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Palaeonitella trifurcata n. sp., a cortoid-building charophyte from the Lower Cretaceous of Catalonia

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ABSTRACT

Palaeonitella trifurcata n. sp. is a minute ecorticate thallus of a charophyte from a non-marine upper Barremian–Lower Aptian section of the Garraf Massif, near Barcelona (Catalonia, Spain). Whorls of trifurcated branchlets built glomerules about 1 mm across. Small radial branchlets were trifurcated once in three terminal acuminate dactyls. Longer and more robust branches, two per whorl emerge from a basal trifurcation, bore opposite secondary branchlets and ended in three terminal branchlets bearing one oospore. The whole set of characters suggests affinity with *Nitella*, making of this fossil one of the oldest and unique possible records of thalli of this extant genus.

The thallus of *P. trifurcata* n. sp. was encrusted by a thin micrite film, and additionally, the whorls were coated by a thicker crust while the plant was still alive. It is suggested that this crust was formed upon the periphyton which grew perhaps upon a mucilage covering the whorls and apical heads, as it happens in extant *Nitella*. After encrustation, a small (ca. 5 mm across) constructive micrite envelope, called a cortoid, was formed attached to the plant, preserving in the inside the thallus articulated and slightly encrusted. Once the plant died, such cortoids accumulated on the lake bottom and were buried and lithified, forming a “cortolite”. This is the first report of constructive micrite envelopes protecting delicate and poorly calcified charophyte thalli from being destroyed.

1. Introduction

Genus *Nitella* is the extant charophyte genus with the poorest fossil record. The main reason for this is the low calcification potential of their thalli and its inability to generate gyrogonites, only organic oospores are produced after the oogonia are fertilized. One well-documented fossil record of *Nitella* is formed by silicified oospores described by Musacchio (2010) from the Upper Cretaceous volcanic bearing floodplain succession of El Zampal in Patagonia, Argentina. A more dubious fossil affine to *Nitella* is *Nitellites sahnii* Horn af Rantzien, 1957 from the Raajmahal series in India, Lower Cretaceous in age (Feist et al., 1991), which corresponds to an organic oospore displaying an ornamentation reminiscent of extant *Nitella mucronata*. However, this fossil does not show any mark of the oosphere sister cells, which together with the ornamentation are diagnostic features of these oospores.

So far, there are no records of fossil thalli that can be assigned straightforward to *Nitella*. Ecorticate fossil thalli of charophytes are usually classified within genus *Palaeonitella* (Pia, 1927) Martín-Closas and Diéguez, 1998, however this organ-genus includes ecorticate thalli that may belong to several charophyte groups. For instance, *Palaeonitella cranii* Kidston and Lang, 1921 from the Upper Devonian of the Rhynie chert in Scotland was first considered to represent a fossil *Nitella*, but Kelman et al. (2004) showed that its oospores were paleocharacean-type rather than characean. The new species described herein may represent the oldest fossil thallus with strong affinities to *Nitella*. The very particular type of cortoids (sensu Flügel, 2004) developed upon *Palaeonitella trifurcata* n. sp., allowed the exceptional preservation of *Nitella*-like thalli in the Lower Cretaceous of Catalonia.

2. Material and methods

The section called Les Piques that provided the material is located in the municipality of Olivella, near the farm called Can Grau. It can be reached following a small, paved road that joins the villages of La Plana Novella and Olivella across the Garraf Natural Park, about 20 km southwest from Barcelona, Catalonia (Fig. 1). Base coordinates of the Les Piques section are 41°18′13.3″N 1°50′43.1″E. Fieldwork and sampling were authorized by the headquarters of the Garraf Natural Park with reference number S46145 (2013).

The studied beds belong to the marls and charophyte-rich limestones of the basal part of El Peu de la Serra lithostratigraphic unit

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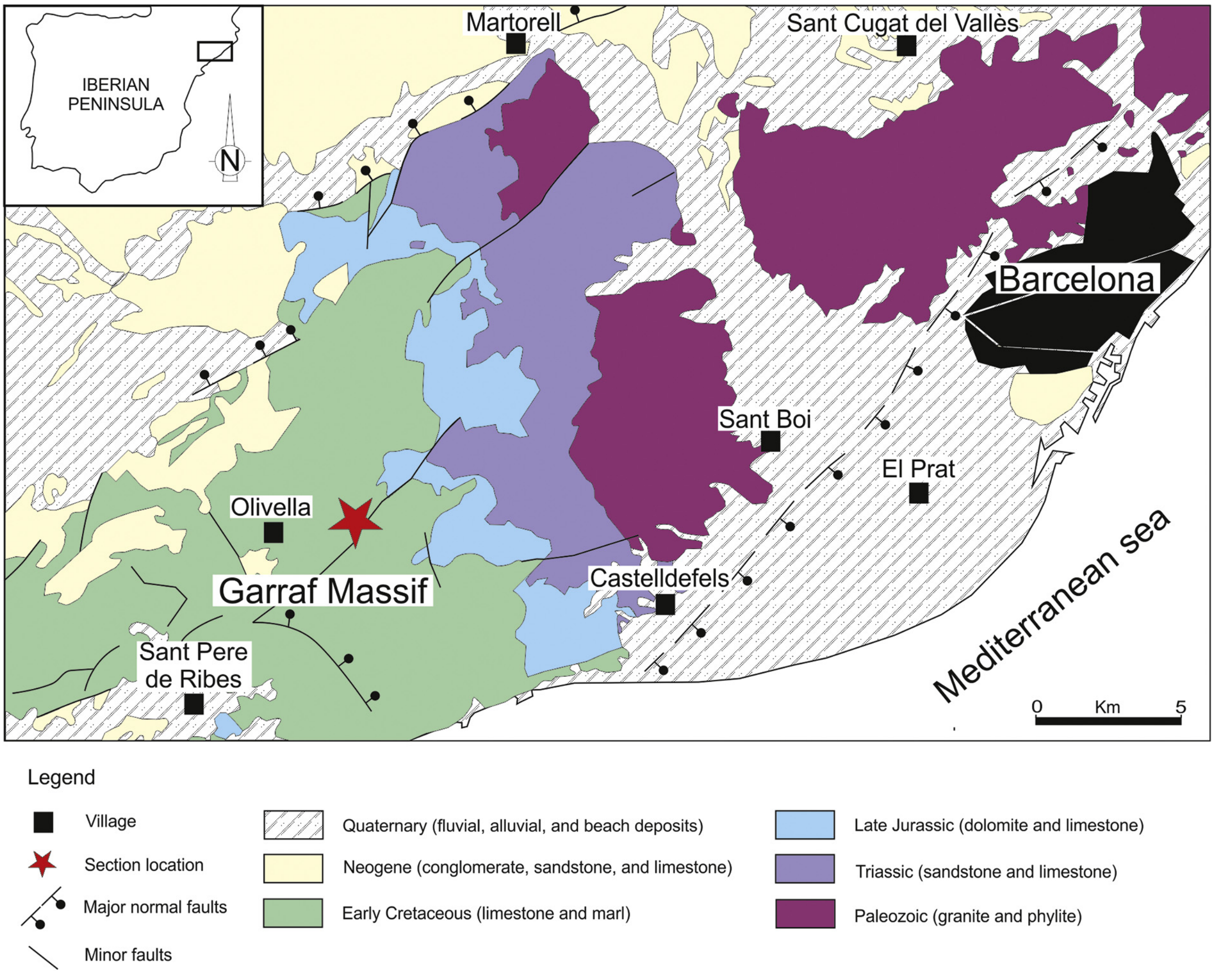

Fig. 1. Geological map of the study area, with location of the Les Piques section (star) (modified from Roca i Adrover and Miranda i Canals, 2010).

defined by Salas and Moreno (2008). Limestones were systematically sampled and prepared as thin sections of ca. 30 μm thick. Fourteen thin sections containing dozens of small cortoids, enclosing portions of charophyte thalli in their nuclei, have been studied. The thin sections containing the material illustrated are stored in the Museu Geològic del Seminari Conciliar de Barcelona with numbers MGSCB 86463–86475, while the remaining material is housed in the Departament de Dinàmica de la Terra i de l'Oceà at the Facultat de Ciències de la Terra-UB.

The microfossils were studied, measured and photographed at the University of Barcelona using the software Motic Images Plus 2.0 ML in a stereomicroscope Motic BA310. The charophyte plant reconstruction provided herein was undertaken by joining the different portions of the plant preserved in the inside of cortoids and that corresponded one to another as in a jigsaw-puzzle, following the procedure previously used for the reconstruction of fossilized charophyte plants from thin sections (e.g., Villalba-Breva and Martín-Closas, 2011; Pérez-Cano et al., 2020).

3. Geological setting

The Garraf Massif is the northernmost part of the Catalan Coastal Chain displaying a Cretaceous sedimentary record, which is part of the Iberian rift. This Mesozoic rift system generated by intraplate extension concomitant to the opening of the North Atlantic and the Bay of Biscay (Salas et al., 2001; Tugend et al., 2015). The sedimentary record of the Mesozoic Iberian rift was strongly controlled by tectonic subsidence, although other factors, such as paleogeography and paleoclimate, had a significant influence. The first rifting phase of the Iberian Rift extended from the latemost Permian until the Late Triassic Salas and Casas, 1993). This phase was followed by a period of thermal subsidence lasting for most of the Early and Middle Jurassic. From the Kimmeridgian (Late Jurassic) to the early Albian (Early Cretaceous) there were two tectonic rifting phases separated by a period of post-rift lasting from the late Berriasian to the late Hauterivian (Salas et al. in Martín-Chivelet et al., 2019).

Most of the stratigraphic succession cropping out in the Garraf Massif developed during the Late Jurassic-Early Cretaceous rifting phases (Fig. 2). The sedimentary succession from that interval is characterized at the base by Upper Jurassic dolomites (Les Agulles unit) including some intervals of lagoonal dark limestones that provided Kimmeridgian plant remains (Barale and Calzada, 1985). These dolomites are covered by a unit, up to 50 m thick, formed of finely laminated limestones with fenestral porosity known as La Pleta de Garraf Formation, which was attributed to tidal flat deposits by Rosell-Ortiz (1978-79) and may be partially dolomitized (Garraf Upper Dolomite unit). This formation is overlain by a 50 m-thick unit of palustrine and lacustrine limestones called the Els Mangraners Formation, latest Berriasian in age (Albrich et al., 2006). Upward, the succession turned into a ca. 100 m-thick unit of shallow marine limestone known as the Polacos Formation assigned to lower Valanginian (Salas et al., 2001). This unit is cut at its top by a sedimentary discontinuity corresponding to a major depositional gap of regional extension, including most of the Valanginian and the whole Hauterivian stages, i.e., a period of about 10 My

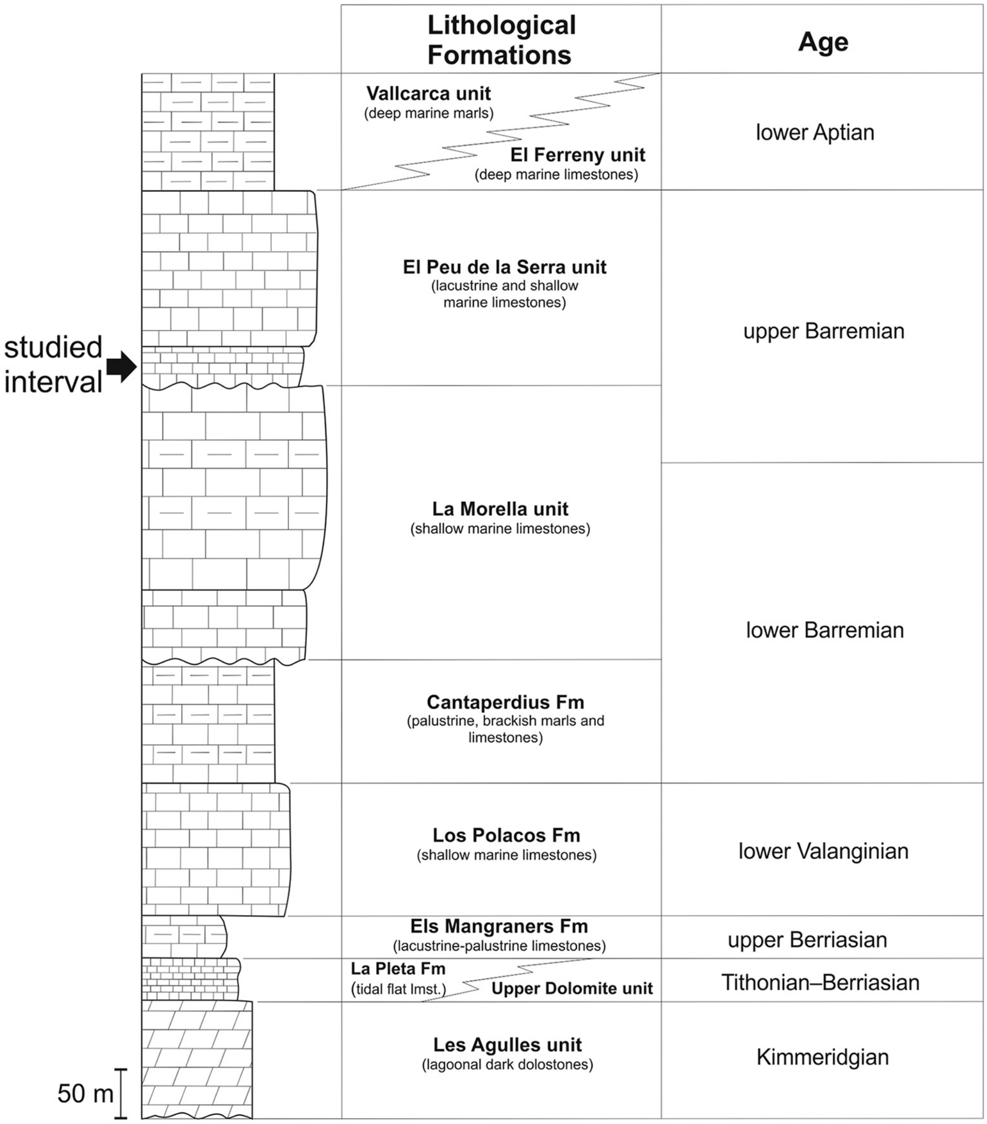

Fig. 2. Lithostratigraphic framework of the Kimmeridgian–Lower Aptian of the Garraf Massif (modified from Albrich et al., 2006 and Salas and Moreno, 2008).

(Albrich et al., 2006). Upon this discontinuity a ca. 500 m-thick Barremian succession begins, mainly formed by shallow marine limestone, rich in benthic foraminifera. At its base it shows a characteristic charophyte-rich bed with *Porochara* sp. gyrogonites followed by a 40 m-thick succession of palustrine limestones and marls with edaphic structures and oysters that indicate brackish conditions and characterize the Cantaperdius Formation. The remaining thickness is called La Morella Limestone and Marl unit (Salas and Moreno, 2008). It is formed by well-bedded limestones rich in orbitolinids and green algae (dasycladaleans and halimedaceans) of lower and upper Barremian age (Albrich et al., 2006). The top of these limestones is well-marked by a deeply karstified surface, which in the study area forms orange-colored lateritic pockets, 1–2 m thick and several meters across. The studied unit is located immediately upon this karstified surface. Salas and Moreno (2008) named this largely non-marine and shallow marine deposit El Peu de la Serra Limestone and Marl unit and attributed it to the upper Barremian (Fig. 2).

The section studied is 60 m thick and begins with the basal laterite marking the base of the El Peu de la Serra unit. Above the laterite, non-marine deposits rich in charophytes evolve gradually to shallow marine limestones rich in foraminifera (Fig. 3). Up to four non-marine to marine parasequences are displayed in the Les Piques section, which indicate a deepening-upwards trend (Fig. 3). The facies associations of each non-marine limestone rich in charophytes is in turn organized in a basal interval rich in charophyte-bearing “cortolites”, i.e., a rock rich in cortoids (Fig. 4), which are coated grains showing a single micrite envelope), followed by a limestone where these cortoids are found together with dasycladaleans (*Salpingoporella* sp.), and topped by a miliolid-rich limestone (Fig. 3). These small order parasequences show an increased marine influence towards the upper part of the El Peu de la Serra unit, which finally includes 75 m-thick shallow marine limestones (Fig. 3) rich in rudists, *Chondrodonta* bivalves and benthic foraminifera, mainly *Palorbitolina lenticularis* and *Choffatella decipiens*, late Barremian in age (Albrich et al., 2006; Salas and Moreno, 2008).

The upper part of the Lower Cretaceous sedimentary record at the Garraf Massif includes deeper marine deposits of Lower Aptian age, known as the Vallcarca Marl lithostratigraphic unit (up to 250 m thick) and El Ferreny Limestone unit (40 m thick). They yield a rich ammonite fauna described and biostratigraphically analyzed by Moreno (2007), Moreno-Bedmar and García (2009), Moreno-Bedmar et al. (2009) and Matamales-Andreu and Moreno-Bedmar (2016). Finally, the Upper Aptian El Pujol Florit unit, up to 110 m thick, is formed by shallower marine facies with rudists and orbitolinids.

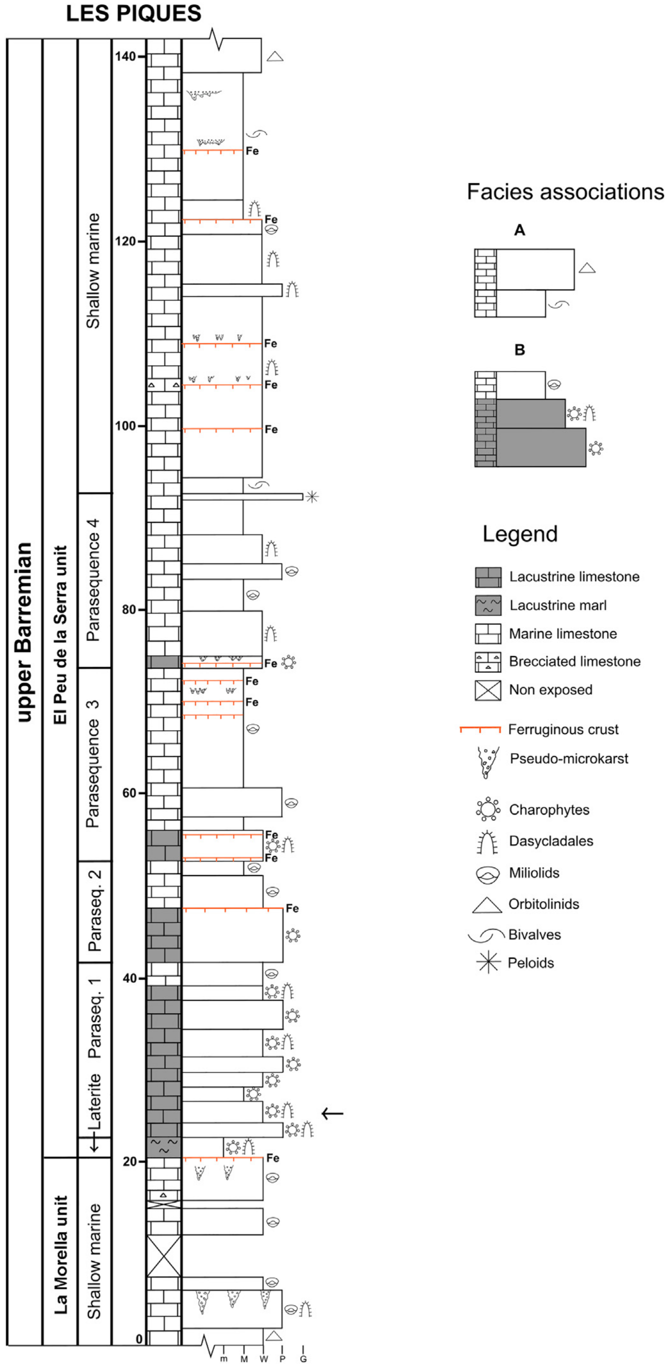

Fig. 3. Stratigraphic section of the El Peu de la Serra unit at Les Piques, showing alternation of non-marine intervals with charophytes (shadowed) and marine intervals rich in dasycladales and foraminifera. The shadowed intervals provided the samples studied.

4. Systematic paleontology

Division: CHAROPHYTA Migula, 1897

Class: CHAROPHYCEAE Smith, 1938

Order: Charales Lindley, 1836

Family: Characeae Richard. ex C.A. Agardh, 1824

Genus: ***Palaeonitella*** (Pia, 1927) Martín-Closas and Diéguez, 1998

Palaeonitella trifurcata Martín-Closas, Segura-Altés, Pérez-Cano, Bover-Arnal et Sanjuan n. sp.

Plate I 1–15, Fig. 5.

Etymology: Referred to the characteristic basal trifurcation of larger branches (Fig. 5).

Diagnosis: Small plant. Thallus ecorticate, slightly encrusted. Internodes up to 200 μm in diameter and whorls about 1 mm across. Nodes slightly swollen. Smaller branchlets typically 8–10 per node, finishing in three acute dactyls. Two larger branches per node show a basal trifurcation, with the central axis showing secondary opposite lateral branching and three terminal bracts with the same structure as other branchlets. Oospores borne at the junction of these three terminal bracts.

Locality: Road margin 2 km southeast from the farm called Can Grau, within the municipality of Olivella, Garraf Natural Park, Catalonia (Spain). Coordinates: 41°18′13.29″N, 1° 50′42.98″E.

Holotype: Specimen illustrated in Plate I, 1. Thin section number 86463 from the Museu Geològic del Seminari Conciliar de Barcelona.

Additional material (Paratypes): Specimens illustrated in Plate I, 2–3, 5, 8, 10–12 and 14. Thin sections numbers 86463, 86464, 86466, 86469, 86470, 86473 and 86474 from the Museu Geològic del Seminari Conciliar de Barcelona.

Stratigraphic horizon: Cortoid-rich limestone ("Cortolite") occurring near the base of the El Peu de la Serra unit, 6 m above the ferruginous laterite. This unit was attributed to the upper Barremian based on orbitolinid foraminifera and the lithostratigraphic framework.

Description: Thallus is ecorticate and very small. Internodes are cylindrical, 87–168 μm in diameter and 347–2124 μm long. Nodes are swollen, about 185–310 μm across, bearing bushy whorls, forming sub-sphaerical glomerules (Plate I, 4–6). Apical heads of thalli are conical and tufted (Plate I, 1–3). Two types of branchlets occur on the same node. Small branchlets, 8–10 in number, 370–714 μm long and 63–90 μm in diameter, are directed radially in all directions around the node (Plate I, 4–5). They furcate once in three terminal, acute dactyls, about 113–229 μm long and 45–54 μm across (Plate I, 9–11). Two larger and more robust branches arise opposite in the node from a basal trifurcation (Plate I, 1, 2, 8). The two lateral branchlets of this trifurcation are at least 228–560 μm long and 43–50 μm in diameter. They run subparallel to the adjacent internodes and furcate once in three acute dactyls (Plate I, 5, 7, 10). The central axis of the trifurcation is more robust, about 90 μm across and runs almost perpendicular as regards the main axis (Plate I, 1–2). This branchlet furcates 2 or 3 times in opposite secondary lateral branchlets bearing three acute dactyls each, and ends with three terminal branchlets with equally three dactyls each (Plate I, 8, 14). Lime-encrusted oospores are 275–372 μm in transversal section are borne individually at the junction of these three terminal branchlets of the central branch (Plate I, 14–15). A reconstruction of the plant is proposed in Fig. 5.

Comparisons: The new species of *Palaeonitella* differs from other species of the same genus by the unique features of the branchlets. Thus, *Palaeonitella vermicularis* Martín-Closas et Diéguez 1998 from the upper Barremian of the Las Hoyas paleontological site (Cuenca, Spain) bore nodes with regularly six short, non-ramified branchlets. *Palaeonitella tarafiyensis* Hill and El-Khayal, 1983 from the Upper Permian of Saudi Arabia shows a similar structure to *P. vermicularis* but with long internodes and extremely inflated nodes. Finally, *P. cranii* Kidston et Lang 1921 from the Upper Devonian of the Rhynie Chert shows repeatedly furcate branchlets bearing three or more dactyls, all with the same structure.

5. Taphonomy and paleoecology

5.1. Origin and formation of the cortoids with Palaeonitella trifurcata n. sp

Charophyte thalli of *P. trifurcata* occur in the inside of small globular constructive micrite envelopes, generally 1 mm large, but up to 5 mm across, called cortoids (sensu Flügel, 2004). Most of the cortoids, show internally a whorl of branchlets attached to the node and including a portion of the adjacent internodes (Plate I, 8–11, cortoid represented at the base of Fig. 5). More rarely, two adjacent whorls attached to the intermediate internode are preserved within a cortoid. This type of

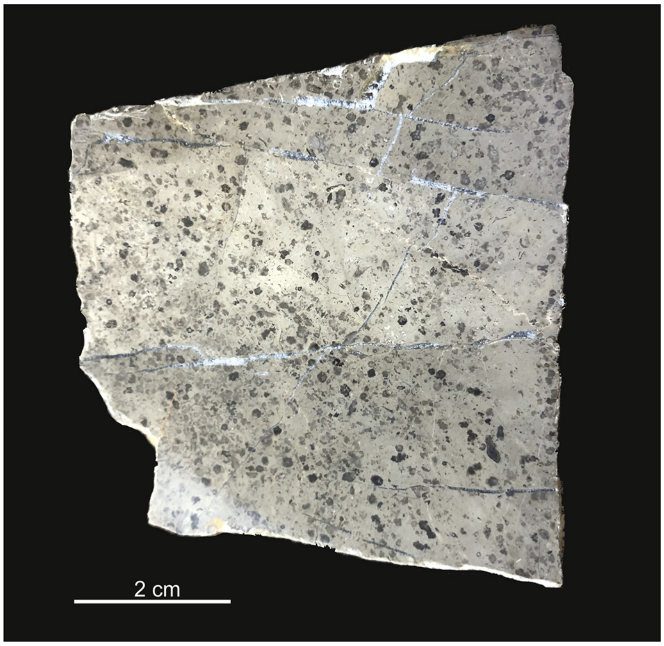

Fig. 4. Cross section of slab from the "cortolite" cropping out at the base of the El Peu de La Serra Formation. Minute cortoids (black dots) are about 1 mm across and hold in the inside a portion of the charophyte thalli studied here.

cortoid is bone-shaped (Plate I, 4–6, cortoid represented in the centre of Fig. 5). Exceptionally three whorls are preserved within a cortoid. Other cortoids include apical heads of the charophyte thallus, bearing short and incompletely developed internodes. In this case the cortoid shape is approximately conical (Plate I, 1–3, cortoid represented in the upper part of Fig. 5). All charophyte thalli within the cortoid are slightly lime-encrusted, suggesting that calcification occurred during the life of the plant, probably within the cortoid, since no other charophyte remains from the same species occur in the sediment outside cortoids.

Constructive micrite envelopes are about 100 µm thick, coating a loose nucleus formed by the charophyte remain. The external coating is mainly formed by dark micrite that displays a clotted internal fabric and is always interrupted at its junction with the internodes, leaving the section of the internodal cell open (Plate I, 1–3). This suggests that the cortoid was formed while the plant was still upright, probably during its lifetime, rather than by growth of a laminated micrite cortex around a deposited structure that turned on the lake bottom, which is the usual mechanism of oncoid formation (Flügel, 2004). The filmy shape of this coating and its internal microstructure suggest that it would correspond to a microbial film. Clotted fabrics have been shown to be often the products of microbially induced carbonate precipitation (Riding and Tomás, 2006; Flügel, 2004). These microbes might have been growing as periphyton upon the whorls of the living charophyte (Fig. 6A, B). By way of comparison, some extant species of genus *Nitella*, to which *Palaeonitella trifurcata* resembles, cover the dactyls and other delicate parts of their thallus with a protective mucilage, that can contain a periphyton made of other algae and microbes (Fig. 7).

The inside of the cortoid is filled in by a large proportion of sparite cement and a minor part of lime mud. Two generations of cement were recognized. The first is microsparitic and fills in the porosity between the micrite coating and the thallus, while the second, formed by larger sparite cristals, fills in the internal porosity of the thalli, such as the inside of the internodal cells.

After the plant died, the already indurated cortoid was deposited on the lake bottom. During burial, the sediment percolated in the cortoid through the uncoated internode opening (Fig. 6C). This is deduced by the infilling of the internode portion close to the opening (Plate I, 1–3). The abundance of microsparitic cement inside the micrite envelope suggests a large degree of inner porosity. During and after burial (fossildiagenesis), the cortoid lithification occurred and its different internal cavities were filled in with sparite cement (Fig. 6D).

5.2. Taphonomy and paleoecology of the microfossil assemblage

The "cortolites" generated by the deposition of cortoids bearing portions of *Palaeonitella trifurcata* thalli occur in a limestone with wackestone fabrics along with other microfossils (Plate II 1–19). Charophyte thalli associated with *P. trifurcata* are *Charaxis spicatus* Martín-Closas et Diéguez (1998) Pérez-Cano, Bover-Arnal et Martín-Closas 2020, *Clavatoraxis* sp., and *Favargerella* sp. The thalli of *C. spicatus* are exceptionally well-preserved, showing anatomical connection between the different parts (Plate II, 1–2). The remains of *Clavatoraxis* sp. and *Favargerella* sp. are less complete since only portions of the internodes and the phylloids, with their characteristic spine-cell rosettes, were found (Plate II, 5–9). Other charophyte remains include poorly calcified, undetermined atopocharoid and clavatoroid utricles (Plate II, 3–4, 11–13). All charophyte remains were probably autochthonous to parautochthonous in the depositional setting. Along with charophytes there were shallow marine fossils (Plate II, 7, 14–19). These include portions of thalli of the dasycladalean *Salpingoporella* sp. (Plate II, 15–17), ostracods (Plate II, 14), cyanobacterial bush (Plate II, 18), and skeletons of small benthic foraminifera, such as miliolids (Plate II, 7) and biseriate foraminifera (Plate II, 17–19). These fossils do not show any evidence of transport and occur as well in the marine intervals intercalated with the freshwater facies that are the object of our study. The occurrence of marine fossils associated with probably freshwater charophytes, in the absence of any paleobiological indication of brackish water, suggests that the assemblage represents a time-averaged sedimentation of two different environmental settings – marine and freshwater – in a coastal lake.

6. Discussion

Palaeonitella trifurcata n. sp. represents a fossil charophyte thallus with strong affinities to thalli of extant *Nitella*, especially because of its ecorticate structure, the structure of branchlets ended in three acute dactyls and the occurrence of longer branches with several furcations. The confirmation of this affinity would require the finding of the oosphere sister cells of the fructification, which is a rather difficult finding for a slightly encrusted oospore, when only thin sections are available for study. The late Barremian age of this plant, based in orbitolinids and the lithostratigraphic context, makes it one of the oldest putative *Nitella* thalli in the fossil record. This age falls within the same time interval, latest Jurassic–Early Cretaceous, reported for the first occurrences of other early characeans with extant representatives, such as genus *Sphaerochara* (Kimmeridgian, according to Schudack, 1993), *Tolypella* (Barremian, according to Martín-Closas et al., 2018) and *Nitella*, which is Early Cretaceous, according to Feist et al. (1991) for *Nitellites sahnii* Horn af Rantzien, 1957.

Palaeonitella trifurcata occurs within small micrite envelopes forming cortoids in freshwater facies of a coastal lake. The cortoids were formed upon the plant whorls, while still attached to the thallus. Most of the coated grains formed by microbes are the result of microbial growth upon a nucleus already deposited on the sedimentary surface and submitted to a hydrodynamic process allowing the turning of the grain on the sea or lake bottom, e.g., oncoids (Flügel, 2004). However, we document here a type of lacustrine microbially induced micrite coating that was probably formed by the periphyton encrustation of a mucilage upon the whorls of charophyte thalli when the plant was still standing upright on the lake bottom, like it happens today in some species of genus *Nitella*. This would allow the exceptional preservation within the cortoid of the otherwise delicate and poorly calcified *Nitella*-like thalli. After the death of the bearing charophyte these already indurated cortoids accumulated in the lake bottom and were

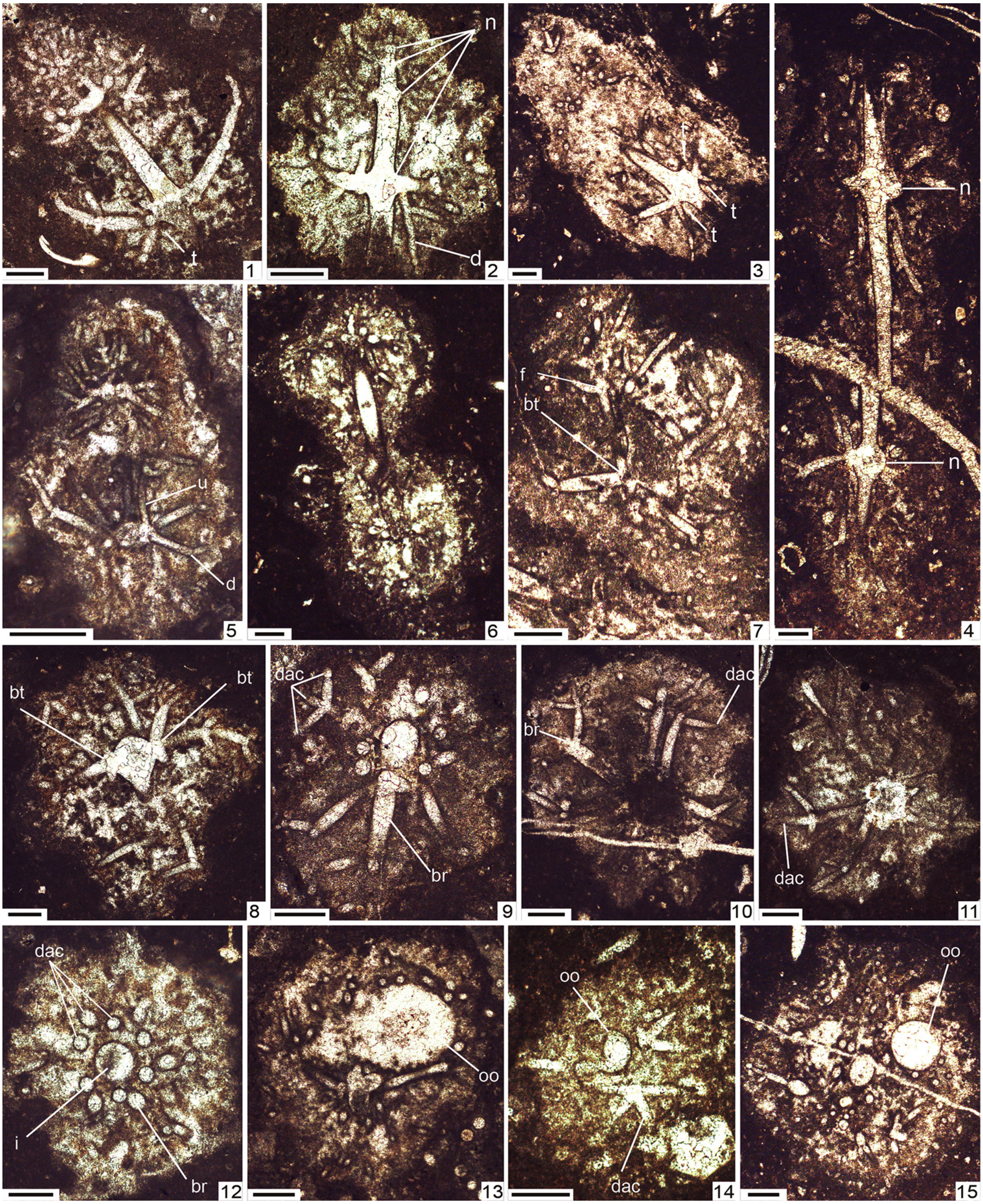

Plate I. *Palaeonitella trifurcata* n. sp. 1: Holotype. Longitudinal section through a conical cortoid showing the apical head of the plant. (t) indicates basal trifurcation of large branches (sample 5_0; thin section no. 86463 MGSCB). 2: Paratype. Longitudinal section through a conical cortoid showing the apical head of the thallus with four nodes (n). Lateral basal branchlet from trifurcation of a large branch growing downwards (d). Note sediment percolation into the internode, indicating it was not covered by the external coating (sample 17; thin section no 86474 MGSCB). 3: Paratype. Oblique section through thallus of conical cortoid showing several nodes of the apical head of the plant. (t) indicates basal trifurcation of large branches with the three basal branchlets separated at angles close to 120°. Note sediment percolation into the internode. (sample 5_3; thin section no. 86466 MGSCB). 4: Longitudinal section through thallus from a two-node cortoid showing globular morphology of nodes (n) (sample 5_2; thin section no. 86465 MGSCB). 5: Paratype. Longitudinal section through two nodes of thallus not centered along the internode, showing upwards (u) and downwards (d) oriented branchlets forming bushy globular whorls (sample 5_1; thin section no. 86464 MGSCB). 6: Oblique section through thallus of a bone-shaped cortoid, showing a well-developed coating (sample 5_1; thin section no. 86464 MGSCB). 7: Section through a branch showing the three branchlets of basal trifurcation (bt) separated at almost 120° and furcation (f) of central branchlet (sample 5_8; thin section no. 86468 MGSCB). 8: Paratype. Almost transversal section, close to the node, showing two opposite branches with basal trifurcation (bt), the right branch showing two furcations. 9: Section through a globular cortoid showing almost transversal section of thallus close to a node. Smaller branchlets with three dactyls (dac) coexist with one large branch (br) (sample 5_10; thin section no. 86469 MGSCB). 10: Paratype. Section through globular cortoid with a transversal section of the thallus close to the node. Acute dactyls (dac) occur on smaller branchlets and in one larger branch (br) (Sample 5_0, thin section no. 86463 MGSCB). 11: Paratype. Transversal section through a node, showing about 6–8 branchlets terminated in three dactils (dac) each (sample 5_11; thin section no. 86470 MGSCB). 12: Paratype. Transversal section through the internode (i) showing transversal sections of dactyls (dac) in groups of three (sample 6; thin section no. 86473 MGSCB). 13: Transversal section through an oospore (oo) surrounded by dactyls in transversal section. Note the crenulated outline of the oospore wall (sample 17; thin section no. 86474 MGSCB). 14: Paratype. Transversal section through an oospore (oo) surrounded by terminal dactyls (dac) showing furcations (sample 5_0; thin section no. 86463 MGSCB). 15: Section through globular cortoid with almost transversal section of the internode (cortoid center), showing section of one isolated oospore (oo), and many smaller transversal sections of branchlets and dactyls (sample 5_0; thin section no. 86463 MGSCB). Scale bars equal 200 μm.

Fig. 5. Reconstruction of the *Palaeonitella trifurcata* plant.

Fig. 7. Thallus of extant *N. tenuissima* (right) showing minute whorls of branchlets embedded in a mucilage. In the older whorls, to the bottom of the picture, a brownish periphyton is growing in the mucilage.

finally buried in lime mud and internally filled in with mud and cement to form a “cortolite”.

7. Conclusions

The preservation within cortoids of articulated, delicate thalli of *Palaeonitella trifurcata* nov. sp., in the Late Barremian–Early Aptian sequences of the Garraf Massif, Catalonia, is an exceptional finding of a putative *Nitella* ancestor. The features of the thallus, especially the globular-shaped whorls, the occurrence of three terminal dactyls on each branchlet and the development of longer branches with several furcations are characters proper of *Nitella*. The remains of this genus are rarely preserved in the fossil record since they are weakly calcified or do not calcify at all, being this the third time that a fossil remain attributed to this genus is recorded worldwide before the Quaternary. However, the affinities of *Palaeonitella trifurcata* with extant *Nitella* should be confirmed by the finding of the multipartite oospore sister cells.

Here we report for the first time an example of cortoid generation upon a living charophyte. The constructive micrite lamina was probably formed by biocalcification of a periphyton crust, generally upon the charophyte whorls, while the charophyte was still alive. Indeed, microbial and algal periphyton grows in extant *Nitella* upon a mucilage that covers parts of the living thallus. After the plant died, the indurated

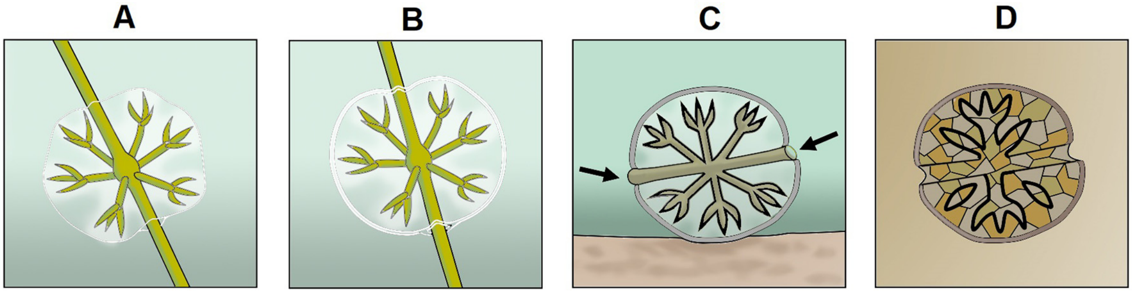

Fig. 6. Cartoon explaining the formation of a *Palaeonitella trifurcata*-bearing cortoids. A. Living plant with whorl coated by a protective mucilage, B. Living plant with thick periphyton coat growing upon mucilage, C. Cortoid (section is shown) deposited on the lake bottom after decay of organic matter and showing encrusted thallus and calcified cortoid wall. Arrows show the open apertures of cortoid, corresponding to the internodal section, D. Lithified cortoid contained in rock (thin section is shown) with the original inner porosity filled in with microsparite crystals.

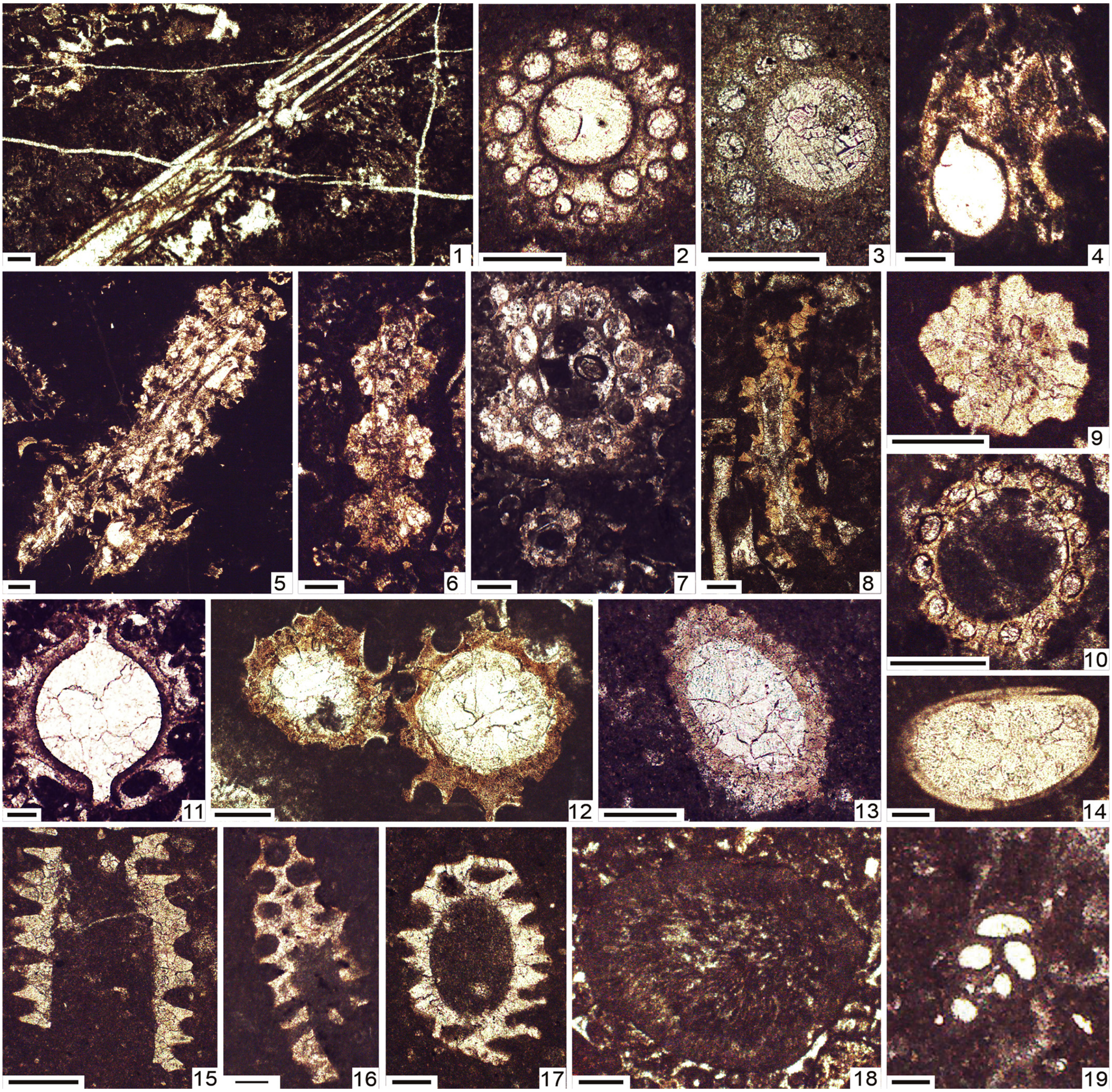

Plate II. Fossil remains associated with *Palaeonitella trifurcata*. 1–2: *Charaxis spicatus*. 1: Longitudinal long section through an internode and node with branchlets (sample 13; thin section no. 86472 MGSCB). 2: Transversal section through a upper part of a internode showing intercalation of pairs of secondary cortical cells separated by larger primary cortical cells (sample 17; thin section no. 86474 MGSCB). 3: Transversal section through a clavatoracean utricle (sample 17; thin section no. 86474 MGSCB). 4: Longitudinal section through a clavatoracean utricle showing apical neck (sample 6; thin section no. 86473 MGSCB). 5–7: *Clavatoraxis* sp. thalli. 5: Longitudinal section through corticated thallus showing spine-cell rosettes (sample 22; thin section no. 86475 MGSCB). 6: Longitudinal section through an ecorticated branchlet showing spine-cell rosettes organized in whorls (sample 13; thin section no. 86472 MGSCB). 7: Transversal section through an internode showing cortication and spine-cell rosettes. A miliolid skeleton can be seen in the internode infilling (sample 13; thin section no. 86472 MGSCB). 8–9 *Favargerella* sp. 8: Longitudinal section through a branchlet (sample 13; thin section no. 86472 MGSCB). 9: Transversal-oblique section through a node (sample 22; thin section no. 86475 MGSCB). 10: Transversal section through a *Charaxis* sp. thallus (sample 13; thin section 86472 MGSCB). 11–12: *Atopochara* sp. utricles. 11: Longitudinal section through a utricle (sample 13; thin section no. 86472 MGSCB). 12: Transversal sections of utricles (sample 22; thin section no. 86475 MGSCB). 13: Oblique section of a clavatoroid utricle (sample 17; thin section no. 86474 MGSCB). 14: Non-cyprídean ostracod (sample 5_0; thin section no. 86463 MGSCB). 15–17: *Salpingoporella* sp. 15: Longitudinal section (sample 5_6; thin section no. 86467 MGSCB). 16–17: Oblique sections (sample 5_13; thin section no. 86471 MGSCB and sample 5_10; thin section no. 86469 MGSCB). 18: Cyanobacterial bush (sample 13; thin section no. 86472 MGSCB). 19: Biseriate foraminifer (sample 5_0; thin section no. 86463 MGSCB). Scale bars equal 200 μm, except 17–19 scale bars, which equal 100 μm.

cortoids accumulated on the lake bottom and became eventually buried to form a “cortolite.”

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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