PALÆO
VERTEBRATA

ARTICLE

Additions to the elasmobranch assemblage from the Bandah Formation (middle Eocene, Bartonian), Jaisalmer District, Rajasthan, India, and the palaeobiogeographic implications of the fauna

Rajendra Singh RANA[a], Raman PATEL[a], David J. CICIMURRI[b], & Jun A. EBERSOLE*[c]

[a]Department of Geology, Hemvati Nandan Bahuguna (H.N.B.) Garhwal University Srinagar Garhwal-246174, Uttarakhand, India
[b]South Carolina State Museum, 301 Gervais Street, Columbia, South Carolina 29201, USA
[c]McWane Science Center, 200 19th Street North, Birmingham, Alabama 35203, USA

**Corresponding author: jebersole@mcwane.org*

Abstract: Isolated elasmobranch teeth (sharks and rays) from the middle Eocene (Bartonian) Bandah Formation in the Jaisalmer District of Rajasthan, India are described. The remains improve our knowledge of the environment represented by this lithostratigraphic unit and the ecology preserved therein. Seventeen unequivocal taxa were identified, including *Nebrius* sp., *Striatolamia* aff. *S. macrota*, *Brachycarcharias atlasi*, *B. lerichei*, cf. *Jaekelotodus* sp., *Carcharhinus mancinae*, *Rhizoprionodon* sp., *Physogaleus* sp., *Galeocerdo clarkensis*, *G. eaglesomei*, *Odontorhytis* aff. *O. pappenheimi*, "*Rhinobatos*" sp., "*Dasyatis*" sp., *Coupatezia* sp., "*Aetomylaeus*" sp., "*Rhinoptera*" sp., and *Ouledia* aff. *O. lacuna*. Of these, "*Aetomylaeus*" sp., *B. atlasi*, *C. mancinae*, *G. clarkensis*, *G. eaglesomei*, cf. *Jaekelotodus* sp., *Nebrius* sp., *Odontorhytis* aff. *O. pappenheimi*, *Ouledia* aff. *O. lacuna*, and "*Rhinoptera*" sp. are reported from the middle Eocene of India for the first time. The Bandah Formation elasmobranch palaeofauna has close affinities to the Palaeocene-Eocene Tethyan/Paratethyan faunas of Africa, Madagascar, Asia, and Europe, and some taxa indicate a western hemisphere influence from North America. The Bandah Formation palaeofauna indicates that deposition occurred in a moderately shallow marine environment. The Bartonian age is primarily based on foraminifera but is corroborated by the presence of elasmobranch taxa that also occur in contemporaneous deposits elsewhere. The marine regression started during the early Palaeogene, and our study indicates that the sea completely withdrew from the Jaisalmer Basin after the deposition of the Bandah Formation. This event may have been synchronous with the middle Eocene uplift of the Himalayan-Tibetan Plateau.

Keywords: Palaeogene, Chondrichthyes, Elasmobranchii, South Asia, Indian Ocean

Submitted 19 January 2021, Accepted 19 March 2021
Published Online 23 June 2021, doi: 10.18563/pv.44.2.e1

INTRODUCTION

The Palaeogene basin of the Jaisalmer District in Rajasthan, India has long been recognized for its rich diversity of fossil invertebrates, but vertebrate fossils from the region are comparatively poorly known (Kumar *et al*., 2007; Pandey *et al*., 2018; Kumar *et al*., 2017; Kumar *et al*., 2020). The paucity of studies on the vertebrate fossils in this region is due to a combination of factors, one being the poor state of preservation of much of the material. Of the few published studies on fossil vertebrates from the Jaisalmer District, Kumar *et al*. (2017) and Kumar *et al*. (2020) described small vertebrate faunas from the middle Eocene Bandah Formation in Rajasthan. Kumar *et al.* (2017) identified teeth as *Isurus* sp., *Lamna* sp., *Striatolamia* sp. and *Galeocerdo* sp., and Kumar *et al*. (2020) reported the occurrence of *Isurus* cf. *I. oxyrhinchus*, *Carcharias* cf. *C. tricuspidatus*, *Galeocerdo* sp., and *Myliobatis* sp. These preliminary reports are of interest because the fossils were obtained from the same locality and formation as the present study, but the material was surface collected from a different outcrop where the lithologic beds are more difficult to discern.

Outside of the Jaisalmer District, several Palaeogene elasmobranch faunas have been reported from the Indian subcontinent, the oldest of which occur in upper Palaeocene (Thanetian) to lower Eocene (Ypresian) strata of the Akli and Kapurdi formations in the Barmer District of Rajasthan (Rana *et al*., 2005, 2006; Rajkumari & Prasad, 2020), and the similarly-aged Kakara Formation of the Shimla District in Himachal Pradesh (Gupta & Kumar, 2013). Early Eocene elasmobranch faunas have been documented from the Cambay Shale of the Surat District (Rana *et al*., 2004), the Subathu Formation of the Solan District of Himachal Pradesh (Sahni *et al*., 1984; Kumar & Loyal, 1987), Nilkanth of the Pauri District of Uttarakhand (Kumar, 1989) and Rajouri District of Jammu and Kashmir (Khare, 1976). Additional selachian faunas were described by Sahni & Mishra (1975) from various Eocene units in the Kutch District in Gujarat.

Herein we describe a collection of isolated elasmobranch teeth recovered *in situ* from the Bandah Formation in the Jaisalmer District of Rajasthan that were obtained during a field investigation in the region in February 2020. These specimens are described in detail, and we provide a re-evaluation of the elasmobranch remains previously reported from the locality by Kumar *et al*. (2017) and Kumar *et al*. (2020). Additionally, we discuss taxonomic issues and the palaeobiogeographic distributions of the species we identified, and we provide a palaeoenvironmental interpretation for the fossiliferous horizon based on the fossils that have been collected.

GEOLOGIC SETTING AND AGE

The Palaeogene surface sequence of the Jaisalmer Basin is represented by the Sanu, Khuiala and Bandah formations (Fig. 1). The basal sequence is the Palaeocene Sanu Formation, which overlies the Cretaceous Habur Formation. Investigations of the surface exposures of the latter formation have thus far shown it to be devoid of fossils. The Sanu Formation is overlain by the lower Eocene Khuiala Formation. Although macrofossils are generally lacking in surface exposures of the Khuiala Formation, abundant vertebrate and invertebrate microfossils are known from the basal part of this unit (Singh, 1996; Kumar *et al*., 2007; Pandey *et al*., 2018; Raju, 2018; and references therein). The middle Eocene Bandah Formation is the uppermost unit within the Palaeogene sequence. This unit conformably overlies the Khuiala Formation and is disconformably overlain by the Pleistocene Sumer Formation (Singh, 1996). The elasmobranch sample described herein was collected *in situ* from the upper portion of the middle Eocene Bandah Formation.

The collecting locality for the present study is located approximately 2.5 km northeast of Bandah Village along Bandah-Ramgarh Road within the Jaisalmer District in Rajasthan, India (N 27°09’00.91”; E 70°28’02.56”). Although a complete section of the Bandah Formation is not exposed at our collecting locality (most of the area is covered by Recent sand from the Thar Desert), an 8.60 m thick section of the upper part of the formation was available to study. This portion of the formation consists of four beds, which include (in ascending order) “bed d” – 3.0 m of greyish-green to khaki gypsiferous shale intercalated with thin bands of dirty white to yellowish foraminifera-bearing limestone and marl (each 0.30 m thick); “bed c” – 1.50 m of yellowish to brownish foraminifera-bearing limestone; “bed b” – 3.50 m of yellowish to chalky white oyster-bearing argillaceous limestone, and; “bed a” – 0.60 m of dirty white to yellowish compact limestone that is finally capped by Recent alluvium. The elasmobranch fossils described herein were collected from the upper part of “bed b” of the Bandah Formation at our collecting locality (see Fig. 2). Although our collecting site is situated close to the study location of Kumar *et al.* (2017) and Kumar *et al.* (2020), our stratigraphic section

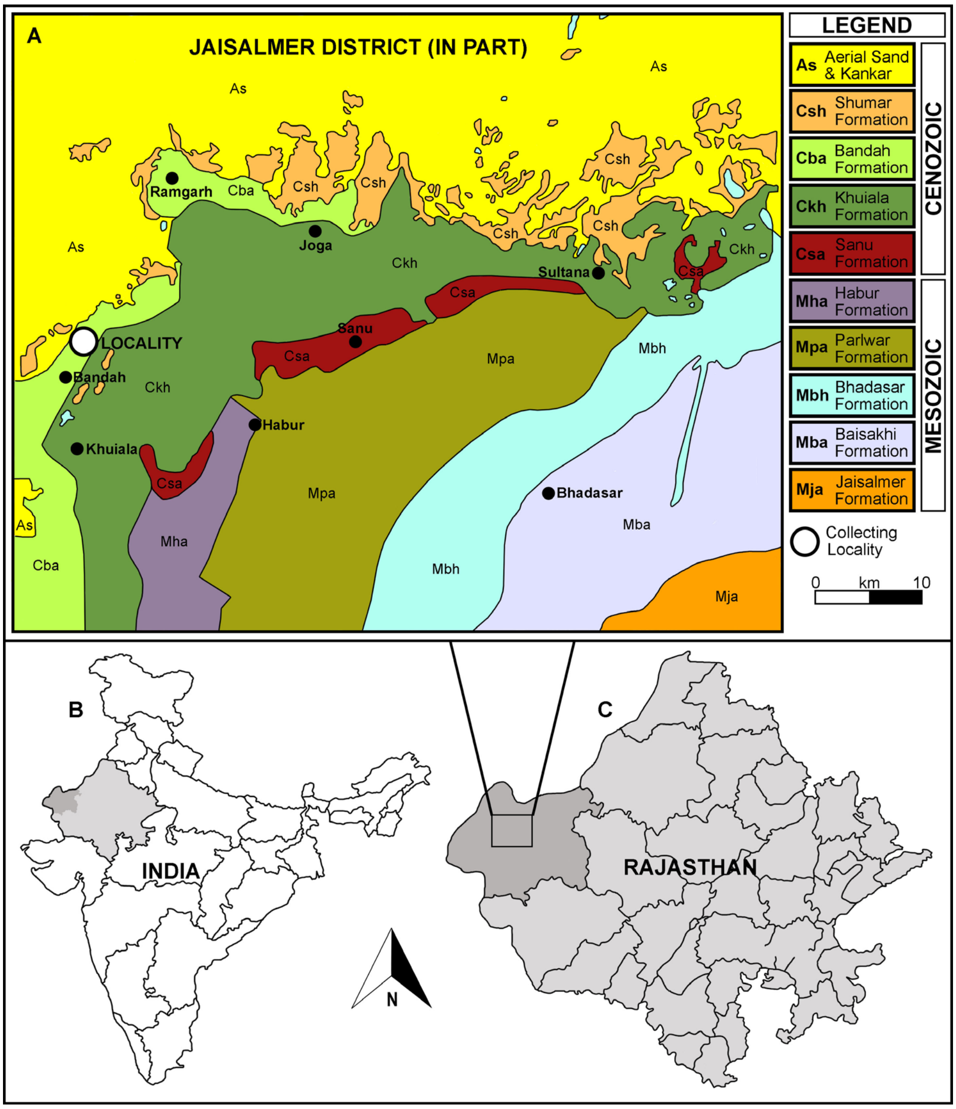

Figure 1. Location of the collecting site in the Jaisalmer District of Rajasthan, India. **A.** Callout of a section of the Jaisalmer District showing the exposed stratigraphic units and collecting locality. **B.** Map of India showing the location of Rajasthan and the Jaisalmer District. **C.** Map of Rajasthan showing the location of the Jaisalmer District. Geologic map modified from Kumar *et al.* (2020).

shown in Figure 2 differs from the interpretations presented in those two prior reports. At our particular location, the various beds within the Bandah Formation are well-exposed and easy to differentiate, whereas the individual beds are more difficult to discern at the area of collection reported by Kumar *et al.* (2017) and Kumar *et al.* (2020). We therefore consider our section to be the more accurate representation of the lithostratigraphic composition of the Bandah Formation in this area.

Based on surface and subsurface sections from elsewhere, more complete sections of the Bandah Formation consist of (in ascending order) gypsiferous bentonitic clay at the base, ochreous marl, bioclastic limestone, fragmental limestone, and hard, fine-grained, compact crystalline limestone. The Bandah Formation as a whole contains abundant foraminifera and molluscs, and various studies of the foraminifera from other subsurface localities have dated the unit to the Bartonian Stage within the middle Eocene based on mega- and planktonic taxa, including *Nummulites acutus* (Sowerby, 1840), *N. maculatus* Nuttall, 1926a, *N. beaumonti* d'Archiac & Haime, 1853, *N. pengaronensis* Verbeek, 1871, *N. fabianni* (Prever in Fabiani, 1905), *Assilina papillata* Nuttall, 1926a, *A. spira* (Roissy, 1805), *Discocyclina javana* (Verbeek, 1880), *Dictyoconoides cooki* Nuttall, 1925, *Globigerinatheka kugleri* (Bolli *et al*., 1957), *Truncorotaloides rohri* Brönnimann & Bermudez, 1953, *T. topilensis* (Cushman, 1925a), and *Turborotalia cerroazulensis* (Cole, 1928) (Singh, 1996, 2007; Raju, 2018; and references therein). Based on subsurface data, the oyster-bearing “bed b” at our locality falls within planktonic foraminifera zones P13 and P14 (i.e., E12 and E13), large benthonic foraminifer zone SBZ17, and calcareous nannofossil zone NP17 (Singh, 1996, 2007; Raju, 2018; Rai *et al*., 2014). These studies confirm a middle Eocene Bartonian age for the elasmobranch assemblage described herein.

MATERIAL AND METHODS

All of the specimens in this study were collected from a single locality located approximately 2.5 km northeast (N 27° 09’00”91”; E 70° 28’02”56”) of Bandah Village, along Bandah-Ramgarh Road in the Jaisalmer District of Rajasthan, India (Fig. 1). The fossils were recovered by surface collecting as well as through the processing of approximately 100 kg of *in situ* bulk matrix. Bulk matrix was screen washed in the laboratory at Garhwal University, Uttarakhand, India, and the resulting concentrates were sorted under a binocular microscope. These methods resulted in the recovery of fossils down to microscopic sizes (less than 2 mm), which yields a more comprehensive representation of the palaeofauna compared to surface collecting alone (i.e., Kumar *et al*. 2017; Kumar *et al*., 2020). Microphotography was done with an Olympus S Z 61 microscope and Nikon D5300 digital camera with 18-55 AF-P lens, and the accompanying figures were produced in CorelDRAW X7 software. All specimens are housed at the Vertebrate Palaeontology laboratory in the Department of Geology at Hemvati Nandan Bahuguna (H.N.B.) Garhwal University, Srinagar Garhwal, Uttarakhand, India. The specimens are catalogued with the prefix “GU/B”, with “GU” indicating Garhwal University and “B” the Bandah Formation. The nomenclature utilized largely follows that of Cappetta (2012) and Ebersole *et al*. (2019), and higher taxonomic rankings follow that of Nelson *et al*. (2016).

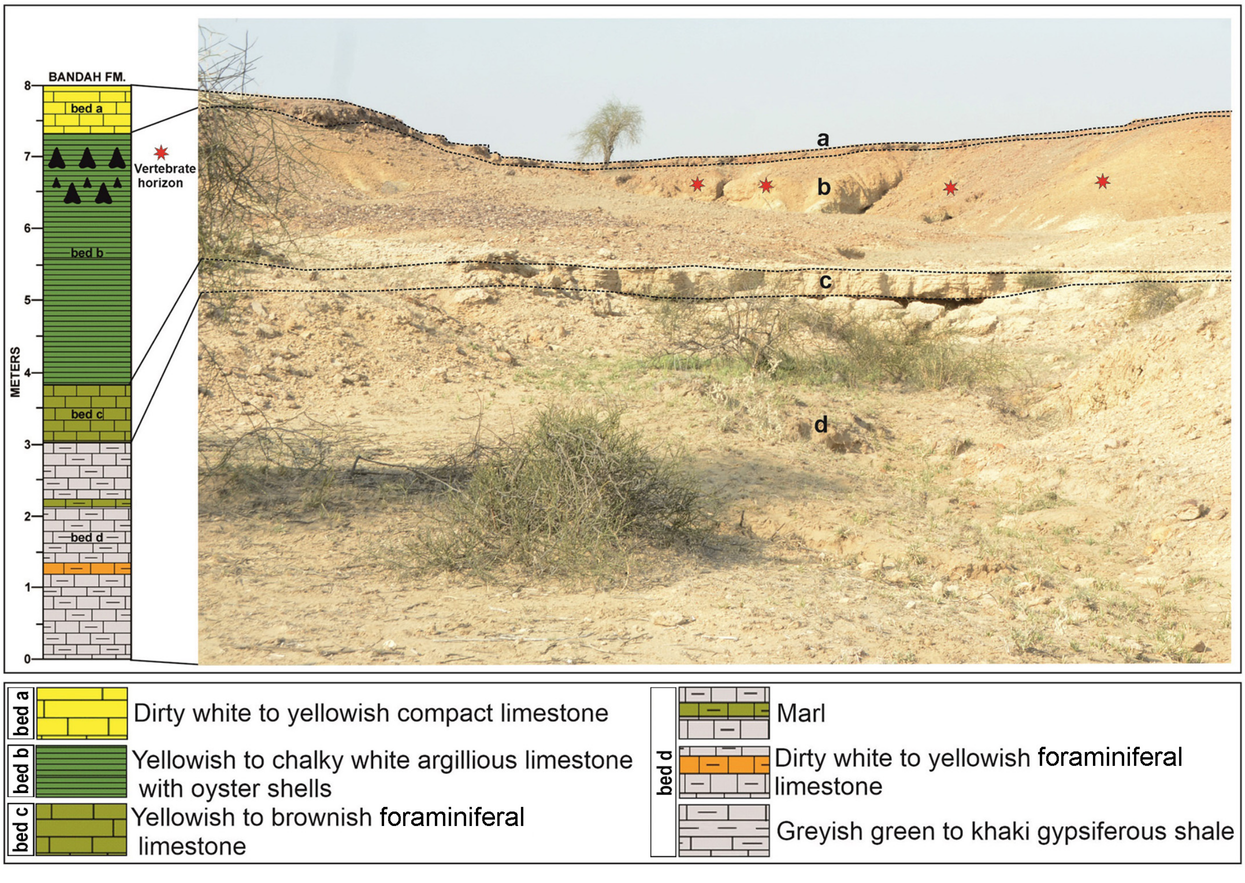

Figure 2. Measured section and lithostratigraphic descriptions of the exposed beds of the Bandah Formation at the collecting locality.

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes Huxley, 1880
Subclass Euselachii Hay, 1902
Infraclass Elasmobranchii Bonaparte, 1838
Division Selachii Cope, 1871
Superorder Galeomorphi (*sensu* Nelson, Grande, & Wilson, 2016)
Order Orectolobiformes Applegate, 1974
Suborder Orectoloboidei Applegate, 1974
Superfamily Hemiscyllioidea Naylor *et al*., 2012
Family Ginglymostomatidae Gill, 1862
Genus *Nebrius* Rüppell, 1837
***Nebrius* sp.**

Referred specimen – GU/B 2005 (Fig. 3).

Description – GU/B 2005 is an asymmetrical lateral tooth that is broader than high. There is a distally inclined main cusp that is much larger than the lateral cusplets occurring on the mesial and distal sides. The mesial cutting edge is very convex basally but becomes straight as it extends to the main cusp, and there are nine cusplets that increase in size apically. The distal cutting edge is short, weakly convex, and bears five cusplets that increase in size apically. The main cusp has smooth cutting edges and is separated from the mesial and distal cusplets by a deep notch. The cutting edges on the lateral cusplets are smooth. The labial crown face is convex (particularly medially) and middle of the crown foot is developed into a basally extended apron. The lingual crown face is convex, and both crown faces are smooth. The root is poorly preserved, but a broadly elliptical foramen is visible medially on the lingual root face.

Discussion – The Bandah Formation tooth (GU/B 2005) is assigned to *Nebrius* based on the large number of mesial and distal cusplets, which contrasts with the 1-4 accessory cusplets seen on teeth of other ginglymostomatids. The Bandah Formation tooth is superficially similar to specimens identified as *Ginglymostoma sokotoense* White, 1934 and *Ginglymostoma* sp. from the late Palaeocene to Eocene Akli and Khuiala formations of Rajasthan, and Kakra Formation of Himachal Pradesh (Rana *et al.*, 2005; Kumar *et al*., 2007; Gupta & Kumar, 2013; Rajkumari & Prasad, 2020). However, it differs by having a greater number of mesial and distal cusplets. The overall morphology of GU/B 2005, including the number of mesial and distal cusplets, is more consistent with teeth described elsewhere as *N. thielensi* (Winkler, 1873), but we herein only assign it to the generic level due to the poor preservation of the specimen. Although this specimen is similar to teeth described as *N. obliquus* (Leidy, 1877), examination of the dentition of Recent *N. ferrugineus* (Lesson, 1831) led Ebersole *et al*. (2019) to conclude that *N. obliquus* is conspecific with *N. thielensi* because the lone characteristic used to separate the two, the shape of the labial apron (see Cappetta & Case, 2016), could reflect heterodonty within a single species and is therefore not taxonomically significant.

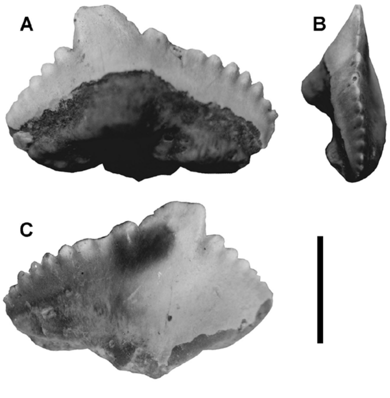

Figure 3. *Nebrius* sp. tooth. **A-C.** GU/B 2005 in A. lingual, B. mesial, and C. labial views. Scale bar = 2 mm.

Extant *Nebrius* species are known to inhabit tropical and sub-tropical continental and insular shelf environments (Compagno, 2005). *Nebrius thielensi* is known primarily from middle and upper Eocene deposits occurring in North America (Müller, 1999; Case & Borodin, 2000; Cicimurri & Knight, 2019; Ebersole *et al*., 2019), Europe (Van den Eeckhaut & De Schutter 2010), and Africa (Case & Cappetta, 1990; Adnet *et al*., 2020).

Order Lamniformes Garman, 1885
Family Mitsukurinidae Jordan, 1898
Genus *Striatolamia* Glikman, 1964
***Striatolamia* aff. S. *macrota* (Agassiz, 1838)**

Referred specimens – GU/B 2010, GU/B 2011, GU/B 2012, GU/B 2013, GU/B 2015, GU/B 2016, GU/B 2017, GU/B 2018, GU/B 2020 (Fig. 4).

Description – Anterior teeth have a very tall and narrow main cusp. The cusp may be straight and erect or slightly distally curved. The sides of the main cusp are parallel on the lower one-half to two-thirds, but apically the sides are convex and meet at the apex. The cutting edges are smooth, sharp, and extend from the apex but end well short of the cusp base. The

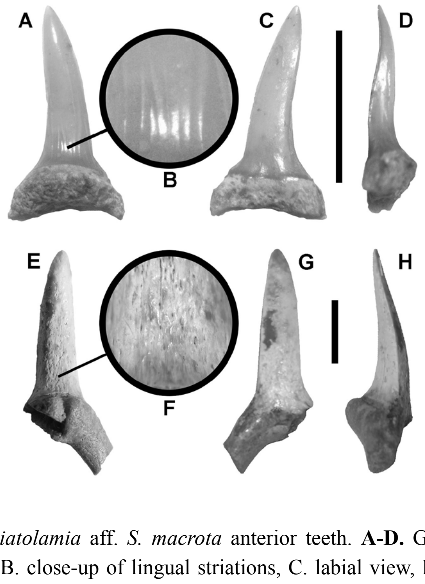

Figure 4. *Striatolamia* aff. *S. macrota* anterior teeth. **A-D.** GU/B 2020, A. lingual view, B. close-up of lingual striations, C. labial view, D. distal view. **E-H.** GU/B 2010, E. lingual view, F. close-up of lingual striations, G. labial view, H. distal view. Scale bars = 5 mm.

labial face is flat to only weakly convex, and the enameloid is smooth. In contrast, the lingual face is very convex and bears numerous fine longitudinal ridges that extend up to three-quarters of the cusp height. The main cusp is flanked by a single pair of diminutive lateral cusplets. Roots are often incompletely preserved, but they are bilobate with elongated, narrow, diverging lobes. A lingual protuberance is bisected by a deep nutritive groove.

Discussion – The anterior teeth recovered from the Bandah Formation have close morphological affinities with *Striatolamia macrota* from the lower-to-middle Eocene Claiborne Group of Alabama, USA (Ebersole *et al*., 2019) and the middle-to-late Eocene sequence of Fayum, Egypt (Case & Cappetta, 1990). The anterior teeth we assigned to *Striatolamia* differ from those of *Brachycarcharias* by having a comparatively taller and narrower main cusp with parallel sides. In contrast, *Brachycarcharias* anterior teeth are more broadly triangular. Additionally, the cusplets preserved on the *Striatolamia* teeth are much smaller and gracile than those on *Brachycarcharias* anterior teeth. *Jaekelotodus* differs by having stout teeth with smooth faces, cutting edges that extend to the base of the main cusp, small and medially curved lateral cusplets, and a distinct lingual protuberance.

Family Odontaspididae Müller & Henle, 1839
Genus *Brachycarcharias* Cappetta & Nolf, 2005
Brachycarcharias atlasi (Arambourg, 1952)

Referred specimens – GU/B 2022, GU/B 2025 (Fig. 5A-F).

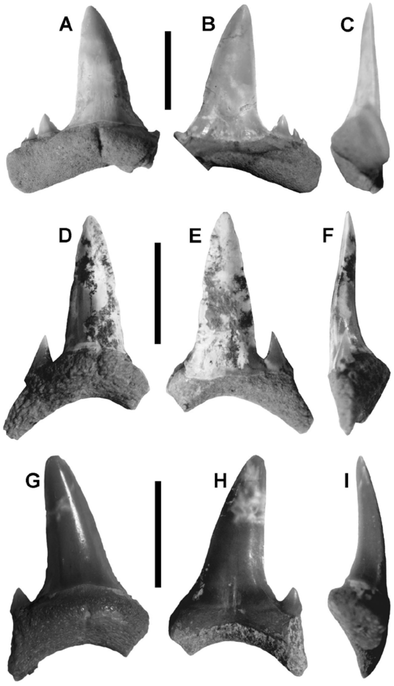

Figure 5. *Brachycarcharias* spp. teeth. **A-C.** GU/B 2025, *B. atlasi* lateral tooth in A. lingual, B. labial, and C. mesial views. **D-F.** GU/B 2022, *B. atlasi* anterior tooth in D. lingual, E. labial, and F. mesial views. **G-I.** GU/B 2021, *B. lerichei* anterolateral tooth in G. lingual, H. labial, and I. mesial views. Scale bars = 5 mm.

Description – Anterior teeth have a broadly triangular, sharply tapering main cusp. The labial face is nearly flat, whereas the lingual face is very convex. Although the labial face is smooth, the lingual face bears conspicuous longitudinal ridges. The cutting edges are smooth and extend to the crown base. The main cusp is flanked by a pair of large, sharply pointed lateral cusplets. The cusplets bear coarse longitudinal ridges. The root is bilobate, with elongated, rather thin and widely separated lobes. A nutritive groove bisects the lingual protuberance.

Lateral teeth have a broader but labio-lingually thinner main cusp than the anterior teeth. The lingual face is flat and smooth, whereas the lingual face is convex and bears numerous longitudinal ridges. The cutting edge is smooth and continuous. The main cusp is flanked by two to three pairs of lateral cusplets, with the distal-most pair being diminutive. The root is bilobate with a lingual protuberance bisected by a nutritive groove. Root lobes are more rectangular and widely separated than seen on anterior teeth.

Discussion – Although similar to teeth of the several coeval lamniform sharks occurring in the Bandah Formation, *Brachycarcharias atlasi* is distinguished by the combination of characteristics that includes cutting edges that extend to the crown base, coarse longitudinal lingual crown ridges, and one to three pairs of large lateral cusplets that also bear longitudinal ridges. *Brachycarcharias atlasi* was recently recognized in the middle Eocene of Alabama, USA (Ebersole *et al*., 2019), and the species is known from various locations in Africa (i.e., Arambourg, 1952).

Brachycarcharias lerichei Casier, 1946

Referred specimens – GU/B 2021, GU/B 2023, GU/B 2024 (Fig. 5G-I).

Description – The anterior teeth have a triangular and tall main cusp that is erect, and faint lingual basal striations are visible on some teeth. On unworn specimens, the distal and mesial cutting edges are sharp and continuous on both anterior and lateral teeth, extending from the apex of the main cusp across the lateral cusplets. The lateral cusplets are triangular, anteriorly sharp, pointed, and basally wider. The labial and lingual crown faces are slightly convex or somewhat flattened and thinner towards the edges, with thin enameloid. The root is bilobed, laterally diverging, and has a shallow groove separating elongated lobes. The lingual root protuberance is indistinct.

Discussion – Although similar to the teeth we identified as *Brachycarcharias atlasi*, those we assigned to *B. lerichei* have comparatively lower but broader lateral cusplets, and the lingual crown ornamentation, if present, is much finer. Additionally, lingual ornamentation occurs on the lateral cusplets of *B. atlasi* teeth, but not on those of *B. lerichei*. Anterior teeth of *B. lerichei* can be distinguished from those of *S. macrota* by their lower but broader main cusp, more complete cutting edges, and larger lateral cusplets. *Brachycarcharias* lateral teeth have sharply pointed lateral cusplets that are of the same size, whereas those of *Striatolamia* are lower and more rounded, and the distal cusplets are generally larger than the mesial ones.

Genus *Jaekelotodus* Menner, 1928
cf. *Jaekelotodus* sp.

Referred specimens – GU/B 2008, GU/B 2014 (Fig. 6).

Description – GU/B 2008 has a tall, triangular main cusp that is rather thick labio-lingually. The main cusp is erect but slightly distally curved. The mesial and distal cutting edges are smooth and extend to the crown foot. The mesial edge is very weakly convex, whereas the distal edge is concave basally but more convex apically. The labial face of the main cusp is flat, but the lingual face is very convex, and both faces are smooth. There is a single pair of very small, needle-like cusplets. The root has a robust lingual protuberance and pointed lobes (mesial lobe is shorter).

GU/B 2014 is incomplete. The main cusp is very broadly triangular but distally hooked. The cutting edges are smooth and extend to the crown foot, with the mesial edge being convex and the distal edge concave. The labial face is flat, but the lingual face is convex, and both faces are smooth. A single pair of cusplets occurs at the base of the main cusp, with the mesial cusplet being smaller and not as well separated from the main cusp. Cutting edges on the cusplets are smooth. The root is broken, but the lingual protuberance is shelf-like.

Discussion – Both specimens are referred to *Jaekelotodus* based on the robustness of the main cusp, completeness of the cutting edges, and diminutive size of the cusplets compared to the size of the main cusp. The anterior tooth differs from those of Odontaspididae indet. (see below) and *Striatolamia* by having complete cutting edges (cutting edges of other taxa end before the crown foot). Additionally, the crown of GU/B 2008 is smooth, whereas the crown on the anterior teeth of *Striatolamia* and *Brachycarcharias* (especially *B. atlasi*) bear lingual longitudinal ridges.

The lateral tooth (GU/B 2014) differs from those of *Striatolamia* in lacking lingual ornament, having a very broad but sharply tapering, hooked rather than lingually inclined main cusp, and the lateral cusplets are narrower and more pointed. The specimen is also broader than lateral teeth of *Brachycarcharias*, it is lingually hooked (as opposed to inclined), and the lingual enameloid is smooth.

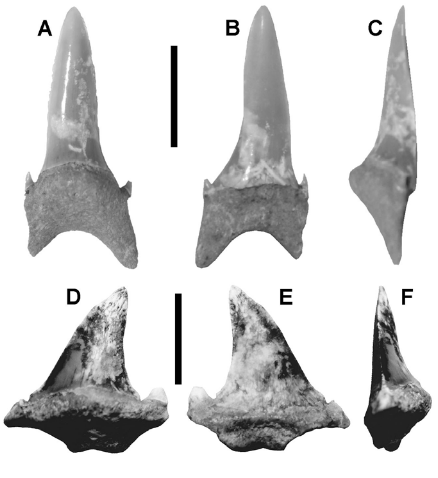

Figure 6. cf. *Jaekelotodus* sp. teeth. **A-C.** GU/B 2008, anterior tooth in A. lingual, B. labial, and C. distal views. **D-F.** GU/B 2014, lateral tooth in D. lingual, E. labial, and F. mesial views. Scale bars = 5 mm.

Odontaspididae indet.

Referred specimens – GU/B 2006, GU/B 2007, GU/B 2009, GU/B 2026, GU/B 2027 (Fig. 7).

Description – GU/B 2006 is complete except for the broken apex and mesial root lobe. The crown consists of a large main cusp flanked by a single pair of lateral cusplets. The main cusp is robust, tall, and rather narrow. In labial view, the main cusp curves slightly distally, and in profile view it is strongly lingually curved. The cutting edges are smooth and sub-parallel at the lower two-thirds of the main cusp but become convex apically. The cutting edges reach the crown foot. The labial crown face is flat and smooth, and the distal face is very convex and smooth. The lateral cusplets are needle-like and slightly diverging. The root is bilobate, with a distal lobe that appears to have been more elongated and divergent than the mesial lobe. A large lingual protuberance is bisected by a narrow nutritive groove.

GU/B 2007 and GU/B 2009 are broken anterior teeth. The anterior teeth are very narrow, rather thin labio-lingually, and slightly sinuous in profile view. Cutting edges are smooth and nearly continuous to the crown foot. The labial face is very weakly convex and smooth, whereas the lingual face is convex and bears fine longitudinal ridges. When preserved, the lateral cusplets are rather small and needle-like. The root is bilobate, and a lingual protuberance bears a narrow nutritive groove.

GU/B 2026 and GU/B 2027 are broken teeth having a triangular and rather labio-lingually narrow, broad-based but sharply tapering main cusp. In profile view, the cusp is straight and may be labially curved at the apex. The cutting edges are smooth and continuous across the crown, reaching the crown foot. The labial face is flat and smooth, whereas the lingual face is convex and smooth. Lateral cusplets are not preserved. The roots are incomplete, but GU/B 2027 shows evidence that it was bilobate and it has an inconspicuous lingual nutritive groove.

Discussion – The specimens examined largely consist of teeth that do not conform to any of the other taxa described above. They have incomplete cutting edges, thus seemingly differentiating them from *Jaekelotodus* and even *Hypotodus*. They differ from *Striatolamia* in being thicker labio-lingually and by having larger lateral cusplets. GU/B 2007 may be a *Brachycarcharias lerichei* anterior tooth, but the cusplets are smaller and narrower than what is generally seen as typical of this species, and the lingual ornamentation is as robust as that observed on *Striatolamia* teeth. GU/B 2026 and GU/B 2027 may represent anterior and/or antero-lateral teeth of *B. lerichei*, but they are too broken for precise identification. One specimen, GU/B 2006, is morphologically similar to the lower fourth anterior tooth of extant *Carcharias taurus* Rafinesque, 1810b and the middle to late Eocene *Mennerotodus parmleyi* Cicimurri *et al*., 2020. However, the specimen is weathered and a distinguishing feature of *Mennerotodus*, denticles or a short edge at the mesial and/or distal crown foot, are not evident.

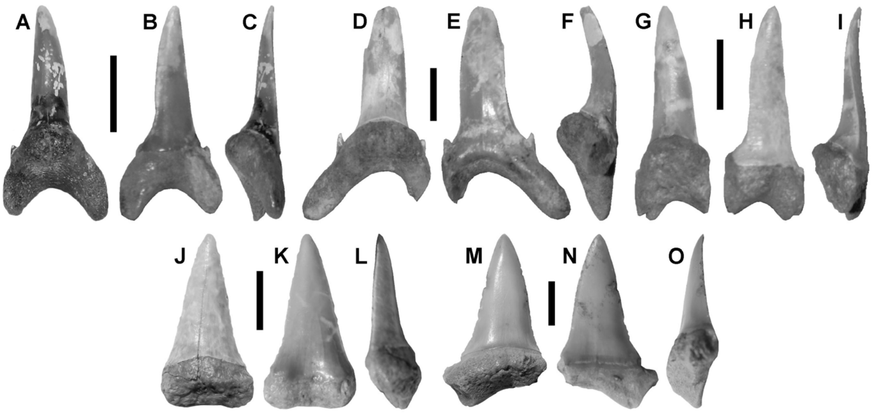

Figure 7. Odontaspididae indet. teeth. **A-C.** GU/B 2007, anterior tooth in A. lingual, B. labial, and C. distal views. **D-F.** GU/B 2006, lower 4th anterior tooth in D. lingual, E. labial, and F. distal views. **G-I.** GU/B 2009 anterior tooth in G. lingual, H. labial, and I. distal views. **J-L.** GU/B 2026, anterior tooth in G. lingual, H. labial, and I. distal views. **M-O.** GU/B 2027, tooth in M. lingual, N. labial, and O. distal views. Scale bars = 5 mm.

Order Carcharhiniformes Compagano, 1973

Family Carcharhinidae Jordan & Evermann, 1896

Genus *Carcharhinus* de Blainville, 1816

Carcharhinus mancinae Ebersole, Cicimurri & Stringer, 2019

Referred specimens – GU/B 2033, GU/B 2035, GU/B 2036, GU/B 2040, GU/B 2041, GU/B 2046, GU/B 2048, GU/B 2049, GU/B 2051, GU/B 2052, GU/B 2071, GU/B 2072 (Fig. 8).

Description – Most of the specimens are incomplete, but most appear to have been similar to GU/B 2071, GU/B 2072. For these specimens, the crown is generally broadly triangular. The mesial cutting edge ranges from straight to sinuous, to very convex. This edge is coarsely serrated, particularly at the medial portion, with serrations becoming finer apically. Serrations are weakly compound. The distal edge is strongly concave, with the apical portion being straight to weakly convex, vertical to inclined, and finely serrated. This edge forms an erect to lingually inclined cusp with the apical part of the mesial edge. Additionally, the distal edge joins an elongated distal heel through a sloping transition (not a distinct notch). The transition from distal edge to distal heel is also marked by a very large serration that is usually weakly compound. Serrations on the distal heel are weakly compound and decrease in size towards the crown foot. The labial crown face is flat to very weakly convex, whereas the lingual face is very convex. Both faces are smooth. The root is high when viewed lingually, and there is a massive lingual protuberance bisected by a narrow, shallow, elongated nutritive groove. The root lobes are sub-rectangular, very widely divergent, and separated by a U-shaped to V-shaped interlobe area.

GU/B 2048 and GU/B 2049 differ from other teeth by having concave mesial and distal edges. On these teeth, the upper part of the crown is developed into a more distinctive, erect cusp that transitions to elongated heels without the formation of a conspicuous notch. The cutting edges are coarsely serrated on the heels, but the cusp bears much finer serrations. The serrations are weakly compound and/or doubly serrate. The root is bilobate, with thin, sub-rectangular lobes that are separated by a V-shaped or U-shaped interlobe area. The massive lingual protuberance is bisected by a narrow, elongated nutritive groove.

An additional specimen, GU/B 2052, has a rather low crown with an elongated and straight mesial cutting edge that forms a conspicuous cusp with the much shorter distal cutting edge. This cusp is strongly distally inclined and separated from a distal heel by a more obvious notch. The mesial and distal cutting edges are finely serrated, whereas the distal heel is coarsely serrated, with serrations decreasing in size towards the crown foot. The labial face is flat, and the lingual face is convex, with both faces being smooth. The root is bilobate with widely diverging, sub-rectangular lobes that are separated by a V-shaped interlobe area. The lingual protuberance is shelf-like, and there is an inconspicuous, medially located nutritive groove.

Discussion – The teeth in this sample are morphologically variable, but we believe that GU/B 2052 represents a postero-lateral tooth, GU/B 2048 and GU/B 2049 are lower anterior teeth, and the remainder are upper anterior and upper/lower lateral teeth. These teeth are easily distinguished from *Galeocerdo eaglesomei* by their weakly compound (or

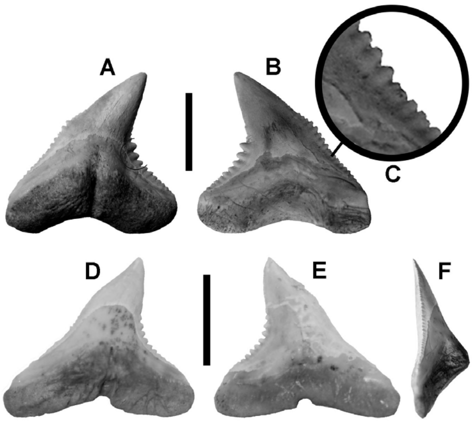

Figure 8. *Carcharhinus mancinae* teeth. **A-C.** GU/B 2071, upper lateral tooth in A. lingual, and B. labial views, C. close-up of compound/doubly serrate mesial serrations. **D-F.** GU/B 2072, lower lateral tooth in D. lingual, E. labial, and F. mesial views. Scale bars = 5 mm.

"double") serrations and more gracile crown appearance. They differ from *Rhizoprionodon* and *Physogaleus*, which both have smooth distal cutting edges, virtually smooth mesial cutting edges, relatively few cusplets on the distal heel that are not compound, and a distinctive notch between the distal cutting edge and distal heel. Although teeth of *Galeocerdo clarkensis* are similar to those of *C. mancinae*, they can be distinguished by their larger overall size, broader width, more distinctive separation of the cusp from the distal heel, more convex labial crown foot, more elongated root lobes separated by a deeper interlobe area, and a less conspicuous lingual protuberance.

Serrated *Carcharhinus* teeth similar to those of extant species are known to occur as early as the Bartonian, and several middle to late Eocene (Priabonian) species have been named (Case & Cappetta, 1990; Reinecke *et al*., 2005; Adnet *et al*., 2007; Underwood *et al*., 2011; Underwood & Gunter, 2012; Ebersole *et al*., 2019; Samonds *et al*., 2019; Adnet *et al*., 2020). Citing a personal communication from D.J. Ward, Ebersole *et al.* (2019) reported that teeth of *Carcharhinus underwoodi* Samonds *et al*. 2019 have simple serrations, and this taxon is not known to exhibit dignathic heterodonty (Samonds *et al*. 2019). In contrast, teeth of *C. mancinae* exhibit compound serrations, and dignathic heterodonty is evident (Ebersole *et al*., 2019). The Bandah Formation teeth can be distinguished from named Bartonian to Rupelian species and from those identified as *Carcharhinus* spp. by the combination of features that include: serrations nearly to the apex of the mesial and distal cutting edges, serrations weakly compound and/or doubly serrate, and sloping transition from distal cutting edge to distal heel that is also indicated by the location of a very large distal heel serration.

The validity of another species, *C. balochensis* Adnet *et al*., 2007, from the late Eocene and early Oligocene of Pakistan, has been questioned. Samonds *et al*. (2019) considered most of the type suite to be conspecific with *Galeocerdo eaglesomei* White, 1955, and the remaining tooth was synonymized with *C. underwoodi*. However, Ebersole *et al*. (2019) considered the dentition of *C. balochensis* to have been similar to *C. mancinae*, and Adnet *et al*. (2020) also maintained usage of *C. balochensis*. In any event, these taxa differ from *C. mancinae* by lacking compound serrations.

The teeth of *C. kasserinensis* Adnet *et al*. (2020) have a more uniformly convex mesial cutting edge, coarser serrations, and more clearly defined separation of the distal heel from the distal cutting edge compared to *C. mancinae*. A single tooth of *Carcharhinus* sp. from the middle Eocene of Jamaica has variously been identified as conspecific with *C. kasserinensis* (i.e., Adnet *et al*., 2020) or *C. underwoodi* (i.e., Samonds *et al*., 2019), but these taxa are distinguished from *C. mancinae* based on the features discussed above. The morphological features of the Bandha Formation *Carcharhinus* teeth leads us to conclude that they are conspecific with *C. mancinae* rather than other superficially similar taxa previously reported from the Tethyan and Paratethyan regions.

If all of the aforementioned species are considered valid, at least three species of *Carcharhinus* (i.e., *C. kasserinensis*, *C. mancinae*, and *C. underwoodi*) were coeval within the Tethys and Indian Ocean regions during the Bartonian. The sudden diversification of this genus during the middle Eocene is not surprising, as the radiation of the Carcharhiniformes during the Eocene has been well documented (Kriwet & Benton, 2004; Adnet *et al*., 2007; Underwood *et al*., 2011; Cappetta, 2012; Iserbyt & De Schutter, 2012; Marramà *et al*., 2018b; Ebersole *et al*., 2019). Furthermore, in their biostratigraphic study of the fossil elasmobranchs of the Gulf Coastal Plain of the USA, Ebersole *et al*. (2019) observed an increase in carcharhiniform diversity specifically during the Bartonian, which included the first stratigraphic occurrence of *C. mancinae*. These studies suggest that the diversification of the carcharhiniforms was driven by the Eocene Thermal Maximum, which likely provided optimal climatic conditions favourable for the radiation of this group. That several coeval fossil species of *Carcharhinus* have been identified within the same region is also not surprising given the diversity of extant species of this genus (34 species; Nelson *et al*., 2016), as at least 18 species are known from the present day Indian Ocean (Voigt & Weber, 2011).

Genus *Rhizoprionodon* Whitley, 1929

Rhizoprionodon sp.

Referred specimens – GU/B 2055, GU/B 2057, GU/B 2058, GU/B 2060, GU/B 2061, GU/B 2062, GU/B 2063, GU/B 2064, GU/B 2065 (Fig. 9).

Description – All of the specimens are incomplete, but none are wider than 5 mm. The crown consists of a triangular cusp and a distal heel. The sharp mesial cutting edge is elongated, smooth, and ranges from concave, to sinuous, to weakly convex. The distal edge is approximately two-thirds the length of the mesial edge, and together the edges form a cusp that varies in width but is always sharply pointed. The distal cutting edge is smooth and sharp, ranges from nearly vertical to strongly distally inclined, and is straight to weakly convex. The distal heel is short and convex, has a sharp and smooth cutting edge, and forms a distinctive notch with the distal cutting edge. The labial crown face is flat, including at the crown foot, whereas the lingual face is convex. The crown enameloid is smooth. The root is bilobate with rather short but very widely spaced, labio-lingually thin lobes. The lobes are bisected by a lingual nutritive groove.

Discussion – We believe that the specimens within our sample that have a very concave mesial cutting edge and somewhat erect cusp were from a male dentition. The specimens can be differentiated from *Scoliodon*, a genus that has been reported from middle Eocene strata of the USA (Cappetta & Case, 2016; Ebersole *et al*., 2019), in that the cusp does not extend beyond the margin of the distal heel. The specimens in our sample can be distinguished from *Physogaleus* (see below) by lacking denticulation on the mesial cutting edge and by having only a rather convex distal heel as opposed to bearing multiple distal

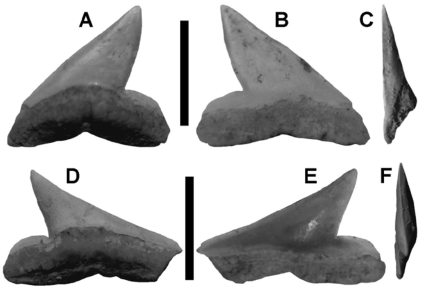

Figure 9. *Rhizoprionodon* sp. teeth. **A-C.** GU/B 2057, lower anterior tooth in A. lingual, and B. labial, and C. mesial views. **D-F.** GU/B 2058, lower lateral tooth in D. lingual, E. labial, and F. distal views. Scale bars = 2 mm.

denticles. They are easily separated from *Galeocerdo* and *Carcharhinus* in lacking serrations on their cutting edges.

Extant *Rhizoprionodon* has a worldwide distribution in tropical marine oceans. The fossil record of this genus is known from Palaeogene and Neogene formations in Egypt, Morocco, Nigeria, Tunisia, Europe, the USA, India, and Pakistan (Case & Cappetta, 1990; Case & West, 1991; Rana *et al*., 2004; Adnet *et al*., 2007; Strougo *et al*., 2007; Underwood *et al*., 2011; Ebersole *et al*., 2019; Adnet *et al*., 2020). Few Eocene species have been named, as the teeth maintained a relatively conservative morphology through to the present day.

Genus *Physogaleus* Cappetta, 1980a

Physogaleus sp.

Referred specimens – GU/B 2056, GU/B 2059, GU/B 2067 (Fig. 10).

Description – The crown of specimen GU/B 2056 is low and consists of a highly distally inclined main cusp and a short distal heel. The mesial cutting edge is elongated, smooth and somewhat convex, and it forms an acute, distally directed cusp apex with the distal cutting edge. The distal cutting edge is short, straight, and smooth. The distal heel is short and bears two weak cusplets, but the cutting edge is smooth. The distal heel forms a distinct notch with the base of the distal cutting edge. The root is ablated but is bilobate, with high, sub-rectangular lobes that are widely diverging. A lingual nutritive groove is inconspicuous.

Specimen GU/B 2059 is damaged at its mesial base. The crown consists of a large cusp and low distal heel. The cusp is broad, triangular, and appears distally directed due to the oblique mesial cutting edge and the more vertical distal edge. The mesial cutting edge is sinuous and smooth except at the base, where indistinct crenulations are separated by a slight notch. The distal cutting edge is rather straight, nearly vertical, and smooth. The distal heel is very low, weakly convex with a smooth cutting edge, and forms nearly a 90˚ angle with the distal cutting edge. The root is incompletely preserved, but the lobes are sub-rectangular and highly divergent, with almost no indication of an interlobe area.

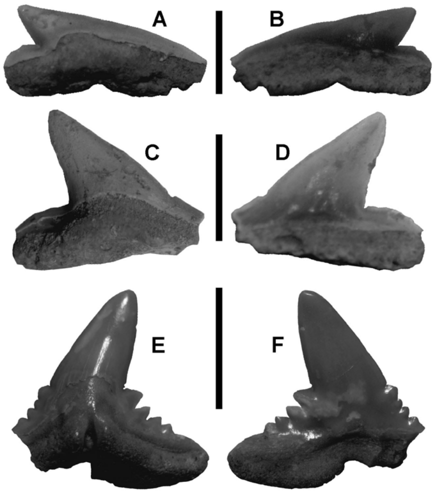

Figure 10. *Physogaleus* sp. teeth. **A-B.** GU/B 2056, upper lateral tooth in A. lingual and B. labial views. **C-D.** GU/B 2059, lower lateral tooth in C. lingual and D. labial views. **E-F.** GU/B 2067, anterior tooth in E. lingual and F. labial views. Scale bars = 5 mm.

GU/B 2067 is damaged at the mesial side but consists of a broad and roughly triangular crown and low root. The crown bears a triangular main cusp that is distally inclined and is flanked by four pairs of triangular lateral cusplets (the crown base is broken and there may have been more cusplets on the mesial side). The mesial cusplets are smaller and less pointed than those on the distal side. The cutting edge is smooth and continuous from the main cusp apex to the crown base. The labial crown face is less convex than the lingual face. The root is bilobate, with very short but elongated, widely diverging lobes. A nutritive groove occurs on the lingual protuberance.

Discussion – We consider GU/B 2059 to represent a male lower anterior tooth due to the unique shape of the main cusp, which is consistent with previous interpretations of this morphology (Cappetta, 1980a; Cappetta & Case, 2016; Ebersole *et al*., 2019). The smooth, unserrated cutting edges and distal heel easily distinguish these teeth from those of coeval *Galeocerdo* and *Carcharhinus* in the Bandah Formation.

Specimen GU/B 2067 is somewhat similar to teeth of coeval *Galeocerdo* and *Carcharhinus* reported herein. However, it is easily distinguished by its smooth cutting edges on the upper half of the crown. In contrast, the latter two taxa have teeth with mesial and distal serrations extending nearly to the crown apex, as well as coarse, weakly compound serrations on the distal heel and lower half of the mesial cutting edge. This specimen is somewhat similar to *Pseudabdounia claibornensis* (White, 1956) from the Bartonian of the USA (Ebersole *et al*., 2019: fig. 32, a–r), but it differs by having a short and low distal heel and a comparatively tall and narrow main cusp in comparison to total tooth size. Additionally, mesial and distal cusplets of *P. claibornensis* are of roughly equal size, whereas the cusplets of GU/B 2067 are clearly larger on the distal side.

The lack of cusplets on the mesial edge and distal heel of GU/B 2056 and GU/B 2059 would indicate identification as *Physogaleus secundus* (Winkler, 1874), whereas the numerous larger serrations on GU/B 2067 are indicative of *P. alabamensis* (Leriche, 1942), both of which were found to be coeval in middle Eocene deposits of the Gulf Coastal Plain of the USA (Ebersole *et al*., 2019). A larger sample size is needed in order to more accurately identify the specimens in our sample.

Family Galeocerdidae Whitley, 1934

Genus *Galeocerdo* Müller & Henle, 1837

Galeocerdo clarkensis White, 1956

Referred specimens – GU/B 2037, GU/B 2045, GU/B 2047, GU/B 2068, GU/B 2069, GU/B 2070, GU/B 2073, GU/B 2074, GU/B 2075 (Fig. 11A-E).

Description – The teeth consist of a broad crown and low root. The crown has an elongated mesial cutting edge that ranges from nearly straight to very convex. This edge is serrated from the base nearly to the apex, with serrations being coarsest in the medial, most convex portion and diminishing in size apically. These serrations are compound and/or doubly serrate. A much shorter distal cutting edge is straight to weakly convex, lingually inclined to nearly vertical, and bears fine serrations nearly to the apex. The distal edge forms a small, distally directed cusp with the mesial edge, and the angle these edges form is acute. A distal heel is elongated, straight to weakly concave, and very coarsely serrated. The serrations are largest below the distal cutting edge but diminish in size towards the distal margin. The labial and lingual crown faces may be equally convex, and the enameloid is always smooth. The root is bilobate, with diverging, somewhat elongated, rounded to sub-rectangular lobes. The lobes are separated by a U-shaped interlobe area. In lingual view, the root appears much higher than in labial view.

Discussion – Two species of *Galeocerdo* have been identified in our Bandah Formation sample, including *G. clarkensis* White, 1956 and *G. eaglesomei* White, 1955 (see below). The teeth assigned to *G. clarkensis* appear to be conspecific with the type specimens named from the Priabonian Yazoo Clay in Alabama, USA (see White, 1956, pl. 11, figs. 12-14), and this species has subsequently been confirmed from Bartonian deposits in the same state (see Ebersole *et al*., 2019). *Galeocerdo clarkensis* teeth can be separated from those of *G. eaglesomei* by having a combination of an evenly convex mesial edge and serrations that are compound and/or doubly serrate. *Galeocerdo clarkensis* also lacks the unique triangular anterior morphology observed within the dentition of *G. eaglesomei*. The *Galeocerdo* teeth from the Bandah Formation are somewhat similar to the teeth of coeval *Physogaleus* sp. but can be differentiated by the presence of fine mesial and distal serrations that extend nearly to the apex of the main cusp. *Galeocerdo clarkensis* teeth can be differentiated from the lateroposterior teeth of *Carcharhinus mancinae* by having a lingual root protuberance that is much less pronounced and not as mesiodistally constricted.

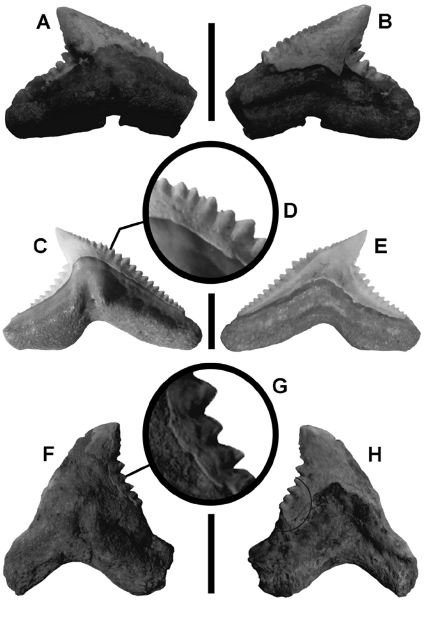

Figure 11. *Galeocerdo* spp. teeth. **A-B.** GU/B 2069, *Galeocerdo clarkensis* lateral tooth in A. lingual and B. labial views. **C-E.** GU/B 2070, *G. clarkensis* lateral tooth, C. lingual view, D. close-up of mesial serrations, and E. labial view. **F-H.** GU/B 2031, *Galeocerdo eaglesomei* anterior tooth, E. lingual view, F. close-up of distal serrations, and F. labial view. Scale bars = 5 mm.

Galeocerdo eaglesomei White, 1955

Referred specimens – GU/B 2031, GU/B 2032, GU/B 2034 (Fig. 11F-H).

Description – The sample consists of three broken teeth. GU/B 2031 is the best preserved specimen, and overall, it is broadly triangular, rather high, with a distally curving crown apex. The mesial edge is damaged at its lower half, but it appears to have been relatively convex. There are simple serrations on the preserved upper part, but these do not reach the apex (likely due to wear). The distal cutting edge is very short, nearly vertical, weakly convex, and bears fine simple serrations that do not reach the apex (likely due to wear). Together, the mesial and distal cutting edges form a rather small cusp. The distal heel is very elongated, almost as high as the crown, and extends at an oblique angle basally away from the cusp. The heel is not separated from the distal edge by a notch, but instead a very large serration marks the transition from distal edge to distal heel. The serrations on the distal heel are simple and decrease in size towards the crown base. The labial crown face is flat to convex, whereas the lingual face is convex. There is no enameloid ornamentation. The root is bilobate with somewhat rectangular, widely diverging lobes that are separated by a U-shaped interlobe area. A shallow, wide nutritive groove occurs on a low lingual protuberance.

Discussion – GU/B 2032 and GU/B 2034 are incomplete crowns, but the preserved portions allow us to consider them to be conspecific with GU/B 2031. In particular, all of the serrations are simple. This feature allows one to distinguish *G. eaglesomei* from *G. clarkensis* and *Carcharhinus mancinae*, which have compound and/or double serrations, and further from *G. clarkensis* by having a very small cusp compared to overall tooth height. *Galeocerdo eaglesomei* is distinguished from *Physogaleus* sp. and *Pseudabdounia claibornensis* (White, 1956) by having coarse but simple serrations extending nearly to the cusp apex, as opposed to being smooth or serrated only on the lower half of the crown. Although teeth of *Hemipristis curvatus* Dames, 1883 are superficially similar to those of *G. eaglesomei*, they are distinguished by having fewer serrations on the mesial edge (generally only on the lower one third) and a cusp that has smooth mesial and distal cutting edges.

Ebersole *et al*. (2019) reviewed the taxonomic history and palaeobiogeographic distribution of *Galeocerdo eaglesomei*. The taxon has been documented from Africa (Stromer, 1910; White, 1926, 1931; Arambourg, 1952) and from Alabama, USA (Ebersole *et al*. 2019).

Order *Incertae sedis*
Family *Incertae sedis*
Genus *Odontorhytis* Böhm, 1926
Odontorhytis aff. *O. pappenheimi* Böhm, 1926

Referred specimens – GU/B 2001, GU/B 2002, GU/B 2003, GU/B 2004 (Fig. 12).

Description – The teeth are less than 7.0 mm in greatest height and consist of a needle-like crown and low root. The crown is roughly conical but laterally compressed to varying degrees. In profile view, the crown is nearly straight to lingually curving. The labial and lingual faces are narrow and may be very rounded to sharp. The mesial and distal faces are biconvex, and the enameloid is ornamented with faint but distinct ridges that are parallel to the long axis of the crown. The ridges extend up to three-quarters the height of the crown. The root is unusual in being very low and expanded slightly beyond the crown in all directions. In profile view, the root is concave with an elongated labial projection, and the labial and lingual surfaces are convex. In basal view, the root outline is teardrop-shaped. A distinctive median furrow divides the root into two parts, with each part having a convex basal attachment surface. An elliptical nutritive foramen occurs within the furrow.

Discussion – The peculiar morphology of the specimens in our sample, with the simple cuspidate crown and lack of bilobed root, are characteristic of *Odontorhytis.* These enigmatic teeth were discussed by Priem (1905, 1909), who thought that middle Eocene teeth from Egypt were either indeterminate percoid fish or possibly belonged to batoids. Bhöm (1926) later described *O. pappenheimi* teeth from the late Eocene of Namibia and assigned them to the family Lophiidae (Neopterygii). Cappetta (1981) reported *O. pappenheimi* from the early Eocene of Morocco and concluded that the structure of the root closely resembled that of selachians. Although the genus is currently recognized as a galeomorph, its ordinal and familial affiliations remain in doubt.

The morphology of the Bandah Formation teeth is generally comparable to those of the three described *Odontorhytis* species, including *O. bahariensis* Salame & Asan, 2019, *O. pappenheimi*, and *O. priemi* Sambou *et al*., 2020, all of which have been reported from the Palaeogene of Africa (Case & Cappetta, 1990; Tabuce *et al*., 2005; Strougo *et al*., 2007; Murray *et al*., 2010; Underwood *et al*., 2011; Salame & Asan, 2019; Adnet *et al*., 2020; Sambou *et al*., 2020) and Pakistan (Case & West, 1991). The oldest species, *O. priemi* from the Thanetian to Lutetian of north and west Africa, clearly differs from the Bandah Formation teeth by having distinctive lateral cutting edges as well as somewhat cuspidate heels at the cusp base. Both *O. pappenheimi* and *O. bahariensis* have a cusp bearing a posterior apical barb and conspicuous labial longitudinal cutting edge. Differences between *O. pappenheimi* and *O. bahariensis* include the latter having a smaller but more extensively ornamented crown with shorter labial cutting edge compared *O. pappenheimi* (Salame & Asan, 2019; Adnet *et al*., 2020). Adnet *et al*. (2020) hinted that *O. bahariensis* represents ontogenetic heterodonty within *O. pappenheimi* (with the former representing juvenile and the latter adult forms of the same species) because both species occur in the same areas within deposits of approximately the same age.

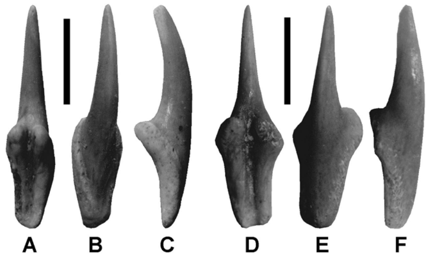

Figure 12. *Odontorhytis* aff. *O. pappenheimi* teeth. **A-C.** GU/B 2001 in A. lingual, B. labial, and C. profile views. **D-F.** GU/B 2002 in D. lingual, E. labial, and F. profile views. Scale bars = 2 mm.

Although the teeth in our sample are most closely aligned with *O. pappenheimi*, there are slight morphological differences between the teeth, and the Bandah Formation specimens are nearly a third taller than *O. pappenheimi* teeth reported from elsewhere. However, these differences could reflect heterodonty (dignathic, ontogenetic) rather than different biological species, and therefore we provisionally assign the Bandah teeth to *Odontorhytis pappenheimi* until a larger sample size can be examined.

Division Batomorphi Cappetta, 1980b

Order Rhinopristiformes Naylor *et al*., 2012

Family Rhinobatidae Bonaparte, 1835

Genus *Rhinobatos* Linck, 1790

***“Rhinobatos”* sp.**

Referred specimens – GU/B 2081, GU/B 2082, GU/B 2083, GU/B 2084 (Fig. 13).

Description – These ablated teeth measure up to 1 mm in width. In oral view, the crown consists of labial and lingual faces that are delineated by a transverse crest. The labial face is inclined, smooth, and flat to weakly convex. The labial crown foot conspicuously overhangs the root. The lingual face has a more vertical orientation and is mesio-distally convex. Lingually there is an elongated medial uvula that protrudes onto the root. A pair of lateral uvulae occur at the crown margins that are oblique to, or parallel with, the medial uvula. These lateral uvulae vary in length and are separated from the medial uvula by deep V-shaped or shallow U-shaped embayments. All crown enameloid is smooth. The root is massive and extends slightly beyond the crown laterally and substantially beyond the lingual crown margin. There is a pair of margino-lingual foramina, one on each side of the medial uvula. The root is bilobate, with large lobes being separated by a very wide but shallow nutritive

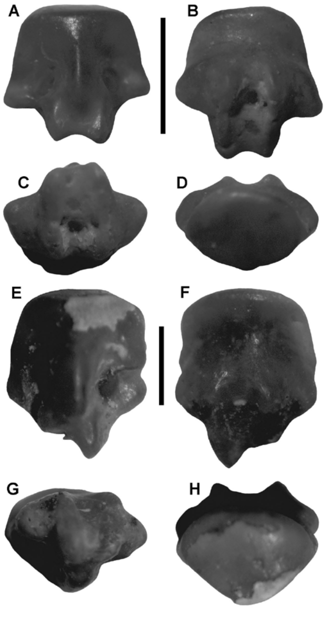

Figure 13. “*Rhinobatos*” sp. teeth. **A-D.** GU/B 2081 in A. lingual, B. labial, C. basal, and D. occlusal views. **E-H.** GU/B 2082 high crowned morphology in E. lingual, F. labial, G. basal, and H. occlusal views. Scale bars = 1 mm.

groove. The basal attachment surfaces are sub-triangular and weakly convex. There are one or more foramina within the nutritive groove.

Discussion – The taxonomic assignment of this tooth morphology has been cast into doubt in recent years. Cappetta & Case (2016), and more recently Adnet *et al*. (2020), referred such specimens to Pristidae (i.e., *Pristis*), although the morphology has typically been assigned to *Rhinobatos* or some similar taxon (i.e., Ebersole *et al*., 2019). This tooth morphology, which occurs as far back as the lower Cretaceous (Cappetta, 2012), is characterized by an elongated central lingual uvula that is flanked by lateral uvulae of various lengths (depending on the species). In contrast, Recent and fossil teeth of Pristidae have a central uvula but lack lateral uvulae (i.e., Carrillo-Briceño *et al*., 2015; 2016). Previous assignment of such teeth to Pristidae could simply be related to their co-occurrence with rostral spines. However, sawfish spines are thus far unknown from the Bandah Formation, and they are absent altogether in the Cretaceous. The similarity of tooth morphology between Rhinobatidae and Pristidae may not be surprising given the close phylogenetic relationship between the two taxa (both reside within the Rhinopristiformes). Based on the work of Marramà *et al*. (2020), we retain this tooth morphology in Rhinobatidae due to their similarity to Cretaceous taxa such as *Rhinobatos casieri* Herman in Cappetta & Case, 1975 and *R. ibericus* Cappetta & Corral, 1999.

Several Eocene *Rhinobatos* species have been described, and the Bandah Formation specimens resemble *R. bruxelliensis* Jaekel, 1894 by having a robust transverse crest, convex labial crown foot, elongated medial lingual uvula, and shorter and diverging lateral uvulae, but the crowns are comparatively narrower. *Rhinobatos steurbauti* Cappetta & Nolf, 1981 appears to have a lower crown with a more convex apex than the Bandah Formation specimens, and the medial uvula is wider. Teeth of *R. auribatensis* Adnet, 2006 have a comparatively straighter labial crown foot (in profile) and the medial lingual uvula is much shorter and wider. Teeth of the Eocene *Pseudorhinobatos* Marramà *et al*., 2020 differ from the Bandah Formation teeth by having very small, low-crowned teeth with diminutive lateral uvulae. Although the Bandah Formation teeth are similar to those of *Eorhinobatos* Marramà *et al*., 2020, they are larger, higher crowned, and have a narrower and longer central uvula.

The lack of associated skeletal material makes it impossible to accurately determine if the Bandah Formation specimens represent *Rhinobatos* or some similar taxon. Villalobos-Segura & Underwood (2020) recently suggested that *Rhinobatos* may have diverged from a common ancestor during the middle Eocene, and there is a possibility that the Bandah Formation taxon may belong to this ancestral genus. For the purposes of this report, we assign the Bandah Formation teeth to "*Rhinobatos*" sp. due to their similarity to other Eocene teeth referred to this genus, but acknowledge the possibility that the specimens may belong to a different, possibly undescribed, genus.

Order Myliobatiformes Compagno, 1973
Suborder Myliobatoidei Compagno, 1973
Family Dasyatidae Jordan & Gilbert, 1879
Genus *Dasyatis* Rafinesque, 1810a
"*Dasyatis*" sp.

Referred specimens – GU/B 2088, GU/B 2090, GU/B 2091, GU/B 2092, GU/B 2093, GU/B 2094, GU/B 2095, GU/B 2096, GU/B 2097 (Fig. 14).

Description – Two *Dasyatis*-like tooth morphologies are present in our sample, including those with a low, rounded apical margin, and those with a tall pointed apical margin. All of these teeth are affiliated based on the convex nature of the labial face, which bears nodular ornamentation to varying degrees. In oral view, all of the teeth are somewhat diamond-shaped, being wider (mesio-distal) than long (labio-lingual). The labial and lingual crown margins are convex (the lingual margin more so), but the lateral margins are sharply pointed. The labial face is weakly to strongly convex, but some teeth exhibit a weakly concave portion. Ornamentation on the labial face ranges from weakly to strongly rugose. A transverse crest separates the labial face from the lingual face. This crest is generally wide and blunt, but some teeth have sharper lateral edges. The lingual face is smooth, and it is convex mesio-distally but concave apico-basally. In basal view, the root is small in comparison to the crown outline. The root is bilobate, with small lobes being separated by a very wide, deep nutritive groove. The lobes have small pentagonal- to triangular-shaped basal attachment surfaces, which are flat to convex. The crown overhangs the root on the labial and lateral sides, but the root extends beyond the lingual crown foot.

Discussion – The low and tall-crowned morphologies in our sample are considered to be conspecific because all crown faces are convex and bear rugose ornamentation to varying degrees. It is possible that the sample reflects gynandric heterodonty, with the higher, pointed teeth belonging to males. Alternatively, males and females of some extant dasyatid species have cuspidate teeth. In the case of the Bandah Formation sample, the presence of the two morphologies indicates heterodonty (gynandric) within the population (i.e., Kajiura & Tricas, 1996).

The Bandah Formation "*Dasyatis*" sp. differs from the teeth of two other dasyatoids that were reported from the Ypresian

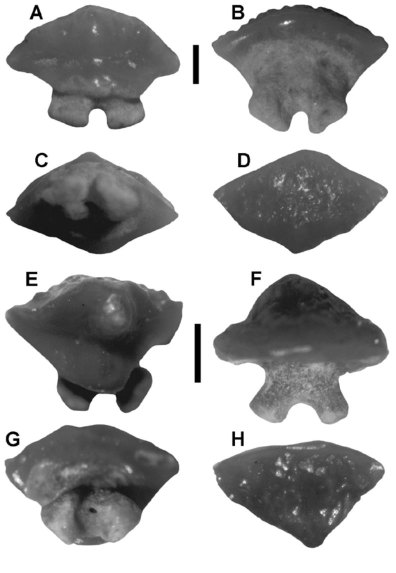

Figure 14. "*Dasyatis*" sp. teeth. **A-D.** GU/B 2090 in A. lingual, B. labial, C. basal, and D. occlusal views. **E-H.** GU/B 2095, high crowned morphology in E. lingual, F. labial, G. basal, and H. occlusal views. Scale bars = 1 mm.

Subathu Formation to the south in the Solan District, including *Dasyatis rafinesquei* Kumar & Loyal, 1987, and *D. vicaryi* Kumar & Loyal, 1987. These differences are significant and include a pitted labial ornamentation on both the *D. rafinesquei* (fine) and *D. vicaryi* (coarse) morphologies, and the cuspidate (male) morphology of *D. rafinesquei* has a narrower crown. The Bandah Formation taxon also differs from *Dasyatis* sp. 2 from the Ypresian Cambay Shale in the Surat District (Rana *et al*. 2004) in bearing coarse nodular ornamentation, whereas the latter taxon has smooth labial faces. However, the Bandah Formation teeth bear close morphological affinities with the teeth of *Dasyatis* sp.1 from the Cambay Shale (Rana *et al*. 2004), but they differ in size. Because it is unclear whether this size difference is taxonomically significant or the result of ontogeny, the Bandah Formation teeth are left to open nomenclature.

Teeth with the above morphology have traditionally been referred to the genus *Dasyatis* (see Cappetta, 2012). However, recent phylogenetic analyses on extant members of the Dasyatidae have shown the family to be paraphyletic, resulting in the splitting of the clade into four distinct subfamilies and at least eight different genera (Last *et al*., 2016; Nelson *et al*., 2016). This has a direct bearing on the taxonomy of fossil members of the Dasyatidae because it is currently unclear to what subfamily and/or genus any of the previously named fossil *Dasyatis* species should now be assigned. As a result, the Bandah Formation teeth are herein referred to as "*Dasyatis*" with the understanding that these specimens may not necessarily belong to this genus.

Genus *Coupatezia* Cappetta, 1982

Coupatezia sp.

Referred specimen – GU/B 2100 (Fig. 15).

Description – The small tooth has a crown measuring approximately 2.5 mm in width (mesio-distal). In occlusal view, the crown has a reniform outline, and the lingual margin is marked by a large transverse crest. The medial portion of the labial face is concave along its width, and the labial limit of this furrow is marked by another, somewhat less robust transverse crest. The labial crown foot is convex and medially embayed. The lingual face is mesio-distally convex, and in lingual view, the middle of the crown rim is apically arched. In basal view the root is large, occupying much the same area as the crown. The root is bilobate and is divided into two rather high lobes by a deep, wide nutritive groove. The basal attachment surface of each lobe is D-shaped and convex. The labial crown foot overhangs the root, but the lobes reach the lateral margins of the crown and extend beyond the lingual crown margin.

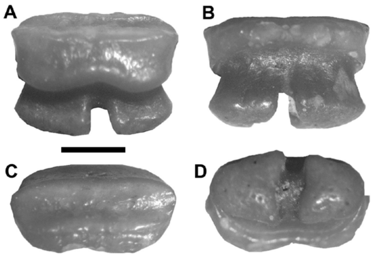

Figure 15. *Coupatezia* sp. tooth. **A-D.** GU/B 2100 in A. lingual, B. basiolabial, C. occlusal, and D. basal views. Scale bar = 1 mm.

Discussion – This specimen conforms to teeth of *Coupatezia* based on its reniform oral outline, concave labial face framed by sharp crests and margins, and large root compared to crown size. Kumar *et al*. (2007) reported the only other known record of *Coupatezia* from the Jaisalmer region, and both male and female morphologies were represented. The specimen identified as *Gymnura* sp. by Kumar *et al.* (2007; pl. 3, figs. 9-12) is in our opinion the male *Coupatezia* morphology, whereas teeth shown in pl. 3, figs. 18-21 are comparable to our Bandah Formation specimen. It is difficult to compare the Bandah Formation tooth to those discussed by Kumar *et al*. (2007), which were recovered from the underlying (Ypresian) Khuiala Formation, based on the limited views they provided and the abraded nature of our only specimen. The Bandah Formation specimen is also similar to middle Eocene *C. cristata* Adnet *et al*., 2020, particularly in the reniform nature of the teeth, the robust lingual transverse crest, and distinctive transverse crest at the labial crown foot. However, additional and well-preserved specimens are needed to more accurately determine the Bandah Formation species.

Dasyatidae indet.

Referred specimen – GU/B 2098 (Fig. 16).

Description – The tooth measures 2.5 mm in crown width. In occlusal view, the crown has a roughly circular outline. A distinguishing feature of this tooth is that much of the crown consists of a high cusp. In profile view, the cusp has a rather flat, oblique labial face that extends from the crown foot to the cusp apex. The lingual side of the cusp is vertical and mesio-distally convex. The lateral and lingual crown foot extends slightly beyond the cusp base, forming a nearly continuous rim. In basal view the crown foot is convex, and the labial part exhibits an embayment such that the enameloid does not extend as far under the crown as on the other sides. The crown enameloid is smooth. The root is smaller than the crown, bilobate, with lobes separated by a wide and deep nutritive groove. The basal attachment surfaces are of unequal size, but both are convex and have a reniform outline.

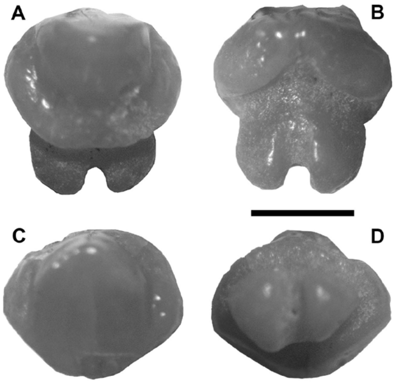

Figure 16. Dasyatidae indet. tooth. **A-D.** GU/B 2098 in A. orolingual, B. basiolabial, C. occlusal, and basal views. Scale bar = 1 mm.

Discussion – In terms of gross morphology, the specimen superficially resembles lateral teeth of *Merdiania convexa* Case, 1994, a taxon known from the Thanetian to Bartonian of the USA (Case, 1994; Cicimurri, 2010; Ebersole *et al*., 2019). However, GU/B 2098 differs by its lack of a transverse furrow at the lingual crown foot, the underside of the labial crown foot is conspicuously embayed, and the root has comparatively smaller lobes. We cannot assign the tooth to "*Dasyatis*" sp. described above due to the unusual morphology of the cusp, and this morphology does not compare with any known species of *Coupatezia*. Additional specimens are needed to determine the identity of this tooth.

Family Myliobatidae Bonaparte, 1835

Subfamily Myliobatinae Bonaparte, 1835

Genus *Aetomylaeus* Garman, 1908

"*Aetomylaeus*" sp.

Referred specimen – GU/B 2116 (Fig. 17A-C).

Description – The specimen is broken but measures approximately 12 mm in width (mesio-distal). In oral view, the crown is U-shaped, with the labial margin being concave and lingual margin convex. The labial face bears a network of reticulated ridges. The root is high and polyaulocorhize, with numerous thin, widely spaced lamellae.

Discussion – Although superficially similar to "*Rhinoptera*" sp. teeth described below, GU/B 2116 differs by the ornamentation of the labial and lingual faces. Whereas "*Rhinoptera*" sp. teeth have longitudinal furrows and ridges on vertical crown faces, the "*Aetomylaeus*" sp. tooth bears reticulated ridges on the labial face. Additionally, the transverse ridge at the lingual crown foot of "*Aetomylaeus*" sp. is thin and sharp, but it is thick and rounded on "*Rhinoptera*" sp. The combination of reticulated labial crown ornament and thin, sharp lingual transverse ridge at the crown base serve to distinguish "*Aetomylaeus*" sp. teeth from those of *Myliobatis*, which exhibits vertical ridges and grooves on crown faces and a thick and rounded lingual transverse ridge. Like the other members of the Myliobatinae, recent molecular divergence estimates by Villalobos-Segura & Underwood (2020) indicate that extant *Aetomylaeus* diverged from an ancestral taxon at some point during the late Miocene. As a result, we refer the Bandah Formation teeth to "*Aetomylaeus*" sp. with the understanding that they likely belong to an ancestral, undescribed member of extant *Aetomylaeus* lineage.

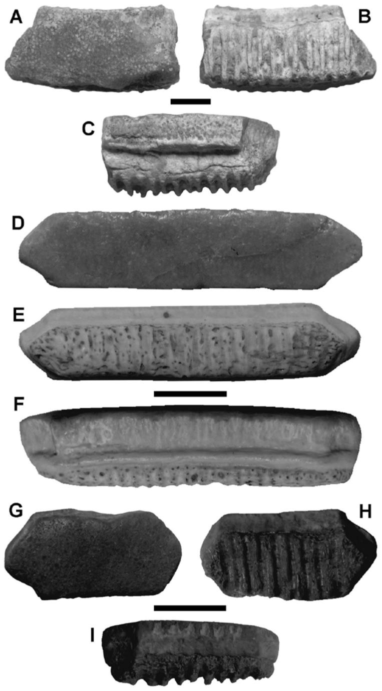

Figure 17. Myliobatidae teeth. **A-C.** GU/B 2116, "*Aetomylaeus*" sp. in A. occlusal, B. basal, and C. labial views. **D-F.** GU/B 2114, "*Rhinoptera*" sp. median tooth in D. occlusal, E. basal, and F. labial views. **G-I.** GU/B 2112, "*Rhinoptera*" sp. medio-lateral tooth in G. occlusal, H. basal, and I. labial views. Scale bars = 2 mm.

Subfamily Rhinopterinae Jordan & Evermann, 1896

Genus *Rhinoptera* Cuvier, 1829

"*Rhinoptera*" sp.

Referred specimens – GU/B 2099, GU/B 2110, GU/B 2112, GU/B 2113, GU/B 2114, GU/B 2115, GU/B 2117, GU/B 2118 (Fig. 17D-I).

Description – Symphyseal/medial teeth are very wide but relatively narrow. In oral view, the lateral angles are sharp and medially located. In labial/lingual view, the crown may be straight to slightly convex, and of uniform thickness along width. In profile view, the crown has a square to rectangular outline, depending on tooth wear. The labial and lingual faces are flat, vertical, and ornamented with wide longitudinal ridges and furrows that are overprinted with fine longitudinal ridges. The lingual crown foot bears a thick shelf-like transverse ridge. The root is low and polyaulocorhize, with lamellae being perpendicular to crown width and ranging from wide and widely spaced, to narrow and narrowly spaced (thickness of lamellae is about equal to the width of the nutritive grooves). The crown overhangs the root labially and laterally, but the lamellae reach (but do not extend beyond) the lingual crown foot.

Proximal lateral teeth are similar in morphology to symphyseal teeth. Two exceptions are that these lateral teeth are higher on the mesial side than on the distal side, and the root lamellae are oblique to crown width. A single distal lateral tooth is roughly hexagonal in occlusal view, but it is otherwise comparable to symphyseal and proximal lateral teeth.

Discussion – Specimens previously reported by Kumar *et al*. (2017) and Kumar *et al*. (2020) from the same horizon of the Bandah Formation were identified as *Myliobatis* sp. These teeth are morphologically identical to those described above, and we consider the material to be conspecific. However, we believe that the morphology is more similar to extant *Rhinoptera* than to *Myliobatis* based on various features, including: labial and lingual crown faces that are flat and vertical (as opposed to concave-convex and inclined); labial and lingual ornament consisting of vertical ridges that are finer and discontinuous (versus robust and contiguous); root lamellae with vertical labial face and not extending beyond the lingual crown foot (in contrast to oblique labial face and extending beyond the lingual crown foot); lateral teeth gradually decreasing in size towards the commissure, with the mesial side of the crown higher than distal side, and root lamellae oblique to crown width (as opposed to abruptly nearly symmetrically hexagonal, with uniformly thick crown and lamellae perpendicular to crown width). Based on these criteria, we conclude that specimens previously reported as *Myliobatis* in the fossil record (Eocene to Miocene) of India (Mishra, 1980; Sahni & Mehrotra, 1981; Kumar & Loyal, 1987, Bajpai & Thewissen, 2000; Rana *et al*., 2004; Rana *et al*., 2006) are more similar to *Rhinoptera* than to *Myliobatis*.

Recent phylogenetic analyses of batoids utilizing molecular divergence data (Villalobos-Segura & Underwood, 2020) suggested that the genus *Rhinoptera* may not have diverged from its ancestral taxon until the late Miocene. If these analyses are correct, they suggest that all pre-Neogene teeth that are morphologically similar to extant *Rhinoptera* may not necessarily belong to this genus. Because of this, we choose to refer the Bandah Formation teeth to "*Rhinoptera*" sp. with the understanding that they may belong to an ancestral genus within the extant *Rhinoptera* lineage.

Family Gymnuridae? Fowler, 1934

Genus *Ouledia* Cappetta, 1986

***Ouledia* aff. *O. lacuna* Adnet *et al*., 2020**

Referred specimens – GU/B 2101, GU/B 2102, GU/B 2103, GU/B 2104, GU/B 2105, GU/B 2106, GU/B 2107, GU/B 2108 (Fig. 18).

Description – The teeth are small, with no specimen exceeding 1 mm in width. The teeth are distinctive by their simple crown and unusual root structure. The crown is wider (mesio-distal) than long (labio-lingual), and in oral view, it is divided by a transverse ridge into (smaller) labial and (larger) lingual faces. The labial face ranges from weakly concave to flat, whereas the lingual face is always convex. In labial/lingual views, the apex of the transverse ridge may be uniformly convex, medially pointed, or form the tip of a distinctive cusp. Crown enameloid is smooth. In profile view, the labial crown foot is approximately even with the root margin, but lingually the root projects well beyond the crown base. The root is rather low and may be slightly wider or slightly less wide than the crown. A wide nutritive groove divides the root into two large lobes. At least one nutritive foramen occurs within the groove.

Discussion – The tooth morphologies in the Bandah Formation sample conform to the various species of *Ouledia* Cappetta, 1986, including *O. casieri* (Kumar & Loyal, 1987), *O. sigei* Cappetta, 1986 and *O. lacuna* Adnet *et al*., 2020. Two tooth morphologies are represented, one with a broadly convex to somewhat pointed apical cutting edge, and one with a distinct pointed cusp and sharp transverse cutting edge. These variations have been attributed to gynandric heterodonty within the genus (Cappetta, 1986), with the cuspidate teeth representing males.

The *casieri* morphology, from the Ypresian of India, was originally named as a new taxon, *Subathunura* Kumar & Loyal, 1987, but this genus has since been synonymized with *Ouledia* (Adnet *et al*., 2008; Adnet *et al*., 2020). *Ouledia casieri* differs from the Bandah Formation specimens by having a transverse furrow on the crown as opposed to a transverse ridge. In terms of overall morphology, the Bandah Formation non-cuspidate variant is very similar to that of *O. sigei* and *O. lacuna*. The Bandah Formation cuspidate morphology is comparable to that of *O. sigei*, but potentially significant differences include a narrower (mesio-distal) crown with flatter labial face. Additionally, none of the teeth from the Bandah Formation are as mesio-distally narrow as some specimens of *O. sigei* (Cappetta, 1986). The Bandah Formation specimens have in common with *O. lacuna*, including specimens that were previously identified only to the generic level (i.e., Adnet *et al*., 2008, Underwood *et al*., 2011) but synonymized with *O. lacuna* (Adnet *et al*., 2020), a labio-lingually thinner and mesio-distally concave labial face. However, due to the poor preservation of the recovered specimens, we conservatively assign the Bandah Formation teeth to *O. lacuna*

DISCUSSION

Review of the Bandah Formation elasmobranch assemblage

Two prior studies, Kumar *et al*. (2017) and Kumar *et al*. (2020), reported elasmobranch remains from the Bandah Formation in the same part of the Jaisalmer Basin of Rajasthan as the present study. Those reports described a small number of shark and ray teeth from approximately the same locality and horizon that we sampled. However, the specimens were surface collected from an outcrop where the lithologic beds are not easily discerned. Furthermore, the identifications of the teeth were largely inaccurate or cannot be known with certainty due to the poor preservation of the specimens. However, when combined with the fossils discussed herein, the composition of the Bandah Formation elasmobranch assemblage becomes clearer (Table 1).

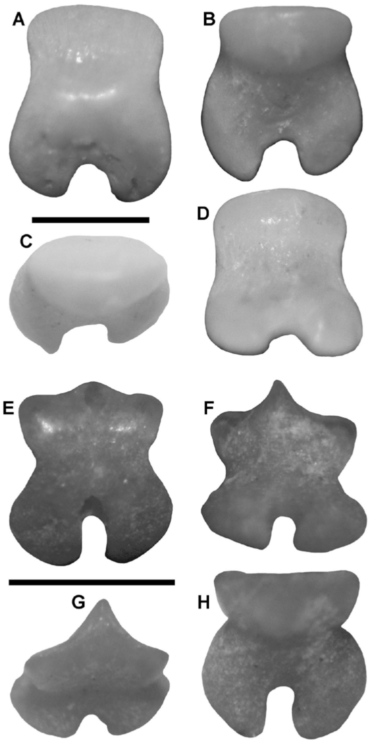

Figure 18. *Ouledia* aff. *O. lacuna* teeth. **A-D.** GU/B 2102 in A. lingual, B. occlusal, C. basal, and D. labial views. **E-H.** GU/B 2105, high crowned-morphology in E. lingual, F. occlusal, G. basal, and H. labial views. Scale bars = 2 mm.

The single *Nebrius* sp. tooth available to us is the only representative of Ginglymostomatidae in our sample, and the specimen differs from similar teeth of *Ginglymostoma* sp. by having more mesial and distal cusplets flanking the main cusp (*sensu* Ebersole *et al*., 2019). Although *Ginglymostoma* sp. and *G. sokotoense* have been identified from the upper Palaeocene and lower Eocene deposits of Barmer, Jaisalmer, and Himachal Pradesh, India (Rana *et al*., 2005; Kumar *et al*., 2007; Gupta & Kumar, 2013; Rajkumari & Prasad, 2020), these specimens generally have fewer lateral cusplets and the labial apron is very small and poorly differentiated from the remainder of the labial crown foot. The Bandah Formation tooth represents the first record of *Nebrius* in the middle Eocene of India.

Mitsukurinidae is represented by *Striatolamia* aff. *S. macrota*. The teeth are poorly preserved, but they were attributed to this genus based on the very tall and narrow main cusp that bears fine longitudinal ridges, and the presence of diminutive lateral cusplets. *Striatolamia* has been reported from the Bandah Formation by Kumar *et al*. (2017), but some teeth identified as *Carcharias* cf. *tricupidatus* Day, 1878 by Kumar *et al*. (2020: pl. 2, fig. j-l) also appear to represent *Striatolamia*.

Two genera of Odontaspididae have been identified, including *Brachycarcharias* and *Jaekelotodus*. There are two species of *Brachycarcharias*, including *B. atlasi* and *B. lerichei*, that were differentiated based on the size and number of lateral cusplets and the coarseness of the lingual ornamentation. The morphological features and palaeobiogeographic distributions of these species were recently reviewed by Ebersole *et al*. (2019). In the two previous reports on Bandah Formation elasmobranchs, we believe that specimens previously identified as *Lamna* sp. (Kumar *et al*., 2017: pl. 2, fig. e–f) and *Carcharias* cf. *tricuspidatus* (Kumar *et al*., 2020: pl. 2, figs. g–i, p–r) are more appropriately identified as *B. lerichei*. The *B. atlasi* specimens reported herein represent the first confirmed occurrence of this species in India.

The single lateral tooth referred to cf. *Jaekelotodus* sp. has a broadly triangular, recurved main cusp with nearly complete cutting edges, and the lateral cusplets, although poorly preserved, are triangular and pointed. A tooth identified by Kumar *et al*. (2017: pl. 2, fig. g–h) is interesting because it bears a strong resemblance to *Tethylamna dunni* Cappetta & Case, 2016, with one of the distinguishing features being the broadly triangular lateral cusplets that are distally directed (Cappetta & Case, 2016; Ebersole *et al*., 2019). Kumar *et al*. (2017) figured another specimen (pl. 2, fig. i–j) that is similar to some teeth of *Hypotodus verticalis* (Agassiz, 1843). It is possible that these taxa are represented in our Bandah Formation sample, but were identified as Odontaspididae or Lamniformes indet. because they are poorly preserved. Additional specimens are needed to corroborate the presence of *Jaekelotodus*, *Tethylamna*, and *Hypotodus* in the middle Eocene of India.

Several teeth in our sample are too fragmentary and ablated to identify beyond Lamniformes. These include crowns and partial teeth that could represent any of the odontaspidids or even *Striatolamia*. Into this group we would place specimens from the Bandah Formation that have previously been identified as *Isurus* sp. (Kumar *et al*. 2017: pl. 2, fig. a–d), *I*. cf. *oxyhrynchus* (Kumar *et al*. 2020: pl. 2, fig. a–f), and *Carcharias* cf. *tricuspidatus* (Kumar *et al*. 2020: pl. 2, fig. m–o).

Three genera of Carcharhinidae have been identified, including *Carcharhinus*, *Rhizoprionodon*, and *Physogaleus*. The *Carcharhinus* teeth are assigned to *C. mancinae*, a taxon recently reported from the middle Eocene (Bartonian) of Alabama (Ebersole *et al*., 2019), based on their overall morphology, the presence of compound serrations, and by having a dentition that exhibits clear dignathic heterodonty. We believe that some specimens identified as *Galeocerdo* sp. in previous Bandah Formation elasmobranch studies by Kumar *et al*. (2017: pl. 2, fig. n–o) and Kumar *et al*. (2020: pl. 2, fig. s–u) are conspecific with teeth we identify herein as *C. mancinae*. The presence of *Carcharhinus mancinae* in the Rajasthan region of India is of interest because the species was heretofore restricted to the Bartonian of Alabama (Ebersole *et al*., 2019), and the temporal range of the species serves to corroborate the age of the Bandah Formation. Furthermore, the Bandah Formation specimens not only represent the first confirmed records of *C. mancinae* in India, but also the first occurrence of this taxon from outside of its type locality of southwestern Alabama, USA.

Although denticulations occur on the distal heel of *Physogaleus* and may occur on the base of the mesial cutting edge, teeth lack serrations on the upper half of the mesial edge and on the distal cutting edge. The limited development of denticulation on the mesial cutting edge and distal heel of the *Physogaleus* teeth are indicative of *P. secundus*, as opposed to the coeval taxon *P. alabamensis* (Ebersole *et al*., 2019). Kumar *et al*. (2020) illustrated a specimen (pl. 2, fig. v–x) that they identified as *Galeocerdo* sp., but our evaluation of the figured specimens leads us to conclude that the material is more similar to *Physogaleus alabamensis*. Our identification is based on the heavy denticulation on the mesial cutting edge and distal heel, and the lack of serrations on the cusp as seen on *Galeocerdo* teeth. Additional specimens are needed to confirm the presence of *P. alabamensis* in the Bandah Formation, but Ebersole *et al*. (2019) reported *P. secundus* and *P. alabamensis* as being coeval in the middle Eocene of Alabama.

The *Rhizoprionodon* teeth in our sample were differentiated from *Physogaleus* lateral teeth based on the lack of mesial denticulation and the single convex to pointed cutting edge on the distal heel. The Bandah Formation teeth may be *R. ganntourensis* (Arambourg, 1952), a species originally described from northern Africa, but a larger sample is needed to make this determination. One additional specimen reported by Kumar *et al*. (2017: pl. 2, fig. p–q), also identified as *Galeocerdo* sp., is of note. The specimen is rather large, and although the basal mesial cutting edge and distal heel are coarsely denticulated, the edges otherwise lack serrations on the upper half of mesial edge and the distal cutting edge. Additionally, the labial crown foot is convex and slightly overhangs the root. This combination of features leads us to believe that the material is more appropriately identified as *Galeorhinus*, rather than *Galeocerdo* or *Physogaleus*.

Two species of Galeocerdidae are present, including *Galeocerdo clarkensis* and *G. eaglesomei*. These species are differentiated from each other by their serrations and the morphology of the mesial and distal sides of the crown. On *G. clarkensis*, the mesial serrations are largest at the middle of the cutting edge, serrations are weakly compound, and the distal heel is separated from the distal cutting edge by a deep notch. In contrast, serrations on *G. eaglesomei* are of rather uniform size, they are simple (i.e., lack additional minute serrations), and there is a sloping transition from the distal cutting edge to the distal heel. As noted above, specimens from the Bandah Formation previously identified as *Galeocerdo* are more appropriately assigned to *Carcharhinus mancinae*, *Physogaleus alabamensis*, and perhaps *Galeorhinus*. The *G. clarkensis* teeth identified in our sample represent the first occurrence of this taxon in India, and the first confirmed occurrence of this species outside of the Atlantic and Gulf coastal plains of the USA (see Ebersole *et al*., 2019). Although *G. eaglesomei* is known from Africa and Alabama in the USA (Stromer, 1910; White, 1926; Ebersole *et al*., 2019), the specimens reported herein represent the first documented record for the taxon in India.

Odontorhytis aff. *O. pappenheimi* is reported for the first time from the middle Eocene of India. The genus is primarily known from the Eocene of Africa, including Namibia, Nigeria, Morocco, Egypt, and Tunisia, but it also occurs in Pakistan (Böhm, 1926; Cappetta, 1981, 1987; Case & West, 1991; Tabuce *et al*., 2005; Strougo *et al*., 2007; Murray *et al*., 2010; Adnet *et al*., 2011; Underwood *et al*., 2011; Adnet *et al*., 2020). *Odontorhytis* was a euryhaline shark that predominantly occurs in deposits representing shallow marine environments, but the taxon appears to have also tolerated brackish and freshwater environments (Murray *et al*., 2010).

The Bandah Formation elasmobranch assemblage contains four batoid families, including Rhinobatidae, Dasyatidae, Myliobatidae, and Gymnuridae. Several poorly preserved teeth are identified as "*Rhinobatos*" sp. due to their superficial similarity to the teeth of this extant genus, and they represent the first occurrence of this taxon in the fossil record of the region. The Bandah Formation Dasyatidae includes "*Dasyatis*" sp. and *Coupatezia* sp. Only one *Coupatezia* tooth has been identified thus far, but it differs from teeth of "*Dasyatis*" in lacking labial ornamentation other than a weak basal transverse crest. The "*Dasyatis*" teeth bear some similarity to specimens identified as *Dasyatis* sp. 1 from the lower Eocene Khuiala Formation, but we could not make a critical comparison of the two samples. It is entirely possible that they represent a new dasyatoid species. We prefer to use "*Dasyatis*" when identifying the Bandah Formation teeth because the family is known to be paraphyletic (Last *et al*., 2016) and, although similar, the teeth could represent some taxon other than *Dasyatis*. An additional tooth is herein assigned to Dasyatidae indet. because it differs from the Bandah Formation "*Dasyatis*" sp. and *Coupatezia* sp. morphologies. The uniqueness of this specimen precluded further identification, but additional specimens may show that a third member of the Dasyatidae occurs in the Bandah Formation.

Two similar Myliobatidae tooth morphologies were identified that are referred to herein as "*Rhinoptera*" sp. and "*Aetomylaeus*" sp., denoting their similarity to teeth of extant species of these genera. Specimens referred to "*Rhinoptera*" sp. have straight, nearly vertical labial and lingual faces that bear coarse vertical crenulations, whereas teeth of "*Aetomylaeus*" sp. have a lingually inclined, pitted and concave labial face and tuberculated, convex lingual face (*sensu* Ebersole *et al*., 2019). Teeth from the Bandah Formation that were identified as *Myliobatis* sp. by Kumar *et al*. (2017: pl. 1, fig. a–d) and Kumar *et al*. (2020: pl. 3, a-d) are in our opinion "*Rhinoptera*" sp. based on their overall morphology, including the higher mesial side compared to the distal side. The "*Rhinoptera*" sp. and "*Aetomylaeus*" sp. teeth described herein represent the first confirmation of these taxa in the fossil record of India.

Ouledia is known from the late Palaeocene to late Eocene of northern Africa and southwestern Asia, where it apparently constitutes part of nearshore marine elasmobranch palaeofaunas (Cappetta, 1986; Rana *et al*., 2005; Tabuce *et al*., 2005; Adnet *et al*., 2007; Strougo *et al*., 2007; Adnet *et al*., 2008, Adnet *et al*., 2011; Underwood *et al*., 2011). The Bandah Formation teeth are morphologically more similar to middle Eocene *O. lacuna* than to the Ypresian species *O. casieri* and *O. sigei*. The specimens in our sample represent the first occurrence of *Ouledia* in the middle Eocene of India and are only the second record of the genus from the subcontinent (Ypresian *O. casieri*).

Palaeobiogeographic implications of the Bandah Formation elasmobranch palaeofauna

Seventeen unequivocal taxa were identified in our Bandah Formation sample. Of these, ten taxa represent first occurrences for India, eight of which could be identified to a species. Because no new taxa were recognized in our Bandah Formation sample, this assemblage presents several interesting palaeobiogeographic implications because each of the identified species were originally identified from elsewhere. For example, *Brachycarcharias lerichei* was named for specimens derived from the Ypresian of Belgium (Casier, 1946). This taxon has since been reported from Antarctica (Marramà *et al*., 2018a), France (Dutheil & Merle, 1992), Germany (Diedrich, 2012), Italy (Marramà *et al*, 2018b), Japan (Tanaka *et al*., 2006), Mexico (Gonzàlez-Barba & Theis, 2000), Morocco (Arambourg, 1952), the Netherlands (Souverein & Stoel, 1995), Spain (Bauzà & Gomez Pallerola, 1988), and the United Kingdom (Cappetta & Nolf, 2005), and Alabama (Ebersole *et al*., 2019), Maryland and Virginia (Ward & Weist, 1990) in the USA. This indicates that *B. lerichei* had a nearly circumglobal range in the Palaeogene that included the Atlantic, Indian, Pacific, and Southern oceans, as well as the Gulf of Mexico and Tethys/Paratethys. *Striatolamia macrota* appears to have had a similar geographic range (see Cappetta, 2012).

Galeocerdo eaglesomei (White, 1926), which was originally named for teeth from the central Atlantic Ocean in Nigeria, had a slightly more restricted geographic range, as it has been confirmed from the northern Atlantic Ocean (Case & Borodin, 2000) and Gulf of Mexico (Ebersole *et al*., 2019) in the USA, and the Indian Ocean in Madagascar (Samonds *et al*., 2019). Even more restricted are the occurrences of *Odontorhytis pappenheimi*, which has only been reported from the southern Atlantic Ocean in Namibia (Böhm, 1926), northern Atlantic Ocean in Morocco (Cappetta, 1981), the Tethys Sea in Egypt (Case & Cappetta, 1990) and Tunisia (Adnet *et al*., 2020), and the Indian Ocean in Pakistan (Case & West, 1991). The same can be said for *Galeocerdo clarkensis*, which has only been confirmed from the northern Atlantic Ocean and Gulf of Mexico in Alabama and South Carolina in the USA (Ebersole *et al*., 2019). Finally, *Ouledia lacuna* has only been reported from the Tethys region in Europe and northern Africa (see Adnet *et al*., 2020), and *Carcharhinus mancinae* has been confirmed only from the Gulf of Mexico in Alabama, USA.

As a whole, the Bandah Formation palaeofauna is comprised of taxa with palaeobiogeographic ranges from every major ocean and every continent. With the exception of *Carcharhinus mancinae*, *Galeocerdo clarkensis*, and *G. eaglesomei*, all of the remaining species have palaeobiogeographic ranges that previously included the Tethys Sea, indicating that this body of water played an essential role in the distribution of sharks and rays between the Atlantic, Indian, Pacific, and Southern oceans during the Palaeogene. Although the occurrences of *C. mancinae* and *G. clarkensis* in the Rajasthan region of India constitutes a palaeobiogeographic range extension of nearly 20,000 km from their type locality of southwestern Alabama, USA, this should not be surprising because modern species like *Carcharhinus leucas* (Müller & Henle, 1839), *C. obscurus* (Lesueur, 1818), and *Galeocerdo cuvier* (Péron

Table 1. Chondrichthyan taxa confirmed from the Bandah Formation in the Jaisalmer District of Rajasthan, India. *Denotes first record of this taxon in India.

Taxon	Reference	Figure
Nebrius sp.*	This study	Fig. 3
Striatolamia aff. *S. macrota*	This study Kumar *et al.* (2017) Kumar *et al.* (2020)	Fig. 4 pl. 2, fig. k-l pl. 2, fig. j-l
*Brachycarcharias atlasi**	This study	Fig. 5A-F
Brachycarcharias lerichei	This study Kumar *et al.* (2017) Kumar *et al.* (2020)	Fig. 5G-I pl. 2, fig. e-f pl. 2, fig. g-l, p-r
cf. *Jaekelotodus* sp.*	This study	Fig. 6
Odontaspididae indet.	This study	Fig. 7
?*Tethylamna dunni* *	Kumar *et al.* (2017)	pl. 2, fig. g-h
?*Hypotodus verticalis**	Kumar *et al.* (2017)	pl. 2, fig. i-j
Lamniformes indet.	Kumar *et al.* (2017) Kumar *et al.* (2020)	pl. 2, fig. a-d, m pl. 2, fig. a-f, m-o
*Carcharhinus mancinae**	This study Kumar *et al.* (2017) Kumar *et al.* (2020)	Fig. 8 pl. 2, fig. n-o pl. 2, fig. s-u
Rhizoprionodon sp.	This study	Fig. 9
Physogaleus sp.	This study	Fig. 10
?*Physogaleus alabamensis* *	Kumar *et al.* (2020)	pl. 2, fig. v-x
Galeorhinus sp.	Kumar *et al.* (2017)	pl. 2, fig. p-q
*Galeocerdo clarkensis**	This study	Fig. 11A-E
*Galeocerdo eaglesomei**	This study	Fig. 11F-H
Odontorhytis aff. *O. pappenheimi**	This study	Fig. 12
"*Rhinobatos*" sp.	This study	Fig. 13
"*Dasyatis*" sp.	This study	Fig. 14
Coupatezia sp.	This study	Fig. 15
Dasyatidae indet.	This study	Fig. 16
"*Aetomylaeus*" sp.*	This study	Fig. 17A-C
"*Rhinoptera*" sp.*	This study Kumar *et al.* (2017) Kumar *et al.* (2020)	Fig. 17D-I pl. 1, fig. a-d pl. 3, a-d
Ouledia aff. *O. lacuna**	This study	Fig. 18

& Lesueur, 1822) have circumglobal distributions. With the Eocene Tethys Sea creating a corridor connecting the northern Atlantic Ocean and the Indian Ocean, the occurrence of taxa such as *C. mancinae* and *G. clarkensis* in the Bandah Formation indicates that many selachian taxa could move freely between these two distant oceans.

Palaeoenvironment and Palaeoecology of the Bandah Formation

In a general view, the Jaisalmer Basin represents the central part of the Rajasthan shelf and the eastern shelf part of the Indus Basin and its eastern extension of the Tethys Sea. During the early Palaeogene, the whole margin of peninsular India (including the western Rajasthan shelf) was submerged due to marine transgression. The region was also connected by the foreland basin of the young Himalaya Mountains, and it is presumed that this was synchronous with the continental collision between India and Asia. It is also assumed that the Himalayan foreland basin extended the Arabian Sea and Tethys realm through the western Rajasthan shelf and the Sanchor and Cambay basins. The development of fine, clastic marl and carbonate sequences in the Sanu, Khuiala and Bandah formations indicates that the Eocene sequence of the Jaisalmer Basin was deposited in a stable environment.

Singh (1976, 1984, 1996, 2003, 2007) provided detailed studies of the Cenozoic surface and subsurface sequences within the Jaisalmer Basin and suggested there was a considerable hiatus in sedimentation in the region at the end of the Mesozoic Era. Although surface exposures of the Sanu Formation have not yielded micro- or macrofossils, subsurface benthic foraminifera such as *Planorotalites pusilla* Bolli, 1957*, P. pseudomenardii* (Bolli, 1957)*, Morozovella velascoensis* (Cushman, 1925b), *Assilina dandotica* Davies & Pinfold, 1937, and *Discocyclina seunesi* Douvillé, 1922 indicate that the first marine transgression in the Jaisalmer Basin occurred during the late Palaeocene, and the sea fluctuated between inner to outer shelf zones (40 to 150 m; Singh, 1984, 2007). Marked shallowing of the sea is recorded by strata near the top of Sanu Formation.

During the early Eocene the shoreline extended much farther east than during the Palaeocene, and this was followed by a renewed deepening of the sea during deposition of the Khuiala Formation. The foraminifera assemblage within the Khuiala Formation is represented by *Assilina granulosa* (d'Archiac, 1850), *A. daviesi* Cizancourt, 1938, *A. lacunata* Cizancourt, 1946, *Nummulites mamilla* Roissy, 1805, *N. burdigalensis* Rozlozsnik & de la Harpe, 1926, and *N. irregularis* Deshayes, 1838, taxa indicating that deposition of the Khuiala Formation represented an inner to middle shelf environment (50 to 100 m; Singh, 2007). Singh (2007) also suggested that there were widespread regressions throughout a short period before the commencement of middle Eocene (Lutetian) transgression, and a similar transgression has also reported from the Bikaner and Kutch basins (Singh, 1971; Biswas, 1971). A short depositional hiatus is preserved at the top of the Khuiala Formation and followed by renewed middle Eocene (Lutetian) transgression. The limestone sequences represented by the Batrewala and Bakhari-Tibba Members of the Bandah Formation formed during this transgression. Subsurface and surface foraminifera from this formation include *Fasciolites elliptica* Sowerby, 1840, *Assilina spira* (Roissy, 1805), *A. papillata* Nuttall, 1926a, *A. subpapillata* Nuttall, 1926b, *Nummulites bagelensis* Verbeek, 1891, *N. pengaronensis* Verbeek, 1871, *N. beaumonti* d'Archiac & Haime, 1953*, N. maculatus* Nuttall, 1926a, *Dictyoconoides cooki* Nuttall, 1925*, Discocyclinap* sp., and *Baculogypsinoides* sp. (Singh, 1984, 2007). Overall, the foraminifera and other invertebrate fossils occurring within limestone beds of the Bandah Formation indicate a moderately deep to shallow (inner to middle shelf of 30-100 m depth) environments existed at various intervals during the middle Eocene, and the deposition of carbonate-rich and gypsiferous shale indicates the climate was warm and tropical. By the end of Eocene, the Tethys Sea had completely withdrawn from the Jaisalmer Basin and shelf.

The interpretation that the Bandah Formation represents a warm and tropical palaeoenvironment is corroborated by the elasmobranch assemblage, which includes taxa that have been reported from middle Eocene strata elsewhere that indicate tropical areas (see Cappetta, 2012; Ebersole *et al*., 2019; references cited herein). Foraminiferal and molluskan species suggest that some beds within the Bandah Formation accumulated in moderately deep to shallow waters. Two taxa within our sample, *Odontorhytis* and *Ouledia*, have been interpreted as preferring nearshore marine or even brackish environments (Cappetta, 1986; Rana *et al*., 2005; Tabuce *et al*., 2005; Adnet *et al*., 2007; Strougo *et al*., 2007; Adnet *et al*., 2008; Murray *et al*., 2010; Adnet *et al*., 2011; Underwood *et al*., 2011). Furthermore, identification of the genera *Nebrius* and "*Rhinoptera*" is of interest because each have extant representatives that prefer extremely shallow waters. For example, the only extant species of *Nebrius*, *N. ferrugineus* (Lesson, 1831), has a depth preference of 70 meters or less

(Froese & Pauly, 2019). Similarly, the eight extant species of *Rhinoptera* are generally found at depths of no less than 65 meters (Froese & Pauly, 2019; Bray & Gomon, 2020). The presence of these four genera at the collecting locality suggests that at least "bed b" of the Bandah Formation represents a shallow-water inner shelf (less than 50 m depth), possibly shallow neritic, environment. This is further corroborated by oyster-bearing limestone within this horizon (see Fig. 2), which is generally indicative of intertidal or subtidal zones (Shepard *et al*., 2018). Such a depositional environment could also explain the broken and ablated nature of the elasmobranch teeth and disarticulation of bivalve shells.

CONCLUSIONS

Our sample from the Bandah Formation of the Jaisalmer Basin yielded a total of 17 unequivocal taxa, with two additional morphologies assigned to Odontaspididae indet. and Dasyatidae indet., that possibly represent additional unique taxa. A reanalysis of specimens figured in two prior studies (Kumar *et al*., 2017; Kumar *et al*., 2020) suggests the presence of *Galeorhinus* sp. in the Bandah Formation, and possibly additional taxa to include *Hypotodus verticalis*, *Physogaleus alabamensis*, and *Tethylamna dunni* (see Table 1). Of the confirmed taxa, 10 represent first occurrences for the fossil record of India, including "*Aetomylaeus*" sp., *Brachycarcharias atlasi*, *Carcharhinus mancinae*, *Galeocerdo clarkensis*, *G. eaglesomei*, cf. *Jaekelotodus* sp., *Odontorhytis* aff. *O. pappenheimi*, *Ouledia* aff. *O. lacuna*, and "*Rhinoptera*" sp. The elasmobranch palaeofauna within "bed b" at our Bandah Formation locality indicates that deposition of this unit likely occurred within a warm, tropical, shallow-water, continental shelf or inner neritic environment, and the presence of *C. mancinae* helps corroborate a Bartonian age. The co-occurrence of diverse taxa otherwise known from widely separated regions suggests that the Tethys Sea played an important role in the distribution of elasmobranchs during the middle Eocene, allowing certain taxa to attain nearly circumglobal distributions.

ACKNOWLEDGEMENTS

We thank Emeritus Professor Ashok Sahni, Panjab University, Chandigarh for providing valuable comments to an earlier version of this manuscript. We also thank Vice-Chancellor Professor Annpurna Nautiyal for providing financial assistance and permission to conduct fieldwork in the region. The students of M.Sc. II semester 2019 -2021 batch are thanked for helping with fieldwork, and Mohd Waqas, Mahendra Kumar, Naveen Singh, and Rohit Yadav are thanked for their assistance with the laboratory work. Finally, we thank two anonymous reviewers, journal editor Rodolphe Tabuce, and the handling editor, Sylvain Adnet, for their insightful comments that greatly improved an earlier version of this study.

BIBLIOGRAPHY

Adnet, S., 2006. Nouvelles faunes de Sélaciens (Elasmobranchii, Neoselachii) de l'Eocène moyen des Landes (Sud-Ouest, France). Implication dans la connaisance des communautés de sélaciens d'eaux profondes. Palaeo Ichthyologica 10, 1-128.

Adnet, S., Cappetta, H., Beard, K. C., Marivaux, L., Marandat, B., Chaimanee, Y., Jaeger, J.-J., Tun, S. T., Soe, A. N., 2008. First myliobatiform teeth (Elasmobranchii, Neoselachii) from the Pondaung Formation (late middle Eocene) of Central Myanmar. Neues Jahrbuch für Geologie un Paläontologie, Abhandlungen 247, 335-340. https://doi.org/10.1127/0077-7749/2008/0247-0335

Adnet, S., Antoine, P.-O., Baqri, S .R. H., Crochet, J.-Y., Marivaux. L., Welcomme, J.-L., Metais, G., 2007. New tropical carcharhinids (Chondrichthyes, Carcharhiniformes) from the late Eocene-early Oligocene of Balochistan, Pakistan: Paleoenvironmental and paleogeographic implications. Journal of Asian Earth Sciences 30, 303-323. https://doi.org/10.1016/j.jseaes.2006.10.002

Adnet, S., Cappetta, H., Elnahas, S., Strougo, S., 2011. A new Priabonian chondrichthyan assemblage from the Western desert, Egypt: Correlation with the Fayum Oasis. Journal of African Earth Sciences 61, 27-37. https://doi.org/10.1016/j.jafrearsci.2011.04.005

Adnet, S., Marivaux, L., Cappetta, H., Charruault, A. L., Essid, E. M., Jiquel, S., Ammar, H. K., Marandat, B., Marzougui, W., Merzeraud, G., Temani, R., Liaud, M. V., Tabuce, R., 2020. Diversity and renewal of tropical elasmobranchs around the Middle Eocene Climatic Optimum (MECO) in North Africa: New data from the lagoonal deposits of Djebel el Kébar, Central Tunisia. Palaeontologia Electronica 23, a38. https://doi.org/10.26879/1085

Agassiz, L. 1838. Recherches sur les poissons fossiles, 11th livraison (November 1838). Petitpierre et Prince (text) and H. Nicolet (plates), Neuchâtel.

Agassiz, L. 1843. Recherches sur les Poissons fossiles. Imprimerie de Petitpierre, Neuchâtel. https://doi.org/10.5962/bhl.title.4275

Applegate S. P., 1974. A revision of the higher taxa of Orectoloboids. Journal of the Marine Biological Association of India 14(2), 743-751.

Arambourg, C., 1952. Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). Notes et Mémoires du Service géologique du Maroc 92, 1-372.

Archiac, E. J. A. D. d'., 1850. Description des fossiles du groupe nummulititique recueillis par M. S.P. Pratt et M. J. Delbos aux environs de Bayonne et de Dax. Mémoire de la Société Géologique de France 2(3), 397-456.

Archiac, E. J. A. D., d', Haime, J., 1853. Description des animaux fossiles du groupe nummulitique de l'Inde: précédée d'un résumé géologique et d'une monographie des nummulites. Gide et Baudry, Paris.

Bajpai, S., Thewissen, J. G. M., 2000. A new, diminutive whale from Kachchh (Gujarat, India) and its implications for locomotor evolution of cetaceans. Current Science 79, 1478-1482.

Bauzà, R. J., Gomez Pallerola, J. E., 1988. Contribución al conocimiento de la ictiología fósil de España. Boletin de la Sociedad de Historia Natural de Baleares 32, 115-138.

Biswas, S. K., 1971. Note on the Geology of Kutch. The Quarterly Journal of the Geological, Mining, and Metallurgical Society of India 43, 223-235.

Blainville, H. M. D., de, 1816. Prodrome d'une nouvelle distribution sytématique du règne animal. Bulletin des Sciences, par la Société Philomatique de Paris 8, 105-124.

Böhm, J., 1926. Über tertiäre versteinerungen von den Bogenfelsen diamantfeldern. In: Kaiser, E. (Ed.), Die Diamantwüste Südwestafrikas. Berlin, pp. 55-87.

Bolli, H. M., 1957. The genera *Globigerina* and *Globorotalia* in the Paleocene-Lower Eocene Lizard Springs Formation of Trinidad, B.W.I . Bulletin of the U.S. National Museum 215, 61-82.

Bolli, H. M., Loeblich, A. R., Tappan, H., 1957. Planktonic foraminiferal families Hantkeninidae, Orbulinidae, Globorotaliidae and Globotruncanidae. In: Loeblich, A. R., Jr., Tappan, H., Beckmann, J. P., Bolli, H. M., Montanaro Gallitelli, E., Troelsen, J. C. (Eds.), Studies in Foraminifera. U.S. National Museum Bulletin 215, 3-50.

Bonaparte, C. L., 1835. Prodromus systematis ichthyologiae. Nuovi

Annali delle Scienze Naturali Bologna Series 1 2 (40), 181-196, 272-277.

Bonaparte, C. L., 1838. Selachorum tabula analytica. Nuovi Annali della Science Naturali Bologna 1(2), 195-214.

Bray, D. J., Gomon, M. F. (Eds.), 2020. Fishes of Australia. Museums Victoria and OzFishNet, accessed [12/2020], http://fishesofaustralia.net.au

Brönnimann, P., Bermudez, P. J., 1953. *Truncorotaloides*, a new foraminiferal genus from the Eocene of Trinidad, B.W.I. Journal of Paleontology 27, 817-820.

Cappetta, H., 1980a. Modification du statut générique de quelques espèces de sélaciens crétacés et tertiaires. Palaeovertebrata 10(1), 29-42.

Cappetta, H., 1980b. Les sélaciens du Crétacé supérieur du Liban. II, Batoïdes. Palaeontolographica Abteilung A 168 (5-6), 149-229.

Cappetta, H., 1981. Additions à la faune de sélaciens fossiles du Maroc. 1: Sur la présence des genres *Heptranchias*, *Alopias* et *Odontorhytis* dans l'Yprésien des Ouled Abdoun. Géobios 14, 563-575. https://doi.org/10.1016/S0016-6995(81)80137-4

Cappetta, H., 1982. Révision de *Cestracion duponti* Winkler, 1874 (Selachii, Batomorphii) du Bruxellien de Woluwe-Saint-Lambert (Eocène moyen de Belgique). Mededelingen Van De Werkgroep Voor Tertiaire En Kwartaire Geologie 19(4), 113-125.

Cappetta, H., 1986. Myliobatidae nouveaux (Neoselachii, Batomorphii) de l'Yprésien des Ouled Abdoun, Maroc. Geologica et Palaeontologica 20, 185-207.

Cappetta, H., 1987. Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii. Handbook of Palaeoichthyology. Gustav Fischer Verlag, Stuttgart.

Cappetta, H., 2012. Chondrichthyes (Mesozoic and Cenozoic Elasmobranchii, Teeth). Handbook of Palaeoichthyology. Verlag Friedrich Pfeil, München.

Cappetta, H., Case, G. R., 1975. Sélaciens nouveaux du Crétacé du Texas. Géobios 8(4), 303-307. https://doi.org/10.1016/S0016-6995(75)80028-3

Cappetta, H., Case, G. R., 2016. A selachian fauna from the middle Eocene (Lutetian, Lisbon Formation) of Andalusia, Covington County, Alabama, U.S.A. Palaeontographica Abteilung A 307, 43-103.

Cappetta, H., Corral, J.C., 1999. Upper Maastrichtian selachians from the Condado de Treviño (Basque-Cantabrian region, Iberian Peninsula). Estudios del Museo de Ciencias Naturales de Alava 14, 339-372.

Cappetta, H., Nolf, D., 1981. Les sélaciens de l'Auversien de Ronquerolles (Eocène Supérieur du bassin de Paris). Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie 81, 87-107.

Cappetta, H., Nolf, D., 2005. Révision de quelques Odontaspididae (Neoselachii, Lamniformes) du Paléocène et de l'Eocène du Bassin de la Mer du Nord. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Science de la Terre 75, 237-266.

Carrillo-Briceño, J. D., Aguilera, O. A., De Gracia, C., Aguirre-Fernández, G., Kindlmann, R., Sánchez-Villagra, M. R., 2016. An early Neogene elasmobranch fauna from the southern Caribbean (western Venezuela). Palaeontologia Electronica 10948074. https://doi.org/10.26879/664

Carrillo-Briceño, J. D., Maxwell, E., Aguilera, O. A., Sánchez, R., Sánchez-Villagra, M. R., 2015. Sawfishes and other elasmobranch assemblages from the Mio-Pliocene of the South Caribbean (Urumaco Sequence, northwestern Venezuela). PLoS One 10(10), e0139230. https://doi.org/10.1371/journal.pone.0139230

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. Palaeontographica Abteilung A 230 (4-6): 97-138.

Case, G. R., Borodin, P. D., 2000. A middle Eocene Selachian Fauna from the Castle Hayne Limestone Formation of Duplin County, North Carolina. Münchner Geowissenschaftliche Abhandlungen (A) 39, 17-32.

Case, G. R., Cappetta, H., 1990. The Eocene selachian fauna from the Fayum Depression in Egypt. Palaeontographica Abteilung A 212, 1-30.

Case, G. R., West, R. M., 1991. Geology and palaeontology of the Eocene Drazinda Shale Member of the Khirthar Formation, central western Pakistan, Part II: late Eocene fishes. Tertiary Research 12, 105-120.

Casier, E., 1946. La faune ichthyologique de l'Yprésien de la Belgique. Mémoires du Musée Royal d'Histoire Naturelle de Belgique 104, 1-267.

Cicimurri, D. J., 2010. On the dentition of *Meridiania convexa* Case (Myliobatoidea), an extinct early Eocene ray from the United States. Cainozoic Research 7(1-2), 99-107.

Cicimurri, D. J., Ebersole, J. A., Martin, G., 2020. Two new species of *Mennerotodus* Zhelesko, 1994 (Chondrichthyes: Lamniformes: Odontaspididae) from the Paleogene of the southeastern United States. Fossil Record 23, 117-140. https://doi.org/10.5194/fr-23-117-2020

Cicimurri, D. J., Knight, J. L., 2019. Late Eocene (Priabonian) elasmobranchs from the Dry Branch Formation (Barnwell Group) of Aiken County, South Carolina, USA. PaleoBios 36, 1-31.

Cizancourt, H., de, 1938. Nummulites et Assilines du flysch de Gardez et du Khost, Afghanistan oriental. In: Cizancourt, A. de, Cox, L. R. (Eds.), Contribution à l'étude des faunes tertiaires de l'Afghanistan. Mémoire de la Société Géologique de France (new series) 39, 5-28.

Cizancourt, H., de, 1946. Dénominations nouvelles pour *Assilina umbilicata* Mme de. Cizancourt et *Assilina subumbilicata* Mme de Cizancourt 1938. - C. R. Société Géologique de France 16, 335.

Cole, W. S., 1928. A foraminiferal fauna from the Chapapote formation in Mexico. Bulletins of American Paleontology 14(53), 1-33.

Compagno, L. J. V., 1973. Interrelationships of living elasmobranchs. Zoological Journal of the Linnaean Society 53 (Supplement 1), 15-61.

Compagno, L. J. V., 2005. Global checklist of living chondrichthyan fishes. In: Fowler, S. L., Cavanagh, R. D., Camhi, M., Burgess, G. H., Cailliet, G. M., Fordham, S. V., Simpfendorfer, C. A., Musick, J. A. (Eds.), Sharks, Rays and Chimaeras, the Status of Chondrichthyan Fishes. International Union for the Conservation of Nature, Gland, Switzerland, pp. 401-423.

Cope, E. D., 1871. Observations on the systematic relations of the fishes. The American Naturalist 5, 579-593. http://dx.doi.org/10.1086/270831

Cushman, J. A., 1925a. New foraminifera from the upper Eocene of Mexico. Contributions from the Cushman Laboratory for Foraminiferal Research 1, 4-9.

Cushman, J. A., 1925b. Some new Foraminifera from the Velasco Shale of Mexico. Contributions from the Cushman Laboratory for Foraminiferal Research 1, 18-23.

Cuvier, G., 1829. Le règne animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée, Edition 2. Chez Déterville, Paris. https://doi.org/10.5962/bhl.title.49223

Dames, W., 1883. Über eine tertiäre Wirbelthierfauna von der westlichen Insel der Birket-EI-Qrûn im Fajum (Aegypten). Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin 6, 129-153.

Davies, L. M., Pinfold, E. S., 1937. The Eocene Beds of the Punjab Salt Range. Palaeontologica Indica (new series) 24, 1-79.

Day, F., 1878. The fishes of India; being a natural history of the fishes known to inhabit the seas and fresh waters of India,, Burma, and Ceylon. Bernard Quaritch, London.

Deshayes, G. P., 1838. Description des coquilles fossiles recueillies en Crimée par M. de Verneuil, et observations générales à leur sujet. Mémoires de la Société Géologique de France 1(3), 37-69.

Diedrich, C. G., 2012. Eocene (Lutetian) shark-rich coastal paleoenvironments of the southern North Sea Basin in Europe: biodiversity of the marine Fürstenau Formation including early white and megatooth sharks. International Journal of Oceanography 2012, 565326. https://doi.org/10.1155/2012/565326

Douvillé, H., 1922. Révision des Orbitoïdes. Deuxième partie: Orbitoïdes du Danien et de l'Éocène. Bulletin de la Société Géologique de France 4(22), 55-100.

Dutheil, D. B., Merle, D., 1992. Les chondrichthiens elasmobranches de la Tuilerie de Gan (Pyrénées Atlantiques, France). Cossmanniana 1(2–4), 15-26.

Ebersole, J. A., Cicimurri, D. J., Stringer, G. L., 2019. Taxonomy and biostratigraphy of the elasmobranchs and bony fishes (Chondrichthyes and Osteichthyes) of the lower-to-middle Eocene (Ypresian to Bartonian) Claiborne Group in Alabama, U.S.A., including an analysis of otoliths. European Journal of Taxonomy 585, 1-274. https://doi.org/10.5852/ejt.2019.585

Fabiani, R., 1905. Studio geo-paleontologico dei Colli Berici: Nota preventiva. Atti R. Ist. Veneto Sci., Lettere ed Arti Venezia 64, 1797-1839.

Fowler, H. W., 1934. Descriptions of new fishes obtained 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. Proceedings of the Academy of Natural Sciences of Philadelphia 85 (for 1933), 233-367.

Froese, R., Pauly, D. (eds.). 2019. FishBase, version (12/2019). World Wide Web electronic publication, accessed [12/2020], www.fishbase.org

Garman, S. 1885. *Chlamydoselachus anguineus* Garm. - A living species of Cladodont shark. Bulletin of the Museum of Comparative Zoology at Harvard College 12(1), 1–35.

Garman, S., 1908. New Plagiostomia and Chismopnea. Bulletin of the Museum of Comparative Zoology, Harvard 51, 249-256.

Gill, T.,N., 1862. XXXII.-Analytical synopsis of the Order of Squali and revision of the nomenclature of the genera. Annals of the Lyceum of Natural History of New York 7(32), 367-408. http://dx.doi.org/10.1111/j.1749-6632.1862.tb00166.x

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

Gonzàlez-Barba, G., Theis, D., 2000. Asociaciones faunisticas de condrictios en el Cenozoico de la Peninsula de Baja California, Mexico. Profil 18, 1-4.

Gupta, S., Kumar, K., 2013. Ziphodont crocodilian and other biotic remains from the Paleocene-basal Eocene Kakara Formation, NW Sub-Himalaya: palaeogeographic and palaeoecologic implications. Himalayan Geology 34, 172-182.

Hay, O. P., 1902. Bibliography and catalogue of the fossil Vertebrata of North America. Bulletin of the United States Geological and Geographical Survey of the Territories 179, 1-868. https://doi.org/10.5962/bhl.title.20094

Huxley, T. H., 1880. On the application of the laws of evolution to the arrangement of the vertebrata and more particularly of the Mammalia. Proceedings of the Zoological Society of London 1880, 649-662.

Iserbty, A., De Schutter, P.J., 2012. Quantitative analysis of Elasmobranch assemblages from two successive Ypresian (early Eocene) facies at Marke, western Belgium. Geologica Belgica 15(3), 146–153.

Jaekel, O., 1894. Die eocänen Selachier vom Monte Bolca: ein Beitrag zur Morphogenie der Wirbelthiere / von Otto Jaekel. J. Springer, Berlin. https://doi.org/10.5962/bhl.title.8458

Jordan, D. S., 1898. Description of a species of fish (*Mitsukurina owstoni*) from Japan, the type of a distinct family of lamnoid sharks. Proceedings of the California Academy of Sciences (Series 3, Zoology) 1(6), 199-204.

Jordan, D. S., Evermann, B. W., 1896. The fishes of north and middle America, a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Part I. Bulletin of the United States National Museum 47, 1-1240. https://doi.org/10.5962/bhl.title.46755

Jordan, D. S., Gilbert, C. H., 1879. Notes on the fishes of Beaufort Harbor, North Carolina. Proceedings of the United States National Museum 1(55), 365-388. https://doi.org/10.5479/si.00963801.1-55.365.

Kajiura, S. M., Tricas, T. C. 1996. Seasonal dynamics of dental sexual dimorphism on the Atlantic stingray, *Dasyatis sabina.* Journal of Experimental Biology 199(10), 2297-2306.

Khare, S. K., 1976. Eocene fishes and arid turtles from the Subathu Formation, Beragua coal mine, Jammu and Kashmir. Journal of the Palaeontological Society of India 18, 36-43.

Kriwet, J., Benton, M. J., 2004. Neoselachian (Chondrichthyes, Elasmobranchii) diversity across the Cretaceous-Tertiary boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 214(3), 181-194. http://dx.doi.org/doi:10.1016/j.palaeo.2004.02.049

Kumar, K., 1989. A report on the occurrence of microvertebrates in the Subathu Formation (Montian-early Lutetian) near Nilkanth, Garhwal Himalaya, Uttar Pradesh, India. Current Science 58, 743-746.

Kumar, K., Loyal, R. S., 1987. Eocene Ichthyofauna from the Subathu Formation, northwestern Himalaya, India. Journal of the Paleontological Society of India 32, 60-84.

Kumar, K., Pandey, P., Kulshreshtha, S. K., Bhattacharya, D., Bhattacharya D., 2017. First record of Vertebrate fauna from Bandah Formation (middle Eocene) of the Jaisalmer Basin, Western Rajasthan, India. Indian Journal of Geoscience 71, 635-644.

Kumar, K., Pandey, P., Bajpai, S., Bhattacharya, D., Bhattacharya D., 2020. Middle Eocene (Bartonian) vertebrate fauna from Bandah Formation, Jaisalmer Basin, Rajasthan, Western India. Historical Biology. https://doi.org/10.1080/08912963.2020.1776708

Kumar, K., Rana, R. S., Singh, H., 2007. Fishes of the Khuiala Formation (early Eocene) of the Jaisalmer Basin, Western Rajasthan, India. Current Science 93, 553-559.

Last, P. R., Naylor, G. J. P., Mabel Manjaji-Matsumoto, B. 2016. A revised classification of the family Dasyatidae (Chondrichthyes, Myliobatiformes) based on new morphological and molecular insights. Zootaxa 4139(3), 345-368. http://dx.doi.org/10.11646/zootaxa.4139.3.2

Leidy, J., 1877. Description of vertebrate remains, chiefly from the Phosphate Beds of South Carolina. Journal of the Academy of Natural Sciences of Philadelphia 8, 209-261.

Leriche, M., 1942. Contribution à l'étude des faunes ichthyologiques marines des terrains tertiaires de la Plaine Côtière Atlantique et du centre des Etats-Unis. Les synchronismes des formations tertiaires des deux côtés de l'Atlantique. Mémoires de la Société géologique de France 45(2-4), 1-110.

Lesueur, C. A., 1818. Description of several new species of North American fishes. Journal of the Academy of Natural Sciences of Philadelphia 1(1), 222-235. https://doi.org/10.5479/si.00963801.84.235

Lesson R. P., 1831. Poissons. In: Duperrey L.I. (Ed.), 1826–1830. Voyage autour du Monde, exécuté par Ordre du Roi, sur la Corvette de la Majeste, La Coquille, pendant les anneés, 1822, 1823, 1824 et, 1825: Arthus Bertrand, Paris, pp. 66-238.

Linck, H. F., 1790. Versuch einer Eintheilung der Fische nach den Zähnen. Magazin für das Neueste aus der Physik und Naturgeschichte 6(3), 28-38.

Marramà, G., Carnevale, G., Englebrecht, A., Claeson, K. M., Zorzin, R., 2018b. A synoptic review of the Eocene (Ypresian) cartilaginous fishes (Chondrichthyes: Holocephali, Elasmobranchii) of the Bolca Konservat-Lagerstätte, Italy. Paläontologische Zeitschrift, 92(2), 283-313. https://doi.org/10.1007/s12542-017-0387-z

Marramà, G., Carnevale, G., Naylor, G. J., Varese, M., Guisberti, L., Kriwet, J., 2020. Anatomy, taxonomy and phylogeny of the Eocene guitarfishes from the Bolca Lagertatten, Italy, provide new insights into the relationships of the Rhinopristiformes (Elasmobranchii: Batomorphii). Zoological Journal of the Linnaean Society 2020, zlaa125. https://doi.org/10.1093/zoolinnean/zlaa125

Marramà, G., Englebrecht, A., Mörs, T., Reguero, M., Kriwet, J., 2018a. The southernmost occurrence of *Brachycarcharias* (Lamniformes, Odontaspididae) from the Eocene of Antarctica provides new information about the paleobiogeography and paleobiology of Paleogene sand tiger sharks. Rivista Italiana di Paleontologia e Stratigrafia 124(2), 283-297. https://doi.org/10.13130/2039-4942/9985

Menner, V. V., 1928. Les sélaciens du Paléógène de Manghyschlack, d'Emba et du versant oriental d'Oural. Bulletin de la Société Impériale des Naturalistes de Moscou, Section Géologique 6(3-4), 292-338.

Mishra, V.P., 1980. A new species of *Myliobatis* and some shark teeth from the middle Eocene of Kutch, Western India. Journal of the Palaeontological Society of India 23/24, 81–85.

Müller, A., 1999. Ichthyofaunen aus dem atlantischen Tertiär der USA. Leipziger Geowissenschaften 9-10, 1-360.

Müller, J., Henle, F. G.,J., 1837. Gattungen der Haifische und Rochen nach einer von ihm mit Hrn. Henle unternommenen gemeinschaftlichen Arbeit über die Naturgeschichte der Knorpelfische. Berichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin, 111-118.

Müller, J., Henle, F. G. J., 1839. Systematische Beschreibung der Plagiostomen. Veit and Company, Berlin. https://doi.org/10.5962/bhl.title.6906

Murray, A. M., Cook, T. D., Attia, Y. S., Chatrath, P., Simons, E. L., 2010. A freshwater ichthyofauna from the late Eocene Birket Qarun Formation, Fayum, Egypt. Journal of Vertebrate Paleontology 30, 665-680. https://doi.org/10.1080/02724631003758060

Naylor, G. J. P., Caira, J. N., Jensen, K., Rosana, K. A. M., Straube, N., Lakner, C., 2012. Elasmobranch phylogeny, a mitochondrial estimate based on 595 Species. In: Carrier, J. C., Musick, J. A., Heithaus, R. M. (eds,), Biology of Sharks and their Relatives, Edition 2. CRC Press, Boca Raton, pp. 31–56.

Nelson, J. S., Grande, T. C., Wilson, M.V.H., 2016. Fishes of the World, fifth edition. John Wiley & Sons, Inc., Hoboken.

Nuttall, W. L. F., 1925. .XLVIII.-Two species of Eocene Foraminifera from India. *Alveolina elliptica* and *Dictyoconoides cooki*. Annals and Magazine of Natural History, Series 9 16(94), 378-388. https://doi.org/10.1080/00222932508633324

Nuttall, W. L. F., 1926a. The zonal distribution and description of the larger foraminifera of the middle and lower Kirthar Series (Middle Eocene) of parts of western India. Records of the Geological Survey of India 59, 115-164. https://doi.org/10.1017/S0016756800085472

Nuttall, W. L. F., 1926b. The Larger Foraminifera of the Upper Ranikot Series (Lower Eocene) of Sind, India. Geological Magazine 63(3), 112-121. https://doi.org/10.1017/S0016756800083850

Pandey, D. K., Chaskar, K., Case, G. R., 2018. Two fossil shark teeth from lower Eocene shales of the Khuiala Formation, Jaisalmer Basin, India. Journal of the Palaeontological Society of India 63, 155-161.

Péron, F., Lesueur, C. A., 1822. Description of a *Squalus*, of a very large size, which was taken on the coast of New Jersey. Journal of the Academy of Natural Sciences of Philadelphia 2 (1), 343-352.

Priem, F., 1905. Sur des poissons fossiles de l'Éocène moyen d'Égypte. Bulletin de la Société géologique de France 4, 633-641.

Priem, M. F., 1909. Note sur les poissons fossiles des phosphates de Tunisie et d'Algérie. Extrait du Bulletin de la Société Géologique de France 4(9), 315-324.

Rafinesque, C. S., 1810a. Caratteri di alcuni nuovi generi e nuove specie di animali e pinate della Sicilia, con varie osservazioni sopra i medisimi, lère partie 1, 3-69.

Rafinesque, C.S., 1810b. Indice d'ittiologia siciliana; ossia, catalogo metodico dei nomi latini, italiani, e siciliani dei psci, che si rinvengono in Sicilia disposti secondo un metodo naturale e seguito da un appendice che contiene la descrizione di alcu. ni nuovi pesci siciliani. Presso Giovanni del Nobolo, Messina. https://doi.org/10.5962/bhl.title.58965

Rai, J., Singh, A., Gulati, D., 2014. Bartonian age calcareous nannofossil biostratigraphy of Tanot well-1, Jaisalmer Basin and its implications. Journal of the Palaeontological Society of India 59(1), 29-44.

Raju, D. S .N., 2018. Paleogene stratigraphy of India: an overview. In: Bajpai, S., Tripathi, S. C., Prasad, V. (Eds.), The Indian Paleogene. Springer International Publishing AG, Gewerbestrasse, Switzerland, pp. 1-89.

Rajkumari, P., Prasad, G. V. R., 2020. New chondrichthyan fauna from the Palaeogene deposits of Barmer District, Rajasthan, western India: Age, palaeoenvironment and intercontinental affinities. Geobios 58, 55-72. https://doi.org/10.1016/j.geobios.2019.11.002

Rana, R. S., Kumar, K., Loyal, R. S., Sahni, A., Rose, K. D., Mussell, J., Singh, H., Kulshreshtha, S. K., 2006. Selachians from the early Eocene Kapurdi Formation (Fuller's Earth), Barmer District, Rajasthan, India. Journal of the Geological Society of India 67, 509-522.

Rana, R. S., Kumar, K., Singh, H., 2004. Vertebrate fauna from the subsurface Cambay Shale (Lower Eocene), Vastan Lignite Mine, Gujarat, India. Current Science 89, 1026-1033.

Rana, R. S., Kumar, K., Singh, H., 2005. Lower vertebrates from the Late Palaeocene–Earliest Eocene Akli formation, Giral Lignite Mine, Barmer District, Western India. Current Science 89, 1606-1612.

Reinecke, T., Moths, H., Grant, A., Breitkreuz, H., 2005. Die Elasmobranchier des norddeutschen Chattiums, insbesondere des Sternberger Gesteins (Eochattium, Oligozän). Palaeontos 8: 1-135.

Roissy, F., 1805. Histoire naturelle générale et particulière des Mollusques; livre faisant suite aux œuvres de Buffon, et partie du cours complet d'Histoire naturelle rédigé par C. S. Sonnini. Paris, Dufart. https://doi.org/10.5962/bhl.title.51804

Rozlozsnik, P., Harpe, P., de la, 1926. Matériaux pour servir à une monographie des Nummulines et Assilines. D'après les manuscrits inédits de Prof. Philippe de La Harpe. Magyar Királyi Földtani Intézet évkönyve 27(1), 1-102.

Rüppell, W. P. E. S., 1835-1838. Neue Wirbeltiere zu der Fauna von Abyssinien gehörig. Fische des Rothen Meeres. Schmerber, Frankfurt am Main. https://doi.org/10.5962/bhl.title.53778

Sahni, A., Mehrotra, D. K., 1981. The elasmobranch fauna of coastal Miocene sediments of peninsular India. Biological Memoirs Lucknow 5, 83-121.

Sahni, A., Mishra, V. P., 1975. Lower Tertiary vertebrates from Western India. Monograph of the Palaeontological Society of India 3, 1-48.

Sahni, A., Batra, R. S., Bhatia, S. B., 1984. Vertebrate assemblage from the Upper Subathu (Middle Eocene) of the Bilaspur area, Himachal Pradesh, India. Proceedings of the 10th Indian Colloquium of Micropaleontology and Stratigraphy, 357-368.

Salame, I., Asan, A., 2019. A new *Odontorhytis* species (Chondrichthyes) from the Middle Eocene of Elgedida mine, Bahariya oasis, Egypt. Egyptian Journal of Geology 63, 407-415.

Sambou, B. S., Hautier, L., Sarr, R., Tabuce, R., Lihoreau, F., Thiamb, M., Lebrun, R., Martin, J. E., Cappetta, H., Adnet, S., 2020. Contribution to the reappraisal of the mid Paleogene ichtyofauna of Western Africa with three new enigmatical elasmobranchs from Thanetian–Lutetian of Senegal. Annales de Paléontologie 106, 102400. http://doi.org/10.1016/j.annpal.2020.102400

Samonds, K. E., Andrianavalona, T. H., Wallett, L. A., Zalmout, I. S., Ward, D. J., 2019. A Middle-late Eocene neoselachian assemblage from nearshore marine deposits, Mahajanga Basin, northwestern Madagascar. PLoS ONE 14(2), e0211789. http://doi.org/10.1371/journal.pone.0211789

Shepard, C., Brenner, J., Goodin, K. L., Ames, K. W., 2018. Chapter 5: Ecological Resilience Indicators for Oyster Ecosystems. In: Goodin, K. L., Faber-Langendoen, D., Brenner, J., Allen, S. T., Day, R. H., Congdon, V. M., Shepard, C., Cummings, K. E., Stagg, C. L., Gabler, C. A., Dunton, K. H., Ruzicka, R. R., Semon-Lunz, K., Reed, D., Ames, K. W., Love, M. (Eds.), Ecological Resilience Indicators for Five Northern Gulf of

Mexico Ecosystems. NatureServe, Arlington, VA. 40 pages.

Singh, N. P., 1976. Micropalaeontological control in subsurface Tertiary sequence of Jaisalmer Basin, Western Rajasthan, India. Proceedings of the 6th Indian Colloquium Micropalaeontology Stratigraphy, 259-278.

Singh, N. P., 1984. Addition to the Tertiary biostratigraphy of Jaisalmer Basin. Petroleum Asia Journal 2(1), 106-128.

Singh, N. P., 1996. Mesozoic-Tertiary biostratigraphy and biogeochronological datum planes in Jaisalmer Basin, Rajasthan. In: Pandey, J., Azmi, R. J., Bhandari, A., Deva, A. (Eds.), Proceedings of the 15th Indian Colloquium of Micropaleontology and Stratigraphy 1996, 63-89.

Singh N. P., 2003. Contribution of biostratigraphic studies in stratigraphic evaluation of west Rajasthan shelf. Gondwana Geology Magazine Special Volume 6, 79-104.

Singh, N. P., 2007. Cenozoic lithostratigraphy of the Jaisalmer Basin, Rajasthan. Journal of the Palaeontological Society of India 52(2), 129-154.

Singh, S. N., 1971. Planktonic Foraminifera in Eocene Stratigraphy of Rajasthan. Proceedings of the 2nd Planktonic Conference, Roma, 1169-1181.

Souverein, P., Stoel, P. B., 1995. Fossiele haaietanden uit het Tertiair van Cadzand. Grondboor en Hamer 49(3/4), 51-53.

Sowerby, J., 1840. Systematic list of organic remains, Appendix to Grant, C. W., Memoir to illustrate a geological map of Cutch. Transactions of the Geological Society of London. 2(5), 327-329.

Stromer, E., 1910. Reptilien- und Fischreste aus dem marinen Alttertiär von Südtogo (Westafrika). Monatsbericht der deutschen geologischen Gesellschaft 62(7), 478-505.

Strougo, A., Cappetta, H., Elnahas, S. A., 2007. Remarkable Eocene ichthyofauna from the ElGedida glauconitic sandstone, Bahariya oasis, Egypt, and its stratigraphic implications. MERC Ain Shams University, Earth Sciences Series 21, 81-98.

Tabuce, R., Adnet, S., Cappetta, H., Noubhani, A., Quillevéré, F., 2005. Aznag (bassin d'Ouarzazate, Maroc), nouvelle localité à sélaciens et mammifères de l'Eocène moyen (Lutétien) d'Afrique. Bulletin de la Société géologique de France 176, 381-400. http://doi.org/10.2113/176.4.381

Tanaka, T., Fujita, Y., Morinobu, S., 2006. Fossil shark teeth from the Namigata Formation in Ibara City, Okayama Prefecture, Central Japan and their biostratigraphical significance. Bulletin of the Mizunami Fossil Museum 33, 103-109.

Underwood, C. J., Gunter, G. C., 2012. The shark *Carcharhinus* sp. from the middle Eocene of Jamaica and the Eocene record of *Carcharhinus*. Caribbean Journal of Earth Science 44, 25-30.

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. Proceedings of the Geologists' Association 122, 47-66. http://doi.org/10.1016/j.pgeola.2010.09.004

Van den Eeckhaut, G., De Schutter, P., 2009. The elasmobranch fauna of the Lede Sand Formation at Oosterzele (Lutetian, middle Eocene of Belgium). Palaeofocus 1, 1-57.

Verbeek, R. D. M., 1871. Die Nummuliten des Borneo-Kalksteines. Neues Jahrbuch für Mineralogie und Geologie B9, 1-14.

Verbeek, R. D. M., 1880. Geologische Notizen über die Inseln des Niederländisch-Indischen Archipels im Allgemeinen, und über die fossilführenden Sumatra's im Besonderen. Palaeontographica. 1880(9), 7-28.

Verbeek, R. D. M., 1891. Voorlopig bericht over den Nummulieten, Orbitoiden en Alveolinen van Java, en over den ouderdom der gesteenten waarin zij optreden. Natuurkundig tijdschrift voor Nederlandsch Indië, 51(12), 101-139.

Villalobos-Segura, E., Underwood, C. J., 2020. Radiation and divergence times of Batoidea. Journal of Vertebrate Paleontology, e1777147, 1-11. http://doi:10.1080/02724634.1777147

Voigt, M., Weber, D., 2011. Field Guide for Sharks of the Genus *Carcharhinus*. Verlag Dr. Friedrich Pfiel, München.

Ward, D. J., Wiest, R. L., 1990. A checklist of Palaeocene and Eocene sharks and rays (Chondrichthyes) from the Pamunkey Group, Maryland and Virginia, USA. Tertiary Research 12(2), 81-88.

White, E. I., 1926. Eocene fishes from Nigeria. Bulletin of the Geological Survey of Nigeria 10, 1-82. https://doi.org/10.1093/oxfordjournals.afraf.a100500

White, E. I., 1931. The vertebrate faunas of the English Eocene: Vol. 1. From the Thanet Sands to the Basement Bed of the London Clay. British Museum (Natural History), London. https://doi.org/10.1017/S0016756800095820

White, E. I., 1934. Fossil fishes of Sokoto province. Bulletin of the Geological Survey of Nigeria 14, 1-78.

White, E. I., 1955. Notes on African Tertiary sharks. Bulletin of the Geological Survey of Nigeria 5(3), 319-325.

White, E. I., 1956. The Eocene fishes of Alabama. Bulletins of American Paleontology 36, 123-150.

Whitley, G. P., 1929. Additions to the check-list of the fishes of New South Wales. No. 2. Australian Zoologist 5(4), 353-357. https://doi.org/10.5962/bhl.title.21645

Whitley, G. P., 1934. Notes on some Australian sharks. Memoirs of the Queensland Museum 10(4), 180-200.

Winkler, T. C., 1873. Deuxième mémoire sur des dents de poissons fossiles du terrain bruxellien. Archives du Musée Teyler 4(1),16-48.

Winkler, T. C., 1874. Mémoire sur des dents de poissons du terrain bruxellien. Archives du Musée Teyler 3, 285-304.