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 Tunisie**

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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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**Résumé**


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 harrissii 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 palae-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 Peri-tethyan 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.
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 Sphaerocysta verticillata var. kebariensis Trabelsi 2010, Clavator harrisi var. zavialensis (Grambast-Fessard, 1980) Martin-Closas, 1996 and Atopochara trivolvis var. trivolvis

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

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).
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 Martin-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 Albanian 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* (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 Morris- son 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. Grambost, 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 Martin-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 brachy cercus* (Grambast, 1962) emend. Martín-Closas, 1996 represents a triplication of the same utricle 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 utricle bracts than its ancestor, *C. brachy cercus*, 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* Grambat, 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 utricle structure, because *Globator* completely lacks the internal whorl of *Echinochara*’s utricle, although it retains one of the two successive trifurcations of the external utricle 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 utricle’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.

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