

# Filling the gap in the evolution of the genus *Echinochara* Peck (Clavatoraceae, Charophyta)

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## ABSTRACT

*Echinochara* is a poorly known charophyte genus of the extinct family Clavatoraceae that thrived in the Middle Jurassic–Early Cretaceous of North America, Europe, and North Africa. It represents the most ancient and plesiomorphic genus of this family. However, the fossil record of *Echinochara* is discontinuous, showing several gaps, one of them especially significant in evolutionary terms between the Kimmeridgian and the early Barremian. The new species *Echinochara pontis* sp. nov., described here from the late Berriasian of the Maestrat Basin (NE Spain), bridges, in part, this gap, shedding light on the evolution of the genus during the earliest Cretaceous. The fructification (utricle) has bilateral symmetry, formed by two superimposed series of bract cells that abaxially cover the gyrogonite. The inner series has three long cells that are born by a short basal cell and reach the oospore apex. The outer series shows a central fan of bract cells, composed of a small basal cell, triangular in shape, that bears three long cells growing upwards, which are in turn flanked by two long bract cells on each side. The central basal cell and these two lateral cells are directly attached to the base of the utricle. The thallus is corticated with cells twisting at an angle of 30°. The utricle of *Echinochara pontis* displays a combination of features present in *Echinochara peckii* (Bathonian?–Kimmeridgian) and *Echinochara lazarii* (Barremian–early Aptian). For instance, the bilateral symmetry of the utricle and the morphology of the inner bract-cell series allow comparison with *E. lazarii*, whilst the morphology of the outer bract-cell series is closer to *E. peckii*. Moreover, the thallus of the new species shows cortical cells with a twisting angle intermediate between that of *Echinochara peckii* (40°–45°) and *Echinochara lazarii* (not twisted). The unique combination of morphological characters in the utricle of *Echinochara pontis* fits well with its intermediate chronostratigraphic position between the two former species. *Echinochara pontis* formed monospecific meadows in brackish settings. A preference for brackish settings is also observed for *Echinochara peckii* and in the older populations of *Echinochara lazarii*, suggesting that this habitat is probably a basal character in the evolution of the genus *Echinochara*.

## 1. Introduction

The Clavatoraceae is a fossil charophyte family that was first recorded in the Middle Jurassic (Trabelsi et al., 2024), thrived worldwide during the Late Jurassic and Early Cretaceous (e.g. Grambast, 1974; Martín-Closas, 2000), declined during the latest Cretaceous (e.g. Grambast, 1974), and survived vegetatively as a relict local group in the earliest Paleocene (Vicente et al., 2019). The fossil record of this family is mainly composed of their calcified fructifications called utricles, on which their taxonomy is based. However, vegetative remains have also

been intensively studied in the recent years. Due to the high diversity and evolutionary rates of the utricles, and their abundance in non-marine facies, they are frequently used as biostratigraphic and palaeoenvironmental tools, especially in Cretaceous deposits (e.g., Grambast, 1968, 1974; Riveline et al., 1996; Vicente et al., 2016; Pérez-Cano et al., 2022a, 2022b).

The evolution of the Clavatoraceae is reasonably well understood (e.g., Grambast, 1974; Schudack, 1993a; Martín-Closas, 1996). However, there are still significant gaps to be clarified, such as the evolution of the genus *Echinochara* Peck, 1957, which is the focus of the present work.

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This fossil genus is especially significant since it is considered to hold the oldest and more plesiomorphic fructification of the Clavatoraceae (Grambast, 1974; Martín-Closas, 1996; Trabelsi et al., 2024). The fossil record of this genus is highly discontinuous, showing several long gaps, the first between the Bathonian and the Kimmeridgian, the second and longest between the Kimmeridgian and the early Barremian, and the third during the late Aptian. These gaps challenge our understanding of its evolution. Three distinct species have been described within the genus *Echinochara*: 1) *Echinochara peckii* (Mädler, 1952) Grambast, 1965 emend. Schudack, 1993a, which ranged from the Bathonian to the Kimmeridgian. This species was first described in the Kimmeridgian from Germany and the United States (Schudack, 1993a; Schudack et al., 1998). *Echinochara spinosa* Peck, 1957 from the Kimmeridgian of the United States is possibly a younger synonym of *E. peckii* according to Schudack (1990). Recently, utricle affines to *E. peckii* have also been reported in the Bathonian (Middle Jurassic) of France (Trabelsi et al., 2024); 2) *Echinochara lazarii* (Martín-Closas, 2000) Mojon ex Pérez-Cano, Bover-Arnal et Martín-Closas 2020, from the early Barremian–early Aptian of Western Europe and North Africa (Martín-Closas, 2000; Trabelsi et al., 2016; Pérez-Cano et al., 2020, 2023); and 3) *Echinochara triplicata* Trabelsi et Martín-Closas 2012 from the early–middle Albian of Tunisia (Trabelsi and Martín-Closas, 2012).

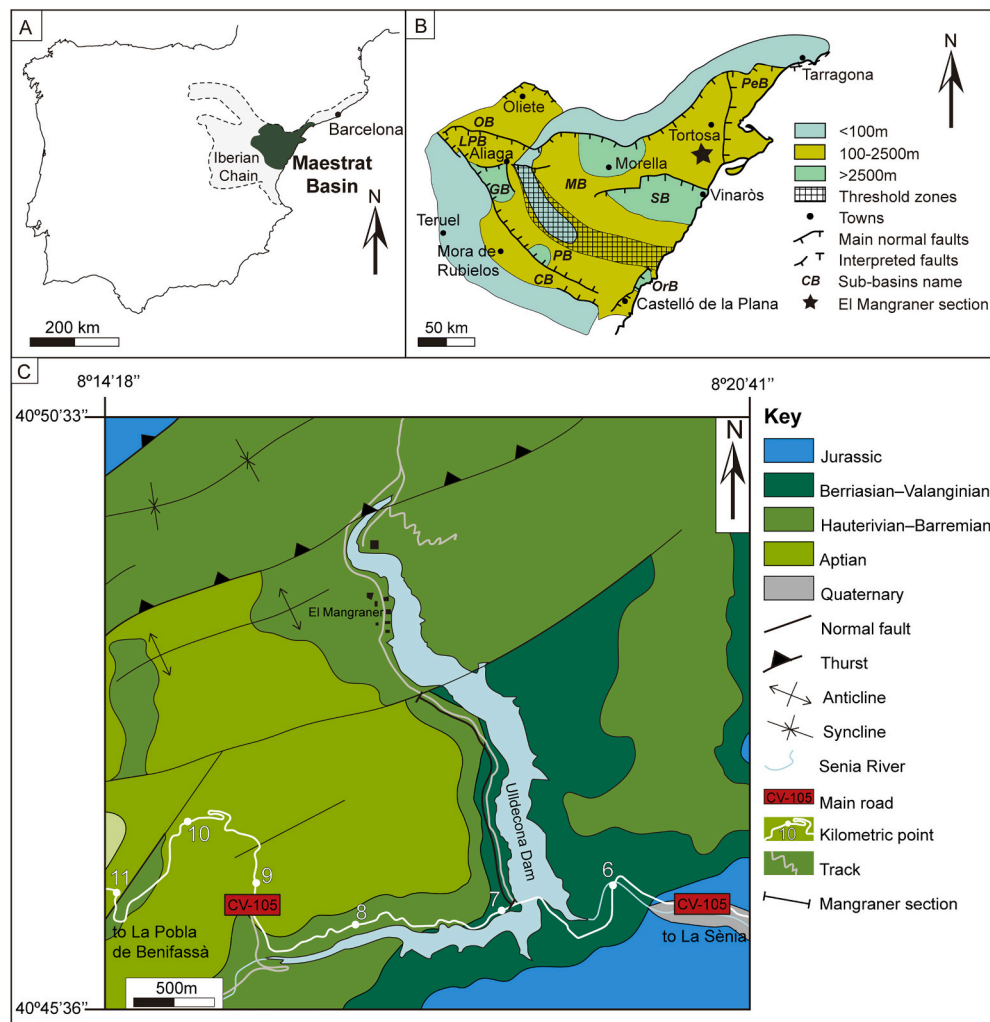
The present work describes a new species of *Echinochara* in the late

Berriasian from the Maestrat Basin, Eastern Iberian Chain (NE Spain). The results allow us to bridge the gap in the fossil record of the genus between the Kimmeridgian and the Barremian, shedding light on its evolutionary patterns and its palaeoecology.

## 2. Geological setting

The Maestrat Basin is located in the Eastern Iberian Chain (Fig. 1A) and was formed during the Late Jurassic–Early Cretaceous as a result of successive rift and post-rift stages (Salas et al. in Martín-Chivelet et al., 2019), comprising 1) Kimmeridgian–late Berriasian rifting; 2) late Berriasian–late Hauterivian post-rift, and 3) Barremian–early Albian rifting. The activity of listric faults caused local subsidence furrows and uplifts that led to the division of the Maestrat Basin into several sub-basins (Salas et al., in Martín-Chivelet et al., 2019). Tectonic inversion of these faults during the Alpine Orogeny (late Eocene–early Miocene) caused the active margins of the Iberian Chain to thrust over the Ebro Basin (Nebot and Guimerà, 2018).

The fossils studied here were found in the Els Mangraners section, which is located in the eastern part of the Morella Sub-basin (Fig. 1B), along the western shore of the Uldecona dam (Fig. 1C). This section, which is several hundred metres thick, has been extensively studied due to the stratigraphic continuity of the Lower Cretaceous non-marine



**Fig. 1.** A. Location of the Maestrat Basin in the Iberian Peninsula. B. Sub-basins of the Maestrat Basin (modified from Salas et al. in Martín-Chivelet et al., 2019), with indication of the thickness of Upper Jurassic to Lower Cretaceous deposits. CB: Cedramán Sub-Basin; GB: Galve Sub-Basin; LB: Las Parras Sub-Basin; MB: Morella Sub-Basin; OB: Oliete Sub-Basin; OrB: Orpesa Sub-Basin; PB: Penyagolosa Sub-Basin; PeB: El Perelló Sub-Basin; SB: Salzedella Sub-Basin. C. Geologic map around the Uldecona dam and location of the stratigraphic section (Modified from García de Domingo and López-Olmedo, 1982).

deposits (e.g., Combes et al., 1966; Grambast, 1974; Martín-Closas and Salas, 1994; Salas and Martín-Closas, 1995). The base of the section is the Tithonian–early Berriasian dolomite and limestone of the El Bovalar Formation. This unit passes upwards and laterally to the finely laminated tidal limestones of the La Pleta Formation, which reached the middle Berriasian (e.g., Martín-Closas and Salas, 1994; Salas et al., 2001; Fig. 2). The Els Mangraners Formation, which is late Berriasian–lowermost Valanginian in age, overlies the La Pleta Formation, and is

composed of charophyte-rich marls and limestones (Fig. 2; Martín-Closas and Salas, 1994). Its age was well constrained by Martín-Closas and Salas (1994) based on the occurrence of two charophyte assemblages. The basal layer, where the charophytes studied here were found, contains *Atopochara trivolis micrandra* (Grambast, 1967), *Globator maillardii nurrensis* (Pecorini 1969) and *Clavator harrisii dongjingsensis* (Hu et Zeng, 1981), belonging to the *Globator maillardii nurrensis* charophyte biozone, which is late Berriasian in age (Riveline et al., 1996), while the

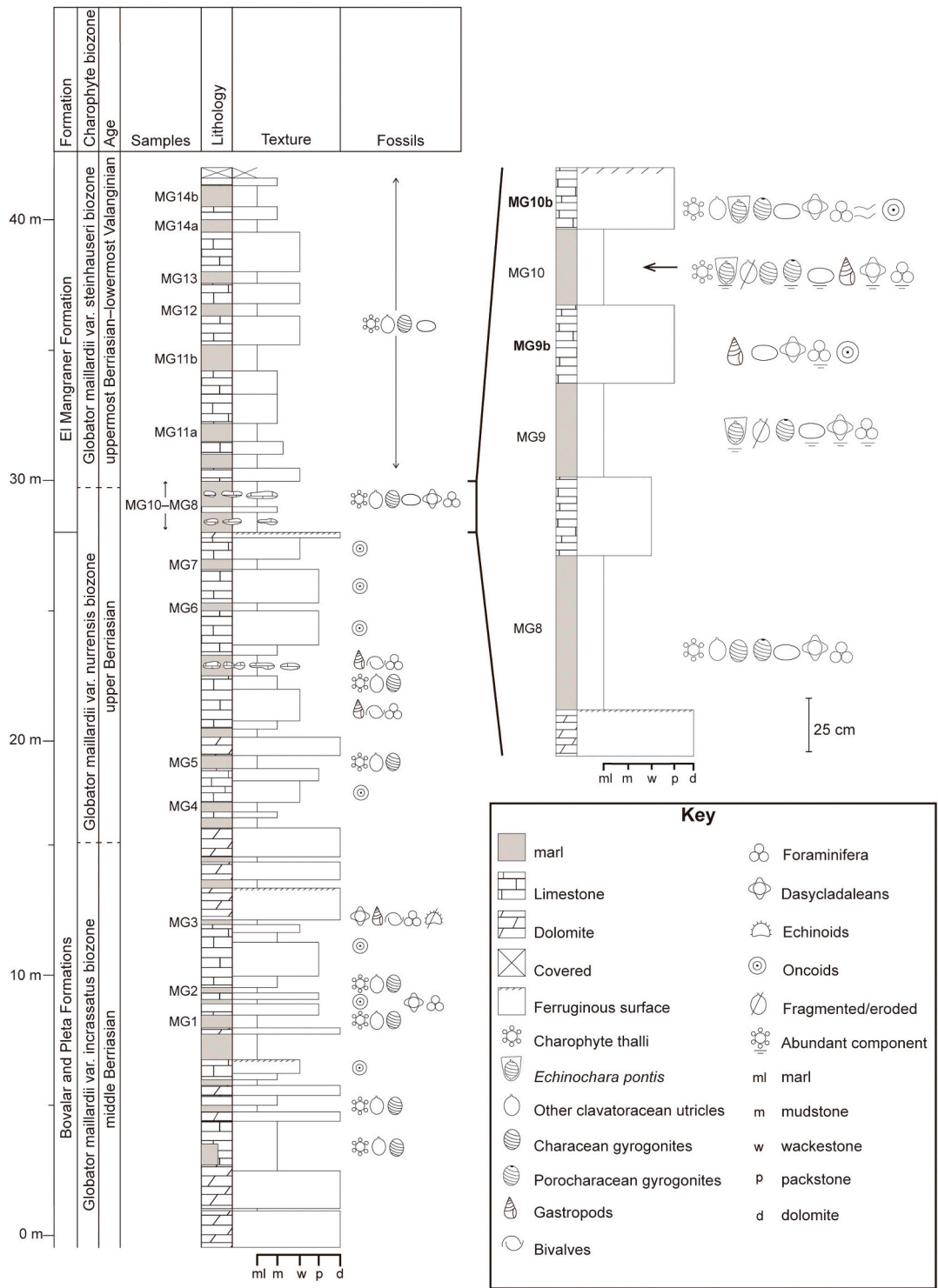


Fig. 2. Stratigraphic section. Base of the Els Mangraners section (modified from Martín-Closas and Salas, 1994), showing the detail of the interval in which *Echinochara pontis* sp. nov. appears. The arrow indicates the type layer of *Echinochara pontis* nov. sp. (MG10). The age is according to the charophyte biostratigraphy of Riveline et al., 1996 and provided by Salas and Martín-Closas (1995).

upper part of the formation contains *Atopochara trivolis micrandra* (Grambast, 1967), *Atopochara trivolis ancora* (Grambast, 1967), *Globator maillardii steinhauseri* (Détraz et Mojon, 1989), *Clavator harrisii donjiangensis*, *Clavator harrisii harrisii* (Peck 1941), and *Ascidella stellata* (Martín-Closas et Grambast-Fessard, 1986), belonging to the *Globator maillardii steinhauseri* biozone, which is early Valanginian and Hauterivian in age (Riveline et al., 1996). The Els Mangraners Formation laterally and vertically changes to the shallow marine limestones of the Polacos Formation (Martín-Closas and Salas, 1998; Salas et al., 2001), which is early Valanginian in age as constrained by the orbitolinid foraminifer *Valdanchella milianii* Schroeder, 1968 (Martín-Closas and Salas, 1988). Charophyte-rich limestones of the Herbers Formation (Valanginian–Hauterivian), and the Cantaperdius Formation (uppermost Hauterivian–lower Barremian), and shallow marine limestones and marls of the Artoles Formation build up the upper part of the Els Mangraners section (Martín-Closas and Salas, 1994).

### 3. Materials and methods

The base of the Els Mangraners section is located at 40°40′15.39″ N and 0°13′51.36″ E and the top at 40°40′54.30″ N and 0°13′32.37″ E (Fig. 1C). One limestone and two marl beds were studied from the base of the Els Mangraners Formation (Fig. 2). Around 3 kg of marl were collected and later disaggregated in a solution of water, oxygen peroxide (H<sub>2</sub>O<sub>2</sub>) and sodium carbonate (Na<sub>2</sub>CO<sub>3</sub>). This marl was then sieved, using three meshes whose openings were 1, 0.5 and 0.2 mm, respectively. Microfossils, including charophyte fructifications, thalli, ostracods, benthic foraminifera, and dasycladaleans, were hand-picked using small brushes under a binocular microscope. Some specimens were treated with a sodium hexametaphosphate solution in order to eliminate the micrite around them and were later photographed with a Quanta 250 scanning electron microscope (SEM) housed at the Scientific and Technological Centres of the University of Barcelona (CCiTUB). Two limestone samples were obtained from the base and the top of the limestone bed MG10B. Two types of thin sections were prepared for each, one parallel and the second perpendicular to the stratification. This double sectioning of the rock sample has is useful when studying charophyte fossils, especially for elongated components such as thalli, but also for other organs, such as utricles (e.g., Pérez-Cano et al., 2020; Martín-Closas et al., 2021). Figured specimens and thin sections of figured specimens were deposited at the Museu de Geologia del Seminari Conciliar de Barcelona (MGSCB) with the numbers MGSCB 89137–89149 and 89150–89154, respectively. The hand-picked material is being stored in the Department of Earth and Ocean Dynamics at the University of Barcelona.

A combined sedimentological and taphonomic analysis was performed to understand the palaeoecology of the charophyte association. The sedimentological study provided information about the environment in which the fossils were deposited. The taphonomic study allowed us to discriminate between autochthonous and allochthonous remains in the depositional setting. This included evaluation of the erosion and fragmentation of the microfossil remains, as well as their completeness, disarticulation, or anatomical connection. This methodology is useful for inferring the palaeoecology of fossil organisms (e.g., Martín, 1999).

### 4. Systematic palaeontology

*Division:* Charophyta Migula, 1897

*Class:* Charophyceae Smith, 1938

*Order:* CHARALES Lindley, 1836

*Family:* CLAVATORACEAE Pia, 1927

*Subfamily:* ATOPOCHAROIDAE Grambast, 1968 emend. Martín-Closas ex Schudack 1993a

*Genus:* *Echinochara* (Peck, 1957) emend. Pérez-Cano, Bover-Arnal et Martín-Closas 2020.

*Echinochara pontis* sp. nov. Pérez-Cano et Martín-Closas.

Figs. 3–5.

*Diagnosis:* Bilaterally symmetrical atopocharoid fructification. Oospore atopocharoid, non-calcified. Utricle with two superimposed series of bract cells, placed only on the abaxial side of the oospore. Inner series with three cells forked from the utricle basal node. Outer series with a central fan formed by a small triangular cell bearing three long bract cells, framed on each side by two long twin bract cells.

*Derivation of the name:* From the Latin “pons, pontis” (bridge). The name refers to the combination of characters shown by the utricle and the thalli, which bridges the plesiomorphic species *E. peckii* and the more derived species *E. lazarii*.

*Material:* 700 specimens, including utricles, complete whorls, and portions of thalli and branchlets.

*Holotype:* Fig. 3F (MGSCB 89137).

*Paratypes:* Fig. 3A–E, G (MGSCB: 89138, 89139, 89140, 89141, 89142, 89143); Fig. 4A–F (MGSCB: 89144, 89145, 89146, 89147, 89148, 89149).

*Type locality:* El Mangraner section, along the road from the Ulldecona dam to the El Mangraner neighbourhood. Municipality of La Pobla de Benifassà (Castelló Province, Comunitat Valenciana, Spain).

*Type layer:* Marl bed located 29 m from the base of the Els Mangraners section (Spain). Sample MG10 of the stratigraphic log by Martín-Closas and Salas (1994) (Fig. 2).

*Description:* The fructification is composed of an uncalcified oospore and the utricle. The oospore morphology is known from (1) the occurrence of sparitic internal casts scattered in the sediment or attached to the utricle (Fig. 3A), and (2) by partially to complete impressions of the oospore upon the inner utricle wall (Figs. 3B–E; 5B). The morphology of the oospore is ellipsoidal perprolate with apical and basal necks. It is c. 596 µm high and 339 µm wide with an isopolarity index between 155 and 200. At least 10–12 turns appear in the lateral view (Fig. 3C–E).

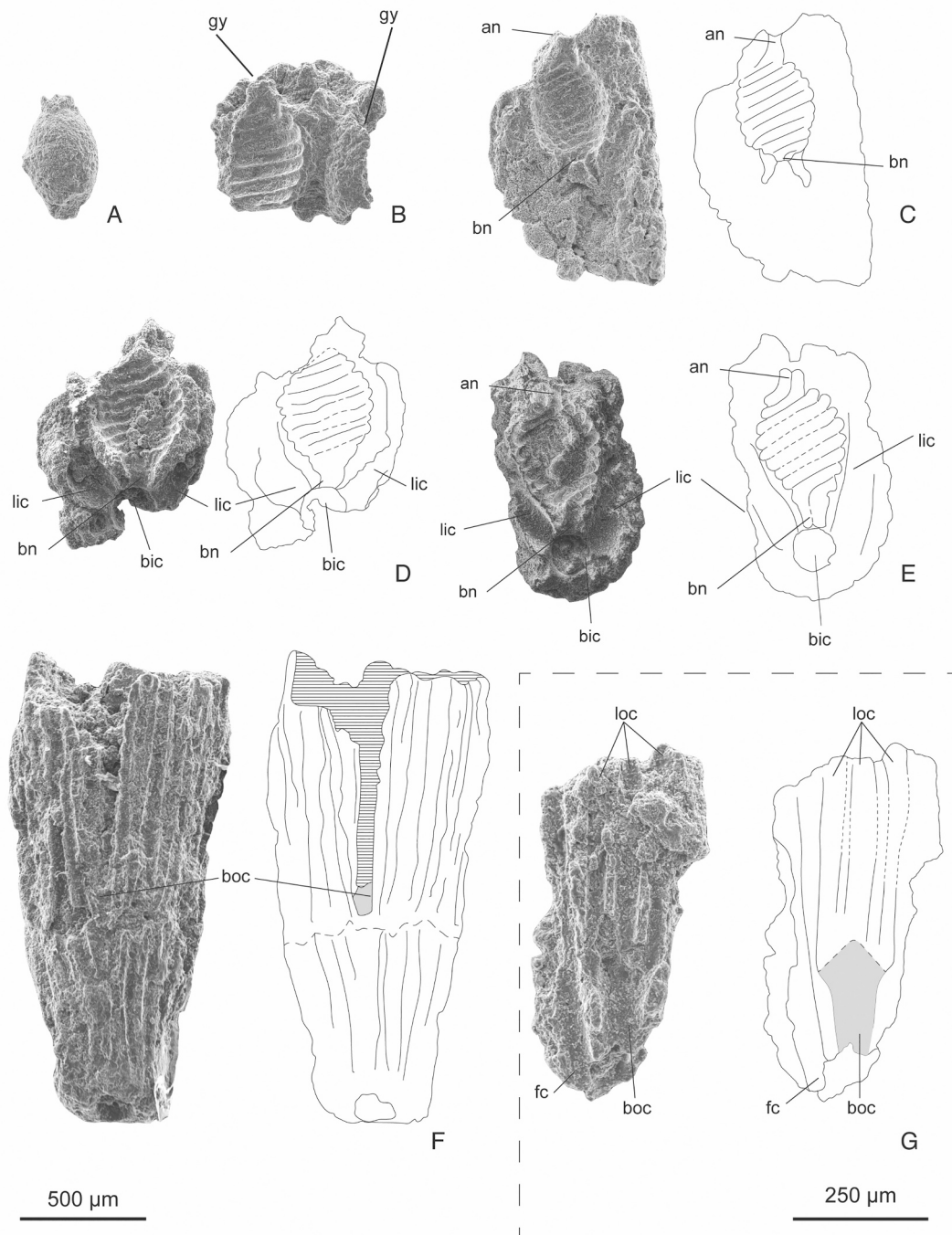
The utricle includes two superimposed series of bract cells, and exclusively occurs in the abaxial part of the oospore, opposite the phylloid. The inner series is composed by a fork-like unit composed of a very short basal cell holding three long slightly curved cells that grow upwards to reach the oospore apex (Figs. 3D–E, 6). These bract cells are preserved as empty tubes, sometimes filled with sediment. The outer series is formed by a single unit of bract cells that completely cover the inner series (Fig. 3F). The bract cells of the outer series are fused to each other, resulting in a solid plate (Fig. 3F). They form one central fan of bract cells framed by two twin cells on each side. The lateral twin cells and the base of the central fan are directly attached to the base of the fructification (Fig. 3F–G, 6). The central fan of cells contains a small, elongated, broadly triangular basal cell, which is trifurcated apically into three long and thin cells (Fig. 3F–G, 6). The tips of the long bract cells from the outer series may be intercalated with the bract cells from the inner series in the upper part of the utricle, as observed in thin sections of complete fertile whorls (Fig. 5C).

Fertile whorls are constituted by six closely packed utricles (Fig. 3F, 6). The preserved remains of these fertile whorls (2–3 utricles found attached, Fig. 3B) show that the oospores were placed very close to one another. On the other hand, specimens showing two superimposed fertile whorls show that the long bract cells of the outer series of the lower whorl overlap the base of the utricles from the next whorl, making it difficult to discriminate between the successive fertile whorls (Figs. 3F, 5A).

Vegetative remains ascribed to *Echinochara pontis* correspond to corticate thalli and branchlets. Thalli remains are generally made of internode portions with lengths varying between 0.5 and 2 mm and separated by nodes (Fig. 4A–C). Nodes are formed by six large globular cells (Fig. 4E–F). Three branchlets extend upwards from each node in groups of three cells (Fig. 4D–F). They are clearly distinguished from cortical cells because they are totally straight (Fig. 4E–F).

The internodes obtained from the laevigates display enough characters to determine them as belonging to the genus *Echinochara*, particularly the high twisting angle (30–35°) of the cortical cells and the



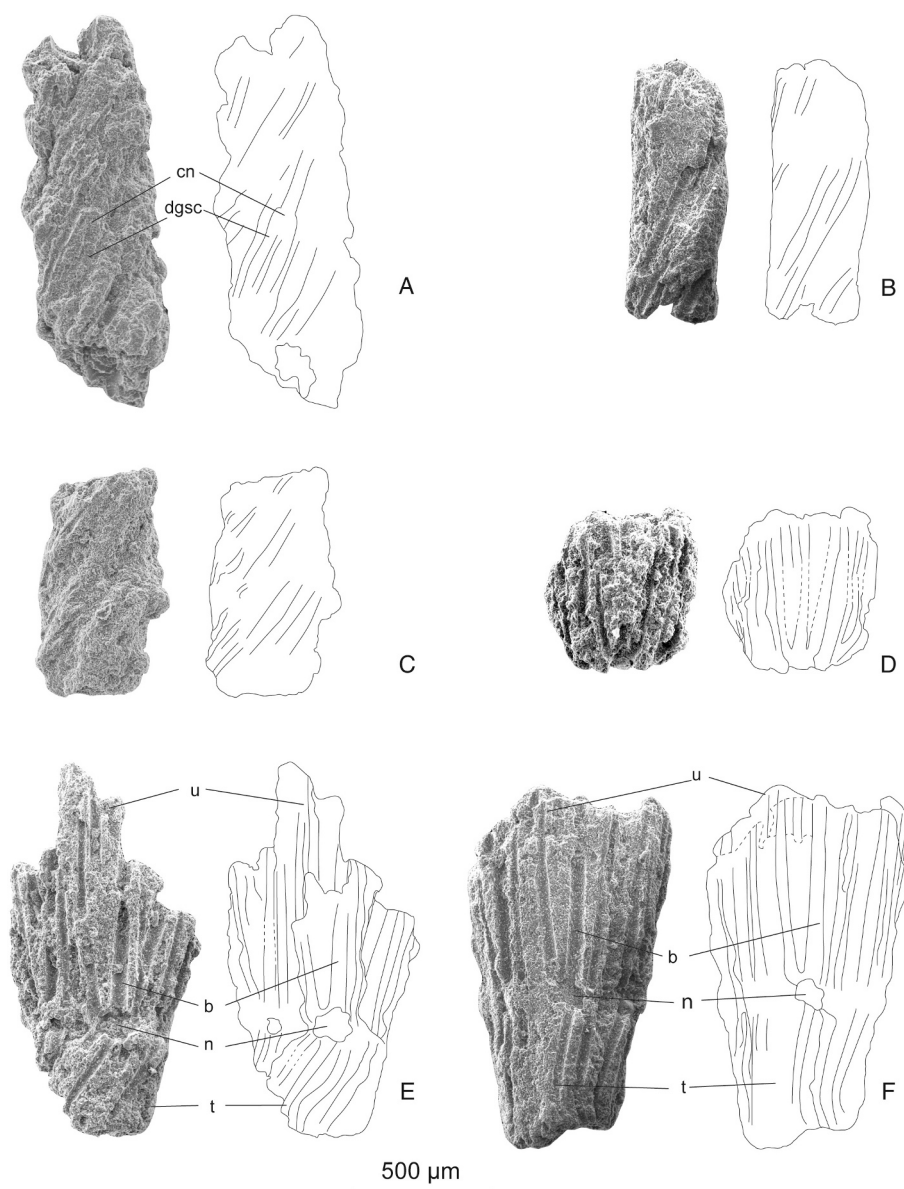


**Fig. 3.** SEM pictures and drawings of the oospore and utricle of *Echinochara pontis* sp. nov. (sample MG10). A. Sparitic mould of a gyrogonite (MGSCB 89138). B. Partial view of the inner part of a fertile whorl with two gyrogonites extremely close to each other (MGSCB 89139). C. Outer cast of a gyrogonite showing the spiral cells, and the apical (ap) and basal (bn) necks, typical features of the clavatoroid gyrogonites (MGSCB 89140). D–E. Cast of the gyrogonite (gy) showing the spiral cells and the basal (bn) and apical (an) necks and the cells of the inner bract-cell series, including the basal cell (bic) and two out of three cells derived from the basal one (lic) (MBSCB 89141 and 89137). F. Complete fertile whorl showing the outer bract-cell series that shows the basal cell of the central trifurcation (bo) (MGSCB 89142). G. Detail of the central trifurcation of the outer bract-cell series, showing the central fan with the basal cell (boc) and three long cells growing upwards (loc) and one cell flanking the central fan (fc) (MGSCB 89143). A drawing of the cells on the SEM pictures can be seen in Supplementary Material 1.

complex cortication structure. Internodes include a large internodal cell that is covered by an intricate structure of cortical cells (Fig. 4A–C). Three primary cortical cells emerge from each nodal cell: a longer and wider one that is flanked by two thinner cells. The width of the central cortical cell may suddenly increase, forming a cortical node (Figs. 4A, 5E). Two pairs of secondary cortical cells emerge from the cortical node. The first pair grows distally, flanking the larger primary cells (Fig. 5E) and resulting, in the distal part of the internode, in a triplostichous

isostichous cortication, with 18 cells covering the internodal cell (Fig. 5H). The second pair of secondary cortical cells grow apically and are considerably thinner than the primary cell (Fig. 5D, G), forming a characteristic triplostichous anisostichous cortication.

**Remarks:** The utricle of *Echinochara pontis* sp. nov. displays a combination of characters from both *Echinochara peckii* (Bathonian?–Kimmeridgian) and *Echinochara lazarii* (early Barremian–early Aptian). However, it also has unique morphological features that enable its



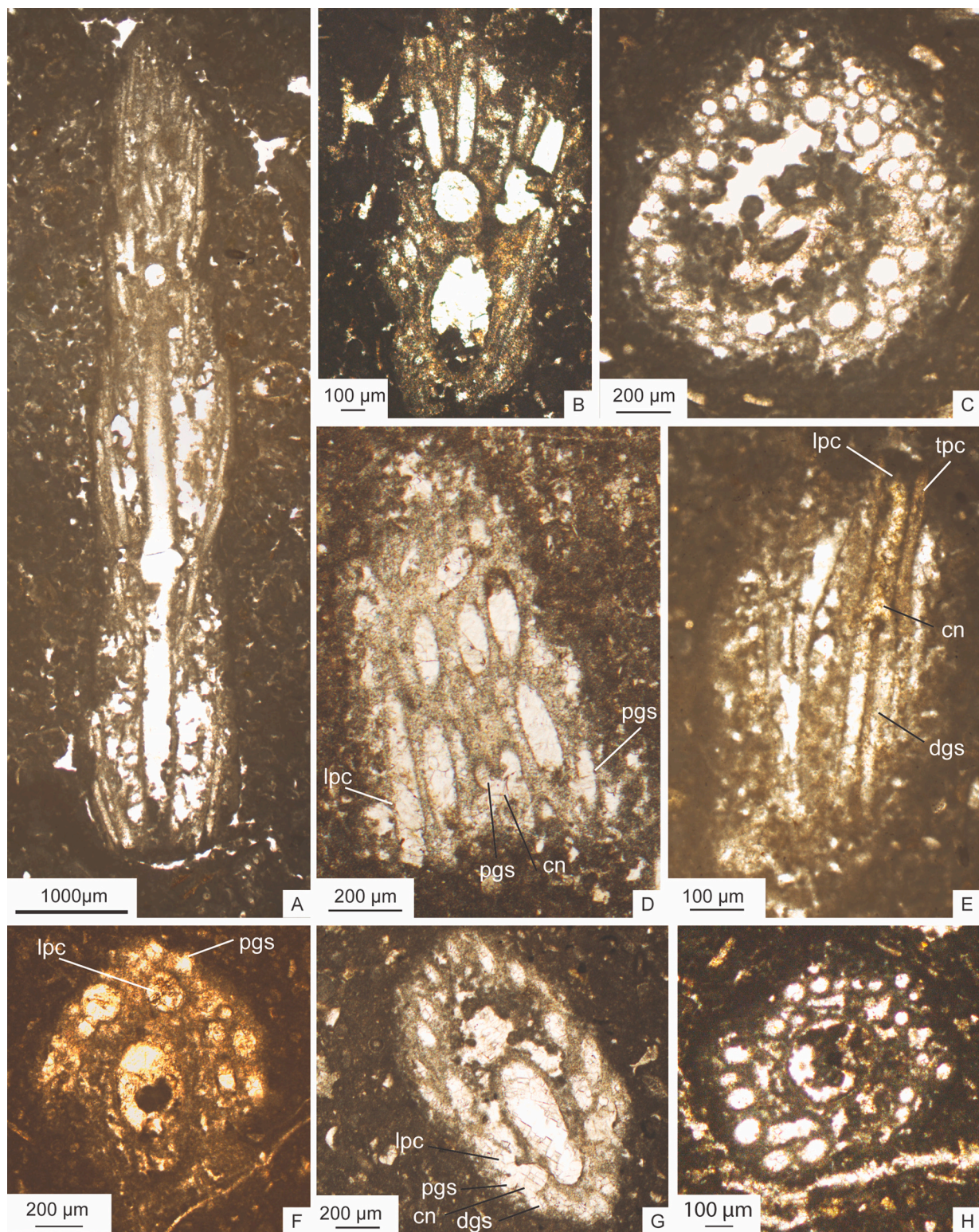
**Fig. 4.** SEM pictures and drawings of thalli and branchlets of *Echinochara pontis* sp. nov. (sample MG10). A–C. Thalli portions showing the high degree of twisting of cortical cells around the internodal cell (i), and the key features of the double triplostichous cortication such as the cortical node (cn), the cells growing downwards (dgsc) and the cells growing upwards (pgsc) (MGSCB 89144, 89145, 89146). D. Isolated branchlets borne in groups of three (MGSCB 89147). E–F. Thalli (t) anatomically attached to branchlets (b) and utricles (u), the latter covered by the branchlets. Note that branchlets and cortical cells are borne from the node (n) and are clearly distinguished by the angle of twisting (MGSCB 89148 and 89149). The difference in twisting between the cells of the utricle and branchlets is clear. A drawing of the cells on the SEM pictures can be seen in Supplementary Material 2.

distinction from every other species of *Echinochara* described to date. In common with the oldest species, *Echinochara peckii*, the utricle of the new species has trifurcations in the outer bract-cell series. However, *Echinochara pontis* sp. nov. only has one trifurcation, while *E. peckii* has two trifurcations (Mädler, 1952; Schudack, 1993a). On the other hand, the bilateral symmetry of the utricle in the newly described species *Echinochara pontis* sp. nov. is like the symmetry in the Barremian–early Aptian *Echinochara lazarii*. Moreover, these two species also have in common the morphology of the inner bract-cell series. The only difference is the width of the cells, which is higher in *Echinochara pontis* sp. nov.

The morphology and structure of the thallus of *Echinochara pontis* sp. nov. suggest that the cortication was double-triplostichous. This structure was first described by Pérez-Cano et al. (2020) for *Charaxis spicatus* (Martín-Closas et Diéguez 1998) emend. Pérez-Cano, Bover-Arnal et

Martín-Closas, which is the thallus found attached to *Echinochara lazarii*. The cortication of *Echinochara peckii* was not described originally. However, thin sections from the Kimmeridgian of Switzerland with thalli ascribed to *Echinochara peckii* by Mojon and Mouchet (1992, pl. II figs. D–E and pl. III figs. A–B) present strong similarities with sections of *Charaxis spicatus*, particularly the double triplostichous cortication. It is thus possible that this character is shared by the thalli of all *Echinochara* species. The main difference between the thalli of the different species of *Echinochara* is their twisting angle. Thus, in *Echinochara peckii* and *Echinochara spinosa*, the angle between the cells and the internodal axis is high, in the range of 40–45° (measured from specimens illustrated respectively by Mädler, 1952, pl. A fig. 4 and by Peck, 1957, pl. 1 fig. 9). This angle decreases over time, being of only 30°–35° for *Echinochara pontis* sp. nov., while in *Echinochara lazarii* the cells are not twisted, i.e., parallel to the internodal axis (Pérez-Cano et al., 2020).





**Fig. 5.** Thin sections of *Echinochara pontis* sp. nov. (sample MG10B). A. Longitudinal section through a tip of a thallus showing three anatomically connected whorls (thin section MGSCB 89150). B. Longitudinal-oblique section through two superimposed fertile whorls showing utricles and oospores (thin section MGSCB 89151). C. Transverse section through the apical part of a fertile whorl. Note that the utricle is only in the outer part of the whorl; the inner space, filled with sediment and cement, would host the oospores (not preserved). Bract cells of the inner series of the utricle are larger cells, whilst thinner cells would correspond to sections of bract-cells from the outer series (thin section MGSCB 89152). D. Tangential section through a proximal part of the internode, showing primary cortical cells (lpc) and secondary cortical cells growing upwards (pgs) (thin section MGSCB 89153). E. Tangential section of a distal part of the internode showing thin and large primary cortical cells (tpc and lpc respectively), the latter subdividing in the distal direction (dpc) (thin section MGSCB 89150). F. Oblique section of the proximal part of the internode (thin section MGSCB 89152) indicating the long primary cell (lpc) that is covered by two small cells that are growing upwards (pgs). G. Transverse section of the middle part of the internode, showing the cortical node (cn) part of the internode (thin section MGSCB 89154). H. Transverse section through a distal section of an internode, characterized by 18 cortical cells with a similar diameter (thin section MGSCB 89151).



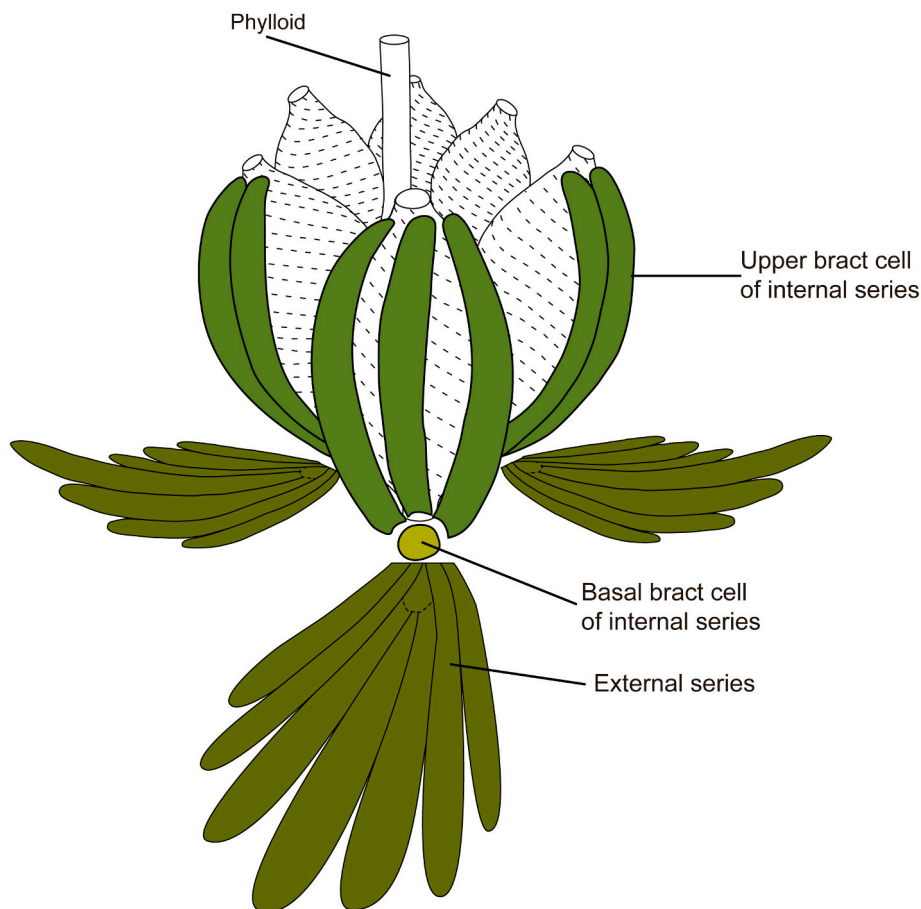


Fig. 6. Reconstruction of the fertile whorl of *Echinochara pontis* sp. nov. The outer bract-cell series opened to show the inner utricule series.

**Age:** The age of the new species in its type locality is late Berriasian, as determined by Martín-Closas and Salas (1994). Samples MG9 and MG10 occur in the upper part of the Els Mangraners Formation and its age is constrained between the upper part of the early–middle late Berriasian *Globator maillardii nurrensis* charophyte biozone of Riveline et al. (1996) identified in sample MG8, and the base of the latest Berriasian–Hauterivian *Globator maillardii steinhauseri* biozone of Riveline et al. (1996) identified in sample MG11a. The occurrence of the benthic foraminifer *Valdanchella miliani*, which is early Valanginian in age (Azéma et al., 1976), in a bed of the Polacos Formation directly overlying the studied deposits also helps constrain the age of the new species to the latest Berriasian.

## 5. Discussion

### 5.1. Evolution of genus *Echinochara* Peck 1957 between the Kimmeridgian and early Barremian

The utricule of *Echinochara pontis* sp. nov. displays a combination of morphological characters from *Echinochara peckii* and *Echinochara lazarii*, which fits well with its intermediate chronostratigraphic position between these two taxa (Fig. 7). The succession of these three species sheds light on the evolution of the utricule in the genus *Echinochara* during the Late Jurassic and Early Cretaceous.

The major trend in the evolution of the genus *Echinochara* is the simplification of the utricule structure. Thus, the outer and inner bract-cell series show a clear evolutionary decrease in the number of trifurcations, with two trifurcations being observed in the outer bract-cell series of *E. peckii*, one in *E. pontis* sp. nov. and none in *E. lazarii* and *E. triplicata* (Fig. 7). The inner bract-cell series of *E. peckii* displays a long

basal cell in the trifurcation, while very short basal cells occur in the inner bract-cell series of *E. pontis* sp. nov. and *E. lazarii* (Fig. 7). The inner series of *E. triplicata* is not yet known but given the trend described it may be similar to the inner bract-cell series of *E. pontis* sp. nov. and *E. lazarii*.

The evolutionary trends observed in the utricles of the genus *Echinochara* are not unique, since similar trends were observed in the other two atopocharoid genera, i.e. *Globator* and *Atopochara* (Grambast, 1974; Martín-Closas, 1996). These two genera are very common in the fossil record, and their evolution is well understood, forming gradualistic lineages, interpreted as anagenetic series by Schudack (1993a) and Martín-Closas (1996). In particular, as already noted by Martín-Closas (1996), the outer bract-cell series of *Echinochara* resembles that of *Globator maillardii*. Now we can confirm that they share a similar evolutionary trend towards a decrease in the size of the basal trifurcations until the complete reduction in the Barremian (Grambast, 1974). Martín-Closas (1996) also noticed the similarity of the inner bract-cell series of *Echinochara* with the utricule of *Atopochara trivolvis*. Now it can be shown that both taxa shared the same evolutionary trend towards loss of the basal cell of the trifurcations, called the “primordial cell” or “P-cell” by Grambast (1968). In the genus *Echinochara* this cell became smaller between the Kimmeridgian and the Berriasian, while in the genus *Atopochara* a parallel reduction occurred short before the Barremian. The length of the apical cells of the utricule gradually increased in all members of the Atopocharoidae.

In addition, the symmetry of the utricule in the genus *Echinochara* evolved from triradiated to bilaterally symmetrical. The ancestral species *Echinochara peckii* had a triradially symmetrical utricule, with three inner bract-cell series and presumably the same number of outer bract-cell units according to Schudack (1993a). However, the radial symmetry



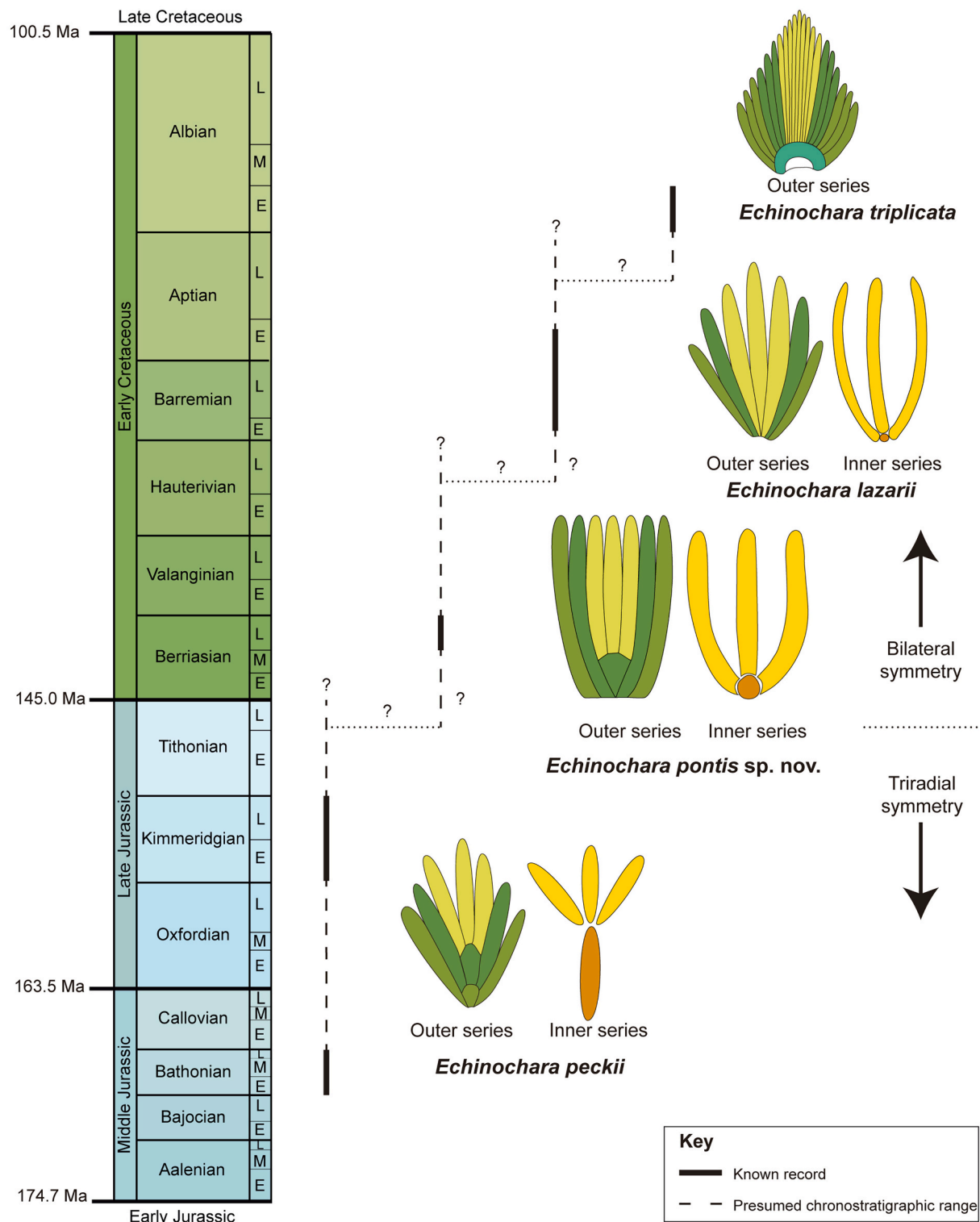


Fig. 7. Phylogeny of *Echinochara*, showing the morphological changes that occurred among *Echinochara peckii*, *Echinochara pontis* sp. nov., *Echinochara lazarii*, and *Echinochara triplicata*. The inner series of *Echinochara triplicata* is unknown.

of the outer series is less convincing when looking at the illustrations he provided. Triradial symmetry is a basal character for Atopocharoidae, as it is shared by all taxa of the subfamily (Grambast, 1968; Martín-Closas, 1996). *Echinochara pontis* demonstrates that the utricle was already completely bilateral in symmetry in the late Berriasian, the same symmetry continuing in *E. lazarii* in the Barremian (Pérez-Cano et al., 2020).

The evolutionary lineage formed by the succession of *Echinochara*

*peckii*, *E. pontis*, *E. lazarii* also gives an insight into the evolution of the thallus. The cortication structure seems to have remained unchanged during its evolution, being permanently double triplostichous. However, the twisting angle of the cortication decreased over time, being highly twisted in *Echinochara peckii*, intermediate in *E. pontis*, and without any twisting in the thallus *Charaxis spicatus* belonging to *Echinochara lazarii*. As a consequence, the high degree of twisting of the cortical cells must

be considered a basal character for the genus *Echinochara*.

## 5.2. Taphonomy and palaeoecology of *Echinochara pontis* sp. nov

*Echinochara pontis* sp. nov. is found in marls where it is the dominant charophyte taxon. Complete fertile whorls of this species are abundant with usually two fertile whorls anatomically connected (Fig. 3F). Internode portions are frequent and usually long (>1000 µm) and sometimes show the branchlets still attached (Fig. 4E–F). These taphonomic observations suggest that *Echinochara pontis* is autochthonous in the assemblage from the type locality. Other charophyte remains associated with *E. pontis* belong to clavatoraceans and porocharaceans. Clavatoracean utricles include *Globator maillardii* var. *steinhauseri*, *Atopochara trivolvii* var. *micrandra*, and *Nodosoclavator bradleyi*, and gyrogonites of aff. *Mesochara harrisi*, while thalli are represented by small portions of *Clavatoraxis* sp. and *Favargerella* cf. *aquavivae*. All these clavatoracean and characean remains are rare and show superficial erosion, suggesting transport, i.e. they are parautochthonous to allochthonous in the depositional setting. Porocharacean gyrogonites associated with *E. pontis* belong to *Porochara* gr. *kimmeridgensis* subgr. *westerbeckerensis* (Mädler, 1952) Mädler 1955, as defined by Martín-Closas (2000). They are frequent and generally well preserved, with only some of them showing superficial erosion and fragmentation. Ostracods are also abundant fossils associated with *E. pontis*. Cypridean ostracods are rare. In contrast, non-cypridean ostracods are abundant and well-preserved with both valves in anatomical connection, indicating autochthony. Marine-affinity fossils found in the same sample are dasycladalean thalli and benthic foraminifera, such as lithuolids. In particular, dasycladaleans are diverse with at least four different genera, including *Salpingoporella* Pia, *Clypeina* Michelin (*Clypeina* sp. and *Clypeina parasolkani* Farinacci et Radoičić), *Holosporella* Pia, and *Bakalovaella* Bucur or *Orternstella* Granier, Masse et Berthou (B. Granier personal communication, 2024).

The occurrence of rare fossils of freshwater affinity, some of them showing evidence of transport, such as clavatoracean utricles and cypridean ostracod carapaces, together with more abundant and well-preserved fossils from brackish to marine fossils (porocharacean gyrogonites, non-cypridean ostracods, dasycladales, benthic foraminifera) suggests the interaction of marine and non-marine conditions in the depositional setting, probably resulting in dominant brackish to euryhaline environments. *Echinochara pontis* sp. nov. probably thrived in such environments, where it may have formed monospecific or paucispecific meadows.

The ability of the genus *Echinochara* to thrive in brackish settings has been extensively reported. Kimmeridgian *Echinochara peckii* and *Echinochara spinosa* were interpreted as growing in brackish settings (e.g., Schudack, 1993a, 1993b, 1995, 1996; Schudack et al., 1998) while *Echinochara lazarii* was limited to classically influenced brackish settings during the early Barremian. During the late early Barremian, this latter species was also able to colonize also freshwater environments, widening its palaeoecological distribution (Pérez-Cano et al., 2022b). In sum, *Echinochara pontis* sp. nov. appears to display similar ecological requirements to the Kimmeridgian *Echinochara peckii* and the early Barremian *Echinochara lazarii*, highlighting that the genus is a reliable indicator of brackish environments at least until the late Barremian.

## 6. Conclusions

*Echinochara pontis* sp. nov. is described in the late Berriasian from the Maestrat Basin, bridging a gap of ca. 23 My in the evolution of the genus *Echinochara*. This new species shows a unique combination of characters in the utricle, such as the occurrence of trifurcations in the outer bract-cell series, which are considered plesiomorphic for the genus, and derived characters, such as the bilateral symmetry of both utricle units. This is consistent with its intermediate chronostratigraphic position between the previously known species, *Echinochara peckii* from the

Bathonian to Kimmeridgian and the Barremian–early Aptian *Echinochara lazarii*. The new utricle structure described considerably improves our understanding of the evolution in the genus *Echinochara* during the earliest Cretaceous. The main evolutionary changes in this genus include the shift from a triradiated utricle structure to a bilaterally symmetrical utricle by the late Berriasian, the reduction of the basal trifurcation of the inner utricle series before the Berriasian, and the reduction to disappearance of all trifurcations of the outer utricle series between the Berriasian and the Barremian. In parallel the twisting of the cortical cells of the internodes disappeared during the same interval.

The palaeoecology of *Echinochara pontis* sp. nov. suggests that this genus was restricted to brackish settings, at least until the early Barremian. The finding of new *Echinochara* fossils, especially from the Bajocian to Kimmeridgian, Valanginian to Hauterivian and late Aptian, will help us understand completely more clearly the evolution, biostratigraphy, palaeoecology, and biogeography of this still poorly known charophyte genus.

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## 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.

## Data availability

Data will be made available on request.

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