

The Albian-Cenomanian transition in a shelf-basin transect: Biostratigraphy, sedimentology and paleontology of Jebel Mghila, Central Tunisia

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ABSTRACT

Twenty-two ammonite species are identified in the upper Albian *Mortoniceras* (*Subschloenbachia*) *rostratum*, *Mortoniceras* (*Subschloenbachia*) *perinflatum* and *Stoliczkaia* (*Shumarinaia*) *africana* Zones, and in the lower Cenomanian *Mantelliceras mantelli* Zone. The species *Placentoceras Saadensis* Thomas and (Thomas and Peron, 1890, 1890 is revised, including *Engonoceras Thomasi* Pervinquier, 1907, and is placed within the genus *Hypengonoceras* Spath, 1922. This accurate biostratigraphic framework allowed to evidence, at the Albian-Cenomanian transition (*S. (S.) africana* Zone), a significant sea level drop, responsible for emergence and erosion to the SE, and for deposition of a Lowstand wedge to the NW, fed by erosional channels on the shelf slope. Plesiosaur remains found in the upper Albian series (base of *M. (S.) rostratum* Zone) represent one of the few elasmosaurids known worldwide in the Albian, and the first plesiosaurian reported from Tunisia.

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1. Introduction

The Albian stage is one of the longest stages in Mesozoic times (≈ 12 Ma), and records many sedimentological and geodynamic events, such as a major marine transgression (Haq, 2014), the widespread demise of carbonate shelves (Skelton et al., 2003), Oceanic Anoxic Events (OAE) (e.g., Schlanger and Jenkyns, 1976; Luciani et al., 2007), local synsedimentary tectonic events, and the opening of the equatorial Atlantic Ocean (Klingelhoefer et al., 2016). In spite of these important features, this period is still poorly known and understood, mainly because of its thick and monotonous, chiefly argillaceous succession, which rarely offers good exposures.

The south-Tethyan margin of Tunisia offers the opportunity of studying the sedimentary record of the Albian stage, thanks to good outcrops, to fossiliferous successions, and to good exposures along the shelf to basin transition, in the central and northern parts of the country. In this work, we present a study of the uppermost Albian deposits and their transition to the Cenomanian sediments in Jebel Mghila, which is located in Central Tunisia, and presents an outer shelf succession of marls and thin limestone beds. The collection of about fifteen ammonite levels and the sedimentological study of three 20–50 m thick sections, make possible to refine the latest Albian ammonite succession, to explore the transition between the Albian and Cenomanian stages, and to describe the first plesiosaurian specimen discovered in Tunisia.

2. Geological and historical background

During Mesozoic times, Tunisia is part of the South-Tethyan passive continental margin, the rifting of which occurred in Triassic times. The Mesogean sea is assumed to open in the Cretaceous (Dercourt et al., 1986), reactivating the extensional rifting

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structures. From the late Eocene onwards, the Alpine compression deformed the Mesozoic series into NE-trending folds, giving way to the present-day structural domains. These are the Tellian nappes in northernmost Tunisia, the intracontinental folded belt of the Atlas chain in Northern and Central Tunisia, and the almost undeformed Saharan platform to the South. The northern part of the Atlas domain is marked by numerous diapirs, and is sometimes referred to as the diapir zone (e.g., Snoke et al., 1988; Amri et al., 2020). The Atlas domain is separated from the eastern lowlands around Kairouan by a complex zone of folds and faults, the North-South Axis, which also acted as a major normal fault (Fig. 1).

During the Cretaceous, Tunisia comprised four paleogeographic domains (Fig. 1; Fournié and Pacaud, 1973; Zghal and Arnaud, 2005; Soua, 2015). The southern Saharan platform is a stable domain, which received a thin, incomplete sedimentary succession. It is separated from Central Tunisia, by the subsident Chott depression. The Central Tunisian platform is a little subsident zone, marked by the deposition of abundant Cretaceous shelf carbonates and by a long lasting hiatus that encompasses part of the Albian stage. The North Tunisian Basin corresponds to the Northern Atlas and the Tell nappes. It received mainly outer shelf marls and shales during the Cretaceous.

After pioneer exploratory works by French geologists in the late 19th century, Pervinquier (1903, 1907) was the first to establish a stratigraphy of the Mesozoic strata of Tunisia, based on detailed paleontological studies. This synthesis has been then used for the publication of numerous geological maps, and enlarged by Burollet (1956) to Central and Northern Tunisia, by means of numerous field sections, and the collection of abundant fauna. At the same time, Dubourdieu (1956) stated the geology and stratigraphy of north-eastern Algeria and northwestern Tunisia. Since then, many sedimentological works have been carried out, leading to a better understanding of the Cretaceous evolution of the Tunisian margin. Regarding the Albian-Cenomanian succession, detailed stratigraphic works on the Cretaceous succession in Tunisia have been published by Bismuth (1973), Bismuth et al. (1981, 1982), M'Rabet (1981), Philip et al. (1989), Robaszynski et al. (1993a, 1993b, 2008), M'Rabet et al. (1995), Zghal et al. (1997), Jaillard et al. (2005), Lehmann et al. (2009), Chihaoui et al. (2010), Latil (2011), Ben Fadhel et al. (2011), Layeb et al. (2012), Meister and Abdallah (2012) and Kennedy and Gale (2015).

According to these works, the Aptian carbonate shelf became emergent in most of Central Tunisia, around the Aptian-Albian boundary (Burollet, 1956; M'Rabet et al., 1995; Tour et al., 2015). Subsequently, the Albian marine transgression progressively overwhelmed the emergent part of Central Tunisia. It began in earliest Albian times around Tajerouine (Chihaoui et al., 2010; Latil, 2011), and in late Albian times in most of Central Tunisia (Bismuth et al., 1982; M'Rabet et al., 1995; Tour et al., 2015). The latest Albian time-span is marked by a shallowing upward trend, which triggered the northward progradation of shelf carbonates (Bismuth et al., 1982). The Albian-Cenomanian boundary is poorly constrained in Southern and Central Tunisia, where it is usually merged into a single Zebbag Formation, made of massive shelf limestones with evaporite intercalations (M'Rabet et al., 1995; Jaballah and Negra, 2016). Farther North, the Albian-Cenomanian boundary is marked by a limestone intercalation within the shaly marls of the Fahdene Formation (Burollet, 1956; Robaszynski et al., 1993b; Jaillard et al., 2005).

Jebel Mghila is a NE-trending anticline, the axis of which plunges to the SW toward the city of Sbeitla (Fig. 2). Because it is comprised between the underlying Aptian shelf carbonates and the overlying Turonian shelf limestone, the Albian and Cenomanian marls are well exposed in a "U" shaped depression crossed by a road joining the localities of Jilma to the SE, and Sbiba to the NW.

Pervinquier (1903) was the first to describe the Albian-Cenomanian succession in this locality. Then, Tour et al. (1989) summarized the upper Albian-Campanian sedimentation of Jebel Mghila, and Kennedy and Gale (2015) described the ammonite succession of the Cenomanian series of this area, following a work by Hancock.

Here, we present three sections of the upper Albian-lowermost Cenomanian succession (Fahdene Formation) studied in Jebel Mghila. Two sections have been studied on the western flank of the anticline (MR and MHC, Fig. 2B) and one on the eastern flank of the structure (MH, Fig. 2B). The lower part of the upper Albian marly succession and its lower contact with the Aptian massive dolomites (Serdj Formation) is difficult to observed, due to abundant soil and cultivated fields.

3. Biostratigraphy

Pervinquier (1903) described two outcrops at the South-East (South of Fom el Guelta) and at the South (Kef Si Abd el Kader) of Jebel Mghila. He did recognize the "Vraconnien" stage, also called "zone à *Mortoniceras inflatum*" at the base of his Cenomanian (units 1–3 of Pervinquier, 1903) with "*Stoliczkaia dispar* d'Orb., *Mortoniceras inflatum* Sow." and "*Turrilites Bergeri* Brong."

Hancock, Kennedy and Gale (Kennedy and Gale, 2015) investigated the Cenomanian to lowermost Turonian successions, which were originally described in Pervinquier (1903), but they did not investigate the uppermost Albian interval, providing only new descriptions of the material collected by Pervinquier.

As pointed out by Kennedy and Gale (2015), the uppermost Albian zonal succession developed in western Europe (Amédéo, 1992, 2002; Amédéo et al., 2004; Latil, 1995; Kennedy and Latil, 2007) can be used in Tunisia, keeping in mind that Robaszynski et al. (2008) interpreted the *Stoliczkaia africana* Zone as a regional equivalent of the West-European *Pleurohoplites briacensis* Zone, which is supported by our field observations. The biostratigraphic scheme herein adopted for the uppermost Albian comprises three lineage zones [*Mortoniceras* (*M.*) *fallax*, *Mortoniceras* (*S.*) *rostratum*, *M.* (*S.*) *perinflatum* Zones] and one interval zone [*Stoliczkaia* (*S.*) *africana* Zone].

Our measured sections correspond to units 1–4 of Pervinquier (1903), and the massive beds located at their top correspond to the "laterally extensive dolomitic limestone" of Kennedy and Gale (2015). They allow us to provide a detailed biostratigraphic scheme for the uppermost Albian (Fig. 3).

The *Mortoniceras* (*M.*) *fallax* Zone has not been recognized in the absence of fossil material, even though this zone is most probably represented in the lower part of the Mghila East section (MH.1–11, Fig. 3).

The *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone has been identified at the base of the Mghila West section (beds MR.1 and 2) and in the Mghila East section (beds MH.11–17; Fig. 3) with the following assemblage:

Puzosia sp. juv.

Hypenoceras saadense (Thomas and Peron, 1890).

Stoliczkaia (*Stoliczkaia*) *clavigera* (Neumayr, 1875).

Stoliczkaia (*Stoliczkaia*) sp. juv.

Mortoniceras (*Subschloenbachia*) *rostratum* (J. Sowerby, 1817).

Cantabrigites spinosum (Pervinquier, 1907).

?*Cantabrigites* sp. nov.

Lechites gaudini (Pictet and Campiche, 1861)

Anisoceras armatum (J. Sowerby, 1817).

The *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone is well expressed in the three sections (beds MH.17–19, MR.3–3b and MHC.3; Fig. 3), yielding the following assemblage:

Desmoceras (*Desmoceras*) *latidorsatum* (Michelin, 1838).

Hypenoceras saadense (Thomas and Peron, 1890).
Stoliczkaia (*Stoliczkaia*) *clavigera* Neumayr, 1875.
Mortoniceras (*Mortoniceras*) *pachys* (Seeley, 1865).
Mortoniceras (*Subschloenbachia*) *perinflatum* (Spath, 1922).
Cantabrigites spinosum (Pervinquier, 1907).
Scaphites aff. *meriani* Pictet and Campiche, 1861.

In the absence of the index species, the *Stoliczkaia* (*S.*) *africana* Zone is herein defined by default between the last *Mortoniceras* occurrence and the first occurrence of true Cenomanian ammonites, below the discontinuity at the base of the laterally extensive sandy dolomitic bed (beds MH.22-24 and MR.3-5). The following assemblage has been collected within this interval (Fig. 3): *Puzosia* aff. *mayoriana* (Orbigny, 1841) (large specimen). *Hypenoceras saadense* (Thomas & Peron, 1890). *Mariella* (*Mariella*) *bergeri* (Brongniart, 1822).

The Albian-Cenomanian boundary in Mont Risou, Southeastern France, given by Kennedy et al. (2004, see also Petrizzo et al., 2015), is defined by “the level 36 m below the top of the Marnes Bleues, which corresponds to first occurrence of the planktonic foraminiferan *Rotalipora globotruncanoides*.” This boundary lies within the west-European *Pleurohoplites briacensis* Zone (Kennedy et al., 2004). The occurrence of evolved morphologies of *Mariella* (*M.*) *bergeri* in the *Stoliczkaia* (*S.*) *africana* Zone of the eastern MH section, strongly suggests that the Albian-Cenomanian boundary lies within the latter ammonite zone.

The lower Cenomanian *Neostlingoceras carcitanense* Subzone of the *Mantelliceras mantelli* Zone is possibly known in the Mghila Centre section (Bed MHC.4-10) with the occurrence of the following assemblage (Fig. 3):

Stoliczkaia (*Stoliczkaia*) aff. *clavigera* Neumayr, 1875.
Mantelliceras couloui (d'Orbigny, 1850).
Mariella (*Mariella*) *dorsetensis* Spath, 1926.

The upper *Mantelliceras mantelli* Zone is well expressed in the three studied sections (above beds MH.25, MR.7 and MHC.10), yielding the following assemblage:

Pachydesmoceras aff. *denisonianum* (Stoliczka, 1865).
Sharpeiceras florencae Spath, 1925.
Mantelliceras couloui (d'Orbigny, 1850).
Mantelliceras lymense (Spath, 1926).
Graysonites cobbani (Amédéo, 1994).
Mariella (*Mariella*) *dorsetensis* Spath, 1926.
Mariella (*Mariella*) *lewesiensis* (Spath, 1926).

4. Sedimentology

4.1. Jebel Mghila

Four major discontinuities have been identified in Jebel Mghila sections (Fig. 4).

The first one (D1) corresponds to the contact with the Aptian dolomites (Serdj Formation). The top of the latter is partly brecciated, mineralized and karstified. Karst cavities are filled up with yellow, dolomitic sandstone, presenting bioturbation, ferruginous bivalves and gastropods, and locally, cross bedding. The iron rich cap contains aeolian quartz grains, lithoclasts and marine fauna (brachiopods, sea-urchins), indicating a marine transgression that follows a long-lasting emergence. The latter corresponds to the post-Aptian hiatus known in most of Central Tunisia (Burollet, 1956). This discontinuity likely contains several amalgamated surfaces.

The second discontinuity (D2) is marked by an erosional surface overlain by dolomitic sandstone containing aeolian quartz and sandstone lithoclasts. In section MR (Fig. 4), a small channel is infilled with biogenic calcarenite containing rounded quartz, lithoclasts, gastropods, nautilus and ammonites. Plesiosaur vertebrae,

found loose close to this outcrop, most likely proceed from the infilling of this channel, interpreted as a small-scale incised valley. No evidence of emergence has been found, but the lithoclasts, channelized deposits and reworking evidence indicate an erosional hiatus.

The third discontinuity (D3) is well marked in the three studied sections. In sections MR and MH, it is marked by an erosional surface at the base of a set of yellow/orange, massive, coarsely sandy, dolomitic beds, which can be followed all along the outcrop of Jebel Mghila (unit 2 of Pervinquier, 1903; base of the sections described by Kennedy and Gale, 2015). In section MHC, it is marked, 5 m below the sandy dolomitic beds, by an erosional surface overlain by sandy dolomitic marls containing coarse quartz grains and reworked pebbles of calcareous marl, up to 12 cm large. In all sections, it marks an abrupt lithologic change, with respect to the mainly shaly-marly, underlying series.

The fourth discontinuity (D4) is marked in all sections by a bioturbated, phosphate- and glauconite-rich, sandy marl bed, overlying a first, noticeable massive sandy dolomite bed. This level contains ammonites, irregular sea-urchins, scarce rudistids, ankerite and aeolian quartz grains. The abundance of phosphate, glauconite and bioturbation indicates a condensation level, while the fauna indicates an outer shelf, open marine environment. The

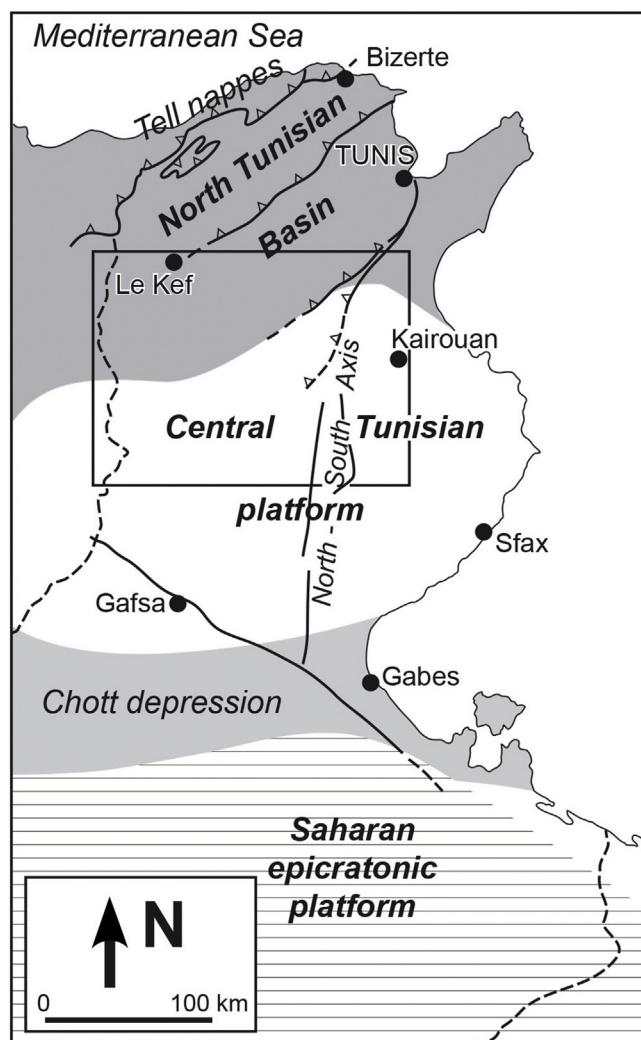


Fig. 1. Main Cretaceous sedimentary domains in Tunisia, and location of Fig. 2.

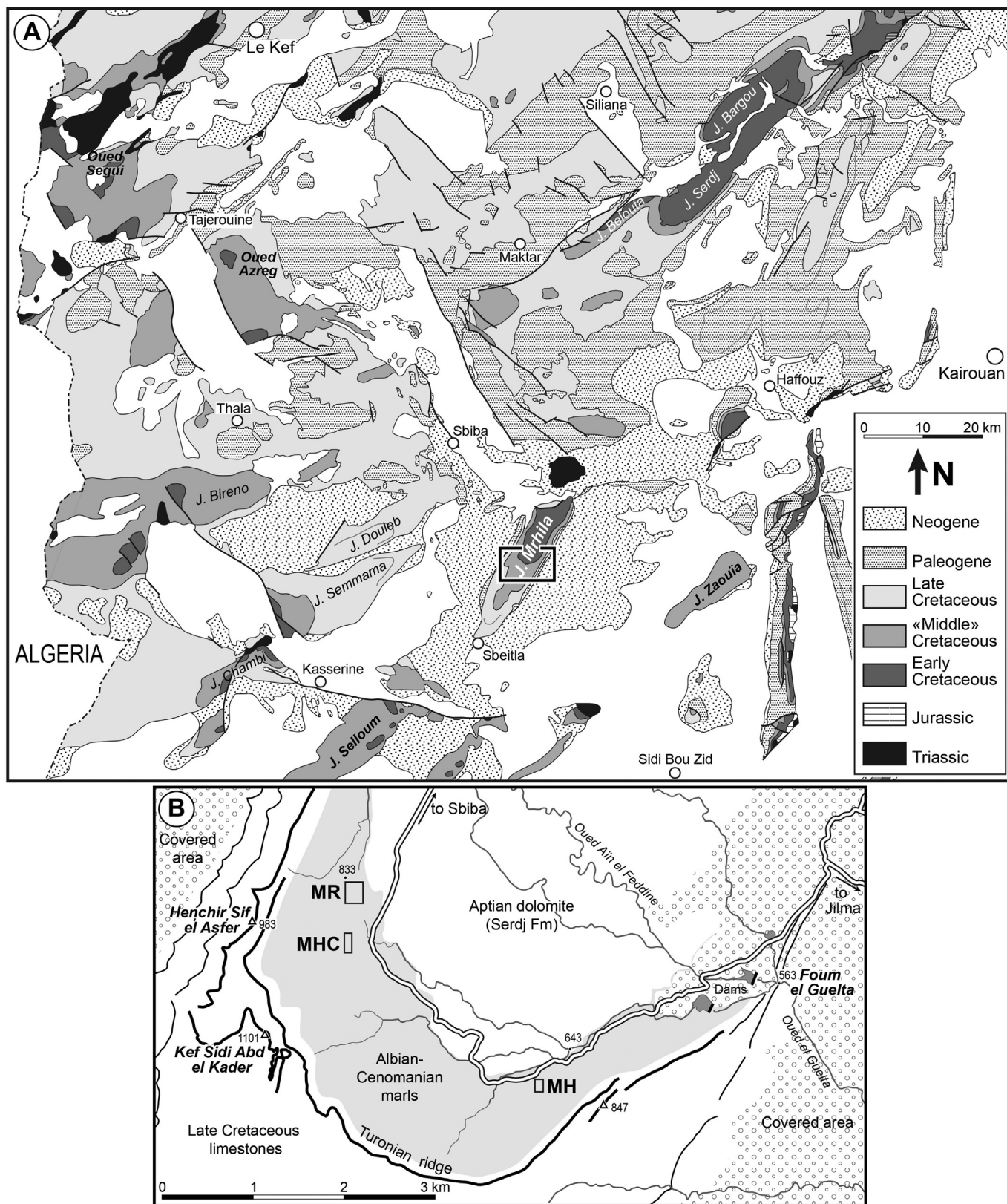


Fig. 2. Geological sketch of Central Tunisia (A), and location of the studied sections (B).

base of the sandy dolomite bed may be interpreted either as a sequence or parasequence boundary, while the condensed bed itself (D4) would represent the subsequent transgressive surface.

The fifth discontinuity (D5) resembles the fourth one. It is located at the top of a second well marked massive sandy dolomite bed (top of unit 2 of Pervinquier, 1903; top of the “laterally extensive dolomitic limestone” of Kennedy and Gale, 2015). It is a thin, glauconite- and phosphate-rich bed, containing bioclasts, ammonites and sea-urchins. The base of the underlying dolomitic and sandy bed is interpreted either as a sequence or parasequence boundary, the phosphate bed (D5) corresponding to a transgressive surface.

These sedimentary discontinuities define three third order depositional sequences (Fig. 4 and 5).

The first one is poorly exposed. In the eastern section (MH), it consists of a succession of sandy dolomitic beds, with few marl interbeds. The occurrence of gastropods, pectinids and fragments of other bivalves, as well as abundant glauconite, indicate a marine environment. Bioturbation is also present. Sedimentary features consist of some cross bedding and current ripples near the base, and of horizontal laminae in the upper part, suggesting a shallow marine deposition. The last sandy dolomite bed presents iron-rich mineralization and stromatolitic laminae, suggesting an intertidal environment and a subsequent emergence period. Available data allow to ascribe this sequence to the *M. (M.) fallax* (?) and the very base of the *M. (S.) rostratum* ammonite zones.

The base of the second depositional sequence (S2) is exposed in the western (MR) and eastern section (MH), where it is affected by

minor faults that may disturb the observed succession. To the East (MH section), it begins with white, slightly sandy, calcareous marl beds bearing fish remains (vertebrae and teeth) oysters and pectinids, indicating a shallow marine environment. They are overlain by white calcareous marls and green clayey marl containing benthic fauna (oysters, pectinids and other bivalves, scarce fish remains) and abundant ammonites, suggesting a transgressive trend. To the West (MR section), above the plesiosaurian-bearing channel, the lower part of the sequence contains both benthic (brachiopods, echinoids, scarce bivalves) and pelagic fauna (ammonites, belemnites), while the upper part only contains ammonites, indicating an outer shelf environment and supporting the transgressive trend. Pyrite is locally abundant. The top of this sequence seems to have been eroded below the overlying erosional discontinuity. It has been deposited during the late *M. (S.) rostratum*, the *M. (S.) perinflatum* and part of the *S. (S.) africana* ammonite zones.

The base of the third sequence (S3) presents variable successions. In the western and eastern sections, S3 begins with a bed of yellow to reddish, sandy dolomite or limestone, which presents an erosional base and contains quartz gravels and lithoclasts up to 1 cm in diameter (D3). This bed is overlain by the phosphate-rich bioturbated, sandy marls with sandy dolomitic marl bed, interpreted as D4. The faunal content (irregular sea-urchins, rudistids (*Sauvagesia nicaisei* of Pervinquier, 1903) and ammonites) suggests a shallow, open marine environment.

In the MHC section, the succession is more complete. It begins (bed 4, Fig. 4) with some beds of clayey, dolomitic sandstone, which

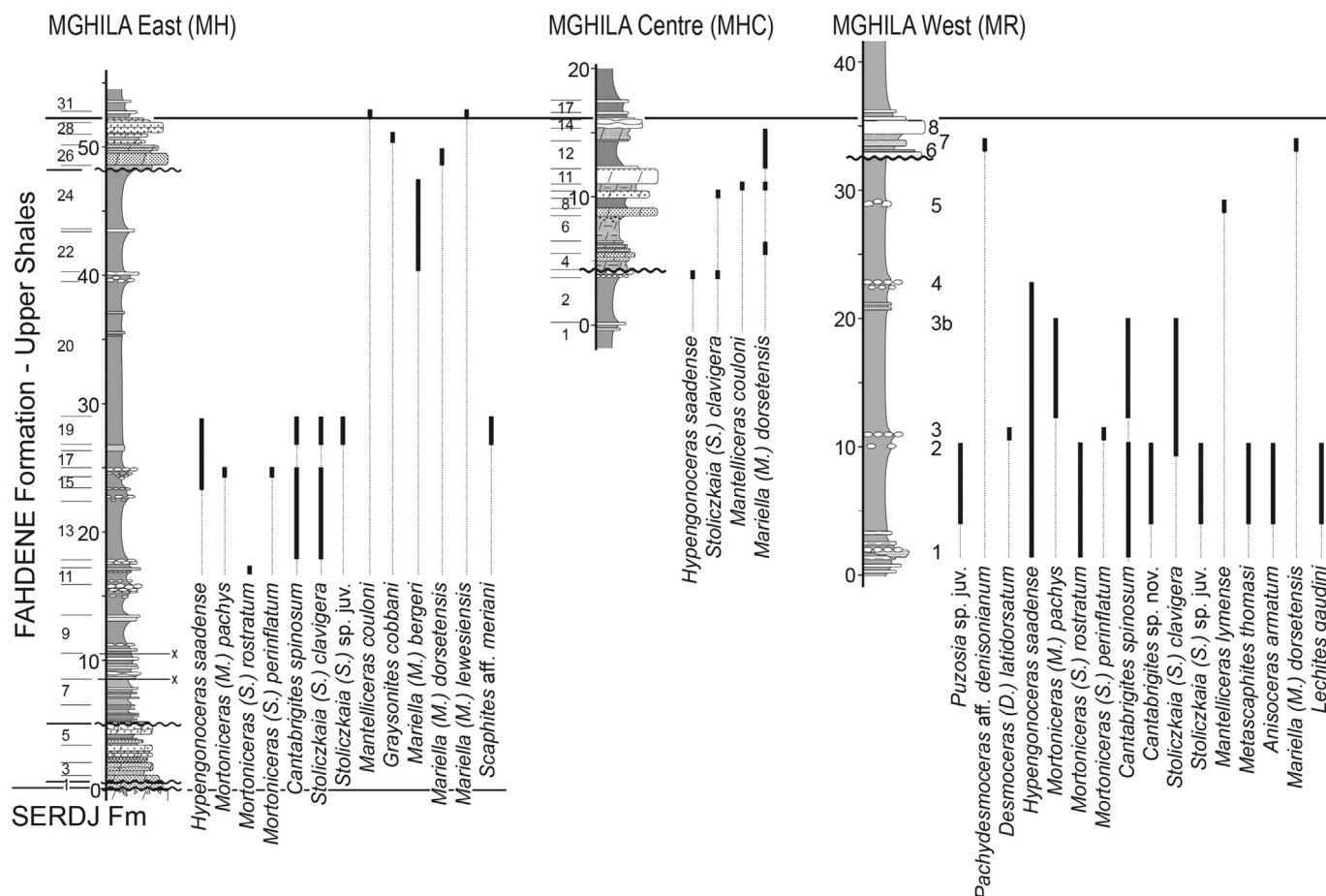


Fig. 3. Ammonite distribution along the Albian-Cenomanian transition in Jebel Mghila (location on Fig. 2B).

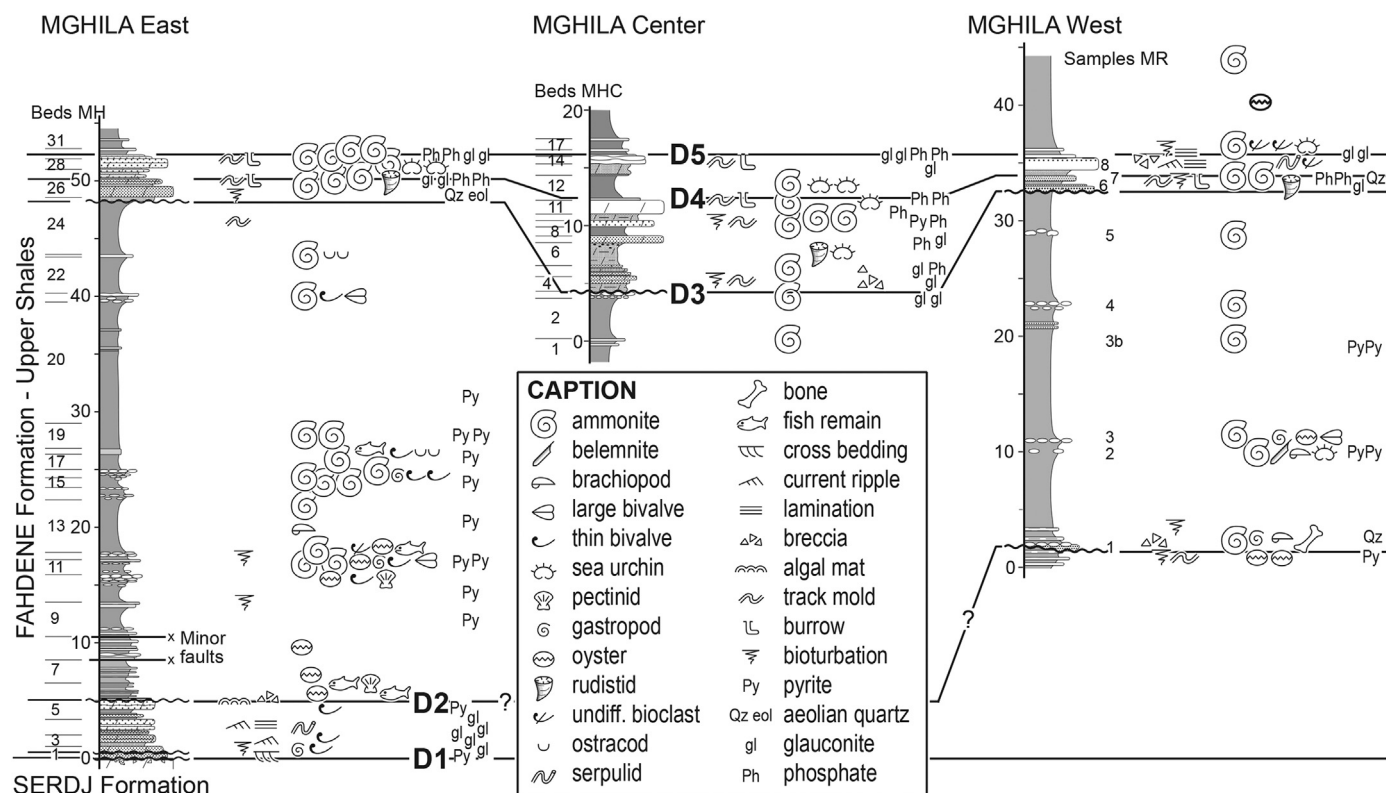


Fig. 4. Sedimentological sections of the Albian-Cenomanian transition in Jebel Mghila (location on Fig. 2B).

contains reworked pebbles of the underlying nodular calcareous marl and quartz gravels, and is capped by a Fe–Mg rich crust (hard ground). These are overlain by coarse sandstone rich in phosphate, grading upward into sandy and dolomitic marls containing scarce regular sea-urchins, rudistids and ammonites (beds 5 and 6). They are overlain by massive beds of coarse grained to gravelly dolomitic sandstone (beds 7–11, Fig. 4), capped by D4.

In all sections, the phosphate- and glauconite-rich marl bed capped by D4 is overlain by bioturbated, sandy marl beds still rich in phosphate and glauconite, bearing irregular urchins, bioclasts, serpulids and ammonites, suggesting a submarine condensed sedimentation. These phosphate-rich layers are overlain by a massive bed of bioturbated sandy dolostone, showing locally laminae and ripples. The top of the sandy dolomite is capped by a glauconite- and phosphate-rich marly layer, locally bearing bioclasts and ammonites (D5). Overlying this thin layer interpreted as a Transgressive Surface, is a thick succession of green clayey marl, the base of which yields scarce oysters and ammonites (unit 3 of Pervinquier, 1903; see also Kennedy and Gale, 2015). None of the late Albian ammonites described by Touir et al. (1989) above D5 have been found, and in agreement with Kennedy and Gale (2015), we consider the overlying sequence as early Cenomanian in age (Fig. 5).

In total, the D3–D5 interval is 12 m thick in section MHC, whereas it is 3–3.5 m in the other sections. Therefore, combined with the biostratigraphic data that evidence an erosion of the upper part of sequence 2 in section MHC, the base of sequence 3 in the latter section is interpreted as the infilling of a channel caved in sequence 2, and infilled by lowstand deposits. In this interpretation, a significant erosion occurred during the Albian-Cenomanian transition period (*S. (S.) africana* ammonite zone) in the area of Jebel Mghila. No evidence of an emergence period has been found (karst, desiccation, paleosols ...) in Jebel Mghila, which can be due

to the marly nature of the underlying deposits. Therefore, it is not possible to specify certainly whether erosion took place in a submarine or subaerial environment.

4.2. Comparison with neighbouring areas

In Central Tunisia, uppermost Albian deposits bear evidences of a shallowing upward trend. In Jebels Selloum and Semmama (Fig. 2), the upper Albian marls grade upward into locally cross-bedded, coarse-grained bioclastic limestones (Bismuth, 1973; Bismuth et al., 1982; Philip et al., 1989, Fig. 6). The latter were deposited in a high energy, very shallow marine environment, and their top is marked by emergence features (Bismuth et al., 1982; Philip et al., 1989). The high lateral thickness variations of the bioclastic limestones suggest that either they are deeply channelized, or more probably, they were strongly eroded. These observations show that a subaerial erosion at the top of the upper Albian marls of Jebel Mghila is likely.

In Jebel Semmama, the top of the bioclastic limestones yielded “*Submantelliceras* sp.”, associated with poorly preserved specimens of “*Paraturrilites*”, “*Mortonicer*” and “*?Knemiceras*” (Philip et al., 1989). Since “*Submantelliceras*” is a Cenomanian genus and the other ones are late Albian in age, either the latter are reworked, or *Submantelliceras* sp.” has been misidentified. In Jebel Selloum, the shallow marine bioclastic limestones are overlain by limestone of open marine environment, in turn overlain by shallow marine rudistid-rich limestones. This open marine limestone yielded “*Submantelliceras* gr. *couloni*” and “*Mantelliceras* cf. *picteti*” (Philip et al., 1989), which indicate the upper part of the “*Mantelliceras mantelli*” Zone of early Cenomanian age. In Jebel Zaouia (Fig. 2 and 6), the Aptian dolomites are overlain by a comparable sequence, which yielded ammonites of the *M. mantelli* Zone (“*Submantelliceras martinpreyi*”, “*Mantelliceras lymense*”, “*M. saxbii*”, “*M.*

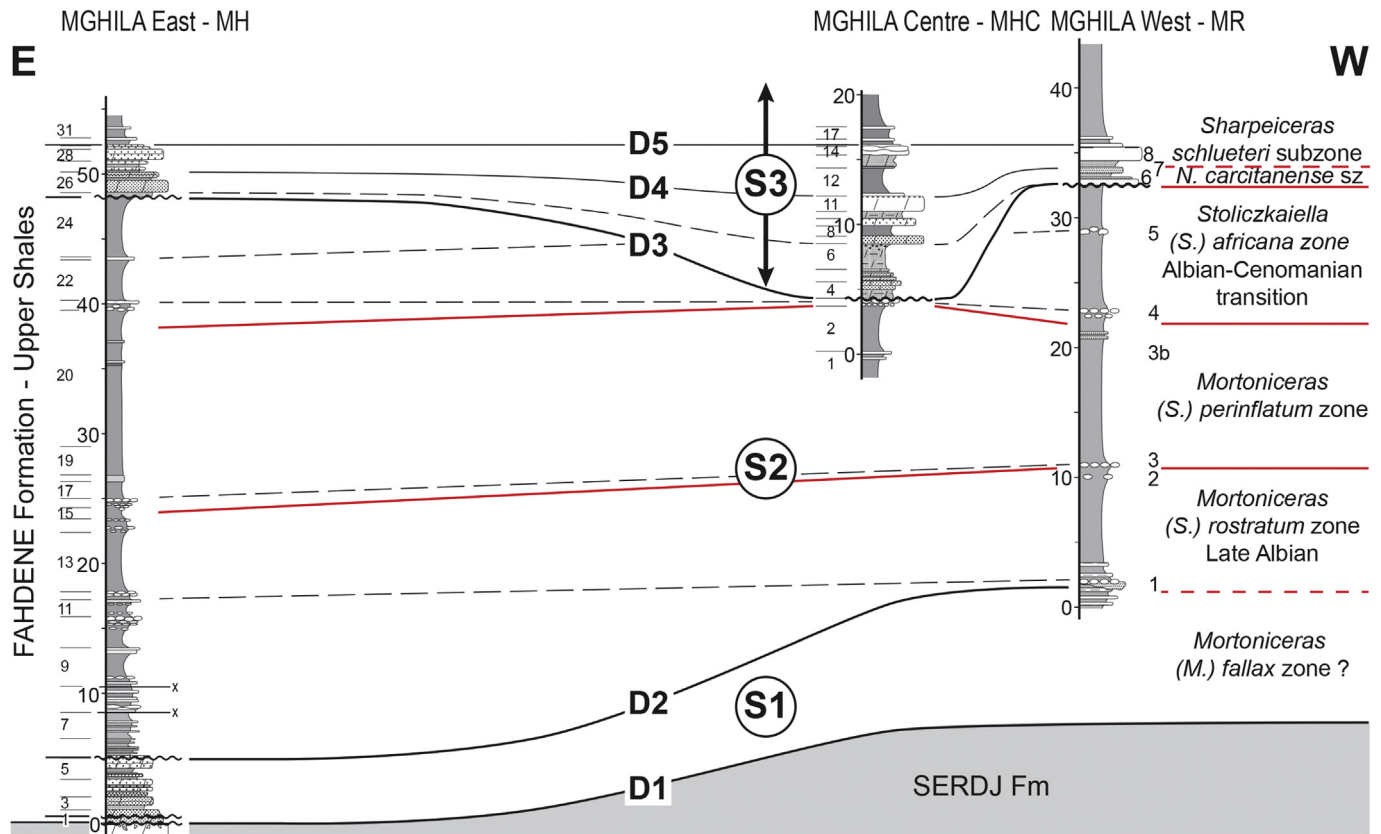


Fig. 5. Sequence stratigraphy interpretation and age of the Albian-Cenomanian transition in Jebel Mghila.

gr. dixonii", "M. cf. mantelli", "M. tenue"; Philip et al., 1989). The overlying, oyster-rich marls yielded "Sharpeiceras laticlavium" and "Mantelliceras lymense" of early Cenomanian age (Philip et al., 1989).

In Northern Tunisia, uppermost Albian marls also record a shallowing upward trend, since mud mounds and isolated corals and rudistids have been mentioned (Robaszynski et al., 1993b; Jaillard et al., 2005; Layeb et al., 2012). East of Jebel Jerissa (Oued Azreg, Fig. 2), Robaszynski et al. (1993a; 1993b; 2008) described at the top of the upper Albian marls, a 20 m thick, thickening upward succession marked by shallow erosional channels, interpreted as a lowstand deposits (Shelf margin wedge), which contains the Albian-Cenomanian boundary defined by foraminifera (Fig. 6). It is capped by three phosphate- and ammonite-rich channelized beds, which were ascribed to two local, newly defined ammonite zones (G. azregensis and G. cobbani Zones) of earliest Cenomanian age (Robaszynski et al., 1993a; 2008). Kennedy and Gale (2015) consider the G. cobbani ammonite zone as corresponding to the Sharpeiceras schlueteri Subzone (earliest Cenomanian) of the M. mantelli Zone.

Farther northwest (Oued Segui, Fig. 2; erroneously named Oued Zerga in Jaillard et al., 2005), the "Late Albian" marls are overlain by a 30 m thick thickening- and shallowing-upward sequence culminating with sandy limestones showing current features and shallow marine fauna (isolated rudistids, echinoids) (Jaillard et al., 2005, Fig. 6). This sequence yielded latest Albian ammonites and contains the Albian-Cenomanian boundary defined by foraminifera (Fig. 5). It is first overlain by a ≈ 20 m thick aggrading strata set, in which appear the first typical Cenomanian ammonites. Above, a thinning-upward succession yielded ammonites from both the G. azregensis and G. cobbani Zones, and is interpreted as a transgressive (retrogradational) sedimentary body (Jaillard et al., 2005).

4.3. Correlations and interpretation

These data make possible the following correlations and interpretations (Fig. 6). During the late Albian (S2), a shallowing upward trend is indicated in the southeastern sections by the appearance of biogenic limestones and in the northeastern sections by the occurrence of benthic fauna (rudistids, corals, mudmounds ...). This shallowing upward succession is interrupted to the Northwest by the abrupt contact of relatively shallow deposits resting on deep outerself marl, and to the Southeast by emergence features. In agreement with Robaszynski et al. (1993a; 1993b), we interpret this contact as a Sequence boundary of late Albian age (D3 in Fig. 6) that caps our S2 depositional sequence.

The latter is overlain in the northwestern sections by Lowstand deposits (LST), well expressed in the Oued Segui section by a first prograding (thickening upward), then aggrading succession bearing benthic fauna of outer shelf environment. This part of the succession contains the Albian-Cenomanian boundary defined by planktic foraminifera (Robaszynski et al., 1993a, 1993b; Jaillard et al., 2005). In Oued Segui, the aggrading strata set is overlain by a thinning upward series that may likely represent a transgressive deposit that evolves into deep outer shelf marls (Fig. 6). The top of the aggrading succession is interpreted as a Transgressive surface, which seems to grade laterally southeastward into condensed, phosphate-rich beds. In this interpretation, on one hand the superimposed phosphate-rich beds identified in the Oued Azreg and Jebel Mghila sections would correspond to transgressive parasequences at the base of a third order Transgressive Systems Tract (TST). On the other hand, the channels filled by the phosphate-rich marls in Oued Azreg and Jebel Mghila were carved during the LST on the slope joining the southeastern emergent areas to the northwestern basin domain. This erosion was likely due to the

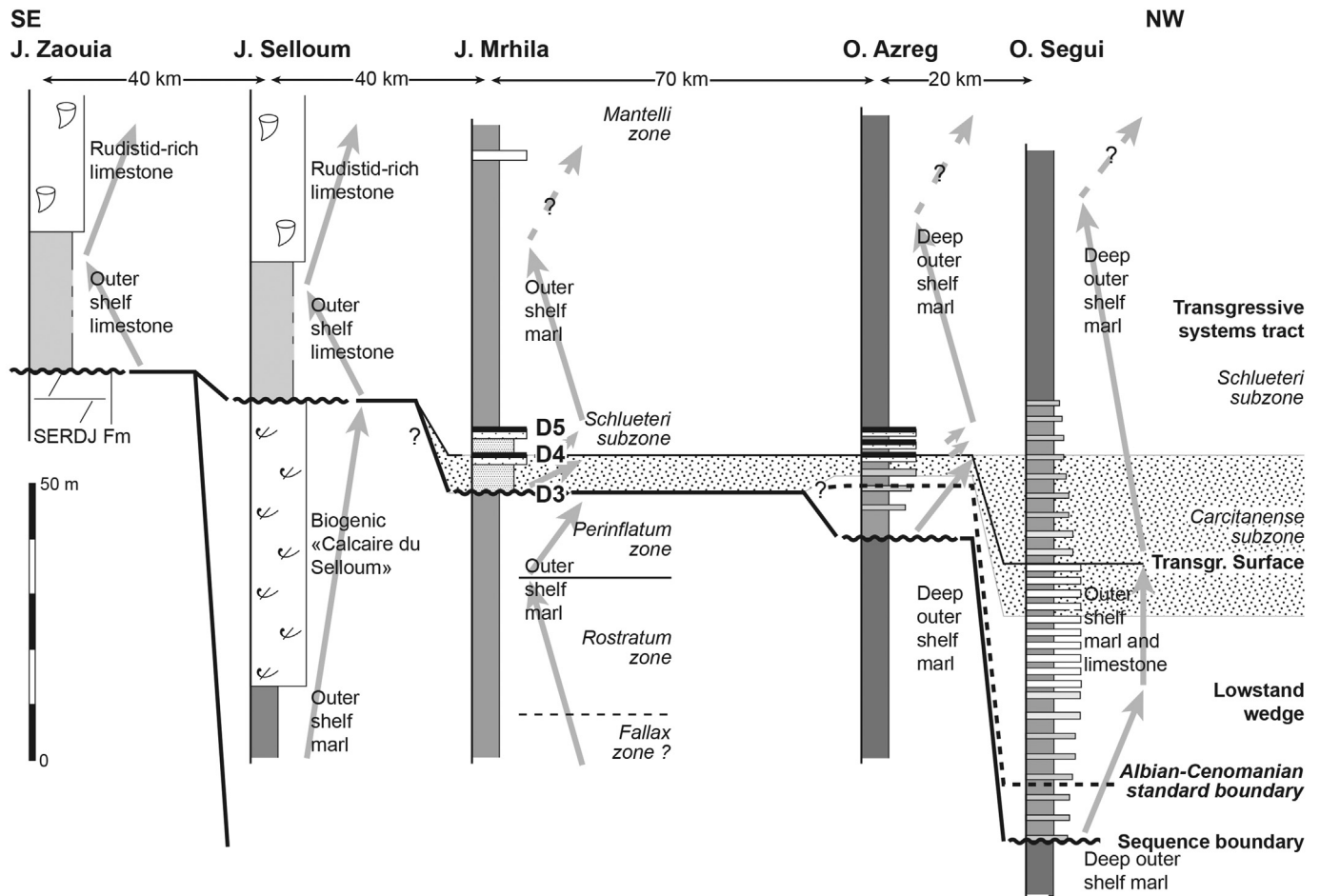


Fig. 6. Correlation and interpretation of the Albian-Cenomanian transition in Central Tunisia. Location of the sections on Fig. 2B. Data are from Philip et al. (1989) for jebels Zaouia and Selloum, from Robaszynski et al. (1993a, 1993b) for Oued Azreg, and from Jaillard et al. (2005) for oued Segui.

transport of products resulting from the erosion of the emergent areas. These products may be represented by the limestone beds of the LST deposits in the Oued Segui section, and by the lens shaped limestone beds locally identified in Oued Azreg (Robaszynski et al., 1993a, 1993b).

The first transgressive deposits are of earliest Cenomanian age (*N. carcitanense* Subzone, Fig. 5), while the late part of the TST seems to mainly correspond to the *Sharpeiceras schluteri* Subzone. The Early Cenomanian transgression may have reached the southeastern areas (Jebel Selloum and Jebel Zaouia) during the *S. schluteri* Subzone. In the latter sections, the transgressive deposits are overlain by shallow marine, rudistid-bearing limestones (Philip et al., 1989) interpreted as the Highstand Systems Tract (HST) of the third order sequence S3. Data are lacking so far in the northwestern sections to document such evolution.

5. Systematic paleontology

5.1. Ammonites

Dimensions are given in millimetres: D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus; v = width of the venter. Figures in parentheses are dimensions as a percentage of the diameter. The suture terminology is that of Korn et al. (2003):

E = external lobe; A = adventive lobe (= lateral lobe, L, of Kullmann and Wiedmann, 1970); U = umbilical lobe; I = internal lobe.

The repositories of specimens are:

UJF-ID: ISTerre, Université of Grenoble Alpes, ex Institut Dolomieu collections.

MNH: Laboratoire de Paléontologie of the Muséum National d'Histoire Naturelle, Paris.

BMNH: British Museum of Natural History, London.

Order Ammonoidea Zittel, 1884

Suborder Ammonitina Hyatt, 1889

Superfamily Desmoceratoidea Zittel, 1895

Family Puzosiidae Spath, 1922

Subfamily: Puzosiinae Spath, 1922

Genus *Puzosia* Bayle, 1878

Subgenus *Puzosia* Bayle, 1878

(= *Matsumotoceras* Hoepen, 1968; ?*Hyperpuzosia* Matsumoto, 1988).

Type species: *Ammonites planulatus* J. de C. Sowerby, 1827, p. 38, by subsequent designation of H. Douvillé, 1879, p. 91.

***Puzosia* sp. juv.**

Fig. 7n

Material. UJF-ID.15003 from the bed MR.2 from the Mghila West section, upper Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone.

Description and remarks. A tiny limonitic nucleus (Fig. 7n), 10 mm in diameter, with rather evolute coiling ($U/D = 0.3$), a whorl section as high as broad, low vertical umbilical wall, rounded umbilical shoulders, feebly convex flanks and rounded venter. There are four sigmoidal constrictions on the last preserved whorl and no indication of ribs. This specimen cannot be identified at a specific level. Pervinquier (1907, pl. 6, figs 25–32) figured several small pyritized specimens from the latest Albian of Pont du Fahs and Guern Er Rhezal, northern Tunisia, which do not show the strongly sigmoidal constrictions of our specimen.

Genus *Pachydesmoceras* Spath, 1922

Type species: *Ammonites denisonianus* Stoliczka, 1865, p. 153, pl. 66a, by the original designation of Spath 1922, p. 127.

***Pachydesmoceras* aff. *denisonianum* (Stoliczka, 1865)**

Figs 8c, d

1865 *Ammonites denisonianum* n. sp., Stoliczka, p. 153, pl. 66, fig. 2.
1961 *Pachydesmoceras denisoni* Stoliczka: Collignon, p. 39, pl. 8, fig. 1.

1988 *Pachydesmoceras denisonianum* (Stoliczka): Matsumoto, p. 109, figs 48–49 (with full synonymy).

Non 1998 *Pachydesmoceras denisonianum* (Stoliczka): Kaplan et al., p. 80, fig. 36; pls 7, 8.

?2015 *Pachydesmoceras* sp.: Kennedy, p. 251, fig. 8.

Material. UJF-ID. 15050 from the bed MR.7 from the Mghila West section, early Cenomanian, *Mantelliceras mantelli* Zone.

Description and remarks. A poorly preserved internal mould of an incomplete phragmocone, about 160 mm in diameter (Figs 8c, d). The coiling is evolute, the umbilicus comprising about 30% of the total preserved diameter. The umbilicus is deep, with a broadly rounded umbilical shoulder. The oval whorl section is too distorted to be measured. The weathered flanks show numerous, slightly flexuous, narrow, widely spaced ribs.

This specimen differs from the material described by Matsumoto (1988, p. 109, figs 48, 49) from the Cenomanian of Japan, by its denser ribbing and by its intercalatory ribs that arise lower on the flanks. Our specimen seems to be closer to the specimen figured by Collignon (1961, pl. 8, fig. 1) from the late Albian of Sakondry (Madagascar).

Family Desmoceratidae Zittel, 1895

Subfamily Desmoceratinae Zittel, 1895

Genus and subgenus *Desmoceras* Zittel, 1884

Type species: *Ammonites latidorsatus* Michelin, 1838, p. 101, pl. 12, fig. 9, by the subsequent designation of Böhm, 1895, p. 364.

***Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838)**

Figs 8a, b

1838 *Ammonites latidorsatus* Michelin, p. 101, pl. 12, fig. 9.

2011 *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838): Klein and Vašíček, p. 144 (with full synonymy).

2013a *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838): Kennedy and Klinger, p. 40, figs 1–5.

2014 *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838): Kennedy and Fatmi, p. 58, text-figs 11a–h.

2015 *Desmoceras* (*Desmoceras*) cf. *latidorsatum* (Michelin, 1838): Kennedy, p. 252, pl. 3, fig. 5.

Material. UJF-ID. 15051 from the bed MR.3 from the Mghila West section, upper Albian, *Mortonicer* (*Subschloenbachia*) *perinflatum* Zone.

Description and remarks. A poorly preserved 90° sector of phragmocone, with a whorl height of 60 mm (Figs 8a, b). Although strongly weathered, the whorl section is subelliptical and slightly

compressed ($Wb/Wh = 0.9$), with a maximum of width at the inner third of the flanks. The flanks are smooth and convex, converging to a narrowly rounded venter.

Superfamily Engonoceratoidea Hyatt, 1900

Family Knemiceratidae Hyatt, 1903

Genus *Hypengonoceras* Spath, 1922

Type species: *Placenticer* *Warthii* Kossmat, 1895, by the original designation of Spath, 1922, p. 112.

***Hypengonoceras saadense* (Thomas and Peron, 1890).**

Figs 9a–o, 10a, b, 11a–e.

1890 *Placenticer* *Saadensis* Thomas and Peron, p. 19, pl. 16, figs 3–7.
1903 *Placenticer* *Saadense* Thomas et Peron: Pervinquier, p. 68, non 80, 92.

1903 *Engonoceras*, Pervinquier, p. 66, 92.

1907 *Placenticer* *Saadense* Thomas et Peron: Pervinquier, p. 198, text-fig. 76.

1907 *Engonoceras Thomasi* Pervinquier, p. 202, pl. 9, fig. 6, text-fig. 77.

?1912 *Engonoceras saadense* Peron: H. Douvillé, p. 318, figs 69, 70.

1938 *Engonoceras Thomasi* Pervinquier, Roman, p. 490, text-fig. 468 bis.

1940a *Knemiceras* aff. *saadense* Thom. et Per. sp.: Breistroffer, p. 87.

1940b *Knemiceras* aff. *saadense* Thom. et Per. sp.: Breistroffer, p. 129.

1983 *Engonhoplitoides* cf. *vicorpense* Basse: Breistroffer, p. 56.

1989 *Engonoceras saadense* (Thomas and Peron): Latil, p. 54, pl. 1, figs 1, 2.

1989 *Engonoceras* sp.: Latil, p. 57, pl. 1, fig. 3.

2010 *Knemiceras saadense* Peron and Thomas: Bujtor, 2010, p. 8.

2012 *Hypengonoceras saadense* (Thomas and Peron): Latil and Aly, p. 165.

2014 *Hypengonoceras saadense* (Thomas and Peron, 1890): Klein, p. 195.

2015 *Placenticer* *saadense* Thomas and Peron, 1890: Kennedy, in Kennedy and Gale, 2015, p. 255, pl. 1, figs 5, 7, 8; text-fig. 11.

Even though *Engonoceras Thomasi* Pervinquier and *Placenticer* *Saadensis* Thomas and Peron are very difficult to compare because of their different preservational states (juvenile pyritized for the first species, calcareous subadult and adults for the second one), these two species are herein placed in synonymy as a result of the position of the pyritized faunas, which are interposed between the first calcareous faunas of the *Mortonicer* (*Subschloenbachia*) *rostratum* Zone and the last calcareous specimen of the *Stoliczkaia* (*Shumariinaia*) *africana* Zone, strongly suggesting that *Engonoceras Thomasi* represents the juvenile growth stages of *Hypengonoceras saadense*. Neotype. Thomas and Peron (1890) described the species *Placenticer* *saadensis* on the basis of several fragments from Bou Saada (Algeria), Jebel Mghila and Jebel Roumana (Tunisia) and they figured only two fragments from Jebel Mghila. Breistroffer (1940b, p. 131) designated as the holotype, one of the fragments from the type locality of Bou Saada: 'Quoi qu'il en soit, il s'agit d'une forme au moins très voisine de l'espèce du Vraconien sup (à *Mariella Bergeri* Brgn. sp.) ou du Cénomani basal (à *Hypoturrilites caritanensis* Mather. sp.) d'Algérie (Bou Saada = local.-typ.: holotype non fig., Khenchela) et de Tunisie (Dj. Meghila, Dj. Roumana, Dj. Meghila, D. Adira)'. In the 1980', one of us (J.-L.L.) tried to trace the Algerian material in the Sorbonne collections, unsuccessfully. Consequently, Latil (1989, p. 54) designated a neotype from the two Tunisian fragments figured by Thomas and Peron: MNHN.R52073, the original figured by Thomas and Peron (1890, pl. 16, figs 5, 7, refigured by Latil, 1989, p. 54, pl. 1, fig. 1). The original material figured by Thomas and Peron has been refigured by Latil (1989, pl. 1, fig. 1, 2), by Kennedy et al. (2015, pl. 1, fig. 5, 7), and is available online on the website of the Museum National d'Histoire Naturelle de Paris

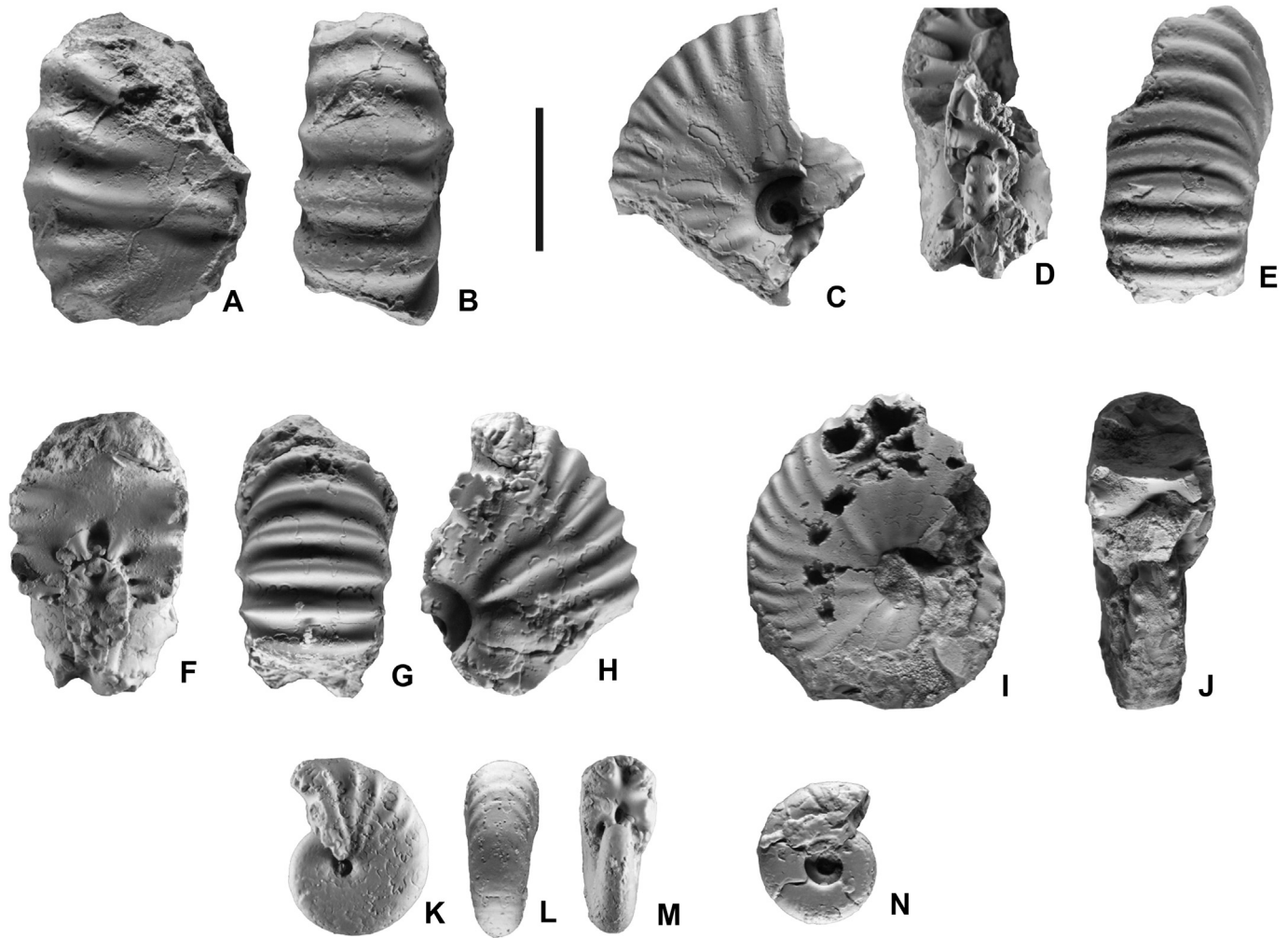


Fig. 7. (a, b) *Stoliczkaia* (*Stoliczkaia*) sp. juv. indet., UJF-ID.15010, from Bed 2 of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone; (c–e) *Stoliczkaia* (*Stoliczkaia*) sp. juv., UJF-ID.15011, from Bed 2 of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone; (f–h) *Stoliczkaia* (*Stoliczkaia*) sp. juv., from Bed 19 of Mghila East section, late Albian, *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone; (i, j) *Stoliczkaia* (*Stoliczkaia*) *clavigera* Neumayr, 1875, from Bed 2 of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone; (k–m) *Metascaphites thomasi* Pervinquier, 1907, UJF-ID.15009, from Bed 2 of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone; (n) *Puzosia* sp. juv., UJF-ID.15003 from Bed MR.2 of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone. Scale bar is 10 mm.

(<https://science.mnhn.fr/institution/mnhn/collection/f/item/r52073?listIndex=2&listCount=13>).

Material. Two fragments from Bed 1, five specimens from Bed 2 of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone; eleven fragments from Bed 3 of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone; one fragment from Bed 4 of Mghila West section, late Albian, *Stoliczkaia* (*Shumarinaia*) *africana* Zone; one fragment from Bed 3 of Mghila Centre section, late Albian, *Stoliczkaia* (*Shumarinaia*) *africana* Zone; two fragments from interval 15–17, and 4 specimens from Bed 19 of Mghila East section, late Albian, *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone; the original material figured by Thomas and Peron, and the holotype of *Engonoceras thomasi* Pervinquier, 1907 from the late Albian of Fom El Guelta, Jebel Mghila.

Measurements.

UJF-ID.15032: D: 6.0; Wh: 2.5 (0.42); Wb: 2.5 (0.42); U: 2.0 (0.33); Wb/Wh: 1.00.

UJF-ID.15025: D: 18.0; Wh: 10.0 (0.56); Wb: 5.8 (0.32); U: 2.4 (0.13); Wb/Wh: 0.58.

The holotype of *Engonoceras thomasi* Pervinquier, MNHN unregistered specimen:

D: 32; Wh: 18.5 (0.58); Wb: 9.3 (0.29); U: 2.7 (0.08); Wb/Wh: 0.50. UJF-ID.15047: D: 360; Wh: 200 (0.55); Wb: 100 (0.28); U: ? (?); Wb/Wh: 0.50.

Description. The early stages of the ontogeny are known by the inner whorls of a well-preserved juvenile pyritized specimen, 6 mm in diameter (UJF-ID.15032: Figs 9h, i). At this stage of the ontogeny, the coiling is moderately involute ($U/D = 0.33$), the flanks and the venter are convex, the whorl section is still almost circular and the last preserved whorl shows 6 radially elongated latero-umbilical tubercles, which most probably disappear soon after.

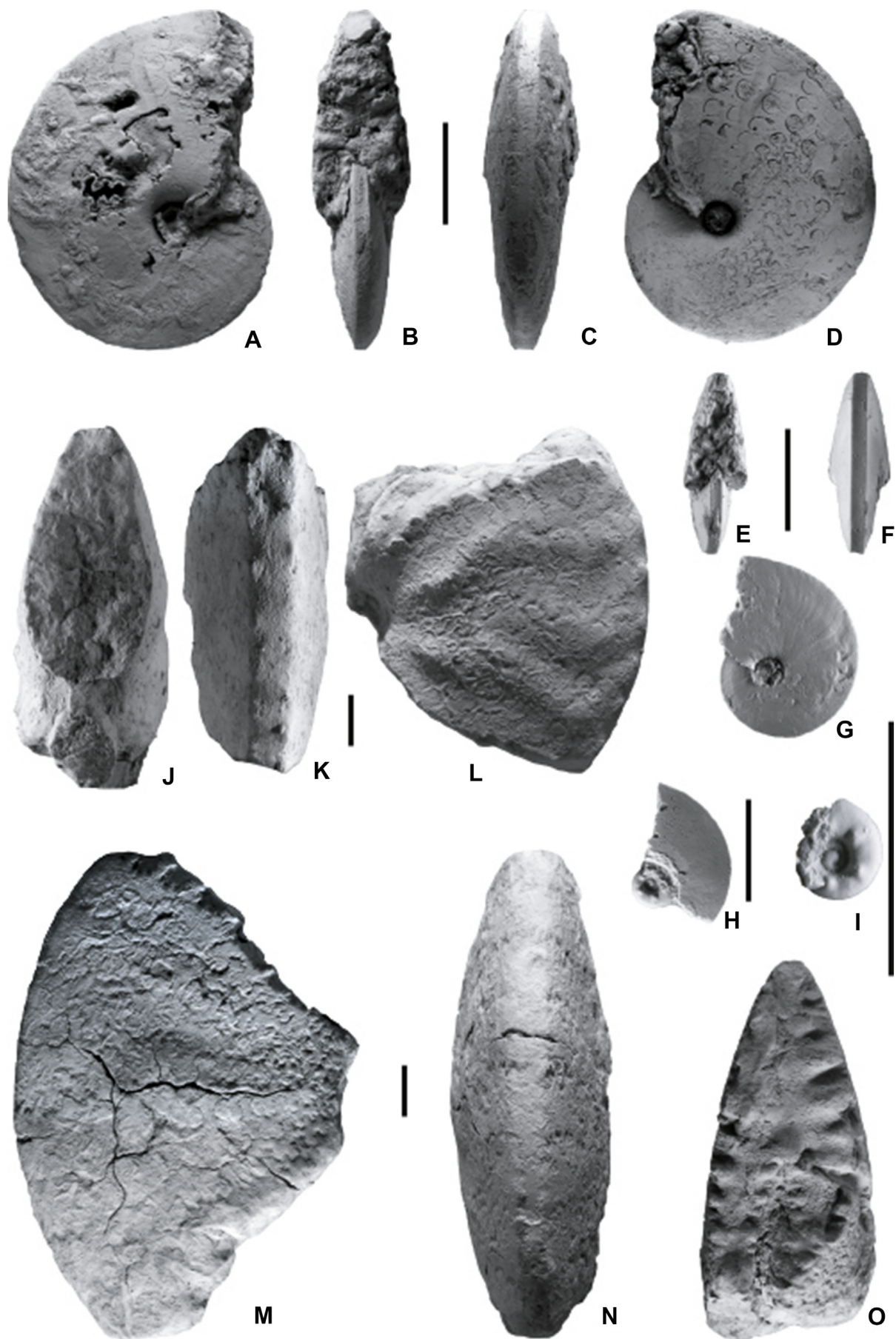
At a diameter of 10 mm and beyond, the coiling is involute ($UD = 0.13$), with shallow steep umbilical wall, narrowly rounded umbilical edge, the whorl section is subtriangular and compressed ($Wb/D = 0.58$), with smooth flattened flanks ending with a sharp ventrolateral edge, and the venter is narrow, smooth and flat (e.g. UJF-ID.15025, Figs 9e–g).

The largest known pyritized specimen from Jebel Mghila is the holotype of *Engonoceras thomasi* Pervinquier, 1907 (unregistered MNHN specimen, Figs 9a–d).

It is a well preserved pyritized internal mould, 32 mm in diameter. The shell is discoidal, high-whorled ($Wh/D = 0.59$), with a



Fig. 8. (a, b) *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838), UJF-ID. 15051 from the bed 3 of the Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone; (c, d) *Pachydesmoceras* aff. *denisonianum* (Stoliczka, 1865), UJF-ID. 15050 from the bed 7 of the Mghila West section, early Cenomanian, *Mantelliceras mantelli* Zone. Scale bar is 10 mm.



compressed subtriangular whorl section ($Wb/Wh = 0.5$), feebly convex flanks with a maximum breadth just above the umbilicus. Coiling is very involute, the umbilicus comprising 8% of the diameter. The umbilical wall is shallow and the umbilical edge is broadly rounded. The flanks converge to a narrow and flat venter ($v/D = 0.11$). The ornament is made of few sigmoidal striae on the adapical part of the last preserved whorl, which are visible only on the upper half of the flanks (Figs 9a, d).

Additional material from the *Mortonicer* (*Subschloenbachia*) *perinflatum* Zone of the Azreg section, Tajerouine area, Central Tunisia, allowed us to follow the early sutural ontogeny (Fig. 11a–e). It should be noted that the saddles are exceptionally indented in Fig. 11d (UJF-ID. 15085). The suture line figured by Pervinquier (1907, fig. 77) is herein refigured (Fig. 11e).

The growth stages between the larger pyritized specimen, 32 mm of diameter, and the smaller known calcareous fragments, with an estimated diameter of 70 mm, are not known.

Beyond a diameter of 70 mm, the species is known from numerous fragments preserved as slightly weathered calcareous internal moulds. At that stage of the growth, the whorl section is always compressed (Wb/Wh ranging from 0.47 to 0.57), subtriangular, with very narrow umbilicus, shallow umbilical wall, narrowly rounded umbilical edge, slightly convex flanks, converging to a rather sharp ventrolateral edge. The venter is generally flat, rarely slightly concave or slightly convex, more or less narrow (the ratio of venter thickness to whorl height ranging from 0.05 to 0.15). There are spirally elongated ventrolateral tubercles, alternating across the venter, which are more or less expressed depending on the state of preservation and the thickness of the venter. The flanks are generally smooth (e.g. UJF-ID.15043, Figs 9m–o) but some specimens show radially elongated periumbilical swellings giving rise to feeble, coarse ribs on the inner half of the flanks (UJF-ID.15038, Figs 9j–k).

A large specimen (UJF-ID.15047, Figs 10a, b), 370 mm in diameter is preserved as an internal mould of a phragmocone. The coiling is very involute, the whorl section is becoming more elliptical, with smooth, convex flanks and a maximum of thickness on the inner third of the flanks. The umbilicus is shallow, the umbilical edge is broadly rounded. The venter is very narrow ($v/Wh = 0.06$), retaining ventrolateral tubercles up to a diameter of about 180 mm. Beyond this diameter, the venter becomes smooth, narrow and convex. The body chamber is unknown.

Remarks. The fragment figured by Latil (1989, p. 57, pl. 1, fig. 3) as *Engonoceras* sp., from the *Mortonicer* (*Subschloenbachia*) *perinflatum* Zone of Salazac (Gard, France), which was identified as *Engonhoplitoidea* cf. *vicorpense* Basse by Breistroffer (1983, p. 56), does not differ in any way from the Tunisian fragment UJF-ID.15038 (Figs 9j–k).

The fragment identified as *Hypengonoceras* sp. in Latil (1989, p. 54, pl. 1, fig. 4), from just above the phosphatized level of the *Mortonicer* (*Mortonicer*) *fallax* Zone of Salazac, Gard, France, is very probably an adult phragmocone of *Hypengonoceras duboisi* (Latil, 1989).

As suggested by Latil and Aly (2012), the present species is closely related to *Hypengonoceras warthi* (Kossmat, 1895). Roy and Bardhan (2019) recently re-figured the type material of *Hypengonoceras warthi* (Kossmat, 1895) from the late Albian of India. Our species is closely allied to *H. warthi*, from which it differs mainly by its much larger size and its non-vertical umbilical wall. Kennedy

et al., (2015) has placed the Tunisian species in the genus *Placenticer* Meek, 1876, but as shown by Roy and Bardhan, *Hypengonoceras warthi*, and then *H. saadense*, clearly belong to the Engonoceratoidea.

Occurrence. The species is known from the uppermost Albian, *Mortonicer* (*Subschloenbachia*) *rostratum* to *Stoliczkaia* (*Shumarinaia*) *africana* Zones of Jebel Mghila. It has also been recorded in Tunisia from Jebel Roumana and the area of Jebel Adira and Jebel el Hamra. Pervinquier (1903, p. 80) and we found it farther north, in the Tajerouine area. We were unable to trace the Algerian material from Bou Saada and Khenchela, in Algeria, mentioned by Thomas and Peron (1890).

Superfamily Acanthoceratoidea De Grossouvre, 1894

Family Brancoceratidae Spath, 1934

Subfamily Mortoniceratinae H. Douvillé, 1912

Genus *Mortonicer* Meek, 1876.

Type species: *Ammonites vespertinus* Morton, 1834, p. 40, pl. 17, fig. 1, by the original designation of Meek, 1876, p. 448.

Subgenus *Mortonicer* Meek, 1876.

***Mortonicer* (*Mortonicer*) *pachys* (Seeley, 1865).**

Figs 12j, k

1865 *Ammonites pachys* Seeley, p. 227; pl. 9, fig. 4.

1930 *Mortonicer* (*Pervinquieria*) *inflatum* (Sowerby): Besairie, p. 555, pl. 16 fig. 1.

1932 *Mortonicer* (*Pervinquieria*) *pachys* (Seeley): Spath, p. 405; text-fig. 130d, 138–139.

1979 *Pervinquieria* (*Pervinquieria*) *pachys* (Seeley): Scholz, p. 110, pl. 29, fig. 9a, 9b.

1997 *Mortonicer* groupe *pachys* (Seeley): Delamette et al., pl. 36, fig. 2, 3.

2008 *Mortonicer* (*Mortonicer*) *pachys* (Seeley): Kennedy et al., p. 43.

2017 *Mortonicer* (*Mortonicer*) *pachys* (Seeley, 1865): Benzagagh et al., p. 90, fig. 1211, 1212, 1213.

2018. *Mortonicer* (*Mortonicer*) *pachys pachys* (Seeley, 1865): Klein, p. 118 (with additional synonymy).

Type. The holotype, SMC B54 from the reworked upper Albian phosphates at the base of the Cenomanian Cambridge Greensand in eastern England (Seeley, 1865; Spath, 1932), redescribed by Kennedy et al. (2008, p. 42; pl. 10, figs. 9–11).

Material. Two fragments from Bed 3b of Mghila West section (UJF-ID.15007–08), one fragment from Bed 16 of Mghila East section (UJF-ID.15086), late Albian, *Mortonicer* (*Subschloenbachia*) *perinflatum* Zone.

Description. UJF-ID.15007 is a fragment of a juvenile specimen, 29 mm long, preserved as calcareous internal mould with a diameter of about 25 mm. Coiling is moderately evolute. The umbilical wall is feebly convex, the umbilical shoulder broadly rounded. The intercostal whorl section is as broad as high, trapezoidal, the ventrolateral shoulders broadly rounded, the venter flattened, with a strong siphonal keel. Coarse ribs arise on the umbilical wall and strengthen into minute, umbilical radially elongated clavi. The tubercles give rise to generally two, rarely one, radial to slightly prorsiradiate ribs. The ribs bear inconspicuous ventrolateral bullae, from which the ribs become slightly projected forward on the

Fig. 9. *Hypengonoceras saadense* (Thomas and Peron, 1890). (a–d) The holotype of *Engonoceras Thomasi* Pervinquier, 1907 (p. 202, pl. 9, fig. 6, text-fig. 77), unregistered specimen from the Sorbonne collections, now housed in the Museum d'Histoire Naturelle de Paris, from the late Albian of Fom El Guelta, Jebel Mghila; (e–g) UJF-ID.15025, from MH.19, *Mortonicer* (*Subschloenbachia*) *perinflatum* Zone; (h, i) UJF-ID.15032, from MR.2, *Mortonicer* (*Subschloenbachia*) *rostratum* Zone; (j–l) UJF-ID.15038, from MR.3, *Mortonicer* (*Subschloenbachia*) *perinflatum* Zone; (m–o) UJF-ID.15043, from MR.3, *Mortonicer* (*Subschloenbachia*) *perinflatum* Zone. Scale bar is 10 mm.



Fig. 10. (a, b) *Hypengonoceras saadense* (Thomas and Peron, 1890), UJF-ID.15047, from MR.3, *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone. Scale bar is 50 mm.

venter. A narrow smooth zone separates the ribs from the siphonal keel.

UJF-ID.15008 (Fig. 12j, k) is a larger fragment of phragmocone, with a whorl height of 31 mm, that has a slightly higher than broad, trapezoidal whorl section. The ribs are slightly flexuous, arising at the base of the umbilical wall, bifurcates above the umbilical

shoulder from an only slight, radially elongated swelling, decline on the inner third of the flanks, become coarser on the outer part of the flanks, developing tiny inner ventrolateral tubercles that tend to disappear with age, and are slightly projected forward on the venter. UJF-ID.15086, a fragment of phragmocone preserved as calcareous internal mould, is more characteristic of the species,

with radially elongated umbilical tubercles, depression on the inner third of the flanks, minute lateral tubercle and a well marked ventrolateral tubercle.

Remarks. Our material differs from *Mortonicer* (*Mortonicer*) *pachys* only by its almost inconspicuous tuberculation, which is tentatively interpreted as an unexpected survivor of the species at the base of the *Mortonicer* (*Subschloenbachia*) *perinflatum* Zone. **Occurrence.** *Mortonicer* (*Subschloenbachia*) *perinflatum* Zone of Jebel Mghila, Tunisia. The species was previously known in the *Mortonicer* (*Mortonicer*) *fallax* Zone of France, Belgium, England, Hungary, Poland, Morocco and Madagascar.

Subgenus *Subschloenbachia* Spath, 1921

(= *Durnovarites* Spath, 1932, p. 380; *Reyreicer* Collignon, 1979, p. 34).

Type species: *Ammonites rostratus* J. Sowerby, 1817, p. 163, pl. 173, by original designation by Spath, 1921, p. 284.

***Mortonicer* (*Subschloenbachia*) *rostratum* (J. Sowerby, 1817).**

Figs 12a-i

1817 *Ammonites rostratus* J. Sowerby, p. 163, pl. 173.

1898 *Schloenbachia inflata* Sow. Typische form; Kossmat, p. 190 (40) (pars), pl. 23 (19), fig. 2; pl. 24, fig. 1.

1995 *Mortonicer rostratum* (J. Sowerby, 1817): Latil, pl. 1, fig. 1 (= specimen of Sowerby, 1817, pl. 173), pl. 2, fig. 1.

2007 *Mortonicer* (*Subschloenbachia*) *rostratum* (J. Sowerby, 1817): Kennedy and Latil, p. 463, pl. 3, fig. 2; pl. 3, figs 3, 6–9; pl. 4, figs 7, 8 (with additional synonymy).

2010 *Mortonicer* (*Mortonicer*) *rostratum* (J. de C. Sowerby): Owen et al., p. 190, pl. 35, fig. 1.

non 2018 *Mortonicer* (*Subschloenbachia*) cf. *rostratum* (J. Sowerby, 1817): El Qot, p. 38, fig. 11F, 11G, 11H.

2018 *Mortonicer* (*Mortonicer*) *rostratum* (J. Sowerby, 1817): Klein, pp. 101, 122 (with additional synonymy).

2019. *Pervinquieria* (*Subschloenbachia*) *rostrata* (J. Sowerby, 1817), Kennedy, p. 214, pl. 13, pl. 14, figs 1, 2.

Type. The holotype, by monotypy, is OUM K 835, the original of *Ammonites rostratus* J. Sowerby, 1817, p. 163, pl. 173, from the Upper Greensand of Roke, 1.5 km NNE of Benson, Oxfordshire, refixed by Latil (1995, pl. 1, fig. 1).

Material. Nine fragments from Bed 1 and two fragments from Bed 2 of Mghila West section, two fragments from Bed 11b of Mghila East section, late Albian, *Mortonicer* (*Subschloenbachia*) *rostratum* Zone.

Description. UJF-ID.15004 and 15005 (Figs 12f-i) are juvenile specimens preserved as pyritized internal mould with a diameter of about 25 mm. Coiling is moderately evolute. The umbilical wall is feebly convex, the umbilical shoulder broadly rounded. The intercostal whorl section is depressed (Wb/Wh at about 1.05) trapezoidal, the ventrolateral shoulders broadly rounded, the venter flattened, with a strong siphonal keel. Coarse ribs arise on the umbilical wall and strengthen into strong, conical umbilical tubercle. The tubercles give rise to generally two, rarely one, radial to slightly prorsiradiate ribs. The ribs bear inconspicuous outer lateral bullae, a small inner ventrolateral conical tubercle, from which the ribs become slightly projected forward, giving rise to a small outer ventrolateral conical tubercle and declining on the venter. A narrow smooth zone separates the ribs from the siphonal keel.

The material from Bed 1 of Mghila West section and Bed 11b of Mghila East section comprises weathered fragments of subadult and adult specimens, preserved as limestone internal moulds (Figs 12a-e). At a diameter of about 40 mm, the lateral bullae become stronger and migrate to the mid-flanks. At a larger diameter, the ribs are regularly alternating, one primary for one intercalatory, the

lateral tubercles are stronger, tending to become radially elongated, and the inner and outer ventrolateral tubercles tend to merge in a single bulge. The adult body chamber (Wh at about 40 mm and more) is characterized by the lack of umbilical tubercles, the lack of intercalatory ribs, the presence of radially elongated lateral tubercles and the presence of coarse, ventrolateral bulge/tubercle. Close to the aperture (Wh at about 50 mm), the tubercles are disappearing and the ribs are strongly projected forward on the venter.

Remarks. The specimen figured by El Qot (2018, p. 163, fig. 11F-H) from the upper Albian of Wadi El Karm (Sinai, Egypt) is merely a *Mortonicer* (*Mortonicer*) *inflatum*. At that size, *M. (S.) rostratum* still shows strong lateral tubercles.

Occurrence. *Mortonicer* (*Subschloenbachia*) *rostratum* Zone of south Tunisia. The species is widespread in the upper Albian of Bulgaria, Caucasus, Crimea (Ukraine), France, England, Germany,

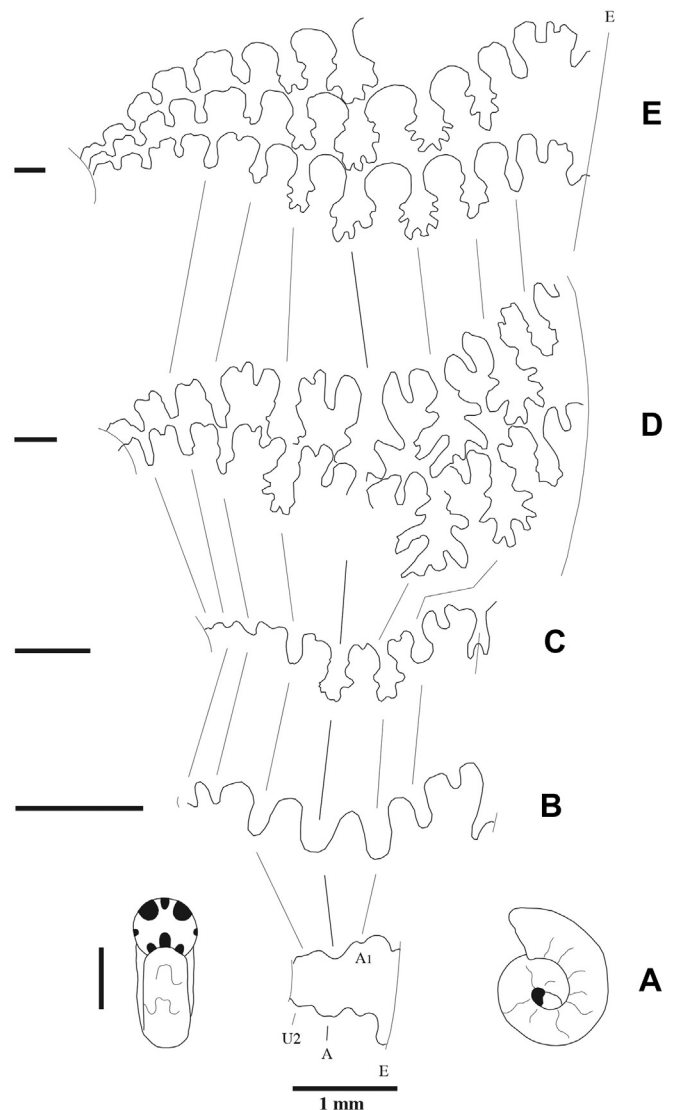


Fig. 11. *Hypengonoceras saadense* (Thomas and Peron, 1890); (a–c) suture of the early whorls of a destroyed specimen from AG.6, Azreg section, central Tunisia, *Mortonicer* (*Subschloenbachia*) *perinflatum* Zone; (d) UJF-ID.15085, an atypical specimen with deeply indented saddles, from AG.6, Azreg section, central Tunisia, *Mortonicer* (*Subschloenbachia*) *perinflatum* Zone; (e) The holotype of *Engonoceras Thomasi* Pervinquier, 1907 (text-fig. 77), unregistered specimen from the Sorbonne collections, now housed in the Museum d'Histoire Naturelle de Paris, from the late Albian of Fom El Guelta, Jebel Mghila. Scale bar is 1 mm.

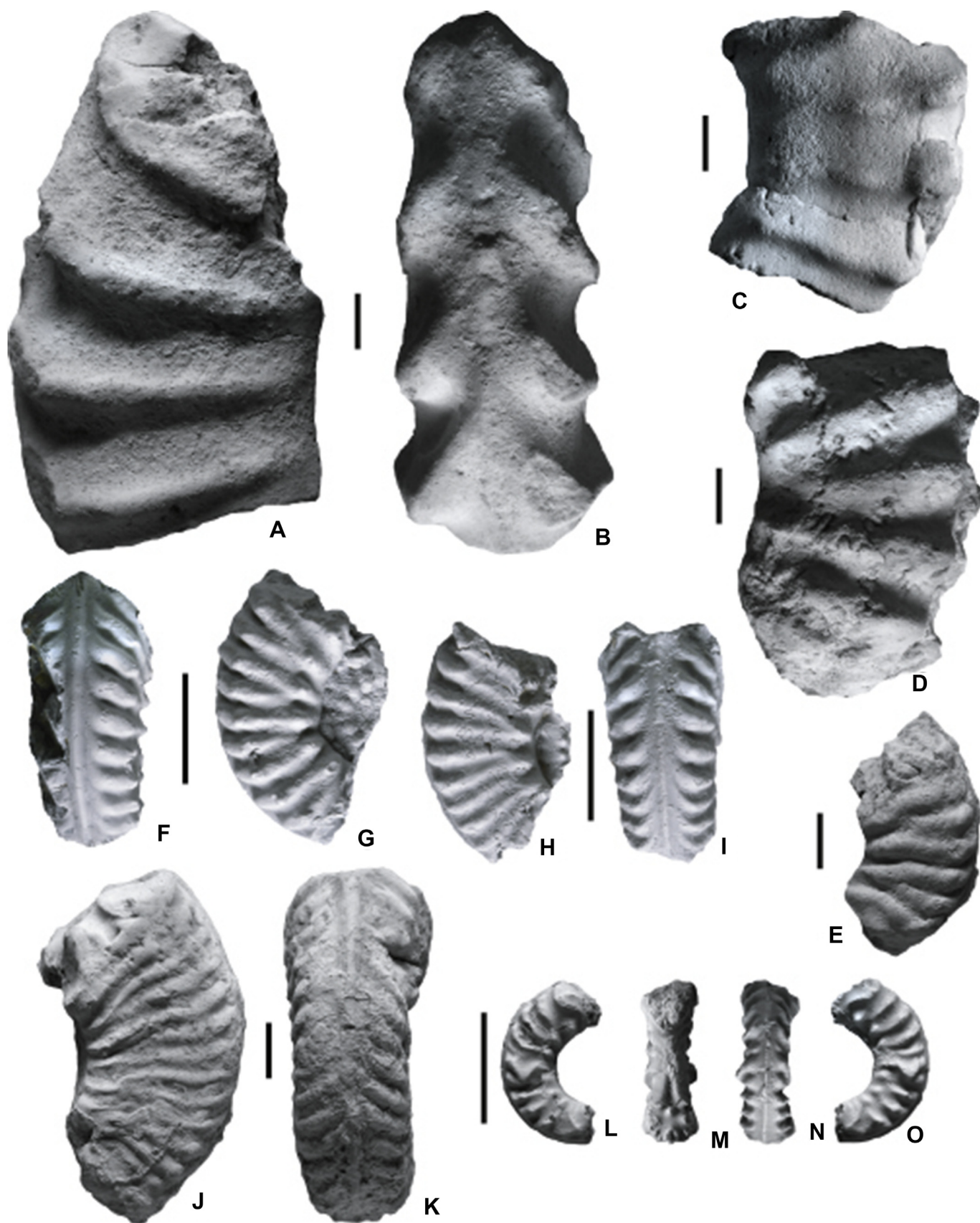


Fig. 12. (a–i) *Mortoniceras* (*Subschloenbachia*) *rostratum* (J. Sowerby, 1817). (a, b) UJF-ID.15006, (c) UJF-ID.15008, (d) UJF-ID.15007, (e) UJF-ID.15009 from bed MR.1, Mghila West section; (f, g) UJF-ID.15004, (h, i) UJF-ID.15005 from bed MR.2, Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone. (j, k) *Mortoniceras* (*Mortoniceras*) *pachys* (Seeley, 1865), UJF-ID.15008 from bed MR. 3, Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone; (l–o) ?*Cantabrigites* sp. nov., UJF-ID.15006 from Bed 2 of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone. Scale bar is 10 mm.

Hungary, Poland, ?Romania, Spain, Switzerland, Angola, Madagascar, Iran, Texas (United States), India and Japan.

***Mortoniceras (Subschloenbachia) perinflatum* (Spath, 1922a)**

Figs 13a–f

- 1860 *Ammonites inflatus* Pictet and Campiche (non J. Sowerby): p. 178, pl. 21, fig. 5; pl. 22, fig. 3.
 1903 *Mortoniceras inflatum* Sowerby: Pervinquier, p. 66.
 1907 *Mortoniceras inflatum* Sowerby: Pervinquier, p. 229 (pars).
 1922 *Inflatoceras (Subschloenbachia) perinflata* Spath, p. 113.
 1933 *Mortoniceras (Durnovarites) perinflata* Sowerby: Spath, p. 430, pl. 40, fig. 238; text-fig. 150.
 1979 *Mortoniceras (Durnovarites) perinflatum* (Spath, 1922): Cooper and Kennedy, p. 269, figs 3g, 61, 62d–i, 63, 64 (with synonymy).
 2005 *Mortoniceras (Durnovarites) perinflatum* (Spath, 1922): Kennedy et al., p. 365, text-figs 10a, 11a–f (with additional synonymy).
 2007 *Mortoniceras (Subschloenbachia) perinflatum* (Spath, 1922): Kennedy and Latil, p. 465, pl. 3, figs 2, 4, 5 (with additional synonymy).
 2011 *Mortoniceras (Subschloenbachia) perinflatum* (Spath, 1922): Kennedy in Gale et al., p. 76, text-figs 28a, f, g, 29f.
 2011 *Mortoniceras (Subschloenbachia) perinflatum* (Spath, 1922): Meister et al., p. 690, text-fig. 5a, b.
 2013 *Mortoniceras (Subschloenbachia) cf. perinflatum* (Spath, 1922): Wilmsen et al., p. 501, text-fig. 7a–c.
 2015 *Mortoniceras (Subschloenbachia) perinflatum* (Spath, 1922): Kennedy, p. 256, pl. 4, figs 3, 4, 6.
 2018 *Mortoniceras (Durnovarites) perinflatum* (Spath, 1921): Klein, p. 140 (with additional synonymy).

Type. The holotype, by monotypy, is the original of Pictet and Campiche, 1860, pl. 22, fig. 3, in the collections of the Museum d'Histoire Naturelle, Geneva, from the late Albian of La Vraconne, Saint Croix, Switzerland. It was refigured by Renz (1968, pl. 9, fig. 1), Wiedmann and Dieni (1968, pl. 14, fig. 4) and Meister et al. (2011, text-fig. 5a, b).

Material. Fifteen fragments from Bed 3 of Mghila West section, four fragments from Bed 16A, two fragments from Bed 16B of Mghila East section, late Albian, *Mortoniceras (Subschloenbachia) perinflatum* Zone (unit 1 of Pervinquier, 1903, text-fig. 14).

Description. Kennedy (Kennedy and Gale, 2015, pl. 4, figs 3, 4, 6) has described and figured the three unregistered specimens in the Sorbonne Collections, mentioned by Pervinquier [1903, p. 64; 1907, p. 229 (pars)], from Fom el Guelta and Kef et Tella. Our material is made of fragments of juvenile and adult phragmocones preserved as calcareous internal moulds. The whorl section is variable, from slightly compressed to strongly depressed (Wb/Wh between 0.90 and 1.40) (Figs 13a–f). The flanks are flat to slightly convex, the ornament is characteristic of the species, with low to elevated, coarse ribs, weak to strong, radially elongated periumbilical tubercles, rather small, conical, lateral tubercles, weak to strong, radially elongated inner ventrolateral tubercles and weak to rather strong conical, outer ventrolateral tubercles. It should be noted that the strength of the ornament is not correlated with the shape of the section. At the end of the phragmocone, the ribs tend to become single, bearing coarse, radially elongated periumbilical swellings, strong, coarse outer lateral tubercles and strong inner ventrolateral tubercles, which tend to merge with attenuated, coarse, outer ventrolateral bulges. A small distorted and strongly weathered piece of body chamber is known from a single fragment and seems to show coarse, single ribs bearing strong lateral tubercles and probably merged inner and outer ventrolateral tubercles.
Remarks. Our material comes from the base of the *Mortoniceras (Subschloenbachia) perinflatum* Zone in both Mghila East and

Mghila West sections. The absence of the species in higher stratigraphic levels is very probably due to the scarcity of the species in marly levels: *Mortoniceras (S.) rostratum* represents only 3–5% of the mortoniceratids fauna in underlying beds with pyritized fossils and the beds of the upper part of the *Mortoniceras (Subschloenbachia) perinflatum* Zone are very poor in pyritized fossils. Our material shows a high morphological variability, the more compressed morphologies being very similar to *Mortoniceras (S.) rostratum* when only phragmocones are preserved.

Occurrence. *Mortoniceras (Subschloenbachia) perinflatum* Zone of Jebel Mghila, Tunisia. The species is also known from southern England, southeastern France, Hungary, Poland, Romania, Sardinia, ?northern Spain, Switzerland, Crimea, the Lesser Caucasus, Iran, USA (Texas), Angola, Nigeria, Tunisia, and South Africa.

Genus *Cantabrigites* Spath, 1932.

Type species. *Mortoniceras (Cantabrigites) cantabrigense* Spath, 1932, p. 380, pl. 41, fig. 3, by the original designation of Spath, 1933, p. 436.

***Cantabrigites spinosum* (Pervinquier, 1907)**

Figs 14a–q

- 1907 *Mortoniceras inflatum* Var. *spinosa* Pervinquier, p. 229, pl. 11, fig. 3.
 1920 *Schloenbachia* sp.: Adkins, pl. 1, fig. 5; pl. 4, fig. 1.
 1920 *Mortoniceras worthense* Adkins, p. 91, pl. 1, fig. 7, 8, 10, 18, 19, 26; non pl. 1, fig. 6, 9; text-fig. 12 (= *Cantabrigites wenoense*).
 1928 *Neokentroceras worthense* Adkins, p. 235, pl. 20, fig. 4, 6 (=Adkins, 1920, pl. 1, fig. 5, 7), fig. 5, pl. 11, fig. 9 (=Adkins, 1920, pl. 1, fig. 19).
 1931 *Neokentroceras worthense* Adkins: Spath, p. 378.
 1933 *Mortoniceras worthense* Adkins: Spath, p. 434.
 1934 “*Mortoniceras inflatum* var. *spinosa*” Spath, p. 435.
 1934a *Mortoniceras (Durnovarites) worthense* Adkins: Spath, p. 445.
 ?1955 *Pervinquieria spinosa* (Adkins): Eristavi, p. 140, pl. 6, fig. 2.
 1968 *Mortoniceras (Cantabrigites) picteti* Renz, p. 60, pl. 10, figs 11–13; textfigs. 20c, d, 21d.
 1968 *Mortoniceras (Cantabrigites) valdense* Renz, p. 60, pl. 10, fig. 14a, 14b; text-fig. 20e, 21e.
 ?1968 *Mortoniceras (Cantabrigites) curvatum* Renz, p. 61, pl. 11, fig. 1a, 1b, 2a, 2b, 2c; text-fig. 20g, 21f.
 ?1968 *Mortoniceras (Mortoniceras?) nanoides* Wiedmann and Dieni, p. 141, pl. 13, fig. 11; text-fig. 94.
 ?1968 *Mortoniceras (Durnovarites) neokentroides* Wiedmann and Dieni, p. 146, pl. 13, fig. 5; text-fig. 89.
 1979 *Cantabrigites curvatum* Cooper and Kennedy, p. 292, fig. 78, 79.
 1994 *Prohysteroceas worthense* (Adkins): Emerson et al., p. 130.
 2004 *Cantabrigites spinosum* (Pervinquier): Kennedy, p. 877, fig. 7A–E, fig. 10A, 10B (= Adkins, 1920, pl. 1, fig. 5, 18), fig. 10C, 10D (= specimen Adkins, 1920, pl. 1, fig. 10), fig. 10E (= specimen Adkins, 1920, pl. 1, fig. 26), fig. 10F, 10G (= specimen Adkins, 1920, pl. 1, fig. 19), fig. 10H, 10I (= specimen Adkins, 1920, pl. 1, fig. 8), fig. 10J, 10K (= specimen A Adkins, 1920, pl. 1, fig. 7), fig. 12H–W, 13.
 2005 *Cantabrigites spinosum* (Pervinquier): Kennedy et al., p. 363, fig. 4F–J.
 2011 *Cantabrigites spinosum* (Pervinquier): Szives and Barrágan, in Barrágan et al., p. 450, fig. 3E–G.
 2018 *Cantabrigites spinosum* (Pervinquier): Klein, p. 183.
 2019 *Cantabrigites spinosum* (Pervinquier): Kennedy, p. 215, pl. 4, figs 17, 18.

Type. The lectotype, designated by Kennedy, 2004, p. 877, is the original of *Mortoniceras inflatum* Var. *spinosa* Pervinquier, p. 229, pl. 11, fig. 3a, 3b of Jebel Zrissa (Djerissa), central Tunisia, an unregistered specimen in the Sorbonne collections, now housed in the

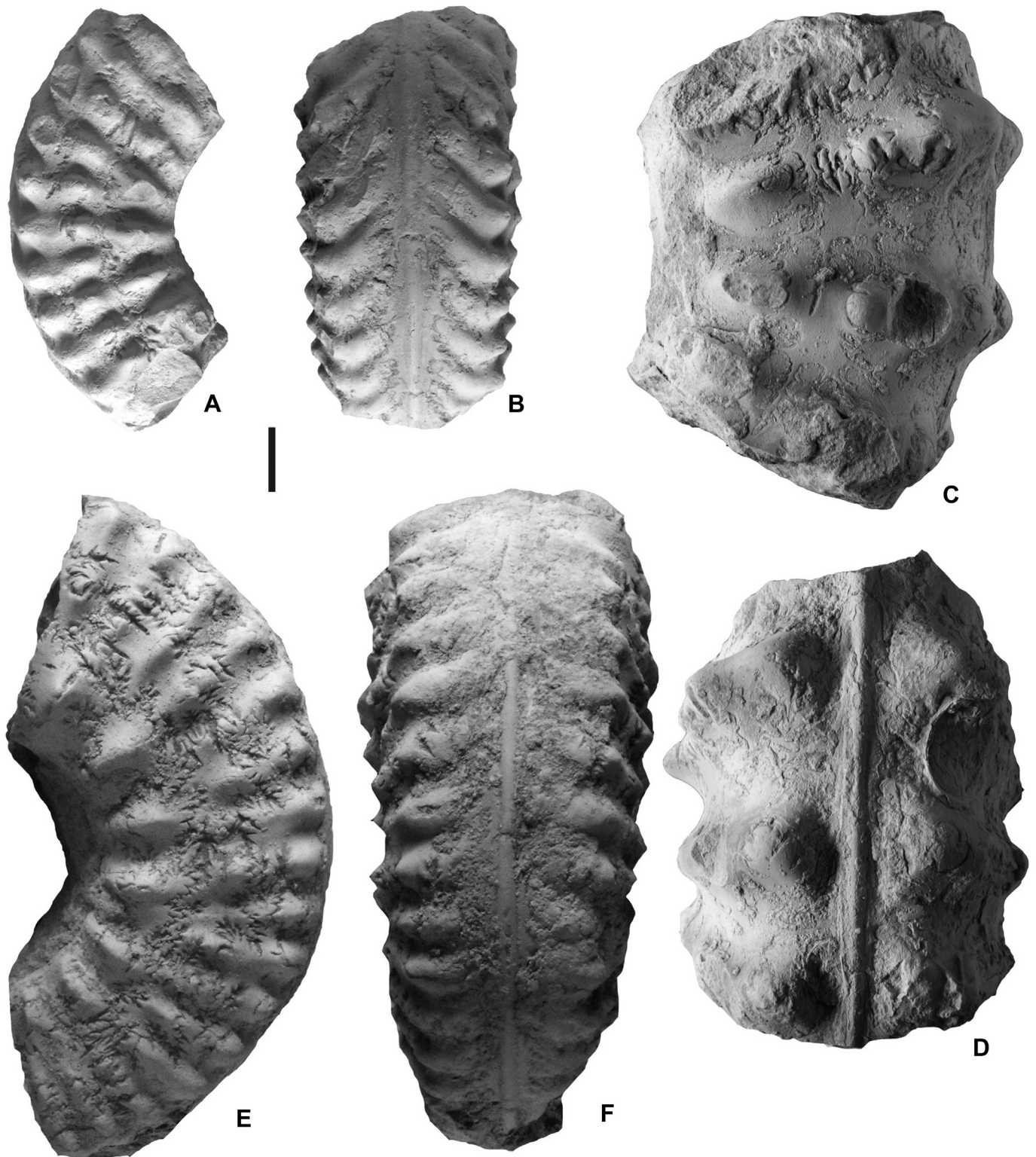


Fig. 13. *Mortonicerias (Subschloenbachia) perinflatum* (Spath, 1922). (a–b) UJF-ID.15087, (c, d) UJF-ID.15087, from bed MR. 3, Mghila West section, late Albian, *Mortonicerias (Subschloenbachia) perinflatum* Zone; (e, f) UJF-ID.15088, from Bed 16A of Mghila east section, late Albian, *Mortonicerias (Subschloenbachia) perinflatum* Zone. Scale bar is 10 mm.

Museum National d'Histoire naturelle, Paris with the number MNHN.F.J04325.

Material. One specimen from Bed 1, seventy-two pyritized specimens from Bed 2 of Mghila West section, late Albian, *Mortonicerias (Subschloenbachia) rostratum* Zone; six pyritized specimens from Bed 3b of Mghila West section; six pyritized specimens from Bed

13–15, two pyritized specimens from Bed 15–17, eight specimens from Bed 19 of Mghila East section; late Albian, *Mortonicerias (Subschloenbachia) perinflatum* Zone.

Measurements.

UJF-ID.15089: D: 14.5; Wh: 5.0 (0.34); Wb: 5.0 (0.34); U: 6.0 (0.41); Wb/Wh: 1.00.

UJF-ID.15090: D: 16.2; Wh: 5.0 (0.31); Wb: 4.7 (0.29); U: 6.8 (0.42); Wb/Wh: 0.94.

UJF-ID.15092: D: 21.0; Wh: 7.0 (0.33); Wb: 6.5 (0.31); U: 9.5 (0.45); Wb/Wh: 0.93.

UJF-ID.15093: D: 24.0; Wh: 8.0 (0.33); Wb: 7.5 (0.31); U: 10.0 (0.42); Wb/Wh: 0.94.

Description. The inner whorls are characterized by smooth flanks (Figs 14c, e, f, o), the keel appearing very early in the ontogeny, prior to a diameter of 5 mm. At about 6 mm, fine, sharp ribs are appearing on the ventrolateral edge, bearing inner and outer ventrolateral minute tubercles. At a diameter of 6–7 mm, the ribs are extending on the outer half of the flanks. At a diameter of 9 mm, all the ribs have reached the umbilical shoulder, developing a minute umbilical tubercle. Beyond a diameter of 10 mm, the ribs arise from a periumbilical, conical tubercle, alone or by two, are coarse and somewhat effaced on the inner part of the flanks, strengthen into an inner ventrolateral conical tubercle, which is linked to an outer ventrolateral tubercle by a coarse, rather strong rib, which is perpendicular to the keel or slightly projected forward. The tubercles generally become stronger with age and the ribs tend to become single on the adult body chamber. The whorl section is subquadratic, only slightly higher than broad (Wb/Wh between 0.93 and 1.00). UJF-ID.15095 (Fig. 14j) is an adult 90° sector of body chamber, with a well marked depression of the ribs on the inner half of the flanks, develops minute lateral tubercles. Two specimens show a radical change on the body chamber, where the ribs are sharp and always bifurcating and the tubercles become minute, tending to disappear with age.

Remarks. The morphological variability of our material does not seem to be considerable. It should be noted that there are four, poorly preserved, juvenile specimens, less than 16 mm in diameter, with compressed whorl section, that show dense, fine ribbing and minute tubercles. As pointed out by Kennedy (2004, p. 879), ‘There are a number of species from western Europe that have the same basic style of ribbing and tuberculation, but all come from condensed units, and limits of intraspecific variation are unclear’. Our material, close to the one figured by Kennedy (2004) from the *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone of northeast Texas, does not allow to solve this problem.

Occurrence. Late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* and *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zones of Jebel Mghila, Tunisia. The species is also known from the latest Albian of Algeria, Angola, Sardinia, SE France, Switzerland, Hungary, USA (Texas) and India.

***Cantabrigites* sp. nov.**

Figs 12l–o

Material. A single pyritized specimens from Bed 2 of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone.

Description. UJF-ID.15006 (Figs 12l–o) is a fragment of a micromorph ammonite preserved as a pyritized internal mould, comprising the very end of the phragmocone and a 130° sector of body chamber, with an estimated diameter of 15 mm. The coiling is evolute. The intercostal whorl section is subquadrangular. The umbilical wall is shallow and rounded. The ribs arise on the umbilical wall, develop small conical bullae on the umbilical shoulder, giving one or two straight, slightly prorsiradiate, coarse ribs, which all bear a small inner conical ventrolateral tubercles and a small, slightly spirally elongated, outer ventrolateral tubercle. Every four ribs, a rib is strongly projected backward and then forward on the outer part of the flanks, colliding the preceding rib, developing a characteristic v-shape bulge, and ending like the other ribs with an outer ventrolateral tubercle, the inner ventrolateral tubercle being present or not. The ribs are projected forward on the phragmocone and

the beginning of the body chamber, and tend to be perpendicular to the keel on the outer part of the body chamber. The suture is simple.

Remarks. This enigmatic specimen shows all the characteristics of *Cantabrigites spinosum*, except that it periodically develops outer lateral bulges. The regularity of their apparitions and their presence on both sides exclude any kind of teratology. This specimen is herein interpreted as a potential new species of the genus *Cantabrigites*.

Occurrence. Late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone, of Jebel Mghila, Tunisia.

Family Acanthoceratidae Grossouvre, 1894

Subfamily: Stoliczkaiinae Breistroffer, 1953

Remarks. As previously suggested (Latil, 1995, p. 348), the stoliczkaiinae are very probably not phylogenetically connected with the Iyelliceratids, the suture of early Stoliczkaiinae (e.g., *Neophlycticeras* Spath, 1922), rather suggesting a rooting among the Desmoceratoidea Zittel, 1895. On the other hand, the lineage Stoliczkaiinae–Mantelliceratinae is now well documented. Consequently, the Stoliczkaiinae is herein interpreted as a subfamily of the Acanthoceratidae Grossouvre, 1894.

Genus and Subgenus *Stoliczkaia* Neumayr, 1875.

(= *Stoliczkaiella* Cooper, 2012).

Type species: *Ammonites dispar* d'Orbigny, 1841, p. 142, pl. 45, figs 1, 2, by the subsequent designation of Diener, 1925, p. 179.

Remarks. Cooper (2012, p. 185) regarded *Stoliczkaia* Neumayr, 1875 as a ‘junior homonym of *Stoliczkaia* (sic) Jerdon, 1870 (Serpentes, Colubridae, Xenodermatinae)’. Klinger (2018, p. 349) has shown that the correct spelling of Jerdon's genus is *Stoliczkaia* and that the valid name of the ammonite genus remains *Stoliczkaia* Neumayr, 1875.

***Stoliczkaia* (*Stoliczkaia*) *clavigera* Neumayr, 1875.**

Figs 15a–r, 7i, j

1864 *Ammonites dispar* Stoliczka, p. 85, pl. 45, fig. 1 only.

1875 *Stoliczkaia clavigera* Neumayr, p. 933.

1903 *Stoliczkaia dispar* d'Orbigny: Pervinquier, p. 66.

1907 *Stoliczkaia dispar* d'Orbigny: Pervinquier, p. 388 (pars), non pl. 12, figs 9, 10, pl. 16, figs 19–23, text-figs 149–151.

1988 *Stoliczkaia* (*Stoliczkaia*) *clavigera* Neumayr, 1875: Delanoy and Latil, p. 755, pl. 2, figs 1, 3; pl. 5, fig. 1.

1994 *Stoliczkaia* (*Stoliczkaia*) *clavigera* Neumayr, 1875: Wright and Kennedy, p. 576, text-figs 5b; 11k–m, q–r; 12e–h, k–n; 13a–c; 14a–c (with synonymy).

2007 *Stoliczkaia* (*Stoliczkaia*) *clavigera* (Neumayr, 1875): Szives, p. 105, pl. 20, fig. 1 (with additional synonymy).

2007 *Stoliczkaia* (*Stoliczkaia*) *clavigera* (Neumayr, 1875): Kennedy and Latil, p. 466, pl. 4, fig. 1; pl. 5, figs 1–7; pl. 6, fig. 1 (with additional synonymy).

2013b *Stoliczkaia* (*Stoliczkaia*) *clavigera* (Neumayr, 1875): Kennedy and Klinger, p. 4, text-figs 6a–u; 7a–i; 8a–c, f–h; 14k, l; 15d, e (with additional synonymy).

2015 *Stoliczkaiella* (*Stoliczkaiella*) *dispar* (d'Orbigny, 1841): Kennedy, p. 258, pl. 3, fig. 4; pl. 4, fig. 1.

2018 *Stoliczkaia* (*Stoliczkaia*) *clavigera* (Neumayr, 1875): Klein, p. 222 (with additional synonymy).

Type. The holotype, by monotypy, is the original of *Stoliczkaia*, 1865, pl. 45, fig. 1 only, GSI. 191 from the Uttatur Group of Moravitoor, India. A cast of this specimen was figured by Delanoy and Latil (1988, pl. 5, fig. 1).

Material. Ten pyritized specimens from Bed 2 of Mghila West section, two pyritized specimens from Bed 13–15 of Mghila East section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone,

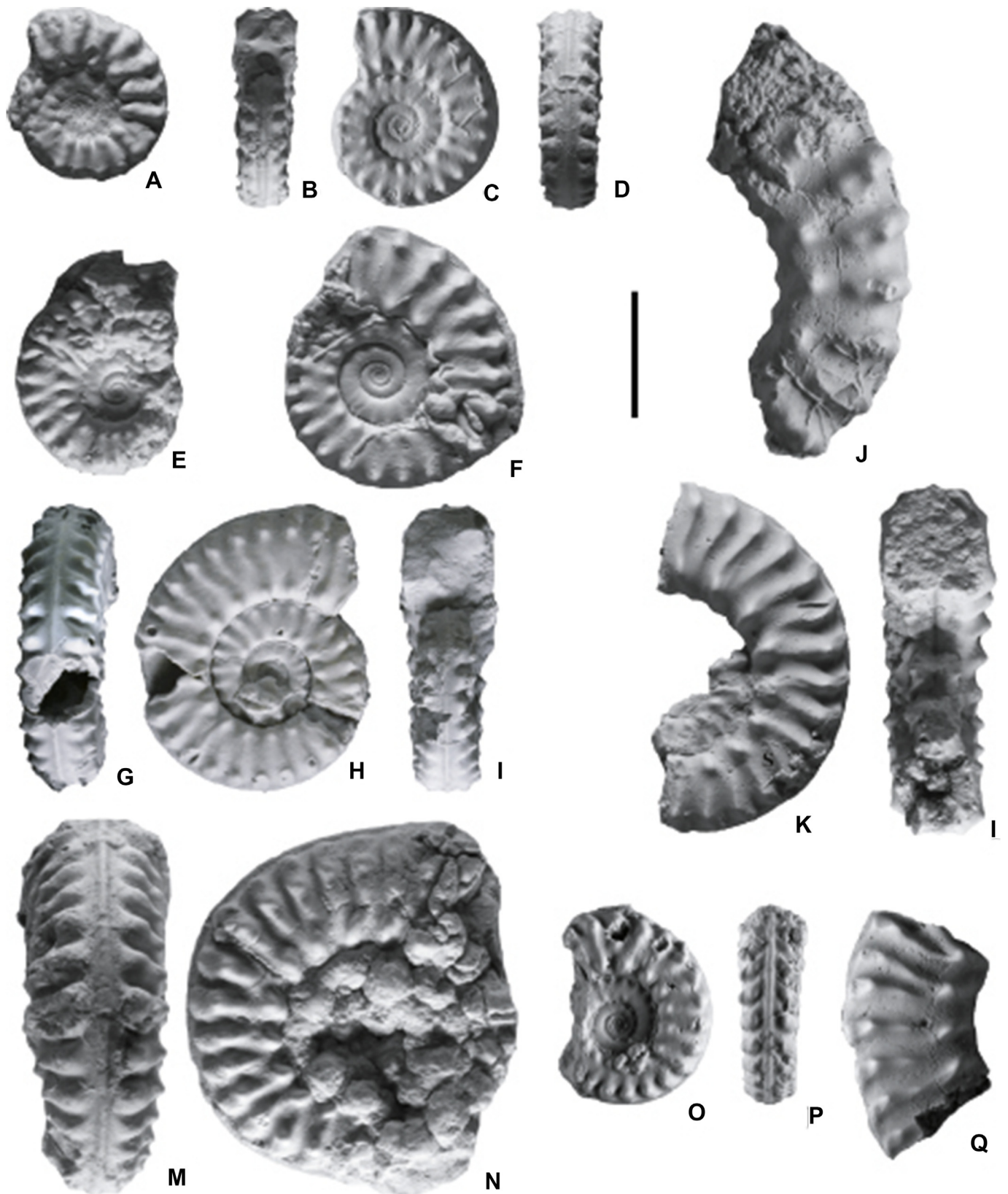


Fig. 14. *Cantabrigites spinosum* (Pervinquier, 1907). (a) UJF-ID.15089, (b–d) UJF-ID.15090, (e) UJF-ID.15091, (f) UJF-ID.15092, (g–i) UJF-ID.15093, (j) UJF-ID.15094, (k, l) UJF-ID.15095, from Bed 2 of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone; (m, n) UJF-ID.15096, from Bed 19 of Mghila East section, (o, p) UJF-ID.15097 from Bed 15–17 of Mghila East section, (q) UJF-ID.15098 from Bed 3b of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone. Scale bar is 10 mm.

four fragments from Bed 3, and one pyritized specimens from Bed 3b of Mghila West section, one fragment from bed 3 of Mghila Centre section, and three pyritized specimens from bed 19 of Mghila East section, late Albian, *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone. A specimen (UJF-ID.15083), from Bed 10 of Mghila Centre section, early Cenomanian, *Neostlingoceras carcitanense* Subzone?, is closely related to this species.

Measurements.

UJF-ID. 15013: D: 15.0 mm; Wh: 7.0 (.47); Wb: 5.4 (.36); U: 2.5 (.17); Wb/Wh: 0.77.

UJF-ID. 15014: D: 13.5 mm; Wh: 6.9 (.51); Wb: 5.0 (.37); U: 2.4 (.17); Wb/Wh: 0.72.

UJF-ID. 15015: D: 17.9 mm; Wh: 9.0 (.50); Wb: 6.5 (.36); U: 3.0 (.17); Wb/Wh: 0.72.

UJF-ID. 15016: D: 21.5 mm; Wh: 11.2 (.52); Wb: 7.6 (.35); U: 2.7 (.13); Wb/Wh: .68.

UJF-ID. 15017: D: 18.7 mm; Wh: 9.6 (.51); Wb: 7.4 (.40); U: 2.7 (.14); Wb/Wh: .77.

UJF-ID. 15018: D: 21.2 mm; Wh: 10.7 (.50); Wb: 9.0 (.42); U: 3.0 (.14); Wb/Wh: .84.

UJF-ID. 15019: D: 22.0 mm; Wh: 10.5 (.47); Wb: 7.8 (.35); U: 3.4 (.15); Wb/Wh: .74.

Description. The early whorls, prior to a diameter of 5 mm, are unknown. Coiling is moderately involute, the umbilicus of moderate depth, with a feebly convex wall and narrowly rounded umbilical shoulder. The whorl section is compressed, with Wb/Wh between 0.68 and 0.84 and a maximum of width at about mid-flanks. The flanks are flattened and subparallel, tending to be slightly convex with age, the ventrolateral shoulders broadly rounded, the venter very feebly convex. The ornament appears very early in the ontogeny. Up to a diameter of 10 mm (Figs. 15g-r), the ribs are regularly alternating, one primary for one intercalatory rib, the primaries arising on the periumbilical shoulder, the intercalatories on the inner third of the flanks. The ribs are slightly flexuous and rectiradiate, ending with a more or less expressed ventrolateral tubercle, and the siphonal area is smooth. Beyond a diameter of 10 mm (Figs. 15g-r, 7i, j), the primary ribs are less numerous and stronger than the intercalatories, arising on the umbilical wall and strengthening on the periumbilical shoulder, developing radially elongated swellings. All the ribs are crossing the venter without interruption. The ventrolateral tubercles are present at a diameter of 18–20 mm and then tend to disappear.

The adult phragmocone, about 65 mm in diameter, is known from 3 poorly preserved fragments preserved as calcareous internal moulds, having a compressed whorl section with Wb/Wh at about 0.75, slightly convex flanks, a rather narrow convex venter, and showing irregular, fine and dense ribbing. UJF-ID.15020 (Figs 15c, d), about 80 mm in diameter, shows the beginning of the body chamber. Two other fragments, UJF-ID.15021–22 (Figs 15a, b, e, f) both comprise 100° sectors of body chamber, for an estimated diameter of 110 mm. On the body chamber, the ornament is made of regularly alternating primary and intercalatory ribs. The primaries arise on the umbilical seam, are slightly flexuous on the flanks and strengthen on the upper half of the flanks and the venter where they are coarse. The intercalatories arise at mid-flank or on the upper third of the flanks. The whorl section is slightly less compressed. At the very end of the body chamber, the ornament disappears suddenly and the whorl section is becoming narrower toward the aperture.

UJF-ID.15083 is a 180° sector of body chamber, 95 mm in diameter, preserved as a weathered calcareous internal mould of a body chamber. The ornament is poorly preserved, but the subscaphitoid coiling in relation with the narrowing of the whorl section close to the aperture, and the apparent attenuation of the ribbing on the flanks toward the aperture, suggest that this specimen is closely related to *Stoliczkaia* (*S.*) *clavigera*.

Remarks. The two fragments figured by Kennedy et al. (2015, p. 258, pl. 3, fig. 4, Pl. 4, fig. 1) as *Stoliczkaia* (*Stoliczkaia*) *dispar* (d'Orbigny, 1841) from the late Albian of Mghila (Pervinquièrre Collection), are strongly weathered. Since the true *Stoliczkaia* (*S.*) *dispar* is not known from us in Tunisia, we merely refer these specimens to *S.* (*S.*) *clavigera*.

As pointed out by Kennedy and Klinger (2013b): « *Stoliczkaia* (*S.*) *dorsetensis* Spath, 1931 (p. 337, pl. 31, figs 2, 3, 10, 13, 14; pl. 32, fig. 7; pl. 33, fig. 1 (including var. *compressa*), originally described from the condensed *perinflatum* Zone of south Dorset, was regarded as a synonym of *clavigera* by Wright and Kennedy (1994, p. 576), and some juveniles are very similar; however, the adult stages are not known from the type area. ». After a re-examination of the type material, *S.* (*S.*) *dorsetensis*, with its wide venter, flattened flanks, and its wide, low ribs on the venter, where they are slightly curved forward, is herein regarded as a valid species. Wright and Kennedy also suggest that the juveniles of *S.* (*S.*) *clavigera* are less compressed than the juveniles of *S.* (*S.*) *dispar*, which, from our experience, does not seem to be supported by the facts. Everywhere, the juveniles are very difficult to identify at a specific level when the adult stages are lacking and the synonymies should be revised.

Occurrence. Late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone and *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone of Jebel Mghila, Tunisia.

Stoliczkaia (*Stoliczkaia*) sp. juv.

Fig. 7c-h

Material. Five pyritized and one calcareous specimens from Bed 2 of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone, three pyritized specimens from Bed 19 of Mghila East section, late Albian, *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone.

Description. The early whorls, prior to a diameter of 5 mm, are known only from UJF-ID.15011 (Fig. 7c-e), and are almost smooth with only well-expressed oblique ventrolateral tubercles. The ventrolateral tubercles disappear early in the ontogeny, probably at a diameter of 10–15 mm. At about 20 mm in diameter, the flanks are convex, the ventrolateral shoulders are narrowly rounded and the venter is rather broad.

Remarks. At the same size, at about 20 mm in diameter, this juvenile material differs from *S.* (*S.*) *clavigera* by its more convex flanks, its broader venter and an earlier loss of the ventro-lateral tubercles. This kind of morphology is known only by juvenile fragments preserved as pyritized internal moulds and a small calcareous fragment, which are twice less numerous than the juveniles of *S.* (*S.*) *clavigera*. It should be noted that these morphologies do not seem to occur further north, in the Tazerouine area. Our material differs from *S.* (*S.*) *dorsetensis* by its narrower and more convex venter, its more convex flanks and its ribs that are not curved on the venter.

Occurrence. Late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone and *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone of Jebel Mghila, Tunisia.

Subfamily Mantelliceratinae Hyatt, 1903

Genus *Mantelliceras* Hyatt, 1903

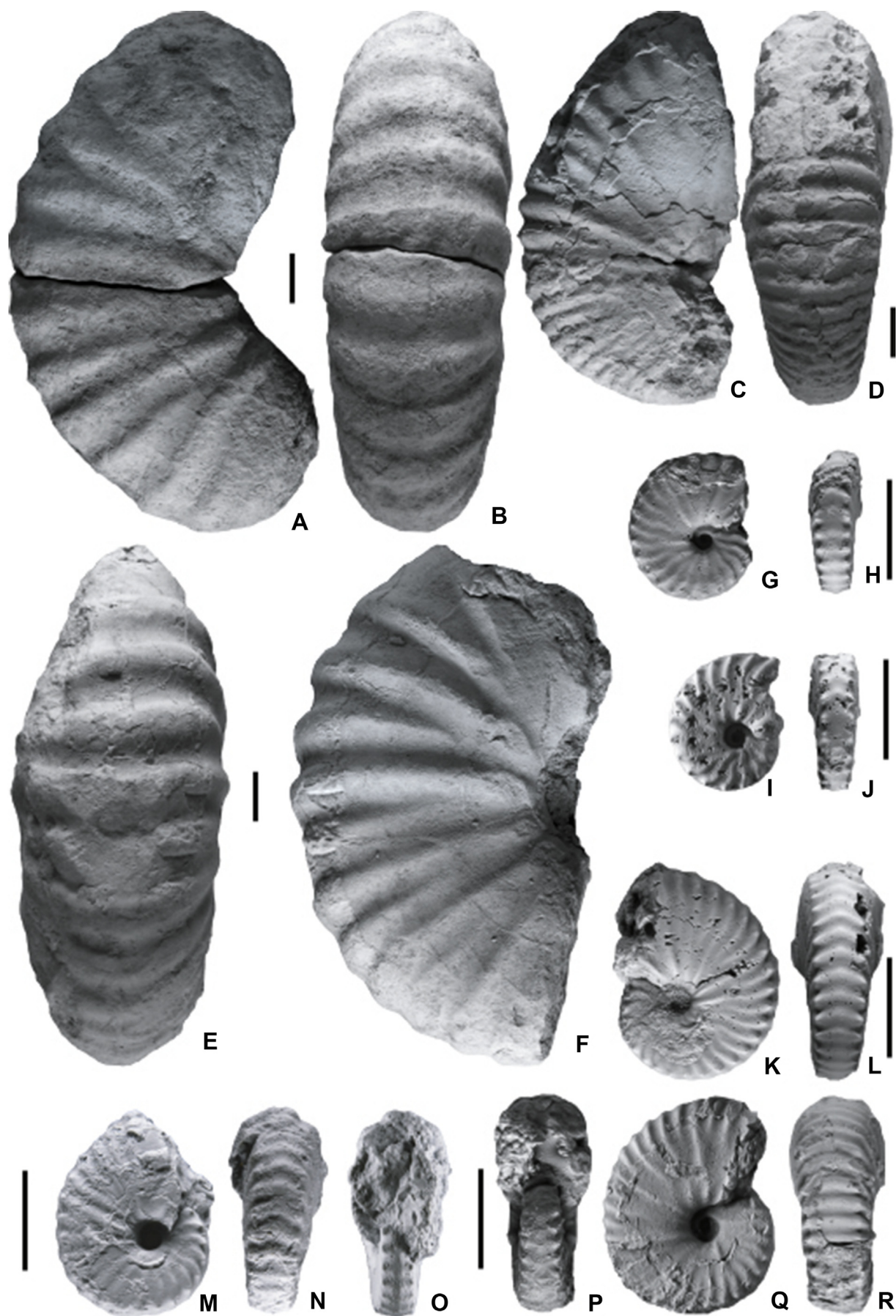
Type Species: *Ammonites mantelli* J. Sowerby, 1814, p. 199, by the original designation of Hyatt, 1903, p. 113 (ICZN Specific Name No. 1634).

Mantelliceras lymense (Spath, 1926).

Figs 16a, b.

1926 *Eucalycoceras lymense* Spath, pp. 427, 431.

1984 *Mantelliceras lymense* (Spath, 1926): Wright and Kennedy, p. 102, pl. 10, fig. 9, pl. 22, figs 1–6, pl. 23, figs 1–3, pl. 31, figs 1, 2,



pl. 36, fig. 4, text-figs 19, 24a, b, 26d, 28f-j (with full synonymy).

2004 *Mantelliceras lymense* (Spath, 1926): Amédéo, in Robaszynski et al., p. 406, pl. 10, figs 1, 2.

2011 *Mantelliceras lymense* (Spath, 1926): Mosavinia and Wilmsen, p. 182, text-figs 4d, e (with additional synonymy).

2015 *Mantelliceras lymense* (Spath, 1926): Kennedy, in Kennedy and Gale, p. 265, pl. 3, fig. 1; pl. 7, figs 1, 6; pl. 8, figs 2, 6; pl. 23, fig. 2; text-fig. 14.

2019 *Mantelliceras lymense* (Spath, 1926): Kennedy, in Gale et al., p. 223, pl. 21, figs 1, 8; pl. 22, Figs 3, 4.

Type. The lectotype, by the subsequent designation of Wright and Kennedy 1984, p. 102, is the original of Pervinquier 1907, pl. 16, fig. 16, refigured by Wright and Kennedy 1984, text-fig. 24a, b, from south of Bargou, Tunisia, an unregistered specimen in the collections of the École des Mines, Paris, currently housed in the collections of the Université de Lyon 1-Villeurbanne.

Material. A loose fragment (UJF-ID.15082) from above Bed 5 in Mghila West section, early Cenomanian, *Neostlingoceras carcitanense* Subzone or *Sharpeiceras schlueteri* Subzone of the *Mantelliceras mantelli* Zone.

Description. UJF-ID.15082 (Figs 16a, b) is a small sector of body chamber, preserved as calcareous internal mould, with a maximum preserved whorl height of 57 mm. The intercostal whorl section is compressed (Wb/Wh = 0.90), subquadrangular with feebly convex flanks, broadly rounded umbilical edge and broadly rounded ventrolateral shoulders. The venter broad and feebly convex. There are six parts of ribs on the fragment, three primaries and three intercalatories. The primaries arise at the umbilical seam, and are low and sharp on the umbilical wall, with inconspicuous clavate bullae on the ventrolateral shoulder. The ribs are broadening on the venter.

Discussion. See Kennedy, in Kennedy and Gale, 2015, p. 265.

Occurrence. Early Cenomanian, southern England, Northern Ireland, France, Algeria, Tunisia, Madagascar, Tamil Nadu, and possibly Germany and Iran.

***Mantelliceras couloni* (d'Orbigny, 1850)**

Fig. 16c, d

1841 *Ammonites Mantelli* Sowerby, Orbigny, p. 340 (pars), pl. 104, figs 1–4.

1850 *Ammonites Couloni* d'Orbigny, p. 147.

1984 *Mantelliceras couloni* (d'Orbigny, 1850): Wright and Kennedy, p. 119, pl. 21, fig. 1, pl. 23, figs 5, 6, pl. 29, figs 1–3, pl. 30, figs 1, 2, pl. 31, figs 3–5, pl. 36, fig. 5, textfigs 25f, h, 27a–d (with full synonymy).

2015 *Mantelliceras couloni* (d'Orbigny, 1850): Kennedy, in Kennedy and Gale, p. 268, pl. 7, figs 2, 5; Pl. 8, fig. 3 (with synonymy).

Type. The lectotype, by the subsequent designation of Juignet and Kennedy (1976, p. 95) is R8011 (collections of the Laboratoire de Paléontologie of the Muséum National d'Histoire Naturelle, Paris), from the early Cenomanian of Lamnay, Sarthe, France, refigured by Wright and Kennedy (1984, text-fig. 20G–I) and Kennedy and Juignet in Gauthier (2006, pl. 51, fig. 1).

Material. A fragment (UJF-ID.15084) from Bed 10 of Mghila Centre section, and one fragment (UJF-ID.15089) from Bed 30 of Mghila East section, early Cenomanian, *Mantelliceras mantelli* Zone.

Description. UJF-ID.15084 is a 90° sector of phragmocone, preserved as a slightly crushed internal mould, with a maximum preserved whorl height of 50 mm. The whorl section is subogival, with a maximum of width above the umbilical edge. The umbilical wall is low and broadly rounded, the flanks are flattened, converging to broadly rounded ventrolateral shoulders. The venter is narrow and flattened. The ornament is made of regularly alternating primary and intercalatory ribs. The primaries arise on the umbilical seam, developing radially elongated swellings at the umbilical edge. The intercalatories arise on the inner third of the flanks. All the ribs bear coarse, rounded, inner ventrolateral tubercles, and strong outer ventrolateral clavi. The venter is smooth between the tubercles UJF-ID.15089, differs only by its ribs crossing the venter (Fig. 16c, d).

Discussion. Our specimen is closely related to *Mantelliceras couloni*, differing only by the persistence of the inner ventrolateral tubercles.

Occurrence. Early Cenomanian of England, France, Iran, ?Romania, Central Tunisia, Japan, and South Africa.

Genus *Graysonites* Young, 1958

Type species: *Graysonites lozoi* Young, 1958, p. 172, pl. 27, figs 1–11; text-fig 1b, c, d, f, by original designation = *Mantelliceras wacoense* Böse, 1928, p. 215, pl. 5, figs 9–25, pl. 6, figs 1–4.

***Graysonites cobbani* (Amédéo, 1994).**

Fig. 16e, f

1994 *Mantelliceras cobbani* Amédéo, p. 424, pl. 10, figs 8, 10, 11; pl. 11, fig. 5; text fig. 34b.

Type. Holotype: MNHN.F.R62636 from Kef el Azreg section (KZ.21, 20 and KZ.26), early Cenomanian, *Graysonites cobbani* Zone of Amédéo, 1994.

Material. A fragment (UJF-ID.15079) from Bed 27 of Mghila East section, early Cenomanian, *Mantelliceras mantelli* Zone of the standard zonation, *Graysonites cobbani* Zone of Amédéo, 1994.

Description. UJF-ID.15079 (Fig. 16e, f) is a small sector of phragmocone, preserved as a slightly crushed calcareous internal mould, with a maximum preserved whorl height of 24 mm. The whorl section is distorted. There are five ribs on the fragment preserved, three primaries and two intercalatories. The primaries arise on the umbilical seam, develop small radially elongated bullae at the umbilical edge, almost inconspicuous lateral swellings, stronger inner ventrolateral conical tubercles (spines) and strong outer ventrolateral tubercles (spines). The venter is almost smooth. The intercalatories differs only from the primaries by the lack of peri-umbilical bullae.

Discussion. Our fragment differs in no respect from the holotype figured by Amédéo (1994, pl. 10, fig. 11).

Occurrence. The species is known from the early Cenomanian of central Tunisia, *Mantelliceras mantelli* Zone of the standard zonation, regional *Graysonites cobbani* Zone of Amédéo, 1994.

Genus *Sharpeiceras* Hyatt, 1903.

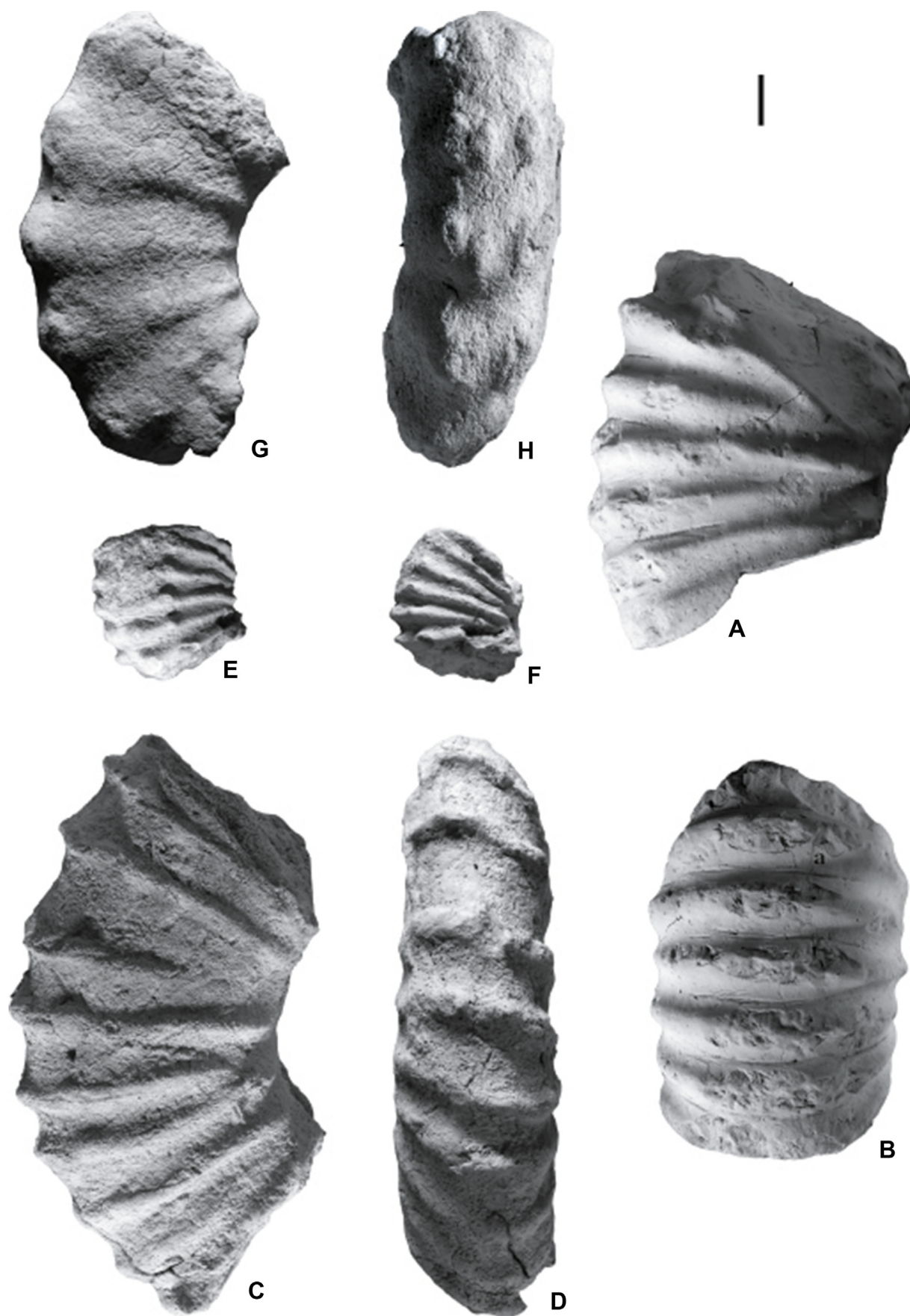
Type species: *Ammonites laticlavus* Sharpe, 1855, p. 31, pl. 14, fig. 1, by the original designation of Hyatt, 1903, p. 111.

***Sharpeiceras florencae* Spath, 1925**

Fig. 16g, h

1925 *Sharpeiceras florencae* Spath, p. 198, pl. 37.

Fig. 15. *Stoliczkaia* (*Stoliczkaia*) *clavigera* Neumayr, 1875. (a, b) UJF-ID.15022, from Bed 3 of Mghila Center East section; (c, d) UJF-ID.15020, from Bed 3 of Mghila West section; (e, f) UJF-ID.15021, from Bed 3 of Mghila West section; (g, h) UJF-ID.15013, from Bed 19 of Mghila East section; (i, j) UJF-ID.15014, from Bed 14–15 of Mghila East section, late Albian, *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone; (k, l) UJF-ID.15016, from Bed 2 of Mghila West section; (m–o) UJF-ID.15017, from Bed 2 of Mghila West section, (p–r) UJF-ID.15018, from Bed 2 of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone. Scale bar is 10 mm.



- 2015 *Sharpeiceras florencae* Spath, 1925: Kennedy et al., p. 14, text-figs 7g–j, p, q, u, w; 12j, k, p, q; 16f–h; 17f–i; 19; 20; 21; 22c–e (with full synonymy).
- 2015 *Sharpeiceras florencae* Spath, 1925: Kennedy, in Kennedy and Gale, p. 276, pl. 11, fig. 3; text-fig. 19 (with synonymy).
- 2019 *Sharpeiceras florencae* Spath, 1925: Kennedy, in Gale et al., p. 226.

Type. The holotype, by monotypy, is the original of Spath, 1925, p. 19, pl. 37, in the collections of the Ditsong Museum of Natural History (formerly the Transvaal Museum), Pretoria, from north-eastern KwaZulu-Natal, South Africa ('Pondoland').

Material. A loose fragment (UJF-ID.15080) from above Bed 25 in Mghila East section and a loose fragment (UJF-ID.15081) from above Bed 12 of Mghila Centre section, early Cenomanian, *Mantelliceras mantelli* Zone.

Description. UJF-ID.15080 (Fig. 16g, h) is a 190° sector of phragmocone, preserved as slightly crushed internal mould, with a maximum preserved whorl height of 42 mm. The intercostal whorl section is compressed, with feebly convex flanks, broadly rounded umbilical edge and broadly rounded ventrolateral shoulders. The venter relatively narrow, and flattened to very feebly convex. There are five widely separated primary ribs on the fragment. They arise at the umbilical seam, and are low and broad on the umbilical wall, with inconspicuous bullae on the umbilical shoulder. The ribs on the flanks are low, broad and coarse, bearing coarse mid-lateral tubercles, strong conical inner ventrolateral tubercles and smaller outer ventrolateral clavi. The venter is smooth between the clavi. UJF-ID.15081 is a strongly weathered fragment, comprising a 120° sector of body chamber, with a maximum preserved whorl height of 65 mm. Parts of six ribs are preserved on the fragment, with well-developed mid-lateral tubercles (the umbilical area is too weathered), strong, coarse inner ventrolateral tubercles and outer ventrolateral tubercles.

Occurrence. Early Cenomanian of northeastern KwaZulu-Natal, South Africa ('Maputo land'), Madagascar, India, Angola, Peru, and northern Mexico.

Family Flickiidae Adkins, 1928

Subfamily: Salaziceratinae Kennedy and Wright, 1984

Genus *Metascaphites* Wiedmann, 1962

Type species: *Scaphites* (?) *Thomasi* Pervinquier, 1907, p. 121, pl. 4, fig. 30, 31; text-fig. 39, by the original designation of Wiedmann, 1962, p. 212.

Remarks. According to Wright (1996, p. 261), *Scaphites* (?) *thomasi* Pervinquier, appears to be a fragment of a late form of *Scaphites equalis* J. Sowerby, 1813. This statement is not supported by the facts: *Metascaphites thomasi* is older than *Scaphites equalis* and is a micromorph ammonite that have no shaft and no hook.

***Metascaphites thomasi* Pervinquier, 1907**

Fig. 7k-m.

- 1907 *Scaphites* (?) *Thomasi* Pervinquier, p. 121, pl. 4, fig. 30, 31; text-fig. 39.
- 1962 *Scaphites* (*Metascaphites*) *thomasi* Pervinquier: Wiedmann, p. 212, 213, 219.
- 1965 *Scaphites* (*Metascaphites*) *thomasi* Pervinquier: Wiedmann, p. 427, pl. 58, fig. 1.

1979 *Salaziceras* (*Noskytes*) *thomasi* (Pervinquier, 1907): Scholz, p. 101, pl. 22, fig. 6; text-fig. 27 T.

1982 *Salaziceras* (*Noskytes*) *thomasi* (Pervinquier): Braga et al., p. 709, pl. 3, fig. 2.

1984 *Metascaphites thomasi* (Pervinquier, 1907): Kennedy and Wright, p. 163, text-fig. 1A-F.

1990 *Metascaphites thomasi* (Pervinquier, 1907): Latil, p. 33.

1992 *Salaziceras* (*Metascaphites*) *thomasi* (Pervinquier): Cooper, fig. 1H.

1994 *Metascaphites thomasi* (Pervinquier, 1907): Wright and Kennedy, p. 558, fig. 3.

1996 *Scaphites* (?) *thomasi* Pervinquier: Wright p. 261.

non 2007 *Metascaphites thomasi* Pervinquier, 1907: Szives, p. 119, pl. 16, fig. 16.

non 2017 *Metascaphites thomasi* (Pervinquier, 1907): Kennedy and Morris, p. 9, fig. 4B, 70-T.

2018 *Metascaphites thomasi* (Pervinquier, 1907): Klein, p. 249.

Type. The holotype by monotypy is the specimen figured and described by Pervinquier (1907, p. 121, pl. 4, fig. 30, 31, text-fig. 39) from the latest Albian of Jebel Mghila, Tunisia. The origin of the specimen is given by Pervinquier (1907, p. 122): 'recueilli par M. Ph. Thomas à la base du Cénomanien du Dj. Mghila, en dessous du Kef Si Abd el Kader'. It should be noted that according to Pervinquier (1903, p. 70, fig. 15) the base of the Cenomanian corresponds to the units 1 and 2 of the Kef Si Abd el Kader section, which are an equivalent of his Vraconian stage. The holotype has been very probably collected in the upper part of the Albian.

Material. A single pyritized specimens, UJF-ID. 15009 from Bed 2 of Mghila West section, late Albian, Mortonicerat (Subschloenbachia) rostratum Zone.

Measurements.

Holotype: D: 14.0 mm; Wh: 7.5 (.54); Wb: 6.0 (.43); U: 1.5 (.11); Wb/Wh: .80.

UJF-ID. 15009: D: 12.5 mm; Wh: 7.0 (.56); Wb: 5.2 (.42); U: 1.2 (.10); Wb/Wh: .75.

Description. This is a wholly septate specimen, 12.5 mm in diameter (Fig. 7k-m). Coiling is very involute, the umbilicus comprising 10 per cent of the diameter, with a shallow, convex umbilical wall. The whorl section is compressed subquadrangular, with whorl breadth to height ratios of 0.75 and maximum of width at about mid-flanks. The flanks are feebly convex, the outer flanks converging to broadly rounded ventrolateral shoulders, and the venter is convex on the juvenile, becoming feebly convex with age. Up to a diameter of 9 mm, the internal mould is totally smooth, then feeble, prorsiradiate, slightly flexuous, primary ribs arise on the umbilical shoulder and are slightly projected forward on the ventrolateral shoulder. Intercalatoxy ribs (one between each primary ribs), arise on the inner third of the flanks. At this stage of the ontogeny, both ribs cross the venter without interruption. The first ventrolateral bullae appear on the last preserved rib, at a diameter of 12.5 mm.

Remarks. As pointed out by Kennedy and Morris (2017, p. 10), 'The *Metascaphites thomasi* of Szives (2007, p. 119, pl. 16, fig. 16) has flank tubercles, linked over the venter by relatively strong ribs and belongs to some other taxon.' The specimens figured by Kennedy and Morris (2017, p. 9, fig. 4B, 70-T) from the early Cenomanian of Tanzania are younger than the present species, they are more evolute at the same size (the ratio U/D given by Pervinquier is

Fig. 16. (a, b) *Mantelliceras lymense* (Spath, 1926), UJF-ID.15082), from above Bed 5 in Mghila West section, early Cenomanian, *Neostlingoceras carcitanense* Subzone or *Sharpeiceras schlueteri* Subzone of the *Mantelliceras mantelli* Zone; (c, d) *Mantelliceras couloni* (d'd'Orbigny, 1850), UJF-ID.15089, from Bed 30 of Mghila East section, early Cenomanian, *Mantelliceras mantelli* Zone; (e, f) *Graysonites cobbani* (Amédéo, 1994), UJF-ID.15079, from Bed 27 of Mghila East section, early Cenomanian, *Mantelliceras mantelli* Zone of the standard zonation, *Graysonites cobbani* Zone of Amédéo, 1994; (g, h.) *Sharpeiceras florencae* Spath, 1925, UJF-ID.15080, from above Bed 25 in Mghila East section, early Cenomanian, *Mantelliceras mantelli* Zone. Scale bar is 10 mm.

erroneous) and develop an ornamentation at an earlier ontogenetic stage. The Tanzanian material is herein assigned to a new species: *Metascaphites morrisi* nov. sp., holotype specimen n° OUM KX15754 figured by Kennedy and Morris (2017, fig. 4B, 70-Q).

Occurrence. Upper Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone of Jebel Mhrila, South Tunisia. The species is also known from the latest Albian of Hungary and Spain.

Suborder Ancyloceratina Wiedmann, 1966

Superfamily Turrilitoidea Gill, 1871

Family Anisoceratidae Hyatt, 1900

Genus *Anisoceras* Pictet, 1854

Type species: *Hamites saussureanus* Pictet, 1847, p. 118, pl. 13, figs 1–4, by the original designation of Pictet, 1854, p. 374.

Anisoceras armatum (J. Sowerby, 1817).

Fig. 17a, b

1817 *Hamites armatus* J. Sowerby, p. 153, pl. 168.

1908 *Anisoceras armatum* var. *Živković* Petković, p. 99, pl. II, fig. 3.

1965 *Anisoceras armatum* (J. Sowerby): Clark, p. 25, pl. 5, fig. 4; pl. 6, fig. 6; text-fig. 7a.

1979 *Anisoceras* (*Anisoceras*) *armatum* (J. Sowerby, 1817): Cooper and Kennedy, p. 200, figs. 13a, b, 14d, e, 16z, c, e, i, 17–19 (with full synonymy).

1979 *Anisoceras* (*Anisoceras*) *armatum* (J. Sowerby): Scholz, p. 25 (pars), pl. 2, figs. 1, 5, 7 only.

non 1979 *Anisoceras* sp. aff. *armatum* J. Sow.: Collignon, p. 7, pl. 1, fig. 1.

1996 *Anisoceras armatum* (J. Sowerby, 1817): Kennedy, p. 573, figs. 24d–f, h.

1998 *Anisoceras armatum* (J. Sowerby, 1817): Kennedy et al., p. 34, figs. 30, 31, 32a–c, 33d–f, 36f.

2004 *Anisoceras armatum* (J. Sowerby, 1817): Kennedy, p. 890, figs. 25G, H, Q, R, Y–D1, 26.

2007 *Anisoceras armatum* (J. Sowerby, 1817): Kennedy and Latil, p. 467, pl. 7, fig. 7, pl. 10, fig. 11, 14.

2015 *Anisoceras armatum* (J. Sowerby, 1817): Klein, p. 35, with synonymy.

2015 *Anisoceras jacob* Breistroffer, 1947: Klein, p. 35, with synonymy.

Type. Holotype, by monotypy, is the original of J. Sowerby, 1817, pl. 168, refigured by Kennedy et al. (1998, fig. 30). no. K673a, b in the collections of the Oxford University Museum of Natural History, from the late Albian, Upper Greensand of Roke, 1.5 km NNE of Benson, Oxfordshire, England.

Material. UJF-ID.15001, from Bed 2 of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone.

Description. UJF-ID.15001 (Fig. 17a, b) is a small fragment of recurvated sector, preserved as a pyritized internal mould. The whorl section is compressed oval, with a maximum preserved whorl height of 8 mm. The ribs are unobscured, single and coarse on the dorsum. There is one primary for one intercalatory rib. The primary ribs develop strong conical dorsolateral tubercles, elongated parallel to the shaft, tend to be divided into two ribs on the flanks which are linked to strong clavate ventrolateral tubercles; the ventrolateral tubercles are linked across the venter by a wide coarse rib. The intercalatory ribs are single and non tuberculated.

Remarks. This small fragment is very similar to the type specimen of *Anisoceras picteti* Spath, 1926, but we follow Cooper and Kennedy (1979), considering that *Anisoceras picteti* is a junior synonym of *A. armatum*.

Occurrence. Late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone of Mhrila area, South Tunisia. The species is known from the latest Albian of Belgium, southern England, France, Germany,

Switzerland, Hungary, Serbia, Spain, South Africa, Mozambique, Texas, Georgia and South India.

Family Turrilitidae Gill, 1871

Genus and subgenus *Mariella* Nowak, 1916

Type species: *Turrilites bergeri* Brongniart, 1822, p. 395, pl. 7, fig. 3, by the original designation of Nowak, 1916, p. 10.

Mariella* (*Mariella*) *bergeri (Brongniart, 1822)

Fig. 17c–e

1822 *Turrilites bergeri* Brongniart, p. 395, pl. 7, fig. 3.

1985 *Mariella* (*Mariella*) *bergeri* (Brongniart, 1822): Atabekian, p. 27, pl. 2, figs 4, 5; pl. 3, figs 1–11; pl. 4, figs 1–7 (with synonymy).

2009 *Mariella* (*Mariella*) *bergeri* (Brongniart, 1822): Kennedy and Bilotte, p. 62, pl. 6, figs 31–44, 745; pl. 7, figs 1–8, 10 (with additional synonymy).

2014 *Mariella* (*Mariella*) *bergeri* (Brongniart, 1822): Mosavinia et al., p. 84, fig. 8C1, 8C2, 8C3.

2015 *Mariella* (*Mariella*) *bergeri* (Brongniart, 1822): Kennedy, p. 311, pl. 24, figs 14, 17.

2016 *Mariella bergeri bergeri* (Brongniart, 1822): Klein, p. 133 (with additional synonymy).

2017 *Mariella bergeri* (Brongniart, 1822): Tajika et al., p. 42, fig. 11D, I, K.

2019 *Mariella* (*Mariella*) *bergeri* (Brongniart, 1822): Gautam et al., p. 25, figs 7D–F.

Type. The holotype, by monotypy, is the original of Brongniart (1822, pl. 7, fig. 3), from the Montagne de Fiz, Savoie, France. The specimen has not been traced.

Material. Two fragments (UJF-ID.15052–53) from the interval 22–24 and 5 fragments from Bed 23 (UJF-ID.15054–58) of Mghila East section, late Albian, *Stoliczkaia* (*Shumarinaia*) *africana* Zone.

Description. UJF-ID.15052–53 are juvenile, preserved as crushed, pyritized internal moulds, with a maximum preserved whorl height of about 10 mm. On the upper part of the flanks, they are feebly prorsiradiate ribs, ending to small transversely elongated tubercles. A smooth zone separates them from a second row of feebly transversely elongated tubercles, displaced aperturally at mid-flank. Another smooth zone separates this row from a third row of conical to feebly transversely elongated tubercles, again displaced aperturally. A third smooth zone separates this row from the fourth row of smaller tubercles, again displaced aperturally, and housed in notches in the junction of the outer and upper whorl faces of the succeeding whorl. They give rise to single radial ribs on the lower whorl face (Fig. 17c).

UJF-ID.15054–58 are slightly distorted fragments, preserved as weathered internal moulds, with a maximum preserved whorl height of about 37 mm. At this stage of growth, the upper row of tubercles has moved at just above mid-flanks and the two lower rows of tubercles are closer each other (Fig. 17d, e).

Occurrence. Widespread in the uppermost Albian *Mortoniceras* (*S.*) *perinflatum* and *Arrhaphoceras briacensis* Zones. Southern England, France, Switzerland, Germany, Spain, Italy, Hungary, Romania, Crimea, Caucasus, Turkmenistan, Kopet Dag, Iran, Morocco, Algeria, Tunisia, India, South Africa, Venezuela and California.

Mariella* (*Mariella*) *dorsetensis Spath, 1926

Fig. 17i–k.

1857 *Turrilites bergeri* Brongniart: Sharpe, p. 65 (pars), pl. 26, figs 9, 11 only.

1926 *Turrilites dorsetensis* Spath, pp. 429, 431.

1996 *Mariella* (*Mariella*) *dorsetensis* Spath, 1926: Wright and Kennedy, p. 344, pl. 100, figs 5, 11, 17, 19, 22, 25; pl. 102, fig. 7; text-fig. 136b, e (with full synonymy).

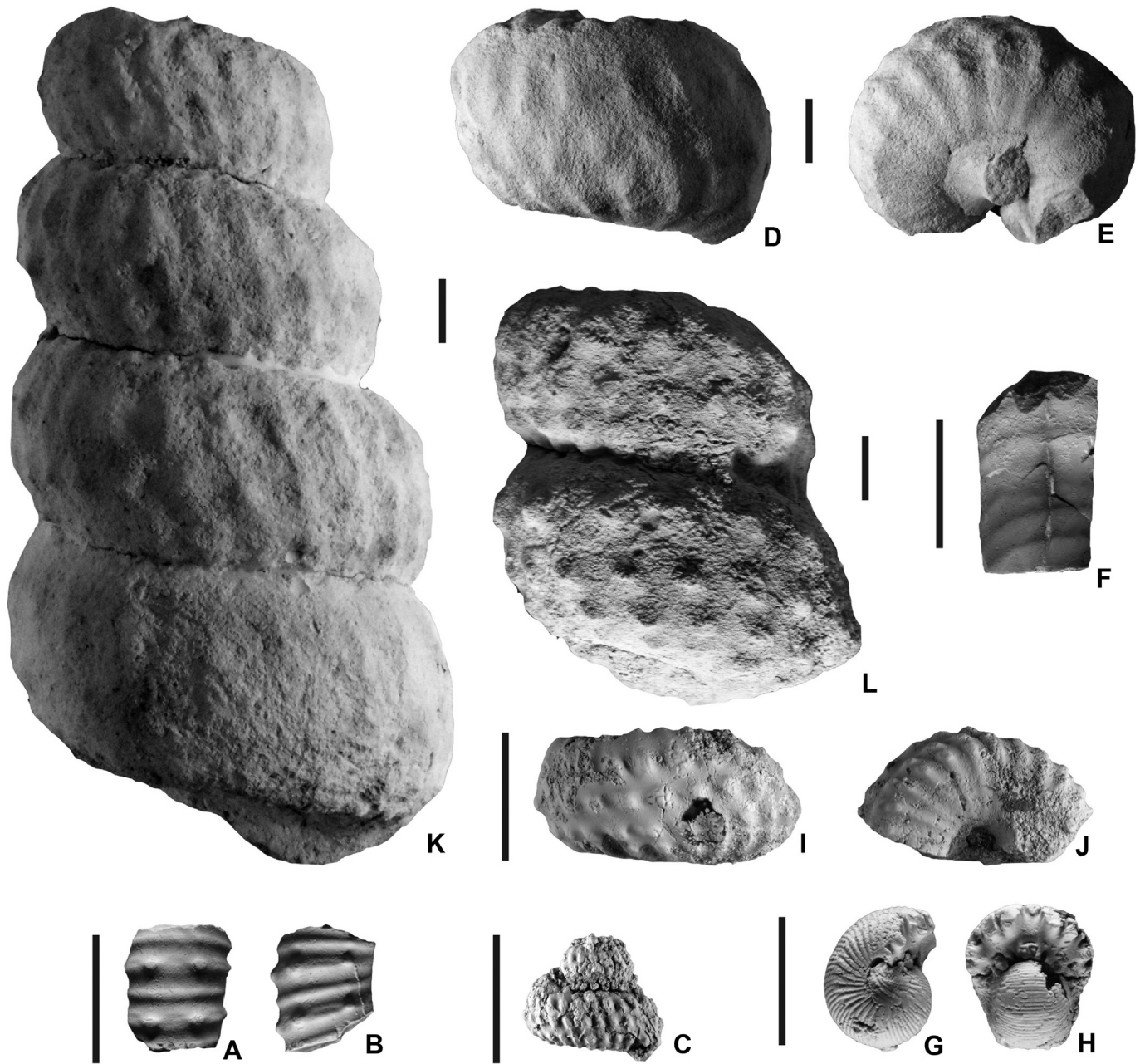


Fig. 17. (a, b) *Anisoceras armatum* (J. Sowerby, 1817), UJF-ID.15001, from Bed 2 of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone; (c) *Mariella* (*Mariella*) *bergeri* (Brongniart, 1822), UJF-ID.15052 from the interval 22–24 of Mghila East section, late Albian, *Stoliczkaia* (*Shumarinaia*) *africana* Zone; (d, e) *Mariella* (*Mariella*) *bergeri* (Brongniart, 1822), UJF-ID.15054, from Bed 23 of Mghila East section, late Albian, *Stoliczkaia* (*Shumarinaia*) *africana* Zone; (f) *Lechites gaudini* (Pictet et Campiche, 1861), UJF-ID.15000, from Bed 2 of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone; (g, h) *Scaphites* aff. *meriani* Pictet et Campiche, 1861, UJF-ID.15002, from Bed 19 of Mghila East section, late Albian, *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone; (i, j) *Mariella* (*Mariella*) *dorsetensis* Spath, 1926, UJF-ID.15067, from bed 5 of Mghila Centre section; early Cenomanian, ?*Neostlingoceras carcitanense* Subzone of the *Mantelliceras mantelli* Zone; (k) *Mariella* (*Mariella*) *dorsetensis* Spath, 1926, UJF-ID.15067, from Bed 26 of Mghila East section, early Cenomanian, ?*Neostlingoceras carcitanense* Subzone of the *Mantelliceras mantelli* Zone; (l) *Mariella* (*Mariella*) *lewesiensis* (Spath, 1926), UJF-ID.15077, from Bed 30 of Mghila East section; early Cenomanian, *Mantelliceras mantelli* Zone. Scale bar is 10 mm.

2015 *Mariella* (*Mariella*) aff. *dorsetensis* Spath, 1926: Kennedy, p. 312, pl. 24, fig. 15.

2016 *Mariella dorsetensis* Spath, 1926: Klein, p. 141 (with additional synonymy).

Type. The holotype, by monotypy, is BMNH C3834, the original of Sharpe, 1857, pl. 26, fig. 11, refigured by Wright and Kennedy, 1996, pl. 100, fig. 5, from Chardstock, Devon.

Material. A series of badly preserved fragments: 3 fragments (UJF-ID.15061–63) from Bed 7 (UJF-ID.15054–58) of Mghila West section;

3 fragments (UJF-ID.15064–66) from Bed 26 of Mghila East section; 5 fragments (UJF-ID.15067–71) from bed 5, 2 fragments (UJF-ID.15059–60) from Bed 10, and 4 fragments (UJF-ID.15054–58) from Bed 12–13 of Mghila Centre section; early Cenomanian, *Neostlingoceras carcitanense* Subzone and *Sharpeiceras schlueteri* Subzone of the *Mantelliceras mantelli* Zone.

Description. (UJF-ID.15067–72) are juvenile, preserved as calcareous internal moulds, with a maximum preserved whorl height of 10 mm (Fig. 17i, j). There are four rows of tubercles, the tubercles of

successive rows displace adaperturally. The tubercles of the upper row and the second row are subequal, and rounded to slightly transversely elongated. The first row is above the middle of the exposed whorl face, the second row is in the middle part. The tubercles of the third row are subequal to those of the previous rows, and lie towards the bottom of the exposed whorl face. The tubercles of the fourth row are smaller, and partially concealed in the notches in the inter-whorl contact zone. A very juvenile specimen, with a maximum preserved whorl height of 6 mm, with a broad smooth area between the first and the second row of tubercles, seems to be transitional to *Mariella* (*Mariella*) *lewesiensis* (Spath, 1926). The calcareous fragments are strongly weathered. UJF-ID.15066 is an adult, consisting of four whorls, including the phragmocone and part of the body chamber, with a maximum preserved whorl height of 35 mm (Fig. 17k). This specimen is as described by Kennedy et al., (2015, p. 312).

Occurrence. *Mariella* (*Mariella*) *dorsetensis* is known from the lower part of early Cenomanian of southern England, northern France, Poland, Turkmenistan, Iran, Madagascar and Peru.

***Mariella* (*Mariella*) *lewesiensis* (Spath, 1926)**

Figs 17l

1857 *Turrilites bergeri* Sharpe, p. 65 (pars), pl. 26, fig. 110 only.

1926 *Turrilites lewesiensis* Spath, pp. 429, 431.

1996 *Mariella* (*Mariella*) *lewesiensis* (Spath, 1926): Wright and Kennedy, p. 339, pl. 100, fig. 4; pl. 101, figs 2, 3; pl. 103, figs 6–8 (with synonymy).

2015 *Cenomariella lewesiensis lewesiensis* (Spath, 1926): Klein, p. 153 (with full synonymy).

2017 *Mariella lewesiensis* (Spath, 1926): Mosavinia and Wilmsen, p. 118, text-fig. 4b, g (with additional synonymy).

2019 *Mariella* (*Mariella*) *lewesiensis* (Spath, 1926): Kennedy, p. 287, pl. 52, figs 7, 12.

Type. The holotype, by monotypy, is BMNH 33558, the original of Sharpe 1857, pl. 26, fig. 10, from the Chalk Marl near Lewes, Sussex, refigured by Wright and Kennedy (1996, pl. 101, fig. 3).

Material. Two badly preserved fragments (UJF-ID.15077–78) from Bed 30 of Mghila East section; early Cenomanian, *Mantelliceras mantelli* Zone.

Description. UJF-ID.15077 is an adult, preserved as a weathered calcareous internal mould, consisting of two whorls, with a maximum preserved whorl height of 30 mm (Figs 17l). The outer whorl face is convex in intercostal section, the junction of outer and lower whorl faces rounded, the lower whorl face flattened. There are four rows of tubercles, four in a distance equal to the whorl height, the tubercles of successive rows displace adaperturally. The tubercles of the upper row are strong and conical, and are separated from the second row by a broad smooth zone. The tubercles of the upper row are slightly less numerous than those of the second row. The second row have slightly smaller conical tubercles, and a narrow smooth zone separates the second and third rows, the latter lying just above the junction of the outer and lower whorl faces. A fourth row of tubercles, close to the third one is located in the inter-whorl suture and the tubercles are slightly smaller and conical; they give rise to weak radial ribs that extend across the base of the whorl.

Remarks. This species differs from *Mariella* (*M.*) *dorsetensis* by its conical, less numerous tubercles, its broader smooth area between the first and second row of tubercles, and less numerous tubercles of the first row.

Occurrence. Early Cenomanian, *Mantelliceras mantelli* Zone of Jebel Mghila, Tunisia. The species is also known from the early Cenomanian, southern England, France, Germany, Switzerland, Poland,

Iran, Turkmenistan, South Africa, Madagascar, India, Japan, and Peru.

Family Baculitidae Gill, 1871

Genus *Lechites* Nowak, 1908

Type species: *Baculites gaudini* Pictet and Campiche, 1861, p. 112, pl. 55, figs 5–9, by the original designation of Nowak, 1908, p. 350.

***Lechites gaudini* (Pictet et Campiche, 1861)**

Fig. 17f

1861 *Baculites gaudini* Pictet and Campiche, p. 112, pl. 55, figs 5–9.

1977 *Lechites gaudini* (Pictet and Campiche): Cooper and Kennedy, p. 644, text-figs 1.1–1.38; 2.1–2.30; 3; 4.1–4.18; 5.115; 6; 7; 8.16–26 (with synonymy).

2016a *Lechites* (*Lechites*) *gaudini* (Pictet and Campiche, 1861): Klein, pp. 2, 4 (with synonymy).

2016a *Lechites* (*Lechites*) *communis* Spath, 1941: Klein, pp. 2, 3 (with synonymy).

2016a *Lechites* (*Lechites*) *campichei* Renz, 1968: Klein, pp. 2, 3 (with synonymy).

2016a *Lechites* (*Lechites*) *italicus* Wiedmann and Dieni, 1968: Klein, pp. 2, 6 (with synonymy).

2016a *Lechites* (*Lechites*) *raricostatus* Breistroffer, 1947: Klein, pp. 2, 3 (with synonymy).

2016a *Lechites* (*Lechites*) *vraconensis* Renz, 1968: Klein, pp. 2, 8 (with synonymy).

2019 *Lechites* (*Lechites*) *gaudini* (Pictet and Campiche, 1861): Kennedy, in Gale, Kennedy and Walaszczyk, p. 291, pl. 58, Fig. 5.

Lectotype. The original of Pictet and Campiche 1861, p. 112, pl. 55, fig. 5, by the subsequent designation of Spath 1941, p. 663, refigured by Renz 1968, pl. 17, fig. 3 (collections of the Musée Geologique, Lausanne, GEOLREG: 40012, 2A, 2/2, 3349) from the condensed uppermost Albian of Sainte-Croix, Vaud, Switzerland.

Material. UJF-ID.15000, from Bed 2 of Mghila West section, late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone.

Description. UJF-ID.15000 (Figs 17f) is a 17 mm long fragment, preserved as a crushed pyritized internal mould. The whorl section oval, with a maximum preserved whorl height of 10 mm. The ribs are feeble, effaced on the dorsum, narrow and widely spaced on the flanks, where they are straight and prorsiradiate, crossing the venter without interruption.

Occurrence. Late Albian, *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone of Mghila area, South Tunisia. The species is known from the late Albian of southern England, France, Switzerland, Hungary, Romania, Sardinia, Iran, Algeria, Central Tunisia, Madagascar, South Africa, Madagascar, South India, Japan, Mexico, Australia and Alexander Island, Antarctica.

Superfamily Scaphitoidea

Family Scaphitinae Gill, 1871

Genus *Scaphites* Parkinson, 1811

Type species: *Scaphites equalis* J. Sowerby, 1813, p. 53, by subsequent designation of Meek, 1876, p. 413.

***Scaphites* aff. *meriani* Pictet et Campiche, 1861**

Fig. 17g, h

1861 *Scaphites meriani* Pictet and Campiche, p. 16, pl. 44, figs 1–4, 8 only.

1965 *Scaphites* (*Scaphites*) *meriani* Pictet and Campiche: Wiedmann, p. 426, pl. 54, fig. 6; pl. 57, figs 3–4 (with synonymy).

1968 *Scaphites* (*Scaphites*) *meriani* Pictet and Campiche: Wiedmann and Dieni, p. 84, pl. 7, fig. 4; pl. 8, fig. 4; pl. 15, fig. 8.

1968 *Scaphites* (*Scaphites*) n. sp.: Renz, p. 94, pl. 18, fig. 19; textfig. 33b.

1979 *Scaphites* (*Scaphites*) *meriani* Pictet and Campiche: Scholz, p. 44, pl. 1, figs 26–28.

1981 *Scaphites meriani tenuis* Chiriac, p. 75, pl. 7, fig. 8.

2008 *Scaphites meriani* Pictet and Campiche: Joly and Delamette, fig. 8G.

2016b *Scaphites meriani meriani* Pictet and Campiche, 1861: Klein, p. 84 (with full synonymy).

Lectotype. The adult specimen figured by Pictet and Campiche (1861, pl. 44, fig. 1, designed and refigured by Wiedmann (1965, p. 426, pl. 54, fig. 6).

Material. UJF-ID.15002, from Bed 19 of Mghila East section, late Albian, *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone.

Description. UJF-ID.15002 (Fig. 17g, h) is a 11.5 mm fragment, preserved as a pyritized internal mould, comprising the initial whorls until the very beginning of the shaft. The whorl section is depressed, with rounded ventrolateral margins and broad feebly convex venter. The ribs are very fine, tending to be divided into 2–3 ribs on the venter from minute ventrolateral bullae.

Remarks. Cooper (1990) considers that *S. meriani* is a synonym of *Scaphites hugardianus* d'Orbigny, 1842, on the basis of a study of morphological intraspecific variation of the species without taking into account the biostratigraphic range of both taxa. Scholz (1979) mentions that *S. meriani* could be younger than *S. hugardianus*. We herein regard both species as independent and valid pending a revision on the basis of stratigraphically well documented material. **Occurrence.** South Tunisia, late Albian, *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone. The species is also known from the latest Albian of France, Hungary, Romania, Sardinia, Switzerland and ?Madagascar.

5.2. *Plesiosaur*

The repositories of specimens is UJF-ID: ISTerre, Université Grenoble Alpes, formerly Institut Dolomieu collections.

Order Sauroptrygia Owen, 1860

Plesiosauria Blainville de, 1835

Superfamily Plesiosauroidae (Williston) Welles, 1943

Family Elasmosauridae Cope, 1869

Genus et species indetermined.

Material. UJF-ID.16000, five vertebrae found at the Mghila West section, late Albian, base of the Sequence 2, base of the *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone.

General preservation

Five incomplete vertebrae have been discovered. They have been found at the surface, near a small erosive channel filled with fine sandstone. So, they probably have been reworked during a transgressive phase in a channel, firstly dug during an emersion and then flooded during the transgression and acting temporarily as a tidal channel. As a result of both action (current exposure in desert environment and syn-sedimentary reworking), the bones are poorly preserved, with very few of the original periostic surface bone kept, revealing a highly spongy internal structure. The centra exhibit also some distortion, indicating that a syn-sedimentary compression probably occurred during diagenesis. Only the centra are preserved and none is complete, rendering their identification along the vertebral column difficult. However, the fact that these centra have been found all close together, combined with their similar size, indicate that they most probably belong to the same individual and from an adjacent part of the vertebral column.

Description

Cervical centrum (H = 9,5 cm, W = 8,5 cm, L = 7 cm) (Fig. 18 A-D) – This centrum is slightly laterally compressed and partially preserved. It is slightly higher than wide than long but these measurements remain approximate due to its poor preservation. The articular surfaces are almost amphiplate and bear a large horizontally oval (2 × 1 cm) notochordal pit. In dorsal view, the typically hourglass-shaped neural canal is well visible, flanked laterally in its median part by two oval foramina. Laterally to the neural canal, there is a large ovoid surface (better preserved on left side), which sutural zone is still visible, and corresponding to the neural arch insertion. The right lateral surface preserves on its posteroventral part a pronounced knob that probably corresponds to the transverse process of the rib. The ventral surface is regularly rounded without any keel and bears two almost central nutritive foramina. Two larger and more laterally located foramina are also present. On the basis of all these characters, this centrum could correspond to one of the last cervical vertebra (see for example Welles, 1943).

Pectoral centrum (H = 9,5 cm, W = 8 cm, L = 6 cm) (Fig. 18 E-H) – This centrum is distorted and broken, so that the median plane of symmetry was difficult to determine. In anterior/posterior view, the centrum has a roughly triangular shape. The articular surfaces, though eroded, were most probably almost amphiplate with a large horizontally oval (2 × 1 cm) notochordal pit. In dorsal view, only one part of the neural canal with a median foramen is preserved. Laterally to the neural canal, a large roughly oval rugous surface and protuberance indicate that the rib transverse process was probably located on both the centrum and the neural arch, as usual in pectoral vertebrae (Brown, 1981). The lateral surfaces of the centrum are regularly convex and bear at least three pairs of nutritive foramina, regularly spaced. Because the rib process is highly situated and located on both the centrum and neural arch, this centrum could be one of the latest pectoral vertebra.

Dorsal centrum (H = 9 cm, W = 9 cm, L = 6 cm) (Fig. 18 I-K) – Though also partially preserved, this centrum is the best preserved. The proportions are mostly similar to the pectoral centrum but the articular surfaces are rounded. They are almost amphiplate with a large and distinct horizontally oval (2 × 1 cm) notochordal pit. The dorsal surface bears the trace of the neural canal flanked laterally by two oval foramina, and laterally by a large ovoid surface corresponding to the neural arch insertion which suture is visible. The lateral surfaces of the centrum, though badly preserved seems regularly convex and bear ventrally three nutritive foramina regularly spaced. This centrum whose lateral surfaces lacks any rib facet is interpreted as a dorsal one (Brown, 1981).

? Cervical centrum fragment (L = 8,5 cm) (Fig. 18 L) – Only the dorsal surface, exhibiting the neural canal and the neural arch insertion suture is relatively well preserved. The length of this centrum could however be appreciated as parts of both amphiplate articular surfaces are preserved, showing that it is longer than the other centra here described. This, combined to the occurrence of two close nutritive foramina preserved on the midline of the bone, could indicate an anterior cervical centrum. The other surfaces are all damaged, precluding any detailed description.

Unidentified centrum – A bone fragment probably corresponds to a centrum because of its internal microstructure, very similar to the other described centra. A zone could correspond to the neural canal and a rounded surface to transverse process insertion zone, so that

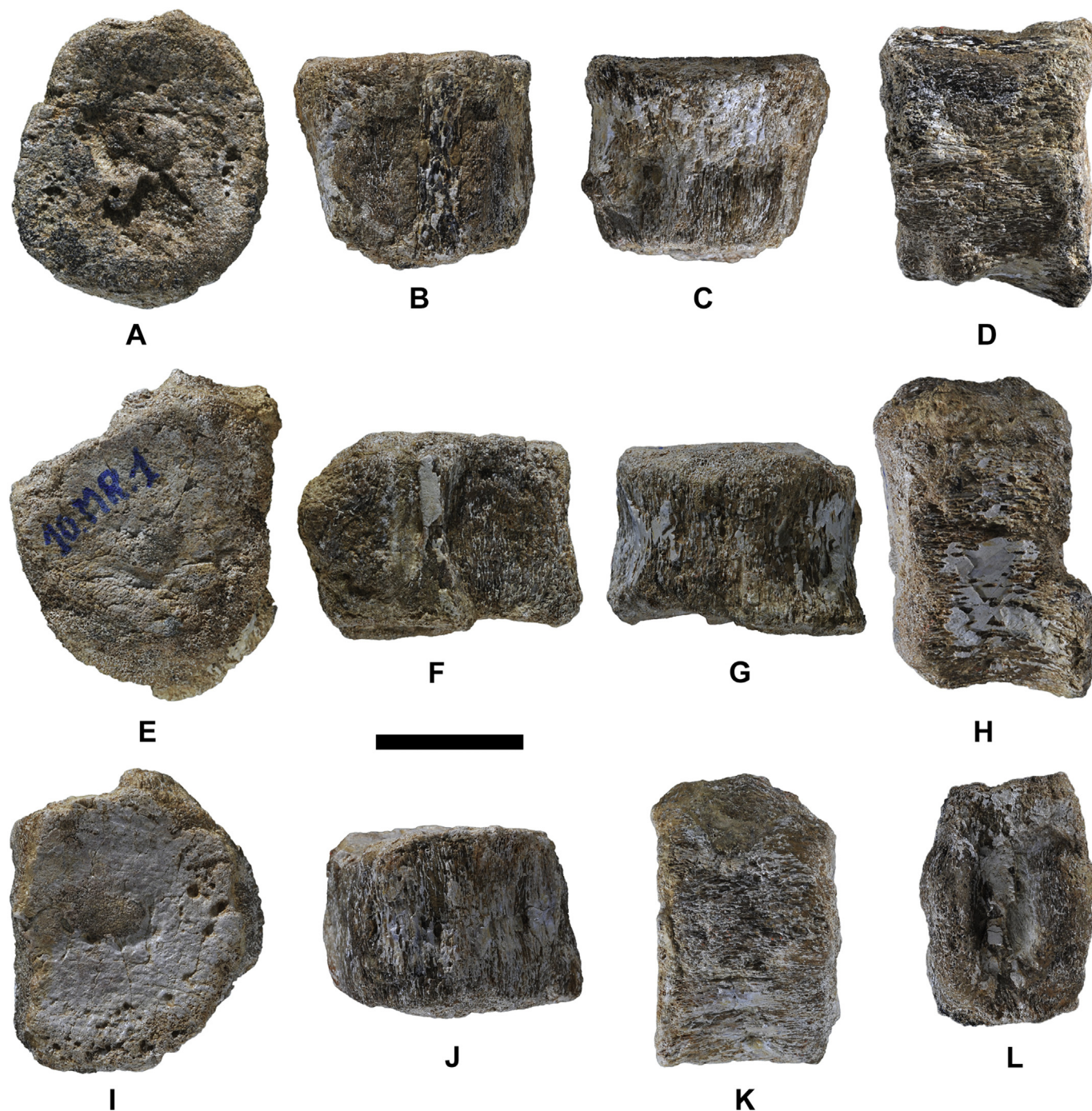


Fig. 18. Indeterminate elasmosaurid from the base of the Sequence 2, Mghila West section, late Albian, UJF-ID.16000. A–D: posterior cervical centrum in anterior (A), dorsal (B), ventral (C) and left lateral (D) views; E–H: pectoral centrum in anterior (E), dorsal (F), ventral (G) and left lateral (H) views; I–K: dorsal centrum in anterior (I), dorsal (J), and left lateral (K) views; L: ? cervical centrum in dorsal view. Scale is 5 cm.

it could correspond either to one of the last pectorals, or to one of the first dorsals.

Systematical attribution

Despite their poor state of preservation, these centra exhibit at least three characteristics permitting to refer them to the clade Plesiosauria (i.e. Brown, 1981; Storrs, 1991, 1993): 1) amphicoelous articular surfaces; 2) occurrence of paired nutritive foramina sub-centrally on the ventral and lateral surfaces of the centra; 3) highly spongy microanatomy. The amphiplat (or acoelous) articular surfaces, as well as elongated cervical vertebrae are typical of Cretaceous long-necked forms, more especially of Elasmosauridae (i.e. Druckenmiller and Russell, 2008; Ketchum and Benson, 2010). In pliosauroids and polycotyloid plesiosauroids on the contrary, the centra are always distinctively amphicoelous and shorter ($L < H$). The proportions of the cervical centrum described here, broader than long and high, are usually found in the posterior cervicals of elasmosaurids (e.g., SGO.PV.6506, *Lagenanectes richterae*, *Albertonectes vanderveldei*; Kubo et al., 2012; Otero et al., 2014; Sachs et al., 2017). As a result, these vertebrae could tentatively be referred to as an indeterminate elasmosaurid. Moreover, the occurrence of a large notochordal pit probably indicates an immature state of ontogenetic growth (Brown, 1981). Unfortunately, the poor preservation and lack of any specific diagnostic character preserved on the material preclude for a more precise systematical determination at the infra-familial level.

Palaeobiogeographical implications

Plesiosaurs were widespread during Cretaceous time, having being found in all continents, including in high latitude environments like those of Antarctica and Australia (Gasparini et al., 2003; Kear, 2006; Bardet et al., 2014). They were mainly represented by numerous genera belonging to Plesiosauroidea (short-necked polycotylics and leptocleidids, as well as long-necked elasmosaurids) and by scarcer Pliosauroida (short-necked pliosaurids). As far as elasmosaurids are concerned, they are mainly known during the Late Cretaceous whereas they remain scarcer in the Early Cretaceous (Ketchum and Benson, 2010; Bardet et al., 2014; Benson and Druckenmiller, 2014; Serratos et al., 2017; Sachs et al., 2017). During Albian time, elasmosaurids remain scarce but were widely expanded, having being reported from Canada by *Wapuskianectes betsynichollsae* Druckenmiller and Russell, 2006 and an indeterminate specimen (Druckenmiller and Russell, 2006), Venezuela by *Alzadasaurus tropicus* Colbert, 1949 (Colbert, 1949), Australia by *Eromangasaurus australis* (Sachs, 2005) and an indeterminate specimen (Sachs, 2005; Kear, 2006, 2007), and Europe by several indeterminate or partial specimens (e.g., Persson, 1963; Bardet et al., 2016; Vincent et al., 2020).

Plesiosaurs are known in Africa by leptocleidids in the Valanginian of South Africa (Andrews, 1911; Cruickshank, 1997), pliosaurids (Angst and Bardet, 2015) and polycotylics (Bardet et al., 2003; Buchy et al., 2005; Allemand et al., 2018, 2019) in the Turonian of Morocco. As far as they are concerned, African elasmosaurids are known in Morocco, both in the Turonian (Buchy, 2006; Sachs and Kear, 2017; Allemand et al., 2017, 2018, 2019) and the Maastichtian (Vincent et al., 2011, 2013), as well as in the Maastichtian of Angola (Araújo et al., 2015) and the Maastichtian of Egypt (Werner and Bardet, 1996) (see Vincent et al., 2011 for details). The plesiosaur remains from the Albian of Tunisia here described, though being fragmentary, thus represent one of the few occurrences of elasmosaurids from the Albian worldwide and the first plesiosaurian specimen described from Tunisia.

6. Concluding remarks

- Based on our new collections, twenty-two ammonite species are recognised in the uppermost Albian and lowermost Cenomanian of Djebel Mghila. The *Mortonicer* (*Subschloenbachia*) *rostratum* and the *Mortonicer* (*Subschloenbachia*) *perinflatum* Zones of latest Albian age, are recognised on the basis of the occurrence of their key marker species. At the Albian-Cenomanian transition, despite the lack of the index species, the *Stoliczkaia* (*Shumarinaia*) *africana* Zone is also identified by the disappearance of the mortoniceratids. The *Neostlingoceras carcitense* Subzone of the Lower Cenomanian *Mantelliceras mantelli* Zone is doubtfully recorded in Mghila Centre section, while the *Sharpeiceras schlueteri* Subzone of the Lower Cenomanian *Mantelliceras mantelli* Zone is recognised everywhere, on the basis of the occurrence of key marker species.
- The species *Placenticer* *saadensis* Thomas and Peron, 1890 is revised, including *Engonoceras thomasi* Pervinquière, 1907, and is placed within the genus *Hypengonoceras* Spath, 1922.
- The definition of an accurate biostratigraphic framework and identification of sedimentary discontinuities allowed to define 3 depositional sequences in the latest Albian and earliest Cenomanian. Correlation with other well-dated sections shows that the Albian-Cenomanian transition (*S. (S.) africana* Zone) is marked by a major sea level drop. The latter triggered the emergence of the southeastern areas and the deposition of a lowstand wedge to the NW, fed by erosional channels in the intermediate bypass zone that includes Jebel Mghila.
- The subsequent earliest Cenomanian transgression (*N.s carcitense* Subzone) is associated with diachronous, condensed, phosphate-rich deposits in the bypass zone that represents the shelf slope.
- Five vertebrae found at the base of Sequence 2 (base of the *M.s (S.) rostratum* Zone) are ascribed to an undetermined plesiosaur. They constitute the first plesiosaurian remains reported from Tunisia, and represent one of the few elasmosaurids known in the Albian world.

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