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A new giraffid *Bramiscus micros* nov. gen. nov. sp. (Ruminantia, Giraffidae) from the Miocene of northern Pakistan

María Ríos, Sayyed Ghyour Abbas, Muhammad Akbar Khan, and Nikos Solounias

ABSTRACT

We report new cranial, dental, and postcranial remains of a new early giraffid from the Middle Miocene of Pakistan: *Bramiscus micros* nov. gen. nov. sp. (Ruminantia, Giraffidae). The material comes from the fossil site Dhok Bun Amir Khatoon (Chinji Formation 14-11.4 Ma, Lower Siwaliks), located in the Chakwal district (Punjab, Pakistan). Additional remains were identified from the Hasvard Siwaliks Collection. The new findings show fused anterior ossicones, as in *Bramatherium*. The metatarsals possess a strong medial ridge and a weak lateral ridge, a feature encountered only in *Bramatherium perimense*. The size of our taxon is smaller than *Bramatherium*, hence the name. *Bramiscus micros* nov. gen. nov. sp. coexisted at the same time with other giraffids, such as *Progiraffa exigua, Giraffokeryx punjabiensis, Giraffa priscilla, Giraffa punjabiensis,* and other still unnamed taxa.

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Keywords: new species, new genus, Vertebrate; Mammalia; Giraffidae; Chinji; Miocene; Siwaliks

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INTRODUCTION

Early Miocene Giraffidae are less diverse and abundant than during the later Miocene, with most of the evidence coming from the Chinji Formation of Pakistan (Ullah et al., 2006; Khan et al., 2009, 2013; Aftab et al., 2013; Mahmood et al., 2015). There are also giraffid fossils from Kalodirr, Loperot, and Moruorot Hill at the Lothidok Formation of West Turkana (Kenya), as well as Rusinga Island at the Hiwegi Formation (Kenya), and from Gebel Zelten (Libya) (Churcher, 1970; Hamilton, 1973, 1978; Grossman and Solounias, 2014). The only known Early Miocene genera are *"Progiraffa"* and *Canthumeryx*. By the Middle Miocene, there are several additional species (e.g., *Giraffokeryx*, *Giraffa*) and an adaptive radiation had occurred (Solounias, 2007), with several more giraffid taxa appearing in the Chinji Formation (Pakistan), in Fort Ternan (Kenya), as well as in Chios, Greece (Paraskevaidis, 1940; de Bonis et al., 1997) and more occurrences from Africa and Middle East (Harris et al., 2010). In the upper Chinji and younger Siwaliks there is an increase in species diversity with the appearance of large sivatherine giraffids *Bramatherium, Libytherium,* and *Sivatherium* (Aftab et al., 2016; Ríos et al., 2019, 2022a). Research on these occurrences is presented in an extensive number of studies, such as Lydekker (1883), Pilgrim (1911), Paraskevaidis (1940), Churcher (1970), Hamilton (1973, 1978), de Bonis et al. (1997), Barry et al. (2005), Geraads and Aslan (2003), Solounias (2007), and Aftab et al. (2016).

The present article deals with the description of a new genus and species from the Middle Miocene of the Chinji Formation. The holotype is a

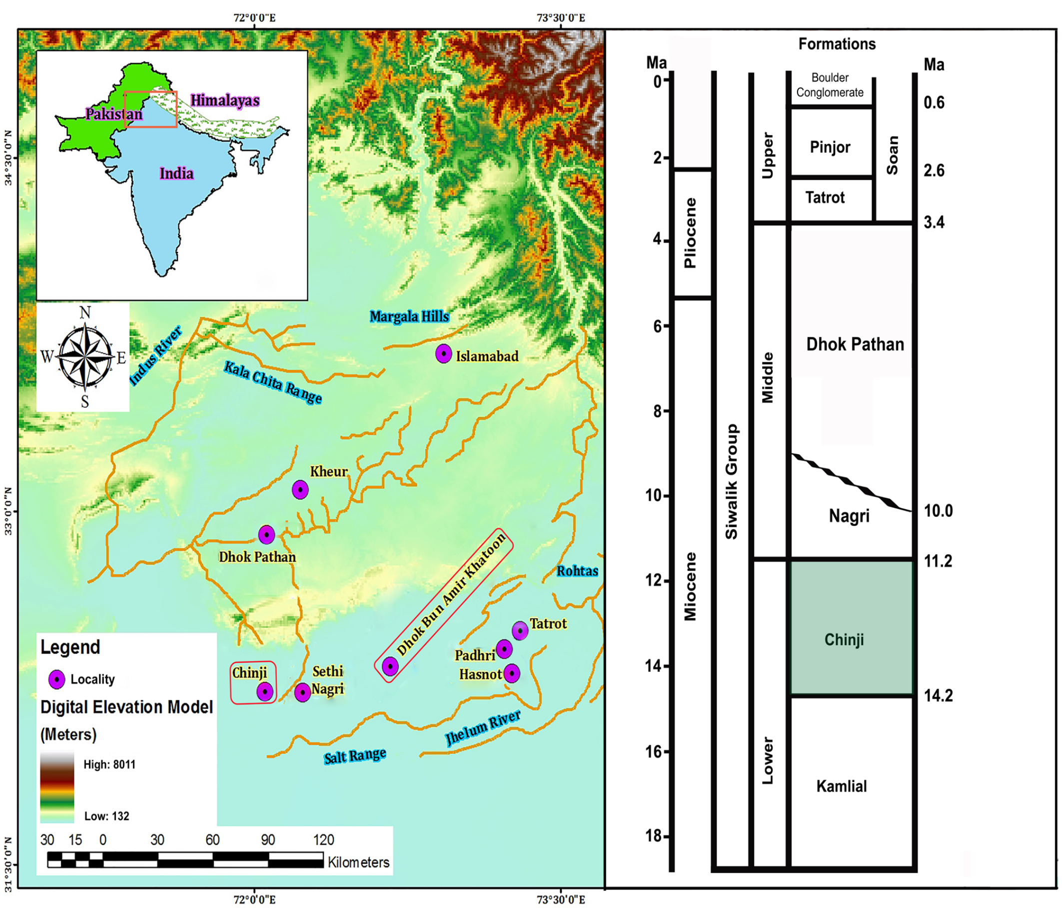

FIGURE 1. Left: Geographic location of the Potwar Plateau in northern Pakistan. (Purple circle indicates location of the localities discussed). **Right:** Chronostratigraphic context of the Siwaliks Neogene-Quaternary deposits showing the distribution of Siwalik *Bramiscus micros* nov. gen. nov. sp. (Range of the taxon in light blue).

frontal bearing two anterior ossicones. It comes from the site of Dhok Bun Amir Khatoon, which contains the well exposed Chinji Formation deposits and is in the Chakwal district (Punjab, Pakistan) (Figure 1). The site has yielded two frontals and isolated teeth, as well as posterior ossicones. Additional metapodials were collected during the Harvard-GSP expeditions. The age of the fossil site is 14-11.4 Ma, while the metatarsal Y-GSP-14999 is of later age (9.286-9.265 Ma).

Geological Setting

The Siwalik Group contains a rich vertebrate fossil succession (Lydekker, 1883; Colbert, 1935; Barry et al., 2002; Nanda, 2002; Khan et al., 2009, 2010; Aftab et al., 2016) and is stratigraphically divided into the Lower, Middle, and Upper Siwalik subgroups (Barry et al., 2002). The Lower Siwalik Subgroup (Kamlial and Chinji formations) corresponds with the Astaracian and Vallesian mammall ages (18-11.4 Ma) (Barry et al., 2013).

The Dhok Bun Amir Khatoon outcrops represent fluvial deposits of the Chinji Formation (Lower Siwaliks). They are situated 52.48 km East from the Chinji stratotype (Chakwal district, Pakistan, Figure 1) (Aftab et al., 2016). The geographical coordinates of the site are Lat. 32°47'N, Long. 72°55'E. The outcrops comprise shales, silt/mudstones, and sandstones deposited in a fluvial environment, mainly filled by unweathered igneous minerals. The shale and silts/mudstones are brick red, a characteristic of the Chinji Formation at the type section. The silts/mudstones comprise about 70% of the outcrop, while the sandstone only represents about 30%. The sandstone is dull to bright gray, and mostly present as grit. At certain places bright or brick red colored conglomerates and breccia are interbedded between the silt/mud layers. This lithology corresponds to the Chinji type section. In the Chinji Rest House area, conglomerates are thicker than the well-exposed sediments at Dhok Bun Amir Khatoon. Based on lithological and biostratigraphic data (see Johnson et al., 1985; Cheema et al., 1997; Cheema, 2003; Khan et al., 2008, 2009, 2013, 2017), the fossil bearing section of the site has been dated as Middle Miocene-early Late Miocene. The biostratigraphic range of the included faunal assemblage suggests an age between 14 and 11.4 Ma (Cheema, 2003; Khan et al., 2008, 2011, 2013, 2017; Barry et al., 2013).

This paper also includes a unique metatarsal described from the later Dhok Pathan Formation (Upper Miocene). The type section of the Dhok Pathan Formation is present around the Dhok Pathan Rest House, near the Dhok Pathan village at the bank of Soan River, Chakwal, Pakistan (Pilgrim, 1911; Pilbeam et al., 1977, 1980). Like the Chinji stratotype, Dhok Pathan stratotype is also over 10 km long (Pilgrim, 1911). This formation is characterized by the cyclic deposition of the varied colored sandstone and light-yellow clay and between these two strata, conglomerate is sandwiched or lenses out (Pilgrim, 1911; Barry et al., 2002, 2013). The Dhok Pathan Formation determined age is 9.8 to ca. 3.5 Ma (Barry et al., 2013).

Institutional/Technical Abbreviations

AMNH: American Museum of Natural History (New York, USA)
GSI-B: Geological Survey of India – Brown Collection
GSP-H: Geological Survey of Pakistan – Howard University Project
GSP-Y, Y-GSP: Geological Survey of Pakistan - Harvard University Project
GSP-S: Geological Survey of Pakistan – Sind collection
PUPC: Punjab University Palaeontological Collection, Lahore, Pakistan
PU: Punjab University, Lahore, Pakistan

MATERIALS AND METHODS

Materials

The material comprises 13 specimens including the frontals with ossicones, isolated ossicones, isolated upper and lower premolars and molars, and a mandibular fragment. Y-GSP material is of known age (Johnson et al., 1985, 1988; McRae, 1990; Badgley et al., 1998).

Repository

The specimens are stored at the Dr. Abu Bakr Fossil Display and Research Centre, University of the Punjab, Lahore, Pakistan (PUPC IDs) and Harvard Peabody Museum, USA (Y-GSP IDs). The material of the new species is also represented in the Harvard-GSP project (Y-GSP) collections and belongs to the Geological Survey of Pakistan. While the final deposition of the fossils is uncertain, they currently are all at Harvard Peabody Museum in the Department of Human Evolutionary Biology's Paleoanthropology Lab.

Methods

Measurements and terminology. We took all measurements with digital calipers. We follow the measurements and terminology proposed for rumi-

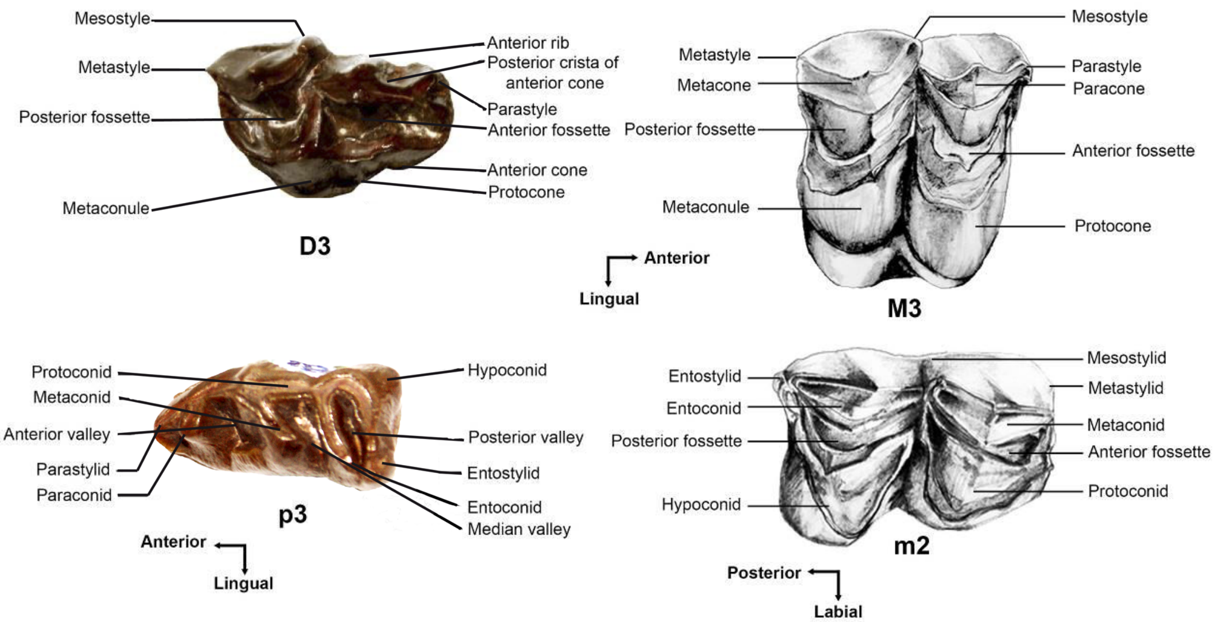

FIGURE 2. Terminology used in the text, based on Bärmann and Rössner (2011) and Hamilton (1978). **Upper left:** DP4; **upper right:** M3; **lower left:** p3; **lower right:** m2.

nants by Hamilton (1973) and by Bärmann and Rössner (2011) (Figure 2). The measurements used to compare the material were collected during visits to the American Museum of Natural History (New York, USA), the Institut Català de Paleontologia-Miquel Crusafont (Barcelona, Spain), the Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain), the Musèum National d'Histoire Naturelle (Paris, France), and the Natural History Museum (London, UK). The rest of the morphological and biometrical information in this paper was collected from several publications (Gaudry, 1861; Rodler and Weithofer, 1890; Pilgrim, 1911; de Mecquenem, 1924; Bohlin, 1926; Dietrich, 1937, 1942; Singer and Boné, 1960; Churcher, 1970, 1978; Hendey, 1970; Hamilton, 1973, 1978; Melentis, 1974; Heintz et al., 1981; Brunet and Heintz, 1983; Harris, 1976a, b, 1991; Kostopoulos et al., 1996; de Bonis et al., 1997; Geraads, 1994, 2009; Kostopoulos, 2009; Robinson, 2011).

Maximum parsimony analysis. We used the character list from Ríos et al. (2017) and included the *Bramiscus micros* nov. gen. nov. sp. data into their matrix. The data matrices including the new data are presented as supporting information (Appendix 1). We compiled the data matrices using Mesquite 3.04 (Windows version). We performed a Maximum Parsimony analysis to check the phylogenetic position of *Bramiscus micros* nov. gen. nov. sp. within the Giraffidae. The resulting dataset consists of 111 characters (cranial, dental, and postcranial), and 32 taxa. We used TNT v1.5-beta software (Goloboff et al., 2008) to analyze the dataset. All characters are non-additive and unweighted. We analyzed the trees using a Traditional Search method (heuristic algorithm) with Tree Bisection Reconnection (TBR) and 1000 replicates (holding the 10 most parsimonious trees for each replicate). We used the Bremer included in the script (BREMER.RUN) to assess branch support.

SYSTEMATIC PALAEONTOLOGY

Superfamily GIRAFFOIDEA Gray, 1821
Family GIRAFFIDAE Gray, 1821
Genus *BRAMISCUS* nov. gen.

zoobank.org/ECF5AE35-4F43-491F-8C9C-117AD2DAADCA

BRAMISCUS MICROS nov. sp.

zoobank.org/EBEC061A-707C-402E-A3C1-43EB04486CA5

Figures 3-5

Diagnosis. Small-sized giraffid with probably two pairs of ossicones. The ossicones of the anterior pair are fused at their base (*Bramatherium*-like). The posterior pair is straight and possibly directed laterally. All ossicones have an oval cross-section at the base and are vaguely circular at the apex. The ossicone surface is covered with longitudinal ridges of medium depth. The ridges or grooves are

FIGURE 3. PUPC 22/01, frontal and ossicones of *Bramiscus micros* nov. gen. nov. sp. from Dhok Bun Amir Khatoon (Middle Miocene, Potwar plateau, Pakistan): **A,** anterior view; **B,** posterior view; **C,** lateral right view; **D,** lateral left view; **E,** dorsal views. Scale bar equals 30 mm.

deeper and larger distally on the apical part and laterally than dorsally on the proximal part and medially. The dentition is brachydont and shows a rugose enamel. The upper molars have a post-metaconule fold and a labial cingulum, as well as a developed entostyle. The lower p2 has a crest on the anterior valley. The lower p3 has a well-developed paraconid and parastylid. The metaconid is narrower than the entoconid. The lower molars have a slightly rounded protoconid and hypoconid. Labially, they have rugose enamel and an anterolabial cingulum. A *Palaeomeryx* fold of the lower molars is absent (sensu Sánchez et al., 2011). The lower molars have a high L/W index of ~2. The metatarsal has a characteristic large medial ridge and a low lateral ridge.

Holotype. PUPC 22/01, fragment of frontal bone bearing a pair of ossicones with their fused bases (Figure 3).

Paratype. PUPC 13/375, pair of ossicones with their fused bases (Figure 4).

Etymology. *Bramiscus* refers to the morphological similarities between the ossicones of *Bramiscus* and *Bramatherium*, and means small *Bramatherium: -iscus* means very small in Greek. *Micros* also means small.

Geographic distribution and age. Chinji Formation (14 Ma, Astaracian) to Dhok Pathan Formation (9.265 Ma, Vallesian), Lower to Middle Siwaliks, Punjab, Pakistan.

Anatomical Description

Ossicones. PUPC 22/01 is a fragment of an ossicone-bearing frontal bone fragment (Figure 3). The right ossicone is complete while the left is broken in the middle. Both ossicones are fused at the base like in the paratype PUPC 13/375 (Figure 4). The maximum preserved length of the ossicone fused bases is 127.90 mm and that of width is 92.95 mm. The fused bases form a convex structure anteriorly and mostly flat but a bit concave posteriorly. The ossicones are tilting laterally, hence they form a V-shape in rostral view. Their fused bases form an

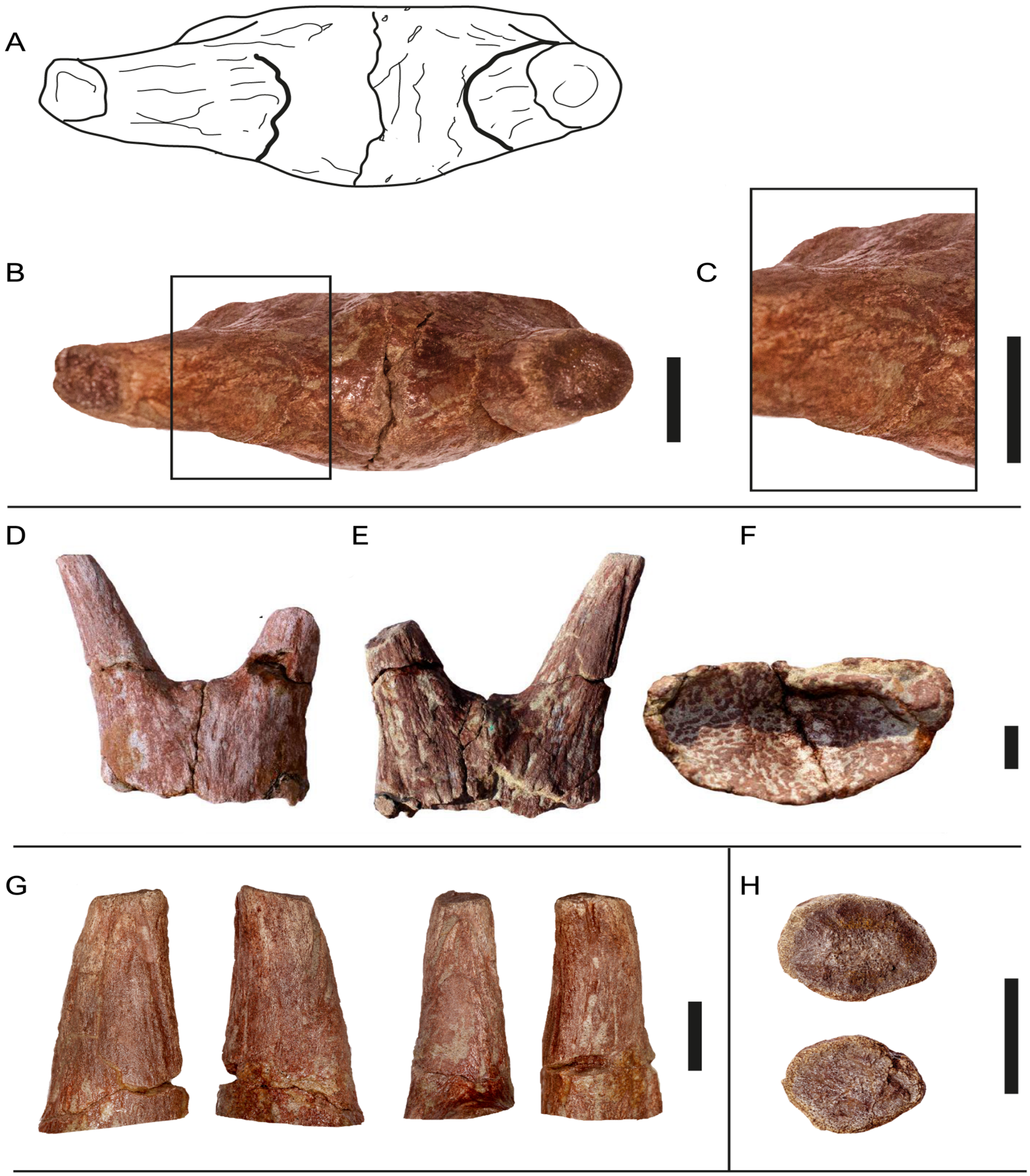

FIGURE 4. PUPC13/375, frontal and ossicones of *Bramiscus micros* nov. gen. nov. sp. from Dhok Bun Amir Khatoon (Middle Miocene, Potwar Plateau, Pakistan): **A-C,** dorsal view, 1) schematic drawing representing the main features referred in the text, **B-C,** detail; **D,** anterior view; **E,** posterior view; **F,** distal view; **G,** ossicone in anterior, posterior, medial and lateral views; **H,** cross section of the ossicones near the apex in dorsal view. Scale bars equal 30 mm.

angle of approximately 110º with each other. They both have deep grooves running over the surface, but the lateral groove is extremely deep. The ossicones are straight with a slight twist that can be seen from the running grooves as well. As the ossicones move in opposite directions from their base to their apex, and away from the sagittal plane of the frontal, they create an outward orientation. Small bumps are present over the surface of the ossicones, especially the right one. The cross sec-

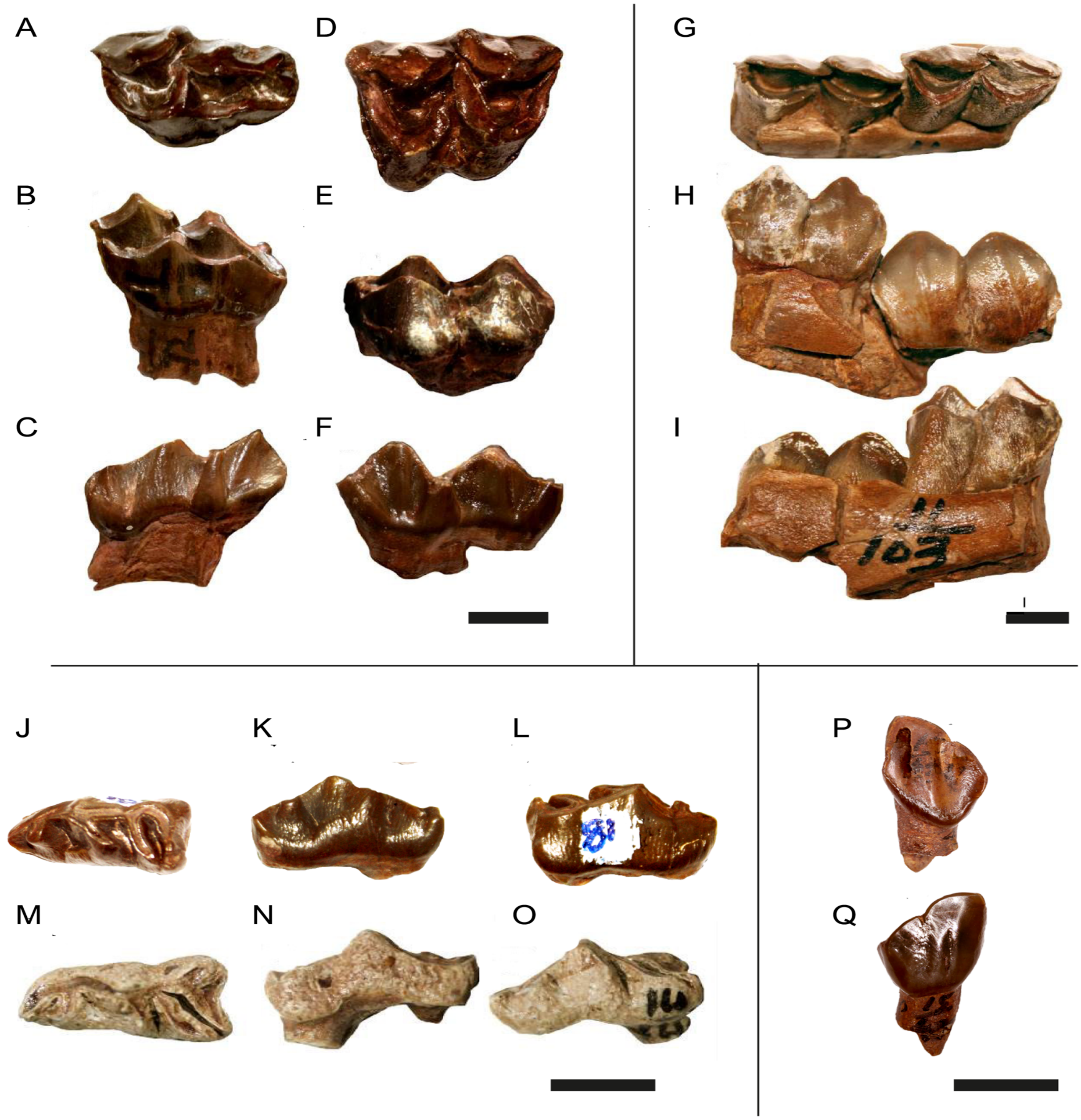

FIGURE 5. Dental remains of *Bramiscus micros* nov. gen. nov. sp. from Dhok Bun Amir Khatoon (Middle Miocene, Potwar plateau, Pakistan): **A-C,** right D3 PUPC 11/72 in **A**) occlusal, **B**) lingual, **C**) labial views; **D-F,** right M1 PUPC 11/70 in **D**) occlusal, **E**) lingual, **F**) labial views; **G-I,** right mandible fragment with m1-2 PUPC 11/103 in **G**) occlusal, **H**) lingual, **I**) labial views; **J-L,** left p2 PUPC 14/142 in **J**) occlusal, **K**) labial, **L**) lingual views; **M-O,** left p3 PUPC 14/143 in **M**) occlusal, **N**) labial, **O**) lingual views; **P-Q,** right canine PUPC 11/31 in **P**) lingual, **Q**) labial views. Scale bar equals 10 mm.

tion at the free distal base is oval, gradually becoming circular towards the apex, and the anteroposterior and transversal diameters (DAP and DT) of the ossicones also decrease towards the apex. There is no hint of a suture line, probably indicating that the individual was fully adult. Small bumps on the ossicones indicate that they belong to an older individual as it has been commonly observed in many giraffid genera including *Palaeomeryx, Schansitherium, Decennatheirum,* and *Giraffa,* where the number of bumps increase with age, and are only found in adult individuals (Ríos and Solounias, 2019, Ríos et al., 2022b).

PUPC 13/375 bears two ossicones (Figure 4) that are fused at their base. The fusion forms a long plate of bone. From a proximal view the portion of the ossicones bases has an irregular surface. It is divided into three areas with two lateral triangular concave areas and a deeper middle section. The estimated preserved length of the ossicones is 175 mm from the base of the skull. The ossicones form an angle with the skull fragment of approximately 90º (practically straight angle). The ossicones are straight. The section at the ossicone base is oval (Figure 4H), with the long axis of the oval oriented approximately 34º outwards from the sagittal plane of the fragment. The section becomes slightly semicircular towards the apex of the ossicone, with a flattened anteromedial side. The ossicones narrow gradually towards the apex. The surface of the ossicone is rugose, ornamented with longitudinal grooves that run along all the surface of the ossicone, with the lateral groove being also deeper than the rest.

Although a complete cranium has not been found, there is a high possibility that the isolated ossicones found at the site belong to the same taxon as they share a similar proportions and morphology. The isolated ossicones found at Dhok Bun Amir Khatoon (Figure 4G) resemble the morphology of the posterior ossicones of *Bramatherium*, and as the anterior ossicones also resemble *Bramatherium*, we conclude that there is a high probability that these specimens represent the broken-off posterior ossicones belonging to the frontals found at the same site. However, it is important to note that there is no direct evidence to support this claim. While the new taxon may have similar anterior ossicones, it cannot be assumed that it had the exact same posterior ossicone morphology. However, being similar in size, the presumed posterior ossicones are also described here. They are straight and contain compact bone as in *Bramatherium*. The surface is smooth. and they contain two canals separated internally by a thin plate of bone. One canal is bigger than the other. The ossicones terminate in a small knob.

Upper dentition. The available specimens are all isolated teeth. The DP3 (Figure 5A-C) is bilobed, slightly molarized, and longer than wide. In occlusal view the anterior lobe is longer and semicircular, and the posterior lobe is shorter, wider, and triangular in shape. The enamel is smooth and shiny lingually and more rugose labially. The parastyle, mesostyle, and metastyle are thick basally but narrow towards the apices. Labially, the stylids are strong. The paracone and metacone are strongly developed. Lingually, strong cingulum is present at the base of the protocone whereas a weak cingulum is present posteriorly. The posterior fossette is triangular. A shallow median valley is present. The postprotocrista reaches the premetaconulecrista. The premetaconulecrista is prominent.

The M1 (Figure 5D-F) has a labial wall with stronger parastyle and mesostyle and a slightly weaker metastyle. The paracone and metacone are very strong. Lingually, the protocone and metaconule are V-shaped, with the posterior lobe slightly buccolingually wider than the anterior one. The anterior fossette is semicircular whereas the posterior fossette is crescent shaped. The transverse valley represents a weak entostyle. The preprotocrista is more elongated than the postprotocrista. The enamel is rugose and there is a lingual cingulum.

Lower dentition. The available specimens consist of a canine, isolated premolars, and a mandible fragment with well-preserved m1 and m2. The canine (Figure 5P-Q) has a pointy larger anterior lobe while the smaller posterior lobe is rounded and represents 45% of the total width of the tooth.

The p2, is a simple tooth, elongated and with a slightly pointed protoconid. The metaconid and the entoconid are separated. The anterior lingual valley is wider than the posterior one and there is a crest in it (Figure 5J-L).

The p3 (Figure 5.M-O) shows a well-developed paraconid and parastylid. The paraconid is well distinguished from the parastylid and compressed laterally. The metaconid is posteriorly oriented and is separated from the entoconid, which is also posteriorly projected. The postparacristid is wider than the extremely thin preparacristid and they are oriented lingually. The metaconid is strong and coniform. The hypoconid is prominent.

The lower molars (Figure 5J-L) are brachydont with sharp and pointed conids. They have a lingual wall with prominent entostylid, mesostylid, and metastylid. The stylids are broader at the base and gradually narrow towards the tip. Labially, there is a short and robust ectostylid. The anteroposterior cingulum is present. The *Palaeomeryx*-fold is absent (Sánchez et al., 2010). The fossettes are crescent shaped and only slightly pointed.

Metatarsal. Y-GSP-14999 is a well-preserved right proximal metatarsal (Figure 6). In proximal view there is an asymmetry between the lateral and the medial profiles. The kidney-shaped articulation facet for the ectomesocuneiform is similar in size to the semicircular navicular-cuboid facet. The ento-

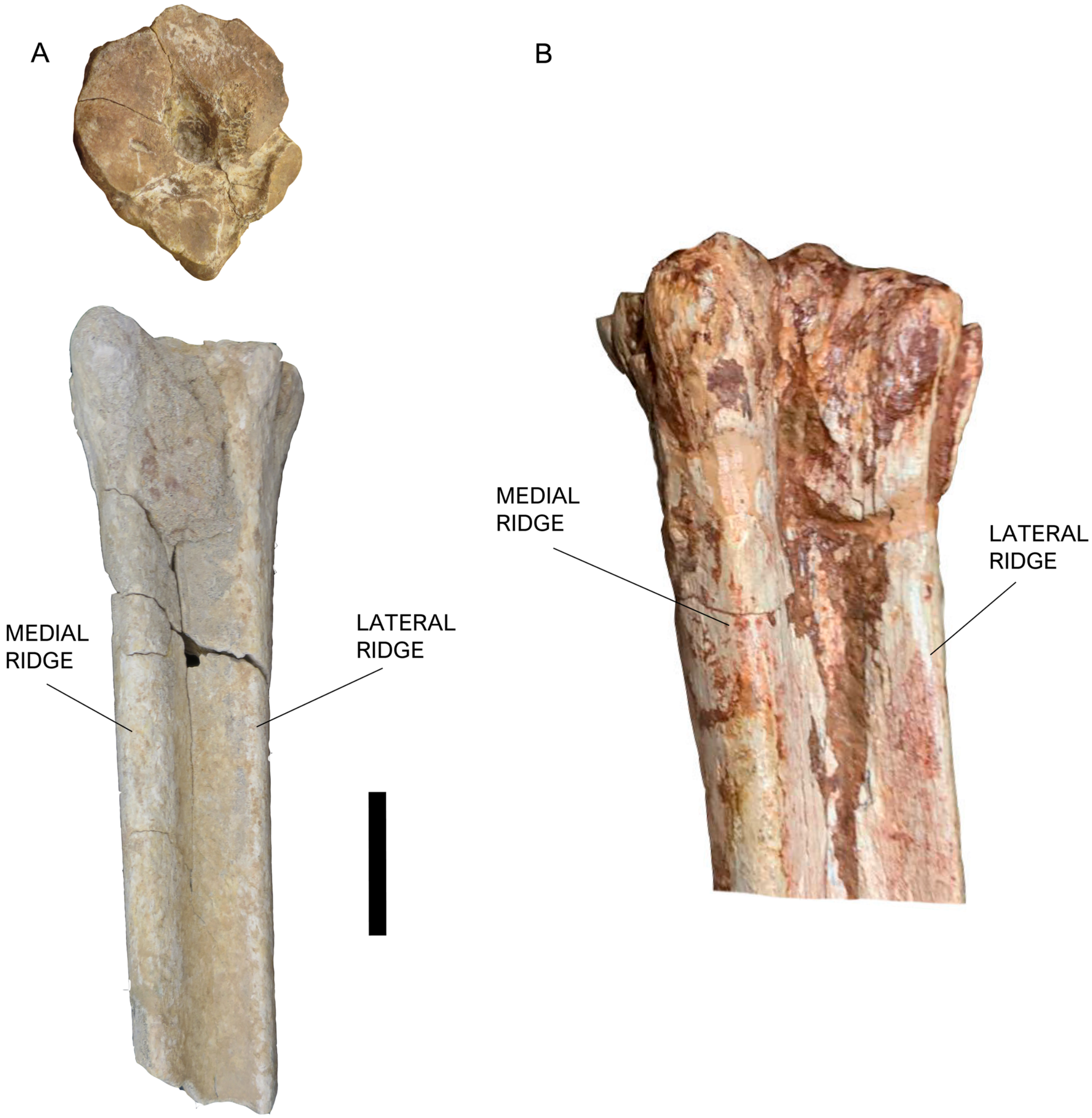

FIGURE 6. Right metatarsals showing the plantar similarities. **A,** *Bramiscus micros* nov. gen. nov. sp. (Y-GSP-14999) proximal and plantar views and, **B,** *Bramatherium megacephalum* from the Siwaliks of Pakistan (AMNH-19688). Scale bar equals 50 mm.

cuneiform facet is relatively large and subtriangular, and it does not contact the ectomesocuneiform facet. The synovial fossa is oval and deep. The medial epicondyle is large with a large plantar head, the distal aspect of which continues onto the medial ridge. The lateral epicondyle is split into a dorsal and plantar head by a deep longitudinal groove on the lateral shaft. The plantar head is continuous distally with the weak lateral ridge. Both heads of the lateral and medial epicondyles are oriented longitudinally, however the dorsal heads slightly flare outward. The medial ridge is high and rounded and the lateral ridge is sharp and thinner. The central trough is intermediate in depth, and it flattens distally. The most distinctive feature is the presence of an acute asymmetry in the medial and lateral diaphysis plantar ridges. Y-GSP-1196 shares the same morphology, with a high and wide medial ridge while the lateral is thinner and lower.

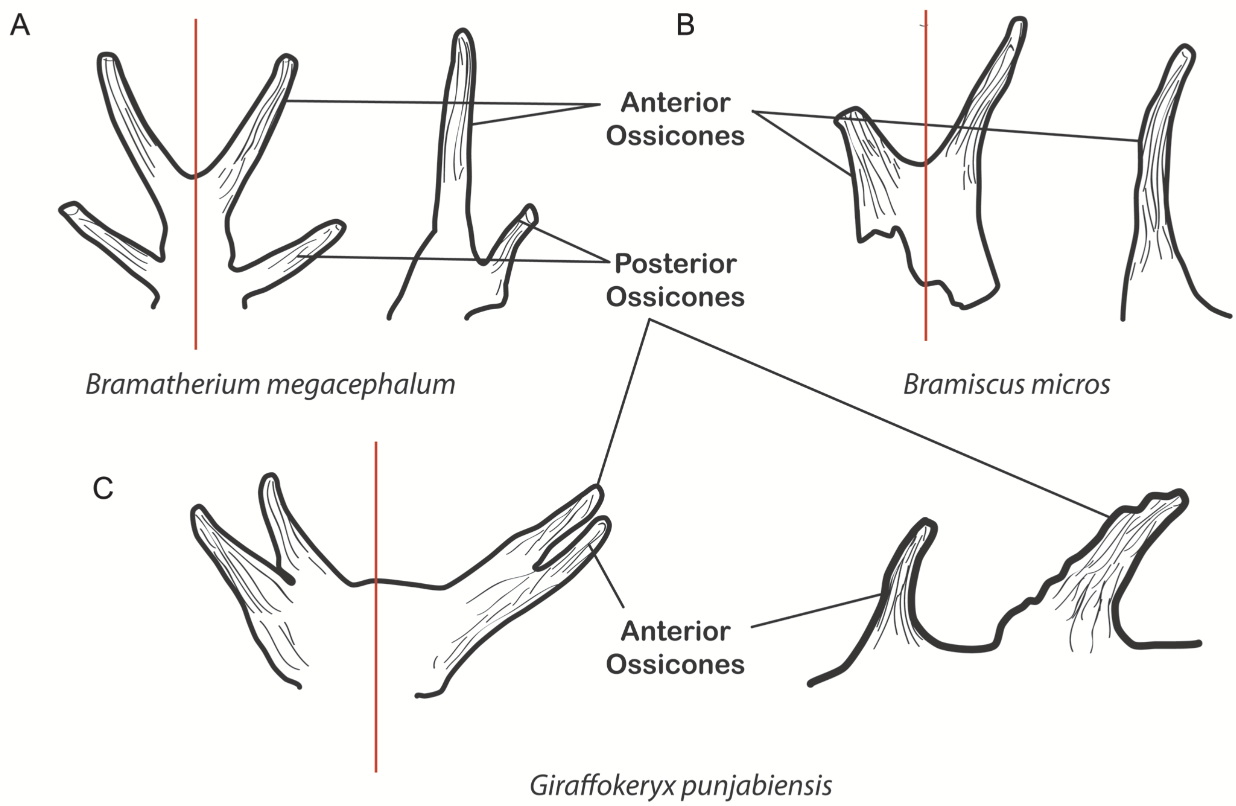

FIGURE 7. Ossicones of several giraffid taxa. **A,** *Bramiscus micros* nov. gen. nov. sp. (Y-GSP-14999), **B,** *Bramatherium megacephalum* from the Siwaliks of Pakistan (AMNH-19688), **C,** G*iraffokeryx punjabiensis* from the Siwaliks of Pakistan (AMNH-19688). Images not to scale.

RESULTS

The morphology and proportions of the specimens from Dhok Bun Amir Khatoon (Chinji) analyzed in this article appear to indicate that they belong to a new Middle Miocene giraffid taxon: *Bramiscus micros* nov. gen. nov. sp.

Ossicones

Orientation and Curvature. The ossicones of PUPC 13/375 are only slightly, and moderately in PUPC 22/01, posterolaterally oriented, while the other early taxa as *Giraffokeryx, Canthumeryx, Injanatherium,* and *Georgiomeryx* have ossicones that are oriented more laterally, with a much higher divergence angle (Ríos et al., 2017). The ossicones of PUPC 13/375 and PUPC 22/01 show barely any curvature towards the apex, while this curvature is marked in *Giraffokeryx* (Colbert, 1933), and *Decennatherium asiaticum* (Ríos et al., 2019). Also, the ossicones of *Giraffokeryx* are directed laterally and not vertically as in *Bramiscus.* The long transverse axis of the ossicone is oriented approximately 34º outwards from the sagittal plane in *Bramiscus* while in *Giraffokeryx* the same angle is 52º (see Colbert, 1933) (Figure 7). Interestingly, the orientation and space between the ossicones of *Bramiscus* is like that found in *Bramatherium megacephalum*.

Ornamentation. The surface of the ossicone is rugose, but not as rugose as in *Giraffokeryx*, and *Decennatherium*, and not as smooth as in *Samotherium* (faint ridges) or *Palaeotragus* (no ridges). These ridges in PUPC 13/375 and PUPC 22/01 are deeper and larger on the distal and lateral sides as in *Bramatherium*.

Size. The estimated length of the anterior ossicones from the base of the skull is small, being similar in length to some *Giraffa* specimens, although both show significant morphological differences, e.g., *Giraffa* demonstrates greater girth than *Bramiscus* (Solounias, 2007). They are similar in size to the anterior ossicones of *Giraffokeryx*. The dimensions of the ossicones of PUPC 13/375 and PUPC 22/01 also exclude most giraffids that bear larger ossicones as *Decennatherium, Birgerbohlinia, Bramatherium,* and *Sivatherium* as this reaches lengths of 5x the length of *Bramiscus*

(Ríos et al., 2017). They are also very different in size and morphology when compared to the bovid horns with marked keels found in the same locality.

Morphology of the ossicone bases. The bases of the ossicones in PUPC 13/375 and PUPC 22/01 are fused forming a structure that connects the ossicones with the frontal. This creates a space between the skull and the flaring part of the ossicones. Such a condition is found in two giraffid genera where the bases of the ossicones are fused, *Bramatherium*, and *Giraffokeryx*; one palaeomerycid, *Prolibytherium*; and three bovid genera, *Tsaidamotherium, Plesiaddax,* and *Urmiatherium* (Falconer, 1845; Bettington, 1846; Rodler, 1889; Colbert, 1933; Bohlin, 1935; Lewis, 1939; Kostopoulos, 2009; Jafarzadeh et al., 2012; Shi et al., 2016). However, only *Bramatherium* has a large structure formed by fused bases, whereas in *Giraffokeryx* only a small portion is formed by the fusion of the ossicone bases and the space between the ossicones and frontal is very small (Figure 7). *Prolibytherium* also shows the fused ossicone bases, but these bases are very close, even merging, with the frontal bone. The bovid genera also show a partial fusion of horn core bases, but it is not as great as *Bramatherium* or *Bramiscus*.

To summarize, the anterior ossicones of *Bramiscus* narrow gradually towards the apex and have the same "V" shape as the ossicones of *Bramatherium megacephalum* (e.g., YPM-13881) and *Bramatherium perimense.* The ossicones are fused at their base similarly to the figured anterior ossicones of *B. megacephalum* (Lewis, 1939: plate 2, YPM-13881), and *B. perimense* (AMNH-27016; Falconer, 1845; Bettington, 1846: plate 1 MRCS 1436 and NMHUK 20009 cast; Colbert, 1935, fig. 174, AMNH 19771; Lydekker, 1876, plate 7, fig. 13, AMNH-27016). The possible posterior ossicones of *Bramiscus* are straight as the posterior ossicones of *Bramatherium perimense* AMNH 19688. The posterior ossicones of *B. megacephalum* also share with *Bramiscus* the presence of two internal canals.

Dentition

Differences with primitive Giraffomorpha. Our specimens also differ from other primitive Giraffomorpha such as *Propalaeoryx, Climacoceras, Prolibytherium* and *Nyanzameryx* by the presence of a more prominent and well-separated metastylid in the p3 (Sánchez et al., 2010). *Climacoceras* has narrower upper molars and in *Nyanzameryx* and *Prolibytherium* the lingual conids are compressed and the lingual wall of the hypoconulid is incomplete in the m3 (Barry et al., 2005).

Due to the high morphological stability in the Giraffidae (Hamilton, 1978; Solounias, 2007) the dentition of *Bramiscus micros* nov. gen. nov. sp. differs little in morphology and size to the dentition of other early giraffids, such as *"Progiraffa exigua", Canthumeryx sirtensis,* or *Giraffokeryx punjabiensis*, as they sport small, simple teeth. Despite this, there are some morphological differences, especially regarding the p3, which is one of the most diagnostic teeth in giraffids (Hamilton, 1978; Ríos et al., 2016a, 2017).

p3. Regarding the p3 Length/Width index (L/W index), the remains from Dhok Bun Amir Khatoon show average values of 2.06 (N=3), with a minimum value of 1.86 and a maximum of 2.37. These are very close to the average values of most of the other Early and Middle Miocene giraffids *"Progiraffa exigua", Canthumeryx sirtensis,* and *Georgiomeryx georgalasi* and higher than other early giraffids such as *Injanatherium arabicum*, which never reaches a L/W value higher than 1.74. Crown giraffids from the late Miocene and the Plio-Pleistocene show lower L/W index values (Ríos et al., 2017).

Morphologically, the p3 PUPC 14/143 is like *"Progiraffa exigua*" specimen S 412 from Locality S 2 at the Zinda Pir Dome (upper unit of the Chitarwata Formation and the overlying Vihowa Formation, 20 to 17 Ma, Pakistan, Barry et al., 2005: fig. 9:1; Lindsay et al., 2005), although in S 412, the metaconid, entoconid, and posterior stylid are more parallel. The *"Progiraffa exigua"* specimen Y 31797 (Barry et al., 2005: fig. 9:2) from the Locality Y 747 (base of the Potwar sequence, ca. 18.3, Pakistan) is smaller and does not have a developed posterolabial lobe. However, is important to recall that the basicranium ascribed to *"Progiraffa exigua"* by Barry et al. (2005), was later used to establish the new taxon *Prolibytherium fusus* (Danowitz et al., 2016) so the teeth taken as *"Progiraffa"* by Barry et al. (2005) may belong to *Prolibytherium fusus* as well, although this needs further analysis. The premolars ascribed by Aftab et al. (2016) to *"Progiraffa exigua"* are also questionable, and they come from the same formation as the cranial appendages of *Bramiscus*. The original *"Progiraffa exigua"* material is older, as it comes from the earlier Kamlial Formation (ca 18.3–14.2 Ma). *Canthumeryx sirtensis* has a less developed entoconid on the p3, and *Giraffokeryx punjabiensis* has a p3 with a more developed metaconid that projects posteriorly and an entoconid that reaches the lin-

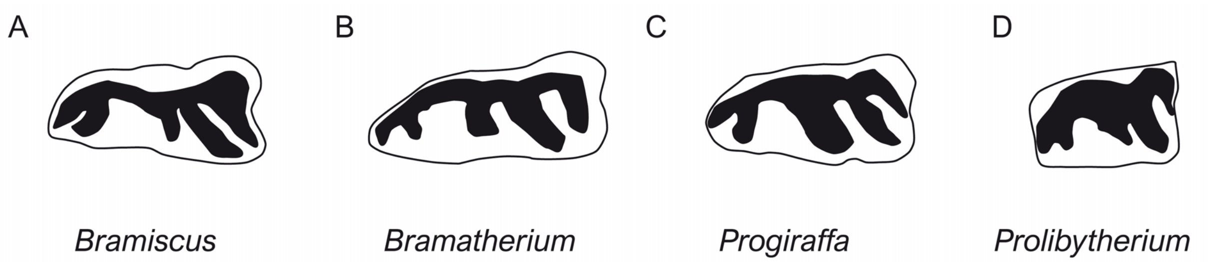

FIGURE 8. Dental remains of several giraffid taxa. **A,** *Bramiscus micros* nov. gen. nov. sp. (Y-GSP-14999) and, **B,** *Bramatherium megacephalum* from the Siwaliks of Pakistan (AMNH-19688), **C,** *"Progiraffa exigua"* from the Siwaliks of Pakistan (AMNH-19688). Images not to scale.

gual side of the tooth (Figure 8, Hamilton, 1978). *Georgiomeryx georgalasi* from the early Middle Miocene of Thymiana (Greece) (de Bonis et al., 1997). This species shares similar size and proportions with *Bramiscus* specimens, particularly PUPC 11/141. However, it can be distinguished by the absence of the metaconid and a less parallel entoconid and entostylid.

The p3 of *Bramatherium* is much larger and has a lower L/W index but retains an almost identical morphology otherwise.

Lower molars. Concerning the lower molars, they are simple and small, like those of "*Progiraffa exigua*" (Barry et al., 2005: fig. 10:1-5), but in *P. exigua* the m1, m2, and m3 anterior and posterior lobes are labially more pointed and with a more acute V-shape (Figure 5). They are also smaller in size and differ in their L/W Index as *"P. exigua"* has a much lower index than *Bramiscus* specimen PUPC 11/102 (m1: 1.66 vs 2.04; m2: 1.51 vs. 2.00; Pilgrim, 1911; Barry et al., 2005).

The lower molars of *Canthumeryx sirtensis, Georgiomeryx georgalasi, Injanatherium arabicum, Giraffokeryx primaevus,* and *Giraffokeryx punjabiensis* and the late Miocene *Palaeotragus rouenii*, have a similar size but are slightly larger and have lower L/W values than the new specimens from Dhok Bun Amir Khatoon. The other late Miocene and Plio-Pleistocene giraffids all have much larger lengths.

Giraffa priscilla, another one of the middle Miocene giraffid found in the area (based on a single tooth), shows more brachydont teeth and differs also in several upper molar characters (e.g., plus upper molars with lower L/W index values, smaller anterior and posterior fossettes and a rounder metaconule and protocone) (Matthew, 1929; Bhatti et al., 2012; Aftab et al., 2013, 2016).

Metatarsals. As mentioned above, the most distinctive feature is the presence of a very particular and acute asymmetry in the medial and lateral diaphysis ridges, only seen so far in *Bramatherium* (Ríos et al., 2016). Y-GSP-14999 has a high and wide medial ridge while the lateral is thinner and lower. The same is true for *Bramatherium perimense* AMNH 19688 (Figure 6). However, *Bramatherium* has longer and less gracile metapodials (Ríos et al., 2016). In *Giraffokeryx*, the metatarsal (unpublished data) has two ridges that are of equal development, while *Giraffa* has very elongated metapodials, which exclude them as possible matches for these specimens.

Results of the phylogenetic analysis. Our data matrix (Appendix 1) includes 32 taxa and 111 characters (cranial, dental, mandibular, and postcranial). The Maximum Parsimony (MP) search produced three Most Parsimonious Trees (MPT), which resulted in a consensus tree (Strict, Nielsen) of 277 steps (Figure 9) and recovered a monophyletic Giraffidae (node A). The most basal off-shoot is the stratigraphically older *Canthumeryx sirtensis,* followed by *Bramiscus micros* and *Georgiomeryx georgalasi* (node B). The remaining taxa (node C) are grouped into two clades: a group including *Injanatherium hazimi, Injanatherium arabicum, Giraffokeryx punjabiensis,* and *Giraffokeryx primaevus* (node D), and the large group of younger giraffids (node E). Our resulting MPT matches the results of Ríos et al. (2017).

DISCUSSION

The ossicones found from Dhok Bun Amir Khatoon (Pakistan) and Chinji are the first ones recovered with this morphology. The recently identified species is smaller in size, yet it shares similarities with *Bramatherium* in terms of its cranial appendage's distinctive V-shaped morphology. Additionally, it exhibits a notable and sharp asymmetry in the medial and lateral diaphysis ridges of its metatarsals, akin to that observed in *Bramathe-*

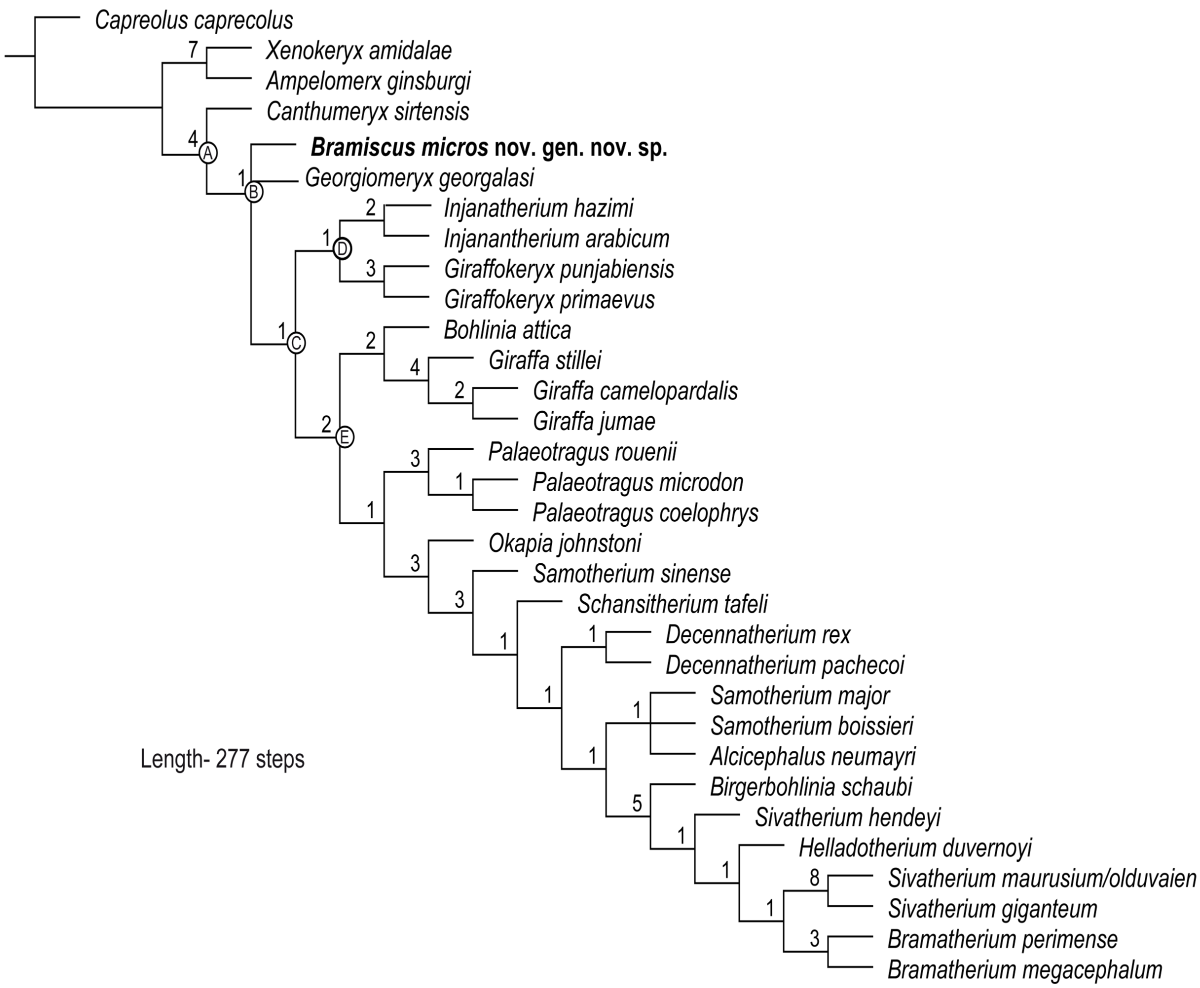

FIGURE 9. Most Parsimonious Tree (MPT) including *Bramiscus micros* nov. gen. nov. sp. MPT of 277 steps. Bremer values are present over each node.

rium. Therefore, and despite *Bramiscus micros* nov. gen. nov. sp. pertaining to a much more basal clade of giraffids, we have named this new genus after *Bramatherium* because of the morphological similarity of its ossicones to those of the younger and larger *Bramatherium* species also found in Pakistan. The anterior ossicones are shaped and fused in a similar way. Due to the age of the material, as well as the presence of bumps in the ossicones, a feature related to ontogenetic development in certain giraffids and only found in adult individuals (Ríos et al., 2020) we don't think that the frontals with ossicones belong to a young *Bramatherium*.

We acknowledge the similarities with *Bramatherium*, and that the trichotomy in our cladogram is potentially an issue of missing data. However, the estimated length of the anterior ossicones from the base of the skull is significantly smaller in *Bramiscus*. Additionally, the p3 of *Bramatherium* is much larger and has a lower L/W index than *Bramiscus*, and *Bramatherium* has longer and less gracile metapodials than *Bramiscus*, which all together grants a generic difference.

Bramiscus micros nov. gen. nov. sp., had most likely two pairs of ossicones that differ from other Early and Middle Miocene giraffids and giraffomorphs ossicones in size, orientation, and ornamentation. *Giraffokeryx punjabiensis* shares with PUPC 13/375 and PUPC 22/01, an ossicone surface ornamented with longitudinal ridges and an oval section of posterior pair (Colbert, 1935). PUPC 13/375 are also similar in size to the anterior ossicones of the adult *Giraffokeryx punjabiensis* skull AMNH-19475, but PUPC 13/375 and PUPC 22/01 ossicones otherwise differ from those of *G. punjabiensis* in several features, such as the size of the bases, the inclination, and the curvature, as they are less curved and inclined and are not so laterally projected. In addition, PUPC 13/375 and PUPC 22/01 ossicones show less shallow longitudinal grooves (see Ríos et al., 2017, figures 3-4).

The ossicones of PUPC 13/375 and PUPC 22/01 also differ from the ossicones of the other most basal giraffids recovered in our MPT, *Canthumeryx sirtensis, Georgiomeryx georgalasi, Injanatherium arabicum,* and *Injanatherium hazimi* (Heintz et al., 1981; Churcher, 1990; de Bonis et al., 1997, and literature within), which have a much more horizontal insertion to the skull.

There are no known *"Progiraffa exigua"* ossicones yet. In fact, the description of the species *P. exigua* was based only on non-very diagnostic lower molars from the Upper Nari beds (now the Chitarwata Formation of Dako Nala in the Bugti Hills of Baluchistan, Pakistan), and therefore we suggest it to be considered a nomem nudum or to be used very cautiously (Pilgrim, 1908). The basicranium ascribed to *"Progiraffa exigua"* by Barry et al. (2005) (see Barry et al., 2005: figure 13), was later used to establish the new taxon *Prolibytherium fusus* (Danowitz et al., 2016).

The ossicones of PUPC 13/375 and PUPC 22/01 also differ from other early Giraffomorpha as they are much larger and lack the typical characteristics of the ossicones of those taxa. They lack the spikes of the horns of Climacoceratids, the disposition, and the fused and narrow base of *Prolibytherium* female appendages, and the morphology and number of palaeomerycid protuberances (Hamilton, 1973, 1978; Barry et al., 2005; Solounias, 2007; Sanchez et al., 2010, 2015). The frontal is small and has thin lateral walls as in the material of early giraffids from Gebel Zelten (Africa) and Wadi Moghara (Egypt) (Pickford et al., 2001).

Regarding the teeth attributed to *"Progiraffa exigua"* only the two lower molars identified by Pilgrim (1908) can definitively be linked to this taxon. However, these molars lack distinct characteristics and closely resemble the lower molars of other early giraffids. Consequently, the giraffid material from the Chinji formation, designated as *"P. exigua"* by Aftab et al. (2016), raises doubts about its attribution (refer to Aftab et al., 2016: fig. 3J-L, fig. 3M-O). It's worth noting that the specimens presented by Aftab et al. (2016) originate from the same formation as the cranial appendages of *Bramiscus* (rP2 PUPC 81/91, Ghungrila; lP3 PUPC 71/70, Rakh Wasnal). Furthermore, the original *"P. exigua"* material (consisting of two lower molars) is older, originating from the earlier Kamlial Formation (approximately 18.3-14.2 Ma). As a result, any comparisons of the premolars from Dhok Bun Amir Khatoon to "P. exigua" are based on material that is not contemporaneous with the holotype material of *"P. exigua."* Thus, in this study, these premolars are more appropriately tentatively assigned to *Bramiscus*, given that other giraffids from the same time period in the region, such as *Giraffokeryx* and *Giraffa*, exhibit distinct morphologies (see Results section).

Finally, the metatarsals Y-GSP-14999 and Y-GSP 1196 strike a high resemblance to those of *Bramatherium megacephalum* (e.g., AMNH 19688). The combination of a high and wide medial ridge and, especially, a small lateral ridge (within giraffids only *Bramatherium* has this feature) defines *Bramatherium* as unique and our species *Bramiscus* as similar to it in that aspect (Ríos et al., 2016b). So, this unites the two taxa as well as the ossicone morphology. However, it is important to note that *Bramatherium* comes from later deposits corresponding with the Late Miocene and *Bramiscus micros* nov. gen. nov. sp. metatarsals are somewhat older (Middle Miocene-Late Miocene Boundary, 11.827- 9.265 Ma). Our phylogenetic analysis suggests that further analysis of these similarities is warranted, as they belong to different offshoots of the giraffid tree based on our current data.

CONCLUSIONS

We describe a new giraffid genus and species: *Bramiscus micros* nov. gen. nov. sp. based on the ossicones and dentition recovered from the Middle Miocene of Dhok Bun Amir Khatoon (Pakistan, 14-11.4 Ma) and the Chinji stratotype and which are stored at the Dr. Abu Bakr Fossil Display & Research Centre, University of the Punjab (Lahore, Pakistan) and at the Harvard Museum (USA). These represent the earliest example of ossicones that arise from a fused base, like what is observed in the posterior ossicones of the later and much larger *Bramatherium megacephalum* However, according to the phylogenetic analysis, these two genera are placed in different offshoots of the giraffid tree and further analysis is required. The dental, cranial, and postcranial information provided by this new material helps us understand the early evolution of this enigmatic family and contribute to elucidating the true nature of giraffoid ossicones and provide evidence of epiphyseal ossicones in this taxon.

Bramiscus micros nov. gen. nov. sp. coexisted in the same area with *"Progiraffa exigua", Giraffokeryx punjabiensis,* and *Giraffa priscilla.* Finally, our material represents the earliest record of giraffids with true ossicones in the Indian subcontinent.

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APPENDIX 1.

Data matrix for the Giraffidae including *Btamiscus micros.* Based on Ríos et al. (2017). Character matrix of the analyzed taxa. xlsx, TNT versions. Appendix material available for download from https://palaeo-electronica.org/content/2024/5228-new-giraffid-genus.