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An unexpected late paroxyclaenid (Mammalia, Cimolesta) out of Europe: dental evidence from the Oligocene of the Bugti Hills, Pakistan

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Abstract

Eight isolated mammal molars were discovered from lower Oligocene deposits of the Bugti Hills, Pakistan (Paali Nala, Dera Bugti locus C2; lower Chitarwata Formation). Because of their unusual morphology, these molars have long remained enigmatic. Extensive comparisons with fossil eutherian and metatherian mammals and the recent description of new paroxyclaenids (Mammalia, Cimolesta) from the early Eocene (Ypresian) of Europe have highlighted the plausible affinities of these teeth from the Oligocene of Pakistan, and suggest a referral to Paroxyclaenidae. The dental morphology of this taxon is singular among Paroxyclaenidae, and as such it allows us to propose here a new species and a new genus: *Welcommoides gurki*. The occurrence of a paroxyclaenid in the Oligocene of Pakistan remains somewhat unexpected inasmuch as these mammals have so far been known only from the Eocene of Europe. At c. 4.2 kg, *W. gurki* is the largest paroxyclaenid ever discovered, and is assigned to the subfamily Merialinae, which became extinct in Europe around the Ypresian–Lutetian transition, long before the occurrence of this new taxon from Pakistan. *Welcommoides* has a suite of unusual characters compared with merialines, suggesting that this South Asian lineage had diverged for some time from its European Ypresian counterparts. Such a hypothesis is supported by the faunal similarities between European and Indian subcontinent faunas during the Ypresian. Moreover, our discovery strengthens support for the hypothesis that low latitudes of South Asia were a tropical refugium, at least during the first steps of the global climatic deterioration started at the Eocene–Oligocene transition.

Key words

Europe

Indian subcontinent

Mammalia

Palaeogene

palaeobiogeography

palaeoecology

INTRODUCTION

PAROXYCLAENIDAE are an enigmatic family of archaic and moderately small placental mammals, known only from Europe and that occurred from the Ypresian (early Eocene) up to the Priabonian (late Eocene) (e.g. [Matthes 1952](#); [Van Valen 1965](#); [Russell & Godinot 1988](#); [Solé et al. 2019](#)). Paroxyclaenidae are divided into two subfamilies: Paroxyclaeninae and Merialinae. Paroxyclaenines are the most diverse within the Paroxyclaenidae, with eight species representing six genera: *Paroxyclaenus* Teilhard de Chardin, 1922; *Kopidodon* Weitzel, 1933; *Vulpavoides* Matthes, 1952; *Pugiodens* Matthes, 1952; *Paravulpavoides* Harrison, 2009; and *Sororodon* Solé, Plateau, Le Verger & Phélizon, 2019. Paroxyclaenines first appeared in the Ypresian – with *Sororodon* from Mutigny (France, locality close to the reference level MP8 + 9 (MP = Mammal Palaeogene reference-levels of the mammalian biochronological scale for the European Palaeogene; [BiochroM'97 1997](#)) ([Solé et al. 2019](#)) – and last occurred in the Bartonian – represented by *Paravulpavoides* from Creechbarrow (England, MP16) ([Harrison 2009](#)). In contrast, the stratigraphical range of the merialines had long appeared shorter than that of paroxyclaenines: they were only known in the Ypresian ([Solé et al. 2019](#)). Five species representing four genera were known thus far: *Merialus* Russell & Godinot, 1988; *Spaniella* Crusafont-Pairó & Russell, 1967; *Fratrodon* Solé, Plateau, Le Verger & Phélizon, 2019; and *Paraspaniella* Solé, Plateau, Le Verger & Phélizon, 2019. As noted by Crusafont-Pairó & Russell (1967), paroxyclaenids are quite rare in fossil mammal assemblages: each known species is represented by only one or two individuals. Consequently, paroxyclaenids have remained poorly known and rarely studied. The main reviews dealing with the systematics and evolution of the Paroxyclaenidae are those of Russell & Godinot (1988), in which they described the oldest paroxyclaenid ever found – *Merialus martinae* from Palette (early Ypresian; France) – and those of Solé et al. (2019), in which the separation of the Paroxyclaeninae and Merialinae is discussed based on four new species from the Ypresian. It is noteworthy that paroxyclaenids were so far known and limited to Europe.

The fossil mammals from the Bugti Hills (Balochistan, Pakistan; Fig. 1) have long been famous and the subject of several studies thanks to the numerous specimens that were collected early in the twentieth century (e.g. [Pilgrim 1912](#); [Forster-Cooper 1915](#)). Collaborative field expeditions (1995–2004) in the North and South Zin anticline of the Bugti Hills (Fig. 1) led by the ‘*Mission Paléontologique Française au Baloutchistan*’ (MPFB) in collaboration with the Geology Department of the University of Balochistan, Quetta (1995–2000), and the Earth Sciences Division of the Pakistan Museum of Natural History, Islamabad (2001–2004), allowed for the clarification of the stratigraphical position of the fossil vertebrates along the thick Oligocene–Miocene terrestrial sequence exposed in the Bugti region, as well as the ages of the successive distinct Bugti faunas ([Welcomme et al. 2001](#); [Métais et al. 2009](#); [Antoine et al. 2013](#)). These most recent field expeditions in the Bugti Hills have notably led to the discovery of a particularly rich fossil-bearing lens of fluvio-deltaic sands at Paali Nala (DBC2 [Dera Bugti locus C2]), situated in the lowermost levels of the

Oligocene continental sequence (Bugti Member, lower Chitarwata Formation; e.g. [Marivaux et al. 1999](#); [Welcomme et al. 2001](#); [Antoine et al. 2003a](#); [Métais et al. 2009](#)). Wet screenings have yielded a diverse assemblage of marine, deltaic and aquatic invertebrates and vertebrates, together with terrestrial mammals (such as rodents, bats, eulypotyphles, primates, carnivores, creodonts, artiodactyls, perissodactyls, dermopterans, and marsupials). The descriptions of the abundant and highly diversified rodents, primates, ruminants as well as colugos ([Marivaux et al. 1999, 2001, 2002a, 2005, 2006](#); [Marivaux & Welcomme 2003](#); [Métais et al. 2009, 2017](#)), have considerably enhanced our knowledge of the poorly known Oligocene terrestrial mammalian communities of the Indian subcontinent and South Asia in general. This early Oligocene fauna is particularly informative for documenting the mammal palaeodiversity of the Indian subcontinent, but it only partially bridges a gap between the former known early to middle Eocene vertebrate faunas (e.g. [Thewissen et al. 2001](#); [Smith et al. 2006, 2007](#); [Rana et al. 2008](#); [Rose et al. 2009a, 2009b, 2018](#)) and the famous Neogene faunas of the Siwaliks (e.g. [Barry et al. 2002](#); [Métais et al. 2009](#); [Antoine et al. 2013](#)).

In this paper we describe a set of isolated teeth (upper and lower molars) from the Paali Nala locality that were discovered between 1999 and 2004 in the framework of the wet-screening operations of the sediments. Due to their unusual morphology, these teeth have long remained enigmatic. Here we underscore their plausible paroxyclaenid affinities, erect a new genus and species (*Welcommoides gurki* gen. et sp. nov.) on the basis of the uniqueness of several dental features, and then discuss the evolutionary history of this mammalian group with a special emphasis on the palaeobiogeographical significance of this new taxon from Pakistan.

MATERIAL & METHODS

Material

The fossils from the Paali Nala locality (DBC2; Dera Bugti level C2) are housed in the palaeontological collections of the *Université de Montpellier* (UM), Montpellier, France.

Institutional and collection abbreviations. MNHN: *Muséum national d'Histoire naturelle* (Paris, France); MNHN.F.Av: Avenay; MNHN.F.CEB: Condé-en-Brie; MNHN.F.GR: Grauves; MNHN.F.Louis.Py: Pourcy, Collection Louis; MNHN.F.Louis-X-Mut: Mutigny, Collection Louis; RBINS Cast-Vert: Royal Belgian Institute of Natural Sciences (Brussels, Belgium), collection of casts of fossil vertebrates; MNHN.F.SLP-29-PE, MNHN.F.SLP-29-PR: Prémontré; UM/DBC2: *Université de Montpellier*, Dera Bugti level C2; UM/POY: Pourcy.

High-resolution μ CT-scan

We used X-ray microtomography (μ CT-scan) for obtaining three-dimensional digital models (3D surface renderings) of the fossil teeth. The specimens were scanned with a resolution of 5 μ m, using a μ CT-scanning station EasyTom 150 / Rx Solutions (Montpellier RIO Imaging [MRI], ISE-M, Montpellier, France). The crown and roots of each tooth were virtually delimited by manual segmentation under AVIZO 2020.2 software (Visualization Sciences Group). The teeth were prepared within a 'Label Field' module of AVIZO, using the segmentation threshold selection tool. The 3D digital models (surfaces) of the different dental specimens described in this paper are available on MorphoMuseum (Solé & Marivaux 2024), an online open access platform that aims at enhancing accessibility to 3D models (<http://morphomuseum.com>).

Dental terminology and measurements

We followed the dental terminology of Szalay (1969). We measured the maximum length (L) and width (W) on each specimen when possible.

Body mass analysis

As in Solé *et al.* (2019), we estimated the body mass of the new paroxyclaenid species based on the approach developed by Legendre (1986) to estimate the body mass of extinct species. We used the parameters established (1) for all mammals, (2) for large mammals (> 500 g) and (3) for herbivores. We estimated the length and width of the first lower molar (m1) of *Welcommoides gurki* based on comparisons of the size of its first upper molar (M1) with that of the homologous dental loci in *Fratrodon tresvauxi* and *Paraspaniella gunnelli* (Solé *et al.* 2019). Our choice was based on the fact that these paroxyclaenids are close to the Bugti taxon (best analogues), and because the m1 and M1 are known for these two taxa.

SYSTEMATIC PALAEOLOGY

Order **CIMOLESTA** McKenna, 1975

Suborder **PANTOLESTA** McKenna, 1975

Family **PAROXYCLAENIDAE** Weitzel, 1933

Subfamily **MERIALINAE** Russell & Godinot, 1988

Genus **WELCOMMROIDES** nov.

LSID

<https://zoobank.org/NomenclaturalActs/3fe4a444-e925-491c-8f7b-626bec75a391>

Derivation of name

The genus name pays tribute to our late colleague and friend, Jean-Loup Welcomme (1950–2021), who greatly contributed to our knowledge of Cenozoic mammals, especially from the Bugti Hills of Pakistan (1995–2004).

Diagnosis

As for the type and only species.

Type species

Welcommoides gurki sp. nov.

Welcommoides gurki sp. nov.

Figures 2, 3

LSID

<https://zoobank.org/NomenclaturalActs/62d4982f-8d6b-4ce4-a7cf-bc95f8f4e2a4>

Derivation of name

‘Gurk’ (in *balochi*) meaning ‘wolf’ (*loup* in French); *Gurk* was Jean-Loup Welcomme's nickname in the field, fondly given by our Bugti fellows.

Diagnosis

Largest species of paroxyclaenids. It differs from other paroxyclaenids in the clear separation of the entoconid and hypoconulid on lower molars; m3 more mesiodistally elongated; presence of labial cingulid and of a postcingulid on m3; the presence of a pseudo-stylocone on upper molars and of a second stylar cusp (cusp C) on M1 and M2; the presence of large pre- and post- cingula on upper molars.

Holotype

UM/DBC 2226, Rm3 (Fig. 3E–H).

Referred specimens

UM/DBC 2230, RDP4 (Fig. 2A–B); UM/DBC 2228, RM1 (Fig. 2C–D); UM/DBC 2229, RM2 (Fig. 2E–F); UM/DBC 2236, LM2 (Fig. 2G–H); UM/DBC 2231, LM3 (Fig. 2I–J); UM/DBC 2232, LM3 (Fig. 2K–L); UM/DBC 2233, LM3 (Fig. 2O–P); UM/DBC 2234, LM3 (Fig. 2M–N); UM/DBC 2225, Lm3 (Fig. 3A–D); UM/DBC 2227, fragment of Rm3 corresponding to the trigonid (Fig. 3I–L).

Measurements

Listed in Table 1.

Type locality

Paali Nala, Dera Bugti locus C2; Bugti Member, lower Chitarwata Formation; early Oligocene; Bugti Hills, Balochistan, Pakistan.

Description

One isolated upper tooth is here considered as a DP4 (Fig. 2A–B). This tooth is triangular in occlusal view. The parastyle and postmetacrista are projected mesially and distally, respectively. The stylar shelf is transversely short, the ectocingulum is developed and it bears two stylar cusps which are probably neomorphic cusps. The ectoflexus is modestly deep. The paracone and metacone are widely separated and mesiodistally elongated. The metacone is slightly higher and larger than the paracone. The paraconule and metaconule are well defined. The paraconule is larger than the metaconule. The preparaconule crista joins the ectocingulum. The protocone is wide and long; its apex is mesially inclined. The postcingulum is larger than the precingulum.

One tooth is identified as a M1 (Fig. 2C–D). The M1 was triangular in occlusal view because the postmetacrista area seems to be shifted distally. The paracone and metacone are widely separated, and the paracone is slightly higher than the metacone. The centrocrista is thin and straight. The stylar shelf is buccolingually long and the ectoflexus is very shallow. The parastyle is clearly defined. As on the DP4, the ectocingulum is well defined and high, and a strong and conical stylar cusp is present, located postero-buccal to the paracone, and devoid of any crest. By its position well separated from the parastylar lobe, and the lack of link to the paracone, this stylar cusp is either a stylar cusp C or a neomorphic structure, but not strictly homologous to a stylocone (Butler 1978). Moreover, a second stylar cusp (cusp C), smaller than the main stylar cusp (hereafter named pseudo-stylocone), and not connected to it, is

visible. The paraconule and metaconule are bulbous. The preparaconule crista joins the parastylar area. The protocone is large. Its apex is shifted mesially. It is as high as the metacone and paracone. The pre- and post- cingula are present and linked (lingual cingulum); the postcingulum is larger than the precingulum.

The M2s (Fig. 2E–H) are smaller than the M1, but both teeth are morphologically similar (e.g. presence of a pseudo-stylocone and a second stylar cusp – broken on UM/DBC 2229; separated paracone and metacone; presence of pre- and post- cingula; large paraconule and metaconule).

The M3s (Fig. 2I–P) are smaller than M1 and M2 but have the same features as the M2: presence of a pseudo-stylocone; separated paracone and metacone; large paraconule and metaconule; presence of pre- and post- cingula. They differ from M1 and M2 in lacking the stylar cusp C and in the absence of a metastylar area.

Among the three lower molars (two complete teeth and one fragment of trigonid; Fig. 3) two are considered as m3 because of the distal position of the hypoconulid and of their sizes: the molars are indeed smaller than the approximate size of m1 that can be estimated based on the area of M1 (UM/DBC 2228): L = 6.55–6.85 mm and W = 4.32–4.91 mm. The paraconid is mesiodistally appressed to the metaconid (the trigonid is therefore compressed mesiodistally). These two cuspid are weakly separated, but a distinct groove between them is visible in occlusal and lingual views. The paraconid is as lingually located as the metaconid. It is slightly lower than the metaconid. The protoconid is only slightly higher than the metaconid and paraconid. The paracristid is rather straight, bears a notch medially, and shows cuspid-like enamel swellings on its distal part, close to the cuspidate paraconid. The trigonid has a 'V'-shape morphology in occlusal view. The talonid is as wide buccolingually as the trigonid. The hypoconid is the largest cuspid of the talonid. The hypoconulid is very distally located and lingually displaced, close to the entoconid; both cuspid remaining separated, nonetheless. They are as high as the hypoconid. The cristid obliqua is mesiolingually oriented and reaches the trigonid wall at a point located halfway between the protoconid and the metaconid; the cristid obliqua runs part way up the distal trigonid wall. A cuspid-like enamel swelling (mesoconid?) is situated on the mesial portion of the cristid obliqua on the holotype and the specimen UM/DBC 2225 (Fig. 3A, E); it is individualized from the hypoconid and separated by a notch. No mesoconid-like cuspid is present on UM/DCB 2226 but instead a swelling of the cristid obliqua close to the hypoconid (Fig. 3E). The entocristid is high and it bears an entoconulid, and even a small metastylid distally (Fig. 3). A notch is present between the entocristid and the metaconid. A thin precingulid is present along the mesial part of the teeth (on both the paraconid and protoconid). The hypoflexid is deep and distinctly separates the protoconid from the hypoconid. A labial cingulid and a postcingulid are well defined on UM/DBC 2226 (Fig. 3E); they are not present on UM/DBC 2225.

Comparisons

The unusual dental morphology of *Welcommoides gurki* (Fig. 4) documents a distinctive new mammal that does not show incontestable affinities to any known clades, making it atypical whatever the considered taxon. At a most basic level, the dental morphology and formula of *Welcommoides* (which remains unclear on the basis of isolated teeth) does not allow to establish with certainty the eutherian affinities of this new taxon. Consequently, in the course of this study, we compared these teeth of *W. gurki* to various groups of mammals including metatherians, which are all mammals more closely related to living marsupials than to living placentals and monotremes. The molars of *Welcommoides* are clearly distinct from those of 'alphadontids', typical 'pediomyoids', peradectids or herpetotheriids, which all have a smaller protocone, larger styler shelf generally bearing five distinct styler cusps, a stylocone (if present) connected to the paracone, with the paracone being generally larger than the metacone, the ectoflexus present and generally deep. However, *Welcommoides* shares a number of similarities with relatively bunodont metatherians such as *Glasbius*, *Protodidelphys*, basal polydolopimorphians (including the anatoliadelphids) or even basal paucituberculatans like *Bardalestes* from the early-middle Eocene of Argentina (Goin *et al.* 2009). *Bardalestes* is only known by two upper molars (the ultimate molar is missing), which show several characters similar to those of *Welcommoides* such as a strong styler cusp B (StB) and a smaller styler cusp corresponding to StC + StD, a broad and transversely long trigon, but *Bardalestes*' upper molars also differ in their V-shaped centrocrista, metaconule larger than paraconule, lack of lingual cingulum, and smaller protocone.

The upper molars of the Late Cretaceous genus *Glasbius* differ from those of *Welcommoides* in their smaller protocone, the position of conules, which are close to the protocone, the presence of an ectoflexus, a centrocrista labially convex, and the styler cups (A to E) nearly as large as the paracone and metacone (Clemens 1966). *Glasbius* have lower molars with broadly expanded talonid and a labial cingulid, but the paraconid is not closely appressed to the metaconid as in *Welcommoides*, so that the trigonid forms a wider angle lingually opened, and the cristid obliqua meets the trigonid more labially than in *Welcommoides*; both genera have labial cingulids and postcingulids on lower molars but the distal position of the hypoconid and the absence of entoconulid on lower molars of *Glasbius* (related to the lesser development of the protocone on upper molars) set the Late Cretaceous North American metatherian *Glasbius* clearly apart from *Welcommoides*.

Likewise, resemblance of *Welcommoides* with the extinct protodidelphid *Protodidelphys* is noticeable (Marshall 1987). Both show upper molars lacking the ectoflexus, with a moderate styler area, and the tendency to develop large styler cusps (B and D in *Protodidelphys*, whereas it is the pseudo-stylocone and C in *Welcommoides*). Differences include more

bulbous cusps on upper molars and less developed conules, smaller talonid, and strong entoconid on lower molars of *Protodidelphys*.

The molars of *Welcommoides* share also dental features with polydolopimorphians, a diverse group of Palaeogene metatherians known in South America, Antarctic (Gelfo *et al.* 2019), Australia (Sigé *et al.* 2009). Recently, they have also been reported in Central Turkey where two genera have been reported (Maga & Beck 2017; Métais *et al.* 2018; Beard *et al.* 2023). The type of *Welcommoides* is an ultimate molar, which resembles the m4 of *Orhaniyeia nauta* in many aspects: paraconid and metaconid large, closely appressed, and in lingual position so that the paracristid and protocristid retain a primitive transverse orientation, the cristid obliqua meets the trigonid slightly lingual to the midpoint of the protoconid, relatively straight postcristid connecting hypoconid and hypoconulid, neomorphic cuspids on the well-developed pre-entocristid. In *Orhaniyeia*, the hypoconulid and entoconid are twinned, as is frequently the case in metatherians, which is variably seen in *Welcommoides* (hypoconulid and entoconid are almost twinned in the holotype UM/DBC 2226 whereas they are further away in UM/DBC 2225), suggesting that these similarities with anatoliadelphids are likely to be convergent. This is confirmed with the morphology of upper molars which are much more bulbous in *Orhaniyeia* than in *Welcommoides*. Other differences include the development of exodaenodonty, and postmetacrista longer than the preparacrista on M1–3, the presence of five styler cups with enlargement of styler cusps B and D, a transversely narrow trigon, and an asymmetrical and anteriorly canted protocone in *Orhaniyeia*. Mesial and distal cingula are present on M1–3, but not extending below the protocone, and the metaconule is much larger, whereas the paraconule is entirely subsumed within the preprotocrista.

In summary, although the features just mentioned combine to produce a superficial similarity between certain metatherians and *Welcommoides*, there are also numerous differences in detail that indicate that a close relationship is unlikely. Moreover, it is worth noting that while weight estimation for *W. gurki* is *c.* 4 kg, most Cenozoic metatherians have small body size (< 500 g) (Beck 2022).

Among eutherians, the dental morphology exhibited by *Welcommoides* is very particular, and it appears autapomorphic whatever the considered clade. Plagiomenids are known from the Palaeogene of North America and have often been related to extant colugos (Dermoptera); they share with *Welcommoides* the presence of accessory styler cusps with neomorphic cuspules, strong conules and lack of hypocone on upper molars; low-crowned lower molars with very broad talonid basins and comparatively low, and anteroposteriorly-compressed trigonids, twinned hypoconulid-entoconid. Moreover, plagiomenids have a reduced third molar (Rose 2006). Beyond this relative resemblance, plagiomenids generally lack the paraconid on lower molars, and they further differ from *Welcommoides* in their upper molars typically divided by a deep transverse valley that runs from the labial edge between the paracone and the metacone to the protocone; a similar transverse valley separates the trigonid from the talonid in the lower molariforms.

The relatively bunodont dental morphology led us to extend our comparisons to condylarthrans. Among the broad sweep of these primitive ‘ungulates’, individual features of *Welcommoides* are shared with numerous taxa, but a smaller number of groups show sufficient similarity to warrant more detailed comparisons. These include some mostly North American Paleocene ‘condylarths’ such as the mioclaenid *Promiocleanus* to which paraxylaenids were first thought to be somewhat related (Russell & McKenna 1961), or the arctocyonids *Chriacus* and *Thryptacodon*. Like *Welcommoides*, *Promiocleanus*, which is common in the Paleocene of North America, shows a m3 trigonid with closely appressed and lingual metaconid and paraconid, but the paraconid is substantially smaller, the cristid obliqua contacts the distal aspect of the trigonid directly below the protocristid notch. *Promiocleanus* also differs in its transversely narrow and shorter mesio-distally talonid, and its hypoconulid and entoconid tend to be reduced to a smooth ridge (Williamson 1996). The upper molars of *Promiocleanus* differ in their lack of styler area replaced by a thick labial cingulum devoid of cusp, a mesiodistally-directed preparacrista, the presence of a hypocone (even tiny), a postcingulum with a lingual extremity that is more elevated, and the lack of lingual cingulum. Likewise, the upper molars of *Promiocleanus* do not show this extremely remote paracone and metacone linked by a strong and somewhat straight centrocrista.

Like *Welcommoides*, the arctocyonids *Chriacus* and *Thryptacodon* display a developed paraconid (reduced in *Thryptacodon*) that is lingually located but not closely appressed to the metaconid so that the trigonid is somewhat open lingually, the talonid is transversely wide but the cristid obliqua generally connects to the trigonid labial to the protocristid notch (below this notch in *Chriacus truncatus* (Rose 1996)), and the labial cingulid and postcingulid are variably developed, *Chriacus truncatus* retains the entoconulid on m3 but the hypoconulid is generally reduced in the m3 of arctocyonids (Rose *et al.* 2012). Although the upper molars of *Chriacus* and *Thryptacodon* show some resemblances with those of *Welcommoides*, such as large conules, the presence of a lingual cingulum, well-separated paracone and metacone, they lack a styler shelf that is, similarly to *Promiocleanus*, replaced by a thick labial cingulum; they also differ notably in their squared upper molars in occlusal view and the presence of a continuous lingual cingulum, bearing a hypocone in some species. Although *Welcommoides* shares a number of dental similarities with some Paleocene ‘condylarths’, those are generally primitive eutherian features, and *Welcommoides*, although retaining many plesiomorphic dental features is temporally late, and its similarities with mostly Paleocene primitive ungulates are likely to be convergent.

Another atypical group of mammals deserves thorough comparison with *Welcommoides*, namely the Ptolemaiida, a poorly-known order whose relationships with other placental mammals remain unresolved. The ptolemaidan dentition combines a primitive tribosphenic molar pattern with a set of unique dental specializations not seen in other mammals. Ptolemaidans are exclusively documented in Africa and known from the late Eocene to Middle Miocene of Africa. They have long been known exclusively by three genera that are all restricted to the lower Oligocene of the Fayum Depression in Egypt (Gunnell *et al.* 2010):

Ptolemaia, *Qarunavus* and *Cleopatrodon*, and by *Kelba*, which is now known from several Miocene localities in East Africa (Cote *et al.* 2007). By its overall morphology, the dentition of *Kelba* displays strongest affinities with that of *Welcommoides*. The upper molars of *Kelba* share the mesial and distal cingula well developed, paracone and metacone widely separated; but differ in the reduction of the styler shelf devoid of cusps, the strong development of the precingulum compared to the postcingulum, the lack of pre-paracrista, the presence of a mesostyle, and the variable presence of the paraconule, metaconule and hypocone (Cote *et al.* 2007). As in the holotype of *Welcommoides*, the lower molar m3 of *Kelba* has a tall protoconid and a strong paraconid, but it is not as closely appressed to the metaconid as it is in *Welcommoides*. The entoconid is reduced (absent on m1–2) and crescentiform in *Kelba*'s ultimate molar, and the hypoconulid is much smaller than in *Welcommoides*. There is a small shelf present at the hypoflexid, but the cingulids are less developed in m3 than in m1–2 (Cote *et al.* 2007). Despite these limited similarities, there are numerous substantial differences between *Welcommoides* and *Ptolemaia* that make a close relationship appears unlikely.

Finally, the most convincing comparisons were made with 'Cimolesta', a wastebasket taxon and polyphyletic group of various primitive extinct placental groups of uncertain affinity, and encompassing medium-sized to large herbivores (e.g. Pantodonta) and tiny carnivorous/insectivorous (e.g. Cimolestidae) mammals (Rose 2006). Among Cimolesta, *Welcommoides* compares best with some Pantolesta which regroups several Palaeogene families that include taxa with lower-crowned molars with somewhat rounded cusps. The Pantolestidae are known from the early Paleocene in North America (Dorr 1977) and Europe (De Bast & Smith 2017), and by the late Eocene in Asia with the Dyspterninae, which have been considered to be closely related to the Paroxyclaenidae (Russell & Godinot 1988). In pantolestans, the lower molars show relatively lower trigonids and broader, basined talonids. Upper molars have a generally narrower styler shelf and a wide posterolingual cingulum, often bearing a distinct hypocone. The Pentacodontidae (sometimes considered a subfamily of Pantolestidae), are distinguished by their unusual swollen fourth premolars, which are often much larger than the molars, and a tendency to wear the cheek teeth very heavily, features suggesting a greater emphasis on crushing and grinding than in cimolestids and adaptation to a hard (durophagous) diet (Rose 2006). The early Paleocene pentacodontid *Eurolestes* from Hainin (Belgium) shares with *Welcommoides* a similar occlusal outline, broad trigon, straight centrocrista, with well-developed conules and cingula, and a styler region bearing several small styler cusps (De Bast & Smith 2017). However, *Eurolestes* displays a small hypocone and another accessory cusp between the protocone and the metaconule, and a shallow ectoflexus, and lacks conical styler cusps. Differences are also significant when considering lower molars, and especially the m3, which is slightly smaller than m1 and displays a relatively high trigonid, a reduced and not fully in lingual position paraconid, a reduced and transversely narrow talonid basin lacking labial cingulid and postcingulid, and with a descending pre-entocristid devoid of any cusp.

The pantolestid *Palaeosinopa* is known from the late Paleocene to middle Eocene (late middle Tiffanian, Ti4, to earliest Bridgerian, Br1; Rankin 2015) of North America and the early Eocene of Europe (Smith 2001). In *Palaeosinopa*, the trigonid is much higher than the talonid, the paraconid is reduced and not as lingually positioned as the metaconid; as in *Welcommoides*, there are median notches both on protocrisid and paracrisid, the talonid is less broad in all direction, and is about the same breadth transversely as the trigonid, the hypoconid is slightly larger than the entoconid, which is not positioned distally as in *Welcommoides*, while the smaller hypoconulid is anteroposteriorly compressed and slightly more lingual than on m1. Moreover, the talonid of *Welcommoides* is closed lingually by the enteloconulid and accessory cuspids situated medial to it. The talonid is longer and narrower than the trigonid, while they are about the same breath in *Welcommoides*. In *Palaeosinopa*, the molar paraconid is reduced and the entoconid and hypoconulid are more closely appressed to one another than in the other molars. As on m1 and m2, the entocrisid does not reach the postvallid surface and the talonid basin is left open lingually. In sum, despite some similarities, there are numerous substantial differences that make a close relationship between *Welcommoides* and *Palaeosinopa* fairly unlikely. As mentioned above, pantolestids have also been tentatively reported (and included in the Dyspterninae) from the Eocene of Asia with *Kiinkerishella zaisanica* Gabuniya & Biryukov 1978, *Oboia argillaceous* Gabuniya 1989, and *Gobiopithecus khan* Dashzeveg & Russell 1992, all from Ergilian strata (late Eocene) of the Zaysan Basin in Eastern Kazakstan. They are known by their lower dentition only, and are similar in having a mesiodistally short but transversely wide talonid on lower molars, the paraconid is very reduced (lost in *Kiinkerishella*) and not lingually positioned, the hypoconid is distinctly higher than the other talonid cupids; the m3 has a mesiodistally reduced talonid; this ultimate molar is distinctive in *Kiinkerishella* in being of rounded occlusal outline and peg-like (Lucas & Emry 2004). These potential Asian pantolestids remain poorly documented and, as far as their lower dentition is concerned, highly autapomorphic compared with *Welcommoides*.

Comparisons with the Paroxyclaenidae

Finally, it appears that the unusual dental morphology of *Welcommoides gurki* matches best with the Paroxyclaenidae. The upper molars from DBC2 are similar to those of the paroxyclaenids in the presence of separated paracone and metacone of equal height, of a mesiodistally long protocone that is as high as the metacone and paracone, of a stylar shelf that is buccolingually long, of a high ectocingulum, and of large metaconule and paraconule (Fig. 5). Lower molars of paroxyclaenids are typified by a paraconid placed lingually (Russell & Godinot 1988). This feature is clearly illustrated by the trigonid of the m3s found in Paali Nala (Fig. 6V–X). The latter are also morphologically similar to those of the paroxyclaenids – especially the merialines *Fratrodon* and *Paraspaniella* (Fig. 6) – in being high-crowned and in having a trigonid that is only slightly higher than the talonid. Paroxyclaenids also share the wide talonid and the entocrisid that encloses the postfossid. All paroxyclaenids have molars

that decrease in size from M1/m1 to M3/m3. This feature is supported by the upper molars found in DBC2 (Fig. 4).

The classification of the Paroxyclaenidae includes two subfamilies: the Merialinae and Paroxyclaeninae. Paroxyclaenines differ from merialines notably in the wide separation of the paraconid and metaconid on molars, while merialines possess lower molars with closely situated paraconid and metaconid (Russell & Godinot 1988; Solé *et al.* 2019). Based on this feature, it seems that the fossils from Paali Nala would better belong to the Merialinae rather than to the Paroxyclaeninae. The Merialinae are represented by four genera (five species): *Merialus* (two species), *Spaniella*, *Fratrodon*, and *Paraspaniella*. They are all known from Ypresian localities (Fig. 7A) (Crusafont-Pairó & Russell 1967; Russell & Godinot 1988; Solé *et al.* 2019).

Regarding the morphology of the upper (deciduous and permanent) teeth, the fossils from the Paali Nala locality differs substantially from *Fratrodon* and *Paraspaniella* in the presence of a large pseudo-stylocone on DP4 and molars, and of a styler cusp C on DP4, M1 and M2 (Fig. 5). Only an incipient pseudo-stylocone is present on the M1 of *Fratrodon* (Fig. 5B); in *Paraspaniella*, there is a cusplation of the ectocingulum. The styler shelf is clearly buccolingually longer in the Bugti specimens than in *Paraspaniella* and *Spaniella*. The large size of the styler shelf recalls more *F. tresvauxi* than *P. gunnelli*.

The lower molars from Paali Nala are similar to those of *Merialus* and *Fratrodon* – the oldest merialines – in the presence of a separation of the metaconid and paraconid. This feature discards any assignment to *Paraspaniella* and *Spaniella* (the youngest merialines) in which there is no groove between the paraconid and the metaconid (Fig. 6). Moreover, the entocristid is lower on the Bugti m3s than on those of *Paraspaniella* and *Spaniella*. The presence of a precingulid on UM/DBC 2225 (Fig. 3A), UM/DBC 2226 (Fig. 3E) and UM/DBC 2227 (Fig. 3I) recalls the condition observed in *Merialus* and *Fratrodon*; the precingulid is strongly reduced in *Spaniella* and *Paraspaniella* (Fig. 6).

Merialines, as paroxyclaenines, are characterized by the reduction or loss of the entoconid, as noted by Russell & Godinot (1988). The entoconid and hypoconulid are not distinguishable on merialines; they are replaced by a very thin cusplation on the postcristid and entocristid (Solé *et al.* 2019). Moreover, the postcristid and entocristid are even fused. These features are visible on the m3s of European merialines (Fig. 6). The m3s from Paali Nala are interesting in the presence of a large entoconid (as high as the hypoconid); this feature is similar to the condition observed in *Paraspaniella* (Fig. 6). There is no cusplation of the entocristid and/or postcristid on the Bugti specimens. The hypoconulid on UM/DBC 2225 (Fig. 3A) and UM/DBC 2226 (Fig. 3E) is clearly separated from the entoconid; this, however, differs from lower molars of *Paraspaniella* in which the hypoconulid is reduced and low. The entocristid in the Bugti specimens is also lower than in merialines. The talonid is interestingly mesiodistally elongated on the Bugti m3s; in merialines, the talonid of m3s is mesiodistally short (as on m1s and m2s) (Fig. 6).

Upper and lower molars of the Bugti taxon are also original in the presence of large pre- and post- cingula, of a labial cingulid, and of a postcingulid. Such structures are unknown in other known Paroxyclaenidae. The Bugti fossils, despite their Oligocene age, however, appear conservative compared to other merialines in having a mesiodistally-elongated talonid on m3, a low entocristid, the entoconid and hypoconulid separated, and a large stylar shelf. Indeed, the presence of a mesiodistally-elongated talonid recalls the m3 of *Merialus bruneti* in which this feature is observed (Ypresian; UM/POY12; Fig. 6D; Solé *et al.* 2019).

We estimated the ratio ‘mesiodistal length/buccolingual width’ for the DP4, M1, M2 and m3 of the Bugti taxon to compare their shape with that of the European taxa. The DP4 from Paali Nala (Fig. 2A–B) is slightly more mesiodistally elongated (1.01 for UM/DBC 2230 vs. 0.92 in *P. gunnelli*; Solé *et al.* 2019, table 3). The same trend is noticed when considering the ratios of M1 and M2: the Bugti specimens are more mesiodistally elongated than in the European merialines. The values for the M1 range between 0.7 (*P. gunnelli*) and 0.76 (*F. tresvauxi* from Avenay) for European merialines (Solé *et al.* 2019, table 3), while it equals 0.81 for UM/DBC 2228 (Fig. 2D; Table 1). The values for the M2 range between 0.68 (*F. tresvauxi* from Avenay) and 0.73 (*Spaniella carezi*) for European merialines (Solé *et al.* 2019, table 3), while it equals 0.8 for UM/DBC 2229 (Fig. 2F; Table 1). The ratio for the m3s from Paali Nala ranges from 1.64 to 1.68 (mean = 1.66; n = 2; Table 1). These values are very different from those of European merialines: the values for the m3 range between 1.07 (*F. tresvauxi* from Condé-en-Brie) and 1.33 (*S. carezi*) (Solé *et al.* 2019, table 4). Therefore, the m3s from Paali Nala are clearly more mesiodistally elongated than those of the European species. The substantial difference in the compared values for the m3 with respect to the DP4, M1, and M2 from Pakistan might be due to the position of the hypoconulid, which tends to be very distally located on the third molar in mammals (as it does on UM/DBC 2225 and UM/DBC 2226; Fig. 3); whereas it is not the case in European merialines as highlighted by Solé *et al.* (2019). However, it is undeniable that the upper molars from the Paali Nala locality are more mesiodistally elongated than those of European merialines.

Given their many unique characteristics, the fossils discovered at the Paali Nala locality cannot be referred to any known merialine taxa. This is why we erect here a new genus and species: *Welcommoides gurki*.

DISCUSSION

Affinities of *Welcommoides gurki* and palaeobiogeographical considerations

The current classification of the Paroxyclaenidae distinguishes two subfamilies: Merialinae and Paroxyclaeninae. As shown in the comparison section, *Welcommoides gurki* is

morphologically closer to the merialine paroxyclaenids (i.e. taxa showing closely appressed paraconid and metaconid on lower molars). The closest taxa are *Fratrodon tresvauxi* (MP8 + 9) and *Paraspaniella gunnelli* (MP10). The Bugti paroxyclaenid shares with them a talonid that is higher than in species of *Merialus*. For some characters, *Welcommoides* seem to be closer to *Merialus/Fratrodon* than to *Spaniella/Paraspaniella*: separation of the metaconid and paraconid distinguishable; lower entocristid; presence of a precingulid; larger styler shelf; larger parastylar area; presence of a pseudo-stylocone. However, *Welcommoides* differs from *Merialus* and *Fratrodon* in having a paraconid as high as the metaconid and protoconid (derived feature among paroxyclaenids; e.g. Solé *et al.* 2019); the paraconid is distinctly lower than the metaconid and protoconid in *Merialus* and *Fratrodon* (plesiomorphic feature). The upper molars of *Welcommoides* also differ from those of *Merialus* and *Fratrodon* in being more mesiodistally elongated, which may be a primitive feature, as *Fratrodon*, *Paraspaniella* and *Spaniella* tend to have more buccolingually elongated molars than *Merialus* (Solé *et al.* 2019). Moreover, as mentioned above, *Welcommoides* differs from these taxa in numerous autapomorphic features: presence of a neomorphic pseudo-stylocone, a second styler cusp, a labial cingulid, a postcingulid, and development of pre- and post- cingula. It also differs in conserving a hypoconulid on m3s that is individualized and distally located; this feature recalls the m3 of *Merialus bruneti* among Merialinae (Fig. 6). The entoconid is also well separated from the hypoconid on m3s of *Welcommoides*; this feature is primitive among Paroxyclaenidae. As noted by Solé *et al.* (2019), one of the trends among the merialines is the reduction of the hypoconid and, to a lesser extent, the entoconid.

Taking into consideration the presence of an individualized hypoconulid and the similarities with *Merialus* and *Fratrodon* (known in Mutigny, Avenay and Condé-en-Brie, MP8 + 9), it may be expected that *Welcommoides* could have diverged from European merialines early in the history of this group. This separation clearly occurred before the appearance of *Paraspaniella* (known in Prémontré, MP10) and *Spaniella*. The microfossil assemblages from the Prémontré Sands allowed estimating that the deposition of the Prémontré mammal fauna (MP10) was around 50.4 Ma (Steurbaut *et al.* 2016) and that together, Mutigny, Avenay and Condé-en-Brie (MP8 + 9) cover a time interval spanning c. 54–51 Ma (Hooker 1996; Neal 1996; Escarguel 1999; Smith & Smith 2013; Solé *et al.* 2019). In that context, we hypothesize that the lineage that includes *Welcommoides gurki*, diverged from European merialines between 54 Ma and 50 Ma (Fig. 7A). Therefore, the paroxyclaenid from Pakistan described herein possibly separated from the European taxa early during the Ypresian, thereby suggesting an early dispersal of this group from Europe to the Indian subcontinent (Fig. 7). Such dispersal suggests the existence of land connections between Europe and the Indian subcontinent during the Ypresian. But the pathway(s) of these dispersals remain unresolved. No paroxyclaenid is known from the early Eocene of Pakistan from the Gandhera Quarry, Mami Khel Formation, Kuldana Formation, Chorgali Formation, Ghazij Formation or Kirthar Formation (Russel & Gingerich 1981; Gingerich *et al.* 1997, 1999, 2001; Gingerich 2003; Thewissen *et al.* 2001; Missiaen & Gingerich 2014), nor from the early Eocene of India (Kapur *et al.* 2022), and as such no data is provided in support of a dispersal of the paroxyclaenids

during the Ypresian. The known Eocene mammal faunas from Pakistan have no strong affinities with the Eocene faunas of Europe and North America, and besides they greatly differ from those of the Eocene of the 'mainland' Asia. Accordingly, Thewissen *et al.* (2001) concluded that these mammal faunas were endemic and relatively isolated. Thus, there are no data available in Pakistan for this period to support the existence of land connections between Europe and the Indian subcontinent.

The Cambay Shale Formation, exposed at the Vastan open cast lignite mine near the Vastan village, about 40 km northeast of Surat, Gujarat, western India, is known for its well-preserved diverse fauna of terrestrial mammals as well as other vertebrates (e.g. Rana *et al.* 2004; Bajpai *et al.* 2005; Rose *et al.* 2006). Besides, it is the oldest known South Asian Cenozoic mammalian assemblage (Kapur *et al.* 2022). The mammalian fauna of the Cambay Shale Formation is represented by the earliest modern mammals from the Indian subcontinent, including the highest diversity of early bats (Rana *et al.* 2005; Smith *et al.* 2007), lagomorphs (Rose *et al.* 2008), ailuravine rodents (Rana *et al.* 2008), basal adapiform and omomyiform primates (Rose *et al.* 2009a; Dunn *et al.* 2016), stem artiodactyls (Kumar *et al.* 2010), tillodonts (Rose *et al.* 2009b, 2013), hyaenodontids (Bajpai *et al.* 2009; Rana *et al.* 2015), tapiroid perissodactyls (Smith *et al.* 2016), perissodactyl-like cambaytheres (Bajpai *et al.* 2006; Rose *et al.* 2014), adapisoriculids (Kapur *et al.* 2017), and apatemyids (Solé *et al.* 2020). This diverse fauna is interesting for questioning the mammalian palaeobiogeography during the Ypresian because the land-mammal affinities suggest terrestrial connections between Europe, Asia and the Indian subcontinent at that time, and faunal dispersals as a result (Kapur *et al.* 2022). Indeed, several mammalian orders from the Vastan local fauna (such as bats, rodents, primates, and tillodonts) suggest faunal connections between Europe and India during the early Eocene (Smith *et al.* 2007, 2016; Rana *et al.* 2008; Rose *et al.* 2009a, b; Solé *et al.* 2020; Kapur *et al.* 2022). The direction and timing of these dispersals remain uncertain, but they presumably occurred during the early Ypresian or even earlier. Because of some affinities between Vastan mammals and early Eocene mammals from Asia, Kapur *et al.* (2022) envisaged significant faunal exchanges between India and Asia at or before the Paleocene-Eocene boundary (c. 56 Ma). This implies an initial contact between the two landmasses at this time. European mammals probably dispersed to India via land connections across the Turgai Strait and/or along the Tethyan shore – the southern route (Fig. 7B). However, paroxyclaenids or representatives of most of mammal orders documented in Western Europe or India during the early-middle Eocene have not been recognized in the highly endemic Balkanatolian fauna from the middle Eocene of Anatolia (Métais *et al.* 2018; Licht *et al.* 2022), suggesting sharp biogeographical boundaries in the area at crossroads of Europe, Africa, Asia, and India.

Paroxyclaenids had so far never been reported from South Asia (Indian subcontinent, South-East Asia, and southern China), and the record from Pakistan discussed here represents the first mention of this group in this large palaeobiogeographical province. Given the extreme rarity of this group, we might expect that *Welcommoides* from the early Oligocene of

the Bugti Hills to have evolved locally/endemically in some part of the Indian subcontinent since the Ypresian. The autapomorphic appearance of *Welcommoides*, the latest paroxyclaenid to be known thus far, would be the result of the local evolution of its lineage to specific environmental regional conditions. Nevertheless, such unexpected occurrence is likely to trigger the recognition of paroxyclaenids in other parts of tropical Asia, notably through re-examination of unidentified mammal specimens in collections.

Implication of the body mass of *Welcommoides gurki*

Based on comparisons of the sizes of the M1 of *W. gurki* with those of the m1s and M1s of *Fratrodon tresvauxi* and *Paraspaniella gunnelli*, we estimated the length and width of the M1 of *W. gurki* as follows: L = 6.85 mm and W = 4.32 mm (based on *P. gunnelli*); L = 6.55 mm and W = 4.91 mm (based on *F. tresvauxi*). Based on these values, we estimated the body mass of *W. gurki* following the method developed by Legendre (1986). The results based on the established parameters are listed in Table 2 for: (1) all mammals; (2) large mammals (> 500 g); and (3) herbivores.

The heaviest paroxyclaenid previously known was *Spaniella carezi* (mean 3731 g; Solé *et al.* 2019, suppl. file 2). The mean body mass estimates calculated for *W. gurki* (3990 g and 4476 g, based on comparison with *Fratrodon tresvauxi* and *Paraspaniella gunnelli*, respectively; Table 2) exceed those estimated by Solé *et al.* (2019) for all European paroxyclaenid species. Therefore, given its dimensions, *W. gurki* would be the largest-bodied paroxyclaenid ever recognized. Solé *et al.* (2019) noticed that the largest representatives of paroxyclaenids occurred around the Ypresian/Lutetian boundary. They thus hypothesized that the warm climatic conditions recorded during the Early Eocene Climatic Optimum (EECO; Zachos *et al.* 2008) may have favoured the large body mass of several paroxyclaenids (i.e. the merialine *Spaniella* and the paroxyclaenine *Kopidodon*; Crusafont-Pairó & Russell 1967; Koenigswald 1983). Conversely, they observed a decrease in paroxyclaenid body size during the Lutetian, and then hypothesized that the continuous decrease in temperatures coupled to an increase in seasonality after the Ypresian/Lutetian boundary (Mosbrugger *et al.* 2005) may have favoured smaller-bodied forms (Solé *et al.* 2019). However, the underlying processes that might explain these correlations remain unknown.

The higher body mass estimated for *Welcommoides* (compared with its older paroxyclaenid counterparts) suggests that this South Asian Oligocene paroxyclaenid lived in an environment as favourable as the European one at the Ypresian/Lutetian boundary. The discovery of *W. gurki* thus supports the hypothesis that the palaeoenvironmental and palaeoclimatic conditions in the Bugti Hills area were forested, warm and humid during the early Oligocene as previously envisaged based on the great diversity of primates (Marivaux *et al.* 2001, 2002a, 2005), the presence of cynocephalid dermopterans (Marivaux *et al.* 2006) and traguloid ruminants (Métais *et al.* 2009, 2017) discovered in the same deposits (DBC2,

Paali Nala). These tropical palaeoenvironmental conditions are also supported by floristic and isotopic data. De Franceschi *et al.* (2008), based on wood and pollen, envisaged the presence of a moist tropical forested habitat for Central Pakistan during the time of deposition of the lowermost Chitarwata Formation, notably with ferns and palmae.

Indian subcontinent as a tropical refugium for the ultimate Paroxyclaenidae

As presented above, the region of the Bugti Hills seemingly displayed palaeoclimatic conditions favourable to rainforest ecosystems during the early Oligocene (Marivaux *et al.* 2006; De Franceschi *et al.* 2008). As noted by Marivaux *et al.* (2006), because of the northward drift of the Indian Plate, the reconstructed palaeolatitude of the Bugti Hills was ~14° farther south (i.e. c. 15°N, equivalent to the present-day latitude of Bangkok in Thailand) than in recent times (29°N). The hypothesis of warm and humid environmental conditions is well illustrated by the great diversity of primates and rodents discovered in this area, as well as the presence of traguloid artiodactyls and a cynocephalid dermopteran during the early Oligocene (Marivaux *et al.* 2001, 2002a, 2005, 2006; Marivaux 2006; Métais *et al.* 2009, 2017). The identification of a large paroxyclaenid strengthens this palaeoenvironmental hypothesis.

While paroxyclaenids disappeared from Europe at the end of the Eocene, it may seem surprising that a representative of this clade is still present in the Oligocene of the Indian subcontinent. The last European paroxyclaenid to be known is *Paravulpavoides* from Creechbarrow (England; Bartonian MP16; Harrison 2009). Its disappearance thus preceded the major turnover that occurred at the Eocene–Oligocene boundary: the ‘Grande Coupure’ (or ‘Grande Coupure de Stehlin’) (e.g. Stehlin 1909; Legendre & Marandat 1986; Legendre 1987; Legendre 1989; Legendre & Hartenberger 1992). The ‘Grande Coupure’ is related to the intense and rapid global cooling characterizing the Eocene–Oligocene transition, notably at the Oligocene Oi-1 event (e.g. Zachos *et al.* 2001, 2008). In Western Europe, this faunal turnover was marked by an abrupt event of mammalian extinctions, during which about 60 % of existing lineages disappeared (Legendre 1989; Legendre & Hartenberger 1992; Blondel 2001; Escarguel & Legendre 2006; Escarguel *et al.* 2008; Maitre 2014; Vianey-Liaud & Marivaux 2017; Weppe *et al.* 2021; Solé *et al.* 2022). Several studies also indicated that the renewal of the European fauna already started in the late Priabonian (Legendre & Hartenberger 1992; Solé *et al.* 2022): the ‘Grande Coupure’ corresponds to a gradual renewal. The gradual shift in mammalian communities mirrors the vegetational shift: tropical and subtropical forests were replaced by temperate, mixed deciduous floras and more open habitats (Gruas-Cavagnatto 1974; Collinson & Hooker 1987; Ollivier-Pierre *et al.* 1987; Cavagnetto & Anadón 1996). Therefore, the extirpation of the European paroxyclaenids can be considered as related to the ‘Grande Coupure’.

The European primates greatly suffered from the 'Grande Coupure': Eocene primates show a considerable diversity notably in their body size, while only a mouse-sized omomyid was retained in Western Europe, 2 myr after the Eocene–Oligocene transition (Köhler & Moyà-Solà 1999; Vianey-Liaud *et al.* 2019). As evidenced by Marivaux *et al.* (2006), the palaeoenvironmental conditions on the drifting Indian Plate and in South-East Asia during the Oligocene contrast markedly with those recorded on the rest of the Eurasian continent. The conditions in South Asia (Indian subcontinent + South-East Asia) continued to support the presence of primates (tarsiids, amphipithecids, eosimiids, and sivaladapids), but also of rodents, tree shrews, some artiodactyls (tragulids) and dermopterans. Therefore, it is clear that this region, which extended into lower latitudes, provided a continuous access to tropical refugia during the climatic deterioration characterizing the late Eocene to early Oligocene interval, which was seemingly lethal for primate communities elsewhere across the Holarctic continent (Jaeger *et al.* 1998; Marivaux *et al.* 2002a, b, 2004, 2005, 2006; Antoine *et al.* 2003a, b; Jablonski 2003, 2005; Dawson *et al.* 2006, Rust *et al.* 2023).

Our conclusions regarding the taxonomical affinities of *Welcommoides gurki* suggest closer relationships with merialines than with paroxyclaenines. In Western Europe, it seems that Merialinae become extinct at the end of the Ypresian, long before the 'Grande Coupure'. Solé *et al.* (2019) hypothesized that a faunal turnover took place at the end of the Ypresian in Europe ('Ypresian-Lutetian Mammal Turnover') when a transient cooling is recorded in the *Basin de Paris* (Huyghe *et al.* 2015), that is, after the Early Eocene Climatic Optimum (EECO; 50–47 Ma). In North America, the climatic deterioration after the EECO resulted in major diversity loss (Bridgerian Crash; Woodburne *et al.* 2009). The disappearance of the Merialinae in Europe might then be related to this climatic deterioration. Accordingly, South Asia seems to have already acted as a tropical refugium for the merialine paroxyclaenids at the end of the Ypresian and later.

CONCLUSION

This new paroxyclaenid species from the lower Oligocene of Pakistan underscores the existence of connections between Europe and the Indian subcontinent during the Ypresian. It also illustrates the case of a mammal group that disappeared from Europe at the end of the Ypresian (c. 50 Ma), but survived somewhere for almost 20 myr and appeared in the Indian subcontinent by c. 30 Ma. However, the evolutionary history of this paroxyclaenid lineage in South Asia remains entirely unknown. Paroxyclaenids have so far never been recorded in Eocene fossil-bearing localities of the Indian subcontinent, South Asia, or Asia in general. This total blank in the fossil record obscures our understanding of the evolutionary history of this enigmatic mammal group in this South Asian Province. Basically, very little is known about the terrestrial palaeobiodiversity of the tropical areas of South and Southeast Asia during most of

the Palaeogene. For the Indian subcontinent, the main localities available to palaeontologists are Vastan in India (Ypresian) and few other early to middle Eocene localities in Pakistan and India, as well as the foothills of the Sulaiman Range for the Oligocene. We hope that such an unexpected occurrence would trigger new occurrences of paroxyclaenids in other parts of Asia, notably through re-examination of unidentified mammal specimens in collections.

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DATA ARCHIVING STATEMENT

Data for 3D models of fossil teeth described in this study are available in MorphoMuseum (<https://doi.org/10.18563/journal.m3.182>). This published work and the nomenclatural acts it contains, have been registered in ZooBank: <https://zoobank.org/references/58AE237E-50D4-4353-A947-727D4EE863F5>

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TABLES

Table 1. Measurements (in mm) of the specimens of *Welcommoides gurki* gen. et sp. nov. from Paali Nala locality (Dera Bugti locus C2; lower Chitarwata Formation; Bugti Member; Bugti Hills; Balochistan; Pakistan).

Specimen	Locus	Mesiodistal length	Buccolingual width	Mesiodistal length / Buccolingual width
UM/DBC 2225	m3	5.67	3.45	1.64
UM/DBC 2226	m3	5.60	3.34	1.68
UM/DBC 2227	m3	-	3.17	-
UM/DBC 2230	DP4	5.17	5.13	1.01
UM/DBC 2228	M1	5.43	6.74	0.81
UM/DBC 2229	M2	4.64	5.77	0.8
UM/DBC 2231	M3	4.44	5.06	0.88
UM/DBC 2232	M3	3.93	5.13	0.77
UM/DBC 2233	M3 (worn enamel)	3.49	4.82	-
UM/DBC 2234	M3	4.56	-	-
UM/DBC 2236	M2	4.90	6.38	-

Table 2. Body mass estimates (in g) for *Welcommoides gurki**

M1 estimated based on comparison with	All mammals	Large Mammals (> 500 g)	Herbivores	Mean
<i>Paraspaniella gunnelli</i>	3058	4219	4692	3990
<i>Fratrodon tresvauxi</i>	3467	4689	5271	4476

* based on the method developed by Legendre (1986).

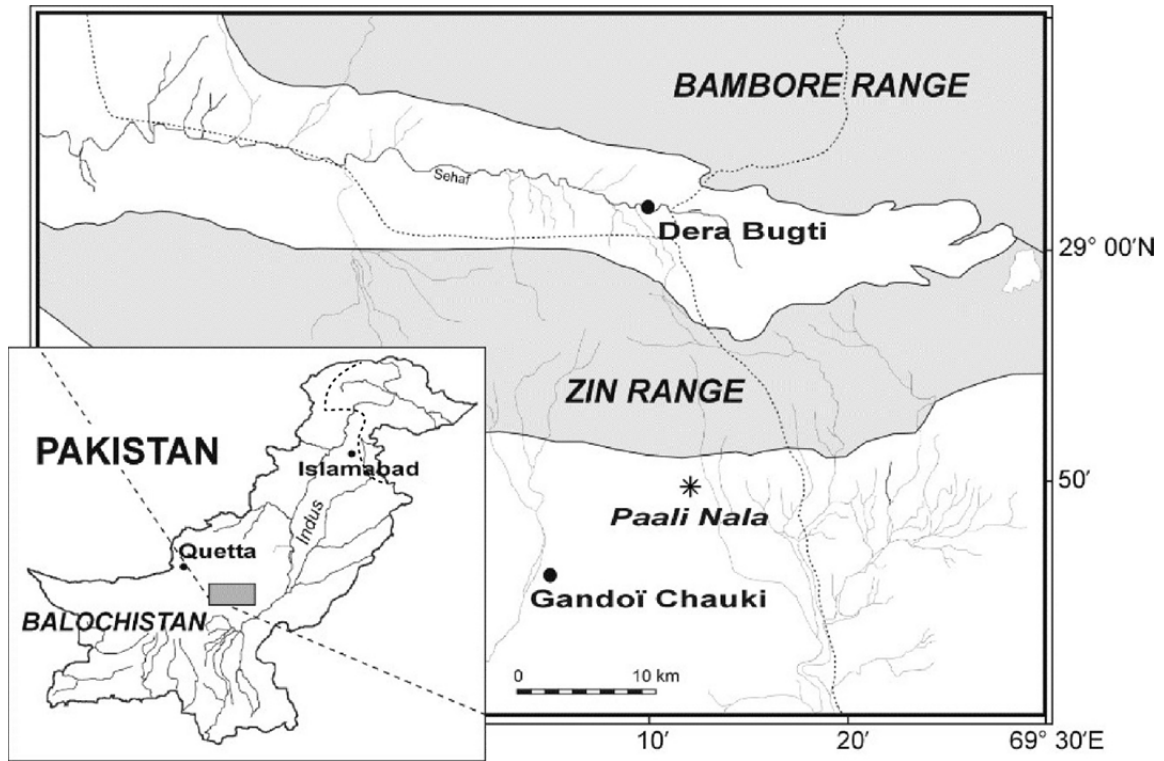


Fig. 1. Location map of the early Oligocene Paali Nala DBC2 fossil-bearing locality (Bugti Hills, eastern Balochistan, Pakistan).

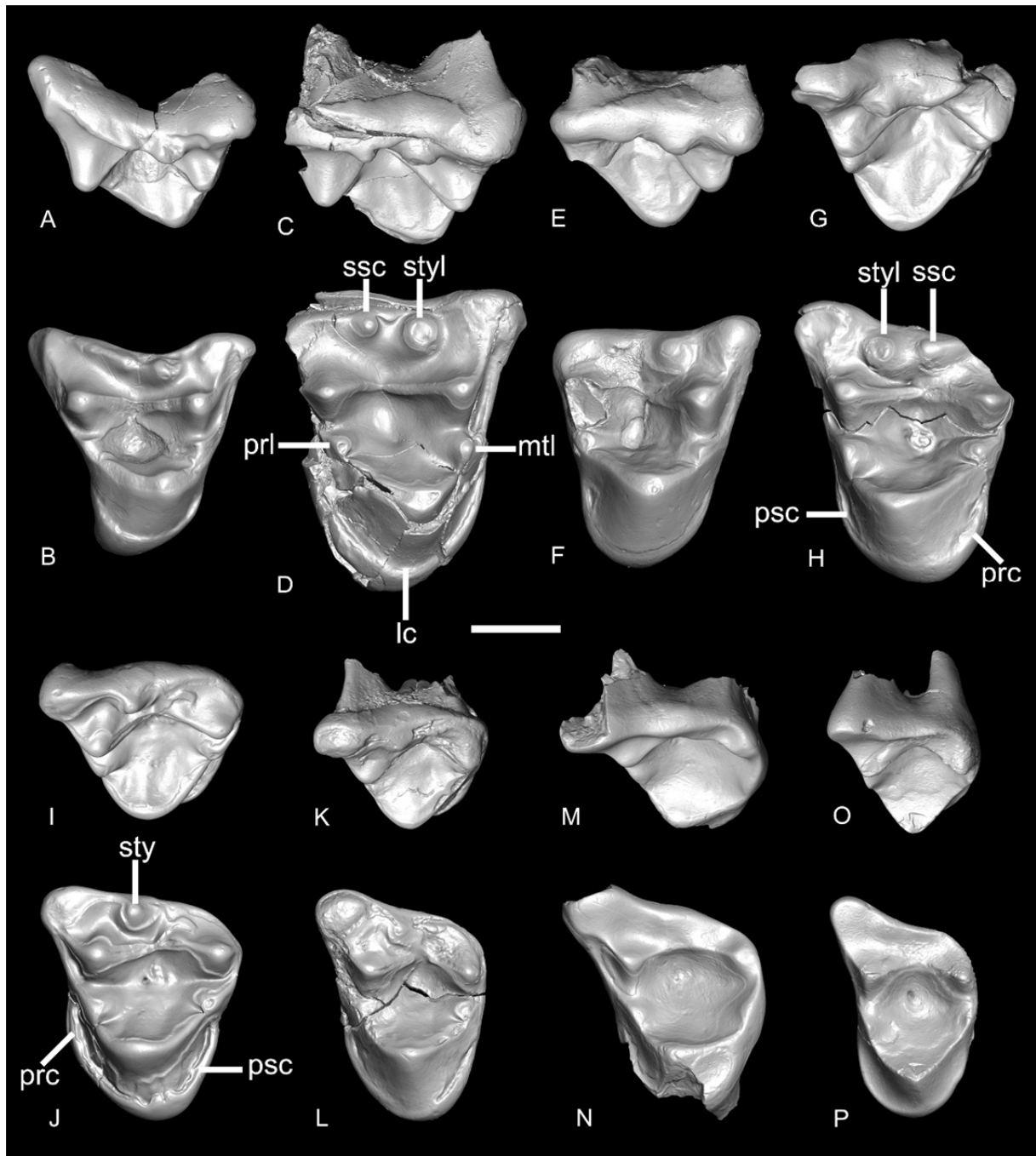


Fig. 2. Upper teeth of *Welcommoides gurki* gen. et sp. nov. from the Paali Nala DBC2 locality (Dera Bugti locus C2; Bugti Member, lower Chitarwata Formation; Bugti Hills; Balochistan; Pakistan). **A–B**, UM/DBC 2230, right (R) DP4 in labial (A) and occlusal (B) views; **C–D**, UM/DBC 2228, RM1 in labial (C) and occlusal (D) views; **E–F**, UM/DBC 2229, RM2 in labial (E) and occlusal (F) views; **G–H**, UM/DBC 2236, left (L) M2 in labial (G) and occlusal (H) views; **I–J**, UM/DBC 2231, LM3 in labial (I) and occlusal (J) views; **K–L**, UM/DBC 2232, LM3 in labial (K) and occlusal (L) views; **M–N**, UM/DBC 2234, LM3 in labial (M) and occlusal (N) views; **O–P**, UM/DBC 2233, LM3 in labial (O) and occlusal (P) views. **Abbreviations:** *lc*, lingual cingulum; *mtl*, metaconule; *prc*, precingulum; *prl*, paraconule; *ps*, parastyle; *psc*, postcingulum; *ssc*, second stylocone (cusp C); *styl*, pseudo-stylocone. Scale bar represents 2 mm.

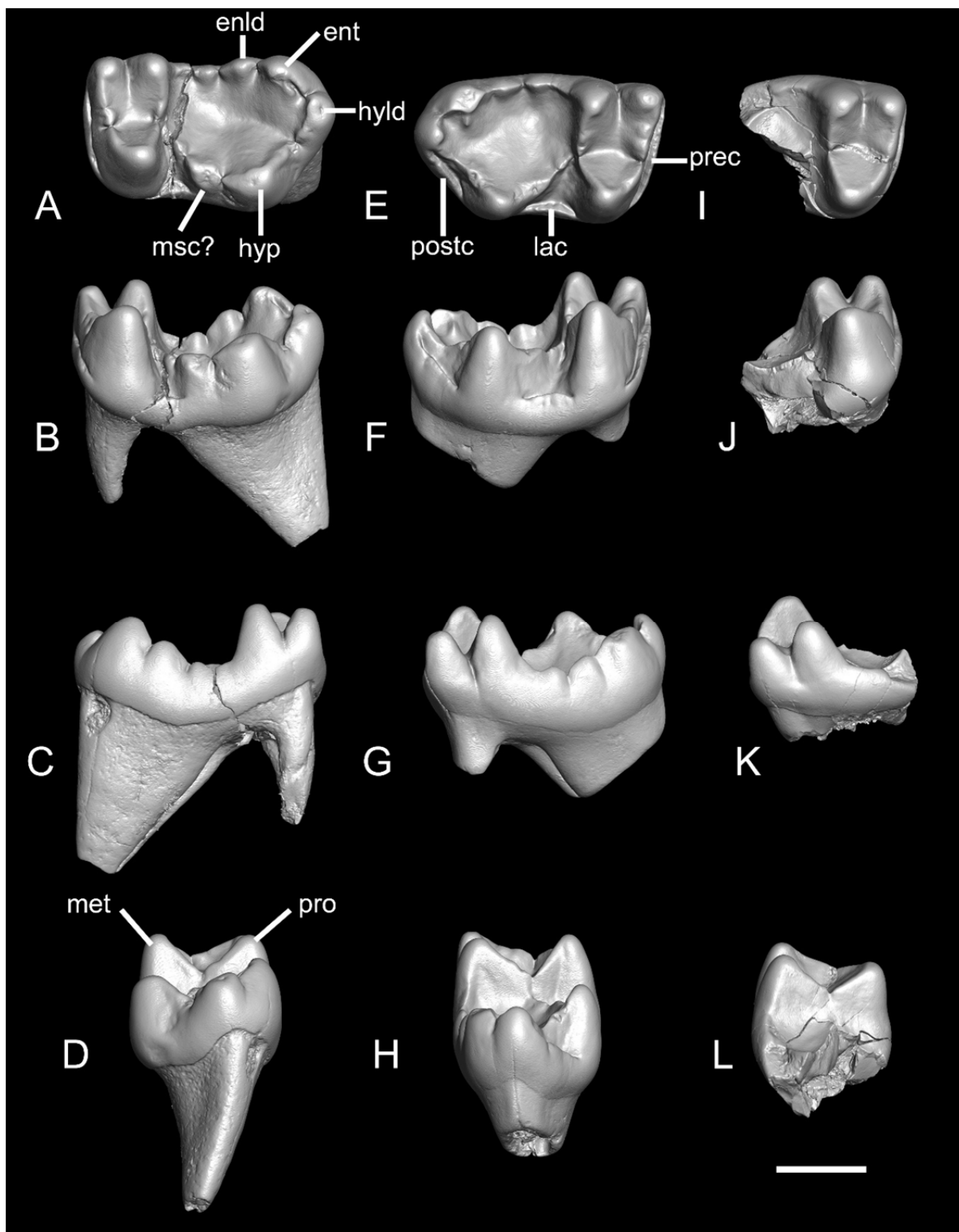


Fig. 3. Lower teeth of *Welcommoides gurki* gen. et sp. nov. from the Paali Nala DBC2 locality (Dera Bugti locus C2; Bugti Member, lower Chitarwata Formation; Bugti Hills; Balochistan; Pakistan). **A–D**, UM/DBC 2225, Lm3 in occlusal (A), labial (B), lingual (C), and distal (D) views; **E–H**, UM/DBC 2226 (Holotype), Rm3 in occlusal (E), labial (F), lingual (G), and distal (H) views; **I–L**, UM/DBC 2227, Rm3 in occlusal (I), labial (J), lingual (K), and distal (L) views. **Abbreviations:** **enld**, entoconulid; **ent**, entoconid; **hyld**, hypoconulid; **hyp**, hypoconid; **lac**, labial cingulid; **met**, metaconid; **msc?**, mesoconid?; **postc**, postcingulid; **prec**, precingulid; **pro**, protoconid. Scale bar represents 2 mm.

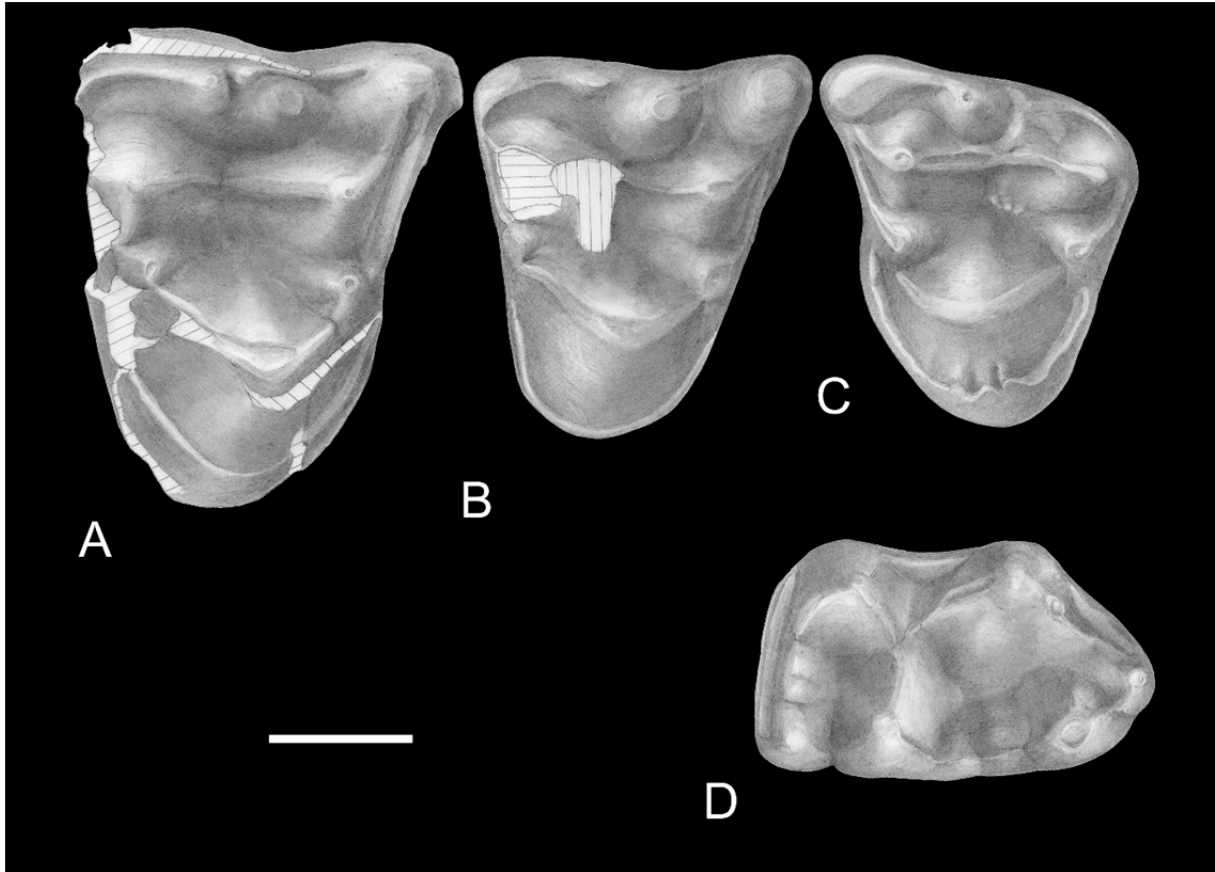


Fig. 4. Reconstruction of the upper and lower molar series of *Welcommoides gurki* gen. et sp. nov. from the Paali Nala DBC2 locality (Dera Bugti locus C2; Bugti Member, lower Chitarwata Formation; Bugti Hills; Balochistan; Pakistan). **A**, UM/DBC 2228, RM1; **B**, UM/DBC 2229, RM2; **C**, UM/DBC 2231, LM3; **D**, UM/DBC 2226, Rm3. Images A and B are reversed. Scale bar represents 2 mm. Drawings are from L. Meslin (Centre National de la Recherche Scientifique).

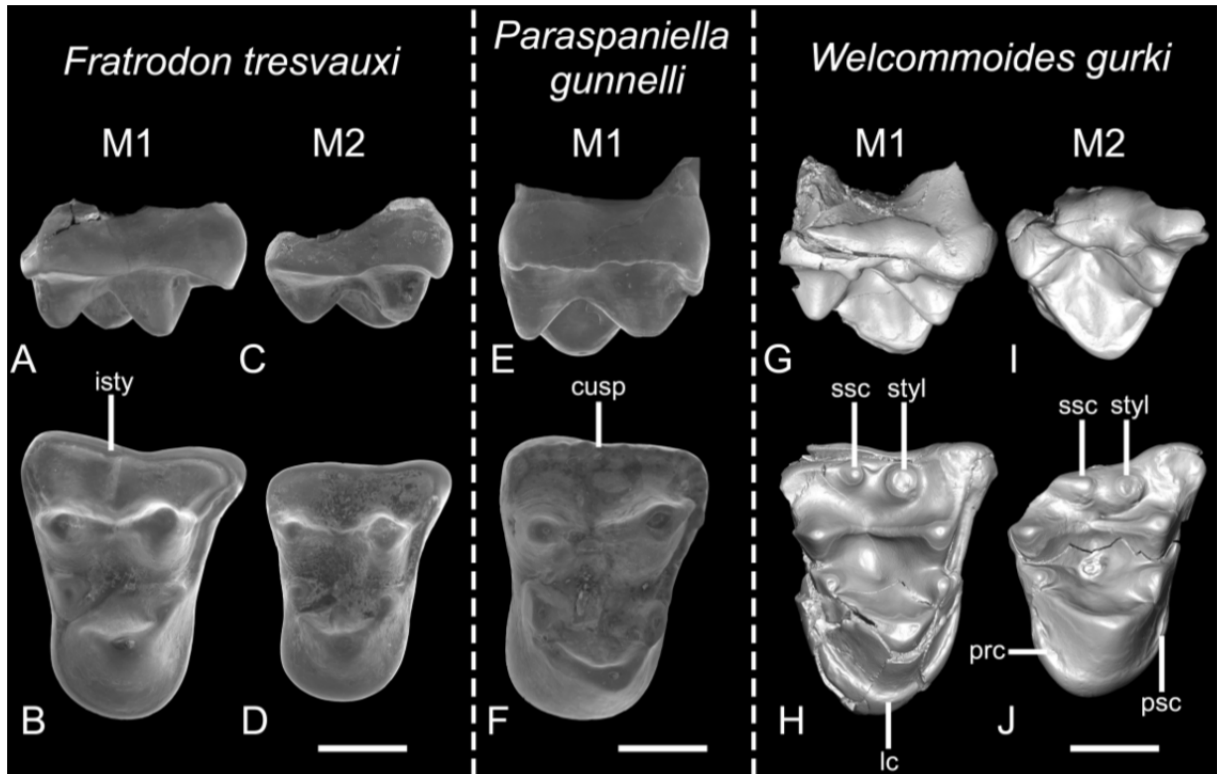


Fig. 5. Comparison of merialine upper molars. *Fratrodon tresvauxi*: **A–B**, RBINS Cast-Vert-32468-2240, LM1 in labial (A) and occlusal (B) views; **C–D**, MNHN.F.AV5714, LM2; in labial (C) and occlusal (D) views. *Paraspaniella gunnelli*: **E–F**, MNHN.F.SLP-PR-29 2097, RM1 in labial (E) and occlusal (F) views. *Welcommoides gurki* gen. et sp. nov.: **G–H**, UM/DBC 2228, RM1 in labial (G) and occlusal (H) views; **I–J**, UM/DBC 2236, LM2 in labial (I) and occlusal (J) views. **Abbreviations:** **cusp**, cusplation; **lc**, lingual cingulum; **styl**, pseudo-stylocone; **ssc**, second stylar cusp (cusp C); **prc**, precingulum; **psc**, postcingulum. Images A–D and I–J are reversed. All scale bars represent 2 mm.

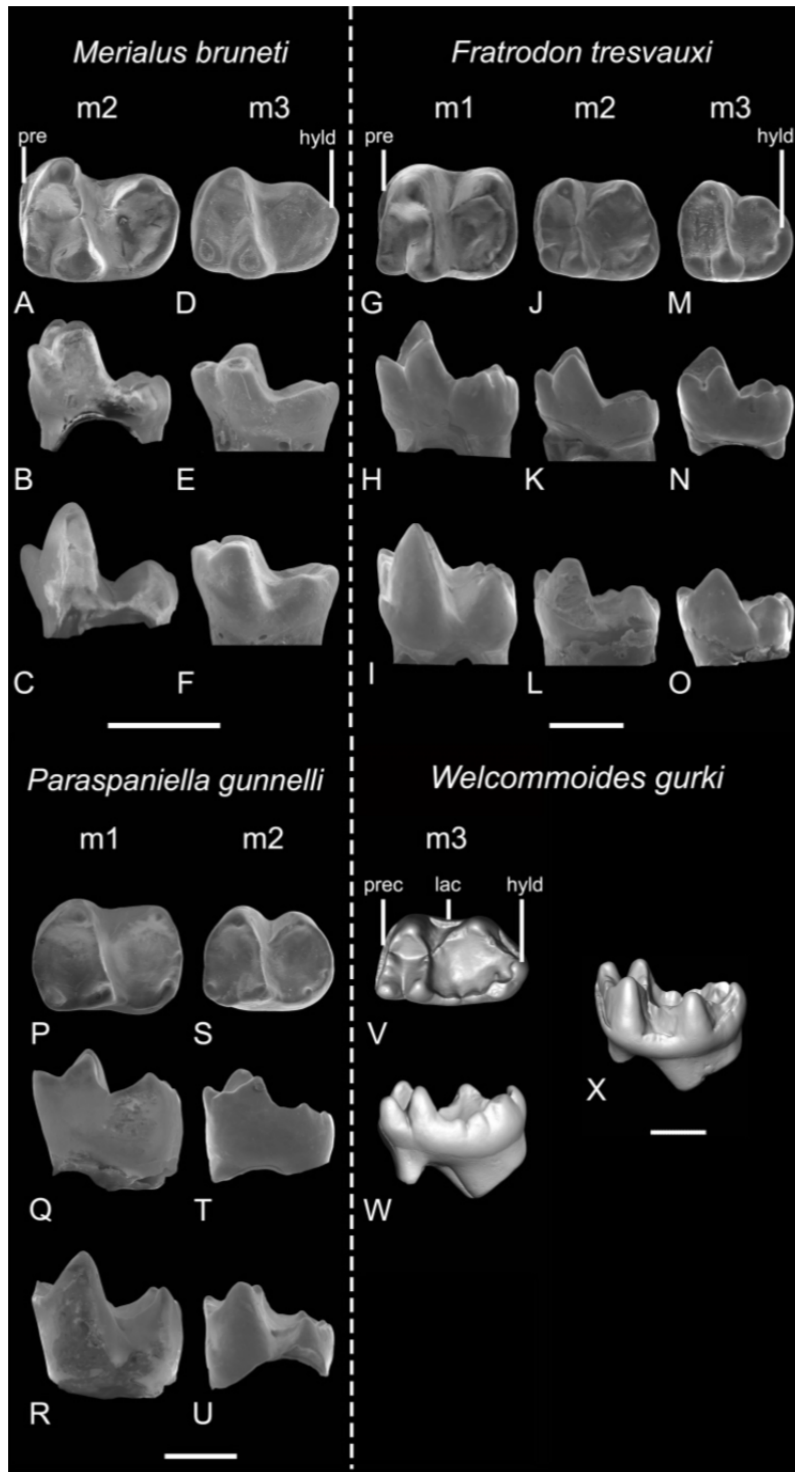


Fig. 6. Comparison of merialine lower molars. *Merialus bruneti*: **A–C**, MNHN.F.Louis23.Py, Lm2 in occlusal (A), lingual (B), and labial (C) views; **D–F**, UM/POY12, Lm3 in occlusal (D), lingual (E), and labial (F) views. *Fratrodon tresvauxi*: **G–I**, MNHN.F.Louis189Mu, Rm1 in occlusal (G), lingual (H), and labial (I) views; **J–L**, MNHN.F.Louis190Mu, Rm2 in occlusal (J), lingual (K), and labial (L) views; **M–O**, MNHN.F.CEB 550, Rm3 in occlusal (M), lingual (N), and labial (O) views. *Paraspaniella gunnelli*: **P–R**, MNHN.F.SLP-29-PE 1327, Lm1 in occlusal (P), lingual (Q), and labial (R) views; **S–U**, MNHN.F.GR 7601, Rm2 in occlusal (S), lingual (T), and labial (U) views. *Welcommoides gurki* gen. et sp. nov.: **V–X**, UM/DBC 2226, Rm3 in occlusal (V), lingual (W), and labial (X) views. **Abbreviations**: **prec**, precingulid; **hyld**, hypoconulid; **lac**, labial cingulid. Images A–B, D–E, I, L, O, P–Q, U and X are reversed. All scale bars represent 2 mm.

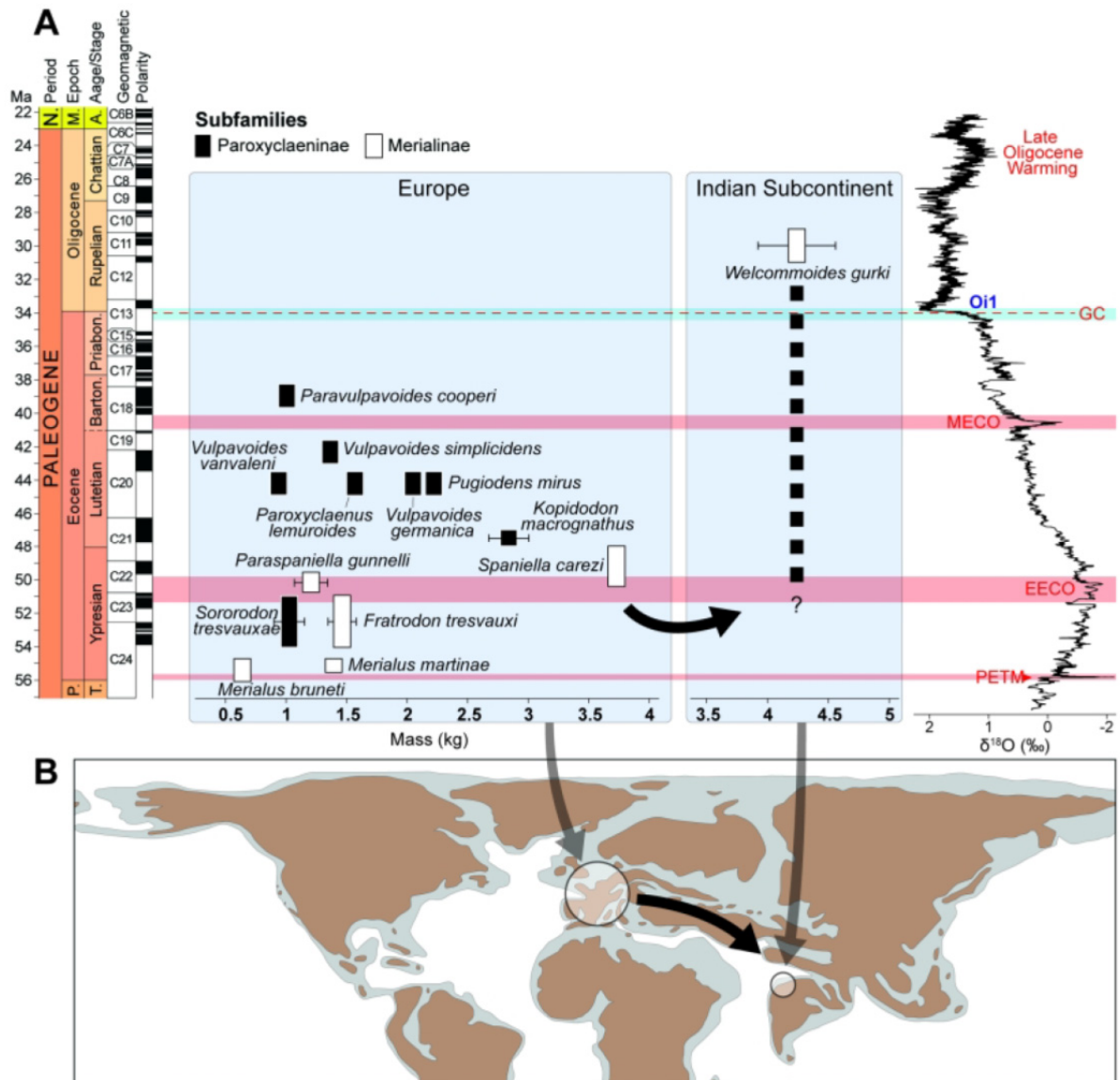


Fig. 7. Evolutionary history and paleogeography of paroxyclaenids. **A**, temporal and change in body mass in paroxyclaenids. **B**, geographical distribution. The values plotted are the averages of the body masses estimated using the method designed by Legendre (1986); the data are available in Solé *et al.* (2019) and Table 2. The exact timing and dispersal route of the dispersal of Paroxyclaenidae in India is unknown but probably occurred in the Ypresian (black arrow on B). The most notable Eocene climatic warming phases are highlighted with pink horizontal bars; climatic cooling at the onset of the Oligocene is indicated with the blue bar. **Abbreviations:** EECO, Early Eocene Climatic Optimum; GC, ‘Grande Coupure’; MECO, Middle Eocene Climatic Optimum; Oi-1, Oligocene Oi-1 event; PETM, Paleocene-Eocene Thermal Maximum. Palaeogeographical map adapted from Barrier *et al.* (2008).