MIOCENE SHARK TEETH ASSEMBLAGES AND ANCILLARY FISH TAXA FROM BARIPADA, ORISSA: TAXONOMIC REVISION AND A GLOBAL PALAEOBIOGEOGRAPHIC OVERVIEW

SUBHRONIL MONDAL, SEBABRATA DAS, SUMANTA MALICK and DEBAPRIYA ADHIKARY

DEPARTMENT OF GEOLOGICAL SCIENCES, JADAVPUR UNIVERSITY, KOLKATA-700032
Corresponding author: Email: subhronil_m@rediffmail.com

ABSTRACT

New assemblages of fossil fish remains have been collected from the Miocene marine beds of Baripada, Orissa, along the river Burhabalang. Although several authors previously described various taxa from the same locality, little was known about their stratigraphic distribution. Present work includes a detailed systematic study, based on numerous specimens along with the establishment of regional stratigraphy and depositional environment. Five new species of sharks are reported here. Among them Isurus desori, Carcharhinus aff. balochenisis and Carcharhinus aff. perseus are described for the first time from the Indian subcontinent; whereas Isurus oxyrinchus and Galeocerdo cuvieri were not previously reported from Baripada.

The state-of-the-art of the Miocene shark assemblages of the world has been reevaluated in the light of new data. The most diverse shark teeth assemblage has been found to be in Baripada. Diversity patterns have been studied. The species-level faunal correlation using Jaccard similarity coefficient method suggests the persistence of endemism among the major bio-provinces during the early Miocene and reasons for this have been explored.

Keywords: Shark teeth, Miocene, India, Palaeobiogeography, Transgression

INTRODUCTION

The Miocene Epoch was an eventful time interval during which much of the configuration and topography of the modern world began to assume (Theodor, 2005). The tectonism, separation and reassembly of continents triggered a sudden increase of biodiversity both in marine and terrestrial ecosystems. Faunal radiation and modernity especially in marine vertebrates also took place during that time (Theodor, 2005). The early Miocene also experienced global marine transgression and many parts of several continents were under water (Vail et al., 1977). Miocene rocks are therefore reported from many coastal parts of the world as well as India (see Sahni and Mehrotra, 1981) and from adjoining areas (see Vredenburg, 1928). The beds yield diverse shark teeth fossils and other marine biota such as bivalves and gastropods.

In the present endeavor, we have described a rich haul of shark teeth assemblages from areas in and around Baripada, Orissa (Fig.1). Although shark teeth have been previously reported from Baripada (Ghosh, 1959; Mehrotra et al., 1973), their stratigraphic information was inadequate. In the present study, we have collected specimens from several geological sections and the collection includes a sizable number, more than 130 specimens. They all were collected assiduously and systematically with precise stratigraphic background.

The shark teeth assemblages include twelve species belonging to six genera of three families. Five species are the new record from Baripada, of which three are not previously reported from the Indian subcontinent. They are Isurus desori, Carcharhinus aff. balochenisis and Carcharhinus aff. perseus. In systematic revision, we have taxonomically updated many previously described forms, for example, Hyprorhin macloti has been redesignated as Carcharhinus macloti following www.futen.fi.

Sedimentological analysis reveals that fossil shark teeth are found in several beds including the tops of hardground at different levels. Similar co-occurrence of shark teeth and hardground has been found in many areas and stratigraphic levels (e.g. see Tiwari et al., 1998; Adnet et al., 2007).

The elasmobranch faunal radiation that took place during late Eocene-early Oligocene time (Adnet et al., 2007) reached a new height during the early Miocene which coincided with a global marine transgression (Vail et al., 1977; Hallam, 1981; Haq et al., 1987) and elasmobranchs became truly cosmopolitan (details will be discussed later). They were paleobiogeographically widespread and invaded all the faunal provinces. The analysis of the distribution patterns suggests a latitudinal gradient of the elasmobranch diversity which decreases with increasing latitudes. Subtropics were the diversity hotspots. The most diverse assemblage has been found in the present area, Baripada (based on present analysis and literature scanning), although exposures are extremely patchy.

The faunal correlation among the Miocene shark assemblages of the world reveals poor similarity coefficient, which perhaps indicates the persistence of species-level endemism in different bio-provinces. This may be due to intense tectonic activities (Garfunkel, 1998, 2004; Golonka, 2004; Adnet et al., 2007), which culminated in the early Miocene and resulted in creating ecological and geographical barriers, thus facilitated rapid and diverse endemic speciation.

GEOLOGICAL SETTING

Miocene marine beds at Baripada crop out at different places along the eastern bank of the river Burhabalang. The Miocene sediments show lateral facies variation as well as variation along the thickness of each facies. However, some beds are regionally persistent and thus help in stratigraphic correlation. A regional stratigraphic classification, based on several sections, has been shown here (Fig. 2).
Baripada marine lithological units overlie a fluvial suite of sediments comprising pebbly sandstone (base not exposed), and overlying greenish shale (Mondal et al., 2007). The sandstone is poorly sorted, immature and contains numerous highly rounded pebbles and conglomerates of different composition. Cross-stratifications are crudely developed. Shale is intercalated with thin silt layers at places. It is laterally persistent and devoid of any macrofossils.

The lowermost marine unit is coarse-grained immature sandstone with calcareous matrix (Bed no. 1). Its top is highly irregular. This is one of the main fossil-yielding horizons. Besides shark teeth and other fish remains, molluscan fossils (gastropods and bivalves) are also present. Among bivalves, different species of Ostrea (Bhalla and Dev, 1975) are the most abundant and are attached at the top of this bed. Most of the shells are articulated and exhibits an *in situ* orientation, i.e. attached left valve lying below. The average thickness of the bed is 0.6m. This bed is overlain by a whitish limestone (Bed no. 2), which has average thickness of 0.4m. The bed shows no primary structure. Its upper part is very undulating and is characterized by having scours and undercuts. Both the surface of undercuts and scours are infested with borings made by organisms like sponges and encrusted by corals and bryozoans mats. Many borings are occupied by their creators, i.e. calcareous sponges or filled in by the material of the overlying bed. Over this bed lies a 0.5m thick sandstone unit (Bed no. 3). This bed is much similar to the lowermost marine sandstone (Bed no. 1). It is also very coarse to pebbly with calcareous matrix and the top of it is very irregular forming typical karst topography. This bed yields maximum number of shark teeth specimens and other fish remains are also equally abundant. Molluscan fossils are found all through, but oyster shells are mainly restricted to the base. The bed also contains large blocks (average diameter 15-20 cm) of the underlying limestone bed and many of the pebbles and boulders bear all around boring marks. Majority of the limestone clasts are irregular in shape, with sharp boundaries. Oysters are found mostly scattered and disarticulated and having no preferred orientation. The next successive bed is fine sandstone (Bed no. 4) having on an average 2.1m thickness. The grains are well sorted and the bed is whitish in colour. The bed yields new shark teeth assemblage dominated by new species of *Carcharhinus*, besides sparse fossils of gastropods and bivalves. The bed is overlain by a 1.65m thick, highly weathered argillaceous unit. The bed is reported to have a few shark teeth specimens (Chaudhuri, 1958). In spite of our extensive search, we have, not found a single shark tooth fossil. Besides, no other marine fossils has been reported form this horizon. The shark teeth reported by Chaudhuri (1958) may have been exhumed from the older beds and found in this upper horizon.

The shark assemblages described here include species of characteristic Miocene age. However, some are more time-diagnostic forms, for example *C. carcharias* is a characteristic Burdigalian species (lower Miocene), while *I. oxyrinchus* and *H. serra* suggest still older age (Aquitanian- Burdigalian) within lower Miocene (see also Sahni et al., 1981).

Three intra-formational, bored and planar hardgrounds have been recognized in the sequence. They are generally characterized by boring and encrusting organisms. Hardgrounds are ferruginous at places. Association of oyster bivalves and occasional mud cracks suggest very shallow water environments. Presence of scours and undercuts also indicates prevalence of high turbulence (cf. Fursich et al., 1992).

This is also supported by the dominance of boring and attached benthic taxa. The carbonate deposition was the product of

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**EXPLANATION OF PLATE I**

(All X 3)

1. *Carcharhinus aff. bolochenisis* Adnet et al., lingual view. Note stronger serrations at the middle and smooth tip and highly reduced crown.
3. *Carcharhinus (Prionodon) gangeticus* Muller and Henle, labial view.
4. *C. (Prionodon) gangeticus*, same specimen, lingual view.
5. *C. (Prionodon) gangeticus*, lingual view.
6. *Carcharhinus macloti* (Muller and Henle), lingual view.
7. *C. macloti*, same specimen, labial view.
8. *Carcharhinus aff. perseus* Adnet et al., lingual view.
15. *H. serra*, same specimen, lingual view.
early Miocene transgression and the hardground surface at its top may be taken as a maximum flooding surface (MFS) (cf. Bardhan et al., 2002; Fürsich and Pandey, 2003).

SYSTEMATIC PALEONTOLOGY

(All specimens are archived in the Department of Geological Sciences, Jadavpur University, Kolkata-32. Dimensions (in millimeter) are: H(t) = total height of the root, H(c) = height of crown, H(r) = height of root, W(c) = width of crown, W(r) = width of root, T(c) = thickness of crown, T(r) = thickness of root). Measurements of parameters are according to Sahni and Mehrotra (1981), and are followed here.)

**Class** Chondrichthyes Huxley, 1880
**Subclass** Elasmobranchii Bonaparte, 1838
**Order** Carchariniformes Compagno, 1973
**Family** Carcharhinidae Jordan and Evermann, 1896
**Genus** Carcharhinus Blainville, 1816
**Type Species:** Carcharias melanopterus Quoy and Gaimard, 1824

_Carcharhinus aff. balocensis Adnet et al._

(Pl. I, figs. 1-2)

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

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

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

*Galeocerdo sp.* Baijapai and Thewissen, 2002, txt-fig.2f.

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

*Carcharhinus balocensis* Adnet et al., 2007, p. 307-309, fig. 3.

**Material:** A single specimen from Bed 1 of Mohulia; Baripada, Orissa (see Fig. 2).

**Description:** Tooth large, crown triangular in outline, almost equilateral. Both mesial and distal cutting edges are serrated, serrations are coarser at the middle part of the mesial edge and are absent at the tip; the mesial cutting edge is concave while the distal cutting edge is gently convex. The base of the crown is highly reduced, raised and tapered medially towards the tip, this feature is especially prominent in lingual view, in labial view the root-crown boundary is, however not raised and indistinct. The root crown boundary becomes parallel with the mesial edge near the base. The root is robust, fully developed and larger than the crown. A longitudinal furrow at the base of the root which is described as the nutritive groove (cf. Adnet et al., 2007) is not well discernible in lingual view. Several longitudinal feeble striations are visible both in crown and root, they are better seen in the lingual view. Numerous pits are visible on the root; in cross-section root is thicker and gradually becomes thinner towards cutting edge. The cusp is pointed towards the external side.

**Discussion:** Adnet et al. (2007) described the species based on numerous specimens. Previously the holotype and other material were included into *Galeocerdo latidens* by Welcomme et al. (1997). Adnet et al. (2007) convincingly demonstrated that the present species bears synapomorphic characters of *Carcharhinus* present in both upper and lower teeth. They also compared the present species with many Palaeogene and Neogene species of *Carcharhinus*. We here describe the species based on a single upper tooth. It strongly resembles the type material described by Adnet et al. (2007), but our solitary specimen differs only in having some feeble striation marks present in both root and crown. The root-crown boundary in labial view is indistinct. Distinction of the present species from the other *Carcharhinus* species present in Baripada will be discussed in the respective discussion part of the species.

**Specimens**

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*Carcharhinus (Prionodon) gangeticus* (Müller and Henle)

(Pl. I, figs. 3-5)

*Carcharhinus (Prionodon) gangeticus* Müller and Henle, 1841, pl. 2, fig. 22.

*Carcharias (Prionodon) gangeticus* Noetling, 1901, pl. 25.

*Carcharhinus (Prionodon) gangeticus* Mehrotra et al., 1973, p. 183, pl. 1, fig. 2.

**Material:** Seven upper teeth from Bed 4 of Mohulia and Mukurmatia, Baripada, Orissa.

**Description:** Tooth moderately large, with maximum height and width are 14.99 mm and 15.6 mm respectively. Shape of the tooth is triangular, but typically asymmetrical, where width exceeds height; tooth is oblique with serrations on both the edges, covering both tip and the heel, however serrations are more prominent towards the base. External surface of the crown...
is generally flat, but for larger specimen it may have a shallow feeble triangular pit at the centre; internal surface is always convex, anterior margin is broadly convex in outline and large, while posterior margin is small with a prominent concavity near the base. Root is relatively broad, greater than height of the crown, thick, with a bifurcating base, nutritive groove is well discernible in some specimens, which is deep, wide and continues up to the basal margin of the root.

Discussion: Mehrotra et al. (1973) described the species from the same locality at Baripada. However, their description was based on a single, small specimen and therefore, intraspecific variability has not been mentioned.

Mehrotra et al. (1973) also described a new species, *C. jhingrani* from Piram Island, Gujarat. (pl. 1. fig. 1) and mentioned that *C. (P.) gangeticus* is distinguished from *C. jhingrani* by having concavity at the base of the crown, uniform serrations and broader root.

The present species can also be compared with the *Carcharhinus* sp. 2 described by Adnet et al. (2007) from the early Oligocene horizons of Balochistan, Pakistan. Both are having oblique upper teeth, which are uniformly serrated; width exceeds height and prominent nutritive groove. However, the population of *C. sp. 2* is smaller in size with maximum height and widths are 9 mm and 10 mm respectively, whereas the Baripada species may attain a maximum size of about 15 mm height and 15.6 mm width.

Because of the smaller size and older stratigraphy of *C. sp. 2*, we refrain ourselves from synonymising it with the present species.

*C. (P.) gangeticus* is also comparable with *C. aff. balochenisis* described earlier. Both have serrations on both the cutting edges, width is greater than the height and large size of tooth. But, *C. aff. balochenisis* differs in having raised root-crown boundary and longitudinal striations on both root and crown, better visible at lingual view.

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*Carcharhinus macloti* (Müller and Henle)  
(Pl. I, figs. 6-7)

*Hypoprion macloti* Müller and Henle, 1841, pl. 1, fig. 21.  
*Hypoprion macloti* Mehrotra et al., 1973, p. 186, pl. 1, fig. 7.

Material: Two specimens from Bed 4 of Mohulia; Baripada, Orissa.

Description: Tooth very small and triangular in shape, higher than broad; crown erect to oblique, and slightly incurved outward at the apex. Mesial edge with a prominent notch; mesial and distal cutting edges are straight, edges are smooth; at anterior margin near base four prominent denticles present. Labial surface is flat, while lingual surface is convex; crown-root boundary in labial view is straight, while in lingual view it is convex; root broader than high, thicker than cusp and feebly bifurcated; a nutritive channel is present lingually at the middle of the root.

Discussion: The present species has been previously described under *Hypoprion* and is re-assigned here within *Carcharhinus* following www.funet.fi (May, 2008).

Mehrotra et al. (1973) described the species based on a
broken specimen from Kutch. Their specimen strongly resembles the Baripada material in many respects. However, Kutch specimen is slightly broader than high, while all the present specimens have greater values of height. This may be due to incomplete preservation of the Kutch specimen.

*C. maclotti* may be compared with the contemporary *C. aff. balochenensis* described here. Both species have similar oblique crown, bifurcated root and convex inner and flat outer surface. But, *C. maclotti* can be distinguished by its smaller size, smooth cutting edges and presence of denticles near the base.

*C. maclotti* also shows marked similarities with another Baripada species, *C. (P.) gangeticus* in having similar nature of external and internal surfaces, being higher than broad and bifurcated root. However, *C. maclotti* is non-serrated and has basal denticles which are lacking in *C. (P.) gangeticus*.

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*Carcharhinus aff. perseus* Adnet et al.

(Pl.I. figs. 8-10)

*Carcharhinus aff. perseus* Adnet et al., 2007, p. 309-312, fig. 4.

**Material:** Five specimens from Beds 1 and 3 of Mohulia; Baripada, Orissa.

**Description:** Tooth medium in size (maximum being 13.87 mm height and width; 7.74 mm); crown resembling equilateral triangle in outline, higher than broad, compressed in nature, erect to slightly oblique. Mesial heel is absent in the upper jaw and slightly developed in lower jaw, distal heel well developed and extends below the root-crown boundary; both mesial and distal cutting edges are ornamented with fine and uniform serrations; both cutting edges are concave, however degree of concavity varies. Distal heel is serrated; crown is larger than root, but in some variants they may be more or less equal; root-crown boundary is mostly convex in lingual view, but may be straight; root is always thicker than crown; a narrow, constricted nutritive groove is present at the middle of the root in lingual side; in labial view a short groove mainly restricted near the base of the crown may be present.

**Discussion:** *C. aff. perseus* has been vividly described by Adnet et al. (2007). The Baripada specimens closely correspond with Balochistan material in major morphological detail. However, the present teeth are mostly smaller in size and differ in some other morphological aspects, for example, Balochistan material have serrations on cutting edges which are stronger near the base, whereas in the present assemblage the serrations are uniform. Moreover, the ratio between the crown and the root is higher for Baripada specimen (1.5) than those of Balochistan (1.2).

Adnet et al. (2007) compared C. aff. perseus with some fossil shark teeth from other regions. *C. jhingrani* which was reported from the Miocene of Piram island in India (see Mehrotra et al. 1973, pl. 1, fig. 1; Sahni and Mehrotra, 1981, pl. 2, fig. 3) can be compared with *C. aff. perseus* in having "equilateral crown, broad root and vertical root extremities" (Adnet et al., 2007, p.310). But, *C. jhingrani* can be distinguished by its "lesser arched basal edge of the root and a deep nutritive groove" (Adnet et al., 2007, p.310).

*C. aff. perseus* may be compared with *C. aff. balochenensis* described here. Both species have similar oblique crown, bifurcated root and convex inner and flat outer surface. But, *C. maclotti* can be distinguished by smaller size, smooth cutting edges and presence of denticles near the base.

*C. aff. perseus* also shows marked similarities with another Baripada species, *C. (P.) gangeticus* in having similar nature of external and internal surface, being higher than broad and having bifurcated root. However *C. maclotti* is non-serrated and has basal denticles which are lacking in *C. (P.) gangeticus*.

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**Genus Galeocerdo** Müller and Henle, 1837

**Type species:** *Galeocerdo cuvier* Peron and Le Sueur, 1822

*Galeocerdo cuvier* Le Sueur

(Pl.I. figs. 11-12)

*Galeocerdo cuvier* Mehrotra et al., 1973, p. 184, pl. 1, fig. 3.

*Galeocerdo cuvier* Sahni and Mehrotra, 1981, p. 109, pl.2, fig. 12.

**Material:** A single tooth from Bed 4 of Mohulia; Baripada, Orissa.

**Description:** Tooth large, sub-triangular, irregular in shape, broader than high and highly oblique. Crown is labio-lingually thickened; the mesial cutting edge has a deep notch, distal margin strongly convex; both cutting margins are serrated; strength of serrations becomes weak to obsolete near the apex; at distal cutting edge strength of serrations are coarser at the middle, decreases towards the base and the apex, whereas mesial edge serrations are finer and uniform. Mesial heel is extended, with numerous denticles, size of the denticles increases proximally. On the labial surface a prominent triangular pit is present at the middle near the root; labial surface bears few longitudinal striations; crown-root boundaries at both faces are convex, convexity more pronounced in lingual side. Root higher than crown; in cross-section it is labio-lingually arched and thicker at the middle part; in profile the tooth deflects outward.

**Discussion:** *G. cuvier* has been reported from the lower Miocene beds of different localities in Gujarat. The figured specimens of this species described by Mehrotra et al. 1973 (pl. 1 fig. 3) from Kutch and Sahni et al. (pl. 2, fig. 12, locality not specified) are almost identical to the present specimen. This suggests that the species shows no geographic variations. Mehrotra et al. (1973) described a new species *G. wyniei* (pl.1, fig. 4a and 4b) from the same locality and stratigraphic level of Kutch. It is distinguished from *G. cuvier* by its compressed shape and broader tooth (height one-third of the width). Furthermore, serrations are present at the apical part of the *G. wyniei* while it is weak to obsolete in *G. cuvier*.

*G. aduncus* has been reported by Sahni et al. (1981, pl. 2, fig. 15) from the lower Miocene horizon of Kutch. *G. aduncus* resembles *G. cuvier* in overall shape of the cutting edges. The species is distinctly less broad than *G. cuvier* and has much coarser serrations on the anterior margin, which continue up to the apex without showing any sign of attenuation.

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**Family Hemigaleidae** Hasse, 1879

**Genus Hemipristis** Agassiz, 1843

**Type Species:** *Hemipristis serra* Agassiz, 1843
Hemipristis serra Agassiz
(Pl. I, figs. 13-15)

Hemipristis serra Ghosh, 1959, p. 677, pl. 88, fig. 1, 6.

Hemipristis serra Mehrotra et al., 1973, p. 185, pl. 1, fig. 5.

Hemipristis serra Tiwari et al., 1998, p. 11, pl. 1, fig. 1.

Material: Two specimens from Bed 4 of Mohulia; Baripada, Orissa.

Description: Tooth medium in size, crown triangular, higher than broad and slanted distally. Both labial and lingual faces of crown and root are convex; mesial and distal cutting edges are serrated, serration conspicuous at the middle, coarser in the mesial surface than that of distal surface. Denticles are present at the base of the mesial edge and strength of denticles increases upward, apex is characteristically devoid of any serration. Labial surface is flat to convex, whereas lingual surface is always convex. In labial view a long longitudinal groove is present at the middle that extends from crown-root boundary towards apex; in lingual view few longitudinal striations are present on the crown. Heels are prominent at both edges; crown-root boundary in the lingual view is convex towards apex and straight labially. Root thickened, broader than high, thicker at middle and bifurcated. A longitudinal furrow at the base of the root which is described as the nutritive groove (cf. Adnet et al., 2007) is deep, continuing up to the base and situated on a 'lingual protuberances' of the root.

Discussion: H. serra is a spatiotemporally widely distributed species (see Tiwari et al., 1998 and Adnet et al., 2007). In India it is reported from both eastern and western coasts including the present locality Baripada (Ghosh, 1959). Mehrotra et al. (1973) commented that C. feddeni of Tewari et al. (1964) described from Kutch, is identical with H. serra and they synonymized the two species.

Mehrotra et al. (1973) described a new species H. sureshi co-occurring with H. serra in Kutch. They distinguished H. sureshi from H. serra in being smaller in size, more oblique and having smooth distal margin. Adnet et al. (2007) compared H. serra with Eocene species H. curvatus from the Eocene bed of Pakistan. They found that H. curvatus is larger in size and its mesial edge has more than three denticles on upper teeth. In the present material H. serra also has denticles as many as five.

Hemipristis cf. H. serra described by Adnet et al. (2007) shows gradation between H. curvatus and H. serra, especially with respect to serration in mesial cutting edge. H. curvatus is an Eocene species while H. serra ranges from Oligocene to Neogene (Cappetta, 1987 and references therein). Adnet et al. (2007) therefore, believed that H. serra evolved from H. curvatus.

Specimens H(t) H(c) H(r) W(c) W(r) T(c) T(r)
1 13.19 8.06 5.38 11.19 — 2.24 2.49
2 14.93 8.68 5.8 12.71 12.8 2.34 2.35
3 17.34 9.41 7.63 13.65 13.2 3.13 3.18
4 — 9.63 — — — 3.56 3.69
5 15.21 9.31 6.34 12.02 12.09 — —
6 17.36 11.91 5.83 16.18 15.61 2.17 —
7 16.69 10.86 8.66 14.82 14.86 2.93 2.99
8 12.65 9.24 3.23 — 2.1 3.05
9 18.24 11.34 9.13 16.69 16.26 3.51 3.69
10 15.58 8.96 6.55 15.25 — 3.05 3.16
11 8.04 5.28 2.72 5.81 6.72 1.27 1.29
12 — 7.32 — — — 1.84 2.21
13 10.43 5.68 4.85 7.01 — 2.3 2.64
14 11.49 6.73 4.5 10.07 10.03 1.57 2.23
15 8.78 5.64 3 5.81 7.5 1.2 1.32
16 9.62 5.43 4.95 7.85 8.04 1.52 1.79
17 — 9.19 — — 2.63 —
18 14.38 8.01 5.78 9.44 10.49 2 2.36
19 12.48 6.11 5.08 10.09 10.58 1.94 2.12
20 — 8.43 — — 2.81 —
21 — 11.79 — — 2.62 —
22 13.48 9.2 4.7 11.78 13.24 2.04 2.29
23 16.18 8.12 7.06 12.6 14.07 2.27 2.54
24 12.84 8.44 5.18 10.61 10.48 2.12 2.34
25 — 7.9 — — 2.62 2.72
26 11.25 6.36 8.41 10.48 — 2.23 3.03
27 10.23 6.7 3.82 — 1.78 2.16
28 — 6.51 — — 1.58 1.63
29 18.79 — 17.43 — — —
30 8.51 4.65 3.64 — 1.31 1.55
31 — — — — — —
32 — — — 6.3 6.46 1.43 1.51
33 — 7.59 — — 1.9 2.35
34 5.52 2.73 2.19 3.87 5.65 0.8 1.7
35 — 6.95 — — 1.58 2.9
36 — 6.61 — — 2.1 —
37 — — 2.24 7.38 — 1.53 1.52
38 7.46 4.72 2.59 5.45 — 1.13 1.49
39 6.53 3.25 2.46 5.06 5.36 0.75 1.1
40 4.6 3.47 2.9 — — 0.75 —
41 4.63 2.89 1.71 4.44 4.88 0.75 0.59
42 — — — — 1.41 —
43 5.12 2.76 2.36 — 0.86 1.43

Remarks: Mehrotra et al. (1973) provided a detailed description of the species and they reported it from Baripada, Orissa and Kutch, Gujarat. Their description however based on two specimens. Our present collection includes forty six specimens of different ontogenetic stages. We therefore here provide, in addition, intraspecific variability of some characters. Majority of the teeth having height greater than width, but in some variants the height and the width may be more or less equal (see Plate II, figures 1 and 2). Although serrations of the cutting edges are uniform, serrations are relatively coarser towards the base in larger specimens. Mesial edge is more concave than distal edge, mesial concavity shows wide variations, some are feebly concave or straight (see Plate II, figure 3 and 4). Labial surface is diagnostically flat, however at the tip it may be slightly inwardly curved. Nutritive groove is seen in some specimens, it is short, narrow and restricted towards the base of the root which may be feebly bifurcated or flat.

Order Lamniformes Garman, 1885
Family Lamnidae Müller and Henle, 1838
Genus Carcharodon Müller and Henle, 1841
Type Species: Squalus carcharias Linnaeus, 1758
Carcharodon carcharias Linnaeus
(Pl. II, figs. 1-4)

Carcharodon carcharias Mehrotra et al., 1973, p. 191-192, pl. 2, figs. 2, 6 a-b.
Carcharodon carcharias Tiwari et al., 1998, p. 12, pl. 1, fig. 5, 6.

Material: Forty six specimens from Beds 1, 3 and 4 of Mohulia, Mukurmatia, Balipal and Baghdahi; Baripada, Orissa.
Carcharodon megalodon Agassiz  
(Pl. II, figs. 5-6)

Carcharodon megalodon Ghosh, 1959, p. 675-676, pl. 88, figs. 10, 19.  
Carcharodon megalodon robustus Ghosh, 1959, p. 676, pl. 88, fig. 5, 16.  
Carcharodon megalodon robustus Mehrotra et al., 1973, p. 189, pl. 2, 1.

Material: Eight specimens from Beds 1, 3 and 4 of Molihula, Mukurmatia and Baghadhia; Baripada, Orissa.

Remarks: The present species has been previously described by Ghosh (1959) from Baripada. Subsequently Mehrotra et al. (1973) reported it from Kutkut. The early specimens from Baripada are very large (height: 42.5 and width: 36.5) and Ghosh described a subspecies C. megalodon robustus also from Baripada. The present specimens are smaller in size and their maximum height is 18.18 mm. But they correspond well with the shape and other characters including the diagnostic collar near root-crown boundary.

Specimens  H(t)  H(e)  H(r)  W(c)  W(r)  T(c)  T(r)  
1  17.74  9.26  2.64  8.9  14.55  2.53  3.17  
2  16.16  8.72  6.16  11.99  11.38  2.28  3.03  
3  13.51  6.58  6.42  12.12  13.16  1.75  2.52  
4  8  8.15  2.11  2.44  
5  14.89  7.67  6.96  13.52  13.1  2.11  2.44  
6  18.18  10.1  5.98  11.84  —  2.4  4.52  
7  12.71  7.61  3.43  12.05  10.57  2.01  2.58  
8  12.5  7.68  4.02  8.3  10.21  1.73  2.09  

Genus Isurus Rafinesque, 1810

Type species: Isurus oxyrinchus Rafinesque, 1810

Isurus desori Sismonda  
(Pl. II, figs. 7-11)

Material: Thirty eight specimens from Beds 1 and 3 of Molihula, Mukurmatia and Baghadhia, Baripada, Orissa.

Description: Tooth triangular, equilateral, slender; crown much higher than broad and erect; both mesial and distal cutting edges are uniformly and finely serrated. Labial surface is flat with a prominent triangular groove present at the middle near the root and never reaches the apex. Lingual side is strongly convex; lateral heels are present, equipped with serrations; root-crown boundary is convex lingually. Root is broader than high and may be strongly bifurcated; in cross-section the root is swollen at the middle and becoming thinner distally; a long, constricted nutritive groove is present lingually at the middle of the root and it continues up to the base of the root; in profile, cutting edges are sigmoid, apex pointing externally.

Discussion: The present finding of I. desori is a new record from Baripada as well as from India. Previously it has been reported from North and South America, Netherland and Chile (www.buriedtreasurefossils.com). I. desori is an extinct species, ranging between early to middle Miocene (www.naturepreserved.com). It is believed that I. desori gave rise to I. oxyrinchus and the evolution was anagenetic (www.fossilguj.com). Detailed comparison and evolutionary relationship between I. desori and I. oxyrinchus will be discussed in the discussion part of I. oxyrinchus.

Specimens H(t) H(e) H(r) W(c) W(r) T(c) T(r)  
1  13.73  8.29  5.33  4.6  10.81  2.72  2.85  
2  11.24  4.53  3.1  —  
3  14  8.56  5.96  3.82  2.52  3.65  
4  13.71  7.59  6.02  4.16  2.81  3.53  
5  15.68  8.54  7.49  3.68  2.42  3.81  
6  14.06  8.08  6.24  4.42  9.46  2.58  3.72  
7  13.71  7.61  6.37  8.96  2.87  3.83  
8  15.12  8.18  5.34  5.3  10.55  3.29  
9  9.1  5.32  3.21  3.7  
10  9.7  5.64  3.35  2.96  1.82  1.97  
11  12.74  7.55  4.77  3.89  2.52  3.81  
12  10.74  6.29  4.69  2.65  3.91  
13  7.92  3.13  2.39  2.98  
14  6.93  4.03  2.23  
15  9.25  6.32  3.23  5.43  1.06  1.49  
16  11.1  6.15  5.01  2.8  2.08  2.92  
17  10.83  5.49  5.13  4.23  7.02  
18  4.75  2.93  7.79  1.66  2.2  
19  8.57  5  3.58  2.76  5.57  1.37  1.56  
20  8.86  4.05  4.36  1.63  7.65  1.24  2.21  
21  8.11  5.14  3.01  2.42  6.35  1.42  1.8  
22  4.47  3.15  9.64  1.64  2.68  
23  3.62  3.41  6.65  1.36  1.79  
24  10.06  —  —  —  
25  7.86  3.12  1.77  
26  7.62  3.37  2.62  1.49  1.45  
27  1.54  —  1.98  2.3  
28  6.56  4.47  2.34  2.2  5.18  0.81  1.09  
29  5.93  3.65  2.43  1.63  1.06  1.5  
30  5.89  3.58  1.16  1.58  
31  10.86  6.36  4.53  4.14  10.65  2.24  2.01  
32  4.34  2.96  2.74  1.22  1.69  
33  6.23  3.09  1.53  
34  6.35  1.21  1.24  
35  9.07  1.8  2.04  
36  5.09  2.78  2.3  1.48  6.21  0.81  1.33

EXPLANATION OF PLATE II  
(All X 3)

1. Carcharodon carcharias Linnaeus, lingual view.
2. C. carcharias, same specimen, labial view. Note height: width ratio is almost equal.
3. C. carcharias, labial view.
4. Carcharodon carcharias, labial view.
6. C. megalodon, same specimen, labial view.
7. Isurus desori Sismonda, labial view. Note a triangular pit at the middle near the base.
8. I. desori, labial view.
10. I. desori, lingual view. Note a long, constricted nutritive groove at the middle of the groove.
11. I. desori, labio-lingual view.
12. Isurus oxyrinchus Rafinesque, labio-lingual view.
13. I. oxyrinchus, same specimen, lingual view.
14. I. oxyrinchus, labial view.
15. I. oxyrinchus, same specimen, lingual view.
Isurus oxyrinchus Rafinesque
(Pl. II, figs. 12-15)

Isurus spallanzani Bonaparte, 1839, pl. 1, fig. 1.
Carchariolamna heroni Hora, 1939, pl.13, fig. 1-4, text-fig. 1b
Carchariolamna heroni Tewari, 1954, p.14
Carchariolamna heroni Tewari, 1959, p. 232a, pl. X
Isurus spallanzanii Mehrotra et al., 1973, p. 187, pl. 1, fig. 10, a-b
Isurus spallanzanii Sahni and Mehrotra, 1981, pl. 1, fig. 2.
Isurus spallanzanii Tiwari et al., 1998, p. 12, pl. 1, fig. 7, 8.

Material: Fifteen specimens from Beds 1 and 3 of Mukurmata, Bagadiha and Mohulia; Baripada, Orissa.

Description: Tooth slender, erect, higher than broad; crown thick and chisel shaped; crown surface smooth and blades are prominent near apex; both lingual and labial surfaces convex, but become flatter near apex. Root is swollen at middle part, strongly bifurcated with short and thick lateral branches; crown-root boundary is convex in lingual side and straight in labial view; in profile the tooth is sigmoid, with apex pointing towards external side.

Discussion: Hora (1939) previously described the species as Carchariolamna heroni from Balasore, Orissa. Again, Tewari (1954, 1959) reported and described the same species from the Miocene beds of Kutch, western India. Based on their description and illustrations it is evident that C. heroni is conspecific with I. oxyrinchus since there are many similarities of the diagnostic characters. However, the present Baripada specimens differ from the specimens of both Hora (1939) and Tewari (1959) only in relative thickness of the teeth, Baripada specimens being thicker.

Isurus spallanzani previously described from many places including India (Mehrotra et al., 1973; Tiwari et al., 1998). Recently it has been found to be conspecific with I. oxyrinchus (see www.catalogueoflife.org) and therefore I. spallanzanii has been included in the synonymy list.

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<th>H(c)</th>
<th>H(r)</th>
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Family Odontaspidae Müller and Henle, 1839
Genus Carcharias Rafinesque, 1810
Carcharias baripadensis Mehrotra et al. (Pl. III, figs. 4)

EXPLANATION OF PLATE III
(All x 3 except, fig. 4, where scale is given.)

1. Isurus pagoda Noetling, lingual view. Note strong bifurcating root and prominent arrow head.
2. I. pagoda, labio-lingual view.
3. I. pagoda, labial view.
4. Carcharias baripadensis Mehrotra et al., Optical microscope photograph.
5. Aetobatus narinari Euphasian, labial view.
7. A. narinari, labial view.
8. A. narinari, same specimen, lingual view. Note fine and dense ridges.
9. Rhinoptera rauburni White, labial view.
10. R. rauburni, labial view.
11. R. rauburni, labial view. Note prominent longitudinal groove between root and crown.
13. H. aff. Sylvestris
15. Dentex sp., same specimen.
16. Dentex sp. Note the vertical striations.
17. Dentex sp., same specimen.
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Carcharias baripadensis Mehrotra et al., 1973, p. 193, pl. 2, fig. 10, a-b.

Material: Single specimen from Bed 3 of Mohulia; Baripada, Orissa.

Remarks: The species was previously described from Baripada and was based on the monotypic holotype. The present collection includes another specimen. It strongly resembles many diagnostic characters of the present species like minute size, identical shape, which is higher than broad and has much posterior obliquity. However, the crown of the present specimen is more or less straight near the apex, which is directed outward in the type specimen.

Specimens | H(t) | H(c) | H(r) | W(c) | W(r) | T(c) | T(r) |
-----------|------|------|------|------|------|------|------|
1          | 25.37| 1.68 | 1.13 | 0.63 | 2.28 | 0.83 | 1.17 |

Order Rajiformes Berg, 1940
Family Myliobatidae Bonaparte, 1838
Genus Aetobatus Müller and Henle, 1841
Type Species: Raja aquila Linnaeus, 1758
Aetobatus narinari Euphrasen (Pl. III, figs.5-8)
Aetobatus arcuatus baripadensis Ghosh, 1959, p. 678, pl. 88, figs. 12, 17, 18.

Material: Seven specimens from Beds 1 and 3 of Mohulia, Baripada, Orissa.

Remarks: The present species was previously described by Ghosh (1959) from Baripada. He described it as a new subspecies Aetobatus arcuatus baripadensis, based on some ridges which bifurcate near the root (pl. 88, figs.12, 17, 18). Our specimens lack this character like A. arcuatus s. st. In both labial and lingual views the present tooth meets the arcuate root acutely, instead of vertically (as in A. arcuatus baripadensis). Besides, number of ridges are more and relatively fine, than A. arcuatus baripadensis (42 ridges in 33mm breadth for our sample, whereas 24 in 29 mm breadth for A. arcuatus baripadensis).

Specimens | Breadth | Length | Width |
----------|---------|--------|-------|
1         | 3.5     | 1.9    | 0.4   |
2         | 1.8     | 1.8    | 0.3   |
3         | 1.6     | 1      | 0.2   |
4         | 1.2     | 0.8    | 0.1   |
5         | 0.6     | 1.1    | 0.1   |
6         | 0.7     | 0.6    | 0.2   |
7         | 0.8     | 1.1    | —     |

Order Myliobatiformes Compagno, 1973
Family Rhinopteridae Jordan and Evermann, 1896
Genus Rhinoptera (Zygobates) Müller, 1834
Type Species: Myliobatis marginata Saint-Hilaire, 1817
Rhinoptera raeburni White (Pl. III, figs. 9-11)
Rhinoptera raeburni Ghosh, 1959, p. 677, pl. 88, fig. 11.

Material: Eight specimens from Beds 1 and 3 of Mohulia; Baripada, Orissa.

Remarks: The present species was previously described from Baripada by Ghosh (1959). His description was based on two fragmentary specimens. Here, we have additional material and a few observations may be further made. The ridge interval increases during ontogeny. In the occlusal view enamel surface is flat, sloping distally. In the lingual view, a prominent longitudinal groove is present between root and crown.

Specimens | Breadth | Length | Width |
----------|---------|--------|-------|
1         | 1.9     | 0.8    | 0.4   |
2         | 1.5     | 0.6    | 0.4   |
3         | 1.6     | 0.4    | 0.3   |
4         | 1.1     | 0.3    | 0.4   |
5         | 1.1     | 0.8    | 0.7   |
6         | 0.5     | 0.4    | 0.3   |
7         | 0.9     | 0.4    | 0.3   |
8         | 0.5     | 0.3    | 0.2   |

Family Trygonidae Müller and Henle, 1837
Genus Hypolophus Müller & Henle, 1841
Type Species: Hypolophus sephens Müller and Henle, 1841
Hypolophus aff. sylvestris White (Pl. III, figs. 12-13)

Hypolophus sylvestris mohuliyi Ghosh, 1959, p. 678, pl. 88, figs. 2, 9; text-fig.1

Material: Eight specimens from Beds 1 and 3 of Mohulia; Baripada, Orissa.

Remarks: Ghosh (1959) previously described this species from Baripada. He had introduced a new subspecies (Hypolophus sylvestris mohuliyi) on the basis of a complete isolated specimen. The present species is poorly represented in Baripada. Most of the specimens of the present collection are small and fragmented. However they strongly resemble the H. sylvestris mohuliyi in having low crown which is similar in length with that of root; flatter base and the characteristic ridges which are only prominent on the enamel surface.

In a recent systematic revision the generic and family level affinities of sylvestris have been changed following www.zipcodezoo.com. We, have however, provisionally retained the previous phylogenetic framework.

Specimens | Breadth | Length | Width |
----------|---------|--------|-------|
1         | 0.9     | 1      | 5     |
2         | 0.8     | 0.7    | 0.45  |
3         | 0.9     | 0.4    | 0.2   |
4         | 0.7     | 0.3    | 0.5   |
5         | 0.7     | 0.5    | 0.5   |
6         | 0.9     | 0.4    | 0.5   |
7         | 0.7     | 0.2    | 0.4   |
8         | 0.3     | 0.6    | 0.4   |

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii Klein, 1885
Order Acantopterygii Johnson and Patterson, 1993
Family Denticidae
Genus Dentex Cuvier, 1817
Type Species: Sparus dentex Linnaeus, 1758
Dentex sp. (Pl. III, figs. 14-17)

Material: Two specimens from Bed 3 of Mohulia; Baripada, Orissa.

Remarks: The present species was described by Tiwari et al. (1998) from Mizoram, North-East India. They described it on the basis of an isolated sample. Our two specimens (root not preserved) resemble in many morphological aspects. However, in Mizoram specimen the vertical striations are mainly restricted near the base whereas, in the present specimens the striations are continuous from apex to base. Moreover, the Baripada specimens are larger in size than Mizoram specimen.
Table 2: Jaccard similarity coefficients of the Miocene shark genera between area pairs in different important fossil bearing areas of the world. Sources as mentioned in Table 1.

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Table 3: Jaccard similarity coefficients of the Miocene shark species between area pairs in different important fossil bearing areas of the world. Sources as mentioned in Table 1.

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Specimens
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Remarks

Tertiary diversity of selachians was established right from the Eocene-Oligocene times, but they were geographically restricted only in Atlantic, Mediterranean, Central Asia and in some parts of the Eastern Tethys (Adnet et al., 2007 and references therein). The diversity reached its peak during the Miocene (Theodor, 2005) and selachians became truly cosmopolitan. The updated genus and species level lists of Miocene sharks have been shown in the Table 1. Mainly two families dominated the Miocene shark community. Carcharhinidae constituted almost 39.4% of all Miocene selachian species and are represented mainly by three genera, Carcharhinus, Galeocerdo and Hypoprion. Lamnidae (= Isuridae, family level taxonomic revision has been done following Compagnano, 1984) constituted 23.6% of all Miocene selachian species and are represented by two genera.
Table 4: Jaccard similarity coefficients of the Miocene shark genera between area pairs in different important fossil bearing areas of the Indian subcontinents.

<table>
<thead>
<tr>
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<th>West Coast</th>
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Table 5: Jaccard similarity coefficients of the Miocene shark species between area pairs in different important fossil bearing areas of the Indian subcontinents.

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<th>Sri Lanka</th>
<th>Burma</th>
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</table>

*Carcharodon* and *Isurus*. Carcharhinids are shallow water neritic forms, whereas lamnids are pelagic (Sahni and Mehrotra, 1981; Adnet et al., 2007).

Palaeobiogeographic distribution and diversity in important fossil localities at species level of the Miocene selachians is shown in Fig. 3. Miocene sharks are distributed in almost all continents, but the diversity appears to be controlled by latitudinal factors. Diversity is more in the subtropical areas, falling within 30° N and S of the palaeoequator. Beyond this, towards higher latitude the diversity drops. Most of the fossil shark bearing areas and maximum diversity, however, lies in the northern hemisphere. The present-day distribution also depicts more or less the same pattern and latitudinal gradient. Arctic and higher latitude sharks are rare and extant sharks flourish best within 20° C isotherm (see Sahni and Mehrotra, 1981).

Sahni and Mehrotra (1981) have dealt in considerable detail the similarities among important shark fossil-bearing regions of the world and they also compared the Indian Miocene assemblages with other areas. Their two main observations regarding Lower Miocene fossil shark communities are: (1) Indian east and west coast assemblages are different and (2) East coast assemblage (Baripada) shows closer affinity with Burma and New Zealand; while west coast shows much faunal similarity with Mediterranean, Portugal, North America and South Africa.

In the present endeavor, we have revisited the faunal similarities across major fossil-yielding regions based on updated and revised faunal list. We have analyzed the genus and species level data distributed in important areas to calculate the similarity co-efficient by Jaccard method (cf. Campbell and Valentine, 1977). The results are shown in Tables 2 and 3 respectively. The genus-level global correlation coefficient chart (Table 2) provides higher Jaccardian values, implying more or less circum-global distribution of dominant genera. Species-level global result (Table 3), however, reveals poor coefficient values, which perhaps indicates persistence of endemism at this taxonomic category (cf. Bardhan et al., 2007).

The species-level faunal correlation (Table 3) suggests that there existed indistinct faunal provinces with respect to shark assemblages in the Miocene oceans. Even within the Atlantic, the correlation coefficient values range from 0.13 to 0.75. Jaccard correlation coefficient between Brazil and Cuba, however, is higher (0.75). But, again Cuba and different North American Atlantic coasts (Florida, North and South Carolina) show poor values ranging from 0.16 to 0.38. Along the Pacific areas, Peru and Chile show maximum faunal homogeneity (0.42). Between California - Chile and California - Peru the values are 0.23 and 0.33 respectively. While the two North American important fossil bearing localities on either side, i.e. California and Carolina (North and South), having similar latitude (spanning 23° N to 42° N) show poor affinity (Jaccard values 0.13 between California and North Carolina and 0.21 between California and South Carolina respectively), which may suggest that Panama Isthmus might have acted as ecological and geographical barrier. These observations may be supported by the poor correlation between Brazil and Chile and Brazil and Peru (Jaccard value 0.14 and 0.13 respectively). However, poor faunal similarities may not be always attributed to ecology-induced endemism, it may be due to difference in stratigraphy (Adnet et al., 2007). In the present database two species are omnipresent in all faunal localities listed here. One is *Carcharodon megalodon*, but it has a wider stratigraphic range, i.e. Eocene to Pliocene (Sahni and Mehrotra, 1981). On the other hand, *Hemipristis serra*, the other cosmopolitan species, is time-diagnostic only to Miocene and therefore the
stratigraphic factor may be excluded (Sahni et al., 1998). Similar poor faunal similarity is also observed among the fossil localities of the Indian subcontinent (see Tables 4 and 5). Sahni et al. (1981) suggested a marked similarity among shark assemblages of western coast of India, Mediterranean Portugal, North America and South Africa. We have reevaluated the faunal correlation coefficient among these areas based on updated and revised data and the values are 0.15 (with Portugal), 0.16 (with Carolina), 0.11 (with California), and 0.18 (with South Africa). Similarly, eastern coast of India (Baripada) also shows poor similarity coefficient with Burma and New Zealand (0.36 and 0.11 respectively). In fact, poor faunal similarities among shark assemblages of the world persisted from the Palaeogene. Adnet et al. (2007) demonstrated that during the Eocene-Oligocene times, although assemblages were clustered only in few areas, i.e. Western Tethys, North and Central Atlantic and the Eastern Tethys, the faunas were less similar among them. Even within the Eastern Tethys, Balochistan (Pakistan) fauna is poorly correlated with the adjacent Qatar, Egypt and India (Kutch). They observed that this faunal inhomogeneity persisted up to the Paleogene-Neogene transition and may be attributed to tectonism that resulted in the convergence of South Eurasian and African-Arabian plates. Major tectonic changes in many part of the world, for example, the formation of San Andreas Fault Zone of North America; upliftment of the Andes in South America and Great Rift Valley in Africa affected both atmospheric and oceanic circulation patterns of the world. In Eurasia, the continuous elevation of the Tibetan Plateau resulting from the collision between Indian and Asian plates and the separation of Australia from Antarctica drastically affected the oceanic circulation scenario of the world (Raymo, 1994). Poor faunal similarities between western India, Portugal, North America and South Africa may be explained by 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)" during the late-early Miocene (Adnet et al., 2007, p.303; see also Popov et al., 1993; Rögl, 1998, 1999; Adams et al., 1999).

Faunal homogeneity at generic level and disjunct distribution at species level may speak for a close interplay between evolution of sharks and physical changes of the earth during Miocene. Thus, endemism and poor faunal similarities may be explained by the vicariance biogeographic model (cf. Grande, 1990).

In India, Miocene shark assemblages are diverse in Kutch, Gogha coast and Piram Island in western coast and Baripada, the present studied locality, in eastern coast. They show relatively good faunal similarities (Jaccard value 0.33). Both areas were dominated by *Carcharhinus* (12 species in Baripada and 7 species in west coast). The dominance of Carcharhinids indicates tropical near-shore environment and they were found in many littoral habitats of the world, associated with hardground and other shallow-water faunas (Adnet et al., 2007 and references therein). The present Baripada assemblage is also associated with hard ground, mud cracks, in situ oyster bearing horizons, which collectively suggest very shallow water environment. Baripada is situated far inland (almost 60 km. from the present-day coast line) and the fossil shark-bearing marine facies directly overlie the fluvial sediments, when a narrow arm of the Indian Ocean invaded the eastern coast in response to global marine transgression during the early Miocene (Fig. 4).

ACKNOWLEDGEMENTS

We are thankful to Prof. Subhendu Bardhan, Jadavpur University, Kolkata-32 for his guidance and valuable suggestions to make our work successful. Our special thanks go to Prof. P. K. Bose, Dr. Subir Sarkar and Dr. Dipak C. Pal, Jadavpur University for discussion. We express our sincere thanks to Mr. Sabyasachi Shome, Geolgical Survey of India, Mr. Pinaki Roy and Mr. Rabi De, Jadavpur University for their help in photography. Authors are grateful to the reviewer, Prof. Ashok Sahni, Panjab University, Chandigarh for providing valuable suggestions. We are also grateful to our classmates for their co-operation in our fieldwork during 2007. The help rendered by the local people of Baripada and adjacent villages are also acknowledged.

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Manuscript Accepted May 2009