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"*Escharella*" *massiliana* n. sp., Marseille, Planier Canyon, 115 m depth.

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On some "*Hemicyclopora*" Norman, 1894 and "*Escharella*" Gray, 1848 species (Bryozoa, Cheilostomatida) from the Atlantic-Mediterranean region. Re-examination of their generic status and description of new species and a new genus

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ABSTRACT
The long-established difference between the bryozoan genera *Hemicyclopora* Norman, 1894 and *Escharella* Gray, 1848 is the occurrence of a lyrula in the autozooidal orifices of *Escharella* species. The examination of abundant material from the Mediterranean and NE Atlantic using re-assessed specific criteria revealed an unexpected diversity involving several undescribed typical *Hemicyclopora* species, and also species displaying transitional features between the morphological concepts of these two genera. The overall diversity of the examined material comprises ten species with five new species (*Hemicyclopora neatonensis* n. sp., *H. hexaspinae* n. sp., "*Hemicyclopora*" *celtica* n. sp., "*H.*" *pytheasi* n. sp., "*Escharella*" *massiliana* n. sp.), and two species of *Hemicyclopora* left unnamed because of insufficient material. A new genus, *Scutocyclopora* n. gen., is erected for the Mediterranean species *Hemicyclopora dentata* López de la Cuadra & García-Gómez, 1991, which diverges in the absence of oral spines and the production of a non-tatiform ancestrula. Six species are distinguished in the Mediterranean material (5-205 m) and seven species in the Atlantic material (128-1050 m). All these species live in deep water, on small, discrete, poorly-lit substrates, mostly of biogenic origin, except for two Mediterranean species (*H. hexaspinae* n. sp., *S. dentata* (López de la Cuadra & García-Gómez, 1991) n. comb.), which can also live in dark, shallow submarine caves.

KEY WORDS
Escharellidae, morphological criteria, species complex, biogeography, scattered microhabitats, stepping-stone dispersal, dark habitats, new combination, new species, new genus.

RÉSUMÉ
*Sur quelques espèces d'"*Hemicyclopora*" et d'"*Escharella*" (Bryozoa, Cheilostomatida) de la région atlantico-méditerranéenne. Réexamen de leur statut générique et description de nouvelles espèces et d'un nouveau genre.*
Il est admis depuis longtemps que les genres de bryozoaires chéilostomes *Hemicyclopora* Norman, 1894 et *Escharella* Gray, 1848 se différencient par la présence d'une lyrule dans l'orifice des autozooides d'*Escharella*. L'examen d'un abondant matériel de Méditerranée et de l'Atlantique NE en utilisant des critères spécifiques réévalués a révélé une diversité insoupçonnée impliquant plusieurs espèces non-décrites, typiques du genre *Hemicyclopora*, mais aussi des espèces présentant des caractères morphologiques intermédiaires entre les deux genres ci-dessus. Globalement, la diversité du matériel examiné comprend dix espèces, dont cinq nouvelles (*Hemicyclopora neatonensis* n. sp., *H. hexaspinae* n. sp., *"Hemicyclopora" celtica* n. sp., "*H.*" *pytheasi* n. sp., "*Escharella*" *massiliana* n. sp.), et deux espèces non décrites par manque de matériel suffisant. Un nouveau genre, *Scutocyclopora* n. gen., est érigé pour l'espèce méditerranéenne *Hemicyclopora dentata* López de la Cuadra & García-Gómez, 1991, dont les caractères divergent par l'absence d'épines orales et la production d'une ancestrule non tatiforme. Six espèces sont considérées dans le matériel méditerranéen (5-205 m) et sept espèces dans le matériel atlantique (128-1050 m). Toutes ces espèces vivent en eau profonde sur des petits substrats peu éclairés, principalement d'origine biogène, à l'exception de deux espèces en Méditerranée (*H. hexaspinae* n. sp., *S. dentata* (López de la Cuadra & García-Gómez, 1991) n. comb.), qui peuvent aussi vivre à faible profondeur dans des grottes sous-marines obscures.

MOTS CLÉS
Escharellidae,
critères morphologiques,
complexe d'espèces,
biogéographie,
microhabitats éparpillés,
dispersion pas-à-pas,
habitats obscurs,
combinaison nouvelle,
espèces nouvelles,
genre nouveau.

INTRODUCTION

Bryozoan species show a great diversity of colony shapes, sizes, life cycles, ecological requirements and capacity to cope with interspecific competition (Taylor 2020 for a review, and references therein). Encrusting species developing only small, multiserial, unilaminar colonies form a morphological group frequently present among bryozoans. This morphological group is widely represented in microhabitats and ecological niches involving relatively reduced risks of spatial competition from large and dynamic components of sessile communities. The refuge function of these microhabitats results mainly from severe limitations in terms of energy supply and/or substrate availability and perenniality, which are environmental conditions required for the expansion of large, dynamic sessile competitors. Among cheilostome bryozoans, all species ascribed to the genus *Hemicyclopora* Norman, 1894, i.e., nine fossil and nine living species as currently recognised (Bryozoa.net, accessed on 20.IV.2022), belong to this morphological group. None of the living species of *Hemicyclopora* have been recorded in euphotic conditions of shallow habitats. In contrast, they live in mesophotic or aphotic, poorly productive habitats or microhabitats with a dotted distribution either on deep-water bottoms, e.g. on undersides of pebbles, empty shells or other mineralized biotic remains, and in shallow, dark submarine caves in the coastal zone. *Hemicyclopora polita* (Norman, 1864), the type-species of the genus, is thus typically established off-shore on shells, stones and skeletons of deep-water corals (Norman 1864; Ryland 1963; Hayward & Ryland 1979 and personal JGH data). The small size of *Hemicyclopora* colonies and the scattered condition of the substrates they colonize make collecting them rather haphazardly. Moreover, during benthic sampling of oceanographic surveys, substrates of this kind are usually not specifically kept in collections or made available to bryozoan specialists. For these reasons, one can assume that the nine living species presently listed, and particularly those recorded in the Atlantic-Mediterranean region [five in the Mediterranean basin with *H. admirabilis* Ramalho, Rodríguez-Aporta & Gofas, 2022 adding to the four species listed in Rosso & Di Martino (2016)], only represent the visible part of a taxonomic iceberg. Obviously, the morphological criteria used to distinguish between *Hemicyclopora* species need to be better defined. Moreover, the relationships between the genera *Hemicyclopora* and *Escharella* Gray, 1848, essentially differentiated by the presence or the absence of a lyrula (Norman 1894, 1909; Ryland 1963), have to be examined critically. In this paper, these two key issues are tackled thanks to abundant material from both the Mediterranean and the Atlantic stored by the authors. This revision takes into consideration 11 species, including ten species from the authors' material, five species of which are described as new, two species are left unnamed, and a new genus is erected. Except for three "unrelated" taxa, including the type species of the new genus, these species were grouped into four species complexes. In two of them, species are assumed to form a link between the genera *Hemicyclopora* and *Escharella*.

MATERIAL AND METHODS

Origin of material

Material mostly originates from several oceanographic surveys performed during the last 40-50 years and using dredges or trawls for sampling. Further specimens were collected by diving in submarine caves. These collections of specimens and substrates potentially bearing *Hemicylopora* colonies were stored at both authors' laboratories.

Specimen repositories

Type material of the new species, figured specimens and other material were deposited at the Muséum national d'Histoire naturelle, Paris, and in the Rosso Collection at the Museum of Palaeontology of the University of Catania.

Methods of study

Morphological characters of species were examined under stereomicroscopes and SEM. Specimens selected for SEM observations were treated or not with bleach, and either gold-palladium coated for examination with a Hitachi S-570 (SME, Marseille) and a TESCAN VEGA 3 SBU (IMM, Marseille), or uncoated using a TESCAN VEGA 2 LMU in backscattered-electron/low-vacuum mode (Microscopical Laboratory of the University of Catania). Measurements were taken with an eyepiece micrometer and from scales of SEM photos. Drawings were made by JGH from sketches combining observations with SEM and stereomicroscope.

Abbreviations

col.	colony;
COR	coralligenous bottom;
DC	detritic sandy bottom;
Div	sampling by diving;
Dre	sampling by dredging or trawling;
Is.	Island;
R/V	research vessel;
SEM	scanning electronic microscope;
Stn	sampling station.

Measurements

AZ	autozooid;
L	length;
OV	ovicell;
SD	standard deviation;
W	width;
X	mean.

Institutions

IMM	Institut de Microbiologie de la Méditerranée, CNRS, Marseille;
MIO	Mediterranean Institute of Oceanography, Marseille;
MNHN	Muséum national d'Histoire naturelle, Paris;
PMC	Museum of Palaeontology of the University of Catania;
SME	Station marine d'Endoume, Marseille.

RESULTS

Systematic accounts

The species presented below were placed in the family Escharellidae Levinsen, 1909, though temporarily in one case (see below). The alternative placement of *Escharella* and *Hemicyclopora* in Romancheinidae Jullien, 1888 (e.g. Souto *et al.* 2014; Rosso & Di Martino 2016; Martha *et al.* 2020; Ramalho *et al.* 2022; Bryozoa.net, accessed on 20.IV.22;) is not appropriate considering the polyphyly of this family (Orr *et al.* 2021, 2022). Seven species among the ten presented below were grouped into four species complexes. These groups were arbitrarily erected considering discernible morphological similitudes between specimens from the examined material and/or described in the literature. Two of these groups gather species presenting intermediate features between the genera *Hemicyclopora* and *Escharella*. As noticed by Norman (1909: 308) about *Hemicyclopora multispinata* (Busk, 1861): "The genus is allied to *Escharella* (synonym of *Mucronella*) but without the denticle (lyrula) within the lower lip". Ryland (1963: 26) also defines *Hemicyclopora* as "like *Escharella* but lacking a lyrula". Other differences pointed out by Hayward & Ryland (1999) involve: 1) the condyles in the primary orifice, small when present in *Escharella*, well-marked in *Hemicyclopora*; and 2) the ovicell, cleithral (closed by the autozooid operculum) in *Hemicyclopora*, acleithral (not closed by the operculum) in *Escharella*. Both genera are umbonuloid and their frontal shield presents only marginal pores, small or medium sized in one or double row in *Hemicyclopora* and generally larger (areolae) and in a single row in *Escharella*. However, these generic features may be poorly perceptible or equivocal in certain species, and their generic assignation remains critical without genetic appraisal. Lyrula, a well-established feature of *Escharella* species, may be typically anvil-shaped and large, such as in *E. immersa* (Fleming, 1848), the type species of the genus (e.g. Hayward & Ryland 1999; Souto *et al.* 2007), or a smaller denticle, quadrate (e.g. *E. quadrata* Lopez de la Cuadra & Garcia Gómez, 2001) or triangular (e.g. *E. praealta* (Calvet, 1907). However, it can also be reduced to a low bulge hidden behind the proximal lip of the orifice, hardly perceptible without precise SEM examination. The efficiency of this structure for partitioning the orifice and peristome and facilitating water exchanges through the ascus (Berning *et al.* 2014) is thus much variable among species. The identification of the type of ovicell closure (acleithral, cleithral, semi-cleithral, subcleithral; Ostrovsky 2013) is another source of uncertainty when the decision of generic assignment is based on this character. Precise identification should require sections in properly preserved specimens. The correct recognition of this character may be quite problematic when only the skeletal parts of specimens are available. In this case, the respective position of the maternal orifice with its opercule and that of the ovicell opening may suggest a certain type of closure, which remains a subjective interpretation. The constancy of a certain type of closure among species of each of the genera *Hemicyclopora* and *Escharella* remains to be established, and the use of this character for differentiating them is thus disputable. As noted by Souto *et al.* (2007: 368), the number of oral spines is an important feature for differentiating species of *Escharella*. The same is admitted for species of *Hemicyclopora* [e.g. characterization of *H. multispinata* with eight spines and *H. polita* (Norman, 1864) with six spines by Hayward & Ryland (1999: 140)]. However, examination of a large number of specimens showed that, at least in colonies of certain species, non-ovicellate zooids may present a lower number of spines than the majority of them (assumed cause: failure of the ovicell development in these autozooids, see below). In contrast, the number of spines in ovicellate zooids appears to be constant within

most species, while its change in certain local populations might indicate a genetic divergence. The number of spines in ancestrulae, around the opesia and the cryptocyst, is often used for characterizing species (e.g. Hayward & Ryland 1999: 11 spines in *H. polita*, ten spines in *H. multispinata*). However, as noticed by Ryland (1963), this number may slightly vary within the same species (Fig. 14C: an ancestrula of *H. polita* with 12 spines), even among ancestrulae settled on the same substrate.

Suborder FLUSTRINA Smitt, 1868
Superfamily LEPRALIELLOIDEA Vigneaux, 1949
Family ESCHARELLIDAE Levinsen, 1909

Species complex 1: "*multispinata*"

REMARK

Hemicyclopora multispinata (Busk, 1861) is the oldest described taxon among the 18 *Hemicyclopora* species listed in Bryozoa.net (accessed on 20.IV.22). The lack of precision in the original description and the specific name pointing to the presence of numerous oral spines, a feature shared with several congeneric species, have led to repeated misinterpretations of this taxon. Despite gaps and deficiencies in the knowledge of the morphology of the true *H. multispinata*, the available data on this species (see below) indicate that several specimens from our material are morphologically close to it. These specimens are distributed in two geographically distinct series, which form a species complex with *H. multispinata*. The best documented series is constituted by Mediterranean specimens, for which a new species is here designated. The second series is limited to few specimens from two localities of the Azores, which are left unnamed (*Hemicyclopora* sp. 1).

Hemicyclopora multispinata (Busk, 1861)
(Fig. 1A-C)

Lepralia multispinata Busk, 1861: 78, pl. 32, figs 5, 6.

?*Hemicyclopora multispinata* – Cook 1968: 216. — Hayward & Ryland 1999: 146 (pars). — Ramalho *et al.* 2020b: 455, 457 (table 2), 459 (table 3).

Not *Hemicyclopora multispinata* – Norman 1909: 308, pl. 42, figs 6-7. — Nichols 1911: 21. — Harmelin 1976: 230, table 3 (= *"E." massiliana* n. sp.). — Zabala 1986: 444. — Boronat Tormo 1987: 107, pl. 10A, B (= *H. discrepans* (Jullien *in* Jullien & Calvet, 1903)). — Zabala & Maluquer 1988: 126, fig. 283b (= *H. discrepans*). — Rosso 1989: tables 3c, 4c, 6c, pl. 8, fig. A (= *H. neatonensis* n. sp.); 1996a: 195, 210, pl. 4, fig. A; 1996b: 60 (table 1) (= *H. neatonensis* n. sp.). — Di Geronimo *et al.* 1990, table 1. — López de la Cuadra & Garcia Gómez 1994: 11 — Chimenz & Faraglia 1995: 40, pl. 2, figs A, B (= *H. neatonensis* n. sp.). — Morri *et al.* 1999: 733 (table 1). — Hayward & Ryland 1999, figs 46D, 49 (= "*H." pytheasi* n. sp. or *H. celtica* n. sp). — Chimenz Gusso *et al.* 2014: 172, fig. 88a-d (= *H. neatonensis* n. sp.). — Denisenko *et al.* 2016: 13 & table 1. — Rosso & Di Martino 2016: 579 (table 1).

TYPE LOCALITY. — Madeira.

MATERIAL EXAMINED. — **Atlantic, Portugal, Madeira • Type**. Dry specimen in slide 99.7.1.1802; NHMUK, Busk collection; labelled "*Mucronella peachii* var. *multispinata*, one small, unfertile colony on a shell fragment, collected by J. Y. Johnson; macrophotos sent by Mary Spencer Jones"; 14.II.2022; here, Fig. 1C).

REMARKS

The available optical photos of the type of *H. multispinata* (Fig. 1C) reveal a small specimen, in mediocre condition, without ovicells, but with an ancestrula apparently bearing 10 spines. Visible features of the orifices confirm the correctness of Busk's figures (Busk 1861, pl. 32, figs 5-6; here, Fig. 1A, B) and original description ("… *orifice arched, with an entire, straight lower lip; peristome raised, thick, forming a cup in front of the orifice; 8-10 marginal spines*"). Busk's figure 6 shows an autozooid with six spines, but in figure 5 three autozooids bear at least eight spines (Fig. 1A, B). In both figures, orifices are slightly longer than broad, with a moderately concave proximal edge and an arched proximal thickening with a moderate vertical elevation. Therefore, the assertion by Hayward & Ryland (1999: 146) that the orifice of *H. multispinata* is characterized by a "*proximal edge produced medially as a prominent lip*" do not correspond to Busk's description and figures. Their figures illustrating *H. multispinata* (Hayward & Ryland 1999, figs 46D; 49) may actually correspond to one of the species treated below. Consequently, *H. multispinata* has often been erroneously recorded, particularly from the northern Atlantic and the Mediterranean (see below). The record of *H. multispinata* by Norman (1909: 308, pl. 42, figs 6-7) at Madeira (70 fathoms depth) is quite puzzling as this specimen is depicted with eight oral spines, an orifice with a proximal edge more 'pouting' than in *H. polita*, and also with large spatulate avicularia (Norman 1909, pl. 42, fig. 7; here, Fig. 1E). This latter feature obviously excludes this specimen from the genus *Hemicyclopora* as it is unlikely that Norman had misinterpreted the occurrence of an adjacent colony belonging to another, very different, species provided with large avicularia. A plausible hypothesis is that this specimen belongs to another family, and quite possibly to a species of the atlantisinid genus *Bathycyclopora* Berning, Harmelin & Bader, 2017. This genus "superficially resembles the escharellid genera *Hemicyclopora* and *Escharella*" (Berning *et al.* 2017: 31). For example, *B. suroiti* Berning, Harmelin & Bader, 2017, from Atlantis Seamount, has eight long oral spines, an orifice with a prominent proximal edge, tiny paired adventitious avicularia, poorly visible without SEM, and large spatulate interzooidal avicularia with a rostrum similar in shape to those illustrated by Norman (here, Fig. 1F, G). Therefore, one may suppose that a deep-water species close to *B. suroiti* exists at Madeira and has been confused with *H. multispinata* by Norman (1909).

Cook (1968: 216) considered that *H. multispinata* was synonymous with *H. canalifera* (Busk, 1884) after examination of the types of both species. However, this synonymy was rejected by Berning & Spencer Jones (2023), who designated the specimen figured by Busk (1884: pl. 22, fig. 2) as the lectotype of *Mucronella canalifera*. The morphological features of an Azorean specimen from the collection of Jullien and Calvet listed as *H. multispinata* in the MNHN col-

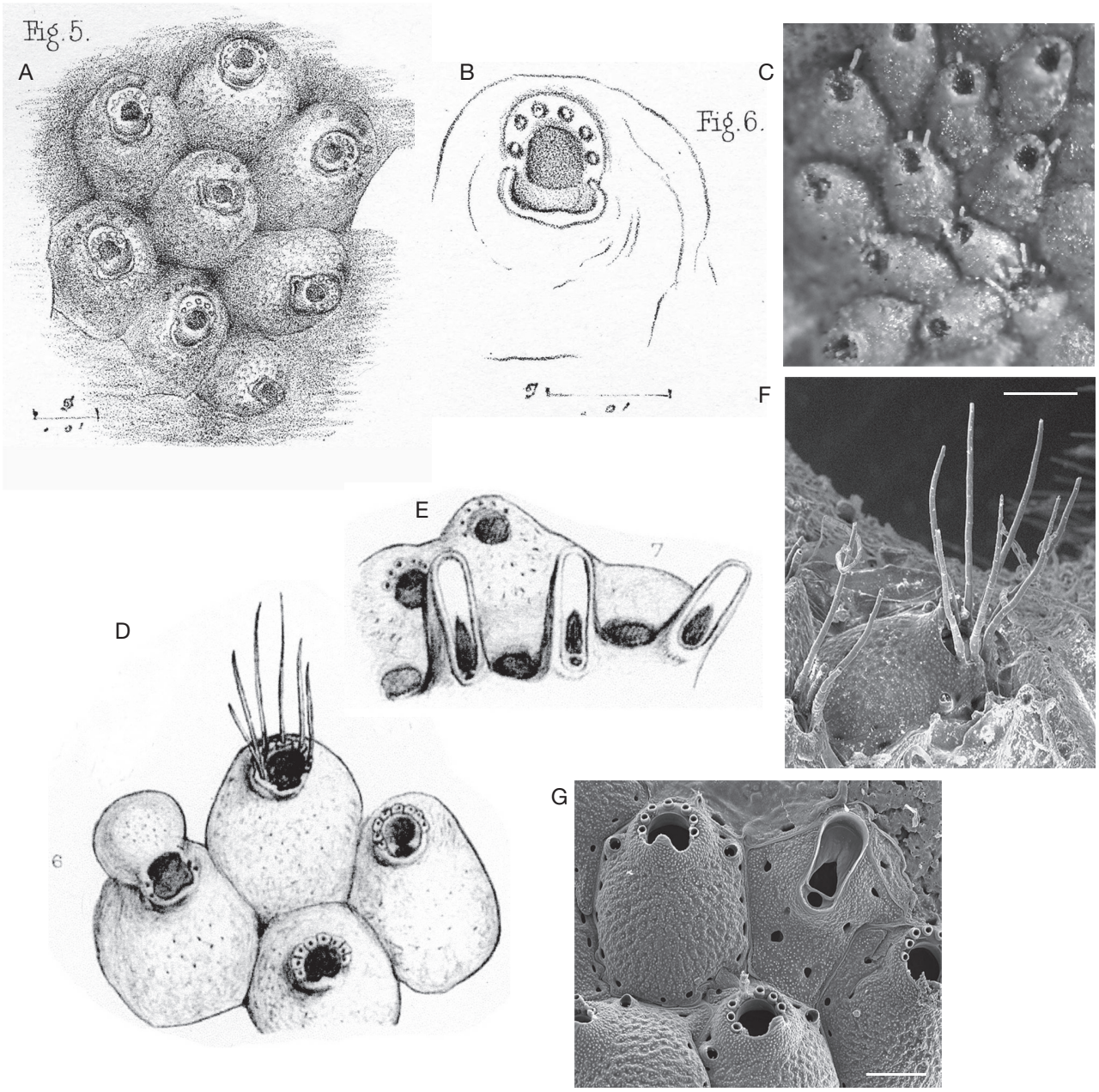

FIG. 1. — **A**, **B**, original figures of *Lepralia multispinata* Busk, 1861, from Madeira; part of colony with eight non-ovicellate zooids (**A**), distal part of a non-ovicellate zooid (**B**) illustrating the bases of six spines, the orifice shape and the proximal peristomial thickening; **C**, part of the type specimen of *Lepralia multispinata* (Busk collection 99.7.1.1802), with ancestrula and 11 non ovicellate zooids, photo courtesy of Mary Spencer Jones; **D**, **E**, *Hemicyclopora multispinata* (Busk, 1861) from Madeira, figured by Norman (1909, figs 6-7), ovicellate and non-ovicellate zooids, note the long spines and the orifice with a convex proximal edge of two zooids (**D**), and the large spatulate avicularia (**E**); **F**, **G**, *Bathycyclopora suroiti* Berning, Harmelin & Bader, 2017. Origin: Atlantis Seamount, RV Suroit, Seamount 2, DW258, derivative of figures 12G and 12E (both SEM photos by JGH) in Berning *et al.* (2017). Scale bars: F, G, 200 µm.

lections (MNHN-IB-2008-2436: Talisman 1883, Dr. 125, 13.VIII.1883, Fayal-Pico, 80-115 m), are visible at https://www.mnhn.fr/fr/collections/collection-groups/marine-invertebrates/bryozoans-and-brachiopods/hemicyclopora) thanks to 10 SEM photos taken by B. Berning in 2012 (MNHN project RECOLNAT ANR-11-INBS-0004). This specimen, very different from the Busk's type of *H. multispinata*, was assigned to *H. canalifera* by Berning & Spencer Jones (2023, fig. 5). Records of *H. multispinata* from boreal areas (e.g. Nichols 1911, Denisenko *et al.* 2016) are doubtful.

Hemicyclopora neatonensis n. sp.
(Figs 2A-F; 3A-F; 10A-C; Tables 1; 2; 4)

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Hemicyclopora multispinata – Rosso 1989: tables 3c, 4c, 6c, pl. 8, fig. A.; 1996a: 195, 210, pl. 4, fig. A.; 1996b: 60 (table 1) — Di Geronimo *et al.* 1994: 103 (table 3). — Chimenz & Faraglia 1995: 40, pl. 2, figs A, B. — ? Morri *et al.* 1999: 733 (table 1). — Rosso & Sanfilippo 2005: 111 (table 1). — Chimenz Gusso *et al.* 2014: 172, fig. 88a-d. — Rosso & Di Martino 2016: 579 (table 1).

TABLE 1. — Comparative measurements of the length and width of non-ovicellate zooids (**AZ L** & **AZ W**), and width of ovicells (**OV W**) in specimens assigned to *Hemicyclopora* Norman, 1894, *Escharella* Gray, 1848 and *Scutocyclopora* n. gen.: *H. neatonensis* n. sp. (**HN**), *H. hexaspinae* n. sp. (**HH**), *H. discrepans* (Jullien *in* Jullien & Calvet, 1903) (**HD**), "*H.*" *celtica* n. sp. (**HC**), *E. similis* Ramalho, Rodríguez-Aporta & Gofas, 2022 (**ES**), "*E.*" *massiliana* n. sp. (**EM**), "*H.*" *pytheasi* n. sp. (**HP**), *S. dentata* (López de la Cuadra & García-Gómez, 1991) n. comb. (**SD**). Specimens from the Mediterranean (**Med**) and the Atlantic (**Atl**) in the following areas: Gulf of Cadiz (**GC**), seamounts (**SM**), Iberian coast (**IC**), Bay of Biscay (**BB**) and Armorican margin (**AM**). Number of measured colonies in brackets. Mean ± standard deviation (range; number of data), measurements in microns.

	AZ L	**AZ W**	**OV W**
HN – Med (6)	747 ± 79 (610-1040; 60)	516 ± 50 (390-580; 60)	448 ± 35 (375-500; 22)
HH – Med (5)	637 ± 71 (435-750; 49)	502 ± 52 (435-635; 49)	302 ± 14 (280-328; 13)
HH – Atl GC (2)	636 ± 66 (485-725; 17)	446 ± 54 (365-560; 17)	299 ± 6 (290-305; 5)
HD – Med (2)	603 ± 39 (560-680; 8)	470 ± 74 (415-630; 8)	294 ± 8 (280-305; 9)
HD – Atl SM (3)	705 ± 68 (630-890; 12)	447 ± 25 (410-485; 12)	287 ± 11 (280-305; 5)
HD – Atl IC (2)	720 ± 35 (655-775; 18)	518 ± 59 (390-650; 18)	314 ± 20 (290-340; 7)
HC – Atl AM (7)	752 ± 84 (535-920; 76)	590 ±110 (390-970; 76)	334 ± 39 (245-410; 33)
HP – Atl BB-AM (3)	683 ± 67 (560-845; 25)	460 ± 39 (365-535; 25)	297 ± 39 (255-380; 17)
ES – Med-Atl (4)	658 ± 78 (510-800; 59)	452 ± 50 (365-580; 59)	270 ± 21 (235-305; 30)
EM – Med (2)	593 ± 66 (465-730; 14)	379 ± 42 (320-440; 14)	258 ± 13 (230-270; 11)
SD – Med (7)	721 ± 79 (560-975; 47)	517 ± 69 (365-680; 47)	434 ± 26 (390-480; 8)

TABLE 2. — Features of *Hemicyclopora neatonensis* n. sp., *H. discrepans* (Jullien *in* Jullien & Calvet, 1903), *H. hexaspinae* n. sp. Abbreviations: **BKz**, associated to basal kenozoid; **Cle**, cleithral; **crypt**, cryptocyst; **DAz**, associated to distal autozooid; **IKz**, associated to interzooidal kenozooid; **Op**, opesia; **Rec**, recumbent; **Scl**, semicleithral.

Features	***H. neatonensis* n. sp.**	***H. hexaspinae* n. sp.**	***H. discrepans***
Frontal shield	Spaced round granules	Small granules	Pointed granules
Marginal pores	Large (20-30 µm)	Tiny to medium-large (5-20 µm)	Medium (15-20 µm)
Peristome proximal part	Semi-circular collar joining the 1st pair of spines	Smooth	Smooth
Orifice proximal edge	Concave	Straight or slightly concave	Slightly concave
Orifice inner relief	No lyrula or denticle	No lyrula or denticle	No lyrula or denticle
Condyles	Prominent, triangular, downcurved	Prominent, triangular	Prominent, triangular
Oral spine number	8 (6, 7, 9)/6	6 (7)/6 – thick bases	8 (9)/8 (6-7)
Ovicell	BKz-DAz-IKz, W > L, Cle	Rec, BKz, W > L, Scl	Rec, BKz, W > L, Cle?
Porous IKZ	Present	No	Present
Ancestrula, spine number - length	Op: 6-7, crypt: 5-6 L: 410-560 µm	Op: 6 (7), crypt: 4 L: 500-560 µm, extensive cryptocyst	Op: 6, crypt: 4-5 L: 430 µm
Depth range	27-120 m	5-150 m	115-320 m
Substrate	Shells, rhodoliths	Dark cave walls, biogenic debris	Shells, biogenic debris
Origin of material	Central Mediterranean	Mediterranean & G. of Cadiz	Mediterranean & G. of Cadiz

TYPE LOCALITY. — Italy, SE Sicily, Gulf of Noto.

TYPE MATERIAL. — **Holotype. Mediterranean, Italy, Ionian Sea, SE Sicily, Gulf of Noto** • 1 large colony with several ovicells; Gulf of Noto, Stn PS 81-9D; 36°45'N, 15°12'E; 78 m depth; VII.1981; on a small rhodolith; Dre; I. Di Geronimo leg.; PMC. B34.1.4.2021a. **Paratypes. Mediterranean, Italy, Ionian Sea, SE Sicily, Gulf of Noto** • 1 colony with 3 autozooids and ancestrula; same data as the holotype; on a small rhodolith; PMC. B34.1.4.2021b1 • 1 dead ovicellate colony; same data as the holotype; on a small rhodolith; PMC. B34.1.4.2021b2 • 1 living ovicellate colony; same data as the holotype; on a small rhodolith; PMC. B34.1.4.2021b3 • 1 living ovicellate colony; same data as the holotype; on a bivalve shell; PMC. B34.1.4.2021b4 • 1 living ovicellate colony; SE Sicily, Gulf of Noto; Stn PS 81-CR1; 36°44'N, 15°10'E; 45 m depth; on a bivalve shell; PMC. B34.1.4.2021b5 • 1 living colony; same data as PMC. B34.1.4.2021b5; on a rhodolith fragment; PMC. B34.1.4.2021b6 • 1 coated colony, same data as PMC. B34.1.4.2021b5; MNHN-IB-2017.769. All samples collected in VII.1981; Dre; I. Di Geronimo leg.

OTHER EXAMINED MATERIAL. — **Mediterranean, Italy, Ionian Sea, SE Sicily, Gulf of Noto** • 18 fragments; Stn PS 81-9D; same data as the holotype; PMC Rosso-Collection I. H. B. 92a • fragments, Stn PS 81-2XB; 120 m depth; PMC Rosso-Collection I. H. B. 92a • fragments, Stn PS81-6D; 96 m depth; PMC • 25 fragments; Stn PS 81-9C; 83-74 m depth; on rhodoliths, mollusc and brachiopod shells; PMC Rosso-Collection I. H. B. 92a • fragments; Stn PS 81-2C; 60 m depth. All samples collected in VII.1981; Dre; I. Di Geronimo leg.; PMC Rosso-Collection I. H. B. 92a.

SEM PHOTOS EXAMINED. — **Italy** • Adriatic Sea, Puglia, Brindisi, 27 m depth, CR bottom, C. Chimenz leg. (sent to JGH, 30.VI.1995).

ETYMOLOGY. — From *Neaton*, ancient Greek name of the town of Noto, SE Sicily, close to the shore of the Gulf of Noto.

DIAGNOSIS. — Autozooids bulged, frontal shield with round granules, marginal pores medium- to large-sized. Orifice terminal or subterminal, primary orifice with prominent and down-curved condyles; proximal edge concave, bordered by a low semi-circular collar. Oral spines usually eight in non-ovicellate and six in ovicellate zooids. Ovicell recumbent on the frontal shield of the distal zooid, with a low proximal visor, ooecium produced by a small basal kenozooid, occasionally fusing with a distal zooid or an interzooidal kenozooid. Large interzooidal kenozooids occasional. Ancestrula with opesia, cryptocyst and gymnocyst equally extended, 12 or 13 spines, the opesia with a concave proximal edge.

DESCRIPTION

Colony encrusting, unilaminar, small- to medium-sized (i.e., less than 100 zooids). Autozooids quincuncially arranged, relatively large (Figs 2; 3; 10A, B; Table 1); frontal shield bulged, its surface relief with small knobs; marginal areolar

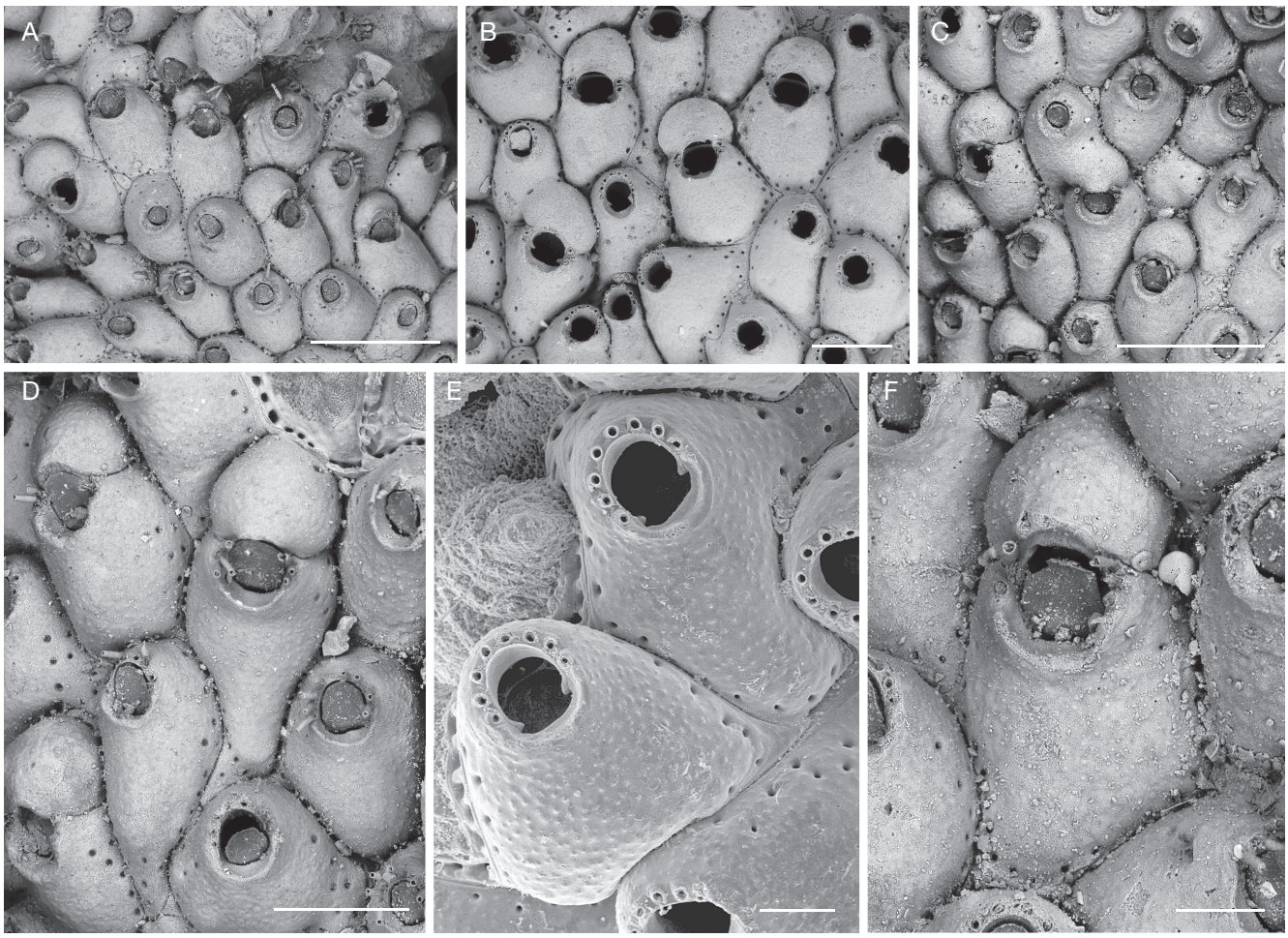

Fig. 2. — *Hemicyclopora neatoniensis* n. sp.: **A**-**C**, general aspect of the colony with ovicellate and non-ovicellate autozooids and rare interspersed kenozooids. Note the variability in the size and shape of autozooids and in the nature of the ovicells; **D**, close-up of some zooids with the typical peristomes; **E**, non-ovicellate autozooids; **F**, an ovicellate autozooids with four oral spines. Origin: **A**-**F**, holotype, PMC. B34.1.4.2021a; Sicily, Gulf of Noto, 78 m; **E**, paratype, MNHN-IB-20174-769, Gulf of Noto, 45 m. Scale bars: A, C, 1 mm; B, D, 500 µm; E, F, 200 µm.

pores relatively large (20-30 µm; Fig. 2D, E), generally in a single row with another one or two pores in an upper position at the level of the orifice (Fig. 2D). Pore-chambers small and numerous (10-12 on each side) (Figs 2E; 3E, F). Distal wall vertical or sub-vertical (Figs 2E; 3E). Orifice of non-ovicellate zooids distal or sub-distal, longer than wide (Table 1, ratio L/W: 1.13), wider in ovicellate zooids (25-30% in Sicilian specimens), proximal edge (poster) slightly concave, condyles large, triangular, more or less blunt (Figs 2E; 3C, E; 10A, B). A low, semi-circular collar proximal to the poster, higher when joining the most proximal pair of oral spines (Figs 2D-F; 10A). Oral spines eight, occasionally six, seven or nine, in non-ovicellate zooids, six in ovicellate zooids (Figs 2D, F; 3D). Ovicell ovoid, wider than long, cleithral (Figs 2B, D, F; 3C), with a small, low, more or less arched vizor above the proximal edge, recumbent on a small ooecium-producing basal kenozooid (Fig. 2D, F), occasionally fusing with the frontal shield of distal daughter autozooid (Figs 2B, C; 3C), or an interzooidal kenozooid (Fig. 3B). Interzooidal kenozooids present, nearly as large as autozooids (i.e., vicarious: Fig. 3E) or smaller at varying extents, irregularly shaped, the frontal shield finely granular with areolar pores irregularly distributed in a peripheral band. Ancestrula with 12 spines (occasionally 13), including six or seven around the opesia, this latter with a concave proximal edge; opesia, cryptocyst and proximal gymnocyst similarly sized when measured along the central axis (Figs 3F; 10C); three distal and latero-distal daughter autozooids budded by the ancestrula, similar to the following ones, but slightly smaller.

Remarks

As in other *Hemicyclopora* species, the most readily accessible distinctive features of the specimens assigned here to *H. neatonensis* n. sp. are provided by the distal part of the zooids, i.e., the structure and shape of the orifice area, the number of oral spines, and the structure of the ovicell. Like in the type of *H. multispinata*, the orifice of *H. neatonensis* n. sp. is a little longer than broad, with a slightly concave proximal edge, proximally bordered by a low, arched crest, which becomes higher when it meets the most proximal pair of oral spines, and the condyles (not described in *H. multispinata*) are large and roughly triangular. The oral spines are eight in

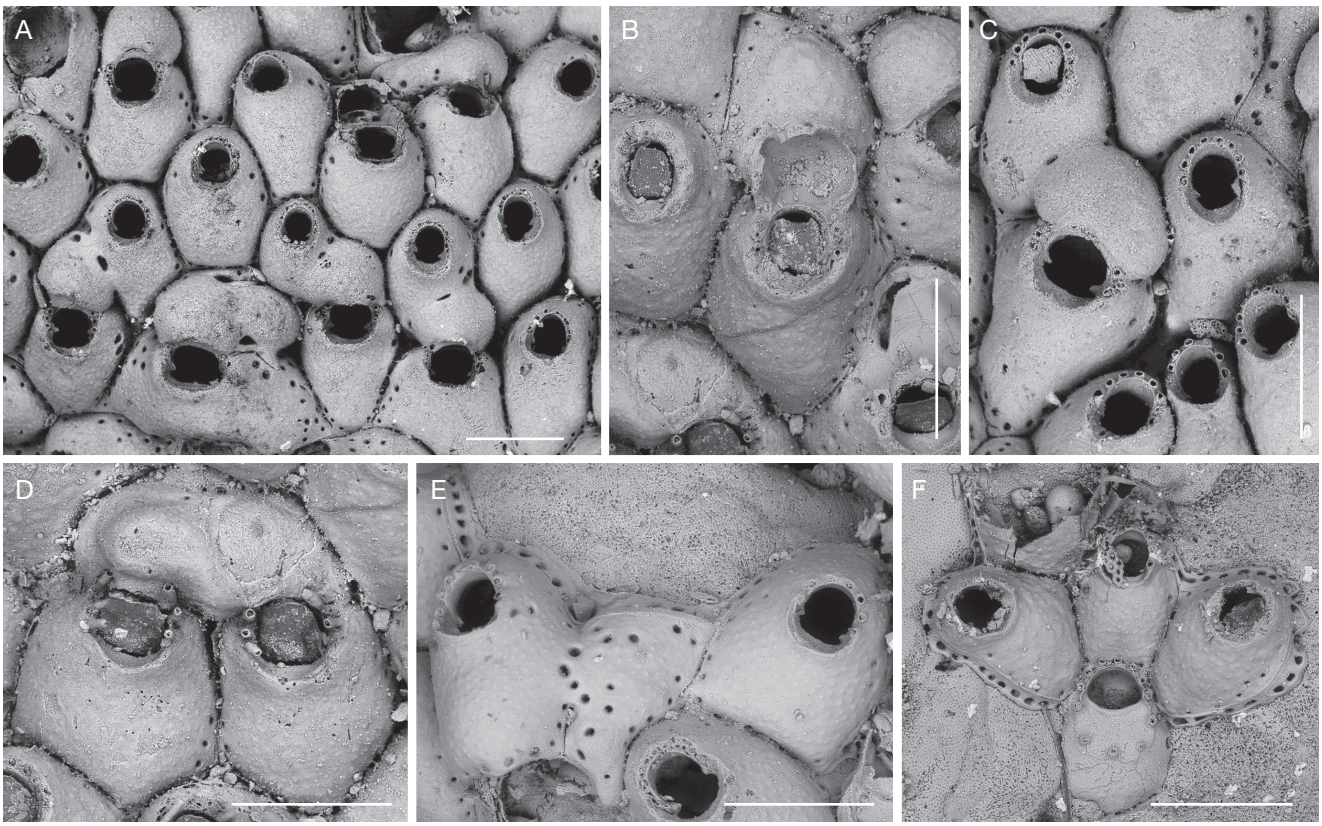

FIG. 3. — *Hemicyclopora neatoniensis* n. sp.: **A**, cluster of autozooids, several with ovicells associated with distal zooids smaller or developing teratologic morphologies; **B**, ovicell complex formed by a maternal autozooid and a distal kenozooid; **C**, ovicellate zooid with a very broad ovicell associated with a distal non-ovicellate zooid. Note the dimorphic orifices with eight, occasionally seven spines, and the condyles morphology; **D**, contiguous autozooids with fused ovicells; **E**, polygonal porous kenozooid at the colony periphery; **F**, ancestrula with three daughter zooids exposing their basal pore chambers; Origin: Sicily, Gulf of Noto; **A**-**E**, PMC. B34.1.4.2021b2; **F**, PMC. B34.1.4.2021b1. Scale bars: 500 µm.

most cases (occasionally six, seven or nine) in non-ovicellate zooids, invariably six in ovicellate zooids, and articulated on thick bases. Ovicells bear a short, arched crest near the edge of the orifice, apparently formed by the cryptocystal layer of the endooecium. The latter is built by a small basal kenozooid (Fig. 3B) but also, sometimes in a same colony, by a distal autozooid or an interzooidal kenozooid. The ancestrula has the same shape in these Mediterranean specimens and in the type specimen of *H. multispinata*, with the opesia, the cryptocyst and the proximal gymnocyst similarly extended (Figs 3F; 10C), but with, seemingly, a greater number of ancestrular spines (12 or 13) in *H. neatonensis* n. sp. In some colonies from Sicily, a few ovicells and adjacent autozooids show a deformity (Fig. 3A, D) possibly resulting from their fusion. The occurrence of interzooidal kenozooids in *H. neatonensis* n. sp. (Fig. 3E), as well as in *H. polita*, *H. discrepans* (Jullien *in* Jullien & Calvet, 1903) and *E. similis* Ramalho, Rodríguez-Aporta & Gofas, 2022 (see below), suggests that this feature may have a taxonomic value. These heteromorphs allow filling empty surfaces unsuitable to the growth of autozooids and thus ensure colony continuity between lobes (Cheetham & Cook 1983), such as in areas where irregularities in the substratum lead to a disrupted autozooid arrangement (Hayward & Ryland 1999). Such kenozooids are observed in several cheilostome taxa such as Cribrilinidae Hincks, 1879 (e.g. Harmelin 1978), *Setosella* Hincks, 1877 (Rosso *et al.* 2020) and *Microporella* Hincks, 1877 (Di Martino & Rosso 2021).

HABITAT DISTRIBUTION

The present material assigned to *H. neatonensis* n. sp. came in most cases from coastal shelf habitats, particularly detritic biogenic bottoms often including empty shells and/or algal concretions (Rosso 1989; 1996a; Chimenz Gusso *et al.* 2014 – recorded as *H. multispinata*), hosting the Coastal Detritic Biocoenosis and the Shelf-edge Detritic Biocoenosis (Pérès & Picard 1964; Pérès 1967). In the Gulf of Noto, the species was usually very rare, except in station PS 81-9D where several colonies encrusted small (1-2 cm), exceptionally larger, rhodoliths. The only colony from the Adriatic Sea (see below) was collected in a Coralligenous rocky bottom. Considering the sampling depths (27-120 m) and the sheltered position of colonies on the substrata, this species can be categorized as sciaphilic.

GEOGRAPHICAL DISTRIBUTION

Hemicyclopora neatonensis n. sp. has been collected in the Ionian Sea (Rosso 1989; 1996a, b), in the southern Adriatic Sea off Apulia (Chimenz & Faraglia 1995), and in the Tyrrhenian Sea off the Pontine Isles (Chimenz Gusso *et al.* 2014)

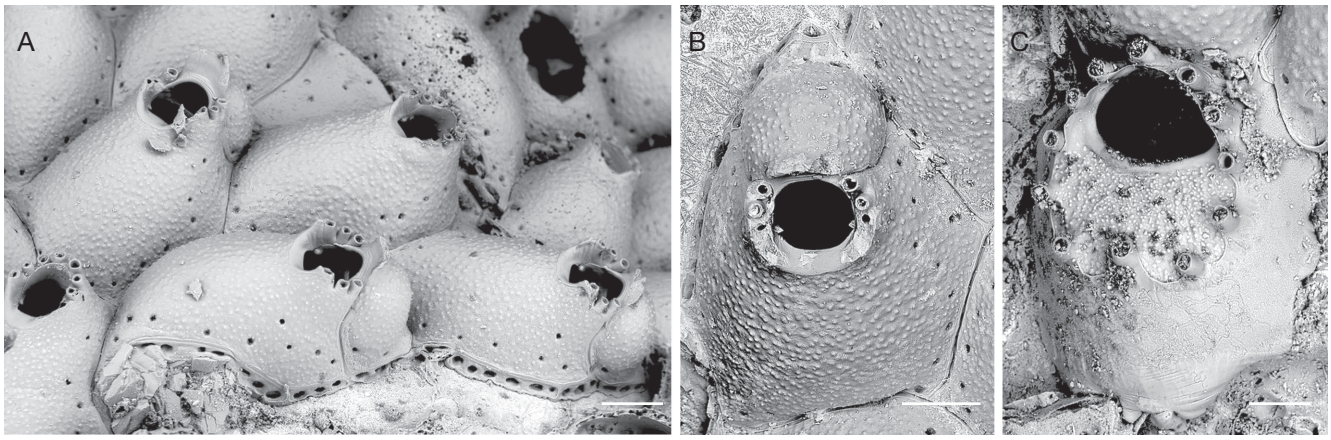

FIG. 4. — *Hemicyclopora* sp. 1: **A**, lateral view of ovicellate and non-ovicellate zooids with granular frontal shield, marginal pores and basal pore chambers, note the structure of the orifices and the ovicells with vizor, recumbent on a basal kenozooid; **B**, frontal view of an ovicellate zooid with typical features; **C**, ancestrula with 12 spines. Origin: Azores; Biaçores Stn 145-146; MNHN-IB-2017-1558. Scale bars: A, B, 200 µm; C, 100 µm.

(Table 4). However, it is likely that this species is more evenly distributed in the Mediterranean and that the present gaps are mainly due to the small colony size and the poor accessibility of local populations.

GEOLOGICAL DISTRIBUTION

Hemicyclopora neatonensis n. sp. also occurs in Early Pleistocene deposits of W Sicily (Belice section) (Di Geronimo *et al.* 1994; Rosso & Sanfilippo 2005), pointing to its persistence in this area.

Hemicyclopora sp. 1
(Fig. 4A-C; Table 4)

MATERIAL EXAMINED. — **Portugal, Azores, São Miguel Island** • 1 colony; R/V *Jean Charcot*; Biaçores, Stn 145, 37°41'N, 25°33.5'W; 135-148 m depth; 30.X.1971; on shell; Dre; H. Zibrowius leg.; MNHN • 2 ovicellate colonies; S of São Miguel; R/V *Jean Charcot*; Biaçores Stn 146, 37°39.8'N, 25°35.8'W; 330-334 m depth; 30.X.1971; on scoria and biogenic concretion; Dre; H. Zibrowius leg.; MNHN-IB-2017-1558.

DESCRIPTION

Colony encrusting, unilaminar. Autozooids quincuncially arranged, frontal shield bulged, granular, marginal pores medium-sized (18-25 µm), arranged in a single row split in two below the proximal edge of orifice; pore-chambers oval and flattened, numerous along the vertical walls. Orifice terminal, slightly longer than wide in non-ovicellate zooids, wider in ovicellate zooids, condyles prominent, triangular, proximal edge slightly concave or straight, a collar proximal to the orifice edge, low but becoming high when adjoining the proximalmost pair of spines. Oral spines eight in non-ovicellate zooids and six in ovicellate ones, with bases relatively high and thick. Ovicell vertically recumbent on a basal kenozooid, endooecium with the same granular surface as the frontal shield, proximal edge smooth with a vizor more or less high. Occasional occurrence of interzooidal kenozooids with porous shield. Ancestrula with 12 spines, five of which around the opesia, cryptocyst finely granular, peripheral and proximal gymnocyst widely extended.

REMARKS

These Azorean specimens are close to *H. neatonensis* n. sp. Their common traits include the granular surface of the bulged frontal shield, the shape of the orifice area including the primary orifice with prominent triangular condyles, a slightly concave proximal edge (poster), the number of oral spines (eight in non-ovicellate zooids and six in ovicellate ones), a low, arched crest below the poster, which is attached to the base of the most proximal spines, the structure of the ovicell, produced by a basal kenozooid, with a vizor above the orifice edge (Fig. 4A, B), the presence of interzooidal kenozooids (Fig. 4A), and a similarly-shaped ancestrula with 12 spines (Fig. 4C). Apparent differences with *H. neatonensis* n. sp. concern mainly the length and width of autozooids, which are larger, while ovicells are narrower (Table 1), less swollen, with a vizor which is differently shaped and sized. However, this comparison is based on only three Azorean colonies. These colonies were compared to unpublished SEM photos of another specimen from the Azores collected in a locality close to those of *Hemicyclopora* sp. 1 (R/V *Jean Charcot*, Biaçores 1971, Stn 167, 130 m, 37°46'0"N, 25°48'8"W; JGH leg.). This specimen differs clearly from the latter in having ovicellate and non-ovicellate zooids with six oral spines in most cases, an orifice with a concave proximal edge, bordered by a very high, arched collar, and ovicells bearing an erect, highly prominent vizor. These features resemble *H. canalifera*, which, therefore, would co-occur with *Hemicyclopora* sp. 1.

The clarification of the "*multispinata*" species complex would require detailed morphological and genetic analyses of new material from Madeira with features similar to those of Busk's type, and compared with other material from the Atlantic, including the Azores, and from the Mediterranean (*H. neatonensis* n. sp.).

Species complex 2: "*discrepans*"

Hemicyclopora discrepans
(Jullien *in* Jullien & Calvet, 1903)
(Fig. 5A-G; Tables 1; 2; 4)

Lepralia discrepans Jullien *in* Jullien & Calvet, 1903: 72, pl. 10, fig. 1.

Hemicyclopora discrepans – López de la Cuadra & Garcia-Gómez 1991: 218. — Harmelin & d'Hondt 1992: 30 (part). — Reverter-Gil & Fernández-Pulpeiro 1999: 1411, fig. 4A-C. — Souto & Reverter-Gil 2021: 3, 5, table 1 (part).

Hemicyclopora multispinata (Busk, 1861) – Boronat Tormo 1987: 107, plate 10A, B.

?*Hemicyclopora admirabilis* Ramalho, Rodríguez-Aporta & Gofas, 2022: 22, fig. 10.

?*Hemicyclopora* sp. – Souto *et al.* 2014: 140, fig. 5B, D.

Not *Hemicyclopora discrepans* (Jullien, 1903) – Harmelin 1997: 144 (table 2) (see below = *Hemicyclopora hexaspinae* n. sp.).

MATERIAL EXAMINED. — **Mediterranean. Alboran Sea** • 3 small ovicellate colonies; R/V *Cryos*; Balgim Stn DW132, 35°25.7'N, 4°18.8'W; 170 m depth; 15.VI.1984, on shell (2 col. together with 2 col. of *Escharella similis*) and biogenic concretion; Dre; JGH leg.: listed by Harmelin & d'Hondt (1992); MNHN.
NE Atlantic – Ibero-Moroccan Gulf • 2 ovicellate colonies; R/V *Noroit*; Seamount 1, Gorringe Bank, Stn DW5, 36°32.0'N, 11°37.9'W, 180 m depth; 22.IX.1987; Dre; JGH leg.; MNHN • 1 small colony; R/V *Noroit*; Seamount 1, Gorringe Bank, Stn DW15, 36°33.44'N, 11°28.8'W, 320 m depth; 24.IV.1987, on stone; Dre; JGH leg.; MNHN • 1 small colony; R/V *Noroit*; Seamount 1, Ampère Seamount, Stn CP99, 35°03.8'N, 12°55.4'W, 250 m depth, on shell; Dre; JGH leg.; MNHN
Spain, NW Iberian Peninsula • 3 small ovicellate colonies; 42°38'30"N, 9°23'42"W; 128 m depth; V.1997; on shell and fragment of a whale bone; Dre; O. Reverter-Gil leg.; MNHN (1.VI.1998: material examined by Reverter-Gil & Fernández-Pulpeiro 1999 and listed by Souto & Reverter-Gil 2021).

DESCRIPTION

Colony encrusting, unilaminar, forming small lobate patches of less than 100 zooids. Autozooids elongated, hexagonal or polygonal, quincuncially arranged; frontal shield bulged, most prominent at mid-length and proximally to the orifice, its surface covered with evenly spaced, hemispherical to conical and pointed granules, 5-15 µm in diameter (Fig. 5B, F, G); marginal pores medium-sized (up to 15-20 µm), in a single row along the proximal half of the zooid, and distributed distally in two or three rows up to the orifice level (Fig. 5B, D, F, G). Pore-chambers small and numerous (up to 15 on each side), opening along a *c.* 50 µm wide basal margin (Fig. 5F). Distal wall vertical or sub-vertical (Fig. 5B, D, G). Orifice distal or sub-distal, often somewhat inclined distally, a little longer than wide in non-ovicellate zooids, significantly wider than long in ovicellate zooids, proximal edge (poster) slightly concave, without any collar or umbo, sometimes with a thin rim of gymnocystal calcification connected laterally to the proximal pair of spines; condyles protuberant, thick, triangular, slightly curved proximally, with more or less blunt tips (Fig. 5B, E, G). Oral spines articulated on stout bases, long (up to *c.* 750 µm), outwardly arched, particularly the distalmost pair, eight in non-ovicellate zooids, occasionally nine, and eight, seven or six in ovicellate zooids (Fig. 5), this number being constant or variable within colonies (see below). Ovicell globular, wider than long, attached to the distal wall of maternal zooid, sometimes adjoining the proximal part of the frontal shield of distal zooid; endooecium with the same granular texture as the frontal shield of autozooids, without umbo or vizor, sometimes with a narrow, thin rim of gymnocystal calcification along the opening (Fig. 5C, D, F, G), presumably cleithral, "terminal", produced by a basal kenozooid not visible frontally, only detected at early stage and in broken ovicells (Fig. 5D, F). Interzooidal kenozooids infrequent, relatively large (e.g. 600 × 550 µm), with few frontal pores. Ancestrula with three roughly equally extended parts, an opesia with six distal spines and a concave proximal edge, a cryptocyst with a granular surface, edged by four or five spines, and a proximal gymnocyst (Boronat Tormo 1987: 107, pl. 10B; Reverter-Gil & Fernández-Pulpeiro 1999: 1411, fig. 4B; specimen from Seamount 1 Stn DW15).

REMARKS

Morphological features and taxonomic issues

Except for the number of spines in ovicellate zooids, which may vary within and between colonies (see below), the morphological features of our material from the Mediterranean (Alboran Sea) and the NE Atlantic comply with the original figure of *H. discrepans* by Jullien (1903: pl. 10, fig. 1), the redescription of this species by Reverter-Gil & Fernández-Pulpeiro (1999), and our own examination of part of their material (letter, SEM photos and material sent by O. Reverter-Gil to JGH, 1.VI.1998). This species (or species complex) is characterized by zooids with a bulged frontal shield without any thickening or umbo adjoining the orifice and the ovicell, a primary orifice with clearly protruding condyles, the particular aspect of the frontal shield and endooecium with granules which tend to be pointed, relatively large marginal pores distributed in several rows laterally to the orifice, eight oral spines with large and thick bases in non-ovicellate zooids, and globular ovicells produced by a small, basal, terminal kenozooid, later recumbent on the frontal shield of the distal zooid. However, these features are also shared with *H. admirabilis*, recently described from the Alboran Sea (Ramalho *et al.* 2022), and with *Hemicyclopora* sp. (Souto *et al.* 2014) from southern Portugal. Except for minor differences (e.g. the precise shape of condyles) that may indicate local variability, both *H. admirabilis* and the specimens described by Souto *et al.* (2014) as *Hemicyclopora* sp. only differ from *H. discrepans* in the lower number of spines in ovicellate zooids (six vs eight). In our material from the Mediterranean (Alboran Sea) and the nearby Atlantic, several colonies show features combining those of *H. discrepans* and *H. admirabilis*, particularly the number of spines in ovicellate zooids. This number can vary within a single colony, as in a specimen from the Alboran Sea (Balgim DW132, Fig. 5A), in which it is six or eight. Therefore, this specimen should be intermediate between *H. discrepans* and *H. admirabilis*.

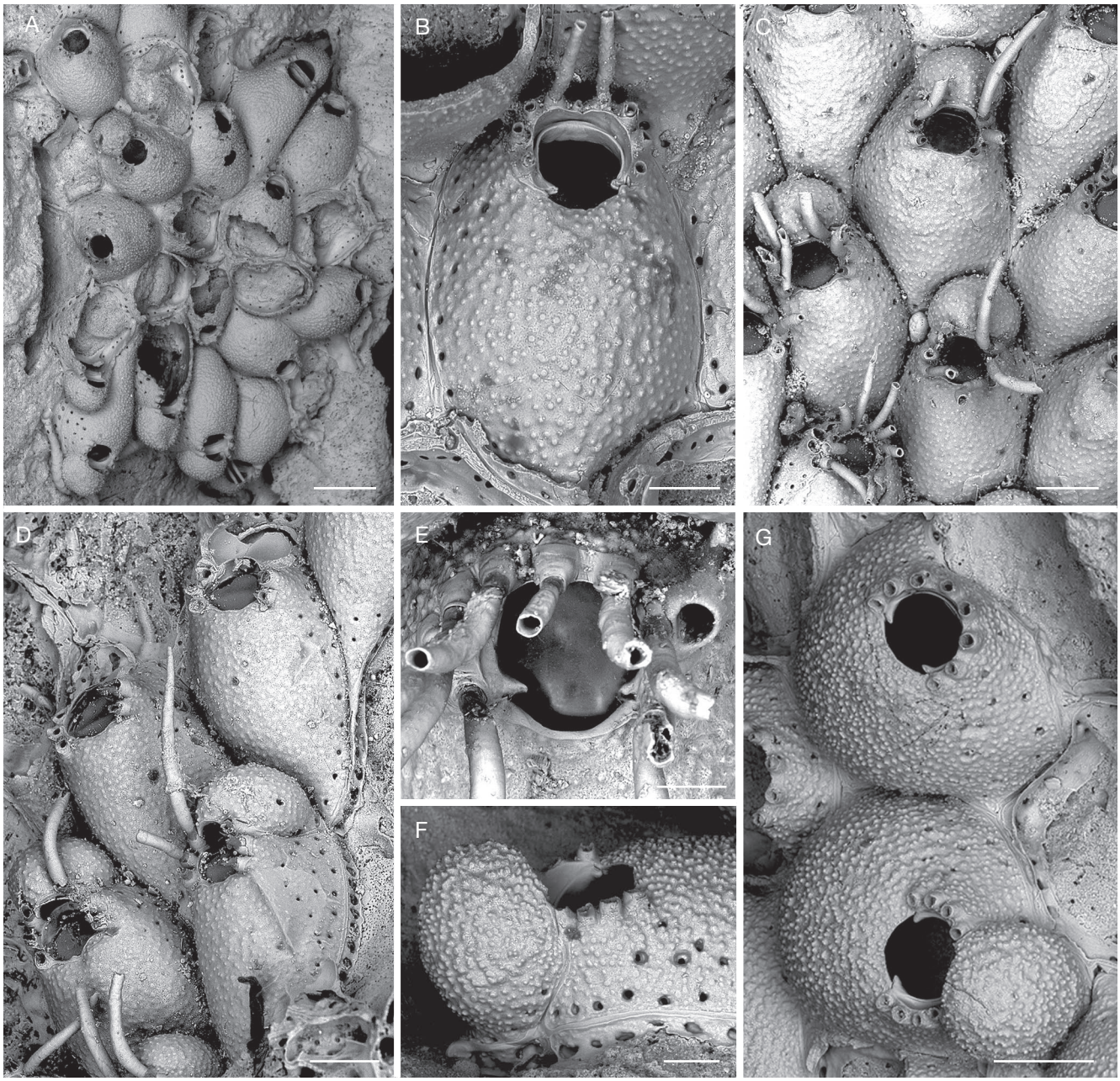

FIG. 5. — *Hemicyclopora discrepans* (Jullien *in* Jullien & Calvet, 1903): **A**, colony with ovicellate zooids bearing six, seven, or eight oral spines; **B**, non-ovicellate zooid with eight spines, primary orifice with internal arch and protruding condyles, and granular frontal shield; **C**, three ovicellate zooids with six spines and ovicells inserted between the base of distal autozooids; **D**, zooids with long, curved spines, large porous area lateral to orifice and ovicells attached to distal maternal wall, one under construction; **E**, orifice with triangular, down-curved condyles, concave proximal edge with a narrow rim of gymnocyst; **F**, lateral view of the distal part of an ovicellate zooid with eight spines, large marginal pores and the ovicell with the basal kenozooid; **G**, two zooids, one ovicellate, both with eight spines, frontal shield and endooecium with pointed granules. Origin: **A**, **B**, **F**, **G**, Alboran Sea, Balgim DW132, 170 m; **C**, **D**, **E**, Atlantic, Gorringe Bank, Seamount 1 DW5, 180 m. Scales bars: A, 400 µm; B, F, 100 µm; C, D, G, 200 µm; E, 50 µm.

Furthermore, specimens from the Atlantic seamounts (Gorringe Bank: DW5, DW15; Ampère Seamount: CP99) have six spines in ovicellate zooids, as in *H. admirabilis*, but a colony from Ampère Seamount diverges from the Bauplan of the latter in having a majority of non-ovicellate zooids with nine spines (seven cases: 70%) instead of eight spines (three cases: 30%). This divergence recalls cases of speciation driven by geographic isolation on Atlantic seamounts observed within the Atlantisinidae Berning, Harmelin & Bader, 2017 (Berning *et al.* 2017). In particular, the species *Atlantisina gorringensis* Berning, Harmelin & Bader, 2017 was likely endemic to Gorringe Bank and Ampère Seamount. In conclusion, the present material questions the actual type of ovicell closure and the taxonomic relationships between *H. discrepans*, *H. admirabilis* and *Hemicyclopora* sp. (Souto *et al.* 2014). Are they a complex of species or a series of vari-

ants of the same species (*H. discrepans*) having a particular plasticity? Obviously, this case study would require molecular analyses to give proper answers. Unfortunately, colonies of *Hemicyclopora*, particularly in this case, are very small, rare, and their habitat is not easily accessible.

Habitat distribution

The examined material was collected from 128 m to 320 m depth on sandy bottoms. Deeper records of *H. discrepans* are provided by Calvet (1907: 717 m) from the western entrance of the Strait of Gibraltar, and Reverter-Gil & Fernández-Pulpeiro (1999) from the NW Iberian Peninsula (Thalassa U844, 695-760 m). This last specimen, not illustrated by SEM, is held at the MNHN and its specific assignation should be verified. The two deep-water colonies from Portugal recorded as *Hemicyclopora* sp. by Souto *et al.* (2014: 800-900 m) may represent the deepest record of *H. discrepans*. Colonies were established on small biogenic substrates: empty shells, concretions, and even on fragments of whale bones (Reverter-Gil & Fernández-Pulpeiro 1999; Souto & Reverter-Gil 2021).

Geographical distribution

Hemicyclopora discrepans has an Atlantic-Mediterranean distribution (Table 4). In the Mediterranean, the species was collected exclusively in the Alboran Sea (present material; Boronat Tormo 1987; Harmelin & d'Hondt 1992). In the Atlantic, specimens were recorded from seamounts and banks located SW of the Gibraltar Strait and along the NW Iberian Peninsula.

Species complex 3: "*lopezfei*"

This species complex gathers the new species described below, provisionally ascribed to the genus *Hemicyclopora*, and *Escharella lopezfei* Souto, Berning & Ostrovsky, 2016. Both share many features, except for the number of spines in ovicellate zooids and the lack of a lyrula in the new species.

"*Hemicyclopora*" *celtica* n. sp.
(Fig. 6A-I; Tables 1; 3; 4)

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Type locality. — Armorican margin, NE Atlantic Ocean.

Type material. — **Holotype. NE Atlantic, France, Armorican margin** • 1 large colony, *c.* 100 autozooids with 15 ovicells; R/V *Thalassa*; Stn Z398; 47°36.0'N, 7°16.8'W; 330 m depth; 22.X.1973; on *Chlamys* shell, together with 1 ancestrula with a single daughter zooid; JGH leg.; Dre; MNHN-IB-2017-778.
Paratypes. NE Atlantic, France, Armorican margin • 1 large ovicellate colony, *c.* 70 autozooids; R/V *Thalassa*; Stn Z417, Little Sole Bank, 48°12.0'N, 9°09.5'W; 865 m depth; 24.X.1973; on *M. oculata* Linnaeus, 1758; Dre; JGH leg.; MNHN-IB-2017-779 • 1 ovicellate colony, coated for SEM examination; R/V *Thalassa*; Stn Z435, off Brittany, 48°39.7'N, 09°53.2'W; 1050 m depth; 26.X.1973; with *H. polita* on *Desmophyllum pertusum* (Linnaeus, 1759); Dre; JGH leg.; MNHN-IB-2017-780 • 1 ovicellate colony, *c.* 65 autozooids with 26 ovicells; R/V *Thalassa*; Stn Z398; same data as holotype; on shell; PMC. B35.5.5.2021.
Ireland • 3 small colonies; Trawler Heliotrope, Porcupine Seabight, 51°30'N, 11°30'W; 1000 m depth; II.1977: on shells and coral skeleton; Dre; JGH leg.; MNHN-IB-2017-781.

Other material examined. — **NE Atlantic – France, Armorican margin** • 1 colony; R/V *Thalassa*; Stn Z392, Armorican Margin; 47°34.9'N, 7°01.3'W; 390 m depth; 21.X.1973; MNHN • 3 colonies; R/V *Thalassa*; Stn Z398, same data as holotype • 1 colony; R/V *Thalassa*; Stn Z402, 47°39.5'N, 07°28.5'W; 450 m depth; 22.X.1973; MNHN • 1 colony; R/V *Thalassa*; Stn Z427; 48°27'N, 09°48.4'W; 330 m depth; 25.X.1973; on *D. pertusum*; MNHN • 1 colony; R/V *Thalassa*; Stn Z417; on *M. oculata*; same data as paratype MNHN-IB-2017-779 • 1 colony; R/V *Thalassa*; Stn Z435; 1050 m depth; on *D. pertusum;* same data as paratype MNHN-IB-2017-780.

Etymology. — Latin adjective, feminine of *celticus*, in reference to the frequency of this species in the Celtic Sea.

Diagnosis. — Autozooids bulged, relatively large, frontal shield with small, rounded granules, small marginal pores. Orifice terminal to subterminal, condyles prominent, with blunt tips, proximal edge convex, with a narrow gymnocystal rim, without proximal inner thickening. Oral spines typically eight, but sometimes six or seven in non-ovicellate zooids, always six in ovicellate zooids. Ovicells with a narrow gymnocystal proximal rim, lying on the distal, ooecium-builder autozooid. Ancestrula with opesia, cryptocyst and gymnocyst equally extended along central long axis, 11, 12 or 13 spines.

Description

Colony encrusting, unilaminar, small to medium-sized. Autozooids distinctly separated by deep grooves, laid out in quincunx, relatively large, oval to hexagonal, the width often much variable; frontal shield convex, evenly covered by small, rounded granules; marginal pores small (10-15 µm), arranged in a single row which becomes double laterally to the orifice (Fig. 6C-E). Basal pore-chambers oval to elongated, grouped by four to five in elongated windows, two disto-lateral and one distal (Fig. 6C-E). Distal wall subvertical (Fig. 6B-E). Orifice terminal or subterminal, as long as wide or slightly longer than wide in non-ovicellate zooids (Fig. 6C, D, G, H), wider in ovicellate zooids (Fig. 6C); proximal edge often clearly convex, i.e., in shape of a parabola (Fig. 6C, D, H), but sometimes nearly straight (Fig. 6B, G), without umbo or distinct cryptocystal thickening; primary orifice with prominent condyles, medium-sized, with blunt or triangular tips (Fig. 6D, G, H), inner side of the proximal edge smooth, without any gymnocystal thickening (Fig. 6I). Oral spines long, slender, with acute tip, seemingly composed of two jointed segments, peristomial bases conical and thick, eight in a majority of non-ovicellate zooids, but also seven or six (see below), always six in ovicellate zooids (Fig. 6). Ovicell adnate on the distal ooecium-producing daughter autozooid, apparently acleithral, endooecial surface granular as the frontal shield, with a narrow, smooth gymnocystal thickening bordering the proximal edge of the orifice (Fig. 6C, E, F). Ancestrula with six spines distally around the opesia and five, six or seven spines proximally around the cryptocyst; gymnocyst well developed (30-40% of total length along the proximo-distal axis).

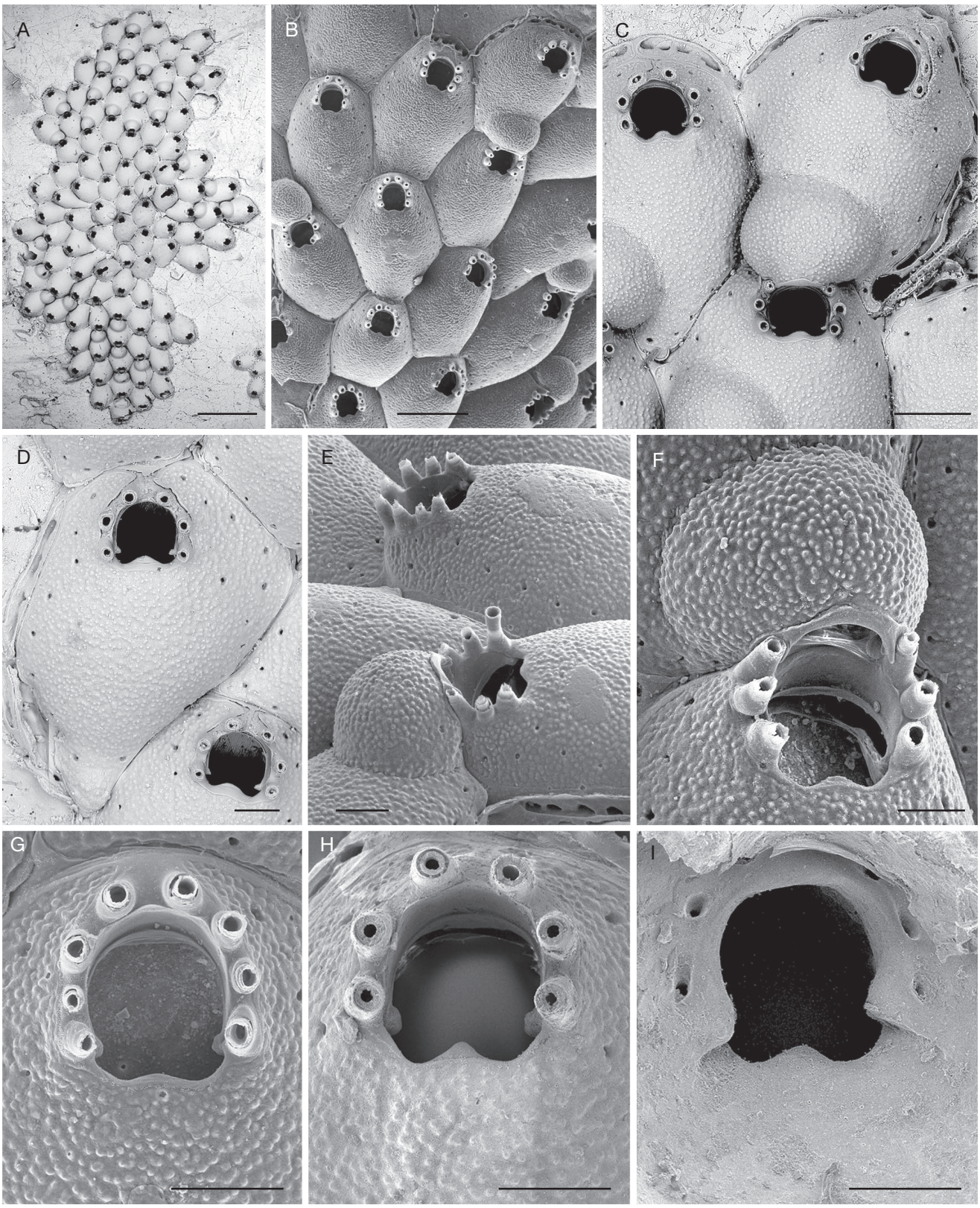

FIG. 6. — *Hemicyclopora celtica* n. sp.: **A**, colony with clustered ovicells; **B**, small portion of a colony, note the occurrence of six, seven or eight spines in non-ovicellate zooids, and 6 spines in ovicellate zooids; **C**, non-ovicellate and ovicellate zooids, all with six spines, ovicells associated with a distal autozooid; **D**, non-ovicellate zooids with small marginal pores, subterminal orifice edged by six spines, prominent condyles and markedly convex proximal edge; **E**, **F**, non-ovicellate and ovicellate zooids, note the granular frontal shield with tiny marginal pores, the terminal orifice of the non-ovicellate zooid with eight prominent basal parts of spines, and ovicells with endooecium formed by the distal autozooid; **G**, **H**, frontal view of two orifices, with eight spines and a moderately convex proximal edge (**G**) and six spines and a triangular proximal edge (**H**); **I**, inner side of an orifice with smooth surface and basal pores of spines. Origin: Armorican Margin, **A**, **C**, **D**, Thalassa Z398, paratype PMC.B35.2021; **B**, **E**-**I**, Thalassa Z435, paratype MNHN-IB-2017-780. Scale bars: A, 1 mm; B, 400 µm; C, 200 µm; D-F, G-I, 100 µm.

TABLE 3. — Features of three species of the complex *'similis'* (*Escharella similis* Ramalho, Rodríguez-Aporta & Gofas, 2022, original description by Ramalho *et al.* 2022 and present material; "*Escharella" massiliana* n. sp.; "*Hemicyclopora" pytheasi* n. sp.), and of "*H." celtica* n. sp. Abbreviations: **Acl**, acleithral; **BKz**, associated to a basal kenozoid; **crypt**, cryptocyst; **DAz**, associated to a distal autozooid; **Op**, opesia; **Rec**, recumbent.

Features	*E. similis* (original description)	*E. similis* (present material)	"*E.*" *massiliana* n. sp.	"*H.*" *pytheasi* n. sp.	"*H.*" *celtica* n. sp.
Frontal shield	Finely granular	Slightly hummocky	Slightly hummocky	Slightly hummocky	Markedly granular
Marginal pores	Small	Medium-Large (15-20 µm)	Large (20-35 µm)	Large (20-25 µm)	Small (10-15 µm)
Peristome proximal part	Small, triangular proximal umbo	Thick triangular umbo	No umbo	No umbo	No umbo
Orifice proximal edge	Well-developed peristome	Convex with rounded or pointed tip	Convex, hyperbolic, rounded tip,	Convex, hyperbolic, rounded tip	Convex, hyperbolic, rounded tip
Poster inner relief	Small, triangular lyrula	Marked thickening: distinct bulge	Thick, rectangular edge with a tiny bulge	No thickening, smooth surface	No thickening, smooth surface
Condyles	Not prominent	Not prominent	Not prominent	Not prominent	Prominent, thick
Oral spine number	8/8 - 1st pair converging	8/8 - 1st pair converging	8/8 - 1st pair converging	8/8 - 1st pair converging	8 (6-7)/6
Ovicell	BKz, W > L, Acl	Rec, BKz, W > L, Acl	Rec, BKz, W > L, Acl	Rec, BKz, W > L, Acl	DAz, W > L, Acle?
Ancestrula spines - size	Op: 8 + crypt: 5 L: 380 µm	Op: 6 + crypt: 5 L: 360 µm	Op: 5 + crypt: 5 L: 440 µm (Calvi)	Op: 4-5-6 + crypt: 5 L: 375-380 µm	Op: 6 + crypt: 5-6-7 L: 375-430 µm
Depth range	95-120 m	145-205 m	115-130 m	190-610 m	330-1050 m
Substrate	Erect bryozoans, serpulid tubes, shells	Calcareous biogenic debris	Calcareous biogenic debris	Stones, coral skeletons, shells	coral skeletons
Origin of material	Alboran Sea	Alboran Sea & G. of Cadiz	NW Mediterranean	Bay of Biscay, Armorican Margin	Armorican Margin

TABLE 4. — Geographical distribution of the examined species. Abbreviations: **HN**, *Hemicyclopora neatonensis* n. sp.; **HH**, *H. hexaspinae* n. sp.; **HD**, *H. discrepans*; **HC**, "*H." celtica* n. sp.; **HP**, "*H." pytheasi* n. sp.; **ES**, *Escharella similis* Ramalho, Rodríguez-Aporta & Gofas, 2022; **EM**, "*E." massiliana* n. sp.; **SD**, *Scutocyclopora dentata* (Lopez de la Cuadra & Garcia-Gomez, 1991) n. comb.; **Hsp1**, *Hemicyclopora* sp. 1; **Hsp2**, *Hemicyclopora* sp. 2.; **MED**, Mediterranean; **ATL**, Atlantic. **Alb**, Alboran Sea; **NW Med**, north-western Mediterranean; **CE Med**, central Mediterranean extended to the southern Tyrrhenian Sea and the Adriatic. **GuCa**, Gulf of Cadiz and close seamounts; **Ibe Atl**, Iberian Atlantic coast; **Bis Ar**, Bay of Biscay and Armorican margin; **Az Is**, Azores Islands.

	HN	HH	HD	HC	HP	ES	EM	SD	Hsp1	Hsp2
MED	×	×	×	–	–	×	×	×	–	–
ATL	–	×	×	×	×	×	–	–	×	×
Alb	–	–	×	–	–	×	–	×	–	–
NW Med	–	×	–	–	–	–	×	×	–	–
CE Med	×	×	–	–	–	–	–	×	–	–
Gu Ca	–	×	×	–	–	×	–	–	–	–
Ibe Atl	–	–	×	–	–	–	–	–	–	×
Bis Ar	–	–	–	×	×	–	–	–	–	–
Az Is	–	–	–	–	–	–	–	–	×	–

REMARKS

Morphological features

"Hemicyclopora" celtica n. sp. is characterized by the following features: 1) orifice with a distally-curved proximal edge whose convexity is more or less pronounced, and without umbo; 2) condyles prominent with triangular or rounded tips; 3) inner side of proximal part of primary orifice with smooth and flat surface; 4) invariably six spines in ovicellate zooids (117 ovicells examined); 5) ovicell recumbent on the proximal part of the frontal shield of the distally adjacent autozooid into which it is integrated; 6) ovicell opening edged with a smooth narrow gymnocystal rim, apparently acleithral, as suggested by examination of the holotype with a stereomicroscope and SEM photos of bleached specimens (Fig. 6F); however, accurate identification of the ovicell closure requires examination of living colonies and anatomical studies (Ostrovsky 2013); and 7) small marginal pores (Table 3). The number of spines in non-ovicellate zooids is usually eight but can be lower (Fig. 6B-E). In 160 non-ovicellate zooids from 12 colonies (7 localities, 330-1050 m) the number of spines was eight (45%), seven (39%) or six (16%). This variability is apparently not induced by factors of the microenvironment. This assertion is substantiated by colonies of similar size and condition occurring on the same fragment of coral skeleton (two cases: Thalassa Z402 and Z417) which presented inverse ranking in their proportions of spine numbers. The occurrence of eight spines in non-ovicellate zooids is assumed to be a fundamental trait of "*H." celtica* n. sp. while a lower number, six or seven spines, would result from an aborted development of the ovicell. The proportion of ovicellate zooids per colony can be high (Fig. 6A), but is in general moderate (about 8-17%; mean = 11 ± 4%). Another source of morphological variability in "*H." celtica* n. sp. is the shape of autozooids due to the great range of the autozooid width

(Table 1). This feature is reflected by the value of the coefficient of variation (SD × 100/X), which is higher for width than for length (18% vs 11%).

Taxonomic issues

"*Hemicyclopora*" *celtica* n. sp. is morphologically very close to *Escharella lopezfei* Souto, Berning & Ostrovsky, 2016, from the Galicia Bank (NE Atlantic). These species display several similar external features: same aspect of the frontal shield with small rounded granules and small marginal pores, same layout of the pore-chambers, proximal edge of the orifice and condyles similarly shaped, usually eight oral spines in non-ovicellate zooids, ovicells associated to the frontal shield of a distal autozooid. Obviously, the series of traits shared by these two entities raises the problem of their specific and generic assignment. The decision to separate our material from *E. lopezfei* at both species and genus ranks was justified by the conjunction of: 1) the constant difference in the number of oral spines in maternal zooids (always six in "*H".* *celtica* n. sp. and eight in *E. lopezfei*), verified in numerous colonies of "*H.*" *celtica* n. sp.; 2) the absence in the internal side of the orifice of "*H".* *celtica* n. sp., below its convex edge and above the level of condyles, of any thicknening forming a lyrula similar to the triangular denticle recorded in *E. lopezfei* and *E. praealta* (Calvet, 1907), a closely related species according to Souto *et al.* (2016); and 3) the distribution of these two entities in two distant geographical areas. Precise information on the shape of this denticle in *E. praealta* is provided by López de la Cuadra & Garcia Gómez (1993: fig. 2; 2001: fig. 1D-F) and unpublished SEM pictures of specimens of this species from Mediterranean cryptic habitats kept in our collection (JGH & AR). Undoubtedly, the structure of the orifice of *E. praealta* (and thus of *E. lopezfei*) differs from that of "*H.*" *celtica* n. sp. As stressed by Pica *et al.* (2022), "subtle differences are often considered species-specific" in Bryozoa according to the modern species taxon concept. Therefore, considering the lack of denticle or thickening in the orifice (Fig. 6I) which could play the role of a lyrula (Berning *et al.* 2014) and the uncertainty concerning the type of ovicell closure and its value as discriminating feature, "*H".* *celtica* n. sp. was arbitrarily attributed to the genus *Hemicyclopora*. Obviously, this species constitutes a 'borderline case', such as the entities forming the species complex *similis* (see below). Both cases challenge the distinction between the genera *Hemicyclopora* and *Escharella.*

The proximal edge of the orifice of "*H".* *celtica* n. sp. can be covered by a narrow rim of smooth gymnocystal calcification when it is convex (Fig. 6C, D, H), as in *E. lopezfei* (Souto *et al.* 2016: figs 78-79). However, this feature is not constant in "*H.*" *celtica* n. sp., and the whole poster edge can be covered by the secondary cryptocystal calcification of the frontal shield (Fig. 6E, G). Moreover, the convexity of the poster edge is variable and can be insignificant (Fig. 6B). When visible in frontal view, the gymnocystal rim of the convex poster is clearly continuous with the gymnocystal frame of the orifice, including the spines, and often remains visible distally, between the distalmost pair of spines (Fig. 6D). This structure indicates more a deficiency in cryptocystal calcification than the emergence of a lyrula-like denticle with a peristomial position. Thus, pending molecular analyses providing a clarification of the phylogenetic relationships between *Hemicyclopora* and *Escharella*, this new species is conditionally left in *Hemicyclopora*.

"Hemicyclopora" celtica n. sp. resembles "*H".* *pytheasi* n. sp. (see below) in having a similar orifice shape and eight oral spines in non-ovicellate autozooids (Figs 6B, G; 9F) but they clearly differ in the shape of the condyles and the type of ovicell (see below).

HABITAT DISTRIBUTION

"Hemicyclopora" celtica n. sp. is a deep-water species found in seven stations ranging from 330 m to 1050 m depth, mostly located close to or along the shelf break. Colonies encrusted shells, biogenic debris and were frequent on skeletons of 'cold-water' corals (*M. oculata* Linnaeus, 1758, *D. pertusum* (Linnaeus, 1759)). These fragmented coral skeletons indicate the proximity of banks built by these large branching scleractinians along the edge of the continental shelf where a strong thermocline is established and currents bring nutrient-rich waters (White & Dorschel 2010). In the three deepest stations (Thalassa Z417, Z435, Heliotrope: 865-1050 m), "*H".* *celtica* n. sp. co-occurred with *H. polita*, often on the same fragment of coral skeleton.

GEOGRAPHICAL DISTRIBUTION

"*Hemicyclopora*" *celtica* n. sp. was recorded in the northeast Atlantic from the Armorican margin to west Ireland (Table 3). However, its actual distribution is most likely wider, particularly in deep-water locations of the northern Atlantic.

Species complex 4: "*similis*"

A set of Mediterranean and Atlantic specimens with a common range of morphological traits constitutes a species complex displaying a remarkable example of a morphological cline. Three geographically separated morphotypes, differing mainly in the structure of their orifice, are considered to be different species, two of which being new to science. The orifice structure of these species poses the fundamental question of the boundary between the genera *Escharella* and *Hemicyclopora*.

Escharella similis
Ramalho, Rodríguez-Aporta & Gofas, 2022
(Figs 7A-F; 10G-I; Tables 1; 3; 4)

Escharella similis Ramalho, Rodríguez-Aporta & Gofas, 2022: 71, fig. 9, table 2.

Escharella sp. – Ramalho *et al.* 2020a: 106, table 2.

Hemicyclopora discrepans – Harmelin & d'Hondt 1992: 30 (part).

MATERIAL EXAMINED. — **Mediterranean, Alboran Sea** • 1 small colony; R/V *Cryos*, Balgim Stn DR130, 35°25.3'N, 4°19.3'W; 145 m depth; 15.VI.1984; on shell; Dre; JGH leg. • 4 colonies;

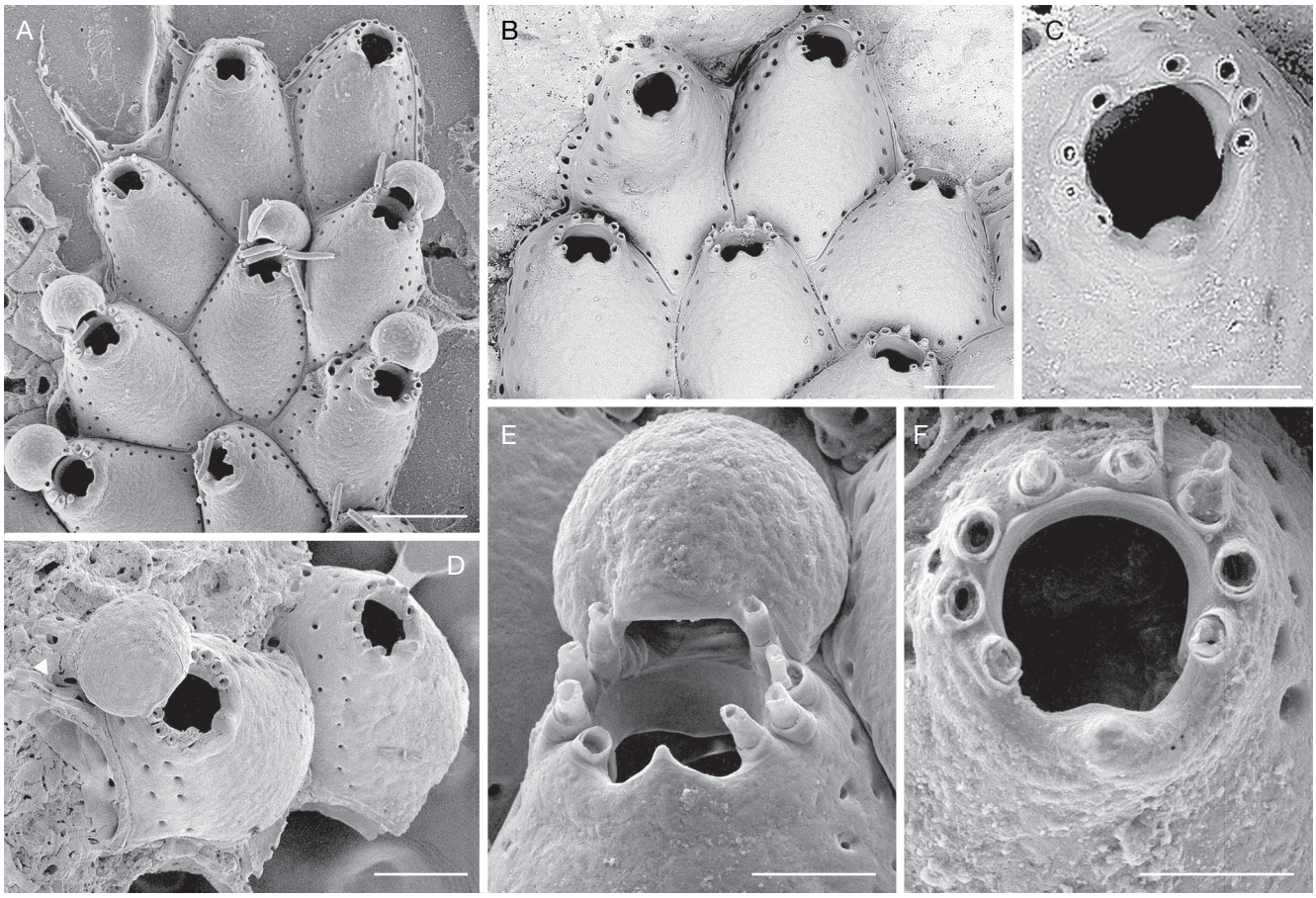

Fig. 7. — *Escharella similis* Ramalho, Rodríguez-Aporta & Gofas, 2022: **A**, edge of colony with five ovicellate zooids; **B**, non-ovicellate zooids with eight oral spines and a triangular proximal umbo; **C**, orifice of non-ovicellate zooid showing the lyrula-like inner bump and the proximal peristomial umbo in vertical view; **D**, two zooids, one with a terminal ovicell associated to a tiny basal kenozooid and orifice with a lyrula-like bump; **E**, distal part of an ovicellate zooid with 8 spines, a triangular peristomial umbo, and the orifice of the ovicell in an upper position; **F**, orifice of a non-ovicellate zooid with a low inner protuberance and step-shaped condyles. Origin: **A**, **B**, **C**, **E**, **F**, Alboran Sea, Balgim DW132; **D**, Atlantic, Gulf of Cadiz, Balgim DR42. Scale bars: A, 400 µm; B, D, 200 µm; C, E, F, 100 µm.

R/V *Cryos*, Balgim Stn DW132, 35°25.7'N, 4°18.8'W; 170 m depth; 15.VI.1984, on shells; Dre; JGH leg. • 1 ovicellate colony with ancestrula, *c.* 30 autozooids (4 ovicells) + 1 small colony, R/V *Cryos*, Balgim Stn DW134, 35°25.8'N, 4°17.0'W; 205 m depth; 15.VI.1984; on biogenic concretion and shell; Dre; JGH leg.; MNHN.
NE Atlantic, **Ibero-Moroccan Gulf** • 1 ovicellate colony, *c.* 60 autozooids + 1 small colony coated for SEM; R/V *Cryos*, Balgim Stn DR42, 35°54.5'N, 6°13.3'W; 135 m depth; 2.VI.1984; Dre; JGH leg.; MNHN.

Description

Colony encrusting, unilaminar, small. Autozooids moderately sized, elongated (L/W ratio = 1.46), distinctly separated by deep grooves, laid out in quincunx; frontal shield convex, smooth, slightly mamillated; marginal pores medium-sized (10-20 µm), distally arranged in a double or triple row and proximally in a single row (Fig. 7A, B, D). Pore chambers large, oval, numerous, laterally distributed in a single, long area (Fig. 7B, D). Distal wall subvertical (Fig. 7A, B, D). Orifice distal; primary orifice as long as wide, or slightly longer, the internal arch wide, with step-shaped proximal ends, i.e., without prominent condyles (Fig. 7C, F); a more or less prominent bulge on the inner side of the proximal edge of the orifice (Fig. 7C, D, F); outer side of the secondary orifice, forming a thick, convex lip with a short umbo, often triangular or conical (Fig. 7A-F). Oral spines eight in both ovicellate and non-ovicellate zooids, long (200-250 µm), articulated on thick, prominent bases, the proximalmost pair being clearly convergent (Figs 7C-E, F; 10G-H), the distalmost resting against the ovicell. Ovicells frequent, with endooecial surface similar to that of autozooids, without proximal protuberance, not closed by the operculum, recumbent against the vertical distal wall of the maternal zooid, produced by a small, poorly visible, basal kenozooid, often placed at the colony margin, or inserted between two distal zooids (Fig. 7A, D, E). Ancestrula relatively small, with oval opesia, proximal gymnocyst broad, five spines at the periphery of the cryptocyst and six spines (present material from Alboran Sea) distally bordering the opesia (Fig. 10I).

Remarks

Morphological features

The generic affiliation of *Escharella similis*, recently described from the Alboran Sea (Ramalho *et al.* 2022), was validated by the presence of a triangular denticle at a central place on the inner side of the orifice, below the convexity of the orifice outer edge (Ramalho *et al.* 2022, fig. 7D). Indeed, the

occurrence of a lyrula in the primary orifice determines the difference between *Escharella* and *Hemicyclopora* (Norman 1909: 308; Ryland 1963: 25, 27), and this triangular denticle has the same function as a typical anvil-shaped lyrula (Berning *et al.* 2014). The type of ovicell closure, cleithral vs acleithral, which also contributes to discriminating these two genera according to Hayward & Ryland (1999), is often not easy to identify. Colonies examined here, from the Alboran Sea and the near-Atlantic, show most diagnostic features of *E. similis* (proximal edge of orifice thick, convex and with a short, pointed umbo, non-prominent condyles, eight spines in both ovicellate and non-ovicellate zooids, kenozooidal ovicells). However, the lyrula-like protuberance in the inner side of the poster is much lower (Fig. 7C, D, F) than the triangular denticle originally described in this species. This difference likely denotes intraspecific variability, which also includes the number of ancestrular spines around the opesia, ranging from eight (Ramalho *et al.* 2022) to six (present material), while there are invariably five spines around the cryptocyst.

Habitat distribution

The nine examined colonies of *E. similis* were collected by dredging in soft bottoms within a relatively narrow depth range (135-205 m) across the outer continental shelf. The substrates were empty shells and biogenic concretions. These habitat features are similar to those indicated by Ramalho *et al.* (2022) for this species.

Geographical distribution

Escharella similis is known from several localities of the Alboran Sea (Harmelin & d'Hondt 1992, as *H. discrepans*; Ramalho *et al.* 2020a, as *Escharella* sp.; Ramalho *et al.* 2022; present material). Its occurrence in the Gulf of Cadiz, i.e., not far from the western entrance of the Gibraltar Strait might indicate the existence of a local population founded by the transfer of Mediterranean larvae to the Atlantic *via* the Mediterranean Outflow Water (MOW) (e.g. Singh *et al.* 2015).

"*Escharella*" *massiliana* n. sp.
(Fig. 8A-G; Tables 1; 3; 4)

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Hemicyclopora multispinata – Harmelin 1976: 230 (table 3).

Escharella octodentata – Madurell *et al.* 2013: 126 (table 2).

Type locality. — Marseille, Planier Canyon, Mediterranean Sea.

Type material. — **Holotype. Mediterranean – France** • 1 ovicellate colony, coated for SEM examination, *c.* 38 autozooids (16 ovicells); JGH-Stn 72.15; Marseille, Planier Canyon; 43°07'20"N, 5°12'51"E; 115 m depth; 18.IV.1972; on empty shell; Dre; JGH leg.; MNHN-IB-2017-774.
Paratype. Mediterranean – France • 1 small ovicellate colony; Corsica, off Calvi; R/V *Catherine Laurence*; Bracors-3, Stn CL 74-84; 42°47'32"N, 9°08'17"E; 110-150 m depth; VII.1984; on biogenic debris; Dre; Fredj & Di Geronimo leg.; PMC. B36; 5.5.2021.

Other material examined. — **Mediterranean – France** • 1 small, dead colony; JGH-Stn 72.15; same data as holotype; MNHN • 2 colonies; Marseille-Cassis, Cassidaigne Canyon, JGH-Stn 72.9; 43°08'53"N, 5°25'55"E; 115-130 m depth; 22.III.1972; Dre; JGH leg.; MNHN • 1 small colony; Marseille-Cassis, Cassidaigne Canyon; 130 m depth; 19.IV.1971; on leather debris; Dre; H. Zibrowius leg.; MNHN.
Spain • 1 ovicellate colony; Catalonia, off Cap de Creus; INDEMARES 1, Stn 12; 42°21'36.0"N, 3°19'37.2"E; 148 m depth; 23.IX.2009; detrital sand; 2 SEM photos, T. Madurell & M. Zabala leg.; MNHN.

Etymology. — From Massilia, ancient Latin name of Marseille.

Diagnosis. — Autozooids separated by deep grooves, frontal shield convex with slightly hummocky surface, marginal pores large. Distal and lateral walls subvertical. Orifice terminal, slightly longer than wide, proximal edge a flat, thick, parabolic convexity, bearing a small bump on the inner side, condyles indistinct, very short and blunt. Oral spines eight in both ovicellate and non-ovicellate zooids. Ovicells not closed by operculum, attached to distal wall of maternal zooid, kenozooidal; endooecium without proximal prominence, with similar surface relief as frontal shield. Ancestrula with opesia, cryptocyst and gymnocyst equally extended, ten spines (5 + 5).

Description

Colony encrusting, unilaminar, small. Autozooids elongated (L/W ratio = 1.56), oval to pentagonal, distinctly separated by deep grooves, laid out in quincunx; frontal shield uniformly convex except for the proximal raising end, smooth, slightly mamillated; marginal pores large (20-40 µm) in a single row + 1-2 in an upper position below the proximal edge of orifice. Distal wall vertical (Fig. 8). Orifice distal, as long as wide, or slightly longer; internal arch wide, with indistinct short and blunt condyles at proximal ends (Fig. 8A, F); proximal edge clearly convex, with rounded (parabolic) tip, very thick with a square rim covered by a gymnocystal layer, uniformly flat on the upper side and with a small hump on the inner side. Oral spines eight in ovicellate and non-ovicellate zooids, articulated on thick, prominent bases, the proximalmost pair clearly convergent (Fig. 8A-C), the distalmost resting against the ovicell. Ovicells frequent (42% of zooids in the holotype), globular, acleithral, attached to the vertical distal wall of the maternal zooid, associated to a basal ooecium-producing kenozooid, frequently at the colony margin or inserted between two distal autozooids, with some marginal pores visible at the base of the endooecium and 2-3 pore-chambers below them belonging to the kenozooidal base; surface topography of the endooecium similar to that of the frontal shield; well calcified floor visible in ovicell under construction (Fig. 8A-C, G). Ancestrula with 10 spines, i.e., five spines around both the opesia and the cryptocyst (one case observed, Fig. 8D).

Remarks

Morphological features and taxonomic issues

This species shares many morphological features with *E. similis*, but differs from it essentially in the structure of the orifice. In *"E." massiliana* n. sp. the proximal edge of the orifice is also typically convex, but with a square rim, uniformly thick and flat, without an umbo on the upper side, but with a very low protuberance on the inner side, only visible with SEM (Fig. 8A, E, F). This tiny bump may be considered as a

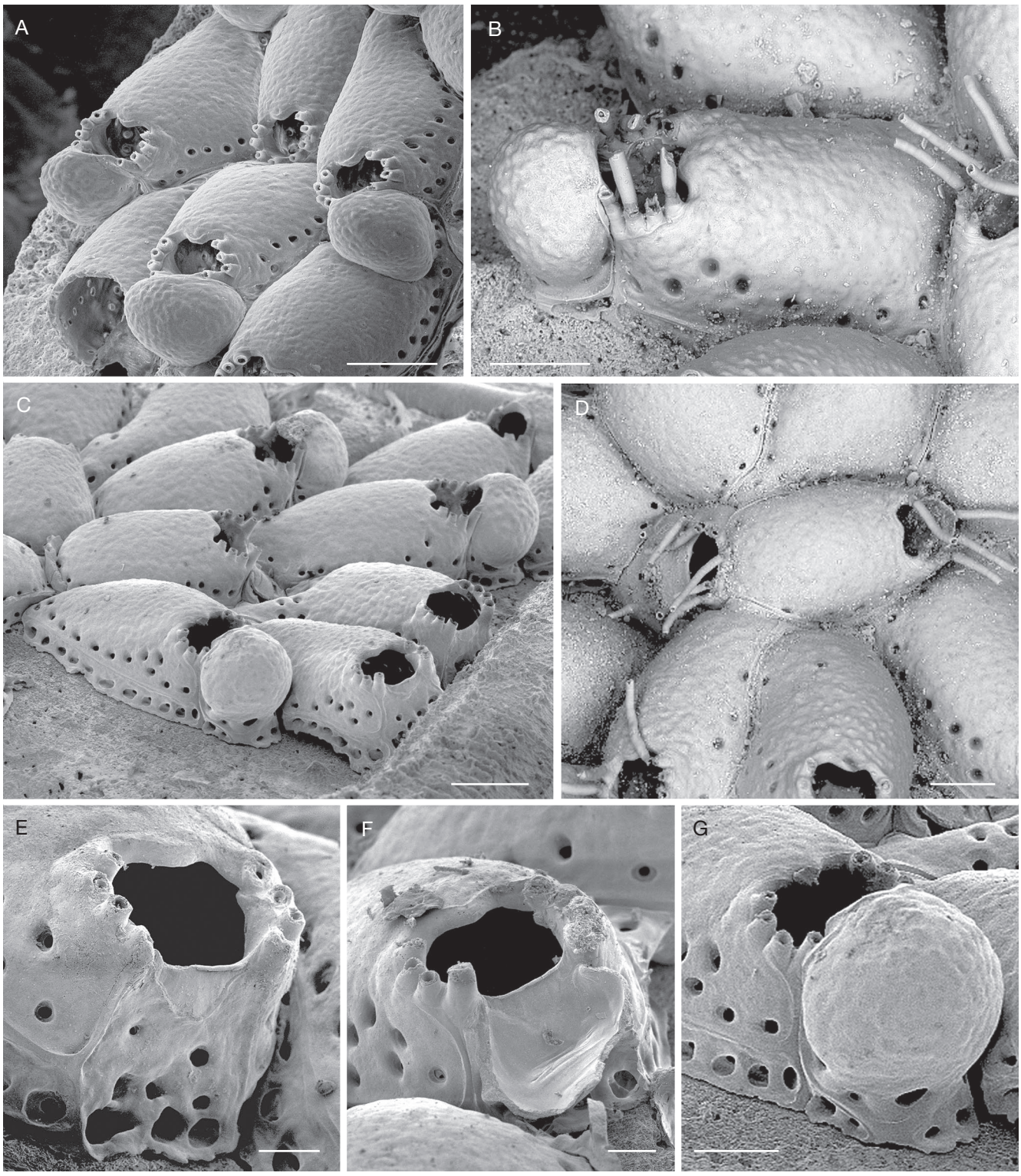

FIG. 8. — "*Escharella*" *massiliana* n. sp.: **A**, zooids of the colony edge with hummocky frontal shield and three terminal, recumbent ovicells; **B**, lateral view of an ovicellate zooid, note the small basal kenozooid and the large marginal pores; **C**, **E**, **F**, **G**, edge of the same colony as **A**, with different stages in the ovicell construction involving a small basal kenozooid, note the thickness of the proximal edge of the orifice; **D**, ancestrula and periancestrular zooids. Origin: **A**, **C**, **E**-**G**, Marseille, Planier canyon, holotype MNHN-IB-2017-774; **B**, **D**, Calvi, paratype PMC. B36. 5.5.2021. Scale bars: A, B, C, D, 200 µm; E, F, 50 µm; G, 100 µm.

primary lyrula, characterizing an intermediate stage between the genera *Escharella* and *Hemicyclopora*. This species was thus doubtfully placed in *Escharella*. The average length and width of autozooids, and the range of these dimensions (Table 1) are smaller in *"E." massiliana* n. sp. than in *E. similis* and the L/W ratio is higher, i.e., autozooids are more elongate. How-

ever, this comparison is based on few data. The number of ancestrular spines around the opesia is also different (five vs eight in *E. similis*).

Habitat distribution

The six examined colonies encrusted biogenic debris in four stations with similar habitat traits: detrital soft bottoms within the same depth range (110-150 m).

Geographical distribution

The present records of *"E." massiliana* n. sp. only concern two areas in the north-western Mediterranean: Marseille (Provence) and Calvi (Corsica).

"*Hemicyclopora*" *pytheasi* n. sp.
(Fig. 9A-G; Tables 1; 3; 4)

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?*Hemicyclopora multispinata* – Hayward & Ryland 1999, fig. 46D.

Type locality. — La Chapelle Bank, Armorican margin.

Type material. — **Holotype. NE Atlantic. France** • 1 large colony, *c.* 80 zooids with a great proportion of ovicells (> 50%) and large interzoecial kenozooids; R/V *Jean Charcot*; Biaçores Stn 259; off Brittany, La Chapelle Bank; 48°01.3'N, 7°51.5'W; 190 m depth; 19.XI.1971; on shell; Dre; H. Zibrowius leg.; MNHN-IB-2017-770. **Paratypes. NE Atlantic. France** • 1 large colony, *c.* 60 autozooids (18 ovicells) + 2 ancestrulae budding 1 and 3 daughter zooids; R/V *Jean Charcot*; Biaçores Stn 259, off Brittany, La Chapelle Bank; 48°01.3'N, 7°51.5'W; 190 m depth; 19.XI.1971; on shell; Dre; H. Zibrowius leg.; PMC. B33.5.5.2021 • coated fragment of colony and detached orifices, same origin as holotype; MNHN-IB-2017-775 • 3 ovicellate colonies; JPL-Stn G61 (710), Bay of Biscay, 44°54'N, 02°11'W; 200 m depth; III.1967; on pebble; Dre; J. P. Lagardère leg.; MNHN-IB-2017-776 • juvenile colony with ancestrula, coated, same origin as holotype; MNHN-IB-2017-777.

Other material examined. — **NE Atlantic. France** • 1 colony; R/V *Jean Charcot*; Biaçores Stn 257, 47°57'N, 07°51.5'W; 335 m depth; 19.XI.1971; on *Madrepora oculata*; Dre, H. Zibrowius leg.; MNHN • 1 colony; R/V *Jean Charcot*; Biaçores Stn 259; same data as holotype and paratype PMC. B33.5.5.2021; on bivalve shell.

Etymology. — In honour of Pytheas, famous antique astronomer and sailor, citizen of Massalia (ancient Greek name of Marseille), who explored the northern seas during the 4th century B.C., and in reference to the geographical distribution of this species.

Diagnosis. — Autozooids separated by deep grooves, frontal shield convex with mamillate texture, marginal pores large. Distal wall subvertical. Orifice terminal, condyles indistinct and relatively square, without lyrula-like protuberance; proximal edge of secondary orifice clearly convex with round top. Oral spines eight in both ovicellate and non-ovicellate zooids; spines of the proximalmost pair clearly converging; in ovicellate zooids, bases of the distal pair adjoining the ovicell. Ovicell apparently acleithral, attached to distal wall of maternal zooid, terminal and produced by a small, basal kenozooid; endooecium smooth, without proximal thickening. Large, interzooidal, porous kenozooids occasionally present. Ancestrula with opesia, cryptocyst and gymnocyst equally extended, five spines around the cryptocyst, 4-6 spines around the opesia.

Description

Colony encrusting, unilaminar, small to medium-sized. Autozooids large, elongated (L/W ratio = 1.48), distinctly separated by deep grooves, laid out in quincunx; frontal shield convex, smooth, slightly mamillated; marginal pores large (15-30 µm), distally arranged in a double or triple row and proximally in a single row (Fig. 9A-C). Distal wall subvertical (Fig. 9B, C, E), its inner side visible in ovicellate zooids as a broad, vertical frame below the ovicell opening and between the distalmost pair of spines (Fig. 9D). Orifice distal; primary orifice as long as wide or slightly longer, its calcified ring with step-shaped proximal ends, i.e., without prominent condyles; inner proximal side smooth and without any protuberance (Fig. 9G); proximal edge of secondary orifice clearly convex, with round top and without umbo (Fig. 9B-D, F). Oral spines eight in ovicellate and non-ovicellate zooids, long (200-250 µm), huddled together, with thick, prominent bases, the proximalmost pair clearly convergent (Fig. 9D, F). Ovicells frequent, globular, sometimes remarkably wide, with surface structure of endooecium similar to that of frontal shield, without proximal protuberance, seemingly not closed by the operculum, attached to the vertical distal wall of the maternal zooid, apparently terminal and free (Ostrovsky 2013: 125, 129), but produced by a small, poorly visible, basal kenozooid at the colony margin (Fig. 9B, C). Pore chambers numerous. Large interzooidal kenozooids occasional, with porous frontal shield (Fig. 9D). Ancestrula with proximal rim of opesia concave, proximal gymnocyst broad, five spines at the cryptocyst periphery, and four, five or six spines bordering the opesia (Fig. 9E).

Remarks

Morphological features

The morphological features of "*H.*" *pytheasi* n. sp. are very similar to those of *E. similis* and "*E.*" *massiliana* n. sp., except for the structure of the primary orifice. Unlike other species of the same species complex, the internal side of the convex proximal edge of the orifice of "*H.*" *pytheasi* n. sp. is smooth, without any bulge that could be identified as a lyrula (Fig. 9G). In the absence of such structure, does the convex edge of the orifice play the function of a lyrula and can stop the open operculum in a vertical position? The respective position of the maternal orifice and the ovicell suggests that the latter is acleithral (Fig. 9C, D), as in typical *Escharella* species. However, this feature remains incertain without specific anatomical investigation. Therefore, pending a molecular approach, this species was placed in the genus *Hemicyclopora* in quotation marks. Colonies of "*H*". *pytheasi* n. sp. often have a great proportion of ovicellate zooids, e.g. > 50% in the holotype specimen, and even more in two other colonies (Stn JPL-G61: 59%; Biaçores Stn 259: 74%). This high fertility was observed in most colonies (mean: 39 ± 24%) and likely has a specific significance. The occurrence of large interzoecial kenozooids (Fig. 12D) has been only observed in specimens from the Armorican Margin (Biaçores st. 259).

Taxonomic issues

"*Hemicyclopora*" *pytheasi* n. sp. shows obvious morphological similarities with "*H.*" *celtica* n. sp. with which it can coexist

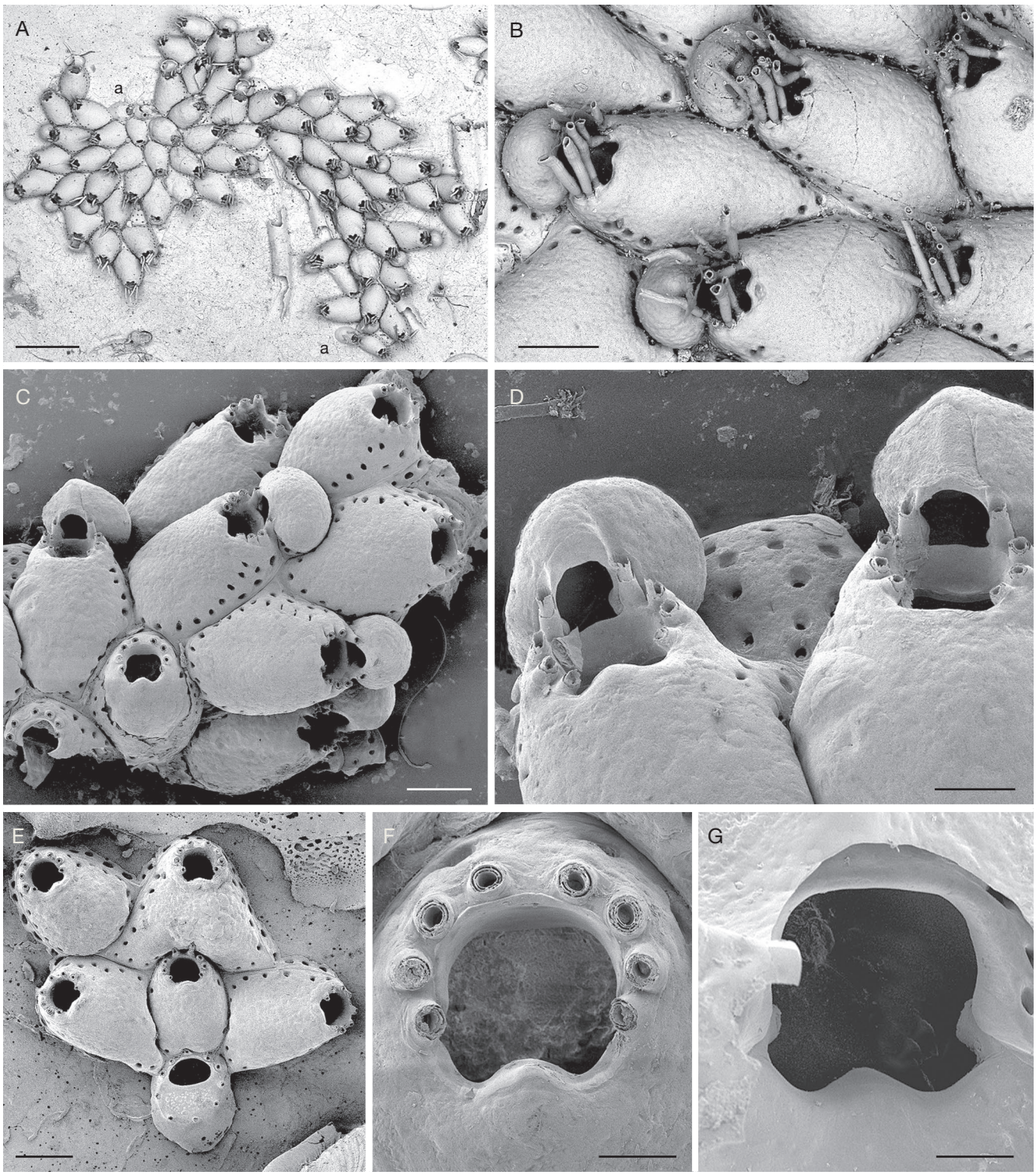

FIG. 9. — *"Hemicyclopora" pytheasi* n. sp.: **A**, colony with many ovicells and its ancestrula; another ancestrula with a single daughter zooid, both marked (a); **B**, ovicellate zooids with converging oral spines; **C**, ovicellate and non-ovicellate zooids, with a small zooid regenerated inside a broken cystid; **D**, distal part of two ovicellate zooids and an interzooidal porous kenozooid; **E**, juvenile colony with ancestrula; **F**, distal part of a non-ovicellate zooid, orifice with typically convex proximal edge; **G**, inner side of an orifice showing the lyrula-like suboral umbo and three basal pores of spines (partly visible on the right side). Origin: Atlantic, Armorican margin; Biaçores Stn 259; **A**, **B**, paratype PMC-B33.5.52021; **C**, **D**, **F**, **G**, paratype MNHN-IB-2017-775; **E**, paratype MNHN-IB-2017-777. Scale bars: A, 1 mm; B, C, E, 200 µm; D, 100 µm; F, G, 50 µm.

along the Armorican margin. These species share the same shape of the secondary orifice and the presence of eight spines in non-ovicellate zooids. However, "*H.*" *pytheasi* n. sp. differs in the external aspect of the frontal shield and endooecium (mamillated vs granular), the size of the marginal pores (large vs tiny), the condyles (step-shaped vs protuberant), and the

ovicellate zooids. The latter differ in the number of spines in ovicellate zooids (eight in "*H.*" *pytheasi* n. sp. vs six in "*H.*" *celtica* n. sp.), and the building of ovicells, which involves a basal kenozooid ("*H.*" *pytheasi* n. sp.), instead of a distal autozooid ("*H.*" *celtica* n. sp.) (Table 3). The co-occurrence of these two species in the same depth zone of the same geographical area (Armorican margin) confirms the validity of these observed differences for discriminating them at species level. The specimen figured without indication of origin by Hayward & Ryland (1999: fig. 46D) and attributed to *H. multispinata* shows some typical features of "*H.*" *pytheasi* n. sp.: proximal edge of the orifice typically convex, ovicellate zooid with eight spines, and large marginal pores. On the other hand, the drawing illustrating *H. multispinata* by the same authors (Hayward & Ryland 1999: fig. 49) might be attributed as well to "*H.*" *pytheasi* n. sp. or to "*H.*" *celtica* n. sp. because of the lack of information concerning the ovicellate zooids and the shape of condyles.

Habitat distribution

Colonies of "*H.*" *pytheasi* n. sp. encrusted small substrates (empty shells, fragmented skeletons of *Madrepora oculata*, pebbles) at the edge of the continental shelf (190-335 m).

Geographical distribution

The examined material came from the Armorican margin and the Bay of Biscay.

Additional *Hemicyclopora* species

Hemicyclopora hexaspinae n. sp.
(Figs 10D-F; 11A-G; 12A-E; Tables 1; 2; 4)

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Hemicyclopora discrepans – Harmelin 1997: 144, table 2.

Hemicyclopora multispinata – Di Geronimo *et al.* 1990: table 1.

Type locality. — France, La Ciotat, 3PP Cave.

Type material. — **Holotype**. **Mediterranean, France** • 1 colony, *c.* 20 zooids (5 ovicells) + ancestrula; La Ciotat, 3PP Cave, 25 m depth from entrance; 73°09'47.9"N, 5°35'59.8"E; 20 m depth; 15.I.1993; Div.; JGH leg.; MNHN-IB-2017-771.
Paratypes. **Mediterranean, France** • 1 coated colony, *c.* 23 autozooids (4 ovicells); La Ciotat, 3PP Cave, 40 m from entrance; 73°09'47.9"N, 5°35'59.8"E; 21 m depth; 28.XI.1991; Div.; JGH leg.; MNHN-IB-2017-772 • 1 coated colony, *c.* 30 autozooids (1 ovicell); Marseille, 'Calanques' Coast, Cape Morgiou Cave; 73°12'05.8"N, 05°27'08.11"E; 27 m depth; 26.IX.1967; Div.; JGH leg.; MNHN-IB-2017-773.
Italy • 1 ovicellate colony with ancestrula; Ustica Island, Apollo Bank; *c.* 38°7'N, 13°1'E; 60 m depth; VI.1986; Dre; AR leg.; PMC. B32.12.12.2020.

Other material examined. — **Mediterranean, France** • 1 colony; Marseilles, 'Calanques' Coast, Eissadon Cave; 73°12'07"N, 5°29'24.2"E; 5 m depth; 17.VI.1992; Div.; JGH leg.; MNHN • *c.* 13 colonies (12 sampled spots); La Ciotat, 3PP Cave; 19-25 m depth; same site as for holotype; from XI.1991 to XI.1994; Div.; JGH leg.; MNHN. **Italy** • 7 colonies + fragments; S Tyrrhenian Sea, Ustica Island, Apollo Bank, same data as for paratype PMC. B32.12.12.2020; PMC Rosso-Collection I. H. B.91a • 4 colonies; W Ionian Sea, SE Sicily, Catania, off Acitrezza Marine Protected Area, 110 m depth (2 col.); Ciclopi survey; VII.2000; Stn 8I; 95 m depth (1 col.) & Stn 9G; 63 m depth (1 col.); coarse DC with Würmian biogenic remains; Dre; AR leg.; PMC Rosso-Collection I. H. B.91b. **Atlantic Ocean, western approach of Gibraltar Strait** • 1 small colony on shell; R/V *Cryos*; Balgim Expedition; Stn DR42; 35°54.5'N, 6°13.3'W; 133-137 m depth; 2.VI.1984; Dre; JGH leg.; MNHN • 2 small colonies; R/V *Cryos*; Balgim Expedition; Stn DW 43; 35°54.1'N, 6°14.5'W; 150 m depth; 2.VI.1984; Dre; JGH leg.; MNHN • 1 small colony on shell; R/V *Cryos*, Balgim Expedition; Stn DR49; 35°53.0'N, 6°32.8'W; 518-524 m depth; MNHN.

Etymology. — From Latin *hexa* (six) and *spinae* (spines), in apposition, for the typical number of oral spines of this species in both ovicellate and non-ovicellate autozooids.

Diagnosis. — Autozooids bulged, frontal shield finely granular with usually small to medium-sized marginal pores. Orifice terminal, condyles prominent with blunt tips, proximal edge more or less concave, without suboral umbo. Oral spines six in both non-ovicellate and ovicellate autozooids with the proximal pair arched inwardly and the distal ones outwardly. Ovicell presumably semicleithral, attached to the distal wall of the maternal zooid, produced by a small, basal kenozooid, narrower than autozooids; endooecium finely granular, without proximal thickening. Ancestrula with an extended cryptocyst and a narrow proximal gymnocyst, and 10-11 spines, four of them edging the cryptocyst.

Description

Colony encrusting, unilaminar, small (in most cases, less than 30 zooids). Autozooids relatively small (Table 1), longer than wide (L/W: 1.31), relatively poorly calcified, cystid with maximum thickness at orifice level; frontal shield markedly bulging, finely granular (Figs 11A, D; 12B); marginal pores very small and poorly visible in specimens from caves (about 5-7 µm; Fig. 11A-C) or larger in colonies from open soft bottoms (20-25 µm; Figs 11D, E; 12B); disto-lateral and distal walls subvertical, with numerous small basal pore chambers (Fig. 11A-D). Orifice distal, slightly broader than long; proximal edge (= poster) slightly concave or nearly straight, without proximal umbo or thickened rim; condyles triangular, slightly curved proximally, located just above the poster corners (Figs 10D, E; 11A, F). Six oral spines in both non-ovicellate and ovicellate autozooids, exceptionally seven in non-ovicellate zooids (about 2% in available samples from Mediterranean caves), relatively short, with an open tip, articulated on thick, barrel-shaped bases (Figs 10D; 11E-G); in both non-ovicellate and ovicellate zooids, spines of the proximal pair arched inwardly while spines of the distal pair arched outwardly (Fig. 11A-G). Ovicells kenozooidal, present at the colony margin (Fig. 11A-E), attached to the distal wall of the maternal zooid and on a tiny kenozooidal base, ovoid, significantly narrower than the maximum width of the maternal autozooid, presumably semicleithral (Fig. 11C); endooecium finely granular, imperforate, a small, triangular labellum sporadically present, with smooth surface suggesting a gymnocystal origin (outer fold of the ooecium floor?). Ancestrula with typical structure, opesia

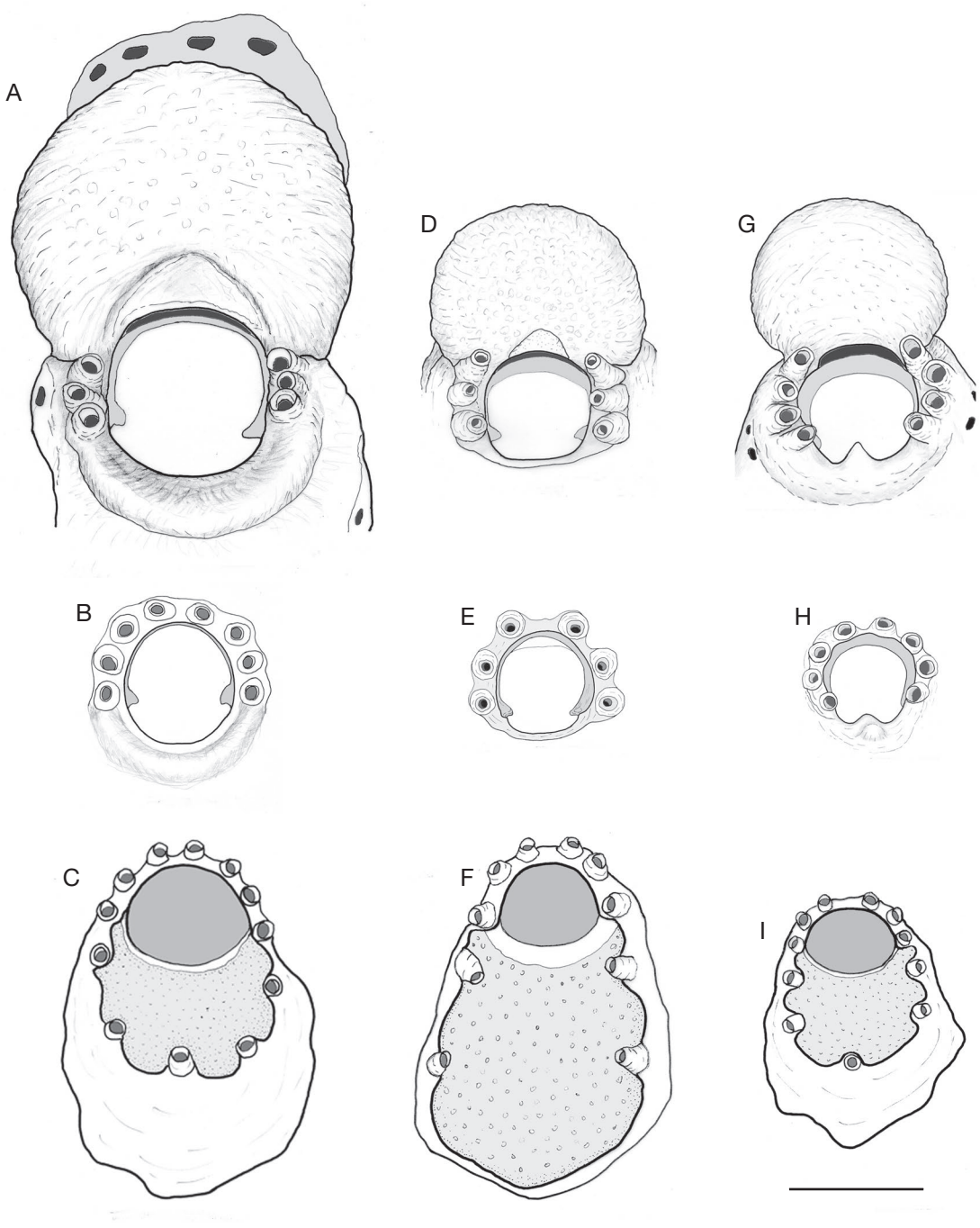

FIG. 10. — Distal part of ovicellate and non-ovicellate zooids, and ancestrulae, all at the same scale: **A**-**C**, *Hemicyclopora neatonensis* n. sp.; **D**-**F**, *H. hexaspinae* n. sp.; **G**- **I**, *Escharella similis* Ramalho, Rodríguez-Aporta & Gofas, 2022. Drawings from SEM pictures and examination under stereomicroscope. Origin: **A**-**C**, Sicily; **D**-**F**, Provence; **G**-**I**, Alboran Sea. Scale bar: 200 µm.

with a concave proximal border rimmed by a narrow band of smooth calcification, cryptocyst particularly extensive, and gymnocyst wide laterally but drastically narrowing proximally, four spines bordering the distal half of the cryptocyst and six, exceptionally seven, opesial spines; one autozooid budded distally (Figs 10F; 12B, D). The ancestrula or an autozooid can occasionally produce a tubule from a lateral pore chamber, at the extremity of which an autozooid may be budded (Fig. 12C-E).

REMARKS

Morphological features

The most obvious distinctive features of *H. hexaspinae* n. sp. are: 1) the number of oral spines, six in both ovicellate and non-ovicellate zooids, which are articulated on particularly large, barrel-shaped bases; 2) the distinctly terminal orifice, with a strait or slightly concave proximal edge, without a proximal umbo; 3) the very convex frontal shield of autozooids; 4) the downcurved, triangular shape of the condyles;

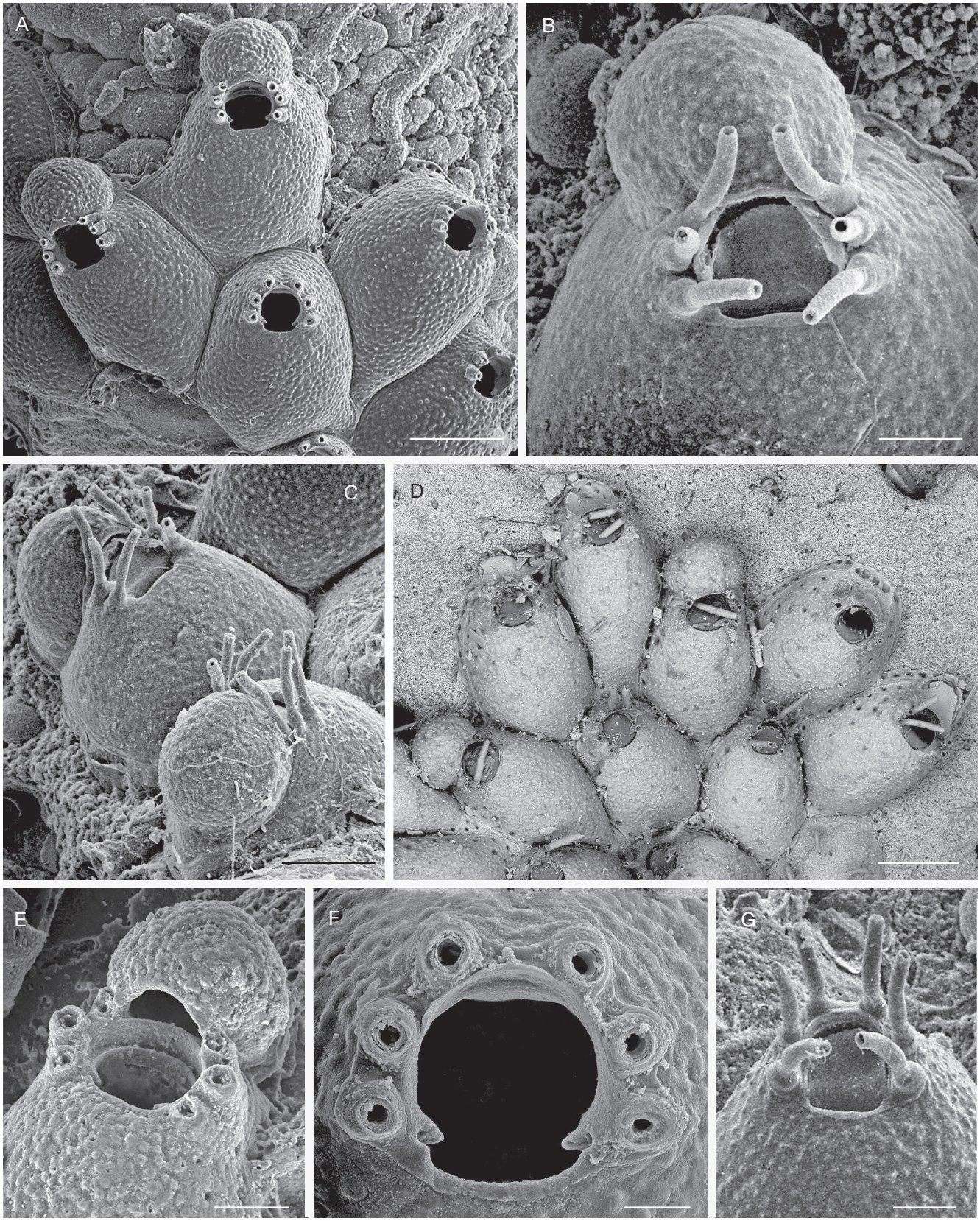

FIG. 11. — *Hemicyclopora hexaspinae* n. sp.: **A**, ovicellate and non-ovicellate zooids at the edge of a small colony, with frontal shield bulged and granular; **B**, **C**, ovicellate zooids: terminal ovicells with six curved spines, attached to maternal distal wall and lying on a small kenozooid responsible for ovicell formation; **D**, colony edge with six ovicells: two fully grown and four under construction from a basal kenozooid; **E**, ovicellate zooid with thick bases of spines; **F**, orifice of non-ovicellate zooid: six basal parts of spines, concave proximal edge and prominent condyles; **G**, shape of the oral spines in a non-ovicellate zooid:. Origin: **A**, **B**, **F**, **G**, paratype MNHN-IB-2017-772, Provence, 3PP Cave; **C**, paratype MNHN-IB-2017-773, Provence, Cape Morgiou Cave; **D**, paratype PMC.B29.8.11.2020; Ustica Is., Apollo Bank; **E**, Atlantic, Balgim DR49. Scale bars: A, D, 300 µm; B, E, G, 100 µm; C, 200 µm; F, 50 µm.

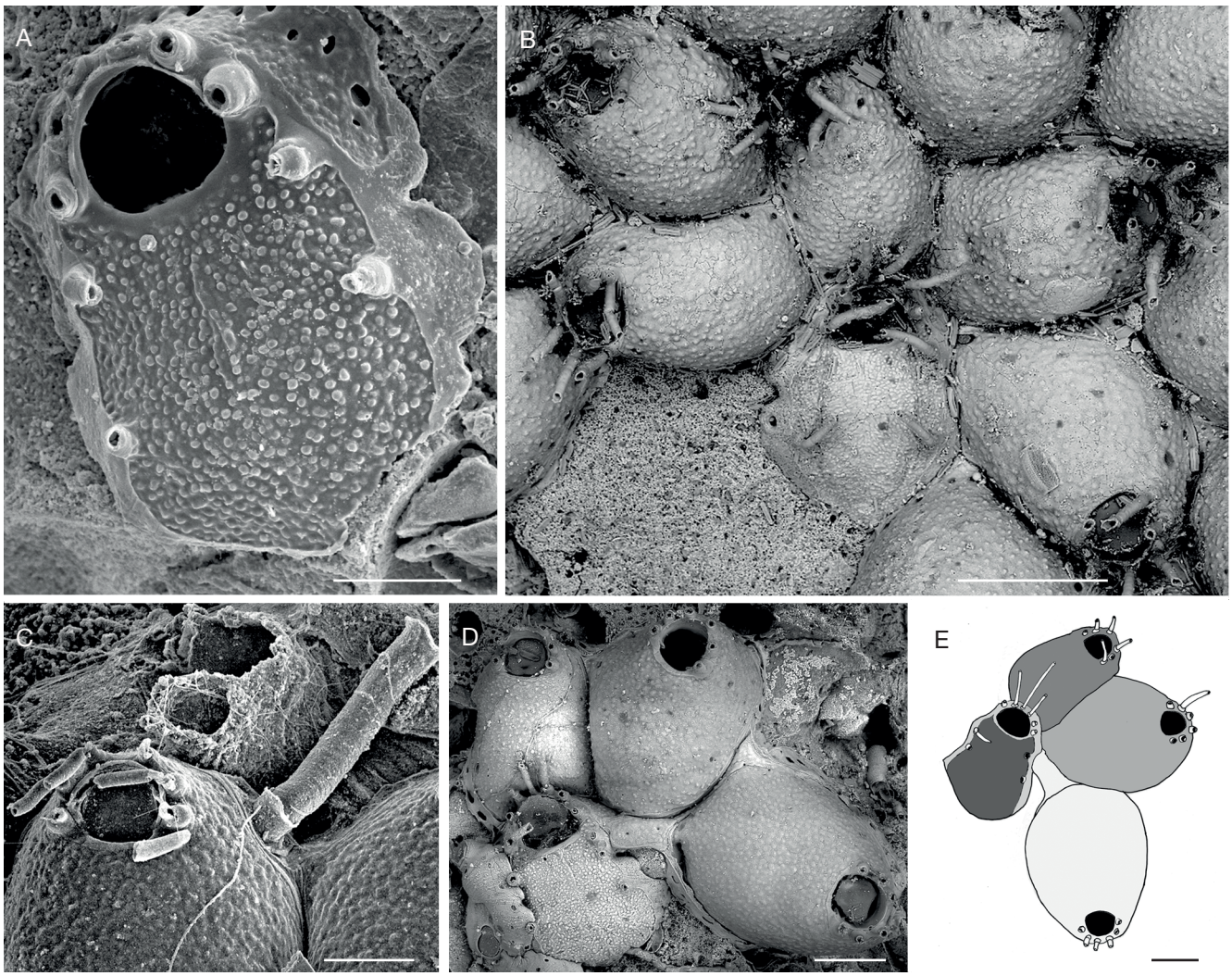

Fig. 12. — *Hemicyclopora hexaspinae* n. sp.: **A**, ancestrula, note the large size of the cryptocyst; **B**, ancestrula and daughter zooids; **C**, autozooid with a tubule budded from a distolateral pore-chamber; **D**, ancestrula with three successive daughter zooids, the third one with a basal tubular part budded by the ancestrula; **E**, same ancestrula and zooids, sketch from stereomicroscopic examination: darkening by Mn-Fe oxides increasing from the youngest zooid to the ancestrula attesting to the very slow growth in confined dark caves. Origin: **A**, **C**-**E**, Provence, 3PP Cave; **B**, Ustica Island, Apollo Bank. Scale bars: A, 50 µm; B, 300 µm; C-E, 100 µm.

5) the comparably small, nearly isodiametrical ovicells produced by a tiny basal kenozooid; and 6) the ancestrula with a broad cryptocyst and a very narrow proximal gymnocyst. The small size of colonies with a high frequency of ovicells and the predominantly peripheral position of the latter are also typical. Samples from the large, dark 3PP cave attest to these features: the number of autozooids of 17 collected colonies ranged from three to 30 (mean = 13 ± 6 AZ, but many zoecia were empty), with a high proportion of ovicellate ones (71%). The occurrence of ovicells is predominant at the colony margin (74%). This peripheral location may indicate a growth stop of the colony due to insufficient energy allocation after reproduction, a condition observed in dark caves when food inputs are sporadic (Harmelin 1997). Specimens from soft bottoms in the open sea differ from those from dark caves essentially in the larger size of their marginal pores. This difference might be related to the dynamics of growth in these two environments, which is very slow in dark caves with poor exchanges with the open sea (Harmelin 2000, see below). The semicleithral type of the ovicell closure was identified by A. Ostrovsky (personal communication to JGH, 18.X.2022) from a SEM picture (Fig. 11C) showing an ovicell partially closed by the ooecial vesicule and a sclerite.

Taxonomic issues

Hemicyclopora hexaspinae n. sp. differs from Mediterranean congeners particularly in the number of oral spines, shape of the orifice, and type of ovicells (Table 2). This species has several characters in common with *H. discrepans* (Table 2): a bulged frontal shield with a granular texture, absence of a thickening or umbo proximally to the orifice and on the ovicell, protuberant triangular condyles, poster concave or straight, oral spines with very thick bases, distal wall subvertical,

ovicell apparently terminal but associated with a small basal kenozooid. However, *H. hexaspinae* n. sp. differs clearly from *H. discrepans* in having constantly six spines instead of eight in non-ovicellate zooids, and an ancestrula with the proximal gymnocyst poorly developed and the cryptocyst area widely extended proximally (Figs 10F; 12A). Among other Recent *Hemicyclopora* species, the boreal *H. emucronata* (Smitt, 1872), also has six oral spines in both ovicellate and non-ovicellate zooids (Smitt 1872: fig. 27; Kluge 1962: fig. 270). However, available SEM pictures of Smitt's type and of a specimen from Spitsbergen (Kuklinski *et al.*, website *Atlas of Arctic Bryozoa*, accessed on 30.IX.2020) show that *H. emucronata* clearly differs from *H. hexaspinae* n. sp. The former has zooids with a flatter frontal shield, the ovicell endooecium is continuous with the frontal shield of the distal zooid, and the ancestrula has a different structure.

Habitat distribution

The available material of *H. hexaspinae* n. sp. was collected in two habitats which are quite opposite in terms of environmental conditions and type of substrates: walls of dark parts of shallow submarine caves vs biogenic remains at the surface of relatively deep soft bottoms (60-150 m) in the open sea. In underwater caves from the Marseille area, *H. hexaspinae* n. sp. was present with tiny, frequently ovicellate colonies ("spot colonies", Bishop 1989; Okamura *et al.* 2001). However, in dark caves with low energy inputs from the outside, the occurrence of ovicells in tiny colonies is not a sign of early fertility and high offspring production, such as in r-selected species (e.g. Pianka 1970) from productive environments. On the contrary, in dark caves, the growth of bryozoan colonies is limited to a very low yearly production of zooids. This feature is revealed by the external aspect of zooids, which are more or less blackened by deposits of Mn and Fe oxides that increase over time (Allouc & Harmelin 2001), a common phenomenon in aphotic habitats. This is exemplified by a tiny colony from 3PP Cave composed of the ancestrula and three autozooids (Fig. 12D, E), each budded very sporadically as shown by the increasing darkening of the frontal wall and spines from the third, youngest, zooid to the ancestrula. Such populations and colony features are signs of an adaptive strategy for life in highly cryptic and oligotrophic habitats where energy inputs from the outside are very limited and sporadic (Harmelin 2000; Okamura *et al.* 2001). Another peculiarity of the occurrence of *H. hexaspinae* n. sp. in cryptic habitat is its uneven distribution among caves clustered in the same area. Along the coast from Marseille to La Ciotat, despite the great frequency of this habitat (mostly karstic cavities), specimens were recorded in only three caves. Most of them were collected in the vast 3PP Cave, but none in the similarly large Trémies Cave, close to the former (linear distance: < 8 km), despite extensive sampling of its dark parts (e.g. Harmelin 1969, 1986). Differences in the inner thermal regime of these two caves might be the cause of this uneven distribution. In 3PP Cave, because of a descending profile (Harmelin 1997), yearly fluctuations are reduced (12.8-14.5°C) and close to those of the homothermic deep-sea. In contrast, in the Trémies Cave, due to a karstic origin, the inner ascending profile leads to the trapping of warm water bodies in the upper dark parts (Harmelin 1969). However, *H. hexaspinae* n. sp. was also present in two other shallow caves (Cape Morgiou, Eissadon) where the inner thermal regime fluctuates as in the open sea at the same depth. The punctuated distribution of *H. hexaspinae* n. sp. in caves of the Provence region suggests that connectivity between caves is very low and recruitment is mostly autochthonous. In the same region, *H. hexaspinae* n. sp. was never recorded in deep-water samples (100-300 m, rock fragments, dead shells, coral skeletons) from the shelf and the neighbouring Cassidaigne Canyon (Harmelin 1976, table III and unpublished data). In southern Italy, small living and dead colonies of *H. hexaspinae* n. sp. were found on the outer shelf, in thanatocoenoses occurring at the surface of detritic biogenic bottoms (Ionian Sea, eastern Sicily), and also at the top of the Apollo Bank where rocky outcrops with *Laminaria rodriguezii* Bornet, 1888 alternate with coarse detritic sand. Living colonies were mostly colonising small rhodoliths, fragments of coralline algae, dead branches of erect bryozoans [e.g. *Adeonella calveti* Canu & Bassler, 1930 and *Smittina cervicornis* (Pallas, 1766)] and shells.

Geographical distribution

Obviously, the small size of colonies of *H. hexaspinae* n. sp., the types of substrates on which they grow, and their scattered condition increase considerably the stochasticity of records. Therefore, its actual geographical distribution is poorly known. Most records were from the western Mediterranean Sea, in Provence, in the southern Tyrrhenian Sea, and in the western Ionian Sea (Sicily). This species has also been collected in the NE Atlantic, close to the western entrance of the Gibraltar Strait (Table 4). This occurrence in the Gulf of Cadiz, down to 524 m depth, may suggest a possible influence of the Mediterranean outflow water (e.g. Bashmachnikov *et al.* 2015) on the composition of the bottom fauna.

Hemicyclopora sp. 2
(Figs 13A-C; Tables 1; 4)

Material examined. — **Spain. N Iberian Peninsula** • 1 living ovicellate colony (30 autozooids, 3 ovicells); R/V *Thalassa*; Stn X301; Asturias; 44°07.7'N, 05°09.4'W; 980-1020 m depth; 12.X.1971; on *D. pertusum*; Dre; H. Zibrowius leg.; MNHN-IB-2017-1559.

Description

Colony encrusting, unilaminar. Autozooids quincuncially arranged, roughly hexagonal, large (L ≥ 1 mm, Table 1), some peripheral zooids nearly triangular due to a considerable proximal widening (Fig. 13A); frontal shield bulged, remarkably high at the level of the orifice (Fig. 13B). Orifice sub-terminal, longer than wide (ratio L/W up to 1.3); proximal edge straight or very slightly concave, without umbo or lower thickening; condyles prominent, triangular

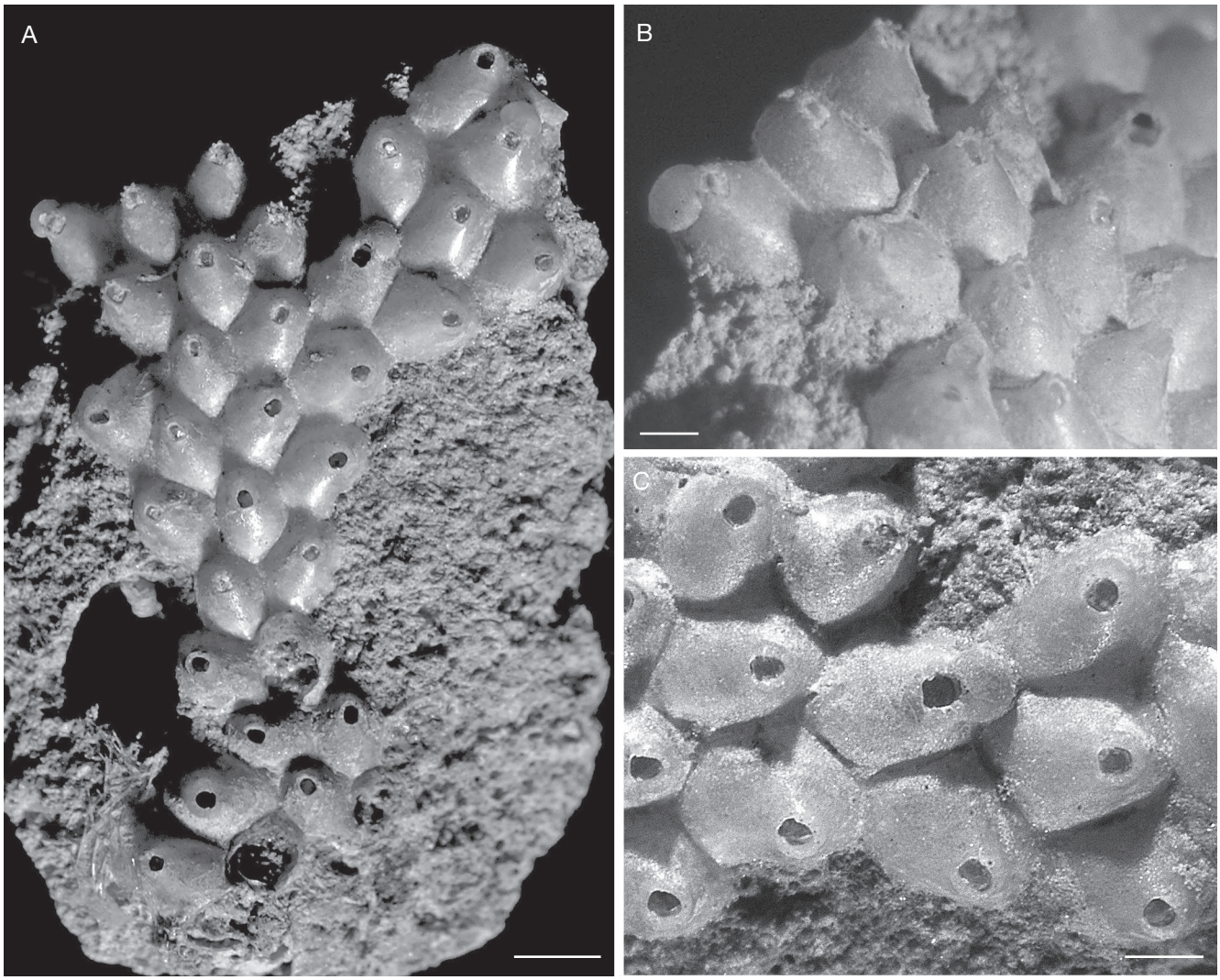

FIG. 13. — *Hemicyclopora* sp. 2: **A**, colony on a fragment of coral skeleton; **B**, same colony, zooids showing a typical profile with a great distal thickness, a terminal orifice, a vertical distal wall, and a terminal, highly recumbent ovicell; **C**, frontal view of non-ovicellate and ovicellate zooids. Origin: Asturias, Thalassa X301; MNHN-IB-2017-1559. Scale bars: A, 1 mm; B, C, 400 µm.

(Fig. 13C). Oral spines eight in non-ovicellate zooids, six in ovicellate ones. Ovicell cleithral, distinctly attached to the distal wall of the maternal zooid, likely associated to a basal kenozooid, rather flattened and wide (Fig. 13B, C), with a low mucro above the proximal edge.

REMARKS

This single, small colony most likely belongs to an undescribed species, but its peculiarities need to be verified and precised on more abundant material before introducing a new species name. It differs from the other *Hemicyclopora* first by the combination of obviously visible characters: large size and particular shape of zooids, shape of the orifice, type and shape of the ovicell. Small characters were not visible on this colony left uncleaned and not observed with SEM. It is probably an exclusively deep-water species, perhaps preferentially associated to the community of cold-water scleractinians.

Genus *Scutocyclopora* n. gen.

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TYPE SPECIES. — *Hemicyclopora dentata* López de la Cuadra & García-Gómez, 1991.

DIAGNOSIS. — Colony encrusting, unilaminar, multiserial. Autozooid frontal shield umbonuloid, imperforate except for marginal pores aligned in rows; communication by small basal pore-chambers. Orifice with slightly protruding or non-protuberant condyles, encircled by a high, flared peristome, without oral spines. Ovicell hyperstomial, attached to distal wall of maternal zooid, not associated with a distal daughter autozooid. Ancestrula morphologically similar to succeeding autozooids, with umbonuloid frontal shield and without spines.

ETYMOLOGY. — From the Latin noun *scutum*: shield, in reference to the frontal shield of the ancestrula.

Scutocyclopora dentata
(López de la Cuadra & García-Gómez, 1991) n. comb.
(Figs 14B; 15A-F; Tables 1; 4)

Hemicyclopora dentata López de la Cuadra & García-Gómez, 1991: 213, fig. 2A-C, pl. 1.

Hemicyclopora collarina Canu & Lecointre, 1930. — Harmelin 2003: 108, fig. 4. — Ayari-Kliti *et al.* 2012: 90, pl. 3, fig. 2A-C.

Hemicyclopora sp. – Zabala 1993: 567.

Hemicyclopora sp. 1 – Rosso *et al.* 2021a: fig. 6H, table 1.

Not *Hemicyclopora collarina* Canu & Lecointre, 1930: 106, pl. 14, fig. 3-5. — Buge 1957: 313. — Moissette 1988: 158, pl. 26, fig. 1, 4.

MATERIAL EXAMINED. — **France, Provence** • 3 colonies; Cassis, Trémies Cave; 43°12'00"N, 5°30'43.5"E; 6 m depth; 7.I.1982; dark zone; on stalactite and bryozoan nodules; Div; JGH leg.; MNHN • 1 colony; Port-Cros Is., Bagaud Cave; 43°00'46"N, 6°21'36"E; 5 m depth; III.1985; dark zone; on rocky wall; Div; JGH leg.; MNHN. **Spain**, **Balearic Archipelago** • 1 colony; Mallorca Is.; Stn MZ_M.120 (13); 7 m depth, on *Posidonia* rhizome; Div; M. Zabala leg.; MNHN • 1 colony; Cabrera Is.; Stn MZ M.8 (27); depth missing, on *Posidonia* root; Div; M. Zabala leg.; MNHN • 1 small ovicellate colony; Mallorca Is.; Stn MZ 415; depth missing, on lower side of a biogenic concretion; Div; M. Zabala leg.; MNHN. **Italy** • 1 dead colony fragment; Tyrrhenian Sea, Campania, Palinuro Cape, Scaletta Cave; 40°1'35"N, 15°16'7"E; 46 m depth; 14.IX.2009; dark zone; Div; R. Leonardi leg.; PMC Rosso-Collection I. H. B. 93a.• 1 living and two dead small ovicellate colonies; lu Lampiùne Cave; 40°08'05.7"N, 18°31'00.4"E; 8 m depth; 2003; dark zone; Div; G. Belmonte leg.; MNHN • 1 colony with ancestrula; Sicily, Ionian Sea, off Avola, *c.* 100 m depth; 2005; coralligenous bottoms; fishermen Dre; AR leg.; PMC Rosso-Collection I. H. B. 93b • 1 ovicellate colony fragment; NW Sardinia, Capo Caccia-Isola Piana MPA, Bisbe Cave; 40°35'40"N, 8°11'39"E; 5 m depth; VI.2009; on wall of semi-dark zone; Div; V. Di Martino leg.; PMC Rosso-Collection I. H. B. 93c.

SEM PHOTOS EXAMINED. — **Spain** • Holotype; La Atunara; López de la Cuadra leg. (personal communication to JGH, XII.1988); paratypes I & II stored at the MNHN: MNHN-IB-2008-12741, data available at http://coldb.mnhn.fr/catalognumber/mnhn/ib/2008-12741 • 1 large colony with 5 ovicells and ancestrula; Cape Castel, Montgri; Stn ST 9144; 42°4'57.22"N, 3°12'6.67"E; 27 m depth; T. Madurell leg. (personal communication to JGH, 05.III.2020). **Croatia** • 1 large colony; Kornati Archipelago; 33 m depth; COR with gorgonians; M. Novosel leg. (personal communication to JGH, 20.I.2011).

DESCRIPTION
Colony small, encrusting, multiserial, unilaminar. Autozooids separated by deep grooves, arranged quincuncially; frontal shield clearly convex, surface distinctly structured by large (*c.* 20-30 µm in diameter) hemispherical tubercles (Fig. 15B-E) with a glassy appearance, imperforate except for relatively large (19-35 µm) marginal pores, arranged in a single row which doubles distally, laterally to the orifice (Fig. 15A, D). Pore-chambers small (*c.* 30 µm wide), numerous (>10 on each side). Primary orifice rounded, wider than long in both non-ovicellate and ovicellate autozooids, with proximal edge slightly concave, condyles step-shaped at the extremities of a wide internal arc (Fig. 15A, D, E); operculum light yellow. No oral spines. Secondary orifice of non-ovicellate zooids forming a high, collar-shaped peristome, more or less flared with an upper rim irregularly waved or with some indentations, interrupted proximally by a rounded notch sometimes indented with a triangular process (pseudo-spine) at the upper corners (Fig. 15B, D); in ovicellate zooids, peristomial collar higher, often indented with irregularly triangular pseudo-spines, distally contiguous to the ovicell (Fig. 15A, C, E). Ovicell hyperstomial, cleithral, attached to the distal wall of maternal zooid, most likely associated with a small, basal kenozooid, endooecium noticeably tuberculate, with proximal rim (distal edge of orifice) topped by a prominent vizor with smooth surface and convex to triangular upper edge, which can be indented in specimens from caves (Fig. 15A, C, E). Ancestrula resembling later zooids (Figs 14B; 15F), with umbonuloid frontal shield, entirely calcified, markedly convex and nodular; orifice rounded, without spines but encircled by a flared peristome with the edge waved or scalloped, with some indentations separated by few small triangular processes (pseudo-spines), a little smaller than in "adult" zooids, but slightly wider than the periancestrular zooids.

REMARKS
Morphological features and taxonomic issues

All specimens of *Scutocyclopora dentata* n. comb. from our collections or examined from SEM photos (14 colonies from 12 Mediterranean localities and various habitats: see below) showed the same readily apparent morphological traits that clearly discriminate this species from all *Hemicyclopora* species. The frontal shield and the endooecium, covered with large nodules, have a very particular aspect, but the obvious uniqueness of this species is given by features of the orifice area and the ancestrula. The lack of oral spines, which are replaced by a high and more or less serrated collar, prolonged with a prominent, arched vizor on the ovicell, is a constant feature. Similarly, all observed ancestrulae, including the one of the type (López de la Cuadra & Garcia-Gómez 1991, text-fig. 2B; pl. 1, fig. 1 and SEM photo sent to JGH), are similar to the following autozooids, just a little smaller (Figs 14B; 15F; Table 1). Therefore, this type of ancestrula differs drastically from the tatiform ancestrula characterizing both *Hemicyclopora* (e.g. *H. polita*, the type species of the genus: Fig. 14A) and *Escharella*. The latter type shows in frontal view three distinct parts, a distal opesia with a slightly concave proximal edge that is framed by oral spines, a cryptocystal area, also edged by several spines, and a lateral and proximal gymnocystal area. Curiously, the ancestrula of *S. dentata* n. comb. bears a superficial resemblance with that of the hippoporidrid *Scorpiodinipora costulata* (Canu & Bassler, 1929) (Harmelin *et al.* 2012: fig. 6). Variability of these discriminating characters only concerns the shape of the peristomial collar, more or less scalloped, with indentations and pointed processes that may be reduced or form pseudo-spines (Fig. 15A-D). However, some morphological traits are similar to those of *Hemicylopora*, such as the colony shape, the general structure of the orifice, the ovicell and the frontal shield.

Recent material of *S. dentata* n. comb. was attributed by Harmelin (2003) and Ayari-Kliti *et al.* (2012) to the fossil

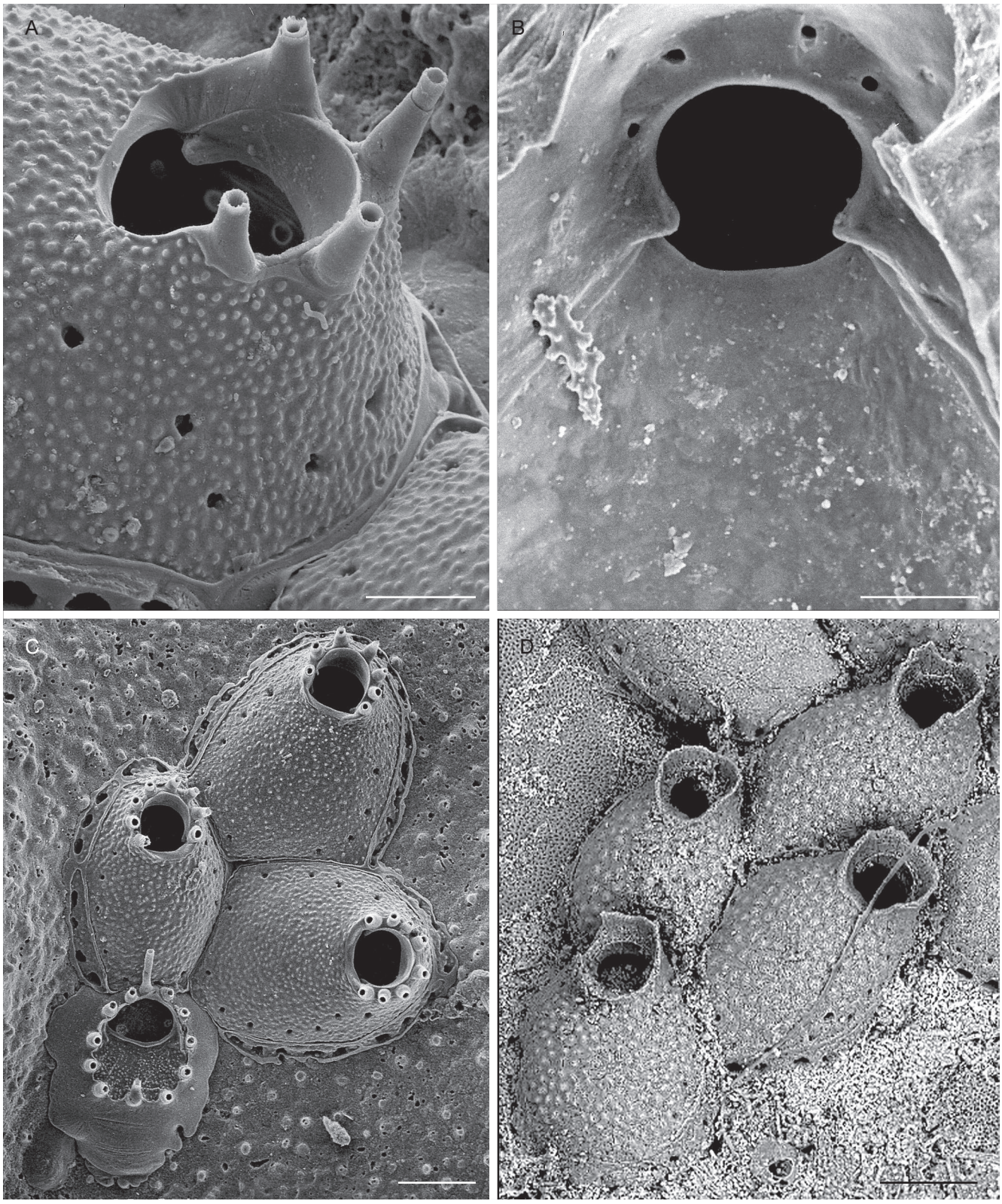

Fig. 14. — Oral spines in a non-ovicellate zooid of *Hemicyclopora polita* (Norman, 1864): **A**, outside view of four spines with tall bases; **B**, inside view of the orifice area showing four pores corresponding to the opening of spines into the coelom and the distal part of the umbonuloid frontal shield. Ancestrula and early astogeny in the genera *Hemicyclopora* and *Scutocyclopora* n. gen.: **C**, *H. polita*, **D**, *S. dentata* n. comb, Origin: **A**-**C**, NE Atlantic, Armorican Margin, 1050 m, R/V *Thalassa* Z435; **D**, Ionian Sea, Sicily, off Avola, 100 m. Scale bars: A, B, 100 µm; C, D, 200 µm.

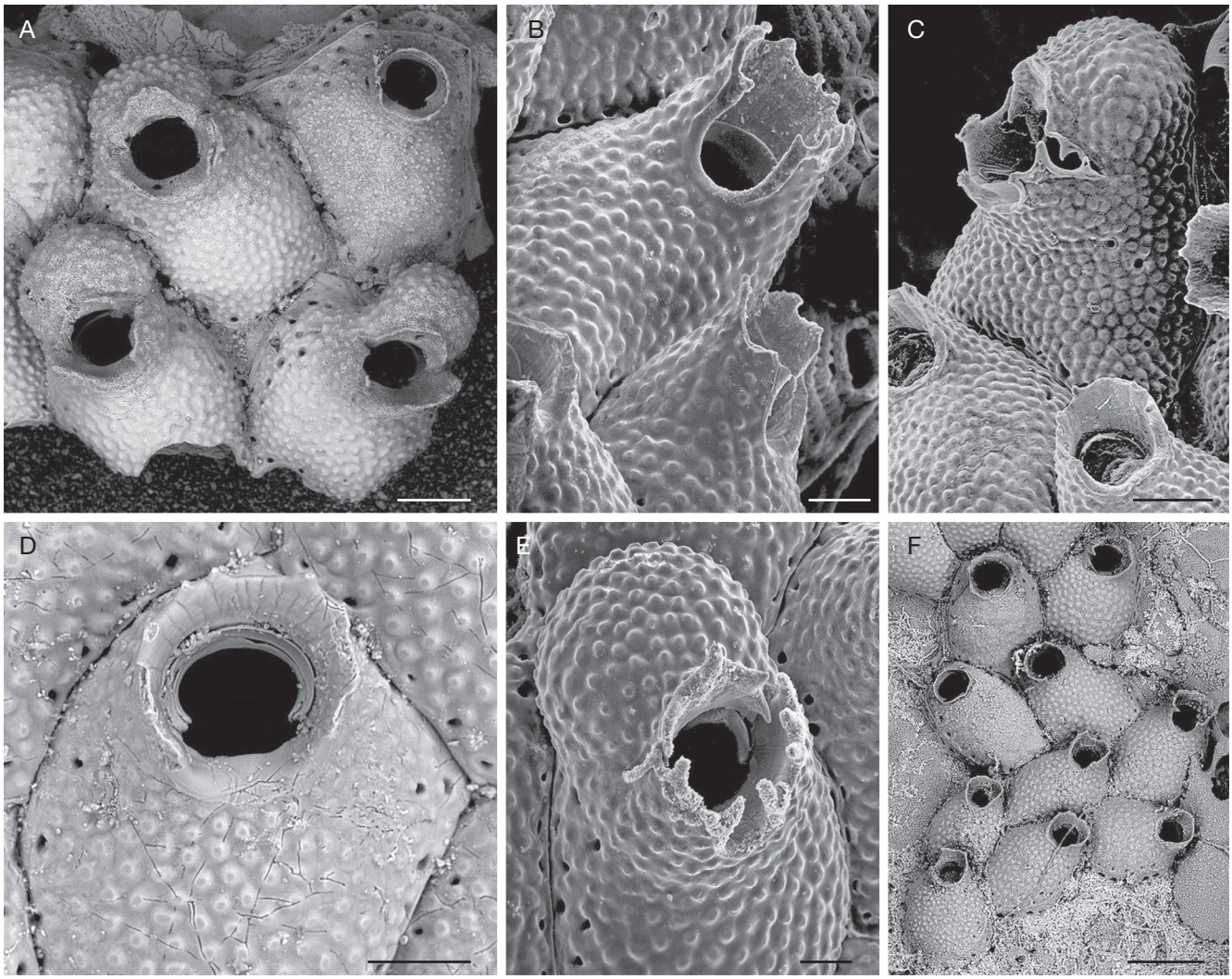

FIG. 15. — *Scutocyclopora dentata* (López de la Cuadra & García-Gómez, 1991) n. comb.: **A**, one non-ovicellate and three ovicellate zooids; **B**, two non-ovicellate zooids with high, indented peristome; **C**, **E**, ovicellate zooid with nodular frontal shield and endooecium and orifice edged by a vizor on the ovicell and a collar with pseudo-spines; **D**, non-ovicellate zooid with indented collar, orifice with internal arch ending in step-shaped condyles, and small marginal pores; **F**, young stage of a colony with ancestrula. Origin of specimens: **A**, Italy, Campania, Palinuro Cape, Scaletta Cave, 47 m; **B**, **E**, France, Port-Cros, Bagaud Cave, 5 m; **C**, France, Provence, Trémies cave, 6 m; **D**, **F**, Italy, Sicily, off Avola, 100 m. Scale bars: A, C, 200 µm; B, D, E, 100 µm; F, 300 µm.

species *Hemicyclopora collarina* Canu & Lecointre, 1930 from the Faluns of Touraine and Anjou. This species was defined by Canu & Lecointre (1930: 106) with the following characters "Les zoécies sont distinctes, séparées par un sillon profond, un peu allongées, ovoïdes ou subhexagonales […] frontale très convexe […] entourée de minuscules pores aréolaires […] deux cardelles profondes […] grand anter, plus petit poster droit ou concave, […] péristomie très évasée, très irrégulière, dont la lèvre proximale est très large, […] L'ovicelle est grande, très globuleuse, lisse […]", and 4-6 spines are present. This species was similarly characterized by Buge (1957: 313). The figures given by Canu & Lecointre (1930: pl. 14, figs 3-5) show true spines and not spinous indentations of the peristomial collar, such as in Recent specimens of *S. dentata* n. comb. Moreover, the remark by Canu & Lecointre (1930: 107) that *H. collarina* resembles *H. labiosa* (Jullien, 1903), a typical *Hemicyclopora* species from the Azores with six to eight spines and a high peristome, implies a clear difference to *S. dentata* n. comb. The description and SEM figures of fossil specimens from the Messinian of Oran (Algeria) ascribed to *H. collarina* by Moissette (1988) depict a very convex and finely granular frontal shield, an orifice with a straight proximal edge and small condyles, a peristome with high lateral wings, and four spines with large bases in ovicellate zooids. The ancestrula of *H. collarina* is not known.

Scutocyclopora dentata n. comb. shows some superficial similarities with *Hemiphylactella pulchra* Vigneaux, 1949, the type species of the genus *Hemiphylactella* Vigneaux, 1949, from the early Miocene of Aquitaine (France) (Di Martino & Taylor 2017: 784, fig. 1A-E). The two species share a nodular frontal shield with peripheral pores and a large, flared peristome which extends on the proximal rim of the ovicell. However, *H. pulchra* has 1-3 oral spines and a wider, flatter and thicker peristome, besides autozooids with a less convex frontal shield and fewer but larger areolar pores, and relatively smaller ovicells.

The placement of *Scutocyclopora* n. gen. in the same family as *Hemicyclopora* and *Escharella*, i.e., in Escharellidae, is quite questionable considering the features of the ancestrula. Obviously, the phylogenic relationships of this taxon will require a molecular approach.

Habitat distribution

Scutocyclopora dentata n. comb. is distributed in a wide variety of coastal habitats with apparently contrasting ecological features within the Infralittoral and the Circalittoral zones (depth range: 5-100 m), but with a clear tendency to sciaphily, i.e., a preference for mesophotic and dark habitats or microhabitats. This species was first found (López de la Cuadra & García-Gómez 1991) on stones and shell fragments at 30-50 m depth. Subsequent records span widely across different types of habitats: 1) coarse debris on detritic sand in northern Tunisia (Ayari-Kliti *et al.* 2012); 2) rocky walls of submarine caves in complete darkness at shallow depth in Provence (Harmelin 2003), southern Italy and Sardinia (Rosso *et al.* 2021a, present paper), and Catalonia (Medes Isles: T. Madurell & M. Zabala, person. com. to JGH, 1.II.2021); 3) biogenic concretions and stones in coralligenous bottoms with *Paramuricea clavata* (Risso, 1826) (Croatia, 33 m, M. Novosel leg.; Catalonia, 26-41 m, T. Madurell & M. Zabala, person. com.); and 4) debris of rhizomes and roots of *Posidonia oceanica* (Delile) from the Balearic Islands (Zabala 1993 and leg.; T. Madurell & M. Zabala, person. com. to JGH, 1.II.2021). However, the apparent ecological heterogeneity of these microhabitats may be misleading as undersides of small substrata may offer to tiny encrusting bryozoan colonies conditions similar to those of a large cavity (e.g. Harmelin 2000, 2003).

Geographical distribution

The examined material of *Scutocyclopora dentata* n. comb. was collected in various localities of the Mediterranean: in Spain (Andalusia, López de la Cuadra & Garcia-Gómez 1991; Catalonia, Madurell & Zabala, unpublished data; Balearic Islands, Zabala 1993 as *Hemicyclopora* sp. & unpublished data), France (Provence: Harmelin 2003 and present material), Italy (Campania, SE Sicily, S Apulia and NW Sardinia: Rosso *et al.* 2021a, present material), Croatia (Kornati Archipelago: M. Novosel, unpublished data), and northern Tunisia (east of Zembra Island: Ayari-Kliti *et al.* 2012).

DISCUSSION

Taxonomic decisions

The present work, first dedicated to the revision of the *Hemicyclopora* species of only the Mediterranean basin, brought evidence of 1) the necessity to also assess material from the NE Atlantic; 2) an unexpected hidden diversity despite the long history of the study of bryozoans in the Atlantic-Mediterranean region; 3) an obvious blurring of boundaries between the genera *Hemicyclopora* and *Escharella*, with species constituting a link between them; and 4) the clear divergence of the species *H. dentata* from the morphological plan of these two genera, leading to the erection of a new genus.

Of the four *Hemicyclopora* species listed by Rosso & Di Martino (2016) in their compendium of the Mediterranean bryozoan diversity, only two, *H. discrepans* and *H. dentata*, were kept as occurring in the region, but the second one was designated as the type species of the new genus *Scutocyclopora* n. gen. The overall species diversity of the examined material from the Mediterranean encompasses six or seven species (depending on the validity of the synonymy of *H. admirabilis* with *H. discrepans*) assigned to three genera (*Hemicyclopora*, *Escharella*, *Scutocyclopora* n. gen.), and including three new species (*H. neatonensis* n. sp., *H. hexaspinae* n. sp., "*E.*" *massiliana* n. sp.). Eight species were identified in our Atlantic material, including *H. polita*, not considered in this study (but see fig. 14A-C), which co-occurs on deep-water corals along the Armorican margin with "*H.*" *celtica* n. sp. and "*E.*" *pytheasi* n. sp., three species also recorded in the Mediterranean (*H. discrepans*, *H. hexaspinae* n. sp., *E. similis*), and two species left unnamed. As already mentioned, the studied species, except for *S. dentata* n. comb., were assigned to the family Escharellidae rather than to the polyphyletic Romacheinidae. The family assignation of *Scutocyclopora* n. gen. remains disputable.

This study thus confirms the great diversity of cheilostomate bryozoans in the Mediterranean revealed by recent works (e.g. *Schizomavella* Canu & Bassler, 1917: Reverter-Gil *et al.* 2016; *Collarina* Jullien, 1886: Harmelin *et al.* 2019; *Setosella*: Rosso *et al.* 2020; *Microporella*: Di Martino & Rosso 2021). This revision also revealed that several taxa, here split into species complexes, exemplify the close relationships between the genera *Hemicyclopora* and *Escharella*. These species present clinal changes in the morphology of their primary orifice, leading to the emergence of a lyrula. The absence of lyrula in *Hemicyclopora* was soon considered as the fundamental difference between these two genera (Norman 1894, 1909; Ryland 1963). According to Hayward & Ryland (1999), this generic distinction is also based on the type of ovicell closure, cleithral (*Hemicyclopora*) or acleithral (*Escharella*). The present material offered examples of intermediate stages between a lyrula-like denticle (*E. similis*), a tiny bump ("*E.*" *massiliana* n. sp.) only perceptible with SEM examination, and the absence of any protuberance ("*H.*" *pytheasi* n. sp, "*H.*" *celtica* n. sp.). Obviously, this allegated morphological cline, which questions the differentiation of *Hemicyclopora* from *Escharella*, needs to be tested with molecular tools and phylogenetic analyses.

The re-examination of the morphological traits of *S. dentata* n. comb. highlighted a clear divergence from all other *Hemicyclopora* or *Escharella* species. These differences (nontatiform ancestrula with an umbonuloid nodular frontal shield, secondary orifice with a high collar without oral spines) are constant in all specimens irrespective of their habitat. This morphological divergence justifies the erection of a new genus, *Scutocyclopora* n. gen., whose phylogenetical relationships would also require a molecular approach.

The absence of avicularia is a common trait of both *Hemicyclopora* and *Escharella*. Thus, the record and illustration of a specimen of *H. multispinata* from Madeira with large vicarious avicularia by Norman (1909), despite being the

author of the genus *Hemicyclopora* (Norman 1894), remained an enigma. As suggested here, this specimen may belong in fact to a species of *Bathycyclopora*, i.e., a genus of Atlantisinidae, a deep-sea family distributed in seamounts of the NE Atlantic (Berning *et al.* 2017), and seemingly absent from the present-day Mediterranean despite it thrived there in the Gelasian (Early Pleistocene) with at least one species (*Atlantisina mylaensis* Rosso & Sciuto, 2019), *c.* 2 million years ago (Rosso & Sciuto 2019).

Morphological features

A broad variety of diagnostic morphological traits was used for characterizing the different species examined here (Tables 2; 3). They were provided by particular traits of the frontal shield (shape, surficial relief, size and distribution of marginal pores), the orifice (shape, size, position, including those of condyles, development of the secondary orifice: umbo, peristome), the number of oral spines and shape of their basal part, the ovicell (shape, size, position, structure and formation of the ooecium), and the ancestrula (number and distribution of spines, relative size of the opesia, cryptocyst and proximal gymnocyst). These features often need the use of SEM to be accurately characterized. The number of specimens that can be examined in that way is thus limited, leading to the difficulty to distinguish individual peculiarities (single colony level) from features present at a much wider scale (regional population, species). Moreover, the available material in collection was often limited to a very small number of tiny colonies.

In his redescription of *H. polita*, Ryland (1963) noted that the number of spines of both the orifice and the ancestrula may vary within *Hemicyclopora* species. Indeed, on coral skeletons from the Celtic Sea (Thalassa Z435) bearing both "*H". celtica* n. sp. and *H. polita*, non-ovicellate zooids of the latter (124 in five colonies) presented a varying number of oral spines (four: 37.9%; five: 14.5%; six: 47.6%). Cases of non-ovicellate zooids with a lower number of spines than the dominant number was particularly frequent in a deep-sea population of "*H". celtica* n. sp. This variability, which contrasts with the stability of the number of spines in ovicellate zooids, was attributed to repeated abortion of ovicells. A reverse trend was noted in the species complex "*discrepans*" with the number of spines in ovicellate zooids varying according to the geographic origin of the specimens (e.g., Alboran Sea vs Atlantic seamounts), and also within a single specimen (Fig. 5A). This instability might indicate a particular genetic plasticity of these specimens. The choice of splitting material previously attributed to *E. similis* and *E. lopezfei*, leading to the erection of three new species ("*H.*" *celtica* n. sp., "*E.*" *massiliana* n. sp., "*H.*" *pytheasi* n. sp.), was sustained by the geographical discontinuity of their populations and stable morphological differences. This decision is consistent with the admitted good agreement between genetical and morphological classifications in cheilostomes (e.g. Jackson & Cheetham 1994; Orr *et al.* 2021).

Oral spines are hollow tubes, apparently with an open tip, jointed with a chitinous annular part at calcified bases, which are more or less prominent. These bases of spines, also tubular, open with large pores on the inner side of the oral part of the cystid, as revealed by SEM examination (Fig. 6I: "*H.*" *celtica* n. sp.; Fig. 9G: "*E.*" *pytheasi* n. sp.; Fig. 14A, B: *H. polita*). Besides functions of oral spines already debated (review by Schack *et al.* 2019), the occurrence of these internal pores suggests direct communication between the perigastric coelom and the spines. Do these exchanges allow the spines to move according to outside stimuli? Are the spines also sensory organs? Is this structure of the oral spines of *Hemicyclopora* also present in *Escharella*? Are the ancestrular spines similarly designed? These questions are left open.

In all species except two, ovicells were hyperstomial, attached to the maternal distal wall and associated with a small, basal, ooecium-producing kenozooid. Basal kenozooids can be very small and not easy to see, even with SEM, except in incompletely formed ovicells at the colony margin. For this reason, in some species (e.g. *H. hexaspinae* n. sp., "*H." pytheasi* n. sp., "*E.*" *massiliana* n. sp.), ovicells may appear to be terminal and free, resting directly on the substrate. The Mediterranean *H. neatonensis* n. sp. presents a transitional condition with ovicells constructed either by a small basal kenozooid, a large distal interzooidal kenozooid, or a distal autozooid. In contrast, "*H." celtica* n. sp. invariably shows ovicells immersed in the distal daughter autozooid, which is responsible for the ooecium building. In this well-calcified, deep-water species, this type of ovicell is assumed to offer better protection to the embryos, but likely at the expense of a slower construction than a kenozooidal ovicell.

Geographical and ecological distribution patterns

Most generally, the populations of these Atlantic-Mediterranean species appear to be very scattered, both at a local scale (e.g. *H. hexaspinae* n. sp. in the network of submarine caves in the Marseille area), and at the scale of a whole basin (e.g. *H. neatonensis* n. sp., only recorded in some areas of southern Italy). This scattering may result from both the limited dispersal potential of bryozoans with non-planktotrophic larvae (e.g. Ryland 1976; Jackson 1986; Watts *et al.* 1998; Watts & Thorpe 2006) and failure in the circulation of water bodies at any scale, leading to isolation of local populations and possible cryptic speciation. The species pair of *E. similis*, in the Alboran Sea, and "*E." massiliana* n. sp. in Provence might be an example. Conversely, species may have an extensive geographical distribution despite the poor dispersal capacity of their pelagic larvae, as stressed by Winston (2012). Among the diverse pathways enabling the geographical expansion of these species, hopping using small substrates as stepping-stones appears to be the most realistic one for *Hemicyclopora* species. The role of whale bones as scattered reservoirs of biodiversity (Wilson & Kaufmann 1987; Winston 2012) enabling deep-sea dispersal of species was strikingly attested by the finding of *H. discrepans* together with a diverse assemblage of bryozoans on this kind of substrate (Reverter-Gil & Fernández-Pulpeiro 1999; Souto & Reverter-Gil 2021). But empty shells and other biogenic substrates, frequently colonized by *Hemicyclopora* species, are much more common stepping-stones. Obviously, molecular analyses of disjunct populations of morphospecies

assigned here to "*Hemicyclopora*" and "*Escharella*" could critically appraise the taxonomic decisions taken on the basis of morphological features, and thus could provide a more realistic assessment of the biogeography of these species in the Atlantic-Mediterranean region. Unfortunately, the scarcity and small size of colonies and their occurrence in poorly accessible habitats may represent a major hurdle for this approach.

The depth distribution of species in our material ranged from 5 m to 205 m in the Mediterranean and from 128 m to 1050 m in the Atlantic, from the nearshore zone in underwater caves to offshore upper-bathyal bottoms. The apparent absence of *Hemicyclopora* species at shallow depth in the Atlantic may result from the lack of available material from nearshore caves or equivalent cryptic habitats. In each of the reported habitats, ambient light was considerably diminished or null where the bryozoans grew, and colonies were protected from sediment deposition. The large branched scleractinians (i.e., 'cold-water-corals') from the shelf break and the upper bathyal are islands of diversity (e.g. Freiwald *et al.* 2004) for many bryozoan species (Zabala *et al.* 1993; Mastrototaro *et al.* 2010; Rosso *et al.* 2010, 2018; Souto *et al.* 2016; Berning *et al.* 2017), including *Hemicyclopora* species in the Atlantic, but apparently not in the Mediterranean.

Present-day and past distribution of *Hemicyclopora*. The actual present-day diversity of the genus *Hemicyclopora* is obviously underestimated, even if one only considers its limited, traditional concept. The same is likely true for the general geographical distribution of this genus. The distributions of the new species described here overlap with that of already known living taxa [*H. discrepans*, *H. emucronata*, *H. labiosa* (Jullien *in* Jullien & Calvet, 1903), *H. labrata* Hayward, 1994, *H. multispinata*, *H. polita*, *H. polita mucronata* Ryland, 1963], reported from Madeira to the Arctic. In the same area, *Hemicyclopora* has a long, but incomplete, fossil history with several species known from Europe and North Africa at least since the late Eocene. In contrast, only one Cenozoic species, *H. parajuncta* Canu & Bassler, 1917, was present in North America (Canu & Bassler 1917), whose record in the Eocene of Europe (Zágorsek & Kázmér 1999) remains doubtful. At least three species, *H. brevis* Canu & Lecointre, 1930, *H. dimorpha* Canu & Lecointre, 1930, and *H. collarina*, occurred in the Miocene in North Africa (El Hajjaji 1992; Moissette 1993; Moissette *et al.* 2006). Three other species reported from the Iberian-Moroccan region as *Hemicyclopora* sp. (El Hajjaji 1992; Berning 2006). *Hemicyclopora steenhuisi* (Lagaaij, 1952) and *H. disjuncta* are known from the Pliocene, and *H. neatonensis* n. sp. from the early Pleistocene of Sicily (see above). This latter species is the only one with both fossil and present-day representatives. The oldest *Hemicyclopora* species are *H. dissidens* Gordon & Taylor, 2015 and *H. ventricosa* Gordon & Taylor, 2015, from the Early Eocene in New Zealand (Gordon & Taylor 2015), where the genus occurred up to the Burdigalian with *H. inermis* (Stoliczka, 1865). Another remote fossil record is that of *H. noshiroensis* Hayami, 1975 from the Pliocene of Japan (Hayami 1975). Assuming a correct generic attribution for all fossil species (most miss SEM micrographs), the origination of the genus might be in the New Zealand region, from where it has spread westward through the Tethys gateway. The present-day geographical distribution pattern might result from local extinction in the southern hemisphere and diversification in the Atlantic-Mediterranean region.

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