PALÆO VERTEBRATA

New *Squalicorax* species (Neoselachii: Lamniformes) from the Lower Maastrichtian of Ganntour phosphate deposit, Morocco

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Abstract: Two new *Squalicorax* species, *S. benguerirensis* nov. sp. and *S. microserratus* nov. sp. are described from the Lower Maastrichtian of the Benguérir phosphate open mine, Ganntour deposit, Morocco. The species *S. benguerirensis* nov. sp. was classically assigned to *S. yangaensis* by Arambourg (1952) and has been also recognized in coeval deposits from eastern USA to Mid-East. The species *S. microserratus* nov. sp. corresponds to the lateral teeth of *S. kaupi* as reported by Arambourg (1952) and which is now referred to *S. bassanii.* The comparison of these two new species with other anacoracids, known from Morocco or elsewhere, allows the great taxonomic and ecological diversities of this family during the Cretaceous to be highlighted.

Keywords: Chondrichthyes, Lamniformes, Anacoracidae, new species, Maastrichtian, Morocco

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INTRODUCTION

Anacoracid sharks are one of the dominant and characteristic elements of the Cretaceous elasmobranch faunas, occurring from Albian up to the Late Maastrichtian. Their geographical distribution is very broad since teeth of *Squalicorax* are found worldwide (Cappetta, 2012).

In Morocco, *Squalicorax* is common in all stratigraphic levels of the Maastrichtian phosphatic series of the Ouled Abdoun and Ganntour deposits (Noubhani & Cappetta, 1997), but also in other localities south of the High-Atlas (Oued Erguita) and in the Middle-Atlas (Bekrit, Timhadit).

Fieldwork undertaken near the Benguérir city (Ganntour deposit) made it possible to highlight the rich assemblages of Anacoracidae containing up to five species of *Squalicorax* associated in the same time period (see Cappetta *et al*., 2014): *Squalicorax* aff. *pristodontus* Agassiz, 1835, *S. africanus* Cappetta, 1991, *S. bassanii* Gemmellaro, 1920, and two new species described here (namely *Squalicorax* sp. nov 1 and *Squalicorax* sp. nov. 2 in Cappetta *et al*., 2014).

MATERIAL AND METHODS

The phosphatic deposits of Morocco, known since 1908, have been exploited since the 1920s (Office Chérifien des Phosphates, 1989). They crop out in several deposits, the main ones being at Ouled Abdoun and Ganntour, located between Casablanca and Marrakech (Fig. 1). Stratigraphically, these phosphatic strata range from the uppermost Cretaceous (lowermost Maastrichtian) to basal mid-Eocene (Lutetian), spanning the longest time interval of all Tethyan phosphate deposits (Lucas and Prévôt-Lucas, 1996). The fossils studied in this work come from the phosphate ore of Benguérir, located on the Ganntour Plateau, about 12 km east of the Benguérir locality, north of the El Kelaa des Sraghna road (Fig. 1). They were collected in two phases, initially during a field trip carried out in 1979 by the senior author (HC), prior to the start of mining operations, and then during various trips carried out between 1998 and 2008. The industrial exploitation of the phosphatic series located at the East of the locality of Benguérir was at the point of starting in 1979, and only a few pits of variable size gave access to some parts of the phosphatic series. One of these pits ("Tranchée d'essai"; GPS coordinates: 32° 13' 58.083" N, 7° 49' 08.63" W), large, and dug just north of the Benguérir-El Kelaa des Sraghna road (see Fig. 1), exposed the base of the Maastrichtian, (Level 6 of the miners, see Cappetta *et al*. 2014) which was very fossiliferous. This Level, between 30 and 40 cm thick, consists of a soft, coarse phosphate, grey coloured, very rich in fish remains (including elasmobranch teeth) which is overlain by a bed of marl and siliceous marl and chert, of about 1.10 m thickness (Fig. 2). Currently this is mainly observable at the bottom of many old trenches in the northern part of the Benguérir deposit. This Level 6 is a true unconsolidated bone-bed, very detrital at its base, with in particular many small very rounded quartz pebbles, resting directly on yellow nonfossiliferous upper Campanian and lowermost Maastrichtian clays, the top of which are bioturbated, with many burrows (Boujo, 1976; Cappetta *et al*., 2014). Currently, the succession of the Levels of Benguérir is well exposed thanks to immense trenches several kilometers long, aligned in a north-south direction, which were opened for phosphate exploitation in the Ganntour plateau. This phosphatic series shows relatively thick and fossiliferous Maastrichtian deposits, reaching a thickness of about twenty meters with five exploited main stratigraphic Levels named Level 6 (base) to Level 2 (top) and resumed as L6 - L2 thereafter for brevity. The geology and stratigraphy of the Ganntour deposit were mainly studied by Boujo (1968, 1976). More recently Cappetta *et al.* (2014) studied in detail

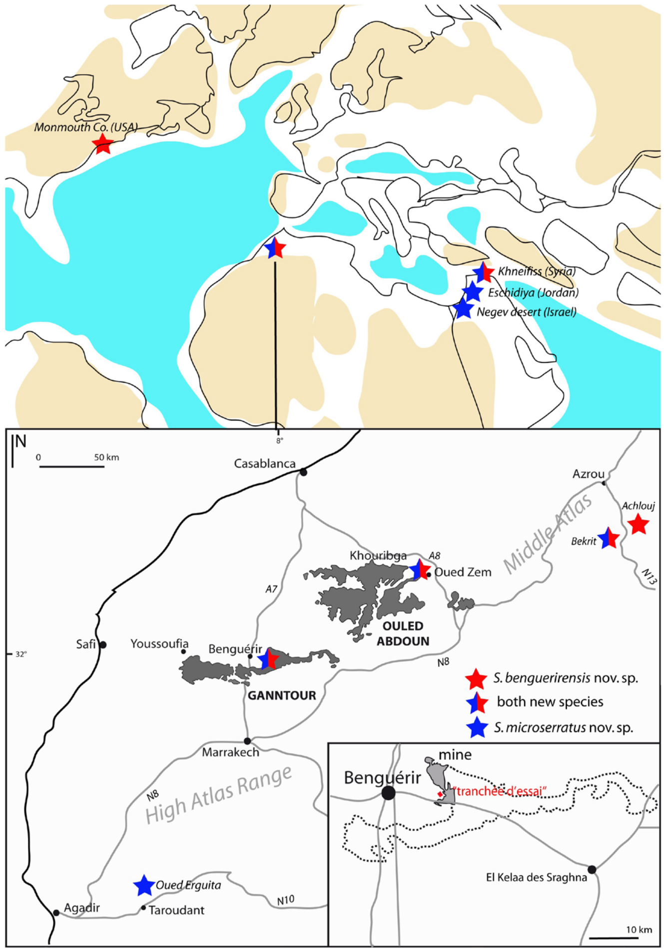

Figure 1. Paleomap of the Maastrichtian tethysan realm with locations of the main fossil deposits where at least one of both *Squalicorax* new species occurs. Enlargement on Moroccan and Benguérir deposits.

the fossiliferous series outcropping in Benguérir ores, particularly its succession of marine vertebrate associations (reptiles, bony fishes and elasmobranchs), clarifying the age of the fossiliferous deposits as being from the Lower Maastrichtian (L6 to L5) to the Upper Maastrichtian (L4 to L2).

Elasmobranch fossil teeth were obtained partly by surface collecting in the trenches, first in the "Tranchée d'essai" (see above), but also in three different areas of the northern zone where the L6 constitutes the bottom of the trenches (GPS coordinates: 32° 18' 15.22" N, 7° 51' 26.67 W; 32° 18' 19.28" N, 7° 50' 44.23 W; 32° 18' 01.93" N, 7° 51' 05.03 W). Teeth were also collected in areas where the different phosphate levels are kept separately in different storage areas by miners, and not mixed (see Cappetta *et al*. 2014 for details). This peculiarity allowed the collection of numerous teeth in these stocks from identified Levels, supplementing the sampling made in the trenches themselves. Hundreds of kilograms of sediment from the different Levels were also sieved, using mesh sizes down to 400 µm. The elasmobranch teeth are by far the most abundant vertebrate fossils at all Levels of the phosphatic series (Cappetta *et al*., 2014). A total of 60 species belonging to 32 genera have been identified in Maastrichtian Levels (Cappetta *et al*., 2014) including five species of the genus *Squalicorax*, one of the most famous Cretaceous anacoracids, showing a worldwide distribution.

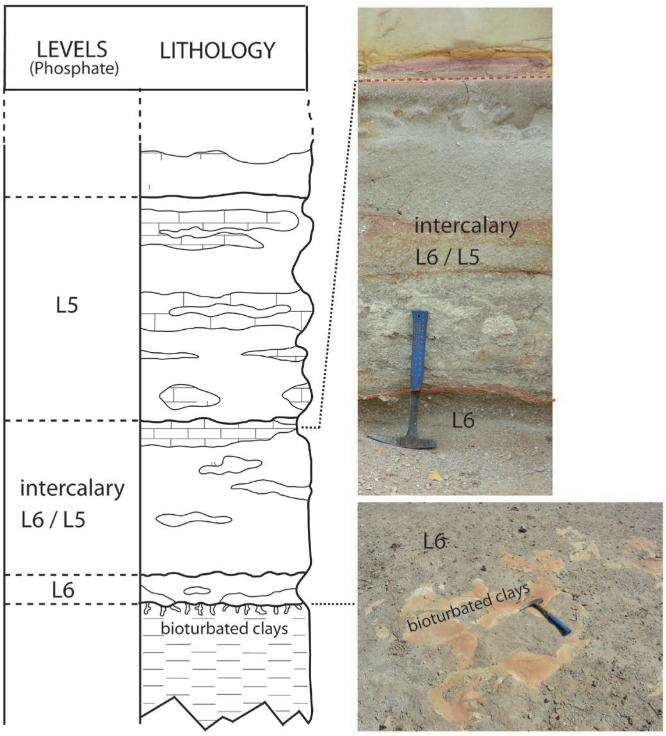

Figure 2. Left, partial composite section of the Maastrichtian phosphatic series East of Benguérir, simplified from Cappetta *et al*., 2014. Right, illustrations of local outcrops (areas of the northern zone) with focusing on L6 and L5.

Beyond the paleobiological interest in better defining the tooth morphology of this genus, interesting variations of its diversity can be observed in the material from Benguérir (Pomes, 2003). In fact, isolated teeth of *Squalicorax* are abundant at all Levels of the Benguérir series, but the L6 (the base of the series) contains the most diverse specific assemblage of this genus, with five coeval species (see Cappetta *et al*., 2014), three of them representing a large portion of the *Squalicorax* specimens, consisting of *S.* aff. *pristodontus* and the two new species presented here. The two other species, *Squalicorax bassanii* and *S. africanus* constitute only a minute part of this assemblage. Thereafter, diversity of *Squalicorax* decreases toward the top of the series (Upper Maastrichtian) where *S. pristodontus* represents almost all *Squalicorax* teeth (99%) in L2 together with *Squalicorax bassanii* (1%).

The present work completes the previous study of Cappetta *et al*. (2014), in describing for the first time the two unnamed species of *Squalicorax* which occur in the Lower and Upper Maastrichtian of the Benguérir deposit.

SYSTEMATIC PALAEONTOLOGY

Systematics and terminology follows Cappetta 1987, 2006 and 2012. All figured teeth with collection number BEG-C6 (for Benguérir - L6) are housed at the University Montpellier 2. Apart from the holotypes of both new species, which come from the "Tranchée d'essai", the other studied specimens come mainly from the northern zone of the deposit and from the stores (see Materials and Methods above, and Cappetta *et al*., 2014).

Order LAMNIFORMES Berg, 1958

Family ANACORACIDAE Casier, 1947

The family includes the genera *Squalicorax* Whitley, 1939, *Ptychocorax* Glikman & Istchenko *in* Glikman, 1980, *Scindocorax* Bourdon, Wright, Lucas, Spielmann & Pence, 2011 and *Nanocorax* Cappetta, 2012. The genera *Pseudocorax* Priem, 1897 and *Galeocorax* Cappetta, 2012, previously assigned to Anacoracidae are currently included in the family Pseudocoracidae Cappetta, 2012.

Genus *Squalicorax* Whitley, 1939

(*Corax* Agassiz, 1835; *Anacorax* White & Moy-Thomas, 1940; *Palaeocorax* Glikman, 1956; *Sinkorax* Whitley, 1965; *Eoanacorax* Glickman & Shvazhaite, 1971; *Palaeoanacorax* Glickman *in* Glikman & Shvazhaite, 1971; *Microanacorax* Glikman, 1980; *Paraanacorax* Glikman, 1980; *Praeptychocorax* Glikman, 1980)

Type species: *Corax pristodontus* Agassiz, 1835; Maastrichtian of Maastricht, The Netherlands.

The genus *Squalicorax*, erected by Whitley (1939) to replace the genus *Corax* Agassiz, 1835, preoccupied by *Corax* Ledru, 1810 (Aves), was split into several distinct genera by Russian authors (Glikman, 1956, 1980; Glikman & Shvazhaite, 1971) based more on their stratigraphic distribution than on well-defined morphological features (see appendix).

The teeth morphologies and sizes occurring among the around forty species of *Squalicorax* strongly vary from one species to another. For instance, the teeth morphology in *S. pawpawensis* Siverson *et al.*, 2007 (upper Albian, Texas) appears very different from that of *S. pristodontus* (Agassiz, 1835) (Maastrichtian, The Netherlands). However, other species have intermediate morphologies that make the transition between these extreme species. This situation is quite similar to what is observed in recent species of the genus *Carcharhinus*, showing extreme teeth morphologies, but with a series of intermediate shapes. In this situation, any splitting of the genus would be completely arbitrary.

Therefore, we will continue to use the genus *Squalicorax* (see Cappetta, 2012), even if the genus *Palaeoanacorax* Glikman *in* Glikman & Shvazhaite, 1971 has been regarded as valid by some authors (Siverson *et al.*, 2007; Underwood & Cumbaa, 2010). More recently, the genus *Scindocorax* was described by Bourdon *et al.*, 2011, for some teeth belonging to a new species (*Sc. novimexicanus*) collected in the Santonian of New Mexico, North America.

Currently, the genus *Squalicorax* includes 53 nominal species ranging from Albian to Maastrichtian. Among these species, several are certainly synonymous but only an overall revision, which greatly exceeds the scope of this current work, would make it possible to discuss in detail these questions of synonymy. A very scarce occurrence of the genus in Cenozoic deposits was sometimes noted (Winkler, 1876; Noetling, 1885; Burris, 1998, 1999; Dutheil, 1996; Eaton *et al.*, 1989) but these occurrences cannot be regarded as reliable reports. In all cases, it is either the result of reworking, or a problem of erroneous labelling in collections, and all the *Squalicorax* representatives disappeared at the end of the Cretaceous (e.g. Kriwet & Benton, 2004).

Squalicorax benguerirensis **nov. sp.**

(Fig. 3 A-J)

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1952 - *Corax yangaensis* Dartevelle & Casier, 1943; Arambourg, p. 116, pl. 21, fig. 1-3.

2000 - *Squalicorax* cf. *yangaensis* Dartevelle & Casier; Bardet *et al*., p. 273, p. 276, fig. 4 k-l.

2014 - *Squalicorax* nov. sp. 2; Cappetta *et al*., p. 227, fig. 7 O-P.

Material: many teeth from the type locality and from the other sampled sites (see above).

Type locality: “Tranchée d’essai” of Benguérir, Ganntour deposit.

Age: Lower Maastrichtian, L6.

Derivatio nominis: from the name of the type locality, Benguérir.

Holotype: BEG-C6.19, fig. 3 D.

Paratypes: fig. 3 B, 3 G, 3 I, 3 J.

Mensurations (in mm): BEG-C6.16 : 15.47 Width, 14.53 Height, 4.22 Thickness; BEG-C6.17: 19.84 W, 17.65 H, 4.19 T; BEG-C6.18: 19.92 W, 18.96 H, 4.65 T; BEG-C6.19: 22.95 W, 18.27 H, 4.45 T; BEG-C6.20: 12.63 W, 9.25 H, 2.63 T; BEG-C6.21: 20.05 W, 16.67 H, 3.33 T; BEG-C6.22: 20.68 W, 15.41 H, 4.26 T; BEG-C6.23: 19.02 W, 12.55 H, 4.16 T; BEG-C6.24: 18.91 W, 13.42 H, 3.86 T; BEG-C6.25: 25.53 W, 20.89 H, 5.91T.

Diagnosis

Species characterized by its rather labio-lingually compressed teeth and being able to reach a relatively large size (up to about 25 mm total width). Cutting edges with strong serrations secondarily serrated; root high; cusp with acute apex less than 90°; distal notch absent on the anterior and antero-lateral teeth but present on lateral and very lateral ones. Presence of a flatness of the root at the site of the lingual protuberance; labial face of the crown with a barely significant basal bulge.

Description

The holotype (fig. 3 D) is an anterolateral tooth. The crown is broad, rather flat and triangular. Its mesial edge is regularly convex; its distal edge is subrectilinear and oblique. There is a very short distal heel separated from the distal edge of the cusp by a very blunt angle. The lingual margin of enameloid, convex as a whole, forms a clear median concavity. The labial face of the crown is slightly convex; the margin of enameloid is concave medially and there is no differentiated basal bulge.

The edges are remarkable due to the presence of secondarily formed strong serrations; one can count 14 mesial serrations and 10 distal ones. The serration of the distal heel is simple.

The root is not thick and broad. Its basal face is flat, especially laterally, more convex medially. It exhibits a very particular character: medially, under the crown, it shows a depressed zone continuing on the base of the crown. On the marginal areas distinct margino-lingual faces are quite distinct from the basal face. The side edges of the root are oblique and divergent in labial (or lingual) view. On the basal face, three circular foramina open, mesially located relative to the center of the tooth.

The labial face of the root is relatively low; it shows many elliptic and vertical foramina aligned under the margin of enameloid, and this over practically the whole width of the face. These foramina determine indentations in the border of the enameloid. The basal notch of the root is broad and not very deep, slightly angular medially.

On a probably upper anterior tooth (fig. 3 J), the cusp is slightly straightened. The mesial cutting edge is very convex just above the contact with the root, which is marked by a distinct notch. In its more apical part, it is rather rectilinear up to the apex of the cusp. The distal cutting edge is initially slightly convex, then is connected to the distal heel by a regular concavity.

The variations observed mainly result from a gradual heterodonty. The lateral teeth (figs. 3 F-H) are relatively less high, with a sharper and more distally bent cusp. The distal edge, initially regularly concave in more anterior teeth, becomes angular, with a distal heel well separated from the cusp. The mesial cutting edge is less convex than in more anterior files, and sometimes almost straight (fig. 3 F). In labial

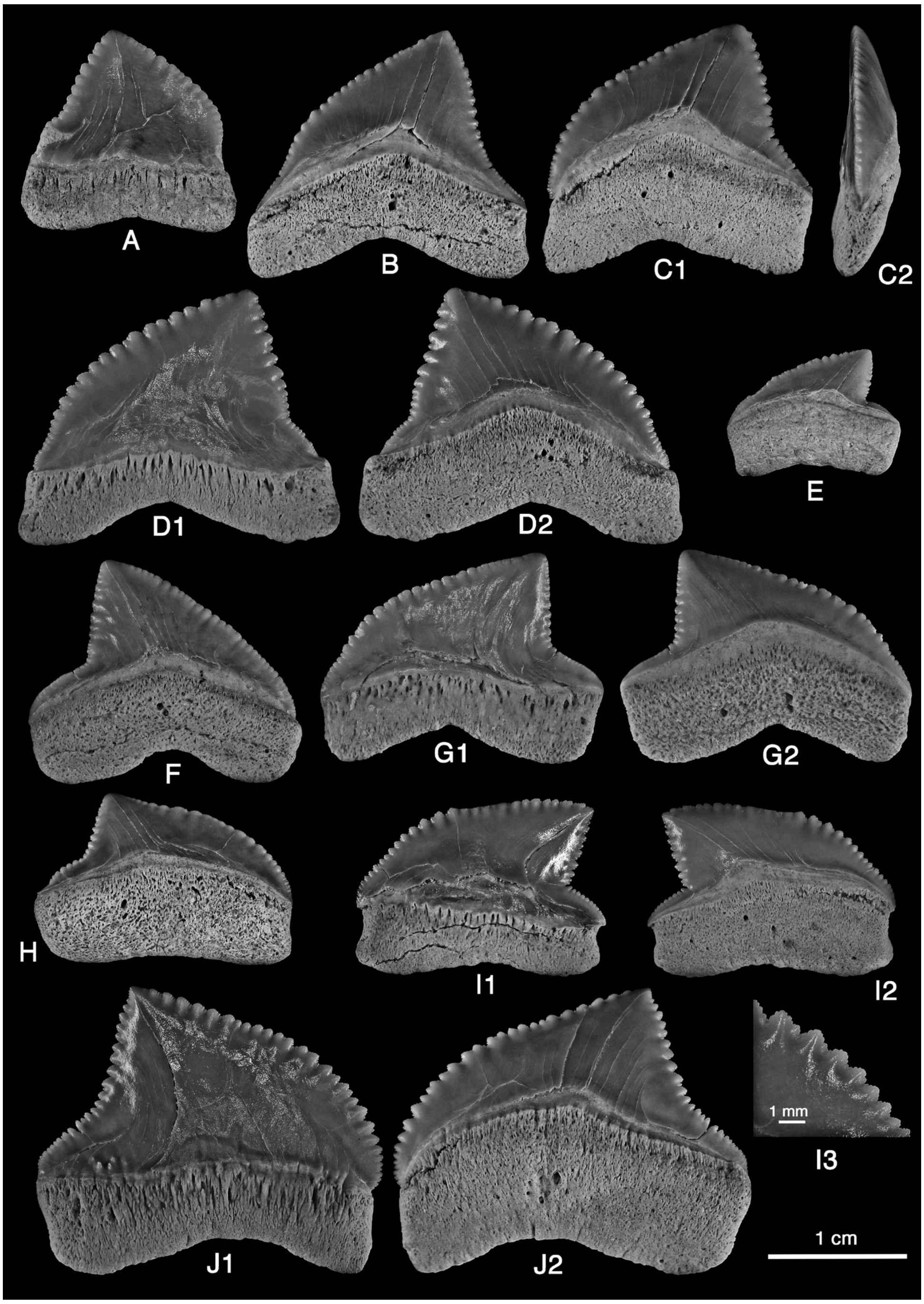

Figure 3. *Squalicorax benguerirensis* nov. sp. **A**, (BEG-C6.16) parasymphyseal tooth, labial view. **B**, (BEG-C6.17), **paratype**, anterior tooth, labial view. **C**, (BEG-C6.18) anterolateral tooth. C1 lingual view. C2 profile. **D**, (BEG-C6.19), **holotype**, anterolateral tooth. D1 labial view. D2 lingual view. **E**, (BEG-C6.20) very lateral tooth, lingual view. **F**, (BEG-C6.21): lateral tooth, lingual view. **G**, (BEG-C6.22), **paratype**, lateral tooth. G1 labial view. G2 lingual view. **H**, (BEG-C6.23) lateral tooth, lingual view. **I**, (BEG-C6.24), **paratype**, very lateral tooth. I1 labial view. I2 lingual view. I3 detail of the mesial edge. **J**, (BEG-C6.25), **paratype**, anterior tooth. J1labial view. J2 lingual view.

view, the basal notch of the root also tends to grow blurred. It can be concave (fig. 3 F) or angular medially (fig. 3 G). The very lateral teeth show a cusp that is strongly bent distally (fig. 3 E, I). The apex of the cusp is also sharper. There is a distal heel well separated from the distal cutting edge of the cusp by a sharp notch. The distal cutting edge of the cusp is slightly convex (fig. 3 E) or straight (fig. 3 I). The edge of the basal face of the root is slightly concave medially.

Discussion

This new species occurs in Morocco only in the lower Levels of the lower Maastrichtian: L6 and L5 of Benguérir (Cappetta *et al*., 2014), lowermost Level with internal moulds of *Roudereia* of Sidi Daoui, to the north of the Oued Zem locality, in the Ouled Abdoun deposit, and in the basal Maastrichtian of the black phosphate deposits of the Bekrit area, in the Middle-Atlas.

This species can reach a rather large size, the largest specimens exceeding 25 mm in total width. The teeth of this species can be immediately distinguished by their double serrated edges. Only another older species, *S. yangaensis* (Dartevelle & Casier, 1943), presents this characteristic. Arambourg (1952) had assigned the teeth from Oued Erguita with this morphology to *S. yangaensis*, a species described after specimens coming from the Upper Cretaceous of Lake Yanga, Enclave of Cabinda, in western Africa. The age of the Lake Yanga series ranges from Santonian to lower Campanian (Taverne, 1970).

In reality, compared to the teeth of *S. benguerirensis*, the typical teeth of *S. yangaensis* are of smaller size and their morphological characteristics are quite different, with, in particular, an always acute cusp, a mesial edge usually gibbous carrying strong irregular serrations and a distal notch always well marked, even on the anterior teeth, separating the distal edge of the cusp from the heel (see Antunes & Cappetta, 2002).

The new species from the Maastrichtian of Morocco thus differs from *S. yangaensis* by its larger size, the absence of a distal notch on the anterior and anterolateral files and by a cusp with a broader apex, especially in the anterior files.

Some teeth from the late Upper Cretaceous of Tumuna (Manha Matadi), Enclave of Cabinda, illustrated by Dartevelle and Casier (1959, pl. 24, fig. 10-12), are completely comparable with the specimens from Lake Yanga and correspond well to the morphology of *S. yangaensis*. This is the same for some specimens from the Santonian to lower Campanian of Angola, collected south of the Zaire river and illustrated by Antunes & Cappetta (2002). Glikman (1980) chose the species *yangaensis* as the type-species of his genus *Microanacorax*. In Morocco, apart from the phosphatic deposits of the Méséta, a single specimen of the new species *benguerirensis* was encountered at the base of the phosphatic series of the Oudiksou syncline, and other specimens were collected from the base of the phosphatic Maastrichtian series of Bekrit (Middle-Atlas). However, it was never collected from the lowermost Levels of the Maastrichtian series of Oued Erguita, north of Taroudant, south of the High-Atlas. It is also present in the lower Maastrichtian phosphates of Syria, particularly in the mine of Khneifiss (Bardet *et al*., 2000). Two *Squalicorax* teeth with double serrated cutting edges were illustrated by Schwimmer *et al*., 1997 (as *S. kaupi*), one from the Early Campanian (lower Bluffton Fm.), Russell Co., Alabama, and another one from the middle Campanian (upper Bluffton Fm.), Stewart Co., Georgia, USA. However, these teeth have a general morphology close to that of *S. bassanii*, very different from that of *S. benguerirensis* nov. sp. A single tooth from the Early Maastrichtian of Monmouth Co., New Jersey, described as *Squalicorax* sp. (see Case & Cappetta, 2004, pl. 3, fig. 2 a-b) exhibits a mesial cutting edge with a double serration, very similar to the condition observed in *S. benguerirensis*. However, as the distal cutting edge of this tooth only has single serrations, its inclusion in the latter species remains hypothetical.

***Squalicorax microserratus* nov. sp.**

(Fig. 4 A-J)

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1952 - *Corax kaupi* Agassiz, 1835; Arambourg, p. 113, pl. 20, fig. 18-23, 25-26 (non 11-17, 24).

2014 - *Squalicorax* nov. sp. 1; Cappetta *et al*., p. 227, fig. 7 M-N.

Material: many teeth from the type locality and from the other sampled sites (see above).

Type locality: “Tranchée d’essai” of Benguérir, Ganntour deposit.

Age: lower Maastrichtian, L6.

Derivatio nominis: species so named because of the very fine and regular serrations of the cutting edges.

Holotype: BEG-C6.33, fig. 4 H.

Paratypes: figs. 4 B, 4 F, 4 J.

Mensurations (in mm): BEG-C6.26: 17.54 Width, 15.72 Height, 6.35 Thickness; BEG-C6.27: 15.92 W, 15.24 H, 5.52 T; BEG-C6.28: 17.23 W, 15.17 H, 5.37 T; BEG-C6.29: 20.48 W, 14.99 H, 4.55 T; BEG-C6.30: 18.61 W, 15.09 H, 4.61 T; BEG-C6.31: 17.97 W, 12.24 H, 4.17 T; BEG-C6.32: 16.90 W, 11.64 H, 3.89 T.

Diagnosis

Species with thick teeth that can reach up to about 20 mm in total width, characterized by regularly and very finely serrated cutting edges. The mesial cutting edge is long and slightly convex, while the distal one is much shorter, straight or slightly concave; there is a short and low distal heel separated from the distal cutting edge by a notch making an angle of more than 90°, except in anterior and anterolateral teeth that lack a notch. The labial face of the crown is flat, without a transverse bulge at its base; lingual face moderately convex. Bulky root with an overall rectangular outline, with a small marked median concavity. Marginal edges of the root straight or more often with a concave notch more marked mesially.

Description

The holotype is a tooth broader than high of probably lower anterior position (fig. 4 H). The cusp is triangular, rather erect, with an acute apex. The mesial cutting edge is very oblique and slightly convex. It is formed by fine and regular simple serrations throughout its length.

The distal edge of the cusp is rectilinear and practically vertical. There is a short, convex, and relatively low distal heel.

The junction is via a rather sharp notch. The distal edge, as with the heel, is formed by fine and regular serrations. The lingual margin of enameloid is well marked and regularly convex. The lingual face of the crown is very convex tranversely and its labial face is practically flat; its lower edge is subrectilinear, slightly concave medially, without a differentiated bulge.

The root is high, rectangular on the whole. Its basal face is very developed and higher than the crown in lingual view. The lobes are almost symmetrical. The distal margin is subvertical, slightly concave; the mesial margin is clearly concave. The basal notch is neither very deep nor very broad. The labial face of the root is also well developed and flat. Under the limit of enameloid one observes more or less aligned and irregularly spaced elliptic foramina.

A more anterior tooth (fig. 4 B) is relatively higher. Its mesial cutting edge is more convex, the distal heel is longer and the notch separating it from the distal edge of the cusp is very blunt. In mesial profile view (fig. 4 B2), the crown is slightly sigmoidal at the level of the cusp.

In more anterior files, the root is comparatively thicker than

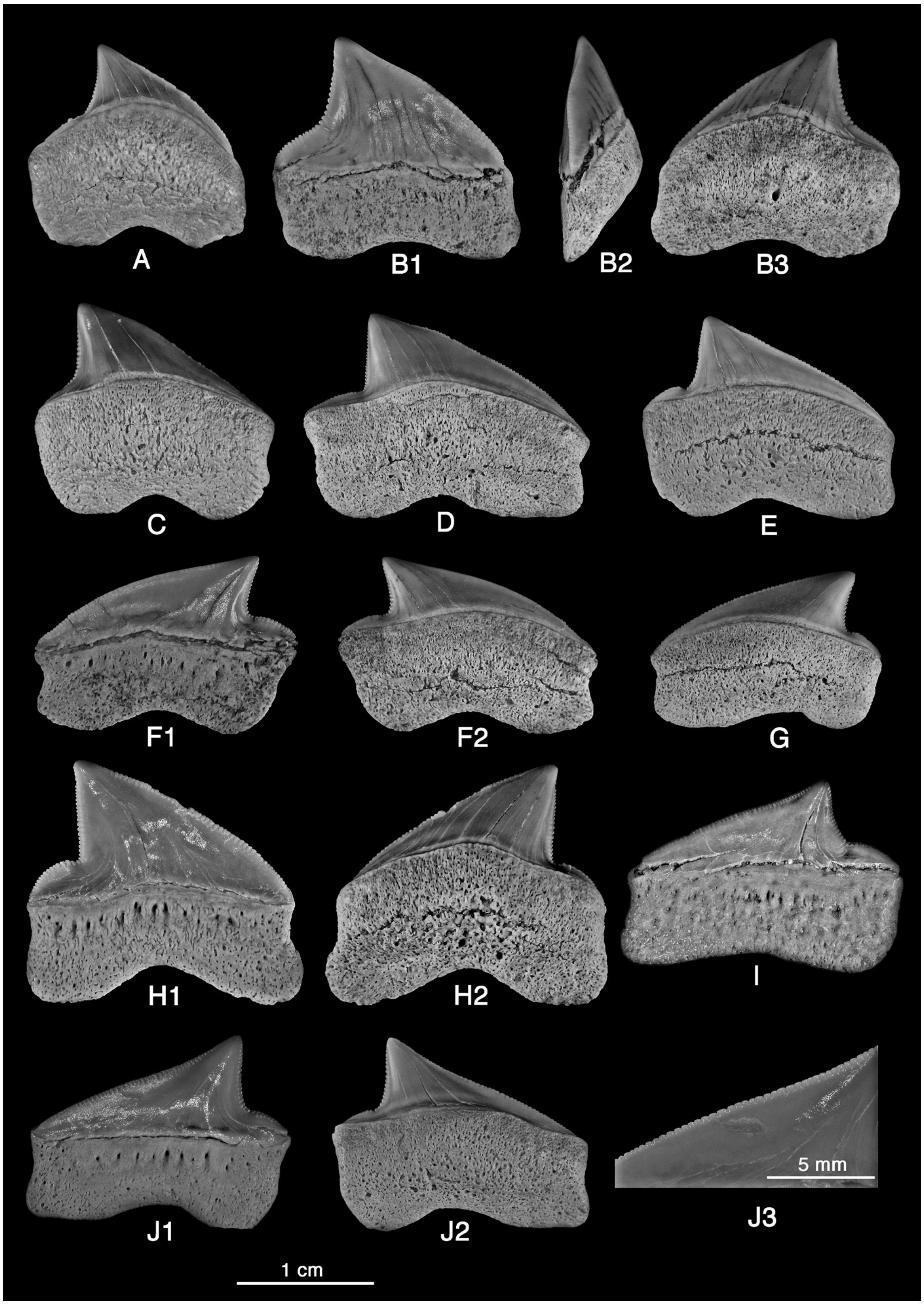

Figure 4. *Squalicorax microserratus* nov. sp. **A**, (BEG-C6.26) anterior tooth. **B**. (BEG-C6.27), **paratype**, anterior tooth. B1 labial view. B2 profile. B3 lingual view. **C**, (BEG-C6.28) anterior tooth, lingual view. **D**, (BEG-C61.29) lateral tooth, lingual view. **E**, (BEG-C6.30) lateral tooth, lingual view. **F**, (BEG-C6.31), **paratype**, lateral tooth. F1 labial view. F2 lingual view. **G**, (BEG-C6.32) lateral tooth, lingual view. **H**, (BEG-C6.33), **holotype**, anterolateral tooth. H1 labial view. H2 lingual view. **I**, (BEG-C6.34) lateral tooth, labial view. **J**, (BEG-C6.35), **paratype**, lateral tooth. J1 labial view. J2 lingual view. J3 detail of the mesial edge, labial view.

in lateral files, with a very convex basal face (fig. 4 A).

In the lateral files (fig. 4 D-G), the teeth are transversely elongated but the cusp maintains a rather constant slope. The mesial cutting edge is slightly convex, the distal one is rectilinear to slightly concave. The distal heel is well individualized but relatively low. The notch of the distal margin of the root is either regularly concave (fig. 4 F), or angular (fig. 4 D), blunt (fig. 4 G, I-J) with a well detached heel differentiating even a kind of cusplet close to the notch (fig. 4 E, G).

The root, always thick, tends to have a trapezoid outline, with oblique and clearly concave margins. The basal notch is rather lightly marked. The mesial lobe is often longer and narrower than the distal one and, in general, the root is slightly higher distally. In the very lateral teeth, probably lower, the crown is low but the cusp remains always relatively straight (fig. 4 I-J), the root becoming almost rectangular and very thick.

Discussion

This species is immediately distinguishable from the other contemporaneous species of *Squalicorax* occurring in the same layer by its teeth with a crown of relatively low development, especially in lingual view, with a rather acute cusp and especially by a high, thick root with a rectangular to trapezoidal contour, with, generally, well marked marginal notches. Its teeth also have cutting edges with fine and regular serrations, which easily separates them from the teeth of *S. pristodontus*, which shows much more developed serrations of irregular size, especially on the mesial edge.

Another species, *S. coquandi* Vullo *et al*., 2007, from the Turonian of western France, shows a very similar serration on the cutting edges. However, this species reaches a larger size (up to about 23.5 mm width) than *S. microserratus* nov. sp. and its cusp is more acute and elongated, compared to *S. microserratus* nov. sp. Moreover, the root of *S. coquandi* is less high and thinner than in *S. microserratus* nov. sp..

Arambourg has illustrated teeth of *S. microserratus* nov. sp. from the lower Maastrichtian of Oued Erguita (1952, pl. 20, fig. 18-23, 25-26), but he associated them with anterior teeth, which he named *S. kaupi*, interpreting them as lateral teeth of this last species. The teeth he named *S. kaupi* correspond in reality to teeth of the species *S. bassanii* Gemmellaro, 1920, for a long time considered to be a synonym of *S. kaupi*, but the morphology of which, quite particular and characteristic, makes this species perfectly valid. The assumption of Arambourg, associating this type of teeth with teeth of *S. bassanii* was not to be rejected *a priori* and could appear as logical until new sampling by the senior author in the lower Maastrichtian of Jordan (unpubl. data). The associations of Jordanian Anacoracidae allow the rejection of this assumption. Indeed, in Level A3 (basal Maastrichtian) of the Eshidiya phosphate mine (Jallad *et al*., 1989; Prabhulingaiah *et al*., 2014), teeth of *S. bassanii* are abundant, and even dominant, whereas the teeth with a *S. microserratus* nov. sp. morphology are extremely rare; these last teeth cannot thus correspond to lateral teeth of *S. bassanii*. In L6 of Benguérir, Morocco, on the other hand, the teeth of *S. microserratus* nov. sp. nov. sp. are frequent whereas those of *S. bassanii* are much scarcer. These observations constitute an additional argument for considering the teeth of *S. bassanii* and *S. microserratus* nov. sp. as representing distinct species. It must also be added that the new species *S. microserratus* nov. sp. is represented by teeth from different positions in the mouth, confirming that it does not correspond to a component of the dentition of another species.

S. microserratus nov. sp. is a widespread species. Besides Morocco, it occurs in the lower Maastrichtian of Syria and Jordan where it remains rare, as in the lower Maastrichtian of the Negev desert, Israel (HC, unpubl. data). In terms of its stratigraphical range, this species is particularly abundant at the base of the Maastrichtian of Benguérir (L6); higher in the series, it becomes much scarcer and disappears completely after L2, corresponding to the upper Maastrichtian.

CONCLUSIONS

The genus *Squalicorax* currently includes more than fifty nominal species, of which about thirty (the exact number varies according to the authors consulted) can be regarded as valid. Even if the phyletic relationships between species of the genus are much more complex than was accepted some years ago, several general evolutionary trends can be identified within the genus *Squalicorax* (*sensu* Cappetta, 2012). A clear increase in tooth size can be noted as the most general evolutionary trend in the genus *Squalicorax*. Besides that, one can observe an increasingly blunt apical angle, a gradually decreasing distal heel in relation to the cusp, with the disappearance of the notch separating the heel from the distal cutting edge of the cusp, a progressive enlargement and a more and more marked labio-lingual flattening, a greater development of the basal face of the root, and finally an increasing emphasis of the serration of the cutting edges. A very specialized cutting-grinding type dentition occurs in *Ptychocorax*, with anterior teeth of a classical *Squalicorax* morphology and with grinding-type, apically flattened lateral teeth, differentiating strong folds at the surface of the crown.

It was generally accepted that *Squalicorax* represents a homogeneous group with a “lineage”, already cited by Leriche (1929, p. 222; *S. falcatus* - *S. kaupi* - *S. pristodontus*) showing the evolutionary trends cited above. In the light of the numerous species described over the last decades, it seems that the evolution of this “lineage”, and more generally of the genus *Squalicorax*, is much more complex than previously conceived. Indeed, one does not observe a simple anagenetic evolution from one species to another, but a co-existence of supposed ancestral species with more derived species. For instance, one can note the simultaneous occurrence of *S. kaupi* and *S. pristodontus* in many localities (Cappetta & Case 1975). Some species also exhibit a mosaic of primitive and derived characters as in *S. africanus* Cappetta 1991 (a very small size, a significant bulge at the base of the labial face of the crown, and a strong labio-lingual flattening of the teeth). Only a broad review of all species will permit a better understanding of their interrelationships. In some lineages, a secondary serration superimposed on the main serration may appear in *S. yangaensis* and *S. benguerirensis* nov. sp., as in the Pliocene and Recent *Galeocerdo*. The small-sized teeth genera *Nanocorax* and *Scindocorax* still remain poorly known, but they are probably related to the lower Cretaceous stock, from which *Squalicorax* evolved.

The family shows a very clear morphological convergence regarding the dentition, as it can be reconstructed as well as teeth morphologies, with the Carcharhinidae: the dentition of *Squalicorax* is reminiscent of some *Carcharhinus*, at least for the upper teeth; the dentition of *S. yangaensis* is very close to that of the Recent *Galeocerdo cuvier* with double serrated teeth. Such similarities probably result from a similar way of life and identical or at least very similar trophic practices that led to similar dental adaptations. The occurrence of this double serration in different teeth morphologies corresponding to different *Squalicorax* lineages (*S. yangaensis*- *S. benguerirensis* nov. sp. on one side, and *Squalicorax* sp. as figured by Schwimmer *et al*., 1997) indicates that this derived feature appeared independently in different *Squalicorax* lineages.

The anacoracid assemblages vary significantly between the Albian and the Maastrichtian. At the generic level, only the genus *Squalicorax* occurs between the Albian and the Turonian. Thereafter, the number of genera increases, with three genera in the Coniacian (*Squalicorax*, *Ptychocorax* and *Nanocorax*) and four in the Santonian (*Squalicorax*, *Ptychocorax*, *Nanocorax* and *Scindocorax*). After this peak of diversity, their numbers decrease, with three genera in the Campanian (*Squalicorax*, *Ptychocorax* and *Nanocorax*) and only *Squalicorax* in the Maastrichtian.

At the level of the specific assemblages, the curve follows approximately that of the genera. One can note a clear increase in species number between the Albian (four) and the Cenomanian (seven). There is then a small decrease in the Turonian and the Coniacian (six) before an important peak during the Santonian (eleven). After that their number decreases again in the Campanian (ten) and mainly in the Maastrichtian (seven).

Finally, this study allows an extension of the faunal list, already long, of the fossil selachians of Morocco (Noubhani & Cappetta, 1997). The family of Anacoracidae is thus enriched by two new species: *Squalicorax benguerirensis* nov. sp. and *S. microserratus* nov. sp.

These two new species had already been observed by Arambourg (1952), but this author did not recognize their distinctiveness, instead assigning them to already known species, one to *S. yangaensis*, the other one regarded as being the lateral teeth of a species he named *S. kaupi*, and representing, in reality, teeth of a different species, *S. bassanii*.

This study highlights the great diversity of Anacoracidae in the Maastrichtian, at the end of which the family completely disappears. In Benguérir, L6 shows a maximum of *Squalicorax* diversity with the coexistence of five distinct species (*S. africanus*, *S. bassanii*, *S. benguerirensis* nov. sp., *S. microserratus* nov. sp. and *S.* cf. *pristodontus*). However, this diversity decreases rapidly, as one can note when ascending the stratigraphic sequence, and, in the upper Maastrichtian Level of Benguérir (L2), only *S. pristodontus* and *S. bassanii* are present, but only in very low numbers for this last species. Even *S.* cf. *pristodontus*, abundant in the lower Levels of the series (L5 to L3) becomes much scarcer, compared with other Lamniformes like *Cretolamna maroccana*. One can thus perceive a progressive, but relatively rapid, reduction of the diversity of the genus prior to its total extinction at the K/Pg boundary.

A concurrence with other apex predators belonging to Lamniformes can be invoked to explain the rapid decrease of *Squalicorax* in the successive faunal associations of Benguérir. Indeed, at the base of the Maastrichtian (L6), the teeth of *Squalicorax* are highly abundant, whereas teeth of other lamniforms, for instance *Cretolamna*, are much scarcer and smaller. Higher in the series (L4 and L3), the teeth of *Cretolamna maroccana* become abundant and their large size is indicative of large sharks that could compete with the genus *Squalicorax*. In L2, *Squalicorax* appears to be declining, as evidenced by their smaller number compared to that of *Cretolamna.* In the same Level, *Serratolamna serrata* becomes abundant, compounding the competitive pressure of *Cretolamna*. However, it should be noted that important morphological differences in the dentitions of *Squalicorax* and *Cretolamna* could be indicative of prey partitioning decreasing the food competition, therefore not a direct cause of *Squalicorax* extinction.

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APPENDIX

List of nominal Anacoracidae genera

Anacorax White & Moy-Thomas, 1940.
Type species: *Corax* (as *Galeus*) *pristodontus* Agassiz, 1835: Maastrichtian; Maastricht, The Netherlands. A type species was not explicitely designed by White & Moy-Thomas; yet, *pristodontus* is considered as the type species of the genus *Corax* Agassiz, 1835. [Syn. of *Squalicorax* Whitley, 1939].

Corax Agassiz, 1835.
Type species: *Corax* (as *Galeus*) *pristodontus* Agassiz, 1835: Maastrichtian; Maastricht, The Netherlands. Name preoccupied by *Corax* Ledru, 1810 (Aves). [Syn. of *Squalicorax* Whitley, 1939].

Eoanacorax Glikman & Shvazhaite, 1971: p. 186.
Type species: *Eoanacorax dalinkevichiusi* Glikman & Shvazhaite, 1971: lower Cenomanian; Jiesia Series, close to Vareikiai, Lithuania. [Syn. of *Squalicorax* Whitley, 1939].

Hermanodus Landemaine, 1991.
Type species: *Acrodus* (*Palaeobates*) *dolloi* Leriche, 1911 (figured by Leriche in 1929): Upper Santonian; Lonzée, Namur Province, Belgium. [Syn. of *Ptychocorax* Glikman & Istchenko *in* Glikman, 1980].

Microanacorax Glikman, 1980.
Type species: *Corax yangaensis* Dartevelle & Casier, 1943: Senonian (probably Santonian or Campanian); Yanga Lake, Enclave of Cabinda, western Africa. [Syn. of *Squalicorax* Whitley, 1939].

Microcorax Cappetta & Case, 1975.
Type species: *Microcorax crassus* Cappetta & Case, 1975: Cenomanian (Woodbine Fm., Lower Arlington Sandstone Member); Amon Carter Airfield, Tarrant Co., Texas, U.S.A. [Syn. of *Nanocorax* Cappetta, 2012].

Nanocorax Cappetta, 2012: p. 246. (= *Microcorax* Cappetta & Case, 1975).
Type species: *Microcorax crassus* Cappetta & Case, 1975. Cenomanian (Woodbine Fm., Lower Arlington Sandstone Member); Amon Carter Airfield, Tarrant Co., Texas, U.S.A. *Nanocorax* Cappetta, 2012 replaces *Microcorax* Cappetta & Case, 1975, junior synonym of *Microcorax* Sharpe, 1877, a corvid genus.

Palaeoanacorax Glikman *in* Glikman & Shvazhaite, 1971.
Type species: *Palaeoanacorax volgensis* Glikman, 1971. Middle Cenomanian; Nizhnaya Bannovka village, Saratov Province, Russia. [Syn. of the genus *Squalicorax* Whitley, 1939].

Palaeocorax Glikman, 1956.
Type species: *Corax falcatus* Agassiz, 1835: Upper Cretaceous (White Chalk); Near Brighton, Kent and Sussex, Great Britain; Pläner de Strehlen, close to Dresde; Quedlimbourg, Germany. *Palaeocorax* Glikman, 1956 is preoccupied by *Palaeocorax* Forbes, 1892 (Aves). [Syn. of *Squalicorax* Whitley, 1939].

Paraanacorax Glikman, 1980.
Type species: *Corax bassanii* Gemmellaro, 1920: Campanian -Maastrichtian; Sciarauna-el-Ghibli, Gebel Duwi, Gebel Nakheil, Egypte. *Paraanacoras* by misprint. [Syn. of *Squalicorax* Whitley, 1939].

Phychocorax Glikman & Istchenko *in* Glikman, 1980.
Type species: *Acrodus (Palaeobates) dolloi* Leriche, 1911: Santonian; "Glauconie de Lonzée", Belgium. [Syn. of *Ptychocorax* Glikman & Istchenko *in* Glikman, 1980 (misprint)].

Praeptychocorax Glikman, 1980.
Type species: *Corax curvatus* Williston, 1900b: Cenomanian (Benton Fm.); Ellsworth Co., Kansas, U.S.A. [Syn. of *Squalicorax* Whitley, 1939].

Ptachocorax Glikman & Istchenko *in* Glikman, 1980.
Type species: *Acrodus* (*Palaeobates*) *dolloi* Leriche, 1911: Upper Santonian; Lonzée, Namur Province, Belgium. [Syn. of *Ptychocorax* Glikman & Istchenko *in* Glikman, 1980 (misprint)].

Ptychocorax Glikman & Istchenko *in* Glikman, 1980.
(= *Phychocorax* Glikman & Istchenko *in* Glikman, 1980; = *Ptachocorax* Glikman & Istchenko *in* Glikman, 1980; = *Hermanodus* Landemaine, 1991.
Type species: *Acrodus* (*Palaeobates*) *dolloi* Leriche, 1911: Upper Santonian; Lonzée, Namur Province, Belgium.

Scindocorax Bourdon, Wright, Lucas, Spielmann & Pence, 2011.
Type species: *Scindocorax novimexicanus* Bourdon, Wright, Lucas, Spielmann & Pence, 2011. Santonian (Hosta Tongue Mb. of the Point Lookout Sandstone); NMMNH locality 297, Bernalillo Co., New Mexico, U.S.A., North America.

Sinkorax Whitley, 1965.
Type species: *Corax falcatus* Agassiz, 1835: Upper Cretaceous (White Chalk); near Brighton, Kent and Sussex, Great Britain; Pläner of Strehla, close to Dresde; Quedlimbourg, Germany. Replaces *Palaeocorax* Glikman, 1956, preoccupied by *Palaeocorax* Forbes, 1892 (Aves). [Syn. of *Squalicorax* Whitley, 1939].

Squalicorax Whitley, 1939.
(= *Corax* Agassiz, 1835; = *Anacorax* White & Moy-Thomas, 1940; = *Palaeocorax* Glikman, 1956; = *Sinkorax* Whitley, 1965; = *Eoanacorax* Glikman & Shvazhaite, 1971; = *Palaeoanacorax* Glikman *in* Glikman & Shvazhaite, 1971; = *Microanacorax* Glikman, 1980; = *Paraanacorax* Glikman, 1980; = *Praeptychocorax* Glikman, 1980).
Type species: *Corax pristodontus* Agassiz, 1835: Maastrichtian; Maastricht, The Netherlands.

List of nominal Anacoracidae species

This list does not take in consideration the problems of species synonymies, which are outside of the framework of the present work.

africanus (*Squalicorax*) Cappetta, 1991: p. 20, pl. 1, fig. 1-7; lower Maastrichtian, Abu Ahmed Mine, Bed 3, Mohamed Rabah area, region of Safaga, Egypt.

antiquus (*Squalicorax*) (Eudes-Deslongchamps, 1877): *Corax*; p. 4, pl. 1, fig. 4-5; Jurassic (Lower Oolithe), Normandy, France. The occurrence of the genus *Squalicorax* in Jurassic is doubtful and unlikely.

arnaudi (*Squalicorax*) (Coquand, 1860): *Oxyrhina*; p. 133 (no figuration); Santonian, Lavie, close to Cognac, Charente, southwestern France.

aulaticus (*Ptychocorax*) Glikman & Istchenko *in* Glikman, 1980: *Ptachocorax* (*sic*); p. 104, pl. 13, fig. 19, 20, 23; see Nessov *et al.*, 1994.

baharijensis (*Squalicorax*) (Stromer, 1927): *Corax*; p. 5, pl. 1, fig. 25-27; upper Cenomanian, 500 m west of Gebel Maghrafe, Bahariya, Egypt.

bassanii (*Squalicorax*) (Gemmellaro, 1920): *Corax*; p. 182, pl. 2, fig. 4-19; Campanian-Maastrichtian, Sciarauna-el-Ghibli, Gebel Duwi, Gebel Nakheil, Egypt. (Type species of the genus *Paraanacorax* Glikman, 1980).

bernardezi (*Squalicorax*) Guinot, Underwood, Cappetta & Ward, 2013: p. 629, p. 627, fig. X-F'. Middle Turonian (*T. lata* Zone), Justine-Herbigny, Ardennes, France.

boreaui (*Squalicorax*) (Coquand, 1860): *Corax*; p. 134 (no figuration); Santonian, Toutblanc, close to Cognac, Charente-Maritime, southwestern France.

coquandi (*Squalicorax*) Vullo, Cappetta & Neraudeau, 2007: p. 105, p. 103, fig. 2. Lower Turonian (lower part of Unité T1m), Port-des-Barques, Charente-Maritime, southwestern France.

crassidens (*Squalicorax*) (Cope, 1872): *Galeocerdo*; p. 355 (no figuration. Types figured by Hussakof, 1908, p. 30, fig. 6); Upper Cretaceous (Niobrara Chalk), Smoky Hill River, Kansas, U.S.A.

crassus (*Microcorax*) Cappetta & Case, 1975: p. 304, p. 305, fig. 2; upper Cenomanian (Woodbine Fm., Lower Arlington Sandstone Member), Amon Carter Airfield, Tarrant Co., Texas, U.S.A. (Type species of the genera *Microcorax* Cappetta & Case, 1975 and *Nanocorax* Cappetta, 2012).

curvatus (*Squalicorax*) (Williston, 1900b): *Corax*; p. 41, pl. 12, fig. 7-8; Cenomanian (Benton Fm.), Ellsworth Co., Kansas, U.S.A. (Type species of the genus *Praeptychocorax* Glikman, 1980).

dalinkeviciusi (*Squalicorax*) (Glikman & Shvazhaite, 1971): *Eoanacorax*; p. 186, pl. 1, fig. 1-4; lower Cenomanian, Jiesia Series, close to Vareikiai, Lithuania. (Type species of the genus *Eoanacorax* Glikman & Shvazhaite, 1971).

dolloi (*Ptychocorax*) (Leriche, 1911): *Acrodus* (*Palaeobates*); p. 7 (name only; figured by Leriche, 1929, p. 228, fig. 6-7) Upper Santonian, Lonzée, Namur Province, Belgium. [Type species of the genus *Ptychocorax* Glikman & Istchenko *in* Glikman, 1980 (= *Phychocorax* Glikman & Istchenko *in* Glikman, 1980, *Ptachocorax* Glikman & Istchenko *in* Glikman, 1980 (misprints) and *Hermanodus* Landemaine, 1991].

dubius (*Squalicorax*) (Noetling, 1885): *Galeocerdo*; p. 97, pl. 5, fig. 6a-c; Zone A1, Samland, Enclave of Kaliningrad, Russia. Cretaceous teeth reworked in the Tertiary.

elongatus (*Squalicorax*) (Coquand, 1860): *Corax*; p. 97 (no figuration); Turonian (= Carentonian), Sillac, near Angoulême, Charente-Maritime, southwestern France.

falcatus (*Squalicorax*) (Agassiz, 1835): *Corax*; p. 226, pl. 26, fig. 14, pl. 26a, fig. 1-15 (as *Galeus pristodontus*); Upper Cretaceous (White Chalk), Near Brighton, Kent and Sussex, Great Britain; Pläner of Strehla, close to Dresde; Quedlimbourg, Germany. (Type species of the genera *Palaeocorax* Glikman, 1956 and *Sinkorax* Whitley, 1965).

falcatus/praecursor (*Squalicorax*) (Sokolov, 1978): *Palaeoanacorax*; Albien supérieur (Vraconien), east of Mangyshlak, western Kazakhstan, central Asia.

gutierrezmarcoi (*Squalicorax*) Bernardez, 2002: p. 282, pl. 39. Upper Cenomanian, Cab-1, Asturias, northwestern Spain. Species described in an unpublished PhD thesis (Univ. of Oviédo, Spain); *nomen nudum*.

hartwellii (*Squalicorax*) (Cope, 1872): *Galeocerdo*; p. 355 (no figuration); Upper Cretaceous (Niobrara Chalk), Smoky Hill River, Kansas, U.S.A. Type figured by Hussakof, 1908, p. 30, fig. 6.

heterodon (*Squalicorax*) (Reuss, 1845): *Corax*; p. 3, pl. 3, fig. 49-71; Upper Cretaceous, Bohemia, Czech Republic.

hybodontoides (*Ptychocorax*) Glikman, 1980: p. 104, pl. 13, fig. 24, 27; Campanian, Lake Sultansandjar, Uzbekistan, Central Asia.

incisus (*Squalicorax*) (Egerton, 1844): *Corax*; p. 168; Upper Cretaceous, Pondicherry, India.

intermedius (*Squalicorax*) (Glikman, 1971): *Palaeoanacorax*; p. 189, pl. 1, fig. 13-14; upper Turonian, Aksyrtau Mountain, Mangyshlak, western Kazakhstan, Central Asia.

kaupi (*Squalicorax*) (Agassiz, 1835): *Corax*; p. 225, pl. 26, fig. 4-8, pl. 26a, fig. 25-34; Upper Cretaceous, Aachen and Haldem, Germany. Species name spelled *kaupii* in the original publication.

kugleri (*Squalicorax*) (Leriche, 1938): *Corax*; p. 25, pl. 4, fig. 8-8'; Maastrichtian, ossiferous glauconite of Vista Bella, Isle of Trinidad, West Indies.

laevis (*Squalicorax*) Giebel, 1848: p. 371 (name only; no figuration); Turonian, Quedlinburg, Sachsen-Anhalt, northern Germany.

lindstromi (*Squalicorax*) (Davis, 1890): *Corax*; p. 412, pl. 42, fig. 3-11; Upper Cretaceous, Oppmanna and Ignaberga, Scanie, Sweden.

maretsensis (*Squalicorax*) (Winkler, 1876): *Galeocerdo*; p. 10, pl. 1, fig. 10-12. Selandian (= Heersian), Maret, Orp-le-Grand, Belgium. This species is based on fragments of *Squalicorax* teeth reworked from Cretaceous deposits. Species to reject.

maximus (*Squalicorax*) (Dixon, 1850): *Corax*; p. 366, pl. 30, fig. 17; Upper Cretaceous, Houghton, Great Britain.

microserratodon (*Nanocorax*) (Shimada, 2008): *Squalicorax*; p. 1189, fig. 1, p. 1190, fig. 2, p. 1191, fig. 3, p. 1192, fig. 4D. Upper Coniacian (Smoky Hill Chalk Mb., Niobrara Chalk). No precise locality; southwest of Trego Co., Kansas, USA. The type specimen is a part of dentition with 18 teeth.

minor (*Squalicorax*) (Giebel, 1847): *Carcharodon*; p. 349 (name only, no figuration); Maastrichtien, Maastricht, The Netherlands.

mississippiensis (*Squalicorax*) (Sokolov, 1978): *Anacorax*; p. 28 (see *Galeocerdo falcatus* Leidy, 1873, p. 301-302, pl. 18, fig. 32-37); upper Santonian - lower Campanian (Columbus Fm.), Mississippi, U.S.A.

novimexicanus (*Scindocorax*) Bourdon, Wright, Lucas, Spielmann & Pence, 2011: p. 11, p. 13, fig. 7, p. 14, fig. 8. Santonian (Hosta Tongue Mb. of the Point Lookout Sandstone), NMMNH locality 297, Bernalillo Co., New Mexico, U.S.A. [Type-species of the genus *Scindocorax* Bourdon, Wright, Lucas, Spielmann & Pence, 2011].

obliquus (*Squalicorax*) (Reuss, 1845): *Corax*; p. 4, pl. 4, fig. 1-3; Turonian, Bohêmia, Czech Republic.

obliquus/subserratus (*Squalicorax*) (Glikman, 1980): *Palaeoanacorax*; p. 99 [see *Palaeocorax falcatus*, Glikman, 1964, p. 76, pl. 3, fig. 7; cited *in* Zhelezko (1997, p. 9); see Mertiniene, 1978 (p. 143)]; upper Cenomanian, Saratov, Russia.

obruchevi (*Squalicorax*) (Glikman, 1980): *Paraanacroax* (*sic*); p. 102, pl. 30, fig. 13-19 (see *Anacorax kaupi*, Glikman, 1964, pl. 3, fig. 1-3); Campanian, Alymtau Mountain, southern Kazakhstan, central Asia.

pamiricus (*Squalicorax*) (Glikman *in* Glikman & Shvazaite, 1971): *Palaeoanacorax*; p. 188, pl. 1, fig. 11-12; Turonian, Tadjikistan, central Asia. The type specimens are two indeterminable fragmentary crown.

papulovi (*Squalicorax*) (Zhelezko, 1987): *Anacorax*; Santonian (Koldenen-Temir Fm.), Kublej River, region of Aktjubinsk, western Kazakhstan, central Asia. See Zhelezko (1990, p. 126).

parallelus (*Squalicorax*) (Coquand, 1860): *Corax*; p. 97 (no figuration); Carentonian (= Turonian), Sillac, near Angoulême, Charente-Maritime, soutwestern France.

pawpawensis (*Squalicorax*) Siverson, Lindgren & Kelley, 2007: p. 945, p. 941, fig. 2A, pl. 1. Upper Albian (Pawpaw Fm.), The Motorola site of Blake & Reid, 1998, Tarrant Co., Texas, U.S.A.

praeyangaensis (*Squalicorax*) (Glikman, 1980): *Microanacorax*; p. 116, pl. 30, fig. 11-12; upper Santonian, Tyk-Butak River, region of Aktjubinsk, western Kazakhstan, central Asia.

primigenius (*Squalicorax*) Landemaine, 1991: *Oxyrhina* (?) *primaeva*. Type (designed by Landemaine): pl. 5, fig. 118 a-c, non fig. 114-117, Dalinkevicius, 1935; upper Albian, rivers Sventoji and Neris, Lithuania. Figures *in* Landemaine, 1991: p. 21, pl. 10, fig. 1-11 (Albian, Haute-Marne, France).

primulus (*Squalicorax*) (Müller & Diedrich, 1991): *Pseudocorax*; p. 40, pl. 22, fig. 1-5; lower-middle Cenomanian, Werther-Ascheloh, forest of Teutoburger, close to Münster, northwestern Germany.

priscoserratus (*Squalicorax*) Siverson, Lindgren & Kelley, 2007: p. 941, fig. 2B, p. 943, fig. 3A-P. Upper Albian (Pawpaw Fm.), The Motorola site of Blake & Reid, 1998, Tarrant Co., Texas, U.S.A.

pristodontus (*Squalicorax*) (Agassiz, 1835): *Corax*; p. 224, pl. 26, fig. 9-13 (as *Galeus pristodontus*); Maastrichtian, Maastricht, The Netherlands. (Type species of genera *Corax* Agassiz, 1835 [preoccupied by *Corax* Ledru, 1810 (Aves], *Squalicorax* Whitley, 1939 and *Anacorax* White & Moy-Thomas, 1940a).

pristodontus/plicatus (*Squalicorax*) (Priem, 1898): *Corax pristodontus* var. *plicatus*; p. 236, pl. 2, fig. 5; Upper Cretaceous, Meudon, Paris Basin.

sagisicus (*Squalicorax*) Glikman, 1980: p. 106, pl. 30, fig. 25; Coniacian, Nugaity Creek, Sagis River, western Kazakhstan, central Asia. Species created by Glikman & Zhelezko *in* Zhelezko, 1977, but nor described nor figured, and therefore *nomen nudum* at that time.

santonicus (*Squalicorax*) (Glikman & Zhelezko, 1979): *Anacorax*; p. 91, pl. 1, fig. 1-2. Upper Santonian, Sugursaj River, Aktjubinsk region, western Kazakhstan, Central Asia. Species erected by Glikman & Zhelezko *in* Zhelezko, 1977, but not described or illustrated, and therefore *nomen nudum* at this time; validated *in* Glikman & Zhelezko, 1979. Mentioned again as a new species *in* Glikman, 1980.

trapezoidalis (*Squalicorax*) (Coquand, 1860): *Corax*; p. 97 (no figuration); Turonian (= Carentonian), Sillac, near Angoulême, Charente-Maritime, southwestern France.

uilicus (*Squalicorax*) (Glikman & Zhelezko *in* Zhelezko, 1977): *Anacorax*; p. 9 (nor description, nor figuration); Campanian, Kazakhstan. Species created by Glikman & Zhelezko *in* Zhelezko, 1977, but nor described nor figured, and therefore *nomen nudum* at that time. Species cited later by Zhelezko (1995, p. 26).

volgensis, *Squalicorax* (Glikman *in* Glikman & Shvazhaite, 1971):

Palaeoanacorax; p. 187, pl. 1, fig. 5-7. Middle Cenomanian, Nizhnaya Bannovka village, Saratov Province, Russia. (Type species of the genus *Palaeoanacorax* Glikman *in* Glikman & Shvazhaite, 1971).

yangaensis (*Squalicorax*) (Dartevelle & Casier, 1943): *Corax*; p. 96, pl. 1, fig. 14-29; Senonian (probably Santonian or Campanian), Yanga Lake, Enclave of Cabinda, western Africa. (Type species of the genus *Microanacorax* Glikman, 1980).