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Nongmaithem Amardas SINGH, Deepak CHOUDHARY, Y. Priyananda SINGH, Ningthoujam Premjit SINGH, Rajeev PATNAIK, R. P. TIWARI & K. Milankumar SHARMA

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Chondrichthyan and osteichthyan fauna from the middle Miocene deposits of Palasava, Kutch, India: implication for paleoenvironment and paleobiogeography

Nongmaithem Amardas SINGH
Department of Geology, Central University of Punjab, Bathinda-151401 (India)

Deepak CHOUDHARY
Centre of Advanced study in Geology, Panjab University, Chandigarh-160014 (India)

Y. Priyananda SINGH
Department of Geology, Central University of Punjab, Bathinda-151401 (India)

Ningthoujam Premjit SINGH
Biostratigraphy Division, Wadia Institute of Himalayan Geology, Dehradun-248001 (India)

Rajeev PATNAIK
Centre of Advanced study in Geology, Panjab University, Chandigarh-160014 (India)

R. P. TIWARI
Department of Geology, Central University of Punjab, Bathinda-151401 (India)

K. Milankumar SHARMA
Department of Geology, Central University of Punjab, Bathinda-151401 (India)
and Department of Geology, Central University of South Bihar, Gaya-824236 (India)
milankumar.sharma@gmail.com (corresponding author)

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ABSTRACT

The Neogene of Kutch, India is well known for its rich marine and terrestrial vertebrate assemblages. However, the data of piscean fauna from the middle Miocene of India is very scarce. We report here additional chondrichthyan and osteichthyan remains from the middle Miocene deposit of Chhasra Formation, Palasava site, Kutch, Gujarat, India. The elasmobranchs include *Carcharhinus* Blainville, 1816 (*C. brevipinna* (Müller & Henle, 1839), *C. falciformis* (Müller & Henle, 1839), *C.* cf. *leucas*, *C.* aff. *perezi*, *Carcharhinus* sp.), *Negaprion* Whitley, 1940 (*Negaprion* sp.), *Aetobatus* Blainville, 1816 (*Aetobatus* sp.), *Myliobatis* Cuvier, 1816 (*Myliobatis* sp.), *Dasyatis* Rafinesque, 1810

(*D. probsti* Cappetta, 1970, *D. rugosa* Probst, 1877), *Himantura* Müller & Henle, 1837 (*H. menoni* Sahni & Mehrotra, 1981), *Pastinachus* Rüppell, 1829 (*Pastinachus* sp.), and *Taeniurops* Garman, 1913 (*Taeniurops* sp.). The teleosts of Palasava are represented by four families including Bagridae Bleeker, 1858, Channidae Fowler, 1934, Characidae Latreille, 1925 and Cyprinidae Cuvier, 1817. Sørensen-Dice coefficient data of Palasava elasmobranchs show a good similarity index with their counterparts in the Mediterranean Sea suggesting the existence of short-lived reopening of the marine pathway. However, a much higher faunal affinity with those of Eastern Pacific indicates a gradual shift in migration path through the Pacific Ocean to Indo-Pacific region after the permanent landbridge was formed. The vertebrate fauna from the Palasava suggests a coastal, marginal marine, near-shore littoral to neritic environment of deposition with the influence of freshwater riverine system. The integration of the floras and faunas from Palasava locality indicates the presence of warm, humid/wet, tropical to sub-tropical environmental conditions during the middle Miocene.

KEY WORDS
India,
Kutch,
middle Miocene,
sharks,
batoids,
paleoenvironment,
paleobiogeography.

RÉSUMÉ

Faune de chondrichtyens et d'ostéichtyens provenant des dépôts du Miocène moyen de Palasava, Kutch, Inde : implication pour le paléoenvironnement et la paléobiogéographie.

Le Néogène de Kutch, en Inde, est bien connu pour ses riches assemblages de vertébrés marins et terrestres. Cependant, les données sur la faune de chondrichthyens du Miocène moyen de l'Inde sont très rares. Nous rapportons ici des restes supplémentaires de chondrichtyens et d'ostéichtyens provenant du dépôt du Miocène moyen de la formation Chhasra, site de Palasava, Kutch, Gujarat, Inde. Les élasmobranches incluent *Carcharhinus* Blainville, 1816 (*C. brevipinna* (Müller & Henle, 1839), *C. falciformis* (Müller & Henle, 1839), *C.* cf. *leucas*, *C.* aff. *perezi*, *Carcharhinus* sp.), *Negaprion* Whitley, 1940 (*Negaprion* sp.), *Aetobatus* Blainville, 1816 (*Aetobatus* sp.), *Myliobatis* Cuvier, 1816 (*Myliobatis* sp.), *Dasyatis* Rafinesque, 1810 (*D. probsti* Cappetta, 1970, *D. rugosa* Probst, 1877), *Himantura* Müller & Henle, 1837 (*H. menoni* Sahni & Mehrotra, 1981), *Pastinachus* Rüppell, 1829 (*Pastinachus* sp.), et *Taeniurops* Garman, 1913 (*Taeniurops* sp.). Les téléostéens de Palasava sont représentés par quatre familles : Bagridae Bleeker, 1858, Channidae Fowler, 1934, Characidae Latreille, 1925 et Cyprinidae Cuvier, 1817. Les données du coefficient de Sørensen-Dice des élasmobranches de Palasava montrent un bon indice de similitude avec leurs homologues de la mer Méditerranée, ce qui suggère l'existence d'une réouverture éphémère de la voie marine. Cependant, une affinité faunistique beaucoup plus élevée avec ceux du Pacifique oriental indique un changement progressif de la voie de migration à travers l'océan Pacifique vers la région Indo-Pacifique après la formation du pont terrestre permanent. La faune de vertébrés provenant de Palasava suggère un environnement de dépôt côtier, marin marginal, littoral proche du rivage ou néritique avec l'influence d'un système fluvial d'eau douce. L'intégration des flores et des faunes de la localité de Palasava indique la présence de conditions environnementales chaudes, humides, tropicales à subtropicales pendant le Miocène moyen.

MOTS CLÉS
Inde,
Kutch,
Miocène moyen,
requins,
batoïdes,
paléoenvironnement,
paléobiogéographie.

INTRODUCTION

The Miocene deposits of Kutch, India is well known for its diverse fossil assemblages comprising of foraminifers, molluscs, chondrichthyan, teleostean, reptilian and mammalian remains (Wynne 1872; Lydekker 1876; Venkatappaya 1955; Sahni & Mishra 1975; Sahni & Mehrotra 1981; Bhandari *et al.* 2009, 2015, 2018; Kulkarni *et al.* 2010; Patnaik *et al.* 2014; Kapur *et al.* 2019; Singh *et al.* 2019, 2020; Sharma *et al.* 2021; and references therein). Recent, geological field work conducted in the middle Miocene (*c.* 14 ± 2 Ma, Kapur *et al.* 2019) deposits of Chhasra Formation at Palasava localities of Kutch, Gujarat, India have yielded teeth of elasmobranch, teeth, bones and spines of teleosts. The Palasava village of Kutch, Gujarat India is also known to report diverse mammalian taxa such as *Sanitherium* Meyer, 1865, *Sivameryx* Lydekker, 1878, *Brachypotherium* Roger, 1904, *Zygolophodon* Vacek, 1877, *Gomphotherium* Burmeister, 1837, and *Deinotherium* Kaup, 1829 along with fishes, chelonians, crocodiles, snakes and birds (Kapur *et al.* 2019). The paleobotanical data from the Palasava deposits comprise of certain palynomorphs (Verma *et al.* 2013) and fossil wood (Shukla *et al.* 2014).

Earlier elasmobranch finds are from the early Miocene Khari Nadi Formation and includes *Megaselachus chubutensis* Ameghino, 1906, *Carcharadon carcharias* Linnaeus, 1758, *Carcharadon* sp., *Galeocerdo cuvier* Le Sueur, 1822, *Hemipristris serra* Agassiz, 1843, *Rhizoprionodon* sp., *Carcharhinus* sp., *Sphyrna lewini* (Griffith & Smith, 1834), *Sphyrna* sp., Lamnidae indet., *Myliobatis* sp., and *Aetobatus* sp. (Patnaik *et al.* 2014; Sharma *et al.* 2021; and references therein). Sahni & Mishra (1975) reported a diverse elasmobranch assemblage from the early Miocene of Kutch belonging to the

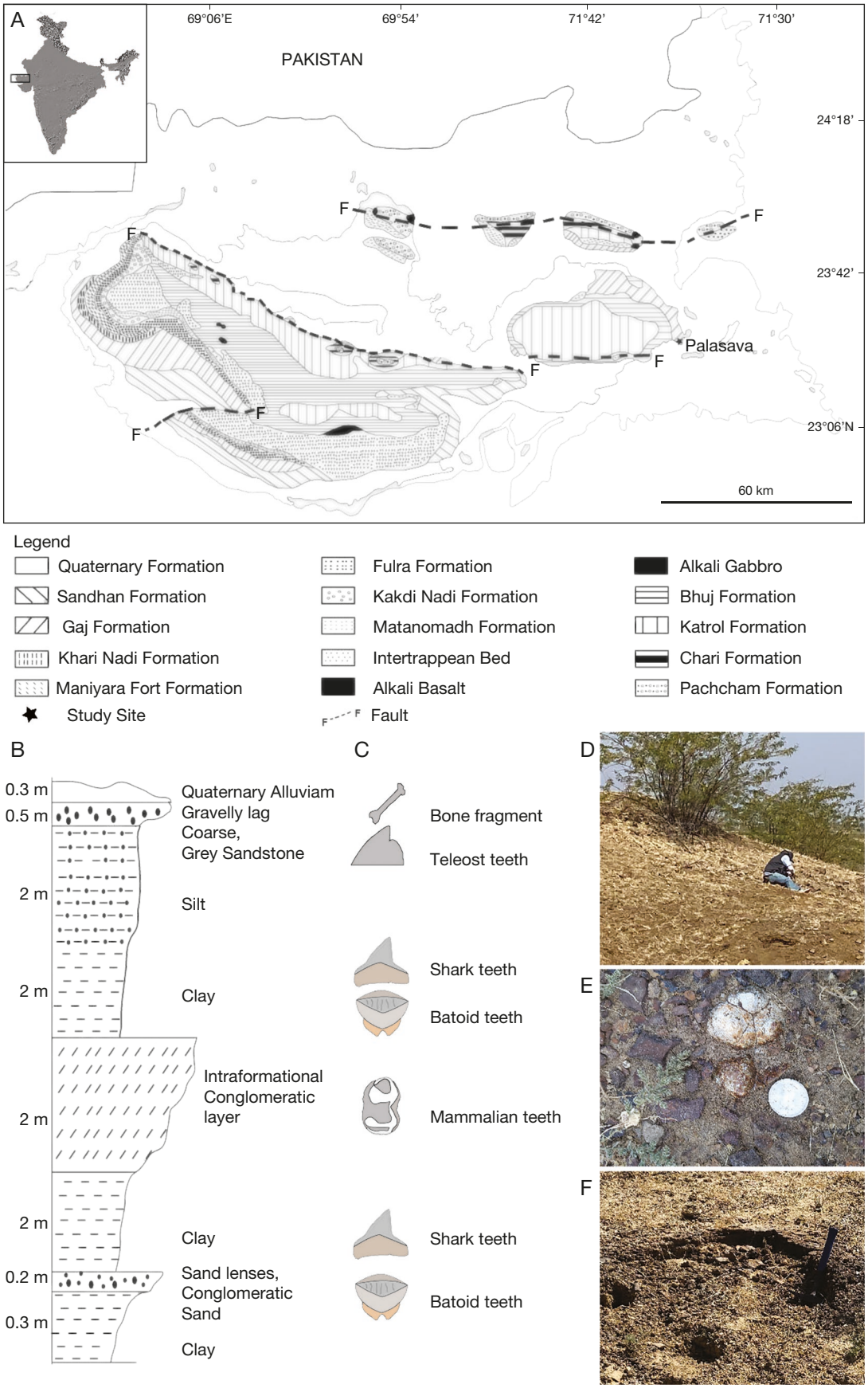

Fig. 1. — **A**, Map of India showing the study locality (represented by **rectangular box**); **B**, geological map of Kutch (GSI, 2012); **C**, stratigraphic column of the Palasava locality (after Kapur *et al*. 2019); **D**-**F**, field photograph of middle Miocene Chhasra Formation as exposed at the Palasava section.

families Charcharinidae, Isuridae, Alopiidae, Sphyrnidae and teleosteans including the families of Diodontidae, Sphyraenidae and Scombridae. Elasmobranchs from the late Miocene of Kutch are represented by *Carcharhinus* sp., *D. rugosa* Probst, 1877, *D.* cf. *probsti*, *Dasyatis* sp., *Pastinachus* Rüppell, 1829, *Himantura* Müller & Henle, 1837, and *Pristis* Linck, 1790, whereas the teleosts are represented by Cyprinidae Cuvier, 1817, Bagridae Bleeker, 1858, Siluriformes Cuvier, 1817, and Perciformes Bleeker, 1859 (Bhandari *et al.* 2009; Singh *et al.* 2019; Sharma *et al.* 2021). However, elasmobranch and teleost fauna from the middle Miocene are represented by *Carcharhinus* Blainville, 1816, *Myliobatis* Cuvier, 1816, *Pristis*, and *Cyprinids* Cuvier, 1817 (see, Kapur *et al.* 2019).

The sharks and batoids from the early and late Miocene marine sediments of India are very common (Sahni & Mehrotra 1981; Ralte *et al.* 2011; Tiwari & Ralte 2012; Sharma 2013; Sharma & Patnaik 2013, 2014; Sharma *et al.* 2021; and references therein). However, the record of chondrichthyan and osteichthyan faunas from the middle Miocene deposits of India and their systematic study is very meager and our understanding of their taxonomic diversity and faunal relationships is poor. The present paper documents certain chondrichthyan and osteichthyan fauna from the middle Miocene Palasava locality. The collected gnathostome remains and their associated faunas have been used here for paleoenvironmental and paleobiogeographic assessment. Faunal correlation of sharks and batoids from the middle Miocene deposits of western coast of India with some coeval deposits of America, Europe and Indo-Pacific region has also been reassessed.

GEOLOGICAL SETTING

The Kutch basin of Gujarat, India is well known for metazoan fossils ranging in age from the Mesozoic to Pleistocene (Biswas 1992; and reference therein). Neogene deposits of Kutch are divisible into three formations: Khari Nadi, Chhasra and Sandhan formations (Biswas 1992). The Geological Survey of India (2012) classified the Neogene rocks of the Kutch as Khari Nadi Formation (Oligocene to lower Miocene age), Gaj Formation (lower Miocene to middle Miocene age) and Sandhan Formation (Pliocene age) (also see Fig. 1). The Gaj Formation is equivalent to the Chhasra Formation of Biswas (1992). Lithologically, the Khari Nadi Formation overlying the Maniyara Fort Formation (Oligocene) has a conformable contact with the younger Gaj/Chhasra Formation. The Khari Nadi Formation is dated as early Miocene (23.03 – 20.43 +/– 0.05 Ma, see, Gradstein *et al.* 2004) and has a weak erosional unconformity with the underlying Oligocene Maniyara Fort Formation (Catuneanu & Dave 2017; Sharma *et al.* 2021). The Gaj/Chhasra Formation comprises mainly of olive green shale, gypseous shale and claystone with alternations of thin argillaceous limestone beds and disconformable upper contact with the younger rocks of Sandhan Formation (?Miocene-Pliocene) (Biswas 1992) (also see Fig. 1B-E). The Chhasra Formation, named after the Chhasra village, was earlier dated as early Miocene (Burdigalian) by Biswas (1992). However, based on the mammalian assemblages at the Palasava site, it is reassigned to middle Miocene (Langhian-Serravallian; *c.* 14 ± 2 Ma) age for the ossiferous sedimentary succession (Kapur *et al.* 2019). The Sandhan Formation is comprised of clay with concretions, pelleted rock, siltstone, parallel to cross-laminated sandstone beds intermittent with conglomerate beds comprising of calcareous nodules, agate pebbles, very coarse sand and mudclasts.

MATERIAL AND METHODS

The specimens described here were collected in-situ from the field and were also recovered from the maceration of bulk samples of approximately 500 kg from Palasava fossil site (23°26'23.60"N, 70°59'2.31"E) Rapar Taluka, District Kutch, Gujarat state in western India (Fig. 1). The Palasava fossil site is located around 6-7 km east of Palasava village, Taluka Rapar, District Kutch, Gujarat State, western India (Fig. 1A). The maceration technique follows Sharma *et al.* (2021). The dried macerated residues were sieved through mesh sizes ranging from 74 to 595 µm and were seen under Leica Stereozoom Microscope (ASPO 9) for picking the microvertebrate remains. The collected fossils were studied and photographed under a Leica M205C Stereozoom Trinocular Microscope housed at BIOPS Lab, Central University of Punjab, Bathinda. The tooth terminology of elasmobranch follows Cappetta (2012). The described specimens are deposited at the BIOPS Lab., Department of Geology, Central University of Punjab Bathinda-151401 (India) and Department of Geology, Panjab University, Chandigarh under the catalogue numbers: BIOPS/CUP/KP and PUKPS.

ABBREVIATIONS

Institutional abbreviations

BIOPS/CUP/KP	Biostratigraphy, Paleontology and Sedimentology laboratory/ Central University of Punjab/ Kutch Palasava;
PUKPS	Panjab University Kutch Palasava.

SYSTEMATIC PALEONTOLOGY

Order CARCHARHINIFORMES Compagno, 1977
Family CARCHARHINIDAE Jordan & Evermann, 1896
Genus *Carcharhinus* Agassiz, 1843

Carcharhinus brevipinna
Müller & Henle, 1839
(Fig. 2A-C)

Carcharhinus brevipinna Müller & Henle, 1839: 31, pl. 9.

REFERRED SPECIMENS. — One isolated upper tooth under the specimen number PUKPS-784.

LOCALITY AND HORIZON. — Middle Miocene (Langhian age) greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

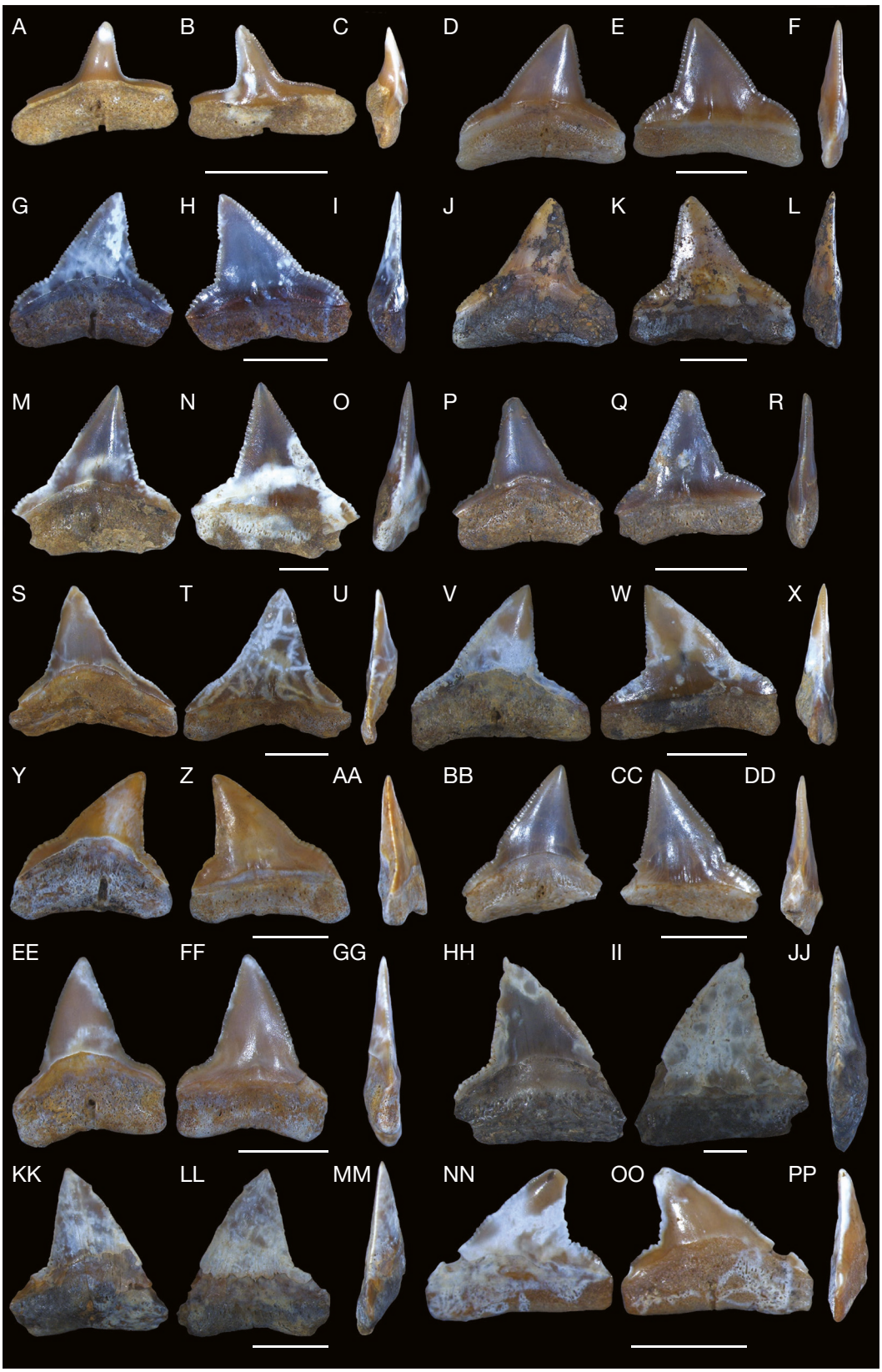

Fig. 2. — **A**-**C**, *Carcharhinus brevipinna* Muller & Henle, 1839 (PUKPS-784) upper teeth, jaw position indet., views: **A**, lingual; **B**, labial; **C**, lateral; **D**-**R**, *Carcharhinus falciformis* (Müller & Henle, 1839) (PUKPS-781, 782, 783, 785, 786) upper lateral teeth, views: **D**, **G**, **J**, **M**, **P**, lingual; **E**, **H**, **K**, **N**, **Q**, labial; **F**, **I**, **L**, **O**, **R**, lateral; **S**-**U**, *Carcharhinus* cf. *leucas* (PUKPS-787) upper teeth, jaw position indet., views: **S**, lingual; **T**, labial; **U**, lateral; **V**-**GG**, *Carcharhinus perezi* (PUKPS- 788, 789, 790, 791) upper teeth, jaw position indet., views: **V**, **Y**, **BB**, **EE**, **HH**, lingual; **W**, **Z**, **CC**, **FF**, labial; **X**, **AA**, **DD**, **GG**, lateral; **HH**-**MM**, *Carcharhinus* aff. *plumbeus* (PUKPS-792, 793) upper teeth, jaw position indet., views: **HH**, **KK**, lingual; **II**, **LL**, labial; **JJ**, **MM**, lateral; **NN**-**PP**, *Carcharhinus* sp. 1 (PUKPS-794) upper teeth, jaw position indet., views: **NN**, lingual; **OO**, labial; **PP**, lateral. Scale bars: A-L, P-GG, KK-PP, 5 mm; M-O, HH-JJ, 2 mm.

Description

Specimen PUKPS-782 is a small size tooth, crown is triangular in shape, distally inclined, both the mesial and distal cutting edges are finely serrated (Fig. 2A-C). The serration is slightly coarser towards the median portion of the cusp. The lingual face of the tooth is convex while the labial face is slightly flattened towards the apex, convex at the median portion and slightly concave towards the base of the crown. The mesial edge of the cusp is distally inclined and the distal edge forms a nearly vertical notch to the heel. The crown of the tooth is curved lingually (Fig. 2C). The root is bilobate, wider than the height, with a prominent median groove that separates each lobe and the base of the root is nearly straight to slightly concave. The crown-root boundary is convex. The crown height of the tooth is 2.45 mm, width of the root is 6.76 mm and the total height of the tooth is 4.44 mm.

Remarks

Carcharhinus brevipinna (Müller & Henle, 1839) is distinguished from other *Carcharhinus* taxa in having a short cusp with a lingually curved crown (Perez *et al.* 2017). The upper teeth of *C. brevipinna* are closely similar to *C. limbatus,* however it differs in having a shorter cusp, asymmetric crown and finer serration at teeth shoulder (Perez *et al.* 2017). The upper teeth of *C. limbatus* are differentiable from *C. brevipinna* in having coarser serrations at the heels especially at the distal heel (see, Perez *et al.* 2017). The differentiation of the present specimen into upper or lower tooth is very difficult. However, we prefer to describe it as upper tooth of *C. brevipinna*, which is often slightly broader (also see Perez *et al.* 2017). The present specimen resembles to those of *C. brevipinna* reported from the late Miocene of Lago Bayano, Panama (Perez *et al.* 2017) in having a shorter and more asymmetric crown, lingually curved towards the apex and extended root. Previously, dermal denticle of *C. brevipinna* had been reported from the late Miocene deposit of Baripada beds as *C. maculipinnis* (Sahni & Mehrotra 1981). This is the first report of *C. brevipinna* from the Miocene sediments of Kutch, India.

Carcharhinus falciformis (Bibron, 1841 *in* Müller & Henle, 1839-1841) (Fig. 2D-R)

Carcharias (*Prionodon*) *falciformis* Bibron *in* Müller & Henle, 1841: 47.

Carcharhinus falciformis – Purdy *et al.*, 2001: 151, fig. 53b-f.

Referred specimens. — Five isolated upper lateral teeth under the specimen numbers PUKPS-781, 782, 783, 785 and 786.

Locality and horizon. — Middle Miocene (Langhian age) greyish coarse sandstone gravelly lag bed of Chhassra Formation at Palasava site, Kutch, Gujarat.

Description

The specimens PUKPS-781, 782, 783, 785 and 786 are triangular in shape, crown broader at the base and narrowly pointed towards the apex. The mesial cuttings are straight to slightly convex and arched distally. The distal cutting edge is straight and nearly perpendicular to the basal margin (Fig. 2D-R). Both the mesial and distal cutting edges bear strong serrations which are slightly coarser towards the base and also separated from the coarsely serrated heels by a shallow angular notch (Fig. 2D-R). The lingual faces are convex while the labial faces are flattened, the crown base of the teeth are compressed labio-lingually (Fig. 2D, E, G, H, J, K, M-P). The basal margins of the teeth are curved upward at the lingual side and are nearly straight and horizontal at the labial side. The specimen PUKPS-786 shows a gap in serrations at the median portion of the mesial cutting edge (Fig. 2P-R). The serrations at the basal part of tooth of specimen PUKPS-785 are not clearly visible due to abrasion and worn out (Fig. 2M, N). The roots are bilobate, slightly thicker at the lingual side, base of the lobes are nearly curved to straight and each lobe is divided by a shallow nutritive groove. The crown height ranges from 5.76-4.03 mm, width of the root is 12.29-6.7 mm and the total height of the tooth is 9.85-6.87 mm.

Remarks

Carcharhinus falciformis differs from other *Carcharhinus* taxa in having a gap in serrations between the apex and the base of teeth on the mesial cutting edge, the straightness of the mesial cutting edge and narrowed crown with a notch on both cutting edges (Purdy *et al.* 2001; Marsili *et al.* 2007; Perez *et al.* 2017). However, extant species of *C. falciformis* can have variable morphology including the absence of serration gap and more distally inclined crown (Purdy *et al.* 2001). The absence of noticeable serration gap at mesial cutting edges of the present specimens corresponds to upper lateral teeth (also see Purdy 1990). Teeth of *C. falciformis* are comparable with those of *Carcharhinus amboinensis* (Müller & Henle, 1839) (Bass *et al.* 1973; Naylor & Marcus 1994; Koscic *et al.* 2018) in having broader crown base, angular, distally placed notch, perpendicular distal cutting edges, and horizontal root base but it differs from the later in the presence of a shallow notch on the mesial cutting edge. *Carcharhinus falciformis* has been reported from the early Miocene of Malta, Venezuela (Ward & Bonavia 2001; Carrillo-Briceño *et al.* 2016b) and late Miocene of Borneo, Panama (Pimiento *et al.* 2013; Perez *et al.* 2017; Koscic *et al.* 2018). Earlier, *C. falciformis* was reported from late Miocene Baripada Beds of Orissa, late Miocene Piram Beds and (?) middle Miocene deposits of Gogha coast of Kathiawar (Sahni & Mehrotra 1981). The present specimens are the first report of *C. falciformis* from the Miocene sediments of Kutch, India.

Genus *Carcharhinus* Agassiz, 1843

Carcharhinus cf. ***leucas*** Müller & Henle, 1839 (Fig. 2S-U)

Carcharhinus leucas Müller & Henle, 1839: 42.

Referred specimen. — One isolated upper tooth, specimen number PUKPS-787.

Locality and horizon. — Middle Miocene (Langhian age) greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description

Specimen PUKPS-787 is a small tooth having a broad and triangular crown, cusp is erect and slant apically (Fig. 2S-U). Tooth is partially worn out, but the serrations at both mesial and distal cutting edges are still visible. The serrations at both the cutting edges are coarser towards the heel. The mesial cutting edge is uneven or weakly sigmoid and extend towards the heel without showing any distinctive notch. The distal cutting edge is nearly straight to slightly concave, and separated from the heel by a shallow distal notch. The lingual face of the crown is convex while the labial face is flat (Fig. 2S). The neck in between the crown base and the root is curved upward in the lingual view and nearly straight or slight curved in the labial view. The root is high, broad and bilobate, basal part of the root is arched upward (Fig. 2U). The height of the crown is 6.35 mm, width of the root is 13.26 mm and the total height of the tooth is 11 mm.

Remarks

Teeth of *C. leucas* are distinguishable from those of other species of the genus *Carcharhinus* in having a more symmetrical crown shape, crown merging smoothly with the root without a distinct notch on the mesial cutting edge (also see Compagno 1984; Pimiento *et al.* 2013). The upper teeth of *C. leucas* are comparable in shape with those of *C. longimanus* but differ from the latter in having a much larger crown and straight basal margin (Purdy *et al.* 2001; Marsili *et al.* 2007). It also differs from *C. obscurus* in having a distally deflected apex of the cusp and convex mesial cutting edge (Purdy *et al.* 2001; Marsili *et al.* 2007). The present specimen resembles *Carcharhinus leucas* reported from the late Miocene of Panama (Pimiento *et al.* 2013) and early Miocene of Egypt (Cook *et al.* 2010) in having symmetrical teeth, nearly narrow crown, absence of distinct notch on mesial cutting edge and presence of straight or slightly curved distal cutting edge. Previously, dermal dental remains of *Carcharhinus leucas* were reported from the late Miocene deposit of Baripada Beds (Sahni & Mehrotra 1981). *Carcharhinus leucas* is considered a circum-tropical epipelagic shark which is well adapted to tropical waters, rivers, and coastal lakes below 30 m depths (Compagno 1984, 1988; Pimiento *et al.* 2013).

Carcharhinus perezi (Poey, 1876)
(Fig. 2V-GG)

Platypodon perezii Poey, 1876: 390 (194), pl. 9, figs 2, 3.

Carcharhinus perezii – Compagno, 1984: 492.

Referred specimens. — Four isolated upper teeth, specimen numbers PUKPS-788, 789, 790 and 791.

Locality and horizon. — Middle Miocene (Langhian age) greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat, India.

Description

The specimens PUKPS-788, 789, 790 are triangular in shape teeth, crowns are narrow and distally arched, the mesial cutting edges of the cusps are convex and distal cutting edges are straight to slightly concave (Fig. 2V-GG). The cutting edges bear serrations which are coarser towards the base. A well distinct or shallow angular notch is present at the distal edge of the crown separating the cusp from the heel. The mesial cutting edges are either present in a shallow notch or a distinct notch is absent. The crowns are flat in labial face and convex in lingual side (Fig. 2V-Z, BB-FF). The specimen PUKPS-791 (Fig. 2EE-GG) has a high and erect crown which is sub-triangular in shape. The distal cutting edge is straight and the mesial cutting edge is convex, both having nearly uniform serration. Distal cutting edge of the crown is separated from the heel by a shallow notch and the mesial heel of the tooth is worn out. The basal margin of the tooth is curved at lingual side and horizontal in labial view. The root is robust, bilobate and a nutritive groove is present on the lingual side separating the two lobes; the basal part of root is curved or nearly straight. The crown height ranged from 5.42-4.93 mm, width of the roots range from 11.13-8.6 mm, and the total height of the teeth ranged between 9.97-8.81mm.

Remarks

The present report is the first record of *Carcharhinus perezi* from the Miocene deposits of India. Teeth of *Carcharhinus perezi* are distinguished from those of the other species of *Carcharhinus* by having distally curved mesial cutting edge and coarsely serrated crown (Pimiento *et al.* 2013). The upper teeth of *C. perezi* differ from those of *C. obscurus* in having broad crown and distally deflected apex, and from *C. brachyurus* in apical convexity of cutting edge (Purdy *et al.* 2001; Marsili *et al.* 2007). *Carcharhinus perezi* has been reported from the late Miocene deposit of Gutun Formation, Panama (Pimiento *et al.* 2013); early Miocene of Pirabas Formation, Brazil, Cantaure Formation, Venezuela (also see Dos Reis 2005; Carrillo-Briceño *et al.* 2016b; Aguilera *et al.* 2017), Miocene deposits of Lee Creek, North Carolina (Purdy *et al.* 2001), Pollack Farm site, Delaware (Purdy 1998), Northern Venezuela (Sánchez-Villagra *et al.* 2000), Alvalade basin, Portugal (Antunes *et al.* 1999; Antunes & Balbino 2006) and Pliocene of Tuscany, Italy (Marsili *et al.* 2007). The present specimens are similar to *Carcharhinus* sp. reported earlier from middle Miocene of Palasava, Kutch (Kapur *et al.* 2019).

Carcharhinus aff. ***plumbeus***
(Fig. 2HH-MM)

Squalus plumbeus Nardo, 1827: 26.

Referred specimens. — Two isolated upper teeth specimen numbers PUKPS-792 and 793.

Locality and horizon. — Middle Miocene (Langhian age) greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description

The specimens PUKPS-792 and 793 are poorly preserved triangular shaped teeth, crown broad, partially worn out and labio-lingually compressed (Fig. 2HH-MM). Slightly worn out serrations are present on both the mesial and distal cutting edges. The mesial edges of the crowns are slightly convex to straight, mesial heel and root of the teeth are broken, distal cutting edge is straight. The serration is finer towards the apex, coarser at the crown base and near the distal notch which separates the distal edge of the crown from the heel. The labial face is flat and the lingual face is convex (Fig. 2HH, II, KK, LL), basal margin of the crown is straight in labial view. The root is high, robust, bulged on the lingual side and flattened on the labial side. Basal part of the root is nearly horizontal and a weak median nutritive groove is present. The crown heights of the PUKPS-792, 793 are 4.73 mm, 6.14 mm and total heights are 8.53 mm and 10.54 mm respectively.

Remarks

The present specimens resemble the upper teeth of *Carcharhinus obscurus* in having broad and triangular crown, apically convex mesial cutting edge and a nearly vertical distal cutting edge. Teeth of *C. plumbeus* and *C. obscurus* are very similar and difficult to distinguish. However, *C. plumbeus* has a narrower and more elongated crown and convexity at the cutting edges of apex, whereas, *C. obscurus* has a broader crown (also see Purdy *et al.* 2001; Pimiento *et al.* 2013). The lack of distally deflected apex of the teeth as in *C. obscurus* (also see Purdy *et al.* 2001; Marsili *et al.* 2007; Pimiento *et al.* 2013; Perez *et al.* 2017) makes us convinced to assign the present specimens as *C.* aff. *plumbeus.* It also differs from other species of *Carcharhinus* in having broad, thin and labio-lingually compressed crown (Cappetta & Nolf 1991), convex mesial cutting edge, straight distal cutting edge and distally deflected tooth apex (Purdy *et al.* 2001; Marsili *et al.* 2007). *Carcharhinus plumbeus* has been reported from late Miocene deposits of Gatun Formation (Pimiento *et al.* 2013), Pungo River Formation (Purdy *et al.* 2001), Chagres Formation (Carrillo-Briceño *et al.* 2015), late Miocene Chucunaque Formation of Lago Bayano, Panama (Perez *et al.* 2017), Miocene deposits of Venezuela and Cuba (Iturralde-Vinent *et al.* 1996; Aguilera & De Aguilera 2001; MacPhee *et al.* 2003). This is the first report of *Carcharhinus* aff. *Plumbeus* from the Miocene of Indian subcontinent.

Carcharhinus sp. 1
(Fig. 2NN-PP)

Referred specimens. — One isolated upper tooth under the specimen number PUKPS-794.

Locality and horizon. — Middle Miocene (Langhian age) greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description

The specimen PUKPS-794 is a small size tooth, crown is triangular in shape, labio-lingually flattened, distally arched and crown base is broad (Fig. 2NN, OO). The crown height of the tooth is 3.22 mm, width of the root is 8.25 mm and total height of the tooth is 6.27 mm. The lingual face of the crown is convex and the labial side is flat. The cutting edges of the tooth are partially worn out. The distal cutting edge is concave and mesial cutting edge is convex. The serrations at both edges are coarser toward the base of the crown. The distal cutting edge is separated from the coarsely serrated heel by a shallow distal notch, whereas the coarsely serrated mesial cutting edge extends up to the mesial heel without having any notch. The root is thin, bilobate, median nutritive groove is present; the root is as wide as the heel of the crown and the basal part of the root is straight.

Remarks

The present specimen is ill preserved, partially worn out and broken at the apex and hence proper identification up to species level is difficult. The present specimen is different from *C. pricus* (Schultz 1977; Karasawa 1989; Szabó & Kocsis 2016) and *C. egertoni* (Sharma & Patnaik 2014) in having broad crown and thicker root. Teeth of the genus *Carcharhinus* have earlier been reported from lower Miocene of Kutch (Patnaik *et al.* 2014), and middle Miocene of Kutch (Kapur *et al.* 2019), late Miocene of Baripada Beds (Sharma & Patnaik 2014; Sharma *et al.* 2021), late Miocene of Kutch (Bhandhari *et al.* 2015), Miocene deposit of Bhuban Formation, Mizoram (Ralte *et al.* 2011).

Carcharhinus sp. 2
(Fig. 3A-F)

Referred specimens. — One isolated anterior lower tooth under the specimen number PUKPS-795 and one upper tooth under the specimen number PUKPS-796.

Locality and horizon. — Middle Miocene (Langhian age) greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description

Specimen PUKPS-795 is a lower tooth having narrowly erected, high, pointed and symmetrical crown. The specimen is worn out, root is broken and ill preserved. The cutting edges are ornamented with uniformly fine serrations and which are absent on the heel (Fig. 3A-C). The labial face is flat and the lingual face is convex (Fig. 3C). The crown of the tooth is lingually curved and again recurved labially towards the apex (Fig. 3C). Root is thin, its basal part is concave and a median nutritive groove divides the root into two lobes. The height of the crown is 6.72 mm, height of the root is 3.46 mm, width of

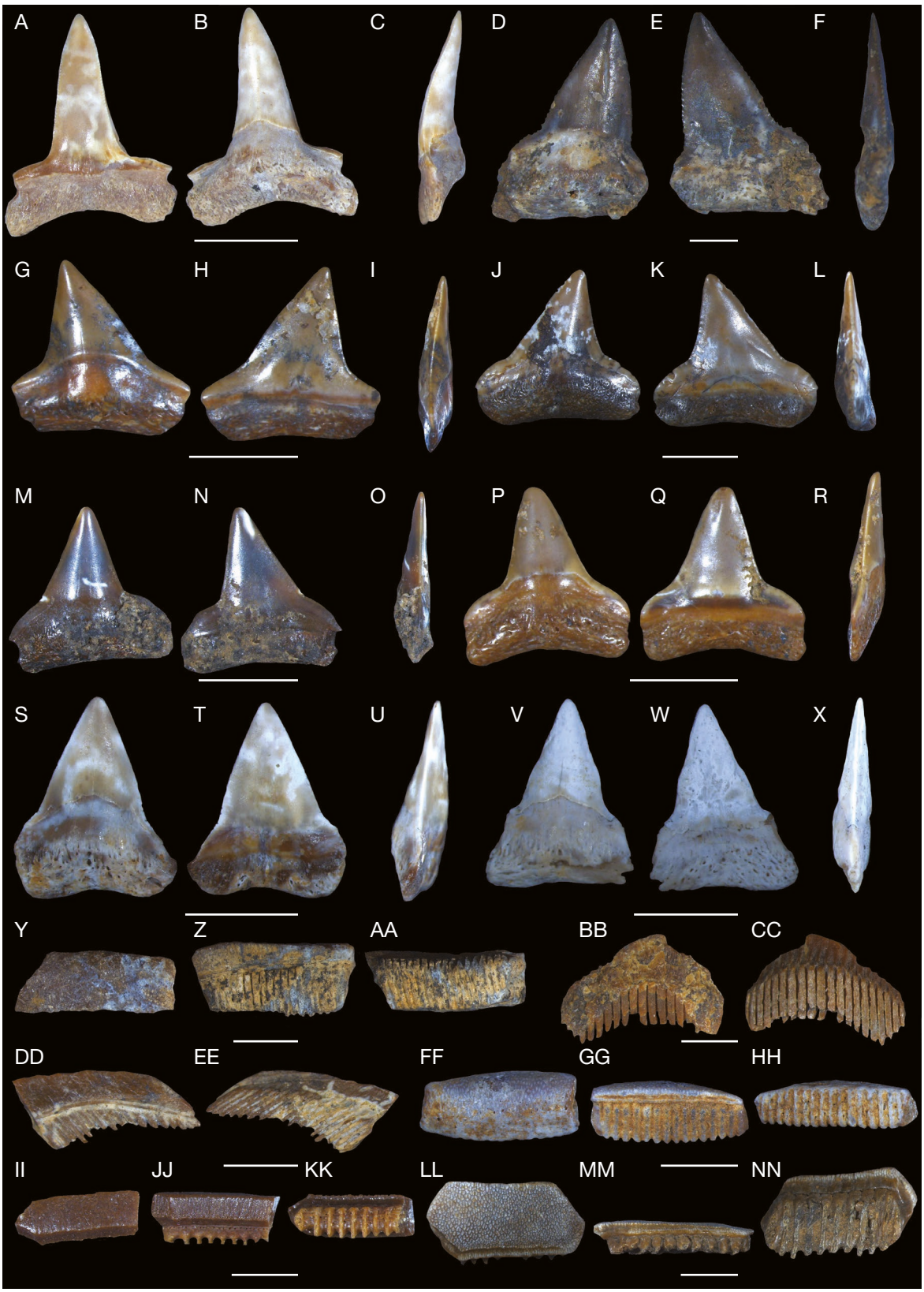

Fig. 3. — **A**-**F**, *Carcharhinus* sp. 2 (PUKPS-795, 796) isolated anterior lower tooth, views: **A**, **D**, lingual; **B**, **E**, labial; **C**, **F**, lateral; **G**-**R**, *Negaprion* sp. (PUKPS-797, 798, 799, 800) upper lateral teeth, views: **G**, **J**, **M**, **P**, lingual; **H**, **K**, **N**, **Q**, labial; **I**, **L**, **O**, **R**, lateral; **S**-**X**, Carcharhinidae indet. (PUKPS-801, 802) upper teeth, jaw position indet., views: **S**, **V**, lingual; **T**, **W**, labial; **O**, **R**, **U**, **X**, lateral; **Y**-**AA**, *Myliobatis* sp. (BIOPS/CUP/KP-35.) jaw position indet., views: **Y**, occlusal; **Z**, lingual; **AA**, basal; **BB**-**HH**, *Aetobatus* sp. jaw position indet. (BIOPS/CUP/KP-36, PUKPS- 803, 804), views: **BB**, **DD**, **FF**, occlusal; **GG**, lingual; **CC**, **EE**, **HH**, basal; **II**-**NN**, *Rhinoptera* sp. (BIOPS/CUP/KP-37: lateral teeth, PUKPS-804: median), views: **II**, **LL**, occlusal; **JJ**, **MM**, lingual; **KK**, **NN**, basal. Scale bars: 5 mm.

the root is 8.3 mm and total height of the tooth is 10.18 mm. The specimen PUKPS-796 is of moderate size poorly preserved upper tooth, crown is erect and sub-triangular in shape. Both the mesial and distal cutting edges are coarsely serrated and the serrations continue up to the heel of the teeth. However, serrations are either very week or totally disappear toward the apex. Mesial cutting edge is sinuous, convex at the middle and recurved mesially towards the apex, and the distal cutting edge is convex (Fig. 3D-F). Labial face of the teeth is nearly flat and lingual face is curved (Fig. 3F). The crown height is 5.59 mm, and the total height of the tooth is 8.23 mm.

Remarks

Species level identification of lower teeth of *Carcharhinus* is very difficult and it is also a much debated subject (Kent 1994; Naylor & Marcus 1994; Purdy *et al.* 2001; Pimiento *et al.* 2013). Specimen PUKPS-795 is similar to a lower anterior tooth of *Carcharhinus* sp. described from the late Miocene deposits of Lago Bayano, Panama (Perez *et al.* 2017) in having a narrow elongated crown with lingual curve at the base and re-curve at the apex. It is considered that upper lateral teeth are the most diagnostic teeth within the dentition of *Carcharhinus* sharks for accurate taxonomic identification (Naylor & Marcus 1994). Lower teeth of *Carcharhinus* are very similar to the lower teeth of *Negaprion* Whitley, 1940 but can be distinguished from the latter by having a shorter crown (Perez *et al.* 2017) and fine serrations at the cutting edges (Pimiento *et al.* 2013). Specimen PUKPS-796 is very poorly preserved and its species level identification is difficult. Earlier, *Carcharhinus* sharks have been described from lower and middle Miocene of Kutch and Saurashtra, Gujarat in the western coast of India (also see Sahni & Mehrotra 1981; Patnaik *et al.* 2014; Kapur *et al.* 2019; Sharma *et al.* 2021), late Miocene of Baripada Beds, Odisha in the Eastern Coast of India (Sahni & Mehrotra 1981; Mondal *et al.* 2009; Sharma & Patnaik 2014; and references therein) and lower Miocene Bhuban Formation, Mizoram (Ralte *et al.* 2011).

Genus *Negaprion* Whitley, 1940

Negaprion sp.
(Fig. 3G-R)

Referred specimens. — Four isolated upper lateral teeth under the specimen numbers PUKPS-797, 798, 799 and 800.

Locality and horizon. — Middle Miocene (Langhian age) greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description

The specimens PUKPS-797-800 are small size teeth, crown is triangular in shape and broader towards the base. The labial faces of the teeth are flat and lingual faces are convex. The mesial cutting edges are slightly inclined distally with pointed apex. The cutting edges bear no serration and are smooth and extend onto the heels (Fig. 3G-R). The mesial edges are straight to slightly curved and the distal edges are straight. PUKPS-799 is having a nearly perpendicular distal cutting edge (Fig. 3M, N). The basal margins of the teeth are curved on the lingual side and nearly straight on the labial sides. Roots are low, bilobate, broad and have a slightly curved to nearly straight base, central foramen is present in the median portion of the root. The crown height of the teeth ranges from 4.1- 5.05 mm, root width from 7.48-8.04 mm and the total height of the teeth from 7.5-8.41mm.

Remarks

Previously, teeth of the *Negaprion brevirostris* and *N. Eurybathrodon* were reported from the late Miocene of Baripada Beds in the eastern coast of India (Sharma & Patnaik 2014) and from the lower Miocene Bhuban Formation of Mizoram (Ralte *et al.* 2011). This is the first record of *Negaprion* sharks from the middle Miocene of Kutch. Extinct species of *Negaprion eurybathrodon* (Cappetta 1987; Purdy *et al.* 2001) is considered to be analogous with the extant species *Negaprion brevirostris* (Pimiento *et al.* 2013) based on similarity of the teeth morphotypes. The present specimens are differentiable from *Negaprion brevirostris* in having broader and shorter crown instead of tall and narrow crown in the later. Teeth of the genus *Sphyrna* having a deep distal notch are also easily distinguishable from the present specimen. *Negaprion* sharks are also reported from the late Miocene of Lago Bayano Panama (Perez *et al.* 2017 as *N. brevirostris*), early Neogene of Western Venezuela (Carrillo-Briceño *et al.* 2016b as *N. eurybathrodon*).

Carcharhinidae indet.
(Fig. 3S-X)

Referred specimens. — Two isolated upper teeth under the specimen numbers PUKPS-801, 802.

Locality and horizon. — Middle Miocene (Langhian age) greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description

The specimens PUKPS-801, 802 are small size teeth, crown is broad and triangular in shape, heavily worn out. The mesial and distal cutting edges are straight with pointed apex and smooth cutting edges without serration (Fig. 3S-X). Labial face is flat and lingual face is curved. The crown is high. The root is incomplete, thick, broad and slightly curved to straight at the base, a central foramen is present at the median part of root base. The crown height of the teeth ranges from 4.46-4.96 mm, root width is 6.9 mm and total height of the teeth ranges from 8.2-8.81mm.

Remarks

The present specimens are incomplete and highly worn out and difficult for proper taxonomic allocation. The specimens are comparable to *Carcharodon* taxa reported from the Miocene,

Bhuban Formation, Mizoram (Ralte *et al.* 2011) in having a broad and triangular shape crown in PUKPS-801, however the absence of serration at the cutting edges of tooth and poor nature of preservation makes it difficult to diagnose them as belonging to *Carcharodon*. Certain sharks of the family Carcharhinidae have been earlier reported from the Miocene deposits of India including the Kutch and Saurashtra, Gujarat in the western coast of India (Sahni & Mehrotra 1981; Patnaik *et al.* 2014; Sharma *et al.* 2021), Baripada Beds, Odisha in the Eastern Coast of India (Sahni & Mehrotra 1981; Mondal *et al.* 2009; Sharma & Patnaik 2014; and references therein) and Bhuban Formation, Mizoram (Ralte *et al.* 2011).

Order MYLIOBATIFORMES Compagno, 1973
Family MYLIOBATIDAE Bonaparte, 1838
Genus *Myliobatis* Dumeril in Cuvier, 1817

Myliobatis sp.
(Fig. 3Y-AA)

REFERRED SPECIMENS. — Isolated teeth BIOPS/CUP/KP-35.

LOCATION AND HORIZON. — Middle Miocene greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

DESCRIPTION
The specimen BIOPS/CUP/KP-35 is an incomplete tooth, medium sized and crown is rectangular to hexagonal in shape. The surface of the crown is flat and ornamented with shallow pitted tubercles (Fig. 3Y). The crown is low and slightly overhanging on the labial side, and the root is separated from the crown by a shallow trench running along the tooth length (Fig. 3Z). The lingual face of the crown presents a slightly oblique shelf. The root of the tooth is totally under the crown and it is also ornamented with small rectilinear furrows.

REMARKS
Teeth of *Myliobatis* have been earlier reported from the middle Miocene of Palasava, Kutch, Chhasra Formation (Kapur *et al.* 2019). *Myliobatis* are commonly reported from the early Miocene of deposits of Khari Nadi Formation, Kutch (Patnaik *et al.* 2014; Sharma *et al.* 2021), early Miocene of Bhuban Formation of Mizoram (Ralte *et al.* 2011), late Miocene Baripada Beds (Sahni & Mehrotra 1981; Sharma 2013; Sharma & Patnaik 2013). Teeth of the genus *Myliobatis* and *Rhinoptera* closely resemble to each other and their precise identification is quite difficult (Gillette 1984). Teeth of *Myliobatis* are characterised by higher crown, more angular occlusal surface, and a thicker lingual cingulum (Laurito & Valerio 2008; Perez *et al.* 2017) and differ from those of *Rhinoptera* in having a significant interlocking design and asymmetrical feature and greater width/length ratio (also see Gillette 1984; Kocsis *et al.* 2018; Sharma *et al.* 2021). The presence of lingual shelf and less angular crown deemed fit to assign the present specimen under the genus *Myliobatis*. The genus *Myliobatis* is considered to be globally distributed (Last *et al.* 2016), and the reliable records of *Myliobatis* extend back to the Late Cretaceous (Claeson *et al.* 2010; Cappetta 2012). *Myliobatis* teeth have been reported from the early Miocene Brazil (Dos Reis 2005), Egypt (Cook *et al.* 2010), Madagascar (Andrianavalona *et al.* 2015) and Germany (Aguilera *et al.* 2017; Villafaña *et al.* 2020; and reference therein), middle Miocene of Hungary (Gillette 1984), Panama (Szabó & Kocsis 2016), Portugal (Fialho *et al.* 2019) and late Miocene Chile (Staig *et al.* 2015), Borneo (Kocsis *et al.* 2018), Panama (Pimiento *et al.* 2013), Peru (Landini *et al.* 2017b), Portugal (Antunes & Balbino 2006), Venezeula (Carrillo-Briceño *et al.* 2015).

Genus *Aetobatus* Blainville, 1816

Aetobatus sp.
(Fig. 3BB-HH)

REFERRED SPECIMENS. — Three isolated teeth under the specimen numbers BIOPS/CUP/KP-36, PUKPS-803, 804.

LOCATION AND HORIZON. — Middle Miocene greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

DESCRIPTION
Specimen BIOPS/CUP/KP-36 is a medium size tooth and strongly curved lingually. The crown is wider at the median portion of tooth. The surface of tooth crown is highly abraded and the root boundary is not distinct (Fig. 3BB). The labial face/side of the crown is ornamented with ridge and trench (Fig. 3CC). The root of the tooth is extremely extended lingually and is dorso-ventrally flattened. Specimen PUKPS-803 is strongly curved lingually and broken on the lateral side of teeth (Fig. 3DD, EE). In occlusal view, the crown surface is flat and crown is wider at the median portion of the tooth. The labial side of the crown is straight and the lingual side is nearly curved at the margin. The crown and the root of the tooth are separated by a trench running along the length of the tooth, root is extended lingually. Specimen PUKPS-804 differ from the tooth morphology of BIOPS/CUP/KP-36 and PUKPS-803. The crown surface of the tooth is curved and ornamented with small pits, the crown height is maximum in the median region of the file (Fig. 3FF-HH). The root is arched lingually and it consists of alternate grooves and laminae. The root is higher than the crown. A small ridge line runs in between the crown and root (Fig. 3GG) and on the labial side, the root penetrates the crown face (Fig. 3HH).

REMARKS
The teeth of the genus *Aetobatus* are distinguished from those of *Rhinoptera* in having lower crown, oblique root lobe which are extremely extended from the crown (Sharma & Patnaik 2013; Sharma *et al.* 2021; and references therein). Strongly curved and extreme extension of root at the lingual side of

teeth in the present specimens deem fit to assign it as *Aetobatus*. Earlier, *Aetobatus* sp. had been reported from the early Miocene Khari Nadi Formation of Kutch, (Sahni & Mishra 1975; Sharma *et al.* 2021); Miocene of Bhuban Formation of Mizoram (Tiwari & Ralte 2012) and late Miocene of Baripada Beds (Ghosh 1959; Mondal *et al.* 2009; Sharma & Patnaik 2013). Teeth of the *Aetobatus* are also known from the early Miocene France (Goedert *et al.* 2017), Switzerland (Jost *et al.* 2016), Venezuela (Carrillo-Briceño *et al.* 2016b), Egypt (Cook *et al.* 2010) and Germany (Villafaña *et al.* 2020) middle Miocene of France (Vialle *et al.* 2011), Panama (Gillette 1984) and Portugal (Fialho *et al.* 2019), late Miocene of Chile (Long 1993), Peru (Landaini *et al.* 2017b), Borneo (Kocsis *et al.* 2018), Panama (Pimiento *et al.* 2013; Carrillo-Briceño *et al.* 2015; Perez *et al.* 2017), Portugal (Antunes & Balbino 2006).

Genus *Rhinoptera* Cuvier, 1829

Rhinoptera sp.
(Fig. 3II-NN)

Referred specimens. — Two isolated lateral teeth BIOPS/CUP/KP-37, median PUKPS-804.

Location and horizon. — Middle Miocene greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description

Specimen PUKPS-804 is a small tooth having a high, symmetrical and angular crown margin and is wider than long in occlusal view. The lateral portion of the specimen PUKPS-804 is broken (Fig. 3II- KK), the lingual and labial faces are slant. The labial and lingual faces of the tooth are ornamented with wrinkles. The crown of the tooth is slightly overhanging towards the labial side and it is also separated from the root by a shallow trench (Fig. 3JJ). The specimen is having nine root lobes and each lobe is separated by an alternating groove (Fig. 3KK). BIOPS/CUP/KP-37 is a small tooth, crown is low, hexagonal in shape, slightly asymmetric in occlusal view, and the root is slightly extended lingually (Fig. 3LL-NN). The crown surface is flat with reticulated ornamentation. The lingual face of the crown has a slightly oblique shelf (Fig. 3KK). The labial face of the crown is overhanging the root (Fig. 3NN) and crown is slightly thicker on the mesial side compared to the distal sides (Fig. 3NN). On the lingual side, the crown and root boundary is separated by a ridge running along the entire length of the tooth. The root is as high as the crown and shows a polyaulacorhizid vascularisation type represented by eleven parallel laminae separated by deep nutritive grooves in basal view (Fig. 3NN).

Remarks

The present specimen PUKPS-804 is comparable with *Rhinoptera sherborni* White, 1926 in having width, asymmetrical, hexagonal shape crown in occlusal view, presence of prominent ridge separating the crown and root at lingual side of the tooth. However, it differs from the later in having a thinner crown, and a highly inclined labial face of the crown. BIOPS/CUP/KP-37 is differentiable from *Rhinoptera studeri* and *Rhinoptera raeburni* in having thinner and asymmetric crown. The incomplete preservation and scarcity of the specimens makes it difficult for a precise identification up to the species level and hence been assigned here as *Rhinoptera* sp. Teeth of the genus *Rhinoptera* have been reported from the late Miocene of Baripada Beds, Odisha (Orissa), India (Sharma & Patnaik 2013), early Miocene of Brazil (Távora *et al.* 2010; Aguilera *et al.* 2017), early Miocene of France (Cappetta 1970; Goedert *et al.* 2017), Germany (Villafaña *et al.* 2020; and references therein), Switzerland (Bolliger *et al.* 1995), Venezuela (Aguilera & De Aguilera 2001; Carrillo-Briceño *et al.* 2016b; Goedert *et al.* 2017), the United States (Case 1980), middle Miocene of Portugal, Panama (Gillette 1984; Fialho *et al.* 2019), late Miocene of Borneo (Kocsis *et al.* 2019), Panama (Pimiento *et al.* 2013; Perez *et al.* 2017).

Family Dasyatidae Jordan, 1888
Genus *Dasyatis* Rafinesque, 1810

Dasyatis rugosa (Probst, 1877)
(Fig. 4A-C)

Raja rugosa Probst, 1877: 76, pl. 1, figs 5-9.

Dasyatis rugosa – Cappetta, 1970: 95-97, pl. 21, figs 1-14.

Referred Specimens. — Isolated female lateral tooth BIOPS/CUP/KP-38.

Location and Horizon. — Middle Miocene greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description

Specimen BIOPS/CUP/KP-38 is a small size tooth, a broad and prominent transverse crest divides the crown into lingual and labial faces (Fig. 4A-C). The labial and lingual visors are semi-circular to sub-angular in shape. The labial face of the crown presents wrinkles like reticulated ornamentations and a prominent narrow and extended labial median hollow. The labial visor is smooth in basal views and labial part of the root is depressed (Fig. 4C). The lingual face of the crown is flat to slightly concave and a median lingual ridge is weakly developed. The root is bilobate, robust, lingually projected, each lobe separated by a wide furrow (Fig. 4C). The basal face of the root is flat and triangular in shape.

Remarks

Teeth of *Dasyatis rugosa* had been earlier reported from late Miocene Tapar site of Kutch, India (Sharma *et al.* 2021). *Dasyatis rugosa* is different from the other species of *Dasyatis* in having narrow extended lateral median hollow and recticulated ornamention of labial zone (Vialle *et al.* 2011). The female teeth of *D. rugosa* are differentiated from the male

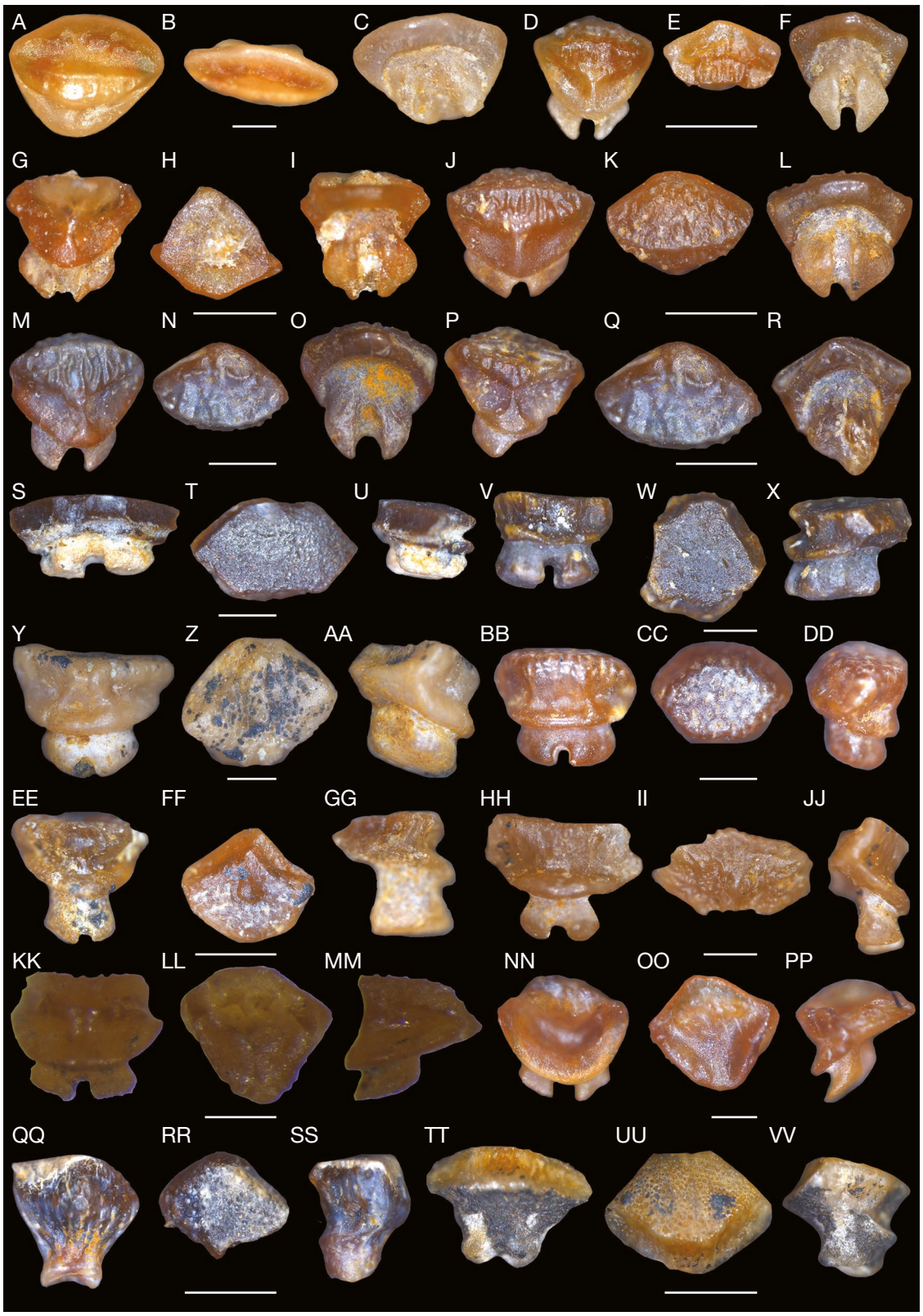

Fig. 4. — **A**-**C**, *Dasyatis rugosa* Probst, 1877 (BIOPS/CUP/KP-38) female lateral teeth, views: **A**, lingual; **B**, occlusal; **C**, profile; **D**-**I**, *Dasyatis* aff. *probsti* (BIOPS/CUP/KP-39, 40) female lateral teeth, views: **D**, **G**, lingual; **B**, **E**, **H**, occlusal; **C**, **F**, **I**, profile; **J**-**R**, *Himantura menoni* (BIOPS/CUP/KP-41, 42, 43) isolated antero-lateral teeth, views: **J**, **M**, **P**, lingual; **K**, **N**, **Q**, occlusal; **L**, **O**, **R**, profile; **S**-**JJ**, *Pastinachus* sp.: **S**-**DD**, isolated upper lateral teeth: BIOPS/CUP/KP-44, 45, views: **S**, **V**, **Y**, **BB**, lingual; **T**, **W**, **Z**, **CC**, occlusal; **U**, **X**, **AA**, **DD**, profile; **EE**-**JJ**, upper syphysal teeth: BIOPS/CUP/KP-46, 47, 48, 49, views: **EE**, **HH**, lingual; **FF**, **II**, occlusal; **GG**, **JJ**, profile; **KK**-**PP**, *Taeniurops* sp. (BIOPS/CUP/KP-50, 51) jaw position indet., views: **KK**, **NN**, lingual; **LL**, **OO**, occlusal; **MM**, **PP**, profile; **QQ**-**VV**, Batoidae indet. (BIOPS/CUP/KP-52, 53), views: **QQ**, **TT**, lingual; **RR**, **UU**, occlusal; **SS**, **VV**, profile. Scale bars: A-C, G-I, HH-PP, 0.5 mm; D-F, J-R, Y-GG, QQ-VV, 1 mm; S-X, 2 mm.

teeth by having a convex labial face, wide transverse crest, often with sinuous labial crown margin (in basal view), robust root lobes and the absence of pointed crest bent toward the rear (Cappetta 1970; Reinecke *et al.* 2005; Haye *et al.* 2008; Cicimurri & Knight 2009; Vialle *et al.* 2011). *Dasyatis rugosa* has also been reported from middle Miocene Nyirád, Hungary (Szabó & Kocsis 2016), early Miocene of Germany, Switzerland (Sach & Heizmann 2001; Reinecke *et al.* 2011; Jost *et al.* 2016; Villafaña *et al.* 2020), middle Miocene of France, Hungary (Vialle *et al.* 2011; Szabó & Kocsis 2016).

Dasyatis probsti Cappetta, 1970
(Fig. 4D-I)

Dasyatis probsti Cappetta, 1970: 91, pl.21, figs 15-23.

Referred specimens. — One isolated female lateral tooth under the specimen number BIOPS/CUP/KP-39 and one male tooth under the specimen number BIOPS/CUP/KP-40.

Location and horizon. — Middle Miocene greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description

Specimen BIOPS/CUP/KP-39 is a small size female tooth, crown is higher than root, globular to rhombic in shape, fairly angular (Fig. 4D-F). The median transverse crest is prominently broad and high which lowers quickly towards the latero-posterior side. The labial face of the crown possesses a crescent shape median labial hollow depression (Fig. 4E) ornamented with irregular reticulations of ridge and furrow (Fig. 3E). BIOPS/CUP/KP-40 represents a male tooth (Fig. 4G-I). The transverse crest is high, pointed lingually, smooth, forms a broad V-shape, the marginal angle of the crown is sharp and angular. The labial visor is smooth, angular in shape in basal view and meets the lingual visor at a marginal angle. The lingual faces of the crown are smooth, concave and a strong lingual median ridge divides the lingual face into two. The roots of the teeth are robust, strong, bilobate, lingually projected and each lobe is separated by a deep median groove. The basal face of the root is flat and triangular in shape.

Remarks

The present specimens are identical to those of *Dasyatis probsti* Cappetta, 1970 reported from the late Miocene of Tapar site of Kutch (Sharma *et al.* 2021). Teeth of the genus *Dasyatis* are always misinterpreted as those of *Taeniura.* However, teeth of *Taeniura* differ from *Dasyatis* in having much sharper transversal edge and more concave occlusal face (Vialle *et al.* 2011; Sharma *et al.* 2021). *Dasyatis probsti* closely resembles *Taeniura cavernosa* (Probst, 1877). However, teeth of *D. probsti* are comparatively less high, median transverse crest is more sinuous and median labial hollow is more circular to subcircular than those of *Taeniura cavernosa* having triangular shape median labial hollow (Cappetta 1970; Vialle *et al.* 2011). *Dasyatis probsti* differs from *D. rugosa* in having a strong median lingual ridge and a nearly circular depression on the labial face of the crown in occlusal view (also see Cappetta 1970; Pollerspöck & Beaury 2014; Sharma *et al.* 2021). *Dasyatis* teeth have also been previously described from the Miocene deposits of Baripada Beds, Orissa, India (Sahni & Mehrotra 1981; Sharma 2013; Sharma & Patnaik 2013), early Miocene of Brazil (Aguilera *et al.* 2017), Venezuela Carrillo (Aguilera *et al.* 2017), Germany (Villafaña *et al.* 2020), early Miocene of Panama (Gillette 1984) and late Miocene of France, Panama (Gagnaison 2017; Perez *et al.* 2017). *Dasyatis probsti* has also been reported from early Miocene of the Simssee area of Bavaria, Germany (Villafaña *et al.* 2020), middle Miocene of Mazan, France (Vialle *et al.* 2011), from the Langhian of Herault (Cappetta 1970), and from the Serravallian of Vaucluse, southern France (Brisswalter 2008).

Order MYLIOBATIFORMES Compagno, 1973
Family Dasyatidae Jordan, 1888
Genus *Himantura* Müller & Henle, 1837

Himantura menoni Sahni & Mehrotra, 1981
(Fig. 4J-R)

Himantura menoni Sahni & Mehrotra, 1981: 83, pl. 3, fig. 9A.

Referred specimens. — Three isolated antero-lateral teeth under the specimen numbers BIOPS/CUP/KP-41, 42 and 43.

Location and horizon. — Middle Miocene greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description

Specimens BIOPS/CUP/KP-41, 42, 43 are small teeth and high crowned rhombic in shape in occlusal view (Fig. 4J-R). The crown of the tooth is divided into labial and lingual zones by the presence of a prominent transverse crest. The labial face of the crown is convex, shallow, a median hollow is present, crown enameloid is ornamented with wrinkles (Fig. 4K, L, Q). The lingual face of the crown is concave and a prominent median lingual ridge is present. However, the labial faces of the crowns are ornamented by irregular pits and wrinkles (Fig. 4J, K, M, N, P, Q). The labial visors are wide and nearly semi-circular to subangular in outline, and the lingual visors are narrow and angular. Median lingual ridge separates the lingual faces into two equal parts which are smooth and concave. The roots of the teeth are strong, lingually arched, bilobate and each root lobe is separated by a deep median groove (Fig. 4J, L, M, O, P, R). Labial part of the root is depressed, while the basal face of the root is nearly flat and triangular in shape.

Remarks

Himantura menoni has earlier been reported from the late Miocene Tapar locality of Kutch, India (Sharma *et al.* 2021), late Miocene of Baripada Beds of eastern India as *Dasyatis menoni* (Sahni & Mehrotra 1981; Sharma & Patnaik 2013) which was later re-assigned to the genus *Himantura* (Andrianavalona *et al.* 2015). The present teeth resemble

the female teeth as they are devoid of pointed transverse crest that bend towards the rear side (also see Kocsis *et al.* 2018; Sharma *et al.* 2021). Teeth of the genus *Himantura* were earlier reported from middle to late Eocene of Egypt (Underwood *et al.* 2011), Morocco and Pakistan (Case & West 1991; Adnet *et al.* 2007, 2010) from the Rupelian of Pakistan and Oman (Thomas *et al.* 1989; Adnet *et al.* 2007), Miocene of deposit of Northwestern Madagascar (Andrianavalona *et al.* 2015), from the Pliocene of Italy (Cappetta & Cavallo 2006). *Himantura* is also reported from the early Miocene of Brazil (Aguilera *et al.* 2017), late Miocene of Borneo (Kocsis *et al.* 2018), from the Pliocene of Italy (Cappetta 2012) and is also known for its wide distribution in Indo-Pacific region (also see Borsa *et al.* 2013; Andrianavalona *et al.* 2015; Weigmann 2016; Borsa 2017). The present day biogeographic distribution of the genus *Himantura* is in the Indo-Pacific region includes the coast of India and Madagascar (Borsa *et al.* 2013; Andrianavalona *et al.* 2015; Weigman 2016; Borsa 2017; Sharma *et al.* 2021).

Genus *Pastinachus* Rüppell, 1829

Pastinachus sp.
(Fig. 4S-JJ)

Referred specimens. — Two isolated upper lateral teeth under the specimen numbers BIOPS/CUP/KP-44, 45, and upper symphysial teeth under the specimen numbers BIOPS/CUP/KP-46, 47, 48, 49.

Location and horizon. — Middle Miocene greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description

Specimens BIOPS/CUP/KP-44, 45, 46, 47, 48 and 49 are small sized teeth, the crowns are hexagonal to rhombic in shape, wider than high (Fig. 4S-DD). The crown is thick, and in occlusal view the surfaces of the crown are flat, smooth, and enameloid is irregularly pitted, a prominent transverse crest separates the labial face from the highly depressed lingual face (Fig. 4S-X). In specimen BIOPS/CUP/KP-46, 47 (Fig. 4Y-DD), the crown is ornamented with median transverse crest, labial faces of the crown are slightly concave to flat in BIOPS/CUP/KP-46 (Fig. 4Z, AA) or convex with slightly overhanging the labial visor in BIOPS/CUP/KP-47 (Fig. 4CC, DD). The lingual visor is smooth and curved, lingual face is concave and lingual marginal face is slightly compressed, median lingual lobe is absent. Specimens BIOPS/CUP/KP-48, 49 (Fig. 4EE-JJ) are having high, thin and hexagonal shaped crown, labial faces of the crown are nearly flat and slightly overhanging towards the labial visor. Roots are robust, bilobate, the two lobes are separated by wide and deep grooves. The basal face of the root is flat and sub triangular to semicircular in shape. In specimens BIOPS/CUP/KP-48 and 49, the roots are small, elongated and lingually arched, bilobate and the diverging lobes are separated by wide and deep grooves (Fig. 4EE, HH).

Remarks

Earlier teeth of the genus *Pastinachus* have been reported from Tapar sites of the late Miocene deposits of Kutch, India (Sharma *et al.* 2021). The present report is the first record of *Pastinachus* from the middle Miocene deposits of India. The lateral teeth of the *Pastinachus* are characterised by their thick, large robust size, rhombic to hexagonal shape, and presence of a salient bulge on the labial face of the crown (Herman *et al.* 1998; Cappetta 2012; Adnet *et al.* 2019; Sharma *et al.* 2021). The anterior teeth of *Pastinachus* are comparatively smaller and have a slightly higher crown extending labio-lingually, symphyseal teeth are distinguishable by their thin crown with curved lingual face (also see Adnet *et al.* 2019). The present specimens are closely similar to *Pastinachus kebarensis* Adnet, Mouana, Charruault, Essid, Ammar, Marzougui, Merzeraud, Tabuce, Vianey-Liaud & Marivaux, 2019 (Adnet *et al.* 2019) in having hexagonal shape high crown, wide teeth crown, flat crown surface, robust roots, etc. However, a more detailed morphological comparison will be required to assign the present specimens to a particular species even though there is a high possibility of them belonging to *Pastinachus* from India (Sahni & Mehrotra 1981; Sharma & Patnaik 2013; Sharma *et al.* 2021) to *Pastinachus kebarensis* (also see Adnet *et al.* 2019; Sharma *et al.* 2021). Previously, teeth of *Pastinachus* were reported from the early Miocene of Libya (Argyriou *et al.* 2015), the Neogene of Taiwan as *Dasyatis* sp. by Uyeno (1978) (also see Cappetta & Cavallo 2006; Cappetta 2012), from the Miocene deposits of Borneo (Kocsis *et al.* 2018). Earlier *Pastinachus* sp. has also been reported from the late Miocene of Baripada Beds in the eastern coast of India as *Dasyatis sylvestris* (also see Sahni & Mehrotra 1981; Sharma & Patnaik 2013). Fossils of *Pastinachus* sp. have been described from shallow marine fossil-bearing deposits of Djebel el Kébar (Merzeraud *et al.* 2016). The species of *Pastinachus aquitinicus* has been reported from France, Lisbon Province, Portugal and Alachua County, Florida, United States (also see Leriche 1942; Zbyszewski 1949; Cahuzac *et al.* 2007; Gagnaison 2017).

Genus *Taeniurops* Garman, 1913

Taeniurops sp.
(Fig. 4KK-PP)

Referred specimens. — Several isolated teeth under the specimen numbers BIOPS/CUP/KP-50, 51.

Location and horizon. — Middle Miocene greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description

Specimens BIOPS/CUP/KP-50, 51 are small sized female teeth, crowns are broad, high and acute (Fig. 4KK-PP). The crown is divided into lingual and labial parts by a sharp transverse crest. The labial and lingual visors of the crown join at sharp marginal angles; labial margins are less arched than the lingual margins. An elongated transverse hollow is present

in the labial face of the crown (Fig. 4LL-OO). Labial faces of the crowns present a deep depression along the transverse crest, and reticulated folded ornamentation of enameloid is present at the labial margin (Fig. 4LL, OO). The lingual face of the crown is slightly concave, and median lingual ridge is absent (Fig. 4KK, NN). Root is small, bilobate and a wide and deep groove is present in between the two lobes, that is lingually projected. The basal face of the root is flat and triangular in shape.

Remarks

The present record is the first report of fossil remains of *Taeniurops* from Miocene deposits of India. *Taeniurops* differs from *Dasyatis* by a sharp transversal edge and an occlusal face that is quite concave (Cappetta & Gayet 2013; Villafaña *et al.* 2020). It is also separable from the teeth of *Dasyatis* in having distinct depression in the labial visor which is bordered by a sharp crest (Cappetta & Gayet 2013; Villafaña *et al.* 2020). The present specimens represent female teeth as they lack the male diagnostic characters of having highly pointed crown. Besides, this male teeth have strong cuspidate and lingually oriented cusps (Villafaña *et al.* 2020). Earlier records of *Taeniurops* are from the lower to the middle Miocene of Germany (also see Reinecke *et al.* 2011; Cappetta 2012), early Miocene of Germany (Probst 1877, as *Raja cavernosa* Probst, 1877, as *Dasyatis cavernosa*; Reinecke *et al.* 2011; Villafaña *et al.* 2020), Portugal (Antunes *et al.* 1981, as *Dasyatis cavernosa*), Switzerland (Fischli 1930, as *Trygon cavernosus*; Bolliger *et al.* 1995), the United States (Case 1980), early Miocene of Switzerland, Brazil (Jost *et al.* 2016; Aguilera *et al.* 2017) and late Miocene of Panama (Pimiento *et al.* 2013).

Batoidae indet.
(Fig. 4QQ-VV)

Referred specimens. — Two isolated female teeth indeterminate position under the specimen numbers BIOPS/CUP/KP-52, 53.

Location and horizon. — Middle Miocene greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description

The specimens BIOPS/CUP/KP-52, 53 are poorly preserved, small sized teeth having high crown, rhombic to asymmetric, reticular shape (Fig. 4QQ-VV). The labial faces of the crown are ornamented with small pits in occlusal views (Fig. 4RR, UU). The thick labial and lingual visor are ornamented with irregular ridge and furrows running nearly vertical (Fig. 4QQ-VV). The face is curved and absence of median lingual ridges. Root of the tooth is small, weak, divided by a shallow nutritive groove (Fig. 4TT).

Remarks

The present specimens are comparable to *Pastinachus* sp. reported from the late Miocene of Kutch, India (Sharma *et al.* 2021) in having rhombic to irregular rectangular crown shape, weak root and shallow nutritive grooves. However, BIOPS 52, 53 differ from the late Miocene specimens in having very high crown tapering down towards the root portion, depressed or curve furrow, comparatively very small root. The incomplete nature of preservation of teeth makes it difficult for species level identification of the specimens.

Class OSTEICHTHYES Huxley, 1880
Subclass ACTINOPTERYGII Klein, 1885
Division TELEOSTEI Müller, 1846
Order CYPRINIFORMES Bleeker, 1859
Family Cyprinidae Cuvier, 1817

Cyprinidae indet.
(Fig. 5A-J)

Referred specimens. — Several isolated teeth under the specimen numbers BIOPS/CUP/KP-54, 55, 56, 57 and 58.

Location and horizon. — Middle Miocene greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description

The teeth are classified into four morphotypes based on morphological variations.

Morphotype 1 (Fig. 5A, B)

BIOPS/CUP/KP-54 is globular in shape, elongated and distally curved towards the apical crown. In lateral view, the tooth is terminated distally with blunt and short hook. In occlusal view, the masticatory area is depressed and bounded by two small lateral cusps (Fig. 5B). The central part of the masticatory area is uneven and ornamented with a shallow crest and furrow.

Morphotype 2 (Fig. 5D, E)

BIOPS/CUP/KP-55 is partially broken. The tooth terminates distally in a blunt well-marked hook. The masticatory area is bounded by well-developed crests on either side and is ornamented with another row of crests in the central part.

Morphotype 3 (Fig. 5E, F)

BIOPS/CUP/KP-56 is anteroposterioly compressed, trapezoidal in shape and elongated. In occlusal view, the crown surface is oval in outline. In lateral view, the crown is slightly curved. The masticatory surface is strongly oblique to the longitudinal axis of the crown.

Morphotype 4 (Fig. 5G-J)

BIOPS/CUP/K-57 and 58 are short, cylindrical in shape and have a circular crown. The grinding surface of the teeth is fully exposed with slightly depressed medially on the crown surface. The lateral margin of teeth is slightly constricted at the median portion of teeth.

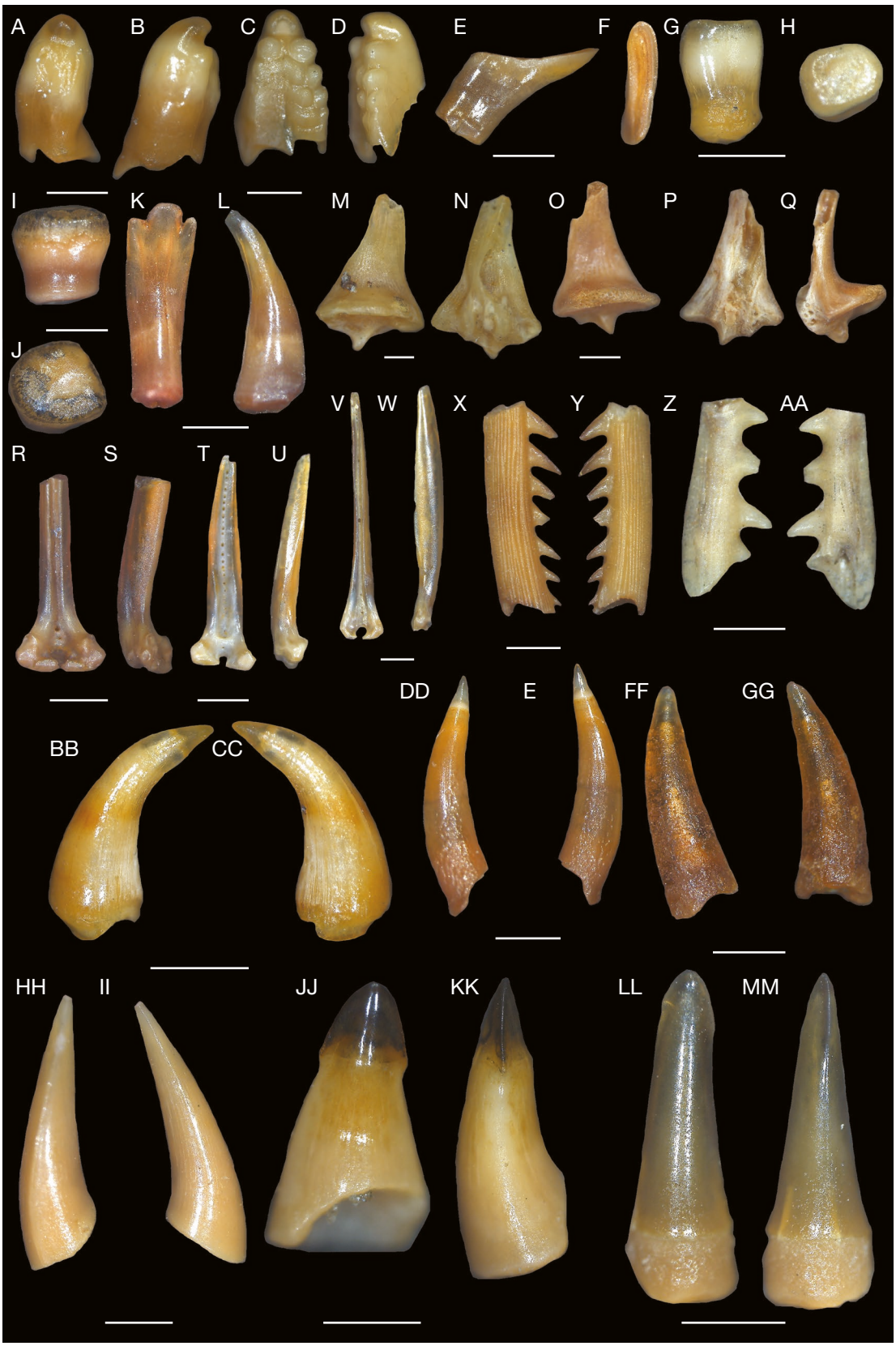

Fig. 5. — **A**-**J**, Cyprinidae indet. (BIOPS/CUP/KP-54, 55, 56, 57, 58), views: **A**, **C**, anterior; **B**, **D**, **E**, **G**, **I**, lateral; **F**, **H**, **J**, occlusal; **K**, **L**, Characidae Latreille, 1825 (BIOPS/CUP/KP-59), views: **K**, anterior; **L**, lateral; **M**-**X**, Bagridae indet. (BIOPS/CUP/KP-60, 61, 62, 63, 64), views: **M**, **O**, **R**, **T**, **V**, anterior; **N**, **P**, basal; **Q**, **S**, **U**, **W**, **X**, lateral; **Y**-**AA**, siluriformes (BIOPS/CUP/KP-65, 66), views: **Y**-**AA**, lateral; **BB**-**II**, Channidae (BIOPS-67, 68, 69, 70), views: **BB**-**II**, lateral; **JJ**-**MM**, Teleostei indet., views: **JJ**, **LL**, anterior; **KK**, **MM**, lateral. Scale bars: A-Q, BB-MM, 1 mm; R-AA, 2 mm.

Remarks

BIOPS/CUP/KP-54 is comparable to those cyprinid pharyngeal teeth reported from the middle Miocene Ramnagar, Jammu and Kashmir (Parmar & Prasad 2012) and the late Miocene of Tapar, Kutch (Singh *et al.* 2019) respectively by having similar features such as short conical hook distally and depressed masticatory area bounded by small crests on either side. The present specimen also exhibits similarity to globular and abraded type of cyprinid (species of barb) teeth reported from the Baynunah Formation of late Miocene, Abu-Dhabi Emirate (Otero 2018), *Tor tor* (Hamilton, 1822) reported from the Late Neogene-Quaternary Lukundol Formation of Nepal (West *et al.* 1988) and to *Barbus* sp. reported from the Oligocene-Miocene of Switzerland and France (Gaudant *et al.* 2002). Because of sharing similar features with different genera of cyprinid, the allocation of this specimen to a particular genus is impossible. BIOPS/CUP/KP-55 also has well-developed crest on the tooth edge and the presence of another row of crest on masticatory area attributes to the pharyngeal teeth of cyprinid (Tiwari *et al.* 1991; Parmar & Prasad 2012; Singh *et al.* 2019). BIOPS 56 compares well to *Labeo* by having a laterally flattened crown, oblique occlusal surface and slightly enlarged crown teeth distally (Otero *et al.* 2009) but differs on account of having an anteroposteriorly narrow crown. However, the present specimen can be assigned to cyprinid without doubt based on its trapezoidal shape, anteroposteriorly narrower, laterally flattened and broader occlusal surface (Tiwari *et al.* 1991; Kotlia & Mathur 1997; Singh *et al.* 2019). BIOPS/CUP/KP-57 and 58 are similar to those teleostei teeth reported from the early Miocene of Jabal Zaltan, Libya (Argyriou *et al.* 2015) on account of being short, cylindrical in shape and having a circular crown. Recently, Parmar & Prasad (2012) reported similar pharyngeal teeth from the middle Miocene of Ramnagar, Jammu and Kashmir and assigned them to Cyprinidae indet.

Order CHARACIFORMES Latreille, 1825
Family Characidae Latreille, 1825

Characidae indet.
(Fig. 5K, L)

Referred specimens. — Several isolated teeth under the specimen numbers BIOPS/CUP/KP-59.

Location and horizon. — Middle Miocene greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description

Specimen BIOPS/CUP/KP-59 (Fig. 5K, L) is a medium size tooth, tricuspidate, subcylindrical in shape, and labiolingually compressed. At the crown, the three cusps are aligned and the middle one is more elongated and prominent. In the basal section, the teeth present a central pulp cavity.

Remarks

The present specimen resembles characids reported from the late Miocene of Baripada. Bed, Orissa (Sharma & Patnaik 2013) and the Lower Oligocene and Miocene of the Arabian Plate (Otero 2001) by having tricuspidate cusps, subcylindrical in shape, labio-lingually compressed, and the middle cusp is more elongated than the two lateral cusps. However, the limited fossils do not allow more precise taxonomic allocation.

Order SILURIFORMES Cuvier, 1817
Family Bagridae Bleeker, 1858

Bagridae indet.
(Fig. 5M-W)

Referred specimens. — Pectoral and dorsal spine under the specimen numbers BIOPS/CUP/KP-60, 61, 62, 63 and 64.

Location and horizon. — Middle Miocene greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description

Specimens BIOPS/CUP/KP-60, 61, (Fig. 5M-Q) represent pectoral spines which are highly damaged and preserve only the proximal part with three articular processes (dorsal, ventral and axial processes). The dorsal process (or condyle) is semi-circular in shape with fine striations developed on their surface. The ventral process is greatly reduced and located opposite to the dorsal process. The axial process is also reduced and slightly pointed. Serrations and denticles are absent on the lateral margins.

Specimen BIOPS/CUP/KP-62, 63, 64 (Fig. 5R-W) are the dorsal spines, characterised by a well preserved articular head, a medium to moderately large rounded articular foramen, and slightly curved and compressed. A wide groove is developed which is continuous throughout the length of the spine. Serrations or denticles are absent on the lateral margins of all the spines.

Remarks

BIOPS-60 and 61 differ from the clariid by having an axial process. Gayet (1987) described that clariid spines do not exhibit any form of axial process and the condyle represents only a quarter of circle. The pictoral spines of ariid are also devoid of any surface ornamentation (Hora 1939; Singh *et al.* 2019), whereas the condyle surfaces of the present specimens are marked by the striations. BIOPS-60 and 61 are attributed to the pectoral spine of bagrid by the presence of striations on condyle, the presence of three articular processes and the absence of serrations or denticles on the shafts (Sahni & Khare 1977; Gayet 1987; Otero & Gayet 2001; Singh *et al.* 2019). BIOPS-62, 63 and 64 are closely similar to bagrid dorsal spines (Gayet 1987; Parmar & Prasad 2012; Singh *et al.* 2019), having a well preserved articular head, a medium to moderately large rounded articular foramen, slightly curved and compressed and devoid of serrations or denticles on the

lateral margins. However, the precise taxonomic allocation of the present specimens is not possible until complete spines are found.

Order SILURIFORMES Cuvier, 1817

Siluriformes indet.
(Fig. 5X-AA)

Referred specimens. — Spines fragments under the specimen numbers BIOPS/CUP/KP-65, 66.

Location and horizon. — Middle Miocene greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description
The present spines are broken off and no distal and proximal parts are preserved. They are dorso-ventrally convex, and are ornamented with striations on both sides. The posterior denticles are prominent with well-developed, whereas the anterior denticles are absent (Fig. 5X-AA). The denticles are conical in shape and are closely spaced. The shafts are wider towards the proximal end and narrower towards the distal end.

Remarks
BIOPS/CUP/KP-65 and 66 differed from the pectoral spines of ariid, e.g. *Arius* Valenciennes, 1840 from Baripada Beds of Miocene (Hora 1939) and *Arius sahni* Khare, 1976 from middle Eocene Subathu Formation of Beragua Coal Mine, Jammu and Kashmir (Khare 1976) by having denticles on posterior margin. A bagrid spine reported by Gayet (1987) from the lower-middle Eocene Kuldana Formation, Pakistan (Gayet 1987) also differs from BIOPS/CUP/KP-65 and 66 in having both anterior and posterior dentitions. The present specimens compare well to those of clariid such as *Clarias batrachus* (Linnaeus, 1758) and *C. falconeri* Lydekker, 1886 (Sahni & Khare 1977) reported from the Middle Siwalik deposits of Ladhyani and Lehri-Sarail, Himachal Pradesh on account of having denticles on the shaft and the presence of longitudinal striations on both dorsal and ventral surfaces. However, *C. batrachus* and *C. falconeri* are characterised by their minute denticles on the anterior margin, whereas the denticles on the shaft of BIOPS/CUP/KP-65 and 66 are present only on the posterior margin. Because of all these differences and lack of diagnostic features, it is difficult to assign these spines to any family.

Order PERCIFORMES Bleeker, 1859
Family Channidae Fowler, 1934

Channidae indet.
(Fig. 5BB-II)

Referred specimens. — Several teeth under the specimen numbers BIOPS/CUP/KP-67, 68, 69, 70.

Location and horizon. — Middle Miocene greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description
The present teeth are pointed, conical in shape, bulging towards the base. Most of the teeth surfaces are ornamented with weak wrinkle and longitudinal serration (Fig. 5DD-GG), whereas some have smooth surfaces (Fig. 5BB, CC, HH, II). The tooth referred to BIOPS-70 is large and straight, whereas BIOPS-67, 68 and 69 are small and apically curved.

Remarks
The present specimens are closely similar to the channid reported from the Upper Siwalik deposits of Surai Khola, Nepal (Kotlia & Mathur 1997) and lower Siwalik beds of Jammu (Parmar & Prasad 2012) by having conical shape, pointed apical part, thin enameloid layer and striations on the crown as well as at the base. BIOPS-67, 68 and 69 also compare well to recent *Channa* Scopoli, 1777 such as *C. stratus* Day, 1878 (synonym of *Ophicephalus striatus* Day, 1878) and *C. mullius* F. Hamilton, 1822 described by Kotlia & Mathur (1997) on account of having curved apex and base with wrinkles and striations, but the recent *Channa* sp. is characterised by being anteriorly narrower and posteriorly broader, unlike the present specimens. Because of sharing of the above mentioned tooth morphological features except for being anteriorly narrow and posteriorly broad, the present specimens are attributed here to Channidae.

Division TELEOSTEI Müller, 1846

Teleostei indet.
(Fig. 5JJ-MM)

Referred specimens. — Two isolated teeth the specimen numbers BIOPS/CUP/KP-71, 72.

Location and horizon. — Middle Miocene greyish coarse sandstone gravelly lag bed of Chhasra Formation at Palasava site, Kutch, Gujarat.

Description
BIOPS/CUP/KP-71 and 72 are high, conical in shape, bulging towards the base and compressed towards the apex (Fig. 5JJ-MM). The tip is lanceolate and slightly constricted below the labio-lingually flattened part of the crown. Both specimens are devoid of serration.

Remarks
The present specimens are slightly similar to Amiiformes on account of lanceolate shape with the presence of thin enameloid at the tip (see, Poyato-Ariza & Martín-Abad 2013). However, the fossil records of Amiidae fish from the Miocene are very meager. Therefore, BIOPS-71 and 72 are assigned to teleostei indet.

DISCUSSION

Faunal composition and paleoenvironment

The middle Miocene Palasava section of Kutch, India has yielded a diverse faunal assemblage comprising of elasmobranchs, teleosts, chelonians, crocodiles, snakes, birds and mammals (Kapur *et al.* 2019) (also see Fig. 6). The mammalian fauna (11 families, nine genera and nine species) is the most diverse, followed by the batoids (three families, eight genera and ten species) and teleosts (three families, genera and species unidentified), crocodiles (two families, two genera and two species), turtles (two families, three genera and species unidentified), birds (two families, genera and species unidentified), sharks (one family, two genera and seven species), snake (one family, one genus and one species) (also see Fig. 6A, B). The fish fauna (sharks, batoids and teleosts) of Chhasra Formation with a total of seven families, ten genera and 17 species is quite diverse (also see Fig. 6A, B). The chondrichthyans from Palasava are represented by the families Carcharhinidae, Myliobatidae, Dasyatidae and Pristidae. The shark assemblage is dominated by the genus *Carcharhinu*s, comprising *C. brevipinna*, *C. falciformes* and *C. leucas* which are mostly circum-tropical in distribution, except for *C. perezi* which is mainly restricted to the Caribbean Sea (also see Compagno 1984; Pollerspöck & Straube 2019; Villafaña *et al.* 2020). *Carcharhinus* sharks are considered to be adapted to a wide range of habitats ranging from inshore to offshore environment, from tropical, subtropical to temperate climate (Compagno 1984; Cappetta 2012; Sharma *et al.* 2021). Extant species of *Carcharhinus* including *C. brevipinna*, *C. leucas*, *C. perezi* and *Negaprion* inhabit continental, coastal and insular shelves at depths of 0-200 m (Weigmann 2016) (also see Fig. 7C), *C. leucas* and *C. perezi* are usually found at depths of 30 m (Pimiento *et al.* 2013; Carrillo-Briceño *et al.* 2016b). *Carcharhinus leucas* is also considered to be adapted to freshwater conditions (Compagno 1984; Cook *et al.* 2010). *Carcharhinus brevipinna* is mainly found in warm temperate to tropical areas in the Atlantic, Mediterranean and Indo West Pacific (Compagno 1984; Reiner 1996; Burgess 2009; Perez *et al.* 2017). *Carcharhinus falciformes* is found in open ocean, occasionally insular shelves and inshore at depths of 18 to 500 m (Compagno 1984; Purdy *et al.* 2001; Pimiento *et al.* 2013) (Fig. 6C) whereas *C. perezi* is known to be found in open ocean at the depth of 380 m (Weigmann 2016) (also see Fig. 6C). *Carcharhinus brevipinna*, *C. falciforme* and *C. leucas* are in present-day Indian Ocean (Akhilesh *et al.* 2014). *Negaprionodon* sharks mainly inhabit estuarine and intertidal through offshore waters at depths of 92 m in the Atlantic and the Pacific Ocean (Compagno 1984; Kent 1994). Among the *Negaprion*, *N. brevirostris* frequently inhabit mangrove environments and coral reefs, but occasionally can be found in the open ocean near surface waters for migration purposes and occur in tropical and temperate, estuarine and marine waters generally at depths of 0-92 m (Compagno 1984; Kent 1994; Compagno *et al.* 2005). *Negaprion* is commonly adapted to warm waters (Cappetta 1987) and mainly feeds on actinopterygians, small shark, squid and octopus, etc. (Compagno 1984). Among the batoids, *Myliobatis* and *Taeniurop* are known to inhabit brackish and marine open sea environments (Compagno 1984; Carrillo-Briceño *et al.* 2016b). *Aetobatus*, *Dasyatis*, *Himantura*, *Pastinachus* and *Pristis* are mostly found in shallow shelves, shallow estuaries, lagoons and fresh water (Compagno 1984; Sharma *et al.* 2021) (Fig. 7A, C). *Dasyatis* and *Taeniura* are usually found in water depths of 50 m (Carrillo-Briceño *et al.* 2016b) (Fig. 7A, C). However, the species *D. rugosa* and *T. cavernosa* are found at water depths of up to 500 m (Vialle *et al.* 2011; Carrillo-Briceño *et al.* 2016b). Species of the genus *Himantura* are well adapted to a wide range of habitats, from sandy bottoms in large rivers (5 to 20 m depth), estuaries, brackish waters to tropical shallow marine environments, open shallow subtidal, coastal marine, fluvio-deltaic environment (Marzullo *et al.* 2011; Andrianavalona *et al.* 2015; Aguilera *et al.* 2017; Sharma *et al.* 2021). Some genera of rays, such as *Himantura* or *Pastinachus*, have also been reported from estuaries and fresh water (Kocsis *et al.* 2018). The record of *Pastinachus* associated with certain mammal bones from Tunisia is considered to have been deposited in a forestland (Dartevelle & Casier 1943; Adnet *et al.* 2010; Murray *et al.* 2010), close to coastal environment from the early late Eocene of Egypt (Murray *et al.* 2010), shallow marine inshore (Adnet *et al.* 2010; Underwood *et al.* 2011), shallow and macrotidal environments between dune or channel bar sets (Underwood *et al.* 2011). *Pastinachus* is considered as amphidromous, resting on shallow-water inshore sandflats and frequently venturing far into estuaries and freshwaters (Adnet *et al.* 2019). *Dasyatis rugosa* is known from the marginal marine environment, and depths ranging from 0-480 m (Compagno *et al.* 2005; Kyne & Simpfendorfer 2007; Vialle *et al.* 2011). The elasmobranch faunas recorded from Palasava are mostly adapted to tropical to subtropical, warm and humid climate.

The osteichthyans of Palasava comprising of Cyprinidae, Bagridae, Characidae and Channidae are commonly found in freshwater river and brackish water conditions (Nelson 2006). The present ecology of these extant taxa shows that they live in freshwater and brackish water conditions throughout Africa and Asia (also see Roberts 1975; Mo 1991). Among the extant freshwater teleosts, cyprinids including carps, barbs and loaches are the most common and occur essentially in lakes and rivers (McClelland 1839; Daniels 2000). Bagrids dwell in diverse habitats such as upland streams, large river channels and seasonal floodplain lagoons (Winemiller 1996). Channids inhabit a variety of freshwater conditions ranging from lakes, ponds, rice paddies, swamps, and peat swamp forests, to large rivers, creeks, and hill streams (Rüber *et al.* 2020). Records of elasmobranch, teleosts, and various mammalians, reptiles and birds (Fig. 6A) (Kapur *et al.* 2019) suggest a warm and humid, tropical to sub-tropical environmental condition in the middle Miocene (*c.* 14 ± 2 Ma). The teleosts described above are found mostly in freshwater and sometimes in brackish water (Nelson 2006). The present piscean fauna associated with other marine and terrestrial vertebrate remains from this section suggest a coastal, marginal marine, near shore littoral to neritic environment of deposition with the influence of freshwater riverine system.

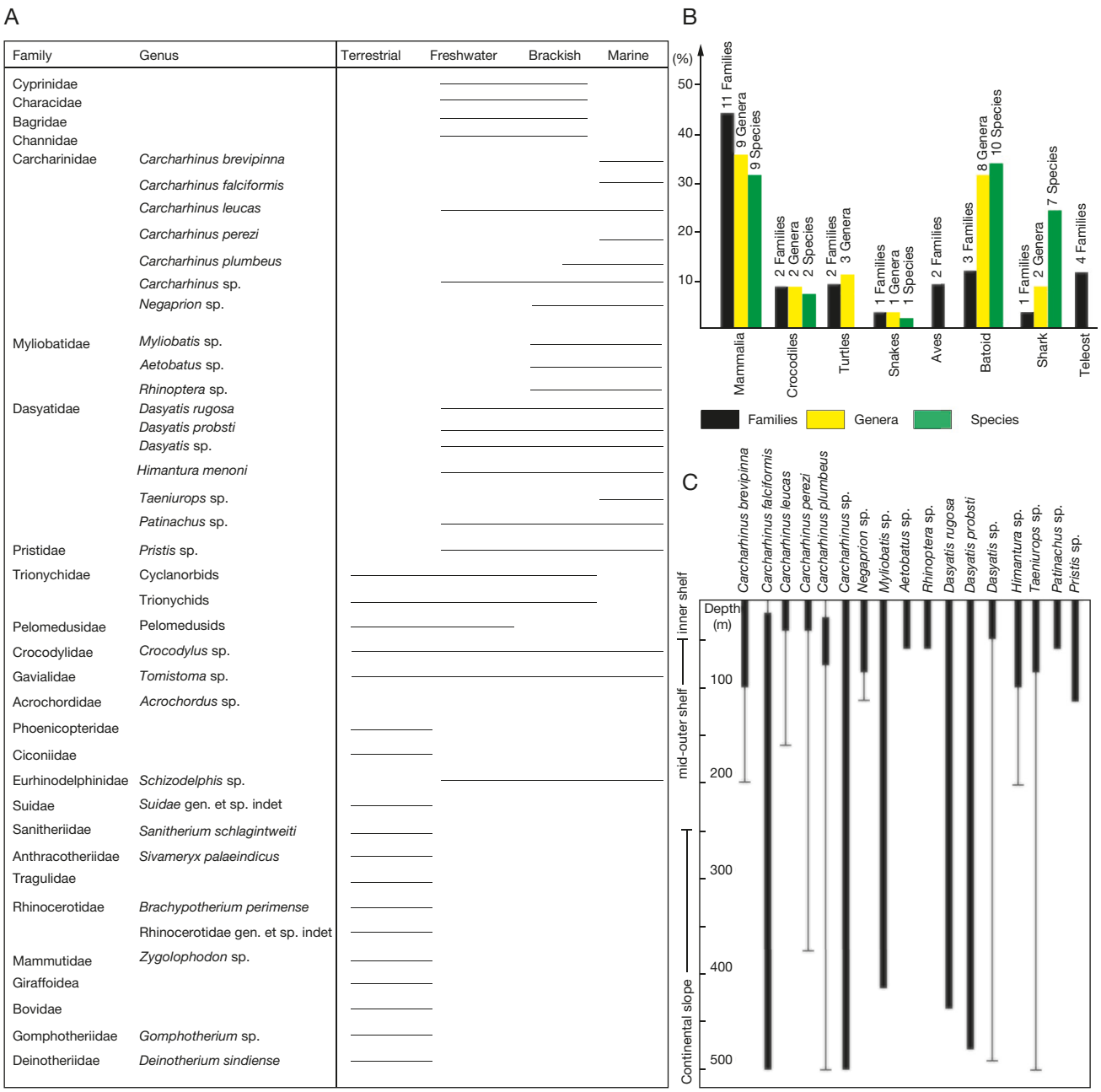

Fig. 6. — **A**, Paleoenvironment distribution of the middle Miocene fauna of Palasava site, Kutch, India (also see Compagno 1984; Carrillo-Briceño *et al*. 2016; Kapur *et al*. 2019; Sharma *et al*. 2021; present study); **B**, faunal Assemblage of the middle Miocene of Palasava site, Kutch, India (sources: Kapur *et al*. 2019; present study); **C**, depth preferences of the elasmobranch from middle Miocene of Palasava site (also see Compagno 1984; Pimiento *et al*. 2013; Weigmann 2016; Carrillo-Briceño *et al*. 2016; and references therein).

The present faunal assemblage of elasmobranchs and teleosts, in association with other vertebrates including chelonians, crocodiles, snakes, birds and mammals such as *Sanitherium*, *Sivameryx*, *Brachypotherium*, *Zygolophodon*, *Gomphotherium*, and *Deinotherium* from the Palasava site indicates the presence of a riverine-estuarine system(s) linked to the sea, i.e., the depositional centres were quite close to the sea (also see Kapur *et al.* 2019). Previous reports of angiospermous palynomorph assemblages from this locality comprising *Spinizonocolpites*, *Spinomonocolpites*, *Retitrescolpites*, *Meliapollis*, *Ctenolophonidites*, *Palaeomalvaceaepollis*, *Graminidites*, and *Ericipites* indicates the existence of mangroves near the tropical to subtropical forests under warm and humid climatic conditions (Verma *et al.* 2013). The existence of woodland forest in the vicinity of freshwater and marine environments is also evidenced by the assemblages of many fossilised wood (Shukla *et al.* 2014), mammalian fossil fauna including proboscids, rhinocerotids, giraffid, tragulids, etc. (Kapur *et al.* 2019) and the existence of a warm humid climatic condition is also indicated by the presence of herpetofaunal assemblages (Singh *et al.* 2022). Based on the presence of permineralized fossil woods including *Bauhinium palaeomalabaricum* and *Ebenoxylon indicum*

TABLE 1. — Faunal similarity (Dice' similarity) of early and middle Miocene elasmobranch of Kutch, India and other early and middle Miocene deposits of Mediterranean and Indo-Pacific regions. The data of early Miocene elasmobranch of Kutch, India are from Sharma *et al.* (2021) and references therein.

Country	Localities	Number of genera	Share number genera	Dice's similarity index	References
Faunal similarity (Dice' Similarity) of early Miocene elasmobranch of Kutch, India and other early Miocene deposits of Mediterranean and Indo-Pacific regions					
Spain	Elche, CalaSantVicenç	11	6	0.444	Vicens & Rodríguez-Perea 2003; Villafaña *et al.* 2020
France	Bordeaux, Breyra Valley, Gironde, Léognan, Montpellier, Saucats	41	13	0.456	Cappetta 1970; Goedert *et al.* 2017; Villafaña *et al.* 2020
Switzerland	Benken, Zurich; Lucerne, Gallen	41	9	0.316	Fischli 1930; Bolliger *et al.* 1995; Jost *et al.* 2016
Italy	MontagnadellaMaiella	7	4	0.348	Marsili *et al.* 2007
Malta	Rasir-Reqqa, Bahrija, Rdumii-Vigarju	15	8	0.516	Ward & Bonavia 2001
Germany	Simsee	31	12	0.511	Villafaña *et al.* 2020
Austria	Eggenburg, Maigen, Kletzenmarkt, Oberösterreich, Plesching, Wallern	46	9	0.290	Schultz 2013; Pollerspöck *et al.* 2018
Slovakia	Cerova, Lieskove	30	8	0.348	Underwood & Schlögl 2013
Hungary	Ipolytarnoc	20	7	0.389	Kordos & Solt 1982; Kocsis 2007
Egypt	Moghra	9	6	0.480	Cook *et al.* 2010
Libya	Jabal Zaltan	9	6	0.480	Argyriou *et al.* 2015
Grenadines	Lesser Antilles	5	3	0.286	Portell *et al.* 2008
Colombia	Guajira Peninsula	11	5	0.385	Carrillo-Briceño *et al.* 2016a
Venezuela	Falcón Basin	24	11	0.550	Carrillo-Briceño *et al.* 2016b
Brazil	Northern Brazil	21	12	0.649	Dos Reis 2005; Aguilera *et al.* 2017
Chile	Central Chile	16	5	0.313	Suarez et al. 2006; Villafaña *et al.* 2020
Panama	Central Panama	9	4	0.320	Pimiento *et al.* 2013
Japan	Mizunami	5	2	0.267	Takakuwa & Ando 2018
Middle Miocene faunal similarity between the Kutch fauna and other middle Miocene deposit of Mediterranean and Indo-Pacific regions					
Poland	Holy Cross Mountains	15	4	0.320	Schultz 1977
Hungary	Nyirád	14	5	0.417	Szabó & Kocsis 2016
Spain	El Chorrillo	11	1	0.095	Perez *et al.* 2017
France	Mazan	29	5	0.256	Vialle *et al.* 2011
Panama	Sabanita	12	5	0.455	Gillette 1984
Peru	Ica Valley	10	2	0.20	Collareta *et al.* 2021
Grenadines	Lesser Antilles	5	1	0.133	Portell *et al.* 2008
Japan	Central Japan	34	4	0.182	Karasawa 1989; Takakuwa 2006; Takakuwa *et al.* 2009; Suziki 2012
South Korea	Pohang City	5	1	0.133	Yun 2020

from Palasava, Shukla *et al.* (2014) concluded the prevalence of tropical forests with high precipitation and low seasonality during the middle Miocene deposition of Palasava area. Thus, integration of the flora and fauna from Palasava locality is in favour of warm, humid/wet, tropical to sub-tropical environmental conditions during the middle Miocene (*c.* 14 ± 2 Ma) (also see Kapur *et al.* 2019).

PALAEOBIOGEOGRAPHIC CONSIDERATIONS

The Kutch basin in western coast of India and its fossil records are significant for Neogene paleobiogeographic reconstruction of Africa and Eurasia owing to its rich marine and terrestrial fauna ranging from early to late Miocene (Patnaik *et al.* 2014; Kapur *et al.* 2019; Singh *et al.* 2020; Sharma *et al.* 2021). The paleobiogeographic distribution of Neogene marine and terrestrial fauna is considered as direct or indirect evidence of collision tectonics of African-Arabian plate and subsequent rearrangement of the Tethyan Sea connecting the Indian Ocean, Atlantic Ocean and Mediterranean Sea along with changes in the oceanic circulation pattern (also see Spezzaferri 1995; Rögl 1999; Hardenbol *et al.* 1998; Harzhauser *et al.* 2002, 2007; Patnaik 2016; and references therein). A close faunal similarity is observed between the early Miocene elasmobranch of the Western coast of India and their counterparts from Red sea and Mediterranean Sea (also see Sharma *et al.* 2021), Western Atlantic Ocean: Lesser Antilles (26%), Venezuela (65%), Brazil (58%) (also see Dos Reis 2005; Portell *et al.* 2008; Carrillo-Briceño *et al.* 2015, 2016b; Aguilera *et al.* 2017; and references therein) and Eastern Pacific Ocean- Panama (37%), Colombia (34%) Chile (20%) (Suarez *et al.* 2006; Pimiento *et al.* 2013; Carrillo-Briceño *et al.* 2016a) (also see Table 1). This similarity indicates the presence of a Tethyan seaway passage till the early Aquitanian (Rögl 1999; Piller *et al.* 2007) connecting the Indian Ocean with the Atlantic Ocean (Sahni & Mehrotra 1981; Adnet *et al.* 2007). Such a marine connection could have favored the migration of the elasmobranchs from Mediterranean Sea to the India Ocean (Sharma *et al.* 2021; and references therein), and even after Tethys was reduced to Mediterranean, the isthmus of Panama was still open till the late Miocene (*c.* 9 ma) (Perez *et al.* 2017), which might

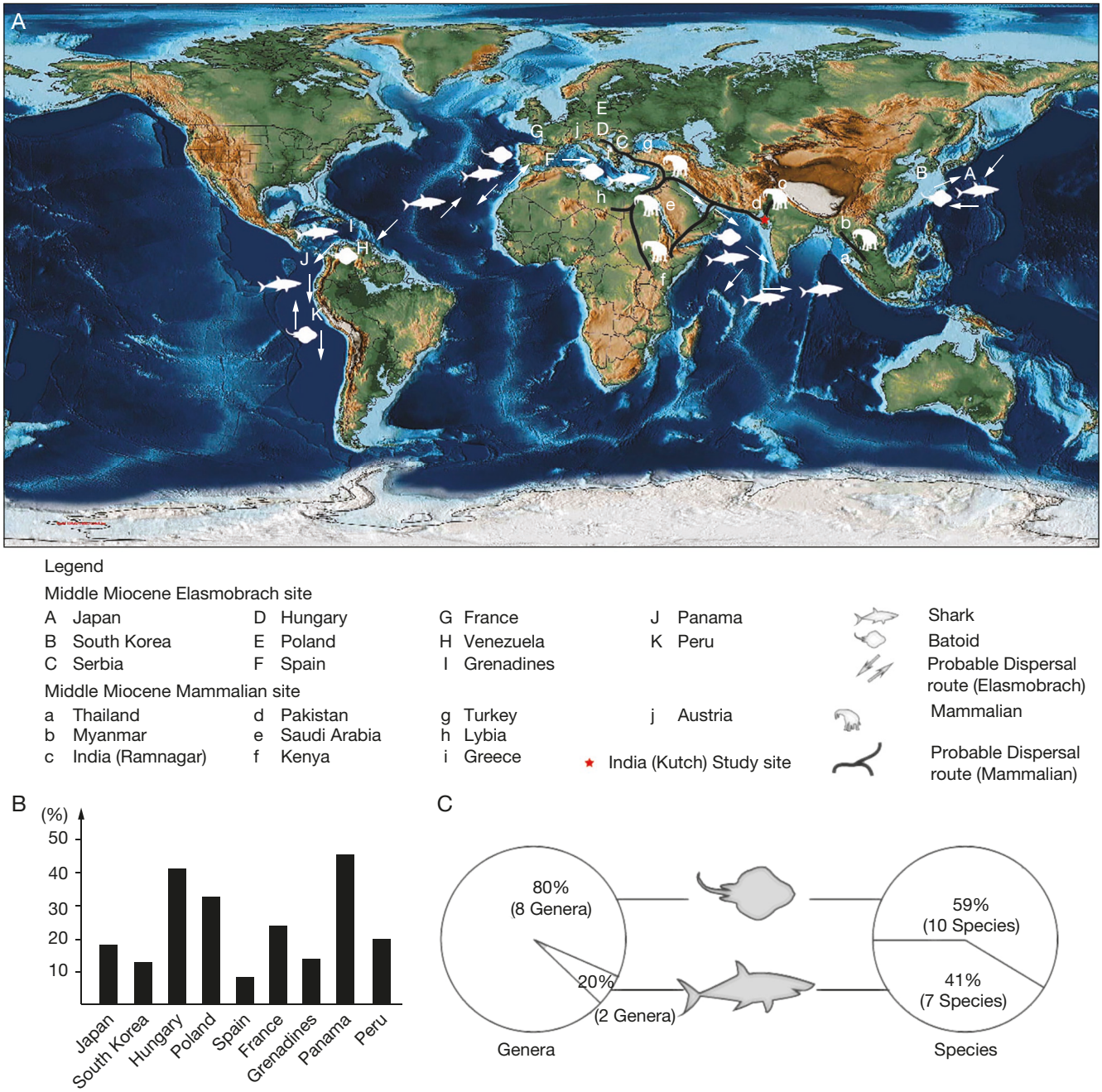

Fig. 7. — A, Paleobiogeographic map of the middle Miocene Elasmobranchs (sources: Schultz 1977; Gillette 1984; Karasawa 1989; Aguilera & De Aguilera 2001; Takakuwa 2006; Portell *et al*. 2008; Suziki 2012; Takakuwa *et al*. 2009; Vialle *et al*. 2011; Szabó & Kocsis 2016; Perez *et al*. 2017; Jovanović *et al*. 2019; Yun 2020; Collareta *et al*. 2021) (sources: Patnaik 2016; Kapur *et al*. 2019); **B**, dice's Similarity Index graph of elasmobranch faunas in middle Miocene; **C**, percent relative abundance chart of elasmobranch genera and species. Credits: A, PALEOMAP PaleoAtlas (GPlates).

have allowed the migration of sharks from eastern Pacific to Indo-Pacific Ocean through the Mediterranean sea (Fig. 6B).

The present elasmobranch assemblage from the middle Miocene deposits of the western coast of India still shows a good similarity index with their counterparts of Mediterranean Sea namely, France (33%), Portugal (27%), Spain (19%) and Hungary (40%). As compared to the similarity data of early Miocene fauna, the middle Miocene data shows a slight decline in the similarity index. However, this similarity may be attributed either to the diversification of Indian fauna from the remnant water of the Tethys Sea (also see Sahni & Mehrotra 1981; Mondal *et al.* 2009; Sharma & Patnaik 2014) or intermittent migrations of a marine fauna between Mediterranean and Indian Ocean during some short-term reopening of the Tethyan Seaway around 15-14 Ma (Harzhauser *et al.* 2007; and references therein), before a permanent closure of the seaway took place. Such a permanent land bridge would have permitted the migration and diversification of terrestrial fauna across Africa and Eurasia (also see Rögl 1999; Harzhauser *et al.* 2007; Patnaik 2016; Kapur *et al.* 2019). However, a higher

faunal affinity has been observed with Eastern Pacific-Panama (50%); Indo-Pacific-Japan (41%), South Korea (24%) and Caribbean Sea-Lesser Antilles (24%), Eastern Atlantic-Poland (43%) (also see Gillette 1984; Karasawa 1989; Portell *et al.* 2008; Yun 2020) (Table 1; Fig. 7). A closer faunal similarity of middle Miocene Palasava fishes with those from Japan, South Korea, Lesser Antilles and Panama (also see Gillette 1984; Karasawa 1989; Portell *et al.* 2008; Yun 2020) might point towards a gradual shift in migration path through the Pacific Ocean to Indo-Pacific region (Fig. 7). Such a shift coincides with the Neogene worldwide invasion of large Carcharhinidae through other possible gateways of open Panama isthmus and/or South African strait which would have promoted the diversification of Indo-Pacific marine groups (Briggs 1999; Adnet *et al.* 2007).

The teleosts belonging to Cyprinidae, Bagridae, Clariidae and Channidae inhabited both Africa and Asia in the Miocene (Nelson 1994, 2006; Singh *et al.* 2019). The dispersal history of different taxa of teleost families between Eurasia and Afro-Arabia is linked to the connection and separation of landmasses (Patterson 1993; Doadrio 1994; Nelson 2006). The extant cyprinids represent the most diverse family of bony fishes in Eurasia and Africa (Nelson 2006), and fossil cyprinids have also been reported from Asia (Li *et al.* 1983; Tiwari *et al.* 1991; Lee 2004; Chang & Chen 2008; Parmar & Prasad 2012; Sharma *et al.* 2015; Singh *et al.* 2019), Europe (Gaudant & Rousset 1979; Cavender 1991; Gaudant *et al.* 2002) and Afro-Arabic Plate (Otero 2001). However, the family is widely considered to have originated in China (Briggs 1999; Gaudant *et al.* 2002). Their dispersal can be correlated with the first Tertiary land connection between the Afro-Arabia and Asia (Rögl & Steininger 1983; Adams *et al.* 1983; Thomas 1985). Miocene bagrids and clariids have also been reported from many localities of Asia, Europe, Afro-Arabia (also see James & Slaughter 1974; Thomas 1981; Frostick & Reid 1986; Stewart 2001; Otero & Gayet 2001; Parmar & Prasad 2012; Argyriou *et al.* 2015; Singh *et al.* 2019). Although they are since the Palaeogene times in both Asia and Afro-Arabia, their dispersal history could not be resolved as there was no terrestrial connection between the two continents before (Otero & Gayet 2001). The snakehead (channids) fishes were restricted to tropical south Himalayan regions such as Baluchistan, Pakistan, India and Nepal (Böhme 2004) during the early Miocene. After this, they expanded rapidly into subtropical Western Eurasia and have been recorded from many localities of Western Eurasia during 17.5-13 Ma (Böhme & Ilg 2003; Böhme 2004). But, these fishes were absent in the southern parts of Western Eurasia (Mediterranean region, Eastern Europe and Arabia), Eastern Eurasia (Mongolia, China and Japan), and Africa during 17.5-13 Ma. At the beginning of late middle Miocene, they disappeared from Western Eurasia and were restricted to central and south Asia approximately between 13-8 Ma (Böhme 2004). However, a species level identification of the assemblage is required to evaluate any fresh-water connection between Afro-Arabia and Southwestern Asia during the Miocene.

CONCLUSION

The Chondrichthyan fauna from the middle Miocene of Palasava localities of Kutch comprises of *C. brevipinna*, *C. falciformis*, *C.* cf. *leucas*, *C. perezi*, *Carcharhinus* sp., *Negaprion* sp. *Aetobatus* sp., *Myliobatis* sp. *D. probsti*, *D. rugosa*, *Himantura* sp. *Pastinachus* sp. and *Taeniurops* sp. The osteichthyan fauna is represented by four families comprising of Bagridae, Channidae, Characidae and Cyprinidae.

The ichthyofauna described above and other associated marine and terrestrial vertebrate remains from middle Miocene (*c.* 14 ± 2 Ma) suggest a coastal, marginal marine, near shore littoral to neritic environment of deposition with the influence of freshwater riverine system. The integration of the flora and fauna from Palasava points towards the presence of a warm, humid/wet, tropical to sub-tropical environmental conditions during the middle Miocene.

The elasmobranchs described above show a good similarity index with their counterparts in the Mediterranean Sea suggesting a short-term reopening of the marine pathway during Langhian. However, a much higher faunal affinity with those of Eastern Pacific indicates a gradual shift towards migration between Pacific Ocean and Indo-Pacific region once a permanent landbridge was established.

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