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## Late Miocene fossil calibration from Yunnan Province for the striped rabbit *Nesolagus*

Lawrence J. FLYNN<sup>1</sup> JIN Chang-Zhu<sup>2</sup> Jay KELLEY<sup>3,4</sup> Nina G. JABLONSKI<sup>5</sup>  
JI Xue-Ping<sup>6</sup> Denise F. SU<sup>7</sup> DENG Tao<sup>2,8,9</sup> LI Qiang<sup>2,8</sup>

(1 Department of Human Evolutionary Biology, Harvard University Cambridge MA 02138, USA ljflynn@fas.harvard.edu)

(2 Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044, China)

(3 Institute of Human Origins and School of Human Evolution and Social Change, Arizona State University Tempe, AZ 85287, USA)

(4 Department of Paleobiology, National Museum of Natural History, Smithsonian Institution Washington, DC 20560, USA)

(5 Department of Anthropology, The Pennsylvania State University University Park, PA 16802, USA)

(6 Department of Paleoanthropology, Yunnan Institute of Cultural Relics and Archaeology Kunming 650118, China)

(7 Department of Paleobotany and Paleoecology, Cleveland Museum of Natural History Cleveland, OH 44106, USA)

(8 CAS Center for Excellence in Life and Paleoenvironment Beijing 100044, China)

(9 University of Chinese Academy of Sciences Beijing 100049, China)

**Abstract** The rabbit from the Late Miocene Shuitangba site in Yunnan Province represents the same species as that from the older site of Lufeng, Yunnan. Both settings record a wet, swampy habitat. Premolar morphology shows that the species is an early representative of the extant striped rabbit genus, which today lives in moist habitat, and should be designated *Nesolagus longisinuosus* (Qiu & Han, 1986). Fossil evidence for *Nesolagus* by about 7 Ma in the fossil record of South China is consistent with mitochondrial evidence for the Late Miocene split of the extant species of *Nesolagus*. We reconstruct a scenario for the origin of *Nesolagus* after 8 Ma, followed by rapid spread through Southeast Asia into present-day Sumatra.

**Key words** Shuitangba, Yunnan, South China; Miocene; Leporidae, *Nesolagus*; mitochondria

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### 1 Introduction

The developing fossil record of South China, especially Yunnan Province, holds the solutions to several evolutionary and biogeographic puzzles. In contrast to the Late Miocene vertebrate record of North China (Baodean Mammal Stage-Age), which is well-represented by many localities, the South China theater of evolution has yielded few assemblages documenting the different fauna and paleoecology of the region. Late Miocene fossils of South

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China include distinctive taxa at the species and higher taxonomic levels, some of which may be precursors of Recent Southeast Asian mammalian lineages. The new species *Tapirus yunnanensis* Ji et al., 2015 and *Muntiacus zhaotongensis* Dong et al., 2014 are examples. Small mammal fossils, such as tree shrews are no exception. The site of Lufeng with *Prodendrogale yunnanica* Qiu, 1986, records a northern record of the tree shrew family. Here, the Late Miocene Lufeng and Shuitangba sites elucidate the origin of an enigmatic lagomorph.

The living striped rabbits of Sumatra and mainland Southeast Asia (*Nesolagus netscheri* and *N. timminsi*) had no known precursor until Qiu and Han (1986) drew the tentative conclusion that the origin of *Nesolagus* involved an endemic species from Lufeng, Yunnan, then placed in the fossil genus *Alilepus*. Jin et al. (2010) agreed when they found Pleistocene *Nesolagus* in neighboring Guangxi Province. The rich Late Miocene mammal locality at Lufeng (7 to 6 Ma, Qi et al., 2006), spans about five meters of lignite with diverse mammalian fossils in a swampy paleoecological environment. Among the small mammal component is a leporine rabbit named on evidence previously available as a species of *Alilepus*, *A. longisinosus*. Morphological variants among the dozens of specimens suggested to Qiu and Han (1986) that *A. longisinosus* might represent a transition toward extant *Nesolagus*.

In recent years, new rabbit fossils have been recovered from Shuitangba, another Late Miocene site in Yunnan (Fig. 1). Near Zhaotong, 300 km northeast of Lufeng, the site is close to the northern limit of the South China paleobiogeographic region and has a fauna very much like that of Lufeng (Jablonski et al., 2014). At ~6.2 Ma (Ji et al., 2013) Shuitangba is younger, includes lignite beds, and samples a wet, water-side paleoenvironment. Its rabbit cannot be distinguished from Lufeng *Alilepus longisinosus* but, unlike the sample from Lufeng, the new material uniformly presents *Nesolagus* morphology that is advanced with respect to typical *Alilepus*. However, new leporid fossils from Shuitangba are still few. Mandibular specimen ZT 2015-0285 with complete dentition was found appressed to a block of dark clay during the intensive quarrying by IVPP in March 2015. Later in that field season edentulous jaw ZT 2015-0207 was retrieved. Collecting under the direction of Ji Xueping the year before produced palate fragment ZT 2014-0391. Previous field seasons involved trial wet screening and yielded a jaw fragment and an isolated premolar.

Here we document the new leporid fossils from Shuitangba, showing their affinity to the Lufeng rabbit and to extant *Nesolagus*. As an early representative of *Nesolagus*, *N. longisinosus* confirms a Late Miocene time frame for the differentiation of the modern genus lineage.

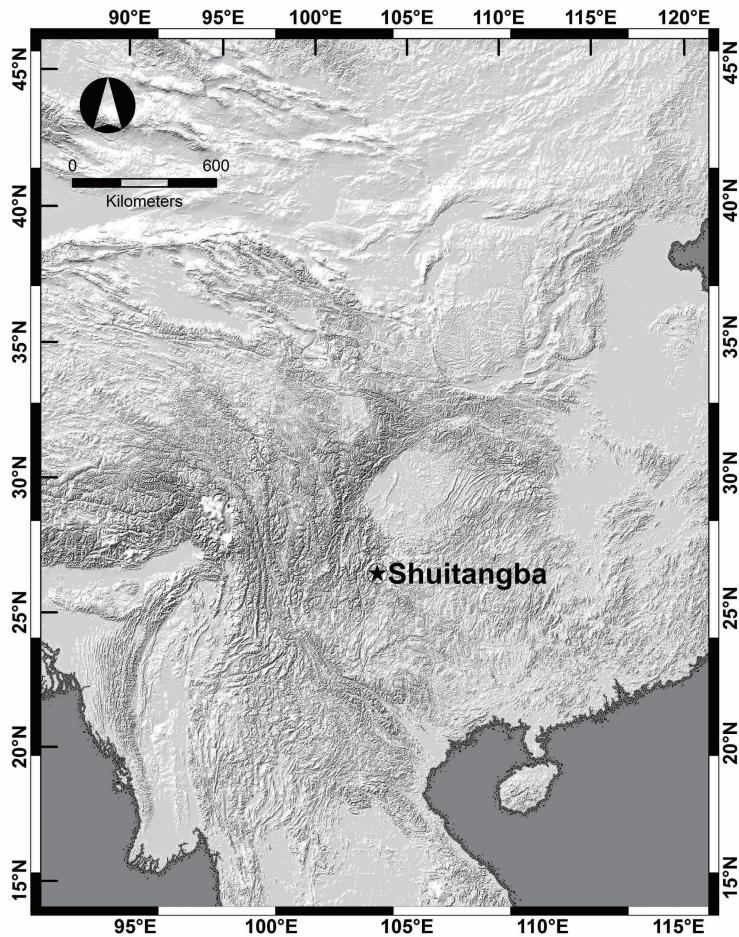


Fig. 1 Location of fossil site Shuitangba in Yunnan Province, South China

## 2 Systematic paleontology

### Order Lagomorpha Brandt, 1885

#### Family Leporidae Gray, 1821

#### Genus *Nesolagus* Forsyth Major, 1899

#### *Nesolagus longisinosus* (Qiu & Han, 1986)

*Alilepus longisinosus* Qiu & Han, 1986

*Alilepus* sp. Ji et al., 2013

*Alilepus longisinosus* Jablonski et al., 2014

*Alilepus longisinosus* Ji et al., 2015

**Referred material** ZT 2007-2-0063, isolated right p3; ZT 2010-3-0345, left dentary fragment with p3–4, m1; ZT 2014-0391, right maxilla and palatine fragment with all cheek tooth alveoli, P4 and M1–2; ZT 2015-0207, edentulous right mandible with all alveoli; ZT 2015-0285, left mandible with incisor, p3–4, m1–3.

**Locality** Shuitangba, local spring and lignite quarry in Zhaotong Basin, northeastern Yunnan Province. All specimens from the same “peaty clay” unit that yielded the *Lufengpithecus* skull reported by Ji et al. (2013), provenance is about 1 m above the skull at the 8-meter level in fig. 2e of Ji et al. (2013).

**Age** Faunal data place the assemblage in the Late Miocene; paleomagnetic correlation to a long Zhaotong Basin section dates the site to ~6.2 Ma (Ji et al., 2013).

**Emended diagnosis** Close in size to *Nesolagus sinensis* Jin et al., 2010, premolars toward the lower end of the size range for *N. sinensis*, but molars slightly longer relative to *N. sinensis*; short diastema, slightly longer than that of *N. sinensis*; prominent anterior and posterior external reentrants of p3 contain cement, but the reentrant in the anterior internal position is undeveloped and lacks cement (reentrant terminology of Jin et al., 2010 modified slightly in Fig. 2); trigonid unexpanded anteroposteriorly, unlike *Alilepus*; posterointernal reentrant of p3 variable, progressively reduced by expansion of the opposed posteroexternal reentrant, with the median bridge displaced to the lingual wall of p3 and the posterointernal reentrant eliminated; other features after Qiu and Han (1986): anterolingual fold shallow and anterobuccal fold distinct on P2, incisive foramen ends at anterior portion of P2.

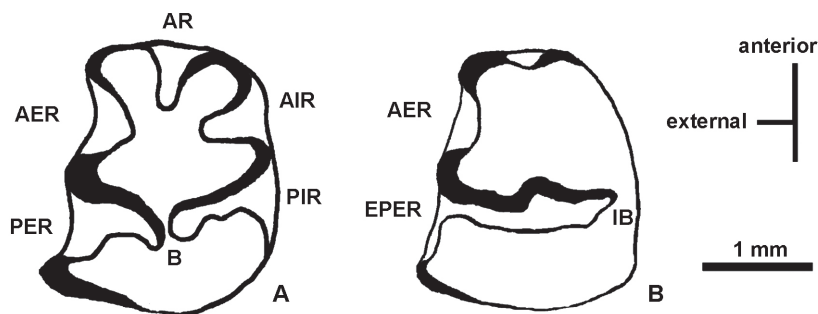


Fig. 2 Simplified leporid p3 dental terminology

A. idealized p3 showing reentrant positions and central trigonid-talonid bridge (B); B. *Nesolagus*-like p3 showing extended posteroexternal reentrant (EPER) and the bridge in internal position (IB)

AR. anterior reentrant; AER. anteroexternal reentrant; AIR. anterointernal reentrant;  
PER. posteroexternal reentrant; PIR. posterointernal reentrant

**Measurements** See Table 1; cheek tooth lengths and widths include upper dentition for ZT 2014-0391. Lengths of tooth rows at the alveolus level are greater than at the occlusal level of the crowns where teeth converge slightly; diastema length for damaged ZT 2015-0207 is approximate.

**Description** ZT 2015-0285 (Fig. 3) is a complete dentary of a young adult with dentition, except for the posterior extremity of the gonial angle and parts of the ascending ramus. Typical for leporids, p3 is the largest and most complex cheek tooth. The trigonid is short, but broadly rounded anteriorly, and the main buccal reentrant encroaches on the lingual wall of p3, as in young individuals of *Nesolagus*. Widths of cheek teeth progressively decrease posteriorly. The smallest tooth, m3, has a reduced posterior lobe and its base curves posteriorly so that the alveolus is elongated. The flat face of the incisor, 3.15 mm across, is angled

laterally; perpendicular to this surface, the incisor axis in cross section is 2.45 mm. Enamel extends around most of the medial side of the incisor (Fig.3). The mental foramen is above the midlevel of the diastema, 3.7 mm anterior to p3. The diastema is not exceptionally long; the ratio of diastema length to diastema plus alveolar row length is 0.48.

The edentulous mandible ZT 2015-0207 (Fig. 4) is somewhat larger than ZT 2015-0285. The coronoid rises steeply, but is not vertical, and the mental foramen, 3.5 mm anterior to p3, is high on the diastema; mandibular depth is 12 mm from the p4 alveolar margin to the inferior margin of the dentary.



Fig. 3 Left mandible ZT 2015-0285 in early wear, with incisor and all cheek teeth, p3–4, m1–3  
Lingual view above, buccal view below, occlusal view in the middle shows anterior to the left



Fig. 4 Buccal (right) and lingual (left) views of edentulous right mandible ZT 2015-0207



Fig. 5 Left dentary fragment ZT 2010-0345 with p3–4 and m1. Buccal view above, lingual view below, occlusal view in the middle. Cementum in the buccal folds of p3 is well developed

The maxilla and its dentition are represented by only one specimen, ZT 2014-0391 (Fig. 7), a right maxilla with P4 and M1–2 and all cheek tooth alveoli, and preserving a portion of the palatine bone. The latter extends anteriorly to opposite P4, where the palatine foramen is located. The incisive foramen extends posteriorly to a point opposite the middle of P2. Judging by the alveoli of the missing teeth, M3 is smallest, while P2 is oval and larger. P3 is asymmetrical with a buccally expanded metacone. The preserved cheek teeth are uniform in morphology, showing a deep internal reentrant with thin, gently wrinkled enamel, and heavy cementum within the reentrant exposed lingually. The root of the zygomatic process juts laterally opposite P4 and P3, and superior to the cheek teeth, about 3 mm above the alveolar margin.

ZT 2010-0345 (Fig. 5) is a partial mandible of an apparently older individual. The mental foramen is about 2.5 mm anterior to p3. The thin enamel of the anterior walls of the talonids of p4 and m1 undulates gently. The deep buccal reentrants are filled with cementum; the anteroexternal reentrant of p3 also bears cementum, but there is none on the lingual side of the teeth. The p3 resembles the isolated p3, ZT 2007-0063 (Fig. 6), which preserves 11 mm of crown height. The main buccal reentrant (PER) of both is very deep, extending nearly to the lingual wall of the tooth. A very thin connection of dentine is exposed there. There is no median bridge of dentine, but just buccal to the midline the thick enamel of the posterior wall of the trigonid flexes toward the talonid. Both teeth have a more triangular and anteroposteriorly longer trigonid than the p3 of ZT 2015-0285, a feature more typical of *Alilepus* than *Nesolagus*.

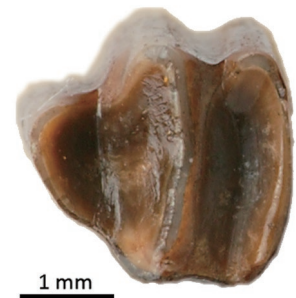


Fig. 6 Occlusal view of isolated right p3, ZT 2007-2-0063

**Table 1** Tooth dimensions of *Nesolagus longisnuosus* from Shuitangba (mm)

Specimen	p3 L	p3 W	p4 L	p4 W	m1 L	m1 W	m2 L	m2 W	m3 L	m3 W	L: alveoli	L: occlusal	Diastema
ZT 2015-0285	2.95	2.62	2.44	3.29	2.78	3.18	2.81	3.01	1.9	1.65	15	12.3	14
ZT 2015-0207											17.2		15
ZT 2007-0063	2.92	2.75											
ZT 2010-0345	2.99	2.95	2.48	3.05	2.7	2.96							
			P4 L	P4 W	M1 L	M1 W	M2 L	M2 W					
ZT 2014-0391			2.04	3.65	2.17	3.68	1.86	3.55			15.1		

Abbreviations: L. length; W. width.



Fig. 7 Right maxilla and palatine fragment ZT 2014-0391 with all cheek tooth alveoli, P4 and M1–2  
Lateral view left, ventral view right

### 3 Discussion

*Alilepus* is a Miocene age leporine that evolved in North America and spread to Eurasia around 8 Ma (Flynn et al., 2014). Its dentition is distinctive, particularly p3 with a shallow anteroexternal reentrant, and deep posteroexternal and posterointernal reentrants. The two posterior reentrants flank a narrow central bridge between the trigonid and talonid. In describing the large sample of rabbits from Lufeng, Qiu and Han (1986) noted that many specimens of the diagnostic lower premolar (p3) resembled the genotypic species *Alilepus annectens* (Schlosser, 1924), although the p3 midline bridge between the trigonid and talonid was quite narrow when present.

The opposed external and internal posterior reentrants of *Alilepus* are fully transformed in extant *Nesolagus*. The posteroexternal reentrant extends lingually to the internal wall of the tooth; the central bridge is eliminated, and there is no posterointernal reentrant. Either the trigonid and talonid are completely isolated, or a thin connection persists at the internal lingual wall. The single specimen of Pleistocene *Nesolagus sinensis* would show a thin lingual dentine connection in late ontogeny (toward the base of the p3 crown), although at an earlier wear stage (the surface of p3) the trigonid and talonid were totally isolated (Jin et al., 2010).

The Lufeng fossil sample shows a range of p3 morphologies from *Alilepus*-like premolars to a minority in which the trigonid and talonid are isolated (Fig. 8). Some Lufeng p3 have a very deep posteroexternal reentrant without a central bridge but retain a thin connection at

the lingual extremity of the crown. The absence of the bridge with a consequent long external reentrant as a variant in the Lufeng sample led to the name *Alilepus longisinuus* Qiu & Han, 1986 and the proposal that the species might lie near the ancestry of *Nesolagus*.

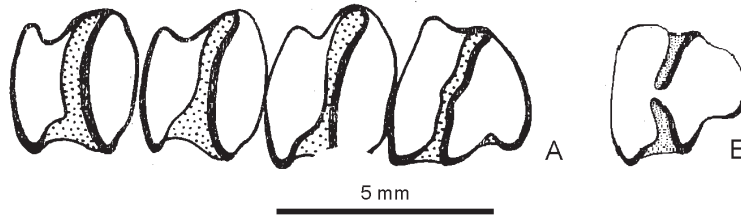


Fig. 8 Examples of Lufeng premolar variation from Qiu and Han (1986)

- A. holotype IVPP V 8131 dentition of *Nesolagus longisinuus*, right p3–4 and m1–2, anterior to right;  
 B. reversed image of p3 V 8132.41 at same scale. A shows a deep PER (no PIR) on p3 as in *Nesolagus*;  
 B shows the *Alilepus* morphotype with retained bridge joining trigonid and talonid

The geographically (and temporally) closest rabbit locality to Shuitangba is Lufeng. Dental sizes for the Shuitangba specimens fall near the means or toward the lower end of the ranges of those from Lufeng (Qiu and Han, 1986). The morphology of the three p3 from Shuitangba is identical to that of the advanced Lufeng morphotype in lacking a dentine bridge between trigonid and talonid. The p3 crown is dominated by a very deep external reentrant reaching the lingual wall of the tooth; the posterointernal reentrant is absent and the complete lingual wall borders a thin fold of dentine connecting trigonid to talonid. As in similar Lufeng specimens, an enamel flexure buccal to the midline of the tooth marks the former position of the bridge.

Remains of the Shuitangba rabbit are compatible with those of the Lufeng rabbit but differ in that all three p3 from Shuitangba show *Nesolagus* morphology. The geologically younger material from Shuitangba currently available shows that the premolars, variably derived at Lufeng, were more consistently like *Nesolagus* at Shuitangba. The absence of the trigonid bridge, with consequent long posteroexternal reentrant and lost posterointernal reentrant are derived *Nesolagus* traits necessitating transfer of *A. longisinuus* to that genus. *N. longisinuus* illustrates progressive intraspecific transformation toward typical *Nesolagus* morphology and origin of the genus in the Late Miocene wet habitat of Yunnan.

**Comparison** In recognizing fossil *Nesolagus* for the first time, Jin et al. (2010) based *N. sinensis* on a Pleistocene mandible from Guangxi Province in which a median bridge on p3 is entirely lacking. The talonid and trigonid are joined lingually by enamel and dentine low on the crown toward the root. About the size of *N. longisinuus* from Yunnan, *N. sinensis* is also close to extant *Nesolagus* in size. Jin et al. (2010) endorsed explicitly the ancestral relationship of “*Alilepus*” *longisinuus* to *N. sinensis* and later species of *Nesolagus*.

*Nesolagus sinensis* shows complete separation of the p3 trigonid from the talonid at an early stage of wear (lingual connection in late wear), unlike most *N. longisinuus* from Lufeng, for which the p3 retains a central or lingual connection. Other differences are minor.



The lower teeth of *N. sinensis* are somewhat larger than the Shuitangba *Nesolagus* specimens (compare Table 1 with Jin et al., 2010); p3 size for Shuitangba *N. longisinosus* is near that of *N. sinensis*, but the molars are relatively longer and narrower in the former. Shuitangba *Nesolagus* has a diastema length ratio of 0.48, close to that of the Lufeng sample (with ratio of 0.50 based on measurements of Qiu and Han, 1986). Both are close to the 0.46 ratio of *Nesolagus sinensis* cited by Jin et al. (2010).

**Paleoecology** Both the Lufeng and Shuitangba sites contain very dark clays, shell beds, fossil wood, and aquatic vertebrate fossils. Sediments accumulated in a reducing swamp environment, and faunal elements from both sites, for example a beaver and bamboo rats, indicate wet conditions. The Shuitangba fauna included a tapir (Ji et al., 2015) and diverse waterfowl. At Shuitangba a large otter (Wang et al., 2018) also attests to water. The Shuitangba ape (Ji et al., 2013) is very similar to *Lufengpithecus lufengensis*, and these suggest dependable sources of food (likely fruit) at both sites. As for these elements of the fauna, the paleoecological setting for Yunnan *Nesolagus* is waterside intermountain basins with wet conditions likely for much of the year. Fossil *Nesolagus* habitat contrasts with that of the cursorial *Alilepus*, its Holarctic predecessor.

The nocturnal Annamite striped rabbit of Laos and Viet Nam, *Nesolagus timminsi*, lives in moist habitat without an appreciable dry season (Schai-Braun and Hackländer, 2016), and may present a reasonable analogue for *Nesolagus longisinosus*. Today other rabbits favor a waterside niche, an example being the North American swamp rabbit, *Sylvilagus aquaticus*, which swims readily.

## 4 Conclusion

The diagnostic *Nesolagus* premolar morphology, occasionally present in the Lufeng specimens that were previously assigned to *Alilepus longisinosus*, appears to be more prevalent in the younger Shuitangba sample of that species. Its occurrence and then predominance in the species requires systematic transfer of the species to *Nesolagus*, as *N. longisinosus*. The wet habitat occupied by *N. longisinosus* contrasts with the presumed open habitat of *Alilepus annectens* of North China. Prior to the Late Miocene (~8 Ma, Flynn et al., 2014) modern leporines were absent from the Old World. Late Miocene leporines traversed high latitude steppe and woodland terrain in dispersing from North America to northern Asia. Rabbits later penetrated the mesic habitat of South China in the form of early representatives of *Nesolagus*. Neither *Nesolagus* nor *Alilepus* are known from the older Yuanmou sites of Yunnan Province, dating to ~8 Ma (Qi et al., 2006).

The Late Miocene swamp rabbit of Yunnan successfully occupied South China wetlands by about 7 Ma (the greater limit for Lufeng age estimate being about 6.9 Ma, Qi et al., 2006). SurrIDGE et al. (1999) reported their initial mitochondrial analysis of the two living species of *Nesolagus* and estimated that the considerable difference between them suggested genetic

origin about eight million years ago. The current paleontological record of 7 Ma is a minimum age for calibration of the origin of the genus and is reasonably concordant with the Late Miocene 8 Ma molecular split estimate. The fossil evidence calls for distinction of *Nesolagus* by ~7 Ma, and *Nesolagus* presumably spread through Southeast Asia to Sumatra about that time. Characteristic in the wet habitat of the Late Miocene of South China, the Yunnan *Nesolagus* lineage survives to the present as the modern striped rabbits of Southeast Asia.

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## 云南晚中新世苏门答腊兔(*Nesolagus*)分离时间的标定

Lawrence J. FLYNN<sup>1</sup> 金昌柱<sup>2</sup> Jay KELLEY<sup>3,4</sup> Nina G. JABLONSKI<sup>5</sup>  
吉学平<sup>6</sup> Denise F. SU<sup>7</sup> 邓涛<sup>2,8,9</sup> 李强<sup>2,8</sup>

(1 美国哈佛大学人类演化生物学学院 剑桥 02138)

(2 中国科学院古脊椎动物与古人类研究所, 中国科学院脊椎动物演化与人类起源重点实验室 北京 100044)

(3 美国亚利桑那大学人类起源学院和人类演化与社会变化学院 坦佩 85287)

(4 美国国家自然历史博物馆古生物部, 史密森研究所 华盛顿 20560)

(5 美国宾夕法尼亚州立大学帕克分校人类学系 帕克 16802)

(6 云南省文物考古研究所古人类部 昆明 650118)

(7 美国克利夫兰自然历史博物馆古植物与古生态研究室 克利夫兰 44106)

(8 中国科学院生物演化与环境卓越创新中心 北京 100044)

(9 中国科学院大学 北京 100049)

**摘要:** 报道了发现于云南昭通水塘坝的晚中新世兔类, 它与时代较早的云南禄丰地点的长褶“翼兔”(“*Alilepus*” *longisinuus*)属于同一个种, 两者栖息的环境均为潮湿的沼泽地区。前臼齿的形态表明该种是现今生活在湿润地区条纹兔(即苏门答腊兔*Nesolagus*)的早期代表, 因此将该种更名为长褶苏门答腊兔*Nesolagus longisinuus* (Qiu & Han, 1986)。*Nesolagus*化石记录在大约7 Ma的华南地区的证据与线粒体学研究推测*Nesolagus*的现生种类在晚中新世从兔科演化主线上分出来的结论一致。重建了苏门答腊兔演化历史的大致一幕, 即其在8 Ma后出现, 随即迅速地扩散到整个东南亚并最终到达现今的苏门答腊地区。

**关键词:** 云南水塘坝, 中新世, 兔科, 苏门答腊兔, 线粒体

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