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Barbourofelines from the Middle-Late Miocene of the Siwaliks, Pakistan

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MAK provided concept and designed the study. KM acquired, analyzed and interpreted the data. MAB and MA worked in photography and mapping. SGA drafted the manuscript.

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ABSTRACT

The family Nimravidae is poorly known from the Siwalik Group that comprises freshwater deposits having an age that spans 18.0-0.6 Ma. The new material recovered from the Dhok Ban Ameer Khatoon (Chinji Formation) and Sethi Nagri (type locality of the Nagri Formation) is assigned to *Sansanosmilus rhomboidalis* based on the morphology of canine. The recovered material is unique and rare in the Siwaliks of northern Pakistan. It also increases the stratigraphic range of this barbourofelines species from the Chinji Formation to the Nagri Formation.

INTRODUCTION

Nimravidae is a carnivoran family that was present during the middle to late Miocene deposits of Eurasia, Africa and America (Bryant, 1991). The family diversified substantially in the Miocene and became extinct near the Pliocene (Morlo, 2006), and most of the species are present in the subfamily Barbourofelinae. Barbourofelines are regarded within Nimravidae because both have reduced talonid basin and have tends to be slightly convex, giving the anterior cuspid a slightly inflated morphology of m1 (Wang *et al*., 2020). According to Barrett *et al*. (2021) the recovered phylogeny implies a migration of nimravine taxa into Africa at MN2, which gave rise to the earliest barbourofelins. The subfamily Barbourofelinae is represented by seven genera which are reported from the America, Kenya and Uganda, Namibia and Spain, Libya, Central Europe, Tunisia, and Eurasia and these include *Barbourofelis*, *Ginsburgsmilus*, *Afrosmilus*, *Syrtosmilus*, *Prosansanosmilus*, and *Sansanosmilus* (Schultz *et al*., 1970; Kurten, 1976; Ginsburg, 1978; Geraads and Gulec, 1997; Morlo *et al*., 2004, 2007; Morlo, 2006; Nagel *et al*., 2009; Werdelin and Peigne, 2010; Tseng *et al*., 2010; Robles *et al*., 2013). The remains of these barbourofeline genera are scarce (Robles *et al*., 2013) and every new specimen is extremely valuable. The Siwalik barbourofelines have not been entertained in detail after (Colbert, 1935) and in this regard, there is no detailed taxonomic, evolutionary, and paleobiogeographic study available. Not only the origin of the Siwalik barbourofelines is unknown but also that of the whole subfamily. It is probable that barbourofelines underwent an early radiation in the Early Miocene of Africa (Morales *et al*., 2001; Morlo *et al*., 2004), later dispersing into Eurasia during the late early Miocene. Barbourofelines are first recorded there by *Prosansanosmilus peregrinus* and *Afrosmilus hispanicus* in MN4 (Morales *et al*., 2001; Morlo *et al*., 2004), although *Prosansanosmilus eggeri* from MN5 of Europe is apparently more plesiomorphic (Morlo *et al*., 2004). Further, the question of whether *Sansanosmilus* descended from *P. eggeri* or represents another immigration of Barbourofelinae in MN6 cannot be answered yet (Nagel *et al*., 2009).

In the Siwalik group of the Indian subcontinent, the record of this family Nimravidae and its subfamily

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Abbreviations
MNHN, Muséum National d'histoire Naturelle Paris (F); Smns, Staatliches Museum für Naturkunde Stuttgart (D); UNSM, University of Nebraska State Museum, Lincoln, NE (USA).

Barbourofelinae is extremely poor. Pilgrim (1932) has reported some fragmentary specimens of doubtful allocation to this family. Currently, three species, *Sansanosmilus rhomboidalis*, *Sansanosmilus serratus* and *Sivasmilus copei* are recognized from the Siwaliks based on the fragmentary material assigned as holotype (see discussion). No further material was reported or described from the Siwaliks and there remained a gap in the study of this family and carnivoran in general. In this situation, every new specimen is valuable for the taxonomic and biogeographic implications of this family. In the current study, we are describing two specimens from late middle (Chinji Formation) and early late Miocene (Nagri Formation) deposits of the Siwaliks of Pakistan. We also briefly discuss the validity of Pilgrim's material.

The Dhok Ban Ameer Khatoon village is located to the southeast of Chakwal at the Chakwal to Choa Saidan Shah Road (Fig. 1). The village is located on the Nagri sandstone and Chinji Formation outcrops are present to the south and west of the village (Cheema, 2003; Samiullah, 2010; Khan *et al*., 2017; Abbas, 2018). These outcrops show the characteristic lithology of the Chinji Formation. The outcrops are best exposed west of the village, an area locally known as Jallo Wala (Lat. 32° 79' 13.6" N: 72° 92' 90.0" E; Altitude 1891.18 ft), and in this portion of the outcrops the hard, coarse-grained, siliceous sandstone (grit) and conglomerates mainly preserve mammalian remains. The faunal remains of these groups clearly indicate a middle to earliest late Miocene age of the outcrops ranging from 14 to 11.4 Ma, the age of the Chinji Formation (Figs. 1, 2).

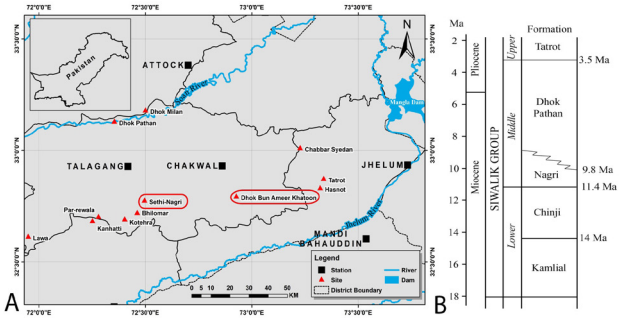

Fig. 1. Map of Potwar Plateau showing localities (enbox) in the Siwaliks of Northern Pakistan bearing carnivoran remains.

Nagri Formation type locality (Y311) is located in Sethi-Nagri near Dhok Saltar (Lat. 32° 46' 28.5" N: Long. 72° 29' 43.4" E), district Chakwal, Punjab, Pakistan (Fig. 1). The section of Nagri Formation depict that it has thick massive sandstone with occasionally occurring shale beds.

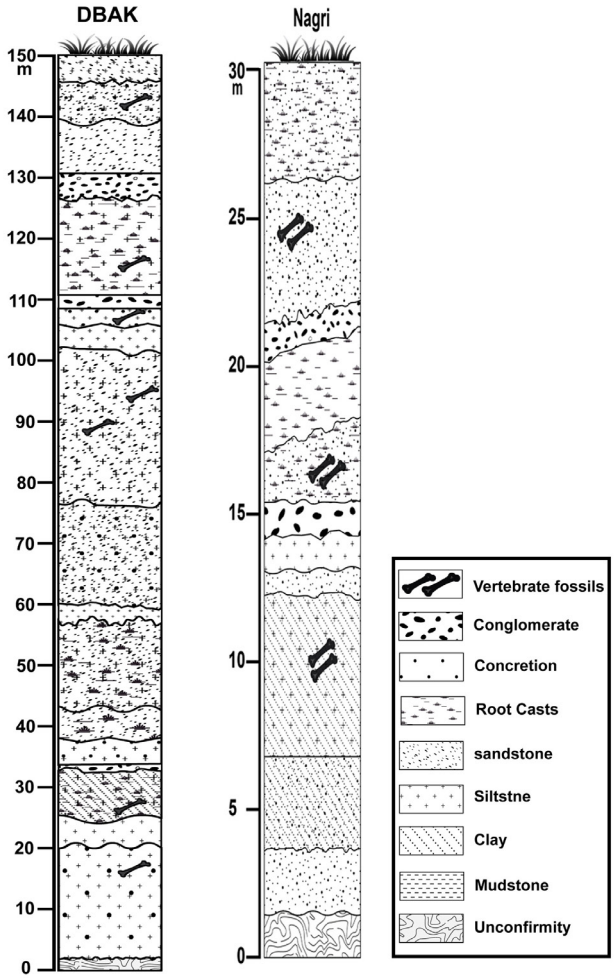

Fig. 2. Lithostratigraphic section of the Dhok Bun Ameer Khatoon (DBAK) Sethi Nagri (Y311) (redrawn after Pilbeam *et al*., 1980; Cheema, 2003).

Sandstone is less compacted and has both vertical and horizontal layering (Dehm, 1963; Pilbeam *et al*., 1980; Shah, 1980; Mahmood and Khan, 2020). The fossiliferous layer is five meter thick and has three divisions. The first division is having the sandstone conglomerates and having single celled dead organisms and layer of algae within it. The second division is also fossiliferous, having a sandstone-conglomerate complex. The conglomerate having silt, clay, and carbonate and iron-rich nodules and the stromatolites and onkolites are absent. The iron-rich nodules have imparted a dark, red-brown stain to many of the conglomerate lenses. This level represents a shallow channel complex, whose axes shifted laterally through time over about one km at the locality. In part of the locality, the lowest and middle levels are separated by non-fossiliferous silt. The middle level grades upward directly into the

highest fossiliferous level. This level includes layers of interfingering red-brown clayey silt, and gray-green sandy silt (Fig. 2). The sediments are extremely bioturbated. Molluscs and a few leaf impressions are present. In some parts of this level, there are autochthonous, dense nodule horizons (Dehm, 1963; Pilbeam *et al*., 1980; Shah, 1980). The Nagri Formation is assigned an age from 10.8 to 8.5 Ma (Barry *et al*., 2013) on the basis of magnetic stratigraphic studies while Y311 (Johnson *et al*., 1982). The Nagri Formation also preserves the oldest hipparionine record in the Siwaliks (Hussain, 1971; Wolf *et al*., 2013).

MATERIALS AND METHODS

The material described in this article consists of an upper canine and a third upper premolar collected from the Dhok Ban Ameer Khatoon and Sethi Nagri, Potwar Plateau, Pakistan. It is housed in the Dr. Abu Bakr Fossil Display and Research Centre, University of the Punjab, Lahore, Pakistan. The crown terminology and measurement manners follow that of Smith and Dodson (2003). The measurements were taken with digital Vernier caliper and expressed in millimeters (mm). The photographs were taken by a digital camera (Canon 6D) and the plate prepared in an Adobe Photoshop (trial version). The locality name is provided in parentheses in the new material.

SYSTEMATIC PALAEONTOLOGY

Order: Carnivora Bowdich, 1821
Suborder: Feliformia Kretzoi, 1945
Family: Nimravidae Cope, 1880
Subfamily: Barbourofelinae Schultz *et al*., 1970
Genus: *Sansanosmilus* Kretzoi, 1929

Sansanosmilus rhomboidalis Pilgrim, 1932

Holotype

GSI-D 154, the left maxilla containing the canine and the base of the crown of P3 (Pilgrim, 1932).

Type locality

Chinji, Chakwal, Punjab, Pakistan (Pilgrim, 1932).

Diagnosis

A primitive barbourofelid of smaller size than *Sansanosmilus palmidens* with a very short slender upper canine, having the root much longer than the crown, of an elongate rhomboidal cross-section, with crenulated edges, with hinder keel straight and not curved; p4 probably slender; infra-orbital foramen high and narrow (Pilgrim, 1932).

Stratigraphic range

Chinji Formation of Lower Siwaliks (Pilgrim, 1932), Nagri Formation of Middle Siwaliks (reference herein).

Referred material

PUPC 20/60, lC (Sethi Nagri); PUPC 16/127, lP3 (Dhok Bun Ameer Khatoon).

Description

PUPC 20/60 is well-preserved upper canine which is compressed labiolingually and high crowned (Fig. 3). Its distal edge is highly crenulated, while at the mesial edge, this character is slightly inconspicuous. It is extremely convex laterally and only faintly concave medially near the tip otherwise it is straight. The lingual side shows two shallow longitudinal grooves and the lateral side has a deep and wide groove which present at the distal side of the tooth. The cross section is rounded rhomboidal due to an inflated portion in the middle of the medial and lateral side. Also, a faint crest is present in the middle portion of the medial side extending up to the tip. The maximum crown height is 25.7 mm at the medial side and that of 21.4 mm at the lateral side. The root is also well preserved and the maximum preserved length is 24.7 mm (from labial side).

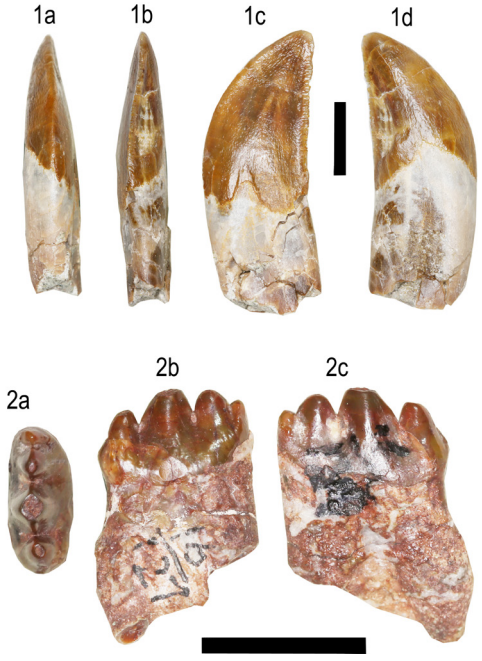

Fig. 3. *Sansanosmilus rhomboidalis*. 1. PUPC 20/60, lC. Views: a. Anterior; b. Posterior; c. Medial; d. Lateral. 2. PUPC 16/127, lP3. Views; a, Occlusal; b, Lingual; c, Labial. Scale bar 10 mm.

The P3 PUPC 16/127 is well-preserved, slightly compressed labiolingually, slightly worn, and bears four cuspids (Fig. 3). All the cusps are united at the base, and separated by small notches at the apex. The anterior-most cusp is extremely small and bears a small crenulated cingulum lingually. The second cusp is moderate in size and is well-separated from the next well-developed and largest cusp. The apex of the third and largest cusp is most worn, this cusp has large mesial and distal crests. The last and fourth cusp is also moderately developed like the second cusp. This cusp bears a small cingulum at its posterior base. Two roots are also well-preserved (Fig. 1).

Remarks

The canine is compressed and has longitudinal furrows labiolingually, and mesiodistal crenulated edges are present. These characteristics are found in the various species of *Sansanosmilus*, *Paramachaerodus*, *Propontosmilus* (=*Paramachaerodus*), and *Sivasmilus* of the Indian subcontinent; *Prosansanosmilus*, *Amphimachairodus*, *Machairodus*, *Ginsburgsmilus*, *Syrtosmilus*, *Afrosmilus*, *Oriensmilus*, *Nimravides*, and *Barbourofelis* of Eurasia, America, and Africa (Pilgrim, 1915, 1932; Baskin, 1981; Morlo *et al*., 2004; Morales *et al*., 2001; Morlo, 2006; Robles *et al*., 2013; Li and Spassov, 2017; Wang *et al*., 2020; Ruiz-Ramoni *et al*., 2020) and fits the diagnostic features of Barbourofelinae provided by Morlo *et al*. (2004) markedly compressed, sabertoothed C1 with crenulations on, at least, their posterior border, and with vertical grooves. The complete upper canine of *Sansanosmilus rhomboidalis* from Chinji (Chinji Formation, Lower Siwalik subgroup) is known while the canines of *Paramachaerodus pilgrimi* from Kotal Kund (Dhok Pathan Formation, Middle Siwalik subgroup) and *Paramachaerodus indicus* from Hasnot (Dhok Pathan Formation, Middle Siwalik subgroup) are known from their bases (Pilgrim, 1915, 1932), however, the upper canines of others species of these genera of Siwalik genera, are unknown till present. The lower canines of *Propontosmilus* and *Sivasmilus* are known (Pilgrim, 1932), so, no comparison can be made with these genera. As judged from the figure (Pilgrim, 1932, Fig. 4), the canine of *Sansanosmilus rhomboidalis* is more convex/rounded mesiolabially and sharp/pointed distally, the cross section of the said canine is narrow with a diamond shape (Pilgrim, 1932, p. 184) that is close to the morphology and cross section of the studied specimen (PUPC 20/60). The cross section of upper canine of *Paramachaerodus indicus* is oval but extremely elongated (Pilgrim, 1932). The more oval cross section and also the more rounded lingual side of GSI-D 261 is different from the studied specimen. *Paramachaerodus pilgrimi* appears by its root (Pilgrim, 1915, p. 142), it is semi-oval to triangular in cross section and its morphology differs markedly from the studied specimen (PUPC 20/60). On the other hand, the upper canines are unknown in *Prosansanosmilus* species; *P. peregrinus and P. eggeri, Syrtosmilus syrtensis*, and *Afrosmillis turkane,* comparison with these species is not possible. The upper canines (and deciduous upper canine) of *Sansanosmilus jourdani* (=*Albanosmilus jourdani*) and *S. palmidens* are more narrow and strongly curved (Morlo, 2006, p. 341) resulting in a highly compressed cross section. The upper canines of *Amphimachairodus coloradensis* and *Paramachaerodus transasiaticus* are slightly recurved mesiodistally (Li and Spassov, 2017; Ruiz-Ramoni *et al*., 2020) like the studied specimens but the canines of both these species are labially more convex. The upper canines of various *Machairodus* species are clearly differentiated from the studied specimens having the regular oval cross section instead of rhomboidal cross section. Presence of the distal groove clearly differentiate the studied specimen from the *Ginsburgsmilus napakensis* (Morales *et al*., 2001, p. 98). The canine of *Oriensmilus liupanensis* (Wang *et al*., 2020) is much longer and slightly more curved lingually. The cross section of the studied specimen matches well with the cross section of *Barbourofelis lovei* and *Nimravides galiani* (Baskin, 1981, p. 127, 132) but the canine of *Barbourofelis lovei* is much longer than the studied specimen, however, the size of *Nimravides galiani* is close to the studied specimen.

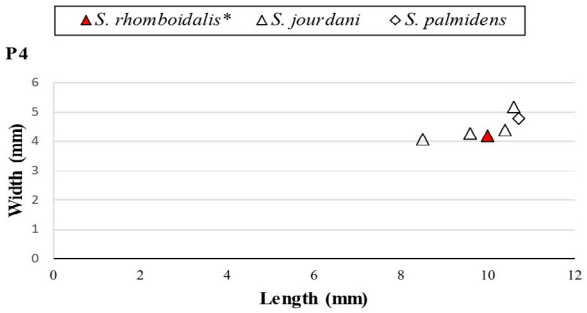

Fig. 4. Scatter plot depicting the dental variation of *Sansanosmilus rhomboidalis* from the Siwaliks. * shows the specimen under study. The comparative data are taken from Pilgrim (1932); Morlo *et al*. (2004); Robeles *et al*. (2013).

The P3 is compressed labiolingually and has blunt and crenulated cusps. These are the features of various barbourofelids and machairodont felids (Pilgrim, 1932; Colbert, 1935; Robles *et al*., 2013a). The Siwalik barbourofelids include, *Sansanosmilus*, *Sivasmilus*, and *Propontosmilus* (Pilgrim, 1932) and machairodonts

Table I. Measurements (in millimeters) of cheek teeth of *Sansanosmilus rhomboidalis*. (*) shows studied specimen. The comparative data are taken from Pilgrim (1932), Morlo *et al.* (2004), Robeles *et al.* (2013).

Taxa	Inventory number	Tooth position	Length	Width	W/L ratio
Sansanosmilus rhomboidalis	PUPC 20/60*	lC	14.6	7.00	0.59
	PUPC 16/127*	lP3	10.0	4.20	0.42
Sansanosmilus jourdani	IPS2034	P3	10.6	5.20	0.49
	IPS46487c	P3	8.50	4.10	0.48
	PS49575	rP3	10.4	4.40	0.42
	IPS49575	lP3	9.60	4.30	0.45
Sansanosmilus palmidens	MNHN-Sa 451	P3	10.7	4.80	0.45
Prosansanosmilus peregrinus	SMNS 41482	C	8.00	5.50	0.69
Prosansanosmilus eggeri	BSP1959 II 8055	P3	11.2	6.20	0.55
Ginsburgsmilus napakensis	UM Nap IX 1966	P3	11.0	5.80	0.53
	SO-5670	P3	10.1	5.70	0.56

include, *Paramachaerodus*, *Epimachairodus*, and *Machairodus* (Pilgrim, 1932). Not a single P3 of Siwalik barbourofelids and machairodont felids is known till present, however, the P3 of barbourofelids and machairodont felids is well-known from other regions of the world including the Eurasia, Afria and America (Pilgrim, 1932: Werdelin and Peingne, 2010; Morlo *et al*., 2004; Morlo, 2006; Robles *et al*., 2013). The described P3 is clearly different from that of *Sansanosmilus jourdani* (=*Albanosmilus jourdani*), *Ginsburgsmilus napakensis*, *Afrosmilus turkanae*, and *Prosansanosmilus peregrinus*, in that it is more developed, less compressed and curved, with well-developed four cusps and of small size. The P3 of various species of *Machairodus* and *Barbourofelis* are much larger and are more pointed and sharper except the *Barbourofelis lovei* (Fig. 4) (Schultz *et al*., 1970).

DISCUSSION

Pilgrim (1932) erected two species of barbourofelines from the Siwalik Group, *Sansanosmilus serratus*, and *Sansanosmilus rhomboidalis*, and a third species, *Sivasmilus copei*, was added by Kretzoi (1929). These species were mainly erected on the fragmentary material and there may be a case of misidentification. *Sansanosmilus serratus* was based on the left fragmentary mandibular ramus containing the p4-m1 (GSI-D 165), Figure 3 in the plate 8 of Pilgrim's monographic work. Both the teeth were partially broken. In m1, the protoconid was missing and in p4 only the posterior accessory cusp was perfect. The preserved edges of the both teeth are crenulated (Pilgrim, 1932: Fig. 3) which helped Pilgrim to place this specimen in the Machaerodontinae. The specimen shows the morphology of *Machairodus* despite the breakage of cusps but even more to that of the recently erected species, *Oriensmilus liupanensis*, by Wang *et al*. (2020) from late Miocene of China. Contrastingly, the high backward orientation of the preserved teeth cusps matches well with *Prosansanosmilus peregrinus* (Heizmann, 1973). Hence, a more detailed analysis of the specimen is need to properly evaluate it taxonomic position, and this needs in hand observation of the specimen.

The other species of the genus *Sansanosmilus*, *Sansanosmilus rhomboidalis* was based on a left maxillary fragment with canine and roots of P3 (Pilgrim, 1932: pl. 8, Fig. 4). The morphology of P4 (GSI-D 153) attributed to *Sansanosmilus* (?) cf. *rhomboidalis* is close to that of *Machairodus giganteus*. According to Pilgrim (1932), (p. 185, line 1 and 2), the protocone must have been reduced if present. Then he writes (p. 185, line 4) although it is partially broken, the protocone must have been almost non-existent because the cross section of the root is hardly expanded laterally. The canine was shown only in buccal view. It is quite different from other barbourofelids and machairodont felids. So, the erection of this new species seems justified but there are considerable intraspecific variations in the canines of the barbourofelids (Pilgrim, 1932; Schultz *et al*., 1970; Morlo *et al*., 2004; Morlo, 2006; Werdelin and Peingne, 2010; Robles *et al*., 2013a). Similarly, *Sivasmilus copei* was originally described as *Sivaelurus chinjiensis* by Pilgrim (1915). Kretzoi (1929), based on the morphology of the premolars of GSI-D 151, a left mandibular ramus with the canine and p2 to p4, designated it as *Sivasmilus copei* and Pilgrim (1932) accepted it as such. The association of this specimen to *Sivasmilus*, and hence to a barbourofelid, was based on the reduction of p3 and its crenulated enamel. The crown of the canine outside of the alveolus is missing, only the alveolus of p2 is present, p3 is complete, and the talonid of the p4 is preserved. Pilgrim (1915), (p. 149) writes

about the canine "The root of the canine is elliptical in cross section without the distinct indication of a posterior trenchant edge." This makes it closer to macharirodonts rather than barbourofelids. In essence, it can be concluded that the Siwalik barbourofelid species need a revision but more material is needed along with the inspection of previously described material.

CONCLUSIONS

Dhok Ban Ameer Khatoon and Nagri Formation are very important localities because of their faunal elements. But carnivoran remains are very rare in the Siwaliks. This study describes the two new specimens belonging to *Sansanosmilus rhomboidalis*, recovered from the both of these localities ranging in age from late middle to early late Miocene of the Siwaliks of Pakistan. *Sansanosmilus rhomboidalis* differs from *S. palmidens* and *S. jourdani* due to canine morphology.

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Statement of conflict of interest

The authors have declared no conflict of interest.

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