***Astrocoryne cabela*, gen. nov. et sp. nov. (Hydrozoa : Sphaerocorynidae), a new sponge-associated hydrozoan**

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The family Sphaerocorynidae includes two valid genera and five species, most of which have a confusing taxonomic history. Here, a new genus and species, *Astrocoryne cabela*, gen. et sp. nov., is described from the Maldives and the Red Sea, based on both morphological and molecular evidence. *Astrocoryne cabela* has an apomorphy represented by the type of tentacles, here named ‘dicapitate’, and consisting of capitate tentacles with a halfway *capitulum*-like cluster of nematocysts. Molecular analyses confirmed the monophyly of this species, as well as its belonging to the Sphaerocorynidae, together with *Sphaerocoryne* spp. and *Heterocoryne caribbensis*, for which we present molecular data for the first time. Moreover, the high divergence of *A. cabela* from other species of the family justifies the establishment of a new genus. Interestingly, specimens from the Maldives and the Red Sea showed marked morphological variation in the polyp stage, although only a slight genetic divergence was detected. This study highlights that a comprehensive morpho-molecular assessment of Sphaerocorynidae is strongly needed in order to clarify the taxonomic issues and the diversity of this taxon.

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Astrocoryne cabela, gen. et sp. nov.

TOC Summary

Additional keywords: Capitata, new genus, new species, Maldives, Red Sea.

Introduction

Hydrozoan polyps are involved in interspecific associations with several other organisms, including cnidarians, sponges, bryozoans, arthropods, annelids, molluscs, echinoderms, chordates, seaweeds and seagrasses (Gili and Hughes 1995; Boero and Bouillon 2005; Puce *et al.* 2008). In some cases, hydroids are obligatorily associated with their hosts, and these intimate associations are assumed to be achieved by the selectivity of hydrozoan larvae (e.g. Conover and Sieburth 1964; Piraino *et al.* 1994; Orlov 1997). In particular, the drivers of planula settlement of some hydroid species on specific hosts are known to be

species-specific bacterial cues, such as for *Hydractinia echinata* (Fleming, 1828), for which the larval settlement and metamorphosis on gastropod shells inhabited by hermit crabs are regulated by *Pseudoalteromonas espejiana* (see Müller and Leitz 2002 for a review). Sponges are one of the most common hosts for hydrozoans (Puce *et al.* 2008), and associations may range from occasional to highly specific (Puce *et al.* 2005). To date, 26 hydrozoan species are known to live, at least partially, embedded by tissues of 28 species of sponges (Puce *et al.* 2005, 2008; Schuchert and Reiswig 2006; Brinckmann-Voss and Lindner 2008), whereas more than 100 species have been reported as occasional epibionts (Shimabukuro 2007). The specifically associated species show variable levels of integration with their sponge hosts: (i) hydranths grow into the canal system of the sponge; (ii) they protrude from the surface, but can retract into the host body; or (iii) they protrude from the surface and cannot retract into the sponge (Puce *et al.* 2005). The latter case is represented by the family Sphaerocorynidae Prévot, 1959, which has hydranths arising from the sponge surface, with the hydrorhiza embedded by host tissues. This family is composed of the two genera *Sphaerocoryne* Pictet, 1893 and *Heterocoryne* Wedler & Larson, 1986. Although *Sphaerocoryne* is rarely found on other substrates, such as corals (Calder *et al.* 2003), coral rubble (Calder 2010), bivalves (Calder 1971), serpulid tubes (Galea 2008) and other hydrozoans (Mergner and Wedler 1977; Shimabukuro *et al.* 2006), both genera are considered obligate sponge-associated taxa, especially *Heterocoryne*, which is exclusively found on sponges (Wedler and Larson 1986; Galea 2013).

The family Sphaerocorynidae was erected by Prévot (1959), and formerly included only *Sphaerocoryne*, which had been assigned to Corynidae Johnston, 1836 by previous authors. *Heterocoryne* was later discovered by Wedler and Larson (1986), and was then assigned to the same family by Petersen (1990). Molecular analyses revealed that Sphaerocorynidae belongs to the clade Capitata *sensu stricto*, and it seems to be one of the basal taxa of the superfamily Zancleida (Nawrocki *et al.* 2010; Maggioni *et al.* 2016). However, the analysis of concatenated 16S, 18S and 28S rRNA included only two *Sphaerocoryne* species and did not provide strong statistical support for their placement within Zancleida, due to either undersampling or the fact that no 18S rRNA sequences were obtained for those species.

The taxonomic histories of most species of the family Sphaerocorynidae are confusing and the validity of some taxa still needs to be assessed. To date, four valid species belong to *Sphaerocoryne*, even though for two species, *S. cocometra* (Bigelow, 1909) and *S. peterseni* Bouillon, 1984, only the medusa stage is known (Bouillon 1984; Bigelow 1909). The remaining two species, *S. agassizii* (McCrady, 1859) and *S. bedoti* Pictet, 1893, show little morphological variation, and the diagnostic characters are mainly limited to the position of medusa buds on polyps, the arrangement of nematocysts in medusa buds, the number of tentacles, and the presence of ocelli in medusae at release (Calder 2010). Moreover, these two species were previously assigned to two genera (i.e. *Corynetes* Haeckel, 1879 and *Sphaerocoryne*, respectively) and Calder (2010) and Schuchert (2010) suggested retaining the two genera as distinct, at least until a molecular phylogeny clarifies their relationship. However, no conclusions on this issue have been drawn, due to the lack of precise knowledge of life cycles and morphology. *Heterocoryne* contains a single well-established species, *H. caribbensis* Wedler & Larson 1986, whose morphological differences to *Sphaerocoryne* are clearly

represented by the arrangement of tentacles and the reproductive structures (Wedler and Larson 1986; Petersen 1990). Indeed, *Sphaerocoryne* is characterised by the presence of three to five whorls of capitate tentacles below the hypostome of the polyp, whereas *Heterocoryne* has a distal whorl of simple capitate tentacles and a proximal whorl of trifold capitate tentacles. Regarding the gonosome, *Sphaerocoryne* species reproduce via free-living medusae, whereas *Heterocoryne* bears gonophores reduced to single eumedusoids (Petersen 1990).

In this study, we describe the polyp and newly released medusa of a previously unknown species of Sphaerocorynidae collected from the Maldives and the Red Sea. By morphological and molecular analyses, the new species is assigned to a new genus, and the phylogenetic placement of the family within Zancleida is reconsidered using both mitochondrial and nuclear gene markers.

Materials and methods

Colonies of Sphaerocorynidae were collected during three separate field surveys conducted at St Eustatius, Dutch Caribbean, in June 2015, Thuwal, Saudi Arabian Red Sea in December 2015 and Magoodhoo Island, Faafu Atoll, Republic of Maldives in February 2016. Fragments of sponges associated with hydroids were sampled using plastic bags by SCUBA diving (maximum depth in all dives: 30 m), and after dives were promptly placed in water tanks at the Reef Ecology Laboratory (King Abdullah University of Science and Technology, Saudi Arabia), the Marine Research and High Education (MaRHE) Center (Università degli Studi di Milano-Bicocca, Maldives) and the Caribbean Netherlands Science Institute (CNSI). Hydroid colonies were reared in laboratory to allow the release of medusae, which were cultivated for one week. Both polyps and newly released medusae were maintained in small oxygenated bowls at room temperature, and water was replaced daily. Samples were fixed in 6% or 10% formalin and in 99% ethanol for morphological and molecular characterisations, respectively. A Zeiss Axioskope 40 microscope was used to study the morphology of medusae and polyps, the latter after being carefully detached from their host under a Leica EZ4 D stereo microscope, using syringe needles and micropipettes. All pictures were taken with a Nikon AW100 camera, and measurements were obtained with an ocular micrometer. Drawings were made by hand based on photographs and were subsequently vectorised using CorelDRAW X7.

DNA from ethanol-preserved samples was extracted following a protocol modified from Zietara *et al.* (2000). Three molecular markers were amplified: a portion of the nuclear 28S rRNA (~1700 bp) and 18S rRNA (~1700 bp), and a portion of the mitochondrial 16S rRNA (~600 bp). The PCRs were set up using the same protocols and primers described in Maggioni *et al.* (2016), Medlin *et al.* (1988), and Cunningham and Buss (1993), respectively. All PCR products were purified and directly sequenced in forwards and reverse directions using an ABI 3730xl DNA Analyzer (Applied Biosystems, Foster City, CA, USA). The sequences obtained were deposited with the EMBL (GenBank accession numbers: LT714173–LT714187), and were aligned with other representatives of Zancleida and outgroups (Table 1), using MAFFT 7.110 (Katoh and Standley 2013) with the E-INS-i option. The obtained alignments were run through Gblocks (Castresana 2000; Talavera and Castresana 2007) to remove ambiguously aligned regions, using the default ‘less

stringent' settings. The sequences were combined into a concatenated dataset and PartitionFinder 1.1.1 (Lanfear *et al.* 2012) was used to determine the partition scheme and the molecular models. Bayesian inference (BI) and maximum likelihood (ML) were used to infer phylogenetic relationships of both multi- and single-locus datasets. Bayesian inference analyses were performed using MrBayes 3.2 (Ronquist *et al.* 2012). Four parallel Markov chain Monte Carlo (MCMC) runs were carried out for 3×10^6 generations. Trees were sampled every 100th generation, and burn-in was set to 25%. Maximum likelihood trees were built with Garli 2.01 (Zwickl 2006) and read into the SumTrees 4.0.0 program in the DendroPy 4.0.0 package (Sukumaran and Holder 2010) to calculate non-parametric bootstrap support (BS) values from 1000 replicates, each based on five heuristic search replicates, and to map them on the best ML tree. Bayesian posterior probabilities (BPP) and BS values were indicated at each node. The genetic distances (uncorrected p-distance, 1000 bootstrap replicates) between samples from the Red Sea and the Maldives were also estimated using MEGA6 (Tamura *et al.* 2013).

Type material of the new species was deposited at Museo Civico di Storia Naturale di Milano (MSNM), Milan, Italy.

Results

Phylogenetic analyses

The total alignment of the concatenated *16S-18S-28S* dataset was 4006 bp long (3876 bp long after Gblock treatment), and included representatives of all the main families belonging to Capitata. The general topology of the phylogenetic trees based on BI and ML analyses were almost identical, and therefore only the Bayesian topology is shown (Fig. 1). Nuclear single-locus analyses recovered highly concordant topologies, whereas *16S* analysis showed less resolution at deeper nodes.

The overall statistical support of the tree is higher in the concatenated analysis, with most nodes supported by BPP > 0.95 or BS > 75 or both, and we therefore consider it as our most robust phylogenetic hypothesis. Our results are concordant with previous works (Nawrocki *et al.* 2010; Maggioni *et al.* 2016), recovering the superfamily Zancleida as a monophyletic lineage, with the clade composed of Pennariidae and Hydrocorynidae being the sister group of the remaining families. All our specimens of *Astrocoryneabela*, gen. et sp. nov. form a fully supported monophyletic clade that clusters with *Sphaerocoryne* spp. and *Heterocoryne caribbensis*, constituting the family Sphaerocorynidae. This family diverged early from the other taxa of Zancleida, just after the Pennariidae-Hydrocorynidae group. Moreover, the addition of new taxa and newly obtained *18S* sequences of *Sphaerocoryne* sp. to the dataset improved the statistical support of this node. All the specimens of *A. abela* share the same nuclear haplotypes for both *18S* and *28S* loci, whereas *16S* sequences of samples from the Red Sea and the Maldives are slightly divergent, with a genetic distance of 1.1(±0.5)%.

Systematics

According to the morphological features and phylogenetic placement described in ‘Phylogeny’, we describe a new species and genus of hydrozoan belonging to the family Sphaerocorynidae.

Phylum **CNIDARIA** Verrill

Class **HYDROZOA** Owen

Order **ANTHOATHECATA** Cornelius

Family **SPHAEROCORYNIDAE** Prévot

Amended diagnosis

Polyp stage

Colonies either stolonial or erect; hydrorhiza creeping; hydrocauli long, unbranched or sparingly branched, with terminal hydranths; perisarc thin, reaching hydranth base or stopping at the insertion with the hydrorhiza; hydranth pyriform, with bulbous base and proboscis-like hypostome; no oral tentacles, but single, trifid or dicapitate tentacles in one to five whorls around broadest part of body; gonophores arising above or among tentacles as free medusae or sessile eumedusoids.

Medusa stage

Eumedusoid or free medusa with thick bell-shaped or conical umbrella; apical projection, when present, conical or dome-shaped, with thick mesoglea and broad apical chamber; manubrium flask-shaped, quadrate, or cruciform, narrowing towards the mouth, the latter simple, round or cruciform; two or four tentacles with adaxial, evenly distributed, spirally arranged or absent nematocyst clusters, with a terminal, ellipsoid or spherical capitulation; marginal bulbs large, clasping exumbrella, each with adaxial expansion; ocelli abaxial, not always present in newly liberated medusae; gonads adradial, confluent in perradii in mature specimens.

Remarks

The diagnosis of the family Sphaerocorynidae is broadened by adding the unique characteristics (i.e. tentacles in hydroids and medusae) of *A.abela*. The family now includes three valid genera:

Sphaerocoryne, *Heterocoryne* and *Astrocorone*, gen. nov. *Heterocoryne* and *Astrocorone* are monotypic genera, whereas *Sphaerocoryne* includes *S. agassizii*, *S. peterseni*, *S. coccometra* and *S. bedoti*, the latter being the type species of the family.

Genus *Astrocorone*, gen. nov.

(Figs 2–4)

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Diagnosis

Polyp stage

Hydroid forming stolonial colonies; hydrocaulus short to moderately long, simple, arising from a hydrorhiza embedded in tissue of host sponge; perisarc thin, covering both the hydrorhiza and the hydrocaulus; hydranth slightly pyriform, with dicapitate tentacles in one or two alternating whorls around broadest part of the body; hypostome proboscis-like, contractile; gonophores developing among tentacles on short blastostyles.

Medusa stage

Newly liberated medusae with bell-shaped umbrella and scattered nematocysts on exumbrella; four tentacular bulbs, two of which bear an opposite tentacle, with a terminal spherical knob of nematocysts; manubrium cylindrical, with circular mouth.

Remarks

The genus *Astrocoryne*, gen. nov. differs from *Sphaerocoryne* according to the arrangement of tentacles in polyps and to the type of tentacles in both polyps and medusae. Unlike *Astrocoryne*, *Heterocoryne* bears fixed gonophores, and the proximal parts of the tentacles are partially fused in superimposed groups of three, only their distal parts remaining free from each other (see Table S1, available as supplementary material to this paper, for main diagnostic characters for all sphaerocorynid species). The genus *Bibrachium* Stechow, 1919, a poorly known sponge-associated hydroid, has two opposite capitate tentacles with an adoral cluster of nematocysts just below the terminal capitulation (Schulze 1880), the latter feature being similar to *Astrocoryne*. However, in *Bibrachium*, the cluster of nematocysts below the capitulation is restricted to the adoral side, the polyp has only two tentacles, and there is no information regarding its reproduction. The genus *Tricyclusa* Stechow, 1919 has tentacles similar to those of *Astrocoryne*, but the proximal cluster of nematocysts is often incomplete and, in some cases, three intermediate clusters, besides the terminal one, can be found (Vervoort 1949), thus resembling imperfect moniliform tentacles.

Regarding the medusa stage, *Astrocoryne* is similar to *Dicnida* Bouillon, 1978, in having a simple mouth, four bulbs, two opposed tentacles with a terminal knob of nematocysts, and an identical cnidome. However, *Dicnida* has a prominent apical projection also in juveniles, the manubrium is quadrate, tentacles are (exceedingly) long and particularly rigid and, in some cases, bear halfway secondary ramifications, each with its own terminal capitulation, non-tentaculate bulbs are extending on the exumbrella, and both the polyp stage and the size and shape of nematocysts are not known (Bouillon 1978). Consequently, *Astrocoryne* is established here as a distinct new genus.

Etymology

Astrocoryne derives from the combination of the Ancient Greek ἀστήρ ('aster'), meaning star and referring to the star-shaped aspect of the hydranth, and *Coryne*, following the structure of names of the other two genera ascribed to Sphaerocorynidae. It is a feminine noun.

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Material examined

Holotype. Sample MA16053, Maldives: Magoodhoo Island, Faafu Atoll, 3°4'1.2"N, 72°57'0"E, depth 25 m, 8.ii.2016, fertile colony growing on *Clathria* sp. sponge, preserved in 99% EtOH [ethanol] and 10% formalin, MSNMCoe341.

Paratype. Sample MA16053, **Maldives:** Magoodhoo Island, Faafu Atoll, 3°4'1.2"N, 72°57'0"E, 8.ii.2016, two-day-old medusae collected from parental colony (MSNMCoe341) and reared at the MaRHE Center in Magoodhoo Island, preserved in 10% formalin, MSNMCoe342.

Other material. Sample MA16052, **Maldives:** Magoodhoo Island, Faafu Atoll, 3°4'1.2"N, 72°57'0"E, depth 12 m, 8.ii.2016, colony growing on *Haliclona* sp. sponge, preserved in 99% EtOH and 6% formalin. Sample KA175, **Saudi Arabia:** Shark reef, Thuwal, Red Sea, 22°25'1.2"N, 38°58'58.8"E, depth 18 m, 17.xii.2015, colony growing on an unidentified tube sponge, preserved in 99% EtOH.

Diagnosis

Same as for the genus.

Description

Polyp stage

Colonies monomorphic, living in association with different sponges (Fig. 2A–C). Hydrorhiza tubular, branched, 50–65 µm in diameter, covered by moderately thick and slightly wrinkled perisarc (3–6 µm thick) (Fig. 2G), embedded by sponge tissues and giving rise to several hydranths. Pedicels short (90–190 µm) in Maldivian specimens to moderately long (450–580 µm) in specimens from the Red Sea, unbranched, covered by a smooth, thin (1–2 µm), cup-shaped or elongated perisarc (Fig. 2G, H), with a diameter at the distal portion of 50–100 µm. Hydranth slightly pyriform, up to 0.8 mm long, with variable diameter (90–100 µm at the base; 200–240 µm at the tentacle-bearing portion; 60–70 µm at the base of hypostome). Hypostome proboscis-like, contractile, 200–400 µm long and 60–100 µm thick, with a distal circular mouth (Figs 2D, 4A, B). Up to 10 tentacles (generally 8–10) arranged in either one (specimens from the Maldives) or two close whorls (specimens from the Red Sea) in the broadest part of the polyp (Figs 2D, 4A, B). Each tentacle with a terminal, nematocyst-rich capitulum (diameter: 50–85 µm in the distal whorl; 25–30 µm in the proximal whorl) and another, sub-terminal, spherical cluster of nematocysts (diameter: 70–110 µm in the distal whorl; 35–45 in the proximal whorl) (Fig. 2E). Tentacles around 500 µm long (350–530 µm) in the distal whorl, shorter in the proximal whorl (200–320 µm) when present. Nematocyst clusters ~100 µm distant from one other, moved closer by the contraction of the distal part of tentacles (Fig. 2F). Up to 11 medusa buds at different stages of maturation develop among tentacles (Fig. 2I), singly or in couple on blastostyles up to 100 µm long (Fig. 2I). Living hydranths transparent, with white mouths and whitish or light orange gastric cavities (Fig. 2A–C). Nematocysts of all types occurring simultaneously and

concentrated in the terminal and proximal capitations, as well as scattered in the hydrorhiza, more rarely in the hydranth. Cnidome: desmonemes (undischarged: $7-9 \times 4-5 \mu\text{m}$; discharged capsule: $6-8 \times 4-5 \mu\text{m}$; shaft: $5 \times 5 \mu\text{m}$, coiling three times) (Figs 2K, 4H); microbasic euryteles (undischarged: $13-15 \times 5-6 \mu\text{m}$; discharged capsule: $10-12 \times 4-5 \mu\text{m}$; shaft: $9-11 \mu\text{m}$) (Figs 2L, 4I); large stenoteles (undischarged: $18-21 \times 13-17 \mu\text{m}$; discharged capsule: $15-18 \times 11-15 \mu\text{m}$) (Figs 2M, 4D); medium-sized stenoteles (undischarged: $9-10 \times 6-7 \mu\text{m}$; discharged capsule: $8-9 \times 5 \mu\text{m}$) (Figs 2M, 4E); small stenoteles (undischarged: $5-6 \times 4-5 \mu\text{m}$; discharged capsule: $5 \times 4-5 \mu\text{m}$) (Figs 2M, 4F).

Medusa stage

Newly liberated medusa hemispherical, $460-500 \mu\text{m}$ wide and $480-500 \mu\text{m}$ high, with a velar opening of $300-350 \mu\text{m}$, and with nematocysts scattered on the exumbrella (Figs 2A, B, 3C). A short protrusion on the apical part of the exumbrella might result from liberation from the blastostyle (Fig. 3C). Manubrium cylindrical, $150-200 \mu\text{m}$ long and $80-110$ wide at the base, spanning from one-third to half of the bell height, distally provided with a circular mouth (diameter $50-75 \mu\text{m}$), with no additional oral structures and no incipient gonads (Fig. 3B, C). Four radial canals end in four bulbs with a diameter of $60-70 \mu\text{m}$, linked by a circular canal (Fig. 3D). Both bulbs and circular canal contain nematocysts. When released, medusae with no tentacles, but all bulbs show swellings filled with nematocysts (Fig. 3A). Two days after release, medusae with two opposite tentacles (Fig. 3B, D). Tentacles up to $300 \mu\text{m}$ long, armed with terminal spherical nematocyst-rich capitations with diameter $70-85 \mu\text{m}$ (Fig. 3E, F). Ocelli not present at release. Nematocysts scattered on the exumbrella (microbasic mastigophores and rarely microbasic euryteles similar to those found in polyps), in the circular canal (stenoteles), in the bulb swellings and in the terminal capitations of tentacles (stenoteles and desmonemes). Cnidome: microbasic euryteles (undischarged: $14 \times 5 \mu\text{m}$) (Fig. 3G, 3I); microbasic mastigophores (undischarged: $6-7 \times 5-7 \mu\text{m}$; discharged capsule: $5 \times 5 \mu\text{m}$; shaft: $5 \mu\text{m}$) (Figs 3H, 4G); stenoteles ($9-11 \times 8-10 \mu\text{m}$; discharged capsule: $8-9 \times 7 \mu\text{m}$) (Figs 3I, 4E); desmonemes (undischarged: $7-8 \times 4-5 \mu\text{m}$; discharged capsule: $6 \times 4 \mu\text{m}$; shaft: $5 \times 5 \mu\text{m}$, coiling three times) (Figs 3J, 4H).

Relationship with the host, habitat and distribution

Astrocoryne cabela, gen. et sp. nov. was found in association with three different sponges: *Haliclona* sp., *Clathria* sp. and an unidentified tube sponge. However, specimens of these sponges were found at the same areas and depths with no associated hydroids. The hydrozoan colonies occupied in all cases a small area of the sponges and the polyps were distributed with no apparent spatial preferences on the host. Slight differences were noticed in the reaction of sponges to the presence of hydroids: *Clathria* sp. surrounds the base of the polyps forming a cone-shaped collar (Fig. 2A), whereas *Haliclona* sp. and the tube sponge show no apparent modifications (Fig. 2B, C). Interestingly, the material from the Red Sea shared the sponge host with a colony of *Sphaerocoryne* sp., for which the identification to species level was not possible due to the lack of reproductive structures. *Astrocoryne cabela* was observed between 12 and 25 m depth, although deeper or shallower distribution limits cannot be excluded. The known geographic distribution is limited to the central Red Sea (Thuwal) and to the central Maldives (Faafu Atoll).

Remarks

Astrocoryne cabela from the Red Sea and the Maldives shows variation in the arrangement of tentacles and in the length of the pedicel (Table 2). Specimens from the Maldives have one whorl of tentacles, whereas polyps from the Red Sea have two whorls of tentacles, the proximal one being shorter and provided with smaller nematocyst knobs. However, they both share the apomorphy of having a proximal cluster of nematocyst in all tentacles and we named this new type of tentacle ‘dicapitate’. The perisarc in Maldivian specimens stops at the base of polyps, resulting in a short pedicel, while in the Red Sea samples the pedicel is longer and the perisarc almost reaches the proximal whorl of tentacles. As the colonies found in the Red Sea were not fertile, the medusa was not observed, leaving uncertainties about other possible morphological differences in the two populations in this life-cycle stage. The Maldivian medusae developed two opposite tentacles two days after their release and were cultivated for a total of seven days, during which they did not show any further morphological variation. However, we cannot exclude that the adult medusa might develop four tentacles, similarly to what happens in *Sphaerocoryne agassizii* (McCrady 1859) and further surveys are needed to describe the morphology of mature medusae and fully characterise the life cycle of this species.

Etymology

The species name *cabela* refers to the name of the house where the parents of DM live, in recognition of their support over the years.

Discussion

Sponges provide habitat for a large number of species belonging to several taxa (Wulff 2006), and due to the richness of their associated fauna, they have been called ‘living hotels’ (Pearse 1950). Many of the associated organisms live inside the canal system, where they can find food and shelter (Tyler and Böhlke 1972; Rützler 1978), whereas others live epibiontically on their outer surface, where, for instance, they might benefit from the water renewal generated by the sponge itself (e.g. Uriz *et al.* 1992). Only two species of hydrozoans are known to live as sponge endosymbionts and correspond to *Bibrachium euplectellae* (Schulze, 1880) and *Brinckmannia hexactinellidophila* Schuchert & Reiswig, 2006, both associated with hexactinellid sponges (Schulze 1880; Schuchert and Reiswig 2006). However, most of the sponge-associated hydrozoans can be considered as partial endosymbionts, as their hydrorhizae are surrounded by the host and the hydranths protrude from sponge tissues (Puce *et al.* 2005). The families Tubulariidae Goldfuss, 1818, Corynidae and Sphaerocorynidae contain the highest number of sponge-associated species, but only the latter is known to have all its members specifically associated with sponges (Puce *et al.* 2005). This idea is confirmed by the description of *Astrocoryne*, which was exclusively found in association with sponges. The hydroids of *A. cabela* were clearly assignable to Sphaerocorynidae due to their morphology and, in particular, to the pyriform shape of the hydranth, the proboscis-like hypostome and the tentacles arranged in one or a few whorls below the hypostome, among which the gonophores arise. However, this species shows an apomorphy, represented by the peculiar type of tentacles that necessitated creation of a new genus. Additionally, molecular phylogenetic analyses confirmed the position of this species within

Sphaerocorynidae and showed a high genetic divergence from *Sphaerocoryne* species and *Heterocoryne caribbensis*, supporting the establishment of a new genus.

The type of tentacles represents one of the main differences among the hydranths belonging to different genera of Sphaerocorynidae (Petersen 1990) (Fig. 5; Table S1), and both *Astrocorone* and *Heterocoryne* bear apomorphic tentacles. In *Sphaerocoryne*, the tentacles are simple capitate (Fig. 5A) and, in some cases, have been reported as grouped in longitudinal rows (Yamada and Konno 1973). Tentacles of the proximal whorl in *H. caribbensis* consist of three capitate tentacles partially fused longitudinally in their proximal halves, but still showing their own rows of endodermal cells (Fig. 5B) (Wedler and Larson 1986; Galea 2013), slightly resembling the ramified capitate tentacles of *Cladocoryne* Rotch, 1871, the latter having nevertheless the endoderm of the axis of tentacle and ramifications fused (Prévot 1959). Finally, *A.abela* has capitate tentacles with a proximal cluster of nematocysts resembling a halfway capitulum (Fig. 5C). According to Prévot (1959), the most ancestral state of tentacles is represented by a nematocyst button, followed by the capitate tentacle, and all other types of tentacles evolved from this condition. Following this classification, *Sphaerocoryne* has the most ancestral tentacles among Sphaerocorynidae, having all capitate tentacles, whereas *Astrocorone* and *Heterocoryne* have more derived tentacles. The double capitation in *Astrocorone* polyps may derive from a duplication event in the proximal-distal axis of tentacles (Fig. 6). Less-regulated duplication events may be responsible for other peculiar tentacles, such as those of *Tricyclusa singularis* (Schulze, 1876), and repeated events may be the explanation for moniliform tentacles. The unique condition of proximal tentacles in *Heterocoryne* polyps may be either the result of partial duplication events along the mid-lateral axis of capitate tentacles or the partial fusion of already divided tentacles (Fig. 6). Therefore, detailed histological analyses, as well as the study of the expression patterns of homeotic genes involved in the development of tentacles, are needed to shed light on the evolution of tentacles in both sphaerocorynid and other capitate hydrozoans.

The association between hydroids and their hosts is usually constant (Puce *et al.* 2005) and, in some cases, molecular analyses demonstrated that hydrozoan species associated with different hosts actually constitute species complexes, with different molecular groups associated with specific hosts (Montano *et al.* 2015, 2017; Maggioni *et al.* 2016). Sphaerocorynid polyps have been mostly reported growing on unidentified sponges, and only in few cases the identification of the host, at least at genus level, was provided. In particular, *Sphaerocoryne bedoti* is known to be associated with at least nine sponge genera and as many species (Calder 1971; Yamada and Konno 1973; Wedler and Larson 1986; Varela 2012), whereas *H. caribbensis* has been reported so far to live in association with sponges probably belonging to the genus *Mycale* Gray, 1867 (Wedler and Larson 1986) (see Table S1 for known sponge hosts). Throughout our surveys, we found *A.abela* on three different sponges and, in one case, we recorded it as sharing the same sponge host together with a colony of *Sphaerocoryne*, suggesting that the former species could be a generalist symbiont of poriferans. Therefore, according to the literature and our results, hydrozoans ascribed to Sphaerocorynidae do not seem to have evolved species-specific relationships with their hosts, although further in-depth multi-disciplinary analyses of these associations are needed to address this question. For

instance, sponge-associated micro-organisms may have a role in the settlement and metamorphosis of sphaerocorynid planulae, similarly to what happens for instance for *Hydractinia echinata* (Müller and Leitz 2002), and microbiome-related studies may help identifying specific shared microbial components among different sponges.

The analysed specimens of *A. cabela* from the Red Sea and the Maldives showed some morphological differences in the polyp stage, that is, the length of the pedicel and the number of tentacle whorls, and these variations might normally be marked enough to allow the distinction of the samples from the two localities as two distinct species. Nevertheless, according to the molecular analyses, all samples show only a slight genetic divergence that can be observed solely in the mitochondrial marker, and that is likely to be due to the geographic distance other than a speciation event. These differences seem therefore to be better explained by intra-specific morphological variation, a common phenomenon in hydrozoans that can be related to environmental conditions and ontogeny (Cunha *et al.* 2016). It is likely that unexplored biotic and abiotic ecological factors might contribute, synergistically or not, to the observed morphological variation. For instance, differences in hydranths might be related to salinity (e.g. Kinne 1957; Kinne and Paffenhöfer 1965), which differs by about five psu between the two sampling localities (Reimer *et al.* 2017; Seveso *et al.* 2017), and variations in the pedicel might be due to distinct reactions of the polyps to different hosts. However, the Red Sea is known to be a hotspot of biodiversity and endemism (Hughes *et al.* 2002), and is characterised by a peculiar geological history and several barriers (see DiBattista *et al.* 2016 for a review) that might be responsible for ongoing speciation between populations from the Maldives and Saudi Arabia. *Astrocoryne cabela* is likely to be present also in other localities in the Red Sea and in the Indo-Pacific, and both the inclusion of other geographic areas in the molecular analyses and the morphological study of all life stages for all populations may clarify the diversity and genetic structure of this hydroid. Finally, a comprehensive molecular and morphological appraisal of the whole Sphaerocorynidae family is necessary to clarify the taxonomic problems of all species and genera, and to assess the diversity, biogeography and evolution of these often reported, but poorly known, hydrozoans.

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Fig. 1. Bayesian inference tree obtained from the concatenated dataset of nuclear *18S* and *28S* loci and mitochondrial *16S* gene under the GTR+G+I model. Black circles on nodes indicate Bayesian posterior probabilities (BPP) > 0.95 and bootstrap support (BS) > 75 on combined analysis, whereas grey circles indicate BS > 75 and white circles indicate BPP > 0.95. Node values represent BPP on single-gene *16S-18S-28S* analyses; × indicates that one of the taxa is not included in the analysis; - indicates that the node does not exist.

Fig. 2. (A–M) Polyp stage of *Astrocoryneabela*, gen. et sp. nov. (A) Fertile colony associated with *Clathria* sp. from the Maldives; (B) polyp growing on *Haliclona* sp. from the Maldives; (C) specimen associated with a tube sponge from Saudi Arabia; (D) photomicrograph of an anesthetised fertile polyp; (E) extended tentacle showing the two clusters of nematocysts; (F) contracted tentacle; (G) detail of the insertion of the pedicel into the hydrorhiza; (H) cup-shaped perisarc covering the basal part of hydranth; (I) fertile polyp with 11 medusa buds at different stages of maturation; (J) blastostyle bearing two medusa buds; (K) desmonemes; (L) microbasic eurytele; (M) stenoteles of three size classes. Scale bars = A–C 250 µm; D, I 100 µm; E–H, J 40 µm; K–M 5 µm. Abbreviations: Hy, hydrorhiza; Pe, pedicel; Sp, sponge; sS, small stenotele; mS, medium-sized stenotele; lS, large stenotele.

Fig. 3. (A–J) Medusa stage of *Astrocoryneabela*, gen. et sp. nov. from the Maldives. (A) Medusa, a few minutes after release; (B) two-day-old medusa with comparatively longer manubrium and two opposite tentacles; (C) detail of the manubrium and the protrusions on the apical part of exumbrella; (D) basal view of a medusa; (E) extended tentacle; (F) detail of the nematocyst-rich terminal swelling of a tentacle; (G) microbasic eurytele; (H) microbasic mastigophore; (I) stenotele; (J) desmonemes. Scale bars = A, B 100 μ m; C–E 50 μ m; F–J 5 μ m.

Fig. 4. (A–I) *Astrocoryneabela*, gen. et sp. nov. (A) Fertile polyp from the Maldives; (B) polyp from Saudi Arabia; (C) medusa from the Maldives; (D) large stenotele; (E) medium-sized stenotele; (F) small stenotele; (G) microbasic mastigophore; (H) desmoneme; (I) microbasic eurytele. Scale bar = A–C 200 μ m; D–I 20 μ m.

Fig. 5. Type and arrangement of tentacles in Sphaerocorynidae: (A) *Sphaerocoryne*; (B) *Heterocoryne*; (C) *Astrocoryne*.

Fig. 6. Different type of tentacles and their possible evolution. (A) Primordial nematocyst button; (B) capitate tentacle; (C) dicapitate tentacle; (D) moniliform tentacle; (E) capitate tentacles in multiple whorls; (F) partially fused capitate tentacles that may have derived from partial duplication (black arrow) or partial fusion (white arrow) events.

Table 1. Specimens included in the analyses and associated GenBank accession numbers

Family	Genus	Species	Specimen code	Locality	GenBank accession numbers		
					16S	18S	28S
Asyncorynidae	<i>Asyncoryne</i>	<i>ryniensis</i>	KUNHM2639	Japan	EU8765 52	EU87657 8	GQ42428 9
Cladocorynidae	<i>Cladocoryne</i>	<i>floccosa</i>	LEM S40/AL1407	Brazil	KT2666 07	EU27260 8	KT75717 3
Cladocorynidae	<i>Cladocoryne</i>	<i>haddon</i>	MA200	Maldives	LT5938 65	LT59387 5	LT59387 0
Cladocorynidae	<i>Pteroclava</i>	<i>krempfi</i>	MA181	Maldives	LT1582 09	LT59387 6	LT22203 9
Hydrocorynidae	<i>Hydrocoryne</i>	<i>miurensis</i>	KUNHM2814	Japan	GQ3953 26	–	GQ42431 3
Milleporidae	<i>Millepora</i>	<i>alcicornis</i>	AGC2001/AMN20 08	–	EU8765 51	AF35808 8	EU87995 0
Moerisiidae	<i>Moerisia</i>	<i>inkermani</i>	LEM m3x S41	Brazil	KT2666 26	KT72240 8	KT75716 1
Moerisiidae	<i>Odessia</i>	<i>maeotica</i>	MHNGINVE5364 2	France	GQ3953 4	GQ42434 1	GQ42434
Pennariidae	<i>Pennaria</i>	<i>disticha</i>	MZUSP:1670	Brazil	KT2666 35	KT72242 1	KT75712 9
Porpitidae	<i>Porpita</i>	<i>porpita</i>	CWD147	–	AY9353 22	GQ42431 9	EU88355 1
Porpitidae	<i>Velella</i>	<i>velella</i>	Sch71	France	EU3054 87	EU87657 6	EU87994 9
Solanderiidae	<i>Solanderia</i>	<i>ericopsis</i>	MHNGINVE2959 3	New Zealand	AY5125 30	EU27263 6	EU27259 3
Solanderiidae	<i>Solanderia</i>	<i>secunda</i>	KUNHM 2611	Japan	EU3054 84	EU30550 2	EU30553 3
Sphaerocorynidae	<i>Astrocoryne</i>	<i>cabela</i>	KA175	Saudi Arabia	LT7141 73	LT71417 4	LT71417 5
Sphaerocorynidae	<i>Astrocoryne</i>	<i>cabela</i>	MA217	Maldives	LT7141 76	LT71417 7	LT71417 8
Sphaerocorynidae	<i>Astrocoryne</i>	<i>cabela</i>	MA218	Maldives	LT7141 79	LT71418 0	LT71418 1
Sphaerocorynidae	<i>Heterocoryne</i>	<i>caribbensis</i>	SE005	St Eustatius	LT7141 85	LT71418 6	LT71418 7
Sphaerocorynidae	<i>Sphaerocoryne</i>	sp.	MA205	Maldives	LT7141 82	LT71418 3	LT71418 4

Sphaerocorynidae	<i>Sphaerocoryne</i>	<i>agassizii</i>	PCSphAg/PC005	Florida	GQ395323	–	GQ424318
Zancleidae	<i>Zanclea</i>	<i>costata</i>	MHNGINVE26507	France	AY512531	EU876579	EU879951
Zancleidae	<i>Zanclea</i>	<i>gallii</i>	MA058	Maldives	LN714107	LT593874	LT593869
Zancleidae?	<i>Zanclea</i>	<i>prolifera</i>	KUNHM2793	Japan	EU305488	EU272639	EU272598
Outgroups							
Corynidae	<i>Stauridiosarsia</i>	<i>ophiogaster</i>	KUNHM 2803	Japan	EU305473	EU272615	EU272560
Corynidae	<i>Sarsia</i>	<i>striata</i>	MHNGINVE35765	Scotland	GQ395328	GQ424338	GQ424311
Corynidae	<i>Coryne</i>	<i>uchidai</i>	MHNGINVE49102	Japan	GQ395320	GQ424332	GQ424306
Corynidae	<i>Scrippsia</i>	<i>pacifica</i>	–	California	AY512551	AF358091	AY920804
Cladonematidae	<i>Staurocladia</i>	<i>wellingtoni</i>	MHNGINVE25379	New Zealand	AY787882	GQ424323	EU879948
Ptilocodiidae	<i>Hydrichthella</i>	<i>epigorgia</i>	KUNHM 2665	Japan	EU305478	EU272622	EU272569
Candelabridae	<i>Candelabrum</i>	<i>cocksii</i>	MHNGINVE29591	France	AY512520	EU876556	EU879928
Olindiidae	<i>Olindias</i>	<i>phosphorica</i>	MHNGINVE29811	Spain	AY512509	AY920753	EU247808

Table 2. Comparative measurements of *Astrocoryneabela* (in micrometre) based on specimens from the Maldives and Saudi Arabia

	Locality	
	Maldives	Red Sea
Hydranth		
Length	600–800	400–600
Diameter at base	90–100	65–75
Diameter at tentacle portion	200–240	200–250
Diameter at the base of hypostome	65–70	40–50
Length of hypostome	200–250	100–120
Pedicle		
Shape	Cup-shaped	Tubular
Length	90–190	450–480
Diameter	80–100	50–65
Tentacles		
Number	8–10	8–9
Length	350–500	200–500
Whorls	1	2
Diameter of terminal capitula	50–85	55–60
Diameter of proximal ‘capitula’	80–110	65–70
Cnidome		
Small stenoteles	5–6 × 4–5	6 × 4–5
Medium-sized stenoteles	9–10 × 5–6	8–9 × 5–7
Large stenoteles	18–21 × 13–16	19–20 × 14–17
Desmonemes	7–8 × 4	7–9 × 4–5
Microbasic euryteles	13–15 × 5–6	14–15 × 5–6

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6