



Observations on some Actinoporellas (Chlorophyta, Polyphysaceae). Revision of the Jacques EMBERGER Collection. Part 1

Bruno GRANIER ¹

Abstract: On the occasion of the inventory of the J. EMBERGER Collection, specimens from the "Lower Cretaceous" (Valanginian and Hauterivian) of Algeria, which are referable to the genus *Actinoporella* (GÜMBEL in ALTH) and which were earlier identified to its type-species *A. podolica* (ALTH) by CONRAD *et al.*, are re-examined. They correspond to two discrete species, one of which could be a junior synonym of *A. podolica*, a synonymy that remains pending because it would require a new sampling at the original locality in western Ukraine some 140 years after the original specimens, now lost, were collected. Regarding their age ascription, they are Tithonian and/or Berriasian in age, *i.e.*, latest Jurassic (*sensu* OPPEL) in age, not earliest Cretaceous. In addition to these two Actinoporellas, a third discrete species, initially described as *Clypeina nigra* (CONRAD & PEYBERNÈS), but later referred to the genus *Actinoporella*, is revised. New data justify its re-ascription to the genus *Bakalovaella* BUCUR. Finally, it is now confirmed that both the Polyphysaceae and the modern Dasycladaceae derive from the Diploporaceae either directly or indirectly through the ancestral Dasycladaceae.

Key-words:

- systematics;
- paleophycology;
- phylogenetics;
- Dasycladales;
- Algeria;
- France;
- Ukraine;
- Tithonian;
- Berriasian;
- Valanginian;
- Hauterivian;
- Barremian

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Résumé : *Observations sur quelques Actinoporellas (Chlorophyta, Polyphysaceae). Révision de la Collection Jacques EMBERGER. Part 1.* - À l'occasion de l'inventaire de la Collection J. EMBERGER, des spécimens du "Crétacé inférieur" (Valanginien et Hauterivien) d'Algérie, qui se rapportent au genre *Actinoporella* (GÜMBEL in ALTH) et qui avaient précédemment été attribués à son espèce type *A. podolica* (ALTH) by CONRAD *et al.*, sont réexaminés. Ils correspondent à deux espèces distinctes, dont l'une pourrait être un synonyme junior d'*A. podolica*, une synonymie en suspens parce qu'elle nécessiterait un nouvel échantillonnage de la localité originelle d'Ukraine occidentale quelque 140 années après que le matériel type, aujourd'hui perdu, y ait été récolté. Concernant l'attribution stratigraphique, ils sont d'âges tithonien et/ou berriasien, c'est-à-dire du Jurassique terminal (*sensu* OPPEL) et non du Crétacé basal. En plus de ces deux Actinoporellas, une troisième espèce, originellement décrite comme *Clypeina nigra* (CONRAD & PEYBERNÈS), mais ultérieurement attribuée au genre *Actinoporella*, est révisée. De nouvelles données justifient sa réattribution au genre *Bakalovaella* BUCUR. Enfin, il est désormais confirmé que les Polyphysaceae et les Dasycladaceae modernes sont issues de Diploporaceae, soit directement, soit indirectement par le biais des Dasycladaceae ancestrales.

¹ Dépt. STU, Fac. Sci. Tech., UBO, 6 avenue Le Gorgeu, CS 93837, F-29238 Brest (France)
bgranier@univ-brest.fr

**Mots-clefs :**

- systématique ;
- paléophycologie ;
- phylogénétique ;
- Dasycladales ;
- Algérie ;
- France ;
- Ukraine ;
- Tithonien ;
- Berriasien ;
- Valanginien ;
- Hauterivien ;
- Barremien

1. Introduction

During his career, the late Jacques EMBERGER (02/01/1923-09/03/1978), son of Louis EMBERGER (23/01/1897-30/11/1969), assembled a private library of scientific literature (offprints, periodicals, books, ...) dedicated to the calcareous algae. Besides that, he collected a significant number of samples of which thin sections were prepared. There are more than 9000 references in this collection, with up to 10 thin sections for each sample. A fraction of this material that corresponds to igneous and metamorphic rocks has been put aside. More recently, some more material was taken out of the collection: that was the type-material of algae studied by Mme Marie LEMOINE, which was shipped to the Muséum d'Histoire Naturelle de Paris for integration in her collection of calcareous red algae. Despite that, the J. EMBERGER Collection remains a very valuable resource for paleophycological investigations (see GRANIER, 1989, 2018a, 2018b). J. EMBERGER was not a prolific author. As a matter of fact, he is mostly known for the bibliographic syntheses that he published in the "*Bulletin de l'Institut de Géologie du Bassin d'Aquitaine*" (J. EMBERGER, 1976, 1978, 1979) but he wrote very few contributions dedicated to the algae (J. EMBERGER, 1956, 1958a, 1958b, 1958c; J. EMBERGER & MAGNÉ, 1957; M. LEMOINE & J. EMBERGER, 1967; CANÉROT & J. EMBERGER, 1970; BULLE & J. EMBERGER, 1973). He did not pay either much attention to formally define some taxa of his own. That was the case with his "*Zergatella suprajurensis*" (J. EMBERGER, 1960; GRANIER, 1989, 2010) but that was also the case with his "*Clypeina harrazaensis*" (J. EMBERGER, 1960), which is one of the species described in this first part of the "Revision of the Jacques EMBERGER Collection", together with *Clypeina lucasi* J. EMBERGER, 1956. Both *Clypeinas* are referable to the genus *Actinoporella* (GÜMBEL in ALTH, 1882). Although J. EMBERGER did not identify it his collection includes a third species that was once considered as another *Actinoporella*; it will prove to be a Dasycladacean, not a Polyphysacean alga.

2. A digest on *Actinoporella podolica* (ALTH, 1878)

ALTH (1878: Pl. VI, figs. 1-8; herein Fig. 1) describes *Gyroporella podolica* from Upper Jurassic limestones of the locality of Nyzhniv ("Nižniow") and of its immediate vicinity ("góry Tanutyńskij" / "Tanutynska Gora"): Fig. 2. He also mentions two other localities of the Ivano-Frankivsk Oblast in W Ukraine: Bukivna ("Bukowna", some 10 km W of Nyzhniv) and Kutyshche ("Kutysk", some 5 km S of Nyzhniv), where the alga is less common. Later, GÜMBEL (in ALTH, 1882) introduces the genus *Actinoporella* based on *Gyroporella podolica* (ALTH, 1878, Pl. VI, figs. 1-4, 6-8), whereas ALTH (*op.cit.*) introduces a new species "*Actinoporella Gumbeli*" based on specimens originally ascribed to *Gyroporella podolica* (ALTH, 1878, Pl. VI, fig. 5). However, after comparing 40 specimens ascribed to *Actinoporella podolica* and 13 specimens of *Actinoporella guembeli*, PIA (1920) concludes that both species are synonymous. ALTH's, GÜMBEL's and PIA's materials are lost. They were probably destroyed during the Second World War (CONRAD *et al.*, 1974).

The original locality of each specimen illustrated by ALTH (1878, Pl. VI, figs. 1-8; here Fig. 1) is not provided, which is not the case with PIA's (1920, Pl. VII, figs. 1-7; herein Fig. 3) drawings but there are other issues:

- according to CONRAD *et al.* (1974), two specimens they illustrate (*op.cit.*, Fig. 7.a-b), which "are reminiscent of the specimen" on PIA's figure 1 of plate VII (1920), "are attributable to a new species of *Clypeina* or *Teutloporella*";
- according to RADOIČIĆ (1969), PIA's figure 3 of plate VII (1920) is "very different from ALTH's specimens of *Actinoporella podolica*, and might correspond to some mesozoic [*sic*] *Clypeina*" (CONRAD *et al.*, 1974). PIA's (1920: Fig. 19) erroneous reconstruction of the species, reused by BERGER and KAEVER (1992: Fig. 2.20.e), is based on this single specimen;
- PIA's figure 4 of plate VII (1920) is also questionable (see discussion below).

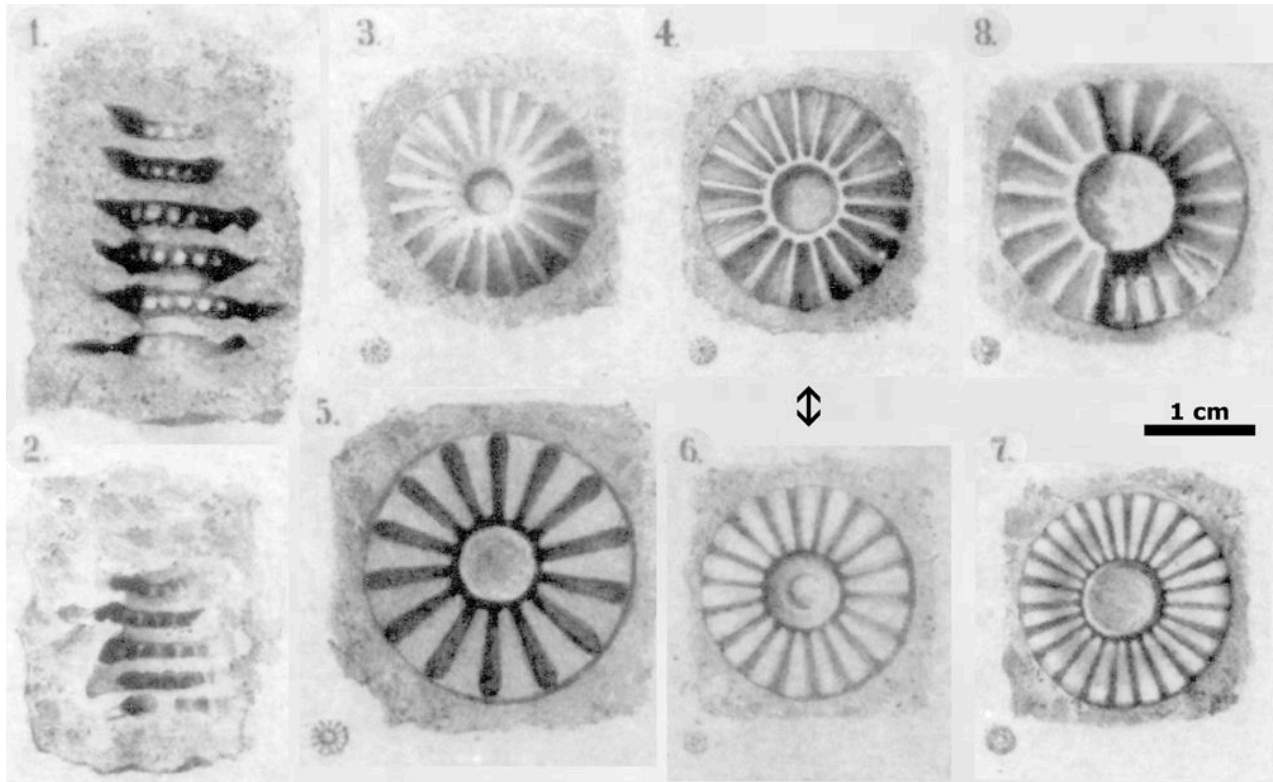


Figure 1: *Gyroporella podolica* fide ALTH (1878). 1) oblique break; 2) oblique break; 3) mould of whorl; 4) mould of whorl (corresponding to imprint 6); 5) imprint of whorl (corresponding to "*Actinoporella guembeli* ALTH, 1882"); 6) imprint of whorl (corresponding to mould 4); 7) imprint of whorl; 8) mould of whorl. Scale bar 1 cm (from the book).

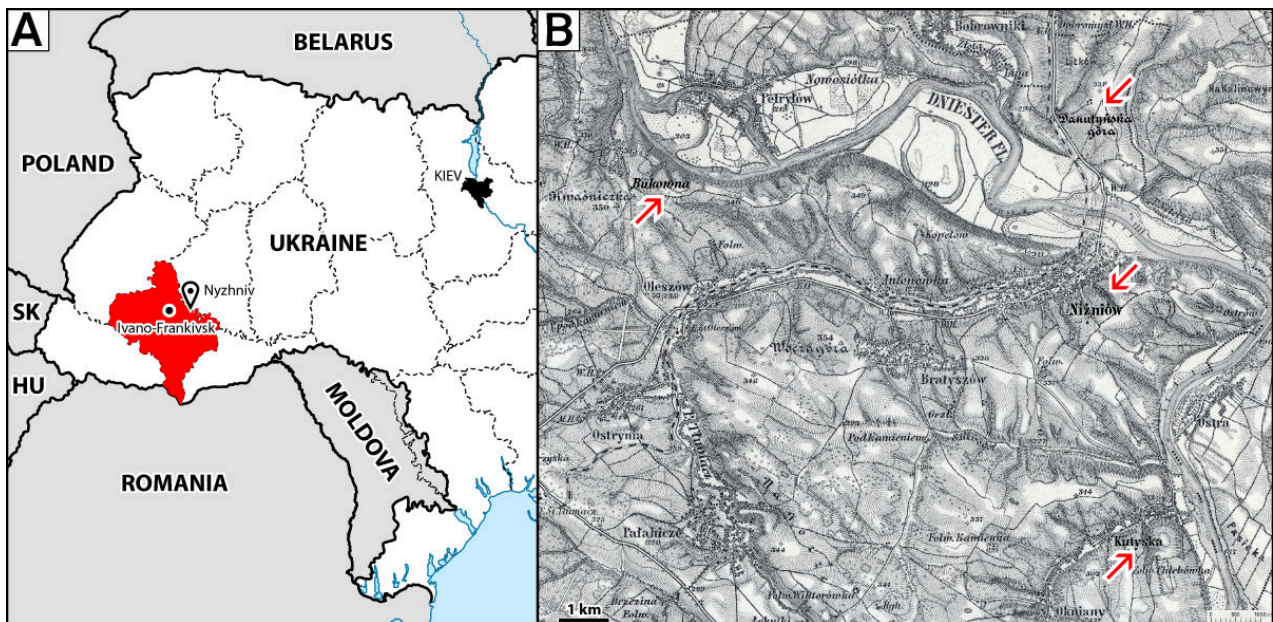


Figure 2: Location map of the original localities sampled by ALTH (1878) in the Nyzhniw area, W Ukraine: "Nizniw", "Danutyńska góra", "Bukowna", "Kutyska".

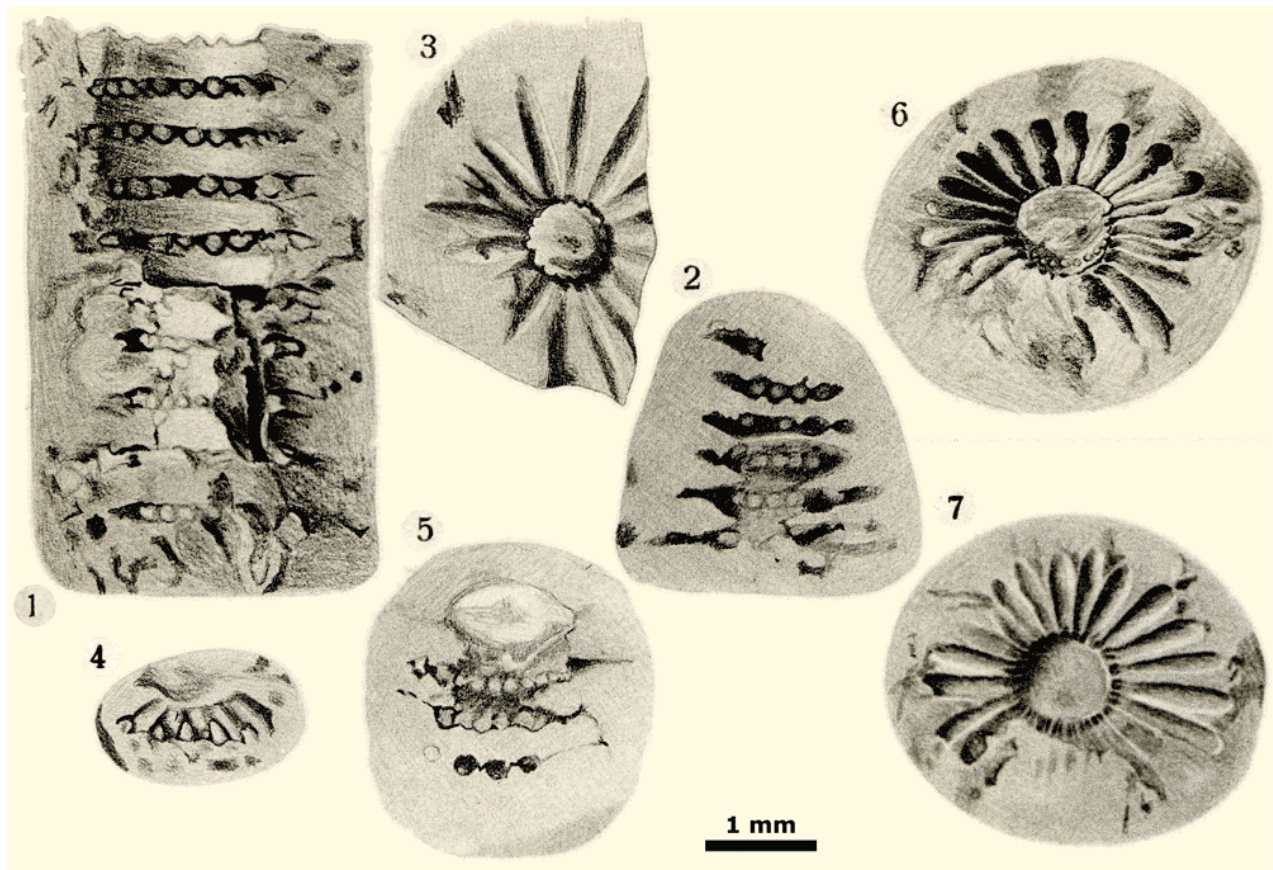


Figure 3: *Actinoporella podolica* fide PIA (1920). 1) longitudinal break; 2) oblique break; 3) mould of whorl; 4) imprint of whorl; 5) oblique break; 6) mould and 7) imprint of whorl. Scale bar 1 mm.

The specimens illustrated on PIA's figures 1 and 4 of plate VII (1920) were collected at "Tanutynska Gora" whereas the specimen illustrated on figure 3 was collected at Bukivna. In conclusion, one is left with four of PIA's figures (1920, Pl. VII, figs. 2, 5-7) of specimens that were all collected at Nyzhniv:

- PIA's figure 2 of plate VII (1920), which corresponds to ALTH's figure 1 of plate VI (1878), and PIA's figure 5 of plate VII (1920). Both of them are oblique breaks;
- PIA's figures 6 and 7 of plate VII (1920), which are respectively the mould and the imprint of the same single whorl.

In conclusion, the type locality of *Actinoporella podolica* should be Nyzhniv itself, not "Tanutynska Gora" as stated by CONRAD *et al.* (1974). This toponym, which is not visible on ALTH's map (1882, p. 185), was misspelled for "Danutyńska góra", as reported on the 1:75,000 military map of "Tyśmienica und Tłumacz" (1877-1912). Relative to Nyzhniv, it is located on the opposite bank of the river Dniester, and corresponds to Dibrova, Ivano-Frankivsk Oblast.

In a subchapter entitled "*Actinoporella podolica* in its type-locality of Upper Jurassic age", CONRAD *et al.* (1974) state that "the reason why

the dimensions given by" PIA "for d and D are different from" their "own observations is not known". However, it is crystal clear:

- their material was not collected at Nyzhniv, the type-locality, but probably in another locality;
- the measurements of their specimens are not only "different" but significantly out of ranges compared to those given by ALTH (1878) and PIA (1920). For instance, D, the diameter of a whorl, is significantly smaller, ranging from 2.1 to 3.2 mm according to PIA (1920) versus from 0.7 to 1.0 mm according to CONRAD *et al.* (1974); similarly, d, the diameter of the main axis, ranges from 0.4 to 1.1 mm according to PIA (1920) versus from 0.18 to 0.28 mm according to CONRAD *et al.* (1974);
- most specimens of figure 6 of CONRAD *et al.* (1974: Fig. 6.a-f) are "poorly preserved". It looks like they consist of mouldic pores, left empty after the leaching of the original aragonitic coating;
- their figures 4.a-b (CONRAD *et al.*, 1974; herein Fig. 4.a-b) and 6.g (CONRAD *et al.*, 1974; herein Pl. 1, fig. a) might correspond either to *Clypeina ? isabellae* MASSE *et al.*, 1999 (see Pl. 1, figs. b-f), or to *Clypeina ? loferensis* SCHLAGINTWEIT *et al.*, 2009.

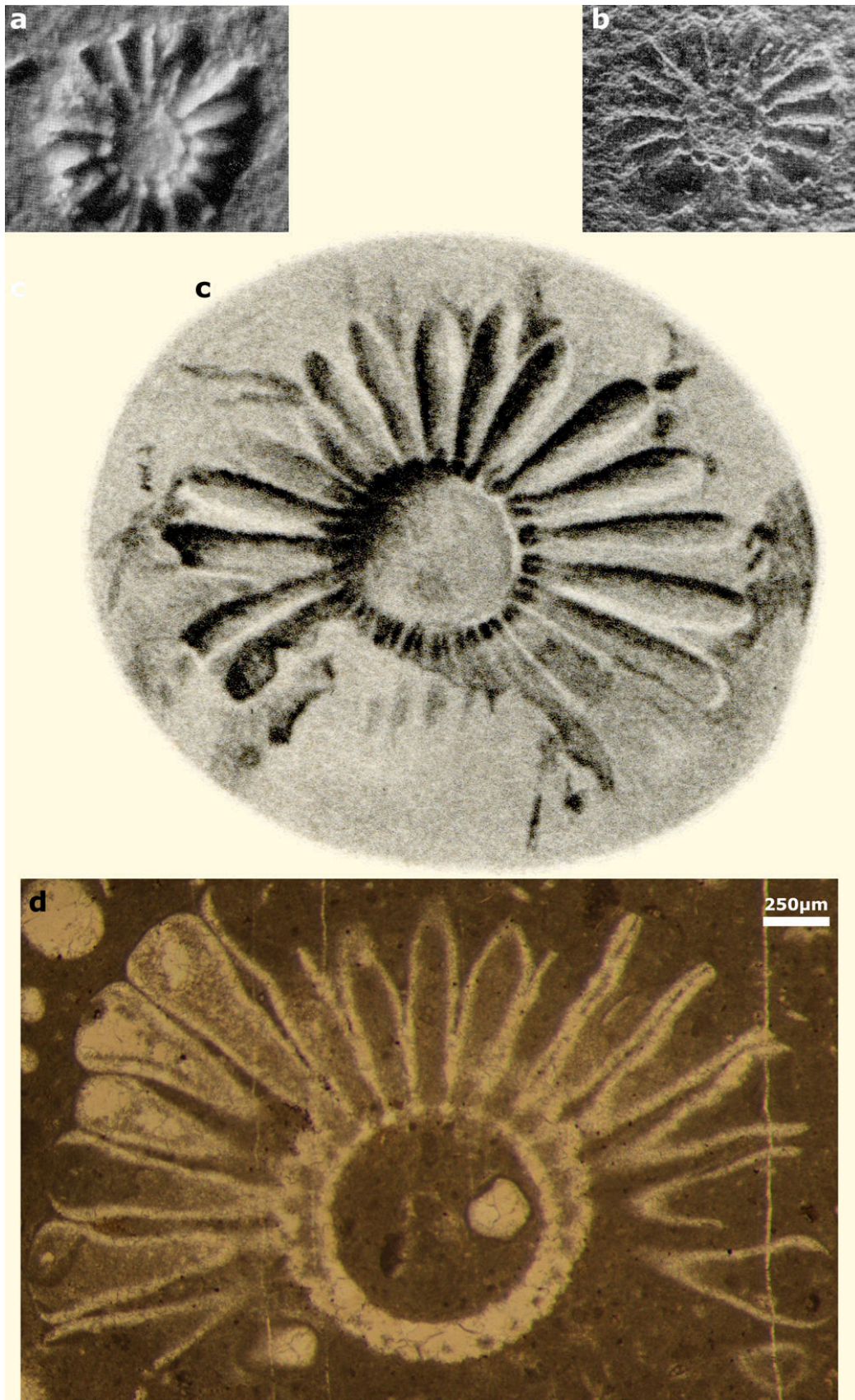


Figure 4: a-b) 14-15 laterals, excerpts from CONRAD *et al.* (1974: Fig. 4.a-b); c) 22 laterals, excerpt from PIA (1920: Pl. VII, fig. 7); d) holotype of *Actinoporella harrazaensis* n.sp., subtransverse section of a single row with 25 club-shaped laterals, thin section 444B. See J. EMBERGER's 1960 Fig. 27 (Djebel Harraza, J. EMBERGER Collection). Scale bar 250 μ m.



All that suggests that one should seriously question the identification of CONRAD *et al.*'s (1974) new material as *Actinoporella podolica* (ALTH, 1878), as well as the relevancy of their synonymy list.

3. *Actinoporella* specimens from Algeria

In a subchapter entitled "On *Clypeina lucasi* (= *A. podolica*) and other specimens from the Neocomian age", CONRAD *et al.* (1974) state that *Clypeina harrazaensis*, *nom. nud.* (J. EMBERGER, 1960), from the Hauterivian of Algeria, and *Clypeina lucasi* J. EMBERGER, 1956, from the "Valanginian" of Algeria, are junior synonyms of *Actinoporella podolica*. However, pending a new survey of the Ukrainian type-locality, the result of which would provide a conclusion to the synonymy of one of these Algerian species with *Actinoporella podolica*, it is assumed below that we are dealing with two discrete species.

Remains of the first species mostly consist of isolated rows with in average 15 subcylindrical fertile ampullae that, due to their morphology, are distally diverging (Pl. 2) whereas the rows of the second species bear up to 25 phloiophorous fertile ampullae forming a rather continuous "clipeus" (Fig. 4.d).

Actinoporella harrazaensis

J. EMBERGER *ex* GRANIER, *herein*

(Fig. 4.d; Pl. 3, figs. a-h; Pl. 4, figs. a-j; Pl. 5, figs. a-n; Pl. 6, figs. a-d)

Synonymy:

nom. nud. 1960 *Clypeina harrazaensis* n.sp.- J. EMBERGER, p. 143, Fig. 27 (1) (herein Fig. 4.d; Pl. 4, figs. a-b, g)

1972 *Clypeina lucasi*.- REY, Pl. VIII, fig. 2

1974 *Actinoporella podolica*.- CONRAD *et al.*, Fig. 9.a-c

1992 *Actinoporella lucasi* n.comb.- GRANIER, Pl. 1, figs. 5-6

Origin of the name: from Djebel Harraza (Ain Rich, Algeria).

Holotype: Fig. 4.d, also illustrated by J. EMBERGER (1960: Fig. 27.1 *pars*), subtransverse section of a single row, thin section 444B, J. EMBERGER Collection.

Paratypes : Pl. 3, figs. a-h; Pl. 4, figs. a-e, g, i-j; Pl. 5, figs. a-n, various subaxial, tangential and oblique sections 444A, 444B, 444C, 444D, 444E, and 444F from the same rock sample.

Type-level: In level 15 of the Djebel Harraza section (J. EMBERGER, 1960: Fig. 26), it is found associated with *Pseudocyclammina lituus* (YOKOYAMA) and *Coscinoconus* sp. In the Djebel Ladjdar section (e.g., in sample 873 of the J. EMBERGER Collection, "Ain Melah" (Ain El Melh), S of Bou-Saâda), it is found with calpionellids. Accordingly it is not "Hauterivian" in age as suggested by CONRAD *et al.* (1974), but Berriasian.

Diagnosis: A rather large representative of the genus *Actinoporella* (GÜMBEL in ALTH, 1882), commonly found in the form of dissociated fertile rows, ranging from 1.5 to 3.2 mm in diameter. Presence of both upper and lower coronae. About two dozens of club-shaped fertile ampullae per row forming a flat clipeus-like verticil. These morphologic and metric (below) parameters are diagnostic of the species.

Description and measurements: The photomicrographs (Fig. 4.d; Pl. 3, figs. a-h; Pl. 4, figs. a-j; Pl. 5, figs. a-n; Pl. 6, figs. a-d) represent a comprehensive catalogue of the material referable to this species found in the J. EMBERGER Collection. A unique large subtransverse section of a row comprising some 25 laterals (Fig. 4.d), already illustrated by J. EMBERGER (1960: Fig. 27.1 *pars*), is selected as the holotype. Its outer diameter D is 3.2 mm whereas its inner diameter d is 0.88 mm, which results in a d/D ratio of 27.5%. Some specimens are smaller, with D equal to 1.5 mm, but the distal part of the lateral was not preserved. With d equal to 0.33 mm; the ratio d/D varies from 18.8% to 37.6%. The thickness/height of a whorl, H (comprising the coronae), measures 0.46 mm in average. The fertile ampullae are typically club-shaped with a width increasing gradually from 0.09 mm in the proximal part up to 0.33 mm in the distal part. They are probably slightly vertically compressed, *i.e.*, thinner (in axial or tangential sections) than wider (in transverse section), and their length may exceed 1 mm. Some measurements (d/D, w) make it close to *Actinoporella guembeli sensu* ALTH (1882); however, it is still not possible to conclude to a synonymy because ALTH 's original material is lost.

Actinoporella lucasi

(J. EMBERGER, 1956), GRANIER, 1992

(Pl. 2, figs. a-f, g *pars*; Pl. 6, figs. e, g-k; Pl. 7, figs. a-g)

Synonymy:

1956 *Clypeina lucasi* n.sp.- J. EMBERGER, p. 549-550, Fig. 3 *pars*; Pl. XXIV, figs. 1-2 (holotype), 7 *pars*

1960 *Clypeina lucasi*.- J. EMBERGER, Fig. 21.1

1974 *Clypeina lucasi* EMBERGER (= *Actinoporella podolica*).- CONRAD *et al.*, Fig. 8.a-b

? 1966 *Clypeina* aff. *hanabatensis* n. sp.- MOUTY, Pl. 4, figs. 1-2

non 1992 *Actinoporella lucasi* n.comb.- GRANIER, Pl. 1, figs. 5-6

According to CONRAD *et al.* (1974), "the thalli (...) are hollow and epigenized by large dolomite rhombs" and "no suitable sections could be made". However, in addition to the isolated rows (J. EMBERGER, 1956: Fig. 3 *pars*; Pl. XXIV, figs. 1-2, 7 *pars*; CONRAD *et al.*, 1974: Fig. 8.a-b; herein: Pl. 2, figs. a-f, g *pars*), there is a significant number of thin sections made from the same rock samples in the J. EMBERGER Collection (herein: Pl. 6, figs. e, g-k; Pl. 7, figs. a-g).



According to J. EMBERGER (1956), the outer diameter D of a whorl ranges from 2.5 to 3.0 mm and the inner diameter d ranges from 0.35 to 0.48 mm. The distal part of the fertile ampullae is commonly broken. Two isolated rows with some complete ampullae are measured: A) Pl. 2, fig. a sample has $D = 2.2$ mm with $d = 0.4$ mm, *i.e.*, $d/D = 18\%$, and B) Pl. 2, fig. b sample has $D = 2.9$ mm with $d = 0.5$ mm, *i.e.*, again $d/D = 18\%$. In thin section, because measurements of D are commonly underestimated and d ranges from 0.33 to 0.65 mm, the ratio d/D is commonly overestimated (it reaches up to 25 %). The thickness of a whorl, *i.e.*, its height, H (comprising the coronae), ranges from 0.3 to 0.5 mm, and is probably almost equal to the distance from the center of a whorl to the center of the next one, h . Accordingly, the ratio H/h should be close to 1. The diameter of the fertile ampullae, p , may reach up to 0.56 mm at their distal part (versus 0.5 mm according to J. EMBERGER, 1956), and their length may exceed 1 mm (up to 1.1 mm according to J. EMBERGER, 1956). The number of ampullae per whorl is 15 in on average. Some values (d/D , w) make it close to *Actinoporella podolica sensu* ALTH (1882). As for *A. harrazaensis* n.sp. above, it is not possible to conclude on their synonymy.

Remark: In the Djebel Ladjdar section (J. EMBERGER, 1960: Fig. 20), this species is found associated with *Salpingoporella annulata* CAROZZI and *Coscinoconus* sp., below strata with *Anchispirocyclina lusitanica* (EGGER) and calpionellids. Accordingly it is not "Valanginian" in age as suggested by CONRAD *et al.* (1974), but probably Tithonian - (?) early Berriasian.

4. Notes on *Actinoporella nigra* (CONRAD & PEYBERNÈS, 1978), GRANIER, 1994

***Bakalovaella nigra* CONRAD & PEYBERNÈS, 1978, n.comb. (Pl. 1, figs. g-ab, ae-ak)**

Synonymy:

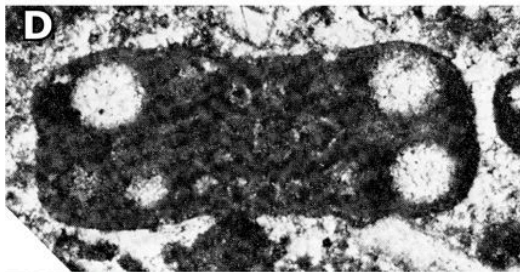
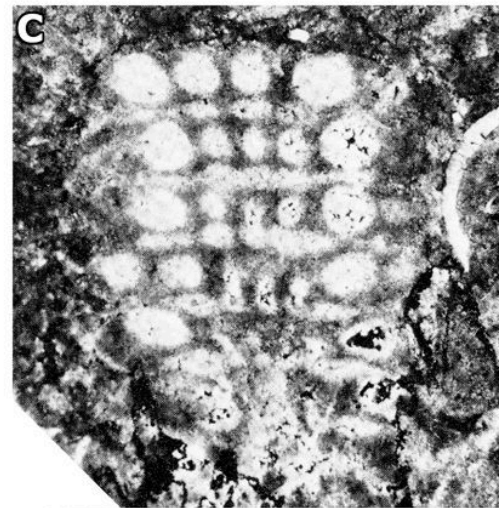
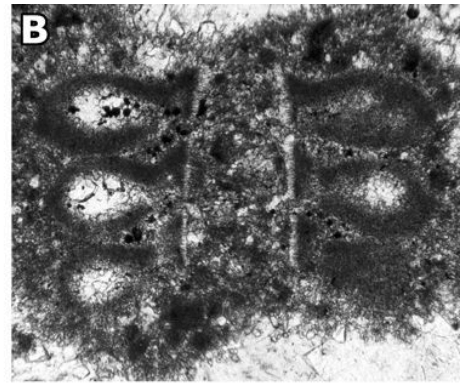
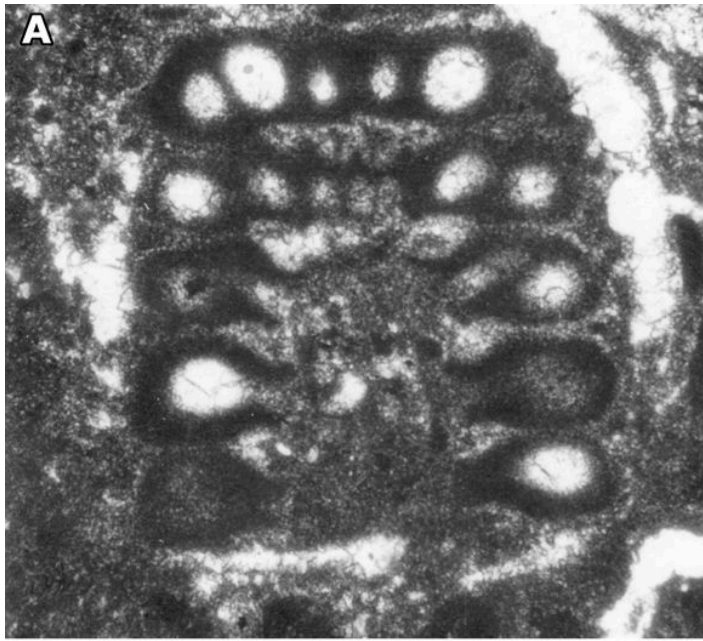
- 1976** *Clypeina* sp. 1.- CONRAD & PEYBERNÈS, p. 180, Fig. 6
1978 *Clypeina nigra* n.sp.- CONRAD & PEYBERNÈS, p. 80-82, Figs. 1, 2 (= CONRAD & PEYBERNÈS, 1976: Fig. 6), 3 (holotype), 4-5
1979 *Clypeina nigra*.- PEYBERNÈS *et al.*, p. 80-82, Pl. 3, fig. 4
1980 *Clypeina nigra*.- ARNAUD-VANNEAU, Pl. 112, figs. 1-3
1994 *Actinoporella nigra* n.comb.- GRANIER, p. 114-115, Pl. 3, figs. 1, 2 (= ARNAUD-VANNEAU, 1980, Pl. 112, fig. 2), 3 (= ARNAUD-VANNEAU, 1980, Pl. 112, fig. 3), 4
2002 *Actinoporella nigra*.- BUCUR, p. 44, Pl. III, fig. 7

A set of ten thin sections, 4 labelled 7237 and 6 more labelled 7238, with the alga was identified in the J. EMBERGER Collection. The rock samples were picked from core 4 of the Esso REP STE1 borehole, at Saint-Trosse (Municipality of Pontenx-les-Forges, Landes, France). The borehole location, WGS84 44°17'39.0"N 1°03'17.0"W, is derived from the Infoterre website of the B.R.G.M. (2019).

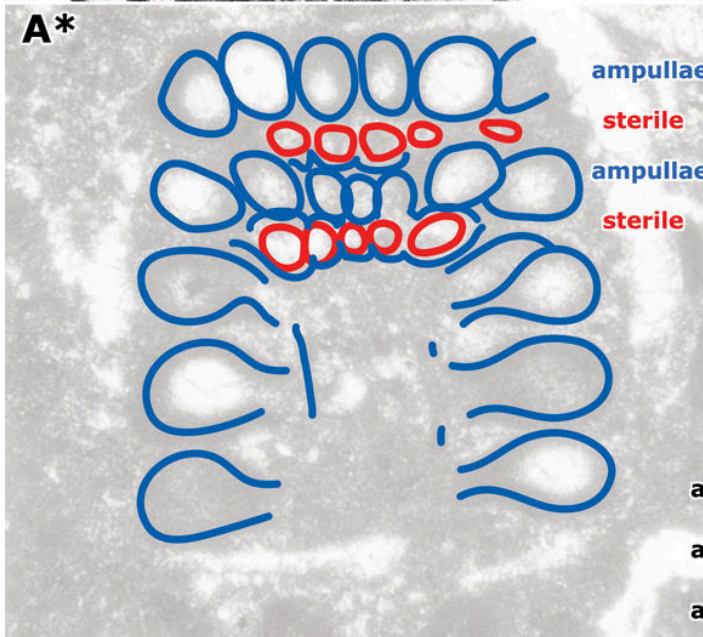
According to CONRAD and PEYBERNÈS (1976), the diagnosis is "Small, simple and cylindrical thallus, bearing laterals arranged in regularly spaced whorls. Club-shaped laterals, closed at their distal ends, filled in with hyaline calcite, and connected to the axial siphon by a narrow pore. The siphon as well as the laterals are embedded in a black and microgranular carbonate cast. The non-calcified space separating the whorls is divided by fine radial partition walls that are also microgranular in nature" [translated from the French: "Petit thalle simple et cylindrique, porteur de rameaux disposés en verticilles régulièrement espacés. Rameaux en forme de massue, fermés à leurs extrémités distales, garnis de calcite hyaline, et communiquant avec le siphon axial par un pore étroit. Le siphon, ainsi que les rameaux sont enrobés par une masse carbonatée noire et microgranulaire. L'espace non calcifié séparant les verticilles est parcouru par de fines cloisons radiales, également de nature microgranulaire"].

According to GRANIER (1994), the amended diagnosis is "Small articulated *Actinoporella* species with a cylindrical main axis bearing close-set whorls of branches. Branch consisting of a vestibule followed by a vesicular to short club-shaped gametophore, by an open pore on one side of the whorl, and by an "excrescence" on the opposite side. Gametophore perpendicular to the main axis and closed at its distal part. Calcareous sheath consisting of microgranular calcite wall".

The algal structure is fully reinterpreted here (Fig. 5). The ampulla is ovoid and short, which can hardly compare with the long ampullae of the *Actinoporellas*. The "excrescence" of GRANIER (1994), visible on one side of the whorl, at the base of the ampulla, could be an artifact whereas the pore on the opposite side of the whorl is effectively connecting the ampulla to the sterile lateral. Those structures observed in the interverticillar space and described by CONRAD and PEYBERNÈS (1976) as "cloisons radiales (...) microgranulaires" or as "indentations de l'enveloppe calcaire entre les verticilles" correspond to poorly mineralized walls between neighbouring sterile laterals. The structure of the alga is that of a *Bakalovaella* (see GRANIER & BUCUR, 2019), hence the new combination.



250µm

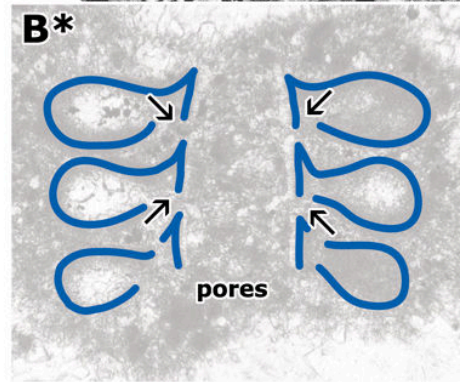


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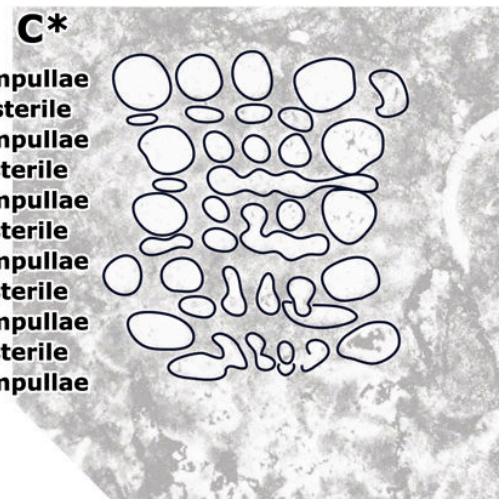
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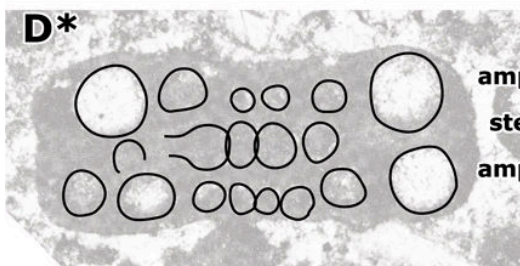
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sterile

ampullae



◀ **Figure 5:** *Bakalovaella nigra* (CONRAD & PEYBERNÈS), n.comb. A-A*) subaxial to oblique section with 5 whorls. Unpublished photomicrograph by J. EMBERGER, STE1, Saint-Trosse, France; B-B*) subaxial section with 3 whorls. Excerpts from GRANIER, 1994: Pl. 3, fig. 1. É. FOURCADE Collection, sample G.1280, Spain; C-C*) tangential section with 6 whorls. Excerpt of CONRAD & PEYBERNÈS, 1978: Pl. II, fig. 2. PEYBERNÈS Collection, Bas de Cagire, France; D-D*) tangential section with 2 whorls. Holotype, excerpt of CONRAD & PEYBERNÈS, 1978: Pl. II, fig. 3. PEYBERNÈS Collection, Bas de Cagire, France. Scale bar 250 µm.

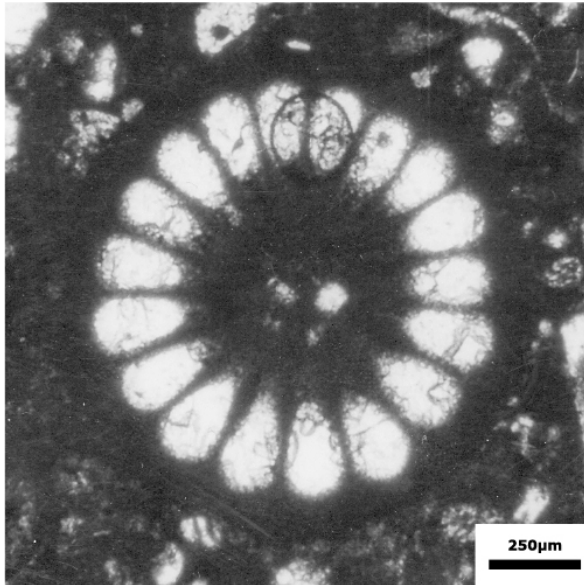


Figure 6 : *Bakalovaella nigra* (CONRAD & PEYBERNÈS), n.comb.: transverse section of a whorl with 25 ampullae. Unpublished photomicrograph by J. EMBERGER, STE1, Saint-Trosse, France. Scale bar 250 µm.

A transverse section of a whorl in one photomicrograph of the J. EMBERGER Collection (Fig. 6) bears 25 ampullae (compared with 18-20 according to CONRAD and PEYBERNÈS, 1976); it reaches 1.1 mm in outer diameter (compared with 0.6-0.8 mm according to CONRAD and PEYBERNÈS, 1976).

At Saint-Trosse, the species is found associated to *Choffatella* gr. *decipiens* SCHLUMBERGER and *Palorbitolina lenticularis* (BLUMENBACH) in strata ascribed to the Barremian-lower Aptian. The specimens from the Rocher de Cluses (Pl. 1, figs. ab, ak) should be referred to the upper Hauterivian. The alga is known from Bulgaria (CONRAD & PEYBERNÈS, 1978; PEYBERNÈS *et al.*, 1979), France (CONRAD & PEYBERNÈS, 1976, 1978; ARNAUD-VANNEAU, 1980), Romania (BUCUR, 2002), Spain (GRANIER, 1994), and Switzerland (SCHLAGINTWEIT, unpublished data, personal communication, 20/04/2019), all these occurrences are currently restricted to the northern Neotethyan margins.

5. Elements of phylogeny

The various use of "vestibule" in modern Polyphysaceae and fossil Diploporaceae generates some confusion because it refers to discrete structures: A) In the living Polyphysaceae, the vestibule is an expansion of the main axis at the base of the fertile lateral, both being separated by a partition with an opening (BERGER & KAEVER, 1992). Therefore, it comes before the common base of the corona(s) and the fertile ampulla; B) In the Diploporaceae, the vestibule is the common base of a tuft of laterals. In some forms, it can even expand slightly to form some sort of short primary lateral (see discussion in BUCUR & ENOS, 2001), called a "composite vestibule" by MAMET and ROUX (1981). Accordingly, for some authors, when the primary is much shorter than the secondaries, it could legitimately be called a vestibule.

It was previously suggested that the Family Bor-netellaceae GRANIER & BUCUR (in GRANIER *et al.*, 2013) arose from the Family Triploporellaceae (PIA) with transition forms from *Triploporella* STEINMANN to *Zitellina* L. et J. MORELLET (see BUCUR *et al.*, 2010). Similarly, ancestors of the Family Thyrsoporellaceae GRANIER & BUCUR, 2013, should also be found in the Triploporellaceae.

In contrast, the Family Dasycladaceae (KÜTZING) probably arose from the Family Diploporaceae (PIA) with possible affiliations of A) *Granieria* BARATTOLO & ROMANO to *Barattoloporellopsis* GRANIER *et al.* or to *Bakalovaella* BUCUR, then *Montiella* (L. et J. MORELLET), and of B) *Eodasycladus* CROS & LEMOINE to *Indopolia* PIA and/or to *Cymopolia* J.V. LAMOUREUX. In both cases (A and B), it is assumed that the driving force honoured the "piston lifting" model of GRANIER and BUCUR (2019) rather than the "escalator" model of L. EMBERGER (1968) or the cladospore to choristopore evolution as suspected by ELLIOTT (1989). In the "piston lifting" model, the primary lateral becomes increasingly longer whereas the fertile ampulla remains rather small. Ancestors of the Family Polyphysaceae (KÜTZING) should also be found in the Diploporaceae or in ancestral Dasycladaceae (e.g., *Eodasycladus*) with possible affiliations of *Actinoporella* to *Halycoryne* HARVEY and/or *Acetabularia* J.V. LAMOUREUX. Some sort of "communicating vessels" model should apply here because, in complete contrast to the previous model, the primary remains rather small whereas the fertile ampulla becomes increasingly larger.

Ultimately, it is a different scenario (Fig. 7) than those proposed earlier by micropaleontologists (e.g., PIA, 1920; ELLIOTT, 1989; GRANIER in BERGER *et al.*, 2004) or phycologists (BERGER and KAEVER, 1992; OLSEN *et al.*, 1994; VERBRUGGEN *et al.*, 2009).

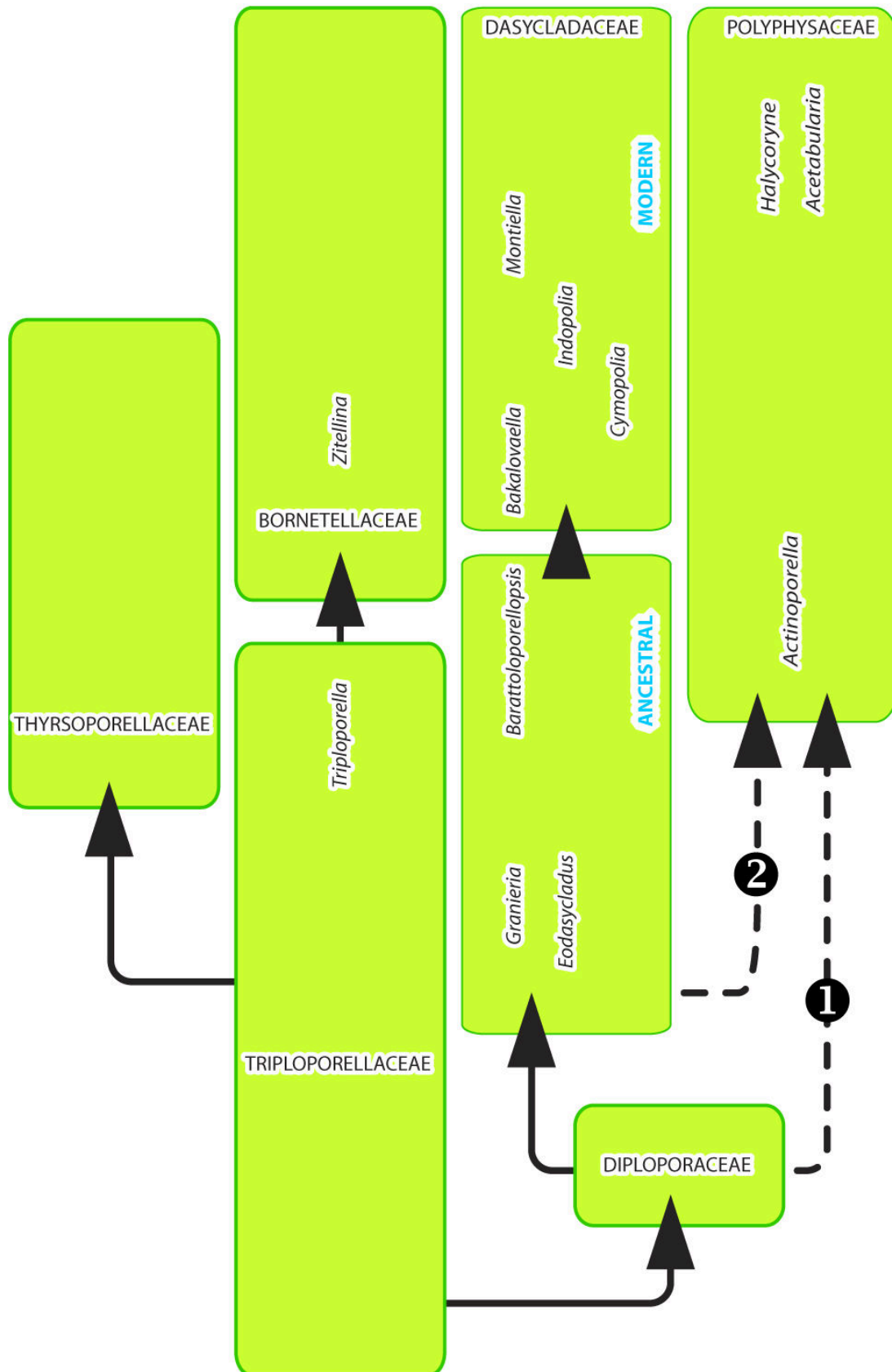


Figure 7: Sketch of a new phylogenetic canvas for the euspondyl Dasycladales (hence excluding the aspondyl Family Seletonellaceae KORDE): 1) hypothesis of a direct filiation of the Polyphysaceae from the Diploporaceae, 2) hypothesis of an indirect filiation of the Polyphysaceae from the Diploporaceae through the "ancestral" Dasycladaceae (favourite hypothesis).



6. Conclusions

With respect to stratigraphy, the Oulad Nail area requires revision. There are obvious problems as, for instance, when J. EMBERGER (1960: p. 127) cites "*Iberina lusitanica*(EGGER)" in strata overlying strata with "*Calpionellites darderi* (COLOM)" at Djebel Zireg. More importantly, EMBERGER's Valanginian and Hauterivian probably refer to Tithonian and Berriasian strata. For instance, and as already pointed out by MAYNC (1959), the *Choffatella zireggensis* SIGAL, 1952, from the so-called "Hauterivien", is a junior synonym of *Anchispirocyclus lusitanica* (EGGER); it is nowadays considered a marker of the Tithonian-lower Berriasian interval (e.g., GRANIER, 2019).

With respect to the systematics of the Actinoporellas:

- the type-locality of *Actinoporella podolica* (ALTH) should be re-sampled in search for specimens approaching the original descriptions of ALTH (1878) and PIA (1920), which is not the case with the material presented by CONRAD *et al.* (1974);
- although it cannot be demonstrated that *Actinoporella podolica* (ALTH) is the senior synonym of *A. lucasi* (J. EMBERGER) or of *A. harrazaensis* n.sp., the latter two are well anchored in the genus and should be considered as discrete species.

In addition, *Clypeina nigra* CONRAD & PEYBERNÈS is excluded from the Polyphysaceae. It is neither an *Actinoporella*, nor a *Clypeina*. A set of evidence anchors it to the Dasycladaceae as *Bakalovaella nigra* (CONRAD & PEYBERNÈS), n. comb.

With respect to the phylogeny of the Dasycladales, it is assumed that the modern Dasycladaceae and Polyphysaceae, both choristospore (one with "short ampullae", the other with "long ampullae"/"spicule"), should derive from the fossil Diploporaceae (either indirectly, through ancestral Dasycladaceae, or directly), whereas the modern Bornetellaceae, goniospore, derive from the Triploporaceae, which represents a new phylogenetic scenario.

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Plates

Plate 1: a) *Actinoporella podolica* fide CONRAD *et al.* (1974: Fig. 6.g); b-f) cf. *Clypeina ? isabellae* MASSE *et al.*, 1999: b-d) subtransverse sections; e) oblique section of one whorl; f) oblique section with two whorls. Thin sections: b-e) 443, f) 427 (upper Berriasian, Sierra Mariola, Spain, B. GRANIER Collection); g-aa, ae-aj) *Bakalovaella nigra*, n.comb. g-q, t, v, x-aa, ae, ag-aj) random sections of a single whorls; r) two isolated whorls; s, w) two connected whorls; t, af) oblique sections of two whorls. Thin sections: g-j, v) 7237A; k-l) 7237B; m, o) 7238E; n, q, s, w) 7238F; p, t) 7238B; r) 7238A; u, ag, ai-aj) 7237C; x-y) 7238D; z-aa, ae) 7238C; af, ah) 7237D (Saint-Trosse, France, J. EMBERGER Collection); ab, ak) *Bakalovaella nigra*, n.comb. Thin section: GT (1) 45 (Rocher de Cluses, France, sequence Ha6 "Urgonian", Gunter TRABOLD Collection, D.G.P., Geneva University); ac) *Choffatella* gr. *decipiens* SCHLUMBERGER. Thin section: 7237D (Saint-Trosse, France, J. EMBERGER Collection); ad) *Palorbitolina lenticularis* (BLUMENBACH). Thin section: 7238D (Saint-Trosse, France, J. EMBERGER Collection).

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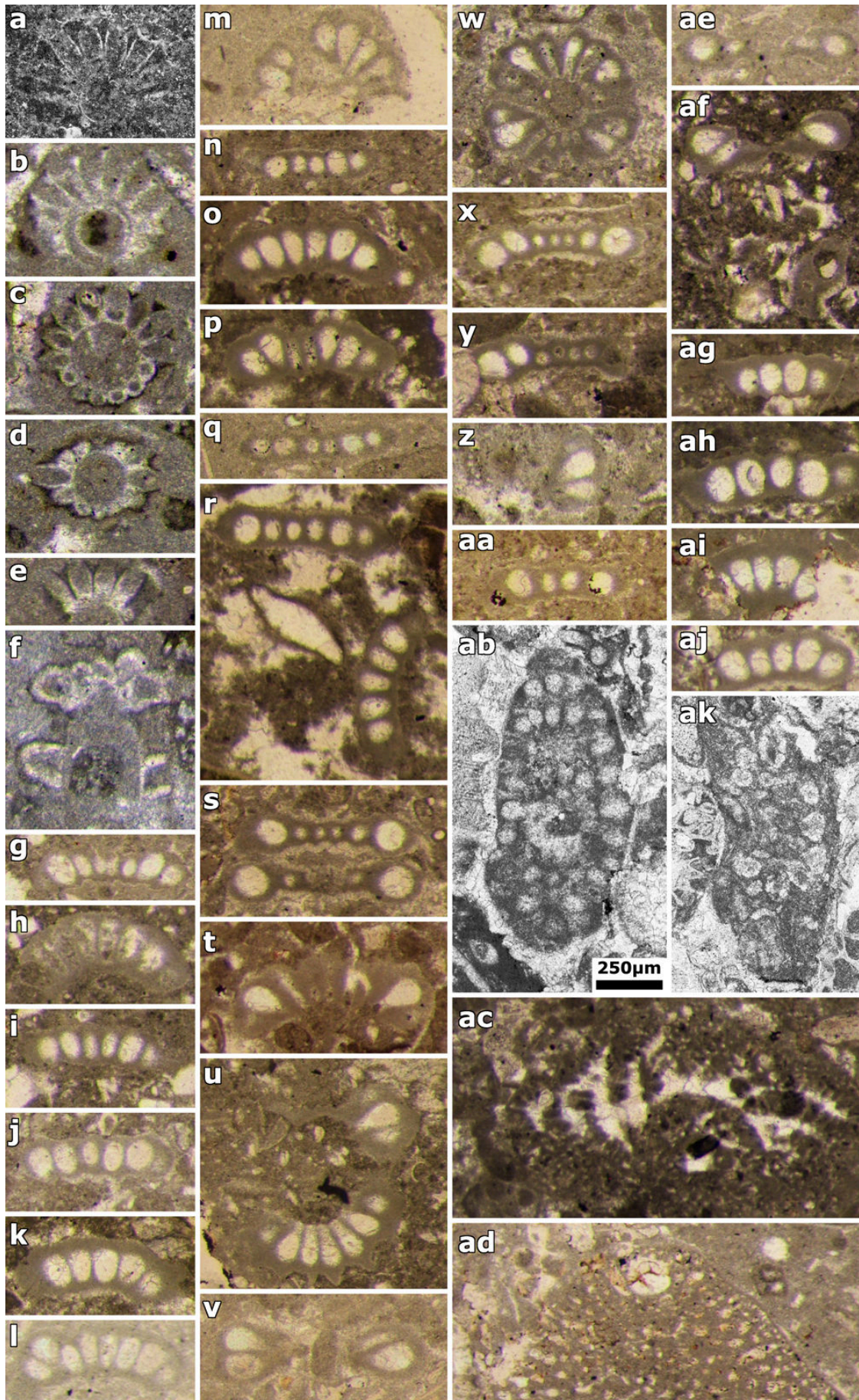




Plate 2: *Actinoporella lucasi*. a-f) lower and upper side of isolated rows. The distal part of the ampullae is commonly broken. g) The piece of rock after acidic leaching with *Actinoporella lucasi*, *Salpingoporella annulata* and *Coscinococcus* sp. originally illustrated by J. EMBERGER (1956: Pl. XXIV, fig. 7). Djebel Zireg, J. EMBERGER Collection.

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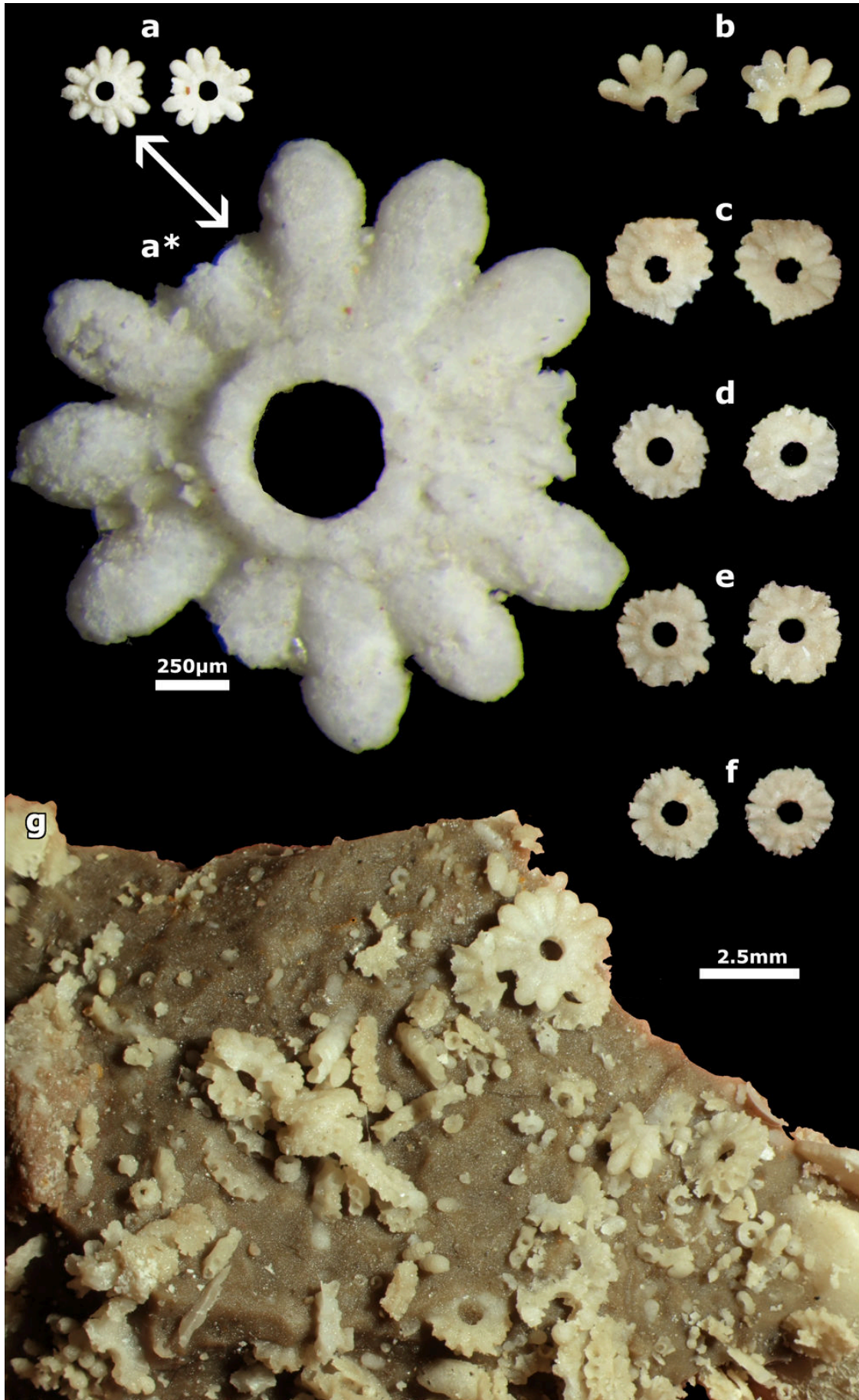




Plate 3: *Actinoporella harrazaensis* n.sp. a-e) oblique sections of single rows; f-h) tangential sections of single rows. Thin sections: a, d-g) 444A; b-c) 444D; h) 444B (Djebel Harraza, J. EMBERGER Collection).

Scale bar 250 μ m.

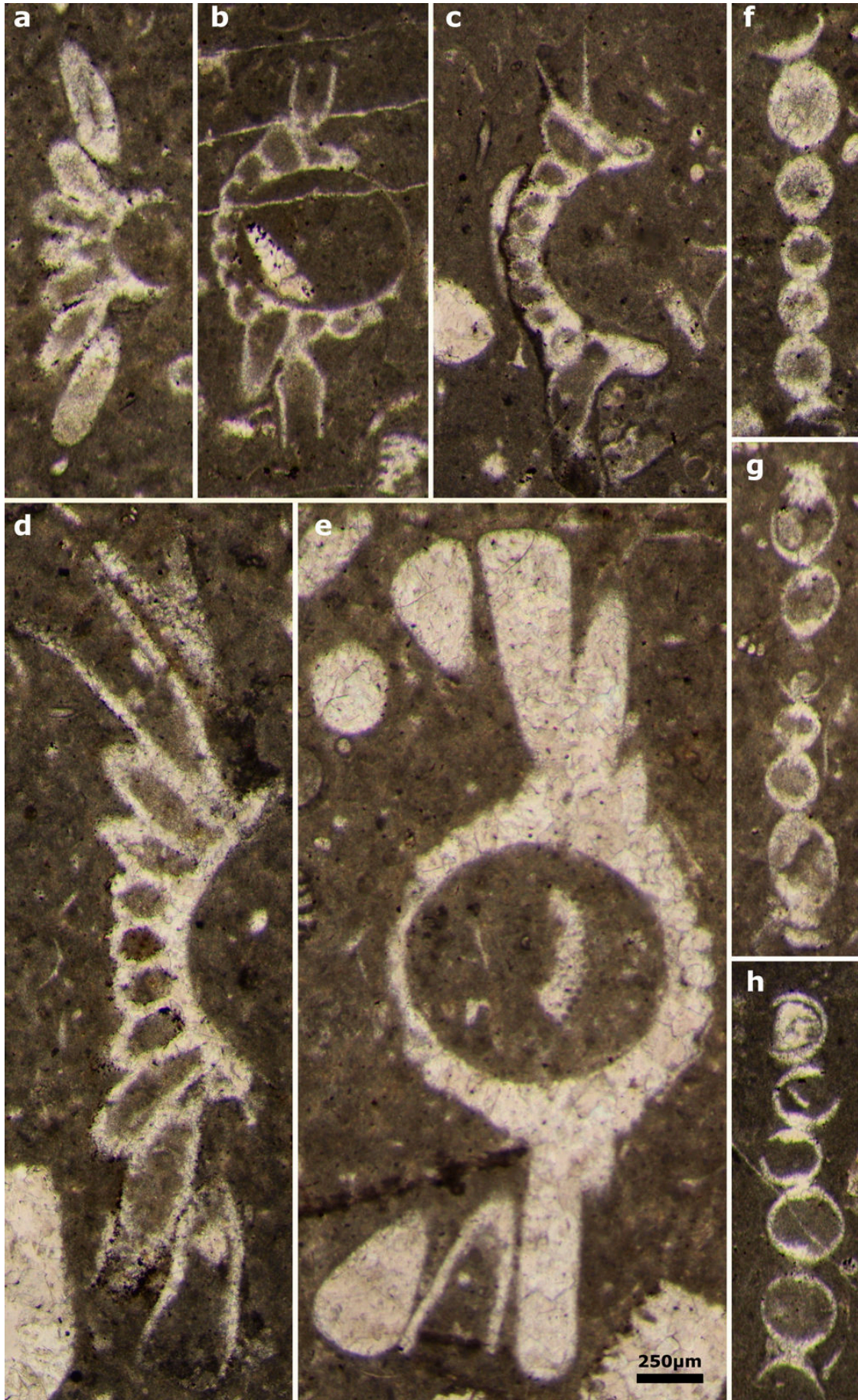




Plate 4: *Actinoporella harrazaensis* n.sp. a, f-g) deep tangential sections of single row; b-e) subaxial sections of single rows; h-j) oblique sections of single rows. Thin sections: a-d, g, j) 444B; e) 444D; f) 443A; h) 443B; i) 444E (Djebel Harraza, J. EMBERGER Collection).

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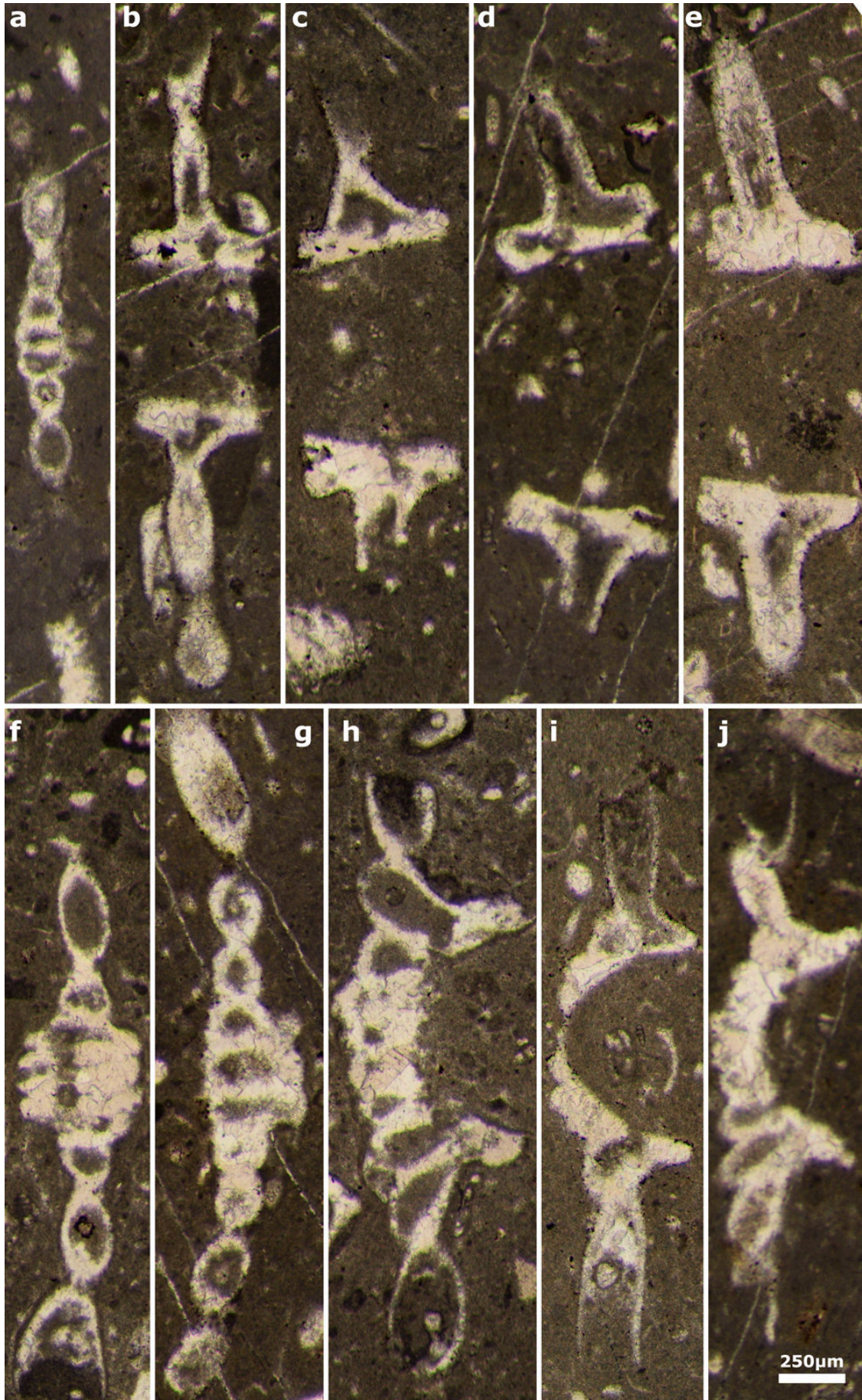




Plate 5: *Actinoporella harrazaensis* n.sp. a-c) deep tangential sections of single row; d-e) sections of single broken rows; g) subaxial sections of a single row; h-j) tangential sections of single rows; k-n) oblique sections of single rows. Thin sections: a, l-m) 444E; b, e) 444G; c, g) 444F; d, i, k) 444B; f, j, n) 444D; h) 444A (Djebel Harraza, J. EMBERGER Collection).

Scale bar 250 μ m.

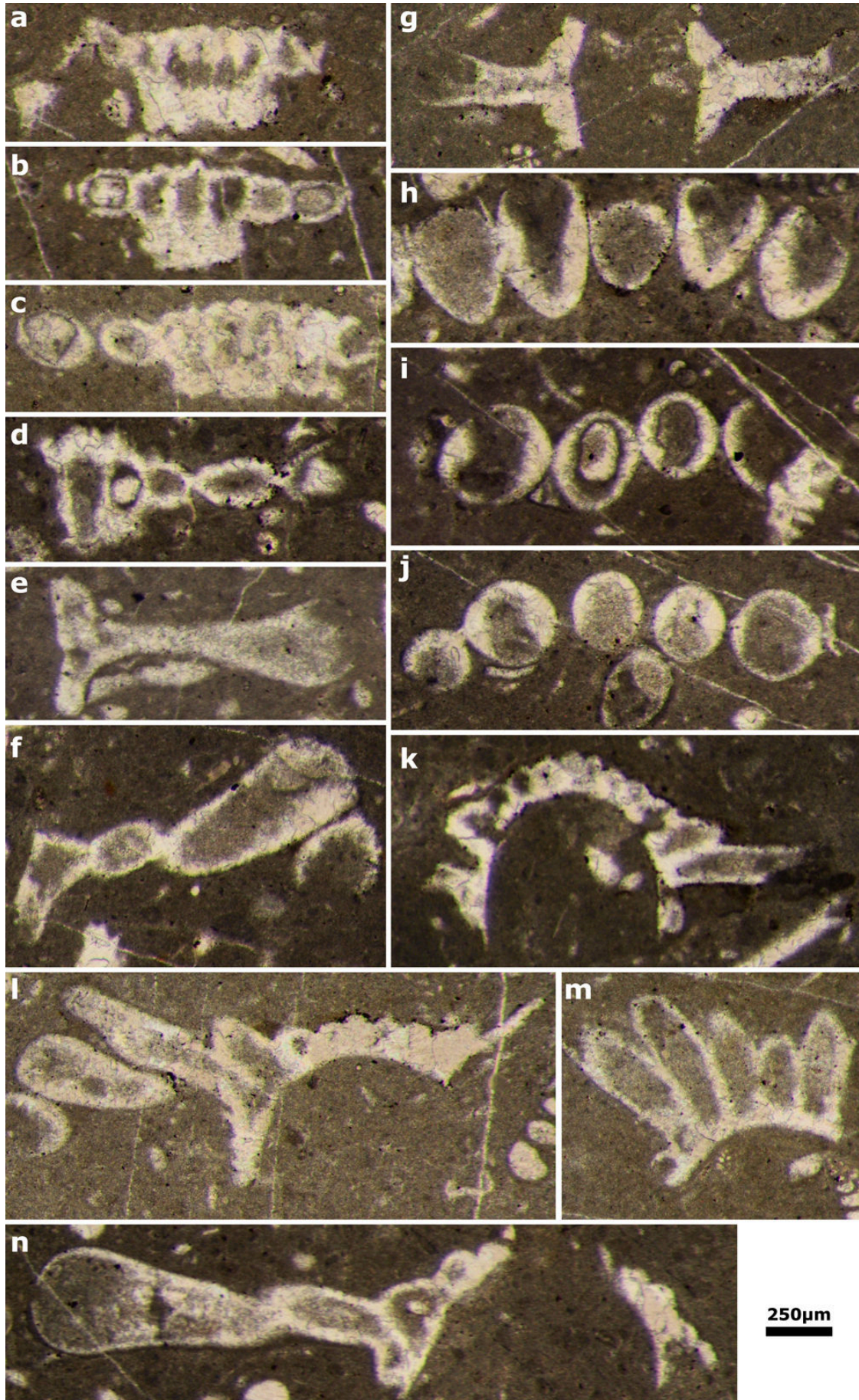




Plate 6: a-d) *Actinoporella harrazaensis* n.sp.: a-b) oblique sections of single rows; c) tangential to oblique section of a single row; d) subaxial section of a single row (Djebel Ladjdar, Aïn El Melh, J. EMBERGER Collection). e, g-k) *Actinoporella lucasi*: e) tangential section of a single row. See J. EMBERGER's 1960 Fig. 21; g-h) oblique sections of single rows; i) oblique section of a single row; j-k) subaxial sections of single rows. f) Calpionellid. Thin sections: a-b) 873C; c) 873D; d) 873B; e, i-k) 21; f) 873A; g) 19; h) 18 (Djebel Zireg, Aïn El Melh, J. EMBERGER Collection).

Scale bar 250 μ m.

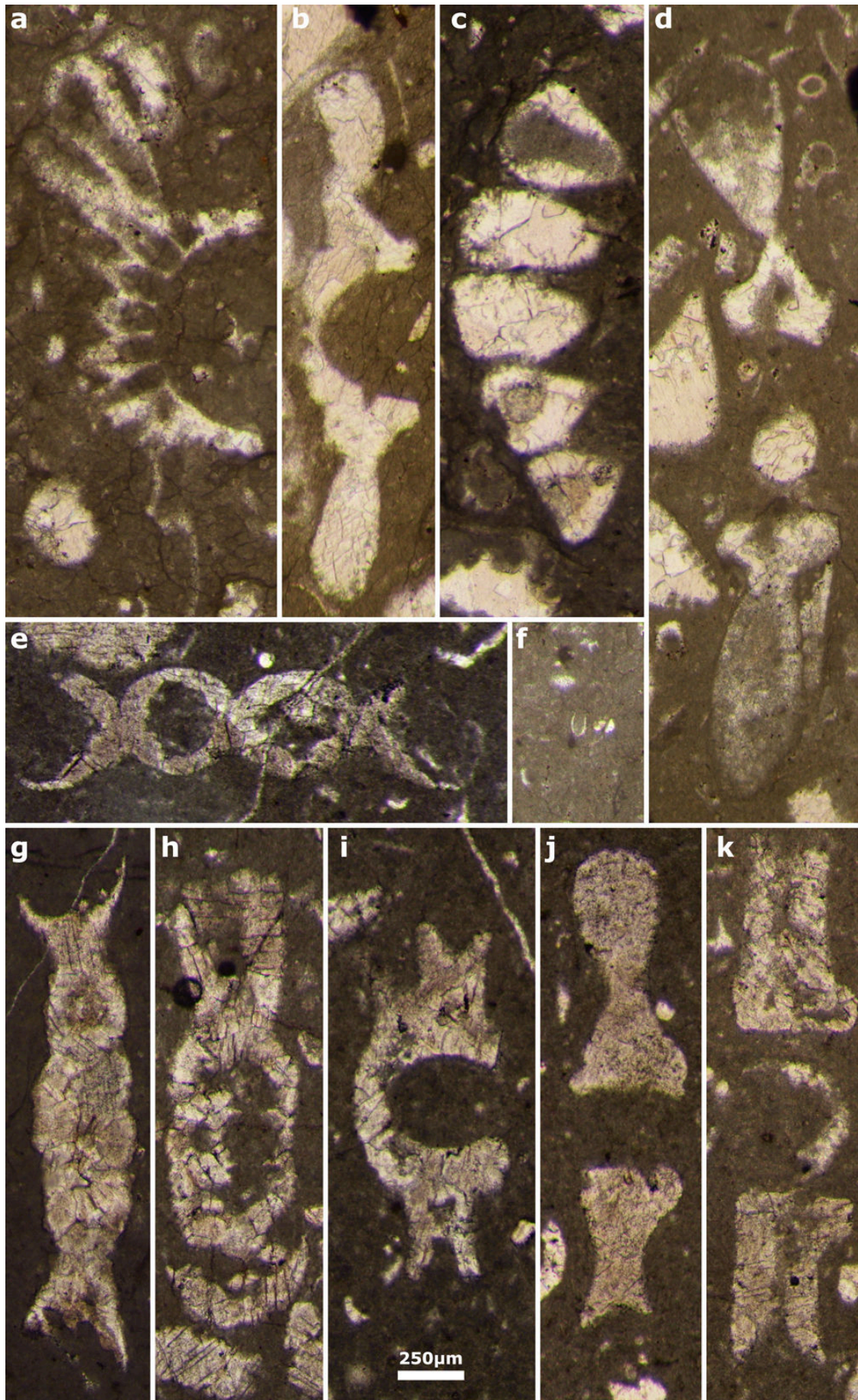




Plate 7: *Actinoporella lucasi*. a) oblique section of a single row; b) subaxial and tangential sections of two rows; c-f) oblique sections of single rows; g) subtransverse section of a single row. d is used in a drawing of J. EMBERGER (1956: Fig. 3). Thin sections: a-c, f) 21; d) 22; e, g) 18 (Djebel Zireg, J. EMBERGER Collection).

Scale bar 250 μm .

