6. A new species of the extinct shrew *Paenelimnoecus* from the Pliocene of Yinan, Shandong Province, northern China

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Abstract. A new species of a small allosoricine shrew from Late Pliocene cave deposits in Yinan County is described under the name *Paenelimnoecus chinensis*, and its systematic position is discussed. Detailed description of the species reveals morphological characters that distinguish it from the known species of *Paenelimnoecus*. Comparisons with the known species indicate close relationships between this new species and *P. pannonicus* from the Pliocene of Europe. Owing to lack of reliable Pliocene records in the literature, *P. chinensis* first demonstrates the Pliocene distribution of *Paenelimnoecus* in East Asia, although this genus was very recently described from the Late Miocene of Inner Mongolia. It is inferred that *Paenelimnoecus* was widely distributed from Europe to north China across the northern part of Eurasia in the Late Pliocene.

Key words : New species, north China, Paenelimnoecus, Pliocene, shrew

Introduction

(1996b).

Paenelimnoecus is a small allosoricine shrew, which is known mainly from the Miocene and Pliocene of Europe. The taxonomy of the genus was greatly confused until the revision by Reumer (1984). He concluded that the generic names *Petenyiella, Suncus, Pachyura* and *Allopachyura* previously used for this shrew were untenable, and that the generic name *Paenelimnoecus* was appropriate for the shrew.

In China, Cai (1987) referred a small soricid mandible from the lower part of the Nihewan beds to *Paenelimnoecus* sp. This was the only record of the genus hitherto known in East Asia, but unfortunately, his unillustrated description is too simple to confirm the generic allocation of the mandible. Recently, Storch (1995) described a new species of *Paenelimnoecus* from the Late Miocene of Inner Mongolia, which indicates its distribution in East Asia during Late Miocene time.

Pliocene cave deposits recovered on the Qipanshan Hill near Xingtunzhi in Yinan County have yielded a great number of mammalian remains, which include two forms of shrew with striking difference in size. The larger form, *Lunanosorex lii*, was already described in our preceding paper (Jin and Kawamura, 1996b), while the smaller form is assignable to a new species of *Paenelimnoecus* and is described herein. The specimens of this species comprise a skull, a mandible, and maxillary and mandibular fragments, which were obtained from Layer 6 of the cave deposits. A geological account of the deposits is given in Jin and Kawamura Terminology and measuring method

Jin and Kawamura (1996a) provided the terminology and measuring method for a soricid skull, mandible and dentition, which are also used herein. Measurements were taken by using a measurescope (Nikon: MM-11) with an electric digital counter (Nikon: CM-65).

Systematic paleontology

Order Insectivora Bowdich, 1821 Family Soricidae Gray, 1821 Subfamily Allosoricinae Fejfar, 1966 Genus **Paenelimnoecus** Baudelot, 1972

Remarks.—We follow the conclusion of Reumer (1992), in which this genus is allocated to the subfamily Allosoricinae instead of to the Limnoecinae, Crocidurinae, Soricinae, or Crocidosoricinae.

Paenelimnoecus chinensis sp. nov.

Figures 1-6

Holotype.—Right mandible with first lower incisor, P_4 , M_1 and M_2 (V10814, 1).

Paratype.—Fragmentary skull with left P^4 , M^1 and M^2 (V10814, 2).

Referred specimens.—A left maxilla with P⁴, M¹ and M² (V10815, 1); a right maxilla with P⁴, M¹ and M² (V10816); a left maxillary fragment with P⁴ (V10815, 3); a right mandibular fragment with M₂ (V10815, 2).

Repository.—All the specimens described are stored in the Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing.

Geographic and geologic distribution.-Known only from the locality of Yinan; Late Pliocene.

Name derivation.-chinensis, denoting its occurrence in China.

Diagnosis.—A *Paenelimnoecus* species with four alveolar pits for upper antemolars between first upper incisor and P⁴; teeth pigmented red to orange; infraorbital foramen ranging from the position above paracone of P⁴ to that above mesostyle of M¹; lacrimal foramen opening above postectoflexus of M¹; alveolus of first lower incisor ending below protoconid of M₁; mental foramen positioned below hypoflexid of M₁; upper facet triangular; interarticular area very short and narrow; lower facet rectangular with no emargination on its lower margin, and its lingual protrusion weaker

than in *P. micromorphus, P. crouzeli* and *P. repenningi*; lower sigmoid notch narrow dorsoventrally in lateral view; first lower incisor with very weak serration on its cutting edge, and without buccal cingulum; M_1 and M_2 completely lacking entoconid and entoconid crest; overlap of M_2 on M_1 weak relative to *P. pannonicus*.

Description.-

Skull: In lateral view, the rostrum extends almost straight forward (Figure 1B) in contrast to *Sorex* where it is strongly bent anteroventrally. The lateral wall of the rostrum is weakly depressed above the alveoli of the antemolars. The infraorbital foramen is a large oval depression ranging from the position above the paracone of P⁴ to that above the mesostyle of M¹ (Figure 2A). Two small foramina open in the depression near its anterior margin. The posteroventral corner of the depression is almost right-angled. A slender vertical bar separates the lacrimal foramen from the depression. The foramen has a round outline, and is placed above the post-ectoflexus of M¹. The anterior margin of the orbit is almost vertical and situated above the pre-ectoflexus of M². The rostral part of the bony palate is broader and



Figure 1. Paenelimnoecus chinensis sp. nov. Fragmentary skull with left P^4 , M^1 and M^2 (paratype; V10814, 2). **A**: palatal view, **B**: left lateral view. **aa**: alveolar pits for antemolars, **af**: alveolar pit for first upper incisor, **d**: depression probably formed by the damage of the maxillary wall, **df**: displaced fragment of P^4 , **P**⁴: alveolus of P^4 .

shorter than that of Sorex (Figure 1A). Four alveolar pits for antemolars are present between the first upper incisor and P4. The most anterior alveolus has a gourd-shaped outline larger posteriorly, and with a marked central constriction. It is considered to be the alveolus of A¹ and A², in accordance with Rzebik-Kowalska's interpretation (1990). The second discrete alveolus is round, and is much smaller than the preceding one. The third and fourth are of nearly the same size, and have round outlines. They are much larger than the second. Of the alveoli of P4, the anterior and lingual ones are observable on the right side of the bony palate of V10814, 2 (Figure 1A). The former has a round outline, and is nearly the same size as the fourth antemolar alveolus. The lingual one is a large curved depression, elongated anteroposteriorly, with anterior and posterior ends being deep pits. The posterior palatal foramina open lingually to the position between the hypocone and the posterior margin of M¹. The bony palate is elevated along its posterior margin to form a low transverse ridge. The mesopterygoid fossa is observed behind this ridge. The anterior margin of the fossa is arcuate.

P⁴: The occlusal outline is a rounded trapezoid with its posterior margin markedly emarginated. The parastyle is a low, small conical cusp placed at the anterobuccal corner of the crown, where it forms a distinct protrusion of the anterior margin of the crown. The paracone, the highest cusp in the crown, is separated from the parastyle by a distinct notch. A high sharp ridge extending from the paracone to the posterobuccal corner of the crown is obtusely V-shaped in

occlusal view. This ridge and the paracone is stained red to orange, whereas other parts of the crown are not pigmented. The protocone is a small conical cusp on the middle of the anterior margin of the crown. It is lower and smaller than the parastyle. A ridge connecting the protocone to the parastyle is slender and distinct in V10815, 3 (Figure 3A), while it is broad and indistinct in V10816 and V10815, 1 (Figures 2B and 3B). A low blunt ridge, into which the hypocone is merged, runs along the lingual margin of the crown. The anterior tip of the ridge is separated from the protocone by a broad shallow valley. In the valley, a supplementary low cusplet is observed in V10815, 1 (Figure 3B), but it is absent in V10815, 3 and V10816. On the buccal face of the crown, there is a weak cingulum in V10815, 1 and V10815, 3, whereas no cingulum is present in V10816.

 M^1 and M^2 : The occlusal outline is roughly a broad oblong with its posterior margin strongly emarginated. The ectoloph is stained red to orange, while the remaining part of the crown is unpigmented. The paracone is situated near the anterior margin of the crown. This cusp is much lower and smaller than the metacone in M^1 , while the differences between them are slighter in M^2 . The mesostyle is rather conical and not completely merged into the ectoloph. At a position somewhat lingual to the apex of the mesostyle, the ridge extending from the paracone meets that from the metacone. A slender flange extends from the posterior base of the metacone to that of the metastyle along the posterior margin of the crown. The pre-ectoflexus is much smaller than the post-ectoflexus in M^1 , while the two are



Figure 2. Paenelimnoecus chinensis sp. nov. Right maxilla with P⁴, M¹ and M² (V10816). A : right lateral view, B : palatal view.



Figure 3. Paenelimnoecus chinensis sp. nov. **A**: left maxillary fragment with P⁴ in palatal view (V10815, 3), **B**: left maxilla with P⁴, M¹ and M² in palatal view (V10815, 1).

nearly the same size in M². On the buccal face of the crown, no cingulum is present in V10815, 1 and V10816, but there is a weak cingulum in V10814, 2 (Figure 1B). The protocone, situated near the anterior margin of the crown, is much lower than the ectoloph. From the protocone, a

distinct ridge extends buccally along the anterior margin of the crown, and another ridge extends straight posteriorly. The latter ridge is separated from the lingual base of the metacone, and thereby the trigon basin is continuous with the talon basin. The hypocone is indistinct and merged into



Figure 4. Paenelimnoecus chinensis sp. nov. Right mandible with first lower incisor, P_4 , M_1 and M_2 (holotype : V10814, 1). A : buccal view, B : lingual view.



Figure 5. Paenelimnoecus chinensis sp. nov. Ascending ramus of the holotype (V10814, 1). A: posterior view, B: dorsal view, C: ventral view. cs: coronoid spicule, ia: interarticular area, If: lower facet, mf: mandibular foramen, uf: upper facet.

a low ridge running along the posterior half of the lingual margin of the crown. This ridge is almost parallel to the above-mentioned posterior ridge of the protocone. These two ridges are separated by a shallow valley continuous with the talon basin.

Mandible: The horizontal ramus is slender and delicate. and has an almost straight lower margin in lateral view. It shows nearly the same height from front to rear in buccal view, whereas it attains its maximum height below M1 in lingual view (Figure 4). The alveolus of the lower incisor ends below the protoconid of M₁. The mental foramen is small, and opens below the hypoflexid of M1. The symphysis forms an elliptical swelling, with a central groove elongated anteroposteriorly, and terminates below the metaconid of M₁. The morphology of the ascending ramus is generally similar to that of Sorex. The deflection of the ascending ramus toward the buccal side is relatively slight (Figure 5A), to the same extent as in Sorex. The tip of the coronoid process is thickened to form a rounded surface with no depression. The coronoid spicule is well developed, and situated at midheight of the coronoid process. The external temporal fossa is clearly observed between the tip of the process and the spicule, but is indistinct below the spicule. The upper sigmoid notch is slightly emarginated ventrally in lateral view. There is no ptervgoid spicule. The upper ptervgoid fossa is broadly excavated on the dorsolingual face of the condyle, and forms a strong lingual emargination of the interarticular area. In posterior view, this area is very short, and much narrower than the upper facet (Figure 5A). The buccal margin of the area is straight. The upper facet is triangular in posterior and ventral views, and a narrow ellipse in dorsal view (Figures 5A-C). The lower facet is rectangular in posterior and ventral views, and protrudes lingually far beyond the lingual tip of the upper facet. Its lower margin is straight and not emarginated dorsally in posterior view



Figure 6. Paenelimnoecus chinensis sp. nov. Dentition of the holotype in occlusal view (V10814, 1).

(Figure 5A). In dorsal and ventral views, its lingual margin is rather straight and not pointed lingually (Figures 5B and 5C). The lower facet can be seen from the buccal side (Figure 4A). A small foramen is observed just anterior to the lower facet (Figure 5C). The lower sigmoid notch is deeply emarginated into the ascending ramus, and is narrow dorsoventrally in lateral view. The internal temporal fossa is very large and deep, and exhibits a rounded triangular shape. Its basal margin lies nearly on the same level as the upper margin of the horizontal ramus. The mandibular foramen is relatively small, and opens below and somewhat anterior to the middle of the basal margin of the internal temporal fossa. It extends anteriorly, and is not connected to the internal temporal fossa. The lingual face of the angular process is depressed to form the lower pterygoid fossa.

First lower incisor: The crown is relatively long and extends straight forward in dorsal view (Figure 6). Its anterior part is stained red to orange. The tip of the crown is somewhat upturned. In the specimen observed (holotype only), this tooth seems to be somewhat displaced anteriorly on the buccal face of the horizontal ramus. Judging from the posterior end of the alveolus of this tooth, the original position of the posterior margin of its crown is probably below the protoconid of M_1 . The cutting edge undulates very weakly, possibly corresponding to the weakly "monocuspulate" or "bicuspulate" character states of Reumer (1984). No cingulum is observed along the posterior margin

of the crown. There is a shallow broad groove on the lingual face of the crown.

 P_4 : Both lingual and buccal faces of the crown are damaged. The main cusp with orange pigmentation is situated at the anterior tip of the crown. From the cusp, a ridge extends posterobuccally and gradually descends to the middle of the crown, where it turns posterolingually and rises slightly to form another cusp without pigmentation. From this cusp, the ridge descends again in the same direction and extends to the posterior margin of the crown. The ridge therefore exhibits a broad V-shape in occlusal view (Figure 6), and is notched between the cusps in lateral view (Figure 4). A broad indistinct valley occurs on the lingual side of the ridge.

 M_1 and M_2 : The occlusal outline is trapezoidal. The buccal face of the ectolophid is stained orange. The paraconid at the anterior tip of the crown is remote from the protoconid, and the ridge between them is strongly notched. In occusal view, the posterior half of this ridge is parallel to the lingual margin of the crown (Figure 6). On the other hand, the metaconid is situated near the protoconid (especially in M_1), and the notch in the ridge between them is much weaker. The metaconid is more conical than other main cusps. The hypoflexid is deep (especially in M_2), and almost reaches the buccal cingulum. A ridge extending anterolingually from the hypoconid attaches to the posterior face of the protoconid, and steeply descends toward the

Element	Parameter	V10814, 2	V10815, 1	V10815, 3	V10816	V10814, 1	V10815, 2
P⁴	BL	_	1.18	1.16	1.14		
	LL	· _	0.80	0.73	0.80	—	—
	PE	_	0.65	0.58	0.71		—
	W	_	1.14	1.19	1.27	—	—
M۱	BL	1.19	1.05	—	1.16	_	_
	LL	1.23	—	—	1.13		—
	PE	0.88	—	—	0.94	—	—
	AW	1.32	—	—	1.30	—	—
	PW	1.45	_	—	1.42	—	—
M²	BL	1.06	1.02	—	1.05	—	_
	LL	1.17	1.04	—	1.12	—	—
	PE	0.87	0.84		0.89	—	—
	AW	1.31	1.25	_	1.31	_	_
	PW	1.26	1.23		1.26	—	—
Mandible	LMH	—	_	_		3.32	_
	HC	—		—	_	2.94	_
	LUF	_	_	_	—	0.61	_
First lower incisor	L	—	_	_	—	2.95	
Mı	L		_	_		1.20	_
	TRW	_	_	_		0.60	
	TAW	_	_	_	—	0.65	_
M_2	L		_	_	_	1.12	_
	TRW		—	—	_	0.70	_
	TAW	_	—	_		0.62	0.65

Table 1. Measurements of Paenelimnoecus chinensis sp. nov.

Abbreviations AW: anterior width, BL: buccal length, HC: height of the coronoid process, L: length, LL: lingual length, LMH: length from the mental foramen to the uppermost point of the lower margin of the ascending ramus, LUF: length of the upper facet, PE: length to the posterior emargination, PW: posterior width, TAW: talonid width, TRW: trigonid width, W: width. For detailed explanation see Jin and Kawamura (1996a).

protoconid. The hypoconulid (entostylid in Reumer, 1984) is a ridgelike cusp, which is lower than the hypoconid. The ridge between them is weakly notched. There is neither entoconid nor entoconid crest, so that the talonid basin opens broadly to the lingual side. The buccal cingulum is well developed and not undulated, while the lingual one is weak in M_1 and indistinct in M_2 . In buccal view, the anterior part of M_2 overlaps the posterior end of M_1 (Figure 4A). In lingual view, the lower margin of the crown is arcuate ventrally, more extremely so in M_1 than in M_2 (Figure 4B).

Measurements.—The measurements of the teeth and mandible are given in Table 1. As regards M^1 and M^2 , the PE index of Reumer (1984) is calculated in order to quantify the degree of the posterior emargination (PE index= {(LL+BL)/2PE}-1). Values for M^1 are 0.37 in V10814, 2 and 0.22 in V10816, while those for M^2 are 0.28 in V10814, 2 and 0.22 in V10815, 1 and V10816.

Systematic position.-The specimens described above have the following diagnostic characters: the upper facet triangular; the interarticular area very short; entoconid and entoconid crest completely absent; the ridge connecting the paraconid to the protoconid long, and its posterior half parallel to the longitudinal axis of the mandible; the metaconid placed near the protoconid. These coincide with the diagnostic characters of the tribe Allosoricini given by Reumer (1984), and are applicable to the subfamily Allosoricinae of Reumer (1992), who dropped the tribal treatment he used previously. The present specimens are therefore referred to Allosoricinae. According to Reumer (1992), the subfamily comprises only two genera, Allosorex and Paenelimnoecus. The detailed description of Allosorex given by Feifar (1966) indicates that this genus differs greatly in much larger size, a unique shape in the ascending ramus (coronoid process very short and strongly deflected buccally ; upper pterygoid fossa very large; lower facet placed very anteriorly, etc.), and in having the teeth unpigmented, the lower incisor strongly upturned in its apical part, the lower molars without cingula and with the protoconid placed much nearer to the metaconid, and M₁ larger relative to M₂.

On the other hand, the morphological characters of the maxillae, mandibles and teeth of *Paenelimnoecus* hitherto described (Engesser, 1979, 1980; Reumer, 1984, 1992; Rzebik-Kowalska, 1990) are consistent with those of the present specimens. This justifies their allocation to the genus *Paenelimnoecus*.

Reumer (1992) listed four species for the genus, and gave their temporal ranges. They are : *P. micromorphus* (Doben-Florin, 1964) from the Early Miocene, *P. crouzeli* Baudelot, 1972 from the Middle Miocene, *P. repenningi* (Bachmayer and Wilson, 1970) from the Late Miocene, and *P. pannonicus* (Kormos, 1934) from the Pliocene.

Doben-Florin (1964) and Ziegler (1989) described and figured the morphology of *P. micromorphus*. The present specimens are distinguishable from *P. micromorphus* in having the mental foramen positioned more posteriorly, the alveolus of the lower incisor ending more posteriorly in buccal view, the condyle with remarkable lingual emargination (the condyle of *P. micromorphus* with buccal emargination as stated by Ziegler, 1989), the lingual protrusion of the lower facet weaker, the lower margin of the lower facet not emarginated dorsally, the lower sigmoid notch much narrower in lateral view, the mandibular foramen positioned more anteriorly, the lower incisor without cingulum (buccal cingulum is present in *P. micromorphus*, judging from fig. 3 of Pl. 5 in Ziegler, 1989), and the teeth distinctly pigmented. In addition to these, the infraorbital and lacrimal foramina seem to be placed more anteriorly in the specimens.

On the basis of the illustrations and descriptions in Engesser (1979, 1980) and Reumer (1992), *P. crouzeli* resembles *P. micromorphus* in the position of the mental foramen and that of the alveolus of the lower incisor, and in the morphology of the lower facet and lower sigmoid notch. These characters therefore distinguish the present specimens from *P. crouzeli*. Furthermore, the present specimens are distinct from *P. crouzeli* in having the coronoid process slenderer and less stout, the interarticular area narrower, and the internal temporal fossa smaller.

The descriptions and illustrations of P. repenningi given by Bachmayer and Wilson (1970, 1978) indicate that the present specimens differ from P. repenningi in having the teeth clearly pigmented, the posterior border of the infraorbital foramen positioned more anteriorly, the anterior margin of the coronoid process sloping down more gently (in P. repenningi, it makes a near-right angle with the horizontal ramus), in the buccal shape of the condyle (in *P. repenningi*, the lower facet distinctly protrudes ventrally), and in having the lower sigmoid notch much narrower in lateral view. The buccal view of the fragmentary skull of P. repenningi is illustrated in Bachmayer and Wilson (1978; Pl. 1, fig. 3), where three antemolars are observable. In the figure, the most anterior and middle ones are much larger than the most posterior one. This possibly suggests that P. repenningi has a different alveolar pattern from the present specimens.

The morphological characters of *P. pannonicus* given by Reumer (1984) and Rzebik-Kowalska (1990) are compared with those of the present specimens. The specimens are distinguished from *P. pannonicus* in having the lacrimal foramen positioned more anteriorly, an additional alveolar pit for upper antemolars probably indicating the presence of an additional antemolar, the interarticular area narrower in relation to the width of the upper facet, the lower incisor with a less serrated cutting edge, and weaker overlap of M_2 on M_1 (thereby the posterior face of the hypoconid is not concave in M_1). Moreover, the pigmentation of the teeth seems heavier (red to orange) than in *P. pannonicus* (light orange, according to Reumer, 1984).

Additionally, the Late Miocene species *P. obtusus* recently described by Storch (1995) is compared with the present specimens on the basis of his description and figures. The specimens are clearly distinct from *P. obtusus* in having somewhat larger size; P^4 and M^1 with much stronger posterior emargination; the coronoid process not leaning anterior-ly; the mandibular condyle with stronger lingual emargination, with a narrower interarticular area and with a triangular upper facet; the lower sigmoid notch much narrower; and M_1 and M_2 with more roundish occlusal outlines, with buccal cingula sloping posteriorly and with no entoconid.

The specimens are therefore different from all the known

species of *Paenelimnoecus*. We can conclude that they represent a new species of the genus, which we name *P. chinensis*.

Discussion.-Among the Paenelimnoecus species hitherto described, the information on skulls and upper teeth is poor or absent for the Early and Middle Miocene species P. micromorphus and P. crouzeli. It is therefore impossible to discuss the relationships among the two species and P. chinensis on the basis of these parts. On the other hand, the morphology of mandibles is comparable among all the species of the genus. P. micromorphus and P. crouzeli are distinct from P. chinensis in the anterior position of the mental foramen and that of the alveolus of the lower incisor. in the morphology of the lower facet (with strong lingual protrusion and emargination on its lower margin), and in having a much broader lower sigmoid notch. According to Bachmayer and Wilson (1970), a Late Miocene species, P. repenningi, has the position of the mental foramen near that in P. chinensis, but it is distinct from P. chinensis in the morphology of the ascending ramus (morphology of its anterior border, lower condyle and lower sigmoid notch). The other Late Miocene species, P. obtusus, clearly differs from P. chinensis in having the coronoid process leaning anteriorly and lower sigmoid notch much broader, and in the morphology of the condyle (oval upper facet, much weaker lingual emargination and broader interarticular area).

The difference in mandibular morphology between *P. chinensis* and the Pliocene *P. pannonicus* is less than that between *P. chinensis* and the above-mentioned Miocene species. The mandible of *P. chinensis* is similar to that of *P. pannonicus* in the position of the mental foramen and that of the alveolus of the lower incisor, and in the morphology of the ascending ramus (narrow lower sigmoid notch, weak lingual protrusion of the lower facet and no emargination on its lower margin, and curvature of the anterior margin of the ramus). *P. chinensis* is therefore considered to be closely related to *P. pannonicus*.

Our recognition of P. chinensis confirms the existence of Paenelimnoecus in East Asia during Late Pliocene time. In the Early Miocene, this genus appeared in Europe, and survived there until the Late Pliocene. In East Asia, the genus first appeared in the Late Miocene, which is indicated by P. obtusus from Inner Mongolia. P. obtusus is not a direct ancestor of P. chinensis, because there is great morphological difference between them. P. chinensis was possibly derived from a form close to the European species, P. pannonicus, while the lineage of P. obtusus had possibly become extinct before the Pliocene. It is inferred that the ancestor of P. chinensis migrated from Europe in the Early Pliocene, and speciated into P. chinensis. Again in the Late Pliocene Paenelimnoecus was widely distributed from Europe to north China across the northern part of Eurasia. Such a distribution pattern in Pliocene time is also inferred for another soricid genus, Beremendia (Jin and Kawamura, 1996a).

Conclusions

Small shrew remains from Late Pliocene cave deposits of

Yinan County are assigned to a new species of the genus Paenelimnoecus and named P. chinensis. This species is characterized by pigmented teeth, four alveolar pits for upper antemolars, anteriorly positioned infraorbital and lacrimal foramina, posteriorly positioned alveolus of the lower incisor, posteriorly positioned mental foramen, short and narrow interarticular area, rectangular lower facet with weak lingual protrusion, narrow lower sigmoid notch, absence of buccal cingulum in the lower incisor and weak serration on its cutting edge, and weak overlap of M₂ on M₁. These characters distinguish P. chinensis from the known species of the genus, P. micromorphus, P. crouzeli, P. repenningi, P. obtusus and P. pannonicus. Of these known species, the morphological difference from P. chinensis is smallest for the Pliocene species, P. pannonicus. It is therefore inferred that P. chinensis originated from a form close to P. pannonicus of the Late Miocene or the Early Pliocene. P. chinensis confirms the distribution of Paenelimnoecus in East Asia during the Late Pliocene. In this time, Paenelimnoecus was widely distributed from Europe to north China across the northern part of Eurasia.

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