



The taxonomic position of the pelagic ‘staurozoan’ *Tessera gemmaria* as a ceriantharian larva

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Abstract

Based on 16 specimens from the Southwestern Atlantic coast (Argentina and Brazil) we reinterpret the taxonomic position of *Tessera gemmaria* Goy, 1979, a stauromedusa considered as *incertae sedis* for a long time. Using external morphology, histological preparations and molecular data (16S and COI) we conclude that *T. gemmaria* is an early stage of a cerinula, the long-lived planktonic larval stage of the Ceriantharia (Anthozoa).

Keywords: Taxonomy, Cnidaria, Anthozoa, plankton

Introduction

In the marine realm, most invertebrates have indirect development with larvae differing from adults in size, morphology, habitat, feeding habit, or locomotion (Valentine 2004; Young 2006). About 120 types of larvae are described for the marine invertebrates (Young 2006), the majority inhabiting the plankton. In the past, pelagic larvae of many invertebrates were not recognized as such and, as a consequence, they were identified as separate species, causing taxonomic confusion and false conclusions (e.g. Hannerz 1956; Giangrande *et al.* 1994).

Among cnidarians, larval and adult stages of a single species have been described under different genera and species names, or even in different classes (e.g. Miranda *et al.* 2010). Some of these species names have persisted in common usage even after the two forms have been recognized as successive stages in the life cycle of one species (Mills *et al.* 2007).

The species *Tessera gemmaria* Goy, 1979 is one example of taxonomic confusion. The family Tesseridae (subfamily Tesseranthinae) was proposed by Haeckel (1880) to encompass three new genera and four new species of Stauromedusae (*Tessera princeps*, *Tessera typus*, *Tesserantha connectens*, and *Tesseraria scyphomeda*), based on four specimens collected in different surveys; type specimens of these species do not exist in the Phyletisches Museum in Jena (PMJ), the repository of type specimens of most of the species described by Haeckel (Stiasny 1922; Morandini pers. obs.). Mayer (1910: 522) reinterpreted the three genera and four species described by Haeckel as successive ontogenetic stages of one species, but he did not state which species name would be valid. New records for the group appeared a century later, when Goy (1979) assigned two specimens, collected by the Calypso off Santos (Brazil), to the genus *Tessera* based on the number of gastric filaments (4), the number of tentacles (8), and the terminal button of nematocysts in each tentacle. She described these specimens (measuring 1.8 and 2.2 mm in height, 1 mm in diameter) as a new species, *Tessera gemmaria*. Although she did not designate a holotype, both specimens were deposited at the Muséum National d’histoire Naturelle de Paris (MNHN Inv. M. - 1712), and so constitute syntypes of the species (International Commission on Zoological Nomenclature 1999: ICZN Arti-

cle 72.1.1). However, only one specimen is now available and it was possible to examine only its gross morphology because of its poor condition. Goy (1979) also remarked on the need of histological and cnidome studies to corroborate the characteristics of the genus, but she did not do them.

The pelagic *Tessera* is an exception in the Staurozoa, a group known as ‘stalked jellyfish’ (see definitions in Marques & Collins 2004, Collins *et al.* 2006, van Iken *et al.* 2006). The family Tesseridae Haeckel, 1880, to which *T. gemmaria* was assigned, has been considered as *incertae sedis* (Mianzan & Cornelius 1999; Migotto *et al.* 2002; Marques *et al.* 2003) or ignored in studies of southern hemisphere Stauromedusae (Grohmann *et al.* 1999). Furthermore, some characters of Tesseridae, like the presence of solid tentacles and a long oral tube, do not fit with the known morphology of staurozoans (see Mayer 1910; Thiel 1936; Mills & Larson 2007). The lack of appropriate analyses on the specimens of Haeckel and Goy create doubts about the taxonomic position of Tesseridae within Staurozoa.

Specimens recently collected along the southwestern Atlantic Ocean conform to the description of Goy’s *Tessera gemmaria*. The goal of this study is to reinterpret the taxonomic position of this doubtful taxon based on evidence of external morphology, anatomy, and molecular data.

Material and Methods

Sixteen specimens were collected from four localities along 2,200 km of the coast of Argentina and Brazil (Table 1). The samples were collected with Bongo or simple plankton nets (200 – 220 µm mesh) and the specimens were preserved in 5% formaldehyde solution. One specimen collected in the São Sebastião Channel (SE Brazil, 23°50’54’’S 45°25’42’’W) was kept alive for observations and a piece of its tentacle was preserved in ethanol for molecular analysis. Voucher specimens are deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP 1478) and Estación Costera Nágera, Universidad Nacional de Mar del Plata (UNMdP – INIDEP).

TABLE 1. Specimens collected (the first locality is in Argentina, the others in Brazil).

Coordinates	Expedition	Date	# larvae
38°46’S 57°68’W	EPEA (Estación Permanente de Estudios Ambientales)	03/2005	13
23°50’02’’S 44°01’01’’W	--	04/2009	1
23°18’36’’S 42°41’49’’W	--	05/2009	1
23°50’54’’S 45°25’42’’W	--	05/2009	1

Morphological observations

Three specimens from Argentina and two from Brazil were photographed and then used for histology, dehydrated in ethanol series, cleared in xylene, and embedded in Paraplast®. The specimens were serial sectioned at 5µm and stained with Weigert hematoxylin and Mallory trichromic or hematoxylin and eosin stain (Morandini & Silveira 2001). Diagrams of the mesenterial arrangement (cf. McMurrich 1910; Leloup 1960, 1964) were based on histological preparations.

Molecular data

16S and COI amplification

DNA was extracted using InstaGene (Bio-Rad). Genes were amplified using PCR, then purified with AMPure® (Agencourt®). The PCR primers CB1 (forward - TCGACTGTTTACCAAAAACATA) and CB2 (reverse - ACGGAATGAACTCAAATCATGTAAG) (Cunningham & Buss 1993) were used to amplify the target fragment of mitochondrial DNA 16S and the primers LCO1490 (forward - GGTCAACAAATCATAAAGATAT-TGG) and HCO-2198 (reverse - TAAACTTCAGGGTGACCAAAAATCA) were used to mitochondrial DNA COI. DNA sequencing used BigDye® Terminator v3.1 kit (Applied Biosystems) and the same primers of PCR in an ABI PRISM®3100 genetic analyzer (Hitachi). The utility of the Cytochrome Oxidase I gene (COI) for barcoding species has been demonstrated in many marine taxa, including cnidarians, mainly medusozoans (see overview

in Ortman *et al.* 2010; and a recent example in Collins *et al.* 2011). However, the efficiency of its use in Anthozoa is disputed: it has been found not to be suitable by some (Herbert *et al.* 2003; Huang *et al.* 2008), although others have used it at the genus level for some groups (Reimer & Sinniger 2010; Reimer *et al.* 2011), and even at the species level (Sinniger *et al.* 2008; Benzoni *et al.* 2010).

Taxa selected for comparison

We compared our sequence to those from representative cnidarians, including at least one species from each class, downloaded from GenBank. We also added two sequences from adult ceriantharians (*Isarachnanthus* and *Ceriantheomorpha*) from Brazil (Table 2).



FIGURE 1. *Cerinula* larva collected in this study; arrows show that mesenteries almost reach the aboral end. Scale bar = 0.5 mm.

DNA analysis

Sequences were edited to make decisions on ambiguous sites, and then assembled in SEQUENCHER 4.10.1. Contig sequences were edited in GENEIOUS™ 5.3.4 and aligned using BioEdit© (shell for ClustalW Multiple Alignment) (Thompson *et al.* 1994) software with corrections by eye in the case of 16S. New sequences have been submitted to GenBank (Tab. 2) and aligned data sets are available from TreeBase (11498 - <http://purl.org/phylo/treebase/phylo/study/TB2:S11498>). Kimura's two-parameter model of base substitution was used to calculate genetic distances in MEGA4 software (Tamura *et al.* 2007) and results contrasted with similar procedures carried out in GENEIOUS™ 5.3.4. Maximum Likelihood (ML) analyses were performed using PALM (Phylogenetic Inference with Automatic Likelihood Model Selectors) (Chen *et al.* 2009). The most appropriate model for each of the datasets was chosen by employing the Akaike information criterion (AIC) and then the model 'GTR+ G' was applied. Branch support was estimated by bootstrapping with 1,000 replicates for the ML (PALM) analyses. ML analyses were also contrasted with similar procedures carried out in MEGA 4.

Table. 2 – Taxonomic data, GenBank sequence numbers and references of species used for molecular comparison in this study.

Class	Order	Family	Genus	Species	16S	COI	Reference	
--	--	--	--	Larvae	JF915192	JF915197	This work	
Anthozoa	Ceriantharia	Arachnactidae	<i>Isarachnanthus</i>	sp.	JF915194	JF915196	This work	
		Cerianthidae	<i>Ceriantheomorpha</i>	<i>brasiliensis</i>	JF915193	JF915195	This work	
	Scleractinia	Acroporidae	<i>Ceriantheopsis</i>	<i>americanus</i>	U40289			France <i>et al.</i> , 1996
			<i>Cerianthus</i>	<i>borealis</i>	U40288			France <i>et al.</i> , 1996
		<i>Acropora</i>	<i>palifera</i>	AF265593			Romano & Cairns, unpublished	
		<i>Acropora</i>	<i>palmata</i>	--	AY451341		Shearer & Coffroth, 2008	
		Gardineriidae	<i>Gardineria</i>	<i>hawaiiensis</i>	GQ868702		Stolarski <i>et al.</i> , unpublished	
		Hormathiidae	<i>Hormathia</i>	<i>pectinata</i>	FJ489430		Gusmão & Daly, 2010	
		Actinostolidae	<i>Stomphia</i>	<i>selaginella</i>	GU473298		Rodriguez & Daly, 2010	
		Edwardsiidae	<i>Edwardsia</i>	<i>timida</i>	GU473299		Rodriguez & Daly, 2010	
Zoanthidea	Zoanthidae	<i>Nematostella</i>	<i>vectensis</i>	--	DQ538492		Reitzel <i>et al.</i> , 2008	
		<i>Zoanthus</i>	<i>sociatus</i>	HM130477			Reimer <i>et al.</i> , 2010	
	Alcyonacea	Primnoidae	<i>Acrozoanthus</i>	<i>australiae</i>	--	HM171914		Reimer <i>et al.</i> , 2010
			<i>Primnoa</i>	<i>pacifica</i>	FJ526210			France & Pante, unpublished
		Gorgoniidae	<i>Lophogorgia</i>	<i>chilensis</i>	U40305		--	France <i>et al.</i> , 1996
			<i>Eunicella</i>	<i>singularis</i>	--	AY827538		Calderon <i>et al.</i> , 2006
	Pennatulacea	Renillidae	<i>Renilla</i>	<i>muelleri</i>	U19372			Bridge <i>et al.</i> , 1995
		Antipatharia	<i>Allopathes</i>	<i>robillardi</i>	HM015358			Miller <i>et al.</i> , 2010
	Staurozoa	Lucernariidae	<i>Stichopathes</i>	<i>variabilis</i>	HM015353			Miller <i>et al.</i> , 2010
			<i>Halichystus</i>	<i>tennis</i>	HM022154			Miranda <i>et al.</i> , 2010
Depastridae		<i>Halichystus</i>	<i>antarcticus</i>	FJ874775			Miranda <i>et al.</i> , 2010	
		<i>Halichystus</i>	<i>californiensis</i>		GU201830		Kahn <i>et al.</i> , 2010	
		<i>Cratelorophus</i>	<i>convolutus</i>		GQ120102		Ortman <i>et al.</i> , 2010	
Scyphozoa		Ulmariidae	<i>Aurelia</i>	<i>aurita</i>	AF461398			Schroth <i>et al.</i> , 2002
			<i>Drymonema</i>	<i>dalmatinum</i>		HQ234621		Bayha & Dawson, 2010
		Rhizostomeae	<i>Cassiopea</i>	sp.	U19374			Bridge <i>et al.</i> , 1995
			<i>Nausithoe</i>	<i>atlantica</i>		GQ120089		Ortman <i>et al.</i> , 2010
Hydrozoa		Anthoathecata	<i>Hydrocorynidae</i>	<i>Hydrocoryne</i>	GQ389713			Nawrocki <i>et al.</i> , 2010
	Leptothecata	Phialellidae	<i>Phialella</i>	FJ550474			Leclère <i>et al.</i> , 2009	
	Limnomedusae	Oliandiasidae	<i>Oliandias</i>	EU293977			Collins <i>et al.</i> , 2008	
Cubozoa	Tamoyidae	Carybdeidae	<i>Carybdea</i>	AF360118			Ender & Schierwater, unpublished	
		<i>Tamoya</i>	<i>ohboya</i>		GQ150264		Collins <i>et al.</i> , 2011	

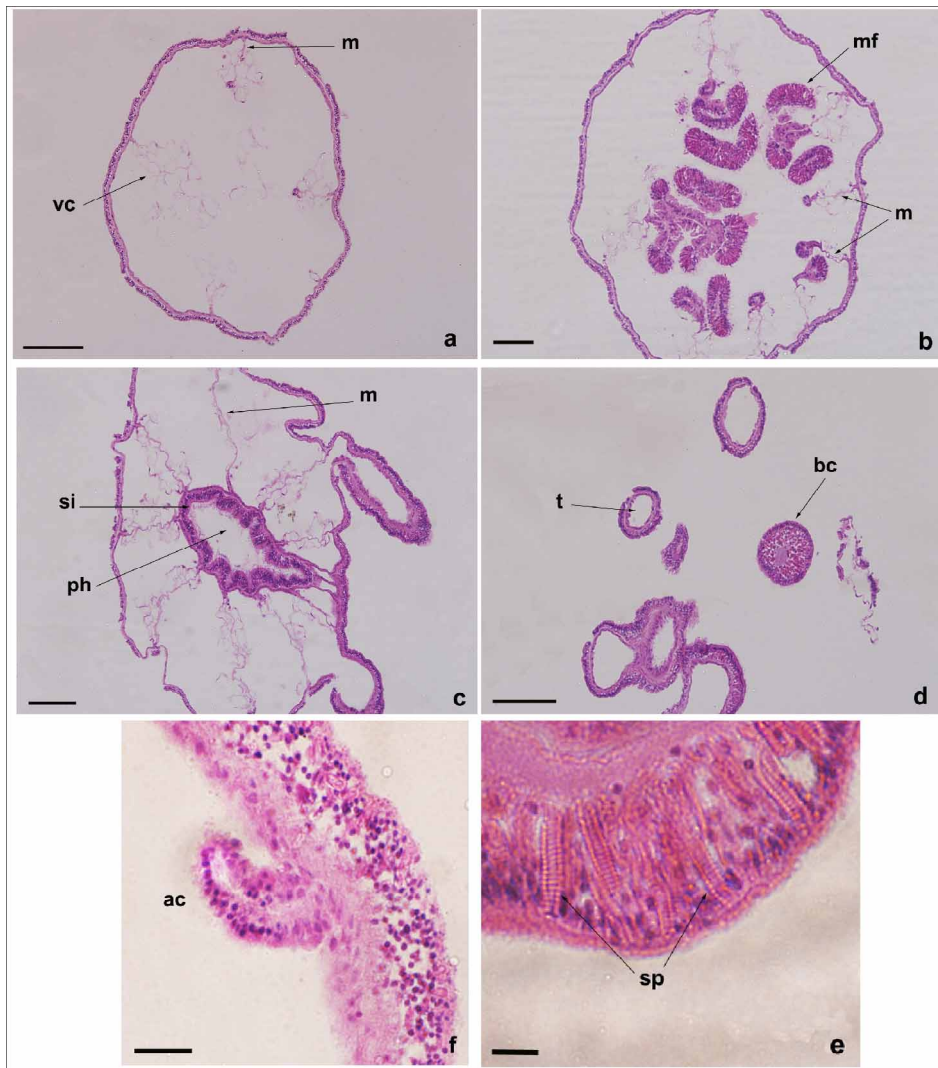


FIGURE 2. Histological preparations: a—Detail of the gastrovascular cavity with four mesenteries. b—Detail of the gastrovascular cavity with 8 mesenteries and folded mesenterial filaments. c—Detail of actinopharynx and two mesenteries being formed. d—Detail of hollow tentacles and the tentacle tip with a button of cnidocysts. e—Spirocyst in the aboral pore. f—Detail of acontioids. ac—acontioids, bc—terminal buttons of cnidocysts, m—mesenteries, mf—mesenterial filaments, ph—actinopharynx, si—siphonoglyph, sp—spirocyst, t—tentacles, vc—vacuolated cells. Scale bar a-d = 0.05 mm, e = 10 μ m, f = 20 μ m.

Results

Morphological data

External morphology of the 16 specimens collected from Argentinean and Brazilian coasts correspond with the description of *Tessera gemmaria* by Goy (1979). The specimens are conical, and vary in size from 1.31 mm to 2.46 mm in height and from 0.50 mm to 1.58 mm in diameter. The transparent body allows observation of four mesenteries with filaments almost reaching the aboral pore (Fig. 1 arrows). Four to thirteen tentacles are arranged in two concentric circles, each tentacle with a cnidocyst button at the tip. The aboral pore has a cnidocyst area.

Histological preparations show the actinopharynx with one siphonoglyph, mesenteries, folded mesenterial filaments and acontioids (Fig. 2). Moreover, one of the most remarkable characters observed in our specimens was the presence of spirocysts (Fig. 2e). A schematic diagram of the mesenterial arrangement is shown in Figure 3.

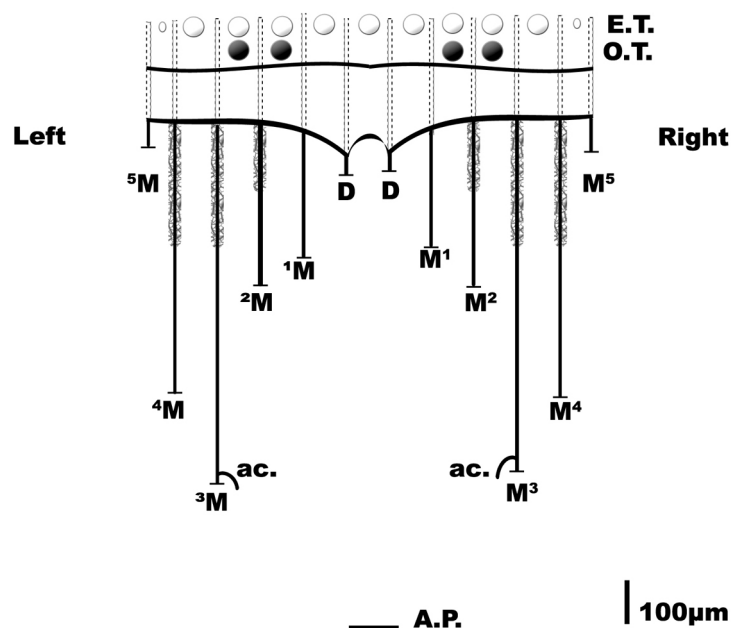


FIGURE 3. Mesenterial arrangement diagram of cerinula larva collected in this study. ac—acontoids, d—directive mesenteries, m—mesenteries, t—tentacles, ap—aboral pore.

Molecular study

The sequences of the larva morphologically identical with *T. gemmaria* are more similar to those of ceriantharians than to those of staurozoans. The DNA distance matrix supports the taxonomic position of the studied specimens within Ceriantharia, having no differences from the 16S and COI sequences of *Isarachnanthus* sp. (Table 3). ML topology (Fig. 4) agrees with distance matrix, supporting the studied material as falling within Ceriantharia and not within Staurozoa.

TABLE 3. DNA distance matrix between the larva similar to '*Tessera gemmaria*' from the Brazilian coast and other cnidarian species (Anthozoa, Cubozoa, Hydrozoa, Scyphozoa, and Staurozoa) based on 16S and COI sequences.

	Larva	16S	COI
<i>Isarachnanthus</i> sp.		0.000	0.000
<i>Ceriantheomorpha brasiliensis</i>		0.061	0.187
<i>Ceriantheopsis americanus</i>		0.077	--
<i>Cerianthus borealis</i>		0.094	--
<i>Acropora palifera</i>		0.245	--
<i>Craterolophus convolvulus</i>		--	0.281
<i>Acropora palmate</i>		--	0.317
<i>Edwardsia timida</i>		0.253	--
<i>Hormathia pectinata</i>		0.265	--
<i>Stomphia selaginella</i>		0.264	--
<i>Gardineria hawaiiensis</i>		0.276	--
<i>Zoanthus sociatus</i>		0.285	--
<i>Haliclystus californiensis</i>		--	0.328
<i>Primnoa pacifica</i>		0.345	--
<i>Lophogorgia chilensis</i>		0.333	--
<i>Nematostella vectensis</i>		--	0.340
<i>Nausithoe atlantica</i>		--	0.350
<i>Tamoya ohboya</i>		--	0.350
<i>Drymonema dalmatinum</i>		--	0.370
<i>Hydrocoryne iemanja</i>		0.384	--

<i>Haliclystus tenuis</i>	0.423	--
<i>Haliclystus antarcticus</i>	0.427	--
<i>Aurelia aurita</i>	0.369	--
<i>Cassiopea</i> sp.	0.392	--
<i>Renilla muelleri</i>	0.334	--
<i>Allopathes robillardi</i>	0.330	--
<i>Olindias sambaquiensis</i>	0.416	--
<i>Eunicella singularis</i>	--	0.429
<i>Carybdea marsupialis</i>	0.440	--
<i>Phialella quadrata</i>	0.445	--
<i>Stichopathes variabilis</i>	0.447	--

Discussion

Both morphological and molecular data support our specimens as an anthozoan, probably a cerinula (the long-lived planktonic larva of Ceriantharia), and not a planktonic staurozoan. According to Berntson *et al.* (2001), Won *et al.* (2001), and Daly *et al.* (2002, 2003, 2007) this group is basal in Hexacorallia, but see alternative views on the phylogenetic position of Ceriantharia in Collins *et al.* (2006: Fig. 3) and Bruger & France (2007: Fig. 5a).

Although the mitochondrial markers we used, especially COI, are useful in barcoding medusozoans, they may have limited efficiency for anthozoans. However, only two ceriantharian COI sequences were previously deposited in Genbank (Table 2) and we add two more as well as the “*Tessera*” sequence. These five sequences differ subtly among themselves and at the level of less inclusive groups in Ceriantharia and also show differences between the haplotypes of Ceriantharia and other anthozoan groups (Table 3, Fig. 4). We consider it premature to propose assignments to a specific family or genus based on the sequences.

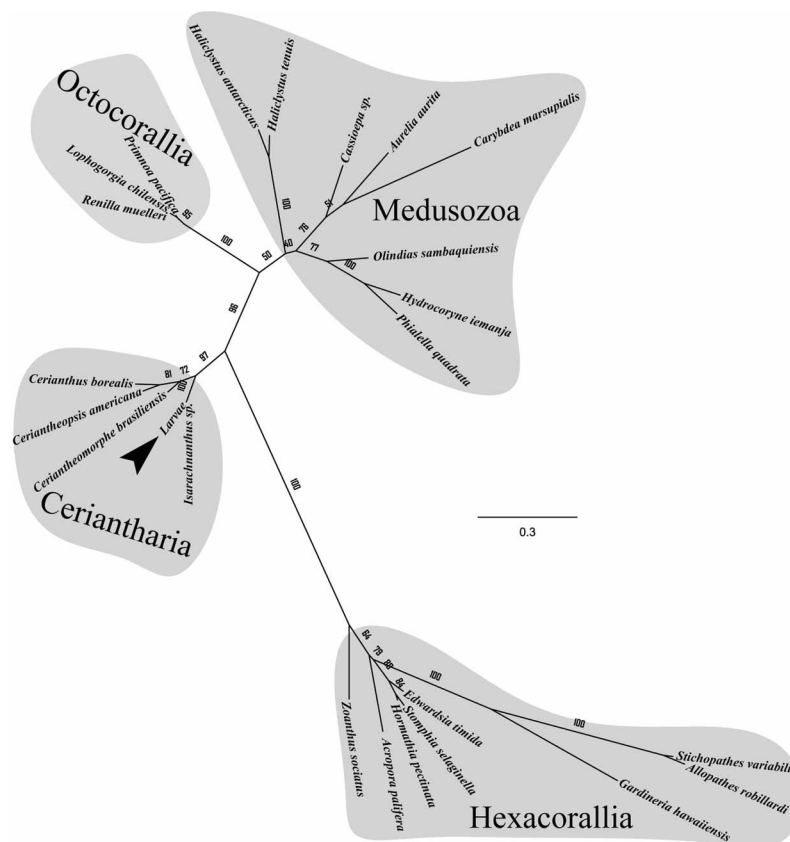


FIGURE 4. Phylogenetic hypothesis (ML) based on mitochondrial 16S for the specimens similar to ‘*Tessera gemmaria*’ and other representatives of Anthozoa and Medusozoa. Numbers associated to branches are bootstrap proportions after 1,000 replicates. Arrow indicates the material studied.

The taxonomic position of *Tessera gemmaria* Goy, 1979 was based on misinterpretation of morphological traits. In an external examination of the specimens, the gastrovascular cavity of *T. gemmaria* was described as divided by four mesenteries (Goy, 1979). In fact, a cerinula larva may have from eight to some dozens mesenteries (Leloup 1964) that, during ontogeny, are added to the ventral intermesenterial compartment (Daly *et al.* 2008). The larger specimens we studied have two mesenteries being formed (Figs 2c – 3). In ceriantharian larvae, only some of the mesenteries reach the aboral end, and the most recently formed mesenteries extend only a short distance proximal to the end of the pharynx (Hyman 1940). In our material, three or four mesenteries almost reach the aboral end (Fig. 1 arrows). The pendant gonads described by Goy (1979) are the folded mesenterial filaments (Fig. 2b). Moreover, spirocysts are restricted to Anthozoa Hexacorallia (Daly *et al.* 2003) (Fig. 2e), therefore the presence of spirocysts in our specimens is a decisive evidence that they are not staurozoans, a result also supported by molecular data. We did not find ptychocysts in our specimens, a type of cnida found exclusively in Ceriantharia and used for building the tubes (Mariscal *et al.* 1977); perhaps they develop ptychocysts at later stages.

The specimens described by Goy (1979) are not staurozoans; we interpret them as cerinula larvae. Our specimens conform to the description of Goy's *Tessera gemmaria*, but generic placement of *T. gemmaria* can never be resolved with the existing syntype because of its poor preservation.

The results of our study also raise doubts about the reality of the Tesseridae, as already speculated by Krumbach (1925). He considered *Tessera princeps* as a “romantic archetype” or as ontogenetic steps of a unique organism (Krumbach 1925: 530). In fact, Haeckel (1880, 1882) had access to only four specimens from three widespread locations. Although the internal anatomy of Haeckel's specimens was described, it is not clear whether Haeckel studied them by means of histological sections. Haeckel (1880, 1882) described the specimens as having solid tentacles and a long oral tube, but these characters do not fit into the known morphology of either staurozoans (Mayer 1910; Thiel 1936; Mills & Larson 2007) or ceriantharians (van Beneden 1897; Carlgren 1912, 1924; Leloup 1964).

Finally, we believe that the taxonomy of the planktonic forms of Ceriantharia needs to be thoroughly revised because almost every described species may be likely a stage in the life cycle of an already described benthic form (cf. Molodtsova 2004).

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