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A morphological review of the jellyfish genus *Nausithoe* Kölliker, 1853 (Nausithoideae, Coronatae, Scyphozoa, Cnidaria)

CLARISSA G. MOLINARI[1,2*], ALLEN G. COLLINS[3,4] & ANDRÉ C. MORANDINI[1,5]

[1]*Departamento de Zoologia, Instituto Biociências, Universidade de São Paulo, Rua do Matão, travessa 14, n. 101, Cidade Universitária, São Paulo, SP, 05508-090, Brazil*
acmorand@ib.usp.br; https://orcid.org/0000-0003-3747-8748
[2]*School of Environment and Science, Gold Coast Campus, Griffith University, Southport, QLD 4222, Australia*
[3]*National Systematics Laboratory, Office of Science and Technology, NOAA National Marine Fisheries Service, MRC-153, Washington, DC 20013-7012, USA*
allen.collins@noaa.gov; https://orcid.org/0000-0002-3664-9691
[4]*Department of Invertebrate Zoology, Smithsonian National Museum of Natural History, MRC-163, Washington, DC 20013-7012, USA*
[5]*Centro de Biologia Marinha, Universidade de São Paulo, Rodovia Manuel Hypólito do Rego km 131.5, São Sebastião, SP, 11612-109, Brazil*
**Corresponding author: clarissamolinari@gmail.com; https://orcid.org/0000-0003-4086-6020*

Abstract

In this study we address the diversity of the scyphozoan jellyfish genus *Nausithoe* Kölliker, 1853 (Nausithoidae, Coronatae), questioning the feasibility of using some characters of the medusa stage to identify species and filling in gaps concerning species of the genus and their distributions. Like most scyphozoans, the vast majority of the 21 *Nausithoe* species have a metagenetic life cycle, but similarity of most polyps within the genus highlights the need for studying morphology of the medusa stage. By analyzing morphological features on preserved and live specimens (polyps and medusae) and comparing these data with the original descriptions, we were able to validate twenty species of the group, providing new information for some of them.

Key words: Deep-sea, medusae, polyp, periderm tube, taxonomy, systematics

Introduction

Among the scyphomedusae (Cnidaria, Scyphozoa) the order Coronatae Vanhöffen, 1892 comprises six families: Atollidae Hickson, 1906; Atorellidae Vanhöffen, 1902; Linuchidae Haeckel, 1880; Nausithoidae Haeckel, 1880; Paraphyllinidae Maas, 1903; and Periphyllidae Haeckel, 1880; totaling 60 accepted species (Jarms & Morandini 2019, WoRMS). Most coronate diversity is represented by deep-sea animals (38 species) (Kramp 1961). The main diagnostic feature of coronates is the coronal furrow (groove) on the exumbrella (Mayer 1910). Prior to this work, the genus *Nausithoe* Kölliker, 1853 (family Nausithoidae) comprised 21 accepted species that together have a wide distributional range, occurring from shallow waters to at depths of at least 2,600m (Jarms & Morandini 2019, Molinari *et al.* 2020). *Nausithoe* medusae are mainly small, with 16 marginal lappets, eight rhopalia and eight tentacles, alternating between lappets, and eight adradial gonads beneath or outside the coronal furrow (Fig. 1)

Several authors (*e.g.,* Werner 1973; Jarms 1990; Silveira & Morandini 1997) have emphasized the importance of studying life cycles as a means for unravelling the taxonomic identity of coronate species. Most *Nausithoe* species have typical metagenesis (Jarms 1990; Silveira & Morandini 1997) and study of the adult form (*i.e.*, the medusa stage) is imperative to differentiate them (Jarms 1990). This is because most *Nausithoe* polyps exhibit great morphological similarity, making it difficult to identify species by only examining this semaphoront of the life cycle. The identification of preserved polyps almost always remains at the family or generic level (Jarms *et al*. 2002a; Molinari & Morandini 2019); although for certain species the polyp tubes can be identified to species (*e.g.*, Morandini & Jarms 2005, 2010, 2012). Moreover, not all *Nausithoe* species exhibit the typical metagenetic life

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cycle. *Nausithoe planulophora* (Werner, 1971) and *N. racemosa* (Komai, 1936), for example, do not have medusa stages (Werner 1970; Werner & Hentschel 1983).

Nausithoe medusae are members of planktonic communities of different environments. Although they have been reported in historical surveys (*e.g.,* Gegenbaur *et al.* 1853; Agassiz & Mayer 1902; Vanhöffen 1902; Stiasny 1935; Bigelow 1938), they are rarely reported in more recent studies (Pagès *et al.* 1992; Suárez-Morales *et al.* 2002; Gershwin & Zeidler 2003; León *et al.* 2005; Neumann-Leitão *et al.* 2008; Nogueira *et al.* 2015). In more recent years (since 2016), with the widespread use of smartphones and social media (mainly Facebook® and Instagram®), it has become more common to find groups of amateur and professional divers and underwater photographers that from time-to-time post photos of *Nausithoe* polyps and medusae.

As the differentiation of *Nausithoe* species can be difficult, in this study we present a review of the morphological characters that can be used to define and distinguish its species. To support this review, we studied 379 medusae, approximately 130 ephyrae, 112 solitary polyps and 5 colonies (with more than 50 polyps each) of the group, available in four museums and our own laboratory cultures and collections. We also propose a new terminology to describe the bell morphology of *Nausithoe* medusae, which should also have utility when applied to other coronate groups.

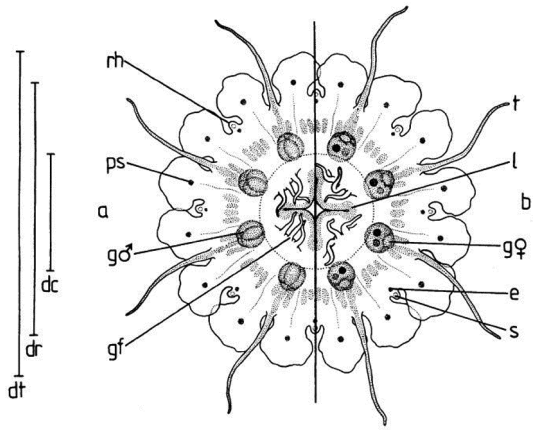

FIGURE 1. Schematic view of an adult medusa of the genus *Nausithoe* (based on the species *N. aurea* = *N. maculata*) illustrating the characters to be observed. Note that on the right side (**b**) a female medusa is represented, and on the left side (**a**) a male individual. **dc**—diameter of the coronal groove; **dr**—diameter between rhopalia; **dt**—total diameter; **gf**—bud of gastric filament; **l**—lips around mouth; **ml**—marginal lappets; **rh**—rhopalium; **t**—tentacle; **e**—eyespot; **g—**male and female gonads; **ps**—pigment spot; **s**—statolith; (adapted from Jarms *et al*. 2002b).

Methods

Our morphological data were derived from observations of living and preserved specimens (4% formalin-seawater solution or 70% ethanol), in addition to photos obtained from professional divers, underwater photographers and the Monterey Bay Aquarium Research Institute (MBARI) Video Annotation and Reference System (VARS) database (dsg.mbari.org/dsg/datause). Living polyps and medusae were mostly obtained from collections along the Brazilian coast and from the laboratory of Prof. Dr. Gerhard Jarms (Universität Hamburg, Germany); the living animals were kept in the Zoology Department (Biosciences Institute—University of São Paulo, Brazil). Preserved specimens were obtained from different museum collections (Table 1 and Supplementary Materials S1 and S2), and observations were conducted at the Smithsonian's National Museum of Natural History (NMNH) Museum Support Center (Suitland MD) and the Department of Invertebrate Zoology of the Natural History Building (Washington DC, USA). As coronate specimens (either polyps or medusae) are challenging to identify and some identifications were performed by non-experts in the group, we re-examined all specimens and images of individuals available, assessing the main features recognized in Nausithoidae medusae and polyps as stated by Jarms *et al.* (2002b) and represented in Fig. 1. Specifically, examinations considered the following: color and thickness of the mesoglea; shape, length and number of marginal lappets; shape and size of mouth lips; rhopalium organization and form; thickness and shape of subumbrellar musculature; shape and subdivisions of gastrovascular cavity; shape, size and

color of gonads; shape and size of tentacles; arrangement and number of gastric filaments; presence of nematocysts clusters; general shape of umbrella and central dome; as well as additional features observed in some specimens.

TABLE 1. Number of lots analyzed from each museum.

Species	Museum	Locality	N of lots
N. rubra, N. punctata, N. maculata, N. marginata, N. simplex, N. racemosa, N. challengeri	Smithsonian's National Museum of Natural History (NMNH)	Washington, D.C., USA	79
N. atlantica, N. challengeri, N. globifera, N. punctata.	Natural History Museum (NHM)	London, United Kingdom	13
Nausithoe rubra	American Museum of Natural History (AMNH)	New York, USA	1
N. hagenbecki, N. marginata, N. werneri, N. punctata, N. simplex	Zoological Museum Hamburg (ZMH)	Hamburg, Germany	19
Nausithoe picta	Zoological Museum Amsterdam (ZMA)	Amsterdam, Germany	1
Nausithoe striata	Berlin Zoological Museum (ZMB)	Berlin, Germany	1

Results

We note several issues that complicated examination of some of the specimens from the collections. Some were not possible to identify because of poor preservation, lack of diagnostic characters, or for being too young (adult morphology not yet achieved). We also excluded those specimens wrongly identified as *Nausithoe* (*e.g.*, *Paraphyllina* sp.—NHM 1970.10.8.225).

In total, we observed 626 specimens (polyps, ephyrae, medusae) from museum collections in addition to live specimens from laboratory cultures, annotating every individual for the characters mentioned above, except for: thickness and shape of subumbrellar musculature and shape and subdivisions of the gastrovascular cavity. These characters were barely visible in most specimens due to preservation techniques and time in preservative. We also recorded the specimens' pigmentation even though it is known that fixatives might impact pigmentation.

We propose new terms to help distinguish and define bell outlines of *Nausithoe* medusae in a more standardized way. The terminology described below is based on the height of the central disk in relation to the rest of the umbrella of adult medusae. There are three different types (Fig. 2): **hypodome** (Greek *hypo* = under, less than + Latin *domus* = roof)—dome height smaller than the distance from groove to bell margin; **isodome** (Greek *isos* = equal, like + Latin *domus* = roof)—dome height about the same (± 1.2x) size as the distance from groove to bell margin; and **hyperdome** (Greek *hyper* = beyond, over + Latin *domus* = roof)—dome higher than the distance from groove to bell margin.

We observed 15 of the 21 described species of the genus. All species and their descriptions are presented below and summarized in Supplementary Materials (S3). A list of valid species is summarized in Table 2 and depth distribution of the species that have this information available is represented in Fig. 3. As a result of our review, we synonymize *Nausithoe albida* Gegenbaur, 1856 and *Nausithoe punctata* Kölliker, 1853, at least partly based on the shared type locality of both species (Mediterranean Sea). *Nausithoe albida* is poorly described, with no image and no holotype material available to be analyzed. We believe the specimens used to describe this species are likely to be *N. punctata*, perhaps in a different stage of maturity or ontogenetic growth, but without sufficient detail to allow the two species to be differentiated.

TABLE 2. Updated list of the 20 valid species of the genus *Nausithoe* Kölliker, 1853, and brief information about life cycle and geographical distribution (with new localities for some species, obtained from museum specimens).

valid Species name	Polyp	Medusa	Synonyms	Distribution	New localities
Nausithoe albatrossi	Not known	Present		E Pacific, deep sea	-
			Nauphanta albatrossi	E Pacific, deep sea	
Nausithoe atlantica	Not known	Present		N Atlantic, deep sea	NE Pacific, USA
Nausithoe challengeri	Not known	Present		S Atlantic, deep sea	Mid N Atlantic
			Nauphanta challengeri	S Atlantic, deep sea	
Nausithoe clausi	Not known	Present		N Pacific, E of Caroline islands	-
Nausithoe eumedusoides	Solitary	Reduced		Mediterranean, submarine caves	-
			Stephanoscyphus eumedusoides	Mediterranean, submarine caves	
Nausithoe globifera	Solitary	Present		NE Atlantic, deep sea	Mediterranean
Nausithoe hagenbecki	Solitary	Present		unknown, aquarium animal	-
Nausithoe limpida	Not known	Present		NW Atlantic, deep sea	-
Nausithoe maculata	Solitary	Present		W Atlantic, shallow water	-
			Nausithoe aurea	SW Atlantic, shallow water	
Nausithoe marginata	Solitary	Present		Mediterranean, shallow water	Puerto Rico
Nausithoe picta	Not known	Present		Malayan Archipelago and CE Pacific	-
Nausithoe planulophora	Solitary	Absent		Mediterranean, submarine caves	-
			Stephanoscyphus planulophorus	Mediterranean, submarine caves	
Nausithoe punctata	Colonial	Present		Worldwide(?), shallow water	-
			Stephanoscyphus mirabilis	Antibes, France	
			Nausithoe albida	Messin, Italy	
			Nausicaa phaecum	Corfu, Greece	
			Liniscus cyamopterus	Cape Verde, W Africa	
			Nausithoe punctata var. *pacifica*	Suva Island, Fiji	
Nausithoe racemosa	Colonial	Reduced		Japan, shallow water	-
			Stephanoscyphus racemosus	Japan, shallow water	
Nausithoe rubra	Not known	Present		Worldwide(?), deep sea	-
Nausithoe simplex	Solitary	Not known		NW Atlantic, deep sea	-
			Stephanoscyphus simplex	S Greenland	
			Stephanoscyphistoma simplex	S Greenland	
Nausithoe sorbei	Solitary	Present		NE Atlantic, deep sea	-
Nausithoe striata	Solitary	Not known		Antarctica, deep sea	-
			Tubularia striata	Antarctica, deep sea	
			Scyphistoma striatum	Antarctica, deep sea	
			Stephanoscyphus striatus	Antarctica, deep sea	
			Stephanoscyphistoma striatus	Antarctica, deep sea	
Nausithoe thieli	Solitary	Present (only ephyra known)		Red Sea, deep sea	-
Nausithoe werneri	Solitary	Present		NE and SW Atlantic, Mediterranean and Artic Ocean, deep sea	-

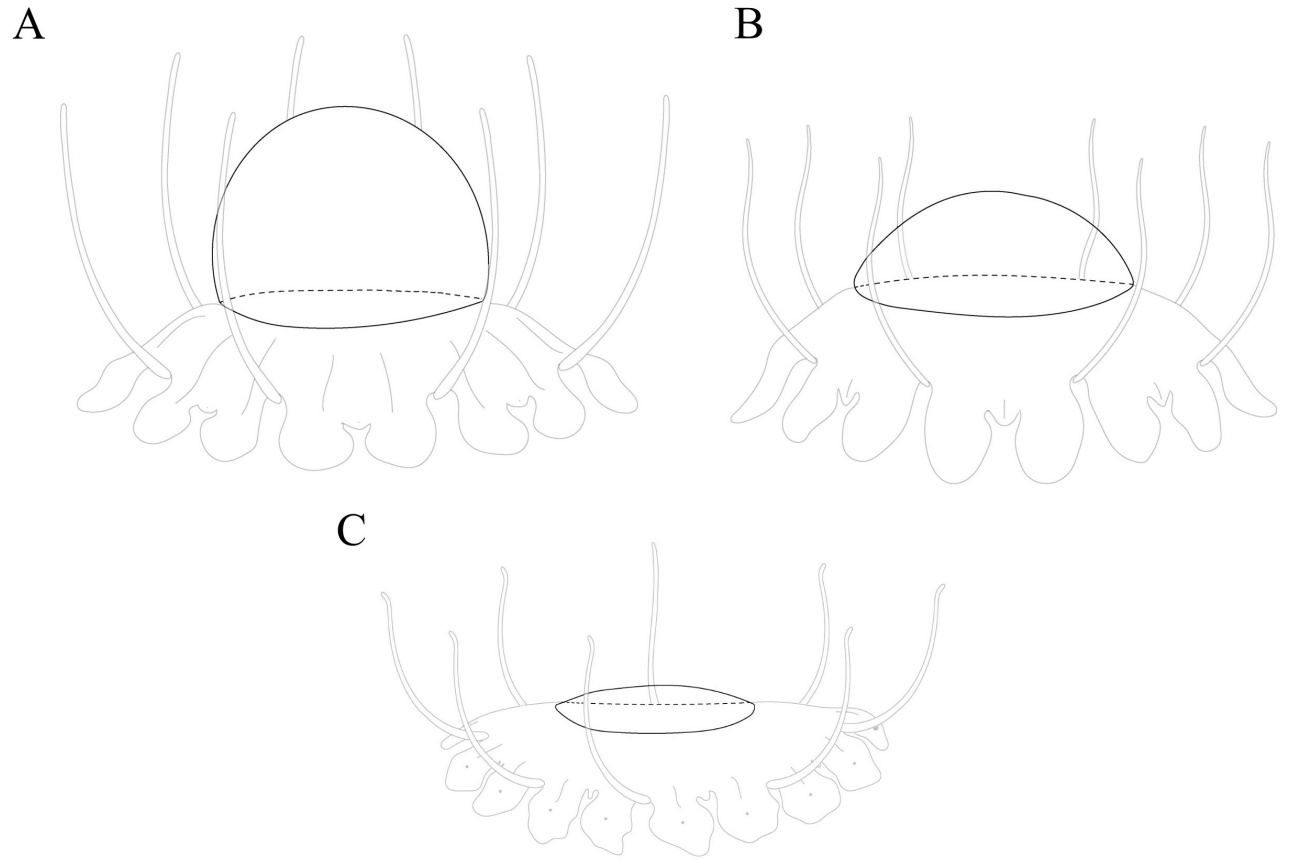

FIGURE 2. Proposed terminology to distinguish umbrella outlines in *Nausithoe* medusa according to the height of the central disc in comparison to the rest of the body when the animal is relaxed. **A**—Hyperdome (dome higher than the distance from groove to bell margin); **B**—Isodome (dome with about the same size of the distance from groove to bell margin); **C**—Hypodome (dome smaller than the distance from groove to bell margin).

Nausithoe albatrossi (Maas, 1897)

Nauphanta albatrossi Maas, 1897: 83, pl. XIV.
Nausithoe albatrossi—Vanhöffen, 1902: 29.

Holotype not known, possibly not extant.

Material examined: None.

Diagnosis: medusa—isodome bell with gastric filaments organized in 16 clusters of 5 filaments each.

Description: Based on Maas (1897), Bigelow (1928), Mayer (1910), and Kramp (1961). Adult medusa 35 to 40 mm in diameter and 35 mm high; narrow and elongate lappets, with rounded ends; smooth central disc; gonads oblong; gastric filaments organized in 16 clusters of 5 filaments (4 clusters per quadrant, a total of 80 filaments). No information about the rhopalia. No information about a polyp stage.

Type locality: Gulf of Panama (no information on depth).

Distribution: Pacific coast of South America.

Remarks: The organization of gastric filaments is not seen in any other species of the genus.

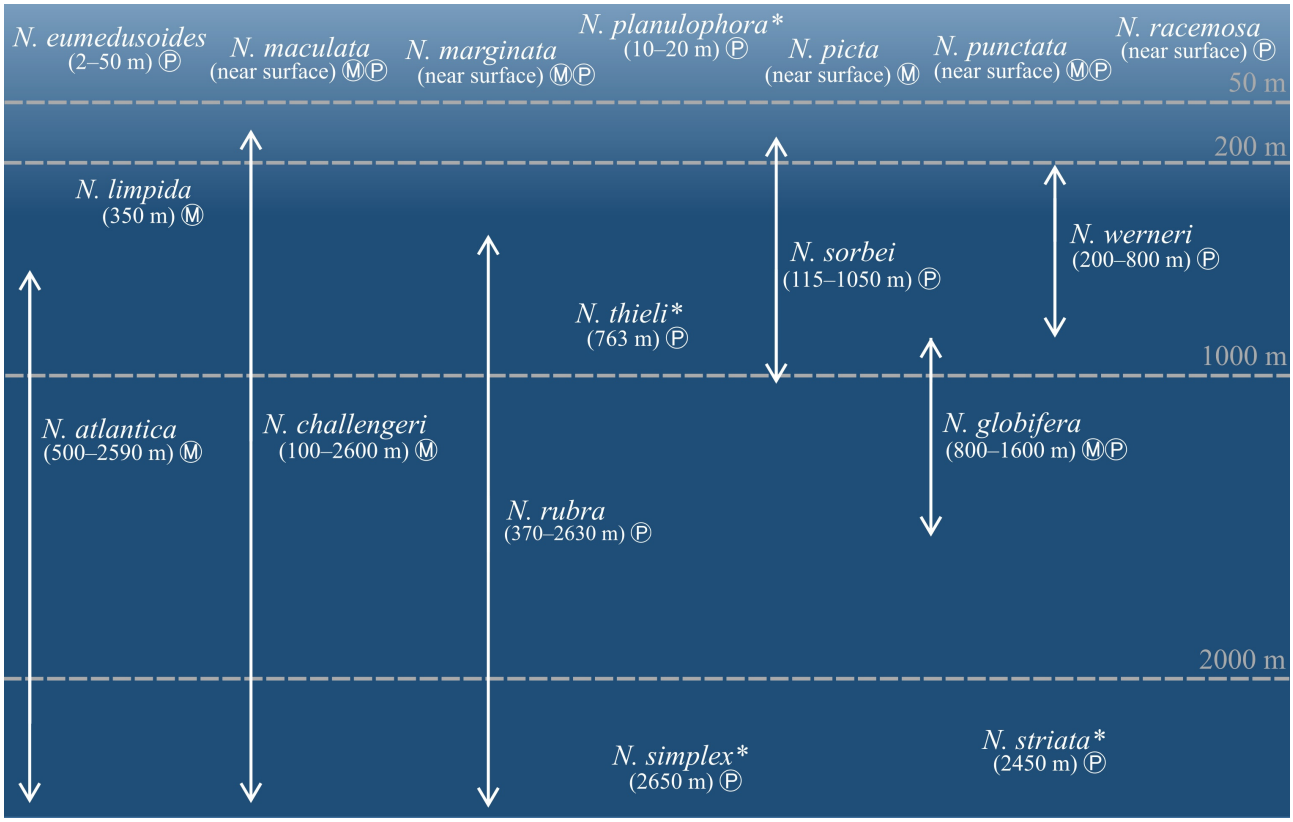

FIGURE 3. Depth distribution of *Nausithoe* species. Species with no information on depth are not represented and the image is out of scale. M—indicates that the distribution is based on medusae records. P—indicates that the distribution is based on polyp records. *Species that have only the polyp stage described.

Nausithoe atlantica **Broch, 1913**

(Fig. 4)

Nausithoe atlantica Broch, 1913: 9–10, pl. I figs 1–4.

Holotype not known, possibly not extant.

Material examined: NHM 1982.11.30.125, NHM 1982.11.30.128 (two specimens from Portugal 1982, no information on depth) and MBARI database (identity-reference 35 from Gulf of California 2015, USA 25°45'N 109°85', depth: 2,590m; identity-reference 24 from coast of Oregon 2006, USA 45°40'N 126°72'W, depth: 2,334m).

Diagnosis: medusa—isodome bell with dark colored umbrella.

Description: Based on Broch (1913), Russell (1956), and Kramp (1961), due to poor condition of specimens. Adult medusa up to 35 mm in diameter, 19 mm of this the central disc; umbrella smooth, dark yellowish-brown (almost black); somewhat arched central disc; slightly elongate marginal lappets with rounded margins; rhopalia with statocyst and deeply colored ventral sensory bulb; circular to slightly oblong gonads; more than 160 gastric filaments in total. No information about polyp stage.

Type locality: North Atlantic (36°53'N 29°47'W, 500 m depth).

Distribution: North Atlantic and Pacific coasts of North America.

Remarks: The only two specimens examined (NHM 1982.11.30.125, NHM 1982.11.30.128) were damaged, precluding the observation of important characters. Both animals had a smooth umbrella with remnants of red-brownish pigmentation (almost vanishing). Tentacles with a very thick base. Gonads disc-shaped (early development), elongated distally and near to the margin of coronal muscle. It was not possible to see the gastrovascular cavity and lappets, and the rhopalia were too damaged to be observed and described. Tentacles were as long as the estimated

total diameter of specimens, around 20 mm. Based on MBARI images, gonads apparently form two aboral extensions in later development.

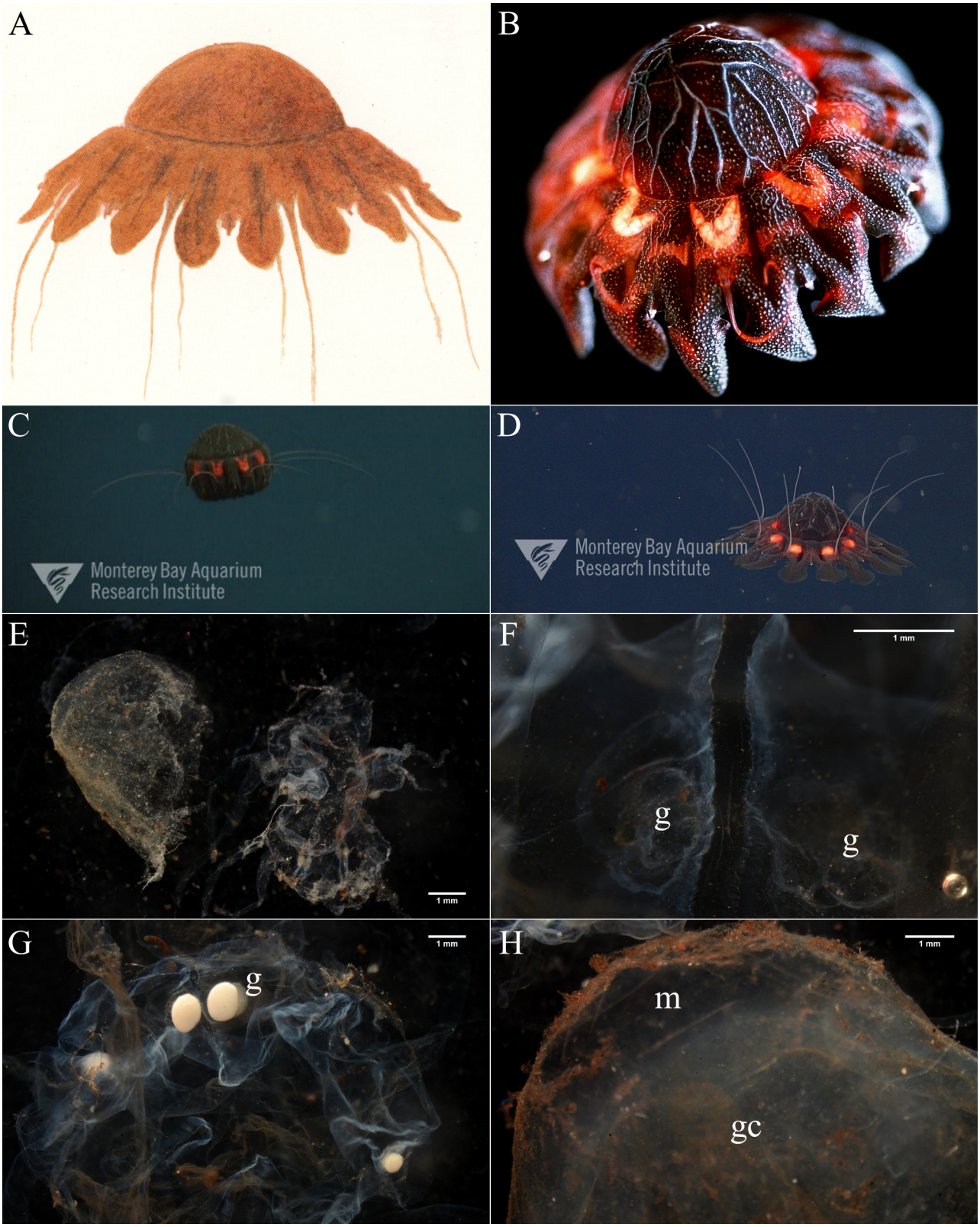

FIGURE 4. *Nausithoe atlantica*. **A**—part of plate drawing by Russell 1970. **B**—Adult medusa (photo: P. R. Flood © Bathybiologica). **C**—Adult medusa (© MBARI 2006—VARS database; identity-reference 24). **D**—Adult medusa (© 2015 MBARI—VARS database; identity-reference 35). **E—**Extremely damaged specimen with dome detached from the rest of the body (NHM 1982.11.30.128). F–H: NHM 1982.11.30.125. **F**—Beginning of gonad (**g**) formation. **G—**View of mature gonads. **H—**Exumbrellar red pigmentation vanishing; central disc with mesoglea (**m**) and gastrovascular cavity (**gc**).

***Nausithoe challengeri* (Haeckel, 1880)**
(Fig. 5)

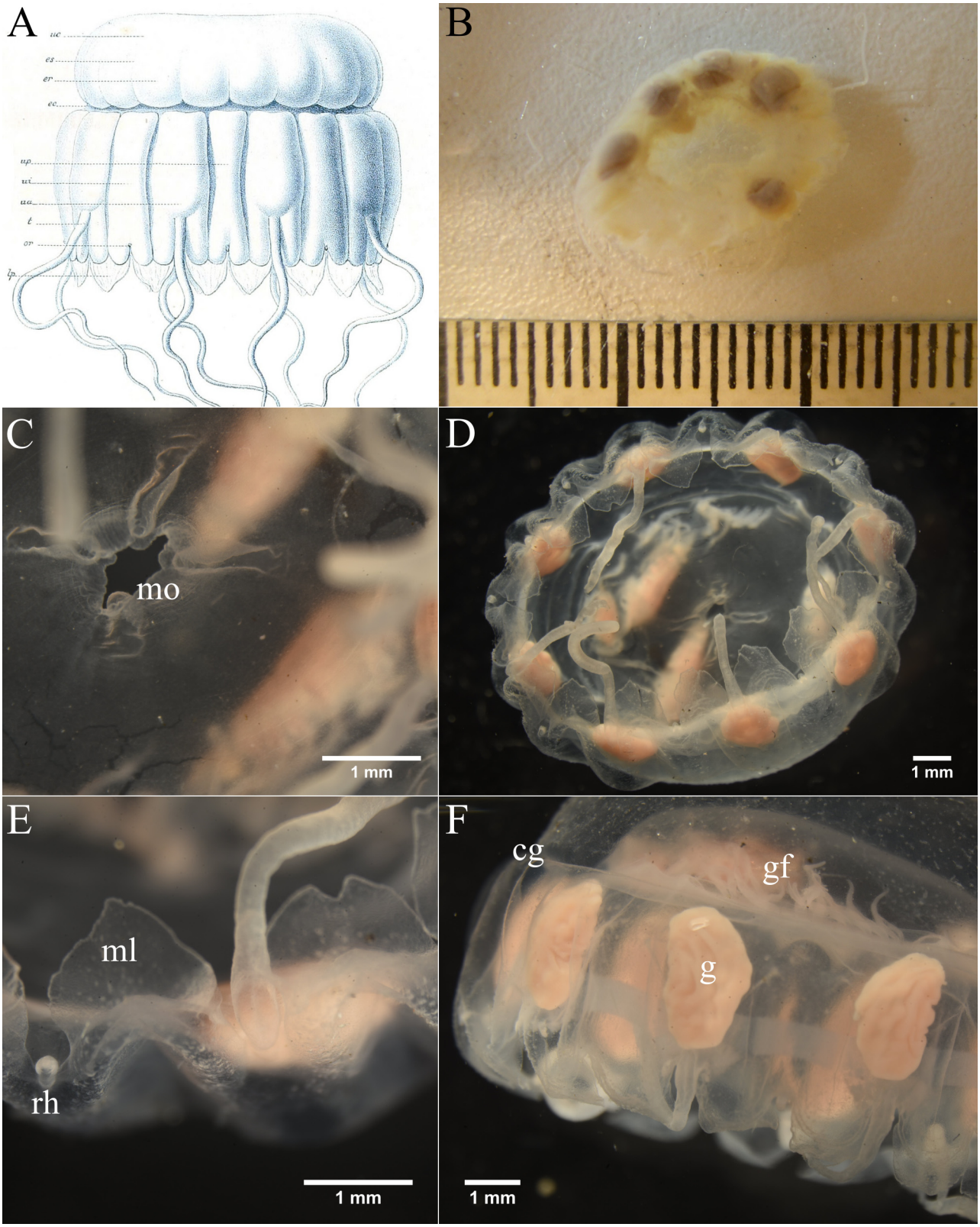

FIGURE 5. *Nausithoe challengeri*. **A**—Drawing by Haeckel 1880. **B**—Holotype NHM 1882.10.9.1. C–F: NMNH 58264. **C**—Oral view of the whole medusa, with focus on tentacles (**t**) and marginal lappets. **D**—Closer look of the mouth (**mo**) without manubrium. **E**—Detail of the marginal lappets (**ml**) and rhopalium (**rh**). **F—**Side view showing the bean-shaped gonads (**g**), the coronal groove (**cg**) and gastrovascular cavity with gastric filaments (**gf**).

Nauphanta challengeri Haeckel, 1880: 487. Haeckel, 1882: 103–111, pls. XXVI–XXVII.
Nausithoe challengeri—Vanhöffen, 1902: 28.

Holotype NHM 1882.10.9.1.

Material examined: NMNH 58264 (one specimen from the Mid North Atlantic Ocean, 1978, depth: 0–100 m); NHM 1882.10.9.1 (holotype).

Diagnosis: medusa—isodome bell and no mouth lips and manubrium.

Description: Based on original description, Bigelow (1928), Mayer (1910), and Kramp (1961). Adult medusa 12 mm in diameter; deep annular furrow marking the transition from pedalia to central disc; somewhat less in diameter than bell-radius; thin and long tentacles (longer than bell-radius); large bean-shaped gonads; one cluster of gastric filaments per quadrant, each one with about 24 filaments (96 total). No information about polyp stage.

Type locality: Tristan da Cunha Island, central South Atlantic (32°24'S 13°5'W, 2,600m depth)

Distribution: Only known from type locality, and a new record here (mid North Atlantic).

Remarks: The examined specimen (NMNH 58264) matches well with the original description. The animal had a very thick transparent umbrella, with high dome and marginal disc cylindrical, i.e., parallel to the oral-aboral axis. Gastrovascular cavity with 32 short gastric filaments in total and no manubrium (mouth opens directly to the cavity). Sixteen wide marginal lappets with pointed tips and eight rhopalia with statoliths and no ocellus. Eight yellowish-orange oval gonads. Total diameter 13 mm and tentacles up to 4 mm long (probably contracted due to preservation). The absence of mouth lips and manubrium is typical of *N. marginata*, however, the umbrella shape, the position of the gonads and the animal size match Haeckel's description of *Nausithoe challengeri*.

Nausithoe clausi Vanhöffen, 1892

(Fig. 6: A–D)

Nausithoe clausi Vanhöffen, 1892: 3–28, pl. IV. figs 1–2.

Holotype not known, possibly not extant.

Material examined: None.

Diagnosis: medusa—hypodome with transparent umbrella.

Description: Based on original description of a single specimen. Medusa 9 mm in diameter, 5 mm of this the central disc; 2.5 mm high; smooth transparent umbrella; marginal lappets short and broad, with rounded edges; tentacles equal to bell radius; numerous gastric filaments; small round gonads; no data about statocyst.

Type locality: tropical N Pacific, E of Caroline islands (no information on depth).

Distribution: Only known from type locality.

Remarks: This species description is based on a single specimen, possibly a juvenile according to the size of the gonads. Morphology resembles *N. picta* and *N. punctata.*

Nausithoe eumedusoides (Werner, 1974)

(Fig. 6: E–H)

Stephanoscyphus eumedusoides Werner, 1974: 439–461, figs 1–5.
Nausithoe eumedusoides—Jarms, 1990: 11.

Holotype ZMH C9797.

Material examined: Living polyps kept in laboratory cultures (from submarine caves in Mljet, Croatia, 2002; 26m depth; H. Zibrowius col.).

Diagnosis: medusoid—tetrameric form with no manubrium, can be hermaphroditic; polyp—solitary with single cusp closer to the base.

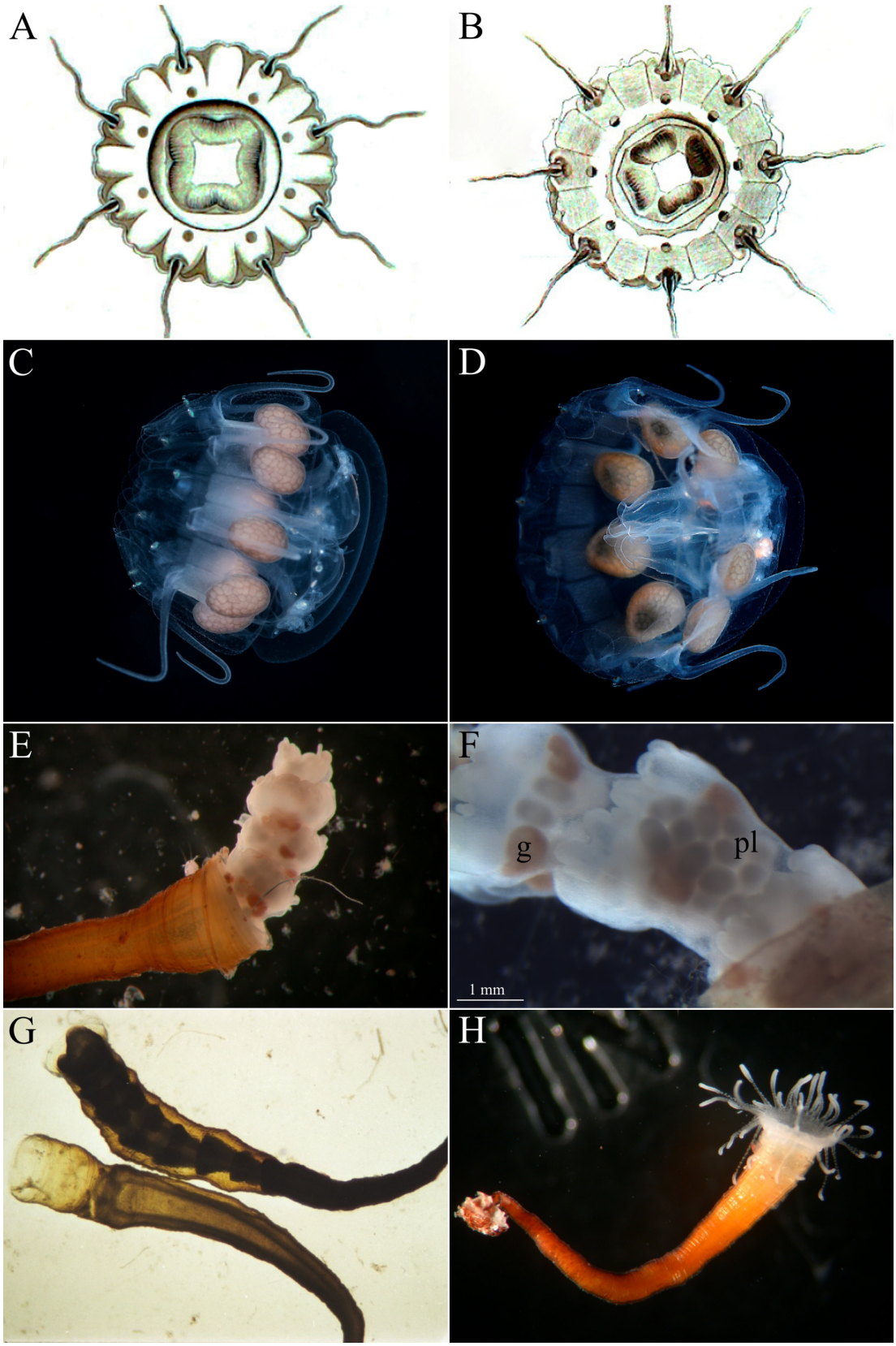

FIGURE 6. *Nausithoe clausi* (A–D) and *Nausithoe eumedusoides* (E–H). **A** and **B**—Drawing from Vanhöffen 1892: aboral view (A) and oral view (B) of adult medusa. **C** and **D**—Lateral view (C) and oral view (D) of a possible adult medusa of *N. clausi* from Anilao, Philippines, shallow waters (photos: © Suzan Meldonian 2019). **E**—Polyp strobilating and releasing the eumedusoids. **F**—Closer view of medusoid showing the gonads (**g**) and planulae (**pl**). **G**—Two polyps in culture; the upper polyp is strobilating. **H**—Polyp with tentacles extended; notice the wide collar.

Description: Based on Werner (1970) and original description. Medusoid 1–1.5 mm in umbrella width and 1–1.2 mm in height; quasi-tetrameric; lack of manubrium; rhopalia with minimally developed sense organ; absence of coronal groove until the final moments of strobilation; no gastric filaments; reduced umbrella musculature with 4 thin longitudinal muscle strands; beating flagella on the epidermis; four gonads in total (eight merged in pairs), bean-shaped or oblong, with yellow to brown pigmentation; can be hermaphroditic (with even the production of both eggs and sperm cells at the same time in the same gonad) or single sexed. Polyp solitary; 22.2 mm in total length; 1–2 single cusp closer to the base (arranged vertically one above the other); produces 4–5 medusoids per strobilation.

Type locality: Submarine caves near Marseille, France.

Distribution: Marine caves probably of all Mediterranean (2–50 m depth).

Remarks: Only *N. eumedusoides* and *N. racemosa* have a medusoid described in their life cycle, but the polyps are extremely different from each other. *N. eumedusoides* is a solitary species while *N. racemosa* is colonial (and with significant soft body differences, *e.g.*, oral disc, symbiosis with algae).

Nausithoe globifera Broch, 1913

(Fig. 7: A–D)

Nausithoe globifera Broch, 1913: 10–11, pl. I figs 5–8.

Holotype not known, possibly not extant.

Material examined: NHM 1956.7.31.4 and NHM 1956.7.31.5-10 (seven specimens from France—Italy 1956, no information on depth), NHM 1982.11.30.136 (one specimen from Portugal 1959, depth: 1,600 m), NHM 1982.11.30.139 (one specimen with no info about locality, 1982, depth: 1,600 m).

Diagnosis: medusa—hyperdome bell and deep purple-reddish stomach; polyp—solitary with eight cusps per whorl.

Description: Based on original description, Bigelow (1928), Kramp (1961), and Jarms (1997). Adult medusae up to 22 mm in diameter, 10 mm of this the central disc; umbrella smooth, transparent, with high-domed central disc (hyperdome); lappets wide and rounded; rhopalia with statocyst and slightly colored ventral bulb; 80 or more gastric filaments in total; stomach deep purple-reddish; marginal tentacles, orange-red; gonads slightly mitten-shaped with a slight cleft, white to reddish brown. The polyp described for this species was 6.86 mm long and 0.92 mm in aperture diameter. It had eight cusps per whorl and four whorls in total. Soft body with a maximum of 40 tentacles. Strobilation produces 24 ephyrae.

Type locality: North Atlantic (45°26’N 25°45’W, 1,000m depth).

Distribution: Eastern part of North Atlantic.

Remarks: The four examined specimens were too damaged, preventing observations of the structure of the rhopalia. Gonads were oblong to slightly quadrangular, with a cleft, rendering them asymmetrical, located above the coronal groove. Four triangular gastric septa with more than 15 gastric filaments each (apparently more than 60 in total). Transparent umbrella with deep-red central gastrovascular cavity and manubrium (some specimens lost color completely). Tentacles were as long as the estimated total diameter of specimens, measuring around 20 mm long.

Nausithoe hagenbecki Jarms, 2001

(Fig. 7: E–H)

Nausithoe hagenbecki Jarms, 2001: 14–18, figs 1–5.

Holotype ZMH C11659.

Material examined: ZMH C11659.

Diagnosis: medusa—hypodome bell with short tentacles and gonads arranged in pairs; polyp—solitary with 16 cusps per whorl and collar surrounded by multiple club-like lips.

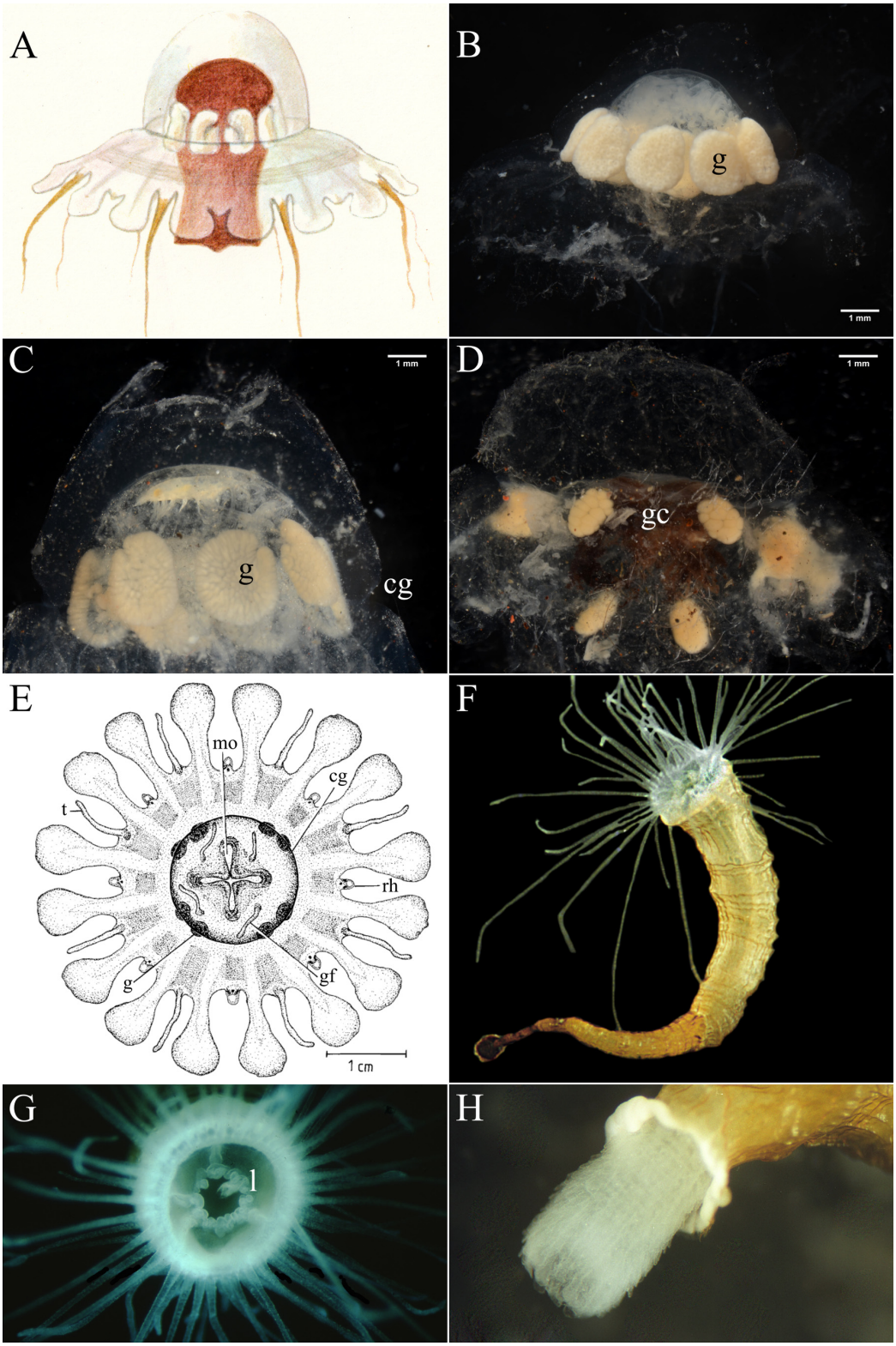

FIGURE 7. *Nausithoe globifera* (A–D) and *Nausithoe hagenbecki* (E–H). **A**—Drawing from Russell 1970. B and C: NHM 1982.11.30.139; D: NHM 1982.11.30.136. **B**—side view of female medusa; note the high dome-shaped central disc and the oval gonads (**g**) with hundreds of eggs. **C**—side view of male medusa, focusing on the deep coronal groove (**cg**) and gonads (**g**); it is also possible to see a small crustacean prey inside the gastrovascular cavity. **D—**side view of a male with the red pigmentation of the gastrovascular cavity and the gastric filaments (**gf**) still preserved. **E**—Image adapted from Jarms 2001; representation of an adult female medusa with coronal groove (**cg**), gastric filament (**gf**), gonads (**g**), mouth (**mo**) with lips, rhopalium (**rh**) with statolith and ocellus, tentacle (**t**). **F**—Polyp as collected in the tank of Hagenbeck's Tierpark. **G**—Oral view of polyp with multiple club-like lips (**l**). **H**—Strobilating polyp with dense packed ephyrae.

Description: Based on original description. Adult medusae 5 mm in diameter, 3.7 mm between rhopalia and 1.6 mm being the flat central disc (hypodome); rhopalia with statolith and a dark red pigmented ocellus; stout and short tentacles (shorter than the lappets); one gastric filament per quadrant (four in total); spherical gonads arranged in pairs situated beneath the coronal groove. Polyp solitary with at least two whorls of 16 cusps; 28.8 mm in total length; soft body with four lobes at the collar and mouth surrounded by four bigger (coming from the gastric septae) and 16 smaller (from the mouth margin) club-like lips; up to 8.2 mm-long slender tentacles.

Type locality: found in the tropical aquarium of the Hagenbeck Zoo in Hamburg, Germany.

Distribution: Unknown, not yet found in the wild.

Remarks: The polyp's soft body morphology in this species is remarkably different from other animals of the genus, with four lobes at the collar and mouth surrounded by four bigger and 16 smaller club-like lips. The shape and positioning of the gonads, arranged in pairs, are the most distinctive characteristics of the medusae.

Nausithoe limpida Hartlaub, 1909

Nausithoe limpida Hartlaub, 1909: 474–476, pl. LXXVII figs 3, 5.

Holotype not known, possibly not extant.

Material examined: None.

Diagnosis: medusa—hypodome bell with violet manubrium.

Description: Based on original description, Bigelow (1928), and Kramp (1961). Adult medusae 16 mm in diameter, 6 mm of this the central disc; tentacles measuring 6 mm in length and with enlarged base; flattened, almost discoidal, umbrella (hypodome) with smooth central disc; manubrium violet; broad and slightly elongated marginal lappets (3 mm long); rhopalia with statocyst and ocellus (not described, based on figure); 96 gastric filaments in total (4 groups of 24); gonads irregularly heart-shaped, females with many dark eggs.

Type locality: North Atlantic (75°47'N 12°59'W, 350m depth).

Distribution: Only known from type locality.

Remarks: This species might be synonymous with *N. rubra* because the number of gastric filaments and gonad shape are the same in both species. However, the adult diameter in *N. limpida* is considerably smaller.

Nausithoe maculata Jarms, 1990
(Fig. 8)

Nausithoe maculata Jarms, 1990: 21–24, figs 15–17, pl. V.
Nausithoe aurea Silveira & Morandini, 1997: 236–239, figs 1–7, pls I–II.

Holotype ZMH C11534.

Material examined: NMNH 57648, 57650, 57651, 57657, 57660, 57656, 57658 and 57659 (more than 100 specimens from Puerto Rico 1975, no information on depth), NMNH 43306 (eight specimens from Dry Tortugas 1929, no information on depth), NMNH 57764, 57765, 57766, 57767, 57768, 57772 and 57773 (more than 50 specimens from Belize 1978, no information on depth); 24 medusae from culture (polyps from Cuba 2001 and São Sebastião, Brazil 2018, shallow waters) and photo from underwater photographers, Linda Ianniello and Suzan Meldonian (SE Florida, USA 2015–2016, depth: 6–12 m).

Diagnosis: medusa—hypodome bell with one yellow pigment spot in each lappet; polyp—solitary with 16 cusps per whorl.

Description: Based on original description. Adult medusa 4 mm in diameter, 2 mm of this the central disc; flattened transparent umbrella (hypodome) with a yellow pigment spot in the center of each lappet; rounded lappets with pointed tips; rhopalia with statocyst and red ocellus; 7 gastric filaments per quadrant (28 in total); spherical gonads (in life female blue, male brownish). Polyp solitary; living in shallow waters (5–10 m); 13 mm total length; 16 cusps per whorl; maximum of 8 whorls of cusps. When describing *Nausithoe aurea*, Morandini & Silveira (2001a, b) highlighted the production of a planuloid by the polyp, apart from the typical strobilation resulting in ephyrae. This feature has not been observed in polyps from Cuba or Puerto Rico.

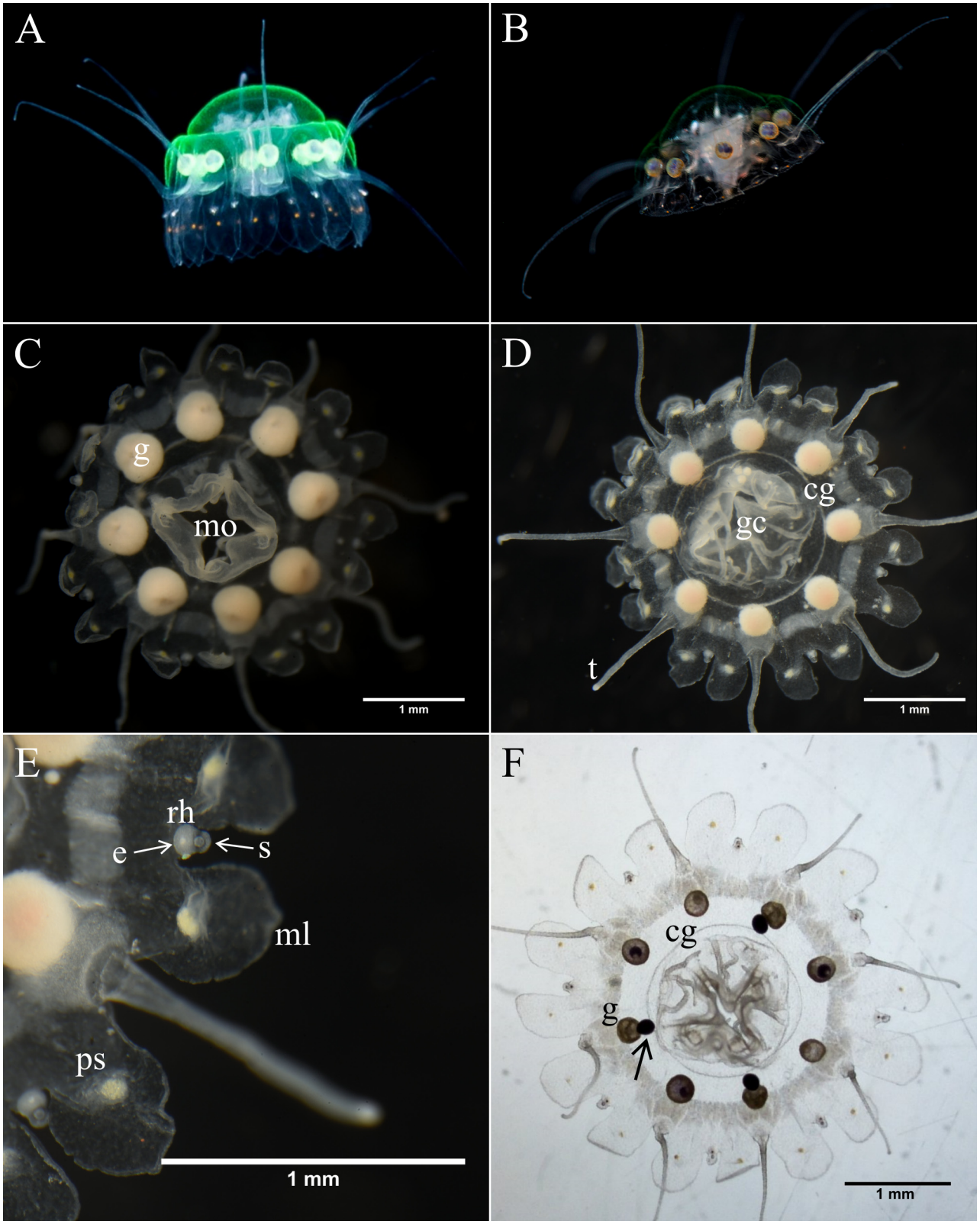

FIGURE 8. *Nausithoe maculata*. C–E: NMNH 57660. **A**—Side view of adult medusa from SE Florida (photo: © Linda Ianniello 2015). **B**—Side view of adult medusa from W Palm Beach, Florida, note the dark eggs inside the gonads (photo: © Suzan Meldonian 2016). **C**—Oral view of the medusa, showing the mouth (**mo**) and gonads (**g**). **D**—Aboral view of the medusa, showing the coronal groove (**cg**) and gastrovascular cavity (**gc**) with cirri. **E**—Detail of rhopalium (**rh**), with statocyst (**s**) and ocellus (**e**), and marginal lappets (**ml**) with the yellow pigment spot (**ps**), essential for identifying this species.

Type locality: Puerto Rico (shallow waters).

Distribution: Caribbean, Florida (USA), Brazil.

Remarks: Examined specimens had from three to seven gastric filaments per quadrant. The gonads were round, varying in color from dark brown to yellowish-white. Specimens had a maximum total diameter of 6 mm and tentacles were about 3 mm long. There is a report of *N. aurea* from the Cape Verde Islands (León *et al.* 2005), but no image is provided and the identity could not be checked.

Nausithoe marginata Kölliker, 1853

(Fig. 9)

Nausithoe marginata Kölliker, 1853: 323.

Holotype not known, possibly not extant.

Material examined: ZMH C9774 and 9776 (11 specimens from France and Italy, no information on depth), NMNH 57649 (more than 30 specimens from Puerto Rico 1975, no information on depth) and photo from underwater photographer, Linda Ianniello (SE Florida, USA 2020, depth: 6–12 m).

Diagnosis: medusa—isodome bell with no mouth lips nor manubrium; polyp—solitary with 8 cusps per whorl.

Description: Based on original description and Jarms (1990). Adult medusa 4–5 mm in diameter, 2 mm of this the central disc; rhopalia with statoliths and no ocellus; marginal lappets triangular; mouth without lips; tentacles shorter than total body length; transparent umbrella; gonads elongated. Polyp solitary; more than 5 mm in total length; aperture 0.6–0.8 mm in diameter; 5 to 10 whorls of cusps with 8 cusps each.

Type locality: Messina, Italy (shallow waters).

Distribution: Mediterranean and new report for Puerto Rico.

Remarks: Examined specimens were extremely damaged. Very delicate umbrella, transparent, with high dome. Gastrovascular cavity with 12 short gastric filaments in total (4 clusters in each quadrant) and no manubrium (mouth opens directly to the cavity). Eight white oblong gonads. Total diameter up to 3 mm.

Nausithoe picta Agassiz & Mayer, 1902

(Fig. 10)

Nausithoe picta Agassiz & Mayer, 1902:

Holotype not known, possibly not extant.

Material examined: ZMA2048 (8 specimens from Indonesia, Maluku, no information on depth) and photo from underwater photographer, Fabien Michenet (Tahiti, depth: 20m).

Diagnosis: medusa—hypodome with transparent umbrella and blue gastric filaments.

Description: Based on original description and Mayer (1910). Medusae 15–22 mm in diameter; smooth transparent umbrella; marginal lappets as long as wide, with rounded edges; tentacles length equal to bell radius; 4 groups of about 12 blue gastric filaments each; large brown gonads; rhopalia with brown ocellus.

Type locality: Rangiora Island, French Polynesia (near surface).

Distribution: French Polynesia and Central E Pacific Ocean.

Remarks: The morphology of this species resembles that of *N. clausi* and *N. punctata*, except for the blue gastric filaments, rendering this as the only feature that distinguishes the medusa of *N. picta*.

Nausithoe planulophora (Werner, 1971)

(Fig. 11)

Stephanoscyphus planulophorus Werner, 1971: 125–135, figs 2–8.
Nausithoe planulophora—Jarms, 1990: 11.

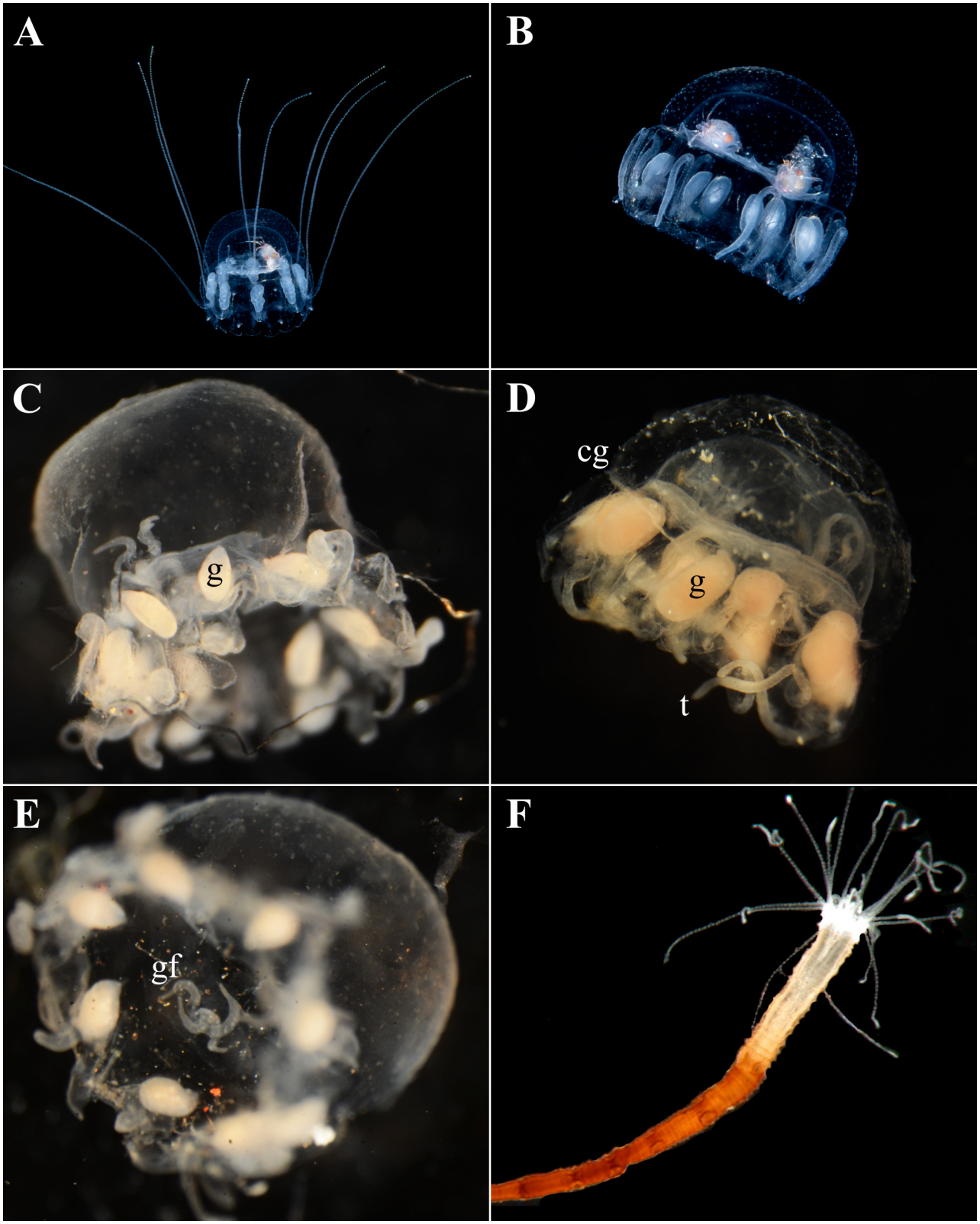

FIGURE 9. *Nausithoe marginata*. **A** and **B**—Lateral view of two adult medusae from the coast of SE Florida with small prey inside the gastrovascular cavity (photos: © Linda Ianniello 2020). C and E: ZMH C9774; D: NMNH 57649. **C** and **D**—Side view of adult medusa, emphasizing the gonads (**g**), coronal groove (**cg**) and tentacles (**t**). **E**—Oral view of the gastrovascular cavity showing one of the gastric cirri clusters (**gf**). **F**—Live polyp on lab culture.

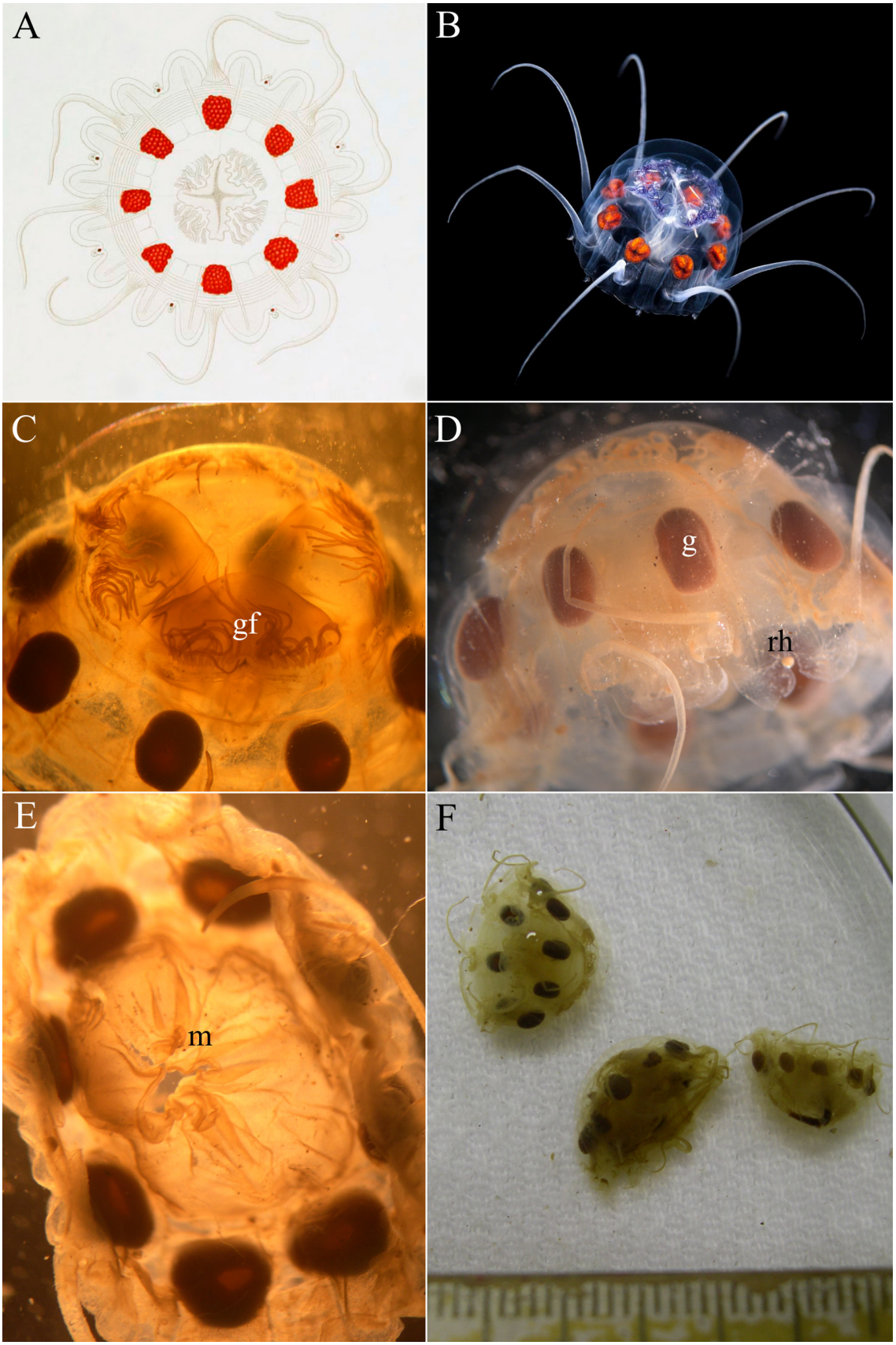

FIGURE 10. *Nausithoe picta*. **A**—Original illustration by Agassiz & Mayer 1902. **B**—Adult medusae from the coast of Tahiti (photo: © Fabien Michenet 2012). C, D, E and F: ZMA2048. **C**—aboral view of the gastrovascular cavity showing the gastric filaments (**gf**). **D**—Lateral view of medusa showing the gonads (**g**) and rhopalium (**rh**). E—Oral view of medusa emphasizing the mouth (**m**) and manubrium. **F**—Lateral view of three adult medusae from the museum collection.

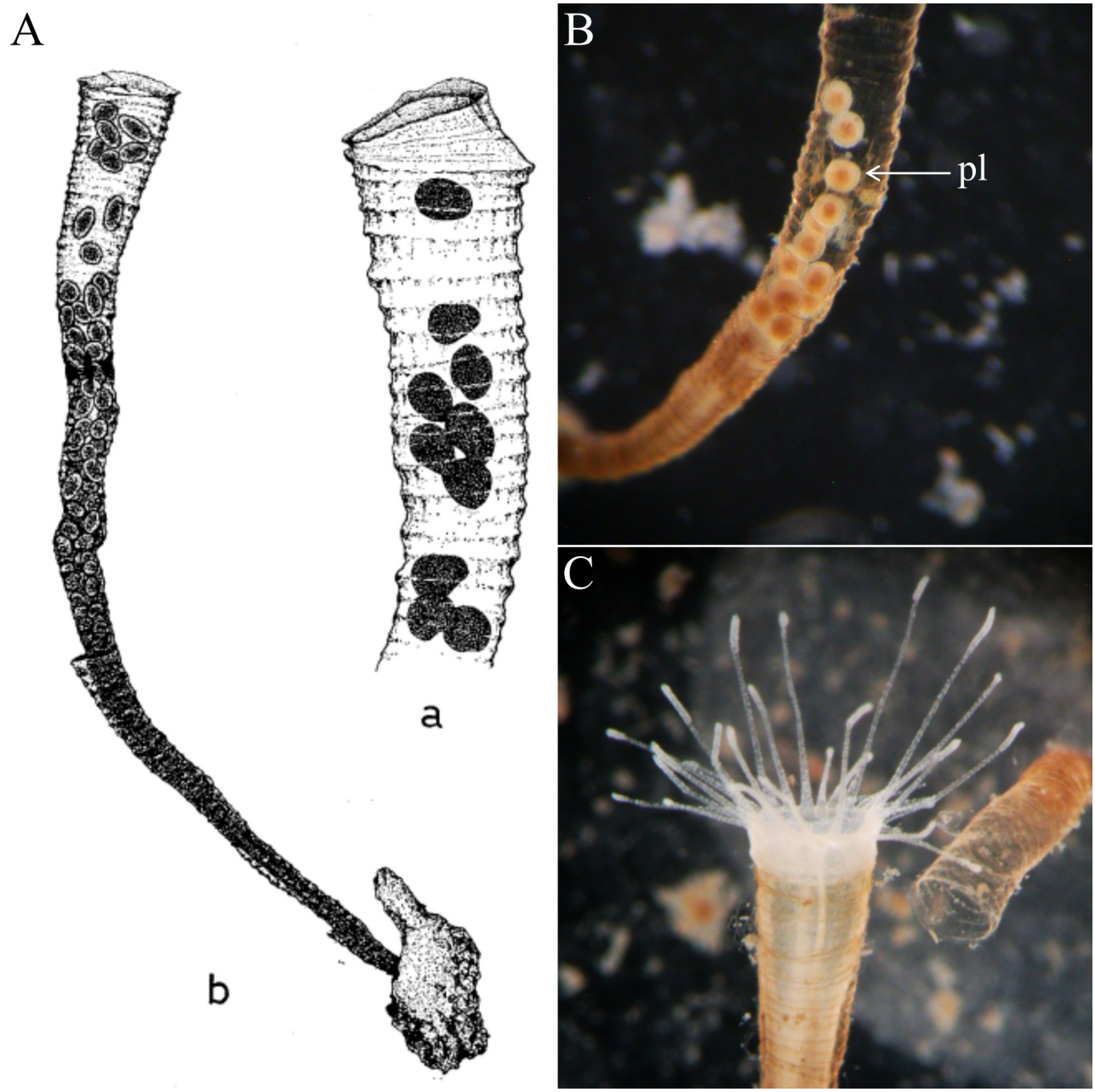

FIGURE 11. *Nausithoe planulophora*. **A**—Image extracted from Werner (1971, fig. 6); **a**: intermediate stage of the transformation of the ephyrae into planulae; **b**: fully developed flagellated planulae. **B**—Polyp from laboratory culture releasing planulae (**pl**). **C**—Polyp with tentacle crown extended.

Neotype ZMH C9742.

Material examined: Living polyps kept in laboratory cultures (from Werner's original culture; submarine caves in Marseille, France, 1969; 10–20 m depth; H. Zibrowius col.).

Diagnosis: polyp—solitary with 16 cusps per whorl.

Description: Based on original description, and Werner & Hentschel (1983). No medusa. Polyp solitary; longest specimen measuring 20 mm in total length; 1 mm aperture diameter; 0.2 mm basal disc diameter; 16 cusps per whorl and 4–5 whorls; 30 tentacles. Planuloid less than 0.5 mm in diameter; body at first spherical, then ellipsoidal.

Type locality: Marseille, France (submarine caves, 10–20 m depth).

Distribution: Mediterranean coast of France and Italy.

Remarks: The observation of life cycle (planuloid production) is essential to differentiate this species.

***Nausithoe punctata* Kölliker, 1853**
(Fig. 12)

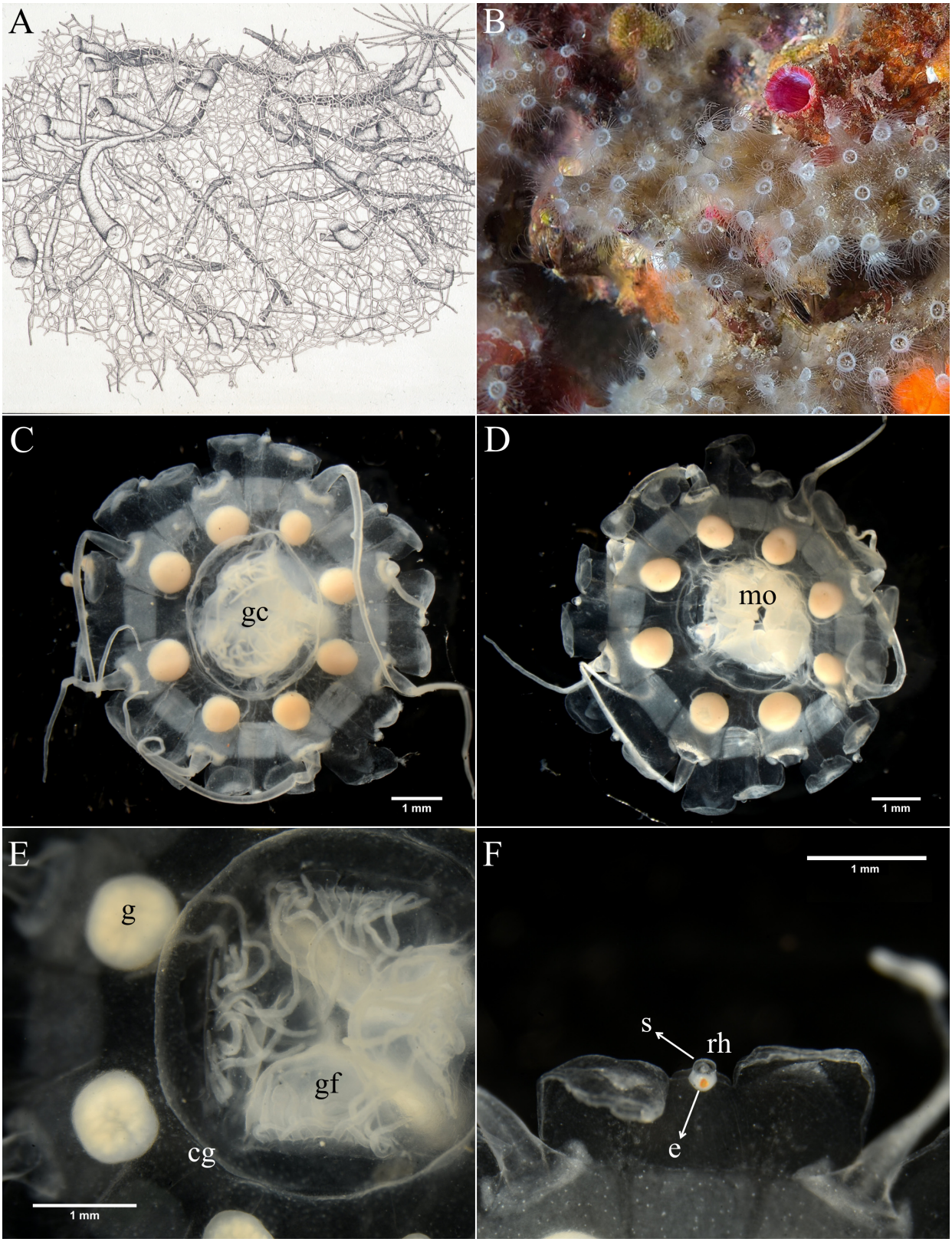

FIGURE 12. *Nausithoe punctata*. **A**—Original drawing by B. Werner of the polyp colony inside a sponge. **B**—Colony in Sant'Angelo, Naples, Italy; only the terminal end of the polyps, with the tentacle crown, is visible (photo: © Fabio Russo 2017). C–F: NMNH 57654. **C**—Aboral view of adult medusa showing the gastrovascular cavity (**gc**). **D**—Oral view of adult medusa showing the mouth (**mo**) with manubrium. **E**—Detail of the gastrovascular cavity showing the gastric filaments (**gf**), gonads (**g**) and coronal groove (**cg**). **F**—Detail of the rhopalium (**rh**), with statocyst (**s**) and ocellus (**e**).

Nausithoe punctata Kölliker, 1853: 323.
Nausithoe albida Gegenbaur, 1856: 211–214.
Stephanoscyphus mirabilis Allman, 1874: 65, pl. XIV.
Nausicaa phaecum Haeckel, 1880: 485–486.
Liniscus cyamopterus Haeckel, 1880: 497–498.
Nausithoe punctata var. *pacifica* Agassiz & Mayer, 1899: 170.

Holotype not known, possibly not extant.

Material examined: NHM 1902.7.29.32, NHM 1950.3.1.195 (six specimens from Naples, Italy 1902 and 1905, no information on depth), NHM 1930.12.9.86.89 (four specimens from Ceylon, Sri Lanka 1930, no information on depth), ZMH C7263, C7350 (five specimens from Naples, Italy, no information on depth), NMNH 58427 (two specimens from the NE Atlantic Ocean 1978, no information on depth), NMNH 41723 (one specimen from Bermuda 1914, no information on depth), NMNH 57649 (one specimen from Puerto Rico 1975, no information on depth), NMNH 57652, 57654 (15 specimens from Saint Croix, USA Virgin Islands 1975, no information on depth), NMNH 57770, 57775, 57776, 57777, 57779 (more than 30 specimens from Belize 1976, no information on depth) and photo from underwater photographer, Fabio Russo (Red Sea, Egypt 2018).

Diagnosis: medusa—hypodome bell with transparent umbrella; polyp—colonial, living inside sponges and with a single small basal disc holding the complete colony.

Description: Based on original description, Bigelow (1928), Mayer (1910), Vanhöffen (1913), Kramp (1961), and Werner (1970). Adult medusa 12 mm in diameter, 6 mm of this the central disc, 6 mm height; flattened transparent umbrella (hypodome) with pale pink disc and yellowish lappets; rounded marginal lappets; rhopalia with statocyst and ocellus; gonads can vary from white yellow (more immature) to dark brown or blue; females with 2 to 4 eggs per gonad. Polyp colonial, living inside sponges; a primary polyp with a single small basal disc holds the complete colony; individually, the polyps have a typical coronate polyp appearance; soft body with no algal symbiont.

Type locality: Messina, Italy.

Distribution: possibly a worldwide species in shallow waters.

Remarks: In the examined specimens, eggs are bigger in relation to the animal size when compared to those of *N. globifera* and *N. rubra*. Specimens had from 20 to 32 gastric filaments in total (5 to 8 per quadrant). The maximum total diameter was 9 mm and tentacles reached up to 4 mm long. The absence of pigmentation in the lappets was the character we used to differentiate these specimens from *N. maculata*, because all the other morphological features seem to be conflicting. Nevertheless, this pigmentation might vanish when the animal is kept in formalin for too long, so we also considered body size (*N. punctata* is slightly bigger) and excluded from analyses young specimens to avoid misidentifications.

Nausithoe racemosa **(Komai, 1936)**
(Fig. 13)

Stephanoscyphus racemosus Komai, 1936: 182.
Nausithoe racemosa—Jarms, 1990: 11.

Holotype not known, possibly not extant.

Material examined: Living polyps kept in laboratory cultures (Shirahama, Japan, 2004; 5m depth; S. Kubota col.).

Diagnosis: medusoid—no gastric filaments, developed mouth or tentacles; polyp—colonial without internal cusps and broad oral disc with small tentacles.

Description: Based on original description, and Werner (1970, 1971, 1973). A reduced medusa, medusoid with no gastric filaments, developed mouth or tentacles; males develop four elongated gonads while in the strobilation chain, so that the upper distal medusoid releases the spermatozoa before the others; females detach before shedding the large size eggs from the mouth, embedded in a mucus strand with nematocysts; the medusoid has a well-developed muscular system, but is not able to swim. Polyp colonial; there is a central/primary polyp from which secondary polyps emerge, as a "stem with nodes", not randomly, but at an oblique angle; no internal cusps; soft body with enlarged oral crown, broad ring around the mouth and small delicate tentacles; the tentacle's crown has kind

of a square shape; dark yellow/brown coloration of tissues due to the large amount of as-yet uncharacterized algal symbiont.

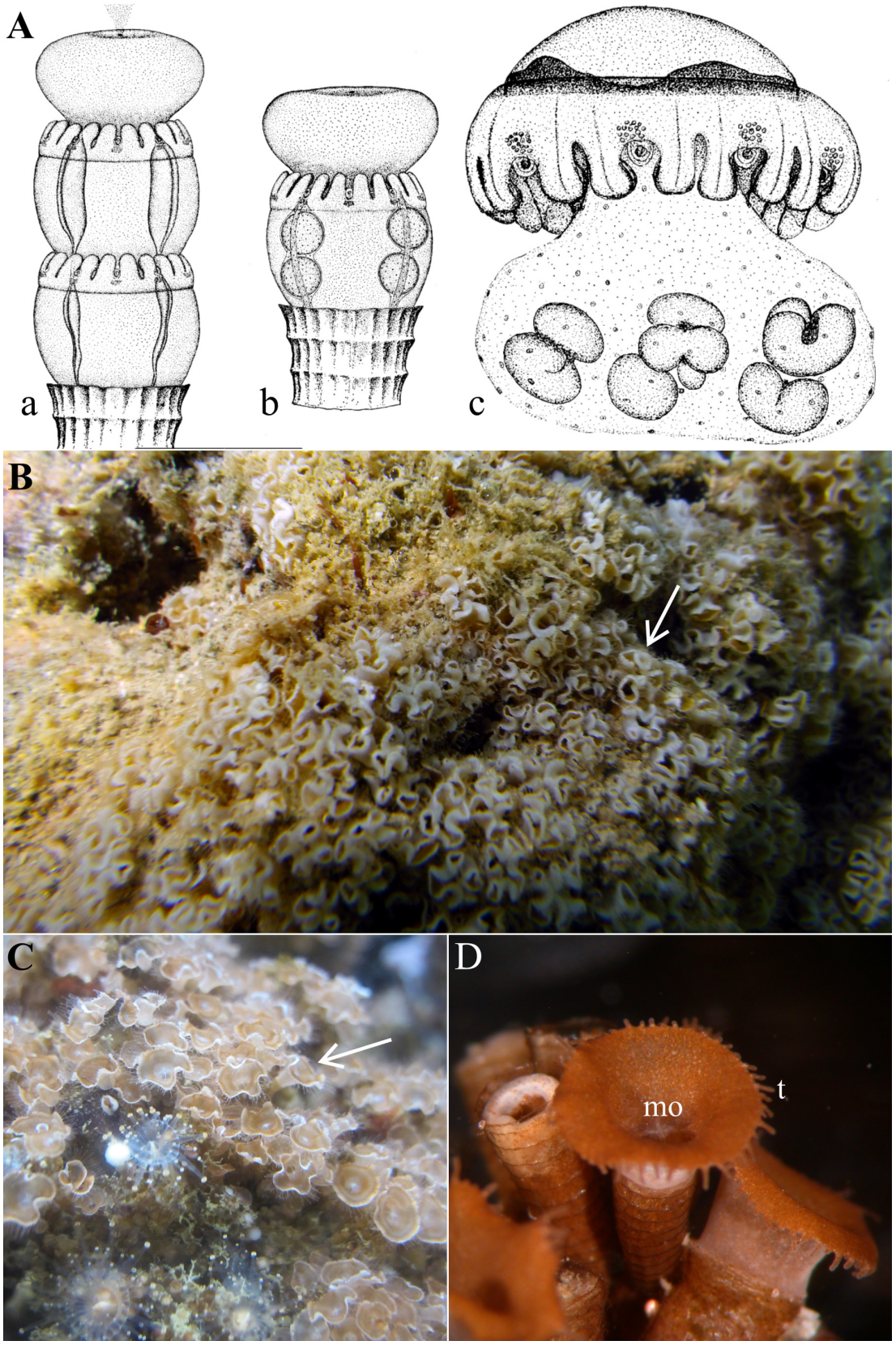

FIGURE 13. *Nausithoe racemosa*. **A**—Images adapted from Werner (1971, fig. 3, 4, 5); a: male polyp shedding off spermatozoa from the central opening of the operculum; b: female polyp showing the distal eumedusoid outside the tube; c: female eumedusoid releasing eggs embedded in a mass of mucus. **B** and **C**—Polyp colony, pointing to one individual polyp. **D**—Oral view of polyp showing the flat extended collar with the mouth (**mo**) and small tentacles (**t**).

Type locality: Seto, Japan.

Distribution: Japan, NW Pacific Ocean (shallow waters).

Remarks: This species is easily differentiated from other *Nausithoe* because of the colony's structure and the polyps' enlarged oral crown and small tentacles.

Nausithoe rubra **Vanhöffen, 1902**

(Fig. 14)

Nausithoe rubra Vanhöffen, 1902: 30–31, pl. I.

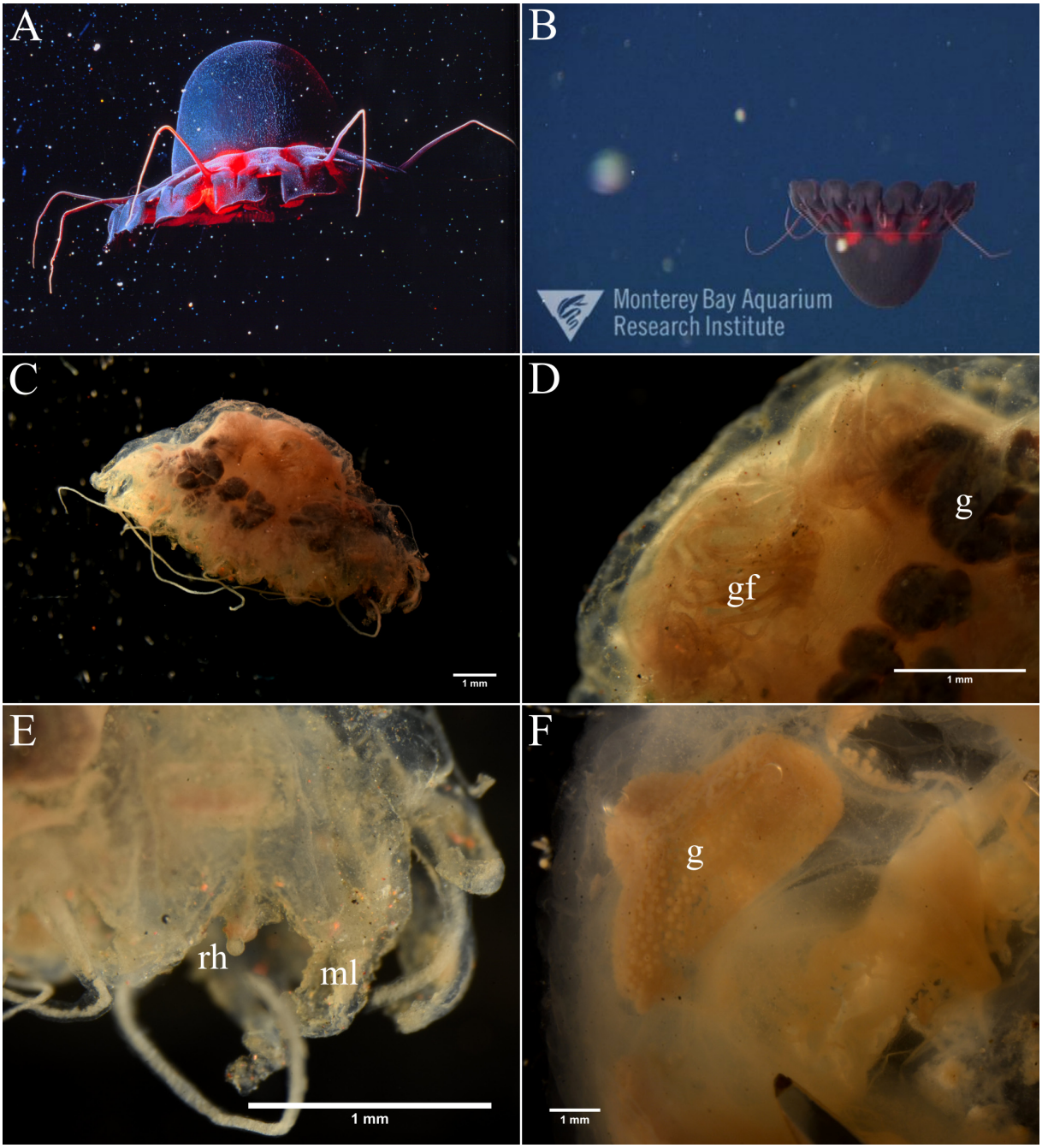

FIGURE 14. *Nausithoe rubra*. **A**—Side view of adult medusa from the coast of California (photo: George Matsumoto © 2000 MBARI). **B**—Adult medusa from the coast of California (© 2013 MBARI—VARS database; identity-reference 46). C–E: AMNH 2113. **C**—Side view of adult medusa. **D**—Detail of gastrovascular cavity with gastric filaments (**gf**). **E**—Detail of rhopalium (**rh**), note the bulb with darker pigmentation, and marginal lappets (**ml**). **F**—Detail of the gonads (**g**) with triangular shape (specimen NMNH 55931).

Holotype ZMB 14808.

Material examined: NMNH 28128 and 28129 (two specimens from Peru, no information on depth), NMNH 55931 (one specimen from California, USA 1975, depth: 900m), AMNH 2113 (one specimen from Tower Island, Galapagos 1925, depth: 372m) and MBARI database (identity-reference 46, coast of California 2013, 36°39'N 122°67'W, depth: 1,210m).

Diagnosis: medusa—hyperdome red-purple bell with blue stomach.

Description: Based on original description, Bigelow (1928), Mayer (1910), and Kramp (1961). Adult medusa up to 15 mm in diameter; exumbrella surface of central disc covered with nematocysts; pointed marginal lappets; tentacles and bell red-purple, stomach blue; gastric septae broadly triangular; narrow perradial gastric ostia. No information about a polyp stage.

Type locality: East Atlantic (9°31'N 9°46'E, Benguela current, 2,000m depth).

Distribution: possibly a worldwide species in deeper waters.

Remarks: Examined specimens with brownish smooth umbrella, with narrow pointed lappets (in some specimens the marginal lappets were very damaged, making it difficult to verify their morphology). Eight rhopalia with statocyst and a darker brown bulb at the base. Triangular faint orange or dark purple gonads, pointing to the margin and containing hundreds of eggs. More than 50 gastric filaments in total, close to 12 per quadrant. Some specimens had dense, white "warts" (nematocysts?) on the exumbrellar surface. The largest animal was 20 mm in diameter and had tentacles as long as 15 mm.

Nausithoe simplex (Kirkpatrick, 1890)

(Fig. 15: A–B)

Stephanoscyphus simplex Kirkpatrick, 1890: 14, pl. III.
Stephanoscyphistoma simplex—Jarms, 1990: 11.
Nausithoe simplex—Morandini & Jarms, 2012: 62–63, figs 1–4.

Lectotype NHM 1878.3.26.11a.

Material examined: NHM 1878.3.26.11a, b, d.

Diagnosis: polyp—solitary with 1 whorl of 4 cusps.

Description: Based on original description, and Morandini & Jarms (2012). Only known from the polyp stage. Polyp 4.56 mm in total length; a single series with 4 internal quadratic cusps.

Type locality: S of Greenland (56°11'N 37°41'W), ~2650m depth.

Distribution: Only known from type locality.

Remarks: The precise identification of this species demands visualization of the internal cusps (shape and number). We analyzed one specimen previously identified as *N. simplex* (NMNH 53831—North Carolina/ USA 1966), but observation of the internal cusps to confirm the identification was not possible without damaging the specimen.

Nausithoe sorbei Jarms, Tiemann & Altuna Prados, 2003

(Fig. 15: C–F)

Nausithoe sorbei Jarms *et al.*, 2003: 3–8, figs 3–5.

Holotype ZMH C11682.

Material examined: Live specimens from laboratory culture (polyps from Gavdos island, Greece, 2005; 115m depth; H. Zibrowius col.).

Diagnosis: young medusa—transparent body with red mouth and stomach; polyp—solitary with one cup-shaped cusp per whorl.

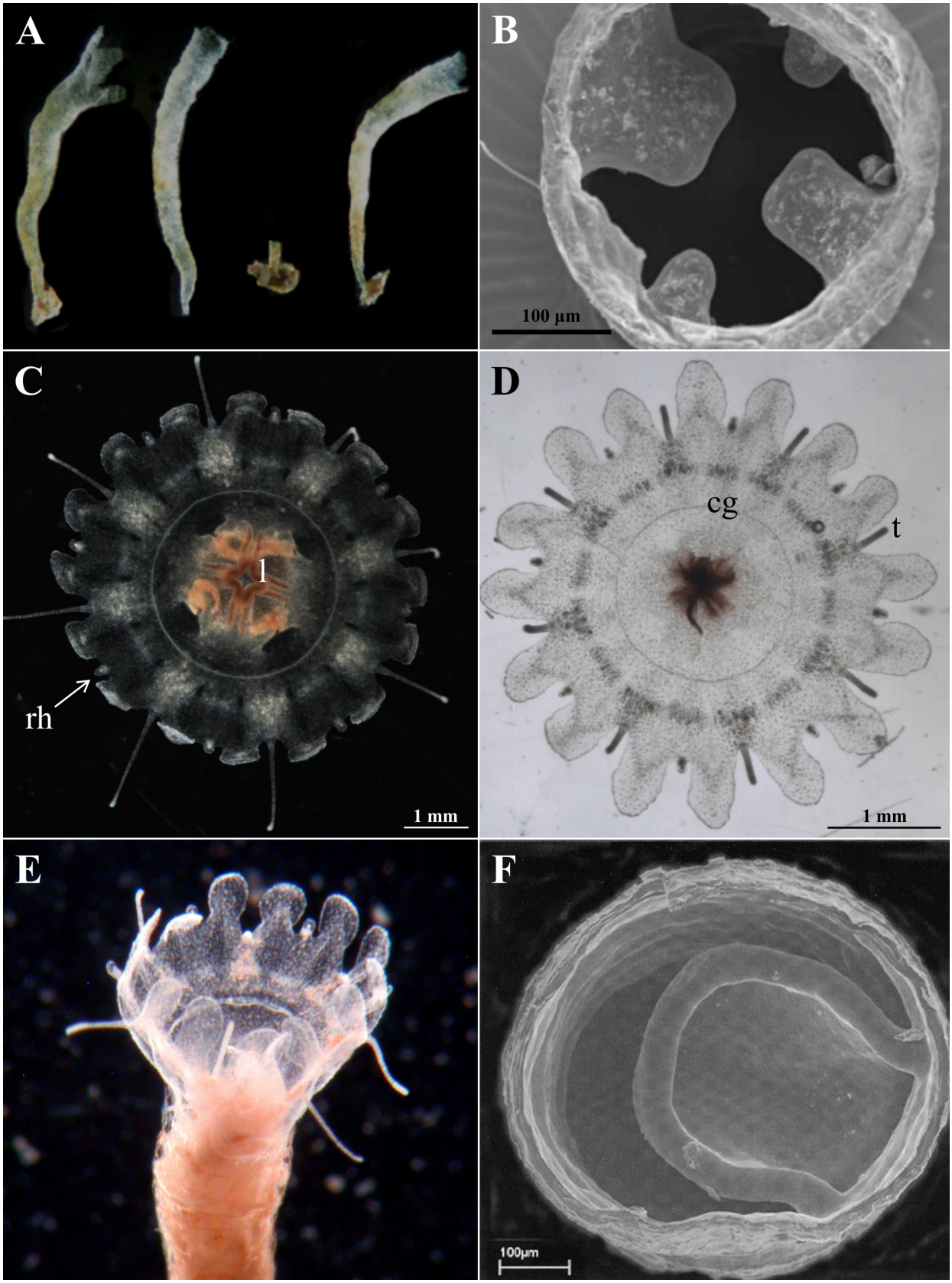

FIGURE 15. *Nausithoe simplex* (A–B) and *Nausithoe sorbei* (C–F). **A**—Lectotype NHM 1878.3.26.11a. **B**—Scanning electronic microscopy of internal whorl of cusps (NHM 1878.3.26.11d); image adapted from Morandini & Jarms 2012. **C**—Young medusa showing the rhopalium (**rh**) and red mouth lips (**l**). **D**—Just-released ephyra showing the coronal groove (**cg**) and tentacles (**t**). **E**—Polyp strobilating. **F**—Scanning electronic microscopy of the single internal cusp; image extracted from Jarms *et al*. 2003.

Description: Based on original description, Jarms & Morandini (2019), and own observations on live specimens. The ephyrae are released at 4.7–5.0 mm in diameter, tentacles and transparent body with red mouth and stomach. Polyp solitary; 13.1 mm total length; periderm tube rings more prominent; 1–4 whorls per tube, consisting of a single cup-shaped cusp each.

Type locality: Bay of Biscay (400–1050 m depth).

Distribution: NE Atlantic Ocean (coast of Europe).

Remarks: Besides the original description, only Jarms & Morandini (2019) presented data on the species including observation of live specimens. Despite several attempts to raise the species in captivity, ephyrae did not grow into adults.

Nausithoe striata (Vanhöffen, 1910)

(Fig. 16: A–B)

Tubularia striata Vanhöffen, 1910: 280, fig. 6.
Scyphistoma striatum—Vanhöffen, 1910: vii.
Stephanoscyphus striatus—Leloup, 1937: 64.
Stephanoscyphistoma striatus—Jarms, 1990: 11.
Nausithoe striata—Morandini & Jarms, 2005: 120–122, figs 7–9.

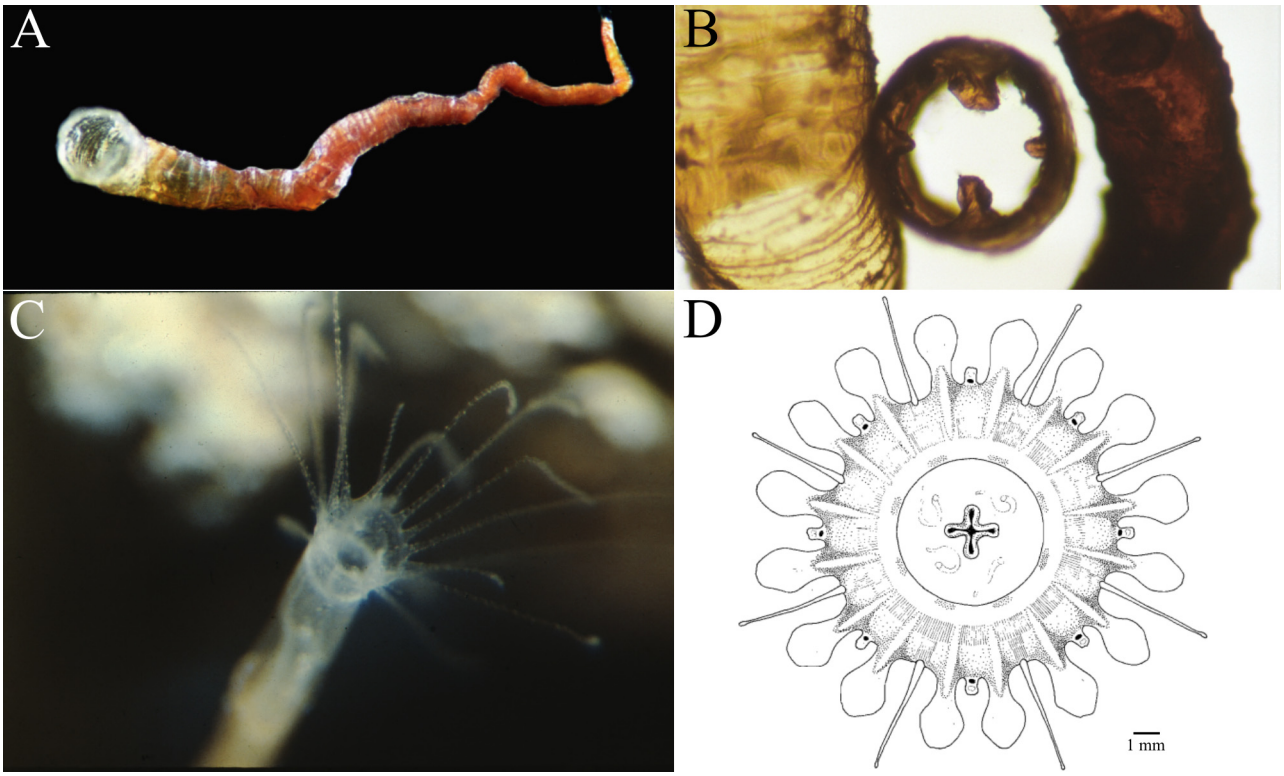

FIGURE 16. *Nausithoe striata* (A–B) and *Nausithoe thieli* (C–D). **A**—Holotype (ZMB CNI 14816). **B**—Distal whorl of internal cusps of the holotype (ZMB CNI 14816). **C**—Polyp with thin collar and few tentacles. **D**—Image of young medusa adapted from Jarms 1990.

Holotype ZMB CNI 14816.

Material examined: ZMB CNI 14816.

Diagnosis: polyp—solitary with 4 cusps per whorl.

Description: Based on original description, and Morandini & Jarms (2005). Only known from the polyp stage. Polyp solitary; 8.4 mm in total length; light brown color; 0.58 mm basal disc; 0.14 mm diameter just above the basal disc; 0.34 mm diameter at 2 mm height and 0.64 at 5 mm height; aperture 0.96 mm in diameter; 5 whorls of 4 internal cusps.

Type locality: Antarctic Ocean (65°S 85°E), 2,450m depth.

Distribution: Only known from type locality.

Remarks: This species was diagnosed based on one polyp SEM, which revealed 4 internal cusps per whorl, the same as *N. simplex*. Nevertheless, *N. simplex* has only one whorl of internal cusps and was described from Greenland.

Nausithoe thieli Jarms, 1990

(Fig. 16: C–D)

Nausithoe thieli Jarms, 1990: 17–21, figs 8–11, pl. IV.

Holotype ZMH C11532.

Material examined: None.

Diagnosis: ephyra—transparent with 4 small buds of gastric filaments; polyp—solitary with 2, 4 and 8 cusps per whorl.

Description: Based on original description. Polyp solitary; 19.58 mm in total length; 2, 4 and 8 cusps per whorl (number increases from base to aperture of tube) and maximum of 7 whorls; smooth cusps; 0.5 mm in diameter at basal disc; 0.08 mm in diameter above the basal disc; 30–40 tentacles; 20 ephyrae per strobilation. Newly released ephyra transparent; 2 mm diameter; 0.7 mm of this the central disc; rhopalia with statocyst and ocelli; 4 small buds of gastric filaments. Adult medusa unknown.

Type locality: Central Red Sea (763m depth).

Distribution: Only known from type locality.

Remarks: Cultivation of ephyrae into mature medusae not yet successful.

Nausithoe werneri Jarms, 1990

(Fig. 17)

Nausithoe werneri Jarms, 1990: 12–17, figs 1–7, pls I–III.

Holotype ZMH C11530.

Material examined: ZMH C10693 (four specimens from Portugal, no information on depth), ZMH C10602 (eight specimens from Morocco 1967, no information on depth), more than 27 specimens kept in culture (polyps from Morocco 1980, depth: 800–3,000 m; Mediterranean Sea 2008, depth: 200m; and Rio de Janeiro, Brazil 2002, depth: 200–227 m).

Diagnosis: medusa—hyperdome bell, translucid, with straw hat shape; polyp—solitary with 8 cusps per whorl.

Description: Based on original description and own observations. Adult medusae 5.7–12 mm in diameter with 3.85–7.74 mm of this the central disc, with a high translucid hyperdome bell with straw hat shape; marginal lobes partially overlapping, rounded; tentacles up to 7 mm long; rhopalia with statocyst and ocelli; rounded, brown/yellowish, gonads located above the coronal groove (dioecious). Polyp solitary; 2.56–31.43 mm in total length; aperture diameter 0.33–1.65 mm; 0.08–0.40 mm diameter just above the basal disc; 8 cusps per whorl and a maximum of 14 whorls, cusps have additional teeth on the surface; 40–50 tentacles; over 100 ephyrae per strobilation.

Type locality: Morocco coast, 415–420 m depth.

Distribution: NE Atlantic Ocean, SW Atlantic Ocean, Mediterranean and Arctic Ocean.

Remarks: Examined specimens with a thimble-shaped transparent central disc, with 4 to 8 gastric filaments, which made their identification as *N. werneri* possible. Gonads are round and yellowish, located under or outside the coronal grove. Maximum diameter of specimens was 7 mm and tentacles were up to 3 mm long. All specimens from Brazil were males.

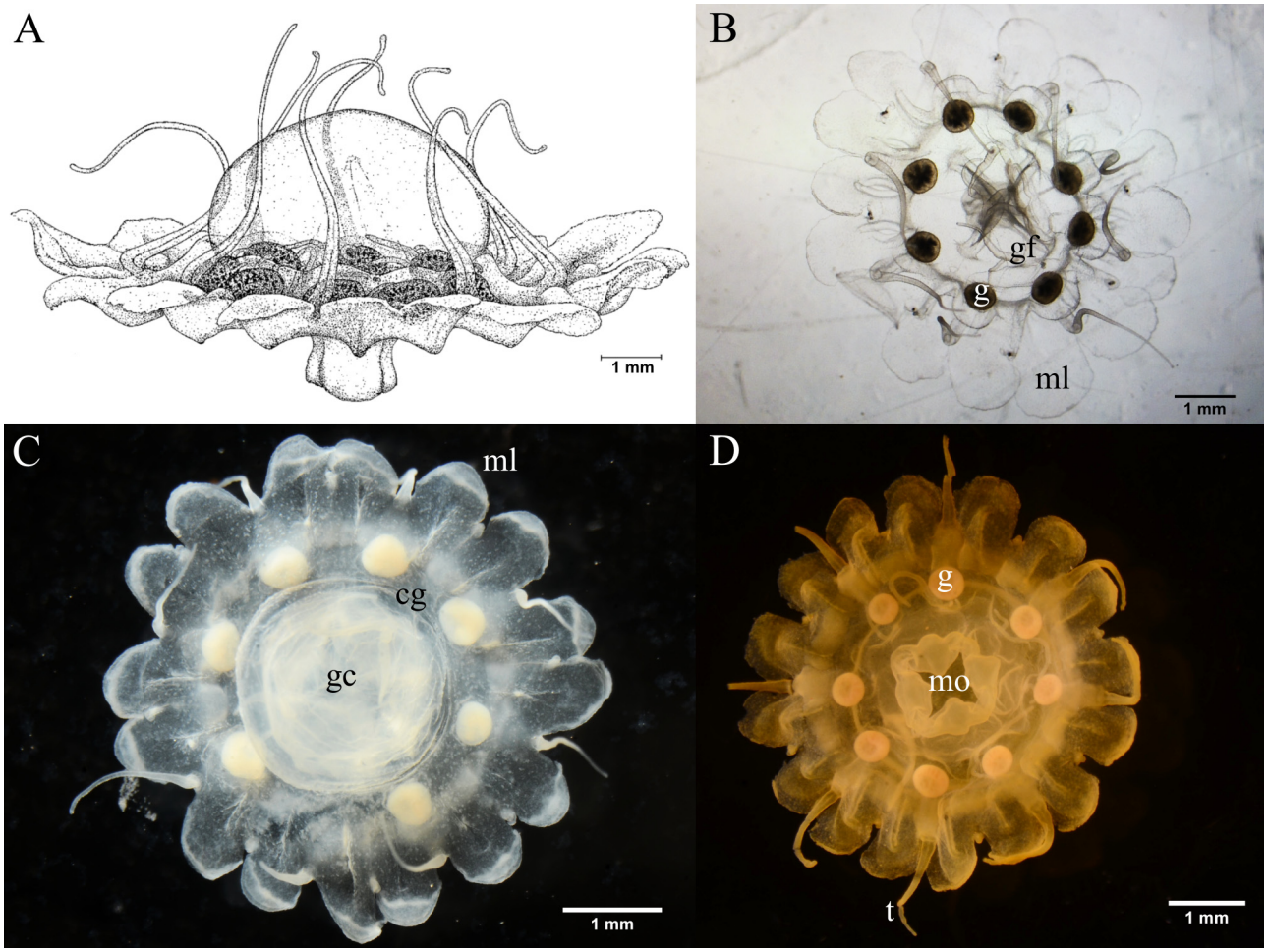

FIGURE 17. *Nausithoe werneri*. A—Side view of adult medusa showing the hyperdome bell; illustration from Jarms 1990. B—Aboral view of male medusa from laboratory culture showing the gastric filaments (**gf**), the gonads (**g**) and the wide marginal lappets (**ml**) overlapping. **C**—Aboral view of medusa (ZMH C10693) showing the coronal groove (**cg**), gastrovascular cavity (**gc**) and marginal lappets (**ml**); **D**—Oral view of medusa (ZMH C10602), emphasizing the mouth (**mo**), gonads (**g**) and tentacles (**t**).

Discussion

The order Coronatae is widely known as being composed of deep-sea medusae species, although a significant part of its species diversity also occurs in shallow waters (around 35%). Several species of the genus *Nausithoe* were described more than 100 years ago and have never been found again (*N. albatrossi*, *N. albida*, *N. clausi*, *N. limpida*, *N. picta*). Unfortunately, in such cases their morphological features could not be reviewed or compared to more recently described species, mostly due to the absence of specimens available for inspection. Comparing our observations of different specimens from distinct locations with the original descriptions helped to elucidate the diversity of the group.

Although relatively poorly known, members of the genus *Nausithoe* are regularly found among specimens reported in different studies, either considering the medusa (Gershwin & Zeidler 2003; León *et al.* 2005; Pagès *et al.* 2006; Neumann-Leitão *et al.* 2008) or the polyp stage (Sterrer 1986; Galil & Zibrowius 1998; Cebrián & Ballesteros 2004; Morandini & Jarms 2010). It is difficult to clearly state if the different species are common or not, perhaps also being misidentified or inaccurately observed; thus, based on current knowledge, we cannot highlight the importance of these species in planktonic and/or benthic communities. However, it should be noted that some pelagic stages can bloom (S. Toshino *pers. comm.* 2018, Okinawa, Japan), and some benthic species can colonize wide areas (ACM *pers. observ.* 2013, São Sebastião, Brazil); while others can inflict painful stings (Oiso *et al.* 2004).

In general, studying the morphology of gelatinous animals can be a difficult task. Preservation techniques and different fixation substances can affect the shape and pigmentation of jellyfish species. Thus, relying on the shape and color of a preserved specimen can be somewhat tricky. Still, while studying the genus *Nausithoe* we noticed that the general shape of the bell, mainly the central disk morphology, especially the dome height in relation to the bell radius, could be an important character for differentiating certain species. In the case of *N. rubra*, previous descriptions did not mention the shape of the central disk. However, when analyzing the preserved animals, we can infer that this species' umbrella is flatter than in *N. globifera*, but not as flat as described for *N. punctata* or *N. maculata*. Our proposal to use the terminology "hypodome", "isodome" and "hyperdome" is intended to help standardize the nomenclature and provide a better comparative framework for describing the morphology of *Nausithoe* jellyfishes. Additionally, the need for this terminology was also perceived when we found some inconsistencies while comparing descriptions with the specimen itself. Russell (1970) described the umbrella of *N. atlantica* as "somewhat flat" when compared to *N. globifera*. But the umbrella is in fact more intermediate in *N. atlantica* (= isodome), and this is readily distinguishable from the flatter hypodome umbrellas of *N. maculata* or *N. punctata*. Our aim was to avoid general or confusing terms that would prevent a precise definition of the morphological feature being studied.

The recent accumulation of photos of live animals has been crucial to this review. Although there are some complications stemming from comparing preserved to living animals, our bell morphology terminology worked quite well for the species that we could observe both in living form and as preserved specimens (*e.g.*, *N. atlantica*, *N. maculata*, *N. marginata*, *N. punctata*, *N. rubra* and *N. werneri*).

The importance of the bell shape to identify *Nausithoe* specimens was also apparent when comparing a museum specimen with Haeckel's (1882: 103–111, pls. XXVI–XXVII) description of *N. challengeri* ("cap-shaped; with horizontal apex and vertical side wall; sometimes as wide as high"). The drawing provided by the author closely resembles a specimen we observed: NMNH 58264, Fig. 5. This individual lacked the manubrium, which is an uncommon feature, prior to this work only ascribed to the species *N. marginata*. However, all the other morphological characters correspond to the *N. challengeri* description; therefore, we consider *N. challengeri* to be a valid species, disagreeing with some authors (Bigelow 1928; Kramp 1961).

Another character which has traditionally been used for the distinction of *Nausithoe* species is the number of gastric filaments. Based on our findings, we consider this character problematic and in need of further study. The species *N. punctata* and *N. maculata* may have the same number of gastric filaments, apparently depending on the size of the medusae. *N. rubra*, *N. atlantica* and *N. globifera*, which have more than a hundred gastric filaments (Russell 1970), are recognized to be much larger than *N. maculata* and *N. punctata*. If the size of the animal is determinant for the number of gastric filaments in their cavities, we should reconsider the utility of this feature as a diagnostic character for the group and explore if it could be normalized based on medusa size. It might be more informative to only take into consideration the arrangement of filaments within the gastrovascular cavity (isolated vs. in clusters),

The shape of the gonads was also a point of discrepancy between our observations and the available literature. Depending on the degree of maturity, gonads might change in shape, in most cases varying from bean-shaped or oval to clearly round (more developed), as was observed in *N. maculata*, *N. punctata* and *N. werneri*. This type of incongruence was expected before our analysis of museum specimens due to the experience in cultivated animals and considering intraspecific variation observed by some authors (*e.g.,* Morandini & Silveira 2001, for *N. aurea* = *N. maculata*).

It is well known that *Nausithoe* polyps are very similar one to the next and the morphological characters proposed by Jarms (1990) are not always enough to identify specimens (Molinari & Morandini 2019), although for some species, measurements of polyps are useful (Morandini & Jarms 2005, 2012). The number, arrangement, and shape of the internal cusps in the polyp tubes continues to be an important and effective feature. But the observation of a few individuals might not be sufficient to assess the true variation among polyps. It would be necessary (and desired) to compare a significant number of polyps, with an effective observation of all series of internal cusps (*e.g.* using SEM techniques) to account for intraspecific variation in this character. We are aware that there are limitations in collecting polyps, especially deep-sea species, and that such observations require the polyps to be cut, therefore damaging the sample. Computed microtomography could be a useful tool for less destructive analysis to characterize of rare material (as Holst *et al.* 2021).

We were able to differentiate all species of *Nausithoe* analyzed: *N. atlantica*, *N. challengeri*, *N. eumedusoides*,

N. globifera, *N. maculata*, *N. marginata*, *N. punctata, N. racemosa*, *N. rubra*, *N. sorbei* and *N. werneri*. Bigelow (1928) and Kramp (1961) suggested that *N. rubra* and *N. atlantica* should be synonymized based on the species morphology and original descriptions. We agree that both species' descriptions are similar; however, taking into consideration our observations on fixed animals and MBARI deep sea images, we conclude that they are likely to be distinct species. *N. rubra* has a hyperdome umbrella and triangular gonads, wheras *N. atlantica* has an isodome umbrella and oblong gonads that can develop two apically oriented projections making them appear V-shaped.

Although we recognize *Nausithoe punctata* as a valid species, its reported distribution might be erroneous due to the difficulty in identifying these animals. When comparing the original descriptions of *Nausithoe albida*, *Nausithoe clausi* Vanhöffen, 1892, *Nausithoe limpida* Hartlaub, 1909 and *Nausithoe picta* Agassiz & Mayer, 1902, they all seem morphologically to be similar to *N. punctata*. Kramp (1961) had already pointed out the similarity of *N. clausi* and *N. picta* to *N. punctata*. Nevertheless, these species were superficially described and were not collected at the same location: *N. albida* is only known from its type locality in Italy; *N. clausi* is only known from the type locality east of the Caroline islands (tropical North Pacific Ocean); *N. limpida* is only known from the type locality in the North Atlantic Ocean; and *N. picta* is known from the Central Indo-Pacific. Taking into consideration the distribution, the only species described for the same region as the type locality of *N. punctata* (Mediterranean Sea) is *N. albida.* For that reason, we consider this species as a synonym of *N. punctata*, even though the holotype of *N. albida* is not extant and there are no images of the specimens. In conclusion, we retain as valid 20 of the 21 previously accepted species for the genus *Nausithoe* (Table 2), pending collection and detailed morphological and genetic characterization of specimens representing the full diversity of the genus.

Jellyfish systematics in general is quite difficult due to the soft nature of the animals, the limited number of morphological features to compare, and their life cycles involving multiple life history stages. The systematics of the genus *Nausithoe* is no different. Several species have been described based on a few specimens, obscuring information on intraspecific variation, and the characters used did not embrace the array of species we know today. Here we state that a combination of features (coloration, bell and gonad shape, gastric filaments arrangement, the number of internal cusps in polyp tubes, and of course genetic data) is the best way to define and distinguish species of the genus *Nausithoe*. Molecular data for coronates available in GenBank at present are questionable. There are numerous cases of published sequences not being associated with vouchers or even locality information (see Marques *et al*. 2013). Further, many identifications have been made by non-specialists in the group, and many species have been identified only to the generic level (as "sp."). Unfortunately, there is no way at present to check/validate these genetic sources, limiting their utility for systematics; the data must be augmented by new genetic sequences associated with morphologically characterized voucher specimens. A deep understanding of Coronatae diversity is crucial to unravel the evolutionary history of the group, including life cycles (*e.g.,* Jarms 1990; Silveira & Morandini 1997). As often stated in the literature on the group, integrating observations of living specimens, including life cycles, coloration, cnidomes, anatomy, and genetics will be critical for understanding the biodiversity of Coronatae.

Conclusion

Our review and study highlight that there are still many gaps in knowledge about the diversity and the geographic and depth distributions of coronate jellyfishes of the genus *Nausithoe*. By comparing the original descriptions with specimens from museum collections, laboratory reared specimens and underwater photos, we retain as valid 20 of the 21 previously accepted species for the genus and propose that some of the morphological diagnostic characters traditionally used to identify these species should be questioned or refined.

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References

Agassiz, A. & Mayer, A.G. (1899) Acalephs from the Fiji Islands. *Bulletin of the Museum of Comparative Zoology at Harvard University*, 32, 157–189.

Agassiz, A. & Mayer, A.G. (1902) Reports on the scientific results of the expedition to the tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "Albatross", from August 1899 to March 1900, Command Jefferson F. Moser, U.S.N., commanding. III. *Medusae Memoirs of the Museum of Comparative Zoology at Harvard College*, 26 (3), 139–176.

Allman, G.J. (1874) Reports on the Hydroida collected during the Expeditions of H.M.S. 'Porcupine'. *Transactions of the Zoological Society of London*, 8 (8), 65.
https://doi.org/10.1111/j.1096-3642.1874.tb00566.x

Bigelow, H. (1928) Scyphomedusae from the Arcturus Oceanographic Expedition. Museum of Comparative Zoology. *Zoologica*, VIII (10), 497–501.
https://doi.org/10.5962/p.184695

Bigelow, H.B. (1938) Plankton of the Bermuda oceanographic expeditions, VIII. Medusae taken during 1929 and 1930. *Zoologica*, 23 (2), 99–189.
https://doi.org/10.5962/p.203655

Broch, H. (1913) Hydroida. *Reports and Scientific Results of the "Michael Sars" North Atlantic Deep-Sea Expedition, 1910*, Zoology, 3 (4), 9–10.

Cebrián, E. & Ballesteros, E. (2004) Zonation patterns of benthic communities in an upwelling area from the Western Mediterranean (La Herradura, Alboran Sea). *Scientia Marina*, 68 (1), 69–84.
https://doi.org/10.3989/scimar.2004.68n169

Galil, B. & Zibrowius, H. (1998) First benthos samples from Eratosthenes seamount, eastern Mediterranean. *Senckenbergiana Maritima*, 28 (4/6), 111–121.
https://doi.org/10.1007/BF03043142

Gegenbaur, C., Kölliker, A. & Müller, H. (1853) Bericht über einige Herbste 1852 in Messina angestellte vergleichend-anatomische Untersuchungen. *Zeitschrift für wissenschaftliche Zoologie*, 4 (3/4), 299–370.

Gegenbaur, C. (1856) Versuch eines Systemes der Medusen, mit Beschreibung neuer oder wenig gekannter Formen; zugleich ein Beitrag zur Kenntniss der Fauna des Mittelmeeres. *Zeitschrift für Wissenschaftliche Zoologie*, 8, 202–273, tafs vii–x.

Gershwin, L. & Zeidler, W. (2003) Encounter 2002 Expedition to the isles of St Francis, South Australia: medusae, siphonophores and ctenophores. *Transactions of the Royal Society of South Australia*, 127 (2), 205–241.

Haeckel, E. (1880) s.n. *In*: *Das System der Medusen I. 2: System der Acraspeden*. Verlag von Gustav Fischer, Jena, pp. 361–672.

Haeckel, E. (1882) Report on the deep-sea medusae dredged by H.M.S. Challenger during the years of 1873–1876. *Report on the scientific results of the voyage of H.M.S. Challenger during the years of 1873–1876. Zoology*, 4 (2), i–cv + 1–154.

Hartlaub, C. (1909) Méduses. *Croisière Océanographique, Mer du Grönland 1905*, 464–478.

Hickson, S.J. (1906) Coelenterata: Anthozoa = Actinozoa—general characters—Alcyonaria. *In*: Harmer, S.F. & Shipley, A.E. (Eds.), *The Cambridge Natural History*, 1, pp. 326–364.

Holst, S., Miranda, L.S., Meyer, P., Michalik, P. & Sötje, I. (2021) Morphological analyses of the adult and juvenile stages of the stalked jellyfish *Craterolophus convolvulus* (Johnston, 1835) (Cnidaria: Staurozoa: Stauromedusae: Craterolophidae) using micro-CT. *Zoologischer Anzeiger*, 292, 240–260.
https://doi.org/10.1016/j.jcz.2021.04.005

Jarms, G. (1990) Neubeschreibung dreier Arten der Gattung *Nausithoe* (Coronatae, Scyphozoa) sowie Wiederbeschreibung der Art *Nausithoe marginata* Kölliker, 1853. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 87, 7–39.

Jarms, G. (1997) The polyps of Coronatae (Scyphozoa), a review and some new results. *In*: den Hartog, J.C. (Ed.), *Proceedings of the 6th International Conference on Coelenterate Biology, 1995*. Nationaal Natuurhistorisch Museum, Leiden, pp. 271–278.

Jarms, G. (2001) The life cycle of *Nausithoe hagenbecki* sp. nov. (Scyphozoa, Coronatae). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 98, 13–22.

Jarms, G., Morandini, A.C. & Silveira, F.L. (2002a) Polyps of the families Atorellidae and Nausithoidae (Scyphozoa: Coronatae)

new to the Brazilian fauna. *Biota Neotropica*, 2 (1), 11.
https://doi.org/10.1590/S1676-06032002000100004
Jarms, G., Morandini, A.C. & Silveira, F.L. (2002b) Cultivation of polyps and medusae of Coronatae (Cnidaria, Scyphozoa) with a brief review of important characters. *Helgoland Marine Research*, 56, 203–210.
https://doi.org/10.1007/s10152-002-0113-3
Jarms, G., Tiemann, H. & Prados, A.A. (2003) A new bathybenthic coronate polyp, *Nausithoe sorbei* sp. nov. (Scyphozoa, Coronatae), from the Bay of Biscay and off Azores. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 100, 1–11.
Jarms, G. (2010) The early life history of Scyphozoa with emphasis on Coronatae. A review with a list of described life cycles. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg*, 45, 17–31.
Jarms, G. & Morandini, A.C. (2019) Coronamedusae. *In*: Jarms, G. & Morandini, A.C. (Eds.), *World Atlas of Jellyfish*. *1st Edition*. Dölling und Galitz Verlag, Hamburg, pp. 111–259.
Kirkpatrick, R. (1890) Report upon the Hydrozoa and Polyzoa collected by P.W. Basset-Smith, Esq., Surgeon R.N., during the Survey of the Tizard and Macclesfield Banks, in the China Sea, by H.M.S. 'Rambler', Commander W.U. Moore. *The Annals and Magazine of Natural History*, 6 (5), 11–24.
https://doi.org/10.1080/00222939009460773
Kölliker, A. (1853) Bericht uber einige im Herbst 1852 in Messina angestellte vergleichendanatomische Untersuchungen. 11. *Zeitschrift für wissenschaftliche Zoologie*, 4, 299–370.
Komai, T. (1936) On another form of *Stephanoscyphus* found in waters of Japan. *Memoirs of the College of Science, Kyoto Imperial University*, Series B, 11, 175–183.
Kramp, P.L. (1961) Synopsis of the Medusae of the World. *Journal of the Marine Biological Association of the United Kingdom*, 40, 7–469.
https://doi.org/10.1017/S0025315400007347
Leloup, E. (1937) Hydropolypes et scyphopolypes recueillis par C. Dawydoff sur les côtes de l'Indochine française. II. Scyphopolypes. *Mémoires du Muséum d'Histoire Naturelle de Belgique*, Series 2, 12, 1–73.
León, M.E., Tejera, E., Hernández, F. & Conway, D.V.P. (2005) Medusas de las islas de Cabo Verde: resultados de la campaña TFMCBM/98 Cabo Verde. *Vieraea*, 33, 11–28.
https://doi.org/10.31939/vieraea.2005.33.02
Maas, O. (1897) Reports on an exploration off West coasts of Mexico, Central and South America, and off the Galapagos islands, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "Albatross", during 1891, Lieut. Commander Z.L. Tanner, U.S.N., commanding. XXI. Die Medusen. *Memoirs of the Museum of Comparative Zoölogy at Harvard College*, 23, 8–92.
Maas, O. (1903) Die Scyphomedusen der Siboga-Expedition. *Siboga-Expeditie*, 11, 1–91.
Marques, A.C., Maronna, M.M. & Collins, A.G. (2013) Putting GenBank data on the map. *Science*, 341 (6152), 1341.
https://doi.org/10.1126/science.341.6152.1341-a
Mayer, A.G. (1910) *Medusae of the world. Vol. III. The Scyphomedusae.* Carnegie Institution of Washington. Washington, D.C., 735 pp.
Molinari, C.G. & Morandini, A.C. (2019) Update on benthic scyphozoans from the Brazilian coast (Cnidaria: Scyphozoa: Coronatae). *Revista Brasileira de Zoociências*, 20 (2), 1–14.
https://doi.org/10.34019/2596-3325.2019.v20.27610
Molinari, C.G., Maronna, M.M., Morandini, A.C. (2020) New record of *Nausithoe werneri* (Scyphozoa, Coronatae, Nausithoidae) from the Brazilian coast and a new synonymy for *Nausithoe maculata*. *ZooKeys*, 984, 1–21.
Morandini, A.C. & Silveira, F.L. (2001a) New observations and new record of *Nausithoe aurea* (Scyphozoa, Coronatae). *Papéis Avulsos de Zoologia*, 41 (27), 519–527.
Morandini, A.C. & Silveira, F.L. (2001b) Sexual reproduction of *Nausithoe aurea* (Scyphozoa, Coronatae). Gametogenesis, egg release, embryonic development, and gastrulation. *Scientia Marina*, 65 (2), 139–149.
https://doi.org/10.3897/zookeys.984.56380
Morandini, A.C. (2003) Deep-Sea medusae (Cnidaria: Cubozoa, Hydrozoa and Scyphozoa) from the coast of Bahia (western South Atlantic, Brazil). *Mitteilungen aus dem hamburgischen zoologischen Museum und Institut, Hamburg*, 100, 13–25.
Morandini, A.C. & Jarms, G. (2005) New combinations for two coronate polyp species (Atorellidae and Nausithoidae, Coronatae, Scyphozoa, Cnidaria). *Contributions to Zoology*, 74, 117–123.
https://doi.org/10.1163/18759866-0740102008
Morandini, A.C. & Jarms, G. (2010) The identification of the coronate polyp from the Arctic Ocean: *Nausithoe werneri* Jarms, 1990 (Cnidaria, Scyphozoa, Coronatae), with notes on the biology. *Steenstrupia*, 32, 69–77.
Morandini, A.C. & Jarms, G. (2012) Discovery and redescription of type material of *Nausithoe simplex* (Kirkpatrick, 1890), comb. nov. (Cnidaria: Scyphozoa: Coronatae: Nausithoidae) from the North Atlantic. *Zootaxa*, 3320 (1), 61–68.
https://doi.org/10.11646/zootaxa.3320.1.5
Neumann-Leitão, S., Sant'anna, E.M.E., Gusmão, L.M.O., Do Nascimento-Vieira, D.A., Paranaguá, M.N. & Schwamborn, R. (2008) Diversity and distribution of the mesozooplankton in the tropical Southwestern Atlantic. *Journal of Plankton Research*, 30 (7), 795–805.
https://doi.org/10.1093/plankt/fbn040

Nogueira Jr., M., Brandini, F.P., & Codina, J.C.U. (2015) Diel vertical dynamics of gelatinous zooplankton (Cnidaria, Ctenophora and Thaliacea) in a subtropical stratified ecosystem (South Brazilian Bight). *PLoS ONE*, 10 (12), e0144161. https://doi.org/10.1371/journal.pone.0144161

Oiso, N., Fukai, K., Ishii, M., Okita, K. & Kubota, S. (2004) Systemic reaction associated with Iramo scyphopolyp, *Stephanoscyphus racemosum* Komai. *Clinical and Experimental Dermatology*, 29, 681–682. https://doi.org/10.1111/j.1365-2230.2004.01634.x

Pagès, F., Gili, J.-M. & Bouillon, J. (1992) Medusae (Hydrozoa, Scyphozoa, Cubozoa) of the Benguela Current (southeastern Atlantic). *Scientia Marina*, 56 (Supplement 1), 1–64.

Pagès, F., Flood, P. & Youngbluth, M. (2006) Gelatinous zooplankton net-collected in the Gulf of Maine and adjacent submarine canyons: new species, new family (Jeanbouilloniidae), taxonomic remarks and some parasites. *Scientia Marina*, 70 (3), 363–379. https://doi.org/10.3989/scimar.2006.70n3363

Péron, F. & Lesueur, C.A. (1810) Tableau des caractères génériques et spécifiques de toutes les espèces de Méduses connues jusqu'à ce jour. *Annales du Muséum National d'Histoire Naturelle, Paris*, 14, 325–366.

Russell, F.S. (1956) On the scyphomedusae *Nausithoë atlantica* Broch and *Nausithoë globifera* Broch. *Journal of the Marine Biological Association of the United Kingdom*, 35 (2), 363–370. https://doi.org/10.1017/S0025315400010195

Russell, F.S. (1970) Nausithoeïdae. *In*: Russell, F.S. (Ed.), *The Medusae of the British Isles II. Pelagic Scyphozoa with a Supplement to the First Volume on Hydromedusae.* Cambridge University Press, London, pp. 29–37.

Silveira, F.L. & Morandini, A.C. (1997) *Nausithoe aurea* n. sp. (Scyphozoa, Coronatae, Nausithoidae), a species with two pathways of reproduction after strobilation: sexual and asexual. *Contributions to Zoology*, 66, 235–246. https://doi.org/10.1163/26660644-06604004

Sötje, I. & Jarms, G. (2009) Derivation of the reduced life cycle of *Thecoscyphus zibrowii* Werner, 1984 (Cnidaria, Scyphozoa). *Marine Biology*, 156, 2331–2341. https://doi.org/10.1007/s00227-009-1261-7

Sterrer, W. (1986) Class Scyphozoa (jellyfish). *In*: Sterrer, W. (Ed.), *Marine fauna and flora of Bermuda*. Wiley-Interscience, New York, New York, pp. 155–159.

Stiasny, G. (1935) Die Scyphomedusen der Snellius Expedition. *Verhandelingen der Koninklijke Akademie van Wetenschappen*, Sectie 2, Afdeeling natuurkunde, 34 (6), 1–44.

Suárez-Morales, E., Gasca, R., Segura-Puertas, L. & Biggs, D.C. (2002) Planktonic cnidarians in a cold-core ring in the Gulf of Mexico. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México*, Serie Zoología, 73 (1), 19–36.

Vanhöffen, E. (1892) Die Akalephen der Plankton-Expedition. *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, 2, 3–28.

Vanhöffen, E. (1902) Die Acraspeden Medusen der deutschen Tiefsee-expedition 1898–1899. *Wissenschaftliche Ergebnisse der deutschen Tiefsee-expedition auf dem dampfer Valdivia 1898–1899*, 3, 3–52. https://doi.org/10.5962/bhl.title.1404

Vanhöffen, E. (1910) Die Hydroiden der Deutschen Südpolar-Expedition 1901–1903. *Deutsch Südpolar-Expedition*, 11, 269–340.

Vanhoffen, E. (1913) Uber Westindische Medusen. *Zoologische Jahrbücher*, 11, 413–432.

Werner, B. (1970) Contribution to the evolution in the genus *Stephanoscyphus* (Scyphozoa Coronatae) and ecology and regeneration qualities of *Stephanoscyphus racemosus* Komai. *Publications of the Seto Marine Biological Laboratory*, 18, 1–20. https://doi.org/10.5134/175623

Werner, B. (1971) *Stephanoscyphus planulophorus* n. spec., ein neuer Scyphopolyp mit einem neuen Entwicklungsmodus. *Helgoländer wissenschaftliche Meeresuntersuchungen*, 22, 120–140. https://doi.org/10.1007/BF01611366

Werner, B. (1973) New investigations on systematics and evolution of the class Scyphozoa and the phylum Cnidaria. *Publications of the Seto Marine Biological Laboratory*, 20, 35–61. https://doi.org/10.5134/175791

Werner, B. (1974) *Stephanoscyphus eumedusoides* n. spec. (Scyphozoa, Coronatae), ein Höhlenpolyp mit einem neuen Entwicklungsmodus. *Helgoländer wissenschaftliche Meeresuntersuchungen*, 26, 434–463. https://doi.org/10.1007/BF01627626

Werner, B. & Hentschel, J. (1983) Apogamous life cycle of *Stephanoscyphus planulophorus*. *Marine Biology*, 74, 301–304. https://doi.org/10.1007/BF00403455