Elasmobranchs from the upper Paleocene of Togo

Guillaume Guinot, Yawovi Zikpi Amoudji, Koffi Evenyon Kassegne, Raphaël Sarr, Ampah Kodjo C. Johnson, Pauline Yawoa D. da Costa, Lionel Hautier

Elasmobranchs from the upper Paleocene of Togo

Guillaume Guinot[a]*, Yawovi Zikpi Amoudji[b], Koffi Evenyon Kassegne[b], Raphaël Sarr[c], Ampah Kodjo C. Johnson[b], Pauline Yawoa D. Da Costa[b], Lionel Hautier[a]

[a] Institut des Sciences de l'Evolution de Montpellier (ISE-M, UMR 5554, CNRS/UM/IRD/EPHE), Université de Montpellier, 34095 Montpellier Cedex 5, France

[b] Département de Géologie, Faculté des Sciences, Université de Lomé, B.P.1515 Lomé, Togo

[c] Laboratoire de Sédimentologie et Biostratigraphie, Département de Géologie, Faculté des Sciences et Techniques, Université Cheikh Anta Diop de Dakar, B. P. 5005 Dakar-Fann, Sénégal

* Corresponding author. E-mail address: guillaume.guinot@umontpellier.fr (G. Guinot).

Abstract

Bulk sampling and surface collecting of two glauconitic horizons located in Southern Togo yielded a diverse elasmobranch fauna described here. This fauna includes 30 species and is dominated by carcharhiniforms (11 species), myliobatiforms (nine species) and lamniforms (five species) and also comprises three orectolobiform, whereas the squatiniforms and rhinopristiforms are represented by species each. Although the poor preservation of the specimens hampered numerous species-level identifications, the vast majority of taxa identified were formerly reported from the Paleocene-Ypresian interval, six of which being exclusively known from the upper Paleocene. This, along with the six benthic foraminifera species, indicate a late Thanetian age for the sampled horizons and provide age constraints on a geographically widespread benchmark horizon in Western Africa. The composition of the elasmobranch assemblage shows strong resemblances with upper Paleocene faunas from Morocco and differs markedly from known assemblages from geographically closer localities in Niger and Nigeria, which suggests strong palaeoenvironmental control on the distribution of Thanetian elasmobranch diversity.

Keywords:

Chondrichthyans

Benthic foraminifera

Stratigraphy

Paleobiogeography

1. Introduction

The Paleocene epoch witnessed a major reorganization of both marine and terrestrial ecosystems. Among marine vertebrates, this epoch includes the diversification of numerous fish clades in the aftermath of the Cretaceous-Paleogene extinction and the settlement of the modern groups in the late Paleocene-Eocene interval (Guinot and Cavin, 2016). More specifically, the late Paleocene is marked by the diversification of several elasmobranch groups including lamniforms, carcharhiniforms, and myliobatiforms. Yet, the Paleocene elasmobranch fossil record is rather poorly known compared to the late Maastrichtian and post Paleocene Cainozoic (Guinot and Cavin, 2016). Furthermore, knowledge on late Paleocene elasmobranch assemblages is geographically heterogeneously documented and the dating of many of them is poor. Most reported faunas are restricted to North Africa (e.g., Arambourg, 1952; Noubhani and Cappetta, 1997) and northern Europe (e.g., Baut and Genault, 1995; Casier, 1967, 1943; Herman, 1977; Moreau and Mathis, 2000), whereas other reports include Jordan (Cappetta et al., 2000), Angola and Democratic Republic of Congo (Dartevelle and Casier, 1959, 1943), Niger (Cappetta, 1972), Nigeria (White, 1934), and USA (Case, 1994; Ward and Wiest, 1990). Stromer (1910) described several elasmobranchs and other vertebrates from southern Togo that were attributed to the Eocene. Some elasmobranch specimens reported by Stromer (1910) originated from Dagbati (Djagbati in original publication), an area where only middle Eocene rocks outcrop (Johnson et al., 2000). However, other taxa were sampled from limestones in Adabion, a locality on the banks of the Mono River close to village of Tokpli, with additional material collected from exposures near the neighbouring city of Tabligbo. These limestones were subsequently attributed to the middle-late Paleocene (Da Costa et al., 2013b, 2013c). According to Stromer (1910), these horizons yielded *Myliobatis dixoni*, *Odontaspis elegans* var. *substriata*, *Xenodolamia* aff. *simplex*, *Ginglymostoma* aff. *thielense*, and *Hypolophites myliobatoides* along with

actinopterygian and tetrapod remains. Recent fieldwork in the Tabligbo area allowed the identification of a late Paleocene vertebrate-rich glauconitic horizon covering the limestone series. The fauna reported here adds to the knowledge on elasmobranch diversity as well as on their distribution along the Atlantic coast of Africa and provide age constraints on a geographically widespread benchmark horizon in Western Africa.

2. Geographical and geological Settings

The localities sampled are situated near the village of Tabligbo (Fig. 1(A)), southern Togo (Maritime Region). This region is part of the Togolese coastal sedimentary basin, which comprises a thick Upper Cretaceous to Neogene monoclinal sequence dipping South. The Campanian-Maastrichtian overlies the Dahomeyan basement and is characterized by various clastic facies that are mostly known from cores (Da Costa et al., 2009, 2013c, 2013b). This series is covered by a carbonate-dominated Paleogene sequence (Da Costa et al., 2013c; Johnson et al., 2000) that precedes Eocene shales, clays, and phosphorite series (Johnson et al., 2000). The sections studied in the present work (Fig. 1(B)) were accessed in the cement quarries WACEM (coordinates: 06°35’34.7’'N, 1°33’25.8’’E) and ScanTogo (coordinates: 06°36’35.4’'N, 001°34’05.4’’E) respectively located 6 km and 8 km northeast of the city of Tabligbo. The lower part of the observable Paleocene succession is composed of a unit of yellow-weathering bioclastic limestone about four metres thick. This coquina limestone contains abundant bivalves, gastropods and echinoderms (including *Togocyamus seefriedi* Oppenheim, 1915) as well as rare foraminifera and numerous ostracods. The ostracod assemblage correlates with the Ewekoro Formation (Johnson et al., 2000) in the biozone P3 (Adegoke, 1977). Stromer (1910) reported vertebrate remains that he received from Mr Koert, which originate from the banks of the Mono river at Adabion near the locality of Tokpli as well as additional material sampled from exposures near Tabligbo. Although the horizon from

which the specimens were sampled is not specified, Stromer (1910) indicated that the specimens he studied were preserved in an indurated yellow limestone containing abundant shells and gastropods, which most likely corresponds to the *T. seefriedi* limestones. In addition, prospections carried out in the area on the banks of the Mono river (close to the village of Sika-Kondji) resulted in the identification of the yellow limestones. While outcrops were overgrown and/or flooded, samples confirmed that these limestones are equivalent to the coquina *T. seefriedi* horizon described above. A diverse and abundant invertebrate fauna was subsequently described from the same area by Oppenheim (1915) and was later revised and completed by Furon and Kouriatchy (1948) who provided additional material from Adabion and Togblékopé. Although Furon & Kouriatchy (1948) indicated that their material was sampled from their layer 6 (glauconitic limestone, see below), it is clear from the faunal content that their specimens originate from the underlying *T. seefriedi* limestones (layer 7). These limestones are unconformably overlain by a compact limestone of two meters thickness, which comprises in its upper part a 30 cm thick oyster level and another unconformity. This is covered by a glauconitic series of less than one meter thick that includes a glauconitic biomicrite in its lower part and a 20 cm thick glauconitic sandstone in its upper part, which yielded the bulk of the elasmobranch described here. Numerous bioturbations containing crustacean remains mark the limit between the glauconitic biomicrite and the glauconitic sandstone. The glauconitic biomicrite level yielded planktonic foraminifera that suggest an upper Paleocene age (Biozone P4) (Da Costa et al., 2009, 2013d; Johnson et al., 2000), whereas previous biostratigraphic data provided contentious results for the glauconitic sandstone. Based on planktonic foraminifera, this level was assigned to the biozones P5-P6 (Da Costa et al., 2013a, 2009), whereas calcareous nannofossils indicate an age within the biozones NP9-10 (Da Costa et al., 2013c). Our samplings from this glauconitic sandstone layer yielded six species of benthic foramina (Fig. 2): *Frondicularia microdisca*

Reuss, 1860 known from the Upper Cretaceous of Germany and North America; *Frondicularia phosphatica* Russo, 1934 that ranges from the Thanetian of Senegal and North Africa; *Frondicularia vertebralis* Russo, 1934, known from the upper Paleocene of Senegal; *Lenticulina incisa* (Terquem, 1858) that ranges from the Paleocene and lower Eocene of Senegal and Ivory Coast; *Palmula sigmoicosta* Ten Dam & Sigal, 1950 known from the Paleocene of Algeria and Tunisia and *Nodosaria affinis* d'Orbigny, 1846, that ranges from the Upper Cretaceous of North America to the Paleocene of Senegal. This assemblage suggests a Thanetian age for this glauconitic sandstone horizon. The carbonate-dominated series is overlain by a thick (100 m) shaly series containing numerous benthic and planktonic foramina that are either attributed to various biozones (P3 to P6), which suggests condensation of the series (Johnson et al 2000) or to the basal Ypresian biozone P6 (Da Costa et al., 2013c, 2013a, 2009).

3. Material and methods

About 40 kg of rock were bulk sampled from the glauconitic sandstone horizon and washed with water or diluted (7%) hydrogen peroxide. Small fossil remains were picked from residues that were formerly sieved down to 0.7mm mesh size, whereas most large specimens were surface picked in the field. One third of the rock samples were sieved with a 0.4mm mesh size, which did not yield additional identifiable elasmobranch specimens. About 300 identifiable elasmobranch teeth were recovered. Specimen preservation is generally poor, most of fossils being broken due to sediment compaction and/or worn, while surface-collected samples show various degrees of surface alteration. The crowns of all elasmobranch teeth have a typical dark grey color and show a similar preservation with no signs of partial reworking. Elasmobranch teeth represent the largest fraction of the fossil material recovered, along with benthic foraminifera and fragmentary crustacean remains. Other associated fossils

include (listed by order of abundance): pycnodont and other incomplete actinopterygian teeth, gastropods (preserved as internal moulds), nautilid shells, rare coral polyps, chelonian and bivalve shell fragments.

Specimens from the underlying glauconitic limestone were sampled from 1 kg of rock that was processed using 7.5% buffered formic acid and sieved down to a 0.4mm mesh size. This sample yielded five elasmobranch teeth and numerous actinopterygian bone and tooth fragments, gastropods and crustacean fragments as well as cidaroid spines.

All figured and unfigured specimens are housed in the collections of the Geology Department of the University of Lomé. Official specimen numbers are preceded by 'ULDG TAB' (shorten here to 'TAB2' and 'TAB3' for specimens from the glauconitic sandstones and glauconitic limestones, respectively).

4. Systematic palaeontology

Order Squatiniformes Buen, 1926

Family Squatinidae Bonaparte, 1838

Genus ***Squatina*** Dumeril, 1806

Squatina cf. *prima* (Winkler, 1876)

Fig. 3(A-B)

Material: Five incomplete teeth and several isolated crowns from the glauconitic sandstones.

Description: Teeth are small (less than 1.5mm high) and generally as broad as high. The crown comprises a triangular and erect main cusp flanked by a pair of lateral heels that are slightly inclined to the base and faintly oriented lingually. The cutting edges are moderately developed and run continuously from one heel to the other. An apron is present at the base of the labial root face, below the main cusp. This can vary in size and shape, being generally narrow and slightly displaced from the axis of the main cusp in anterior teeth or being wide

and short in laterals. The apron always extends below the basal root edge in labial view. The root has a concave basal face pierced by a large central foramen. The lingual root face displays a marked lingual protuberance, which is pierced by a central foramen.

Remarks. The morphology of these teeth is typical of the genus *Squatina*. Teeth of the species *S. prima* (Winkler, 1876a), described from the Selandian of Belgium (see also Herman, 1977), bears resemblances with the material reported here. However, the teeth described here are smaller than most of specimens referred to *S. prima*, but the poor preservation of the Togolese specimens preclude further identification of this taxon.

Order Orectolobiformes Appelgate, 1972

Family Hemiscylliidae Gill, 1862

Genus ***Chiloscyllium*** Müller & Henle, 1837

Chiloscyllium sp.

Fig. 3(C-D)

Material: Three incomplete teeth: two from the glauconitic sandstones and one from the glauconitic limestones.

Description: Teeth of this species are characterized by a rather short and wide main cusp that broadens in its lower region and connects to a pair of incipient but broad lateral cusplets. The cutting edges are faint but continuous from the apex of the main cusp to the lateral cusplets. The labial crown face is slightly convex in profile view and tends to display an irregular surface in some teeth (Fig. 3(C)). The apron is short, wide and bifid in labial view with a markedly concave central region. The concave marginal area of the basal crown face separates the apron from the lateral cusplets. Anterior teeth are more mesio-distally compressed.

Remarks: Species of this genus have a conservative morphology and the poor preservation does not allow precise identification of the specimens reported here.

Family Ginglymostomatidae Gill, 1862

Genus ***Hologinglymostoma*** Noubhani & Cappetta, 1997

Hologinglymostoma sp.

Fig. 3(E-F)

Material: Two incomplete teeth from the glauconitic sandstones.

Description: The crown comprises an erect triangular main cusp flanked by low heels that bear three low and broad cusplets, well separated from each other and from the main cusp by notches. The apron is short, broad and concave in its median region, in labial view. The lingual face bears a broad and lingually developed uvula with a rounded lingual edge.

Remarks: This genus is so far represented by a single nominal species, *H. jaegeri* Noubhani and Cappetta, 1997 from the upper Paleocene of Morocco. Although incomplete, the specimens reported here concur with the diagnosis of the genus including a markedly concave labial crown face in profile view, a main cusp well separated from the heels, which bear several low and sharp (but broad) cusplets. Teeth of *H. jaegeri* have a holaulacorhize root, which was seemingly the case in one tooth with incomplete root from Tabligbo. These characters differentiate teeth of *Hologinglymostoma* sp. from those of *Ginglymostoma* sp. described below.

Genus ***Ginglymostoma*** Müller & Henle, 1837

'Ginglymostoma' sp.

Fig. 3(G-I)

Material: Four incomplete teeth from the glauconitic sandstones.

Description: Anterolateral teeth are as broad as wide. The main cusp is labio-lingually compressed, broad and triangular. At least three mesial cusplets of decreasing size towards the mesial crown edge are present, separated from each other by narrow notches. Both the main cusp and cusplets are inclined to the commissure. The apron is moderately broad with a flat basal edge. In labial view, the apron is well separated from the basal edge of the labial crown face by two concavities. Lateral teeth are broader than high with three cusplets on the distal heel and a fourth, incipient cusplet on the distal edge. The distal crown edge bears a vertical ridge oriented lingually that connects to the incipient cusplet. Four cusplets are present on the mesial heel. All cusplets and main cusp are strongly bent to the commissure. The apron is broad, moderately developed and protrudes labially, which confers a concave outline to the labial crown face in profile view. The apron is mesially positioned relative to the main cusp and is separated from the rest of the crown by concavities of the basal crown edge. A labial ridge is present on the distal half of the basal crown face in labial view. The ridge runs from the distal edge of the apron to the apex of the most distal cusplets and follows the basal edge outline of the labial crown face.

Remarks: Although lacking roots, the specimens described here resemble those of a number of Paleocene ginglymostomatids from Morocco including *G. botmaense* Noubhani and Cappetta, 1997, *G. erramii* Noubhani and Cappetta, 1997, and *G. pectinatum* Noubhani and Cappetta, 1997, which were included within the Recent genus *Ginglymostoma*. Yet, these species have strongly asymmetrical crowns with frequent labial ornament and more than two pairs of lateral cusplets in lateral teeth. In addition, the specimens described here and other Moroccan species (*G. botmaense*, *G. erramii*) bear a broad and relatively developed apron, placed mesially relative to the main cusp. These characters differ from the Recent *Ginglymostoma* and recall those found in the Recent *Nebrius* species (*N. ferrugineus*). The labial ridge on the distal half of the basal crown face present in the Togolese species is also

present in commissural teeth of the Recent *N. ferrugineus* (Herman et al., 1992). However, teeth of *N. ferrugineus* have a much more developed (both basally and labially) apron, which calls to a needed revision of Paleogene ginglymostomatids to elucidate the systematic position of these taxa. The character combination presents on the crown of the Togolese specimens (especially the mesio-lingual ridge and the labial ridge on the distal half of the basal crown face in lateral teeth) distinguish themfrom all other ginglymostomatids, but the scarcity and incompleteness of the specimens precludes the formal description of this species.

Order Lamniformes Berg, 1937

Family Serratolamnidae Landemaine, 1991

Genus ***Serratolamna*** Landemaine, 1991

Serratolamna aschersoni (Stromer, 1905)

Fig. 4(A-B)

Material: One tooth from the glauconitic sandstones.

Description: This tooth is 24 mm high and is characterized by its broad triangular main cusp strongly bent to the commissure. A pair of high and broad triangular cusplets is present, separated from the main cusp by a narrow but deep notch. The cusplets are strongly diverging and the distal one is curved to the posterior and shows a slight anticlockwise torsion in apical view. Two additional small external cusplets are present (the mesial one is broken) but reduced and erect. The main cusp and cusplets have a convex lingual face. The labial face of the cusplets is less markedly convex. The labial face of the main cusp shows a bulge that excludes the region near the cutting edges, which are well developed and sharp. The base of the labial crown face is bulged but does not overhang the root, except below the main cusp. One large median vertical notch corresponding to a vertical enameloid folding is present on the base of the main cusp, and some less marked additional ones are present on the margins of

the main cusp and below the distal cusplet. The root is moderately high and fairly labio-lingually compressed. The basal and labial faces are flat, the latter being slightly inclined labially. The lateral extremities of the root lobes are rounded, whereas the basal edge of the labial lobe faces are straight and joint medially in a broad triangular concavity in labial view. A large medio-lingual foramina opens on the angle between the lingual and basal root face, where there is no lingual bulge.

Remarks: This species, which has a complex taxonomic history (Case and Cappetta, 1990), was limited to the Ypresian and Lutetian of Africa and USA but Case (1994) reported this species from the uppermost Thanetian or lowermost Ypresian of Mississippi (Tuscahoma Fm.). However, it is unclear whether the specimens from Mississippi come from the Ypresian Bashi Formation and/or Tuscahoma Formation. In addition, specimens illustrated in Case (1994) differ from the sub-complete tooth series illustrated by Arambourg (1952) from the Ypresian of Morocco in having a root with an incipient medio-lingual notch as well as lower and broader cusplets with the distal one not being curved distally; which may indicate closer affinities with *Lamna gafsana* White, 1926. Both species were included in the genus *Serratolamna* by Landemaine (1991), along with the species *O. serrata* Agassiz, 1843, *L. caraibaea* Leriche, 1938, *O. amonensis* Cappetta and Case, 1975 and *O. koerti* Stromer 1910, although the latter two species belong to distinct genera and families (Cappetta 2006, Vullo et al. 2016). Arambourg (1952, p. 110) also indicated that *S. aschersoni* is present in the Thanetian of Morocco, which has not been confirmed in Noubhani and Cappetta (1997). In the absence of illustrations, these Thanetian records were difficult to assess. The probable upper lateral tooth described here shows typical characters of *S. aschersoni* (morphology and number of cusplets, labial crown face, medio-central foramina) and represents the first definite Thanetian record of this species.

Family Otodontidae Glickman, 1964

Genus ***Otodus*** Agassiz, 1838

Subgenus *Otodus* Agassiz, 1838

Otodus (Otodus) obliquus Agassiz, 1838

Fig. 4(C-U)

Material: 36 mostly complete teeth and several tooth fragments from the glauconitic sandstones.

Description: Two morphs were recovered from our samplings. The first morph (Fig. 4(C-I)) comprises incomplete teeth that are large and robust. Incomplete teeth from anterior files can reach 70 mm high and have an erect triangular main cusp with a strongly convex lingual face and a moderately convex labial face. The main cusp is relatively wide in its basal region but narrows toward a sharp apex. Some anteriors show a constriction of the crown base, near the cusplets. The lower edge of the labial crown face has a characteristic deep triangular notch. The cutting edges are well developed and smooth. The lingual root face bears a strong lingual protuberance pierced by a central foramen. Lower lateral teeth are of the same morphology but smaller with a flat labial crown face and less marked lingual protuberance. In upper laterals the main cusp is strongly inclined distally; its apex is slightly bent labially. The labial crown face is somewhat flat with a vertical concavity and a slight basal bulge. The pair of cusplets is well separated from the main cusp by a notch that is wider in the distal region. Cusplets are triangular and large, the distal one being more elongate and more diverging. The lingual collar is wide and the lingual root protuberance is marked, although less developed than in anteriors. Root lobes are well developed and separated by a broad and deep concavity of the basal edge of the root in labial view. The distal root lobe has a squared outline, whereas the mesial one is more rounded. Posterior teeth have the same morphology as laterals, but more mesio-distally elongate with a lower and more distally bend main cusp. Teeth of the

second, smaller morph (Fig. 4(J-U)) do not exceed 25 mm high. Anterior teeth have a narrow triangular and biconvex main cusp with a more bulged lingual face. A pair of strongly diverging cusplets is present, separated from the main cusp by a deep but narrow notch. The cusplets are biconvex with parallel mesial and distal margins in their lower region. The lingual root protuberance is wide and moderately developed. Root lobes are oriented labially and separated by a wide concavity. Both mesial and distal lobes are rather thin, the mesial one being narrower with a sharp extremity. The root lobes are wider and shorter in more lateral files where cusplets tend to have a concave outer edge. Upper lateral teeth are strongly mesio-distally developed with distally inclined main cusp showing a flat labial face. Root lobes have a squared outline and the lingual protuberance is wide. Posterior teeth have the same general morphology as laterals but with lower and proportionally wider cusplets and markedly square-shaped root lobes.

Remarks: This species is rather common in Paleocene-Ypresian samplings from Atlantic and Tethys oceans. The type specimens were described by Agassiz (1838) and originate from the Ypresian of Sheppey Island (see also Casier, 1966). Agassiz noted the marked size and morphological differences among the specimens he figured, which he attributed to heterodonty (monognathic, dignathic and ontogenic) indicating that large teeth with inclined main cusp were laterals (pl. 31 Figs. 1-2, 6-7) and that large teeth were from upper files (pl. 31, Fig. 13), whereas more slender ones were from lower files (pl. 31, Figs. 8-9). He noticed the same variation in smaller teeth, which he concluded belonged to younger individuals (pl. 36 Figs. 26-27), although he suggested that some of them might be upper intermediates of adult individuals. Subsequent records from numerous localities in the Selandian and Ypresian of the Cabinda enclave and in the Selandian of Democratic Republic of Congo (Dartevelle and Casier, 1959, 1943), from the Ypresian of Belgium (Casier, 1966) as well as from the upper Paleocene and Ypresian of Morocco (Arambourg, 1952), all include both the small and

large morphs and the same distribution is present in the samplings from Togo. Considering that teeth recovered from both morphs represent virtually all tooth files each, it is indeed reasonable to consider that the small morph represents teeth of young individuals. However, a number of records of this species were based exclusively on teeth of the small morph, which can be sometimes very difficult to differentiate from teeth of Paleocene *Cretolamna* species (Casier, 1966; Dartevelle and Casier, 1943). These reports include the Thanetian of France (Baut and Genault, 1995; Moreau and Mathis, 2000) and the Selandian and Danian of Alabama (Ehret and Ebersole, 2014), the latter being possibly the oldest record of the species but the lack of associated larger typical *O. obliquus* teeth make this record tentative. Other additional records include the Thanetian and Ypresian of Kazakhstan (King et al., 2013), although Zhelezko and Kozlov (1999) reported several subspecies in the pre-Thanetian Paleogene and the Ypresian of Uzbekistan (Malyshkina and Ward, 2016 - tooth fragment) and Romania (Neugeboren, 1851). Agassiz also described *Otodus lanceolatus* (Agassiz, 1843, p. 269, pl. 37, Figs. 19-23) from the base of the ferrugenic sands of Kressenberg (probably Kressenberg Fm, Ypresian), which he acknowledged was possibly synonymous with *O. obliquus* but differed in having larger cusplets and less marked lingual bulge of the crown. However, it appears that these variations fit the intraspecific variability seen in *O. obliquus* and so that *O. lanceolatus* is a junior synonym of *O. obliquus*.

Family Odontaspididae *sensu lato*

Genus ***Jaekelotodus*** Menner, 1928

Jaekelotodus africanus (Arambourg, 1952)

Fig. 5(A-I)

1952. *Odontaspis robusta* var. *africana* - Arambourg, p. 64, pl. 6, pl. 7, Figs. 1-6.

Material: 21 incomplete teeth and several isolated crowns from the glauconitic sandstones.

Description: Anterior teeth are higher than broad and can reach 30 mm in height. The main cusp is elongate and strongly sigmoid in profile view with a slight torsion of the apex in some specimens. The lingual face is strongly convex, whereas the labial face is only weakly convex to flat with a vertical central concavity on the lower half of the main cusp. The cutting edges are thin and taper in the basal region, where the main cusp broadens. The basal edge of the labial crown face is markedly concave and shows no bulge but it overhangs the root at all points in profile view. Very short and faint vertical folds are present on the basal edge of the labial crown face. The lingual collar is well marked. Lateral heels are very low and inclined basally. The heels bear a pair of lateral cusplets, which are short and curved both lingually and toward the main cusp. The root is bilobate with thin, V-shaped and elongated root branches. A very developed and relatively narrow lingual root protuberance is crossed by a deep nutritive groove. Lateral teeth are lower, more massive and mesio-distally developed. The main cusp is wide, biconvex and curved to the posterior in teeth from the upper files, whereas it is only slightly bent in lower teeth. The cutting edges are continuous from the apex of the main cusp to the notch separating the cusplets. The heels are low and short and bear a pair of lateral cusplets of similar shape and orientation as in anteriors, although smaller and less inclined towards the main cusp. The root lobes are rounded, labio-lingually compressed and rather developed but become reduced in more posterior files. The lingual root protuberance is wide but weakly developed. Posterior teeth are mesio-distally expanded and broader than high. The main cusp is low, triangular and inclined to the commissure and lingually. A pair of erect mesial cusplets and one distal cusplet is present, separated from the main cusp and from each other by a narrow notch. Cusplets adjacent to the main cusp are broad and low

Remarks: Previously, *Jaekelotodus africanus* was restricted to the upper Paleocene and Ypresian of Morocco and Tunisia (Arambourg, 1952, Noubhani and Cappetta, 1997). Teeth

of this species differ from those of *J. robustus* (Leriche, 1921) in being less massive and smaller with more gracile, more elongate and falciform upper lateral teeth. *Jaekelotodus speyeri* (Dartevelle and Casier, 1943) differs in having teeth with two pairs of cusplets as well as low and triangular main cusp, whereas *J. borystenicus* Glikman, 1964 have smaller and less elongate teeth with two pairs of cusplets. Neugeboren (1851) described *Lamna cavidens* from the Ypresian of Romania based on incomplete specimens among which only one (Pl.5, Fig. 58) might belong to an undetermined *Jaekelotodus* species.

Genus ***Palaeohypotodus*** Glikman, 1964 *non* Zhelezko, 1989

Palaeohypotodus sp.

Fig. 5(J-K)

Material: Two incomplete teeth from the glauconitic sandstones.

Description: The anterior tooth displays a 3 mm high erect main cusp with convex lingual face and weakly convex labial face with fine incomplete cutting edges. The heels are missing and the basal edge of the labial crown face bears a line of protruding and erect tubercles that are more developed below the heels than below the main cusp. The crown of the lateral tooth displays a main cusp strongly bent distally and two mesial cusplets, well separated from each other and from the main cusp. The mesial-most cusplet is reduced and weakly inclined, whereas the second cusplet is more elongate and strongly bent towards the commissure.

Remarks: By their slender and widely separated cusplets and labial ornament made of protruding tubercles, the teeth described here can be assigned to the genus *Palaeohypotodus* but the lack of complete specimens precludes more precise identification.

Family Lamnidae Müller & Henle, 1838

Genus ***Isurolamna*** Cappetta, 1976

Isurolamna sp.

Fig. 5(L-R)

Material: Eight incomplete teeth from the glauconitic sandstones

Description: Anterior teeth can reach 20 mm high and have an elongate and rather narrow main cusp with a slightly sigmoid profile. The main cusp is nearly straight in presumed lower anteriors, whereas it is slightly oriented toward the commissure in teeth from upper files. The crown is smooth with a convex lingual face and flat labial face. The cutting edges are thin and taper just before reaching the heels, which are extremely low, poorly differentiated and inclined basally and labially. The basal edge of the labial crown face slightly overhangs the root by a weak bulge. The root bears a wide and moderately developed lingual protuberance where a short nutritive groove opens. The root branches are well differentiated and oriented labially. Teeth from anterolateral files are more asymmetrical with distally oriented main cusp and more developed distal root branch. Lateral teeth are mesio-distally expanded and lower with shorter root branches. The presence of cusplets cannot be excluded but the heels of most of them are poorly preserved.

Remarks: Two nominal *Isurolamna* species are commonly reported from Paleocene to lower Eocene deposits. *Isurolamna affinis* (Casier, 1946) was described from the Ypresian of Belgium and has been reported from various Ypresian and Lutetian localities. *Isurolamna inflata* (Leriche, 1906) was erected as a variety of *Lamna vincenti* (Winkler, 1876a) based on material from the Lutetian of Belgium with no illustration nor designation of type specimen and it is possible that *I. affinis* represents a junior synonym of *I. inflata* (Cappetta and Case, 2016; Malyshkina and Ward, 2016). In addition, several reports of *Isurolamna* from Paleocene localities were assigned to *I. inflata* (Baut and Genault, 1995; Moreau and Mathis, 2000; Noubhani and Cappetta, 1997) but these reports are based on more gracile and smaller teeth that might represent different species (Cappetta, 2012). The material reported here falls

within this latter category, along with specimens reported by Dartevelle and Casier (1959) as undetermined Lamniformes (pl. 30, fig. 4) from the lower Selandian of the Cabinda enclave.

Order Carcharhiniformes Compagno, 1973

Family Scyliorhinidae Gill, 1862

Genus ***Foumtizia*** Noubhani & Cappetta, 1997

Foumtizia aff. *gadaensis* Noubhani & Cappetta, 1997

Fig. 6(A-D)

Material: Six incomplete teeth from the glauconitic sandstones.

Description: The main cusp is triangular with a sharp apex and broad lower region that is widely united to high heels. The heels are elongate and oblique and can display up to four cusplets. The cusplets are low and poorly individualized from each other. The basal edge of the labial crown face is bulged and strongly concave. The labial bulge is scalloped by very short vertical folds that are unevenly distributed but mainly restricted to the basal crown edge.

Remarks: This genus ranges from the Danian (Nilsson, 2003; Noubhani and Cappetta, 1997) to the Priabonian (Malyshkina, 2006) and comprises seven nominal species. With the exception of an unnamed species from the Danian of Sweden (Nilsson, 2003), Paleocene species are restricted to Morocco (Noubhani and Cappetta, 1997) and include *Foumtizia abdouni* (Danian-Thanetian), *F. arba* (Danian), and *F. gadaensis* (Danian). Teeth of these species differ from those of their Eocene relatives (*F. deschutteri, F. pattersoni, F. poudenxae,* and *F. zhelezkoi*) by their weaker labial crown ornament. Considering the preservation of the material recovered from Togo, these specimens cannot be confidently assigned to any nominal species of this genus. However, the weak ornament restricted to the basal edge of the labial crown face and the number of cusplets of some lateral teeth of

Foumtizia sp. indicate close relationships with Paleocene *Foumtizia* species, particularly *F. gadaensis* based on similarities in the numbers of denticles and crown ornament.

Genus ***Premontreia*** Cappetta, 1992

Subgenus *Oxyscyllium* Noubhani & Cappetta, 1997

Premontreia (Oxyscyllium) subulidens (Arambourg, 1952)

Fig. 6(E-K)

For synonymy, see Noubhani & Cappetta (1997) and add:

1997. *Premontreia (Oxyscyllium) subulidens* (Arambourg, 1952) - Noubhani & Cappetta, p. 55, pl. 21, Figs. 1-11.

Material: Seven incomplete and several fragmentary teeth from the glauconitic sandstones.

Description: The main cusp is high, triangular, and fairly slender in anterior teeth. The lingual face of the main cusp is convex, whereas the labial face is nearly flat. The main cusp is slightly inclined lingually and flanked by a pair of lateral cusplets. Cusplets are sharp with a rather narrow and slightly diverging apex. Cusplets are well separated from the main cusp by a notch that does not interrupt the developed and sharp cutting edges, running from the apex of the main cusp to the margins of the cusplets. Faint vertical folds can be present but are restricted to the base of the labial face, below the main cusp and cusplets. The root has a flared and flat basal face with a wide and developed lingual protuberance. The nutritive groove is rather wide and shallow except on the lingual protuberance where it is deeper. In labial view, the margino-lingual edges of the root are strongly concave. A pair of foramina is present on each margino-lingual face. Lateral teeth have a broader and more distally bent main cusp with more diverging cusplets and occasionally an incipient second mesial cusplets. Posterior teeth are lower, with main cusp and cusplets strongly bent to the commissure as well as more marked and more numerous vertical folds on the basal edge of the labial crown face.

Remarks: Although incomplete, the teeth reported here display a morphology, ornament and heterodonty that concur with that of *P. (O.) subulidens*, known from the Danian to lower Ypresian of Morocco (Arambourg, 1952; Noubhani and Cappetta, 1997) and Ypresian of Tunisia (Arambourg, 1952). Teeth of this species differ from those of *P. (O.) carinatus* (Reinecke and Engelhard, 1997) from the Paleocene of Germany and *P. (O.) peypouqueti* Noubhani and Cappetta, 1997 from the upper Paleocene of Morocco in lacking crown ornament in anteriors and in having more gracile and elongate cusplets.

Premontreia (Oxyscyllium) sp.

Fig. 6(L-O)

Material: Nine incomplete teeth and numerous isolated cusps from the glauconitic sandstones.

Description: Teeth of this species show an elongate and gracile main cusp with a fairly narrow basal region. The lingual face of the main cusp is convex, whereas the labial face is reduced and flat. A pair of cusplets, although not preserved, appears well separated from the main cusp. A second pair of cusplets can be present in lateral teeth (Fig. 6(O)). The heel region is oriented labially. The basal edge of the labial crown face overhangs the root. Labial ornament is made of numerous fine but salient subvertical folds at the base of the labial crown face. The longest folds alternate with shorter folds and reach the base of the main cusp as well as most of the height of the cusplets. Folds below the cusplets converge towards the cusplets' apex, whereas those below the main cusp are oriented towards the apex of the latter. None of the specimens have their root preserved but some teeth show well developed root lobes with flared marginal extremities that are oriented laterally.

Remarks: These teeth differ from those of *P. (O.) subulidens* by a more gracile general morphology, fine but more salient vertical folds on the labial crown face that taper higher on

the crown, and by their basal edge of the labial crown face that overhangs the root in profile view.

Genus ***Porodermoides*** Noubhani & Cappetta, 1997

Porodermoides spanios Noubhani & Cappetta, 1997

Fig. 6(P-R)

1997. *Porodermoides spanios* nov. sp. - Noubhani & Cappetta, p. 69, pl. 34, Figs. 1-7.

Material: One incomplete tooth and one tooth fragment from the glauconitic sandstones.

Description: The incomplete tooth has an elongate, biconvex, and sharp main cusp. The upper two thirds of main cusp are bent towards the commissure and very slightly inclined lingually. The distal cusplet is not preserved but the mesial cusplet is rather low, triangular, and situated slightly more labially than the main cusp in profile view. The cusplet is weakly diverging and the apex is inclined lingually. The cutting edges run continuously from the apex of the main cusp to the marginal base of the cusplets. On the main cusp, the cutting edges are sigmoid in profile view and markedly positioned lingually in the upper half. In profile view, the base of the labial and marginal crown regions is constricted and slightly overhangs the root. The crown is smooth with the exception of the slight vertical ridge on the lower half of the labial cusplet face. The root is broader than high with a slightly convex and heart-shaped basal face. The root lobes are rounded, moderately developed and oriented mesio-distally. The labial and marginal faces of the root are strongly flared. The lingual protuberance of the root is broad and marked. The root lobes are separated by a wide nutritive groove that is deeper in the area of the lingual protuberance. Rather large marginolingual foramina open in the depression between the lingual protuberance and the root lobe.

Remarks: Although scarce, the material recovered here agrees with the morphology of the type series of *P. spanios*, described from the upper Paleocene of the Ouled-Abdoun Basin in

Morocco (Noubhani and Cappetta, 1997). Noubhani and Cappetta (1997) also reported a single tooth attributed to *P.* aff. *spanios*, from the Danian of the Ganntour Basin (Morocco), which differs from *P. spanios* by its strong labial ornament. This morphology was not recovered in our samplings and the tooth from the Ganntour Basin might correspond to a second, older *Porodermoides* species.

Family Triakidae Gray, 1851

Genus ***Palaeogaleus*** Gurr, 1962

Palaeogaleus sp.

Fig. 6(S-V)

Material: Eleven incomplete teeth and several isolated cusps from the glauconitic sandstones.

Description: These teeth have a short and broad main cusp that is strongly inclined to the commissure and do not reach the distal crown edge. The mesial heel is high, broadly convex with a sharp cutting edge that is not separated from that of the main cusp, where it tapers at mid height. Distal cusplets (up to three) are broad, triangular and strongly bent to the commissure. The basal edge of the labial crown face is irregular, sometimes scalloped, and bears a marked bulge with rare light folds on its marginal faces. The lingual crown face is smooth.

Remarks: These teeth show typical features of members of the genus *Palaeogaleus* (short and strongly distally inclined main cusp, marked labial bulge of the crown, low distal cusplets). Several *Palaeogaleus* species occur in the Paleocene: *P. brivesi* (Arambourg, 1952), *P. larachei* Noubhani and Cappetta, 1997, *P. prior* (Arambourg, 1952), and *P. vincenti* (Daimeries, 1888), as well as unnamed species from the Danian of Denmark (Adolfssen and Ward, 2015, 2014) and Sweden (Nilsson, 2003). Teeth of *Palaeogaleus* sp. differ from those of *P. prior*, *P. brivesi*, *P. vincenti*, and the specimens of Denmark and Sweden in the absence

of mesial cusplets. The Togolese material resembles the less ornamented specimens of *P. larachei*, but the latter have less developed distal cusplet and the preservation of the material reported here precludes its precise specific attribution.

Genus ***Galeorhinus*** Blainville, 1816

Galeorhinus mesetaensis Noubhani & Cappetta, 1997

Fig. 6(W-X)

1997. *Galeorhinus mesetaensis* nov. sp. - Noubhani & Cappetta, p. 80, pl. 43, Figs. 1-8 & pl. 44, Fig. 1.

Material: 24 incomplete teeth and several tooth fragments from the glauconitic sandstones and two incomplete teeth from the glauconitic limestones.

Description: Teeth are generally broader than high except in anterior files where they are slightly higher than wide. The main cusp is thin, elongate, and bent towards the commissure with a convex lingual face and a slightly convex to nearly flat labial face. The mesial cutting edge of the main cusp is sharp, rectilinear to sigmoid in labial/lingual view, and continuous with the mesial heel. The mesial heel is sharp, oblique and moderately high, except in posterior files where it is more developed. The mesial heel has an irregular cutting edge. The distal cutting edge of the main cusp is convex and separated from the distal heel by a notch. The distal heel is more oblique and bears generally three and occasionally four cusplets oriented distally and decreasing in size toward the base of the crown. The basal edge of the labial crown face is concave. The lower part of the labial crown face is developed labially, especially below the heels where a strong bulge overhangs the root. These marginal labial bulges are covered with short, discontinuous, and flexuous folds that do not reach the heels. Fine vertical folds are present on lingual face but restricted to the area below the mesial heel. The root is holaulacorhize and low with a flat basal face and a slightly flared labial edge. The

marginal faces of the lingual root edge are concave in basal view and separated by a narrow lingual protuberance.

Remarks: The general morphology, number of cusplets, labial bulge of the basal crown edge below the heels and crown ornament all agree with the morphology of the type series of *G. mesetaensis* described from the upper Paleocene of the Ouled Abdoun Basin in Morocco (Noubhani and Cappetta, 1997). This species was also reported from the Danian of the Ganntour Basin (Noubhani and Cappetta, 1997). This is the first record of this species outside Morocco.

Galeorhinus sp.

Fig. 6(Y-A')

? 1994. *Galeorhinus affinis* Probst - Case, p. 117, pl. 9, Figs. 186-194.

Material: Three teeth from the glauconitic sandstones.

Description: The main cusp is broad, inclined to the commissure and biconvex with slightly convex mesial and distal cutting edges. The mesial heel is oblique, low, and bears two to three incipient cusplets on its mesial half. The distal heel bears two wide triangular cusplets close to the main cusp and two low and broad incipient cusplets near the distal crown edge. The basal edge of the labial crown face is concave and buldged with short and coarse vertical folds. Slight vertical folds are present on the lingual face, below the mesial heel. The root is moderately high with a wide but poorly developed lingual protuberance.

Remarks: Teeth of this species resemble those of *G. mesetaensis* but differ in being larger and more robust with a wider and less sigmoid main cusp. Teeth of *Galeorhinus* sp. also have a higher root, less flared basal edge of labial crown face with shorter and coarser labial ornament, as well as finer lingual folds. In addition, the mesial heel is lower with individualized cusplets in *Galeorhinus* sp. whereas the mesial heel is only irregular in *G.*

mesetaensis. Case (1994) reported teeth from the Tuschoama and Bashi Formations (respectively uppermost Thanetian/lowermost Ypresian and Ypresian) of Mississippi that he assigned to the species '*Galeorhinus' affinis* (Probst, 1878). However, this species should be included in the genus *Chaenogaleus* and is restricted to the Miocene. The morphology of specimens from Mississippi specimens closely resembles that of the material reported here and might be conspecific or closely-related.

Genus ***Triakis*** Müller & Henle, 1838

Triakis sp.

Fig. 7(A-C)

Material: Three incomplete teeth from the glauconitic sandstones.

Description: Anterior teeth are slightly higher than broad with a relatively broad and triangular main cusp bent to the commeasure. The main cusp has a flat or slightly convex labial face and is flanked by pair of broad and low cusplets. Cusplets are well separated from the main cusp by a notch, although the latter occurs high on the crown. The mesial cusplet is lower and more erect than the distal one. The basal edge of the labial crown face is concave and overhangs the root. The labial crown faces is ornamented by strong vertical ridges that are very pronounced and blade-like on the basal edge. These ridges cover the labial face of the cusplets but taper towards half-height of the main cusp. Slight lingual vertical folds are present on the cusplets and at the base of the main cusp. More lateral teeth are slightly broader than high with developed oblique heels marginal to the pair of cusplets. Labial ornamentation runs up to the apex of the crown.

Remarks: The morphology of teeth of this species, with broad and low cusplets that are united to the main cusp on a large portion of the crown and strong labial ridges associated with lingual ornament, indicates close affinities with the genus *Triakis*. Although a number of

triakid species are known from the Paleocene, *Triakis*-like taxa are seldom during this time interval. Teeth of *Triakis antunesi* Noubhani and Cappetta, 1997 (upper Paleocene of Morocco) resemble those of the species described here but differ in having two pairs of cusplets and a less regular labial ornament on the main cusp. An unnamed species was reported from the Danian of Sweden (Nilsson, 2003) based on fragmentary specimens; its teeth display a comparable morphology to the Togolese ones but with more developed cutting edges and scarcer labial ridges.

Triakidae ? indet.

Fig. 7(D-J)

1997. *Scyliorhinus* sp. - Noubhani & Cappetta, p. 62, pl. 28, Fig. 7.

Material: Five incomplete teeth from the glauconitic sandstones.

Description: The crown is low with a stubby and lingually oriented main cusp as well as a labially developed basal region of the labial face. The cutting edges are marked and continuous with oblique heels that bear a pair of incipient cusplets weakly individualized from the main cusp. The basal edge of the labial crown face is strongly concave in its median region, whereas its areas are markedly convex. The lingual crown face is bulbous below the main cusp and cusplets. The labial ornament consists of strong vertical ridges that taper near the heels and the base of the main cusp. The lingual ornament is composed of finer ridges vertically oriented below the heels and toward the apex of the crown on the main cusp, where they can be flexuous near the basal crown edge.

Remarks: These teeth share characters with those of Recent triakids with crushing dentitions (*Mustelus* and *Scylliogaleus*) including a low and wide main cusp, a developed basal region of the labial crown face, and the presence of labial and lingual ornamentation. They differ from Recent triakids, however, by the presence of a concave basal edge of the labial crown face,

which is devoid of apron, and by the absence of uvula. Although the genus *Mustelus* is present in the Thanetian (Baut and Genault, 1995; Moreau and Mathis, 2000; Reinecke and Engelhard, 1997), the material reported here probably belongs to another unnamed taxon. Noubhani and Cappetta (1997) reported a single incomplete tooth as *Scyliorhinus* sp. from the Danian of Morocco that compares well with the Togolese material and may be congeneric, if not conspecific.

Family Carcharhinidae Jordan & Evermann, 1896

Genus ***Abdounia*** Cappetta, 1980

Abdounia africana (Arambourg, 1952)

Fig. 7(K-T)

1952. *Scyliorhinus africanus* nov. sp. - Arambourg, p. 126, pl. 23, Figs. 60-83.

1997. *Abdounia africana* Arambourg - Noubhani & Cappetta, p. 89, pl. 48, Figs. 1-13.

Material: Four incomplete and 16 incomplete teeth from the glauconitic sandstones.

Description: Anterior teeth are higher than wide with an erect main cusp inclined lingually, strongly convex lingual face, and a nearly flat labial face. The heels are oblique and bear a pair of fairly broad triangular cusplets, not reaching the lingually oriented lateral extremities of the heels, where an incipient cusplet can be present on the mesial edge. The cusplets are diverging and slightly protrude labially relative to the main cusp. These are well separated from the main cusp by a wide concavity, although both are largely united at their base. The base of the labial crown face slightly overhangs the root and is rectilinear to slightly concave below the main cusp. The root is high and bilobate with flared basal edge of the labial face. The distal root lobe is narrower and more elongate than the mesial one. A broad but short medio-lingual protuberance is present and divided by a wide nutritive groove that runs over the entire basal root face. Two foramina are present on each concave margino-lingual face.

The antero-lateral teeth are of similar morphology but as high as wide and occasionally bear a second pair of cusplets. Lateral teeth are more mesio-distally elongate with strongly distally inclined main cusp and a pair of lower, broader and more diverging cusplets that are less protruding labially. Latero-posterior teeth resemble laterals but are lower and can bear labial and lingual ornament on the lower part of the crown, which consists of fine vertical folds. Symphysial teeth are small, symmetrical with a short heel, a pair of low triangular cusplets, and a root with short lobes flared labially.

Remarks: This species was so far restricted to the Paleocene of Morocco (Arambourg, 1952; Noubhani and Cappetta, 1997). *Abdounia beaugei* (Arambourg, 1935) is known from the uppermost Thanetian/lowermost Ypresian (Case, 1994) to the Upper Eocene (Leder, 2013). It is represented by teeth of comparable general morphology, which differ from those of *A. africana* by their larger size and more common presence of two and often three lateral cusplets. Other records of Paleocene *Abdounia* include a taxon reported as *A. minutissima* (Winkler, 1874) from the Thanetian of France (Baut and Genault, 1995). However, the morphology of teeth illustrated by Baut and Genault (1995) does not agree with the type material from Belgium and one tooth (pl. 9, Fig. 5) resembles teeth of *A. africana*. *Abdounia biauriculata* (Casier, 1946) was reported from the Thanetian of France (Moreau and Mathis, 2000), but the material was not illustrated, and this species seems to be restricted to the Ypresian (Casier, 1946) and Lutetian (Cappetta and Case, 2016).

Genus ***Physogaleus*** Cappetta, 1980

Physogaleus sp.

Fig. 7(U-Y)

1995. *Physogaleus secundus* (Winkler) - Baut & Genault, p. 208, pl. 9, Figs. 3-4.

Material: Two complete and numerous incomplete teeth from the glauconitic sandstones.

Description: Teeth are wider than high, not exceeding 3.5 mm wide. The main cusp is biconvex, but more developed lingually. The main cusp is lingually inclined and strongly bent towards the commissure with a marked sigmoid profile. The mesial heel is high and oblique, weakly separated from the main cusp, and with a blunt mesial edge. The distal heel bears two poorly differentiated cusplets that are oriented distally and well separated from the main cusp by a narrow and deep notch. The mesial cusplet is low and broader than the second, which is incipient. The distal edge of the distal heel is lingually oriented. The base of the labial crown face slightly overhangs the root/crown edge in the marginal faces of lateral teeth. The root is fairly low with a slightly flared and flat basal face, except on the extremities of the root lobes where it is convex and apically oriented. The lingual protuberance is developed and broad. A large nutritive groove is present on the basal face. The groove is deeper and narrower on the lingual region of the labial face, where a central foramen opens. The root lobes are laterally oriented with lingually curved extremities. The margino-lingual edges of the basal root face are strongly concave. Each margino-lingual root face bears four foramina that are lined up below the crow/root edge, the distal ones being more compressed, whereas mesial margino-lingual foramina often confer a scalloped basal edge. Several foramina open on the protruding lower half the labial root face, the largest foramen being close to the concavity of the nutritive groove in labial view.

Remarks: The morphology of these teeth is close to that of *P. secundus* (Winkler, 1876b) but much smaller with less cusplets on the distal heel, wider nutritive groove, and more marked concavities on the margino-lingual root edges in basal view. Teeth attributed to *P. secundus* from the Thanetian of France (Baut and Genault, 1995) closely resemble those of *Physogaleus* sp. described here, whereas a subsequent report from another French Thanetian locality by Moreau and Mathis (2000) lacks illustrations and cannot be assessed. This unnamed taxon represents one of the oldest record of the genus *Physogaleus*, along with

Physogaleus americanus Case, 1994 (uppermost Thanetian/lowermost Ypresian and Ypresian of Mississippi), which differs from teeth of most Paleocene and early Eocene species by its larger size and the presence of cusplets on both mesial and distal edges.

Superorder Batomorphii Cappetta, 1980

Order Rhinopristiformes Naylor, Caira, Jensen, Rosana, Straube & Lakner, 2012

Family Rhinobatidae Müller & Henle, 1838

Genus ***Pseudobatos*** Last, Séret & Naylor, 2016

Pseudobatos matzensis (Baut & Genault, 1995) comb. nov.

Fig. 7(Z-B')

1995. *'Rhinobatos' matzensis* nov. sp. - Baut & Genault; p. 211, pl. 10, Figs. 3-5.

Material: Four teeth from the glauconitic sandstones and one tooth from the glauconitic limestone.

Description: Anterior teeth are as high as wide and do not reach more than 1 mm. Teeth are of crushing morphology with convex labial face separated from the lingual face by a labially convex transverse crest, which is weak and does not reach the marginal angles. The lingual face bears a large median uvula, which is as high as wide and of irregular outline. The median uvula is weakly protruding lingually and faintly separated from the lateral uvulae by short and narrow notches. Lateral uvulae are little developed, weakly individualized from the rest of the crown, and connected to the marginal angles by a straight to slightly concave edge. The labial face has a triangular outline in occlusal view with rectilinear marginal edges that reach a weak apron with a straight labial edge. The root is rather high, faintly lingually projected, and holaulacorhize with a large nutritive groove, which is pierced by a large central and several paracentral foramina. The basal face of each root lobe is flat and inclined towards the median groove. The root lobes are triangular in basal view and devoid of individualized lingual

expansions. A pair of margino-lingual foramen is present in depressions located below the notches separating the median and lateral uvulae. Posterior teeth are smaller, with a flatter labial face, and more reduced lateral uvulae.

Remarks: The morphology of the material reported here agrees with that of the type specimens from the Late Thanetian of Paris Basin (Bracheux sands), which was previously the only occurrence of this species. Similar heterodonty is found between the French and Togolese specimens despite the low number of specimens in our samplings. Baut and Genault (1995) attributed the small-sized teeth with less developed lateral uvulae to juvenile individuals but these are likely from posterior files. The species *P. matzensis* comb. nov. was tentatively included in the genus *'Rhinobatos'* in the original description. The genus *Rhinobatos* has commonly been used for a variety of fossil taxa of undetermined affinities within Rhinopristiformes (and the same situation prevailed for living species until the revision of this clade by Last et al. (2016)). This was mainly due to the lack of data on tooth morphology in living taxa, which was restricted to line drawings of some species in Cappetta (1980). Subsequent illustrations of teeth of some living members of this order (Cappetta et al., 2016; Herman et al., 1997) enabled to better evaluate the morphological diversity of their teeth, although that of some genera (*Rhynchorhina*, *Acroteriobatus*) remains to be investigated (Guinot et al., 2018). Based on current knowledge, teeth of *P. matzensis* comb. nov. differ from the only living *Rhinobatos* species whose tooth morphology has been adequately illustrated (*R. rhinobatos*) in having a higher root, less individualized lingual expansions of the root lobes, labially convex transverse crest, and lateral uvulae less individualized from the median uvula. *Glaucostegus* teeth (*G. cemiculus*) are bulbous and much larger than those of *P. matzensis* comb. nov. with more developed and generally diverging lateral uvulae as well as more developed and rounded apron and marked lingual expansions of the root lobes. Teeth of living *Trygonorrhina* have a higher root than *P.*

matzensis comb. nov. with wider median uvula and flatten to concave lingual crown face bearing ornament. Teeth of *P. matzensis* comb. nov. share numerous characters with those of *Pseudobatos* (species *P. productus*) (Cappetta, 1980, 2012), including a labially convex transverse crest, lateral uvulae weakly developed and separated from the median uvula by a notch, and a root with triangular lobes devoid of individualized lingual expansions of the lobes. Considering the greater similarities in tooth morphology between the Thanetian species and those of the living *P. productus* in comparison with other rhinopristiforms, this species should be included in the genus *Pseudobatos*. However, this attribution needs to be confirmed by improving knowledge on tooth morphology of living rhinopristiforms, especially for the genera *Rhynchorhina* and *Acroteriobatus*.

Order Myliobatiformes Compagno, 1973

Family Dasyatoidea indet.

Genus ***Arechia*** Cappetta, 1983

Arechia sp.

Fig. 8(A)

Material: A single incomplete tooth from the glauconitic sandstones.

Description: The crown is composed of a reduced, flat and weakly basally inclined labial face with a convex labial edge and concave margin-labial borders. The lingual face is high with slightly concave margino-lingual faces. A high and thick transverse crest separates the lingual and labial faces but does not reach the blunt and somewhat flared marginal angles. The root is incomplete; it is lingually placed and is overhung labially by the crown in occlusal view. Numerous foramina open on the labial root face.

Remarks: This genus is known by the type species *A. arambourgi* Cappetta, 1983 from the Ypresian of Morocco (Cappetta, 1983; Noubhani and Cappetta, 1997) and from other

unpublished reports from the Ypresian of Senegal and Mississippi (Cappetta, 2012), as well as from unfigured material from the Lutetian of Togo (Cappetta and Traverse, 1988) and Morocco (Tabuce et al., 2005). The fragmentary crown recovered here bears a typical broad and well-developed transverse crest not reaching the marginal angles, a developed and concave lingual crown face, as well as a short and basally inclined labial face. This specimen represents the oldest record of the genus.

Genus ***Coupatezia*** Cappetta, 1982

Coupatezia sp.

Fig. 8(B-H)

Material: Three incomplete teeth and one tooth fragment from the glauconitic sandstones.

Description: Female teeth (Fig. 8(B-F)) have a mesio-distally elongate and high crown and do not exceed 2 mm wide. The occlusal face is kidney-shaped and lingually bordered by a broad and marked transverse crest. The transverse crest is sub-rectilinear in its median portion and convex on its margins where it reaches the labial edges. The marginal angles are broad and blunt. The labial edge of the occlusal face strongly overhangs the root and is bevelled in profile view. The median region of the labial edge of the occlusal face is strongly concave and flanked by a pair of margino-labial angles that protrude labially. The lingual half of the occlusal face is strongly depressed and ornamented by fine and dense enameloid irregularities. The labial half of the occlusal face bears a high and irregular transverse ridge, which connects to the lingually positioned transverse crest and does not follow the labial edge of the occlusal face. This labial transverse ridge can bifurcate labially into several randomly arranged folds where concavities are occupied by similar ornament to the depression of the lingual half of the occlusal face. The labial edge of the occlusal face is smooth. The lingual crown face is high, smooth, and slightly flared close to the occlusal face. The lingual crown face is convex

transversally but bears a pair of slight concavities on the margino-lingual faces. The basal edge of the lingual crown face is straight to slightly convex and bears a narrow and shallow median concavity. The male tooth (Fig. 8(G-H)) is as high as wide with a heart-shaped occlusal face. The centre of the occlusal face is only slightly depressed and devoid of ornament. The depression is border labially by a fine discontinuous ridge that follows the labial outline of the crown and lingually by a broad transverse crest (incomplete). The lingual crown face is flared in its lower region and bears a wide and shallow median concavity on its basal edge.

Remarks: Female teeth are very similar to those of the species *Coupatezia woutersi* Cappetta, 1982 but have a higher and more developed lingual crown face and a smooth and regular labial crown edge, whereas it is scalloped in *C. woutersi*. The male tooth described here also differs from those of *C. woutersi* by its reduced ornament of the labial crown face. *Coupatezia woutersi* is restricted to the Lutetian; other reports from the Thanetian and Ypresian of Mississippi (Case, 1994) and Selandian of Maryland (Ward and Wiest, 1990) are based on teeth that do not match the original description of the species (and might be closer to *C. boujoi*) and unfigured material, respectively. Teeth of *Coupatezia* sp. resemble those of *C. boujoi* (middle Ypresian of Morocco) in both size and general shape. However, lateral female teeth of the species described here differ in their much coarser ornament that occupies the labial half of the occlusal face, whereas in the Moroccan species this consists of a fine – sometimes bifurcating – ridge that follows the labial edge of the occlusal face. The incomplete tooth attributed to a male individual strongly resembles, based on the available characters (i.e. only crown), those of the type material of *C. boujoi* and only differs by its smaller size.

Genus ***Dasyatis*** Rafinesque, 1810

'Dasyatis' sudrei Cappetta, 1972

Fig. 8(I-N)

Material: Four incomplete teeth from the glauconitic sandstones.

Description: These dasaytoid teeth are cuspidate and do not exceed 1 mm in width. The crown is labio-lingually compressed and mesio-distally elongate and overhangs the crown in all points in labial view. The labial crown face bears a marked median concavity bounded lingually by a salient transverse crest that tappers just before reaching the marginal angles, where the crest is oriented labially. The median depression is bordered labially by a ridge that follows the slightly convex and irregular labial outline of the crown. Ornamentation is present on the labial crown face and varies from strongly reticulate mostly near the edges of the depression to very finely reticulate. The lingual crown face bears a strong bulge underlying the transverse crest and overhanging the lower part of the lingual face in occlusal view. The bulge is sharp in its lower edge and bears the same ornament as on the labial face with stronger ridges located near the base of the bulge. A developed median cusp originates from the lingual crown face, below the transverse crest. The cusp is lingually oriented with a triangular profile that comprises the basal edge of the lingual face and the transverse crest at is base. The main cusp is mesio-distally compressed with a fine longitudinal ridge, which originates from the transverse crest and almost reaches the apex. The root is low and comprises two triangular and mesio-distally elongate lobes separated by a wide and deep notch where a median foramen opens.

Remarks: The teeth described here show a combination of characters including the main cusp originating from the lingual face (below the transverse crest), lingual and labial reticulate ornamentation, transverse crest morphology and typical profile outline that conform to the description of *'D.' sudrei* from the Thanetian of Niger (Cappetta, 1972). Records of this species have previously been restricted to the type locality as well as undescribed specimens from the Thanetian of Senegal (pers. com. S. Adnet and pers. obs. G. Guinot) and the material

from Togo suggests that *'D.' sudrei* was probably widespread in the Thanetian of western Africa.

'Dasyatis' sp.

Fig. 8(O-Q)

Material: Four incomplete teeth from the glauconitic sandstones.

Description: Non-cuspidate tooth crowns (Fig. 8(O-P)) are globular with a triangular and narrow lower region of the lingual face that is overhung by the rest of the crown in occlusal view. The margino-lingual faces are concave and separated by a narrow and vertical median ridge. The upper portion of the lingual crown face and the labial face are bulbous and ornamented by short irregular folds randomly oriented on the labial face but tend to be vertical on the lingual face. The labial and lingual faces can be separated by a faint and low transverse crest, which is absent in some teeth. The marginal angles are acute; the labial crown edge is convex with a broad and short median expansion. One cuspidate tooth (Fig. 8(Q)) shows the same general morphology but differs in having a more marked transverse crest that is V-shaped in occlusal view, no lingual ornament and very scarce labial folds.

Remarks: These teeth show a typical dasyatid crown morphology and comparable sexual heterodonty. However, considering the Paleocene diversity of this group and the poor preservation of the material, it is not possible to more precisely identify this taxon.

Family Mobulidae Gill, 1893

Genus ***Burnhamia*** Cappetta, 1976

Burnhamia sp.

Fig. 8(U-W)

Material: One fragmentary tooth from the glauconitic sandstones.

Description: This incomplete crown is mesiodistally elongate and labiolingually compressed. The crown is displaced lingually relative to the root. The occlusal face is V-shaped in cross section with a shorter and more abrupt lingual side. The occlusal face has an irregular surface that bears a granulose ornamentation. The lateral extremity of the occlusal face is triangular and oblique. The lingual crown face is convex in its upper region but strongly concave near the basal edge where short, strongly developed and irregular folds are present. The labial crown face is flat with irregular vertical folds.

Remarks: Underwood et al. (2017) erected the genus *Sulcidens* for the species *Myliobatis sulcidens* Dartevelle and Casier, 1943 known from the Paleocene and Ypresian of Morocco and Cabinda Enclave. Differences between *Sulcidens* and *Burnhamia*, both known from associated tooth sets, are tenuous but the dentition of the former is more *Myliobatis*-like with large median teeth and very mesio-distally compressed laterals, whereas *Burhamia* species show a *Rhinoptera*-like gradation of tooth width away from the symphysis (Underwood et al., 2017). Separating species of these two genera on the basis of scarce and fragmentary material is difficult but teeth of *Sulcidens* also differ from those of *Burnhamia* by the presence of an antero-posterior notch on the lateral extremities of the occlusal crown face and by a symmetrical depression on the occlusal face with lingual and labial sides of the depression being of equal size. The tooth fragment recovered here lacks these characters and is therefore attributed to an undetermined *Burnhamia* species.

Family ?Mobulidae Gill, 1893

Genus ***Archaeomanta*** Herman, 1979

Archaeomanta sp.

Figs 8(R-T)

Material: A single tooth from the glauconitic sandstones.

Description: This tooth is less than 2.5 mm high and comprises a high lingually inclined main cusp and short incomplete root. The main cusp shows an erect lower half that is labio-lingually developed and mesio-distally compressed (especially in its labial part), and separated from the root by a collar. The labial and lingual edges of the lower half of the main cusp are slightly convex in profile view. The upper half of the cusp is strongly bent lingually, which confers a sharp labial angle in profile view. A fine labial cutting edge runs from the labial angle to the apex of the cusp where a finer lingual cutting edge originates and tapers before the concavity on the lingual crown face in profile view. The crown is damaged but its preserved lingual portion indicates that it is short and slightly wider than the crown.

Remarks: The genus *Archaeomanta* comprises three nominal species: *A. melenhorsti* Herman, 1979 (the type species) was described from the Ypresian of Belgium and also reported from the Ypresian of Morocco (Noubhani and Cappetta, 1997) and Mississippi (Case, 1994), as well as from the Lutetian of Belgium (Herman, 1979), Uzbekistan (Case et al., 1996) and England (Kemp et al., 1990). *Archaeomanta priemi* Herman, 1979 was described from the upper Paleocene of Morocco (Herman, 1979; Noubhani and Cappetta, 1997) and *A. hermani* Kozlov, 2001 from the Bartonian of Kazakhstan. In addition, numerous reports of this genus have been made including in the Danian-Selandian of Morocco (Noubhani and Cappetta, 1997), Lutetian of Jordan (Cappetta et al., 2000), France (Dutheil, 1997), Togo (Cappetta and Traverse, 1988), Guinea-Bissau (Cappetta, 2012) as well as in the Priabonian of Western Sahara (Adnet et al., 2010), and Egypt (Underwood et al., 2011). The intra-specific dental variation seems rather strong in *Archaeomanta*, which makes it difficult to separate species, especially considering the number of published records without illustrations. Furthermore, the higher-level systematics of this genus is problematic because, although resembling teeth of some filter-feeding mobulids, *Archaeomanta* teeth show a well-developed pulp cavity extending to the apex of the cusp (Underwood et al., 2011), which

would rather indicate affinities with Rajiformes. By its rather marked mesio-distal compression, strong lingual inclination of the cusp and rather pronounced baso-labial angle of the crown, the tooth described here is close to those of *A. melenhorsti* but also bears characters present in teeth of *A. priemi* (collar at the base crown/root edge). However, it differs from the latter species by its smaller size and higher lower half of the crown. Considering the scarcity and preservation of the material from Togo and the lack of knowledge on systematics of the genus *Archaeomanta*, it is preferable to leave the presence species in open nomenclature.

Family Myliobatidae Bonaparte, 1838

Genus ***Myliobatis*** Cuvier, 1816

'Myliobatis' dixoni Agassiz, 1843

Fig. 8(X-Z)

Material: Several incomplete teeth from the glauconitic sandstones.

Description: Teeth are of crushing type with concave labial edge and convex lingual edge in occlusal view with triangular lateral extremities. Labial and lingual curvings are more marked in upper teeth than in those from lower files. The labial crown face is labially inclined and overhangs the lingually displaced root. Ornament on the labial crown face consists of rather large and irregular vertical folds. The lingual crown face is labially inclined with numerous fine vertical folds and a horizontal bulge is present at the basal edge of the lingual face. This bulge is thin and undulating, following the shape of underlying root branches. The root is typically polyaulacorhize with numerous parallel branches of similar size except for the two lateralmost, which are triangular in basal view.

Remarks: The material described here, although fragmentary, agrees with the morphology of the *Myliobatis dixoni* species complex (Baut and Genault, 1995), which is known from a

variety of localities worldwide and is in need of revision. *Myliobatis dixoni* was reported by Stromer (1910) from the limestones of Adabion.

Genus ***Aetomylaeus*** Garman, 1908

Aetomylaeus sp.

Fig. 8(D'-F')

Material: Several incomplete teeth from the glauconitic sandstones and one incomplete tooth from the glauconitic limestone.

Description: This large median myliobatid tooth fragment is labio-lingually compressed and mesio-distally elongate. Judging from the crown morphology, the preserved portion of the specimen represents less than half of the complete tooth size; it measures 45 mm mesio-distally. The crown is thicker at its center than at the edges and has a convex occlusal face in labial view. The lateral crown extremities are rounded and the lingual crown face is high, oblique, and overhangs the root. The lingual crown face bears worn irregular vertical wrinkles and is bordered by a fine basal bulge. The labial crown face bears fine vertical folds and is lower than the lingual face and abrupt, only slightly overhanging the root in occlusal view. The polyaulacorhize root is of similar height from one lateral margin to the other. Root branches are incompletely preserved on both the basal and lingual faces. The labial root face is high and bears narrow vertical notches.

Remarks: The crown of teeth from the median file is thicker at its center than at the edges, which is typical of *Aetomylaeus*. This tooth morphology does not match any published Paleogene myliobatid taxon and may represent one of the earliest reports of the genus, although some species included in *Myliobatis* might belong to *Aetomylaeus* (Cappetta, 2012). The specimens reported here differ from unworn *M. dixoni* teeth by their much larger size: the illustrated specimen although representing about half the length of the original tooth is much

larger (4.8 cm) than the largest complete *M. dixoni* teeth. *Aetomylaeus* sp. further differs from *M. dixoni* by its much higher root and basally inclined distal region of the crown and root.

Family Rhinopteridae Jordan & Evermann, 1896

Genus ***Rhinoptera*** Cuvier, 1829

Rhinoptera cf. *raeburni* White, 1934

Fig. 8(A'-C')

Material: One tooth from the glauconitic sandstones.

Description: This median tooth is 18mm wide and shows strong labio-lingual compression and mesio-distal expansion. The crown is high and of constant thickness from one lateral extremity to the other in lingual view. Lateral extremities are triangular in occlusal view and slightly labially oriented. The occlusal face is flat and worn with no ornament. The lingual face is flat and oblique with a marked lingual root overhang in profile/occlusal views. The lingual crown face bears strong vertical folds that widen and taper near the occlusal edge. A protruding basal vertical bulge is present on the lingual crown face, the base of which is concave in profile view except near the lateral extremities where a vertical fold reaches the basal bulge. The basal bulge is ondulated, each concavity corresponding to the underlying root branches. The labial crown face is oblique labially and strongly overhangs the root. The labial crown face bears strong irregular vertical folds. The root is polyaulacorhize with worn branches and lingually placed relative to the root. A line of labial foramina is present below the crown/root edge. A pair of median foramina is present at the basal edge of each root branch.

Remarks: Teeth of this genus can be separated from those of juvenile myliobatid specimens or small myliobatid species by their constant height from one lateral extremity to the other in lingual view, whereas this is higher in the median region of myliobatid teeth. The (probably)

Danian species *Rhinoptera prisca* Woodward, 1907 from Brazil and the Thanetian *Rhinoptera raeburni* from Nigeria (White, 1934) and Democratic Republic of Congo (Dartevelle and Casier, 1943) are the oldest representatives of the Rhinopteridae. Differences between teeth of these two species are tenuous and precise assessment of their potential synonymy is hampered by the quality of the illustrations of the type material of both species. The tooth recovered here shows strong labio-lingual compression and mesio-distal expansion. As this morphology is present in the type series of *Rhinoptera raeburni* but absent in the associated teeth of the *Rhinoptera prisca* type series, the material reported here is tentatively attributed to the former species.

5. Discussion

The elasmobranch assemblage from the glauconitic sandstone comprises 30 species and is dominated in both number of species and specimens by small nectobenthic carcharhiniforms (11 species) along with lamniforms (five species) and rare but diverse myliobatiforms (nine species). All taxa recovered from the underlying glauconitic limestone bed (*Chiloscyllium* sp., *Galeorhinus mesetaensis*, *Pseudobatos matzensis*, *Aetomylaeus* sp.) were also sampled in the glauconitic sandstone. Although species-level identifications are hampered by the poor preservation of the specimens, the vast majority of taxa identified here were formerly reported from the Danian-Ypresian interval, four of which are exclusively known from the upper Paleocene of Morocco (*Hologinglymostoma, Porodermoides spanios*) or Thanetian of France and Niger (*Pseudobatos matzensis, 'Dasyatis' sudrei*). *Arechia* sp. is the only taxon that was not known prior to the Eocene. This is in line with the benthic foraminifera assemblage reported here that indicates a Thanetian age for the sampled glauconitic sandstone. Both assemblages clarify previous reports on planktonic foraminifera that did not report biomarkers for the glauconitic horizons and indirectly suggested either a

late Paleocene (Slansky, 1962, p. 137) or a late Paleocene-early Eocene (Da Costa et al., 2013b, 2013c, 2013d, 2009) age for this horizon. This glauconitic sandstone layer seems to have a large geographical extent as it has been reported at the base of the Akinbo Formation above the Ewekoro Formation in Nigeria (Adegoke et al., 1972; Petters and Olsson, 1979), covering the *Togocyamus seefriedi* limestones in Benin (Bio-Lokoto et al., 1998) and on the top of Late Paleocene limestones in Ghana (Kjemperud et al., 1992). Yet, no fossils were described nor reported from this horizon. In Benin, a glauconitic level has been dated by radiochronology at 53 ± 2 Ma (Akpiti et al., 1985). However, this horizon is situated within the upper argillaceous series (Akpiti et al., 1985) and it is unclear whether it is equivalent to the glauconitic layer resting directly on top of the limestone series in the same area (Bio-Lokoto et al., 1998) and in Togo, especially considering that other glauconitic levels are also present in the argillaceous series in Togo and Benin (Slansky, 1962) as well as Nigeria (Adegoke, 1977). In Nigeria, radiochronologic analysis of the glauconitic layer that forms the base of the Akinbo Formation and of another glauconitic horizon situated three meters higher within the upper argillaceous series yielded an average age of 54,5 ± 2,7 Ma (Adegoke et al 1972). Yet, glaucony populations typically comprise grains with a long (5 myrs or more) period of genesis, which can result in artificially young absolute radiochronologic ages (Smith et al., 1998) and other biostratigraphic evidence suggest that the Paleocene/Eocene boundary should occur in the middle part of the Akinbo Formation in southwestern Nigeria (Adegoke et al., 1972; Petters and Olsson, 1979). A similar placement (within the overlying shaly argillaceous series) of the Palaeocene/Eocene boundary was made in Togo (Johnson et al., 2000; Slansky, 1962). This is consistent with the Thanetian age suggested by the benthic foraminifera assemblage and by some elements of the elasmobranch fauna reported here and indicates a late Thanetian age for the glauconitic horizons.

The composition of the elasmobranch assemblage described here shows strong resemblances with late Paleocene faunas from Morocco (‘Sillon A’ in the Ganntour Basin, ‘Couche 2a’ in the Ouled Abdoun Basin – see Yans et al. 2014 for discussion on the stratigraphy) including *Hologinglymostoma, Serratolamna aschersoni, Otodus obliquus, Jaekelotodus africanus,* small *Isurolamna* morph, *Foumtizia* aff. *gadaensis, Premontreia (O.) subulidens, Porodermoides spanios, Galeorhinus mesetaensis, Abdounia africana, Myliobatis dixoni*. The absence of *S. aschersoni* and *Arechia* in the Moroccan late Paleocene fauna would indicate that the Moroccan Sillon A and Couche 2a assemblages most likely pre-late Thanetian since these taxa are present in the late Thanetian Togolese fauna and in the younger (likely Ypresian, see Yans et al. 2014) C1/C2 and C1 faunas in Morocco (Noubhani and Cappetta, 1997). This is consistent with the Selandian-early Thanetian age provided by chemostratigraphic analyses for the Couche 2a (Yans et al. 2014). Other differences between the C2/Sillon A faunas (which include squaliforms and hexanchiforms) and the Togolese assemblages (which include *Palaeohypotodus* and small *Physogaleus*) are more likely environment-related or due to endemism (see below). In contrast, very few taxa reported here are represented in the Thanetian of Niger (Cappetta, 1972) and Nigeria (White, 1934), whereas all taxa reported from Nigeria (*Eotorpedo hilgendhorfi, E. jaekeli, Squatiscyllium nigeriensis, Ginglymostoma sokotoense, Hypolophites myliobatoides, Myliobatis wurnoensis*) were found in Niger. Only the ‘species’ *Myliobatis dixoni* occurs both in Togo and Nigeria, but this taxon is in need of revision (see above) and has wide geographical and stratigraphic ranges. Similarly, *‘Dasyatis’ sudrei* is the only species shared by the Togolese and Nigerien faunas, but this species is also known from the Thanetian of Senegal (Sylvain Adnet, pers. com.). Comparison with Thanetian faunas from southeastern Atlantic (Dartevelle and Casier, 1959, 1943) is made difficult by the lack of micro-fossils in corresponding assemblages and because their precise stratigraphic origin is sometimes uncertain. Reappraisal of the

stratigraphic position of Dartevelle and Casier's samplings (Solé et al., 2018) suggests that the only clear Thanetian assemblage that yielded elasmobranch remains is restricted to layer 18 of Landana (Cabinda enclave), which comprises *Sulcidens sulcidens, 'Cretolamna appendiculata'* (possibly *Otodus (O.) obliquus*), *M. dixoni*, and ? *Carcharias substriatus*. A number of other elasmobranch assemblages from Landana (layers 13-16) are Selandian-Thanetian (Zone P4) and include similar species plus *Delpitioscyllium africanum* and *Jaekelotodus speyeri*. Other assemblages from different layers at Manzadi Point VI (Democratic Republic of Congo) are possibly Selandian (Solé et al., 2018) and include *Delpitoscyllium africanum, Otodus (O.) obliquus, 'Cretolamna appendiculata', Myliobatis dixoni, Myliobatis nzadinensis*, and *Rhinoptera raeburni*. Despite the lack of precision on both the stratigraphic origin and the microfauna composition of the Paleogene assemblages reported by Dartevelle and Casier (1959, 1943), some cosmopolitan pelagic taxa from Landana and Democratic Republic of Congo (*Otodus (O.) obliquus*, *Rhinoptera* cf. *raeburni*, *Isurolamna*) were recorded in Togo but not in the faunas from the epicontinental sea of Niger and Nigeria.

The much stronger affinities between the Togolese assemblage and North African faunas compared with Niger and Nigeria is unexpected. This is especially surprising considering the probable connection between the Gulf of Guinea and Niger (and to a greater extent, North Africa) in the Thanetian through the trans-Saharan seaway (Belkhodja and Bignot, 2004) and the closer geographical position of the Togolese locality with Nigeria and Niger. Such variations in faunal composition might be related to different palaeoenvironmental conditions and/or stratigraphic positions. However, dating of Moroccan (Yans et al., 2014), Nigerien, and Nigerian faunas within the Thanetian age is still in need of precision. It is hence difficult to assess the effect of potential stratigraphic differences on the variations in faunal composition of these assemblages. However, although most of the taxa

from Niger and Nigeria are restricted to the Thanetian, the nectobenthic torpediniform *E. hilgendhorfi* ranges from the Selandian (Dartevelle and Casier, 1959, 1943) to Ypresian (Arambourg, 1952; Case et al., 2015) and is absent from the Togolese glauconitic horizons. Conversely, some cosmopolitan taxa from Landana and Democratic Republic of Congo and Morocco (*Otodus (O.) obliquus*, *Isurolamna*) with long stratigraphic ranges were recorded in Togo but not in the faunas from Niger and Nigeria. This tends to indicate that differences in stratigraphic origins, if proven, might not be the sole factor that explains the faunal differences observed. The Thanetian fauna from Morocco ('Sillon A' and 'couche 2a') comprises hexanchiforms, diverse squaliforms, and pristiophoriforms that indicate an open marine environment. Conversely, the Thanetian assemblage from Niger suggests a restricted coastal palaeoenvironment (Cappetta, 1972) with freshwater to coastal osteichthyans (Bagridae, Osteoglossiformes, Dipnoi) and numerous benthic elasmobranchs. Its similarity with the assemblage from Nigeria (White, 1934) suggests a similar environment for the latter. Although devoid of hexanchiforms, squaliforms and pristiophoriforms, the elasmobranch assemblage reported here is dominated by small nectobenthic carcharhiniforms (mostly Triakidae and Scyliorhinidae) and numerous pelagic batomorphs and lamniforms. The benthic foraminiferal assemblage includes members of the Nodosaridae (*Frondicularia*, *Lenticulina*, and *Palmula*), which indicates a coastal and warm environment. This faunal evidence, alongside the absence of continental organisms and presence of nautiloids and rare coral polyps suggests a plainly marine environment on the continental shelf, which may explain the numerous elasmobranch taxa shared with the Moroccan fauna. In addition, the absence in Niger and Nigeria of some cosmopolitan elasmobranch taxa known from Togo, Morocco, and Angola lends support for a palaeonenvironmental control on the distribution of late Paleocene elasmobranch faunas that differentiates an open-sea southeastern Atlantic fauna from a more neritic fauna in the epicontinental trans-Saharan seaway. However, some degree of endemism

is present among the former fauna, as exemplified by the number of taxa in the Togolese assemblage (*Premontreia (Oxyscyllium)* sp., *Palaeogaleus* sp., *'Ginglymostoma'* sp., *Arechia* sp., *Aetomylaeus* sp., *Archaeomanta* sp., and possibly *Coupatezia* sp. and *Burnhamia* sp.) that despite their poor preservation probably correspond to new unnamed species. In addition, none of the species reported from the underlying limestones in the Tabligbo area by Stromer (1910) were recovered in our samplings, excepted *M. dixoni*. Among the other species described by Stromer (1910), *Odontaspis elegans* var. *substriata* Stromer, 1910 was based on a single incomplete specimen that makes the validity of this species dubious. Yet, it was subsequently reported from Angola (Dartevelle and Casier, 1959, 1943) and Niger (Cappetta, 1972) based on specimens that indicate affinities with the genus *Brachycarcharias*. While Stromer's *Xenodolamia* aff. *simplex* is an indeterminate tooth of a probable lamniform and *Ginglymostoma* aff. *thielense* an indeterminate ginglymostomatid, the genus *Hypolophites* Stromer, 1910 is also known from the Thanetian of Niger (Cappetta, 1972), Nigeria (White, 1934) and Angola (Leriche, 1913). The underlying limestones where Stromer's specimens were sampled very likely correspond to a different palaeoenvironment, which may explain those differences, although additional work on the stratigraphy of these levels is needed to confirm their Thanetian age.

Acknowledgements

We wish to thank the Directors of the ScanTogo (M. Eric Goulignac) and WACEM (M. Motaparti Prasad) quarries in Tabligbo as well as employees from these companies for providing access and sampling permissions. Sylvain Adnet and Henri Cappetta are thanked for fruitful discussions on Paleocene elasmobranch taxonomy. Maëva Orliac and Mickaël J. Mourlam (University of Montpellier) helped in the field. Romain Vullo, Charlie J.

Underwood and Todd. D. Cook provided helpful comments on an earlier version of the manuscript. This study was partly supported by a CNRS (PICS) grant n°229424.

References

Adegoke, O.S., 1977. Stratigraphy and paleontology of the Ewekoro formation (Paleocene) of southwestern Nigeria. Bull. Am. Paleontol. 71, 1–379.

Adegoke, O.S., Dessauvagie, T.F.J., Kogbe, C.A., 1972. Radioactive age determination of glauconite from the type locality of the Ewekoro Formation. Presented at the Conference on African Geology, 1970, Ibadan, pp. 277–280.

Adnet, S., Cappetta, H., Tabuce, R., 2010. A Middle–Late Eocene vertebrate fauna (marine fish and mammals) from southwestern Morocco; preliminary report: age and palaeobiogeographical implications. Geol. Mag. 147, 860–870.

Adolfssen, J.S., Ward, D.J., 2015. Neoselachians from the Danian (Early Paleocene) of Denmark. Acta Palaeontol. Pol. 60, 313–338.

Adolfssen, J.S., Ward, D.J., 2014. Crossing the boundary: an elasmobranch fauna from Stevns Klint, Denmark. Palaeontology 57, 591–629.

Agassiz, L. 1843 [1833-1844]. Recherches Sur Les Poissons Fossiles. Vol. 3. Neuchatel & Soleure: Petitpierre, pp. 442.

Akpiti, S., Clauer, N., Houessou, A., Lang, J., Tisserant, D., 1985. Datation isotopique K-Ar d'un niveau de sable glauconieux à la limite Paleocene-Eocene dans le bassin cotier Béninois (Afrique de l'Ouest). J. Afr. Earth Sci. 3, 487–490.

Arambourg, C., 1952. Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). Notes Mém. Serv. Géol. Maroc 92, 1–372.

Arambourg, C., 1935. Note préliminaire sur les vertébrés fossiles des phosphates du Maroc. Bull. Soc. Géol. Fr. 5, 413–439.

Baut, J.-P., Genault, B., 1995. Contribution à l'étude des élasmobranches du Thanétien (Paléocène) du Bassin de Paris. 1. Découverte d'une faune d'élasmobranches dans la partie supérieure des Sables de Bracheux (Thanétien, Paléocène) des régions de Compiègne (Oise) et de Montdidier (Somme), in: Herman, J., Van Waes, H. (Eds.), Elasmobranches et Stratigraphie. Professional Paper of the Belgian Geological Survey, Brussels, pp. 185–259.

Belkhodja, L., Bignot, G., 2004. La transgression thanétienne (Paléocène supérieur) dans l'Aurès occidental (Algérie), d'après les associations de Foraminifères de la coupe d'El

Kantara. Rev. Micropaléontologie 47, 1–12.
Bio-Lokoto, A., Carbonnel, G., de Klasz, I., de Klasz, S., Lang, J., Salard-Cheboldaeff, M., 1998. Données nouvelles biochronologiques et paléoécologiques sur le bassin sédimentaire côtier du Bénin entre le Crétacé supérieur et l'éocène basal (Afrique de l'ouest). Rev. Micropaléontologie 41, 29–57.
Cappetta, H., 2012. Chondrichthyes - Mesozoic and Cenozoic Elasmobranchii: Teeth, Handbook of Paleoichthyology. Verlag F. Pfeil, Munich.
Cappetta, H., 2006. Elasmobranchii Post-Triadici (index specierum), Fossilium Catalogus I: Animalia. Blackhuys Publishers, Leiden.
Cappetta, H., 1992. Carcharhiniformes Nouveaux de l'Ypresien Du Bassin de Paris. Geobios. 25, 639–46.
Cappetta, H., 1983. Additions à la faune de sélaciens fossiles du Maroc. 2: Révision de *Raja praealba* ARAMBOURG, 1952, espèce de l'Yprésien des Ouled Abdoun. Tert. Res. 5, 1–8.
Cappetta, H., 1982. Revision de *Cestracion duponti* Winkler, 1874 (Selachii, Batomorphii) du Bruxellien de Woluwe-Saint-Lambert (Eocene Moyen de Belgique). Contrib. Tert. Quat. Geol. 19, 113–125.
Cappetta, H., 1980. Les sélaciens du Crétacé supérieur du Liban. II : Batoïdes. Palaeontogr. Abt. A 168, 149–229.
Cappetta, H., 1972. Les poissons crétacés et tertiaires du bassin des Iullemmeden (République du Niger). Palaeovertebrata 5, 179–251.
Cappetta, H., Case, G.R., 1975. Sélaciens nouveaux du Crétacé du Texas. Geobios 8, 303–307.
Cappetta, H., Case, G.R., 2016. A selachian fauna from the Middle Eocene (Lutetian, Lisbon Formation) of Andalusia, Covington County, Alabama, USA. Palaeontogr. Abt A 307, 43–103.
Cappetta, H., Gregorová, R., Adnet, S., 2016. New selachian assemblages from the Oligocene of Moravia (Czech Republic). Neues Jahrb. Für Geol. Paläontol. - Abh. 280, 259–284.
Cappetta, H., Pfeil, F., Schmidt-Kittler, N., 2000. New biostratigraphical data on the marine Upper Cretaceous and Palaeogene of Jordan. Newsl. Stratigr. 38, 81–95.
Cappetta, H., Traverse, M., 1988. Une riche faune de sélaciens dans le bassin à phosphate de Kpogamé-Hahotoé (Eocène moyen du Togo): note préliminaire et précisions sur la structure et l'âge du gisement. Geobios 21, 359–365.
Case, G.R., 1994. Fossil fish remains from the Late Paleocene Tuscahoma and Early Eocene

Bashi Formations of Meridian, Lauderdale County, Mississippi. Part I. Selachians. Palaeontogr. Abt A 230, 97–138.

Case, G.R., Cappetta, H., 1990. The Eocene selachian fauna from the Fayoum depression in Egypt. Palaeontogr. Abt. A 212, 1–30.

Case, G.R., Cook, T.D., Wilson, M.V.H., 2015. A new elasmobranch assemblage from the early Eocene (Ypresian) Fishburne Formation of Berkeley County, South Carolina, USA. Can. J. Earth Sci. 52, 1121–1136.

Case, G.R., Udovichenko, N.I., Nessov, L.A., Averianov, A.O., Borodin, P.D., 1996. A middle Eocene selachian fauna from the white mountain formation of the Kizylkum desert, Uzbekistan, C.I.S. Palaeontographica 242, 99–126.

Casier, E., 1967. Le Landénien de Dormaal (Brabant) et sa faune ichthyologique. Mém. Inst. R. Sci. Nat. Belg. 156, 1–66.

Casier, E., 1966. Faune ichthyologique du London Clay. Brit. Mus. Nat. Hist. 496 p.

Casier, E., 1946. La faune ichthyologique de l'Yprésien de la Belgique. Mém. Mus. R. Hist. Nat. Belg. 104, 1–267.

Casier, E., 1943. Contributions à l'étude des Poissons fossiles de la Belgique. IV. Observations sur la faune ichtyologique du Landénien. Bull. Mus. R. Hist. Nat. Belg. 19, 1–16.

Da Costa, P.Y.D., Affaton, P., Borschneck, D., Vidal, L., Sonzogni, C., Johnson, A.K.C., 2013a. Evolution verticale des minéraux argileux de la série crétacé supérieur-tertiaire du bassin côtier togolais et leurs implications paléoclimatiques. Afr. Geosci. Rev. 20, 105–120.

Da Costa, P.Y.D., Affaton, P., Salaj, J., Johnson, A.K.C., Seddoh, K., 2013b. Biozonation des formations sédimentaires du bassin côtier du Togo (Afrique de l'Ouest). Rev. Ivoir. Sci. Technol. 21–22, 45–73.

Da Costa, P.Y.D., Johnson, A.K.C., Affaton, P., 2013c. Les terrains paléozoïques et mésozoïques du bassin côtier togolais : Stratigraphie et Paléogéographie. Stand. Sci. Res. Essays 1, 415–429.

Da Costa, P.Y.D., Johnson, A.K.C., Affaton, P., 2009. Biostratigraphy and geodynamic impact in the uppermost part of the northeastern coastal basin of Togo. Comptes Rendus Palevol 8, 511–526.

Da Costa, P.Y.D., Medus, J., Flicoteaux, R., Salaj, J., Harmsmid, B., Affaton, P., Seddoh, K., 2013d. Biostratigraphie de la bordure septentrionale du bassin côtier togolais. Apport des données palynologiques et structurales. Rev CAMES 1, 6–20.

Daimeries, S.A., 1888. Notes ichthyologiques (Système Landénien) - I. Ann. Société R. Malacol. Belg. 23, 42–43.

Dartevelle, E., Casier, E., 1959. Les poissons fossiles du Bas-Congo et des régions voisines. Ann. Mus. Congo Belge Sér. Min. Géol. Paléontol. 3, 77–98.

Dartevelle, E., Casier, E., 1943. Les poissons fossiles du Bas-Congo et des régions voisines. Ann. Mus. Congo Belge Sér. Min. Géol. Paléontol. 3, 1–200.

Dutheil, D.B., 1997. Presence d'Archaeomanta (Elasmobranchii: Mobulidae) dans l'Eocene Moyen du Bassin de Paris. Cossmanianna 5, 57–60.

Ehret, D.J., Ebersole, J., 2014. Occurrence of the megatoothed sharks (Lamniformes: Otodontidae) in Alabama, USA. PeerJ 2.

Furon, R., Kouriatchy, N., 1948. La faune éocene du Togo. Mém. Muséum Natl. Hist. Nat. 27, 95–114.

Glikman, L.S., 1964. Sharks of Paleogene and their stratigraphic significance. Nauka Press 229 p. Moscow. [in Russian].

Guinot, G., Adnet, S., Shimada, K., Shimada, K., Underwood, C.J., Siversson, M., Ward, D.J., Kriwet, J., Cappetta, H., 2018. On the need of providing tooth morphology in descriptions of extant elasmobranch species. Zootaxa 4461, 118–126.

Guinot, G., Cavin, L., 2016. 'Fish' (Actinopterygii and Elasmobranchii) diversification patterns through deep time. Biol. Rev. 91, 950–981.

Herman, J., 1979. Additions to the Eocene fish fauna of Belgium. 4. Archaeomanta, a new genus from the Belgium and North African Palaeogene. Tert. Res. 2, 61–67.

Herman, J., 1977. Les sélaciens des terrains néocrétacés et paléocènes de Belgique et des contrées limitrophes. Eléments d'une biostratigraphie intercontinentale. Mém. Pour Serv. À Explic. Cartes Géologiques Minières 15, 1–450.

Herman, J., Hovestadt-Euler, M., Hovestadt, D.C., 1997. Part B: Batomorphii. No. 2: Order: Rajiformes - Suborder: Pristoidei - Family: Pristidae - Genera: *Anoxypristis* and *Pristis*; No. 3: Suborder: Rajoidei - Superfamily: Rhinobatoidea - Families: Rhinidae - Genera: *Rhina* and *Rhynchobatus* and Rhinobatidae - Genera: *Aptychotrema, Platyrhina, Plathyrhinoidis, Rhinobatos, Trygonorrhina, Zanobatus* and *Zapteryx*, in: Stehmann, M. (Ed.), Contributions to the Study of the Comparative Morphology of Teeth and Other Relevant Ichthyodorulites in Living Supraspecific Taxa of Chondrichthyan Fishes. Bull. Inst. R. Sc. N. B. – B., 67, pp. 107–162.

Herman, J., Hovestadt-Euler, M., Hovestadt, D.C., 1992. Part A: Selachii. No. 4: Order: Orectolobiformes – Families: Brachaeluridae, Ginglymostomatidae, Hemiscyllidae,

Orectolobidae, Parascyllidae, Rhiniodontidae, Stegostomatidae. Order: Pristiophoriformes – Family: Pristiophoridae. Order: Squatiniformes – Family: Squatinidae, in: Stehmann, M. (Ed.), Contributions to the Study of the Comparative Morphology of Teeth and Other Relevant Ichthyodorulites in Living Supraspecific Taxa of Chondrichthyan Fishes. Bull. Inst. R. Sc. N. B. – B., 62, pp. 193–254.

Johnson, A.K.C., Rat, P., Lang, J., 2000. Le bassin sédimentaire à phosphates du Togo (Maastrichtien-Eocène): stratigraphie, environnements et évolution. J. Afr. Earth Sci. 30, 183–200.

Kemp, D.J., Kemp, L., Ward, D.J., 1990. An Illustrated Guide to the British Middle Eocene Vertebrates. Privately published, London, pp. 59.

King, C., Iakovleva, A., Steurbaut, E., Heilmann-Clausen, C., Ward, D., 2013. The Aktulagay section, west Kazakhstan: a key site for northern mid-latitude Early Eocene stratigraphy. Stratigraphy 10, 171–209.

Kjemperud, A., Agbesinyale, W., Agdestein, T., Gustafsson, C., Yüler, A., 1992. Tectono-stratigraphic history of the Keta Basin, Ghana, with emphasis on tate erosional episodes, in: Géologie Africaine. Presented at the Colloque Géologique, Libreville, pp. 55–69.

Kocsis, L., Gheerbrant, E., Mouflih, M., Cappetta, H., Yans, J., Amaghzaz, M., 2014. Comprehensive stable isotope investigation of marine biogenic apatite from the late Cretaceous–early Eocene phosphate series of Morocco. Palaeogeogr. Palaeoclimatol. Palaeoecol. 394, 74–88.

Kozlov, V.A., 2001. Additions to the Paleogene elasmobranch fauna of western Kazakhstan. Turania, a new shark genus (Odontaspididae) and a new ray species (genus Archaeomanta, Mobulidae). Mater. Po Stratigr. Paleontol. Urala 83–86.

Landemaine, O., 1991. Sélaciens nouveaux du Crétacé supérieur du sud-ouest de la France. Quelques apports à la systématique des élasmobranches. Soc. Amic. Géol. Amat. 1, 1–45.

Last, P.R., Séret, B., Naylor, G.J.P. 2016. A new species of guitarfish, Rhinobatos borneensis sp. nov. with a redefinition of the family-level classification in the order Rhinopristiformes (Chondrichthyes: Batoidea). Zootaxa 4117, 451–475.

Leder, R.M., 2013. Eocene Carcharinidae and Triakidae (Elasmobranchii) of Crimea and Kazakhstan. Leipz. Geowiss. 20, 1–57.

Leriche, M., 1938. Contribution à l'étude des poissons fossiles des pays riverains de la Méditerranée américaine (Venezuela, Trinité, Antilles, Mexique). Mém. Soc. Pal. Suisse 61, 1–42.

Leriche, M., 1921. Sur les restes de Poissons remaniés dans le Néogène de la Belgique. Leur signification au point de vue de l'histoire géologique de la Belgique pendant le tertiaire supérieur. Bull. Société Belge Géologie 30, 115–120.

Leriche, M., 1913. Les poissons paléocènes de Landana (Congo). Les gisements de poissons paléocènes et éocènes de la côte occidentale d'Afrique. Ann. Mus. Congo Belge 1, 67–91.

Leriche, M., 1906. Contribution à l'étude des poissons fossiles du Nord de la France et des régions voisines. Mém. Société Géologique Nord 5, 1–430.

Malyshkina, T.P., Ward, D.J., 2016. The Turanian Basin in the Eocene: the new data on the fossil sharks and rays form the Kyzylkum Desert (Uzbekistan). Proc. Zool. Inst. Russ. Acad. Sci. 320, 50–65.

Moreau, F., Mathis, S., 2000. Les élasmobranches du Thanétien (Paléocène) du Nord de la France, des carrières de Templeuve et de Leforest. Cossmanniana 7, 1–18.

Neugeboren, L., 1851. Die vorweltlichen Squaliden-Zähne aus dem Grobkalke bei Portsesd am Altflusse unweit Talmatsch. Zweite Abtheilung. Arch. Ver. Für Siebenbürg. Landeskd. 4, 151–214.

Nilsson, J., 2003. Carcharhiniforma hajar från Limhamns kalkbrott, Skåne. Examensarbeten Geol. Vid Lunds Univ., pp. 20.

Noubhani, A., Cappetta, H., 1997. Les Orectolobiformes, Carcharhiniformes et Myliobatiformes des bassins à phosphate du Maroc (Maastrichtien-Lutétien basal). Systématique, biostratigraphie, évolution et dynamique des faunes. Palaeo Ichthyol. 8, 1–327.

Oppenheim, P., 1915. Die eocänen Invertebraten. Fauna des Kalksteins in Togo im Zusammenhange mit anderen Tertiärablagerungen Afrikas vergleichend betrachtet. Beitr. Zur Geol. Erforsch. Dtsch. Schutzgebiete 12, 1–26.

Petters, S.W., Olsson, R.K., 1979. Planktonic Foraminifera from the Ewekoro Type Section (Paleocene) Nigeria. Micropaleontology 25, 206–213.

Probst, J., 1878. Beitrag zur Kenntnis der fossilen Fische aus der Molasse von Baltringen. Jahresh. Ver. Für Vaterl. Naturkunde Württ. 34, 113–154.

Reinecke, T., Engelhard, P., 1997. The selachian fauna from Geschiebe of the Lower Selandian basal conglomerate (Thanetian, Late Paleocene) in the Danish subbasin (Sealand, Scania, Western Baltic Sea). Erratica 2.

Slansky, M., 1962. Contribution à l'étude géologique du bassin sédimentaire côtier du Dahomey et du Togo. Technip, Paris., pp. 271.

Smith, P.E., Evensen, N.M., York, D., Odin, G.S., 1998. Single-Grain 40Ar-39Ar Ages of Glauconies: Implications for the Geologic Time Scale and Global Sea Level Variations. Science 279, 1517–1519.

Solé, F., Noiret, C., Desmares, D., Adnet, S., Taverne, L., De Putter, T., Mees, F., Yans, J., Steeman, T., Louwye, S., Folie, A., Stevens, N.J., Gunnell, G.F., Baudet, D., Yaya, N.K., Smith, T., 2018. Reassessment of historical sections from the Paleogene marine margin of the Congo Basin reveals an almost complete absence of Danian deposits. Geosci. Front.

Stromer, E., 1910. Reptilien und Fischreste aus dem marinen Alttertiär von Südtogo (West Africa). Monatsbericht Dtsch. Geol. Ges. 62, 478–505.

Tabuce, R., Adnet, S., Cappetta, H., Noubhani, A., Quillevere, F., 2005. Aznag (bassin d'Ouarzazate, Maroc), nouvelle localité à sélaciens et mammifères de l'Eocène moyen (Lutétien) d'Afrique. Bull. Soc. Géol. Fr. 176, 381–400.

Underwood, C.J., Kolmann, M.A., Ward, D.J., 2017. Paleogene origin of planktivory in the Batoidea. J. Vertebr. Paleontol. 37, e1293068.

Underwood, C.J., Ward, D.J., King, C., Antar, S.M., Zalmout, I.S., Gingerich, P.D., 2011. Shark and ray faunas in the Middle and Late Eocene of the Fayum Area, Egypt. Proc. Geol. Assoc. 122, 47–66.

Vullo, R., Guinot, G., Barbe, G., 2016. The first articulated specimen of the Cretaceous mackerel shark Haimirichia amonensis gen. nov. (Haimirichiidae fam. nov.) reveals a novel ecomorphological adaptation within the Lamniformes (Elasmobranchii). J. Syst. Palaeontol. 14, 1003–1024.

Ward, D.J., Wiest, R.L.J., 1990. A checklist of Palaeocene and Eocene sharks and rays (Chondrichthyes) from the Pamunkey Group, Maryland and Virginia, USA. Tert. Res. 12, 81–88.

White, E.I., 1934. Fossil fishes of Sokoto province. Bull. Geol. Surv. Niger. 14, 1–78.

Winkler, T.C., 1876a. Mémoire sur quelques restes de poissons du système heersien. Arch. Mus. Teyler 4, 1–15.

Winkler, T.C., 1876b. Deuxième mémoire sur des dents de poissons fossiles du terrain bruxellien. Arch. Mus. Teyler 4, 16–48.

Winkler, T.C., 1874. Mémoire sur des dents de poissons du terrain bruxellien. Arch. Mus. Teyler 3, 295–304.

Woodward, A.S., 1907. Notes on some Upper Cretaceous fish-remains from the Provinces of Sergipe and Pernambuco, Brazil. Geol. Mag. 5, 193–197.

Yans, J., Amaghzaz, M., Bouya, B., Cappetta, H., Iacumin, P., Kocsis, L., Mouflih, M., Selloum, O., Sen, S., Storme, J.-Y., Gheerbrant, E., 2014. First carbon isotope chemostratigraphy of the Ouled Abdoun phosphate Basin, Morocco; implications for dating and evolution of earliest African placental mammals. Gondwana Res. 25, 257–269.

Zhelezko, V.I., Kozlov, V.A., 1999. Elasmobranchii and Palaeogene biostratigraphy of Transural and Central Asia. Mater. Po Stratigr. Paleontol. Urala 3, 1–324.

Figure captions

Figure 1. A, General geological map of the Coastal Sedimentary Basin in Southern Togo (Maritime Region) and sampled sites. **B**, synthetic sedimentary log of the WACEM and ScanTogo sections.

Figure 2. Benthic foraminifera sampled from the glauconitic sandstone. **A**: *Frondicularia microdisca* (TAB2-1), **B**: *Frondicularia phosphatica* (TAB2-2), **C**: *Frondicularia vertebralis* (TAB2-3), **D**: *Palmula sigmoicosta* (TAB2-4), **E**: *Nodosaria affinis* (TAB2-5), **F**: *Nodosaria affinis* (TAB2-6), **G**: *Lenticulina incisa* (TAB2-7). Scale bars equal 500 μm, excepted A-B (1 mm).

Figure 3. Squatiniformes and Orectolobiformes. **A-B**: *Squatina* cf. *prima*. **A**: lateral tooth (TAB2-8) in labial view, **B**: anterior tooth (TAB2-9) in labial view. **C-D:** *Chiloscyllium* sp. **C:** anterior tooth (TAB3-1) in labial view and **D**: lateral tooth (TAB2-10) in labial view. **E-F**: *Hologinglymostoma* sp. **E**: lateral tooth (TAB2-11) in occlusal view, **F**: lateral tooth (TAB2-12) in lingual view, **G-I**: *'Ginglymostoma'* sp. **G**: anterior tooth (TAB2-13) in labial view, **H**: anterolateral tooth (TAB2-15) in labial view, **I**: posterior tooth (TAB2-14) in labial view. All scale bars equal 500 μm.

Figure 4. Lamniformes. **A-B**: *Serratolamna aschersoni*, upper lateral tooth (TAB2-16) in **A**, lingual and **B**, labial views. **C-U**: *Otodus (Otodus) obliquus*. **C**: lower anterior tooth (TAB2-17) in lingual view, **D**: lower lateroposterior tooth (TAB2-18) in lingual view, **E-F**: upper lateral tooth (TAB2-19) in **E**, labial and **F**, lingual views; **G**: upper lateral tooth (TAB2-20) in lingual view, **H**: upper lateral tooth (TAB2-21) in lingual view, **I**: upper lateroposterior tooth

(TAB2-22) in lingual view, **J-K**: anterior tooth (TAB2-23) in **J**, lingual and **K**, labial views, **L-M**: upper lateral tooth (TAB2-24) in **L**, lingual and **M**, labial views, **N-O**: upper lateral tooth (TAB2-25) in **N**, lingual and **O**, labial views, **P**: upper intermediate? tooth (TAB2-26) in lingual view, **Q**: upper lateral tooth (TAB2-27) in lingual view, **R-S**: upper lateral tooth (TAB2-28) in **R**, labial and **S**, lingual views, **T**: posterior tooth (TAB2-29) in lingual view, **U**: posterior tooth (TAB2-30) in lingual view. All scale bars equal 1 cm.

Figure 5. Lamniformes. **A-I**: *Jaekelotodus africanus*. **A-C**: anterior tooth (TAB2-31) in **A**, lingual, **B**, labial and **C**, profile views, **D-E**: upper lateral tooth (TAB2-32) in **D**, lingual and **E**, labial views, **F-G**: upper lateral tooth (TAB2-33) in **F**, labial and **G**, lingual views, **H-I**: posterior tooth (TAB2-34) in **H**, lingual and **I**, labial views. **J-K**: *Palaeohypotodus* sp. **J**: lateroposterior tooth (TAB2-35) in lingual view, **K**: anterior tooth (TAB2-36) in labial view. **L-R**: *Isurolamna* sp. **L-N**: upper anterior tooth (TAB2-37) in **L**, lingual, **M**, labial and **N**, profile views. **O-P**: upper lateral tooth (TAB2-38) in **O**, labial and **P**, lingual views, **Q-R**: lower lateral tooth (TAB2-39) in **Q**, labial and **R**, lingual views. Scale bars: 1 cm (A-G), 5 mm (H-I, L-R), 1 mm (J-K).

Figure 6. Carcharhiniformes. **A-D**: *Foumtizia* aff. *gadaensis*. **A**: lateral tooth (TAB2-40) in labial view, **B**: anterior tooth (TAB2-41) in labial view, **C-D**: anterior tooth (TAB2-42) in **C**, lingual and **D**, labial views. **E-K**: *Premontreia (Oxyscyllium) subulidens*. **E**: anterior tooth (TAB2-43) in lingual view, **F-G**: lateral tooth (TAB2-44) in **F**, lingual and **G**, labial views, **H-I**: anterior tooth (TAB2-45) in **H**, labial and **I**, lingual views, **J-K**: posterior tooth (TAB2-46) in **J**, lingual and **K**, labial views. **L-O**: *Premontreia (Oxyscyllium)* sp. **L-M**: lateral tooth (TAB2-47) in **L**, lingual and **M**, labial views, **N**: lateral tooth (TAB2-48) in labial view, **O**, lateral tooth (TAB2-49) in labial view. **P-R**: *Porodermoides spanios*. **P**: anterior tooth

(TAB2-50) in labial view, **Q-R**: anterior tooth (TAB2-51) in **Q**, lingual and **R**, labial views. **S-V**: *Palaeogaleus* sp. **S**: lateral tooth (TAB2-52) in labial view, **T**: lateral tooth (TAB2-53) in labial view, **U**: lateral tooth (TAB2-54) in labial view, **V**: lateral tooth (TAB2-55) in labial view. **W-X:** *Galeorhinus mesetaensis.* **W**: lateral tooth (TAB3-2) in labial view, **X**: anterior tooth (TAB3-3) in labial view. **Y-A'**: *Galeorhinus* sp. **Y-Z**: lateral tooth (TAB2-56) in **Y**, lingual and **Z**, labial views, **A'**: anterior tooth (TAB2-57) in labial view. Scale bars equal 1 mm except A-D and S-V (500 μm).

Figure 7. Carcharhiniformes and Rhinopristiformes. **A-C**: *Triakis* sp. **A**: anterior tooth (TAB2-58) in labial view, **B**: anterior tooth (TAB2-59) in labial view, **C**: lateral tooth (TAB2-60) in labial view. **D-J**: Triakidae ? indet. **D-E**: lateral tooth (TAB2-61) in **D**, labial and **E**, occlusal views, **F**: lateral tooth (TAB2-62) in labial view, **G**: lateral tooth (TAB2-63) in labial view, **H-I**: lateral tooth (TAB2-64) in **H**, lingual and **I**, labial views, **J**: lateral tooth (TAB2-65) in occlusal view. **K-T**: *Abdounia africana*. **K**: symphysial tooth (TAB2-66) in labial view, **L-M**: latero-posterior tooth (TAB2-67) in **L**, labial and **M**, lingual views, **N-O**: anterior tooth (TAB2-68) in **N**, lingual and **O**, labial views, **P-Q**: anterior tooth (TAB2-69) in **P**, basal and **Q**, labial views, **R-S**: lateral tooth (TAB2-70) in **R**, labial and **S**, lingual views, **T**, latero-posterior tooth (TAB2-71) in labial view. **U-Y**: *Physogaleus* sp. **U-V**: lateral tooth (TAB2-72) in **U**, labial and **V**, lingual views, **W-X**, lateral tooth (TAB2-73) in **W**, labial and **X**, lingual views, **Y**: lateral tooth (TAB2-74) in labial view. **Z-B'**: *Pseudobatos matzensis* comb. nov. **Z-A'**: anterior tooth (TAB3-4) in **Z**, lingual and **A'**, basal views, **B'**: posterior tooth (TAB2-75) in lingual view. Scale bars: 1 mm (D-E, N-Y), 500 μm (A-C, F-M, Z-A') and 200 μm (B').

Figure 8. Batomorphii. **A**: *Arechia* sp., tooth (TAB2-76) in lingual view. **B-H**: *Coupatezia* sp. **B-D**: non-cuspidate tooth (TAB2-77) in **B**, lingual, **C**, occlusal and **D**, basal views, **E-F**: non-

cuspidate tooth (TAB2-78) in **E**, lingual and **F**, occlusal views, **G-H**: cuspidate tooth (TAB2-79) in **G**, occlusal and **H**, lingual views. **I-N**: *'Dasyatis' sudrei*. **I**: tooth (TAB2-80) in labial view, **J**: tooth (TAB2-81) in lingual view, **K-L**: tooth (TAB2-82) in **K**, lingual and **L**, basal views, **M-N**: posterior tooth (TAB2-83) in **M**, labial and **N**: basal views. **O-Q**: *'Dasyatis'* sp. **O**: non-cuspidate tooth (TAB2-84) in lingual view, **P**: non-cuspidate tooth (TAB2-86) in occlusal view, **Q**: cuspidate tooth (TAB2-85) in occlusal view. **R-T**: *Archaeomanta* sp., tooth (TAB2-87) in **R**, profile, **S**, labial and **T**, profile views. **U-W**: *Burnhamia* sp., tooth (TAB2-88) in **U**, occlusal, **V**, labial and **W**, lingual views. **X-Z**: *Myliobatis dixoni*, tooth (TAB2-89) in **X**, basal, **Y**, occlusal and **Z**, lingual views. **A'-C'**: *Rhinoptera* cf. *raeburni*, tooth (TAB2-90) in **A'**, occlusal, **B'**, basal and **C'**, lingual views. **D'-F'**: *Aetomylaeus* sp., tooth (TAB3-5) in **D'**, lingual, **E'**, labial and **F'**, occlusal views. Scale bars: 500 μm (A, G-H, I-T), 1 mm (B-F), 3 mm (U-C'), 1 cm (D'-F').

Figure 1

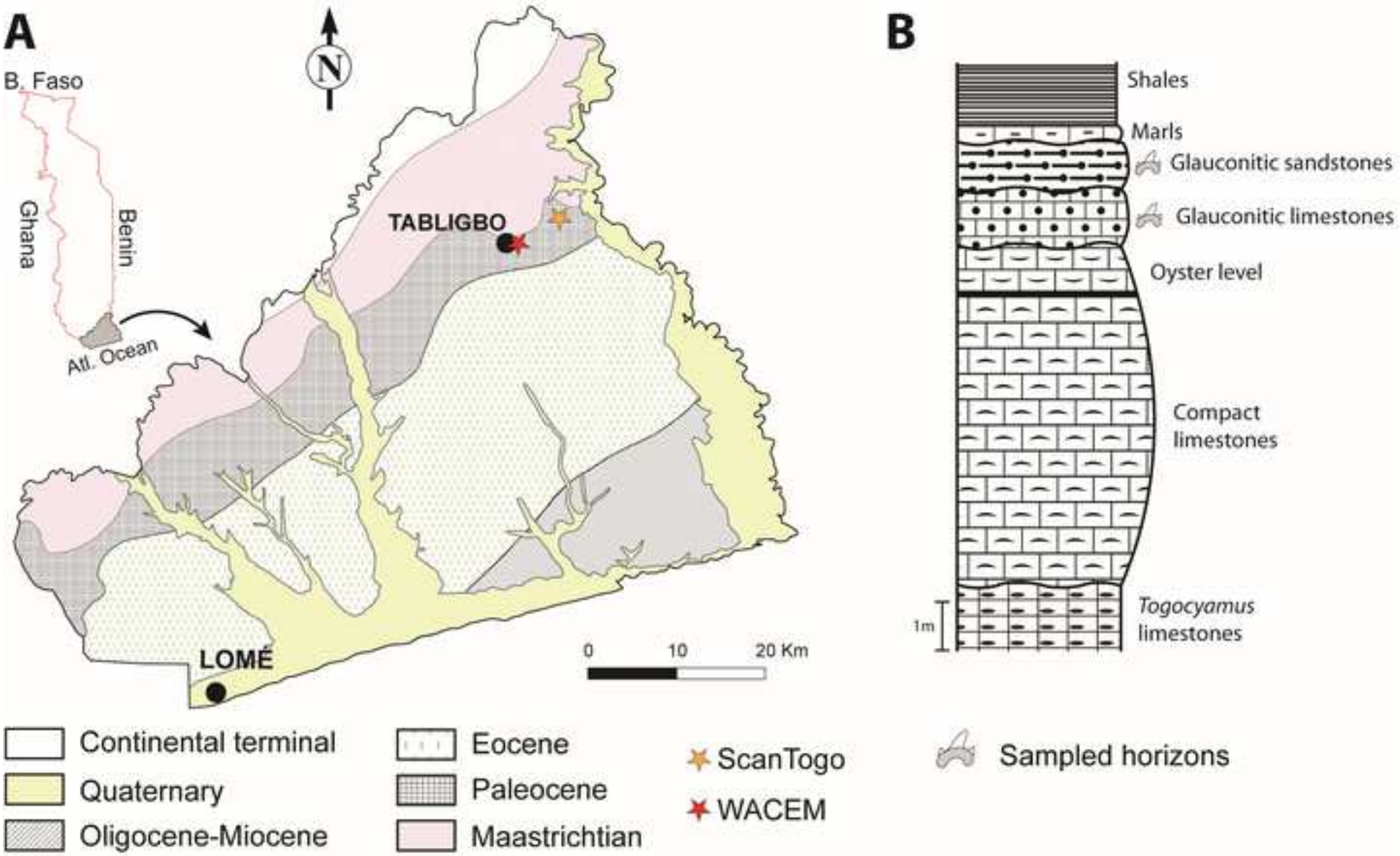

Figure 2

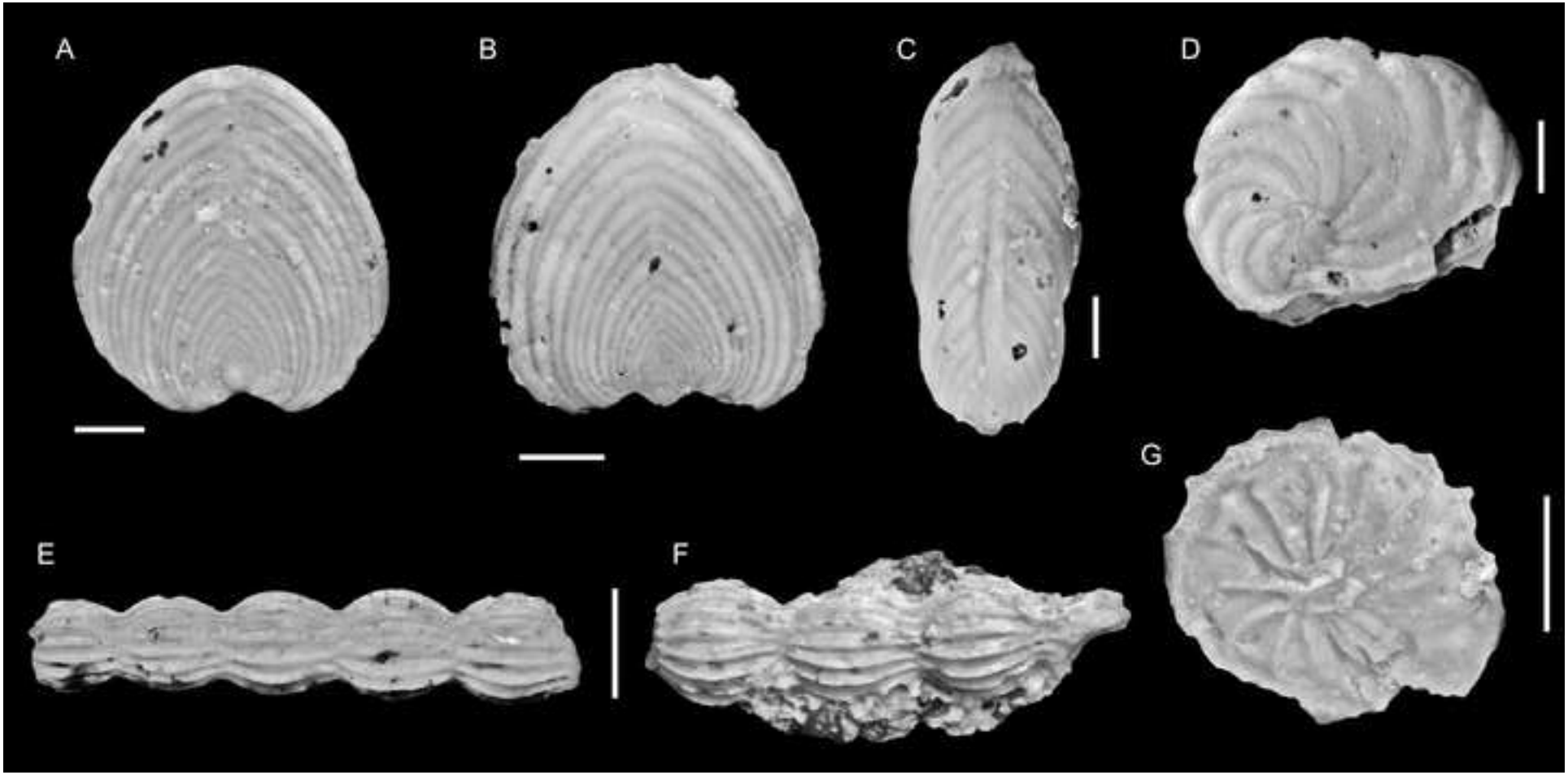

Figure 3

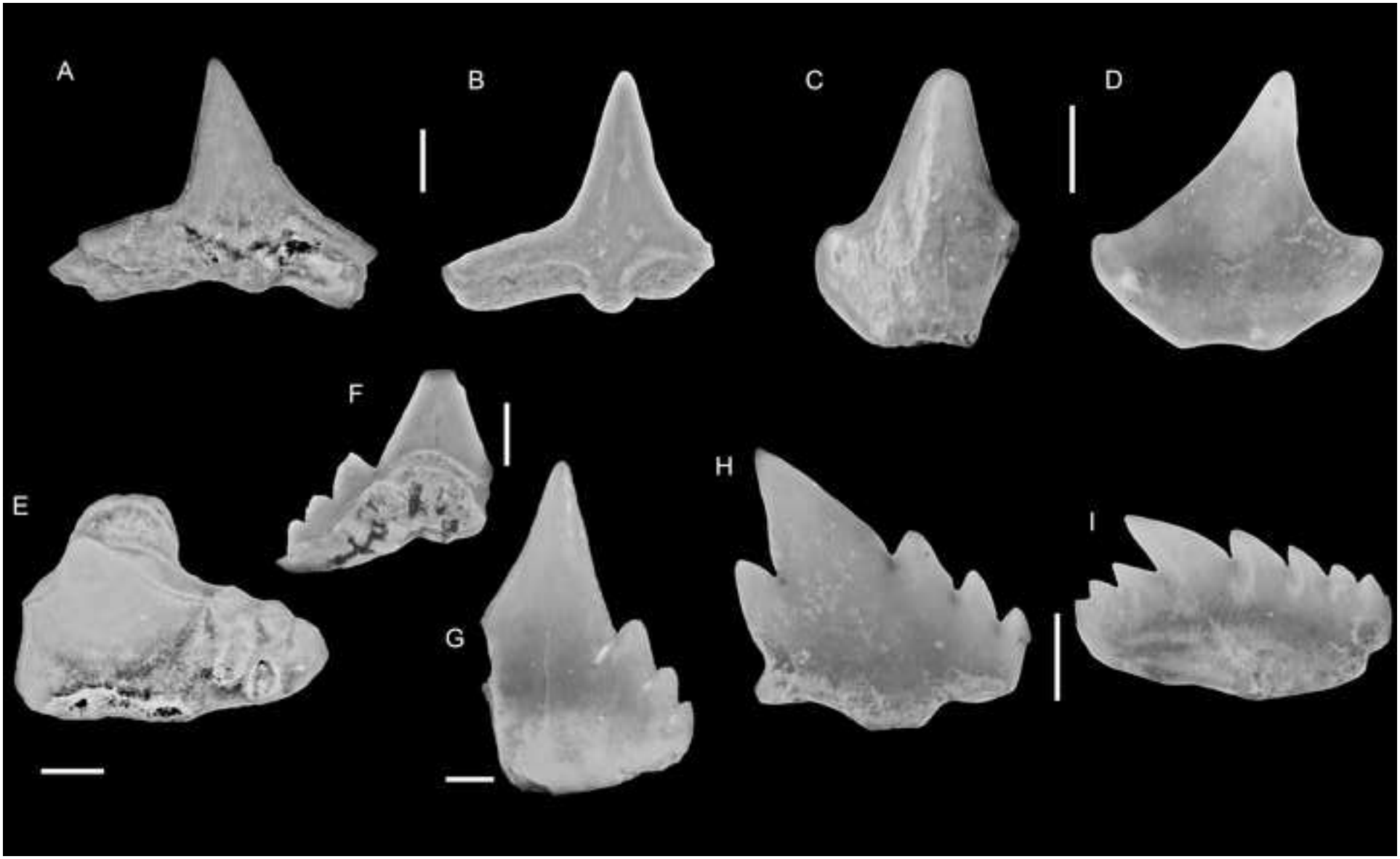

Figure 4

Click here to access/download;Figure;Figure 4_C. aschersoni, O. obliquus-R.tif

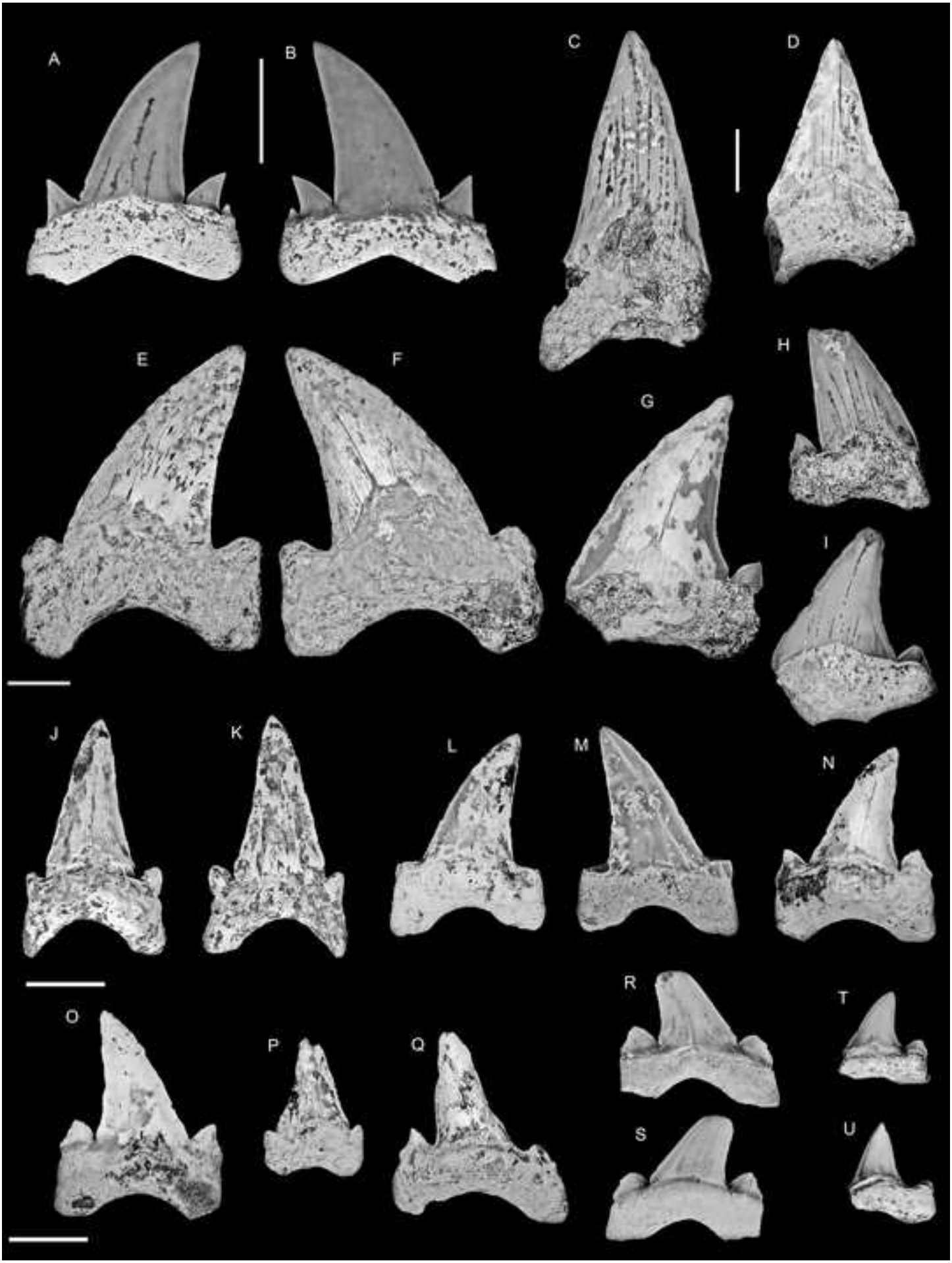

Figure 5

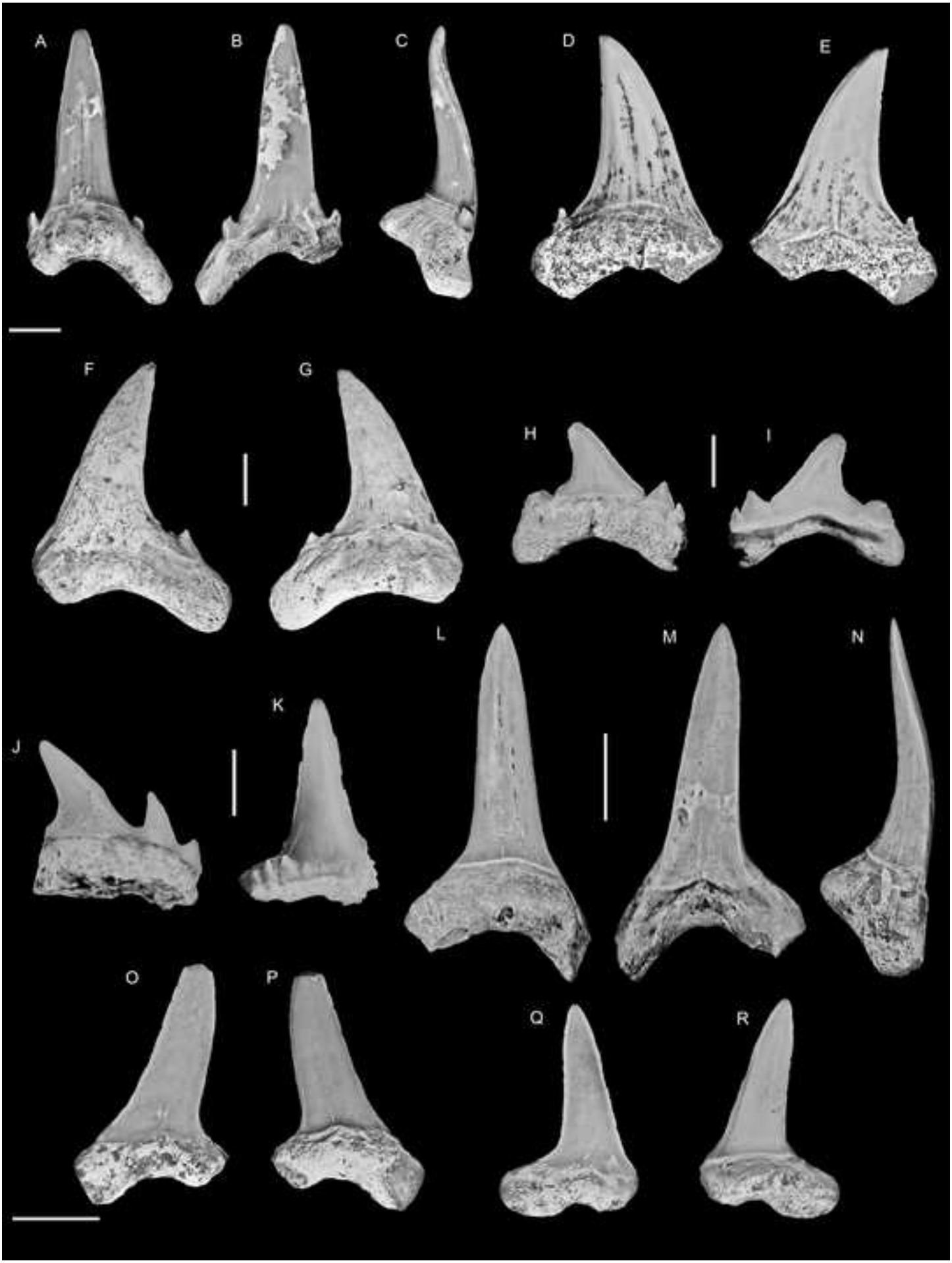

Figure 6

Click here to access/download;Figure;Figure 6_Carchas-R.tif

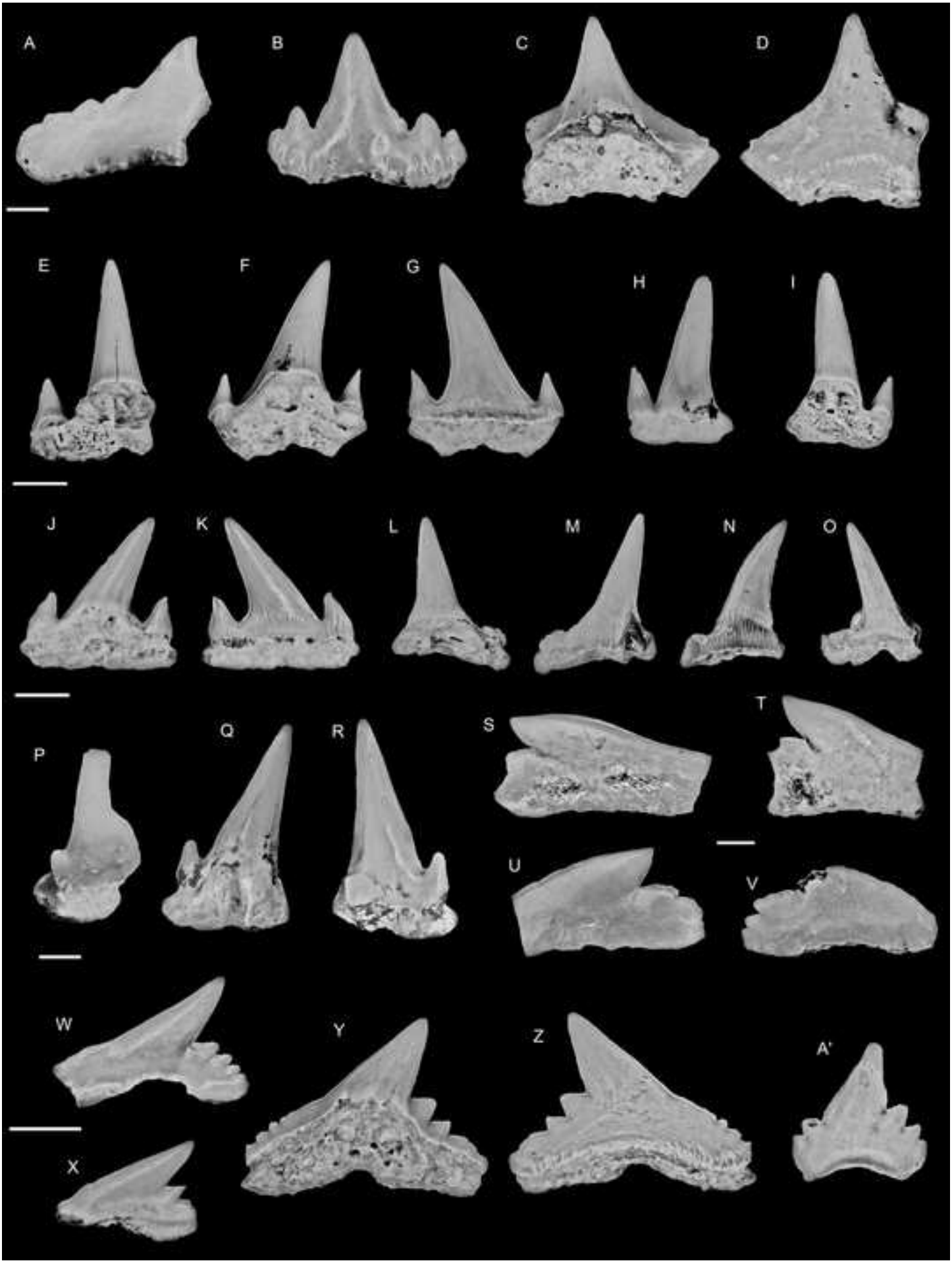

Figure 7

Click here to access/download;Figure;Figure 7_carchas 2-R.tif

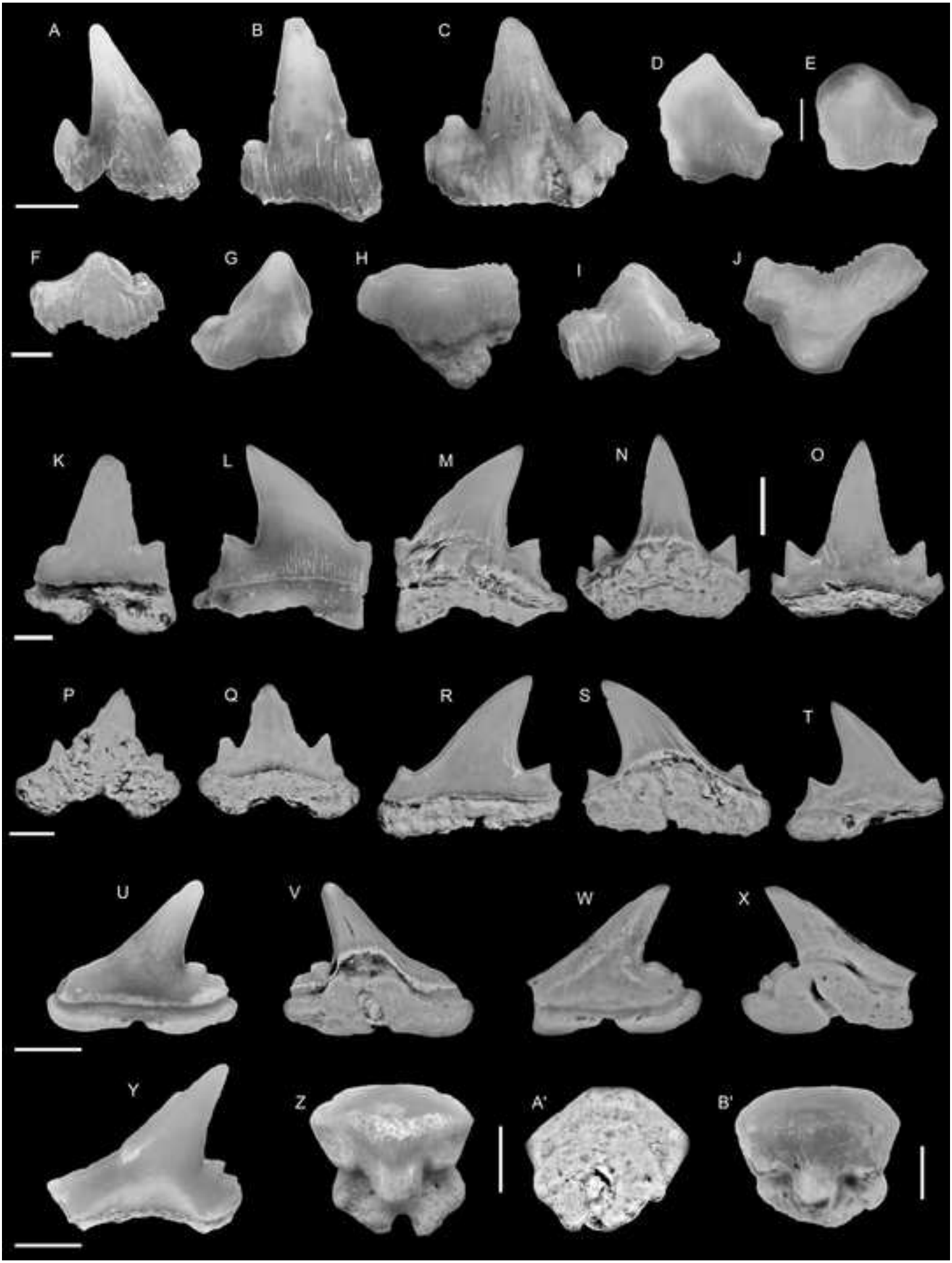

Figure 8

Click here to access/download;Figure;Figure 8_Batoides-R2.tif