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Systematic Palaeontology (Vertebrate Palaeontology)

A new species of Anthracotheriidae, *Merycopotamus medioximus* nov. sp. from the Late Miocene of the Potwar Plateau, Pakistan

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Abstract

New anthracotheriid remains, discovered by the H-GSP in well-dated localities from the Potwar plateau in the North of Pakistan, between 10.4 and 8.6 Ma, are described and attributed to *Merycopotamus medioximus* nov. sp. This new species displays an intermediate morphology between the older *M. pusillus* and the more recent *M. dissimilis*. These results permit to emend the *Merycopotamus* diagnosis. **To cite this article:** F. Lihoreau et al., *C. R. Palevol* 3 (2004).

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Résumé

Une nouvelle espèce d'Anthracotheriidae, *Merycopotamus medioximus* nov. sp. du Miocène récent du plateau du Potwar, Pakistan. Des restes d'Anthracotheriidae, découverts par le H-GSP dans des localités bien datées du plateau du Potwar, au Nord du Pakistan, entre 10,4 et 8,6 Ma, sont décrits et attribués à *Merycopotamus medioximus* nov. sp. Cette nouvelle espèce possède une morphologie intermédiaire entre *M. pusillus*, espèce plus ancienne, et *M. dissimilis*, plus récente. Ces résultats permettent en outre d'émender la diagnose du genre *Merycopotamus*. **Pour citer cet article :** F. Lihoreau et al., *C. R. Palevol* 3 (2004).

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Keywords: Anthracotheriidae; *Merycopotamus*; Late Miocene; Pakistan

Mots clés : Anthracotheriidae ; *Merycopotamus* ; Miocène récent ; Pakistan

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Version française abrégée

Depuis 1973, le H-GSP prospecte les niveaux néogènes du plateau du Potwar, au nord du Pakistan [5] (Fig. 1). La famille des Anthracotheriidae est très diversifiée sur le sous-continent indien depuis l'Éocène moyen [9] et durant le Néogène [6,12,14,17] mais le matériel du Miocène moyen et récent reste peu étudié. Nous décrivons dans ce manuscrit des spécimens inédits d'Anthracotheriidae provenant de localités fossilifères corrélées au Geomagnetic Polarity Time Scale [3,10] avec une précision de $\pm 0,1$ Ma [2]. Ce matériel, découvert dans les régions de Kaur et de Sethi Nagri (Fig. 1) et daté du Miocène récent, est attribué à une nouvelle espèce. Une partie des collections de l'AMNH, établies par Colbert [4], et celles de l'université d'Utrecht [13] sont rapportées à cette espèce. La diagnose du genre *Merycopotamus* est élargie.

Systématique

Artiodactyla Owen, 1848

Anthracotheriidae Leidy, 1869

Bothriodontinae Scott, 1940

Merycopotamus Falconer et Cautley, 1847

Espèce type. *Merycopotamus dissimilis* (Falconer et Cautley), 1836, Miocène récent et Pliocène du Myanmar, d'Inde et du Pakistan.

Espèces incluses. *Merycopotamus pusillus* Lydekker, 1885, Miocène moyen d'Inde et du Pakistan et *Merycopotamus dissimilis*.

Diagnose élargie du genre. Crête faciale oblique en contact avec une tubérosité faciale marquée ; grande extension de la fosse canine ; une à deux cuspides accessoires sur la crête disto-vestibulaire des prémolaires supérieures ; molaires supérieures tétracuspides sélénodontes ; molaires supérieures plus larges que longues ; mésostyle en boucle continue ou divisée ; une seule postprotocrista ; symphyse redressée, au bord ventral concave ; une cuspide accessoire sur la crête mésio-linguale des prémolaires inférieures ; pas de prémétacristide ; préhypocristide et préentocristide atteignent le bord lingual de la dent ; hypoconulide aligné avec les cuspides vestibulaires.

Diagnose différentielle. *Elomeryx* Marsh, 1894 et *Sivameryx* Lydekker, 1878, diffèrent de *Merycopotamus* par l'existence d'un paraconule et de deux postprotocrista sur les molaires supérieures, et par la présence de quatre crêtes issues du métaconule sur les

molaires inférieures. Les préhypocristide et préentocristide n'atteignent pas le bord lingual de la dent et l'hypoconulide n'est pas aligné avec les cuspides vestibulaires, mais avec l'axe médian de la dent sur les molaires inférieures d'*Elomeryx* et d'*Afromeryx* Pickford, 1991. *Elomeryx*, *Afromeryx*, *Sivameryx* et *Hemimeryx* Lydekker, 1883, se distinguent de *Merycopotamus* par leurs symphyses au bord ventral droit. *Elomeryx* diffère par la présence d'une fosse canine courte, d'une crête faciale horizontale et d'une bulle tympanique enflée. *Hemimeryx* ne montre pas de postprotocrista et possède de nombreuses cuspides accessoires sur les prémolaires inférieures. *Libycosaurus* présente des prémolaires supérieures portant plus de deux cuspides accessoires sur leur crête disto-vestibulaire et une absence d'incisure vasculaire.

Merycopotamus medioximus nov. sp.

Liste synonymique. Voir version en anglais.

Holotype. Crâne d'un juvénile avec P4/ et M3/ droites, et M1/–M3/ gauches, Y13310 (Fig. 2A–C), appartenant aux collections du Geological Survey of Pakistan (GSP), conservé pour étude au Peabody Museum, Harvard University.

Paratype. Mandibule gauche avec P3/–M3/, Y14969 (Fig. 2D et E), appartenant aux collections du GSP, conservée pour étude au Peabody Museum, Harvard University.

Localité type. y312, Dhok Mila, Potwar Plateau, Pakistan.

Étymologie. De l'adjectif latin *medioximus*, signifiant intermédiaire, compris entre deux pôles.

Horizon. Formations de Nagri et partie inférieure de Dhok Pathan.

Âge. Miocène récent, entre 10,4 et 8,6 Ma [2].

Matériel. Voir version en anglais

Diagnose. *Merycopotamus* de grande taille ; orbites légèrement surélevées au-dessus du toit crânien ; ouverture des forams palatins principaux au niveau de P1/–P2/ ; molaires supérieures présentant une encoche sur le mésostyle ; de petites crêtes sur les bords mésial et distal des styles ; hypoconulide en boucle ; métapodes larges transversalement dans leur partie distale, main tétradactyle.

Diagnose différentielle. *Merycopotamus pusillus* diffère par la présence d'un mésostyle continu, une hauteur mandibulaire plus faible, un condyle mandibulaire situé plus haut au-dessus de la rangée dentaire, une incisure vasculaire moins prononcée, des molaires

inférieures (M/2 et M/3) plus petites, des membres plus grêles (particulièrement les métapodes et phalanges). *Merycopotamus dissimilis* diffère par l'ouverture des forams palatins principaux antérieurement à P1/, le mésostyle plus profondément divisé en deux styles coniques, la canine inférieure hypsoarhizodonte (voir [19]), la symphyse plus longue et plus redressée, la hauteur mandibulaire relativement plus forte, la présence d'un pli de l'entoconide et la tendance nette à la disparition de la posthypocristulide.

La combinaison de caractères dérivés (élargissement transverse des métapodes (Fig. 4), développement de l'incisure vasculaire, position basse du condyle mandibulaire par rapport à la rangée dentaire) et plésiomorphes (absence de pli entoconide, posthypocristulide bien développée, symphyse peu redressée) chez *Merycopotamus medioximus* nov. sp. permet de redéfinir le genre jusqu'à présent restreint à *M. dissimilis*. *Merycopotamus pusillus* ne doit plus être inclus dans *Hemimeryx* (contra [16]) de par le développement de son protocône, mais doit être inclus dans *Merycopotamus* par la morphologie de sa symphyse, l'absence de prémétacristide et l'importante hauteur mandibulaire. La nouvelle espèce, de par la morphologie de son mésostyle (Fig. 3), de sa canine inférieure (Fig. 2F et G), l'ouverture des forams mandibulaires externes et ses dimensions dentaires (Tableau 1) et mandibulaires (Tableau 2), est une forme intermédiaire entre *M. pusillus*, du Miocène moyen [11], et *M. dissimilis*, de la fin du Miocène et du Pliocène [1,5,18]. Une acquisition de caractères liés à un mode de vie amphibie (élévation des orbites) et une accentuation des caractères pouvant être liés à un comportement de bâillement [8] sont observées dans ce genre au cours du Néogène.

1. Introduction

Since 1973, the Harvard University and Geological Survey of Pakistan joint research project (H-GSP) has conducted geological research on the Potwar plateau in the North of Pakistan [15] (Fig. 1). The complete sequence studied by this team is the longest in the Neogene, dated between 18 and 0.7 Ma [10]. A great number of vertebrate fossils has been discovered and the majority of the fossiliferous localities has been correlated to the Geomagnetic Polarity Time Scale [3] with an accuracy of ± 0.1 Ma [2].

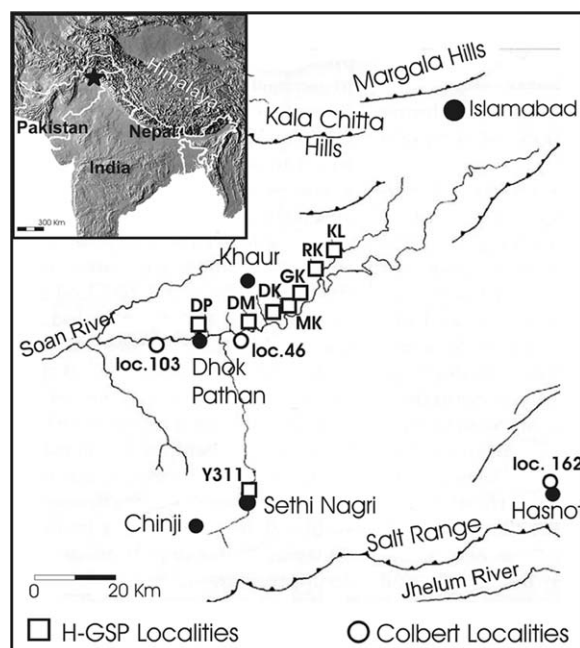


Fig. 1. Geographic distribution of *Merycopotamus medioximus* nov. sp. localities (new material from the H-GSP localities and other material from the Colbert localities and Sethi Nagri). Stratigraphic section abbreviations: DP: Dhok Pathan (loc. 194); DM: Dhok Mila (loc. y193, y310, y312); DK: Dinga Kas (loc. y224, y227, y229); MK: Malhuwala Kas (loc. y408); GK: GandaKas (loc. y239); RK: Ratha Kas (loc. y218, y224, y228, y251); KL: Kaulial (loc. y285). Fig. 1. Distribution géographique de localités ayant livré *Merycopotamus medioximus* nov. sp. (nouveau matériel des localités du H-GSP et autre matériel des localités de Colbert et de Sethi Nagri). Abréviations des sections stratigraphiques: DP: Dhok Pathan (loc. 194); DM: Dhok Mila (loc. y193, y310, y312); DK: Dinga Kas (loc. y224, y227, y229); MK: Malhuwala Kas (loc. y408); GK: GandaKas (loc. y239); RK: Ratha Kas (loc. y218, y224, y228, y251); KL: Kaulial (loc. y285).

The fossil family Anthracotheriidae is known on the Indian sub-continent, from the Middle Eocene [9] to the Late Pliocene [18]. The family was very diversified in this region during the Neogene [6,14,17], but is still unstudied in the Middle and Late Miocene. We describe here a new anthracotheriid species from the Late Miocene (Nagri and Dhok Pathan Formations [2]) of the Potwar plateau (see also [12]) on the basis of new material discovered in the Khaur area and near Sethi Nagri (Fig. 1). Part of the collection of the American Museum of Natural History (AMNH) established by Colbert [4] and that of the Utrecht University [13] are also reported to the new species. Moreover, the diagnosis of the genus *Merycopotamus* is emended.

2. Systematic

Artiodactyla Owen, 1848

Anthracotheriidae Leidy, 1869

Bothriodontinae Scott, 1940

Merycopotamus Falconer and Cautley, 1847

Type species. *Merycopotamus dissimilis* (Falconer and Cautley), 1836, Late Miocene and Pliocene of Myanmar, India and Pakistan.

Referred species. *Merycopotamus pusillus* Lydekker, 1885, Middle Miocene of India and Pakistan and *Merycopotamus dissimilis*.

Emended diagnosis. Oblique facial crest that joins the facial tuberosity; large canine fossa on maxilla; one or two accessory cusps on the disto-buccal crest of upper premolars; selenodont tetracuspitate upper molars; upper molars wider than long; loop-like or divided mesostyle; only one postprotocrista; elevated symphysis with concave ventral border; one accessory cusp on the mesio-lingual crest of lower premolars; no premetacristid; prehypocristid and preentocristid reach the lingual border of the molar; hypoconulid in line with buccal cusps.

Differential diagnosis. *Elomeryx* Marsh, 1894 and *Sivameryx* Lydekker, 1878 differ from *Merycopotamus* in the presence of a paraconule and two postprotocrista on upper molars, and in the presence of four crests on the metaconids of the lower molars. The prehypocristid and preentocristid do not reach the lingual border of the lower molar and the hypoconulid is in line with the buccal cusps in *Elomeryx* and *Afromeryx* Pickford, 1991. *Elomeryx*, *Afromeryx*, *Sivameryx* and *Hemimeryx* Lydekker, 1883, are distinguished from *Merycopotamus* in having a straight ventral border of their symphyses. *Elomeryx* also differs in having a short canine depression on the maxilla, a horizontal facial crest, and an inflated tympanic bulla. *Hemimeryx* lacks a postprotocrista on the upper molar and has a greater number of accessory cusps on the lower premolars. *Libycosaurus* possesses more than two accessory cusps on the disto-buccal crest of upper premolars and has no vascular impression.

Merycopotamus medioximus nov. sp.

Synonymy

vp 1935 *Merycopotamus dissimilis* (Falconer and Cautley); Colbert, p. 276 [4]

v 1977 *Merycopotamus nanus* Lydekker; Pilbeam et al., p. 687 [15]

v 1977 *Merycopotamus dissimilis* (Falconer and Cautley); Pilbeam et al., p. 687 [15]

1978 *Merycopotamus dissimilis* (Falconer and Cautley); Moonen et al., p. 427 [13]

vp 1982 *Merycopotamus dissimilis* (Falconer and Cautley); Barry et al., p. 95–130 [1]

1992 *Hemimeryx*; Steensma and Hussain, p. 104 [18]

vp 1995 *Hemimeryx pusillus* (Lydekker); Flynn et al., p. 255 [5]

vp 2002 *Hemimeryx* spp.; Barry et al., p. 69 [2]

Holotype. Partial skull of a juvenile individual with preserved crowns of the right P4/ and M3/, and left M1/-M3/, Y13310 (Fig. 2A–C), from the Geological Survey of Pakistan (GSP) collections, housed for study in the Peabody Museum, Harvard University.

Paratype. Left mandible with P3-M/3, Y14969 (Fig. 2D–E), from the GSP collections, housed for study in Harvard University.

Type locality. Locality y312, Dhok Mila, Potwar Plateau, Pakistan.

Etymology. From the Latin adjective *medioximus*, meaning intermediate, between two poles.

Horizon. Nagri and lower Dhok Pathan Formations.

Age. Early Late Miocene, between 10.4 and 8.6 Ma [2].

New material. Symphysis with right C-P/2 (Y4191, loc. y166), right M/3 (Y4596, loc. y193), mandible with right (P/3-M/1) M/2-M/3 and left (P/3-M/2) (Y4597, loc. y193), frag. right M/3 (Y4616, loc. y194), left MT4 (Y6065, loc. y218), left M1/-M2/ (Y6169, loc. y224), right M/3 (Y6225, loc. y228), MT3 (Y6444, loc. y311), P4/-M3/ (Y6746, loc. y227), left dP4-M/1 (Y9003, loc. y251), right MC3 (Y10514, loc. y311), left MC2 (Y10535, loc. y312), right M1/ (Y10539, loc. y311), right (M2/-)M3/ (Y10631, loc. y311), left MT3 (Y10847, loc. y310), right MC3 (Y12970, loc. y311), frag. skull with right P4/ and M3/, and left M1/-M3/, (Y13310, loc. y312), frag. right mandible with M1/-M2/ (Y13523, loc. y239), left (M2/-)M3/ (Y14318, loc. y450), right (M2/-)M3/ (Y14515, loc. y269), left (M2/-)M3/ (Y14516, loc. y269), left mandible with P3-M/3 (Y14969, loc. y408), left MC3 (Y15376, loc. y228), right M2/ (Y15572, loc. y285), right dP4/ (Y16657, loc. y578), frag. left mandible with M/3 (Y16657, loc. y578), right M2-M/3 (Y18294, loc. y454), right P4/-M3/ (Y20611, loc. y311), M2/-M3/ (L24154, loc. 194), left

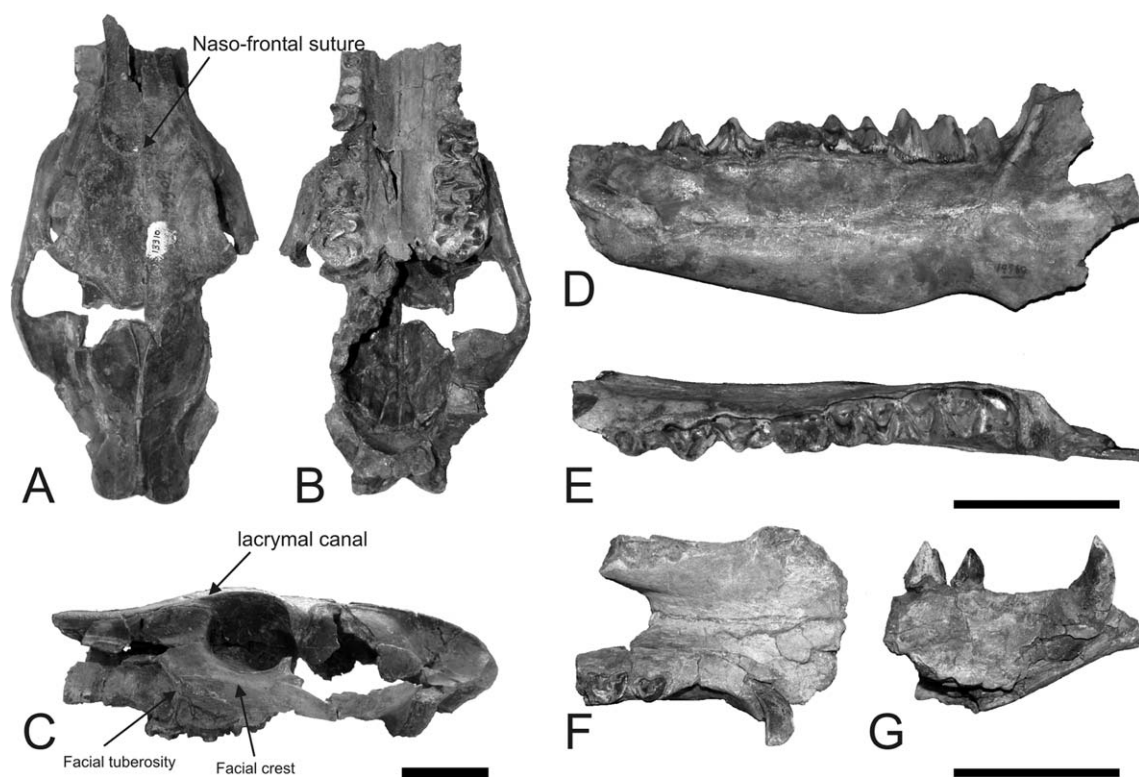


Fig. 2. A–C. Skull of *Merycopotamus medioximus* nov. sp., Y13310, in dorsal (A), ventral (B) and lateral (C) views. D–G. Mandibles of *Merycopotamus medioximus* nov. sp. D–E. Y14969, in lateral (D) and occlusal (E) views. F–G. Y4191 in occlusal (F) and lateral (G) views. Scale bars = 5 cm.

Fig. 2. A–C. Crâne de *Merycopotamus medioximus* nov. sp., Y13310, en vues dorsale (A), ventrale (B) et latérale (C). D–G. Mandibules de *Merycopotamus medioximus* nov. sp. D–E. Y14969, en vues latérale (D) et occlusale (E). F–G. Y4191 en vues occlusale (F) et latérale (G). Barres d'échelle = 5 cm.

M3/ (Y26570, loc. y311), frag. left M/3 (Y26878, loc. y311), right MC3 (Y26879, loc. y311), left M1/ (Y30877, loc. y311), right MC3 (Y46769, loc. y311), left (P/4)-M/3 (Y49562, loc. y891), frag. M/1 (Y50491, loc. y311), left MT4 (Y50633, loc. y450), left M/2 (Y52174, loc. y311), GSP collections, housed for study in Harvard University.

Other material. Left C-M2/ (NG104), frag. right M/3 (NG108), right M/2 (NG111), right P/4-M/2 (NG115), left M/1 (NG181), left M/1 (NG182), from the Utrecht University collection, Sethi Nagri. Right (M1)–M3/ (AM9917, loc. 162), frag. right M2/ (AM9920, loc. indet.), left M1/ (AM9920, loc. indet.), left M1/ and M2/ (two individuals) (AM19371, loc. 114), right M2/ (AM19372, loc. 46), right and left dP4-M1/ (AM19504, loc. 147), right M/3 (AM19698, loc. 103), M1/ (AM19854, loc. 103), left M1/

(AM94618, loc. indet.), mainly from Colbert's collection, housed in AMNH.

Diagnosis. Large *Merycopotamus* species; orbits slightly elevated above the cranial roof; main palatine foramen opening at P1–P2/; upper molars with a mesostyle notch but not fully divided; small crests on the mesial and distal borders of the styles; loop-like hypocondylide on M/3; transverse broadening of the distal parts of metapodials; tetradactyle manus.

Differential diagnosis. *M. pusillus* differs in having a continuous mesostylar loop, a shallower mandible, a mandibular condyle positioned high relatively to the dental row, a less pronounced vascular impression, smaller M/2 and M/3, and slender limbs particularly the metapodials and phalanges. *M. dissimilis* differs in having the main palatine foramen opening mesial to P1/, a fully divided mesostyle with two conical styles, a

hypsoarhizodont lower canine (see [19]), a longer and more slanted symphysis, a deeper mandibular corpus, and the presence of an entoconid fold and in the absence of the posthypocristulid.

3. Description

3.1. Skull

The type of this species is a skull that lacks the anterior part of the maxillae, basicranium and zygomatic arch (Fig. 2A–C). It is a sub-adult with erupting M3/. Nevertheless, the skull is only slightly smaller than that of an adult of *M. dissimilis*. In dorsal view, the naso-frontal suture is rounded (Fig. 2A) as in *M. dissimilis*, whereas it is acutely angled in *M. pusillus* and *Elomeryx* [11]. The superior margin of the orbits shows a continuous divergence anterior to the post-orbital process. Thus, the cranial roof appears triangular (Fig. 2A). The superior borders of the orbits are also slightly elevated with respect to the cranial roof, but less than in *M. dissimilis*.

In ventral view, the maxillo-palatine suture is at the level of the mesial border of M1/ (Fig. 2B) as in *M. pusillus*, whereas it is at the level of the M2/ in *M. dissimilis*. The main palatine foramen opens at P1/–P2/ as in *M. pusillus* and is posterior to that position in *M. dissimilis* (anterior to P1/). The internal choanes open posteriorly to M3/.

In lateral view, the canine fossa is deep and extends to the facial tuberosity, just distal to the infra-orbital foramen, above P4/ (Fig. 2C). The facial crest runs along the jugal, it joins the facial tuberosity and connects obliquely to the anterior border of the lachrymal. A second crest is present on the ventral face of the zygomatic arch, as in *M. dissimilis*. The jugal is prominent with respect to the part of the maxillae that bears the M2/–M3/, a condition similar to that of *M. dissimilis*, whereas the jugal is not prominent in *M. pusillus* [11]. The lachrymal is rectangular and constitutes the anterior margin of the orbit. It has a sizable contact with the nasal. There is no lachrymal foramen but a well-defined groove corresponding to the lachrymal canal lies above the lachrymo-frontal suture (Fig. 2C). The external auditory meatus is situated between the retro-glenoid process and the mastoid process. It is dorso-ventrally orientated (Fig. 2C). The nuchal crests

are separated from the temporal crests that join the zygomatic arch. In occipital view, the supraoccipital shows two strong fossae separated from each other by a medio-occipital crest.

3.2. Upper dentition

Upper incisors are not known. The upper canine shows wrinkled enamel with longitudinal striations. There is a keel running on the distal border of the tooth. The root is not closed in that specimen.

There are four premolars on the maxillary and they form a continuous row. They are separated from the canine by a diastema (28 mm in NG104) that is longer than in *M. dissimilis* (8.6–16.2 mm in M16551 and M16552 from the Natural History Museum, London and in *M. pusillus* (15 mm in Y47189 [11]). The premolars are morphologically identical to those of *M. pusillus* and *M. dissimilis*. The P1/, P2/ and P3/ are biradicate with trapezoidal outlines in occlusal view, and a median constriction that increases in size from P1/ to P3/. Three crests run from the main cusp. The mesio-lingual and mesio-buccal crests are of equal dimensions, while the longer disto-lingual crest bears accessory cusps, whose heights decrease toward the distal border of the crown. The disto-lingual basin increases in size from P1/ to P3/. The P4/ is bicuspid and differs from those of *M. pusillus* and *M. dissimilis* in the presence of small crests developed from the style toward the ribs of the buccal cusp.

The upper molars resemble those of *M. pusillus* and *M. dissimilis*. They are tetracuspidate, broader than long with crescent-like cusps. However, the upper molars differ in the occurrence of a notch on the mesostyle. The mesostyle is more asymmetrical in occlusal view and partly divided in *M. medioximus* nov. sp. (Fig. 3), whereas it is fully divided into two conical cusps in *M. dissimilis* and forms a continuous, symmetrical loop in *M. pusillus*. Moreover, specimens of *M. medioximus* nov. sp. have small crests mesio-distally oriented as observed on P4/ (Fig. 3). This character is more or less accentuated in the specimens of *M. medioximus* nov. sp., but is never observed in other species of *Merycopotamus*. Upper molar dimensions (Table 1) do not discriminate between the species of *Merycopotamus* despite the very marked differences in estimated body weights [11].

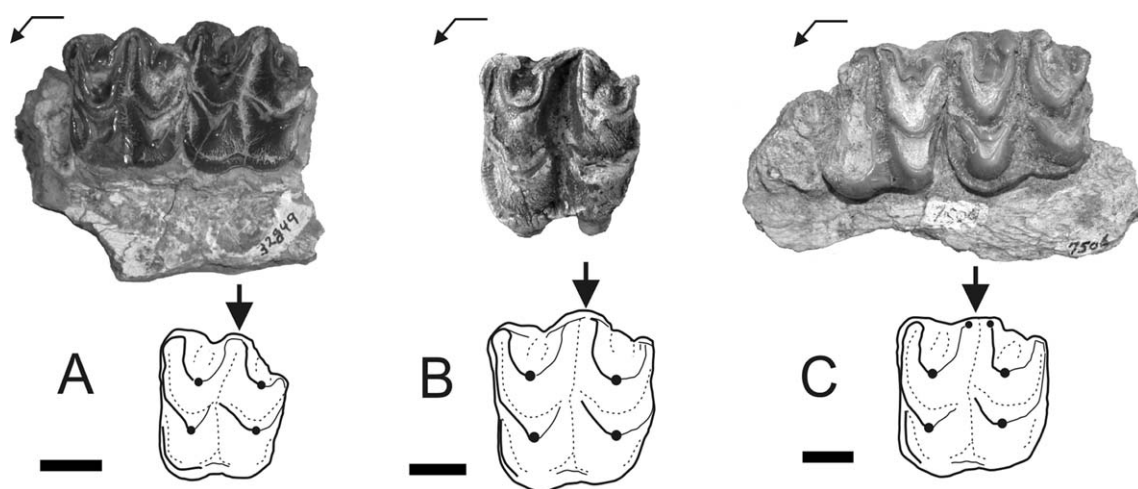


Fig. 3. Comparison of the mesostylar morphology on the upper molars of *M. pusillus* (Y32849, A), *M. medioximus* nov. sp. (Y15572, reversed image B), and *M. dissimilis* (Y7506, C). Scale bar = 1 cm.

Fig. 3. Comparaison de la morphologie du mésostyle des molaires supérieures de *M. pusillus* (Y32849, A), *M. medioximus* nov. sp. (Y15572, image inversée B) et, *M. dissimilis* (Y7506, C). Barre d'échelle = 1 cm.

Table 1

Measurements in millimetres of upper and lower jugal teeth of *M. medioximus* nov. sp. from the Potwar plateau. L_{md} (mesio-distal length); L (maximal width); Sd (standard deviation).

Dimensions en millimètres des dents jugales supérieures et inférieures de *M. medioximus* nov. sp. du plateau du Potwar. L_{md} (longueur méso-distale); L (largeur maximale); Sd (écart type)

		<i>n</i>	Mean	Min	Max	<i>Sd</i>			<i>n</i>	Mean	Min	Max	<i>Sd</i>
P1/	L_{md}	2	14.7	14.0	15.4		M1/	L_{md}	12	20.4	18.0	22.0	1.4
	L	2	11.4	10.9	11.8			L	12	20.6	17.3	23.3	1.8
P2/	L_{md}	3	16.5	16.0	17.3		M2/	L_{md}	9	24.7	21.0	28.0	2.4
	L	2	14.8	13.8	15.8			L	10	24.9	21.6	28.2	2.2
P3/	L_{md}	3	19.0	18.0	20.9		M3/	L_{md}	10	27.3	23.2	31.0	2.3
	L	2	14.4	13.5	15.3			L	7	27.6	23.0	31.5	3.4
P4/	L_{md}	10	15.3	12.4	18.5	1.9							
	L	10	17.2	14.4	21.8	2.1							
P/1	L_{md}	3	11.3	9.9	12.1		M/1	L_{md}	9	20.9	17.3	24.4	2.3
	L	3	7.2	7.0	7.4			L	9	13.9	12.0	15.3	1.0
P/2	L_{md}	1	15.0				M/2	L_{md}	8	24.7	21.6	26.6	1.9
	L	1	10.0					L	8	16.4	14.1	18.5	1.4
P/3	L_{md}	5	17.7	16.8	19.3	1.0	M/3	L_{md}	9	37.7	33.8	42.4	3.0
	L	5	10.6	9.6	11.9	1.0		L	13	17.4	14.4	20.0	1.8
P/4	L_{md}	3	18.2	17.9	18.5								
	L	3	11.3	10.1	13.0								

3.3. Mandible

Merycopotamus medioximus nov. sp. presents a deeper mandibular corpus than *M. pusillus* (Table 2). The vascular impression is deeper than in *M. pusillus*, but is not as deep as in *M. dissimilis*. The gonial area is expanded below the ventral border of the mandible.

The insertions for the masseter muscle protrude more than in *M. pusillus* resembling the condition observed in *M. dissimilis*.

A mental foramen is present on the ventral border of the mandibular symphysis below the I/1–I/2 interspace. One or two external mandibular foramina are posterior to the post-canine depression. The larger one

Table 2

Compared measurements of the mandible symphysis (L_{symp} : symphysis maximal length ; A_{symp} : angle between the tooth row and the ventral border of symphysis), the mandibular depth (H_{md} , measured below M/2) and the C-P/1 diastem length (L_{diast}) of the known species of *Merycopotamus*, in millimetres. Dimensions of *M. pusillus* and *M. dissimilis* include unpublished material from Pakistan [11].

Dimensions comparées de la symphyse mandibulaire (L_{symp} : longueur maximale de la symphyse ; A_{symp} : angle entre la rangée dentaire et le bord ventral de la symphyse), de la hauteur mandibulaire (H_{md} , mesurée sous M/2) et de la longueur du diastème C-P/1 (L_{diast}) des espèces connues de *Merycopotamus*, en millimètres. Les mesures de *M. pusillus* et *M. dissimilis* incluent du matériel inédit du Pakistan [11]

	<i>M. medioximus</i> nov.sp.					<i>M. dissimilis</i>					<i>M. pusillus</i>				
	<i>n</i>	Mean	Min	Max	<i>Sd</i>	<i>n</i>	Mean	Min	Max	<i>Sd</i>	<i>n</i>	Mean	Min	Max	<i>Sd</i>
L_{symp}	6	65.0	48.0	81.3	11.4	4	93.2	79.7	110.5		8	57.7	50.0	66.5	6.5
A_{symp}	8	29.8°	21.1°	38.0°	5.8°	2	45.8°	40.1°	51.5°		8	27.0°	23.0°	30.4°	3.2°
H_{md}	7	55.5	48.9	63.0	6.3	6	68.3	63.6	75.8	4.4	14	45.7	41.9	50.0	3.0
L_{diast}	7	26.0	21.0	31.5	3.5	5	30.3	26.3	33.8	3.1	9	18.4	15.0	25.0	3.5

is at the level of the P/3, while the smaller one is below the P/4 (Fig. 1D) when present. The anterior foramen is always below P/2 in *M. pusillus*, and in *M. dissimilis* the single foramen is always below P/4. The position of this foramen is linked to the development of the canine, the root of which is curved and extends posteriorly to P/2 in *M. pusillus*, to P/4 in *M. dissimilis*, and is in an intermediate position in *M. medioximus* nov. sp.

The mandibular symphysis is fused in adult specimens (Fig. 1F and G). The angle between the ventral border of the symphysis and the lower tooth row, and the dimensions and morphology of the symphysis differ from *M. dissimilis* being less vertical and smaller in *M. medioximus* nov. sp. The variability of the facial morphology of the new species is greater than in *M. pusillus*, as shown by the measurements of the angle of the symphysis (Table 2).

The coronoid apophysis (preserved on Y5122) is perpendicular to the dental row and its height (from the dental row to the apex of the apophysis) is smaller than in *M. pusillus* (AM94619). The coronoid process and the mandibular condyle are lower in *M. dissimilis* and *M. medioximus* nov. sp. than in *M. pusillus*, with an optimisation of the jaw aperture in the two younger species. This character, together with an increase of the canine size and a more pronounced vascular impression, suggests a possible adaptation to a gape behaviour similar to that of extant Hippopotamidae and Taassuidae [8].

3.4. Lower dentition

There are three equal sized alveoli for the lower incisors. The anterior alveolus border is flattened in

dorsal view as in *M. dissimilis* and not curved, as in *M. pusillus* (Fig. 1F). The lower canine is large and buccolingually compressed, with a pronounced distal keel. The canine is curved with the apex directed dorso-laterally (Fig. 1F and G). The root is open in all specimens and it ends under the P/3. The canine is smaller than in *M. dissimilis*, where the root is always widely opened, even in old-aged specimens, and it ends under P/4. The diastem between C and P/1 is longer than in *M. pusillus* and partially overlaps the measurements of *M. dissimilis* (Table 2). The mean length of the diastema is intermediate between those of *M. pusillus* and *M. dissimilis*.

All the premolars are biradicate, with a rectangular outline in occlusal view, and they possess a single central cusp from which run two crests (Fig. 1E). The mesio-lingual crest bears an accessory cusp and the disto-lingual one joins the distal cingulum bordering the occlusal basin. An accessory cusp is present lingual to the disto-lingual crest of the P/4. There is an increase in the size of the occlusal basin from P/1 to P/4.

The lower molars are tetracuspidate, except M/3, which is pentacuspidate. The molars resemble those of *M. pusillus*, although they are larger with minor overlap in their dimensions (Table 1). They differ from those of *M. dissimilis* in the lack of an entoconid fold (a small mesio-distal crest between the hypoconid and the entoconid) and in the well-developed loop-like hypoconulid on M/3 (the posthypoconulid is always absent in *M. dissimilis*) (Fig. 1E).

3.5. Postcranium

Both metacarpals and metatarsals are similar in length to those of *M. pusillus*, but their diaphyses are



Fig. 4. Comparison of MC3 in palmar view. A. Y46769, *Merycopotamus medioximus* nov. sp. B. Y31727, *Merycopotamus pusillus*. Scale bar = 2 cm.

Fig. 4. Comparaison des vues palmaires de MC3. A. Y46769, *Merycopotamus medioximus* nov. sp. B. Y31727, *Merycopotamus pusillus*. Barre d'échelle = 2 cm.

transversely wider (Fig. 4). The MC2 (Y10535) is broad compared to the lateral metacarpals of *M. pusillus*. The proximal surface presents a lateral process with contacts for the magnum and trapezoid. No articular surface is observed on the median face, arguing for the lack of MC1. This condition differs from the pentadactyl hand described in *Elomeryx borbonicus* [7]. The MC3 (Y15376) displays a broad diaphysis compared to the slender metacarpals of *M. pusillus*, although they are of identical proximo-distal lengths. In ventral view, the articular facets for the phalanx and the metapodial keels have a short extension, thus differing from those of suids.

4. Discussion and conclusion

The genus *Merycopotamus* previously consisted of the single species *M. dissimilis* and the generic diagnosis was exclusively based on the division of the mesostyle of the upper molars. The intermediate morphology of the new species indicates that this character cannot longer be used for generic discrimination (Fig. 3). Moreover, the species *M. pusillus* cannot be

attributed to the genus *Hemimeryx*, as first suggested by Pilgrim [16], because of the complete protocone (presence of a postprotocrista) and the small number of accessory cusps on lower premolars. This species must therefore be included into *Merycopotamus* because of its symphysis morphology, the lack of premetacristid, and of the mandibular depth.

Although its size is close to that of *M. dissimilis*, the new species is morphologically between *M. pusillus* from the older Chinji Formation and *M. dissimilis* from the upper part of Dhok Pathan and Tatrot Formations, with a combination of characteristics that define one of the latter two species (absence of the entoconid fold, well-developed posthypocristulid, and weakly elevated and short symphysis, like in *M. pusillus*; broad metapodials and the large vascular impression like in *M. dissimilis*) or/and some other characters intermediate between the two species, like the partial mesostyle division. The evolution of this latter feature is gradual throughout the Miocene in *Merycopotamus* species (Fig. 3). A loop-like mesostyle is interpreted as plesiomorphic in Bothriodontinae, as it is observed in *Elomeryx* and *Sivameryx*. Its complete division is thus an autapomorphy of *M. dissimilis*. The presence of small accessory crests is considered as an intermediate stage, which is only known in the new species. The main external mandibular foramen opens below the P/3. It is positioned more anteriorly in *M. pusillus* and more posteriorly in *M. dissimilis*. This character is correlated with the increase in size of the lower canine and the acquisition of hypsoarhizodonty. The orbits are slightly elevated above the cranial roof, more than in *M. pusillus* and less than in *M. dissimilis*. It corresponds to an adaptation to an amphibious way of life, more stressed in *M. dissimilis*. Taking all these characters into consideration, *Merycopotamus medioximus* nov. sp. can be interpreted as an intermediate species in the *Merycopotamus* lineage in Pakistan between 10.4 and 8.6 Ma.

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