Indian Journal of Geo Marine Sciences
Vol. 53 (12), December 2024, pp. 785-795
DOI: 10.56042/ijms.v53i12.17562

Research Article

A mega-toothed shark, *Otodus megalodon* (Agassiz, 1835) from the Middle Miocene Bhuban Formation of Mizoram, India

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Received 28 November 2024; revised 30 December 2024

The Bhuban Formation of Mizoram is known for its fossil assemblages of invertebrates, foraminiferans, sharks and batoids. Recent fieldwork at Tuithum Quarry of the Bhuban Formation, Mizoram, yielded an isolated tooth of *Otodus megalodon* (Agassiz, 1835), the largest fish that ever lived on earth. The present record of *O. megalodon* is not only the first-time report from the Miocene of Mizoram but also from the entire Northeast India. The *O. megalodon* was a cosmopolitan giant predator, known to inhabit tropical, subtropical, and temperate seas during the early Miocene to early Pliocene epochs. Based on regression analyses, the tooth belonging to this individual specimen is estimated to indicate a total body length of approximately 7.81 meters, suggesting that it was likely a juvenile. The present finding of *O. megalodon* and the earlier record of the elasmobranch fauna and associated invertebrates indicate that a warm, shallow marine (nearshore), high-energy environment prevailed during the deposition of the upper Bhuban Formation.

[**Keywords**: Miocene, *Otodus megalodon*, Paleobiogeography, Paleoenvironment, Sharks]

Introduction

The fossiliferous Bhuban Formation of Mizoram represents a part of the Surma Basin extending towards the Tripura-Mizoram accretionary belt[1,2]. The major lithostratigraphic units of Mizoram are characterised by the presence of an alternate sequence of arenaceous and argillaceous deposits, which are known to have yielded certain molluscs, decapods, echinoids, foraminiferans, corals, elasmobranchs and teleost fishes, and ichnofossils[3-21]. Recent fieldwork conducted at the Bhuban Formation of Mizoram yielded a well-preserved tooth of *Otodus megalodon* (Agassiz, 1835), for the first time from this formation. The species is considered the biggest macropredator shark that ever existed on this planet.

The extinct shark *O. megalodon* existed from the Miocene to the Pliocene and is known globally as a cosmopolitan species, well adapted to both tropical and temperate environments[22-25]. However, the record of megalodon sharks from India is limited to the Baripada Beds on the east coast and questionably from Kutch[26-29]. It is considered that this cosmopolitan giant predator reached a maximum total length (herein, TL) of ~ 15 to 18 m[(refs. 30-33)]. The largest known specimen of *O. megalodon* is estimated to have reached about 20 meters in length[30-32]. These sharks used to roam around the globe during the Miocene (23 Ma) to Pliocene time[33,34]. The species became extinct during the transitional phase of early to late Pliocene (~3.6 Ma), and the reason for the extinction remains a mystery[24,33-36]. Certain workers opined that the extinction of *O. megalodon* may be related to the reduction of productive coastal habitats in the late Pliocene and the advent of probable competitors[36-37]. Presently, *Carcharodon carcharias* is considered as the largest surviving macrophagous shark attaining a body length of approximately 6 to 7 m[(refs. 33,38-40)]. The rise of *C. carcharias* might have been associated with the oceanographic changes during Pliocene, population fragmentation, and competition for food generating a biotic stress which subsequently drove to the extinction of *O. megalodon*[24,41].

Specimens of *O. megalodon* are usually large, and their isolated teeth and vertebrae may be found associated with tooth sets[23,42-45]. Based on the previous reports of large-sized triangular serrated teeth and further study of their feeding habits, the

megatooth shark is considered the largest macro-predatory shark to have ever existed[24,33,35,36,46-49]. In the Indian context, the report of *O. megalodon* is limited to the late Miocene Baripada Beds[26,28,29]. The present paper documents the first report of *O. megalodon* shark from the Lower to Middle Miocene Bhuban Formation, Mizoram and attempts to reconstruct the paleoenvironmental and paleobiogeographic conditions of the region by integrating previous faunal records from the region.

Geological settings

Geologically, the Neogene deposits of the Surma Group of Mizoram, which is a part of the Tripura-Mizoram accretionary, comprise a series of elongated folds having N-S direction trends and arcuate shapes with westward convexity, which runs almost parallel to the suture zone of the Arakan-Yoma subduction[1,2,20,50]. The entire sedimentary column of the area consists of medium to fine-grained sandstone, silty-sandstone to siltstone, mudstone, shale, a few lenses of coquina limestone, calcareous sandstone and conglomerates with intraformational clasts[20]. The Cenozoic deposits of Mizoram can be classified as Oligocene deposits of the Barail Group, Lower to Middle Miocene deposits of the Surma Group and Middle Miocene to Late Pliocene deposits of the Tipam Group (See, Table 1). The deposits of the Surma Group are subclassified into two formations, namely the Bhuban Formation and Bokabil Formation. The Bhuban Formation exposed in Mizoram are again subdivided into the Lower Bhuban, Middle Bhuban and Upper Bhuban units[1,2,9,20,50].

The presently described specimen was collected from the *in-situ* sandstone exposed at Tuithum Quarry in the western limb of the Aizawl anticline within a geographical coordinate of 23°44'00" N; and 92°41'00" E. The exposure of the rock sequence of upper Bhuban Formation in this site is approximately 78.9 m with three prominent lithological units comprising sandstone, silty-shale and conglomerate. Sandstones are fine to medium-grained, grey in colour; parallel to cross lamination and flame structures, mud clasts, and pebbles are also present. Biogenic activities are poorly preserved in the upper part of the sandstone bed. Silty-shale, which occurs as an interbedded layer between sandstone beds, is grey to dark grey in colour. These beds are rich in fossil assemblages consisting of shark teeth, bivalves, gastropods and burrows. A conglomeratic band of 0.3 m thick is present above the sandstone bed at 3.6 m levels. These bands contain extensively bored pebbles, and the fossil assemblage consists of bivalves and burrows.

Material and Methods

The collected sample from the Tuithum locality of Aizawl, Mizoram (Fig. 1) was washed with tap water, and photographs were taken using a Nikon DM 7200 camera for further taxonomic analysis. The terminology used by Cappetta (2012)[23] is followed for a taxonomic description of the tooth. The tooth position is considered using the graphic synthetic representation of teeth used by Gottfried *et al*.[33] and later modified by Pimiento[51]. The total length of the individual is constructed using the regression analyses proposed by Shimada[46]. The specimen is catalogued under the specimen number SF/MZ/BF and deposited at the Geology Department of Mizoram University.

Results

Systematic palaeontology

Class: CHONDRICHTHYES Huxley, 1880
Subclass: ELASMOBRANCHII Bonaparte, 1838
Order: LAMNIFORMES Berg, 1958
Family: OTODONTIDAE Glikman, 1964
Genus: *Otodus* Agassiz, 1838

Table 1 — Lithostratigraphy of Mizoram[9,50]

Age	Group	Formation	Unit	Thickness (in m)	Generalised lithology	Depositional environment
Recent alluvium					Silt, clay and gravel	River deposits
Early Pliocene - late Pliocene	Tipam			+900	Friable sandstone with occasional clay bands	Stream deposits
		Bokabil		+950	Shales with siltstones and sandstones	Shallow marine
Miocene to Upper Oligocene	Surma	Bhuban	Upper Bhuban	+1100	Arenaceous with sandstones, shales and siltstones	Shallow marine, near shore to lagoonal
			Middle Bhuban	+3000	Argillaceous with shales, siltstones	Deltaic complex
			Lower Bhuban	+900	Arenaceous with sandstones and silty shales	Shallow marine
Oligocene	Barail			+3000	Shales, siltstones and sandstones	Shallow marine

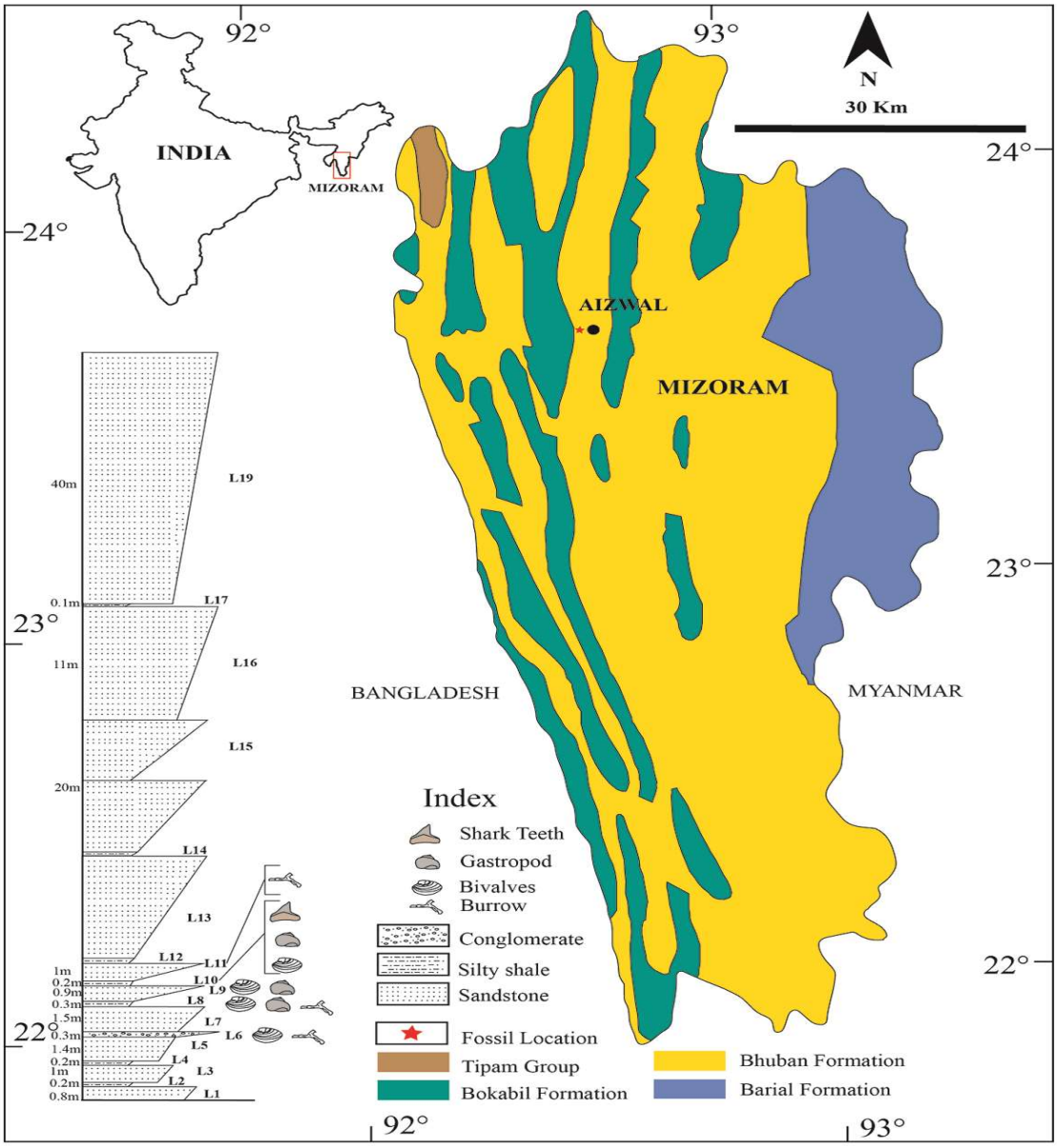


Fig. 1 — Geological map of Mizoram[7] and litholog of *Otodus megalodon* bearing section

†*Otodus (Megaselachus) megalodon* Agassiz, 1835 (Fig. 2a – c)

Type species †*Otodus auriculatus* (Blainville, 1818)

Material and horizon

An isolated tooth under the specimen number SF/MZ/BF-002 was recovered from the medium-grained dark grey sandstone of the Bhuban Formation, Mizoram.

Description

The specimen SF/MZ/BF-002 is a well-preserved large tooth. Crown is broader towards the foot, erect, sub-triangular in shape, straight and symmetrical. The tooth possesses a total height of 5.9 cm, the crown with a height of 4.6 cm, and the root width of the specimen is 4.8 cm. The crown of the tooth is higher than broad. Crown is convex in its lingual surface; its labial face is flattened to some extent and concave towards root. Fine, tiny and regular serrations are present on both the cutting edges of the crown. The crown in both the lingual and labial faces bear longitudinal enamel cracks. The specimen possesses robust, thick, high and well-developed root lobes; however lingual protuberance is lacking. A prominent

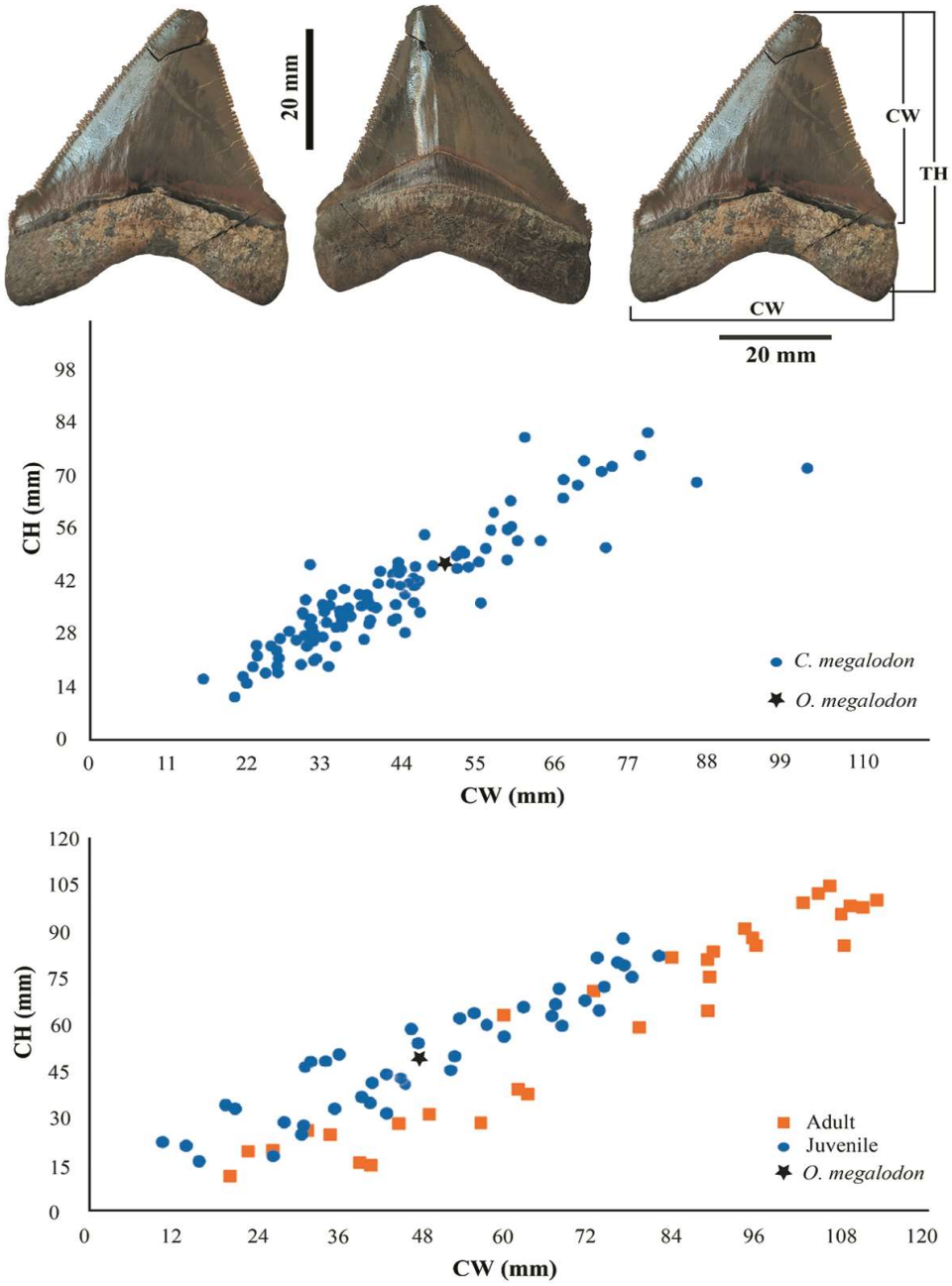


Fig. 2 — (a – c) *Otodus megalodon* (SF/MZ/BF-002): a) labial view, b) lingual view, and c) Measurement on tooth height (TH), crown height (CH) and crown width (CW); d) Scatter plot showing the anatomical data for *O. megalodon* (blue dots)[51,60] and SF/MZ/BF-002 present tooth (black star); and e) scatter plot showing the anatomical data for juvenile (blue dots) and adult (orange squares) of *O. megalodon*[51,60] and SF/MZ/BF-002 present tooth (black star)

inversed 'V-shaped neck' that characterises the megalodon specimen is clearly visible at the lingual view of the crown towards its basal portion. The present specimen may represent one of the first three upper lateral teeth as it is almost symmetrical, triangular in shape and has a slightly curved cutting edge.

Remarks

The teeth of *O. megalodon* are differentiable from those of *Carcharodon carcharias* in having finer, more regular and lobed serrations, and larger teeth with larger roots[52], lacking a crown which is flattened labiolingually[44], and the presence of a neck[53]. The teeth morphology of *O. megalodon* sharks often

changes with age[53]. It is observed that the juvenile teeth of *O. megalodon* may or may not have lateral cusplets[51,53-55]. The tooth possesses diagnostic features such as a large crown, triangular to subtriangular outline, convex lingual face and flattened labial surface. It shows the presence of uniformly fine serration, a chevron 'V' shaped band separating root from the crown in lingual face; shallow basal concavity separating the root lobes, poorly developed lingual roots, protuberance[23,33,51,56-60]. A close comparison of the dental morphologies of *O. megalodon* as diagnosed by Cappetta[23] also confirms that the fossil specimen belongs to *O. megalodon.* Pimiento *et al*.[51] and Pasqua *et al*.[60] compared the CH vs. CW of the megalodon teeth and established the stages of individual specimens to determine whether they belong to a juvenile or adult shark. The data of the present specimen is plotted in their data (Fig. 2d, e) showing that current specimen most likely belongs to a juvenile of *O. megalodon*. The possible total length of the collected specimen SF/MZ/BF-002 is estimated following the regression analyses proposed by Shimada[46], assuming that the specimen may belong to the A1-A3 position in the jaw (Table 2). The total length of the specimen is approximately 7.81 m (Table 2), and it falls in the size range (4-10 m long) of juvenile specimens of *O. megalodon*[51,60].

The teeth of mega-toothed sharks and their taxonomic status have been subject to contention and debate. Based on the morphological characteristics and the presence of serrated edges, *O. megalodon* has been assigned to the genus *Carcharodon* for the first time by Agassiz[61]. The species has also been previously classified into different genera, including *Carcharocles*, *Procarcharodon* and *Megaselachus*[23,37,51]. During the late Cretaceous, lamniform sharks suffered a major adaptive radiation resulting in the intensification of the taxon diversity in the form of *Cretalamna*, *Cretoxyrhina*, *Cardabiodon*, etc., which are also considered to be cosmopolitan in habitat[23]. Subsequently, numerous gigantic fossil taxa of lamniforms, including *Otodus* and *Parotodus*, evolved during the Cenozoic time[23,32,33,35]. *Otodus megalodon* was earlier classified under the family Lamnidae (order Lamniformes), and it is now categorised within the family Otodontidae, which is also considered the closest relative of the living fossil *C. carcharias*[22,33,61].

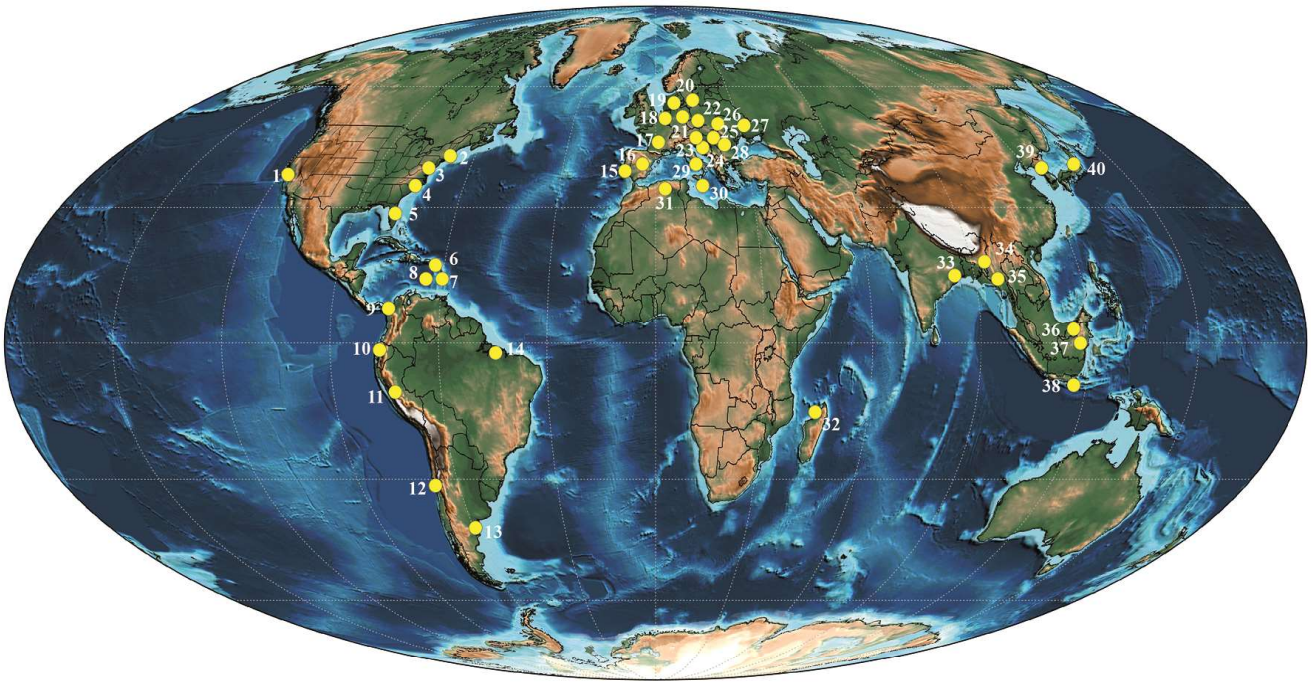
Table 2 — Application of linear regressions at the possible anatomical positions (A1 to A3) of SF/MZ/BF-002 using Shimada[46]; where, Y is the total length of the body (TL), and X is the crown height (CH)

Tooth position	Total Length (TL) regression formula (Shimada, 2003)	Reconstructed size
A1	Y1 = 5.234+11.522; X = 5.234+11.522×59	6.85 m
A2	Y2 = -2.16+12.103; X = -2.16+12.103×59	7.12 m
A3	Y3 = 19.162+15.738; X = 19.162+15.738×59	9.47 m
Average value (meters)		7.81 m

Discussion

The shark of the species *O. megalodon* is considered the largest macrophagous species that ever lived, and their adults are contentiously estimated in size ranging from 10 m to 30 m[33,36,51,62-69]. *Otodus megalodon* is known as a cosmopolitan species for its wide distribution in tropical to warm-temperate coastal habitats[22,33,44]. The species is known to have been reported from certain Miocene and Pliocene deposits of North and South America, Europe, Africa, New Zealand, Australia, Japan and India[28,45-69] (Fig. 3). The associated elasmobranch fauna from Mizoram is also considered to have a close faunal similarity with those of Miocene deposits of the Indian subcontinent *viz*. Myanmar[70,71], Baripada Beds, India[26,28,29,72,73], Kutch, Bhavnagar and Piram Island[26,74-78]. Singh *et al*.[75] established a close similarity index of the Middle Miocene elasmobranch of India with those of the Mediterranean Sea, suggesting the reopening of the seaways during Langhian for a short interval and later on, the faunal similarity was gradually shifted, in which the migration pattern was favouring towards the Eastern Pacific Ocean from Indian Ocean after the final closure of the *Gomphotherium* Landbridge.

Earlier, the elasmobranch remains of the Bhuban Formation have been explored and reported in the unpublished report of the Geological Survey of India[79]. Mehrotra[79] recorded Piscean remains including *Alopias* sp., *Odontaspis* cf. *contortidens*, *Carcharhinus leucas* (sharks) and *Sparus cintus* (teleost) from the Kolasib area of the Bhuban Formation, Mizoram. Later on, Satsangi & Mehrotra[3] reported *Hemipristis serra*, *Carcharodon* cf. *carcharias*, *Carcharhinus* sp., *Odontaspis cuspidata*, *Negaprion* sp., *Isurus* sp., *Dasyatis* sp. and siluroid tooth. However, the first elaborated systematic analysis of elasmobranch from the Upper Bhuban



1	California, USA	9	Panama	17	France	25	Hungary	33	India, Odisha
2	New Jersey, USA	10	Ecuador	18	Netherland	26	Slovakia	34	India, Mizoram
3	Maryland, USA	11	Peru	19	Demark	27	Ukriane	35	Burma
4	Carolina, USA	12	Chile	20	Poland	28	Serbia	36	Brunei,
5	Florida, USA	13	Argentina	21	Germany	29	Italy	37	Borneo
6	Puerto Rico	14	Brazil	22	Czechia	30	Malta	38	Indonesia, Java
7	St. Lucia	15	Portugal	23	Austria	31	Algeria	39	South Korea
8	Lesser Antilles	16	Spain	24	Slovania	32	Madagascar	40	Japan

Fig. 3 — Global biogeographic distribution of *Otodus megalodon*[34,58,86-96 and references therein]

rocks was carried out by Tiwari[5], and he described *Carcharhinus gangeticus*, *Isurus oxyrinchus* and *Carcharodon carcharias* from the Sairang area, Mizoram. Later on, isolated teeth of *Hemipristis serra*, *Negaprion* sp., *Sphyrna zygaena*, *Carcharodon carcharias*, *Isurus oxyrinchus*, *Pristophorous suevicus*, *Dasyatis* sp. and *Dentex* sp. were reported from the Aizawl and Lunglei localities of Bhuban Formation by Tiwari *et al*.[4]. Tiwari & Bannikov[80] also reported three new species of teleost *Decapterus mizoramensis*, *Pentaprion sahnii* and *Bothus? bhubanicus* from the Bhuban rocks of Mizoram. Ralte *et al*.[20] recorded isolated teeth, spines of sharks from Bika Quarry and Ruata Quarry and their specimens comprise of *Lamna* sp., *Carcharodon carcharias*, *Otodus angustidens*, *Carcharodon* sp., *Isurus oxyrinchus*, *Glyphis pagoda*, *Alopias* sp., *Carcharias cf. taurus*, *Carcharias cf. tricuspidatus*, *Odontaspis* sp., *Carcharhinus egertoni*, *Carcharhinus priscus*, *Carcharhinus cf. macloti*, *Carcharhinus bhubanicus*, *Carcharhinus* sp., *Galeocerdo aduncus*, *Negaprion brevirostris*, *Negaprion cf. eurybathrodon*, *Scoliodon laticaudus*, *Hemipristis serra*, *Hemipristis unidenticulata*, *Sphyrna lewini*, *Sphyrna zygaena*, *Galeorhinus* sp., *Squalus* sp., Carcharhinidae gen. et sp. indet., and indeterminate vertebral centra of a selachian. Sharks of the genera *Carcharhinus* and *Sphyrna* are known to inhabit inshore to offshore waters of tropical to temperate climate[23,73,74,81] (Table 3). The occurrence of *Carcharhinus*, *Alopias*, *Carcharadon*, *Sphyrna* and *Galeocerdo* sharks suggested an environment connected to the open ocean, which had normal salinity conditions[23,28,73,81,82,83]. Subsequently, Tiwari & Ralte[21] described fossil batoid and teleost fish remains from the Bhuban Formation, and their collection

Table 3 — Palaeoenvironment distribution of the Miocene sharks and batoids from Bhuban Formation, Mizoram[3,5,20,21,23,28,29,53,72,73,74,73,81, 84,85]

Family/Genus/Species	Marine	Brackish	Freshwater	Depth distribution (m)
Carcharhinidae				
† Carcharhinus bhubanicus	✓			
Carcharhinus (prionodon) gangeticus	✓	✓	✓	
Carcharhinus macloti	✓			0-2000
Carcharhinus nicaraguensis	✓	✓		1-120
† Carcharhinus priscus	✓			
Carcharhinus sp.	✓	✓	✓	
† Galeocerdo aduncus	✓			
Negaprion brevirostris	✓	✓		
† Negaprion eurybathrodon	✓			
Negaprion sp.	✓	✓		
Scoliodon sorrakawah	✓	✓		10-75
Hemigaleidae				
† Hemipristis Serra	✓			
Hemipristis unidenticulata	✓			
Hemipristis sp.	✓			
Sphyrnidae				
Sphyrna diplana	✓	✓		0-1043
Sphyrna zygaena	✓	✓		0-200
Triakidae				
Galeorhinus sp.	✓			
Squalidae	✓			
Squalus sp.	✓	✓		
Lamnidae				
Lamna sp.	✓			
Carcharodon carcharias	✓	✓		0-1200
† Carcharodon angustidens	✓			
Carcharodon sp.	✓	✓		
Isurus spallanzanii	✓			0-750
† Isurus pagoda	✓			
Isurus sp.	✓			
Alopiidae				
Alopias sp.	✓			
Odontaspididae				
Odontaspis cf. *contortidens*	✓			
Odontaspis cuspidata	✓			
Odontaspis taurus	✓			0-232
Odontaspis tricuspidatus	✓			
Odontaspis sp.	✓			
Otodontidae				
† Otodus megalodon	✓			
Pristiophoridae				
Pristiophorus snevieus	✓			
Dasyatidae				
Dasyatis sp.	✓	✓		

consists of *Myliobatis* sp., *Aetobatus* sp. and *Diodon* sp. The batoids such as *Aetobatus* and *Myliobatis* indicate warm to temperate-warm shallow water coastal, shallow marginal marine, inshore, and estuaries to freshwater conditions[74,85,85] (see Table 3). Based on the present status of the elasmobranchian fauna and associated mega invertebrates from the Bhuban Formation of Mizoram, the prevalence of a warm, shallow marine (nearshore), high-energy environment is suggested here.

Conclusion

The present study reports *Otodus megalodon* shark for the first time from the Bhuban Formation, Mizoram, Northeast India. Based on the size of the collected tooth, the total body length of the juvenile individual is estimated to be approximately 7.81 m. The intermigration of sharks from the Mediterranean Sea, and Pacific Ocean to the Indian Ocean through the remnant Tethys Sea water route during the Middle Miocene is revalidated with the present finding, along with the association of sharks and batoids previously reported from the Bhuban Formation. The present finding of *O. megalodon* and earlier records of the elasmobranch fauna and associated invertebrates suggest the prevalence of a warm, shallow marine (nearshore), high-energy environment during the deposition of the upper Bhuban Formation.

Acknowledgements

KMS thanks the Science and Engineering Research Board, India, for the research grants (sanctioned no. CRG/2021/004627). We are thankful to Prof. Ashok Sahni (Panjab University, Chandigarh, India) for his encouragement and suggestions from time to time.

Conflicts of Interest

The authors declare no conflict of interest.

Author Contributions

LF, KMS, RPT & RP: Conceptualisation and formal analysis; KMS: Writing-original draft; RPT & RP: Reviewing and editing of the manuscript. NAS: Preparation of map, photographs; LF, AL, PL & JL: Field work, collection of samples and geological description.

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