

The Mediterranean species  
of *Hornera* Lamouroux, 1821 (Bryozoa, Cyclostomata):  
reassessment of *H. frondiculata* (Lamarck, 1816)  
and description of *H. mediterranea* n. sp.

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*Hornera frondiculata* (Lamarck, 1816), large colony with complex branching pattern. Croatia, Vis Is., 30 m. (Photo: J. G. Harmelin).

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# The Mediterranean species of *Hornera* Lamouroux, 1821 (Bryozoa, Cyclostomata): reassessment of *H. frondiculata* (Lamarck, 1816) and description of *H. mediterranea* n. sp.

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## ABSTRACT

*Hornera* Lamouroux, 1821, a genus which includes large, rigidly erect, ramified and highly calcified cancellate cyclostome species, is represented in the Mediterranean Sea by two species, *H. frondiculata* (Lamarck, 1816), the type species of the genus, and a species previously left unnamed or wrongly attributed to the northern *H. lichenoides* (Linnæus, 1758), and classified under this name as threatened in the Mediterranean (Barcelona Convention, Annex II). On the basis of abundant material including large, well-preserved colonies collected by diving, the distinctive morphological and ecological features of these two species are detailed, leading to the description of a new species, *H. mediterranea* n. sp., and to a better characterization of *H. frondiculata*. The current state of knowledge of the range of the two *Hornera* species suggests that they are endemic to the Mediterranean. Their depth and habitat distributions span from 30 to 100 m on both dimly lit rocky walls and flat bottoms with coarse elements for *H. frondiculata*, and from 55 to 200 m only on flat sandy bottoms for *H. mediterranea* n. sp., but both species can coexist in the same microhabitat. The distribution of *H. frondiculata* in two separate habitats is reflected in a remarkable plasticity of colony shape and branching design which optimizes food particle capture according to local flow conditions.

## KEY WORDS

cyclostomes,  
biogeography,  
habitat distribution,  
colony shape,  
reproduction strategy,  
SPA-BD protocol  
annex II,  
new species.

## RÉSUMÉ

*Les espèces méditerranéennes de Hornera Lamouroux, 1821 (Bryozoa, Cyclostomatida) : réexamen de H. frondiculata (Lamarck, 1816) et description de H. mediterranea n. sp.*

Le genre *Hornera* Lamouroux, 1821, qui comprend un grand nombre d'espèces de cyclostomes Cancellata érigées, rigides, ramifiées et très calcifiées, est représenté en Méditerranée par deux espèces, *H. frondiculata* (Lamarck, 1816), l'espèce-type du genre, et une espèce citée sans nom spécifique ou bien identifiée à tort comme *H. lichenoides* (Linnæus, 1758), une espèce nordique, désignée comme menacée en Méditerranée (Convention de Barcelone, Annexe II). Un matériel abondant incluant de grandes colonies bien préservées, récoltées en plongée, a permis de définir en détail les traits morphologiques et écologiques des deux espèces, conduisant à une meilleure caractérisation de *H. frondiculata* et à la description d'une nouvelle espèce, *H. mediterranea* n. sp. Dans l'état actuel des connaissances, les distributions de ces deux espèces indiquent qu'elles sont endémiques de Méditerranée, vivant entre 30 et 100 m sur des parois rocheuses ombragées ou bien sur des fonds meubles avec des éléments grossiers pour *H. frondiculata*, et entre 55 et 200 m uniquement sur des fonds meubles pour *H. mediterranea* n. sp., mais les deux espèces peuvent cohabiter dans le même microhabitat. L'occupation par *H. frondiculata* de deux types très différents d'habitats se traduit par une remarquable plasticité de la forme des colonies et des ramifications qui permet d'optimiser la capture des particules alimentaires selon les conditions locales de circulation.

**MOTS CLÉS**  
cyclostomes,  
biogéographie,  
distribution écologique,  
forme coloniale,  
stratégie de reproduction,  
protocole ASP-DB  
annexe II,  
espèce nouvelle.

## INTRODUCTION

The genus *Hornera* Lamouroux 1821 is particularly speciose (93 species listed in <http://bryozoa.net/index.html>, accessed on 12/X/2020), with a large proportion (73 %) of fossil species spanning from the Eocene to the Pleistocene (Smith *et al.* 2008). Recent molecular phylogenetic data (Waeschenbach *et al.* 2009; Taylor & Waeschenbach 2015) have upset the traditional generic classification of Cyclostomata with, in particular, the grouping in the same clade of the Cancellata *Hornera* with some Tubuliporina genera, such as *Entalophoroecia* Harmelin, 1976, *Diplosolen* Canu, 1918, *Cardioecia* Canu & Bassler, 1922 and *Fron dipora* Link, 1807. In the Mediterranean Sea and the North Atlantic, *Hornera* species are the largest vinculariiform (cf. Lagaaij & Gautier 1965), or 'multiserial rigidly erect' (basic growth form according to McKinney & Jackson 1989), cyclostomes. One may also assert that *H. frondiculata* (Lamarck, 1816) is the most beautiful bryozoan in the Mediterranean owing to its delicate branching pattern. Like some other large rigidly erect bryozoans occurring in the nearshore coastal zone [e.g. *Reteporella septentrionalis* (Jullien, 1903), *Myriapora truncata* (Pallas, 1766), *Pentapora fascialis* (Pallas, 1766)], it was soon noticed and depicted by early naturalists exploring the Mediterranean. One of them, Count L. F. Marsili, a military engineer and naturalist also known as Marsilli or Marsigli, who came to Marseille to resolve the old debate regarding the vegetal, animal or mineral nature of the precious red coral [*Corallium rubrum* (Linnæus, 1758)], wrote the first oceanographic treatise (Marsilli 1725). In this book, several benthic organisms living with the red coral were depicted and, as already noted by Busk (1856), he gave the first representation of a large colony of *H. frondiculata* (pl. 33, fig. 163, reproduced here: Fig. 1A), placed in the category of 'madréporés rameux'. The finding of *H. frondiculata* by Marsili was not surprising considering that he sampled communities hosting the red coral with local red coral fishermen at sites off

the Marseille-Cassis coast and Riou Island, where many specimens of the present collection were collected.

The genus *Hornera* Lamouroux 1821 is represented in the Mediterranean Sea by *H. frondiculata*, the type species of the genus, considered here to be probably endemic to this sea (see below), and a second species left unnamed or, in many cases, ascribed without significant justification to *H. lichenoides* (Linnæus, 1758), a species mostly known from northern and Arctic seas (e.g. Busk 1875; Hayward & Ryland 1985; Kuklinski & Bader 2007).

As for many *Hornera* species, the morphological criteria characterizing the two Mediterranean species are not clearly defined. Consequently, the species names *frondiculata* and *lichenoides* have often been incorrectly used. For instance, the assertion that *H. frondiculata* is 'a common but highly variable species' (Smith *et al.* 2008) is certainly based on erroneous identifications. The use of the taxon *H. lichenoides*, in particular, is subject to uncertainties, especially because the origin of the material on which Linnæus (1758) erected the species *Millepora lichenoides* is unknown, as well as the real existence of a type. The purpose of the present paper is to give a precise description of the morphology and the ecology of the two Mediterranean *Hornera* species on the basis of abundant material. Furthermore, the taxonomic status which was originally proposed without a valid procedure by Waters (1904) for a second Mediterranean *Hornera* species, i.e., *H. mediterranea* n. sp., will be formally assigned to specimens so far ascribed to *H. lichenoides* or named *Hornera* sp.

Another problem related to the alleged presence of *H. lichenoides* in the Mediterranean involves the Mediterranean Action Plan and the Barcelona Convention for the protection of the marine environment and the coastal region of the Mediterranean (UNEP 2011). In Annex II of this convention are listed species endangered or threatened in the Mediterranean. A single bryozoan, *H. lichenoides*, is included in this list (see Rosso 2009; Rosso *et al.* 2010), and thus put at the same level as the iconic and

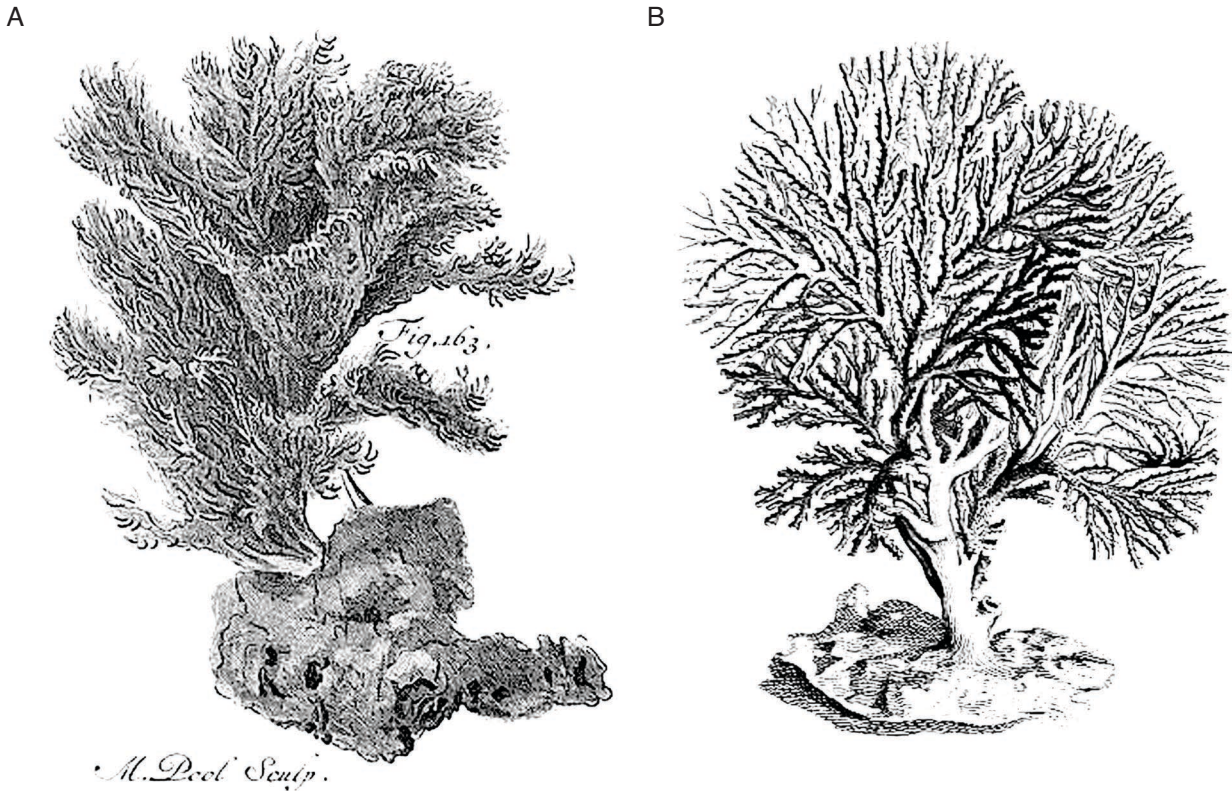


FIG. 1. — *Hornera frondiculata* (Lamarck, 1816), historical depictions of large colonies: **A**, by Marsilli (1725: pl. 33, fig. 63); **B**, by Ellis (in Ellis & Solander 1786: pl. 26, fig. 1).

highly threatened monk seal *Monachus monachus* (Herman, 1779). Apart from the obvious problems of nomenclature already evoked, the choice of this species (by an unknown expert) without any indication of specific threats is quite surprising. In addition to the poor knowledge of the morphological features of the Mediterranean *H. lichenoides*, the ecological requirements, the frequency of occurrence and the vulnerability of this species have never been documented. In contrast, *H. frondiculata* is better known, at least its general features, is more frequent at shallower depth in the nearshore zone exposed to multiple threats, and may be considered as much more attractive to collectors. One of the aims of the present paper is to offer evidence to support an eventual revision of this list.

## MATERIAL AND METHODS

### ORIGIN OF MATERIAL

Most examined specimens of the two *Hornera* species were collected by the author and collaborators by diving, dredging or trawling, and stored at the *Station Marine d'Endoume*, Marseille (SME). Diving enabled the collection of unbroken large specimens that revealed their genuine growth-forms, and supplied information on their microhabitat and local abundance. A collection of specimens of both species from Sicily was loaned by A. Rosso, University of Catania. Other examined material includes specimens stored at the Muséum national d'Histoire naturelle,

Paris (MNHN), specimens collected in Tunisia by S. Sartoretto, Ifremer, Toulon, and underwater photos of *H. frondiculata* by two amateur naturalists, D. Ader and E. Driancourt.

### SPECIMEN REPOSITORIES

Most studied specimens are deposited at the MNHN, including the type material of *H. mediterranea* n. sp. Some fertile specimens of both species were sent to the Natural History Museum, London (NHMUK). Rosso's material is located at the Paleontological Museum of the University of Catania, under the codes 'PMC. Rosso Collection I.Ps-H. B-45' and 'PMC. Rosso Collection I.Ps-H. B-46', respectively for *H. frondiculata* and *H. mediterranea* n. sp.

### METHODS OF STUDY

Morphological traits of specimens were observed with stereomicroscopes and scanning electron microscopes (SEM) after gold-palladium coating: Hitachi S-570 (SME) and Quanta 200, FEI (*Plateforme Microscopie Electronique Timone*, Aix-Marseille University). Measurements were carried out with an eyepiece micrometer and from scales of SEM photos. Macro and underwater photos were taken with an Olympus Pen EPL7 equipped with a 60 mm macro lens.

### TERMINOLOGY

The surface of colonies of *Hornera* presents a great diversity of aspects due to layers of secondary calcification that conceals to

varying extents the zooids under variously shaped structures such as ridges, pustules, hollow spaces and pores. Consequently, the detailed morphology of *Hornera* species is not easy to describe. Several terms naming the particular traits of this calcification have been created, mainly used for fossil material, such as nervus-nervi, sulcus-sulci, vacuole, cancelli (e.g. Busk 1875; Canu 1912; Canu & Bassler 1920; Mongereau 1972; Moissette & Spjeldnaes 1995). Despite definitions given by Canu & Bassler (1920) and Mongereau (1972), and their use by the latter in the diagnosis of the genus *Hornera*, these terms introduce more complexity than clarity in the descriptions. Therefore, following Borg (1926, 1944), they are not used here, except in some cases for indicating equivalence.

#### ABBREVIATIONS

##### List of material

AZ	autozoid;
col.	colonies;
COR	coralligenous rocks;
DC	detritic sandy bottom;
Div	sampling by diving;
Dre	sampling by dredging or trawling;
GZ	gonozoid;
JGH	J.-G. Harmelin;
N	number;
R	range;
SD	standard deviation;
Stn	sampling station;
UW	underwater.

##### Measurements

L	length;
W	width;
X	mean.

##### Institutions

MNHN	Muséum national d'Histoire naturelle, Paris;
MZB	Museu de Zoologia, Barcelona;
NHMUK	Natural History Museum, London;
SME	Station Marine d'Endoume, Marseille.

##### Private collections

Coll. AR	Antonietta Rosso, Catania;
Coll. JGH	Jean-Georges Harmelin, Marseille.

#### RESULTS

Family HORNERIDAE Smitt, 1867  
Genus *Hornera* Lamouroux, 1821

TYPE SPECIES. — *Hornera frondiculata* Lamouroux, 1821 (synonym of *Retepora frondiculata* Lamarck, 1816, see below), by original designation.

### *Hornera frondiculata* (Lamarck, 1816) (Figs 1-4 ; Tables 1-3)

*Retepora frondiculata* Lamarck, 1816: 182.

*Hornera frondiculata* Lamouroux, 1821: 41, pl. 26, fig. 1, pl. 74, figs 7-9 – Milne-Edwards 1838: 17, pl. 9, fig. 1 – Alder 1864: 109, pl. 5, fig. 7 – Heller 1867: 124 – Busk 1875: 17, pl. 20, figs 1-3, 6 – Calvet 1902: 43 – Waters 1904: 94, pl. 91, fig. 3 –

Canu & Bassler 1930: 86, pl. 12, figs 15-16 – Neviani 1939: 69 – O'Donoghue & de Watteville 1939: 8 – Gautier 1955: 268, pl. 4, figs 31-32. – Lagaij & Gautier 1965: chart 1 – Cook 1968: 238 (part: Mediterranean specimens) – Harmelin 1968: 1187; 1976: 223, table I, 229, table III – Mongereau 1972: 329 (part), pl. 5, figs 1-3 – Zabala 1986: 686, fig. 213 – Zabala 1993: 571, fig. 3 – Rosso 1987: 173, 175, 180-181, 188-189, fig. 6; 1996: 209, table 5, pl. 1c, g; 2005: 263, table 3; 2009: 134, 4 figs (not numbered) – Di Geronimo *et al.* 1988: 703, table 1; 1993: 89, 92, tables 2, 3, pl. IX, fig. C; 1994, table 3; 1997: 200, table 3; 1998: 248, table 1; 2003: 135, table 2; 2005: 73, table 4 – Zabala & Maluquer 1988: 182, pl. 36, figs 17-18 – Costa *et al.* 1991: 418, table 2 – Moissette & Spjeldnaes 1995: 786, pl. 2, figs 5-6 – Novosel 2005: 236, fig. 10 – Ballesteros 2006: 156, fig. 17A. – Smith *et al.* 2008: 371, 388, fig. 2A – Souto *et al.* 2010: 38 (list) – Belbacha *et al.* 2011: 46, fig. 53 – Weinberg 2013: 325 – Abdelsalam 2014: 271, fig. 2 – Rosso *et al.* 2013: 169, table 1 – Gerovasileiou & Rosso 2016: 36 (list) – Rosso & Di Martino 2016: 570 – Achilleos *et al.* 2020: 233, table 1.

*Hornera lichenoides* (L., 1758) – Laubier 1966: 223: table – Argyrou *et al.* 2002, figs 5-29 (dubious identification).

*Hornera violacea* Sars, 1863 – Calvet 1902: 44 (erroneous identification).

*Hornera caespitosa* Busk, 1875 – Calvet 1906: 478, pl. 30, figs 11-12 (erroneous identification).

TYPE LOCALITY. — Mediterranean Sea.

MATERIAL EXAMINED. — **France** • several large colonies (up to 11 cm wide); Marseille, South Riou Island; Stn JGH-71.34; 70 m; 3.VII.1971; coarse DC; Dre; with *H. mediterranea* n. sp.; JGH leg. • 2 large colonies (up to 13 cm wide); Marseille, Grand Conglue Is.; 48 m; 7.IX.1968; COR; Div; JGH leg. • several colonies; Marseille, South Riou Island, Impérial du large; Stn JGH-68.33; 65 m; 11.VI.1968; COR; Div; JGH leg. • several colonies; Marseille, South Riou Is.; Stn JGH-72.8; 90 m; 2.III.1972; silted DC; Dre; JGH leg. • fragments; South Riou Is.; Stn JGH-73.9; 90-100 m; 6.IV.1973; Dre; with *H. mediterranea* n. sp.; JGH leg. • 1 colony; Marseille, North Mangespin; 65 m; 18.IV.1972; with *H. mediterranea* n. sp.; JGH leg. • 1 colony; Hyères Islands, South Porquerolles Island; 60-65 m; X.1996; A. Castric leg. • 1 large colony + UW photos; Corsica, Scandola, Palazzu Islet; 42°23'09"N, 8°34'55"E; 35 m; X.1975; COR; Div; JGH leg.

**Italy** • 11 small fragments; SE Sicilia; Gulf of Noto; Stn PS/81 4C; 95-86 m; VII-VIII.1981; A. Rosso leg. • 8 small fragments; SE Sicilia; Gulf of Noto; Stn PS/81 4B; 65 m; VII-VIII.1981; A. Rosso leg. • 30 small fragments (thanatocenosis); North Sicilia; Ustica Island, Apollo Bank; 70 m; VII.1986; A. Rosso leg. • 1 fragment; Ionian Sea; 17 m; A. Tursi leg.

**Tunisia** • 2 colonies; northern coast, West Serrat Cape, Sidi Mechrig, Kavensur; 51-53 m; 28.VII.2006; COR; Div; S. Sartoretto leg.

**Greece** • 1 colony; Corfou, Paleokastritsa; Stn JV-4c; 40 m; 5.VII.1958; Div; J. Vacelet leg. • 1 fragment; South Creta, Kalolimniones; R/V *Calypso*, survey 1964; 80-125 m; 4.V.1964; Dre; JGH leg. • 7 fragments; Aegean Sea, Scarpanto Strait; R/V *Jean Charcot*, Stn 19.MO.67; 35°55'00"N, 27°28'30"E; 29-33 m; 29.VIII.1967; coarse DC; Dre; JGH leg.

OTHER MATERIAL EXAMINED. — Specimens from the MNHN collection (examination on 05.II.2005). • Syntypes; two small colonies from Lamarck collection; labelled by Lamarck: '*Retepora frondiculata* n., *Millepora tubipora* Solander *et al.* p. 139'; MNHN - M6 (R) 1867, no. 177b., presently [MNHN-IB-2008-4691](#) and [MNHN-IB-2008-4694](#) • 1 large colony depicted by Milne-Edwards (1838, pl. 9, fig. 1), labelled '*Hornera frondiculata* Lamour'; MNHN 4690 - M6 (R) 1867 - no. 177e. • 1 colony ca. 3 cm wide; labelled '*Hornera frondiculata* Lamouroux', Bonifacio, R/V *Travailleur*, D24, 40-80 m, 15.VII.1881; coll. Jullien, 11t. 18. • 3 fragments,

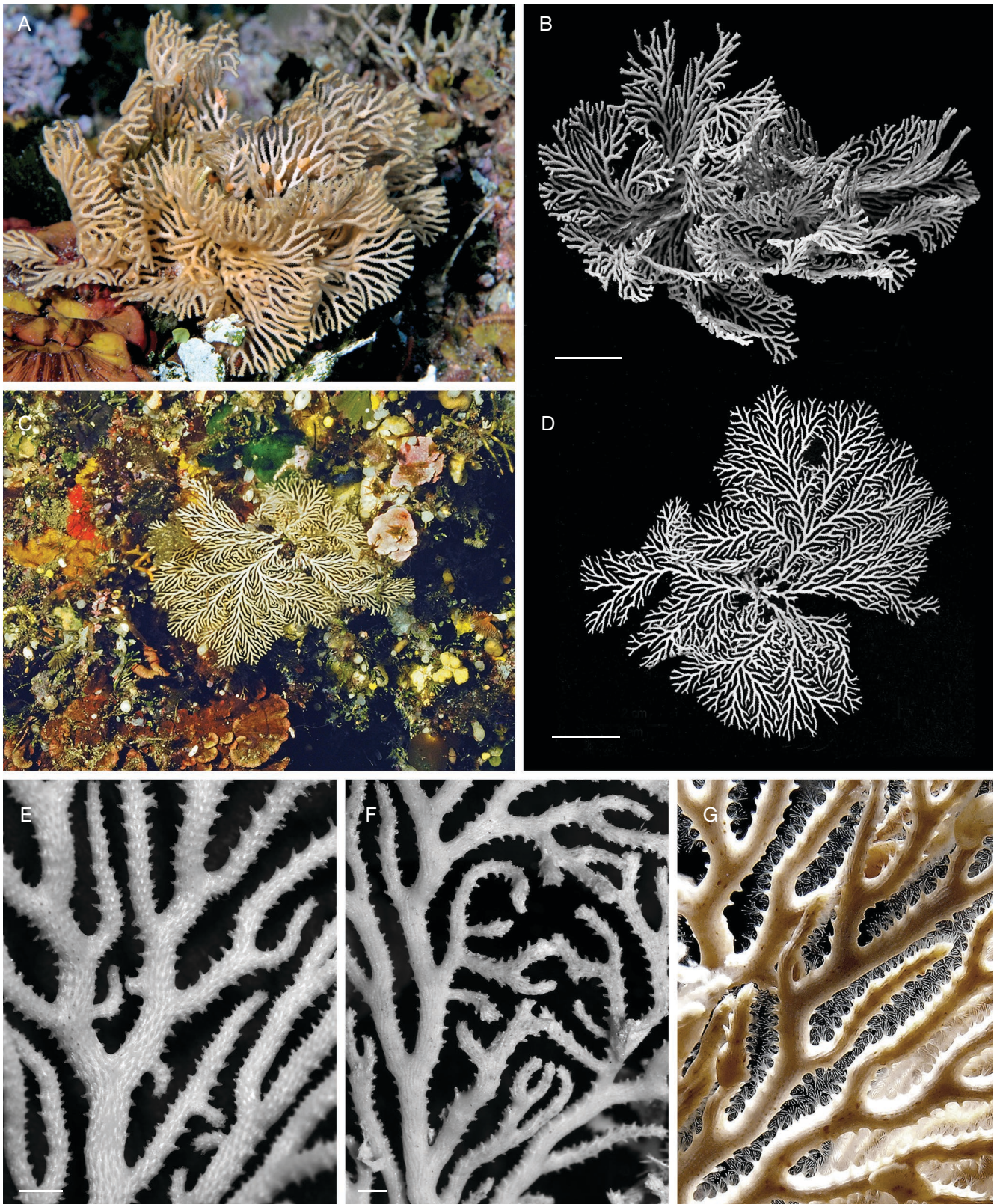


FIG. 2. — *Hornera frondiculata* (Lamarck, 1816), branching features of colonies: **A**, bushy colony on flat bottom with dense cover of seaweeds and invertebrates; **B**, bushy colony on coarse detrital sandy bottom; **C**, sub-planar colony on coralligenous vertical rocky wall; **D**, sub-planar colony from the same habitat; **E-F**, branchlets of second order with growth directed in order to split empty spaces between adjacent branches; **G**, UW close-up of a living colony showing expanded lophophores filling the space between adjacent branches. Origin: **A, G**, Croatia, Vis Is., 30 m, UW photos, 22.IX.2014; **B**, Marseille, Grand-Conglue Is., 48 m; **C**, Corsica, Palazzu Is., 35 m, UW photo, X.1975; **D**, same origin as **C**, colony sent to P. L. Cook, NHMUK in 1975; **E**, Greece, Corfou, Paleokastritsa, 40 m; **F**, Marseille, Riou Is., 70 m. Scale bars: **B, D**, 2 cm; **E-F**, 1 mm. Photos: Jean-Georges Harmelin.

with gonozooid; Bonifacio, R/V *Travailleur*, no. 862, 55-77 m. • 5 fragments; R/V *Travailleur* 1881, D.24 (2° sér.) 55-77 m, coll. Calvet 1892 11t. 18, no. 223. • Several fragments in two boxes; Marseille, coll. Jullien 1858, 2t. 18 no. 102 & 103.

ADDITIONAL PHOTOGRAPHIC RECORDS. — • 1 large colony; France, Marseille, Riou Island, Impérial du large; 38 m; vertical rock; UW photo; E. Driancourt leg. • 2 large colonies; France, Marseille, Riou Island, Impérial du large; 30-35 m; vertical rocky; UW photos; D. Ader leg. • 1 large specimen; France, La Ciotat, Pierre du Levant; 43°09'19"N, 05°37'26.5"E, 65 m; VI.2008; COR; Div; photo of collected specimen; S. Sartoretto leg. • 1 colony, SEM photos; Spain, Menorca Channel; 39°51'1.541"N, 3°30'22.294"E; 60-80 m; VIII.2011; on maerl; INDEMARES IEO exped.; T. Madurell leg. (MZB 2015-8368, STUB 540). • 3 large fertile colonies; Croatia, Vis Island, Bisevo; 30 m; rocky and sandy bottom with seaweeds; 22.IX.2014; UW photos; JGH leg. • 1 colony; Tunisia, Zembra Island; 45 m; UW photo; P. Sánchez-Jérez leg. (as *H. lichenoides* in Argyrou *et al.* 2002, Figs 5-29). • 1 colony; Algeria, Jijel, Aouana Island; 43 m; UW photo; S. Belbacha leg. (in Belbacha *et al.* 2011, Fig. 53). • 1 colony; Italy, Sicilia, Messina strait; 40 m, UW photo; S. Weinberg leg. (in Weinberg 2013: 325).

#### DESCRIPTION

Colony erect, strongly calcified, firmly attached to a substrate by a broad expansion of secondary calcification, branching dichotomously many times with short, variously directed ramifications without anastomoses, and with the further addition of small, secondary lateral branches growing at right angle (Fig. 3F). Resulting growth-form varying from sub-planar to convoluted rosette shape, both reaching large size, up to *ca.* 15 cm in width and height, with narrow spacing between secondary branches, pale salmon pink in colour when alive (Fig. 2A, G). Autozooid apertures distributed on frontal side in 5-8 (6.7 in average) alternating longitudinal (linear) rows (Fig. 3A, D, E). Peristomes short, longer on lateral sides of branches, with distal edge typically lacking, leaving a U- or V-shaped notch, while lateral edges may be prominent and distinctly tapered, particularly in lateral rows (Fig. 3C, D). Horizontal part of autozooid tubes pierced with large, round pores (12.5-15 µm) down to the base of raised peristome, clearly visible in the apical zone of branches, where autozooid walls remain apparent in frontal view (Fig. 3C). Secondary calcification increasing greatly from the branch tips to the basal parts of the colony, rapidly masking the external features of autozooids. In an initial stage, secondary calcification forming thick longitudinal ridges surrounding the peristomes (Fig. 3C). These ridges ('nervi') increasing in thickness and soon joining with flat or convex transversal bridges of calcified layers which partially cover the autozooids, but leaving oblong or rounded windows ('sulci') within which some mural pores remain visible (Fig. 3D). In a further stage, frontal side, except for raised peristomes, entirely covered with a thick layer of secondary calcification densely punctuated with small, round pustules often aligned transversally and, proximally to each peristome, interrupted by 3-5 large, irregularly shaped holes ('vacuoles') (Fig. 3E). Dorsal side of branches convex, with surface structured by a network of longitudinal ridges branching and anastomosing to produce long, concave, spindle-shaped areas pierced with 2-6 large pores, covered with small pustules (Fig. 4E). Fertile colonies

frequent, the large ones bearing a great number of gonozooids of the same colour as branches, but clearly denser (Fig. 4A). Gonozooid chamber large, developed on the dorsal side from an enlarged tube migrated from the frontal side (Fig. 4B), clearly longer than wide when placed between two bifurcations, or roughly triangular or heart-shaped when adjacent to a branch fork; a prominent crest along the upper midline of the chamber, extending on both sides of the ooeciostome (Fig. 4A). Brood chamber wall made of foliated crystallites overlapping according to the direction of wall growth, pierced with mural pores (10.6-14.4 µm), which are rapidly closed by pointed radial spines during the development of the gonozooid (Fig. 4D). External relief of the gonozooid formed by a dense network of small, reticulated ridges, spreading perpendicularly towards the upper crest, bearing a line of small, round pustules, and delimiting spaces ('cancelli-like cavities', Taylor & Jones 1993); ooeciostome large, much broader than the peristomes of autozooids (x 3.8 in average), placed at the middle of the upper crest, curved laterally, with a wide elliptical aperture opening towards the space delimited by the closest lateral branch (Fig. 4A, B). Ancestrula and early astogenetic stages not observed.

#### REMARKS

##### *Taxonomic issues*

The authorship of *H. frondiculata* has long been attributed to Lamouroux (1821) and this designation was maintained by d'Hondt (1994: 302), though he noted that two specimens of this species kept at the MNHN had a handwritten label signed by Lamarck naming them '*Retepora frondiculata*, Méditerranée'. There is no indication that Lamouroux had the opportunity to examine these specimens in Lamarck's collection. However, his knowledge of the species *Retepora frondiculata* created by Lamarck (1816) is attested by the fact that he mentioned it in the synonymy of *H. frondiculata* (Lamouroux 1821: 42, 'Rétépore frondiculé; de Lam. Anim. Sans vert tom. 2, p. 182, no. 3'). In his revision of the European species of *Hornera*, Mongereau (1972) considered only fossil material, except for a Mediterranean specimen from d'Orbigny's collection (MNHN.F.A15367, formerly MNHN no. 13773) designated as the neotype of *H. frondiculata* Auct., arguing that the Lamouroux collection had been destroyed during World War II (Mongereau 1972, see also d'Hondt 1991). As noted by Smith *et al.* (2008), this neotype is not valid. Moreover, Mongereau (1972) distinguished three morphotypes ('formes') of *H. frondiculata* Auct. based on differences in the calcification of the frontal side of branches: *frondiculata*, *lagaaiji* and *striata*, the first one ranging from the Eocene to the Present, the two others being only fossil. The authorship of Lamarck is now admitted (e.g. Bock & Gordon 2019), and attested by high-definition photos (including SEM pictures and original Lamarck handwritten labels) of two syntypes of *Retepora frondiculata* Lamarck, 1816 (MNHN-IB-2008-4691 and MNHN-IB-2008-4694), available on the MNHN website (<https://science.mnhn.fr/all/list?originalCollection-Coll.+Lamarck>). The assertion by Smith *et al.* (2008) that Lamouroux (1821) based his description of *H. frondiculata* on material from Kamtchatka is disputable.



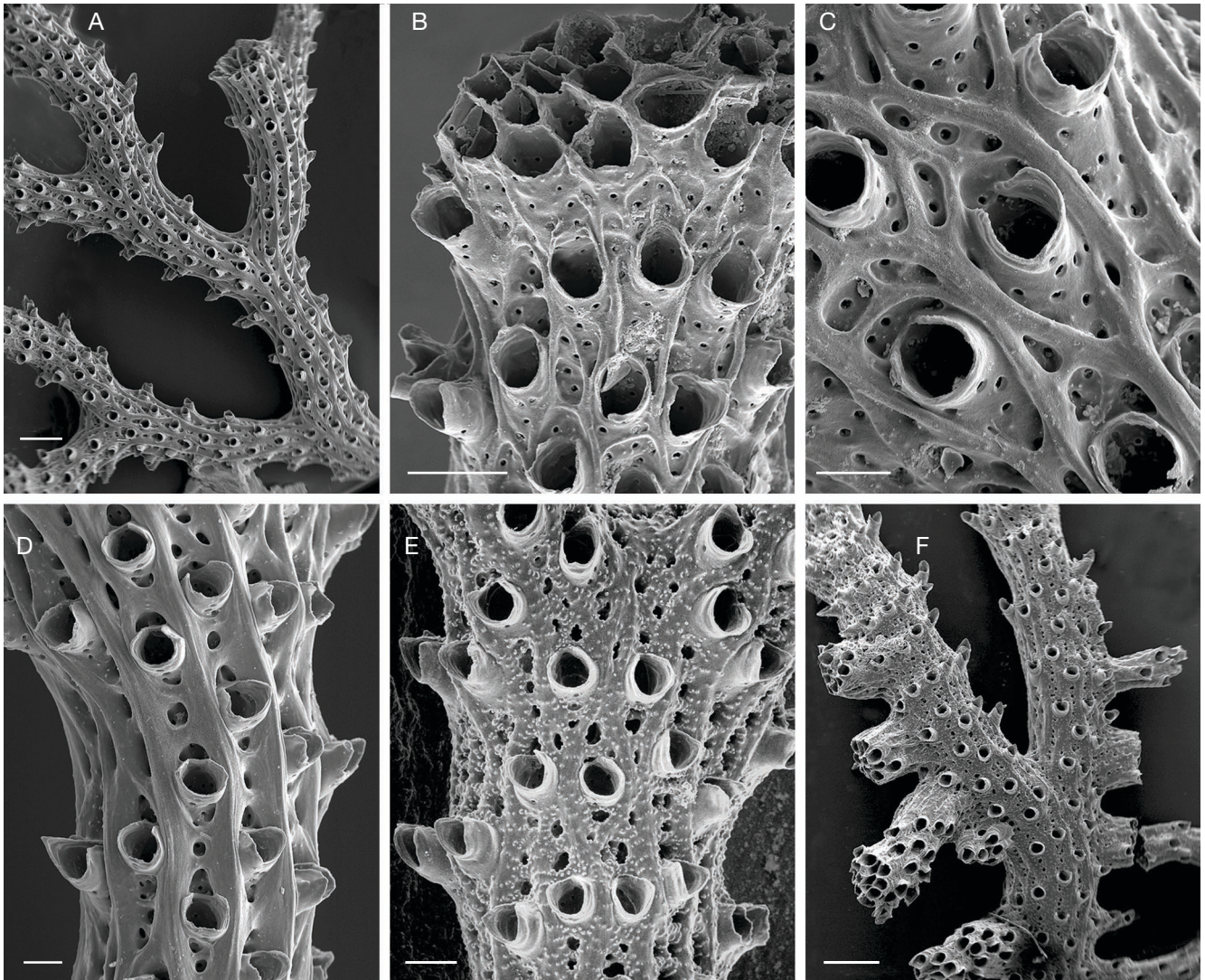


FIG. 3. — *Hornera frondiculata* (Lamarck, 1816), frontal side: **A**, part of colony with five bifurcations; **B**, growing tip of a branch; **C**, initial stage of secondary calcification with ridges encircling autozooids with typically notched peristomes and frontal wall pierced with large mural pores; **D**, intermediate stage of secondary calcification; **E**, older stage of secondary calcification; **F**, part of colony with several lateral branches. Origin: **A-D**, Greece, Scarpanto Strait, 29–33 m, 29.VIII.1967; **E**, Marseille, Riou Is., 70 m, 3.VII.1971; **F**, Riou Is., 90 m, 2.III.1972. Scale bars: **A**, **F**, 500  $\mu\text{m}$ ; **B**, 200  $\mu\text{m}$ ; **C-D**, 100  $\mu\text{m}$ ; **E**, 150  $\mu\text{m}$ . Photos: Jean-Georges Harmelin.

When indicating the distribution of *H. frondiculata*, Lamouroux indeed cited first ‘Kamtchatka, Tilesius’, then later ‘Océan indien et austral, Linné, Ellis’, and finally ‘Méditerranée, de Lamarck’. This succession of localities more probably follows a geographical order (farthest to nearest) rather than indicating that Kamtchatka was the type locality of the species, and a specimen from the Tilesius collection the type specimen of this species. It is more likely that the specimen illustrating the description of *H. frondiculata* (Lamouroux 1821, pl. 74, figs 7–9) was from the Mediterranean. The same origin is highly probable for the large colony, beautifully illustrated, but left unnamed by J. Ellis (Ellis & Solander 1786, pl. 26, fig. 1; here Fig. 1B) and assigned to *H. frondiculata* by Lamouroux (1821, pl. 26, fig. 1), who reproduced Ellis’ plates.

The record in Corsica (Pietranera, North of Bastia, 35 m) by Calvet (1902) of *H. violacea* M. Sars, a species from the North Atlantic now classed in the Stigmatoechidae Brood, 1972

[= *Stigmatoechos violacea* (M. Sars, 1863); Bock & Gordon 2019], is obviously a misidentification. The sampling depth of this occurrence suggests that it might be *H. frondiculata*. The specimens collected by Lagaaij & Gautier (1965) at 128 m and 145 m depth off the mouth of Rhône River may correspond either to *H. frondiculata* or to *H. mediterranea* n. sp. The record of *H. caespitosa* Busk, 1875 by Calvet (1906) at 445 m depth off Cape Sicié (East of Marseille) most likely matches colonies of *H. frondiculata* detached from their substratum and drifted down the slope of Sicié canyon. The report of *H. lichenoides* by Laubier (1966) without comment on coralligenous bottoms at Banyuls-sur-Mer at moderate depth (< 40 m) is probably a misidentification of *H. frondiculata*.

#### Morphological features

The general shape and branching type of colonies of *H. frondiculata* are typical, and cursory examination, even underwater,

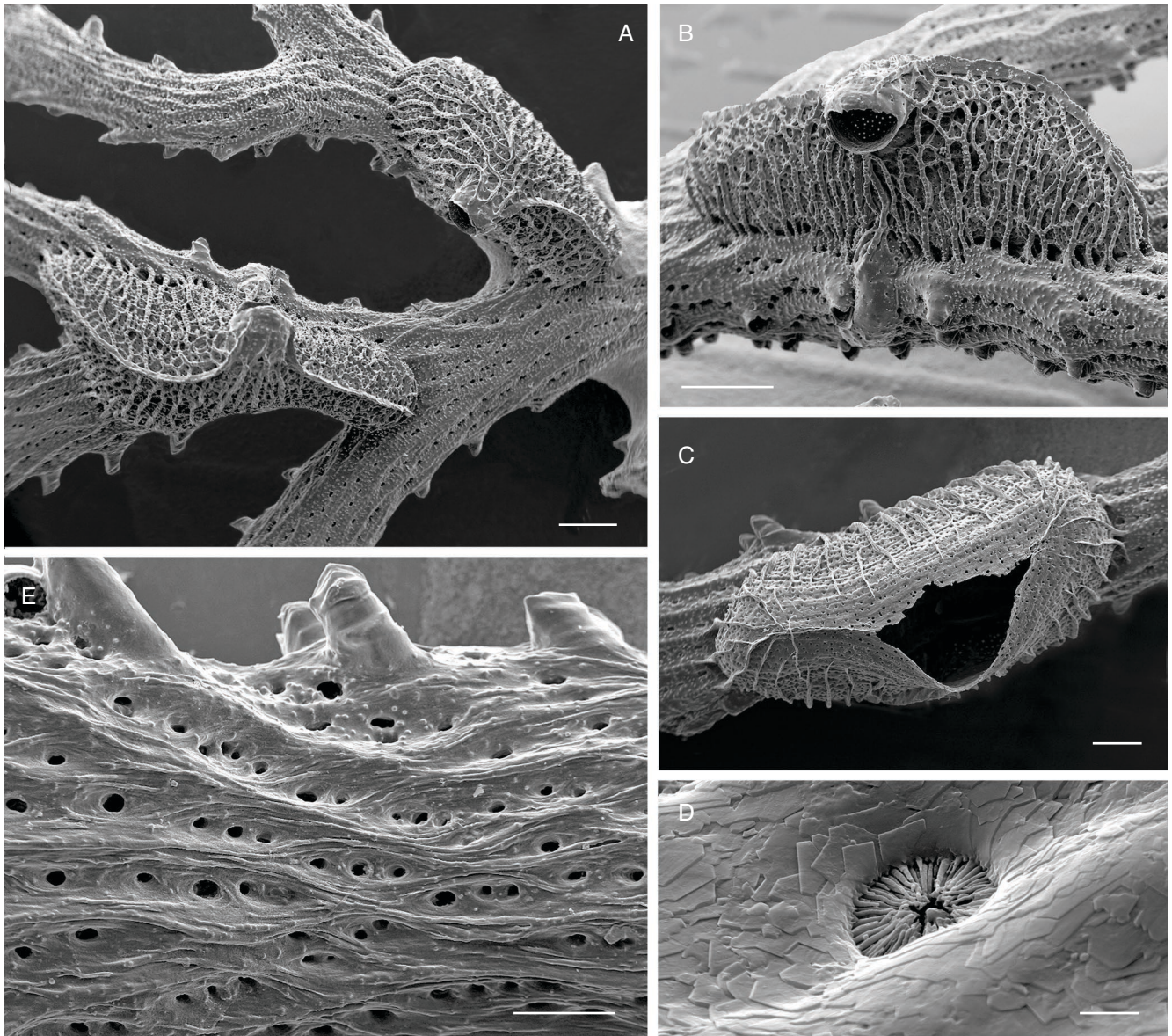


FIG. 4. — *Hornera frondiculata* (Lamarck, 1816), dorsal side: **A**, part of colony with 2 gonozooids; **B**, gonozooid lateral view showing the oocystostome and the basal tube; **C**, frontal view of a gonozooid chamber under construction; **D**, gonozooid wall made of foliated crystallites and mural pore closed by radial spines; **E**, wall of dorsal side with ridges delimiting porous spindle-shaped areas. Origin: **A-E**, Marseille, Riou Is., 70 m, 3.VII.1971. Scale bars: **A-B**, 500  $\mu\text{m}$ ; **C**, 250  $\mu\text{m}$ ; **D**, 5  $\mu\text{m}$ ; **E**, 200  $\mu\text{m}$ . Photos: Jean-Georges Harmelin.

allows a correct identification of the species. Old drawings of large colonies, such as that represented by Marsilli (1725 pl. 33, fig. 163; here Fig. 1A), can therefore be assigned to this species with confidence. The shape of colonies shows a marked habitat-related plasticity, from nearly planar on rocky walls to strongly contorted on coarse detrital sandy bottoms (Fig. 2 A-D, see below in Discussion). However, the detailed structure of the branches is similar in both growth-forms. Lateral branches growing at right angles are frequent in colonies of *H. frondiculata* (Figs 2E, F, 3F) regardless of their shape; they apparently appear to develop subsequently to the distal growth and bifurcation of the branches from which they are budded. Delayed budding of lateral branches is assumed to be an adaptive strategy to increase the fragmentation

of empty spaces between laterally adjacent branches and improve the filtering activity of a colony according to its microenvironment (see below, Discussion). Lateral branches and typical notched peristomes are present on a colony of *H. frondiculata* collected by Abdelsalam (2014, fig. 2) on the Mediterranean coast of Egypt, but the stem and main branches are exceptionally thick and irregularly ramified. This unusual growth-form and remarkable calcification may be induced by peculiar features of the habitat, e.g. shallow depth (20-25 m) and proximity of the Nile delta and the mouth of the Suez Canal. The particular shape of peristomes characterized by a deep distal U-shaped notch (Fig. 3C, D), is a constant and highly discriminating trait of *H. frondiculata*. The main variability in the peristome shape concerns the

TABLE 1. — Distribution of *H. frondiculata* (Lamarck, 1816) in Mediterranean ecoregions (classification according to Notarbartolo di Sciara & Agardy 2010).

Mediterranean ecoregions	References
Algero-Provençal Basin	France: Provence, Harmelin 1976, Coll. JGH; Catalonia, Laubier 1966 as <i>H. lichenoides</i> (dubious identification); West Corsica, Calvet 1902: (dubious identification). Calvet 1906 as <i>H. caespitosa</i> . Spain, Catalonia, Zabala 1986; Balearic Is.: Zabala 1993, Ballesteros 2006, Souto <i>et al.</i> 2010. Algeria: Gautier 1955, Belbacha <i>et al.</i> 2011.
Alboran Sea	?
Tyrrhenian Sea	France: East Corsica, Calvet 1902 (as <i>H. violacea</i> ). Italy: Naples, Waters 1904, Cook 1968; Apollo Bank, Di Geronimo <i>et al.</i> 1988, Coll. AR. North Tunisia: East Tabarka coast, S. Sartoretto leg.; Zembra Is., Argyrou <i>et al.</i> 2002 (figured as <i>H. lichenoides</i> )
Ionian Sea	Italy: South Sicilia, Rosso 1996, Coll. AR, Di Geronimo <i>et al.</i> 1998, Weinberg 2013. Greece: Corfou: Coll. JGH (leg. J. Vacelet)
Tunisian Plateau	East Tunisia: Canu & Bassler 1930. Malta: NHMUK ecatalogue 8645130. Graham Bank, Di Geronimo <i>et al.</i> 1993, Coll. AR
Adriatic Sea	Heller 1867, Neviani 1939, Novosel 2005.
Aegean Sea	Greece: South Creta, Coll. JGH (R/V Calypso survey 1964); Scarpanto Strait: Harmelin 1968; N. Sporades: Simboura <i>et al.</i> 1995.
Levantine Sea	Egypt: O'Donoghue & De Watteville 1939, Abdelsalam 2014. Cyprus: Argyrou <i>et al.</i> 2002 (as <i>H. lichenoides</i> ), Achilleos <i>et al.</i> 2020.

lateral edges, more or less projecting and sometimes clearly triangular (Fig. 3D). The presence of notched peristomes in this species was noted in early publications (e.g. Busk 1875: 17, pl. 20, figs. 2, 3; Waters 1904: 94, pl. 9, fig. 3), but has not been systematically taken into account subsequently as a species-specific feature, leading to erroneous records, particularly of non-Mediterranean living specimens (e.g. Busk 1886), or of fossil material (e.g. Mongereau 1972; Moissette 1993; Moissette *et al.* 2007; Zágorský 2010). Besides having a distal notch, the peristomes of *H. frondiculata* differ from those of *H. mediterranea* n. sp. in their significantly smaller size (Table 2). The mural pores of the autozooid walls, visible in young parts of branches, are particularly large (Fig. 3C), clearly broader than in *H. mediterranea* n. sp. The frontal and dorsal sides of branches of *H. frondiculata* have a typical aspect, with calcified structures and hollows contributing to the distinctiveness of this species when compared to *H. mediterranea* n. sp. (Fig. 3). However, the development of the secondary calcification on branches of *H. frondiculata* is similar to that observed in other *Hornera* species (e.g. *H. antarctica*: Borg 1926, 1944, and below, *H. mediterranea* n. sp.). Schematically, the frontal side of the autozooid walls is first partially covered by longitudinal strips and transversal bars, that then merge to form a thick, complete cover between the raised peristomes, just interrupted by several small, irregularly shaped windows per zooid (Fig. 3B-E). The strengthening of the dorsal side by a cover of secondary calcification presents a distinctive aspect with spindle-shaped, longitudinal depressions (Fig. 4E) containing several pores, which are, like the holes of the frontal side, windows allowing communication between the hypostegal pseudo-coelom and the autozooids. *Hornera frondiculata* is characterized by high fertility, with a large proportion of fertile colonies (Table 2) and a large number of gonozooids per fertile colony. For example, 20 gonozooids were present in a medium-sized colony (H: 7.7 cm, W: 6.6 cm,

Marseille, South Riou, 70 m; 3.VII.1971). On colonies with a contorted shape, gonozooids are generally placed on the convex parts of branches, probably for the efficient export of larvae. As noted by early authors (e.g. Alder 1864: 109, pl. 5, fig. 7), the carinated shape of the gonozooids, with a ridge along the upper side of the chamber ('carina', Borg 1926), is very typical. This prominent longitudinal ridge, which starts at the opposite sides of the long axis of the chamber and ends on both sides of the oeciostome may result from the suture of two lateral valves, as suggested by stages in the development of the gonozooid (Fig. 4C). The tubular origin of the gonozooid from a zooid of the frontal side, well described by Borg (1926), is evident from SEM examination (Fig. 4B).

#### GEOLOGICAL DISTRIBUTION

Records of fossil material attributed to *H. frondiculata* are numerous (e.g. Mongereau 1972; Smith *et al.* 2008). In the list of *Hornera* species available at Bryozoa.net (see above), *H. frondiculata* is considered to span from the Palaeogene to the Recent. The overall appearance of fossil *Hornera* colonies can be misleading. For example, the holotype of *Hornera affinis* Milne Edwards, 1838, from the Tertiary of Sicilia (MNHN-IB-2008-4416), looks like *H. frondiculata*. It is clear that the validity of these fossil occurrences cannot be evaluated if the raised peristomes are eroded (as in most cases), and therefore the presence or not of a distal notch, the most decisive criterion for this species, cannot be checked. This feature is not explicitly considered in the description of fossil material (e.g. Mongereau 1972; Moissette 1988; Moissette *et al.* 2007). The peristomes of a specimen from the Miocene of the Czech Republic assigned to *Hornera cf. frondiculata* by Zágorský (2010, pl. 26, fig. 12) are clearly not notched. However, notched peristomes can be recognised on a Pliocene specimen from Rhodes illustrated by Moissette & Spjeldnaes (1995, pl. 2, fig. 5).

TABLE 2. — Morphometrical data for *Hornera frondiculata* (Lamarck, 1816) and *H. mediterranea* n. sp. Results: mean ± standard deviation (range, number of data). — Morphological features, measurements (µm). Width of peristomes: smallest axis of ellipse, width of gonozooids: smallest dimension in frontal view, length of gonozooids: largest dimension in frontal view. Origin and number of measured colonies, *H. frondiculata*: 11 colonies from 7 sites (Riou Is., Palazzu, Kavensur, Corfou, Scarpanto); *H. mediterranea* n. sp.: 12 colonies from 7 sites (Riou Is., La Ciotat), including the holotype. — Fertility of colonies: N1: total number of examined colonies, N2: total number of fertile colonies, percentage of fertile colonies in brackets; N3: total number of gonozooids, N3/N1: mean number of gonozooids per examined colony, N3/N2: mean number of gonozooids per fertile colony.

	<i>H. frondiculata</i> (Lamarck, 1816)	<i>H. mediterranea</i> n. sp.
	Morphological features	
W branch	974 ± 235 (500-1560, 102)	711 ± 128 (455-1020, 143)
W peristome	122 ± 11 (108-145, 49)	148 ± 12 (125-185, 102)
L gonozooid	2562 ± 480 (1720-3545, 46)	1283 ± 260 (820-1750, 23)
W gonozooid	1154 ± 235 (850-1900, 27)	896 ± 111 (650-1130, 22)
W oocystostome	466 ± 70 (360-605, 32)	216 ± 26 (185-265, 8)
N AZ rows	7.6 ± 1.3 (5-11, 67)	5.4 ± 0.9 (4-7, 59)
	Fertility of colonies	
N1 / N2 (%)	24 / 16 (66.7)	126 / 9 (7.1)
N3 (N3/N1 – N3/N2)	213 (8.9 – 13.3)	14 (0.11 – 1.56)
	Depth of sampled sites (m)	
	56.6 ± 20.8 (30-100, 18)	90.5 ± 34.2 (55-200, 23)

#### HABITAT DISTRIBUTION

As noted by Ballesteros (2006), *H. frondiculata* belongs to the assemblage of species from deep-water coralligenous habitats, together with other large rigidly erect bryozoans which form an intermediate stratum below that of large gorgonians (Belbacha *et al.* 2011). However, *H. frondiculata* exhibits two frequency peaks among the Mediterranean coastal habitats (Table 4), (i) on dimly lit steep rocks of the coralligenous community, in some cases at its upper depth limit (30-35 m), but generally deeper (50-80 m), and (ii) on deep coarse detrital sand. In the coralligenous rocky habitat, *H. frondiculata* occupies only exposed microhabitats (Novosel 2005), such as vertical walls shaded by large gorgonians. In contrast, it is absent from overhangs and cavities, or the entrance of caves. *Hornera frondiculata* can be abundant, forming large bushy colonies on detrital sand covered with coarse biogenic elements in the vicinity of steep rocks, ('débris organogènes', Harmelin 1976). These biogenic mineralized deposits are alive or dead (thanatocenose, Rosso 1996; Di Geronimo *et al.* 2001), coming in part from nearby coralligenous rocks, directly from drifted fragments, or indirectly from larval recruitment onto large erect cnidarians, empty bivalve shells (*Spondylus* Linnæus, 1758, *Arca* Linnæus, 1758) and large bryozoan colonies. In sites swept by bottom currents, the latter may form aggregations of erect colonies at the surface of coarse soft bottoms (Marion 1883: 'graviers à bryozoaires'; Picard & Bourcier 1976: 'fonds détritiques côtiers à grands bryozoaires branchus').

#### GEOGRAPHICAL DISTRIBUTION

There is no reliable indication that *H. frondiculata* occurs outside the Mediterranean. The records of this species at Cape Verde, West Africa by Busk (1886) and Cook (1968) are doubtful as the latter noted 'tubular peristomes', thus apparently without the characteristic distal indentation. The status of endemic to the Mediterranean for *H. frondiculata* is likely, but needs to be verified through the study of material from the near Atlantic. This species has been recorded in seven of the eight ecoregions of the Mediterranean (Table 1).

#### *Hornera mediterranea* n. sp.

Figs 5-8, tables 2-4

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*Hornera mediterranea* Waters, 1904: 94 (*nomen nudum*); 1905: 15 – Smith *et al.* 2008: 390.

*Hornera lichenoides* (Linnæus) – Calvet 1931: 43 (part: st. 344 & 633) – Laubier 1966: 223, table (dubious identification) – Zabala 1986: 820, fig. 244, pl. 29-D; 1993: 572 – Saguar & Boronat 1987: 413, table, figs 3-5 – Zabala & Maluquer 1988: 182, figs 620-624 – Rosso 1989: 270, tabs 5, 23, pl. 1b; 1996: 209, table; 2005: 263, table 3 – Costa *et al.* 1991: 418, table 2 – Harmelin & d'Hondt 1992: 609 – Di Geronimo *et al.* 1993: 92, table 3; 1997: 200, table 3; 1998: 248, table 1; 2001: 282, table 3; 2005: 73, table 4.

'*Hornera lichenoides*' Auctt. not (Linnæus, 1758) – Rosso & Di Martino 2016: 570.

*Hornera frondiculata* Lamouroux, 1821 – Harmelin 1968: 1187.

*Hornera* sp. - Harmelin 1976: 223, table I, 229, table III; 1978: 137 – Abdelsalam 2014: 272, fig. 3 (dubious identification) – Rosso 2009: 134.

*Hornera serrata* Meneghini, 1844 – Neviani 1939: 70 (dubious identification).

*Hornera violacea* var. *proboscina* Busk, 1875 – O'Donoghue & de Watteville 1939: 8 (dubious identification).

TYPE LOCALITY. — France, Marseille, Riou Island.

TYPE MATERIAL. — **Holotype.** France • 1 large fertile colony, ca. 5 cm high, 6.7 cm wide, with long, contorted branches, 58 bifurcations and 6 gonozooids (Fig. 5A); Marseille, SW Riou Island; 43°10'25"N, 5°22'52"E; 60-62 m; VII.1982; coarse DC and low rocks; JGH leg.; [MNHN-IB-2017-225](#).

**Paratypes.** France • 1 fragmented colony with 10 bifurcations and 5 gonozooids; same data as for holotype; JGH leg.; [MNHN-IB-2017-226](#) • 2 fragments of colony with gonozooids; same origin as the holotype; JGH leg.; [MNHN-IB-2017-227](#) • 2 fragments of fertile colony with 2 gonozooids; Marseille, South Riou Island; Stn JGH-71.33; 74 m; 5.VII.1971; Div; [MNHN-IB-2017-228](#) • 2 fragments of well-calcified colony; Marseille, South Riou Is.; Stn JGH-71.34; 70 m; 3.VII.1971; Dre; with *H. frondiculata*; JGH leg.;

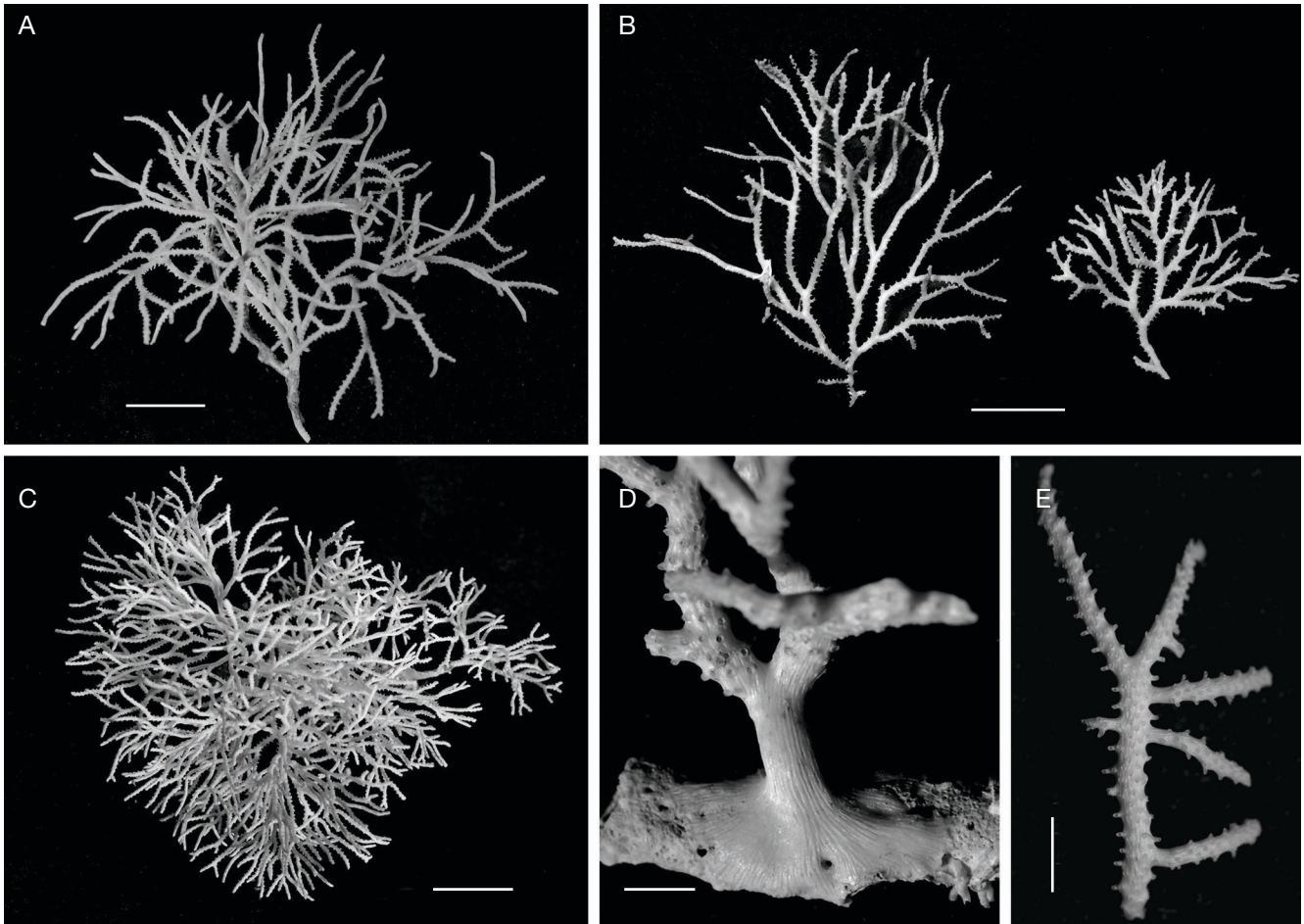


FIG. 5. — *Hornera mediterranea* n. sp., branching features of colonies: **A**, holotype, MNHN-IB-2017-225. **B1**, large colony sparsely branched, **B2**, smaller colony densely ramified; **C**, large bushy colony; **D**, base of a colony encrusting a biogenic fragment; **E**, part of colony with lateral branches. Origin: **A**, **C**, same as holotype, Marseille, Riou Is., 60–65 m. **B1**, La Ciotat, 60 m, 27.VII.1992; **B2**, Marseille, Riou Is., 70 m, 8.XII.1971; **D**, Marseille, Grand-Conglue Is., 90 m, 2.III.1972; **E**, Marseille, Impérial du large, 2.II.1976. Scale bars: **A–B**, 1 cm; **C**, 2 cm; **D–E**, 2 mm. Photos: Jean-Georges Harmelin.

**MNHN-IB-2017-229** • 1 large colony with lateral branches; Marseille, Riou Island, Impérial du large; 55 m; 2.II.1976; coarse DC; JGH leg.; **MNHN-IB-2017-230**.

OTHER MATERIAL EXAMINED. — France • several small colonies, 1 gonozooid; same data as for paratype **MNHN-IB-2017-228**; JGH leg. • 1 colony; same data as for paratype **MNHN-IB-2017-229**; JGH leg. • several fragments; Marseille, South Riou Is.; Stn JGH-71.43; 70 m; 8.XII.1971; coarse DC; Div; JGH leg. • several small colonies; Marseille, South Riou Island; Stn JGH-72.8; 90 m; 2.III.1972; silty DC; Dre; JGH leg. • 1 colony; Marseille, South Riou Is.; Stn JGH-72.22; 100 m; 26.V.1972; silty DC; Dre; JGH leg. • several fragments; Marseille, South Riou Is.; Stn JGH-73.9; 90–100 m; 6.IV.1973; silty DC; Dre; with *H. frondiculata*; JGH leg. • several fragments; Marseille, South Riou Is.; Stn JGH-73.17; 85 m; 12.VII.1973; DC; Dre; JGH leg. • several colonies; Marseille, South Riou Is., Impérial du large; 55 m; 2.II.1976; coarse DC; Div; JGH leg. • several large colonies, some fertile; same data as for holotype; JGH leg. • several fragments; Marseille, North Mangespin; 65 m; 18.IV.1972; Dre; with *H. frondiculata*; JGH leg. • fragments; Marseille, Mangespin, South Veyron; Stn JGH-72.21; 60 m; 25.V.1972; Dre; DC; JGH leg. • fragments; Bay of Cassis; 75 m; XI.1970; DC; Dre; M. Bourcier leg. • fragments; Bay of Cassis; 95 m; silty DC; Dre; M. Bourcier leg. • fragments; Bay of Cassis; 75 m; IX.1971; DC; Dre; M. Bourcier leg. • fragments; off Cassis, East Cassidaigne canyon; 170–200 m;

30.IX.1969; silty DC; Dre; H. Zibrowius leg. • fragments; off Cassis, West Cassidaigne canyon, Stn JGH-71.13; 140–170 m; 5.V.1971; silty DC, Dre; JGH leg. • fragments; off Cassis, West Cassidaigne canyon, Stn JGH-72.9; 115–130 m; 22.III.1972; silty DC; Dre; JGH leg. • 1 colony; Bay of La Ciotat; 60 m; 27.VII.1992; DC; Dre; M. Bourcier leg. • fragments; Hyères Islands, South Porquerolles Island, 2.2 nautical miles South off Cap d'Armes; Stn JGH-76.24; 130 m; 19.VI.1976; coarse DC; Dre; JGH leg. • Hyères Islands, off Levant Island, Magaud Bank; Stn JGH-71.25; 100 m; 24.VI.1971; DC + rocks; Dre; JGH leg. • fragments; Hyères Islands, off Levant Island, Magaud Bank; Stn JGH-71.27; 100 m; 24.VI.1971; DC + rocks; Dre; JGH leg. • fragments; French Riviera, Bay of Cannes; 75 m; IV.1970; silty DC; Dre; M. Bourcier leg.

Italy • 10 small fragments; South Sicilia, Gulf of Noto; Stn PS/81 4C; 95–86 m; A. Rosso leg. • 7 fragments; South Sicilia, Gulf of Noto; Stn PS/81 4X; 102–93 m; A. Rosso leg. • 4 fragments; Sicilia Strait; Stn V 2B; 125 m; A. Rosso leg. • 1 small fragment; Sicilia Strait; Stn V 3; 120 m; A. Rosso leg. • 1 fragment; Sicilia Strait; Stn V 4; 120 m; A. Rosso leg. • 2 small fragments; Sicilia Strait; Stn V 9; 129 m; A. Rosso leg. • 1 small fragment; Sicilia Strait; Stn V 17; 120 m; A. Rosso leg.

Greece • 1 small fragment; Santorini; R/V Jean Charcot, Stn 32.MO.67; 36°32.3'N, 25°17.85'E.; 110–128m; 4.IX.1967; coarse DC and biogenic concretions; Dre; JGH leg. (as *H. frondiculata* in Harmelin 1968).

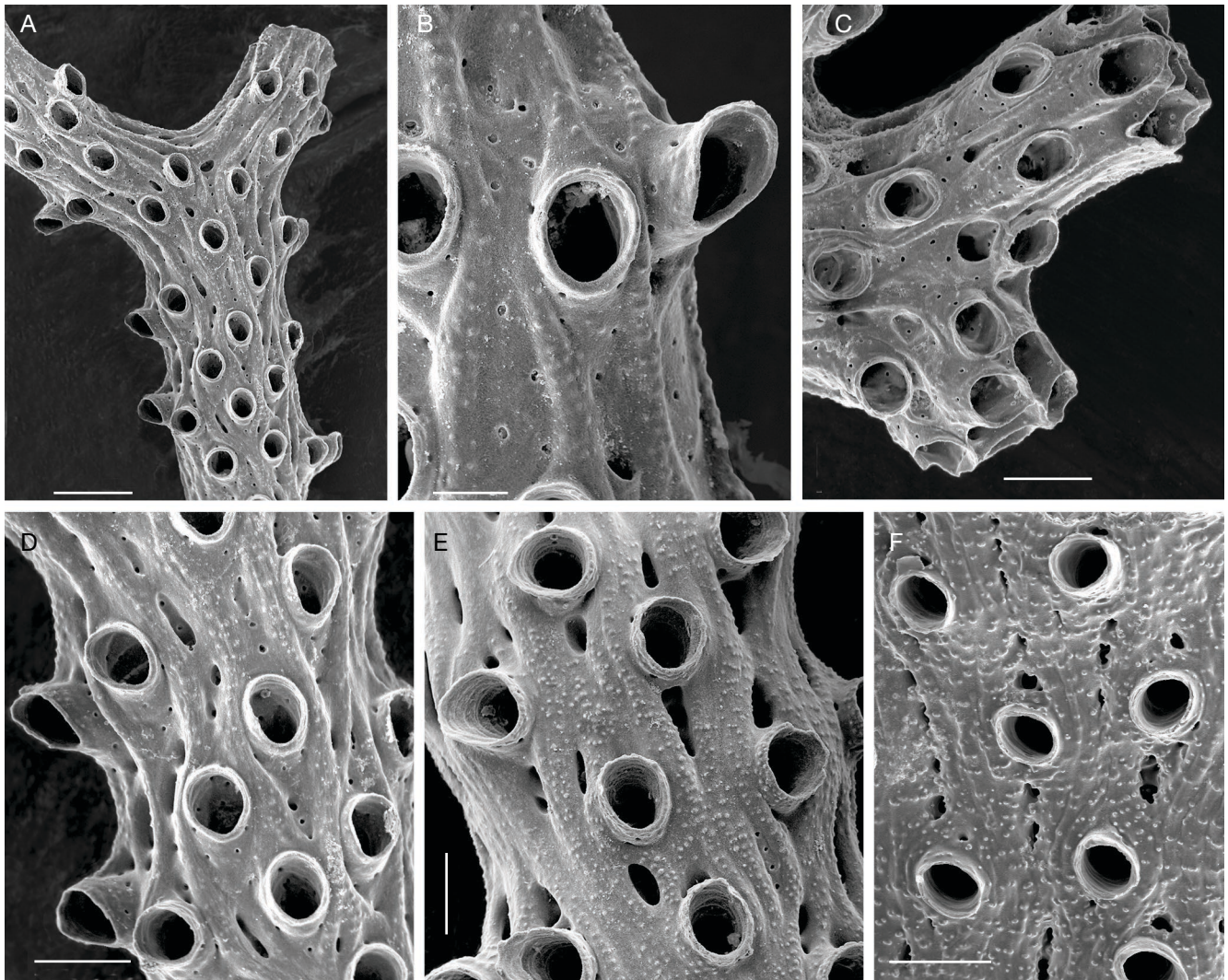


FIG. 6. — *Hornera mediterranea* n. sp., frontal side: **A**, bifurcated distal part of branch; **B**, edge of branch, note the shape of peristomes; **C**, branch tip without secondary calcification; **D-E**, two stages of secondary calcification; **F**, part of branch with heavy secondary calcification. Origin: **A, C-E**, Marseille, Riou Is., 85 m, 2/VII/1973; **B, F**, Riou Is., 74 m, 5/VII/1971. Scale bars: **A**, 400  $\mu$ m; **B**, 100  $\mu$ m; **C-F**, 200  $\mu$ m. Photos: Jean-Georges Harmelin.

ADDITIONAL MATERIAL. — Museum specimens from the Atlantic and boreal seas not belonging to *H. mediterranea* n. sp., attributed to *Hornera lichenoides* • 6 SEM photos; Greenland, 70°30'N, 54°44'W, 175 fms, HMS *Valorous* expedition 1875, NHM 1911.10.1.181; P. Kuklinski leg., sent by P. D. Taylor on 27.V.2005 • 1 colony; Bay of Biscay; R/V *Travailleur* 1881; 392 m; Dre. 40, Calvet 1906; MNHN no. 866, examination on 15.II.2005 • 1 colony; Norway, Finnmark, Jarfjord; Pouchet expedition 1891; Dre. 26; L. Calvet, 11 t. 18; MNHN no. 222, examination on 15.II.2005 • 1 colony; Finnmark, Loppen; Smitt, M6 (R) -1867; MNHN no. 177g, examination on 15.II.2005.

ETYMOLOGY. — *mediterranea*: from the Mediterranean Sea, the source of all specimens examined for the present description.

DIAGNOSIS. — Zoarium erect, ramified dichotomously with narrow, isodiametric branches oriented in several directions. Frontal side of branches occupied by rows of autozooids pierced by small mural pores, with short, relatively broad peristomes with ellipsoidal apertures. Gonozooid globular or oval, built from a broad basal tube, covered with a stratified network of calcified strings, ooeciostome opening laterally. Secondary calcification of frontal side leading to a uniform cover punctuated by small pustules, with 1-3 small windows

per autozooid. Dorsal side convex with longitudinal ridges bearing small pustules aligned transversally.

#### DESCRIPTION

Zoarium erect, firmly fixed on small, discrete substrata by layers of secondary calcification expanding widely (Fig. 5D), white in colour, bushy, reaching large size (> 10 cm), but often smaller, ramified dichotomously many times without anastomoses, with slender, nearly cylindrical, isodiametric branches, bent in several directions, often with long segments between two bifurcations (up to 1-1.5 cm) (Fig. 5A-C); lateral branches growing at right angle present, but not frequent (Fig. 5E). Frontal side occupied by autozooids opening alternatively along 4-7 longitudinal rows on the frontal side (Fig. 5A, D), with wall pierced by round pores (about 8-11  $\mu$ m), scattered all around the tube except above the base of the peristomes (Fig. 6B); peristomes short, longer on branch sides (180-210  $\mu$ m), with aperture entire, ellipsoidal, slightly broader distally, with long axis oriented longitudinally in medial rows, more obliquely

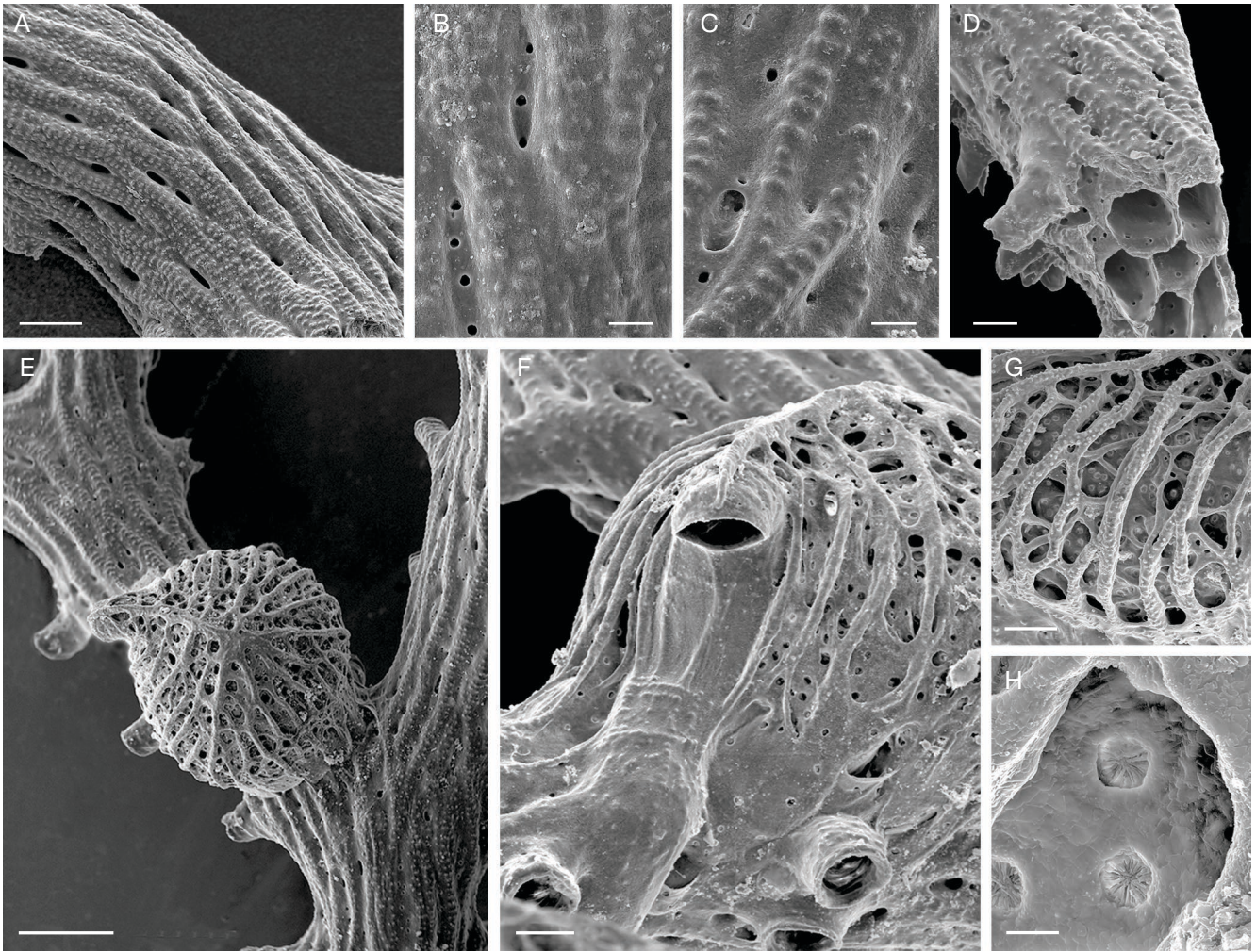


FIG. 7. — *Hornera mediterranea* n. sp., dorsal side: **A-C**, secondary calcification of dorsal side with ridges bearing transversally aligned pustules and pores in narrow spindle-shaped areas; **D**, branch tip; **E**, gonozooid in frontal view; **F**, gonozooid in lateral view, basal tube and oocystostome; **G**, network of secondary calcification covering the gonozooid wall; **H**, gonozooid wall with 3 mural pores closed by radial spines. Origin: **A-C**, Riou Is., 85 m, 12.VII.1973; **D-F**, Riou Is., 74 m, 5.VII.1971; **G**, Riou Is., 70 m, 3.VII.1971. Scale bars: **A**, 200  $\mu$ m; **B-C**, 50  $\mu$ m; **D**, **F-G**, 100  $\mu$ m; **E**, 400  $\mu$ m; **H**, 10  $\mu$ m. Photos: Jean-Georges Harmelin.

on lateral rows (Fig. 5B). External aspect of autozooids varying markedly from the branch tips to the base of the colony according to the increase with age in the amount of secondary calcification; four schematic stages perceivable in this progression (Fig. 5C-F): (stage 1) apical area of branches (Fig. 6A-C), autozooids with raised peristome and primary frontal wall fully exposed, 8-10 mural pores and both sides slightly thickened by a smooth longitudinal ridge, a large empty space (40-60  $\mu$ m) bordered with the base of the lateral ridges at the proximal end of frontal wall, (stage 2) (Fig. 6D) thickening and broadening of the lateral ridges that tend to cover the whole frontal wall, leaving only few mural pores visible, which can be included within narrow, longitudinally oblong windows, (stage 3) in older parts (Fig. 6E), peristomes emerge from a thick cover of secondary calcification formed by thick, convex, longitudinal 'mouldings' covered with transverse lines of pustules, which border 1-2 large, oblong windows, (stage 4) in more basal parts (Fig. 6F) peristomes hardly emerging from a uniform mass of secondary calcification, which is densely punctuated

by small pustules distributed transversally, and interrupted by small, irregularly shaped windows, 1 to 3 per zooid. Dorsal side markedly convex, entirely covered by layers of secondary calcification deposited straight from the branch tip, deeply striated with narrow, longitudinal, anastomosed ridges with rounded surface covered with tiny pustules aligned transversally, leaving long, narrow spindle-shaped empty spaces between them, open or closed by a wall pierced by 2-5 small pores (10-13  $\mu$ m wide) (Fig. 7A-C). Gonozooid chamber on the dorsal side, globular with ovoidal or roundish outline, broader than the branch on which it is placed (Fig. 7E); basal part made of a tube migrated from the frontal side and markedly widened ( $W = 220-260 \mu$ m) before building the floor of the gonozooid across a large part of the branch width (Fig. 7F); cover of fully grown gonozooid densely reticulated by a complex network made of stratified layers of anastomosed strings of secondary calcification converging towards the top of the gonozooid and forming a low crest towards the oocystostome (Fig. 7E, G); areas between the strings irregularly shaped and sized, some closed

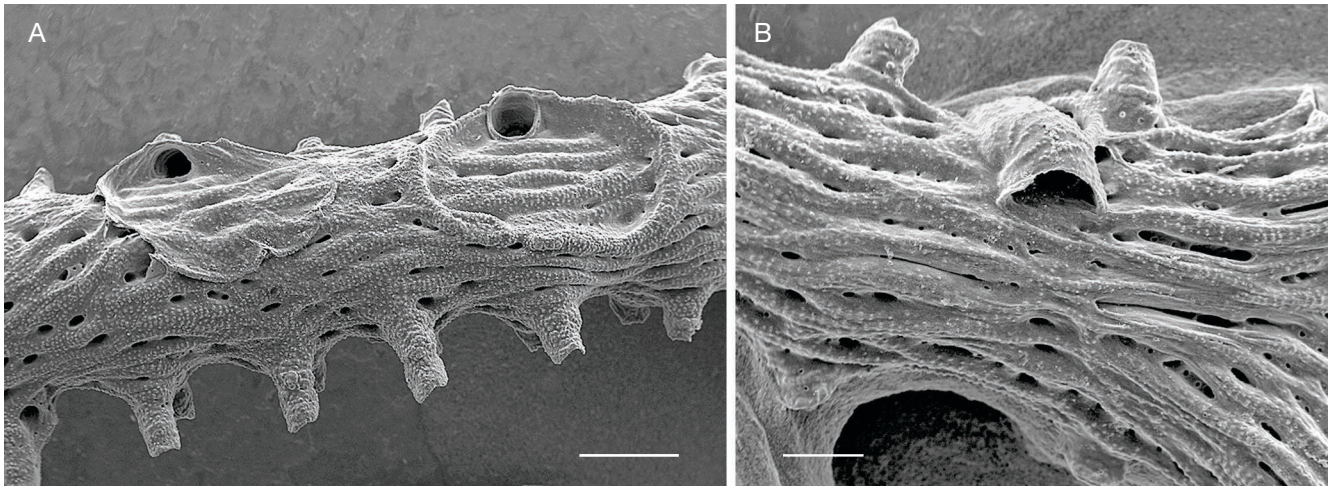


FIG. 8. — *Hornera mediterranea* n. sp., vestiges of brood chambers: **A**, two floors covered by secondary calcification; **B**, basal tube of a gonozooid. Origin: **A-B**, Riou Is., 74 m, 5/VII/1971. Scale bars: **A**, 400 µm; **B**, 200 µm. Photos: Jean-Georges Harmelin.

TABLE 3. — Distribution of *H. mediterranea* n. sp. in Mediterranean ecoregions.

Mediterranean ecoregions	Records
Algero-Provençal Basin	France: Provence, Harmelin 1976, Coll. JGH; Monaco, Calvet 1931. Spain: Catalonia, Zabala 1986; Levante coast, Sagar & Boronat 1987; Balearic Is., Zabala 1993
Alboran Sea	Harmelin & d'Hondt 1992
Tyrrhenian Sea	Italy: Naples, Waters 1904, 1905; NE Sicilia, Di Geronimo <i>et al.</i> 2001
Ionian Sea	Italy: South Sicilia, Calvet 1931, Rosso 1989, 1996, Coll. AR; Taranto Gulf, Di Geronimo <i>et al.</i> 1998
Tunisian Plateau	?
Adriatic Sea	Neviani 1939 (dubious identification)
Aegean Sea	Greece: Santorin: Coll. JGH
Levantine Sea	Egypt: O'Donoghue & de Watteville 1939, Abdelsalam 2014 (dubious identification)

by calcified, porous wall; primary gonozooid wall pierced with rounded pores closed by a diaphragm made of converging pointed processes (Fig. 7H). Ooeciostome a short tube opening laterally, slightly curved downwards, placed just above the basal tube of the gonozooid and seemingly prolonging it, frequently with a low crest on the upper midline, ooeciopore oval, a little broader than the autozooid peristomes (x 1.5 in average) (Fig. 7F). Frequency of fertile colonies and number of gonozooids on them relatively low (Table 2); floor of gonozooids sometimes remaining on branches after loss of the upper parts (Fig. 8). Ancestrula and early astogenetic stages not observed.

REMARKS

*Taxonomic issues*

The species name *mediterranea* was introduced by Waters (1904: 94, 1905: 15) for a specimen from Naples, first assigned by him to *H. lichenoides* (Linnæus) because of similarities in the gonozooid, but differing from the latter by colony and autozooid features. However, this new species name fails to comply with article 12 of the ICZN as Waters did not give a real description of this taxon, nor a figure, and has not deposited type material, nor specimen bearing this name in the museums known to house his material (NHMUK, Museum of Manchester). Therefore,

although there is a strong presumption that Waters designated under the name *H. mediterranea* a specimen belonging to the species described here, this specific name is considered to be a *nomen nudum*, and thus available. In tribute to A. W. Waters, the species name *mediterranea* is given here for the second *Hornera* species present in the Mediterranean.

Records in the literature of Mediterranean bryozoans that can be referred with some confidence to *H. mediterranea* n. sp. are the following which were originally cited as (i) *H. lichenoides* (Linnæus) (Calvet 1931; Zabala 1986; Zabala & Maluquer 1988; Harmelin & d'Hondt 1992; Di Geronimo *et al.* 1993; Rosso & Di Geronimo 1998), (ii) *H. lichenoides* Auctt. not Linnæus (Rosso & Di Martino 2016), (iii) *H. 'lichenoides'* (Rosso *et al.* 2010; Rosso & Di Martino 2016), and (iv) *Hornera* sp. (Harmelin 1976, 1978; Rosso 2009; Abdelsalam 2014). These records are recent specimens, but there are also fossils from the Plio-Pleistocene (Zabala 1986; Sagar & Boronat 1987; Zabala & Maluquer 1988; Rosso 1989; Rosso & Di Geronimo 1998; Abdelsalam 2014).

*Morphological features*

Colonies of *H. mediterranea* n. sp. are readily distinguishable from those of *H. frondiculata*. They are typically formed of



TABLE 4. — Occurrence frequency (% Occ.) of *H. frondiculata* (Lamarck, 1816) (*H. f.*) and *H. mediterranea* n. sp. (*H. m.*) in six habitat categories from the coastal zone of the French Mediterranean coast. Data from Harmelin (1976, table 1). Depth range (mean in brackets) of samplings. COR: coralligenous rocky bottoms; GSO: semi-dark cavities.

Habitat	Depth range (m)	N samples	<i>H. f.</i> % Occ.	<i>H. m.</i> % Occ.
Shallow COR-GSO	8-46 (20.4)	23	0	0
Deep COR	55-75 (63.4)	9	11.1	0
Biogenic deposits	40-75 (61.0)	7	42.9	42.9
Coarse detrital sand	60-100 (78.9)	15	53.3	33.3
Silty detrital sand	105-200 (150.0)	13	7.7	38.5
Silty sand	205-350 (268.5)	10	0	0

narrow, often curved, subcylindrical branches, irregularly bifurcating in three dimensions. These colonies are fragile and easily fragmented, but sampling by diving has shown that they can reach a large size (> 10 cm, Fig. 5C) in favourable sites, such as that of the holotype. Lateral branching is present, but less common than in *H. frondiculata*. The autozooids differ from those of *H. frondiculata* in their larger diameter (Table 2), smaller mural pores, and shorter peristomes with an ellipsoidal aperture, slightly broader distally. The development of secondary calcification on the frontal side follows the same succession of stages as in *H. frondiculata*, with a similar pattern of thickening, that can be divided into 4 stages (Fig. 6). The main difference concerns the windows ('lacunes'), which are less numerous and smaller in the last stages of calcification in *H. mediterranea* n. sp. (Fig. 6F). The thickening of the convex dorsal side is typically achieved by distinct ribs with rounded outline, covered by transverse lines of small pustules, a structure resembling that of *H. branchoensis* Calvet, 1906 from Cape Verde Islands. Within depressions between these ribs, pores are smaller than in *H. frondiculata*, in which they are included in spindle-shaped depressions. As in *H. frondiculata*, the gonozooid is broader than the branch on which it is developed, but its relative size is smaller, its shape is rounded or oval, and it is not carinated. Unlike *H. frondiculata*, *H. mediterranea* n. sp. produces few gonozooids (Table 2). The occurrence on branches of *H. mediterranea* n. sp. of vestiges of brood chambers consisting of floors more or less covered by secondary calcification (Fig. 8A), or limited to the basal tube of the chamber (Fig. 8B), can be diversely interpreted. These remains might be signs of aborted growth due as well to strong limitations in time of suitable conditions for the development of gonozooids as to vulnerability to particular adverse conditions. However, according to Batson *et al.* (2020), similar vestiges of gonozooid floors observed in *Hornera* colonies from New-Zealand would result from the resorption of brood chamber walls.

#### Fossil records

*Hornera lichenoides* Auctt. was recorded together with *H. frondiculata* in fossil deep coral assemblages from the Early Middle Pleistocene of southern Italy by Di Geronimo *et al.* (2005) and in other deposits of the same age (Rosso & Di Geronimo 1998; Rosso 2005). The occurrence of this species in Early Pleistocene deposits in southern Italy was considered by Rosso & Di Geronimo (1998) as an indication that this species was a 'residual boreal guest' that had

colonized the Mediterranean during the glacial intervals. These Pleistocene specimens attributed to *H. lichenoides* can be identified as *H. mediterranea* n. sp. considering that the differences between the two species were recognized by Rosso (i.e. Rosso 2009; Rosso & Di Martino 2016) and extant specimens of *H. mediterranea* n. sp. from Rosso's collection have been examined here. The hypothesis that *H. mediterranea* n. sp. results from a speciation from boreal populations of *H. lichenoides* having entered the Mediterranean during phases of glaciation can be regarded as tenable. On the other hand, the record of *H. lichenoides* from the Middle Miocene in Hungary by Moissette *et al.* (2007), without morphological details, remains questionable.

#### HABITAT DISTRIBUTION

All examined specimens of *H. mediterranea* n. sp. were collected within the depth range of 55-200 m (Table 4), on soft bottoms ranging from the circalittoral zone (*sensu* Pérès & Picard 1964) to the upper limit of the bathyal zone. The shallowest sampling stations were close to deep coralligenous outcrops or lower discrete rocks, and presented a large part of coarse detrital elements indicating the frequent occurrence of bottom currents. The largest specimens (Fig. 5A, C) were collected in this category of stations. In deeper soft bottoms (100-200 m), more distant from the coast and comprising a greater proportion of fine particles, colonies were smaller. Unlike *H. frondiculata*, colonies of this species were never collected on rocky walls, but all were lying free at the surface of soft bottoms, leaning on their lateral branches, the base attached on small to tiny substrates. The record at a very shallow depth (20-25 m) in Egypt by Abdelsalam (2014) of a fragment of colony identified as *Hornera* sp., sampled together with *H. frondiculata*, is questionable and probably does not correspond to *H. mediterranea* n. sp. All examined colonies of *H. mediterranea* n. sp. were free of epibionts except for one from Marseille (JGH-Stn 72.8, Riou Is., 90 m), which was encrusted by two small colonies of *Amphiblestrum lyrulatum* (Calvet, 1907). Interestingly, as pointed out by Lopez de la Cuadra & Garcia-Gomez (1994) in their redescription of this species, *A. lyrulatum* is endemic to the Mediterranean and often confused with '*Ramphonotus minax*' (Busk, 1860) from the northern Atlantic. Thus, as with *H. mediterranea* n. sp., *A. lyrulatum* may be a 'residual northern guest' (Rosso & Di Geronimo 1998), genetically differentiated in the Mediterranean after transfer after transfer of an Atlantic species during glaciation phases.

#### PROTECTION STATUS

As already mentioned, *H. lichenoides* (Linnæus, 1758) is the only bryozoan species in the list of endangered or threatened species in the Mediterranean (Barcelona Convention, Annex II; UNEP 2011). It is not clear which species this name refers to and why it was designated as threatened. Since *H. mediterranea* n. sp. is uncommon and has no spectacular features which would be noticed by anyone other than an expert bryozoologist, it is likely that there was a confusion with *H. frondiculata*.

#### GEOGRAPHICAL DISTRIBUTION

In the present state of knowledge, *H. mediterranea* n. sp. is only known from the Mediterranean. Almost all records of *H. mediterranea* n. sp. are from the western Mediterranean (Table 4). The only available record from the eastern Mediterranean is a small specimen collected at Santorini, Aegean Sea (Harmelin 1968, listed as *H. frondiculata*).

#### GEOLOGICAL DISTRIBUTION

*Hornera mediterranea* n. sp. was recorded (as *H. lichenoides*) in Pleistocene deposits in southern Italy (Costa *et al.* 1991; Di Geronimo *et al.* 1997; Rosso & Di Geronimo 1998; Di Geronimo *et al.* 2003; Rosso 2005) and submerged late Würmian to Holocene deposits from the Sicily Strait (Di Geronimo *et al.* 1993), often co-occurring with *H. frondiculata*.

#### DISCUSSION

##### MORPHOLOGICAL FEATURES

The occurrence of *Hornera frondiculata* and *H. mediterranea* n. sp. in two major habitat categories, hard and soft bottoms, with different colonial morphologies offers interesting examples of linkage between attributes of colonies and environmental features. Colonies of the two Mediterranean *Hornera* species are unilaminar, multiserial, rigidly erect species, with non-linked branches (terminology of McKinney & Jackson 1989). They differ in their general shape, plasticity potential, branching pattern and width of branches. The absence of anastomoses between adjacent branches, in contrast to some other *Hornera* species, such as *H. antarctica* Waters, 1904 (Borg 1944), may increase the fragility of the colonial skeleton, particularly when it is formed by narrow branches with widely spaced successive bifurcations. However, thick layers of secondary calcification on the frontal and dorsal sides, a generic trait, improve the strength of branches and their resistance to breakage of branches. Hence, colonies of *H. mediterranea* n. sp., which have narrower branches with bifurcations often widely spaced (Fig. 5A, B1), are clearly more fragile than those of *H. frondiculata*. These differences in the architectural design of colonies are species-specific and/or linked to local environmental conditions, and may offer good models for testing the influence of biotic and physical drivers on the habitat distribution and the capacity for food acquisition (e.g. Abelson *et al.* 1993; Helmuth & Sebens 1993; Eckman & Okamura 1998; Okamura *et al.* 2001).

Plasticity of colony shape is an advantageous feature allowing species to occupy different environments and habitats (Jackson 1979). Striking examples of intraspecific high plasticity of growth forms according to habitat features are found among cyclostomes, such as *Platonea stoechas* Harmelin, 1976 or '*Cardioecia watersi*' (O'Donoghue & de Watteville, 1939) (Harmelin 1975, 1976). *Hornera frondiculata* presents an obvious plasticity with colony shapes recalling those of retiform *Reteporella* species living in the same habitats. Their colony shapes exhibit a similar range with two opposite branching designs, i.e., planar vs complexly folded. Widely flared cup-shaped colonies resulting from planar branching are typical of *R. mediterranea* (Hass, 1948) and *H. frondiculata* (Fig. 2C, D) when they co-occur on deep, dimly-lit rocky walls. On the other hand, the complex growth-shape with branches or colony parts bent in all directions is shared by *H. frondiculata* (Fig. 2A, B) and *R. grimaldii* (Jullien, 1903) when both live at the surface of flat bottoms, free or attached to a tiny substrate. The unifacial location of lophophores in deep water colonies with planar shape growing parallel and close to the substratum can be inferred as an adaptation for exploiting the food resource from a boundary layer in which the flow is steady and unidirectional. In contrast, the multifacial location of lophophores in colonies with complex three-dimensional designs is probably an adaptation to life in a turbulent boundary layer generated by an unsteady flow, partly due to the topographical roughness of the bottom covered with coarse elements. Colonies of *H. mediterranea* n. sp., which thrive on the same flat bottoms, are also bushy. The relative fragility of their narrow branches is not a limitation considering the deeper distribution of this species and may be, on the contrary, an advantage in facilitating the local multiplication of clones (see below). The production of lateral branches (Figs. 2E-F, 3F, 5E), more frequent in *H. frondiculata* than in *H. mediterranea* n. sp., is another expression of the plasticity of the colony shape. This type of ramification occurs preferentially in proximal parts of large colonies and seemingly after the bifurcation of branches distal to them. In most cases, they grow perpendicular to the mother branch and split empty spaces between adjacent branches with, sometimes, drastic changes in the direction of growth (Fig. 2E-F). This pattern allows expanded lophophores to be adequately spaced and can be considered as a functional alternative to retiform branching and a remarkable example of colony integration to increase the efficiency of filtration of food particles by lophophores. Budding of lateral branches in *Hornera* species recalls the similar branching process observed in some Tubuliporina (Harmelin 1976; Jablonski *et al.* 1997), particularly among species of *Annectocyma* (Hayward & Ryland, 1985). In the latter, lateral budding involves skeletal resorption from pseudopores (Harmelin 1976, fig. 7; Batson *et al.* 2020, table 1: 'window resorption'). In *Hornera*, the process allowing the proximal budding of lateral branches is expected to be different considering their skeleton free-walled structure, and has to be investigated more precisely. Whatever its ontogeny, lateral branching contributes to the high potential of *Hornera* species of remodelling their colony shape by resorption and

re-budding stressed by Batson *et al.* (2020) in their synthesis of resorption of mineralized parts in bryozoans.

#### REPRODUCTIVE POTENTIAL

The two *Hornera* species apparently differ in their reproductive output, as suggested by the rarity of gonozooids in *H. mediterranea* n. sp., even if floors of erased brood chambers are taken into account, and their much greater abundance in *H. frondiculata* (Table 2). The question of why these two co-occurrent *Hornera* species differ so much in the energy allocated to reproduction remains open. Does this result from a difference in filtering efficiency, i.e., in available energy, or from more indirect causes? The presumed low reproductive output of *H. mediterranea* n. sp. may be compensated by asexual reproduction through the fragmentation of its fragile, narrow branches. Strong turbulent bottom jets and shocks by mobile benthic animals are expected to be natural sources of fragmentation, but human actions, e.g. through trawling, may be now predominant. It is clear that the presumed high fertility of *H. frondiculata* is not reflected by features of its population. This species has none of the characteristics of an r-selected species (e.g. Pianka 1970), i.e., numerous small individuals, short-lived, subject to a high mortality rate in an unpredictable environment, nor those of an invasive species. The relative rarity of *H. frondiculata* colonies within upper circalittoral communities (i.e., above 40 m depth) despite their high potentiality in sexual reproduction may imply strong limitations either in survival or dispersal of larvae, recruitment success or ability of post-recruitment stages to cope with the interspecific competition, possibly coupled with a low tolerance for temperature variations (see below). Unfortunately, there was no ancestrula nor juvenile colonies in the studied material of both Mediterranean *Hornera* species. A different sampling methodology would be required to get information on early stages of these species, which could allow comparisons with the early astogeny in other *Hornera* species (Batson *et al.* 2019).

#### DEPTH DISTRIBUTION AND THERMAL REGIME

The two *Hornera* species live in the Circalittoral biozone (*sensu* Pérès & Picard 1964) and can co-exist in the same type of habitat within a relatively broad depth range (Table 4). However, they differ in the average depth and upper limit of their depth distribution (Table 2), which are clearly deeper for *H. mediterranea* n. sp. This disparity could be driven by the vertical distribution of habitats suitable to this species. However, detrital sandy bottoms with coarse elements, on which *H. mediterranea* n. sp. thrives in Provence with large specimens, also occur at depths shallower than the upper limit of the distribution of this species in this region (55 m). This upper depth limitation may be linked to a low tolerance to seasonally variable temperatures. The deep layers (below about 55-60 m) are characterized by a constant temperature of around 13°C while the upper layers are exposed to strong seasonal variations (Bensoussan *et al.* 2010) with, in some regions (e.g. Marseille area), rapid wind-induced temperature drops during summer (Milot 1979). For *H. frondiculata*, a

relationship between depth range in different regions and this type of thermal stress has previously been hypothesized (Harmelin 1988).

#### VULNERABILITY OF THE *HORNERA* SPECIES IN THE MEDITERRANEAN

The epifaunal 'facies' marked by an abundance of large erect bryozoans at the surface of coarse detrital sandy bottoms, which may include both *Hornera* species, once covered widespread patches in the 40-80 m depth zone (Marion 1883). This type of habitat has regressed during the last century because of pollution, silting and trawling, particularly off urbanized coasts, such as the gulf of Marseille or the bay of La Ciotat. In the latter, it has been shown that the restoration of this assemblage of large erect bryozoans after the diminution of stressors has been very slow (Picard & Bourcier 1976). The vulnerability of deep coralligenous outcrops, where *H. frondiculata* can live, is mainly due to silting and pollution (Weinberg 1978; Hong 1983; Ballesteros 2009). Collection or breakage of colonies by divers is deemed to be much more limited considering the depth of the sites where *Hornera* species live and a change in the behaviour of divers, who are now more aware of the need to respect the marine biota.

#### NEEDS FOR THE REVISION OF *H. LICHENOIDES*

The status of *H. lichenoides* Linnæus is not clear while this species name is commonly used. The origin of the material on which Linnæus (1758) based his very short description of *Millepora lichenoides* is unknown, and there is no indication of the current existence of type material. Moreover, it is not certain whether the original material considered by Linnæus was actually part of his own collection or belonged to another naturalist. However, *H. lichenoides* Auctt. was soon, and is still, considered as a northern species, present in the Arctic and northern seas (e.g. Smitt 1867; Busk 1875; Hincks 1880; Borg 1926; Hansen 1962; Kluge 1962; Hayward & Ryland 1985; Ryland & Hayward 1991; Bader & Schäfer 2005; Kuklinski & Bader 2007; Noël 2010; Rouse *et al.* 2018). The most obvious differences between *H. lichenoides* (Linnæus) Auctt. and *H. mediterranea* n. sp. are the degree of secondary calcification, which can be huge in the former, forming a uniform cover hiding the boundaries between the autozooids, and the size of branches, clearly thicker and broader, with a greater number of autozooid rows (e.g. Hayward & Ryland 1985: figs 40-41; SEM pictures made by P. Kuklinski of a specimen from Greenland: NHM 1911.10.1.181), and specimens attributed to *H. lichenoides* examined at the MNHN. On the other hand, the gonozooids of *H. mediterranea* n. sp. (Fig. 7E) and *H. lichenoides* (Linnæus) Auctt. (Hincks 1880: pl. 67, fig. 3; Borg 1926: figs 94-95; Kluge 1975: fig. 83; Hayward & Ryland 1985: fig. 41C; Ryland & Hayward 1991: fig. 24) have the same globular shape. Calvet (1931) considered that the erection of a new species, *H. mediterranea*, by Waters (1904, 1905) for Mediterranean specimens of *H. lichenoides* was unjustified considering that there was no difference in the features of the gonozooid. The apparent resemblance in the shape of the gonozooids in the two species

should be more clearly described in northern specimens of various origins, together with details of the zooidal features at different stages of secondary calcification. Currently, the question of the existence of one or several species under the name *H. lichenoides* Auctt. in the Atlantic and the northern seas remains open and should be thoroughly reviewed with modern tools. It is clear from the present material that the particular features of the colonies and the zooids of *H. mediterranea* n. sp. are constant, suggesting a genetic individualisation in a well-defined habitat.

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