Discovery and description of a mysterious Asian flying squirrel (Rodentia, Sciuridae, Biswamoyopterus) from Mount Gaoligong, southwest China

Quan Li¹, Xue-You Li¹, Stephen M. Jackson²,³,⁴,⁵,⁶, Fei Li⁷, Ming Jiang⁸, Wei Zhao⁸, Wen-Yu Song¹,², Xue-Long Jiang¹

¹ State Key Laboratory of Genetic Resources and Evolution, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China ² Kunming College of Life Science, University of Chinese Academy of Sciences, Kunming, China ³ Biosecurity NSW, NSW Department of Primary Industries, Orange, New South Wales 2800, Australia ⁴ School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia ⁵ Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, United States of America ⁶ Australian Museum Research Institute, Australian Museum, 1 William St. Sydney, New South Wales 2010, Australia ⁷ Kadoorie Conservation China, Kadoorie Farm & Botanic Garden, Lam Kam Road, Tai Po, Hong Kong, China ⁸ Baoshan Management Bureau of Gaoligongshan National Nature Reserve, Baoshan, Yunnan, China

Corresponding author: Xuelong Jiang (jiangxl@mail.kiz.ac.cn)

Academic editor: R. López-Antonanzas | Received 5 February 2019 | Accepted 30 April 2019 | Published 18 July 2019

http://zoobank.org/246FA0BE-1170-4DB6-94C7-6C240A43A9C4C

Citation: Li Q, Li X-Y, Jackson SM, Li F, Jiang M, Zhao W, Song W-Y, Jiang X-Y (2019) Discovery and description of a mysterious Asian flying squirrel (Rodentia, Sciuridae, Biswamoyopterus) from Mount Gaoligong, southwest China. ZooKeys 864: 147–160. https://doi.org/10.3897/zookeys.864.33678

Abstract

The flying squirrels of the tribe Pteromyini (Family Sciuridae) currently include 15 genera of which the genus Biswamoyopterus comprises two recognized species, B. biswasi Saha, 1981 and B. laoensis Sanamxay et al., 2013. These two species were each described from only one specimen that are separated from each other by 1,250 kilometres in southern Asia, where they occur in northeast India and central Lao PDR respectively. In 2017 and 2018, two specimens of Biswamoyopterus were discovered from Mount Gaoligong, west Yunnan province, southwest China (between the type locality of the two recognized species). This study aimed to evaluate the taxonomic status of these two newly acquired specimens of Biswamoyopterus by comparing their morphology with the two described species of the genus. The results of this study showed that the specimens from Yunnan province (China) differed from...
both *B. laoensis* and *B. biswasi* in both pelage colour and craniology, and should be recognised as a distinct species, *B. gaoligongensis* sp. nov., which is formally described here. This study contributes to the understanding of the flying squirrels of southern Asia and identifies an additional species that appears to be endemic to southwest China; however, more research is required to provide details of its ecology, distribution, and conservation status.

**Keywords**
Biodiversity, conservation, mammal, Pteromyini, systematics, taxonomy, threatened, wildlife, Yunnan

**Introduction**

The flying squirrels of the tribe Pteromyini (Family Sciuridae) currently comprise 52 species of recent mammals that are placed in 15 genera. A number of fossil species have also been described and includes in several of the genera containing extant species as well as 13 additional extinct genera (Jackson and Thorington 2012; Jackson and Schouten 2012; Koprowski et al. 2016). The genus *Biswamoyopterus* Saha, 1981 is the most recently described in the tribe and initially only included *Biswamoyopterus biswasi* Saha, 1981 based on a single specimen collected in Namdapha National Park, northeast India (Saha 1981). *Biswamoyopterus biswasi* was placed in its own genus by Saha (1981) as it was considered to exhibit a unique combination of characters that distinguish it from other genera including: 1) large body size, cylindrical tail, and well-developed uropatagium (tail membrane or interfemoral membrane) similar to *Petaurista*, *Aeretes* and *Aeromys*; 2) the presence of ear tufts similar to *Belomys* and *Trogopterus*; and 3) cuspidate brachyodont dentition similar to *Hylopetes* and *Aeromys*. In addition to these characters, *Biswamoyopterus* was recognised to have pale-yellow incisors similar to *Aeromys* and *Eupetaurus* (Corbet and Hill 1992). In reference to these characters, Sanamxay et al. (2013) described a second species of *Biswamoyopterus* (*B. laoensis*) based on a single specimen collected from central Lao PDR. So far, all knowledge of *Biswamoyopterus* comes from the morphological description of these two holotypes. As a result, the International Union for Conservation of Nature (IUCN) listed *Biswamoyopterus biswasi* as critically endangered due to hunting and habitat loss from logging (Molur 2016) and *Biswamoyopterus laoensis* as data deficient (Kennerley 2017).

There is a gap of 1,250 km between the type localities of the two described *Biswamoyopterus* species (Sanamxay et al. 2013). Western Yunnan, southwest China occurs between the two type localities of *Biswamoyopterus* (Fig. 1). In 2017 and 2018, two specimens of *Biswamoyopterus* sp. were collected in Mount Gaoligong (the watershed of the Irrawaddy River and the Nu River [Salween River]), west Yunnan (Fig. 1) that appeared to have different pelage and cranial characters from the two described species of *Biswamoyopterus*. Therefore, the aim of this study was to: 1) undertake a detailed comparison of the specimens collected in Yunnan province, China with the two described species; and 2) if these Yunnan specimens proved to be distinct, formally describe and name a new species of *Biswamoyopterus*. 
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Materials and methods

Ethics statement

Animals used for this study were approved by the Animal Ethics Committee of the Kunming Institute of Zoology, Chinese Academy of Sciences (approval ID: SMKX2018021).

Repositories

ZSI  Zoological Collection of the Zoological Survey of India, Kolkata [Calcutta], India.
NUoL  Zoological collection of the Faculty of Environmental Sciences, National University of Laos, Vientiane, Lao PDR.
KIZ  Kunming Natural History Museum of Zoology, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China.

Specimens examined

Holotype

CHINA • 1♂, holotype of Biswamoyopterus gaoligongensis sp. nov., skin and skull available; Yunnan province, Baoshan city, Longyang county, Lujian township, Baihualin village; 25.298N, 98.785E; 2040 m a.s.l.; Jan. 2017; Quan Li leg.; Broad-leaved evergreen forests; KIZ 034924 (field No. bs1628).

INDIA • 1♂, holotype of Biswamoyopterus biswasi, skin and skull available; Tirap District, Namdapha, 26 km east of Miao, Deban; ca. 350 m a.s.l.; Apr. 1981; Shyamrup Biswas leg.; collected from a tall Nahar tree (Mesua ferrea) at 20:15 pm; ZSI 20705.
LAO PDR • 1♀, holotype of *Biswamoyopterus laoensis*, skin and skull available; Bolikhamsai Province, Pak Kading District, Ban (village) Thongnami, Thongnami market (Purchased from the market by the collectors. The collectors speculated that the original collection site might be Nam Kading National Biodiversity Conservation Areas or Khammouan Limestone National Biodiversity Conservation Areas (NBCA), which is about 5 km Northeast of Thongnami and Khammouan Limestone NBCA, and about 25 km Southeast of Ban village); 18.172N, 104.24E; Sep. 2012; Daosavanh San-amxay, Sysouphanh Xayavong, and Vilakhan Xayaphet leg.; NUoL FES.MM.12.163.

Paratype
CHINA • 1 sex unknown, paratype of *Biswamoyopterus gaoligongensis* sp. nov., skin of head and skull available; same locality as for KIZ 034924; Dec. 2018; a native of the area leg.; KIZ 035622 (field No. 201812001).

**Morphological techniques**

The external and craniodental measurements of type specimen of *Biswamoyopterus biswasi* and *Biswamoyopterus laoensis* were employed from the literature (Saha 1981; Sanamxay et al. 2013). External measurements of *Biswamoyopterus* sp. nov. were copied from the label tied on the specimen, included body mass, head and body length, tail length, hind feet length, and ear length. Craniodental measurements of *Biswamoyopterus* sp. nov. were taken with digital caliper to the nearest 0.01 mm; the mensural points follow Saha (1981) and Sanamxay et al. (2013) to facilitate the subsequent comparison (Fig. 2). A total of 28 craniodental measurements were used, including:

- **BB** Breadth of braincase,
- **BH** Braincase height,
- **CBL** Condylar length,
- **DL** Diastema length,
- **FL** Frontal length,
- **GPB** Greatest palatal breadth,
- **IBG** Inter bullae gap,
- **IOB** Interorbital breadth,
- **LAB** Length of auditory bulla,
- **LBP** Length of bony palate,
- **LIF** Length of the incisive foramina,
- **MB** Mastoid breadth,
- **MH** Mandible height,
- **ML** Mandible length,
- **MRTL** Mandibular tooth row length,
- **MWN** Maximum width of nasals,
- **MYTL** Maxillary tooth row length,
- **NL** Nasal length,
- **OB** Orbit breadth,
- **ONL** Occipitonasal length,
- **PL** Palate length,
- **POB** Postorbital breadth,
- **PPL** Postpalatal length,
- **RB** Rostrum breadth,
- **WAAM** Width of auditory bullae across the external auditory meati,
- **WPFM** Width of the bony palate at the first upper molar,
- **ZB** Zygomatic breadth,
- **ZH** Zygomatic height.

Superscript (P<sup>X</sup>, M<sup>X</sup>) upper premolars and upper molars, and

Subscript (P<sub>X</sub>, M<sub>X</sub>) lower premolars and lower molars.
Figure 2. Twenty-eight craniodental measurements taken for this study. See text for definitions. The different coloured arrows have no special meaning, they make it easier to see the starting and ending points of different measurements. Photo credit: Sanamxay et al. (2013).

The nomenclature of cheek teeth structures followed Tong (2007) and Thorington et al. (1996) (Fig. 3).

Pelage colour comparisons were made among all four available specimens. Skull and teeth were studied using a stereo binocular microscope. As only four skull specimens were available, statistical analysis was not possible.

**Taxonomy**

Class Mammalia Linnaeus, 1758  
Order Rodentia Bowdich, 1821  
Family Sciuridae Fischer, 1817  
Subfamily Sciurinae Fischer, 1817  
Tribe Pteromyini Brandt, 1855  
Genus Biswamoyopterus Saha, 1981  

*Biswamoyopterus gaoligongensis* sp. nov.  
http://zoobank.org/21C9D58C-EDC9-4016-8148-3F81DB51D9D3

**Common name.** Mount Gaoligong Flying Squirrel. Chinese common name "高黎贡比氏鼯鼠".

**Holotype.** Specimen KIZ: 034924 (field number bs1628), an adult male, skull, dried skin, baculum, and remaining body part in alcohol deposited in the Kunming
Figure 3. Nomenclature of cheek teeth of *Biswamoyopterus*. Maxillary tooth row (top), Mandibular tooth row (bottom).

Natural History Museum of Zoology, Kunming Institute of Zoology, Chinese Academy of Science (KIZ).

**Type locality.** Baihualin village [25.298167N, 98.784683E], Lujiang township, Longyang County, Baoshan City, Yunnan, China. The locality is located on the eastern slope of the southern Mount Gaoligong.

**Etymology.** The specific name is derived from Mount Gaoligong, the type locality of the new species and –*ensis*, Latin for belonging to.

**Diagnosis.** *Biswamoyopterus gaoligongensis* sp. nov. can be distinguished from the other two described species of *Biswamoyopterus* by the following combination of traits: 1) The ear tufts at the base of the posterior margins of ears are bicolored, basally white and terminal black. The scrotum is dark brown which strongly contrasts with the yellowish-white abdominal pelage. 2) The muzzle is very short, and the zygomatic arch is distinctly expanding outward, making the outline of the skull short and wide. The outer margin of the nasal bone, the orbital margin of the frontal bone, and the post-orbital margin of the frontal bone are almost parallel to the midline of skull on the
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Description. Biswamoyopterus gaoligongensis sp. nov. is a large flying squirrel (head and body length: 440 mm, tail length: 520 mm, and body mass: 1370 g) with a very developed uropatagium that extends approximately one-third of the proximal tail length in fresh specimen (Fig. 4). The back and upper surface of patagium are predominantly reddish brown, while the back between the shoulder and uropatagium is speckled with numerous white-tip furs that are absent from the head, shoulder, plagiopatagium, outer edge of uropatagium, limbs, and tail (Fig. 4). Similar to the shoulder, the head is reddish brown, but showing some yellowish grey in the crown. The ear is naked, with two bunches of long hairs (i.e., ear tufts) at the ear base, the anterior tufts are black, and the posterior tufts are basally white and terminal black. The back of each manus is reddish brown and the digits are black, while the whole pes and digits are black. The tail is cylindrical, the part beyond the uropatagium is black, and the part within the uropatagium is the same colour as the uropatagium. Throat, belly, and ventral surface of patagium are yellowish white. However, the scrotum is dark brown which strongly contrasts with the abdominal pelage.

Skull is large with a short muzzle and an expanded outward zygomatic arch, making the outline of skull short and wide (Fig. 5). The frontal depression is deep and postorbital processes are large and well developed. The outer margin of the nasal bone, the orbital margin of the frontal bone, and the post-orbital margin of the frontal bone are almost parallel to the midline of skull on the dorsal view. The auditory bullae are relatively large, with a honeycomb pattern of complex septae. The interpremaxillary foramen is well opened, which is not common in most flying squirrel genera. The mandible is generally similar to that of other flying squirrels. The coronoid process is less developed, only slightly higher than condylar process when the mandible is placed on a plane.

The anterior surface of incisors is pale yellow. Cheek teeth are strongly cuspidate brachyodont, with slightly pitted enamel.

Maxillary teeth: P3 is strong and unicuspid. Parastryle is prominent on P4 and dwindle on the following molars in an anterior to posterior gradient. Paracone is prominent on P4, M1, M2, and M3. Metacone is prominent on P4, M1, and M2, and indistinct on M3. Between protocone and metacone, at the exit of the middle valley of P4, M1, M2, and M3, there are two mesostyles form a projecting gutter. Protocone is prominent on P4, M1, M2, and M3. Hypocone is small, separated from protocone by a notch, distinct on M1 and M2, small on P4, and absent on M3. The anteroloph and posteroloph are indistinct on P4 and M3; distinct on M1 and M2, but they do not develop into a ridge as high as the protoloph and metaloph. A protoloph connecting the protocone with the paracone on M1, M2, and M3, and notched on P4. A metaloph connecting the protocone with the metacone on M2, interrupted by one big or two small metaconules on P4 and M1, and absent on M3.
Mandibular teeth: Four main cusps (protoconid, hypoconid, metaconid, and entoconid) are all distinct on \( P_4, M_1, M_2, \) and \( M_3 \). Mesoconid is present on the buccal side of \( P_4, M_1, M_2, \) and \( M_3 \), the notch between mesoconid and hypoconid is distinct, seems to be formed by the intense wear and tear. Mesostylid is small and fused with metaconid on \( P_4 \) and \( M_1 \), indistinct on \( M_2 \) and \( M_3 \).

**Comparison.** Body size, \( B. gaoligongensis \) sp. nov. is similar to \( B. biswasi \) but clearly smaller than \( B. laoensis \) (Table 1). Pelage colour becomes dark gradually from \( B. biswasi \) to \( B. gaoligongensis \) sp. nov. and to \( B. laoensis \). The back, \( B. biswasi \) is morocco-red speckled with white, \( B. gaoligongensis \) sp. nov. is reddish brown speckled with white, and \( B. laoensis \) is dark reddish brown speckled with white. The belly, \( B. biswasi \) is white, \( B. gaoligongensis \) sp. nov. is yellowish-white, and \( B. laoensis \) is pale orange. The tail beyond uropatagium, \( B. biswasi \) is pale smoky grey, with a dark tip, both \( B. gaoligongensis \) sp. nov. and \( B. laoensis \) are black (Fig. 4). The ear tufts, \( B. biswasi \) are white, \( B. gaoligongensis \)
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sp. nov. are bicolour (the anterior tufts are black, and the posterior tufts are basally white and terminal black), and B. laoensis are black (Fig. 6).

The muzzle of B. gaoligongensis sp. nov. is very short, B. biswasi is intermediate, and B. laoensis is much longer (Fig. 5, Table 1). As a result, the outline of skull of B. gaoligongensis sp. nov. is short and wide, B. biswasi is relatively short, and B. laoensis appears
Table 1. Body Mass (in grams), external and skull measurements (in mm) of four specimens of genus Biswamoyopterus.

| Measurements                        | B. biswasi (ZSI 20705) | B. gaoligongensis sp. nov. (KIZ 034924) | B. gaoligongensis sp. nov. (KIZ 035622) | B. laoensis (NUoL FES.MM.12.163) |
|-------------------------------------|-------------------------|----------------------------------------|----------------------------------------|----------------------------------|
| Body Mass                           | –                       | 1370.0                                 | –                                      | 1800.0                           |
| Head and body length                | 405.0                   | 440.0                                  | –                                      | 455.0                            |
| Tail length                         | 605.0                   | 520.0                                  | –                                      | 620.0                            |
| Hind feet length                    | 78.0                    | 75.0                                   | –                                      | 74.5                             |
| Ear length                          | 46.0                    | 47.0                                   | 46.0                                   | 52.0                             |
| Occipitonasal length (ONL)          | 72.40                   | 69.75                                  | 71.11                                  | 74.39                            |
| Condylar vault length (CBL)         | 70.10                   | 66.37                                  | 67.73                                  | 70.99                            |
| Mastoid breadth (MB)                | –                       | 30.72                                  | 33.50                                  | 30.79                            |
| Zygomatic breadth (ZB)              | 47.50                   | 48.41                                  | 48.30                                  | 47.72                            |
| Zygomatic height (ZH)               | –                       | 4.61                                   | 4.58                                   | 4.86                             |
| Breadth of braincase (BB)           | –                       | 33.86                                  | 34.46                                  | 32.84                            |
| Braincase height (BH)               | –                       | 22.90                                  | 24.15                                  | 22.55                            |
| Rostrum breadth (RB)                | –                       | 19.61                                  | 19.62                                  | 17.04                            |
| Nasal length (NL)                   | 20.90                   | 19.35                                  | 20.70                                  | 22.57                            |
| Maximum width of nasals (MWN)       | –                       | 13.15                                  | 12.51                                  | 13.37                            |
| Interorbital breadth (IOB)          | 19.00                   | 15.75                                  | 16.38                                  | 14.06                            |
| Postorbital breadth (POB)           | –                       | 18.87                                  | 20.55                                  | 17.19                            |
| Length of the incisive foramina (LIF)| 6.40                 | 5.65                                   | 5.86                                   | 5.85                             |
| Length of bony palate (LBP)         | –                       | 20.08                                  | 22.01                                  | 23.83                            |
| Post palatal length (PPL)           | –                       | 28.72                                  | 29.68                                  | 28.77                            |
| Length of auditory bulla (LAB)      | 15.50                   | 14.68                                  | 14.57                                  | 17.33                            |
| Width of auditory bullae across the | –                       | 35.88                                  | 36.76                                  | 35.96                            |
| external auditory meati (WAAM)      |                         |                                        |                                        |                                  |
| Inter bullae gap (IBG)              | –                       | 6.52                                   | 6.76                                   | 5.01                             |
| Maxillary tooth row length (MYTL)   | 15.50                   | 15.92                                  | 16.23                                  | 16.33                            |
| Greatest palatal breadth (GPB)      | –                       | 18.26                                  | 18.61                                  | 19.37                            |
| Width of the bony palate at the first| –                       | 8.58                                   | 8.03                                   | 8.05                             |
| upper molar (WPFM)                  |                         |                                        |                                        |                                  |
| Mandibular tooth row length (MRTL)  | –                       | 15.24                                  | 15.41                                  | 15.33                            |
| Mandible length (ML)                | –                       | 44.44                                  | 46.53                                  | 45.36                            |
| Mandible height (MH)                | –                       | 27.10                                  | 27.37                                  | 29.78                            |
| Palate length (PL)                  | 34.70                   | 32.60                                  | 32.87                                  | –                                |
| Diastema length (DL)                | 15.70                   | 13.70                                  | 15.03                                  | –                                |
| Orbit breadth (OB)                  | 24.60                   | 26.17                                  | 26.50                                  | –                                |
| Frontal length (FL)                 | 28.60                   | 27.66                                  | 30.63                                  | –                                |

long. On the dorsal view of skull, the outer margin of the nasal bone, the orbital margin of the frontal bone, and the post orbital margin of the frontal bone of B. gaoligongensis sp. nov. are almost parallel to the midline of skull, while B. biswasi slanted, and B. laoensis slanted even more. The postorbital processes of B. gaoligongensis sp. nov. and B. biswasi are clearly larger than B. laoensis. The preglenoid process of B. gaoligongensis sp. nov. and B. laoensis are almost flat, whereas that of B. biswasi obviously protruding forward (Fig. 7). The sutures of frontal and squamosal bone of B. gaoligongensis sp. nov. are bulging, while B. biswasi and B. laoensis are almost flat. The auditory bullae of
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*Biswamoyopterus* gaoligongensis sp. nov. and *B. biswasi* are distinctly smaller than those of *B. laoensis*. The posterior margin of the palatal bones of *B. gaoligongensis* sp. nov. and *B. biswasi* is concave forward, while *B. laoensis* is flat. The central point of the posterior margin of the palatal bones of *B. gaoligongensis* sp. nov. lies in front of the posterior margin of $M^3$, *B. biswasi* just meet, and *B. laoensis* lies behind (Fig. 7).

The metacone and hypocone of $M^1$ and $M^2$ of *B. gaoligongensis* sp. nov. are most developed among three species, followed by *B. laoensis*, again *B. biswasi*. As a result, $M^1$ and $M^2$ of *B. gaoligongensis* sp. nov. are almost equal to $P^4$, while those of *B. laoensis* and *B. biswasi* are smaller than $P^4$. In addition, the outline of $M^1$ and $M^2$ of *B. gaoligongensis* sp. nov. is sub-square, *B. laoensis* is sub-rectangle, and *B. biswasi* is sub-triangular. The hypoconid of *B. gaoligongensis* sp. nov. is strongest among three species, followed by *B. biswasi*, again *B. laoensis* (Fig. 5).

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**Figure 6.** Ear tufts of the three *Biswamoyopterus* species, the red arrow indicates the anterior tufts, and the yellow arrow indicates the posterior tufts A (ZSI 20705, holotype) *Biswamoyopterus biswasi* B (KIZ 034924, holotype) *Biswamoyopterus gaoligongensis* sp. nov. C (NUoL FES.MM.12.163, holotype) *Biswamoyopterus laoensis*. The image C was derived from Sanamxay et al. (2013).

**Figure 7.** The posterior margin of the palatal bones relative to the posterior margin of $M^3$ (dotted line) and shape of the pre-glenoid process (arrow) of the three *Biswamoyopterus* species A (ZSI 20705, holotype) *Biswamoyopterus biswasi* B (KIZ 034924, holotype) *Biswamoyopterus gaoligongensis* sp. nov., C (NUoL FES. MM.12.163, holotype) *Biswamoyopterus laoensis*. The image C was derived from Sanamxay et al. (2013).
**Distribution.** Apart from the locality of the holotype, there are two more localities in Yunnan, China, where the *Biswamoyopterus gaoligongensis* sp. nov. was photographed. These include Linjiapu (25.28693N, 98.70102E), 10 km west of the type locality; and Banchang (25.145876N, 98.796026E), 9 km south of the type locality (Fig. 1). Although these three localities cover the east and west slopes of Mount Gaoligong (the watershed of the Irrawaddy River and the Nu River [Salween River]), they are all restricted in a small area of southern Mount Gaoligong.

**Natural history.** Little is known about the natural history of *Biswamoyopterus gaoligongensis* sp. nov. The holotype was collected from evergreen broad-leaved forest at an altitude of 2,000 meters above sea level. A set of photos taken in Linjiapu showed a *Biswamoyopterus gaoligongensis* sp. nov. resting on the branches of *Daphniphyllum* sp. *Petaurista yunanensis*, *P. elegans*, and *Hylopetes alboniger* were also collected in the same habitat where the holotype was collected.

**Conservation status.** The limited available information suggests that *Biswamoyopterus gaoligongensis* sp. nov. has a relatively low abundance. Because low-altitude forests inhabited by *Biswamoyopterus gaoligongensis* sp. nov. are close to human settlements, they are vulnerable to human activities. The currently known threats are agricultural reclamation and poaching.

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**Key to the three known species of Biswamoyopterus**

1 Pale orange belly and marked with numerous, black, discontinuous lines; ear tufts black; long muzzle; large auditory bulla; the posterior edge of the palatal bones is flat.............................................................. *Biswamoyopterus laoensis*
   – Light-coloured belly; ear tufts bicour or white; short muzzle; smaller auditory bulla; the posterior edge of the palatal bones is concave forward.........2

2 Parti-coloured tail with a dark tip; ear tufts white; the central point of the posterior margin of the palatal bones just meet the posterior margin of M₃; the outline of M¹ and M₂ is sub-triangular; smaller hypoconid .................
   ........................................................................................................... *Biswamoyopterus biswasi*
   – Black tail; ear tufts bicour; the central point of the posterior margin of the palatal bones lies in front of the posterior margin of M₃; the outline of M¹ and M₂ is sub-square; strong hypoconid .................................................................
   ................................................................................................................. *Biswamoyopterus gaoligongensis* sp. nov.

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**Discussion**

This study describes a third species of *Biswamoyopterus* in the middle of the isolated ranges of two previously known species, suggesting that the distribution of *Biswamoyopterus* is much broader than previously known. Although the genetic analysis within *Biswamoyopterus* was not available in this study, the morphological comparison shows that *Biswamoyopterus gaoligongensis* sp. nov. markedly differs from *Biswamoyopterus bis-
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wasi and Biswamoyopterus laoensis in pelage colour and craniodental traits (Figs 4, 5; Table 2). Within the distribution of Biswamoyopterus and adjacent areas (Fig. 1), they occur sympatriically with a number of flying squirrels including Belomys pearsonii, Eu-petaurus sp., Hylopetes alboniger, H. phayrei, Petaurista alborufus, P. caniceps, P. elegans, P. petaurista, P. philippensis, P. yunanensis and Trogopterus xanthipes (Jackson and Thornton 2012; Jackson and Schouten 2012). This high diversity of both genera and species may be the result of the region acted both as refugia and diversification centre since the late Miocene (Lu et al. 2013; Mercer and Roth 2003).

**Acknowledgements**

We thank Mr. Dazhou Peng, Mr. Jinlin Qian, and Mr. Chunliao Qian for their assistance in the field. We are grateful to Dr. Rong Li for identification of plant species, and Dr. Qigao Jiangzuo for some morphologic terms. We appreciate Baoshan Management Bureau of Gaoligongshan National Nature Reserve for their assistance in field work. Our research is supported by National Key Research and Development Program of China (#2017YFC0505202) and the Yunnan University “Double First-Class” Construction Program (C176240107).

**Table 2. Comparison of the three species of Biswamoyopterus.**

| Species       | B. biswasi       | B. gaoligongensis sp. nov. | B. laoensis |
|---------------|------------------|---------------------------|-------------|
| Size          | Relatively small | Relatively small          | Large       |
| Dorsal coloration | Morocco-red speckled with white | Reddish brown speckled with white | Dark reddish brown speckled with whitish-grey |
| Ventral Coloration | White           | Yellowish-white           | Pale orange and marked with numerous, black, discontinuous lines |
| Coloration of tail beyond the uropatagium | Pale smoky grey with a dark tip | Black | Black |
| Ear tufts | White | The anterior tufts are black, and the posterior tufts are basally white and terminal black | Black |
| Muzzle | Short | Shorter | Long |
| Outer margin of the nasal bone, orbital margin of the frontal bone, and post-orbital margin of the frontal bone vs. midline of the skull | Inclined | Almost parallel | More inclined |
| Postorbital processes | Large | Large | Relatively small |
| Preglenoid process | Forward protruding | Almost flat | Almost flat |
| Sutures of frontal and squamosal bone | Almost flat | Bulge | Almost flat |
| Auditory bulla | Relatively small | Relatively small | Large |
| Posterior margin of the palatal bones | Concave forward, the central point just meets the posterior margin of M3 | Concave forward, the central point lies in front of the posterior margin of M3 | Flat, the central point lies behind the posterior margin of M3 |
| M1 and M2 | Feeble metacone and hypocone, outline of M1 and M2 is sub-triangular | Most developed metacone and hypocone, outline of M1 and M2 is sub-square | Second developed metacone and hypocone, outline of M1 and M2 is sub-rectangle |
| M1 and M2 | Second developed hypoconid | Most developed hypoconid | Feeble hypoconid |
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