**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 clasmotheres, teleoceratins, and rhinoceroses recorded in Eurasia and Africa. The new taxon displays morphological characters close to *Aceratherium*. However, the presence of plesiomorphic characters on the teeth (presence of P1, continuous lingual 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 haadeanensis*’. Though the latter displays more derived features than *P. rodleri*, their phylogenetic relationships allow inclusion of both species in the same new genus.


**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 Azerbajan 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 volcaniclastic 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; Meccquenem 1905, 1911, 1925; Tobien, 1968; Campbell et al., 1980; Bernor, 1986; Bernor et al., 1996; Ataabadi et al., 2013). 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 Meccquenem, 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.

**ARTICLE MATERIALS 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...
A new Miocene rhinocerotid from Iran (e1040118-2)

Pandolfi

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Family RHINOCEROTIDAE Owen, 1845
Tribe ACERATHERINI 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) medifossette 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.

<table>
<thead>
<tr>
<th></th>
<th>P. rodleri</th>
<th>P. huadeensis</th>
<th>H. tetradactylum</th>
<th>A. incisivum</th>
<th>A. lufengensis</th>
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<tr>
<td>P1</td>
<td>18.4</td>
<td>15.6</td>
<td>18.5</td>
<td>21.5–29</td>
<td>17.5–24</td>
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<tr>
<td>P2</td>
<td>41–41.4</td>
<td>41.9–42.4</td>
<td>45.2–46.3</td>
<td>30–36.5</td>
<td>33–41.5</td>
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<tr>
<td>P3</td>
<td>50.5–50.7</td>
<td>ca. 55–55.8</td>
<td>54.5–54.8</td>
<td>32–40.5</td>
<td>40.5–50</td>
</tr>
<tr>
<td>P4</td>
<td>44–46</td>
<td>ca. 57</td>
<td>36.5–43</td>
<td>44–51–43</td>
<td>40–49</td>
</tr>
<tr>
<td>M1</td>
<td>58.7–59.6</td>
<td>60.4–60.6</td>
<td>42–50</td>
<td>45–53.5</td>
<td>47–63</td>
</tr>
<tr>
<td>M2</td>
<td>61.6–61.8</td>
<td>62.2–62.7</td>
<td>46–51</td>
<td>44–52.5</td>
<td>47–63</td>
</tr>
<tr>
<td>DP4</td>
<td>51.7</td>
<td>48.2</td>
<td>40–50</td>
<td>35–42–52</td>
<td>40–50</td>
</tr>
</tbody>
</table>

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 hypoglossal foramen is mesiolaterally displaced in the condyloid fossa and the basilar process has a sagittal crest; the postglenoid foramen is mesiolaterally displaced in the condyloid fossa and displays a convex anterior–lateral border. The hyoglossal 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 paracone fold is very worn; at this stage of wear the protocone 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 crochet is single and well developed; the median valley is open despite the development of the crochet. 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 crochet is 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 Mequetem, 1905; Antoine, 2002). Compared to P. rodleri, I. morgani has larger teeth, weak enamel folds, and abundant cement (specimens at NHMW; de Mequetem 1905, 1911; Antoine, 2002; Deng, 2005).

Ceratherium 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, MGCC; 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 Brachytherium (B. brachyclus, B. goldfussi, B. perimene, 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 medidfossette 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 basioccipital 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 sasaniense, Gaindatherium browni, Dihoplus, and the extant genera (Dicerorhinus, Rhinoceros, Ceratotherium, and Dicerorhinus; 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 medidfossette is absent on the premolars, the metacone 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? primae- vium, 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 medidfossette 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).

Paradiceros mkirii 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 medidfossette 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 medidfossettes 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. yuamouensis, A. faeni- gensis, A. taisadamensis, A. hezechengensis, and A. fuguens), Chilotherium (Ch. schlosseri, Ch. kowalevski, Ch. wimanii, and Ch. anderssonii), Hoploaceratherium tetractylum, Shansirhinus ringstromei, Subchilotherium intermedium, Alicorns simor- rense, and Alicorns 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 medidfossette 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. primige- nius, 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 chilotheriines and was referred to Aceratherium by Geraads and Koufos (1990). In this species, the antecrochet is developed on M1, the medidfossette 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. Ger- aads and Koufos, 1990). Hoploaceratherium tetractylum 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 medidfos- sette is absent on the premolars, the hypocone is slightly larger than the protocone on P2, the hypocone is rounded on the pre- molars, 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). Chilo- theridium 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 medidfossette is absent on the premolars, the protocone constriction is strong on M1, and the antecrochet is well developed (Hooijer, 1971; Geraads, 2010). In Turkanaetherium 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 Hispanotherium and the type species of Hispanotherium results in monophyly 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 (Alicorns simorrense, A. complanatum) clade branched off, at the second, the Aceratherium clade branched off, and at the third, H. tetractylum 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 (Shanshirhins Chilotherium) Acerorhinus)), supported by five unambiguous synapomorphies. The relationship between P. roldleri and ‘A.’ huaeensis, together with the position of Aceratherium incisivum and the species of Acerorhinus, leads me to propose that ‘A.’ huaeensis 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. yaamuouensis) (A. hezhengensis A. tsai-damensis)). The (Shanshirhins Chilotherium) clade (node F) is supported by nine unambiguous synapomorphies. In agreement with Lu (2013), A. lufengensis appears as sister taxon of (Acerorhinus (Shanshirhins, 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 roldleri. The holotype and only specimen assigned to it is clearly distinguished from the three species collected in the same locality: Ianotherion morgani, Ceratoth- rium neumayri, and Chilotherium persiae. Comparison with several late Miocene species from Africa and Eurasia allowed distinction of P. roldleri from the known species, given numerous morphological differences. The phylogenetic analysis places P. roldleri within Aceratheriini and related it to the species ‘A.’ huaeensis. 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 huaeensis displays more derived features than P. roldleri: 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. huaeensis. 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 huaeensis is the fourth species of Rhinocerotidae recognized in the lower Maragheh interval; in fact, P. rodleri, I. morgani, and upper Maragheh intervals.

PERSIATHERIUM ROLLERI 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. Ceratothrium neumayri was adapted to tough low-level vegetation but was not a strict grazer (Geraads and Spassov, 2009). Ianotherium 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 roldleri 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. roldleri, but new detailed investigations are needed to understand the paleoecology (e.g., paleodiet) and interrelationships among the Maragheh Rhinocerotidae.

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