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A colubrid snake from the late Miocene of Kutch, Gujarat, India

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Fossil snakes are extremely rare in the Indian Neogene records. We report the first record of isolated precloacal vertebrae of a "colubrine" snake from a late Miocene site, Tapar section in Kutch, Gujarat (India). The present specimens differ from the earlier finding of a colubrid from a younger deposit of Labli Member, Utterbaini Formation of Upper Siwaliks (Jammu and Kashmir) by the absence of hyapophyses. The "colubrine" snakes of late Miocene (~11-10 Ma) perhaps lived in a relatively wetter environment compared to the present "colubrine" from Kutch.

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INTRODUCTION

Kutch is well known for its Neogene vertebrates since mid 18th century (Grant, 1840; Wynne, 1872; Lydekker, 1876, 1880). In recent years, more fossil specimens have been unearthed from these sediments, particularly from the late Miocene sites of Tapar and Pasuda that include teleost, batoids, turtles, crocodylians, lizards, snakes, suids, equids, giraffids, rhinocerotids, and elephants (also see, Bhandari *et al*., 2010, 2015; Patnaik *et al*., 2014; Singh *et al*., 2019, 2020, Sharma *et al.* 2021, Čerňanský *et al.* 2021, Singh *et al*. in press). Recently, Bhandari *et al*. (2018) reported the first record of hominoid *Sivapithecus* from the late Miocene locality of Tapar. However, the report of snakes from the Palaeogene-Neogene of Kutch is very scanty. Only a few records from the Lower Eocene Cambay Shale of Panandhro Lignite Mine (Rage *et al*., 2003), early Eocene of Vastan Lignite Mine of Kutch, Gujarat (Rage *et al*., 2008), early to middle Miocene of Kutch (Head *et al*., 2007 and Kapur *et al*., 2019) are known till date.

During the recent field survey (2017-2019) of the late Miocene deposits exposed around Tapar, we recovered several vertebrae of "colubrine" snakes. These have been described and compared here and the paleoecological significance has been discussed.

GEOLOGICAL SETTING AND AGE

Kutch basin is well known for its fossiliferous litho-stratigraphic sequences ranging in age from the Mesozoic to Pleistocene (Biswas, 1992). The tertiary sediments were deposited over the older sediments of Mesozoic age capped by the Deccan Traps. Biswas (1992) classified the Neogene deposits of Kutch into three formations namely, Khari Nadi Formation, Chhasra Formation, and Sandhan Formation. The Khari Nadi Formation comprises siltstone, sandstone, limestone, and clay is also known as the Arenaceous Group (Wynne, 1872) and Gaj Bed (Poddar, 1959; Mohan and Bhatt, 1968). 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). The lithology of the Khari Nadi Formation is comprised of laminated to very thin-bedded siltstone, fine-grained sandstone, and gypseous claystone. Khari Nadi Formation is considered as early Miocene in age (Aquitanian: 23.03–20.43± 0.05 Ma., Gradstein *et al.,* 2004, Patnaik *et al.,* 2014) and it is having a conformable and gradational contact with the younger Gaj Formation (Chhasra Formation as in Biswas, 1992, Catuneanu and Dave, 2017). The rocks of the Gaj/Chhasra Formation were dated as early Miocene Burdigalian (Biswas, 1992) and as Lower Miocene to Middle Miocene by the Geological Survey of India (2012). This formation is comprised of olive green shale, gypseous shale, and claystone with alternations of thin argillaceous limestone beds. It is considered that this formation is having a disconformable upper contact with the younger rocks of the Sandhan Formation (?Miocene –Pliocene) (also see Biswas, 1992). The Sandhan Formation is comprised of clay with concretion, pelleted rock, siltstone, parallel to cross-laminated sandstone beds intermittent with conglomerate beds comprising of calcareous nodules, agate pebbles, very coarse sand, and mudclasts.

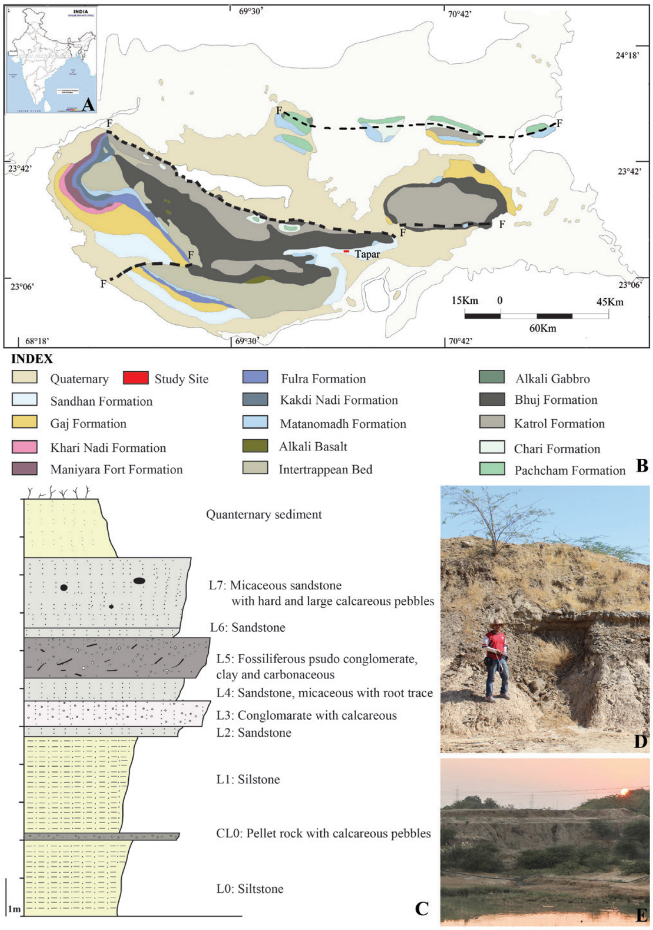


Figure 1: A) Map of India showing the study area by a rectangular box, B) Geological map of the study area (Kutch) modified after Geological Survey of India, 2012 (Fossil location indicated by red box mark), C) Lithosection exposed at the fossil location (Study site), D-E) Photograph showing fossil-bearing lithounit of the Tapar section.

The present specimens of colubrid snake have been recovered from the conglomerate beds of the Sandhan Formation exposed at the Tapar site (Fig. 1). The lithosection exposed in the study area is comprised of massive sand, silt, and clay layers along with intermittent conglomerate beds (Figs. 1. C, D, E). The lithologies exposed in this section were supposed to have been deposited in a floodplain setting with occasional cannibalization of pre-existing deposits as the rivers and streams meandered over the floodplain (Bhandari *et al*., 2015). The Tapar section is also known to have yielded certain vertebrates including fragmented teeth of *Deinotherium, Gomphotherium*, rhinos, giraffids, equids, bovid, suids, crocodiles, turtles, fishes teeth (Bhandari *et al.*, 2010, 2015; Singh *et al*., 2019, 2020). Based on the presence of First Appearance Datum (FAD) of *Hipparion* teeth and other associated faunas Bhandari *et al.* (2015) opined the fossiliferous batoids bearing site of Tapar section to be of Late Miocene (11-10 Ma) age. The recent findings of rodents including an advanced *Myocricetodon,* a new murine *Kutchimys prasadi* gen. et sp. nov., also of *Progonomys morganae, Kanisamys kutchensis* and a new sciurine *Tamias gilaharee* sp. nov. from the Tapar section suggested a precise age of ~10 Ma (also see, Patnaik *et al.* in press) which supported by the recent finding of a new *Listriodon* species, *Listriodon dukkar* nov. sp. from Pasuda dated the age of the sediment to be around ~ 10 Ma (Made *et al.* in press).

MATERIALS AND METHODS

Small snake vertebrae were recovered from bulk samples of calcareous ferruginous conglomerate by wet and dry sieving techniques. The sediments were broken into fragments and then soaked in plastic tubs with buffered acetic acid and water. The loose samples were washed with water by using different mesh sieve sizes 20, 40, and 60 (ISTM). Mostly, the snake fossils could be recovered from the mesh sieve sizes 20 and 40. Images were obtained under the Leica Stereozoom Microscope M205C housed at the Department of Geology, Central University of Punjab, Bathinda at a magnification of x 1.5 and x 2. The terminology of snake vertebrae followed here is that of Rage (1984). *Institutional Abbreviation-* VPL/PU/KT**,** Vertebrate Palaeontology Laboratory, Centre for Advanced Study in Geology, Panjab University, Chandigarh (India); PBL/CUP/MKSAS/R, Palaeontogy and Biostratigraphy Lab., Central University of Punjab, Bathinda (India); H-GSP, Harvard-Geological Survey of Pakistan (Pakistan).

SYSTEMATICS

SERPENTES Linnaeus, 1758
COLUBRIDAE Oppel, 1811
"**COLUBRINAE**" Oppel, 1811

"**COLUBRINAE**" indet.
(Pl. I and II).

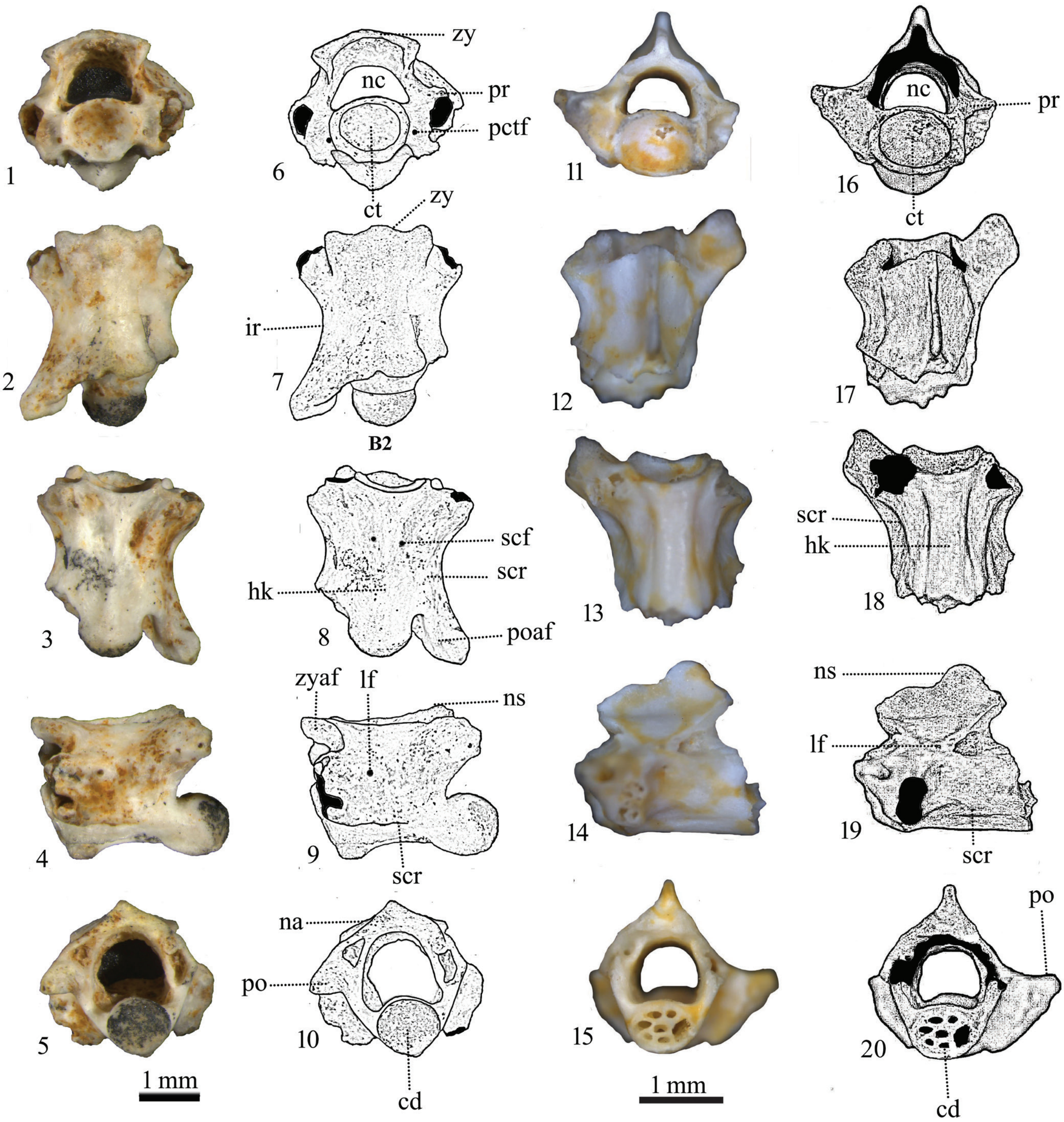
Fossil Locality: Tapar, Kutch (Gujarat).
*Age***:** Late Miocene (~11-10 Ma) Sandhan Formation.
*Materials***-** VPL/PU/KT-3, PBL/CUP/MKSAS-2, PBL/CUP/MKSAS-3, PBL/CUP/MKSAS-4; precloacal vertebrae.

*Description***:** Recovered specimens are mostly incomplete in form. They are characterized by having very small centrum length ranging from 2.7 mm to 3.8 mm. The neural spine is variably damaged in all specimens. The additional measurements are provided in Table 1.

In anterior views, the cotyle is relatively small being oval and slightly wider than tall. The zygosphene roof is preserved with an arched shape in the specimen PBL/CUP/MKSAS-2 and its zygosphenal articular facets are steep and high-angled (P1. I, Figs. 1, 6). Paracotylar foramina are seen on either side of the cotyle in two specimens PBL/CUP/MKSAS-2 and PBL/CUP/MKSAS-3 (Pl. I, Fgs. 1, 6 and Pl. II, Figs. 1, 6). The neural canal is wide, convex near the margin of zygosphene, and slightly straight to convex at the base (Pl. I, Figs. 1, 6, 11, 16). The prezygapophyses are damaged in all specimens.

In posterior views, the condyle is prominent and rounded. The neural arch is vaulted or domed (Pl. I, Figs. 5, 10, 15, 20).

Plate I



EXPLANATION OF PLATE I

"Colubrinae" indet. Fig. 1-10, PBL/CUP/MKSAS-2; Fig. 11-20, PBL/CUP/MKSAS-4. Anterior views (Fig. 1, 6, 11, 16); dorsal views (Fig. 2, 7, 12, 17); lateral views (Fig. 4, 9, 14, 19); posterior views (Fig. 5, 10, 15, 20); ventral views (Fig. 3, 8, 13, 18). Abbreviations: cd, condyle; ct, cotyle; hk, haemal keel; ir, interzygapophyseal ridge; lf, lateral foramina; na, neural arch; nc, neural canal; ns, neural spine; pctf, paracotylar foramina; po, postzygapophysis; poaf, postzygapophyseal articular facet; pr, prezygapophysis; scf, sub-central foramina; scr, sub-central ridge; zy, zygosphene; zyaf, zygosphenal articular facet.

Table 1. Measurement (in mm) of the four precloacal vertebrae (PBL/CUP/MKSAS-2, PBL/CUP/MKSAS-4, PBL/CUP/MKSAS-3, VPL/PU/KT-3).

	PBL/CUP/ MKSAS-2	PBL/CUP/ MKSAS-4	PBL/CUP/ MKSAS-3	VPL/PU/ KT-3
Maximum height of cotyle	1.0	0.7	0.9	1.4
Maximum width of cotyle	1.2	0.9	1.0	1.7
Maximum height of condyle	0.9	0.6	0.97	1.4
Maximum width of condyle	1.0	0.9	0.9	1.5
Width of zygosphene	1.6	-	1.9	-
Height of neural canal	1.1	-	-	-
Width of neural canal	1.3	-	-	-
Width of prezygopophysis	2.6	-	-	-
Width of postzygopophysis	-	-	-	-
Length of neural spine	-	-		-
Length of centrum	2.7	-	3	3.8
Width of interzygapophyseal constriction	1.9	1.5	1.8	-

Deep and wide zygantral area with endozygantral foramina are present in the specimen PBL/CUP/MKSAS-2 (Pl. I, Figs. 5, 10). Only one side of postzygapophysis is present in all the specimens and not expanded laterally as in the Siwalik specimens.

In dorsal views, most of the specimens are damaged except the specimen PBL/CUP/MKSAS-2. The interzygapophyseal ridge is smoothly concave. The zygosphenal lip is moderately convex, pointed lobes and wide medial lobe.

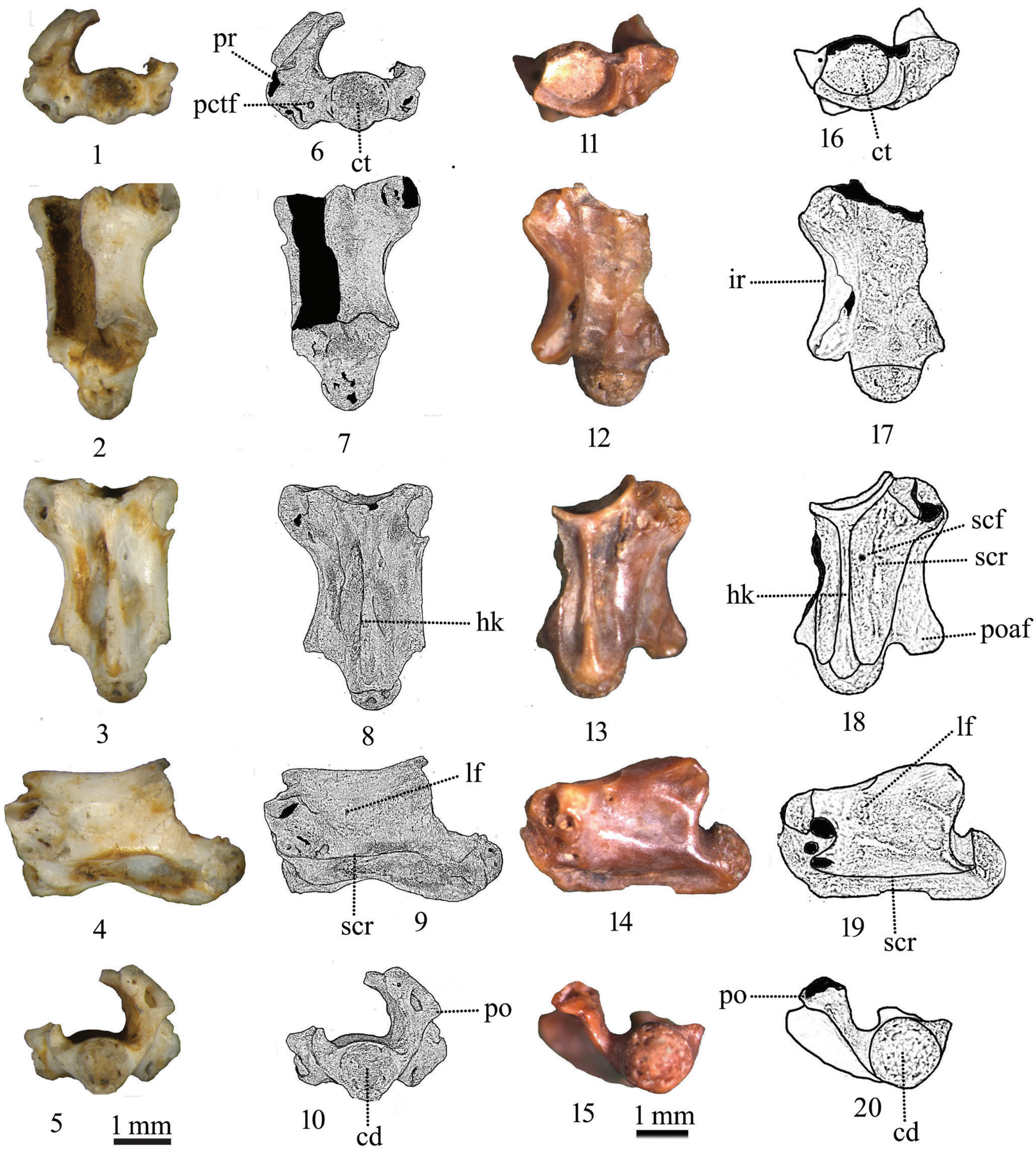
In the ventral views, the centrum is elongated and is of a triangular shape. Paired subcentral foramina and sub-central channels/grooves are present but the specimen PBL/CUP/MKSAS-4 lacks sub-central foramina. The specimen PBL/CUP/MKSAS-2 preserves postzygapophyseal articular facet on one side with an oval shape (Pl. I, Figs. 3, 8). The haemal keel is well developed.

In the lateral view, the inter zygapophyseal and subcentral ridges are straight. The lateral foramina are present and they occur in deep depressions just ventral to the inter zygapophyseal ridges (Pl. I, Figs. 4, 9, 14, 19; Pl. II Figs. 4, 9, 14, 19). The foramina are more anteriorly placed. Parapophysis, dyapophysis and neural spine are damaged in all specimens. Hyapophysis is absent.

COMPARISON AND DISCUSSION

All the present vertebrae from Tapar sections are attributed to the family Colubridae based on the trunk vertebrae usually lightly built and being longer than wide, the prominent sub-central ridges and sub-central foramina, and the presence of a well-developed haemal keel (Holman, 2000; Ikeda, 2007). Within the family Colubridae the informal name "Natricinae" and "Colubrinae", are used widely by palaeontologists as a sub familial rank. "Natricinae" possess hypapophyses in their precaudal vertebrae (Venczel, 2011), whereas in "Colubrinae" hypapophyses are restricted to the anterior trunk (i.e., cervical) vertebrae, and this structure in succeeding mid trunk and posterior trunk vertebrae is substituted by a haemal keel (see Georgalis *et al*., 2017). The present specimens are recognized as the mid trunk or posterior trunk vertebrae of "Colubrinae" based on the absence of hypapophyses of the trunk vertebrae (Venczel, 2011; Georgalis *et al*., 2017) and the presence of a well-developed haemal keel (Szyndlar, 1991; Head, 2005). "Colubrinae" includes several genera such as *Coluber* (Linnaeus, 1758), *Elaphe* (Wagler, 1833), *Coronella* (Laurenti, 1768), *Telescopus* (Wagler, 1830), and *Texasophis* (Holmann, 1977). *Coluber* (North American genus) and *Elaphe* (European genus) are identified based on the distinct differences of skull bones and axial elements (Szyndlar, 1985, 1988). Regarding vertebrae, "colubrine" snakes have been classified into two informal groups to facilitate the taxonomic allocation of fossils such as small-sized "colubrine" and large-sized "colubrine" (Szyndlar, 1984). The large-sized group includes snakes with the centra of large trunk vertebrae exceeding in the length of 6 mm and the small-sized "colubrines" include snakes with the trunk vertebral centra rarely reaching a length of 5mm. The present specimens differ from *Coluber, Elaphe,* and *Coronella* by having smaller-sized trunk vertebrae and lacking prezygapophyseal accessory processes. Head (2005) established a new taxon *Chotaophis padhriensis* (H-GSP 24346) from the Late Miocene of Siwalik, Pakistan, and recognized the unique combination of anteriorly positioned lateral foramina, presence of parazygantral foramina, and elongated centrum as the characters of *Chotaophis*. However, the presence of parazygantral foramina cannot be considered as a diagnostic feature of this genus because all "colubrines" possess this character. The anatomical characters of the present specimens are slightly matching with the specimen described by Head (2005) but differ from *Chotaophis* by their convex zygosphenal lip, relatively not much elongated than *Chotaophis*, and short or poor prezygapophyses. Čerňanský *et al*. (2017) described *Texasophis* and *Telescopus* from the middle Miocene of Hambach, northwestern Germany. These two taxa are almost similar on account of anatomical characters and having small size but the only difference is the straight anterior border of *Telescopus* zygosphenal lip and slightly convex zygosphenal lip in *Texasophis*. The present specimens appear to be more related to *Texasophis* rather than *Telescopus* on account of small size, convex zygosphenal lip, elongated form, strongly built haemal keel, and distinct subcentral ridges (Čerňanský *et al*., 2017). However, *Texasophis* is considered to be a problematic taxon because it has an unclear relationship with the recent "colubrines". Rage *et al*. (2001) reported colubrid snakes from the Neogene Siwalik beds of Jammu and Kashmir, India. The specimens from the Neogene Siwalik beds of Jammu and Kashmir (Rage *et al*., 2001) possess a strong hyapophysis, whereas the present specimens are lacking this feature. Also, the Tapar vertebrae are comparable to those of Eocene colubroid reported from Panandhro Lignite Mine and Vastan Lignite Mine of Kutch, Gujarat (Rage *et al*., 2003, 2008) but differ on the basis of having a thin zygosphene

Plate II



EXPLANATION OF PLATE II

"Colubrinae" indet. Fig. 1-10, PBL/CUP/MKSAS-3; Fig. 11-20, VPL/PU/KT-3. Anterior views (Fig. 1, 6, 11, 16); dorsal views (Fig. 2, 7, 12, 17); lateral views (Fig. 4, 9, 14, 19); posterior views (Fig. 5, 10, 15, 20); ventral views (Fig. 3, 8, 13, 18). Abbreviations: cd, condyle; ct, cotyle; hk, haemal keel; ir, interzygapophyseal ridge; lf, lateral foramina; pctf, paracotylar foramina; po, postzygapophysis; poaf, postzygapophyseal articular facet; pr, prezygapophysis; scf, sub-central foramina; scr, sub-central ridge.

with its roof convex dorsally. From the above discussion, it is concluded that the Tapar (Kutch) "colubrine" is difficult to assign to any known genus.

Palaeoecology: Head (2005) observed that there was a change in the Siwalik snake community record from middle to late Miocene coinciding with the intensification of the monsoon. The intensification of monsoon is generally constrained between 11 to 9 Ma (see Kroon *et al*., 1991). Before the monsoon intensification, the percentage of "colubrine" was less in the Siwalik record, which increased after the intensification leading to diversification (see Head, 2005). Therefore, the occurrence of "Colubrinae" in the late Miocene Tapar, Gujarat (~11-10 Ma; Bhandari *et al*., 2015) and from the late Miocene Siwalik of Pakistan (7-8.5 Ma; Head, 2005) appears broadly concurrent with the timing of this monsoonal intensification. During this period the climate entered a phase of cooler and drier conditions promoting the dominance of C4 grassland in the Siwalik (Patnaik and Prasad, 2016).

Today, "colubrines" are found in many tropical areas. The majority of "colubrines" are terrestrial dwellers, besides some aquatic, arboreal, and fossorial forms (Amr *et al*., 2011). The genera vary greatly in habitat and behavior depending on different species and subspecies. For example, *Elaphe obsoleta obsoleta* (Conant and Collins, 1991) prefers heavily wooded habitats and on rocky hillsides of mountains, whereas *Elaphe obsoleta quadrivittata* (Palmmer and Braswell, 1995) prefers river swamps as habitats (Burton and Burton, 1969). The genus *Texasophis* is mostly a ground-dwelling carnivore (Holman, 1977; Szyndlar, 1984). The genus *Coronella* is terrestrial and rather secretive, spending much of their time undercover (Steward, 1971). As the present specimens appear to be more related to the extinct genus *Texasophis* (Holman, 2000), it could be a ground-dwelling form. Kutch, nowadays, experiences seasonal and arid conditions (temperature varies from 12°C during winter and as high as 43°C during the hot summer days) with 838 mm annual precipitation. The extant genera of Colubridae such as *Wallaceophis gujaratensis* and *Coronella brachyuran* have been found in Gujarat. These species prefer to live in dry and arid conditions (Mirza *et al*., 2016; Vyas *et al*., 2017; Mirza and Patel, 2017). In contrast to the present ecological conditions of colubrids in Gujarat, the Tapar "colubrine" might have lived in a wetter and more humid condition during the late Miocene. This is corroborated by a rich reptilian and mammalian fauna comprising turtles, crocodiles, suids, equids, giraffids, rhinocerotids, and proboscides (Bhandari *et al*., 2015). The wet and humid condition is also suggested by the stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope composition of dental enamel of Tapar proboscideans (Patnaik *et al*., 2019).

CONCLUSIONS

The finding of the "colubrine" snakes from Tapar site, Kutch Gujarat, India, and Siwaliks of Pakistan indicates that similar monsoonal conditions prevailed in the region throughout Indo-Pakistan during the late Miocene period. The present "colubrines" snake from the late Miocene (~11-10 Ma) might have lived in a moderately wetter condition than the present Kutch "colubrines".

ACKNOWLEDGMENTS

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continued from back cover

Palynofacies of the early Cretaceous Pariwar Formation, Jaisalmer Basin, Rajasthan, India: Palaeoenvironmental interpretation 251

Raj Kumar, Neelam Das, Neha Aggarwal & Bindhyachal Pandey

Confocal Laser Scanning Microscopy (CLSM) of newly recovered microfossil assemblage from the Kurnool Group, South India: New insights on microfossil morphology 258

Yogesh Kumar, Yogmaya Shukla1, Veeru Kant Singh, Mukund Sharma & Shreerup Goswami

The early Cambrian (Series 2, Stage 3) burrows from the Nagaur Sandstone, Marwar Supergroup, Rajasthan, India: palaeoenvironmental and palaeoecological considerations 271

Shamim Ahmad, S. K. Pandey, Mukund Sharma & Ayushi Srivastava

Carbonate Fan Fabric Structures (FFS) in time and space: A case study from the Palaeoproterozoic Kajrahat Limestone, Vindhyan Supergroup, India 290

Divya Singh, Mukund Sharma, Uday Bhan, Bindhyachal Pandey, S. K. Pandey & Deepak Singh

Palaeobotanical evidence for Artinskian wildfire in the Talcher Coalfield, Mahanadi Basin, India 303

Deveshwar Prakash Mishra, Srikanta Murthy, Bindhyachal Pandey & Ashish Kumar Singh

A note on the Fan-Fabric Structures in the late Palaeoproterozoic Kajrahat Limestone, Katni, M.P., India 315

Uday Bhan, Divya Singh, Mukund Sharma, Deepak Singh & S.K. Pandey

A study of morphometric characters of *Ammonia* species in the Chilika lagoon, Odisha, India 323

Utsha Dasgupta & Anupam Ghosh

Turonian (Late Cretaceous) Heterodont Subfamilies: Lucininae, Eriphylinae and Opinae (Bivalvia: Veneroida) from the Narmada Basin, central India 336

A. K. Jaitly, Susheel Kumar, Bindhyachal Pandey, J. P. Gautam & Deep Narayan Tiwari

A study of marsh foraminifera microhabitat in Harshad, Gujarat, India 346

Suchandrani Dutta, Ishita Das, Dipankar Buragohain & Anupam Ghosh

x x x x x x x x x

Diachronism in Late Neogene-Quaternary planktic foraminiferal events in Northern and Eastern Indian Ocean: Palaeoceanographic implications 357

Ashutosh K. Singh, Devesh K. Sinha, Kirtiranjan Mallick, Vikram Pratap Singh & Ankush Shrivastava

New Record of *Ptilophyllum* and related leaf fossils from Kimmeridgian sediments of the Kachchh Basin, western India 375

Dhirendra Kumar Pandey, Neeru Prakash, Franz T. Fürsich, Matthias Alberti, Rajesh Singh Shekhawat, Neelam Das, Suraj Bhosale, Ketan Chaskar & Kevin N. Page

A colubrid snake from the late Miocene of Kutch, Gujarat, India 381

Ningthoujam Premjit Singh, Nongmaithem Amardas Singh, K. Milankumar Sharma, Rajeev Patnaik, Yumlembam Priyananda Singh & Deepak Chaudhary