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FOSSIL LIZARDS AND SNAKES FROM THE MIDDLE PLEISTOCENE OF CHINA

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Published accounts of fossil squamates (lizards and snakes) from China are not abundant, especially those from Neogene and Quaternary deposits, which are even less well understood, with only a few reports from the Miocene (Sun, 1961; Li et al., 1983) and the Pleistocene (Bien, 1934; Sun et al., 1992; Li and Xue, 2002; Li et al., 2004; Mead et al., 2014). The following squamate taxa were briefly reported for the Pleistocene: Lacertidae and an ophidian (Bien, 1934), Colubridae (Sun et al., 1992), and lizards (Mead et al., 2014). Apart from these, some lizards (*Tinosaurus luonanensis*, *Conicodontosaurus qinlingensis*, *Eumeces* sp., and *Eremias* sp.) were described by Li and Xue (2002) and Li et al. (2004). Snake vertebrae from the Zhoukoudian and Haimao faunas have not been described in detail (Bien, 1934; Sun et al., 1992).

In recent years, we have found some squamates, identified as the skink, cf. *Eumeces capito*, and snake, cf. *Natrix* sp., from the Longyadong Cave fauna, which was excavated by the Shaanxi Provincial Institute of Archaeology of China during 1995–1997. Thermoluminescence (TL) dating of the fossiliferous strata containing these fossils (Layer 4 of Unit 5) suggests an age of 356.6 ± 17.8 to 273.9 ± 13.7 ka BP (Wang and Huang, 2001; Shaanxi Provincial Institute of Archaeology and Museum of Luonan County, 2008). Xue et al. (1999), Xue (1987), and Li et al. (2016) reported fossil teeth of *Homo erectus* and mammalian fossils from Longyadong Cave fauna, and Wang and Huang (2001, 2002) reported a large number of lithic artifacts from the locality. This paper focuses on the squamates from this well-known fossil locality.

Institutional Abbreviations—LV, fossil from Longyadong Cave, Shaanxi Provincial Institute of Archaeology, Xi'an, Shaanxi, China; NWUV, Northwestern University, vertebrate specimen.

SYSTEMATIC PALEONTOLOGY

SQUAMATA Oppel, 1811
LACERTILIA Owen, 1842
SCINCIDAE Gray, 1825
EUMECES Wiegmann, 1834

Cf. *EUMECES CAPITO* Bocourt, 1879
(Fig. 1)

Material—LV1, a partial right maxilla; LV2, an incomplete left maxilla; LV3, a left dentary.

Locality and Horizon—Layer 4 of Unit 5 of Longyadong Cave, Shaanxi, China; middle Pleistocene.

Description

Maxilla—Specimen LV1 is a partial right maxillary, preserving 10 teeth and an additional four tooth sockets (Fig. 1A, B). The teeth are narrow, flattened cones, and pleurodont. The nasal margin forms an anterodorsal notch in the maxilla, and four supralabial foramina form a line across the lateral surface of the bone. Specimen LV2 is a slightly more complete left maxilla but exhibits worn-out tooth sockets (Fig. 1C).

Dentary—Specimen LV3, a right dentary (Fig. 1D, E), is better preserved than the maxillae. It is a long (10.0 mm in length), ventrally straight bone, with a slight medial curvature at its anterior end. In medial view, the Meckelian canal is narrow anteriorly and open posteriorly. The dentary preserves 18 broken teeth and an additional 10 alveoli. The tooth morphology is the same as for the upper teeth. The cusps of the teeth are prominent and slightly curved lingually. In lateral view, there are five mental foramina on the anterior surface, of which the anterior-most one is low, close to the ventral edge of the dentary.

As with the maxillary teeth, the dentary teeth are all homodont, pleurodont, and single-cusped, but only slightly smaller anteriorly. The length of the tooth row is 7.5 mm. The greatest height of a tooth is 0.9 mm, and tooth width at the base is 0.2 mm (in medial view).

Discussion

Quaternary skink fossils have only rarely been reported from China, and many aspects of the evolution of these lizards are still poorly understood. Bien (1934) reported that the fossil Lacertidae (cf. *Eremias argus*) teeth from Zhoukoudian are obtusely conical and the posterior ones have moderately serrated mesial edges. Mead et al. (2014) mentioned skink (Scincidae) right lower jaw fragments from five caves in Chongzuo, southern China. Li and Xue (2002) and Li et al. (2004) reported some fossil skinks (*Eumeces* sp.) from Luonan in a more detailed description.

Li et al. (2004) reported three lizard fossils of the middle Pleistocene (493 ± 55 ka BP) from Qinling caves in Luonan County,

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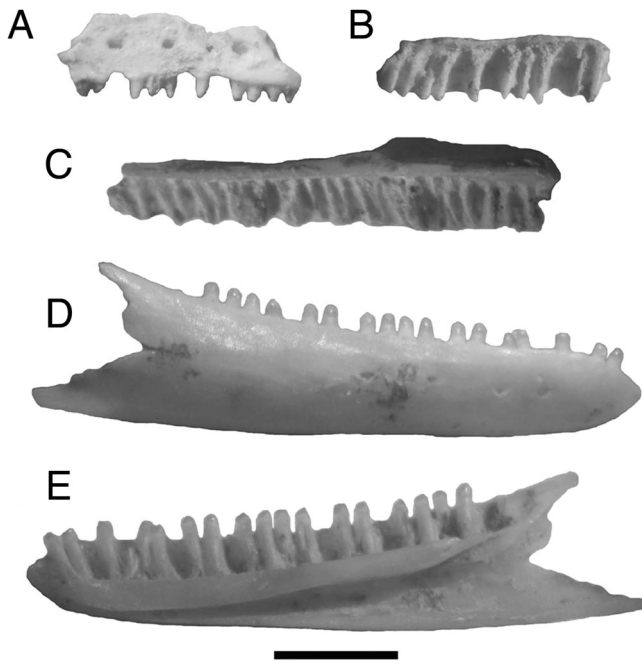


FIGURE 1. *Eumeces capito*. LV1, partial right maxilla, in **A**, medial and **B**, lateral views. **C**, LV2, partial left maxilla, in lateral view. LV3, right dentary, in **D**, lateral and **E**, medial views. Scale bar equals 2 mm.

SERPENTES Linnaeus, 1758
COLUBRIDAE Oppel, 1811
NATRIX Linnaeus, 1758

CF. *NATRIX* SP.
(Fig. 2)

Material—LV4, a trunk vertebra; LV5, three articulated vertebrae.

Locality and Horizon—Layer 4 of Unit 5 of Longyadong Cave, Shaanxi, China; middle Pleistocene.

Description

The material attributed to cf. *Natrix* sp. includes four trunk vertebrae. Specimen LV4 is an isolated vertebra, and the other three, LV5, are cemented together by calcite. The vertebrae of LV5 have the same morphology as that of LV4.

Specimen LV4 (Fig. 2A–E) is a small and fairly well-preserved trunk vertebra, although the left prezygapophysis, the neural spine, and the hypapophysis are damaged. The right prezygapophysis is well preserved. Its articular facet is rectangular and obliquely extended forward and outward in dorsal view. The prezygapophyseal accessory process is pointed on either side. Their articular facets are rectangular and obliquely extended backward and outward. Prominent epizygapophyseal spines are present at the posterolateral margins of the postzygapophyses. The zygantrum is broad and deep, and the superior border invagination is forward. Large parazygantral foramina are present lateral to the zygantral margins (Fig. 2B). The neural canal is triangular and trilobated. The neural spine is low and straight in lateral view (LV5; Fig. 2J, K). The synapophysis is composed of a rounded diapophysis superiorly and a flattened parapophysis below. The parapophysial articular facet is larger in size than the diapophysial articular facet. The parapophysis process projects obliquely downward. The cotyle and the condyle are suboval in anterior and posterior views. The interzygapophyseal ridge is straight in lateral view, and the subcentral ridge is convex in lateral view (Fig. 2C). The hypapophysis is short, strongly sigmoid ventrally, and caudally directed to stand out from the condyle (LV5; Fig. 2F–K). Measurements are presented in Table 2.

Shaanxi, China, including a right dentary identified as *Eumeces* sp. The characteristics of the dentary and the teeth are similar to the modern *Eumeces capito* (see Table 1), but considering that the specimens are few and incomplete, they have been identified as *Eumeces* sp. (Li et al., 2004).

Eumeces with an open Meckelian groove is different from *Emoia* (Meckelian canal enclosed) (Zhao et al., 1999) and *Asymblypharus* (with a fused Meckelian canal, and now considered to be restricted to the Tianshan and Altay mountains; Darevsky and Tshumakov, 1962). The narrow, flat conical teeth of *Eumeces* are different from the conical, columnar teeth of *Ateuchosaurus*, *Mabuya*, and *Scincella* (*Leiopolisma*) (Zhao et al., 1999; Li et al., 2004).

Previous studies (Li et al., 2003) have shown that the teeth of the modern skink *Eumeces capito* are homodont, pleurodont, single-cusped, and number ≥ 25 –30. The teeth are usually slender and closely spaced. The lizard remains (LV1–LV3) reported here from the Longyadong Cave have similar characteristics but are smaller in size (Table 1). Therefore, here we classify the fossil specimens tentatively as cf. *Eumeces capito*.

This is the second report of this fossil skink in China. *Eumeces capito* is endemic to China, mainly distributed along the boundary of the two zoogeographic areas in the Qinling Mountains (Zhang, 1999).

Discussion

Quaternary snake fossils in China are quite rare, having been reported from only three locations: the middle Pleistocene of Zhoukoudian (Bien, 1934), the lower Pleistocene in Haimao (Sun et al., 1992), and the lower Pleistocene of Renzidong Cave (Mead et al., 2016). Snake (Colubridae) remains from the Haimao fauna comprise broken dentaries with teeth and vertebrae, but the vertebrae have not been described (Sun et al., 1992). Bien (1934) reported a mandible with teeth of a small

TABLE 1. Comparison of the teeth of some *Eumeces*.

Species/Specimen	Dentition	Pattern	Crown	Tooth profile	Number	Length (mm)
<i>Eumeces chinensis</i> ^a	Homodont	Pleurodont	Single-cusped	Narrow, pillar-like	25	15
cf. <i>Eumeces capito</i> ^a	Homodont	Pleurodont	Single-cusped	Narrow, pillar-like	25–30	15
LV3	Homodont	Pleurodont	Single-cusped	Narrow, pillar-like	28	7.5
NWUV1141 ^b	Homodont	Pleurodont	Single-cusped	Narrow, pillar-like	26	7

^aModern species after Li et al. (2003).

^bFossil species after Li et al. (2004).

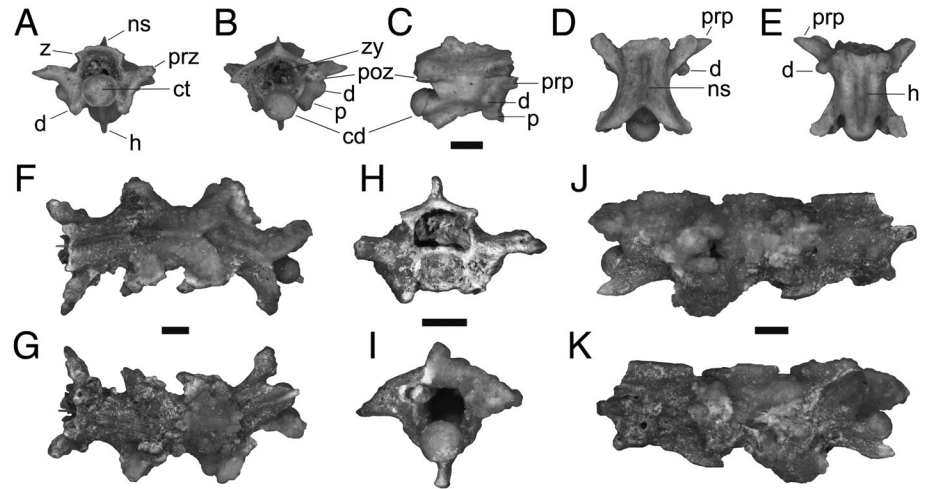


FIGURE 2. *Natrix* sp. LV4, trunk vertebra, in **A**, anterior, **B**, posterior, **C**, right lateral, **D**, dorsal, and **E**, ventral views. LV5, three articulated vertebrae, in **F**, dorsal, **G**, ventral, **H**, anterior, **I**, posterior, **J**, right lateral, and **K**, left lateral views. **Abbreviations:** **cd**, condyle; **ct**, cotyle; **d**, diapophysis; **h**, hypapophysis (hemal keel); **ns**, neural spine; **p**, parapophysis; **poz**, postzygapophysis; **prp**, prezygapophyseal process; **prz**, prezygapophysis; **z**, zygosphenes; **zy**, zygantrum. Scale bars equal 1 mm.

TABLE 2. Comparison of trunk vertebrae of cf. *Natrix* sp. and some Colubridae.

Taxon	Locality	cl	naw	cl/ naw	Age (ka)
cf. <i>Natrix</i> sp. ¹	China	3.0	1.6	2.06	356.6–273.9
<i>Elaphe</i> sp. ²	China	7.0	5.0	1.4	500–230
cf. <i>Elaphe</i> sp. ³	China	5.95	5.73	1.04	early Pleistocene
<i>Mionatrix diatomus</i> ⁴	China	3.6	3.4*	1.06	middle Miocene
<i>Natrix longivertebra</i> ⁵	Poland	4.27–5.58	—	1.76–2.22	middle Pliocene
<i>N. natrix</i> ⁵	Poland	3.81–5.9	—	1.45–2.07	late Pleistocene
<i>Coluber gemonensis</i> ⁶	Poland	3.42–4.58	—	1.29–1.50	late Pleistocene
<i>Vipera berus</i> ⁵	Poland	3.40–3.95	—	1.7–1.88	middle Pleistocene
Colubridae A ⁷	Brazil	9.8	8.7	1.13	late Miocene
Colubridae B ⁷	Brazil	6.4	4.8	1.33	late Miocene
Colubridae C ⁷	Brazil	9.2	6.9	1.33	late Miocene

Measurements in mm. **Abbreviations:** **cl**, centrum length; **naw**, neural arch width at interzygapophyseal constriction.¹From Longyadong Cave; ²Bien (1934); ³Mead et al. (2016); ⁴Sun (1961); ⁵Szyndlar (1991b); ⁶Szyndlar (1991a); ⁷Hsiou and Albino (2010). *Measured on figure.

snake from the fossiliferous deposits at Locality 2 of the Zhoukoudian fauna.

Comparing the specimens from Longyadong Cave with the trunk vertebrae from Zhoukoudian, there is an obvious difference in shape and in the orientation of their hypapophyses. In the former, the hypapophysis extends posteriorly from the condyle, whereas in the latter it is anteroventrally directed. Moreover, the Longyadong Cave form is small (Table 2), slender, and its prezygapophyseal process is longer and sharper than that of the Zhoukoudian vertebrae (Fig. 2C–E). Sun (1961) reported fossil snakes from the Miocene Shanwang fauna and noted that the short hypapophyses extend throughout the entire vertebral column; Sun suggested that this condition is close to that in *Natrix* and named the fossil species *Mionatrix diatomus*. Fossils from Longyadong Cave differ from that species in the long, posteriorly extended hypapophyses of the trunk vertebrae. The lack of a continuous presence of a hypapophysis on the Renzidong vertebral series illustrates that the specimen does not belong to Natricinae (Mead et al., 2016). *Rhabdophis tigrinus* and *Elaphe dione* are two species of Colubridae living in the study area (Fang and Song, 1981; Zhao et al., 1999), and the vertebrae of *E. dione* differ from the fossils from Longyadong Cave by not having a sigmoid, extended hypapophysis. *Rhabdophis tigrinus* differs from the fossils from Longyadong Cave in having a long and thin sigmoid hypapophysis and a cylindrical

diapophysis, and that the prezygapophyseal process extends posterolaterally.

Ikeda (2007) studied 54 species and subspecies of snakes from Japan and a few other east and southeast Asian countries. Comparing all of those taxa (including *Amphiesma*), the fossils from Longyadong Cave differ from those species in the sigmoid hypapophysis, which is one of the valid characteristics used in diagnosing natricine snakes versus others (LaDuke, 1991; Ikeda, 2007). Following Head (2005), the fossils from Longyadong Cave with the parazygantral foramina and epizygapophyseal spines (Fig. 2B, C) should be assigned to Natricinae.

In their report of a new snake from the Miocene of South America, Hsiou and Albino (2010) mentioned that the Colubridae are a monophyletic group of snakes supported by at least seven synapomorphies, but none of these are from the postcranium. Based only on vertebral morphology, the colubrids are traditionally identified by the following combination of characters: (1) delicate vertebrae, longer than wide; (2) thin zygosphenes and neural spine thin and slender; (3) paradiapophyses differentiated; (4) paracotylar foramina usually present; and (5) prezygapophyseal processes well developed. Most of these characters can be observed in the fossil from Longyadong Cave, but it differs from ‘Colubridae’ of South America in having a wide flat zygosphenes, development of a hypapophysis, and a very small centrum.

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- As previously pointed out (Szyndlar, 1991b), it is generally true that examination of geologically relatively young snake fossils is a more complex task than in the case of older materials; even early Miocene snakes closely resemble their living relatives. Obviously, this resemblance is more striking in the case of Pliocene and, especially, Pleistocene fossils. Although snake remains have been found quite often in fossil materials from central and east European sites, few of these were identified below the subordinal level or described in detail. For example, a catalog of Pleistocene vertebrate faunas from Hungary compiled by Jánossy (1986) lists 38 localities yielding snake remains. Materials from almost one-third of the numbered sites were defined as either ‘abundant’ or ‘common’ or they counted thousands of bones. Of them, however, only the fossils from Villány 3 were identified to the species level (Kretzoi, 1956), whereas those from the remaining 37 localities were defined as ‘Ophidia indet.’ just as in the case in the Zhoukoudian of China (Bien, 1934), where fossils were assigned to the suborder ‘Ophidia.’
- Natrix longivertebra*, *Natrix natrix*, and *Vipera berus* are among the small snakes from Europe reported by Szyndlar (1991a, 1991b) in which trunk vertebrae are characterized by a thin, high hypapophysis.
- Vipera berus* is the smallest viper (Szyndlar, 1991b:fig. 16). The centrum length of 25 trunk vertebrae of a living example of *V. berus* is 3.4–3.95 mm, and the centrum is 1.7–1.88 times longer than wide. Its trunk vertebrae have a high hypapophysis that extends posteriorly but it obviously differs from the fossils in Longyadong Cave in that the neural spine is short and flat and the hypapophysis is thin and acute.
- Natrix natrix* from the upper Pleistocene of Poland is quite similar to the fossils from Longyadong Cave based on a smaller centrum (Table 2). Notably, its hypapophysis is higher and extends posteriorly (Szyndlar, 1991b:fig. 4).
- Natrix longivertebra* (Szyndlar, 1991b:fig. 3) is another extinct species from the upper Miocene of Poland. Trunk vertebrae of this snake differ from those of other members of the genus *Natrix* by having stout and dorsoventrally flattened prezygapophyseal processes and a narrow centrum with the hypapophyseal base continuing anteriorly in a salient ridge. The most distinct feature is an extreme elongation of the vertebrae. However, considering that the extinct *N. longivertebra* and the extant *N. natrix* are very similar, proper identification based exclusively on the vertebrae is problematic. In some rare cases, trunk vertebrae of *N. natrix* (like those of *N. longivertebra*) display extreme elongation of the centrum, with the length/width ratio reaching as much as 2.07 (Szyndlar, 1984).
- Comprehensive analysis shows that the snake specimens from Longyadong Cave are consistent with *Natrix* in centrum size and shape, and especially in its well-developed and sigmoid, extended hypapophysis (Table 2). Considering that the extinct species within the genus and the living species are very similar, proper identification based exclusively on the vertebrae is problematic. Based on neontology (Zhao et al., 1998), living *Natrix* is a large snake restricted to western Xinjiang of China and does not occur in the study area. Adequate comparative skeletons of living snakes of eastern Asia are noticeably absent in museums, making identifications of fossil specimens less than satisfactory. Therefore, the fossils from Longyadong Cave are classified as cf. *Natrix* sp.
- Following Mead et al. (2016), given the lack of descriptions of cranial and vertebral remains of the living snakes of eastern Asia, we recognize that our assignment of the Longyadong snake specimens to *Natrix* is tentative. Clearly more detailed work on the modern species from eastern Asia, especially China, is desperately needed, and additional attention is required in the recovery of cranial and vertebral remains of fossil squamate species.
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