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PRIABONIAN SHARKS AND RAYS (LATE EOCENE: NEOSELACHII) FROM MINQAR TABAGHBAGH IN THE WESTERN QATTARA DEPRESSION, EGYPT

BY

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Abstract — A Priabonian (late Eocene) neoselachian fauna of sharks and rays is known from marine strata in the foothills of Minqar Tabaghbagh, near the southwestern corner of the Qattara Depression in the Western Desert of Egypt. Neoselachian remains were collected from the lower glauconitic shales and mudstones of the Daba'a Formation, which is a western equivalent of the Qasr El-Sagha Formation found in the eastern part of the Western Desert. Neoselachians studied here are macro-scale, collected on the surface, and known either from teeth or rostral remains. Taxonomic evaluation shows that the neoselachians belong to five orders, 11 families, 19 genera, and 24 species. The species are: *Hexanchus agassizi*, *Carcharias* sp., *Otodus* cf. *O. sokolowi*, *Brachycarcharias* cf. *B. twiggsensis*, *Macrorhizodus praecursor*, *Xiphodolamia serrata*, *Alopias alabamensis*, *Alopias* sp., *Abdounia* aff. *A. minutissima*, *Misrichthys stromeri*, *Carcharhinus* sp. 1, *Carcharhinus* sp. 2, *Galeocerdo* sp. 1, *Galeocerdo* sp. 2, *Negaprion frequens*, *Negaprion* sp., *Physogalus* sp., *Rhizoprionodon* sp., *Anoxypristis* sp., *Propristis schweinfurthi*, *Pristis lathami*, *Myliobatis* sp. 1, *Myliobatis* sp. 2, and an indeterminate sting ray spine.

Teeth of *Otodus* cf. *O. sokolowi* and *Macrorhizodus praecursor* are the most abundant remains recovered from the locality. Recovery of *Xiphodolamia serrata* confirms the late Eocene age of the faunal Minqar Tabaghbagh assemblage. *Xiphodolamia serrata*, previously known only from Priabonian late Eocene Tethyan deposits of central and north Africa and western Asia, is reported from Egypt for the first time.

Taxa recovered from the base of the Daba'a Formation have been reported from late Eocene Tethyan deposits of Iran, Syria, Jordan, Egypt, Morocco, Angola, Nigeria, Europe, and North America. The Tabaghbagh fauna is important stratigraphically because it enables surface and subsurface correlation of late Eocene sedimentary deposits across the Western Desert of Egypt, to the Arabian Peninsula and western Asia in the east, and to African sites farther to the west and south.

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INTRODUCTION

The Western Desert of Egypt has an extensive cover of Eocene sedimentary strata that are exceptionally well exposed along escarpments and terraces of valleys and large basins (depressions) that formed and evolved during the late Miocene through Pliocene and Pleistocene (Beadnell, 1905; Greenwood, 1972; Albritton et al., 1990). These strata have been a major source of Eocene vertebrate fossils for two centuries. Among these, Neoselachii (sharks and rays) are the most abundant and diverse group. More than a hundred species of sharks and rays are known from the late Eocene of Egypt, most of which come from sediments of Fayum and vicinity (Priem, 1897a, 1897b, 1899a, 1899b, 1905, 1907, and 1914; Dames, 1883 and 1888; Woodward, 1893; Stromer, 1903, 1905a and 1905b; Andrews, 1906; Fraas, 1907; Leriche, 1922; Weiler,1929; Case and Cappetta 1990; Gingerich, 1992; Strougo et al., 2008; Vliet and Abu el Khair, 2010; Underwood et al. 2011; Underwood and Ward, 2011; Murray et al., 2011; Adnet et al., 2011).

The purpose of this paper is to document a macro-scale neoselachian fauna from late Eocene bone-bearing beds exposed along the foothills of Minqar Tabaghbagh (Figs. 1 and 2) in the southwest corner of the Qattara Depression (Gaenslen et al. 1946; Shata, 1953; Vliet and Abu el Khair, 2010). Fossils studied here were obtained by surface prospecting during joint Egyptian Environmental Affairs Agency and University of Michigan Museum of Paleontology expeditions in 2009 and 2010. The new fauna is important for understanding taxonomic relationships, and for understanding the stratigraphic and paleogeographic distribution of sharks and rays from western and southwestern Asia across Egypt to northern and central Africa.

GEOLOGY AND STRATIGRAPHY

The fauna described here was collected from an eight-meter thick interval of glauconite and glauconitic shale and sand at the base of Minqar Tabaghbagh that is similar to the base of the Daba'a Formation described by Norton (1967). El

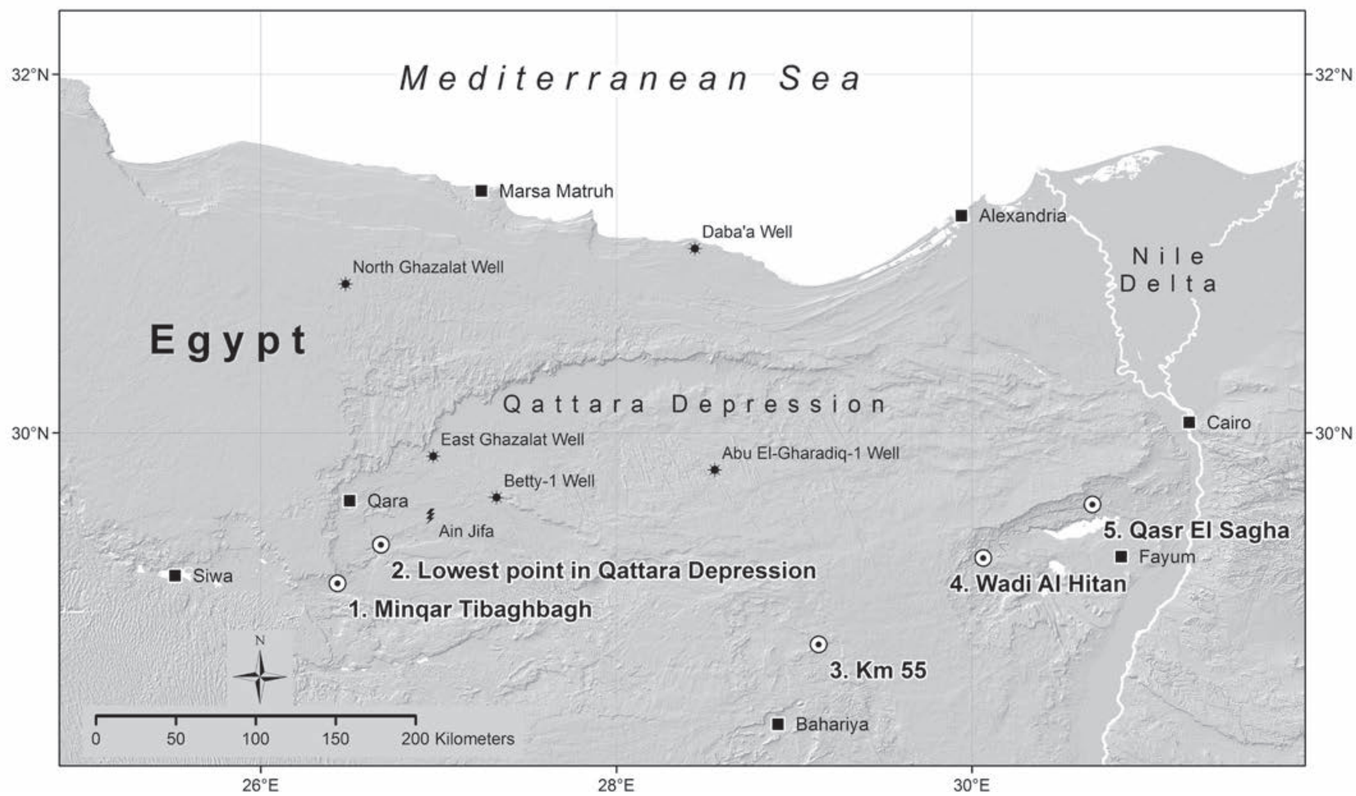

FIGURE 1 — Map of northern Egypt showing the location of Minqar Tabaghbagh and the corresponding late Eocene fossil locality (locality 1) producing the neoselachians described here. Locality 1 is 95 km east of Siwa Oasis and 60 km south of Qara Oasis, at the southwestern end of the Qattara Depression in the Western Desert of Egypt. Localities are numbered from west to east. **1**, Minqar Tabaghbagh (Shata, 1953; Vliet and Abu el Khair, 2010). **2**, lowest point of the Qattara Depression (Anonymous, 1982). **3**, Km 55 locality near the highway between Bahariya and Wadi Al Hitan (Adnet et al., 2011). **4**, Wadi Al Hitan (Case and Cappetta, 1990; Underwood et al., 2011; and Underwood and Ward, 2011). **5**, Qasr el-Sagha (Stromer, 1905; Andrews, 1906; Case and Cappetta, 1990, Murray et al., 2011, and Underwood et al., 2011). All localities produced neoselachian teeth and marine mammal remains. Some boreholes and wells in the Western Desert that have Daba'a Formation in the subsurface are labeled on the map.

FIGURE 2 — Glauconitic shale and sand in the lower part of the upper Eocene Daba'a Formation at the foot of Minqar Tabaghbagh. **A**, greenish and iron-stained beds that produced many neoselachian teeth and skeletons of marine mammals. **B**, scattered teeth of *Otodus* cf. *O. sokolowi* on the surface of the glauconitic shale at the foot of Minqar Tabaghbagh. The teeth of this species are the most common neoselachian remains at localities 1 and 2 of Figure 1. This is the actual distribution of the teeth on the surface when they were found, with no disturbance or alteration of the image. All teeth of this specimen were left in the field for further assessment.

Ramly (1967) illustrates this too in his geological cross-section connecting Qara Oasis and Sitra Lake. The glauconitic sand and shale facies appears to be continuous laterally in an east-west direction (Shata, 1953; Albritton et al, 1990). Albritton et al. (1990) stated that the Daba'a Formation is predominantly clastic in origin and contains calcareous sandstone and sandy limestone, and is a lateral equivalent of the Qasr el-Sagha Formation farther to the east. Marine vertebrate fossils of the same age and farcies were also collected from several localities near the lowest point of the Qattara Depression (Fig. 1, point 4 on the map) as published informally by Slaughter and Gillette (in *Science Digest*, December 1982).

The late Eocene-Oligocene Daba'a Formation (Norton, 1967) and/or its lateral equivalent was recognized from subsurface cores at the Daba'a-I well in the northern part of the Western Desert (Fig. 1). At the type section, the formation consists of a several hundred meters of thick marine shales with occasional carbonate and sandstones. The base of the Daba'a Formation rests unconformably on the middle Eocene nummulitic limestone of the Apollonia Formation, which is equivalent to the Wadi El-Rayan Series in the Fayum region. The top of the Daba'a Formation is conformably or unconformably capped by the early Miocene Moghara and Mamura formations (Hantar, 1990).

The Daba'a Formation is exposed in the foothills of Minqar Tabaghbagh and two kilometers farther south at a prominent local hill known as Qaret Gehannam (this locality has nothing to do with Qaret Gehannam nor with the Gehannam Formation known in Fayum), where it is 64 meters thick (Shata, 1953). Shata reported abundant shark teeth weathering out from a dark shale here. According to Shata (1953), the upper Eocene shale of the Minqar Tabaghbagh section is capped by a thick band of glauconitic sandstone and marl with abundant Eocene nautiloids, echinoids, and gastropods, followed directly by a yellowish brown and green shale beds of Miocene age. Shata's 1953 lithological and faunal descriptions certainly refer to the same level that has produced marine vertebrates reported by Vliet and abu el Khair (2010) and the shark and ray teeth collected and discussed here (Fig. 2A,B).

Sheikh and Faris (1985) studied calcareous nannoplankton and planktonic foraminiferans from the Daba'a Formation in three boreholes from the Western Desert (north Ghazalat-1, Daba'a-I, and Mubarak-3). Their study showed that the basal shale and clay of the Daba'a Formation is upper Eocene in age as indicated by the existence of calcareous nannoplankton zone NP 21 and planktonic foraminiferal zones P15-P17 (see also Said 1990: 467-468). Marzouk (2004) studied the calcareous nannoplanktonic zonation of the Daba'a Formation in Abu Gharadig Oil Field in the Western Desert and found that the lower part is purely late Eocene in age, ranging between NP18-NP 20.

INSTITUTIONAL ABBREVIATION

CGM — Egyptian Geological Museum, Cairo (Egypt)

SYSTEMATIC PALEONTOLOGY

Systematic organization and taxonomic nomenclature for the specimens described here follow Cappetta (1987).

Class CHONDRICHTHYES Huxley, 1872
Subclass ELASMOBRANCHII Bonaparte, 1838
Cohort SELACHII or EUSELACHII Hay, 1902
Subcohort NEOSELACHII Compagno, 1977
Superorder SQUALOMORPHII Compagno, 1973
Order HEXANCHIFORMES de Buen, 1926
Suborder HEXANCHOIDEI Garman, 1913
Family HEXANCHIDAE Gray, 1851

Genus *Hexanchus* Rafinesque,1810

Hexanchus agassizi Cappetta, 1976
Fig. 3A

Material.— CGM 60458 (one specimen).

Description.— CGM 60458 is a lower lateral tooth which is 4 mm high, 9 mm wide, and 1 mm thick lingolabially. Seven small cusps are preserved, which decrease gradually in height distally toward the oral cavity.

Discussion.— Modern *Hexanchus*, the cow shark or sixgill shark, may attain five meters in length. Teeth of *Hexanchus agassizi* are very rare at Tabaghbagh and other localities of middle and late Eocene age in the western desert of Egypt (Underwood et al., 2011). The main reason why they are rare is because *Hexanchus* is a deep pelagic shark that does not visit shallower water very frequently.

Order LAMNIFORMES Berg, 1958
Family ODONTASPIDIDAE Müller and Henle,1839

Genus *Carcharias* Rafinesque, 1810

Carcharias sp.
Fig. 3B-E

Material.— CGM 60453-60457 and 60465 (six specimens).

Description.— Most teeth obtained here are anterior teeth ranging between 11 and 30 mm in total height and between 10 and 17 mm in total width. The teeth have a long and slender central blade, and small lateral cusplets, mostly broken in the specimens figured in this report.

Discussion.— The genus goes back to the Cretaceous (Cappetta and Case, 1975a,b), however it has a wider distribution and diversity in the Paleogene (Cappetta, 1987). *Carcharias* seems to be very rare in the Eocene of Egypt.

Family OTODONTIDAE Glikman, 1964

Genus *Otodus* Jordan and Hannibal, 1923

Otodus cf. *O. sokolowi* (Jaekel, 1895)
Fig. 3F-BB

Material.— CGM 60201-60334 and 60502-60508 (141 specimens).

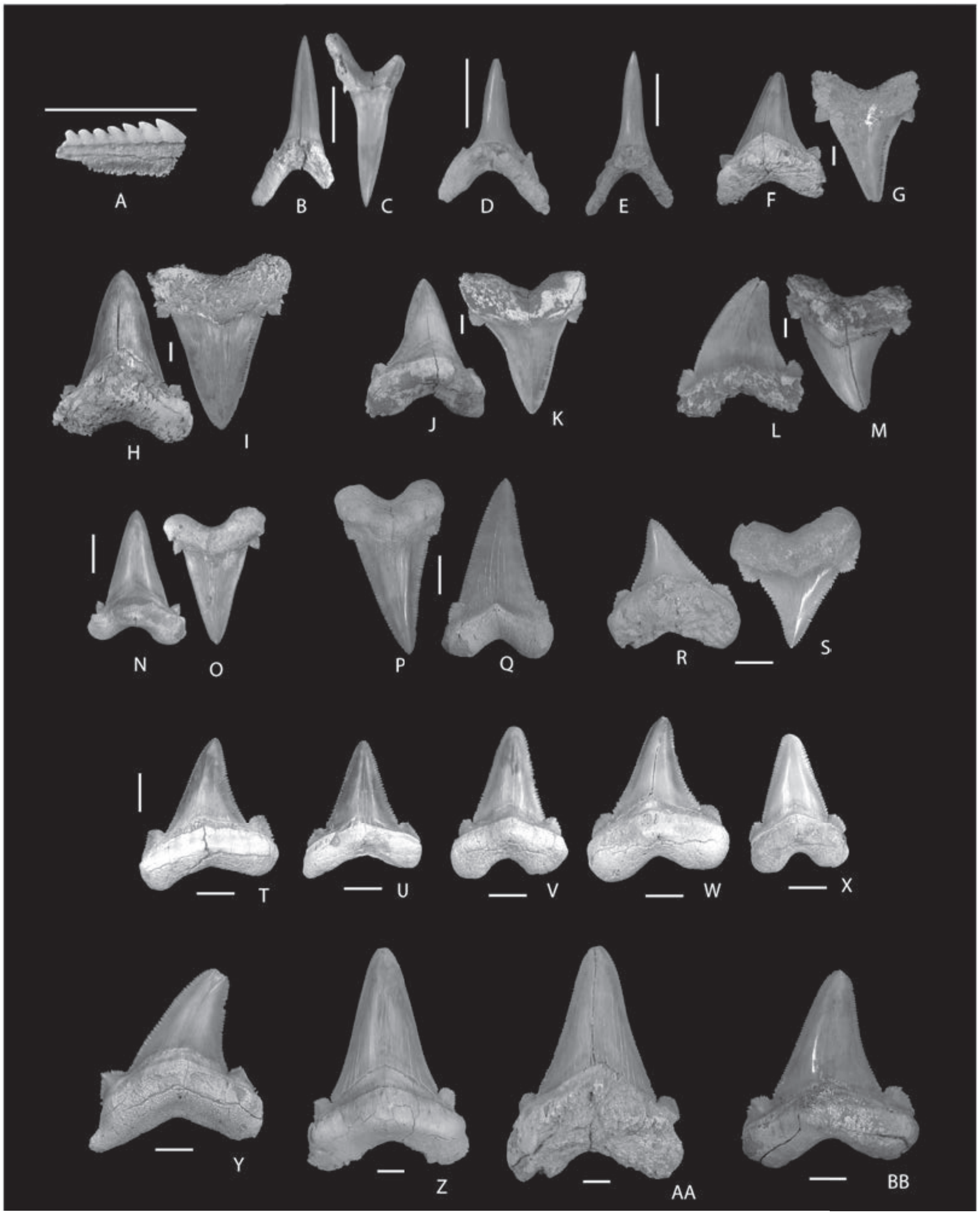

FIGURE 3 — Priabonian (late Eocene) shark teeth of the orders Hexanchiformes and Lamniformes coming from the lower Daba'a Formation exposed near the foot of Minqar Tabaghbagh. Scalebar is 1 cm for all specimens. **A, *Hexanchus* sp.**: CGM 60458, lateral tooth in lingual view. **B-E, *Carcharias* sp.**: B-C, 60455, anterior tooth in lingual and labial views; D, 60454, lateral tooth in a lingual view; E, 60456, anterior tooth in lingual view (lateral cusplets are broken). **F-BB, *Otodus* cf. *O. sokolowi***: F-G, CGM 60208, upper lateral tooth in lingual and labial views; H-I, 60201, lower anterior tooth in lingual and labial views; J-K, 60207, lower anterior tooth in lingual and labial views; L-M, 60211, lower anterior tooth in lingual and labial views; N-O, 60214, lower lateral tooth in lingual and labial views; P-Q, 60252, upper anterior tooth in lingual and labial views; R-S, 60328, upper posterior tooth in lingual and labial views; T, 60220, lower lateral tooth in lingual view; U, 60229, lower lateral tooth in lingual view; V, 60221, lower lateral tooth in lingual view; W, 60231, upper lateral tooth in lingual view; X, 60222, upper anterior tooth in lingual view; Y, 60503, lower lateral tooth in lingual view; Z, 60296, lower anterior tooth in lingual view; AA, 60299, lower anterior tooth in lingual view; BB, 60304, lower lateral tooth in lingual view.

Description.— Large teeth that may reach 97 mm in height and 75 mm in width. Central blades are large and bear fine and regular serrations along both cutting edges; small lateral cusplets are triangular in shape and bear serrations as well.

Discussion.— *Otodus sokolowi* is an extinct mackerel shark. Teeth of *Otodus*, also known as *Carcharocles*, are very common in many middle and late Eocene Tethyan deposits in North Africa, the Middle East, and North America. However, Minqar Tabaghbagh in the Western Desert of Egypt is the only place where *Otodus* cf. *O. sokolowi* teeth are extremely abundant (Fig. 2,B). Teeth of similar morphology are known from the middle Eocene of Syria (Siqneux, 1959), Jordan (Bender, 1968, Cappettta et al., 2000, Mustafa and Zalmout, 2002; Smadi et al., 2003; Mustafa et al., 2005), Egypt (Stromer, 1905A; Case and Cappetta, 1990; Vliet and Abu el Khair, 2010; Underwood et al., 2011), Morocco (Adnet et al., 2010), and Nigeria, Congo, and Angola (White, 1926; Dartevelle and Casier, 1942, 1943, 1949, 1959). In North America *Otodus* (*Carcharocles*) is known from Castle Hayne Formation of North Carolina (Bourdon and Chandler, 2007), the Irwinton Sand Member of the Barnwell Formation in Georgia (Case and Borodin, 2000), and was also reported from the middle Eocene of Alabama (White, 1956).

Family LAMNIDAE Müller and Henle, 1838

Genus *Macrorhizodus* (*Cosmopolitodus* = *Isurus*) Glikman, 1964

Macrorhizodus praecursor (Leriche, 1905)
Fig. 4A-V

Material.— CGM 60335-60407 (73 specimens).

Description.— Medium sized lamniform teeth with a triangular to sigmoidal central blade bearing smooth cutting edges. The teeth may reach 44 mm in total height anteriorly, and 30 mm in total width laterally. Anterior teeth generally have a height that is twice their width, the central blade is sigmoidal, and the roots are bilobed and rounded. Lateral and posterior teeth have height and width more or less equal, their central blade is triangular in shape, and the root is flattened labiolingually.

Discussion.— Teeth of *Macrorhizodus praecursor* are widely known from all middle and late Eocene Tethyan deposits of Europe, and North America. However, some late Eocene marine vertebrate localities in Egypt (Adnet et al., 2011) and Morocco (Adnet et al., 2010) lack this taxon, which is attributed to either environmental factors or the methods used to collect the sample studied.

Family CRETOXYRHINIDAE Glikman, 1958

Genus *Brachycarcharias* Cappetta and Nolf, 2005

Brachycarcharias cf. *B. twiggsensis* (Case, 1981)
Fig. 4W-X

Material.— CGM 60481-60482 (two specimens).

Description.— Both teeth are incomplete and weathered. CGM 60481 is a lateral tooth that is more than 21 mm high and more than 17 mm wide; the central blade is triangular in shape but incomplete as the tip is worn off. Two lateral cusps are preserved, one on each side of the central blade; these cusps are triangular in shape, low, and flat. The root is partially weathered anteriorly and posteriorly.

Discussion.— This species is known from the middle and late Eocene of the Western Desert of Egypt (Underwood et al., 2011; Adnet et al., 2011; Strougo et al., 2008; Case and Cappetta 1990; Stromer, 1905a). Case and Cappetta (1990) described this species from the Fayum as *Cretolamna twiggsensis*. Specimens figured in their monograph (Case and Cappetta, 1990: plate 3) show that teeth of this species have a lateral cusplet in addition to the lateral cusp. However, because the material from Tabaghbagh is incomplete, we were unable to assign these teeth directly to *Brachycarcharias twiggsensis*.

Family LAMNIDAE Müller and Henle, 1838, incertae sedis

Genus *Xiphodolamia* Leidy, 1877

Xiphodolamia serrata Adnet et al., 2009
Fig. 4Y-Z

Material.— CGM 60408 (one specimen).

Description.— Only one specimen was found, missing part of the tip of the root. Tooth height is 16 mm measured straight from the base of the root to the tip of the central blade. The root is oval in shape and measures 8 × 11 mm. The central blade is compressed mesiodistally and is very smooth and blunt lingually, while it has a sharp and finely serrated labial cutting edge. The central blade measures 15 mm long lingually, and 24 mm long labially along the serrated side.

Discussion.— *Xiphodolamia serrata* was recently named by Adnet et al. (2009). It is known only from Tethyan Priabonian faunas (Adnet et al., 2009 and 2010). This is the first record of the species in the Western Desert of Egypt. Careful review of the neoselachian faunas of the middle and late Eocene of the Fayum region, including Wadi Al Hitan (Underwood et al., 2011), shows that this species is absent from the Fayum sequence. However, presence of the species in surrounding basins will facilitate regional correlation between the late Eocene Iranian fauna to the east and Moroccan fauna to the west.

Family ALOPIIDAE Bonaparte, 1838

Genus *Alopias* Rafinesque, 1810

Alopias alabamensis White, 1956
Fig. 4AA

Material.— CGM 60473-60474, 60409, and 60464 (four specimens).

Description.— *Alopias alabamensis* teeth are small, measuring 11-12 mm in total height and 10-13 mm in total width. The central blade (crown) is triangular in shape, with sharp cutting edges on both sides; it is straight and flat labially, and slightly concave in lingually. The root-crown contact is slightly concave on the lingual surface of anterior teeth. It is broad at the base and extends mesially and distally along the root without developing

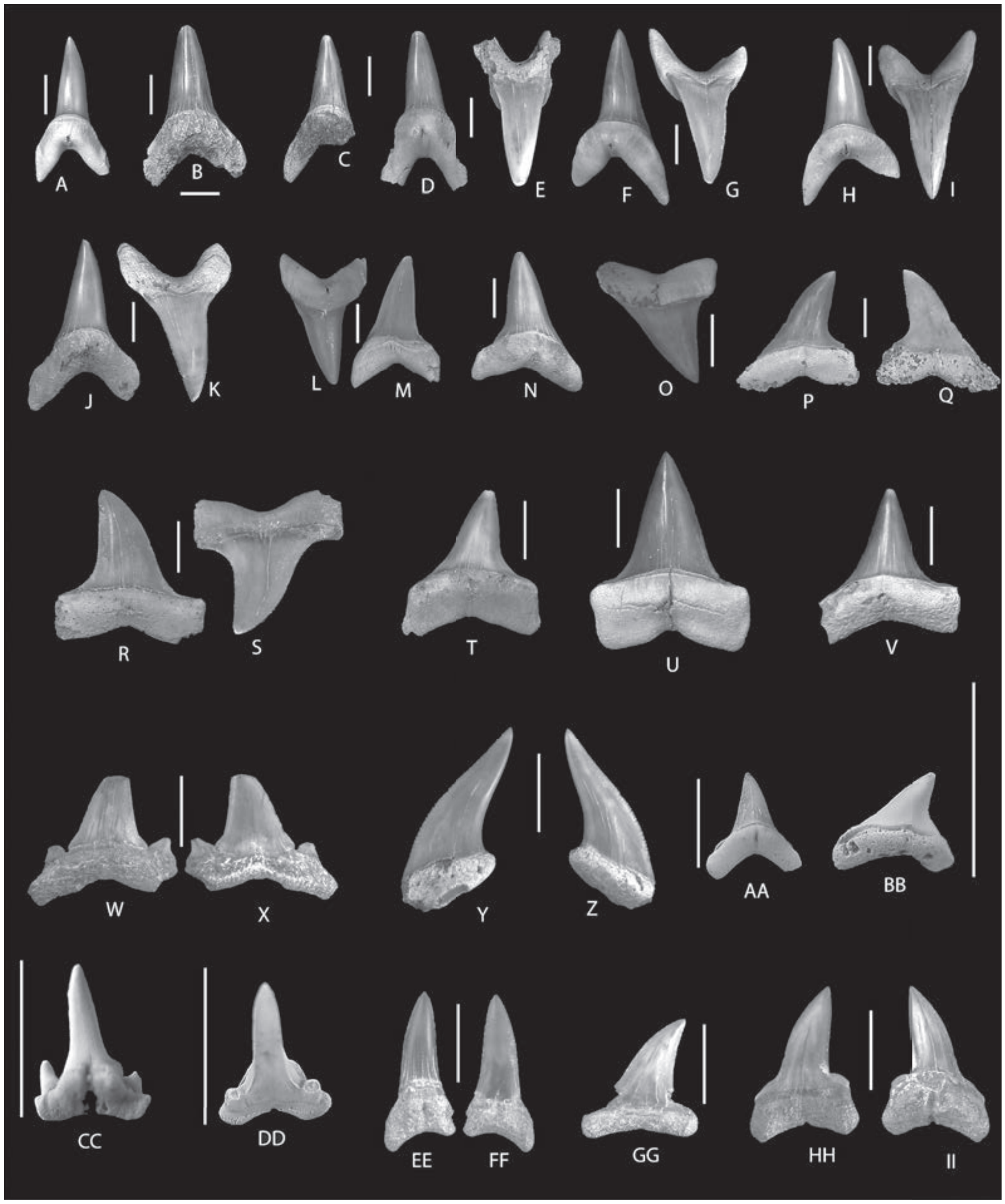

FIGURE 4 — Priabonian (late Eocene) shark teeth of the orders Lamniformes and Carcharhiniformes coming from the lower Daba'a Formation exposed near the foot of Minqar Tabaghbagh. Scalebar is 1 cm for all specimens. **A-V, *Macrorhizodus praecursor***: A, CGM 60360, upper most anterior tooth in lingual view; B, 60357, lower anterior tooth in lingual view; C, 60351, lower anterior tooth in lingual view; D-E, 60361, upper anterior tooth in lingual and labial views; F-G, 60353, upper anterolateral tooth in lingual and labial views; H-I, 60356, upper anterolateral tooth in lingual and labial views; J-K, 60354, upper anterolateral tooth in lingual and labial views; L-M, 60399, upper lateral tooth in lingual and labial views; N, 60358, upper tooth of more lateral position in lingual view; O, 60377, upper lateral tooth in lingual view; P-Q, 60393, upper posterolateral tooth in lingual and labial views; R-S, 60376, lower lateral tooth in lingual and labial view; T 60350, lower lateral tooth in lingual view; U, 60352, lower anterolateral tooth in lingual view; V, 60355, lower posterolateral tooth in lingual view. **W-X, *Brachycarcharias* cf. *B. twiggsensis***: CGM 60481, lower lateral tooth in lingual labial views. **Y-Z, *Xiphodolamia serrata***: CGM 60408, anterior tooth in distolabial and mesiolabial views. **AA, *Alopias alabamensis***: CGM 60473, upper anterolateral tooth in lingual view. **BB, *Alopias* sp.**: CGM 60472, lateral tooth in lingual view. **CC-DD, *Abdounia* aff. *A. minutissima***: CC, CGM 60475, anterior tooth in lingual view; DD, 60476, anterior tooth in labial view. **EE-II, *Misrichthys stromeri***: EE-FF, CGM 60467, lower anterior tooth in labial and lingual views; GG, 60466, upper anterolateral tooth in labial view; HH-II 60468, upper most anterolateral tooth in labial and lingual views.

any cusplets or denticles. The root-crown contact is straight in lateral teeth, where the blade is directed orally. Cutting edges of both lateral and anterior teeth run continuously without any interruption or indentations. The root has a prominent and robust apron lingually, and becomes thinner and flatter toward the end of each lobe.

Discussion.— Teeth described here are very close in size and morphology to those illustrated by Case and Cappetta (1990: plate 3). Similar species were collected and described from the middle and late Eocene of the western desert of Egypt (Stromer, 1903; Case and Cappetta, 1990; Underwood et al., 2011).

Alopias sp.
Fig. 4BB

Material.— CGM 60472 (one specimen).

Description.— *Alopias* sp. is only known from one lateral tooth. It measures 6 mm high and 6 mm wide. The cutting edge of the central blade is interrupted by a weak notch on the distal side.

Discussion.— Teeth of this species are different from *Alopias alabamensis* (White, 1956) in bearing a notch on the distal side of the central blade.

Order CARCHARHINIFORMES, Compagno, 1973
Family: CARCHARHINIDAE Jordan and Evermann, 1896

Genus *Abdounia* Cappetta, 1980

Abdounia aff. *A. minutissima* (Winkler, 1874)
Fig. 4CC-DD

Material.— CGM 60475-60480 (six specimens).

Description.— Teeth of this species measure between 9-10 mm in total height, and 6-8 mm in width. The teeth are concave toward the oral cavity. The central blade is conical in shape, slender, and connected to a smaller conical lateral cusp mesially and distally near the base of the crown. The root bears a strong apron lingually that is divided symmetrically by a furrow. Labially, the central blade has a convex surface, it is broad at its lower third with an occasional fine ridge-like striation running parallel to its main axis. The root is notched lingually where the lingual furrow reaches the base of the crown.

Discussion.— Teeth of *Abdounia* aff. *A. minutissima* from Minqar Tabaghbagh are very similar to those previously described from Wadi Al Hitan as *Abdounia* sp. by Case and Cappetta (1990) and those illustrated by Underwood et al. (2011). The genus ranges from the lower Eocene to upper Eocene (Cappetta, 1987).

Genus *Misrichthys* Case and Cappetta, 1990

Misrichthys stromeri Case and Cappetta, 1990
Fig. 4EE-II

Material.— CGM 60466-60468 (three specimens).

Description.— This species was described in detail from upper and lower teeth obtained from the Birket Qarun and Qasr el-Sagha formations (Case and Cappetta, 1990: 14-15, plates 5-7).

Discussion.— Only three teeth were obtained from Minqar Tabaghbagh, but teeth of *Misrichthys stromeri* are abundant 300 km to the east in the Fayum area from middle and late Eocene sediments.

The species is known from Egypt (Case and Cappetta, 1990; Underwood et al., 2011; Adnet et al., 2011) Jordan (Mustafa and Zalmout, 2002), and Morocco (Adnet et al., 2010). *Misrichthys* sp. from the middle Eocene Midawara Formation (Underwood et al., 2011) is the oldest and the smallest record of this genus.

Genus *Carcharhinus* Blainville 1816

Carcharhinus sp. 1
Fig. 5E-F

Material.— CGM 60459-60462 (four specimens).

Discussion.— Teeth of this species measure about 11 mm in height, and 11 to 12 mm wide. The central blade is triangular in shape and extends mesiodistally into shoulders; the shoulders are sharp and separated from the main blade by slightly developed notches. The roots have a shallow furrow in the middle of the lingual portion.

Discussion.— Teeth of *Carcharhinus* sp. 1 differ from those of *Carcharhinus* spp. of Case and Cappetta (1990), in having no serrations of any kind on their blades. They differ from *Carcharhinus* sp. or *Negaprion* sp. teeth described and figured in Adnet et al. (2011) from Km 55 in the Western Desert of Egypt in having either sharp cutting edges lacking any serrations or in having the shoulders dip mesially and distally, rather than being straight (fig. 3 in Adnet et al., 2011).

Carcharhinus sp. 2
Fig. 5G-H

Material.— CGM 60469-60471 (three specimens).

Description.— Teeth of this species are about 10 and 11 mm in height, and 13 mm wide. The central blade is spear-like with a curved end that forms a notch where it meets the lateral shoulders or heels. The root is furrowed by deep canal that exposes a foramina in the middle.

Discussion.— The main differences between *Carcharhinus* sp. 1 and *Carcharhinus* sp. 2 is the shape of the blade and the deep canal in the lingual face of the root.

Genus *Galeocerdo* Müller and Henle, 1838

Galeocerdo sp. 1
Fig. 5I

Material.— CGM 60483 (one specimen).

Description.— CGM 60483 is an anterolateral tooth from the Daba'a Formation that preserves most of the crown and root morphology. It is 10 mm high, 14 mm wide, and 3 mm thick labiolingually across the root, being generally flattened labiolingually. The crown is elevated, with a short triangular

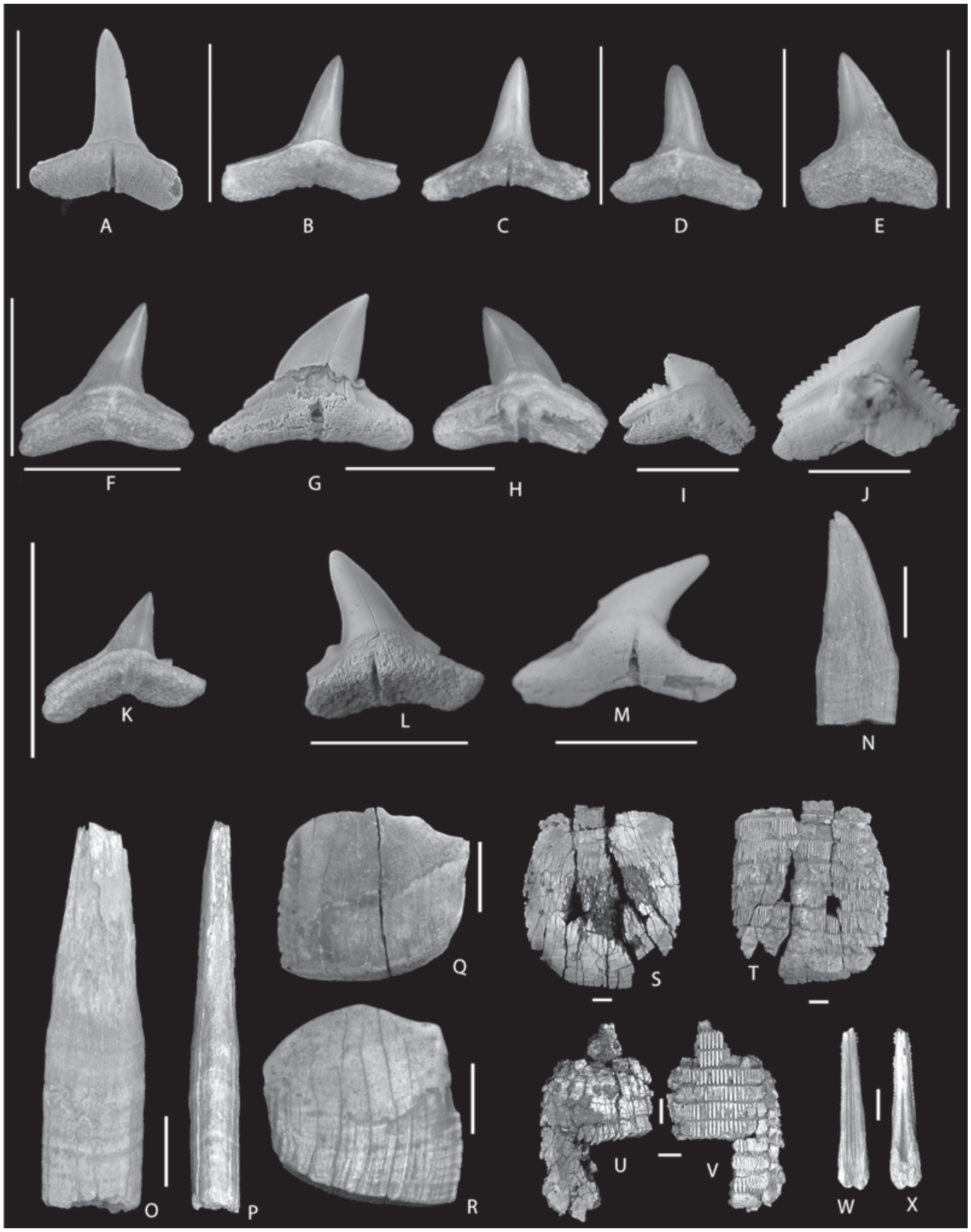

FIGURE 5 — Priabonian (late Eocene) shark teeth of the orders Carcharhiniformes, Rajaformes, and Myliobatiformes coming from the lower Daba'a Formation exposed near the foot of Minqar Tabaghbagh. Scalebar is 1 cm for all specimens. **A-D, *Negaprion frequens***: A, CGM 60441, upper anterior tooth in lingual view; B, 60443, lower lateral tooth in lingual view; C, 60444, lower anterolateral tooth in lingual view; D, 60445, lower lateroposterior tooth in lingual view. **E-F, *Carcharhinus* sp. 1**: E, CGM 60459, lateral tooth in lingual view; F, 60460, lateral tooth in lingual view. **G-H, *Carcharhinus* sp. 2**: G, CGM 60470, lateral tooth in lingual view; H, 60471, lateral tooth in lingual view. **I, *Galeocerdo* sp. 1**: CGM 60483, upper lateral tooth in lingual view. **J, *Galeocerdo* sp. 2**: CGM 60484, anterolateral tooth in lingual view. **K, *Rhizoprionodon* sp.**: CGM 60451, lateral tooth in lingual view. **L, *Negaprion* sp.**: CGM 60483, lateral tooth in lingual view. **M, *Physogaleus* sp.**: CGM 60485, lateral tooth in lingual view. **N, *Anoxypristis* sp.**: CGM 60490, rostral tooth in dorsal view. **O-P, *Pristis lathami***: CGM 60491, rostral tooth in dorsal and anterior views. **Q-R, *Propristis schweinfurthi***: Q, CGM 60492, rostral tooth in dorsal view; R, 60493, rostral tooth in dorsal view. **S-T, *Myliobatis* sp. 1**: CGM 60495, lower dental plate in dorsal and ventral views. **U-V, *Myliobatis* sp. 2**: CGM 60497, lower dental plate in dorsal and ventral views. **W-X, Stingray spine**: CGM 60488, in ventral and dorsal views.

central blade. The mesial side of the crown is convex, and the cutting edges are serrated mesially and distally (including the shoulders or heels). The distal shoulder possesses stronger serrations than the mesial shoulder. Mesial and distal ends of the central blade are finely serrated, and these serrations get stronger from the apex of the central blade toward the mesial end of the cutting edge. The central blade is separated from the distal shoulder by a strong notch. The root is elevated labially and lingually, and it constitutes most of the lingual side of the tooth, and almost half of the labial side. The lingual side of the root has a very weak furrow. Mesial and distal ends of the root have rounded or curved lobes.

Discussion.— This is one of two species of *Galeocerdo* preserved in the Daba'a Formation and represents the smaller of the two (larger samples needed to confirm this). *Galeocerdo* sp. 1 differs from the specimens of *Galeocerdo latidens* illustrated in Case and Cappetta (1990) in having very fine serrations or crenulations on the central cusp. Case and Cappetta (1990) mentioned a second species from the late Eocene El-Sagha Formation in their monograph and called it *Galeocerdo* sp. (Case and Cappetta, 1990: plate 5, figs 92-95). It differs from CGM 60483 in being larger, and in having weak serrations on the distal shoulder. The crown, labially and lingually, covers a large area of the tooth.

Teeth of *Galeocerdo* have previously been reported in Egypt by Stromer (1905a) and Priem (1897b). Vliet and Abu El-Khair (2010) listed *Galeocerdo* sp. from Minqar Tabaghbagh, along with other neoselachian species.

Galeocerdo sp. 2
Fig. 5J

Material.— CGM 60484 (one specimen).

Description.— CGM 60484 is the lateral tooth of a larger species of *Galeocerdo* from the foot of Minqar Tabaghbagh. It is 19 mm high, and more than 19 mm wide. The crown is more or less triangular in shape. The central blade is small and directed distally towards the oral cavity. Cutting edges are strongly serrated on both mesial and distal edges. The central blade is finely serrated as well, both mesially and distally. The mesial cutting edge runs straight from the mesial end of the crown to the apex, while the distal cutting edge is concave, forming a shoulder and making an angle with the central blade. A strong notch is present in the middle of the distal cutting edge.

Discussion.— *Galeocerdo* sp. 2 is different from *Galeocerdo* sp. 1 in being larger and in having stronger serrations, a straight mesial cutting edge, and a concave distal cutting edge.

Genus *Negaprion* Whitley, 1940

Negaprion frequens (Dames, 1883)
Fig. 5A-D

Material.— CGM 60410-60450 (41 specimens).

Description.— Teeth of *Negaprion frequens* are relatively small, ranging from 7 to 12 mm in total height, from 5 to 12 mm in total width (mesiodistally), and from 2 to 3 mm in lingolabial thickness in the middle of the root. Lower teeth generally have a slender cusp, while upper teeth have a triangular blade (Case and Cappetta, 1990). In the specimens figured here from Minqar Tabaghbagh, the lower most anterior teeth show a narrow root, and the more lateral teeth have wider roots.

Discussion.— Teeth of this species are best known from the Birket Qarun and Qasr el-Sagha formations of Wadi Al Hitan (Case and Cappetta, 1990; Underwood et al., 2011). Additional Egyptian material was reported from the Qasr El-Sagha Formation at Km 55 on the desert highway connecting Cairo and Bahariya (Adnet et al., 2011).

Negaprion frequens is also known from the middle and late Eocene outside Egypt. Teeth of this species have been reported from the middle Eocene of the Midra and Saila shales of Qatar (Casier, 1971); the late Eocene of Jordan (Cappetta et al., 2000; Mustafa and Zalmout, 2002); and the late middle Eocene to late Eocene of southwestern Morocco (Adnet et al., 2010).

Negaprion sp.
Fig. 5L

Material.— CGM 60463 (one specimen).

Description.— CGM 60463 is a medium-sized upper lateral tooth. It measures 11 mm high, 12 mm wide, and 12 mm thick lingolabially at the root center. The crown has a triangular central blade curved toward the rear, with smooth cutting edges and shoulders. However, the distal cutting edge possesses a diminutive and blunt low cusp. The mesial heel or shoulder makes an angle of 160° with the central blade. The labial side of the crown is flat, however its tip curves slightly labially. The root is asymmetrical around the vestigial canal on the lingual face.

Discussion.— This species could have been assigned easily to *Negaprion frequens*, however teeth of *Negaprion frequens* have more slender central blades and less robust roots than *Negaprion* sp.

Genus *Physogaleus* Cappetta, 1980

Physogaleus sp.
Fig. 5M

Material.— CGM 60485 (one specimen).

Description.— CGM 60485 is partially preserved, measuring 9 mm high, 14 mm wide, and 4 mm thick labiolingually at the middle of the root. The central blade is wide at the base, recurved, and tapering out toward the apex. Both mesial and distal shoulders are broken off and absent. The root is robust and show a strongs apron that is furrowed in the middle.

Discussion.— It is extremely difficult to assign this species to any known species because of the missing parts of the blades. Case and Cappetta (1990) illustrated some teeth of *Physogaleus* sp. that have serrations on both mesial and distal edges of the central blade (Case and Cappetta, 1990: plate 5).

Genus *Rhizoprionodon* Whitley, 1929

Rhizoprionodon sp.
Fig. 5K

Material.— CGM 60451-60452 (two specimens).

Description.— *Rhizoprionodon* sp. is small. CGM 60451 is 5 mm high, 8 mm wide, and 2 mm thick. The crown is has a triangular central blade connected to low heels. All cutting edges are sharp and unserrated. The mesial cutting edge is concave. The central blade is almost perpendicular to the distal cutting edge. The root extends mesiodistally, with a shallow lingual furrow in the middle.

Discussion.— *Rhizoprionodon* sp. seems to be rare in the late Eocene Daba'a Formation at Minqar Tabaghbagh. However, the species is very common in the Fayum area (Underwood et al., 2011).

Superorder BATOMORPHII Cappetta 1980
(= BATOIDEA Compagno, 1973)
Order RAJIFORMES Berg, 1940
Family PRISTIDAE Bonaparte, 1838

Genus *Anoxypristis* White and Moy-Thomas, 1941

Anoxypristis sp.
Fig. 5N

Material.— CGM 60490 (one specimen).

Description.— CGM 60490 is a complete and slightly weathered left rostral tooth. It is compressed dorsoventrally, pointed at the tip, and curves posteriorly. It is 30 mm high mediolaterally, 11 mm wide anteroposteriorly, and 4 mm thick dorsoventrally at the base where it joined the rostrum. The base has an oval cross-section. The medial third is square in shape and ringed with growth lines. The more lateral part of the tooth is more or less a flattened cone, slightly concave upward, that tapers to an apex. Anterior and posterior edges are bluntly convex and lack any grooves or gutters.

Discussion.— *Anoxypristis mucrodens* rostral teeth were reported from the middle and late Eocene of Fayum (Priem, 1905; Stromer, 1905; Case and Cappetta, 1990; Murray et al., 2011; Underwood et al., 2011). *Anoxypristis* sp. from Minqar Tabaghbagh is more compressed dorsoventrally than the teeth of *Anoxypristis mucrodens*. Rostral teeth of the living species *Anoxypristis cuspidata* of Latham (1794) are slightly different from the fossil tooth from Minqar Tabaghbagh (see Herman et al., 1997: plates 8-9).

Genus *Propristis* Dames, 1883

Propristis schweinfurthi Dames, 1883
Fig. 5Q-R

Material.— CGM 60492-60493 (two specimens).

Description.— Both cataloged specimens represent rostral teeth. CGM 60492 has 6 complete rostral teeth and fragments. The height of these ranges from 21 to 28 mm, the anterior-posterior length ranges from 23 to 30 mm, and the dorsoventral thickness ranges from 7 to 8 mm. The rostral teeth have rectangular to trapezoidal outlines, are compressed dorsoventrally, are thick basally (medially), and taper to thin blades (1mm) at the extreme lateral end. The base of each tooth is concave, with a lenticular cross-section. There is a groove that extends along the anterior surface to form a lip that overlaps the posterior end of the preceding tooth. Anterior cutting edges are shorter than the posterior ones, and they are angular to convex in shape with a barb sticking out in most of the specimens if it is not eroded. Posterior edges are normally convex without any interruption. The medial halves of all teeth preserve fine ridges running mediolaterally and growth rings running anteroposteriorly on both dorsal and ventral faces.

Discussion.— The type species *Propristis schweinfurthi* was based on isolated rostral teeth (Dames, 1883: 136-140, plate III) from the late Eocene beds exposed north of Birket Qarun in the Fayum region of Egypt. Since then many records of rostra and rostral teeth of this species have been recognized from middle and late Eocene deposits of Africa and North America (Case, 1981; Cappetta, 1987; Case and Bordin, 2000). The species is common in the middle and late Eocene of Egypt. Fraas (1907) reported a 2.15 m long rostrum of *Propristis schweinfurthi* from Fayum that was collected by R. Markgraf. Fraas concluded that there were 40 visible alveoli for rostral teeth on each side of the rostrum. Although there were only 3 rostral teeth associated with the rostrum (each approximately 21 mm high and 21 mm wide), Fraas stated that only 22 of these alveoli were filled with their counterparts. Fraas's assumption that there are only 22 teeth on the rostrum at the time the animal expired was based on the fine stippling on the front alveoli.

Case and Cappetta (1990) reported *Propristis schweinfurthi* from the middle and late Eocene of Fayum; Adnet et al. (2010) reported rostral teeth from both middle and late Eocene beds of southwest Morocco; and Underwood et al. (2011) recorded the species in all formations of the middle and late Eocene at Wadi Al-Hitan. Oral teeth have not yet been found in association with a rostrum, however Adnet et al. (2011) assigned oral teeth that are similar to those of *Rhinobatos* to ?*Propristis* sp.

Genus *Pristis* Latham, 1794

Pristis lathami Galeotti, 1837
Fig. 5O-P

Material.— CGM 60491 (one specimen). Some rostra associated with rostral teeth were observed and left in the field.

Description.— The only specimen at hand is a slightly weathered rostral tooth that is 53 mm long (mediolaterally) measured along the longest axis; 14 mm wide measured anteroposteriorly, and 7 mm thick measured dorsoventrally at the base of the crown. The proximal half of the tooth is thickest, and the tooth tapers distally to a much thinner 3 mm. The anterior edge of the tooth is thick and blunt, while the posterior edge is concave, a shallow gutter that runs from the base of the tooth to the distal end.

Discussion.— Rostral teeth of this species may reach 133 mm in total length, as measured on UMMP 101214 collected from the late Eocene of Wadi Al Hitan. The specimen is not related to *Anoxypristis* sp. because the posterior edge of the rostral tooth is concave while that of *Anoxypristis* is bluntly convex. *Pristis lathami* is known from almost complete rostra with variable lengths and variable numbers and configuration of rostral teeth.

Pristis lathami is known from lower and upper Eocene deposits in Africa and North America (see Cappetta, 1987). In Egypt the species is known from the Eocene of the Fayum and Bahariya regions (Stromer, 1905B; Case and Cappetta, 1990; Underwood et al., 2011; Murray et al., 2011; Adnet et al., 2011). The type specimen is known from a 42-cm long calcified cartilaginous rostrum from the Paris Basin (Galeotti, 1837). Casier (1949) recorded two additional rostra from the Eocene of the Paris Basin that measured 92 and 62 cm in extreme lengths. Cicimurri (2007) described a partial rostrum of *Pristis lathami* from the late Eocene of South Carolina, and also reviewed the fossil record of *Pristis lathami* in North America. Farther east, *Pristis lathami* is known from the Eocene of Qatar (Casier, 1971). It is also known from the middle and late Eocene of central Pakistan (Zalmout and Gingerich, personal observations).

Order MYLIOBATIFORMES sensu Compagno, 1973
Family MYLIOBATIDAE Bonaparte, 1838

Genus *Myliobatis* Cuvier, 1817

Myliobatis sp. 1
Fig. 5S-T

Material.— CGM 60494-60496 (three specimens).

Description.— CGM 60495 is a relatively complete lower dental plate. It is a lower toothplate because there is no bend or concavity in the basal surface (see Herman et al., 2000, to differentiate between upper and lower jaws of this genus). The toothplate has a median file of seven teeth in a row from front to back, flanked by one file of lateral teeth on each side. The occlusal surface is convex in the front two thirds and slightly concave in the posterior third, while the basal surface is flat. The toothplate is 90 mm long, 80 mm wide, 23 mm thick in the middle at the 5th tooth from the front, and 4-6 mm thick at the posterolateral corner. The median teeth reach a maximum of 11 mm in anteroposterior length, and measure between 69 and 74 mm in transverse width. Interlocking sutures are obscured on the occlusal surface of the toothplate, marked only by a thin line. Individual teeth are more discernable on the basal surface. Roots are polyaulacorhizous (fide Cappetta, 1987: 14). The lateral teeth are small and have rhombic to oval outlines. Each tooth is elongated anteroposteriorly, with a length of about 10 mm and a width of about 4 mm.

CGM 60494 includes a piece of a dental plate with three teeth from a median file, and CGM 60496 is a partial dental plate including four teeth from a median file. Both specimens resemble median teeth of CGM 60495 in size and morphology.

Discussion.— *Myliobatis* is diverse and widespread geographically in the Eocene of Egypt. *Myliobatis pentoni*, the first large taxon of the group to be described from Egypt, came from the Mokattam Limestone (Woodward, 1893). Woodward described material including an association of large upper and lower jaws, and reported the upper jaw to be 180 long and 135 mm wide, while the lower jaw is 160 mm long and 130 mm wide. This is almost twice the size of the lower tooth-plate of CGM 60494 from Minqar Tabaghbagh. In addition, the upper toothplate of Woodward has two files of small teeth lateral to the median file on each side, while the lower toothplate has three files of small teeth lateral to the median file on each side.

Stromer (1905b) described and measured several middle and late Eocene toothplates of *Myliobatis* from the vicinity of Cairo and Fayum, showing that this taxon is very diverse in the Eocene of Egypt. Case and Cappetta (1990) described another toothplate from the late Eocene Qasr El-Sagha Formation that seems to be half the size of our specimens here. Underwood et al. (2011) reported several teeth and toothplates from middle and late Eocene deposits in the vicinity of Fayum, concluding that these plates are common in the Qasr el-Sagha Formation.

Myliobatis sp. 2
Fig. 5U-V

Material.— CGM 60497 (one specimen).

Description.— CGM 60497 is the partially preserved lower dental plate of a medium-sized ray. The dental plate is slightly convex, with the anterior margin being a little thinner than the thickest part of the plate and the posterior margin tapering to a thin lamina. The anteroposterior length of the toothplate as preserved is 81 mm, and the width as preserved is 47 mm. The full width may have been as great as 62 mm. CGM 60497 preserves a median file of at least 11 teeth, each up to 8 mm in length, as measured anteroposteriorly on the occlusal surface, and 41 mm in width. The greatest height of median teeth is 18 mm. The right side of the dental plate shows two lateral files of smaller teeth and there is little or no room for a third. We expect the condition on the left side to have been the same. Teeth of the first lateral file are 8 mm long anteroposteriorly and 7 mm wide mediolaterally. The tooth root has three groves. The second file of lateral teeth is partially preserved; one nearly complete tooth measures 8 mm anteroposteriorly and 4 mm mediolaterally, with a base to occlusal surface height of about 4 mm.

The dental plate as a whole is lenticular in transverse cross-section. The occlusal surface is relatively smooth. The basal surface is straight anteroposteriorly rather than curved, and the roots are low and polyaulacorhizous.

Discussion.— The lower dental plate of *Myliobatis* sp. 2 is differs from that of *Myliobatis* sp. 1 in being smaller, in having a lenticular cross section, and in having an additional file of lateral teeth. The dental plate illustrated in Case and Cappetta (1990: plate 9, fig. 199-200) has a length/width ratio of 5:4, while in CGM 60497 this ratio appears to have been closer to 4:3.

FAMILY INDET.

Stingray spines
Fig. 5W-X

Material.— CGM 60468 and 60487-60489 (four specimens).

Description.— CGM 60488 is a nearly complete stingray spine that is missing its distal tip. The spine is 51 mm long. It has thick longitudinal ridges on the dorsal surface, and a convex ventral surface marked by a 21 mm long, and 2 mm deep groove. The cranialmost 14 mm of the spine is 10 mm wide, while the rest of the spine tapers to a width less than 4 mm. Barbs are small, and arranged on both lateral edges of the distal half of the spine.

Other Fishes

Barracuda jaws and puffer fish dental plates (CGM 60498) were found in association with the shark and ray teeth.

DISCUSSION

The late Eocene sharks and rays of Tabaghbagh are interesting for what they indicate about the diversity, age, and paleobiogeographic relationships of the Tabaghbagh fauna.

Diversity of the Tabaghbagh Fauna

The neoselachian fauna of Minqar Tabaghbagh includes five orders, and 24 species, identified from a collection of 304 identified teeth or spines. Most species are Carcharhiniformes (10 species; 42%), followed by Lamniformes (7 species; 23%), Rajiformes (3 species; 13%), Myliobatiformes (3 species; 13%), and Hexanchiformes (1 species; 4%). The same ranking can be done for specimens. In contrast to the ranking based on species, most specimens are Lamniformes (228 specimens; 75%), followed by Carcharihiniformes (63 specimens; 21%), Myliobatiformes (8 specimens, 3%), Rajiformes (4 specimens; 1%), and Hexanchiformes (1 specimen; 0%). These numbers are influenced by the size and visibility of specimens in the field, by collecting methods used in the field (surface prospecting vs. screen-washing), by the focus of collectors while sampling (taxonomical representation vs. relative abundance of taxa), and finally by the intensity of systematic study.

Age of the Tabaghbagh Fauna

The age of the neoselachian fauna at Minqar Tabaghbagh is Priabonian (late Eocene), based on the composition of the fauna itself and based on marine mammals found in the lower part of the Daba'a Formation. *Xiphodolamia serrata* Adnet et al., 2009, is a clear indicator of late Eocene age, as it has been reported recently from late Eocene strata in Iran, Jordan, Morocco, and Angola (Adnet et al., 2009; Adnet et al., 2010).

Marine mammals associated with the neoselachian fauna at Tabaghbagh include primitive Sirenia and archaeocete Cetacea. *Basilosaurus* sp., *Masracetus* sp., and *Eotheroides* sp. are the main components of the marine mammal fauna at Tabaghbagh, and these coexisted together in the Priabonian late Eocene Gehannam and Birket Qarun formations at Wadi Al-Hitan, some 300 km east of Minqar Tabaghbagh.

Paleoenvironment

At Tabaghbagh, the order Hexanchiformes is represented by a single species that we refer to *Hexanchus* sp. Recent representatives of this species prefer deeper waters, and feed on small sharks, rays, marine mammals, and also invertebrates (Compagno, 1984a).

Lamniformes include eight carnivorous and scavenging species. Teeth of *Otodus* cf. *O. sokolowi* and *Macrorhizodus praecursor* are abundant, and in some cases associations of 40 teeth or more from different tooth positions representing the same species, and probably same individual shark, were found scattered within an area one to two meters in diameter (Fig. 2b). *Otodus* cf. *O. sokolowi* and *Macrorhizodus praecursor* were large predators that may have hunted in groups.

Adnet et al. (2009) stated that the teeth of *Xiphodolamia serrata* may have been specialized for cutting and tearing, which is a fuctional similarity to *Hexanchus*. *Brachycarcharias* cf. *B. twiggsensis* and *Carcharias* sp. are rare at Minqar Tabaghbagh. They are heterodont in having anterior teeth bearing straight cusps, and lateral teeth with triangular distally-inclined central blades. *Alopias alabamensis*, *Alopias* sp., and *Abdounia* aff. *A. minutissima*, are moderately common. Their dentitions are small and they probably took smaller pelagic and benthic prey (Compagno, 1984a).

Carcharhiniformes is the most diverse neoselachian order in the Tabaghbagh fauna. Teeth of *Negaprion frequens* are common, while teeth of the other Carcharhiniformes are known from relatively few specimens. The presence of 10 carcharhiniform species means that the area was inhabited by an abundance of smaller vertebrates and invertebrates that constitute the main diet of this group.

Rajiformes includes *Anoxypristis* sp., *Propristis schweinfurthi* and *Pristis lathami*, which are all known from rostral teeth but not oral teeth. These are specialized shallow bottom feeders, that crush crustaceans and grazing invertebrates (Graman, 1913). Their rostra and rostral teeth are used for defense and prey detection while agitating and combing soft sediment on the sea floor. They live in lagoons and estuaries, and sometimes range into rivers.

Myliobatiformes is represented by two species identified from dental plates. *Myliobatis* species are benthic soft-bottom feeders that often trap prey by flapping their broad ventral body surface and using suction for ingestion. Sting rays are known only from spines, but these too feed primarily on crustaceans, molluscs, and occasionally small fish

Carcharhiniformes, Rajiformes, and Myliobatiformes in the Minqar Tabaghbagh fauna indicate a nearshore marine environment, possibly a bay or an estuary close to land that was connected to rivers and deltas. A majority of living representatives of these three orders are shallow marine to fresh water inhabitants. The abundance and diversity of Lamniformes in the Tabaghbagh fauna may reflect input of nutrients from rivers flowing northward from the African continent supporting an abundance of invertebrates, smaller fishes, and marine mammals. The setting is tropical to subtropical with warm shallow waters, possibly resembling the modern northern and western coasts of Australia (Compagno, 1984B; Last and Stevens, 2009) or the Gulf of Guinea (Schneider, 1990).

The late Eocene neoselachian fauna of Minqar Tabaghbagh was part of a much larger marine vertebrate and invertebrate community that included diverse bony fishes, turtles, crocodiles, archaeocete whales, and sirenians.

Paleobiogeographic Relationships of the Tabaghbagh Fauna

The Tabaghbagh neoselachian fauna described here can be compared to other contemporaneous Priabonian faunas in Tethys. For this four faunas from localities in North Africa and Arabia were selected. The localities and taxa for all five faunas are listed in Appendices I-V. The comparative faunas were compiled and published by different authors (Case and Cappetta, 1990, Cappetta et al., 2000; Mustafa and Zalmout, 2002; Adnet et al., 2010; Adnet et al. 2011; Underwood et al., 2011; Underwood and Ward, 2011). All of the selected faunas were found in similar regional and environmental settings in that they were obtained from marginal marine glauconitic and/or phosphatic clastic sedimentary facies where they were associated with skeletal remains of bony fishes and marine mammals such as archaeocete whales and sea cows.

The easternmost late Eocene neoselachian fauna to be discussed here is that from glauconite in the Wadi Esh-Shallala Formation chalk and marl at Qa' Faydat ad Dahikiya in the Eastern Desert of Jordan (Cappetta et al., 2000; Mustafa and Zalmout, 2002). Dahikiya produced 41 species representing eight orders. Carcharhiniformes dominate the Jordanian fauna (49%), followed by Lamniformes (12%), Rajiformes (12%), Myliobatiformes (10%), Orectolobiformes (5%), Pristiophoriformes (5%), Hexanchiformes (5%), and Torpediniformes (2%).

The Wadi Al Hitan World Heritage Site in the eastern part of the Western Desert of Egypt has the greatest number of neoselachian taxa (10 orders, 80 species; Case and Cappetta, 1990; Underwood et al., 2011, Underwood and Ward, 2011; Murray et al., 2011). These were collected from the Gehannam, Birket Qarun, and Qasr El-Sagha formations of late Eocene age. Myliobatiformes dominate the Wadi Al Hitan fauna (35%), followed by Carcharhiniformes (27%), Rajiformes (12%), Lamniformes (10%), Orectolobiformes (7%), Torpediniformes (3%), Neoselechii incertae sedis (1%), Heterodontiformes (1%), Squatiniformes (1%), Pristiophoriformes (1%), and Hexanchiformes (1%). The high diversity is directly related to screen-washing, which was carried out intensively and extensively over large areas of Wadi Al-Hitan.

Locality Km 55 is another late Eocene locality in the eastern part of the Western Desert of Egypt. This fauna came from the Qasr el-Sagha Formation between Fayum and Bahariya oases. Km 55 produced 22 neoselachian species representing five orders (Adnet et al., 2011). Myliobatiformes dominate the Km 55 fauna (46%), followed by Carcharhiniformes (32%), Rajiformes (14%), Lamniformes (5%), and Neoselechii incertae sedis (1%).

Farther to the west the Minqar Tabaghbagh late Eocene site is in the western part of the Western Desert of Egypt. The neoselachians came from the lower part of the Daba'a Formation east of Siwa. As noted above, Carcharhiniformes dominate the Tabaghbagh fauna (42%), followed by Lamniformes (23%), Rajiformes (13%), Myliobatiformes (13%), and Hexanchiformes (4%).

The most western neoselachian fauna considered here is from Ad Dakhla in the Moroccan Sahara, southwestern Morocco (Adnet et al., 2010) . The fauna includes 41 species of sharks belonging to six or possibly seven orders. Carcharhiniformes (31%) and Myliobatiformes (29%) predominate, followed by Lamniformes (17%), Rajiformes (12%), Orectolobiformes (5%), Torpediniformes (2%), and finally Selachian incertae sedis (2%). Adnet et al. (2010: 867) considered the neoselachian fauna at Ad Dakhla to support a Priabonian age but did not rule out the possibility of an older Bartonian age.

The composition of neoselachian faunas from each of the five localities compared here, Dahikiya in Jordan Wadi Al Hitan, Km 55, and Tabaghbagh in Egypt; and Ad Dakhla in Morocco, are illustrated graphically in Figure 6. Here comparison is made on the basis of ordinal level taxa present at Tabaghbagh, and each fauna is represented in terms of the relative number of species in each of the orders considered, normalized to 100%. Two localities, Dahikiya and Tabaghbagh, stand out in having relatively few Myliobatiformes, but faunal composition is otherwise similar across the whole east-west transect. We attribute the paucity of Myliobatiformes to less intensive screen-washing at Dahikiya and Tabaghbagh compared to that at Wadi Al Hitan, Km 55, and Ad Dakhla. We attribute the similarity in faunal composition observed here across the Middle East and North Africa to the equability of late Eocene climate and the broad geographic distribution of similar marine environments paralleling the northern margins of Arabia and North Africa.

CONCLUSIONS

The neoselachian fauna of Minqar Tabaghbagh includes five orders, and 24 species, identified from a collection of 304 identified teeth or spines. Most species are Carcharhiniformes (10 species; 42%), followed by Lamniformes (7 species; 23%), Rajiformes (3 species; 13%), Myliobatiformes (3 species; 13%),and Hexanchiformes (1 species; 4%). The age of the neoselachian fauna at Minqar Tabaghbagh is Priabonian late Eocene, based on the composition of the neoselachian fauna itself and based on marine mammals found in the lower part of the Daba'a Formation.

Carcharhiniformes, Rajiformes, and Myliobatiformes in the Minqar Tabaghbagh fauna indicate a nearshore marine environment, possibly a bay or an estuary close to land that was connected to rivers and deltas. The abundance and diversity of Lamniformes in the Tabaghbagh fauna may reflect input of nutrients from rivers flowing northward from the African continent supporting an abundance of invertebrates, smaller fishes, and marine mammals. Paleoenvironmentally, the setting is tropical to subtropical with warm shallow waters, possibly

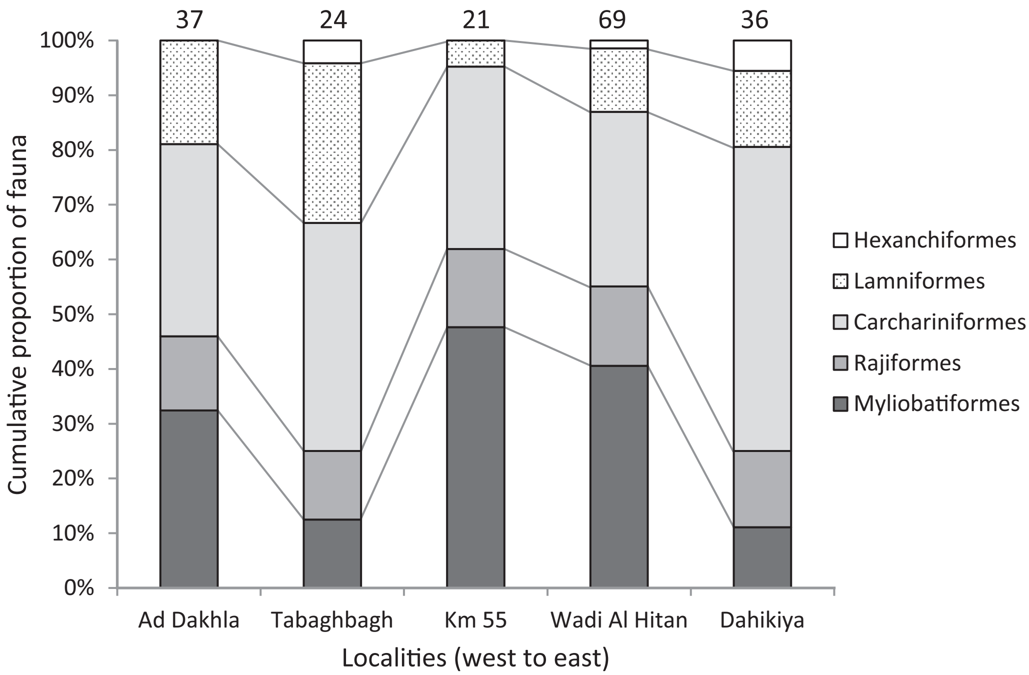

FIGURE 6 — Proportions of late Eocene neoselachian faunas spanning North Africa and the Arabian Peninsula, based on the relative species richness of the orders Hexanchiformes, Lamniformes, Carchariniformes, Rajiformes, and Myliobatiformes. Faunas come from the middle to late Eocene of ad-Dakhla in the Western Sahara of southwestern Morocco (Adnet et al., 2010; Appendix III); late Eocene of Minqar Tabaghbagh (this study, Appendix I); Km 55 in the Western Desert of Egypt (Adnet et al., 2011; Appendix V); late Eocene of Wadi Al Hitan (Underwood at. al., 2011; Appendix II); and late Eocene of Qa' Faydat ad Dahikiya of the Eastern Desert of Jordan (Cappetta et al., 2000; Mustafa and Zalmout, 2002; Appendix IV). Species richness for each fauna is given at the top of each column. Note the general similarity of faunal composition across localities, but varying proportions depending on the intensity of collecting in general, and intensity of screen-washing in particular. The coefficient of determination R^2 for regression of ordinal representation on species richness is 0.99 for Rajiformes, 0.77 for Myliobatiformes, and 0.71 for Carchariniformes, but only 0.39 for Lamniformes and 0.07 for Hexanchiformes.

resembling the modern northern and western coasts of Australia or the Gulf of Guinea.

The neoselachian fauna from Minqar Tabaghbagh resembles that known from other marine localities in the Middle East and North Africa. We attribute the observed faunal similarity to equability of the late Eocene climate and to a broad distribution of similar marine living environments along coasts at more or less the same latitude.

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APPENDICES

Selachian faunal lists for five sites compared here. Genera and species are listed by taxonomic order. See Figure 6 for a graphical comparison of faunal composition at the five sites.

APPENDIX I — Neoselachian fauna of late Eocene age at the foot of Minqar Tabaghbagh, Daba'a Formation, in the Western Desert of Egypt (this report; and Vliet and Abu el Khair, 2010).

- Hexanchiformes
  - *Hexanchus agassizi*
- Lamniformes
- *Carcharias* sp.
  - *Otodus* cf. *O. sokolowi*
  - *Brachycarcharias* cf. *B. twiggsensis*
  - *Macrorhizodus praecursor*
  - *Xiphodolamia serrata*
  - *Alopias alabamensis*
  - *Alopias* sp.
- Carcharhiniformes
  - *Abdounia* aff. *A. minutissima*
  - *Misrichthys stromeri*
  - *Carcharhinus* sp. 1
  - *Carcharhinus* sp. 2
  - *Galeocerdo* sp. 1
  - *Galeocerdo* sp. 2
  - *Negaprion frequens*
  - *Negaprion* sp.
  - *Physogalus* sp.
  - *Rhizoprionodon* sp.
- Rajiformes
  - *Anoxypristis* sp.
  - *Propristis schweinfurthi*
  - *Pristis lathami*
- Myliobatiformes
  - *Myliobatis* sp. 1
  - *Myliobatis* sp. 2
- Family indet. (stingray)

APPENDIX II — Neoselachian fauna of late Eocene age from **Wadi Al-Hitan**, Gehannam, Birket Qarun, and Qasr el-Sagha formations, in Fayum Province, Western Desert of Egypt (Case and Cappetta, 1990; Underwood et al., 2011).

- Hexanchiformes
  - *Hexanchus* ex. gr. *agassizi*
- Pristiophoriformes
  - *Pristiophorus* sp.
- Squatiniformes
  - *Squatina* sp.
- Heterodontiformes
  - *Heterodontus* sp.
- Orectolobiformes
  - *Nebrius* sp.
  - *Hemiscyllium* sp.
  - *Chiloscyllium* sp.
  - ?*Pararhincodon* sp.
  - *Eostegostoma* sp.
  - ?*Stegostoma* sp.
- Lamniformes
  - *Carcharias* sp.
  - *Anomotodon* ?*cravenensis*
  - *Macrorhizodus praecursor*
  - *Brachycarcharias twiggsensis*
  - *Brachycarcharias* cf. *B. twiggsensis*
  - *Carcharocles sokolowi*
  - *Parotodus mangyshlakensis*
  - *Alopias alabamensis*
- Carcharhiniformes
  - *Abdounia* aff. *A. minutissima*
  - *Abdounia* sp.
  - *Galeocerdo*? *aegypticus*
  - *Galeocerdo latidens*
  - *Hemipristis curvatus*
  - *Moerigaleus vitreodon*
  - *Carcharhinus* sp. 1
  - *Carcharhinus* sp. 2
  - *Negaprion frequens*
  - *Negaprion* sp.
  - *Misrichthys stromeri*
  - *Rhizoprionodon* sp.
  - *Physogaleus* sp.
  - '*Triakis*' aff. *T. wardi*
  - ?*Triakis* sp.
  - *Mustelus* sp.
  - *Leptocharias* sp.
  - *Premontreia* (*P.*) sp.
  - *Premontreia* (*Oxyscyllium*) sp.
  - *Megascyliorhinus* sp.
  - *Scyliorhinus* sp.
  - *Crassescyliorhinus* sp.
- Neoselachii *incertae ordinis*
  - *Odontorhytis pappenheimi*
- Rajiformes
  - *Propristis schweinfurthi*
  - *Anoxypristis mucrodens*
  - *Anoxypristis* sp.
  - *Pristis* ex. gr. *lathami*
  - *Pristis* sp. 1
  - *Pristis* sp. 2
  - *Rhinobatos* sp.
  - *Rhynchobatus* sp. 1
  - *Rhynchobatus* sp. 2
  - *Rhynchobatus* sp. 3
- Torpediniformes
  - *Torpedo* sp.
  - *Narcine* sp.
- Myliobatiformes
  - *Platyrhinoidis* sp.
  - ?*Platyrhina* sp.
  - *Dasyatis* sp.
  - Dasyatidae sp. 2
  - Dasyatidae sp. 3
  - ?*Neotrygon* sp.
  - *Ouledia* sp.
  - *Gymnura* sp.
  - ?*Jacquhermania attiai*
  - *Coupatezia* sp.
  - *Burnhamia* sp.
  - ff. *Burnhamia* sp.
  - *Archaeomanta* sp. 1.
  - *Archaeomanta* sp. 2.
  - ?Mobulidae sp.
  - *Eoplinthicus* sp.
  - *Pseudaetobatus* sp.
  - '*Myliobatis*' sp.
  - '*Myliobatis*' sp.
  - '*Myliobatis*' sp.
  - *Rhinoptera* sp.
  - ?*Rhinoptera* sp.
  - '*Aetobatus*' sp.
  - *Garabatis* sp.
  - *Lophobatis* sp.
  - *Leidybatis* sp.
  - *Pastinachus* sp.
  - *Taeniura* sp.

APPENDIX III — Neoselachian fauna of latest Bartonian to Priabonian age from **Ad Dakhla**, unnamed formation, in Moroccan Sahara (Adnet et al., 2010).

Orectolobiformes
- *Nebrius* cf. *N. obliquus*
- *Chiloscyllium* spp.

Lamniformes
- *Otodus* cf. *O. sokolovi*
- ‘*Cretolamna*’ *twiggsensis*
- ‘*Carcharias*’ *koerti*
- *Macrorhizodus praecursor*
- *Carcharias* sp.
- *Alopias* aff. *A. alabamensis*
- *Xiphodolamia serrata*

Carcharhiniformes
- *Scyliorhinus* spp.
- *Carcharhinus frequens*
- *Carcharhinus* spp.
- *Rhizoprionodon* sp.
- *Misrichthys stromeri*
- *Abdounia* spp.
- *Galeocerdo* cf. *G. eaglesomei*
- *Galeocerdo* sp.
- *Physogaleus* sp.
- *Hemipristis curvatus*
- *Paragaleus* sp.
- *Galeorhinus* spp.
- *Sphyrna* sp.

Rajiformes
- *Rhynchobatus* sp.
- *Rhinobatos* spp.
- *Pristis* cf. *P. lathami*
- *Propristis schweinfurthi*
- *Anoxypristis* sp.

Torpediniformes
- cf. *Narcine* sp.

Myliobatiformes
- *Dasyatis* spp.
- *Himantura* spp.
- *Gymnura* sp.
- *Ouledia* sp.
- *Aturobatis* sp.
- *Myliobatis* spp.
- *Rhinoptera* sp.
- *Aetobatus* cf. *A. irregularis*
- *Garabatis* sp.
- *Archaeomanta* sp.
- *Burnhamia* sp.
- *Mobula* sp.

Selachii *incertae sedis*
- *Odontorhytis* sp.

APPENDIX IV — Neoselachian fauna from the late Eocene **Qa’ Faydat ad Dahikiya** locality, Wadi Esh-Shallala Formation, in the Eastern Desert of Jordan (Cappetta et al., 2000; Mustafa and Zalmout, 2002).

Hexanchiformes
- *Hexanchus* sp.
- *Heptranchias* sp.

Pristiophoriformes
- *Centrophours* sp.
- *Pristiophorus* sp.

Orectolobiformes
- *Brachaelurus* sp.
- *Pararhincodon* sp.

Lamniformes
- *Carcharias* sp.
- *Macrorhizodus* aff. *Praecursor* sp.
- *Otodus* aff. *O. sokolovi*
- *Alopias* sp.
- *Xiphodolamia serrata*

Carcharhiniformes
- *Abdounia beaugie*
- *Abdounia lapierrei*
- *Abdounia* sp.
- *Scyliorhinus* sp.
- *Microscyliorhinus leggetti*
- *Physogaleus* sp.
- *Galeocerdo latidens*
- *Galeocerdo* sp. 1
- *Galeocerdo* sp. 2
- *Scoliodon terraenovae*
- *Misrichthys stromeri*
- *Carcharhinus* cf. *C. frequens*
- *Carcharhinus* sp. 1
- *Carcharhinus* sp. 2
- *Carcharhinus* sp. 3
- *Rhizoprionodon* sp.
- *Hypogaleus* sp.
- *Hemipristis curvatus*
- *Hemipristis* sp.
- Hemigaleidae sp.

Rajiformes
- *Triakis* sp.
- *Rhynchobatus* cf. *R. vincenti*
- *Rhynchobatus* sp.
- *Rhinobatos* sp. 1
- *Rhinobatos* sp. 2

Torpediniformes
- *Torpedo* sp.

Myliobatiformes
- *Dasyatis* sp. 1
- *Dasyatis* sp. 2
- *Gymnura* sp.
- *Myliobatis* sp.

APPENDIX V — Neoselachian fauna of late Eocene age from the **Km 55 locality**, Qasr El-Sagha Formation, in the Western Desert of Egypt (Adnet et al., 2011).

Lamniformes
- *Brachycarcharias twiggsensis*

Carcharhiniformes
- *Misrichthys stromeri*
- *Carcharhinus* sp. 1
- *Negaprion frequens*
- *Negaprion* aff. *N. frequens*
- *Rhizoprionodon* sp.
- ?*Sphyrna* sp.
- *Scyliorhinus* spp.

Neoselachii incertae ordinis
- *Odontorhytis pappenheimi*

Rajiformes
- *Anoxypristis* sp.
- *Propristis schweinfurthi*
- *Pristis lathami*

Myliobatiformes
- *Myliobatis* sp. 1
- *Myliobatis* sp. 2

Dasyatidae spp.
- *Taeniura* sp.
- *Pastinachus* sp.
- *Coupatezia* sp.
- ?*Jacquhermania attiai*
- *Himantura* spp.
- *Ouledia* sp.
- *Rhinoptera* sp.