

Biodiversity of bathyal coral gardens
– portrait of a uniserial bryozoan endemic
to the South Azorean Seamount Chain:
an unexpected evolutionary testbed?

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Harmelinus uniserialis (Harmelin, 1978) on *Madrepora oculata* Linnaeus, 1758, NE Atlantic Ocean, Hyères seamount, 1060 m.

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Biodiversity of bathyal coral gardens – portrait of a uniserial bryozoan endemic to the South Azorean Seamount Chain: an unexpected evolutionary testbed?

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ABSTRACT

On slopes of the bathyal zone, branched scleractinian corals produce three-dimensional constructions and rubble which provide hard substrates particularly suitable for encrusting bryozoans. Samples of “cold water corals”, mainly *Madrepora oculata* Linnaeus, 1758, collected on six seamounts of the South Azorean Seamount Chain (SASC), allowed a close re-examination of a poorly-known uniserial encrusting cheilostome bryozoan, *Harmelinus uniserialis* (Harmelin, 1978), revealing unexpected morphological features. In contradistinction to the apparent simplicity of its colony shape formed by ramifying chains of autozooids and vicarious kenozooids, this species presents a great structural complexity shaped by different types of polymorphs. The vicarious kenozooids are the basis of a disparity cline including the distal kenozooidal part of ovicelled and non-ovicelled autozooids, and five differently-shaped adventitious avicularia, which is validated by a puzzling morphological trait (tiny porous knobs) shared by most of them. The common origin of kenozooids and avicularia represents an innovation among cheilostome bryozoans, apparently with little or hidden evolutionary development. The functions of these polymorphs are unclear except for a role as connecting tools and oocial cover of kenozooids integrated with autozooids. Vicarious kenozooids are assumed to store metabolites in their large chamber and to dispatch them through the mesenchymatous network. The different types of avicularia, budded by the same colony and even by the same autozooid, might have a common role of water renewal at the colony surface, improving the supply of particulate food. The high frequency of processes of zooid repair by intramural budding and still living fragments of colony, the thickness of walls and the great rarity of both ovicells and ancestrulae indicate that colonies are particularly long-lived and have a very low reproduction rate. These features and the confinement of colonies within the boundary layer of substrates result in very limited larval dispersal and the endemism of this species to the 600-1500 m depth zone of the South Azorean Seamount Chain and the southern bathyal slope of the Azores. Several traits of *H. uniserialis* suggest that it may be a relict species.

KEY WORDS

Cold-water corals,
Bryozoa,
growth-form,
polymorphism,
avicularia,
kenozooids,
intramural budding,
phenotypic plasticity,
relict species,
Harmelinus.

RÉSUMÉ

Biodiversité des jardins de coraux bathyaux – portait d’un bryozoaire unisériel endémique de la chaîne de monts sous-marins du sud des Açores : un banc d’essai évolutif?

Sur les pentes de l’étage bathyal, les coraux scléactiniaires branchus produisent des constructions tridimensionnelles et des débris qui sont des substrats durs particulièrement favorables aux bryozoaires. Des prélèvements de « coraux d’eau froide », principalement *Madrepora oculata* Linnaeus, 1758, récoltés sur six monts sous-marins au sud des Açores (South Azorean Seamount Chain : SASC) ont permis un réexamen approfondi d’un bryozoaire chéilostome encroûtant unisériel, *Harmelininus uniserialis* (Harmelin, 1978), qui a révélé des traits morphologiques inattendus. Contrairement à l’apparente simplicité de sa forme de croissance constituée par des chaînes ramifiées d’autozoïdes et de kénozoïdes vicariants, cette espèce présente une grande complexité structurale causée par différents types de polymorphes. Les kénozoïdes vicariants sont à la base d’une variation clinale incluant la partie distale kénozoïdale des autozoïdes ovicellés ou non, et cinq types différents d’aviculaires, attestée par un trait morphologique commun, minuscule et surprenant. L’origine commune des kénozoïdes et des aviculaires est une innovation chez les bryozoaires chéilostomes, apparemment sans débouchés évolutifs nets. Les fonctions de ces polymorphes ne sont pas claires, à l’exception des rôles d’organe de connectivité et de protection joués par les kénozoïdes intégrés aux autozoïdes. Les kénozoïdes vicariants sont supposés stocker des métabolites dans leur grande chambre pour les redistribuer par le réseau mésenchymateux. La fonction des différents aviculaires reste énigmatique, en particulier quand différents types sont bourgeonnés par le même autozoïde. Une fonction commune des cinq types d’aviculaires pourrait être le renouvellement de l’eau au niveau de la colonie, favorisant l’apport de particules nutritives. La grande fréquence de zoïdes réparés par bourgeonnement intramural et de fragments de colonies encore vivants, l’épaisseur des parois et la grande rareté des ovicelles et des ancestrales indiquent que les colonies ont une très longue durée de vie et un taux de reproduction très bas. Ces traits et le confinement des colonies dans la couche limite sur les substrats des constructions coralliennes ont pour effet une très faible dispersion des larves et un endémisme de cette espèce à une profondeur de 600-1500 m au sud des Açores sur la pente bathyale et les monts sous-marins (SASC). Plusieurs traits de *H. uniserialis* suggèrent que c’est une espèce relictée.

MOTS CLÉS

Coraux d’eau froide,
Bryozoa,
forme de croissance,
polymorphisme,
aviculaires,
kénozoïdes,
bourgeonnement intramural,
plasticité phénotypique,
espèce relictée,
Harmelininus.

INTRODUCTION

The three-dimensional biogenic habitats created by assemblages of large azooxanthellate branched corals and other erect invertebrates developed on rugged rocky continental slopes, offshore banks and seamounts are hotspots of biodiversity in the deep-sea. These world-wide distributed deep-sea coral gardens, popularised as “cold-water corals” and included in the trendy general category of “animal forests” (e.g. Rossi *et al.* 2017), have engendered a vast amount of literature (e.g. Le Danois 1948; Freiwald *et al.* 2004; Mortensen & Fosså 2006; Roberts *et al.* 2006; McClain 2007; Buhl-Mortensen *et al.* 2010; Henry & Roberts 2017; Wienberg & Titschack 2017; Ramos *et al.* 2017; Orejas *et al.* 2021; Zhao *et al.* 2023 and references therein). Bryozoans are regular epibiotic components of the deep-sea scleractinian corals and the first synthetic data on them were published by Le Danois (1948: 176-177). In this pioneering book, a list of 53 species from coral mounds distributed from W Ireland to Galicia was compiled from works of Calvet (1906a, b; 1931), Jullien & Calvet (1903) and Nichols (1911). Further data on bryozoans living on deep-sea corals in the Atlantic and the Mediterranean are still relatively few or part of more general surveys (e.g. Gautier 1958; Ryland 1963; Harmelin 1974; Zabala *et al.* 1993; Harmelin 2006; López-Fé 2006; Souto *et al.* 2016; Berning *et al.* 2017; Rosso *et al.* 2018; Ramalho *et al.* 2020).

The present contribution to the knowledge of the bryozoan fauna of bathyal coral gardens focusses on a tiny, uniserial cribrimorph bryozoan which is particularly common on branched corals from seamounts of the South Azorean Seamount Chain (SASC). This species, initially named *Cribrilina uniserialis* Harmelin, 1978, was described from two colonies collected on the bathyal slope of São Miguel Island, Azores (Harmelin 1978). The inadequate generic affiliation of *C. uniserialis* was corrected by A. Rosso (Rosso *et al.* 2018), who assigned it to a new genus, *Harmelininus* Rosso, 2018. Abundant stored material collected during two oceanographic surveys (R/V *Calypso* 1959, R/V *Suroit Seamount 2*) on six seamounts composing the SASC allowed a more thorough examination of this species. Most colonies of this tiny uniserial species encrusted bare skeletal parts of two large, deep-water, framework-forming scleractinian corals, *Madrepora oculata* Linnaeus, 1758 and *Solenosmilia variabilis* Duncan, 1873 (e.g. Zibrowius 1980). Close scrutiny of this material by light microscopy and SEM revealed great structural complexity in both colonies and zooids, with a surprisingly high level of polymorphism, unexpected in a uniserial species. The great abundance and particular features common to variously-shaped kenozooids and avicularia raised the question of their structural relationships, functional role, and possible phyletic links with other genera. Considering the costate frontal shield of

the autozooids, *H. uniserialis* may provisionally be placed among cribrimorphs, a morphological grouping. However, its assignment to the Cribrilinae Hincks, 1879 was not maintained considering the now proved polyphyly of this family (López-Gappa *et al.* 2021; Orr *et al.* 2022).

MATERIAL AND METHODS

ORIGIN OF MATERIAL AND SPECIMEN REPOSITORY

The two type specimens of *Cribrilina uniserialis* were collected during the Biaçores cruise of the R/V *Jean Charcot* in 1971. The material examined here was dredged during cruises of the R/V *Calypso* in 1959 (1 specimen) and Seamount 2 of the R/V *Le Suroit* in 1993 (all other specimens). All these specimens were legacy of H. Zibrowius (CNRS, SME), who sorted the bryozoan-bearing material, and are deposited at the MNHN.

METHODS OF STUDY

Stereomicroscopes and SEM were used for examining and picturing the morphological characters of specimens, which were kept dry. Specimens selected for SEM observations were treated or not with bleach, and gold-palladium coated for examination with a Hitachi S-570 (SME, Marseille) and a TESCAN VEGA 3 SBU (IMM, Marseille). Measurements were taken with an eyepiece micrometre and from scales of SEM photos. Drawings were made from sketches combining observations with SEM and stereomicroscope.

ABBREVIATIONS

Col.	colony;
CWC c	old water corals;
Is.	Island;
R/V	research vessel;
SASC	South Azorean seamount chain;
SEM	scanning electronic microscope;
SMT	seamount;
Stn	sampling station.

Measurements

AV	avicularium;
AZ	autozooid;
L	length;
OV	ovicell;
KZ	kenozooid;
SD	standard deviation;
W	width;
X	mean.

Institutions

CNRS	Centre national de la Recherche scientifique, France;
IMM	Institut de Microbiologie de la Méditerranée, CNRS, Marseille;
MNHN	Muséum national d'Histoire naturelle, Paris;
SME	Station marine d'Endoume, Marseille.

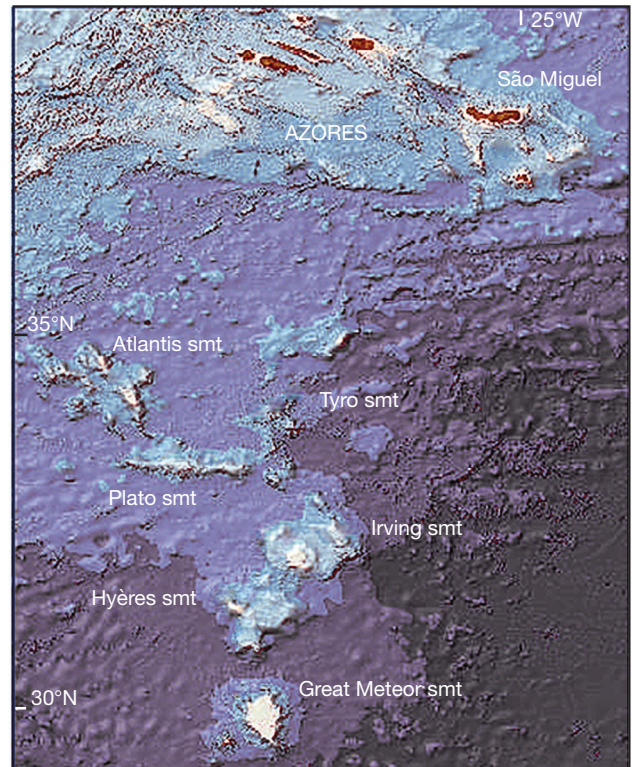


FIG. 1. — Geographical location and depth distribution of the 19 sampling stations of *Harmelinus uniserialis* (Harmelin, 1978). Abbreviations: **AT**, Atlantis Seamount; **IR**, Irving Seamount; **HY**, Hyères Seamount; **ME**, Great Meteor Seamount; **PL**, Plato Seamount; **SM**, Azores, São Miguel; **TY**, Tyro Seamount. Map downloaded from GEBCO 2019 Gridded Bathymetry Data.

RESULTS

Phylum BRYOZOA Ehrenberg, 1831
Order CHEILOSTOMATIDA Busk, 1852

Suborder FLUSTRINA Smitt, 1868

Cribrilina uniserialis Harmelin, 1978: 177, fig. 2; pl. I, fig. 2.

Harmelinus uniserialis – Rosso *in* Rosso *et al.* 2018: 430, figs 85-86.

MATERIAL EXAMINED. — **Azores Archipelago. São Miguel Is.** • Holotype of *Cribrilina uniserialis*; 1 large colony with 1 ovicelled zooid, on *Madrepora oculata*; R/V *Jean Charcot*; Biaçores Stn 197; 815 m depth; 37°49.5'N, 25°01.5'W; E São Miguel; 5.XI.1971;

MNHN-IB-2008-7908 • Paratype of *Cribrilina uniserialis*: 1 small colony, on *M. oculata*; R/V *Jean Charcot*, Biazores Stn 240; 825-810 m depth; 37°35'N, 25°32.5'W; S of São Miguel Is.; 12.XI.1971; MNHN-IB-2008-7910.

South Azorean Seamount Chain. Atlantis Seamount • Several colonies on *M. oculata*; R/V *Suroit*; Seamount 2; Stn DW262; 1160 m depth; 34°23.40'N, 30°29.10'W; 3.II.1993; MNHN • 1 colony on *Madrepora oculata*; R/V *Suroit*; Seamount 2; Stn DW263; 610 m depth; 34°25.90'N, 30°32.50'W; 3.II.1993; MNHN.

Tyro Seamount • Several colonies on *Solenosmilia variabilis*; R/V *Suroit*; Seamount 2; Stn DW276; 1520 m depth; 34°02.10'N, 28°19.00'W; 6.II.1993; MNHN • Several colonies on *M. oculata*; R/V *Suroit*; Seamount 2; Stn DW277; 1000-845 m depth; 33°59.92'N, 28°20.56'W; 6.II.1993; MNHN • Several colonies on *M. oculata*; R/V *Suroit*; Seamount Stn DW278; 890 m depth; 33°57.80'N, 28°22.40'W; 6.II.1993; MNHN • Several colonies on fragments of *M. oculata*; R/V *Suroit*; Seamount 2; Stn DW279; 805 m depth; 33°55.60'N, 28°23.70'W; 6.II.1993; MNHN.

Plato Seamount • Small colonies on spines of sea-urchin; R/V *Suroit*; Seamount 2; Stn DW248; 670-735 m depth; 33°13.58'N, 29°32.49'W; 1.II.1993; MNHN • 1 colony, on pebble darkened by Mn-Fe oxides; R/V *Suroit*; Seamount 2; Stn DW251; 900-935 m depth; 33°13.47'N, 29°38.39'W; 1.II.1993; MNHN.

Irving Seamount • Several colonies on fragments of *M. oculata*; R/V *Suroit*; Seamount 2, Stn DW221; 1160-1180 m depth; 32°17.84'N, 28°15.32'W; 28.I.1993; MNHN • Several colonies on fragments of *M. oculata*; R/V *Suroit*; Seamount 2; Stn DW223; 995 m depth; 32°19.69'N, 28°16.50'W; 28.I.1993; MNHN • Several colonies on fragments of *M. oculata*; R/V *Suroit*; Seamount 2; Stn DE227; 695 m depth; 32°07.20'N, 28°08.70'W; 28.I.1993; MNHN • Several colonies on fragments of *M. oculata*; R/V *Suroit*; Seamount 2, Stn DW 231; 745-740 m depth; 32°01.5'N, 27°24.50'W; 29.I.1993; MNHN.

Hyeres Seamount • 1 colony (SEM pictures) on stylasterid skeleton; R/V *Calypso*, survey 1959, 620-700 m depth, 31°27.7'N, 28°55.6'W; 13.VIII.1959; MNHN • Several colonies on skeleton of *M. oculata*; R/V *Suroit*; Seamount 2; Stn DW184; 706-675 m depth; 31°24.40'N, 28°52.3'W; 13.I.1993; MNHN • Several colonies, on skeleton of *M. oculata*; R/V *Suroit*; Seamount 2; Stn DW200; 1060 m depth; 31°19.10'N, 28°36.00'W; 18.I.1993; MNHN • 1 colony, on skeleton of *M. oculata*; R/V *Suroit*; Seamount 2; Stn DW203; 845 m depth; 31°09.50'N, 28°43.50'W; 19.I.1993; MNHN.

Great Meteor Bank • 1 fragmented colony, on rock fragment darkened by Mn-Fe oxides; R/V *Suroit*; Seamount 2; Stn DW180; 1575-1610 m depth; 30°04.09'N, 28°45.09'W; 15.I.1993; MNHN.

AMENDED DESCRIPTION

Colony encrusting, fundamentally uniserial, consisting of a primary linear chain formed by distally budded caudate autozooids and kenozooids, from which secondary ramifications are bilaterally budded (Fig. 2C-E), their development possibly leading to the spotty formation of reticulate or pseudo-pluriserial subcolonies (Fig. 3C, E). Reticulate structure formed in three ways: 1) intersecting of two overlapping branches; 2) real connection of two branches via their communication pores; and 3) distal zooid of a branch abutted onto the lateral side of another branch (Figs 3A; 8C). Small pseudo-pluriserial subcolonies can develop by disordered aggregation of autozooids with reduced cauda and kenozooids, both being more or less interconnected.

Autozooids with a cormidial structure, typically with a proximal cauda budded by the parent zooid, widening distally to form the autozooidal chamber with gymnocrystal lateral walls and a costate shield and, distally to the orifice

TABLE 1. — *Harmelinus uniserialis* (Harmelin, 1978) – Meristic and size data. Origin of data – Azores bathyal slope: Biazores Stn 197; SASC: Seamount 2 - Hyeres SMT (DW 184, DW 200), Irving SMT (DE 227), Atlantis SMT (DW 264), Tyro SMT (DW 276, SW 278, DW 279). Mean ± SD (range; data number).

	AZ non Ov	AZ Ov
Costal shield L	342 ± 25 (290-410; 46)	374 ± 57 (255-475; 13)
Costal shield W	250 ± 34 (180-105; 46)	307 ± 45 (255-400; 13)
Costae N	16.8 ± 1.8 (14-21; 142)	15-19 (6)
Costae oral bar W	64 ± 13 (45-95; 16)	–
Costae below oral bar W	39 ± 7 (25-50; 16)	–
Orifice L	83 ± 8 (75-97; 21)	100 ± 10 (85-112; 6)
Orifice W	106 ± 12 (85-120; 21)	128 ± 7 (120+135; 5)
Ov L	–	255 ± 48 (220-340; 9)
Ov W	–	266 ± 37 (220-340; 9)
KZ L	411 ± 90 (315-590; 16)	–
KZ W	312 ± 68 (180+450; 16)	–
Foramen diameter	20-23	18-20

and fully integrated to it, a distal kenozooid forming a cap from which is budded a daughter autozooid or a vicarious kenozooid. Caudae semi-cylindrical, long (200–400 µm) and narrow or much shorter (40 µm) or nearly absent, with a smooth gymnocrystal wall through which a tubular coelomic lumen is visible, broadening distally to become the proximal part of the main chamber. Main chamber with lateral walls with a greater or lesser degree of slope, bearing one to three elongated pore chambers on each side, a costate frontal shield made of 14–21 costae (Table 1). Costae with upper surface rounded, smooth and without pematidia (lumen pores), separated on each side by a slit without intercostal bridges, generally narrow but occasionally much wider; paired costae sometimes of different width, fused in the midline and forming a low, irregular bulge; distalmost pair of costae playing the role of an apertural bar, similar to the proximal ones but wider (60–80 µm vs 35–50 µm), sometimes forming an obtuse angle; costae of the proximal corner of the costate shield much smaller than the others. Orifice large, terminal, laterally and distally delimited by a semicircular calcified frame, sometimes very thick and made of multiple calcified layers produced by intramural budding (see below), proximally edged by the distalmost pair of costae; operculum with a slightly convex proximal edge. Oral spines absent. Distal kenozooid prolonging the autozooidal chamber below the level of the orifice, in the shape of the upper half of a truncated cone (“kenozooidal cap”) at the top of which is budded a distal daughter zooid (Fig. 4A-D), its chamber connected to the maternal autozooid by a foramen, i.e., a large, circular pore (18–25 µm in diameter) open through the transverse wall (Figs 4A, B; 9E), assumed to function as a gigantic pore chamber.

Ovicelled zooids very infrequent (< 1.5% of autozooids, Fig. 3A), often grouped, with costate shield, apertural bar and orifice broader than in non-ovicelled zooids (Table 1). Ovicell prominent, apparently cleithral (Fig. 5); brood chamber budded from the transverse wall of the maternal autozooid (Fig. 5C, D); oecium bilobed with a frontal medial suture, produced by a basal oecial kenozooid with

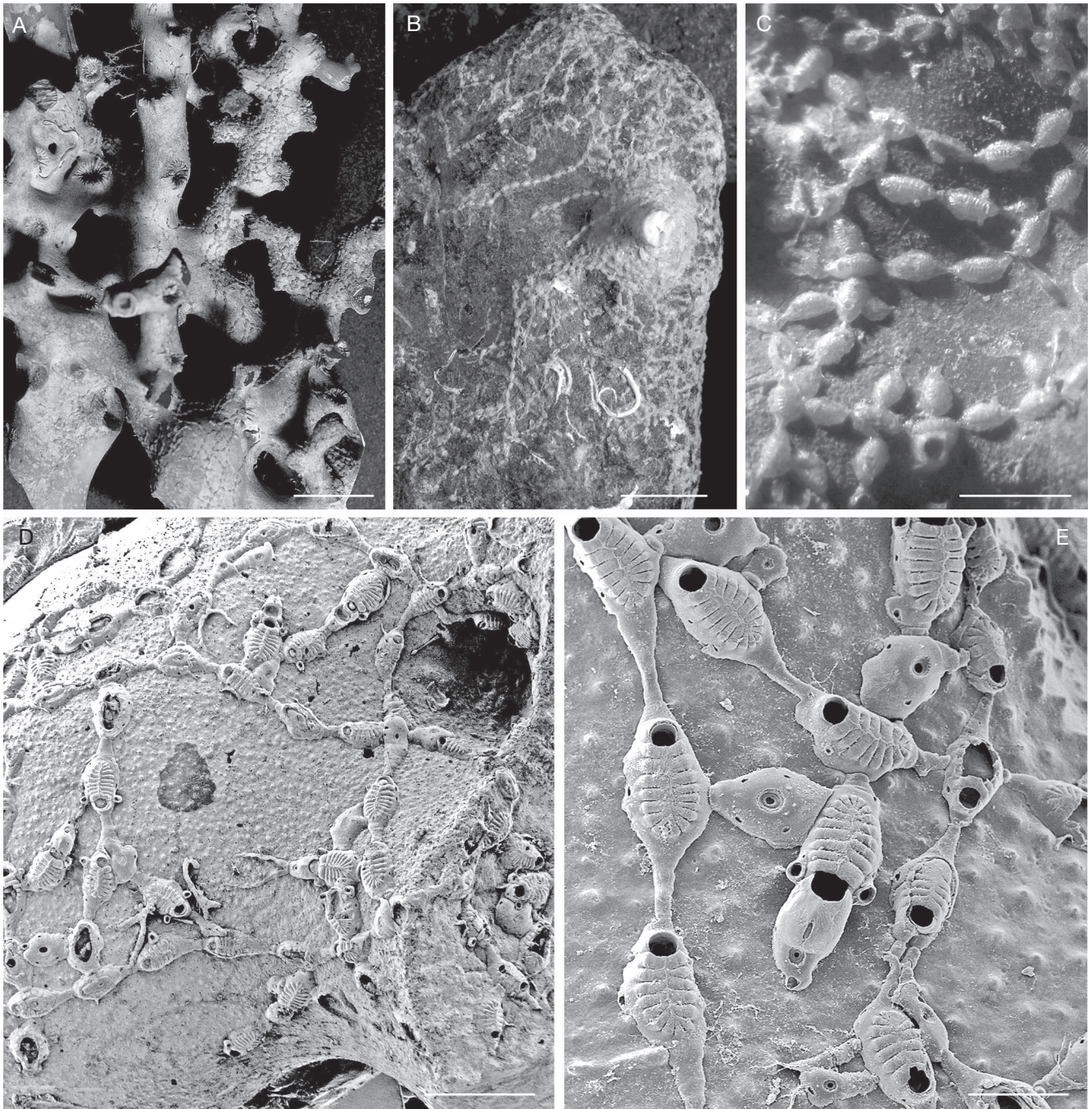


FIG. 2. — *Harmelinus uniserialis* (Harmelin, 1978), colonized substrates and general aspect of colonies: **A**, fragment of *Madrepora oculata* Linnaeus, 1758; **B**, pebble; **C**, part of colony showing non-caudate autozooids, optical view; **D**, other aspect of the same colony, SEM view; **E**, part of colony with typical features. Origin: A, C, D, Hyères SMT, Stn DW 184; B, Irving SMT, Stn DW 251; E, Tyro SMT, Stn DW 276. Scale bars: A, B, 1 cm; C, D, 1 mm; E, 400 μ m.

a frontally apparent distal part from which is budded a distal zooid (Fig. 5A, B). Ooecial kenozooid communicating with the maternal autozooid by a foramen (Fig. 5C, D) identical to that connecting a non-ovicelled autozooid to its distal cap; basal part with a pore-chamber on each side, producing a bilobate outfold with a smooth surface without pores, a thick (20 μ m), alveolar wall (ectooecium), which is proximally and basally divided in two sheets forming each lobe (Fig. 5D). Medial suture of the two lobes closed or

partially open with an elongated distal window reaching the distal edge of the ovicell (Fig. 5A, B). Distal, frontally apparent part of the ooecial kenozooid (Fig. 5A, C, D) larger than the distal cap of non-ovicelled zooids, with a frontal, circular window open near the distal edge of the medial suture, similar to that present on vicarious kenozooids (see below), opening on a thick, multi-layered wall and a small central opesia; porous knobs (see below) present near this window (Fig. 5A, B).

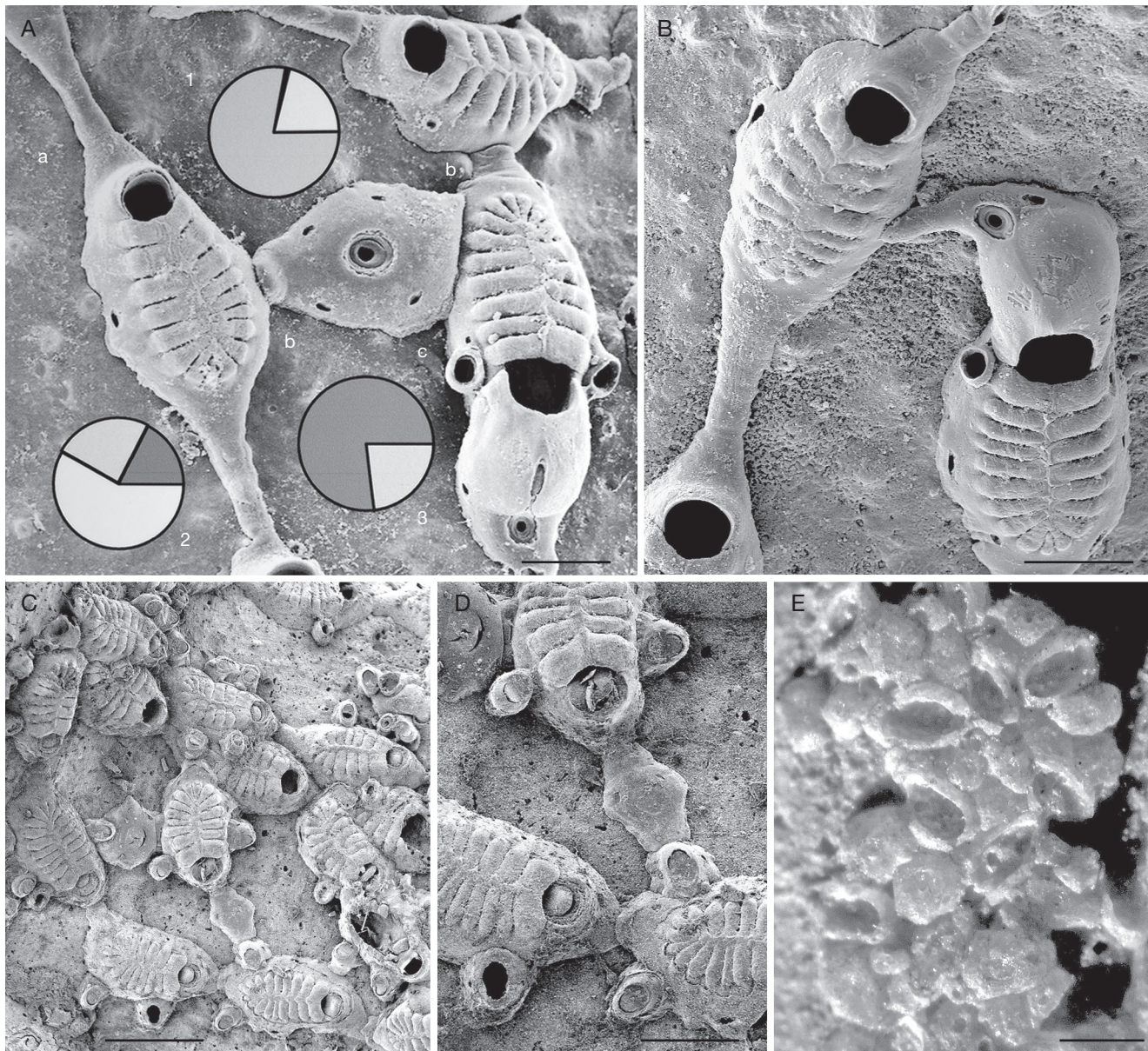


FIG. 3. — *Harmelinus uniserialis* (Harmelin, 1978), structure of colonies and graphs of zooid proportions: **A - a**, distal budding of autozooids with long cauda; **b**, lateral budding of autozooid (AZ) and kenozooid (KZ); **c**, abutment of kenozooid on ovicelled AZ - 1, KZ (21% white), non-ovicelled AZ (78% grey), ovicelled AZ (1% black); 2, non-ovicelled AZ without avicularium (AV) (59% white), with one AV (24% grey), with two AV (17% dark); 3, ovicelled AZ, with one AV (23% grey), with two AV (77% dark); **B**, ovicellar kenozooid connected to the lateral pore chamber of an adjacent AZ; **C**, zooidal aggregation with 12 AZ without cauda, 28 AV and three KZ; **D**, clustering of three AZ without cauda, involving a small vicarious kenozooid abutted on to an avicularium (AV4) in proximal position, co-occurring with another AV type (AV2); **E**, dense aggregation of KZ. Origin: A, B, Tyro SMT, Stn DW 276; C, D, E, Tyro SMT, Stn DW 278. Scale bars: A, C, E, 400 µm; B, D, 200 µm.

TABLE 2. — *Harmelinus uniserialis* (Harmelin, 1978) – Avicularia types. Occurrence on the Azores bathyal slope, São Miguel (**ABS**) and four seamounts of the SASC of the five types of avicularia on autozooids ovicelled (**AZOv**) or not (**AZnoOv**), and on vicarious kenozooids (**KZ**), bearing or not porous knobs (**PK**). Origin of data: **ABS**, Bjaçores Stn 197, 240; **Tyro** (DW 276, DW 278, DW 279); **Plato** (DW 251); **Irving** (DW 221, DW 223, DW 227, DW 231); Hyères (DW 184, DW200).

AV types	AZnoOv	AZOv	KZ	PK	ABS	Tyro	Plato	Irving	Hyères
AV1: Columnar	+	+	-	-	AZ	AZ	-	-	AZ
AV2: Globular	+	+	-	-	-	AZ	AZ	AZ	AZ
AV3: Adnate	-	+	-	+	-	AZ	-	AZ	AZ
AV4: Pyramidal	+	+	+	+	-	AZ, KZ	AZ	AZ	AZ
AV5: Giant	-	-	+	+	-	AZ, KZ	-	-	-

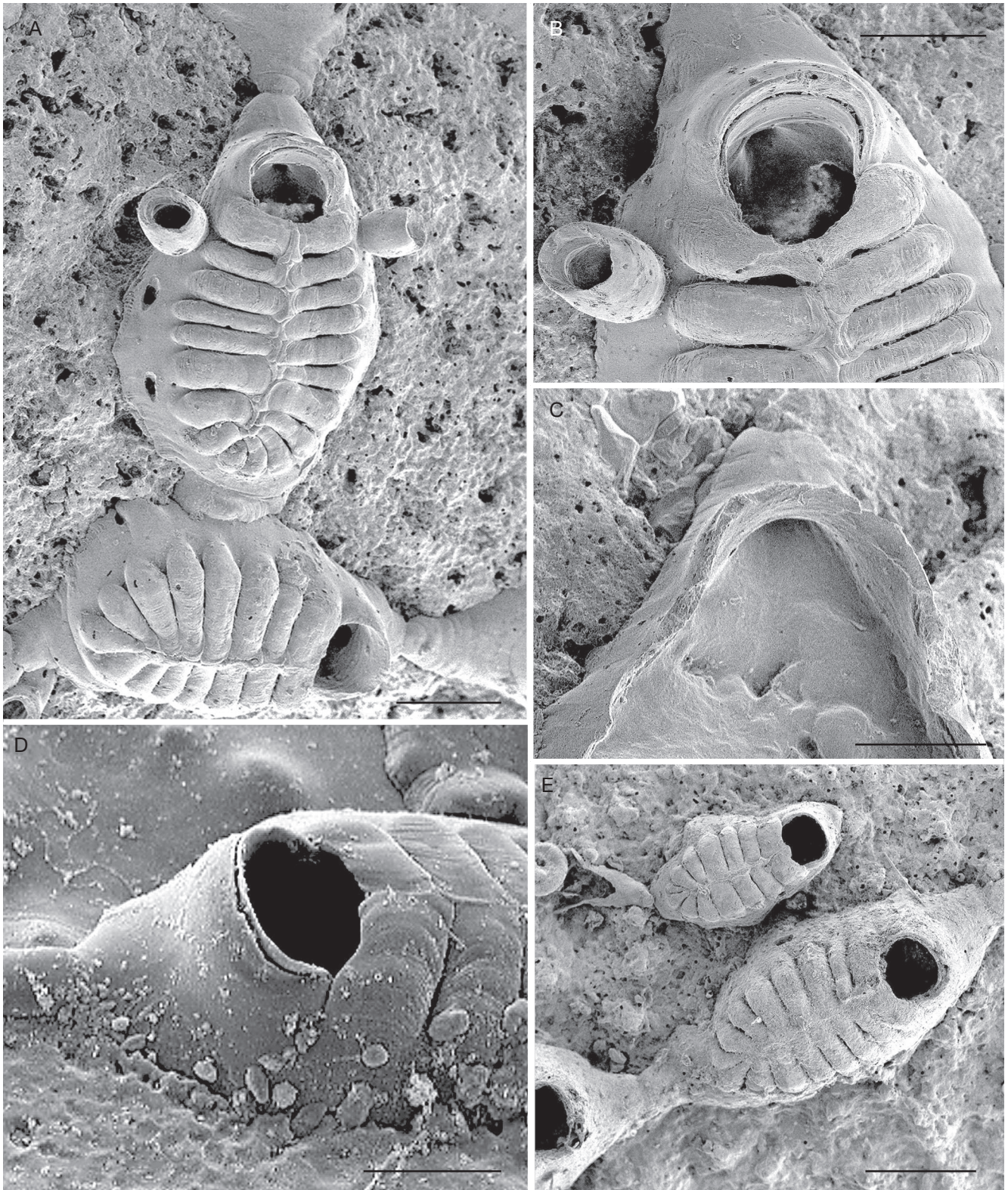


FIG. 4. — *Harmelinus uniserialis* (Harmelin, 1978), morphology of non ovicelled autozooids and ancestrula: **A**, autozooid (AZ) with two avicularia (AV1) and distal budding from the kenozooidal cap, budded from the lateral side of another AZ; **B**, AZ distal part with a AV1 avicularium, note the foramen through the transverse wall separating the AZ orifice from the kenozooidal cap (idem in **A**), the concave proximal edge of the orifice and the unequal size of costae; **C**, eroded kenozooidal cap showing its subconical chamber and the broken base of the AZ transverse wall; **D**, distal part of AZ showing the boundary between the kenozooidal cap and the orifice frame; **E**, ancestrula and AZ, note their contrasting sizes and the proximal budding by the ancestrula. Origin: A, B, C, Hyères SMT, Stn DW 200; D, E, Tyro SMT, Stn DW 276. Scale bars: A, B, E, 200 μ m; C, D, 100 μ m.

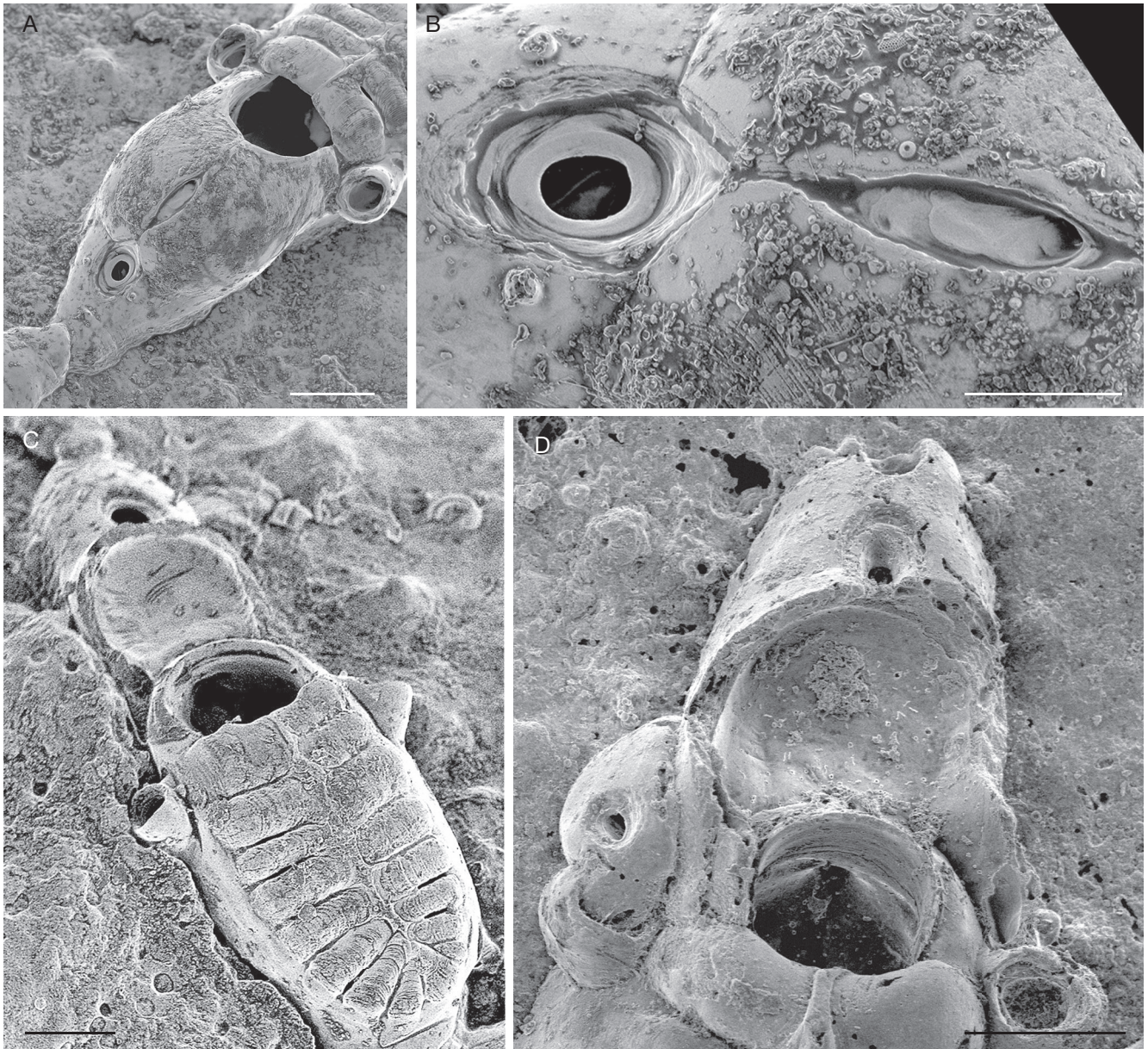


FIG. 5. — *Harmelinus uniserialis* (Harmelin, 1978), structure of the ovicell: **A**, distal part of an ovicelled autozooid bearing two adnate avicularia (AV3), with open medial slit, and oocyst kenozooid budding a distal zooid; **B**, close-up of the same ovicell, medial slit showing the two layers of the bivalved oocyst wall, the dorsal window of the distal kenozooid with thick gymnocyst layers and oval opesia, and two lateral porous knobs; **C**, ovicell in formation showing the floor of the brood chamber budded by the maternal autozooid; **D**, broken ovicell showing the thickness of the frontal wall and the two proximal layers, and the foramen open through the transverse wall. Origin: A, B, C, Tyro SMT, Stn DW 276; D, Hyères SMT, Stn DW 184. Scale bars: A, C, D, 100 µm; B, 50 µm.

Avicularia displaying a variety of shapes assigned to five different morphs (AV 1-5), budded by autozooids (AV 1-5) or vicarious kenozooids (AV 4 & 5) (Figs 6; 8). All avicularian morphs with semicircular rostrum and mandible, not prominent, operculum and opesia rounded with a narrow cryptocyst, no pivot bar or hinges, and two large basal pores; present on all ovicelled autozooids, less frequently present on non-ovicelled zooids (Table 2).

AV1: “columnar” (Figs 6B; 8D), with a slightly barrel-shaped column, two large basal pores in opposite position on the proximal and distal sides, infrequent, adventitious on ovicelled and

non-ovicelled autozooids, single or paired, budded on the vertical wall between the apertural bar or the preceding costa, uncalcified area oval, with semicircular opesia a little broader than the mandible, a narrow rim of cryptocyst slightly broader proximally.

AV2: “globular” (Figs 6G, H; 8E), similar to AV1 but shorter and rostrum with a wider, rounded rim, adventitious on ovicelled and non-ovicelled autozooids

AV3: “adnate” (Figs 6A, D; 8A), with a triangular silhouette, adventitious on ovicelled zooids, two large basal pores in opposite position similar to those of AV1, occurrence of peripheral porous knobs (Figs 6D; 8A).

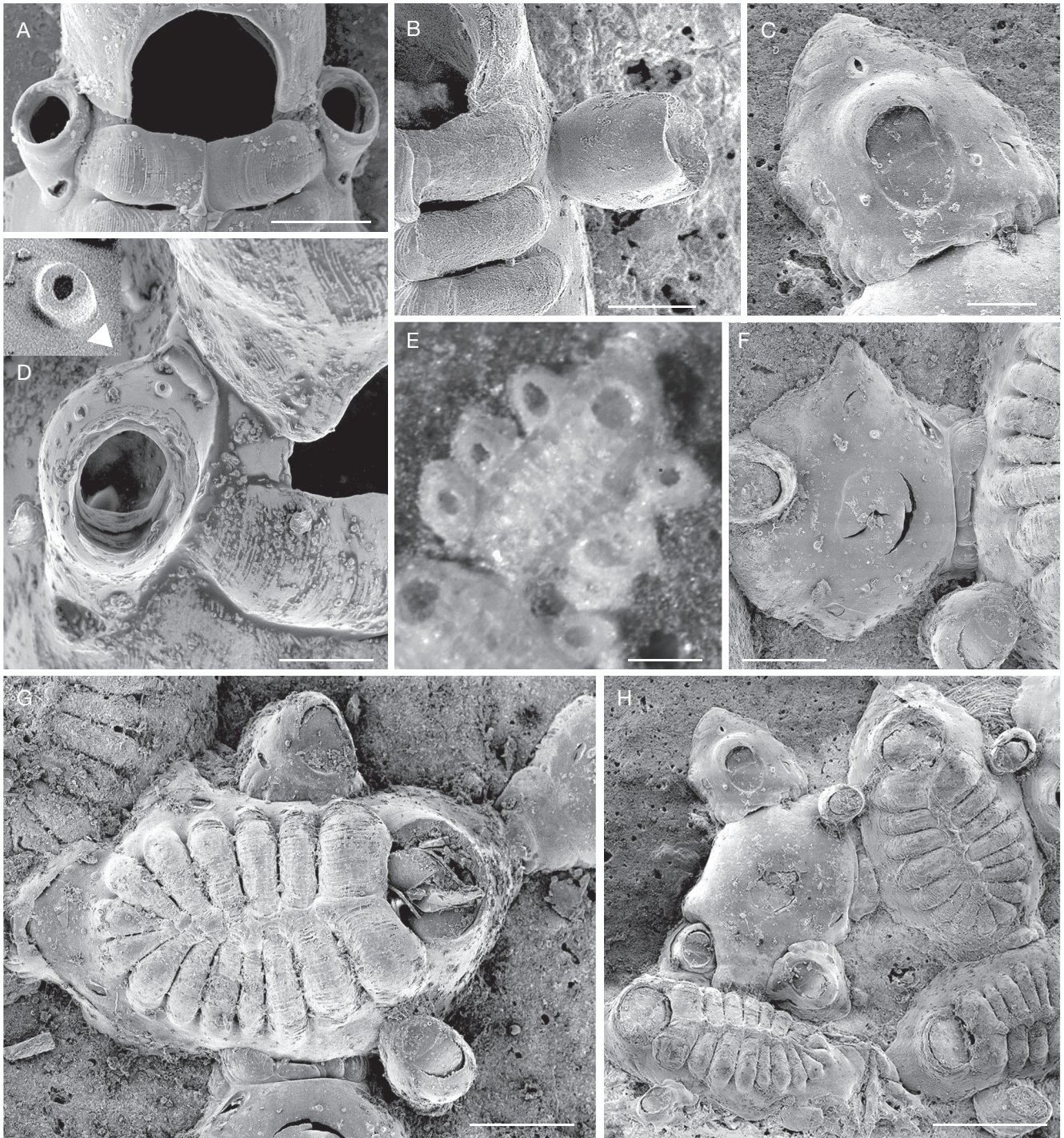


FIG. 6. — *Harmelinus uniserialis* (Harmelin, 1978), different types of avicularia: **A**, “adnate” type (AV3) on an ovicelled AZ; **B**, “columnar” type (AV1); **C**, “giant” type (AV5) with three porous knobs, one incompletely formed, distal to the slightly prominent rostrum; **D**, “adnate” type, adventitious to an ovicelled AZ, with a large pore chamber and three porous knobs (inset: enlarged view of a knob); **E**, autozooid with five “pyramidal” morphs (AV4) budded from lateral walls; **F**, vicarious kenozooid with thickened cuticle persisting on the frontal gymnocyst and the central window; **G**, globular and pyramidal avicularia budded by the same AZ; **H**, three globular (AV2), one “giant” (AV5) and one “pyramidal” (AV4) avicularia budded by two AZ and a vicarious KZ with persistent cuticular layer; Origin: A, D, Tyro SMT, Stn DW 276; B, Hyères SMT, Stn DW 200; C, E, F, G, H, Tyro SMT, Stn DW 278. Scale bars: B, C, D, 50 μ m; A, F, G, 100 μ m; D, H, 200 μ m.

AV4: “pyramidal” (Figs 6E, G; 8B), with a broad base partly resting on the substratum, column sculpted by vertical grooves, single, sometimes paired with AV2 when distolaterally budded by a non-ovicelled zooid (Fig. 6G), or several, up to five, laterally budded from both sides of

an autozooid (Fig. 6E), occasionally budded by a vicarious kenozooid (Fig. 6H); presence of 2-3 porous knobs (Fig. 8B).

AV5: “giant” (Figs 6C, H; 8C), rare (only two cases observed), laterally budded by a vicarious kenozooid (Fig. 6H)

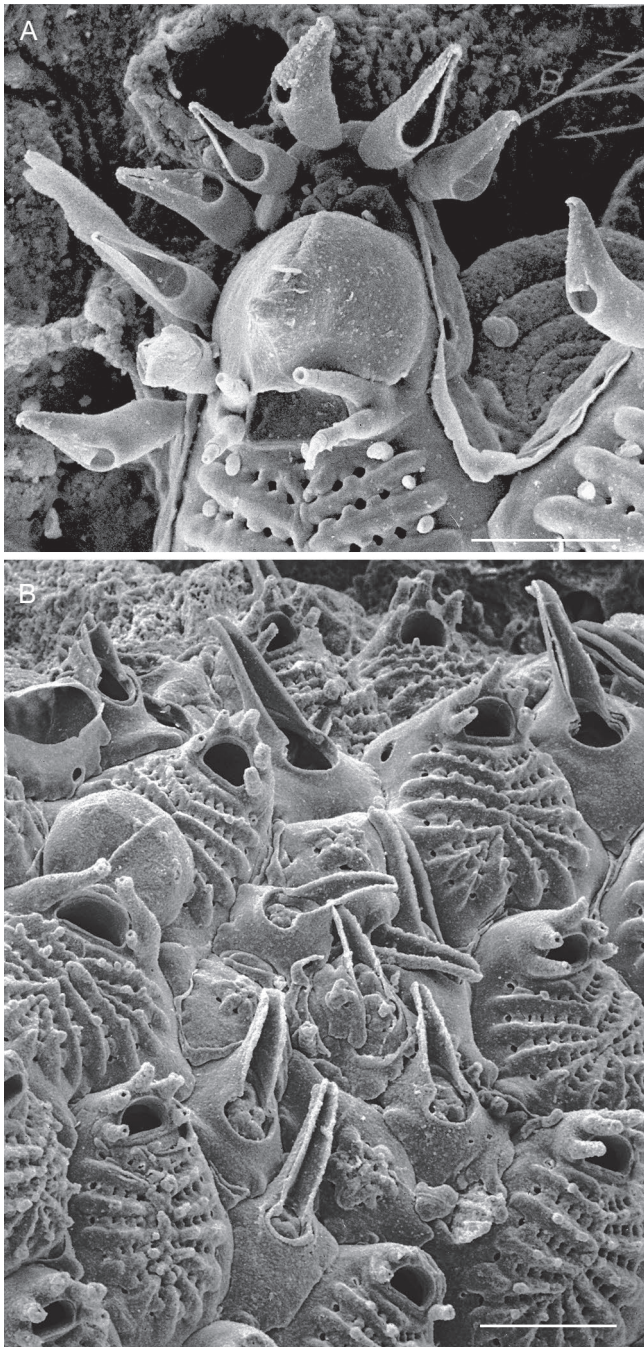


FIG. 7. — **A**, *Glabrilaria pedunculata* (Gautier, 1956), ovicelled zooid crowned by seven pedunculate avicularia; **B**, *Cribrilaria cassidainsis* Harmelin, 1984, colony edge with ten interzooidal avicularia. Origin: A, B, Mediterranean Sea, France, La Ciotat, 3PP Cave, 40–60 m inside; A, B, 20–24 m depth. Scale bars: A, 100 μ m; B, 200 μ m.

or a non-ovicelled autozooid; chamber very large, slightly convex, roughly pentagonal with a broad base resting on the substratum, adjoining the parental zooid with wrinkles at the budding locus, a pair of lateral pore chambers; mandible and opesia area centrally located, both similarly semicircular, the rostrum a little smaller and edged by a low rim; occurrence of porous knobs (see below), one distal to the rostrum and four around the opesia (Figs 6C; 8C).

Vicarious kenozooids (“vicariozooids”, Silèn 1977; Schack *et al.* 2019) frequent (mean: 21% up to 56% on a pebble from DW251; Fig. 3E), produced by distal or lateral budding from an autozooid or a kenozooid, irregularly shaped and sized (Figs 3A, 3D; 9A–F; 10A; Table 1), often as large as an autozooid, sometimes larger or much smaller, polygonal with rounded corners, eventually with a short conical cauda when included in a zooid chain, proximal base upwardly protruding on the wall of the parental zooid when laterally budded (Figs 3A; 9D, E); distal edge very wide and rectilinear when abutting on to the lateral side of an autozooid (Figs 3A; 8C, D). Calcified frontal wall a smooth, convex gymnocyst, entirely covered by a thick, persistent cuticle (6F, H) with a pair of fusiform pore chambers placed at half height on each lateral side and a large central window (90–110 μ m) oval to circular, opening onto the thick, stratified gymnocystal wall (Fig. 9D–F), the innermost layer, a smooth cryptocystal rim surrounding a small, rounded opesia (diameter: 30–40 μ m) opening on a large, irregularly shaped coelomic chamber visible by light microscopy (Fig. 8A, B), with lateral tubular extensions connected to adjacent zooids, whose assumed function is to ensure the continuity of the funicular system. Presence on the frontal wall, close to the central window, of several (up to 7) short porous knobs (diameter: 8–11 μ m) with open tips (Figs 8E, F). Secondary kenozooids eventually produced by intramural budding within the cystid of a damaged or senescent autozooid (see below).

Ancestrula rare, similar to non-ovicelled autozooids but considerably smaller (Fig. 4E); orifice relatively large, costate frontal shield composed of 14 costae, with a broad apertural bar; distal cap small. Zone of astogenetic change consisting of a uniserial file of daughter zooids similar in shape and size to the ancestrula, produced by the latter from a distal or a proximal budding locus (Fig. 4E).

DISCUSSION

MORPHOLOGICAL TRAITS

The initial examination of two specimens of this species (Harmelin 1978) by light microscopy revealed the most apparent morphological traits: 1) a uniserial encrusting growth-form resulting from the distal and bilateral budding of caudate autozooids and large vicarious kenozooids with a central pore and an internal chamber, considered to be aborted autozooids; 2) autozooids with a costate shield made of 13–16 contiguous costae without pelmata, including an unmodified apertural bar; 3) an orifice without spines; and 4) a prominent, cleithral ovicell with a medial slit, associated with a basal and distal kenozooid bearing a structure identified as an avicularium. The existence of an intercostal space without bridges between successive costae was later described by Rosso *et al.* (2018) from two SEM pictures of the holotype. The new, abundant material of *H. uniserialis* from the SASC and the SEM examination of several specimens have confirmed most of these traits, but also revealed unexpected features contributing to a remarkable morphological complexity at both colony and zooid levels.

Branching patterns: variations around uniserial growth-form

The colony of *H. uniserialis* is fundamentally uniserial with a primary chain of distally budded caudate autozooids and large, vesicular kenozooids from which secondary branches are bilaterally budded. Distal budding from autozooids is always achieved from a frontally apparent kenozooidal chamber (“interzoooid”; Silén 1977: 206), consisting of a distal cap in non-ovicelled autozooids, and an ooecial kenozooid in ovicelled zooids, both functioning as a gigantic pore chamber communicating with the proximal autozooid chamber through a foramen (Figs 4A, B; 5D; 10E). Lateral budding is produced from one or several budding loci. The wide spacing of lophophores along branches, characteristic of uniserial colonies, is amplified in *H. uniserialis* by the long proximal cauda of autozooids (up to *c.* 400 µm in unbranched files) and the frequent occurrence of large, vicarious kenozooids. Zooid spacing may be diminished by the more or less well-ordered reticulation of branches or their juxtaposition (Figs 2C; 3C), that may occur on particular locations on the substrate. Reticulate branching is achieved in three ways: 1) crossing of branches by simple overgrowth; 2) bonding of the distal end of a branch to the lateral side of another branch (abutment); and 3) connection through pores between zooids (AZ, KZ, AV) of two distinct colony parts, one distal and one lateral (Figs 2D, E; 3). In this latter case, connectivity between branches enables potential exchanges of metabolites and information by the way of the funicular system (Lutaud 1983; Lidgard & Jackson 1989, fig. 1. Best & Thorpe 2002; Schwaha *et al.* 2020). When a kenozooid forms a lateral bridge between two branches placed side by side, its proximal end, budded by the parent zooid, is recognizable by its folded shape while its distal end, simply abutted on to the other branch, is in most cases very wide (Fig. 3A). These different patterns of growth can lead to a disordered aggregation of zooids, creating pseudo-pluriserial subcolonies (Fig. 3C, E), assumed to be induced by particular micro-environmental conditions (see below). Partial mortality and fission of colonies are regular processes in encrusting bryozoans (Jackson & Winston 1981; Winston 1981; McKinney & Jackson 1989). The long-lived, poorly dynamic, uniserial colonies of *H. uniserialis* are particularly subject to fragmentation of zooid chains. Moreover, the early stages of colonies are rarely detectable due to the rarity of an ancestrula. Boundaries of colonies are therefore quite indistinct. A similar multiplication of colony fragments or ramets was described in two uniserial fossil species, the cyclostome *Corynotrypa* Bassler, 1911 (Taylor 1985) and the cheilostome *Herpetopora* Lang, 1914 (Taylor 1988), the latter possessing similar modes of branch connection (see below).

Costate shield: imperfectly designed and weakly protective

The present material confirms the observation by Rosso *et al.* (2018) that the successive costae are separated by a linear space not interrupted by bridges. However, the width of these intercostal spaces varies notably among sites, between coexisting colonies, and even within a colony. Spacing of

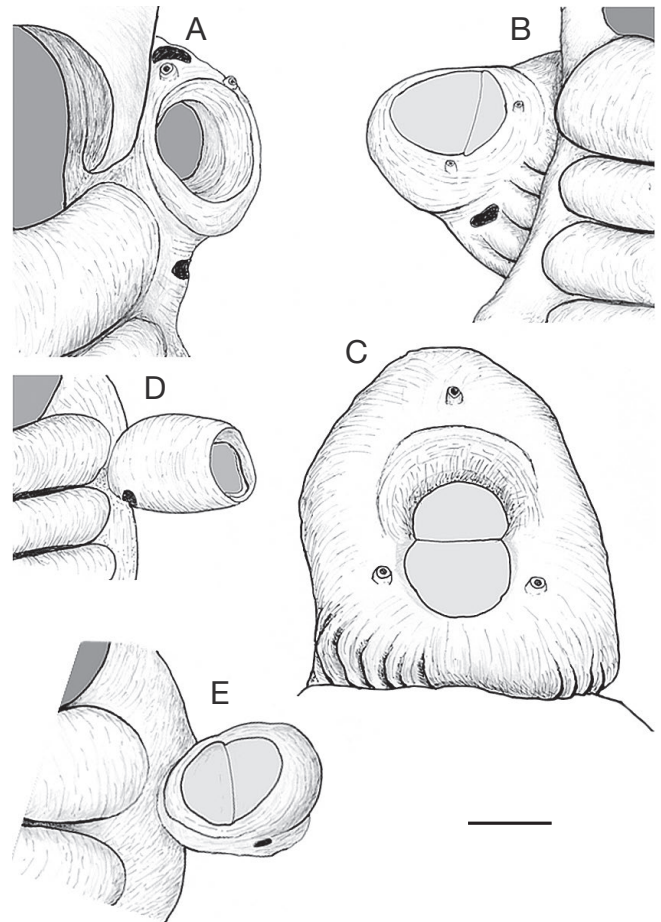


FIG. 8. — *Harmelinus uniserialis* (Harmelin, 1978), drawings of five types of avicularia: A, “adnate” (AV3); B, “pyramidal” (AV4); C, “giant” (AV5); D, “columnar” (AV1); E, “globular” (AV2). Origin: copied from diverse SEM pictures. Scale bar: 50 µm.

costae can be very narrow (e.g. in colonies from Stn DW200) or, in contrast, very wide, as in some zooids of the deepest specimen in the collection, encrusting a rock fragment from the Great Meteor Bank (Stn DW180, 1600 m depth). SEM examination of specimens has shown that costae are not flat, as noted by A. Rosso (Rosso *et al.* 2018), but have a convex frontal surface (Fig. 10). In contrast with the common structure of the spinocyst of cribrimorphs, which is formed with similarly-sized paired costae, the costate shield of *H. uniserialis* can comprise narrow and very wide costae intercalated between normally-sized costae (Figs 3Ac; 4A, B; 5C). Features of the distalmost pair of costae edging the orifice may vary considerably, even within the same colony, with the distal edge more or less rectilinear or concave, the two costae unequal in size and also considerably wider than the other costae of the same frontal shield (Figs 4B; 5C; 6G). Interestingly, the encrusting pluriserial electrid *Aspidelectra melolontha* (Landsborough, 1852) shows a similar asymmetry and variability in the width of the spinous processes over-arching the opesia (cf. photo by Hans De Blauwe, WoRMS Image, accessed on 22.V.2023).

Ovicell: rare, complex and armored

Ovicelled zooids are rare in *H. uniserialis* (Fig. 3A). Consequently, details of the successive stages of ovicell construction were not observed. Moreover, as stressed by Ostrovsky (2013), the type of oecium formation is better defined in conjunction with anatomical studies, which were not possible with this material stored dry. The structure of the brood chamber was interpreted from SEM examination of an old broken brood chamber and another in formation (Fig. 5C, D). The floor of the brood chamber is apparently budded by the maternal zooid at an early stage (Fig. 5C). Furthermore, given the similar position of the foramen in the orifice of both non-ovicelled and ovicelled autozooids (Figs 4B vs 5B), one may argue that the distal cap of non-ovicelled zooids has the same ontogenetic origin as the oecial kenozooid. However, the successive stages of the construction of this oecium with a composite structure are enigmatic. In particular, does this structure with very thick walls and two-layered valves result from a primary construction, or from secondary events including intramural budding (see below)? The two layers of the valves are visible within the window which may remain open at the medial suture (Fig. 5B), and also in the proximal part of a broken ovicell (Fig. 5D). The frontally exposed part of the oecial kenozooid exhibits typical features of the vicarious kenozooids of this species, i.e., a membranous frontal wall covering a thick, multilayered calcified wall with an inner rounded opesia and, around this window, three porous knobs (Fig. 5B). The ovicelled autozooids of *H. uniserialis* are thus a distinctive example of a cormidial unit (Schack *et al.* 2019), with the oecial kenozooid and the adventitious avicularia as submodules. Considering the likely origin of the floor of the brood chamber, apparently produced by the distal wall of the maternal zooid, and that of the oecium wall, built by an intimately associated kenozooid, the ovicell of *H. uniserialis* may belong to the type 2 defined by Ostrovsky (2013). Given the great thickness of the oecial walls, the brood chamber provides a high degree of protection to embryos, which may partly compensate the rarity of ovicells. Brooding is expected to be energy-expensive (McKinney & Jackson 1989) while the microenvironment in which *H. uniserialis* grows is assumed to be highly oligotrophic with unpredictable food inputs (see below). It is therefore likely that the concentration of ovicells in a few locations is driven by food availability, such as aggregations of autozooids.

Avicularia: basic structure but outstanding phenotypic diversity

Avicularia are the most enigmatic trait of *H. uniserialis*. The abundance and shape diversity of these polymorphs contrast strikingly with their rarity in other uniserial cheilostomes. For example, among the seven uniserial calloporid genera listed by Rosso & Taylor (2002), only two Cretaceous ones (*Hapsidora* Lang, 1917; *Marssonopora* Lang, 1914) are provided with avicularia. Many other examples can be found in other cheilostome genera. Only one pair of avicularia was present in the original material of *Cribrilina uniserialis* from the Azores. These avicularia were adventitious on an ovicelled zooid, described as “petits, arrondis”, figured with

a short column, oval in section (Harmelin 1978, fig. 2), corresponding to the columnar type (AV1). Data on the frequency of avicularia in colonies from six seamounts of the SASC (Fig. 3A) confirm that all ovicelled zooids bear one or two adventitious avicularia while only 42% of non-ovicelled autozooids bear one or several avicularia. Avicularia-bearing zooids are less frequent in linear chains than in colony parts where zooids are aggregated. In such aggregations, avicularia can be more numerous than autozooids and kenozooids (Fig. 3C). These avicularia exhibit five different morphotypes (columnar, globular, adnate, pyramidal and giant; Figs 6; 8), whose distinctive traits are better distinguished by SEM. In all these avicularia, whatever their general shape, the opesia and mandibular areas are poorly differentiated, with a simple morphological structure without pivot bar or prominent hinges, short and rounded rostrum and mandible, and the inner cryptocyst forming a continuous narrow rim without clear distinction between the opesia and the mandibular areas. However, the five avicularian morphotypes differ in the extent of parental integration. Two of them, columnar and adnate, are typically adventitious, a dominant type in deep-sea species (Hayward 1981). By contrast, the giant type (AV5; Fig. 6C, F) is laterally-budded and rests on the substratum, only connected to the parent zooid by its proximal side. In uniserial colonies, this pattern may be equivalent to that of interzooidal avicularia in pluriserial colonies (see Carter *et al.* 2010a, b and Schack *et al.* 2018 for the features of the four types of avicularia). The shape and position of the globular and pyramidal morphotypes (Figs 6G, H; 8B, E), may indicate an intermediate status between the two adventitious avicularia and the “interzooidal” giant avicularian morph. Other puzzling peculiarities characterize these avicularia: 1) possible budding of two different morphs by a parental zooid, e.g. globular and pyramidal symmetrically placed on the distolateral sides of a non-ovicelled autozooid (Fig. 6G), or pyramidal and giant jointly budded by a parental kenozooid (Fig. 6H) or autozooid (not illustrated, Seamount 2, DW 279, Tyro SMT); 2) occurrence of several avicularia of the same type on the sides of a single autozooid (Fig. 6E: five pyramidal morphs), implying budding loci without pre-existing communication pores, a pattern previously noted by Silén (1977), Winston (1984: 20) and Lidgard *et al.* (2012); and 3) occurrence of porous knobs at the periphery of the rostrum or the opesia of three avicularian morphs (adnate, pyramidal, giant; Figs 6D, F; 8A-C). Interestingly, this enigmatic trait is shared with vicarious and oecial kenozooids (see below), suggesting that kenozooids and three avicularian morphs may have the same evolutionary origin. Such possible relationships between kenozooids and avicularia had already been noted by Powell (1966: 167; “It is clearly evident that avicularia, kenozoecia and zooecia intergrade in structure in certain Anascan and primitive Ascophora species”). The lack of porous knobs on columnar (AV1) and globular (AV2) avicularian morphs and the strict association of the latter with the orificial area might either imply that they are more-evolved stages in the graded morphogenesis of avicularia (Fig. 7), or that they have a different origin. The inferred relationships

between vicarious kenozooids and three avicularian morphs bearing porous knobs differ strikingly from the admitted origin of avicularia. Primitive avicularia are considered to be slightly modified autozooids whose first occurrence in the fossil record was discovered in the Mid-Cretaceous genus *Wilbertopora* Cheetham, 1954 (Cheetham *et al.* 2006; Carter 2008). Present-day clues of the autozooidal origin of avicularia are given by B-zooids, with an enlarged operculum and a still active feeding polypide (e.g. Banta 1973; Silén 1977; Carter 2008), and also by variations in the shape of avicularia in species of *Crassimarginatella* Canu, 1900 (Cook 1968; Cheetham *et al.* 2006; Lidgard *et al.* 2012; Schack *et al.* 2019).

The question of the functional role of these differently-shaped avicularia is challenging. Budding and metabolism of these numerous avicularia have a cost to the colony, but for what purpose? Paradoxically, several clues, e.g. uniserial shape and low fecundity of colonies, microhabitat features, suggest that food resources are most likely extremely limited and irregularly supplied to feeding zooids. Thickness of colonies with exerted lophophores do not exceed 1 mm, implying the confinement of zooids within the viscous sublayer of the boundary layer (see below) where energy supply is highly restricted. Therefore, given these conditions, is it conceivable that this unusual diversity of avicularia can be an example of adaptive division of labour (Lidgard *et al.* 2012)? This would imply a high degree of specialization within this polymorph category while risks of starvation are predominant. Budding of two different, relatively large avicularia by a single zooid (Fig. 6G) is thus particularly intriguing. The widely-accepted hypothesis of the chief function of avicularia is defense against epibiotic micropredators (e.g. Kaufmann 1971; Winston 1986; Lidgard 2008; Lidgard *et al.* 2012; Taylor 2020). According to this hypothesis, it could be assumed that each avicularian morph is specialized for a particular category of micropredators and that the latter are exceptionally abundant and diversified on hard substrates of the SASC. Also, is the occasional budding of numerous avicularia by a single zooid (Fig. 6E) triggered by a particularly high and focused predation risk? Similar cases of multiple avicularian budding by a single zooid were observed among cribrimorphs living on walls of a coastal dark cave (3PP Cave, La Ciotat, French Mediterranean coast) in which environmental conditions are close to those of the upper bathyal zone (Harmelin 1997). This pattern was observed in two species, *Glabrilaria pedunculata* (Gautier, 1956), with a crown of four or six pedunculate avicularia budded by ovicellar kenozooids (Fig. 7A), and *Cribrilaria cassidainsis* Harmelin, 1984, with an aggregation of 10 interzooidal avicularia (Fig. 7B). Another intriguing case of avicularia clustering occurs in *H. uniserialis* when zooids are aggregated on particular spots (Fig. 3C): are their highly localized occurrence and dominance over autozooids and kenozooids induced by massive and recurrent attacks of micropredators on these spots? The abundance and diversity of benthic micropredators on deep-sea hard substrates has not yet been recorded and the remark of Hughes & Jackson (1990: 902) that “Nothing is known of the extent to which micropredation varies with habitat” is particularly relevant

to that of *H. uniserialis*. An alternative hypothesis of the role of the avicularia of *H. uniserialis*, whatever their type, could be a common function related to the scarcity of food available to colonies. This function could be the production of microcurrents by movements of their mandibles, which are similarly-shaped, broad with a rounded edge, in the five morphotypes. Thanks to this shape, their movements might provide an efficient re-suspension of particulate organic matter deposited on the substratum, provided by the marine snow (e.g. Alldredge & Silver 1988) and/or the coral living tissues. The localized grouping of avicularia, autozooids and kenozooids in *H. uniserialis*, inferred to improve the colony functioning, recalls the grouping of autozooids in chimneys and may thus correspond to a “local group behaviour” (Shunatova & Ostrovsky 2002).

The origins of the morphogenetic variations of avicularia in *H. uniserialis* remain enigmatic. The outstanding diversification of the shape of avicularia, which can occur within a group of zooids or in a single zooid, can hardly be considered a polyphenic trait (e.g. Moczek & Nijhout 2003) triggered by selective demands from external drivers. These different avicularia might rather result from several random trials of morphological innovation from a common base, that is kinds of morphological prototypes (“protoavicularia”). Their placement in one of the conceptual categories dealing with phenotypic changes is obviously highly debatable. They might conform to the concept of “paradaptation”, a term coined by Bock (1980) for random phenotypic variations appearing in several species under the same selective conditions. However, in the case of *H. uniserialis*, these phenotypic variations can coexist within colonies (i.e., individuals), and even within zooids. These phenotypic variants might also be “spandrels”, an architectural term applied to biological evolution by Gould & Lewontin (1979), that are “byproducts of another decision in design, and not as adaptations for direct utility in themselves” (Gould 1997), not issuing from adaptive selection. Another alternative evolutionary category might be “nonadaptations” proposed by Gould & Vrba (1982) for structures that would provide a potential “source of raw material for further selection” (Gould & Vrba 1982: 12).

Kenozooids: multipurpose polymorphic modules

Kenozooids are major contributors to the surprising complexity of *H. uniserialis* by their abundance and their close relationships with the avicularia. These fundamental modules display two distinct levels of colonial integration: they are vicarious components of zooid chains and ramifications, and also an essential structural part, intimately integrated to ovicelled and non-ovicelled autozooids. The large vicarious kenozooids frequently replace autozooids in zooid chains and are capable of budding either an autozooid, a kenozooid (Fig. 9C) or an avicularium (Fig. 6H). They therefore conform to the definition of “vicariozooid”, although they are large and their role cannot be to “increase colony rigidity and margin robustness” (Schack *et al.* 2019), such as vicariozooids of pluriserial species. They can display an aggregative pattern in some limited parts of colonies and be more abundant than autozooids (Fig. 3E).

This trait recalls the proliferation of small, clustered kenozooids with a central opesia characterizing *Callistopora agassizii* (Smitt, 1873), a bathyal, erect, pluriserial cribrilinid from the Caribbean Sea (Smitt 1873; Winston 2005: 8, figs 7-14). The outer cuticular part (ectocyst) of the frontal membrane that covers the large, convex body of vicarious kenozooids can be particularly thick and persistent, extending over the centrally-placed, oval to subcircular, opesia (Figs 6F, H). Edges of this opening reveal a thick, multilayered gymnocyst (Fig. 8E, F), which provides a high level of protection to the inner chamber and attests the age of colonies.

The inner chamber, visible by light microscopy, is edged with peripheral canals connecting the proximal parent zooid to the distal daughter zooid and lateral zooid chains (Fig. 9A, B). The funicular system ensures the continuity of the transfer of metabolites between zooids (Ryland 1979; Lutaud 1983; Lidgard & Jackson 1989; Best & Thorpe 2002). The large size of these kenozooids and their vast inner chamber connected to peripheral zooids suggest that they may also have the function of storing metabolites delivered by feeding autozooids during short periods of optimal food inputs, and of redistributing them through mesenchymatous strands of the funicular system. One may thus consider that the vicarious kenozooids of *H. uniserialis* form a network of nutrient storage-and-dispatch centers allowing the survival of the colony during periods of food shortage, a condition supposed to be recurrent in the microhabitat of this species.

Heterozooids with a particularly large chamber are a distinctive trait of several deep-sea uniserial species. For example, vesicular vicarious kenozooids, sometimes with a small central opesia, occur in *Klugerella bifurca* (Powell, 1967) with a great similarity in shape and connection patterns with *H. uniserialis* (Gordon 1986, pl. 5b), also in *Pyriporoides bathyalis* (Rosso & Taylor, 2002) (Rosso & Taylor 2002, fig. 3A), *Teresaspis lineata* (Canu & Bassler, 1928) (Rosso *et al.* 2018, figs 70-76) and the fossil *Herpetopora* (see below). In *Callopora bathyalis* Harmelin, 1975, this storage function might be played by avicularia with a large chamber (Harmelin 1975, fig. 1), one of the three avicularian types present in this species. As noted by Powell (1966 and references therein), large vicarious kenozooids with a central opesia are found in some pluriserial species, such as *Membraniporella distans* MacGillivray, 1882 and *Figularia spinea* Brown, 1952 (Powell 1966, figs 1-2). In *Distansescharella* d'Orbigny, 1853, both vicarious kenozooids and avicularia can have a large chamber (Fig. 8G, I; see below). Kenozooids built by intramural budding within the frame of an autozooid may have the same structure and function (see below and Taylor 1988). Besides the putative storage function of vicarious kenozooids, the functions of kenozooids forming a cap intimately integrated to the distal part of non-ovicelled zooids and of oocial kenozooids are more evident in being oversized pore-chambers and a thick protective cover of the oecium. The common occurrence of porous knobs in the two types of kenozooids and three avicularian morphotypes is a strong indication that these heterozooids have the same modular origin (Figs 5B; 6C, D; 9E, F). The origin and role of these tiny structures is enigmatic. They might be vestigial

bases of spines as formerly supposed (Harmelin 1978), and they might have the same origin as the small spines encircling the opesia of kenozooids of *Distansescharella* (Fig. 9H and below).

Zooid repair by intramural budding: a regular process

Reparative processes of zooids by intramural budding within empty cystids (Taylor 2020, chapter 5.2.5) generate an increase of the wall thickness and, when repeated within the same autozooid, the orifice size is considerably reduced by the nested deposits of calcified layers (mode A). Another mode of zooidal reparative process by intramural budding produces closure plates entirely filling the cystids (mode B). These processes have been recorded in fossil species, such as the Ordovician uniserial stenolaemate *Corynotrypa* sp. Taylor 2020, fig. 5.7G), *Wilbertopora listokinae* Cheetham, Sanner, Taylor & Ostrovsky, 2006 (Cheetham *et al.* 2006, figs 6.4 & 6.5), *Allantopora irregularis* (Gabb & Horn, 1860) (Cheetham & Cook 1983, fig. 77.2) and the uniserial electrid *Herpetopora laxata* (d'Orbigny, 1852) (Taylor 1988; Taylor *et al.* 2018). They are also common in the extant bathyal uniserial species *Pyriporoides bathyalis* (Rosso & Taylor 2002, Fig. 3C, D) and *Teresaspis lineata*. In the latter, nested orificial rims and closure plates of orifices and kenozooids occur in old autozooids (Rosso *et al.* 2018, figs 66, 68, 76). They are also observed in cribrilinids living in cryptic habitats (see below). In *H. uniserialis*, the two processes of intramural budding are also frequent in old parts of colonies. The internal replication of a fully-formed zooid within the initial skeletal frame of a cystid, supposedly emptied after the decay of living tissues, can be repeated several times, the repaired autozooid remaining functional (Fig. 10A-E). The same process can occur in vicarious kenozooids (Fig. 9F) and in avicularia (Fig. 10B). Repeated events of intramural budding of this mode generate a considerable increase in relative wall thickness. Stratified calcified layers indicating the succession of budding events are visible on the lateral walls and in the orifice. Up to seven nested rims were observed in some orifices (Fig. 10A, B), leading to a strong reduction of the surface area of the orifice, which can reach 60%. Constraints on polypide exertion and depletion of feeding efficiency likely result from this reduction of orifice size. The second mode of zooid repair by intramural budding, i.e., a closure plate entirely filling the whole cystid, generally occurs when autozooids have already undergone several repair processes of mode A (Fig. 10F, G). Closure plates present a frontal area similar to that of vicarious kenozooids, with a central, rounded window (Fig. 10G) opening onto a very thick wall ("intramural opesiate kenozooid", Taylor 1988), but without the porous knobs which occur around the opesia of vicarious kenozooids (see above). Therefore, in changing an autozooid into a kenozooid, the production of a closure plate is an ultimate process allowing persistence of connectivity between zooids in a uniserial chain. In *H. uniserialis*, avicularia with few nested cystid frames (Fig. 10B) can also occur, but are uncommon. In contrast, avicularia with several piled cystids resulting from successive intramural budding are frequent in cribrilinids living in coastal cryptic habitats (cavities, caves, lower faces of piled pebbles) or the

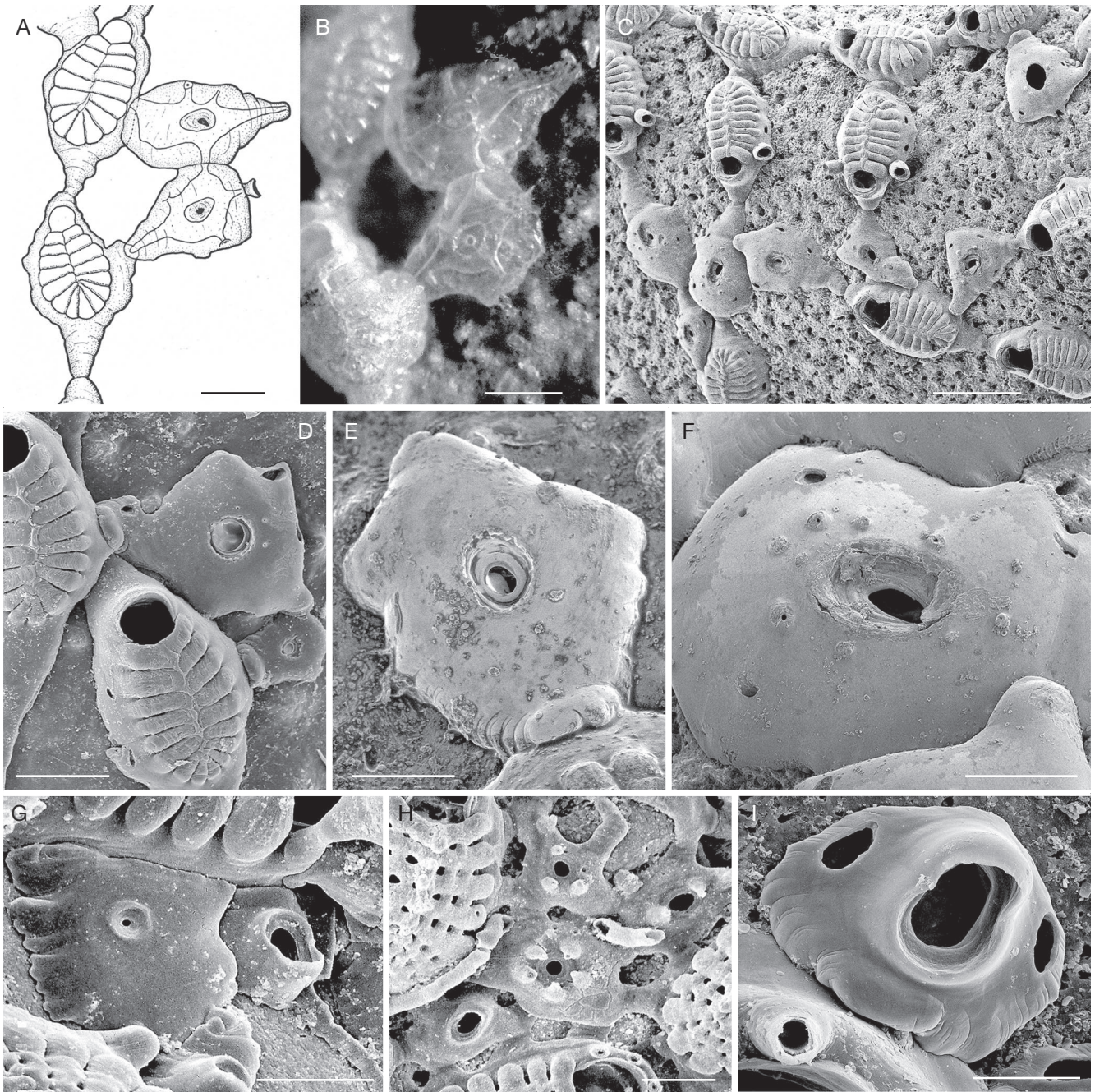


FIG. 9. — *Harmelinia uniserialis* (Harmelin, 1978), vicarious kenozooids: **A**, drawing of two interconnected KZ, laterally budded by 2 AZ; **B**, light photography of the same zooids; **C**, part of colony with seven variously shaped KZ connected to several AZ; **D**, two differently sized KZ budded from the lateral walls of two AZ; **E**, pentagonal KZ with proximal corner folded on the budding locus of the maternal zooid; **F**, frontal wall of a large KZ with central window open on a thick, multilayered wall, surrounded by seven porous knobs. *Distansescharella* d'Orbigny, 1853: **G**, *D. alcicornis* (Jullien, 1882), large vicarious KZ with central window, abutted on to an AZ and close to an adventitious avicularium; **H**, *D. seguenzai* Cipolla, 1921, reticulum formed by three small KZ with a central window surrounded by 2-5 conical spinous processes with a likely porous tip; **I**, *D. alcicornis*, avicularium with opesia and rostrum poorly differentiated, and proximal side folded on the maternal zooid. Origin: A, B, Azores, São Miguel bathyal slope, Białos Stn 197, 815 m (9A copied from Harmelin 1978, fig. 2); C, F, Hyères SMT, Stn DW 200; D, E, Tyro SMT, Stn DW 276; G, I, R/V *Thalassa*, Y434, 620 m, on *Lophelia prolifera* (Linnaeus, 1758); H, R/V *Calypso*, Stn 1902, Libya. Scale bars: A, B, D, F, 200 μ m; C, 400 μ m; E, G, H, 100 μ m; I, 50 μ m.

upper-bathyal zone. This trait is particularly common among species of *Cribrilaria* Canu & Bassler, 1929, such as the Mediterranean *C. venusta* Canu & Bassler, 1925 (Harmelin 1970: “aviculaires à structure emboîtée”, pl. 1, fig. k; pl. 2, fig. 3, as *C. crenulata* Harmelin, 1970; Lidgard *et al.* 2012, fig. 4a, as *Puellina venusta* (Canu & Bassler, 1925)). Intramural budding

is frequent in five *Collarina* species living in cryptic habitats (Harmelin *et al.* 2019: fig. 17). In contrast, short-lived colonies of *C. balzaci* Audouin, 1826, which encrust ephemeral seagrass leaves, never present piled avicularia, suggesting a relationship between the occurrence of intramural budding and the life span of colonies. The assumption that sublethal

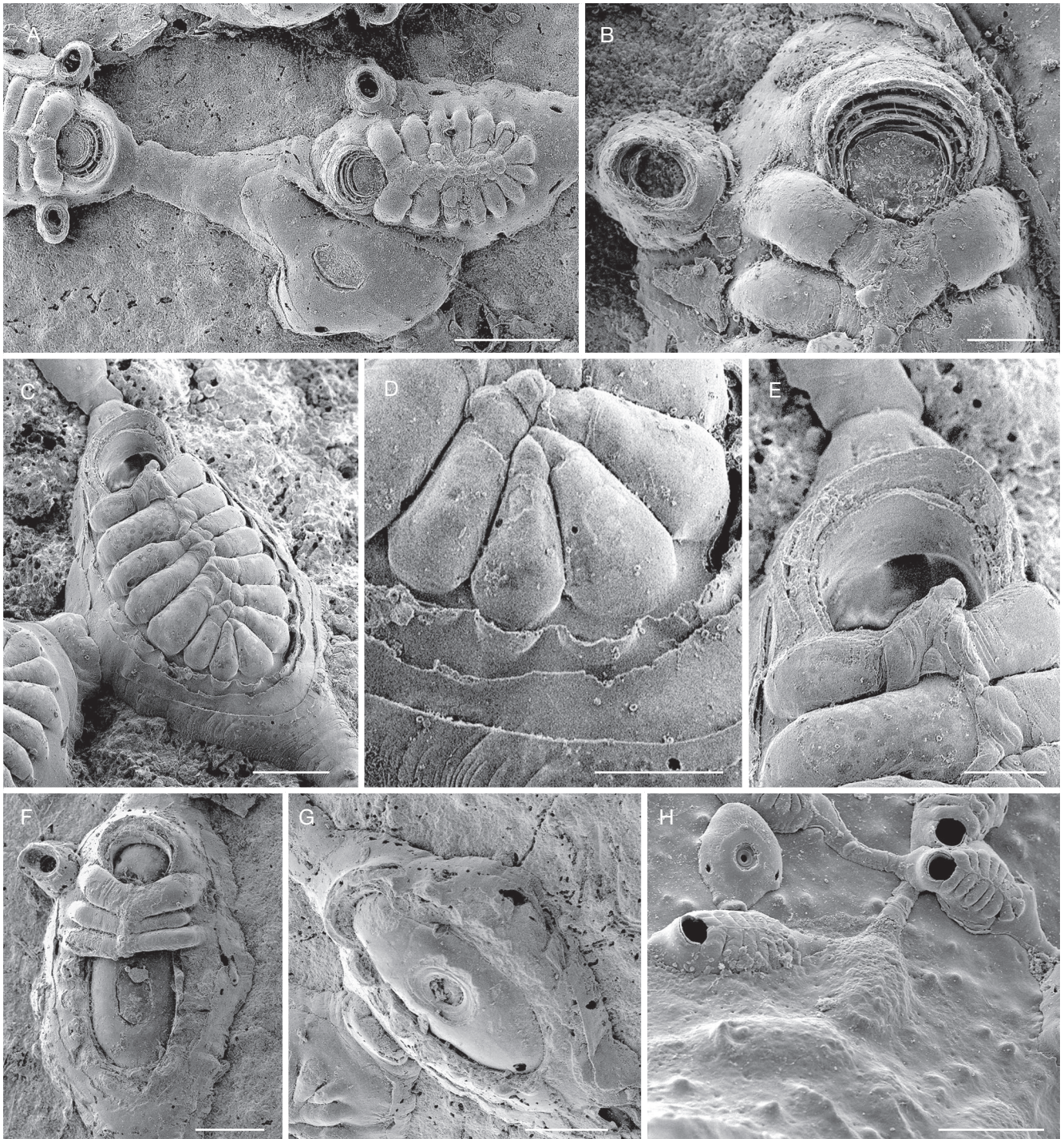


FIG. 10. — *Harmelinia uniserialis* (Harmelin, 1978), intramural budding: **A**, two old AZ and a KZ showing marks of repeated intramural budding; **B**, distal part of an old AZ with multiple nested calcified layers reducing the size of the orifice and of the opesia of the avicularium; **C**, AZ with lateral wall presenting several nested calcified layers; **D**, same AZ, proximal part of the costal shield and nested layers of the lateral wall; **E**, same AZ, distal part showing the reduced size of the orifice and the foramen; **F**, old AZ with a closure plate below the damaged costal shield; **G**, cystid of an old damaged AZ filled with a KZ with a central window; **H**, distal part of a colony covered by calcified deposits produced by tissues of a corallite of *Solenosmilia variabilis* Duncan, 1873. Origin: A, B, F, G, Hyères SMT, Stn DW 184; C, D, E, Hyères SMT, Stn DW 200; H, Tyro SMT, Stn DW 276. Scale bars: A, 200 μ m; B, D, E, 50 μ m; C, F, G, 100 μ m; H, 400 μ m.

predation is the direct cause of zooid repair by intramural budding was thoroughly discussed and supported by Berning (2008), who illustrated several repaired orifices with, in most cases, a single additional orificial rim. The hypothesis

that the causative agent of repeated intramural budding in avicularia, as observed in cribrilinids, is predation by single-zooid predators specifically targeted on avicularia is rather unrealistic and should be tested experimentally.

In *H. uniserialis*, the two types of reparative structures by intramural budding in zooids are assumed to be processes allowing the preservation of their functions, including connectivity between zooids, despite adverse conditions (food shortage, senescence, breakage of frontal shield).

Ancestrula: a mini-autozooid with a bi-polar budding capacity
The ancestrula of *H. uniserialis* is very similar to an ‘adult’ autozooid (Fig. 4E), except for its much smaller size, its less developed kenozooidal distal cap, and the relative size of the orifice, which is clearly larger. The ratio of the orifice width to that of the costate shield is 0.6 in the illustrated ancestrula and 0.4 in the autozooid close to it (Fig. 4E). In the four ancestrulae observed in the present material, the frontal shield was made up of 14 costae. The capacity of the ancestrula of *H. uniserialis* of budding a daughter zooid from both its small distal kenozooidal cap and a proximal budding locus on the lateral wall is noticeable. This budding bipolarity is shared with some other uniserial species, such as the Icelandic bathyal calloporid *Pyriporoides bathyalis* (Rosso & Taylor, 2002), and the Cretaceous electrid *Herpetopora* (Taylor 1988) (see below). This pattern of bipolar budding may provide uniserial colonies better chances to grow in directions favourable to their development.

TAXONOMIC AFFILIATION AND RELATIONSHIPS WITH OTHER CHEILOSTOMES

The incorrect generic affiliation of *Cribrilina uniserialis* was discussed by Rosso (in Rosso *et al.* 2018) together with that of *C. lineata* Canu & Bassler, 1928, another deep-sea uniserial “*Cribrilina*” from the Caribbean Sea, and two new genera were erected: *Harmelinius* Rosso, 2018 for *C. uniserialis* and *Teresaspis* Rosso, 2018 (Rosso *et al.* 2018) for *C. lineata*.

Morphological analogies between *H. uniserialis* and other extant uniserial species are not evident, but there is a remarkable convergence in the shape of autozooids and kenozooids with *Klugerella bifurca* (Powell, 1967) (see Gordon 1986, fig. 5B). Analogies reported below involve species belonging to Cretaceous genera, an anascan electrid (*Herpetopora*) and two ascophoran “cribriliniids” (*Andriopora*, *Distansescharella*), which are extinct or poorly represented at the present time. Ascribing *H. uniserialis* to a clade formerly included in the cribriliniids remains disputable considering the profound systematic shift brought by recent molecular analyses (Orr *et al.* 2022). Moreover, several features of this species, particularly the atypical co-occurrence of several avicularian polymorphs and their apparent morphological relationships with vicariant kenozooids might denote an evolutionary dead-end and a status of relict species. Its endemism in a geographically limited deep-water area in the Atlantic Ocean (see below) could also argue for this status. Features of *H. uniserialis* might also indicate that it is one of the possible links between anascan and ascophoran cribrimorphs (e.g. Gordon 2000; Dick *et al.* 2009; Orr *et al.* 2022).

Andriopora Lang, 1916

Similitudes of *H. uniserialis* with *Andriopora* were noted by Harmelin (1978). This Cretaceous genus is characterized by uniserial encrusting colonies with autozooids having a frontal

shield formed of arched costae, “more or less intimately fused” (Lang 1921), without pelmata or pelmatidia, avicularia generally present and six oral spines when present. A SEM photo (courtesy of S. Martha, 9.I.2023) of the holotype of *A. homunculus* Lang, 1916, the type-species of this genus, shows a uniserial succession of autozooids with a costate frontal shield, a relatively narrow lateral and proximal gymnocyst without a cauda, paired avicularia placed distally to the orifice, and a broken ovicell associated with a distal autozooid. Other fossil specimens ascribed to *Andriopora* may resemble *H. uniserialis*, such as one from the Lower Maastrichtian, Rügen, identified as *A. aggregata* by E. Voigt (unpublished SEM photo sent to JGH on January 1993). This specimen exhibits autozooids which are distally and laterally interconnected by uniserial series of narrow kenozooids which superficially recall the caudae of *H. uniserialis*. The morphological similitudes between *H. uniserialis* and this fossil genus may represent more a convergence in their zoarial structure than a close relationship between these two taxa.

Herpetopora Lang, 1914

Several features are shared between *H. uniserialis* and another Cretaceous genus, the anascan electrid *Herpetopora*, particularly with *H. laxata* (d’Orbigny, 1852) from the Chalk (Taylor 1988; Taylor *et al.* 2018). Convergent morphological patterns include 1) uniserial branching with distal and lateral budding leading to a reticulate colony, autozooids with a long or shorter proximal cauda; 2) kenozooids with a central opesia (“opesiate kenozooids”, Taylor 1988); 3) reticulation of colony achieved by the overgrowth of branches (Type 2, Taylor 1988: text-fig. 7), by the abutment of a distal zooid to the lateral side of a zooid of another branch (Type 1, Taylor 1988) and by the junction of the distal zooid of a branch to the pore window of another branch (Type 3: “pore location”, Taylor 1988); 4) the capacity of repairing damaged or dead autozooids by “intramural reparative budding” (Taylor 1988; Taylor *et al.* 2018) producing a kenozooid filling the empty cystid or a succession of nested secondary autozooids; and 5) the ancestrula, smaller than autozooids and with two budding loci, distal and proximal. Therefore, *H. uniserialis* and *Herpetopora laxata* present striking similitudes concerning the colony branching patterns and several zooidal features, including the ancestrula bipolarity and processes of zooid repair by intramural budding. However, obviously, *H. uniserialis* has a much more complex structure with a spinocystal shield, complex ovicells and several categories of polymorphs, that may indicate an evolutionary gap between these two taxa.

Distansescharella d’Orbigny, 1853

Several morphological features of *Distansescharella* are akin to those of *H. uniserialis*. This genus, considered by Lang (1921) to be close to *Andriopora*, classified as Cribriliniidae (WoRMS, access on 8.IV.2024), comprises 14 species including six Cretaceous species and four extant species (P. Bock, Bryozoa.net, access on 8.IV.2024). Extant species are distributed in the NE Atlantic and the Mediterranean on bathyal hard substrates (Harmelin 1978; Harmelin *et al.*

1989; López-Fé 2006; Souto *et al.* 2016), but, curiously enough, also on empty shells collected at low tide on shores of the English Channel (*D. seguenzai* Cipolla, 1921; De Blauwe 2019). Features common to *Distansescharella* and *Harmelinus* concern the costate shield, the avicularia and the kenozooids. In *Distansescharella*: 1) costae have a smooth surface without pematidia or pematia and the distalmost pair delimit the proximal edge of the orifice; 2) avicularia are adventitious and have a similar basic structure with poorly differentiated opesial and mandibular areas without hinges (Fig. 8I); and 3) large, similarly shaped vicarious kenozooids with a small central opesia (Fig 8G; Harmelin 1978: fig. 4; López-Fé 2006: fig. 8; Souto *et al.* 2016: figs 39, 44, 46, 50, 51). The common occurrence of this last feature in these two genera has been formerly noted in *D. alcicornis* (Jullien, 1882) (Harmelin 1978: 179 “[...]kénozoïdes de grande taille[...] vésicules non costulées et pourvues d’un pore central [...]sont similaires à ceux émis par *Cribrilina uniserialis*”). Another analogy between these two genera is the morphological relationship between the avicularia and the vicarious kenozooids revealed by a published SEM photo of *D. alcicornis* from Galicia Bank (Souto *et al.* 2016, fig. 44): the lower of the two large interzooidal heterozooids labelled as kenozooids exhibits an extensive gymnocystal chamber and an avicularian structure near the distal edge, with rounded opesial and mandibular areas, and a slightly prominent distal rim. These traits are similar to those of the adjacent adventitious avicularia in the same specimen, and also of the large avicularium (AV5: “giant”) of *H. uniserialis*. In the extinct species *D. fallax* Voigt, 1949 and *D. familiaris* (Hagenow, 1839), type-species of *Distansescharella*, vicarious avicularia are numerous and also have a large chamber (Martha *et al.* 2019: fig. 69a-d). The occurrence of a large chamber in both avicularia and kenozooids in these two genera may provide the same functional advantage, i.e., metabolite storage (see above). Therefore, the boundary between these two categories of heterozooids is unclear in both *Distansescharella* and *Harmelinus*. Another trait suggesting a possible relationship between these two genera is the presence in *D. seguenzai* of a disjunct colonial structure, with autozooids linked by a mesh bearing small interzooidal kenozooids with 2-5 small pointed processes, apparently with an open tip, encircling the central, rounded opesia (Fig. 8H). These spinous processes, first identified as vestigial costae (Harmelin *et al.* 1989, pl. I, figs 1, 4), are reminiscent of the tiny porous knobs present around the opesia of interzooidal kenozooids and on avicularia of *H. uniserialis*. Moreover, this reticulate mesh formed by tubules connecting the autozooids might correspond to an intermediate evolutionary step between uniserality and pluriserality of colonies. Obviously, however, extant species of *Distansescharella* (Harmelin 1978; Harmelin *et al.* 1989; López-Fé 2006; Souto *et al.* 2016; De Blauwe 2019) clearly differ from *H. uniserialis* in having a frontal shield with successive costae connected by 4-5 bridges, four oral spines, an oecium produced by the distal autozooid and a tafiform ancestrula with branched spines (Harmelin 1978, fig. 3; López-Fé 2006). The occurrence of “opesiate kenozooids”,

vicarious or filling an autozooid by intramural budding in *Figularia spinea* Brown, 1952 and *Membraniporella distans* MacGillivray, 1882, recorded by Powell (1966), might also be clues of evolutionary relationships.

HABITAT

Habitat conditions

The habitat of *H. uniserialis* is restricted to the upper-bathyal zone as revealed by the depth range of the 19 stations hosting colonies of this species (610-1590 m, mean: 927 ± 273 m; Fig. 1). The absence of *H. uniserialis* at shallower bathyal depths in the same area (28 stations on seamounts Atlantis, Irving, Plato, Hyères and Great Meteor, 270-490 m) was established during previous taxonomic studies (Harmelin 2006; Berning *et al.* 2017) and an unpublished preliminary listing of cribrimorphs (collection stored at the MNHN, Paris). The high topographic complexity and complex hydrodynamic patterns that occur on the sides of seamounts foster the development of reef-building branched scleractinian corals and associated biota (e.g. Le Danois 1948; Jensen & Fredericksen 1992; Freiwald 2002; Freiwald *et al.* 2004; Buhl-Mortensen *et al.* 2010). These bathyal branched corals develop large frameworks with a complex 3D architecture offering to associated biota three types of habitats: 1) the living apical parts of the coral branches, covered by the coral tissues; 2) the older parts with bare surfaces, prone to be colonized by sessile biota; and 3) coral rubble, accumulated at the base of coral colonies, also highly suitable to small invertebrates. Most colonies of *H. uniserialis* (14 stations, 610-1160 m) encrusted *Madrepora oculata*, a large bathyal branched coral with a vast geographical range (e.g. Zibrowius 1980; Orejas *et al.* 2021). The occurrence of *H. uniserialis* on *Solenosmilia variabilis*, another large branched coral, was only noted in one of the deepest stations (Tyro, 1520 m; Seamount 2 DW 276). Another widely distributed reef-forming branched coral, *Desmophyllum pertusum* (Linnaeus, 1768), also present in the SASC and potentially colonized by *H. uniserialis*, was unfortunately not present in the examined material. Like *Teresaspis lineata* (Canu & Bassler, 1928) (Rosso *et al.* 2018), *H. uniserialis* is frequent on bathyal branched corals but can also occupy small hard substrates likely mixed with coral rubble: a stylasterid skeleton (Hyères Smt, 620 m, Calypso Exped.), spines of sea-urchin (Plato Smt, DW 248), and rock fragments (Plato Smt, DW 251: fig. 2B; Great Meteor Bank, DW 180). The occurrence of *H. uniserialis* on these non-coral substrates is probably more frequent than indicated by the present material. However, the abundance of *H. uniserialis* in the complex framework of *M. oculata* and *S. variabilis* testifies to the suitability of this habitat to the ecological needs of this uniserial bryozoan.

Relationships between growth-form and ecological conditions

The uniserial encrusting growth-form (= runner; Jackson 1979) is the least frequent colony shape among the different clades of bryozoans (McKinney & Jackson 1989). Uniserial species are poor competitors, occupying refuges whose predictability or unpredictability was discussed by Bishop *et al.* (1989). The relative frequency of runners in the bathyal zone

(McKinney & Jackson 1989; Rosso & Taylor 2002) suggests that they may be well adapted to the constraints of life on deep-water hard substrates. In the bathyal zone, branched corals and other hard substrates colonized by runners are perennial and predictable spatial refuges, but colonies encrusting them are exposed to unpredictable harsh microenvironmental conditions. The development of a network of linear, uniserial files of zooids allows maximization of the colonization of substrate bare surfaces in all directions with a low number of zooids, increasing the chance for some of them to find good conditions (e.g. nutrients inputs, limited silting). Interestingly, Winston (1976) showed that cultured colonies of *Conopeum tenuissimum* Calvet, 1908 formed uniserial branches growing in several directions when food was scarce. She also noted that in these colonies “most zooids are lacking polypides and are heavily calcified”, a phenotypic change recalling features of *H. uniserialis*. Similarly, the production of abnormal uniserial colonies in *Electra pilosa* (Linnaeus, 1767) was supposed to be induced by the scarcity of food (Silén 1987). As noted by McKinney & Jackson (1989), in contrast with multiserial encrusting species, zooids composing a uniserial chain are not protected by laterally adjacent zooids and are directly exposed to adverse events. Fragmentation of the zooid chains and processes of zooid repair by intramural budding are thus frequent. Because of the wide spacing of lophophores and lack of elevation relative to the substrate, autozooids probably have poor food-capture efficiency. They are confined within the inner layer of the benthic boundary layer (e.g. Zhang *et al.* 2014), i.e., in the very thin “diffusive boundary layer”, i.e., the lower part of the viscous bed layer against the substrate where molecular viscosity is predominant (Buhl-Mortensen *et al.* 2010, fig. 7). Therefore, *H. uniserialis* represents an interesting case of the food acquisition model (Eckman & Okamura 1998; Okamura *et al.* 2001), shared with other uniserial species from the same habitat, such as *Crepis* spp. The development of pseudo-pluriserial parts and the aggregative distribution of ovicelled zooids in colonies of *H. uniserialis* are inferred to be linked to micro-topographic features allowing better food supply at the substrate surface and export of larvae. Considering the physical microenvironment surrounding the lophophores of *H. uniserialis*, the question of the feeding strategy of this species can thus be addressed: is it a suspension feeder or a deposit feeder of sedimented organic particles? This question was already addressed by Schopf (1969) for deep-water colonies of *Euginoma* Jullien, 1882 growing parallel to the bottom and whose polypides can be in contact with deposited organic particles. The same assumption was proposed by De Blauwe (2019) for bryozoans encrusting the concave side of disarticulated shells from nearshore bottoms. In coastal habitats, encrusting colonies established in confined conditions, e.g. in reef microcavities or on undersides of piled stones, may also have the same food habit.

A partial list of other deep-sea uniserial encrusting bryozoans includes cyclostome species with a stomatoporiiform shape (Harmelin *et al.* 1974, 1979), several calloporid genera (list in Rosso & Taylor 2002), species of *Crepis* Jullien, 1882, *Klugerella* Moyano, 1991, *Mosaicoporina* Gordon &

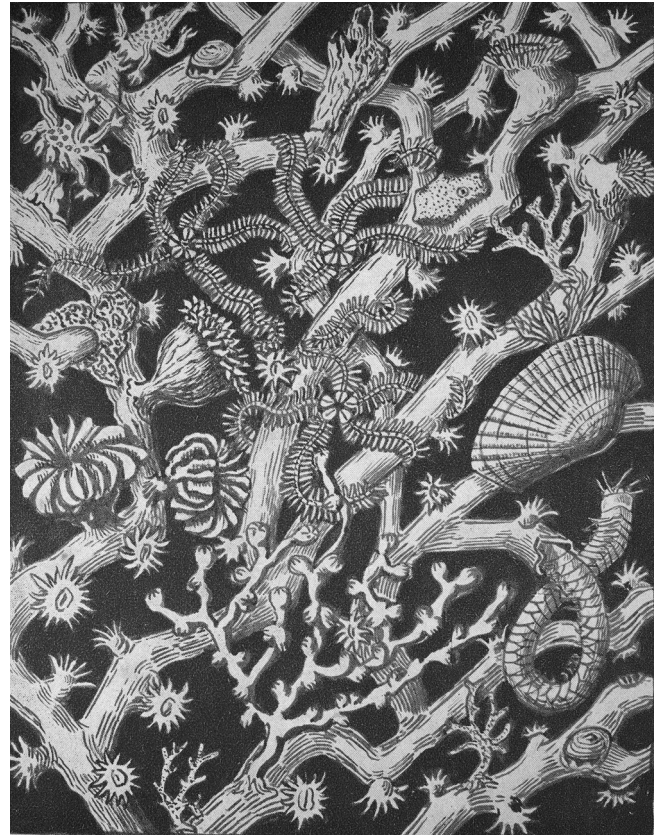


FIG. 11. — Epifaunal assemblage associated to *Madrepora oculata* Linnaeus, 1758 on the bathyal slope off Brittany. Reproduction of plate 6 of the book “Les profondeurs de la mer” by Y. Le Danois (1948), Payot, Paris.

d’Hondt, 1997, *Reginelloides* Soule, Soule & Chaney, 1995, and *Teresaspis* Rosso, 2018. In the NE Atlantic Ocean, species of *Crepis* (Reverter-Gil *et al.* 2011) occupy the same habitat as *H. uniserialis*, with the same zoecial shape and branching pattern. At shallow depth, species with the same growth form can occur in tiny cavities, such as the calloporid *Allan-topora minuta* (Harmelin, 1973), a Mediterranean runner species with long cauda and the same branching pattern as *H. uniserialis*, discovered in microcavities of an old bioherm (Harmelin 1973).

Interactions with hosting corals

Most colonies of *H. uniserialis* occupied bare portions of branches of large scleractinians corals, below apical ends covered with tissues of living corallites. In contrast, some colonies interacted with these soft tissues. This interaction was observed on corallites of *Solenosmilia variabilis* (Stn DW 276). Some zooids of a colony of *H. uniserialis* placed close to the apex of corallites were partly or totally coated by a thin calcareous layer produced by the coral soft tissues (Fig. 9H). This interaction implied three successive stages: 1) growth of the bryozoan colony on bare parts of the corallite following the shrinkage of the coral tissues during a decline in activity; 2) recovery of corallite activity with re-extension of its soft tissues along the column, which cover newly grown zooids of *H. uniserialis*; and 3) secretion by the coral of a

new calcareous layer, which coats the peripheral zooids of the bryozoan colony. The latter can thus contribute to the thickening of the coral skeleton. A similar light mutualistic interaction is commonly observed in nearshore coralligenous rocky bottoms of the Mediterranean between small scleractinian corals and several encrusting cheilostome bryozoans, among which the cribrilid *Cribrilaria radiata* (Moll, 1803) is dominant (Harmelin 1990). Old parts of coral branches and bryozoans encrusting them were blackened by a dark coating corresponding to deposits of Fe-Mn oxides. The same darkening was observed by Grischenko (2022) on bryozoan colonies encrusting the surface of cobalt-rich Fe-Mn crusts on substrates of Magellan seamounts. This dark coating of substrates and old bryozoan colonies by Fe-Mn deposits is commonly observed in both deep-sea habitats and dark parts of shallow-water cavities (Laborel & Vacelet 1959; Harmelin 2000). The microbial origin of Mn-Fe deposits seems obvious as well in coastal caves (Allouc & Harmelin 2001) as on deep-sea substrates (Peng *et al.* 2016).

GEOGRAPHICAL DISTRIBUTION

The geographical range of H. uniserialis: a remote and tiny area in the NE Atlantic

The occurrence of *H. uniserialis* was initially reported from only two bathyal stations close to the island of São Miguel (Fig. 1). This limited distribution along the southern slope of the Azores may denote a sampling deficiency. However, this species was not recorded in other bathyal samples collected along this slope during the Jean-Charcot Białores expedition (unpublished personal data). By contrast, the occurrence of *H. uniserialis* across a vast southern area encompassing the six main seamounts of volcanic origin composing the SASC was attested by the present material (Fig. 1). These seamounts have a complex history and are variously aged, from 11-16 million years (Meteor) to 40 million years (Plato) (Caballero-Herrera *et al.* 2023 and references therein). The SASC forms a bathyal archipelago far from the eastern mainland (c. 1500 km) and the Madeiran and Canary archipelagos (> 1100 km; Caballero-Herrera *et al.* 2023, fig. 1). The very strong topographic heterogeneity of the SASC area leads to complex circulation patterns of the bottom water bodies, highly variable in space and time (for the Great Meteor Bank, see Mouriño *et al.* 2001). These inferred bottom circulation patterns may trap larvae within the SASC (Roberts *et al.* 2006), increasing the isolation of local populations. Moreover, a Lagrangian ocean modelling of the Azores region at depths including the habitat of *H. uniserialis* and other endemic taxa (Sala *et al.* 2013; fig. 11: 300-500 m; fig. 12: 600-2000 m) indicates predominant northward transport pathways.

The South Azorean Seamount Chain: a center of speciation and endemism?

As emphasized by Richer de Forges *et al.* (2000), groups of seamounts are similar to archipelagos functioning as centers of speciation. How relevant is this observation to the SASC for the benthic fauna and particularly the bryozoans and the present species? The “seamount endemism hypothesis” is

TABLE 3. — Bryozoan species endemic to the Azores bathyal slope (ABS) and/or to seamounts of the South Azorean Seamount Chain (SASC). Authorities of species: *Cribrilaria atlantis* (Harmelin, 2006); *C. hexaspinosa* Harmelin, 1978; *C. octospinosa* Harmelin, 1978; “*Stomatopora*” *corrugata* Harmelin, 1979; *Atlantisina atlantis* Berning, Harmelin & Bader, 2017, *Atlantisina meteor* Berning, Harmelin & Bader, 2017, *B. vibraculata* (Calvet, 1931), *B. suroiti* Berning & Harmelin & Bader & Cibio, 2017, *Calvetopora otapostasis* Berning, Harmelin & Bader, 2017. Seamounts: At, Atlantis; Hy, Hyères; Ir, Irving; Me, Meteor; Pl, Plato; Ty, Tyro.

Species	ABS	SASC	Depth (m)
“ <i>Stomatopora</i> ” <i>corrugata</i>	W Flores, S São Miguel	–	610-1400
<i>Cribrilaria atlantis</i>	S Faial	At, Ir, Hy, Me	250-610
<i>Cribrilaria hexaspinosa</i>	–	Hy, Me	300-1500
<i>Cribrilaria octospinosa</i>	–	Hy	290
<i>Atlantisina atlantis</i>	–	At	280-460
<i>Atlantisina meteor</i>	–	Ir, Hy, Me	270-480
<i>Bathycyclopora vibraculata</i>	NW Terceira	–	599
<i>Bathycyclopora suroiti</i>	–	At	330-460
<i>Calvetopora otapostasis</i>	–	At	275-460
<i>Calvetopora</i> sp.	–	Me	333-403
<i>H. uniserialis</i>	S São Miguel	At, Ty, Pl, Ir, Hy, Me	610-1590

open to debate and cannot be generalized (e.g. Rogers 1994; Thoma *et al.* 2009; Rowden *et al.* 2010). Speciation and endemism of benthic biota associated with seamounts are conditioned by two large sets of factors: 1) oceanographic and geographical drivers, i.e., the general ocean circulation, the physical patterns of the water masses within the SMT system (Mouriño *et al.* 2001; Lavelle & Mohn 2010), the distance to peripheral bottoms with suitable habitats; and 2) the biology and ecology of biota (e.g. McClain 2007; Shank 2010). Species dispersal patterns may be modified according to climate-driven changes in ocean circulation (Wilson *et al.* 2016). However, biological features of clonal benthic species are obviously fundamental factors of endemism (e.g. Jackson 1989), particularly the absence of pelagic, long-lived larvae or asexual propagules, which can be exported over long distances towards potentially colonizable bottoms.

According to Hoffman & Freiwald (2021), the occurrence of taxa endemic to the Azores and allied SMT started during the Neogene, that is after the formation of the islands and the SMT. The relevance of this assertion to *H. uniserialis* has, however, still to be assessed. The function of the SASC as a centre of endemism is well documented for Gastropoda with lecithotrophic larvae or direct development (e.g. Gofas 2007; Hoffman & Freiwald 2021; Caballero-Herrera *et al.* 2023 and references therein) and Harpacticoid copepods (Crustacea) (George & Schminke 2005; Mohn 2010). In contrast, the polychaete fauna of the SASC includes few endemic species (Gillet & Dauvin 2000). As regards the bryozoan fauna, previous analyses showed that the SASC and the southern bathyal slope of Azores harboured 11 endemic species, including three *Cribrilaria* species (Table 3). Amongst the latter, *Cribrilaria atlantis* (Harmelin, 2006) is endemic to four seamounts of the SASC (Atlantis, Irving, Hyères, Great Meteor) and the bathyal slope S of Pico Is., with a distribution limited to the 250-600 m depth range. This species is part of a species

complex including two other species distributed in the NE Atlantic (*P. arrecta* Bishop & Househam, 1987; *P. macaronensis* Harmelin 2006) and eight other species or unnamed morphs scattered in other seas, suggesting speciation from a common ancestor. An opposite scenario is displayed by *H. uniserialis*, which apparently has no closely related uniserial species in Recent seas, and whose possible evolutionary relationships with the pluriserial genus *Distansescharella* (see above) have to be specified.

A major problem with the designation of a species as endemic to a SMT area is undersampling (McClain 2007), i.e., the lack of investigations in other areas with similar conditions. However, the endemism of *H. uniserialis* to the SASC and the southern bathyal of the Azores is highly probable. Despite being easily recognizable, this species has never been recorded from other NE Atlantic bathyal locations examined during previous studies (e.g. Harmelin 2006; Souto *et al.* 2016; Berning *et al.* 2017; Harmelin & Rosso 2023). Its endemism to the south Azorean seamounts and the bathyal slope of the southern Azores is restricted to a depth range of 600–1500 m, as asserted by its absence in shallower samples from the same area examined during previous surveys (Harmelin 2006 and unpublished personal study of cribrilins). The scarcity of ovicelled zooids in all examined colonies suggests that the production of larvae is very low. Moreover, apart some exceptional conditions, the larvae are likely confined within the viscous sublayer of the boundary layer where parent colonies live. Therefore, the export of larvae outside the 3-D calcareous framework of corals is most probably dependent on exceptional hydrological events. Most evidently, the long-distance rafting of colonies on light substrates and dispersal of fragmented hard substrates bearing colonies, by any of the means reported by Winston (2012), is impossible. Chances of dispersal of larvae of *H. uniserialis* towards other seamounts, offshore banks or the African and European continental margins are thus virtually zero.

CONCLUSIONS

Mounds formed by bathyal branched scleractinian corals (“cold-water coral reefs”) on continental margins and offshore seamounts are large three-dimensional habitats and well-known hot-spots of biodiversity in the deep sea. Seamounts also offer fascinating examples of the colonization of islands. In the abundant literature dealing with the associated fauna of this deep-sea habitat, bryozoans have a relatively modest part, even though they contribute significantly to its biodiversity. Despite its small size and apparent simplicity, the encrusting uniserial cheilostome species *Harmelinus uniserialis*, redescribed here, exhibits innovative traits concerning the modular structure of bryozoans, likely related to the ecological conditions within the coral framework and the biogeography of seamounts.

In cheilostome bryozoans, uniserial growth of a colony does not always imply a basic modular structure, as evidenced by Taylor (1988) in *Herpetopora*. The present species exhibits a

striking complexity at both colonial and zooidal levels, with a surprisingly high degree of polymorphism. Colonies, whose limits are indistinct due to the crossing and fragmentation of branches, display multiple variations in the branching patterns and the layout of zooids. Zooids are widely spaced in long, linear or ramified chains, which can alternate with patches of aggregated zooids simulating a multiserial growth-form. At first sight, the modular structure of *H. uniserialis* is shaped by autozooids, vicarious kenozooids and avicularia, but a closer view reveals a much more complex structure.

Kenozooids are the main source of the modular complexity of this species. Morphological clues consisting of enigmatic tiny porous knobs shared by different modular parts may suggest that the large vicarious kenozooids interspersed between autozooids are the initial basis of two paths of evolutionary changes occurring with strong morphological disparities. The first one is represented by kenozooids highly integrated with autozooids, i.e., the distal cap of non-ovicelled zooids and the oecial cover of ovicelled zooids including a distal part, both functioning as a distal pore chamber and budding locus. The second path consists in the production of avicularian morphs, at least those three which have porous knobs, with an increasing colony integration, that can co-occur in the same colony and even the same autozooid. The presumed kenozooidal origin of avicularia, or the common origin of these polymorphs, and the intracolony persistence of successive steps in the morphogenesis of avicularia are striking oddities of *H. uniserialis*. The emergence of such innovations at zooid level is an example of facilitation provided by the modular construction of bryozoan colonies (e.g. Schopf 1973; Carter *et al.* 2011; Lidgard *et al.* 2012). These innovations might also be interpreted as expressions of an evolutionary stasis (e.g. Cheetham 2001) with no evident posterity (evolutionary dead-end?), except for a putative relationship with the genus *Distansescharella*. Functional benefits of these different polymorphs, i.e., kenozooids and avicularia, remain questionable. However, the kenozooids intimately integrated with autozooids ensure connectivity with distally budded zooids and protection of the oecium. Moreover, the high frequency of vicarious kenozooids with a large chamber is assumed to be linked to the trophic constraints that likely occur at substrate level, i.e., in the viscous boundary sublayer. These large kenozooids are supposed to form a network of storage-and-dispatch centers, accumulating nutrients during periods of food inputs, and dispatching nutrient through mesenchymatous strands of the funicular system (Lutaud 1983; Best & Thorpe 2002; Schwaha *et al.* 2020). The relative frequency of heterozooids with a large chamber in bathyal encrusting species may sustain this hypothesis.

Even more enigmatic is the function of the five avicularian morphotypes. Does their morphological diversity illustrate the division of labour that characterizes modular organisms (Lidgard *et al.* 2012)? Defense against single-zooid invertebrate predators is the better documented and often alleged function of avicularia (e.g. Lidgard 2008; Lidgard *et al.* 2012). Are these different avicularia of *H. uniserialis* highly

specialized polyphenic responses induced by several categories of predators present at the surface of the bathyal branched corals? This exceptional biodiversity of small predators associated to deep-sea corals has never been recorded. On the contrary, one might consider that these different avicularia are just “protoavicularia”, i.e., phenotypic trials generated by successive neutral mutations, coexisting without precise roles, except perhaps a common one. Considering the micro-environmental constraints faced by colonies, this common function might be enhancing the renewal of water and supply of deposited particulate organic matter near the orifice of autozooids by movements of their rounded mandible. In the stagnant microenvironment (lower part of the boundary layer) where colonies are established, risks of starvation appear to be more serious than predation. However, thorough studies of the anatomy of the five avicularian morphs (e.g. Carter *et al.* 2010b), could provide a better understanding of their functioning and possible role.

Another confusing trait of this species is the rarity of ovicells and young astogenetic stages, which contrasts with the frequency of colonies of *H. uniserialis* on the examined substrates. This trait, together with the thickness of walls and the abundance of zooids exhibiting repair processes (intramural budding, closure plates), are clues that colonies, entire or fragmented after partial mortality, are extremely long-lived despite limited food availability. It is also highly probable that *H. uniserialis* has a very low potential of larval dispersal, even at short scales, due to the rarity of ovicells and confinement of colonies in the steady water layers covering their substrates. Most likely this trait, allied to an unfavorable general oceanic circulation, are the main drivers of the endemism of *H. uniserialis* to the region encompassing the South Azorean Seamount Chain and the southern bathyal slope of the Azores.

Given the distances between the seamounts colonized by *H. uniserialis*, it is likely that the different subpopulations of this species are for the most part self-recruiting and, therefore, the gene flow between them is probably much reduced. The present study does not provide clear evidence of morphological differences between these sub-populations. However, the hypothesis of a species complex including several sibling species (e.g. Knowlton 1993) distributed across the SASC should not be discarded. Assessment of this hypothesis would require future research including more thorough morphological analyses and new samples for a genetic study.

Considering some of its traits, it may be argued that *H. uniserialis* is a relict species. These traits include similarity to several Cretaceous species, endemism to distinct microhabitats in a limited deep-sea area with an unsteady geological past, and above all, morphological peculiarities not identified in other extant species, particularly the co-occurrence of several avicularian morphotypes having morphological relationships with kenozooids. For this species, the area encompassing the South Azorean Seamount Chain and the southern bathyal slope of São Miguel Is. may have functioned as an ecological refuge (Vermeij 1986).

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