New Material of Listriodon guptai Pilgrim, 1926 (Mammalia, Suidae) from the Basal Manchar Formation, Sindh, Pakistan: Biochronological and Paleobiogeographic Implications

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New material of *Listriodon guptai* Pilgrim, 1926 (Mammalia, Suidae) from the basal Manchar Formation, Sindh, Pakistan: biochronological and paleobiogeographic implications

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Abstract. New fossil material from the latest early Miocene Manchar Formation in the Ranikot area (Sindh, Pakistan) provides information about the poorly known listriodontine suid *Listriodon guptai* Pilgrim, 1926. Recognition of this taxon, initially described on the basis of a fragmentary upper molar, allows biochronologic correlations for the base of the Manchar Formation with penecontemporaneous formations of Pakistan where this taxon also occurs (Sulaiman Range and Potwar Plateau). *Listriodon guptai* may be closely related to the bunolophodont species *Listriodon affinis* of doubtful stratigraphic provenance and age in the Bugti Hills, as well as to the fully lophodont *Listriodon pentapotamiae* which occurs throughout the Chinji Formation in the Potwar Plateau. The early occurrence of these taxa pleads for an early diversification of the listriodonts in the Indo-Pakistan Subcontinent during the late early Miocene.

Key words: Listriodon, Manchar, Pakistan, Suidae

Introduction

The Listriodontinae is a subfamily of suids that developed sublophodont to lophodont cheek teeth during the early and middle Miocene probably as an adaptation to folivory (Hunter and Fortelius, 1994). The earliest known representatives of the subfamily are from the early Miocene of Asia (MN1-2) and Europe (MN 4), but by the middle Miocene, their geographic distribution comprised the entire Old World (Pickford, 1993). Early listriodontines are generally bunodont, but their skulls already show many of the classic osteological features that characterize the genus *Listriodon*, which has fully lophodont cheek teeth. The group went extinct around the middle–late Miocene transition in Asia and Africa and during the early late Miocene in Europe (van der Made, 1996).

Three listriodont species are traditionally recognized in the Miocene of the Indian subcontinent: *Listriodon pentapotamiae* (Falconer, 1868), *L. affinis* (Pilgrim, 1908), and *L. guptai* Pilgrim, 1926. *Listriodon pentapotamiae* occurs throughout the Chinji Formation in the Potwar Plateau (middle Miocene; Barry *et al.*, 2002) (equivalent to MN 6-7/8 of Europe). *Listriodon affinis*, known only by its type specimen (Pilgrim, 1908), was collected at Kumbi, Bugti Hills, Balochistan (Figure 1) and it is most probably early Miocene in age (level 4 correlated with the early Miocene ?MN2, Welcomme *et al*., 2001; Métais *et al*., 2009; Orliac *et al*., 2009). *Listriodon affinis* is classically considered to be the earliest known listriodont (van der Made, 1996), but the type and only specimen (a maxilla fragment with heavily worn P4-M1) housed in the Indian Museum, Calcutta may even not be a *Listriodon*. It could be related to or belong to the kubanochoere suid *Libycochoerus fategadensis* (Prasad, 1967) from early Miocene strata (equivalent MN2-3) of the Kachchh Peninsula, Gujarat, Western India (Pickford, 1988, p. 35). *L. guptai* was named by Pilgrim (1926) on the basis of specimens originating from the basal part of the Manchar Formation in the locality of Bhagothoro, in the Sindh (Figure 1). The age of the base of the Manchar Formation is still a matter of debate, but it is generally considered to be late early Miocene (Raza *et al*., 1984; Raza *et al*., 2002) or basal middle Miocene, more or less equivalent to MN 5 of the European Land Mammal zonation (van der Made, 1999).

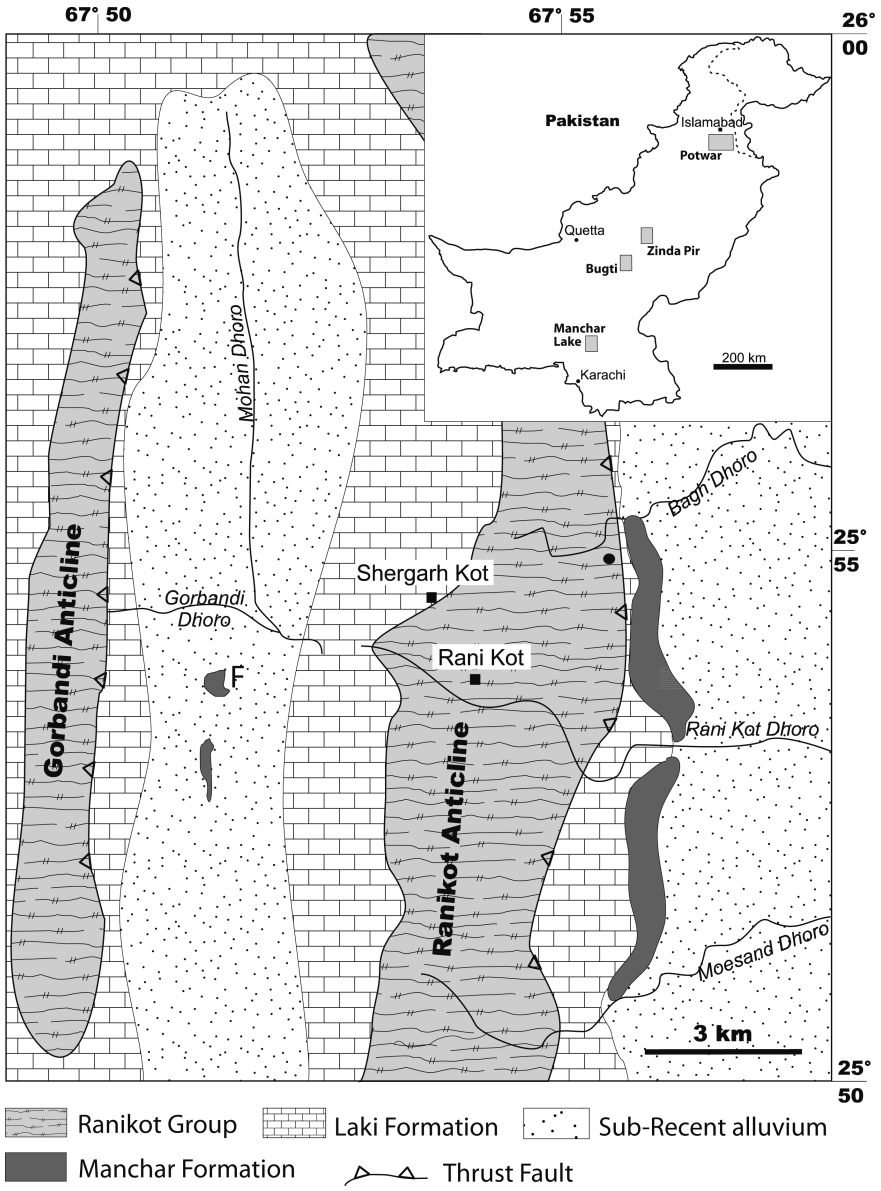

Figure 1. Location and geological map of the Ranikot area. 'F' indicates the outcrop of the lowermost Manchar Formation from which the specimen here attributed to *Listriodon guptai* was found.

The fragmentary maxilla reported here was collected from the lowermost beds of the Manchar Formation exposed in the Ranikot area, Sindh (Figure 1). The fossil specimen probably comes from the ferruginous, variegated sandstone and silt sequence about 5 metres thick that overlies the lower Eocene Laki Formation in this locality. East of the Ranikot anticline, the Manchar Formation overlies directly but unconformably the limestone of the Eocene marine Laki Formation. The specimen was found in the large depression which separates the N-S trending Laki and Gorbandi anticlines (Figure 1). In this depression, the exposures of Manchar rocks were lightly affected by Plio-Pleistocene tectonic deformation (Schelling, 1999). Small hills that can attain a relief of 10 metres consisting of reddish-brownish sediments of the Manchar Formation are exposed at some places. Although some infrequent outcrops of the Manchar Formation were mentioned in this area by Jones (1961), no fossil vertebrates have so far been reported from there. The locality lies about 50 km south of the classical locality of Bhagothoro (Pilgrim, 1926).

The new listriodontine material described here consists

of a fragmentary maxilla preserving left M2-3. Although slightly worn, the specimen belongs to a relatively young adult individual, and the crest pattern of the upper molars is clearly visible. Orliac *et al*. (2009) described material from Kumbi and Dera Bugti (stratigraphic level 6 in the local biostratigraphy—upper lower Miocene, see Welcomme *et al*., 2001; Métais *et al*., 2009; Antoine *et al*., 2013) that they attributed to *Listriodon guptai*. This report of new material from the basal Manchar is thus of interest as it yields important data concerning the temporal and geographic distribution of this taxon, and allows biochronological correlations between different formations of Pakistan (exposed in the Upper and Lower Indus Basin, over a distance of 1000 km), and thus helps to constrain the age of the Manchar Formation. Moreover, this discovery throws light on the early history of the listriodonts in the Indo-Pakistan Subcontinent.

Material and methods

The new maxilla described here was collected by one of us (MAW) during the course of field geology for the students of the University of Sindh. Comparisons were mostly made with material of the Muséum National d'Histoire Naturelle, Paris, France (MNHN). The material is compared to dental remains referred to *Listriodon guptai* from Bhagothoro and various Howard-Geological Survey of Pakistan (H-GSP) localities (van der Made, 1996). The material is also compared to the type specimen of *L. affinis* (figured in Pilgrim, 1926, pl. 11, fig. 1) and to a fragmentary M1 from Samane-4 (MNHN PAK 24254) of the Bugti Hills, and referred to the latter taxon.

The dental nomenclature follows Wilkinson (1976), Pickford (1988) and Hünermann (1968).

Tooth measurements were taken with an electronic caliper (precision of 0.2 mm); the length and width correspond to the maximal dimensions of the tooth. Dental nomenclature follows Boisserie *et al*. (2010) and van der Made (1996). 'M' designates the upper molar. Measurements are in millimetres. MNHN = Muséum National d'Histoire Naturelle, Paris; MNHT = Muséum d'Histoire Naturelle de Toulouse. Toponymy: the spellings of place names in the Indo-Pakistan subcontinent have varied over the past century and a half during which palaeontological studies have been undertaken. We provide a short list of the currently accepted spellings of places in the Sindh, along with variants encountered in the literature. Balochistan: Baluchistan, Bhagatoro: Bhagathoro, Kumbi: Khumbi, Manchar: Manchchar, Potwar: Potohar, Sindh: Sind.

Systematic paleontology

Family Suidae Gray, 1821
Subfamily Listriodontinae Gervais, 1859
Genus ***Listriodon*** von Meyer, 1846

Listriodon guptai Pilgrim, 1926

Figure 2

Holotype.—A right M3 (the distal lobe is damaged), figured by Pilgrim (1926, pl. 11, fig. 2).

Type locality.—"The basal beds of the Lower Manchars of Sind at Bhagothoro," Sindh (Pilgrim, 1926).

Geographical range.—HGSP 8321, 8311, 8322, 8223, 8412, and 8127, Lake Manchar, Sindh (van der Made, 1996); Z124, Z210, and Z120, Zinda Pir Dome, Balochistan (Lindsay *et al*., 2005); Kumbi 6 and Dera Bugti 6, Bugti Hills, Balochistan (Orliac *et al*., 2009).

Stratigraphical range.—late early Miocene (van der Made, 1996; Lindsay *et al*., 2005; Métais *et al*., 2009; Antoine *et al*., 2013). Lower Manchar Formation in Sindh (Raza *et al*., 1984), base of the Vihowa Formation in the Zinda Pir (Lindsay *et al*., 2005) and in the Bugti Hills (Métais *et al*., 2009).

Differential diagnosis (after Orliac *et al*., 2009).—Listriodontinae with upper incisors with several apical lobes and the crown divided by a major groove that is absent in European bunolophodont listriodonts; distal part of the upper incisor crown with a basal break slope, as in *Eurolistriodon*; upper and lower molars more lophodont than in *Listriodon lockharti*, i.e., with complete mesial lophs and lophids, wide mesial basin, and distal lobe of the M3 lacking distocone and reduced to a small depression; distal lophs and lophids interrupted by a median groove, unlike *L. pentapotamiae* and *Listriodon splendens* that exhibit complete posterior lophs and lophids (Figure 3).

Referred material.—CPAG.RAN.Ma.V.1. This specimen belongs to the Ranikot (RAN) fossil collections of the Centre of Pure and Applied Geology (CPAG), University of Sindh, Jamshoro.

Description

The two teeth preserved on the maxilla exhibit the same basic structures, with high and sharp cusps, full mesial loph, and an incomplete distal one. The endocristae of the mesial loph are slight and reduced, forming a wide mesial basin, wider in the M2. The mesial loph is formed by the two mesial precristae and by the paraconule. The distal loph is incomplete since the centroconule lies in mesial position and not as a continuation of the premetacrista. Both teeth exhibit a sharp postectoprotocrista and ecto-

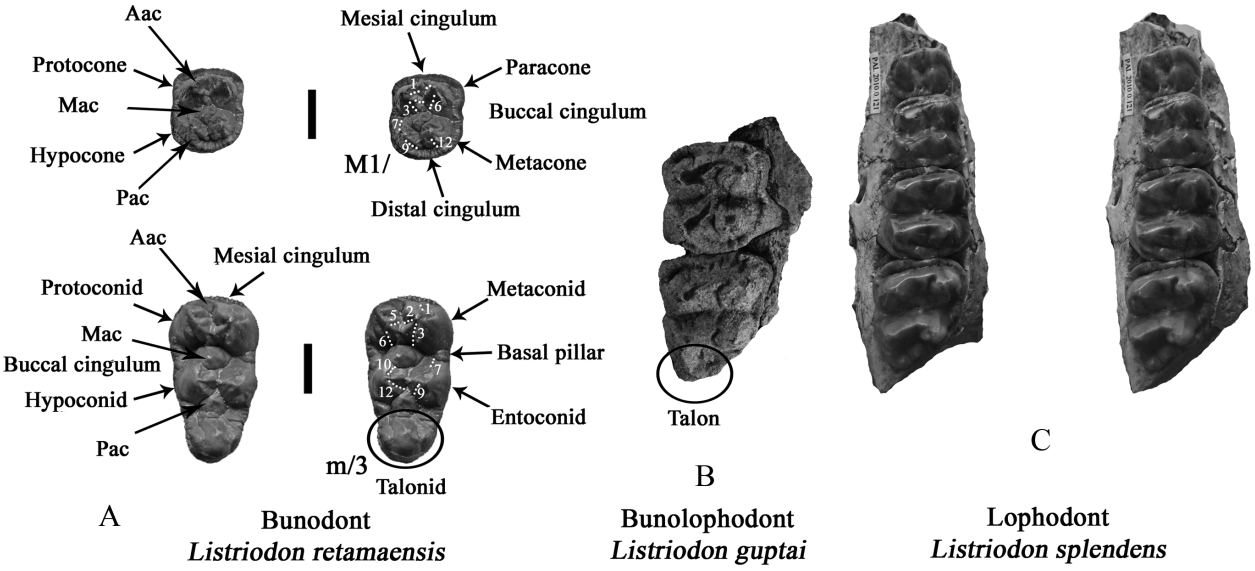

Figure 2. Dental nomenclature of upper molars in some listriodontine suids (Hünermann, 1968; Wilkinson, 1976; Pickford, 1988). The numbers 1 to 12 on 3A are the Fürchen defined by Hünermann (1968). Notice the intermediate upper molar bunolophodont dental pattern of *Listriodon guptai* with respect to the bunodont *L. retamaensis* (Mahou, MN 5 base, Spain), and the lophodont *L. splendens* (Villefranche d'Astarac, MN 6/7, France). Scale bar = 1 cm. (A) and (C) are stereo-photos.

metacristule, forming a "V-shaped" structure. The M2 measures 27 mm mesiodistally, and 25 mm buccolingually.

The M3 displays the same structure as the M2 except that it has a short talon distally, with a fully transversal mesial loph and an extensive mesial basin. The post-metacristule is wide and connects lingually to the distal cingulum. The distal loph, as in fully lophodont species, does not have a distocone and presents a depression which opens distally. The M3 measures 31 mm mesiodistally, and 24 mm buccolingually.

Comparisons

Pilgrim (1926) did not provide the buccolingual diameter of the holotype, but the figures are supposed to be at natural size, and if so then the diameter is about 23 mm for this M3 which is damaged distally preventing measurement of the mesiodistal diameter. The specimen from Ranikot is slightly larger than the holotype, and significantly larger than *Listriodon guptai* from the Bugti beds DB6 (Orliac *et al*., 2009). Moreover, the proportion of the M3 is different: the M3 from the Bugti beds is squarer in outline than the specimen described here. The number of available specimens is presently too low for a definite conclusion, and we cannot completely rule out that CPAG.RAN.Ma.V.1 might belong to another species.

Pilgrim (1926) considered *Listriodon guptai* to be very close to *L. lockharti*: "I am inclined to think that the differences from *L. lockharti* noted above point to the Bugti species (*L. affinis*) being at a more primitive stage. *L. guptai* in some ways occupies a position intermediate between the other two species". The advanced state of lophodonty contests the attribution of this listriodont material to *L. lockharti* or to the poorly known species *L. affinis* that is also more bunodont (van der Made, 1996). Regarding the latter species, Orliac *et al*. (2009) identified a fragmentary upper molar that probably belong to *L. affinis* from lower Miocene strata in the Bugti Hills (Welcomme *et al*., 2001; Métais *et al*., 2009; Antoine *et al*., 2013) that might be the equivalent of Kumbi 4, where the holotype and unique specimen of *L. affinis* is supposed to have been collected. The measurements and the few features preserved in the specimen are congruent with the type specimen of *L. affinis*. Both specimens present an interloph narrower and shallower than the specimen from Dera Bugti-6 (DB6) and Kumbi-6, which indicates a somewhat more bunodont condition. The dental morphology of the specimen CPAG.RAN.Ma.V.1 is more consistent with that of *L. guptai* which shows more advanced lophodonty. Moreover, the incomplete distal loph prevents the attribution of this material to one of the fully lophodont species such as *L. pentapotamiae* from the Chinji Formation or *L. splendens* from the middle Miocene (MN6-7/8) of Western Europe (Figure 3). It is worth noting that *L. guptai* is close to the African species *L. akatikubas* from the lower Miocene of Maboko (Kenya, *ca*. 16.5 Ma). The latter species also displays a full mesial loph and an incomplete distal one. In the

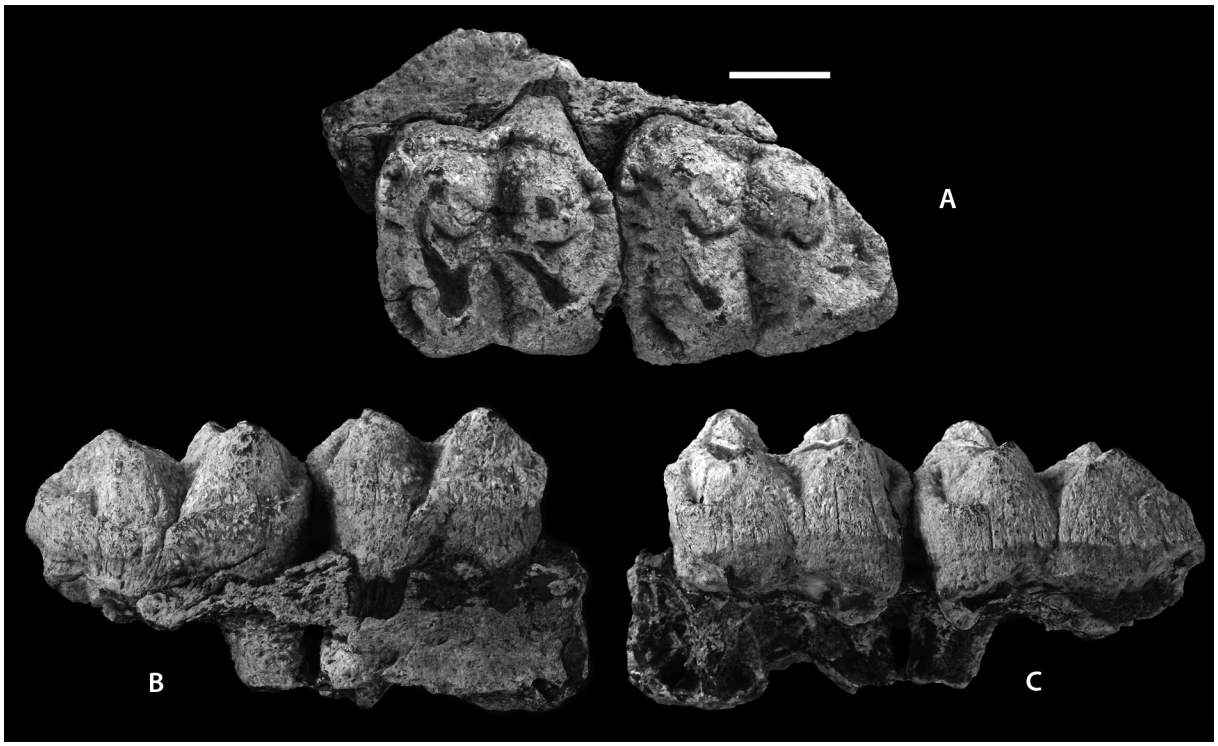

Figure 3. The fossil specimen CPAG.RAN.Ma.V.1 consisting of a fragment of maxilla containing left M2 and M3 in occlusal (**a**), lingual (**b**), and buccal (**c**) views. Scale bar = 1 cm.

Indo-Pakistan Subcontinent, and pending additional information on the primitive species *L. affinis*, it appears clear that there is an Asian lineage of listriodonts characterized by an increase in lophodonty of the cheek teeth from *L. guptai* to *L. pentapotamiae* (van der Made, 1996).

Discussion

The biochronological correlations of the Manchar with the Bugti-Zinda Pir and Siwaliks are still a matter of debate (e.g. Antoine *et al*., 2013). An additional problem concerns correlation between the thick Gaj River series and the Bhaghotoro sections (Raza *et al*., 1984), and more generally with other Neogene fossil faunas of Pakistan. Pilgrim (1917) defined 3 different zones in the ca 400 m thick section at Bhaghotoro. According to Pilgrim (1917) the fossils of the "lower Manchar fauna" at Bhagothoro come from approximately the lower 100 meters of the formation. This lack of precise stratigraphic provenance of the fossils introduces confusion about the exact time range registered in the Manchar Formation. The Bhagothoro section is subdivided into the same three stratigraphic units as those established for the Gaj River, although its thickness is five times lower (Raza *et al*., 1984). Only the lowest unit has produced remains of *Listriodon guptai*, the higher part of the Manchar Formation having yielded *L. pentapotamiae*. In the Ranikot area, the transitional estuarine deposits between the Gaj and Manchar Formation with associated marine and terrestrial taxa is not present suggesting lateral variation of the depositional environment or diachronism between Bhagothoro, the Manchar lake area and the Ranikot area. Although the fauna in this area is still poorly documented, we consider that the level that yielded the fossil reported here belongs to the lowermost stratigraphic subdivision of the Manchar Formation (Figure 4).

Pilgrim (1926) mentioned that the holotype of *Listriodon guptai* came "from the basal beds of the Lower Manchhars of Sind at Bhagothoro, which correspond to the Kamlial horizon of the Salt Range". In the Siwaliks, the base of the Kamlial Formation is dated to 18.3 Ma (Barry *et al*., 2002), and in the Zinda Pir, the *L. guptai*-yielding levels (lower part of the Vihowa Formation) are aged ca. 19 Ma (Lindsay *et al*., 2005). The earliest occurrence of *L. guptai* in the Bugti Hills appear to be roughly coeval and can be correlated with the European MN3 (late Orleanian European Land Mammal Age, Antoine *et al*., 2013). In the Siwaliks, the species *guptai* is not registered and the first occurrence of the genus is represented by *Listriodon pentapotamiae* and dated to ~14 Ma which

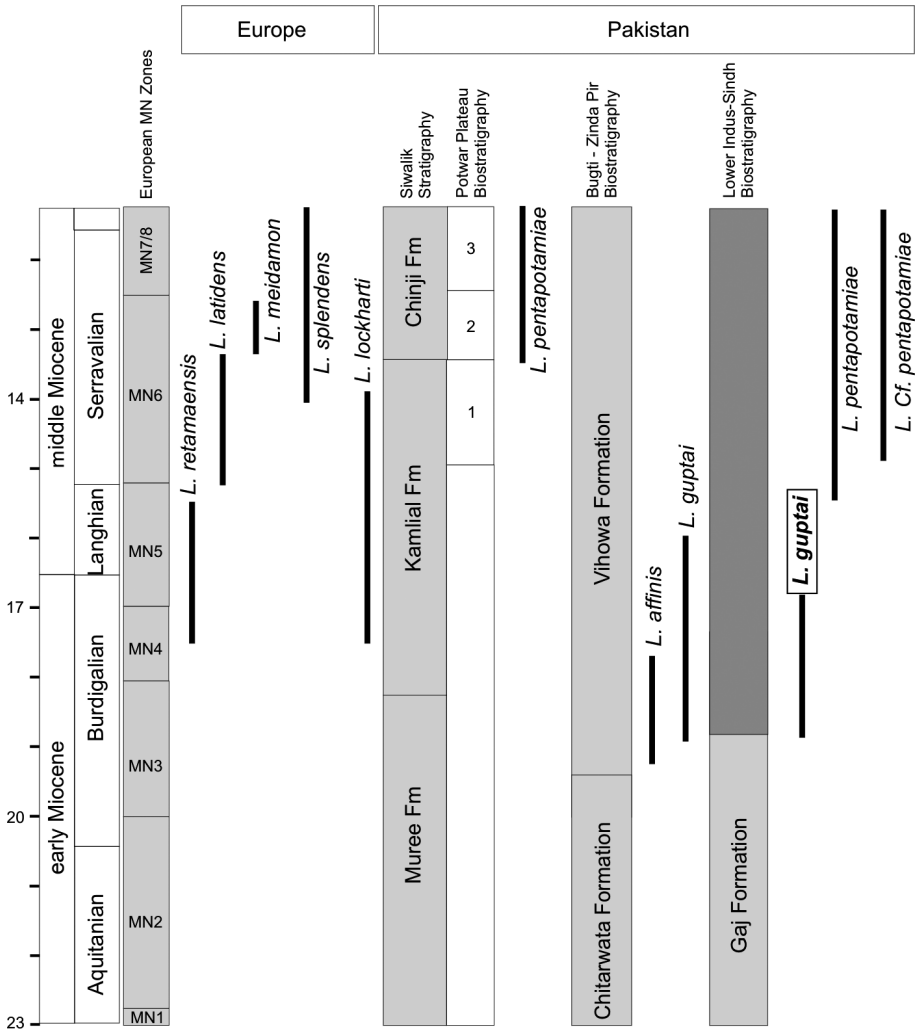

Figure 4. Tentative biochronologic correlations between the base of the Manchar Formation and penecontemporaneous formations in Pakistan, Asia Minor and Europe (from Raza *et al*., 1984; Barry *et al*., 2002; Antoine *et al*., 2013).

correspond to the uppermost Kamlial (Barry *et al*., 2002). The stratigraphical range of *L. guptai* is not precisely known but in no locality is it associated with *L. pentapotamiae*, suggesting that these species did not overlap in time, and are thus reliable biochronological markers. As a consequence, and pending radiometric data, the base of the Manchar Formation is probably correlative with other Local Faunas of Pakistan that have yielded this taxon: ~19 Ma (middle early Miocene).

Conclusion

A restricted sample of a listriodont suid from the Basal Manchar Formation at Ranikot is of interest in that it throws light on the anatomy and systematic position of a taxon which is close to the origin of lophodont listriodonts. The specimen can be attributed to *Listriodon guptai*, a species in which the molars are close to achieving full lophodonty as in the middle and late Miocene *L. pentapotamiae*. *L. affinis* and *L. guptai* document the early history of the subfamily in the Indo-Pakistan Subcontinent and may predate the earliest records in Europe and Africa (MN4, van der Made, 1996). Further investigation of the exposures of the Manchar Formation on the flanks of the Laki Rage are needed to refine the relationships (in term of age and depositional environments) between this fossil assemblage and the classic ones situated at Bhagathoro about 50 km to the North.

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