

## First discovery of fossil *Diplothrix* (Muridae, Rodentia) outside the Ryukyu Islands, Japan

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The first *Diplothrix* (Muridae, Rodentia) fossils of the early Early Pleistocene are described as *D. yangziensis* sp. nov., which were collected from the Renzidong Cave deposits in Anhui Province, Eastern China. *Diplothrix* was previously represented by a single species, *D. legata*, whose geographical distribution during the Late Pleistocene is restricted to the Ryukyu Islands, Japan. With straight chevrons on M1, distinct t3 and t9 on upper molars, primitive M3, mlc on m1, and developed a-lab on m2 and m3, the new species is morphologically distinct from other large murids in East Asia, and should belong to the genus *Diplothrix*. There are also differences in molar morphology between the new species and *D. legata*, the type species of *Diplothrix*, as well as other known fossils. For example, *D. yangziensis* sp. nov. has a smaller size, a more elongated crown, developed precingulum and pc on M1, more primitive M3, weaker mlc and more primitive pc on m1, and stronger plc and pc on m3. In short, *Diplothrix yangziensis* sp. nov. is evidently more primitive than *D. legata*, suggesting that the former is likely the ancestor of the latter. *Diplothrix yangziensis* sp. nov. is the first discovery of the genus outside the Ryukyu Islands, Japan and is also the earliest and most primitive species of the genus in Eurasia. Its discovery has significant implications for reconstructing the evolution and dispersal pattern of *Diplothrix*, as well as for discussing its palaeoecological variation.

### Renzidong Cave, Anhui Province, early Early Pleistocene, *Diplothrix*

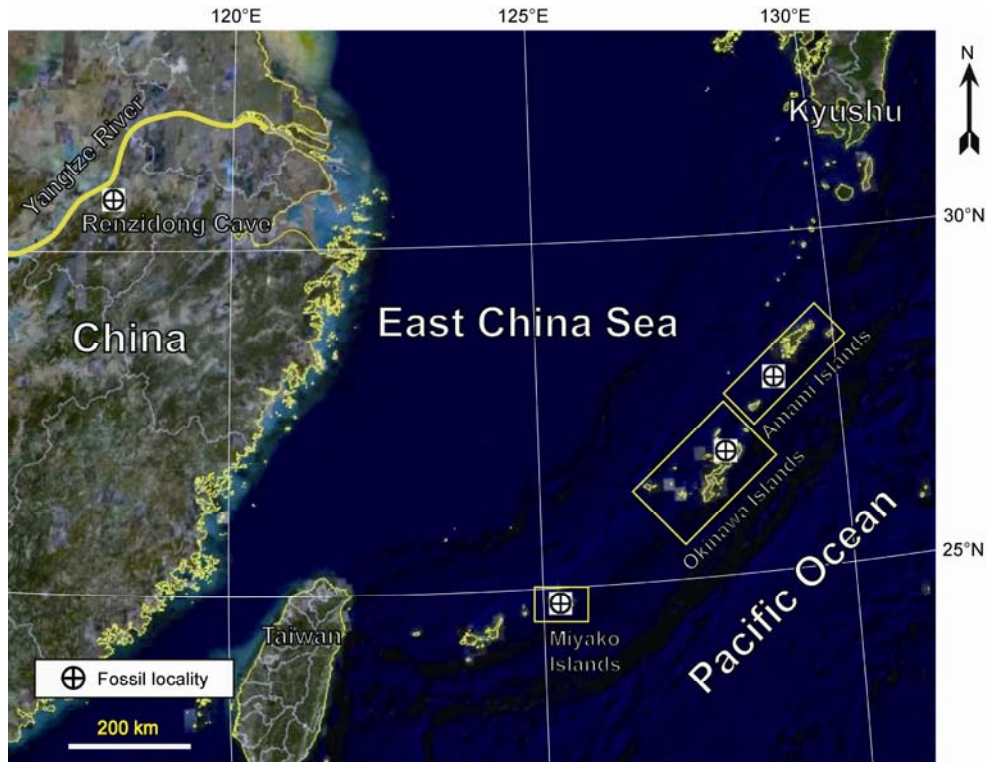
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The extant *Diplothrix*, with a single and rare species *D. legata*, is a large-sized arboreal murid and well-known for its long body hair. Its geographical distribution is restricted to Okinawa Islands and Amami Islands of the Ryukyu Islands, Japan (Figure 1) [1]. Due to the exiguity of the fossil record, the origin and evolution of the genus *Diplothrix* remained obscure for a long time. According to the updated production of molecular phylogeny, the genus *Diplothrix* shows close relationship with *Rattus* [2].

From 1998 to 2005, an excavation team, consisting of researchers from the Institute of Vertebrate Paleontology

and Paleoanthropology, Chinese Academy of Sciences and the Anhui Museum, launched systematic excavations at the Renzidong Cave. The sediments of the cave have yielded numerous mammalian remains, which are called Renzidong fauna, in association with stone and bone artifacts [3,4]. According to the faunal analysis, the age of Renzidong fauna is assigned to the time interval between 2.0 and 2.4 Ma [3,4], which falls into the early Early Pleistocene of the chronological standard scheme generally accepted in China. The most conspicuous micro-mammalian remains from these cave sediments are dozens of maxillas and mandibles and hundreds of isolated molars of a large murid morphologically similar to *Diplothrix*. On the basis of the preliminary re-

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**Figure 1** Geographical distribution of fossil *Diplothrix*.

ports of these materials by Jin [4] and Wang [5], this paper aims to conduct the systematic inferences from the morphological studies of these *Diplothrix* remains, introducing a new species, concluding evolutionary trends and discussing the origin of the genus.

For the terminology of murid dentition we follow Musser [6], for mandible nomenclature Yang [7] (Figure 2).

The fossil locality of Renzidong Cave is situated near the south bank of the Yangtze River in Fanchang County, Province Anhui, China (Figure 1). The cave deposits are about 30 m in depth and can generally be divided into two sedimentation cycles, reflecting different depositional and environmental conditions [3,4]. The first 7 layers comprise the upper part of the sediments, which is composed mainly of brown to reddish brown mud or sandy mud with limestone breccia. This part yielded abundant mammalian remains including the *Diplothrix* fossils described here. The lower part of sediments consists of eighth layers, composed mainly of gray sandy mud, sand and rounded gravel.

## 1 Systematic paleontology

### Family Muridae Gray, 1821

#### Genus *Diplothrix* Thomas, 1916

**Synonym.** *Leopardamys*, Otsuka H (2002). The formation of the Ryukyu Arc and Migration of Biota to the Arc,

Naha: Ryukyu Times. 116 [8].

**Type species.** *Diplothrix legata* (Thomas, 1906).

**Included species.** *Diplothrix yangziensis* sp. nov.; *Diplothrix* sp.

**Stratigraphic range.** The early Pleistocene to the present.

**Amended diagnosis.** Large-sized murid with robust cusps. Stout mandible with heavily built lower masseteric crest. M1 with straight chevrons, distinct t3 and t9, absent t7 and 4 or 5 roots; M2 with distinct t3 and 4 roots; M3 with distinct t3, disconnection between middle and posterior chevrons, and 3-rooted. m1 without a-cen, link between paired anteroconids and protoconid-metaconid, and developed anterior mure and medial mure while m1 with present mlc, distinct plc and 4 roots; m2 with developed a-lab, plc and 3 roots; m3 with developed a-lab and 3 roots.

#### *Diplothrix yangziensis* sp. nov.

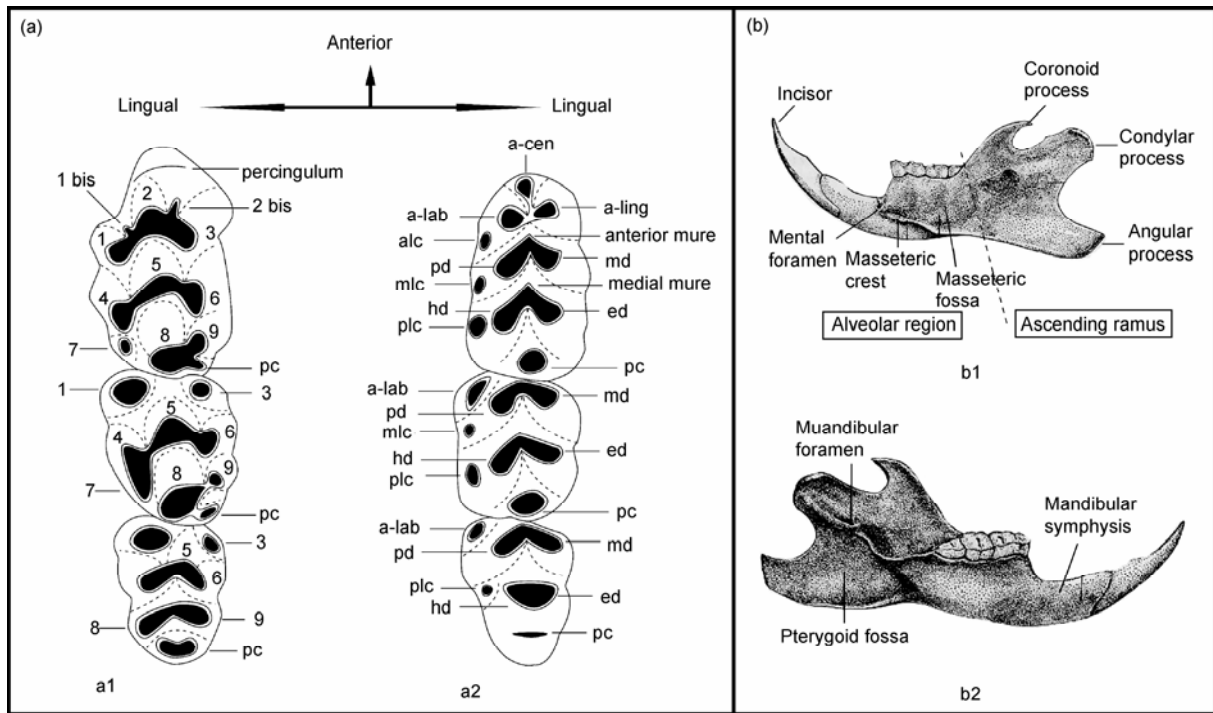
(Figures 3 and 4)

**Synonym.** *Diplothrix* sp., Jin (2009). Paleolithic Site—the Renzidong Cave, Fanchang, Anhui province. Beijing: Science Press. 218–220 [4].

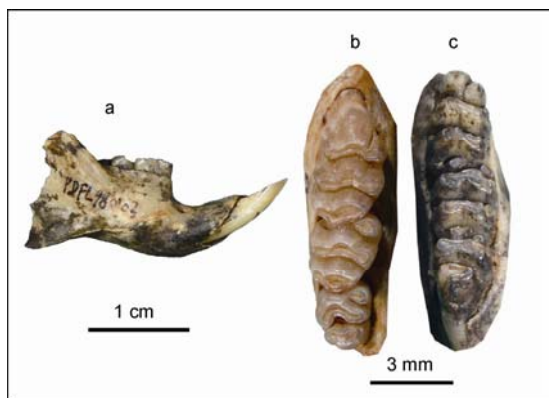
**Holotype.** Fragmentary right ramus of a maxilla with M1 to M3 (IVPP V14002.001).

**Paratype.** Relatively complete right ramus of a mandible with lower incisor, m1 to m3, fragmentary coronoid and angular process (V 14002.002).

**Hypodigm.** A fragmentary skull with left M1 to M3,

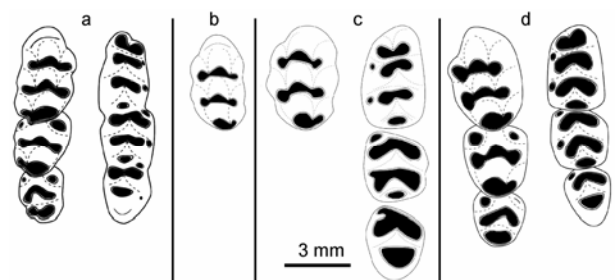


**Figure 2** Terminology of dental (a) and mandible (b) structures of Muridae. a1, Left upper molars, occlusal view; a2, left lower molars, occlusal view; b1, mandible, labial view; b2, mandible, lingual view. Abbreviations: t1–t9: tubercles, pc: posterior cingulum, a-cen: anterocentral cusp, a-lab: anterolabial cusp, a-ling: anterolingual cusp, pd: protoconid, hd: hypoconid, md: metaconid, ed: entoconid, alc: anterior labial cusplet, mlc: middle labial cusplet, plc: posterior labial cusplet.



**Figure 3** Morphology of *Diplothrix yangziensis* sp. nov. a, Right ramus of mandible (paratype, V14002.004), labial view; b, right M1–M3 (holotype, V14002.001), occlusal view; c, right m1–m3 (V14002.040), occlusal view.

right M1 and fractional palatal bridge (V14002.003); 21 fragmentary maxillas with upper molars (V 14002.004–024); 7 fragmentary left ramus of mandibles with m1 to m3 (V14002.025–031); 3 fragmentary left ramus of mandibles with m1 and m2 (V 14002.032–034); 28 fragment-



**Figure 4** Evolutionary trends within *Diplothrix*. a, *Diplothrix yangziensis* sp. nov. (the early Early Pleistocene, V14002.001, V14002.040); b, *Diplothrix* sp. (the middle Early Pleistocene) [9]; c, *D. legata* (the Late Pleistocene) [10]; d, extant *D. legata*<sup>1)</sup>.

ary left or right ramus of mandibles with lower molars (V 14002.035–052); 70 isolated M1 (V 14002.053–122); 28 isolated M2 (V 14002.123–150); 22 isolated M3 (V 14002.151–172); 45 isolated m1 (V 14002.173–217); 17 isolated m2 (V 14002.218–234); 6 isolated m3 (V 14002.235–240).

**Type locality and horizon.** Layer 3 to 7, the upper part of the Renzidong Cave, Fanchang Country, Anhui Province,

1) The molar map of extant *D. Legata* was drawn after a cast of *D. Legata* made by Prof. Jin Changzhu when he stayed in Kagoshima University, Japan. We also consulted the molar maps of extant *D. Legata* stored in National Museum of Nature and Science, Japan drawn by Prof. Kawamura Y from Aichi University of Education, Japan.

Eastern China.

**Geological age.** The early Early Pleistocene (possibly between 2.0–2.4 Ma).

**Etymology.** Named after the Yangzi River, which is located near the fossil site.

**Diagnosis.** Relatively large-sized murid with comparatively brachyodont and strongly inclined cusps. Short diastema, deep masseteric fossa and heavily built lower masseteric crest on mandible. Developed precingulum, pc, t3 and t9, straighter chevrons, and mainly 4 roots on M1; distinct t3 and t9 on M2; little degeneration, distinct t3 and t9, disconnection between middle and posterior chevrons on M3. Late connection between paired anteroconids, disconnection between paired anteroconids and protoconid-metaconid, weak mlc, distinct plc, missing anterior mure and medial mure, small pc and 4 roots on m1; distinct a-lab, plc and 3 roots on m2; developed a-lab, small proportion of plc, large proportion of pc and 3 roots on m3.

**Measurements.** See Table 1.

**Description.** Large size. A fragmentary skull with only frictional frontal, parietal, maxilla, palatine, left M1 to M3 and right M1. The width of the palatal bridge between M1s is about 4.5 mm. The posterior margin of the incisor foramen is just located at the same level with the anterior margin of M1.

Relative brachyodont and non-stephanodont. Cusps are robust and strongly inclined.

**M1.** A strong precingulum exists on the gentle slope on 91% of total specimens. Distinct t1 and t3 are nearly the same size and both isolated from t2. The cusps of the first lamina lie almost at the same level. The t4 and t6 are nearly the same size and almost at the same level while t5 is a little anteriorly placed. The anterior and middle chevrons are straight while the middle chevron is a bit wider than the anterior one. There is little inflation of t1 and t4 to the lingual side. The t2 and t5 just slightly extend transversely while t8 distinctly extends transversely. The t7 is absent, whereas t9 is well developed and located more anteriorly. The anterior side of t9 is at the same level of the middle part

of t8. Pc is distinct. In lingual view, cusps are strongly inclined posteriorly and the boundary between the crown and root is nearly straight. Specimens with 5 roots account for 34% of the total sample and the rest are the 4-rooted with the two lingual roots being fused.

**M2.** The t1 is large and isolated; t3 is distinct, low-positioned and ridge-shaped. The t1 and t3 are connected with a weak ridge on specimens of young individuals. The t4 and t6 are nearly the same size and almost at the same level while t5 is a little anteriorly placed. The middle chevron is straight. The t7 is absent, but t8 extends transversely. The t9 is well developed but slightly smaller than that of M1. Pc is absent. In lingual view, cusps are also strongly inclined posteriorly and the boundary between the crown and root is slightly convex dorsally. All M2 specimens are 4-rooted.

**M3.** The tooth is slender and primitive. The t1 is large and isolated and t3 small but distinct with low-position. The t4 obviously inflates lingually. The t6 is reduced and close to t5. The three cusps of the middle lamina earlier incorporate into a bow-shaped chevron. The t7 is absent. The t8 is reduced and confluent with t9 into a short and straight chevron. The middle and posterior chevrons are separated by a deep valley. Pc is absent. In labial view, the boundary between the crown and root is nearly straight. All M3s are 3-rooted.

The mandible is robust with short diastema. The mandibular symphysis just ends under the anterior root of m2. Ascending ramus, with clearly posteriorly inclination, begins at the posterior margin of m2 and only covers the latter part of m3 from labial view. Mental foramen is large, oval and situated anterior to the front end of masseteric crest. Masseteric fossa is broad and deep. The upper masseteric crest is missing while the lower masseteric crest is heavily built and extends forward below the roots of m1. The occlusal surface of the molars is slightly higher than the top of the lower incisor, which extends backward to the rear of labial side of m3 and owns triangular transect.

**Table 1** Measurements of mandibles and molars of *Diplothrix yangziensis* sp. nov. (mm)

	N	Length			Width			W/L
		Range (Min. –Max.)	Mean	Sd	Range (Min. –Max.)	Mean	Sd	
M1	72	3.96–4.76	4.38	0.21	2.34–2.87	2.59	0.13	0.59
M2	29	2.75–3.50	3.14	0.19	2.22–2.79	2.48	0.15	0.78
M3	22	2.21–2.64	2.48	0.11	1.90–2.23	2.1	0.1	0.84
M1–M3	9	8.64–9.31	8.93	0.19				
Diastema length	9	6.24–7.92	7.11	0.34				
Mandible height (below m1)	16	5.87–7.62	6.87	0.36				
m1	50	3.37–4.09	3.74	0.17	2.07–2.47	2.25	0.11	0.6
m2	17	2.58–3.23	2.91	0.16	2.38–2.78	2.54	0.1	0.87
m3	6	2.32–2.90	2.57	0.15	1.92–2.31	2.16	0.1	0.84
m1–m3	17	7.75–8.54	8.22	0.19				

**m1.** The tooth is wider posteriorly than anteriorly. The a-cen is missing. The a-lab is smaller and more back-placed than the a-ling. The connection between paired anteroconids is late. The paired anteroconids and protoconid-metaconid are lacking X-shaped connection and separated by a deep valley. The main four cusps are about the same size. The anterior walls of chevrons formed by protoconid-metaconid and hypoconid-entoconid are generally straight while the posterior walls are a little concave onwards. The anterior mure, medial mure and alc are absent. 93% of total specimens bear a small, ridge-shaped and low-positioned mlc affixing the labial side of protoconid. The plc is well developed. The width of the pc, which is small, oval and low-positioned, accounts for about 1/3 that of the tooth. From labial view, cusps are strongly inclined anteriorly and the boundary between crown and root is slightly bulged upwards. All specimens are 4-rooted.

**m2.** The crown is almost rectangular. The a-lab is large and plc is distinct. The width of the pc, which is a bit wider than that of m1, accounts for about 1/2 that of the tooth. From labial view, cusps are strongly inclined anteriorly and the boundary between crown and root is slightly bulged upwards. All specimens are 3-rooted.

**m3.** About 95% of total specimens bear a-lab, which merge with the protoconid with wear. The weak plc appears on 30% of total specimens and reduced pc are present on 75% of total specimens. In labial view, cusps are strongly

inclined anteriorly and the boundary between crown and root is slightly bulged upwards. All specimens are 3-rooted.

## 2 Comparisons and discussion

### 2.1 Comparison with other Quaternary large-sized murids from China

With distinct t3 and t9 on upper molars, strong precingulum and weak pc on M1, less reduced M3, weak mlc and small pc on m1, developed a-lab on m2 and m3, weak plc and pc on m3, *Diplothrix yangziensis* sp. nov. is distinguishable from other Chinese Quaternary large murids by its body size and morphology (Table 2). The detailed differences are as the following.

*Leopoldamys edwardsioides* from the Early Pleistocene of Longgupo Cave in Wushan County, Chongqing can be distinguished from *Diplothrix yangziensis* sp. nov. by its larger molars, bent chevrons on M1, shorter and wider M2, connection between middle and posterior chevrons on M3, and 2-rooted m2 and m3 [10]. *Wushanomys brachyodus*, also from the Early Pleistocene Longgupo Cave, differs from *Diplothrix yangziensis* sp. nov. in bearing weak t1bis, bent chevrons on M1, an accessory cusp behind t6, 3 or 4 roots on M1, connection between middle and posterior chevrons on M3, and 2 roots on lower molars [11]. *Beryl-*

**Table 2** Comparison of morphological characters among *Diplothrix yangziensis* sp. nov., the recent *D. legata* and other large-sized murids

		<i>Wushanomys brachyodus</i> [9]	<i>Niviventer andersoni</i> [9]	<i>Rattus Norvergicus</i> [9]	<i>Leopoldamys Edwardsioides</i> [9]	<i>Berylmys bowersi</i> [9]	<i>Bandicota indica</i> [10,11]	<i>Diplothrix legata</i> [15]	<i>Diplothrix yangziensis</i> sp. nov.
Number of roots	M1	3–4	5	5	4	4	4	5	4–5
	m1	2	4	4	4	4	4	4	4
	m2	2	2	3	2	3	2	3	3
	m3	2	2	3	2	3	2	3	3
t3	M1	small	small	small	small	naught	small	distinct	distinct
	M2	small	naught	small	small	small	naught	distinct	small
	M3	naught	naught	naught	naught	naught	naught	small	small
t9	M1	small	small	distinct	small	distinct	small	distinct	distinct
	M2	small	naught	distinct	naught	small	naught	distinct	distinct
	M3	naught	naught	distinct	naught	naught	naught	small	distinct
Precingulum on M1		weak	naught	strong	naught	naught	naught	naught	strong
Pc on M1		naught	naught	naught	naught	naught	naught	naught	weak
a-lab	m2	small	small	distinct	small	small	distinct	distinct	distinct
	m3	small	naught	distinct	naught	small	small	distinct	distinct
Mlc	m1	naught	naught	distinct	naught	naught	naught	distinct	small
Plc	m1	small	small	distinct	small	distinct	distinct	distinct	distinct
	m2	small	small	distinct	small	distinct	distinct	distinct	distinct
	m3	naught	naught	naught	naught	naught	naught	naught	small
Pc on m3		naught	naught	naught	naught	naught	naught	naught	weak
Width of the pc in relation to the m1 width		>1/2	>1/2	<1/2	circa1/2	<1/2	<1/2	circa1/2	circa1/3

*mys bowersi* from the Middle Pleistocene Sichuan-Guizhou area is distinct from *Diplothrix yangziensis* sp. nov. by larger molars, wider crown, absent inclined cusps, bent chevrons on M1, an earlier link of paired anteroconids and a X-shaped connection between paired anteroconids and protoconid-metaconid on m1, and a 2-rooted m2 and m3 [11]. *N. andersoni*, the largest species of *Niviventer*, differs from *Diplothrix yangziensis* sp. nov. by having smaller molars with higher crowns, the more posterior position of t1 and lingual inflation of t1 and t4 on M1, an earlier link of the paired anteroconids and X-shaped connection between the paired anteroconids and protoconid-metaconid on m1, and 2-rooted m2 and m3 [9]. The largest species of *Rattus*, *R. norvegicus*, is similar to *Diplothrix yangziensis* sp. nov. in having a distinct t9 on upper molars, a strong precingulum on M1, present mlc on m1, and developed a-lab on m2 and m3. However, the former still differs from the latter in having smaller size, the more posterior situation of t1 and inflation to lingual side of t1 and t4 on M1, missing t3 and connection between middle and posterior chevrons on M3, the earlier link between paired anteroconids and X-shaped connection between paired anteroconids and protoconid-metaconid on m1 [11]. The extant *Bandicota indica* and its fossils from Late Pleistocene resemble *Diplothrix yangziensis* sp. nov. by straighter chevrons, missing X-shaped connection between paired anteroconids and protoconid-metaconid on m1 and more degenerative pc on lower molars. But the former is different from the latter in possessing much larger size, hypsodonty, longer diastema, significantly wider molars, distinctly transverse extended t2 and t5 on M1, and 2-rooted m2 and m3 [12,13].

## 2.2 Comparison with other *Diplothrix* species

The morphological characters of *Diplothrix yangziensis* sp. nov. are very similar to those of *Diplothrix legata* from the Ryukyu Islands, Japan. Both species possess a heavily built mandible, robust cusps, straight chevrons and developed t3 and t9 on M1, disconnection between middle and posterior chevrons on M3; disconnection between paired anteroconids and protoconid-metaconid, missing medial mure, present mlc and distinct plc on m1; distinct a-lab and plc on m2; developed a-lab on m3; similarity on roots number of molars.

In 1906, Thomas first proposed the type species of *Diplothrix* as a new species of genus *Lenothrix* [14]. After ten years, he erected the new genus *Diplothrix* and revised *L. legata* as *Diplothrix legata* (Thomas, 1916) [15]. The geographical distribution of fossil *Diplothrix* is restricted to Okinawa Islands, Amami Islands and Miyako Islands of the Ryukyu Islands, Japan from Late Pleistocene (Figure 1) [10,16–18]. By far the earliest fossils *Diplothrix* are two M1 from the Imadomari-Akagimata fauna of southern Okinawa Islands [8]. Fission-track dating of the fossil-bearing strata gives an approximate age of 1.5 Ma, namely the middle

Early Pleistocene [18]. In this paper, the two M1, previously referred to as *Leopaldamys edwardsioides* [9], are revised as *Diplothrix* sp. (Figure 4).

*Diplothrix* sp. resembles *Diplothrix yangziensis* sp. nov. by having similar size of molars, brachydonty, strong inclination of cusps, distinct cusps and developed t3 and t9 on M1. Nonetheless, the former bears more advanced characters such as weak precingulum, absolute 5 roots and missing pc on M1.

The extant *D. legata* and its Late Pleistocene records from the Ryukyu Islands are considered much more advanced than *Diplothrix yangziensis* sp. nov. because of the following traits: much bigger size, weak inclination of cusps, hypsodont, shorter and wider crown; absent precingulum and pc, absolute 5 roots on M1; reduced M3; the earlier link between paired anteroconids, more developed mlc on m1; wider pc on lower molars and missing plc and pc on m3.

Based on the comparisons, we think the morphologically primitive species *Diplothrix yangziensis* sp. nov. should have a close relationship to *D. legata* from the Ryukyu Islands. The former is likely to be the direct ancestor of the latter while the middle Early Pleistocene *Diplothrix* sp. could represent a transitional stage.

We also recognize the following evolutionary trends within the genus *Diplothrix*: The body size increases significantly and the inclination of cusps decreases. The crown becomes higher, shorter and wider. The precingulum and pc of M1 vary from distinct to absent. The roots of M1 change from 4 or 5 to absolute 5. The elongated M3 becomes reduced. The link between paired anteroconids on m1 alters from late to early. The weak mlc of m1 becomes developed. The pc on m1 and m2 varies from small to large. The plc and pc on m3 change from partial developed to absence (Figure 4).

## 2.3 Zoogeographical implications of *D. yangziensis* sp. nov.

The discovery of *Diplothrix yangziensis* sp. nov. of the early Early Pleistocene from eastern China provides important evidence for discussing the geographical origin, distribution and dispersal of the genus *Diplothrix*. Based on the *Diplothrix* fossils from Renzidong Cave, Wang [5] considered that *D. legata* from the Ryukyu Islands was possibly derived from China. *Diplothrix yangziensis* sp. nov. migrated from Renzidong Cave to the Ryukyu Islands by the “Ryukyu Land Bridge”, which connected southeastern China and the Ryukyu Islands during Early Pleistocene. According to paleontological and geological data, Otsuka [9] considered the Ryukyu Islands were connected to Asian Mainland by the “Ryukyu Land Bridge” during the early Early Pleistocene, driving the migration of terrestrial vertebrates from the mainland to islands. So the discovery of *Diplothrix* remains in Renzidong Cave provides new evidence for above viewpoint. From faunal analysis, the Renzidong fauna is in the

transitional zone between the Palaeartic and Oriental Regions but with more Palaeartic types than other Chinese transitional faunas. It implies that there should be a cooling event at the beginning of the Pleistocene pushing southward migration of the Palaeartic elements [3,4]. Obviously, the migration of *Diplothrix yangziensis* sp. nov. was closely related to this cooling event.

### 3 Conclusions

(1) *Diplothrix yangziensis* sp. nov. from Renzidong Cave, Anhui Province differs remarkably from other Chinese large-sized murids in the morphology of molars, maxilla and mandible. *Diplothrix yangziensis* sp. nov. also bears more primitive characters than the extant *D. legata* and its fossil representatives.

(2) *Diplothrix yangziensis* sp. nov. is the first discovery of the genus outside the Ryukyu Islands, Japan and is also the earliest and most primitive species of the genus in Eurasia. Its discovery has significant implications for reconstructing the evolution and migratory pattern of *Diplothrix*, as well as for discussing its palaeoecological adaptation. According to present data, the earliest record of fossil *Diplothrix* in the Ryukyu Islands dates to the middle Early Pleistocene (approximately 1.5 Ma) whereas *Diplothrix yangziensis* sp. nov. is of the early Early Pleistocene age (circa 2.0–2.4 Ma). Therefore, *Diplothrix* originated obviously on the Chinese mainland and not on the Ryukyu Islands, Japan.

(3) Renzidong is situated in the transitional zone between the Palaeartic and the Oriental zoogeographical regions. The fossil fauna from this site implies a cooling event at the beginning of the Pleistocene causing a southward migration shift of Palaeartic elements. *Diplothrix yangziensis* sp. nov. migrated possibly from Renzidong Cave to the Ryukyu Islands by the “Ryukyu Land Bridge” during the Early Pleistocene and evolved to present.

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