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A new vole from Xizang, China and the molecular phylogeny of the genus *Neodon* (Cricetidae: Arvicolinae)

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Abstract

During a faunal survey in southern Xizang, we collected 27 specimens of voles that could not be identified as any known species in the Arvicolinae. These specimens shared the following morphological characteristics, not corresponding with any other arvicoline species: the first lower molar possessed five closed triangles, the third upper molar exhibited either four or three inner angles, and the tails of all specimens measured 30% of the body length. Their proximal baculum of the glans was very sturdy and trumpet-shaped, the distal baculum was tongue-like and sturdy, and the lateral bacula were very short. Molecular phylogenetic analyses based on nucleotide sequences of the mitochondrial cytochrome *b* (cyt *b*) gene clustered these specimens as a distinct lineage within the genus *Neodon.* According to the morphological and molecular data, we described them as a new species, *Neodon linzhiensis*. Our phylogenetic analysis strongly supported that *Lasiopodomys fuscus, Phaiomys leucurus, Neodon sikimensis, N. irene* and the new species formed a monophyletic group, not including *N. juldaschi.* We suggested that *L. fuscus* and *P. leucurus* should be transferred to *Neodon* and that *N. juldaschi* should be removed from this genus. Following our new delineation of *Neodon*, we proposed a redefinition of the morphological diagnostic characters of the genus.

Key words: new species, Arvicolinae, *Neodon*, *Lasiopodomys fuscus*, Tibet

Introduction

The genus *Neodon* Horsfield 1841 is classified within the subfamily Arvicolinae (Musser & Carleton 2005). The taxon is variously treated as a genus (Hinton 1923, 1926; Ellerman 1941; Musser & Carleton 2005), subgenus of *Pitymys* (Ellerman & Morison-Scott 1951; Corbet 1978; Luo 2000), and a subgenus of *Microtus* (Allen 1940; Gromov & Polyakov 1977; Musser & Carleton 1993). Hinton (1923) includes the following species within the genus *Neodon*: *sikimensis, forresti, irene, oniscus* and *carruthersi*. Musser and Carleton (2005) only recognized four species: *sikimensis, forresti*, *irene* and *juldaschi*; they treat *oniscus* as a subspecies of *N. irene* and *carruthersi* as subspecies of *N. juldaschi*. The diagnostic characteristics of this genus, such as described by Hinton (1926), are as follows: first lower molar with three closed triangles in advance of the posterior transverse prism; fourth and fifth spaces of first molar widely confluent and separated from the anterior trefoil; moderate size ears with a distinct antitragus; fore and hind claws equally developed; palate typical of *Microtus* where posterior edge of the bony palate consists of a thick medium projection bordered on either side by deep, open pits; and slight development of spongy bone within the auditory bulla.

During autumn 2007 and 2008, more than 400 small mammal specimens were collected as part of two biodiversity programs: the Rapid Biodiversity Assessment program of Peking University at Linzhi, Xizang, and the Baseline Survey of Gongbu Nature Reserve by the Sichuan Academy of Forestry. During the field work, 27 speci-

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mens of voles belonging to the Arvicolinae could not be morphologically identified to any known species within the subfamily, although they shared with *Lasiopodomys fuscus* and *L. brandtii* the same structure of M^1, M^2, M_2 and M_3, and a relatively short tail.

Herein, based on a combination of molecular phylogenetic analysis and morphological observations, we assess the taxonomic status of those newly collected individuals within Asian voles. The phylogeny is used to suggest taxonomic changes.

Material and methods

Morphological study. In total, 90 preserved specimens of *Neodon* and related genera, including *N. sikimensis*, *N. irene*, *Phaiomys leucurus*, *Lasiopodomys fuscus* and the unassigned specimens were morphologically examined. A number of external, cranial, and dental characters were recorded for each specimen. For comparison, 98 specimens of arvicoline rodents (*Lasiopodomys brandtii*, *L. mandarinus*, *Microtus arvalis*, *M. fortis*, *M. ilaeus*, *M. limnophilus*, *M. maximowiczii*, *M. mongolicus* and *M. oeconomus*) were also examined (Appendix I). Abbreviations used in the morphological comparison followed Liu *et al*. (2007): tail length (TL), ear length (EL), head body length measuring from snout to the anus (HBL), hind foot length excluding the claws (HFL), weight (g) of the fresh specimen, claw length of the forefinger (CLF), skull greatest length (SGL), skull basal length (SBL), condylobasal length (CBL), zygomatic breadth (ZB), mastoidal breadth (MB), least interorbital width (IOW), skull height (SH), length of maxillary toothrow (LMxT), width across molars (M-M), length of the mandibular toothrow (LMbT), and breadth across the two upper incisor breadth (TUIB).

Preparation of the glans penis followed Hooper (1958) and Lidicker (1968). Bacular structures were assessed from translucent preparations of the glans. Measurements and abbreviations for the glans and bacula were based on Hooper (1958), Yang and Fang (1988) and Yang *et al*. (1992) as follows: length of glans (LG); diameter of glans (DG), total length of bony baculum (TLBB), proximal baculum length (PBL), width of proximal baculum base (WPBB), width of proximal baculum at the middle point (WPB), height of proximal baculum base (HPBB), distal baculum length (DBL), width of distal baculum (WDB), and lateral baculum length (LBL).

Statistical analyses of the morphological data were performed using SPSS v.12.0 for Windows (SPSS Inc. 1999). Descriptive statistics (mean, standard deviation, and observed range) were computed for each species. Principal component analysis (PCA) was used to obtain a general view of intra- and interspecific variation. We projected the most informative factors of individuals to detect differentiation of morphological measurements between the unassigned specimens and species of *Lasiopodomys*, *Microtus* and *Neodon*. A canonical discriminant analysis was used to morphologically associate the new specimens with an established genus. Two discriminant functions, based on the measurements of 76 specimens of *Neodon*, *Microtus* and *Lasiopodomys*, were a priori determined to be significant at a probability of 0.01. Because the unassigned specimens and *M. limnophilus* were poorly distinguished in the projection of individuals over the 1st, 2nd and 3rd factors, we conducted *t*-tests to identify significant differences between the two species.

Field work was conducted in accordance with animal care and used guidelines established by the American Society of Mammalogists (Animal Care and Use Committee 1998).

Molecular phylogenetic study. A total of 27 samples, representing two putative species of *Neodon* (*N. sikimensis* and *N. irene*) and the unassigned specimens, were analyzed using the mitochondrial cytochrome *b* (cyt *b*) gene. Additionally, 22 specimens representing four species from related genera (*Lasiopodomys fuscus*, *L. brandtii*, *Microtus fortis* and *M. limnophilus*) of Arvicolinae were included and sequenced. Four sequences of *Neodon* were retrieved from GenBank, along with 29 representatives of different genera in the Arvicolini and different subgenera of *Microtus*, as follows: *Lasiopodomys mandarinus* (2 sequences), *Chionomys nivalis* (1), *Blanfordimys bucharensis* (1), *Arvicola terrestris* (1), and 24 sequences representing 18 species from ten subgenera of *Microtus* (Appendix II). We selected additional taxa for a more speciose phylogenetic analysis based on the prior studies of Jaarola (2004) and Galewski *et al*. (2006). A member of subfamily Cricetinae, *Mesocricetus auratus*, was chosen as the primary outgroup because previously the subfamily was resolved as the sister group of Arvicolinae (Galewski *et al*. 2006). Sample localities were indicated in Fig. 1 and detailed information was given in Appendix II.

Total DNA was extracted from 95% alcohol-preserved liver or muscle tissue using the standard method of phenol / chloroform (Sambrook & Russell 2001). The entire cyt *b* gene was amplified using primers described in

Delisle and Strobeck (2002). Prior to sequencing, PCR products were purified using a commercial kit (Watson Bio-Medical). Double-stranded PCR products were directly sequenced from both directions using an ABI 3730 Genetic Analyzer (Applied Biosystems) following the manufacturer's protocols.

Alignment of cyt *b* was straightforward as there were no indels. The inadvertent amplification of pseudogenes (Zhang & Hewitt 1996) was checked by translating the sequences into amino acid sequences using Mega 3.0 (Kumar *et al*. 2004).

Maximum likelihood (ML) and Bayesian inferences (BI) methods were used to hypothesize phylogenetic (matrilineal) relationships. The ML analysis was completed in RaxML (Stamatakis *et al*. 2008) with default parameters. For BI, the sequences were partitioned by codon position, and three partitions were given (codon position 1, pos. 2, pos. 3). The best-fit evolutionary models for each partition were assessed with MrModeltest 2.3 using the AIC criterion (Huelsenbeck & Crandall 1997; Posada & Crandall 1998, 2001). BI was implemented using the program MrBayes 3.1 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). The following models were selected: SYM+I+G (first codon positions), GTR+I (second codon positions), and GTR+I+G (third codon positions). Three runs were performed with four Markov chains (three heated chains and a single cold chain) starting from a random tree. Each of these runs was conducted with a total of 60 million generations and sampled every 1000 generations. Stationarity was confirmed by inspecting plots of ln (*L*) against generation (Rambaut & Drummond 2003) in the program Tracer 1.2; the first 1000 generations were discarded as burn-in. Posterior probabilities (PP) for nodes were assembled from all post burn-in sampled trees.

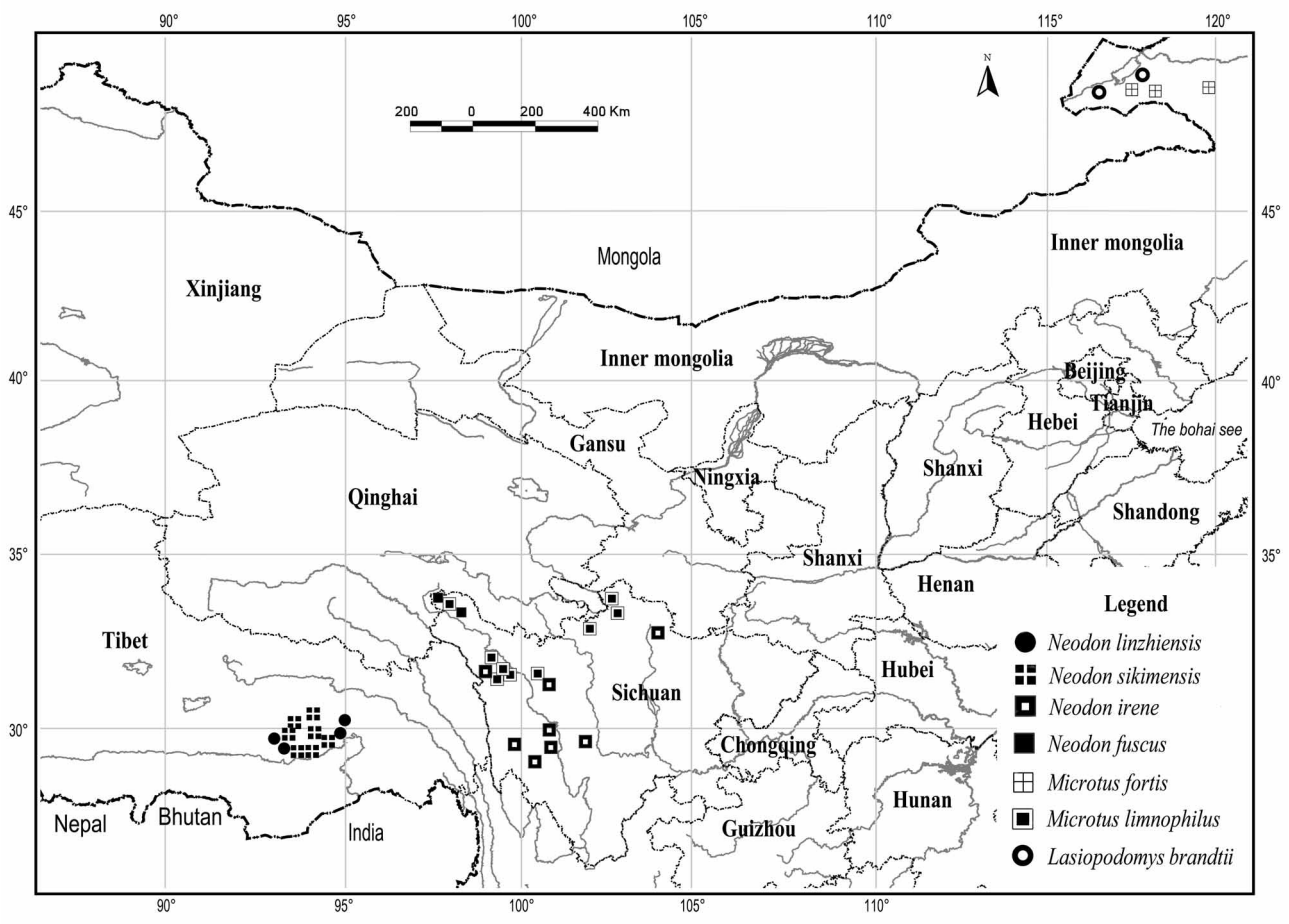

FIGURE 1. Collection localities of samples of voles sequenced in this work.

Results

Morphological study. Detailed morphological characters of the unidentified specimens and comparison with related taxa were listed in Tables 1–3 and Figs 2–3.

TABLE 1. External and cranial measurements (mm) of five species of *Neodon* from China (see methods for abbreviations).

Taxa	*N. linzhiensis* **sp. nov.**		*N. sikimensis*	*N. irene*	*N. leucurus*	*N. fuscus*
	holotype	other specimens				
W(g)	44	36.2(26–48)$^{n=24}$	40.5(27–49)$^{n=16}$	28.8(23–38)$^{n=19}$	50.1(38–56)$^{n=14}$	46.13(34–73)$^{n=8}$
HBL	100	104.2(92.0–115.0)$^{n=24}$	110.38(102.0–121.0)$^{n=16}$	97(82.0–105.0)$^{n=19}$	112.8(102.0–120.0)$^{n=17}$	102.75(95.0–122.0)$^{n=8}$
TL	37	32.6(24.0–39.0)$^{n=24}$	43.27(36.6–52.0)$^{n=15}$	30.1(23.0–35.0)$^{n=19}$	31.1(26.0–33.0)$^{n=17}$	32.38(28.0–42.0)$^{n=8}$
HFL	17	17.4(16.0–20.0)$^{n=24}$	19.72(18.0–22.0)$^{n=16}$	15.8(18.0–18.0)$^{n=19}$	18.1(17.0–19.0)$^{n=17}$	19.63(18.5–22.0)$^{n=8}$
EL	15	13.8(12.0–15.0)$^{n=24}$	14.34(13.0–15.5)$^{n=16}$	13.1(11.0–15.0)$^{n=19}$	12.3(12.0–13.0)$^{n=17}$	13.63(12.5–14.5)$^{n=8}$
SGL	26.64	25.67(23.74–27.80)$^{n=15}$	27.34(25.22–28.28)$^{n=16}$	23.29(21.06–24.94)$^{n=15}$	28.8(27.0–30.0)$^{n=6}$	28.39(27.78–29.50)$^{n=3}$
SBL	24.4	23.97(21.88–26.34)$^{n=15}$	25.42(23.62–26.70)$^{n=15}$	21.88(19.66–23.10)$^{n=18}$	26.85(25.1–28.26)$^{n=6}$	27.01(26.46–27.60)$^{n=3}$
CBL	25.5	24.9(23.32–27.06)$^{n=14}$	26.74(24.64–27.80)$^{n=16}$	23.05(20.96–24.10)$^{n=19}$	27.5(26.1–28.74)$^{n=5}$	27.61(27.28–28.12)$^{n=3}$
ZB	14.94	14.53(13.22–15.98)$^{n=16}$	15.26(13.94–16.20)$^{n=13}$	13.45(11.80–14.78)$^{n=17}$	17.26(16.3–17.96)$^{n=7}$	16.37(15.74–17.26)$^{n=3}$
IOW	3.22	3.32(3.12–3.54)$^{n=19}$	3.9(2.76–4.18)$^{n=16}$	3.19(2.94–3.58)$^{n=19}$	3.91(3.68–4.06)$^{n=9}$	3.34(2.92–3.48)$^{n=5}$
MB	12.54	12.22(11.50–12.92)$^{n=16}$	12.73(12.00–13.30)$^{n=15}$	11.16(10.40–11.90)$^{n=19}$	13.94(13.26–14.92)$^{n=10}$	13.87(13.68–14.12)$^{n=3}$
SH	9.42	9.55(9.18–10.00)$^{n=16}$	9.99(9.18–10.60)$^{n=15}$	8.58(7.84–9.42)$^{n=19}$	11.22(10.42–11.76)$^{n=9}$	11.27(10.62–11.78)$^{n=3}$
ABL	7.42	7.13(6.58–7.54)$^{n=19}$	7(6.38–7.50)$^{n=16}$	6.06(5.20–7.12)$^{n=19}$	8.11(7.54–8.64)$^{n=11}$	7.93(7.42–8.36)$^{n=8}$
LMxT	5.8	5.74(5.34–6.12)$^{n=24}$	6.16(5.80–6.38)$^{n=16}$	5.1(4.40–5.54)$^{n=19}$	6.8(5.18–6.32)$^{n=9}$	5.65(5.10–6.70)$^{n=8}$
LMbT	5.72	5.72(5.30–6.12)$^{n=24}$	6.18(5.75–6.44)$^{n=16}$	5.09(4.42–5.66)$^{n=19}$	6.85(5.94–7.32)$^{n=16}$	5.69(5.18–6.58)$^{n=7}$
M-M	5	4.94(4.72–5.32)$^{n=24}$	5.26(4.94–5.56)$^{n=16}$	4.46(4.08–4.78)$^{n=19}$	5.78(5.94–7.4)$^{n=16}$	5.22(4.82–5.84)$^{n=7}$

TABLE 2. Morphological comparison among *Neodon*, *Microtus* and *Lasiopodomys* (EL, HBL, and CLF: mm) (see methods for abbreviations).

Genera	Species	EL	TL/HBL	SH/ZB	ZB/SGL	CLF	Ear and hindfeet
Neodon	*linzhiensis* sp. nov.	13.8	0.31	0.78	0.57	2.34	Frontal base of the ears without long hairs; back of hindfeet covered with short and sparse hairs; the back of toes had few hairs; plantar hairs short and sparse
	sikimensis	14.3	0.39	0.78	0.56	2.60	
	irene	13.1	0.31	0.77	0.58	2.30	
	fuscus	13.6	0.32	0.81	0.58	2.93	
	leucurus	12.3	0.28	0.65	0.60	2.83	
Lasiopodomys	*brandtii*	11.8	0.20	0.68	0.58	3.17	Frontal base of the ears with long hairs, which covered upon external auditory canal; back of hindfeet and toes covered with long and dense hairs; plantar hairs dense
	mandarinus	10.2	0.22	0.58	0.63	2.89	
Microtus	*limnophilus*	13.8	0.36	0.83	0.54	2.12	
	fortis	12.9	0.39	0.76	0.52	2.49	Frontal base of the ears without long hairs; back of hindfeet and toes covered with short and sparse hairs; plantar hairs short and sparse
	oeconomus	12.5	0.38	0.68	0.54	2.65	
	arvalis	11.2	0.32	0.65	0.56	2.72	
	mongolicus	13.0	0.38	0.68	0.55	2.79	
	ilaeus	11.4	0.32	0.65	0.57	2.81	
	maximowiczii	14.0	0.41	0.68	0.55	3.13	

TABLE 3. Comparison of glans penis and morphology among five species of *Neodon* (PB: Proximal baculum; DB: Distal baculum; LB: Lateral baculum; DP: Dorsal papilla; OCP: Outer crater papilla; UL: Urethral lappet; see methods for other abbreviations)

Characters	*Neodon linzhiensis* **sp. nov.** (n=9–25)	*Neodon sikimensis* (n=4–16)	*Neodon irene* (n=6–19)
LG	4.11(3.80–4.50)	4.15(4.00–4.30)	4.23(4.00–4.50)
DG	2.42(2.30–2.70)	2.63(2.40–2.80)	2.29(2.20–2.50)
PB	Bone, sturdy, trumpet-shaped	Bone, anterior part pole-like, proximal part rhombus	Bone, anterior part pole-like, proximal part rhombus
DB	Bone, tongue-like	Bone, stick-like and distal part getting smaller	Bone, stick-like, symmetrically
LB	Bone, stick-like, medium ossified	Bone, stick-like but slightly ossified	Bone, medium ossified
DP	Conical-like	Conical-like	Two forks
OCP	No obvious papilla	No obvious papilla	No obvious papilla
UL	Three forks, and equal height	Three forks, and equal height	Two forks
TLBB	3.89 (3.30–4.20)	4.28 (4.00–4.60)	4.20 (4.10–4.30)
PBL	2.86 (2.25–3.20)	3.15 (3.00–3.50)	2.90 (2.80–3.00)
WPBB	1.54 (1.40–1.70)	1.95 (1.90–2.00)	1.49 (1.33–1.90)
WPB	0.46 (0.35–0.65)	0.43 (0.40–0.50)	0.44 (0.42–0.50)
HPBB	0.44 (0.30–0.60)	0.58 (0.50–9.70)	0.62 (0.50–0.75)
DBL	1.01 (0.90–1.20)	1.13 (1.00–1.20)	1.25 (1.17–1.33)
WDB	0.48 (0.40–0.60)	0.65 (0.60–0.70)	0.37 (0.30–0.42)
LBL	0.58 (0.50–0.70)	0.70 (0.60–0.80)	0.64 (0.58–0.80)
The first lower molar	Five closed triangles; six angles in the inner side, and four in the outer side	Three closed triangles; six angles in the inner side, and four in the outer side	Three closed triangles; five angles in the inner side, and four in the outer side
The third upper molar	50% specimens have four inner angles in M^3, the rest have three inner angles	Four inner angles in the inner side	Three inner angles in the inner side
Temporal ridges	Very distinct temporal ridges, fused to a linear median interorbital crest; the squamosals, frontals, and parietals modified with ridges	Very distinct temporal ridges, fused to a linear median interorbital crest; the squamosals, frontals, and parietals modified with ridges	Temporal ridges a little weak and not distinct; the squamosals, frontals, and parietals not modified with ridges

continued.

Characters	*Neodon leucurus* (n=5–17)	*Neodon fuscus* (n=2–8)
LG	4.44(4.40–4.50)	4.90(4.80–5.00)
DG	2.62(2.50–2.80)	2.90(2.80–3.00)
PB	Bone, anterior part welding head like, proximal part flask-like, and the bottom flat	Bone, anterior part welding head like, proximal part rhombus
DB	Bone, triangular	Bone, triangular
LB	Cartilaginous	Bone, stick-like but minusculely ossified
DP	Conical-like	Two forks
OCP	Three-four papilla every side, very small	No obvious papilla
UL	Two forks	Three forks, and equal height
TLBB	4.30 (4.00–4.50)	4.10 (3.90–4.30)

continued next page

TABLE 3. (continued)

Characters	*Neodon leucurus* (n=5–17)	*Neodon fuscus* (n=2–8)
PBL	3.22 (3.00–3.40)	3.00 (2.90–3.10)
WPBB	2.00 (1.90–2.10)	2.00 (1.90–3.10)
WPB	0.68 (0.60–0.80)	0.45 (0.40–0.50)
HPBB	0.54 (0.40–0.70)	0.81 (0.70–0.92)
DBL	1.02 (0.90–1.20)	1.05 (1.00–1.10)
WDB	0.56 (0.50–0.60)	0.60 (0.60–0.60)
LBL	Cartilaginous	0.36 (0.30–0.42)
The first lower molar	Three closed triangles; five angles in the inner side, and three in the outer side	Four closed triangles; five angles in the inner side, and four in the outer side
The third upper molar	Three inner angles in the inner side	Three inner angles in the inner side
Temporal ridges	Very distinct temporal ridges, but hardly fused to a linear median interorbital crest; the squamosals, frontals, and parietals modified with very distinct ridges	Very distinct temporal ridges, fused to a linear median interorbital crest; the squamosals, frontals, and parietals modified with very distinct ridges

Morphologically, the unidentified specimens shared the following characteristics with the putative members of *Neodon*: (1) medium size head and body length, 100–110 mm (Table 1), (2) similar ratio of tail to body length (Table 2), (3) similar palate shape, and 1st and 2nd upper molar patterns (Fig. 2), and (4) similar morphological characteristics of glans penis, possessing a sturdy proximal and distal bacula, two slightly ossified lateral bacula, and no outer crater papilla (Table 3; Fig. 3).

A Principal Component Analysis (PCA) was conducted to evaluate morphological variation in 16 morphological measurements (HBL, TL, EL, SGL, SBL, CBL, ZB, IOW, MB, SH, ABL, M-M, LMxT, LMbT, LM and LIL) among the unidentified specimens and the species of the genera *Lasiopodomys*, *Microtus* and *Neodon*. All variables had positive loadings of high magnitude on the 1st component (accounting for 57.4% of the variance), indicating most of the variation involved size. The first three components explained about 84.0% of the total variance (Appendix III). Thirteen measurements, except TL, IOW and EL, contributed more than 67% to the 1st factor. TL and IOW contributed more than 69% to the 2nd factor and EL contributed 96.1% to the 3rd factor. Results of the multivariate analysis were shown in Fig. 4. The trivariate scatter plot of specimen scores on components 1, 2 and 3 showed that the unidentified specimens were distinct from the other 10 species and that the three genera could be distinguished clearly. The unidentified specimens clustered with three species of *Neodon* and *Lasiopodomys fuscus* at the lower left corner of the plot while four species of *Microtus* (excluding *M. limnophilus*) clustered at the top of the plot and two species of *Lasiopodomys* clustered at the lower right corner of the plot.

A canonical discriminant analysis separated and correctly classified most of the original specimens of *Microtus* and *Lasiopodomys*. Of the 76 original specimens from the three genera, 98.7% were correctly classified, which verified the validity of two discriminant functions. Twelve of 14 (85.7%) unidentified specimens grouped into *Neodon* (Appendix IV).

Results from Levene's test showed that variances of 16 morphological measurements of the 11 species and unidentified specimens were equal. Thus, a *t*-test was applied to test for equality of means among 16 measurements from the unidentified specimens and *M. limnophilus* (Appendix V). The results of the *t*-test showed significant differences between the two species in TL, ZB, MB, SH, ABL, M-M, LMxT, LMbT, and LIL.

The unidentified specimens could not be morphologically associated with any known species, and they were clearly differentiated from all other species of Asian voles. Thus, the null hypothesis of conspecificity was rejected by the morphological data.

Molecular analysis. After alignment, 1140 base pairs were obtained from 33 samples, representing 20 different haplotypes (excluding sequences retrieved from GenBank). No deletions, insertions or stop codons were found, indicating that paralogous nuclear insertions likely had not been amplified. New sequences were deposited in GenBank (accession numbers: HQ123593–HQ123620; Appendix II). The ML and BI trees were generally identical in topology; conflicting nodes observed between the two analyses were generally poorly supported (Figs. 5 and 6).

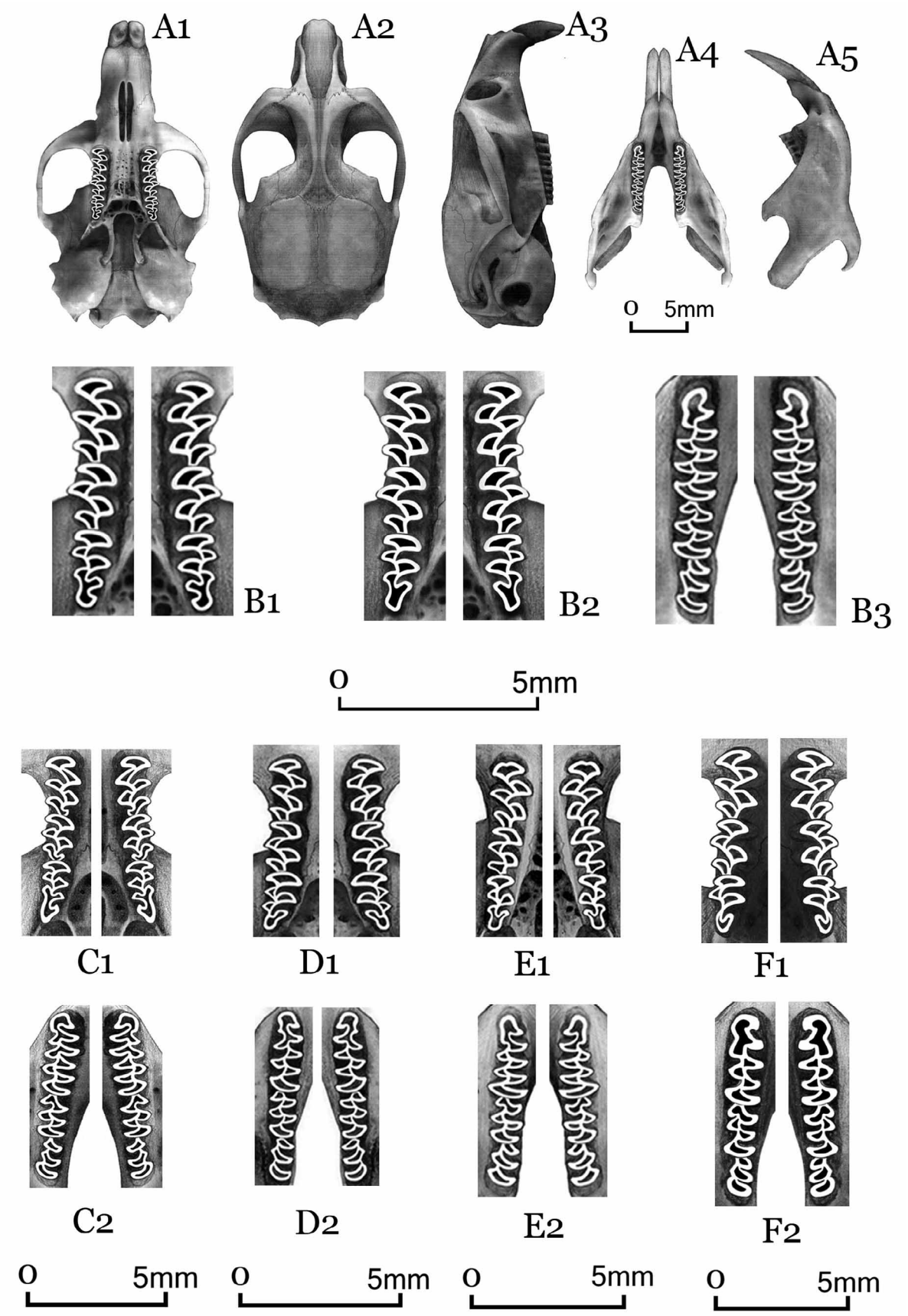

FIGURE 2. Skull of the new species *Neodon linzhiensis* (A1: ventral view; A2: dorsal view; A3: lateral view; A4: lower jaw (ventral); A5: lower jaw (lateral)), and teethrows of five species of *Neodon* (B1, B2 and B3: *N. linzhiensis*; C1 and C2: *N. sikimensis*; D1 and D2: *N. irene*; E1 and E2: *N. fuscus*; F1 and F2: *N. leucurus*).

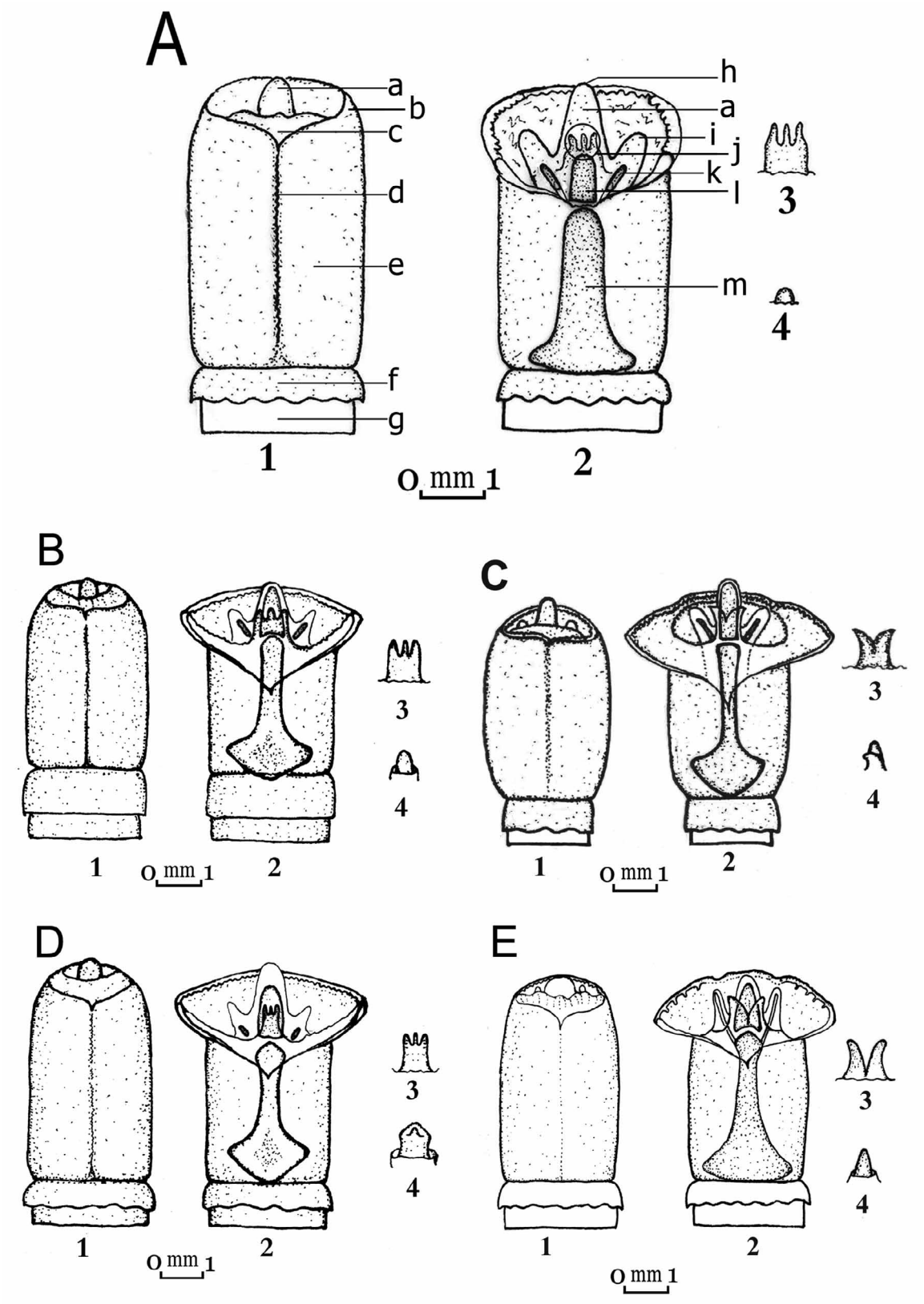

FIGURE 3. Comparison of the glans penis of six voles (A: *Neodon linzhiensis*; B: *N. sikimensis*; C: *N. irene*; D: *N. fuscus;* E. *N. leucurus*). Numbered views are 1: glans; 2: midventral cut view; 3: urethral lappet; 4: dorsal papilla. For *N. linzhiensis*, lettered structural features are: a. distal baculum; b. outer crater; c. inner crater; d. ventral groove; e. glans; f. prepuce; g. penis body; h. station of dorsal papilla; i. lateral baculum (cartilage); j. urethral lappet; k. lateral baculum (bony part); l. distal baculum (bony part); and m. proximal baculum.

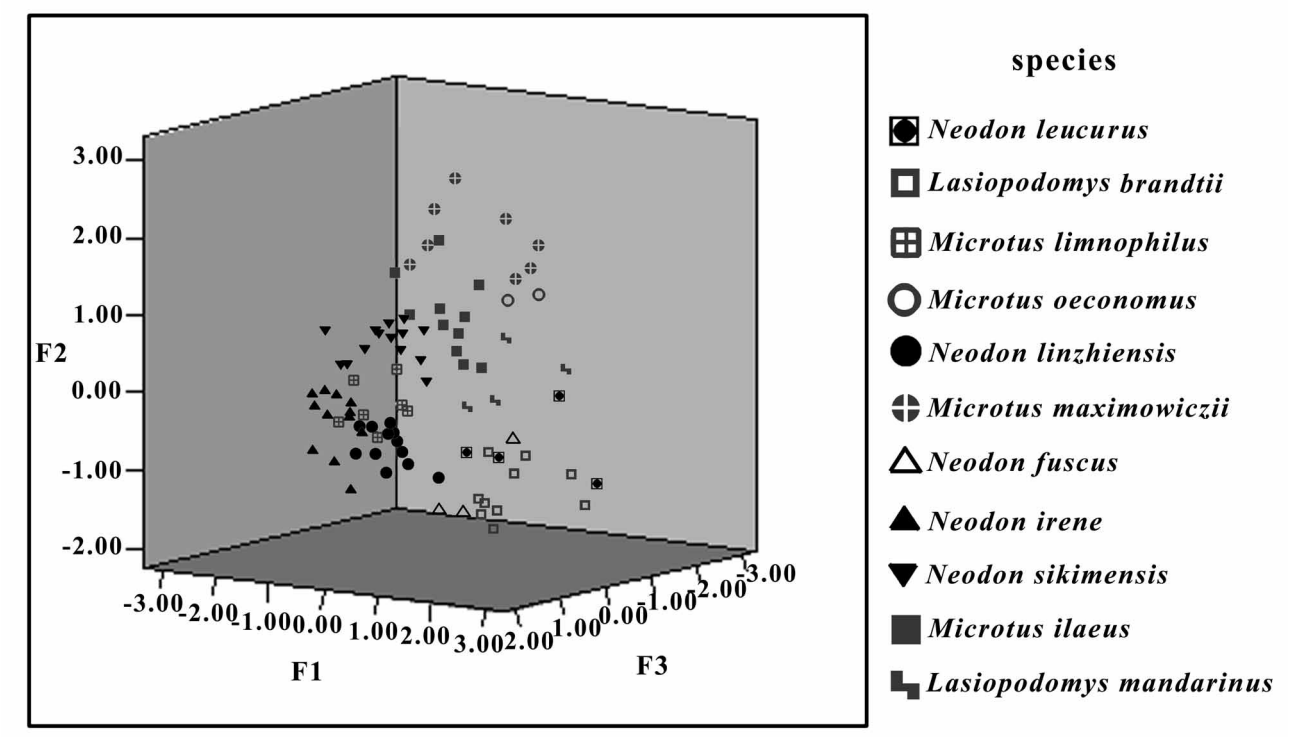

FIGURE 4. Multivariate relationships among 11 species of the genera *Lasiopodomys*, *Microtus* and *Neodon*. Projections of individual specimen scores from principal component analysis on the 1st, 2nd and 3rd factors (F1 to F3, respectively).

Two putative representatives of *Neodon* (*N. sikimensis* and *N. irene*), *Phaiomys leucurus*, *Lasiopodomys fuscus* and four unidentified specimens grouped as a strongly supported lineage in both analysis (PP=100%, BS=91%). Within this lineage, *L. fuscus* showed a sister-group relationship with *P. leucurus*. Excluded from this cluster, *Neodon juldaschi* grouped with *Blanfordimys bucharensis*. Interesting, two species of *Lasiopodomys* (*L. brandtii* and *L. mandarinus*) were very distantly related to *L. fuscus* (Figs. 5 and 6); they either rooted at the base of the tree or formed the sister-lineage of *Microtus gregalis*. The latter group branched in the middle part of the tree within the tribe Arvicolini; the group never clustered near *L. fuscus* (Figs. 5 and 6).

Our sampling included the type species of *Lasiopodomys* (*L. brandtii*). The consistent clustering of *L. fuscus* within *Neodon* and the consistent separation of *L. fuscus* from the other two representatives of *Lasiopodomys*, including *L. brandtii*, required reassignment of *L. fuscus* to *Neodon* as *Neodon fuscus* (Büchner, 1889). Further, *Phaiomys leucurus* consistently clustered within the genus *Neodon*. Therefore, we assigned the species as *Neodon leucurus* (Blyth, 1863). *Neodon juldaschi* consistently clustered with *Blanfordimys bucharensis*, the type species of its genus. Therefore, we assigned *N. juldaschi* as *Blanfordimys juldaschi* (Severtzov, 1879). On the basis of these results, we assigned the unidentified specimens to a new species of *Neodon*.

Species description

Neodon linzhiensis Liu, Sun, Liu, Wang, Guo and Murphy sp. nov

Holotype: Adult female, collected by Shaoying Liu, Yang Liu and Rui Liao on 22 August 2007. The specimen was prepared as a skin with cleaned skull and deposited in Sichuan Academy of Forestry (XZLL02002).

Type locality: Gongbu Nature Reserve, eastern Linzhi, Xizang, China, 29.72891° N and 94.75630° E, 3890 m above sea level (a.s.l.; Fig. 1).

Measurements of holotype: Weight: 44 g; HBL: 100 mm; TL: 37 mm; HFL: 17 mm; EL: 15 mm; SGL: 26.64 mm; SBL: 24.4 mm; CBL: 25.5 mm; ZB: 14.94 mm; IOW: 3.22 mm; MB: 12.54 mm; SH: 9.42 mm; ABL: 7.42 mm; LMxT: 5.80 mm; LMbT: 5.72 mm; M-M: 5.00 mm (Table 1).

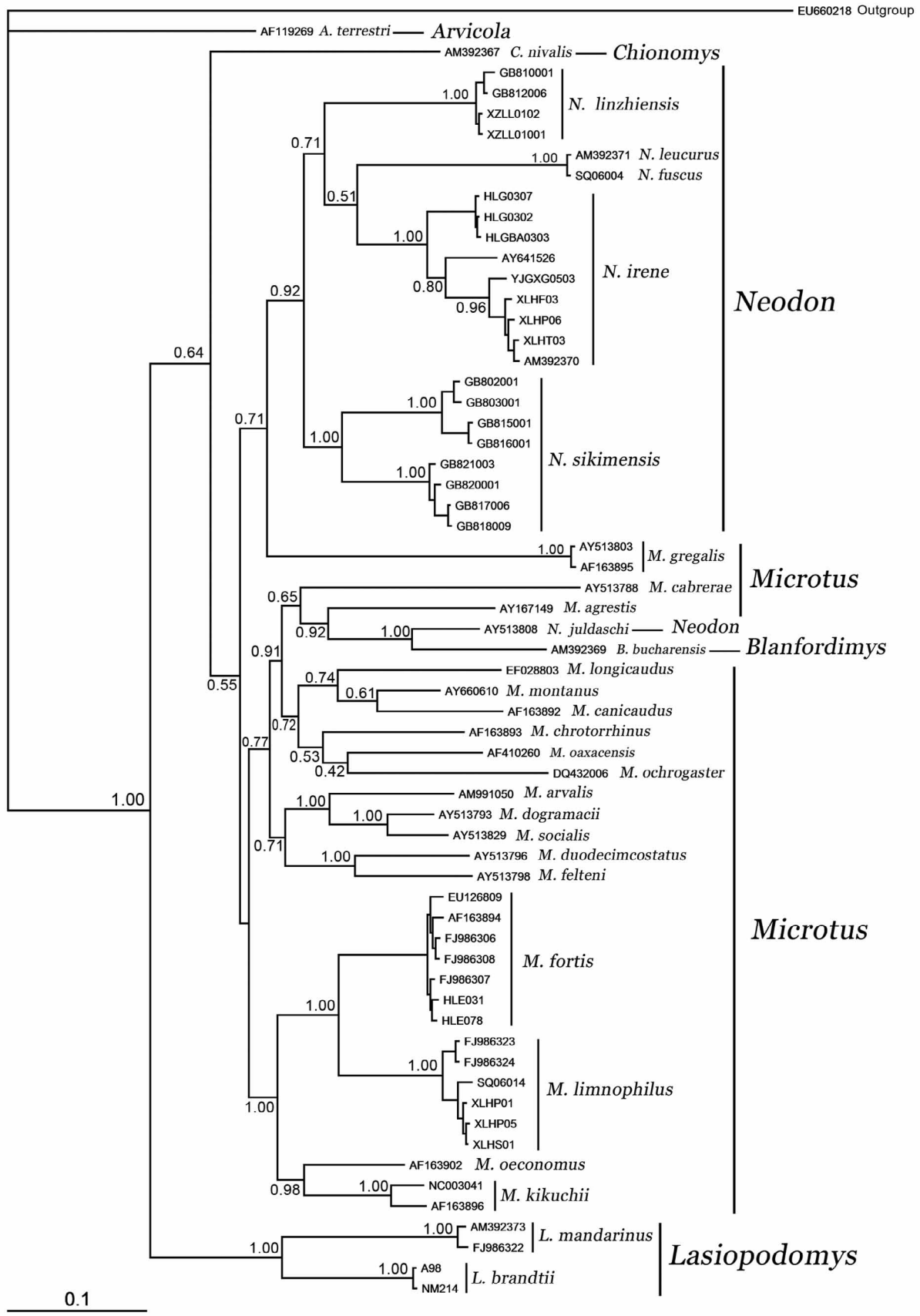

FIGURE 5. Fifty percent majority rule consensus tree from a Bayesian inference analysis of cytochrome *b* nucleotide sequences. Numbers at nodes represent posterior probabilities.

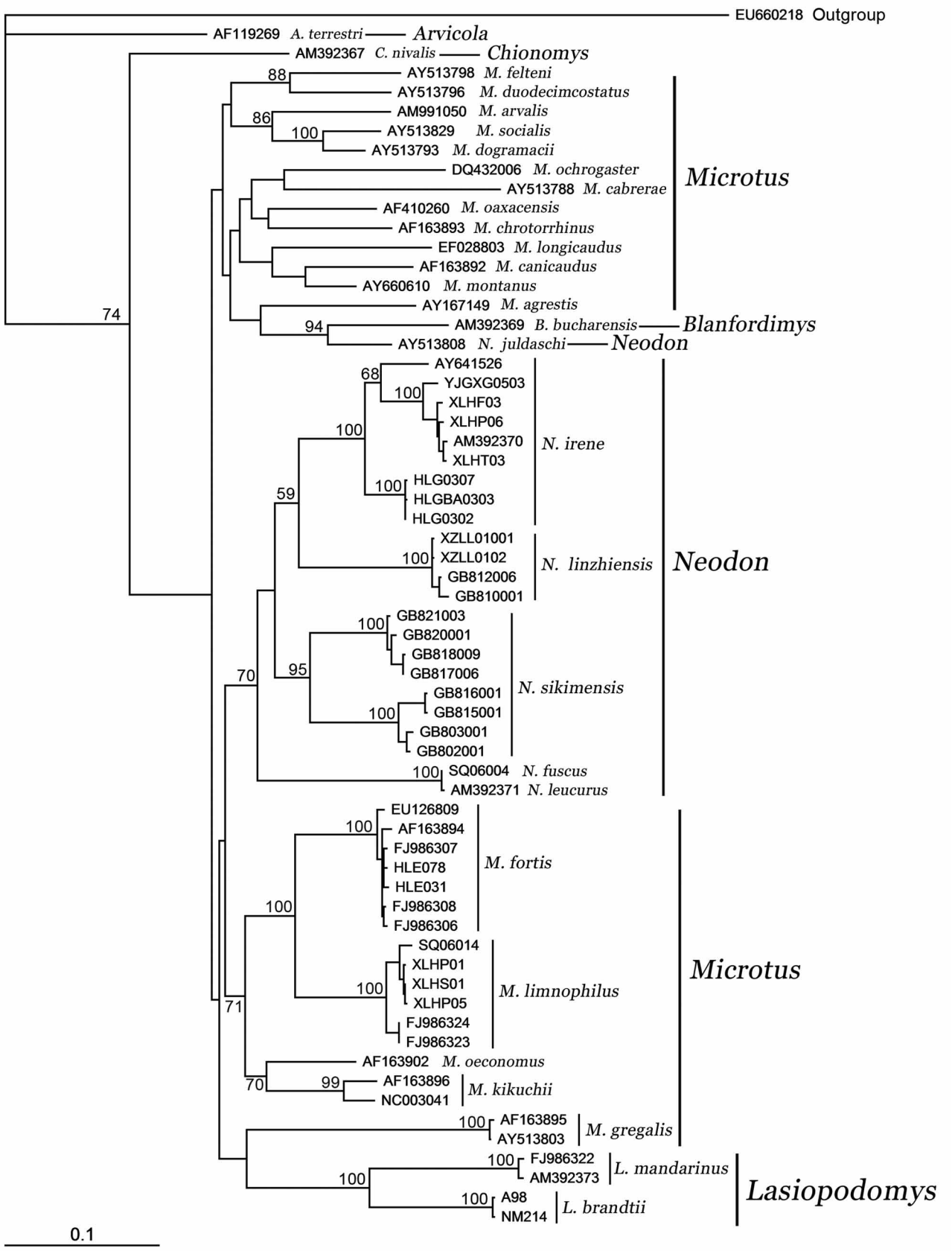

FIGURE 6. Maximum likelihood (ML) tree reconstructed from cytochrome *b* nucleotide sequences based on GTR + I + G model and rooted with *Mesocricetus auratus*. Bootstrap support above 50% is shown at nodes.

Paratypes: Sixteen specimens, skins with skulls; male specimens with glans penes. Twelve specimens (XZLL01001, ♀; XZLL01002, ♂; XZLL01003, ♂; XZLL01004, ♂; GB09N188, ♀; GB09N189, ♂; GB09N190, ♂; GB09N201, ♂; GB09N205, ♀; GB09N206, ♀; GB09N207, ♀; and GB09N211, ♂) were collected from Lunang Town (29.72894° N, 94.72942° E, 3890 m a.s.l., 2 kilometers west of the type locality), Linzhi County, Xizang, China. Another specimen (XZLL02003, ♂) was collected from the type locality. Three specimens (GB081001, ♂; GB081101, ♀; and GB081102, ♂) from Langxian County (29.70298°–29.74884° N; 93.3300°9–93.35358° E, 3640–3770 m a.s.l.) Xizang, China.

Additional specimens. Ten specimens. Three (XZLL02001, ♂; GB09N204, ♂; and GB09N210, ♂, with skull broken) were from the type locality; three (XZLL01005, ♀, with skull broken; XZLL01006, juvenile, ♀; and XZLL01007, juvenile, ♂) were from 2 kilometers west of the type locality; four specimens (GB080505, ♂; GB080406, ♀; B081103, ♀; and B081206, ♀, with skulls broken) came from Langxian County, China.

Geographic distribution. The new species is recorded only from Gongbu Nature Reserve, Linzhi, China (Fig. 1). The type locality consists of an abandoned field adjacent to cropland plants with highland barley (*Hordeum vulgare* L. var. *nudum* Hook f.).

Etymology. The name is derived from the type locality, Linzhi County.

Diagnosis. An arvicoline rodent with the typical palate of *Microtus*. The 1st lower molar has five closed triangles and six inner and five outer angles. The inner side of the 3rd upper molar of 50% specimens exhibits four angles; the remaining specimens have three. The 1st transversal loop of the 3rd lower molar lacks an outer angle, thus the 3rd lower molar exhibits only two outer angles and three inner angles. The tail is short, only 30% of head and body length. Fore and hind claws moderately developed. Frontal base of ears without long hairs. Back of hindfeet covered with short, sparse hairs. Back of toes with few hairs and plantar hairs short and sparse. Skull with very distinct temporal ridges fused to form a linear median interorbital crest. Squamosals, frontals, and parietals modified with ridges. The baculum is unique, with the proximal baculum trumpet-shaped and sturdy, the distal baculum tongue-shaped and sturdy, and the lateral bacula slightly ossified. The mean cyt *b* distances (p-distance) between *Neodon linzhiensis* and other species of *Neodon* are 10.9–12.6%.

Description. Generally, the holotype is black-brown in pelage. Dorsum is covered with hairs. Hairs are thin and long, about 8–10 mm. The proximal end of fur is black-grey, and the distal end is black-brown and dense over the body. Among furs, there are sparse guard hairs which were black, longer and firmer than the undercoat. The ventrum is more lightly colored than the dorsum. The ventral fur is black-gray at the base and off-white at the tip, with no guard or pile hairs; the color from the throat to belly and anus is uniform, but the tips of hairs on the ventral middle are faint yellow. The transition between the darker dorsal and lighter ventral pelage is not abrupt. The margin of lip is grey-white. The pelage of the paratypes is similar to that of the holotype.

Mystacial vibrissae are mostly white, but some are black (18–20 each side). The shortest vibrissa is about 7 mm, and the longest one is about 28 mm.

The ears project slightly above the pelage, with the rim on the front of the ears covered with dense fur; pelage is gray at the base and black-brown at the tip; the back of the ears has thin black-gray fur. The dorsal tail is black-brown and the underside is light gray-white. The hairs of the tip of the tail are slightly long. Hairs on the forelimbs are black-gray, and the base of the hairs on the dorsal surface of the forefoot is black-gray; the tip is grey-white. The pelage on the hindlimbs is dark-gray. Hairs on the dorsal surface of the hindfoot are almost similar with those of the forefoot. The dorsal part of claws is black and ventral part is grey-white and translucent. There are five palmar pads and six plantar pads. Females have eight mammae consisting of two pectoral pairs and two inguinal pairs.

The skull is sturdy (Fig. 2 A), with the dorsal profile straight, and the brain case flattened. The nasals are broad anteriorly and narrow posteriorly. The posterior margin of the nasals is circinal, and protrudes in front of the maxilla. The posterior and anterior of the frontal bone are broad, while narrow in the middle. The interparietal bone is broad and irregularly indented, with the anterior middle part protruding to the frontal bones. Ridges in the interorbital space are very distinct; in an old specimen the two ridges syncretizes into a crest. There are two ridges behind the temporal bone and above the auditory bulla. The squamosals, frontals, and parietals are modified with ridges. The zygomatic arches are sturdy. Auditory bullae are medium-size. The incisory foramen is long and narrow, averaging 1.2 mm in width and 5.2 mm in length. The posterior palate is typical of that of *Microtus*, continuing as a narrow bridge, sloping dorsally to join the anterior edge of the mesopteryoid fossa, and separating the two lateral pits. Many small nutritive foramina occur on the palatine and pterygoid, and the mandibles are sturdy.

The upper incisors are narrow (TUIB = 1.91 mm) and orange in color. Molars are rootless. The 1st upper molar (Fig.2 B1 and B2) exhibits five closed triangles (two inner and three outer). The 2nd upper molar has four closed triangles (two inner and two outer), the inner triangles are large and the outer triangles are small, forming two inner and three outer angles (Fig.2 B1 and B2). In 50% of the specimens examined, the 3rd upper molar consists of a transverse prism followed by two small outer, and a larger inner, closed triangles, and a C-shaped loop, so this tooth forms four inner and three outer angles (Fig.2 B1). In other specimens, the 3rd upper molar consists of a transverse prism followed by two small outer and a larger inner closed triangles, and a Y-shaped loop, so this tooth forms three inner and three outer angles (Fig.2 B2).

The length of the lower incisors exceeds that of the concave of the mandibular condyle and the coronoid process, and is about 86% of the mandible length. The 1st lower molar (Fig. 2 B3) has five closed triangles in front of the posterior transverse space, the anterior space large and anomalistic forming two inner angles, so that this molar has six inner and four outer angles. The 2nd lower molar (Fig. 2 B3) has four closed triangles in front of the posterior transverse space, the most anterior triangle being the smallest. This molar has three outer and three inner angles. The 3rd lower molar (Fig. 2 B3) consists of three transverse lobes, of which the anteriormost has no external projection. This molar has three inner and two outer angles.

The glans penis of the new species (Fig. 3 A) is broad (Table 3). The exterior of the glans is pole-shaped and has a ventral groove. There are no outer crater papillae. The urethral lappet forks into three branches. The dorsal papilla is conical-like and as high as the outer dorsal crater. The proximal baculum is bony, broad and trumpet-shaped. The distinct distal baculum also is bony and tongue-shaped, but the lateral bacular processes are only slightly ossified (Table 3).

Habitat. The specimens were collected from abandoned farmland and along the footpath of a rice field where highland barley was grown.

Comparison with other species. The new species shares the following characters with other members of *Neodon:* same pattern of M^1, M^2, M_2, and M_3; and same ratio of tail length to head and body length. The new species can be distinguished from its congeners by the following characters: head and body length larger than in *N. irene* and *N. fuscus*, and smaller than in *N. sikimensis* and *N. leucurus* (Table 1); first lower molar with five closed triangles (*N. fuscus* has four closed triangles, and the other species of *Neodon* only three closed triangles. Table 3); inner side of first lower molar with six angles (trait shared with *N. sikimensis*, but different from the other species of *Neodon*, which have only five inner angles); third upper molar multivariate with three or four inner angles (*N. sikimensis* has four inner angles and the other species of *Neodon* have only three. Table 3 and Fig. 2); and the skull is modified with ridges on the squamosals, temporal, frontals, and parietals (differs only from *N. irene*, which is void of skull ridges; Table 3). Characteristics of the five species of *Neodon* as newly defined are listed in Tables 1–3 and Figs. 2 and 3.

The new species shares several characteristics with the known species of *Lasiopodomys*. For example, they have the same structure of M^1, M^2, M_2 and M_3, and the glans penis is without outer crater papilla, and the dorsal papilla is bean-like (Yang *et al.* 1992). The new species can be distinguished by the length of the ear and tail, the number of the inner angles in M^3 and M_1 (Table 2), and the lateral bacula (Yang *et al*. 1992) as follows: M_1 of *Lasiopodomys* has only three inner angles, and M^3 shows only five inner angles. *Lasiopodomys* has a shorter ear, shorter tail length ratio, smaller skull height ratio, broader zygomatic breadth ratio, and longer forefinger claw; and the palmar and plantar possess denser hairs, and the base of front of the ears develops dense and long hairs. The lateral bacula of *Lasiopodomys brandtii* are cartilaginous.

Compared with *Microtus*, the new species is morphologically most similar to *M. limnophilus*, with which it shares the same pattern of M^1, M^2, M_2, and M_3, and the same ratio of the tail length to body length. However, 50% of the M^3 of the new species have three inner angles, whereas *M. limnophilus* has four inner angles, and the first lower molar of the new species exhibits five closed triangles and six inner angles, whereas *M. limnophilus* has only four closed triangles and five inner angles. The results of the *t*-test showed significant differences in TL, ZB, MB, SH, ABL, M-M, LMxT, LMbT and LIL between both species (Appendix V).

Morphologically, the glans penis of the new species shares the following characteristics with other members of *Neodon*: no outer or very thin crater papillae; the distal baculum is comparatively short; the lateral bacula only slightly ossified (that of *N. leucurus* is cartilaginous). The new species is unique in having a trumpet-like proximal baculum and a tongue-shaped distal baculum; all other species of *Neodon* have a rhombic or flask-like proximal

baculum and a stick-shaped or triangular distal baculum. Further, the urethral lappet of the new species has three forks, similar to that of *N. sikimensis* and *N. fuscus*, but differing from the two forks of *N. irene* and *N. leucurus*. Similar to *N. sikimensis* and *N. leucurus*, the dorsal lappet of the new species is conical shaped, but this condition differs from *N. irene* and *N. fuscus*, which consists of two forks (Fig.3; Table 3).

Intraspecific variation. Specimens of *Neodon linzhiensis* were collected from two localities along the Yaluzhanbu River. They formed two lineages in the cyt *b* gene tree. The mean uncorrected p-distance of the two lineages was 0.83% and the pairwise genetic distance of the four individuals ranged from 0.17% to 1.05%.

Discussion

Our phylogenetic analyses resolve a strongly supported monophyletic genus *Neodon* that now includes *N. fuscus*, *N. irene*, *N. leucurus*, *N. linzhiensis*, and *N. sikimensis*. Our results are consistent with taxonomic hypotheses generated by Hinton (1923, 1926), Ellerman (1941) and Musser and Carleton (2005), but go against that of Robovsky *et al*. (2008), whom considered *Neodon* (including *Neodon*, *Phaiomys* and *Microtus clarkei*) as a subgenus of *Microtus*.

Neodon fuscus was originally identified as a variant of *Microtus strauchi*, *M. strauchi* var. *fuscus* (Buchner 1889). Ellerman (1941) transferred the species into *Phaiomys* as *P. fuscus*. Subsequently, Ellerman and Morrison-Scott (1951) treated it as *Microtus leucurus fuscus*. Zheng *et al*. (1980), followed by Nowak (1999), Luo *et al*. (2000), Wang (2003) and Musser and Carleton (1993, 2005), assigned it to *Lasiopodomys fuscus*. However, our results do not agree with these taxonomic arrangements. Both the BI and ML trees nest this taxon within *Neodon* and as the sister-species of *N. leucurus* (Figs. 5 and 6).

The sister species relationship between *N. fuscus* and *N. leucurus* is also supported by several morphological traits. The two species share a wide zygomatic arch, a well-marked sagittal interorbital crest, a squamosal with a distinct, marked, blunt protrusion into the posterior region of the orbit, a short, broad nasal that largely falls behind the tip of the premaxilla, a sturdy teeth-row of molars, the upper incisors slightly incline forward, and long (on average exceeding 2.8 mm), black claws on the forelimbs. However, the two species are diagnosed easily by their morphology as follows: whereas *N. fuscus* has four closed triangles in the first lower molar, *N. leucurus* has three; and the fur color of *N. fuscus* is much lighter than that of *N. leucurus*. They are distributed in the same region, the Tanggulashan Mountains of southern Qinghai, yet allopatrically (Zheng 1980). Although these species have a very small pairwise genetic distance (0.1%), we provisionally consider them as being distinct pending further analyses based on additional sequence data, especially data from nuclear genes.

The generic allocation of *Neodon juldaschi* has been unstable. It was originally described as *Arvicola juldaschi* by Severtzov (1879). Corbet (1978) assigned it to the genus *Pitymys* and this allocation was followed by some mammalogists (Feng *et al*.1986; Musser & Carleton 1993; Luo *et al*. 2000). Musser and Carleton (2005) assigned it to the genus *Neodon*. More recently, most mammalogists have suggested that this taxon was a close relative of *N. sikimensis* and *N. irene*. Our molecular analyses did not resolve *N. juldaschi* as belonging to *Neodon*. *Neodon juldaschi* formed a strongly supported clade with *Blanfordimys bucharensis*, and together they clustered with *Microtus agrestis* and *M. cabrerae*. The molecular phylogenies of *Microtus* by Buzan and Kyrstufek (2008), Robovsky *et al*. (2008) and Bannikova *et al*. (2010) also clustered *N. juldaschi* with *Blanfordimys*, and not *Neodon*. *Blanfordimys* was considered to be a subgenus of *Pitymys* (Corbet & Hill 1986), an association not supported by our analyses. Certainly, *N. juldaschi* should be removed from *Neodon*, and perhaps *Blanfordimys* is invalid. In the interest of nomenclatorial stability, we refrain from making formal changes at this stage, pending the availability of additional sequences.

Phallic morphology within the Microtini commonly is used in systematic analyses of European and Asian rodents (Hamilton 1946; Hooper 1958; Anderson 1960; Hooper & Hart 1962). The most important study by Hooper and Hart (1962) assess 33 species of microtines. Some characters of the glans penes of the new species and members of *Neodon* are very distinct from other microtines. Differences include the distal baculum being tongue-like or triangular, the lateral bacula being slightly ossified despite variation in length and the absence of outer crater papilla. Penis morphology may serve to diagnose genera and species. The characters are highly consistent within both genera and species. Although intergeneric and interspecific differences exist, the extent of interspecific divergence within a genus does not necessarily correspond with phyletic history. For example, *N. leucurus* and *N. fuscus*

are sister-species, yet their glans penes have many differences. Several traits of the new species also differ from those of all other species of *Neodon*. For example, whereas the proximal baculum of *N. linzhiensis* is trumpet-shaped and sturdy and the distal ends are tongue-shaped and sturdy, the proximal baculum of the other species of *Neodon* is rhombic or flask-like and the distal baculum is stick-shaped or triangular.

A plethora of molecular studies exists for microtine rodents (e.g. Conroy & Cook 2000; Jaarola *et al*. 2004; Luo *et al*. 2004; Galewski *et al*. 2006; Buzan & Kyrstufek 2008; Buzan *et al*. 2008; Robovsky *et al*. 2008; Bannikova *et al*. 2010). However, few studies consider species of *Neodon* and none focus on the genus itself. Based on the results from our morphological comparison and molecular phylogeny, we conclude that the genus *Neodon* contains five species: *N. sikimensis*, *N. irene*, *N. leucurus*, *N. fuscus* and *N. linzhiensis*. Because samples of *N. forresti* are unavailable, we cannot evaluate the validity of this taxon.

Traditionally, *Neodon* is diagnosed by the first lower molar, which exhibits three closed triangles. However, with the revision of this genus and examination of more specimens, this character tends to be more complex and is not unique to this genus. For example, *N. fuscus* has four closed triangles, and the new species has five, which is normally found in *Microtus* (*M. limnophilus* and *M. oeconomus* have four) and *Lasiopodomys*. Compared to *Microtus*, *Neodon* has a shorter tail length ratio, a slightly longer ear, higher skull height ratio, and a shorter forefinger claw (Table 2). Additionally, *Neodon* and *Microtus* occur in different areas. *Neodon* is only found in the Trans-Himalayan ranges and the Qinghai-Tibetan Plateau, but *Microtus* occurs throughout the Palearctic realm. The ear of *Neodon* species is proposed to have a distinct antitragus and a slight development of spongy bone within the auditory bulla (Hinton 1926). However, in our study all the examined specimens of *Neodon*, *Microtus* and *Lasiopodomys* have an antitragus. Therefore, the antitragus cannot be used as a generic diagnostic character for *Neodon*. The degree of development of the spongy bone within the auditory bulla of *Neodon* varies among species. Whereas the spongy bone of *N. fuscus* has a very high level of development (the same as in *M. limnophilus*), that of *N. sikimensis* is less developed, and other species of *Neodon* have only a slight development (same as in *M. fortis*).

Given our findings, we revise the diagnosis of the genus *Neodon* as follows: tail length about 30% of the head and body length; fore and hind claws moderately developed; frontal base of ears without long hairs; back of hind-feet sparsely covered with short hairs; back of toes with few hairs and plantar hairs short and sparse; temporal ridges distinct (Table 3); squamosals, frontals, and parietals with weak or distinct ridges; first lower molar generally showing three closed triangles, rarely four or five; when the first lower molar has four closed triangles, its body length would be large, and its skull exceeds 28 mm in length; when the first lower molar has five closed triangles, its third upper molar is multivariate in inner angles—50% of the specimens have four inner angles, and the others have three inner angles (Table 3); lateral bacula only slightly ossified or cartilaginous. This genus is distributed only in Trans-Himalayan ranges and the Qinghai-Tibetan Plateau.

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APPENDIX I. Specimens examined in this study.

Neodon linzhiensis: 27 specimens (15♂♂, 12♀♀), 25 adults, 2 juveniles. 20 specimens from Linzhi County; 7 specimens from Langxian County, Xizang Municipality.
Neodon sikimensis: 19 specimens (7♂♂, 12♀♀), 16 adults, 3 juveniles. 9 specimens from Langxian County, 10 specimens from Linzhi County, Xizang Municipality.
Neodon irene: 19 specimens (7♂♂, 12♀♀), adults. 11 specimens from Litang County; 4 specimens from Yajiang County; 2 specimens from Danba County; 1 specimen from Songpan County; 1 specimen from Luhuo County, Sichuan province.
Neodon fuscus: 8 specimens (5♂♂, 3♀♀), adults. From Shiqu County, Sichuan province.
Neodon leucurus: 17 specimens (10♂♂, 7♀♀), adults. All from Xizang Municipality. 1 specimen from Xietongmen County; 2 specimens from Shajia County; 15 specimens from Lasha, Xizang Municipality.
Microtus limnophilus: 16 specimens (11♂♂, 5♀♀), adults. 8 specimens from Ruoergai County; 5 specimens from Dege County; 2 specimens from Luhuo County; 1 specimen from Aba County, Sichuan province.
Microtus ilaeus: 9 specimens (4♂♂, 5♀♀), adults. Three (♀♀) from Emin County, Xinjiang Municipality; 6 (4♂♂, 2♀♀) from Tacheng County, Xinjiang Municipality.
Microtus maximowiczii: 10 specimens (6♂♂, 4♀♀), adults. From Chinese National Zoological Museum.
Microtus arvalis: 10 specimens (7♂♂,3♀♀), adults. From Chinese National Zoological Museum.
Microtus mongolicus:17 specimens (10♂♂, 7♀♀), adults. From Chinese National zoological museum.
Microtus oeconomus: 6 specimens(3♂♂, 3♀♀), adults. From Chinese National Zoological Museum.
Microtus fortis: 11 specimens (6♂♂, 5♀♀), adults. From Inner Mongolia of Neimeng Municipality.
Lasiopodomys brandtii: 13 specimens (7♂♂, 6♀♀), adults. From Chinese National Zoological Museum.
Lasiopodomys mandarinus: 5 specimens (4♂♂, 1♀), adults. From Chinese National Zoological Museum.

APPENDIX II. Specimens used in the molecular study (*retrieved from GenBank).

Genus	Subgenus	Species	Field Number	Locality	GenBank Accession No.
Neodon		*N. linzhiensis*	XZLL01002	Linzhi, Tibet	HQ123617
		N. linzhiensis	XZLL01001	Linzhi, Tibet	HQ123618
		N. linzhiensis	XZLL0103	Linzhi, Tibet	
		N. linzhiensis	XZLL0104	Linzhi, Tibet	
		N. linzhiensis	GB810001	Linzhi, Tibet	HQ123593
		N. linzhiensis	GB812006	Linzhi, Tibet	HQ123594
		N. sikimensis	GB802001	Linzhi, Tibet	HQ123599
		N. sikimensis	GB803001	Linzhi, Tibet	HQ123600
		N. sikimensis	GB815001	Linzhi, Tibet	HQ123601
		N. sikimensis	GB816001	Linzhi, Tibet	HQ123602
		N. sikimensis	GB817006	Linzhi, Tibet	HQ123603
		N. sikimensis	GB818009	Linzhi, Tibet	HQ123604
		N. sikimensis	GB819002	Linzhi, Tibet	HQ123605
		N. sikimensis	GB820001	Linzhi, Tibet	
		N. sikimensis	GB821003	Linzhi, Tibet	HQ123606
		N. irene	YJGXG0503	Yajiang, Sichuan	HQ123619
		N. irene	XLHF03	Dege, Sichuan	HQ123611
		N. irene	XLHP03	Dege, Sichuan	HQ123614
		N. irene	XLHP06	Dege, Sichuan	
		N. irene	XLHP09	Dege, Sichuan	
		N. irene	XLHT03	Dege, Sichuan	HQ123616
		N. irene	HLG0305	Luding, Sichuan	HQ123596
		N. irene	HLG0306	Luding, Sichuan	
		N. irene	HLG0307	Luding, Sichuan	
		N. irene	HLG0302	Luding, Sichuan	HQ123595
		N. irene	HLG0303	Luding, Sichuan	HQ123597
		N. irene	HLG0304	Luding, Sichuan	
		N. irene			AM392370*
		N. fuscus	SQ06004	Siqu, Sichuan	HQ123609
		N. fuscus	SQ06003	Siqu, Sichuan	
		N. fuscus	SQ06005	Siqu, Sichuan	
		N. fuscus	SQ06007	Siqu, Sichuan	
		N. fuscus	SQ06008	Siqu, Sichuan	
		N. fuscus	SQ06010	Siqu, Sichuan	
		N. leucurus			AM392371*
		N. juldaschi			AY513808*
Microtus	*Alexandromys*	*M. fortis*			FJ986306*
		M. fortis			FJ986307*
		M. fortis			FJ986308*
		M. fortis			EU126809*
		M. fortis			AF163894*

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APPENDIX II. (continued)

Genus	Subgenus	Species	Field Number	Locality	GenBank Accession No.
		M. fortis	HLE078	Hailaer, Inner Mongolia	HQ123608
		M. fortis	HLE031	Hailaer, Inner Mongolia	HQ123607
		M. fortis	HLE006	Hailaer, Inner Mongolia	
		M. fortis	HLE032	Hailaer, Inner Mongolia	
		M. fortis	HLE035	Hailaer, Inner Mongolia	
		M. limnophilus			FJ986323*
		M. limnophilus			FJ986324*
		M. limnophilus	SQ06014	Siqu, Sichuan	HQ123610
		M. limnophilus	SQ06016	Siqu, Sichuan	
		M. limnophilus	XLHP01	Dege, Sichuan	HQ123612
		M. limnophilus	XLHS01	Dege, Sichuan	HQ123615
		M. limnophilus	XLHS02	Dege, Sichuan	
		M. limnophilus	XLHS03	Dege, Sichuan	
		M. limnophilus	XLHP05	Dege, Sichuan	HQ123613
	Pallasiinus	*M. oeconomus*			AF163902*
		M. kikuchii			NC003041*
		M. kikuchii			AF163896*
	Agricola	*M. agrestis*			AY167149*
		M. cabrerae			AY513788*
	Microtus	*M. arvalis*			AM991050*
		M. dogramacii			AY513793*
		M. socialis			AY513829*
		M. clarkei			AY641526*
	Terricola	*M. duodecimcostatus*			AY513796*
		M. felteni			AY513798*
	Stenorcanius	*M. gregalis*			AY513803*
		M. gregalis			AF163895*
	Aulacomys	*M. chrotorrhinus*			AF163893*
		M. longicaudus			EF028803*
	Myomes	*M. canicaudus*			AF163892*
		M. montanus			AY660610*
	Pitymys	*M. oaxacensis*			AF410260*
	Pedomys	*Microtus ochrogaster*			DQ432006*
Lasiopodonmys		*L. brandtii*	NM214	Hailaer, Inner Mongolia	HQ123620
		L. brandtii	A98	Hailaer, Inner Mongolia	HQ123598
		L. brandtii	BJ235	Hailaer, Inner Mongolia	
		L. brandtii	BJ262	Hailaer, Inner Mongolia	
		L. mandarinus			AM392373*
		L. mandarinus			FJ986322*
Chionomys		*C. nivalis*			AM392367*
Blanfordimys		*B. bucharensis*			AM392369*
Arvicola		*A. terrestri*			AF119269*
Outgroup		*Mesocricetus auratus*			EU660218*

APPENDIX III. Character loading and percentage of variance explained on the first three components of the principal component analysis; morphological measurements from adult specimens of 11 species of the genera *Lasiopodomys*, *Microtus* and *Neodon.*

Variables	Component		
	1	2	3
M	0.902	0.217	0.068
ZB	0.887	0.256	0.039
LMxT	0.876	0.342	0.043
LM	0.867	0.384	0.101
MB	0.862	-0.187	0.275
SBL	0.86	0.445	0.113
SGL	0.859	0.454	0.151
SH	0.857	0.279	0.113
CBL	0.828	0.494	0.142
LMbT	0.817	0.454	0.060
ABL	0.797	0.289	-0.224
LIL	0.701	0.395	0.228
HBL	0.677	0.358	-0.026
TL	0.206	0.861	0.308
IOW	0.346	0.695	-0.125
EL	0.103	0.112	0.961
Variance exlained (%)	57.408	18.431	8.139

APPENDIX IV. Results of canonical discriminant analysis

		Predicted group membership			Total
		Neodon	*Microtus*	*Lasiopodomys*	
Neodon	Original Counts	33	0	1	34
Microtus		0	28	0	28
Lasiopodomys		0	0	14	14
N. linzhiensis sp. nov.		12	1	1	14
Neodon	Percent (%)	97.1	0	2.9	100
Microtus		0	100	0	100
Lasiopodomys		0	0	100	100
N. linzhiensis sp. nov.		85.7	7.1	7.1	100

APPENDIX V. *t*-test for equality of means of 16 measurements in *Neodon linzhiensis* **sp. nov.** and *Microtus limnophilus*. *significant difference (0.05); ** highly significant difference (0.01).

Characters	t	df	Sig. (two-tailed)
HBL	0.355	19	0.727
TL	-2.351	19	0.030*
EL	1.055	19	0.305
SGL	1.149	19	0.265
SBL	1.043	19	0.310
CBL	0.968	19	0.345
ZB	2.718	19	0.014*
IOW	0.643	18.879	0.528
MB	2.153	19	0.044*
SH	-2.115	19	0.048*
ABL	-2.459	18.854	0.024*
M-M	5.458	19	0.000**
LMxT	2.42	19	0.026*
LMbT	2.889	19	0.009**
LM	1.988	19	0.061
LIL	3.754	19	0.001**