



Original Investigation

Reevaluation of several taxa of Chinese lagomorphs (Mammalia: Lagomorpha) described on the basis of pelage phenotype variation

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ABSTRACT

Melanism is a common phenomenon in the animal kingdom. While the occurrence of melanism in lagomorphs has been less studied, this phenomenon has led to systematic confusion among different forms of pikas (*Ochotona*) and hares (*Lepus*). Within *Ochotona*, the Pianma black pika (*O. nigritia*) was established primarily based on its pelage phenotype variation compared with the sympatric Forrest's pika (*O. forresti*). The Gaoligong pika (*O. gaoligongensis*) was also described based on pelage color differences with *O. forresti*. However, the specific status of these two taxa has been questioned for several years. We conducted a detailed examination of the cranial characters used for the initial diagnosis of each of these forms (*O. forresti*, *O. gaoligongensis* and *O. nigritia*). Insignificant differences were displayed among these species, thus contradicting the classification of *O. gaoligongensis* and *O. nigritia* as separate species. Within *Lepus*, the Manchurian black hare (*Lepus melainus*) was also initially described based on the melanistic pelage possessed by this form. We conducted a detailed examination of the cranial characteristics of *L. melainus* and the sympatric Manchurian hare (*L. mandshuricus*) and confirmed the synonymy of these forms; *L. melainus* represents melanistic individuals of *L. mandshuricus*. These taxonomic mistakes probably resulted from underestimating the prevalence of melanism and the potential for adaptive variation of pelage coloration in nature. A more detailed study on the genetic background leading to the occurrence of melanistic lagomorphs is needed.

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Introduction

The Order Lagomorpha includes two families, Leporidae and Ochotonidae, with approximately 90 extant species (Hoffmann and Smith 2005). Taxonomy of lagomorphs remains weakly developed partly because of the morphological similarity among related species, relatively conservative karyotypes, lack of extensive molecular work, and occurrence of hybridization among taxa (Robinson et al. 1983; Alves et al. 2008; Payseur 2009; Hafner and Smith 2010).

Twenty-four species of pika (*Ochotona*) and nine species of hare (*Lepus*) have been reported to occur in China, although the status of several of these species is still questionable (Hoffmann and Smith 2005; Smith and Xie 2008). For example, Gong et al. (2000) described a new species, the Pianma black pika (*O. nigritia*), based on three specimens from Pianma, Yunnan Province

(25°58' N, 98°42' E). The main characters used to distinguish this form from other species were the black pelage, the 'less prominent' frontal compared with other species, and presence of a completely confluent incisive and palatal foramen. The overall shape of this foramen was described as 'long pear-shaped'. Biological data for this species are absent, and it is listed as 'Data Deficient' by the International Union for Conservation of Nature and Natural Resources (IUCN) (Smith and Johnston 2011a). Hoffmann and Smith (2005) and Smith and Xie (2008) pointed out that the specimens used to describe this species may belong to melanistic individuals of Forrest's pika (*O. forresti*).

Another pika species, the Gaoligong pika (*O. gaoligongensis*), from a nearby region (Mt. Gaoligong, Yunnan Province; 27°45' N, 98°27' E) was also described based on its pelage coloration in combination with the shape of the incisive and palatal foramen (Wang et al. 1988). The specific status of *O. gaoligongensis* has been accepted in several publications (Pan et al. 2007), however, Hoffmann and Smith (2005) considered that it 'may be a sister taxa or possibly a synonym of *O. forresti*' (Smith and Xie 2008). The conservation status of this species is also 'Data Deficient' (Smith and Johnston 2011b).

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Li and Luo (1979) described a new species, the Manchurian black hare (*Lepus melainus*), based on seven specimens from Zhanhe, Heilongjiang Province (48°99' N, 127°91' E). The primary diagnostic character used to distinguish it from the sympatric Manchurian hare (*L. mandshuricus*) was its black pelage. Overall morphological differences of the skulls between the two species were minor; only a small difference in the occlusal surface of the first premolar was reported (Li and Luo 1979; Luo 1988). Flux and Angermann (1990) listed *L. melainus* as a separate species. This point of view was reflected later in some important publications (Zhang 1997; Wu et al. 2005). However, Hoffmann and Smith (2005) did not consider it a separate species, and this point of view was accepted in recent monographs devoted to the mammals of China (Pan et al. 2007; Smith and Xie 2008). The conflicting views highlighted above make the species status of *L. melainus* ambiguous, while neither a statistical analysis nor a detailed discussion comparing the two forms are available in the literature.

It has already been reported that a weak knowledge of melanism in pikas and hares has led to systematic confusion (Smith et al. 1990). Thus, the purpose of our study was to evaluate the frequency of this phenomenon and to provide a detailed morphometric study of melanistic and ordinary specimens from the taxa listed above.

Material and methods

Specimens examined

We examined about 7500 pelage specimens belonging to various species of pika and hare from several collections in China and Russia (National Zoological Museum of China, Institute of Zoology, Chinese Academy of Sciences - IOZCAS - about 2000 pikas and 500 hares, Kunming Natural History Museum of Zoology - KNHMZ - about 260 pikas and 80 hares, Northwest Institute of Plateau Biology, Chinese Academy of Sciences - NIPBCAS - about 1000 pikas and 300 hares, Epidemic Prevention Institute of Yunnan - EPIY - 39 pikas and 6 hares, Zoological Museum of Moscow State University - ZMMU - about 1500 pikas and 800 hares, and Zoological Institute, Saint-Petersburg - ZISP - about 600 pikas and 400 hares). All specimens studied were adult animals.

Samples available for morphometric analysis of *Ochotona* are listed in Appendix 1. Specimens of *O. nigritia* include the holotype from KNHMZ and three specimens from KNHMZ and IOZCAS collected at or near the type locality (Pianma). Two paratypes of this species, which should be preserved in EPIY based on the original description, have been lost according to institute curators. Specimens of *O. gaoligongensis* include the holotype (field number 107) from EPIY, two paratypes from KNHMZ (according to museum records and the original date in the description, the field number for these two specimens had been changed; these two paratypes include a male, original field number 87, new field number 830,340, museum collection number 013,311 and a female, original field number 90, new field number 830,341, collection number 013,312), and three additional specimens collected from the type locality. To facilitate comparison with these forms, we examined 13 specimens of *O. forresti* from a region near Gongshan, Yunnan (10 of them with complete cranium, and three of them with a broken post-cranium but with the incisive and palatal foramen available for analysis) and 16 sympatric specimens of the Moupin pika (*O. thibetana*) from Yunnan. Three specimens (two adult) assigned to *O. forresti duoxionglaensis* by Chen and Li (2009); (see also Feng et al. 1986), are housed at NIPBCAS and were included in our morphometrics analysis. Due to condition of some specimens, smaller sample sizes were utilized in our comparative analyses.

Because of the putative relationship between *O. nigritia* and *O. gaoligongensis* with *O. forresti*, we also attempted to locate, and when possible measure, all existing specimens of *forresti* for

comparison (Appendix 1). The type of *O. forresti* and 19 additional specimens are housed in the Natural History Museum, London (NHMUK). These specimens were examined by Lissovsky, but not included in the present morphometrics analysis so as to avoid measurement errors between researchers. One specimen putatively listed as *forresti* is accessioned in the Smithsonian National Museum of Natural History (NMNH); however, the museum tag of this specimen reads *O. roylei*, and the ear measurement of 26 mm lies outside the range of all known *forresti*. The skull of this specimen has been lost. While positive identification is not possible, it is clear that this specimen does not represent an *O. forresti*. Weston (1982) utilized one specimen of *O. forresti* (labeled *O. thibetana forresti* at the time of her analysis) collected from Lijiang, Yunnan Province (American Museum of Natural History collection, AMNH, number 44000). The analysis of Weston (1982) and careful inspection of this specimen by Robert Hoffmann (personal communication) make clear that it represents *thibetana* and not *forresti*; additionally, the MaNIS database (<http://manisnet.org>) indicates that this specimen is currently accessioned as *O. thibetana thibetana* in the AMNH collection. The *forresti* specimen used in Ye et al. (2011), was never accessioned into a collection and has been subsequently lost.

To test potential morphological differences between *L. melainus* and sympatric *L. mandshuricus*, measurements of *L. melainus* and *L. mandshuricus* published by Li and Luo (1979) and Luo (1988) were analyzed. In addition, the paratype of *L. melainus* from IOZCAS was compared with different phenotypes of *L. mandshuricus* using illustrations.

Methods

Photographs

We compared the coloration of each specimen in the above analysis (Appendix 1) using photographs of museum skins, and also photographed skulls for quantitative analysis. Photographs were taken with a Canon PowerShot S5IS with macro-focusing lens and saved in a JPEG format. Digital photos were taken using a scale bar, parallel to the longitudinal axis of the body or the cranium. Images were standardized for specimen position, camera lens plane and the distance between the camera lens and the specimen.

Morphometric analysis

Information from body measurements included body length, ear length and hind foot length. These data were taken from museum field labels and analyzed for differences among species by ANOVA.

The sutures on the posterior cranium of adult pikas are ossified, and thus it was difficult to capture enough shape information from crania using identifiable landmarks (Bookstein 1991). Instead, Makefan6 (Sheets 2003) was used to set equally separate guidelines so as to recognize shape information along the contour of the cranium and the incisive and palatal foramen; this shape information was defined by the establishment of semi-landmarks. The dorsal and ventral (excluding the shape of incisive and palatal foramina) views, as well as the outline of the skull in lateral view and outline of incisive and palatal foramen, were analyzed separately. Landmarks and semi-landmarks were digitized in TpsDig (Rohlf 2005); their location is shown in Fig. 1 and identification marks are listed in Appendix 2. The matrix created in TpsDig was aligned in TpsRelw (Rohlf 2003) using generalized orthogonal least-squares Procrustes (GPA) procedures (Rohlf and Slice 1990). A consensus configuration was obtained through this alignment, then a matrix of partial warp and uniform component scores was constructed based on the consensus configuration, and a matrix of relative warp scores was extracted. To visualize shape differences among *O. gaoligongensis*, *O. nigritia*, *O. forresti*, *O. f. duoxionglaensis* and *O. thibetana*, the first two axes of relative warps scores were plotted. Size and shape differences among sample groups were calculated by two-way

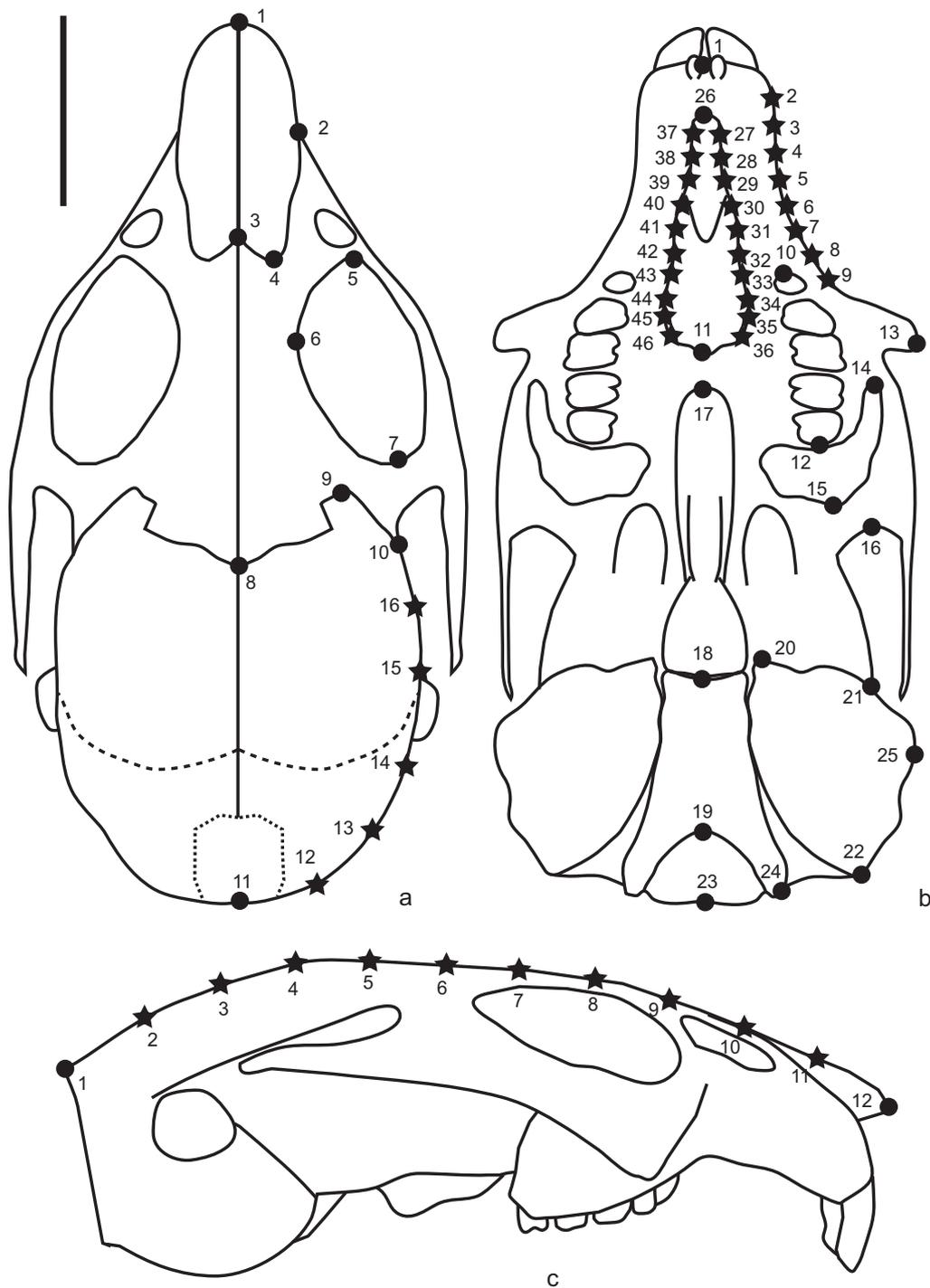


Fig. 1. Landmark and semi-landmark locations on skulls of *Ochotona* (see Appendix 2). (a) Dorsal view; (b) ventral view; (c) lateral view. Shape information along incisive and palatal foramen and were digitized for separate analysis. Landmarks were given by dots, semilandmarks were given by stars. Scale: 1.0 cm.

analysis of variance (ANOVA) applied to the centroid size in dorsal view, and a two-way multivariate analysis of variance (MANOVA) was applied to relative warp scores both in dorsal and ventral views. These statistical analyses were performed in SPSS (version 17.0).

Additionally, 19 linear skull measurements of 16 intact specimens in the *O. forresti* complex from Chinese collections (Appendix I; with both maxillary and mandible complete; the other 14 specimens were either damaged or unavailable for these measurements) were taken using a micrometer (ERLING IP 54). This sample included 10 *O. forresti*, two paratypes of *O. gaoligongensis*, one specimen collected from the type locality of

O. gaoligongensis, the holotype of *O. nigritia* and two specimens collected from the type locality of *O. nigritia*.

Seventeen linear measurements of *Lepus* specimens published by Li and Luo (1979) and Luo (1988) were reanalyzed using Principal Component Analysis (PCA) in NTSYSpc (version 2.2). These measurements included: profile length (PL), zygomatic width (ZW), length of palate (LP), length of the maxillary diastema (LMD), palatal bridge length (PBL), post palatal width (PW), diameter of the tympanic bullae (GTB), least diameter of the tympanic bullae (LTB), distance between the tympanic bullae (DTB), greatest mastoid breadth (GMB), first upper incisor section width (UIW),

incisive foramen length (FL), crown length of maxillary cheek tooth row (CLC), crown length of mandible cheek tooth row (CCM), total length of the mandible (TLM), preorbital width (PROW) and the postorbital width (POW). The first three principle component axes were used to depict shape differences between these two species.

Previous studies have demonstrated that sexual dimorphism in *Ochotona* and *Lepus* is insignificant, thus we combined males and females in all of our analyses (Weston 1982; Smith and Weston 1990; Lu 2003).

Results

Melanistic lagomorphs in museum collections

Color variants, including melanism and albinism, were documented in our review of museum collections; they were, however, particularly rare in meadow-dwelling pikas (*O. curzoniae* and *O. dauurica*; Smith et al. 1990). Extremes of pigmentation and coloration were found in the plateau pika (*O. curzoniae*; Fig. 2), including a completely melanistic individual (IOZCAS 18722; Fig. 2a) and a completely albinistic individual (NIPBCAS 0006357; Fig. 2e; see also Animal Diversity Web 2011). In each case these specimens were part of a larger series containing the normal (sandy brown) coloration of the species, as depicted in Fig. 2b and c, the coloration of which also varies: b appears black in the basal 3/4 length of the fur, while yellow gray at the tips, and c appears brownish-gray in the dorsal part of the pelage but whitish gray near the hind legs. Fig. 2d portrays a yellowish gray coloration from dorsal view which appears to represent a case of xanthochromism in *O. curzoniae*.

Melanistic forms are very rare in the ecologically similar *O. dauurica*. This species has been collected annually since 1959 by staff at the Tuva Anti-Plague Station near the Shara-Kharagay River, Mongun-Taiga region, Tuva, and a single melanistic specimen was collected in 1975 (N. Formozov, personal communication).

Melanism was found more frequently in talus-dwelling pikas (see Smith et al. 1990). A sample of the alpine pika (*O. alpina*) from the former Sayan Reserve, Irkutsk region, Russia (54°7' N, 96°40' E), includes two partly melanistic specimens (ZMMU S-44482, ZMMU S-44481) in a collection of 45 specimens with normal coloration (cassia brown; Fig. 3). Additionally, one melanistic specimen (ZMMU S-13296) was found among three specimens collected from the Kuragan River, central Altai, Russia (50°8' N, 86°10' E), and one melanistic individual (ZMMU S-14741) was found in a

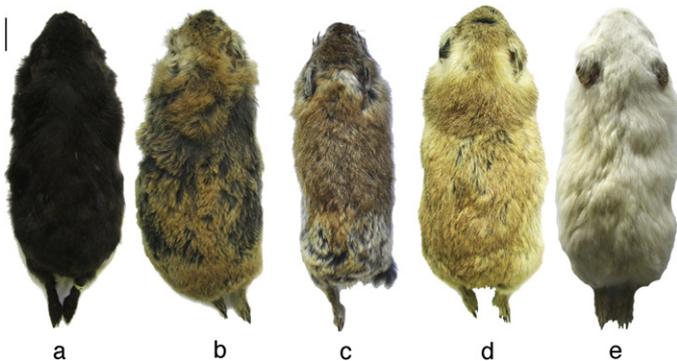


Fig. 2. Comparison of pelage phenotypes of *O. curzoniae*. (a) IOZCAS 18722; (b) IOZCAS 18678; (c) IOZCAS 18680; (d) IOZCAS 18534; (e) NIPBCAS 0006357. (a–c) were collected from the same locality during summer (Jialing Lake, Maduo County, Qinghai; 34°54' N, 98°12' E); (d) was collected from Tianjun, Qinghai; (e) was collected from Menyuan County, Qinghai (34°54' N, 98°12' E). Scale: 2.0 cm. For comparison, pikas portrayed in a, d and e were all collected as a part of a larger series containing the normal (sandy-brown) coloration of the species represented by (b) and (c); see text.



Fig. 3. Comparison of pelage phenotypes of *O. hyperborea*. (a) ZMMU S-63735; (b) ZMMU S-63737. (a) and (b) were both collected together at Karzanak Mountain, Manskiy District, Krasnoyarskiy Territory, Russia. Scale: 2.0 cm.

sample of 29 specimens from the Chulyshman River Valley, Republic of Gorniy Altai, Russia (50°37' N, 88°45' E). Three melanistic specimens were used for the initial description of *O. alpina atra* (Eversmann 1842) (ZISP 84398, ZISP 84399, ZISP 48490) based on specimens from Uymon, Gorniy Altai, Russia (50°12' N, 86°02' E).

Occurrence of melanism was also found in the northern pika (*O. hyperborea*). One melanistic specimen (ZMMU S-123561) from Terney District, Primorskiy Territory, Russia (45°03' N, 136°37' E) was collected together with four others with normal coloration (bright russet). Additionally, two melanistic (ZMMU S-63737, ZMMU S-63733) and one deep brown (ZMMU S-63732) specimens were collected with three other specimens of normal coloration from Karzanak Mountain, Manskiy District, Krasnoyarskiy Territory, Russia (54°49' N, 94°07' E) (Fig. 3); one melanistic animal (ZMMU S-148012) was collected with 17 normal individuals at Torgalyg River, Tuva Republic, Russia (51°04' N, 92°50' E); one melanistic individual (ZMMU S-150657) and one of normal coloration were collected together near Seymchan, Magadan Region, Russia (55°46' N, 152°18' E); and one melanistic pika (ZMMU S-133344) was collected at Batsumber, Tuv Aimag, Mongolia (48°22' N, 106°52' E). It is unknown if melanistic individuals of *O. alpina* and *O. hyperborea* have been collected disproportionately to their actual occurrence in nature.

The type series of the Turuchan pika (*O. turuchanensis*) includes six specimens. One paratype collected in Uchami, Turuchansk District, Krasnoyarskiy Territory, Russia (63°54' N, 96°22' E) (ZISP 28865) is melanistic, while the other five specimens have normal pelage.

Pelage color variation in species under discussion

Comparative study of pelage color variation in the *O. forresti* (*O. forresti*, *O. gaoligongensis*, *O. nigritia*) and *L. mandshuricus* (*L. mandshuricus*, *L. melainus*) complexes (Figs. 4–6) indicates that seasonal variation and partial melanism occur commonly. The three type specimens used for erecting *O. gaoligongensis*, collected in October, were generally similar to *O. forresti* specimens, but with their head and neck a brilliant brown-rufous, and the back a rufous-black (Fig. 4a and b). However, one specimen collected at the type locality of *O. gaoligongensis* in May (Fig. 4c) showed a



Fig. 4. Comparison of pelage phenotypic variation between *O. gaoligongensis* and *O. forresti*. (a) Holotype of *O. gaoligongensis* (EPIY 107); (b) paratype of *O. gaoligongensis* (KNHMZ 013311); (c) *O. gaoligongensis* specimen collected at the same locality (KNHMZ 013314); (d)–(e) *O. forresti* (KNHMZ 005266, KNHMZ 006560). Scale: 2.0 cm.

coloration that was extremely similar to that of typical *O. forresti* (Fig. 4d and e). The pelage of the holotype of *O. nigritia* bears thick and darker hairs, it looks generally black from a distance, but shows a grayish-yellow coloration inspected at a close distance (Fig. 5d). Two other specimens collected near the type locality of *O. nigritia* showed differences in coloration; the specimen collected in winter showed a similar pattern to the type of *O. gaoligongensis*



Fig. 5. Comparison of pelage phenotypic variation between *O. nigritia*, *O. gaoligongensis* and, *O. f. duoxionglaensis*. (a) Paratype of *O. gaoligongensis* (KNHMZ 013312); (b) specimen collected at the type locality of *O. nigritia* in winter (KNHMZ 012486); (c) specimen collected at the type locality of *O. nigritia* in summer (IOZCAS 5047); (d) holotype of *O. nigritia* (KNHMZ 013316); (e) *O. f. duoxionglaensis* (NIPBCAS 0006341). Scale: 2.0 cm.

(compare Fig. 5a with b), while the specimen collected in summer displayed a darker coloration (Fig. 5c).

The pelage of the holotype of *O. f. duoxionglaensis* was dark reddish-brown with a prominent gray region encircling the neck



Fig. 6. Comparison of pelage phenotypic variation and cranium and mandible characteristics between *L. mandshuricus* and *L. melainus*. (a) and (d) Dorsal and ventral view - paratype of *L. melainus* (IOZCAS 26866); (b) and (e) dorsal and ventral view - black phenotype of *L. mandshuricus* (IOZCAS HJ03002); (c) and (f) dorsal and ventral view - brownish gray phenotype of *L. mandshuricus* (IOZCAS 00837); (g)–(j) dorsal, ventral, and lateral view of cranium and mandible of *L. melainus*; (k)–(n) dorsal, ventral, and lateral view of cranium and mandible of *L. mandshuricus*. Scales: (a)–(f) 5.0 cm; (g)–(n) 1.0 cm.

Table 1Statistical analysis on the body form and linear measurements of the skulls of *Ochotona forresti*, *O. gaoligongensis* and *O. nigritia*.

	<i>O. forresti</i>		<i>O. gaoligongensis</i>		<i>O. nigritia</i>		<i>p</i> values (<i>df</i> =2)
	Average	SE	Average	SE	Average	SE	
BL	163.06	9.79	164.5	8.76	163.75	8.54	<i>p</i> = 0.949
HL	28.13	1.15	28.16	1.72	28.25	2.63	<i>p</i> = 0.989
EL	19.94	2.05	20.00	1.26	20.25	2.06	<i>p</i> = 0.958
PL	38.64	1.05	38.49	0.28	38.59	1.03	<i>p</i> = 1.0
SBL	35.82	1.20	36.88	0.21	35.85	1.56	<i>p</i> = 0.951
BAL	32.57	1.59	33.01	0.28	32.28	0.62	<i>p</i> = 0.792
GLN	12.36	0.67	12.40	0.49	12.62	0.36	<i>p</i> = 0.825
GHO	6.84	0.26	6.53	0.11	6.81	0.22	<i>p</i> = 0.963
GSL	12.68	0.43	12.72	0.38	12.05	0.85	<i>p</i> = 0.249
PSL	10.03	0.50	9.57	0.51	9.81	0.25	<i>p</i> = 0.938
IFL	9.61	0.60	10.20	0.13	9.79	0.35	<i>p</i> = 0.923
IFW	3.51	0.25	3.39	0.13	3.48	0.03	<i>p</i> = 0.997
ZB	19.31	0.53	19.48	0.22	18.82	0.38	<i>p</i> = 0.317
SBO	4.83	0.21	4.70	0.20	4.72	0.26	<i>p</i> = 0.857
LDM1	8.12	0.45	8.19	0.39	8.45	0.20	<i>p</i> = 0.533
LDM2	5.75	0.50	5.97	0.67	5.62	0.51	<i>p</i> = 0.869
GNB	17.01	0.59	17.60	1.05	16.96	0.47	<i>p</i> = 0.791
DTB	3.55	0.32	3.36	0.38	3.91	0.05	<i>p</i> = 0.248
LCM1	7.46	0.25	7.78	0.15	7.63	0.12	<i>p</i> = 0.436
LCM2	6.74	0.27	7.13	0.38	6.90	0.34	<i>p</i> = 0.966
TLM	25.46	1.18	25.80	0.74	25.10	1.50	<i>p</i> = 0.846
HVR	15.23	0.61	15.42	0.42	14.35	0.36	<i>p</i> = 0.095

Abbreviations. Standard error, SE; body length, BL; hind leg length, HL; ear length, EL; profile length, PL; skull basilar length, SBL; basal length, BAL; greatest length of the nasals, GLN; greatest inner height of the orbit, GHO; coronal suture length, GSL; parietal suture length, PSL; incisive foramen length, IFL; incisive foramen width, IFW; zygomatic breadth, ZB; smallest breadth across the orbit, SBO; length of the diastema in maxillary, LDM1; length of the diastema of mandible, LDM2; greatest neurocranium breadth, GNB; distance between the tympanic bullae, DTB; length of the cheek tooth row at base in maxillary, LCM1; length of the cheek tooth row in mandible, LCM2; total length of the mandible, TLM; height of the vertical ramus, HVR. The length of body, and length of ear and hind leg were obtained from museum records (17 *O. forresti*, 5 *O. gaoligongensis* and 3 *O. nigritia*). Linear measurements of skulls were obtained from 16 intact specimens (10 *O. forresti*, 3 *O. gaoligongensis* and 3 *O. nigritia*).

(Fig. 5e). The ear of this holotype was also covered by gray fur. The pelage of the paratype has been largely destroyed, however a grayish region could also be observed along the neck region.

A large number of melanistic specimens of *L. mandshuricus* were found along with partial melanistic and gray phenotypes in museum collections. For example, 11 specimens (four males, six females and one juvenile without gender information) were collected at Liudaogou, Langxiang, Heilongjiang Province (41°35' N, 127°11' E), in October 2003 (IOZCAS H03019-H03029), and three of them possessed a black coat (IOZCAS H03019-03021). In the black phenotype specimens, the dorsal part of the pelage is black, while the throat and abdomen are white; thus these specimens are only partially melanistic (Fig. 6b and e). The coloration of the paratype of *L. melainus* (IOZCAS 26866) is compared with the black and brown phenotypes of *L. mandshuricus* (IOZCAS HLJ03002, IOZCAS 00837) in Fig. 6; the dorsal pelage of the type of *L. melainus* is thicker than in *L. mandshuricus*.

Morphometric analysis

The general body length of the specimens of *O. forresti*, *O. gaoligongensis*, and *O. nigritia*, is similar (Table 1; *p* = 0.949); the average value is about 163 mm. *Ochotona thibetana* from a nearby region is prominently smaller (*p* < 0.05), with an average size of about 145 mm. Average lengths of hind feet and ears are similar in the three forms in the *O. forresti* complex (*p* = 0.989 and *p* = 0.958, respectively, Table 1).

Analysis of 19 skull measurements demonstrated insignificant differences among *O. forresti*, *O. gaoligongensis* and *O. nigritia* in all measurements (*p* values ranged from 0.095 to 1.0, Table 1). ANOVA analysis based on centroid size in a dorsal view also demonstrated significant differences among *O. thibetana* and each of *O. forresti*, *O. gaoligongensis* and *O. nigritia* (*p* < 0.001), while insignificant differences were observed among *O. forresti*, *O. gaoligongensis*, and *O. nigritia*. Relative warps analysis of the ventral view showed

that the first two axes of relative warps scores captured 28.71% and 14.78% of shape variation respectively. In the dorsal view, the first two axes of relative warps scores explained 33.94% and 24.24% of the shape variation. While there were no distinct differences among these four taxa, there was wide overlap in the shape space. The shape variation of the lateral view was also too weak to distinguish the species under discussion; however, shape variation of the incisive and palatal foramina discriminated the samples into two groups. The first group included *O. forresti*, *O. gaoligongensis*, and *O. nigritia*, and the second group included *O. thibetana* (Fig. 7p and q). Nevertheless, *O. gaoligongensis* could not be separated from *O. nigritia* based on shape variation of the palatine foramen. For example, the holotype of *O. gaoligongensis* (Fig. 7a) was similar to *O. forresti* (Fig. 7h and i), the paratypes of *O. gaoligongensis* (Fig. 7b and c) were similar to the specimen collected at the type locality of *O. nigritia* (Fig. 7g) and the other *O. forresti* (Fig. 7j). MANOVA analysis based on the relative warps scores both for dorsal and ventral views revealed no significant differences among *O. forresti*, *O. gaoligongensis*, and *O. nigritia*, while when these forms were combined, they differed significantly from *O. thibetana* (*p* < 0.001).

The holotype and adult paratype used to erect *O. f. duoxionglaensis* were greatly different in the shape of their respective incisive and palatal foramen. The outline of this region in the holotype (Fig. 7k) is similar to the shape of *O. forresti*. However, there is a prominent inclined plane on the lateral margin, which was not present in other specimens of *O. forresti* (Fig. 7a–j). The paratype of *O. f. duoxionglaensis* (Fig. 7l) showed a shape of incisive and palatal foramen similar to that found in *O. thibetana* (Fig. 7m–o). The differences of this region in these two specimens were also apparent by geometric morphometrics analysis (Fig. 7p and q).

Skull shape of *L. melainus* was similar to both the black and gray phenotypes of *L. mandshuricus* in bearing an indistinct anterior branch of the supraorbital processes in the cranium and a very well-developed ascending ramus in the mandible (Fig. 6). PCA

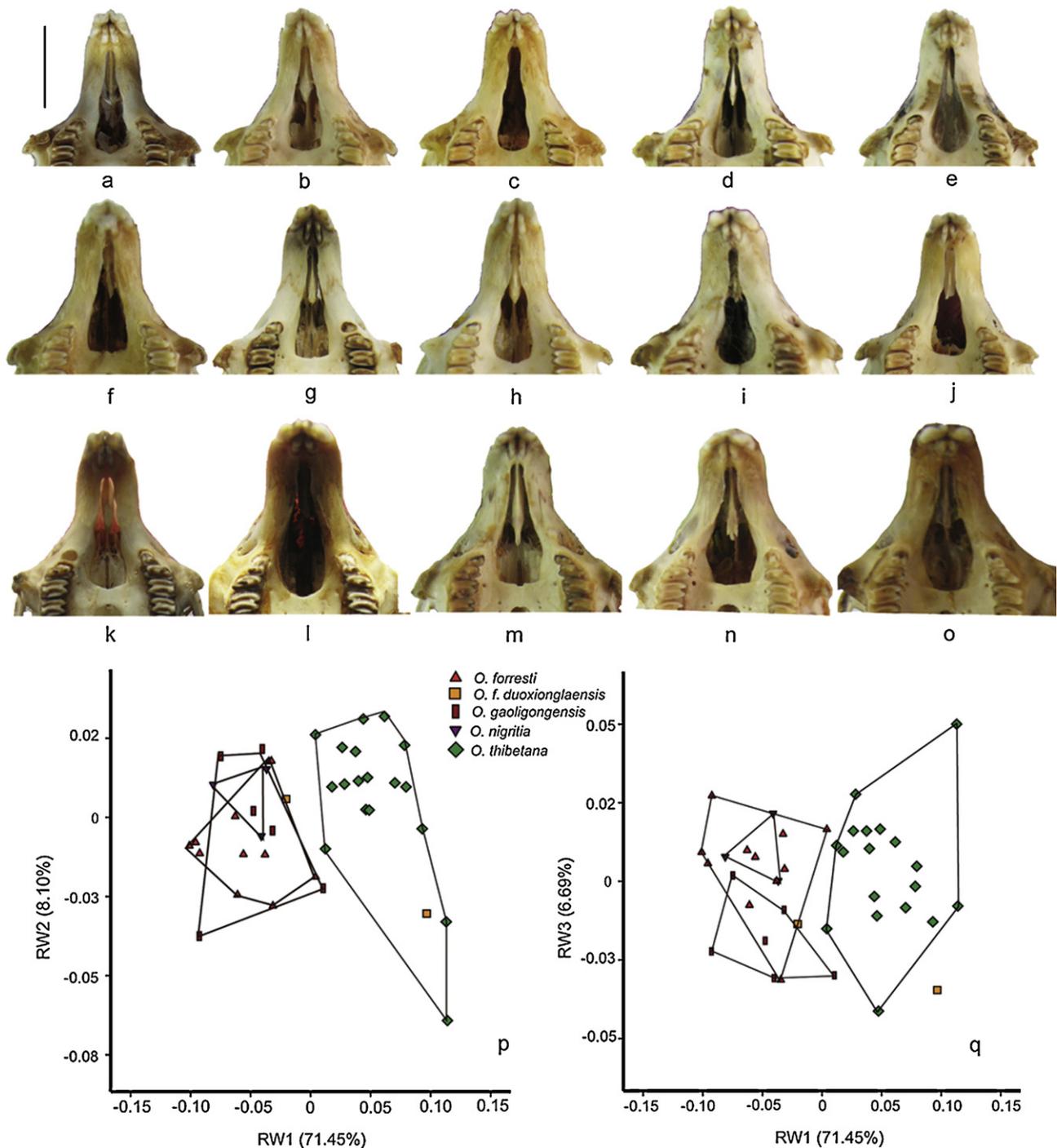


Fig. 7. Shape variation of the incisive and palatal foramen in *O. gaoligongensis*, *O. nigritia*, *O. forresti*, *O. f. duoxionglensis* and *O. thibetana*. (a)–(e) *O. gaoligongensis*: (a) holotype (EPIY 107); (b) and (c) paratypes (KNHMZ 013311, KNHMZ 013312); (d) and (e) specimens collected at the same locality (KNHMZ 013314, KNHMZ 013315); (f) and (g) *O. nigritia*: f. holotype (KNHMZ 013316); (g) specimen collected at the type locality (IOZCAS 5009); (h)–(j) *O. forresti*: (h) KNHMZ 005260; (i) KNHMZ 005264; (j) KNHMZ 005265; (k) and (l) holotype and paratype of *O. f. duoxionglensis*; (k) NIPBCAS 0006341, (l) NIPBCAS 0006342; (m)–(o) *O. thibetana*: (m) KNHMZ 004824; (n) KNHMZ 005333; (o) KNHMZ 005332; (p) and (q) relative warps analysis on the shape variation of incisive and palatal foramen. Scale: 1.0 cm. (a)–(o) Show the similarity and shape variation in the incisive and palatal foramen of *O. gaoligongensis*, *O. nigritia*, *O. forresti*, as well as their differences with *O. f. duoxionglensis* and *O. thibetana*; (p) and (q) show the differences as depicted by geometric morphometrics.

analysis based on 17 linear measurements demonstrated insignificant shape variation among these three phenotypes (Fig. 8a); the first three axes explained 29.30%, 13.33% and 8.62% of shape variation. Occurrence of those phenotypes in China overlapped widely, in which melanistic individuals were generally confined to the Lesser Khingan and vicinity, while the brown type showed a much wider distribution (Fig. 8b).

Discussion

Occurrence of melanism in lagomorphs

Melanism occurs as a ubiquitous polymorphism in animals, and this phenomenon has been widely reported in fish, birds and mammals. In mammals, felids (Searle 1968; Robinson 1978), canids

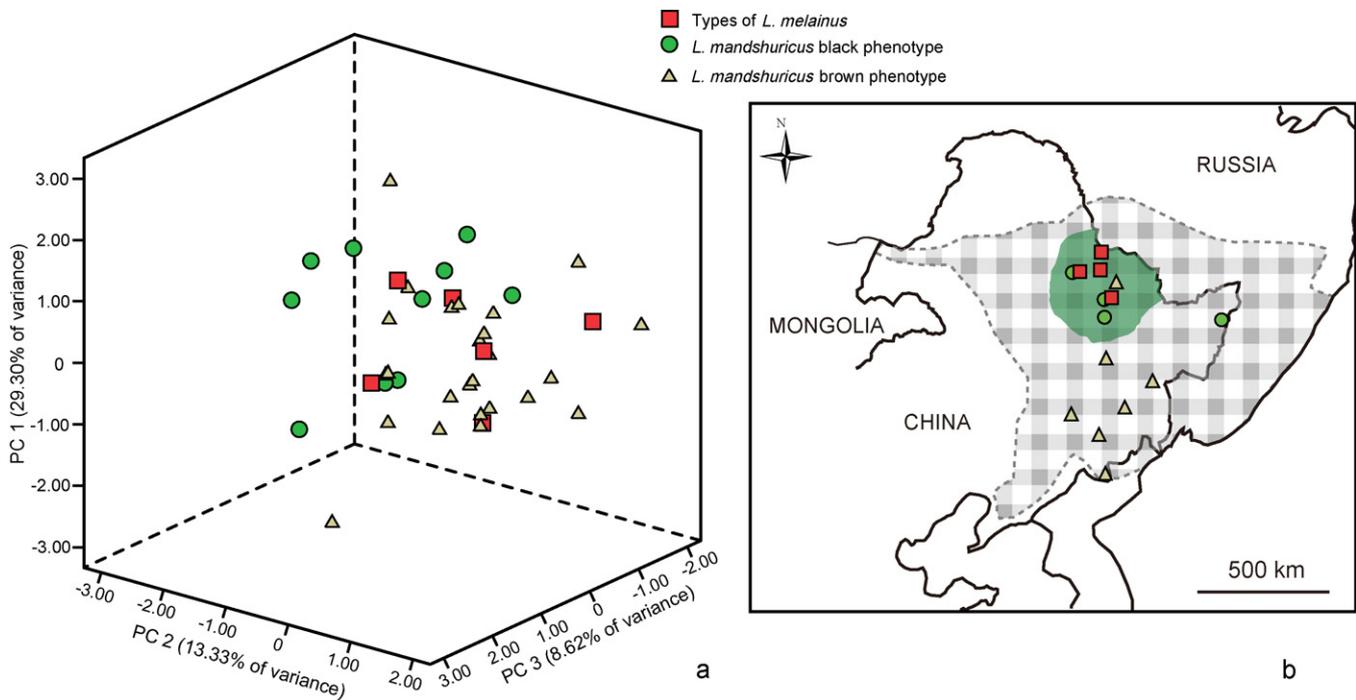


Fig. 8. Shape variation and sample localities in China of *L. mandshuricus*. (a) PCA analysis on the 17 linear measurements published by Luo (1988); (b) sample localities in China used in PCA analysis. The grid shaded area gives the distribution range of *L. mandshuricus* (Smith and Xie 2008), the green shaded area gives the range of the species in the Lesser Khingan Range.

(Anderson et al. 2009), deer (Baccus and Posey 1999), primates (Nakayama et al. 2008) and several species of rodents (Lai et al. 2008) show this kind of pigment diversity. Changes in coat color in animals are mainly associated with mutations in the melanocortin-1-receptor gene (*MC1R*) coding region (Majerus and Mundy 2003; Nachman et al. 2003). It has been suggested that coat color polymorphisms of animals could be associated with different ecological settings. For example, as an anti-predator strategy dark coat color has been observed more frequently in humid and closed habitats, while pale coat color may be found in drier, more open habitats (Lai et al. 2008). Additionally, correlation between coloration of the substrate and pelage color has been noted in several rodent species (Benson 1933; Belk and Smith 1996; Krupa and Geluso 2000; Nachman et al. 2003).

In spite of this rich knowledge about melanism in nature and recent studies on the genetic background for the occurrence of this phenomena, melanism has been less studied in both families of lagomorph. There are short reports on the occurrence of melanistic coloration in the snowshoe hare (*L. americanus*), the European hare (*L. europaeus*), the Manchurian hare (*L. mandshuricus*), cottontails (*Sylvilagus floridanus*, *S. palustris*), and northern and alpine pikas (*O. hyperborea*, *O. alpina*) (Blair 1936; Aldous 1939; Ognev 1940; Gordon 1954; Velich 1956; Yudakov and Nikolaev 1974; Marin 1984; Sokolov et al. 1994). Many of these reports are more than 60 years old, and they are limited to certain geographical regions. In many cases the prevalence of melanism has led to systematic confusion.

A meta-analysis of coat color variation in lagomorphs reported that the overall pelage coloration tends to match environmental background and to change with seasons (Stoner et al. 2003). Additionally, it was determined that darkened pigmentation at ear tips and tail tips may have communicative roles, that a darker pelage is probably associated with adaptation to forest habitats, and that a red coloration may be adapted to rock environments (Stoner et al. 2003). For example, the pelage of the mountain hare (*L. timidus*) appears largely adapted to the polar and mountainous habitats it

occupies; additionally it shows a significant difference from summer to winter (Stoner et al. 2003). A high proportion of melanism also occurs in cold and moist regions. About 0.5% of populations of *L. mandshuricus* from Primorye display signs of melanism. This proportion is bigger in the Bira and Bidjan River valleys (Yudakov and Nikolaev 1974; Sokolov et al. 1994). Melanistic Altai pikas (*O. alpina*) in the taiga zone may even reach 20% of the population (Marin 1984). The occurrence of melanism in *O. princeps* and *O. macrotis* has also been reported (Sludskiy et al. 1980; Smith et al. 1990). The present study provides the first case for occurrence of melanism and albinism in *O. curzoniae*, although the proportion of melanism in *O. curzoniae* on the Qinghai-Tibet plateau appears much lower than for *O. alpina* in the taiga zone of north Asia. These data further confirm the possibility of pigment diversity in different species of lagomorphs and indicate that these polymorphisms may be due to environmental conditions.

Different natural conditions may induce occurrence of pigment diversity in wild populations of lagomorphs. The partial melanistic individual that was used to erect *O. nigritia* and the black phenotypes of *L. mandshuricus* also serve to portray the gradient variation of these phenomena in lagomorphs.

It is worth noting that the underlying causes and evolutionary process leading to the occurrence of melanism are still unclear. It would be interesting to know whether the expression of melanism in different lagomorphs is induced independently or is a plesiomorphic character. Also important is our need to understand more clearly the selection pressures which may lead to expressions of melanism. We hope our data may initiate new interest to this topic.

Remarks on the taxonomy of *Ochotona forresti*

Thomas described *O. forresti* based on two specimens collected in northwest Yunnan (northwest flank Li-Kiang Range; Thomas 1923). The species was established based mainly on differences with the sympatric *O. thibetana*. Following its original description

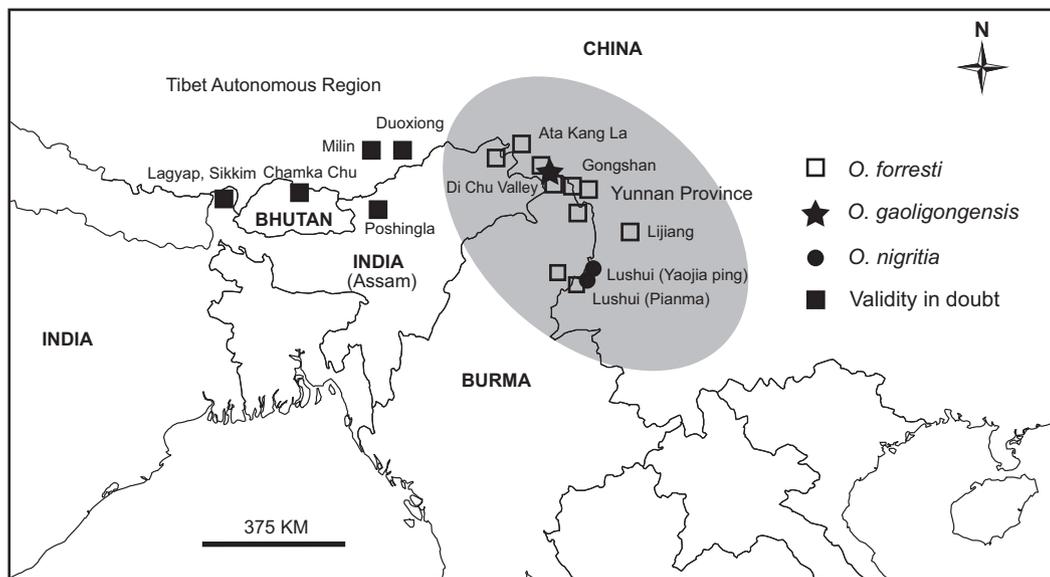


Fig. 9. The known distribution of specimens attributed to *O. forresti* (squares), *O. gaoligongensis* (stars) and *O. nigritia* (circles). Localities of *O. forresti* that are of questionable validity are represented by solid squares.

the form was assigned to the Moupin pika *O. thibetana* (Gurev 1964; Feng and Kao 1974; Weston 1982), the steppe pika *O. pusilla* (Ellerman and Morrison-Scott 1951) and to Royle's pika *O. roylei* (Corbet 1978). Recently the taxonomic status of this species has been widely accepted (Allen 1938; Feng and Zheng 1985; Yu et al. 1992; Niu et al. 2004; Smith and Xie 2008; Ye et al. 2011). The distinctive characters between *O. forresti* and *O. thibetana* include the following aspects: the average body size of *O. forresti* is larger than *O. thibetana*, the length of fore leg claws in *O. forresti* is longer than in *O. thibetana*, and the incisive and palatal foramen of *O. forresti* is narrower than that of *O. thibetana* near the palatal bridge (Feng et al. 1986; Smith et al. 1990).

There are 19 specimens which have been identified as *O. forresti* in the British Natural History Museum. Lisovsky measured the holotype (NHMUK 23.4.1.91) several years ago, and these measurements all fall within the variation of the specimens preserved in China (SBL 36.25, IFL 9.52, ZB 19.32, SBO 4.86, LDM 8.22, DTB 3.86, LCM1 7.49, HVR 14.55). Among those specimens, seven were collected in Myanmar, four collected in Assam, one collected from Sikkim, four collected in Yunnan, and three of them were collected from Tibet (Appendix 1). Three specimens collected from Tibet were originally labeled as *O. roylei chinensis*. The skulls of these specimens are either missing or very badly broken, and the remaining incisive and palatal foramina are similar in shape to *O. thibetana*. However, these specimens from Ata Kang La have been examined closely by Robert Hoffmann and determined to be *O. forresti*. Two specimens collected from Poshingla, Assam (NHMUK 82.881 and NHMUK 82.882), are shorter in body length (127 and 110 mm, respectively) when compared with the average value of *O. forresti*. One specimen collected from Lagyap, Sikkim (NHMUK37.3.14.32) was originally labeled as *O. roylei nepalensis*; the skull of this specimen is also very badly broken, but the incisive and palatal foramina show a similar shape to *O. roylei*. One specimen labeled as *O. forresti* from Bhutan preserved in the NMNH has likely been misidentified (see above). In addition to these specimens, KNHMZ hosts the biggest collection of the *O. forresti* complex (24 specimens). EPIY hosts one specimen, and IOZCAS contains two specimens. A reexamination of all *O. forresti* in collections outside of China is warranted, given the likelihood of frequent mislabeling of specimens attributed to *O. forresti*. Taking into consideration only those specimens that are likely to represent *O. forresti*, the distribution of the species mainly encompasses a small region confined by

the Gaoligong ranges (Fig. 9). The vegetation at the altitude of 2600–4400 m, where *O. forresti* lives, is mainly mixed broadleaf-coniferous forest (Smith and Xie 2008).

Descriptions of *O. nigritia* and *O. gaoligongensis* were based on very limited samples, thus color variation caused by seasonal changes or contrasting habitats were probably neglected. Furthermore, overall body size and cranial characteristics of these forms are within the range of *O. forresti* (Table 1 and Fig. 7p and q). The evidence we have provided contradict the specific status of *O. nigritia* and *O. gaoligongensis*, and confirm the speculations proposed by Hoffmann and Smith (2005) that these forms should be considered synonyms of *O. forresti* (Hoffmann and Smith 2005; Smith and Johnston 2011c; Smith and Xie 2008). This conclusion also provides a new benchmark for IUCN to assess the conservation status of *O. forresti*.

Description of *O. f. duoxionglaensis* was also based on limited samples (two adults and one juvenile; Chen and Li 2009). The shape of the incisive and palatal foramen differed greatly in the adults that were established as holotype and paratype. The common name for *O. forresti* was translated into Chinese as “gray-necked pika,” thus erecting these specimens from Tibet as a subspecies of *O. forresti* could have been misled by the presentation of a grayish region around the neck, while according to our observations, a gray-colored neck is commonly found in other species of pikas. The original determination of these specimens as *O. forresti* by Feng et al. (1986) compared them to *O. thibetana*. This comparison shows very similar external measurements between the two species in this region. Additionally, our morphometric analysis places one of these specimens clearly in the range of *O. thibetana* and significantly different from *O. forresti*, *O. gaoligongensis* and *O. nigritia* (Fig. 7p and q). The second specimen falls near the border of the distributions of these two complexes. It appears that these forms may represent *O. thibetana*, rather than *O. forresti*, although further collection in this region is necessary to make a final determination. In our analysis, we do not consider these specimens as a western range extension of *O. forresti*.

Remarks on the taxonomy of *Lepus mandshuricus*

Lepus mandshuricus was established based on specimens from Khabarovskii Krai, Russia (Radde 1861). Sowerby (1923) noted the occurrence of melanistic individuals, and melanistic individuals

of this species were used to establish *L. mandshuricus* subphase *melanotonus* by Ognev (1922) and *L. melainus* by Li and Luo (1979). Surprisingly, these new designations were adopted in several important monographs (Flux and Angermann 1990; Zhang 1997; Wu et al. 2005). Here we demonstrate that the occurrence of *L. melainus* within China is largely confined within the distribution of *L. mandshuricus*. Additionally, our reanalysis of the measurements provided in the original description showed insignificant differences among the three pelage types (gray coloration, partial melanistic individuals, and complete melanistic individuals). The distribution of melanistic forms of *L. mandshuricus* in Russia has been summarized by Sokolov et al. (1994). In the coastal area of southern Primorsk only about 0.5% of hares are partial melanists, while an increased frequency has been noted in the valleys of the Bira and Bidzham rivers, as well as in the southern Amur region. It is unclear whether the degree of melanism is correlated with vegetation coverage; a more comprehensive study on the genetic background of this phenomenon is needed.

Conclusions

Our results demonstrated that the occurrence of melanism is common in various species of lagomorph, that establishing new species or subspecies mainly based on color variation of the pelage from a limited number of specimens is speculative, and that a more detailed investigation using multiple avenues of morphological information is needed for an accurate and comprehensive study of these species. The forms *O. nigritia* and *O. gaoligongensis* should be recognized as color morphs of *O. forresti*; similarly, *L. melainus* should be considered a color morph of *L. mandshuricus*.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi: 10.1016/j.mambio.2011.09.009.

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