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内蒙古四子王旗额尔登敖包晚始新世紧齿犀类一新属[1)]

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摘要: 描述了内蒙古四子王旗额尔登敖包晚始新世乌兰戈楚组(?)(中白层)的紧齿犀亚科(Eggysodontinae)一新属种: 邱氏原紧齿犀(*Proeggysodon qiui*),标本为破损的下颌骨。新属种与其他渐新世紧齿犀的区别在于个体较小,具有两对发育的铲形下门齿,下前臼齿没有臼齿化,p4的下斜脊更向舌侧倾斜延伸,下臼齿下斜脊与下次脊连接处呈角状,下臼齿无颊侧齿带。紧齿犀类和柯氏犀类(forstercooperes)可能有较近的系统发育关系,它们具有以下的共近裔性状: 短而粗壮的大犬齿,相对短的齿隙(犬齿和前臼齿之间),下颌联合部短而高,从而使门齿趋向直立。新标本的发现填补了早－中始新世柯氏犀类和渐新世紧齿犀类在时代上的空白,也使紧齿犀类成为欧洲始新世/渐新世之交的"大间断"之后哺乳动物群自亚洲迁入欧洲的又一例证。

关键词: 内蒙古四子王旗,始新世,紧齿犀,柯氏犀,"大间断"

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PROEGGYSODON GEN. NOV., A PRIMITIVE EOCENE EGGYSODONTINE(MAMMALIA, PERISSODACTYLA) FROM ERDEN OBO, SIZIWANGQI, NEI MONGOL, CHINA

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Abstract Previously, rhinocerotoid eggysodontines have been confined to Oligocene deposits from Europe and Asia. Here we report a new primitive Late Eocene eggysodontine, *Proeggysodon qiui* gen. et sp. nov., from Erden Obo, Siziwangqi, Nei Mongol, China. *Proeggysodon* differs from other eggysodontines in being smaller; in having two pairs of well-developed, spatulate lower incisors, non-molarized lower premolars, a more lingually aligned cristid obliqua of p4, and an angled junction between the cristid obliqua and the hypolophid of each lower molar; and in lacking buccal cingulids on the lower cheek teeth. Furthermore, we propose that eggysodontines and forstercooperes are closely related, mainly because they share the following features: large and erect canine, relatively short diastema

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between canine and cheek teeth, and dorsoventrally deep and anteroposteriorly abbreviated symphysis associated with nearly vertically implanted incisors. The new specimen narrows the time gap between the Early to Middle Eocene forstercooperes and the Oligocene eggysodontines. The discovery of *Proeggysodon* in Asia also suggests that eggysodontines dispersed from this continent into Europe after the "Grande Coupure".

Key words Siziwangqi, Nei Mongol; Eocene; eggysodontines; forstercooperes; "Grande Coupure"

1 Introduction

The subfamily Eggysodontinae is a group of medium-sized rhinocerotoids, including the European *Eggysodon* and the Asian *Allacerops*. The Eggysodontinae was originally placed in the Rhinocerotidae (Roman, 1911), but was either placed in the Hyracodontidae (Radinsky, 1967a; Uhlig, 1999) or treated as a separate family Eggysodontidae (Qiu and Wang, 2007). Although Heissig (1989) also included *Prohyracodon* and *Ilianodon* in the subfamily Eggysodontinae, the phylogenetic position of these genera is open to argument (McKenna and Bell, 1997; Qiu and Wang, 2007). The research history of the group was summarized by Qiu and Wang (1999), and we follow these authors in considering that: 1) *Allacerops* is a valid genus with *A. turgaica* (Borissiak, 1915) as its type species; 2) *Eggysodon* and *Allacerops* are different genera; and 3) Allaceropinae is a junior synonym of Eggysodontinae. Specimens referable to the subfamily are relatively rare and previously known only from the Oligocene, and the group is more abundant and diverse in Europe than in Asia where it originated (Becker, 2009; de Bonis and Brunet, 1995; Heissig, 1989; Qiu and Wang, 1999; Reshetov et al., 1993; Uhlig, 1999). Only two eggysodontine specimens have previously been reported from China. An anterior half of a juvenile mandible from the Oligocene Xianshuihe Formation in the Lanzhou Basin, Gansu Province, has been identified as *Allacerops* cf. *A. turgaica* (Qiu and Wang, 1999), while a segment of a left lower jaw with m1 from the Early Oligocene Paoniuquan Formation, Danghe area, Gansu Province, was assigned to *Allacerops* sp. by Wang and Qiu (2004).

Here we report a primitive eggysodontine from the upper Eocene of Erden Obo (= Urtyn Obo), Naomugeng (= Nomogen) Sumu, Siziwangqi, Nei Mongol, China (Fig. 1). The bed from which the specimen was recovered is equivalent to the "Middle White" or "Gray" layer shown in a sketch made by Walter Granger at Erden Obo during the Central Asiatic Expedition (CAE) (Osborn, 1929: fig. 2). The new material provides important information about the origin and evolution of Eggysodontinae, as well as their phylogenetic relationship with other rhinocerotoids. Terminology for tooth structures in this paper follows Bai et al. (2010).

2 Systematic paleontology

Order Perissodactyla Owen, 1848
Superfamily Rhinocerotoidea Gray, 1825
Family Eggysodontidae Breuning, 1923
Subfamily Eggysodontinae Breuning, 1923
Proeggysodon gen. nov.

Type species *Proeggysodon qiui* gen. et sp. nov.
Included species Only the type species.
Etymology Allusion to *Eggysodon*. The Greek prefix *'pro-'* means before.
Diagnosis As for the type and only species.

Fig. 1 The location of Siziwangqi, Nei Mongol, and those of some nearby localities
The black dot marks the locality where the specimen described in this paper was found; the names in the parentheses were used by the CAE members or subsequent authors; coordinates correspond to Siziwangqi

Proeggysodon qiui gen. et sp. nov.

(Fig. 2)

Holotype IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing) V 18099, broken paired mandibles without ascending rami, preserving i1 – 2, c, and p2 – m3 on the right and root of i1, broken p3 – m1, and roots of m2 – 3 on the left, in addition to associated tooth fragments including broken crown of left i2, crown of left canine, and some broken cheek teeth.

Etymology The specific name honors Prof. Dr. Zhanxiang Qiu, who described the first Chinese eggysodontines, for his great contributions to the study of Chinese perissodactyls.

Diagnosis Small eggysodontine. Differs from other eggysodontines in having two pairs of well-developed, spatulate lower incisors, non-molarized lower premolars, more lingually oblique cristid obliqua of p4, and angled junction between cristid obliqua and hypolophid of each lower molar, and in lacking buccal cingulids on lower cheek teeth.

Type locality and horizon Erden Obo, Nomogen, Siziwangqi, Nei Mongol, China; Ulan Gochu Formation(?) (upper part of "Middle White"); Late Eocene.

Description Incisor, canine and premolar measurements from the right mandible (length/width in mm): i1, 12.8/9.7; i2(12.7/9.8), c(18.4/17.7), p2(16.5/?), p3 (17.1/10.3), and p4(18.1/14.6). Molar measurements from the right mandible(length/(trigonid width)/(talonid width) in mm): m1(21.4/16.7/17.7), m2(27.7/17.3/18.7), and m3(29.1/20.3/?).

The lower jaw is of an old individual, and the left horizontal ramus is slightly dorsoventrally

compressed. The ventral part of the symphyseal region is nearly absent due to weathering, so the roots of the incisors are visible buccally. The bone between the right canine and p2 is also damaged (Fig. 2).

Although the symphyseal region is partly broken, it appears shallow and broad in dorsal view (Fig. 2B). The posterior border of the mandibular symphysis is situated slightly anterior to the level of p2. The incisors and canine are widely spaced, and the incisors are more or less vertically implanted. The diastema between the canine and p2 is very short (ca. 27.2 mm). From the lateral view, it is reasonable to infer that the symphysis is dorsoventrally deep and anteroposteriorly abbreviated. The symphysis rises upwards, forming an angle of about 43° with the long axis of the horizontal ramus (Fig. 2C). The horizontal ramus is slender, with a lower border that is slightly concave anteriorly and convex posteriorly. Two mental foramina are placed

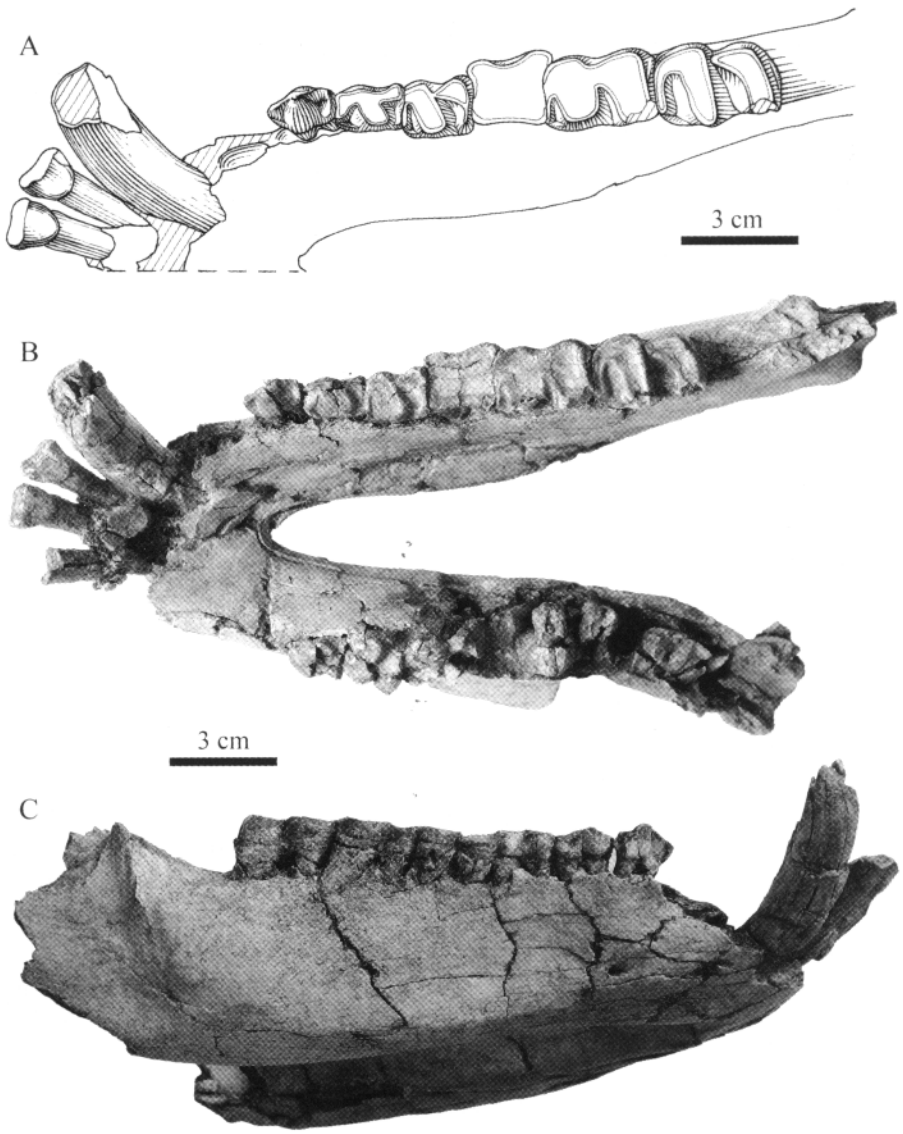

Fig. 2　The lower jaw of *Proeggysodon qiui* (IVPP V 18099)
A. line drawing of right lower dentition in occlusal view; B. dorsal view of lower jaw; C. lateral view of lower jaw

at the same horizontal level and separated by a distance of about 22 mm. The posterior foramen is the larger of the two, and is situated slightly below the dorsoventral midpoint of the horizontal ramus at the level of the boundary between p2 and p3. In the lateral view the horizontal ramus in fact appears somewhat swollen below m3. A space separates m3 from the ascending ramus. Posterior to this space, a short and prominent ridge on the lateral surface of the mandible extends ventrally and slightly anteriorly, delimiting the anterior border of the masseteric fossa. The medial surface of the ascending ramus bears a broken mandibular foramen located 48 mm posterior to m3 and at roughly the same level as the alveolar border.

The crown of i1 is very robust and spatulate, with flat buccal and lingual facets, but the lingual facet tilts slightly forward (Fig. 2A – B). The occlusal surface of i1 is heavily worn, and forms an oval facet that is flat and buccolingually compressed. In buccal view, the upper edge of the crown is slightly concave in the middle. The root is considerably longer than the crown and tapers apically. The mesial, buccal and distal surfaces of the root are nearly flat, while the lingual side is slightly convex. The i2 is roughly similar to i1, but the crown of i2 is concave with the mesial portion extending upward. In buccal view, the upper edge of the crown is deeply concave in the middle. In lingual view, a worn, somewhat depressed oval facet is present along the distal side of the tooth. The root of i2 is similar to that of i1, but the former is slightly laterally compressed with convex buccal and lingual sides.

The tip of the right canine is broken, but the corresponding area is intact in the isolated left canine. The canine is vertical and tusk-like with a long, robust root, and is considerably larger than the incisors. A flat wear facet is present on the distal side of the left canine, making the cross-section of the canine into a triangle with a distal base and a mesial apex.

The cheek teeth are all heavily worn, with the exception of m3 (Fig. 2A – B). An alveolus is present mesial to the right p2, indicating the presence of a p1 or dp1. However, the socket is absent on the left side. The half-preserved right p2 is double-rooted, whereas the left p2 has only one root as inferred from the shape of the alveolus. The broken p2 has a single main cusp (protoconid), with two ridges that respectively extend mesially and distally. The mesial ridge descends gently, terminating relatively high on the paraconid rather than at the base. A prominent contact facet is discernible on the mesial surface of the paraconid, another indication of the presence of a p1 or dp1. A shallow, narrow groove between the main cusp and the paraconid represents the trigonid. The distal ridge is steeper and shorter than the mesial one, ending at the hypoconid at the same height as the contact between the mesial ridge and the paraconid. The talonid is much larger and deeper than the trigonid, and the entoconid is absent. Only a weak mesiolingual cingulid is present at the base of the trigonid, while the lingual part of the main cusp and the distal border lack cingulids entirely. The p3 is rectangular in occlusal view, being longer than wide. The trigonid is roughly V-shaped, having a strong metalophid and a confluent protolophid and paralophid that are short and extend mesiolingually from the protoconid. The paraconid is distinct and conical. The metaconid is slightly lower and more distally situated than the protoconid, and the metalophid is distolingually oriented. The talonid is about half the length of the trigonid. The cristid obliqua is short and extends mesially from the hypoconid to the distal part of the protoconid. The entoconid and hypolophid are absent. The ectoflexid forms a small depression. Only a short, but prominent, lingual cingulid is present at the base of the trigonid. The p4 is relatively wider than p3. The metalophid of p4 is slightly less oblique than that of p3, and the metaconid is as high as the protoconid. The protolophid extends a short distance mesiolingually from the protoconid, then curves lingually and slightly mesially to form a ridge-like paralophid; the angle between the metalophid and the protolophid is about 80°. The talonid of p4 is deeper than that of p3, and slightly shorter than the trigonid. The cristid obliqua extends mesially and slightly lingually from the hypoconid to the metalophid, resulting in a relatively deep ectoflexid. The entoconid of p4 is more prominent than that of p3.

However, the hypolophid of p4, which borders the talonid distally, is rather weak and ridge-like. The cingulid of p4 is similar to that of p3.

The m1 and m2 are heavily worn. The morphological characters of m1, apart from its nearly rectangular outline, are hardly discernible. The trigonid and talonid of m2 are similar to those of p4 except that the metalophid of m2 is less oblique than that of p4, the angle between the metalophid and the protolophid of m2 is only about 74 °, and the hypolophid is better developed. In this heavily worn example of m2, the hypolophid is transverse. However, the originally distolingually oriented hypolophid would become transverse with wear, assuming the distal wall of the hypolophid had a buccal part that was inclined forward and an erect lingual part. Thus, the hypolophid of m2 may be oblique at the early-wear stage, rather than transverse throughout its existence. The lingual cingulid is more prominent than that of p4, closing off the base of the trigonid. In addition, a rather weak cingulid is present buccally on the distal part of the tooth. The m3 is moderately worn, and differs slightly from m1 and m2 in its morphology. The trigonid of m3 is U-shaped. The metalophid is nearly transverse. A ridge extends mesially and slightly lingually from the protoconid to form the protolophid, then turns lingually to form a long paralophid that lies parallel to the metalophid. The angle between the metalophid and the protolophid is slightly less than 90°. The talonid of m3 is slightly narrower than the trigonid. The hypolophid of m3 is slightly oblique, and the cristid obliqua extends mesially from the hypoconid to the distal part of the protoconid. The hypolophid and cristid obliqua meet at an angle slightly exceeding 90°, and the distobuccal corner of this angle is rather sharp than rounded. The cingulids of m3 are similar to those of m2 except that the weak mesiobuccal and distal cingulids are present.

3　Comparisons and discussion

The mandible of *Proeggysodon* has two paired of well-developed, spatulate incisors, large, vertical canines, very short diastemae between the canines and cheek teeth, relatively prominent ectoflexids on the cheek teeth, and lower molars that are not elongated. The large, vertical canines exclude the specimen from true rhinoceroses and hyracodontids (Radinsky, 1967a), while the relatively prominent ectoflexids on the cheek teeth and the fact that the lower molars are not elongated exclude the specimen from amynodontids (Wall, 1989). On the other hand, the large, vertical canines and very short diastemae between the canines and cheek teeth are characteristic of eggysodontines (Qiu and Wang, 1999; Roman, 1911).

The Asian eggysodontine genus *Allacerops* includes two species: *A. turgaica* and *A. minor*. *A. turgaica* was first described by Borissiak (1915), as *Epiaceratherium turgaica*, from lower Oligocene deposits in the Turgai Region, Kazakhstan. Wood (1932) then erected the genus *Allacerops*, with *A. turgaica* as the type species. The species has also been reported from the Myneske-Suyek and Tort-Mola localities in Kazakhstan, and from Gansu Province in China (Birjukov, 1961; Qiu and Wang, 1999; Reshetov et al., 1993; Wang and Qiu, 2004). *A. minor* was first described as a subspecies of *A. turgaica* from the lower Oligocene Hsanda Gol Formation of Tatal Gol, Mongolia (Beliajeva, 1954; Dashzeveg, 1991). Borsuk-Białynicka (1968) regarded the taxon as a separate species, based on some new information provided by a fragmentary lower jaw from the Early Oligocene Hsanda Gol Formation of Ulan Ganga, Western Gobi Desert, Mongolia (Dashzeveg, 1991). The Central Asian horizons bearing the *Allacerops* material were originally considered Middle Oligocene, but are actually Early Oligocene in age (Berggren and Prothero, 1992; Daxner-Höck et al., 2010). An unusual specimen, identified as *Allacerops* sp., was reported from the Upper Eocene (Ergilian) of Khoer Dzan, Eastern Gobi Desert, Mongolia (Dashzeveg, 1991). However, because this specimen is poorly preserved, and much smaller than members of any other known *Allacerops* species, its attribution is doubt-

ful (Qiu and Wang, 1999).

The molar series of *Proeggysodon* is about 19% shorter than that of *Allacerops* (Table 1). The symphyseal region of *Proeggysodon* is similar to that of *A. turgaica* in being dorsoventrally deep and anteroposteriorly abbreviated, and in that its posterior border reaches the level of the anterior edge of p2. However, the symphyseal region of *A. minor* appears less curved upwards than those of *Proeggysodon* and *A. turgaica* (Borsuk-Białynicka, 1968: pl. 19, fig. 1b; Reshetov et al., 1993). Furthermore, *Proeggysodon* has two pairs of lower incisors which are widely placed and similar in size, whereas *A. turgaica* has three pairs of incisors that are closely situated and decrease slightly in size from i1 to i3 (Reshetov et al., 1993). However, the incisors of *Proeggysodon* and *Allacerops* are similar in having a spatulate shape and in that the mesial part of i2 extends upward (Reshetov et al., 1993). Although *A. minor* also has two pairs of incisors, it can be inferred from the alveoli that they are closely appressed (Borsuk-Białynicka, 1968: pl. 20, fig. 1a). The canine of *Proeggysodon* is similar to that of *A. turgaica* in being massive, conical, and in having a big root, however, the latter is smaller and somewhat elongated mesiodistally (Reshetov et al., 1993). The length ratio of the diastema to the cheek teeth is greater in *Proeggysodon* than in *Allacerops* (Table 1). The presence of a p1 or dp1 alveolus on the right mandible of the holotype of *Proeggysodon*, and its absence on the left side, indicates that this character can be variable even in the same individual. The lower cheek teeth of *Proeggysodon* differ from those of *Allacerops* in having the following features: premolars that are less molarized, and also smaller relative to the molars; more elongated molars; a more inclined metalophid and shorter protolophid on p4; a more lingually extended cristid obliqua on m1-2; an angular junction between the cristid obliqua and the hypolophid on each molar; and marked lingual cingulids at the bases of the trigonids on the cheek teeth (Fig. 3; Table 1, 2) (Beliajeva, 1954; Borsuk-Białynicka, 1968; Reshetov et al., 1993). The Ergilian *Allacerops* sp. from Mongolia is more advanced than *Proeggysodon* in having a complete hypolophid fused with the entoconid on p4, and a shorter diastema between the canine and the first premolar (18 mm in *Allacerops* sp.) (Dashzeveg, 1991). On the other hand, the combined length of p2-4 is 67% greater in *Proeggysodon* than in *Allacerops* sp. Both are similar in that the posterior border of the symphysis reaches the level of the anterior edge of p2, and in that two mental foramina are present with the posterior one below p2 or p3 (Dashzeveg, 1991).

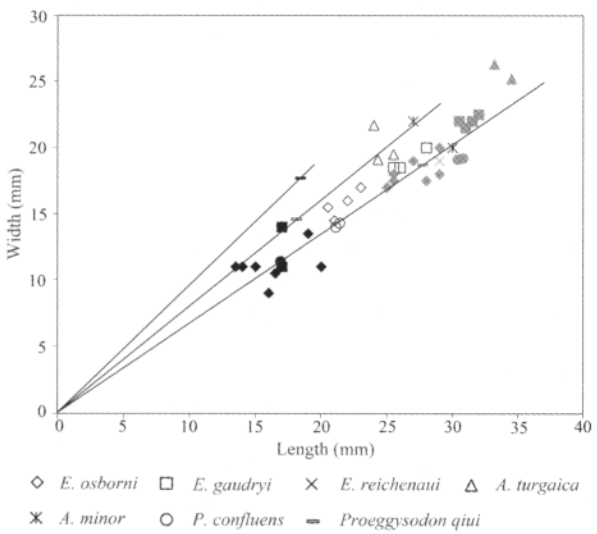

Fig. 3 Bivariate plots of the dimensions of the lower canine (solid black), p4 (unshaded), and m2 (solid gray) in *Eggysodon osborni*, *E. gaudryi*, *E. reichenaui*, *Allacerops turgaica*, *A. minor*, *Pappaceras confluens*, and *Proeggysodon qiui*

The lines connect the points representing the teeth measurements of *Proeggysodon* to the origin; symbols below a given line represent species in which the length/width ratio for the tooth in question is larger than in *Proeggysodon*, whereas symbols above the line represent species in which the ratio is smaller; the data for *Eggysodon* are from Uhlig (1999); for *Allacerops*, from Reshetov et al. (1993) and Beliajeva (1954); for *Pappaceras*, from Wood (1963)

Table 1　Comparison of measurements among *Proeggysodon*, *Allacerops*, *Eggysodon*, and *Pappaceras*　(mm)

Characters	*Proeggysodon qiui*	*Allacerops turgaica*	*Allacerops minor*	*E. osborni*		*Eggysodon gaudryi*	*Eggysodon reichenaui*	*Pappaceras confluens*
				Möhren-13	Klein-blauen			
1. length of p1-4 (p2-4)	(51.7)	82.3 (67.7)	77.0	**69.5** (**56.0**)	(68)	**79.0** (72.0)	—	69.9 (56.0)
2. length of m1-3	79.2	96.7	99.0	**80.0**	86	88.5	84	88.1
3. length of the cheek teeth	(130.9)	179.0 (164.4)	176	149.5 (136.0)	(154)	167.5 (160.5)	—	158.0 (144.1)
4. diastema between c and p1(p2)	27.2	24.0	23	—	39	32.0	—	27.4
5. ratios 1:2	(0.65)	0.85 (0.70)	0.78	0.87 (0.70)	(0.79)	0.89 (0.81)	—	0.79 (0.63)
6. ratios 4:3	(0.21)	0.13 (0.15)	0.13	—	(0.25)	0.19 (0.20)	—	0.17 (0.19)

Note: Numbers in parentheses pertain to the combined length of p2-4(rather than p1-4). Bold indicates values measured from figures. Data for *A. turgaica* from Reshetov et al. (1993: table 1); for *A. minor*, from Borsuk-Białynicka(1968: table 1). Measurements for *E. osborni* are from material from the Möhren 13 locality(Uhlig, 1999: fig. 92), and from Kleinblauen (Uhlig, 1999: table 122). Most measurements for *E. gaudryi* are from material from Latou(Uhlig, 1999: table 142), but the length of p1 was measured from a published plate(Roman, 1911: pl. 6, fig. 1). Data for *E. reichenaui* are from Uhlig(1999: table 148); for *P. confluens*, from Wood(1963: table 2).

There are four *Eggysodon* species from Europe: *E. osborni*, *E. gaudryi*, *E. pomeli* and *E. reichenaui* (de Bonis and Brunet, 1995; Heissig, 1989; Roman, 1911; Uhlig, 1999). In *E. pomeli* the lower dentition is unknown. The known fossil record of *Eggysodon* in Europe extends from MP21 to MP30(Ménouret and Guérin, 2009). *E. osborni* was traditionally considered smaller than *E. gaudryi* and *E. reichenaui*, which were in turn considered smaller than *Allacerops turgaica* (de Bonis and Brunet, 1995). However, recent studies on *E. osborni* show that its size has a wide range of variation, the largest individuals being close to the size of *E. gaudryi* (Fig. 3)(Becker, 2009). The molar length of *Proeggysodon* is similar to that of small specimens of *E. osborni* (de Bonis and Brunet, 1995), while the p2-4 length is about 8% smaller in *Proeggysodon* (Table 1). Accordingly, the premolars are shorter in relative terms in *Proeggysodon* than in *Eggysodon*. *Proeggysodon* is similar to *Eggysodon* in having two pairs of incisors, but the incisors of *Eggysodon* are pointed and i2 is greatly reduced(Osborn, 1900; Uhlig, 1999). The canine of *Proeggysodon* has a rounded cross section at the base and is larger than the more laterally compressed canine of *Eggysodon* (Fig. 3). The ratio of diastema length to the total length of the cheek teeth is smaller in *Proeggysodon* than in *E. osborni*, and slightly greater in *Proeggysodon* than in *E. gaudryi* (Table 1). The premolars of *Proeggysodon* are less molarized than those of *Eggysodon*, since the premolars of the latter taxon have well-developed hypolophids whereas in *Proeggysodon* these structures are absent on p2-3 and rather weak on p4(Table 2). Furthermore, p4 of *Proeggysodon* differs from those of *E. osborni* and *E. gaudryi* in being less elongated (Fig. 3), and in having a more inclined metalophid, a shorter protolophid, a more oblique paralophid, and a slightly more lingually oriented cristid obliqua (Table 2)(de Bonis and Brunet, 1995: pl. 1, fig. 3; Roman, 1911: pl. 6, fig. 2; Uhlig, 1999). The premolars of *Proeggysodon* bear cingulids only lingually at the base of the trigonids, while those of *E. osborni* and *E. gaudryi* each have a continuous buccal cingulid and an interrupted lingual

cingulid at the base of the metaconid(de Bonis and Brunet, 1995; Uhlig, 1999) . The m2 of *Proeggysodon is more similar to those of E. osborni* and *E. reichenaui* than that of *E. gaudryi* in size and in having a more lingually oblique protolophid (Fig. 3) (Roman, 1911; Uhlig, 1999) . The cristid obliqua of m2 in *Eggysodon* usually extends mesially from the hypoconid and is smoothly arched at the junction with the hypolophid(Becker, 2009; de Bonis and Brunet, 1995; Uhlig, 1999) , whereas in *Proeggysodon* the cristid oblique of m2 is more lingually oblique and forms an acute angle with the hypolophid(ca. 81°) (Table 2) . The m3 of *Proeggysodon* is similar to that of *Eggysodon* in that the protolophid is less lingually oblique than that of m2, and in having a nearly transverse metalophid, slightly oblique hypolophid and mesially aligned cristid obliqua(Roman, 1911; Uhlig, 1999) . However, the cristid obliqua of m3 in *Proeggysodon* meets the hypolophid at a sharp angle, in contrast to the relatively gentle arch seen in *Eggysodon*. The molars of *Proeggysodon* are similar to those of *E. osborni* and *E. gaudryi* in having lingual cingulids closing off the trigonids at the bases. However, each molar of *E. osborni* has a cingulid at the base of the ectoflexid, a lingual cingulid at the base of the talonid (Uhlig, 1999) , and/or a well-developed buccal cingulid (de Bonis and Brunet, 1995: pl. 1, fig. 3a) ; each molar of *E. reichenaui* has a prominent cingulid at the base of the ectoflexid and a weak lingual cingulid at the base of the trigonid; each molar of *E. gaudryi* normally has a prominent and complete buccal cingulid (Uhlig, 1999) .

Table 2 Comparison of some dental characters among *Proeggysodon*, *Allacerops*, *Eggysodon*, and *Pappaceras*

Characters	*Proeggysodon qiui*	*Allacerops turgaica*	*Allacerops minor*	*Eggysodon osborni*	*Eggysodon gaudryi*	*Eggysodon reichenaui*	*Pappaceras confluens*
pairs of lower incisors	2	3	2	2	2	—	3
metalophid of p4	inclined	—	transverse	less inclined	nearly transverse	—	inclined
extension of p4 cristid obliqua	antero-lingual	anterior	anterior	anterior	anterior	—	antero-lingual
premolars molarization	non-molariform	molari-form	molari-form	molari-form	molari-form	—	non-molariform
angle between m2 protolophid and metalophid	74°	—	—	70° -80°	80°	70° -80°	~88°
extension of m2 cristid obliqua	slightly lingual	anterior	—	anterior	anterior	anterior	slightly lingual
extension of m1-2 metalophid and hypolophid	inclined or transverse	inclined	inclined	inclined	transverse or slightly inclined	inclined	inclined
junction between the molar cristid obliqua and hypolophid	angled	gently arched	gently arched	gently arched	gently arched	gently arched	angled or slightly arched

Stehlin(1930) described a lower jaw of *Eggysodon* sp. from Puy-Laurens, Tarn, France. De Bonis and Brunet(1995) and Uhlig(1999) referred the specimen to *E. gaudryi* based on its size, as well as the presence of two pairs of incisors, an erect canine, and cingulids comparable in morphology and position to those seen in *E. gaudryi*. Furthermore, the transverse metalophids and hypolophids of the molars are also reminiscent of *E. gaudryi*. However, the m2 trigo-

nid of the Puy-Laurens *Eggysodon* sp. is nearly V-shaped, with an acute angle between the metalophid and the protolophid(Stehlin, 1930: fig. 2) . This condition is similar to that seen in *E. osborni* and *Proeggysodon*, whereas the molar trigonid of *E. gaudryi* is almost U-shaped(Roman, 1911) . Thus, we consider the Puy-Laurens *Eggysodon* sp. specimen to differ from both *E. gaudryi* and *E. osborni*, and the specimen should continue to be regarded as indeterminate at the specific level.

To sum up, *Proeggysodon*, *Eggysodon* and *Allacerops minor* all have two pairs of lower incisors, contrasting with the presence of three pairs in *Allacerops turgaica*. Furthermore, *Proeggysodon* and *Eggysodon* also share relatively elongated molars, and the length ratio of the diastema to the cheek teeth is similar in these genera. These observations probably imply that *Proeggysodon* is more closely related to *Eggysodon* than to *Allacerops*. On the other hand, the holotype mandible of *Proeggysodon* is obviously more primitive than both *Eggysodon* and *Allacerops*, judging by its small size, non-molarized premolars, relatively short premolars (compared to the molars) and lack of buccal cingulids on the cheek teeth. Accordingly, believe that our decision to erect a new genus and species for this mandible is amply justified.

4　Systematic position of eggysodontines

The phylogenetic relationships between Eggysodontinae and other perissodactyl groups are uncertain. Apart from *Eggysodon* and *Allacerops*, the Eggysodontinae also contains *Prohyracodon* and *Ilianodon* according to Heissig(1989) and Uhlig(1999) . However, the referral of *Prohyracodon* to Eggysodontinae was mainly based on an undescribed specimen of *Prohyracodon* (= *Meninatherium*) *teller* from Graz, which was briefly mentioned by Heissig (1989) and bears the root of an erect canine and alveoli for two pairs of incisors; Heissig (1989) also assigned *Ilianodon* to Eggysodontinae mainly because of its elongated premolars, similar to those of *P. teller*, and large canine alveolus(Chow and Xu, 1961) . *Prohyracodon obrutschewi*, another species of *Prohyracodon* whose anterior dentition differs from that of *P. teller*, is more similar to *Ardynia*(Dashzeveg, 1996; Qiu and Wang, 2007) . Accordingly, the assignment of *Prohyracodon* and *Ilianodon* to Eggysondontinae awaits confirmation from new, more complete specimens, as well as a detailed description of *P. teller* from Graz. Dashzeveg(1996) considered the Eggysodontinae to consist of five genera: *Forstercooperia*, *Juxia*, *Armania*, *Eggysodon*, and *Allacerops*(= *Teniseggysodon*) . This assemblage of taxa is not a monophyletic group, given that *Juxia* is a primitive paracerathere and *Armania* is an amynodontids(Dashzeveg, 1996; Qiu and Wang, 2007) . Thus, only *Eggysodon*, *Allacerops* and *Proeggysodon* can undoubtedly be placed in an eggysodontine clade at present. The subfamily Eggysodontinae has been placed within Rhinocerotidae(Roman, 1911) or Hyracodontidae(Radinsky, 1967a; Heissig, 1989; MeKenna and Bell, 1997; Qiu and Wang, 1999) , or probably as a separate family Eggysodontidae within Rhinocerotoidea(Qiu and Wang, 2007) .

Forstercooperiinae is composed of *Forstercooperia* and *Pappaceras*, although the latter was considered to be a junior subjective synonym of the former by Radinsky(1967a) and Lucas et al. (1981) . Following Qiu and Wang(2007) , we consider that *Forstercooperia* and *Pappaceras* are different genera. Lucas et al. (1981) reviewed the species of *Forstercooperia* from Asia and North America, but Holbrook and Lucas (1997) concluded that the North American forms should actually be assigned to a new primitive rhinocerotid genus, which they named *Uintaceras* (see also Wang, 1976) . This would imply that forstercooperes were confined to Asia. *Forstercooperia* and *Pappaceras* are about the same size as *Juxia* and have tooth morphology reflecting a similar evolutionary grade, but both genera are nevertheless readily distinguishable from *Juxia* and from other, later large paraceratheres (Qiu and Wang, 2007) . However, the forstercooperes are still usually regarded as the sister group of the paraceratheres(Lucas and Sobus,

1989; Qiu and Wang, 2007; Radinsky, 1967a; Wang, 1976).

Though Wood(1938) placed *Forstercooperia totadentata* in Rhinocerotidae, he nevertheless noted that "the hypothesis of ancestry to *Eggysodon* (=*Allacerops*) has much to commend it at first sight, except the large size of *Forstercooperia*, especially for its age"(Wood, 1938: 14). He rejected the hypothesis mainly based on two undescribed specimens from Shara Murun and Irdin Manha, which seem to be close to the ancestry of *Eggysodon*(=*Allacerops*) and fairly different from *Forstercooperia*(Wood, 1938). Since then, however, no specimens referable to *Allacerops* have been reported from Nei Mongol, China. Similarly, Wood(1963: 9) also briefly mentioned that "future evidence might make the Eggysodontinae(=Allaceropinae) contain it (*Pappaceras*) logically". Radinsky(1967a) also mentioned that *Allacerops* was probably derived from *Forstercooperia*. However, the hypothesis of a close phylogenetic relationship between Eggysodontinae and Forstercooperiinae was not widely accepted(McKenna and Bell, 1997; Qiu and Wang, 2007; Uhlig, 1999).

The anterior dentition, as along with related characters, plays a more important role than the cheek teeth in studies of rhinocerotoid phylogenetic interrelationships(Prothero et al., 1989; Qiu and Wang, 1999; Radinsky, 1966). We propose that eggysodontines and forstercooperes are closely related mainly on the basis of the following characters: 1) large and erect canines that are considerably larger than the incisors; 2) a very short diastema between the canine and cheek teeth; and 3) a dorsoventrally deep and anteroposteriorly abbreviated symphysis associated with nearly vertically implanted incisors.

The large canine is a plesiomorphic character within Rhinocerotoidea, but the canine is even larger in the eggysodontines and the forstercooperes than in other non-amynodontid rhinocerotoids(Heissig, 1989). In hyracodontids the canine is comparable to the incisors in terms of its size and incisiform character, while the canine of rhinocerotids tends to atrophy(Qiu and Wang, 1999). The primitive paracerathere *Juxia* also has a relatively large canine, but the canine becomes reduced or absent in later forms(Qiu and Wang, 2007). De Bonis and Brunet (1995) pointed out that sexual dimorphism was present in *Eggysodon*, the females having smaller canines. A short diastema was probably a synapomorphic feature of forstercooperes and eggysodontines, since a long diastema is a plesiomorphic character of rhinocerotoids. The primitive rhinocerotoid *Hyrachyus*, for example, has a long diastema compared to the length of the cheek teeth. However, a few non-amynodontid rhinocerotoids, such as *Hyracodon*, *Triplopides*, and *Uintaceras*, have relatively short diastemae, though these taxa lack enlarged canines (Holbrook and Lucas, 1997; Radinsky, 1967a). The shortness of the diastema in these cases is probably a homoplastic character evolved in parallel with the forstercoopere-eggysodontine. The mandibles of both forstercooperes and eggysodontines have dorsoventrally deep, anteroposteriorly abbreviated symphyses and nearly vertically implanted incisors(de Bonis and Brunet, 1995; Qiu and Wang, 1999; Reshetov et al., 1993; Wood, 1963), while those of most of other non-amynodontid rhinocerotoids have symphyses with more horizontal ventral surfaces as well as more procumbent incisors. In addition, the ectolophs and metalophs of M3 come together at a slight angle in both eggysodontines and forstercooperes, whether or not the metacone is highly reduced (Reshetov et al., 1993; Uhlig, 1999; Wood, 1963). Furthermore, *Proeggysodon* and *Pappaceras confluens* display some similarities in the lower cheek teeth, including a non-molarized p3, inclined metalophids on the premolars, an mesiolingually directed protolophid on m2, and a protolophid on m3 that is more buccally directed than that on m2(Table 2) (Wood, 1963). These similarities also support a close relationship between forstercooperes and eggysodontines. However, *Pappaceras* is more primitive than *Proeggysodon* in having three pairs of conical lower incisors, more elongated lower cheek teeth (Fig. 3), and no entoconid or hypolophid on p4 (Wood, 1963).

As a result, we place forstercooperes and eggysodontines in the subfamily Eggysodontinae

(Breuning, 1923), which has chronological priority over Forstercooperiinae (Wood, 1963). However, phylogenetic relationships above the subfamily level are beyond the scope of this paper. It is likely that Eggysodontinae is the sister group of the subfamily Paraceratheriinae, and the two subfamilies are tentatively united by the presence of modified nasal and maxillary bones for the support of an elaborated muscular snout (Lucas and Sobus, 1989). However, the paucity of known skull material for eggysodontines prevents further comparison with the skulls of forstercooperes and paraceratheres, and resolving phylogenetic relationships within and outside Eggysodontinae will require new, more complete specimens.

The Eocene/Oligocene transition reflects an important global climatic change from a warm and humid Eocene to a cool and arid Oligocene (Meng and McKenna, 1998; Zachos et al., 2001). The Eocene/Oligocene faunal turnover in Europe is named the "Grande Coupure", and it is thought that European Eocene faunas were displaced by Oligocene immigrants either from Asia or from North America via Asia (Prothero, 1994). However, the "Mongolian Remodelling", referring to Mongolian faunal reorganization across the Eocene/Oligocene boundary, was probably derived by major climatic change (Meng and McKenna, 1998). The European earliest Oligocene rhinocerotoids, including *Epiaceratherium*, *Ronzotherium*, *Eggysodon*, and *Cadurcotherium*, are assumed to be originally from Asia (Becker, 2009). Both *Ronzotherium* and *Cadurcotherium* had pre-"Grande Coupure" representatives in Asia, having been reported from Late Eocene Ergilian deposits of Mongolia (Becker, 2009; Dashzeveg, 1991; Gromova, 1954; Wall, 1989). A few dental remains of *Epiaceratherium* have been recorded from the Early Oligocene of Pakistan (Antoine et al., 2003). By contrast, the rhinocerotoids were represented in the Eocene of Europe only by *Hyrachyus* and *Prohyracodon* (Radinsky, 1967b; Savage et al., 1966). *Hyrachyus* was considered to be close to the ancestor of all later rhinocerotoids (Qiu and Wang, 2007), and has a distant relationship with the European earliest Oligocene rhinocerotoids. The European *Prohyracodon* was reported from the Middle or Upper Eocene of Romania based only on scant material (Wood, 1929), and the relationship between *Prohyracodon* and eggysodontines is open to debate as discussed above. As a result, it is unlikely that European earliest Oligocene rhinocerotoids originated from the local Eocene faunas. The discovery of *Proeggysodon* in the upper Eocene deposits of Nei Mongol is a further indication that the European Oligocene form *Eggysodon* most likely had an Asian ancestry and accordingly represents a case that fits the hypothesis that the European "Grande Coupure" across the Eocene/Oligocene boundary resulted from immigration from Asia.

5　Stratigraphic distribution of eggysodontines in the Erlian Basin

Forstercooperia totadentata was unearthed from the Irdin Manha Formation, 37 km southeast of Iren Dabasu (Wood, 1938). The site is near the Irdin Manha locality, which lies 32 or 40 km south of Iren Dabasu (Berkey and Morris, 1927; Granger and Berkey, 1922; Meng et al., 2007). Recent field work in the Erlian Basin, Nei Mongol clarified some stratigraphic problems in the Huheboerhe (Camp Margetts) area, which was first explored by the CAE of the American Museum of Natural History in the 1920s (Meng et al., 2007; Wang et al., 2010). Based on detailed stratigraphic correlations, it is reasonable to show that the "Houldjin Formation" recognized in this area by the CAE is actually the Irdin Manha Formation, while the "Irdin Manha Formation" of the CAE is the Arshanto Formation (Meng et al., 2007; Sun et al., 2009; Wang et al., 2010). Consequently, the species *Pappaceras confluens* recorded from the "Irdin Manha Formation" in the Huheboerhe area should actually be from the Arshanto Formation, and should be Early Eocene or earliest Middle Eocene in age (Wang et al., 2010). Most specimens of *Forstercooperia minuta* were also recorded from the "Irdin Manha Formation" of the CAE in the Huheboerhe area (Lucas et al., 1981), but the layers containing *F. minuta*

should be assigned to the Arshanto Formation instead. The discovery of *Proeggysodon* from the Upper Eocene "Middle White" at Erden Obo, which is obviously younger than the Sharamurunian Asian Land Mammal Age(Qiu and Wang, 2007), somewhat narrows the gap between the Early to Middle Eocene forstercooperes and the Oligocene eggysodontines.

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