



Listriodon dukkar sp. nov. (Suidae, Artiodactyla, Mammalia) from the late Miocene of Pasuda (Gujarat, India): the decline and extinction of the Listriodontinae

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Abstract

The Listriodontinae were a common and widespread group of Suidae (pigs) that lived in an area extending from Portugal to China and to southern Africa. Here, we describe the new species *Listriodon dukkar* from Pasuda (Gujarat, India). It shares features with *Li. pentapotamiae*, evolved from it, and is the last representative of this lineage. The Listriodontinae flourished for about 10 million years, reached their maximum diversity and geographic extension during the Mid-Miocene Climatic Optimum (about 17–13.6 Ma), and their last records are close in age and date to ~ 9.8 Ma in the Indian Subcontinent, 9.78 Ma in Europe, and ~ 10 Ma in Africa. We review the environments in which the last listriodont lineages lived and went extinct. Their extinctions occurred against a background of increasing seasonality, vegetation change, a rise in bovid diversity and abundance, and local events, such as the European Vallesian Crisis and a dramatic drop in tragulid abundance in the Siwaliks. However, changes in the atmospheric pCO₂ may have contributed to their decline and extinction in all their geographic distribution. Decreasing pCO₂ is expected to have decreased sugar content and increased protein content of leaves and fruit. Hindgut fermenting Suoidea have higher protein requirements, while foregut fermenting Suoidea are more efficient in digesting sugars. Listriodontinae were probably foregut fermenters and were less well adapted in a low pCO₂ world.

Keywords Suoidea · Vallesian crisis · Folivore · pCO₂ · Atmospheric carbon dioxide · Food protein content

Introduction

The Listriodontinae (Suidae, Suoidea) were a group of pigs that was common and widespread during the Early and Middle Miocene of the Old World (Van der Made 1996a; Pickford and Morales 2003; Orliac 2007, 2009) and that formed

an important part of the ecosystems of their time. Within this group, various lineages evolved towards lophodonty (teeth with transverse crests), a convergence with the tapirs, with which initially they were confused (Nicolet 1844; von Meyer 1846; Lydekker 1876; Rusconi 1937). Tapirs are folivores and frugivores (Wilson and Mittermeier 2011) and a folivorous diet has been inferred for these pigs, as well (Leinders 1977a, b; Hunter and Fortelius 1994).

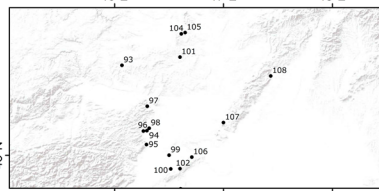
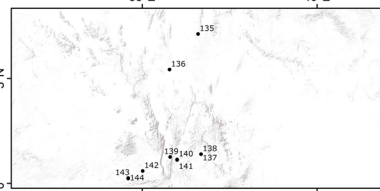
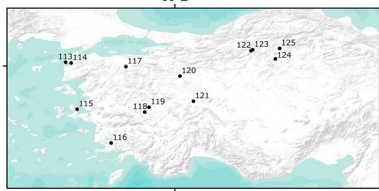
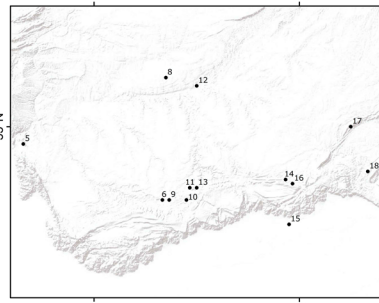
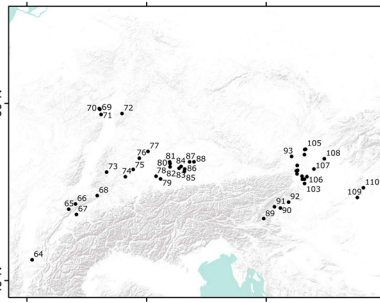
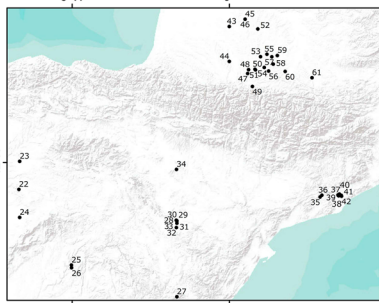
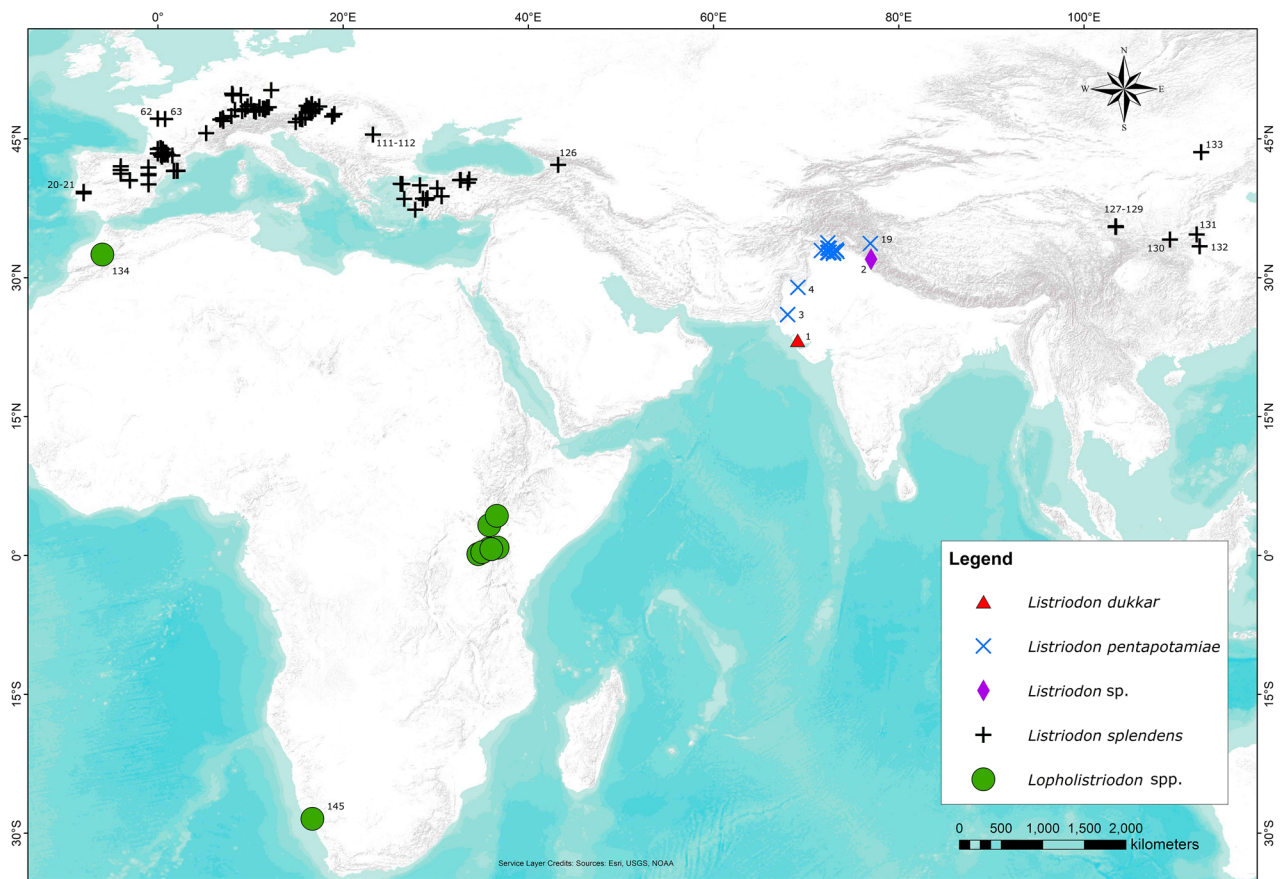
Here, we describe a new species of *Listriodon* from Pasuda (Kutch, India), a suoid species in which not only the molars were perfectly lophodont, but also the premolars. It is more derived than the Indian *Li. pentapotamiae*, with which it shares features and from which it evolved. This suggests that it is the last listriodont species from the Indian Subcontinent, which is in line with earlier interpretation of the age of Pasuda as early Late Miocene (Bhandari et al. 2015).

The Listriodontinae were widely distributed in Europe, the Indian Subcontinent, Asia, and Africa (Fig. 1) covering latitudes from 0 to about 50°. They reached their highest diversity during the Middle Miocene Climatic Optimum,

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no.	Locality	no.	Locality	no.	Locality	no.	Locality
1	Pasuda	21	Azambujeira inf.	42	Castell de Barberá	63	Manthelan
2	Nurrur	22	La Cisterniga	43	Sansan	64	La Grive M, L7, oc
3	Gaj River	23	Cerro del Otero	44	Villefranche d'Astarac	65	Loche
4	Vihova Fm, Bugti Hills	24	Coca	45	Simorre	66	La Chau-de-Fonds
5	Daus Khel 17	25	Paracuellos V	46	Tournan	67	Lac Morat
6	Kundal Nala	26	Paracuellos III	47	Bonnefont	68	Anwill
7	Kushalgar	27	Mas del Olmo	48	Tri-sur-Brise	69	Wissberg
8	Dhulian	28	Arroyo del Val I, IV, VI	49	St. Gaudens	70	Gau Weinhelm
9	Chinji	29	Manchones I & II	50	Larroque de Magnoac	71	Esselborn
10	Bhitomar	30	Mureno	51	Castelnau Magnoac	72	Eppelsheim
11	Kadirpur	31	Torril III	52	Péjouan	73	St. Georgen
12	Khauri	32	Nombrevilla II	53	Orezezan	74	Möskirch
13	Sethi Nagri	33	Solera	54	Boulogne	75	Morsingen
14	Dhok Bun Ameer Khatoon	34	La Ciesma	55	Calsteinau de Barbares	76	Laichingen
15	Lava village	35	Can Mata	56	Escanecrobe	77	Steinheim
16	Dhok Tallan 189	36	Hostalets	57	Mongausy	78	Markt Rettenbach
17	Chabbar Syedan	37	Can Ponsic I	58	L'Isle en Dodon	79	Hammerschmiede
18	Andar Kas Loc. 150	38	Can Feliu	59	Lombez	80	Stätzing
19	Ramagar	39	San Quirze	60	Le Fousseret	81	Friedberg
20	Aveiras de Balxo	40	Santia	61	Saverdun	82	Mering
		41	Can Liobateres 1	62	Doué-la-Fontaine	83	Kleineisenbach
						84	Prittibach
						85	Aumeister
						86	Grosslappen
						87	Massenhausen
						88	Wartenberg
						89	St. Steph
						90	Hasselbach
						91	Gratkorn
						92	Löffelbach
						93	Oberhollabrunn
						94	Mauer
						95	Eichkogel
						96	Atzgersdorf
						97	Nussdorf= Wien Heiligenstadt
						98	Altmandorf bei Heidling
						99	Mannersdorf
						100	Loretto
						101	Klein Hadersdorf
						102	Leithagebirge
						103	St. Margarethen
						104	Stützenhofen
						105	Fünfkirchen
						106	Kaiserssteinbruch
						107	Neudorf Sandberg
						108	Jablonica
						109	Soósút
						110	Szentendre
						111	Menisor
						112	Krivádia railway station
						113	Nebisuyu
						114	Bayraktepe
						115	Mordogan
						116	SarıÇay
						117	Pasalar
						118	Esmé Akçaköy
						119	Akçaköy
						120	Soğca
						121	Yaylaçilar
						122	Inönü 1
						123	Lower Sinap
						124	Candir
						125	Çorak Yerler
						126	Korethi
						127	Laogou
						128	Guonigou
						129	Guanghe
						130	Langshuiquou
						131	Xinan
						132	Erlangang
						133	Tung gur
						134	Beni Mellal
						135	West Stephanie - Buluk
						136	Moruot
						137	Mbagathi
						138	Fort Ternan
						139	Muruyur
						140	Barute, Ngorora Fm Mb A
						141	Ngorora Fm Mbs B, C, D
						142	Nyakach
						143	Maboko
						144	Majiwa
						145	Arisdrift

Fig. 1 Geographic distribution of *Listriodon dukkar*, *Li. pentapotamiae*, *Listriodon* sp. (either *Li. dukkar* or *Li. pentapotamiae*), *Li. splendens*, and *Lopholistriodon* (mainly after Van der Made, 1996a, b). In some cases, one dot is a cluster of localities: Gaj River indicates 14 HGSP localities and Chinji for 18 localities (IVAU and BSP collections)

after which they started to decline everywhere. This contrasts with the latitudinal gradient in extinction seen in most Suoidea, like the Tetraconodontinae (Van der Made 1992, 1999) and Hyotheriinae (Van der Made 2010). This synchronous decline of the Listriodontinae living in areas from the tropics to temperate climates suggests a global cause. Their decline started with the end of the Mid-Miocene Climatic Optimum at 13.6 Ma and their extinction coincided with an event in Europe that was baptised as the mid-Vallesian Crisis, or shorter Vallesian Crisis, that also marked the local extinction of the primitive Hominoidea (Agustí and Moyà Solà 1990; Moyà Solà and Agustí 1990).

This paper aims to describe the new species of *Listriodon*, to interpret the environment in which the Indian *Listriodon* lineage lived, and to discuss the possible reasons for decline and extinction of the Listriodontinae.

Geological background and antecedents on Pasuda

The lithostratigraphic sequence of Kutch basin is known to have lithological exposures with fossil fauna spanning from the Mesozoic to Pleistocene (Biswas 1992) (Fig. 2a, b). The Neogene deposits of the Kutch basins are classified into three formations as Khari Nadi, Chhasra, and Sandhan formations (Biswas 1992). The Oligocene Maniyara Fort Formation is overlain by the Khari Nadi Formation with a weak erosional unconformity due to a transgressive overlap (Catuneanu and Dave 2017). The Khari Nadi Formation comprises siltstone, sandstone, and clay, and is dated as early Miocene (Aquitanian: 23.03–20.43 ± 0.05 Ma; Hilgen et al., 2012). The uppermost part of this formation, with numerous bioturbation structures and pseudoconglomeratic beds on top, yields certain mammalian remains (Patnaik et al. 2014). The contact with the Chhasra Formation is conformable and gradational. This formation consists of grey to khaki green, laminated shale, siltstone, and argillaceous limestone at the lower part, and predominant siltstone and laminated silty shale at the upper part (Biswas 1992). The Chhasra Formation, dated as early Miocene (Burdigalian), has a disconformable contact with the younger Sandhan Formation (Biswas 1992). The Sandhan Formation is characterised by the presence of medium-to-coarse grain micaceous sandstone, quartzose sandstone, clay, siltstone, sandstone, and conglomerate. The coarse-grained sandstone consists

of pebbles and concretionary nodules, and the conglomeratic beds have yielded both marine and terrestrial vertebrate remains (Bhandari et al. 2015; Singh et al. 2019; Sharma et al. 2021).

The present *Listriodon* specimen was recovered from the fossiliferous deposits exposed at Pasuda section (N23°14'27.81" and E70°11'00.59") situated about 1 km west of the Pasuda main road. Pasuda is a small village, situated approximately 65 km east of district Headquarter, Bhuj, of Kutch District of Gujarat, India. The lithostratigraphic section of the Pasuda locality comprises massive sand, silt, clay, and conglomerate beds (Fig. 2c, d). The latter contain calcareous nodules, agate pebbles, very coarse sand, and mudclasts, and has occasionally a coarsening upward sequence, suggesting a crevasse splay deposit (Bhandari et al. 2015). The conglomerate layer consisting of mud pebbles, nodules, and calcareous concretions yielded a rich assemblage of micro- and mega vertebrate fossils. Lithologically, these beds are different from Khari Nadi and Chhasra as the beds show abundant coarse-grained sandstone with pebbly clasts, calcareous nodules, agate pebbles, mud clast, and conglomerate, and show close similarity to the Sandhan Formation (Biswas 1992; Catuneanu and Dave 2017). The Tapar section, exposed nearly 2 km west of Pasuda, has a similar lithological and faunal composition and notably yielded the hominoid, *Sivapithecus*. Based on the presence and First Appearance Datum (FAD) of *Hipparion*, as well as on the associated fauna, Bhandari et al. (2015) proposed a Late Miocene (11–10 Ma) age for fossiliferous sites of Pasuda and Tapar. The Pasuda site is also known for mammalian fauna including murid rodents, *Giraffokeryx punjabiensis*, *Giraffa priscilla* (Bhandari et al. 2015) (see Table 1).

Materials and methods

The fossil from Pasuda described here (PUKP-1) is kept in the Centre of Advanced study in Geology, Panjab University, Chandigarh. This fossil has been compared with other fossils indicated in Table 2 and those described and figured by Van der Made (1996a), as well as many other specimens of *Li. pentapotamiae* housed at the Indian Museum, Kolkata.

The methods of study and tooth nomenclature follow Van der Made (1996a). This nomenclature is applicable to different groups of Artiodactyla, including Suoidea, Anthracotheriidae, and ruminants (which is better than having different nomenclatures for each of these groups). Molar cusps tend to have lobes or crests, usually a maximum of four, though not all are present in all taxonomic groups. These are called pre-, endo-, post-, and ectocrista or—cristid, depending on whether they originate on the anterior, interior, posterior, or exterior side of the tooth. Secondary cusplets or styles may be formed as part of these crests. The names are constructed

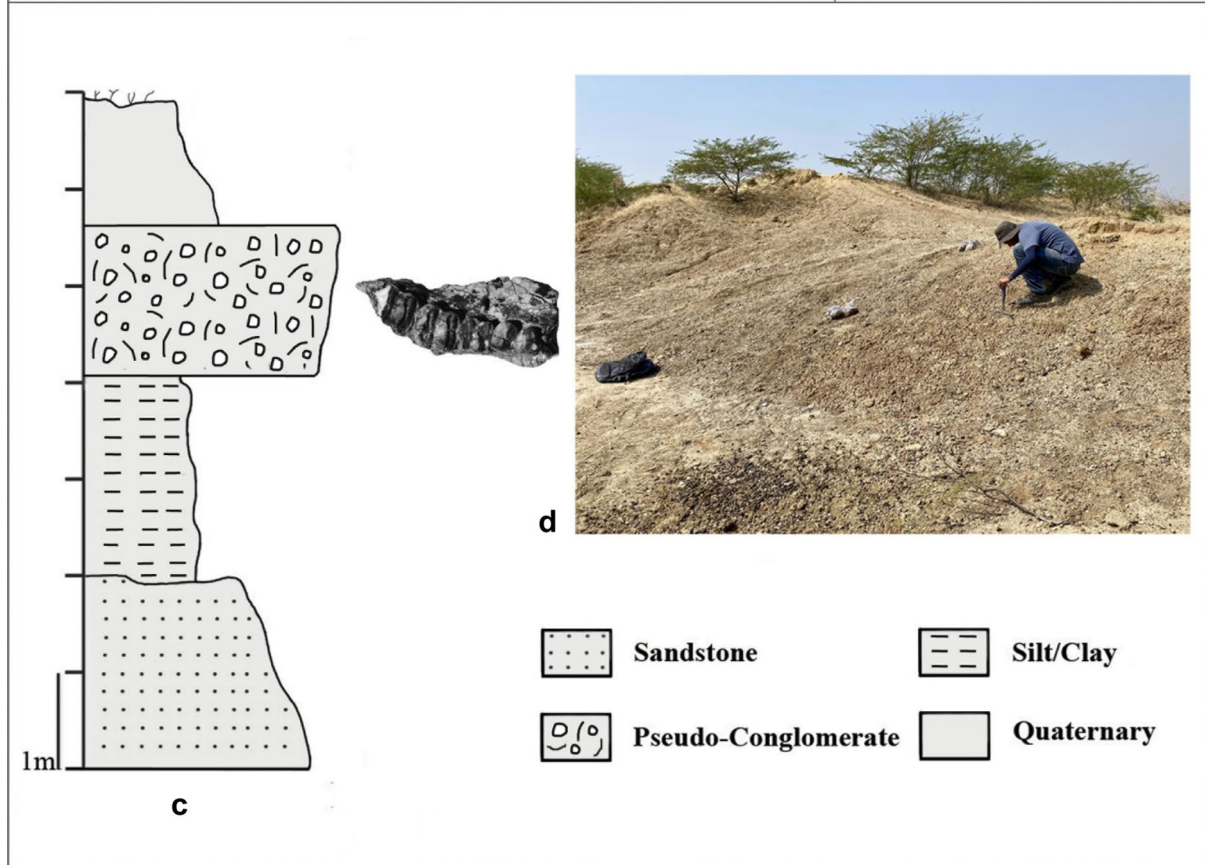
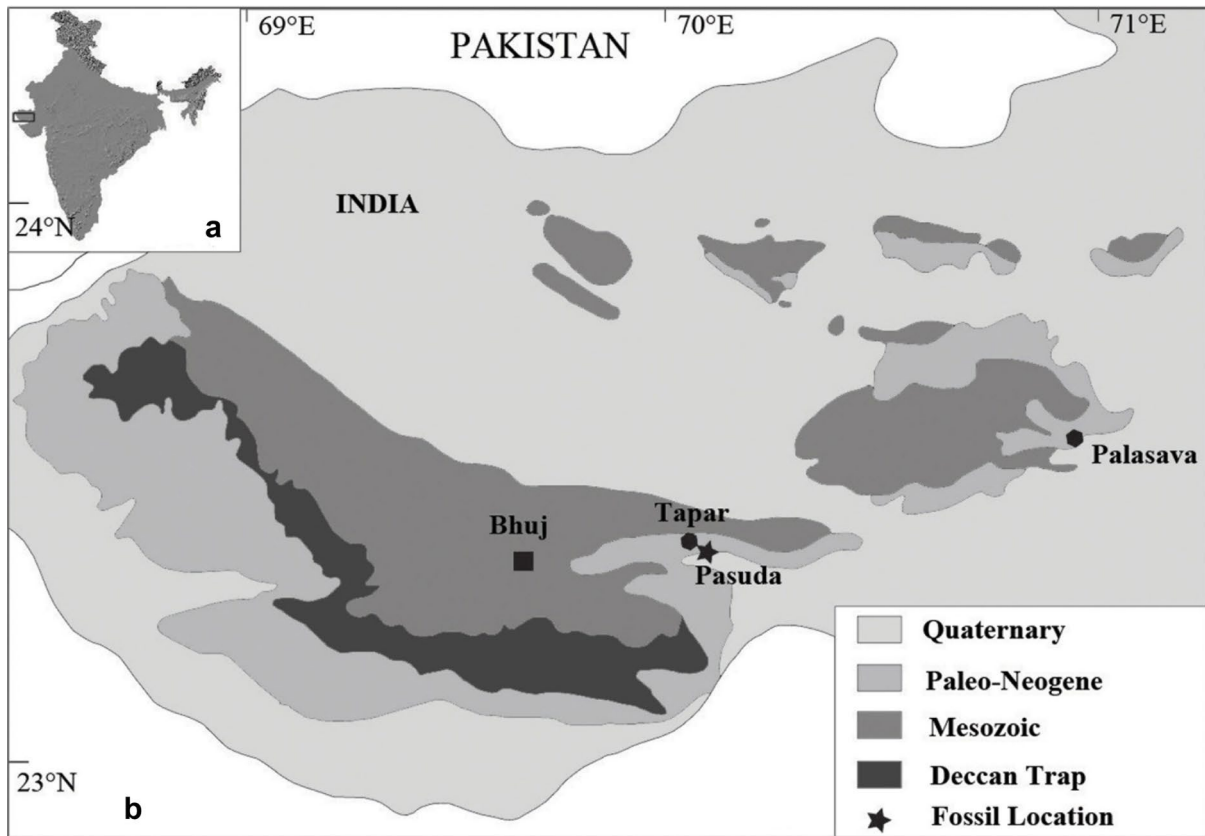


Fig. 2 Geographic and stratigraphic position of the find. **a** Map showing the position of the study area within Kutch, Gujarat, India. **b** Geological map of the Kutch area with the fossil locality indicated by star mark. **c** Stratigraphic column of the Pasuda locality. **d** The site where the fossil of *Listriodon dukkar* sp. nov. was recovered

in a logical way from general to particular: first comes the name of the cusp, then the position of the crest, secondary cusplet, or style. For example: protoprecrista, hypopreculid. The premolars are simpler, but the nomenclature is the same (Fig. 3).

The age of many localities is estimated using magnetostratigraphy and interpolation between the boundaries of the chrons. Dating of the Geomagnetic Polarity Time Scale (GPTS) has improved and the changes are particularly notable in the time period that is of interest here. For instance, the upper boundary of the long chron C5n.2n has varied: 8.87, 8.92, 9.92, 9.987, and 9.984 Ma (La Breque et al. 1977; Berggren et al. 1985; Cande and Kent 1995; Lourens et al. 2004; Hilgen et al. 2012). The Siwalik sequence is a classic example of a long sedimentary sequence dated by magnetostratigraphy (Opdyke et al. 1979; Johnson et al. 1982; Tauxe and Opdyke 1982). The ages given for faunal events in the Siwaliks (e.g., Barry et al. 1982, 1995, 2002; Barry and Flynn 1990) and elsewhere have been recalculated and are given, save in the cases where the differences are minimal. Here, we use the MN units (Mein 1975; De Bruijn et al. 1992) and a local Spanish biozonation (Daams and Freudenthal 1981; Van Dam et al. 1997) for European biostratigraphy. Comparisons of magnetostratigraphically dated micromammal localities (Kálin and Kempf 2009; Van der Meulen et al. 2012) and Suoidea (Van der Made 2020) show the MN units to be diachronous. Recent dates for the MN units are provided by Hilgen et al. (2012), but see also Van der Made (2020).

Systematic palaeontology

The Listriodontinae are a group of Suidae which evolved wide and low incisors and which had a tendency to evolve from bunodont to sublophodont (e.g., species of *Bunolistriodon* and the African *Lopholistriodon*) to lophodont (*Listriodon* and species of *Lopholistriodon*). In *Listriodon*, there are two lineages: *Li. pentapotamiae* in the Indian Subcontinent and *Li. splendens* in an area that extended from Europe to Anatolia and China. Falconer (1868) named *Li. pentapotamiae*, thinking it was a tapir. Lydekker (1878) named *Li. theobaldi*, but Pickford (1988) considered it to be synonym of *Li. pentapotamiae*. The type specimen of *Li. theobaldi* comes from Hasnot. Barry et al. (1982) indicated the temporal range of *Listriodon* in the magnetostratigraphic Hasnot section (about 11.5–10.5 Ma), the last occurrence coinciding

with the first of *Hipparion* in locality Y454. Van der Made (1996a) applied the name *Li. pentapotamiae theobaldi* to the more evolved and younger fossils and *L. p. pentapotamiae* to the older and more primitive ones. For the classification of the Listriodontinae, Van der Made (1996a, b, 2020) is followed here, though alternative classifications exist (Pickford and Morales 2003; Orliac 2007, 2009).

Some lineages of the Palaeochoeridae (or “Old World peccaries”), a primitive group of Suoidea, also evolved towards lophodonty, such as *Yunnanchoerus* and a genus that was called *Schizochorus*. The latter name is a junior homonym of a tapeworm and now is called *Schizoporcus* (Van der Made 2010). *Schizochorus* has been reported from the Siwaliks, but the material more likely represents *Yunnanchoerus* (Van der Made 1997a; Pickford 2017). For the Palaeochoeridae, the classification by Van der Made (2010) is followed here. Lately, a different classification has been proposed (Pickford 2017), but see discussion by Van der Made (2020).

Institutional abbreviations. CASGPU—Centre of Advanced Study in Geology, Panjab University, Chandigarh, India; CJFV—Collection J. F. de Villalta, Barcelona, Spain; FISH—Forschungs-Institut Senckenberg, Frankfurt, Germany; FMNH—Finnish Museum of Natural History, Helsinki, Finland; GML—Geological Museum, Lisbon, Portugal; GSP—Geological Survey of Pakistan, Islamabad, Pakistan; HGSP—Howard University—Geological Survey of Pakistan; IM—Indian Museum, Kolkata, India; IPS—Institut Català de Paleontologia Miquel Crusafont, Sabadell; IVAU—Instituut Voor Aardwetenschappen Utrecht, The Netherlands; IVPP—Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; KNM—Kenya National Museums, Nairobi, Kenya; MHNCF—Musée d'Histoire Naturelle, La Chaux-de-Fonds, Switzerland; MLGSB—Museu i Laboratori de Geologia del Seminari, Barcelona, Spain; MNCN—Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN—Muséum national d'Histoire naturelle, Paris, France; MTA—Maden Tetkik ve Arama, Ankara, Turkey; NMB—Naturhistorisches Museum, Basel; Switzerland; NWW—Naturhistorisches Museum Wien, Vienna; Austria; PDTCFAU—Paleoantropoloji, Dil ve Tarih Coğrafya Facultesi, Ankara Üniversitesi, Ankara, Turkey; PIMUZ—Paläontologisches Institut und Museum der Universität, Zürich, Switzerland; SMNS—Staatliches Museum für Naturkunde, Stuttgart, Germany; SNSB-BSPG—Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; UPM—Laboratoire de sédimentologie et paléontologie, Université de Provence, Marseille, France.

Anatomical abbreviations. In addition to the common ones: C^m and C^f for the upper canines of males and females.

Table 1 Provenance of the data used for comparison

Species	Locality	Collection	Origin of data
<i>Li. dukkar</i> sp. nov.	Pasuda	CASGPU	Choudhari, this paper
<i>Li. pentapotamiae</i>	Chinji Formation	IM, GSP, SNSB-BSPG, IVAU, FISF	Van der Made (1996a)
<i>Li. pentapotamiae</i>	Manchar Formation	HGSP	Van der Made (1996a)
<i>Li. pentapotamiae</i>	Various, Indian Subcontinent	IM	Van der Made, not published
<i>Li. splendens</i>	Arroyo del Val IV	IVAU, IPS	Van der Made (1996a)
	Arroyo del Val VI	IVAU	
	Aveiras de Baixo	GML	
	Çandır	MTA	
	Can Ponsic I	IPS	
	Castell de Barberà	IPS	
	Cerro del Otero	MNCN	
	La Chau-de-Fonds	MNCF	
	Eichkogel	NMW	
	“Gers”	MNHN	
	La Grive	MGL, IGF	
	Hostalets	IPS, MLGSB, CJFV	
	L’Ile-en-Dodon	FMNH (cast)	
	Inönü 1	MTA	
	Leithagebirge	NMW	
	Manchones I	IVAU, IPS	
	Neudorf Sandberg (Dvinska Nova Ves)	NMW	
	Pasalar	PDTCAU, PIMUZ	
	San Quirze	IPS, MGSCB, CJFV	
	Sansan	MNHN	
	Sarıçay	MTA	
	Simorre	MNHN, UPM	
	Sinap Formation, Lower	MNHN, MTA	
	Steinheim	SMNS, NMB	
	Villefranche d’Astarac	MNHN	
	Wartenberg	SNSB-BSPG, IVAU	
	Wien Heiligenstadt	NMW	
	Xinan	IVPP	
<i>Lo. kidogosana</i>	Ngorora Formation	KNM	Van der Made (1996a)
<i>Lo. akatidogus</i>	Fort Ternan	KNM	Van der Made (1996a)
	Beni Mellal	MNHN (cast)	
<i>S. sinapensis</i>	Lower Sinap Formation	MTA	Van der Made (2003a)
<i>S. vallesiensis</i>	Middle Sinap Formation	MNHN	Van der Made (2003a)
	La Tarumba	IPS	
<i>Y. lufengensis</i>	Lufeng	IVPP	Van der Made and Han (1994)

Table 2 Measurements (in mm) of PUKP-1 left P³-M³ of *Listriodon dukkar* sp. nov. from Pasuda

	P ³	P ⁴	M ¹	M ²	M ³
DAP	12.5	10.7	14.1	20.7	23.0
DTa			15.1	19.8	18.7
DTp	13.2	14.8	16.3	19.8	> 18.1

DAP antero-posterior diameter, *DTa* transverse diameter of the anterior lobe, *DTp* transverse diameter of the posterior lobe

Superfamily **Suoidea** Gray, 1821

Family **Suidae** Gray, 1821

Subfamily **Listriodontinae** Gervais, 1859

Tribe **Listriodontini** Gervais, 1859

Listriodon von Meyer, 1846

Type species. Listriodon splendens von Meyer, 1846.

Diagnosis. Lophodont Listriodontinae with high crowned C^m that curve outwards and upwards (after Van der Made, 1996a, b).

Included species. *L. splendens* and *L. pentapotamiae*.

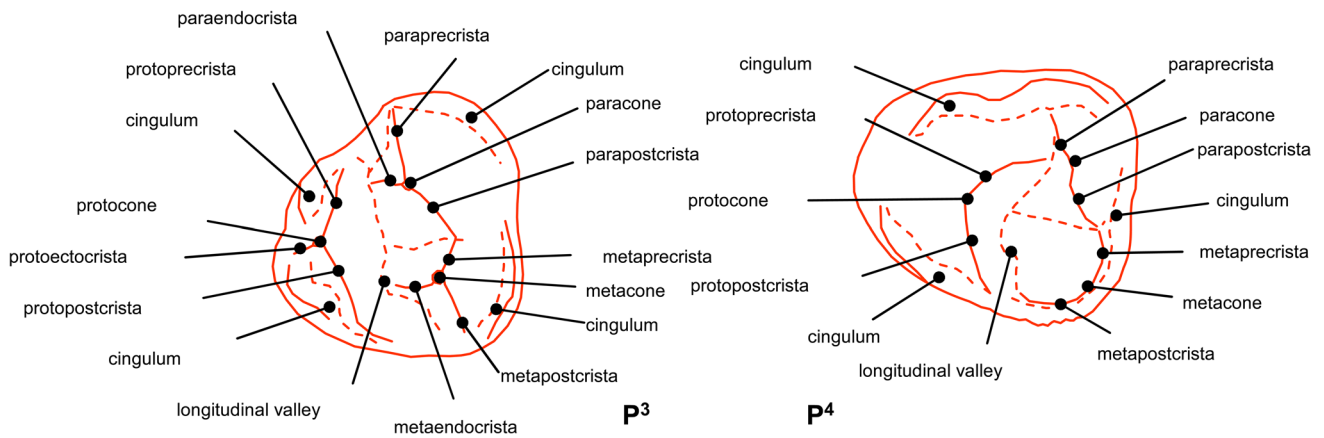


Fig. 3 Nomenclature of the teeth shown on a P³ and P⁴ of *Listriodon splendens*

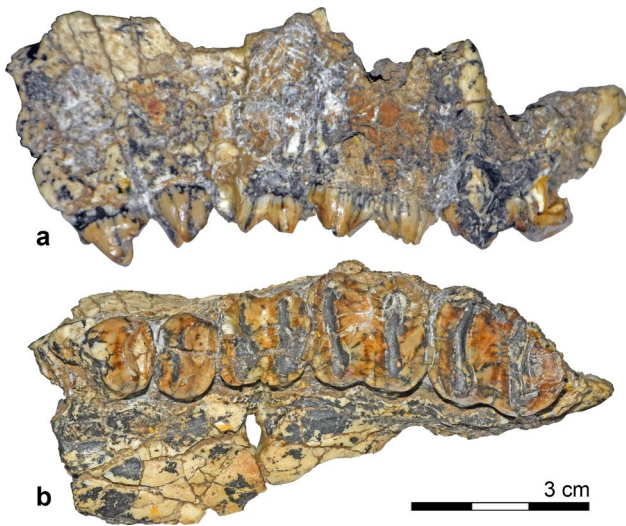


Fig. 4 PUKP-1—*Listriodon dukkar* sp. nov. from Pasuda: collection number—left maxilla with P³-M³: **a** occlusal and **b** buccal views

***Listriodon dukkar* sp. nov.**

Holotype. PUKP-1—left maxilla with P³ till M³ (Fig. 4).

Type locality. Pasuda, Gujarat, India.

Age of the type locality. early Late Miocene (probably a little less than 10 Ma).

Zoobank LSID. urn:lsid:zoobank.org:act:03E63D53-F626-4A75-B671-3E3CFA0B43D9.

Diagnosis. species of *Listriodon* with wide P³⁻⁴ with perfect lophs, formed by the protocone and paracone, and with the posterior part of the crowns shortened as a result of the reduction of the metacone (in the P⁴), parapostocrista and protopostocrista.

Differential diagnosis. *Listriodon dukkar* differs from *L. pentapotamiae* in the P³ having a large protocone and well-developed protolophs and in the P³⁻⁴ having shorter metapostcristae and in being shorter and relatively wide. It differs from *L. splendens* in the P³ having a large protocone and well-developed protoloph and shorter metapostocrista and in the P⁴ lacking completely a metacone, having a more reduced protopostocrista, in the protocone being placed more anteriorly, forming a more perfect protoloph, and in being smaller. It differs from *Lopholistriodon* in having less elongate M¹⁻², less-developed cingula in the P³⁻⁴, in the P³ having a larger protocone and better developed protoloph, and in the P³⁻⁴ having more reduced parapostcristae and in being wider. It differs from *Lo. kidogosana* in being larger. *Listriodon dukkar* differs from *Schizoporcus* in having M^x with a smooth metaloph, without a tetrapreconule protruding from it or a furrow in the middle of its distal side, in the M¹⁻² being less elongate, in the P³⁻⁴ in having a well-developed protoloph and being wider, and in having a palatine groove that does not extend as far forward as the premolars. It differs from *S. sinapensis* in being larger.

Etymology. The species name “dukkar” is from the common Gujarati name for pig or boar.

Description and comparison

Upper molars. The upper molars (Fig. 4) have two transverse crests; they are lophodont. Lophodont molars evolved in different mammals, such as *Deinotherium* (Proboscidea) and *Pyrotherium* (Pyrotheria), which were the size of elephants, and Tapiridae (Perissodactyla) and Suoidea (Artiodactyla), with sizes comparable to the fossils from Pasuda. The anterior cingulum of the upper molars of a tapir forms a cusp

at the buccal side and there are small, but clear, crests on the anterior and posterior sides of the buccal cusps. These features are not present on the molars from Pasuda. Suoidea include fully lophodont species of the genera *Listriodon* and *Lopholistriodon*, sublophodont species of *Bunolistriodon* and *Lopholistriodon* spp. (all Suidae) and the lophodont *Schizoporcus* and *Yunnanochoerus* (Palaeochoeridae).

Fortelius et al. (1996) defined sublophodont as the state when the proximal pair of cusps of a molar forms a loph, but the distal cusps remain entirely or partially separate. If these cusps remain separate, there tends to be a sharp furrow marking the place where the two cusps meet and the wear facets and the dentine islands on the tips remain separate until wear is much advanced. Sublophodont Suoidea may retain a central cusp (tetrapreconule) placed behind the middle of the transverse valley (*Bunolistriodon*), which

may have the posterior loph not straight, but with an angle in the middle, where the tetrapreconule protrudes forwards (*Schizoporcus*, *Yunnanochoerus*). The molars from the specimen from Pasuda are much worn, but it can be seen that the anterior sides of the metalophs are smooth and that there is no indication of a cusplet or crest (tetrapreconule) as in *Schizoporcus* and there is no furrow at the posterior side of the metaloph of the M². The molars are fully lophodont as in *Listriodon* and some species of *Lopholistriodon*.

The molars of *Schizoporcus* are known to be elongate with wide transverse valleys. To some extent, this is obscured by the fact that molars that are more worn also tend to be shorter because of interproximal wear, which affects their proportions. Nevertheless, it is evident that the molars from Pasuda and of *Listriodon* are less elongate than those of *Schizoporcus* and also *Lopholistriodon*. The lines in Fig. 5

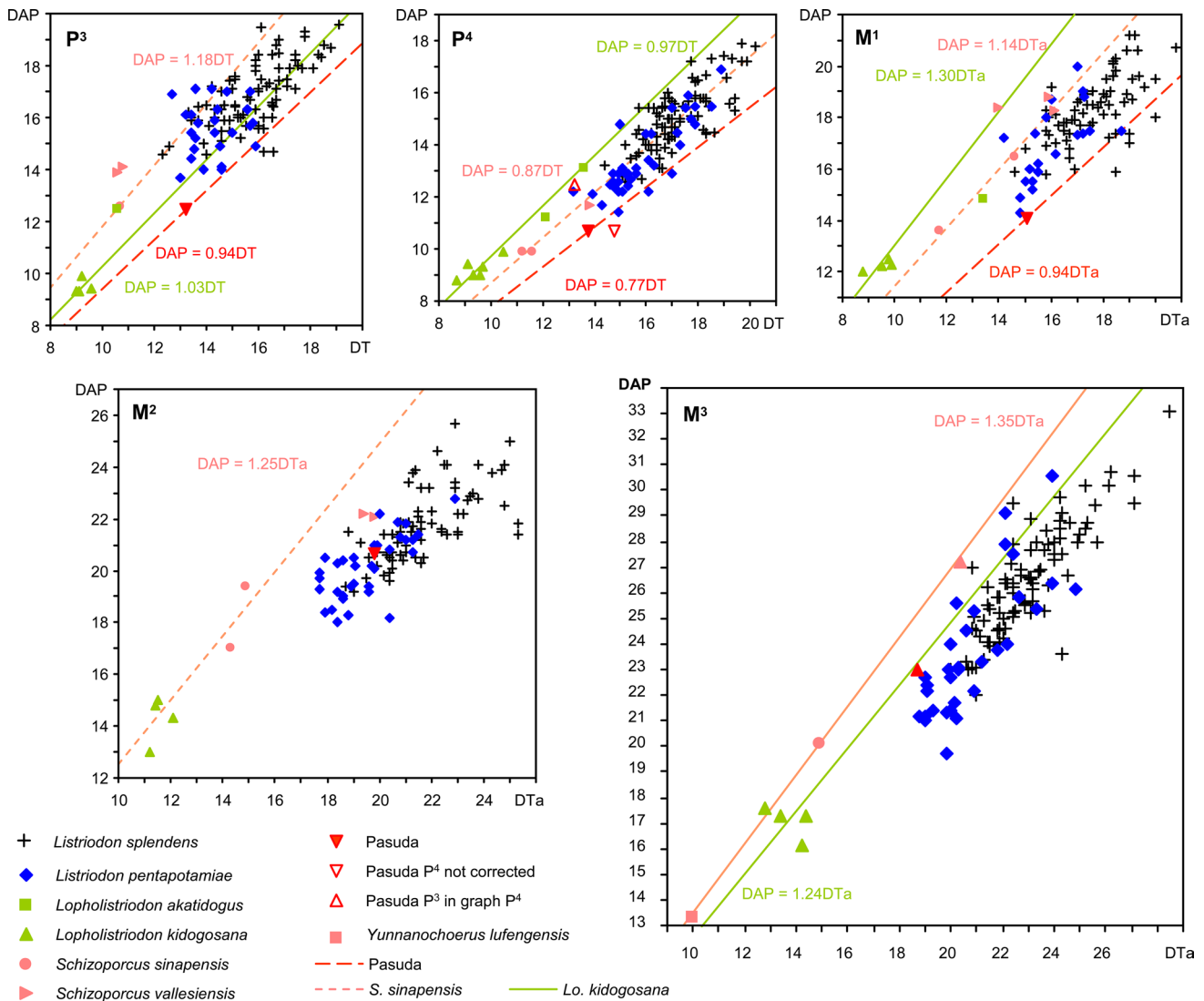


Fig. 5 Bivariate diagrams the DAP (antero-posterior diameter), DT (transverse diameter), and DTa (DT of the anterior lobe) of the upper cheek teeth of selected Suoidea. Provenance of data as indicated in Table 1

indicate the average length–width proportions of the different samples. The M^3 of *Yunnanochoerus* has a very narrow second loph, which is not the case in Pasuda. The molars from Pasuda are comparable in size to *Li. pentapotamiae*, but tend to be smaller than those of *Li. splendens*, while they are larger than those of *Yunnanochoerus lufengensis*, *S. sinapensis*, and *Lo. kidogosana* (Fig. 5).

Palate. What is left of the palate (Fig. 4) shows that there is no deep palatine groove next to the premolars and molars, which is present in *Schizoporcus*. This groove is less marked and extends far less anteriorly in the Suidae.

Fourth upper premolar. The P^4 (Fig. 6b) has one buccal cusp, the paracone, which is connected by a loph with the protocone. Both cusps are about equally high and placed equally far forwards. The parapostcrista is reduced to a small ridge on the back of the paracone and the metacone is completely reduced. The protopostcrista is reduced to a low crest on the back of the protocone. In fact, the tooth consists of a protoloph and little more.

In *Li. splendens*, the metacone is placed more backwards at a level between the protocone and metacone, the protoprecrista curves towards the paracone, and the large protopostcrista curves towards the middle of the posterior cingulum (Fig. 6e). These crests, together with the paracone and metacone, form a longitudinal valley, very unlike in the specimen from Pasuda. There is a distinct metacone, separated on the lingual side from the paracone by a clear furrow. There is no evolutionary tendency to reduce the metacone; instead, it may become more separate from the paracone (Fig. 6e3), which seems to be a tendency towards a molarized P^4 with two lophs, but this morphology was never reached and the longitudinal valley remains open posteriorly (Fig. 6e5). This tendency in the P^4 is related to the trend in the P_4 that the hypoconid becomes higher and placed more buccally and with a better developed hypoendocristid, which is a step in the direction of the formation of a hypolophid. The beginning hypolophid occludes with the cleft between the parapostcrista and metaprecrista of the P^4 . The P^4 from Pasuda became reduced to one loph, suggesting that the hypoconid on the P_4 became reduced.

The earliest *Li. pentapotamiae* have a morphology, which is still close to that of *Li. splendens* (Fig. 6h), but in the course of evolution, the metacone became reduced, and the protocone moved forwards and formed a transverse protoloph with the paracone (Fig. 6j). The protopostcrista also became reduced. This morphology is consistent with the P_4 of this species having less well-developed hypoendocristids than *Li. splendens*. The P^4 in *Li. pentapotamiae* shows an evolution towards the morphology seen in the P^4 from Pasuda.

The P^4 of *Schizoporcus* has the protoprecrista directed anteriorly, ending low near the middle of the anterior cingulum (Fig. 6d1). There is no connection to the paracone and no protoloph is formed. The longitudinal valley is well developed and wide open at the anterior side.

The P^4 of *Lo. akatidogus* may have a well-developed distinct metacone (the tip of protocone in Fig. 6g is damaged) or no metacone at all (Fig. 6f). The latter morphology is close to that of Pasuda, but the protoloph is less well formed and the protopostcrista is strongly developed.

In *Lo. kidogosana*, the P^4 has a well-developed protoloph and much reduced metacone (Fig. 6a). This morphology is close to that of the specimen from Pasuda, but the anterior cingulum is much more developed.

The P^4 from Pasuda has a longitudinal fracture in the middle, which is about 1 mm wide at the base and which becomes narrower till the tip. This fracture increased the width (measured at the base), probably by around 1 mm. In Fig. 5, both measured and corrected widths are indicated. The P^4 is among the widest (relative to the length) compared to *Listriodon* and is clearly much wider than in *Schizoporcus* and *Lopholistriodon*. This great width is probably related to the extreme development of the loph (increasing the width) and the complete reduction of the metacone (decreasing the length). The specimen from Pasuda is a little smaller than those of *Li. pentapotamiae* and clearly smaller than those of *Li. splendens*.

Third upper premolar. The P^3 from Pasuda (Fig. 6b) has a morphology, which is essentially identical to that of the P^4 .

In *Li. splendens* (Fig. 6e), the P^{2-4} form a morphological cline and the protocone is smaller in the anterior premolars. However, there is an evolutionary tendency of this cusp to become larger and placed more forwards, so that the P^3 becomes more similar to the P^4 . There is also a tendency for the metacone to become better developed in the P^3 , and there is even a metaendocrista, which would be a step in the direction of a posterior loph. However, primitive morphologies continue to occur (compare Fig. 6k with no distinct metacone and Fig. 6e). The development of an individual metacone has its counterpart in the development of a hypoconid with a morphology as in the P_4 (Van der Made 1996a, Pl. 42, fig. 2). Even in the most evolved P^3 , the longitudinal valley still opens anteriorly (Fig. 6e4). The different characters of the P^3 of *Li. splendens* are at a more primitive state than in the P^4 , but evolve in the same way, which is away from the morphology seen in the specimen from Pasuda.

In *Li. pentapotamiae* (Fig. 6c), the P^3 is very similar to that of the primitive and earlier *Li. splendens*. The evolutionary change of the protocone in *Li. pentapotamiae* has not been documented in detail, but it seems that in the later *Li. pentapotamiae*, the protoprecrista is somewhat more developed and more directed towards the paracone, which

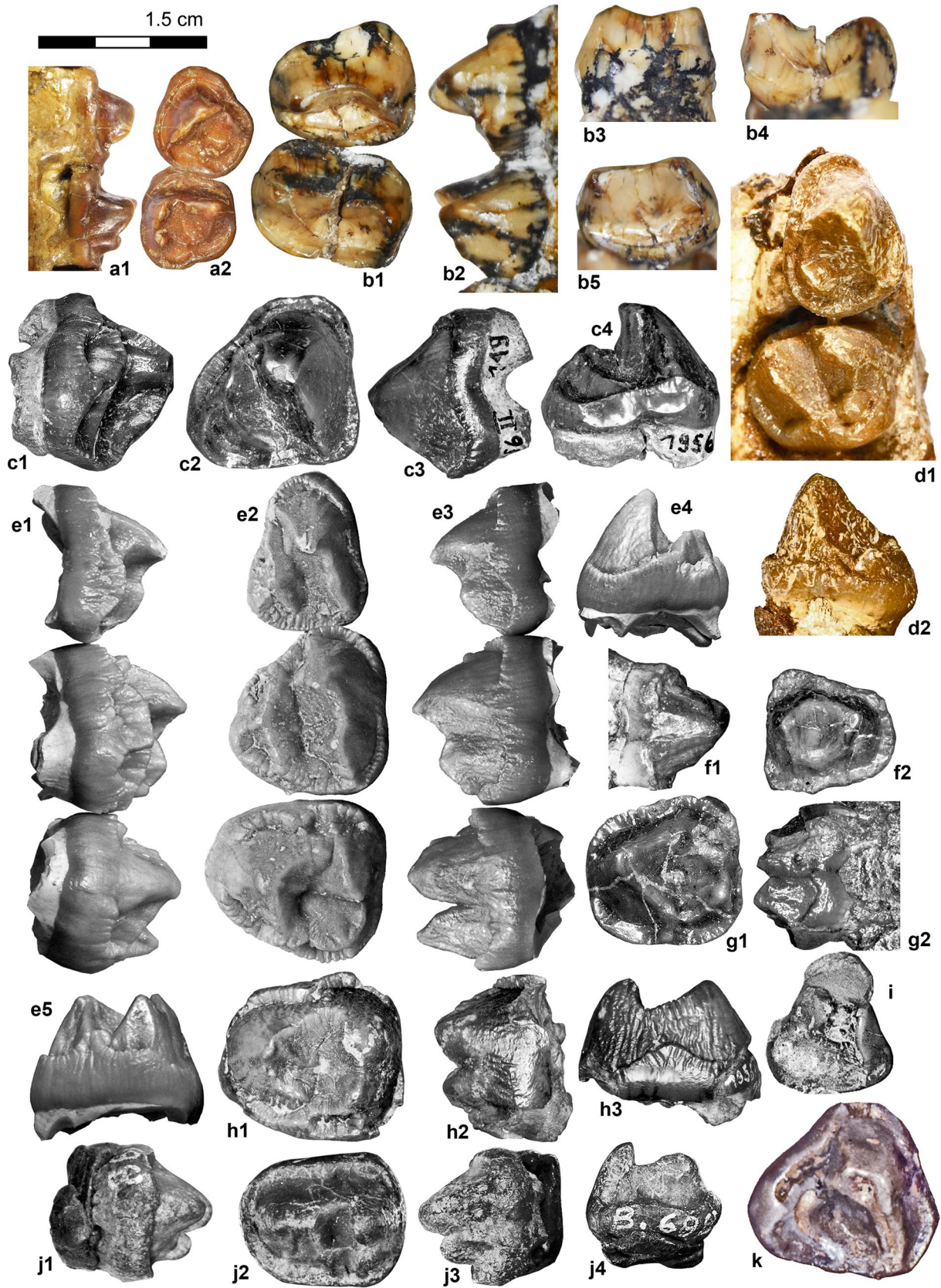


Fig. 6 The premolars of selected Suoidea compared: **a** KNM BN992—right P^{3-4} of *Lopholistriodon kidogosana* from locality 2/10 in member 10 of the Ngorora Formation: (1) buccal and (2) occlusal views. **b** PUKP-1—*Listriodon dukkar* sp. nov. from Pasuda: (1) occlusal view of P^{3-4} , (2) buccal view of P^{3-4} , (3) anterior view of P^3 , (4) posterior view of P^3 , and (5) posterior view of P^4 . **c** BSP 1956III119—left P^3 of *Li. pentapotamiae*: (1) lingual, (2) occlusal, (3) buccal, and (4) posterior views. **d** MNHN 3337—*S. vallesiensis* from the Middle Sinap Formation: (1) occlusal view of left P^{3-4} and (2) lingual view of P^3 . **e** IPS no number—left P^{2-4} of *Li. splendens* from Castell de Barberà: (1) lingual, (2) occlusal, and (3) buccal views, (4) anterior view of the P^3 , and (5) posterior view of the P^4 . **f** KNM FT3319—right P^4 of *Lo. akatidogus* from Fort Ternan: (1) buccal and (2) occlusal views. **g** KNM FT3320—right P^4 of *Lo. akatidogus* from Fort Ternan: (1) occlusal and (2) buccal views. **h** BSP-1956III115—left P^4 of *Li. pentapotamiae* from Kanatti Chak 5, Chinji Formation: (1) occlusal, (2) buccal, and (3) anterior views. **i** MTA 1953—left P^3 of *Schizoporcus sinapensis* from the Lower Sinap Formation: occlusal view. **j** IM B698—left P^4 of *Li. pentapotamiae*: (1) lingual, (2) occlusal, (3) buccal, and (4) anterior views. **k** MNHN no number—left P^3 of *Li. splendens* from the Lower Sinap Formation: lingual view

would be a first step in the direction of the formation of a protoloph as seen in Pasuda. *Li. pentapotamiae* does not have a tendency to develop a separate metacone in the P^3 nor to develop a large hypoconid in the P_3 .

In *Lo. kidogosana* (Fig. 6a), the paracone seems to have shifted towards the middle of the tooth with its protopre-crista and protopostcrista forming a crest that rotated from an antero-posterior to an oblique orientation. Also, the protocone shifted to a more anterior position and rotated its axis. These are steps in the direction of a transverse loph, but they differ in an essential way from the configuration in Pasuda, where the paracone is at the extreme buccal side. Another difference is in the extremely wide cingulum surrounding the whole tooth.

The P^3 from Pasuda is relatively wide (compared to its length) and is one of the widest in Fig. 5. Only a few of the other *Listriodon* specimens are still wider, while the ones of *Schizoporcus* and *Lopholistriodon* are narrower. This great relative width is the result of the increased size of the protocone and its shift to a more anterior position contributing to the formation of the transverse loph, as well as of the reduction of the parapostcrista. The specimen from Pasuda is a little smaller than the P^3 of *Li. pentapotamiae* and clearly smaller than those of *Li. splendens*.

Taxonomic discussion

The molars of the specimen from Pasuda have perfect lophs as in *Listriodon* and some of the species of *Lopholistriodon*. *Lopholistriodon* has several, mostly small species, with premolars that are narrower and with less-developed lophs than in Pasuda. *Lopholistriodon akatidogus* (= *Lo. bartulensis*) approaches Pasuda in size, but has much narrower premolars. The early Late Miocene *Lo. kidogosana* is much

smaller than the species from Pasuda and has much more elongate molars. The molars from Pasuda are most similar to those of *Listriodon*. They are smaller than those of *Li. splendens*, but most of them are within the ranges of *Li. pentapotamiae*.

The well-formed lophs of the P^{3-4} are different from both species of *Listriodon*, though they are most similar to the morphology in *Li. pentapotamiae*. *Listriodon splendens* evolved from early *Li. pentapotamiae*. The protocone on its P^4 retained a more posterior position and a well-developed protopostcrista, which together with the metacone, that evolved to be more separate from the paracone, could evolve into a metaloph. By contrast, in the evolution of *Li. pentapotamiae*, the metacone of the P^4 became reduced, while the protocone moved forwards to form a loph with the paracone. The P^3 shows the same tendencies, with a beginning individualisation of the metacone in *Li. splendens*, but not in *Li. pentapotamiae*. On the corresponding lower premolars, the increased hypoconid and hypoendocristid are a step towards a hypolophid in *Li. splendens*, while if there is any change in *Li. pentapotamiae*, it is towards a reduction of this structure. Both species were on divergent evolutionary pathways. With a totally reduced metacone of the P^4 , the specimen from Pasuda is closer to *Li. pentapotamiae*, but differs in a better developed loph of the P^4 and in a P^3 which has a perfect loph. In addition, both teeth differ from all other Listriodontinae in the reduction of the area behind the paracone or protoloph.

The morphology of the P^3 and P^4 from Pasuda is different from all other Listriodontinae, but also points to close affinities with *Li. pentapotamiae*, which we consider to be its ancestor. Though we assume that the change occurred by local evolution, at present no specimens of intermediate morphology have been published and the separation from *Li. pentapotamiae* is very clear. For these reasons, we name the new species *Listriodon dukkar*.

Discussion

Early late Miocene extinction of the Listriodontinae

Very different opinions are to be found in the literature on the temporal distribution of *Li. pentapotamiae*. According to Pilgrim (1926), this species occurred in the Chinji, Nagri, and Dhok Pathan Formations, but all the material he described or figured came from the Chinji Zone. Matthew (1929) cast doubt on the presence of *Listriodon* in the Middle Siwaliks. However, Colbert (1935) indicated the same distribution as Pilgrim and listed seven items from the lower part of the Middle Siwaliks at Nathor and Phadial. Hussain et al. (1979) and Barry et al. (1982) mentioned the co-occurrence of *Hipparion* and *Listriodon* in Daud Khel

and locality Y454 in the Tatrot-Andar Kas section. Pickford (1988, Fig. 6) indicated in his range chart the occurrence of *Listriodon* in the very lowermost part of the Nagri Formation, overlapping with *Hipparion*. Raza et al. (2002) estimated the temporal overlap of *Listriodon* and *Hipparion* to be less than 0.5 My.

Various papers mention more recent and dated records of *Listriodon*. Flynn et al. (1995) and Barry et al. (2002) indicated the last record of *Li. pentapotamiae* as 9.6 Ma and 10.3 Ma, recalculated as 10.379 Ma and 10.478 Ma, respectively. The date 10.3 Ma has been repeated by various later authors, including Antoine et al. (2013), who also mentioned Listriodontini or *Listriodon* sp. with a last record in the approximate interval from 11 to 10 and perhaps even 8.4 Ma. Barry et al. (2002) mentioned a *Schizochœrus gandakasensis* with a time range of 10.1–8.7 Ma. In reality, this is a species of *Yunnanochœrus*, a sublophodont palaeochœrid which survived long after *Listriodon* (Van der Made 2010; Pickford 2017). The molars of all these genera are lophodont or sublophodont and very similar if worn. The *Listriodon* sp. of Antoine et al. (2013) has not been described, so we cannot discuss it, but given the coincidence in temporal distribution, we do not rule out the possibility that it might represent a *Yunnanochœrus*. Alternatively, it could represent *Li. dukkar*. Khan et al. (2012) described fossils from Sethi Nagri and assigned them to *Li. pentapotamiae*. This locality corresponds to loc. Y311 (Barry et al. 1982, 2002) with an approximate age of 10.72 Ma (range 10.108–10.035 Ma). In the Indian Siwaliks, the last record of *Listriodon pentapotamiae* is from Nurpur and dates to ~ 9.8 Ma (Patnaik 2013). This is based on an upper canine described by Vasihat et al. (1983) from Nurpur. The curvature of the canine forms a large part of the circumference of a circle as is common in *Li. pentapotamiae* and possibly *Li. dukkar*, while in the other Suidae of this time, the curvature forms a lesser part of a circle. This fossil comes from a section that has been magnetostratigraphically dated by Rao (1993) and that was reinterpreted by Sangode and Kumar (2003). This is the youngest dated fossil of the Listriodontinae in the Indian Subcontinent.

Even though we have the date of ~ 9.8 Ma for the last appearance of *Listriodon* in the Indian Subcontinent, we do not know the morphologically relevant features of the youngest samples. Nearly, all material described comes from the Chinji Formation or age equivalent strata (Pilgrim 1926; Colbert 1935; Pickford 1988; Van der Made 1996a). An exception is the paper by Khan et al. (2012), which describes Late Miocene material from Sethi Nagri, the type locality of the Nagri Formation, and assigned it to *Li. pentapotamiae*. The P₄ figured by Khan et al. (2012) has a morphology that is normal for *Li. pentapotamiae*, with a hypoconid near the axis of the tooth and a very modest hypoendocrisid. Although there are no upper premolars, nor P_{2,3} among the

specimens, it seems that this material does not represent *Li. dukkar*, for which we expect a short talonid and reduced hypoconid in the P₄.

The age of Pasuda is early Late Miocene and was roughly estimated to be between 11 and 10 Ma (Bhandari et al. 2015). Because *Li. dukkar* evolved from *Li. pentapotamiae* and because it is unlikely that two nearly identical species lived in a relatively small area, it is the last documented listriodont species known from the Indian Subcontinent, and given the differences in morphology, it should be clearly younger than Sethi Nagri (10.72 Ma). The locality Pasuda and the extinction of the Indian *Listriodon* lineage should also be younger and could be close to the last record of the genus at 9.8 Ma as mentioned by Patnaik (2013). Whereas the fossil record in the northern part of the Indian Subcontinent is particularly rich, in the southern part, it is poor. *Listriodon dukkar* could have retreated to the South and have survived there longer, but we do not have any fossil record, which could confirm or deny this.

In Europe, the last listriodont was *Listriodon splendens*. It was a very common species and is known from over 100 localities of the units MN6 to MN9. In MN9, it is known from Aveiras de Baixo, Azambujeira (both Portugal), Santiago, Can Ponsic I, Can Llobateres 1 (Spain), Doué-la-Fontaine (France) (Van der Made 1996a), and in addition, it is cited from the Vallesian of Can Flaqué, Relea, subsuelo de Sabadell, Creu del Batlle, Can Amat, and St. Miquel (Golple-Posse 1972), but we did not study this material. Its last dated occurrence is at Can Llobateres 1 (Van der Made 1990a, b, 1996a), a locality dated to 9.78 Ma based on magnetostratigraphy and close to the end of MN9, which is estimated as 9.7 Ma (Casanovas Vilar et al. 2014). No locality with *Li. splendens* has been assigned to a younger MN unit or has been dated to less than 9.78 Ma.

Asia is a huge continent. In western Asia, like in Europe, the last occurrence of *Listriodon splendens* is in MN9. It is known from Esme-Akçaköy and Çorak Yerler (Becker-Platen et al. 1975a, b), as well as from the Lower Sinap Formation (Ozansoy 1965). The fossils from Çorak Yerler come from two horizons, but have been studied as a whole, and based on different taxa, different correlations have been proposed, to the Kayadibi and Garkin Faunengruppen (Becker-Platen et al. 1975b). Sen et al. (1998) stated “In summary, there are obviously two different faunas at Çorak Yerler, one possibly of late Astaracian or early Vallesian and the other of late Vallesian or early Turolian.” Geraads (2013) suggested mixing of the collections. Kaya et al. (2016) mentioned two fossiliferous levels and, based on a magnetostratigraphic section with two reversals, favored an age between 8.13 and 7.55 Ma for the upper level, but did not obtain results for the lower level and did not mention *Listriodon*. The faunal list includes *Listriodon* (Becker-Platen 1975b), but *Hippopotamodon major* has also been reported from the

locality (Fortelius et al. 1996). If we accept the presence of two fossiliferous levels of different ages (as suggested by Sen et al. 1998), it is possible that the lower level, with *Listriodon*, correlates to MN9 and the upper one, with *H. major*, to MN10 or 11.

The age of the *Listriodon* record from the Lower Sinap Formation can be estimated. In Ozansoy's (1965) scheme, the Upper, Middle, and Lower Sinap Formation consist of beds 1–19, 20–43, and 44–47, respectively. A small fauna with *Listriodon* comes from bed 46, about 58 m below bed 25, the lowermost fossiliferous level of the Middle Sinap Formation. This fauna is generally considered to be late Middle Miocene or MN8 (e.g., Steininger et al. 1996). More recent work led to the recognition of a dense sequence of over 30 fossil localities in, or correlated to the Sinap Tepe (=Hill) composite magnetostratigraphic section (Kappelman et al. 2003). The entry of the hipparions is in locality 4 at a height of about 45–50 m and localities 88, 64, 104, and 65 are at heights of about 25–45 m in the profile. These four localities are correlated to chron C5n.2n–4n, which implies ages between 11.056 and – 10.7 Ma (Kappelman et al. 2003). This means that they are early Late Miocene (MN9) in age and not Middle Miocene (MN8). These localities do not have *Hipparion*. However, like bed 46, they have short faunal lists and probably lack *Hipparion* for that reason. The lowermost fossiliferous locality is loc. 65 with an interpolated age of 10.899 Ma (recalculated as 11.004 Ma). Probably, Ozansoy's (1965) bed 46 was not much older than locality 65. Ozansoy's Middle Sinap fossiliferous levels (beds 20, 23, 25) were identified as OZ01, OZ02, and S01 and are at a height of 125–130 m of Kappelman's et al.'s (2003) section. Ozansoy's bed 46 would have been 58 m lower than bed 25, which is at a height of about 67 m at the level of locality 93 in Kappelman's et al.'s (2003) section, with an interpolated age of 10.488 Ma (recalculated as 10.576 Ma). It seems reasonable to assume an age for the *Listriodon* from Sinap between 11.004 and 10.576 Ma.

On the other side of Asia, various species of *Listriodon* were named on the basis of Chinese fossils, but these are indistinguishable from *L. splendens* (Van der Made 1996a). Deng et al. (2013) indicated the presence of *Listriodon mongoliensis* and two species of *Hipparion* in the lowermost Upper Miocene of the Guonigou Formation in the Linxia Basin.

The last African listriodont is *Lopholistriodon kidogosana* from Member D of the Ngorora Formation (Pickford and Wilkinson 1975). This member was reported to date to 9.82–9.68 Ma (Bishop and Pickford 1975), but more recent work suggested older ages for the Ngorora Fm (Tauxe et al. 1985; Deino et al. 1990) and Pickford (2001) situated locality 2/11, with the last *Lopholistriodon kidogosana*, between 11.84 and 11.54 Ma. Tsubamoto et al. (2017) described a tooth fragment of a listriodont with an

estimated age of 10 Ma and assumed that *Li. splendens* or *Li. pentapotamiae* dispersed to Africa. This is only a small fragment with a morphology and size that also fit *Lo. akatidogus* (= *Lo. bartulensis*) and such an identification would not need to be explained by an intercontinental dispersal. In contrast to the two species of *Listriodon*, these two species of *Lopholistriodon* are known from fewer localities. In addition, it should be noted that the African upper Middle and lower Upper Miocene fossil record is less abundant than that from the preceding and following times and as a consequence, the time of extinction is less precisely known.

The last appearances of the Listriodontinae are in the early Late Miocene: *Listriodon splendens* in Europe and western Asia after 9.78 Ma, *Listriodon dukkar* in the Indian Subcontinent at or shortly after 9.8 Ma, and a possible *Lopholistriodon akatidobus* in Africa around 10 Ma. The ages of the decrease in abundance leading to extinction, the death of the very last individual, and the youngest recorded fossil of a species are not the same, but the difference is only relevant if we know it to be large compared to the precision we can obtain in dating. Given the temporal range of about 10 My of the Listriodontinae, the extinction of the last three lineages adapted to different climates and environments is remarkably close in time.

Listriodont ecology

Suoidea are specialized in rooting and during seasons when their favourite food is not available; they have access to a source of food for which they do not compete with other large mammals. They may also eat soil that is rich in organic material. Suoidea complement their diet with food of animal origin: animals they catch (e.g., rodents, reptiles, and birds), carrion, animals living in the soil (e.g., earthworms, larvae), and on occasions, this may make up 88% of their diet (Wilson and Mittermeier 2011). The specialized dentition of the Listriodontinae suggests that they did not ingest important quantities of food of animal origin. Skull morphology suggests that the Listriodontinae were never particularly strongly adapted to rooting and incisor morphology and wear indicate that they progressively abandoned the rooting habit (Leinders 1977a; Van der Made 1996a). This has several implications. One is that their diet was not complemented by animals living in the soil and they depended on leaves and fruit for their proteins. The other is that they are expected to have been limited to environments where nutritious leaves (and fruit) were available year-round.

Many Suoidea are very selective when feeding. The snout of *Babyrousa* is narrow and it is reported to select precisely different plant parts and in the case of captive individuals even to shell peanuts and peel bananas (Leus 1994). By contrast, the Listriodontinae have very wide snouts and were probably not very adept in precisely selecting the best plant

parts. This is primarily due to their very wide incisors, which have been interpreted as an adaptation to bulk feeding on forbs but not on grasses (Van der Made 1996a, 2003b).

Because of the dental morphology and macrowear, *Li. splendens* has been interpreted to be a specialized folivore (Leinders 1977a, b) and this is confirmed by microwear analysis (Hunter and Fortelius 1994). Stable isotopes are compatible with folivorous diet, different from that of other Suidae (Quade et al. 1995; Domingo et al. 2012). Except for *Phacochoerus* and *Hylochoerus*, most species of wild pigs and peccaries have a preference for fruit and shift to roots and tubers when fruit is not available and domestic pigs have been reported to have a preference for sweet fruits (Leus 1994). Fruits tend to be rich in carbohydrates (sugar and starch), but tend to have less than 0.5% crude protein of the wet weight. Tapirs have lophodont cheek teeth, like *Listriodon*, and their diets consist of 63–86.5% of leaves, 8.1–37% of fruit, and the rest of twigs, bark, etc. (Wilson and Mittermeier 2011). We are not aware of anyone having addressed the possibility that Listriodontinae ingested important amounts of fruit.

Listriodon splendens lived in environments with abundant fruit. Fuss et al. (2018) documented caries in the hominid *Dryopithecus* from the locality St. Stefan in Austria (about 12.5 Ma), caused by the ingestion of fruit. The environment was forest, dominated by *Quercus*, *Fagus*, *Castanea*, *Carya*, *Pterocarya*, *Engelhardia*, and *Juglans*. Nine fossil plant species, mostly from the understory of the forest produced ripe sugar-rich fruits during the months June–December: *Prunus* sp. 1 and 2, *Vitis* sp., *Elaeagnus* sp., *Morus* cf. *nigra*, *Arbutus* sp., *Castanea* sp., *Carya* sp., and *Toddalia* sp. *Listriodon splendens* is one of the most abundant species from this locality and may have fed on the same fruits.

Suoidea may ingest large quantities of protein-rich nuts and acorns. Acorns allow *Sus scrofa* to gain weight to get through the winter. Their bunodont dentition is well suited for such a diet. Whether Listriodontinae ingested important quantities of nuts is unknown, but their lophodont dentition seems less suited for such a diet. The dental adaptations of *Li. pentapotamiae* and the last *Lopholistriodon* species are similar to those of *Li. splendens* and we assume that this was also the case with their diets.

Herbivores depend on a symbiosis with microorganisms which digest cellulose for them and thus also make cell contents available. Cellulose fermentation takes place in fermentation chambers either in the foregut or hindgut, and the position has further implications (Janis, 1976). Ruminants are the most specialized foregut fermenters. They are more efficient in digesting cellulose than hindgut fermenters, and take more time to digest food, and their digestive tract and contents comprise a larger proportion of the total bodyweight. Whereas food intake in ruminants is limited by rumen fill, hindgut fermenters may increase intake, decrease

digestion time and efficiency, and, as a result, increase total nutrients obtained. Sugar is fermented along with cellulose in the rumen, and as a result, ruminants have lower blood sugar levels, while hindgut fermenters absorb the sugar before it reaches the place where fermentation takes place. The way nitrogen becomes available to the herbivore is different and seems to be more efficient in foregut fermenters. Ruminants have the most complex forestomachs, but also camels, hippopotamuses, peccaries, and the babirusas are foregut fermenters, while *Potamochoerus*, *Phacochoerus*, and *Sus* are hindgut fermenters (Langer 1986; Leus et al. 1999; Clauss et al. 2008). Peccaries and babirusas benefit from the formation of microbial proteins by fermentation in the forestomach. Those microbial proteins are subsequently digested in the stomach, resulting in higher protein digestibility and lower protein requirements. The hindgut fermenting Suidae have a more efficient access to sugars in fruit and leaves. Either foregut fermentation evolved several times in the Artiodactyla or it is the ancestral state and some Suidae became hindgut fermenters. Listriodontinae, which split off early from the other Suidae, may have been foregut fermenters, like the babirusas and peccaries. This may have had consequences for the protein requirements of the Listriodontinae.

The energy and protein requirements of several species of ungulates have been studied in detail. Borges et al. (2017) and Nogueira-Filho et al. (2014) gave the minimum daily protein intakes in relation to body weight: *Pecari tayacu* 514 mg N/kg^{0.75}, *Tayassu pecari* 336.5 mg N/kg^{0.75}, *Cervus elaphus* 680 mg N/kg^{0.75}, *Odocoileus virginianus* 710 mg N/kg^{0.75}, and *Philantomba monticola* 643 mg N/kg^{0.75}. The requirements are also expressed as a minimum % of crude protein of the diet (dry matter), which is 5.4% for *Pecari tayacu*, 4.5% for *Tayassu pecari*, 4–7.1% for *Babyrousa babyrousa*, 6.98% for *Boselaphus*, and 8.27% for *Antilope cervicapra*, but 12% for domestic pigs and even 15% for lactating sows (Das et al., 2012; Wilson and Mittermeier 2011; Nogueira-Filho et al. 2014; Borges et al. 2017). Though we cannot measure the protein requirements of the Listriodontinae, these may have been more similar to those of the peccaries and babirusas and even ruminants than of *Sus scrofa*. While the Listriodontinae were probably not omnivorous, did not root, nor eat nuts, their diet may have consisted of protein-rich leaves and possibly protein-poor, but sweet, fruit. Fruit has relatively low protein contents and fruit bats (Pteropodiade) overingest energy to meet their protein requirements (Thomas 1984). Obesity is a problem in overfed zoo babirusas to an extent that it may interfere with reproduction (Leus 1994), so overfeeding on low protein food may not have been an option for the Suoidea.

The extremely large male canines of *Li. splendens*, *Bunolistriodon latidens*, and *B. meidamon* have been

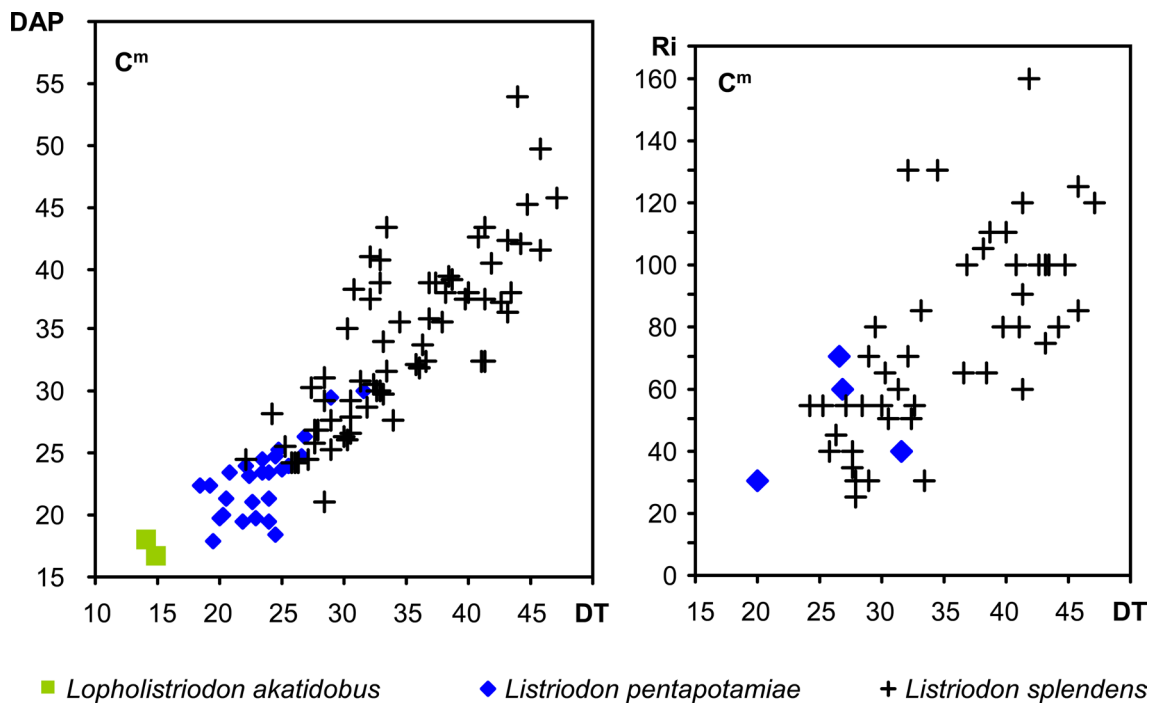


Fig. 7 Bivariate diagrams of the DAP, DT, and Ri (inner radius of curvature) of the male upper canine (C^m) of selected Listriodontinae. Provenance of data as indicated in Table 1

interpreted to be used in display in inter-male interactions, suggesting a preference for habitats with good visibility at a distance and thus relatively open landscapes (Van der Made 1996a, 2003b). These canines reached heights (“lengths”) of about 30 cm, and had large diameters and large radii of curvature. While the height of these teeth can be measured only in relatively few complete specimens, the diameters and radii of curvature can be measured in many broken specimens. Although cheek teeth of *Li. pentapotamiae* are only a little smaller than those of *Li. splendens*, the canines of the males are much smaller (Fig. 7). Most Listriodontinae, including *Lopholistriodon* and *Li. pentapotamiae*, retained modest canines, suggesting that these species may have lived in closed habitats, feeding on herbaceous vegetation in the under story or fallen fruit, while *Li. splendens* may have lived near the interface of closed and open environments or in a mosaic landscape.

Body weight is an important parameter in ecology: it affects strength, speed, the relationship with predators, energy and protein requirements, food selection, and through intestine length and the passage time through the intestines, and it also affects digestion. Various ways to estimate body weight have been proposed, based on the length x width of the first lower molar (Legendre 1986), the length of the second upper molar (Fortelius et al. 1996), or the length

x width of the astragalus (Martinez and Sudre 1995). The body weights of *Li. dukkar*, *Lo. akatidobus*, and *Lo. akatikubas* are estimated on the basis of the M^2 as: 92 ($n=1$), 77 ($n=1$), and 23, 31, and 35 kg (minimum, mean, maximum; $n=4$). The body weight (minimum, mean, maximum) of *Li. pentapotamiae* is estimated as 82, 122, and 182 kg ($n=11$; M_1), 61, 87, and 124 kg ($n=41$; M^2), and 32, 57, and 73 kg ($n=4$; astragalus). For *Li. splendens* this is: 102, 148, and 281 kg ($n=58$; M_1), 70, 108, and 177 ($n=92$; M^2), and 88, 111, and 131 kg ($n=19$; astragalus).

Legendre (1986) used cenograms to study ecology. As he used them, these are diagrams with the natural logarithm of the average body weight of a species on the vertical axis and the species ordered from large to small on the horizontal axis. He noted that there is a gap between the large and small mammals and that intermediate sizes are absent. This gap is very large in deserts, smaller in savannah and woodland, and absent in rain forest. This is logical in view of the anti predator behaviour: sprint and hide in small mammals living in or near closed environments, outrun the predators in the intermediate sized mammals living in more open landscapes, and defence in the large mammals. The short-legged Suidae are not the type of animals that outrun a predator, and especially small species like *Lo. akatikubas* would not venture far in an open environment.

Listriodont extinction in the European context

The context of the extinction of the last *Listriodon* in Europe is better known than for other regions of the world. Its last record is in Can Llobateres 1 (9.78 Ma) and coincides there with the last records of other species of Suoidea. An important turnover in the Suoidea in Spain and elsewhere in Europe, resulting in a major decrease in species richness, was documented (Van der Made 1988, 1990a, b, 1991, 1997c). This appeared to be part of a faunal event, which also involved the extinction of Hominoidea and was called the mid-Vallesian Crisis (Agustí and Moyà Solà 1990; Moyà Solà and Agustí 1990), later shortened to Vallesian Crisis. This event was also noted in the Bovidae: existing lineages went extinct and new arrivals included *Tragoportax* and *Protorox* (Moyà Solà 1983; Moyà Solà and Agustí, 1990; Alcalá and Montoya, 1990).

The causes and extent of the Vallesian Crisis have been much debated in the literature. The Vallesian Crisis was believed to have been caused by a change towards more open

and dry landscapes or to increased seasonality, resulting in an increase of deciduous vegetation and seasonal variations in the availability of fruit (Van Dam 1997; Suc et al. 1999; Agustí et al. 2003). It has also been correlated to Mi7, an oxygen isotope event around 9.7 Ma, reflecting decreased global temperatures (Agustí et al. 2013). The Vallesian Crisis has been considered to be continent-wide (e.g., Fortelius et al. 1996a) or only local (e.g., Madern et al. 2018). Hominoidea went extinct in western and central Europe, but are known from younger localities in Greece, Bulgaria, Turkey, and Georgia (Koufos and De Bonis 2006; Spassov et al. 2012; Kaya et al. 2016; Agustí et al. 2020), which has its parallel in longer survival of palaeotropical plants in SE Europe and the Caucasus (Kovar-Eder et al. 1996). The existence of the Vallesian Crisis has been doubted, based on the micromammal record (Casanovas Vilar et al. 2014).

The fossil record of the Suoidea supports the existence of the Vallesian Crisis (Fig. 8). *Listriodon splendens*, *Propotamochoerus palaeochoerus*, and *Parachleuastochoerus steinheimensis* were common species with temporal ranges

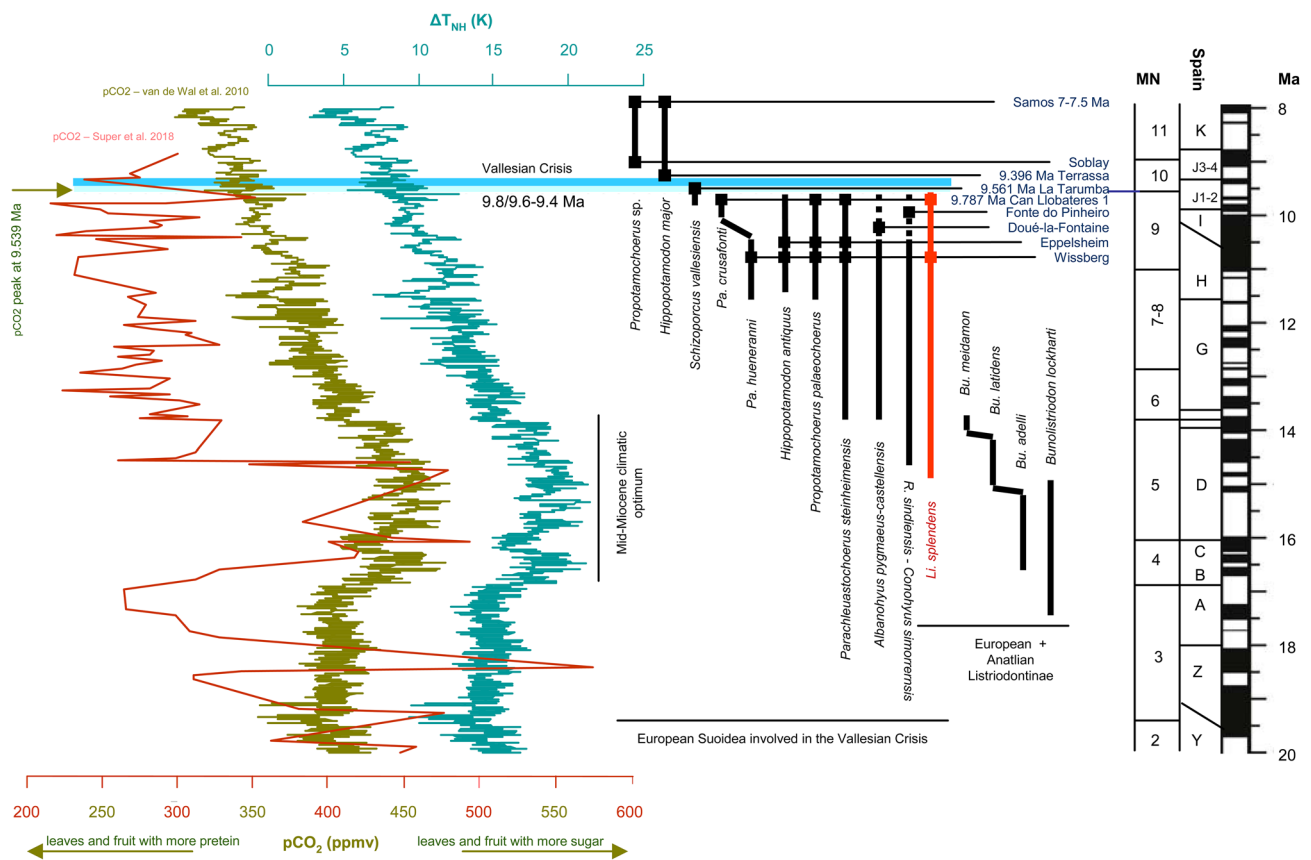


Fig. 8 Temporal distribution of the European Listriodontinae and of the European and Anatolian Suoidea in relation to the Vallesian Crisis. The localities and squares indicate the first or last dated records of the Suoidea involved in this crisis, preferentially in dated sites. Ages of the dated sites after Casanovas-Vilar et al. (2014), Kappelman

et al. (2003) and Van der Made (2003a). To the left reconstructed Northern Hemisphere air temperatures (relative to the present) and pCO₂ estimated from δ¹⁸O (data from Van de Wal et al. 2011) and pCO₂ based on the alkenone proxy (Super et al. 2018)

lasting 5–2 My and their last record is at Can Llobateres. None of these species has been identified from any locality younger than MN9 (or 9.7 Ma) or dated younger than Can Llobateres 1 (9.78 Ma). *Parachleuastochoerus crusafonti* and *Schizoporcus* are less common, but both have their last record at La Tarumba (Van der Made 1990a, b, 1997c). La Tarumba is placed in MN10, is dated to 9.56 Ma (Casnovas Vilar et al. 2016), and is only very little younger than Can Llobateres 1. *Conohyus* is not very abundant and *Albanohyus* is rare, but both have their last record in MN9 (11.2–9.7 Ma), though no precise ages are available for these localities (Van der Made 1996b; Van der Made and Morales 2003). Nowhere in Europe or Anatolia, these Suoidea survived, nor do any of them co-occur with *H. major*, a very common species from MN10 onwards. Within the genus *Hippopotamodon* (= *Microstonyx*), *H. antiquus* was replaced by *H. major* (Van der Made 1990a, b), which happened either late in MN9 or early in MN10. With up to eight contemporaneous species in Europe and up to five species in one locality before and one or two contemporaneous species after the Vallesian Crisis, European suoid species richness never recovered. While variations in sampling density may affect local sequences, this pattern is observed all over Europe. None of the mentioned species survived

anywhere in Europe after MN9. Everywhere in Europe species richness decreased.

Agustí et al. (2003) described floral change coincident with the Vallesian Crisis. Previous to the crisis and still in Can Llobateres 1, there was a humid subtropical flora, while flora from Terrassa—Talud Sud Autopista (9.02 and 9.23 Ma) consists of 36 taxa, of which about 45% are deciduous trees, 15% Mediterranean elements, 33% evergreen trees, and 7% warm evergreen elements, suggesting about 1000 mm mean annual precipitation, mean annual temperatures between 16 and 19°C, and seasonal availability of fruit. *Listriodon* may have lived in other habitats in Europe, and, for instance, is known from localities in the interior of Spain, which today and probably also in the Miocene were drier. However, its last records are in Can Llobateres and other localities in the same area, or with an expected similar environment, and the documented increase in seasonality, restricting the staple food of *Listriodon*, may have been decisive.

As far as the Suoidea are concerned, the Vallesian Crisis is a reality and *Listriodon splendens* became extinct as part of this crisis. If the study of other taxonomical groups cannot confirm the existence of the crisis or of environmental change, this can be because these groups were not affected

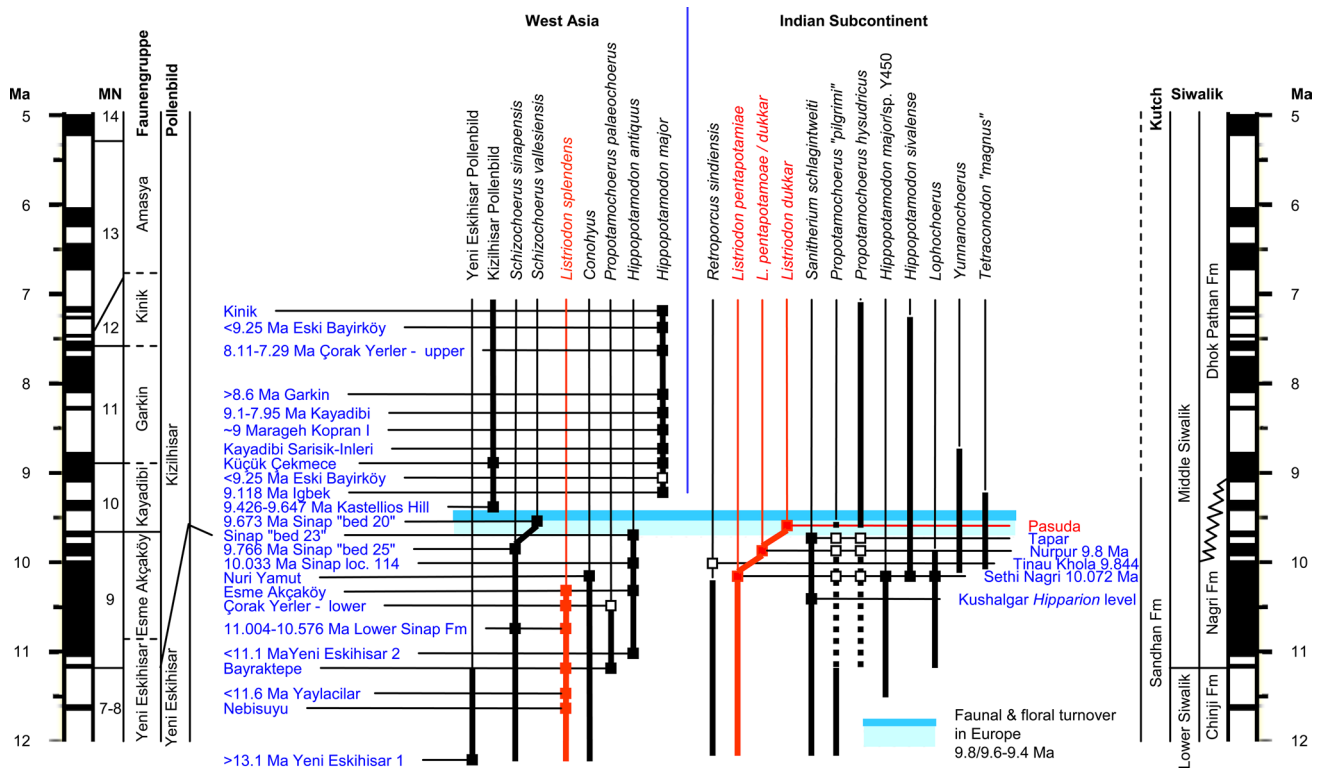


Fig. 9 Temporal distribution of the Anatolian Suoidea in relation to the Faunengruppen and Pollenbilder, defined on Turkish sites (Becker-Platen et al. 1975a, b). The localities and squares indicate the first or last dated records of the Suoidea, preferentially in dated sites

(see text). Ages of the dated sites after Becker-Platen et al. (1975b, 1977), Steininger et al. (1996) and Kappelman et al. (2003), updated after Hilgen et al. (2012)

in the same way. Though generally the age of the crisis is considered 9.7 Ma, the extinction of *Listriodon* and other Suoidea occurred after 9.78 Ma, that of still other Suoidea after 9.56 Ma, and the first dates for the replacing suid and new vegetation date to 9.4 Ma. Therefore, if there were two events, they occurred in the period from 9.78 to 9.4 Ma, and if it was only one, it was between 9.56 and 9.4 Ma. From the foregoing it appears that environmental change and increase in seasonality restricted the availability of the food of *L. splendens*, which may well have been the cause of its extinction in Europe.

Listriodont extinction in the West Asian context

The Anatolian fossil record is less complete than that of the whole of Europe and relevant material of the Suoidea has not yet been published, but the available data fit perfectly the pattern observed in Europe. Figure 9 shows the various species of Suoidea from Anatolia, which in Europe were involved in the Vallesian Crisis and shows a selection of relevant sites with their dates or with an approximate position according to biostratigraphy. The “Faunengruppen” (faunal associations), indicated in the figure, were defined by Becker-Platen et al. (1975a) on the basis of Turkish localities. These Faunengruppen were never widely used because of the MN units which were introduced at the same time (Mein 1975). As argued above, the locality Çorak Yerler has two different levels, one with *Listriodon* and another one with *Hippopotamodon major*. The Alçitepe Mb of the Eceabat Formation on the Gallipoli (Gelibolu) peninsula has several units: the Nebisuyu, Sigindere, and Degirmendere units, correlated to the Aragonian, Vallesian, and Turolian, respectively (Van der Made and Tuna 1999). The locality Nuri Yamut is in the Sigindere unit.

Several of the sites in Fig. 9 overlie or underlie dated tuffs (Becker-Platen et al. 1975a, 1975b, 1977). A composite faunal list of the two localities Yeni Eskihsar 1 and 2 was used to define the Faunengruppe of this name. However, Yeni Eskihsar 2, mainly a micromammal locality, is overlain by two tuffs, dated 13.2 ± 0.35 Ma and 11.1 ± 0.2 Ma, which again are overlain by Yeni Eskihsar 1, which is mainly a large mammal locality. The latter locality has *Hippopotamodon antiquus* (Fortelius et al. 1996) and together with the date, this points to the locality being MN9 and Vallesian, while the other locality is MN7+8 and Aragonian. The localities Bayirköy and Eski Bayirköy overlie a tuff dated to 10.2 ± 0.15 Ma and apparently also one dated 9.25 ± 0.2 Ma (Becker-Platen et al. 1977, Fig. 9), but are correlated to the Kayadibi and Kinik Faunengruppe, respectively (Becker-Platen et al. 1975b). Ozansoy’s Middle Sinap fossiliferous beds 20, 23, and 25 correspond to OZ01, OZ02, and S01 of Kappelman et al. (2003), and have interpolated ages of 9.683–9.590 Ma (recalculated as 9.766–9.673 Ma).

As can be seen in Fig. 9, the Suoidea show the same pattern as in Europe. *Hippopotamodon antiquus* occurs in MN9, while localities of MN10 and younger have *H. major*, like in Europe. Even though *H. major* is known from many sites (e.g., Pickford and Ertürk 1979; Fortelius et al. 1996; Van der Made et al. 2013), none of these sites is dated and known to be older than Igbek, nor any is placed in an MN unit older than MN10. Bayirköy and Eski Bayirköy have *Hippopotamodon*, but we did not study the one from Bayirköy. Five of the eight species that went extinct or were replaced during the Vallesian Crisis in Europe did the same here, including *Li. splendens*. This happened between Sinap “bed 20” (9.673 Ma) and Igbek (9.118 Ma). Beyond Anatolia, the western Asian fossil record is not very well known, but the *Hippopotamodon* from Marageh Kopran I (Iran; about 9 Ma; Fortelius et al. 1996; Bernor et al. 1996), as well as in Udabno (Georgia; MN10) and Eldar (Azerbaijan; MN10/11) are compatible with the event having occurred in a larger part of western Asia. Even though dating is less precise, the turnover may have happened at the same time. In Europe, the Vallesian Crisis occurred between 9.78/9.56 and 9.369 Ma and the faunal turnover in Anatolia occurred at about the same time between 9.659 and 9.118 Ma.

This faunal event in Anatolia seems to coincide with a change in the flora. In Turkey, a series of “Pollenbilder” or sporomorph associations (“zones”) have been defined and are correlated to the Faunengruppen and MN units (Benda et al. 1975; Benda and Meulenkamp 1990). These provide information on the environment in which *Listriodon splendens* lived and went extinct. The Eskihsar Pollenbild includes many tropical and few subtropical elements and the following Yeni-Eskihsar association is transitional. *Listriodon splendens* is present in localities correlated to those Pollenbilder, but not in sites correlated to the next one. The following Kizilhisar association has but few subtropical elements, but more conifers, species related to oaks, and sedges and grasses, indicative of steppe like to semi-arid conditions (Benda and Meulenkamp 1990). The Yeni Eskihsar Pollenbild is defined on a sample from the level of the Yeni Eskihsar 1 micromammal locality, but is said to be typical of the upper part of the Sekköy Formation (which also includes Yeni Eskihsar 2, < 11.1 Ma) (Becker-Platen et al. 1977). The Yeni Eskihsar Pollenbild is known only from a few sites with fossil mammals, but has been correlated to mammal sites. The transition to the Kizilhisar floral associations occurs between the Yeni Eskihsar 1 and Kayadibi mammal associations, and possibly within the Esme Akçaköy Faunengruppe (Benda et al. 1975). The locality Küçük Çekmece is of the Kayadibi faunal association, which has *H. major* and the Kizilhisar pollen association. Benda and Meulenkamp (1990) indicated that Kastellios Hill 1 in Crete has the Kizilhisar pollen association. This locality is placed in MN10 and correlated to chron C4Ar.2r (Steininger et al. 1996). This places the transition between the two pollen zones, which

marks a decrease in temperature and a change to a landscape with more grasses between 11.1 ± 0.2 and $9.426\text{--}9.647$ Ma. The whole Esme Akçaköy faunal association is between these two dates and precedes the faunal change, which also marks the MN9–10 transition. Benda's Pollenbilder are not used anymore, and their use in correlation for the Lower and Middle Miocene has been criticised. However, these Pollenbilder have been found in or lithostratigraphically correlated to sites with fossil mammals of which the age is known and the environmental interpretation for these sites or times should remain valid. More recent work confirms in a broad sense a transition of more humid environments that included subtropical forests to steppe (Yavuz-Isik and Toprak 2010; Bouchal et al. 2017; Steinhorsdottir et al. 2021).

The available data show or suggest that: (1) the extinction of *Listriodon* in western Asia formed part of a turnover event, which involved the same species of Suoidea as the European Vallesian Crisis; (2) the events in both areas are coincident; and (3) also in western Asia, these faunal events may have coincided with a major floral change.

Listriodont extinction in the context of the Indian Subcontinent

Whereas suoid species richness in Europe declined during the Vallesian Crisis, it remained high in the Indian Subcontinent till well into the Pliocene (Van der Made 1991). Barry et al. (2002) found a generally low level of faunal turnover in the Siwaliks in the interval of $10.7\text{--}5.7$ Ma, with peaks at 10.3, 7.8, and $7.3\text{--}7.0$ Ma. The event at 10.3 Ma involved also non-suid taxa, but coincides with the last appearance of *Li. pentapotamiae* and *Conohyus sindiensis*. The last appearance of *?Hippopotamodon* “Y450 unnamed species” and the first appearance of *Hippopotamodon sivalense* and *Propotamochoerus hysudricus* was indicated to be at 10.2 Ma. The temporal ranges of these and other Suoidea as given in the literature are indicated with thick lines in Fig. 9.

As we have seen already, there are records of *Listriodon* in the Indian Subcontinent, which are considerably younger than the 10.3 Ma, indicated by Barry et al. (2002), but this is not the only one. *Conohyus sindiense* (= *Retroporcus*) was cited from a magnetostratigraphic section at Tinau Khola (Munthe et al. 1983). This record is from a long interval with normal polarisation, correlated to C5n.2n, and, based on Hilgen et al. (2012), its interpolated age is 9.984 Ma.

Von Meyer (1866) described fossils from three different fossiliferous levels at Kushalgar and named *Sanitherium schlagintweiti* on the basis of material from a level with *Hipparion*. Later authors stated that the specimen came from Chinji-equivalent strata (Pilgrim 1926; Colbert 1935). The description of new material from Tapar from a level with *Hipparion* shows that the species did indeed survive till after the arrival of that equid (Bhandari et al. 2015).

Hippopotamodon major is present in Sethi Nagri (10.072 Ma), where it existed along with *H. sivalense* (Van der Made and Hussain 1989). This *H. major* may correspond to *Dicoryphochoerus robustus* and *D. titanoides* of Pilgrim (1926) and to *?Hippopotamodon* “Y450 unnamed species” of Barry et al. (2002), because it is the only other *Hippopotamodon* mentioned by these authors. If this is correct, the curious situation exists that in the Indian Subcontinent, around 10.2 Ma, *H. major* is replaced by the larger *H. sivalense*, whereas in Europe and Anatolia, between 9.78 and 9.4 Ma, *H. major* replaced the large *H. antiquus*, which is very close to *H. sivalense*.

In Pickford's (1988) scheme, *Hyotherium pilgrimi* occurred in the Chinji Formation and the very base of the Nagri Formation, and was replaced by *Propotamochoerus hysudricus* in the Nagri, Dhok Pathan, and Soan formations. Pickford (1988) named *H. pilgrimi* and listed in its synonymy the following species named by Pilgrim (1926): *Propotamochoerus salinus*, *P. uliginosus*, *Dicoryphochoerus chisholmi*, *?D. haydeni*, and *D. instabilis*. All these species would have priority over *H. pilgrimi*, but this was not sufficiently discussed. The species *P. salinus* was described from Tapar as a new genus *Kachchoerus* (Bhandari et al. 2015). Pickford's (1988) generic diagnosis of *Hyotherium* states that the P⁴ is without sagittal cusplets. According to this criterion, the holotype of *H. pilgrimi* does not fit *Hyotherium* and it is more likely that Pilgrim (1926) was right and that it belongs to *Propotamochoerus*. Whatever the names applied, the primitive species of *Propotamochoerus* was replaced by *P. hysudricus* and this may have happened around 11 Ma (more conform to Pickford 1988) or around 10.3 Ma (more in line with Barry et al. 2002) or at a still other date, but this remains to be documented.

Lophochoerus nagrii was not mentioned by Barry et al. (2002), but according to Pickford (1988), it made a short appearance in Nagri times, but went extinct afterwards. Barry et al. (2002) gave the temporal distribution of *Tetraconodon magnus* as $10.0\text{--}9.3$ Ma. In fact, there is a size increase in the lineage *T. minor*—*T. intermedius*—*T. magnus* (Van der Made 1999), but we lack precise data on the temporal distribution of these species. According to Barry et al. (2002), *Schizochoerus gandakasensis* appeared between 10.1 and 8.7 Ma. This genus is a junior homonym and its replacement name is *Schizoporcus* (Van der Made 2010), but this species belongs to *Yunnanocherus* (Van der Made 1997a; Pickford 2017).

It appears, thus, that there is some evidence for a turnover in the Suoidea around $10.3\text{--}10.2$ Ma according to the data of Barry et al. (2002), but that data from India and Nepal indicate that *Listriodon* and *R. sindiense* survived till around 9.8 Ma. The species involved are closely related to those in Europe and Anatolia, but not identical.

Barry et al. (2002) also gave data concerning a faunal turnover in the Tragulidae, with two species last occurring at 10.5–10.4 Ma and three species appearing at 10.4–10.3 Ma. It is not quite clear how this compares with the data presented by Barry (2014), showing that Tragulidae made up 30–> 60% of Tragulidae and Bovidae combined until 10 Ma, around 50% at 10 Ma and a decrease from about 20–5% from 9 to 6 Ma. This spectacular drop occurs broadly coincidentally with the final extinction of *Listriodon*. Living Tragulidae are primarily frugivores, but may feed on leaves and occasionally eat carrion or may catch animals (Wilson and Mittermeier 2011). Many of the fossil tragulid species reached much larger sizes than the living species and may have been folivorous. Bovidae range from browsing folivores to grazing bulk feeders and their rise in abundance was probably related to a shift in vegetation.

Stable isotopes from soil carbonates and from teeth provide information on the environment and diet. However, this information is mainly restricted to differentiating C₃ and C₄ vegetation. After 7.3 Ma, C₃ vegetation (probably trees and shrubs) is replaced by C₄ vegetation (grasslands) in the Siwaliks of Pakistan (Cerling et al. 1993; Quade and Cerling 1995). Sanyal et al. (2004) studied soil carbonates near Haripur (India) and found a similar change around 6 Ma. Stable isotopes from tooth enamel of fossils from the Indian part of Siwaliks show Late Miocene dietary shifts among various mammalian taxa including primates (Patnaik 2015; Patnaik et al. 2014, 2019). Also it has been hypothesised that this shift in vegetation could have led to extinction of the hominoids in the Siwaliks (Patnaik et al. 2005). Stable isotope data suggest that *Li. pentapotamiae* lived in environments with C₃ vegetation, which is in line with its dental morphology, and that it went extinct long before C₄ grasses started to dominate the landscapes.

The Siwaliks of northern India and Nepal have an abundant record in leaf and fossil wood floras (Prasad 1971; Awasthi 1992; Prasad and Awasthi 1996; Prasad and Pandey 2008), but most of these fossil plant sites are situated in India (Awasthi 1992) and further to the east than the sites with *Li. pentapotamiae*. The fossil plants indicate a luxuriant humid forest environment, which in the Upper Siwaliks became drier, more open and with grasses. Of particular interest is a sedimentary sequence containing 52 horizons with plant macrofossils and 584 pollen samples at Surai Khola, tied to a magnetostratigraphic section, described by Corvinus and Rimal (2001). They interpreted tropical broad leaved evergreen rainforest and swampy environments from 13 Ma onwards, which is compatible with the sedimentology of the Chinji Formation in Pakistan (Zaleha 1997; Willis and Behrensmeyer 1995), a gradual shift towards moist semi-evergreen forest between some 10 Ma and 9 Ma, after about 7.5 Ma a shift to dry deciduous forest, and still later a shift to

grasslands. They noted that the shift towards grasses in their section is much later than in Pakistan. The evergreen rain forest included trees like *Dipterocarpus*, which may be up to 50 m tall. Srivastava et al. (2018) used the plant fossils in the same section to estimate the principal climatic parameters for the period between 13 and 11 Ma as 1748–2869 mm mean annual precipitation and a mean annual temperature of 21.1–25.4 °C. For the period from 9.5 to 6.8 Ma, they estimated 2592–3151 mm mean annual precipitation (which is an increase) and a mean annual temperature of 26–27 °C and estimated that seasonality in precipitation increased. This increase in precipitation contrasts with the smaller river channels in the Dhok Pathan Formation in Pakistan. Perhaps, one of the two is a local phenomenon. It should be taken into account that the Himalaya was already rising and that, at present, there is a narrow area of high precipitation along the mountain front, so fossil plant sites may not be representative of the environment more to the South and West, where most of the fossil mammals are found. Quade et al. (1995) analysed stable isotopes from soil carbonates at Surai Khola and found a similar pattern as in Pakistan.

The available geochemical, paleontological, and sedimentological information suggests that *Li. pentapotamiae* may have lived in humid environments with a luxuriant C₃ vegetation, probably forest and that it may have fed on leaves of the plants of the understorey and perhaps also fruit. It survived into times with increasing seasonality. Its last records, around 9.8 Ma, date from a time when there was an increase in deciduous vegetation and an opening of the landscape, and coincided with the frugivorous Tragulidae becoming less abundant and Bovidae becoming more abundant. *Listriodon* went extinct well before landscapes became dominated by C₄ grasses.

Listriodont extinction in the African context

In Europe and the Indian Subcontinent, suoid diversity was high with Cainochoerinae, Tetraconodontinae, Suinae, and Taucanaminae living along with the Listriodontinae, as testified by the co-occurrence of several of these in many localities (Van der Made, 1990a, b, 1991). By contrast, in Africa, diversity of the Listriodontinae was higher, while that of other Suoidea was much less (Van der Made, 1996a, b). A species of *Lopholistriodon* survived till about 10 Ma (Fig. 10).

Within the 10 My duration of the Listriodontinae in Africa, there were three major peaks in faunal turnover, around 17, 13.7, and 9.7 Ma (Van der Made 2014). The first two coincide with turnover in the Listriodontinae and sandwich the Mid-Miocene Climatic Optimum, which is when listriodonts reached their maximum geographic extension and diversity. The event around 9.7 Ma is close to the

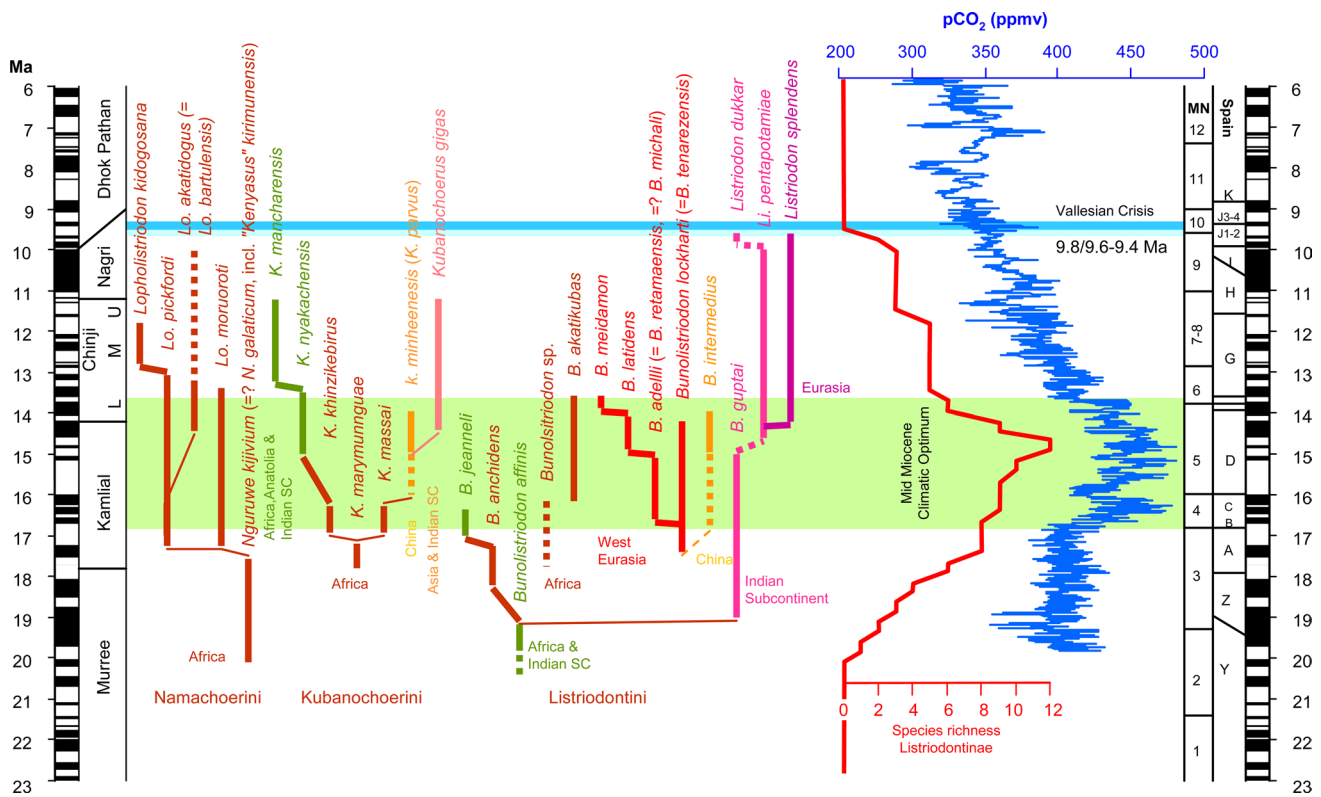


Fig. 10 Temporal distribution of the Listriodontinae (after Van der Made 1996a, 2020; updated), their species richness, and pCO₂ estimated from δ¹⁸O (data from Van de Wal et al. 2011)

extinction of the Listriodontinae at ~ 10 Ma. It is noteworthy that the extinction of the last Listriodontinae and a major peak in faunal turnover in Africa are so close to the European Vallesian Crisis.

Initially, Bovidae formed a small proportion of the large mammals in Africa, but their diversity started to increase leading to a spectacular diversity of the Quaternary (Van der Made 2014, fig. 6). Other Suidae may have escaped direct competition, because of their omnivorous diet and rooting habits, but dental morphology suggests that *Lopholistriodon* was folivorous and more prone to suffering from the bovid radiation.

The eastern African palaeobotanic record is not very dense, but the best sequence of sites is from the Ngorora and Mpesida Formations in the Tugen Hills (Kenya; Jacobs et al. 2010), which also records the latest African Listriodontinae. The flora from Kabarsero (12.6 Ma) has 11 out of 25 taxa that grow today in wet forests or rain forests, including herbaceous plants and grasses that are found in the understory of wet forests (Jacobs and Kabuye 1987; Jacobs and Winkler 1992). Accordingly, the environment was interpreted as moist to wet forest. The flora from Waril (about 10 Ma) is dominated by a species of legume growing in seasonally dry environments (Jacobs et al. 1999). The last *Lopholistriodon*

species must have lived in this environment and will have fed on this legume. The paleoflora from Kapturo (7.2–6.7 Ma) was interpreted as deciduous woodland with seasonality in the moisture (Jacobs and Deino 1996). The silicified wood from Rurmoch (> 6.37 Ma) with stem diameters of > 90 cm suggests trees over 50 m tall, and the association was interpreted as indicative of wet lowland rainforest, while stable isotopes from paleosols and tooth enamel indicate the presence of locally open habitats (Kingston et al. 2002).

These data suggest that *Lopholistriodon* lived in wet forest, may have fed on leguminous plants, and went extinct when the vegetation was on its way to become more seasonal and drier and when bovid diversity increased.

Possible reasons for the extinction of the Listriodontinae

The last record of the Listriodontinae in Europe is at 9.78 Ma, which is before the Vallesian Crisis, (9.78/9.56–9.396 Ma), in the Indian Subcontinent at ~ 9.8 Ma or somewhat later, and in Africa around 10 Ma. The extinctions in these areas seem to have occurred within a remarkably short period, suggesting a common cause. The three different lineages

that went extinct lived at different latitudes in Europe and Anatolia (about 38–50° N), the Indian Subcontinent (about 21–34° N), and Africa (about 0°) and consequently in different climates and environments. If there is a common cause for these three extinctions in different continents, it has to be a global event or process, but most of the changes which coincided with the extinction of the Listriodontinae are local or gradual.

It has been suggested that the Vallesian Crisis was related to the Mi7 event (Agustí et al. 2013). Such events are global. Miller et al. (1991) named the Mi events for rapid increases in the values of the record of $\delta^{18}\text{O}$ from the skeletons of benthic foraminifera in the Miocene. These events reflect sudden decreases in temperature and eustatic sea level and increases in global glacial ice volume. The timing of these events seems to be related to 400 ky, 100 ky, and 180 ky cyclic variations in precession, obliquity, and asymmetry of the obliquity cycle. Pagani et al. (1999b) situated the Mi6 event around 9.6 Ma and coincident with a peak value of $p\text{CO}_2$, reaching the highest value (about 310 ppmv) in a period of over 15 My. The Mi7 event could date to 9.56, 9.40, 9.31, 9.22, 9.14, 9.04, or be still younger (Westerhold et al. 2005). It is possible that a temperature decrease combined with pronounced seasonality may have caused seasonal limitation of nutritive plant parts, causing the extinction of *Suoidea* and early European hominids, but it is more difficult to see how this may have affected the Listriodontinae living at the Equator.

Variations in atmospheric CO_2 concentration are global and have a great impact on the vegetation and on herbivores, as well as humans. The projected increase in CO_2 levels by 2050 is considered to put at risk 148.4 million people, who depend mainly on rice, wheat, barley, and potato for their protein intake (Medek et al. 2017). The protein content of these foods is expected to drop by 6–14%. Two billion people suffer from dietary iron and zinc deficiencies, which cause millions of death, and the problem is expected to increase with rising $p\text{CO}_2$ (Myers et al. 2014). A rise in $p\text{CO}_2$ will enhance productivity and will increase carbohydrate and sugar content in leaves, grains, and fruit (e.g., Högy and Fangmeier 2008; Dong et al. 2018; Yang et al. 2020), and it also leads to a decrease in zinc and iron, and protein content (Ehleringer et al., 2020). Low protein, zinc and iron intake affects growth and may lead to a series of pathologies. There is evidence that elevated $p\text{CO}_2$ may lead to reduced growth rates in cattle (Ehleringer et al., 2020). Meeting the protein requirements of captive ruminants is a concern (e.g., Priebe and Brown 1987; Crissey 2005). There is reason to believe that changes in $p\text{CO}_2$ may have affected the nutrition of Miocene ungulates.

There are various ways to reconstruct the $p\text{CO}_2$ of the past (e.g., Pagani et al. 1999a; Pearson and Palmer 2000; Demicco et al. 2003; Sosdian et al. 2018) and the results

may differ according to the method applied. During the past 200 My, atmospheric CO_2 concentrations of over 1000 were common and peaks of over 2000 ppmv (parts per million volume) occurred (Pearson and Palmer 2000), but the Miocene $p\text{CO}_2$ was much lower. Most methods give relatively low values for the Miocene (below 600 ppmv), but higher values would fit better existing climate models (Steinhilber et al., 2021). In addition, some of the records lack detail; others are of short periods or have long hiatuses. Van de Wal et al. (2011) reconstructed detailed records of $p\text{CO}_2$ and temperature for the past 20 My. Temperatures and $p\text{CO}_2$ were high between about 17 and 13.6 Ma, a period that has been called the Mid-Miocene Climatic Optimum (Figs. 8, 10). Around 13.6 Ma, there was a rapid decline in temperatures and $p\text{CO}_2$ and then a more gradual decline until about 8 Ma, punctuated by several moments of acceleration. Notably, at 9.539 Ma, a record low value of $p\text{CO}_2$ was reached. Super et al. (2018) used the alkenone proxy and the resulting curve (Fig. 8) differs from that of Van de Wal et al. (2011) in generally lower values, but both curves resemble each other in general shape with high values for the Mid-Miocene Climatic Optimum and lower values later. There is a peak low value at 9.4 Ma, but the record is not very dense with the next older data point at 9.7 Ma. Sosdian et al. (2018) used boron isotopes to reconstruct $p\text{CO}_2$, gave various variants based on different assumptions and methods, but all resulted in higher estimated values. The general shapes of these $p\text{CO}_2$ curves are similar to the curve by Van de Wal et al. (2011) in a marked decrease in the $p\text{CO}_2$ after the Mid-Miocene Climatic Optimum and in having a peak low value at 9.874 Ma, though the density of the record is low, with the next data points at 10.604 and 9.244 Ma. The parts with denser data show important fluctuations, but the lesser densely sampled times cannot show such fluctuations.

The onset of the Middle Miocene Climatic Optimum coincided with faunal turnover events in Africa and Europe (Van der Made, 2014). It also marks the onset of the radiation of the Listriodontinae in Africa and Europe (Figs. 8, 10). Later during this period, *Lopholistriodon* in Africa and *Listriodon* in the Indian Subcontinent evolved perfect lophodonty, became specialized folivores, and *Listriodon* acquired a Eurasian distribution from Portugal to China. The end of the Mid-Miocene Climatic Optimum, around 13.6 Ma, coincides with the major peak in faunal turnover in Africa between 16 and 10 Ma (Van der Made, 2014) and coincides with the end of several listriodont lineages (Figs. 8, 10). Apparently Listriodontinae did well during this period of high temperatures and high $p\text{CO}_2$ as they reached their greatest geographic expansion and diversity (Fig. 10). The decrease in $p\text{CO}_2$ from 13.6 Ma onwards is mirrored by the rise in Bovidae in Africa (Van der Made 2014, fig. 6) and elsewhere, and in the decrease in browsers noted by Janis et al. (2000, 2004). The final extinction of the

Listriodontinae around 9.8–9.4 Ma and a spectacular drop in the abundance of the Tragulidae in the Indian Subcontinent (Barry 2014), where they were most diverse, coincide with one of the moments when the decrease in pCO₂ accelerated (Figs. 8, 10). The pCO₂ according to Van de Wal et al. (2011) shows several peaks with each time lower values from about 9.75 Ma onward and a sustained decrease in values from about 9.62 Ma onward, reaching a record low at about 9.58 Ma and continued to decrease till 9.539 Ma and peaked several times about 100, 200, and 300 ka later. The temporal duration of these events covers or overlaps the last records of the last listriodont lineages. The curves by Super et al. (2018) and Sosdian et al. (2018) show peak low values at 9.7 and 9.874, which are close, given the lesser temporal precision due to their less dense records.

The increase in sugar and reduction of protein, Zn, and Fe contents of fruit and vegetables is well studied in relation to the possible rise in pCO₂ in the near future, starting from the present levels around 400 ppm. Little or nothing is known about the effect of the drop in pCO₂, from over 450 ppm during the Middle Miocene Climatic Optimum till about 350 ppm around 9.8–9.4 Ma, on sugar, starch, protein, Zn, and Fe contents of leaves and fruit. The fact that during this period, the high diversity of browsers, including Tragulidae, declined markedly, suggests that a decrease of sugar and starch in fruit and leaves could have been prejudicial to them and that this was not compensated by the higher content in other nutrients.

Janis (1989) classified living and fossil Artiodactyla in three categories, those with: (1) little or no fermentation (Suidae, Tayassuidae, Entelodontidae and Palaeogene families); (2) some foregut fermentation (for example Tragulidae, Anthracotheriidae); and (3) full foregut fermentation plus rumination (including ruminants and camels). Category 2 is somewhat adapted to a fibrous diet, but category 3 consists of “cell wall specialists”, still better adapted to the digestion of cellulose. She noted that, during the Late Eocene and Oligocene, primitive foregut fermenters (type 2) diversified at the cost of hindgut fermenters and that from the Middle Miocene onward, ruminating artiodactyls (type 3) replaced less specialized foregut fermenters and the Listriodontinae. At present, Tayassuidae and *Babyroussa* are considered to be foregut fermenters, while *Phacochoerus* and *Sus* (both Suidae) and *Potamochoerus* are considered to be hindgut fermenters (Langer 1986; Leus et al. 1999; Clauss et al. 2008).

The living Suinae are hindgut fermenters, and the available data suggest that they have higher protein requirements than the peccaries and babirusas, which are foregut fermenters. *Propotamochoerus* from the Chinji Formation is the first representative of this subfamily and was probably a hindgut fermenter. This subfamily radiated and progressively replaced other Suoidea, most of which are likely to have been foregut fermenters (Palaeochoeridae, Listriodontinae,

Cainochoerinae, perhaps Hyotheriinae). At the time when pCO₂ decrease suggests an increase in protein content, Suinae, which were less efficient, replaced other Suoidea, which were more efficient in the digestion of proteins. At the same time, there was a decrease in sugar content and the hindgut fermenting Suinae handle sugars more efficiently. Either access to protein may have been a limiting factor or more efficient sugar digestion may have been a plus, or both may have been decisive in the spread of hindgut fermenting Suoidea. Listriodontinae may have been more competitive in a high pCO₂ world, because they were more protein efficient, while they could afford to be less sugar efficient.

Though many data are still lacking, it seems possible that the decreasing pCO₂ led to changes in the nutrient composition of the vegetation, favoring some herbivores and omnivores over others. The extinction of the Listriodontinae in the different continents may have occurred when a critical pCO₂ threshold was met.

Conclusions

We studied a new fossil from Pasuda and placed it in a wider context. Our work led to the following conclusions:

- The specimen from Pasuda belongs to the new species *Listriodon dukkar*.
- The new species has P³⁻⁴ with perfect lophs and evolved more towards perfect lophodonty than any other Suoidea, reflecting the highest degree of adaptation to folivory.
- *Listriodon dukkar* shares features with *Li. pentapotamiae* and evolved from it.
- The *Listriodon pentapotamiae*–*Li. dukkar* lineage was folivorous and lived in humid environments with a low degree of seasonality, probably including tropical evergreen forest.
- The last records of the three distinct lineages of Listriodontinae in the Indian Subcontinent (~ 9.8 Ma), Europe (9.78 Ma), and Africa (~ 10 Ma) are close in age and suggest a cause that was likely of global nature, acting in the different environments of these continents.
- These extinctions coincided with a variety of local events, including increasing seasonality, changes in vegetation, turnover in the mammals, and the European Vallesian Crisis. They also occurred against a background of the decline of the browsers and the rise of the Bovidae, but these trends occurred at different rates in the different continents. Though all these events may have contributed to the demise of the Listriodontinae, none explains the extinction of the Listriodontinae in all their geographic distribution and apparently in a short period.

- The Listriodontinae radiated and did well when atmospheric pCO₂ was relatively high, but went extinct during a period when pCO₂ decreased. Changes in atmospheric pCO₂ are independent of latitude and affect nutrient contents of plants and, thus, the competition between herbivores with different types of digestion and protein requirements. These observations suggest a causal relationship that may have acted at the same time throughout the area of distribution of the Listriodontinae

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Author contributions JvdM, DC, and RP wrote the paper, and field work and collecting were done by DC, NPS, KMS, NAS, and RP. All the authors read and approved the manuscript.

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Availability of data and materials The fossil from Pasuda described here (PUKP-1) is kept in the Centre of Advanced study in Geology, Panjab University, Chandigarh. The data are either published or given in Table 2.

Code availability Not applicable.

Declarations

Conflict of interest We do not have conflicts of interest.

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