ADDITIONAL VERTEBRATE REMAINS FROM THE EARLY MIOCENE OF KUTCH, GUJARAT

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ABSTRACT

We present here a list of the vertebrate fauna collected during fieldwork carried out in Kutch between 2010-2011 from several early Miocene localities in the Lower Miocene. We describe and comment on fossil remains of fishes (Chondrichthyes and Osteichthyes), reptiles (tomistomid crocodiles) and mammals (Deinotherium sp., Gomphotheriidae indet. and Brachypotherium sp.) from an early Miocene ferruginous Khari Nadi Formation exposed at localities Jangadia, Samda, Pasuda and Baadra. We report for the first time a shark, Megaselachus chubutensis from India and a batoid Rhinoptera from Kutch. A fossil latid fish has also been recorded for the first time from India. Our findings indicate that these fossils were deposited under tropical-subtropical conditions. The present terrestrial and freshwater fauna has common elements in North Africa and Europe and supports hypotheses of faunal exchange between these regions caused by the opening of land route between Afro-Arabian plate and Eurasia in the early Miocene time. However, this land connection might have been disrupted intermittently by marine incursions as appears by the presence of similar shark fauna in all of these areas.

Key words: Early Miocene, Vertebrates, Kutch, Palaeoecology, Palaeogeography.

INTRODUCTION

Kutch Tertiary sequences divided into Matanomadh, Naredi, Harudi, Fulra Limestone, Maniyara Fort, Khari Nadi, Chhasra and Sandhan Formations are exposed circumferentially outwards from the Deccan volcanics, dipping very gently due SSW (Fig. 1.). Right at the boundary of Maniyara Fort and Khari Nadi Formations there exists a ferruginous conglomerate that has yielded an extensive vertebrate fauna including fishes, reptiles and both marine and terrestrial mammals (Wynn, 1872; Prasad, 1964; Mishra, 1976; Sahni and Mishra, 1975; Bajpai and Domning 1997; Bajpai et al. 2006; Thewissen and Bajpai, 2008; 2009; Bhandari et al., 2009). These fossils belong to Khari Nadi Formation that has been considered to be of Aquitanian (23-20 Ma) (Biswas and Raju, 1973; Biswas, 1992; Kumar et al., 2009) or Aquitanian to Burdigalian (Sahni and Mishra, 1975) age. Bhandari et al. (2009), based on a “proboscidean datum” argued that these deposits are around 16.5 Ma old.

A diverse fish assemblage was recovered by Sahni and Mishra (1975) from the early Miocene of Kutch belonging to cartilaginous (Class: Chondrichthyes; subclass: Elasmobranchii) and bony fishes (Class: Osteichthyes; subclass: Actinopterygii). Several taxa of cartilaginous fish belonging to the families Charcharindae, Isuridae, Alopiidae, Sphyrnidae and Carcharidiidae were recovered by these authors. Among the bony fishes perciformes assigned to Diodontidae, Sphyraenidae and Scombridae were also reported (Sahni & Mishra, 1975).

We carried out fieldwork in 2010-2011 covering almost all of the geologic formations of Kutch. We present here our findings from the early Miocene ossiferous ferruginous conglomerate exposed at Jangadaia, Samda, Pasuda and Baadra. We also discuss the paaleobiogeographic significance of our findings.
Fig. 1. A. Broad geological map of Kutch and Kathiawar (Gujarat), showing the distribution of Deccan Volcanics (green) and Tertiary deposits (yellow) and the Early Miocene fossil locality of Pasuda, B. Location and geological map of the study area, Kutch (modified after Biswas, 1992), C. stratigraphic section near Matanomadh showing the vertebrate-bearing horizon (modified after Sahni and Mishra, 1975), D and E exposure of ossiferous ferruginous sandstone and conglomerate near Jangadia and Samda respectively.

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<td>Crocodile snout (KF -40)</td>
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MATERIAL AND METHODS

List of fossil vertebrates reported here is given in Table 1. Enamel samples were prepared for observation under the SEM (JEOL-JSM6490) at Department of Geology, Panjab University. The procedure includes sawing/grinding according to various planes of observation, polishing with abrasive powder, etching with 5% HCl for 60 seconds, cleaning ultrasonically and sputter-coating with gold-palladium. Description of the enamel microstructure was done at hierarchically increasing levels of complexity (see Koenigswald and Clemens 1992). Abbreviations: KF-Kutch Fossils, deposited in the Vertebrate Palaeontology Laboratory, Department of Geology, Panjab University, Chandigarh, India.

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes
**Order Lamniformes** Berg, 1958

*Family Ottodontidae* Glickman, 1964

*Genus Megaselachus* Glickman, 1964

*Megaselachus chubutensis* (Ameghino, 1906)  
(Pl. 1, figs. 1, 2)

**Material, Horizon and Locality:** Four isolated incomplete teeth bearing nos. KF-17A, KF-17B, KF-17C, KF-17D from the Lower Miocene conglomerate bed exposed at Jangadia, Kutch.

**Description:** KF 17a and KF 17b (Plate 1: fig. 1-2) are large, median cusps are broad and triangular; apex of the teeth is nearly pointed, crown higher than the root; labial face of the teeth is flat while the lingual face is smooth and convex. Both of the cutting edges bear fine and regular serrations right from the apex to the crown foot. The median cusp is flanked by a weakly developed lateral cusp. The lingual neck is well developed in both the specimens and is thickest at the median region. The roots are robust and bilobate; lingual protuberances are feebly developed, median nutritive groove is well developed.

**Remarks:** The present specimen is the first report of *Megaselachus chubutensis* from India. Teeth of *Megaselachus* are widely distributed and have been reported from the Miocene and Pliocene deposits of Europe, North and South America, Africa, Australia and Asia (Cappetta, 2006; Cook *et al.*, 2010). Earlier, *Megaselachus chubutensis* was described as *Carcharodon chubutensis* from the Miocene of Argentina (Ameghino, 1906). *Megaselachus chubutensis* has also been reported from the Miocene deposit of Moghra, Egypt (Cook *et al.*, 2010). It is difficult to differentiate *Megaselachus chubutensis* from the juvenile teeth of *M. megalodon* as the later teeth also bear a lateral cusplet (Purdy *et al.*, 2001; Ward and Bonavia, 2001) and both species have also been found in the same deposits (Kent, 1994). The present specimen from Kutch is identical to those of *Megaselachus chubutensis* from the Lower Miocene deposits of Moghra, Egypt (Cook *et al.*, 2010) in having a pair of weakly developed lateral cusplets flanking the median cusp and the size of the specimens are also quite comparable.

**Order Carchirhiniformes** Compagno, 1973

*Family Hemigaleidae* Agassiz, 1843

*Genus Hemipristis* Agassiz, 1943

*Hemipristis serra* (Agassiz, 1843)  
(Pl. 1, fig. 3)

**Material, Horizon and Locality:** An isolated tooth, KF-17E from the Lower Miocene conglomerate bed exposed at Jangadia, Kutch.

**Comments:** Incomplete tooth is of medium size, triangular, higher than broad and the crown is slanted distally. Lingual face of the crown is convex, the labial face of the crown is slightly concave, the root is not preserved and the apex is deflected strongly. Both the mesial and distal edges are serrated and serration at the upper part of the mesial edge is stronger and decreases in size towards the base. *Hemipristis serra* was distributed worldwide during the Miocene and Pliocene (Portell *et al.*, 2008). It has also been described from both the eastern and western coasts of India including the Late Miocene Baripada Beds in the eastern coast (Modak, 1952; Ghosh, 1959; Mohanty, 1966, 1980; Mishra, 1985; Mondal *et al.*, 2009; Milankumar, 2013) and the Lower Miocene shale of Matanumadh and Lakpat (Mehrotra *et al.*, 1973; Sahni and Mehrotra, 1981) in the western coast. Occurrence of *Hemipristis serra* has also been noted from the Late Eocene-Early Oligocene of Balochistan (Adnet *et al.*, 2007) and from the Lower Miocene deposits of Moghra, Egypt (Cook *et al.*, 2010).

**Galeocerdo cuvieri** Le Sueur, 1822  
(Plate 1, fig. 12)

**Material, Horizon and Locality:** An isolated tooth, KF-66 from the Lower Miocene shale bed of Baadra, Kutch.

**Comments:** Teeth of the genus *Galeocerdo* have been described earlier by various workers from the Tertiary of Kutch, Gujarat (Mehrotra *et al.*, 1973; Mishra, 1980; Sahni and Mehrotra, 1981). Previous records of fossil species of *Galeocerdo* described from Kutch include *G. cuvieri* (Mishra, 1980; Mehrotra *et al.*, 1973), *G. aduncas* (Mishra, 1980), *G. cf. semilivis* (Sahni and Mehrotra, 1981), *Galeocerdo wynnei* (Mehrotra *et al.*, 1973). *Galeocerdo cuvieri* has also been reported from the Miocene deposit of Baripada Beds (Mondal *et al.*, 2009; Milankumar, 2013) and *G. aduncas* has been described from the Bhuban Formation, Surma Group of Mizoram (Ralte *et al.*, 2011).

**Order Lamniformes** Berg, 1958

*Family Lamnidae* Muller and Henly, 1838

*Genus Carcharodon* Linnaeus, 1758

*Carcharodon bigelowi* (Mehrotra *et al.*, 1973)  
(Pl. 1, fig. 4)

**Material, Horizon and Locality:** An isolated tooth, KF-
EXPLANATION OF PLATE 1

1-2. *Megaselachus chubutensis* (KF-17A, KF-17B), 3. *Hemipristis serra*, Agassiz 1843 (KF-17E). 4. *Carcharodon bigelowi* (KF-17E), 5. *Carcharodon carcharias* (KF-17G), 6-7. *Carcharhinus* sp. (KF-17J and KF-17K), 8-9. *Myliobatis* sp. (KF-17H and KF-17I), 10. *Rhinoptera* sp. (KF-17L), 11. *Pristis* sp.(KF-17G), 12. *Galeocerdo cuvieri* (KF-66). Figs. 1a, 2a, 3a, 4a, 5a, 6a, 7a, 8a, 9a and 10a are in lingual view and Figs. 1b, 2b, 3b, 4b, 5b, 6b, 7b, 12 are in labial view. Figs. 8b, 9b and 10b are occlusal view, Fig. 11 in lateral view.
**Carcharodon carcharias** Linnaeus, 1758  
(Pl. 1, fig. 5)

*Material, Horizon and Locality:* An incomplete tooth, KF-17G from the Lower Miocene conglomerate bed exposed at Jangadía, Kutch.

*Comments:* Teeth of *Carcharodon carcharias* have been described from Lower Miocene shale of Lakhpat (Mehrotra et al., 1973; Sahni and Mehrotra, 1981), Late Miocene deposits of the Baripada Beds (Ghosh, 1959; Sahni and Mehrotra, 1981; Mondal et al., 2009; Milankumar, 2013), from the Bhawan Formation of Mizoram (Tiwari et al., 1998; Ralte et al., 2011). The present specimen is imperfectly preserved, is of medium size, slightly oblique, margin of the crown is serrated; higher than broad, equilateral triangular in shape, the lingual face is convex and the labial face is flat, lateral cusplet absent, root collar is present, root is bilobate; root thickness is more than the thickness of the crown. The species is found throughout the Miocene to Pliocene deposits of coastal and pelagic zones of tropical and subtropical seas (Serralheiro, 1954; Antunes and Jonet, 1970).

*Order Carcharhiniformes* Compagno, 1973  
*Family Carcharhinidae* Jordan and Evermann, 1896  
*Genus Carcharhinus* Blainville, 1816  
*Carcharhinus* sp.  
(Pl. 1, figs. 6, 7)

*Material, Horizon and Locality:* Isolated teeth, KF-17J and KF-17K from the Lower Miocene conglomerate bed exposed at Jangadía, Kutch.

*Comments:* The teeth of the genus *Carcharhinus* have been reported earlier from the Miocene fossiliferous deposits of Western Coast of India including Piram Island, Kutch, Gogha coast (Sahni and Mishra, 1975; Mehrotra, 1979), from Miocene deposits of Baripada Beds (Ghosh 1959; Mehrotra et al., 1973; Sahni and Mehrotra, 1981; Mondal et al., 2009; Milankumar, 2013) and Miocene deposits of Mizoram (Ralte et al., 2011). KF-17J and KF-17K are incomplete medium size teeth, with oblique crown which is a scalene triangle in shape, asymmetrical, crown oblique; both the mesial and distal cutting edges are finely serrated which are more pronounced towards the base. Lingual face is convex and the labial face is flat, small groove is present in between the root and the crown. Height of the root is nearly equal to the height of the crown (Plate 1: fig. 6). The root is bilobate, broad, lingual face convex and labial face flat. The present taxon is comparable to that of *Carcharhinus* (Prionodon) *gangeticus* in having a scalene triangle shaped crown and nearly equal height of the root and the crown. However, the present taxon possess a more inclined crown which is lacking uniform serration.

*Order Rajiformes* Berg, 1940  
*Family Myliobatidae* Bonaparte, 1838  
*Genus Myliobatis* Dumeril (In Cuvier, 1817: 137)  
*Myliobatis* sp.  
(Pl. 1, figs. 8, 9)

*Material, Horizon and Locality:* Isolated teeth, KF-17H and KF-17I from the Lower Miocene conglomerate bed exposed at Jangadía, Kutch.

*Comments:* KF-17H and KF-17I are small to medium size, incomplete teeth (Plate 1: figs. 8, 9); crown height is nearly equal to the height of the root. In the basal view all of the teeth show roots with prominent ridges and grooves, the loblets generally extend slightly beyond the lingual edge of the crown (Plate 1: figs. 8b, 9b). KF-17H preserves 14 prominent ridges and grooves. The crowns are smooth. The present specimens are comparable to those of *Myliobatis* sp. 1 of Case and Cappetta (1990; p. 19-20, pl. 9, figure 216) and *Myliobatis* sp. 5 (Milankumar and Patnaik, 2013) in having a deep transverse lingual groove between the root and the crown. However, KF-17H (Plate 1: Fig. 8) is comparatively smaller than those specimens. In India, teeth of *Myliobatis* sp. have been reported earlier from the Eocene of Kutch (Mishra, 1980; Bajpai and Thewissen, 2002), Palaeogene-Lower Eocene of Gujarat (Rana et al., 2004), Early Eocene Kapurdi Formation of Rajasthan (Rana et al., 2006), Miocene deposit of Mizoram (2012), Miocene of Baripada Beds (Sahni and Mehrotra, 1981; Mondal et al., 2009; Milankumar and Patnaik, 2013), Eocene deposit of Subathu Formation (Kumar and Loyal, 1987).

*Order Myliobatiformes* Compagno, 1973  
*Family Rhinopteridae* Jordan and Evermann, 1896  
*Genus Rhinoptera* Cuvier, 1829  
*Rhinoptera* sp.  
(Pl. 1, fig. 10)

*Material, Horizon and Locality:* Isolated tooth, KF-17L from the Lower Miocene conglomerate bed exposed at Jangadía, Kutch.

*Comments:* KF-17L (Plate 1: fig. 10) is an incomplete medium size tooth, hexagonal in shape; anterior and posterior faces are slightly slanting; crown is thick and
sloping forward, the anterior and posterior faces are seldom vertical; the root coarsely ridged and grooved; enamel surface is slightly worn out, root is damaged, longitudinal groove is present in between the root and the crown. The present specimen is the first record of *Rhinoptera* teeth from the Lower Miocene deposit of Kutch. Earlier, Rhynopteridae teeth have been described from the Palaeogene-Lower Eocene of Gujarat (Rana et al., 2004), *Rhinoptera raeburni* from Late Miocene shale of Baripada Beds (Ghosh, 1956, 1959 and Mondal et al., 2009; Milankumar and Patnaik, 2013, in press) and *Rhinoptera aff. sherburni* from the limestone of Baripada (Milankumar and Patnaik, 2013, in press).

**Superorder Pristoidea**

**Family Pristidae** Bonaparte, 1838

**Genus Pristis** Link, 1790

*Pristis sp.*

(Pl. 1, fig. 11)

**Material, Horizon and Locality:** KF-17G is an isolated rostral tooth from the Lower Miocene conglomerate bed of Jangadia, Kutch.

**Comments:** The specimen is poorly preserved, incomplete and its identification is very difficult. Earlier, rostral tooth of *Pristis aquitinicus* have been described from the limestone bed of Baripada Beds (Ghosh, 1959; Milankumar and Patnaik, 2013). This is the first record of the fossil remains of the genus *Pristis* from the Lower Miocene deposit of Kutch.

**Teleostei** Müller, 1846

**Perciformes** Bleeker, 1859

**Latidae** Jordan, 1923

*Latidae indet.*

(Pl. 2, figs. A, B and C)

**Material, Horizon and Locality:** KF-30 is a neurocranium from the Lower Miocene conglomerate bed exposed at Jangadia, Kutch.

**Comments:** The specimen is weathered but shows the diagnostic feature of a latid neurocranium such as the presence of a supraoccipital crest extending far forward between the frontals. It has a wide and strongly ossified neurocranium similar to that found in extant latid species such as *Psammoperca waigiensis*, *Lates niloticus*, *L. calcarifer*, *L. longispinis* and *L. macrophthalmus* (Greenwood, 1976; Otero, 2004). The specimen recorded here requires further preparation and will be described in detail later on. Most of the fossil latids come from the Paleogene and Neogene of North Africa and Europe (Murray and Attia, 2004; Otero, 2004).

**Class Reptilia**

**Crocodyliformes** Clark in Benton and Clark, 1988

**Mesoeucrocodylia** Whetstone and Whybrow, 1983

**Neosuchia** Clark In Benton and Clark, 1988

**Eusuchia** Huxley, 1875

**Crocodilia** Gmelin, 1789

**Family Crocodylidae** Cuvier, 1807

**Subfamily Tomistominae** Kälin, 1955

*Tomistominae indet.*

(Pl. 3, figs. A and B)

**Material, Horizon and Locality:** A snout KF-40 from the Lower Miocene conglomerate bed exposed at...
Samda, Kutch.

**Description:** The premaxilla is completely preserved. The anterior plate in front of the external narial aperture is thin-walled and steep and does not have the perforation for the 1st mandibular tooth. The posterodorsal processes of the premaxillae reach backward to the level of the anterior part of the third maxillary alveolus. The premaxillary foramen, foramen incisivum, is triangular in shape and is situated between the 2nd and 3rd premaxillary teeth. There are five pairs of premaxillary alveoli preserved. The anteriormost, the 3rd and the 4th pair of alveoli are quite large and the posteriormost pair is the smallest. In ventral aspect, the premaxillo-maxillary suture is irregularly shaped and reaches backward to the level of the second maxillary alveolus. There is a clear lateral constriction between the premaxillae and the maxillae. The nasals are in contact with the premaxillae. The nasal-premaxillary suture is W-shaped. The nasals are isolated from the posterior border of the external naris by the premaxillae. The dorsal surface of the snout is slightly sculptured by numerous small shallow pits. Features such a nasal-premaxillary contact and enlarged anterior maxillary alveoli supports a tomistomine affinity.

**Class Mammalia**

**Order Proboscidea** Illiger, 1811

**Family Deinotheriidae** Bonaparte, 1841

**Genus Deinotherium** Kaup, 1829

*Deinotherium* sp. Indet.  
(Pl. 4, fig. A; Pl. 5, figs. A-E)

**Material, Horizon and Locality:** Two upper molars (M1, M2) KF-27 embedded in the Lower Miocene conglomerate bed exposed at Samda, Kutch.

**Description:** The two molars are eroded along the longitudinal section exposing the dentine and the enamel (Plate 4 A). The molars appear bilophodont and show presence of anterior and posterior cingulii. The approximate molar length is 6 cm. The crown height is approximately 5 cm. Near the EDJ (Enamel Dentine Junction), the 3DE (3 Dimensional Enamel) is developed showing decussating bundles of prisms (Plate 5 B and D). From the middle to the outer surface of the enamel (OES), HSB (Hunter Schreger Band) and RE (Radial Enamel) can be seen (Plate 5 A). In the RE prisms are nearly perpendicular to the OES (Plate 5C). Key-hole Pattern 3 prisms vary in diameter from 5 to 7 µm (Plate 5 E).

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**EXPLANATION OF PLATE 3**

A. Dorsal and B. ventral views of the premaxilla of Tomistominae indet (KF-40).
EXPLANATION OF PLATE 4

A. *Deinotherium* molars embedded in the ferruginous conglomerate (KF-27). B and C cross section and surface view of Gomphotheridae indet. molar fragment (KF-76). Scale bar represents 1 cm.
EXPLANATION OF PLATE 5

A. Vertical section of *Deinotherium* molar enamel (KF-27). Depending on the direction of the light relative to prism orientation, single bundles of prisms (a, b) appear as either light or dark bands. B. Enamel zone with bifurcating HSB. C. Outer enamel zone with nearly parallel prisms showing radial enamel (RE) close to OES. D. Close up of the B image showing cracks running parallel to HSBs. E. A typical keyhole enamel pattern.
Family Gomphotheriidae Hay, 1922  
Genus and species indet.  
(Pl. 4, figs. B, C; Pl. 6, figs. A-D)  
Material, Horizon and Locality: A molar enamel fragment KF-76 from Lower Miocene conglomerate bed exposed at Pasuda, Kutch.  
Description: The outer enamel surface of the molar fragment KF-76 shows corruagtion and has small ridges and tubercles (Plate 4 C). A vertical section of gomphotheriidae molar shows a thick enamel layer (Plate 4 B). Prism bundles are oriented towards the occlusal surface of the molar. Three enamel layers can be distinguished at the mid-crown, on the basis of prism orientation. An inner layer with 3DE (Plate 6A, B and C) is present at the enamel dentine junction. This zone represents ~15% of the total enamel thickness (Plate 6A). The middle layer is formed by HSB and RE and the outer layer composed of RE with prisms nearly perpendicular to the OES (Plate 6A). Fan-shaped Pattern 3 prisms vary in diameter from 7 to 9 µm (Plate 6 D).  
Comments on the proboscidean enamel microstructure: The proboscidean dental enamel has evolved in response to dietary preferences and mechanical adaptation, which is reflected in its microstructure. The variation so developed helps in understanding the phylogenetic relationships among various taxa. Since the fossils collected here are fragmentary in nature we have attempted to compare their molar enamel microstructure to those of well studied forms such as Barytherium (Bertrand 1988, 1989), Moeritherium (Bertrand 1988, 1989; Přefetzschner 1994), Deinotherium (Bertrand 1988, 1989; Přefetzschner 1994), Palaeomastodon (Kozawa 1978; Bertrand 1988, 1989; Přefetzschner 1994), Phiomia (Bertrand 1988, 1989; Přefetzschner 1994), Gomphotherium (Fox 2000), Stegodon and Elephas (Ferreti, 2008; Kozawa, 1978). Differences between various taxa can be seen in the morphology of the prism cross-section in molars. Prisms showing a typical keyhole pattern with a nearly rounded prism head is seen in Moeritherium, Deinotherium and Phiomia. Gomphotherium and Anancus prisms show a fan-shaped head. Stegodon and Elephas are characterised by a Gingko-leaf pattern (Kozawa 1978). Proboscideans show three basic types of prismatic enamel: radial enamel (RE), Hunter-Schreger Bands (HSB), and 3D enamel (3DE). In Moeritherium molars, at mid-crown, HSB are relatively thin, of nearly constant thickness and straight (Bertrand 1988; Přefetzschner 1994). In contrast, the elephantoid molars show more complex HSB, characterized by an undulated path, irregular thickness and frequent bifurcations of the bands. A three-layered (3DE-HSB-RE) schmelzmuster is found in Gomphotherium, Anancus, Stegodon and Elephas. Deinothieves and “barytherioids” markedly differ from the pattern of Moeritherium and the Elephantiformes (i.e., Palaeomastodon, Phiomia plus Elephantoidea) in having an almost completely decussated enamel consisting of 3DE (Bertrand 1988, 1989). But, contrary to previous observations, we have observed presence of HSBs in Deinotherium, as well as 3DE.

Order Perissodactyla Owen, 1848  
Superfamily Rhinoceroidea Owen, 1845  
Family Rhinocerotidae Gray, 1821  
Tribe Teleoceratini Hay, 1902  
Genus Brachypotherium Roger, 1904  
(Type Species: Rhinoceros brachypus Lartet, 1837)  
Brachypotherium sp.  
(Pl. 7, figs. A, B, C, D, E and F)  
Material, Horizon and Locality: An m3 KF-9A and a mandible with p2 KF-9B from the Lower Miocene conglomerate bed exposed at Jangadia respectively, Kutch.  
Description: The p2 is a part of the mandible KF-9. It is small and simple-structured. The trigonid valley is semi-open and is V-shaped, the paraconid make an u-turn posteriorly (Plate 7 D). The m3 (KF-9A) posterior (talonid) end is missing. Thus the hypolophid is not preserved, but a small part of the hypoconid is preserved. A shallow buccal groove is present that separates the two lobes. The remainder of the elements - paraconid, paralophid, protoconid, protolophid, metaconid and metalophids - are well preserved (Plate 7 A). The crown is high (Plate 7 C). The paraconid is curved posteriorly making the trigonid valley semi-open. The trigonid valley is V-shaped.  
Comments: Bhandari et al. (2009) have described Brachypotherium upper molars from the Pasuda locality (see Fig. 1A). Brachypotherium has been recorded from equatorial areas of Asia, North America, Europe, and Africa (Heissig, 1989). There are several species belonging to this genus, for example Brachypotherium brachypus, Brachypotherium americanum, Brachypotherium perimense, Brachypotherium heinzeltini, and Brachypotherium lewisi. Rhinocerotids were abundant in the Chinji and Nagri formations of the Siwalik Group (Heissig 1972, 2003). They have
EXPLANATION OF PLATE 6

A. Vertical section of Gomphotheridae molar enamel (KF-76). Prism bundles oriented in different directions (a, b). B. Enamel zone with 3DE and HSB. C. Enamel zone showing 3DE. D. Fan-shaped enamel pattern.
EXPLANATION OF PLATE 7

*Brachypotherium* sp. KF-9A, m3 in occlusal (A), lingual (B) and labial (C) views. KF-9B, p2 in occlusal (A), lingual (B) and labial (C) views. Scale bar = 1 cm.

been reported from the Murree and equivalents in India (Kumar and Kad, 2003) and Pakistan (Antoine and Welcomme, 2000).

**DISCUSSION**

**Palaeobiogeography of Selachians**

The present record of selachian species *Megaselachus chubutensis* is new from the Indian Subcontinent. Record of *Megaselachus chubutensis* has been described from the Lower Miocene deposits of Moghra, Egypt (Cook *et al.*, 2010). The fossil specimens of *Pristis* sp. and *Rhinoptera* sp. are also new from the Lower Miocene deposits of Kutch. Earlier, fossil teeth of *Pristis* sp. and *Rhinoptera* sp. were described from the Eastern coast of India (Baripada Beds) (Sahni and Mehrotra, 1981; Milankumar and Patnaik, 2013, in press). The present taxa have close similarity to the selachian fossils from Baripada Beds. *Hemipristis* is particularly abundant in the Miocene deposits of Europe and North America, as well as in the coeval deposits of Java, India, Australia, Western Africa and Japan and, persists until the Pliocene in Angola and Zanzibar (Marsili, 2007; Cappetta, 1987; Cappetta, 1970; Sahni and Mehrotra, 1981; Milankumar, 2013 and reference therein). They are most commonly found in neretic deposits containing warm water fauna (Cappetta, 1987). This species is widespread during the Miocene and is now localized in the Indian Ocean, where it is found in the neretic environment (Cappetta, 1987). The fossil teeth of *Carcharodon carcharias* have also been well documented from the Tertiary deposits of Caribbean Faunal Province (Longbottom, 1979; Gillette, 1984), Pliocene deposits of Angola (Antunes, 1978), Miocene Pirabas Formation of Northern Brazil (Reis, 2005). The genus *Carcharodon* occurs as early as Burdigalian, in Switzerland (Leriche, 1927). The genus *Carcharhinus* is commonly found all along the Indian coast line and had a wide distribution from the seas of India to Japan.
ADDITIONAL VERTEBRATE REMAINS FROM THE EARLY MIOCENE OF KUTCH, GUJARAT

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The fossil teeth of *Carcharhinus* is found in the Miocene of Ecuador, Tertiary of Caribbean province (Longbottom, 1979; Gillette, 1984), Pliocene of Angola (Antunes, 1978), Miocene of Pirabas Formation of Brazil (Reis, 2005), Eocene to Oligocene of Baluchistan Pakistan (Adnet et al., 2007). *Carcharhinus* is well adapted in the coastal-pelagic, inshore, warm-temperate and tropical waters of continental and insular shelves and their adjacent oceanic waters (Portell et al., 2008). The genus *Galeocerdo* is widely distributed throughout the world with the exception of the Mediterranean Sea and are most commonly adapted to near shore environment of temperate to tropical conditions (Sahni and Mehrotra, 1981; Lineaver and Backus, 1973). The teeth of *Rhinoptera* has also been reported from the Early Eocene of Nigeria and Angola (White, 1934; Dartevelle and Casier, 1959), from the Early Eocene of Virginia (Kent, 1999); the Middle Eocene of England (Kemp et al., 1990), Nigeria (White, 1926), Morocco (Arambourg, 1952) and Uzbekistan (Case et al., 1996) and the late Eocene of Egypt (Murray et al., 2011). It appears, therefore, that most of the present taxa have relatively extensive geological time spans and biogeographical ranges as the Tethys Sea during the Early Miocene was well connected to both the Atlantic Ocean and Pacific Ocean (Harzauser and Pillar, 2007). Therefore, the Miocene fossil fauna known from India is also correlatable to the fossil taxa from Africa, North and South America, Australia, New Zealand etc. as this Tethyan realm likely provided the marine connection between the two areas for many other marine faunal components (Sahni and Mehrrotra, 1981; Cook et al., 2010; Milankumar and Patnaik, 2013, in press).

**Palaeobiogeography of Tomistomine crocodiles**

*Tomistoma tandoni* was described on the basis of cranial and vertebral remains from the Middle Eocene of the Indian subcontinent (Sahni and Mishra, 1975). Tomistomine crocodiles have been reported from other Miocene sites of the Indian subcontinent: Tomistomidae indet. comes from the Early Miocene of Kutch (Vijayasarathi and Sabale, 1985), *Tomistoma* sp. from the Middle–Late Miocene Nepal Siwalik (West et al., 1991) and the large *Ramphosuchus crassidens* (Falconer and Cautley, 1840) from the Middle Miocene (Head 2001). The affinities of the Miocene tomistomine of India is still not clear: whether directly descended from the Asian Palaeogene forms or dispersed eastward out of Africa after the collision of the Afro-Arabian plate with Eurasia in the Early Miocene. Tomistomine remains from Early Miocene deposits all around the Mediterranean are considered as *Tomistoma lusitanica* Antunes, 1961 (Brochu and Gingerich, 2000). From North Africa, tomistomines have been reported from Wadi Moghara, Egypt (Fourtau, 1918), and Gebel Zelten (Savage and Hamilton, 1973). Other records from Africa are from the late Miocene of Uganda, *Tomistoma coppensi* and from Early Pliocene of Zaire (Pickford, 1994).

**Palaeobiogeography of mammals.**

It is widely considered that before the Early Miocene, the open Tethyan Seaway obstructed the migration of land mammals between Africa and Eurasia to a great degree. Proboscideans were supposed to be endemic to Africa during the Paleogene. After the mid-Burdigalian collision of the Afro-Arabian plates with Eurasia produced a terrestrial passage, called the “Gomphotherium Landbridge” (Rögl, 1999), allowing faunal exchange between Africa and Eurasia. The phenomenon of this migration is termed as the “Proboscidean Datum Event” (Madden and van Couvering, 1976). Later work showed that there were multiple immigration events (Tassy 1989, 1996; Koufos et al., 2003). Harzhauser et al. (2007) documented two or more proboscidean datums close to the end of the Early Miocene. These were an earlier gomphothere event at about 18 +/- 0.5 Ma and later deinother event at 17 +/- 0.5 Ma. This was recently confirmed by the findings of mammals from Kutch by Bhandari et al (2009). Böhme (2004) suggested migration of the channids from India to Europe at around 17.5 Ma, based on presence of monsoon-like conditions in both these regions. Presence of widespread tropical to sub-tropical palaeoclimatic conditions during this time is further attested by the presence of sharks (Table 2) and tomistomine crocodiles. The large mammals are thought to have required tropical forests for survival.
Table 2. Occurrence of fishes in the Miocene deposits of Western coast of India in Kutch, Piram Island and Gogha Coast and their palaeoclimatic and palaeoenvironmental implications (Sources: Mehrotra, 1979; Mehrotra et al. 1973; Sahni and Mehrotra, 1981; Sahni and Mishra; 1975; Mishra, 1980; Compagno, 1984 and 1999; Smith and Heemstra, 1986; Cappetta, 1989; Rana et al., 2004; Milankumar, 2013, Unpublished thesis, en.wikipedia.org).

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CONCLUSIONS

We present here some new finds of fossil marine and fresh water fishes from the early Miocene of India, that have common elements elsewhere in Africa and Europe. Our findings further strengthen the idea that there were land connections between Africa, Europe and the Indian subcontinent during early Miocene times and that all these regions experienced similar tropical to subtropical conditions. However, presence of common marine elements in these regions may suggest that this land bridge was breached intermittently by the formation of marine passages.

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REFERENCES


Murray, A.M., Cook, T. D. Attia, Y. S., Chatrath, P. and Si-mons,


