

***PUELLINA SALDANHAI* N. SP., A NEW CRIBRIMORPH
CHEILOSTOME (BRYOZOA: GYMNOLAEMATA) FROM DARK
CAVE ENVIRONMENT OF SOUTHERN PORTUGAL**

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With 9 figures and 1 table

ABSTRACT. A new species of cribrimorph bryozoan, *Puellina saldanhai* n.sp., is described from material collected in dark recesses of a submarine cave of Sagres area (southern Portugal). It is closely related to *P. cassidainsis* Harmelin, which occupies similar cave habitat in the Mediterranean, and with which Canarian specimens of *Puellina saldanhai* have been formerly mistaken. Differences between these species concern mainly the structure of the suboral bar and that of the ovicell.

RESUMO. Uma nova espécie de briozoário cribrimorfo, *Puellina saldanhai* n. sp. é descrita a partir do material colhido nos recantos escuros de uma gruta submarina em Sagres (Portugal). Esta espécie tem afinidades com *P. cassidainsis* Harmelin, que ocupa um habitat semelhante no Mar Mediterrâneo e com a qual, espécimes agora identificadas como *P. saldanhai* oriundos das Ilhas Canárias, haviam sido confundidos. As principais diferenças entre as duas espécies dizem respeito às estruturas da barra sub-oral e do oviceleto.

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INTRODUCTION

The biogeography of the Atlanto-Mediterranean region is particularly interesting considering the complex geologic history of this area. The major geologic and climatic changes that have occurred since the closing of the Indian Ocean (20 MY) have considerably affected the exchanges between the Atlantic and Mediterranean basins, and were responsible of successive phases of faunal transfers with periods of isolation, extinction, and renewal (PÉRÈS, 1985). The present-day hydrology through the Straits of Gibraltar and in adjacent areas is marked (since 18,000 years; VERGNAUD-GRAZZINI *et al.*, 1989) by an upper Atlantic inflow and a deep Mediterranean outflow. This pattern has shaped the recent Atlantic-Mediterranean faunal exchanges, favouring the transfer of propagules available in the Atlantic upper layers (< 200 m depth) towards the Mediterranean.

The bryozoan fauna of the Atlanto-Mediterranean region comprises a majority of species common to both the north east Atlantic and the Mediterranean basin (GAUTIER, 1962; HARMELIN, 1992; HAYWARD, 1974; LÓPEZ de la CUADRA & GARCÍA-GÓMEZ, 1994; ZABALA, 1986), species with wider geographic distribution (including some alleged cosmopolitan species), and a large number of Mediterranean endemics. However, many species classified within these categories need a thorough re-evaluation of their status. Several species with an Atlanto-Mediterranean distribution display distinct Atlantic and Mediterranean morphotypes, as revealed by detailed morphological studies. These more or less pronounced but constant differences address the question of their significance as systematic criteria: are they only indicative of present-day environmental control on local populations (*e. g.* due to differences in hydrology or trophic resources), or phenetic signatures of profound genetic divergence between Atlantic and Mediterranean allopatric populations? For some of these species, characterization of distinct morphotypes has not led to any systematic decision (*e. g.* *Crassimarginatella crassimarginata*: HARMELIN & d'HONDT, 1993, Figs. 7-8; *Puellina cassidainsis*: HARMELIN & ARISTEGUI, 1988, Fig. 10 G-H). In other species (*e. g.* *Puellina setiformis*, *P. pseudoradiata*: HARMELIN & ARISTEGUI, 1988; *Escharina dutertrei*: ZABALA *et al.*, 1993), the Atlantic and Mediterranean morphotypes have been classified in different subspecies.

Shallow-water submarine caves are particularly valuable as reference habitat for between-region faunal comparisons, specially because their dark and quiet environment shows a noted worldwide homogeneity (HARMELIN *et al.*, 1985). This habitat appears to be specially favourable to some bryozoan genera, which generally show a second distribution peak on the upper slope (“crypto-bathyal” species, HARMELIN, 1986). The cribrimorph genus *Puellina* Jullien, 1886 is most typical of this distribution pattern (HARMELIN, 1986): around 70% of the 14 *Puellina* species recorded in the regional pool (0-500 m depth) from Provence (French Mediterranean)

inhabit nearshore dark caves. Life in dark caves and/or on deep-water hard substrates implies fragmented spatial distribution and higher probability for allopatric speciation. Thus, better knowledge of the Atlantic cave biota should bring stimulating comparisons with their Mediterranean counterparts. The area of Sagres (southern Portugal) is a key region for investigating these relationships because of its geographical location (western approaches of the Straits of Gibraltar) and the frequency of submarine caves along its rocky shore.

A survey of the communities of eight caves of Sagres area was performed in October 1986 within the frame of the Portuguese-French cooperation programme for scientific research in oceanography (BOURY-ESNAULT *et al.*, 2001).

During this survey, an abundant collection of cave bryozoans was made, including a *Puellina* species formerly ascribed to *P. cassidainsis* (HARMELIN, 1984). Morphological analyses of this material and comparisons with *P. cassidainsis* from Mediterranean localities confirmed the occurrence of phenetic differences already stressed on Canarian specimens (ARISTEGUI, 1984; HARMELIN, 1984). A species status, *P. saldanhai* n. sp., was thus attributed to these Atlantic specimens.

MATERIAL AND METHODS

Studied site

A large population of *P. saldanhai* was sampled by SCUBA diving in a dark room of Donzelle Cave, one of the eight caves of Sagres area that have been explored during the 1986 survey. This cave contrasted with the other caves of this area by its quieter environment in terms of water movements due to its topography which determined more cryptic conditions. This cave comprised a main chamber whose entrance was located at 15-18 m depth under a vast overhang at the bottom of a cliff, and an upper small room (3-5 m depth) communicating with the former through a short and narrow corridor. This upper room presented walls darkened by ferro-manganese oxides, which are typical of totally dark cave and deep-sea environments (HARMELIN *et al.*, 1985). The sessile fauna of this dark room (BOURY-ESNAULT *et al.*, 2001) was characterized by the abundance in *Isops intuata* (Porifera; identification by N. BOURY-ESNAULT), brachiopods, Scyphozoa, and *Pourtalosmilia anthophyllites* (Ellis & Solander, 1786), a colonial scleractinian (identification by H. ZIBROWIUS). The rocky substrata of this room and the skeletons of *P. anthophyllites* were encrusted by a rich bryozoan assemblage (> 30 species) including numerous colonies of *P. saldanhai* n. sp.

Study methods

Cleaned (sodium hypochlorite) and uncleaned colonies of *P. saldanhai* were examined with a stereomicroscope and a Hitachi S-570 SEM after gold coating. Measurements (Fig. 1) and counts (costae, oral spines) were carried out on at least 6

colonies under the stereomicroscope at high magnification using a micrometric eyepiece according to the procedure used by BISHOP & HOUSEHAM (1987) and HARMELIN & ARISTEGUI (1988). For the autozooidal dimensions (L1, L2), 10 measurements were made per colony. Means were calculated from pooled data. The colonial structure, i.e. the proportions in non-ovicellate autozooids, ovicellate autozooids, avicularia, and kenozooids occurring in each colony, was assessed from counts made on several (5-10 per colony), small (around 2 mm²) colony portions using either the SEM or the stereomicroscope. Twelve colonies of *P. saldanhai* were considered for this assessment.

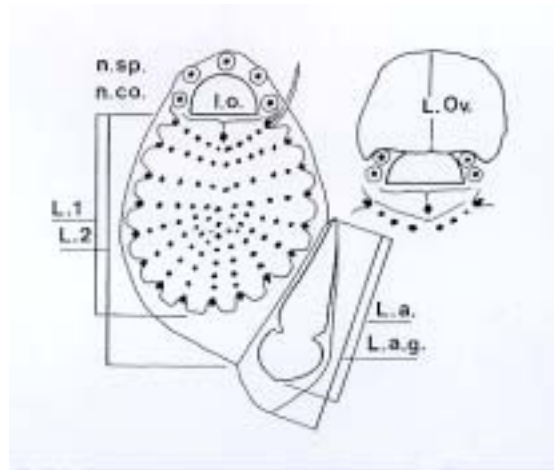


Fig. 1 - Measurements taken into account. Abbreviations; L1: length of frontal shield of autozooid; L2: length of frontal shield + proximal gymnocyst; l. o.: width of non-ovicellate orifice; n. co.: number of costae; L. Ov.: length of ovicell; L. a.: length of avicularium without proximal gymnocyst; L. a. g.: length of avicularium with proximal gymnocyst. From HARMELIN & ARISTEGUI (1988).

RESULTS

Puellina saldanhai n.sp.

- Type specimens. Holotype: Muséum National d'Histoire Naturelle de Paris (LBIMM.BRY 20209).

Paratypes: Museu Municipal do Funchal (MMF 30421); Muséum National d'Histoire Naturelle de Paris (LBIMM.BRY 20210).

- Type-locality: Donzelle Cave, 3-5 m depth, Sagres, Southern Portugal.

- *Derivatio nominis*: This species is dedicated to late Professor LUIZ SALDANHA, University of Lisboa and Guia Marine Laboratory, who was the coordinator of the survey of the submarine cave communities of Sagres area in 1986.

Synonymy

Cribrilaria setosa: HARMELIN, 1978; p. 189.

Cribrilaria cassidainsis: ARISTEGUI, 1984; p. 220, Figs. 47b, 48b, 50a; Pl. 10, Figs. 1-2.

Cribrilaria cassidainsis: HARMELIN, 1984; p. 86 (*pars*), Fig. 13.

Puellina cassidainsis: HARMELIN & ARISTEGUI, 1988, Fig. 10G.

? *Cribrilaria radiata*: COOK, 1985, Pl. 9, Fig. E (= BMNH 1972.3.3.1).

Description

Colony encrusting, unilaminar, of moderate size (commonly less than 100 zooids), often with ribbon-like shape. Autozooids generally longer than broad. Gymnocyte narrow laterally, of moderate width proximally (Fig. 2). Frontal shield (pericyte) of autozooid sub-oval, well calcified, flat or slightly convex, with 10-16 costae (usually 12-14). Costae smooth, with basal portion rounded and slightly prominent, bearing a small pelmatidium often occluded by calcification, sometimes forming an irregular thickening at the center of the shield (Fig. 5). First (distal) pair of costae generally more prominent and thicker than the other costae (Fig. 2). Intercostal pores small to very small, except for those of the distal row (i. e. just below the apertural bar), reniform, with one (occasionally two) median denticle on the inner side, often occluded by calcification (Fig. 4).

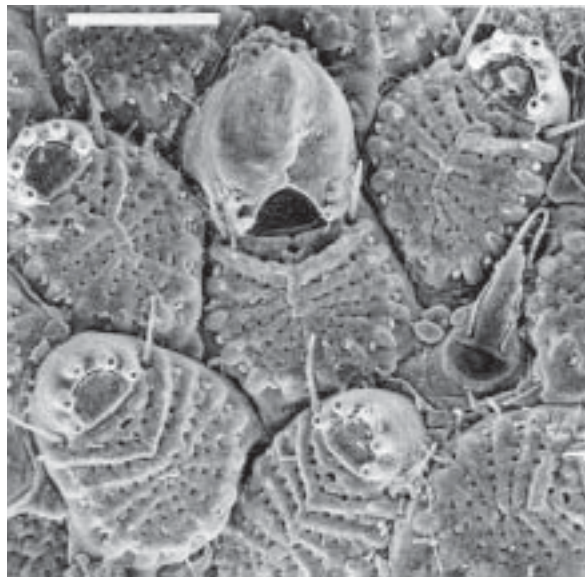


Fig. 2 - *P. saldanhai* n. sp., portion of uncleaned colony with 5 autozooids including one ovicellate (ovicell of type B) zooid, and one avicularium. Donzelle Cave, Sagres. Scale bar: 200 μ m.

Distal setoid papillae robust and long (length = $1/2$ to $2/3$ x L1; Fig. 1). Orifice of non-ovicellate autozoid D-shaped, wider than long (width = 1.25 - 1.38 x length); orifice of ovicellate autozoid broader than the former (Fig. 2). Oral spines 5 in non-ovicellate autozoid (Figs. 2, 4), 4 in ovicellate zoid (Figs. 2, 7), with thick, conical, basal portion, apparently without apophysis above the joint. Apertural bar triangular, of variable height, with two low distal tubercles bearing a pematidium, a well open median sub-oral lacuna with a small proximal denticle, located centrally on the bar or on its proximal half (Fig. 4). Ovicells relatively infrequent (Fig. 3), of type A (majority) and type B (around 40%; Figs. 7, 9; see below), both co-occurring in fertile colonies; ovicell length not significantly different from width (LOV / wOV = 0.97 ± 0.11 ; n = 21), with a median rounded crest often flanked by 2-4 radiating lateral crests or knobs. Avicularia moderately variable in size, shape, and location; with gymnocyst generally well developed laterally and proximally, often grouped at the lateral border of colony (Figs. 2, 5); rostrum pointed, with sides slightly convex at mid-height or straight, with beak often curved downwards; old avicularia with proximal uncalcified area occluded by a minute costate shield (Fig. 5). Kenozooids with radiate costate shield, not rare (cf. below).

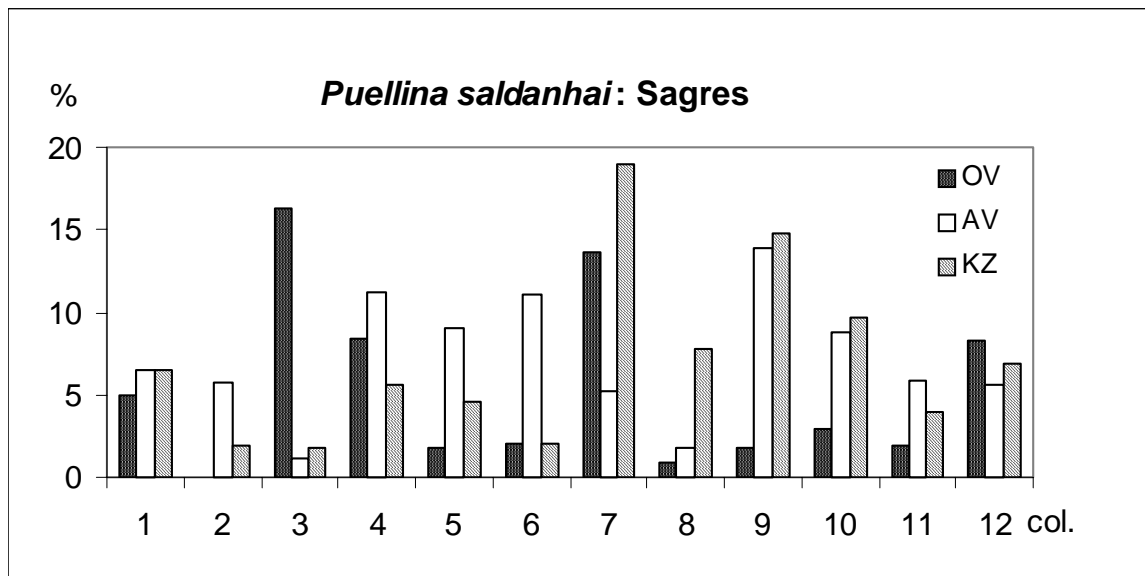
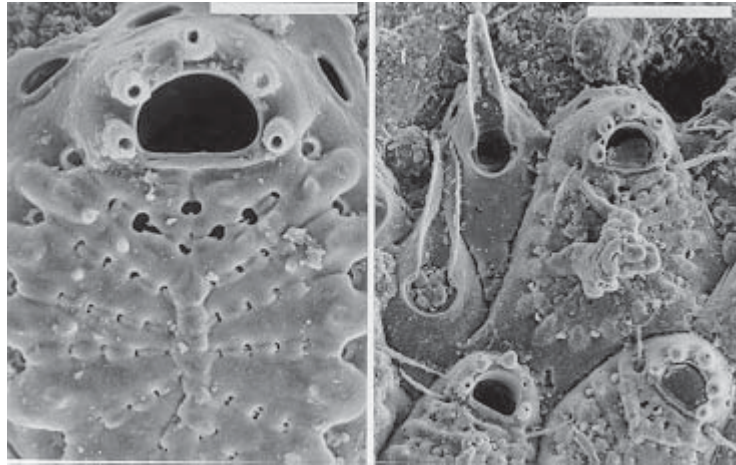


Fig. 3 - Proportions in ovicellate zooids (OV), avicularia (AV), and kenozooids (KZ) relative to the whole number of zooids (non-ovicellate autozooids not plotted) in 12 colonies of *Puellina saldanhai* n. sp. collected in Donzelle Cave, Sagres (southern Portugal).



P. saldanhai n. sp. from Donzelle Cave, Sagres. Fig. 4 (left) - Distal portion of a marginal autozoid showing the distal pore-chambers, the orifice and apertural zone, and the intercostal lacunae. Scale bar: 200 μ m. Fig. 5 (right) - Lateral border of a colony with 2 avicularia (the lower is regenerated and an autozoid bearing an irregularly bulging frontal shield due to extra-growth of some costae. Scale bar: 200 μ m.

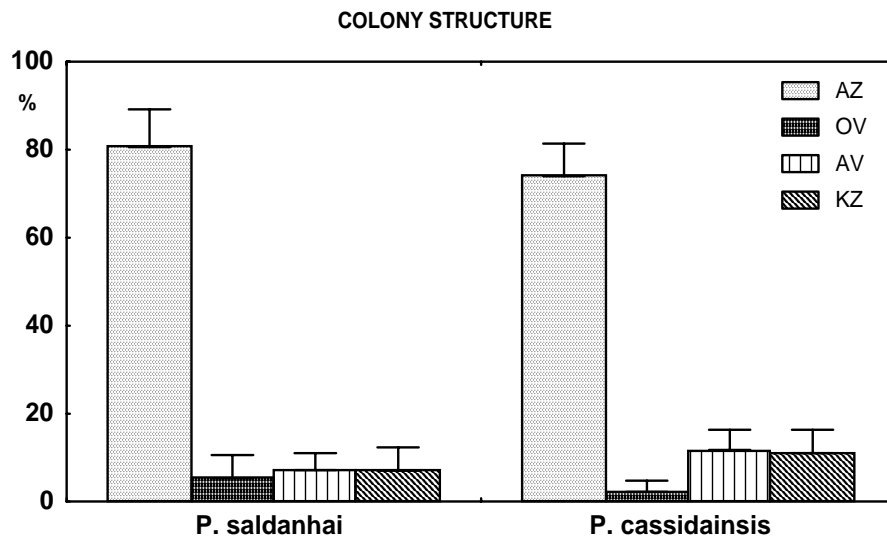


Fig. 6 - Colony structure of *Puellina saldanhai* and *P. cassidainis*: mean proportions in non-ovicellate zooids (AZ), ovicellate zooids (OV), avicularia (AV), and kenozooids (KZ) from samples (*P. s.*: 12 colonies, 1220 zooids; *P. c.*: 10 colonies, 952 zooids) collected in type-localities (*P. s.*: Donzelle Cave, Sagres; *P. c.*: Trémies Cave, Cassis).



Ovicellate autozooids. Fig. 7 (left) - *Puellina saldanhai* n. sp. (Donzelle Cave, Sagres), with ovicell of type B (associated to a distal kenozooid) and orifice bearing 4 spines. Scale bar: 100 μ m. Figure 8 (right) - *Puellina cassidainsis* (3PP Cave, La Ciotat, French Mediterranean), with ovicell of type A (associated to a distal autozooid) and orifice bearing 2 spines. Scale bar: 100 μ m.

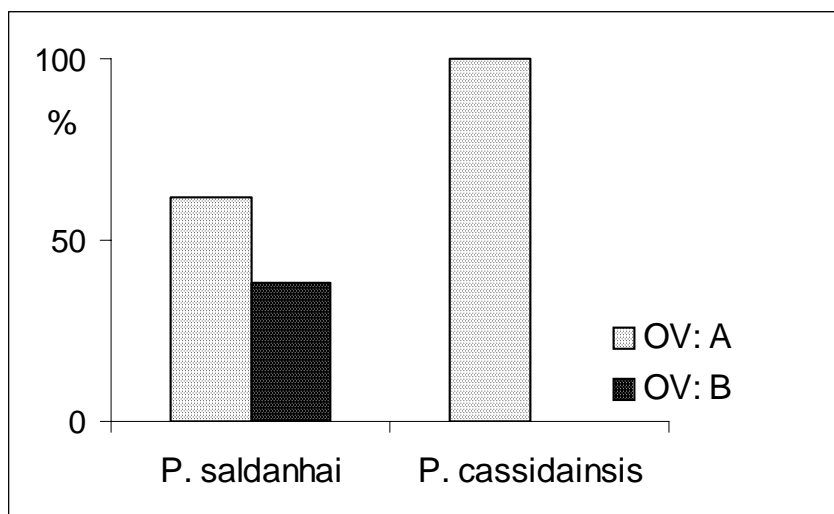


Fig. 9 - Proportions in ovicells of category A (associated to distal autozooid) and category B (associated to distal kenozooid) in *Puellina saldanhai* (110 ovicells; 20 colonies from type-locality) and *P. cassidainsis* (110 colonies; 32 colonies from type-locality and 8 other localities).

Variability of characters and comparison with *P. cassidainsis*

The general morphological features of *P. saldanhai* and *P. cassidainsis* are very similar: no major differences were noticed between the shapes of frontal shields, costae, lacunae, ovicells, avicularia of these two species (for *P. cassidainsis*, see HARMELIN, 1984: Figs. 9-13). Colonies of *P. saldanhai* from Sagres cave frequently present irregularly developed costae, which can form an irregular bump in the center of the frontal shield (Fig. 5). This feature may be specific of this local population, as it has not been observed in Canarian specimens.

Two dimensions of *P. saldanhai* and *P. cassidainsis*, the length of the costulate shield (L1) and the avicularium length (LAV), were statistically compared with the same sampling design (six colonies per species and ten measurements per colony for L1; 28 avicularia per species). For both species, colonies came from their type-locality (*P. s.*: Sagres cave; *P. c.*: Trémies Cave, Cassis, French Mediterranean). There were no significant between-species differences in both measurements (1-way ANOVAs on $\sin x$ transformed data; L1: $F = 0.534$; d. f. = 1.118; $p = 0.47$; LAV: $F = 0.023$; d. f. = 1.54; $p = 0.88$). Higher values of the coefficient of variation (CV = 11.4% vs. 8.9% for L1; 13.7% vs. 9.0% for LAV) suggest that variability of both dimensions is greater in *P. saldanhai* than in *P. cassidainsis*. The relative size of the proximal gymnocyst of autozooids is smaller in *P. saldanhai* than in *P. cassidainsis* as attested by the ratio L1/L2 significantly higher in the former (Table 1).

TABLE 1 - Morphometric and meristic characters of *P. saldanhai* and *P. cassidainsis* from similar sampling designs. Abbreviations according to figure 1; n. sp. AZ: number of oral spines on non-ovicellate autozooids; n. sp. Ov.: number of oral spines on ovicellate autozooids. Dimensions in μm . Mean \pm standard deviation (number of measurements).

Measurements	<i>P. saldanhai</i>	<i>P. cassidainsis</i>
L1	240.8 \pm 19.9 (60)	236.4 \pm 22.1 (39)
L2	285.4 \pm 27.0 (60)	300.7 \pm 34.7 (37)
L1 / L2	0.85 \pm 0.04 (60)	0.78 \pm 0.06 (37)
l. o.	68.1 \pm 2.1 (30)	68.3 \pm 4.3 (39)
L. a.	243.6 \pm 33.4 (28)	250.0 \pm 28.3 (28)
L. a. g.	335.4 \pm 43.2 (28)	363.4 \pm 36.5 (28)
L. Ov.	191.0 \pm 19.1 (21)	229.7 \pm 10.4 (16)
n. sp. AZ.	5	5
n. sp. Ov.	4	2
n. co.	13.0 \pm 0.6	11.9 \pm 1.0

However, besides these between-species similarities, several characters appear to show constant differences between *P. saldanhai* and *P. cassidainsis*.

The occurrence of a relatively large lacuna on the median suture of the apertural bar is a constant feature in *P. saldanhai* (Fig. 4), while in *P. cassidainsis*, the apertural bar is typically devoid of median lacuna (Fig. 8). A single exception to this diagnostic trait was found on a deep-water colony (Cassidaigne Canyon, Marseilles region, 300 m depth), which otherwise displayed other characters typical of *P. cassidainsis* (ovicellated orifice with two spines, no ovicell of type B).

The potentialities in developing different ovicell types differ strikingly in the two species, and may be indicative of phyletic relationships. Three subgenera of *Puellina* were distinguished by BISHOP & HOUSEHAM (1987) partly from differences in ovicell types. *Puellina* species classified in subgenus *Cribrilaria* typically have ovicells of category A, which are “produced during the budding of an autozoid distal to the maternal autozoid, and (are) a proximal component of the distal autozoid” (BISHOP & HOUSEHAM, 1987). In subgenus *Glabilaria*, ovicells are of category B, i. e. associated to a distal kenozooid with a costate frontal shield, while ovicells of type C, which are budded prior to distal zooids, characterize the subgenus *Puellina*. However, as noticed by HARMELIN & ARISTEGUI (1988), intermediate features can occur in some species, indicating that these subdivisions correspond more to nodes in a continuum of morphological variability rather than to clearly distinct categories within the genus *Puellina*. Examination of ovicell types showed that *Puellina saldanhai* is one of those species with mixed characters and therefore differs clearly from *P. cassidainsis*. In a sample of 110 ovicells from 20 colonies of *P. saldanhai* from Donzelle Cave, 61.8% of ovicells were of category A and 38.2% of category B (Figs. 7, 9). In *P. cassidainsis*, ovicells of category A (Figs. 8-9) occurred without exception in a sample of same size (110 ovicells from 32 colonies collected in Marseilles’ area in 5 shallow-water dark caves and 4 deep-water sites ranging from 120 to 300 m depth).

Puellina cassidainsis has been first described (HARMELIN, 1984) as having either two oral spines on ovicellate (maternal) autozooids (material from north-western Mediterranean; Fig. 8), or four spines (material from Canary Islands referred here to *P. saldanhai*) as in most species referred to subgenus *Cribrilaria*. In ovicellate Mediterranean specimens of *P. cassidainsis*, the two spines may be occasionally provided with a small, blunt, proximal apophysis (HARMELIN, 1984: Fig. 10), which may be interpreted as remnant of the missing second pair. In *Puellina saldanhai*, ovicellate zooids bear without exception four oral spines (Figs. 2, 7).

Specimens from Canary Islands ascribed to *P. cassidainsis* by ARISTEGUI (1984); HARMELIN (1984) and HARMELIN & ARISTEGUI (1988) show typical characters of *P. saldanhai*: apertural bar with a median lacuna, ovicellated orifices with four oral spines, and ovicells frequently associated to a distal costate kenozooid

(see ARISTEGUI, 1984: Pl. 10, Fig. 1). The Ghanean specimen illustrated by COOK (1985, Pl. 9E) as *Cribrilaria radiata* (a Mediterranean endemic; HARMELIN, 1992) might belong to *P. saldanhai* considering the avicularium and apertural bar features. The diagnostic characters of *P. cassidainsis* evidenced from specimens collected in the north-western Mediterranean, i. e. apertural bar without median lacuna, ovicell of only type A, ovicellated orifice with two spines, were also observed in specimens from Algeria (Annaba, Cap de Fer, 85-130 m depth; R. V. "Ichthys", 1983; HARMELIN, unpublished data), i. e. from a locality washed by the superficial Atlantic waters circulating in the Mediterranean (GUIBOUT, 1987). This may indicate that the phenotype of *P. cassidainsis* is stable enough to be not modified when the Mediterranean hydrological features are modified by the Atlantic flow.

Analysis of colony structure in terms of proportions in different zooid types (Fig. 6) indicates significant differences between *P. saldanhai* and *P. cassidainsis* (2 x 4 contingency table; $\chi^2 = 52.02$; d. f. = 3; $p < 0.001$). The proportion in autozooids is higher in the former ($80.5 \pm 8.6\%$ vs. $74.0 \pm 7.4\%$) while inter-colony variability of this proportion is relatively low in both species (CV = 11 vs. 10%). Avicularia and kenozooids occur in similar proportions (Fig. 6), which are lower in *P. saldanhai* (around 7% vs. 11% in *P. c.*); however, in every case, the inter-colony variability is high (CV ranging from 38.5 % for the avicularia of *P. saldanhai* to 75.1% for the kenozooids of *P. cassidainsis*). In both species, the relative frequency of ovicells is highly variable among colonies (CV = 100-110%; Fig. 3). Consequently, the higher mean proportion in ovicellate zooids observed in *P. saldanhai* (5.3 vs. 2.2%) is not significantly different from that in *P. cassidainsis*.

Remarks about other cribrimorphs coexisting with *P. saldanhai* in Sagres' caves

The cribrimorph fauna dwelling in the caves of Sagres area appears to be noticeably less diverse than the one from north-western Mediterranean caves. Four other cribrimorph species were found in a preliminary census: *Puellina setosa* (WATERS, 1899), *P. hincksi* (FRIEDL, 1917), *Collarina* sp., and *Membraniporella nitida* (JOHNSTON, 1838). *Puellina setosa* was the dominant species of a paucispecific bryozoan assemblage (8 species) from a dark recess of another cave of the same area (Nossa Senhora Cave), which was seemingly submitted to more active water circulation than the room sheltering the population of *P. saldanhai* (BOURY-ESNAULT *et al.*, 2001). Thus, *Puellina* species particularly frequent in Mediterranean caves, such as *P. radiata* (Moll, 1803) and *P. pedunculata* (Gautier, 1956), were not observed despite the occurrence of those "crypto-bathyal" Mediterranean endemics on the western side of the Strait of Gibraltar (Harmelin & d'Hondt, 1993).

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