# First discovery of fossil Nesolagus (Leporidae, Lagomorpha) from Southeast Asia 

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#### Abstract

A new leporid species, Nesolagus sinensis sp. nov., is described here representing the only leporid member of the Early Pleistocene Gigantopithecus fauna from Sanhe Cave, Chongzuo, Guangxi, South China and also the first fossil taxon of the Southeast Asian genus Nesolagus. Compared with two extant Nesolagus species from Indonesia and Vietnam and other related leprids, the new species has a relatively small size and an extraordinarily weak anterior internal reentrant (AIR) on p3, but it also retains the simplified paedomorphic pattern during the ontogenetic process as in extant species, which suggests that the new species is more primitive than and probably directly ancestral to extant Nesolagus species. The new species seems closely related to Alilepus longisinuosus from the Late Miocene strata of Lufeng, Yunnan, and probably diverged from a leporid similar to its ancestral form. It also indicates that Nesolagus originated in Southwest China.


Guangxi of China, Early Pleistocene, Nesolagus sinensis sp. nov., Gigantopithecus fauna

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The genus Nesolagus, also known as Sumatra Short-eared Rabbit or Striped Rabbit, is listed as the rarest species of the family Leporidae and one of the rarest species of mammals. Previously, it was considered endemic to the forest of the Barisan Mountains in western Sumatra, Indonesia. Since Schlegel and Jentink discovered Striped Rabbit in Sumatra in 1880, a new species of Nesolagus, N. timminsi, was found in the Annamite Mountains between Laos and Vietnam recently [1, 2], attracting much attention.

With a relatively small size, buffy gray with seven brown stripes and bright red tail and rump, Nesolagus is characterized by the particularly short ear (the ear length of Nesolagus is only half of Lepus) and limbs. It lives in rain-

[^0]forests at altitudes of $600-1400 \mathrm{~m}$. It is nocturnal, resting in the burrows of other animals. The tooth structure of Nesolagus is rather primitive, especially its similarity with Palaeolagus on upper teeth. This paper is the first report of Nesolagus fossil.

During 2007 and 2008, Chongzuo Biodiversity Research Institute, Peking University collaborated with Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences to carry out geological investigations in Chongzuo, Guangxi, leading to the discovery of new strata with Gigantopithecus blacki fossils in Sanhe Cave on Wuming Mountain. After systematic excavation, abundant mammalian fossils including more than 80 species were collected, such as Gigantopithecus blacki, cf. Hominidae, Pongo sp., Hylobates sp., Ailuropoda wulingshanensis, Sinomastodon yangziensis, Stegodon preorientalias, Di-
coryphochoerus ultimus, Cervavitus fenqii, Typhlomys intermedius, Rhizomys brachyrhizomyoides, Hystrix magna, Niviventer preconfucianus, and Leopoldamys edwardsioides [3, 4]. Especially, a mandible of Nesolagus was recovered in the cave.

The Sanhe Cave $\left(22^{\circ} 16.493^{\prime} \mathrm{N}, 107^{\circ} 30.663^{\prime} \mathrm{E}\right)$ is located in Chongzuo Ecological Park, which is 16 km to the northeast of Chongzuo urban district (Figure 1(a)). This park is also the main habitat for Presbytis leucocephalus, a rare and endangered primate. The cave developed on Permian limestone is the largest tubular Karst cave in this area. The eastern cave entrance, 12.5 m wide and 15.6 m high, is 203 m above sea level and located more than 70 m above the 1 st terrace. The deposits of Sanhe Cave consist of brown sandy clay, yellow-brown sand, and yellow sandy clay. The stratigraphic sequence can be divided into 7 layers from top to bottom with 12 m in thickness (Figure 1(b)) [3]. The mandible of Nesolagus was recovered from the 5th layer.

Based on the faunal analysis, the geological age of Sanhe Cave is estimated to be the middle Early Pleistocene, corresponding to approximately $1.2-1.6 \mathrm{Ma}$ on paleomagnetic dating [3, 4]. The Chongzuo Nesolagus fossil of the Early Pleistocene is the unique extinct representative of the genus, and its discovery has significant implications for discussing its origin, systematic evolution, and dispersal events of Southeast Asia during the Quaternary.

The terminology of p 3 and measuring methods follow White and Morgan [5] with slight modification (Figure 2).

## 1 Systematic paleontology

Order Lagomorpha Brandt, 1885
Family Leporidae Gray, 1821
Genus Nesolagus Forsyth Major, 1899
Type species Nesolagus netscheri (Schlegel, 1880)
Nesolagus sinensis sp. nov. (Figures 3 and 4)
Holotype: Fragmentary ramus of a left mandible with fragmentary incisor and p3 to m3 (IVPP V15932).

Type locality: Wuming Mountain in Chongzuo Ecological Park in Guangxi Zhuang Autonomous Region.

Geological age: Middle Early Pleistocene.
Etymology: Named for the first discovery of Nesolagus fossil in China (after Greek "Sino", pertaining to China and the Chinese).

Diagnosis: Relatively small in size; the diastema is relatively short; the lower incisor is relatively curved and located obviously forward; in p3, the AIR is extremely weak, whereas the cement-filled AER is broad and deep; in p4 to m 2 , the PER extends posteriorly in the lingual side; in m3, the talonid is relatively large.

## Measuremenrs: See Table 1.

Description: In the fragmentary mandible, the diastema is relatively short and more curved than those of Hypolagus and Lepus. The mental foramen is relatively large and located approximately in the middle of diastema. There are two large nutrient foramina beneath the mental foramen. Posterior end of the lower incisor forms a tubercle on the


Figure 1 Maps showing the geographical location (a) and its geological section (b) of Sanhe Cave.

(a)

(b)

(c)

Figure 2 Diagrams of p3 of Leporidae with labeled features. AR, anterior reentrant; AER, anteroexternal reentrant; AIR, anterointernal reentrant; PER, posteroexternal reentrant; PIR, posterointernal reentrant; MB, median dentine bridge; EL, enamel lake (formed from posterointernal reentrant); EPER, extended posteroexternal reentrant; IB, internal dentine bridge; TH, thick enamel in PER; TN, thin enamel in PER.

Table 1 Measurements of cheek teeth and mandible of Nesolagus sinensis sp. nov. ${ }^{\text {a) }}$

|  | i | p 3 | p 4 | m 1 | m 2 | m 3 | LT | LD | LA |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Length (mm) | 2.4 | 3.16 | 2.57 | 2.59 | 2.51 | 1.61 | 13.10 | 13.80 | 15.20 |
| Width (mm) | 3.53 |  |  |  |  |  |  |  |  |
| Width trigonid (mm) |  | 3.18 | 3.71 | 3.47 | 3.17 | 1.92 |  |  |  |
| Width talonid (mm) |  | 2.93 | 2.68 | 2.42 | 2.51 | 1.18 |  |  |  |

a) LT, length of tooth row in occlusal surface; LD, length of diastema; LA, length of alveolar p3-m3.


Figure 3 Fragmentary left mandible of Nesolagus sinensis sp. nov. (V15932; holotype). A1, buccal side; A2, lingual side.


Figure 4 Line drawings of the lower teeth of Nesolagus sinensis sp. nov. (V15932), N. timminsi and N. netscheri (type species) in the occlusal view. (a)-(c) Nesolagus sinensis sp. nov. (V15932, holotype) ((a) p3: the cutting surface below the cross section, p4-m3: occlusal surface; (b) reversed image of the surface above the cross section at 4.5 mm below the occlusal surface of p3; (c) transverse section view of i); (d) N. timminsi (BMNo. 1997.396); (e) N. netscheri (BMNo. 21.1.18.1).
lingual face of dentary. The mandibular height is measured as 11.77 mm on the lingual side of m 1 , while mandibular diastema index (diastema $\mathrm{L} /($ diastema $\mathrm{L}+$ alveolar L )) is approximately 0.463 , which is obviously less than that of Lepus (ca. 0.59).

The position of the posterior end of the robust lower incisor, located anterior to p3, is obviously more forward than Hypolagus, Pliopentalagus and Pentalagus. The lower incisor has a trapezoidal outline in cross section with two prominent angularities on backside. The width of the lower incisor is 3.53 mm .

The p3 has a sub-triangular occlusal outline with a smooth anterior margin instead of an angled one in Hypolagus. The AR and MB linking the trigonid and talonid are both absent. The AIR is extremely weak, whereas the ce-ment-filled AER is broad and deep. In order to better observe lingual structure of the trigonid and talonid, p3 is cut transversally at 4.5 mm below the occlusal surface. The results indicate that p 3 remains simplified paedomorphic pattern. Figure 4(b) shows the reversed image of the surface
above the cross section (cutting plane), while p3 of Figure 4(a) shows the enamel pattern on the surface below the cross section, illustrating the differences in morphology between the upper and lower parts of the tooth. In the early stage of wear, PER extends lingually and fuses with PIR, leading to the complete separation between the trigonid and talonid by cement in p3. In the advanced stage of wear (4.5 mm beneath occlusal surface), the PIR is completely missing and the IB is present, forming the EPER as in Lepus and the linkage between the trigonid and talonid by IB. The trigonid is longer and narrower than talonid whose posterior wall is smooth. The enamel of the posterior margin of trigonid and external wall of the tooth is thickened.

The p 4 to m 2 are similar to each other in morphology. The AER is weak. The PER extends posteriorly in the lingual side and extends nearly to the lingual margin of crown, resulting in the relatively weak IB linking the trigonid and talonid. It is characterized by the thick enamel of anterior wall (TH), the thin enamel of posterior wall (TN), and the weak crenulations on the posterior wall of PER, which are similar to Alilepus longisinuosus, Brachylagus, Hypolagus, Pronolagus and Romerolagus, while are different from Pliopentalagus, Pentalagus and Caprolagus. The tiny differences among p4 through m 2 include the gradual decrease of talonid width, the ordinal shortening of crown length, and the increase of degree of curvature.

The m3 is much smaller than other teeth. The IB connecting the trigonid and talonid is absent. The morphology of trigonid is similar with other teeth but the width of trigonid is narrower than that of m 2 . The talonid degenerates into oblate shape in outline but is still larger than those of Brachylagus, Lepus and Pentalagus.

## 2 Comparisons and discussion

There are still many controversies on taxonomy of the Leporidae on the subfamily level [6, 7]. Based on the presence or absence of the AIR and PIR on p3, White [7] divided the Leporidae into three subfamilies. The first is Palaeolaginae, in which the AIR is absent. The second is Archaeolaginae, in which the AIR and PIR are both absent. The third is Leporinae, in which the AIR and PIR are both present. The above described specimen from Chongzuo, with the AIR and PIR, should be assigned to Leporinae.

So far, Leporinae includes at least 22 genera and can be divided into two groups by the presence or absence of the AR on p3. The first group includes Aztlanolagus, Bunolagus, Caprolagus, Lepus, Nekrolagus, Pentalagus, Pliopentalagus, Pliosiwalagus, Poelagus, Pronolagus, Oryctolagus, Serengetilagus, Sylvilagus, and Trischizolagus, in which the AR is retained on p3. The second group includes Nesolagus, Alilepus, Brachylagus, Pratilepus, Notolagus, Paranotolagus, Pronotolagus, and Romerolagus, in which the AR is absent. The specimen from Chongzuo, without the AR, should be
assigned to the second group. Furthermore, it is most consistent with the genus Nesolagus by the following characters: the connection of the PER and PIR in the early stage of wear, whereas in the advanced stage of wear, the PIR is completely missing and the IB is present.

There are merely two extant species of the genus Nesolagus, N. netscheri (Schlegel, 1880) and N. timminsi Averrianov et al., 2000. The distribution of Nesolagus is restricted to Southeast Asia (Figure 5). The extant Nesolagus is relatively small (generally 35-40 cm in body length), which is slightly larger than Brachylagus (25-29 cm ) and Romerolagus ( $29-31 \mathrm{~cm}$ ), but smaller than Oryctolagus (35-45 cm), Pentalagus (43-47 cm), Pronolagus ( $40-50 \mathrm{~cm}$ ), Caprolagus ( $41-53 \mathrm{~cm}$ ), and Lepus ( $48-68 \mathrm{~cm}$ ). The dental structure of extant Nesolagus is relatively primitive and retains the simplified paedomorphic pattern on p 3 during the ontogenetic process. No fossil record of Nesolagus has been known from anywhere.

The type species of Nesolagus was originally proposed as Lepus netscheri by Schlegel and Jentink [8] when he studied the material from Sumatra, Indonesia. However, Forshyth [9] erected the new genus Nesolagus and revised $L$. netscheri as $N$. netscheri because its structure of skull and teeth is different from other Leporinae, its limbs are much shorter than those of Lepus, and its claws are not so strong as those of Caprolagus hispidus, resulting in its being a poor runner and an occasional burrower. Afterwards, Schreuder [10] described the skull and dental structures of $N$. netscheri in detail. It is characterized by the strong upper


Figure 5 Map showing distribution of the genus Nesolagus in Asia. A, $N$. netscheri (type species); B and C, N. timminsi; D, N. sinensis sp. nov.
incisors, the very shallow internal reentrant with no crenulation on its walls on upper molariforms, two anterior reentrants on p 2 , the smooth enamel of PER with no crenulation on its walls on lower molariforms, and the missing AR and MB on p3. The size of the specimen from Chongzuo falls into the range of the type species $N$. netscheri (the length of the lower alveolar of Chongzuo specimen is 15.2 mm , whereas $N$. netscheri varies between 14 and 17 mm [10]), but the former is still distinguished from the latter by the extremely weak AIR and the broad and deep AER with ce-ment-filled on p3, and the apparent expansion of EPER posteriorly in lingual side and developed IB on the lower molariform teeth ( $\mathrm{p} 4-\mathrm{m} 2$ ).

In 1999, Russian scholars found the trace of Nesolagus in Laos. The distribution of Striped Rabbit has extended to Vietnam [1]. Averiannov et al. [2] presented a detailed osteological description of the Annamite rabbit based on a nearly complete skeleton collected in Vietnam and erected a new species, $N$. timminsi, differing from $N$. netscheri. $N$. timminsi is distinguished from the Chongzuo specimen by its slightly larger size (the length of the lower alveolar of holotype of $N$. timminsi is 16.1 mm [2]), the weak AER without cement-filling and the thick and smooth enamel of the posterior wall of trigonid on p 3 , smooth enamel of the anterior wall of trigonid and weak IB on the lower molariform teeth ( $\mathrm{p} 4-\mathrm{m} 2$ ), and small size, obviously reduced talonid, and the presence of IB on m3.

With relatively small size, short diastema of mandible, the extremely weak AIR and broad and deep AER on p3, the PER expanding posteriorly in the lingual side on p 4 to m 2 , and the relatively large talonid on m 3 , the Chongzuo rabbit specimen is morphologically distinct from the extant species of Nesolagus, and should be assigned to a new species, Nesolagus sinensis sp. nov.

## 3 The phylogeny and origin of Nesolagus sinensis sp. nov.

The body size of Nesolagus is just in the range of Ochtona and Oryctolagus and quite different from Lepus. The body size of Nesolagus is similar to Brachylagus, Romerolagus, Pronolagus, Pentalagus, and Caprolagus with the smaller size, short ears and limbs, the close ratio of the length of the forelimbs and hind limbs, and the presence of AER, PER and PIR on p3. However, it is difficult to judge if they evolved from the same ancestor because their geographical distribution is far to each other. It still deserves further research whether the convergent adaptation is the reason.

As the smallest extant leporines, the genus Brachylagus, with a single species B. idahoensis (Merriam, 1891), is most close to Nesolagus on dental structure. B. idahoensis is different from Nesolagus sinensis sp. nov. by its smaller size, developed TN on p 3 and degenerative m 3 . It is notable that the p3 of both Brachylagus and Nesolagus still retain sim-
plified paedomorphic pattern. Namely, the trigonid and talonid are completely separated by cement on p3 in the early stage of ontogenetic process. From a sample of 219 p3 of $B$. idahoensis, $88 \%$ of them have the trigonid and talonid completely separated, while in the rest $12 \%$ (possibly older individuals) PER extends to the lingual border of the tooth and the trigonid and talonid are linked by IB [7]. Based on the absence of AR on p 3 of both $B$. idahoensis and Nesolagus, it is considered that the two genera probably have a close phylogenic relationship. However, the result of DNA research opposes the above hypothesis [11]. So the morphological similarity may be resulted from the convergent evolution. B. idahoensis may have evolved from an ancestor closely allied to Alilepus Wilsoni [7].

The volcano rabbit, with a single species Romerolagus diazi, merely resides in the mountains of Mexico. Its body shape resembles Ochotona but the morphology is relatively primitive; hence, it is considered as a living fossil. Romerolagus resembles Nesolagus by absence of AR and deep AER with cement-filling on p3. But, the former differs from the latter in possessing no AIR, developed MB and PIR being enamel lake on p 3 , and degenerative talonid on m3. Romerolagus diazi may have close relationship with Pratilepus kansasensis based on the PIR being enamel lake on p3 [5].

The genus Pronolagus (the red rock hares), with the type species $P$. crassicaudatus, includes at least three species, all distributed in southern Africa. Pronolagus differs from Nesolagus by its larger size and wider outline, presence of AR, deep AIR with cement-filling and presence of MB on p3. According to the developed AR and deep PIR, Pronolagus should be closer to Trischizolagus than to Nesolagus.

The genus Pentalagus (Amami Rabbit), with a single species $P$. furnessi, is restricted in Tokunoshima Island and Amami Island of the Ryukyu Islands, Japan. Pentalagus is considered as distantly related to Nesolagus because the former has the following characters: presence of AR with heavy crenulations, PIR and PER both with developed crenulations, and presence of MB on p3, prominent crenulations of PER on p 4 to m 2 , and obvious degradation of m 3 .

The Hispid Hare, Caprolagus hispidus, has been recorded all along the southern foothills of the Himalaya, such as Nepal and Assam of India [12]. It is characterized by thick body hair, strong claws and large-sized teeth. Caprolagus is similar to Nesolagus in possessing the EPER as in Lepus on p3. However, the former is distinct from the latter by the deeply developed AR, AIR and AER and shallow but prominent crenulations of TN on p3.

The genus Alilepus is distributed in both Eurasia and North America, but mainly in Palearctic, with the type species A. annectens from Ertemte, Inner Mongolia of Upper Miocene, A. hibbardi from North America of upper part of Middle Miocene (Clarendonnian), A. lascarevi from Russia of Upper Pliocene, A. ucrainicus from Russia of Upper Mi-
ocene, A. vagus from North America of Lower Pliocene (late Hemphillian), A. Wilsoni from Lower Pleistocene (late Blancan) and A. cf. annectens from Huiyu, Beijing of Lower Pleistocene. There are only two Alilepus records in the transitional zone and Oriental zone; A. lii from Huainan, Anhui and $A$. longisinuosus from Lufeng, Yunnan.
A. lii is distinguishable from Nesolagus sinensis sp. nov. in having developed crenulations of PER on the lower molariform teeth, and heavy crenulations of PIR and PER, and a rather wide MB linking trigonid and talonid on p 3 . So, $A$. lii is possibly the ancestral type of Pliopentalagus [13].
A. longisinuosus from Yunnan resembles Nesolagus sinensis sp. nov. by the small mandibular diastema index (the former is 0.504 and the latter is 0.463 , whereas Lepus is 0.59 ), the extremely weak AIR, degenerated MB and PER confluent with PIR forming elongate EPER on p3 of holotype, and little crenulations of reentrants on the lower molariform teeth. However, the former is considered to be more primitive than the latter by having no cement in AER and developed PIR, and presence of MB in most specimens on p3. Consequently, the two genera probably have close relationship [6].

The suggested evolutional lineage of Nesolagus sinensis sp. nov. with some other leporids are shown in Figure 6.

Alilepus is probably derived from Hypolagus parvipticatus from North America [7]. Dawson [14] proposed East Asia as the origin of Alilepus. But, the updated fossil record prefers North America rather than East Asia as the provenance of Alilepus. The earliest record of A. hibbardi from

North America is about the age of early Late Miocene (Clarendonian) whereas the earliest record from Lufeng, Yunnan of A. longisinuosus [6] stands at the age of Late Miocene (8 Ma). So the appearance of Alilepus from East Asia is slightly later than North America.

As the most primitive Alilepus, A. hibbardi possesses AIR, AER and rather wide MB on p3. It is considered to be the ancestral type of many advanced leporids, such as $A z$ tlanolagus, Caprolagus, Lepus, Nesolagus, Pentalagus, and Pronolagus [6, 7, 15, 16]. The variation of p3 structure is regular and diversified during the process from Alilepus to extant leporids. A. longisinuosus evolved into Nesolagus based on the degeneration of MB and PER confluent with PIR on p3. Pliopentalagus huainanensis is derived from $A$. lii on the basis of PIR closed into enamel lake then the appearance of AR on p3. The evolution on p3 in Pliopentalagus huainanensis can be divided into three branches. Firstly, it evolves into Pentalagus by retaining of MB and enamel lake open to lingual side on p3. Secondly, it evolves into Aztlanolagus by retaining of enamel lake. Thirdly, it evolves into Caprolagus and Poelagus with enamel lake "captured" by PER on p3 and PER extended to lingual border of p3 (Figure 6). During the process of Alilepus evolution, the following morphologic transformations have significant implications for discussing the leporid evolution, such as, PIR with enamel lake, enamel lake "captured" by PER, enamel lake open to lingual side, and degeneration of MB on p3. It still deserves further research concerning the cause of above transformations.


Figure 6 Suggested relationships of Nesolagus sinensis sp. nov. with some other leporids. 1, Incipient AIR and PIR; 2, PIR more deeply incised than AIR; 3, AIR more deeply incised than PIR; 4, AR present; 5, AR absent; 6 , AIR present in most specimens; 7, AIR absent in most specimens; 8 , PIR weakly incised or absent; 9, PIR strong incised; 10, PIR enamel lake forms; 11, PER incised to $50 \%$ of occlusal width or less; 12, PER incised to more than $50 \%$ of occlusal width; 13, AER deeply incised; 14, AER weakly incised; 15, TN in PER folded; 16, TN in PER smooth; 17, AER incised from $34 \%$ to $50 \%$ of occlusal width; 18, AER incised from $25 \%$ to $42 \%$ of occlusal width; 19, enamel lake "captured" by PER; 20, enamel lake opens to lingual side; 21, PER extend to lingual border of p3; 22, inner most portion of PER expanded and deflected anteriorly; 23, TN in PER strongly deflected posteriorly; 24, AIR confluent with AER; 25 , reduction in size; 26, increase in size.

## 4 Conclusions

(1) Nesolagus sinensis sp. nov. of Early Pleistocene is the unique and earliest fossil of Striped Rabbit from Southeast Asia.
(2) With relatively small size, short diastema on mandible, the extremely weak AIR and deep and cement-filled AER on p3, and the relatively large talonid on m3, Nesolagus sinensis sp. nov. is more primitive than the extant Nesolagus. It probably is derived from A. longisinuosus, indicating a Southwest China origin of Nesolagus. The morphology of Nesolagus sinensis sp. nov. is more similar to $N$. netscheri than to $N$. timminsi. So Nesolagus sinensis sp. nov. was dispersed to Sumatran, Indonesia in Early Pleistocene, contemporaneous with the dispersal of Sinomastodon.
(3) Nesolagus sinensis sp. nov. still retains the simplified paedomorphic pattern (the trigonid and talonid are completely separated by cement on p 3 in the early stage of ontogenetic process) during the ontogenetic process like in extant species, which suggests that the new species is probably directly ancestral to extant Nesolagus species.
(4) The evolution of Alilepus can be divided into two branches in South China and one branch in North China after its migration to China from North America in Miocene. The first south branch is represented by A. longisinuosus, which evolved into Nesolagus based on the degeneration of MB and PER confluent with PIR on p3. The second south branch is represented by A. lii, which evolved into Pliopentalagus huainanensis on the basis of developed MB, the presence of AR , and complicated crenulations on p 3 . Meanwhile, the north branch is represented by A. annectens, which has close relationship with the ancestral type of Trischizolagus.
(5) Nesolagus sinensis sp. nov. from the Sanhe Gigantopithecus fauna in Chongzuo, Guangxi coexisted with many Oriental tropical forest animals including Gigantopithecus blacki, Pongo sp., Hylobates sp., Sinomastodon yangziensis, Cervavitus fenqii, Dicoryphochoerus ultimus, Tupaia belangeri, Tylonycteris fulvidus, Belomys parapearsoni, Typhlomys, and Chiropodomys, suggesting Nesolagus sinensis sp. nov. was living in a tropical rain forest environment with a warm and humid climate [3, 4].

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