

## ***Error vacuo*, Detecting Structures in Poorly Calcified Jurassic Dasycladales**

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### **Abstract**

Several Jurassic dasycladalean genera (e.g. *Pseudoclypeina*, *Palaeodasycladus*, *Eodasycladus*, *Chinianella* and *Cylindroporella*) display a complex structure which, owing to a deficit of calcification, is difficult to interpret. This lack of calcification causes a loss of certain soft algal structures and complicates the work of the specialist responsible for interpreting the algal anatomy as well as the corresponding position in the systematics. A key of interpretation is given, and case histories are discussed.

### **Keywords**

Dasycladales, Paleoalgology, Systematics.

### **Introduction**

“*Error vacuo*” is reminiscent of *horror vacui* (in Latin means “fear of empty spaces”) and it can be translated as “the error induced by the presence of the empty spaces”. The study of fossil Dasycladales is commonly based on calcified organs. The distribution of calcium carbonate around the alga is sometimes useful in distinguishing taxa at the species level, but the structure of the calcareous skeleton actually is the only way to understand the anatomical elements of the alga. The ornamentation adding to pores and cavities produced by a deficiency of calcification may lead to a structural misinterpretation. In the present paper, some case studies from Jurassic taxa are provided. Several genera (e.g. *Selliporella*, *Pseudoclypeina*, *Palaeodasycladus*, *Eodasycladus*, *Chinianella* and *Cylindroporella*) display a complex structure. The lack of calcification causes the loss of the soft structures and complicates the scientific interpreting of the algal anatomy and assigning the correct systematic status even to family level.

### **Calcification: function and distribution**

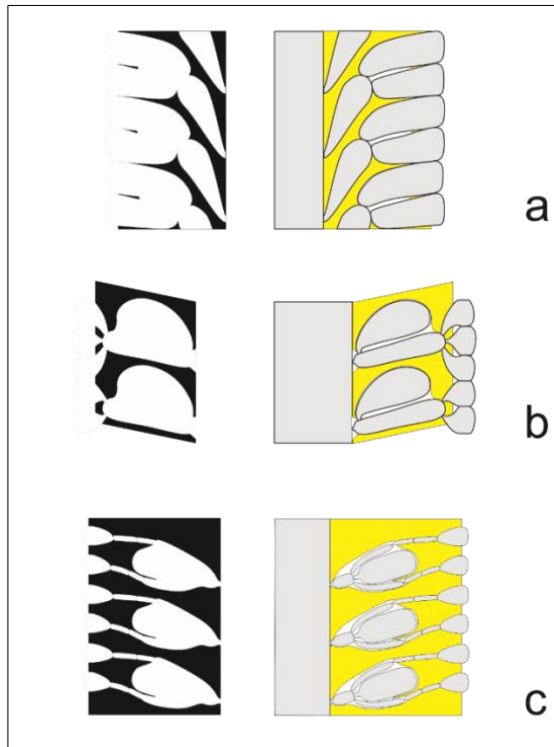
Dasycladales may produce lime-secreting mucilage to coat their soft parts. From a mineralogical point of view, calcium carbonate precipitates as aragonite with a few other minerals (Berger & Kaefer, 1991), but few fossil counterparts testify the presence of an original skeleton of fibrous calcite (e.g. *Pseudoclypeina distomensis*, *Clypeina sulcata*). Calcification is generally extracellular, accumulating around laterals, and less frequently around the central stem. Intracellular calcification, related to reproductive organs, is known in fossil and extant species as well (e.g. *Triploporella remesi* and *Acetabularia schenckii*). Calcification

probably is functional to reproduction in protecting gametangia and gametophores against intense sunrays (De Castro, 1997). The solar shield effect is obtained with different strategies: a) peripheral shield, i.e. a calcareous thin layer set close to the cortex leaving the internal volume completely uncalcified (e.g. *Bornetella oligospora*); b) calcareous sleeve, external reproductive organs (e.g. choristosporate) can be coated or not (e.g. *Cymopolia*); c) calcareous sheath preferentially coating external gametophores (e.g. *Neomeris annulata*); d) intracellular calcification filling the space among gametangia (cysts, e.g. *Acetabularia schenckii*); e) intracellular calcareous thin layer separately coating each gametangium (e.g. *Chalmasia antillana*, *Acetabularia moldavica* Barattolo et al. 2019).

### **Pores, compound pores and empty spaces**

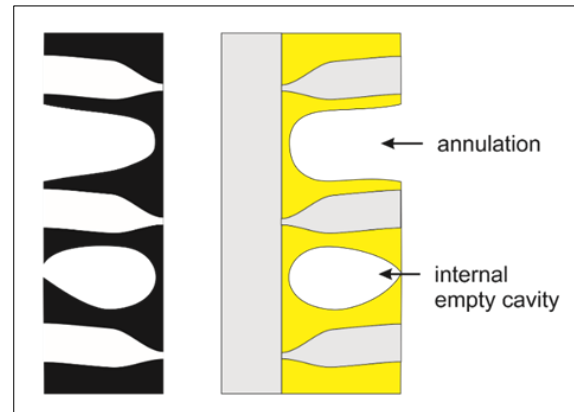
The term “pore” conventionally indicates the external mould of a lateral (Pia, 1920). However, the close relationship between pore and lateral is verified when calcification adheres to the lateral’s wall. In all other cases, the pore may recall the original lateral shape to various degrees. In general, pores showing an irregular outline, lateral protuberances, lateral fusion, counter sinking, could be a sign of a loose pore/lateral relationship. Whether faithfully or not the pore reflects the shape of the corresponding algal soft part, the presence of such a cavity nonetheless indicates the past presence of an organic structure (lateral, reproductive organ, lateral + reproductive organ). The term “pore” should be used under these circumstances, i.e. voids not related to organic structures cannot be termed “pores”. Irregular pores or with bulges are possibly the result of a deficiency of calcification around a tuft of

secondary laterals (e.g. *Dinarella kochi*, Fig. 1a), laterals with a terminal gametophore (*Eodasycladus alanensis*, Fig. 1c), laterals with goniosporate gametophores (*Cylindroporella liasica*, Fig. 1b).



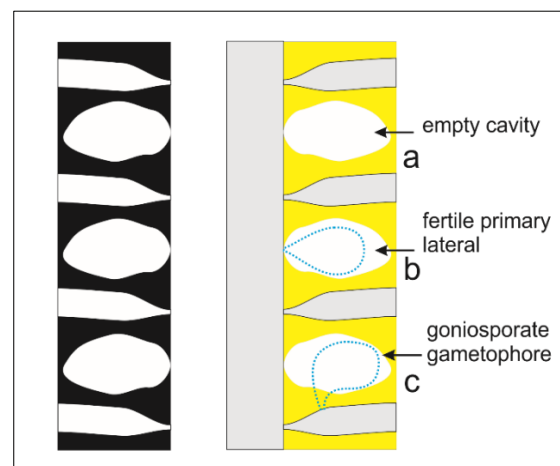
**Fig. 1.** Examples of compound pores. The lack, or deficiency of calcification affects: a) the tuft of secondary laterals, such as in *Dinarella kochi*, redrawn by Sokač & Nikler, 1969; b) the primary lateral and the gametophore, such as in *Cylindroporella ? liasica*, redrawn by Barattolo & Parente, 2000; c) The short primary lateral, secondary laterals, part of tertiary laterals and the gametophore, such as in *Eodasycladus alanensis*, redrawn by Barattolo et al., 2012. Right: gray, (half) central stem and laterals; white, cavities; yellow, calcification. Left: white, (half) central cavity, pores and empty cavities; black, calcification.

Such pores can be termed “compound pores”. Analyses of compound pores in different cuts and regions of the thallus can cast light on the elements destroyed by the deficiency of calcification. Barattolo & Parente (2000) have shown that the large, fertile primary pore of *Uragiella liasica* Lebourché & Lemoine, 1963, is a single large compound pore formed by a gametophore aside the primary lateral (Fig. 1b). Consequently, the taxon, previously thought cladosporous, has been transferred to the genus *Cylindroporella*, that means from the family Triploporellaceae to Dasycladaceae. Taxa with spaced whorls often show articulated calcareous skeletons (annulation, Pia 1920). Annulation is widely open outwards (e.g. *Clypeina solkani*, Lower Cretaceous), but sometimes (e.g. *Cymopolia fragilis*, Middle Eocene) strongly mineralized calcareous sleeves can display empty spaces closed within the calcareous wall (Fig. 2).



**Fig. 2.** Difference between annulation and internal cavity.

Firstly, the empty space between whorls possibly did not efface any organic structure (Fig. 3a), that means they were mere empty spaces and cannot be termed “pores”. Secondly, the occurrence of interposed uncalcified verticils alternated with those calcified can be demonstrated. In the Paleocene *Hamulusella liburnica* (Barattolo, 1998) and *Uteria brocchii* (Génot, 1993) the thin calcification adhering to the central stem displays whorls of pores corresponding to the initial (proximal) part of otherwise not mineralized laterals. The large cavities between whorls of the Lower Jurassic *Chinianella ellebergeri* (Lebourché & Lemoine, 1963) are commonly interpreted as fertile verticils (Fig. 3b). Thirdly, the empty cavity once housed a gametophore attached sideways to the primary lateral (Fig. 3c).

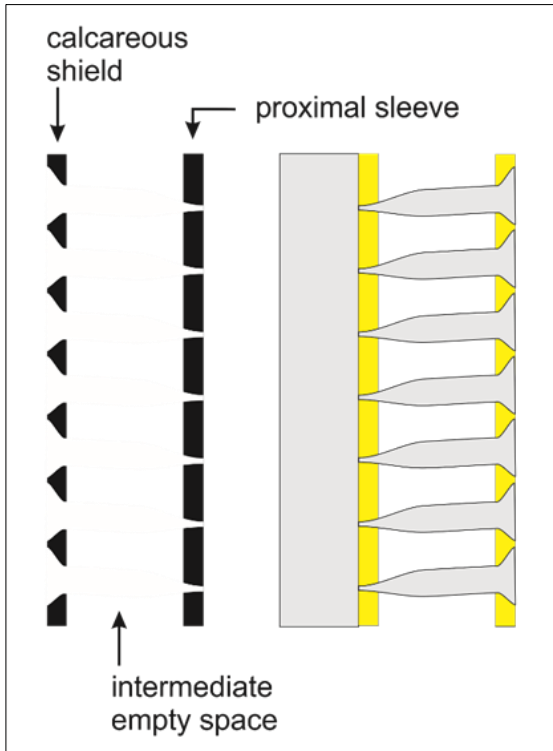


**Fig. 3.** Interpretation of internal empty spaces. a) Empty cavity produced by a lack, or insufficiency of calcification; b) cavity originally occupied by part of a fertile primary lateral; c) cavity originally occupied by a goniosporate gametophore sideways attached to the lateral.

### Large empty spaces

In a number of cases, large cavities occur, comprising more than 50% of the volume originally occupied by laterals. Two possibilities are as follows: a) intermediate empty space and, b) empty room. “Intermediate empty space” (IES)

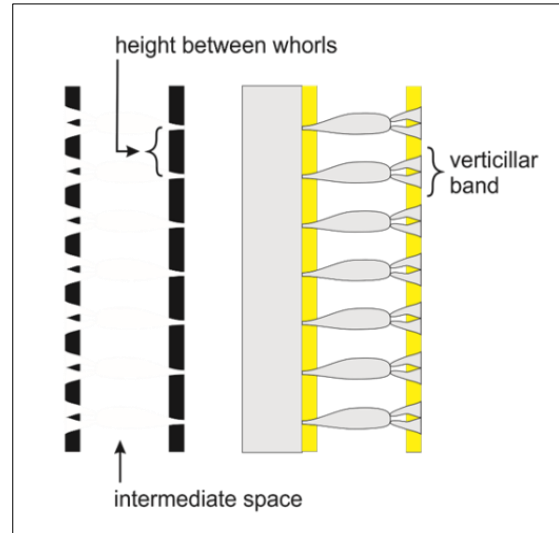
occurs when both the proximal and distal parts of the calcareous skeleton are preserved (Figs. 4-5).



**Fig. 4.** Fertile regions sometimes protected by a peripheral shield and a proximal calcareous sleeve may also occur, forming a large, intermediate uncalcified empty space.

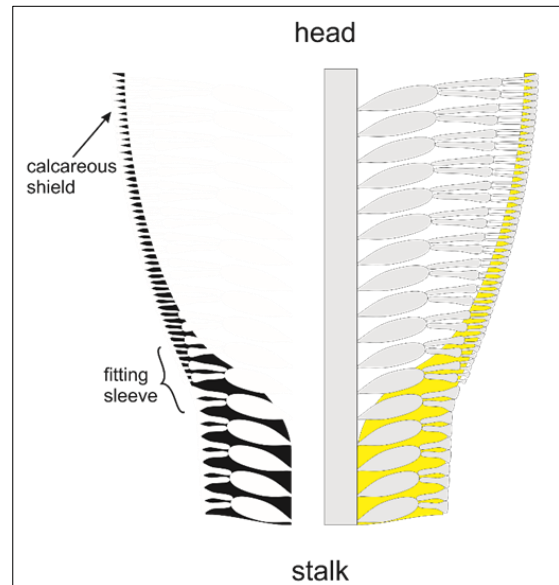
Typically, the central stem is coated by a thin calcareous sheath (the proximal sleeve) containing pores related to the initial, proximal part of the laterals. Therefore, in this situation, the number ( $w$ ) of pores per whorl and the height ( $h$ ) between whorls can be deduced. The outer layer consists of a calcareous shield (De Castro, 1997).

An example of IES occurs in the Tertiary genera *Uteria*, *Zittelina*, *Dactylopora*. The calcareous shield allows the detection of the number of distal pores contained in the verticillar band (Fig. 5), whose height is equal to  $h$ . The proximal number of pores per whorl ( $w_{prox}$ ) can be compared with the number of distal pores ( $w_{dist}$ ) occurring within the verticillar band.  $w_{dist}-w_{prox}$  ratio allows an estimation of the order of ramification and number of pores in a tuft. An “empty room” typically occurs in the upper part of club-shaped thalli (Fig. 6). The calcareous skeleton is reduced to a peripheral shield, thus leaving the internal part completely empty. The lower part (stalk) is generally more calcified than the fertile upper part (head). The transition between the two parts (the fitting sleeve) often allows the structure of the uncalcified parts to be assumed.



**Fig. 5.** The proximal number ( $w_{prox}$ ) of pores per whorl can be compared with the number ( $w_{dist}$ ) of distal pores occurring in the verticillar band. The  $w_{dist}-w_{prox}$  ratio provides an estimate of the order of ramification (branching) and the number of pores per tuft.

Many Jurassic genera (*Palaedasycladus*, *Fanesella*, *Sestrosphaera*, *Tersella*, *Granieria*, *Petrascula*) display this sort of calcification (Barattolo & Bigozzi, 1996; Barattolo et al, 2008; Pia, 1920; Romano & Barattolo, 2009).

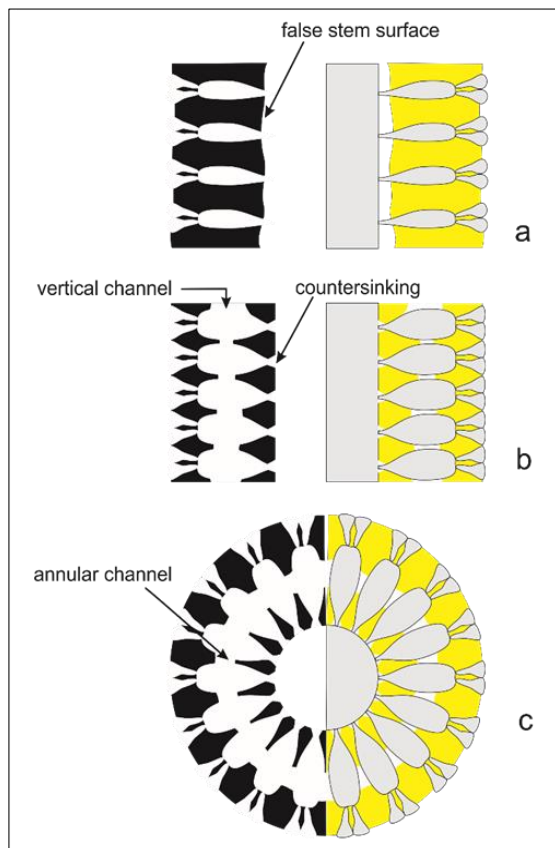


**Fig. 6.** Example of “empty room” in a club-shaped thallus. The lower part (stalk) is generally more calcified than the fertile upper part (head). The transition between the two parts (the fitting sleeve) often allows estimating the original structure of the uncalcified parts of the skeleton.

### Minor empty spaces

Other examples of empty space are related to a deficiency of calcification close to the central stem or by the proximity of laterals. When the calcareous sleeve does not attain the central stem, it is characteristically irregular (false stem surface, Fig. 7a). The lack of calcification can fuse pores

together vertically (Fig. 7b) and/or laterally in a whorl (Fig. 7c, like in the Middle Jurassic *Selliporella donzellii*, Barattolo et al., 1992). Laterals are linked to the main stem through a small pore. Such a large, inward opening (countersink) of the pores may often be related to a lack of calcification (Fig. 7b and c).



**Fig. 7.** Other examples of empty space. a) calcareous sleeves not attaining the central stem are characteristically irregular (false stem surface). b), c) lack or insufficient calcification can fuse pores together vertically (b) and/or horizontally (c) into a whorl. Laterals are joined to the main stem through a small pore. Such large, inward opening (countersink) of the pores may denote an insufficient calcification (b and c).

### Acknowledgements

The author wishes to thank Angela Federico and Marc Conrad for the English revision of the manuscript.

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Submitted: 28 Nov. 2018

Revised: 15 Jan. 2019

Accepted: 22 Mar. 2019