

A New Representative of the Family Raoellidae (Suiformes) from the Middle Eocene of Khaichin-Ula 2, Mongolia

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Abstract—The Middle Eocene fauna of Khaichin-Ula 2 is shown to include a new species of the genus *Haqueina* of the family Raoellidae. In addition to this form, the fauna includes three suiform species, *Gobiohyus reshetovi*, *G. pressidens*, and *Chorlakkia valerii*. New morphological data on *Haqueina* corroborate the validity of the family Raoellidae and allow for the analysis of its relationships.

Key words: Artiodactyla, Suiformes, Middle Eocene, Mongolia, new species.

INTRODUCTION

Remains of Paleogene artiodactyls collected in Mongolia by the Joint Soviet–Mongolian Paleontological Expedition headed by V. Yu. Reshetov in 1970 and 1975 include the upper and lower jaws of a small suiform of the genus *Haqueina*. The specimens come from the Middle Eocene of the Khaichin-Ula 2 locality. The fossil remains were found in the lower part of lacustrine–alluvial deposits of the Khaichin Formation (Shuvalov *et al.*, 1974; Badamgarav and Reshetov, 1985) and were provisionally referred to hypertragulids (Badamgarav and Reshetov, 1985). Along with the genus *Haqueina* of the family Raoellidae, the fauna from Khaichin-Ula 2 was shown to include members of two other families of the superfamily Dichobunoidea, namely, two species of the family Helohyidae (*Gobiohyus reshetovi* and *G. pressidens*) and one species of the family Dichobunidae (*Chorlakkia valerii*) (Vislobokova, 2004).

The collection from Khaichin-Ula 2 considerably enlarges our knowledge of the morphology and distribution of the genus *Haqueina*. The sole species of the genus, *H. haquei*, was described from the Middle Eocene (Lower Charrat) of the Ganda Kas locality (site 21) in Pakistan on the basis of a small lower jaw fragment with two posterior molars (Dehm and Oettingen-Spielberg, 1958). A mandibular fragment with P₄ from site 25 of the same locality was also referred to *H. haquei* (Dehm and Oettingen-Spielberg, 1958). Coombs and Coombs (1977a) reported a find of the lower teeth of this genus in India.

Relatively well-preserved remains of *Haqueina* from Mongolia give fresh information about the taxonomic position of the genus and history of the family Raoellidae.

SYSTEMATIC PALEONTOLOGY

Order Artiodactyla

Suborder Suiformes

Family Raoellidae Sahni, Bhatia, Hartenberger, Jaeger, Kumar, Sudre et Vianey-Liaud, 1981

Genus *Haqueina* Dehm et Oettingen-Spielberg, 1958

Haqueina: Dehm and Oettingen-Spielberg, 1958, pp. 26–29, text-fig. 5, pl. 3, figs. 1 and 2; Coombs and Coombs, 1977a, p. 303; Holroyd and Ciochon, 1995, p. 177.

Type species. *Haqueina haquei* Dehm et Oettingen-Spielberg, 1958; Middle Eocene; Turkey.

Emended diagnosis. Second premolars with pointed and posteriorly curved tip. Paraconule present in P³, P⁴, and molars. Paraconule small and located at approximately equal distances from paracone and protocone in M¹ and closer to protocone in M² and M³. Ectoloph absent. Central valley of upper molars open lingually. Upper molars with continuous cingulum. In M₃, labial arms of hypoconid and hypoconulid border posterior notch; posthypoconid and additional cuspules on hypolophid and between entoconid and hypolophid present.

Species composition. In addition to the type species, *H. haichinensis* sp. nov. from the Middle Eocene of Mongolia.

Comparison. This genus differs from the genus *Raoella* in the absence of ectoloph, lingually open central valley of the upper molars, the position of the paraconule of M¹, and stronger developed cingulum (retention of the posterolingual cingulum) of the upper molars. It differs from the genus *Indohyus* in the more complex structure of the posterior lobe of M₃.

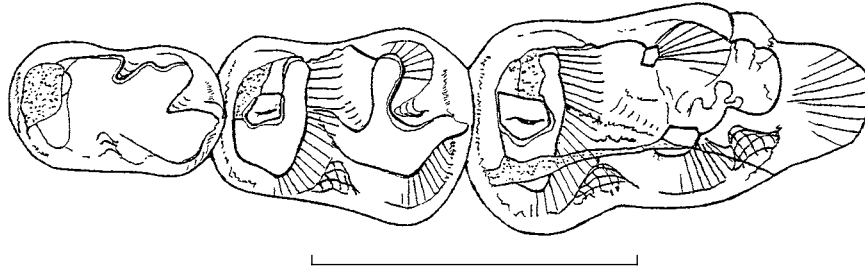


Fig. 1. *Haqueina haichinensis* sp. nov., holotype PIN, no. 3108/468, M_1 – M_3 , dorsal view. Scale bar, 1 cm.

Haqueina haichinensis Vislobokova, sp. nov.

Plate 10, figs. 1 and 2

Hypertragulidae gen. et sp. nov.: Badamgarav and Reshetov, 1985, pp. 42 and 50.

E t y m o l o g y. From the Khaichin locality.

H o l o t y p e. PIN, no. 3107/468, incomplete mandible with preserved P_1 , P_2 , and P_4 – M_3 ; Mongolia, Khaichin-Ula 2; Middle Eocene, Khaichin Formation.

D e s c r i p t i o n (Fig. 1). A well-preserved maxillary tooth row, including P^2 – M^3 (specimen PIN, no. 3107/469), is only slightly worn. The most worn tooth is M^2 , while the posterior half of M^3 is not worn at all.

A small diastema is present between P^2 and P^3 . The premolars are long, whereas the molars are relatively short and brachyodont. The premolar row is longer than the molar row, and P^2 – P^4 are approximately equal in length to M^1 – M^3 .

The crowns of P^2 , P^3 , and P^4 are elongated, relatively high, slightly pointed, triangular in lateral view, and have an elevated paracone. The labial side of the paracone is convex. Each premolar has lingual and labial cingula.

P^2 is narrow, with a strongly concave lingual side. Its tip is slightly curved posteriorly.

P^3 has a small protocone located in the posterior region of the tooth. A short and narrow medial crest deviates labially from the protocone. A relatively large parastyle and a smaller posterior style are well-developed at the postexternal angle of the crown. The style somewhat protrudes labially. The anterior wing of the protocone (preprotocrista) fuses with the lingual cingulum in the point that approximately corresponds to the posterior edge of the anterior third of the crown length. The posterior wing of the protocone (postprotocrista) fuses with the posterior cingulum.

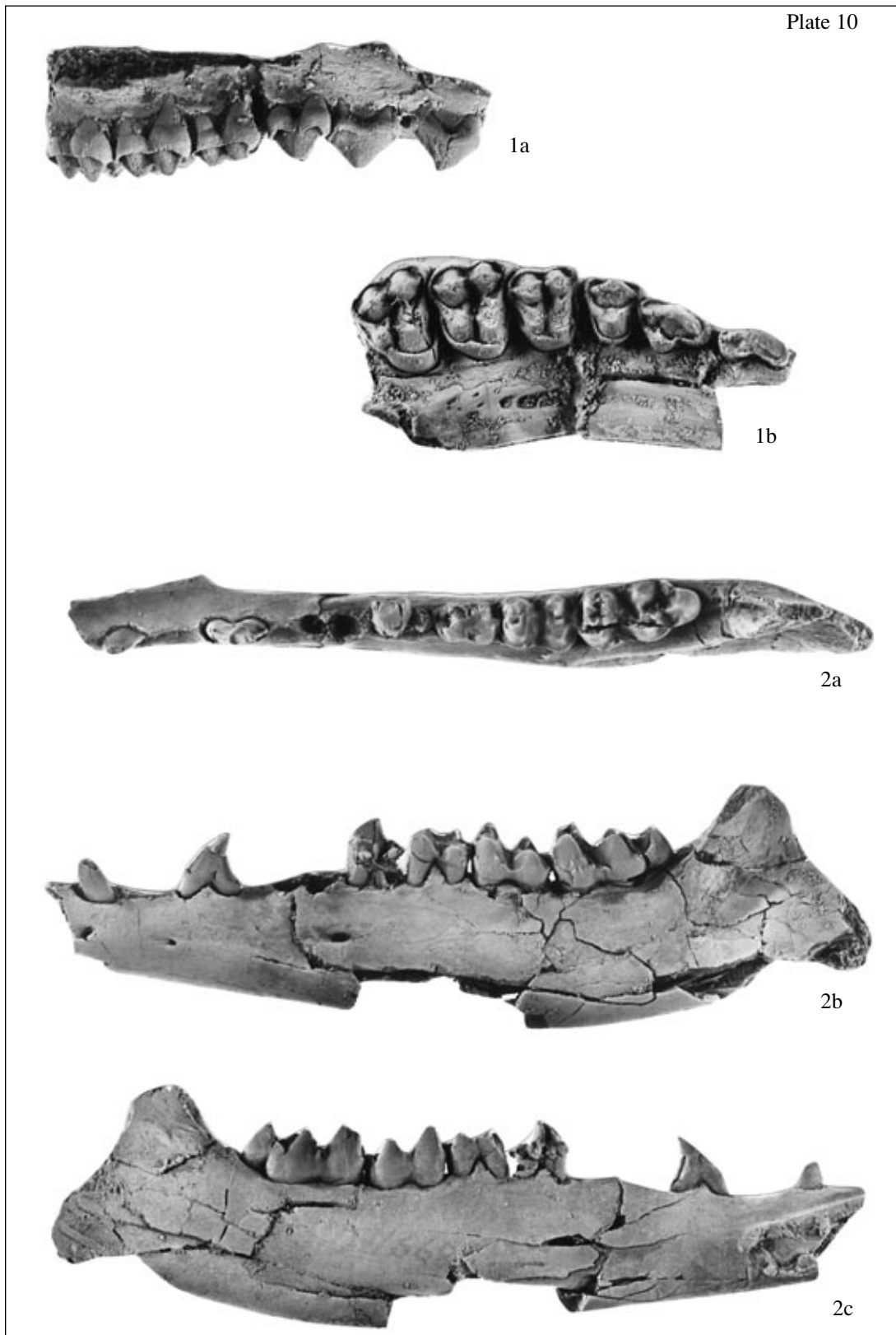
The crown of P^4 is symmetrical, its posteroexternal angle projects somewhat posteroexternally. The well-developed centrally positioned protocone bears a small additional cuspule, the paraconule. The anterior style (parastyle) and the smaller posterior style (at the posteroexternal angle) are well developed. The posterior style slightly protrudes labially. It is fused with the postprotocrista. The preprotocrista fuses anteriorly with the parastyle and the anterior cingulum.

The upper molars have four conical main cusps, i.e., the paracone, metacone, protocone, and metaconule. The metaconule is located in place of an undeveloped hypocone. M^1 is noticeably smaller than M^2 and M^3 . M^3 is larger than M^2 . Their crowns are transversely expanded and narrowed posteriorly, especially strongly in M^3 . The labial side is substantially longer than the lingual side. The ectoflexus is clearly pronounced, M^3 has the entoflexus as well.

The labial cusps (paracone and metacone) are poorly worn in M^1 and M^2 and weakly inclined inward. The anterior and posterior wings of these cusps are approximately aligned. The preparacrista of M^1 and M^2 is directed mesiodistally, while in M^3 , it extends mesiolingually. The parastyle is strongly developed, particularly in M^3 , and projects mesially. It is fused with the anterior crest, which originates from the paraconule (preparaconule crest). The posterior wing of the paracone and the anterior wing of the metacone are not confluent and do not form an ectoloph. The posterior style (metastyle) is poorly developed only in M^3 . The mesostyle is undeveloped.

The lingual cusps (protocone and metaconule) are not fused, but they are more heavily worn and relatively strongly inclined lingually. The postprotocrista is absent. The paraconule is present. It is located closer to the paracone in M^1 and equidistantly from the paracone and protocone in M^2 and M^3 . The posterior crest of the paraconule (postparaconule crest) is directed to the middle of the paracone base, and the anterior crest of the metaconule (premetaconule crest) points to the anterior part of the metacone base. The posterior crest of the metaconule (postmetaconule crest) fuses with the cingulum in M^1 and M^2 , and, in addition to that, with a very weak metastyle in M^3 .

The lower edge of the mandible (holotype) is weakly convex below P_2 – M_3 . The maximum depth of the mandibular body is at the talonid of M_2 . Anteriorly, the mandibular body gradually lowers from P_4 to P_1 and is poorly elongated. The anterior mental foramen is located below P_1 , it is larger than the posterior mental foramen; the latter is located below P_3 and P_4 . An additional vascular foramen is very small and observed between the mental foramina under the anterior edge of P_2 .



Explanation of Plate 10

Fig. 1. *Haqueina haichinensis* sp. nov., specimen PIN, no. 3108/469, $\times 1.5$, fragmentary maxilla, Khaichin-Ula 2, Mongolia; Khaichin Formation, Middle Eocene: (a) buccal and (b) ventral views.

Fig. 2. *Haqueina haichinensis* sp. nov., holotype PIN, no. 3108/468, $\times 1.5$, left mandible, Khaichin-Ula 2, Mongolia; Khaichin Formation; Middle Eocene: (a) dorsal, (b) lingual, and (c) inner views.

Table 1. Measurements of teeth of *Haqueina haichinensis* sp. nov.

Tooth	Length	Width
P ²	7.8	2.9
P ³	8.6	5.3
P ⁴	6.0	6.8
M ¹	8.3	8.7
M ²	9.2	10.5
M ³	9.5	11.5
P ₁	3.7	2.5
P ₂	6.2	2.6
P ₄	–	4.3
M ₁	6.6	4.8
M ₂	8.2	6.4
M ₃	13.3	6.8

The diastemata are present between the canine and P₁, P₁ and P₂, and P₂ and P₃. The longest of them is the diastema between P₁ and P₂. It is slightly shorter than the length of P₂ and twice as long as the diastema between P₂ and P₃.

The first lower premolar is small, caniniform, and single-rooted. It is inclined anteriorly and has a damaged but probably weakly pointed tip, the protoconid. The second premolar is double-rooted, considerably larger and almost twice as long as P₁. It is simple, high, triangular in lateral view, and has a posteriorly inclined pointed tip and a sharp posterior edge. Judging from the alveoli, the third premolar was not longer than P₄.

P₄ is distorted. The protoconid of this tooth was probably somewhat lower than that of P₂, and the metaconid and paraconid were undeveloped.

M₁ is relatively heavily worn, whereas M₃ is virtually lacks wear marks. The molar size sharply increases from M₁ to M₂. The posterior molar, M₃, is stout and broad. In all molars, the trigonid is substantially higher than the talonid. In M₁, the trigonid is slightly narrower than the talonid. In M₂, the talonid is considerably wider than the trigonid. In M₃, the talonid is nearly equal in width to the trigonid.

The lower molars apparently bear six cusps, including two labial (protoconid and hypoconid), three lingual (entoconid and closely spaced metaconid and paraconid), and the centrally positioned hypoconulid. In M₂ and M₃, the protoconid and metaconid are higher than the entoconid. The hypoconulid is small in M₁ and M₂, whereas it is large, broad, and complex in M₃. The hypoconulid is lower than the entoconid. The precingulids and postcingulids are present. A small ectocingulid is developed at the crown base of the lower molars between the protoconid and hypoconid.

In M₁, the anterointernal part of the molar is not preserved, all cusps and cristids are worn.

The wear facet of M₂ superficially resembles the selenodont pattern (Fig. 1). The paraconid is worn. The trigonid notch is deep and forms a small mark. The protocristid and paracristid are equally weakly arched. They are broad-notched, with the paracristid notch being slightly narrower than the notch of the protocristid. The hypolophid is worn. The entoconid is rounded. Posteriorly, the talonid basin is lingually open.

In M₃, which is nearly unworn, a small paraconid is located near and somewhat lingually to the metaconid. The paracristid has a narrow and deep notch, while the protocristid is high and lacks a notch. The cristid oblique is short and only slightly skewed, it adjoins the trigonid slightly labial to the midpoint of the protocristid. The hypolophid is not worn. It is straight, low, and very narrow, with a small cuspule adjoining it near the hypoconid. Crests of the hypoconulid form a loop resembling the structure typical of selenodont forms. The posterior labial wing of the hypoconid (postcristid) is fairly long. It is directed posteriorly and somewhat lingually and reaches a short longitudinally extended labial crest of the hypoconulid. A small cusp (posthypoconid) is located lingually from the point of their fusion. Another small cuspule is present between the entoconid and hypoconulid. The extensive notch at the posteroexternal margin of the crown is delineated by the labial crests of the hypoconid and hypoconulid.

Measurements, mm. Length of P²–P⁴ is 22.5; M¹–M³, 23; P²–M³, 45.3; P₂–P₄, 24; M₁–M₃, 27; M₂–M₃, 21.7; P₂–M₃, 52; P₁–M₃, 62. For other measurements, see Tables 1 and 2.

Table 2. Measurements of the lower teeth of *Haqueina*

Species, tooth	Length	Width of trigonid	Width of talonid	Width of hypoconulid	Length of hypoconulid
<i>H. haquei</i> , M ₂ , holotype (Dehm and Oettingen-Spielberg, 1958)	7.8	5.5	6.0	–	–
<i>H. haquei</i> , M ₃ , holotype (Dehm and Oettingen-Spielberg, 1958)	10.8	6.0	6.0	3.8*	3.5*
<i>H. haichinensis</i> , M ₂ , holotype	8.2	5.7	6.4	–	–
<i>H. haichinensis</i> , M ₃ , holotype	13.3	6.7	6.8	4.0	3.7

* Measured using a photograph (Dehm and Oettingen-Spielberg, 1958).

Comparison. The new species differs from *Haqueina haquei* in the slightly larger measurements of M_2 and M_3 and the presence (or a better development) of the paraconid on M_3 . It is not improbable that, in the holotype of *H. haquei* (Dehm and Oettingen-Spielberg, 1958, pl. 3, fig. 1), the paraconid is obliterated by wear.

Remarks. The genus *Haqueina* shows superficial similarity to the selenodont dental structure (Coombs and Coombs, 1977a). This explains why the form from Khaichin-Ula 2 was originally attributed to tragulids and determined as Hypertragulidae gen. nov. (Badamgarav and Reshetov, 1985).

Material. In addition to the holotype, an upper jaw fragment from the type locality, specimen PIN, no. 3107/469.

DISCUSSION

The taxonomic position of the genus *Haqueina* and the family Raoellidae has long remained uncertain.

This genus was originally attributed to dichobunids (Dehm and Oettingen-Spielberg, 1958). Subsequently, *Haqueina* was included into the family Raoellidae (Sahni *et al.*, 1981; Thewissen *et al.*, 1987), although certain differences between this genus and other raoellids were noticed. Holroyd and Ciochon (1995) proposed that *Haqueina* is more closely related to the Helohyidae. McKenna and Bell (1997), however, retained it in the family Raoellidae without an association of the latter with any superfamily of the Suiformes. Erfurt and Sudre (1996) believed that the family stems from the Diacodexidae. In actual fact, as will be shown below, *Haqueina* retains some primitive characters of this ancient dichobunoid group. According to a cladistic analysis performed by Gentry and Hooker (1988), the family Raoellidae shares many characters with the Helohyidae (*Gobiohyus* and *Helohyus*) and anthracotheriids and relatively early diverged from diacodexids. This hypothesis is corroborated by more primitive conditions of a series of characters in *Haqueina* compared to diacodexids.

In addition to *Haqueina*, the family Raoellidae includes five genera from the Early and Middle Eocene of Asia, *Raoella*, *Indohyus*, *Khirtharia*, *Kunmunella*, and *Meikatius* (McKenna and Bell, 1997). The Mongolian material shows that the genera *Raoella*, *Indohyus*, and *Haqueina* display especially high morphological similarity.

The genus *Raoella* was established on the basis of an incomplete maxilla with P^4 – M^3 (Sahni and Khare, 1971). Initially, it was assigned to the family Anthracotheriidae (Sahni and Khare 1971), later, to the Helohyidae (Coombs and Coombs, 1977a), and, subsequently, to the separate family Raoellidae (Sahni *et al.*, 1981; Thewissen *et al.*, 1987; McKenna and Bell, 1997). The genus *Indohyus* is represented by a fragmentary maxilla with P^4 – M^2 and several mandibles (Young, 1937; Rao, 1971; Coombs and Coombs, 1977a). Similar to

Gobiohyus, this genus was originally assigned to the Choeropotamidae (Rao, 1971).

Haqueina, *Raoella*, and *Indohyus* share the following primitive characters: (1) the absence of the hypocone and the presence of enlarged metaconule in place of the hypocone, (2) the absence of the mesostyle, and (3) weak development of the paraconule. Another common feature of these genera is the presence of the hypolophid.

Similarly to *Raoella* and dissimilar to *Indohyus*, *Haqueina* has a thin paraconule on P^4 . Coombs and Coombs (1977a) considered the presence of the paraconule on P^4 as the unique feature of the genus *Raoella*. In *Haqueina*, this character is observed in P^3 as well.

Haqueina, however, differs from *Raoella* and *Indohyus* in (1) such a primitive character as the absence of a crest between the paracone and metacone, i.e., the ectoloph, which is a primitive character; in *Raoella*, this crest is weak; (2) the lingually open central notch in the upper molars, that is, the absence of a crest between the protocone and metacone, the postprotocrista according to Coombs and Coombs (1977a); (3) the mesiodistally orientated preparacrista; and (4) the stronger developed cingulum, i.e., the preservation of the posterolingual cingulum on the upper molars; in *Raoella*, it is undeveloped. Among the Raoellidae, the ectoloph and postprotocrista are also absent in *Khirtharia*, which is represented by several upper and lower molars (Pilgrim, 1940; Coombs and Coombs, 1977a).

Advanced characters that distinguish *Haqueina* from *Raoella* and *Indohyus* are as follows: (1) the presence of the parastyle on P^3 ; (2) a more labial position of the paraconule on M^1 (in all molars of *Raoella* and *Indohyus*, this cusp is located closer to the protocone than to the paracone); and (3) the development of the metastyle on P^4 and M^3 . In addition, *Haqueina* is more advanced than *Raoella* in the somewhat narrower crowns of the upper molars. The length to width ratio of M^3 of *Raoella* is 0.75 (10.5 to 14) versus 0.83 (9.5 to 11.5) in *Haqueina*.

Haqueina retains some additional primitive characters, in particular, those typical of primitive dichobunoids of the genus *Diacodexis* from the Early and Middle Eocene of Asia and America and the Early Eocene of Europe. In a number of primitive features, *Haqueina* resembles *D. pakistanensis* from the Lower Eocene of the Barbara Banda locality in Pakistan (Thewissen *et al.*, 1983). These include (1) the large size and shape of the upper premolars, (2) a stout labial cingulum on the premolars and molars, (3) considerably smaller first molars compared to the second and third molars, and (4) the predominance of the width over the length in the crowns of the upper molars. Other primitive features include the preservation of a considerable posterior tapering of the upper molars (especially in M^3) and a somewhat anteriorly shifted paraconid of the lower premolars. The labial surface of the upper premolars is primitively convex.

However, such primitive characters of *Haqueina* as the absence of the hypocone and ectoloph, small paracule, and small paraconid positioned close to the metaconid indicate that the Raoellidae originate from a more primitive artiodactyl group than diacodexids or dichobunoids.

Haqueina, like some other genera of the family Raoellidae, shows apparent similarity to the family Helohyidae. This family includes six genera from the Middle Eocene of North America and two genera (*Gobiohyus* and *Pakkohyus*) from the Middle Eocene of Asia. It was long believed to be ancestral to the Anthracotheriidae, but now it is placed among dichobunoids (McKenna and Bell, 1997).

Similarly to the genus *Gobiohyus* of the family Helohyidae from China, Mongolia, and Kazakhstan, *Haqueina*, *Raoella*, and *Indohyus* have the enlarged metaconule in place of the hypocone in the upper molars. Additionally, *Haqueina* resembles *Gobiohyus* in a low hypolophid and a moderately large and centrally positioned hypoconulid on M_3 (Coombs and Coombs, 1977a). However, *Haqueina* differs from *Gobiohyus* in the shape and structure of premolars, certain important morphological features of molars, and their proportions. In *Haqueina*, the crowns of P^2 and P^3 are notably more elongated and have better developed labial cingula. P^4 is distinguished by the presence of the lingual cingulum (which is absent in *Gobiohyus*). The position of the protoconid on P^3 is also dissimilar: it is located distally in *Haqueina* and in the center in *Gobiohyus*. The labial crown sides of P^2 and P^3 are more convex, whereas the lingual side of P_2 is concave. The molars of *Haqueina* differ from those of *Gobiohyus* in the less square outlines and the absence of the ectoloph and "postprotocrista"; M_3 is distinguished by a more complex structure of the third lobe (as opposed to the unicuspid hypoconulid in *Gobiohyus*). A better pronounced selenodonty of *Haqueina* than *Gobiohyus* manifests itself in the development of the postparacule crest. In *Gobiohyus*, this crest is very weak or undeveloped.

In addition, the molars of *Haqueina* are distinguished by the larger size difference between the first and subsequent molars (abrupt enlargement of molars from the first to the second). *Gobiohyus* shows a gradual increase in crown size from the first molar to the third. The most impressive features of *Haqueina*, i.e., large dimensions of the second and third molars and smaller difference between them than in the Helohyidae (Coombs and Coombs, 1977a), are additional evidence for the assignment of these forms to a separate phyletic lineages.

In some morphological characters, *Haqueina* looks similar to the other genus of the Helohyidae, i.e., *Rakkokuhyus* from the Middle Eocene fauna of Pondaung in Myanmar (Holroyd and Ciochon, 1995). Apart from similarities in size, the two genera share (1) the lingually directed cristid oblique, (2) a promi-

nent hypoconulid of M_2 , (3) the metaconid that is slightly smaller than the protoconid, (4) the lingually open talonid basin, (5) a straight hypolophid of M_3 , and (6) the entoconid and hypoconid that are equal in size and height. According to Holroyd and Ciochon (1995), these features indicate the affinity between *Haqueina* and helohyids. However, they most likely indicate the affinity of the families Raoellidae and Helohyidae. *Haqueina* differs from *Rakkokuhyus* in the lower mandibular body, the development of the paraconid, and a more complex structure of the hypoconulid of M_3 .

Size difference between M_1 and M_2 and the complex talon of M_3 are known in *Anthracotherium*, whose oldest record is known from the Middle Eocene of Asia. However, the strong development and the peculiar W-shaped ectoloph, the development of mesostyle, the absence of the hypolophid, and other characteristic anthracotheriid features (Coombs and Coombs, 1977b) suggest that it independently acquired common features with the Raoellidae as a result of parallel evolution.

Haqueina displays a certain similarity to members of the family Haplobunodontidae, in particular, to the genera *Haplobunodon* from the Middle and Late Eocene of Europe and *Rhagatherium* from the Eocene of Europe and, possibly, America and Africa. *Haqueina* resembles *Haplobunodon* in the complex hypoconulid, and it is similar to *Rhagatherium* in the presence of an additional cuspule at the hypolophid (Dehm and Oettingen-Spielberg, 1958; Coombs and Coombs, 1977a). The family Haplobunodontidae is commonly assigned to the superfamily Anthracotherioidea (McKenna and Bell, 1997). Erfurt and Sudre (1995) proposed that haplobunodontids do not belong to anthracotherioids and represent an autochthonous group that probably diverged from diacodexids in the Early Lutetian (at the beginning of the Middle Eocene). The most primitive representative of haplobunodontids, *Hallebune*, from the Middle Eocene of Germany has many common characters with diacodexids (Erfurt and Sudre, 1995) and considerably differs from *Haqueina*.

The specific combination of primitive and derived characters in *Haqueina* supports the independence of the family Raoellidae and its early separation from the Suiformes stem. The similarity to helohyids and some anthracotherioids was most likely gained in parallel. The Raoellidae apparently followed an independent developmental path from primitive artiodactyls and should not be placed in any suiform superfamilies, as was suggested by McKenna and Bell (1977).

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