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General paleontology, systematics and evolution (Biostratigraphy)

Echinochara triplicata sp. nov. (Clavatoraceae, fossil Charophyta) from the Lower Albian of Tunisia*Echinochara triplicata* sp. nov. (Clavatoraceae, Charophytes fossiles) de l'Albien inférieur de TunisieKhaled Trabelsi^{a,*}, Carles Martín-Closas^b^a Faculté des sciences de Sfax, université de Sfax, CP 3000, BP 11-71, Sfax, Tunisia^b Departament d'Estratigrafia, Paleontologia i Geociències marines, facultat de Geologia, universitat de Barcelona, 08028 Barcelona, Catalonia, Spain

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ABSTRACT

Echinochara Peck, 1957 is a poorly known charophyte genus from the Upper Jurassic and Lower Cretaceous of the United States and Europe. Its fossil record is currently limited to two species, *Echinochara spinosa* Peck, 1957 and *Echinochara peckii* (Mädler, 1952) nov. comb. Grambast, 1956 emend. Schudack, 1993, which have obscure phylogenetic relationships. A third species of this genus, *Echinochara triplicata* nov. sp., is described here from the Lower Albian of Jebel Koumine (Central Tunisia) and is hypothesized to derive from the Barremian–Aptian morphotypes of *Echinochara peckii*. The new species represents the first record of the genus in Africa and its more recent record worldwide. It occurs along with the clavatoraceans: *Clavator harrisii zavialensis* and *Atopochara trivolvis trivolvis* and provides an additional tool for the biostratigraphic characterization of non-marine Albian of Europe and North Africa.

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R É S U M É

Echinochara Peck, 1957 est un genre de charophytes très peu connu dans le Jurassique supérieur et le Crétacé inférieur des États-Unis et de l'Europe. Jusqu'à présent, l'enregistrement de ce genre fossile est limité uniquement à deux espèces, *Echinochara spinosa* Peck, 1957 et *Echinochara peckii* (Mädler, 1952) nov. comb. Grambast, 1956 emend. Schudack, 1993, dont les relations phylogénétiques demeurent encore mal élucidées. Une troisième espèce de ce genre, *Echinochara triplicata* nov. sp., est décrite ici dans l'Albien inférieur de Jebel Koumine (Tunisie Centrale) et permet d'émettre l'hypothèse qu'elle dérive à partir des morphotypes du Barrémien–Aptien d'*Echinochara peckii*. La nouvelle espèce représente le premier enregistrement du genre en Afrique, et la forme la plus récente dans le monde. Elle a été trouvée en association avec les Clavatoracées, *Clavator harrisii zavialensis* et *Atopochara trivolvis trivolvis* et fournit alors un outil supplémentaire pour la caractérisation biostratigraphique de l'Albien non-marin de l'Europe et l'Afrique du Nord.

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1. Introduction

During the Aptian–Albian, central Tunisia was one of the large islands in the southern margin of the Tethys Sea (M'Rabet et al., 1979), bearing rich continental deposits with charophytes, called the “Kebar Formation” (Trabelsi et al., 2010). This series, in its type locality, Jebel Kebar, was assigned for the first time to the Lower Albian on the basis of the charophyte assemblage *Sphaerochara verticillata* var. *kebariensis*, *Clavator harrisii* var. *zavialensis* and *Atopochara trivolvis* var. *trivolvis* (Trabelsi et al., 2010) and ostracods (*Cypridea laevigata*, and Timiriaseviinae, *Vecticypris* and Darwinulidae) (Trabelsi et al., 2011). In the North of the Tunisian palaeo-island, in the locality of Jebel Koumine, the same formation contains a rich assemblage of fossil charophytes, including a new species of genus *Echinochara* Peck, 1957, which is the subject of this study.

For the first time, this new species allows us to establish a clear link between two *Echinochara* species and provides a new element for the biostratigraphic characterization of the non-marine Albian of the Peritethyan realm on the basis of charophytes. This is of considerable interest because charophyte assemblages of biostratigraphic interest from

this time interval were less rich in species than those of other chronostratigraphic intervals.

2. Geological and Paleontological Settings

The Jebel Koumine is located in central Tunisia (Fig. 1), less than 10 km south of the city of Sbitla and about 30 km north-west of Jebel Kebar (the type locality of the Kebar Formation). In this area, an anticline oriented East to West allows Aptian to Cenomanian rocks to crop out, directly covered by Cenozoic strata. The Kebar Formation in Jebel Koumine crops out exclusively on the northern flank of the structure (Fig. 2A), with a total thickness of 230 m and lying unconformably on the uppermost member of the dolomitic Orbata Formation, Lower Aptian in age (Masse, 1984; M'Rabet, 1981). This superposition represents a major regional unconformity, documented throughout Central Tunisia (Ben Youssef, 1999; Masse, 1984; M'Rabet, 1981). The Kebar Formation is directly overlain by transgressive marine marls and limestones of the Zebbag Formation, Upper Albian in age (*Stoliskaia dispar* ammonite biozone, according to Ben Youssef, 1999). This stratigraphical context frames the Kebar Formation

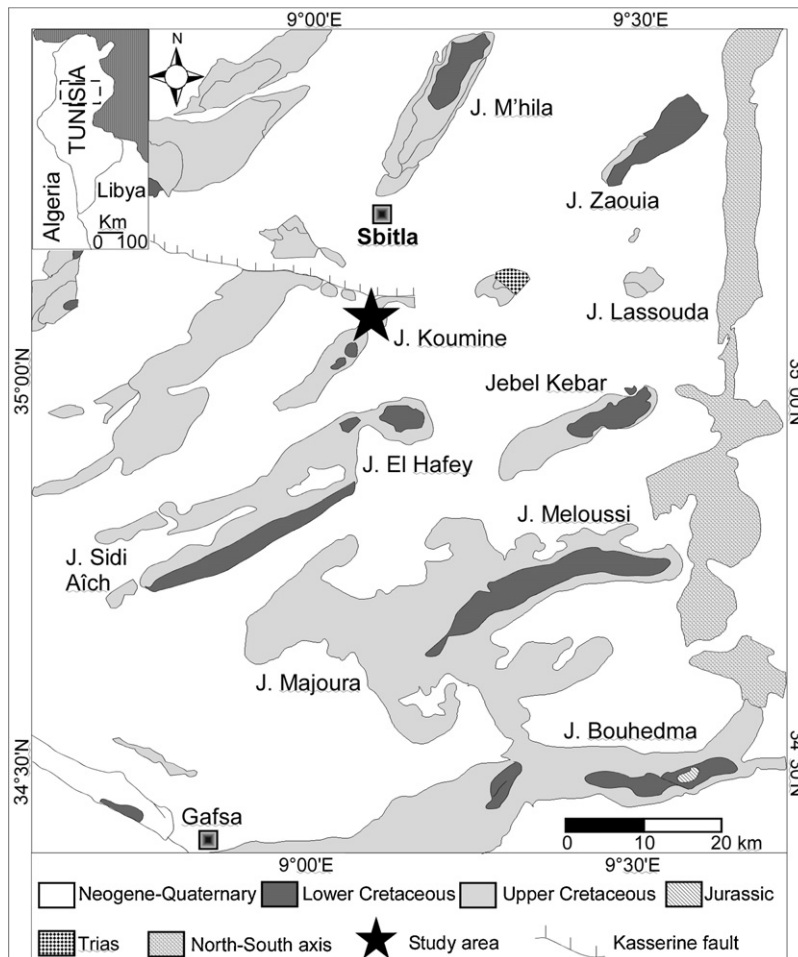


Fig. 1. Geographical and geological setting of the Jebel Koumine (study area).

Fig. 1. Cadre géographique et géologique du secteur étudié (Jebel Koumine).

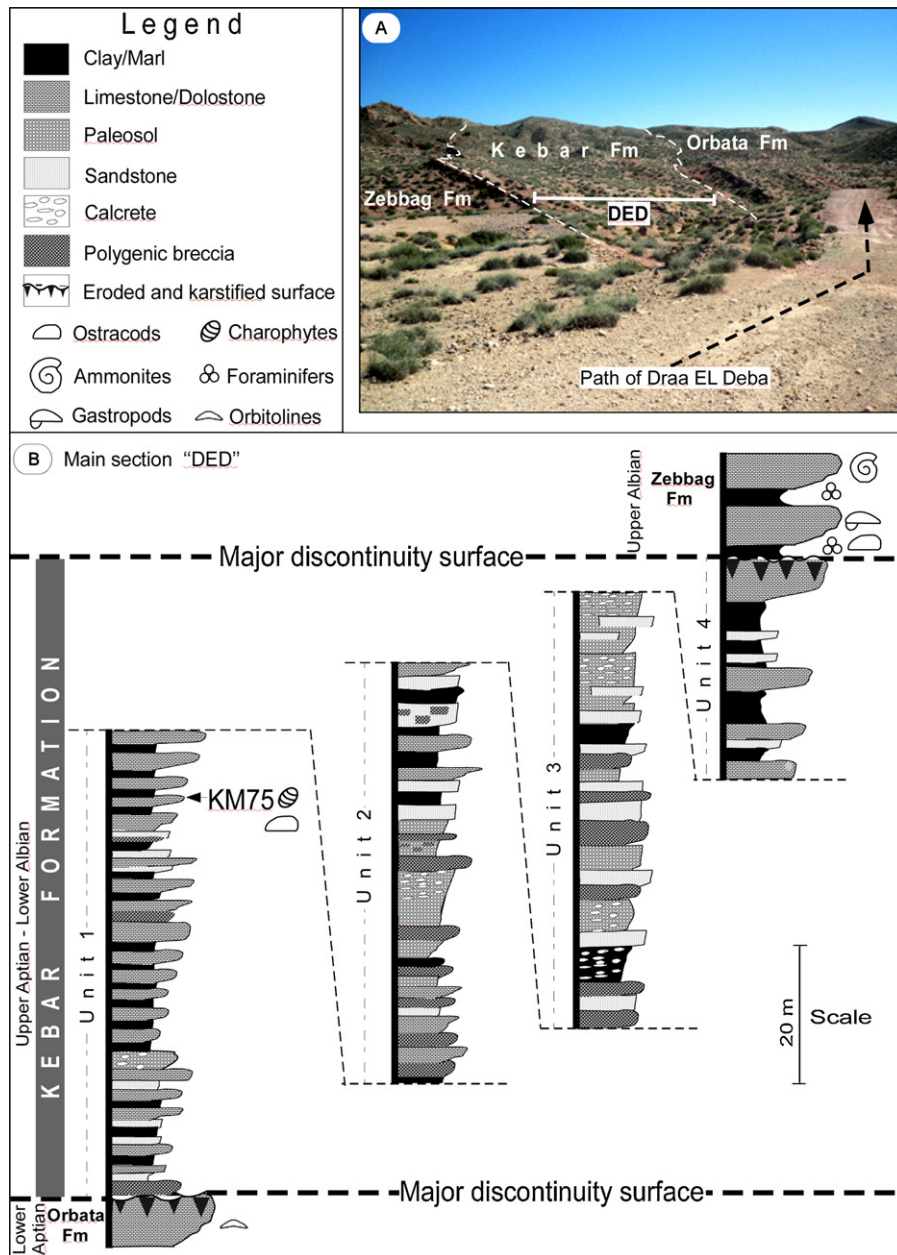


Fig. 2. Studied section of the Kebar Formation in Jebel Koumine. **A.** The Kebar Formation as seen west from the landmark "Path of Draa El Deba". **B.** Lithostratigraphic log of the section "DED" of the Kebar Formation.

Fig. 2. Affleurement principal de la Formation Kebar à Jebel Koumine. Vue générale de la Formation Kebar à l'ouest de « la piste de Draa El Deba ». Log lithostratigraphique de la coupe « DED » de la Formation Kebar.

between the Upper Aptian-Upper Albian interval. Recently, Trabelsi et al. (2010) attributed this formation more precisely to the Lower Albian, based on a charophyte assemblage. This age was also confirmed by a rich assemblage of ostracods (Trabelsi et al., 2011; Trabelsi and Colin, work in progress).

The vertical change in the lithofacies and stacking-pattern in the main section called DED, located near the path of "Draa El Deba" on the northern flank of Jebel Koumine (Fig. 2A), allows us to subdivide the Kebar

Formation into four lithostratigraphic units that represent a fluvio-lacustrine environment (Fig. 2B). Level KM75 from the DED section is a lacustrine limestone, at the top of unit 1 of the Kebar Formation (Fig. 2B), which provided a large amount of well-preserved fructifications (gyrogonites and utricles) of charophytes. Moreover, this bed provided a new species of the genus *Echinochara*, associated with *Sphaerochara verticillata* var. *kebariensis* Trabelsi 2010, *Clavator harrisii* var. *zavialensis* (Grambast-Fessard, 1980) Martín-Closas, 1996 and *Atopochara trivolvus* var. *trivolvus*

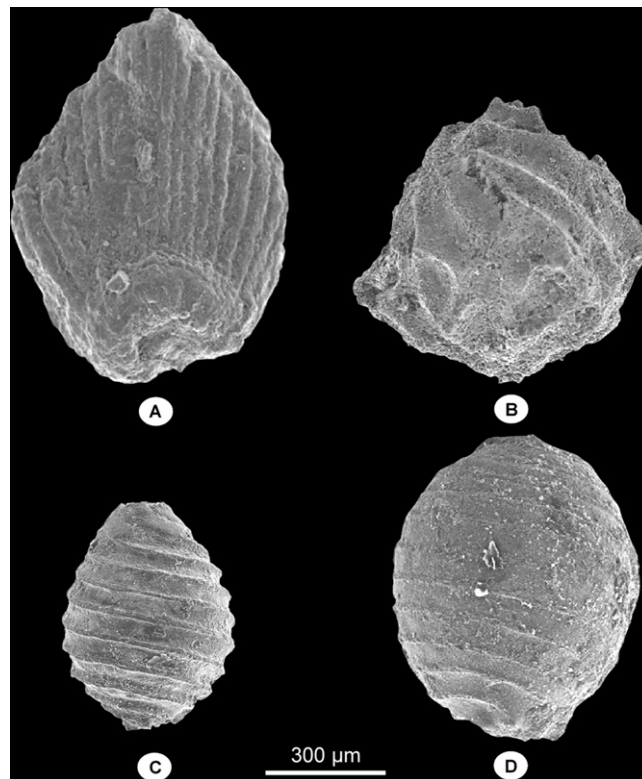


Fig. 3. Charophytes from bed KM75 of the Kebar Formation in Jebel Koumine section. **A.** *Echinochara triplicata* nov. sp. **B.** *Atopochara trivolvis* var. *trivolvis*. **C.** *Clavator harrisii* var. *zavialensis*. **D.** *Sphaerochara verticillata* var. *kebariensis* (all fructifications in lateral view).

Fig. 3. Charophytes du niveau KM75 de la Formation Kebar. **A.** *Echinochara triplicata* nov. sp. **B.** *Atopochara trivolvis* var. *trivolvis*. **C.** *Clavator harrisii* var. *zavialensis*. **D.** *Sphaerochara verticillata* var. *kebariensis* (toutes les fructifications en vue latérale).

Peck, 1938 (Fig. 3B–D). The assemblage formed by the three latter species has recently been described in the Lower Albian of Tunisia by Trabelsi et al. (2010).

3. Material and methods

Samples taken in the consolidated limestone bed KM75 were treated using acetolysis, breaking down the rock by preliminary attack with acetic acid. The efficiency of this method, first advocated by Nötzold (1965) and already applied by Trabelsi et al. (2010), has recently been demonstrated by Rodríguez et al. (2011). It consists in taking the sample of calcareous rock, perfectly dried and mechanically comminuted in fragments about 1–3 mm across, and adding similar amounts of anhydrous acetic acid and anhydrous copper sulfate (acid attacks in an exothermic reaction). After neutralization of the milieu by ammonia, the residue is treated with ultra-sound, then washed and rinsed. The studied material is stored at the Service of Paleontology and Sedimentology of the National Office of Mines of Tunisia under reference SPSONMT Trab., J. Koum. 0018–0035.

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, 1989 ex Schudack, 1993

Genus *Echinochara* Peck, 1957 emend. Schudack, 1993
Echinochara triplicata, Trabelsi et Martín-Closas nov. sp.

Fig. 3A.

Material: One well-preserved specimen, showing a symmetry unit of an *Echinochara* utricle and up to 10 more specimens, poorly preserved but with a similar structure.

Diagnosis: Utricle of *Echinochara* with the external whorl formed by three radially-symmetrical units, each formed by 21 elongated and non-branched vertical bract cells, directly connected to the utricle base, where the scar of the attachment cell can be observed.

Derivation of name: From the Latin adjective *triplicata*, meaning threefold. The new species in fact represents a triplication of the number of cells of the utricle of *Echinochara peckii* var. *lazarii* Martín-Closas, 2000, from which it is hypothesized to derive.

Holotype: Specimen num. SPSONMT Trab., J. Koum. 0025 (Fig. 3A), stored at the Service of Paleontology and Sedimentology of the National Office of the Mines of Tunisia (charophyte collection from J. Koumine, 2011).

Paratypes: Specimens num. SPSONMT Trab., J. Koum. 0026–0031, stored at the Service of Paleontology and Sedimentology of the National Office of the Mines of Tunisia (charophyte collection from J. Koumine, 2011).

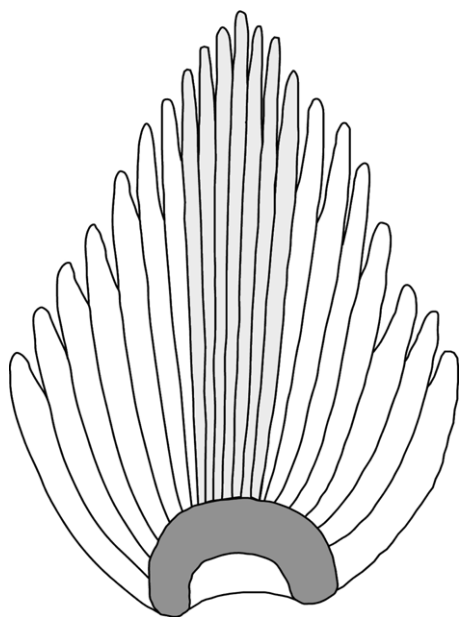


Fig. 4. Structure of one unit of symmetry of the outer whorl of the *Echinochara triplicata* nov. sp. utricle, formed by three sets of seven cells each, which are convergent to a basal attachment scar (dark grey), representing a bract of the internal whorl.

Fig. 4. Structure de l'une des unités de symétrie du verticille externe de l'utricule d'*Echinochara triplicata* nov. sp., formée par trois groupes de sept cellules chacune, qui convergent directement de la base où on observe la marque d'une bractée (gris foncé) du verticille interne.

Type locality: Section DED of the Kebar Formation located in the South East of Draa el Deba in the northern flank of Jebel Koumine. Coordinates: N 35° 70'; E 90 90'.

Type-layer: Limestone level KM75 of section DED, 60 metres from the base and 10 metres from the top of the basal unit (U1) of the Kebar Formation in Jebel Koumine; Lower Albian in age.

Description: Utricles of the new species were found preserved as calcite plates with an arrangement reminiscent of the external plates of the *Echinochara peckii* utricle (Fig. 3). These plates are about 600 µm wide and 850 µm long. On one side of the plate there are 21 vertical furrows, 310 to 540 µm long and 10 to 15 µm wide, converging to the base where they are attached. These 21 furrows are attributed to the bract cells of one symmetrical unit of the external whorl of an *Echinochara* Peck, 1957 utricle, as described by Schudack (1993). The bract cells are grouped in three sets of seven cells each (Fig. 4). The medial set bears thinner and longer bract cells, running linearly throughout the plate from the base to the top. It is embraced on each side by another set of seven cells each, which are slightly convergent to the base but shorter, wider and progressively more curved inwards towards the top. The basal part of the plate shows a rounded attachment scar, about 130 µm across with a prominent peripheral rim, which was attributed to the scar of the abaxial internal bract, *sensu* Schudack (1993). This scar is the only available proof that the internal series of bracts still existed in *Echinochara triplicata* nov.sp., because on the opposite side of the calcite plate the surface

is irregular and unstructured. In consequence, no marks of the gyrogonite are available in the material studied.

Remarks: The organization of the utricle cells in each symmetry unit of the new species recalls the fan-like structure of the utricle wall of *Echinochara peckii* var. *lazarii* Martín-Closas, 2000. As in this morphotype, in the *E. peckii triplicata* nov. sp., all the cells depart directly from the attachment scar, and are not arranged in two successive trifurcations as in the case of *Echinochara peckii* var. *peckii*. However, unlike *E. peckii* var. *lazarii*, the new species bears symmetry units, each formed by 21 cells instead of seven.

Distribution: *Echinochara triplicata*, from the Lower Albian of Tunisia, is the youngest species of the genus *Echinochara* and is also its first African record. Genus *Echinochara* Peck, 1957 shows a rather disjointed distribution in both time and space. The oldest record of the genus is represented by *Echinochara peckii peckii* (Mädler, 1952) which occurs in the Oxfordian of Switzerland (Mojon, 1989) and in the Kimmeridgian of the United States and Germany (Mädler, 1952; Schudack, 1993; Schudack et al., 1998). A second species, *Echinochara spinosa* Peck, 1957, was also described from the Kimmeridgian of the Morrison Fm (United States). Additionally, Mojon and Mouchet (1992) claimed that *Echinochara*-like vegetative remains found in thin sections from the Lower Kimmeridgian of the Jura Mountains (Switzerland) belonged to *E. peckii*, but insufficient evidence was provided to characterize the utricle on which the species is based. There is a significant gap in the record of the genus *Echinochara* from the Tithonian to the Hauterivian. After this gap, a later morphotype of this species (*E. peckii* var. *lazarii*) occurs in the Lower Barremian of the Iberian Peninsula (Martín-Closas, 2000) and in the Upper Barremian and Lower Aptian of the Subalpine Chains, France (Martín-Closas et al., 2009).

5. Evolution of genus *Echinochara* Peck, 1957

The genus *Echinochara* (subfamily Atopocharoidae) is currently represented by the two taxa *Echinochara spinosa* Peck, 1957 and *Echinochara peckii* (Mädler, 1952) nov. comb. Grambast, 1956 emend. Schudack, 1993). The genus as a whole was considered by Martín-Closas (1989, 1996) a paraphyletic ancestral stock from which the remaining Atopocharoidae were derived. *Echinochara spinosa* was interpreted by Martín-Closas (1996) as the ancestral form of the genus on the basis of its utricle, formed by six trifurcated bract cells in the internal whorl, and six profusely trifurcated bract cells in the external whorl. *Echinochara peckii* was seen as a more derived utricle structure, with only three trifurcated bract cells in the internal whorl. The external whorl, described by Schudack (1993), showed a completely new structure, with three symmetrical plates formed by the fusion of bracts, trifurcated twice. The precise phylogenetic relationships between the two species are difficult to ascertain given the present knowledge of their utricle structure.

The new species *Echinochara triplicata* shows clear affinities with *Echinochara peckii*, particularly with the youngest morphotype of this species, *E. peckii* var. *lazarii* Martín-Closas, 2000. Like this variety, *E. triplicata* has the utricle formed by three symmetrical plates with the cells

directly departing from the attachment scar, instead of being organized in two successive trifurcations as in the case of the nominal variety, *Echinochara peckii* var. *peckii* (Mädler, 1952). However, the new species bears symmetry units formed by three times as many bracts as in *E. peckii* var. *lazarii*. Multiplication of parts of the same structure in closely related species is known in other clavatoraceans. For example, according to Martín-Closas (1996), *Clavator brachycerus* (Grambast, 1962) emend. Martín-Closas, 1996 represents a triplication of the same utricule bract structure as its presumed ancestor *Clavator ampullaceus* (Grambast and Lorch, 1968) Martín-Closas, 1996. Again, *Clavator ultimus* (Grambast, 1971) Martín-Closas, 1996 has 50% more utricule bracts than its ancestor, *C. brachycerus*, but there is no change in the original structure. Martín-Closas (1996) suggested that such multiplications could be the result of processes of polyploidy.

According to Martín-Closas (1996), the evolutionary lineage *Globator* Grambast, 1966 was also derived from *Echinochara peckii*; however, this branch separated much earlier than *Echinochara triplicata*, at least in the Tithonian. Also, it represented a more significant change in the utricule structure, because *Globator* completely lacks the internal

whorl of *Echinochara*'s utricule, although it retains one of the two successive trifurcations of the external utricule layer of *Echinochara peckii* var. *peckii*.

6. Discussion and conclusions

Echinochara triplicata nov. sp. represents the third known species within the genus *Echinochara* Peck, 1957. Phylogenetic relationships of the new species are proposed with *E. peckii* var. *lazarii* from the Lower Barremian to Lower Aptian of Europe, on the basis of the non-ramified structure of the utricule's external whorl (Fig. 5). However, compared with its presumed ancestor, the new species displays three times the original number of cells per symmetry unit.

Echinochara triplicata nov. sp. can be considered a new tool for biostratigraphic studies in the non-marine Upper Jurassic-Lower Cretaceous of the Peritethyan Realm. It is especially important because it provides a new taxon for better characterization of the Upper Aptian-Lower Albian biozone of the charophyte biozonation (*Clavator grovesii* lusitanicus biozone) as defined by Riveline et al. (1996), which is poorer in biostratigraphically useful species than other Lower Cretaceous charophyte biozones.

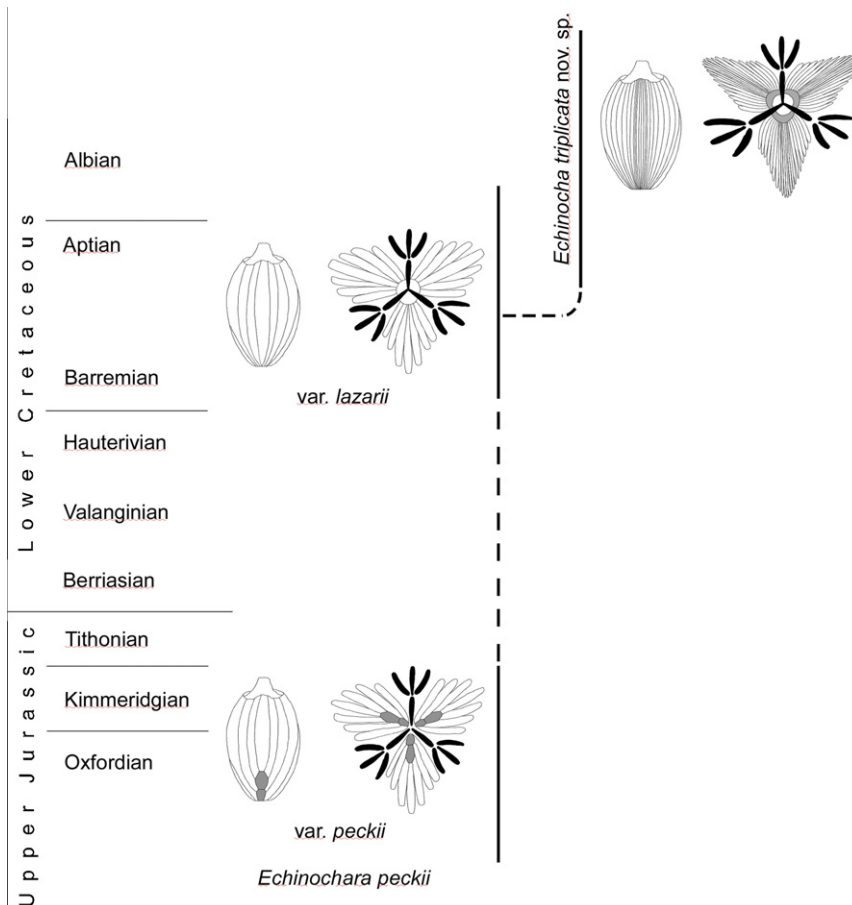


Fig. 5. Phylogenetic link between *Echinochara triplicata* nov. sp. and *Echinochara peckii* (Peck, 1957). Utricule profiles are represented on the left and the whole utricule opened on the basal plane is represented on the right, with the internal whorl in black and the external whorl in white.

Fig. 5. Relation phylogénétique entre *Echinochara triplicata* nov. sp. et *Echinochara peckii* (Peck, 1957). Les profils de l'utricule sont représentés à gauche alors que l'utricule entier ouvert selon un plan basal est représenté à droite, avec le verticille interne en noir et le verticille externe en blanc.

The new species represents the first record of the genus *Echinochara* Peck, 1957 from Africa and the first in the world from the Albian. Its occurrence in the Albian shows that the genus attained a very long chronostratigraphic range, comparable to, or even longer than, the range of the closely related genera *Globator* Grambast, 1966, which extended between the Tithonian and the Lower Aptian, or *Atopochara* Peck, 1938, which extended between the Berriasian and the Maastrichtian (only between the Berriasian and the Cenomanian in the Peritethyan realm). In addition, the total biogeographic range reached during the history of the genus *Echinochara* was very wide, subcosmopolitan in the Northern Hemisphere (North America, Europe and Africa).

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