trunk limb IV, pre-epipodite:	(0) present; (1) absent
28	Trunk limb IV, setae of the internal series:	(0) present; (1) absent
29	Trunk limb IV, setae on gnathobasic filter comb:	(0) 8 or more; (1) 6 or 5; (2) 2 or less
30	Trunk limb IV, setae on exopodite:	(0) 8 or more; (1) 4 to 6; (2) 2 or 3
31	Trunk limb V, setae on exopodite:	(0) 6 or 7; (2) 1 or 2
32	Postabdomen, marginal denticles in transversal rows:	(0) absent; (1) present
33	Postabdomen bilaterally compressed, with a plate-like dorsal expansion:	(0) absent; (1) present
34	Postabdomen, postanal expansion:	(0) absent; (1) present
35	Terminal claw	(0) long and slender; (1) short and robust
36	Gut coiling:	(0) not coiled; (1) coiled

* The duplication is considered present even if only sensillum occurs; ** According Fryer (1976 - Tab. I)

the family, but the other apomorphic characters (4, 22, 29, and 30) have their states changed in more advanced clades.

Within the Macrothricidae, *Grimaldina* Richard,1892 is the most basal genus and the sister group to a clade compounded by the remaining genera (Clade A in figure 1), which is supported by characters 17 (TL I with one seta on gnathobase or none) and 21 (TL II with 1 seta on exopodite). The reduction of the number of the TL I gnathobasic setae in more advanced clades also occurs in the Eurycercoidea (Eurycercidae have 3, while the Chydoridae have 0-2 setae). The present tree topology (Fig. 1), showing the non-Macrothricinae genera as paraphyletic, is in agreement with the supposition of Dumont & Silva-Briano (1998)

Table III. Data matrix, with 12 ingroup (Macrothricidae species) and 3 outgroup taxa (*). (–) Indicates where the character is inapplicable.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Acantholeberis curvirostris *	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neothrix armata *	0	0	0	0	1	2	0	0	0	0	0	0	0	1	1	1	1	2	1	1	2	2	1	0	2	2	1	1	2	2	1	0	0	0	–	0
Ophryoxus gracilis *	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Bunops tuberculata	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	1	0	0	1	1	2	0	0	0	1	1	0	1	1	1	1	0	0	0	0
Drepanothrix dentata	0	0	0	0	1	0	0	1	1	1	0	0	0	0	1	1	1	0	0	1	0	1	1	1	2	1	1	0	2	2	1	1	0	0	0	0
Grimaldina brazzai	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	2	1	0	0	0	2	1	0	1	1	1	0	1	0	0	0
Guernella raphaelis	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	1	1	1	1	2	1	1	0	0	0	1	0
Lathonura rectirostris	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	1	1	1	2	2	1	1	2	2	1	0	0	0	1	0
Macrothrix elegans	0	0	0	1	1	0	2	1	1	1	1	0	1	0	0	1	1	0	1	–	1	2	1	1	2	2	1	0	2	2	1	1	0	0	1	0
Macrothrix laticornis	0	0	0	1	1	0	2	1	1	1	1	0	1	0	0	1	1	0	0	1	1	2	1	1	2	2	1	0	2	2	1	1	0	0	1	0
Macrothrix paulensis	0	0	0	1	1	1	2	1	1	1	1	0	1	0	0	1	1	0	0	1	1	2	1	1	2	2	1	0	2	2	1	1	0	0	1	0
Pseudomoina lemnae	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	1	–	0	1	0	0	1	1	1	1	1	1	1	0	0	1	0	0
Streblocerus pygmaeus	1	0	0	1	1	0	1	1	0	1	1	1	0	0	1	1	1	0	1	–	1	2	1	1	2	2	1	1	2	2	1	1	0	0	1	1
Streblocerus serricaudatus	1	0	0	1	1	0	1	1	1	1	1	1	0	0	1	1	1	0	0	1	1	2	1	1	0	2	1	0	1	1	1	1	0	0	1	1
Wlassicsia pannonica	0	0	0	1	1	0	1	1	1	1	0	0	0	0	0	1	1	0	0	1	1	2	1	1	0	1	1	0	1	1	1	1	0	0	1	0

and Dumont & Negrea (2002), who did not consider the non-Macrothricinae genera as a formal subfamily.

Two main clades could be recognized within Clade A (Fig. 1): the Macrothricinae and the Clade D (consists of the non-macrothricinae genera but *Grimaldina*). The Subfamily Macrothricinae (*sensu* Dumont & Silva-Briano, 1998) is supported by four synapomorphies: the presence of fork-like setae on TL I (Fig. 3), their occurrence on endite 1 (lost in *Streblocerus pygmaeus*, but not in *Streblocerus serricaudatus*), TL II with 5 or 4 gnathobasic filter comb setae, and the arrangement of the postabdominal marginal denticles in transversal rows (characters 8, 9, 22, and 32).

Within the Macrothricinae, *Bunops* Birge,1893 appears as the most basal genus (Fig. 1). Its sister group (*Wlassicsia* (*Drepanothrix* (*Macrothrix* + *Streblocerus*))), named as Clade B, is supported by three characters (10, 23, and 24). Of these, the presence of a fork-like seta on endite 2 of TL I have no parallel in other clades.

Macrothrix and *Streblocerus* are sister groups. The closest relationship between *Macrothrix* and *Streblocerus*, which was also found by Olesen (1998, 2000), is supported here by the sclerotized setae on endite 3-TL I and TL III with 3 or 4 setae on exopodite non filtratory setae on endite. Despite the differences observed among species, *Streblocerus* is well defined by the antennules curved outward, presence of scrapers on endite 3-TL I, and gut coiled (characters 1, 12 and 36). The monophyly of the genus *Macrothrix* is supported by the position of the distalmost seta endite 3-TL I, which is located apart from the others (character 13, Fig. 3). The present result suggests the maintenance of the synonymy of *Macrothrix* with *Iheringula* and *Echinisca*, but an analysis of the group including more terminal taxa is necessary to clarify this question.

The clade D (*Pseudomoina* (*Guernella* (*Lathonura* + *Neothrix*) is supported by presence of a seta on the second segment of antennal exopodite, TL III with 8 or more gnathobasic filter comb setae, and TL IV without internal series of setae (characters 3, 25, and 28). The close relationship between *Guernella* and *Pseudomoina* Sars 1912 was previously suggested by Fryer (1974), but here *Guernella* appears closer to (*Lathonura* + *Neothrix*).

According to the present analysis, *Neothrix* is a very derived genus of Macrothricidae, and its phylogenetic position (Fig. 1) conflicts with the proposition that it represents a separate family (Dumont & Silva-Briano 1998).

The present study has some limitations, beginning with the fact that information for many genera were collected from literature sources, that made the comparison difficult and limited the inclusion of more characters in data matrix. In addition, the characters used were limited by the optic microscopy resolution, which prevented the exploitation of the sensilar and glandular structures of the trunk limbs, as proposed by Dumont & Silva-Briano (1997).

Despite these limitations, the present analysis represents an advance for the comprehension of the relationships within the Macrothricidae. Moreover, not supporting the Neothricidae and suggesting the paraphyly of the non-Macrothricinae genera, this paper argues for the revision of the current classification (cf. Dumont & Negrea 2002).

Table IV. Apomorphy list for the family Macrothricidae. The list shows the unambiguous character support for each clade, excluding the autapomorphy at species level.

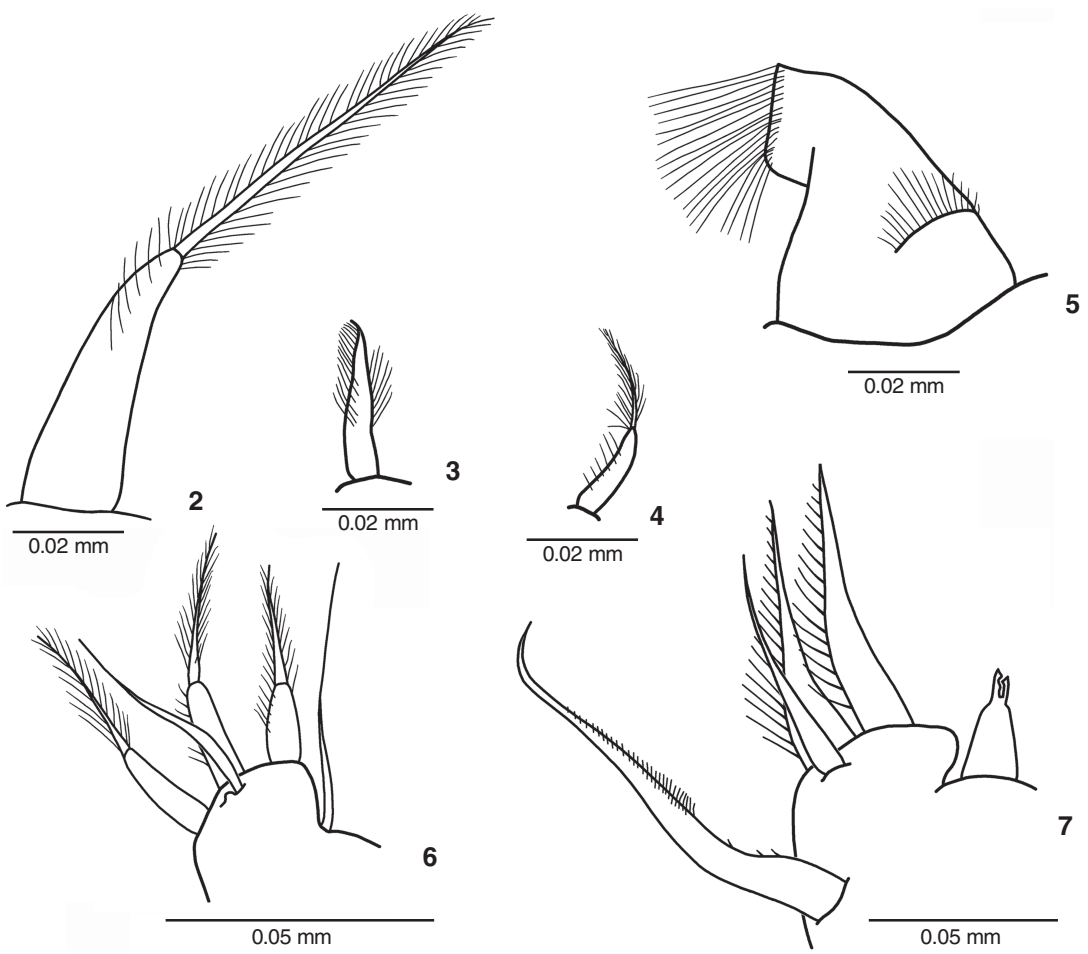
Clade	Character	
Macrothricidae	4 (0 → 1)*	Antenna, seta on third exopodite segment present
	5 (0 → 1)	Five pairs of trunk limbs
	16 (0 → 1)	TL I without seta at exopodite (ODL) base
	20 (0 → 1)	TL II with duplication setae reduced and modified
	22 (0 → 1)*	TL II with 6 or 7 gnathobasic FC setae
	27 (0 → 1)	TL IV without pre-epipodite
	29 (0 → 1)*	TL IV with 5 or 6 gnathobasic FC setae
	30 (0 → 1)*	TL IV with 4 to 6 setae on exopodite
	31 (0 → 1)	TL V with 1 or 2 setae on exopodite
Grimaldina	33 (0 → 1)	Postabdomen with a plate-like dorsal expansion
Clade A	17 (0 → 1)	TL I with 1 FC seta or none
	21 (2 → 1)	TL II with 1 seta on exopodite
Macrothricinae	8 (0 → 1)	TL I with fork-like setae
	9 (0 → 1)*	TL I with fork-like seta on endite 1
	22 (1 → 2)#	TL II with 4 or 5 gnathobasic FC setae
	32 (0 → 1)	Postabdomen, transversal rows of marginal denticles
Bunops	4 (1 → 0) #	Antenna, seta on third exopodite segment absent
Clade B	10 (0 → 1)	TL I with fork-like seta on endite 2
	23 (0 → 1) #	TL III with non filtratory setae on endite external lobe
	24 (0 → 1) #	TL III with distal seta modified as a thick spine
Drepanothrix Sars 1862	4 (1→ 0) #	Antenna, seta on third exopodite segment absent
	21 (1 → 0) #	TL II with 2 or 3 seta on exopodite
	22 (2 → 1)	TL II with 6 or 7 gnathobasic FC setae
Clade C	25 (0 → 2)	TL III without gnathobasic FC setae
	29 (1 → 2) #	TL IV with 2 or less gnathobasic FC setae
	30 (1 → 2)	TL IV with 2 to 3 setae on exopodite
Macrothrix + Streblocerus	11 (0 → 1)	Trunk limb I with sclerotized setae on endite 3
	26 (1 → 2) #	TL III with 3 or 4 setae on exopodite
Macrothrix	13 (0 → 1)	TL I with distalmost seta on endite 3 apart from the others
Streblocerus	1 (0 → 1)	Antennules curved outward
	12 (0 → 1)	TL I with scrapers on endite 3
	36 (0 → 1)	Gut coiled
Clade D	3 (0 → 1)	Antenna with seta on second exopodite segment
	25 (1 → 0)*	TL III with 8 or more gnathobasic FC setae
	28 (0 → 1) #	TL IV without internal series of setae
Pseudomoina	19 (0 → 1) #	TL II without duplication of the row of scrapers
	21 (1 → 0) #	TL II with 2 or 3 seta on exopodite
	34 (0 → 1)	Postabdomen with a postanal expansion
Clade E	23 (0 → 1) #	TL III with non filtratory setae on endite external lobe
	29 (1 → 2) #	TL IV with 2 or less gnathobasic FC setae
	35 (0 → 1) #	Terminal claw short and robust
Guernella	2 (0 → 1)	Antennules thick and flat
	18 (0 → 1)	TL II with 7 scrapers

Continues

Table IV. Continued.

Clade	Character	
Lathonura + *Neothrix*	25 (1 → 2)	TL III without gnathobasic FC setae
	26 (1 → 2) #	TL III with 3 or 4 setae on exopodite
	30 (1 → 2)	TL IV with 2 or 3 setae on exopodite
Lathonura Lilljeborg, 1853	15 (1 → 0)	TL I with 2 setae on exopodite
	24 (0 → 1)#	TL III with distal seta modified as a thick spine
Neothrix	3 (1 → 0)	Antenna, seta on second exopodite segment absent
	4 (1 → 0)#	Antenna, seta on third exopodite segment absent
	6 (0 → 2)	TL I without ejector hooks
	18 (0 → 2)	TL II with 9 scrapers
	19 (0 → 1) #	TL II without duplication of the row of scrapers
	21 (1 → 2)	TL II without seta on exopodite
	22 (1 → 2)	TL II with 4 or 5 gnathobasic FC setae

(*) character state changed in more advanced clade, (#) parallel in one or more taxa, (TL) trunk limb, (FC) gnathobasic filter comb.



Figures 2-7. (2-5) Duplication of the row of scrapers on trunk limb II (character 21): (2) plumose setae (plesiomorphic state); (3-5) reduced and modified setae: (4) *Grimaldina brazzai*; (5) *Macrothrix paulensis*; (6-7) endite 3 of the trunk limb I and the position of the distal seta (character 16): (6) *Grimaldina brazzai*, representing the distal seta close to the others (plesiomorphic state); (7) *Macrothrix paulensis*, showing the distal seta apart from the others (apomorphic state). (ds) Distal seta, (e2) endite 2, (e3) endite 3, (fs) fork-like seta.

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