

Tubiclavoides striatum gen. nov. et sp. nov. (Cnidaria: Hydrozoa) a new bathyal hydroid from the Gulf of Cadiz, north-east Atlantic Ocean

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Tubiclavoides striatum, a new species of an athecate hydroid, was found on mud volcanoes, inactive carbonate chimneys, and cold-water coral stands in the Gulf of Cadiz (south-western Iberian Peninsula, Atlantic Ocean). The new family Tubiclavoididae and the new genus *Tubiclavoides* are proposed to accommodate the new species. The new hydroid is characterized by scattered filiform tentacles, sporosacs developing among the tentacles and hydrocauli covered with striated perisarc, often subdivided into imbricating cones. A full description and illustrations are provided, as well as some notes on the ecology and distribution of the new species.

INTRODUCTION

Communities of benthic animals associated with cold seeps have been discovered only recently at several locations on active and passive continental margins of the Pacific and Atlantic Ocean. These specialized benthic communities are sustained by rising hydrocarbon-rich fluids that serve as microbial energy sources. The high production of organic carbon sustains high biomasses and typical macro-invertebrates that host chemosynthetic endosymbionts. (Sibuet & Olu, 1998; Olu-Le Roy et al., 2004). Contrasting to vast extensions of the rather monotonous bathyal environment, the sea bottom in the Gulf of Cadiz shows a diverse array of habitats that include mud volcanoes with varying degrees of seepage activity, inactive carbonate chimneys fields and dead deep-water coral stands. Through ongoing studies aiming at understanding deep-sea seepage phenomena in the Gulf of Cadiz, it was possible to obtain an important collection of macrofaunal animals living on these little studied special habitats. Their hydrozoan fauna had not been investigated so far and as is often the case when unsampled biotopes are examined in more detail, we found a frequent hydroid that could not be identified with any known species. Although superficially similar to a member of the Oceanidae (see Schuchert, 2004), its unique characteristics made it necessary to create a new genus and new family for it.

MATERIALS AND METHODS

Study area

Located at the junction of the Eurasian and African tectonic plates, the Gulf of Cadiz is geologically complex and its structure is still under debate. One of the most important features is a large olistostrome complex emplaced in an accretionary wedge-type environment (Sartori et al.,

1994; Maldonado et al., 1999; Gutscher et al., 2002) that favours the occurrence of seepage-related geomorphological features such as the mud volcanoes. Since the discovery of the first underwater mud volcano in the Gulf of Cadiz in 1999 (Gardner, 2000, 2001), about 30 other sites at depths ranging from 200 to 3900 m have been located and sampled under the IOC-UNESCO 'Training Through Research (TTR) Programme' (Pinheiro et al., 2003; Van Rensbergen et al., 2005) and more recently the EU funded HERMES project. The Gulf of Cadiz also encompasses other habitats such as inactive carbonate chimneys fields and mostly dead cold-water coral stands that are sometimes heavily colonized by cnidarians.

Collection of samples

Samples were collected during the 'TTR' cruises onboard the RV 'Prof. Logachev'. A TV-assisted grab was used to locate interesting sampling sites in the target environments and a geological dredge was also used in some occasions to recover carbonate chimneys. Box core samples were also collected during the 'Moundfource 2005' onboard the RV 'Pelagia' (NIOZ). Data on the stations yielding the new species are presented in Table 1. The biological material was preserved in 70% or 96% ethanol.

DNA extraction and sequencing

A hydranth of the syntype colony was used to extract DNA and to determine the 16S sequence as given in Schuchert (2005). The sequence was deposited in the EMBL database under the accession number AM403520.

The 16S sequence was compared to numerous other hydrozoan 16S sequences of the suborder Filifera [from Schuchert & Reisinger (2006), AM183123 through AM183141, AY787878, AY787883, AY787884, AY787889, AY787896]

Table 1. Station data for the samples yielding *Tubiclavoides striatum* gen. nov. et sp. nov. Coordinates and depth for dredge samples are mean values.

Site	Cruise	Station	Latitude	Longitude	Depth (m)	Remarks
Jesus Baraza	TTR12	AT-391-Gr	35°35.439'N	7°12.264'W	1105	Mud breccia; active MV
Kidd	TTR14	AT-528-Gr	35°25.304'N	6°43.972'W	489	Mud breccia; active MV
Kidd	TTR14	AT-560-B	35°25.306'N	6°43.976'W	498	Mud breccia; active MV
Meknès	TTR14	AT-541-Gr	34°59.103'N	7°04.435'W	703	Mud breccia; active MV
Meknès	TTR15	AT-581-Gr	34°59.182'N	7°04.344'W	700	Mud breccia; active MV
Meknès	TTR15	AT-585-K	34°59.137'N	7°04.343'W	701	Mud breccia; active MV
Mercator	TTR15	AT-569-Gr	35°17.917'N	6°38.717'W	358	Mud breccia; active MV
Mercator	TTR15	AT-575-B	35°17.903'N	6°38.715'W	355	Mud breccia; active MV
Mercator	TTR15	AT-576-B	35°17.657'N	6°39.672'W	428	Mud breccia; active MV
Gibraltar	TTR14	AT-550-D	35°42.257'N	6°30.000'W	380	Carbonate chimneys
Gibraltar	TTR14	AT-551-D	35°42.683'N	6°30.405'W	419	Carbonate chimneys
Gibraltar	TTR14	AT-552-Gr	35°42.816'N	6°30.234'W	428	Carbonate chimneys
Vernardsky	TTR15	AT-574-D	35°26.066'N	6°46.788'W	510	Carbonate chimneys
TTR	TTR12	AT-416-Gr	35°21.87'N	6°52.00'W	695	Dead scleractinean corals; inactive MV
Pen Duick	TTR12	AT-406-Gr	35°18.148'N	6°47.666'W	550	Dead scleractinean corals
Pen Duick	TTR12	AT-407-Gr	35°17.672'N	6°47.060'W	562	Scleractinean coral debris
Pen Duick	TTR14	AT-565-Gr	35°18.180'N	6°47.656'W	544	Scleractinean coral debris
Pen Duick*	M2005	16A-B	35°18.310'N	6°48.205'W	660	Scleractinean coral debris
Pen Duick	M2005	21-B	35°19.084'N	6°46.397'W	498	Scleractinean coral debris
Pen Duick	M2005	28-B	35°18.200'N	6°48.527'W	622	Scleractinean coral debris

* Type locality; Gr, TV-assisted grab; K, kasten corer; B, box-core; G, gravity core; D, dredge; MV, mud volcano.

as well as some unpublished 16S sequences of *Cordylophora caspia*, *Corydendrium parasiticum*, *Hydrichthys boycei*, *Leuckartiara octona*, *Clava multicornis*, and *Clavactinia gallensis*. Using the methods described in Schuchert (2005), no significant phylogenetic association of *Tubiclavoides striatum* with any other genus could be found.

Abbreviations

DBUA, Department of Biology from the University of Aveiro; HERMES, Hotspot Ecosystem Research on the Margins of European Seas; IOC, Intergovernmental Oceanographic Commission; MHNG, Muséum d'Histoire Naturelle de Genève, Switzerland; MV, mud volcano; ICZN, International Code of Zoological Nomenclature; NIOZ, Nederlands Instituut voor Onderzoek der Zee; TTR, Training Through Research; UNESCO, United Nations Educational, Scientific and Cultural Organization.

SYSTEMATICS

Order ANTHOATHECATA Cornelius, 1992

Suborder FILIFERA Kühn, 1913

TUBICLAVOIDIDAE fam. nov.

Diagnosis

Anthoathecata Filifera hydroids, solitary or colonial, with elongate hydranths bearing filiform tentacles scattered over hydranth body, gonophores develop among the tentacles but independent of them. Stolons ramified. Hydrocauli and stolons covered by perisarc. Nematocysts include microbasid euryteles and desmonemes.

Remarks

With their scattered filiform tentacles, the Tubiclavoididae resemble superficially to the Oceanidae (Schuchert, 2004). They cannot be placed in this family as the Oceanidae never have gonophores among the tentacles; they have them either on the hydrocaulus, stolons or specialized blastostyles. This is a derived condition among the Anthoathecata, while 'gonophores on the hydranth' is a symplesiomorphic trait (Schuchert, 2001, 2004). Scattered filiform tentacles are also known to occur in a few species of Pandeidae, but also in this family, the gonophores are never among or near the tentacles. The Hydractiniidae, in contradistinction, develop their gonophores on the hydranth body or its homologue and some genera like *Clava* or *Clavactinia* have scattered tentacles. However, the gonophores are never among the tentacles and the hydranths always lack a pedicel. The genus *Tubiclavoides* can therefore not be accommodated within the Hydractiniidae without a fundamental change of its scope.

In defining the family we explicitly did not specify the nature of the gonophore and we avoided making the diagnosis too stringent, permitting also future additions of new, slightly different members.

Tubiclavoides gen. nov.

Type species

Tubiclavoides striatum sp. nov.

Diagnosis

Tubiclavoididae with monomorphic hydroids, stolonial or branched, arising from a tubular hydrorhiza. Gonophores reduced to fixed sporosacs developing singly among tentacles.

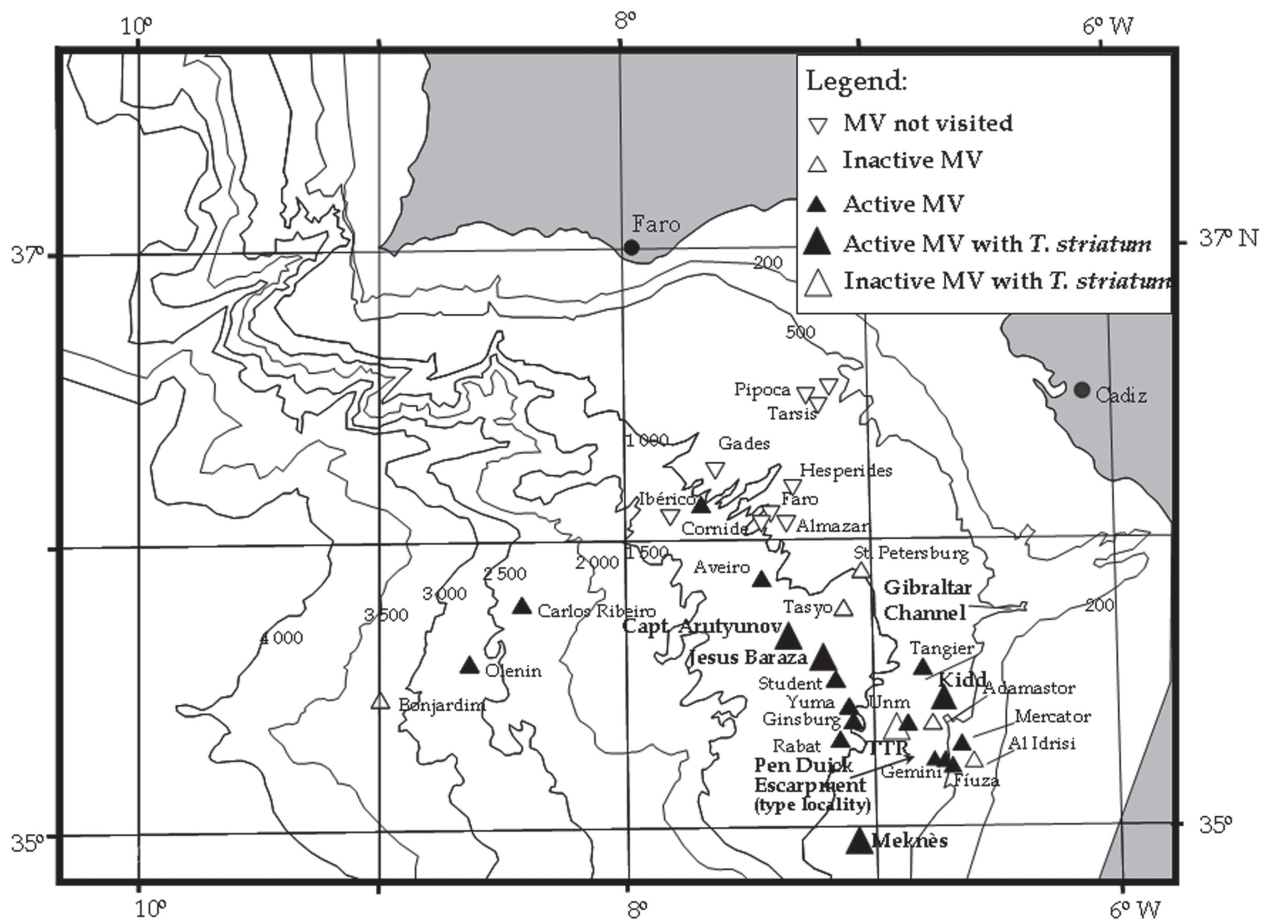


Figure 1. Mud volcanoes in the Gulf of Cadiz and distribution of *Tubiclavoides striatum* gen. nov. et sp. nov.

Remarks

The new genus was named *Tubiclavoides* in order to convey the similarity with *Tubiclava* Allman, 1863. However, *Tubiclava* is more or less a hypothetical genus based on an indeterminate type species (*T. lucerna* Allman, 1863; an intertidal species, perhaps *Turritopsis polycirrho*; see Schuchert, 2004). Whatsoever, in his diagnosis for *Tubiclava*, Allman (1863, 1872) characterizes it by 'gonophores in dense clusters, immediately below the proximal tentacles'. The gonophore position and distribution makes it thus incompatible with our new species.

A valid genus that comes closest to *Tubiclavoides* is *Millardiana* Wedler & Larson, 1988. But again, this genus has its gonophores below the tentacles, albeit on the hydranth body. Additionally, the tentacles are not scattered but concentrated into a band below the hypostome and the zooids are dimorphic. The genus *Millardiana* has been excluded from the Bougainvilliidae, where it was originally placed by Schuchert (2004). It could well belong to the new family Tubiclavoididae, but in this case the diagnosis must be modified. Pending further supportive evidence from a molecular phylogenetic analysis, we refrained here from doing so.

According to article 30.1.4.4 of the ICZN (4th edition, 1999), the gender of a compound genus-group name ending in the suffix -oides is to be treated as masculine if not stated otherwise.

Tubiclavoides striatum sp. nov. (Figures 2 & 3)

Material examined

Holotype: MHNG INVE 39863 Gulf of Cadiz, Pen Duick Escarpment, 35°18.310'N 6°48.205'W, depth 660 m, 26 May 2005, RV 'Pelagia', Moundforce-2005 Station 16A-B, box core, one colony; colony in relatively good condition but some hydrorhizal tubes are broken, dividing the colony into four pieces. One infertile detached polyp was used for DNA analysis, three hydranths were stained and mounted on microslides, the rest of the colony was kept in alcohol.

Paratype: MHNG INVE39862, Pen Duick Escarpment, 35°19.084'N 6°46.397'W, 498 m, 30 May 2005, RV 'Pelagia', M2005 Station 21 B, box core, 1 colony.

Other material (all samples kept by DBUA): all from Gulf of Cadiz. (Table 1 and Figure 1). Jesus Baraza, 35°35.439'N 7°12.264'W, 1105 m, 09 July 2002, RV 'Prof. Logachev', TTR12 Station AT-391-Gr, TV-assisted grab, 4 polyps. – Kidd, 35°25.304'N 6°43.972'W, 489 m, 03 August 2004, RV 'Prof. Logachev', TTR14 Station AT-528-Gr, TV-assisted grab, 9 polyps. – Kidd, 35°25.306'N 6°43.976'W, 08 August 2004, RV 'Prof. Logachev', TTR14 Station AT-560-B, box core, 498 m, 1 polyp. – Meknès, 34°59.103'N 7°04.435'W, 703 m, 05 August 2004, RV 'Prof. Logachev', TTR14 Station AT-541-Gr, TV-assisted grab, 1 polyp. – Meknès, 34°59.182'N 7°04.344'W, 700 m, 28 July 2005,

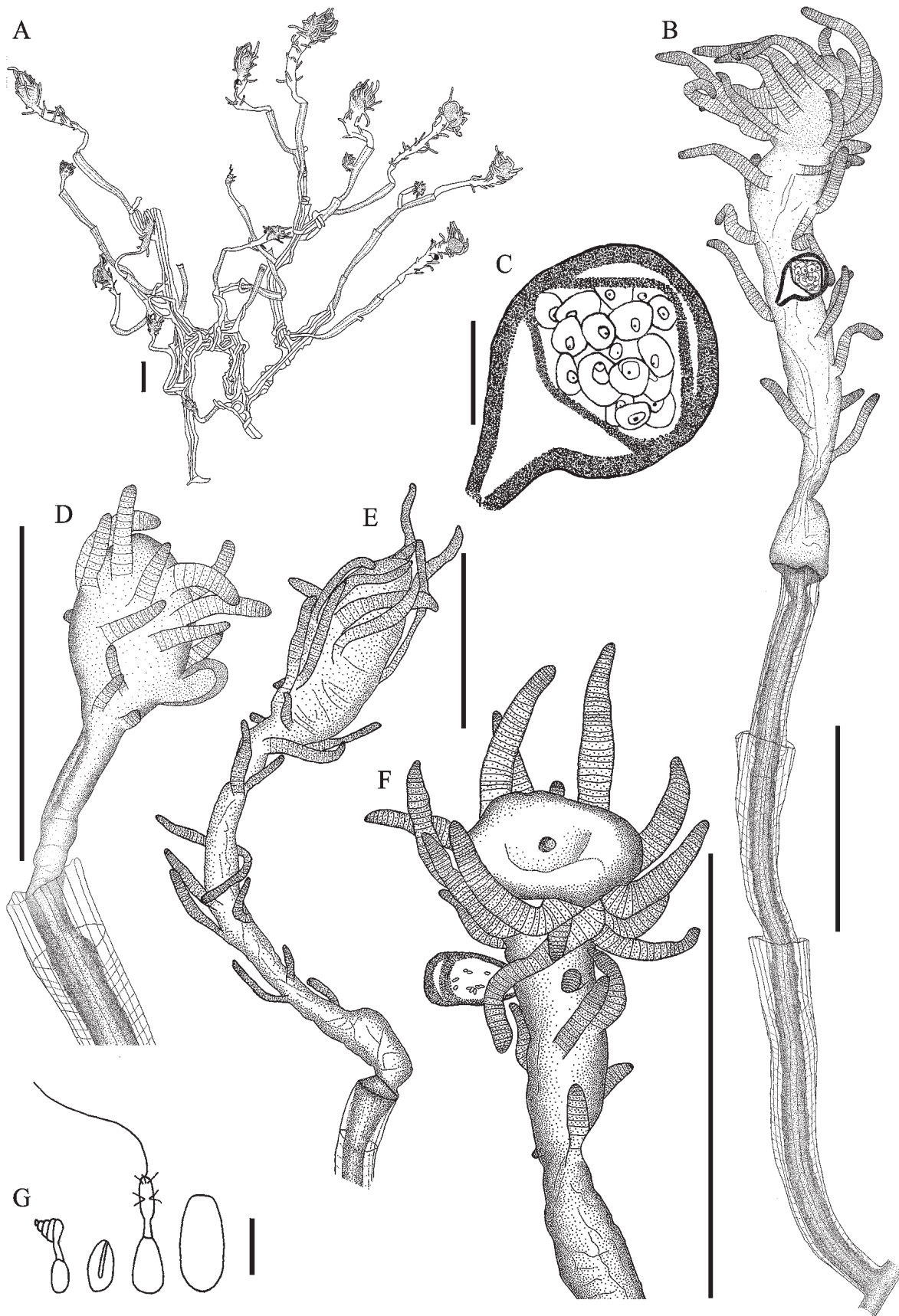


Figure 2. *Tubiclavoides striatum* gen. nov. et sp. nov.; type material. (A) General view of the colony; (B) polyp with hydranth carrying a female sporosac. Note that the perisarc of the hydrocauli is composed of three imbricated cones; (C) schema of the female sporosac with eggs; (D) hydranth with detached external perisarc layer and with a developing female sporosac; (E) sterile hydranth with oval hypostome; (F) small hydranth with a developing sporosac. On the surface of the sporosac are some large nematocyst capsules; (G) nematocysts types: desmoneme, microbasic eurytele undischarged, microbasic eurytele discharged, large unidentified type (from left to right). Scale bars: A, B, D–F, 1 mm; C, 0.1 mm; G, 0.01 mm.

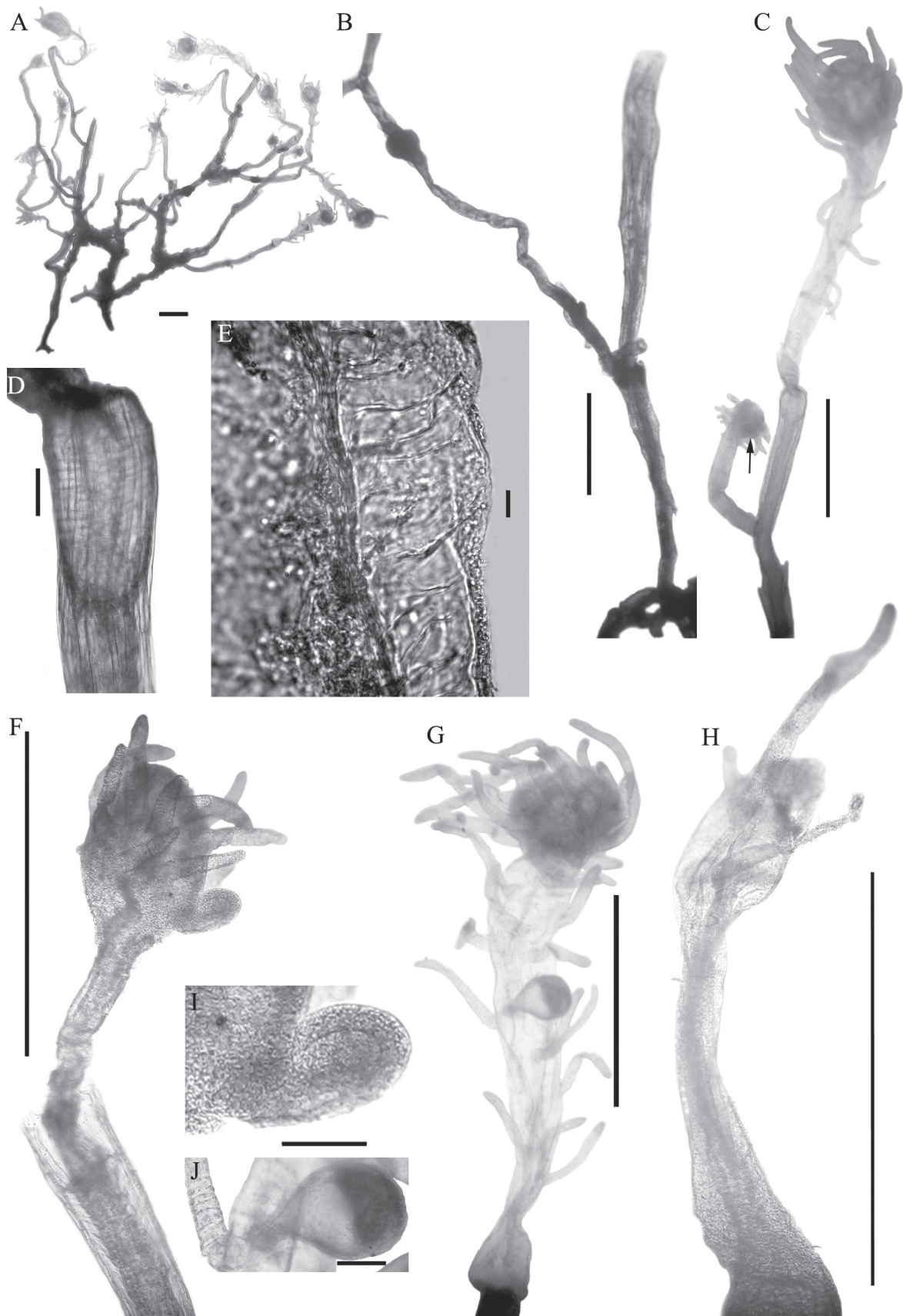


Figure 3. *Tubiclavoides striatum* gen. nov. et sp. nov. (A) General view of a well developed colony; (B) stolons with renovation points; (C) side-branch bearing a small fertile hydranth (arrow); (D) striation of perisarc in distal part of hydrocaulus; (E) higher magnification of perisarc wall of the hydrocaulus, note the two perisarc layers connected by many oblique lamellae; (F) hydranth detached from the external perisarc layer and with a developing female sporosac; (G) elongate hydranth with well-developed female sporosac; (H) unusual hydranth with only five tentacles, being some of the largest found; (I) incipient female sporosac; (J) advanced female sporosac. Scale bars: A–C, F–H, 1 mm; D, I, J, 0.1 mm; E, 0.01 mm. (All photographs from holotype, with exception of B - Station 575B and E - paratype).

RV 'Prof. Logachev', TTR15 Station AT-581-Gr, TV-assisted grab, 1 polyp. – Meknès, 34°59.137'N 7°04.343'W, 701 m, 28 July 2005, RV 'Prof. Logachev', TTR15 Station AT-585-K, kasten corer, 1 polyp. – Mercator, 35°17.917'N 6°38.717'W, 358 m, ? June 2005, RV 'Prof. Logachev', TTR15 Station AT-569-Gr, TV-assisted grab, 3 polyps. – Mercator, 35°17.903'N 6°38.715'W, 355 m, 26 July 2005, RV 'Prof. Logachev', TTR15 Station AT-575-B, box core, 10 polyps. – Mercator, 35°17.657'N 6°39.672'W, 428 m, 26 July 2005, RV 'Prof. Logachev', TTR15 Station AT-576-B, box core, 5 polyps. – Gibraltar Channel, 35°42.257'N 6°30.000'W, 380 m, 07 August 2004, RV 'Prof. Logachev', TTR14 Station AT-550-D, dredge, 1 polyp. – Gibraltar Channel, 35°42.683'N 6°30.405'W, 419 m, 07 August 2004, RV 'Prof. Logachev', TTR14 Station AT-551-D, dredge, 1 polyp. – Gibraltar Channel, 35°42.816'N 6°30.234'W, 428 m, 07 August 2004, RV 'Prof. Logachev', TTR14 Station AT-552-Gr, TV-assisted grab, 1 polyp. – Vernadsky Ridge, 35°26.066'N 6°46.788'W, 510 m, 26 July 2005, RV 'Prof. Logachev', TTR15 Station AT-574-D, dredge, 8 polyps. – TTR, 35°21.87'N 6°52.00'W, 695 m, 17 July 2002, RV 'Prof. Logachev', TTR12 Station AT-416-Gr, TV-assisted grab, 8 polyps. – Pen Duick Escarpment, 35°18.148'N 6°47.666'W, 550 m, 15 July 2002, RV 'Prof. Logachev', TTR12 Station AT-406-Gr, TV-assisted grab, 30 polyps. – Pen Duick Escarpment, 35°17.672'N 6°47.060'W, 562 m, 15 July 2002, RV 'Prof. Logachev', TTR12 Station AT-407-Gr, TV-assisted grab, 4 polyps. – Pen Duick Escarpment, 35°18.180'N 6°47.656'W, 544 m, 09 August 2004, RV 'Prof. Logachev', TTR14 Station AT-565-Gr, TV-assisted grab, 7 polyps. – Pen Duick Escarpment, 35°18.200'N 6°48.527'W, 622 m, 31 May 2005, RV 'Pelagia', M2005 Station 28 B, box core, 1 polyp.

Etymology

The name hints at the conspicuous striation of the perisarc tubes, a characteristic of this species.

Diagnosis

Colonial or solitary hydroids. Stolons often in polysiphonic bundles, with smooth perisarc. Unbranched or sparingly branched erect shoots bearing terminal hydranths. Perisarc of hydrocaulus expanding towards distal end, often subdivided into several imbricating cones, terminating at the base of the hydranth or slightly above; perisarc double-layered, with surface distinctly striated by longitudinal creases; the two perisarc layers connected by many oblique lamellae giving the impression of a cross-striation with the longitudinal striae. Hydranths with rounded hypostome and irregularly scattered filiform tentacles. Spores without perisarc covering, without tentacle rudiments, without ring or radial canals. Female spores with about ten or more eggs. Male gonophores unknown. Cnidome comprises microbasic euryteles, desmonemes, and a further, unidentified capsule.

Description

Erect solitary or colonial polyps, shoots unbranched (Figure 2B) or sparingly branched (Figure 3C) bearing usually a terminal hydranth. Hydroids adhering to hard or muddy substrates by a reticular hydrorhiza composed

of tubular stolons covered by non-striated perisarc. Stolons initially creeping on substrate and in larger colonies forming a network of fascicled stolons; perhaps these colonies are also aggregates of colonies originating through multiple colonization events (Figures 2A & 3A).

Hydrocauli covered by conical, double-layered perisarc; perisarc often regenerated and then subdivided into a set of imbricated cones (Figure 2B); outer surface of perisarc with longitudinal creases giving a fine striation pattern, striae unevenly spaced, occurring over the whole length of the hydrocaulus but getting less conspicuous towards its base. The two perisarc layers are connected by many oblique lamellae giving the impression of a cross-striation with the longitudinal ridges (Figure 3D,E).

Hydranths elongate with prominent rounded hypostome, body provided with scattered filiform tentacles. Tentacle numbers vary from five to more than 30, arranged without defined order all over the hydranth body. Tentacles solid, with central core of gastrodermal cells, tapering gently towards distal, lengths and diameters unequal, the larger ones being mainly found in the distal region. Tentacles covered by microbasic euryteles and desmonemes. An additional, a so far unidentified capsule (macrobasic heteroneme or basitrichous isorhiza), occurs in the remaining tissues, including the spores. Discharged microbasic euryteles with shaft that is about as long as the capsule (Figure 2G).

Gonophores spherical or subspherical spores with relatively long pedicels, one or two spores per hydranth located among the tentacles in the distal 2/3 of the hydranth body, not associated with the tentacles (Figures 2B,F & 3F,G). Female spores (Figures 2C,D & 3I,J) when mature with basal gastrodermal chamber that occupies about half of the volume, thus concentrating the eggs to the distal half, egg number about ten or more; distal epidermal calotte with cavity like a vestige of subumbrella (Figure 2C). According to the commonly used nomenclature (Millard, 1975) the female gonophores correspond thus of the 'heteromedusoid' type. Male spores not seen. Colour of fixed colonies: light-brown to yellow-reddish.

Details and dimensions of the preserved holotype material

Colony composed of 22 polyps connected by stolonal tubes of 0.09–0.16 mm diameter that produce a mat with about 1.3 cm diameter; two shoots without hydranth but with soft tissue in hydranth pedicel; 11 polyps with spores being sometimes somewhat smaller but otherwise apparently not different from sterile polyps; shoots usually unbranched, occasionally with a side branch; perisarc of hydrocauli composed of 1–5 imbricated perisarc cones, each 0.13–7.8 mm long and 0.08–0.43 mm in diameter; shoots 1.3–10.9 mm high; hydranth length 0.6–4 mm; hydranth pedicel diameter 0.06–0.75 mm, height 0.38–3.2 mm; proportion of hydranth length in relation to total shoot height size 53–86%; hypostome 0.2–1 mm and maximum width 0.2–0.8 mm; tentacle number 5–36, distributed in the distal 30–90% of the hydranth body, tentacle length variable from 0.008 to 0.8 mm (more proximal tentacles up to 0.66 mm, more distal tentacles up to 0.76 mm), diameter 0.01–0.14 mm; size of apparently mature spores 0.17–0.47 mm, spores pedicels lengths 0.04–0.2 mm; maximal diameter

of sporosacs 0.09–0.3 mm. Nematocysts: microbasic euryteles 6.3–9.4×3.8–5.6 µm; desmonemes 5–5.9×3.1–5.6 µm; additional capsule that could not be found discharged 11.4–16.9×5.7–7.9 µm.

Remarks

The holotype colony is the best preserved and only fertile material available. All colonies from the other sampling stations had damaged hydranths but the perisarc was rather well preserved. Therefore, branching patterns, skeletal features, associated fauna and substrate type of that material were also studied and taken into account to the description of the new species.

Tubiclavoides striatum was found at 20 sampling stations from the Moroccan margin of the Gulf of Cadiz at depths between 355 and 1105 m (Figure 1). Fertile hydranths were found only in the syntype material collected in March 2005. An identical hydroid has been found in the Porcupine Seabight (south-west of Ireland) by Dr Lea-Ann Henry (Dunstaffnage Marine Laboratory, Scotland; personal communication). This expands the known distribution of *T. striatum* considerably and it has perhaps a much wider distribution than is currently known.

Tubiclavoides striatum occurred in different types of substrate: mud breccia, carbonate chimneys and coral debris of *Madrepora oculata* and *Lophelia pertusa*. It was also found living on a sponge, a polychatete tube, an octocoral and on the hydroid *Diphasia margareta*. *Tubiclavoides striatum* may also be used as a substrate to other species; foraminifera, sponges, other hydrozoan species (e.g. *Halecium* cf. *sessile* and *Clytia* sp.), bryozoans, amphipods and tanaids were observed attached or associated to the new species. *Tubiclavoides striatum* is one of the most frequent species occurring in reducing environments where active methane seepage has been documented (e.g. Jesus Baraza, Meknès and Mercator mud volcanoes) but it also occurred in other habitats such as dead coral strands and fields of inactive carbonate chimneys.

The wide spread and frequent occurrence of *Tubiclavoides striatum* suggests that it is an important and regular faunal element of the deep-sea fauna of the north-east Atlantic.

DISCUSSION

As already discussed under Remarks for the genus, *Tubiclavoides striatum* is evidently a so far undescribed species. Its characteristic features of the perisarc make it easily recognizable, even when infertile or in the absence soft tissues. Of the total 20 sampling stations where this species was found, only the syntype material was in relatively good condition. The specimens from the other stations were quite damaged, but they could reliably be assigned to the same species due to usually well preserved perisarc.

A comparison of the 16S sequence data with several other filiferan species, notably including several genera with scattered tentacles like *Clava*, *Clavactinia*, *Rhizogeton*, *Turritopsis*, *Cordylophora* and *Corydendrium*, did not reveal any significant phylogenetic relationship of *Tubiclavoides striatum*. This indicates that the creation of a new family could be justified, but the 16S gene of hydrozoans is quite rapidly evolving and only suitable to detect relatively close relationships, e.g. at the subfamily, genera and species level (Schuchert, 2005a;

Schuchert & Reisinger, 2006; Moura et al., in preparation). Suitable representatives of potentially more closely related genera, e.g. *Millardiana*, were not present in our analysis.

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