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Fish remains (Elasmobranchii, Actinopterygii) from the Late Cretaceous of the Benue Trough, Nigeria

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Abstract

Selachian and ray-finned fish remains from various Late Cretaceous localities of Nigeria are described. Each locality has yielded only a very few specimens and the diversity is therefore very low. However, some taxa are recorded for the first time in Africa. The Ashaka locality in the Upper Benue Trough (northeastern Nigeria) has yielded a small but interesting late Cenomanian assemblage of microremains, including teeth of "*Carcharias*" *amonensis*, *Rhombopterygia zaborskii* sp. nov., *Hamrabatis* sp., "*Stephanodus*" sp., and a possible ionoscopiform. A large prearticular dentition coming from the early Turonian beds of this locality is assigned to the large pycnodontiform *Acrotemnus*, a poorly known genus here regarded as a senior synonym of *Macropycnodon*. In the Lower Benue Trough (southeastern Nigeria), several localities ranging in age from the late Cenomanian to the early Maastrichtian have yielded various widespread taxa such as *Ptychodus*, *Scapanorhynchus*, *Squalicorax*, Vidalamiinae indet., cf. *Protosphyraena*, and *Eodiaphyodus*. The seaway that occupied the Benue

Trough during transgressive episodes (late Cenomanian–early Turonian and Maastrichtian) created opportunities for the dispersal of many marine fish taxa into new areas, such as the proto-South Atlantic.

Keywords: Elasmobranchii; Actinopterygii; Late Cretaceous; Benue Trough; Nigeria.

1. Introduction

Late Cretaceous fish faunas from Africa are relatively well known (see López-Arbarello, 2004 and Murray, 2000 for a review). In Nigeria, most of the works have dealt with Paleogene material (Odunze et al., 2009, 2012; Stevens et al., 2011; White, 1926, 1934, 1955) whereas only a very few Cretaceous specimens have been reported. Woods (1911) mentioned the presence of *Gigantichthys* (= *Onchosaurus*) sp. in the Turonian of Kumberi (northern part of the Middle Benue Trough) on the basis of some remains collected by J.D. Falconer and A. Longbottom and identified by A.S. Woodward.

White (1934) described some fish remains coming from the southern part of the Iullemmeden Basin (Gilbedi and Kaffe localities, Sokoto State, northwestern Nigeria). On the basis of this material, all Maastrichtian in age, White (1934) identified the following taxa: *Lamna appendiculata* var. *biauriculata* (= *Cretolamna biauriculata*), *Lamna libyca* (= *Serratolamna serrata*), *Schizorhiza stromeri*, ?Pristinae indet., *Stephanodus libycus*, and Pycnodontidae indet., besides “selachian vertebrae and remains of indeterminable bony fishes”. This assemblage was later assigned by Kogbe

(1974) to the Maastrichtian Dukamaje Formation.

Carter et al. (1963) provided two lists of fish taxa collected from two localities in northeastern Nigeria and identified by E.I. White. The first list (i.e., *Onchosaurus pharao*, *Schizorhiza stromeri*, *Enchodus* cf. *lamberti*, *Ceratodus* sp., *Lamna* sp.) corresponds to a fish assemblage collected from a section in the Biriji River, near Gombe, exposing the base of the Yolde Formation (Cenomanian in age). The second list (i.e., *Schizorhiza stromeri*, ?*Stratodus apicalis*, *Lamna*? *serrata*, *Enchodus lamberti*) indicates the fish taxa obtained from a well sunk into the Fika Shales Formation (Turonian?–Coniacian to Santonian–Campanian? in age) at Damagum. The Fika Shales are a clay sedimentary unit occurring in the most northwestern part of the Upper Benue Trough, partly equivalent to the Pindiga Formation. It is worth noting that the known stratigraphical range of some of these species is not consistent with the age of the involved formations, thus suggesting possible misidentifications or sampling bias. Unfortunately, the current whereabouts of the fish material reported by Carter et al. (1963) is unknown and we were unable to re-examine these specimens. The section in the Biriji River near Gombe was visited by one of us (P.C.) in 1990; the outcrops occurring by that time were of variable quality, and it was not possible to obtain further material. Similarly, no good outcrops or fossils were recently obtained from the Fika Shales, despite numerous field observations by one of us (P.C.) in 1990.

Lastly, in a study on ammonites from the Ashaka quarry, Courville (1992: 314) noted the presence of various, well-preserved remains of fishes (selachians, pycnodonts) in three distinct stratigraphical levels; these specimens are described in the present work (see below). In a paper dealing with foraminifera from the same quarry, Gebhardt (1997) also mentioned the occurrence of fish remains in several beds of this section, late

Cenomanian to early Turonian in age.

The material studied in the present work represents the first marine fish remains from the Benue Trough that are well constrained stratigraphically and geographically. All of them were collected by one of us (P.C.) from 1989 to 1991 during field prospections. This material was obtained by surface collecting, except microteeth from one peculiar level of the Ashaka quarry, obtained by screen washing (see below).

2. Geographical and geological settings

In Nigeria, West Africa (Fig. 1A1), the Cretaceous marine formations mainly extend in the eastern part of the country, alongside the Benue River and southern branch of the Niger River. The Benue Trough corresponds to a multiple SW-NE strike-slip basin, which origin is directly related to the Early Cretaceous South Atlantic opening (Benkhelil, 1988, 1989; Guiraud, 1991). Its geographical location is particularly interesting, as: 1) being opened to the Cretaceous oceanic domain (modern Calabar flank; Fig. 1A2); 2) a link to the Saharan areas of northeastern Nigeria (Chad Basin; Fig. 1A2), episodically opened to the Late Cretaceous trans-Saharan seaway related itself to the southern margin of the Tethyan Ocean (Courville, 1993; Courville et al., 1998; Reyment and Dingle, 1987).

The Nigerian Late Cretaceous formations and faunas (mainly ammonites and other invertebrates) from the Benue Trough (northern part: Upper Benue Trough; southern part: Lower Benue Trough) have been studied for long (e.g., Barber, 1958; Carter et al., 1963; Reyment, 1955; Woods, 1911). More recently, the main marine sedimentary units of the Benue Trough have been studied with a particular biostratigraphical and palaeobiological consideration (e.g., Meister, 1989; Zaborski, 1983, 1987, 1990a). A synthesis of the historical and original data was realized by Courville (1993).

In northeastern Nigeria, marine conditions partly occurred during the latest Cenomanian–latest “Senonian” (Campanian–Maastrichtian?) interval; only one main clay–shale-dominated sedimentary unit including basal limestone beds (Pindiga Formation and equivalents; Fig. 1B2), occurs. Further south, marine conditions started earlier and earlier (early Albian around the Niger Delta), and persisted continuously during Late Cretaceous times; several local thick clay–shale formations are piling up (Fig. 1B1).

From the Chad Basin part of the Upper Benue Trough (Fig. 1B2), quite numerous fish remains were obtained from the Gongila Formation (partly equivalent to the Pindiga Formation), at the classic section of the Ashaka quarry (levels 9>, 21> and 26 in Courville, 1992: fig. 3). The level 9> corresponds to a marly sediment including an important sandy fraction and numerous phosphatized elements (mainly fish debris). A few teeth were obtained by screen washing (using 0.5 and 1 mm mesh-sized sieves) of a small amount (~500 g) of matrix from this level. It is considered as latest Cenomanian in age (Saharan Gadeni Zone, partly equivalent to the standard Juddii Zone; Courville, 1993). From the marly–nodular limestone level 21>, vertebrate remains are far less common and include several shark and bony fish teeth and vertebrae, plus several unidentified bone fragments; this level is regarded as the younger local Cenomanian horizon (same biozone as level 9>). Lastly, the level 26 (lowermost Turonian: Saharan Flexuosum Zone = Coloradoense Zone *pars*.) yielded only one large pycnodont dentition.

From the central part of the Upper Benue trough (Fig. 1B2), only poorly-preserved bones belonging to unidentifiable fishes or reptiles were collected from various latest Cenomanian to middle Turonian limestone beds (for outcrop details, see Zaborski, 1990a).

All other fish remains studied here were collected in southern Nigeria, from various formations and palaeogeographic areas (Fig. 1B1):

- The latest Cenomanian to early middle Turonian clay–shale series with nodular limestone beds of the Eze Aku Group was exposed with good conditions in several outcrops along the expressway at Lokpanta, located at the Atlantic side of the Lower Benue Trough (for detailed location and study, see Zaborski, 1987). These outcrops yielded quite common and diverse vertebrate remains, often poorly preserved, including fish teeth, vertebrae, or partial skeletons, as well as reptile bones.
- In the overlying clay–shale Awgu Formation of the same area, only poor outcrops occurred by that time, closely located to the sites mentioned by Reyment (1956); probably latest Coniacian to early Santonian in age (no recent ammonite findings), this series yielded a few shark teeth and poorly-preserved reptile bones. Further north, in the southern part of the Lower Benue Trough, the Nkalagu Limestones [a northern equivalent to the basal Awgu Shales, which is clearly early Coniacian in age (Courville, 1993; Offodile and Reyment, 1977; Zaborski, 1990b)], yielded only one isolated fish tooth.
- In southern Nigeria, the younger Late Cretaceous series examined belong to the fine–detritic Nkporo Shales Formation. Various but very poorly preserved,

mostly unidentifiable vertebrate remains occur in its lower part nearly in each outcrop (P.C. pers. obs.). It is only in the most southern area that good outcrops still existed, studied in details by Zaborski (1983, 1985). Rich ammonite faunas clearly indicate that these fossil assemblages occur below and above the Campanian–Maastrichtian boundary; amongst quite diverse and well-preserved fossil assemblages including bivalves, gastropods and crustaceans, one shark tooth and one fish tooth plate were collected in the early Maastrichtian beds of the "fauna 13" fossil site, 42 km from Calabar (Zaborski, 1985: fig. 1).

3. Systematic palaeontology

Specimen repository. All the material studied in the present work is deposited in the collections of Géosciences Rennes (GR), Université de Rennes 1, France.

Class CHONDRICHTHYES Huxley, 1880
Incerti ordinis (?HYBODONTIFORMES Patterson, 1966)
Family PTYCHODONTIDAE Jaekel, 1898
Genus *Ptychodus* Agassiz, 1838

Ptychodus decurrens Agassiz, 1838
(Fig. 2A)

Material examined. One tooth (GR/PC.1773).

Age and locality. Early Turonian (Nodosoides Zone), Lokpanta (level 31), southeastern Nigeria.

Description. The specimen corresponds to a perfectly preserved tooth. It is wider (12.5 mm) than long (10 mm). The crown is not very high and bears eight transverse, curved ridges that are concave labially. These ridges nearly reach the lateral margins of the crown, where they can bifurcate. The narrow, rectangular marginal area of the crown shows a granular surface, with short, irregular, anastomosed folds. The anaulacorhizous root is relatively low and shows a weak basal concavity. A series of foramina is present all around the specimen, just below the crown–root boundary. The root base is also pierced by a few foramina.

Remarks. The morphology and features (e.g., small size, low crown, high number of ridges) of this tooth allows its assignment to the globally widespread species *Ptychodus decurrens* (see Verma et al., 2012). In Africa, this species was only reported from the Cenomanian of Tunisia (Pervinquière, 1903) and late Turonian of Angola (Antunes and Cappetta, 2002). Some teeth tentatively referred to *P. decurrens* were also reported from the late Cenomanian–early Turonian black shales of Jbel Tselfat in Morocco (Khalloufi et al., 2010).

Order LAMNIFORMES Berg, 1958

Family PSEUDOSCAPANORHYNCHIDAE Herman, 1979

Genus *Protolamna* Cappetta, 1980a

cf. *Protolamna* sp.

(Fig. 2B)

Material examined. Three incomplete teeth (including GR/PC.1774).

Age and locality. Latest Cenomanian (Gadeni Zone), Ashaka quarry (level 21>), northeastern Nigeria.

Description. The best preserved tooth shows an erect, narrow cusp bearing a few slight lingual folds. The labial face is nearly flat whereas the lingual face is strongly convex in apical view. The lingual protuberance of the root is well developed. Lateral cusplets and root lobes are not preserved.

Remarks. Although these teeth are incomplete, the shape and ornamentation of the main cusp combined to root morphology indicate that these specimens can be tentatively assigned to the widespread Cretaceous genus *Protolamna* (Cappetta, 2012). In the other two pseudoscapanorhynchid genera *Leptostyrax* and *Pseudoscapanorhynchus*, the mesiodistal compression at the base of the labial face of the main cusp is stronger (Cappetta, 2012). In Africa, teeth of *Protolamna* and *Leptostyrax* were reported from the Albian of Angola and Tunisia (Antunes and Cappetta, 2002; Cuny et al., 2004).

Family OTODONTIDAE Glikman, 1964

Genus *Cretolamna* Glikman, 1958

Cretolamna sp.

(Fig. 2C)

Material examined. One incomplete tooth (GR/PC.1775).

Age and locality. Coniacian?–Santonian, Awgu, southeastern Nigeria.

Description. The unique specimen corresponds to a large upper lateral tooth. The main cusp bends distally and shows a convex mesial cutting edge. The distal cutting edge is more rectilinear. Only the distal lateral cusplet is preserved. It is triangular, wider than high, and relatively large. The root has a poorly marked lingual protuberance. The root lobes are short and separated by a broad, rounded mediobasal notch.

Remarks. This tooth is very characteristic of this widespread genus. In Africa, teeth of *Cretolamna* are common in Late Cretaceous marine deposits (e.g., Antunes and Cappetta, 2002; Arambourg, 1952; Cuny et al., 2012; Dartevelle and Casier, 1949; White, 1934). A lateral tooth with a similar morphology has been described as *Cretolamna appendiculata* by Antunes and Cappetta (2002: pl. 10, fig. 12) from the late Turonian of Iembe (Angola). Most of *Cretolamna* teeth found in Late Cretaceous deposits have been commonly assigned to the type species *C. appendiculata*, but a recent revision of this genus based on an abundant material from the Cenomanian–Campanian interval shows that several species can be recognized among the *C. appendiculata* group (Siverson et al., in press).

Family ANACORACIDAE Casier, 1947

Genus *Squalicorax* Whitley, 1939

Squalicorax pristodontus (Agassiz, 1843)

(Fig. 2D)

Material examined. One incomplete tooth (GR/PC.1776).

Age and locality. Early Maastrichtian (Neubergicus Zone), Calabar, southeastern Nigeria.

Description. This wide (29 mm), large tooth shows a rather gibbous mesial edge and an attenuated distal heel. Serrations of the cutting edges are well developed. The basal part of the root is not preserved.

Remarks. This widespread species is well known in the latest Cretaceous marine deposits of Africa, especially in the Democratic Republic of the Congo (Dartevelle and Casier, 1943), Morocco (Arambourg, 1952), Egypt (Cappetta, 1991; Gemmellaro, 1920), Angola (Antunes and Cappetta, 2002) and Senegal (Cuny et al., 2012).

Family MITSUKURINIDAE Jordan, 1898

Genus *Scapanorhynchus* Woodward, 1889

Scapanorhynchus cf. *texanus* (Roemer, 1849)

(Fig. 2E, F)

Material examined. Three incomplete teeth (including GR/PC.1777, GR/PC.1778).

Age and locality. Coniacian?–Santonian, Awgu, southeastern Nigeria.

Description. These teeth are large (up to 41 mm in length) and relatively robust. The crown consist of only one main cusp, without lateral cusplets. It is clearly sigmoid in profile view. The lingual face is slightly convex and smooth whereas the labial face is strongly convex and bears up to 25 well marked longitudinal folds. The root has a very pronounced lingual protuberance marked by a short and deep groove. Only the distal lobe of the root is preserved on the best preserved tooth (GR/PC.1777: Fig. 2E). It is relatively robust and has a rounded extremity.

Remarks. The Nigerian specimens studied here are very similar to those figured by Antunes and Cappetta (2002: pl. 9, fig. 4-7) from the late Turonian of Iembe (Angola). However, the root lobes seem more robust in the Nigerian material. These teeth from Awgu would confirm the occurrence of this species in the Late Cretaceous of Africa.

Incertae familiae

Incertae genus

"*Carcharias*" *amonensis* (Cappetta and Case, 1975a)

(Fig. 3A)

Material examined. One tooth (GR/PC.1779).

Age and locality. Late Cenomanian (Gadeni Zone), Ashaka quarry (level 9>), northeastern Nigeria.

Description. The specimen corresponds to an upper lateral tooth. The main cusp is labiolingually compressed and strongly bent distally. There is one pair of triangular lateral cusplets, plus one additional incipient mesial cusplet. The root is damaged and no lingual protuberance, median furrow or lobes can be observed.

Remarks. This small tooth is clearly referable to "*Carcharias*" *amonensis*, a geographically widespread Cenomanian lamniform shark. This taxon corresponds to a good biostratigraphical marker for this stage. It is mainly known from North American and European localities where it can be abundant, while it seems to be slightly less common in Africa. In this continent, it has been found in Morocco (Cavin et al., 2010), Libya (Rage and Cappetta 2002), Egypt (Slaughter and Thurmond, 1974; Werner, 1989), and Angola (Antunes and Cappetta, 2002). It is also present in Lebanon, where a few complete skeletons have been collected (Cappetta, 2012: 208). This species is clearly not an odontaspidid s.l. (e.g., *Odontaspis*, *Carcharias*, and their fossil relatives) and is only assigned to the genus *Carcharias* pending further study on its relationships to other lamniform sharks.

Order RAJIFORMES Berg, 1940

Incertae familiae

Genus *Rhombopterygia* Cappetta, 1980b

Rhombopterygia zaborskii sp. nov.

(Fig. 3B–E)

Holotype. One anterior tooth (GR/PC.1780) (Fig. 3B).

Paratypes. Three anterolateral to lateral teeth (GR/PC.1781, GR/PC.1782, GR/PC.1783) (Fig. 3C–E).

Additional material. Two incomplete teeth.

Age and type locality. Late Cenomanian (Gadeni Zone), Ashaka quarry (level 9>), northeastern Nigeria.

Etymology. Species named in honour to Peter M. P. Zaborski, who led one of the author (P.C.) to the Ashaka quarry.

Diagnosis. New species of *Rhombopterygia* with very small (about 0.5 to 0.8 mm wide) teeth characterized by the following features: 1) cusped crown at least as wide as root, 2) lingual face with concave lateral margins in occlusal view, 3) well-developed median uvula, 4) lateral uvulae reduced but always present.

Differential diagnosis. New species of *Rhombopterygia* with teeth differing from those of *R. rajoides*, the type and only species of the genus, by the following features: 1) anterior teeth narrower with crown as wide as root, 2) lateral margins of lingual face concave in anterior teeth, 3) median uvula narrower and less rounded, 4) more marked lateral uvulae, 5) cusp more developed in anterior teeth and present in lateralmost teeth, 6) smaller size.

Description. Anterior teeth (including the holotype GR/PC.1780: Fig. 3B) have a subrectangular crown in occlusal view. The labial edge of the crown is convex. The lingual face shows a well-developed, subtriangular median uvula that projects lingually, whereas lateral uvulae are much more reduced. Both faces are separated by a transverse crest that rises up into an obtuse central cusp. The root, not very high, is as wide as the crown and shows in lingual view a pair of marginolingual foramina located below the junction of the median and lateral uvulae. In basal view, the root is marked by a deep median furrow that separates two subtriangular lobes. The furrow displays a foramen in central position. Lateral teeth (including the paratype GR/PC.1783: Fig. 3E) have a crown which is more expanded laterally and marked by a transverse crest bearing a lower central cusp. The lingual edge shows a broad, triangular central uvula which is flanked by one pair of smaller, poorly salient lateral uvulae. The root is narrower than the crown.

Remarks. Two “rhinobatoid” taxa have been described from the early Late Cretaceous of Africa. *Isidobatus* is a genus based on isolated “rhinobatoid”-like teeth from the late Cenomanian of Egypt (Werner, 1989). The Ashaka teeth do not display the transverse keels and crest present in those of *Isidobatus* and have less-developed median and lateral uvulae. They can thus be easily distinguished from this peculiar genus. The platyrhinid genus *Tingitanius*, recently described on the basis of a nearly complete specimen from the early Turonian of Morocco (Claeson et al., 2013), has teeth which are rather similar to those found at Ashaka. However, the teeth of *Tingitanius* mainly differ by the lack of a cusp and their higher root.

The teeth from Ashaka are here assigned to the genus *Rhombopterygia* on the basis of its broad crown, the shape of the transverse crest, the presence of a small cusp, and the morphology of the lingual uvulae. This genus has been originally described on the basis of complete skeletons from the Cenomanian of Lebanon representing a single species, *R. rajoides* (Cappetta, 1980b). In addition, isolated teeth assigned to *Rhombopterygia* have been reported from the Cenomanian and Coniacian of Spain (Bernárdez, 2002; Vullo et al., 2009), while there is a doubtful occurrence from the Campanian of Germany (Müller, 1989). The teeth described by Bernárdez (2002: pl. 54, figs. 1-4) as "*R. villae*" (*nomen nudum*) strikingly resembles those of *R. zaborskii* sp. nov. and are also late Cenomanian in age. Therefore, they might represent the same species or closely related forms. Lastly, it can be noted that "*Rhinobatos*" *whitfieldi* from the Cenomanian of Lebanon has similar teeth in overall morphology, but these are smaller and more cuspidate (Cappetta, 1980b). *Rhombopterygia* was placed among the Rhinobatidae by Cappetta (1980b, 2012), but the phylogenetic analysis performed by Claeson et al. (2013) would not support this interpretation. This analysis found "*Rhinobatos*" *whitfieldi* and *Rhombopterygia rajoides* as successive sister taxa to *Zanobatos* and Myliobatiformes. However, it is worth noting that this result was recovered by the 50% majority rule tree but not in the strict consensus.

Genus *Hamrabatis* Cappetta, 1991

Hamrabatis sp.
(Fig. 3F, G)

Material examined. Two teeth (GR/PC.1784, GR/PC.1785).
Age and locality. Late Cenomanian (Gadeni Zone), Ashaka quarry (level 9>), northeastern Nigeria.

Description. The best preserved specimen (GR/PC.1784: Fig. 3F) is a small anterolateral tooth. In occlusal view, it displays a rhombic crown as wide as long and marked by a blunt transverse keel. The lingual area of the occlusal face shows an irregular, alveolate surface whereas the labial area is almost smooth. The lingual face is strongly concave in profile view. The basal part of the lingual face is subhorizontal, flat and falciform in occlusal view. The root is not preserved. A poorly preserved lateral tooth (GR/PC.1785: Fig. 3G) shows a crown more expanded laterally. It is apparently devoid of transverse keel and ornamentation. The basal part of the lingual face is damaged.

Remarks. *Hamrabatis* is known from the Late Cretaceous of Europe, Northern Africa, Near East and North America (see Cappetta, 2012). Thus, the presence of *Hamrabatis* in the Cenomanian of Nigeria represents the southernmost occurrence of this widespread rajiform genus. So far, *H. bernardezi* from France and Spain is the only known Cenomanian species of the genus (Bernárdez, 2002; Vullo et al., 2007, 2009).

The teeth from Ashaka differ from *H. bernardezi* by their crown almost devoid of ornamentation, but this may be due to abrasion. Because of the scarcity and poor preservation of the Ashaka material, these teeth are here referred to *Hamrabatis* sp.

Class OSTEICHTHYES Huxley, 1880
Order PYCNODONTIFORMES Berg, 1937
Family PYCNODONTIDAE Agassiz, 1833
Genus *Acrotemnus* Agassiz, 1836

Acrotemnus sp.
(Fig. 4A)

Material examined. One prearticular dentition (GR/PC.1786).
Age and locality. Early Turonian (Coloradoense Zone), Ashaka quarry (level 26), northeastern Nigeria.

Description. The unique specimen corresponds to a large (92 mm long), complete right prearticular dentition bearing 34 robust teeth. The symphysis is long (52 mm) but not very thick. There are three rows of teeth. The ten teeth of the inner row are large, up to 18 mm wide. They are bean-shaped or oblong and marked medially by a narrow transverse groove. The twelve teeth of the middle row are less transversally extended and are marked by a granular central depression. Lastly, the twelve teeth of the outer row are oval to subcircular, with an unornamented, rounded central depression.

Remarks. *Macropycnodon* is a large genus of pycnodont fish recently erected on the basis of a single vomerine dentition (*M. streckeri*) and isolated teeth (*M. megafrendodon*) from the Turonian of U.S.A. (Kansas and New Mexico, respectively) (Shimada et al., 2010). Therefore, the prearticular dentition of *Macropycnodon* is unknown and no direct comparisons can be made between the North American and the Nigerian material. However, the dental features observed on the large prearticular jaw from the Ashaka quarry are very similar to those present in *Macropycnodon*, especially in the type species *M. streckeri* (specimen KUVP 946; Shimada et al., 2010: fig. 2). In addition, the Nigerian specimen also shares with *Macropycnodon* the Turonian age and the unusual large size. It can be distinguished from the prearticulars of the *Coelodus* species, which bear teeth that are generally smooth and more elongated transversally (Schultz and Paunović, 1997; Poyato-Ariza and Wenz, 2002: fig. 22a).

It is worth noting that some large pycnodont teeth and jaw fragments from the Late Cretaceous (Turonian?) of the Damergou area in Niger (eastern Iullemmeden Basin) have been referred by Arambourg and Joleaud (1943) to the poorly known taxon *Acrotemnus faba*, originally described on the basis of a few associated teeth from the Late Cretaceous (Turonian) of England (Agassiz, 1833–1843; Woodward, 1909). Like *Macropycnodon*, this genus has robust teeth characterized by a sharp transverse apical ridge (Arambourg and Joleaud, 1943: pl. II, figs. 14-17). Furthermore, some teeth from Damergou show a ring-like ridge and a central depression (Arambourg and Joleaud, 1943: pl. II, figs. 11, 13), indicating that the variation in tooth morphology is similar to that observed in *Macropycnodon* and the prearticular dentition from Ashaka. Since *Macropycnodon* and *Acrotemnus* share the same diagnostic features, the former appears to be a junior synonym of the latter. Thus, *Acrotemnus streckeri* may be a subjective junior synonym of *A. faba*, whereas *A. megafrendodon* is clearly a distinct species. The Nigerian specimen here described is assigned to *Acrotemnus* sp. It must be noted that two other Late Cretaceous species were referred to *Acrotemnus*: *A. splendens* from Belgium (Leriche, 1911) and *A. yangaensis* from Angola (Dartevelle and Casier, 1949). While the holotypic material of the former belongs in fact to the enigmatic, purported pycnodontiform genus *Hadrodus*, the holotypic material (a single tooth) of the latter must be regarded as Pycnodontidae indet.

Incerti ordinis (?PYCNODONTIFORMES Berg, 1937)
Incertae familiae
Genus "*Stephanodus*" Zittel, 1888

"*Stephanodus*" sp.
(Fig. 5A)

Material examined. Two teeth (including GR/PC.1787).
Age and locality. Late Cenomanian (Gadeni Zone), Ashaka quarry (level 9>), northeastern Nigeria.

Description. This small hook-shaped branchial tooth shows a strong lateral compression. A flattened discoid extension develops between the base and the hook.

Remarks. This dental morphotype is usually referred to the genus "*Stephanodus*", which may represent a parataxon (see discussion in Berreteaga et al., 2011). Such branchial teeth are mainly present in pycnodontiforms (Kriwet, 1999), but can also be found in other Mesozoic and Cenozoic fish groups. Thus, several authors considered "*Stephanodus*" as a non-pycnodontid fish and referred it to the Eotrigonodontidae within the Tetraodontiformes (e.g., Arambourg, 1952; Bardet et al., 2000; Dartevelle and Casier, 1949; White, 1934).

Order AMIIFORMES Hay, 1929
Family AMIIDAE Bonaparte, 1837
Subfamily VIDALAMIINAE Grande and Bemis, 1998

Genus indet. A
(Fig. 4B, C)

Material examined. Two vertebrae (GR/PC.1788-1789).
Age and locality. Latest Cenomanian (Gadeni Zone), Ashaka quarry (level 21>), northeastern Nigeria.

Description. The larger specimen (GR/PC.1788: Fig. 4B) corresponds to an abdominal vertebral centrum, slightly broader than high and weakly compressed anteroposteriorly. It shows insubstantial parapophyses. The neural and aortal facets are visible dorsally and ventrally, respectively. In dorsoventral view, the smooth lateral surfaces appear markedly concave. The second, smaller specimen (GR/PC.1789: Fig. 4C) is a posterior caudal (ural) centrum, higher than wide.

Remarks. The shape of these vertebral centra is characteristic of those found in the trunk (= abdominal) and caudal region of amiid fishes (Grande and Bemis, 1998). The fact that no well-developed parapophyses are fused to the centrum indicates that these specimens do not belong to the subfamily Amiinae (Grande and Bemis, 1998). Based on their general morphology, these two centra can be assigned to the subfamily Vidalamiinae (Grande and Bemis, 1998). The dorsal vertebral centrum closely resembles that of an indeterminate vidalamiine described from the Late Cretaceous (Maastrichtian) of Brazil (Martinelli et al., 2013). However, the latter does not display the concavity of the lateral surface observed in dorsoventral view in GR/PC.1788. Among other mid-Cretaceous amiids, similar large centra characterized by a weak anteroposterior compression are also observed in the *Pachyamia* from the late Albian of Mexico (Grande and Bemis, 1998) and the early Cenomanian of the Near East (Chalifa and Tchernov, 1982), as well as in a partial vertebral column of a possible indeterminate vidalamiine from the middle Turonian of Brazil (Gallo et al., 2007b).

Genus indet. B
(Fig. 4D)

Material examined. One vertebra (GR/PC.1790).

Age and locality. Coniacian?–Santonian, Awgu, southeastern Nigeria.

Description. This specimen corresponds to a laterally extended vertebral centrum, broader than high and anteroposteriorly compressed. No parapophyses are fused to the centrum. In anteroposterior view, it shows a subrhombic shape, with dorsolateral (i.e, between the neural facets and parapophyses) and ventrolateral (i.e., between the aortal facets and parapophyses) surfaces appearing slightly convex and concave, respectively. This shape indicates a central trunk position.

Remarks. Like the amiid centra from the Ashaka quarry, this centrum shows anatomical features that permit to assign it to the Vidalamiinae. However, it can be distinguished from the Cenomanian abdominal vertebral centrum described above by a stronger anteroposterior compression, a more rhombic outline, and the presence of slight ventrolateral concavities. Thus, the material from Ashaka and Awgu may represent two distinct vidalamiine taxa. Such ventrolateral concavities are an autapomorphic feature of the non-marine (possibly marine?) genus *Melvius* from the Late Cretaceous (Campanian–Maastrichtian) of North America (Bryant, 1987; Grande and Bemis, 1998), in which this character can be much more marked than in the centrum from Ashaka. Unfortunately, the intracolumnar shape variation of the centra remains unknown for the Ashaka vidalamiine, and a deeper comparison with *Melvius* is not possible. Interestingly, the “early Senonian” (Coniacian–Santonian) locality of In Beceten in southern Niger yielded an indeterminate amiid taxon (Broin et al., 1974). An examination of the material (including isolated centra) housed at the Muséum national d’Histoire naturelle of Paris indicates that the amiids from Awgu and In Beceten are at least closely related (R.V. pers. observ.). It is worth noting that this specimen was collected in the Awgu area beside a few teeth of the marine sharks *Cretolamna* and *Scapanorhynchus*. However, all these fossils were found naturally cleaned on an inclined outcrop surface, probably not exactly *in situ*. Furthermore, a different colouring also suggests that the amiid and shark specimens originally came from two distinct beds.

Order IONOSCOPIFORMES Grande and Bemis, 1998

Family and genus indet.

(Fig. 5B)

Material examined. One tooth (GR/PC.1791).

Age and locality. Late Cenomanian (Gadeni Zone), Ashaka quarry (level 9>), northeastern Nigeria.

Description. This small tooth shows a subcircular base, slight longitunal folds, and an apex bearing a transverse, curved carina.

Remarks. This tooth resembles that described from the middle–late Cenomanian of northern Spain (La Cabaña Formation) (Vullo et al., 2009), showing the typical ionoscopiform dental features described by Mudroch and Thies (1996) and Thies and Mudroch (1996). To date, ionoscopiform fishes are known from complete skeletons from Middle Triassic to Early Cretaceous in Europe, Africa, and North and South America (Alvarado-Ortega and Espinosa-Arrubarrena, 2008; Brito and Alvarado-Ortega, 2008). However, *Neorhombolepis*, known from a single incomplete skeleton from the Lower Chalk (Cenomanian) of England (Woodward, 1888), has been considered by some authors as a ionoscopiform genus, closely related or even synonymous to the ophiopsid genus *Macrepistius* from the Albian of Texas (Grande and

Bemis, 1998; Patterson, 1973). In addition, it is noteworthy that the poorly known, monospecific genus *Petalopteryx* from the Cenomanian of Lebanon (Pictet, 1850) closely resembles the ophiopsid genera *Teoichthys* and *Placidichthys* (both from the Early Cretaceous of America), and therefore may belong to this group of ionoscopiforms. Lastly, the presence of some ionoscopiforms in the Cenomanian of Komen (Slovenia) and the Island of Hvar (Croatia) was noted by Wenz and Kellner (1986). All these data and observations would indicate that the temporal range of ionoscopiforms fishes extends into the early Late Cretaceous, and thus would support the assignment of the isolated teeth from the Cenomanian of Spain and Nigeria to this primitive order of marine halecomorph fishes.

Order PACHYCORMIFORMES Berg, 1937

Family PACHYCORMIDAE Woodward, 1895

Genus *Protosphyraena* Leidy, 1860

cf. *Protosphyraena* sp.

(Fig. 4E)

Material examined. One incomplete tooth (GR/PC.1792).

Age and locality. Early Coniacian, Nkalagu, southeastern Nigeria.

Description. The crown is laterally compressed, not very elongated and triangular in lateral view. The apex is broken, showing the very thin layer of enamel in cross-section.

One of the two face displays a single, short enamel fold near the apex. There are two sharp carinae. These anterior and posterior cutting edges are slightly concave and convex, respectively.

Remarks. In Africa, the only report of this genus is a single tooth from the Maastrichtian of Egypt (Gemmellaro, 1920), whereas it is widespread in the Cretaceous of North America and Europe. More recently, a few isolated teeth from the Campanian–Maastrichtian of Saudi Arabia were tentatively assigned to *Protosphyraena* sp. (Kear et al., 2009).

Order CROSSOGNATHIFORMES Taverne, 1987
Suborder PACHYRHIZODONTOIDEI Forey, 1977
Family and genus indet.
(Fig. 6)

Material examined. One caudal skeleton (GR/PC.1793).
Age and locality. Late Cenomanian (Juddii Zone), Lokpanta (level 33), southeastern Nigeria.

Description. The caudal skeleton is embedded at the surface of a flattened, laminated calcareous nodule. About ten preural vertebrae are preserved. Most of the bones of the caudal fin have been removed by weathering and are now preserved as external moulds. There are two well-developed dorsal and ventral caudal scutes. These bones are curved, broaden medially and become thinner, needle-like at their extremities. Posteriormost centra of the preural vertebrae are hardly visible, as well as the ural centra. The basal (proximal) part of an element identified as the parhypural would indicate the position of the first preural centrum (Pu1). Hypural elements seems to be largely fused (Hy1+Hy2 and Hy3+Hy4 condition?). Uroneural elements are damaged, possibly displaced, but rather large and broad element (Un1?) with a pointed distal extremity can be observed. Imprints of lepidotrichs, of which the bases partly overlap the hypurals, indicate a significant degree of hypurostegy. Although distal parts of the caudal fin lobes are not preserved, the symmetry of the tail suggests that it may have been forked and homocercal. The upper and lower lobes show eleven and nine principal rays, respectively. Outermost rays are well segmented. Between these two lobes, the tail displays numerous thin and densely segmented lepidotrichs.

Remarks. Despite its state of preservation, this specimen shows some anatomical features (i.e., well-developed caudal scutes and uroneurals, partly fused hypurals) that are present in most of pachyrhizodontoid fishes, such as *Elopopsis*, *Goulminichthys* and *Pachyrhizodus* (Cavin, 2001: fig. 13). This group of primitive teleosts are well represented in the early Late Cretaceous of Northern Africa, with *Elopopsis* and *Goulminichthys* from the Cenomanian and Turonian of Morocco, respectively (Cavin, 1995, 2001; Taverne, 1976).

Order AULOPIFORMES Rosen, 1973

Family ENCHODONTIDAE Woodward, 1901

Genus *Enchodus* Agassiz, 1835

Enchodus cf. *gladiolus* (Cope, 1872)
(Fig. 5C)

Material examined. Two teeth (including GR/PC.1794).
Age and locality. Late Cenomanian (Gadeni Zone), Ashaka quarry (level 9>), northeastern Nigeria.

Description. The larger and best preserved tooth is sigmoid in lateral view and shows a weak barb in the apical region of the posterior carina. In the posterior part of the crown, there are a few longitudinal folds between the base and the barb.

Remarks. This tooth from Ashaka is very similar to those from the middle–late Cenomanian of North America that are referred to *Enchodus* cf. *gladiolus* (Cumbaa et al., 2010; Nagrodski et al., 2012; Shimada et al., 2006). As mentioned above, *Enchodus* (*E. lamberti*) was reported in Nigeria from the Yolde and Fika Shales formations by Carter et al. (1963).

Order ALBULIFORMES Nelson, 1973
Family PHYLLODONTIDAE Sauvage, 1875
Genus *Eodiaphyodus* Dartevelle and Casier, 1949

Eodiaphyodus cf. *granulosus* Arambourg, 1952

(Fig. 4F)

Material examined. One nearly complete tooth plate (GR/PC.1795).

Age and locality. Early Maastrichtian (Neubergicus Zone), Calabar, southeastern Nigeria.

Description. This oval-shaped tooth plate (47 mm long and 37 mm wide) displays an aggregation of numerous small subcircular teeth (between 2 and 4 mm in diameter). The basal face of the plate shows the tooth bases which are thick, irregular and marked by a central depression. The occlusal face of the plate is more convex and has a smooth surface.

Remarks. This genus was originally described on the basis of complete and fragmentary tooth plates from the Maastrichtian of the Democratic Republic of the Congo and assigned to a new species, *Eodiaphyodus lerichei* (Dartevelle and Casier, 1949). Arambourg (1952) described a second species (i.e., *E. granulosus*) from the Maastrichtian (and Paleocene?) of Morocco. In addition, Arambourg (1952) recognized a third species (i.e., *E. bebianoi*) that had been previously referred to the genus *Pseudoegertonia* by Dartevelle and Casier (1949). This species was described on the basis of a few isolated teeth and tooth plate fragments from the Paleocene of the Democratic Republic of the Congo (Dartevelle and Casier, 1949). *E. bebianoi* might represent a senior synonym of *E. granulosus*, but it is better to consider it as a *nomen dubium* due to the incompleteness of the type material. Estes (1969) tentatively referred the Moroccan species to the genus *Pseudoegertonia* and restricted the genus *Eodiaphyodus* to the species *E. lerichei* alone, but this interpretation is not followed here. As noted by Arambourg (1952), tooth plates of *E. lerichei* differ from those of *E. granulosus* (and *E. bebianoi*) by their teeth that are relatively smaller, more numerous and more slender. In *E. lerichei*, tooth bases are thinner, more regular and more circular, showing a well-developed central depression (Dartevelle and Casier, 1949: pl. 18, fig. 1d). The tooth plate from Calabar described here is morphologically very close to *E. granulosus*, although about twice smaller, and is tentatively referred to this species. In Africa, *Eodiaphyodus* also occurs in the late Campanian–Maastrichtian of Angola (Antunes and Cappetta, 2002) and thus seems to have been a common component of latest Cretaceous to earliest Paleogene ichthyofaunas present along the Atlantic margin.

4. Concluding remarks

In all studied localities, the fish material is generally scarce and poorly diverse, mainly due to sampling bias. Nevertheless, most of these sites have yielded one or several taxa that are recorded for the first time in this part of Africa. Thus, these new occurrences have significant palaeobiogeographical implications. The seaway that occupied intermittently the Benue Trough during transgressive episodes is known to have played a key role in the dispersal of many fish groups (Cavin, 2008; Cavin et al., 2012; Gallo et al., 2007a; Maisey, 2000; Martín-Abad and Poyato-Ariza, 2013) and marine invertebrates (e.g., Courville et al., 1998; Gebhardt, 1999; Néraudeau and Courville, 1997; Néraudeau and Mathey, 2000), especially because it provided a connection between the proto-South Atlantic and the Mediterranean Tethys (via the trans-Saharan seaway) during both the early Late Cretaceous and late Late Cretaceous intervals (e.g., Benkhelil, 1989; Néraudeau and Mathey, 2000; Reyment, 1980a, b; Reyment and Dingle, 1987). The late Cenomanian fish material from Nigeria includes taxa which probably dispersed from the southwestern Europe (Iberian Peninsula) and/or southern Tethyan platforms (Morocco to Lebanon), such as "*Carcharias*" *amonensis*, *Rhombopterygia* and *Hamrabatis*. Thus, "*C.*" *amonensis* was able to reach the South Atlantic (Angola), corresponding to its southernmost and only Southern Hemisphere occurrence (see Kitamura, 2013: fig. 3). As underlined by Cavin (2008), the biogeographical history of pachyrhizodontoid fishes is not well understood. The Nigerian occurrence could have resulted from either a vicariant or dispersal event. The similarity between the vidalamiine from the late Cenomanian of northeastern Nigeria (as well as both closely related forms from the younger beds of southern Nigeria and Niger) and members of this clade from the Late Cretaceous of North and South America may be indicative of an Early Cretaceous vicariant event, like for the genera *Calamopleurus* and *Pachyamia* (Cavin, 2008). However, although most of Late Cretaceous amiid fishes are regarded as non-marine forms, some of these fossils can be recovered from marine deposits, such as the material studied here and the possible vidalamiine specimen described from the Turonian of the Sergipe Basin in northeastern Brazil (Gallo et al., 2007b). If these fragmentary specimens were not washed into the sea and actually correspond to marine forms, a trans-Atlantic dispersal during the early Late Cretaceous cannot therefore be rejected.

The origin and dispersal history of *Ptychodus decurrens* remains unclear. Verma et al. (2012) have suggested that it could have dispersed from Western Australia to

Europe and North America via India or the South Atlantic. This species had a mid to high-palaeolatitudinal distribution (Hoch, 1992; Verma et al., 2012) and its equatorial occurrence in the early Turonian of southern Nigeria may have been due to episodically colder sea water temperatures in this part of the Benue Trough directly connected to the South Atlantic (Néraudeau and Mathey, 2000). Occurrences of this species in the Cenomanian–earliest Turonian of North Africa (e.g., Tunisia, Morocco) would suggest that it migrated southwards during the Turonian to reach the Lower Benue Trough (Nigeria) and Benguela Basin (Angola) in the early and late Turonian, respectively. Interestingly, *P. decurrens* was also reported in the early Turonian of the Sergipe Basin (northeastern Brazil), then located in the northwestern margin of the proto-South Atlantic, roughly at the same palaeolatitude as the Lower Benue Trough (Andrade, 2005; Carvalho and Gallo, 2002). Concerning the genus *Acrotemnus*, it might have dispersed from European seas to the trans-Saharan seaway (Niger) and Benue Trough (Nigeria), and also to the Western Interior Seaway (U.S.A.). A similar pattern of dispersal has been recently proposed by Martín-Abad and Poyato-Ariza (2013) for various Cenomanian–Turonian pycnodontid genera.

Scapanorhynchus texanus might have originated during the Turonian–Santonian interval in the Afro–Arabian plate where it is relatively rare, known only by a few teeth from Angola, Nigeria, and Jordan (Antunes and Cappetta, 2002; Mustafa, 2000; Zalmout and Mustafa, 2001). During the Campanian–Maastrichtian interval, this species seems to have been restricted to North America (Cappetta and Case, 1975b; Case and Schwimmer, 1988; Welton and Farish, 1993) while it was apparently replaced in Africa and Near East by *S. rapax* (Antunes and Cappetta, 2002; Bardet et al., 2000; Quaas, 1902; Retzler et al., 2013). As discussed above, the presence of a vidalamiine fish in the Coniacian?–Santonian beds of Awgu can be the result of either vicariant or dispersal events.

The few Campanian–Maastrichtian occurrences of *Eodiaphyodus* along the South Atlantic coast (Angola, Nigeria) are the oldest ones known for the genus. This suggests that *Eodiaphyodus* originated in this part of Africa and dispersed northwards (via the Atlantic coast of Western Africa or via the trans-Saharan seaway) to reach northwestern Africa, where it is especially common in the late Maastrichtian of Morocco (Arambourg, 1952).

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Figure captions:

Fig. 1. Geographical and stratigraphical position of the fish remains studied here. A, Nigerian geographical framework (A1) and main Nigerian structural and sedimentary units (A2). B, synthetic stratigraphical successions of the Lower Benue Trough, southern Nigeria (B1) and Upper Benue Trough, northeastern Nigeria (B2). Map, stratigraphical successions and other data modified from Courville (1993) and Courville et al. (1998).

Fig. 2. A, *Ptychodus decurrens*, tooth (GR/PC.1773) in occlusal (A1), lingual (A2) and lateral (A3) views. B, cf. *Protolamna* sp., tooth (GR/PC.1774) in lingual (B1) and mesiodistal (B2) views. C, *Cretolamna appendiculata*, tooth (GR/PC.1775) in lingual (C1) and labial (C2) views. D, *Squalicorax pristodontus*, tooth (GR/PC.1776) in lingual (D1) and labial (D2) views. E, F, *Scapanorhynchus* cf. *texanus*, GR/PC.1777 (E) and GR/PC.1778 (F), teeth in lingual (E1, F), labial (E2) and distal (E3) views. Scale bars equal 5 mm (B) and 10 mm (A, C–F).

Fig. 3. A, "*Carcharias*" *amonensis*, tooth (GR/PC.1779) in lingual view. B–E, *Rhombopterygia zaborskii* sp. nov., holotype GR/PC.1780 (B), paratypes GR/PC.1781 (C), GR/PC.1782 (D) and GR/PC.1783 (E), teeth in occlusal (B1, C, D1, E), lingual (B2, D2) and mesiodistal (B3) views. F, G, *Hamrabatis* sp., GR/PC.1784 (F) and GR/PC.1785 (G), teeth in occlusal (F1, G), lingual (F2) and mesiodistal (F3) views. Scale bars equal 500 µm (B–G) and 1 mm (A).

Fig. 4. A, *Acrotemnus* sp., right prearticular dentition (GR/PC.1786) in occlusal view. B, C, Vidalamiinae indet. A, GR/PC.1788 (B) and GR/PC.1789 (C), abdominal and ural centra (respectively) in anterior (B1, C), posterior (B2), dorsal (B3), ventral (B4) and left lateral (B5) views. D, Vidalamiinae indet. B, abdominal centrum (GR/PC.1790) in anterior (D1), posterior (D2), dorsal (D3), ventral (D4) and left lateral (D5) views. E, cf. *Protosphyraena* sp., tooth (GR/PC.1792) in labiolingual views. F, *Eodiaphyodus* cf. *granulosus*, tooth plate (GR/PC.1795) in occlusal (F1), basal (F2) and lateral (F3) views. Scale bars equal 5mm (C, E) and 10 mm (A, B, D, F).

Fig. 5. A, "*Stephanodus*" sp. (?Pycnodontiformes), branchial tooth (GR/PC.1787) in lateral view. B, Ionoscopiformes indet., tooth (GR/PC.1791) in mesiodistal? (B1), labial? (B2) and apical (B3) views. C, *Enchodus* cf. *gladiolus*, tooth (GR/PC.1794) in lateral view. Scale bars equal 500 µm.

Fig. 6. Pachyrhizodontoidei indet., caudal skeleton (GR/PC.1793) in right lateral view. Abbreviations: DCS, dorsal caudal spine; HS, hemal spine; Hy, hypural; Le, lepidotrichs; NS, neural spine; Ph, parhypural, Pu, preural vertebra; U, ural centrum; Un, uroneural; VCS, ventral caudal spine. Scale bar equals 50 mm.

Figure 1

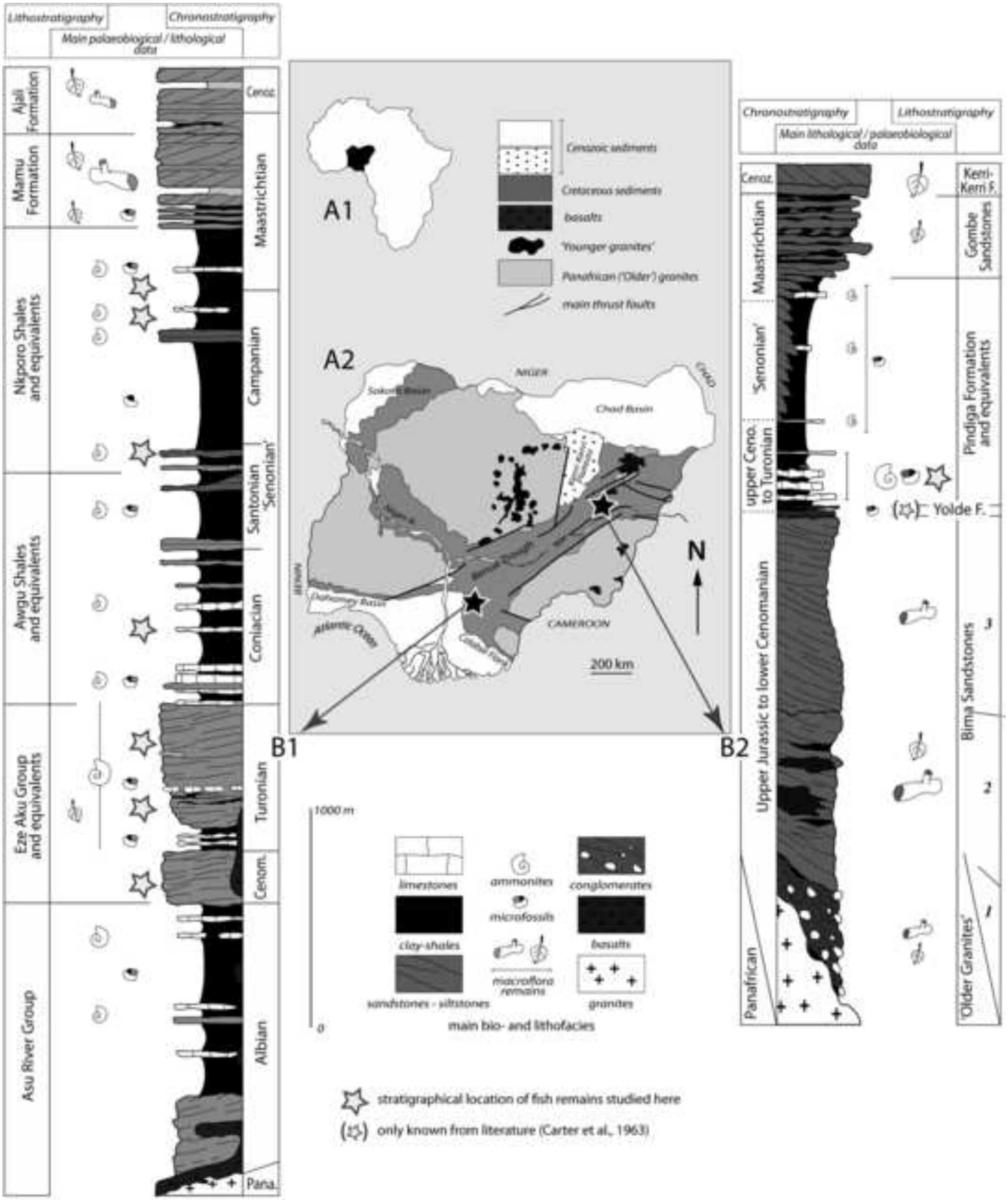

Lithostratigraphy
Chronostratigraphy
Main palaeobiological / lithological data
Ajali Formation
Mamu Formation
Nkporo Shales and equivalents
Awgu Shales and equivalents
Eze Aku Group and equivalents
Asu River Group
Ceno.
Maastrichtian
Campanian
Santonian
'Senonian'
Coniacian
Turonian
Cenom.
Albian
Pana.
A1
A2
Cenozoic sediments
Cretaceous sediments
basalts
'Younger granites'
Panafrican ('Older') granites
main thrust faults
NIGER
CHAD
Sokoto Basin
Chad Basin
BENIN
Dahomey Basin
Atlantic Ocean
CAMEROON
Niger Delta
N
200 km
B1
B2
1000 m
0
limestones
ammonites
conglomerates
clay-shales
microfossils
basalts
sandstones - siltstones
macroflora remains
granites
main bio- and lithofacies
stratigraphical location of fish remains studied here
only known from literature (Carter et al., 1963)
Chronostratigraphy
Lithostratigraphy
Main lithological / palaeobiological data
Ceno.
Maastrichtian
'Senonian'
upper Ceno. to Turonian
Upper Jurassic to lower Cenomanian
Panafrican
Kerri-Kerri F.
Gombe Sandstones
Pindiga Formation and equivalents
Yolde F.
Bima Sandstones
3
2
1
'Older Granites'

Figure 2

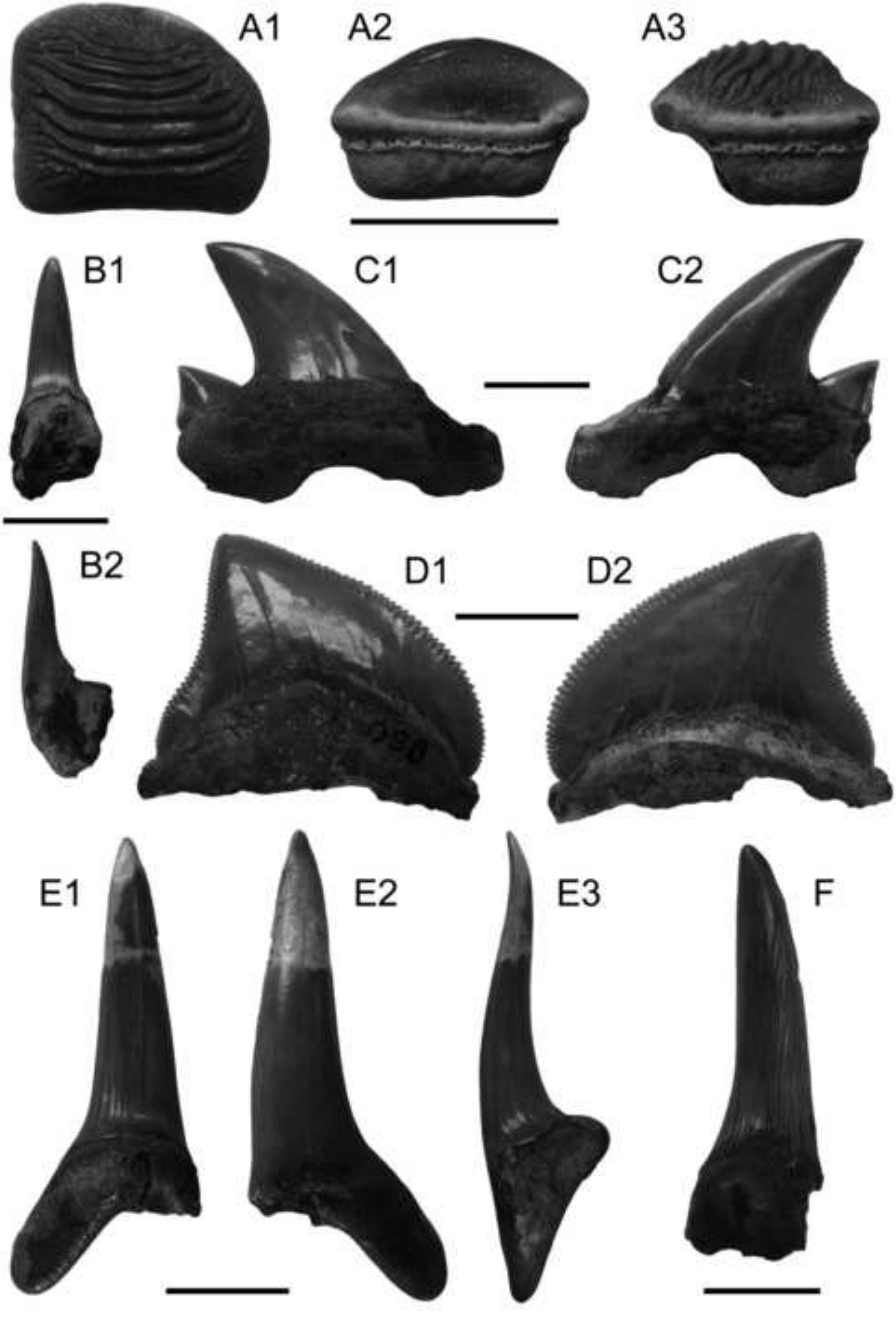


Figure 3

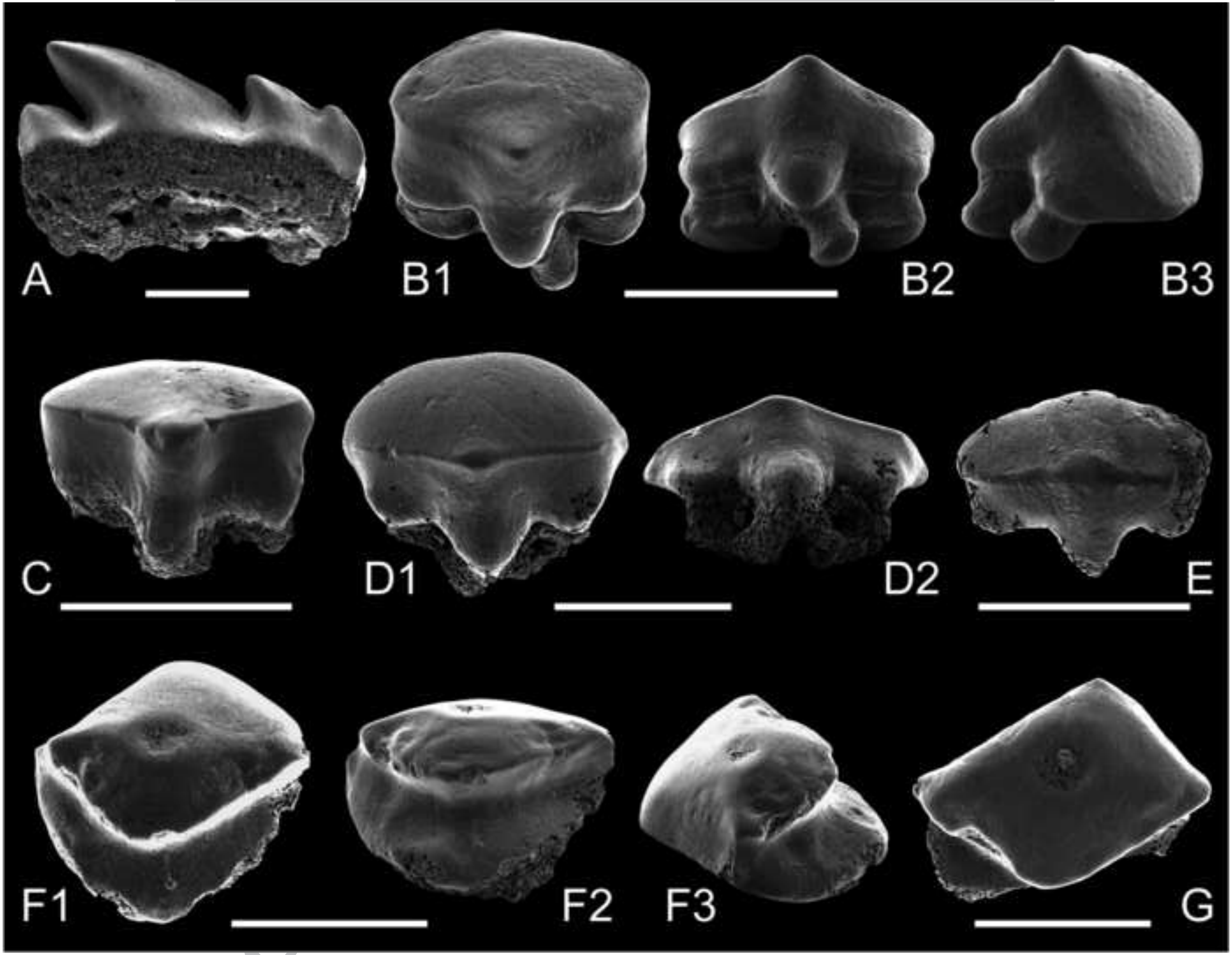


Figure 4

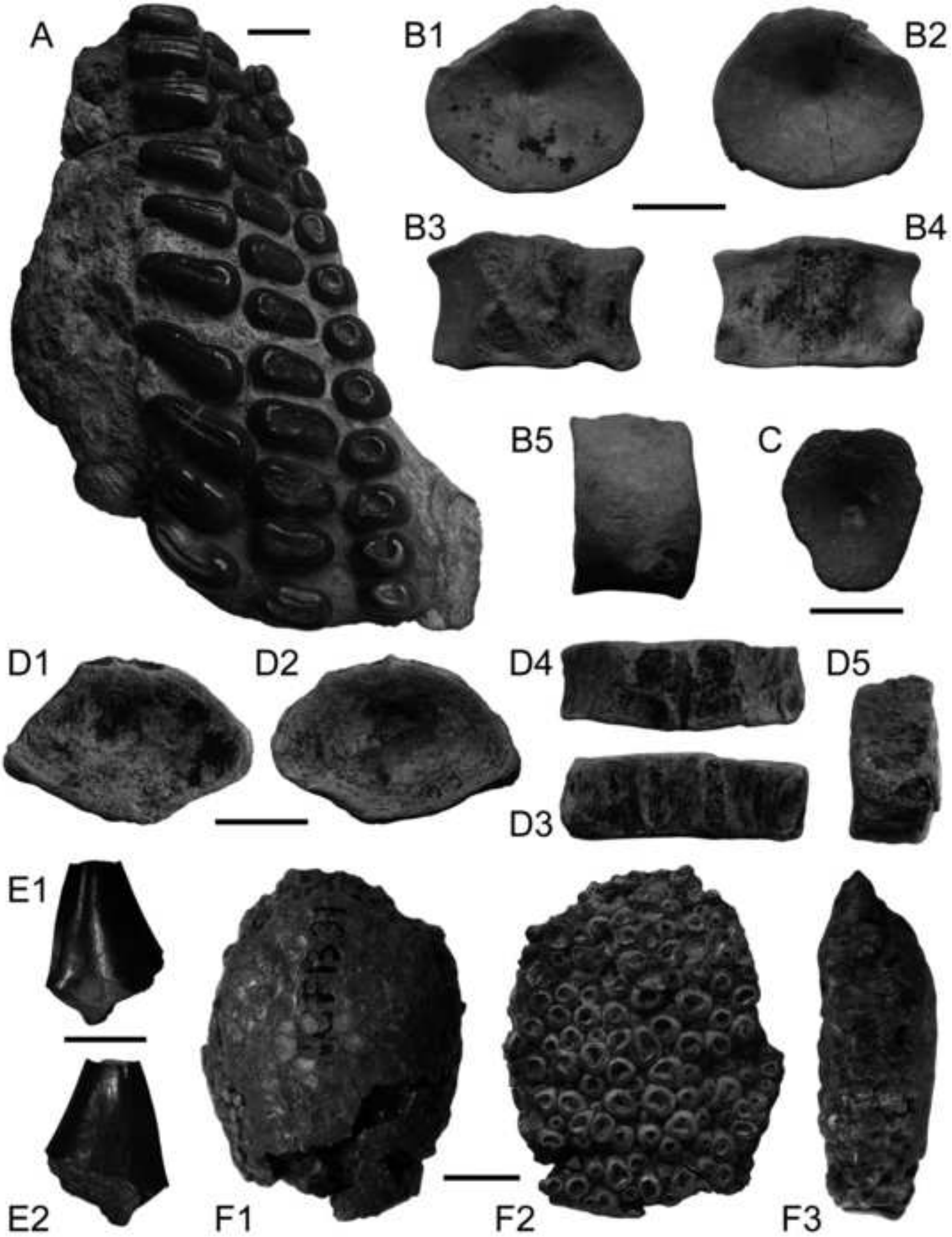


Figure 5

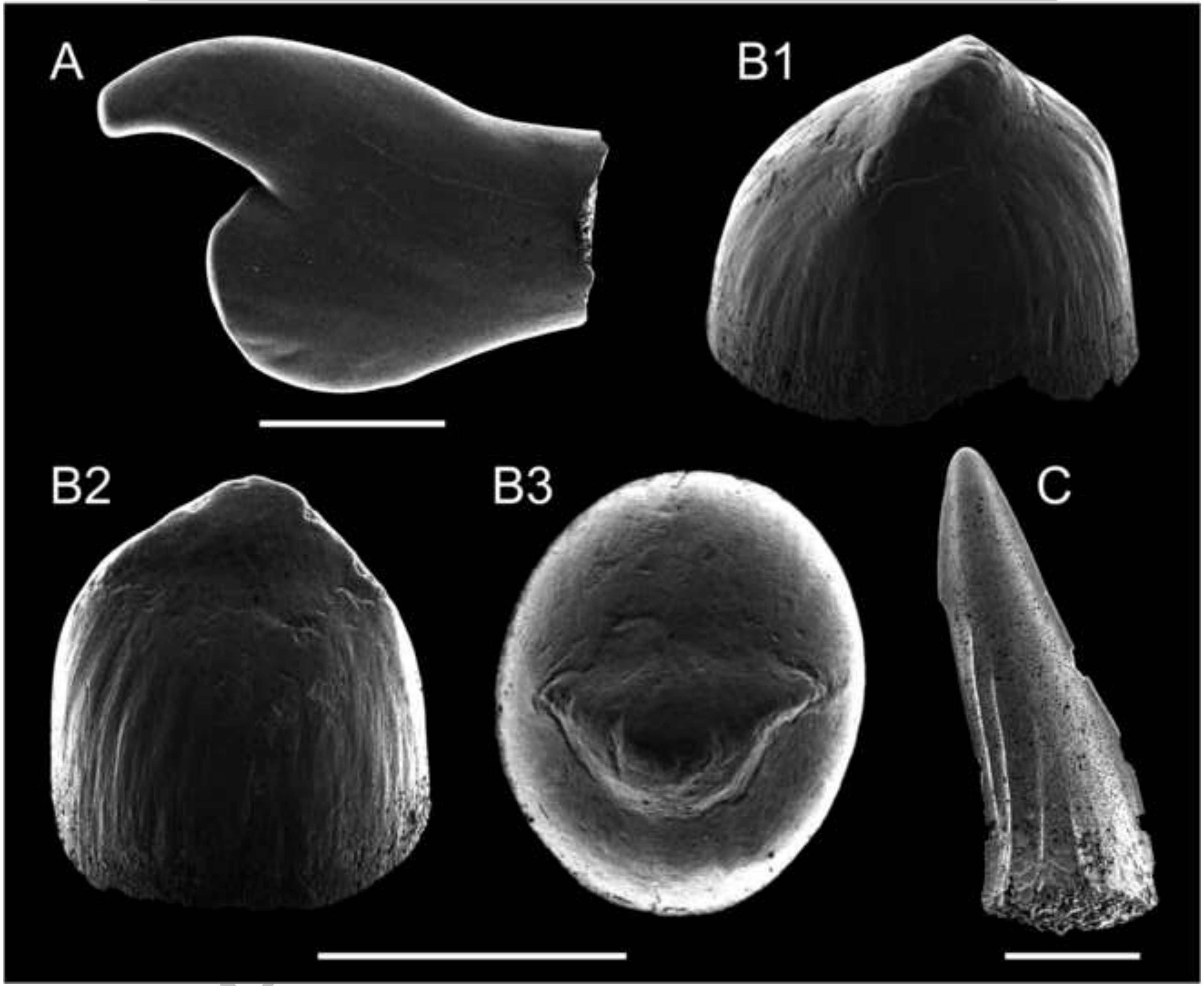
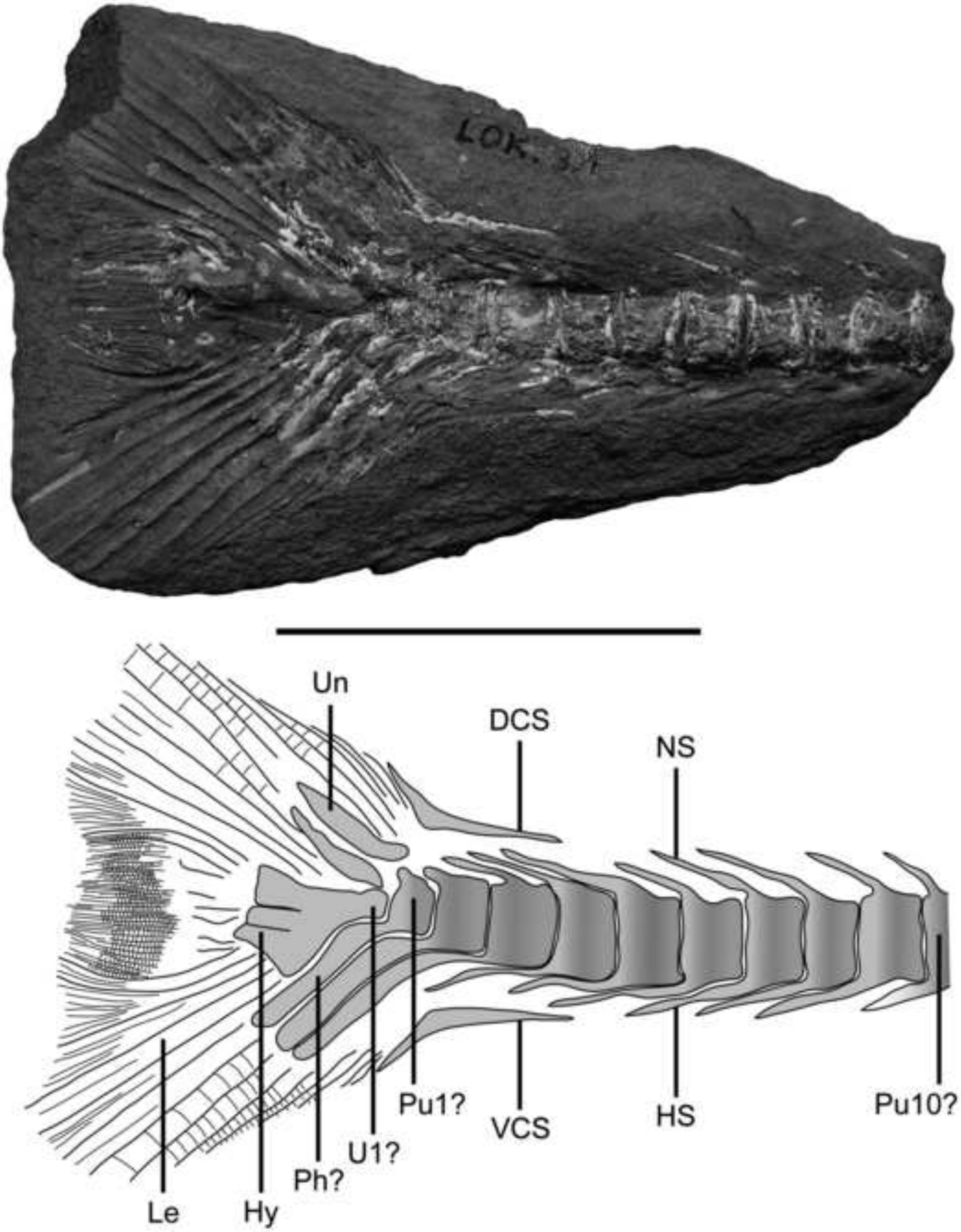


Figure 6



Highlights:

- Selachian and ray-finned fishes are described from the Late Cretaceous of Nigeria.
- Some fish taxa are recorded for the first time in Africa.
- *Rhombopterygia zaborskii* sp. nov. is described from the Cenomanian of Ashaka.
- The Benue Trough created opportunities for the dispersal of many marine fishes.