



## Paleocene ichthyofauna and paleoenvironmental setting, Imo Formation, southeastern Nigeria

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With 3 figures

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**Abstract:** The Paleogene vertebrate fossil record of Nigeria has until recently been limited to marine deposits in the Eocene-age Ameki Formation. New work in the Imo Formation of southeastern Nigeria has revealed a diverse ichthyofauna of Paleocene age. The Imo Formation overlies the Nsukka Formation, and underlies the Ameki Formation. The uppermost bone-bearing interval of the Imo Formation is separated from the overlying Ameki Formation by a NW-SE trending, shoreface-tidally-influenced sandstone ridge that dominates the Ozuitem-Umuahia landscape. The Ameki beds outcrop to the west of the sandstone ridge, whereas the Imo outcrops to the east. Fossils described herein were recovered from an interval of interstratified crudely laminated clay/shale and calcareous lenses of well-sorted sandstone/siltstone which outcrops to the east of the sandstone ridge in the Bende District. The fauna is represented by at least seven taxa, including an actinopterygian, five chondrichthyans (represented by one ray and four shark species), and *Cylindracanthus*, an enigmatic incertae sedis taxon. Five of the species in the Imo fauna appear to have survived into the Eocene, whereas the remaining two are hitherto undocumented in younger faunas of Nigeria.

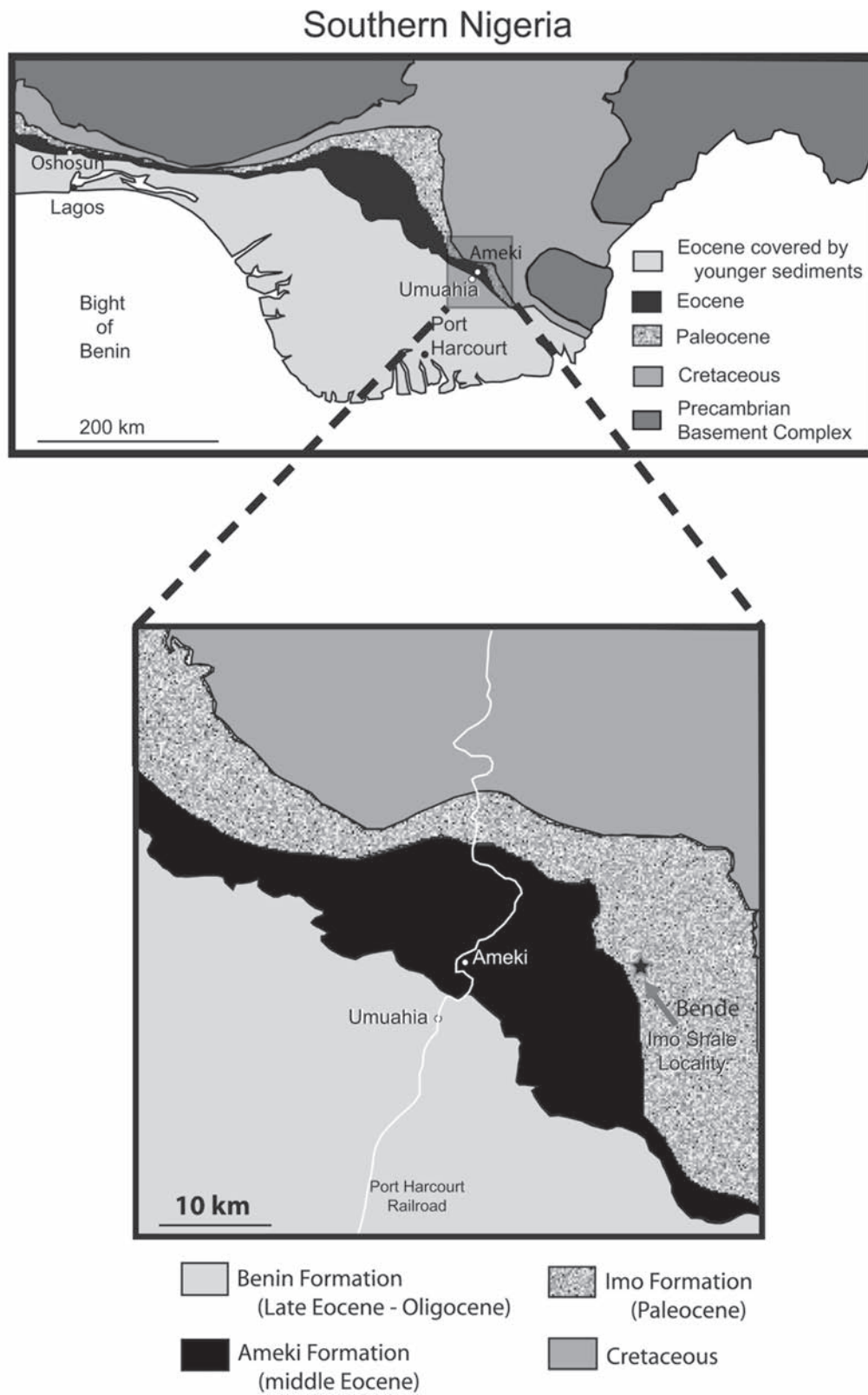
**Key words:** Paleontology, paleoecology, paleobiogeography, Chondrichthyes, Actinopterygii, early Cenozoic, marine environments, Nigeria.

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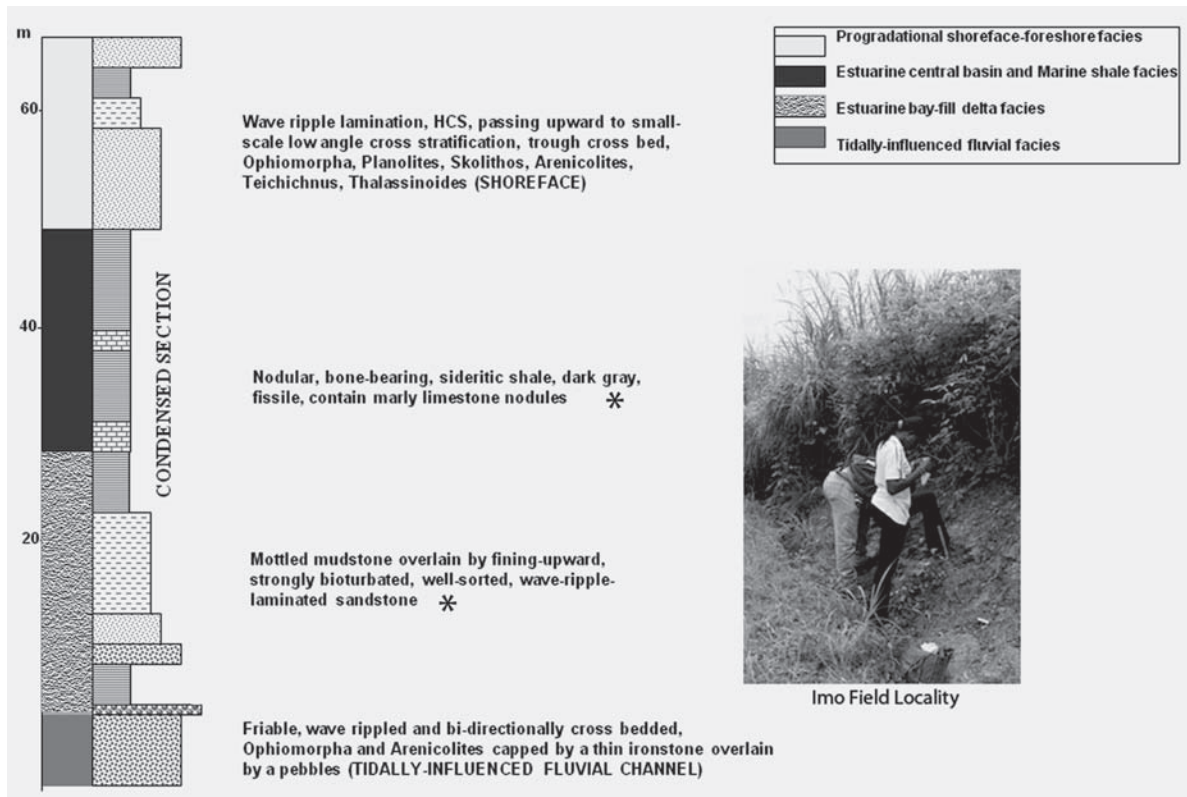
### 1. Introduction

The sedimentary basins of Southern Nigeria reflect the separation of the African and South American landmasses early in the Cretaceous Period (REYMENT 1965; OBOH-IKUENOBE et al. 2005). Paleogene deposition is recorded in the Nsukka Formation, the Imo Formation, and the Ameki Formation (REYMENT 1965; ODUNZE & OBI 2007). Sedimentological evidence suggests that the Nsukka Formation documents a phase of fluvio-deltaic deposition that began close to the end of the Maastrichtian and continued into the Paleocene (OBOH-IKUENOBE 2005). The Imo-Ameki succession contains three lithologically and architecturally similar

depositional cycles, each consisting of a basal fluvial and tidally-influenced fluvial facies, bone-bearing estuarine bay-fill delta/estuarine central basin mudstone facies, and progradational shoreface-foreshore facies assemblages, deposited from the Paleocene well into the Eocene. Vertebrate fossils have hitherto been documented in the region only from Eocene-aged localities such as the type locality of the Ameki Formation at Ameki town, in Ameki deposits near Bende, and in the Oshosun locality north of Lagos (ANDREWS 1920; WHITE 1926). In particular, WHITE (1926) detailed the presence of a diversity of mainly selachian and teleost fishes from Eocene localities, with 29 species documented at Ameki and over a dozen species



**Fig. 1.** Geological map of southern Nigeria above, inset below depicting Imo fossil locality, indicated by an asterisk.



**Fig. 2.** Stratigraphic section of Imo fossil locality, southern Nigeria, with image of team working on an outcrop. \* indicates presence of fossils in a given facies.

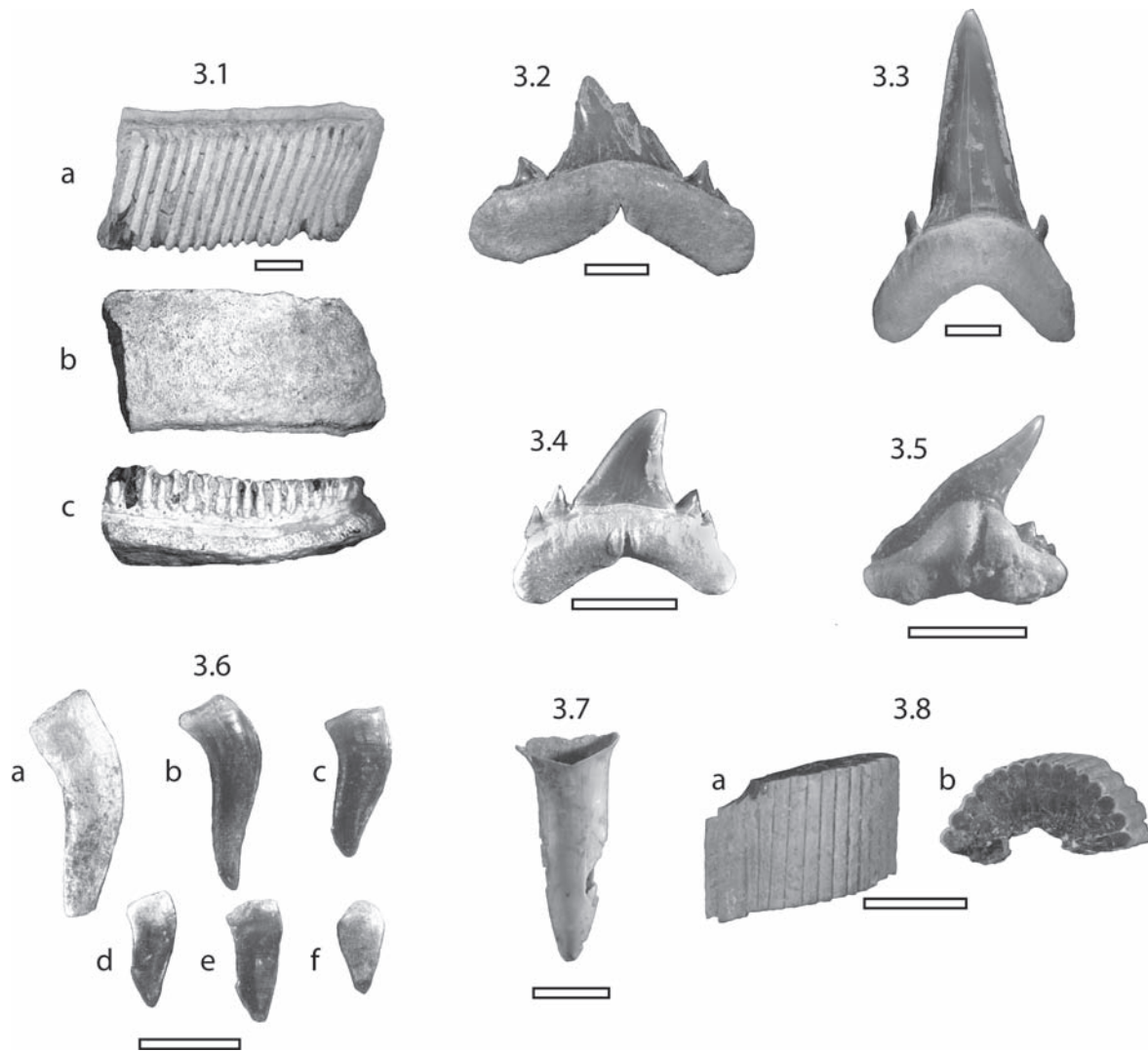
recorded from localities in nearby Oshosun. Far less is known about the vertebrate fauna and paleoenvironmental setting of Paleocene (Imo Formation) depositional units in the region.

The historical town of Bende is located in southeastern Nigeria, and underlain by a succession of the Selandian Imo Formation and the Ypresian Ameki Formation (Fig. 1). In November 2008, a joint expedition was conducted by Ohio University, NEUCOM and Anambra State University, resulting in the discovery of an ichthyofauna somewhat distinctive from that described from the Ameki Formation, in Paleocene-aged deposits near Bende, about 15 km up dip of the Ameki exposure (ODUNZE et al. 2009). Herein the discovery is placed into context using analyses of the sequence architecture and depositional environment of fossil-bearing deposits to inform biostratigraphic and paleobiological inferences.

## 2. Geological setting of paleontological finds

Vertebrate and invertebrate fossils were collected by standard paleontological hand quarrying methods from Imo Formation outcrops near Bende town. Lithofacies analysis demonstrates that the deposits accumulated in a spectrum of coastal and shallow marine environments. Four main depositional facies include (1) fluvial and tidally-influenced fluvial facies, (2) estuarine bay-fill delta, (3) estuarine central basin and marine shale facies, and (4) progradational shoreface-foreshore facies (Fig. 2).

The Bende fossils were recovered from the bay-fill delta and estuarine central basin facies assemblages. The bay-fill delta facies is composed of thin carbonaceous crudely laminated or mottled, gypsiferous clay and clay shale inter-layered with well-sorted, strongly bioturbated/wave ripple laminated fossiliferous fine-medium grained sandstone, siltstone and



**Fig. 3.** Examples of specimens collected at Imo fossil locality on joint Ohio University/Nigeria Anambra State University Uli paleontological expedition. Views are labial unless otherwise noted. **3.1a-c** (NASU 1) *Myliobatis* tooth plate in basal, occlusal and side views respectively; **3.2** (NASU 12) *Isurolamna* tooth; **3.3** (NASU 13) *Odontaspis* tooth; **3.4** (NASU 16) *Cretolamna* tooth; **3.5** (NASU 19) *Physogaleus* tooth; **3.6a-f** (NASU 22-27 respectively) *Trichiurus* teeth; **3.7** (NASU 28) actinopterygian tooth crown; **3.8a-b** (NASU 29-30) *Cyllindracanthus* rostral fragment in dorsal and cross sectional views respectively. Scale bars = 5 mm.

limestone. The presence of gypsiferous and sandy lenticular clays, in association with low diversity burrow types (including *Skolithos*, *Planolites*, *Thalassinoides* and *Teichichnus*), is indicative of a tidally-influenced estuary (ALLEN 1993; ALLEN & POSAMEN-TIER 1993; OBOH-IKUENOBE et al. 2005; PEMBERTON & WIGHTMAN 1992; PROTHERO & SCHWAB 1996; REYMENT 1965).

Bay-fill delta facies deposition likely ended with subsequent transgression across interfluvial areas. This eliminated the estuary and initiated deposition of the bone-bearing shales interbedded with coquinoid limestone and fossiliferous siltstones (ODUNZE & OBI 2007). The transition from shoreface-foreshore facies at the top of the Imo Formation to the overlying tidally-influenced fluvial sandstones marks the

contact between the Imo Formation and the overlying Eocene Ameki depositional cycle (OBOH-IKUENOBE 2005; ODUNZE & OBI 2007) from which vertebrate remains have also been documented (WHITE 1926; ADEGOKE 1969).

The remaining sections detail the fossil ichthyofauna recovered from the Imo Formation, following the classification of NELSON (2006). Terminology for shark tooth morphology follows COMPAGNO (1988).

**Abbreviations:** NASU: Nigeria, Anambra State University Uli, Department of Geology, paleobiological collections accession number.

### 3. Systematic paleontology

Class Chondrichthyes HUXLEY, 1880  
Order Myliobatiformes COMPAGNO, 1973  
Family Myliobatidae BONAPARTE, 1838  
Genus *Myliobatis* CUVIER, 1816

*Myliobatis* sp.

Fig. 3.1

**Description.** – Eleven elements (NASU 01-11) from the median series or file of pavement-like jaw teeth, some arched in coronal plane, representing upper jaw elements (e.g., Fig. 3.1a-b). These are considered components of the median series based upon both their size and shape, as lateral series elements are generally narrower and smaller. All teeth are broken at the lateral ends such that the hexagonal morphology is not evident. The teeth are considerably wider than long, with the largest measuring 37 mm in width, 13 mm in length, and 7.5 mm in thickness. The teeth are identified as those of *Myliobatis*, rather than *Aetobatus*, because the thickness of the crown is equal to or slightly greater than that of the root elements. In *Aetobatus*, the root is thicker than the crown (CAPETTA 1987). Individual root elements are 0.6-1.1 mm wide and the largest plate contains 28 elements. These teeth are most similar to *Myliobatis bothriodon* (WHITE 1926, pl. 10, fig. 12).

**Remarks.** – *Myliobatis* is an extant taxon. Myliobatids feed benthically and employ their pavement-like dentition to grind hard-shelled prey, predominantly mollusks, but also crabs, lobsters, shrimp, and worms. They occur in tropical to warm-temperate continental shelves and offshore waters of the Atlantic, Pacific and Indian oceans. Global fossil distribution and occurrence: worldwide, Early Paleocene-Recent (CAPETTA 1987). African fossil occurrence: Paleocene-Eocene of western Africa including Angola, Egypt, Morocco, Togo and Nigeria (CAPETTA 1987; COOK et al. 2010). WHITE (1926) reported this genus from both Ameki and Oshosun localities.

Order Lamniformes BERG, 1958  
Family Lamnidae MÜLLER & HENLE, 1838  
Genus *Isurolamna* CAPETTA, 1976

*Isurolamna* sp.

Fig. 3.2

**Description.** – One tooth with damaged crown (NASU 12), missing part of median cusp. Crown smooth, relatively low and triangular, with a large root relative to crown size (Fig. 3.2). One prominent vertically oriented triangular cusplet adjacent to each side of crown, with a second small vestigial cusplet mesially and distally from each primary cusplet. Root thick dorsoventrally, moderately arched with modest lingual protuberance and wide shallow transverse (nutrient) groove.

**Remarks.** – An extinct genus in an extant family of pelagic predatory sharks with a fossil occurrence from the Late Paleocene-Early Eocene of Europe and northern Africa (CAPETTA 1987). The root is similar in shape to that of *Isurolamna inflata* from the late Paleocene and early Eocene of northern Africa (pers. comm. TODD COOK). Not reported by WHITE (1926) from his Nigerian localities.

Family Odontaspidae MÜLLER & HENLE, 1839

Genus *Odontaspis* AGASSIZ, 1938

*Odontaspis* sp.

Fig. 3.3

**Description.** – Three teeth with crown heights of 12.2–17.5 mm (NASU 13-15). Crown smooth, narrow and blade-like, vertically oriented with one distinct sharp cusplet on each side (e.g., Fig. 3.3). Tip of crown with slight labially-directed curve. Cutting edges sharp, without serrations, and complete to base of crown. Root highly arched with notable lingual protuberance and modest transverse (nutrient) groove. The crown is relatively higher and narrower and the root is more highly arched than *O. speyeri* from the Paleocene of western Africa (DARTEVELLE & CASIER 1943).

**Remarks.** – An extant genus and family of predominantly coastal sharks with a worldwide modern distribution and occurrence from the Late Cretaceous to Recent. African distribution and occurrence: Paleocene of northern and western Africa (CAPETTA 1987). Reported by WHITE (1926) from Ameki localities.

Family Cretoxyrhinidae GLÜCKMAN, 1958

Genus *Cretolamna* GLÜCKMAN, 1958

*Cretolamna* sp.

Fig. 3.4

**Description.** – Three teeth with crown heights of 5-12 mm (NASU 16-18). Crown smooth, triangular with two distinct cusplets on each side, the inner cusplet about twice the size of the outer (e.g., Fig. 3.4). Crown axis vertically or distally directed. Neck prominent in some teeth. Root lobes short and relatively flat with moderate lingual protuberance and moderate to nonexistent transverse (nutrient) groove.

**Remarks.** – An extinct genus and family. Likely to be *Cretolamna maroccana* (pers. comm. TODD COOK) but additional material will be helpful to further clarify identification. Global distribution and occurrence: nearly worldwide, Early Cretaceous–Early Eocene. African distribution and occurrence: Morocco, Angola, Democratic Republic of the Congo, Niger, Nigeria and Egypt; Late Cretaceous–Eocene (CAPPETTA 1987). Not reported by WHITE (1926) from his Nigerian localities.

Order Carcharhiniformes COMPAGNO, 1973  
Family Carcharhinidae JORDAN & EVERMANN, 1896  
Genus *Physogaleus* CAPPETTA, 1980

*Physogaleus* sp.  
Fig. 3.5

**Description.** – Three relatively small teeth with crown heights of 5.5–7.0 mm (NASU 19–21). Crown smooth, delicate and narrow mesiodistally with no mesial cusplets and three prominent distal cusplets (e.g., Fig. 3.5). Crown axis distally directed; some crowns with labiolingual curve; cutting edges sharp. The crown foot is prominent mesially. Some of the variability in crowns probably represents sexual dimorphism (COMPAGNO 1988). The root is slightly arched with a bulbous lingual protuberance where the two lobes meet; transverse (nutrient) groove also prominent.

**Remarks.** – An extinct genus in an extant family found in Paleocene–Miocene deposits of Europe, Africa and North America, although the Paleocene record from Morocco is questionable (CAPPETTA 1987). African distribution and occurrence: Eocene of Angola, Egypt, Morocco, Namibia, Togo. Reported by WHITE (1926) from the Middle Eocene Oshosun and Ameki localities of Nigeria as *Sphyrna* and *Carcharhinus* (CAPPETTA 1987).

Class Actinopterygii Cope, 1887  
Division Teleostei MÜLLER, 1845  
Order Perciforms BLEEKER, 1859  
Suborder Scombroidei BLEEKER, 1859  
Family Trichiuridae RAFINESQUE-SCHMALTZ, 1815  
Genus *Trichiurus* LINNAEUS, 1758

*Trichiurus* sp.  
Fig. 3.6

**Description.** – Five dentary or premaxillary fang-like anterior teeth, 6–12 mm in length (NASU 22–26; Fig. 3.6a–e), and one small (5 mm) palatine tooth (NASU 27; Fig. 3.6f). The former exhibit a shallow “S” curvature, with edges that are sharp mesially and rounded distally. In four of the five premaxillary teeth, the crown tip bears a slight barb on its distal edge. The palatine tooth is labiolingually compressed, with sharp mesial and distal edges.

**Remarks.** – In a recent review of scombroids from the Cenozoic of England, MONSCH (2004) indicates that cutlassfishes of the genus *Trichiurus* do not exhibit any diagnostic dental characters that permit identification at the species level. Trichiurids are pelagic piscivores found inshore and offshore in the Atlantic, Pacific and Indian oceans. Global fossil distribution and occurrence: worldwide, Eocene–Pleistocene (CARROLL 1988). African occurrence: Eocene. Reported from Nigerian locality Oshosun by WHITE (1926).

Class Actinopterygii

Actinopterygii gen. et sp. indet.  
Fig. 3.7

**Description.** – One actinopterygian tooth crown, 15 mm long (NASU 28). The tooth is hollow from base to tip of crown and possesses thin crown walls, hence the specimen does not represent a chondrichthyan (Fig. 3.7). It is tall and triangular in shape with sharp mesial and distal edges. It is compressed labiolingually and the distal third is slightly curved.

Incertae sedis  
*Cylindracanthus* LEIDY, 1856

*Cylindracanthus* sp.  
Fig. 3.8

**Description.** – Twelve rostral fragments; two more complete than the others (NASU 29–40). Externally the rostrum consists of a series of longitudinal columns and grooves and internally a central canal; the columns are distinct and extend from the surface of the rostrum to the central canal (Fig. 3.8a–b). The two most round and complete pieces do not fit together but each appears to constitute the complete diameter of the rostrum, about 9 mm with a central canal constituting 18–29% of the diameter. Each half is composed of 17 longitudinal columns, thus the entire rostrum consists of about 34 columns separated by grooves. Based on measurements of an intact 500 mm long rostrum of *C. rectus* provided by FARRÉS & ALTIMIRAS (2007), our two 9 mm diameter pieces would be located 100–200 mm from the distal end of the rostrum. The remaining 10 smaller pieces make up less of the diameter of the rostrum, but have the same morphology of longitudinal columns and grooves.

**Remarks.** – A perplexing taxon, *Cylindracanthus* is not known from any material other than rostra. Although *Cylindracanthus* has traditionally been classified among extinct scombroid billfishes (FIERSTINE 2006), some authors are skeptical of this assignment to the point of doubting its identity as a teleost or even a fish (MONSCH 2004). Based on anatomical evidence from the teeth and on the posterior insertions of the rostrum, PARRIS & GRANDSTAFF (2001) concluded that *Cylindracanthus* is a primitive actinopterygian of the order Acipenseriformes (sturgesons and paddle-

fishes), and that the reason no bony *Cylindracanthus* material has been found is that acipenseriforms have a cartilaginous skeleton. This logic is also followed by BECKER et al. (2009) in assigning specimens of *Cylindracanthus* to the Acipenseriformes. NELSON (2006: 430), on the other hand, believes that *Cylindracanthus* cannot confidently be assigned to any order of fishes, a line of reasoning that we follow here. *Cylindracanthus* is usually found in deposits associated with shallow nearshore marine habitats (BECKER et al. 2009). Global fossil distribution and occurrence: Asia, Europe, Africa and North America; Late Cretaceous-Eocene (CARROLL 1988). African occurrence: Late Cretaceous-Eocene. Reported from Eocene Ameki and Oshosun localities by WHITE (1926).

#### 4. Concluding remarks

The Paleocene is thought to be a time of global warmth prior to the differentiation of ocean basins, development of latitudinal temperature gradients and provincialization of the marine fauna (KENNETT 1982; ZACHOS et al. 2001). Our report here on the first vertebrates collected from the Paleocene Imo Formation of southeastern Nigeria offers a glimpse into the composition of the marine fish fauna of the region. The fauna is diverse, represented by at least seven fish taxa, including an actinopterygian, five chondrichthyans (represented by one ray and four shark species), and the enigmatic *Cylindracanthus*, a taxon of uncertain affinities sometimes classified as a billfish or an acipenseriform. Two of the species reported herein are undocumented in the younger Ameki deposits of this region, whereas the remaining five species appear to have survived into the Eocene. As testimony to the temporal persistence of some chondrichthyan and teleostean lineages, we note that of our seven taxa from the Imo Formation, *Myliobatis*, *Odontaspis* and *Trichiurus* are extant today in the waters around southern and western Africa (HEEMSTRA & HEEMSTRA 2004).

Based on the array of species found in Eocene Ameki localities, WHITE (1926) inferred a warm tropical climate for the region at that time, not unlike the coastal environment along western Africa today. A paleoecological reconstruction of the Ameki invertebrate fauna indicated primarily normal marine salinity values for the majority of the Ameki fossiliferous lenses, with occasional slight deviations to more brackish conditions (ARUA 1988). In addition, molluscan families present at Ameki support WHITE'S (1926) assessment of warm water conditions in the region at that time, and echinoids, corals and particularly abundant bivalves suggest well-oxygenated bottom

conditions (ARUA 1988). Although far less is known of Nigerian Paleocene invertebrates to date, the presence of ichthyofauna such as the eagle ray *Myliobatis*, as well as the sand shark *Odontaspis* in the Imo Formation near Bende town is consistent with a warm tropical marine environment during the Paleocene. Future work is planned to recover additional ichthyofauna and other vertebrate and invertebrate fossils.

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