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GEOBIOS

Geobios 43 (2010) 615–628

Original article

Vertebrate microremains from the Early Cretaceous of southern Tunisia[☆]

Microrestes de vertébrés du Crétacé inférieur du Sud tunisien

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Received 14 September 2009; accepted 9 July 2010

Available online 1 October 2010

Abstract

Microremains of various sharks, actinopterygians and crocodiles have been recovered from two sites in the Douiret Formation and three sites in the Ain el Guettar Formation in southern Tunisia. The presence of an actinistian is also suggested based on histological study of hemisegments of lepidotrichia. Convergence in dental enameloid microstructure between neoselachian sharks and actinopterygians sharing a tearing dentition is also documented. The vertebrate assemblage of the Douiret Formation suggests a pre-Aptian age for this formation and the presence of *Bernissartia* in the Ain el Guettar Formation confirms faunal exchange between Africa and Europa during the Early Cretaceous.

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Keywords: Continental Intercalaire; Sharks; Actinopterygians; Actinistians; Crocodiles

Résumé

Des microrestes de plusieurs requins, actinoptérygiens et crocodiles ont été recueillis dans deux sites de la Formation Douiret et trois sites de la Formation Ain el Guettar dans le Sud tunisien. La présence d'un actinistien est également suggérée d'après des études paléohistologiques d'hémisegments de lépidotriches. Une convergence dans la microstructure de l'émailloïde dentaire des requins néosélaciens et des actinoptérygiens partageant une denture de type arracheur est également illustrée. La faune de vertébrés de la Formation Douiret indique un âge pré-Aptien pour cette formation et la présence de *Bernissartia* dans la Formation Ain el Guettar confirme que des échanges faunistiques ont eu lieu entre l'Afrique du Nord et l'Europe durant le Crétacé inférieur.

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Mots clés : Continental Intercalaire ; Requins ; Actinoptérygiens ; Actinistiens ; Crocodiles

1. Introduction

Fossil vertebrate remains have long been reported from the Mid-Cretaceous “continental intercalaire” of the Tataouine region, southern Tunisia (Pervinquièrre, 1912; de Lapparent, 1951, 1960; Tabaste, 1963; Schlüter and Schwarzhans, 1978; Bouaziz et al., 1988). These layers were usually considered as continental deposits, but recent fieldwork in this area from 1995–

2005 has yielded a wealth of new data concerning both fossil vertebrates and plants, which indicate a greater marine influence on the deposits than previously suspected (Barale, 1999, 2007; Benton et al., 2000; Barale and Ouaja, 2001; Buffetaut and Ouaja, 2002; Cuny et al., 2004; Srarfi et al., 2004; Anderson et al., 2007). However, most of the above-mentioned publications focused on rather large, at least centimetric, fossils, and very few studies have been conducted on vertebrate microremains, the size of which lies between 10 and 0.5 mm, except for the study of the shark faunas (Cuny et al., 2004) and taphonomic and geochemical studies (Anderson et al., 2007). Anderson et al. (2007) provided a taxonomic diversity analysis of four localities (Jebel Boulouha North side, Oued el Khil, Touil el Mra and Oum

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ed Diab), but without description of the fossils. They reported the presence of teeth of *Priohybodus* sp., *Hybodus* sp., *Onchopristsis* sp. as well as indeterminate dermal denticles. Concerning actinopterygians, they reported teeth of *Lepidotes* and Caturidae, as well as indeterminate vertebrae, scales and lepidotrichia. They also mentioned reptilian teeth and claws, as well as crocodile teeth and scutes. Taphonomic and geochemical studies of these faunas allowed Anderson et al. (2007) to reach the following conclusions: the Jebel Boulouha North side assemblage (Douiret Formation) was interpreted as a terrestrial carbonate-rich environment with relatively little mixing. The Touil el Mra assemblage (Aïn el Guettar Formation) suggested a marginal marine environment with some mixing of previously interred bones. The Oued el Khil and Oum ed Diab assemblages (Aïn el Guettar Formation) are more equivocal, suggesting mixed freshwater and marine influences.

The present paper aims to describe in detail the most significant vertebrate microremains from these four sites, as well as fossils from Oued Zefrat, a site that was not included in the previous studies by Cuny et al. (2004) and Anderson et al. (2007), and to discuss their importance for a better under-

standing of the evolution of the Tunisian Lower Cretaceous faunas. Description of the chondrichthyan component of the faunas is not repeated here, and we refer instead to Cuny et al. (2004), except for new records not previously reported.

2. Geological setting

The main vertebrate-bearing units within the “continental intercalaire” are of Early Cretaceous age and the localities in the Tataouine Basin are exposed along the Dahar Cliff, which runs for about 300 km in a roughly N-S direction along the northeastern margin of the basin (Fig. 1). The five localities included in this study belong to two different formations: the Douiret Formation, which belongs to the Merbah el Asfer Group and is considered Aptian in age, although it is likely to be a little older (Barremo-Aptian, Le Lœuff et al., 2010), and the Aïn el Guettar Formation, which is early Albian in age and divided into two members, the Chenini Member below and the Oum ed Diab Member above (Oujaja, 2003 in Barale, 2007).

The Douiret Formation is 90 m-thick and consists mainly of sandstone in its lower part and of mudstone in its upper part

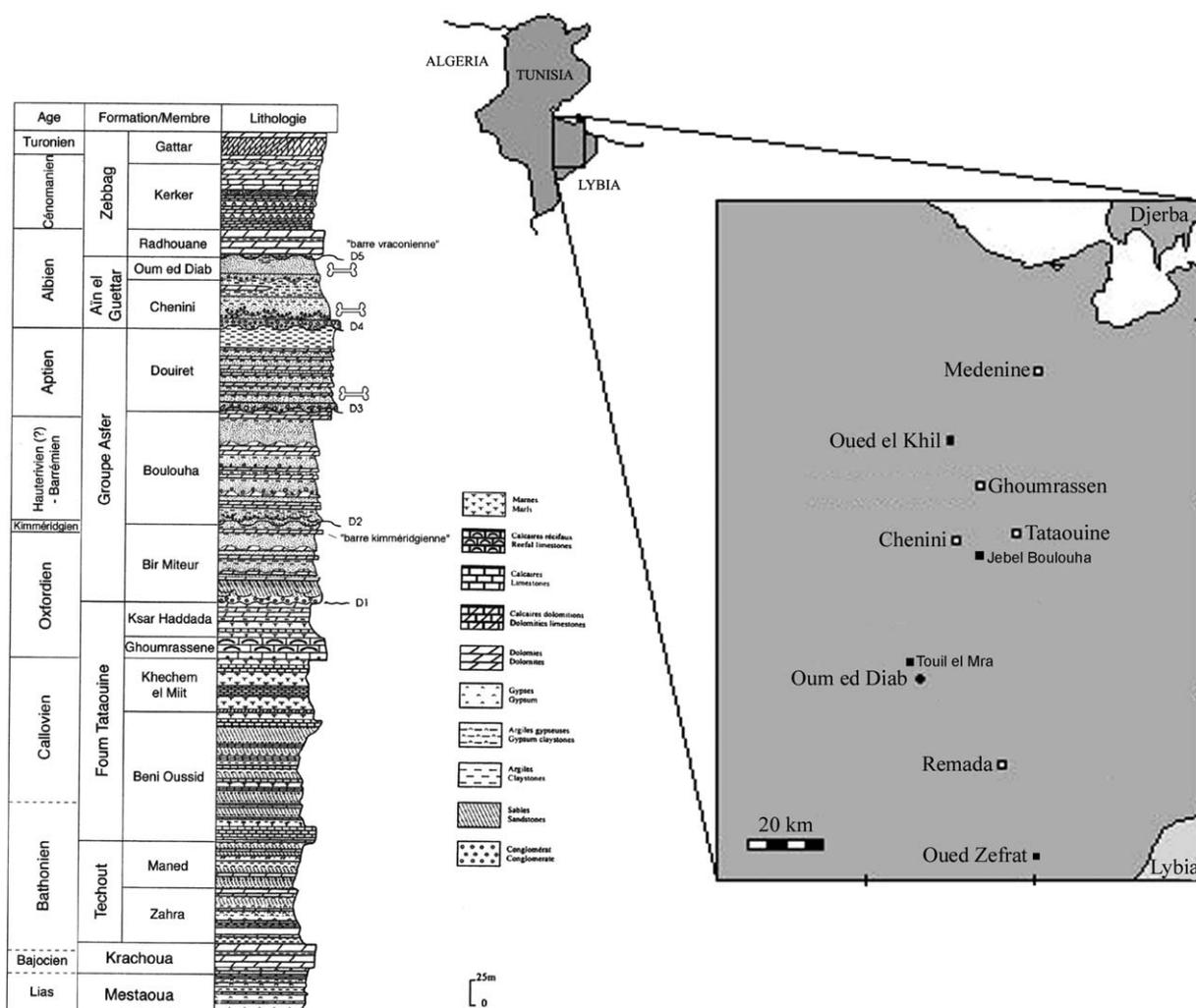


Fig. 1. Stratigraphy and location. Left: simplified stratigraphy of the Jurassic-Cretaceous succession on the Dahar plateau in southern Tunisia (modified from Srafi, 2006). Right: location (black squares) of the localities mentioned in the text (modified from Buffetaut and Oujaja, 2002).

(Srarfi, 2006). It is separated from the overlying Aïn el Guettar Formation by an erosional surface of regional extent called D4 (Ouaja, 2003; Barale, 2007). The Chenini Member of the latter formation is 50 m-thick and consists mainly of coarse sandstones, but also includes interspersed conglomerates, breccias, and mudstones, which contain varied fossil plant material (Anderson et al., 2007). The Oum ed Diab Member is 25 m-thick and consists mainly of sandstones (Srarfi, 2006).

The localities of Jebel Boulouha North side and Oued Zefrat lie in the Douiret Formation, whereas Oued el Khil belongs to the Chenini Member of the Aïn el Guettar Formation and Oum ed Diab and Touil el Mra are situated in the Oum ed Diab Member of the latter formation. For more information on these sites and the geology of the area, we refer to Ouaja (2003), Cuny et al. (2004) and Srarfi (2006).

3. Material and methods

Only poorly consolidated sandstones were sampled and screen-washed in water using 1.7 and 0.5 mm mesh-sized sieves. Eighty kilograms of sediment from Jebel Boulouha North side were processed, as well as 140 kg from Oued el Khil, 100 kg from Oum ed Diab and 100 kg from Touil el Mra. From Oued Zefrat, only a small sample, around 2 kg, was available for processing. The vertebrate microremains were subsequently sorted under a stereoscopic microscope.

The best specimens were then coated with gold and photographed using a Hitachi S-3500N scanning electron microscope (SEM) with an acceleration voltage of 15 kV at the University of Bristol or a JEOL JSM6335F with an acceleration voltage of 7 kV at the Natural History Museum of Denmark. To study their enameloid microstructure with the SEM, some teeth were etched with 10% HCl prior to gold-coating.

All the specimens studied in this work will be deposited in the collection of the Office National des Mines in Tunis.

4. Systematic description

Class CHONDRICHTHYES Huxley, 1880

Subclass ELASMOBRANCHII Bonaparte, 1838

Order HYBODONTIFORMES Maisey, 1987

Family HYBODONTIDAE Owen, 1846

Genus *Egertonodus* Maisey, 1987

Egertonodus sp.

Fig. 2(1)

Material: Oued Zefrat: Thirteen isolated crowns, including OZ1

Description: The largest crown (OZ1) measures 3.6 mm mesio-distally, 1 mm labio-lingually and is 3.7 mm high. It is made of a high main cusp flanked by a pair of well-developed lateral cusplets, reaching a third of the main cusp height. Smaller teeth can sometimes show an additional second pair of minute lateral cusplets. The ornamentation is very similar on both the lingual and labial sides, being made of rather curved, anastomosing ridges. These ridges disappear at mid-height of the main cusp on the labial side, and at two-thirds of this height on the lingual side, whereas they almost attain the apex of the

lateral cusplets on both the lingual and labial sides. The main cusp and lateral cusplets possess well-developed cutting edges running from their base to their apex, which are not interrupted between cusp and cusplets. Both main cusp and lateral cusplets are compressed labio-lingually. The labial side of the main cusp is slightly more convex than the lingual one, and in mesial or distal view, it is slightly sigmoidal in the high, anterior teeth. None of the teeth in our sample shows a preserved root.

Remarks: Due to the presence of sigmoidal curvature of the main cusp as well as high, slender lateral cusplets, the Tunisian teeth are better attributed to *Egertonodus* than to *Hybodus* (Rees and Underwood, 2008). However, none of the Tunisian teeth shows more than two pairs of lateral cusplets, whereas teeth of *E. basanus* show as many as four pairs (Patterson, 1966; Maisey, 1983) and those of *E. duffini* show up to three pairs (Rees and Underwood, 2008). The Tunisian teeth are therefore unlikely to belong to either of the two species currently included in the genus *Egertonodus* (Rees and Underwood, 2008).

Egertonodus was already mentioned in the Lower Cretaceous of Africa by Duffin and Sigogneau-Russell (1993) who described fragmentary crowns from the Anoual Syncline in Morocco (?Berriasian to ?Aptian), which they attributed to *E. basanus*. Their teeth differ from the Tunisian ones by an ornamentation that seems almost to attain the apex of the cusp. However, their material appears to us too fragmentary for identification at species level. It is probably wiser to consider these teeth as belonging to *Egertonodus* sp., and the same applies to the Tunisian teeth. It is however unlikely that they belong to the same species due to a different ornamentation pattern. The record of *Egertonodus* in the Aptian would represent one of the most recent for this genus.

Family INCERTAE SEDIS

Genus *Lissodus* Brough, 1935

aff. *Lissodus* sp.

Fig. 2(2, 3)

Material: Oued Zefrat: Eighteen more or less complete teeth, including OZ2 and OZ3.

Description: The largest crown (OZ2) measures 4 mm mesio-distally, 1.5 mm labio-lingually and is 1.3 mm high. All the crowns show a low, pyramidal main cusp usually flanked by a pair of weakly developed cusplets. The labial peg at the base of the main cusp is weakly developed. A longitudinal crest runs without interruption from the mesial to the distal extremity of the crown and through the apices of each cusp and cusplet. Ornamentation of the crown is quite variable. One to eight ridges ornament both labial and lingual sides of the main cusp. These ridges rarely anastomose to each other, except on the larger teeth, on which ornamentation is better developed than on the smaller ones.

The only complete tooth (OZ3) measures 2.7 mm mesio-distally, 0.7 mm labio-lingually and is 1.4 mm high, the root being approximately half the height of the crown. The root is slightly projected lingually and narrower labio-lingually than the crown. It is perforated by numerous, randomly distributed foramina. Just below the crown, there is a single, somewhat irregular row of smaller foramina. There are more densely distributed on the labial side than on the lingual one. The labial

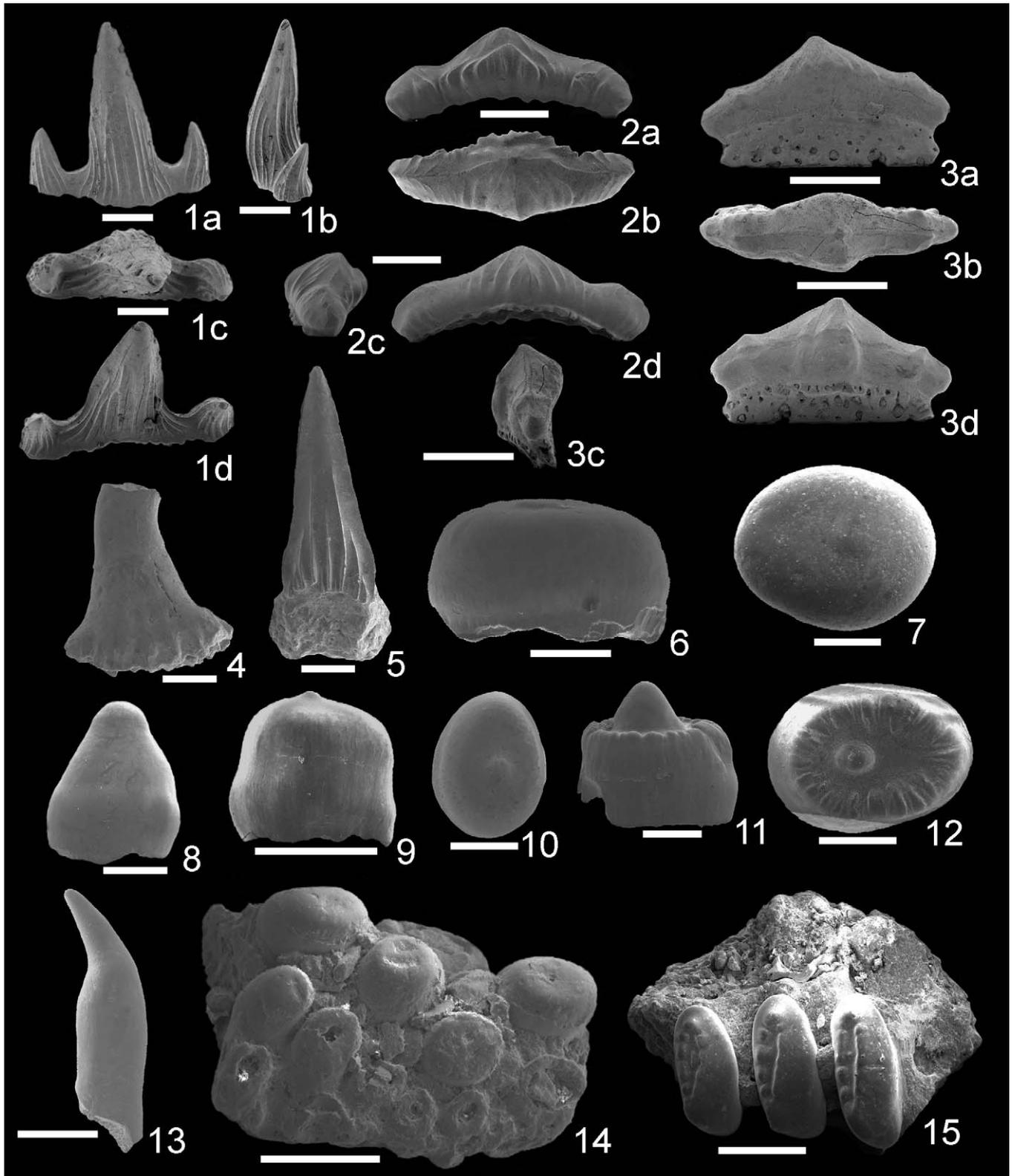


Fig. 2. Vertebrate microremains from the Lower Cretaceous of Tunisia. **1.** Tooth of *Egertonodus* sp. from Oued Zefrat (OZ1): labial (a), mesial or distal (b), apical (c) and lingual (d) views. **2.** Tooth of *Lissodus* sp. from Oued Zefrat (OZ2): lingual (a), apical (b), mesial or distal (c) and labial (d) views. **3.** Tooth of *Lissodus* sp. with root preserved from Oued Zefrat (OZ3): lingual (a), apical (b), mesial or distal (c) and labial (d) views. **4.** Incomplete rostral tooth of *Onchopristis dunklei* from Oued el Khil (OEK5) in ventral or dorsal view. **5.** Incomplete tooth of *?Cretodus* in labial view from Oum ed Diab (OED5). **6.** *Lepidotes* sp., tooth of morphotype 1 from Oued el Khil (OEK6) in lateral view. **7.** *Lepidotes* sp., tooth of morphotype 1 from Oum ed Diab (OED7) in apical view. **8.** *Lepidotes* sp., tooth of morphotype 2 from Oued el Khil (OEK7) in lateral view. **9.** *Lepidotes* sp., tooth of morphotype 1 from Touil el Mra (TEM2) in lateral view. **10.** *Lepidotes* sp., tooth of morphotype 1 from Touil el Mra (TEM3) in apical view. **11.** Tooth of Semionotidae indet. from Oum ed Diab (OED8) in lateral view. **12.** Tooth of Semionotidae indet. from Oum ed Diab

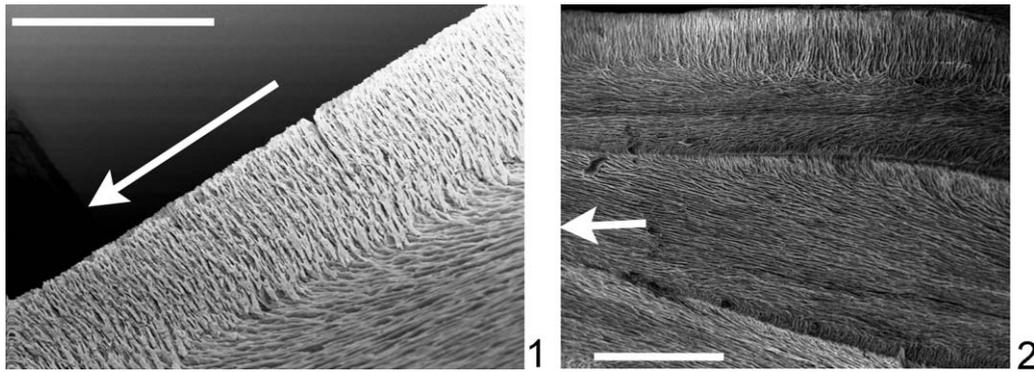


Fig. 3. Comparisons of enameloid microstructure between teeth of *Caturus* sp. and ?*Cretodus* sp. **1.** Cutting edge of a tooth of *Caturus* sp. from Oued el Khil (OEK9) etched 35 seconds in 10% HCl. Note the change of orientation of the bundles of crystallites. **2.** Surface of the tooth of ?*Cretodus* sp. from Oum ed Diab (OED6) etched 30 seconds in 10% HCl revealing its parallel-bundled enameloid. Again, note the change of ornamentation at the level of the cutting edge (top of the image) and ridges ornamenting the surface of the crown. Arrows indicate the direction of the apex of the tooth. Scale bars: 100 µm (1) and 250 µm (2).

side of the root is concave under the row of smaller foramina, whereas the lingual one is almost straight.

Remarks: The general shape of the Tunisian teeth is similar to that of Lonchidiidae and *Lissodus*, although their labial peg is reduced. *Lonchidion* in particular possesses a well-developed labial peg, and the lack of such a feature in the Tunisian teeth precludes their attribution to this genus (Rees and Underwood, 2002). One should however note that this labial peg is quite reduced in the lateral teeth of *Lonchidion marocensis*, approaching the condition observed in the Tunisian teeth (Duffin and Sigogneau-Russell, 1993; Rees and Underwood, 2002). Teeth of *Hylaeobatis* are labio-lingually extended with a reticulate ornamentation and are therefore very different from the Tunisian teeth. The same is true for the teeth of *Vectiselachos*, with granulae ornamenting the surface of their crown. The Tunisian teeth can also be separated easily from those of *Parvodus* as their lateral cusplets are never as well demarcated as in the teeth of the latter. The Tunisian material therefore does not appear to be closely related to any of the four genera currently included in the family Lonchidiidae (Rees, 2008), and it is therefore unlikely to belong to this family. Its affinities might therefore lie closer to *Lissodus*, the familial affinities of which are currently unclear (Rees, 2008). The Tunisian teeth share with the latter a row of small foramina just under the crown on the labial side of the root and a rather well developed ornamentation of the crown. However, the labial peg is not as developed, particularly in anterior teeth, although it is always possible that, taking into account the small size of our sample, the most anterior teeth of the Tunisian taxon are simply lacking. Another difference is that the lateral teeth are not so labio-lingually expanded as the teeth of *Lissodus*. Still, the Tunisian teeth are, in our opinion, closer to *Lissodus* than to any other hybodont genus. They might warrant the erection of a new genus, but the material is insufficient for such an action, and they are provisionally referred to as aff. *Lissodus*, pending the discovery of additional material.

Lissodus has already been found in Tunisia, but in the Oum ed Diab Member of the Ain el Guettar Formation, not from the Douiret Formation (Cuny et al., 2004). The teeth from the Oum ed Diab Member are very different from those from Oued Zefrat with their smooth crown, scalloped lingual side and better developed labial peg. It should be noted that again these teeth are quite unusual for *Lissodus* (Cuny et al., 2004), and they might also, like the teeth from Oued Zefrat, belong to a different, new genus, closely allied to *Lissodus*.

In addition, Oued Zefrat has yielded two teeth of *Priohybodus arambourgi* and seven teeth and three dermal denticles of ‘*Rhinobatos*’ sp. This material is already well known from the Douiret Formation and we refer to the description of Cuny et al. (2004).

Cohort NEOSELACHII Compagno, 1977

Superorder GALEOMORPHII Compagno, 1973

Order LAMNIFORMES Berg, 1958

Family CRETOXYRHINIDAE Gluckman, 1958

Genus ?*Cretodus* Sokolov, 1965

Figs. 2(5) and 3(2)

Material: Oum ed Diab: Two complete main tooth cusps, including OED5 and one broken cusp (OED6).

Description: The largest of these three cusps (OED5) is 6 mm high and exhibits the same characteristics as the *Cretodus* cusps previously recovered from the Chenini Member (see Cuny et al., 2004). The labial side is more flattened than the lingual one. The lingual side is strongly convex and ornamented by up to six ridges, which never attain the apex. One specimen (OED6) had the outer layer of enameloid removed using 10% HCl and was then gold-coated and studied under the SEM to confirm its neoselachian affinities. A parallel-bundled enameloid (PBE) is clearly seen at the surface of the tooth. At the level of the ridges ornamenting the lingual side of the cusp and at the level of the cutting edges, the bundles of crystallites are perpendicular to the axis of the tooth, instead of being parallel to it as in the rest of the crown.

(OED9) in apical view. **13.** Semionotidae or pycnodont, tooth of morphotype 3 (pharyngeal) from Oum ed Diab (OED10) in lateral view. **14.** *Lepidotes* sp., fragmentary dentigenous bone from Touil el Mra (TEM4) in apical view. **15.** Aff. *Gyrodus* sp., fragmentary prearticular from Jebel Boulouha North side (JBNS3) in apical view. Scale bars: 1 mm.

Remarks: The presence of a PBE demonstrates beyond doubt that these cusps belong to a neoselachian shark, and not to a high-cusped hybodont. A precise identification of this material is however difficult because of its fragmentary nature. The rather flexuous ridges ornamenting the crown are quite similar to what can be observed in *Eoptolamna*, but the median crest extending almost to the apex of the crown is lacking (Kriwet et al., 2008). In the other Eoptolamnidae, *Leptostyrax* and *Protolamna*, the labial ornamentation is not as well developed as in the Tunisian specimens (Cappetta and Case, 1999; Rees, 2005; Ward, 2010). The same can be said of most other Lamniformes from the Early Cretaceous, except *Cretodus*. Based on their similarity with the teeth of *Cretodus semiplicatus* found in the Chenini Member (Cuny et al., 2004), the teeth from Oum ed Diab are tentatively attributed to this genus. Note however that the status of the family Cretoxyrhinidae remains unclear at this time (Kriwet, 2006; Siverson, 1999) so that the attribution of *Cretodus* to this family is uncertain.

Interestingly, no neoselachian specimens have previously been recorded from the Oum ed Diab Member, and this has been used to support the hypothesis that this member was deposited in a freshwater environment. Indeed, there is little evidence for freshwater neoselachians prior to the Late Cretaceous (Sweetman and Underwood, 2006). The presence of these cusps brings into question the validity of this suggestion as *Cretodus*, and the Lamniformes in general, have only previously been recorded in marine environments (Williamson et al., 1993; Shimada, 2006; Shimada et al., 2006). Recent geochemical taphonomic studies (Anderson et al., 2007) confirm some marine influence during the deposition of the Oum ed Diab Member of the Ain el Guettar Formation.

The change in orientation of the bundles of the PBE at the level of the ridges ornamenting the surface of the crown is a primitive character among neoselachian sharks, which is well documented in Synchondontiformes (Cuny and Risnes, 2005). Such a primitive character was thus retained by some lamniform sharks, whereas it was lost by others, like the Mitsukurinidae (Cuny and Risnes, 2005).

Cuny et al. (2004) mentioned two cretoxyrhinids in the Chenini Formation: *Cretodus semiplicatus* and cf. *Protolamna* sp. However, the latter kinds of teeth do not belong to *Protolamna* but to *Eoptolamna*. The two latter genera, together with *Leptostyrax*, have been included in the family Eoptolamnidae (Kriwet et al., 2008).

Superorder BATOMORPHII Cappetta, 1980
Order SCLERORHYNCHIFORMES Kriwet, 2004
Family SCLERORHYNCHIDAE Cappetta, 1974
Genus *Onchopristis* Stromer, 1917
Onchopristis dunklei McNulty and Slaughter, 1962
Fig. 2(4)

Material: Oued el Khil: One partial rostral tooth (OEK5).

Description: This rostral tooth has a complete root region but only the base of the cusp is preserved. The root region is ornamented with deep ridging. In basal view, it is compressed ventro-dorsally and shows a rectangular outline. The cusp appears to lack ornamentation but displays a distinctive curve,

and it is quite compressed ventro-dorsally. The root region measures 2.5 mm cranio-caudally and is 3.5 mm high.

Remarks: Sclerorhynchids are represented in the Chenini Member by oral teeth of *Onchopristis dunklei* (Cuny et al., 2004). The rostral teeth of this species correspond well with the fragment described here, sharing small size and a cranio-caudally expanded peduncle with a rectangular base with fluted perimeter (Williamson et al., 1993). Pending further discoveries, it seems therefore that *O. dunklei* is the only sclerorhynchid occurring in the Chenini Member.

Class OSTEICHTHYES Huxley, 1880
Subclass ACTINOPTERYGII Klein, 1885
Superdivision NEOPTERYGII Regan, 1923
Order SEMIONOTIFORMES Arambourg and Bertin, 1958
Family SEMIONOTIDAE Lehman, 1966
Genus *Lepidotes* Agassiz, 1832
Lepidotes sp.
Fig. 2(6–10, 13, 14)

Material: Jebel Boulouha North side: 43 oral hemispherical teeth, 7 marginal teeth and 111 pharyngeal teeth. Oued el Khil: 62 complete, including OEK6, and 10 fragmentary oral hemispherical teeth, 20 marginal teeth, including OEK7, 5 complete pharyngeal teeth, 8 complete scales and 46 fragmentary scales. Oum ed Diab: 176 complete oral teeth, including OED7, 48 oral teeth fragments, 61 marginal teeth and 7 complete pharyngeal teeth, including OED10. Touil el Mra: 10 complete oral teeth, including TEM2-3, and 8 fragments, 7 marginal teeth, 18 pharyngeal teeth, one dentigenous bone fragment (TEM4), one complete scale and one scale fragment.

Description: Three main tooth morphotypes can be recognized among the material. The first consists of hemispherical oral teeth, which reach a maximum diameter of 5 mm in apical view and a maximum height of 3 mm, including the ganoine-covered base (Fig. 2(6–7, 9, 10)). When the latter is preserved, its height is similar to that of the acrodine cap. In apical view, they are spherical to ovoid in outline. Some of these teeth show at their apex a protuberance, which has probably been removed by wear in the other hemispherical teeth recovered from our samples. One bone fragment from Touil el Mra, measuring 3.5 × 2.2 mm bears 12 such teeth (Fig. 2(14)), which appear to be randomly distributed on the surface of the bone.

The second morphotype consists of teeth with a more conical appearance, devoid of ornamentation (Fig. 2(8)). They can reach 3 mm in height whereas their diameter at the base does not exceed 2 mm.

The third morphotype includes elongated teeth, slightly compressed and with a hook-like apical region (Fig. 2(13)). They can reach up to 3 mm in height with a maximum diameter of 1 mm at their base.

The scales are covered with a smooth layer of ganoine. Of the complete specimens two have a posterior edge with a serrated appearance. The scales range in shape from a rounded rhombus to a more angular trapezoid shape and reach up to 4 mm in length. Isolated ganoine covers are smooth on the outer surface but the surface which adjoins the base often shows evidence of growth rings.

Remarks: The association of conical teeth (morphotype 2) on the dentary with hemispherical crowns with a central protuberance (morphotype 1) on the vomer, palatine and dentalosplenic is typical of trituran *Lepidotes* (Bilelo, 1969) and the teeth belonging to morphotype 3 are very similar to the pharyngeal teeth of *Lepidotes gloriae* (Thies, 1989). The association of these three morphotypes at Oued el Khil, Oum ed Diab and Touil el Mra indicates thus the presence of at least one species of trituran *Lepidotes* in each of these locations. However, the material available allows neither a precise identification at specific level, nor to say whether more than one species was present. Moreover, hook-shaped pharyngeal teeth can be found both in Semionotiformes and Pycnodontiformes (Buscalioni et al., 2008), so that it is not possible to be sure that all the morphotype 3 teeth belong to *Lepidotes* as Pycnodontiformes are also known in the Lower Cretaceous of Tunisia (see below).

SEMIONOTIDAE indet.

Fig. 2(11–12)

Material: Oued el Khil: 2 teeth. Oum ed Diab: 5 teeth, including OED8-9.

Description: These teeth possess an enlarged apical protuberance, separated from the rest of the acrodine cap by a groove (Fig. 2(11, 12)). The external margin of this groove is crenulated. The protuberance is not in the centre of the acrodine cap, but is somewhat displaced anteriorly, and the outline of the whole cap of acrodine in apical view is ovoid. The size of these teeth reaches 3 mm on the long axis and 2 mm on the short axis, and their maximum height is 2.5 mm.

Remarks: These teeth could easily be derived from *Lepidotes* teeth of morphotype 1 by the enlargement of the central protuberance together with the appearance of a groove around it. They have however so far been recovered only from Oued el Khil and Oum ed Diab. Whether they represent a new species of *Lepidotes* or a new genus of Semionotidae is difficult to ascertain based on only some isolated teeth. Teeth of similar morphology, but with the central protuberance ornamented with radiating ridges, have also been recovered from the Lower Cretaceous Sao Khua Formation of Thailand (Cuny et al., 2006).

Order PYCNODONTIFORMES Berg, 1937

Family GYRODONTIDAE Berg, 1940

Genus *Gyrodus* Agassiz, 1833

aff. *Gyrodus* sp.

Fig. 2(15)

Material: Jebel Boulouha North side: One prearticular fragment with three teeth (JBNS3) and 33 isolated teeth.

Description: A fragment of bone bears three teeth with an ovoid outline in apical view. They show a slight reduction in size caudally, the most cranial one measuring 1.9 mm on its long axis and 0.7 mm on its short axis, whereas the most caudal one measures 1.5 × 0.7 mm. The teeth show in their caudal part a groove more or less parallel to their long axis. Tubercles are well developed caudally to the groove, but have a tendency to merge to form a ridge cranially to the groove.

Mesially to the tooth row, the bone seems to show depressions that might indicate the presence of at least another

row of teeth parallel to the row formed by the three preserved teeth.

The isolated teeth show a similar ornamentation to the teeth described above or are completely smooth with an ovoid or kidney shape in apical view. One is almost circular in apical view. The largest tooth is 3.5 mm according to its long axis and 2 mm according to its short axis, and thus larger than the teeth still attached to the bone remain.

Remarks: Teeth with a groove and highly developed crenulation are characteristic of the molariform teeth of primitive Pycnodontiformes like *Gyrodus*, *Mesturus* and *Micropycnodon* (Poyato-Ariza and Wenz, 2002), although in these genera, the groove is normally situated in a more central position on the teeth. However, grooves in a similar caudal position have been observed in some aff. *Gyrodus* sp. specimens from the Lower Cretaceous (Hauterivian) of Europe (Kriwet and Schmitz, 2005). Teeth from the vomer show a more circular outline than those of the Tunisian specimens, whereas teeth from the prearticular share a similar ovoid shape with the specimen from Jebel Boulouha. The latter is therefore likely to correspond to a prearticular of a gyrodonid.

It is difficult to say whether the smooth isolated teeth have lost a *Gyrodus*-like ornamentation through wear or not, but we tentatively attribute all the teeth recovered from Jebel Boulouha to a single taxon, as a second one cannot be recognized on the basis of the material available.

PYCNODONTIFORMES? indet.

Fig. 4(2)

Material: Oued el Khil: Seven teeth, including OEK8.

Description: The acrodine cap is circular in outline in apical view, reaching a maximum diameter of 2.9 mm. The teeth are low, not exceeding 1.5 mm in height. The surface of the acrodine cap is densely ornamented, with irregular, radiating and anastomosing ridges. These ridges do not join in the middle of the acrodine cap, leaving a small smooth area in the centre.

Remarks: The circular outline and low profile of these teeth suggest pycnodont affinities, although the ornamentation pattern is somewhat unusual for a pycnodont. A similar radiating ornamentation was however illustrated by Sauvage (1880) in the genus *Athrodon*, although the Tunisian teeth lack a central depression as seen in the latter genus, as well as by Cavin et al. (2009) on teeth from the Lower Cretaceous of Thailand attributed to cf. *Anomoeodus*. Cf. *Anomoeodus* was also mentioned in the Chenini Member of the Aïn el Guettar Formation by Bouaziz et al. (1988), but based on a single kidney-shaped tooth, quite similar to some of the teeth found in the Douiret Formation (see above). However, identification of pycnodonts based on isolated teeth is difficult (Poyato-Ariza, 2003; Kriwet and Schmitz, 2005), and no typical pycnodont teeth have hitherto been found in association with the circular, ornamented teeth from Oued el Khil, so that their attribution to a pycnodont remains tentative.

Order AMIIFORMES Hay, 1929

Suborder CATUROIDEA Owen, 1860

Family CATURIDAE Owen, 1860

Genus *Caturus* Agassiz, 1834

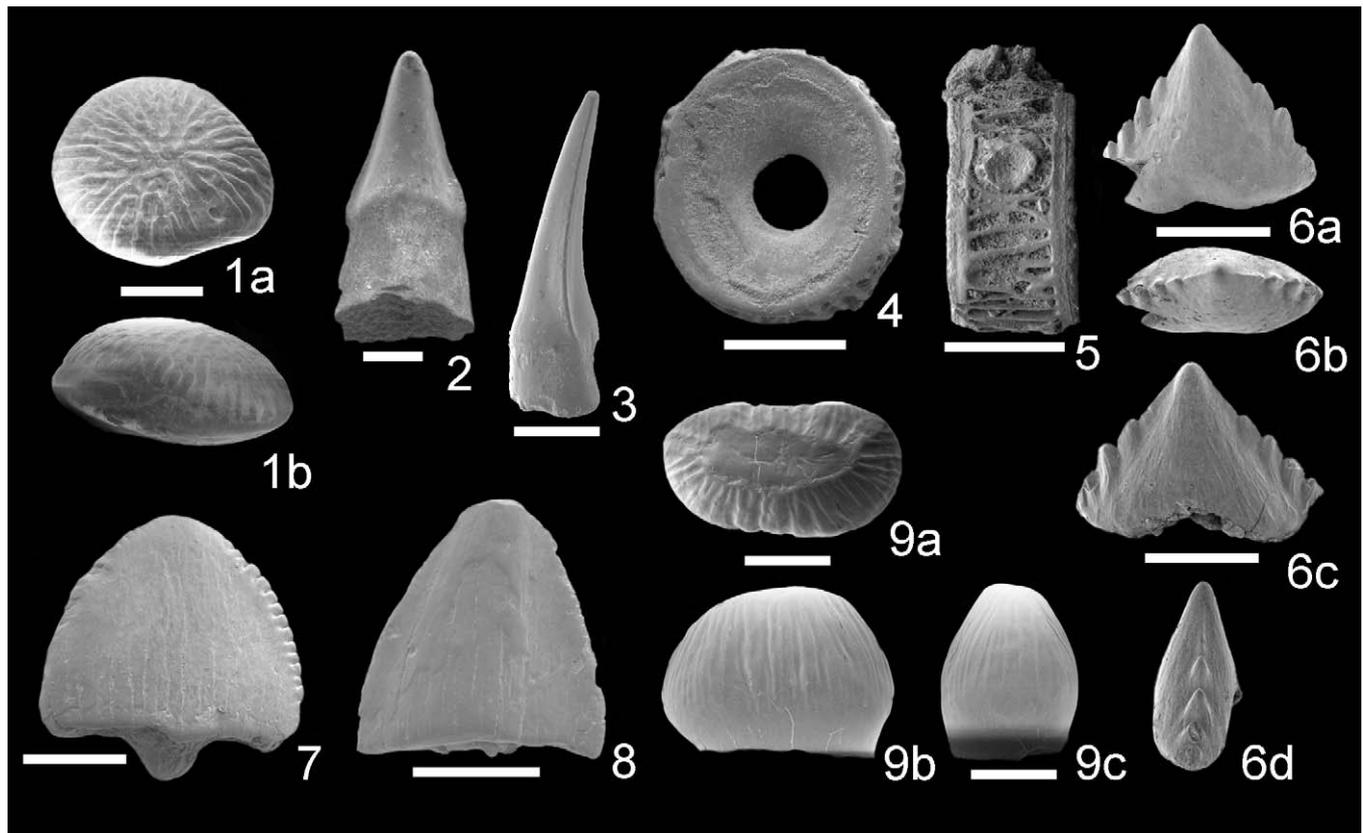


Fig. 4. Vertebrate microremains from the Lower Cretaceous of Tunisia. 1. Tooth of a Pycnodontiformes indet. from Oued el Khil (OEK8): apical (a) and lateral (b) views. 2. Tooth of *Caturus* sp. from Jebel Boulouha North side (JBNS4) in lingual view. 3. Tooth of *Caturus* sp. from Touil el Mra (TEM5) in mesial or distal view. 4. Vertebral centrum of a teleost fish from Jebel Boulouha North side (JBNS5) in cranial or caudal view. 5. Vertebral centrum of a teleost fish from Jebel Boulouha North side (JBNS6) in lateral view. 6. Tooth of an indeterminate archosaur (crocodile?) from Oued Zefrat (OZ4): labial (a), apical (b), lingual (c) and mesial or distal (d) views. 7. Tooth of *Araripesuchus wegeneri* from Oum ed Diab (OED11) in labial or lingual view. 8. Tooth of aff. *Hamadasuchus* sp. from Oued el Khil (OEK12) in lingual view. 9. Molariform tooth of a Bernissartidae from Oum ed Diab (OED12): apical (a), labial (b) and mesial or distal (c) views. Scale bars: 1 mm except in 2, 3 and 9: 500 μ m.

Caturus sp.

Figs. 3(1) and 4(2, 3)

Material: Jebel Boulouha North side: Five complete teeth, including JBNS4, with both ganoine-covered base and acrodine cap present. Oued el Khil: 20 complete teeth and 28 isolated acrodine caps, including OEK9. Oum ed Diab: eight complete teeth and six acrodine caps. Touil el Mra: two complete teeth, including TEM5, and two acrodine caps.

Description: These teeth vary in size from 1 to 5 mm, the specimens from Touil el Mra being the smallest of our samples, not exceeding 1 mm for the complete teeth. In labial or lingual views, the acrodine cap is triangular in outline with a well-developed mesial and distal cutting edge running from its apex to its base. Its surface is smooth, whereas the ganoine-covered base of the crown is ornamented by densely packed, irregular ridges. This ornamentation is sometimes lost through post-mortem wear.

One of the acrodine caps from Oued el Khil was etched in 10% HCl to study its microstructure, which appears very similar to that of the neoselachian shark *Cretodus*. The surface of the cap is made of bundles of crystallites parallel to the axis of the tooth, but these bundles change orientation at the level of the cutting-edge and become perpendicular to the axis of the tooth (Fig. 3(1)).

Remarks: Well-developed cutting edges can also be found in teeth of *Ionoscopus*, but in the latter, the tooth neck has a granulated rather than a ridged surface (Kriwet, 2005; Mudroch and Thies, 1996). Teeth with well-developed cutting-edges are also found in *Calamopleurus africanus* from the ?Albian of Morocco, although in the latter species Forey and Grande (1998) do not mention any ornamentation of the ganoine-covered base of the teeth. The teeth from Tunisia are therefore attributed to the genus *Caturus*. This typical Jurassic marine amiiiform is also present in more terrestrial environments in the Lower Cretaceous of Spain (Buscalioni et al., 2008).

The shape of these teeth indicates a fish preying mostly on soft prey (piercing type of dentition). The similarity in microstructure between the acrodine of *Caturus* and the enameloid of *Cretodus* tends to suggest that these tissues share a similar dual ectodermal and mesodermal origin (Cuny and Risnes, 2005). However, the parallel-bundled enameloid (PBE) is unlikely to be a shared primitive character of Chondrichthyes and Osteichthyes as it was acquired quite late in the chondrichthyan lineage, and only by the galeomorph and squalomorph sharks (Cuny and Risnes, 2005). Among Osteichthyes, this character is restricted to the Actinopterygii, although where exactly in the phylogenetic tree of this clade it appeared for the first time is currently not

documented. The similar organization of the bundles of crystallites is therefore likely to be the result of convergence. The PBE being resistant to tensile stress, its appearance in animals sharing a piercing type of dentition is expected. The change of orientation of the bundles at the level of the cutting edges probably reinforces this latter structure. Similar convergences in microstructure were already noted between teeth of neoselachian sharks and those of carnivorous teleosts by Reif (1979) as well as by Ørvig (1978) in *Birgeria groenlandica*.

Subdivision TELEOSTEI *sensu* Patterson and Rosen, 1977
TELEOSTEI indet.

Fig. 4(4, 5)

Material: Jebel Boulouha North side: 32 centra of vertebrae, including JBNS5 and JNBS6; Oued el Khil: four centra of vertebrae; Oum ed Diab: eight centra of vertebrae; Touil el Mra: 161 centra of vertebrae.

Description: The vertebrae are all deeply amphicoelous and reach a maximum diameter of 6 mm. They show variable length compared to the centrum diameter, but the sides of the centra are always deeply ridged. The notochordal canal in the middle of the centrum is often widely open. The bases of the neural and haemal arches are rarely preserved.

Remarks: Vertebral centra very similar to the Tunisian ones have been attributed to teleost fishes in the Campanian of Alberta (Brinkman and Neuman, 2002). Teleosts were probably abundant in the Lower Cretaceous, but occupied the lowest level of the trophic chain, possessing tiny villiform teeth or even being edentulous (Buscalioni et al., 2008), which would explain that only centra of vertebrae were recovered from the Tunisian sites.

Subclass SARCOPTERYGII Romer, 1955

Order ACTINISTIA Cope, 1871

ACTINISTIA? indet.

Fig. 5

Material: Oued el Khil: Five hemisegments of lepidotrichia, including OEK9-11; Oum ed Diab: 1 hemisegment of lepidotrichia.

Description: The hemisegments of lepidotrichia are made of a bony plate, rectangular in outline with a concave inner face (Fig. 5(1a, b, 2a, b)); these hemisegments bear one or two hook-like structures or odontodes (see below) (Fig. 5(1, 2)). The largest specimen is 2.3 mm wide, 2.1 mm long and 1.5 mm high. Some of these odontodes are well preserved in our sample; they appear to have projected beyond the bony base laterally or anteriorly. Their surface could be smooth or ornamented with delicate, anastomosed ridges. It is not situated in the middle of the bony plate, but it is displaced laterally.

Each odontode is made of a cone of dentine around a pulp cavity (Fig. 5(3a)); the apex is covered by a cap of enamel (Fig. 5(3b)). The dentine shows two superposed layers: a thin birefringent inner one and a thick peripheral one delicately striated by odontoblastic canaliculi (Fig. 5(3c)). The odontode is firmly fixed to the bony hemisegment by a vascularized bone of attachment (Fig. 5(5)). In any case, some little odontodes can be embedded deeply in the hemisegment (Fig. 5(7)). The bony tissue of the hemisegments shows numerous Sharpey's fibres (Fig. 5(6)) and is crossed by thin vascular canals (Fig. 5(4)).

Star-shaped osteocytes with numerous thin radiating canaliculi can be observed (Fig. 5(8)).

Remarks: In the present state of our knowledge, these fish remains cannot be attributed with certainty to any fish in particular, in the absence of fossils found in connection. The presence of cellular bone allows us to reject a derived teleost characterized by acellular bone (Meunier, 1987; Meunier and François, 1992). In extant osteichthyans, dermal odontodes on fin rays can be found in two primitive actinopterygian taxa, polypterids (Géraudie, 1988) and lepisosteids (Sire and Meunier, 1994), but also in some teleostean Siluriformes, Loricaridae (Bhatti, 1938; Sire and Meunier, 1993) and Ageneiosidae (Ferraris, 2003) and in the sarcopterygian coelacanthids (Castanet et al., 1975). The Tunisian material cannot belong to lepisosteids because the hemisegments do not show Williamson canaliculi (Sire and Meunier, 1993). In the two siluriform taxa, the rays that bear odontodes are not subdivided into hemisegments. In the present state of our knowledge, the best hypothesis leads us to an actinistian identification. The rarity of the fossils seems to indicate that these fish were not abundant in the Early Cretaceous of Tunisia, although *Mawsonia* has been already mentioned in the Chenini member of the Aïn el Guettar Formation (Schlüter and Schwarzahns, 1978; Benton et al., 2000).

Division ARCHOSAURIA Cope, 1869

ARCHOSAURIA indet.

Fig. 4(6)

Material: Oued Zefrat: one tooth (OZ4).

Description: OZ4 measures 2 mm mesio-distally, 0.8 mm labio-lingually and is 1.6 mm high. It is triangular in shape in labial or lingual views and compressed labio-lingually. There are four coarse serration mesially and distally, oriented upward. The base of the tooth being quite damaged, more serration might have been present. The lingual (?) side of the crown is wrinkled, whereas the labial (?) one appears almost smooth.

Remarks: The general morphology of this tooth is quite similar to that of hypsilophodontid teeth from the Barremian of Spain (Rauhut, 2002), although the latter teeth possess smooth enamel. The presence of wrinkled enamel on the lingual (?) side of the crown might rather suggest crocodylian affinities for this tooth (Larsson and Sidor, 1999), but with only one damaged tooth at our disposal, we prefer to consider this tooth as belonging to an indeterminate archosaurian pending the discovery of more material.

Superorder CROCODYLOMORPHA Walker, 1970

Order CROCODYLIFORMES Hay, 1930

Division MESOEUCROCODYLIA Whetstone and Whybrow, 1983

Genus *Araripesuchus* Price, 1959

Araripesuchus wegneri Buffetaut, 1981

Fig. 4(7)

Material: Oum ed Diab: two teeth, including OED11; Touil el Mra: one tooth.

Description: The crown is spatulate in labial or lingual view, compressed labio-lingually with both lingual and labial

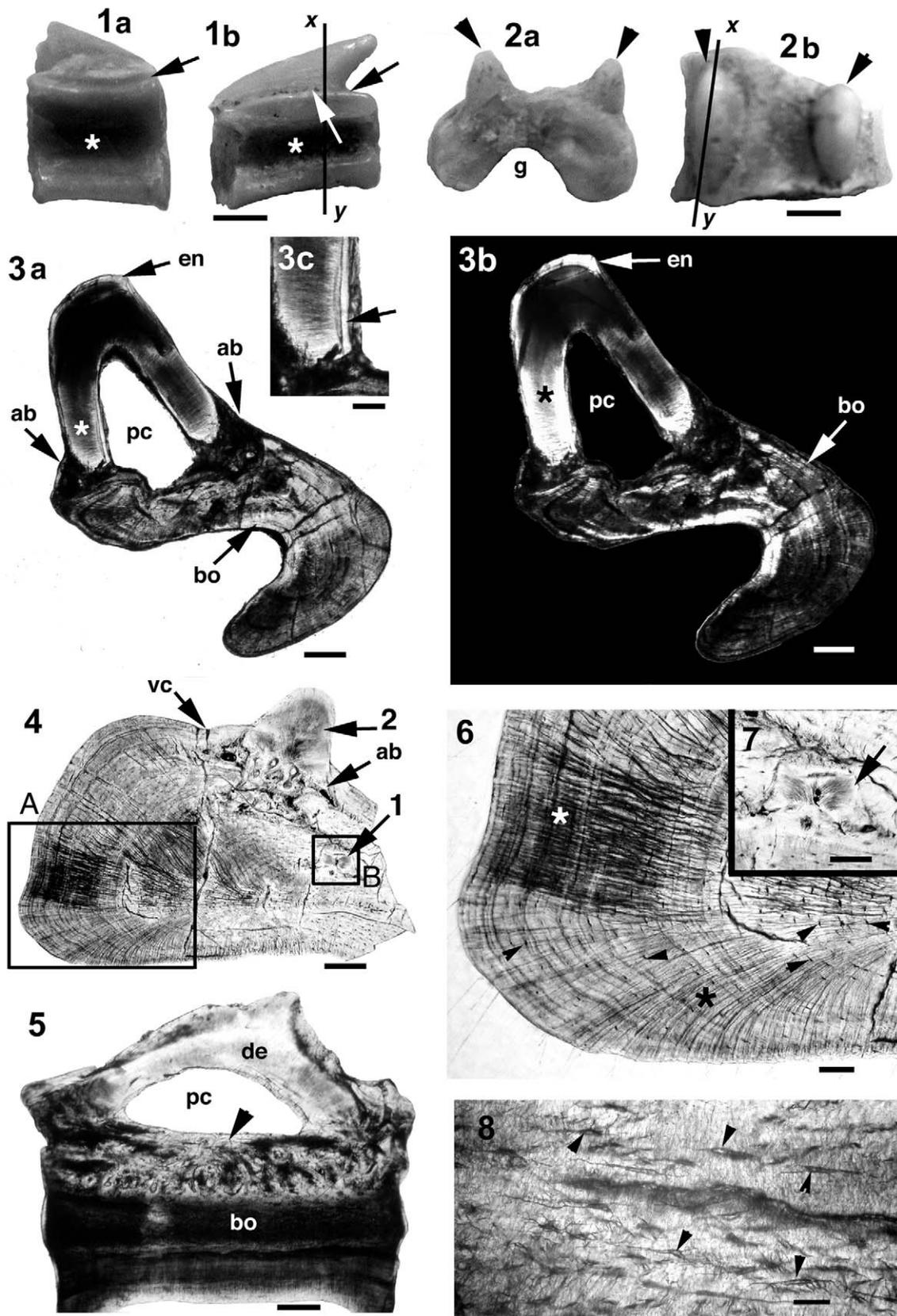


Fig. 5. Hemisegments of lepidotrichia from Oued el Khil. **1.** Two hemisegments of lepidotrichia (inner views) each with one odontode inserted on the lateral side: OEK9 (a) and OEK10 (b). The asterisks signal the groove of the hemisegments. The arrow points the boundary between the odontode and its bony support where vascular apertures can be seen (xy: section of Fig. 3(a, b)) (scale bar: 200 μ m). **2.** A hemisegment of lepidotrichium (OEK11) with two odontodes (arrow heads): distal (a) and outer (b) views (g = groove of the hemisegment) (xy: section of Fig. 5) (scale bar: 200 μ m). **3.** Cross section (xy: Fig. 1(b)) of a hemisegment showing an odontode with its bony base: natural transmitted light (a), polarized light (b) and a detail of dentine (c). The odontode is made of a thin birefringent inner layer of

sides slightly convex. The largest tooth measures 2.5 mm mesio-distally, 0.6 mm labio-lingually and is 2.3 mm high. Both cutting edges are serrated. The rest of the crown is smooth.

Remarks: Although ziphodont teeth occur in a variety of different crocodylians through time, from the subrecent *Mekosuchus* to the Lower Jurassic *Platyognathus*, only two crocodylians show similar teeth in the Lower Cretaceous of Africa: *Araripesuchus wegeneri* and *Hamadasuchus rebouli* (Prasad and de Lapparent de Broin, 2002; Turner, 2006). Similar, low, spatulate teeth with serrated carinae are known in *A. wegeneri*, while the teeth of *H. rebouli* are more triangular in outline (Prasad and de Lapparent de Broin, 2002; Turner, 2006), at least in the mid-portion of the tooth row (Larsson and Sidor, 1999). More posterior teeth of *Hamadasuchus* are also spatulate in outline in labial or lingual views, but their enamel is wrinkled and they are less labio-lingually compressed than the Tunisian teeth (Larsson and Sidor, 1999). The Tunisian teeth are therefore cautiously attributed to *A. wegeneri*.

Infradivision SEBECIA Larsson and Sues, 2007

Family PEIROSAURIDAE Gasparini, 1982

aff. *Hamadasuchus*

Fig. 4(8)

Material: Oued el Khil: one tooth (OEK12).

Description: OEK12 is rather worn. It is triangular in labial or lingual view, compressed labio-lingually with both labial and lingual sides slightly convex. It measures 2 mm mesio-distally at its base and is 2 mm high. One of the well-developed cutting edges shows the remnants of clear serration.

Remarks: This tooth is ziphodont like the preceding one, but shows a more triangular outline in labial or lingual view. It is therefore likely to be closer to *Hamadasuchus* than to *A. wegeneri* (see above).

Infradivision NEOSUCHIA Benton and Clark, 1988

Family BERNISSARTIDAE Dollo, 1883

Fig. 4(9)

Material: Oum ed Diab: one tooth (OED12).

Description: OED12 measures 1.4 mm mesio-distally, 0.8 mm labio-lingually and is 1.1 mm high. It is bulbous in appearance with a neck constricted mesially and distally, and mesio-distally elongated. There is a well developed apical wear facet perpendicular to the axis of the crown. The crown is ornamented by well-developed ridges, which sometimes divide near the wear-facet.

Remarks: Mesio-distally elongated and bulbous molari-form teeth are characteristic of the family Bernissartidae (Buscalioni et al., 2008). If this identification can be confirmed by further material, this could be the first record of this family

from North Africa, which, from a palaeogeographical point of view, is not surprising considering that intermittent migration of European faunas in Africa since the Late Jurassic have been documented (Gheerbrant and Rage, 2006).

MESOEUCROCODYLIA indet.

Material: Jebel Boulouha North side: one tooth; Oum ed Diab: five teeth; Touil el Mra: five teeth.

Description: The tooth from Jebel Boulouha is conical and ornamented with longitudinal ridges. It measures 1.5 mm mesio-distally, 1.3 mm labio-lingually and is 2.1 mm high. The sizes of the teeth from Touil el Mra and Oum ed Diab are similar, but they are generally more compressed labio-lingually and not so well preserved.

Remarks: The shape of the tooth from Jebel Boulouha might correspond to anterior teeth from any of the three crocodiles described above, whereas the preservation of the teeth from Touil el Mra and Oum ed Diab is not good enough to allow a more precise identification than Mesoeucrocodylia indet.

5. Discussion

5.1. Douiret Formation

The Douiret Formation was dated as Aptian based on its geometric relations with underlying and overlying formations (Ouaja, 2003; Srarfi, 2006), but neither biostratigraphic markers, nor radiometric dating confirms this. Here we report from the Douiret Formation a vertebrate assemblage containing: *Egertonodus* sp., aff. *Lissodus* sp., *Priohybodus arambourgi*, ‘*Rhinobatos*’ sp., *Lepidotes* sp., aff. *Gyrodon* sp., *Caturus* sp. and Teleostei, Archosauria and Mesoeucrocodylia indet. None of these taxa are very good biostratigraphic markers but it should be noted that the highest ascertained record of *Egertonodus* is in the Barremian (Rees and Underwood, 2008) and that well dated occurrences of *Priohybodus arambourgi* are from the Late Jurassic (Goodwin et al., 1999; Duffin, 2001). The occurrence of the latter genus in the Aptian has never been demonstrated (Yanbin et al., 2004; López-Arbarello et al., 2008). Similarly, *Caturus* has been recovered in the Barremian of Spain (Buscalioni et al., 2008) but not higher, and the youngest record of *Gyrodon* is in the Hauterivian of Germany (Kriwet and Schmitz, 2005). This faunal assemblage suggests thus a pre-Aptian age for the Douiret Formation. Moreover, Barale and Ouaja (2002) noticed that angiosperms are lacking from the Douiret Formation, a fact that again suggests a pre-Aptian age (Racey and Goodall, 2009). Busson and Albanesi (1967), based on the bivalve and

circumpulpar dentine (black arrow) and a thick outer pallial dentine (asterisk); it is topped by a cap of enamel (en) and is attached to the bony hemisegment by a vascularized attachment bone (a, b) (bo = bone of the hemisegment; pc = pulpar cavity) (scale bar: a, b: 250 μ m; c: 100 μ m). 4. Cross section of a hemisegment showing two odontodes (1, 2). The first one is deeply inserted in the bony tissue of the hemisegment. Numerous Sharpey's fibres are seen in the bone (vc = vascular canal) (scale bar: 250 μ m). 5. Longitudinal section of a hemisegment (xy: Fig. 2(b)) showing an odontode on its bony base (bo) (natural transmitted light); the bone of attachment of the odontode (arrow) is vascularized (de = dentine; pc = pulpar cavity) (scale bar: 250 μ m). 6. Detail (insert A of Fig. 4) of the bone constituting a hemisegment (cross section) to show bone osteocytes (arrow heads) and Sharpey's fibers (asterisks) (scale bar: 100 μ m). 7. Detail (insert B of Fig. 4) of the odontode embedded in bone of the hemisegment; the arrow points to the dentine of the odontode number one (scale bar: 100 μ m). 8. Detail of bone of a hemisegment showing the numerous canalicules starting from the osteocytes' lacunae (arrow heads) (scale bar: 25 μ m).

gastropod faunas, also favoured a Neocomian age for these beds, and a similar conclusion was also recently reached by Le Lœuff et al. (2010).

From a palaeobiogeographic point of view, the fauna recovered is not very informative. *Priohybodus* is a typical Gondwanan element whereas *Egertonodus* and *Gyroodus* indicate the proximity of Europe. In terms of palaeoenvironment, the Douiret Formation remains difficult to interpret. According to Srarfi (2006), it was deposited in an intertidal zone, but Anderson et al. (2007) did not detect any marine influence in these deposits. All of the fish fauna described in the present paper being euryhaline, they do not help to solve this paradox.

5.2. Aïn el Guettar Formation

Both the Chenini and Oum ed Diab members yielded the following faunal content: *Lepidotes* sp., Semionotidae indet., *Caturus* sp., Teleostei indet., Actinistia indet. and maybe *Cretodus*. Such a fauna is of little use for stratigraphical and palaeogeographical purposes. On the other hand, the change in crocodylian fauna between these two members is interesting, showing the replacement of aff. *Hamadasuchus* by *Araripesuchus wegeneri* and the arrival of Bernissartidae from Europe. The presence of the enigmatic teeth of ?Pycnodontiformes in the Chenini Member also suggests that these faunas retain some endemic components. The conditions of deposition of the Aïn el Guettar Formation is equivocal, with mixed freshwater and marine influences (Anderson et al., 2007), and Srarfi (2006) suggested mainly deltaic conditions for most of the fossiliferous sites in this Formation, which is in accordance with their faunal contents.

6. Conclusions

Although the quantities of sediment screen-washed were quite low and encompassed only five sites, a rather diverse assemblage of vertebrate microremains was recovered, including various sharks and actinopterygians, a possible actinistian (based on histological study of hemisegments of lepidotrichia) and various crocodiles. These vertebrate remains allow us to draw some stratigraphic and palaeogeographic conclusions:

- the age of the Douiret Formation is likely to be pre-Aptian;
- faunal exchange of terrestrial faunas between North Africa and Europa during the Early Cretaceous is once again confirmed by the presence of *Bernissartia* in Tunisia.

Moreover, enameloid microstructure analysis documents convergence in dental microstructure between neoselachian sharks and actinopterygians sharing a tearing dentition.

Acknowledgements

This work was made possible through the support of the Office National des Mines in Tunis, the National Geographic Foundation, the Danish Agency for Science Technology and

Innovation and the Natural History Museum of Denmark. We are more particularly indebted to Mustapha Ben Haj Ali (Office National des Mines) for his support of our work. Discussion with Jean Le Lœuff (Musée des Dinosauriens, Espéraza) pointed us towards the potential problems of the dating of the Douiret Formation. We also thank all the persons who helped us in the field, including Habib Algene, Eric Buffetaut, Emmanuel Fara, Faouzi Nasri, Mohamed Ouaja, Dorra Srarfi and Haiyan Tong. Thanks are also due to Tarek Mabrouk for his hospitality during our fieldwork in the Tataouine area.

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