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Fossil sharks from the Early Cretaceous of Tunisia

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Abstract

The Early Cretaceous of Tunisia has yielded rich shark assemblages in the Douiret Formation (Aptian), and both the Chenini Member and the Oum ed Diab Member (Albian) of the Aïn el Guettar Formation. These assemblages are very different from each other, suggesting different palaeoenvironments. The Douiret assemblage is dominated by hybodont sharks (*Hybodus* sp., *Priohybodus arambourgi*) with a marine ray (*"Rhinobatos"* sp.), suggesting a deposit very close to the coast, probably in a large tide-dominated delta. The Chenini assemblage is dominated by neoselachian sharks (*Cretodus semiplicatus*, cf. *Protolamna*, cf. *Scapanorhynchus*, *Onchopristis dunklei*) and a new species of the hybodont *Tribodus*, *T. tunisiensis*, indicating a shallow water marine environment and deposition probably somewhat farther from the coast than the Douiret Formation. On the contrary, the Oum ed Diab assemblage is devoid of neoselachians, strongly indicating a freshwater environment with no marine connection. Its hybodont fauna includes *Hybodus* sp. and *Lissodus* sp. as well as a new genus of Lonchidiidae, *Diabodus tataouinensis*.

Key words

Cretaceous, Tunisia, Elasmobranchii, palaeoenvironment.

Résumé

Requins fossiles du Crétacé inférieur de Tunisie.- Le crétacé inférieur de Tunisie a livré de riches faunes de sélaciens dans la formation Douiret (Aptien) et les membres Chenini et Oum ed Diab (Albien). Ces faunes sont très différentes les unes des autres et suggèrent des milieux de dépôt différents. La faune de Douiret est dominée par des hybodontes (*Hybodus* sp., *Priohybodus arambourgi)* complétés par quelques rares raies (*"Rhinobatos"* sp.). Cela pourrait indiquer un dépôt dans la partie d'un delta soumis à l'influence de la marée. La faune de Chenini est dominée par des requins néosélaciens (*Cretodus semiplicatus*, cf. *Protolamna*, cf. *Scapanorhynchus, Onchopristis dunklei)* et une nouvelle espèce de *Tribodus, T. tunisiensis,* indiquant un milieu marin peu profond, probablement plus éloigné de la côte que celui de la formation Douiret. Au contraire, la faune d'Oum ed Diab est dépourvu de tout néosélacien, indiquant un milieu de dépôt coupé de toute connexion marine. La faune d'hybodontes inclut *Hybodus* sp., *Lissodus* sp. ainsi qu'un nouveau genre de Lonchidiidae, *Diabodus tataouinensis*.

Mots-clés

Crétacé, Tunisie, Elasmobranchii, paléoenvironnement.

INTRODUCTION

Fossil vertebrate remains have long been reported from the mid-Cretaceous of the Tataouine region, southern Tunisia (PERVINQUIÈRE, 1912; DE LAPPARENT, 1951, 1960; TABASTE, 1963; SCHLÜTER & SCHWARZHANS, 1978; BOUAZIZ *et al.*, 1988; BENTON *et al.*, 2000; BUFFETAUT & OUAJA, 2002). They come from two formations (Douiret, Aptian and Aïn el Guettar, Early Albian), which are usually considered to be part of the African Continental Intercalaire, and thus are interpreted as continental deposits (see BENTON *et al.*, 2000 for a review). However, FERRY *et al.* (2002) have recently re-interpreted these deposits as being mainly of tidal origin. We describe here new fossil shark remains that have been recently collected during Tunisian-British-French expeditions in 1999 and 2000, and we discuss whether these shark faunas support deposition of the Douiret and Aïn el Guettar Formations in tidal environments.

1. MATERIAL, SITES AND METHOD

The shark material described in the present work was found at four sites in the Douiret Formation (Jebel Segdel, Bateun el Ghazel, Bateun el Haïma, Jebel

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Boulouha North side), three sites in the Chenini Member of the Aïn el Guettar Formation (Oued el Khil, Ksar Kherachfa, Bateun el Hmaïma), and two sites in the Oum Ed Diab Member of the Aïn el Guettar Formation (Oum Ed Diab, Jebel Touil el Mra). A map of the area can be found in BENTON *et al.* (2000). Fossils have been obtained by screen washing sediments (80 kg from Jebel Boulouha North side, 140 kg from Oued el Khil, 100 kg from Oum ed Diab and 100 kg from Touil el Mra) using 0.5 and 1.7 mm mesh-sized sieves, and by surface collecting for the largest specimens (all sites).

- Jebel Segdel is located 10 km south of Remada and shows fossiliferous indurated sandstones. From surface collecting, these sandstones have yielded teeth of *Priohybodus*, numerous *Lepidotes* teeth and scales, and teeth of large theropod dinosaurs.
- Bateun el Ghazel is located 20 km south of Chenini. The fossiliferous layer is a poorly indurated sandstone set within a dolomitic sequence. It has yielded *Priohybodus* teeth, *Lepidotes* teeth and scales, a poorly preserved fish vertebra, turtle plates, crocodile teeth and dermal plates as well as some dinosaur remains.
- Jebel Boulouha North side is located approximately 10 km southeast of Chenini. The fossils come from poorly indurated sandstones, 50 cm thick, set within a marl-dolomite sequence. This layer has yielded after screen-washing small bivalves, teeth of *Priohybodus*, *Hybodus* and *"Rhinobatos"*, teeth (pharyngeal and oral) and scales of *Lepidotes*, teeth of pycnodonts, teeth of indeterminate non-crushing fishes, and crocodile teeth.
- Bateun el Hmaïma is located approximately 5 km northwest of Ghoumrassen. Two fossiliferous layers were found in the sequence there. Poorly indurated sandstones in the upper part of the Douiret Formation have yielded teeth of *Priohybodus* as well as teeth and scales of *Lepidotes* plus some indeterminate actinopterygian and reptilian (crocodiles and turtles) remains. The second fossiliferous sandstone lies in the lower part of the Chenini Member and has yielded *Cretodus* teeth, dermal bones of *Mawsonia*, toothplates of lungfishes, and some dinosaur (*Spinosaurus*, *?Carcharodontosaurus*, sauropod) and crocodile remains.
- Oued el Khil is located around 15 km northwest of Ghoumrassen, in the lower part of the Chenini Member. The site is a small, disused quarry, the bottom of which is made of a fossiliferous indurated conglomerate in which various dinosaur bones and teeth (*Spinosaurus*, *Carcharodontosaurus*, sauropod, iguanodontid) have been found, associated with wood debris, crocodilian remains, *Lepidotes*, *Cretodus* and *Tribodus* teeth. One meter above the conglomerate, there is a lens of poorly indurated sandstone set within cross-bedded sandstones. After screen-washing, this lens has yielded numerous infracentimetric fossils including *Tribodus*, *?Hybodus*, *Cretodus*, cf. *Protolamna*, and *Onchopristis* oral teeth, various actinopterygian remains (including *Lepidotes*, pycnodont, and *Caturus* oral teeth, plus some pharyngeal teeth, various scales and some vertebrae), a fragmentary toothplate of a lungfish, and some indeterminate reptile teeth. In addition, small internal moulds of gastropods and bivalves were recovered. According to FERRY *et al.* (2002), the indurated conglomerate is a transgressive one and the beds above it were deposited in a tidal facies.
- Ksar Kherachfa is located approximately 3 km northeast of Oued el Khil. The bone bed there has yielded teeth of *Lepidotes*, a large fish vertebra, one tooth of cf. *Protolamna* and one of cf. *Scapanorhynchus*, teeth of crocodiles and *Spinosaurus*, as well as various bone debris.
- Oum ed Diab is located along the Dahar escarpment between Tataouine and Remada, some 25 km north of Remada. The fossiliferous layer is a microconglomerate overlying the sandstones forming the top of the Chenini Member. Fossils include internal moulds of small bivalves, teeth of *Hybodus* and *Lissodus* as well as those of a new lonchidiid genus, one hybodont cephalic spine, various actinopterygian remains (including *Lepidotes*, pycnodont, and *Caturus* oral teeth, *Lepidotes* scales and pharyngeal teeth, various vertebrae, and some jaw fragments), turtle remains, crocodile, iguanodontid and theropod teeth.
- Touil el Mra is located 6 km northwest of Oum ed Diab. The microconglomerate there is very similar to that of Oum ed Diab. It is well to moderately sorted with large, sub-rounded pebbles. Fossils include a hybodont finspine, lonchidiid and hybodontid teeth, various actinopterygian remains (including *Lepidotes*, pycnodont, and *Caturus* oral teeth, *Lepidotes* scales and pharyngeal teeth, various vertebrae and some jaw fragments), toothplates of lungfishes, bone fragments of *Mawsonia*, lepidosauromorph remains, a vertebra possibly belonging to a choristodere, and crocodile teeth. Internal moulds of small bivalves have also been recovered.

All the fossils described in the present study will be housed at the Office National des Mines in Tunis.

2. SYSTEMATIC DESCRIPTION

2.1. Douiret Formation

Class Chondrichthyes HUXLEY, 1880
Subclass Elasmobranchii BONAPARTE, 1838
Order Hybodontiformes MAISEY, 1987
Family Hybodontidae OWEN, 1846
Genus *Hybodus* AGASSIZ, 1837

***Hybodus* sp.**

Material: 62 isolated cusps from Jebel Boulouha North Side.

Description: Only isolated cusps have been recovered, and no complete crowns are known. These small cusps (maximum height: 4 mm) are high and narrow in most specimens. The cross-section of their base is ellipse-shaped. Both the lingual and labial sides are ornamented by up to ten ridges which may anastomose at two third of the height of the cusps. The ridges never reach the apex. The cutting edges are moderately developed, present from the base up to the apex of the cusp, and are never serrated. Some cusps are quite low, but it is difficult to say whether they are accessory cusps of antero-lateral teeth or main cusps of more distal teeth. Only one specimen shows a faint labial node at its base in addition to the ridges ornamenting the surface of the crown.
One cusp shows a shallow root directed lingually. The base of the root is concave with many small foramina. A row of somewhat enlarged foramina can be seen at the base of the lingual side.

Discussion: With no complete tooth and no possibility to assess the heterodonty of this species, a precise identification is impossible. However, the high cusp, the general lack of nodes at their base, their elliptical cross-section, and the pattern of their ornamentation is similar to the genus *Hybodus* (CAPPETTA, 1987). Pending the discovery of more complete teeth, the present material is therefore cautiously attributed to *Hybodus* sp., bearing in mind that *Hybodus* is a form genus in need of revision (UNDERWOOD & REES, 2002).

Genus: *Priohybodus* D'ERASMO, 1960

***Priohybodus arambourgi* D'ERASMO, 1960**
Plate I, figs 1-2

Material: 7 incomplete crowns from Jebel Segdel, 2 poorly preserved crowns from Bateun el Ghazel, 30 incomplete teeth from Bateun el Hmaïma with two showing the root, and 115 more or less complete teeth from Jebel Boulouha North Side, one complete with preserved root (JBNS 1).

Description: Beside *Pororhiza* and *Thaiodus*, *Priohybodus* is one of the very few hybodonts which have achieved a cutting dentition: the crown of its teeth is compressed labio-lingually and possesses serrated edges. The main cusp is high and triangular, flanked by two pairs of diverging accessory cusps. Some teeth may show a very faint third pair of cusps. The cutting edges of both the main and accessory cusps show between three and four serrations per mm according to the size of the teeth, serrations being denser in the smaller teeth. The cutting edge runs from the base up to the apex of all cusps, and is continuous between the main and accessory cusps. The labial side of all cusps is less convex than the lingual side. The latter is always smooth while the labial one may be ornamented by irregular ridges, never attaining the apex (Pl. I, figs 1-2). Although irregular, these ridges are not anastomosed. The largest tooth is 26.5 mm mesio-distally, but its main cusp is not preserved.
The root is compressed labio-lingually, rectangular in shape in labial and lingual view, and slightly projecting lingually. The basal side is flat and rectangular. There is an irregular row of small foramina just below the crown on the labial and lingual side. Below this row of foramina, the labial side is concave while the lingual one is convex. The vascularization is anaulacorhize with some enlarged foramina near the base of the root in some teeth.

Discussion: The Tunisian teeth show no major differences from those of *Priohybodus arambourgi* described from the Late Jurassic of Somalia, Ethiopia and Yemen, the Late Jurassic-Early Cretaceous of Uruguay, and the Early Cretaceous of Tunisia and Libya (D'ERASMO, 1960; TABASTE, 1963; GOODWIN *et al.*, 1999; DUFFIN, 2001a; PEREA *et al.*, 2001) and are best attributed to this species. *Priohybodus* is currently attributed to the family Hybodontidae, mostly based on the fact that its teeth are osteodont (CAPPETTA, 1987; DUFFIN, 2001a). From a morphological point of view, its teeth are also quite similar to those of *"Hybodus" ensis*, whose large teeth are also serrated (UNDERWOOD & REES, 2002). However, contrary to what can be observed in many *Hybodus* species, the material at hand shows no marked heterodonty, apart from the ornamentation of the labial side of the crown that may correspond to a dignathic heterodonty. However, such a homodont dentition appears to be a mechanical result in many sharks possessing a cutting dentition (DUFFIN, 2001a). So we agree that *Priohybodus* is best included into the family Hybodontidae, being possibly quite close to *"Hybodus" ensis*.

Cohort Neoselachii COMPAGNO, 1977
Order Rajiformes BERG, 1940
Suborder "Rhinobatoidei" FOWLER, 1941
Incertae familiae

***"Rhinobatos"* sp.**
Plate I, figs. 3-6.

Material: 36 teeth (including JBNS 2) and one dermal denticle from Jebel Boulouha North Side.

Description: These teeth are small, from 1.5 up to 2.5 mm mesio-distally. The crown shows a very elongated central uvula, attaining the groove on the lingual side of the root. The lateral uvulae are very faint or absent. The apical side of the crown shows a longitudinal crest, in most specimens slightly concave lingually, although one tooth shows a reverse curvature (Pl. I, figs 3, 5). The rest of the crown is smooth. The labial face of the crown overhangs the root, forming a visor with a moderately

developed central protuberance (Pl. I, figs 3-6). None of the teeth shows the development of a cusp, suggesting no gynandric heterodonty.
The lingually projected root is massive and holaulacorhize with a deep central groove. It shows nearly the same height as the crown. There is a well-developed foramen in the centre of the groove, and on the lingual side, there is a large foramen on each side of the uvula. Some small foramina are scattered on the labial side of the root.

Discussion: The absence of a well-developed cusp and/or a longitudinal crest makes the Tunisian teeth easy to separate from those of *Jurobatos, Squatirhina, Engaibatis* and *Rhombopterygia* (CAPPETTA, 1987; UNDERWOOD & MITCHELL, 1999; ARRATIA *et al.*, 2002). The Tunisian teeth are also different from those of *Spathobatis,* the teeth of the latter showing a more developed longitudinal crest and a more massive central uvula (CAVIN *et al.*, 1995; UNDERWOOD & REES, 2002). The general morphology of the crown of the Tunisian teeth is similar to that seen in the genus *Belemnobatis*, but in the latter the labial visor is better developed than in the former (CAVIN *et al.*, 1995; UNDERWOOD & REES, 2002). The teeth from Jebel Boulouha appear also very similar to those found in the Upper Jurassic (?) of Ethiopia, which were attributed to *Rhinobatos* sp. (GOODWIN *et al.*, 1999). There are a number of Cretaceous *"Rhinobatos"* species which possess teeth with no or very weak lateral uvulae: *"R." craddocki* (Maastrichtian, Texas), *"R." halteri* (Barremian and Albian, France and Spain), *"R." intermedius* (Santonian, Lebanon), *"R." latus* (Santonian, Lebanon), *"R." maronita* (Cenomanian, Lebanon), *"R." hakelensis* (Cenomanian, Lebanon), *"R." picteti* (Aptian, France), and *"R." whitfieldi* (Cenomanian, Lebanon). These species probably represent new genera that need to be defined (CAPPETTA & CASE, 1999). Among the Aptian/Albian taxa, the species *halteri* has already been attributed to *Spathobatis* (BIDDLE, 1993, see however KRIWET, 1999 for a different opinion) and the species *picteti* to the genus *Belemnobatis* (UNDERWOOD & REES, 2002). *"R." halteri* shows a constriction at the base of the central uvula (BIDDLE, 1988) that is absent in most of the Tunisian teeth. We have seen that they are in any case different from those of the genera *Belemnobatis* and *Spathobatis*. They probably represent a new genus and species, but we feel that the erection of such a taxon cannot be done without a revision of the Cretaceous *"Rhinobatos"*, which is beyond the scope of this paper. Therefore, we refer these teeth to *"Rhinobatos"* sp. for the time being.
The teeth of this primitive ray are quite rare compared to those of *Priohybodus,* but they do co-occur in the site of Jebel Boulouha, West of Tataouine. These two genera seem also to co-occur in the Late Jurassic (?) of Ethiopia (GOODWIN *et al.*, 1999).

2.2. Chenini Member

Order Hybodontiformes MAISEY, 1987
Family Hybodontidae OWEN, 1846
Genus *Tribodus* BRITO & FERREIRA, 1989

***Tribodus tunisiensis* nov. sp.**
Plate I, figs 7-10

Derivatio nominis: named after Tunisia.

Holotype: T232, a complete tooth with preserved root.

Material: 250+ teeth, 4 of them with preserved root (including T232) and 7 probably belonging to juveniles (including T233). One tooth (T231) has been embedded in resin and cut for SEM study. All teeth come from Oued el Khil.

Diagnosis: a species of the genus *Tribodus* in which the crown of the teeth is devoid of ornamentation, except for three to five grooves that may be present at the base of the labial and/or lingual sides; crown hexagonal to diamond-shaped in apical view; root moderately developed, less than half the height of the crown.

Description: The teeth are hexagonal or diamond-shaped in apical view (Pl. I, figs 8-9), the apical surface being larger than the basal surface of the crown. The largest tooth measures 5 mm mesio-distally, 3 mm labio-lingually and is 3 mm high. Their relative height is highly variable, some being higher than wide labio-lingually, the reverse being true in other teeth. Whether this is linked to a monognathic or dignathic heterodonty cannot be determined. They are devoid of ornamentation, except for three to five coarse grooves that may be present at the base of the labial and/or lingual sides. The lingual side of the crown is slightly concave, and in the highest teeth there is a lingual visor developing at the apex of the crown. The root is small, always less than half the height of the crown (Pl. I, fig. 10), and slightly projected lingually. It shows numerous foramina randomly distributed over its whole surface. There is no basal row of enlarged foramina. A groove separating the root from the crown is absent.
Teeth from juvenile specimens are diamond-shaped and more compressed labio-lingually than the adult ones. Their minimum size is 1 mm mesio-distally and 0.5 mm labio-lingually. Some of them show a faint longitudinal crest, absent in the adult. The apical surface is concave, forming a pseudo-cusp at the mesial and distal extremities of the crown (Pl. I, fig. 7).

Histology: The teeth are osteodont, but there is no obvious arrangement of the vascular canals towards a 'tubular' dentine. The crown is covered by a thick single-crystallite enameloid, reaching 100 μm in thickness on

the apical surface. A similar structure was described by BRITO (1992).

Discussion: The teeth described here are somewhat different from the *Tribodus* teeth described from Brazil by BRITO (1992). The main difference is found in the morphology of the root, which is less developed than in the Brazilian specimens and lacks a baso-central enlarged foramina. However, the latter may be a preservation artefact. Posterior teeth ornamented with ridges and provided with a labially displaced longitudinal crest have not been recorded in our material. According to the high number of teeth recovered, this is unlikely to be a collecting bias. Also, no pseudo-cusps were described in the Brazilian specimens, although these teeth probably belong to a juvenile specimen with a less crushing diet.
The presence of a basal ornamentation on the lingual and/or labial sides of the crown is reminiscent of the teeth of *Hylaeobatis* (?) described from the Loia Series (Valanginian-Barremian) of Congo by CASIER (1961), although the ridges are not as numerous as in casier's specimens. MAISEY (2000) suggested that the teeth from Congo belong indeed to the genus *Tribodus*. WERNER (1994) erected also the species *Tribodus aschersoni*, although she misspelled it *Triodus aschersoni*, based on the teeth of *Aegyptobatus kuehnei* and the fin spines of *Hybodus aschersoni*. The teeth of *Tribodus aschersoni (Aegyptobatus kuehnei)* from the Cenomanian of Egypt differ from those of Tunisia by the presence of a row of specialized foramina in the lingual lower part of the root, a crown more ornamented and more elongated mesio-distally (WERNER, 1989). In Africa, the presence of *Tribodus* has also been suspected in Niger (CAPPETTA & CASE, 1999; DUTHEIL, 1999; MAISEY, 2000), and DUTHEIL (2001) mentioned this genus in Morocco although he did not figure it. The record from Tunisia therefore represents a confirmation of the presence of this South American genus in Africa. At least two species of *Tribodus* were present in Africa, but the presence on this continent of the South American species, *T. limae*, is still to be demonstrated. *Tribodus* was also present in the Cenomanian of South-western France where its teeth were described as *Protolypolophites morlati* (LANDEMAINE, 1991; CAPPETTA & CASE, 1999).

Genus: cf. *Hybodus*

Material: 2 fragmentary crowns from Oued el Khil.

Description: Two fragmentary crown remains, without preserved root, show a low cusp with a longitudinal crest giving origin to ridges which cover the labial and lingual sides of the crown. These ridges do not attain the base of the crown. The maximum size of the fragments is 4 mm.

Discussion: Due to the ornamentation pattern of the crown and the presence of cusps, although very low, these two crown fragments are cautiously attributed to the genus *Hybodus*. If we compare them with the teeth of *Hybodus* sp. described from the Douiret Formation, they appear larger and they have a different ornamentation. The ridges ornamenting the crown of the Douiret teeth attain the base of the crown, contrary to what is seen in the tooth fragments from Oued el Khil.

Cohort Neoselachii COMPAGNO, 1977
Superorder Galea SHIRAI, 1996
Order Lamniformes BERG, 1958
Family: Cretoxyrhinidae GLÜCKMAN, 1958
Genus *Cretodus* SOKOLOV, 1965

Cretodus semiplicatus (MÜNSTER *in* AGASSIZ, 1843)
Plate I, figs 11-16

Material: 67 teeth from Oued el Khil (including OEK 1 and OEK 2), and 2 teeth from Bateun el Hmaïma.

Description: The crown consists of a narrow triangular main cusp flanked by one to two pairs of divergent accessory cusps (Pl. I, figs 12-13). The main cusp becomes broader in posterior teeth. The labial side is almost flat on the main cusp, slightly more convex on the accessory cusps. The ornamentation is made of coarse ridges never attaining the apex of the cusps. The ornamentation is not as well developed as in posterior teeth. The lingual sides of the cusps are strongly convex and ornamented by finer ridges, not attaining the apex. The main cusp is bent lingually, sometimes slightly sigmoid. The cutting edges are well developed, attain the base of the main cusp, and are continuous with those of the accessory cusps.
The root is U-shaped, the lobes being rather thin with a rounded extremity, and is almost as high as the crown. The lingual protuberance is well marked (Pl. I, fig. 11). Anterior teeth may show a central foramen on it, and sometimes a faint groove.
A small tooth (3 mm mesio-distally) shows a broad main cusp flanked by a pair of reduced accessory cusps bent towards the main cusp (Pl. I, figs 14-16). The lobes of the root are almost non-existent. Although this tooth shows a well-developed ornamentation on both the labial and lingual sides, its overall shape is reminiscent of a posterior tooth of *Cretodus semiplicatus* as illustrated by CAPPETTA & CASE (1999, pl. 14, fig. 4).

Discussion: The genus *Cretodus* is generally thought to appear in the Cenomanian and to disappear in the Santonian (CAPPETTA, 1987; SCHWIMMER *et al.*, 2002). However, this genus was mentioned with some doubts in the Albian of Tunisia by CAPPETTA *(in* BOUAZIZ *et al.*, 1988) and in the Albian of France (BIDDLE, 1993). More recently, CAPPETTA & CASE (1999) described *Cretodus semiplicatus* from the Albian of Texas. Like some of the

Tunisian teeth, those described by BIDDLE (1993) show a faint groove on the lingual protuberance of the root.

Genus: cf. *Protolamna* CAPPETTA, 1980
Plate I, figs 17-19; Plate II, figs 1-3

Material: One symphyseal tooth from Oued el Khil (OEK 3) and one anterior tooth from Ksar Kherachfa (KK 1).

Description: The anterior tooth is almost complete, only lacking the tip of one root lobe, and measures 22 mm from the apex of the main cusp to the extremity of the lobes of the root. The main cusp is high and narrow, sigmoid in mesial and distal view (Pl. II, fig. 2). The labial side is slightly convex and shows some coarse and short ridges in the basal part. The lingual side is strongly convex and is ornamented by irregular ridges covering the lower quarter of the cusp. These ridges are thinner than those on the labial side. The cutting edges are well developed, extending from the tip of the cusp to its base, but they are not connected to the accessory cusps. These are well developed, slightly divergent, and separated from the main cusp by a notch (Pl. II, figs 1, 3). They are set labially to the main cusp. Both their labial and lingual sides are convex, the lingual one more so than the labial one. Both are ornamented by faint ridges. The lower boundary of the enameloid on the labial side of the tooth diverges and extends below the lateral accessory cusps. It thus shows a very concave outline. The root is V-shaped with rather short and stout lobes, which are slightly divergent. The lingual protuberance is well developed, with a faint nutrient groove.

The symphyseal tooth is also almost complete, only lacking the tip of one root lobe (Pl. I, figs 17-19), and measures 4 mm from the apex of the main cusp to the extremity of the lobes of the root. The labial side of the main cusp is almost flat and is ornamented with two well-developed ridges, not reaching the apex of the cusp. The cusp is rather compressed at its base, becomes broader, reaching its maximum width at mid-height, and acute again at the apex. The lingual side is strongly convex and ornamented by seven ridges, the median one reaching the apex of the cusp. The cutting edges are well developed and disappear just before the base of the cusp. There is a pair of acuminate lateral accessory cusps, half the height of the main cusp and separated from the latter by a notch. Both sides of the accessory cusps are convex, in particular the lingual one. The lingual side is ornamented by three ridges and the labial one by two ridges. On each side, there is one ridge attaining the apex of the accessory cusps. The accessory cusps are set labially to the main cusp. The lower boundary of the enameloid on the labial side of the tooth diverges and extends below the lateral accessory cusps that are separated by a narrow and deep concavity free of enameloid. The root is V-shaped with rather short lobes, which are slightly divergent. There is a foramen in the lower part of this concavity. The lingual protuberance is not well developed, without a nutrient groove. There is a row of foramina just below the crown on the mesial and distal side of the root.

Discussion: The two teeth described above are reminiscent of both *Leptostyrax* and *Protolamna*. The taxonomy of these two genera is still under discussion (CAPPETTA, 1987; BIDDLE, 1993; SIVERSON, 1996; UNDERWOOD & MITCHELL, 1999).

The type species of *Leptostyrax* is *L. macrorhiza* (COPE, 1875). It is characterized by the distinct offset of the cusplets from the main cusp and the lingual protuberance lacking a nutrient groove. The genus *Protolamna* was established based on lamniform teeth from the Aptian of France by CAPPETTA (1980) with the type species *P. sokolovi*. Characteristic of *Protolamna* is the extraordinarily massive lingual protuberance that is provided with a faint nutrient groove. CAPPETTA (1980) referred all European specimens that had been assigned to *Lamna macrorhiza* (COPE, 1875) to *Protolamna*.

According to WILLIAMSON *et al.* (1993), *Leptostyrax* is diagnosed largely on its peculiar root morphology, with the lower boundary of the enameloid on the labial face of the root diverging and extending below the lateral cusps which are separated by a narrow and deep groove, that is free of enameloid. However, a very similar condition has been described in the teeth of *Protolamna compressidens* from the Turonian/Coniacian of Texas (CAPPETTA & CASE, 1999), suggesting that this character is not useful in discerning these two genera.

We give here a list of features which we believe to distinguish *Leptostyrax* from *Protolamna*. This list is based on literature studies (CAPPETTA, 1980; MÜLLER & DIEDRICH, 1991; BIDDLE, 1993; CAPPETTA & CASE, 1999; KRIWET, 1999; UNDERWOOD & MITCHELL, 1999) and on personal observations. *Leptostyrax* characters are (1) the cutting edges being non-continuous with the cusplets, (2) the main cusp being basally compressed, (3) the rather short root lobes forming a "V", and (4) the lingual protuberance being less well developed than in *Protolamna*. Features characterizing *Protolamna* are (5) the ornamentation of the lingual side of the main cusp and (6) the presence of a nutrient groove on the strongly developed lingual protuberance.

The anterior tooth of the Tunisian material shows characters similar to *Leptostyrax* (1, 3, 4) as well as *Protolamna* (4, 5). The symphyseal tooth, being rather similar to the main cusp of the teeth of *P. compressidens* figured by CAPPETTA & CASE (1999), shows all *Leptostyrax* characters listed above, but also one *Protolamna* character (4).

According to CAPPETTA & CASE (1999), the genus *Leptostyrax* is restricted to North America, but UNDERWOOD & MITCHELL (1999) mention this genus from the Albian of England, although this record is

based on poorly preserved teeth. SIVERSON (1992, 1996) also mentions this genus in the Campanian of Sweden and the Cenomanian of Western Australia, but in both case these occurences are based only on a single tooth. Furthermore, among new, unpublished material from the Lower Cretaceous of Northern Germany, *Leptostyrax* seems to be present as well.

CAPPETTA (*in* BOUAZIZ *et al.*, 1988) mentions and figures a tooth of *Protolamna* from the Albian of Tunisia, but he did not provide a description of this tooth. As the photograph is of rather poor quality, the comparison with our material is difficult.

SCHLÜTER & SCHWARZHANS (1978) mentioned the presence of *Odontaspis* sp. at Ksar Kherachfa, but we strongly suspect that their material corresponds to cf. *Protolamna*.

Based on the discussion above, the attribution of the Tunisian teeth to *Protolamna* rather than to *Leptostyrax* is based on weak evidence: the presence of a very faint groove on the lingual protuberance of the root of the anterior tooth and the ornamentation of the lingual side of the main cusp. Additionally, CAPPETTA & CASE (1999) believe the genus *Leptostyrax* restricted to North America. The discovery of more teeth may lead us to revise this attribution. We also have to bear in mind that the symphyseal tooth may belong to *Cretodus semiplicatus* which is present at the same locality (see WILLIAMSON *et al.*, 1993). For a better understanding of the taxonomy of *Protolamna* and *Leptostyrax*, a revision of these genera is essential.

Family Mitsukurinidae JORDAN, 1898
Genus cf. *Scapanorhynchus* WOODWARD, 1889
Plate II, figs 4-6

Material: One isolated cusp (KK 2) from Ksar Kherachfa.

Description: The cusp is elongated, 17.5 mm long and 5 mm wide at its base, and strongly sigmoid in mesial or distal view (Pl. II, figs 4-6). The labial side is smooth and slightly convex. The lingual side is more convex and ornamented by fine ridges covering the two lower third of the cusp. The cutting edges are well developed from the tip to the base of the cusp.

Discussion: With only a single isolated cusp, a precise identification is almost impossible. This cusp however differs from that of the tooth of cf. *Protolamna* from the same site by its lingual side less convex and more ornamented. It is quite similar to the isolated cusp of an anterior tooth of *Scapanorhynchus* aff. *praeraphiodon* described from the Cenomanian of Texas by CAPPETTA & CASE (1999).

Superorder Squalea SHIRAI, 1996
Order Rajiformes BERG, 1940
Suborder Sclerorhynchoidei CAPPETTA, 1980
Family Sclerorhynchidae CAPPETTA, 1974
Genus *Onchopristis* STROMER, 1917

Onchopristis dunklei McNULTY & SLAUGHTER, 1962
Plate II, figs 7-10

Material: Two anterior (including OEK 4) and two postero-lateral oral teeth from Oued el Khil.

Description: The two anterior teeth have roughly the same size: 1.5 mm labio-lingually and 1 mm mesio-distally. The crown is smooth with a pointed main cusp directed lingually (Pl. II, fig. 8). The labial apron is very well developed, protruding labially over the root, with a square extremity (Pl. II, fig. 7). On one of the two teeth, there is a very faint median ridge on the labial side of the main cusp, starting above the extremity of the labial apron and disappearing before reaching the apex of the main cusp (Pl. II, fig. 10). The uvula is not developed on the anterior teeth (Pl. II, fig. 9). The main cusp is flanked by a pair of accessory cusps. Contrary to the former, the latter are upright and are not oriented lingually. These accessory cusps protrude mesially and distally over the root. The root is almost circular in basal view, and is holaulacorhize with a central groove that widens labially. This groove is almost completely roofed lingually in one of the teeth. There is a large nutrient foramen in the centre of the groove. The margino-lingual foramina are well marked on each side of the main cusp.

The posterior teeth are more elongated mesio-distally with well-developed heels, but without accessory cusps. The teeth reach 2 mm mesio-distally. The longitudinal crest is well developed on the mesial and distal heels but becomes fainter on the main cusp. The main cusp is lower and less bent lingually than in the anterior teeth. It is almost upright in one of the two posterior teeth. There is a faint median ridge on its labial side. The labial apron is less developed than in the anterior teeth but still protrudes over the root, with a square extremity. The lingual uvula is moderately developed, not reaching the groove of the root, with a rather square outline. The root has a similar morphology to that seen in the anterior teeth, but being more elongated mesio-distally.

Discussion: The teeth from Oued el Khil appear quite different from the African ones attributed to *Onchopristis numidus* by WERNER (1989). The latter ones are larger, are more ornamented and possess a more massive labial apron than the Tunisian teeth. According to CAPPETTA & CASE (1999), these teeth do not belong to *Onchopristis numidus*, but to a different, as yet unnamed taxon of Sclerorhynchidae instead. However, they consider that the oral teeth described by WERNER (1989) as *Sechmetia aegyptiaca* belong in fact to *Onchopristis numidus*.

These latter teeth are also different from the Tunisian ones, mainly by their larger size and the possession of a more slender labial apron. On the other hand, the four teeth from Oued el Khil are very similar to those of *Onchopristis dunklei* described from the Cenomanian of Texas by CAPPETTA & CASE (1999). The oral teeth of this species are known as early as the Barremian and their geographic distribution includes the United States, Europe and Africa (CAPPETTA & CASE, 1999; KRIWET, 1999). Their presence in Africa were so far restricted to the Cenomanian of Egypt where they were described as *Sechmetia aegyptiaca* (WERNER, 1989; CAPPETTA & CASE, 1999; KRIWET, 1999). No rostral teeth have been found so far during our work, but it is interesting to note that TABASTE (1963) recorded the presence of rostral teeth of *Onchopristis numidus* in Morocco and Algeria, but not in Tunisia.

2.3. Oum Ed Diab Member

Order Hybodontiformes MAISEY, 1987
Family Lonchidiidae HERMAN, 1977
Genus *Lissodus* BROUGH, 1935

***Lissodus* sp.**
Plate II, figs 11-13

Material: 1 crown from Touil el Mra and 5 crowns from Oum ed Diab (including OED 1).

Description: Only four crowns are complete. Roots are not preserved. The largest crown is 3 mm mesio-distally and 2 mm labio-lingually. Three of these crowns are rather bulky, with an almost triangular outline in apical view (Pl. II, fig. 12). The fourth one, smaller, is more elongated mesio-distally, with a less developed labial peg. It probably corresponds to a more posterior tooth. In the largest teeth in apical view, the lingual side of the crown appears scalloped. There is a faint main cusp and longitudinal crest. Apart from the longitudinal crest, the crowns are smooth (Pl. II, figs 11-13).

Discussion: These teeth are unusual because of their lack of ornamentation and their scalloped labial side in apical view. A lack of ornamentation is more often encountered in *Lonchidion* than in *Lissodus* (REES & UNDERWOOD, 2002; DUFFIN, 2001b; DUFFIN & SIGOGNEAU-RUSSELL, 1993). But in contrast, the low and wide crown-shape with a faint longitudinal crest is a *Lissodus* character that is absent in *Lonchidion*. Therefore, the Tunisian teeth are attributed to *Lissodus* and probably represent a new species. However, taking into account the small number of teeth discovered so far, and the absence of a preserved root, it would be unwise to erect a new species now.

Genus *Diabodus* nov. gen.
Plate II, figs 14-17

***Derivatio nominis*:** from the type locality, Oum ed Diab, and *Odous*, tooth in Greek.

Diagnosis: monospecific genus, same as for species *D. tataouinensis*.

***Diabodus tataouinensis* nov. sp.**

***Derivatio nominis*:** from Tataouine, the governorate in which the type locality, Oum ed Diab, is located.

Holotype: a complete crown from Oum ed Diab (OED 2).

Material: 10 crowns, including the holotype, from Oum ed Diab and one from Touil el Mra.

Diagnosis: Crown smooth with a very strong longitudinal crest set labially or lingually; no cusp on the crown; labial protuberance moderately developed; surface for the root attachment with a triangular outline; dignathic heterodonty with the longitudinal crest set labially or lingually whether the teeth come from the upper or lower jaw; monognathic heterodonty with antero-lateral and lateral teeth broader labio-lingually than the posterior ones.

Description: As only isolated crowns, without root, are available, the orientation of these teeth is problematical, but the outline of the root attachment area is triangular. In *Lissodus angulatus*, *Lissodus nodosus*, and *Lonchidion babulskii* the tip of the triangle is labial and the base is lingual (DUFFIN, 2001b; REES & UNDERWOOD, 2002). We therefore use that character to determine the labial side from the lingual one. The largest tooth is 3 mm mesio-distally and 1 mm labio-lingually. Most of the teeth show a labial protuberance moderately developed, which may disappear in some teeth (Pl. II, figs 15-16). The crowns are smooth, without cusps, but with a very strong longitudinal crest (Pl. II, figs 14-17). In 5 teeth, this crest is set labially, and lingually in 6 teeth. 4 of the teeth with a lingual longitudinal crest show a well marked longitudinal wear facet in the lingual part of the apical side. Most of the teeth are rather broad labio-lingually, except for the two smallest ones that are more compressed. One has a lingual longitudinal crest, the other a labial one, and both show a faint labial protuberance, less developed than in broader teeth. The root attachment area is less extended mesio-distally than the crown.

Discussion: If our orientation of the teeth is correct, the presence of a labial protuberance indicates that they belong to the Lonchidiidae, but their morphology is unlike that of any other genera included in this family.

The absence of cusps separate these teeth from those of *Lissodus, Lonchidion, Vectiselachos,* and *Parvodus,* and the lack of ornamentation separates them from those of *Hylaeobatis* (Rees & Underwood, 2002), justifying the erection of a new genus. The Tunisian teeth are also superficially similar to those of *Bahariyodon bartheli* from the Cenomanian of Egypt, but differ from the latter by the absence of a central cusp and lateral cupslets, and the lingual side of the crown is not expanded lingually to form a shelf-like structure (Duffin, 2001b).
The position of the longitudinal crest, labial or lingual, probably reflects a dignathic heterodonty, allowing a good occlusion between the upper and lower teeth, responsible for the longitudinal wear facets seen in some teeth. In addition to the dignathic heterodonty, there is a monognathic one. The small teeth, rather compressed labio-lingually and provided with a faint labial protuberance are likely to be posterior teeth, because – compared to *Lissodus nodosus* – the anterior teeth usually possess a well-developed labial protuberance (Duffin, 1985). The broader teeth are likely to be antero-lateral and lateral teeth, but the morphology of anterior teeth, if significantly different from that of the antero-lateral ones, remains unknown.

Family Hybodontidae Owen, 1846
Genus *Hybodus* Agassiz, 1837

***Hybodus* sp.**
Plate II, figs 18-20

Material: 93 more or less complete crowns from Oum ed Diab (including OED 3), and 27 ones from Touil el Mra.

Description: The best-preserved crown belongs to a postero-lateral tooth (Pl. II, figs 18-21). It is elongated and asymmetric, with a low main cusp flanked by two low accessory cusps mesially and three distally. The crown is 6 mm mesio-distally and 1 mm labio-lingually. On the labial side, there are five ridges ornamenting the main cusp, and two to three on the lateral accessory cusps. These ridges are not anastomosed, originate at the base of the crown and attain the apex of the cusps. The ridges on the lingual side are sometimes anastomosed and – in contrast to the labial side – they do not originate from the base of the crown. The lingual crown shoulder is smooth. There is a well-developed longitudinal crest ascending all the cusps.
Most of the other crowns are very fragmentary. Some are quite high isolated cusps, slightly compressed labio-lingually, with a similar ornamentation pattern to that described above. They are probably main cusps of anterior teeth. Other fragments show accessory cusps that may become extremely low, almost non-existent. They probably belong to posterior teeth. This species of *Hybodus* appears therefore to show a marked heterodonty. No fragments indicate the presence of more than three lateral accessory cusps in any teeth, and the smaller the teeth, the denser the ornamentation. A rather worn tooth shows a labial node at the base of the main cusp.

Discussion: The absence of labial – except on a single tooth – or lingual nodes on the Tunisian teeth, together with a central cusp oval in outline rather than pyramidal lead us to refer these teeth to *Hybodus* rather than *Polyacrodus*. The pattern of heterodonty that can be inferred from the fragmentary teeth recovered so far is reminiscent of that of *Hybodus parvidens* (Rees, 2002), but the ornamentation is denser in the Tunisian teeth. In addition, the lateral teeth might be more elongated mesio-distally than in *H. parvidens,* although this is difficult to ascertain. We should note that the species *parvidens* is also attributed to *Polyacrodus* (Cappetta, 1987; Underwood & Rees, 2002) based on the presence of a labial keel on the main cusp, absent in the Tunisian teeth. If we compare these teeth with those of Jebel Boulouha North side, the latter are smaller in size, and the ornamentation is denser with more anastomosed ridges. On the contrary, the two fragments from Oued el Khil appear to belong to larger teeth than those from the Oum ed Diab Member, and the ridges ornamenting the crowns are shorter, never attaining the base of the crown. It thus appears likely that there are at least three different species of *Hybodus* in the Lower Cretaceous of Tunisia, but the fragmentary nature of the fossils prevents identification at the species level for the time being.

Hybodontiformes *incertae sedis*
Plate II, figs 22-23

Material: 1 dermal denticle from Touil el Mra, 1 right cephalic spine from Oum ed Diab (OED 4), 1 dorsal fin spine from Oum ed Diab, and 1 from Touil el Mra (TEM 1).

Description: None of the fin spines are complete and only the apical parts are preserved. The largest is the one from Touil el Mra, being 63 mm long (Pl. II, fig. 23). Its section is ovoid with a large central cavity. The lateral sides are ornamented with 10 fine, sub-parallel ridges covered with enameloid. There is a fine anterior keel, also covered with enameloid. On the posterior side, there are two alternating rows of denticles. Each denticle shows an enameloid cover. The fragment from Oum ed Diab is minute, measuring only 2 mm, with the tip missing. Lateral ornamentation is very faint, but there is a single row of well-developed hook-like denticles on the posterior side.
Only the base of the cephalic spine is preserved, measuring 10 mm cranio-caudally (Pl. II, fig. 22). It is convex labio-lingually and asymmetric with a mesial lobe directed more caudally than the lateral one. This

cephalic spine can therefore be recognized as a right one (MAISEY, 1982). Both the lateral and mesial lobes are short and fairly stout, with about equal width and length. The posterior lobe is thin and elongated, becoming broader and flatter distally. The crown is broken at its base but there is no trace of accessory cusp. The cranial side of the base is pointed in apical view, the base of the cusp being in front of the lateral and mesial lobes.
The dermal denticle is minute, being 0.5 mm in diameter. The base is circular in outline with a large basal nutrient foramen. The crown is smooth and globular.

Discussion: As 3 hybodont taxa have been identified from isolated teeth, it is difficult to attribute the spines or the dermal denticle to one or the other of these species in the absence of material found in connection. The dermal denticle is however somewhat unusual for a hybodont with its unornamented crown. It may be easier to get an idea of the affinity of the cephalic spines. In *Hybodus*, and more particularly in the type species *H. reticulatus*, the cranial side of the base is flat, the base of the crown being at the level of the lateral and mesial lobes, contrary to what can be seen in the Tunisian specimen (MAISEY, 1982, 1987). The same flat morphology is seen in *Lissodus cassangensis* (ANTUNES *et al.*, 1990). It is therefore probable that the cephalic spine belongs to a Lonchidiidae (*Diabodus* or *Lissodus)* rather than to a Hybodontidae.

3. PALAEOENVIRONMENT OF THE EARLY CRETACEOUS OF TUNISIA

The Douiret Formation shows the association of *Hybodus* sp., *Priohybodus arambourgi*, and *"Rhinobatos"* sp. From the Late Jurassic onwards, hybodonts appear to be mainly freshwater animals (REES, 1998), and they are indeed very successful in the nonmarine Early Cretaceous of Thailand (CUNY *et al.*, submitted). However, the genus *Hybodus*, which, following CAPPETTA (1987), we consider to include *Meristodon* is found in marine environments in the Late Cretaceous of the United States (CAPPETTA & CASE, 1975, 1999) and is therefore not a useful palaeoenvironmental indicator. *Priohybodus* on the other hand is considered to be restricted to freshwater environments, being found very often in association with dipnoan remains or freshwater unionid bivalves (PEREA *et al.*, 2001). Its palaeogeographic distribution, restricted to the African and South American landmass, seems to confirm this mainly freshwater habitat. The size of the teeth of *Priohybodus* indicates a total body length of more than two metres, although a precise estimate is highly hypothetical in the absence of more complete remains. It was certainly one of the top predators in its environment and probably needed a quite important water depth to be able to survive.
The teeth of *"Rhinobatos"* that are morphologically similar to the Tunisian teeth are mostly found in marine environments in the Barremian-Albian of France (*"R." picteti, "R." halteri)*, the Cenomanian and Santonian of Lebanon (*"R." intermedius, "R." latus, "R." maronita, "R." hakelensis, "R." whitfieldi)*, and the Maastrichtian of Texas (*"R." craddocki)*. Nowadays, the genus *Rhinobatos* is mainly a marine ray, but is known to occasionally venture into estuaries (LAST & STEVENS, 1994). Unfortunately, the systematics of the "Rhinobatoidei" are currently poorly understood (MCEACHRAN *et al.*, 1996), and in the absence of a sound phylogenetic frame, comparison between modern *Rhinobatos* and their fossil counterparts might be misleading. The only other known association between a freshwater *Priohybodus* and a marine *"Rhinobatos"* occurs in the Mugher Mudstone of Ethiopia (GOODWIN *et al.*, 1999). The Ethiopian palaeoenvironment was reconstructed as "a seaward-advance of a flood plain facies where a coastal environment of brackish lagoons gave way to a meandering river system" (GOODWIN *et al.*, 1999, p. 738). In Ethiopia, the small number of teeth

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Plate I

Figs 1-2: Tooth of *Priohybodus arambourgi* (JBNS 1) from Jebel Boulouha North Side in 1: labial view, and 2: lingual view.

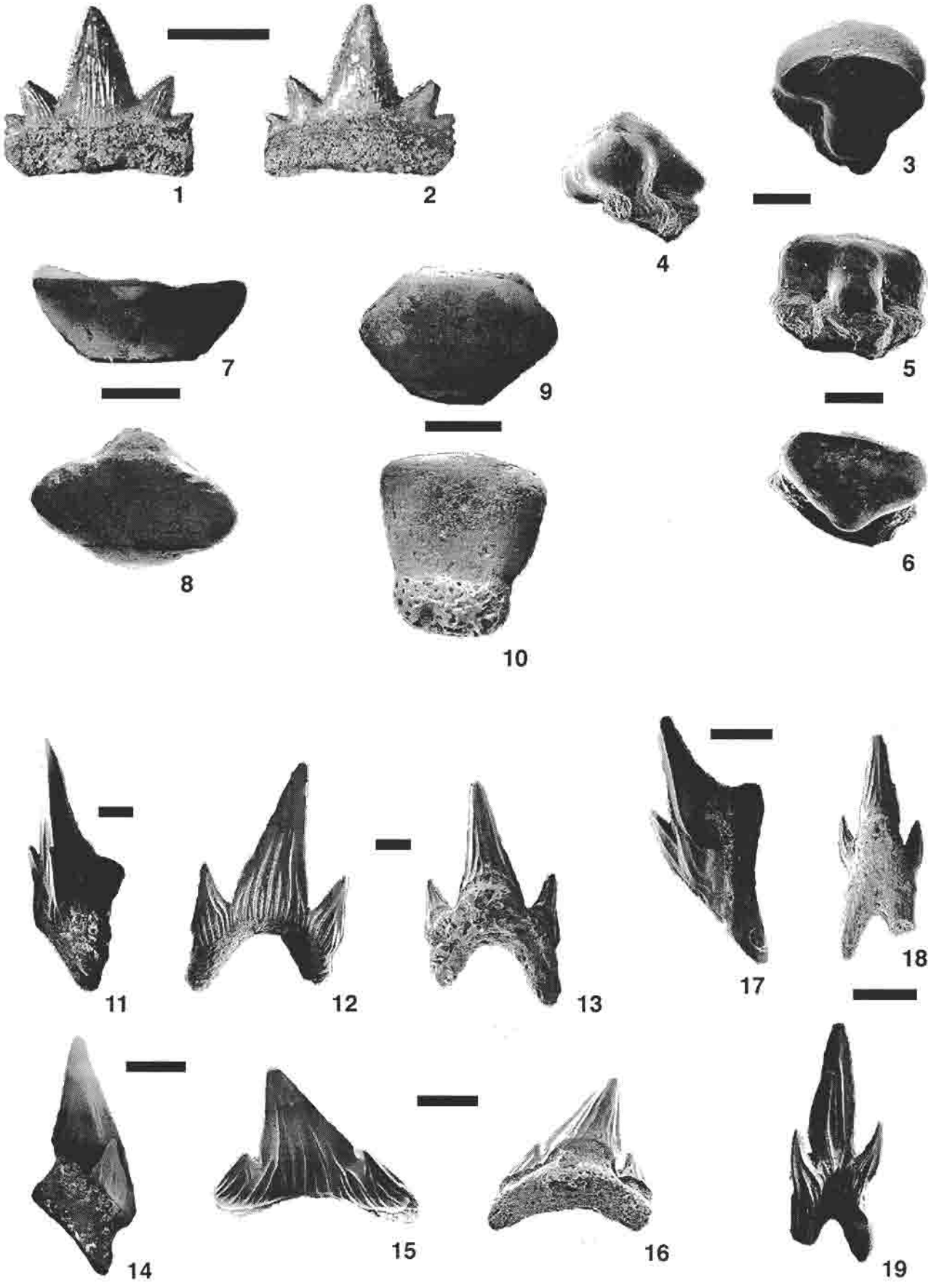
Figs 3-6: Tooth of *"Rhinobatos"* sp. (JBNS 2) from Jebel Boulouha North Side in 3: apical view, 4: mesial or distal view, 5: lingual view, and 6: labial view.

Figs 7-10: *Tribodus tunisiensis* from Oued el Khil. 7-8: Tooth of a juvenile (T233) in 7: lingual and 8: apical view. Tooth of an adult with the root preserved (holotype, T232) in 9: apical and 10: lingual view.

Figs 11-16: *Cretodus semiplicatus* from Oued el Khil. Lateral tooth (OEK 1) in 11: mesial or distal view, 12: labial view, and 13: lingual view. Posterior tooth (OEK 2) in 14: mesial or distal view, 15: labial view, and 16: lingual view.

Figs 17-19: Symphyseal tooth of cf. *Protolamna* (OEK 3) from Oued el Khil in 17: mesial or distal view, 18: lingual view, and 19: labial view.

Scale bars: 1-2: 5mm; 9-10, 14-19: 1 mm; 3-8, 11-13: 0.5 mm.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recovered (3 of *"Rhinobatos"* and 1 of *Priohybodus)* does not allow to discuss the relative abundance of each taxon. In Tunisia however, *Priohybodus* clearly dominates the assemblage (154 teeth against 36 for *"Rhinobatos"),* suggesting a rather strong fluvial influence on the deposit. However, FERRY *et al.* (2002) did not record a single fluvial deposit in the Douiret Formation, which they have interpreted as a transgressive sequence, not a regressive one as in Ethiopia.

The Chenini Member shows the most diverse elasmobranch association, including *Tribodus tunisiensis* nov. sp., cf. *Hybodus*, *Cretodus semiplicatus*, cf. *Protolamna*, cf. *Scapanorhynchus*, and *Onchopristis dunklei*. *Tribodus* is known from marine environments in Brazil (MAISEY, 2000), Egypt (WERNER, 1990), and Congo (CASIER, 1969) and freshwater ones in Niger and Morocco (DUTHEIL, 1999, 2001). The Cretoxyrhinidae are considered as an ecological equivalent of the modern Odontaspididae. These sharks are encountered in coastal environment as well as in open sea, but are not known to enter freshwater (CANUDO *et al.*, 1995). *Cretodus semiplicatus* is rather common in nearshore deposits, but rare in deep-marine deposits (WILLIAMSON *et al.*, 1993). MÜLLER & DIEDRICH (1991) considered *C. semiplicatus* as nectic, pelagic shark. The family Mitsukurinidae (to which belongs *Scapanorhynchus)* is also a family restricted to marine environments (CAPPETTA, 1987), and *Onchopristis dunklei* has been so far mentioned in marine environments only (CAPPETTA & CASE, 1999; KRIWET, 1999). The Chenini Member appears thus to show a typically marine shark assemblage, while the Douiret Formation one shows more freshwater affinities. This is quite paradoxical because the lower part of the Chenini Member shows fluvial deposits, which are absent in the Douiret Formation. This would indicate that the Douiret Formation was deposited farther from the coast than the Chenini Member, while the shark faunas suggest the contrary. The differences in the shark assemblages is unlikely to be due to stratigraphic differences, the Douiret Formation being Aptian while the Chenini Member is Albian, because most of the neoselachians found in the Chenini Member are known as early as the Barremian (*Protolamna*, *Onchopristis*, KRIWET, 1999) or have already been recorded from the Aptian (*Scapanorhynchus*, CAPPETTA, 1987). Interestingly, terrestrial elements (notably dinosaur teeth and bones) are very abundant in the conglomerates of the Chenini Member, where they occur together with teeth of marine sharks. They appear to be less abundant in the Douiret Formation, where the most common tetrapods are aquatic turtles and crocodilians. The tetrapod assemblages from the Douiret Formation and Chenini Member thus seem to suggest palaeoecological interpretations which are at variance with those drawn from the sharks. Further investigations are clearly needed to get a better understanding of the palaeoenvironment of the Douiret Formation and Chenini Member.

The Oum ed Diab Member has yielded exclusively hybodonts, with no neoselachian tooth found so far. Such an assemblage is very similar to that of the Thai Lower Cretaceous, where a marine influence on the deposition has not been recorded. As Oum ed Diab and Touil el Mra are among the most productive bone-beds found so far in the Lower Cretaceous of Tunisia, the absence of neoselachians is unlikely to be the result of a collecting bias. This strongly argues against a marine influence on these deposits. The microconglomerate from which these fossils were found, interpreted as a transgressive beach deposit by OUAJA *et al.* (2002), is therefore more likely to correspond to a lagoonal environment, separated from the sea by a sandbar. The tetrapod assemblage from the Oum ed Diab Member, dominated by crocodilians and iguanodontid dinosaurs, is compatible with such an interpretation.

Plate II

Figs 1-3: Anterior tooth of cf. *Protolamna* (KK 1) from Ksar Kherachfa in 1: labial view, 2: mesial or distal view, and 3: lingual view.

Figs 4-6: Crown of cf. *Scapanorhynchus* (KK 2) from Ksar Kherachfa in 4: lingual view, 5: mesial or distal view, and 6: labial view.

Figs 7-10: Anterior oral tooth of *Onchopristis dunklei* (OEK 4) from Oued el Khil in 7: labial view, 8: mesial or distal view, 9: lingual view, and 10: apical view.

Figs 11-13: Tooth of *Lissodus* sp. (OED 1) from Oum ed Diab in 11: lingual view, 12: apical view, and 13: labial view.

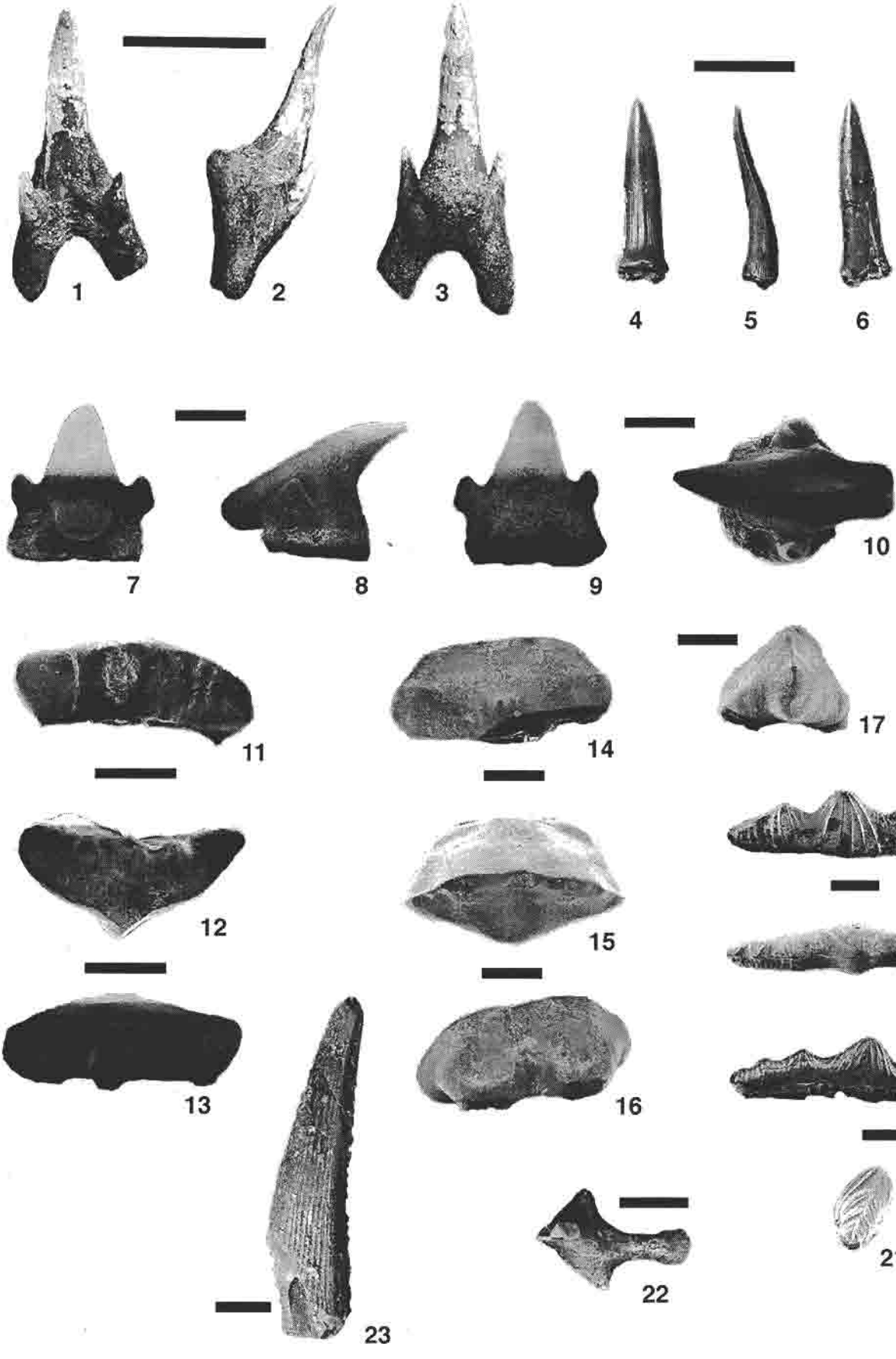
Figs 14-17: Holotype of *Diabodus tataouinensis* (OED 2) from Oum ed Diab in 14: lingual view, 15: apical view, 16: mesio-labial or disto-labial view, and 17: mesial or distal view.

Figs 18-21: Tooth of *Hybodus* sp. (OED 3) from Oum ed Diab in 18: labial view, 19: apical view, 20: lingual view, and 21: mesial or distal view.

Fig. 22: Cephalic spine (OED 4) of a hybodont from Oum ed Diab in apical view.

Fig. 23: Dorsal fin spine (TEM 1) of a hybodont from Touil el Mra in lateral view.

Scale bars: 1-6, 23: 10 mm; 22: 5 mm; 11-13, 18-21: 1 mm; 7-10, 14-17: 0.5 mm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CONCLUSIONS

The Early Cretaceous of Tunisia has yielded rich shark assemblages in the Douiret Formation, Chenini Member, and Oum ed Diab Member. These assemblages are very different from each other, suggesting different palaeoenvironments. The Douiret assemblage is dominated by hybodont sharks (*Hybodus, Priohybodus)* with a few marine rays (*"Rhinobatos"*), suggesting a deposit very close to the coast, probably in a large delta under tidal influence. The Chenini assemblage is dominated by neoselachian sharks (*Cretodus semiplicatus*, cf. *Protolamna*, cf. *Scapanorhynchus*, *Onchopristis dunklei)* and the hybodont *Tribodus*. The presence of *Cretodus semiplicatus* indicates a shallow marine environment and a deposition probably somewhat farther from the coast than the Douiret Formation, although there are sedimentological and palaeontological problems with this interpretation. On the contrary, the Oum ed Diab assemblage is devoid of neoselachians, strongly indicating a freshwater environment with no marine connection.

Our work also indicates that hybodonts with a very specialized dentition such as *Tribodus* were able to successfully co-exist with neoselachian sharks in a marine environment during the Early Cretaceous. The high number of *Tribodus* teeth recovered from Oued el Khil makes it indeed very unlikely that it was an allochtonous, freshwater, component of the fauna.

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