

New findings of lower Aptian charophytes from the Southern High Plateaus (Eastern Meseta, Morocco): biostratigraphic and biogeographic significance

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ABSTRACT

Two stratigraphic sections of the Southern High Plateaus (Eastern Meseta, Morocco) were sampled for the charophyte study. Seven clavatoracean taxa are described and illustrated from the Dekar 1 and Dekar 2 formations, including *Echinohara lazarii*, *Atopochara trivolis* var. *trivolis*, *Clavator grovesii* var. *jiuquanensis*, *Clavator grovesii* var. *corrugatus*, *Clavator harrisii* var. *harrisii*, *Clavator harrisii* var. *reyi*, and *Clavator harrisii* var. *zavialensis*. This assemblage is assigned to the upper part of the Eurasian *Clavator grovesii* var. *jiuquanensis* biozone. The occurrence of intermediate populations of *C. grovesii* var. *jiuquanensis* and *C. grovesii* var. *corrugatus* associated with intermediate populations of *C. harrisii* var. *harrisii*, *C. harrisii* var. *reyi*, and *C. harrisii* var. *zavialensis*, restricts the association to the lower Aptian. These new findings suggest that this area could be important for understanding the evolution of charophytes during the early Aptian. Furthermore, the study provides significant insights into the paleobiogeographic distribution of Lower Cretaceous charophytes, reporting the first record of *C. grovesii* var. *jiuquanensis* (previously described only from Eurasia) and *C. grovesii* var. *corrugatus* (previously known from the Iberian Peninsula and the United States) in Africa, along with the first report of *Echinohara lazarii* in the Western Atlas Domain. Similar lower Aptian assemblages had previously been described only in the Algarve Basin (South Portugal), suggesting a strong paleogeographic connection between these areas.

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1. Introduction

In the Moroccan Atlas Domain (Fig. 1A), the basin fill of the Tethyan Jurassic throughs is succeeded by a thick mainly continental clastic series known as 'Red beds' precede the Late Cretaceous transgression (Choubert and Faure-Muret, 1960–62; Frizon de Lamotte et al., 2008 and references therein). Three lithostratigraphic units (Lower, Middle and Upper Clastic Deposits)

separated by major stratigraphic hiatuses and sporadic volcanic events have been recognized within the Middle Atlas, Central, and Eastern High Atlas series (Charrière and Haddoumi, 2016).

Initially poorly dated due to the absence or scarcity of macrofossils, the age of the Red beds has been the subject of numerous controversies (see summary in Monbaron, 1988). However, many micropaleontologic discoveries (Andreu et al., 1988; Charrière, 1996; Haddoumi et al., 2008, 2010; Mojon et al., 2009; Haddoumi et al., 2019, 2024; Ouaskou et al., 2021), have provided biostratigraphic results at the local scale, followed by regional or Moroccan scale stratigraphic and paleogeographic syntheses.

The biostratigraphic interpretation of Cretaceous Red beds is mainly based on charophyte assemblages, notably Clavatoraceae,

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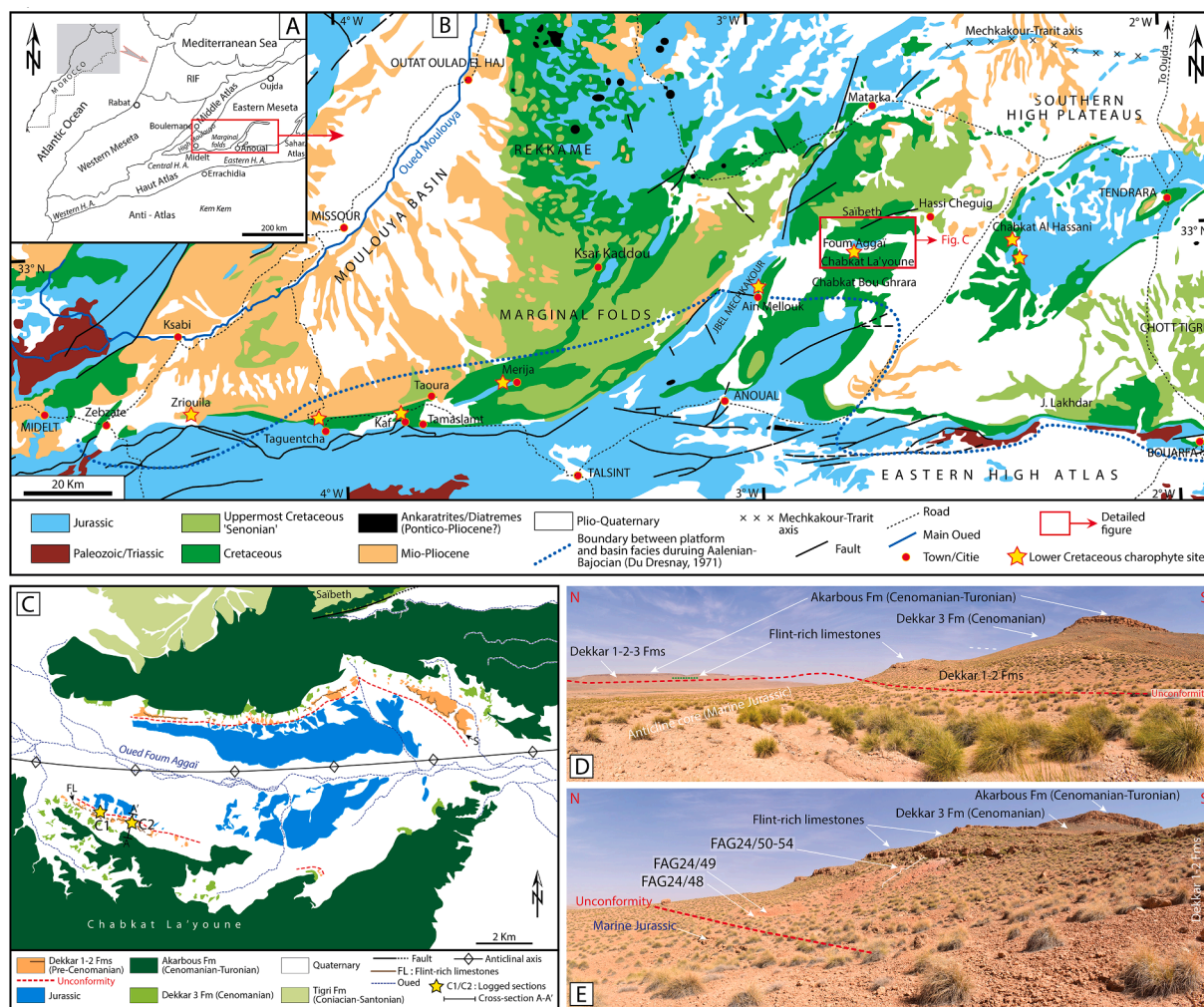


Fig. 1. A. Location of the Atlasic Domain; B. Schematic geological map of the eastern High Atlas, the Marginal Folds region and the southern High Plateaus, showing the study areas and the Lower Cretaceous charophyte sites. Background map modified from [Hollard et al. \(1985\)](#). C. Geological map of the Fom Aggaï anticline showing the location of sections C1 and C2. D. Panoramic view showing the Fom Aggaï anticline and different units of the Cretaceous Red beds, unconformably overlying the marine Jurassic substrate and capped by the Akarbus Formation. E. Close-up view showing the location of the sampled section C2 from the southern limb of the Fom Aggaï anticline. Coordinates of the studied sections: Fom Aggaï: 32°57'48.40" N/2°47'48.60" W and 32°57'40.90" N/2°47'08.44" W; Chabkat Al Hassani: 32°57'51.24" N/2°22'47.47" W and 32°56'14.20" N/2°21'58.99" W.

and sometimes foraminifera from the marine intercalations ([Haddoumi et al., 2019](#); [Ouaskou et al., 2021](#) and references therein). In many regions, clavoceaceans represent an excellent group for biostratigraphic, paleoecologic, and paleobiogeographic studies. Notably, some species show a wide paleogeographic distribution during the Early Cretaceous (e.g. [Martín-Closas and Wang, 2008](#); [Martín-Closas, 2015](#); [Vicente et al., 2024](#)). However, during the Aptian, charophyte assemblages are very rare in the Tethyan area, since they coincide with a marine highstand (e.g., [Bover-Arnal et al., 2022](#)), which challenged the development of continental settings suitable for their preservation. In this context, new findings from the Moroccan Atlas provide crucial data to fill this gap of knowledge. These assemblages not only contribute to the refinement of local biostratigraphic frameworks, but also offer broader insights into the diversity, paleobiogeography, and evolutionary dynamics of charophyte floras during the Aptian.

This study therefore had two main objectives. The first was to describe and illustrate the Aptian charophyte flora from a new site (Fom Aggaï) as well as from a previously reported locality in Eastern Morocco (Tendara dome), with the aim of determining the relative age of the pre-Cenomanian units. The second objective was to analyse the paleobiogeographic distribution of the species,

particularly because some taxa are reported here for the first time from Gondwana, corresponding to the southern margin of the Cretaceous Tethyan Archipelago. The results enhance our understanding of charophyte evolution and biogeography patterns during the Aptian, helping to refine the biostratigraphic and biogeographic models at the intercontinental scale, including North Africa, Europe, Asia and America.

2. Materials and methods

Three stratigraphic sections were systematically sampled for charophyte biostratigraphy and associated fossils. Between 1 and 2 kg of 42 samples of marly and clayey rocks were washed and sieved and 10 thin sections were prepared from indurated rocks in the Laboratory of the Faculty of Sciences, Mohammed First University, Oujda (Morocco), using sieves ranging from 800 to 63 μm . The charophyte assemblage was studied using an AmScope SE305R-PZ-LED binocular microscope under the magnifications of $\times 10$, $\times 20$, $\times 30$, and $\times 60$. An MD500A camera attached to the same microscope and AmLite open access software were used to make the measurements. Some specimens were photographed with a Quanta 200 scanning electron microscope housed at the

Scientific and Technological Centres of the University of Barcelona (CCiTUB). The studied specimens, including those illustrated specimens in the figures, are housed in the paleontological collection of the Applied Geosciences Laboratory of the Faculty of Sciences, Mohammed First University, Oujda. Specimens from Chabkat Al Hassani are numbered HHTN25_01 to HHTN25_08, while samples from Fom Aggaï area are numbered HHFAG25_01 to HHFAG25_24.

3. Geological setting

The studied Fom Aggaï and Tendrara areas belong to the Southern High Plateaus that constitute a distinct structural zone in the Moroccan Eastern Meseta (Fig. 1B). The latter is bordered to the West by the Middle Atlas, to the South by the Eastern High Atlas and continues towards the East in Algeria via the Oran Meseta.

To the south of the Mechakour-Trarit axis (Fig. 1B), the Southern High Plateaus appear as a vast monotonous plain interspersed with some reliefs with relatively rounded shapes and relatively low altitudes. Among these are the Tendrara dome and the Fom Aggaï anticline, where the three charophyte sites studied in this work are located (Fig. 1B): a new site at Fom Aggaï reported for the first time and two sites at Chabkat Al Hassani, SW of Tendrara (Haddoumi et al., 2024), which have been resampled recently.

In the studied areas, the outcrops mainly consist of Cretaceous and Cenozoic series unconformably overlying a Middle Jurassic basement. The latter exhibits basinal facies in the south and carbonate platform facies in the northeast and east in the Southern High Plateaus. The boundary between the platform and basin facies during the Aalenian-Bajocian (Du Dresnay, 1971) is indicated in Fig. 1B. During the Cretaceous, the facies difference is accompanied by a reduction in thickness from the south to the north of the High Plateaus (Médioni, 1960; Haddoumi et al., 2024).

The Cretaceous deposits (Fig. 1B) generally start with the classic deposits of the “Mesocretaceous” (Choubert and Faure-Muret, 1960–1962): pre-Cenomanian, Cenomanian, and Cenomanian–Turonian. In the Southern High Plateaus, the discordant Cretaceous series often starts with the pre-Cenomanian deposits (Médioni, 1960, 1968) sometimes subdivided into two formations: the Dekkar 1 and Dekkar 2 formations (Haddoumi et al., 1998, 2019, 2024). These are composed of conglomerates and sandstones, occasionally associated with limestones or a siliceous layer capped by the Cenomanian versicoloured marlstones, corresponding to the Dekkar 3 Formation, and the upper Cenomanian–Turonian limestones of the Akarbous Formation (Haddoumi et al., 2019). The Akarbous Formation is covered by a predominantly terrigenous uppermost Cretaceous (‘Senonian’) of the Tigri Formation (Médioni, 1970; Haddoumi et al., 2015) and Cenozoic deposits.

The Red beds of the Southern High Plateaus, e.g. in Chabkat Al Hassani and Fom Aggaï (Figs 1 C–E, 2A), are only represented by the upper complex or Dekkar Group (Pre-Cenomanian and Cenomanian in age). This is a relatively reduced series in comparison to the Red beds of the Anoual region located to the SW (Fig. 1B), north of the Eastern High Atlas, near the Fom Aggaï area (Haddoumi et al., 2008; Charrière and Haddoumi, 2016). The Anoual Formation (lower Bathonian) and the Ksar Metlili Formation (Berriasian–Tithonian), forming the lower and middle complexes of the Red beds of Anoual and Ksar Jilali synclines, are missing.

3.1. Fom Aggaï area

The Fom Aggaï area (Fig. 1B–C) is located in an anticline on the Southern High Plateaus, ~40 km NE of Anoual town and ~70 km

SW of Tendrara town (Fig. 1B). This anticline, with an E–W-trending axis and a core of Middle Jurassic terrains, is overlain unconformably by Cretaceous deposits on its flanks, largely covered by Quaternary sediments (Fig. 1C–D). These Cretaceous deposits (Figs. 1C–E and 2A) include pre-Cenomanian strata designated in this study as the Dekkar 1–2 formations. It is difficult to distinguish the boundary between these two units (lateral facies variations and relatively greatly reduced thickness), although they are well distinguished towards the south in the Anoual region. The Dekkar 1–2 succession is topped by the Cenomanian versicoloured marlstones (Dekkar 3 Formation), the Cenomanian–Turonian limestones (Akarbous Formation), and the Coniacian–Santonian deposits (Médioni 1964, 1968) of the Tigri Formation (Médioni, 1970; Haddoumi et al., 2015).

Two sections C1 and C2 (Fig. 2) were measured in the pre-Cenomanian of the southern flank of the Fom Aggaï syncline at Chabkat La'youne (Fig. 1C–E). In these sections, the pre-Cenomanian begins with a 30–50-cm-thick layer of very indurated more or less conglomeratic calcarenites, with essentially calcareous clasts associated with remains of marine fossils, originating from the erosion of the marly-calcareous deposits of the underlying marine Middle Jurassic. In section C2, these calcarenites are overlain by a layer of yellow-green friable clayey calcarenites, rich in calcareous sand and gravel, mixed with remains of reworked Jurassic fossils. This bed, which yielded Cretaceous charophyte remains is followed by reddish mudstone without fossil remains.

After a significant coverage by Quaternary deposits, the Cretaceous section resumes and comprises 12–15 m of purplish marls, which were also sampled. Samples from section C1 revealed an indurated level of marlstones and root tubules. Some samples from sections C1 and C2 (Fig. 2B) yielded well-preserved charophyte remains, sometimes associated with ostracods or fragments of dinosaur eggshells. The upper part of these marls is limy with nodular calcrete transitioning to ~10-m-thick dolomitized flint-rich limestones, constituting a topographic benchmark. No microfossils or bioclasts were observed in thin sections. Above the flint-rich limestones, a nodular calcrete layer up to 8-m-thick was observed in some areas (Fig. 2D). This layer contains nodules whose diameter ranges from several centimetres to a few decimetres thick, separated by purplish marls. This layer is covered by an 8m-thick cross-stratified sandstone bed (Fig. 3E), followed by reddish gypsiferous marlstone and a second cross-stratified sandstone. The base of the gypsiferous marlstone (FAG24/22A sample, Fig. 2B) yielded fish remains with a few teeth of the sclerorhynchiform *Marckgrafia libyca* Weiler (1935), described by Werner (1989) in the Cenomanian beds of the Bahariya Formation (northwestern Desert of Egypt). This taxon was also reported in Morocco from the Kem Kem beds (Dutheil, 2000; Ibrahim et al., 2020) and the Tendrara dome (Haddoumi et al., 2024). The basal calcarenites might be a very reduced lateral equivalent of the Dekkar 1 Formation. The marlstones, flint-rich limestones, and calcretes might also belong to the Dekkar 1 Formation as is the case at Aïn Mellouk (Feist et al., 1999; Haddoumi et al., 2008). In this area (Fig. 1B), located not far from Fom Aggaï, a thick limestone succession with charophytes is considered as resulting from the lateral passage of the terrigenous facies of the Dekkar 1 Formation. Alternatively, they might correspond to the base of the Dekkar 2 Formation as is the case at Chabkat Al Hassani (Haddoumi et al., 2024) and the Marginal Folds (Haddoumi et al., 2019).

The Fom Aggaï flint-rich limestones and the calcretes are likely equivalent of the Aptian Aïn Mellouk limestones (Feist et al., 1999; Haddoumi et al., 2008), and the silicified limestone horizons outcropping further east at Chabkat Al Hassani (Fig. 1B). The red

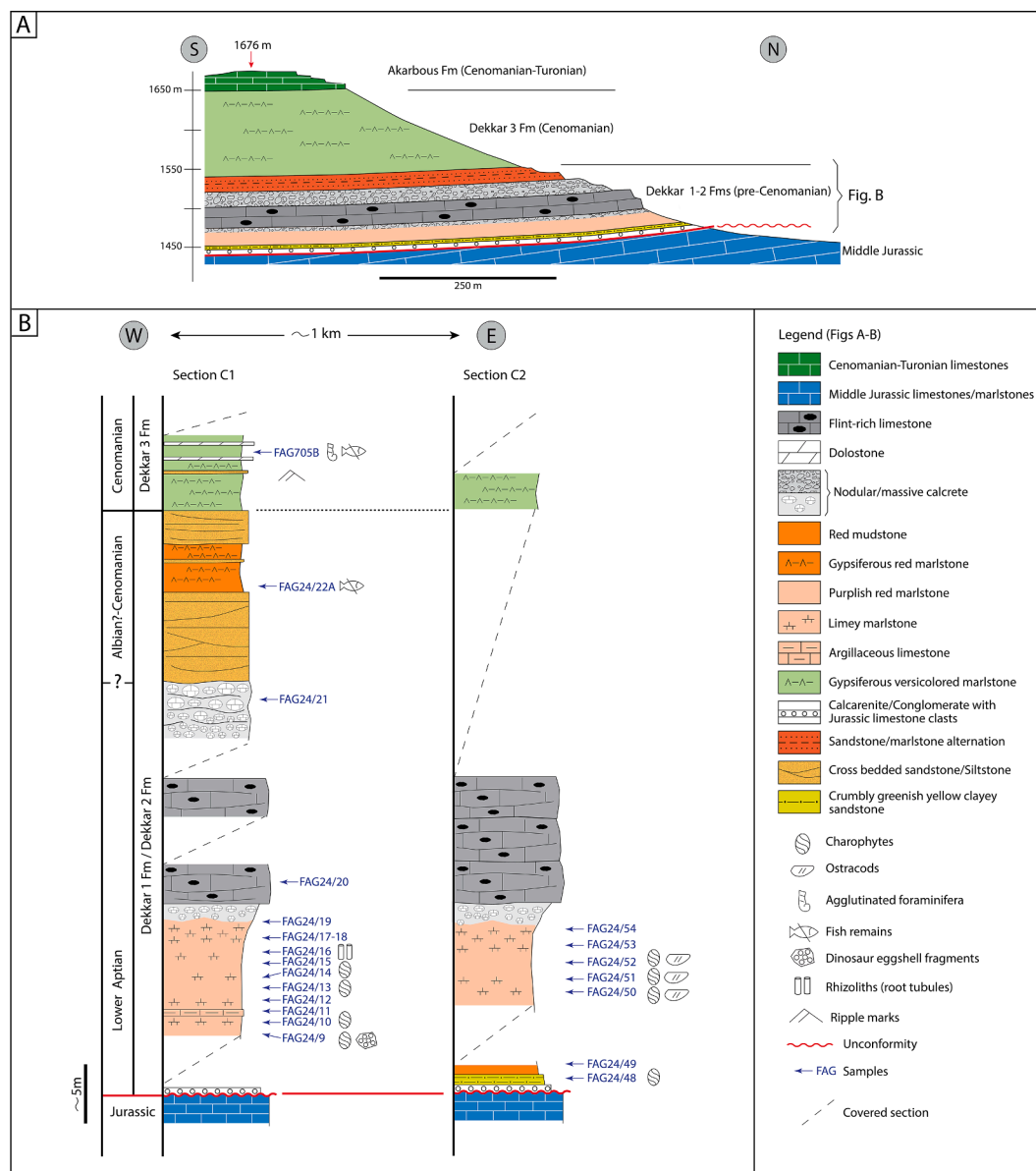


Fig. 2. A. Approximately S–N cross-section A–A' showing different units of the Cretaceous series, unconformably overlying the marine Jurassic substrate, southern limb of the Fom Aggaï anticline, see location in Fig. 1C. B. Sampled stratigraphic logs of sections C1 and C2, southern limb of the Fom Aggaï anticline.

sandstone/gypsiferous marlstone alternation at the top of the Dekkar 1–2 succession most probably belongs to the Dekkar 2 Formation, which are clearly distinguished in the neighbouring Anoual and Ksar Jilali synclines (Haddoumi et al., 1998, 2008). The succession of Dekkar1 and Dekkar 2 formations is overlain by the gypsiferous versicoloured marlstones of the Dekkar 3 Formation, whose base has provided fish remains and undetermined agglutinated foraminifera (sample FAG 705B, Fig. 2B), and the limestones of the generalized Cenomanian-Turonian transgression.

3.2. Chabkat Al Hassani area

This area is located ~40 Km east of the Fom Aggaï site, and yielded charophytes from sites CEH03 (samples TNW13 and TNW14) and CEH04 (sample TNW8, Fig. 3F) of the pre-Cenomanian base, as reported and summary described in brief by Haddoumi et al. (2024). Resampling of large quantities of sediments and a new detailed study led the discovery of new taxa.

3.3. Paleoenvironment

The Dekkar 1–2 succession of the studied areas suggests that deposition occurred in an alluvial to fluvial fan succeeded by a floodplain, with lacustrine-palustrine environments. More or less permanent freshwater bodies evolved into paleosols (semiarid climate) and a silica-rich lake with flint-rich limestones. The succession ends with a palustrine environment and/or a coastal fluvial system with sclerorhynchiform fish remains.

4. Results: systematic paleontology

Nine charophyte taxa were distinguished, including charophyte fructifications and thalli (Table 1).

4.1. Charophyte fructifications

Division Charophyta Migula, 1897

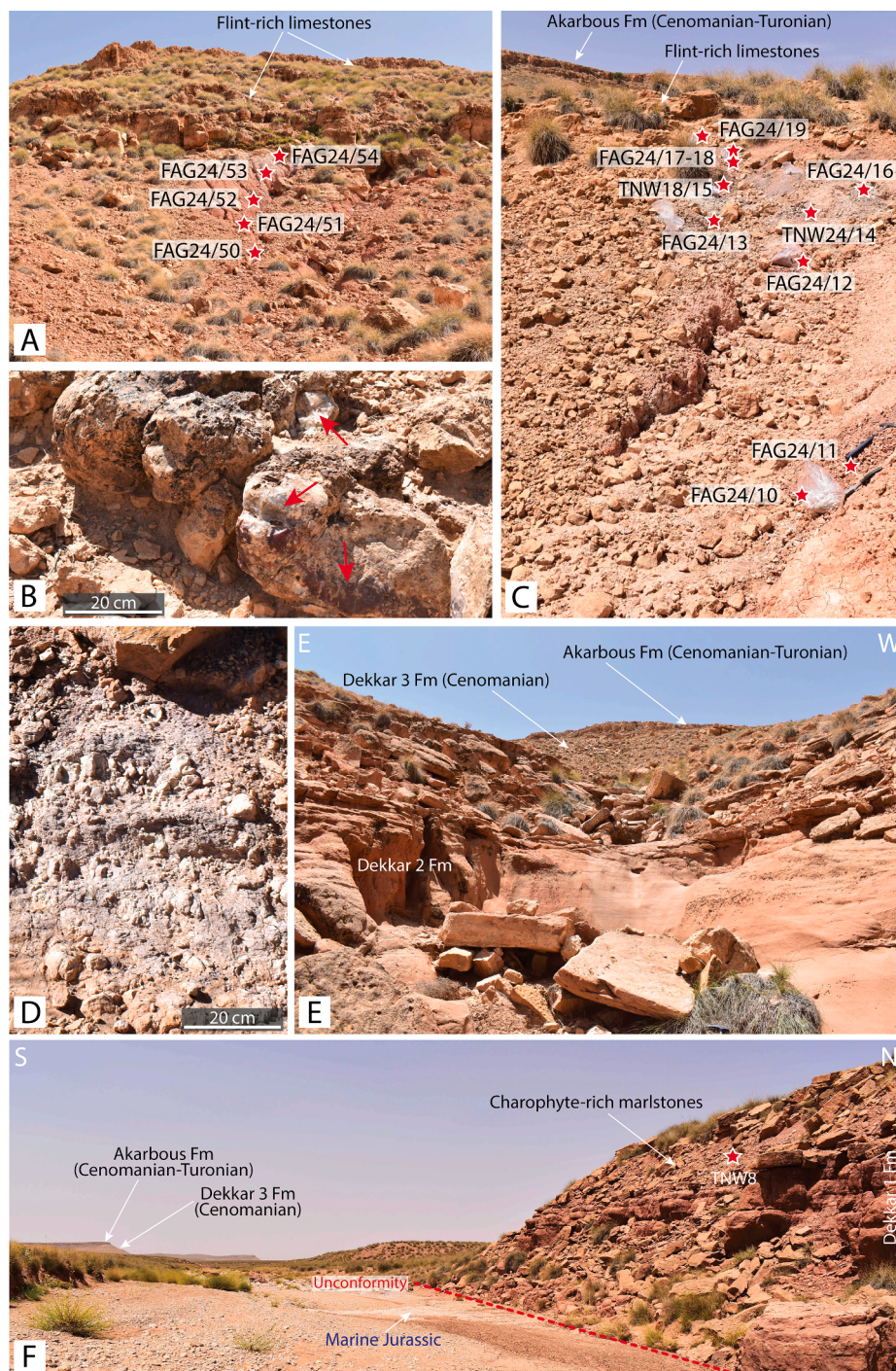


Fig. 3. A. Section C2 and studied samples, Dekkar 1–2 formations, Fom Aggaï area. B. Section C1 and studied samples Dekkar 1–2 formations, Fom Aggaï area. C. Flint-rich limestone showing silicified zone (arrows), Dekkar 1–2 formations, Fom Aggaï area. D. Nodular calcrete. E. Thick cross-stratified sandstone bed of the Dekkar 2 Formation, Fom Aggaï area. F. Field view of the studied charophyte-rich marlstones of Dekkar 1 Fm of site CEH04 (Haddoumi et al., 2024), Chabkat Al Hassani, Tendirara region (see location in Fig. 1B).

Class Charophyceae G.M. (Smith, 1938) emend. Schudack 1993.

Order Charales Lindley, 1836

Family Characeae (Richard ex C. Agardh 1824) emend. Martín-Closas et Schudack 1991

Characeae indet.

Figure 4 A–D.

Material: 45 gyrogonites from sample TNW8 and a smaller population in sample TNW14.

Description: Medium sized gyrogonites measuring between 536 and 663 μm in height and 445–627 μm in width. The shape is prolate with an isopolarity index (ISI) ranging between 102 and 134. Spiral cells are usually concave, but sometimes convex and can have double ridge. The apex is slightly rounded. The base is

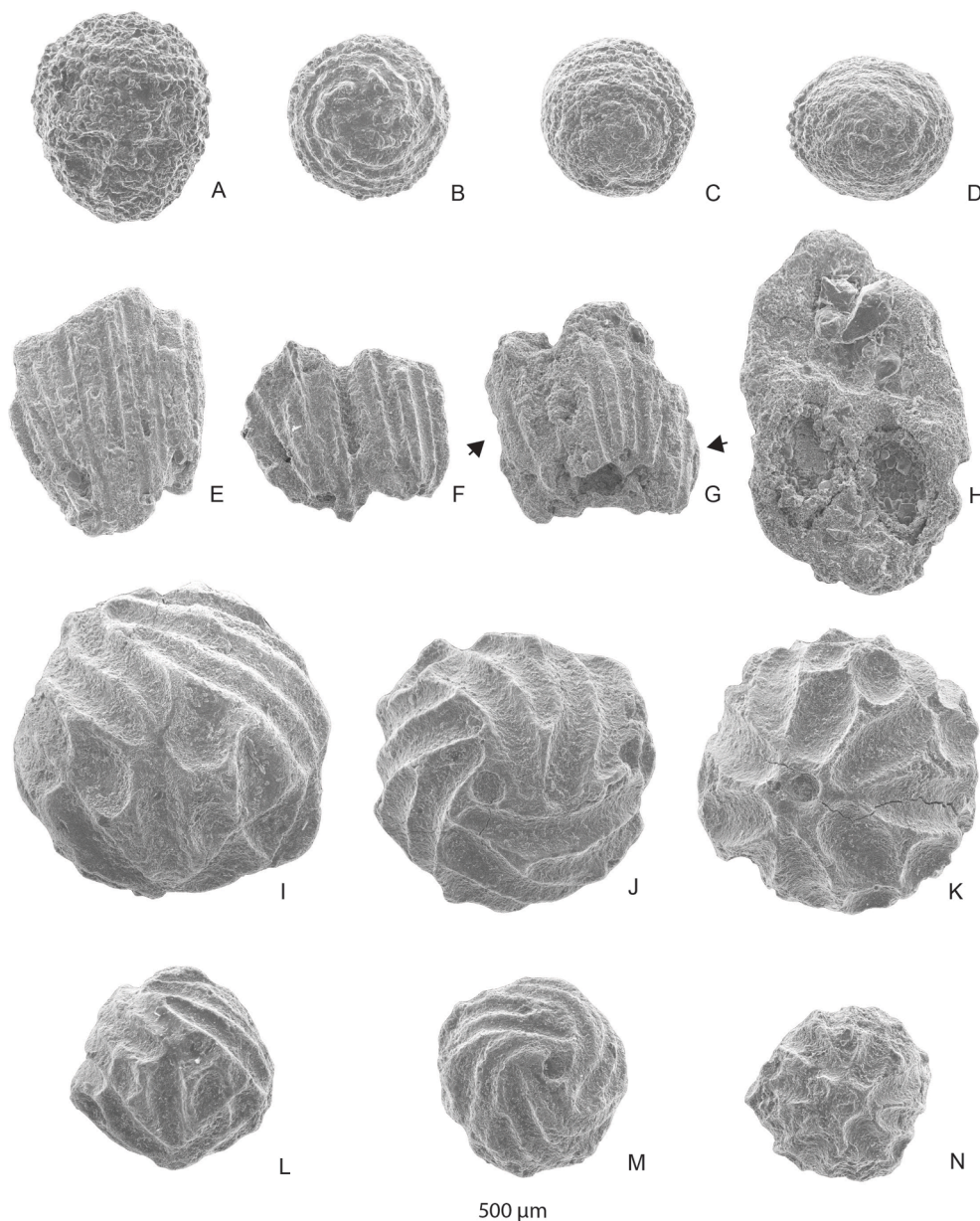


Fig. 4. SEM pictures of charophyte remains. A–D. Characeae indet. (sample TNW8). A. Lateral view (repository number HHTN25_01); B–C. Apical view (repository number HHTN25_02 and HHTN25_03); D. Basal view (repository number HHTN25_04). E–H. *Echinochara lazarii* (sample TNW8). E. Outer bract-cell series (repository number HHTN25_05); F. Two inner bract-cell series attached (repository number HHTN25_06); G. Three inner bract-cell series attached, one in the centre and two laterals (repository number HHTN25_07). The arrows mark the position of the other two utricles; H. Two casts of gyrogonites, partially filled with sparitic calcite (repository number HHTN25_08). I–N. *Atopochara trivolis* var. *trivolis*. I–K. Bigger utricles (sample FAG24/48). I. Lateral view (repository number HHFAG25_01); J. Apical view (repository number HHFAG25_02); K. Basal view (repository number HHFAG25_03). L–N. Small utricles. L. Lateral view (sample FAG24/48; repository number HHFAG25_04); M. Apical view (sample FAG24/48; repository number HHFAG25_05); N. Basal view (sample FAG24/09; repository number HHFAG25_06).

rounded to slightly pointed and can have a small basal funnel (Fig. 4D).

Remarks: The gyrogonites are superficially eroded and sometimes also corroded and do not have enough features preserved to attribute them to a particular genus (Figs. 4 A–D).

Family Clavatoraceae **Pia, 1927**

Sufamily Atopocharoidae (**Grambast, 1968**) emend. Martín-Closas ex **Schudack 1993**

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

Echinochara lazarii (**Martín-Closas, 2000**) Mojon ex Pérez-Cano, Bover-Arnal et Martín-Closas 2020

Figure 4 E–H.

2000 *Echinochara peckii* var. *lazarii* Martín-Closas – Martín-Closas, p. 70, Pl. 6: figs. 1–8, Pl. 7: figs. 1–6.

2003 *Echinochara lazarii* – Mojon p. 459. (*nomen nudum*).

2020 *Echinochara lazarii* (**Martín-Closas, 2000**) comb. nov. Mojon ex Pérez-Cano, Bover-Arnal et Martín-Closas – Pérez-Cano et al. p. 6–8

Material: 43 utricles from sample FAG24/48 and small populations in other samples (Table 1).

Description: Utricles are formed by two superposed bract-cell series (outer and inner series) that cover the gyrogonite in its abaxial part. The outer series is composed of seven bract cell series that are directly attached to the base of the fructification (Fig. 4E). The inner bract-cell series is composed of a short basal bract-cell

Table 1
Distribution of charophyte simples in the samples studied from Fom Aggai and Chabkat Al Hassani

	Fom Aggai						Chabkat Al Hassani		
	FAG 24/9	FAG 24/10	FAG 24/13	FAG 24/14	FAG 24/48	FAG 24/52	TNW8	TNW13	TNW14
Family Characeae									
Characeae indet.							X		X
Family Clavatoraceae									
Subfamily Atopocharoidae									
<i>Echinochara lazarii</i>							X		X
<i>Atopochara trivolvis</i> var. <i>trivolvis</i>	X	X	X	X	X	X	X		X
Subfamily Clavatoroidae									
<i>Clavator grovesii</i> var. <i>jiuquanensis</i>						X			
<i>Clavator grovesii</i> var. <i>corrugatus</i>						X			
<i>Clavator harrisii</i> var. <i>harrisii</i>	X			X	X	X	X	X	X
<i>Clavator harrisii</i> var. <i>reyi</i>	X			X	X	X	X	X	
<i>Clavator harrisii</i> var. <i>zavialensis</i>	X				X	X	X		
Charophyte thalli									
<i>Clavatoraxis</i> sp.					X	X	X		X

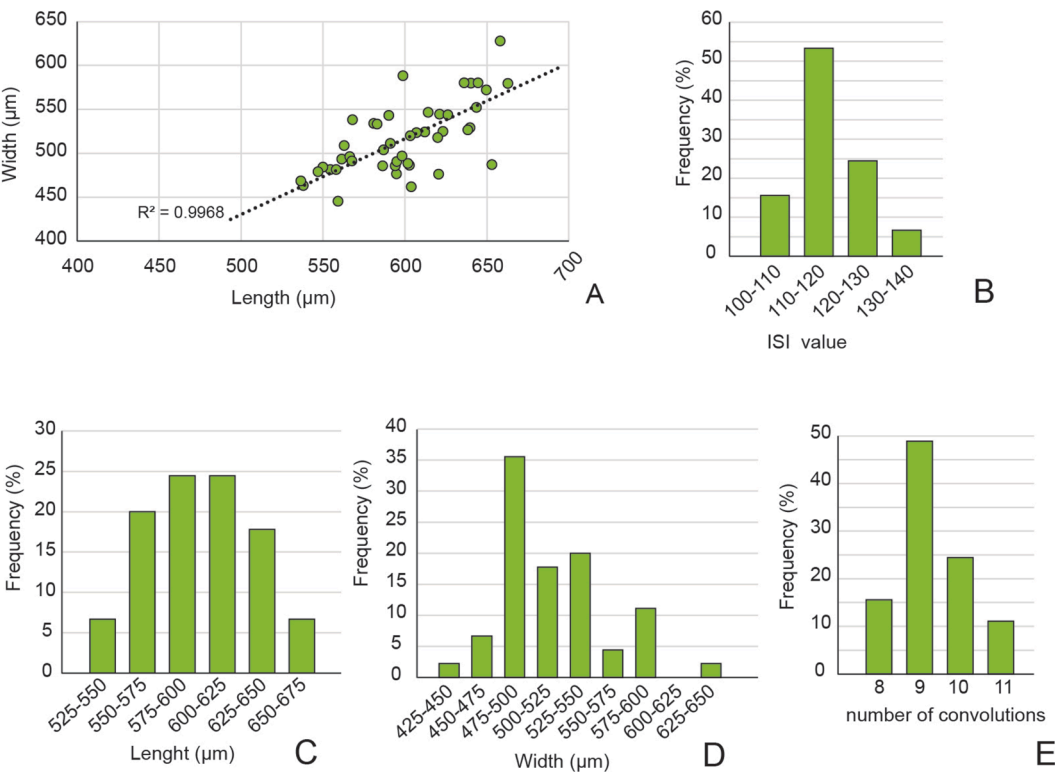


Fig. 5. Biometric analysis of Characeae indet. A. Scatter graph based on the length and width of the gyrogonites. B. Frequency distribution of the gyrogonite length. C. Frequency distribution of gyrogonite width. D. Isopolarity index (ISI). E. Number of convolutions.

and three long bract cells that are attached to the former, forming a fork-like unit (4F). Oospores are ellipsoidal, bottle-shaped, with apical and basal necks (Fig. 4H) and are not calcified and their morphology is known by the occurrence of sparitic moulds attached to the utricle. Partially-preserved fertile whorls, with up to three utricles attached are sometimes found in the studied material (Fig. 4G).

Biostratigraphic and biogeographic distribution: This species is widely distributed in the Barremian – lower Aptian in the Western Tethys area, including the Iberian Chain (Martín-Closas, 2000; Pérez-Cano et al., 2020), Pyrenees (Martín-Closas et al., 2025); Cantabrian Basin (Trabelsi et al., 2024), Algarve (Pérez-Cano et al., 2023), Jura Basin (Martín-Closas et al., 2009), and Eastern Atlas (Trabelsi et al., 2016). This is the first time that this species has been cited in the Moroccan Atlas.

Genus *Atopochara* (Peck, 1938)
Atopochara trivolvis (Peck, 1938) emend. Martín-Closas (1996)
Atopochara trivolvis var. *trivolvis* Peck (1938)
Figure 4 I–N
Material: 43 utricles in sample FAG24/48 and small populations in other samples (Table 1).
Description: This species is characterized by utricle displaying a branched structure that is repeated three times, resulting in tri-radiated symmetry. This structure has three basal cells directly attached to the base. The rightmost cell is upwards trifurcated into two diamond-shaped cells. A very small mark of the antheridium shield is rarely observed between diamond-shaped cells. The central and leftmost cells have the same structure. These cells are apically trifurcated into a small cell on the right and two long and dextrally-coiled cells that reach the top of the fructification.

Biostratigraphic and biogeographic distribution: This species has a cosmopolitan distribution, especially in the Aptian, being described in Eastern Asia, Europe, North Africa, North America, and South America (Martín-Closas and Wang, 2008 and references therein).

Subfamily Clavatoroidae (Grambast, 1969) emend. Martín-Closas ex. Schudack, 1993

Genus *Clavator* (Reid and Groves, 1916) emend. Martín-Closas ex Schudack (1993)

Clavator grovesii Harris 1939

Clavator grovesii var. *jiuquanensis* Wang (1965); Grambast (1970) emend. Martín-Closas (1996)

Figure 6 A–D.

1965 *Perimneste jiuquanensis* sp. nov. – S. Wang, p. 467, Pl. 1.

1970 *Clypeator jiuquanensis* (S. Wang 1965) comb. nov. – Grambast, p. 1965, Fig. D; Pl. 3, figs. 1–5.

1973 *Clypeator europaeus* sp. nov. – Mädlér in Neagu and Georgescu-Donos, p. 178, Pl. I, fig. 7–8; Pl. II.

1996 *Clavator grovesii* var. *jiuquanensis* S. Wang (1965) Grambast (1970) emend. – Martín-Closas, p. 278, Fig. 12.

Material: 37 utricles from sample FAG24/52.

Description: The utricle of this species is characterized by having two lateral and prominent shields composed of 12 cells with the same width. In the anterior part, these cells are interdigitated in a zig-zag line in the middle part. In the basal area of the anterior part there is a short cell at the base, corresponding to the anterior bract. The posterior part shows the impression of three cells, corresponding to the phylloid impression. Some specimens that show one shield that is slightly twisted while the other shield has straight cells (Fig. 6D). Similar specimens have recently been described in the Algarve Basin and identified as transitional morphotypes between *C. grovesii* var. *jiuquanensis* and *C. grovesii* var. *corrugatus* (Pérez-Cano et al., 2023).

Biostratigraphic and biogeographic distribution: The oldest occurrence of this variety is in the early late Barremian from the Maestrat Basin (Pérez-Cano et al., 2020; 2022a) and it is found in the upper Barremian–lower Aptian across Eurasia, from the Iberian Peninsula to Korea (Martín-Closas, 2015; Vicente et al., 2024 and references therein). This is the first time that this variety has been found in Africa.

Clavator grovesii var. *corrugatus* Peck (1941); Martín-Closas 1996 Figure 6 E–H.

1941 *Perimneste corrugata* sp. nov. – Peck, p. 295–297, Pl. 42, figs. 15–24.

1962 *Clypeator corrugatus* (Peck, 1941) comb. nov. – Grambast, p. 295.

1980 *Clypeator lusitanicus* sp. nov. – Grambast-Fessard, p. 39–41, fig. 3; Pl. 1, fig. 10–12; Pl. 2, figs. 1–5; Pl. 3, fig. 3–5.

1996 *Clavator grovesii* var. *corrugatus* (Peck, 1941) comb. nov. – Martín-Closas, p. 278, fig. 11.

1996 *Clavator grovesii* var. *lusitanicus* (Grambast-Fessard, 1980) comb. nov. – Martín-Closas, p. 278, fig. 11.

2000 *Clavator grovesii* var. *corrugatus* Peck (1941) Martín-Closas (1996) – Martín-Closas p. 142–145, Pl. 14, figs. 10–12.

Material: 10 utricles of sample FAG24/52.

Description: The utricle of this species has a bilateral symmetry, showing two lateral shields formed of 14 radial cells twisted dextrally. The posterior part has the imprint of the phylloid and two cells flanking it. The anterior part shows strong and irregular interdigitation of the cells of the lateral shields. Occasionally, this taxon has been found attached to a small portion of *Clavatoraxis* sp., the organ genus corresponding to the phylloid (Fig. 6E).

Biostratigraphic and biogeographic occurrence: Intermediate populations with *Clavator grovesii* var. *jiuquanensis* and *C. grovesii* var. *corrugatus* are found in upper lower Aptian deposits of the Algarve Basin (Pérez-Cano et al., 2023). Homogeneous assemblages of *C. grovesii* var. *corrugatus* have been found in the upper Aptian of the Algarve Basin (e.g., Pérez-Cano et al., 2023; and references therein) and in the lower–middle Albian of the Iberian Chain (Martín-Closas, 2000 and references therein). Outside the Iberian Peninsula, this taxon has also been described in the Aptian–Albian of the United States (Peck, 1941; Soulié-Märsche 1994). This is the first time that it has been found in Africa.

Clavator harrisii (Peck, 1941) emend. Martín-Closas (1996)

Clavator harrisii var. *harrisii* Peck 1941

Figure 6 I–M.

1941 *Clavator harrisii* sp. nov. – Peck, p. 292–294, Pl. 42, figs. 25–37.

1959 *Flabellochara harrisii* (Peck) comb. nov. – Grambast, p. 559.

1996 *Clavator harrisii* var. *harrisii* Peck – Martín-Closas, p. 278–279.

Material: 72 utricles from sample FAG24/52 and smaller populations in other samples (Table 1).

Description: The utricle is composed of two layers, a nodular internal layer and an external layer that covers the nodular one. The external layer has two lateral fans of cells; each composed of 5–7 cells. The posterior part has a phylloid imprint at the base and 5–7 cells around and above of the phylloid imprint. The anterior part is characterized by the presence of a single cell between the two fans. This taxon is occasionally found anatomically attached to a phylloid portion of *Clavatoraxis* sp., where up to three utricles (more commonly one or two) can be found attached to the same phylloid (Fig. 6I–J).

Biostratigraphic and biogeographic distribution: This taxon already occurs in the lower Valanginian deposits, where it is found forming intermediate assemblages with *Clavator harrisii* var. *dongjingensis* Hu and Zeng (1981) Martín-Closas (2000). This type of intermediate assemblage is sometimes also described in the lower Barremian (Pérez-Cano et al., 2020; Trabelsi et al., 2024). *Clavator harrisii* var. *harrisii* usually forms homogeneous populations in the Barremian (Martín-Closas, 2000; Pérez-Cano et al., 2020, 2022a), and rarely also in the Aptian (De Sosa Tomás et al., 2017) and lower–middle Albian (Álvarez-Parra et al., 2021). Nonetheless, in the upper Barremian–lower Aptian deposits, *C. harrisii* var. *harrisii* is usually found associated with *C. harrisii* var. *reyi* (Martín-Closas, 2000; Pérez-Cano et al., 2022a; Trabelsi et al., 2024) while in the upper lower Aptian–Albian beds it is associated with *C. harrisii* var. *zavialensis* (e.g., Martín-Closas 2000; De Sosa Tomás et al., 2017; Pérez-Cano et al., 2023). *C. harrisii* var. *harrisii* shows a cosmopolitan distribution in the Barremian–Albian time interval, being found in North and South America, whole Eurasia, and North Africa (Martín-Closas, 2015, and references therein).

Clavator harrisii var. *reyi* (Grambast-Fessard, 1980) Martín-Closas 1996

Figure 6 N–O.

1980 *Stellatochara reyi* sp. nov. – Grambast-Fessard, p. 42–44, Pl. 3, figs. 6–9.

1996 *Clavator harrisii* var. *reyi* (Grambast-Fessard, 1980) comb. nov. – Martín-Closas p. 279.

2005 *Luzochara reyi* (Grambast-Fessard, 1980) comb. nov. – Pereira and Cabral, p. 173–178, Pl. 1, figs. 1–6.

Material: 21 utricles from sample FAG 24/48 and smaller populations in other samples (Table 1).

Description: Most of the specimens attributed to this taxon have only preserved the gyrogonite with plane to concave spiral cells that are separated by slightly undulated sutures, and only a few of them have partially preserved the nodular layer. Some gyrogonites have different degrees of calcification (Fig. 6O), being considered

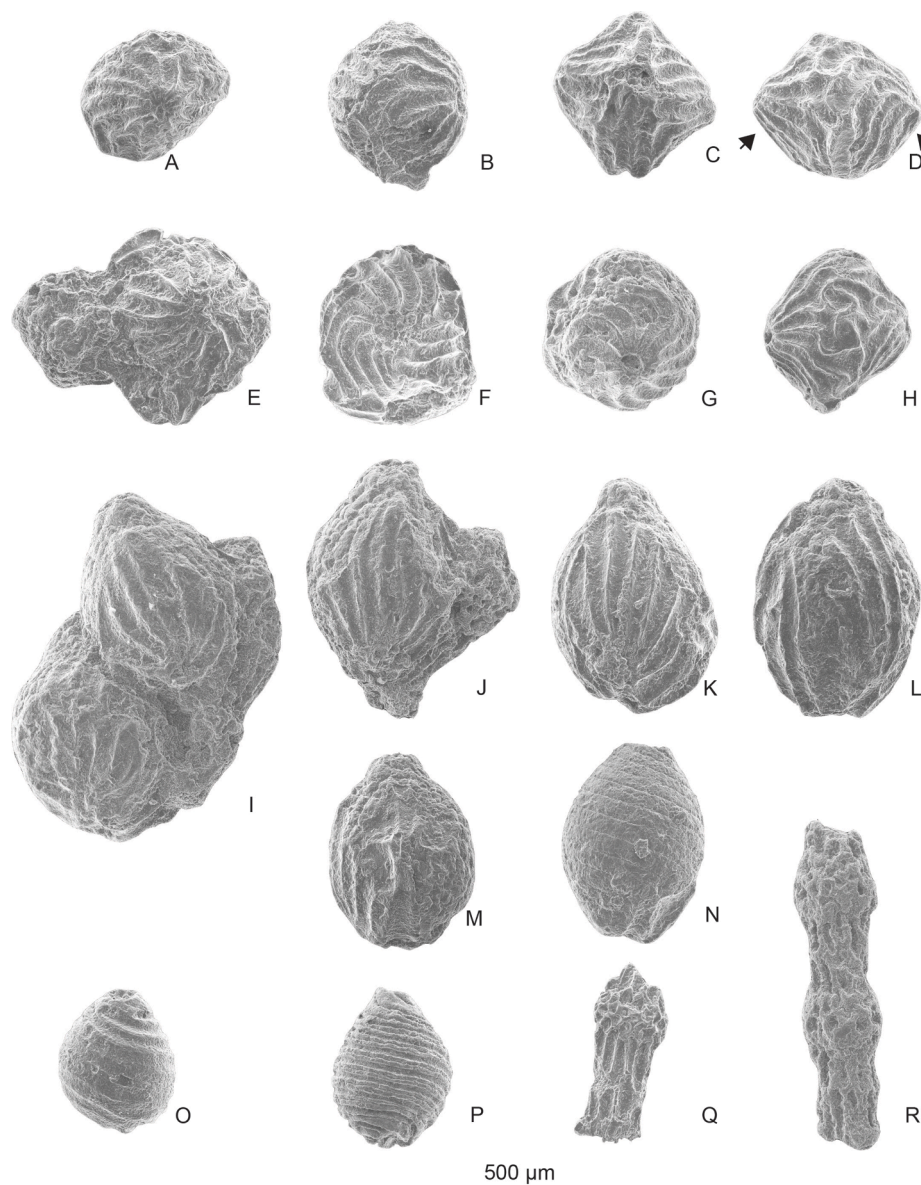


Fig. 6. SEM pictures of charophyte remains. A–C. *Clavator grovesii* var. *jiuquanensis* (sample FAG24/48). A. Lateral view (repository number HHFAG25_07); B. Anterior view (repository number HHFAG25_08); C. Basal view (repository number HHFAG25_09). D. *Clavator grovesii* var. *jiuquanensis* advanced morphotype (sample FAG24/48; repository number HHFAG25_10). Note that the cells of the right shield are slightly twisted while the cells of the left shield are still straight. E–H. *Clavator grovesii* var. *corrugatus* (sample FAG24/48). E–G. Lateral view showing the diversity of morphologies (repository number HHFAG25_11, HHFAG25_12, and HHFAG25_13). The arrow in picture E mark the phylloid attached to the utricle. H. Anterior view (repository number HHFAG25_14). Note the strong interdigitation of the cells of the lateral shields in comparison to *C. grovesii* var. *jiuquanensis* (picture B). I–M. *Clavator harrisii* var. *harrisii* (FAG24/52). I. Two utricles attached to a phylloid portion (repository number HHFAG25_15). J. Lateral view of a utricle attached to a phylloid portion of *Clavatoraxis* sp (repository number HHFAG25_16). K. Lateral view of an isolated utricle (repository number HHFAG25_17). L. Anterior view (repository number HHFAG25_18); M. Posterior view (repository number HHFAG25_19). N. *Clavator harrisii* var. *reyi*, lateral view (sample FAG24/48; repository number HHFAG25_20). O. *Clavator harrisii* var. *reyi* advanced, lateral view (sample FAG24/48; repository number HHFAG25_21). P. *Clavator harrisii* var. *zavialensis*, lateral view (sample FAG24/48; repository number HHFAG25_22). Q–R. *Clavatoraxis* sp. (sample FAG24/52). Q. Internode partially preserved and a node (repository number HHFAG25_23). R. Two nodes and two internodes anatomically attached (repository number HHFAG25_24).

intermediate morphotypes between *C. harrisii* var. *reyi* and *C. harrisii* var. *zavialensis*. Similar specimens were recently reported in the Algarve Basin, Southern Portugal (Pérez-Cano et al., 2023).

Biostratigraphic and biogeographic distribution: This species occurs in the lower Barremian of the Iberian Chain, where a few fructifications of this variety are associated with *C. harrisii* var. *dongjingensis* and *C. harrisii* var. *harrisii*, the latter being the dominant variety in the assemblage (Pérez-Cano et al., 2020; 2022a). *C. harrisii* var. *reyi* is especially common in the upper Barremian–lower Aptian of Western Europe and North Africa,

where it can form homogeneous populations or dominates over *C. harrisii* var. *harrisii* (Martín-Closas, 2000; Pereira and Cabral, 2005; Vicente and Martín-Closas, 2013; Trabelsi et al., 2016; Pérez-Cano et al., 2020; Sanjuan et al., 2021). *C. harrisii* var. *reyi* species has been considered endemic from the European Tethyan Archipelago which includes present day Western Europe and North Africa (Vicente et al., 2024, and references therein).

Clavator harrisii var. *zavialensis* Grambast-Fessard (1980) Martín-Closas (1996).

Figure 6 P.

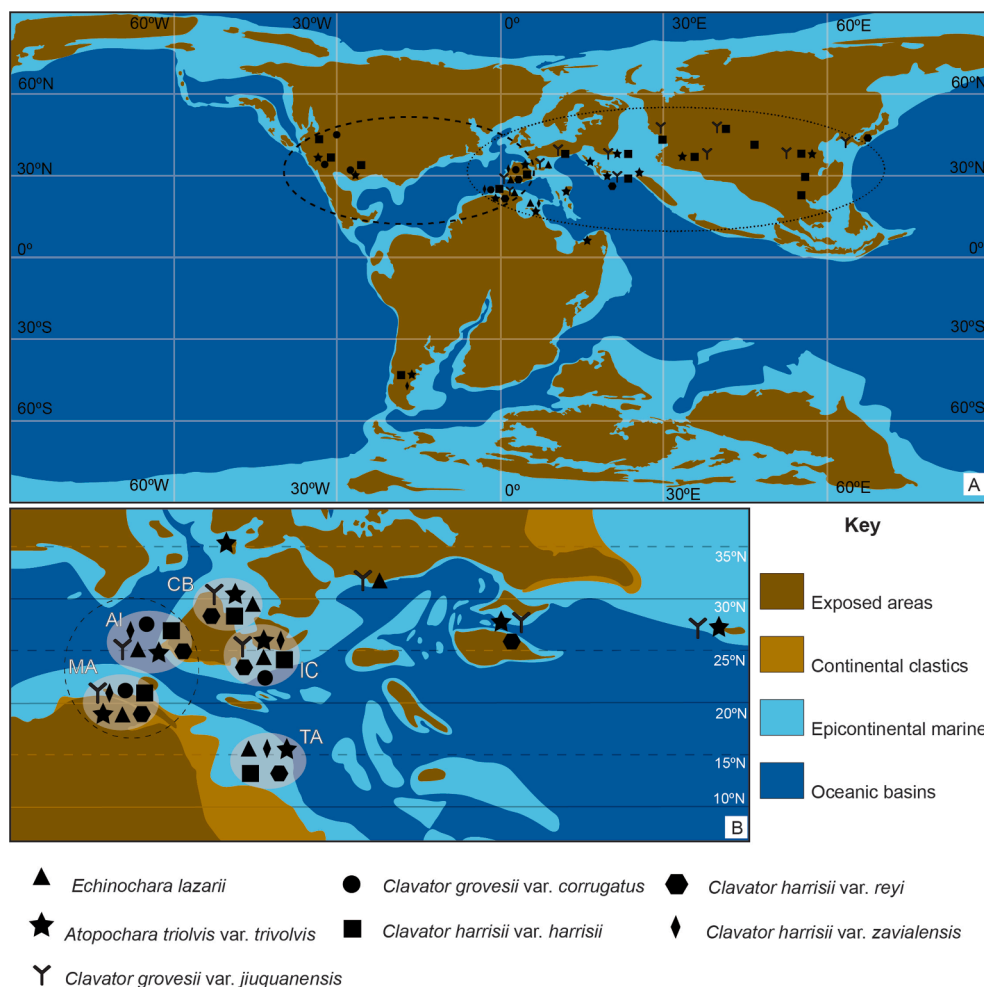


Fig. 7. Paleogeographic maps. A). Global distribution of clavatoracean species described in the Moroccan Atlas. The dotted line indicates the distribution of *Clavator grovesii* var. *jiuquanensis* in the Eurasian Domain, while the dashed line indicates the biogeographic distribution of *Clavator grovesii* var. *corrugatus* in the Atlantic Domain. Paleogeographic map modified from [Scotese et al. \(2024\)](#). B) Detail of the area of the Cretaceous Tethyan Archipelago (present-day Europe and North Africa). Dashed line indicates the area in which intermediate populations of *C. grovesii* var. *jiuquanensis* and *C. grovesii* var. *corrugatus*; and *Clavator harrisii* var. *harrisii*, *C. harrisii* var. *reyi*, and *C. harrisii* var. *zavalensis* are found, the Algarve Basin ([Pérez-Cano et al., 2023](#)) and in the Moroccan Atlas (this work). In the Iberian Chain, *C. grovesii* var. *jiuquanensis* is in the upper Barremian ([Pérez-Cano et al., 2020; 2022a](#)), while *C. grovesii* var. *corrugatus* is found in the Albian ([Martín-Closas 2000](#)). Paleogeographic map modified after Masse (2000) and [Pérez-Cano \(2021\)](#).

1980 *Stenochara zavalensis* sp. nov. – Grambast-Fessard, p. 44, Pl. 3, figs. 10–13.

1996 *Clavator harrisii* var. *zavalensis* ([Grambast Fessard, 1980](#))
comb. nov. – Martín-Closas, p. 279.

Material: 15 utricles in sample FAG 24/48 and smaller populations in other samples ([Table 1](#)).

Description: This is the last variety of the evolutionary lineage of *Clavator harrisii* ([Martín-Closas, 1996](#)), and in the studied populations it is always associated with *C. harrisii* var. *harrisii* and *C. harrisii* var. *reyi* ([Table 1](#)). The utricle of this variety is characterized by a preserved gyrogonite with concave cells. The cells are separated by a double ridge. The Ringstruktur-calcification pattern of [Schudack \(1993\)](#), which is typical of the clavatoroid gyrogonites, can be seen in the apical part of the gyrogonite.

Biostratigraphic and biogeographic distribution: This species occurs in the upper lower Aptian–Albian deposits of the Algarve Basin ([Grambast-Fessard, 1980](#)) where it can be found forming intermediate assemblages with *C. harrisii* var. *harrisii* and *C. harrisii* var. *reyi* ([Pérez-Cano et al., 2023](#)). In the lower Aptian strata, this species has recently been described in the Golfo San Jorge Basin (Patagonia, Argentina) where it is associated with *C. harrisii* var. *harrisii* ([De Sosa](#)

[Tomás et al., 2023](#)). This variety is also found in the upper Aptian–Albian deposits of the Eastern Atlas, forming homogeneous assemblages ([Trabelsi et al., 2016](#)), in the Iberian Chain and the Pyrenees ([Martín-Closas, 2000](#) and references therein).

4.2. Charophyte thalli

Genus *Clavatoraxis* [Martín-Closas et Diéguez 1998](#)
Clavatoraxis sp.

[Figure 6 Q–R.](#)

Material: tens of phylloid portions in samples TNW8, TNW14, FAG 24/48 and FAG 24/52.

Description: The internodes of these thalli are corticated, showing 12 concave cells. Spine-cell rosettes are found in the nodes ([Fig. 6Q–R](#)). In the present study, these thalli portions are sometimes found anatomically attached to utricles of *Clavator harrisii* var. *harrisii* ([Fig. 6I–J](#)) and possibly also to utricles of *C. grovesii* var. *corrugatus* ([Fig. 6E](#)).

Remarks: *Clavatoraxis* differs from the genus *Munieria* in having completely calcified spiral cell and in bearing spine cell-rosettes

on the cortical cells. The internodes of studied thalli superficially show similarities with the internodes of *Munieria*, such as the concave morphology of the cells. However, the genus *Clavatoraxis* has 12 cells while *Munieria* has a minimum 28 (see Pérez-Cano et al., 2020 and references therein). These two morphological features enable the two thalli morphologies to be distinguished.

5. Discussion

5.1. Biostratigraphy

The occurrence of intermediate populations of *Clavator grovesii* var. *jiuquanensis* and *Clavator grovesii* var. *corrugatus*, and intermediate populations of *Clavator harrisii* var. *harrisii*, *Clavator harrisii* var. *reyi*, and *Clavator harrisii* var. *zavialensis* provide high-value biostratigraphic markers. This association belongs to the *Clavator grovesii* var. *jiuquanensis* Eurasian biozone, which is defined as lying between the first occurrence of homogeneous populations of *C. grovesii* var. *jiuquanensis* and the first occurrence of homogeneous populations of *C. grovesii* var. *corrugatus* (Pérez-Cano et al., 2022a). This biozone is equivalent to the European biozone *Asciadiella cruciata*-*Pseudoglobator paucibracteatus*, which is defined as lying between the first occurrence of *Asciadiella cruciata* and *Pseudoglobator paucibracteatus* and the first occurrence of homogeneous populations of *C. grovesii* var. *corrugatus* (Martín-Closas et al., 2009; Pérez-Cano et al., 2023). The age of these biozones is well-constrained to the late Barremian–early

Aptian timespan according to their correlation with the ammonite and dinoflagellate biostratigraphy (Martín-Closas et al., 2009; Pérez-Cano et al., 2023, respectively) and the strontium-isotope stratigraphy (Pérez-Cano et al., 2022a).

The overlap of the previous biostratigraphic correlations with palynology, including dinoflagellates (Pérez-Cano et al., 2023), and pollen (De Sosa-Tomás et al., 2023) places the studied assemblage in the lower Aptian. This excludes the lowermost Aptian, as homogeneous populations of *C. grovesii* var. *jiuquanensis* are still found in Eurasia (e.g., Li et al., 2020).

The new charophyte association allows for a more precise determination of the age of the lower part of the pre-Cenomanian Red beds of the Fom Aggaï area. This age can be extended at least to the neighbouring outcrops of the Southern High Plateaus, as is the case in the Tendara region (Chabkat Al Hassani) where an interval spanning upper Barremian–Aptian has recently been identified (Haddoumi et al., 2024), and in Ain Mellouk (Fig. 1B) where a similar series to those described in the Fom Aggaï outcrops is present. The correlation between different sectors can be seen in Figure 8.

5.2. Paleobiogeography

The charophyte assemblage described in the High Plateaus (Morocco) sheds light on the biogeographic distribution of charophytes during the early Aptian. Notably, *Clavator grovesii* var. *jiuquanensis*, which is found across Eurasia (Vicente et al., 2024

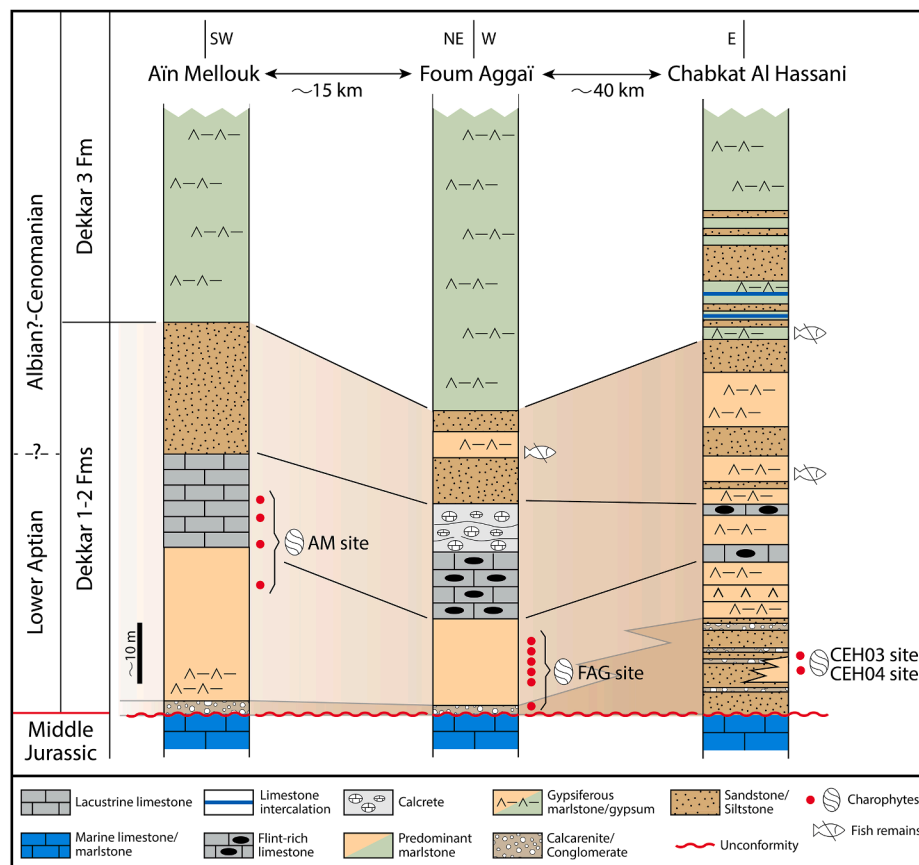


Fig. 8. Correlation of the Lower Cretaceous synthetic logs across the Southern High Plateaus. Ain Mellouk log modified after Feist et al. (1999).

and references therein; Fig. 7A), and *Clavator grovesii* var. *corrugatus*, only described in the 'North Atlantic Domain' (North America and the Iberian Peninsula; Martín-Closas, 2015 and references therein; Fig. 7A), are described for the first time in the paleocontinent of Gondwana. A similar assemblage, including *Echinochara lazarii*, *Atopochara trivolis* var. *trivolis* and intermediate populations of *C. grovesii* var. *jiuquanensis* and *C. grovesii* var. *corrugatus*, and *C. harrisii* var. *harrisii*, *C. harrisii* var. *reyi* and *C. harrisii* var. *zavialensis* has only been described in the lower Aptian deposits of the Algarve Basin (Pérez-Cano et al., 2023, Fig 7B). This suggests strong biogeographic connection between both areas during the Aptian.

The absence of *C. grovesii* var. *jiuquanensis* and *C. grovesii* var. *corrugatus* in the neighbouring Tunisian Atlas could be related to paleoecological restrictions of these species. In this regard, *Echinochara lazarii* has previously been reported in the Tunisian Atlas (Trabelsi et al., 2016) and had wide paleoenvironmental tolerances during the late Barremian, including freshwater and brackish settings (Pérez-Cano et al., 2022b), and probably also during the early Aptian. Similarly, *A. trivolis* var. *trivolis* and *C. harrisii* var. *harrisii* have a wide paleoenvironmental distribution (e.g., Pérez-Cano et al., 2022b and references therein) that could be one of the factors that facilitated their cosmopolitan distribution (Martín-Closas and Wang, 2008; Martín-Closas, 2015, respectively; Fig. 7A). *Clavator grovesii* var. *jiuquanensis* and *Clavator grovesii* var. *corrugatus* seem to have a latitudinal distribution pattern. Paleogeographic reconstructions (e.g., Scotese et al., 2024, Fig. 7A-B) suggest that the Tunisian basins were located at a paleolatitude below 20°N. This paleolatitude may have acted as palaeoclimatic barrier for the distribution of *Clavator grovesii*, persisting throughout the entire evolutionary history of the species, and thus restricting the biogeographic distribution of the species to particular climate areas or environments, as reported by Martín-Closas (2015).

6. Conclusions

Seven charophyte taxa, including *Echinochara lazarii*, *Atopochara trivolis* var. *trivolis*, *Clavator grovesii* var. *jiuquanensis*, *Clavator grovesii* var. *corrugatus*, *Clavator harrisii* var. *harrisii*, *Clavator harrisii* var. *reyi*, and *Clavator harrisii* var. *zavialensis* are described and illustrated in the Lower Cretaceous Red beds in the Moroccan High Plateaus (Eastern Meseta). The study provides new data about the biogeographic distribution of some of these species, especially *Echinochara lazarii*, which is reported here for the first time in the Western Atlas Domain. In addition, *Clavator grovesii* var. *jiuquanensis* and *Clavator grovesii* var. *corrugatus*, which are reported here for the first time in Africa, display a wide distribution in Eurasia and in the Atlantic Domain, respectively, providing a tool with which to perform intercontinental correlations. However, intermediate populations of *Clavator grovesii* var. *jiuquanensis*-*C. grovesii* var. *corrugatus*, and *C. harrisii* var. *harrisii*-*C. harrisii* var. *reyi*-*C. harrisii* var. *zavialensis* have only been described in the Iberian Peninsula, and particularly in the Algarve Basin, reinforcing their inclusion of these basins in the Central Tethyan Archipelago charophyte bioprovince.

The studied assemblage belongs to the *Clavator grovesii* var. *jiuquanensis* Eurasian biozone and to the coeval *Asciidiella cruciata*-*Pseudoglobator paucibracteatus* European biozone. In particular, intermediate populations of *C. grovesii* var. *jiuquanensis* and *C. grovesii* var. *corrugatus* and intermediate assemblages of *C. harrisii* var. *harrisii*, *C. harrisii* var. *reyi*, and *C. harrisii* var. *zavialensis* allow placing the assemblage in the lower Aptian. This study shows that intermediate populations are useful in charophyte biostratigraphy due to their brief chronostratigraphic duration.

CRedit authorship contribution statement

Hamid Haddoumi: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jordi Pérez-Cano:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Rachid Chennouf:** Writing – review & editing, Validation, Resources, Methodology, Investigation. **Jemaa Amakrane:** Writing – review & editing, Validation, Methodology, Investigation. **Sidi Mohamed Mamoun:** Writing – review & editing, Validation, Resources, Methodology, Investigation.

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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Data availability

I have shared all the data in the attached files

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