

New tropical carcharhinids (chondrichthyes, Carcharhiniformes) from the late Eocene–early Oligocene of Balochistan, Pakistan: Paleoenvironmental and paleogeographic implications

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Abstract

New selachians (sharks and rays) have been collected from several late Eocene and early Oligocene marine localities in the Bugti Hills (Balochistan, Pakistan). Two new species of Requiem sharks (close to the Recent “Bull shark”) are described: *Carcharhinus balochensis* and *Carcharhinus perseus*. The rest of the fauna is notable for the strong representation of Carcharhiniformes. These selachian faunas represent a unique tropical association for the Oligocene period and one of the first modern tropical selachian faunas, with modern taxa such as the two new species of “Bull sharks”, *Negaprion* sp. and one of the first occurrences of *Sphyrna* sp. Moreover, these faunas permit paleoenvironmental interpretation of adjacent land masses. The relatively modern aspect of these faunas, compared with other contemporaneous and younger selachian associations from Atlantic and Mediterranean seas, suggests biogeographic isolation of selachian communities living in eastern and western parts of the Tethys before its final closure during the early-middle Miocene.

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1. Introduction

Fossil teeth of sharks and rays from western Tethys and the North and Central Atlantic are relatively common in Paleogene deposits and the subject of numerous publications (e.g., Leriche, 1905; White, 1931; Arambourg, 1952; Casier, 1946, 1966; Nolf, 1988; Ward and Weist, 1990; Kruckow and Thies, 1990; Kemp et al., 1990; Dutheil, 1991; Noubhani and Cappetta, 1997; Zhelezko and Kozlov, 1999; Kent, 1999a,b; Case and Borodin, 2000a,b). In contrast,

fossil selachians from eastern Tethys and the Indo-Pacific are scarcer and published works more limited. Contributing to this is the fact that the eastern part of the Tethys during the Paleogene–Neogene transition is characterized by deformations linked to the convergence of the South Eurasian and African-Arabian plates. The chronological sequence and the tectonic processes involved in these contacts between distinct continental landmasses are complex and actively debated (see Garfunkel, 1998, 2004; Golonka, 2004). The final closure of the eastern strait located in the Middle East, and separating the proto-Mediterranean (Western Tethys) and the new Indo-Pacific Ocean (Eastern Tethys) has been dated as late–early Miocene (Popov et al., 1993; Rögl, 1998, 1999; Adams et al., 1999) but a residual

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seaway between the two new ocean basins may have persisted until the middle Miocene (Rögl, 1999; Meulenkamp and Sissingh, 2003; Golonka, 2004). In this context, the Oligocene time interval appears as a critical and transitional period framed by the end of the circum-Tethys seaway (“Tethys Realm”) and the beginning of new proto-Mediterranean and proto Indo-West Pacific regions (see Briggs, 1995; Harzhauser et al., 2002). Unfortunately, post tectonic activities (resulting from Arabian–Eurasian plate collisions) have complicated the sequence of sedimentary deposition and limited the discoveries of fossil selachians (see Fig. 1).

Most of the Eocene selachian localities from the southern shore of eastern Tethys that have been reported are situated in North Africa (see Murray, 2000) and particularly Egypt with respect to selachians (Dames, 1883; Strömer, 1903; Priem, 1915; Case and Cappetta, 1990). Along the northern shore of Eastern Tethys, Eocene localities that yielded selachians are mostly localised in Central Asia (e.g., Glückman, 1964; Udovichenko, 1989; Case et al., 1996; Zhelezko and Kozlov, 1999) or are often limited to small faunules, consisting of short taxonomic lists, sometimes temporally problematic or limited to the basal Eocene,

including localities in Pakistan (Case and West, 1991), India (Kumar and Loyal, 1987; Bajpai and Thewissen, 2002; Rana et al., 2004, 2005) or in the Arabian plate (Arambourg et al., 1959; Arambourg and Magnier, 1961; Casier, 1971; Thomas et al., 1999). In the Oligocene, the situation is simpler because fossil shark studies from the eastern part of the Tethys are limited to a few localities in Central Asia (Zhelezko and Kozlov, 1999). However, several observations and preliminary taxonomic lists from the lower Oligocene of Egypt (Gebel-el-Quatrani, Murray, 2004 and personal communication 2004) and Oman (Thaytiniti and Taqah localities: Thomas et al., 1989) evidenced the relatively modern features of these selachian faunas. As described below, this is also observed in the selachians from the Bugti Hills, eastern Balochistan (Pakistan). Miocene selachians from the Indian Ocean coasts (East Africa to West Australia) are better known (e.g., Priem, 1907a,b; Leriche, 1954; White, 1927, 1955; Pledge, 1967; Kemp, 1991) but these are often limited to large teeth commonly known worldwide in Miocene seas. Sharks and rays from the Miocene of India (Mehrotra et al., 1973; Sahni and Mehrotra, 1981), are in serious need of review and are not considered in detail in this work.

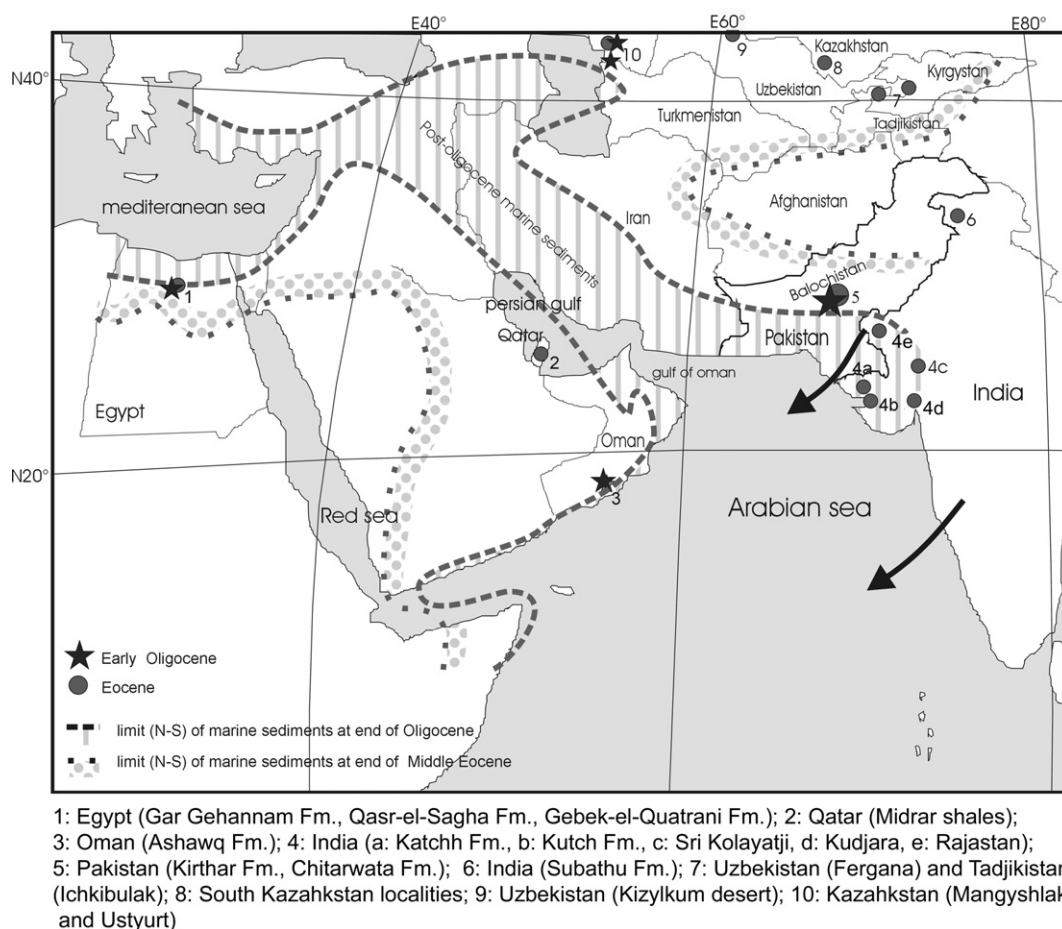


Fig. 1. Map of fossil sharks and rays sites studied in the deposits from the Eocene–Oligocene in the Middle Orient and Central Asian areas. Limits of the marine sediments are compiled and arranged from the works of Meulenkamp and Sissingh (2003) and Golonka (2004). Position of the Indian Plate (and Balochistan subregion) was more southwestward at the end of Paleogene as indicated by the arrows. Abbreviations: Fm, formation.

Herein, we report new fossil selachian faunas from Central Pakistan, ranging from late Eocene to early Oligocene. Two new species of Carcharhinidae are described and the paleobiogeographical implications of these faunas are discussed. This study has been limited to the Carcharhiniforms because they represent the majority of fossil selachians recovered from the Paleogene of the Bugti Hills (in terms of diversity and abundance). Other groups of selachian are listed below, and will be treated elsewhere.

2. Geological setting, materials and methods

Several seasons of fieldwork have been carried out in the eastern part of Balochistan (Fig. 2) since 1997 by the MPFB (“Mission Paléontologique Française au Balouchistan”) gathering members from the University of Montpellier II (Montpellier), Museum National d’Histoire Naturelle (Paris) and the Geology Department of the University of Balochistan (Quetta). Fossil terrestrial vertebrates have long been known in the Bugti Hills (e.g., Pilgrim, 1908, 1912; Forster-Cooper, 1923, 1934) but the new collections of numerous fossil mammals (Antoine and Welcomme, 2000; Antoine et al., 2003, 2004; Marivaux et al., 1999, 2001, 2002, 2005; Marivaux and Welcomme, 2003; Métais et al., 2003; Welcomme et al., 1997, 2001) have revived scientific interest in this area. The survey of old localities and new areas, including some marine deposits, led to the reassessment of the thick Bugti sedimentary series (Welcomme et al., 2001). Selachian teeth studied herein were collected either by surface prospecting (late Eocene localities) or after screen-washing of a matrix, basically sandstone (Oligocene sites). Welcomme et al. (1997) published a preliminary list of the selachian faunas of the Bugti hills, but the important recent collections allow us to expand on that report.

The totality of fossil selachians come from two principal formations (Fig. 2), the Bugti Member of the Chitarwata Formation and the underlying Drazinda Shale Member of the Kirthar Formation. The Oligocene localities (Fig. 2) are stratigraphically in the base (localities of Paali Nala [level 0], Kumbi [level 0], Lundo Chur [level 0], Pazbogi Nala and Hargar [level 0]) and the lower part (Paali Nala, [level C2]) of the Chitarwata Formation (Bugti Member), supposedly early Oligocene (Rupelian) in age (see Welcomme et al., 2001; Marivaux et al., 1999; Marivaux, 2000; Marivaux and Welcomme, 2003). The Eocene localities lie in the upper part of the Drazinda Shale Member of the Kirthar Formation (Locality of Dasht-I-Goran in Welcomme et al., 2001), late Eocene in age (e.g., Gingerich et al., 2001). From East to West, late Eocene and early Oligocene marine deposits are increasingly replaced by terrestrial, fluvio-deltaic clastic deposits (see Welcomme et al., 2001). Supposed marine/estuarine transitions (= base of the Bugti Member) are represented by indurated ferruginous layers unconformably deposited at the base of the fluvial sandy sediments, in which terrestrial vertebrates were discovered, excavated and published (see Welcomme et al., 1997, 2001; Marivaux

and Welcomme, 2003). A composite and simplified section is provided in Fig. 2; further details concerning the biostratigraphy of the Bugti Series are available in Welcomme et al. (2001).

The systematics and dental terminology follow Cappetta (1987) and Compagno (1999) for fossil and Recent taxa, respectively. The material is housed at the Paleontology Department, University of Montpellier II, France and labelled with collection numbers UMC – followed by localities and material abbreviation (Localities of Paali Nala, [level C2] : UMC-DBC-S, other locus of the Bugti Member (base): UMC-DB0-S, Dasht-I-Goran, marine level: UMC-DB-S).

3. Systematic palaeontology

Carcharhiniformes Compagno, 1973

Carcharhinidae Jordan and Evermann, 1896

Carcharhinus Blainville, 1816

Type species. *Carcharias melanopterus* Quoy and Gaimard, 1824

Occurrence. Middle Eocene [fossil species *C. marçaisi* (Arambourg, 1952) and *C. gilmorei* (Leriche, 1942)] to Recent

This genus includes thirty living species of “Requiem” sharks (Compagno, 1999) and conforms to the popular conception of a ‘typical’ shark. Most of them are widely distributed (Compagno, 1984, 1988; Compagno et al., 2005) and ecologically dominant (with other Carcharhinidae) in tropical coastal waters. Our knowledge of the evolutionary history of *Carcharhinus* species remains obscure. Their phylogenetic relationships are still debated (see Compagno, 1988; Naylor, 1992), and the monophyly of the genus remains uncertain (see Naylor, 1992). Likewise, their fossil record has not provided very useful information for understanding their evolutionary history. The earliest *Carcharhinus* are Middle-late Eocene in age and not well-documented (Kriwet, 2005); the morphology of their teeth is very homogeneous and without any consistent link with modern and Recent forms that suddenly appeared in the Miocene. Moreover, fossil *Carcharhinus* species are all based on dental morphology, which unfortunately proves to be problematic in many instances (Naylor and Marcus, 1994; Chiaramonte, 1998). Specific characters of *Carcharhinus* teeth are often difficult to interpret, leading to frequent confusion with other genera in the fossil record (Cappetta, 1987) or between *Carcharhinus* species (Purdy et al., 2001). Naylor and Marcus (1994) developed a morphometric method for analyzing the variation in the upper teeth of *Carcharhinus* that segregates the teeth of many extant species. When completely developed, this method may facilitate the identification of numerous fossil species (Purdy et al., 2001). At the present time, we can observe that almost all *Carcharhinus* fossil teeth from the Eocene show a very homogeneous morphology defined by upper teeth with a principal cusp well individualized from lateral heels and with continuous and no or few serrated cutting edges. On

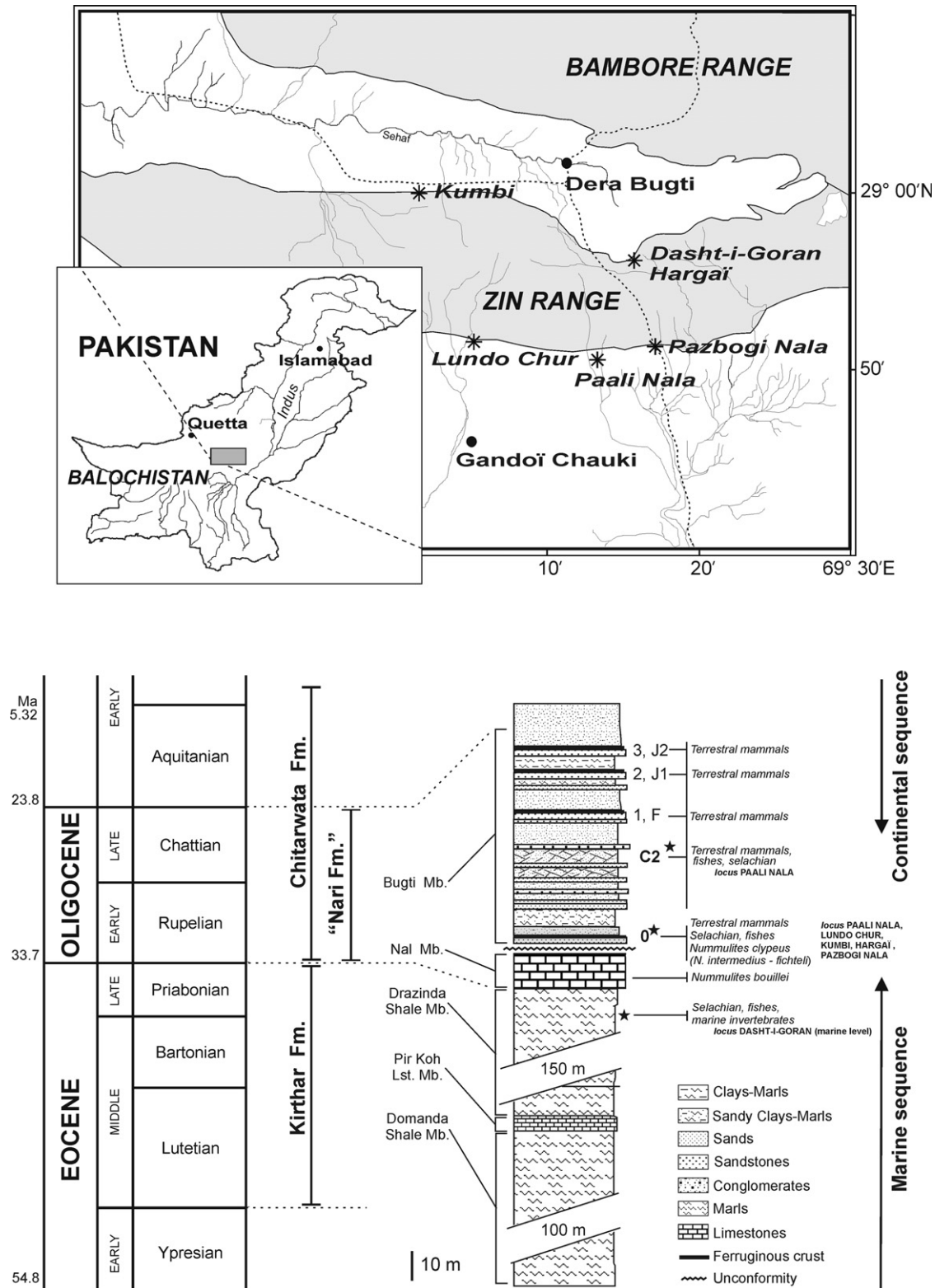


Fig. 2. (Above) Map of Pakistan with enlargement of the Bugti area and the location of fossil sites where the reported and described fossil selachians have been found. Present-day latitudes and longitudes are given. (Below) Composite and simplified section of the Bugti Hills stratigraphic sequence. Fossil Levels and principal geological structures are indicated. Deposit levels with Selachian fossils are figured by star symbol. See Welcomme et al. (2001) for further discussion. Abbreviations: Fm, formation; Mb, member.

the contrary, “post-Oligocene” *Carcharhinus* (many fossils and all the living species except *C. macloiti*) have upper and sometimes lower teeth with the cutting edges of the crown

fully serrated. The transitional forms (Oligocene) have teeth often showing both characters: smoothly to finely serrated cutting edges of cusps. The presence of two new fossil

species of *Carcharhinus* with “post-Oligocene” morphology in the late Eocene and early Oligocene deposits of Bugti Hills unexpectedly changes this point of view. Comparisons with extant species of *Carcharhinus* are based on figures of teeth in Garrick (1982); Compagno (1988); Naylor and Marcus (1994) and on fresh jaws of about fifteen species from the collections of Paleontological Laboratory of Montpellier University. When it is possible, choices of holotypes and descriptions of the two new fossil species are based upon antero-lateral upper teeth, following the recommendations of Naylor and Marcus (1994) to distinguish among species of *Carcharhinus*.

3.1. *Carcharhinus balochensis* new species

Galeocerdo latidens Thomas et al., 1989, in text;

Galeocerdo latidens. Welcomme et al., 1997, in text;

Galeocerdo latidens Case and West, 1991, pl.1.fig. 2;

Galeocerdo sp. Bajpai and Thewissen, 2002, txt-fig. 2f;

Isurus sp. Bajpai and Thewissen, 2002, txt-fig. 2i.

Etymology. From the name of the tribal people and their area (Province of Balochistan) where the new species has been discovered.

Holotype, locality and horizon: UMC-DB-S3. Figs. 3(5)–(7) from Dash i Goran [marine level] in Welcomme et al., 2001, fig. 3. Drazinda Shale Member, Balochistan (Pakistan). late Eocene.

Measurement. Range (mm) height = 13–25, width = 19–26, N = 24;

Other material. Additional material principally consists of a dozen broken teeth from Dash-I-Goran [marine level]: late Eocene; and Kumbi [level 0], Lundo Chur [level 0], Hargai [level 0] (see Welcomme et al., 2001, fig. 3. Nal Member): early Oligocene.

Occurrence. Late Eocene to early Oligocene from Pakistan and Oman. The range may extend back to the early-middle Eocene of Western India (Bajpai and Thewissen, 2002).

Diagnosis. Large fossil carcharhinid species known only by teeth. Dignathic heterodonty with flat, blade-like cusps in upper teeth and weak erected cusps in lower teeth. This species is characterized by upper teeth with triangular crown without distinct heels in anterior and anterolateral files. Cusp is slightly to well curved distally in anterior and lateral files, respectively, its upper mesial edge appears to be deflected distally and both cutting edges are fully serrated and doubly serrated in their lower to middle part. Root is large and well-developed in height, especially in the central part leading to a medially incurved crown-root boundary in labial face. Lower teeth have a cusp with serrated cutting edges from apex to lateral heels and occasionally a deeply arched root in anterior files.

Description. Upper teeth: Teeth reach a maximal 27 mm width even if some fragments suggest a larger size (up to 30 mm). Teeth are rather flat with a triangular crown slightly to well slanted distally, respectively in anterior (Figs. 3(1)–(2)) to lateral files (Figs. 3(10)–(13)). Mesial and

distal cutting edges are fully serrated from the crown-root boundary to the apex of cusp. The serrations are coarser and doubly serrated in the basal half of the crown (Fig. 3(8b)). This peculiar character is present on both mesial and distal cutting edges. In lingual or labial views, the mesial cutting edge appears straight or very slightly concave in its lower part in anterior and antero-lateral files (Figs. 3(1)–(9)) to straight or slightly convex in lateral files (Figs. 3(12)–(13)). In the same view, the distal cutting edge is slightly concave in anterior to the antero-lateral files, regular and without an angle or a distinction of a distal heel. The distal heel is only present in lateral files (Figs. 3(10)–(13)). In labial view, the crown-root boundary is reduced in length, medially arched in the anterior to antero-lateral files (Figs. 3(1),(3),(5), and (7)) to nearly straight in some lateral files (Fig. 3(12)). Root is massive, well-developed in height and greater in length than crown. Shape of the basal border of crown is sometimes irregular, often medially arched (Figs. 3(1), (5)) in anterior and lateral files to straight and only marked by a median notch in lateral files (Fig. 3(12)). Lateral extremities of root are mainly rounded or angular. Root lobes are well developed and separated in lingual view by a nutritive groove, largely open (Fig. 3(2)), shallow to relatively deep in lateral files (Figs. 3(11), (13)). Nutritive groove is often relatively reduced on the largest teeth (Figs. 3(6), (9)).

Lower teeth: They have an erect and central cusp with uninterrupted cutting edges. Lateral heels are weakly developed in very anterior teeth (Figs. 3(17)–(19)) to more developed in antero-lateral files (Figs. 3(14)–(16)) where they are oblique and continuous with cutting edges of cusp. A simple and slight serration is present on the upper two-thirds of the cutting edges (Figs. 3(17), (19)) or is more marked on the full cutting edge of crown (Figs. 3(14), (15)). As in the upper teeth, serrations are often more strongly developed in the lower part of the cutting edges. Labial and lingual faces are convex-concave (Fig. 3(18)) to straight-straight (Fig. 3(16)) in profile. Root is well developed with a thick medio-lingual protuberance in lateral view (Fig. 3(18)). The root lobes have rounded lateral extremities and are separated by a median and deep nutritional groove (Fig. 3(19)) as in upper teeth.

Discussion. Welcomme et al. (1997) referred these large upper teeth (frequently damaged and showing strong and double serration on cutting edges) to *Galeocerdo latidens* (Agassiz, 1843), which is a common taxon in middle and late Eocene tropical seas and was previously recorded in Pakistan (Sanghar Nala; Case and West, 1991). However the distal edge of cusp in upper teeth is regularly curved, serrated and without well-marked notch as in some great *Carcharhinus* upper teeth (except in lateral files). This allocation was confirmed later by the discovery of several lower teeth with fine and symmetrical cusps like on lower jaws of *Carcharhinus* but never observed on *Galeocerdo*. More or less complete additional teeth (Figs. 7–9) were found in the early Oligocene of Kumbi [level 0] and Lundo Chur [level 0]. No significant difference can be noted from the late Eocene material.

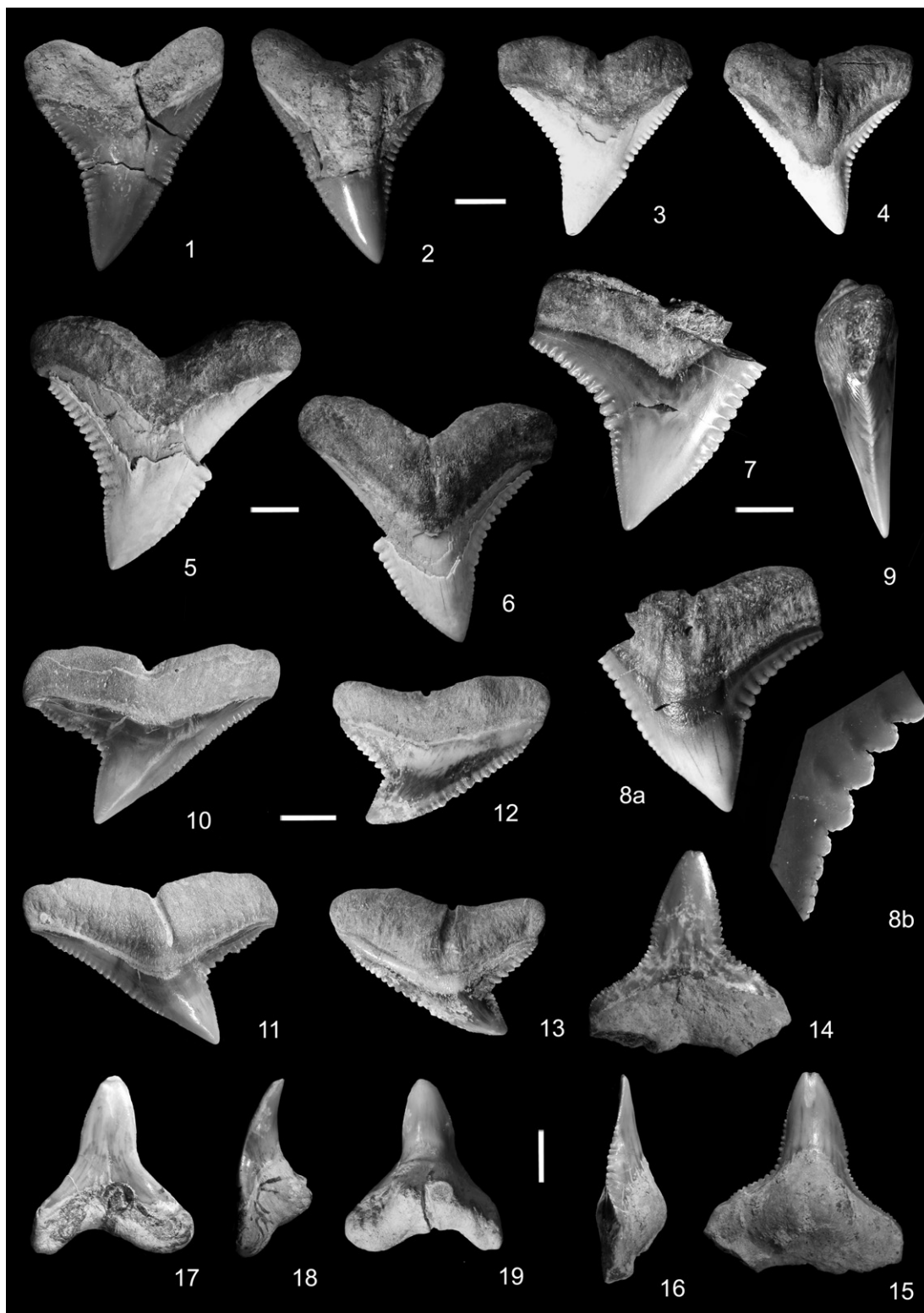


Fig. 3. *Carcharhinus balochensis* n. sp: 1–6, 10–19: from Dash i Goran [marine level], Drazinda Member, Balochistan (Pakistan), late Eocene. 7–9: from Kumbi [level 0], Bugti Member, Balochistan (Pakistan), early Oligocene. 1–2, UMC-DB-S1, anterior upper tooth: 1, labial view; 2, lingual view; 3–4, UMC-DB-S2, antero-lateral upper tooth: 3, labial view; 4, lingual view; 5–6, UMC-DB-S3, Holotype, antero-lateral upper tooth: 5, labial view; 6 lingual view; 7–9, UMC-DB0-S4, antero-lateral upper tooth (root extremities broken): 7, labial view; 8a, lingual view; 8b, detail of distal cutting edge (magnification X3 from 8a), 9, profile; 10–13, UMC-DB-S4 and S5, lateral upper teeth: 10 and 12, labial view; 11 and 13, lingual view; 14–16, UMC-DB-S6, antero-lateral lower tooth: 14, labial view; 15, lingual view; 16, profile; 17–19, UMC-DB-S7, anterior upper tooth: 17, labial view; 18, profile; 19, lingual view. Scale bar = 5 mm.

This species can be easily recognized from all the other Eocene *Carcharhinus* species (see Kriwet, 2005 for details), the few Oligocene remains, and the majority of Neogene and Recent species by the triangular crowns of upper teeth (without individualized mesial and distal heels) and fully serrated cutting edges on the upper and lower teeth. *Carcharhinus balochensis* was compared with some “Post Oligocene” species [*C. egertoni* (Agassiz, 1843) and *C. ackermannii* Da Silva Santos and Travassos, 1960] and some recent species of the genus.

The Neogene species *C. egertoni* is problematic. According to Purdy et al. (2001), the two syntypes of *C. egertoni* (Agassiz, 1843, Pl.36 figs. 6 and 7) actually belong to the Recent species *C. brachyurus* and *Carcharhinus leucas*. Moreover, since Agassiz’s major publications, most of Neogene *Carcharhinus* teeth with modern shape and triangular crown from the American coast (Kruckow and Thies, 1990; Casier, 1958; Longbottom, 1979; Müller, 1999; Aguilera and De Aguilera, 2001; Arratia, 1996) to East Africa (White, 1955) have been placed in this poorly defined species, making the systematics particularly unclear. This fossil taxon thus needs a serious revision and numerous neogene teeth attributed to *C. egertoni* probably belong to other species. *C. balochensis* differs from *C. ackermannii* (Miocene of Brazil) in lacking the triangular crown with angular notch at the base of the mesial cutting edge.

Comparison with Recent Requiem sharks is more appropriate, especially with the *C. leucas* group of Compagno (1988); *leucas-amboinensis* group of Garrick, 1982 as the *C. obscurus* group of Compagno (1988); *obscurus-galapagensis* group in part in Garrick, 1982, 1985, containing the living species *C. leucas*, *Carcharhinus amboinensis* and *C. obscurus*, *C. albimarginatus*, *C. altimus*, *C. plumbeus*, *C. galapagensis*, *C. longimanus*, respectively. Although there is not a consensus on whether or not these groups are valid, they are in use. Both groups display broadly triangular upper teeth with erect to semi-oblique cusp and never a mesial heel, weakly to moderately incised distal edge and both cutting edges fully serrated. Lower teeth have mainly erect cusp and straight to moderately arched basal edge of root. Cappetta (1987) used the name “Bull-group” (named from the Bull shark: *C. leucas*) for all the Recent species having such dental morphology, including the dubious Neogene species *C. egertoni*. As the name of this dental group is roughly explicit, we continue to use this term but no systematic or phylogenetic implications must be deduced from it. Purdy et al. (2001) detailed the morphology and characters of fossil and Recent teeth belonging to this “Bull-group”. According to their results and our personal observation, *C. balochensis* upper teeth are distinguished by: a lower cusp, a lesser pointed apex more deflected distally (Purdy et al., 2001) in anterior files like *C. altimus*, *C. plumbeus*, *C. longimanus*, *C. galapagensis*, *C. leucas*, a basal part of cutting edges more serrated like *C. altimus*, *C. plumbeus* and *C. longimanus*, larger roots nearly lobate, with basal edge medially arched and an enamel boundary on labial face often medially curved like

C. altimus, *C. plumbeus* and *C. longimanus*, *C. galapagensis*, *C. obscurus*. Moreover, *C. balochensis* and the Recent Bull shark *C. leucas* (see Garrick, 1982, fig. 41) have upper and lower teeth having “root with ventral (basal) edges moderately to deeply arched” (Compagno, 1988, p.310). Finally, this is between *C. balochensis* and *C. leucas* that differences are the most tenuous. However, in *C. balochensis*, the cusp of upper teeth is more distally curved with coarser and compound serrations basally, the root is thicker with lobes more developed and individualized. These distinctive dental features justify the specific distinction of *C. balochensis* from *C. leucas*.

Actually, the first fossil evidence of the “Bull-group” has long been reported from the marine Tertiary sediments of Birket-el-Qurun, Fayum (Dames, 1883, Pl.III, Fig. 5; Strömer, 1905, Pl.6 figs. 17–18 under the name *C. egertoni*) and this fossil material was recently dated to the late Eocene (Case and Cappetta, 1990). Another tooth from the Gar Gehannam Formation, Fayum (upper middle Eocene) was figured under the name *Carcharhinus* sp.1 by Case and Cappetta (1990, pl. 7 fig 164–165). This tooth resembles those of *C. balochensis*, but differs substantially from the later in showing important difference in size, a compound serration on the basal part of cutting edges and in having a less obtuse distal cutting edge. Although very incomplete, the tooth from the Drazinda Shale figured by Case and West (1991, pl.1, fig. 2) under the name *Galeocerdo latidens* probably belongs to *C. balochensis*. After examining the fragmentary teeth from the early Oligocene of Oman, we think that several specimens are related to *C. balochensis* and not to *Galeocerdo latidens* (in Thomas et al., 1989). Bajpai and Thewissen (2002) reported rare fossil remains from the Naredi Formation (early Eocene, Kachchh, North-western India, early Eocene) and figured two teeth as *Galeocerdo* sp. (text-fig. 2f) and *Isurus* sp. (text-fig. 2i). These specimens are undoubtedly an upper and a lower tooth of *C. balochensis*, respectively. If these fossil teeth really belong to *C. balochensis*, we suspect a younger age for the Kachchh fauna which is supported by the presence of *Galeocerdo eaglesomi* (White, 1955), only known in the middle Eocene of Africa and North Atlantic basin (White, 1955; Cappetta and Traverse, 1988 ; Case and Borodin, 2000b) and the archaeocete *Kutchicetus minimus*, previously recovered in the middle Eocene (Bajpai and Thewissen, 2000).

According to Purdy et al. (2001, p. 152) and our personal observations on the size range of teeth in the extant species of the “Bull-group”, the largest teeth of *C. balochensis* probably came from individuals of about 4 m long.

3.2. *Carcharhinus perseus* new species

Carcharhinus cf. *Carcharhinus amboinensis* Thomas et al., 1989.

Lamniform Murray, 2004, txt-fig. 7A.

Etymology.— from the name of the ancient Persian Empire (extended from Egypt to Indian boundaries) in reference to the distribution of this new fossil species.

Holotype, Locality and Horizon: UMC-DBC-S9, Figs. 4(5)–(7) from Paali Nala [level C2] in Welcomme et al., 2001, fig. 3. Bugti Member, Chitarwata Fm., Balochistan (Pakistan), early Oligocene.

Measurement. Range (mm) height = 3–16, width = 4–16, N = 191;

Other material. Roughly 200 teeth, Additional material from Pazbogi Nala, Kumbi [level 0], Lundo Chur [level 0], Hargai [level 0] (Bugti Member, Chitarwata Fm.): early Oligocene.

Occurrence. Early Oligocene of Egypt, Oman and Pakistan

Diagnosis. Medium carcharhinid species belonging to the “Bull-group” and only known by teeth. This species is characterized by a very slight dignathic heterodonty with blade-like upper and lower teeth. Teeth of upper and lower jaws are strongly labio-lingually compressed, cutting edges are fully serrated (more developed on upper teeth), root is never larger than crown, arched on its basal edge and having a weak reduction of the nutritive groove on its lingual face.

Description. Medium carcharhinid species. Upper and lower tooth size 12mm and 10mm mean width, respectively.

Upper teeth: Teeth are rather flat with a large and triangular crown erected to slightly slanted distally in anterior (Figs. 4(1)–(2)) and lateral files (Figs. 4(10)–(11)), respectively. There never have a mesial heel and the distal heel is only developed in lateral files. Mesial and distal cutting edges of crown are fully serrated. Serration is strong but simple in the lower half and rapidly decrease in size near the apex of cusp. The mesial cutting edge is very slightly convex in first anterior file (Figs. 4(1)–(2)), more often straight (Figs. 4(3)–(9)) to slightly concave in the lateral file (Figs. 4(10)–(11)). Distal edge is slightly but always concave in this middle part. As a result, the distal edge is never slanted distally even in lateral files (Figs. 4(10)–(11)). Distal heel, when it is present, is serrated too, oblique and marks a small angle with distal edge (Fig. 4(10)). Crown-root boundary is reduced and limited to the fine enamel junction which is convex to relatively straight in labial view (Figs. 4(3) and (5)). Root is strongly labio-lingually compressed (Fig. 4(7)) and never larger than crown. Extremities of lateral lobes are often vertical (Fig. 4(2)) or depressed (Fig. 4(4)) in lingual or labial views. Both lingual and labial faces of root are as flat as those of crown. Root lobes are weakly developed and their basal edges are arched in labial or lingual view. A small but distinct protuberance is sometimes located in the medio-basal part of the lingual face of root and can be observed on labial view (Fig. 4(8)). This protuberance is marked by the basal extremity of the median nutritive groove that is reduced to a fine depression (Fig. 4(9)) or disappears totally on several upper teeth (Figs. 4(2), (4)). Sexual variations have not been observed or remain undeterminable. Ontogenetic variation seems to be slight (denticulation remains strong) and reduces to a more oblique cusp on small specimens. These characters

seem to quickly disappear with growth (up to 8mm of width).

Lower teeth: Dignathic heterodonty seems to be very limited in this species as we can observe in the only living species *C. amboinensis* for which we can compare the dental variation. In fact, lower teeth have a very similar shape with upper teeth. They can be distinguished from upper teeth only by a finer cusp with triangular shape in lateral view, a slighter serration, a mesial cutting edge of crown slightly convex even in antero-lateral (Figs. 4(15)–(18)) and lateral files (Figs. 4(19), (20)); the presence of a slightly mesial heel on the crown of both anterior (Figs. 4(13)–(16)) and lateral files; a weaker root and a nutritive groove better marked than in upper teeth. Symphyseal lower teeth (Fig. 4(12)) have an erect cusp and a reduced crown compared to the root which extends basally.

Discussion. These flat upper and lower teeth of similar shape and with a reduced nutritive groove on the root, have been really problematic. The absence of (or very reduced) nutritive groove is unusual in carcharhinid teeth contrary to other selachian groups (e.g., Lamniformes). Moreover, the reduced dignathic heterodonty is uncommon in Carcharhinid species compared to other fossil and recent species of *Carcharhinus*. Up to now, only one living species of the Leucas group : *C. amboinensis* (Müller and Henle, 1838–41) show similar pattern of dignathic heterodonty. *Carcharhinus perseus* nov sp. exhibits a set of characters that allow us to compare it with *C. amboinensis*. Artificial upper and lower dentition of *C. perseus* have been reconstructed from isolated teeth (Fig. 5) and can be compared to figures of *C. amboinensis* teeth available in the literature Bass et al., 1973, pl.8; Naylor and Marcus, 1994, p.4–5. Although the resemblance is striking, the teeth of *C. perseus* nov. sp. differ from those of *C. amboinensis* in having a crown larger than the root, a cusp more robust (at least on upper teeth) and in having a very limited nutritive groove on upper teeth.

No fossil species could be actually compared to *C. perseus*. Other species of the “Bull-group” are mainly distinct from the new species by a larger size, a stronger serration, and a more pronounced dignathic heterodonty. Cappetta (in Thomas et al., 1989) identified similar teeth from the early Oligocene of Oman Peninsula as *Carcharhinus* aff. *C. amboinensis*. Comparison was relevant but after studying the teeth from Oman, we assign them to *C. perseus*. Mehrotra et al. (1973) reported a new species of *Carcharhinus*: *C. jhingrani* from the Miocene of PIRAM Island, Gujarat (western India), based on an upper tooth (Mehrotra et al., 1973, pl.1, fig 1., LUV 1005). This single specimen was refigured in Sahni and Mehrotra (1981, pl. 2 (fig. 3)) and could be confused with *C. perseus* (equilateral crown, broad root, vertical root extremities). However, it differs in having a lesser arched basal edge of root and a deep nutritive groove. Murray (2004) recently studied fossil fishes from the early Oligocene of Fayum (Egypt) and figured some elasmobranch teeth (text-fig. 7). Some of them are related to the new species (text-fig. 7A in Murray, 2004 and personal communication, 2004) and we conclude that the new

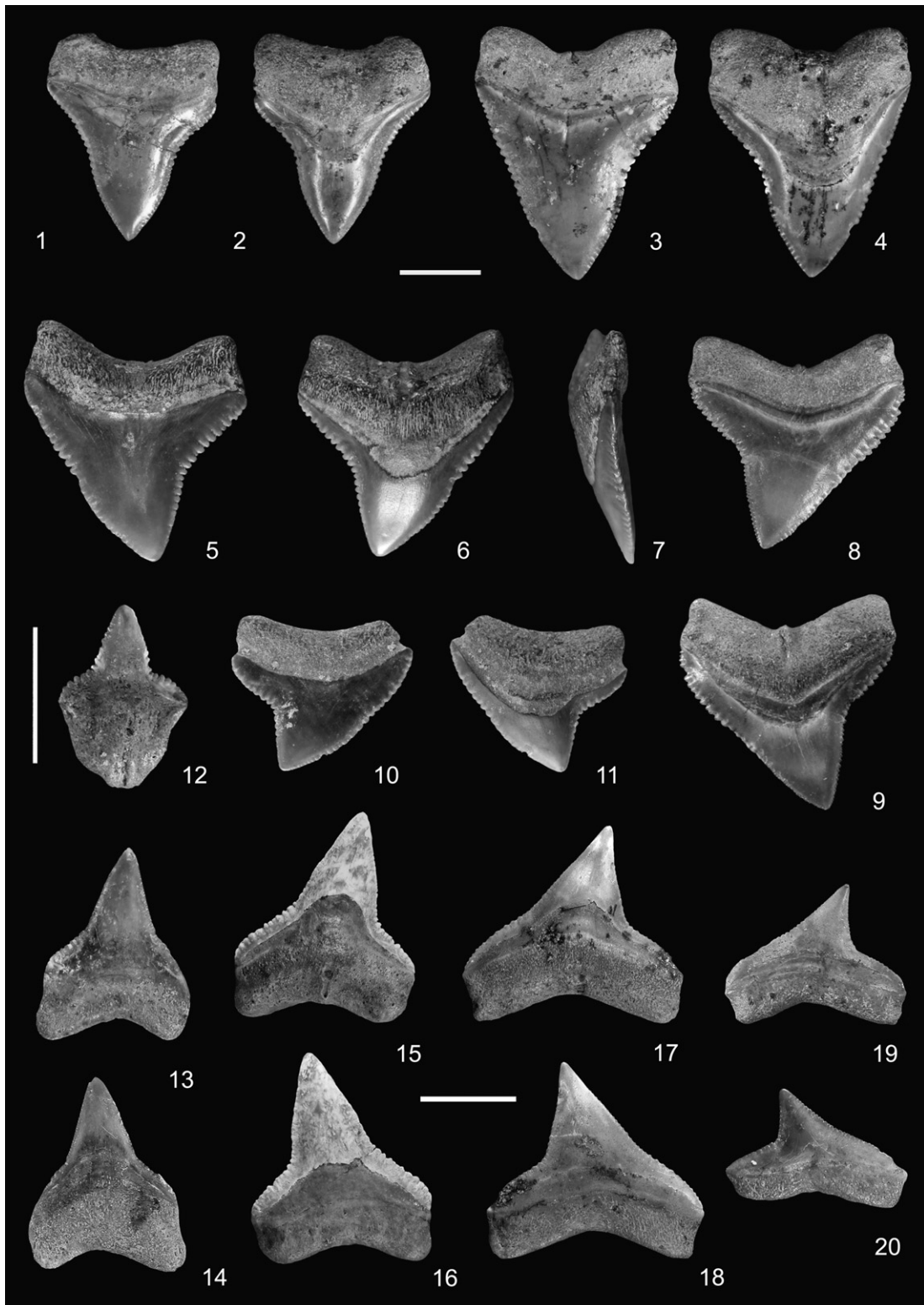


Fig. 4. *Carcharhinus perseus* n. sp.: 1–20, 1–9, 12–20, from Paali Nala [level C2], Bugti Member, Balochistan (Pakistan), early Oligocene. 10–11, from Kumbi [level 0], Bugti Member, Balochistan (Pakistan), early Oligocene. 1–2, UMC-DBC-S1, anterior upper tooth: 1, labial view; 2, lingual view; 3–4, UMC-DBC-S6, anterior upper tooth: 3, labial view; 4, lingual view; 5–7, UMC-DBC-S9, Holotype, antero-lateral upper tooth: 5, labial view; 6, lingual view; 7, profile; 8–9, UMC-DBC-S2, antero-lateral upper tooth: 8, labial view; 9, lingual view; 10–11, UMC-DB0-S5, lateral upper tooth: 10, labial view; 11, lingual view; 12, UMC-DBC-S3, symphyseal lower tooth in lingual view; 13–20, UMC-DBC-S10 to 14, anterior to lateral lower teeth: 13, 16, 18–20 labial view; 14, 15, 17, lingual view. Scale bar = 5 mm.

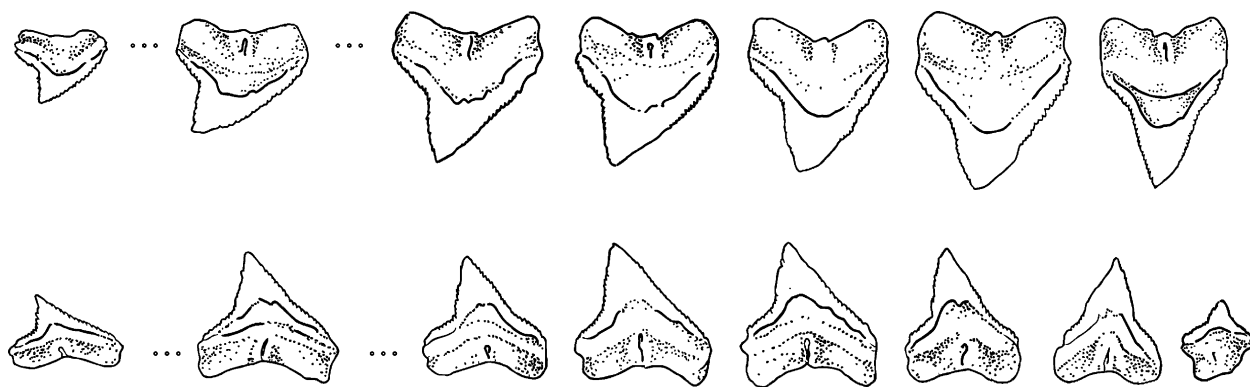


Fig. 5. Reconstituted upper and lower dentition of the fossil species *Carcharhinus perseus* n. sp. (in lingual view) based on isolated teeth from Paali Nala [level C2] (Bugti Member, early Oligocene). Anterior (right) to lateral (left) files.

species *C. perseus* is present in the early Oligocene of Egypt as well.

C. perseus nov. sp. is thus currently restricted to the early Oligocene sediment of Oman, Egypt and Pakistan localities.

3.3. *Carcharhinus* sp.1

Negaprion eurybathrodon Case and West, 1991, pl.1, fig. 5, pl.2, figs. 1–4, 6–7.

Measurement. Range (mm) height = 7–10, width = 8–10, N = 9;

Material. – Figured (UMC-DB-S10 and 11), additional material reduced to about fifteen broken teeth from Dasht-I-Goran [marine level] (Drazinda Member, Kirthar Fm.): late Eocene.

Occurrence. Late Eocene.

Description and discussion. Small species of *Carcharhinus* with teeth slightly smaller than 13 mm width. Upper antero-lateral teeth (Figs. 6(7)–(8)) are characterized by a wide and labio-lingually flattened cusp and two well-individualized heels. The cutting edges of cusp are never serrated. The low and moderately long heels are well separated from the base of the cusp by shallow notches and serration is moderately developed or absent. Lower teeth (Fig. 6(9)) have an erect cusp in central position and the sub-horizontal heels are not or very slightly serrated. Both in upper and lower teeth, roots are elongated, nutritive groove is shallow and forms a small notch on the basal margin of root in labial view (Figs. 6(9), (7))

Even if the material is badly preserved, this *Carcharhinus* species displays a clear dognathic heterodonty. Lower teeth show an erect cusp, a well-developed root with a thick lingual protuberance. Upper teeth have a crown with triangular outline. Case and West (1991) have figured teeth of this species (Case and West, 1991, pl.1, fig. 5; pl.2, figs. 1 and 6–7) from the Sangahr Nala (Kirthar Fm., Pakistan) that they misidentified as the Miocene species *Negaprion eurybathrodon*. Teeth are hardly differentiable from those of the other Eocene *Carcharhinus* species and confusion is therefore possible with *C. frequens* (Dames, 1883) or *C. gilmorei* (Leriche, 1942) (see Müller, 1999). However, unlike *C. frequens*

from the late Eocene of Egypt (see Case and Cappetta, 1990), *Carcharhinus* sp.1 displays a better-individualized cusp, and longer lateral heels on its upper and lower teeth.

3.4. *Carcharhinus* sp.2

Measurement. Range (mm) height = 6–9, width = 8–10, N = 19;

Material. About thirty teeth, figured (UMC-DB0-S9 to 11) from Kumbi [level 0] and others from Lundo Chur [level 0], Paali Nala [level C2] (Bugti Member, Chitarwata Fm.), early Oligocene.

Occurrence. Early Oligocene

Description and discussion. This small species of *Carcharhinus* is characterized by upper teeth with an enlarged central cusp, erect to slightly oblique (Figs. 6(1)–(4)), well-separated from lateral heels by deep notches and with cutting edges totally serrated from apex to the lateral extremities of heels. Lower teeth (Figs. 6(5)–(6)) have a central, erect and fine cusp and two elongated heels subparallel to the straight basal margin of the root. Nutritive groove is large, deep and penetrates the basal margin of the root. Cutting edges are more finely serrated than on the upper teeth.

This species can be easily separated from the other Eocene *Carcharhinus* species in having cutting edges of crown fully serrated on upper and lower teeth. Teeth morphology remains close to that of Recent species like *C. falciiformis* or *C. brachyurus* or that of *C. priscus* (Agassiz, 1843), which is a widespread fossil species known from the late Oligocene (Leriche, 1938) to the Pliocene (Arratia, 1996; Laurito Mora, 1999). However, during the three last decades, numerous Neogene *Carcharhinus* teeth have been placed in *C. priscus* and several of them (including some of the type series of Agassiz) seem to belong to other species (according to Purdy et al., 2001). Moreover, while four teeth of the original type series (Agassiz, 1843, Pl. 26a, figs. 35–38) come from Malta chalk, the others have no precise provenance and Agassiz himself (1843: p. 235) had some doubts in determining some of them. A serious revision of this species is necessary. Moreover, the significantly smaller

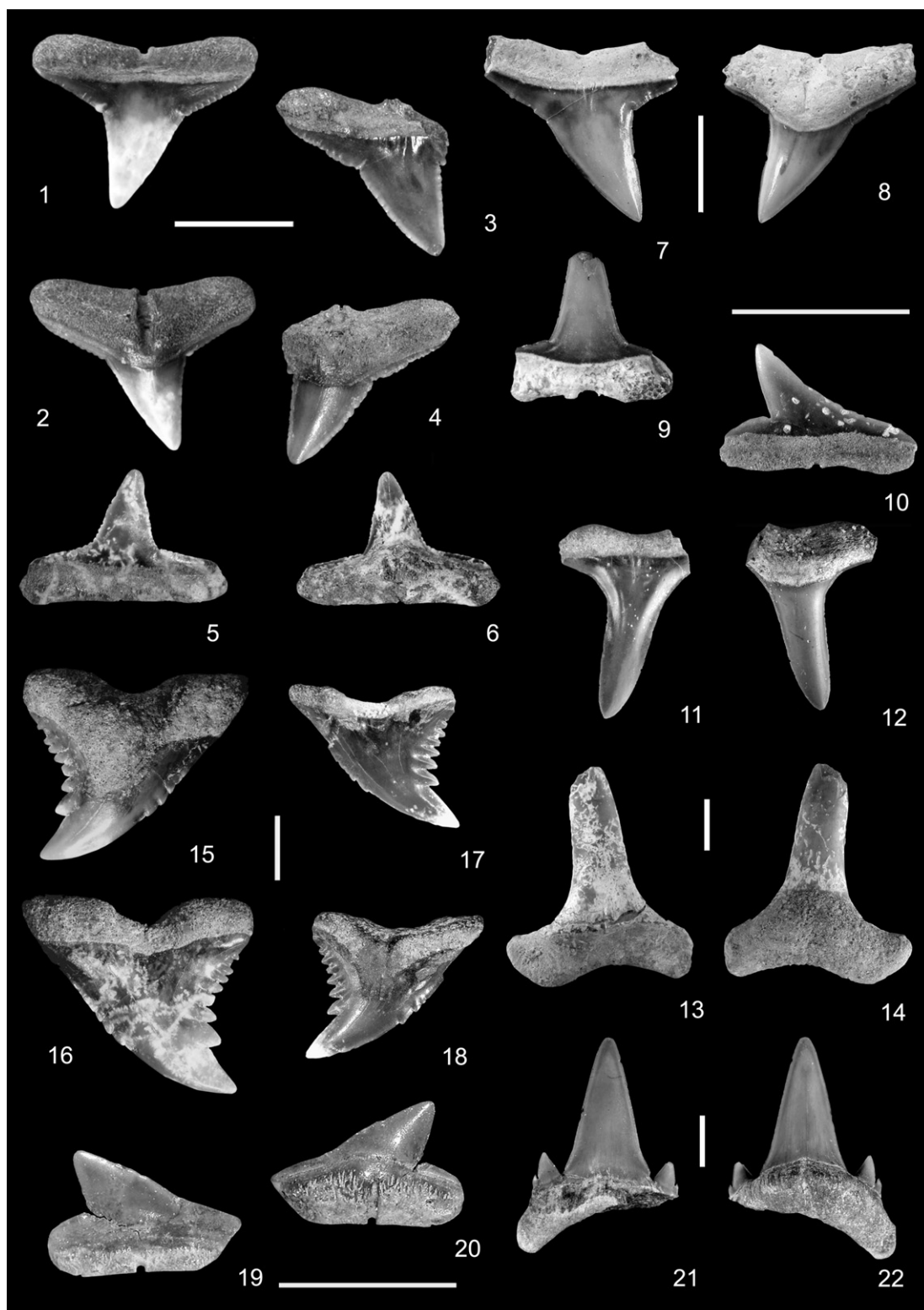


Fig. 6. 1–6, *Carcharhinus* sp.2: UMC-DB0-S9 to1, early Oligocene; Antero-lateral upper teeth: 1 and 3, labial view; 2 and 4, lingual view; 5–6; lateral lower tooth: 5, labial view; 6, lingual view; 7–9, *Carcharhinus* sp.1: UMC-DB-S10 to11, late Eocene. Antero-lateral upper tooth: 7, labial view; 8, lingual view; anterior lower tooth: 9, labial view; 10, *Rhizoprionodon* sp.: UMC-DBC-S21, early Oligocene. Lateral tooth, labial view. 11–14, *Negaprion* sp.: UMC-DB0-S1 and 2, early Oligocene. Anterior upper tooth: 11, labial view; 12, lingual view; anterior lower tooth: 13, labial view; 14, lingual view. 15–18, *Hemipristis* cf. *serra*: UMC-DB0-S12 and 13, early Oligocene. Antero-lateral upper teeth: 15,18, lingual view; 16–17, labial view; 19–20, *Sphyrna* sp.: UMC-DBC-S17 early Oligocene; undertermined file: 19, labial view; 20, lingual view. 21–22, *Cretolamna twiggensis*: UMC-DB-S12, late Eocene. Antero-lateral tooth: 20, labial view; 21, lingual view. Scale bar = 5 mm.

size of the teeth, compared to the typical Neogene forms usually attributed to *C. priscus*, suggests leaving them *incertae sedis* pending further discoveries.

3.5. Genus *Negaprion* Whitley, 1940, *Negaprion* sp.

Measurement. Range (mm) height = 6–23, width = 10–19, N = 7;

Material. Eighteen broken teeth, (figured UMC-DB-S1 and 2) from Kumbi [level 0], (Bugti Member, Chitarwata Fm.), early Oligocene.

Occurrence. Middle Eocene – recent

Description and discussion. Large species of *Negaprion* with anterior teeth (Figs. 6(11)–(12)) reaching a large size (up to 20 mm high). Crown is higher than broad on the anterior teeth and broader than high on laterals. Cusp is acute, vertical with parallel edges to slightly oblique in lateral files. Cutting edges lack serration and are continuous from cusp tip to the lateral extremities of crown. Heels are oblique and may be reduced in the anterior files (Figs. 6(11)–(14)) are horizontal and well-developed in the lateral files. Root lobes are well developed, often asymmetric (Figs. 6(13)–(14)) in anterior and lateral files. Median part of the basal edge of root is concave in anterior files to straight in lateral files. The nutritive groove is shallow and narrow in lingual view and disappear in large teeth (Figs. 6(12), (14)). Teeth of this species are clearly distinct from Neogene *N. eurybathrodon* and other fossil species such as “*N.*” *kraussi* (Probst, 1879) and “*N.*” *gibbesi* (Woodward, 1889) by larger size, the lack of serration on heels and the development of its slender cusp. This unnamed species differs from the Recent *N. brevirostris* (off American coasts) for the same reasons aforementioned and appears closer to the Indo-Pacific extant species *N. acutidens*. The latter possesses upper and lower teeth of similar size and with a similar cusp shape. This lineage is known from the Lower Miocene of South of France (as *N. caunellensis*: Cappetta, 1970) and from the Miocene of the Zanzibar (White, 1955). However, our material differs from these Miocene forms in its larger size, its more developed lateral heels, which lack totally in the anterior teeth of the Miocene material. Indeed, teeth from Balochistan are more like those of Recent Indo-Pacific species than any Miocene species. Some fragmentary cusps from the early Oligocene of Oman may be tentatively related to this great species of *Negaprion*.

3.6. Genus *Rhizoprionodon* Whitley, 1929, *Rhizoprionodon* sp.

Measurement. Range (mm) height = 2–4, width = 2.5–6, N = 5;

Material. Fifteen broken teeth (figured UMC-DBC-S21) from Paali Nala [level C2], Kumbi [level 0] (Bugti Member, Chitarwata Fm.), early Oligocene.

Occurrence. Early Eocene – recent

Description and discussion. Due to the scarcity of the material, only a questionable attribution to the genus

Rhizoprionodon can be made. However the characters (such as the fine, long and erected cusp: Fig. 6(10)) allow us to distinguish our material from that referred to species *R. ganntourensis* (Arambourg, 1952) known in the Eocene of Tethys and North Atlantic (see Case and Cappetta, 1990; Noubhani and Cappetta, 1997). Species from Pakistan appear to be more closely related to the Miocene species such as *R. fisheuri* (Joleaud, 1912), figured by Laurito Mora (1999) and known from the Oligocene of North American coasts (Müller, 1999). This genus was already reported in the early Eocene of West India (Rana et al., 2004) and late Eocene of Pakistan (Case and West, 1991) and it is also present in early Oligocene of Oman.

3.7. *Sphyrnidae* Gill, 1872, Genus *Sphyrna* Rafinesque, 1810, *Sphyrna* sp.

Measurement. Range (mm) height = 3–4.5, width = 5–6, N = 4;

Material. Four teeth, figured (UMII-DBC-S17) and additional four broken teeth from Paali Nala [level C2] (Bugti Member, Chitarwata Fm.), early Oligocene.

Occurrence. Early Oligocene – recent

Description and discussion. Teeth are small (Figs. 6(19)–(20)); the cusp is relatively thick and short; cutting edges lack serration; distal heel is well developed and continuous with the distal cutting edge of cusp; root is as massive as crown and root lobes are well aligned, horizontal and separated by a straight and deep nutritive groove in lingual view (Fig. 6(20)) which largely penetrates the basal margin of the root.

This unnamed species differs from the Miocene species *S. arambourgi* Cappetta, 1970; *S. laevissima* (Cope, 1869 considered as *S. zygaena* by Purdy et al., 2001) and fossil remains of the extant species *S. zygaena* in having a smaller size, a shorter cusp and a massive aspect of crown and root. As mentioned by Cappetta (1987), pre-Miocene species of *Sphyrna* are often erroneously identified, unverified (Cappetta and Traverse, 1988) and actually belong to the genus *Carcharhinus* (Dartevelle and Casier, 1943) or *Physogaleus* (White, 1955; Case, 1981). Teeth of *Sphyrna* are generally distinct by a shorter cusp, a labial face of crown not overhanging the labial face of root and the lack of lingual protuberance on root. The earliest appearance of hammerhead sharks is early Miocene (Cappetta, 1993) but its stratigraphical range should be probably extended to the early Oligocene from the Parisian Basin, France (Dutheil, 1991; Genault, 1993). The scarcity of the material does not allow more precise attribution.

3.8. Family Hemigaleidae Hasse, 1879, Genus *Hemipristis* Agassiz, 1843, *Hemipristis* cf. *H. serra* Agassiz, 1843

Measurement. Range (mm) height = 7–15, width = 11–18, N = 6;

Material. About teen teeth, figured (UMC-DB0-S12 and 13) and additional lower and upper fragmentary teeth from

Kumbi [level 0], Hargar [level 0] (Bugti Member, Chitarwata Fm.), early Oligocene.

Occurrence. Early Oligocene–Plio–Pleistocene

Description and discussion. Upper teeth reach 15 mm in total height. Crown is slanted distally, labio-lingually flattened with slightly sinuous cutting edge in occlusal view. Labial faces of crown and root are concave. Mesial cutting edge bears short denticles (up to 5) in its lower part, which decrease in size basally (Fig. 6(15)). Teeth of lateral files show a slightly serrated mesial edge (Figs. 6(17)–(18)) and a distal edge with no heel and numerous strong denticles decreasing in size from apex to crown-root boundary. Mesial and distal root lobes are enlarged, crown-root boundary is nearly horizontal in labial view (Figs. 6(16)). Nutritive groove is often well-marked and deep (Figs. 6(18)). Lower teeth are narrower mesio-distally with a rather thick crown. The labial face is concave and overlaps the root. Lingual face is strongly convex transversally and root shows a prominent lingual protuberance. One or two pair of small hook-like denticles are present laterally at the base of the cusp.

Hemipristis serra is largely reported during the Oligocene and Neogene (see Cappetta, 1987 and additional references from Kruckow and Thies, 1990; Kemp, 1991; Müller, 1999; Laurito Mora, 1999; Purdy et al., 2001). This species is clearly distinct from the Eocene species *H. curvatus* Dames, 1883 in having a larger size and a mesial edge with more than three denticles on upper teeth. *H. curvatus* occurs in the middle and late Eocene of tropical seas as in Egypt (Case and Cappetta, 1990) and Pakistan localities (Case and West, 1991). The upper teeth of our material are often more denticulated than we can observe in *H. curvatus* (and thus distinct) and they are relatively smaller (Figs. 6(17)–(18)) and serration on the mesial edge of the crown is often slighter and more limited in height than in typical *H. serra* teeth. Ontogenetic variation on upper teeth has been reported in extant species (Compagno, 1988), as well as in *H. serra* (Purdy et al., 2001) and could explain the present variations, especially on the distal cutting edge (Compagno, 1988). However, the presence of a weak serrated mesial cutting edge suggests a transitional form between *H. curvatus* and *H. serra* and thus justifies the present attribution in confer to *H. serra*. Such ambiguities are also recognized in the Oman fauna (early Oligocene) where the two time-successive species have been noted (*H. cf. serra* and *H. cf. curvatus* in Thomas et al., 1989).

3.9. Non-Carcharhiniform sharks (List of fossil selachians is summarized in Table 1)

Several broken teeth (Figs. 6(21)–(22)), recovered in Dasht-I-Goran [marine level] (Drazinda Shale member) belong to *Cretolamna twiggensis* (Case, 1981; Lamniformes, Cretoxyrhinidae), the youngest species of the genus which was discussed and adequately illustrated by Case and Cappetta (1990, p. 9–10, pl. 3). The range of this species is restricted to the middle late Eocene interval and its geo-

graphic distribution extends to paleotropical seas of the Caribbean and oriental Tethys (Case, 1981; Case and Cappetta, 1990; Case and Borodin, 2000b). *C. twiggensis* is noted out in the Eocene Khirthar Formation of Pakistan (Ward and Weist, 1990) and probably in the Midra shales of Qatar under the name *Lamna gafsana* (Casier, 1971). Isolated cups from Kumbi [level 0] have been identified as Odontaspidae. A few teeth from the Dasht-I-Goran [marine level] belong to a fossil nurse shark *Nebrius obliquum* (Leidy, 1877; Ginglymostomatidae) that differs from the contemporaneous and septentrional species *N. thienlenensis* (Winkler, 1873) by larger size, a stronger serration, a unilobed flat apron and a labial face of crown more concave in lateral view. *N. obliquum* is a very common Eocene species with a world-wide distribution in the palaeotropical seas (see Noubhani and Cappetta, 1997) and has been noted in the late Eocene of the Kirthar Formation (Case and West, 1991). A small broken and blunted tooth of this genus has been found in the early Oligocene of the Bugti Hills and is provisionally referred to *N. obliquum*. Two small broken teeth (Kumbi [level 0]) could be only referred to the Orectolobiformes. These damaged teeth show a principal and symmetric cusp, large apron and a pair of well developed hook-like denticles. They are strongly reminiscent of the dental morphology of Hemiscyllidae and the extant genus *Chiloscyllium*, recorded in the lower Oligocene of Oman (Thomas et al., 1989).

3.10. Fossil batoid

Batoids are represented by two families in terms of abundance: Dasyatidae and Rhinobatidae. However, a large fossil sawfish (genus *Pristis*, Pristidae) is present in the Kumbi [level 0] with 2 rostral teeth. One is very large (more than 6 cm of total length) and shows a great similarity with those of the living *P. pristis* (Linnaeus, 1758) or with those of the fossil species *P. lathamii* Galeotii, 1837 which is common in Eocene seas and worldwide (see Case and Cappetta, 1990: p.19 for discussion). *Rhynchobatus cf. pristinus* (Probst, 1877, Rhynchobatidae) has been collected in Kumbi [level 0] and Paali Nala [level C2] localities. This species is principally known in inter-tropical Miocene seas (Priem, 1912, 1914; Case, 1980; Cappetta, 1973; Antunes et al., 1999; Laurito Mora, 1999). Müller (1999) has however reported its presence in the Oligocene deposits of the East Coast of North America. Numerous teeth of *Rhinobatos* sp. (Rhinobatidae) have been collected in Paali Nala sands (level C2: more than 200). Fossils of this Recent genus are relatively common in the Paleocene–Eocene levels including west India (Rana et al., 2004) and are less frequent in younger sediments. Pakistan species differ from Oligo–Miocene species in having a wider size and a larger and better marked nutritive groove. The unique lateral tooth of *R. sahnii* Sahni and Mehrotra, 1981 from lower Miocene of India resembles our material, however several characters suggest that our species is probably new. Concerning the Myliobatiformes order, dasyatid fossils are

Table 1
Distribution of fossil sharks and rays observed in the Bugti Hills, Balochistan (Pakistan) for each sampled level

	Late Eocene				Early Oligocene						
	Midra shale ^a (Qatar)	Qasr-el Sagha ^b (Egypt)	Kirthar Fm. ^c (Pakistan)	Dash-I-goran [mar. lev.]	Kumbi [level 0]	Hargai [~] [level 0]	Lundo Chur [level 0]	Paz-Bogi	Paali Nala [level C2]	Thaytini ^d (Oman)	Mokkatan ^e (Egypt)
Carcharhiniformes											
<i>Carcharhinus balochensis</i>		?	P	+++	+	+	+				
<i>Carcharhinus perseus</i>					++	+	+	+	+++	P	P
<i>Carcharhinus</i> sp.2					++	+	+		+		
<i>Carcharhinus</i> sp.1	?		P	++						?	
<i>Negaprion</i> sp.					++					P	
<i>Rhizoprionodon</i> sp.		P	P	?	+				+	P	
<i>Sphyrna</i> sp.									+		
<i>Hemipristis cf. serra</i>					++	+				P	
Lamniformes											
<i>Cretolamna twiggensis</i>	P	P	P	++							
Odontaspidae					+						
Orectolobiformes											
Orectolobiformes indet.					+					?	
<i>Nebrius obliquum</i>			P	+	?						
Rajiformes											
<i>Pristis cf. lathamii</i>	P	P			+				?		
<i>Rhinobatos</i> sp.									+++	P	
<i>Rhynchobatus cf. pristinus</i>					++				+	P	
Myliobatiformes											
<i>Himantura</i> sp.			P		++				++	P	
<i>Dasyatis</i> sp.					+				++	?	P
<i>Aetobatus</i> sp.	?	P							+	P	
<i>Myliobatis</i> sp.	?	P	P	+	+++	+	+		+		
				Bugti Hills(Balochistan)							

Bugti Hills(Balochistan)

+, rare to; +++, abundant; ?, dubious. Presence of the same species in the principal neighbour areas are labelled by (P).

^a Casier, 1971.

^b Case and Cappetta, 1990.

^c Case and West, 1991.

^d Thomas et al., 1989.

^e Murray, 2004.

common in early Oligocene levels and could correspond to the Recent *Himantura* genus. There is no fossil species of this genus but many fossils attributed to genus *Dasyatis* might probably be reattributed to this last genus and other Dasyatidae according to the new figures of Recent species (Herman et al., 1998, 1999). Although our material is similar to the tooth figured by Case and West (1991, pl.3, fig. 5) from the Drazinda Shale Member under name *D. charlisae* (Case, 1981), it differ from the original description and figures (Case, 1981, pl. 7). This fossil species, probably new, is present in Oman, too (Thaytiniti and Taqah localities). Another dasyatid species is well represented in Paali Nala [level C2]. When compared to usual Cenozoic fossil teeth of genus *Dasyatis*, the teeth from Paali Nala have a small size, a fine and slender crown, a strong antero-lateral compression and enamel without any ridge or ornamentation. Murray (2004, txt-fig. 7C) has figured a tooth from the early Oligocene of Fayum that clearly belongs to this same new species. The Myliobatiforms are also represented by *Myliobatis* sp. from the Drazinda Shale Member and from early Oligocene levels where they are better represented, and by a few specimens of the genus *Aetobatus* in Paali Nala. Fossil

species attributed to the genus *Myliobatis* are numerous and probably some of them are misidentified and belong to other myliobatid genera (Hovestadt and Hovestadt-Euler, 1999). A major revision of the fossil Myliobatidae must be carried out before any additional determination is made.

4. Biostratigraphy, paleozoogeography and paleoenvironment of Baluchistan fossil-bearing sites

Concerning the Drazinda Shale Member (Dasht-I-goran), the Bugti fauna is very similar to that published by Case and West (1991). The fauna is less similar to those of other Eocene localities from Qatar, India and Egypt although these taxonomic differences may be the result of differences in age and/or environment. However, the presence of *Cretolamna twiggensis*, known only from the late Eocene of equatorial seas (Casier, 1971; Case, 1981; Case and Cappetta, 1990; Ward and West, 1990; Case and Borodin, 2000b) confirms the late Eocene age of the top of the Drazinda Shale Member in Bugti Hills. There are few affinities (e.g., *P. lathamii* and *N. obliquum* identified with confidence) between the Pakistani fauna and the well-documented

selachian fauna from Central Asian localities (e.g., Kazakhstan, Uzbekistan, Kirgistan), which were recovered from late Eocene paratethyan marine deposits (Glückman, 1964; Udovichenko, 1989; Averianov and Udovichenko, 1993; Case et al., 1996; Zhelezko and Kozlov, 1999). Such a difference agrees with the current vision that the selachian faunas, as well as the marine invertebrates, from Central Asia are closer to those of the North European Province than to those of the eastern Tethys (Popov et al., 1993; Rögl, 1998; Harzhauser et al., 2002; Zhelezko and Kozlov, 1999). Concerning the environment of the deposit, previous works on fossil fishes from the Drazinda Shale Member (Nolf, 1991; Case and West, 1991) indicated a neritic tropical environment poorly exposed to the oceanic realm and the dominance of carcharhinids as indicators of tropical near shore environment deposits therefore agrees with the previous paleoenvironmental inferences. As stressed by Case and West (1991), the absence of large oceanic predators (e.g., genus *Carcharocles*, *Isurus*, *Alopias*) in the Drazinda Formation is also confirmed by our faunal data. Microfauna is not represented in the late Eocene material probably because of inadequate collecting techniques.

The fossil-bearing sites of the Bugti Member are placed at the base of the Chitarwata Formation and can be considered as roughly contemporaneous (Kumbi [level 0], Lundo Chur [level 0], Hargai [level 0]) or close in time (Paali Nala [level C2]) (see tab.1). There is no clear evidence to detect any substantial difference in age between these localities even if some differences between the assemblages persist (see below). Unlike the faunal association of the Drazinda Shale Member, there are no reliable taxa in the basal Chitarwata Formation to give a precise age. However, faunal correlations with the vertebrate fauna of Oman (Thomas et al., 1989) as well as the data from Fayum (Murray, 2004) confirm an early Oligocene age (see Welcomme and Ginsburg, 1997; Welcomme et al., 2001).

In terms of paleozoogeography, as the Oligocene fauna from eastern Tethys is virtually unknown or poorly studied thus far, comparisons with other faunas from the same bioprovince are necessarily limited. The roughly contemporaneous fauna of Central Asia (Glückman, 1964; Zhelezko and Kozlov, 1999) as well as those of European areas (see Müller, 1983; Brzobohaty, 1987; Dutheil, 1991; Baut and Genault, 1999; Merle et al., 2002) do not exhibit affinities with the material from Pakistan. In fact, most of fossil species recorded in Balochistan (except *H. serra*, *C. twiggensis*, *N. obliquum*, *P. lathamii*, *R. pristinus*) are new or undetermined and seemingly confined to the eastern part of the Tethys (including Egyptian and Oman localities). Moreover, this modern selachian association (dominated by carcharhinids in frequencies and diversity) makes it directly comparable with those of the Mio-Pliocene Atlantic and Mediterranean paleoseas or those of the tropical recent coasts (Compagno, 1990; Compagno and Cook, 1995; Martin, 2004). In fact, the abundance of carcharhinids, dasyatids and Guitar rays are all indicative of an extreme littoral habitat in tropical latitude. In addition, majority of

living sharks and rays systematically close to the Pakistani fossils are mostly euryhaline species known to frequently penetrate tropical rivers (e.g., *C. leucas*, *C. amboinensis*, *Negaprion acutidens* and some other carcharhinids, *Pristis* species, *Rhinobatos* species) as well as to live exclusively in freshwater (some species of *Dasyatis* or *Himantura*). Pelagic fishes are very poorly represented (Lamniformes) or entirely absent from the faunas and the classic benthic fauna of the littoral shelf is lacking (e.g., Scylliorhinidae, Pristiophoridae, Squatinidae, Rajidae). Moreover, sedimentologic observations (micro-dunes and ferruginous hard-ground) and the state of preservation of fossil teeth (rolling patina) are concordant with an extreme littoral environment with possible rapid drainage (like in present deltaic or estuarine environments). The presence of numerous fossil teeth and bones of continental small and large vertebrates of tropical environments (see Marivaux, 2000; Marivaux et al., 2001, 2002, 2005; Marivaux and Welcomme, 2003) in the same deposits provide further support for such a paleoenvironmental interpretation. Similar paleoenvironments have been proposed for both the early Oligocene levels of Fayum (Murray, 2004) and the Oman locality (Thomas et al., 1989; Otero and Gayet, 2001), which present also an equivalent association of selachian species and terrestrial vertebrates. Differences in faunal composition between the early Oligocene localities of Balochistan might be interpreted as an artifact of collecting techniques (for example in Pazbogi Nala) and/or a difference in the depositional environments. Two levels (Paali Nala [level C2] and Kumbi [level 0]), well-represented in terms of richness (more than 200 teeth), illustrate particularly this last point. The Kumbi [level 0] locality has fewer fossils but is more diversified than the Paali Nala [level C2] (13 and 9 species, respectively), with the largest forms (*C. balochensis*, *Negaprion* sp., *Hemipristis* cf. *serra* and *Pristis* cf. *lathamii*) and also more marine forms (Odontaspidae, Orectolobiformes). Paali Nala [level C2] is less diversified in species and has the smallest forms of the Dasyatidae, Rhinobatidae and *C. perseus* which are particularly abundant. Moreover, most of the teeth of *Carcharhinus* sp.2 and particularly those of *C. perseus* are significantly smaller in Paali Nala [level C2] (length of crown: Means = 8.76 mm, $N = 176$; $sd = 2.2$ mm) than in Kumbi [level 0] ($M = 13.78$ mm, $N = 12$, $sd = 1.12$ mm) suggesting that may be an area frequented by young fossil Requiem sharks. Although different in age, no significant difference in form among the teeth has been noticed for the two species. Shark nurseries are often located in protected bays and estuaries (Branstetter, 1990; Simpfendorfer and Molward, 1993; Bush and Holland, 2002) and their observation agrees with our observation about the more deltaic habitat environment assumed for Paali Nala [level C2]. Indeed, the Paali Nala [level C2] sands were probably deposited in a brackish zone of a large river (presence of numerous terrestrial animal remains) near an estuary. The Kumbi [level 0] fauna clearly shows a more marine trend (as attested by shells of marine invertebrates) and may be regarded as representing the tidal zone. The

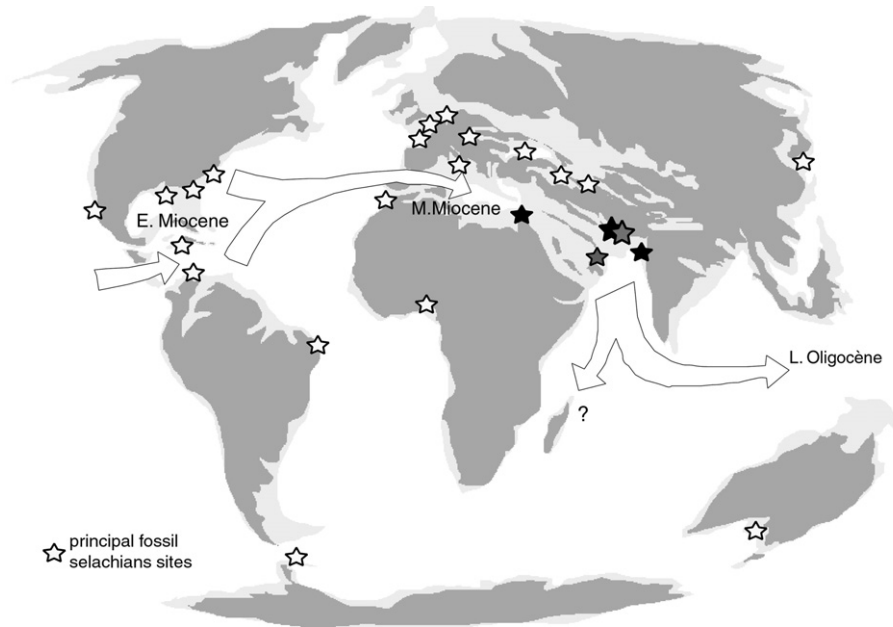


Fig. 7. Simplified Oligocene world map with principal fossil selachians sites from the late Eocene and early Oligocene. Solid stars (black and gray) indicate localities with large *Carcharhinus* belonging to the “Bull-group” (from the late Eocene and the early Oligocene, respectively). Hypothetical migration sea-ways with times for “Bull-group” sharks have been added (see discussion in text).

other localities (Pazbogi Nala, Lundo Chur and Hargai”) may be located between these two topographic positions without further precision due to inadequate sampling. As Paali Nala [level C2] is slightly stratigraphically younger than other levels, the difference in faunal association with Kumbi [level 0] is probably the result of a global and rapid decrease of sea level off Balochistan coast at the beginning of the Oligocene (Welcomme et al., 2001). In any case, the presence of Requiem sharks in brackish/estuarine habitat since the early Oligocene suggests that the ability to invade freshwater habitats was acquired early in the evolution of the genus *Carcharhinus* (only known since the Lower Eocene).

5. Paleogeographic implications

This study considerably enhances our knowledge of the fossil selachian faunas from the eastern Tethys sea (current West Indo-Pacific area) which are otherwise fairly well-known in Atlantic seas for the same time period. The first evidence of modern coastal and tropical selachian associations (with predominance of carcharhinids) was until now only recorded in the Mio-Pliocene. The modern selachian associations that inhabit the extant tropical seas seem to have appeared earlier than previously supposed. Moreover, modern carcharhinid species and groups (such as the “Bull-group” or the hammerhead sharks) appear to be well established in the eastern Indian ocean since the early Oligocene, as attested by available paleotropical sites (e.g., Oman, Egypt, Pakistan, see Fig. 2). The Indo-Pacific region remains are important to the evolution of marine vertebrates during the Paleogene–Neogene transition. This area, representing the residual eastern Tethys, has been consid-

ered as the cradle for numerous Neogene bony fish communities of the proto-Mediterranean (Arambourg, 1943; Cappetta and Ledoux, 1970; Nolf, 1985) and the Atlantic and East Pacific modern tropical fishes and other marine groups (Springer, 1982; Oosterzee, 1997; Briggs, 2003; Anderson, 2000; Mooi and Gill, 2002; Streelman et al., 2002; Teske et al., 2004; Bellwood et al., 2004; Carpenter and Springer, 2005). Eastern Tethys is also thought to have played the role of refuge where modern shark and ray communities evolved (see Musick et al., 2004) although it seems to have been more complex than previously announced (Leviton et al., 1996; Harzhauser et al., 2002). The pattern that characterized the late Eocene–early Oligocene faunal associations of the eastern Tethys when compared to those of the contemporaneous Atlantic and western tethys (Proto-mediterranean) supports this hypothesis (Fig. 7). Likewise, Musick et al. (2004, p. 54) suggested that the rise of Carcharhinidae may parallel in time the rise of higher teleosts in coastal tropical habitats of the Indo-Pacific. The presence of modern species of large *Carcharhinus*, *Negaprion* and one of the first *Sphyrna* in a paleotropical area of eastern Tethys ten million years before their rise in the Atlantic tends to support this assumption. The absence of “Bull-group” fossils in the Proto-Mediterranean prior to the middle Miocene (see Cappetta, 1970; Bartheilt et al., 1991; Holec et al., 1995), despite successive occurrences in Indo-Pacific [late Eocene–early Oligocene: this work], western Pacific [late Oligocene–early Miocene : Uyeno, 1978; Uyeno et al., 1984; Kemp, 1991] and eastern Pacific–western Atlantic coasts [early to middle Miocene : e.g., Sanchez-Villagra et al., 2000; Purdy et al., 2001] is particularly instructive. It seems to confirm the relative isolation of the western Indian–Eastern African Bioprovince

from the Mediterranean–Iranian Bioprovince (see Harzhauser et al., 2002) suggesting the existence of Oligocene ecological barriers in this marine realm before the early Miocene closure of the Tethys (according to Hrbek and Meyer, 2003; Bellwood et al., 2004) and/or physical barrier with partial terrestrial contact between the Asian and African plates (Otero and Gayet, 2001; Marivaux et al., 2001, 2002; Marivaux and Welcomme, 2003). The Neogene worldwide invasion of large Carcharhinidae (as “Bull-group”) through other possible gateways (open Panama isthmus and/or South African strait) seems the most likely scenario as it has been suggested for other Indo-Pacific marine groups (see Briggs, 1999).

6. Conclusion

Until now, the Paleogene fossil selachians were poorly documented for the Indo-Pacific in comparison with the Atlantic. The preliminary faunal list of selachians from the late Eocene–early Oligocene of the Bugti Hills partially fills a gap in our knowledge. Moreover, these fossil selachian associations are the first described tropical Oligocene faunas. Two new species of fossil *Carcharhinus*: *C. balochensis* and *C. perseus* are described, from late Eocene and early Oligocene deposits, respectively. *C. balochensis* is close to the extant Bull shark *C. leucas* and probably reached a considerable size estimated to 4 m long. *C. perseus* is characterized by upper and lower teeth nearly similar in morphology, a character uncommon within the genus and only observed in the living Pigeye sharks: *C. amboinensis*. These two new species represent the first fossil evidence of some modern and large Requiem sharks (termed “Bull group”) that were previously unknown prior the Late Oligocene of East Pacific and early Miocene of Atlantic. Other Carcharhiniformes have been reported and illustrated. One of the first occurrences of hammerhead sharks (Sphyrnidae) and the presence of a modern form of lemon shark (*Negaprion* sp.) are reported. A rapid overview on other elements of the faunas reveals the modern aspect of the entire Bugti selachian assemblage as well as those of some nearby fossil localities. Faunal compositions of each level have confirmed the late Eocene and early Oligocene age previously cited for the highest levels of the Kirthar Formation and the basal levels of the Chitarwata Formation, respectively. This last one is known to have yielded abundant fossils of mammals (Bugti Bone bed, Bugti Member; see Welcomme et al., 2001). Moreover, studies of the selachian association have confirmed the tropical paleoenvironment of these deposits, between a marine inshore for the late Eocene level (Drazinda Shale Mb.) to a coastal zone to brackish estuary/freshwater river for the early Oligocene levels (Chitarwata Fm.). The surprising patterns of the fossil selachian association and species of the eastern Tethys (western Indian Ocean) during the end of the Paleogene provide further evidence for an Indo-Pacific origination of the modern communities of selachians. Moreover, the endemism and modernity of some taxa (e.g., *C. balochensis*,

C. perseus, *Negaprion* sp., *Sphyrna* sp.) compared to those of the contemporaneous localities from Central Asia and western Tethys (European coasts and Palaeocaribbean) suggest an early splitting of the Indo-Pacific and protomediterranean bioprovince. This geographic segregation into several bioprovinces probably began before the supposed closure of the Mediterranean and the end of Tethyan seaway usually dated by the early-middle Miocene. Studies on Indo-Pacific paleoichthyological fauna during the middle Eocene–Oligocene open some new perspectives to better understand the modern zoogeography and evolution of recent selachians and paleogeographic changes.

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