Palaeodiet of Miocene Producer(s) and Depositional Environment(s): Inferences from the First Evidence on Microcoprolites from India

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Abstract: This paper reviews research on coprolites from India, and also provides the first evidence of microcoprolites from the early Miocene (Aquitanian) Khari Nadi Formation sedimentary succession exposed about 1.5 km northeast of the village of Kotada, Kachchh (Kutch) District, Gujarat State, western India. Morphometric and size comparisons (in a statistical framework) within known coprolites from the Mesozoic-Cenozoic successions of India (including the ones recorded herein) and also across the globe suggest that fishes may have been the likely producers of Kotada coprolites. Scanning electron microscopy confirms the presence of fish dental remains within coprolites while both scanning electron microscopy and energy dispersive X-ray spectroscopy reveal the phosphatic nature of the microscopic coprolite specimens (recorded herein) hinting that producer(s) were dominantly consuming a carnivorous (ichthyophagous) diet. Further, X-Ray Fluorescence (XRF) analysis of the host and associated lithologies allow us to contemplate that the Kotada coprolites were deposited in a shallow marine environment with possible aerial exposure of the host lithology at some point after deposition. To the best of our knowledge, the present report is the first record of microscopically small fish coprolites from India, albeit being the first from the Aquitanian of India and the oldest Neogene record from India.

Key words: coprolites, Energy Dispersive Spectroscopy (EDS), Miocene (Aquitanian), palaeodiet, palaeoenvironment, X-Ray Fluorescence (XRF) analysis

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1 Introduction

Buckland (1829) initially used the term “coprolite” (Kopros meaning “dung” + lithos meaning “stone”) when describing fossilized faecal matter associated with ichthyosaur skeletal remains from Yorkshire, United Kingdom. Since Buckland’s (1829) pioneering work, numerous connotations of the term “coprolite” along with related terminologies have been used by palaeontologists (Hunt and Lucas, 2012a and references therein). However, the term “coprolite” is still popularly used and accepted in the scientific literature to describe fossilized faeces or excrement of fauna that thrived in the geological past. In general, previous studies have classified coprolites on the assumption that specific groups of modern vertebrates (including both carnivores and herbivores) produce specifically shaped excrement (Hunt and Lucas, 2012a, 2012b). Furthermore, the morphology of coprolite is often linked to the diet (animal or plant matter) of the producer. In addition, the dietary habit of coprolite producers has been utilized in reconstructing the trophic levels in palaeocommunities (Richter and Baszio, 2001a). The global record of coprolites suggests that these ichnofossils have been reported within various sedimentary regimes spanning almost the entire geological time scale with the oldest record from the early Cambrian deposits of China (Vannier and Chen, 2005).

In India, the oldest coprolite record comes from the Upper Triassic Maleri Formation of south India (Matley, 1939a). Matley (1939a) attributed the spirally coiled coprolites (up to 80mm in longer dimensions) from the Maleri Formation to fishes. However, we observe that the available literature on Indian coprolites is mainly focussed on the Maastrichtian coprolites (particularly Type-A morphotype of Matley 1939b) that are found in association with non-avian dinosaur remains from the infratrappean (i.e., sediments that lay below the initial Deccan volcanic flow) sedimentary successions of central India (Khosla et al., 2015). These investigations aimed to determine the diet and ecology of the largest animals (i.e., non-avian dinosaurs) that thrived in peninsular India and were at the verge of mass extinction. Large-sized (up to 40 mm in diameter) coprolites are also known from the Maastrichtian intertrappean (i.e., sediments that are intercalated between Deccan volcanic flows) deposits exposed within village Bhanpura, Mandsaur District, Madhya Pradesh State, central India (Kapur et al., 2006). Further, a single report documents the occurrence of Palaeogene coprolites in India, i.e., from the Middle Eocene (Lutetian) Harudi Formation of Kutch District, Gujarat State, western India (Sahni and Mishra, 1975). To date, the Neogene coprolite record in India is limited to the Lower Miocene (Burdigalian) Baripada beds of Orissa, eastern India (Sharma and Patnaik, 2010). It is pertinent to mention here that all

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previously known coprolites from India were large (few centimetres in linear dimensions) and linked to large-sized vertebrates such as non-avian dinosaurs, rhynchosaurid reptiles, crocodiles or chelonians. To date, small fish or invertebrate coprolites are not known from India, thus, the microscopically small Miocene (Aquitanian) coprolites recorded here are novel. In addition, we utilized non-destructive techniques (Scanning Electron Microscopy and Energy Dispersive Spectroscopy) to infer the internal texture and chemical nature of the Kotada coprolites. Further, chemical analysis (using Wavelength Dispersive X-Ray Fluorescence technique) of the host (coprolite-yielding) and associated lithologies helped us to gain inferences on the depositional palaeoenvironment.

2 A brief history on coprolite research in India

The well-known coprolite-yielding localities of India are provided in Fig.1. For a graphical representation (timeline) of coprolite research in India over the past 160 years, refer to Fig. 2. Oldham (1859) was the first to document coprolites (only two specimens) from the ferruginous clay exposures of the Late Triassic Maleri Formation, south India, that were collected in the year 1857. However, research on coprolites was in an infancy stage (at least in India) during the latter half of the 19th century and the early part of the 20th century. Therefore, not much attention was given to these trace fossils, considering that previously few workers (King, 1881; Aiyenger, 1937) did confirm the presence of abundant coprolites in the vicinity of village Maleri, Adilabad District, Telangana State (previously Andhra Pradesh State), south India. However, it was Matley (1939a) who documented (in detail) the coprolites from the Late Triassic Maleri Formation of south India. Matley (1939a) attributed these coprolites to the extinct lungfish genus *Ceratodus* owing to a) common presence of isolated dental remains of these fishes within the Maleri Formation (also refer Oldham, 1859; Jain, 1968), and b) due to the conspicuous fusiform and spirally wound morphology of the coprolites. Simultaneously, Matley (1939b) also recorded various morphotypes of coprolites from the Late Cretaceous (Maastrichtian) Lameta Formation deposits of Pisdura, Chandrapur District, Maharashtra State, central India and linked the recovered coprolites to their producer animals. The Pisdura coprolites were classified as Type-A (attributed to titanosaurid dinosaurs), Type-B (attributed to adult chelonians), Type-Ba (attributed to young chelonians), and Type-C (attributed to land reptiles such as small-sized dinosaurs) (Matley, 1939b; see Supplementary Data S1). It is important to note here that all subsequent studies on Indian Maastrichtian coprolites followed Matley's classification (see Khosla et al., 2015 and references therein). Sahni and Mishra (1975) reported large (up to 135mm in longer dimensions) coprolites (without ornamentation) from the Middle Eocene (Lutetian) deposits of Kutch (western India) and attributed these coprolites to crocodiles. Sohn and Chatterjee (1979) reported large coprolites (as compared to the ones reported earlier by Matley in 1939a) from the sedimentary succession of the Maleri Formation exposed close to the village of Achlapur (near Maleri), Adilabad District, Telangana State, south India. Sohn and Chatterjee (1979) attributed the Achlapur coprolites to shell-eating large rhynchosaurian reptile *Paradapedon huxleyi* due to the common occurrence of bones of this animal in the Maleri sediments (Jain et al., 1964). Moreover, considering that Matley (1939b) did not observe any biogenic material within the coprolites, Sohn and Chatterjee's (1979) work gained significance as it recorded the presence of an ostracod (assigned to genus *Darwinula*) for the first time within a coprolite from India. Ascertaining palaeodiet was the focus of many studies of Mesozoic coprolites from the subcontinent (Khosla et al., 2015; Sonkusare et al., 2017 and references therein). Jain (1983), following the classification of spirally coiled coprolites of Williams (1972) enhanced Matley's (1939a) work on the spirally wound coprolites from the Maleri Formation. In contrast to earlier observations of Matley (1939a), Jain (1983) argued against the association of the spirally coiled Maleri coprolites to the known faunal groups (including the lungfish genus *Ceratodus*) from the Maleri Formation. However, Jain (1983) did not completely rule out the possibility of a link between the spirally coiled Maleri coprolites and the intestinal contents of fishes. It should be noted that Jain (1983) recorded numerous coprolites associated with non-avian dinosaur remains within the sediments of the Jurassic Kota Formation, south India. We are unaware of any detailed work on the Jurassic coprolites, but some have noted the presence of oval, ellipsoid, spheroid, and flattened coprolite morphotypes with desiccation marks (Jain, 1983; also p.106 of Gillette and Lockley, 1989). After a gap of about 20 years, Mohabey (2001) recorded plant tissues within the Maastrichtian coprolites from Pisdura, reiterating Matley's (1939b) attribution of Type-A coprolites to plant-eating titanosaurid dinosaurs. Subsequent studies observed the presence of a variety of plant matter (conifers, gymnosperms, and angiosperms) within the Maastrichtian Type-A coprolites from Pisdura (Mohabey and Samant, 2003; Ghosh et al., 2003; Mohabey, 2005). Prasad et al. (2005) recorded grass (Poaceae) phytoliths within the Type-A coprolites from Pisdura. Maastrichtian Type-A coprolites have also yielded chrysophytes, sponges, charophytes, and diatoms apart from vascular plant tissues attributed to Pteridophytes, Gymnosperms, and Angiosperms (Khosla et al., 2015). Recently, Sonkusare et al. (2017) reported palynomorphs (spores and pollen), phytoliths (Poaceae and Dicots), mycorrhizal fungi, thecamoebians, insect remains, diatoms, sponge spicules, and plant debris from within the Type-A coprolites from the infratrappean deposits at Pisdura, Chandrapur District, Maharashtra State, central India. It is should be noted that based on detailed studies on the Indian coprolite material (i.e., Matley's collection housed at the Natural History Museum, London, United Kingdom) from the Late Triassic Maleri Formation and the Late Cretaceous Lameta Formation, Hunt et al. (2007, 2012) proposed ichnotaxonomic nomenclature for these fossils.

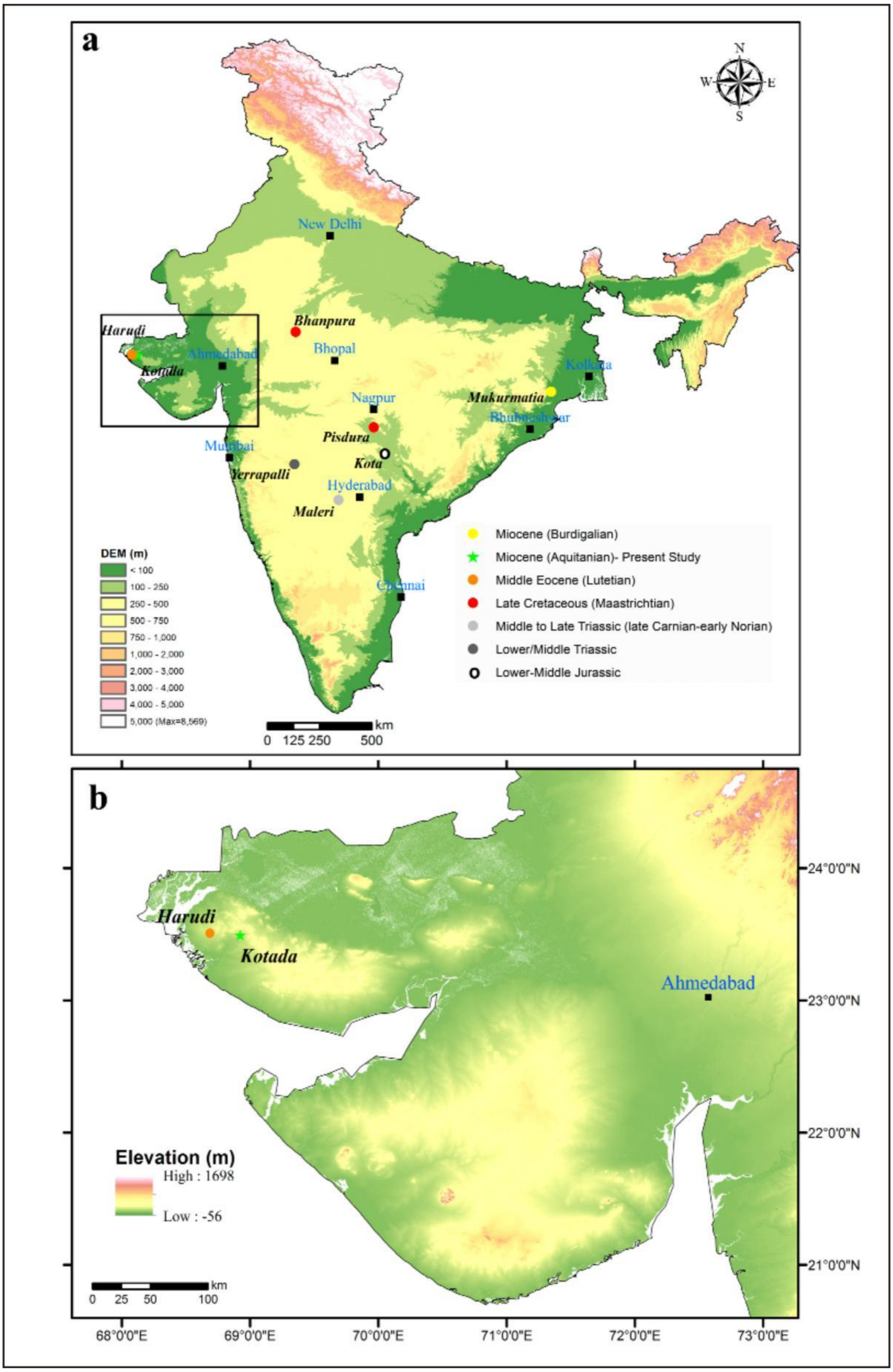


Fig. 1: a) Digital Elevation Model (DEM) map of India showing the well known Mesozoic-Cenozoic coprolite-yielding localities, and b) the DEM map of Gujarat State showing the investigated locality (Kotada, Kachchh District) in the present study.

S1. Detailed information [such as size, locality, age, and linked producer(s)] for the putative fish coprolites (present study)] and the previously recorded coprolites from the Mesozoic-Cenozoic sedimentary successions of India.

S.No	Morphotype	Specimen no.	Length (mm)	Width (mm)	Avg. Length (mm)	Avg. Width (mm)	STDEV Length	STDEV Width	Length/ Width	Log Length	Log width	Log Length/ Width	Location	Age	References	Likely producer(s)
1	Type-A Ellipsoidal	VVK/KOT2042	1.19	0.62	0.83	0.45	0.21	0.11	1.92	0.08	-0.21	0.28	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
2	Type-A Ellipsoidal	VVK/KOT2043	0.93	0.56	-	-	-	-	1.66	-0.03	-0.25	0.22	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
3	Type-A Ellipsoidal	VVK/KOT2051	0.79	0.42	-	-	-	-	1.88	-0.10	-0.38	0.27	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
4	Type-A Ellipsoidal	VVK/KOT2052	0.75	0.39	-	-	-	-	1.92	-0.12	-0.41	0.28	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
5	Type-A Ellipsoidal	VVK/KOT2044	0.59	0.37	-	-	-	-	1.59	-0.23	-0.43	0.20	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
6	Type-A Ellipsoidal	VVK/KOT2053	0.74	0.34	-	-	-	-	2.18	-0.13	-0.47	0.34	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
7	Type-B Cylindrical	VVK/KOT2045	1.45	0.38	1.23	0.39	0.37	0.14	3.85	0.16	-0.42	0.59	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
8	Type-B Cylindrical	VVK/KOT2046	1.49	0.39	-	-	-	-	3.83	0.17	-0.41	0.58	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
9	Type-B Cylindrical	VVK/KOT2047	1.30	0.38	-	-	-	-	3.40	0.11	-0.42	0.53	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
10	Type-B Cylindrical	VVK/KOT2048	1.04	0.31	-	-	-	-	3.41	0.02	-0.51	0.53	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
11	Type-B Cylindrical	VVK/KOT2054	0.88	0.34	-	-	-	-	2.62	-0.06	-0.47	0.42	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
12	Type-B Cylindrical	VVK/KOT2055	0.90	0.28	-	-	-	-	3.21	-0.04	-0.55	0.51	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
13	Type-B Cylindrical	VVK/KOT2049	1.10	0.34	-	-	-	-	3.19	0.04	-0.46	0.50	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
14	Type-B Cylindrical	VVK/KOT2056	1.31	0.36	-	-	-	-	3.64	0.12	-0.44	0.56	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
15	Type-B Cylindrical	VVK/KOT2057	0.87	0.29	-	-	-	-	3.03	-0.06	-0.54	0.48	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
16	Type-B Cylindrical	VVK/KOT2058	1.38	0.41	-	-	-	-	3.35	0.14	-0.38	0.52	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
17	Type-B Cylindrical	VVK/KOT2059	0.91	0.36	-	-	-	-	2.56	-0.04	-0.45	0.41	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
18	Type-B Cylindrical	VVK/KOT2020	2.14	0.80	-	-	-	-	2.69	0.33	-0.10	0.43	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
19	Type-C Spiral	VVK/KOT2060	0.81	0.33	1.11	0.34	0.32	0.07	2.49	-0.09	-0.49	0.40	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
20	Type-C Spiral	VVK/KOT2050	1.56	0.38	-	-	-	-	4.14	0.19	-0.42	0.62	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
21	Type-C Spiral	VVK/KOT2032	1.02	0.25	-	-	-	-	3.35	0.01	-0.51	0.53	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes
22	Type-C Spiral	VVK/KOT2011	1.06	0.41	-	-	-	-	2.63	0.04	-0.38	0.42	Kotada, Gujarat	Miocene (Aquitanian)	Present Study	Fishes

23	Group 1	-	33.80	21.00	33.80	21.00	0.00	0.00	1.61	1.53	1.32	0.21	Mukurmatia, Orissa	Miocene (Burdigalian)	Fig. 2a in Sharma and Pattnaik	Crocodilian
24	Group 2 (Type-1)	-	46.96	33.00	46.96	33.00	0.00	0.00	1.42	1.67	1.52	0.15	Mukurmatia, Orissa	Miocene (Burdigalian)	Fig. 2b in Sharma and Pattnaik	Crocodilian
25	Group 2 (Type-2)	-	34.15	25.00	34.15	25.00	0.00	0.00	1.37	1.53	1.40	0.14	Mukurmatia, Orissa	Miocene (Burdigalian)	Fig. 2c in Sharma and Pattnaik	Crocodilian
26	Group 3 (Type-2)	-	44.70	25.00	44.70	25.00	0.00	0.00	1.79	1.65	1.40	0.25	Mukurmatia, Orissa	Miocene (Burdigalian)	Fig. 2g in Sharma and Pattnaik	Crocodilian
27	Group 3 (Type-3)	-	19.20	8.00	19.20	8.00	0.00	0.00	2.40	1.28	0.90	0.38	Mukurmatia, Orissa	Miocene (Burdigalian)	Fig. 2j in Sharma and Pattnaik	Crocodilian
28	?	LUVP11139a	80.00	28.00	101.25	37.13	30.05	12.90	2.86	1.90	1.45	0.46	Harudi, Gujarat	Middle Eocene (Lutetian)	Plate 2, Fig. 7 in Sahni and Mishra, 1975	Crocodilian
29	?	LUVP11139b	122.50	46.25	-	-	-	-	2.65	2.09	1.67	0.42	Harudi, Gujarat	Middle Eocene (Lutetian)	Plate 2, Fig. 8 in Sahni and Mishra, 1975	Crocodilian
30	Type-A	K42/458	121.00	77.00	110.10	58.30	18.66	18.66	1.57	2.08	1.89	0.20	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Matley et al. 1939b	Titanosaurs
31	Type-A	K42/469	138.00	77.00	-	-	-	-	1.79	2.14	1.89	0.25	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Matley et al. 1939b	Titanosaurs
32	Type-A	K42/434	170.00	86.00	-	-	-	-	1.98	2.23	1.93	0.30	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Matley et al. 1939b	Titanosaurs
33	Type-A	K42/435	166.00	68.00	-	-	-	-	2.44	2.22	1.83	0.39	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Matley et al. 1939b	Titanosaurs
34	Type-A	K42/435a	133.00	65.00	-	-	-	-	2.05	2.12	1.81	0.31	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Matley et al. 1939b	Titanosaurs
35	Type-A	K42/463	108.00	47.00	-	-	-	-	2.30	2.03	1.67	0.36	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Matley et al. 1939b	Titanosaurs
36	Type-A	?	60.00	45.00	-	-	-	-	1.33	1.78	1.65	0.12	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Ambwani and Dutta, 2005	Titanosaurs
37	Type-A	PUAKH10028	81.00	49.00	-	-	-	-	1.65	1.91	1.69	0.22	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Table 2 in Khosla et al., 2015	Titanosaurs
38	Type-A	PUAKH10029	68.00	33.00	-	-	-	-	2.06	1.83	1.52	0.31	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Table 2 in Khosla et al., 2015	Titanosaurs
39	Type-A	PUAKH10030	56.00	36.00	-	-	-	-	1.56	1.75	1.56	0.19	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Table 2 in Khosla et al., 2015	Titanosaurs
40	Type-B	?	63.00	40.00	57.67	37.67	21.43	15.07	1.58	1.80	1.60	0.20	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Plate 35, Fig. 1 in Matley et al. 1939b	Chelonians
41	Type-B	K42/439	91.00	60.00	-	-	-	-	1.52	1.96	1.78	0.18	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Plate 35, Fig. 2 in Matley et al. 1939b	Chelonians
42	Type-B	?	71.00	52.00	-	-	-	-	1.37	1.85	1.72	0.14	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Plate 35, Fig. 3 in Matley et al. 1939b	Chelonians
43	Type-B	?	70.00	42.00	-	-	-	-	1.67	1.85	1.62	0.22	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Plate 35, Fig. 4 in Matley et al. 1939b	Chelonians
44	Type-B	?	75.00	48.00	-	-	-	-	1.56	1.88	1.68	0.19	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Plate 35, Fig. 5 in Matley et al. 1939b	Chelonians
45	Type-B	?	49.00	38.00	-	-	-	-	1.29	1.69	1.58	0.11	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Plate 35, Fig. 6 in Matley et al. 1939b	Chelonians
46	Type-B	PUAKH11000	32.00	21.00	-	-	-	-	1.52	1.51	1.32	0.18	Pisdura,	Late Cretaceous	Table 2 in Khosla et	Chelonians

													Maharashtra	(Maastrichtian)	al., 2015	
47	Type-B	PUAKH11001	39.00	21.00	-	-	-	-	1.86	1.59	1.32	0.27	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Table 2 in Khosla et al., 2015	Chelonians
48	Type-B	PUAKH11002	29.00	17.00	-	-	-	-	1.71	1.46	1.23	0.23	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Table 2 in Khosla et al., 2015	Chelonians
49	Type-Ba	?	52.00	25.00	49.94	27.61	14.83	8.88	2.08	1.72	1.40	0.32	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Plate 36, Fig. 5 in Matley et al. 1939b	Young Chelonians or small-sized dinosaurs
50	Type-Ba	?	38.00	26.00	-	-	-	-	1.46	1.58	1.41	0.16	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Plate 36, Fig. 6 in Matley et al. 1939b	Young Chelonians or small-sized dinosaurs
51	Type-Ba	?	42.50	18.50	-	-	-	-	2.30	1.63	1.27	0.36	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Plate 36, Fig. 7 in Matley et al. 1939b	Young Chelonians or small-sized dinosaurs
52	Type-Ba	?	66.00	33.00	-	-	-	-	2.00	1.82	1.52	0.30	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Plate 36, Fig. 8 in Matley et al. 1939b	Young Chelonians or small-sized dinosaurs
53	Type-Ba	?	39.00	21.50	-	-	-	-	1.81	1.59	1.33	0.26	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Plate 36, Fig. 9 in Matley et al. 1939b	Young Chelonians or small-sized dinosaurs
54	Type-Ba	?	26.50	15.00	-	-	-	-	1.77	1.42	1.18	0.25	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Plate 36, Fig. 10 in Matley et al. 1939b	Young Chelonians or small-sized dinosaurs
55	Type-Ba	?	55.00	39.00	-	-	-	-	1.41	1.74	1.59	0.15	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Plate 36, Fig. 11 in Matley et al. 1939b	Young Chelonians or small-sized dinosaurs
56	Type-Ba	?	57.00	41.00	-	-	-	-	1.39	1.76	1.61	0.14	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Plate 36, Fig. 12 in Matley et al. 1939b	Young Chelonians or small-sized dinosaurs
57	Type-Ba	?	73.50	29.50	-	-	-	-	2.49	1.87	1.47	0.40	Pisdura, Maharashtra	Late Cretaceous (Maastrichtian)	Plate 36, Fig. 13 in Matley et al. 1939b	Young Chelonians or small-sized dinosaurs
58	Type-B or	LT-22	55.60	30.40	52.70	29.53	5.02	1.50	1.83	1.75	1.48	0.26	Bhanpura,	Late Cretaceous	Plate 1, fig. 24 in	Chelonians

	Ba												Madhya Pradesh	(Maastrichtian)	Kapur et al. 2006	or crocodiles
59	Type-B or Ba	LT-23	46.90	30.40	-	-	-	-	1.54	1.67	1.48	0.19	Bhanpura, Madhya Pradesh	Late Cretaceous (Maastrichtian)	Plate 1, fig. 25 in Kapur et al. 2006	Chelonians or crocodiles
60	Type-B or Ba	LT-24	55.60	27.80	-	-	-	-	2.00	1.75	1.44	0.30	Bhanpura, Madhya Pradesh	Late Cretaceous (Maastrichtian)	Plate 1, fig. 26 in Kapur et al. 2006	Chelonians or crocodiles
61	Cylindrical Type	ISI P. 52	35.83	16.60	40.63	19.11	8.16	5.81	2.16	1.55	1.22	0.33	Maleri, Telangana	Middle to Late Triassic (late Carnian - early Norian)	Plate 81, Fig. 1 in Jain, 1983	Rhyncosaurid reptiles
62	Cylindrical Type	ISI P. 53	28.33	9.60	-	-	-	-	2.95	1.45	0.98	0.47	Maleri, Telangana	Middle to Late Triassic (late Carnian - early Norian)	Plate 81, Fig. 2 in Jain, 1983	Rhyncosaurid reptiles
63	Cylindrical Type	ISI P. 54	39.09	15.00	-	-	-	-	2.61	1.59	1.18	0.42	Maleri, Telangana	Middle to Late Triassic (late Carnian - early Norian)	Plate 81, Fig. 3 in Jain, 1983	Rhyncosaurid reptiles
64	Cylindrical Type	ISI P. 50	46.66	25.00	-	-	-	-	1.87	1.67	1.40	0.27	Maleri, Telangana	Middle to Late Triassic (late Carnian - early Norian)	Plate 81, Figs. 4-5 in Jain, 1983	Rhyncosaurid reptiles
65	Cylindrical Type	ISI P. 61	37.72	19.09	-	-	-	-	1.98	1.58	1.28	0.30	Maleri, Telangana	Middle to Late Triassic (late Carnian - early Norian)	Plate 81, Figs. 6-7 in Jain, 1983	Rhyncosaurid reptiles
66	Cylindrical Type	ISI P. 56	53.75	25.00	-	-	-	-	2.15	1.73	1.40	0.33	Maleri, Telangana	Middle to Late Triassic (late Carnian - early Norian)	Plate 81, Figs. 8-9 in Jain, 1983	Rhyncosaurid reptiles
67	Cylindrical Type	ISI P. 71	43.00	23.50	-	-	-	-	1.83	1.63	1.37	0.26	Maleri, Telangana	Middle to Late Triassic (late Carnian - early Norian)	Plate 81, Fig. 10 in Jain, 1983	Rhyncosaurid reptiles
68	Amphipolar Type	ISI P. 49	45.55	21.11	51.94	24.71	9.21	7.73	2.16	1.66	1.32	0.33	Maleri, Telangana	Middle to Late Triassic (late Carnian - early Norian)	Plate 81, Figs. 11-12 in Jain, 1983	Rhyncosaurid reptiles
69	Amphipolar Type	ISI P. 68	62.50	33.59	-	-	-	-	1.86	1.80	1.53	0.27	Maleri, Telangana	Middle to Late Triassic (late Carnian - early Norian)	Plate 81, Figs. 13-14 in Jain, 1983	Rhyncosaurid reptiles
70	Amphipolar Type	ISI P. 69	47.77	19.44	-	-	-	-	2.46	1.68	1.29	0.39	Maleri, Telangana	Middle to Late Triassic (late Carnian - early Norian)	Plate 81, Figs. 15-16 in Jain, 1983	Rhyncosaurid reptiles
71	Heteropolar Type	ISI P. 59	57.14	20.71	54.38	19.75	3.62	3.20	2.76	1.76	1.32	0.44	Maleri, Telangana	Middle to Late Triassic (late Carnian - early Norian)	Plate 82, Figs. 1-2 in Jain, 1983	Rhyncosaurid reptiles
72	Heteropolar Type	ISI P. 70	51.25	15.00	-	-	-	-	3.42	1.71	1.18	0.53	Maleri, Telangana	Middle to Late Triassic (late Carnian - early Norian)	Plate 82, Figs. 3-4 in Jain, 1983	Rhyncosaurid reptiles
73	Heteropolar Type	ISI P. 58	57.86	21.42	-	-	-	-	2.70	1.76	1.33	0.43	Maleri, Telangana	Middle to Late Triassic (late Carnian - early Norian)	Plate 82, Figs. 5-6 in Jain, 1983	Rhyncosaurid reptiles
74	Heteropolar Type	ISI P. 51	51.25	21.87	-	-	-	-	2.34	1.71	1.34	0.37	Maleri, Telangana	Middle to Late Triassic (late Carnian - early Norian)	Plate 82, Figs. 10-11 in Jain, 1983	Rhyncosaurid reptiles

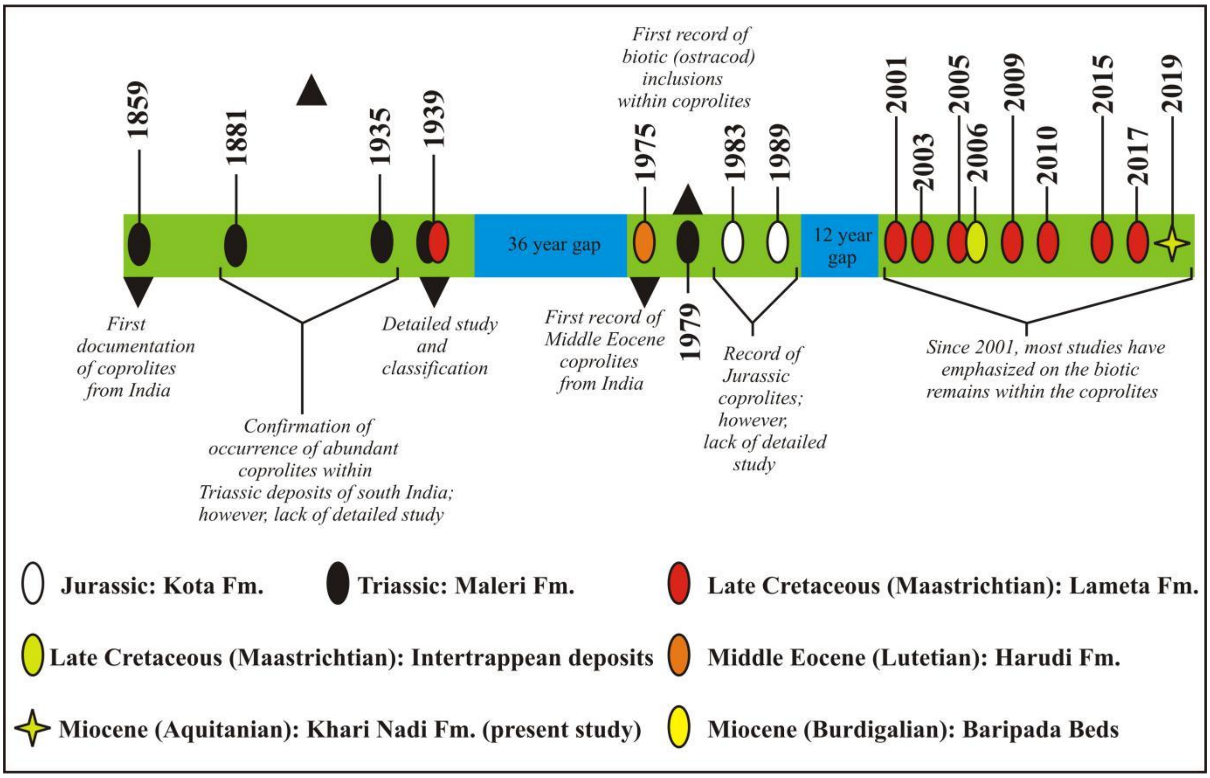


Fig. 2: A graphical representation (timeline) of coprolite research in India over the past 160 years.

3 Geological setting, location, and age

The investigated Khari Nadi Formation was deposited within the Kutch Basin, which is a pericratonic basin in the western part of India. The Kutch Basin encompasses the entire Kutch District and the western part of Banaskantha District of Gujarat State, western India. The Palaeogene-Neogene sequences in Kutch are best exposed as crescentic belts in the south western coastal plains of the Kutch mainland and the periphery of the Mesozoic highs. The Neogene (particularly Miocene) lithostratigraphic units consist of the Khari Nadi Formation, the Chassra Formation and the Sandhan Formation; in ascending chronostratigraphic order (Fig.1 of Biswas, 1992). The Miocene (Aquitanian) Khari Nadi Formation conformably overlies the Oligocene (Rupelian-Chattian) Maniyara Fort Formation. The type section of the Khari Nadi Formation (Biswas, 1992), previously Arenaeous Group (Wynne, 1872) and Gaj Beds (Mohan and Bhatt, 1968), is exposed along the cliffs and banks of the Khari River (vernacular “Khari” meaning salty) near the village of Goyela (Fig. 2 of Biswas, 1992). Lithologically, at the type locality, the approximately 65 meter thick sedimentary succession of the Khari Nadi Formation predominantly consisting of siltstones, sandstones, and claystones is exposed, with the middle and the upper part of the succession consisting of thin beds of marly limestones (Biswas, 1992).

In the present investigation, a coprolite-yielding horizon has been delineated in a stream section, located about 1.5 km northeast of the village of Kotada (Co-ordinates: N23°29’34”; E68°55’18”), District Kutch, Gujarat State, western India (Fig. 3a-d). The studied section is ~3m thick with a ~1m thick, pale yellow marly limestone horizon overlain by an ~1.75m thick sandy silty Clay unit (Fig. 3d). The Clay unit is further overlain by an ~0.25m thick topsoil, while the base of the section is unexposed (Fig. 3d). The coprolite specimens reported in the present study were recovered from within the silty sandy Clay unit of the Khari Nadi Formation at a level ~0.20m above the top of the marly limestone unit (Fig. 3d).

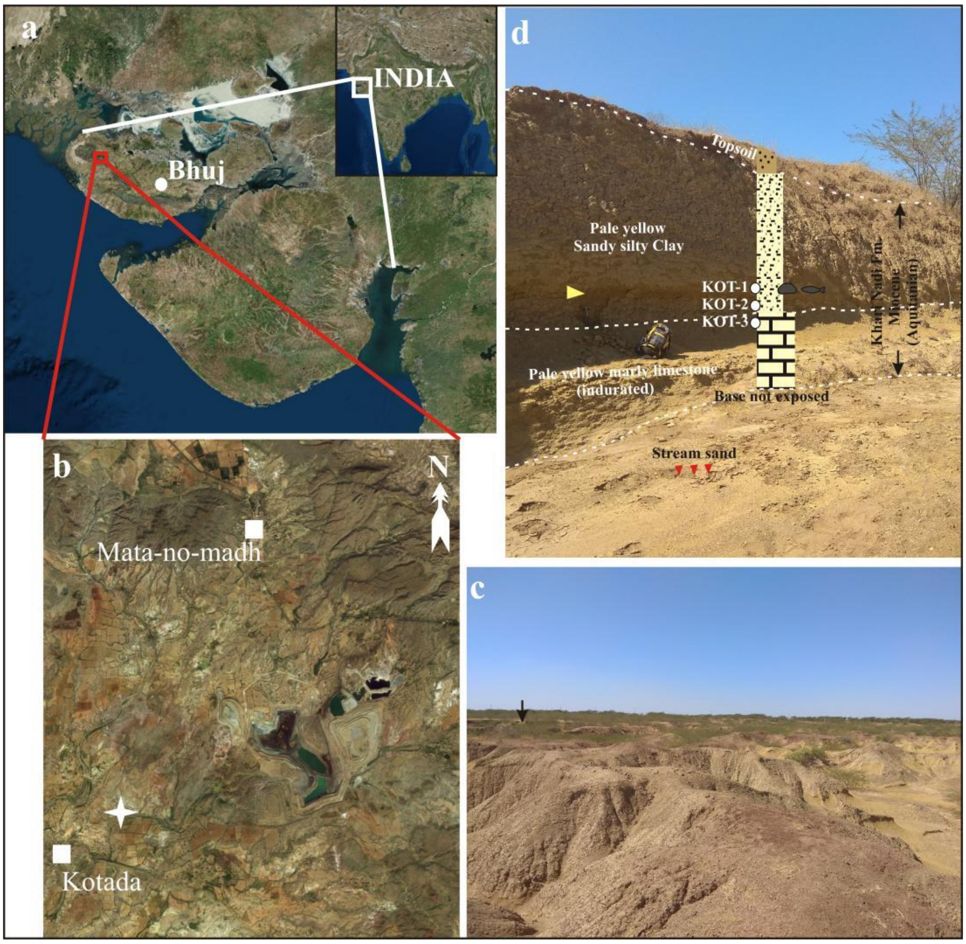


Fig. 3: Location of the studied section and lithology. a) Map of India (inset) along with map of Gujarat State (western India) showing the position of the investigated area (red box), b) a high-resolution Arc-GIS image of the investigated area [location (NE of Kotada) marked by white star], c) panoramic view of the investigated area, and d) photograph of the stream section (NE of the village of Kotada) exposing the sedimentary sequence belonging to Khari Nadi Formation, lithology with positions for KOT-1, KOT-2 and KOT-3 samples. Note: Yellow arrow marks the position of the coprolite-yielding sample (i.e., KOT-1); black arrow marks the location of the investigated stream section; geological hammer (just below the yellow mark in the photograph) is for scaling purpose only.

According to Biswas (1992), the foraminifer *Miogypsina tani* is common in the middle and upper part of the Khari Nadi lithological succession. Based on the occurrence of *M. tani*, an Aquitanian age was determined by Biswas (1992) for the upper part of the Khari Nadi succession, which has been generally followed in subsequent studies including the present investigation. Khari Nadi Formation has been interpreted as tidal flat, littoral to a shallow inner shelf deposit in a slowly transgressive sea over a stable shelf (Biswas 1992).

4 Material and methods

The microscopically small coprolites that have been dealt with in the present investigation were recovered following the methodology provided by Kapur et al. (2018). However, the use of chemicals was avoided during the processing of the sediment samples for recovery of specimens. The specimens were individually examined using a camera mounted stereomicroscope (Model: LeicaS8APO) and Scanning Electron Microscope (Model: JEOL7610F) with EDAX (Model: Octane Plus with TEAM software version V4.2.1) at the Birbal Sahni Institute of Palaeosciences (BSIP), Lucknow, India. All the specimens were measured using Leica Application Suite (LAS) V4.8 software. Additionally, scale bars have been provided along with illustrations of the specimens in the present article. In addition, Principal Component Analysis (PCA) was performed to statistically deduce size differences and association(s) (such as producer animals) of coprolite specimens (recorded herein) and those recorded previously from the Mesozoic-Cenozoic successions of India. Also, the elemental composition [particularly for Calcium (Ca) and Phosphorous (P)] of the specimens was analyzed using the Energy Dispersive Spectroscopy (EDS) with multiple spots analysed for individual specimen (for details refer to "section 5.3"). The host (containing coprolite specimens) and associated lithologies (i.e., a total of three samples: KOT-1, KOT-2 and KOT-3) were analyzed for the presence and quantification of major oxides using Wavelength Dispersive X-Ray Fluorescence (WD-XRF) Spectrometer (Model: PANalytical, axios max, 4 KW) at BSIP. Prior to the WD-XRF analysis, the samples were powdered (up to ~ 300 mesh of ASTM standard) with the help of an agate mortar pestle. Subsequently, with the usage of boric acid as a binder, pressed pellets were formed of the powdered specimens. Further, the individual samples were analyzed using the omnion standardless analysis software that provides semi-quantitative but versatile (as it includes normalization factor for undetected sample matrix) results. All the fossil specimens reported in the present investigation are housed at the Birbal Sahni Institute of Palaeosciences (BSIP), Lucknow, India (BSIP Slide No.164231).

5 Analyses and Results

5.1 Morphotypes

It is pertinent to mention here that most studies on coprolites do not follow a standard methodology for morphological characterization of these ichnofossils; however, a recent study has made a noteworthy contribution to classify coprolites (Hunt and Lucas, 2012a; also refer to Hunt and Lucas, 2012b). Subsequently, Barrios-de Pedro et al. (2018) attempted to further enhance the earlier classification of coprolites by Hunt and Lucas (2012a). Nonetheless, difficulties persist to classify these ichnofossils into different morphotypes due to a variety of factors that are not limited to a) presence of enormous morphological variations within coprolites, b) independent, and varied observations on coprolites by authors without following a proper classification system, and c) imprudent assignments to producer taxa. Thus, owing to lack of a standard methodology, we here follow the classification system provided by the above-mentioned studies; however, to maintain morphological disparity, it became essential to mention additional features in Kotada coprolites.

A total of 22 coprolite specimens (refer to Supplementary Data S1) were recovered in the present investigation from ~1 kilogram of the sediment sample. In general, all the specimens depict shades of green and light to dark brown colour variations (refer Supplementary Data S2). In terms of morphology, the coprolite assemblage (reported herein) can be broadly categorized into three morphotypes that include a) Type-A (Ellipsoidal) coprolites are ellipsoid in overall aspect with elliptic cross-sections and largest diameter in the middle, commonly exhibiting desiccation cracks on the external surface, without spiral markings, and are generally isopolar without displaying any constrictions, b) Type-B (Cylindrical) coprolites exhibit a cylinder shape in overall aspect, lack spiral markings, are generally isopolar without constrictions; however, these coprolites may be anisopolar with one end tapered, but generally maintain constant diameter with circular or oval cross-section, and c) Type-C (Spiral) coprolites are amphipolar, are mostly isopolar and maintain constant diameter with circular or oval cross-section; however, they may be anisopolar with one end tapered. In terms of increasing preponderance in the assemblage recovered, the Type-C (Spiral) specimens are rare (18%), Type-A (Ellipsoidal) specimens are common (27%) while Type-B (Cylindrical) specimens are abundant (54%) (refer to Fig. 4). The criterion followed for measurements of coprolites is provided as Fig. 5. For detailed measurements of the recovered specimens (present investigation) and previously known coprolites from geologically younger as well as older lithological units of India refer to Supplementary Data S1. In the coprolite assemblage recovered herein, the largest coprolite (specimen number: VVK/KOT2042) within the Type-A (Ellipsoidal) category measures 1.19mm (in length) and 0.62mm (in width). However, for Type-A (Ellipsoidal) coprolites, the average length and width are 0.83mm and 0.45mm, respectively (Supplementary Data S1). The largest coprolite (specimen number: VVK/KOT2020) belonging to Type-B (Cylindrical) category measures 2.14mm and 0.80mm in length and width, respectively (Supplementary Data S1). The average length of Type-B (Cylindrical) category coprolites is 1.23mm while an average width is 0.39mm. The average length and width of the Type-C (Spiral) category is 1.11mm to 0.34mm, respectively (Supplementary Data S1). The coprolite (specimen number: VVK/KOT2050) represents the largest specimen in the Type-C (Spiral) category that measures 1.56mm and 0.38mm in length and width, respectively (Supplementary Data S1). In addition, the constructed bivariate plots (Figs. 6a-b) can be visualized to observe the size variation(s) amongst the above-mentioned three categories of coprolites (recovered in the present investigation) and also within those coprolites reported previously from geologically younger or older time slices of India. The observed length/width ratio for the Type-A (Ellipsoidal) coprolites is less than log 10 (0.35) while that for Type-B (Cylindrical) and Type-C (Spiral), it is greater than log 10 (0.35) (refer Fig. 6b). In addition, the Miocene (Aquitanian) Kotada coprolites (reported herein) are conspicuously smaller (also refer Supplementary Data S1 and Fig. 6a-b) in comparison to the previously known coprolites from the Mesozoic-Cenozoic sedimentary successions of India.

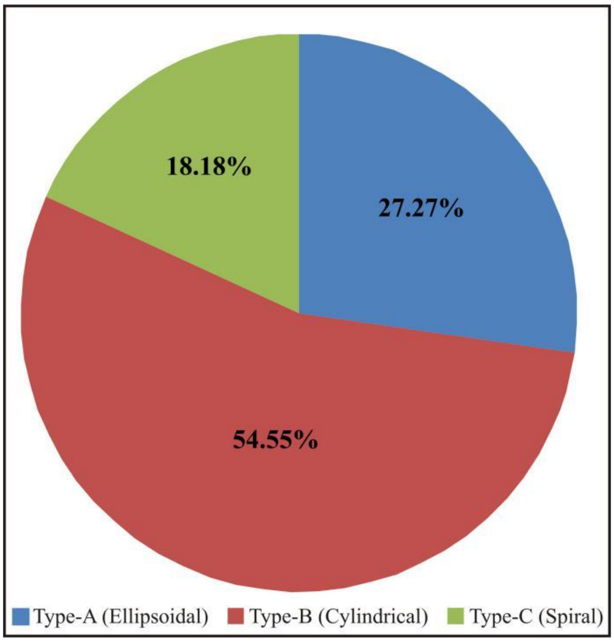


Fig. 4: Pie-chart depicting the relative abundance of the three putative fish coprolite morphotypes, i.e., Type-A (Ellipsoidal), Type-B (Cylindrical), and Type-C (Spiral) that have been recovered in the present study. Note: <25% of total composition has been considered as rare, 25-50% has been considered as common while >50% has been considered as abundant.

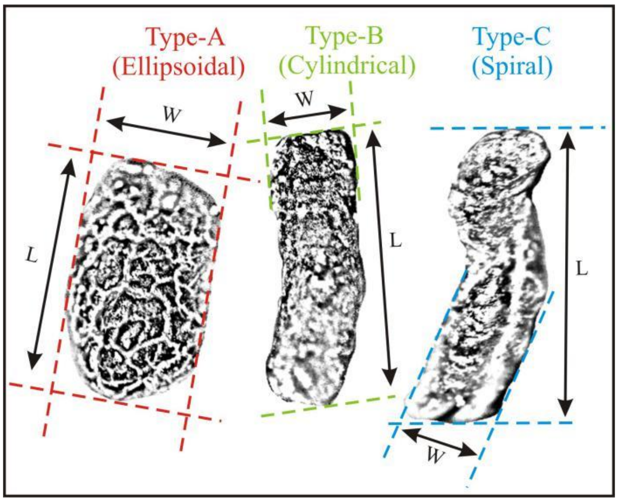
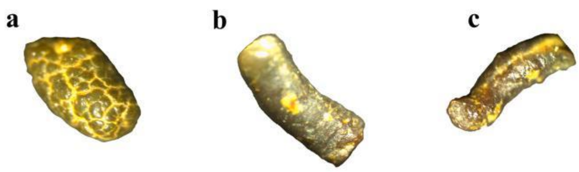


Fig. 5: Criteria followed for the measurements of the three putative fish coprolite morphotypes in the present study. Note: L = length, W = max. width.



S2. Macroscopic (stereomicroscopic) photographs of the putative fish coprolite specimens recovered (present study) from the Miocene (Aquitanian) Khari Nadi Formation sedimentary succession exposed about 1.5 km northeast of the village of Kotada, Kachchh (Kutch) District, Gujarat State, western India. a) Specimen no. VVK/KOT2042; b) Specimen no. VVK/KOT2020 and, c) Specimen no. VVK/KOT2050. For scales refer to Fig. 9.

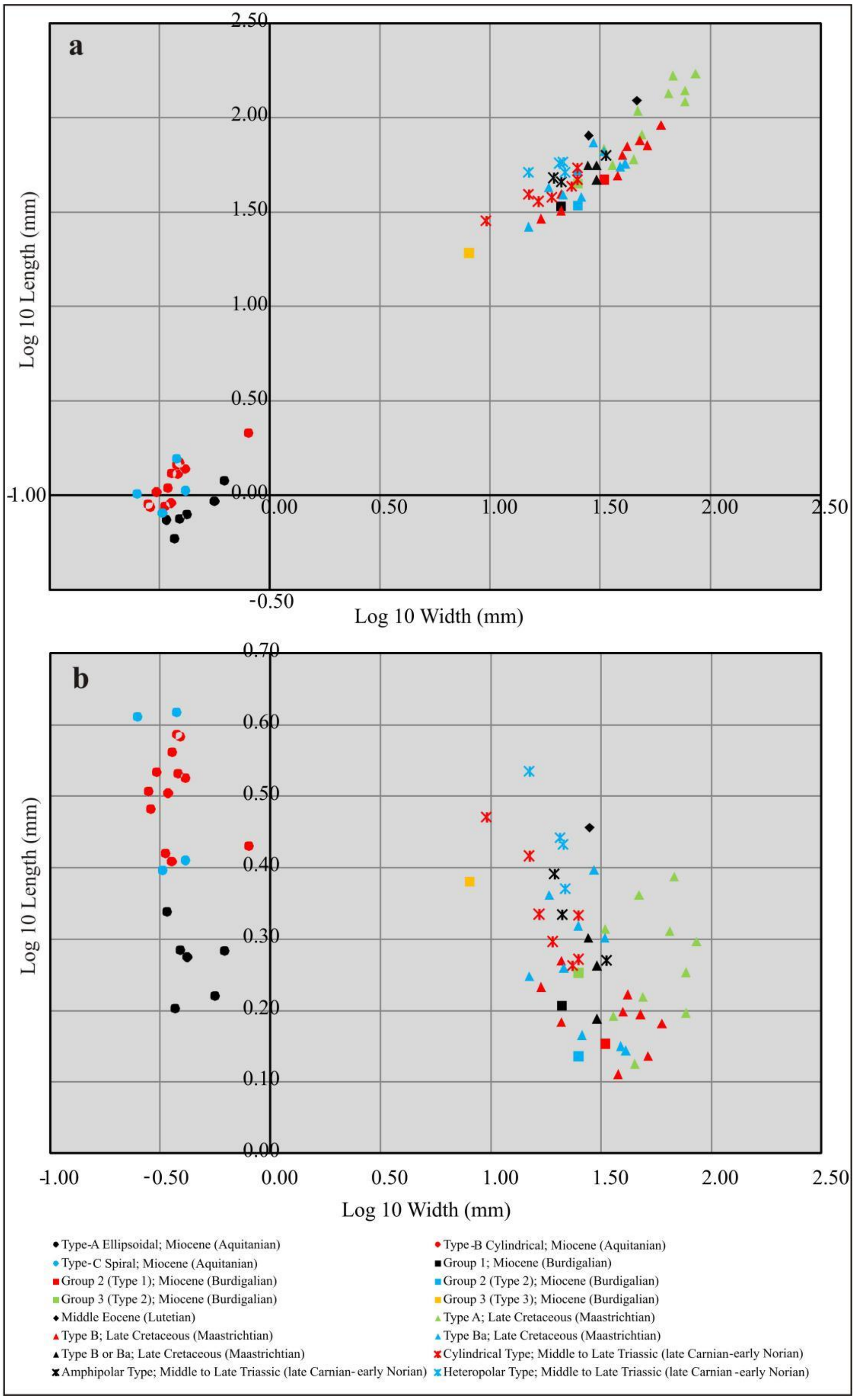


Fig. 6: Bivariate plots showing the size comparisons between putative fish coprolites (present study) and previously known coprolites from the Mesozoic-Cenozoic sedimentary sequences of India. a) Bivariate plot with log10 Width (mm) on the x-axis and log10 Length (mm) on the y-axis, and b) Bivariate plot with log10 Width (mm) on the x-axis and log10 Length/Width on the y-axis. Note: For detailed measurements of the coprolite specimens refer to Supplementary Data S1 in the present study.

5.2 Statistical analysis

We carried out a detailed statistical analysis (Principal Component Analysis) incorporating dataset (on dimensions) available in the published literature on Indian coprolites and the ones recorded in the present investigation (Supplementary Data S1). This has been chiefly attempted to a) gain inferences that may reflect any additional morphological (in terms of size) disparity within the coprolite assemblage from Kotada, b) to statistically compare the size differences between previously known coprolites from India and the ones reported herein, and c) to try to infer any possible association(s) to producer animal(s) based on coprolite dimensions, due to availability of a large dataset from India in published records attributing coprolite specimens to producers (refer to Supplementary Data S1). It is pertinent to mention here that the previously envisaged associations between Indian coprolites and the producer fauna (discussed earlier) have not been tested statistically.

Principal Component Analysis (PCA) of the coprolite specimens from Kotada suggest the presence of at least 2 groups; if we consider the variables a) length/width (LbW) and b) width (W) (refer to Fig. 7a). The PCA biplot allows us to differentiate Type-A coprolites from Type-B and Type-C (Fig. 7a). A differentiation (on the basis of the above-mentioned two variables) cannot be visualized between Type-B and Type-C coprolites; however, Type-C coprolites are spiral in overall aspect, unlike Type-B (refer to section “5.1”). Further, based on the two variables (i.e., LbW and W), differentiation between Kotada coprolites and the previously recorded Mesozoic-Cenozoic coprolites from India can be clearly visualized in the PCA biplot (refer to Fig. 7b). Thus, based on both morphometric and statistical analysis and considering the generally accepted associations (to the producer animals) of the previously recorded coprolites from India (refer to Supplementary Data S1, Figs. 6a-b, 7a-b), we contemplate that the likely producers of the Kotada coprolites weren’t large-sized vertebrates such as rhynchosaurid reptiles, chelonians, crocodilians or dinosaurs. In addition, the biplot (Fig. 7b) clearly demarcates the Type-A (linked to Titanosaurid dinosaurs) from the rest by placing majority (i.e., 6 out of 11) of the specimens at the top right corner (i.e., they have higher positive values of both PCA1 and PCA2 axes). Further, we observe that the Triassic coprolites linked to rhynchosaurid reptiles are mostly (7 out of 13 specimens) placed along the increasing direction of variable LbW in the biplot (refer to Fig. 7b). However, a clear distinction amongst previously recorded coprolites linked to chelonians and crocodilians is not observed, suggesting that the two variables (i.e., LbW and W) are insufficient to differentiate these groups.

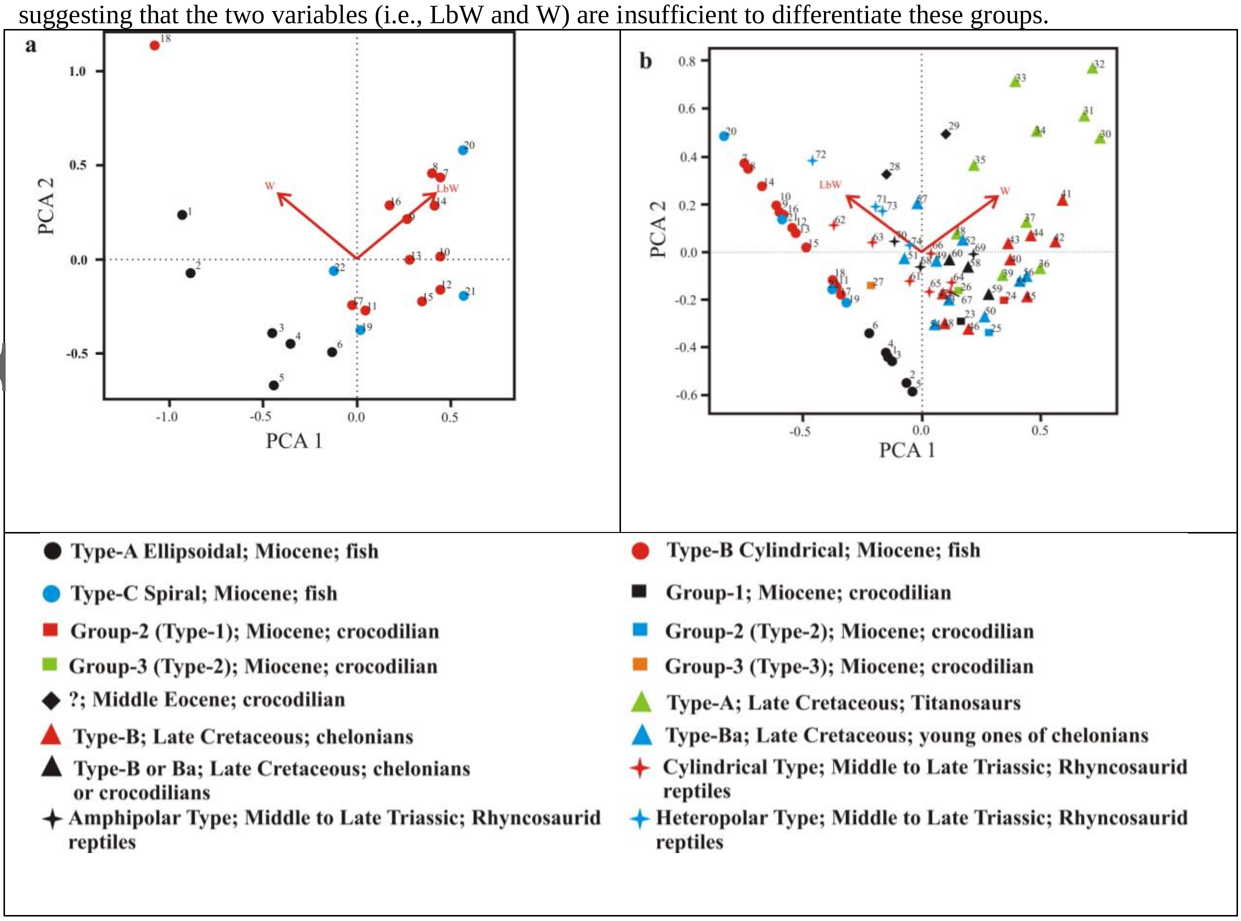


Fig. 7: Results of the PCA analysis: a) incorporating all the putative fish coprolites specimens recovered, in the present study, and b) incorporating putative fish coprolites (present study) and previously recorded coprolites from the Mesozoic-Cenozoic sedimentary succession of India. For further details refer to Supplementary Data S1 and Fig. 6.

Overall, the morphological and statistical data suggest that the Kotada coprolites (reported herein) were most likely produced by small-sized vertebrates and possibly by fishes. The occurrence of numerous indeterminate teleost fish remains (mainly dental elements) in association with the coprolites recorded herein (Fig. 8a-b) also argues in favour of fishes being the likely producers. Further, it should be noted that there is an absence of a strict criterion (based on size) to differentiate coprolites produced by invertebrates and small vertebrates. For instance, up to 3mm (in longer dimensions) ellipsoidal and cylindrical forms of coprolites have been previously assigned to either fishes or echinoderms or crustaceans (Häntzschel et al., 1968 and references therein). Intriguingly, a small constituent of Kotada coprolites (mainly the Type-B: Cylindrical; refer Fig. 9h, k, n) exhibit a rather geometrical (straight with edged ends) shape and are quite comparable in size and morphology to the faecal matter produced by crustaceans (refer Ladle and Griffiths, 1980). Of these, the Kotada specimen VVK/KOT2046 (Fig. 9k) displays a longitudinal groove, which is a case similar to the one observed by Ladle and Griffiths (1980) in the faecal matter produced by the modern crustacean *Asellus aquaticus* (refer Fig. 1n in Ladle and Griffiths, 1980). Moreover, *A. aquaticus* is commonly known to dwell in freshwater and lacustrine habitats, in contrast to the marine Khari Nadi deposits yielding the coprolites reported herein. We here accentuate on the 'putative' assignment of Kotada coprolites to fishes. Ongoing work is expected to provide further inferences on the diversity of fish (and associated biotic component) from the coprolite hosting lithology; however, this aspect would be dealt with (in detail) as a separate study. Thus, it is difficult to assign the Kotada fish coprolites (reported herein) to a particular fish genus, at this stage.

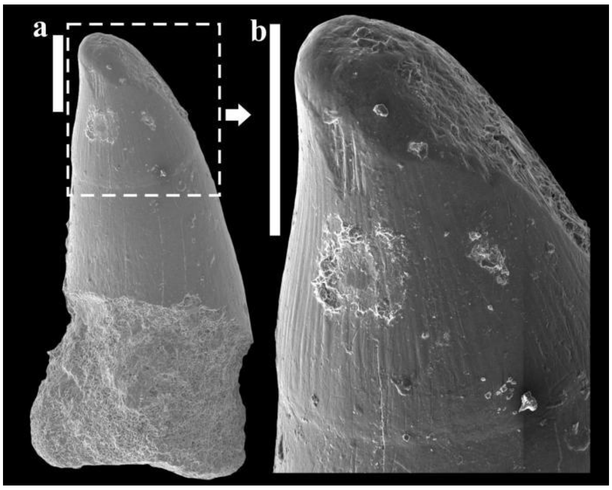


Fig. 8: a) Scanning electron microphotograph of an isolated dental element belonging to Teleost gen. et sp. indet. (Specimen no. VVK/KOT2021) that was recovered from the KOT-1 sample in association with putative fish coprolites recorded in the present investigation, b) a close-up view of the apical portion of the fish tooth showing a conspicuous presence of vertical striations on the external surface. Scale bar equals 300µm for both a, b.

5.3 Scanning Electron Microscopy (SEM) and Energy Dispersive Spectroscopy (EDS)

The scanning electron microphotographs of the coprolite specimens illustrate the three morphotypes (Ellipsoidal, Cylindrical, and Spiral) recovered in the present investigation from Kotada (refer to Fig. 9). Further, the scanning electron microphotographs reveal the internal structure and microtexture of the three morphotypes (discussed earlier) that are typically composed of calcium phosphate microglobules, nano-sized and micron-sized porous structures, and walled egg-like or capsule-like structures (Fig. 9b, f, g, i, j, r). It should be noted that in a previous investigation Lamboy et al. (1994) documented the above-mentioned nano-sized and micron-sized porous structures within Cretaceous-Eocene fish coprolites from North Africa. Subsequently, these porous structures were also observed within fish coprolites recovered from the Upper Miocene to Pliocene sediments of Oman (Purnachandra Rao and Lamboy, 1995). Available literature equivocally supports the idea that the small (nano-sized) and large-sized (~1-10 micron) porous structures (also 'vesicles') and spherical cavities (egg-like mineral spheres) are formed in the presence of gases as a consequence of decomposition of excrement in the presence of sulphur producing bacteria (Northwood, 2005 and references therein). Interestingly, the walled micron-sized microspherulitic spheres (with void spaces) within coprolites have been attributed to mineral pseudomorphs of organic structures (possibly bacteria) of the original excreted material in earlier observations by Hollocher et al. (2010) and Owocki and co-workers [refer to Fig. 3f in Hollocher et al. (2010); Figs. 6a-b in Owocki et al. (2012); Figs. 4a-b in Bajdek et al. (2016)]. The walled egg-like hollow spheres (attributed to bacteria) are also observed within Kotada coprolites in the present investigation (refer to Figs. 9b, j, r). Additionally, but with rarity, crystal sockets can be observed within Kotada coprolites that quite likely belong to pyrite (refer Fig. 9f). Pyrite is commonly known to occur in fossils (including coprolites) and generally precipitates in the presence of sulphur reducing bacteria associated with decaying organic matter (Ehlers et al., 1965; Hollocher et al., 2005; Zhang et al., 2015 and references therein). However, we observe that the Kotada coprolites are devoid of any plant matter.

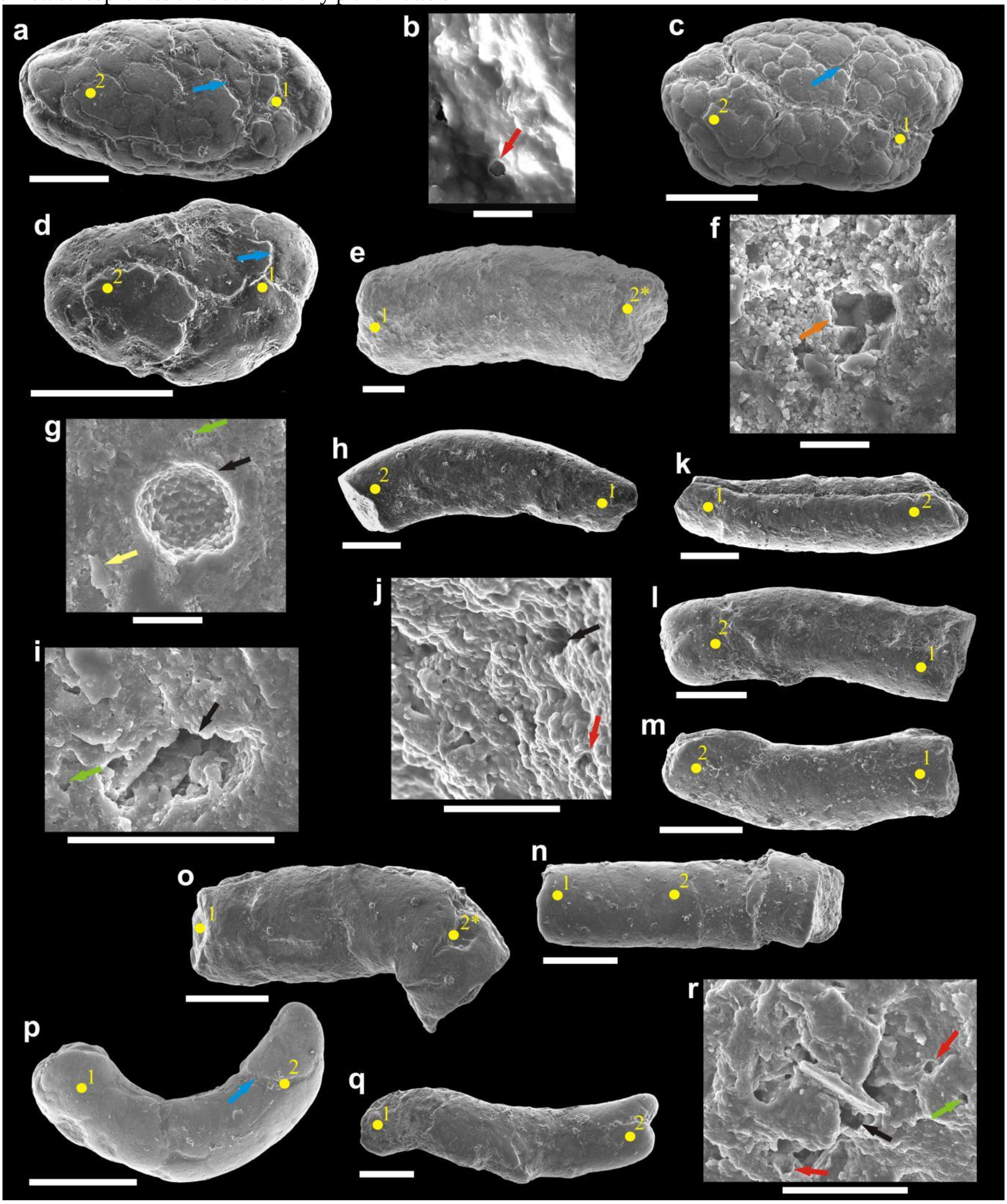


Fig. 9: Scanning electron microphotographs of the putative fish coprolites (recorded in the present study) depicting external morphology and internal structures. **(a-d)** Type-A (Ellipsoidal): (a-b) Specimen no. VVK/KOT2042, (c) Specimen no.VVK/KOT2043, (d) Specimen no.VVK/KOT2044; **(e-n)** Type-B (Cylindrical): (e-g) Specimen no.VVK/KOT2020, (h-j) Specimen no.VVK/KOT2045, (k) Specimen no.VVK/KOT2046, (l) Specimen no.VVK/KOT2047, (m) Specimen no.VVK/KOT2048, (n) Specimen no. VVK/KOT2049; **(o-r)** Type-C (Spiral): (o) Specimen no. VVK/KOT2011, (p) Specimen no.VVK/KOT2032, (q-r) Specimen no.VVK/KOT2050. Note: EDS spots marked by yellow dots on individual specimens.The EDS spot number 2 [with star (*) symbol] in specimens VVK/KOT2020 (Fig. 9e) and VVK/KOT2011 (Fig. 9o) represents original spot number 3 and 7, respectively (for details refer to Fig. 10 and Supplementary Data S3); desiccation crack (blue arrow); large-sized (~10 micron or greater) porous structure (black arrow); small-sized (<10 micron) porous structure (green arrow); walled microspherulite (red arrow); pyrite socket (orange arrow); fish-tooth embedded in

calcium phosphate matrix (yellow arrow) Scale bar equals 300μm for a, c, d, e, h, k, l, m, n, o, p, q; 30μm for i, j, r; 10μm for f, g; and 3μm for b.

Multispot Energy Dispersive Spectroscopy (EDS) analysis on individual specimens suggests the conspicuous presence of elements such as Ca, P, Fe, K, and S, and can be visualized as peaks on the EDS spectra (refer Fig. 10; also refer to Supplementary Data S3). The elemental compositional analysis of individual specimens show that Ca and P exist as major constituents and confirm the phosphatic nature of the Kotada specimens. A conspicuous presence of Ca and P in coprolite generally argues in favour of the producer animal(s) dominantly consuming a carnivorous diet (see Vajda et al., 2016 and references therein). Further, the presence of a fish dental element in the coprolite specimen (VVK/KOT2020; Fig. 9g) hints at an ichthyophagous diet of the producer. The EDS analysis also reveals that Fe, K, and S reflect minor constituents (within Kotada coprolites) as compared to Ca and P. Of the minor constituents, noticeable occurrence (prominent peaks) of S reflected in the Kotada coprolites (Fig. 10) along with the presence of microscopically small porous structures and walled mineral spheres (herein attributed to bacteria) support the idea that the sulphur reducing bacterial activity may have helped in decomposition (to a certain extent) of the faecal matter upon deposition.

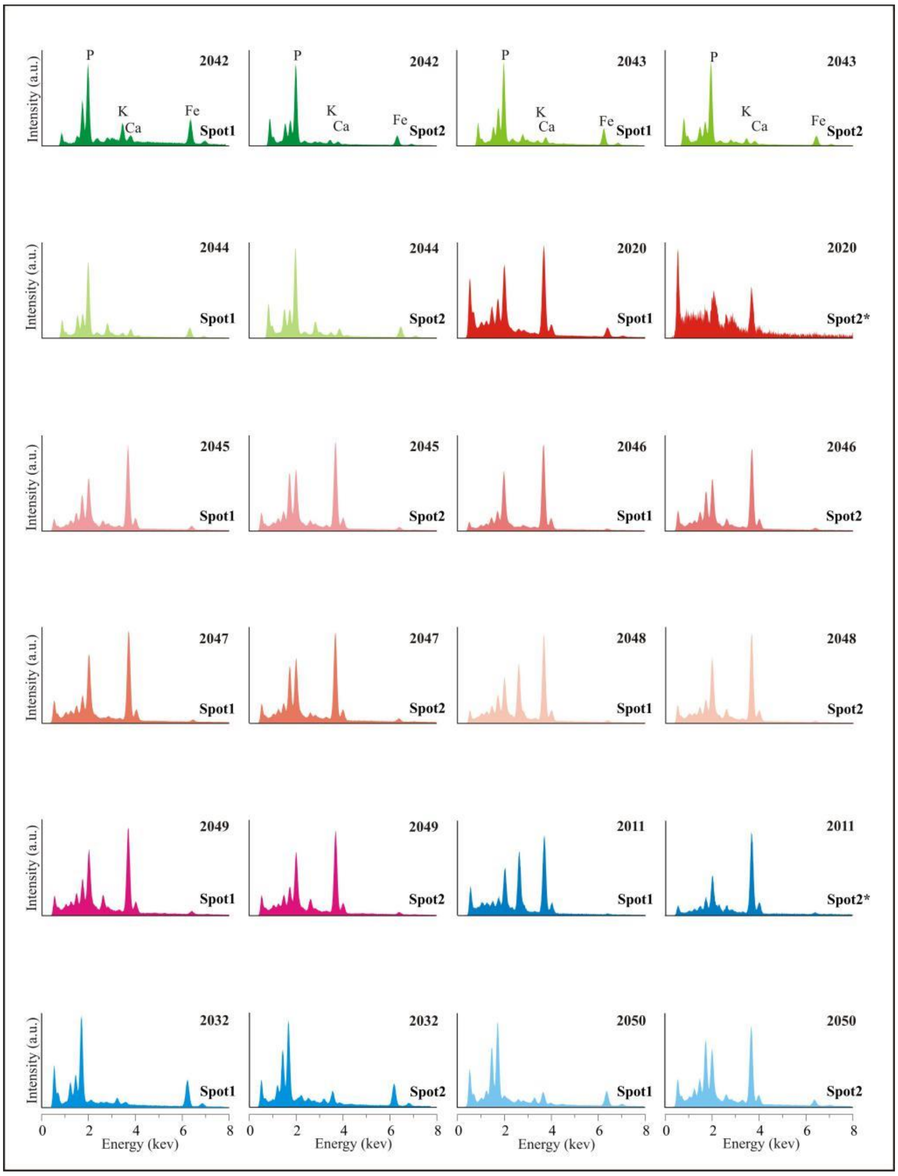


Fig. 10: Profiles of the EDS analysis of the putative fish coprolites recovered from the Miocene (Aquitanian) Khari Nadi Formation sedimentary succession exposed about 1.5 km northeast of the village of Kotada, Kachchh (Kutch) District, Gujarat State, western India. For the position of the individual spots (in each specimen) analyzed refer to Fig. 9.

5.4 XRF analysis of the host lithology and palaeoenvironmental aspects

The results of the XRF analysis (conducted herein) on the host lithology (KOT-1) and associated lithologies

(KOT-2 and KOT-3) show that SiO_2 is the major constituent followed by CaO, Fe_2O_3, and Al_2O_3 (Fig. 11). However, the SiO_2 concentration decreases with depth in the studied succession; the SiO_2 values are 52.38% (KOT-1), 49.76% (KOT-2), and 45.86% (KOT-3) (Fig. 11, Table 1). Further, the concentration of Al_2O_3 and CaO increases with depth in the sequence (Fig 11, Table 1). Thus, a decreased concentration of Al_2O_3 and CaO and an increased SiO_2 concentration in the host lithology (KOT-1) relative to the associated lithologies suggest enhanced chemical weathering (Nesbitt and Young, 1984) of the coprolite-yielding sediments. This may be a consequence of exposure (oxidizing conditions) witnessed by the coprolite-yielding lithology (KOT-1) that was originally deposited in a shallow marine environment. It should be noted that the presence of desiccation cracks on the external surface of coprolites are generally linked to aerial exposure of the original faecal matter (refer Niedźwiedzki et al., 2016). These features (desiccation cracks) can be clearly observed on the external surface of Type-A and in a few cases in Type-C coprolites from the KOT-1 lithology (Fig. 9a, c, d, p) and further support the idea of post-depositional exposure of host sediments. On the contrary, Type-B coprolites from the host lithology (KOT-1) do not show prominent desiccation cracks on their external surfaces. Thereby, reflecting possible selective depositional environments for the three morphotypes, i.e., Type-B and Type-C may have been deposited or buried at a slightly deeper depth as compared to Type-A coprolites. Further, the presence of pyrite (see Fig. 9f) suggests that the Type-B coprolites certainly had a rapid burial and witnessed a reducing environment. In a previous investigation, Jain (1983) documented retention of spiral morphology of faecal matter in extant fishes only up to 24 h. Thus, it seems likely that the Type-C (Spiral) coprolites were also buried quickly after excretion.

Table 1: Chemical concentration (in percentage) of the host (coprolite-yielding; KOT-1) and associated (KOT-2 and KOT-3) lithologies. For a graphical representation of the data, refer to Fig. 11.

Sample no.	SiO2	Al2O3	Fe2O3	Na2O	K2O	CaO	MgO	MnO	TiO2	P2O5	Cl
KOT-1	52.39	20.66	14.09	1.25	2.77	2.00	3.46	0.11	1.19	0.11	1.36
KOT-2	49.77	14.53	15.97	1.01	2.33	5.68	4.67	0.14	1.13	0.12	3.41
KOT-3	45.87	13.07	8.87	0.77	1.34	26.29	1.89	0.25	0.74	0.10	0.21

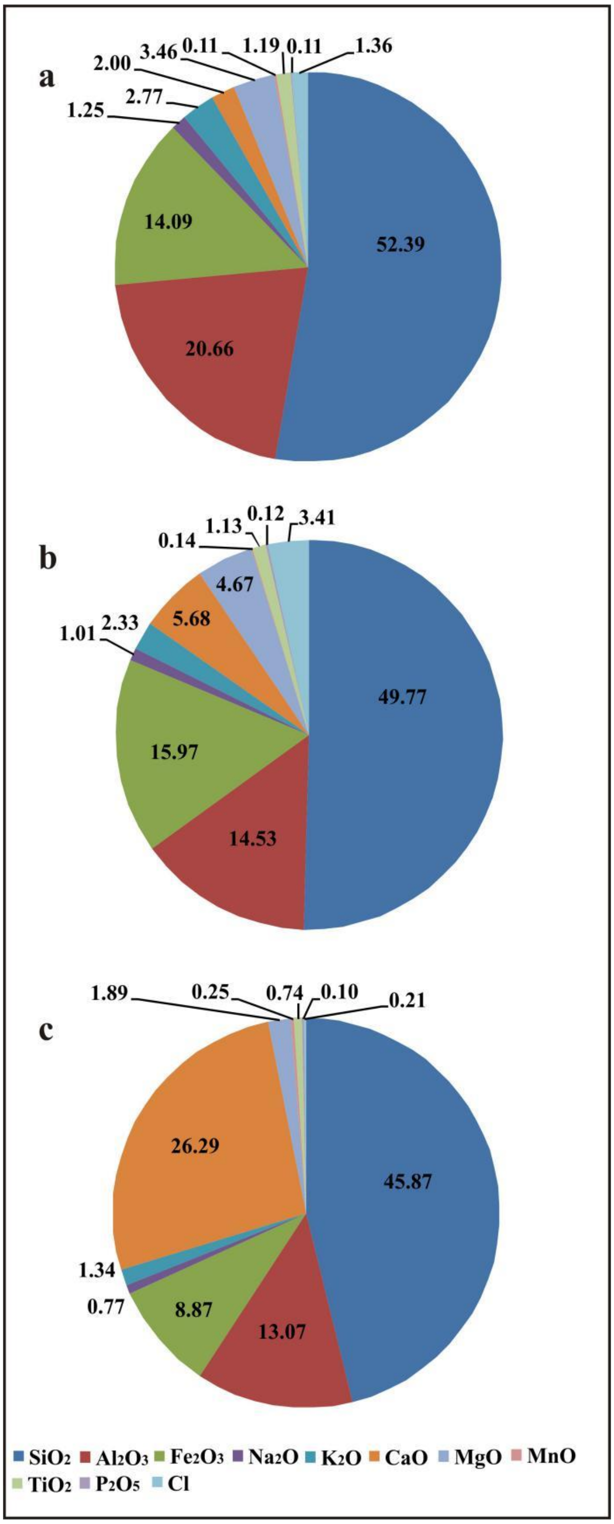


Fig. 11: Pie-chart depicting the chemical concentration (in percentage) of the host (coprolite-yielding) and associated lithologies. Note: a) KOT-1, b) KOT-2, and c) KOT-3.

6 Discussion

Matley (1939a) linked the spirally coiled coprolites from the Middle to Late Triassic Maleri Formation (south India) to the fish genus *Ceratodus*; however, a subsequent detailed study by Jain (1983) argued against such an association. Nonetheless, there are no records of fish coprolites from the post-Triassic geological intervals of India, and none for the microscopically small fish coprolites from India, prior to the present investigation. Outside India, several records of fish coprolites are known. For instance, Broughton et al. (1978) recorded abundant (>10,000 specimens) coprolites (up to 200 mm long) from the Late Cretaceous Whitemud Formation, Saskatchewan Province, Canada and assigned them to holostean fishes. However, none of the coprolites reported by Broughton et al. (1978) is comparable in shape and size to the Kotada coprolites (refer Plate 43, Figs. 1-27 in Broughton et al., 1978; Fig. 9 in present article). Milàn (2010) recorded at least three morphotypes [i.e., a) small-sized (11 to 14 mm long) coprolites having a spherical to drop-like overall aspect and with pointed ends, b) medium-sized (14mm to 23mm long) heteropolar coprolites depicting an overall spiral shape, and c) large-sized (up to 24 mm in diameter) cylindrically shaped coprolites] from the Lower Paleocene (Danian) limestone deposits of Denmark. Of these, the small-sized morphotype was assigned to unknown fishes, while the medium-sized and large-sized morphotypes were linked to sharks and crocodiles, respectively. Considering dissimilarity (in both size and shape) of the Paleocene (Danian) coprolites from Denmark by Milàn (2010) compared to the Kotada coprolites (reported herein) it is unlikely that the Kotada coprolites were produced by either sharks or crocodiles. Numerous fish coprolites have also been reported from the Eocene Messel Pit of Germany (Richter and Baszio, 2001a; 2001b and references therein). Interestingly, the fish coprolites (particularly the Type-B morphotype composed of lithified bacteria and bone fragments) from Messel (refer Fig. 13 in Richter and Baszio, 2001b) are quite similar in size and general morphology compared to the Type-C (reported herein) from Kotada. Further, the SEM analysis does reveal the presence of skeletal elements (e.g., fish dental remains) within the Kotada Type-C specimens (Fig. 9g). In addition, the EDS data also shows a high percentage of Ca and P within the Kotada specimens hinting at a dominantly carnivorous diet of the producer animals as also envisaged for the Type-B coprolites from Messel by Richter and Baszio (2001b). Lamboy et al. (1994) studied (in detail) the nanostructures (using SEM) of numerous fish coprolites (mostly cylindrically shaped and up to 20mm in longer dimensions) and faecal pellets from the Cretaceous-Eocene of North Africa (particularly Egypt, Tunisia, Morocco, Mauritania, and Senegal). These authors observed the typical homogeneous distribution of micron-sized botryoidal apatite particles and ovoid cavities within African fish coprolites (refer to Figs. 2d-g, 3a-d in Lamboy et al., 1994). Further, within the faecal pellets (assigned to either marine bivalves or echinoderms) Lamboy et al. (1994) observed heterogeneous microstructures with apatite particles portraying a crystalline aspect (refer to Figs. 4a-d in Lamboy et al., 1994). Our microscopic analysis of Kotada specimens (present study) revealed homogeneous nano-sized and micron-sized porous structures and ovoid cavities (Fig. 9), without crystalline apatite overgrowths, so it is unlikely that the Kotada coprolites were produced by marine bivalves or echinoderms but rather by fishes. Certainly, future detailed work on the fossilized biotic component (mainly fishes) from the Kotada section in the context of biodiversity and ecological aspects may be quite valuable.

7 Conclusions

a) Research on Indian coprolites spans more than 150 years with much emphasis on Mesozoic-Cenozoic large-sized coprolites linked to rhynchosaurid reptiles, titanosaurid dinosaurs, crocodiles, or chelonians. In a first from India, the present investigation provides evidence for the presence of numerous microcoprolites within the Miocene (Aquitanian), Khari Nadi Formation sedimentary succession exposed about 1.5 km northeast of the village of Kotada, Kachchh (Kutch) District, Gujarat State, western India.

b) The Scanning Electron Microscopy (SEM) and Energy Dispersive Spectroscopy (EDS) reveal the overall morphology, internal texture, and chemical nature of the coprolites (recorded herein) from Kotada. The Kotada specimens show the presence of nano-sized and micron-sized porous structures, walled micro-spherulitic structures, apatite globules, and pyrite that are typical of coprolites. Morphologically, we have here categorized Kotada coprolites into three morphotypes, i.e., Type-A: Ellipsoidal, Type-B: Cylindrical, and Type-C: Spiral. The above-mentioned internal structures along with detection of S (EDS analysis) hints at the decomposition of the original faecal matter in the presence of bacteria. Further, an occurrence of vertebrate remains (fish tooth) within Kotada coprolites and prominent peaks of Ca and P found in the EDS analysis points to a dominantly carnivorous (ichthyophagous) diet consumed by the producer animal(s).

c) Morphometric and size comparisons (in a statistical framework; PCA analysis) with previously known coprolites from the Mesozoic-Cenozoic successions of India and also across the globe implies that the Kotada coprolites weren't produced by large-sized vertebrates such as rhynchosaurid reptiles, titanosaurid dinosaurs, crocodiles or chelonians but quite possibly by fishes.

d) The X-Ray Fluorescence (XRF) analysis carried out in the present investigation on the host and associated lithologies suggests that the Kotada coprolites were deposited in a changing shallow marine environment with possible aerial exposure of the host lithology some point after deposition.

e) In addition, the SEM and EDS data allow us to envisage the idea of selective deposition environment witnessed by the three Kotada morphotypes, i.e., the Type-B and Type-C morphotypes were deposited rapidly after excretion and most likely at a slightly deeper depth as compared to Type-A coprolites.

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