

PERSIATHERIUM RODLERI, GEN. ET SP. NOV. (MAMMALIA, RHINOCEROTIDAE) FROM THE UPPER MIOCENE OF MARAGHEH (NORTHWESTERN IRAN)

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ABSTRACT—A new genus and species of Rhinocerotidae, *Persiatherium rodleri*, gen. et sp. nov., a new acerathere rhinocerotid from the early upper Miocene (ca. 9 Ma) locality of Kopran, Maragheh (northwestern Iran), is described. The new taxon can be clearly distinguished from the three species previously reported at Maragheh: *Iranotherium morgani*, *Ceratotherium neumayri*, and *Chilotherium persiae*. Moreover, *P. rodleri* can be distinguished from the latest middle and late Miocene elasmotheres, teleoceratins, and rhinoceroses recorded in Eurasia and Africa. The new taxon displays morphological characters close to Aceratheriini. However, the presence of plesiomorphic characters on the teeth (presence of P1, continuous lingual cingula on the premolars, labial cingula on the premolars, lingual cingula on the molars, weak protocone constriction on the molars, absence of crista and antecrochet on the molars), of peculiar morphological characters (e.g., lingual side of the protoloph and metaloph directed disto-lingually on P2 with the presence of a lingual groove on the hypocone), as well as some derived characters (e.g., short metaloph on the molars), enable its distinction from other Aceratheriini. A cladistic analysis shows that *P. rodleri* is the sister taxon to ‘*Aceratherium huadeensis*’. Though the latter displays more derived features than *P. rodleri*, their phylogenetic relationships allow inclusion of both species in the same new genus.

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SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

The fossiliferous localities of Maragheh are located on the southern and eastern slopes of the Sahand massif, in eastern Azerbaijan province, northwestern Iran (Campbell et al., 1980:fig. 1; Bernor, 1986:figs. 1–2; Bernor et al., 1996; Ataabadi et al., 2013). The upper Miocene deposits consist of a series of volcanoclastic strata that underlie a broad pediplain at an altitude of 1,450–1,900 m (Campbell et al., 1980:fig. 2). The Maragheh fauna is well known in the literature for the exceptionally abundant and well-preserved mammal remains (Lydekker, 1886; Pohlig, 1886; Rodler, 1889; Rodler and Weithofer, 1890; Mecquenem 1905, 1911, 1925; Tobien, 1968; Campbell et al., 1980; Bernor, 1986; Bernor et al., 1996; Ataabadi et al., 2013, and references therein). This fauna is subdivided into three biostratigraphic intervals—‘Lower Maragheh’ (LM), ‘Middle Maragheh’ (MM), and ‘Upper Maragheh’ (UM)—that span a time of ca. 1.6 Ma (from ca. 9 Ma to 7.4 Ma, latest Vallesian–earliest Middle Turolian; Bernor et al., 1996; Ataabadi et al., 2013). Taxa collected from Maragheh have been studied since the end of the 19th century; however, the rhinocerotid material has not been exhaustively reviewed.

Three species of Rhinocerotidae have been previously reported from Maragheh, *Iranotherium morgani*, *Ceratotherium neumayri*, and *Chilotherium persiae* (Pohlig, 1886; Osborn, 1900; de Mecquenem, 1905, 1911; Geraads, 1988; Antoine, 2002). Systematic revision of the rhinocerotid material collected from the sites of Maragheh and currently housed at Naturhistorisches Museum of Wien and Natural History Museum of London enabled recognition of a fourth species.

Institutional Abbreviations—**HNHM**, Hungarian Natural History Museum, Budapest, Hungary; **MfN**, Museum für Naturkunde, Berlin, Germany; **MGGC**, Museo di Geologia Giovanni Capellini, Bologna, Italy; **MGPPD**, Museo di Geologia e Paleontologia, Padua, Italy; **NHML**, Natural History Museum, London, England; **NHMW mar**, Naturhistorisches Museum, Maragheh Collection, Wien, Austria; **NMB**, Naturhistorisches Museum, Basel, Switzerland.

MATERIAL AND METHODS

The specimen NHMW 2014/0426/0001 (ex mar2126) was compared with the rhinocerotid material collected in the same locality and referred to *I. morgani*, *C. neumayri*, and *Ch. persiae*. The morphological peculiarities of the specimen NHMW 2014/0426/0001 have been already indicated by Geraads and Koufos (1990:163), although these authors referred it to *Aceratherium*. Moreover, the studied specimen was compared with several latest-middle and late Miocene species of Eurasia and Africa (Table S1). The comparisons were based on direct observations of the material housed in several museums and institutions, as well as on the specimens published in several contributions (Table S1). Some differences between the studied specimen and the considered taxa are listed in the text, but other differences are included in the data matrix (online Supplementary Material). The dental terminology follows that of Antoine (2002; Fig. 1) and the morphometric methodology follows that of Guérin (1980). A cladistic analysis was performed in order to investigate the phylogenetic relationships of the new genus and species and

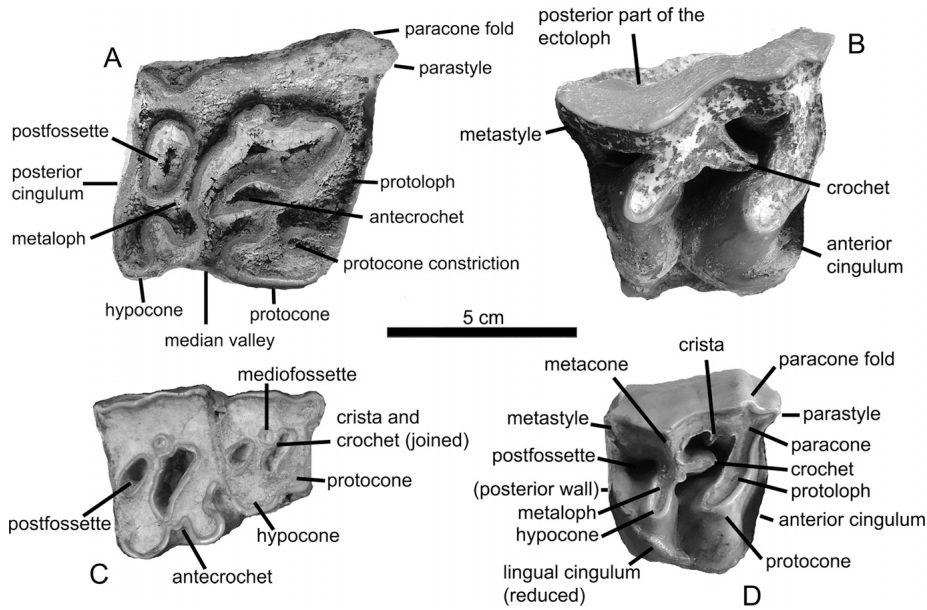


FIGURE 1. Dental nomenclature. **A**, M2 of *Iranotherium morgani* from Maragheh (NHMW 2014/0425/0001 ex mar0392); **B**, M2 of *Ceratotherium neumayri* from Maragheh (NHMW 2014/0424/0001 ex mar0381); **C**, P2–P3 of *Chiloitherium schlosseri* from Samos (MGPPD 25302); and **D**, P4 of *Hoploacera-therium belvederense* from Wien Belvedere (NHMW n°24).

its taxonomic position; 214 characters (70 cranial, 14 mandibular, and 130 dental) described by Antoine (2002), Antoine et al. (2003), and Lu (2013) were considered in this work (Table S2). All characters are equally weighted, 10 characters are unordered (2, 3, 8, 30, 31, 65, 94, 123, 131, 170), and 204 characters are ordered. The analysis was performed in PAUP 4.0β10 (Swofford, 2001) and heuristic search, TBR (tree-bisection-reconnection), and 1,000 replications with additional random sequence, gaps treated as missing. Forty-six taxa were included in this analysis (Table S1), and the selected outgroup was *Trigonias osborni*. The following taxa were added to the list of Lu (2013): *Aceratherium depereti*, *Aceratherium porpani*, *Alicornops complanatum*, *Ceratotherium simum*, *Ceratotherium neumayri*, *Chiloitherium kowalevskii*, *Chiloitherium persiae*, *Chiloitherium schlosseri*, *Diaceratherium aginense*, *Dihoplus schleiermachers*, *Dihoplus pikermiensis*, *Hispanotherium matritense*, *Iranotherium morgani*, *Persiatherium rodleri*, gen. et sp. nov., and *Rhinoceros sondaicus*. The character states were coded following Antoine (2002), Antoine et al. (2003), and Lu (2013) and based on direct observations. The character states of *B. brachypus*, *C. simum*, *D. aginense*, *I. morgani*, and *R. sondaicus* were modified from Antoine (2002) and Antoine et al. (2003). The character states of *Alicornops complanatum* come from Antoine et al. (2003); those of *A. porpani* from Deng et al. (2013); those of *A. depereti* from Boris-siak (1927); and those of *Ch. kowalevskii* are based on Pavlow (1913), whereas those of *C. neumayri*, *D. schleiermachers*, *D. pikermiensis*, *Ch. schlosseri* and *Ch. persiae* were coded from direct observations.

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848
 Family RHINOCEROTIDAE Owen, 1845
 Tribe ACERATHERIINI Dollo, 1885
PERSIATHERIUM, gen. nov.

Etymology—From ‘Persia’, the ancient name of Iranian region, and ‘therium’, Greek name for beast.

Diagnosis—Medium-sized Aceratheriini that differs from other aceratheres in the following characters and combination of characters: (1) P1 present; (2) labial cingula always absent on the

upper molars; (3) cristae always absent on the upper molars; (4) metaloph continuous on M1 and M2.

Type Species—*Persiatherium rodleri*, sp. nov.

Referred Species—*Aceratherium huadeensis* Qiu, 1979 from the late Miocene of Huade (China)

Distribution—Late Miocene (from the latest Vallesian to the late Turolian) of Iran and China.

PERSIATHERIUM RODLERI, sp. nov.
 (Fig. 2; Table 1)

Holotype—NHMW 2014/0426/0001, basal portion of skull with right and left maxillae.

Type Locality and Horizon—Kopran, Maragheh, early upper Miocene, latest Vallesian, Lower Maragheh biostratigraphic unit, ca. 9 Ma.

Etymology—For Alfred Rodler, geologist and paleontologist, who studied the Maragheh fauna at the end of the 19th century and collected the specimen NHMW 2014/0426/0001.

Diagnosis—*Persiatherium rodleri* can be diagnosed by five autapomorphies: (1) external auditory pseudomeatus partially closed ventrally; (2) mediofossette always present on P2–P4; (3) antecrochet absent on the upper molars; (4) lingual cingula present on the upper molars; and (5) mesostyle present on M2. *P. rodleri* is close to ‘*Aceratherium*’ *huadeensis* in size but differs in the following features: (1) protocone and hypocone directed disto-lingually on P2; (2) lingual side of the hypocone flat with a lingual groove on P2 and P3; (3) protocone similar to the hypocone on P3; (4) short metaloph on M1–M2; and (5) presence of lingual cingula on M1 and M2.

DESCRIPTION

Skull

The skull is considerably damaged and only a portion of the basicranium is preserved (Fig. 2). The occipital condyles are missing as well as the premaxillae and part of the palate. The anterior border of the palatine suture is convex, the palatine spine is very weak, and the anterior border of the choanae is regularly convex. The distances between the right and left M2, M1,

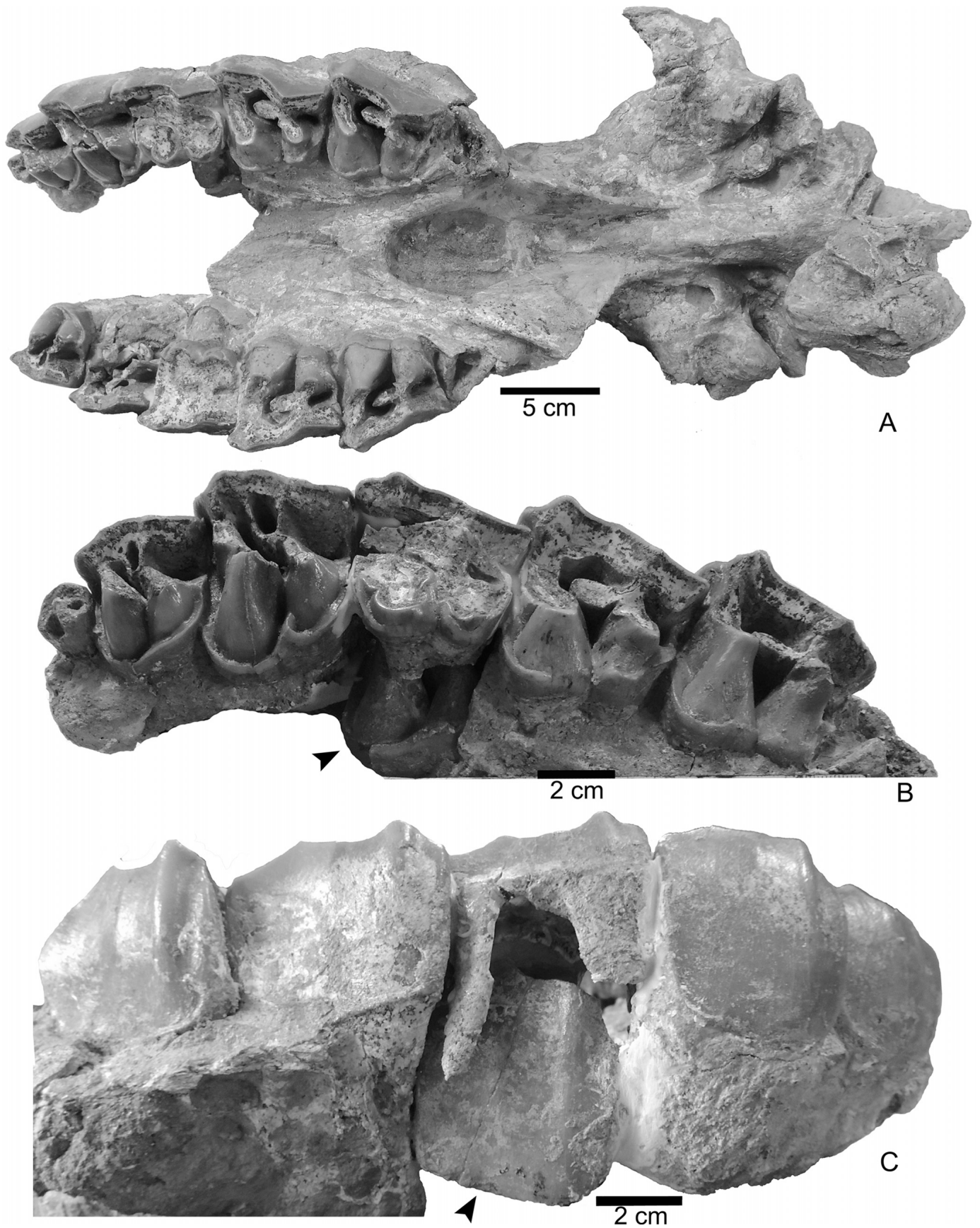


FIGURE 2. Holotype NHMW 2014/0426/0001 of *Persiatherium rodleri*, gen. et sp. nov., from Kopran, Maragheh, Iran. **A**, Ventral view; **B**, occlusal-lingual view of the left cheek teeth; and **C**, labial view of the left cheek teeth. The black arrow indicates the P4 below DP4.

TABLE 1. Measurements (in millimeters) of the upper teeth of *P. rodleri*, gen. et sp. nov. (NHMW 2014/0426/0001 from Maragheh), compared to those of *P. huadeensis* (late Miocene of Huade, China: data from Qiu, 1979), *H. tetradactylum* (Miocene, several European localities: data from Guérin, 1980), *A. incisivum* (Miocene, several European localities: data from Guérin, 1980), and *A. lufengensis* (late Miocene of Lufeng, China: data from Deng and Qi, 2009). L = length; W = width; H = height.

	<i>P. rodleri</i>			<i>P. huadeensis</i>		<i>H. tetradactylum</i>			<i>A. incisivum</i>			<i>A. lufengensis</i>		
	L	W	H	L	W	L	W	H	L	W	H	L	W	H
P1	18.4	15.6	18.5			21–27	17–24		21.5–29	17.5–24				
P2	41–41.4	41.9–42.4	45.2–46.3	37		30–36.5	33–41.5		30–38.5	35–45				
P3	50.5–50.7	ca. 55–55.8	54.5–54.8	44–46	60–61	32–40.5	40.5–50	43–47	34.5–43	41–55		45.6	58.7	31.4
P4			ca. 57	48–49	69–69	36.5–43	44–51.5		40–49	49.5–59.5	42–47			
M1	58.7–59.6	60.4–60.6		61–62	74–75	42–50	46.5–51.5	49–51	45–53.5	47.5–50.5	40–48	57.8	68.7	24.6
M2	61.6–61.8	62.2–62.7		68–69	69–70	46–51	44–52.5		47–63	47.5–61		59.6–62.1	71.3	34.5–36.6
DP4	51.7	48.2				40–50	35–42		40–50	40.5–42.5				

P3, and P2 are, respectively, 80.2, 92.4, 63.7, and 62 mm. The vomer is not visible, the palatine groove is slightly marked, and the pterygoids are damaged but their posterior margins appear nearly horizontal. The posterior lacerate foramen is relatively large, rounded, and very close to the postglenoid process; the latter is well developed and, in ventral view, the main axis of its cross section is oblique with respect to the long axis of the skull and displays a convex anterior–lateral border. The hyoglossal foramen is mesiolaterally displaced in the condyloid fossa and the basilar process has a sagittal crest; the postglenoid foramen is close to the postglenoid process. The oval foramen is evident and distinct from the posterior lacerate foramen. The external auditory pseudomeatus is partially closed ventrally, the paroccipital process is little developed, whereas the post-tympanic one is developed. According to Geraads and Koufos (1990), the basicranial area is short and narrow; its width across the post-tympanic processes, estimated by these authors to approximately 167 mm, is not much greater than the estimated length M1–M3 (Geraads and Koufos, 1990).

Teeth

The upper cheek teeth include P1–P3, M1, M2, erupting P4 and M3, and a much worn DP4 (Fig. 2; Table 1). According to Antoine (2002), P1 can be distinguished from DP1 in being massive and mesio-distally short, but the stage of wear can be also indicative (Geraads and Koufos, 1990); in the studied specimen, the first tooth is not more heavily worn than P2 and can be considered a P1. The length of the left P1–M2 is 229.65 mm. The lingual border of the upper cheek tooth series is concave and the tooth crowns are relatively high with weak cement cover (Table 1). Labial cingula are present on the premolars, whereas they are absent on the molars. Lingual cingula are well developed and continuous on P2–P4 and are also present on M1, M2, and DP4 (Fig. 2).

DP4—The deciduous tooth is very worn; at this stage of wear the paracone fold and mesostyle are weak; the protocone is constricted and the antecrochet is weak; the hypocone and protocone are separated; and the median valley is open.

P1—The left P1 has a high crown and a convex labial wall; the postfossette is relatively wide bucco-lingually and the mesio-lingual cingulum is present.

P2—The labial wall is slightly convex, the parastyle is relatively long, the paracone fold is little developed, the metacone fold is absent, the metastyle is long, and the postfossette is mesio-distally and bucco-lingually wide. The medifossette is present, protoloph and metaloph are slightly oblique, and protocone and hypocone are equal and separated. Protocone and hypocone are directed disto-lingually and the lingual side of the hypocone is flat with a weak lingual groove.

P3—Displays the same morphological characters as P2 but the lingual border of the lingual cingulum has a weak central

depression where a short branch of the cingulum projects to the hypocone. An incipient antecrochet can be also observed.

P4—The lingual cingulum is marked and continuous with a weak depression at the level of the median valley; protocone and hypocone are separated as in P3. The paracone fold is slightly marked.

M1—The parastyle is shorter than on the premolars, the paracone fold is weak, and the mesostyle is very weak. The posterior side of the ectoloph is concave and the metastyle is long. The protoloph is long and the protocone is weakly constricted. The antecrochet is incipient and the crista is absent, whereas the crochets are single and well developed; the median valley is open despite the development of the crochets. The lingual side of the protocone is flat. The metaloph is short, the postfossette is mesio-distally wide, and the posterior cingulum is low.

M2—Displays the same morphological characters as M1 but is less worn and the crochets are not close to the protoloph.

M3—The ectometaloph of M3 is observable on the left side; the tooth is triangular in shape but no other characters can be distinguished.

COMPARISONS

Comparison with Other Species of Rhinocerotidae from Maragheh—Among the rhinocerotid species from Maragheh, *Iranotherium morgani* differs from *P. rodleri* in its dental morphology (de Mecquenem, 1905; Antoine, 2002). Compared to *P. rodleri*, *I. morgani* has larger teeth, weak enamel folds, and abundant cement (specimens at NHMW; de Mecquenem 1905, 1911; Antoine, 2002; Deng, 2005).

Ceratotherium neumayri differs from *P. rodleri* in having a very wavy ectoloph profile on the teeth, having a rounded hypocone on P2 and P3, and in lacking lingual cingula on the molars (specimens from Maragheh, Samos, Pikermi, and other localities at NHML, NHMW, MGGC; Geraads, 1988). Moreover, according to Geraads and Koufos (1990), the basicranial area in *C. neumayri* is longer than in the studied specimen.

In *Chilotherium persiae*, the antecrochet is well developed on the upper premolars, the hypocone is rounded on P2 and P3, and the antecrochet is well developed on the molars and in some cases reaches the entrance of the median valley (specimens from Maragheh at NHML, NHMW).

Comparison with Elasmotheres—Elasmotheriini are generally characterized by increasing crown height of the cheek teeth and reduction of the anterior teeth (Heissig, 1999; Antoine, 2002). Late Miocene species belonging to this group (Table S1) differ from *P. rodleri* in having more hypsodont teeth, enamel folds on the cheek teeth, reduced or absent lingual cingula on the premolars, united protocone and hypocone on P3 and P4, antecrochet on the molars, a long metaloph on M1 and M2, and a lack of labial cingula on the premolars.

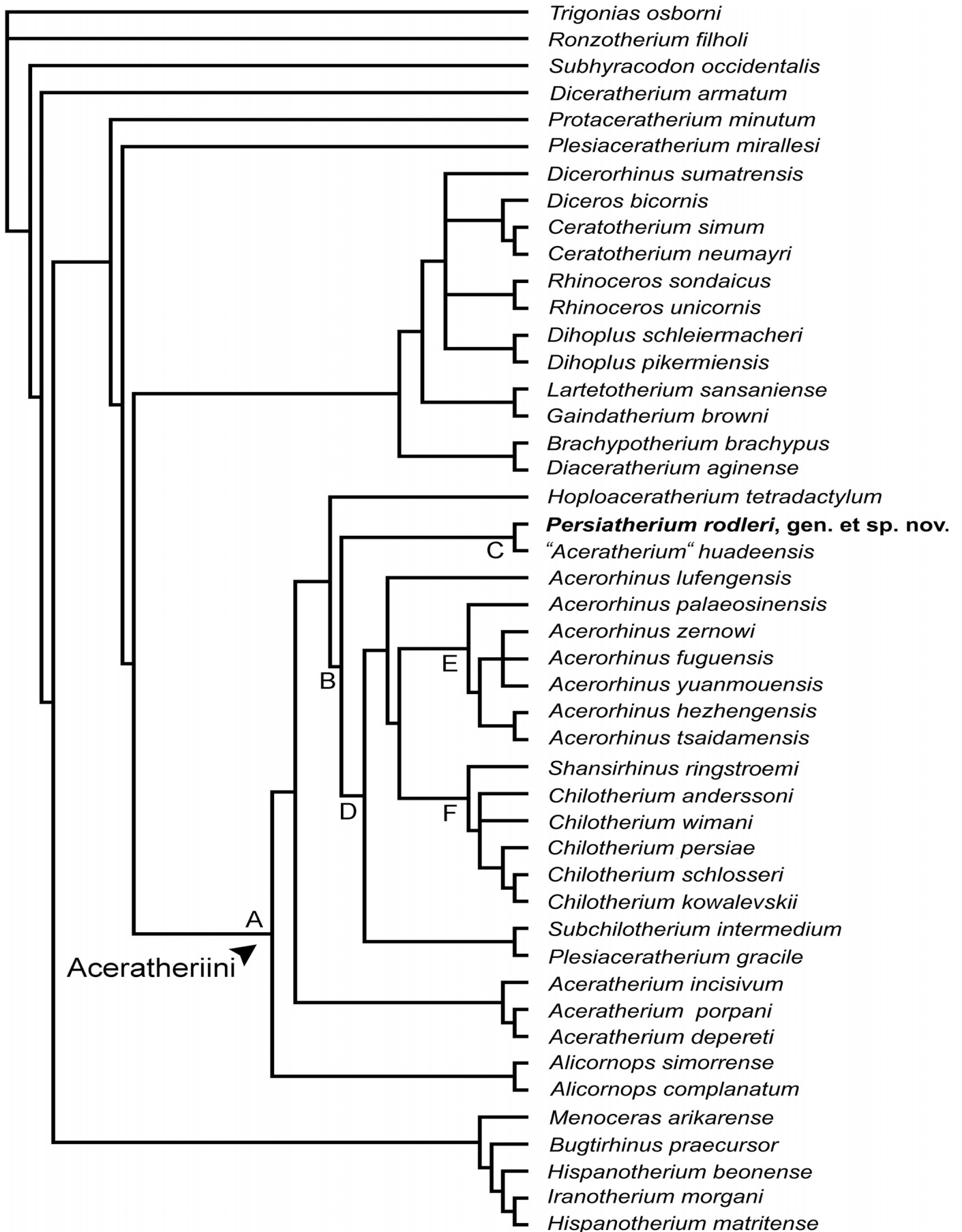


FIGURE 3. Phylogenetic relationships of *Persiatherium rodleri*, gen. et sp. nov., within Aceratheriini (Rhinocerotidae). A–F refer to nodes discussed in the text.

Comparison with Eurasian and African Teleoceratini—Teleoceratini (= Teleoceratina in Antoine, 2002) is a group of Rhinocerotidae generally characterized by shortening of the skull and distal limb segments (Heissig, 1999). The synapomorphies of this group are given by Antoine (2002) and Antoine et al. (2003) but are mostly based on postcranial features. *Persiatherium rodleri* differs from the Miocene *Brachypotherium* (*B. brachypus*, *B. goldfussi*, *B. perimense*, and *B. lewisi*; Table S1) in having cement on the cheek teeth, high-crowned teeth, strong lingual cingula on the upper premolars, a wide postfossette on P2–P4, a medifossette on P3 and P4, a short metaloph on M1 and M2, well-developed lingual cingula on the upper molars, and a lack of labial cingula on the upper molars.

Comparison with Rhinocerotini—Species belonging to Rhinocerotini are characterized by the presence of a nasal and/or a frontal horn (Heissig, 2012; Antoine 2002; Antoine et al., 2003). The short and narrow basicranial area of the studied specimen is a different condition from that observed in any Rhinocerotini (Geraads and Koufos, 1990). The differences between the new taxon and *Lartetotherium sansaniense*, *Gaitherium browni*, *Dihoplus*, and the extant genera (*Dicerorhinus*, *Rhinoceros*, *Ceratotherium*, and *Diceros*; Table S1) can be extrapolated from the data matrix. '*Dicerorhinus*' *steinheimensis* is smaller than *P. rodleri*, the lingual cingula are absent on the premolars and molars, the medifossette is absent on the premolars, the metacone fold is present on P3 and P4, and the paracone fold is strong on M1 and M2 (specimens at NHMW; Guérin, 1980). Among late Miocene African Rhinocerotini, *Ceratotherium? primaevum*, from Algeria is represented by a juvenile skull with erupted M1 and erupting M2 (Arambourg, 1959; Geraads, 2010); this species lacks lingual cingula on M1 and M2, the crochet is less developed than in *P. rodleri*, and the lingual surface of the protocone is rounded. In *Ceratotherium douariense* from Tunisia, lingual cingula are less marked on the premolars than in *P. rodleri*, the medifossette is absent, the protocone is less developed than the hypocone on P2, the lingual cingulum is absent on M1, and the crochet is weak on M1 (cf. Guérin, 1966; Geraads, 2010). *Paradicerus mukirii* from Kenya differs from *P. rodleri* in having the protocone less developed than the hypocone on P2, a transverse metaloph on P3 and P4, a small postfossette on P2–P4, and in lacking P1 and the medifossette on P3 and P4 (casts housed at NHML; Hooijer, 1968; Geraads, 2010).

Comparison with Eurasian and African Aceratheriini—Aceratheriini is represented by species with a long and narrow skull and slender but mediportal limbs (Heissig, 2012). Synapomorphies of this group are given by Antoine et al. (2003) and Lu (2013). This group is here supported by five unambiguous synapomorphies (Node A; Table S3). *Persiatherium rodleri* shares several characters with Eurasian Aceratheriini: presence of well-developed crochets on the molars, well-developed lingual cingula, lingually flattened protocones on the molars, and medifossettes on premolars. Nevertheless, *P. rodleri* can be distinguished from known aceratheriines.

The differences between *P. rodleri* and species of the genera *Aceratherium* (*A. incisivum*, *A. depereti*, and *A. porpani*), *Acerorhinus* (*A. zernowi*, *A. palaeosinensis*, *A. yuanmouensis*, *A. lufengensis*, *A. tsaidamensis*, *A. hezhengensis*, and *A. fuguensis*), *Chilotherium* (*Ch. schlosseri*, *Ch. kowalevskii*, *Ch. wimani*, and *Ch. anderssoni*), *Hoploaceratherium tetradactylum*, *Shansirhinus ringstroemi*, *Subchilotherium intermedium*, *Alicornops simorreense*, and *Alicornops complanatum* can be extrapolated from the data matrix. The comparison is restricted to the main genera or to species not included in the data matrix and represented by limited material or poorly coded specimens.

Compared to *P. rodleri*, *A. laogouense* from Laogou (China; Deng, 2004) has a rounded protocone and hypocone on the premolars, lacks a medifossette on P3, the antecrochet is well developed on M1, and the lingual cingulum is present only on

the entrance to the median valley on M1 and is absent on M2. The genus *Chilotherium* (including *Ch. habereri*, *Ch. primigenius*, and *Ch. samium*) generally differs from *P. rodleri* in the absence or strong reduction of the lingual cingulum on the upper premolars, postfossette posteriorly delimited by an enamel wall on the upper premolars, hypocone and protocone united by a lingual bridge on P2 and P3, presence of a well-developed antecrochet on the upper premolars and molars, strong protocone constriction on the upper molars, and absence of a lingual cingulum on the molars. *Chilotherium kiliasi* from Greece differs slightly from other Eurasian chilotheres and was referred to *Aceratherium* by Geraads and Koufos (1990). In this species, the antecrochet is developed on M1, the medifossette is absent on premolars, the crista is minute on premolars, the hypocone is larger than the protocone on P2, the lingual cingulum is weak and present only at the entrance of the median valley on premolars, the reduced ectoloph profile of P3 and P4 is straight, and the posterior profile of the ectoloph on M1 is straight (cfr. Geraads and Koufos, 1990). *Hoploaceratherium tetradactylum* from Central Europe is smaller than the studied specimen (Table 1). Compared to *P. rodleri*, *H. belvederense* from Wien Belvedere and other eastern European localities (Fig. 1; specimens at NHMW, HNHM; Wang, 1929; cfr. Heissig, 2005) has brachydont teeth, a reduced lingual cingulum on the premolars, the medifossette is absent on the premolars, the hypocone is slightly larger than the protocone on P2, the hypocone is rounded on the premolars, and the lingual cingulum is absent on the molars. Moreover, *S. brancoi* from Shansi differs from *P. rodleri* in having a complex crochet with several folds on M1, a straighter ectoloph on M1 and M2, a crista on M1 and M2, and a lack of lingual cingula on M1 and M2 (specimens at MfN; Schlosser, 1903). *Chilotheridium pattersoni* from Kenya has a ventrally open external auditory pseudomeatus, the lingual cingulum is weak on P2, the protocone is less developed than the hypocone on P2, very reduced lingual cingula are present on P3 and P4, the antecrochet reaches the metaloph on P4, the medifossette is absent on the premolars, the protocone constriction is strong on M1, and the antecrochet is well developed (Hooijer, 1971; Geraads, 2010). In *Turkanatherium acutirostratum* from Kenya, the lophs of the premolars converge lingually, lingual cingula are reduced on the premolars and the postfossette is transversely elongated, the protocone constriction is strong on M1 and M2, and the antecrochet is well developed, whereas the crochet is weak on M1 (Deraniyagala, 1951; Geraads, 2010).

PHYLOGENETIC ANALYSIS

Eight most parsimonious trees were obtained from cladistic analysis in PAUP. The consensus tree is shown in Figure 3 (tree length = 1,244 steps, consistency index = 0.228, retention index = 0.549). The tree topology is similar to that obtained by Lu (2013); however, the added taxa resulted in a new hypothesis of the phylogenetic relationships of the considered taxa. With respect to Lu's (2013) analysis, the inclusion of *Iranotherium* and the type species of *Hispanotherium* results in nonmonophyly of *Hispanotherium*. Paraphyly of this genus was also reported by Deng (2008) and Sanisidro et al. (2012), but different species were considered.

In the present analysis, the tribe Aceratheriini is supported by five unambiguous synapomorphies (node A, Table S3). At the first dichotomy within Aceratheriini the (*Alicornops simorreense*, *A. complanatum*) clade branched off, at the second, the *Aceratherium* clade branched off, and at the third, *H. tetradactylum* branched off. The next node (B) is represented by a dichotomy with a minor clade (node C) composed of *Persiatherium rodleri* and '*Aceratherium*' *huadeensis*, supported by nine synapomorphies, four of which are unambiguous (Table S3), and a major clade (node D) including ((*Subchilotherium intermedium*

Plesiaceratherium gracile) (*Acerorhinus lufengensis* ((*Shansirhinus Chilotherium*) *Acerorhinus*))), supported by five unambiguous synapomorphies. The relationship between *P. rodleri* and 'A.' *huadeensis*, together with the position of *Aceratherium incisivum* and the species of *Acerorhinus*, leads me to propose that 'A.' *huadeensis* be placed in the new genus *Persiatherium*. The clade composed of the species of the genus *Acerorhinus*, excluding *A. lufengensis* (node E), is supported by four unambiguous synapomorphies; this clade includes *Acerorhinus palaeosinensis* as sister taxon of two minor clades of *Acerorhinus* species ((*A. zernowi* *A. fuguensis* *A. yuanmouensis*) (*A. hezhengensis* *A. tsaidamensis*)). The (*Shansirhinus Chilotherium*) clade (node F) is supported by nine unambiguous synapomorphies. In agreement with Lu (2013), *A. lufengensis* appears as sister taxon of (*Acerorhinus* (*Shansirhinus*, *Chilotherium*)), but this result is probably influenced by the limited available material referred to this species.

CONCLUSIONS

The systematic revision of the rhinoceros material collected at Kopran, Maragheh (upper Miocene, northwestern Iran), at the end of the 19th century supports recognition of a new genus and species, *Persiatherium rodleri*. The holotype and only specimen assigned to it is clearly distinguished from the three species collected in the same locality: *Iranotherium morgani*, *Ceratotherium neumayri*, and *Chilotherium persiae*. Comparison with several late Miocene species from Africa and Eurasia allowed distinction of *P. rodleri* from the known species, given numerous morphological differences. The phylogenetic analysis places *P. rodleri* within *Aceratheriini* and relates it to the species 'A.' *huadeensis*. Considering the uncertain generic ascription of this species (Qiu, 1979; Deng et al., 2013; Lu, 2013) and the obtained clade, it is herein included in the new genus *Persiatherium*. *Persiatherium huadeensis* displays more derived features than *P. rodleri*: labial and lingual cingula are absent on the premolars, pseudometaloph is sometimes present on P3, and lingual cingula are absent on the molars. This could be related to the younger age of *P. huadeensis*. The species was collected in the upper Miocene deposit of Huade (Inner Mongolia, China), where *Cervavitus huadeensis* (Mammalia, Cervidae), which is typical of MN12–MN13 (Dong, 2011), also occurred. A younger age than the early Turolian was therefore suggested for this locality (Qiu, 1979; Dong, 2011). *Persiatherium rodleri* occurs only in the lower Maragheh biostratigraphic interval related to the Vallesian (ca. 9 Ma), whereas it is absent from the middle and upper Maragheh intervals.

Persiatherium rodleri is the fourth species of Rhinocerotidae recognized in the lower Maragheh interval; in fact, *I. morgani*, *C. neumayri*, and *Ch. persiae* were collected at Kopran (unpubl. data). The presence of four genera and four species in the same locality and stratigraphic level is an exceptional case within the records of Eurasian Rhinocerotidae and has been reported only at Sansan (middle Miocene, France; Guérin, 1980; Heissig, 2012). It could be related to an abundance of resources in the Maragheh area during the latest Vallesian and/or different niches. *Ceratotherium neumayri* was adapted to tough low-level vegetation but was not a strict grazer (Geraads and Spassov, 2009). *Iranotherium morgani* was a grazer, whereas *Ch. persiae* was probably a mixed feeder like *Ch. habereri*, with hypsodonty index values that fall within the range of extant browser or mixed feeder rhinoceroses (Wei and Zhang, 2004). *Persiatherium rodleri* was probably a mixed feeder; it has less hypsodont teeth than *C. neumayri* and *I. morgani* but they are similar to those of *Ch. persiae*. The latter species is likely more abundant at Maragheh than *P. rodleri*, but new detailed investigations are needed to understand the paleoecology (e.g., paleodiet) and interrelationships among the Maragheh Rhinocerotidae.

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LITERATURE CITED

- Antoine, P.-O. 2002. Phylogénie et évolution des Elasmotheriina (Mammalia, Rhinocerotidae). Mémoires du Muséum national d'Histoire naturelle, Paris 188:1–359.
- Antoine, P.-O., F. Duranthon, and J. L. Welcomme. 2003. *Alicornops* (Mammalia, Rhinocerotidae) dans le Miocène supérieur des Collines Bugti (Balouchistan, Pakistan): implications phylogénétiques. *Geodiversitas* 25:575–603.
- Arambourg, C. 1959. Vertébrés continentaux du Miocène supérieur de l'Afrique du Nord. Service de la Carte géologique de l'Algérie, Mémoire 4:5–159.
- Ataabadi, M. M., R. L. Bernor, D. S. Kostopoulos, D. Wolf, Z. Orak, G. Zare, H. Nakaya, M. Watabe, and M. Fortelius. 2013. Recent advances in paleobiological research of the late Miocene Maragheh fauna, Northwest Iran; pp. 546–565 in X. Wang, M. Fortelius, and L. Flynn (eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. Columbia University Press, New York.
- Bernor, R. L. 1986. Mammalian biostratigraphy, geochronology and zoogeographic relationships of the late Miocene Maragheh fauna, Iran. *Journal of Vertebrate Paleontology* 6:76–91.
- Bernor, R. L., V. Fahlbusch, and H.-W. Mittmann. 1996. The evolution of Western Eurasian Neogene mammal faunas; pp. 1–6 in R. L. Bernor, V. Fahlbusch and H.-W. Mittmann (eds.), *The Evolution of Western Eurasian Neogene Mammal faunas*. Columbia University Press, New York.
- Borissiak, A. 1927. *Aceratherium depereti* nov. sp. from the Jilančik beds. *Bulletin de l'Académie des Sciences de l'URSS* 21:769–786.
- Campbell, B. G., M. H. Amini, R. L. Bernor, W. Dickinson, R. Drake, R. Morris, J. A. Van Couvering, and J. A. H. Van Couvering. 1980. Maragheh: a classical late Miocene vertebrate locality in northwestern Iran. *Nature* 287:837–841.
- de Mecquenem, R. 1905. Le gisement de vertébrés fossiles de Maragha. *Compte Rendu de l'Académie des Sciences Paris* 141:927–929.
- de Mecquenem, R. 1911. Contribution à l'étude du Gisement des vertébrés de Maragha et de ses environs. *Annales d'histoire naturelle Paris* 1:81–98.
- de Mecquenem, R. 1925. Contribution à l'étude des fossiles de Maragha. *Annales de Paléontologie* 14:1–36.
- Deng, T. 2004. A new species of the rhinoceros *Alicornops* from the middle Miocene of the Linxia Basin, Gansu, China. *Palaeontology* 47:1427–1439.
- Deng, T. 2005. New cranial material of *Shansirhinus* (Rhinocerotidae, Perissodactyla) from the lower Pliocene of the Linxia Basin in Gansu, China. *Geobios* 38:301–313.
- Deng, T. 2008. A new elasmothere (Perissodactyla, Rhinocerotidae) from the late Miocene of the Linxia Basin in Gansu, China. *Geobios* 41:719–728.
- Deng, T., and G.-Q. Qi. 2009. Rhinocerotids (Mammalia, Perissodactyla) from *Lufengpithecus* site, Lufeng, Yunnan. *Vertebrata Palasiatica* 47:135–152. [Chinese 135–146; English 146–152]
- Deng, T., R. Hanta, and P. Jintasakul. 2013. A new species of *Aceratherium* (Rhinocerotidae, Perissodactyla) from the late Miocene of

- Nakhon Ratchasima, northeastern Thailand. *Journal of Vertebrate Paleontology* 33:977–985.
- Deraniyagala, P. E. P. 1951. A hornless rhinoceros from the Mio–Pliocene deposits of East Africa. *Spolia Zeylanica* 26:133–135.
- Dollo, L. 1885. Rhinocéros vivants et fossiles. *Revue des Questions Scientifiques* 17:293–299.
- Dong, W. 2011. Reconsideration of the systematics of the early Pleistocene *Cervavitus* (Cervidae, Artiodactyla, Mammalia). *Estudios Geológicos* 67:603–611.
- Geraads, D. 1988. Révision des Rhinocerotidae (Mammalia) du Turolien de Pikermi: comparaison avec les formes voisines. *Annales de Paléontologie* 74:13–41.
- Geraads, D. 2010. Rhinocerotidae; pp. 669–683 in L. Werdelin and W. J. Sanders (eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, California.
- Geraads, D., and G. Koufos. 1990. Upper Miocene Rhinocerotidae (Mammalia) from Pentalophos-1, Macedonia, Greece. *Palaeontographica Abteilung A* 210:151–168.
- Geraads, D., and N. Spassov. 2009. Rhinocerotidae (Mammalia) from the late Miocene of Bulgaria. *Palaeontographica Abteilung A* 287:99–122.
- Guérin, C. 1966. *Diceros douariensis* nov. sp., un Rhinocéros du Mio–Pliocène de Tunisie du nord. *Documents des laboratoires de géologie de la Faculté des sciences de Lyon* 16:1–50.
- Guérin, C. 1980. Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pleistocène supérieur en Europe occidentale: comparaison avec les espèces actuelles. *Documents du laboratoire de géologie de la Faculté des sciences de Lyon* 79:1–1182.
- Heissig, K. 1999. 16. Family Rhinocerotidae; pp. 175–188 in G. E. Rössner and K. Heissig (eds.), *The Miocene Land Mammals of Europe*. Pfeil, Munich.
- Heissig, K. 2005. The fossil rhinoceros of Rudabanya. *Palaeontographica Italica* 90:217–258.
- Heissig, K. 2012. Les Rhinocerotidae (Perissodactyla) de Sansan; pp. 317–485 in S. Peigné and S. Sen (eds.), *Mammifères de Sansan*, Mémoires du Muséum national d’histoire naturelle, Paris.
- Hooijer, D. A. 1968. A rhinoceros from the late Miocene of Fort Ternan, Kenya. *Zoologische Mededelingen* 43:77–92.
- Hooijer, D. A. 1971. A new rhinoceros from the late Miocene of Loperot, Turkana district, Kenya. *Bulletin of the Museum of Comparative Zoology* 142:339–392.
- Lu, X. 2013. A juvenile skull of *Acerorhinus yuanmouensis* (Mammalia: Rhinocerotidae) from the late Miocene hominoid fauna of the Yuanmou Basin (Yunnan, China). *Geobios* 46:539–548.
- Lydekker, R. 1886. On the fossil Mammalia of Maragha, in North-Western Persia. *Quarterly Journal of the Geological Society* 42:173–176.
- Osborn, H. F. 1900. Phylogeny of the rhinoceroses of Europe. *Bulletin of the American Museum of Natural History* 13:229–267.
- Owen, R. 1845. *Odontography or a Treatise on the comparative anatomy of the teeth, their physiological relations, mode of development, and microscopic structure, in the vertebrate animals*: 665 S.; London (Baillière).
- Owen, R. M. 1848. Description of teeth and proportion of jaws of two extinct Anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyopotamus bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N.W. coast of the Isle of Wight: with an attempt to develop Cuvier’s idea of the classification of pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London* 4:103–141.
- Pavlov, M. 1913. Mammifères Tertiaires de la Nouvelle Russie. 1ère Partie: Artiodactyla Perissodactyla (*Aceratherium kowalevskii* n. s.). *Nouveaux mémoires de la Société impériale des naturalistes de Moscou* 17(3):1–67.
- Pohlig, H. 1886. On the Pliocene of Maragha, Persia, and its resemblance to that of Pikermi in Greece; on fossil elephant remains of Caucasia and Persia; and on the results of a monograph of the fossil elephants of Germany and India. *Quarterly Journal of the Geological Society* 42:177–282.
- Qiu, Z.-D. 1979. Some mammalian fossils from the Pliocene of Inner Mongolia and Gansu (Kansu). *Vertebrata Palasiatica* 17:222–235. [Chinese 222–233; English 234–235]
- Rodler, A. 1889. Über *Urmitherium polaki*, einen neuen Sivatheriiden aus dem Knochenfelde von Maragha. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse* 56:307–314.
- Rodler, A., and K. A. Weithofer. 1890. Die Wiederkauer der Fauna von Maragha. *Denkschriften der Kaiserlichen Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Klasse* 57:753–772.
- Sanisidro, O., M. T. Alberdi, and J. Morales. 2012. The first complete skull of *Hispanotherium matritense* (Prado) (Perissodactyla, Rhinocerotidae) from the middle Miocene of the Iberian Peninsula. *Journal of Vertebrate Paleontology* 32:446–455.
- Schlosser, M. 1903. Die fossilen Säugethiere Chinas nebst einer Odontographie der recenten Antilopen. *Abhandlungen der Königlichen Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse* 22:1–221.
- Swofford, D. L. 2001. PAUP* (Phylogenetic Analysis Using Parsimony [*and Other Methods] Version 4.0β10). Sinauer, Sunderland, Massachusetts.
- Tobien, H. 1968. Palaeontologische Ausgrabungen nach Jungtertiären Wirbeltieren auf der Insel Chios (Griechenland) und bei Maragheh (N.W. Iran). *Jahrbuch der Vereinigung “Freunde der Universität Mainz”* 1968:51–58.
- Wang, K. M. 1929. Die fossilen Rhinocerotiden des Wiener Beckens. *Academia Sinica National Research Institute of Geology Memoirs* 7:53–59.
- Wei, M., and X. Zhang. 2004. Ancient diet of two species of late Miocene *Chilotherium* from Fugu, Shaanxi, China: evidence from stable carbon isotopes and hypsodonty index; pp. 43–48 in W. Dong (ed.), *Proceedings of the 9th Annual Meeting of the Chinese Society of Vertebrate Paleontology*, 2004. China Ocean Press, Beijing.

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