Across the great divide: revision of the genus *Eupetaurus* (Sciuridae: Pteromyini), the woolly flying squirrels of the Himalayan region, with the description of two new species

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The woolly flying squirrel, *Eupetaurus cinereus*, is among the rarest and least studied mammals in the world. For much of the 20th century it was thought to be extinct, until it was rediscovered in 1994 in northern Pakistan. This study outlines the first taxonomic and biogeographical review of the genus *Eupetaurus*, which until now has contained only a single species. Careful review of museum specimens and published records of *Eupetaurus* demonstrates that the genus occurs in three widely disjunct areas situated on the western (northern Pakistan and north-western India), north-central (south-central Tibet, northern Sikkim and western Bhutan) and south-eastern margins (north-western Yunnan, China) of the Himalayas. Taxonomic differentiation between these apparently allopatric populations of *Eupetaurus* was assessed with an integrative approach involving both morphological examinations and molecular phylogenetic analyses. Phylogenetic reconstruction was implemented using sequences of three mitochondrial [cytochrome *b* (*Cytb*), mitochondrially encoded 12S and 16S ribosomal RNA (12S, 16S)] and one nuclear [interphotoreceptor retinoid-binding protein (*IRBP*)] gene fragment. Morphological assessments involved qualitative examinations of features preserved on museum skins and skulls, supplemented with principal components analysis of craniometric data. Based on genetic and morphological comparisons, we suggest that the three widely disjunct populations of *Eupetaurus* are each sufficiently differentiated genetically and morphologically to be recognized as distinct species, two of which are described here as new.

ADDITIONAL KEYWORDS: Himalayan uplift – hypsodont – mammals – rodent – south-west China – South Asian river capture – taxonomy – Tibetan Plateau.

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INTRODUCTION

> …no zoologist has dared to describe it.
> Oldfield Thomas (1888: 256) when describing
> *Eupetaurus cinereus*.

Weighing up to 2.5 kg and with a total length up to 1100 mm, the woolly flying squirrel (*Eupetaurus cinereus* Thomas, 1888) is one of the largest gliding mammals (Roberts, 1997; Zahler & Woods, 1997; Zahler, 2001). This enigmatic species has drawn special attention from mammalogists owing to its uniquely high-crowned (hypsodont) dentition, taxonomic uniqueness, poorly known natural history and endangered conservation status (McKenna, 1962; Zahler, 1996, 2010; Jackson & Thorington, 2012). It was originally described by Thomas (1888) from two skins and a skull that came from the Astor (now Astore) and Gilgit districts in northern Pakistan. Between 1924 and 1994 it was thought to be extinct, until it was rediscovered by the scientific community in Pakistan by Peter Zahler of the Wildlife Conservation Society (Lorimer, 1924; Zahler, 1996, 1998). Until recently, available information indicated that *E. cinereus* was limited to several districts within northern Pakistan and north-western India in the western Himalayan region (Pal *et al.*, 2018, 2020). Records of *Eupetaurus* Thomas, 1888 outside of the western Himalayan region can be traced back as far as Anderson (1879), who identified a 'large grey squirrel' specimen collected from Tibet (now the Xizang Autonomous Region of China), deposited in the Naturalis Museum, Leiden, The Netherlands, which is a specimen of *Eupetaurus* (see below, the holotype NML19524). Another specimen was reported from Sikkim, in north-eastern India, by Agrawal & Chakraborty (1970). Wangchuk *et al.* (2004) reported *Eupetaurus* from Bhutan. Two skins, without skulls, lodged at the Kunming Institute of Zoology, Chinese Academy of Sciences, Yunnan, China (KIZ), were collected in 1973 in north-western Yunnan Province in China by staff of the KIZ (Yang & Wang, 1989). Most recently, camera-trap images of *Eupetaurus* were reported from Mount Gaoligong in north-western Yunnan Province, China (Gao *et al.*, 2017).

Before the present study, there were only 17 known skins and four skulls of *Eupetaurus* in museums worldwide, of which 11 were collected from northern Pakistan. This study also benefitted from seven newly collected *Eupetaurus* specimens from north-western Yunnan, China. Taxonomically, *Eupetaurus* has always been considered a monotypic genus (Jentink, 1890; McKenna, 1962; Thorington & Hoffmann, 2005; Thorington *et al.*, 2012), but Yu (2002) and Yu *et al.* (2004) found that woolly flying squirrels from

Tibet and Yunnan are deeply divergent genetically from those in the western Himalayas, probably reflecting a need to recognize more than one species in this genus. There are also clear morphological distinctions between allopatric populations of *Eupetaurus* (Jackson & Schouten, 2012). Therefore, the aim of this study was to undertake an integrative taxonomic review of the genus *Eupetaurus* across its distribution and make taxonomic recommendations based on interpretations of morphological and molecular data.

MATERIAL AND METHODS

SPECIMENS

A total of 24 specimens of *Eupetaurus* are known in natural history museums, including six specimens in the Natural History Museum, London, UK (BMNH); one in the Naturalis Museum, Leiden, The Netherlands (NML); four at the Bombay Natural History Society, Mumbai, India (BNHS); two in the Zoological Collection of the Zoological Survey of India, Kolkata, India (ZSI); two in the Florida Museum of Natural History, Gainesville, FL, USA (FLMNH); and nine in the KIZ (Supporting Information, Supplementary Data SD1). We have examined all of these specimens except the series at BNHS, but the only skull from the BNHS (specimen #7108, now missing according to Zahler & Woods, 1997) was measured and photographed by Joseph Curtis Moore (McKenna 1962). This allowed us to include it in our comparisons. Most available specimens were skins, and only nine skulls were available for study (two juveniles and seven adults; Supporting Information, Supplementary Data SD1). We also made comparisons with specimens of various other flying squirrel genera in these and other collections, including the American Museum of Natural History, New York, NY, USA (AMNH), the Field Museum of Natural History, Chicago, IL, USA (FMNH) and the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

MORPHOMETRIC ANALYSIS

Dental observations were made under a light microscope (Keyence digital microscope system VHX-2000C with a ×50 Kenyence VH-Z00R lens). Morphological nomenclature of the cheek teeth follows a modified version of that by McKenna (1962) and Li *et al.* (2021) (Fig. 1). Dental abbreviations in the text are D for deciduous, P for premolars, M for molars, superscript (P^x, M^x) for upper premolars and upper molars, and subscript (P_x, M_x) for lower premolars and lower molars.
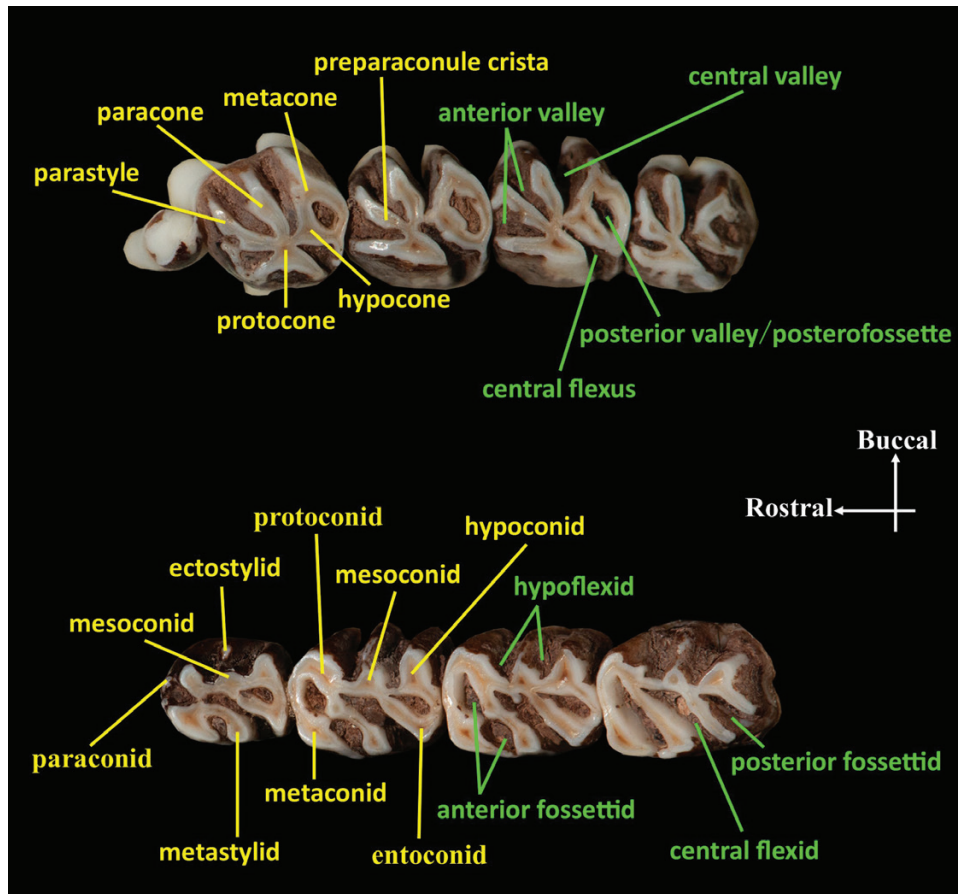
Figure 1. Nomenclature of the *Eupetaurus* cheek teeth: top, upper cheek teeth; bottom, lower cheek teeth.

Craniodental variables were measured with hand-held Vernier callipers (Mitutoyo 500-197; 200 mm) to the nearest 0.01 mm under a desk lamp as necessary, following a modified version of the measurements recorded by Helgen *et al*. (2009) (Fig. 2). The measurements recorded included rostral breadth (RB); width of nasals (WN); length of nasals (LN); interorbital breadth (IOB); postorbital breadth (POB); breadth of braincase (BBC); zygomatic breadth (ZB); width across infraorbital foramen (WAIF); width of incisive foramina (= anterior palatal foramina; WIF); length of incisive foramina (LIF); length of bony palate (LBP); condylobasal length (CBL); maximum skull length (MSL); length of auditory bulla (LAB); width of auditory bullae across external auditory meati (WAAM); width of palate at P^3 (WPP^3); width of palate at P^4 (WPP^4); width of palate at M^1 (WPM^1); width of palate at M^2 (WPM^2); width of palate at M^3 (WPM^3); post-palatal length (PPL); height of braincase, measured from the basioccipital plane to the crown of the braincase (HBC); length of maxillary toothrow (P^3–M^3; LMTR); length of diastema (LD); width of incisors (WI); depth of incisors (DI); width of P^4 (WP^4); width

of M^1 (WM^1); width of M^2 (WM^2); width of M^3 (WM^3); length of angular process (LAP); length of condyloid process (LCP); length of dentary tooth row (LDTR); and width of lower incisor (WLI). Each variable was measured three times, and the mean was used in subsequent analysis.

A principal components analysis based on the covariance matrix was used to evaluate variation in all 34 craniodental variables taken from seven available adult skulls, which were divided into three allopatric populations (west Himalayan population, IMK 9492, FLMNH 28583 and BNHS 7108; central Himalayan population, *NML 19524*; and east Himalayan population, KIZ 034190, KIZ 035087 and KIZ 035088). However, owing to the small sample size, this was only an exploratory analysis. Missing data were filled with the mean of the population. The cheek teeth of FLMNH 28583 were worn excessively; therefore, we replaced its tooth-related measurements with the mean of the population. Raw measurements were log$_{10}$-transformed to standardize variances and improve normality. All analyses were performed using PAST v.4.02 (Hammer *et al.*, 2001).
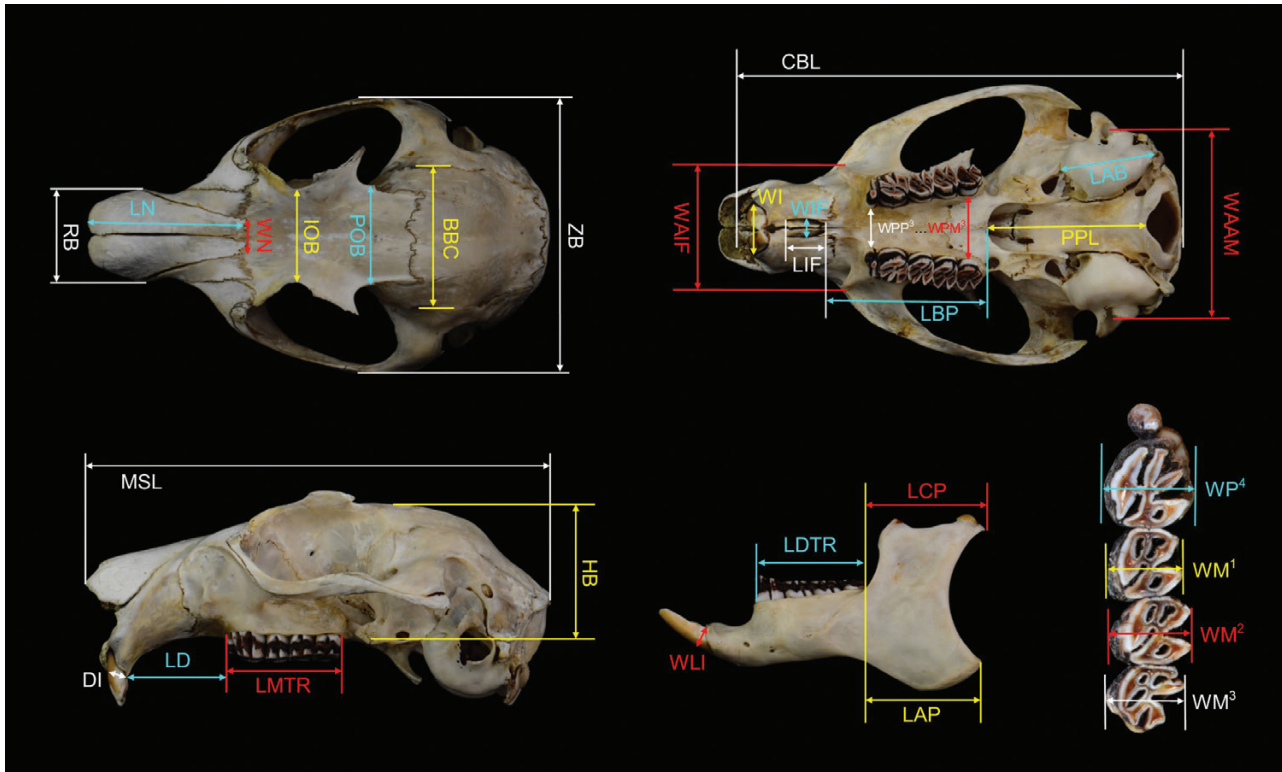
Figure 2. Craniodental measurements taken for this study. See main text for definitions of abbreviations. Owing to space constraints, for WPP³, WPP⁴, WPM¹, WPM² and WPM³ with similar measurement methods we show only the first and last one.

MOLECULAR ANALYSES

Laboratory protocols

Total genomic DNA was extracted from the muscle tissues of four newly collected Yunnan specimens (KIZ 034189–KIZ 034192) using the DNeasy Tissue kit (Qiagen). Three mitochondrial [cytochrome *b* (*Cytb*), 12S ribosomal RNA (12S) and 16S ribosomal RNA (16S)] and one nuclear [interphotoreceptor retinoid-binding protein (*IRBP*)] gene fragment that are commonly used in mammalian molecular studies (e.g. Mercer & Roth, 2003; Yu *et al.*, 2004) were selected for sequencing and analysis. All gene fragments were amplified with rtaq DNA Polymerase (Takara) [primers followed He *et al.* (2010) and Jansa *et al.* (2009) and are presented in Supporting Information, Supplementary Data SD2]. The polymerase chain reaction (PCR) products were purified with the QIAquick PCR Purification kit (Qiagen) and sequenced with the BigDye Terminator Cycle kit v.3.1 using an Applied Biosystems automated sequencer (ABI 3730xl). Sequencing reads were assembled and edited using the DNASTAR LASERGENE v.7.1.

Phylogenetic analyses

We downloaded all previously published sequences for *Eupetaurus* (Yu, 2002; Mercer & Roth, 2003; Yu *et al.*, 2004), in addition to sequence data for various other flying squirrel taxa, from GenBank (Supporting Information, Supplementary Data SD3). We did not include the previously widely used *Aeretes* sequences [GenBank nos AY227593, AY227535 and AY227481] in our analyses, because these come from a misidentified specimen (Roth & Mercer, 2015: 223; Quan Li, pers. obs.). Squirrels from other sciurid subfamilies (Ratufinae and Sciurinae) and the mountain beaver [*Aplodontia rufa* (Rafinesque, 1817), family Aplodontiidae], which is the sister group to all squirrels (Huchon *et al.*, 2002), were selected as the outgroup taxa for phylogenetic analysis.

All gene sequences were aligned using MUSCLE (Edgar, 2004) and assessed manually in MEGA 6 (Tamura *et al.*, 2013). Pairwise *Cytb* divergences were calculated using the Kimura-2 parameter (K2P) model in MEGA 6 (Tamura *et al.*, 2013). Our phylogenetic reconstructions were based on the mitochondrial DNA (mtDNA) plus nuclear DNA

(nDNA) (12S + 16S + *Cytb* + *IRBP*) dataset and the nDNA (*IRBP*) dataset. A partitioning strategy was used to incorporate the variation in evolutionary processes among different sites (Brandley *et al.*, 2005). Appropriate models of DNA evolution for each gene fragment were compared and ranked by the Bayesian information criterion (Luo *et al.*, 2010) in JMODELTEST v.2 (Darriba *et al.*, 2012). The best substitution model for *Cytb* and 12S was GTR+G, and the best model for 16S and *IRBP* was SYM+G. Maximum-likelihood (ML) analyses and Bayesian inference (BI) were performed using RAxML v.7.3.2 (Stamatakis *et al.*, 2008) and BEAST v.1.7.5 (Drummond *et al.*, 2012), respectively.

In ML analysis, the GTRGAMMA model was selected for each partition, and the rapid bootstrapping algorithm was set for running 500 replicates. In BI analysis, we used the relaxed uncorrelated lognormal clock models that allowed the rate in each branch to evolve independently. The BEAST analyses were repeated four times, each analysis for 50 million generations, with a sampling interval of 5000. TRACER v.1.6 was used to confirm the effective sample sizes (ESSs) > 200, and the first 25% of the generations were treated as burn-in. Both ML and BI analyses were performed using resources available in the CIPRES Science Gateway (Miller *et al.*, 2010).

Molecular dating and species delimitations

Divergence times were estimated using BEAST v.1.7.5 (Drummond *et al.*, 2012). The mtDNA + nDNA (12S + 16S + *Cytb* + *IRBP*) dataset was used for molecular dating analyses to avoid overestimation of divergence times. The oldest fossil squirrel, *Douglassciurus jeffersoni* (E. Douglass. 1902), dated to the late Eocene (~37.2–33.9 Mya), was used for calibration (Emry & Thorington, 1984; Goodwin, 2008). We used an exponential distribution for the prior of this calibration and set the lower boundary to 33.9 Mya. All other settings for the analysis were the same as those described for the previous phylogenetic reconstructions.

The single-threshold generalized mixed Yule coalescent (GMYC) model (Pons *et al.*, 2006) was applied to delimit species boundaries and determine the number of putative species. Maximum-likelihood statistics and divergence times were used to estimate the split point from the species to the population level (using the R package 'splits'). We conducted this analysis based on the *Cytb* time-calibrated tree because the availability of *Cytb* sequences for all major geographical regions of occurrence for *Eupetaurus* (from Pakistan, Tibet and Yunnan) best facilitated our examinations of species delimitation in the genus. The Bayesian analysis was based on the Poisson Tree Process model (bPTP, http://species.h-its.org/ptp/; Zhang *et al.*, 2013) with the

ML tree derived from the *Cytb* gene. In addition, the Bayesian species delimitation was evaluated further using BP&P v.3.1 (Yang & Rannala, 2010, 2014), analysed with both A10 and A11 models.

RESULTS

MORPHOLOGICAL COMPARISON

A principal components analysis was used to evaluate morphological variation in 34 craniodental variables among the three allopatric populations of *Eupetaurus*. The first component (PC1) separated individuals mainly on the basis of WIF, WM^1, WM^2, WLI, WM^3 and LAP (63.18% of variation), the second component (PC2) on the basis of WPP^3, IOB, LCP, WN, WP^4 and WIF (16.76% of variation) and the third (PC3) on the basis of WPM^1, WPP^3 and WPP^4 (8.51% of variation; Supporting Information, Supplementary Data SD4). The bivariate scatter plot of specimen scores on PC1 and PC2 clearly distinguished the three allopatric populations from each other (Fig. 3).

External body measurements and masses for each species from the available literature and specimens is found in Table 1. Measurements of variables for all nine available skulls is found in Table 2. Some easily observed distinguishing features of the three species of *Eupetaurus* are summarized in Table 3.

MOLECULAR COMPARISON

Phylogenetic reconstructions generated a similar tree topology with both the mtDNA + nDNA dataset and the nDNA dataset (Fig. 4; Supporting Information, Supplementary Data SD5). In all trees, all *Eupetaurus* samples formed a clade with strong support [i.e. Bayesian posterior probability (PP) ≥ 0.95 and ML bootstrap proportions (BP) ≥ 75]. Within the *Eupetaurus* clade, the samples from Yunnan and Tibet formed a well-supported and independent clade compared with *E. cinereus* from Pakistan (PP = 1.0 and BP = 100; Fig. 4).

Intergeneric relationships of *Eupetaurus* were not recovered consistently in different trees (Fig. 4). In the nDNA tree (Supporting Information, Supplementary Data SD5) and the ML tree of the mtDNA + nDNA dataset (Fig. 4A), *Aeromys* + *Biswamoyopterus* was recovered as the sister clade of *Eupetaurus*, whereas in the BI tree of mtDNA + nDNA dataset (Fig. 4B), *Eupetaurus* showed a sister relationship with a clade comprising *Biswamoyopterus* + *Aeromys* + *Pteromyscus* + *Belomys* + *Trogopterus* + *Pteromys*.

The most recent common ancestor of squirrels can be dated to ~35 Mya. The divergence time between *Eupetaurus* and other flying squirrels is likely to have occurred in the early to mid-Miocene [16.86 Mya; 95%
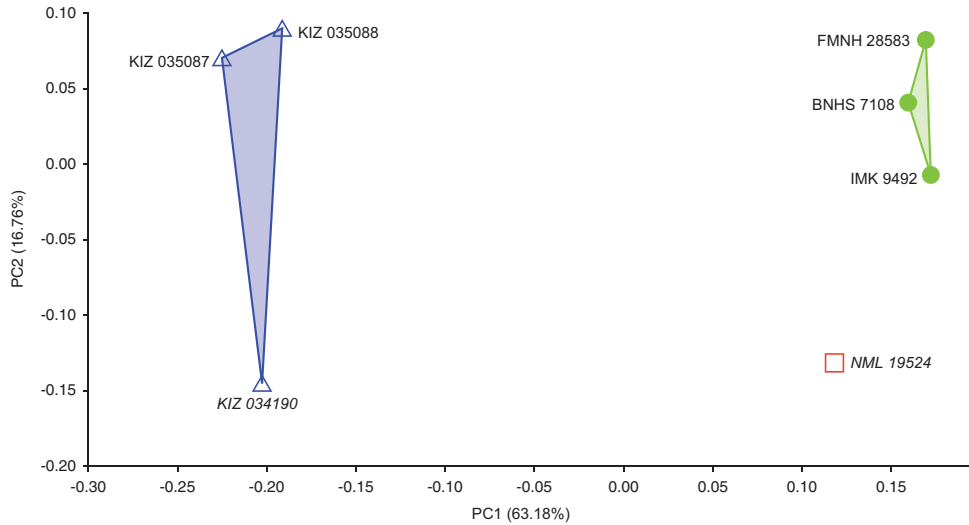
Figure 3. Principal components analysis scatter plot of the skulls of *Eupetaurus*. Key: circles, specimens from Pakistan (*Eupetaurus cinereus*); square, specimen from Tibet (*Eupetaurus tibetensis*); triangles, specimens from Yunnan (*Eupetaurus nivamons*). Abbreviation: PC, principal component.

Table 1. Measurements of external variables recorded from *Eupetaurus*. Measurements of *Eupetaurus cinereus* were taken from Roberts (1997) and Zahler and Woods (1997).

External variables	*Eupetaurus cinereus*	*Eupetaurus tibetensis*	*Eupetaurus nivamons*
Length of head and body (mm)	420–610	468	410–445
Length of tail (mm)	380–545	350+	405–440
Length of ears (mm)	27–49	Unknown	44.5–50
Length of hindfeet (mm)	83–93	Unknown	86–95
Body mass (g)	1420–2500	Unknown	1420–1903

confidence interval (CI) = 13.72–20.46 Mya]. Typical *E. cinereus* from Pakistan probably split from *Eupetaurus* from Yunnan and Tibet by the late Miocene (10.19 Mya; 95% CI = 6.89–13.83 Mya). *Eupetaurus* from Tibet and Yunnan probably split from each other by the Pliocene–Pleistocene boundary (4.46 Mya; 95% CI = 2.28–6.98 Mya).

Molecular divergence within Eupetaurus

Specimens from the three major geographical areas of occurrence for *Eupetaurus* (Pakistan, Tibet and Yunnan) all showed deep respective genetic divergences, grouping into two major clades, east and west. Divergences for *Cytb* measured 14–20% (K2P distance) between specimens from Pakistan and specimens from farther east (Tibet and Yunnan). Divergences for *Cytb* measured 4–5% (K2P distance) between the sample from Tibet and those from Yunnan. These are genetic divergences consistent with or greater than species-level distinctions in many other groups of mammals (Baker & Bradley, 2006), including other squirrel genera (e.g. Harrison *et al.*, 2003; Baker & Bradley,

2006; Helgen *et al.*, 2009). Genetic divergence within *Eupetaurus* samples from Yunnan was considerably smaller, consistent with intraspecific differences (K2P distance = 1.2%). Likewise, minimal genetic difference was observed within samples from Pakistan.

Molecular species delimitation

Cytb tree-based analyses using the single-threshold GMYC model recognized three putative species diverging > 0.51 Mya, indicating that all three regional groupings of *Eupetaurus* (from Pakistan, Tibet and Yunnan) might be recognized taxonomically at the species level (Fig. 5). This was confirmed in our bPTP analysis with strong Bayesian support (PP = 0.814, 0.947 and 0.942, respectively). This level of divergence-time depth is consistent with that between species of squirrels in various other genera (e.g. Hawkins *et al.*, 2016a, b). Furthermore, the delimitation using BP&P has supported the new taxa (PP = 0.99 in A10 model and PP = 0.95 in A11 model; Supporting Information, Supplementary Data SD6).

Table 2. Measurements of skull variables recorded from *Eupetaurus*

Skull variables	ZSI 9492	FLMNH 28583	BNHS 7108*	NML19524	KIZ 034190	KIZ 034192	KIZ 034189	KIZ 035087	KIZ 035088
Age	Adult	Old	Adult	Young adult	Young adult	Juvenile	Juvenile	Adult	Adult
RB	13.37	13.66	16	13.36	14.01	13.57	12.35	16.24	15.86
WN	7.74	7.74	7.7	6.16	6.29	5.83	5.94	7.09	6.38
LN	29.02	26.11	27.5	24.54	27.13	25.05	23.64	26.85	28.77
IOB	19.95	19.95	19	15.78	14.90	14.67	14.08	17.87	15.19
POB	15.02	16.00	16.6	16.43	16.27	16.34	15.96	16.42	16.38
BBC	22.54	21.22	–	22.31	22.34	18.61	19.72	21.74	20.21
ZB	45.73	47.17	46.5	44.43	45.22	41.73	40.09	46.27	47.03
WAIF	19.38	18.33	18.5	17.90	19.93	17.87	17.58	22.57	22.57
WIF	4.86	4.42	–	4.72	3.16	2.70	2.93	2.60	2.77
LIF	7.88	7.19	–	6.40	8.46	5.56	5.61	6.75	6.41
LBP	26.72	27.35	–	25.56	26.07	24.82	24.14	28.00	27.26
CBL	Broken	73.63	72.5	68.52	71.92	65.76	65.66	71.77	73.48
MSL	Broken	76.45	77.5	–	75.30	70.60	69.14	77.30	77.87
LAB	Broken	14.73	15	13.40	14.79	14.31	15.25	15.72	16.07
WAAM	Broken	25.82	–	24.79	29.90	29.14	27.19	31.24	30.47
WPP^3	5.92	7.65	–	6.39	6.08	8.40	7.89	7.76	7.19
WPP^4	6.65	7.65	–	7.44	6.86	7.51	7.43	6.66	5.71
WPM^1	8.46	11.47	–	8.90	8.19	8.82	8.23	8.85	8.37
WPM^2	9.78	11.48	–	10.89	9.44	9.49	9.10	9.96	9.60
WPM^3	11.47	12.33	–	12.39	10.49	9.85	9.68	10.88	10.22
PPL	Broken	Broken	–	23.28	25.60	23.33	22.74	26.10	27.52
HBC	23.40	24.37	–	23.29	23.30	22.34	20.40	22.09	22.54
LMTR	21.59	17.25	21	19.79	18.61	18.55	18.50	20.09	20.76
LD	16.99	18.77	15.5	15.22	16.91	15.15	14.13	16.57	16.60
WI	7.70	8.42	–	7.66	6.68	4.70	5.30	6.29	7.24
DI	3.08	2.80	–	2.57	2.97	2.52	3.15	2.84	2.80
WP^4	5.98	5.16	–	5.20	4.66	4.48	4.15	5.02	5.54
WM^1	5.41	3.34	–	5.07	3.97	3.99	3.92	4.13	4.53
WM^2	5.52	4.60	–	5.09	3.88	4.05	4.22	4.42	4.79
WM^3	4.93	4.24	–	4.53	3.71	3.62	3.68	4.00	4.41
LAP	15.57	16.88	–	15.19	19.24	14.65	18.84	18.85	20.51
LCP	19.79	19.10	–	17.88	16.81	17.41	17.18	19.44	21.03
LDTR	21.12	17.82	21	19.65	19.50	18.84	18.97	21.06	21.61
WLI	3.30	3.02	–	3.11	2.57	2.28	2.29	2.46	2.73

The abbreviations of skull measurements are defined in the main text and illustrated in Figure 2.
*Data from McKenna (1962), measured by Joseph Curtis Moore.

SYSTEMATICS

ORDER RODENTIA BOWDICH, 1821

SUBORDER SCIUROMORPHA BRANDT, 1855

FAMILY SCIURIDAE FISCHER, 1814

SUBFAMILY SCIURINAE FISCHER, 1814

TRIBE PTEROMYINI BRANDT, 1855

GENUS *EUPETAURUS* THOMAS, 1888

Eupetaurus are amongst the largest flying squirrels, with fur that is thick, long and soft. Dorsal coloration ranges from pale grey to brownish grey, and ventral coloration is typically whitish grey. The cylindrical, fox-like tail is long and bushy. The palmar and plantar surfaces are thickly furred between naked pads (Fig. 6).

The skull is generally similar to other flying squirrels (reviewed in detail by McKenna, 1962), with the following diagnostic features (Fig. 7): (1) the snout is long and constricted at the base; (2) the incisors are ungrooved and relatively small, with pale yellow enamel faces; (3) the glenoid fossa opens posteriorly, with the opening placed high on the skull; (4) the coronoid process of the mandible is weak, not rising

Table 3. Easily observed diagnostic features of the three species of *Eupetaurus*

| Character	*Eupetaurus cinereus*	*Eupetaurus tibetensis*	*Eupetaurus nivamons*
Dorsal fur colour	More grey; extensive grey frosting	More brown	More brown
Tail tip colour	Shorter black tail tip, ~5–10% black	Shorter black tail tip, ~10–15% black	Long black tail tip, ~50% black
Rostral breadth	Narrow (13.4–13.7 mm)	Narrow (13.4 mm)	Wide (14–16.2 mm)
Interorbital breadth	Wide (19–20 mm)	Narrow (15.8 mm)	Narrow (14.9–17.9 mm)
Temporal ridge	Posteriorly convergent	Posteriorly convergent	Parallel
Shape of upper cheek teeth	Heart shaped	Heart shaped	Round
Shape of lower cheek teeth	Subsquare	Subrectangular	Subrectangular
Anterior fossettid	A short one	A long one	Two short ones
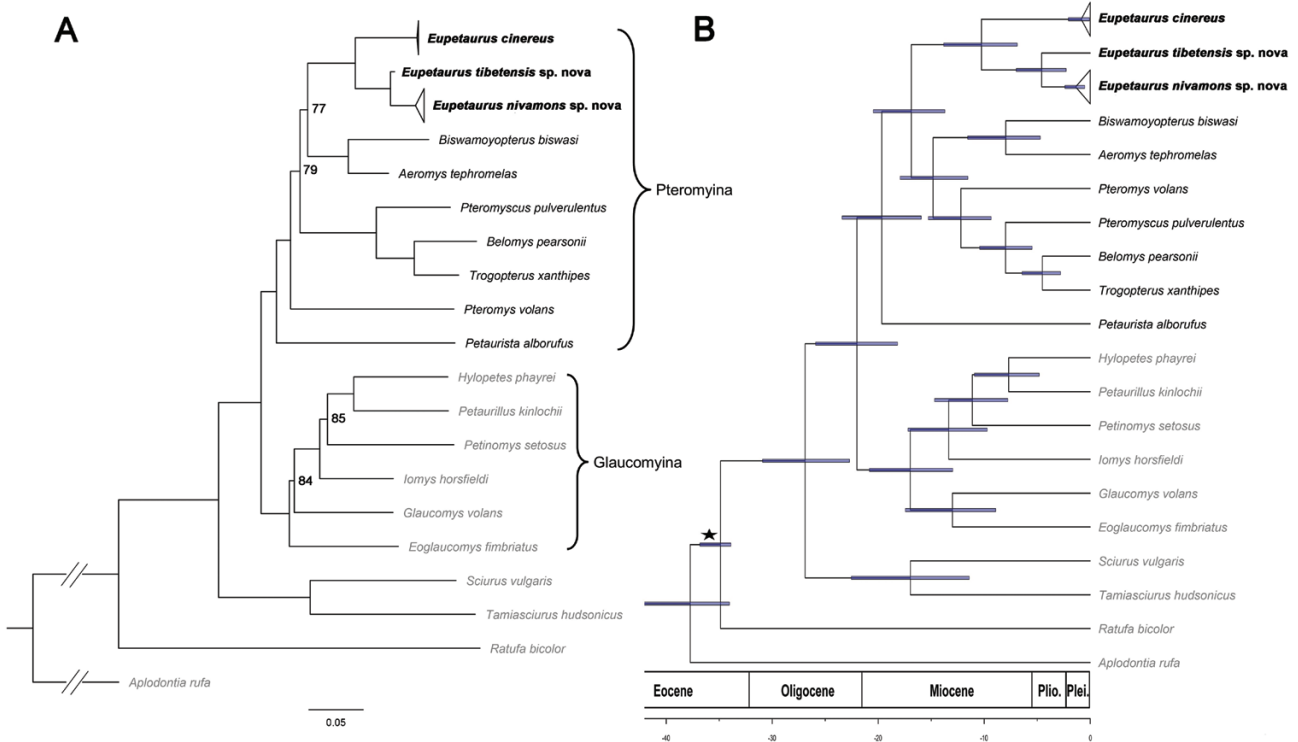
Figure 4. Phylogenetic trees showing the position of the three *Eupetaurus* taxa using combined mitochondrial and nuclear DNA. A, maximum-likelihood tree. B, Bayesian inference tree. We mark only the maximum-likelihood bootstrap proportions < 90 and Bayesian posterior probabilities < 0.9. The star indicates the fossil occurrence used in this study.

above the condyle; (5) the cheek teeth are large, slow to erupt and strongly hypsodont in younger animals (the occlusal surfaces becoming nearly flat after wear); they are enormously expanded vertically (Supporting Information, Supplementary Data SD7), with cusps and their interconnecting ridges combined into lophs and cross-lophs (this remarkable hypsodonty is unlike any other sciurid); (6) the alveolar cavities are strongly swollen to house the unerupted portion of the hypsodont cheek teeth; and (7) 'the pterygoid fossae possess three diagonally elongate pits for the origin of powerful pterygoid musculature' (McKenna,

1962). These diagnostic features appear to relate to *Eupetaurus* feeding primarily on abrasive food, with the incisors reduced in functionality and chewing achieved mainly by anteroposterior trituration of the cheek teeth (McKenna, 1962). Limited available natural history information (mainly for *E. cinereus*) suggests that these squirrels might specialize on eating pine needles (Zahler & Khan, 2003).

The upper cheek-tooth row is strongly convergent anteriorly in adults (although it remains more parallel in juveniles). The P³ is peg-like and strong. The relative size of the upper cheek teeth can be
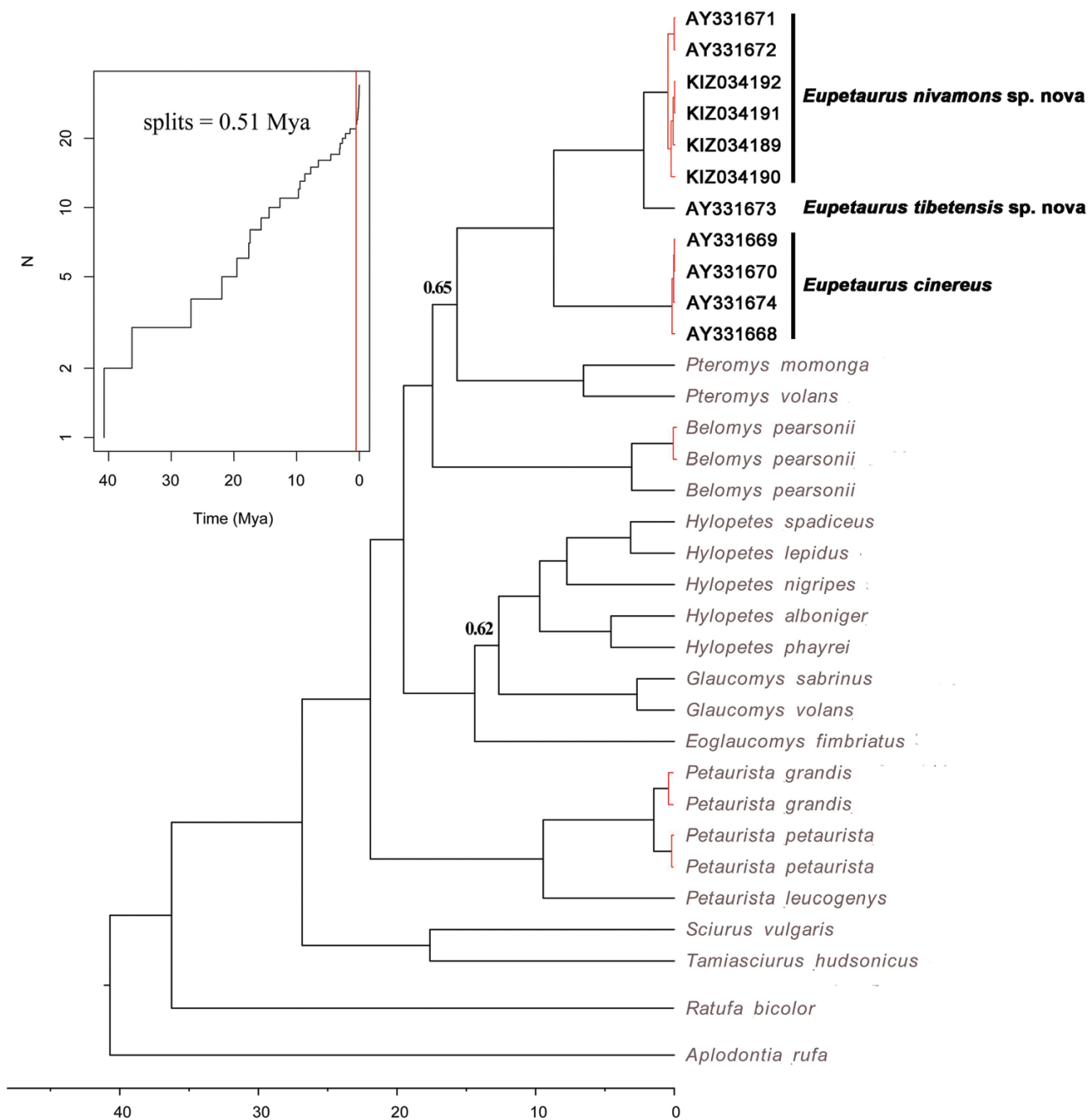
Figure 5. Molecular species delimitation based on generalized mixed Yule coalescent model and *Cytb* data for the three taxa of *Eupetaurus*. Red lines represent intraspecies variation; black lines represent variation above species level.

given as $P^4 > M^1 \approx M^2 > M^3$. The P^4 (and DP^4) and the upper molars have similar structures: the endoloph is strongly folded to form the 'posterolingual diagonal flexus' (see below); the anteroloph, hypertrophic preparaconule crista, paraloph, metaloph and posteroloph are finger-like and connected, in turn, to the buccal side of the endoloph. The anterior valley is wide and divided by the preparaconule crista. When

worn, the preparaconule crista gradually connects with the parastyle to isolate the lingual part of anterior valley into an anterofossette. The central valley is always open. The posterior valley is always closed into a posterofossette, except in the M^3 in early wear.

The relative size of the lower cheek teeth can be given as $P_4 > M_1 \approx M_2 \geq M_3$. The structure of the lower

Figure 6. Skins of the three taxa of *Eupetaurus*. Top row, specimen from Pakistan (*Eupetaurus cinereus* BMNH 14. 2. 10. 1); middle row, Tibet (*Eupetaurus tibetensis NML 19524, holotype*); bottom row, Yunnan (*Eupetaurus nivamons KIZ 034190, holotype*).

molars is relatively simple, with a 'ring' at the front and back, connected by the ectolophid in the middle. The anterior ring is formed by the anterolophid between the protoconid and metaconid, and the protolophid between the protoconid and metastylid. The centre of the anterior ring is one (*E. cinereus* and *E. tibetensis*) or two (*E. nivamons*) anterior fossettids. The lingual edge of the anterior fossettid is not closed in early wear. The posterior ring is formed by the entolophid and posterolophid that run between hypoconid and entoconid. The centre of the posterior ring is one posterior fossettid (talonid basin remnant). The posterior fossettid of M_3 is not closed in early wear. The mesoconid develops into a buccal cusp as strong as the protoconid and hypoconid on the middle of the ectolophid, which divides the hypoflexid into two folds. The central flexid runs from the posterolingual side of the tooth to the base of the anterior fold of the hypoflexid. Generally, DP_4 is similar to the lower molars, but has two opened anterior fossettids and two extra small cusps:an isolated paraconid in front of the buccal anterior fossettid and an isolated ectostylid on the buccal side of the mesoconid (Fig. 8). Also, P_4 possess two open anterior fossettids and an isolated paraconid, but the paraconid will connect with the metaconid and protoconid as the teeth are worn. The mesoconid is very small on P_4 in *Eupetaurus* (Fig. 9F). The entire crown of P_4 is more diagonally oriented than DP_4 and lower molars.

EUPETAURUS CINEREUS THOMAS, 1888

Suggested common name: Western woolly flying squirrel.

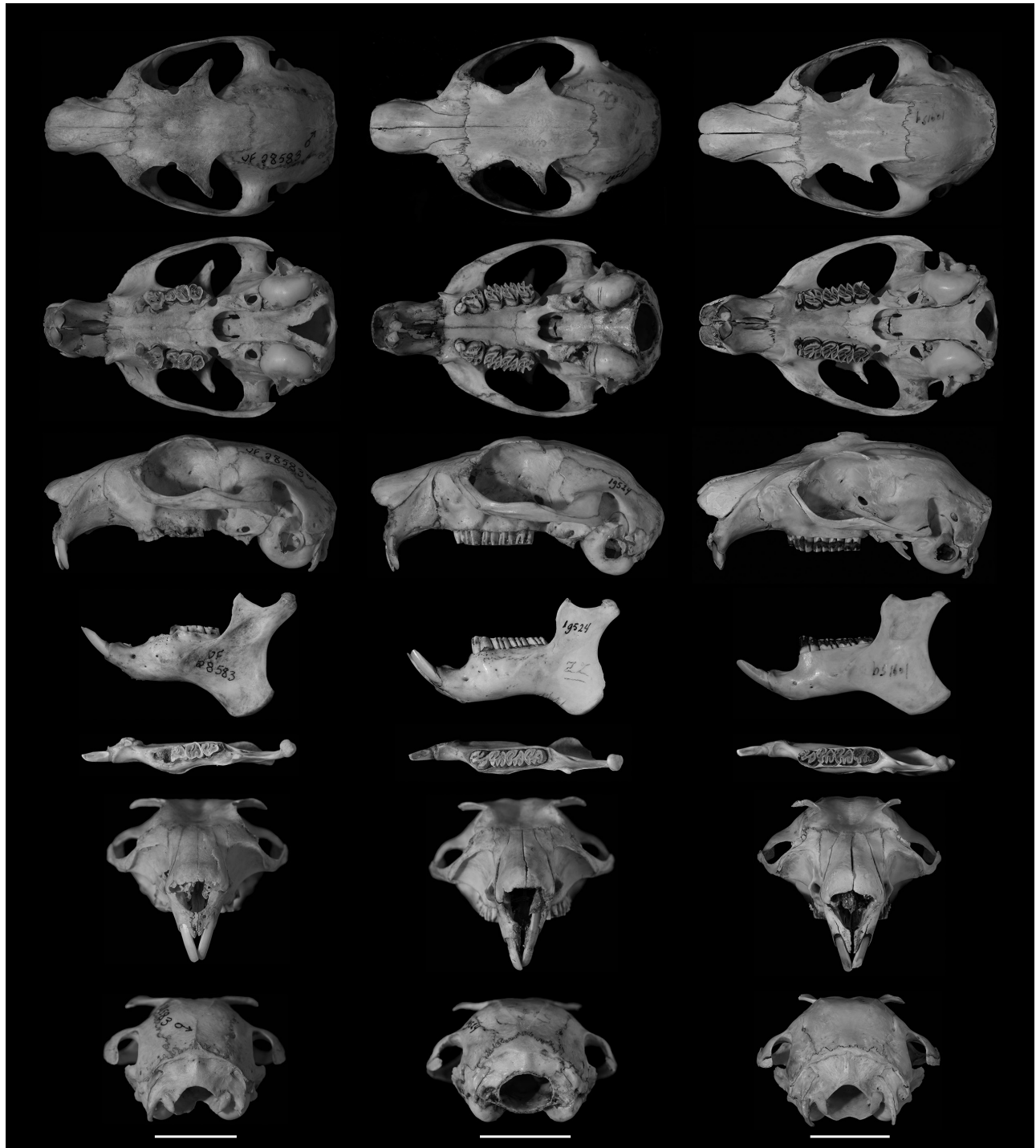*Lectotype:* BMNH 88.9.28.1, adult, skin, 'Astor District' (= Astore, Pakistan).

Figure 7. Skulls of *Eupetaurus*, from left to right: *E. cinereus* (FLMNH 28583) from Pakistan; *E. tibetensis NML 19524*, holotype, from Tibet; and *E. nivamons KIZ 034190*, holotype, from Yunnan. Scale bars (under each skull series): 2 cm.
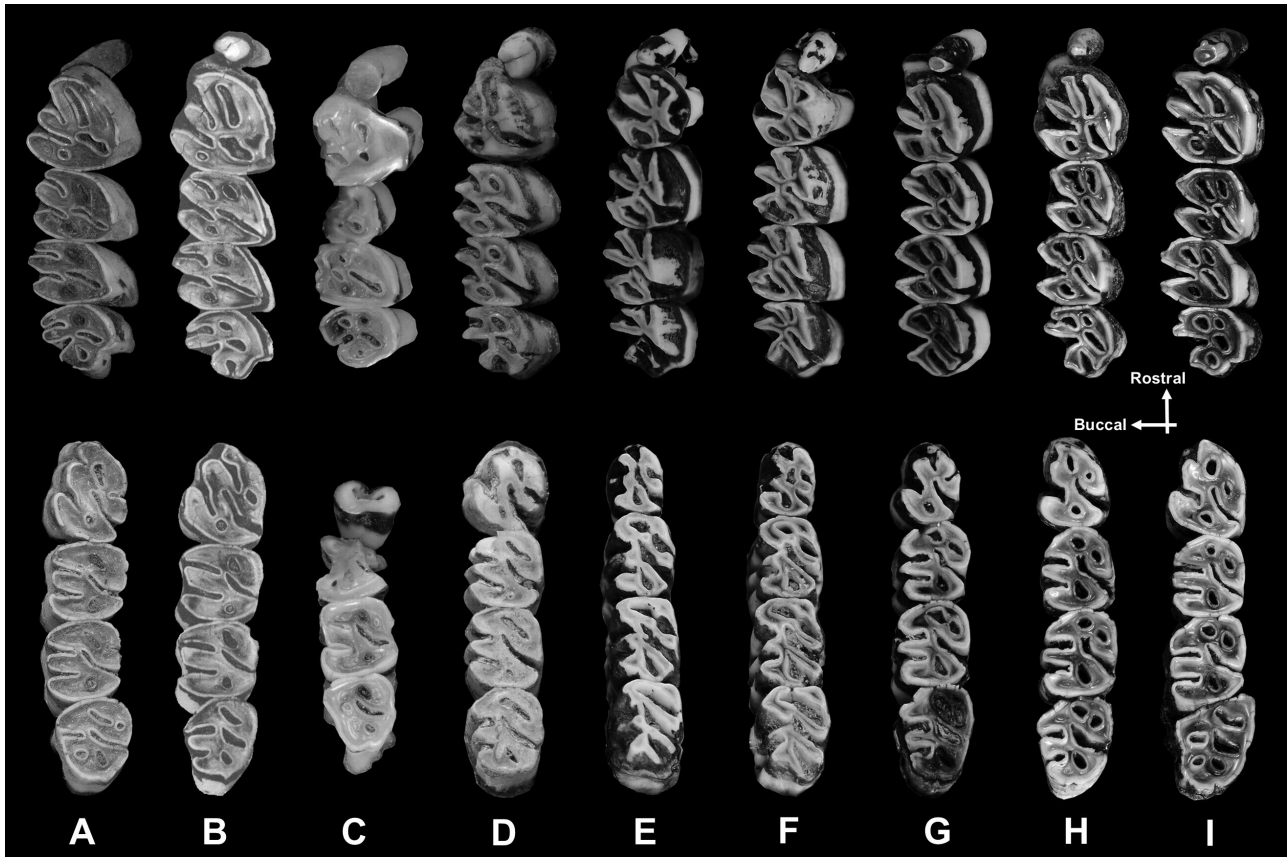
Figure 8. Cheek teeth of the nine known skulls of *Eupetaurus* species: A, *Eupetaurus cinereus* ZSI 9492, adult from Pakistan; B, *E. cinereus* BNHS 7108, adult (now reported lost) from Pakistan (McKenna 1962); C, *E. cinereus* FLMNH 28583, old adult, from Pakistan; D, *Eupetaurus tibetensis NML 19524*, holotype, young adult, from Tibet; E, *Eupetaurus nivamons* KIZ 034189, immature, from Yunnan; F, *E. nivamons* KIZ 034192, immature, from Yunnan; G, *E. nivamons KIZ 034190*, holotype, young adult, from Yunnan; H, *E. nivamons* KIZ 035087, adult, from Yunnan; and I, *E. nivamons* KIZ 035088, adult, from Yunnan. Left side is labial side.

Type locality: 'Astor District, Kashmir' (= Astore District, Pakistan).

Diagnosis: *Eupetaurus cinereus* differs from other *Eupetaurus* species in its overall more grizzled-grey pelage, with more pronounced grey frosting to the dorsal hairs (more saturated brown tones in the pelage of other species). Interspecific distinctions in the skull mainly concern the breadth of the rostrum and the shape of the frontal bones: the rostrum of *E. cinereus* is similar to that of *E. tibetensis* and narrower than that of *E. nivamons*; the interorbital region of *E. cinereus* is broader than in the other two species, and its postorbital processes is larger; the temporal ridges of *E. cinereus* and *E. tibetensis* are convergent posteriorly rather than parallel in *E. nivamons* (Table 3). The cusps and ridges of cheek teeth of *E. cinereus* are markedly more robust than in the other two species. The developed protocone and hypocone make the upper cheek teeth heart shaped,

similar to *E. tibetensis*, and differ from the round ones in *E. nivamons*. Its lower molars are subsquare, also more robust than the subrectangular ones in the other two species. *Eupetaurus cinereus* preserves only one short anterior fosettid (one long anterior fosettid in *E. tibetensis*; two short anterior fosettids in *E. nivamons*) (Figs 7, 8).

Descriptive notes: Size large: head-body length 420–510 mm, tail length 430–545 mm, hind foot length 83–93 mm and mass 2500 g (Zahler & Woods, 1997). The dorsal pelage is typically grizzled greyish, although a melanistic example was recorded by Chakraborty & Agrawal (1977) from Chitral, Pakistan. The pointed ears are hairy, with the outer fur black or brown and the fur of the inner ear greyish. The dorsal surface of the patagium is darker brown. The dorsal surfaces of the forefeet are black and those of the hindfeet are brown. The ventral

Figure 9. Comparison of cheek teeth between *Eupetaurus* and related genera: A, *Petaurista xanthotis* (USNM 144021); B, *Aeretes melanopterus* (USNM 219205); C, *Pteromys volans* (AMNH 19534); D, *Aeromys tephromelas* (USNM 292649); E, *Biswamoyopterus biswasi* (ZSI 20705); F, *Eupetaurus nivamons* (*KIZ 034190*); G, *Trogopterus xanthipes* (FMNH 39835); H, *Belomys pearsonii* (FMNH 35443); and I, *Pteromyscus pulverulentus* (USNM 481186).

pelage is pale brownish grey, with the hairs slate coloured basally and dirty white terminally. The tail is long, cylindrical and exceedingly bushy, with similar coloration to the body, often with the portion of the black tail tip short. The skull and dentition are as described above for the genus *Eupetaurus* and diagnosis of the species.

Distribution: Until recently, *E. cinereus* was known only by specimens and sightings from a few localities

between 2400 and 3600 m a.s.l. in the western Himalayan region, concentrated around Gilgit in northern Pakistan, where its range appears to fall within a small area where the Himalayan, Karakoram and Hindu Kush Mountain Ranges meet (Zahler, 1996; Zahler & Woods, 1997; Molur *et al.*, 2005; Dinets, 2011; Qamar *et al.*, 2012; Din *et al.*, 2015).

More recently, *Eupetaurus* has been recorded by camera traps from the Upper Bhagirathi Basin, Uttarakhand, north-western India, at elevations of 2700 and 4800 m a.s.l. (Pal *et al.*, 2018, 2020). On the basis of the colour of the animals and their geographical location, we regard these records as representing *E. cinereus*. This indicates a wider geographical and elevational range of occurrence for this species along the western margins of the Himalayas. The increasing use of camera-trap survey techniques might demonstrate that the species occurs in areas intermediate between the widely separated known localities in the Gilgit region of Pakistan and the Bhagirathi Basin of India, perhaps even extending into western Nepal.

Natural history: This species resides on cliffs and rock faces at high elevations, and individuals are not normally tree dwellers except when feeding (Roberts, 1997; Zahler & Woods, 1997). Within Pakistan, the habitat of *E. cinereus* is characterized by patchy forests, with herbs and shrubs of the genus *Artemisia* L., juniper (*Juniperus excelsa* M.Bieb.), Chilgoza pine (*Pinus gerardiana* Wall. ex D.Don), blue pine (*Pinus wallichiana* A.B.Jacks.), Morinda spruce [*Picea smithiana* (Wall.) Boiss.] and oaks (*Quercus* L. spp.) > 2000 m a.s.l. (Zahler & Woods, 1997; Zahler & Karim, 1999). In India, alpine vegetation associated with the 2700 m record includes *Bistorta affinis* (D.Don) Greene, *Gentiana* L. spp., *Potentilla* L. spp., *Primula* L. spp., *Rhodiola* L. spp. and *Rhododendron anthopogon* D.Don. The nearest forest was located 4 km downhill of this sighting and was dominated by *Abies pindrow* (Royle ex D.Don) Royle, *Betula utilis* D.Don and *Rhododendron campanulatum* D.Don. The 4800 m record was lacking any woody or arborescent vegetation, which contrasts with other records that typically associate the species with scattered conifers (Pal *et al.*, 2018).

In the original taxonomic description of the genus, Thomas (1888) speculated that it might feed on fungi, lichens, mosses and other rock-loving plants in its high-elevation environment. Roberts (1997) proposed that the buds and cones of the Morinda spruce (*Picea smithiana*) may be an important food source for *E. cinereus*, because buds occur in spring and cones in summer, which are shed in winter. Indeed, Zahler & Woods (1997) found that one captive specimen would eat the buds of Morinda spruce but refused all fruits, nuts and other food offered. More recently, faecal samples from four individuals were found to contain 92–100% pine needles (Zahler & Khan, 2003). Other observations have found this species to consume the buds of blue pine, juniper, spruce, oaks, Chilgoza pine and deodar [*Cedrus deodara* (Roxb. ex D.Don) G.Don]. In August and September, they are also thought to visit walnut trees (*Juglans regia* L.), although it is not clear what parts of the plants they eat (Mirza & Rasool, 2005).

Known predators of *E. cinereus* include the red fox [*Vulpes vulpes* (Linnaeus, 1758)], snow leopard [*Panthera uncia* (Schreber, 1775)] and eagle owl [*Bubo bubo* (Linnaeus, 1758)] (Zahler, 1996, 1998; Zahler & Dietemann, 1999; Qamar *et al.*, 2012; Pal *et al.*, 2020).

This species appears to be nocturnal, solitary and active all year round (Zahler, 1996). A nest attributed to this species was reported from a shelf in a cave at 3230 m a.s.l. in Jutal Nala, northern Pakistan, which was made of bark and branches of juniper and grasses and looked like a flat bowl measuring 500 mm × 400 mm (Oshida *et al.*, 2005). A specimen has also been recorded in Sai Nullah (Gilgit, Pakistan) coming out of an old oak tree at ~2590 m a.s.l. Thus, there appears to be some flexibility in nesting locations if tree hollows are available (Mirza & Rasool, 2005). An immature specimen at BMNH collected on 17 April suggests that breeding occurs early in spring and that two litters in a year could be produced (Roberts, 1997). This is supported by observations of two or three young being produced per litter, with young observed in spring and in late summer (Zahler & Woods, 1997).

Conservation: Eupetaurus cinereus is threatened by habitat loss owing to large-scale clear cutting of forests, particularly the destruction of high-elevation pine woodlands (Zahler & Woods, 1997; Zahler & Khan, 2003). It is also threatened to a lesser extent by expansion of agriculture, small-scale logging, infrastructure development and human settlements (Molur *et al.*, 2005). The total population size was estimated to be between 1000 and 3000 individuals within the known range in Pakistan in the mid-1990s (Zahler & Woods, 1997). It is currently classified as Endangered by the International Union for Conservation of Nature (IUCN) (Zahler, 2010), because it was considered likely to have suffered a recent reduction in population numbers from habitat loss (Rao & Marwat, 2003; Hasan, 2008).

The recent discovery of the species in the state of Uttarakhand in north-western India (Pal *et al.*, 2018, 2020) demonstrates that it might have a considerably wider distribution than previously realized and

indicates that protection and conservation in India is also fundamental for the long-term survival of *E. cinereus*. The species is included in Schedule II (Part II) of the Indian Wildlife (Protection) Act 1972 (Molur *et al.*, 2005; Pal *et al.*, 2018).

Hunting is not thought to be a major threat to this species. The species might receive some traditional respect and *de facto* protection because it is considered be a source of a material called salajit (also spelt *salaajeet* or *shilajit*), which is thought to be a mixture of flying squirrel urine and faecal pellets and rock leachate (Zahler, 1996; Zahler & Karim, 1998; Meena *et al.*, 2010). Salajit is important in traditional medicine (Hooper, 1903) and is collected from caves and sold in medicinal potions used to treat various diseases (Zahler, 1996; Zahler & Karim, 1998; Meena *et al.*, 2010). Historical references regarding the collection and use of salajit (e.g. Hooper, 1903) might provide clues concerning the historical distribution of *E. cinereus* or other *Eupetaurus* species in the Himalayan region, although other high-elevation species of flying squirrels, including the Kashmir flying squirrel [*Eoglaucomys fimbriatus* (Gray, 1837)], might also be sources of the substance (Pyke, 2001).

EUPETAURUS TIBETENSIS JACKSON, HELGEN, Q. LI & JIANG **SP. NOV.**

Suggested common name: Tibetan woolly flying squirrel.

Zoobank registration: urn:lsid:zoobank. org:act:19DA79D4-7E20-4EB6-A1C7-2C22C6F21D58

Holotype: NML 19524, adult, skin and skull, collected in 'Tibet'. Sequences of *Cytb* for this specimen are deposited in GenBank (no. AY331673).

This specimen was first discussed by Anderson (1879), who left it taxonomically unidentified. When describing *E. cinereus* as a new genus and species, Thomas (1888) speculated that Anderson's Tibetan specimen was also a *Eupetaurus*, a point later confirmed by Jentink (1890), who figured the skull of this specimen. Little is known about the collection details for this specimen other than that it is 'said to be from Tibet' (Jentink, 1890: 143). Corbet & Hill (1992: 314) noted that the association of the skull and skin for this specimen suggest that 'it is not a trade skin' (i.e. it is probably a wild-collected animal). To us, this specimen, when considered alongside the paratype skin obtained in a market in the Tibetan town of Gyantse (also spelt Gyangze, 江孜) in 1909, establishes the historical occurrence of this species in the south-central portion of the Tibetan Plateau (see below).

Paratype: BMNH 23.11.10.2, skin, with partial skull *in situ* inside the skin, probably female by examination of the specimen, 'bought in Gyantze Bazaar' (earlier tag reads 'Gyantsi Bazaar'), Tibet, collected in June 1909 by Colonel F. M. Bailey [Bailey was British Trade Agent at Gyantsi and Chumbi (春丕) in Tibet at that time; Bailey, 1945].

Referred specimens: Two specimens from the state of Sikkim in north-eastern India: BMNH 88.9.29.1, skin, with skull fragments removed from skin (anterior of mandibular rami, preserving incisors; anteriormost cranium preserving incisors, premaxillae and nasals), from 'Sikkim?', received from W. T. Blanford from the 'Mandelli collection' (thus apparently collected by L. Mandelli); and ZSI 19103, skin, from 'North Sikkim, alt. 3000 m' (Agrawal & Chakraborty, 1970), elevation also reported as '9000 feet' (Zahler & Woods, 1997).

Type locality: Labels associated with the holotype indicate only that it was collected in 'Tibet'. The paratype specimen at BMNH was obtained from the bazaar at Gyantse (as 'Gyantsi Bazaar'). Here, we accordingly fix the type locality as 'vicinity of Gyantse Town', Tibet (= Xizang). Gyantse is situated at an elevation of 4000 m a.s.l. in the Nyang Chu Valley (年楚河谷), Shigatse (日喀则), southern Tibet.

Diagnosis: Eupetaurus tibetensis differs from *E. cinereus* in having more saturated brown pelage, tinged with reddish tones (typically more clear grey in *E. cinereus*) and from *E. nivamons* in having a black tail tip that is much shorter (approximately half the length of the tail in *E. nivamons*). The rostrum is similar to *E. cinereus* and narrower than *E. nivamons*. The temporal ridges are convergent posteriorly, as in *E. cinereus*, rather than parallel, as in *E. nivamons*. The cusps and ridges of cheek teeth are more robust than in *E. nivamons* but less robust than in *E. cinereus*. Upper cheek teeth are heart shaped, as in *E. cinereus*, and differ from the rounded shape in *E. nivamons*. Lower molars are subrectangular, as in *E. nivamons*, and differ from the subsquare ones in *E. cinereus*, with only one long anterior fosettid per lower molar (two short anterior fosettids in *E. nivamons*; one short anterior fosettid in *E. cinereus*). Overall, the dentition of *E. tibetensis* resembles that of *E. cinereus* more than *E. nivamons*, but the external appearance of *E. tibetensis* is similar to *E. nivamons*.

Descriptive notes: In the available specimens of *E. tibetensis*, overall body size is similar to *E. cinereus*, with a head–body length of 468 mm in the holotype (with the imperfect, broken tail measuring 350 mm). The dorsal pelage is brownish grey, with less extensive

frosting of the fur tips than seen in *E. cinereus*, and with reddish tones sometimes evident along the midline of the dorsum, on the rump and on the proximal portion of the tail. The underparts are greyish, washed with yellow. The dorsal surfaces of the forefeet and hindfeet are brown. The tail is bushy and cylindrical, with coloration similar to the body, except for a short black tip. The skull and dentition are as described above for the genus *Eupetaurus* and diagnosis of the species.

Etymology: The species name is derived from its occurrence in Tibet, where the holotype and paratype originated.

Distribution: Records of occurrence that we attribute to *E. tibetensis* originate from elevations of 2700–4000 m a.s.l. in Tibet (= Xizang) in China, Sikkim in India and (more tentatively) from Bhutan. This species is known for certain from two specimens from Tibet and two specimens from Sikkim, discussed above. *Eupetaurus* has also been reported from Bhutan (Wangchuk *et al.*, 2004), and given the proximity of Bhutan to vouchered records from south-central Tibet and north Sikkim, we suggest that these Bhutanese observations are likely to represent *E. tibetensis*. We are not aware of vouchered specimens or specific published records from Bhutan, only general statements about its occurrence: Wangchuk *et al.* (2004) noted that it was found in coniferous, rhododendron and subalpine forests > 2700 m a.s.l.; Srinivasulu & Srinivasulu (2012) specified that it was known from western Bhutan; and Rinchen (2009) suggested that it might occur in Jigme Dorji National Park in north-western Bhutan. No records of *Eupetaurus* have yet been noted from Nepal (Mitchell, 1979; Thapa *et al.*, 2016).

In summary, we suspect that the distribution of *E. tibetensis* comprises the far southern portion of the central Tibetan Plateau and the northern slopes of the Himalayas in Sikkim and Bhutan (Fig. 10).

Natural history: Currently, there is little known about the ecology of *E. tibetensis*. Commencing research on this species to understand its distribution, ecology and conservation status is an urgent need.

Conservation: The conservation status of *E. tibetensis* remains unknown. We recommend an IUCN Red List categorization of Data Deficient for the species. Surveys are needed to determine the extent of its distribution, including whether it occurs in protected areas, such as Jigme Dorji National Park in Bhutan, and if it is facing particular threats, such as deforestation or hunting.

EUPETAURUS NIVAMONS Q. LI, JIANG, JACKSON & HELGEN **SP. NOV.**

Suggested common name: Yunnan woolly flying squirrel.

Zoobank registration: urn:lsid:zoobank. org:act:BE1BF61A-769A-42D6-8B11-56ECC0A871C8

Holotype: KIZ 034190 (field number BS1601), young adult female, skin, skull, and body preserved in ethanol, collected in January 2017. Sequences for 12S (rRNA) (GenBank no. MW699658), 16S (GenBank no. MW699662), *Cytb* (GenBank no. MW699650) and *IRBP* (GenBank no. MW699654) are deposited in GenBank.

Type locality: The holotype was collected on Biluo Snow Mountain, behind the village of Nageluo (娜格洛) (27°53′23.54″N, 98°45′43.90″E), Bangdang Township (棒当乡), Gongshan County, Nujiang Prefecture, Yunnan Province, China.

Paratypes: Five specimens from the type locality: KIZ 034191 (field number BS1602), immature female, whole body preserved in ethanol; KIZ 034192 (field number BS1603), immature female, cleaned skull with body preserved in ethanol; KIZ 035088 (field number 20171101), adult female, skin, skull with body preserved in ethanol; KIZ 035087 (field number 20171102), adult male, skin, skull with body preserved in ethanol; and KIZ 035086 (field number 20171103), adult male, whole body preserved in ethanol.

Referred specimens: KIZ 034189 (field number GS16078), immature female, skull, skin, and body preserved in ethanol, collected from Nanmowanshan Pass (贡山-巴坡人马驿道丫口), Mount Gaoligong, Gongshan, Yunnan. Two additional skins without skulls (KIZ 003299 and KIZ 003310), purchased at Lijiang or Gongshan, Yunnan in 1973 by Yingxiang Wang (Yang & Wang, 1989) (the original label locality was written as Lijiang, which was later altered to Gongshan).

Diagnosis: *Eupetaurus nivamons* differs from *E. cinereus* in its more saturated brown dorsal pelage (clearer grey dorsal pelage in *E. cinereus*) and closely resembles the external appearance of *E. tibetensis*, but its black tail tip is longer. The rostrum of *E. nivamons* is wider than in *E. cinereus* and *E. tibetensis*; its temporal ridges are parallel rather than posteriorly convergent as in *E. cinereus* and *E. tibetensis* (Table 3). Cheek-teeth cusps and ridges are weakest among the taxa; the protocone and hypocone are not as developed as in the other two species, making the upper cheek teeth round
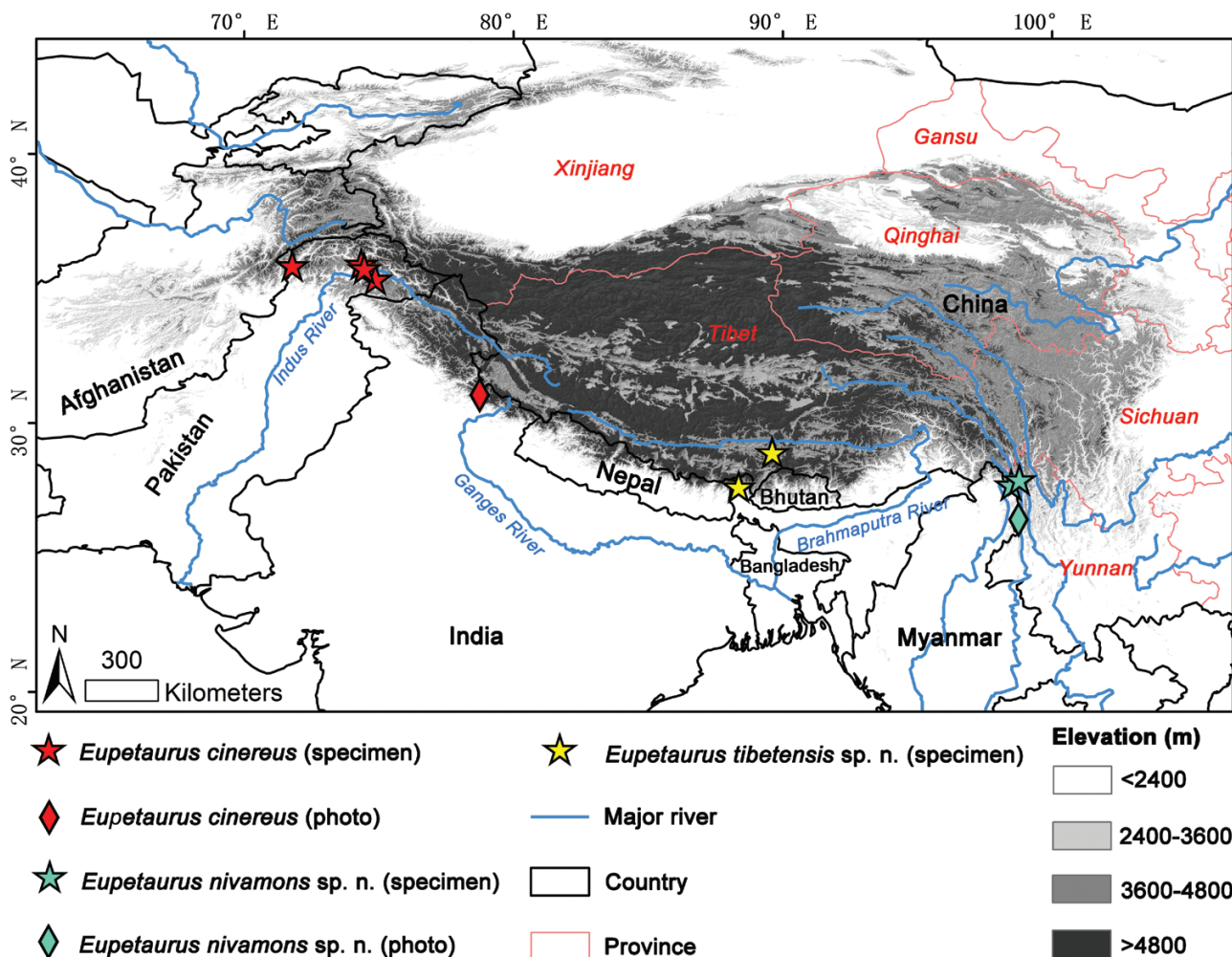
Figure 10. Known localities of the three species of *Eupetaurus*.

in shape rather than heart shaped. Its lower molars are subrectangular, as in *E. tibetensis*, and less robust than the subsquare molars of *E. cinereus*. *Eupetaurus nivamons* has two short anterior fosettids in the lower molars (one long anterior fosettid in *E. tibetensis*; one short anterior fosettid in *E. cinereus*) (Figs 7, 8).

Descriptive notes: *Eupetaurus nivamons* is slightly smaller than *E. cinereus* (holotype head-body length 419 mm, tail length 440 mm, hind foot length 90 mm, ear length 44.5 mm and mass 1420 g). The dorsal pelage is grizzled greyish brown. The same colour extends to the forehead, turning pale grey along the cheeks to the throat. Ventral pelage is light ashy, with a median longitudinal line of coarse hairs. The margin of the patagium is black. The dorsal surfaces of the manus and pes are black, mixed with scattered straw-coloured hairs. The ears are pointed and hairy, externally black and internally white washed with khaki. The proximal half of the tail is similar in colour to the back but browner, and the distal half is black. A pale

marking round the lower half of the otherwise brown body has been observed in one camera-trapped animal at Mount Gaoligong, Yunnan Province, China (Wang Jianhua, pers. obs.). The skull and dentition are as described above for the genus *Eupetaurus* and diagnosis of the species.

Etymology: The specific name is composed of the Latin *nivalis*, snowy, and *mons*, mountain. It is a noun in apposition.

Distribution: According to specimens, camera-trap images/videos and sightings by local people, *E. nivamons* is currently known from the alpine zone (3400–4450 m) on Mount Gaoligong [the watershed of the Ayeyarwady (= Irrawaddy) River and the Nu (= Salween) River] and Biluo Snow Mountain (the watershed of the Nu River and the Mekong River) (Fig. 10). Given that the known distribution runs along the Chinese side of the border with Myanmar, the species is likely to occur in suitable habitats immediately across the border in north-eastern

Myanmar (similar to the case of the recently described gibbon *Hoolock tianxing* Fan *et al.*, 2017). It should also be sought in alpine areas of far south-eastern Tibet situated east of the Brahmaputra River (Fig. 10).

Natural history: The specimen KIZ 034189 was collected from a cliff at an elevation of 3700 m a.s.l. near the spine of Mount Gaoligong. The surrounding natural vegetation is a mosaic of swamp meadows and dense shrubs ~0.5 m high. The main plants are currants (*Ribes* L.), barberries (*Berberis* L.), willows (*Salix* L.), roses (*Rosa* L.), rhododendron (*Rhododendron* L.) and juniper (*Juniperus squamata* Buch.-Ham. ex D.Don). The mean annual temperature is 3.9 °C, ranging from a low of −12.5 °C in January to a high of 19.6 °C in August. Mean annual humidity is 94.4%, ranging from a low of 70% in November to a high of 100% from April to September, except August [data from a nearby combined temperature and humidity meter (ibutton-MAXIM DS1923); Supporting Information, Supplementary Data SD8]. All camera-trap photographs and videos of *E. nivamons* were taken from similar cliff habitats at 3700–4450 m a.s.l. on Mount Gaoligong (Fig. 11).

Large, round faecal pellets and partly eaten plant material were scattered under juniper scrub (*Juniperus squamata*) near the high-elevation cliff of Mount Gaoligong. Given that no other large rodents were documented in this habitat, we interpret this as evidence that juniper is an important food plant for *E. nivamons* in the area.

Potential predators of *E. nivamons* include the tawny owl (*Strix aluco* Linnaeus, 1758), leopard cat [*Prionailurus bengalensis* (Kerr, 1792)] and Siberian weasel (*Mustela sibirica* Pallas, 1773).

Camera-trap observations ($N = 31$) show that *E. nivamons* is active throughout the year, with a peak in October; and it is active from 19.30 to 06.00 h, with
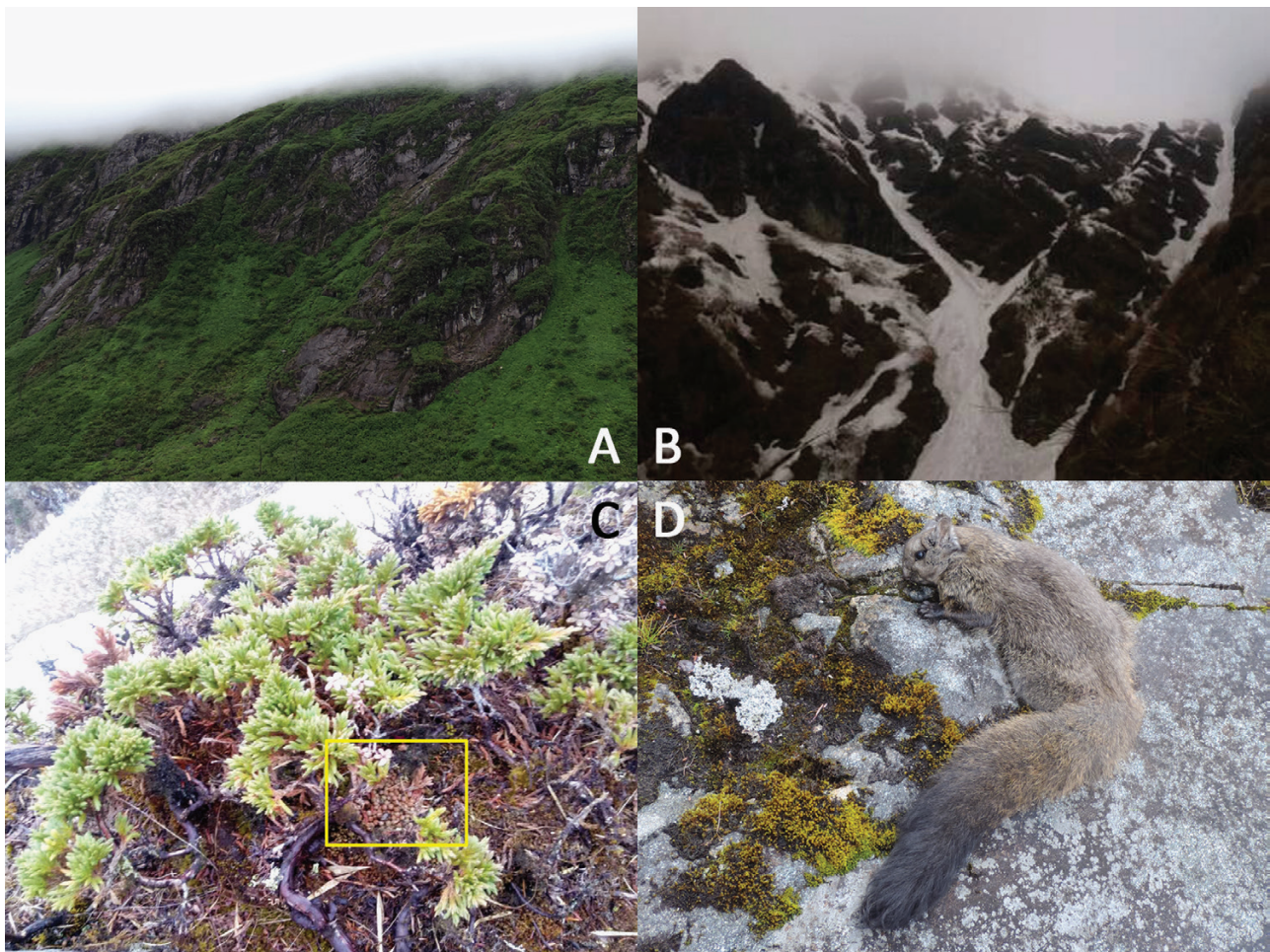

Figure 11. General view of habitat of *Eupetaurus nivamons*: A, summer view; B, winter view; C, faecal pellets and partly eaten plants (yellow square) under *Juniperus squamata*; and D, *E. nivamons*.

a peak from 19.30 to 00.00 h. Even in winter, fresh faecal pellets can be found on top of the snow under juniper shrubs, indicating that *E. nivamons* does not hibernate or migrate from the area during the coldest months of the year (Ge Gao, pers. obs.).

Conservation: We have documented this species at two principal localities, Mount Gaoligong and Biluo Snow Mountain. Mount Gaoligong is within a nationally protected nature reserve, whereas Biluo Snow Mountain has not been gazetted as a protected area. Owing to its high-elevation cliff habitat, far away from human settlements and covered by heavy snow for more than half of the year, *E. nivamons* is probably not heavily affected by human activities. The only known direct threat we documented is poaching for meat by herb collectors who visit the area from June to October. Given the apparent rarity of the animal and relatively small habitat area, we recommend an IUCN Red List classification of Near Threatened for this species. The loss of alpine habitats owing to ongoing climate change is a potential threat to the species in the near future.

DISCUSSION

PHYLOGENETIC POSITION OF *EUPETAURUS*

The high-crowned cheek teeth of *Eupetaurus* have attracted biological interest since the genus was first described (Thomas, 1888). In rodents, the evolution of hypsodont teeth involves modifications that result in cheek-tooth cusps that cease to interlock, which can improve the mechanical strength and effectiveness of cheek teeth, but may also obscure homologous landmarks on premolars and molars, making morphological relationships difficult to decipher (McKenna, 1962). Hypsodonty has evolved repeatedly in various lineages across the Rodentia (Williams & Kay, 2001), but *Eupetaurus* is the only hypsodont member of the Pteromyini. The cheek teeth of *Eupetaurus* are thus superficially different from all other flying squirrels and also different from other hypsodont rodents. In particular, the lower cheek teeth have two obvious buccal flexa and only one prominent lingual flexus, the reverse situation to most hypsodont rodents (a single buccal flexus and two or more lingual ones) (McKenna, 1962).

The genus was removed from Sciuridae and placed in its own family, Eupetauridae, by Schaub (1953: 395) (also Grassé & Dekeyser, 1955; Schaub, 1958) partly because of its highly derived dentition, but also owing to fundamental misconceptions in interpreting published images of the teeth of *Eupetaurus*. However, in a major overview of the relationships and dental anatomy of *Eupetaurus*, McKenna (1962) demonstrated that *Eupetaurus* is clearly referable to the Sciuridae (along with other flying squirrels, recognized at that time within the subfamily Petauristinae). He suggested that *Aeretes* G. M. Allen, 1940, *Eupetaurus* and *Petaurista* Link, 1795 constitute a natural group (the 'Petaurista group') and considered the dentition of *Eupetaurus* to be most like *Petaurista*, probably originating from a cheek-tooth pattern similar to *Petaurista xanthotis* Milne-Edwards, 1872. In a later review, Mein (1970) augmented McKenna's (1962) scheme by also transferring the genera *Belomys* Thomas, 1908, *Pteromys* G. Cuvier, 1800, *Pteromyscus* Thomas, 1908 and *Trogopterus* Heude, 1898 to the 'Petaurista group' based on perceived dental synapomorphies. Thorington *et al*. (2002) later moved an additional genus, *Aeromys* Robinson & Kloss, 1915, to the 'Petaurista group', drawing on a phylogenetic analysis of flying squirrels using 80 morphological characters.

More recent work has focused on reconstructing relationships among the various flying squirrel genera using genetic data. Yu (2002) used partial mitochondrial *Cytb* gene sequences for seven flying squirrel genera to study the relationships of *Eupetaurus* and found that the level of estimated pairwise-sequence divergence observed among *Eupetaurus* and *Petaurista* or *Pteromys* is greater than that observed between *Eupetaurus* and *Belomys*, *Glaucomys* Thomas, 1908, *Hylopetes* Thomas, 1908 or *Trogopterus*. Subsequently, researchers have used three gene fragments (12S, 16S

KEY TO THE SPECIES OF *EUPETAURUS*

1a. Temporal ridges parallel. Rostrum wide. Upper cheek teeth round in shape; lower molars have two anterior fossettids .... ***Eupetaurus nivamons***

1b. Temporal ridges converge posteriorly. Rostrum narrow. Upper cheek teeth heart shaped; lower molars have one anterior fossettid 2

2a. Cusps and ridges of cheek teeth are robust; P^4 and P_4 significantly larger than the following molars; lower molars are subsquare in shape; anterior fossettid short .... ***Eupetaurus cinereus***

2b. Cusps and ridges of cheek teeth are less robust; P^4 and P_4 approximately equal in size to the following molars; lower molars subrectangular in shape; anterior fossettid long .... ***Eupetaurus tibetensis***

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and *IRBP*) to reconstruct the phylogenetic tree of most flying squirrel genera (Mercer & Roth, 2003; Lu *et al.*, 2013; Casanovas-Vilar *et al.*, 2018). These studies found that *Eupetaurus* falls into a major clade with generic membership similar to the *Petaurista* group as proposed by Thorington *et al.* (2002), and more specifically, with *Eupetaurus* recovered as sister to the genus *Aeromys*. More recently, Li *et al.* (2020) included the most recently described flying squirrel genus, *Biswamoyopterus* Saha, 1981 (Sanamxay *et al.*, 2013; Li *et al.*, 2019), not previously included in morphological and genetic comparisons, in a phylogenetic analysis drawing on the same markers (12S, 16S and *IRBP*). That study recovered a sister relationship between *Biswamoyopterus* and *Aeromys*, which together were most closely related to *Eupetaurus*.

In the present study, our ML tree also recovered a sister relationship between *Eupetaurus* and *Aeromys* + *Biswamoyopterus*, but our BI tree showed a different topology, with *Eupetaurus* in a more isolated phylogenetic position, recovered as sister to a larger clade consisting of *Aeromys*, *Belomys*, *Biswamoyopterus*, *Pteromys*, *Pteromyscus* and *Trogopterus* (Fig. 4). Some intergeneric relationships are now clear. Five monophyletic clades can be identified clearly in the Pteromyina by the consensus of our ML and BI trees (Fig. 4): (1) a *Eupetaurus* clade including *Eupetaurus* only; (2) a *Pteromys* clade including *Pteromys* only; (3) a *Petaurista* clade including *Petaurista* and *Aeretes* (genetic samples of *Aeretes* are unavailable, but the close relationship between *Aeretes* and *Petaurista* is a consensus of morphological studies; McKenna, 1962; Mein, 1970; Thorington *et al.*, 2002); (4) an *Aeromys* clade including *Aeromys* and *Biswamoyopterus*; and (5) a *Trogopterus* clade including *Trogopterus*, *Belomys,* and *Pteromyscus*.

More comprehensive molecular phylogenetic comparisons are needed to resolve the deeper intergeneric splits between these lineages fully, including the exact phylogenetic placement of *Eupetaurus*. In the meantime, our morphological comparisons provide additional information that suggests a clearer placement of *Eupetaurus*. We note that: (1) the metaconule is similarly reduced in *Eupetaurus* and the *Aeromys* clade, but prominent in *Pteromys*, the *Petaurista* clade and the *Trogopterus* clade; (2) the interpremaxillary foramen (Hill, 1935) and greater palatine foramina are more expansive in *Eupetaurus* and the *Aeromys* clade than in other flying squirrels; and (3) the enamel faces of the incisors are pale yellow in *Eupetaurus* and *Biswamoyopterus*, but usually orange in other flying squirrels. Presuming that these might represent synapomorphic characters, we hypothesize that our ML tree is a better indication of the true evolutionary relationships in this group of genera: that is,

Eupetaurus is the sister genus of the *Aeromys* clade (*Aeromys* + *Biswamoyopterus*).

NEW INTERPRETATIONS OF SIMILARITY OF CHEEK TEETH

McKenna (1962) proposed that the occlusal morphology of the cheek teeth of *Eupetaurus* was closest to, and derived from, a pattern most similar to *Petaurista*. Evidence for this was that a posterolingual diagonal flexus exists only in *Eupetaurus* and *Petaurista/Aeretes*, and this was interpreted as a homologous apomorphy (Fig. 9). We recognize that there are three different types of flexus/notch on the lingual side of the upper cheek teeth in Pteromyini: one in front of the protocone on the anteroloph (anterior flexus/notch); one between the protocone and hypocone on the endoloph (central flexus/notch); and one between the protocone and the metaconule-derived pseudohypocone on the posteroloph (posterior flexus/notch) (Fig. 9). Flying squirrel taxa can have no lingual flexus/notch or up to three types of lingual flexus/notch. Traces of the protocone and hypocone can be found on two sides of the 'posterolingual diagonal flexus' of *Eupetaurus*, and a possibly homologous central notch can be found in the *Aeromys* and *Trogopterus* clades, which are genetically close to *Eupetaurus*, demonstrating that the 'posterolingual diagonal flexus' of *Eupetaurus* is a central flexus. *Petaurista* and *Aeretes* do not develop the hypocone on the endoloph; their 'posterolingual diagonal flexus' is instead a posterior flexus, which lies between the protocone and the metaconule-derived pseudohypocone.

McKenna (1962) also suggested that the lower cheek teeth of *Eupetaurus* evolved from a pattern most like *Petaurista xanthotis*, suggesting a possible phylogenetic relationship with *Petaurista*. We found that the paraconid and protoconid of *Petaurista/Aeretes/Pteromys* are not merged on the lower molars, revealing four distinct buccal cusps, whereas the paraconid and protoconid of the *Eupetaurus/Aeromys* clade/*Trogopterus* clade are merged on the lower molars, revealing three distinct buccal cusps (Fig. 9).

BIOGEOGRAPHY AND ADAPTATION OF *EUPETAURUS*

Eupetaurus species are endemic to alpine habitats across the Himalayan region, suggesting that their evolution is closely tied to the geological history and environment of the Himalayas. The geological history of the Himalayas and the surrounding area is complex, but some consensus has emerged from recent syntheses (Wang *et al.*, 2014a; Deng & Ding, 2015; Favre *et al.*, 2015; Renner, 2016). One is that a central 'proto-Qinghai–Tibetan Plateau' was uplifted as early as 40 Mya, with subsequent outward extensions

by the early Miocene (Wang *et al*., 2014a). Then the mountains surrounding the Plateau to the south, west and north began to uplift by the late Miocene (Fang *et al*., 2005; Brookfield, 2008; Wang *et al*., 2012; Deng & Ding, 2015). The mountains on the south-eastern edge of the plateau uplifted more recently, mainly between the late Miocene and late Pliocene (Sun *et al*., 2011; Wang *et al*., 2014b).

The Himalayas are an evolutionary hotspot for flying squirrels, where many different genera and species co-exist regionally (Corbet & Hill, 1992; Jackson & Schouten, 2012; Li, 2019). Many taxa demonstrate patterns of elevational stratification, probably reflecting patterns of habitat specialization and local competition between related lineages (Smith & Xie, 2008). *Eupetaurus* occupies the highest elevational range of flying squirrels in the region, and its deep phylogenetic isolation and morphological specializations indicate that it has probably occupied this niche for many millions of years. Our study estimates that the evolutionary divergence between *Eupetaurus* and other flying squirrels occurred during the early to mid-Miocene (95% CI = 13.72–20.46 Mya), similar to the timing when at least the south-west Himalayas probably reached their current elevation (Garzione *et al*., 2000; Murphy *et al*., 2009; Saylor *et al*., 2009; Wang *et al*., 2012).

The Himalayas are not only the highest mountain range on Earth, but also possess the steepest river gorges, such as the Indus, Ganges, Brahmaputra, Salween, Mekong and other major river systems (Brookfield, 1998). These deep gorges cut the alpine habitats suitable for *Eupetaurus* into multiple 'sky islands', between which lowland tropical and subtropical habitats hinder the movement of alpine species, which can consequently result in the isolation of populations and allopatric evolution between 'islands' (He & Jiang, 2014; Ai *et al*., 2018; Wan *et al*., 2018; He *et al*., 2019). However, 10 Mya the drainages were completely unlike those of today, with all the major rivers of South Asia running along parallel structural belts (Brookfield, 1998). After the late Miocene, the uplift of the Himalayas began to be slower than the headward erosion, which extended back onto the plateau to capture major originally latitudinal drainages to form the great sigmoidal bends of the current river system (Brookfield, 1998). River capture first occurred in the Ganges system and later in the Indus and Brahmaputra river systems (Brookfield, 1998). The order of river capture is consistent with the pattern of *Eupetaurus* speciation documented in our study: *E. cinereus* on the west side of the Ganges first split with an eastern lineage (*E. nivamons* + *E. tibetensis*) in the mid- to late Miocene (95% CI = 6.89–13.83 Mya), after which *E. nivamons* on the east of the Brahmaputra split from *E. tibetensis*

on the west side in the late Miocene or at the Pliocene–Pleistocene boundary (95% CI = 2.28–6.98 Mya). We imagine that a common ancestor of living *Eupetaurus* species might once have had a more continuous distribution across Himalayan alpine habitats, with the evolution of river systems since the mid-Miocene promoting allopatric speciation across the region.

RESEARCH OUTLOOK

For most of the 20th century, *Eupetaurus* was the most enigmatic and least studied of all Asian squirrel genera. Only now is the biological diversity represented in the genus becoming understood, with our study demonstrating the presence of three distinctive species of *Eupetaurus* occurring across the Himalayan region. New fieldwork, especially using camera-trapping techniques, continues to expand the known range of the genus, with previously overlooked populations of *E. cinereus* and *E. nivamons* recently discovered in north-western India (Pal *et al*., 2018; 2020) and Yunnan (Gao *et al*., 2017), respectively. There are still large gaps between the known ranges of the three species, and targeted fieldwork is likely to document further populations and perhaps even additional species in the genus. For example, it is not clear whether *Eupetaurus* occurs in the eastern margin of the Tibetan Plateau in the Qinghai, Gansu and Sichuan Provinces of China. It is important to document the current range of occurrence for *E. tibetensis*, which has not been documented by a museum specimen or other firmly documented record for a half century, but the species is likely to occur in Sikkim, southern Tibet and western Bhutan. Considering that the evolution and speciation of *Eupetaurus* are closely related to the Himalayan orogeny, the discovery of additional geographical populations of *Eupetaurus* might further enhance our understanding of geological history of the Himalayas and forming of the major rivers in South Asia, in addition to the ecology and evolution of the largest flying squirrels of the world.

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CONFLICTS OF INTEREST

There were no conflicts of interest.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Supplementary Data SD1. Specimens of *Eupetaurus*.

Supplementary Data SD2. Primers and polymerase chain reaction conditions for amplification and sequencing used in the genetic analyses.

Supplementary Data SD3. GenBank accession numbers for cytochrome *b* (*Cytb*), 12S ribosomal DNA (12S), 16S ribosomal DNA (16S) and interphotoreceptor retinoid-binding protein (*IRBP*) sequences used in this study.

Supplementary Data SD4. Character loading and percentage of variance explained on the components of the principal components analysis; morphological measurements from adult specimens of three geographical populations.

Supplementary Data SD5. Phylogenetic trees using the nuclear DNA (*IRBP*) dataset. The numbers before the slash represent Bayesian posterior probability (PP), and the numbers after the slash represent maximum-likelihood bootstrap proportions (BP); the asterisk means PP ≥ 0.95 or BP ≥ 75.

Supplementary Data SD6. Bayesian species delimitation evaluated using BP&P v.3.1.

Supplementary Data SD7. X-Ray photographs of skull of juvenile *Eupetaurus nivamons* (KIZ 034192), showing DP^4, DP_4 and unerupted P^4 and P_4.

Supplementary Data SD8. Monthly changes of temperature and relative humidity in the Mount Gaoligong habitat of *Eupetaurus nivamons*.