

# Towards a phylogeny of *Euthelepus* (Polychaeta: Terebellidae): the absence of synapomorphies in the subfamily Thelepodinae and genera

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The phylogenetic relationships of *Euthelepus* (Polychaeta: Terebellidae: Thelepodinae) were studied by means of a parsimony analysis of 40 external characters. The ingroup terminals included four species of *Euthelepus*, and the outgroup included 14 species of eight Thelepodinae genera, three belonging to the subfamily Terebellinae, one species of Trichobranchinae, and one species of Polycirrinae. Only two most parsimonious cladograms were found. However, the analysis revealed a large number of homoplastic characters supporting the thelepodin branches. The monophyly of the genus *Euthelepus* was not supported, and the monophyly of the other thelepodin genera, as well as the entire subfamily, is questioned. The large number of homoplasies indicated by the analysis emphasizes the need to further evaluate these hypotheses by using additional characters. A re-classification based on phylogenetic results must be considered.

## INTRODUCTION

The first species of *Euthelepus* to be described was *E. setubalensis* McIntosh, 1885. A further nine species have been assigned to this genus: *E. chilensis* McIntosh, 1885; *E. tenuis* (Verrill, 1900); *E. kinsemboensis* Augener, 1918 (referred by Day (1967) as belonging to the genus *Amphitrite*); *E. malayensis* Caullery, 1944; *E. atlanticus* Hartman & Fauchald, 1971; *E. abranchiatus* Hartman & Fauchald, 1971; *E. pasqua* Fauchald, 1977; *E. serratus* Hutchings & Glasby (1986), and *E. marchinbar* Hutchings, 1997.

Hutchings & Glasby (1986) and Hutchings (1997) revised, redefined, and emended the genus, based on re-examination of type-material and on published descriptions. After such revision, only four species are currently referred to this genus: *Euthelepus setubalensis* McIntosh, 1885 (off Portugal); *E. kinsemboensis* Augener, 1918 (New Caledonia, Angola); *E. serratus* Hutchings & Glasby, 1986 (New South Wales and Queensland, Australia); and *E. marchinbar* Hutchings, 1997 (Northern Territory, Australia). Furthermore, the genus diagnosis, after Hutchings & Glasby (1986a) and Hutchings (1997), includes the presence of lateral lappets on the anterior segments; relatively few, long thick branchial filaments on segments 2 to 4; notochaetae present from segment 3 and continuing for a variable number of segments; and neurochaetae present from segment 5 and continuing to the pygidium.

Hutchings & Glasby (1986b: 116) stated that the presence of lateral lappets in *Euthelepus* is an exclusive feature within all the other thelepodins, which could be an apomorphic character, and therefore a valid generic character. The aim of the present work was to perform a cladistic analysis of *Euthelepus* based on external morphological characters, in order to test the hypothesis of Hutchings & Glasby (1986b). This paper also attempts to explore the relationships of species of *Euthelepus* and

assess the relationships among representatives of the Thelepodinae, testing their monophyly and outlining some implications of these phylogenetic relationships for the classification of the Thelepodinae.

## MATERIALS AND METHODS

The ingroup and outgroup were restricted to examined paratypes or holotypes of each species, or to material collected at or near the respective type localities (Table 1).

The ingroup taxa included all valid *Euthelepus* species, whereas the outgroup included 14 species of eight Thelepodinae genera (Table 1). Furthermore, three species belonging to the subfamily Terebellinae (*Lanice conchilega*, *Eupolymnia nesidensis* and *Loimia ingens*), one species of Trichobranchinae (*Trichobranchus lobiungens*), and one species of Polycirrinae (*Polycirrus broomensis*) were used to aid in assessing the relationships among the representatives of Thelepodinae.

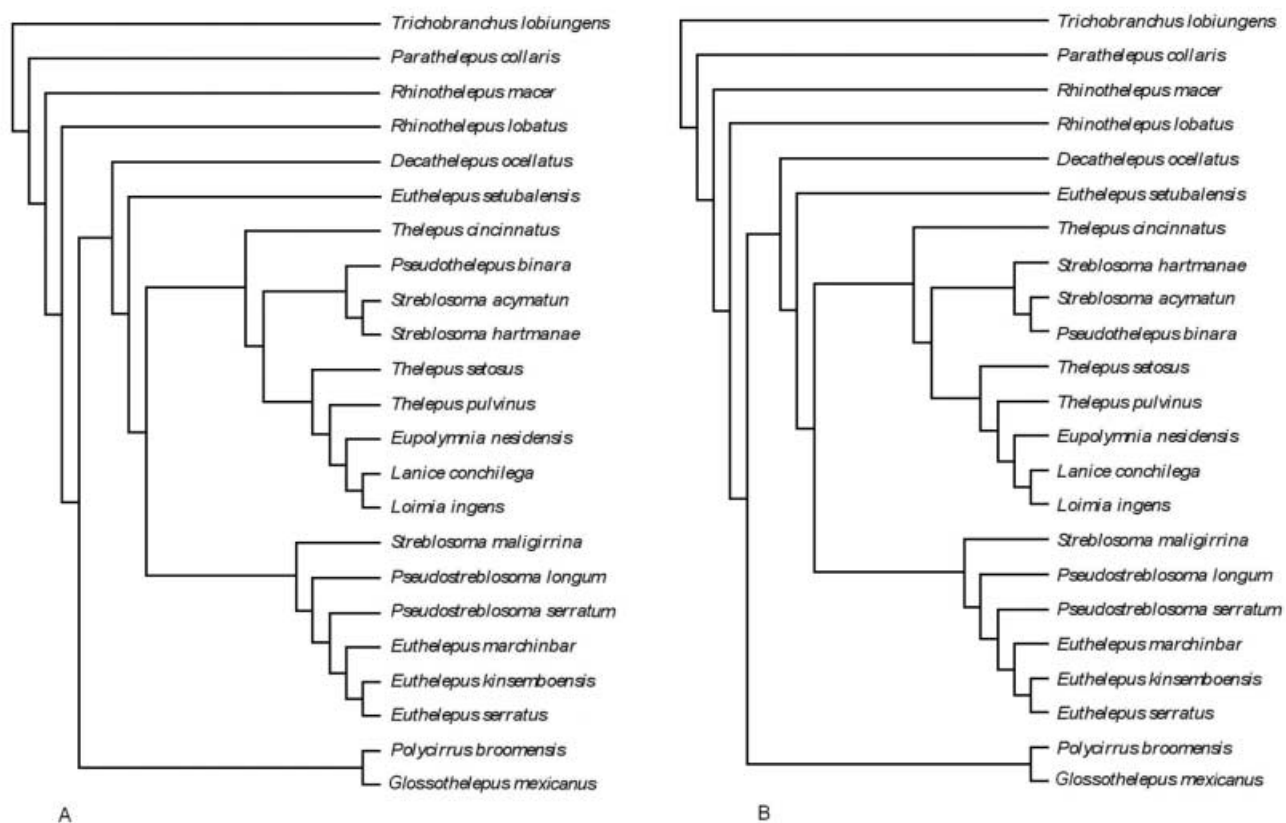
The program NEXUS v. 0.5.0 (Page, 2001) was used for data-matrix editing (Table 3). Parsimony analysis was carried out using the program PAUP v. 4.0b10 (Swofford, 2001). Heuristic tree searches were executed with PAUP default settings, using a random stepwise addition sequence with 100 replicates. Branches of maximum length zero were collapsed, MULPARS options were activated, and ACCTRAN was used for character state optimization. The contingent method was used to code the characters (Forey & Kitching, 2000), and they were treated as unweighted and unordered (Table 2). Unknown or inapplicable characters and missing data were coded as '?'.

### Characters

The numerals within parentheses correspond to characters summarized in Table 2. Illustrations for most

**Table 1.** Examined species, listed in alphabetical order. Abbreviations indicate where the specimens are deposited: AM— Australian Museum, Australia, Sydney; MCEM—Museu do Centro de Estudos do Mar, Brazil, Pontal do Sul; SMF—Senckenberg Museum of Frankfurt, Germany, Frankfurt; NMWZ—Natural Museum of Wales, Wales, Cardiff; BMNH—The Natural History Museum [formerly British Museum (Natural History)], England, London; ZMH—Zoologisches Institut und Zoologisches Museum der Universität, Hamburg, Germany.

Species	Subfamily	Museum
<i>Decathelepus ocellatus</i> Hutchings, 1977	Thelepodinae	AM W6782 (Holotype)
<i>Eupolymnia nesidensis</i> (Delle Chiaje, 1828)	Terebellinae	NMWZ.1989.104.1534
<i>Euthelepus marchinbar</i> Hutchings, 1997	Thelepodinae	AM W21889 (Paratype)
<i>Euthelepus setubalensis</i> McIntosh, 1885	Thelepodinae	BMNH ZK 1885.12.1.358
<i>Euthelepus kinsemboensis</i> Augener, 1918	Thelepodinae	ZMH V896 (Holotype)
<i>Euthelepus serratus</i> Hutchings & Glasby, 1986	Thelepodinae	AM W5443 (Paratype)
<i>Glossothelepus mexicanus</i> Hutchings & Glasby, 1986	Thelepodinae	AM W199659 (Paratype)
<i>Lanice conchilega</i> (Pallas, 1766)	Terebellinae	NMWZ.1991.075.2277
<i>Loimia ingens</i> (Grube, 1878)	Terebellinae	NMWZ.1986.079.0072
<i>Parathelepus collaris</i> (Southern, 1914)	Thelepodinae	NMWZ.1991.075.2215
<i>Polycirrus broomensis</i> Hartmann-Schröder, 1979	Polycirrinae	ZMH P-15532 (Holotype)
<i>Pseudostreblosoma longum</i> (Mohammed, 1973)	Thelepodinae	BMNH ZB 1971.55 (Holotype)
<i>Pseudostreblosoma serratum</i> Hutchings & Murray, 1984	Thelepodinae	AM W195617
<i>Pseudothelepus binara</i> Hutchings, 1997	Thelepodinae	AM W22506 (Paratype)
<i>Rhinothelepus lobatus</i> Hutchings, 1974	Thelepodinae	AM W12618
<i>Rhinothelepus macer</i> Hutchings, 1977	Thelepodinae	AM W8128, AM W17107
<i>Streblosoma acymatum</i> Hutchings & Rainer, 1979	Thelepodinae	AM W8530, AM W10327
<i>Streblosoma maligirrina</i> Hutchings, 1997	Thelepodinae	AM W21891, AM W21892
<i>Streblosoma hartmanae</i> Kritzler, 1971	Thelepodinae	NMWZ.1992.034.0005
<i>Thelepus pulvinus</i> Hutchings, 1986	Thelepodinae	NMWZ.1986.079
<i>Thelepus cinninatus</i> (Fabricius, 1780)	Thelepodinae	NMWZ.1991.075.2173
<i>Thelepus setosus</i> (Quatrefages, 1865)	Thelepodinae	SMF 4607
<i>Trichobranchus lobiungens</i> Hessle, 1917	Trichobranchinae	MCEM BPO 326



**Figure 1.** Two equally parsimonious cladograms with 109 steps, Consistency Index: 0.403 and Retention Index: 0.66 from the analysis of *Euthelepus* and other terebellid species.

**Table 2.** Summary of characters.

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1.	Buccal tentacles shape: (0) all filiforms; (1) filiforms and filiforms with an expanded tip.
2.	Buccal tentacles size: (0) bigger than half of the body; (1) the same length as prostomium and peristomium region.
3.	Eyespots: (0) absent; (1) present.
4.	Eyespots: (0) in irregular rows; (1) arranged in elongated patch.
5.	Upper lip: (0) elongate; (1) expanded; (2) compact.
6.	Shape of the first segment: (0) fused on the ventral side of the animal; (1) lateral lobes can be connected by a broad midventral band.
7.	Branchial trunk: (0) smooth; (1) with annulated surface.
8.	Branchiae position: (0) in pair; (1) a transversal row in dorsal part of the segment.
9.	Branchiae size: (0) all branchiae with the same size; (1) branchiae from the segment 2 longer than the following.
10.	Branchiae position on the segment: (0) median; (1) anterior; (2) posterior.
11.	Branchial filaments: (0) with a medial gap; (1) continuous line in the dorsum.
12.	Branchial filaments on segment 2: (0) displaced slightly laterally; (1) until the notopodia.
13.	Branchiae on segment 2: (0) branching; (1) simple filaments.
14.	Branchiae on segment 3: (0) branching; (1) simple filaments.
15.	Branchiae on segment 4: (0) branching; (1) simple filaments.
16.	Lateral lappets on segment 2: (0) absent; (1) lateral; (2) ventro-lateral; (3) ventral.
17.	Lateral lappets on segment 3: (0) absent; (1) lateral; (2) ventro-lateral; (3) ventral.
18.	Lateral lappets on segment 4: (0) absent; (1) lateral; (2) ventro-lateral.
19.	Ventral shield shape: (0) pads not distinct as ventral and lateral; (1) pads distinct as ventral and lateral.
20.	Nephridial papillae: (0) absent; (1) present.
21.	Nephridial papillae position: (0) posterior; (1) inferior.
22.	Nephridial papillae on segment 3: (0) absent; (1) present.
23.	Nephridial papillae on segment 4: (0) absent; (1) present.
24.	Nephridial papillae on segment 5: (0) absent; (1) present.
25.	Nephridial papillae on segment 6: (0) absent; (1) present.
26.	Nephridial papillae on segment 7: (0) absent; (1) present.
27.	Nephridial papillae on segment 8: (0) absent; (1) present.
28.	Notochaetae on segment 2: (0) absent; (1) present.
29.	Notochaetae on segment 3: (0) absent; (1) present.
30.	Notochaetae on segment 20: (0) absent; (1) present.
31.	Notochaetae on segment 21: (0) absent; (1) present.
32.	Wing position: (0) distal; (1) basal.
33.	Shape of the second row of notochaeta: (0) same shape of the first row; (1) distinct shape of the first row.
34.	Notochaeta serrate-tipped or tip-serrated: (0) absent; (1) present.
35.	Neurochaeta on segment 5: (0) absent; (1) present.
36.	Neurochaeta on segment 6: (0) absent; (1) present.
37.	Neurochaeta on segment 7: (0) absent; (1) present.
38.	Neurochaeta on segment 8: (0) absent; (1) present.
39.	Adult thoracic uncini shape: (0) avicular; (1) long narrow neck; (2) long handled.
40.	Prow in the uncini: (0) absent; (1) present.

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characters can be found in taxonomic revisions of the group (Day, 1967; Holthe, 1986; Hutchings & Glasby, 1986a,b; Hutchings & Glasby, 1987; Hutchings, 1997).

#### *Anterior end (1–6)*

The prostomial grooved buccal tentacle may have two different sizes: longer than half of the body (sometimes longer than the whole individual), or restricted to the anterior region (1) and two different shapes: entirely filiform, or with expanded tip (2). The prostomial eyespots may be absent or present in the posterior region (3), and arranged in irregular rows or as an elongated patch on each side of prostomium (4).

The peristomium upper lip (5) (as defined by Garraffoni & Lana, 2004) may be elongated, expanded, or compact (Hutchings, 2000). However, on the specimens used in the present investigation, an intermediate shape between the expanded and elongate states was observed, but this was more developed than the fine membrane

observed in the compact state. Because few species were analysed, this new peristomium upper-lip state was not coded.

The first segment, always achaetous and visible on the ventral part, may have two different shapes (6), with triangular or oval lobes fused on the ventral side of the animal, or the lateral lobes may be connected by a broad midventral band.

#### *Branchiae (7–15)*

The branchial shape in Thelepodinae (many simple filaments extending across the dorsum in one or more rows on segments 2, 3 or 4) is considered a diagnostic feature for the subfamily (Day, 1967; Hutchings & Glasby, 1987). Some features coded in the present paper are observed only in species of Thelepodinae, such as branchial filaments with medial gap or filaments with continuous line on the dorsum; branchial filaments on segment 2 may be displaced slightly laterally or to the notopodia.



**Table 4.** *The Thelepodinae diagnoses and references.*

Genera	Diagnosis	References
<i>Euthelepus</i>	Upper lip compact, branchiae on segments 2–4, thick filaments, notochaeta from segment 3, continuing for a variable number of segments, notochaeta smooth tipped and serrated, neurochaeta from segment 5, continuing to pygidium, lateral lobes present on segments 2–3 and sometimes 4.	Hutchings & Glasby (1986), Hutchings & Glasby (1987)
<i>Decathelepus</i>	Upper lip compact, two pairs of branchiae, notochaeta from segment 3, 15 pairs neurochaeta from segment 10.	Hutchings, 1977
<i>Glossothelepus</i>	Prostomium expanded with numerous tentacles, numerous simple branchial filaments, notochaeta from segment 3, at least 23 pairs, notochaeta smooth and winged, neurochaeta from segment 9.	Hutchings & Glasby (1986)
<i>Pseudothelepus</i>	Upper lip compact, two pairs of unbranched branchial filaments, notochaeta from segment 3, notochaeta from segment 3, notochaeta smooth and winged, neurochaeta from segment 6, lateral lobes on segment 6.	Hutchings (1997)
<i>Streblosoma</i>	Upper lip compact, branchiae in paired groups, usually on three segments (exceptionally 2), lateral lobes absent, ventral shield usually present, notochaeta from segment 2, notochaeta smooth, neurochaeta from segment 5.	Holthe (1986), Hutchings (1977), Hutchings & Glasby (1987), Kritzler (1971)
<i>Telothlepus</i>	Tentacular lobe large and elongate with numerous tentacles and expanded frilly margin, branchiae as numerous simple filaments on segments 2–3, lateral lobes absent, notochaeta from segment 3, notochaeta smooth-winged, no neurochaeta on the thorax, but present as avicular uncini on the abdomen.	Day (1967), Fauchald (1977)
<i>Thelepus</i>	Two or three pairs of unbranched branchial filaments in transverse rows of free filaments, lateral lobes absent, notochaeta from segment 3, continuing for a variable number of segments, notochaeta smooth, neurochaeta from segment 5, continuing to pygidium.	Holthe (1986), Hutchings (1977), Hutchings & Glasby (1987)
<i>Pseudostreblosoma</i>	Compact prostomium, three pairs of branchiae on segments 2, 3 and 4, each composed of numerous sessile filaments. Lateral lobes absent. Notochaeta narrow-winged capillaries with serrated tips from segment 2, uncini avicular from chaetiger 4 continuing to pygidium.	Hutchings & Murray (1984)

*Lateral lappets (16–18)*

Lateral lappets, when present, may be lateral (on the second and third segments, the lateral lappets are elongated narrow lobes between the noto- and neuropodia), ventro-lateral (on the second and third segments, the lateral lappets are elongated narrow lobes between the notopodia and the ventral shield) and ventral (the lappet is a ring-like collar encompassing the body).

Hutchings & Glasby (1986, 1987) pointed out that the presence of lateral lappets could be used as a feature to define the genera within Thelepodinae. However, this feature was also found in species of the outgroup.

*Ventral shield (19)*

The absence of a ventral shield in *Trichobranchus lobiungens* is an autapomorphy (Garraffoni & Lana, 2004), and was not included in the matrix. However, the ventral shield is present in all other species analysed, as ventral and lateral pads not distinct (all Thelepodinae species), or as distinct ventral and lateral pads.

*Nephridial papillae (20–27)*

Nephridial papillae, when present (20), may be found on the first 3–8 segments (21–27), and may be located posterior, or inferior to the notopodia (between the notopodia and neuropodia).

*Notochaetae and neurochaetae (28–40)*

In adult terebellids, the notochaetae first appear on segment 2 or 3 (28–29). In species that have notochaetae

after segment 21, they occur up to near the pygidium (as seen in the thelepodin species) (30, 31). Therefore, this state was coded as notochaetae on segment 21 absent/present, instead of notochaeta end '<20 segments' as coded by McHugh (1995). Notochaetae are arranged in two rows, and may or may not vary in shape. The chaetae in both rows may have the same shape, with capillaries winged; or may have one row of chaetae with serrated tips, and another with winged capillaries (33).

Garraffoni & Camargo (2006), applying morphometric analysis, defined three different neurochaeta shapes in Terebellidae: 'avicular', which is present in all Thelepodinae and Terebellinae species; 'long narrow neck', which occurs in Polycirrinae; and 'long-handled', which is present in Trichobranchinae (39). Another feature related to the uncini is the so-called prow. This structure, present between the subrostral process and the end of the manubrin (elongated base), is observed only in some thelepodin species (40).

In the present study, the first segment with uncini in *Euthelepus marchinbar* was coded differently from the original description. Hutchings (1997) also reported that the uncini began on segment 4; however, in the specimens analysed, and in the figure in the original description (Hutchings, 1997: 140, figure 2a), they began on segment 5.

## RESULTS AND DISCUSSION

The cladistic analysis of *Euthelepus* yielded two most-parsimonious cladograms (Figure 1A,B) with 109 steps, a consistency index of 0.403 and a retention index of 0.66. These two competing hypotheses of relationship differed

in the positions of *Pseudothelepus binara*, *Streblosoma acymatum*, and *S. hartmanae*. In Figure 1A, *Pseudothelepus binara* appeared as the sister group of *Streblosoma acymatum*, and *S. hartmanae* (*P. binara* (*S. acymatum*, *S. hartmanae*)). In Figure 1B, *S. hartmanae* was the sister group of *S. acymatum* and *Pseudothelepus binara* (*S. hartmanae* (*S. acymatum*, *P. binara*)).

As currently defined by previous papers, the genus *Euthelepus* was not supported as monophyletic in the present analysis. The absence of an apomorphic feature to define the monophyly of the taxon was a surprise, because, as pointed out in the introduction, the presence of laterals is accepted as an apomorphic character (Hutchings & Glasby, 1986). Genera that are reported as very similar in the taxonomic literature (Hutchings, 1977, 1997; Hutchings & Glasby, 1987), such as *Thelepus*, *Euthelepus*, *Pseudothelepus*, *Rinothelepus*, *Decathelepus*, *Parathelepus*, *Streblosoma*, and *Pseudostreblosoma*, did not appear as related groups. Moreover, none of the thelepodin genera used in the present analysis was considered a natural group nor was the entire subfamily (the outgroup species *Eupolymnia nesidensis*, *Lanice conchilega*, *Loimia ingens*, and *Polycirrus broomensis* were nested with some thelepodin species). Glasby et al. (2004), who studied the relationships among terebelliformia species, also found a similar result: that the subfamily Thelepodinae is not monophyletic and the final cladogram had a low bootstrap value, indicating weak support for the subfamily relationships.

Rousset et al. (2003) suggested that the branchial trunk with an annulated surface may be an apomorphy shared by all species of the family based on an analysis that used only species grouped in the subfamily Terebellinae. However, the present study showed that the branchial trunk with annulated surface is a homoplastic feature shared by *Thelepus pulvinus* and *Pseudostreblosoma longum* among the ingroup species, and by *Eupolymnia nesidensis* and *Loimia ingens* among the outgroup species.

According to Glasby et al. (2004), the elongated upper lip (=expanded tentacular lobes) may be an autapomorphy shared by *Rhinothelepus*, *Decathelepus*, *Telothelepus*, and *Glossothelepus*. However, the results of the present analysis did not support this statement (Figure 1A,B).

The sister-group relationships observed in the two most parsimonious cladograms were mostly supported by homoplasies and only a few synapomorphies were found. The first feature was branchiae in the median position on the segment for the clade comprising *Thelepus setosus*, *T. pulvinus*, *Eupolymnia nesidensis*, *Lanice conchilega*, and *Loimia ingens*; second was branchial filaments on segment 2 slightly displaced laterally, and finally nephridial papillae present on segments 6 and 7, in a clade including all the species analysed, except *Trichobranchus lobiungens*, *Parathelepus collaris*, and *Rinothelepus macer*, which were positioned in the basal part of the cladogram. However, all these character states were secondarily lost in less-inclusive clades.

The hypotheses proposed by Hutchings & Glasby (1986) considering several useful features to define the genera within the thelepodins, such as the first segment with noto- and neuropodia, and the tentacular lobe shape, were not supported in the present work. Hutchings & Glasby (1986) observed that these characters could be constant within the genera and recognized them as good

generic diagnostic features, at least for adult specimens. However, many of these characters were revealed as homoplastic, and, as such, do not support the monophyly of any genus in Thelepodinae.

This low support for the studied taxa can be tentatively explained by the deficiencies of most terebellid descriptions, which provide only a few informative characters that are mostly based on external morphology. Furthermore, most of the previous studies did not pay attention to the establishment of the homologies among the different structures. These two problems are easily observed when the diagnoses of the Thelepodinae genera are compared (Table 4).

It is possible to observe that these diagnoses are a group of plesiomorphies, and contain few evolutionary novelties. It is now evident that apomorphies for the thelepodin subfamily and genera are often not considered among the taxonomic characters, and thus they cannot be revealed in cladistic analyses that are based on data from taxonomic descriptions or on a small set of morphological characteristics (Vasily Radashevsky, personal communication).

The main problem detected by the present study is that most of the analysed genera had no support from a phylogenetic viewpoint. Unfortunately, this situation is common in Polychaeta (Rouse & Pleijel, 2003), because most of the diagnoses were not formulated from tree-dependent hypotheses, and represent apomorphies or identification marks for each taxon analysed (Pleijel, 1998). Thus, it is time to rethink our views about the systematics of Terebellidae, and avoid accumulating data only from species descriptions based on limited sets of characters and only on external morphology. The assessment of relationships requires a complete matrix containing substantiated hypotheses of homology (Bartolomaeus et al., 2005). It is necessary to include detailed analyses of the features, to establish a set of relevant characters of external and internal morphology, considering also ultrastructural, ontogenetic, and molecular analyses. A reassessment of the entire set of data on Terebellidae will aid in acquiring more information and in discovering true synapomorphies that will strongly support the phylogenetic relationships of terebellids.

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