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Euricetodon (Rodentia, Mammalia) from the Late Oligocene of the Junggar basin, northern Xinjiang, China

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ABSTRACT

New specimens of *Euricetodon* are described from the Late Oligocene Tiersihabahe Formation of the Junggar basin, northern Xinjiang, China. The relatively abundant material documents the morphological variation within Asian species of the genus. The taxon, identified as *E. aff. E. caducus*, is similar to *E. caducus* from the Oligocene of Kazakhstan and China and *E. occasionalis* from the Early Miocene of Kazakhstan. It also shows noticeable resemblances to *E. longidens* from the Late Oligocene of Europe whose origin is currently in debate. The study confirms the strong morphological affinity between Asian and European species of *Euricetodon* and suggests that the evolutionary trends among paracricetodontines are probably more complex than previously assumed, especially with the new forms discovered from the last decade. A systematic revision of Eurasian paracricetodontines at species level is needed to understand their evolutionary history.

INTRODUCTION

The sedimentary record in the northern Junggar basin, Xinjiang, spans from the Late Cretaceous to Late Miocene (Tong et al., 1987; Wei and Tong, 1992; Ye et al., 2003a; Meng et al., 2008). Recent surveys and studies

of the Tiersihabahe section have revealed that the lower portion of the section, previously recognized as the Late Cretaceous Ulunguhe Formation, is in fact Late Oligocene in age (Ye et al., 2003a). In three seasons from 1998 to 2000, matrix sampled and screen-washed from various localities of the Tiersihabahe

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TABLE 1
Late Oligocene localities of the Junggar basin that yielded *Eucricetodon* material

Locality	Coordinates	Notes on the localization	Years of sampling
XJ 98024	46° 40.363' N–88° 28.325' E	Tietersihabahe section	1998–1999
XJ 99006	46° 40.428' N–88° 28.933' E	near Tietersihabahe section	1999–2000
XJ 20003	46° 35.818' N–87° 43.762' E	Saerduoyila	2000
XJ 200208	46° 40.381' N–88° 28.340' E	near Tietersihabahe section	2002
XJ 200209	46° 40.378' N–88° 28.341' E	near Tietersihabahe section	2002

section yielded new material of small mammals, among which the authors noticed presence of “*Eucricetodon* nov. sp.” (Ye et al., 2003a). Two Late Oligocene localities (XJ 20003 and XJ 20004) were also found in 2000 at Saerduoyila of Halamagai area (Ye et al., 2003b), and *Eucricetodon* was discovered from XJ 20003.

Meng et al. (2006) recognized four lithological units in the section. The lowest one is the Tietersihabahe Formation and contains two Late Oligocene biozones (T-I and T-II). “*Eucricetodon* nov. sp.” was in the “Tietersihabahe faunal assemblage Zone I” (T-I). The age calibration of this biozone, based on magnetostratigraphic correlations, spans from 24.4 to 24.15 Ma (Meng et al., 2006), about 1 Ma before the Oligocene-Miocene boundary (23.03 Ma) according to the recent calibration of the time scale by Gradstein et al. (2004).

Previously, few species of *Eucricetodon* were known in the Oligocene of China (Wang and Qiu, 2000; Wang and Meng 1986; Wang, 1987). The Tietersihabahe localities bear altogether 91 molars, 16 incisors, and two mandibles of *Eucricetodon*, a population that represents a significant advance in our knowledge of the genus in the Late Oligocene of Asia. We present here a detailed description for these specimens and quantify the morphological variation within the population.

Since Lindsay (1978) changed the generic identity of “*Eumys*” *asiaticus* Matthew and Granger, 1923, from the Middle Oligocene of Mongolia to *Eucricetodon asiaticus*, the genus has become critical in understanding the evolutionary history and phylogeny of paracricetodontines in Eurasia. Unfortunately, a systematic comparison between European and Asian *Eucricetodon* has been difficult because of the sparse record of Asian species, in

contrast to a relatively rich record of *Eucricetodon* from many European localities. With the newly discovered material from Xinjiang, the present study presents a comprehensive comparison of Asian forms with European paracricetodontines and tackles the question of the origin of Late Oligocene European *Eucricetodon* species.

MATERIAL AND METHODS

The material studied here comes from five localities (table 1) of the northern Junggar basin that are in the Tietersihabahe section (Tietersihabahe faunal assemblage Zone I; Meng et al., 2006) or its equivalent, based on stratigraphic correlations. The material was collected by screen washing from the localities XJ 98024, XJ 99006, XJ 20003, XJ 200208 and XJ 200209. All specimens are deposited in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) of Beijing, and all specimens are cataloged with the numbers: V15973.1–49 for locality XJ 98024; V15974.1–54 for locality XJ 99006; V15975.1–3 for locality XJ 20003; V15976.1–9 for locality XJ 200208; and V15977.1–17 for locality XJ 200209.

The following description covers the material from the five localities; however, the detailed counting of the morphologic features for specimens from each locality is given in the appendix 1. Tooth measurements for specimens from these localities have been presented separately in table 2, and the specific measurement for each specimen is available on request to the authors. The SEM photographs of teeth were taken from uncoated specimens using a Hitachi SEM at the American Museum of Natural History.

The terminology used to describe the molar (fig. 1) is modified from Huguene (1999) for

TABLE 2
Measurements of upper and lower molars of *Eucricetodon* aff. *E. caducus*.
Abbreviations: n = sample size; min = minimal value; max = maximal value; mean = mean value;
 σ = standard deviation; cv = coefficient of variation [= " σ " / "mean" \times 100].

	Length						Width					
	n	min	max	mean	σ	cv	n	min	max	mean	σ	cv
M1	14	1,85	– 2,25	2,02	$\pm 0,125$	6,204	15	1,28	– 1,53	1,38	$\pm 0,076$	5,497
M2	17	1,28	– 1,67	1,50	$\pm 0,091$	6,034	15	1,21	– 1,51	1,41	$\pm 0,076$	5,369
M3	12	1,14	– 1,37	1,23	$\pm 0,076$	6,133	11	1,11	– 1,28	1,22	$\pm 0,047$	3,822
m1	18	1,44	– 1,90	1,68	$\pm 0,125$	7,442	22	0,96	– 1,37	1,17	$\pm 0,098$	8,361
m2	21	1,09	– 1,72	1,56	$\pm 0,157$	10,063	20	1,07	– 1,39	1,29	$\pm 0,079$	6,120
m3	9	1,32	– 1,61	1,42	$\pm 0,094$	6,629	10	1,08	– 1,33	1,19	$\pm 0,077$	6,495

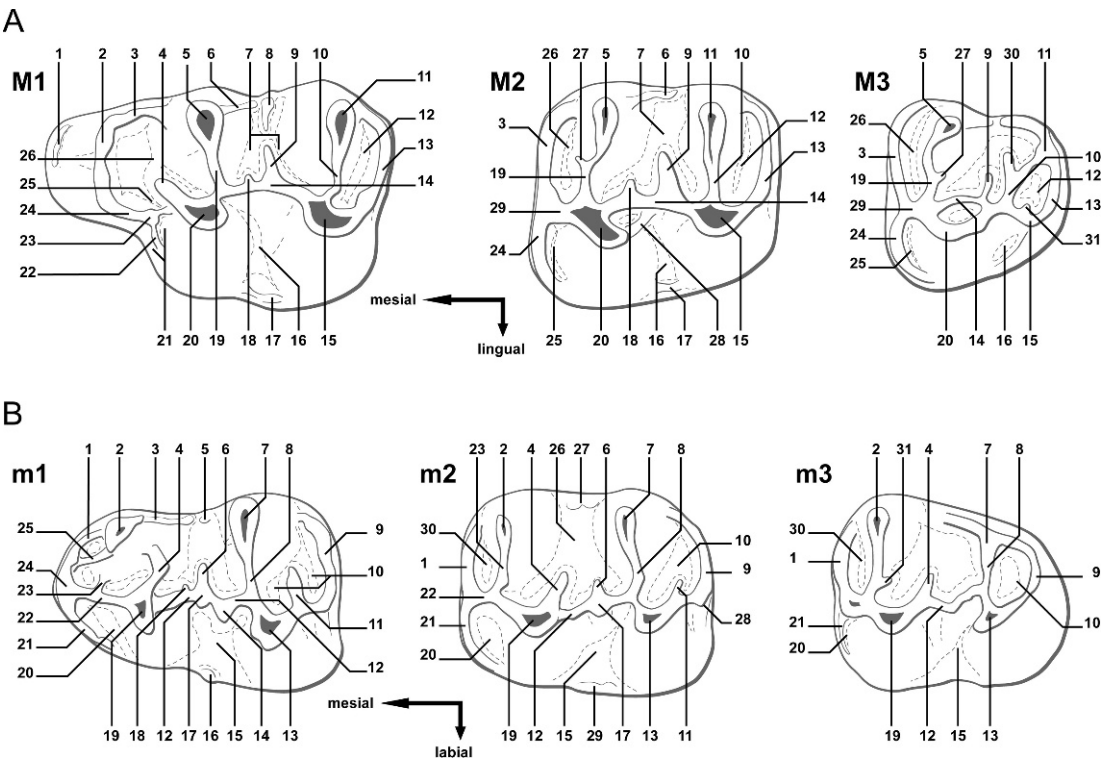


Fig. 1. Terminology used in this paper to described molars, modified from Hugueney (1999) for the first molars and from Freudenthal and Daams (1988) for third molars. (A) Upper molars, M1, M2 and M3: 1. anterior crest; 2. anterocone; 3. labial anteroloph; 4. protocone spur 5. paracone; 6. paracone spur; 7. mesosinus; 8. mesostyle; 9. mesoloph; 10. metalophule; 11. metacone; 12. posterosinus; 13. posteroloph; 14. entoloph; 15. hypocone; 16. sinus; 17. lingual cingulum; 18. 2nd mesoloph; 19. protolophule; 20. protocone; 21. protocone platform; 22. protostyle spur; 23. protostyle; 24. lingual anteroloph; 25. protosinus; 26. anterosinus; 27. protolophule spur; 28. entomesoloph; 29. anterolophule; 30. neomesoloph; 31. neometalophule; (B) Lower molars, m1, m2 and m3: 1. lingual anterolophid; 2. metaconid; 3. metaconid ridge; 4. protoconid hind arm; 5. mesostylid; 6. mesolophid; 7. entoconid; 8. hypolophulid; 9. posterolophid; 10. posterosinusid; 11. hypoconid hind arm; 12. ectolophid; 13. hypoconid; 14. ectomesolophid; 15. sinusoid; 16. ectostylid; 17. mesoconid; 18. 2nd mesolophid; 19. protoconid; 20. protosinusid; 21. labial anterolophid; 22. anterolophulid; 23. metalophulid; 24. anteroconid; 25. metaconid spur; 26. mesosinusid; 27. lingual cingulum; 28. labial posterolophid; 29. labial cingulum; 30. anterosinusid; 31. metalophulid spur.

the first molar and from Freudenthal and Daams (1988) for the third molar. In some publications, however, certain morphological features have been named differently. In the present work the following terms are considered to be equal: protocone spur = protolophule I; protolophule = protolophule II; metalophulid = metalophulid I; protoconid hind arm = metalophulid II.

In accordance with the instructions to authors of the journal, the classification used is the one proposed by McKenna and Bell (1997), in which the subfamily Paracricetodontinae includes not only the genus *Paracricetodon* but also the commonly named Eucricetodontinae (sensu Mein and Freudenthal, 1971).

SYSTEMATIC PALEONTOLOGY

MURIDAE ILLIGER, 1811

PARACRICETODONTINAE MEIN AND FREUDENTHAL, 1971

Eucricetodon Thaler, 1966

Eucricetodon aff. *E. caducus* (Shevyreva, 1967)

Figures 2–4

Eucricetodon, nov. sp., Ye et al. 2003.
Eucricetodon, nov. sp., Meng et al. 2006.

LOCALITIES: XJ 98024, XJ 99006, XJ 20003, XJ 200208, and XJ 200209, northern Junggar basin, Xinjiang, China (see table 1).

HORIZON: Tieersihabahe Formation, Tieersihabahe assemblage Zone I, Late Oligocene.

DESCRIPTION

DENTITION

INCISORS: Two longitudinal, parallel ridges or raised lines are present along the lateral half of the buccal surface of the incisor. In a few incisors, another longitudinal ridge exists along the medial half of the tooth. Faint lines oblique to the longitudinal ridges are present on the lateral face of some teeth (figs. 2P, Q, 4A). Some lower incisors also possess clear undulations of the enamel on the middle of the

anterior face. On upper incisors, the enamel is smoother and there are two longitudinal ridges on the lateral half of the tooth surface and one or two parallel ridges on the medial half. None of the upper incisors possess oblique lines as observed on lower incisors.

UPPER MOLARS: M1 is asymmetric with a narrow anterocone located labial to the longitudinal axis of the tooth. The anterocone widens slightly posteriorly, and in some teeth a constriction is at the anterolingual base of the anterocone. The anterocone is either single or slightly bilobed. A weak cingulum departs from behind the labial side of the anterocone; sometimes undulation can be observed on this cingulum, showing an additional weakly developed style. On the lingual side of the anterocone, the anteroloph is long, reaching the protocone on its lower part. The loph often swells at its posterior extremity to form a small protostyle and in some cases develops a spur that extends toward, or even reaching, the protocone. Anterior to the anterocone, a fine anterior crest exists on some teeth.

The protocone is slightly oblique, extending posterolingually. The protocone spur (protolophule I) is well developed and ends in the anterosinus, close to but never merging with the paracone. The protolophule (protolophule II) joins the paracone on its posterior side. The entoloph is thin and there is no sign of the mesocone. The mesoloph varies in its length, from short to long, and in some cases it is interrupted. The long mesoloph reaches the labial border to merge with the mesostyle. A weak ridge, here termed as the second mesoloph, is occasionally developed anterior to the mesoloph. The entomesoloph is absent, but on the lingual border of the tooth the lingual cingulum is developed and often bears an entostyle. On the labial side, the paracone spur is present on some teeth; when long enough this spur merges with the labial cingulum that is usually dominated by a mesostyle. Unlike the protocone, the hypocone is not obliquely extended. The metalophule joins the hypocone on its anterior part or sometimes in its middle part. The posteroloph is thin and long, reaching the metacone on the posterolabial side to delimit a large posterosinus, and often bears bulges at its extremity.

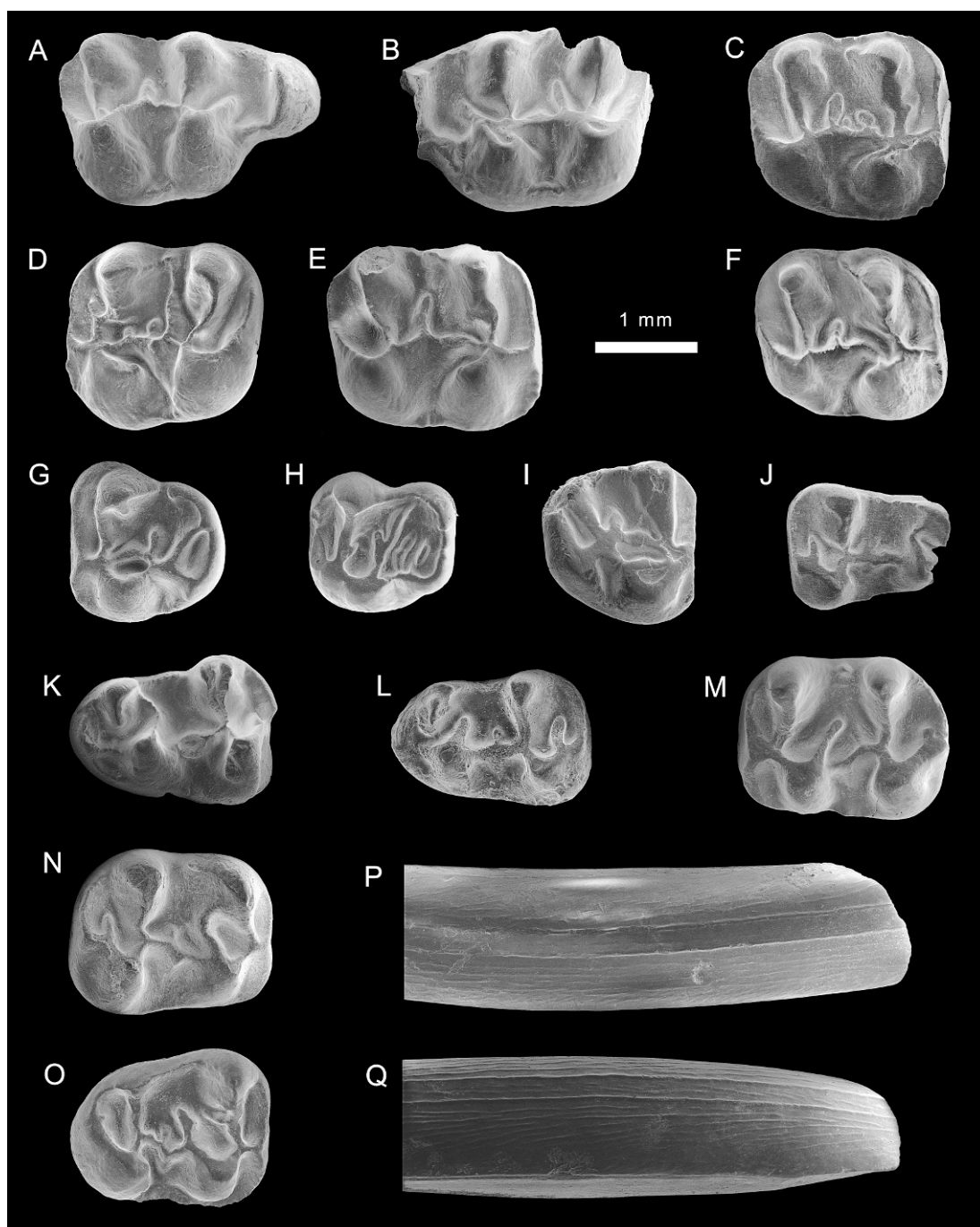


Fig. 2. *Eucricetodon* aff. *E. caducus* from the late Oligocene of the Junggar basin, locality XJ 98024. **A–I.** upper molars (V159873.1–9). **J–O.** lower molars (V159873.10–15). **P–Q.** lower incisors (V159873.16–17).

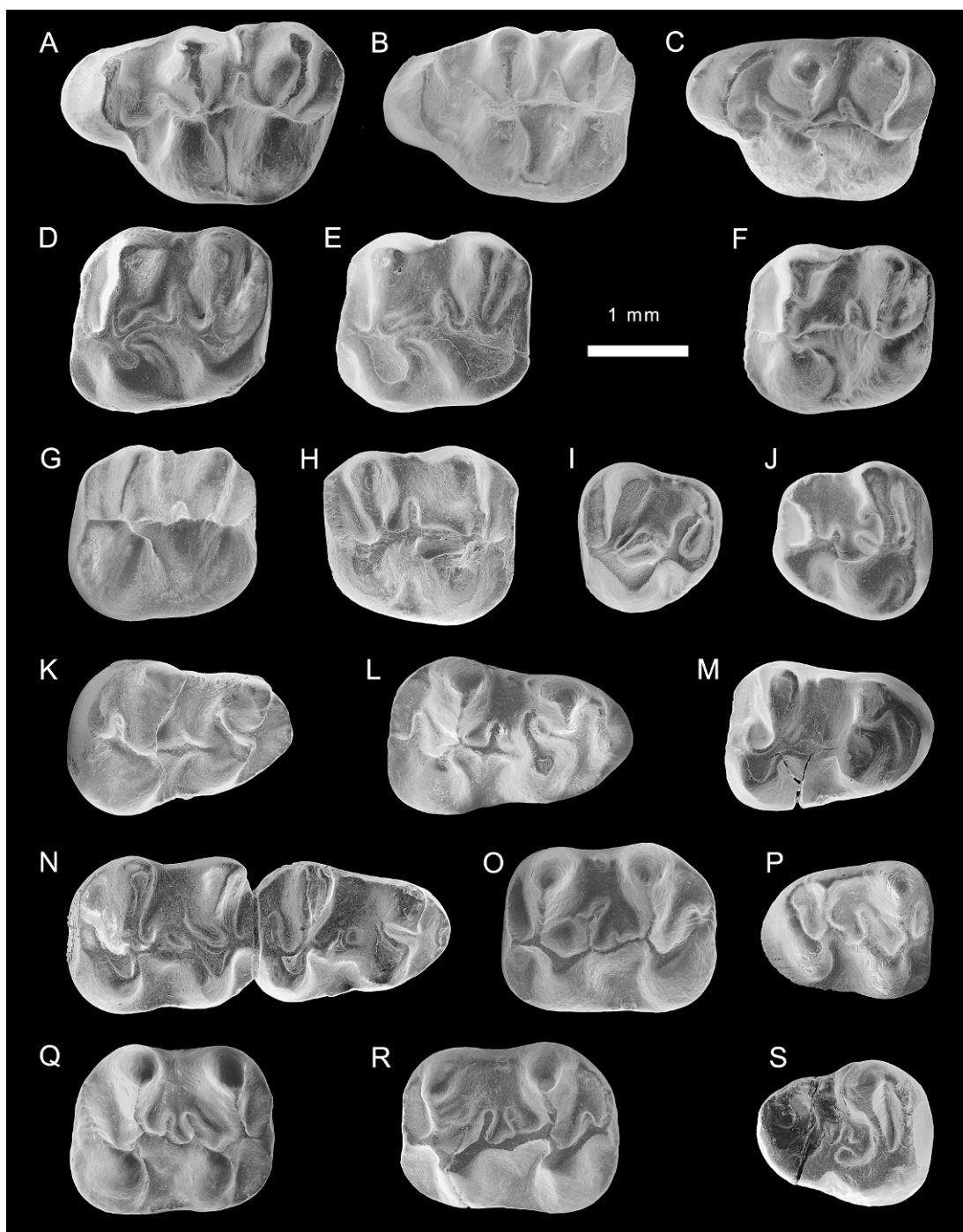


Fig. 3. *Eucricetodon* aff. *E. caducus* from the late Oligocene of the Junggar basin, locality XJ 99006. A–J, upper molars (V15974.1–10). K–S, lower molars (V15974.11–19).

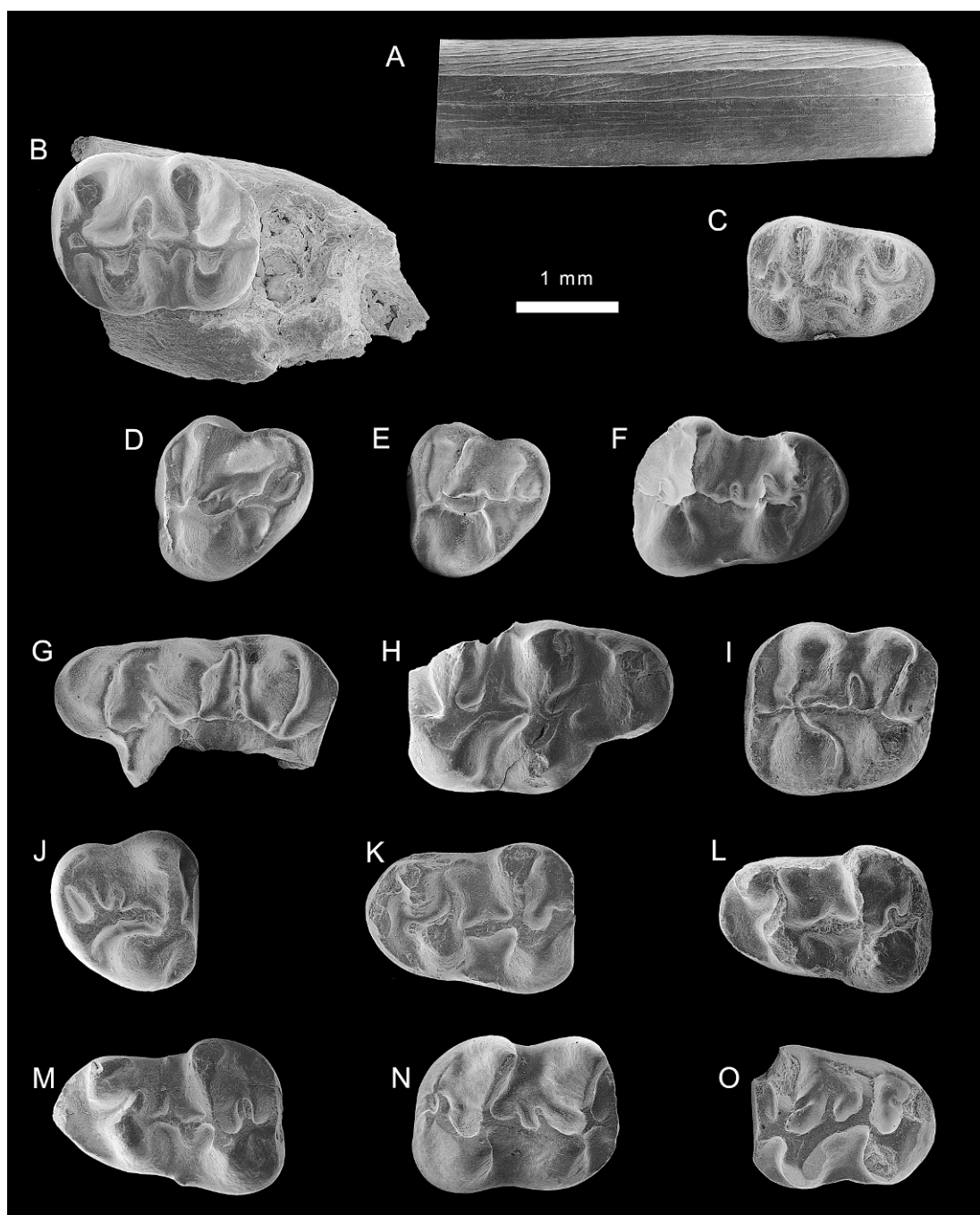


Fig. 4. *Eucricetodon* aff. *E. caducus* from the late Oligocene of the Junggar basin. A–C. lower incisor and molars from XJ 20003 (V15975.1–3). D–F. molars from XJ 200208 (V15976.1–3). G–O. molars from XJ 200209 (V15977.1–9).

M2 is subrectangular, slightly wider anteriorly than posteriorly. Its anterior border is usually straight whereas the posterior one is more rounded. The labial anteroloph is well developed, usually reaching the paracone and with its labial tip bulged in some cases. The lingual anteroloph is more variable, from absent to well developed. The protolophule (protolophule I) joins the anterior part of the protocone and often arches anteriorly. Some teeth bear a protolophule spur that extends from the protolophule into the anterosinus (fig. 2D). As in M1, the paracone spur is often present and merges with the labial cingulum. The labial and lingual cingulums are not so well developed compared to M1, and the mesostyle and entostyle are rarely present. The protocone is oblique, more so than in M1, and even oriented posteriorly in some cases, so that a narrow sinus between the protocone and the entoloph is delimited. On one M2 (fig. 3H) a low entomesoloph connects the posterior part of the protocone to the middle of the entoloph and isolates the narrow sinus from the lingual sinus that reminds one of what is usually observed in the genus *Trakymys* Ünay, 1989, from the Middle Oligocene of Turkey. A mesoloph is always present and sometimes a second or even a third weak mesoloph is present at the anterior part of the entoloph (fig. 2C, D). When multiple mesolophs occur, it is not easy to identify their homologies. The mesocone is not recognizable. The second protolophule does not exist in any of the specimens. The metalophule usually joins the hypocone at its anterior side, rarely at its middle part. The thin posteroloph is long, delimiting a large posterosinus as in M1.

M3 is trapezoidal and the smallest molar. Its anterior portion is similar to that of M2. The protolophule spur projects either anteriorly or posteriorly. The posterior half of the tooth is reduced, so that the hypocone is smaller than the paracone or the protocone, and the metacone is even smaller. The middle part of the tooth shows a high degree of variation. The entoloph usually joins both the protoloph and the posterior arm of the protocone, so it encloses a small pit. The mesoloph extends either from the entoloph or from the protocone if the entoloph is absent.

A neomesoloph branches from the metalophule and extends into the mesosinus, whereas the metalophule varies from being incomplete, long, or divided. In rare cases a neometalophule extends into the posterosinus.

LOWER MOLARS: The m1 is anteroposteriorly elongate. The anteroconid is distinct but smaller than any of the main cuspids. The lingual anterolophid is long, sometimes with a strong bulge; the labial anterolophid may be long or short. The metaconid sometimes has a metaconid ridge, which may join the lingual cingulum; the labial cingulum is usually weakly developed or even absent, with no clear mesostylid. The protoconid and the metaconid are usually linked by the protoconid hind arm (metalophulid II). In most teeth the protoconid possesses a front arm, usually not long enough to be called an anterolophulid. However, one tooth has a metalophulid (metalophulid I) connecting the metaconid to the anterolophulid (V15974.20), and another bears a metaconid spur connecting to the lingual anterolophid (V15974.21). The ectolophid is low, usually connected to the protoconid at its base. The ectolophid is straight and longitudinally oriented, sometimes slightly inclined. The mesolophid is weak or absent, but in a few cases it is long. A second and smaller mesolophid exists in some rare cases. The labial side of the ectolophid often shows a bulge or an ectomesolophid (figs. 4L, M, 3L, 2K, L). The mesoconid is occasionally present. The long posterolophid delimits a large posterosinus. A hypoconid hind arm develops in most teeth and merges with either the entoconid or posterolophid; some teeth also show a small labial posterolophid.

The m2 is somewhat rounded and rectangular in occlusal view. Both anterolophids are well developed, but the labial one is usually shorter and lower. The metalophulid is connected in front of the protoconid (metalophulid I) to the anterolophulid. The protoconid hind arm is long, often bending anteriorly to meet the metaconid. In some cases, the arm can also be divided (fig. 3O). The mesolophid varies from short to long and in some teeth merges with the protoconid hind arm (metalophulid II) in the middle of the mesosinus. The labial side of the ectolophid in some teeth shows a bulge that can be interpreted as a

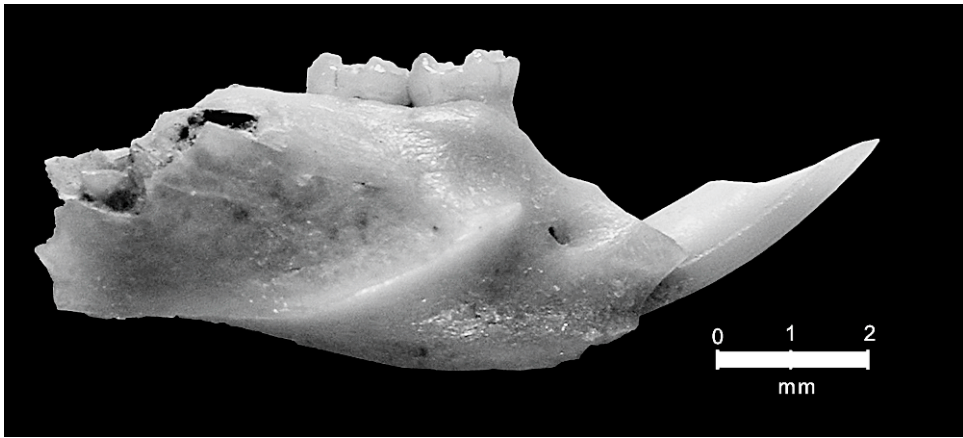


Fig. 5. Mandible of *Eucricetodon* aff. *E. caducus*, labial view, from the late Oligocene of the Junggar basin, locality XJ 99006 (V15974.14).

weak mesoconid, and only a few teeth have a clear mesoconid. The ectostylid rarely exists. The hypoconid slightly extends anterolabially. The hypolophulid is connected to the ectolophid, anterior to the hypoconid. The posterolophid is long, delimiting a broad posterosinusid, but does not always reach the posterolingual side of the entoconid. Some teeth have a hypoconid hind arm or a bulge at the proximal end of the posterolophid.

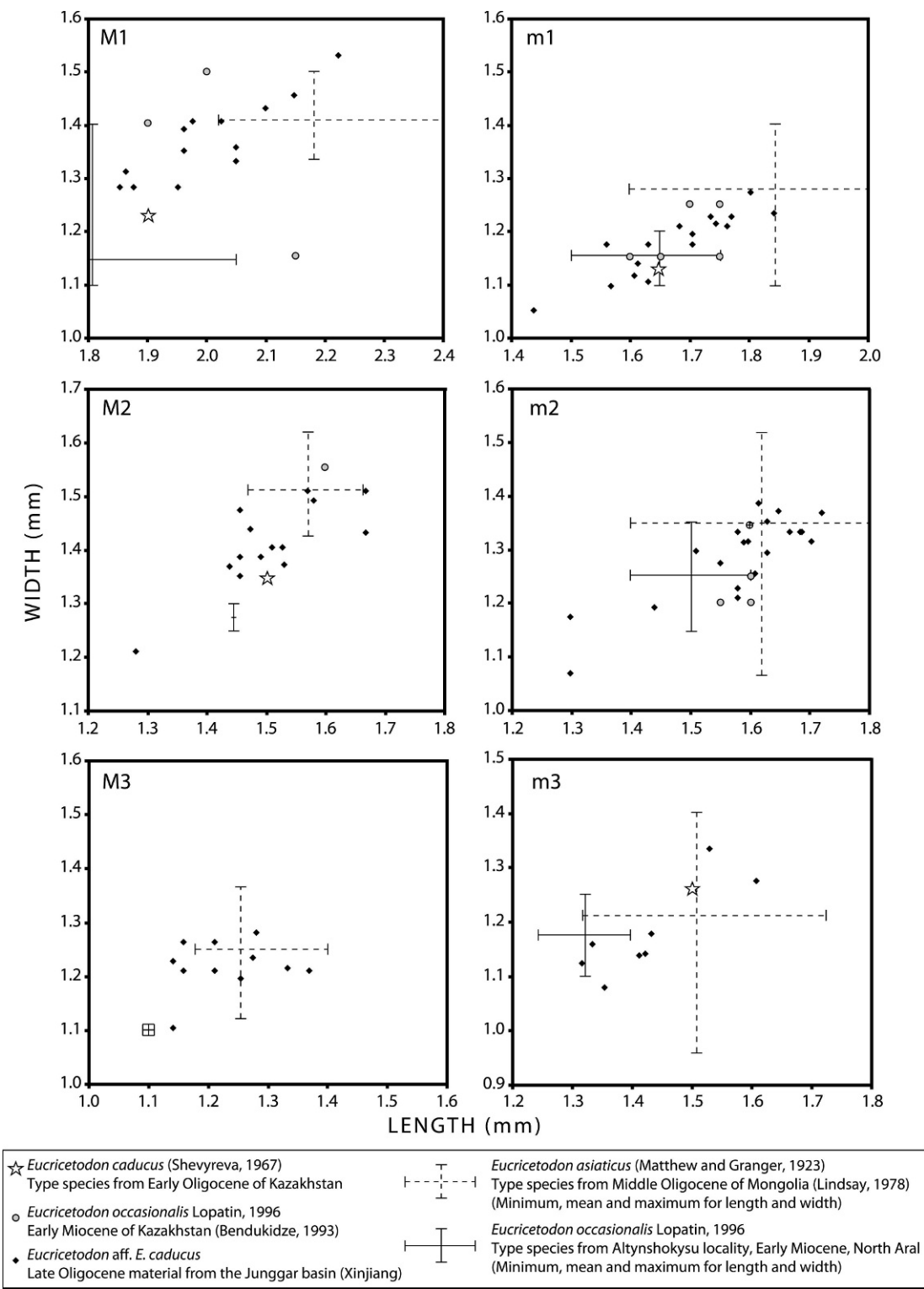
The m3 differs from m1 and m2 in having its posterior half narrower and rounded, with the entoconid reduced. The anterolophids are present, but the labial one is usually smaller. The metalophulid bends anteriorly and joins either the anterolophulid or further anteriorly at the anterolophulid-antrolophid junction. Three teeth have a short posterior metalophulid spur (figs. 2O, 3J, 4O). The protoconid hind arm is short or long; it joins the metaconid or ends in the mesosinusid. The ectolophid is straight or has a sharp bend. The mesolophid is not developed.

DENTARY: Two fragmentary mandibles were collected and the better-preserved one is illustrated (fig. 5). The mandible is slender. Based on what has been preserved, the diastema is shallow and strongly curved. The ascending coronoid ramus starts at a position lateral to m3. The masseter crests are V-shaped; the dorsal crest is weak whereas the ventral one is strong. The dorsal masseter crest joins the ventral one below the middle of the

m1 and the ventral one extends further anteriorly below the anterior edge of m1. The mental foramen is low and large.

SIZE OF TEETH (FIG. 6): Small-sized teeth as in other Paracricetodontinae; on the upper tooththrow M1 and M2 are about the same width whereas M3 is noticeably smaller; on the lower tooththrow no clear differences can be observed between the width of m1, m2 and m3.

The measurements of teeth, the standard deviation and the coefficient of variation are given in table 2. The size is compared in figure 6 with the type species *E. caducus* (Shevyreva, 1967) from the Early Oligocene of Kazakhstan, *Eucricetodon asiaticus* (Matthew and Granger, 1923) from the Middle Oligocene of Mongolia (Lindsay, 1978), and *E. occasionalis* Lopatin, 1996, from two Early Miocene localities of Kazakhstan (Lopatin, 1996; Bendukidze, 1993). The specimens initially described by Bendukidze (1993) as “*E. aff. caducus*” have been put in synonymy with *E. occasionalis* when Lopatin (1996) defined this new species. However, it is noteworthy that specimens of *E. occasionalis* from Altynshokisu (Kazakhstan) are smaller in some cases than the one described by Bendukidze (1993). It is also important to notice that Shevyreva (1967) provided the length but not the width of teeth for *E. caducus*; the width used in the present work for comparison was estimated based on the original figurations of the material.



The observation of size variation shows some irregularities; indeed, based on graphic reading, measurements seem discontinuous (for M2, M3, m1, and m2) due to some smaller teeth found in the five localities. The coefficient of variation is actually high for the width of m1 and the length of m2 (table 2).

The smaller teeth are close to the size of *Pseudocricetodon nawabi* Marivaux et al., 1999, from the Early Oligocene of Pakistan, but the presence of a hypoconid hind arm in m1 (figs. 2J, 4C) excludes it as *Pseudocricetodon*. These small teeth display no morphological peculiarities to date that indicate that they might belong to a species different from the rest of the specimens. Furthermore, the number of teeth does not show a significant difference between these small teeth and the rest of the assemblage. Therefore, in this study all material have been grouped under a single species, but the presence of a second one cannot be excluded. Measurements for teeth from each locality are available on request.

COMPARISON WITH ASIAN *EUCRICETODON*

The described specimens are similar to those of *Eucricetodon asiaticus* (Matthew and Granger, 1923) in several aspects, such as the location of the anterocone, the protocone spur (protolophule I), which never merges with the paracone, and the M1 and M2 mesostyles, which sometimes join the posterior part of the paracone, and a long M3 with a well-developed posterior part, with reduced but distinct hypocone and metacone. In lower teeth we note on m1 an anteroconid that is often isolated from the protoconid (15/20) and a protoconid hind arm that usually joins the posterior side of the metaconid (21/24), and the m3 is elongated with a slightly narrow posterior part.

However, the Junggar specimens differ from *E. asiaticus* in having shorter first and third

molars (fig. 6); an anterocone in M1 that is either single or slightly bilobed (whereas it is always single in *E. asiaticus*); an always well-developed protocone spur (protolophule I); a second weakly developed mesoloph in some specimens; a thin and long posteroloph in M1 and M2 (whereas it is weakly developed in *E. asiaticus*); and a single protoloph connecting the paracone and protocone (whereas the connection is double in *E. asiaticus*). For the lower molars the differences are mainly the rareness of the ectomesolophid and the presence of a small labial posterolophid in some teeth (whereas it is absent in *E. asiaticus*).

The molar morphology and size of *E. caducus* from the Early Oligocene of Kazakhstan (Shevyreva, 1967) are within the variation of the Junggar material (fig. 6), but the incisor was unavailable to Shevyreva. Wang (1987) proposed an emended diagnosis of *E. caducus* based on Early Oligocene material from Inner Mongolia, including three m2s and one incisor. These m2s are similar to the Junggar specimens, but the incisor has three parallel longitudinal lines on its buccal surface, but no ornamentation on the lateral face.

Unlike *E. caducus* and *E. asiaticus*, other Early Oligocene Asian species, such as *E. deploratus* from Kazakhstan (Shevyreva, 1967) and *Atavocricetodon paaliense* from Pakistan (Marivaux et al., 1999), show more differences from the Junggar specimens. *E. deploratus* came from the same locality as *E. caducus*; it differs from the Junggar material and specimens of *E. caducus* in having more massive tooth cusps, and an entoloph more lingually located, so that the lingual cusps are more reduced than the labial ones. In M1 the anterocone is also wider but shorter and in M2 the lingual anteroloph is weakly developed. *A. paaliense* from the Early Oligocene of Pakistan has a more lophodont tooth pattern, with a larger anterocone in M1, a transverse sinus, no

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Fig. 6. Measurements of the molars of *Eucricetodon* aff. *E. caducus* from all the localities, XJ 98024, XJ 99006, XJ 20003, XJ 200208, and XJ 200209. The measurements are compared with the type material of *Eucricetodon caducus* Shevyreva, 1967; the type material of *Eucricetodon asiaticus* from Lindsay, 1978; the type material of *Eucricetodon occasionalis* Lopatin, 1996; and *Eucricetodon occasionalis* from Bendukidze, 1993.

inclination of the protocone on M1 and M2 and no hypoconid hind arm on m1 and m2.

In addition to the Oligocene species, a few Early Miocene species of *Eucricetodon* have been described in Asia. *Eucricetodon youngi* from Qinghai, China (Li and Qiu, 1980), is clearly different from the Junggar specimens in having a short posteroloph, a nearly absent posterosinus, and a nearly transverse sinus. Also, in M1 and M2 the protocone shows no inclination and no protocone spur, the protolophule connects to the posterior side of the protocone and the metalophule connects to the posterior side of the hypocone. These characteristics are usually recognized as the most derived in the evolution of the latest *Eucricetodon*.

Two species have also been recognized from the Early Miocene of Kazakhstan (Agypse) by Bendukidze (1993), *E. sajakensis* Bendukidze, 1993, and *E. aff. caducus* (Shevyreva, 1967). The latter has been recently included in the new species *E. occasionalis* (Lopatin, 1996, 2004). *E. occasionalis* shows noticeable differences from the Junggar specimens; indeed, based on the description and size provided by Lopatin (1996, 2004) the size is slightly smaller; in upper molars no constriction can be observed at the anterolingual base of the anterocone; the posterosinus is narrower; and the mesostyles are less developed. In m1 the anterolophulid is more frequent and the hypoconid hind arm is less frequent, and in m1 and m2 the mesoconids are more developed. Unfortunately, the incisors of this species remain unknown.

According to Bendukidze (1993), *E. sajakensis* was differentiated from *E. caducus* by its robust cusps of upper teeth and its relatively longer mesoloph. However, because these features display a noticeable variation in the Junggar specimens, they may not be sufficient to differentiate the two species. In our view, *E. sajakensis* may prove to be a synonym of *E. caducus*.

Based on the similarities in morphology and size, the differences in incisors, and the lack of information about variation of *E. caducus*, we regard the Junggar material as *Eucricetodon* aff. *E. caducus*. This material also displays some similarities with *E. occasionalis* and could be interpreted as intermediate between

E. caducus and *E. occasionalis*. As discussed later, this determination is made without examination of the potential phylogenetic affinity of this taxon relative to *E. caducus*.

COMPARISON WITH EUROPEAN *EUCRICETODON*

The similarity of the Junggar material with *E. asiaticus* (Matthew and Granger, 1923) makes it necessary to compare it with the European *Atavocricetodon*, because Lindsay (1978) compared *E. asiaticus* with *Atavocricetodon atavus* (Misonne, 1957), which was initially described from the Early Oligocene of Belgium. *Atavocricetodon* includes several species: *A. atavus* (Misonne, 1957), *A. atavoides*, *A. hugueneyae*, *A. nanus*, and *A. minusculus* (Freudenthal, 1996), all known from the Early Oligocene of Europe. Indeed, the outline of the teeth is similar and many morphological resemblances can be observed, such as the position of the anterocone, the posterior connection of the protolophule, the forward connection of the metalophule, the well-developed protocone anterior spur (protolophule I) in M1, the oblique shape of the protocone in M1 and M2, the frequent hypoconid hind arm in m1 and m2, and the elongated shape and often long protoconid hind arm in m3. However some differences exist in *Atavocricetodon*, including the presence of the anterocone posterior spur in M1, the frequent complete presence of the second protolophule in M2, the usually complete anterolophulid, and the well-developed metalophulid, and the absence of lateral ornamentation in the lower incisor.

The differences from other European Oligocene species are also obvious. In the Early and Middle Oligocene, *E. collatus* (Schaub, 1925) shows a well-developed anterocone usually separated from the paracone and protocone by a large anterosinus and the protocone is reduced compared to the other cusps; on lower teeth the lophids are not transverse due to a more forward location of the metaconid and entoconid. The species *E. huerzeleri* Vianey-Liaud, 1972, is noticeably larger in size, the anterocone in M1 is clearly divided, and the M3s are shorter with a more rounded outline.

In the Late Oligocene and Early Miocene (for a review see Hugueney, 1999), *E. hochheimensis*

(Schaub, 1925) and *E. haslachensis* (Schaub, 1925) show a different pattern with more elongated cusps and long undulated lophs; moreover, posterior parts of the third molars are more developed. *E. infralactorensis* (Viret, 1929) differs in having a backward metalophule connection in M1 and posterior protolophule and metalophule connection in M2, as well as a very oblique entoloph. *E. hesperius* Engesser, 1985, is different in having transverse protolophule and metalophule in M2, as well as a weak protoconid hind arm and the absence of hypoconid hind arm and mesolophid in m1. *E. gerandianus* (Schaub, 1925) shows a more reduced and narrow anterocone, a metalophule oriented backward in M1, and a weakly developed protoconid hind arm in m2 and m3. *E. aquitanicus* Baudelot and de Bonis, 1968, is clearly different in its M1, with an anterolophule joining the protocone directly to the anterocone, both protolophule and metalophule connected backward in M2, and the hypoconid of lower molars without any posterior arm.

However, some European species display noticeable resemblances with our specimens from the Junggar basin. As noticed by Engesser (1985) *E. longidens* Huguency, 1969, shows a rather “primitive” pattern compared to the other Late Oligocene–Early Miocene European species. It is worth noting that some of those morphological features can also be observed in *E. aff. E. caducus* from the Junggar basin, such as the frequent hind arm on the hypoconid of lower molars, the long mesolophs on upper molars, and the forward connection of metalophule in M1. The ornamentation described on incisors is also similar to the one described from Junggar, especially on the lateral face. The mandible from Coderet figured by Huguency (1999) is also similar, with an ascending coronoid ramus starting at the posterior part of the m3, a ventral masseter ridge noticeably stronger and longer than the dorsal one, and the anterior end of the masseter crests ending behind and slightly above the mental foramen. The mental foramen is located in the middle of the diastema. However, the position of the foramen is located slightly more anterior in *E. longidens*. Some slight differences can also be noticed on teeth in *E. longidens*, such as a

more transverse connection of metalophule on M1 and M2, a slightly more developed hypocone on M3, and a protoconid hind arm reaching metaconid in m1 that is less frequently long. Also in *E. longidens* the m3 is almost as long as the m1, whereas it is shorter in the specimens from the Junggar basin. Although *E. longidens* is among the smallest Late Oligocene European species, it is still noticeably larger than *E. aff. E. caducus*.

E. dubius from Gaimersheim (Kristkoiz, 1992), *E. longidens* from Coderet (Huguency, 1999), and our specimens from Junggar display noticeable similarities based on the morphology of their mandibles. Also, by comparing with *E. dubius* from Cournon–Les Soumérois (Brunet et al., 1981) we can observe that the general morphology of teeth is similar, and the size is very close to the specimens from Junggar. However, *E. dubius* differs from our specimens in having a frequent mesocone and a mesoloph more posteriorly located in M1. In lower molars the anteroconid is very weakly developed in almost half of the specimens (Dienemann, 1987: pl. 3, fig.1), the ectomesolophid is more frequent than in our specimens, and the hypolophulid and metalophid are more transverse and often interrupted (whereas they are never interrupted in Junggar specimens). The incisor of *E. dubius* shows three longitudinal ridges on the buccal surface but no ornamentation on the lateral face.

The species *E. thezelensis* Comte, 2000, from the Late Oligocene of France (level of Coderet) also presents a lot of resemblances with *E. longidens* and *E. aff. E. caducus*, notably the previously indicated features. Based on features and measurements of the molars, in particular the frequency of the hypoconid hind arm and the rare anterolophulid in m1, and the frequency with which the mesoloph reaches the labial border in M1, the morphology seems even closer to *E. aff. E. caducus*. But still some differences remain (even if those differences are rarely present in *E. thezelensis*), such as the double connection between the paracone and the protocone in M1 and M2 and the lingual anteroloph joining the protocone in M1. The ornamentation of the lower incisor is also very similar to the one of *E. aff. E. caducus*, except that no lines have

been observed on the lateral face by Comte (2000).

The above comparisons confirm the stronger affinity of Asian species with the Oligocene European species as already noted by Lindsay (1978) based on the comparison between Asian and European *Eucricetodon* Thaler, 1966, and the American genus *Eumys* Matthew and Granger, 1923. It is finally noteworthy that *E. longidens*, *E. dubius*, and *E. thezelensis* are the three Late Oligocene European species that show the greatest morphological similarities with the material described in this study, with an especially strong similarity for *E. longidens* in terms of the ornamentation of lower incisors.

ORNAMENTATION OF LOWER INCISORS

In *E. aff. E. caducus* from the Junggar basin, the enamel surface of the lower incisor shows a complicated pattern with longitudinal ridges on both lateral and medial sides of the anterior face, but also oblique lines on both the anterior face and the lateral face. As a matter of fact, the incisors are rarely described for the *Eucricetodon* species and our knowledge about their ornamentation and its variability is poor. However, some authors have provided a description or an illustration of this ornamentation.

Dieneman (1987: 113), Comte (1985: 34, 2000: 104), and Lindsay (1978: 592) provided illustrations of the ornamentation on lower incisors for several species. Based on these illustrations, certain species, like *E. dubius*, *E. gerandianus*, and *E. asiaticus*, show a simple ornamentation with only two or three longitudinal ridges on the lateral side of the anterior face. Unlike other species, *E. incertus*, *E. thezelensis*, *E. huerzeleri*, *E. collatus*, and *A. atavus* show a more complex ornamentation with more ridges and a mixture of both longitudinal and oblique lines on the anterior face. None of these ornamentations is similar to that described in the present study.

Wang (1987) also noticed that the incisor of *E. caducus* from the Early Oligocene of Inner Mongolia is similar to *E. asiaticus*. The specimens observed have two or three longitudinal ridges on the anterior face, but one specimen

also shows no longitudinal lines emphasizing that these features may undergo a strong variability, as also noticed by Hugueney (1999).

Hugueney (1999) also provided some descriptions of lower incisors for *E. hesperius*, *E. gerandianus*, and *E. longidens*. The species *E. hesperius* and *E. gerandianus* both present a simple ornamentation with two ridges on lateral side of the anterior face, similar to what was illustrated by Dieneman (1987) for *E. dubius* and *E. gerandianus* from Germany. Unlike these species, *E. longidens* presents a more complex ornamentation with ridges on both the lateral and internal sides of the anterior face (Hugueney, 1969). Moreover, the incisors of *E. longidens* show a faint oblique ornamentation on the lateral face that so far is unique among the European species, but has been described on the present specimens from the Junggar basin.

Consequently, the comparison of incisor ornamentation seems to confirm the morphological affinities of *E. aff. E. caducus* with *E. longidens* already observed on the molars and the mandibles. However, the diagnostic meaning of the ornamentation is not certain. Comte (1985) compared the ornamentation of lower incisors between different species of *Eucricetodon* (including the species "*A. atavus*") and *Pseudocricetodon* indicating its obvious diagnostic meaning at the genus rank. But to date, too little is known about the ornamentation of incisors and its variability to be sure of its diagnostic meaning at species rank or its evolution. At the very least, these initial observations suggest that particular attention should be paid to these features because they may provide reliable information for clarifying the phyletic relationships among paracricetodontines.

DISCUSSION

GEOGRAPHICAL AND TEMPORAL DISTRIBUTION OF *E. CADUCUS*

The first occurrence of the species *E. caducus* is known from two localities of the earliest Oligocene in Asia: biozones A and B (MP 21–24) in Hsanda Gol Formation in the lakes valley of central Mongolia (Daxner-Höck and Badamgarav, 2007) and the upper part of the Keziletuogayi Formation (locality

XJ200203) of Burqin, Xinjiang, China, which is considered to be equivalent to biozone A of Hsanda Gol Formation (Wu et al., 2004; Ye et al., 2005). In both localities *E. caducus* coexists with *E. asiaticus*. The type locality of *E. caducus* in Kazakhstan is Early Oligocene in age (Shevyreva, 1967).

The specimens from the Late Oligocene of Junggar are regarded as *E. aff. E. caducus* because of their similarity with the type species in morphology and size, suggesting that both taxa are closely related. But due to the lack of intermediate faunas after *E. caducus* in Asia between the Early and the Late Oligocene, the phyletic relationship between *E. aff. E. caducus* and *E. caducus* cannot be further investigated. Indeed, the material of *Eucricetodon* known in China is often insufficient for a clear determination of taxon. Wang and Wang (1991) noticed the presence of *Eucricetodon* spp. in the Early Oligocene of Kekeamu in Inner Mongolia (Kekeamu, initially considered early Middle Oligocene, is now identified as Early Oligocene since the revision of the Eocene-Oligocene boundary [Wang, 1997]), where there were similarities between *E. caducus* and *E. asiaticus*. Wang and Qiu (2000) also described two m2s from *Eucricetodon* sp. from the Late Oligocene of Taben-buluk (Xianshuihe Formation in the Lanzhou basin, Gansu) that show similarities with both *A. atavus* and *E. caducus*.

Bendukidze (1993) described *E. aff. caducus* from the lower Miocene of Kazakhstan. Because Lopatin (2004) included this material in the species *E. occasionalis*, the species *E. caducus* is no longer recognized in the Early Miocene of Kazakhstan.

Concerning the chronological extension of the species, *E. caducus* s.s. is known only in the Early Oligocene of China, Mongolia, and Kazakhstan. The association of *E. caducus* with *E. asiaticus* would then seem restricted to the Early Oligocene of northeastern Asia. From the Early Oligocene to Early Miocene forms morphologically close to *E. caducus* have also been noticed, including the Junggar material, suggesting that *E. caducus* (currently known in China, Mongolia, and Kazakhstan) may have evolved in Asia. Unfortunately, the poor record of *Eucricetodon* in Asia provides little phylogenetic information for this hypoth-

esis. One interesting point to note is that all localities for *E. caducus* and its morphologically similar forms are currently known in an area north of 35° of latitude, indicating that the species probably had a geographical distribution restricted to middle and high latitudes in Asia. Similar geographical patterns are observed for other Chinese *Eucricetodon* species, *E. asiaticus*, and *E. youngi*. This restricted distribution for *E. caducus*, and more generally for *Eucricetodon*, contrasts with the fact that the only other paracricetodontine species, *Eocricetodon meridionalis* (Wang and Meng 1986) and *Oxynocricetodon leptaleos* (Wang and Meng 1986), are found in the Late Eocene of Yunnan at a much lower latitude and display a very different morphological pattern that led Wang (2007) to propose two new genera.

MOLAR EVOLUTIONARY TRENDS

As noticed by Freudenthal (1996) and Hugueney (1999) the general evolution of molar morphology in Eurasian paracricetodontines is clearly different depending on whether one focuses on the Oligocene or on the Miocene. With regard to this observation, the material described in our study is conservative in its morphology compared with the other Late Oligocene species and brings a new insight on these possibly evolutionary trends.

Indeed, some features, usually considered plesiomorphic in the evolutionary history of early paracricetodontines according to Wang (2007), have been observed in the above-described species: the M1 anterocone is not always a loph and can sometimes be a cusp; the m1 ectomesolophid is usually absent or very weakly developed; the m1 and m2 protoconid hind arm (metalophulid II) is usually long and connected to the posterior side of the metaconid. In addition, some other features that were considered apomorphic for some European *Eucricetodon* Miocene lineages (Hugueney, 1999) are observed in our material, such as the posterior connection on the metalophule in M1, the well-developed lingual anteroloph in M2, the rarely present ectomesolophid in m1, and the weakly developed entoconid in m3. Therefore, these

features may appear, or disappear, independently in Asian and European lineages.

Such an observation has implications on the taxonomy of paracricetodontines. For instance, some of the previously cited features have been used to define the genus *Atavocricetodon* based on their supposedly “primitive” nature (Freudenthal, 1996). Because these features have displayed considerable variability, they are not reliable in differentiating paracricetodontines at the genus level and may have no evolutionary or diagnostic significance. For the same reason de Bruijn et al. (2003) proposed that *Atavocricetodon* may be a “morpho-subgenus” containing the oldest forms of *Eucricetodon* known in the Early Oligocene of Europe and may not be considered a clade among paracricetodontines. Consequently, the validity of the genus is doubtful and naming our material under the genus *Atavocricetodon* has not been considered in this study.

More generally, it is noteworthy that the opposite trends usually observed between the Oligocene and the Miocene paracricetodontines have never been explained. One tentative explanation could be considered in the context of climatic changes. Based on marine benthic foraminiferan isotopic analyses, the long-term increase of $\delta^{18}\text{O}$ values from the earliest Oligocene onward reflects a global cooling associated with the expansion of Antarctic continental ice sheets that persisted through the Late Oligocene (Flower and Chisholm, 2006). From that point, apart from some short glaciation events (e.g., Naish et al., 2001), the decrease of $\delta^{18}\text{O}$ values at ca. 26.35 Ma (Flower and Chisholm, 2006) marks a transition toward globally warmer climates that persisted until the end of the Middle Miocene (see Flower and Kennen, 1994). Although the amplitude of the Late Oligocene warming is under debate (Pekar et al., 2006; Pekar and Christie-Blick, 2008), this transition of climatic conditions may be reflected by sedimentary and biotic changes in central Asia (Meng et al., 2006, 2008). The climatic transition could be linked to the morphological variations observed between the Oligocene and Early Miocene paracricetodontines. As opposed to the general trend observed among paracricetodontines, *E. aff. E. caducus* and *E. occasionalis*

display a rather conservative morphology. Being restricted to higher latitudes, they could have been less affected by the Late Oligocene warming event.

RELATIONSHIPS WITH LATE OLIGOCENE EUROPEAN SPECIES

The genus *Eucricetodon* seems much more diverse in Europe than in Asia. In the Oligocene of Europe 10 species of *Eucricetodon* are known (based on Dienemann, 1987; Comte, 1985, 2000; and Vianey-Liaud, 1972) and 10 species in the Early Miocene (Hugueney, 1999). In contrast, only three species of *Eucricetodon* exist in the Oligocene and Early Miocene of China: *E. caducus*, *E. asiaticus*, *E. youngi*. This is partly because some species previously named under *Eucricetodon* have been placed in other genera (Tong, 1992; Wang, 2007). Nonetheless, the identification of many lineages in Europe during the Oligocene and the Miocene suggests that the diversity there have mainly resulted from a local radiation since the Early Oligocene (Dienemann, 1987; Engesser, 1985; Vianey-Liaud, 1972; Comte, 1985). However, the origin of some Oligocene species still remains to be clarified (Comte, 1985). Among the Late Oligocene and Early Miocene European species, *E. longidens* actually shows a strong morphological affinity with *E. aff. E. caducus*. Because of its “primitive” morphology compared to other European Oligocene lineages, Engesser (1985) proposed that *E. longidens* could be an independent lineage that arrived in Europe during the latest Oligocene (Coderet-3: Hugueney, 1969). It is also noteworthy that *E. longidens* is known only from Swiss, German, and northern French localities (above 40° N latitude), indicating that, like *E. caducus* and closely related forms, this species was restricted to high-latitude areas. The same observations can be made for *E. thezelensis*, but this species is actually known from only one locality (Thézels, France).

These observations show that *E. longidens* and *E. thezelensis* could be related to *E. aff. E. caducus* from Xinjiang and *E. occasionalis* from Kazakhstan. As already noted regarding the restricted geographical distribution of

Eucrietodon in Asia, the paracricetodontine species from northern Asia seem to show more morphological affinities with their European relatives. A phylogenetic analysis of Eurasian paracricetodontines is needed to test this hypothesis. The phylogeny at the genus level proposed by Marivaux et al. (2004) already placed paracricetodontines among other early Tertiary rodents and confirmed that *Pappocricetodon*, *Atavocricetodon*, and *Pseudocricetodon* are closely related, but *Eucrietodon* was not included in that phylogenetic analysis. There are several new paracricetodontine genera from the early Tertiary of Asia described in the last decade (e.g., *Raricricetodon* Tong, 1997; *Palasiomys* Tong, 1997; *Oxynocricetodon* Wang, 2007; *Eocricetodon* Wang, 2007; *Ulaancricetodon* Daxner-Höck, 2000). A systematic revision and a phylogenetic study of paracricetodontines in Eurasia at species level (taking into account the intraspecific morphological variability) are now needed: (1) to clarify the evolutionary history of the group and identify the morphological features that have plesiomorphic or apomorphic meaning, (2) to confirm the validity of the existing genus, and (3) to better understand the relationships between European and Asian species.

CONCLUSIONS

Relatively abundant paracricetodontine material was found in the Late Oligocene localities of the Junggar basin. The specimens seem to pertain to one species that is ascribed to *E. aff. E. caducus*. The presence of a second, smaller one is possible, but more material is needed to confirm it. The description of *Eucrietodon aff. E. caducus* is interesting because it provides a view of the morphological variation within Asian *Eucrietodon*. Taking into account this variation, the comparison of this material with other Asian species indicates a resemblance with *E. caducus* from the Early Oligocene of Kazakhstan and China, and *Eucrietodon occasionalis* from the Early Miocene of Kazakhstan. Also, the comparison with the European material confirms the general affinity of the Asian Oligocene *Eucrietodon* with the European species of the genus as initially noticed by

Lindsay (1978). In particular, *Eucrietodon aff. E. caducus* is very similar to that of the Late Oligocene European *E. longidens*, whose origin was suspected to be outside Europe (Engesser, 1985). These new data provide the basis for a thorough phylogenetic analysis of Eurasian paracricetodontines that is critical to understanding both the relationship between the Asian and European species and the potential climatic impact on the morphological changes within the group.

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APPENDIX 1

Morphological variability of the Late Oligocene *Eucrietodon* aff. *E. caducus* from the Junggar Basin

	M1	I			II			III			IV			V			VI				
																					
	XJ 98024 (loc. 1)	6	2	1	3	-	-	-	3	1	1	2	2	2	3	1	1	1	6	-	-
	XJ 99006 (loc. 2)	12	5	5	7	1	2	-	4	4	4	4	6	-	8	2	1	-	9	-	1
	XJ 20003	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	XJ 200208	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	XJ 200209	2	1	1	-	-	1	1	1	-	1	-	1	1	2	-	-	-	1	1	-
	Total	20	8	7	10	1	3	1	8	5	5	5	6	9	13	3	2	1	16	1	1

	M2	I						II			III			IV			V					
																						
	XJ 98024 (loc. 1)	6	4	1	-	1	3	1	2	-	3	1	1	2	3	2	1	-	1	2	-	-
	XJ 99006 (loc. 2)	9	5	2	1	-	7	2	-	2	2	5	3	5	1	2	4	3	-	-	-	-
	XJ 20003	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	XJ 200208	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	XJ 200209	2	1	1	-	-	1	-	1	1	1	1	2	-	-	1	-	1	-	-	-	-
	Total	17	10	4	1	1	11	3	3	3	6	6	6	7	4	5	5	4	1	2	-	-

	M3	I			II			III			IV											
																						
	XJ 98024 (loc. 1)	6	2	2	4	2	4	-	2	-	-	-	-	4	-	1	-	1	-	-	-	-
	XJ 99006 (loc. 2)	5	-	3	2	4	1	2	-	1	1	1	1	1	2	-	-	1	-	1	-	-
	XJ 20003	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	XJ 200208	2	-	2	-	2	-	1	-	1	-	-	-	-	1	1	-	-	-	-	-	-
	XJ 200209	1	1	-	-	1	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-
	Total	14	3	7	4	11	3	7	1	4	1	1	1	8	1	1	1	1	1	1	1	1

The first column provides N, the total number of individuals observed for each locality. Some teeth from XJ 98024 and XJ 99006 are partially broken, so the total number of features observed may be lower than the total number of individuals. Variability is observed on the following morphological features: (M1) I. Division of the anterocone; II. anterior border crest to the anterocone; III. protostyle; IV. paracone spur; V. anterior mesoloph; VI. mesoloph and mesostyle. (M2) I. connection between protocone and entoloph; II. anterior spur on the protolophule; III. lingual anteroloph; IV. paracone spur; V. mesoloph. (M3) I. lingual anteroloph; II. posterior spur on protolophule; III. entoloph and protocone connections; IV. Mesoloph and metalophule.

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