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Source: American Museum Novitates, 2009(3663) : 1-18

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/665.1

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3663, 18 pp., 8 figures, 2 tables August 28, 2009

New Distylomyid Rodents (Mammalia: Rodentia) from the Early Miocene Suosuoquan Formation of Northern Xinjiang, China

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ABSTRACT

Three new distylomyid species, *Distylomys burqinensis*, *Prodistylomys wangae*, and *P. lii*, are described from the Suosuoquan Formation, early Miocene, of Xinjiang Province, northwestern China. Previously unknown cranial materials and upper dentitions add new information for the higher-level taxonomy of distylomyid rodents. Based on these new discoveries, the Family Distylomyidae is resurrected. These fossils demonstrate that distylomyids have a combination of primitive "ctenodactylid" characters and derived hystricognathous ones, possibly indicating a close affinity with South American caviomorph rodents and thereby offering new evidence to challenge the hypothesis that the traditional "Ctenodactyloidea" are monophyletic.

Prodistylomys lii was recovered from Suosuoquan mammal assemblage III (magnetostratigraphically dated as 21.69–21.16 Mya) at the Chibaerwoyi locality. *Distylomys burqinensis* and *Prodistylomys wangae* were collected from a new fossiliferous locality, Locality XJ200601 of Burqin County. The composition of the fauna from this new locality suggests that it represents an assemblage younger than Suosuoquan mammal assemblage III. Preliminary comparison with other faunas suggests that the assemblage is of early Miocene age, approximately 20 Mya old, and is a new fossil level within the Suosuoquan Formation.

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ISSN 0003-0082

INTRODUCTION

Distylomyidae (or Distylomyinae) encompasses a rare and enigmatic group of rodents that has no modern analogue. The type genus *Distylomys*, represented by two species, was named by Wang (1988) on the basis of three mandibles. Originally, Wang established Distylomyidae as a distinct family, referring it provisionally to the superfamily Ctenodactyloidea, particularly because of the sciurognathous lower jaw, although the lower cheek teeth are remarkably similar to those of South American *Cephalomys*. In the following year, Wang and Qi (1989) described a fragmentary lower jaw with cheek teeth and named the second genus of Distylomyidae, *Prodistylomys*, from the latest Oligocene (currently considered early Miocene) Suosuoquan Formation of Chibaerwoyi, Xinjiang. They noted a problem with the inclusion of the Distylomyidae in the Ctenodactyloidea because, unlike any other ctenodactylid rodent, the lower cheek teeth of *Prodistylomys* do not increase in size posteriorly. Wang (1994, 1997) definitely viewed distylomyids as ctenodactylid rodents, demoting them to the status of subfamily within the family Ctenodactylidae. Since Wang and Qi's (1989) publication, only a few additional isolated teeth have been recovered from Inner Mongolia. The scantiness of previous material has obscured the phylogenetic placement of distylomyid rodents.

Our research team, which has conducted field investigations in northern Xinjiang from 1995 to 2008, recovered a large collection of distylomyid rodents among other small mammals from two localities, Chibaerwoyi and a new fossiliferous locality, XJ200601 of Burqin County (fig. 1); the latter has produced more than 70 specimens, including previously unknown cranial materials with upper dentitions of the genus. These materials confirm that the Distylomyidae is a distinct family and offer a new perspective on the higher-level phylogeny of the Superfamily Ctenodactyloidea.

In this paper, we describe the new species from the Suosuoquan Formation of Xinjiang, China. Cranial materials and upper dentitions allow us to diagnose the family and assess its phylogenetic affinity with ctenodactylids and South American caviomorph rodents. We also investigate their biochronologic implications.

METHODS

Nomenclature generally follows Wood and Patterson (1959) with the exception of the term ectolophid = mure.

Teeth and mandibles were measured using a Nikon SMZ 8 microscope set at 20 × magnification; measurements were recorded to the nearest 0.01 mm. The SEM photographs of some teeth were taken from uncoated specimens using a Hitachi scanning electron microscope.

Institutional Abbreviations: AMNH, American Museum of Natural History; IVPP, Institute of Vertebrate of Paleontology and Paleoanthropology, Chinese Academy of Sciences.

SYSTEMATIC PALAEONTOLOGY

ORDER RODENTIA BOWDICH, 1821

FAMILY DISTYLOMYIDAE WANG, 1988

TYPE GENUS: *Distylomys* Wang, 1988.

INCLUDED GENUS: *Prodistylomys* Wang and Qi, 1989.

REVISED DIAGNOSIS: Rodents with hystricomorphous skull and sciurognathous mandible; upper tooth row convergent anteriorly; mandible robust, mental foramen near dorsal surface of diastema, masseteric fossa extending below p4, without dorsal masseteric crest but with well-developed ventral crest; dental formula1/1,0/0,1/1,3/3; cheek teeth hypsodont (high crowned but rooted) or hypselodont (high crowned and rootless), with asymmetrical dental pattern, no significant increase of size posteriorly; P4 nonmolariform, upper molars strongly bilophodont without the mure; p4 molariform, lower molars strongly bilophodont with the mure; incisors with multiserial enamel.

REMARKS: Distylomyids have been known exclusively from lower dentitions (three mandibles and several isolated lower teeth) (Wang, 1997) and discussion of their phylogenetic affinities was limited by lack of cranial and upper dental information. Although Wang (1994, 1997) regarded distylomyid rodents as a subfamily within the family Ctenodactylidae, new cranial and upper dental materials clearly demonstrate that distylomyids are distinguished from other rodents and merit family rank.

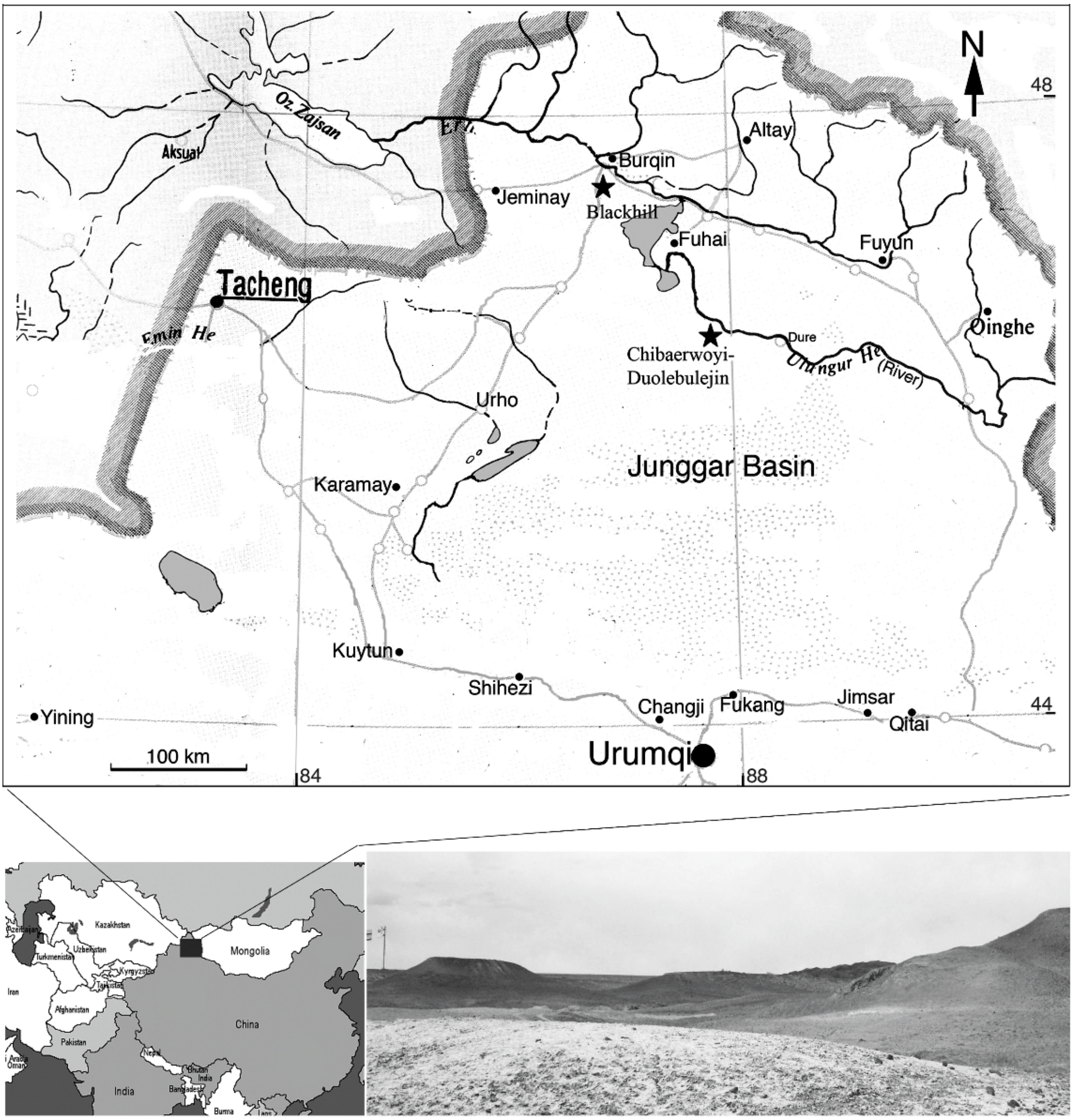

Fig. 1. Location map of study area and photograph of the locality XJ200601 of Burin County. Stars indicate fossilliferous localities.

The earliest members of the family Ctenodactylidae are best represented by *Tataromys*. Distylomyidae share the following characters with *Tataromys*: hystricomorphous infraorbital foramen; sciurognathous lower jaw; incisors with multiserial enamel; strong ventral crest but lacking dorsal crest of the mandible. The family differs from *Tataromys* in having anteriorly convergent tooth rows; smaller incisive foramen; palatine foramen apparently absent; mental foramen on dorsal surface of diastema; cheek teeth not increasing in size posteriorly; bilophodont and hypsodont cheek teeth; and asymmetrical dental pattern. Most characters shared by the Distylomyidae and *Tataromys* also occur in the living ctenodactylids (*Ctenodactylus*, *Felovia*, *Massoutiera*, and *Pectinator*): a broad frontal, the hystricomorphous infraorbital foramen, sciurognathous lower jaw, and incisors with multiserial enamel. In addition, Distylomyidae resemble the living ctenodactylids in having hypsodont and bilophodont cheek teeth; simple occlusal surface pattern. Distylomyidae differ from the latter in having a smaller incisive foramen; cheek teeth not increasing in size posteriorly; ventral masseteric crest extending to the condyle; presence of P4/p4; and asymmetrical dental pattern.

Distylomyidae are also comparable to the South American *Cephalomys* (Wang, 1988). They share hystricomorphous infraorbital foramen; hypsodont and bilophodont cheek teeth; the high degree of penetration of the hypoflexus in the upper molars; incisors with multiserial enamel; and asymmetrical dental pattern. They differ in that in *Cephalomys* the trigon and talon of upper teeth are united labially, the angular process of the lower jaw is hystricognathous, and cheek teeth are somewhat unilaterally hypsodont.

Distylomys Wang, 1988

Type Species: *Distylomys tedfordi* Wang, 1988.

Included Species: *Distylomys qianlishanensis* Wang, 1988; *D. burqinensis*, n. sp.

Geological Range: Late Oligocene to middle Miocene.

Geographic Distribution: Inner Mongolia, Gansu, and Xinjiang, China.

Emended Diagnosis: Incisive foramen small; tooth rows convergent anteriorly; mental foramen in diastema; distinct ventral masseteric crest extending below p4; sciurognathous angular process; dental formula 1/1, 0/0, 1/1, 3/3; cheek teeth hypselodont with asymmetrical pattern; P4 nonmolariform; upper molars bilophodont without the mure; p4 molariform; lower molars bilophodont with the mure; mesoflexid and hypoflexid deep and wide, opposite to each other and with cement; worn occlusal surface of cheek teeth smoothly concave with enamel thin or interrupted at the posterior edge of teeth.

Distylomys burqinensis, n. sp.

Figures 2–5, table 1

Diagnosis: Intermediate sized species, slightly larger than *D. tedfordi* and smaller than *D. qianlishanensis*. Differing from *D. tedfordi* in having p4 longer than m1, a more elongate anterolophid and absence of posterolophid on p4, m1 relatively wider with a more acute lingual apex of the trigonid. Differs from *D. qianlishanensis* in having a more acute anterolophid and subtriangular talonid on p4, lower molar trigonid triangular, and mental foramen higher on the mandible.

Holotype: IVPP V16014.1, anterior partial skull with P4–M3 and associated mandible.

Referred Material: IVPP V16014.2, palate with dentition; V16014.3, palate with broken left P4–M2 and right M1–M3; V16014.4, palate with left M1–M2 and right P4–M2; V16014.5, palate with left M1 and right M1–M2; V16014.6, partial premaxilla with incisors; V16014.7, left premaxilla with broken I2; V16014.8–9, 2 right premaxillae with broken I2; V16014.10–14, 5 left M1; V16014.15, left M2; V16014.16–21, 6 right M1; V16014.22, right M2; V16014.23–26, 4 right M3; V16014.27–32, 6 left fragmentary mandibles with broken i2, and p4–m3; V16014.33–34, 2 left fragmentary mandibles with broken i2 and p4–m2; V16014.35–39, 5 left fragmentary mandibles with p4–m1; V16014.40, left fragmentary mandible with p4; V16014.41, left fragmentary mandible with broken p4–m1; V16014.42, left fragmentary mandible with m1–m2; V16014.43, left fragmentary mandible with m2–m3; V16014.44, left m1; V16014.45–46, 2 left m2; V16014.47, left m3; V16014. 48, right fragmentary mandible with broken i2 and p4–m3; V16014.49, right fragmentary mandible with broken p4 –m1 and complete m2–m3; V16014.50–51, 2 right fragmentary mandibles with p4–m2; V16014.52–55, 4 right fragmentary mandibles with p4; V16014.56–57, 2 right fragmentary mandibles with m1–m2; V16014.58, right fragmentary mandible with m2–m3; V16014.59, right fragmentary mandible with broken m1; V16014.60–61, 2 right p4; V16014.62–64, 3 right m1; V16014.65–66, 2 right m3.

Etymology: the species name refers to Burqin County, where site XJ200601 is located.

Locality and Age: Locality XJ200601 (47°23.198′N, 86°47.981′E), Burqin County, Xinjiang, China. Suosuoquan Formation, early Miocene.

Repository: The specimens are stored in the collections of the Institute of Vertebrate

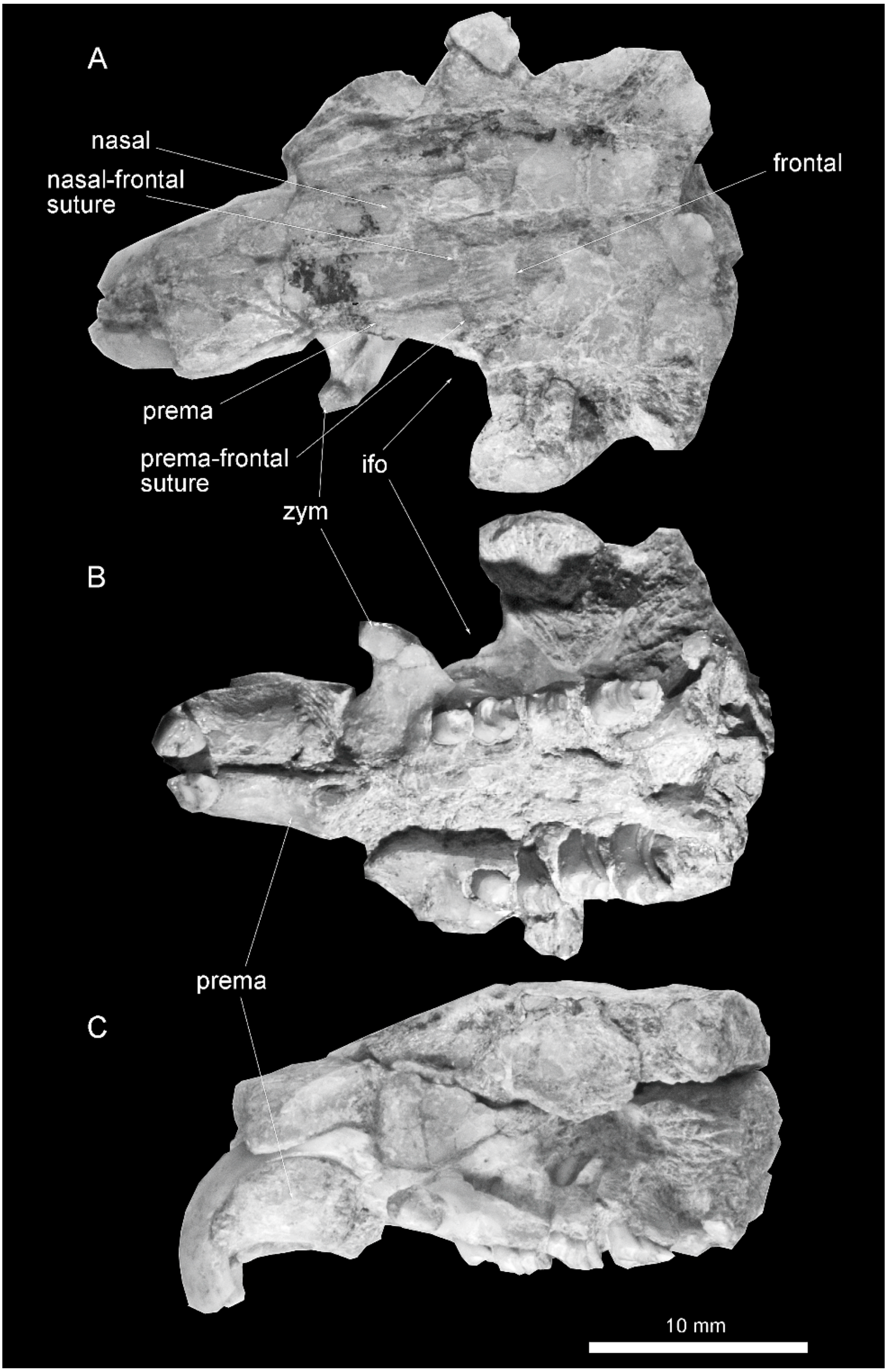

Fig. 2. Dorsal (A), ventral (B), and lateral (C) views of *Distylomys burqinensis* n. sp. (IVPP V16014.1). Abbreviations: **ifo**, infraorbital foramen; **prema**, premaxilla; **zym**, zygomatic root.

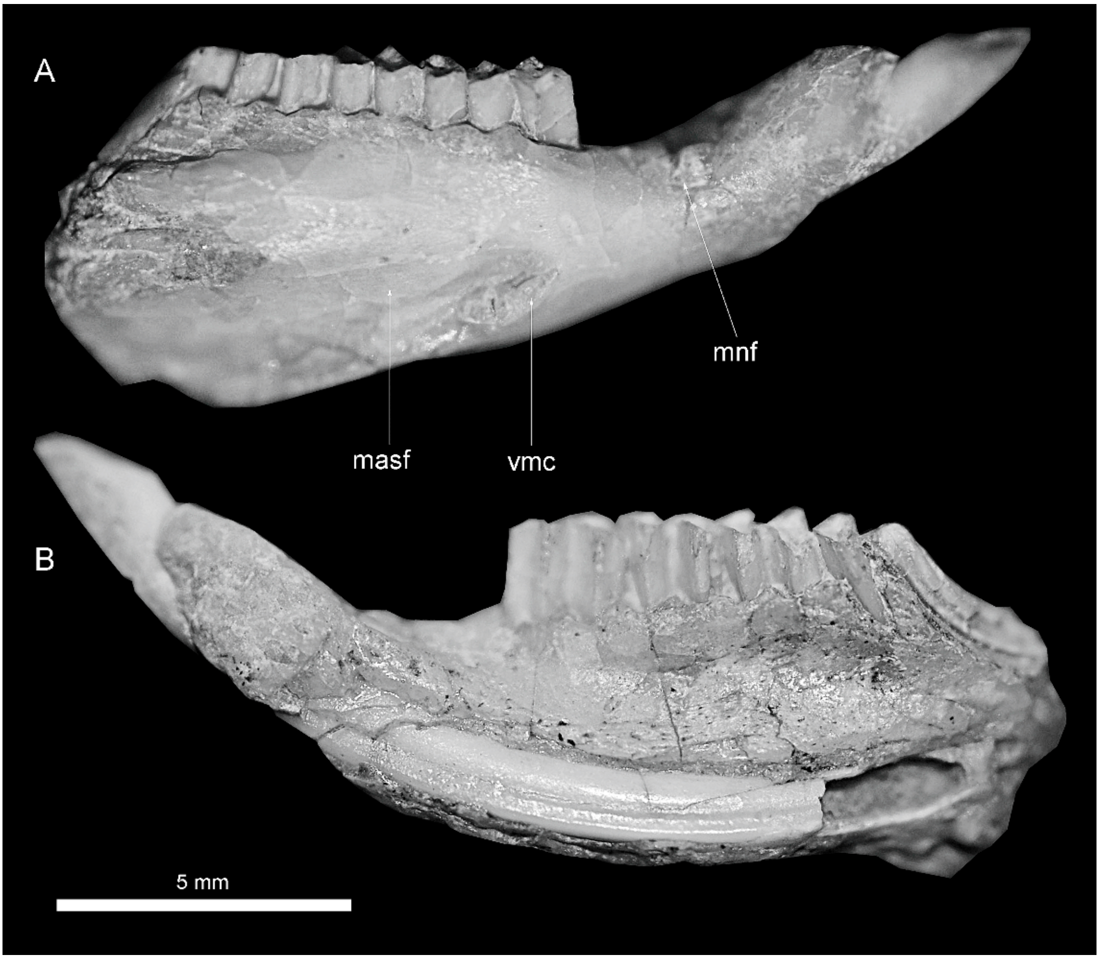

Fig. 3. Labial (A) and lingual (B) views of the mandible of *Distylomys burqinensis* n. sp. (IVPP V16014.1). Abbreviations: **masf**, masseteric fossa; **mnf**, mental foramen; **vmc**, ventral masseteric crest.

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Description: The holotype IVPP V16014.1 is a partial skull with articulated mandible. The skull preserves the anterior half, including the rostrum, palate, and partial frontal (fig. 2) and has been crushed and distorted, with the premaxilla shifted slightly lateroventrally. The incisive foramen is obscured due to distortion. Judging from what is preserved in the holotype and V16014.2 (fig. 4), it is very slender and narrow and ends posteriorly at the level of the center of the anterior zygomatic root. The base of the zygomatic root is preserved and shows that the zygomatic plate is not developed; its anterior margin is located far in front of P4 and its posterior margin is between P4 and M1. The tooth rows are convergent anteriorly. The palate is wider than the length of m1. The palatine-maxillary suture starts from anterior to M1. No palatine foramen can be recognized.

In dorsal view, the nasal bones are narrow and extend posteriorly as far as the premaxillae. Laterally, the premaxillary-maxillary suture extends above M1. The infraorbital foramen, although broken, is evidently large and hystricomorphous. The frontals are flat and broadened relative to the width of the rostrum.

The diastema of the mandible is shallow and shorter than the tooth row (fig. 3). The

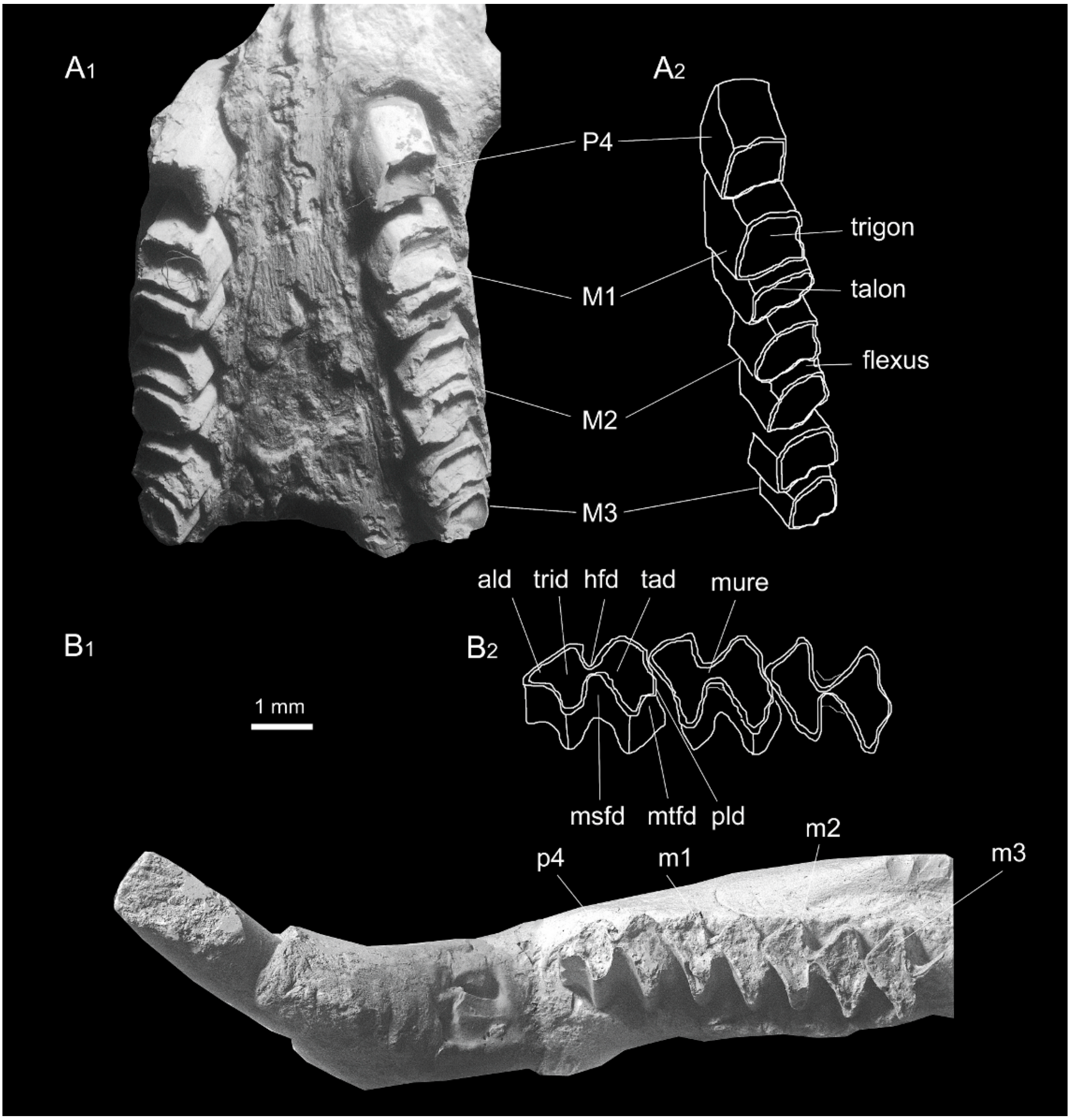

Fig. 4. Scanning micrographs of the palate and mandible of *Distylomys burqinensis*, n. sp., in occlusal view. **A**. Palate of IVPP V16014.2 (A_1) and explanatory drawing of the left cheek teeth (A_2). **B**. Mandible of IVPP V16014.1 (B_1) and explanatory drawing of p4–m2 (B_2). Abbreviations: **ald**, anterolophid; **hfd**, hypoflexid; **msfd**, mesoflexid; **mtfd**, metaflexid; **pld**, posterolophid; **tad**, talonid; **trid**, trigonid.

mental foramen is small and near the dorsal surface of the diastema. The mandible has a robust ventral masseteric crest, but there is no trace for the dorsal crest. The ventral crest terminates slightly anterior to the talonid of p4. Very little of the ascending ramus and angular process is preserved, but what remains suggests that the angular process is in the plane of the incisor within the horizontal ramus, as in other distylomyids.

The dental formula is 1/1, 0/0, 1/1, 3/3. All cheek teeth are hypselodont and at least moderately worn, so that little is known about tooth cusps. The upper incisors are broad and

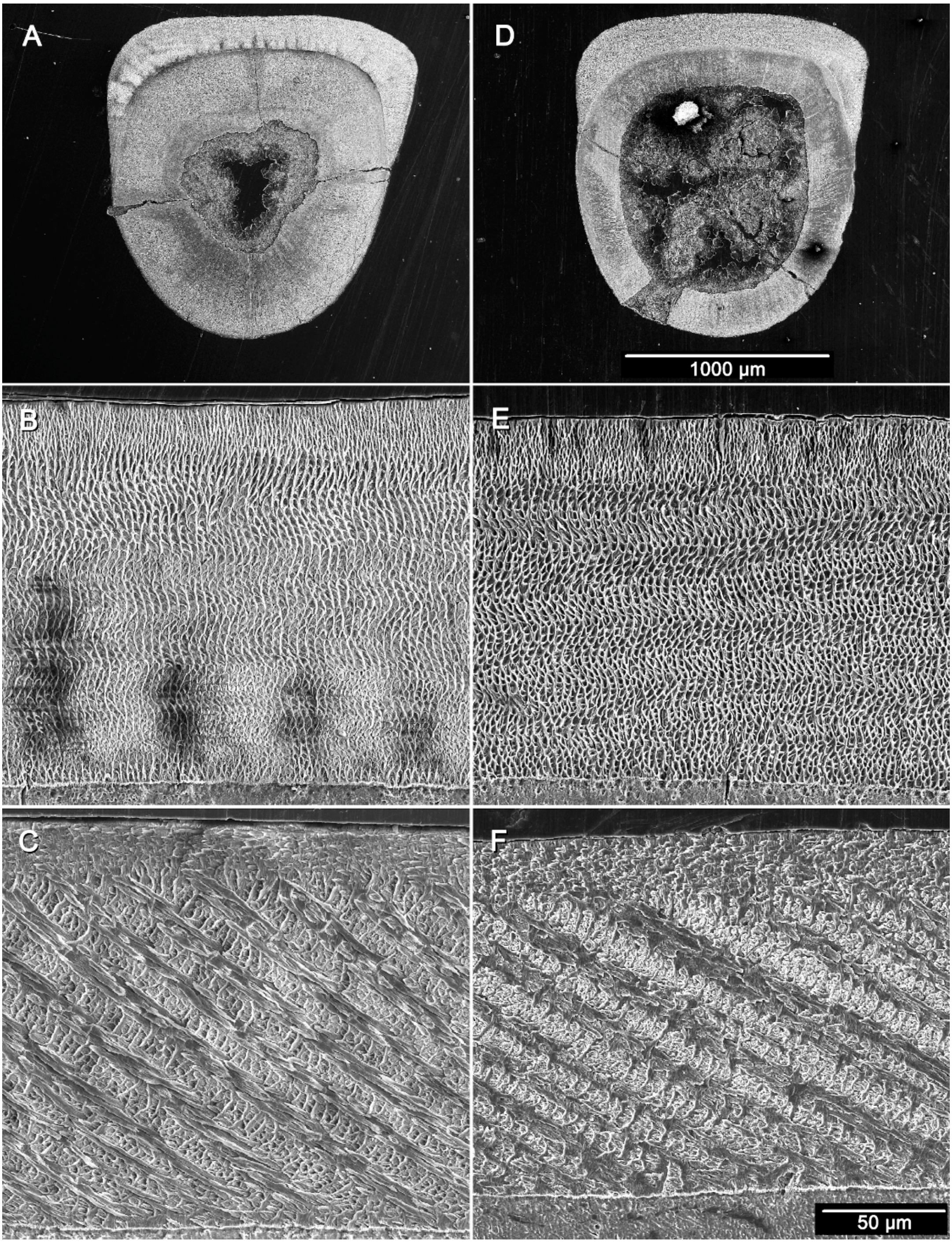

Fig. 5. Incisor enamel microstructure of *Prodistylomys wangae* (IVPP V16016.4; A–C) and *Distylomys burqinensis* (IVPP V16014.28; D–F). **A** and **D**, cross sections of lower incisors; **B** and **E**, microstructures (Hunter-Schreger bands, HSB) in cross-sectional view; **C** and **F**, microstructures (HSB) in longitudinal view.

TABLE 1

Tooth measurements (number of specimens, mean, range, and standard deviation; in mm) of *D. burqinensis*, *P. lii* and *P. wangae*. L, length; W, width; AW, width of the trigon(id); PW, the width of the talon(id)

		D. burqinensis				*P. lii*			*P. wangae*				
Tooth		N	Mean	Range	SD	V16015.1	V16015.2	V16015.3	V16016.1	V16016.2	V16016.3	V16016.4	V16016.5
P4	L	5	0.98	0.90–1.08	0.09								
	W	4	1.21	1.15–1.25	0.05								
M1	L	12	1.71	1.53–1.88	0.10								
	AW	12	1.51	1.40–1.64	0.08								
	PW	11	1.48	1.38–1.65	0.09								
M2	L	6	1.69	1.57–1.81	0.09								
	AW	6	1.42	1.36–1.51	0.06								
	PW	6	1.32	1.20–1.42	0.10								
M3	L	8	1.99	1.79–2.51	0.25		1.98					2.03	
	AW	8	1.52	1.31–1.70	0.16		1.36					1.49	
	PW	8	1.13	0.95–1.27	0.11		1.01					0.97	
p4	L	7	1.98	1.85–2.05	0.06			1.52	1.76		1.71		
	AW	7	1.12	0.99–1.30	0.10			1.01	1.15		1.02		
	PW	7	1.37	1.21–1.50	0.12			1.27	1.39		?		
m1	L	14	1.77	1.66–1.92	0.08	1.68			1.87	1.71	1.74		1.68
	AW	14	1.45	1.27–1.69	0.10	1.72			1.64	?	1.47		1.61
	PW	14	1.52	1.34–1.72	0.10	1.71			1.56	1.43	1.45		1.58
m2	L	18	1.72	1.50–1.88	0.10	1.71			1.82	1.68	1.78		
	AW	18	1.53	1.05–1.75	0.17	1.79			1.73	1.47	1.57		
	PW	16	1.49	1.07–1.75	0.18	1.73			1.65	1.51	1.5		
m3	L	10	1.87	1.65–2.10	0.15	1.56							
	AW	10	1.61	1.45–1.73	0.09	1.59							
	PW	9	1.37	1.21–1.59	0.14	1.33							

flattened anteriorly. Upper cheek teeth are strongly recurved toward the root, and the curvature increases posteriorly (fig. 4).

P4 is nonmolariform, unilobate, and somewhat trapezoidal in occlusal outline, with the posterior border slightly wider than the anterior one (fig. 4). Enamel is thinner at posterior margin.

All upper molars are strongly bilophodont without the mure, so that the trigon and talon form two separated enamel loops. The trigon and talon are straight and parallel to each other. They are separated by a transverse central flexus, which is almost completely filled with cement. In side views, lateral and medial flexi persist to the base of the tooth crown. The trigon is trapezoidal with a flattened lingual wall and a gently convex labial one. The talon is subrectangular, slightly wider than long. Given the tooth curvature, the upper tooth crown inclines posteriorly. Each molar bears four transverse enamel lophs that form the cutting edges of the tooth.

M1 is on average larger than M2 (table 1). In M1, the talon is wider but anteroposteriorly more compressed than the trigon. In M2 the talon is equal to or narrower than the trigon. M3 is larger than the preceding molars. In M3, the talon is reduced and much narrower, but slightly longer than the trigon.

The lower incisors extend posteriorly in the jaw to below m3 (fig. 3). The incisor enamel is thick, relative to the depth of the incisor (fig. 5D–F). It has a flat buccal surface and similarly wraps around to cover the medial and lateral sides of the tooth to a significant extent. The enamel microstructure is multiserial (Korvenkontio, 1934; Wahlert, 1968, 1989; Martin, 1992, 1997), and more specifically it consists of multiserial Hunter-Schreger bands (HSB) with rectangular interprismatic matrix (IPM), a more derived type than the parallel IPM that has an acute angle to the bands (Martin, 1992; 1997). The enamel is 150–165 μm thick, of which the portio interna (PI) and portio externa (PE) account for about 85% and 15%, respectively. Within the PI, each band consists mostly of four prisms. The HSB has a 50°–60° angle to the enamel-dentine junction, as measured following Martin (1992).

Unlike P4, which is nonmolariform, p4 is fully molariform and the largest of lower cheek teeth (fig. 4). The p4 trigonid is narrower than the talonid, with an acute anterior projection; its anterolingual edge is concave. The talonid is shorter but wider than the trigonid. No posterolophid is present except for three specimens that bear a shallow one. In 11 mandibles with check teeth, the premolar is less worn or in the same stage of wear as m1. Therefore we identify it as permanent p4, although Wang (1997) suggested that it may be deciduous p4.

All lower molars are similar in overall morphology. The m1 is longer than m2, but shorter than m3. All molars are bilophodont but have the mure; therefore, the trigonid and talonid are confluent through a narrow neck. The trigonid is triangular, with a tapered and acute lingual apex and straight anterolingual edge. The mesoflexid and hypoflexid intrude transversely halfway across the crown and are filled by thin cement. In side view, both flexids extend to the base of the crown. In m1, the talonid is wider than the trigonid with gently convex posterior edge. In m2, the talonid is equal to or slightly narrower than the trigonid. In m3, the talonid is much narrower than the trigonid.

COMMENT: The type species *D. tedfordi* was described by Wang (1988) on the basis of a single mandible, which was collected in 1928 by the Third Asiatic Expedition, AMNH, from the middle Miocene Tunggur Formation of the Tairum Nor Basin of Inner Mongolia. No additional material has since been referred to the species, restricting the comparison of the new materials to the lower jaw only.

D. burqinensis is similar to *D. tedfordi* and is clearly closely related to it. The type specimen of *D. tedfordi* from Tunggur lies within the lower size range of *D. burqinensis* from Burqin. Morphologically, however, *D. tedfordi* differs from *D. burqinensis* in several aspects: p4 shorter than m1, having a less elongate anterolophid and subelliptical talonid, m1 relatively narrower with an inward curved anterolingual edge and more blunt lingual apex. In *D. tedfordi*, the posterolophid is distinct on p4; in Burqin specimens, it is distinct in three, and absent in eight.

D. burqinensis is smaller than *D. qianlishanensis* and differs in having a more acute anterolophid and subtriangular talonid on p4;

triangular trigonid on lower molars, and higher position of the mental foramen on the mandible.

Wang (1988) thought *D. tedfordi* was morphologically more primitive than *D. qianlishanensis* because it possesses a well-developed posterolophid, a condition considered primitive. This, as Wang noted, is inconsistent with the stratigraphic occurrences of the species because *D. tedfordi* was found in later deposits (middle Miocene) than *D. qianlishanensis* (late Oligocene). *D. burqinensis*, with an early Miocene age, also lacks the posterolophid or has only an incipient one. We therefore offer an alternative interpretation: the presence of the posterolophid is a derived character within the genus, appearing in species with a younger age. If this is true, *D. burqinensis* is morphologically intermediate between *D. qianlishanensis* and *D. tedfordi*, but is more similar to the latter. It should be noted that size decreases in this lineage.

Prodistylomys Wang and Qi, 1989

TYPE SPECIES: *Prodistylomys xinjiangensis* Wang and Qi, 1989.

INCLUDED SPECIES: *Prodistylomys lii*, n. sp.; *P. wangae*, n. sp.

GEOLOGICAL RANGE: Early Miocene.

GEOGRAPHIC DISTRIBUTION: Xinjiang, China

EMENDED DIAGNOSIS: M3 bilophodont without the mure and asymmetrical with the corresponding lower molar, as in *Distylomys*. Differs from *Distylomys* in having rooted, hypsodont cheek teeth, M3 trigon semilunar shaped in outline, p4 with shorter trigonid, m1–2 with short trigonid and narrower talonid than the trigonid, thinner cement in hypoflexid and mesoflexid in lower molars.

Prodistylomys lii, n. sp.

Figures 6–7, table 1

HOLOTYPE: IVPP V16015.1, right fragmentary mandible with broken i2, and m1–m3.

REFERRED MATERIAL: IVPP V16015.2, right M3; V16015.3, right p4.

STRATIGRAPHIC AND GEOGRAPHIC PROVENANCE: Suosuoquan Formation of Chibaerwoyi, Xinjiang. Early Miocene.

ETYMOLOGY: Named for Professor Li Chuankui for his many contributions to the study of Asiatic rodents.

DIAGNOSIS: Similar to *P. xinjiangensis* in size, but differs in having well-developed roots, the absence of the metaflexid, and less hypsodonty.

COMPARATIVE DESCRIPTION: The only preserved upper cheek tooth V16015.2 is a heavily worn M3 (fig. 7–A). The M3 trigon is kidney shaped, whereas it is trapezoidal in *Distylomys burqinensis*. The talon is much narrower than the trigon. At this stage of wear, the flexi are already fused and form a fossette. No cement is present in the fossette. The two strong roots of M3 are fused.

The mandible (fig. 6) is similar to that of the type species, *P. xinjiangensis*. The diastema is short and shallow. The mental foramen opens dorsally and lies on the dorsal side of the diastema. In contrast, in *P. xinjiangensis* the mental foramen opens labially and occurs near the level of the dorsal shelf. The lower incisor is short, extending posteriorly to below m2 as in *P. xinjiangensis* and *D. qianlishanensis*, whereas it extends as far as m3 in *D. burqinensis*. The tip of the lower incisor is broken and its cross section is subrectangular with flat anterior and lingual walls. The enamel thins and extends a short distance onto the labial and lingual walls.

The p4 is not preserved in the holotype, but the alveolus indicates presence of three roots (fig. 6). The only known p4 is IVPP V16015.3 (fig. 7B). The trigonid is shaped like an isosceles triangle with gently concave labial and lingual margins. The anterolophid is short and blunt. The hypoflexid extends only halfway down the tooth, whereas the mesoflexid is much longer, extending to the root. The flexids are U-shaped and have no cement. In *P. xinjiangensis*, the flexids are V-shaped and cement filled. The talonid is wider than the trigonid; the talonid is slightly broken posteriorly, but what remains suggests absence of a metaflexid. This p4 has 3 roots. Although the p4 crown morphology is similar to that of dp4 of *P. xinjiangensis* except for the absence of the posterolophid, we prefer to consider this tooth as p4 because the roots are not splayed apart. If so interpreted, it is probable that p4 and dp4 have similar general crown morphology.

The lower molars have the same bilophodont occlusal pattern as *P. xinjiangensis*, but lack the posterolophid. The flexids extend only to the alveolus, clearly showing well-

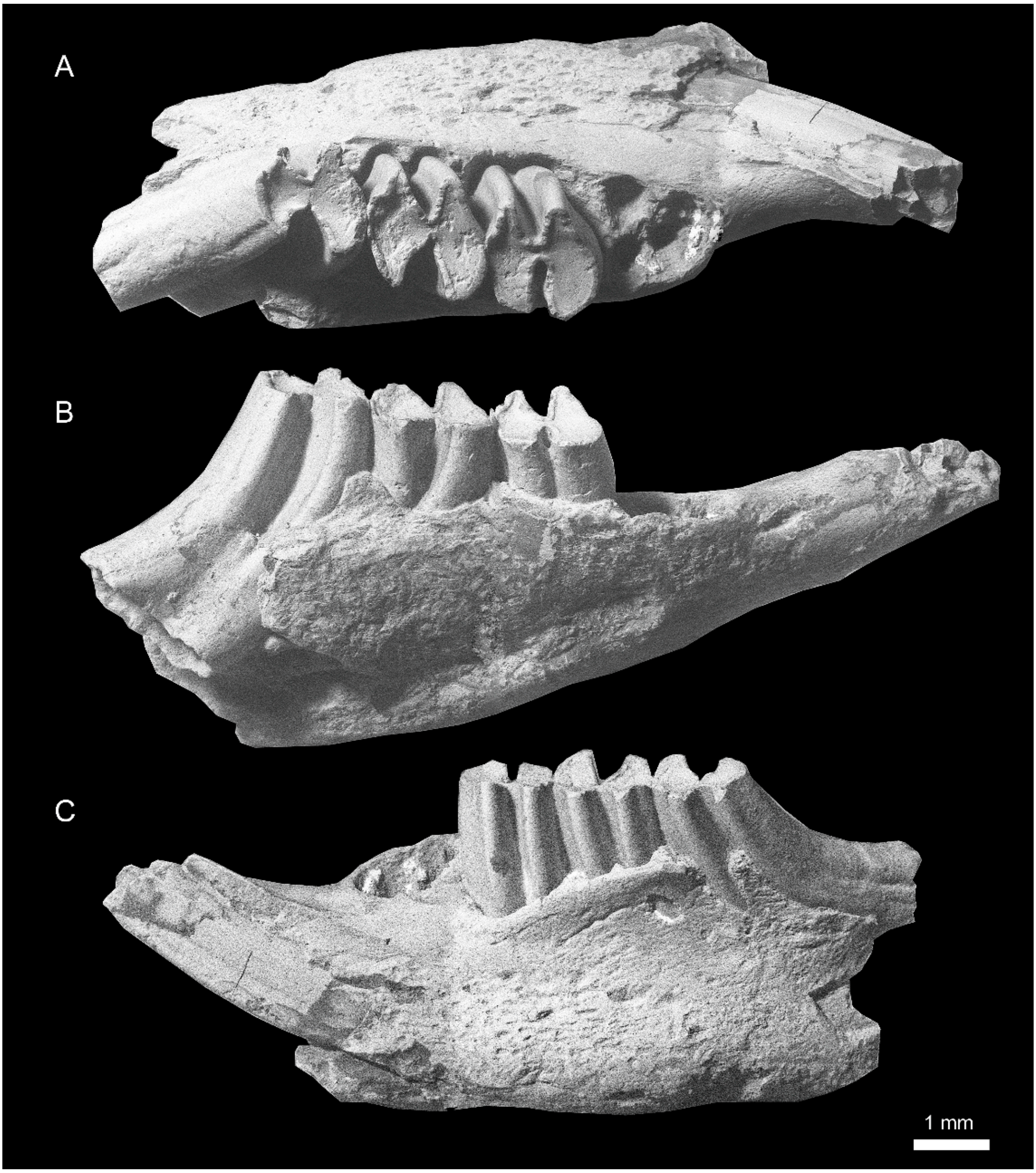

Fig. 6. Occlusal (**A**), labial **(B)**, and the lingual (**C**) views of the mandible of *Prodistylomys lii* (IVPP V16015.1).

developed roots in all the lower molars. In *P. xinjiangensis*, the flexids extend all the way into the tooth base, indicating reduced roots.

COMMENTS: In the Chibaerwoyi locality, fossils were mostly collected from beds A and B (7–12 m, and 14–21 m from the base of the formation, respectively). *P. lii* was collected from Bed A. The exact stratigraphic level of *P. xinjiangensis* was uncertain, but most likely was collected from Bed A. However, *P. lii* is morphologically more primitive than *P. xinjiangensis* in having stronger roots, or less hypsodonty, and lack of posterolophid, suggesting an earlier occurrence.

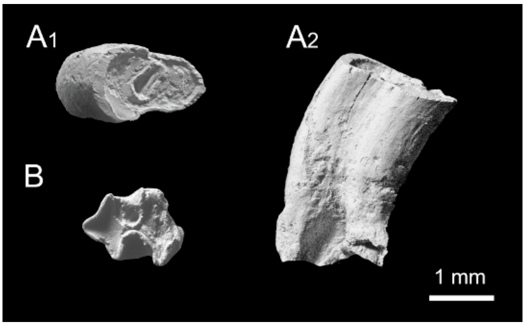

Fig. 7. *Prodistylomys lii*. **A**. occlusal (A_1) and labial (A_2) view of right M3 (IVPP V16015.2). **B**, occlusal view of right p4 (IVPP V16015.3).

Prodistylomys wangae, n. sp.

Figure 8, table 1

HOLOTYPE: IVPP V16016.1, right fragmentary mandible with broken incisor and complete p4–m2.

REFERRED MATERIAL: IVPP V16016.2, right M3; V16016.3, left fragmentary mandible with broken i2–p4, and m1–m2; V16016.4, right fragmentary mandible with broken i2 and p4–m2; V16016.5, left m1.

LOCALITY AND AGE: Locality XJ200601 (47°23.198′N, 86°47.981′E) in Burqin County of Xinjiang, Suosuoquan Formation, early Miocene.

ETYMOLOGY: The species name, *wangae*, is in honor of our colleague, Wang Banyue, for her contribution to the study of distylomyids.

REPOSITORY: The specimens are stored in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing.

DIAGNOSIS: Slightly larger than *P. lii* and *P. xinjiangensis*. Differs from *P. lii* in having weak roots, thicker cement, rounded lingual apex of m1 trigonid, shorter talonid on m2. Differs from *P. xinjiangensis* in having thicker cement, rounded lingual apex of m1 trigonid, and the absence of the metaflexid on lower molars.

DESCRIPTION: The M3 trigon is semicircular in outline, with a straight posterior margin (fig. 8A). The enamel is very thick, becoming thinner on the posterior margin. The hypoflexus extends to the base of the crown and becomes shallower while approaching the base. The mesoflexus extends ¾ of the height of the crown and is fused toward the base, suggesting a rudimentary root. On the contrary, in *P. lii*, both flexi are fused, showing a well-developed root. The talon is circular shaped, much narrower than the trigon.

The state of the masseteric crest is typical for the genus; the ventral crest is strong and extends under p4 and the dorsal crest is absent. The lower incisor extends posteriorly to underneath m3. The lower incisor is similar in its general morphology and microstructure to that of *Distylomys burqinensis* except that the pulp cavity is significantly smaller (fig. 5A, D).

The p4 is shorter than m1 (fig. 8C). The trigonid is much narrower than the talonid compared with that in *P. lii* and *P. xinjiangensis* and has a stout anterolophid. The anterolophid is blunt and lies well toward the labial side of the tooth rather than in the center. Only thin cement is present in the flexids. The talonid has a vestigial posterolophid.

Only m1 and m2 are preserved (fig. 8C; table 1). The lower molars are bilophodont, and hypsodont. The crown expands toward the base. The trigonid is subelliptical with a rounded anterior wall and a long axis oriented slightly anterolabial-posterolingually. The flexids are U-shaped with thin cement; the mesoflexid shallows but extends all the way to the base, and the hypoflexid extends down 2/3 of the height of the crown where it closes, indicating a rudimentary root (fig. 8B). The talonid is narrower than the trigonid, and is compressed with acute labial and lingual angles. The m1 and m2 are identical in crown morphology, but m2 is shorter than m1, and the lingual apex of its trigonid is more acute.

COMMENT: Although the Xinjiang specimens are very similar to *Distylomys* in crown morphology, the rudimentary roots of the cheek teeth, shorter trigonid and narrower talonid on lower molars, and thinner cement suggest that it is better to assign the specimens to the genus *Prodistylomys* rather than to *Distylomys*. *P. wangae* differs substantially from *P. lii* in showing a tendency to the loss of roots and subelliptical trigonid. It differs from *P. xinjiangensis* in the absence of the posterolophid (or metaflexid) and subelliptical trigonid.

DISCUSSION

HIGHER-LEVEL TAXONOMY OF DISTYLOMYIDAE: The superfamily Ctenodactyloidea, having

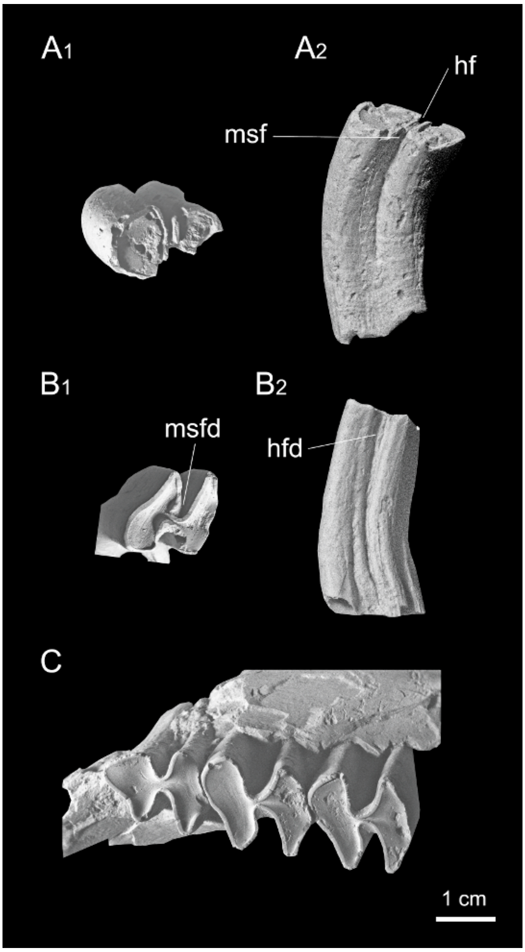

Fig. 8. *Prodistylomys wangae*, n. sp. **A**. occlusal (A_1) and labial (A_2) view of right M3 (IVPP V16016.2). **B**, occlusal (B_1) and labial (B_2) view of left m1(IVPP V16016.5). C, occlusal view of cheekteeth of the holotype (IVPP V16016.1). Abbreviations: **hf**, hypoflexus; **hfd**, hypoflexid; **msf**, mesoflexus; **msfd**,mesoflexid.

the sole family Ctenodactylidae, was used by Simpson (1945) as the least inclusive clade that contains only recent African genera, *Ctenodactylus*, *Pectinator*, *Massoutiera*, and *Felovia*. Subsequently, the superfamily was expanded to encompass extinct taxa from the Tertiary of Asia (Wood, 1977; Dawson et al., 1984; Flynn et al., 1986; Tong, 1997). Currently, in addition to Ctenodactylidae, four extinct families, including as many as 29 genera, have been referred to the superfamily Ctenodactyloidea: Cocomyidae, Tamquammyidae, Yuomyidae, and Chapattimyidae (Tong, 1997; Wang, 1997; Wible et al., 2005). The main character diagnostic of Ctenodactyloidea is a hystricomorphous skull but sciurognathous jaw (Dawson et al., 1984; Flynn et al., 1986).

Recently, the monophyly of the Ctenodactyloidea has been disputed by several studies, especially molecular studies (Martin, 1992; Bryant and McKenna, 1995; Huchon et al., 2000; Adkins et al., 2001; Marivaux et al., 2002; Huchon et al., 2007). Molecular data strongly support the Ctenodactyloidea as part of the stem group of the Hystricognathous rodents. If true, this hypothesis renders the traditional Ctenodactyloidea paraphyletic. To account for the new result, Huchon et al. (2000) proposed "Ctenohystrica" as a more inclusive clade to include all extant groups of ctenodactyloid and hystricognathous rodents. New evidence, particularly that of the upper dentitions, presented here, suggests that distylomyids retain some symplesiomorphies with ctenodactylids on the one hand, but share synapomorphies with some hystricognathous rodents on the other. This suggests an Asian origin of the common ancestor of Ctenodactyloidea-Hystricognathi, echoing the results of both paleontological and molecular studies.

When first described, the distylomyids were known exclusively from mandibles and lower dentitions. Their sciurognathous mandible has played a decisive role in placing the distylomyids within the superfamily Ctenodactyloidea (Wang, 1988, 1994, 1997). However, the sciurognathous mandible is primitive in rodents and gives rise to the hystricognathous condition (Flynn et al., 1986; Dawson et al., 2006). The only preserved skull of distylomyids (IVPP V16014.1) displays a large infraorbital foramen, characteristic of a hystricomorphous skull that is common for ctenodactylid and most hystricognathous rodents.

The incisor enamel of the distylomyids is multiserial and comparable to that of some earlier ctenodactylid rodents, such as *Tataromys plicidens* and *Yindirtemys deflexus* (Martin, 2007). Possessing a multiserial HSB does not necessitate a close relationship of distylomyids with species of Ctenodactylidae because multiserial HSB are known from several major groups of rodents, such as the

Hystricognathi, advanced Ctenodactyloidea, and Pedetidae (Wahlert, 1968; Sahni, 1980, 1985; Martin, 1992, 1995, 1997). Therefore, these characters previously used to diagnose "Ctenodactyloidea" actually are primitive and have little information for relationships between ctenodactylids and distylomyids. However, compared to the earliest ctenodactylid *Tataromys* and *Yindirtemys*, the incisor enamel of the distylomyids has proportionally thinner PE and a more uniform pattern of HSB, which may represent a more derived condition.

Our new discovery also shows that distylomyids display significant differences from the ctenodactylids. The most noticeable feature of the distylomyids is the asymmetrical pattern of upper and lower cheek teeth. The trigon and talon on upper cheek teeth are fully separated, whereas on lower cheek teeth the trigonid is connected with the talonid. By contrast, the occlusal pattern of upper cheek teeth is symmetrical with that of lower check teeth in ctenodactylid rodents. That cheek teeth increase in size posteriorly was considered a synapomorphy for ctenodactylids, and this condition was present in the earliest ctenodactyloid, *Cocomys* (Dawson et al., 1984; Li et al., 1989). In distylomyids, the dentition does not show this size variation. Instead, the smallest cheek tooth is usually M2 and m2 in the upper and lower dentition, respectively, although the size difference between adjacent teeth is not so distinctive.

Finally the posterior edge of the anterior zygomatic root in ctenodactylids is usually leveled with the anterior edge of P4, while in distylomyids it ends at the anterior edge of M1. An anteriorly shifted zygomatic root is probably a derived feature within many clades of rodents.

Interestingly, the tooth morphology of distylomyids is more closely similar to the South American *Cephalomys* than to ctenodactylids by sharing hypsodonty, strong bilophodonty, the high degree of penetration of the hypoflexus in the upper molars, deep mesoflexid and hypoflexid, occlusal pattern lost very early in wear, and the asymmetrical dental pattern in upper and lower cheek teeth. The asymmetrical dental pattern is also seen in the cephalomyid *Soriamys* (Kramarz, 2001). The main character precluding the affinity of distylomyids with the South American caviomorphs is that *Cephalomys* has a hystricognathous mandible, contrasting to the sciurognathous one in distylomyids. Because the morphology of the mandible plays an important role in traditional rodent classification, Wang (1988) had interpreted the dental resemblances between distylomyids and *Cephalomys* to show parallelism. However, as noted above, current views have gradually shifted to favor evolution of the hystricognathous lower jaw from a sciurognathous one. If correct, the dental similarities between distylomyids and *Cephalomys* could be viewed as reflecting a close relationship between the early Miocene distylomyids and South American forms.

Taken together, the characters claimed by previous researchers as evidence for the inclusion of Distylomyidae within Ctenodactyloidea, such as enlarged infraorbital foramen and multiserial incisor enamel, were acquired via common ancestry and do not reflect the relationship. Distylomyidae is apparently different from other ctenodactylid families and represents an independent family. The high degree of penetration of the hypoflexus in the upper molars and the asymmetrical dental pattern in upper and lower cheek teeth, may suggest a close affinity with hystricognathous *Cephalomys*. However, we must admit that more evidence is necessary to resolve the relationships of Distylomyidae with ctenodactylid and hystricognathous rodents.

AGE OF THE LOCALITIES: The Suosuoquan Formation, characterized by a set of reddish sandy mudstones, is broadly exposed in the northern Junggar basin, Xinjiang. It rests comformably, uncomformably, or disconformably on the underlying Oligocene, Eocene, or Paleozoic beds from place to place (Ye et al., 2003). The age of the Suosuoquan fauna has been controversial. It has been considered either late Oligocene (Tong, 1987; Tong et al. 1990; Wu et al., 1998) or early Miocene to middle Miocene (Ye et al., 2000, 2003). More recently, Meng et al. (2006) revised the age for the faunas from the Suosuoquan Formation on the basis of new paleomagnetic and fossil data. Three mammal assemblage biozones have now been recognized in the lower portion of the Suosuoquan

Formation, ranging from latest Oligocene to early Miocene in age.

Prodistylomys lii is recorded from the Chibaerwoyi locality, where fossils mostly occur in beds A and B (7–12 m, and 14–21 m from the base of the formation, respectively). Fossils from those two levels are basically the same and have been united in one assemblage, traditionally known as the Suosuoquan fauna (Ye et al., 2003) or as Suosuoquan Mammal Assemblage Zone III, early Miocene (21.688–21.159 Mya), by Meng et al. (2006).

Locality XJ200601 is a new locality, 25 km southwest of Burqin. At this locality 25.5 m thick sediments of the Suosuoquan Formation are preserved, overlying uncomformably the late Oligocene Tieersihabahe Formation (fig. 1). The fossils were discovered in the red clay 3–6 m above the contact of the two formations. Our preliminary faunal list shows that the fauna greatly resembles the early Miocene Suosuoquan Mammal Assemblage Zone III from the Chibaerwoyi locality, sharing 70% of the taxa at the generic level (table 2). The primary distinction between these two faunas is the dominance of *Distylomys burqinensis* and *Bellatona* sp. and the occurrence of *Prodistylomys wangae* in the XJ200601 fauna.

Distylomyid rodents are geographically restricted to northern China and bear particular chronological value. Three species have been described for *Distylomys*: *D. qialishanensis*, *D. tedfordi*, and *D. burqinensis*. *D. qianlishanensis* was collected from the late Oligocene Yekebulage Formation of Inner Mongolia (Wang, 1988). *D. tedfordi* was described from the AMNH Tairum Nor collection; its precise stratigraphic level was not clear. Wang (1997) suspected that it came from nearby Oligocene deposits. However, additional specimens from the Tairum Nor locality confirm the age estimate of middle Miocene (13–11.8 Mya) for *D. tedfordi* (Wang et al., 2003). As mentioned above, *D. burqinensis* from XJ200601 locality is morphologically intermediate between *D. qianlishanensis* and *D. tedfordi*, suggesting that the XJ200601 fauna is older than the Tairum Nor fauna but younger than the Yekebulage fauna.

TABLE 2

Faunal list of Locality XJ200601 in comparison with Suosuoquan Mammal Assemblage III of Chibaerwoyi (Ye et al., 2003: table 21.4), and A6 assemblage of Qi'an II section (Guo et al., 2002); table 1)

Locality XJ200601	*SIII*	*A6*
Insectivora		
Amphechinus or Mioechinus sp.	+	
Metexallerix sp.	+	
Galerix? sp.		
Lagomorpha		
Sinolagomys sp.	+	+
Bellatona sp.		
Desmatolagus sp.		
Alloptox sp.		
Ochotonidae indet.	+	
Rodentia		
Atlantoxerus sp.	+	
Prodistylomys wangae, n. sp.	+	+
Distylomys burqinensis, n. sp.		+
Litodontomys sp.	+	+
Cricetodon sp.	+	
Tachyoryctoides sp.	+	+
Rodentia, gen. et sp. indet.	+	
Carnivora	+	
Hyaenidae indet.		

P. lii was collected from early Miocene Suosuoquan Mammal Assemblage Zone III. *P. wangae* is more derived than *P. lii* in having reduced roots, suggesting that the XJ200601 fauna is younger than the Suosuoquan Mammal Assemblage Zone III of the early Miocene (21.688–21.159 Mya).

Bellatona sp. from XJ200601 locality may represent the earliest occurrence of the genus since other *Bellatona* species occur prior to the middle Miocene (Dawson, 1961; Erbajeva, 1988; Zhou, 1988); this first appearance datum may mark the beginning of the new stage. Therefore, we consider the XJ200601 fauna as a new mammal assemblage younger than Suosuoquan Mammal Assemblage Zone III.

XJ200601 fauna can be correlated to the A6 assemblage (early Miocene, 20 Mya) from the Qian-I section (Guo et al., 2002; table 2). Based on our preliminary comparison, *D. burqinensis* is most comparable in stage of evolution to *D.* cf. *tedfordi* and *D.* cf. *qianlishanensis* from the A6 assemblage of the Qian-I section. The assemblages also have *Sinolagomys*, *Tachyoryctoides*, *Litodontomys* sp. in common.

ACKNOWLEDGMENTS

We thank Banyue Wang (IVPP) and Mary R. Dawson (Carnegie Museum of Natural History) for discussions; Xie Shuhua for preparation; Emily T. Griffiths for SEM; Zheng Xinwei for field assistance; and Mary R. Dawson and Lawrence J. Flynn for comments on the manuscript. The work was supported by the Knowledge Innovation Program of the Chinese Academy of Sciences (KZCX2-YW-120) and the National Natural Science Foundation of China (40872032). Bi was supported by the IUP Senate Fellowship, and the School of Graduate Studies and Research, Dean's Office of the College of Natural Sciences and Mathematics, and Department of Biology at the Indiana University of Pennsylvania. Additional support was provided by the National Science Foundation (grant EF-0629811 to J.M.).

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