

## ***Aloisalthella*, a new genus of fossil Polyphysacean green algae (Chlorophyta, Dasycladales), with notes on the genus *Clypeina* (Michelin, 1845)**

**Bruno R.C. Granier and Alexandre Lethiers**

### **ABSTRACT**

Following a preliminary historical survey of the Cenozoic *Clypeina marginoporella* Michelin, 1845, which is the type species of the respective genus, and of the Mesozoic *Clypeina sulcata* (Alth, 1882), the point was made that these two species may not be ascribed to the same genus. Accordingly, the new genus *Aloisalthella* is introduced with *Clypeina sulcata* as type-species. In addition, the generic diagnosis of *Clypeina* is amended (i.e., shortened) in order to exclude all features that are not present in its type, e.g., there are no verticils of sterile laterals inserted between successive verticils of fertile laterals. A rather large collection of algae was used to illustrate some key characteristics of these algal taxa as well as a few features rarely observed in *C. sulcata*.

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### **INTRODUCTION**

*Clypeina sulcata* (Alth, 1882) is familiar to any petrographer or micropaleontologist who has ever studied uppermost Jurassic Tethysian series. For palaeophycologists, it remains a peculiar fossil green alga in the sense that most Dasycladalean

algae mineralize in the form of extracellular or intercellular aragonitic coatings whereas very few species are intracellularly mineralized with primary calcite (e.g., Granier, 2012), which is just one aspect of this singular species. Besides pointing out this particular mineralization type, its revision required re-examination of the type-species of the

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genus, i.e., *C. marginoporella* Michelin, 1845, and its definition.

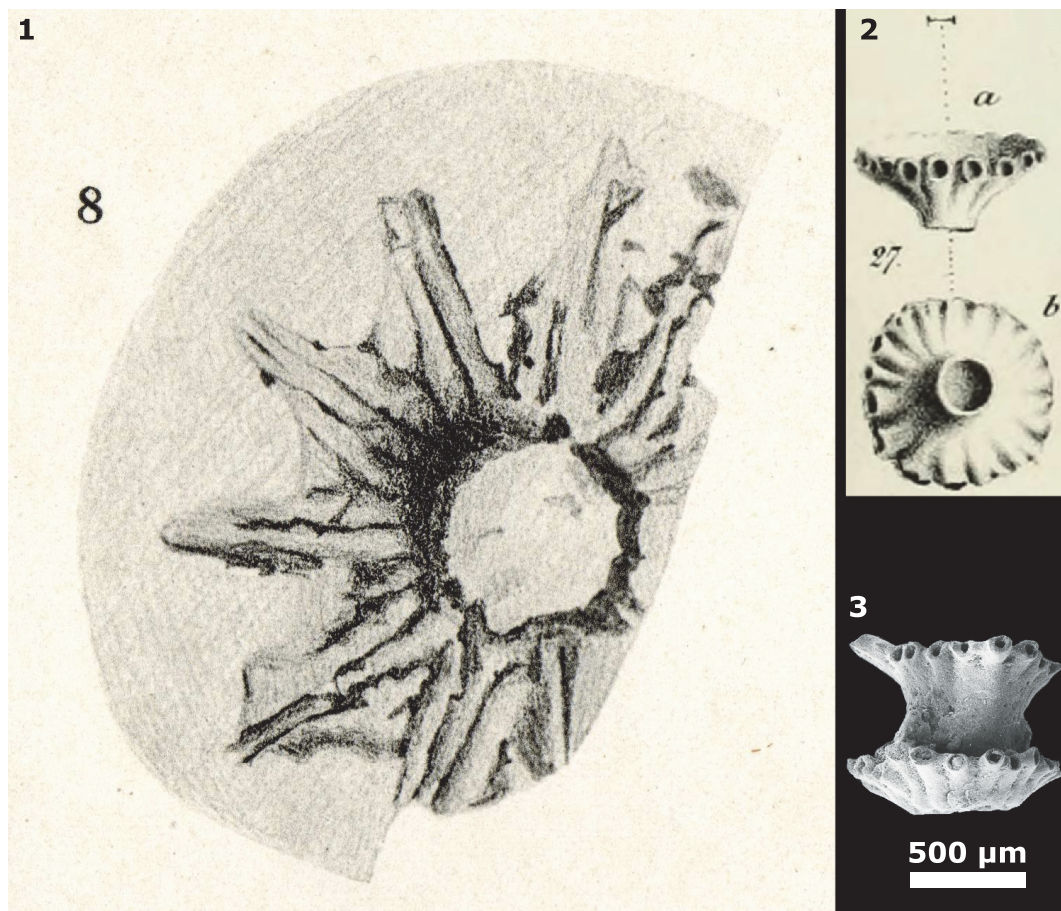
One of the main difficulties faced when studying such large unicellular fossils is that some forms are only found as isolated remains from loose sediment (mostly Cenozoic species, as *Clypeina marginoporella*) whereas others are only known as random cuts in petrographic thin sections of limestones (mostly Mesozoic species, as *C. sulcata*). However, in the case of *C. sulcata*, researchers have collected a variety of material over time: weathered rock surfaces (Figures 1.1, 2), isolated remains (Figures 3-4), petrographic thin sections (Figure 5), and SEM imagery (Figure 4).

The review of the most significant elements contributes 1) to building a 3D model of the species *Clypeina sulcata*, 2) to definitely excluding it from the genus *Clypeina*, and 3) to selecting it as the type of a new genus introduced hereafter.

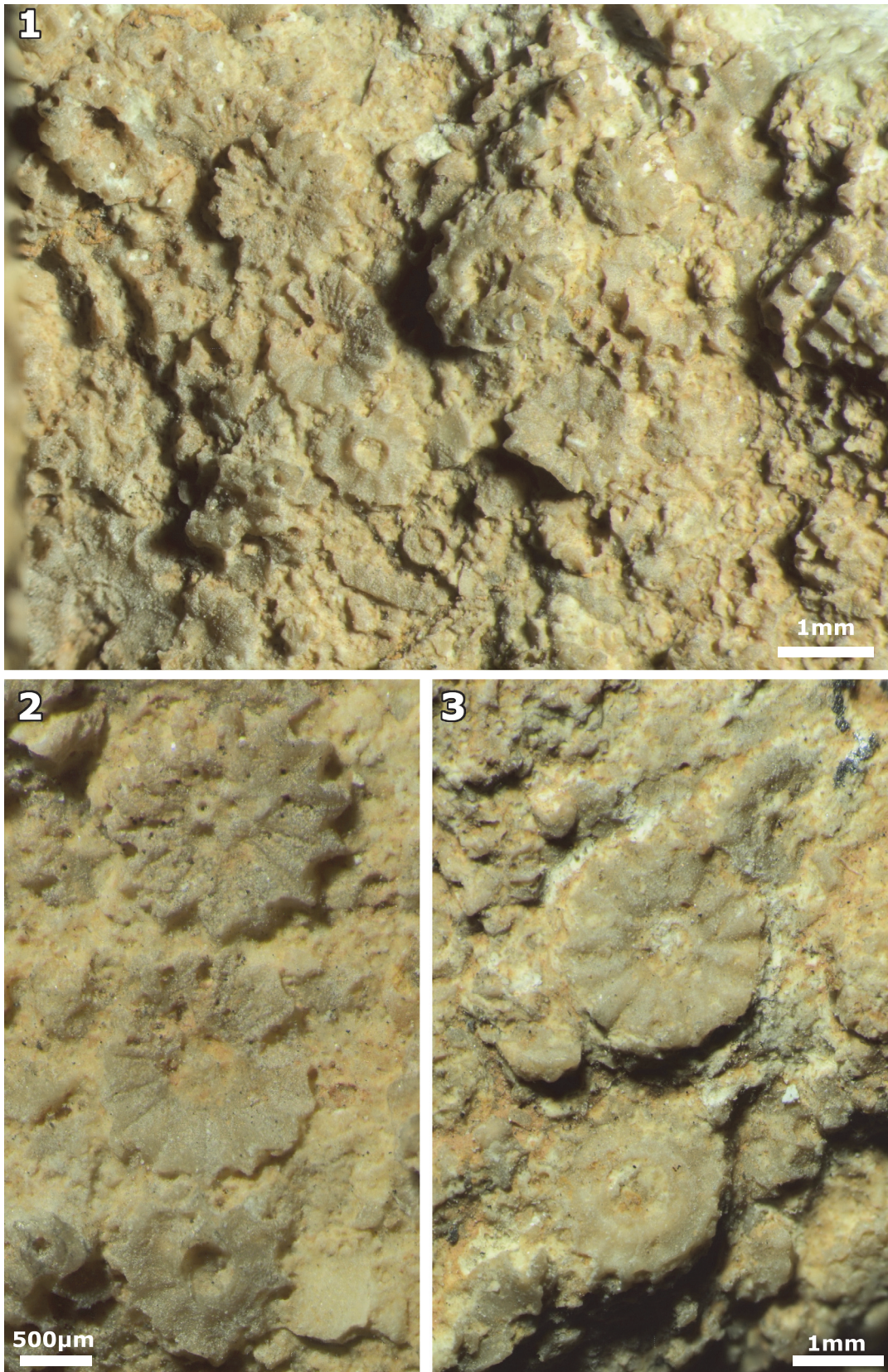
## MATERIAL AND METHODS

Some material published earlier (Michelin, 1845; Pia, 1920; Pfender, 1927a; Génot, 1987; Granier, 1994; Granier and Boichard, 2017) as well as some unpublished material are re-examined here. Some material come from the E.P. Munier-Chalmas and J. Pfender collections currently housed at the Université Pierre et Marie Curie (Paris, France), or from the P. Génot Collection originally stored at the Université de Nantes (France), recently relocated at the Muséum National d'Histoire Naturelle (Paris, France). Finally, most material (the J. Emberger Collection, as well as the first author's collection) is currently housed at the Université de Bretagne occidentale (Brest, France).

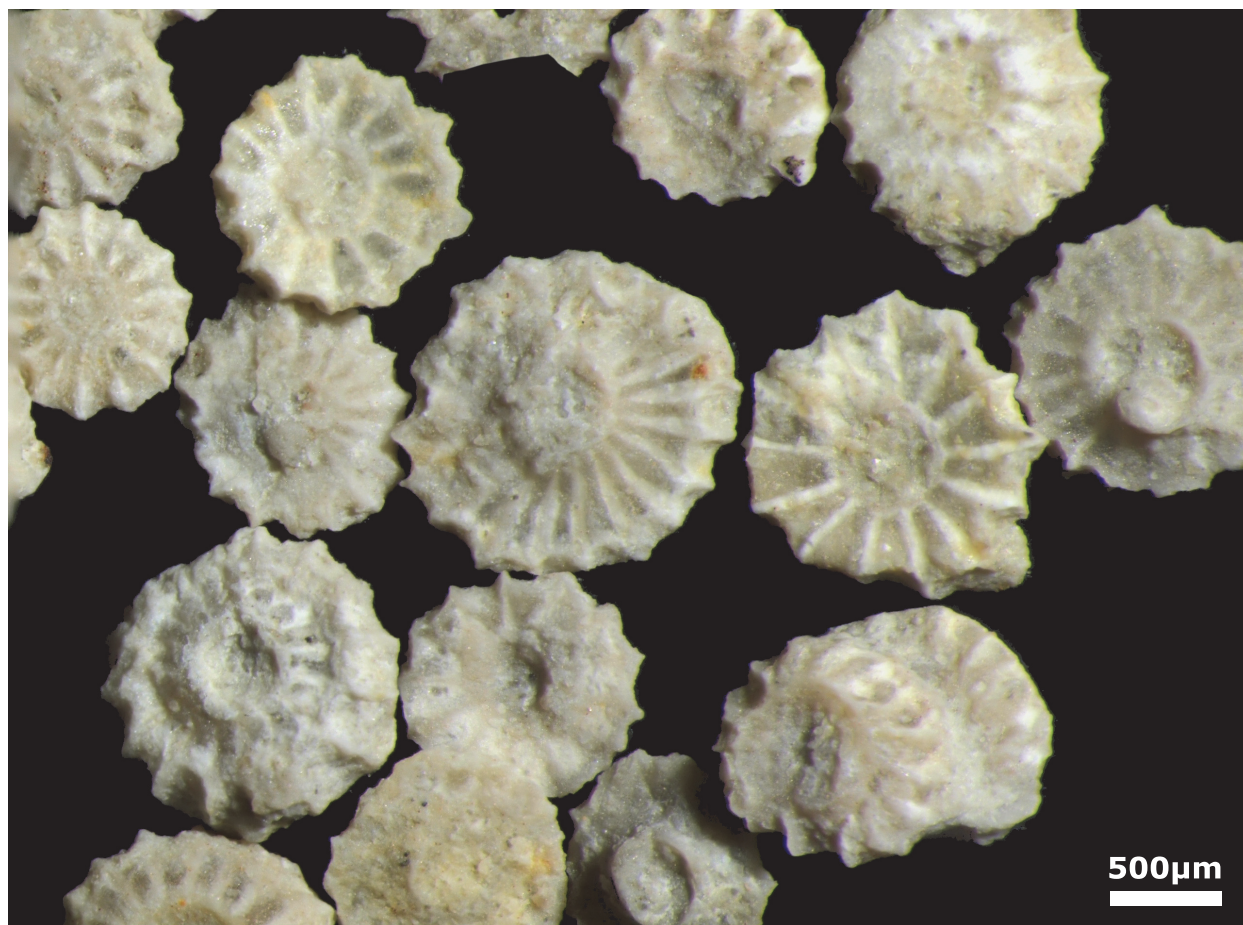
All color photomicrographs were taken under an Olympus SZX7 stereo microscope (with a 5.6X zoom magnification for the thin sections) whereas



**FIGURE 1.** 1. Original drawing of “*Actinoporella sulcata* Alth” (Pia, 1920: plate VII, figure 8). Outer surface of a rock sample from the Tithonian of Nyzhniv, Ukraine. 2. Original drawing of the type of “*Clypeina marginoporella*” [sic] (Michelin, 1845: plate 46, figure 27.a-b). Étampes, Essone, Paris Basin. 3. *Clypeina marginoporella* with two whorls joined together. Lutetian of Chambors, Oise, Paris Basin, E.P. Munier-Chalmas Collection (Génot, 1987: plate 26, figure 5). Note the absence of scars between these two fertile whorls (scale bar equals 500 μm).



**FIGURE 2.** Weathered rock surfaces with *Aloisalthella* gen. nov. *sulcata* comb. nov., from the Upper Jurassic strata of Algeria, leg. R. Karpoff, J. Emberger Collection (1, 3: scale bar equals 1 mm, 2: scale bar equals 500 µm).



**FIGURE 3.** *Aloisalthella* gen. nov. *sulcata* comb. nov., from the Berriasian of Vuache, Savoie, E France, leg. P.O. Mojon, B. Granier Collection (scale bar equals 500  $\mu$ m).

black and white photomicrographs, originally gelatin silver photos, were taken using a Zeiss Photomicroscope III and later scanned. SEM pictures were made at Université de Nantes (France) circa 1987: Figures 1.3, 6.1-3, at the TOTAL Scientific and Research Center (Pessac, France) in 1988: Figure 6.4-5, at Université de Bretagne occidentale (Brest, France) in 2010: Figure 4, and at Universidade Estadual Paulista (Rio Claro, SP, Brazil) in 2015: Figure 6.6-10. Finally, the Blender free software (<https://www.blender.org/>) was used to design 3D reconstructions of the algae.

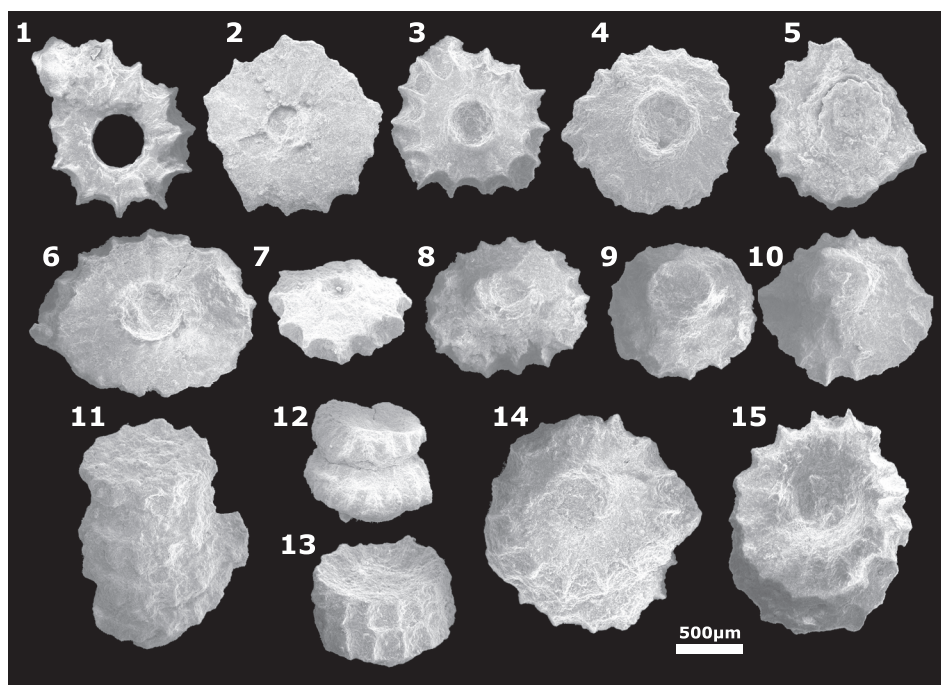
#### HISTORICAL BACKGROUND AND DISCUSSION

##### A Digest on the Genus *Clypeina*, and its Type-Species

The extinct genus *Clypeina* (Michelin, 1845) was initially described as belonging to the Class Anthozoa (Michelin, 1845), and then to the Foraminifera (Parker and Jones, 1860), until Munier-

Chalmas (1877) correctly ascribed it to the “Siphonées verticillées”, i.e., to the Dasycladales. Today, it includes some 40 species (for Jurassic and Cretaceous species see Bassoullet et al., 1978, and Granier and Deloffre, 1993; for Cenozoic species see Deloffre and Génot, 1982 and Deloffre and Granier, 1992). Its type-species is the middle Eocene-lower Oligocene *C. marginoporella* (op. cit.: p. 177-178, plate 46, figure 27.a-b; here Figure 1.2).

The fossil consists of a calcareous coating of the algal main axis and its elongated laterals. These laterals, interpreted as gametophores, are regularly arranged in a series of verticils along the main axis. The tubes corresponding to the calcified laterals are open at both ends: in their proximal end because these pores communicate with the axial cavity (in lieu of the main axis) and in their distal end because their calcareous coating is commonly broken there, hence the specific epithet “*marginoporella*”. The generic name is derived from the Latin *clipeus*, which is a ‘round shield’,



**FIGURE 4.** *Aloisalthella* gen. nov. *sulcata* comb. nov., from the Berriasian of Vuache, Savoie, E France, leg. P.O. Mojon, B. Granier Collection. **1-10.** lower side views of single fertile whorls with a neck and upper side views without neck. **11.** four (?) successive fertile whorls. **12-15.** two (?) successive fertile whorls. All SEM photos same scale (scale bar equals 500 µm).

and the specific epithet from the Latin *margo* and *porus*, respectively ‘side’ and ‘passage’. These close-set tubes are arranged in unfundibuliform rows, i.e., funnel-shaped rows, which are commonly found separated from each other and only rarely attached together.

L. Morellet and J. Morellet (1918) stated that “À côté des ombelles normales, constituées par un verticille de sporanges accolés, s’en trouvent d’autres, d’ailleurs très rares, chez lesquelles la partie évasée de l’entonnoir est fermée par un plancher légèrement bombé, percé de nombreux pores à la façon d’une pomme d’arrosoir. Ce sont les ombelles terminales de la plante” [besides the regular umbels consisting of whorls of joined sporangia, there are other whorls, actually very few, with the flared portion of the funnel sealed by a slightly domed wall, pierced with many holes in the same way as a spray head. They represent the uppermost whorls of the alga]. Few specimens of such algal caps have been documented as “*Clypeina* sp.” by Génot (1987, plate 3, figures 14-15; here Figure 6.1-2; unpublished, here Figure 6.3).

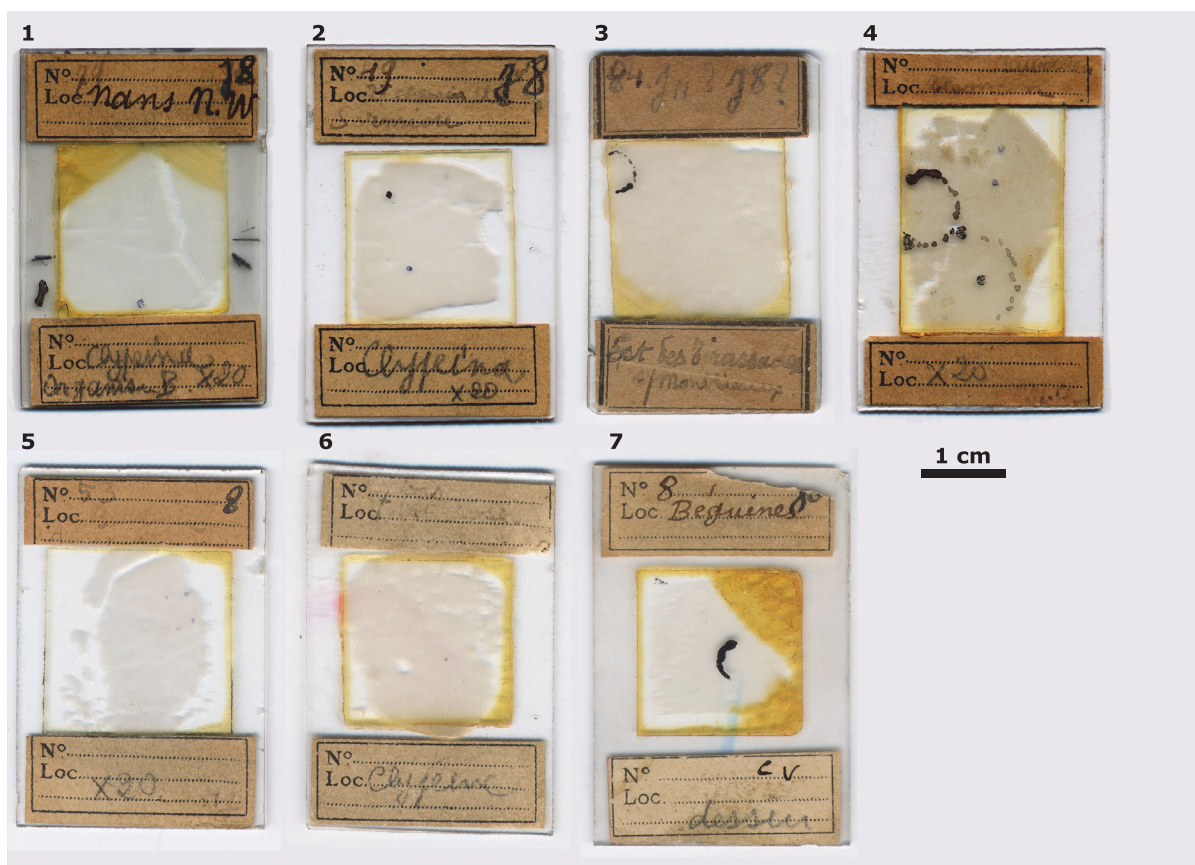
#### Flaws in Earlier Descriptions and Implications

1) L. Morellet and J. Morellet (1918) stated that “Le plus important de ces fragments se com-

pose de huit ombelles (coll. Sorbonne)” [the largest fragment consists of eight umbels (Sorbonne collections)].

This last specimen is not a *Clypeina marginoporella* because the authors probably referred to the specimen that was later illustrated by Génot (1987: plate 3, figure 13) as *C. digitata* (Parker and Jones, 1860). Regarding *C. marginoporella*, Génot (personal communication, 15/10/2016), who investigated the material the Morellet brothers studied and also material of his own, observed a few paired whorls (Génot, 1987: plate 26, figure 5; here Figure 1.3) but never more than two whorls joined together.

2) The Morellet brothers (1918) also stated that “Avec les ombelles, dans les mêmes gisements, existent des fragments de fins tubes calcaires (diamètre moyen 0,3 mm), qui correspondent à la partie stérile de la plante (tige). Ils montrent des verticilles espacés de pores par où sortaient les poils végétatifs” [besides the umbels, in the same localities, there are remains made of thin calcareous tubes (with a 0.3 mm diameter in average), which correspond to the sterile part of the alga (stalk). They show spaced verticils of pores corresponding to exit points of vegetative hairs].



**FIGURE 5.** Original thin sections studied by Pfender (1927a). **1.** no. 79, Nans, Provence, SE France – J. Pfender Collection. **2.** no. 18, Sormiou, Provence, SE France – J. Pfender Collection. **3.** no. 84, Méounes-lès-Montrieux, Provence, SE France – J. Pfender Collection. **4.** without number, Tlemcen, Algeria – leg. Lemesle, E.P. Munier-Chalmas Collection. **5.** no. 53, ? label illegible, Provence, SE France – J. Pfender Collection. **6.** no. 7 bis, ? label illegible, Provence, SE France – J. Pfender Collection. **7.** no. 8, Plan-d'Aups-Sainte-Baume, Provence, SE France – J. Pfender Collection. All photos same scale (scale bar equals 1 cm).

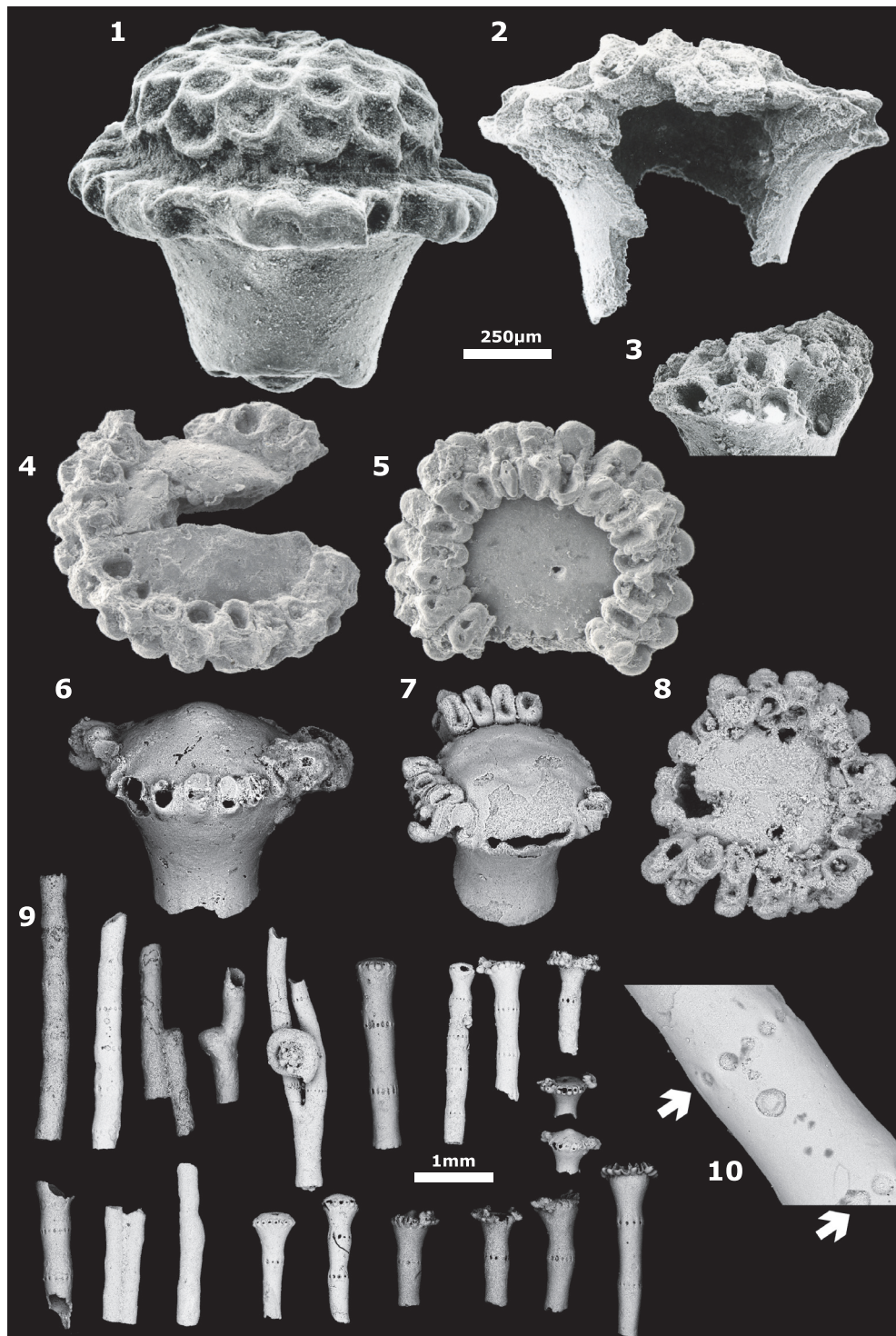
It looks like the authors actually described remains known from modern algal genera, e.g., *Acetabularia* Lamouroux, 1812 (see examples in Granier, 1994: plate 4, figures 5-9; 2012: text-figure 5.A, 5.D; Granier and Boichard, 2017: plate 1, figures 4.a-c, 7; here Figure 6.9-10), but not from *Clypeina* itself. Elliott (1968) fell into that trap because, when quoting Morellets' work, he said that “besides typical fertile whorls they have calcified evidence of the sterile portion of the plant” (...). However, Génot (personal communication, 15/10/2016) reported that he never found or observed such features in all the collection material (e.g., Génot, 1978, 1980, 1987, 2009) he examined during his career.

3) In the same publication (L. Morellet and J. Morellet, 1918), the authors propose a graphical 2D reconstruction of *Clypeina* (*op. cit.*: text-figure 1), that was later re-used by Costantin (1925: text-figure 7.a-b), Pia (1927: text-

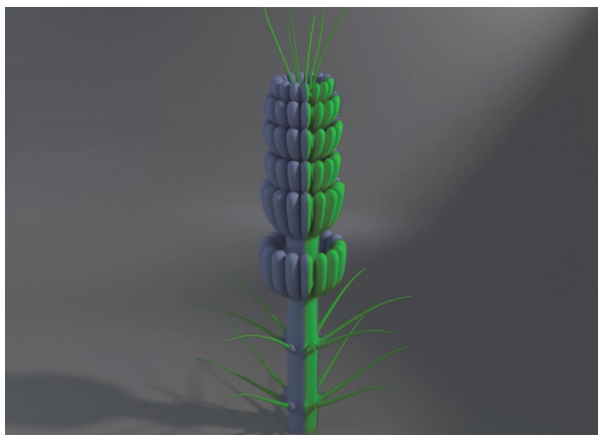
figure 54), Moret (1943: text-figure 16.10), Rezak (1957: text-figure 1), Endo (1961: plate 5, figure 8), Cita (1964: text-figure 62), Elliott (1968: text-figure 3), L. Emberger (1968: text-figure 93), Bignot (1982: text-figure 6.7; 1985: text-figure 6.7), Berger and Kaefer (1992: text-figure 2.20a), and that we used here to build a 3D reconstruction (Figure 7).

To summarize, it looks like the Morellet brothers put forward all the elements, including language elements (e.g., “ombelles”), to definitely link the genus and its representatives to the Family “Acétabulariées” (L. Morellet and J. Morellet, 1918).

As a matter of fact, teratologic cases observed in living *Acetabularia crenulata* (Lamouroux, 1816) with “several superimposed caps” (e.g., Berger and Kaefer, 1992: text-figure 3.61.a-c) or *Polyphysa parvula* (Solms-Laubach) with two superimposed caps (e.g., Valet, 1968: plate 25, fig-



**FIGURE 6.** 1. *Clypeina* sp., Lutetian of Montjavoult, Oise, Paris Basin, E.P. Munier-Chalmas Collection (Génot, 1987: plate 3, figure 14). 2. *Clypeina* sp., Lutetian of Chambors, Oise, Paris Basin, E.P. Munier-Chalmas Collection (Génot, 1987: plate 3, figure 15). 3. *Clypeina* sp., Lutetian of Thiverval-Grignon, Seine-et-Oise, Paris Basin, P. Génot Collection. 4-10. *Acetabularia caliculus* Lamouroux in Quoy and Gaimard, 1824, Holocene of Abu Dhabi, UAE, B. Granier Collection: 4-5, 8: top views of the cap; 6-7: side views of the cap; 9: various views of main axes and caps, with or without coronas (note that one rare specimen has a bifurcated thallus); 10: detail of the calcareous coating of a thallus with scars corresponding to the emplacement of former sessile sterile laterals (arrows). Almost all photos same scale (scale bar equals 250 µm), except 9 (scale bar equals 1 mm).



**FIGURE 7.** 3D reconstruction of the fossil genus *Clypeina* sensu L. and J. Morellet (1918) based on their 2D reconstruction (op. cit.: text-figure 1). Video of image is available at <https://palaeo-electronica.org/content/2019/2333-aloisalthella-and-clypeina> for download.

ure 4) may suggest that the extinct genus *Clypeina* is a direct ancestor of the modern genus *Acetabularia*. However, “the perforate, ‘pepper-pot top’, structure” (Elliott, 1968) observed in few *Clypeina* specimens (e.g., Génot, 1987: plate 3, figures 14-15; here Figure 6.1-2, plus Figure 6.3) allows this hypothesis to be discarded. As a matter of fact, fossil caps of the living *Acetabularia caliculus* Lamouroux in Quoy and Gaimard, 1824, e.g., those documented by Granier and Boichard (2017: plate 1, figures 1-3), may have lost either both the corona structure (Figure 6.9 pars) and the gametophores, sometimes called “spicules”, or only the gametophores (Granier and Boichard, 2017: plate 1, figures 1-3; here Figure 6.4-8, 6.9 pars), but none of them are perforated (Figure 6.4-8).

Worse than that, flaw number 2 is the most questionable argument ever made by the authors. Although it is plausible that the lowermost portion of the algal thallus was bearing only whorls of sterile hairs, as is the case for instance in most claviform genera, i.e., with club-shaped species (e.g., *Petrascula* in Pia, 1920, text-figure 23), or as is commonly observed at both ends of the articles in moniliform genera, i.e., with species looking like a string of beads (e.g., *Cymopolia* in Berger and Kaefer, 1992: text-figure 2.10), there is no such evidence in the material studied either by the Morellets or by Génot.

Lastly Bassoullet et al. (1978) gave an emended diagnosis for the genus that supposedly summarizes all earlier findings. According to the second paragraph of their diagnosis, “On peut noter la présence éventuelle de ramifications

‘stériles’, de forme capillaire, disposées en touffe au sommet de l’algue, en verticilles à sa partie inférieure, et/ou entre les verticilles fertiles” [One can observe the possible presence of hair-like “sterile” laterals, clustered in a tuft at the apex of the algal axis, arranged in verticils in its lower part and/or inserted between the fertile verticils].

By including this last item to cover a feature first observed by Radoičić (1969: text-figure 9.c-d) in “*Clypeina jurassica* Favre and Richard, 1927” (i.e., *Clypeina sulcata*), they added another flaw. Actually, this last feature, absence or presence of sterile rows between fertile rows, is a determining criterion applied in the taxonomic classification of the Dasycladales to split genera, tribes or even families (e.g., the Triploporellaceae versus the Polyphysaceae, e.g., Granier, 2015). In no case should it apply to separate species within a single genus.

In conclusion, narrowing the generic diagnosis of Bassoullet et al. (1978: p. 43-44) is suggested, restricting it to its first paragraph and the first part of its last sentence, keeping in mind the possible occurrence of an apical tuft of sterile hairs but excluding any reference to whorls of sterile laterals, which are either not observed or missing in the fossil material. Furthermore, this narrower definition leads to exclusion of *C. sulcata* and some other species from the genus.

### **A Digest on the Species *Clypeina sulcata***

Modern calcareous green algae (Dasycladales and Bryopsidales) mineralize extracellularly or “intercellularly” (in folds of the cell membrane of these large unicellular organisms) with aragonite. Their fossil counterparts are commonly dissolution molds, either empty (in the subsurface), or partly to fully infilled by late calcitic cement. *Clypeina sulcata* (Alth, 1882) and few allied species mineralize with calcite, commonly yellowish due to organic matter trapped within the crystals (Granier, 2012).

Like the genus *Clypeina*, the species *C. sulcata* went through many nomenclatural vicissitudes, such as having to face competitors that will prove to be junior synonyms (*C. jurassica* Favre and Richard, 1927, and *C. inopinata* Favre, 1932).

When Alth (1882) introduced the genus *Actinoporella* based on his species *Gyroporella podolica* Alth, 1881, from the Upper Jurassic of Galicia (today a Ukrainian western territory), he also described two new species: *Actinoporella gümbeli* and *A. sulcata*.



Later, regarding these last two species, Pia (1920) stated that “Während ich (...) die Selbständigkeit Alths *Actinoporella gümbeli* nicht anzuerkennen vermag, stimme ich mit ihm vollständig in der Meinung überein, daß die wenigen Exemplare, die er als *Actinoporella sulcata* ausgeschieden hat, eine besondere, schon jetzt gut abtrennbare Art vertreten” [Although I may not agree on the singularity of Alth’s *Actinoporella gümbeli*, I fully agree with him to consider that the few specimens he labelled as *Actinoporella sulcata* belong to a singular discrete species]. Pia (1920, plate VII, figure 8) also provided a drawing of a verticil as seen from the outer surface of a rock sample, i.e., the first ever picture of the alga (Figure 1.1).

In the mean time, Joukowsky and Favre (1913) documented in petrographic thin sections an *incertae sedis* that they named “Organisme A” from Purbeckian strata of Switzerland. Later, in 1927, these fossil remains were in two instances concurrently ascribed to the genus *Clypeina*. The first one includes a short note dated February by Pfender (1927b) that announces a forthcoming paper dated September (Pfender, 1927a). The thin sections (Figure 5) she studied are currently stored in the paleontological collections at the Université Pierre et Marie Curie. Four out of five figures of Pfender (1927a: plate V, figures 1-3, 5, not 4; here Figure 8.1, 8.5-6, 8.10), as well as previously unpublished sections from the same material, are documented here in the form of color photomicrographs (Figures 8, 9.6-8, 10.7). The second instance is a short note dated March by Favre (1927) that announces the memoir with the formal definition of *C. jurassica* (Favre and Richard, 1927).

In 1932, Favre again introduces *C. inopinata*, which is “une espèce voisine” [a closely related species], from lowermost Cretaceous strata of Switzerland. However Remane (1969) who revised the type-material of both Favre’s species gave a set of evidences that “make it very doubtful that *C. inopinata* is really an independent species.” Bassoullet et al. (1978) conclude that “*Clypeina inopinata* is probably synonymous of *C. jurassica*.” In turn, Granier and Deloffre (1993) synonymize both species with *C. sulcata*.

There are very few citations of these three taxa in the literature before a paper by J. Morellet (1950), which documents material collected by R. Karpoff in Upper Jurassic strata of Algeria. Color photomicrographs of unpublished material from the same locality and by the same collector, found in the J. Emberger Collection, are illustrated here

(Figure 2). Since J. Morellet’s publication (1950), *C. jurassica* has been cited more than a hundred times with peaks in the 1960s and 1970s.

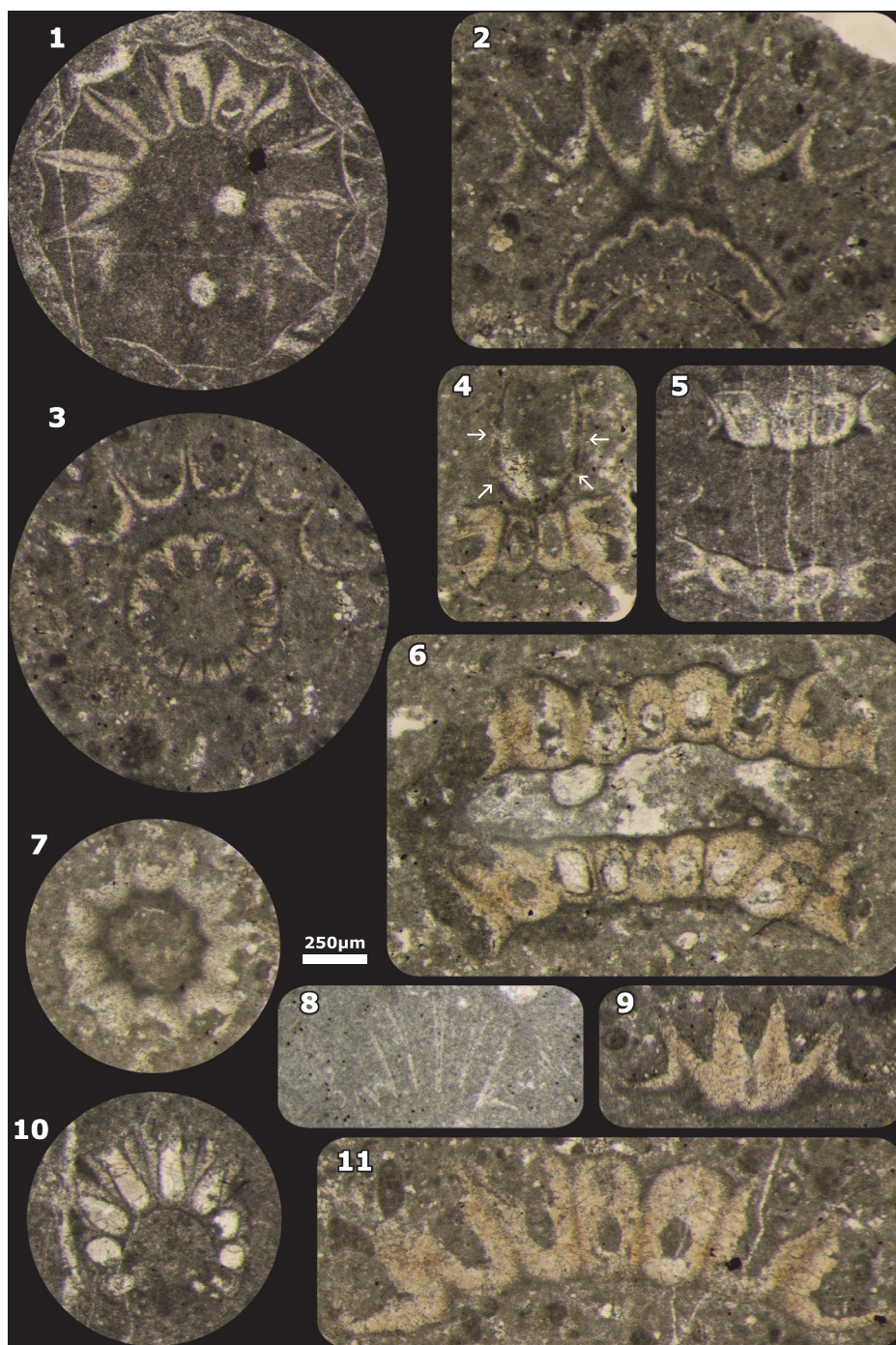
Although Bassoullet et al. (1978) agreed that *Actinoporella sulcata* “is considered to be a synonym of *Clypeina jurassica*,” they did not implement the priority rule (Art. 11 of the ICBN). Thus, Granier and Deloffre (1993) implemented it in the second part of their reappraisal of the fossil Dasycladalean algae. Since then, the new combination *Clypeina sulcata* is regularly cited, implying that this name cannot be rejected and that the name *C. jurassica* cannot be conserved.

The reader is referred to Pfender (1927a), J. Morellet (1950), Elliott (1968), Radoičić (1969), and Bassoullet et al. (1978) for more or less detailed diagnoses or descriptions of the species. However, the identification of rows of hair-like laterals, first due to Radoičić (1969), deserves a short dedicated section, as well as few other features never reported before.

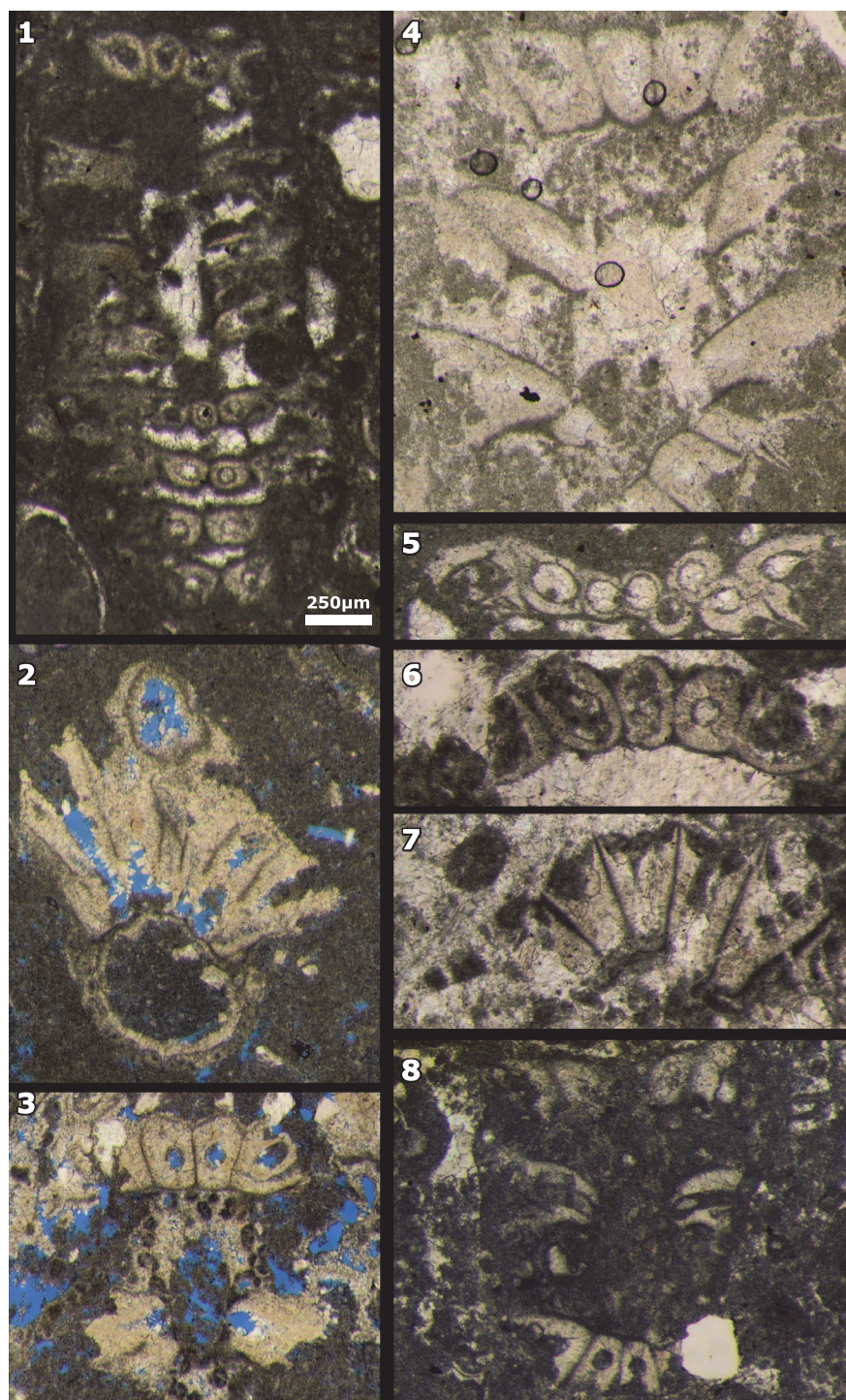
### Whorls of Sterile Laterals

As mentioned earlier, Bassoullet et al. (1978) emended the diagnosis of the genus *Clypeina* in order to encompass *C. sulcata* and its peculiarity: “On peut noter la présence éventuelle de ramifications ‘stériles’, de forme capillaire, disposées (...) en verticilles (...) entre les verticilles fertiles” [One can observe the possible presence of hair-like “sterile” laterals, arranged (...) in verticils (...) inserted between the fertile verticils]. Granier (1986: text-figure 10) modified Remane’s reconstruction (1969: text-figure 23) to take this last remark into account.

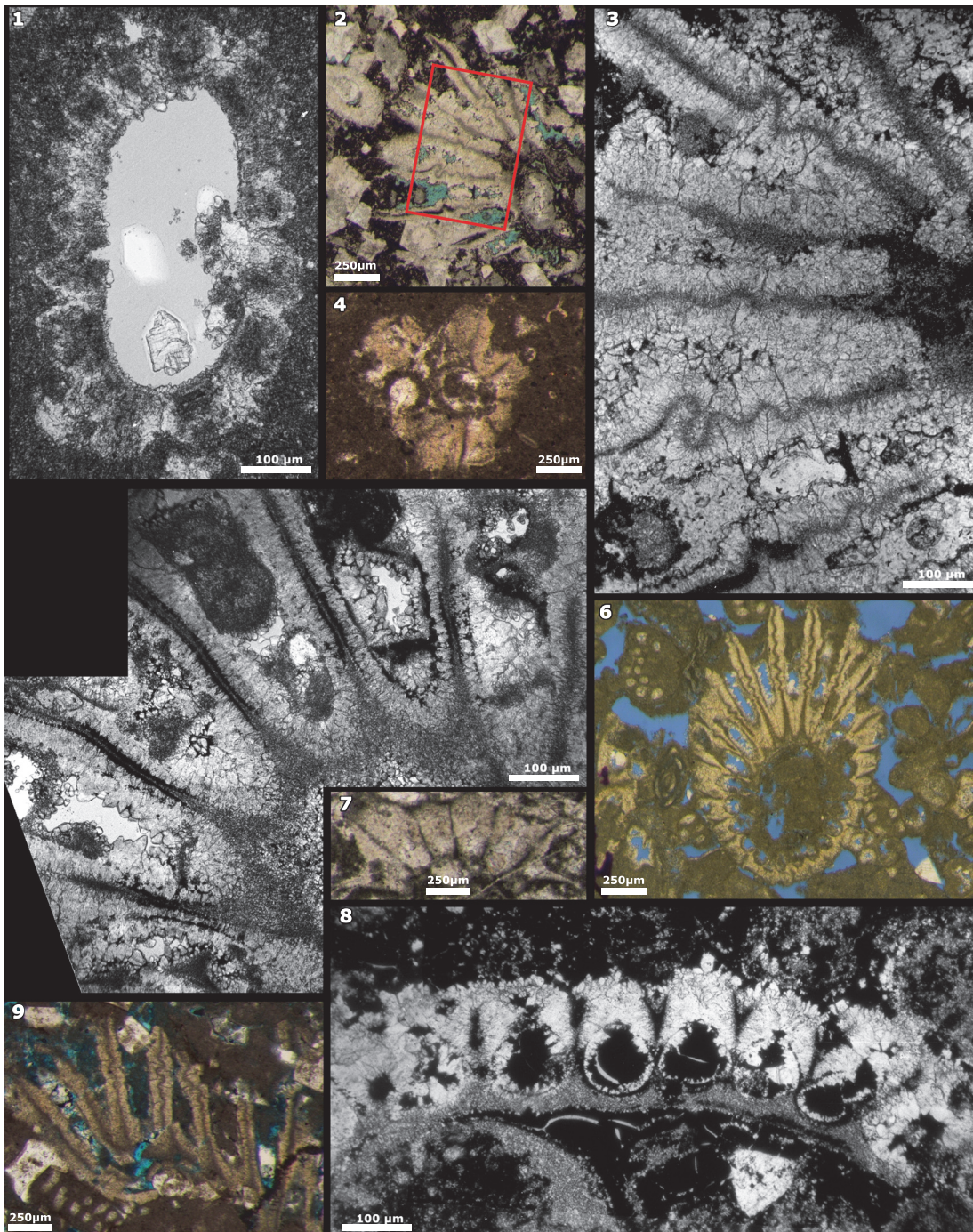
In the modern genus *Acetabularia*, the fine sterile laterals are sessile and do not fossilize, but verticils of scars, left behind after the lateral fall, may be visible (see examples in Granier, 1994: plate 4, figures 5-9; 2012: text-figure 5.A, 5.D; Granier and Boichard, 2017: plate 1, figures 4.a-c, 7; here Figure 6.9-10). Similar features were documented in *Clypeina sulcata* by Radoičić (1969: text-figures 6.c-d, 9.a-d, 10.a-c) and followers (e.g., Granier, 1986: plate 9, figures d, i; De Castro, 1997: plate 19; plate 20, figures 2-3, 5-6; Schlagintweit et al., 2005: text-figure 35b-d). In our opinion, the recently described *C. lagustensis* Sokač et al., 2014, with numerous sterile verticils merely represents an ecological variant of *C. sulcata* (Alth, 1882). Sections documenting these sterile laterals are commonly subaxial (Figures 9.3, 11) or deep tangential, rarely oblique (Figures 8.4, 9.2b, 10.1) or subtransverse (Figure 12.3, 12.6, 12.9), and the



**FIGURE 8.** 1, 5, 10. *Aloisalthella* gen. nov. *sulcata* comb. nov., from the Berriasian of Provence, SE France, J. Pfender Collection. 1: thin section no. 79, Nans, Var: subtransverse section, high in a whorl (= plate V, figure 2 in Pfender, 1927a); 5, 10: thin section no. 49, road from Mazargues to Sormiou, now part of Marseilles' urban area, Bouches-du-Rhône: 5: deep tangential section with two whorls (= plate V, figure 3 in Pfender, 1927a); 10: oblique section in a whorl (= plate V, figure 1 in Pfender, 1927a). 2-4, 6-7, 9, 11. *Aloisalthella* gen. nov. *sulcata* comb. nov., from the Kimmeridgian of Tlemcen, NW Algeria, leg. Lemesle, E.P. Munier-Chalmas Collection. 2: oblique section; 3: subtransverse section, low in a whorl; 4: oblique to subaxial section (arrows point to sterile scars along the main axis); 6: (= plate V, figure 5 in Pfender, 1927a); 7: transverse section, low in a whorl (= text-figure 3.B lower in Pfender, 1927a); 9: tangential oblique section; 11: oblique section of a whorl (= text-figure 3.B upper in Pfender, 1927a). 8. "verticille terminal de poils stériles" according to Pfender (1927a), i.e., uppermost verticil made of sterile hairs (= text-figure 2 in Pfender, 1927a), thin section no. 8, Plan-d'Aups-Sainte-Baume, Var, Berriasian of Provence, SE France, J. Pfender Collection. All photomicrographs same scale (scale bar equals 250 µm).



**FIGURE 9.** *Alosalthella* gen. nov. *sulcata* comb. nov. **1, 4-5.** Thin section no. 519 m, Upper Jurassic, PE-1, core 2, Sierra Perenchiza, Valencia, Spain, leg. R. Deloffre, B. Granier Collection. 1: subaxial section with 8 fertile verticils; d: subaxial section with 3 fertile verticils with clots (scars of sterile laterals) in between; e: longitudinal section of an isolated fertile verticil. **2-3.** Thin section no. 8878035, Upper Kimmeridgian of Abu Dhabi, United Arab Emirates. 2: subtransverse sections of 2 main axes suggesting a branching of a single thallus; 3: subaxial section with 2 fertile verticils with clots (scars of sterile laterals) in between. **6-8.** Berriasian of Provence, SE France, J. Pfender Collection. 6: longitudinal section of an isolated fertile verticil, thin section no. 7 bis, ? label illegible (= text-figure 3.A lower in Pfender, 1927a); 7: subtransverse section of an isolated fertile verticil, thin section no. 53, ? label illegible (= text-figure 3.A middle left in Pfender, 1927a); 8: subaxial section with 3 fertile verticils, thin section no. 84, Méounes-lès-Montrieux, Var (= text-figure 1 in Pfender, 1927a). All photomicrographs same scale (scale bar equals 250 µm).



**FIGURE 10.** *Aloisalthella* gen. nov. *sulcata* comb. nov. **1-3, 5-6, 8-9.** Upper Kimmeridgian of Abu Dhabi, UAE. **1:** subtransverse section of a main axis with pores that correspond to the sterile laterals, thin section no. 8706034; **2-3:** subtransverse section of a fertile verticil and detail of its fertile laterals with twisted walls, thin section no. 9855076; **5:** subtransverse section of a fertile verticil with bitumen linings on the walls of its laterals, thin section no. 8822034; **6:** subtransverse section of a fertile verticil with its fertile laterals with twisted walls, thin section no. 8957035; **8:** oblique section of a fertile verticil with bitumen linings on the walls of its laterals, thin section no. 8902034; **9:** subtransverse section of a fertile verticil with its fertile laterals with twisted walls, thin section no. 9998177. **4.** Subtransverse sections of 2 main axes suggesting a branching of a single thallus, thin section no. 519 m, Upper Jurassic, PE-1, core 2, Sierra Perenchiza, Valencia, Spain, leg. R. Deloffre, B. Granier Collection. **7.** random section of a fertile verticil, thin section no. 53, ? label illegible (= text-figure 3.A upper left in Pfender, 1927a), Berriasian of Provence, SE France, J. Pfender Collection. **1, 3, 5, 8** (scale bar equals 100 µm), and **2, 4, 6-7, 9** (scale bar equals 250 µm).

corresponding pores are rarely visible (except for 2 sections illustrated here: Figures 8.4, 10.1).

## SYSTEMATIC PALAEOLOGY

(B. Granier)

Phylum CHLOROPHYTA Pascher, 1914  
Class DASYCLADOPHYCEAE Hoek et al., 1995  
Order DASYCLADALES Pascher, 1931  
Family POLYPHYSAEAE (Kützing, 1841)  
Genus CLYPEINA Michelin, 1845, emend.

**Type species.** *Clypeina marginoporella* Michelin, 1845, p. 177-178, plate 46, figure 27.a-b; here Figure 1.2.

**Emended diagnosis.** By discarding features that are not observed on *Clypeina marginoporella* Michelin, 1845 (the type-species of the genus), we provide a modified, shortened version of the “diagnose émendée” of Bassoullet et al. (1978). These fossil algae have a thallus usually cylindrical bearing laterals of first order only. The main characteristic of the genus is the occurrence of relatively broad laterals, hence supposedly fertile, markedly longer than thicker. They are varyingly inclined with respect to the main axis communicating with it through a pore at their proximal end; they are either open or closed at their distal end. The calcareous coatings of adjacent laterals are usually welded together in their proximal part. They form single whorls more or less regularly spaced along the main axis, but non-contiguous. In exceptional circumstances, one can find scars marking the former emplacements of sessile hair-like laterals, hence supposedly sterile, clustered in a tuft at the apex of the alga. French version with precise identification of the excerpts from the original text: “Algues fossiles” ayant un thalle “de forme généralement cylindrique, ne possédant que des ramifications de premier ordre. Le genre est surtout caractérisé par la présence de ramifications” relativement développées, nettement plus longues que larges, et donc supposées “fertiles”. Elles ont une “inclinaison variable par rapport à l’axe principal avec lequel elles communiquent par un pore” dans leur partie proximale; elles sont “ouvertes ou fermées à leur extrémité distale”. Les “enveloppes calcaires” de ramifications adjacentes “sont généralement soudées entre elles à leur partie proximale. Elles constituent des verticilles simples plus ou moins régulièrement espacés le long de l’axe, mais non jointifs.” Exceptionnellement, on peut observer des cicatrices marquant l’emplacement “de ramifications stériles, de forme capillaire,”

sessiles, “disposées en touffe au sommet de l’algue”.

Genus ALOISALTHELLA gen. nov.

**Type species.** *Actinoporella sulcata* Alth, 1882, p. 323 (Neotype: plate VII, figure 8 in Pia, 1920; here Figure 1.1).

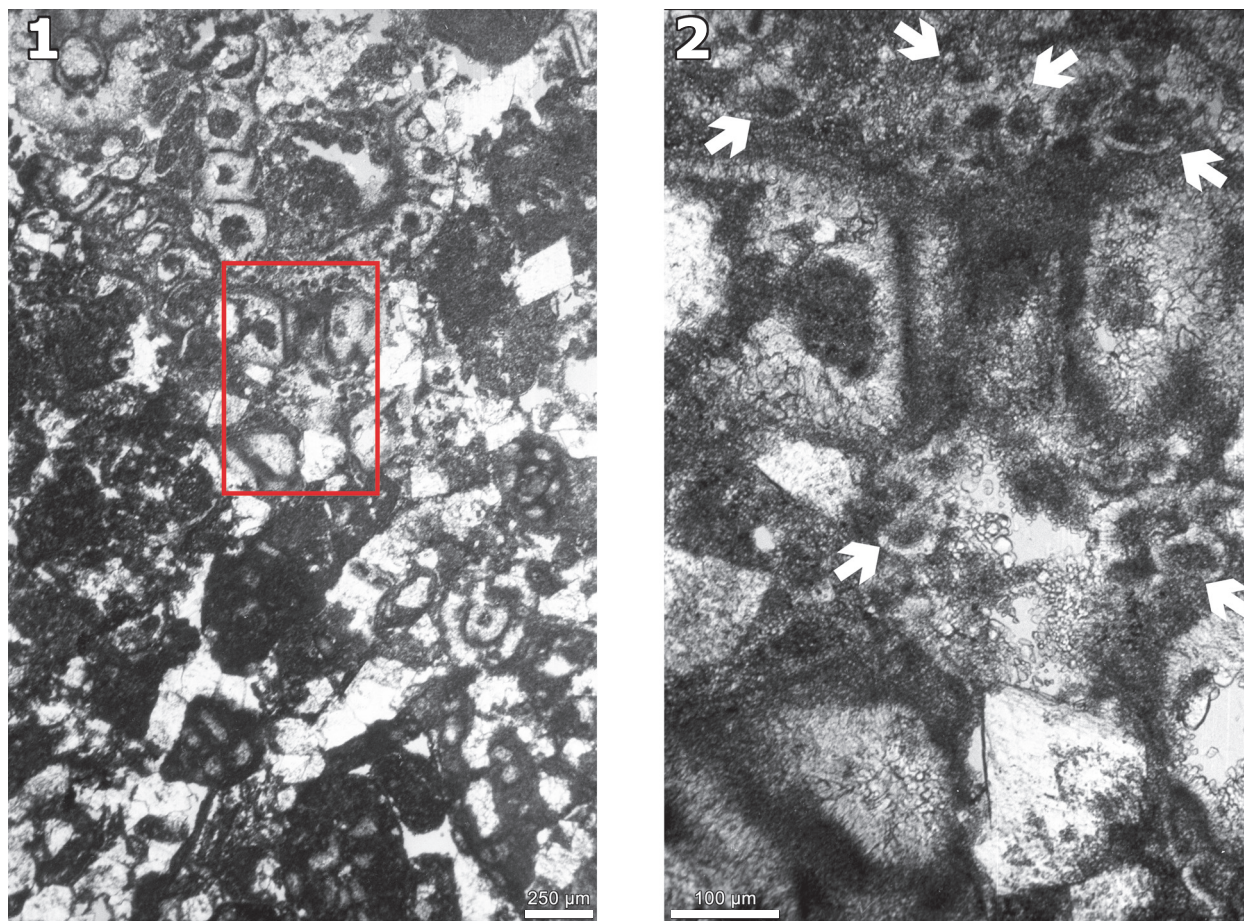
**Diagnosis.** Fossil algae with a subcylindrical main axis (because its diameter may slightly vary within a single specimen) commonly bearing two types of whorls: 1) more or less widely spaced radiating rays of fertile laterals and, when visible, 2) whorls of tiny pores on the locations of sessile sterile laterals. There are usually several whorls of sterile laterals separating two successive rays of fertile laterals. Fertile whorls consisting of first order laterals welded together at least in their proximal part form a round shield. These fossilized laterals are relatively broad, markedly longer than thicker, and either open (broken) or closed at their distal end.

**Etymology.** The new genus is dedicated to Alois (Alojzy) Alth (1819-1886), the author of the species *Actinoporella podolica*, i.e., the type-species of the genus *Actinoporella* (Gümbel in Alth, 1882) (see Granier, 2019a), and of the type-species of the new genus.

*Aloisalthella sulcata* Alth, 1882, comb. nov.

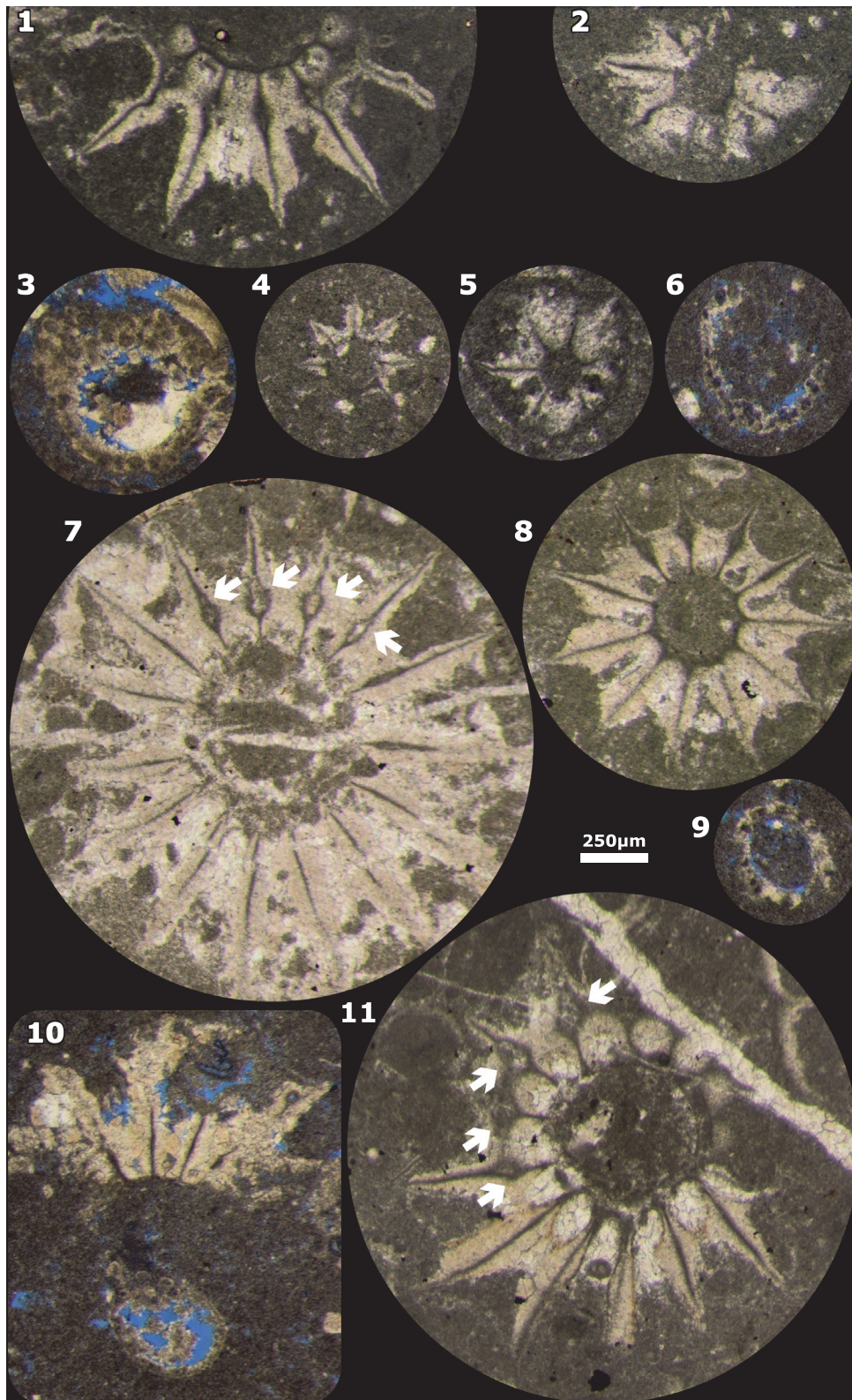
Figures 1.1, 2-4, 8.1-7, 8.9-11, 9-12

- 1882 *A. sulcata* Alth. Alth, p. 323.  
1913 “Organisme A”. Joukowsky and Favre, p. 315, text-figure 6, pl. XIV, figure 2.  
1920 *Actinoporella sulcata* Alth. Pia, p. 100-101, plate VII, figure 8.  
1927b “Organisme A” / *Clypeina*. Pfender, p. 28.  
1927 *Clypeina jurassica*. Favre, p. 49-50.  
1927 *Clypeina jurassica* n. sp. Favre and Richard, p. 34-35, text-figure 10.a-u; plate I, figures 2-3.  
1927a “Organisme A” / *Clypeina jurassica*. Pfender, p. 89-94, France: text-figures 1, 3.A; non text-figure 2; plate V, figures 1-3; Algeria: text-figure 3.B; plate V, figures 4-5; Switzerland: text-figure 4 (= text-figure 6 in Joukowsky and Favre, 1913).  
1932 *Clypeina inopinata* n. sp. Favre, p. 11-16, text-figure 1.1-28.  
1932 *Clypeina jurassica* J. Favre. Favre, text-figure 2.1-17.  
1943 *Clypeina jurassica*. Moret, text-figure 16.13 pars (= text-figure 10.b, 10.e, 10.n in Favre and Richard, 1927).  
1950 *Clypeina jurassica* J. Favre. J. Morellet, plate XXII, figures 1-3.  
1955 *Clypeina jurassica* J. Favre. J. Emberger, p. 545, text-figure 1.1-16.



**FIGURE 11.** *Aloisalthella* gen. nov. *sulcata* comb. nov. Thin section no. 8730034, Upper Kimmeridgian of Abu Dhabi, UAE. **1.** microfacies (scale bar equals 250 µm). **2.** arrows pointing to some scars (clots) of sterile laterals (scale bar equals 100 µm).

- 1960 *Clypeina jurassica* J. Favre. J. Emberger, text-figures 5.a, 10.a, 12.2.
- 1964 *Actinoporella sulcata* Alth. Johnson, p. 12-13, plate 10, figure 7 (= plate VII, figure 8 in Pia, 1920).
- 1968 *Clypeina jurassica* Favre. Elliott, p. 29-32, plate 3, figures 2-5; plate 4, figures 4-6.
- 1968 *Clypeina inopinata* Favre. Elliott, p. 32.
- 1969 *Clypeina jurassica* Favre in Favre and Richard, 1927. Remane, p. 106-108, text-figures 1.a-i, 2.a-d, 3.a-g, 4.a-e, 5.a-e, 6, 7.a-g, 8, 9.a-f, 10.a-h, 11.a-c, 12.a-d, 13.a-c, 14.a-f, 15.a-c, 16.a-d, 17.a-c, 18.a-f, 19, 20.a-b, 21, 22.a-f, 24.a-d, 25.a-e, 26.a-g, 27.a-h, 28.a-d, 29.a-h, 30.a-d, 31-45.
- 1969 *Clypeina jurassica* Favre. Radoičić, p. 81, text-figures 6.a-b, 9.c-d.
- 1969 *Clypeina inopinata* Favre. Radoičić, p. 75-81, text-figures 6.c-d, 7.a-d, 8.a-h, 9.a-b, 10.a-c.
- 1974 *Actinoporella sulcata* Alth. Conrad et al., p. 5, text-figure 2.8 (= plate VII, figure 8 in Pia, 1920).
- 1978 *Clypeina jurassica* Favre and Richard, 1927. Bassoullet et al., p. 49-52, plate 4, figures 4 (= text-figure 9.c in Radoičić, 1969), 5, 7 (= text-figure 10.a-n in Favre and Richard, 1927).
- 1978 *Clypeina inopinata* Favre. Bassoullet et al., p. 48-49.
- 1982 *Clypeina*. Bignot, fig. 6.8.A (= text-figure 24.b in Remane, 1969), 6.8.B (= text-figure 29.c pars in Remane, 1969).
- 1985 "dasycladacean chlorophytes". Bignot, text-figure 6.8.A-B (= text-figure 6.8.A-B in Bignot, 1982).
- 1986 *Clypeina jurassica* Favre in Favre and Richard, 1927. Granier, p. 44-46, plate 9, figures a-d, i-k.
- 1993 *Clypeina sulcata* (Alth). Granier and Deloffre, p. 27.
- 1994 *Clypeina sulcata* (Alth). Granier, p. 81, plate 1, figures 2-3, 5-7.
- 1997 *Clypeina jurassica jurassica* Favre in Favre and Richard, 1927. De Castro, p. 196-197, 230-235, plate 2, figures 1-5; plate 19; plate 20, figures 1-9; plate 21.



**FIGURE 12.** *Aloisalthella* gen. nov. *sulcata* comb. nov. **1-2, 4-5, 7-8, 11.** Upper Jurassic, PE-1, core 2, Sierra Perenchiza, Valencia, Spain, leg. R. Deloffre, B. Granier Collection. 1, 11: thin section no. 519; 2, 8: thin section no. 519.25; 4: thin section no. 519.75; 5: thin section no. 518.50; 7: thin section, 518.75. **3, 6, 9-10.** 8878035, Upper Kimmeridgian of Abu Dhabi, UAE, B. Granier Collection. Arrows in 7 and 11 points to places where the laterals are bent (the "elbow"). All photomicrographs same scale (scale bar equals 250  $\mu\text{m}$ ).

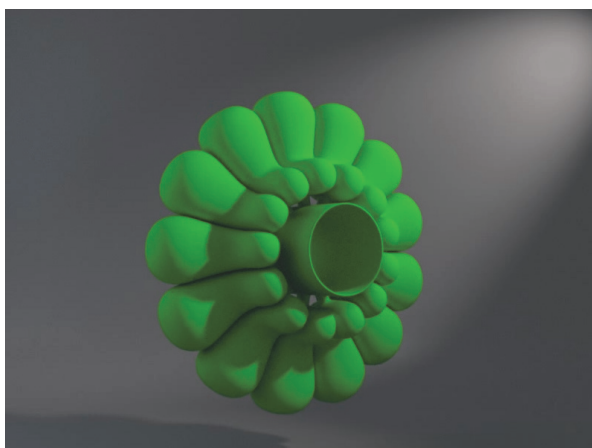
- 2005 *Clypeina sulcata* (Alth). Schlagintweit et al., p. 51-52, text-figure 35.a-d.
- 2009 *Clypeina jurassica* Favre and Richard, 1927. Schlagintweit et al., p. 50-51, text-figure 8.a-b.
- 2011 *Clypeina sulcata* (Alth). Mathieu et al., Photos 48.a-b.
- 2012 *Clypeina sulcata* (Alth). Granier, p. 46, text-figure 7.D.
- 2014 *Clypeina lagustensis* n. sp. Sokač et al., p. 78-80, plate I, figures 1-6; plate II, figures 1-6; plate III, figures 3, 6; plate IV, figures 1-8; plate V, figures 1-10; plate VI, figures 1-12.
- 2014 *Clypeina jurassica* Favre. Sokač et al., p. 79-80, plate III, figures 1-2, 4-5, 7-9.
- 2019b *Clypeina sulcata* (Alth). Granier, p. 251, text-figure 12.K, 12.S
- 2019 *Clypeina sulcata* (Alth). Granier and Lethiers, p. 38, text-figure.

**Remarks.** The few remaining sections, rare and atypical specimens, presented below correspond mostly to subsurface material from the Arab oil reservoir of the Abu Dhabi offshore:

Figure 10.5 is an oblique section, high in a fertile verticil. A black bitumen lining occurs in place of the former cell wall. The outer mineralization is micritic (microcrystalline calcite), possibly after a primary aragonite, whereas the inner mineralization is sparitic and consists of primary yellowish fibrous calcite. This inner calcification is limited and properly outlined in the proximal part of the fertile laterals where it molds possible reproductive structures. It then thickens in the median part of the laterals and thins again in their distal part (see also Schlagintweit et al., 2009: text-figure 8). Figure 10.8 is an oblique section, low in a fertile verticil. Here, bitumen linings split, and large ovoid casts with a sharp outline are now visible on the inner part of the fertile laterals.

Figure 10.2-3, 10.6, 10.9 documents uncommon oblique to subtransverse sections of fertile verticils. The walls of adjacent fertile laterals are twisted, a rare phenomenon that occurred before full mineralization take place, probably because the fertile ampulla was still expanding whereas the mineralization had just started. Consequently the unfolding of the inflating fertile ampulla was fossilized at an early stage.

Thalli of *C. sulcata* are commonly abundant but scattered in the sediment, suggesting that the alga formed dense communities, but not as dense as those of *Neoteutloporella socialis* (Praturlon). Accordingly, the calcareous coatings of neighboring thalli should never join or merge. Figure 9.2 is an odd oblique section. It looks like two thalli have locally joined. A more realistic hypothesis would be



**FIGURE 13.** 3D reconstruction of an uncalcified fertile verticil of *Aloisalthella* gen. nov. *sulcata* comb. nov. It is assumed that on these fertile laterals bulges are located below the row (inferior). Video of image is available at <https://palaeo-electronica.org/content/2019/2333-aloisalthella-and-clypeina> for download.

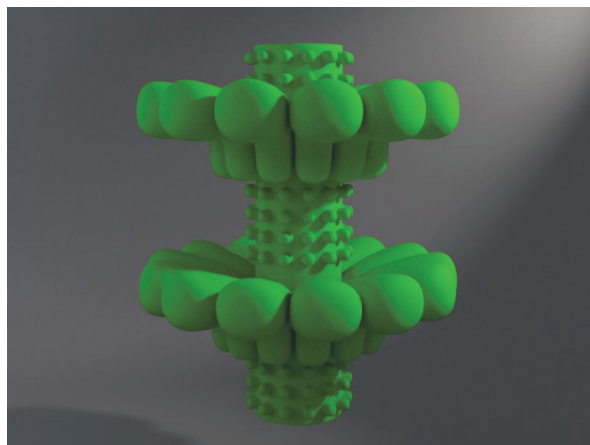
that we are dealing with a single thallus that is branching, and the section cuts the two branches just above the branching. Similarly Figure 10.4 from the Upper Jurassic of Spain represents another odd transverse section. Again, the section would cut the branches above a branching, but this time not so close to the branching. Similar dichotomous branching also rarely occurs in the modern *Acetabularia* (e.g., Valet, 1968: plate 15, figures 5-6; plate 24, figure 3; plate 25, figures 3, 7; Bonotto et al., 1977: text-figure 6; here Figure 6.9 pars).

As for previous 3D reconstructions of algae (Granier, 2010; Granier and Sander, 2013; Granier and Lethiers, 2017), the Blender free software was used to build 3D models of *C. sulcata*. The models presented here focus 1) on the morphology of the fertile laterals (Figure 13) and 2) on the arrangement of the verticils, both sterile (represented by scars) and fertile, along the main axis (Figure 14). Such models enable visualization of truncations of the algal structure (Figure 13) at various angles (Granier and Lethiers, 2019: text-figure; here Figure 15) that can be compared to actual sections (e.g., Figures 8.3, 12.11). In turn these comparisons improve and validate the model.

## CONCLUSIONS

Thalli of representatives of the genus *Clypeina*, obviously those of the Cenozoic *Clypeina marginoporella*, may bear sterile hairs at their distal end, but to date only three specimens are known (Figure 6.1-3). It cannot be excluded that they also bear sterile verticils at their proximal end, close to





**FIGURE 14.** 3D reconstruction of an uncalcified living thallus of *Aloisalthella* gen. nov. *sulcata* comb. nov., with sets of sterile rows (of scars) in alternation with fertile rows. Video of image is available at <https://palaeo-electronica.org/content/2019/2333-aloisalthella-and-clypeina> for download.

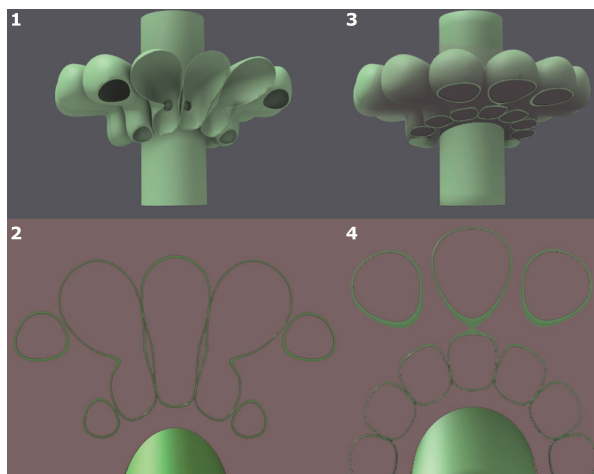
the rhizoid, but that was never observed. In any case, they do not bear any sterile verticils in alternation with fertile verticils. Fertile verticils are commonly imbricated.

In contrast, thalli of representatives of the newly established genus *Aloisalthella*, obviously those of the Mesozoic *Clypeina sulcata*, are commonly bearing more or less widely spaced fertile verticils (not imbricated) with sets of sterile verticils in the intervals, when visible. Unique features of the type-species (possible branching of some thalli and twisted walls of some fertile ampullae) are documented here for the first time.

The corrections made to the generic definition of *Clypeina* imply launching revisions of all the 40 or so species previously referred to this genus.

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This publication follows the “Revision of the Juliette Pfender Collection - Part 1” (Granier and D. Dias-Brito, 2016). It was recently presented on the



**FIGURE 15.** The laterals have the general shape of elbow tubes closed at both ends here (at the start of the reproductive stage). They communicate with the main axis through a small pore on the side of the elbow. **1-2.** oblique sections 3D and 2D to compare with Figure 12.11. **3-4.** oblique sections 3D and 2D to compare with Figure 8.3.

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