

CLADISTIC ANALYSIS AND NEW CLASSIFICATION OF THE FAMILY
TUBULARIIDAE (HYDROZOA, ANTHOMEDUSAE)

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ABSTRACT

A phylogenetic analysis of the species of the family Tubulariidae was performed. The results led to the proposition of two subfamilies. Ectopleurinae subfam. n. is divided in two clades: E. ralphi⁺⁺ group (re-allocated in the new genus Pinauay), supported by the presence of sexually dimorphic blastostyles and medusa buds, and oral tentacles of the hydranth adnate to hypostome, and E. americana⁺ group (which retain the generic name Ectopleura), supported by the presence of a free medusa. The sister group of the subfamily Ectopleurinae is the subfamily Tubulariinae, formed by (Zyzyzus (Bouillonia (Ralpharia (Tubularia, Hybocodon)))).

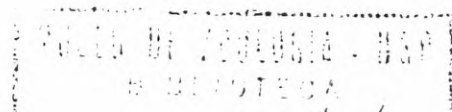
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INTRODUCTION

A phylogenetic hypothesis for the Tubulariidae was recently proposed by Petersen (1990), who considered the genus *Ectopleura* as a basal clade of

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the family, respectively followed by *Bouillonia*, *Zyzyzus*, *Ralpharia* + *Serehyba* and *Hybocodon* + *Tubularia*. Petersen's hypothesis is based on a phylogenetic analysis made "by hand", without addition of a character matrix, and the genera of the family are considered as the terminals of his analysis. The only genus with the species also included in the analysis was *Ectopleura*, for which Petersen found two major groups, mostly characterized by stolon growth pattern and cnidome.

There is much confusion between the genera *Tubularia* and *Ectopleura*, the first traditionally regarded as having sessile gonophores and the latter free medusae (e.g., Millard, 1975:31-32; Bouillon, 1985:112). This problem is not unique to these two genera, but it is related to major principles of hydroid classification. The traditional principles formalized by Rees (1957), who argued in favor of ecological characters defining the medusae species and considered this phase of the life cycle an important attribute of the species, were followed by Brinckmann-Voss (1970), Millard (1975) and Bouillon (1985), among others. For Petersen (1990), the statements of Rees are true only for species, but have no correlation (what we understand as non-applicable) at genus level.

On the contrary, Petersen (1979: 120; 1990: 160) redefined the tubulariid genera exclusively based on features of the hydroid stage discounting the importance of fixed gonophores vs. free medusae. Later, based in his phylogenetic framework, Petersen (1990) demonstrated that medusa reduction is known to occur in parallel events in thirteen capitate families, of which seven have both representatives with and without the medusa stage. Thus, following his conclusions, a classification based on medusa reduction would create para- or polyphyletic groups (Petersen, 1990).

The recent discovery of *Ectopleura obypa* Migotto & Marques (1999) led us to re-evaluate the phylogeny proposed by Petersen (1990), in order to find the best position for that species. We re-studied the characters considered by Petersen, re-coding some of them and discarding others due to uncertainty of distribution and homology establishment, while including some new characters. Moreover, unlike Petersen who adopted mostly genera as the terminals of his analysis (with the exception of the genus *Ectopleura*), we chose the specific level for ours (except for the genus *Tubularia*, considered a unique terminal). Hence, the general goals of this paper were to add and re-organize information of previous phylogenetic hypotheses, improving both the understanding over the characters and the level of the terminals included.

PHYLOGENETIC METHODS

The cladistic analysis of the species of Tubulariidae made herein was based on the principles established by Hennig (1950, 1966) and complemented by several authors (e.g. Eldredge & Cracraft, 1980; Wiley, 1981; Amorim, 1997; Ferrarezzi & Marques, 1997; Kitching *et al.*, 1998).

As terminals, we adopted the species of the genera *Bouillonia*, *Hybocodon*, *Ralpharia*, *Serehyba*, *Zyzyzus*, and the genus *Tubularia* as a unique terminal (*i.e.*, adopted at the genus level). The only genus of Tubulariidae (*sensu* Bouillon, 1985) ignored in the analysis was *Rhabdoon* (Keferstein & Ehlers 1861; = *Rhysomedusa* Vannucci & Soares-Moreira 1966) whose hydranth is unknown, and which would have caused an artifact of non-resolution in our results if included.

Some species of the genus *Ectopleura* had to be excluded for different reasons. Petersen (1990) re-identified *E. pacifica* Thornely, 1900, described by Mammen (1963: 59-61, figs. 27-29) and *E. dumortierii* (van Beneden, 1844), described by Hargitt (1924: 472-473, pl.1, figs. 3-4) as a new species, *E. indica* Petersen, 1990. Nothing in the original description of the species suggests that Petersen examined living or preserved material; on the contrary, actually he assigned as type specimen the figure by Mammen (1963: 60, fig. 27). This is especially important for the phylogenetic inference because the descriptions of Mammen and Hargitt did not mention nematocyst types.

This study was based mostly on literature data, and by no means is presumed to be a revision. On the contrary, it is important the identification of weakly defined characters and muddled areas of the cladogram that deserve further and thorough investigation. Descriptions of species that do not include several of the characters plotted in the matrix, like the species only known from the medusa stage and those known only from their original, brief descriptions [*e.g.* *E. exxonina* (Watson, 1978) and *E. grandis* Fraser, 1944] were not included to avoid a proliferation of missing data in the matrix and consequently a decreased performance in the parsimony analysis, where phylogenetic patterns could be hidden.

The characters were coded as binary and multi-state. The latter was considered ordered when information about contiguity of similarity of states was available and unordered otherwise. Non-available information was coded as a question mark (“?”) and polymorphic data or non-comparable structures were coded in the matrix as a hyphen (“-”).

Cladistic analyses were carried out using the heuristic algorithm “mh*bb*” of the software Hennig86 v.1.5 (Farris, 1988) and its interface software Tree Gardener v.2.2 (Ramos, 1997). Analysis using exact algorithms were not possible due to computer limitations (PC compatible Pentium II, 300 MHz, 256

MB RAM). Strict consensus trees (Sokal & Rohlf, 1981) were adopted when more than one cladogram was produced in the analysis.

Our analysis is composed only by ingroup taxa. The product of it is an unrooted most parsimonious tree, useful for taxonomic purposes only after rooting procedure. The rooting methodology proposed by Nixon & Carpenter (1993) requires multiple outgroup taxa. In this case, outgroup taxa were difficult to establish. Petersen's (1990: 116, 123-124, fig. 3) classification has a suborder Tubulariida including the following groups (in parenthetical notation): ((Corymorphoidea, Tubularioidea) Halocordyloidea, Corynoidea). In the Tubularioidea, the successive sister-groups of Tubulariidae are Paracorynidae, Margelopsidae and Candelabridae. Paracorynidae is a monogeneric family with polymorphic hydroids (cf. Bouillon, 1974); Margelopsidae has pelagic differentiated solitary polyps (Bouillon, 1985), and Candelabridae is characterized by solitary hydroids with peculiar morphology. Therefore, the putative sister-taxa have very derived morphologies, making it difficult to establish comparisons among these families and the tubulariids on the basis of the morphological characters adopted. We considered the Corymorphoidea, the next nearest outgroup of the phylogeny, following Petersen's topology, a distant taxon to be useful for comparisons, although there are some dispute on the relationships between the tubulariid genus *Zyzyzus* and the family Corymorphidae.

Another method to root the network is to adopt ontogenetic information to restrict the possible rooting points (de Pinna, 1994), and some of the characters used in the analysis are suitable for this purpose. Character 4 has an ontogenetic ordering that restricts the rooting point within taxa of *Ectopleura* or between *Ectopleura* and other tubulariids. Character 17 indicates the root point everywhere, except in the terminal *Ectopleura multicirrata* Petersen, 1996. In order to have a working hypothesis, we rooted the network at the same site adopted by Petersen (1990), i.e. in the internal branch between *Ectopleura* and other tubulariids. This is the only evidence we have for rooting before broader relationships (e.g., family level relationships) have been established. This rooting point agrees with the ontogenetic data, and it is also supported by most of the classical taxonomic knowledge on the group (Bouillon, 1985; Petersen, 1990), keeping *Ectopleura* as a monophyletic taxon. However, it is important to note that this approach did not test the monophyly of the ingroup, because no other taxon besides the tubulariids was included in the matrix (Nixon & Carpenter, 1993; Gimenez *et al.*, 1996). A broader analysis including other tubularioids and corymorphoids will be important in the future to prove the monophyly of the family.

Wherever necessary in text we adopted the group⁺ convention (Amorim,

1982), in which a clade is represented by the addition of a + signal to its basal terminal.

CHARACTER LIST AND DISCUSSION

The following characters used by Petersen (1990) were not considered in the analyses due to the impossibility in determining their discrete states, therefore compromising a quantitative analysis: a) type of attachment to the substrate, b) length of stolon and c) color of perisarc. Other characters came from different literature sources and general direct observation. The characters adopted are listed below, summarized in the Table I and illustrated in Figures 1 and 2.

Character 1. Microbasic euryteles (0 - absent; 1 - present)

Character 2. Anisorhizas (0 - present; 1 - absent)

Petersen (1990: 159-160, fig. 19) made a mistake in his considerations about the distribution of this character; the occurrences of anisorhizas and microbasic euryteles were reversed (see characters 2 and 6 of his figure 19B, and his errata). There is a possible link between the presence of microbasic euryteles and anisorhizas, and if so, both would be states of the same character. Petersen (1990) does not assume this hypothesis, and we follow the same codification, considering both as different characters. Our position is corroborated by the presence of both nematocyst types in *Ectopleura crocea* (L. Agassiz, 1862), *Hybocodon prolifer* L. Agassiz, 1862 (Schuchert, 1996: 109, 113-114) and some *Tubularia* (*Tubularia indivisa* Linnaeus, 1758 and *Tubularia ceratogyne* Pérez, 1920; Bouillon, 1974, 1985); therefore the unique character hypothesis failed in the conjunction test (Patterson, 1982; de Pinna, 1991), in which two “states” appearing in the same individual might be considered two different characters. The genus *Zyzyzus* is polymorphic for the character: *Zyzyzus calderi* Petersen, 1990 has microbasic euryteles (Calder, 1988), and *Zyzyzus spongicolus* (von Lendenfeld, 1884) has anisorhizas (Watson, 1978; Bouillon, 1985). The species *Zyzyzus warreni* Calder, 1988 has a unique cnidome, bearing microbasic mastigophores (Migotto & da Silveira, 1987). There is no information on the cnidome of *Zyzyzus floridanus* Petersen, 1990 and *Zyzyzus robustus* Petersen, 1990. In the two species of the genus *Ralpharia* in which the cnidome is known (*Ralpharia magnifica* Watson, 1980 and *Ralpharia coccinea* Watson, 1984), only the first has heterotrichous anisorhizas; microbasic euryteles are not present in both (Watson, 1980: 55, 1984: 10; Bouillon, 1985). *Serehyba sanctisebastiani* da Silveira & Migotto, 1984 also has heterotrichous anisorhizas (da Silveira & Migotto, 1984). The

presence of anisorhizas in *H. prolifer* “is somewhat uncertain as the thread tapered only very gently, thus resembling isorhizas” (Schuchert, 1996: 113-114), a nematocyst type common to other *Hybocodon*. Bouillon (1974, 1985), however, emphasized the presence of microbasic euryteles in the species. The microbasic mastigophores reported in *Hybocodon unicus* (Browne, 1902) (Millard, 1975) was considered by Bouillon (1985: 106) a possible misidentification of an eurytele. Microbasic euryteles were reported in the hydranths of *H. prolifer* (see Schuchert, 1996: 114) and *H. cryptus* Watson, 1984 (see Watson, 1984: 9). Although the cnidome of *Hybocodon* spp. is not well known, the presence of microbasic euryteles seems to be certain and widespread in the genus. *Tubularia* has both types (see Bouillon, 1974, 1985).

Character 3. Medusa release (0 - sessile gonophore; 1 - free medusa)

According to Petersen (1990: 170), the lack of tentacle rudiments in the medusa buds of *Ectopleura grandis* Fraser, 1944, a species known only from the original description, indicates that they “develop into eumedusoid gonophores or non-tentacled aborted medusae”. The medusa of *Ectopleura americana* Petersen, 1990 was observed only attached to the blastostyle (Petersen, 1990: 168). We followed Petersen (1990: 223, fig. 48) and considered both as producing medusa.

Character 4. Ridges or canals in the endoderm of hydrocaulus (0 - up to four v-shaped ridges; 1 - more than eight ridges; 2 - numerous canals with the same diameter; 3 - numerous canals, one wider than the others).

The V-shaped ridges were considered a synapomorphy of *Ectopleura* by Petersen (1990: 160, fig. 19B; character 1). We hypothesized that the V-shaped ridges are the first step of the transformation to the endodermic canals present in all other tubulariids. Following state 0, there would be an increasing number of ridges (state 1, present in *Hybocodon* spp.), the formation of true canals [state 2, in *Zyzyzus* spp. and *Bouillonion cornucopia* (Bonnievie, 1898)], and differentiation of one canal, which becomes wider than the others (state 3, in *Ralpharia*, *Serehyba*, and *Tubularia*) (Petersen, 1990; Watson, 1980; Schuchert, 1996). *Hybocodon prolifer* and *H. unicus* have 8-14 distal endodermal ridges merging into four at the base of hydrocaulus (Petersen, 1990), which suggests that the number of ridges increases during the growth of the hydrocaulus. In *Ralpharia neira* Petersen, 1990, *Ralpharia gorgoniae* Petersen, 1990 and *S. sanctisebastiani*, the endoderm of the distal part of the hydrocaulus forms longitudinal ridges around a central cavity, fusing proximally to form true canals around a center filled with parenchyma (da Silveira & Migotto, 1984; Petersen, 1990), another indication of the transformation of ridges in canals. This important ontogenetical information allowed us to compose the ordination of the character,

assumed by both contiguity of the states and ontogeny. Thus, the character was considered ordered.

Character 5. Region of secretion of neck perisarc (0 - by cells located in a groove around the most basal part of the hydranth. 1 - by cells located in a groove forming the lower edge of an expanded, collar-like upper portion of the neck)

Considered aprioristically by Petersen (1990: 160, fig. 19A character 2, fig. 19B character 1) as a synapomorphy of *Ectopleura*, but should be analyzed together with his character 3 (Petersen, 1990: 160, figure 19A) because, in our view, both are states of the same character (region of perisarc secretion). Specifically for *B. cornucopia* the perisarc is secreted from a groove located in the hydranth immediately under the aboral tentacles, resulting in a very wide perisarc film around the neck region (Petersen, 1990: 156), which could be considered a further step in the evolution of the character, not included herein.

Character 6. Basal disc and stolons (0 - basal disc; 1 - hydrorhiza; 2 - ‘tubers’)

Petersen (1990: 156-158) proposed a different division and transformation series for the states of this character. For him, the ancestral condition would be a “simple circular to nearly circular basal disc” that evolved in two different independent lineages: a) basal disc transformed into the characteristic “tubers” of *Zyzyzus* spp., and b) basal disc successively transformed into the following sequence: “single stolon” [viz. *Ectopleura dumortierii* (van Beneden, 1844)] “simple stolon budding polyps” (viz. *Ectopleura wrighti* Petersen, 1979) “stolon tripod-branching type” (his inclusions about substrate use are considered a different character by us). Although this transformation series is reasonable, we considered a simplified series without intermediary steps because it is difficult to identify these patterns and most descriptions are dubious or lacking in relation to stolon type. The distinct forms of the characteristic rootlets and tubers present in the hydrorhiza of *Zyzyzus* spp. are considered a separate character. Aprioristic considerations for the evolution of this character are difficult to adopt because the contiguity of the states and the ontogenetical data do not suggest a clear ordered series. Hence, the character is considered unordered in the present analysis.

Character 7. Substrate (0 - visible stolons; 1 - stolon buried in gorgonian coenenchyma; 2 - stolon buried in sponges)

The means of attachment to the substrate differs among the species of tubulariids, as previously remarked by Petersen (1990: 157). The stolons are basically divided into two types: those visible (*i.e.*, not buried stolons) and those that are buried in animal structures. Among the species bearing buried stolons, *Ralpharia* and *Serehyba* are often associated with gorgonians (*Serehyba* also

occurs on rocks; pers. obs.), and *Hybocodon* with sponges. *Zyzyzus* is usually associated with sponges, colonial ascidians and ectoprocts, but this association is not obligatory (*Z. warreni* pers. obs; see also Calder, 1988: 50). *Zyzyzus robustus* differs from other species of the genus in having “irregularly shaped hydrorhizal processes forming slender rootlets and swollen tubers, covered by heavy perisarc, which attaches hydroids to rocks, bryozoans, etc.” (Petersen, 1990: 183), thus also having visible stolons. The taxa *Serehyba* and *Z. warreni* are plotted as polymorphic in the matrix. Although *E. multicirrata* has been recorded on shell surfaces (Schuchert, 1996: 110), the small series analyzed by the author made us provisionally include the species in state 0. *Ectopleura japonica* (Hirohito, 1988) is the only species of the genus associated with sponges (see Hirohito, 1988: 20). Character considered unordered.

Character 8. Number of whorls of oral tentacles (0 - two or more; 1 - one)

The data of the matrix were extracted from Petersen’s (1990) diagnoses of tubulariids. The only polymorphic genus is *Zyzyzus*, in which some species have one, two or more closely whorls.

Character 9. Medusa shape (0 - symmetrical umbrella; 1 - asymmetrical umbrella)

Asymmetrical medusa shape is a character of *Hybocodon*. Petersen (1990: 160) pointed out in the description of the genus that the origin of sessile gonophores can be traced from a biradially symmetrical medusa, and he used this character to justify the sister-group relationship between the genus and *Tubularia*. However, the distribution of the character in *Tubularia* appears to be complex; the only described asymmetrical medusae are *T. indivisa* (female eumedusoid, without tentacles) and *Tubularia amoyensis* (Hargitt, 1927) (no sex referred). In some of the other species of *Tubularia* there is an asymmetrical pattern related to the presence of one more developed tentacle or crest, but this does not characterize an asymmetrical umbrella. Therefore, we coded the genus *Tubularia* as polymorphic in the matrix.

Character 10. Umbrellar nematocysts track (0 - absent; 1 - eight meridional; 2 - five meridional)

Ectopleura is diagnosed by the presence of eight meridional nematocyst tracks in the exumbrellar surface (Petersen, 1990: 159; Schuchert, 1996: 107). This is assumed as the primitive condition. The asymmetrical medusa of *Hybocodon* has a characteristic pattern of five of these tracks: one in each smaller radial canal (a reduction from the primitive type), and two along the longest radial canal (a normal type of distribution). However, this pattern is not universal in *Hybocodon*, since *H. unicus* and *Hybocodon cryptus* Watson, 1984 have

nematocysts scattered on the umbrella (Millard, 1975: 34; Petersen, 1990: 195). Species without a medusa stage are coded as non-comparable. Character considered ordered in the analysis, following the explanation above.

Character 11. Sexually dimorphic blastostyles and medusa buds (0 - absent; 1 - present)

Adopted by Petersen (1990: 160, fig 19 B) to distinguish some species of *Ectopleura*, and it is conserved in our analysis. Sexually dimorphic gonophores were described in *E. radiata* (Uchida, 1937) (Yamada, 1950: 3; remarkably, the male gonophore figure by Uchida, 1937: 158 resembles the female one figure by Yamada). As the gonophores of *E. americana* are known only as developing buds, when their morphology is not fully expressed, they were plotted in the matrix as “?”. Male gonophores of *E. multicirrata* were not observed (Schuchert, 1996: 110). Sexually dimorphic species are also present in all species of *Tubularia* (see Petersen, 1990).

Character 12. Asexual reproduction by budding in the tentacular tubercle (0 - absent; 1 - present)

Possible autapomorphy of *H. prolifer* (Petersen, 1990: 192).

Character 13. Form of the tubers in *Zyzyzus* spp. (0 - irregular shaped processes; 1 - three to four bulbs closely connected; 2 - finger like bulbs)

As stated above, there are several different forms of tubers (rooting processes in the sense of Calder, 1988) among the species of *Zyzyzus*: 1) irregular-shaped processes forming slender rootlets and swollen tubers covered by heavy perisarc (*Z. warreni* and *Z. robustus*); 2) processes in the form of 3-4 bulbs closely connected (*Z. floridanus*); 3) processes finger-like, linked to small club-shaped tubers (*Z. spongicolus* and *Z. calderi*). Character considered non-comparable for other tubulariids, and used as ordered in the matrix.

Character 14. Hydrocaulus divided into neck region with filmy perisarc and aboral region with heavier perisarc secreted from area below neck (0 - absent; 1 - present)

Character after Petersen (1990: 160), autapomorphic for the Tubulariidae.

Character 15. Number of tentacles or processes of the medusa or sessile gonophores (0 – four; 1 - two; 2 - one; 3 - zero)

We considered the tentacles of the free medusa related to the processes of the sessile gonophores in the tubulariids. On the margin of the umbrella of several species of *Ectopleura* there are crests rather than tentacles or processes, that we considered as another character. For *E. grandis*, the description of Fraser (1944, see Petersen, 1990: 170) suggests the presence of eumedusoid gonophores or

non-tentacled abortive medusae. *Ectopleura venusta* (Yamada, 1950) is polymorphic with 4-8 (rarely up to 11) tentacles in the female gonophore (Yamada, 1950: 3-4). In *Tubularia* spp. the character is polymorphic since the gonophores are either with (one or more) or without tentacles / processes (Petersen, 1990: 159). The species *H. cryptus* originally described by Watson (1984) has three tentacles arising from the same tentacular bulb; we considered it an autapomorphy of the species, listed in another character. Character unordered.

Character 16. Tentacles transformed into processes (0 – non transformed; 1 - transformed)

One group of species of *Ectopleura*, and the genus *Tubularia*, have processes in the gonophores instead of tentacles. Petersen (1990: 168) called the marginal processes of *E. radiata* medusae tentacles, but later redefined them as processes (Petersen, 1990: 171). Although this character is linked to character 15, they are not considered the same because one concerns the presence of processes and the other the number of processes.

Character 17. Distal tuft of up to 30 tentacle-like processes (0 - absent; 1 - present)

This is a unique character of *E. multicirrata*, possibly derived from the 4 tentacle-like processes condition. In young gonophores the processes are separated into 4 cluster that later increase in number (Schuchert, 1996: 110).

Character 18. Umbrellar crests (0 - processes; 1 - crests)

There are two different structures besides tentacles in the female gonophores: 1) processes (usually 3-8, exceptionally up to 30 in *E. multicirrata*, see Schuchert, 1996) and 2) crests (4 to 8 laterally compressed structures, see Migotto & da Silveira, 1987; Petersen, 1990: 174). As two tubularian species, *Tubularia regalis* Boeck, 1860 and *Tubularia acadia* Petersen, 1990, also have laterally compressed leaf-like crests on the female gonophores (Petersen, 1990), we considered the character polymorphic for the genus.

Character 19. Tentacular bulb (0 – without tentacles or with one tentacle; 1 - with three tentacles)

Three-tentacled marginal bulbs is a unique structure of *H. cryptus* (Petersen, 1990).

Character 20. Blind radial canals from gastric cavity to space between bases of aboral tentacles (0 - absent; 1 - present)

Character 5 of Petersen (1990: 160), present in *Ralpharia*, *Serehyba*, *Tubularia*, and *Hybocodon*.

Character 21. Basitrichous isorhiza (0 - present; 1 - absent)

Adopted after Petersen (1990).

Character 22. Edge of medusa or medusoid umbrella (0 - without raised collar around bell opening; 1 - with internal raised collar around bell opening)

Proposed as a synapomorphy of *Ralpharia* and *Serehyba* by Petersen (1990: 160).

Character 23. Blastostyle main stem (0 - branched; 1 - unbranched)

In the cladogram of Petersen (1990) the evolution of the blastostyle was divided in the following states: 1) main stem unbranched, with many small side branches; 2) main stem branched and with many side branches; 3) without a recognizable main stem, dichotomously branched. In order to simplify the characterization of the states in the species we adopted only two states. The blastostyles of *Ectopleura ralphi* (Bale, 1884) and *E. crocea* (considered closely species by Petersen 1990 and Schuchert 1996) have been described as unbranched (Petersen, 1990: 174-175), but we assumed the branched pattern, as described by Bale (1884, for *E. ralphi*) and Schuchert (1996, for *E. crocea*). *Ectopleura multicirrata* (Schuchert, 1996: 110) diverges from other *Ectopleura* because the “gonophores arise in clusters on unbranched, short blastostyles arising just above aboral tentacles, six or more blastostyles”. To include this species in the genus, Schuchert redefined the diagnosis of *Ectopleura* as “gonophores arise on blastostyles which are dichotomously branched or not”. In the species of *Ralpharia* the blastostyle is branched, like in *R. gorgoniae*, especially the apical end which is profusely branched, transformed into a nematophore (Petersen, 1990: 188). *Ralpharia coccinea* is coded as “?”, because no information is present in the original description.

Character 24. Endodermal canals in hydrocaulus (0 - not forming radiating slits; 1 - forming radiating slits)

Autapomorphy for *Bouillonia* (Petersen, 1990: 160).

Character 25. Hydranth form (0 - urn-shaped; 1 - barrel-shaped)

Autapomorphy for *Bouillonia* (Petersen, 1990: 160). Another possible autapomorphy for this species (not included) would be the cornucopia-like perisarc.

Character 26. Proportion between neck region and total length of the hydrocaulus (0 - neck region up to 1/4 of the total length of the hydrocaulus; 1 - neck region half of the total length of the hydrocaulus)

Autapomorphy for *Zyzyzus* (Petersen, 1990: 160). Although it is a morphometrical relation, there is a clear gap between both states.

Character 27. Stolon (0 - thin, straight; 1 - thickened, contorted)

Considered an autapomorphy for *Ralpharia* (Petersen, 1990: 160) and *Serehyba*.

Character 28. Distal branches of blastostyles with cnidophores (0 - absent; 1 - flatly bell-shaped, truncated; 2 - heart-shaped hollow sac, flatly oval in cross section; 3 - cauliflower shaped)

The nematophore was first pointed out as an autapomorphy for *Serehyba* by Petersen, (1990: 160, considering the species *R. sanctisebastiani*) who had already noticed a complex transformation series of the blastostyles into nematophores in *Ralpharia* spp.: “the cluster of nematophores present in the distal part of the blastostyle in some *Ralpharia* species seems to be transformed medusa buds as evidenced in *R. neira* (see below); the state in this transformation, seen in *R. gorgoniae*, seems to be intermediate between the condition in *R. neira* and the advanced condition in *R. sanctisebastiani*”. However, he did not adopt the character in his analysis. In *R. neira*, the dichotomic blastostyle has distal ramifications with flatly bell-shaped, truncated nematophores in four marginal knobs; in *R. gorgoniae* the branched distal part of the blastostyle carries long and slim clusters of nematophores on short stalks, forming a raceme, each nematophore is like a long triangular or heart-shaped hollow sac, flatly oval in cross-section; finally, the blastostyles of *S. sanctisebastiani* form a dense, cauliflower-like ball of circular, button shaped nematophores, but are similar in the shape of the proximal part to that of *R. gorgoniae*. The nematophores of the three species are armed with anisorhiza nematocysts. Character considered therefore ordered.

Character 29. Hydrocaulus of the main stem (0 - without supporting tubes; 1 - supporting tubes on the lower part)

Autapomorphy of *Tubularia* (Petersen, 1990: 160).

Character 30. Coloniality (0 - colonial; 1 - solitary)

Coloniality varies among and within tubulariid genera. General data were extracted from Petersen (1990) and Schuchert (1996). Although *R. magnifica* was considered polymorphic by Petersen (1990: 186), the original description state is colonial (Watson, 1980: 54), and it is plotted as such in the character matrix because Petersen apparently did not have access to the material.

Character 31. Sexual condition (0 - dioecious; 1 - monoecious)

Calder (1988) diagnosed the genus *Zyzyzus* as monoecious, a character that distinguishes the genus from other tubulariids. However, there is no such information for *Z. robustus* and *Z. floridanus*.

Character 32. Perisarc (0 - heavy and stiff; 1 - light and flexible)

This character defines a group inside *Zyzyzus*, because *Z. robustus* is the only species of the group with heavy perisarc (Petersen, 1990), a shared state with other tubulariids.

Character 33. Transversal section of aboral tentacles (0 - circular; 1 - flattened; 2 - four-sided)

The section of the aboral tentacle is quadratic in *R. neira* and in *E. crocea* (Petersen, 1990). In *H. prolifer* the tentacle cross section is oval (Schuchert, 1996: 114), herein coded as flattened. The missing data (“?”) in the data matrix refers to non-described conditions in the original descriptions and not observed subsequently.

Character 34. Transversal section of oral tentacles (0 - circular; 1 - flattened)

A possible autapomorphy for *R. gorgoniae* (Petersen, 1990).

Character 35. Perisarc around neck region and basal hydranth (0 - non-inflated; 1 - inflated)

Autapomorphy for *B. cornucopia* (Petersen, 1990).

Character 36. Oral tentacles (0 - not adnate to hypostome; 1 - adnate to hypostome)

Present in *H. prolifer* and *H. unicus* (Petersen, 1990), uncertain for *H. cryptus*. In *E. pacifica* the basal part of the oral tentacles is slightly adnate (Petersen, 1990: 165), as in *E. obypa*. The character is also present in some other species of *Ectopleura*, but we do not discount the possibility of a wider distribution, because it may be inconspicuous in some species.

Character 37. Aboral tentacles (0 - not adnate to the base of hydranth; 1 - adnate to the base of hydranth)

Present in *H. prolifer*, *H. unicus* and *Tubularia* spp. (Petersen, 1990), uncertain for *H. cryptus*.

Character 38. Perisarc annulations (0 – present; 1 - absent)**Character 39.** Hydrocaulus diameter (0 - uniform; 1 - widening distally)**Character 40.** Thin ectoderm membrane descends to cover upper half of neck region from part of collar oral to groove (0 absent; 1 - present)

Autapomorphy of *Ectopleura japonica* (Hirohito, 1988).

MATRIX ANALYSIS

The maximum parsimony analysis of the data matrix resulted in 70 trees with length of 82 steps; CI = 0.60; RI = 0.85 (73 steps; CI = 0.56; RI = 0.85 with uninformative characters removed). As explained in the phylogenetic methods section, we rooted the network in the internode between the species traditionally considered in the genus *Ectopleura* and the other tubulariids. The strict consensus tree (L= 84, CI= 0.59, RI= 0.84) is shown in Fig. 1.

Relationships, taxonomy and character evolution in Tubulariidae

After the root assumption, the resulting cladogram shows the genus *Ectopleura* as monophyletic, divided in two subsequent clades: *E. ralphi*⁺⁺ group (supported by the presence of sexually dimorphic blastostyles and medusa buds, and oral tentacles of the hydranth adnate to hypostome) and *E. americana*⁺ group (supported by the presence of free medusa).

Historically, the presence of either free medusae or sessile gonophores was adopted as diagnostic for *Ectopleura* and *Tubularia*, respectively (e.g. Brinckmann-Voss, 1970: 22, 28; Millard, 1975: 32, 35; Bouillon, 1985: 112). Petersen (1979) challenged this definition and later, after a phylogenetic analysis (Petersen, 1990: 222–223), considered the importance of the character diminished, concluding that its maintenance in the definition of the taxa would lead to polyphyletic taxa in *Ectopleura* and *Tubularia*. In order to solve the problem, Petersen (1990) transferred part of the species traditionally attributed to *Tubularia* by having fixed gonophores [e.g. *T. marina* (Torrey, 1902), *T. japonica*, *T. venusta*, among others) to the genus *Ectopleura*.

Our analysis yielded a different interpretation. In fact, the presence of free medusae (presumed apomorphic state after our optimization) is not diagnostic for the whole genus *Ectopleura*, at least regarding all the species included in that genus by Petersen (1990). However, a series of several transformations (viz. Petersen, 1990:223) is not necessary (i.e., is not the most parsimonious hypothesis) to explain the evolution of the character as well. In our hypothesis, the presence of free medusae is diagnostic for a large group of species of *Ectopleura* (*E. americana*⁺), but this condition would be homoplastic with *Hybocodon* spp., indicating only two transformations of this condition in the evolution of the Tubulariidae.

The reappearance of medusa in *Ectopleura* and *Hybocodon* is the most parsimonious optimization for the character in our cladogram. This contrasts with the idea of parallel medusa reduction in the hydroids. Although we

understand that the idea of multiple reductions has an emotional appeal, we must regard that the genomic process of medusa expression is still unknown. In our view, it is possible that some kind of regulatory process (an idea already proposed by Nelson, 1994: 116) may occur in the hydroids and the re-appearance of medusa would be a case of switch on / switch off (for hydroids, see Boero *et al.*, 1997). The other assumption (that only medusa reduction is allowed) would mean the adoption of Dollo parsimony (Farris, 1977), and there is no logical evidence to adopt this procedure.

Previous interpretations regarding the problem of medusa reduction need reevaluation. If it is not wise to assume aprioristically that the presence of medusae or fixed gonophores (or whatever other character) has a higher weight – a character that defines generic level, for instance (*cf.* Rees, 1957) –, it is also unwise to diminish their importance. Both procedures may obscure the phylogenetic meaning of this character. We think that the best approach to the problem is to include the character in the phylogenetic analyses, determine its congruence in relation to other characters and find a parsimonious solution. This procedure can show that the character has phylogenetic sense (*i.e.*, it is a synapomorphy of some group, even if it is also homoplastic with other groups) in some universality level of the analysis.

In order to keep the congruence between the phylogenetic hypothesis obtained and the taxonomy of the group, we propose a new arrangement for the family Tubulariidae. The classification below follows sequencing procedures, and it is proposed up to the generic level:

Family Tubulariidae Allman, 1864

Subfamily Ectopleurinae subfam. nov.

Genus *Pinauay* gen. nov.

Genus *Ectopleura* L. Agassiz, 1862

Subfamily Tubulariinae Allman, 1864

Genus *Zyzyzus* Stechow, 1921

Genus *Bouillonia* Petersen, 1990

Genus *Ralpharia* Watson, 1980

Genus *Tubularia* Linnaeus, 1758

Genus *Hybocodon* L. Agassiz, 1862

The generic name *Pinauay* (etymology: from the Tupi Language *Pináua* = palm tree, *Y* = water, meaning “water palm tree” due to the hydroid shape of the group) is proposed for the distinct clade in our cladogram diagnosed as those tubulariids Ectopleurinae bearing fixed gonophores (character 3), sexually dimorphic blastostyles (character 11) and oral tentacles adnate to hypostome

(character 36). Complementary characters are the colonial polyps with up to 4 ridges in the endoderm (character 4) of the hydrocaulus and annulations on the perisarc (character 38). It includes the species *P. ralphi* (Bale, 1884), *P. crocea* (L. Agassiz, 1862), *P. radiata* (Uchida, 1937), *P. marina* (Torrey, 1902), *P. venusta* (Yamada, 1950), *P. japonica* (Hirohito, 1988), *P. larynx* (Ellis & Solander, 1786) and *P. multicirrata* (Schuchert, 1996). The type species of the genus is herein designated as *Tubularia larynx* Ellis & Solander, 1786.

The species of *Ectopleura* having two-tentacled medusae constitute a monophyletic group (*E. wrighti* +) in which the recently described *E. obypa* (see Migotto & Marques, 1999) is in an apical position. Following the cladogram, the presence of two tentacles is not related to the presence of a single tentacle (autapomorphy of *Hybocodon*), and both states probably appeared independently from the plesiomorphic mode (four tentacles). Besides, *E. obypa* and *E. pacifica* (Thornely, 1900) are phylogenetically different from the remaining two-tentacled species by having the oral tentacles adnate to the hypostome (a character apparently common in the group *Pinauay* spp. and *Hybocodon* spp.), and *E. obypa* has the autapomorphic flattened aboral tentacles (homoplastic with *P. larynx* + *P. multicirrata*, *R. gorgoniae* + *R. sanctisebastiani* and *H. prolifer*).

The sister group of the subfamily Ectopleurinae is Tubulariinae, formed by (*Zyzyzus* (*Bouillonia* (*Ralpharia* (*Tubularia*, *Hybocodon*))))).

The only phylogenetic hypothesis made by Petersen (1990) for the tubulariid taxa that differs from ours (besides the internal relationships of *Ectopleura*) is related solely in the inverted relative position of *Bouillonia* and *Zyzyzus*. Petersen considered *Bouillonia* as the sister group of *Zyzyzus*⁺ whereas here *Zyzyzus* is considered the sister group of *Bouillonia*⁺. This is probably because Petersen postulated as a synapomorphy of *Zyzyzus*⁺ the presence of “endodermal canals in hydrocauline periphery of circular cross-section, formed by fusion of the tissue of T-shaped ridges”, which would be a differentiation from the oblong cross-section longitudinal canal present in *Bouillonia*. Therefore, Petersen considered an ordination in the states of the character, in which the ridges formed oblong cross-section canals and these transformed into the circular cross-section canals. We also considered the character additive, but as there was no information in the ontogeny of the group justifying the transformation of oblong into circular canals, we consider no morphological contiguity between the states. Thus, we prefer to exclude this oblong state from the analysis, possibly pulling *Zyzyzus* down in the tree; on the contrary, the hydrocaulus widening distally is a synapomorphic character of *Bouillonia*⁺. At any rate, it is also interesting to notice that the optimization of the character 4 in our cladogram does not corroborate the ontogenetic ordination assumed, and the state 1 (more than 8 ridges in the endoderm of hydrocaulus) must be interpreted as an

autapomorphy of *Hybocodon* originating from the reduction of the state 2 (numerous canals of the same diameter in the endoderm of hydrocaulus).

Taxonomic implications for *Ralpharia* and *Serehyba*

The monophyly of the tubulariid genera *Ectopleura*, *Hybocodon*, *Bouillonina* and *Tubularia* proposed by Petersen (1990) is corroborated in our analysis. The only taxonomic problem occurs in the complex *Ralpharia*/*Serehyba*.

Nematophores present in the apical region of the blastostyles is a diagnostic character of the genus *Serehyba* da Silveira & Migotto, 1984. Petersen (1990) described two other species bearing these nematophore-like structures, and placed them in the genus *Ralpharia*, pointing out the transformation series from the most simple nematophore (present in *R. neira*) to the most complex (in *S. sanctisebastiani*). In the same study, he proposed *Serehyba* as a junior synonym of *Ralpharia*, arguing that the nematophore would be an insufficient character to justify a separate genus, but he did not propose a phylogenetic analysis for the *Ralpharia* species. The topology from our analysis allows a phylogenetic interpretation of this taxonomic problem. The species *S. sanctisebastiani* is an apical taxon of the *Ralpharia* clade, sister-group of *R. gorgoniae*. As this condition causes the merophyly of *Ralpharia*, there would be two possible approaches to solve this problem:

- 1) the genus *Serehyba* would be considered a junior synonym of *Ralpharia*, and consequently *Ralpharia* would assume a monophyletic condition or;
- 2) the species *R. gorgoniae* that bear nematophores (and perhaps also *R. neira* that bears the most plesiomorphic condition of the nematophore) should be included in *Serehyba*, keeping the monophyly of the latter genus. Nevertheless, this group would have uncertain relationships with the other *Ralpharia*, which is depicted by the basal polytomy formed. This polytomy means that the remaining *Ralpharia* could be a mono- or a merophyletic genus (both hypotheses cannot be resolved by the available data).

In order to preserve nomenclatural stability, we decided to adopt the first approach for the classification of the group. Therefore, we regard *Serehyba* as a synonym of *Ralpharia* based on the phylogenetic topologies presented, agreeing with the subjective opinion of Petersen (1990).

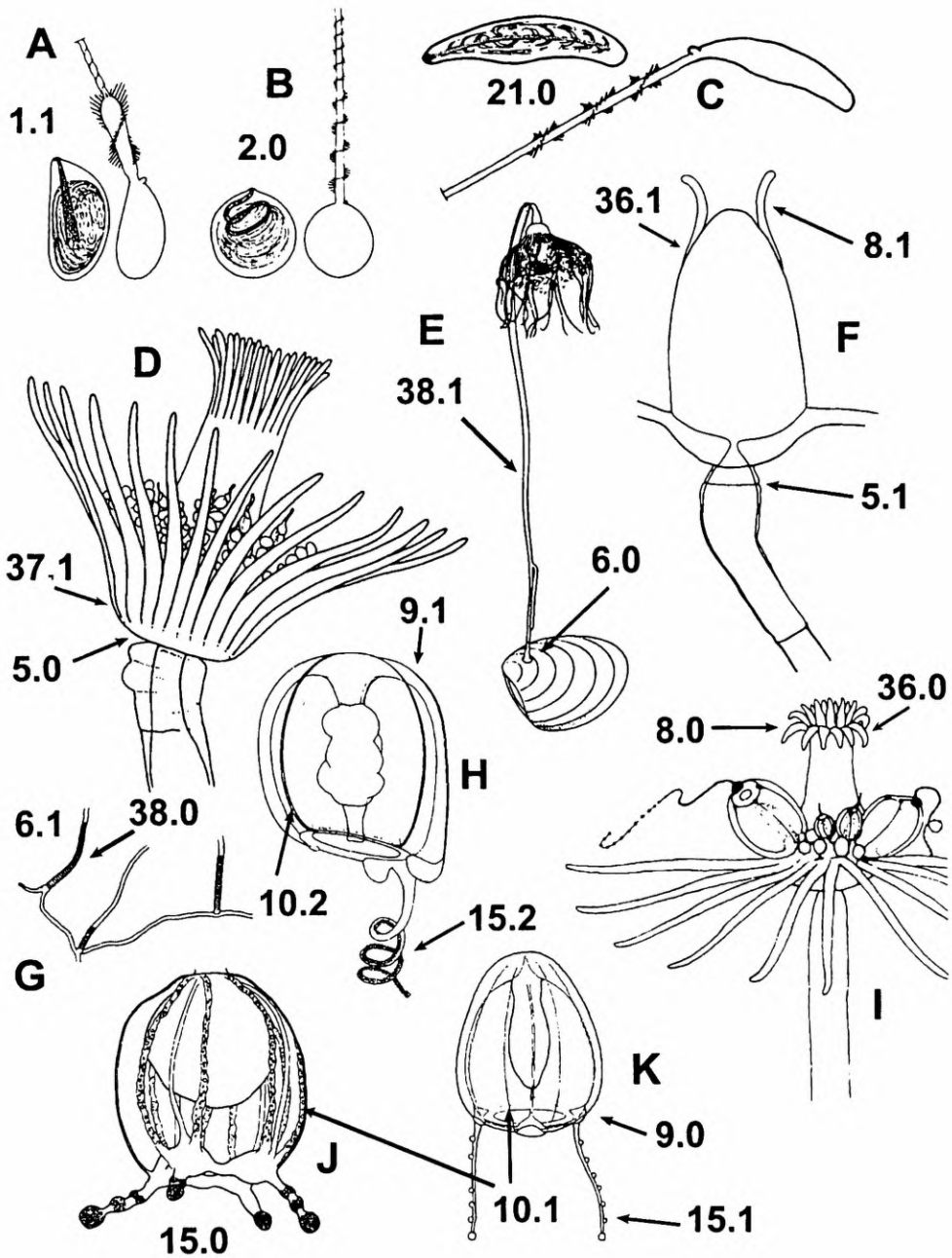


Figure 1. Character states adopted in the cladistic analysis. Numbers refers to the characters listed in the text. A-C. Nematocyst types (modified from Werner, 1965); D. *Hybocodon prolifer* (modified from Schuchert, 1996); E. *Tubularia acadiae* (modified from Petersen, 1990); F. *Ectopleura obypa* (modified from Migotto & Marques, 1999); G. *Pinauay marina* (modified from Petersen, 1990); H. *Hybocodon prolifer* (modified from Schuchert, 1996); I. *Hybocodon unicus* (modified from Millard, 1975); J. *Ectopleura dumortierii* (modified from Hirohito, 1988); K. *Ectopleura* sp. (modified from Schuchert, 1996).

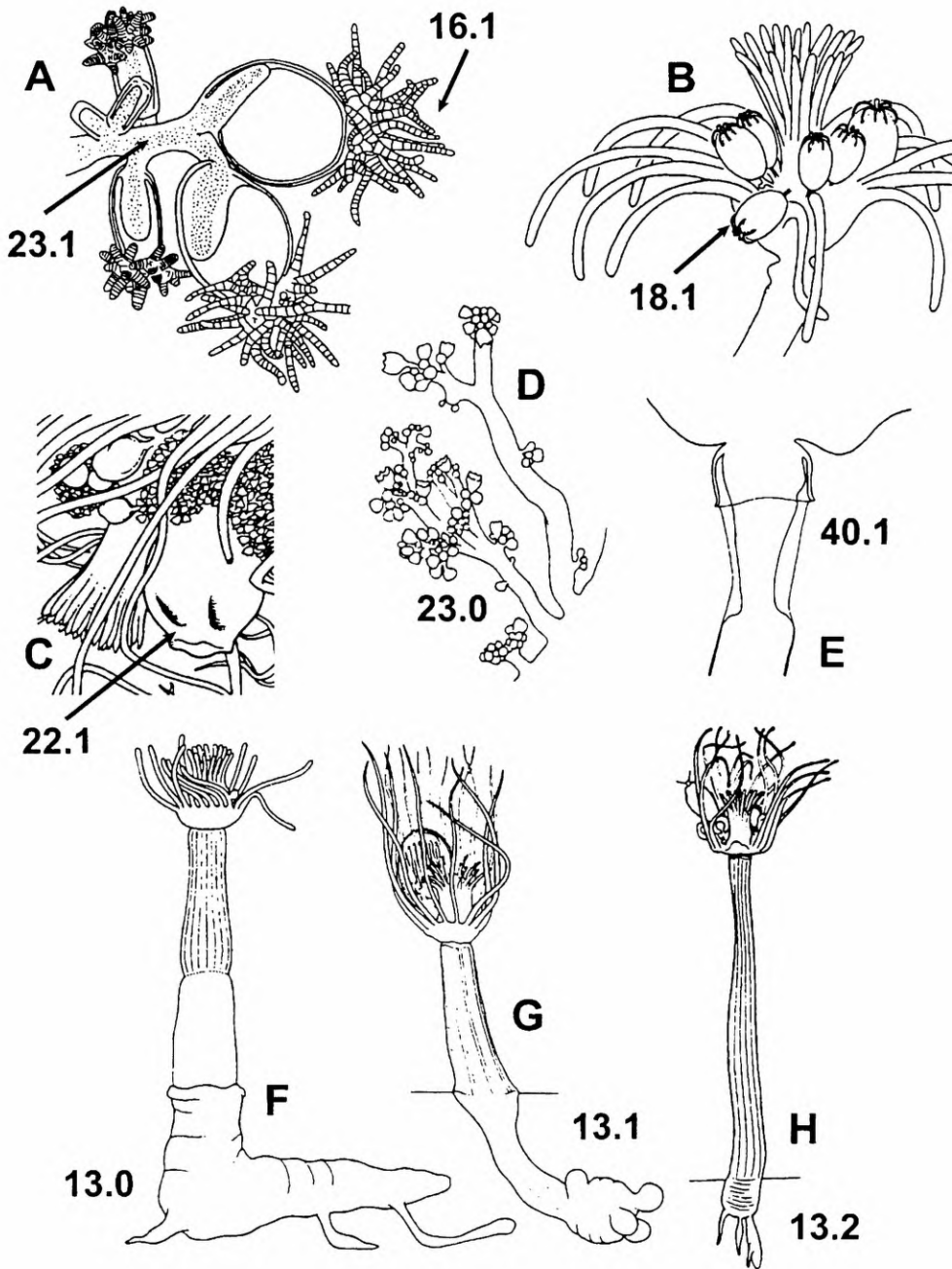


Figure 2. Character states adopted in the cladistic analysis. A. *Pinauay multicirrata* (Schuchert, 1996); B. *Pinauay ralphi* (modified from Migotto & da Silveira, 1987); C. *Ralpharia neira* (modified from Petersen, 1990); D. *Ectopleura americana* (modified from Petersen, 1990); E. *Pinauay japonica* (modified from Hirohito, 1988); F. *Zyzzyzus warreni* (modified from Calder, 1988); G. *Zyzzyzus floridanus* (modified from Petersen, 1990); H. *Zyzzyzus calderi* (modified from Petersen, 1990).

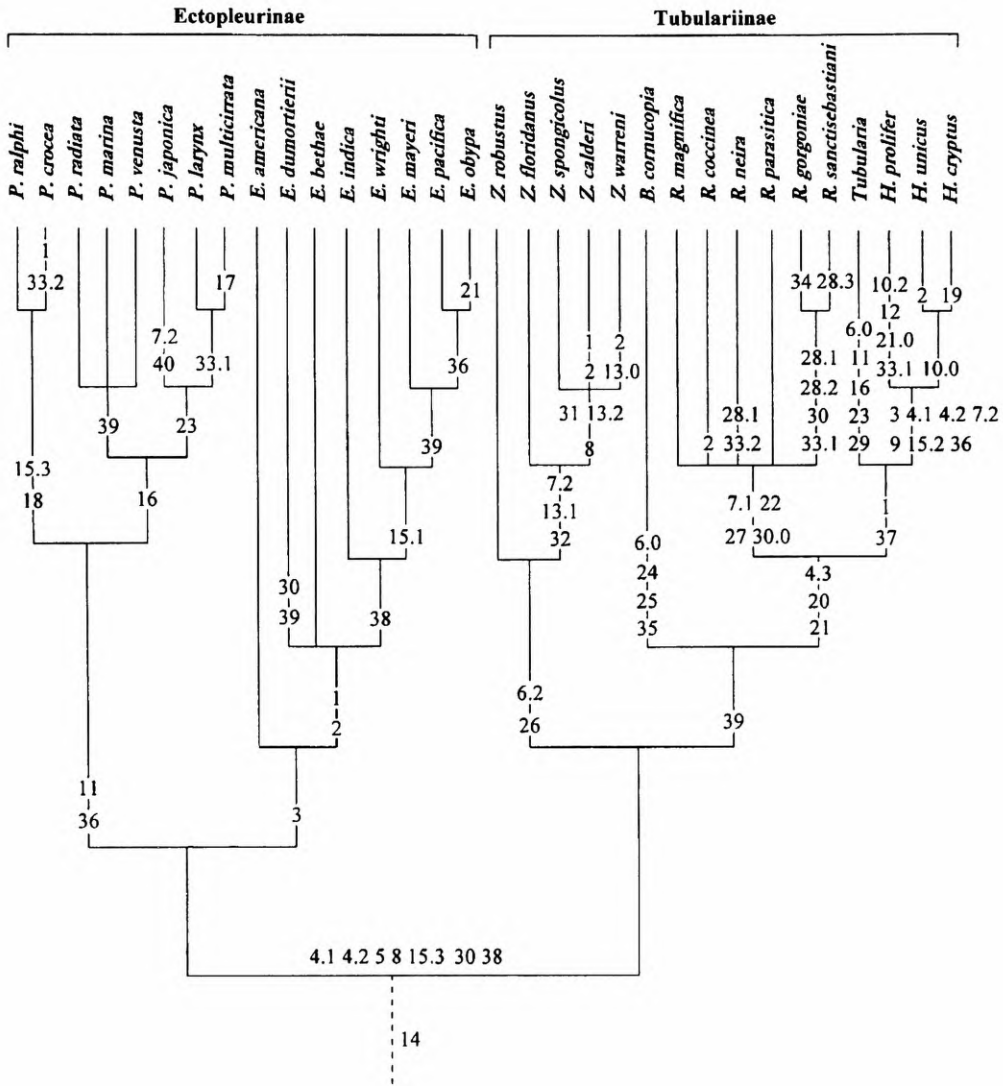


Figure 3. Strict consensus tree (L= 84; CI= 0.59; RI= 0.84) of 70 trees (L= 82; CI= 0.60; RI= 0.85) for the Tubulariidae. The root point, represented by the dashed line, was placed between the *Ectopleura* group and the other tubulariids. The synapomorphy of the family would be the character 14, indicated at the root.

Table I. Data matrix used for phylogenetic analysis of Tubulariidae (see text for descriptions and configurations of the characters). “?” = non-available information; “-” = non-comparable information or polymorphic condition for that taxon.

| Taxa of Tubulariidae | Characters |
|--|---|
| | 1111111111222222222233333333334 |
| | 1234567890123456789012345678901234567890 |
| <i>P. ralphi</i> (Bale, 1884) | 000011010-10-1300100000000000000?00?00?0 |
| <i>P. crocea</i> (L. Agassiz, 1862) | 100011010-10-130010000000000000020010000 |
| <i>P. radiata</i> (Uchida, 1937) | ??0?11010-10-1010000?0000000000000?010 |
| <i>P. marina</i> (Torrey, 1902) | 000011010-10-10100000?00000000000010010 |
| <i>P. venusta</i> (Yamada, 1950) | ??0011010-10-1010000?0000000000000?0010 |
| <i>P. japonica</i> (Hirohito, 1988) | ??0011210-10-1010000?0100000000000?0001 |
| <i>P. larynx</i> (Ellis & Solander, 1786) | 000011010-10-101000000-00000000010010000 |
| <i>P. multicirrata</i> (Schuchert, 1996) | 000011010-?0-101100000100000000010010000 |
| <i>E. americana</i> Petersen, 1990 | 001011010??0-10000000000000000000000000 |
| <i>E. dumortierii</i> (van Beneden, 1844) | 111011010100-1000000000000000010000000010 |
| <i>E. bethae</i> (Warren, 1908) | 111011010100-10000000000000000000000000 |
| <i>E. indica</i> Petersen, 1990 | 111011010100-1000000000000000000000000100 |
| <i>E. wrighti</i> Petersen, 1979 | 111011010100-1100000000000000000000000100 |
| <i>E. mayeri</i> Petersen, 1990 | 111011010100-1100000000000000000000000110 |
| <i>E. pacifica</i> (Thornely, 1900) | 111011010100-11000000000000000000000101?0 |
| <i>E. obypa</i> Migotto & Marques, 1999 | 111011010100-1100000000000000000010010110 |
| <i>B. cornucopia</i> (Bonnie, 1898) | ??0200000-00-130000000011000010000100110 |
| <i>Z. spongicolus</i> (von Lendenfeld, 1884) | 000202210-002130000000000100011100000100 |
| <i>Z. floridanus</i> Petersen, 1990 | ??0202200-0011300000?000010001?100000100 |
| <i>Z. calderi</i> Petersen, 1990 | 110202210-002130000000000100011100000100 |
| <i>Z. warreni</i> Calder, 1988 | 010202-10-000130000000000100011100000100 |
| <i>Z. robustus</i> Petersen, 1990 | ??0202000-0001300000?000010001?000000100 |
| <i>R. magnifica</i> Watson, 1980 | 000301100-00-1300001110000100000??000110 |
| <i>R. coccinea</i> Watson, 1984 | 010301100-00-130000111?000100000??000110 |
| <i>R. neira</i> Petersen, 1990 | ??0301100-00-1300001?10000110000200001?0 |
| <i>R. gorgoniae</i> Petersen, 1990 | ??0301100-00-1300001?10000120100110001?0 |
| <i>R. parasitica</i> (Korotneff, 1887) | ??0301100-00-1?00001?10000100?00??0001?0 |
| <i>R. sanctisebastiani</i> (da Silveira & Migotto, 1984) | 000301-00-00-130000111000013010010000110 |
| <i>H. prolifer</i> L. Agassiz, 1862 | 101101201201-120000100000000010010011110 |
| <i>H. unicus</i> (Browne, 1902) | 111101201000-120000110000000010000011110 |
| <i>H. cryptus</i> Watson, 1984 | 101?01201000-1200011100000000100000??110 |
| <i>Tubularia</i> spp. | 10030000--10-1-10-0110100000110000001-10 |

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