cf. *Trimeresurus* LACÉPÈDE (Reptilia: Squamata: Viperidae: Crotalinae) from the late Early Miocene of Japan

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Abstract. A single middle trunk vertebra from the Sakurado Facies of the Yamanouchi Member of the Akeyo Formation (late Early Miocene), Mizunami City, central Japan, is identified as cf. *Trimeresurus* (a living crotaline genus) based on the very close morphological similarity of the fossil to the modern and Pleistocene species *Trimeresurus flavoviridis* (HALLOWELL, 1861) and on zoogeographic grounds. This is the oldest record of the Crotalinae from Asia. Additional fossil material of this crotaline is needed in order to make a more specific identification.

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I. INTRODUCTION

The oldest viperids known are from the earliest Miocene (ca 23.5-22 Ma) of both the Old and the New World (SZYNDLAR and RAGE, 1999). In Europe the most ancient viperids are the Early Miocene *Provipera boettgeri* from Hessler in Germany (KINKELIN, 1892), *Vipera antiqua* from Weisenau in Germany (SZYNDLAR and BÖHME, 1993), and a possible *Vipera* sp. from the St-Gérand-le Puy complex of sites in France (HOFFSTETTER, 1955). All of these represent the subfamily Viperinae (OPPEL, 1911). In Africa, the most ancient viperids are known from the Early Miocene of Namibia and represent the viperids *Bitis* sp. and either *Daboia* or *Vipera* (RAGE, 2003).

Up until now, the only viperid material known from the Early Miocene of Asia are vertebrae that have not been positively identified to the generic level. A few vertebrae are known from the Early Miocene of Li Mae Long, Thailand (SZYNDLAR and RAGE, 1999); but these small vertebrae (the largest one has a centrum length of 4.3 mm, RAGE and GINSBURG, 1997) cannot be identified below the family level. Other Early Miocene viperid vertebrae have been reported from Central Asia from the Zaisan basin at the Kazakhstan-Chinese boundary by CHKHIKVADZE (1985). He recognized both a small and a large species. The small species may represent the "*Vipera berus* complex" and the large species may represent the "Oriental viper group", but no further information on these fos-

sils has been published. Both of these taxa probably represent the subfamily Viperinae. A fragmentary vertebra identified as "*Vipera* sp." with a relatively large centrum length (ca. 7.5 mm) was reported from the middle Sarmatian (Middle Miocene) of Rustavi in eastern Georgia (ZEROVA et al., 1987). But this vertebra has a centrum that is so distinctly wider than long that it probably represents the Boidae rather than the Viperidae (SZYNDLAR and RAGE, 1999).

In the New World, the most ancient viperid is approximately contemporary to those of the Old World, but is perhaps slightly younger (latest Arikareean North American Land Mammal Age, SZYNDLAR and RAGE, 1999). This vertebral material was reported from western Nebraska, USA, by HOLMAN (1981) who suggested that it resembled the modern pit viper genus *Sistrurus* (actually he should have stated *Sistrurus catenatus*) more than any other New World taxon, but he abstained from any subfamilial assignment. At present there seems no doubt that this Nebraska material represents the Crotalinae.

Turning now to the Late Miocene in the Old World, two forms of Crotalinae gen. et sp. indet. were reported from the Ukranian Late Miocene (MN9a) locality of Gritsev on the basis of maxillae by IVANOV (1999). These fossils were suggested to be related to be pit vipers of the "*Agkistrodon* complex" and to have been Asian immigrants. Also in the Ukraine, a new viperid *Daboia ukranica* was described from the Late Miocene Gritzev locality on the basis of maxillae, skull bones, and vertebrae (ZEROVA, 1992).

The Japanese Locality. The locality (Fig. 1) for *cf. Trimeresurus* (in part, *Protobothrops* of some authors) lies west-southwest of Tokyo in central Japan northeast of Nagoya (also see KIMURA and
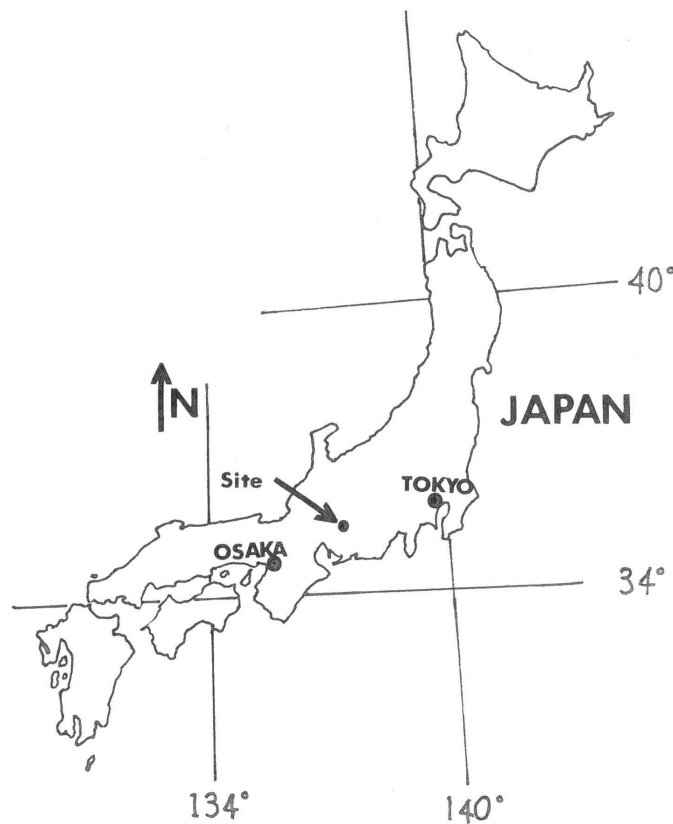

Fig. 1. Location map for the late Early Miocene site (indicated by arrow) in Japan that yielded cf. *Trimeresurus* sp. indet.

OZAWA 2002: Fig. 1, p. 685). The vertebra was collected from the Sakurado Facies, Yamanouchi Member of the Akeyo Formation, Mizanami Group, in Mizunami City, Gifu Prefecture, Japan: latitude 35-22-7 N , longitude 137-14-13 E. The site represents the late Early Miocene (KIMURA and OZAWA , 2002). KOBAYASHI (1989) estimated the age of the Akeyo Formation to be 17.0 - 17.5 Ma on the basis of fission-track data.
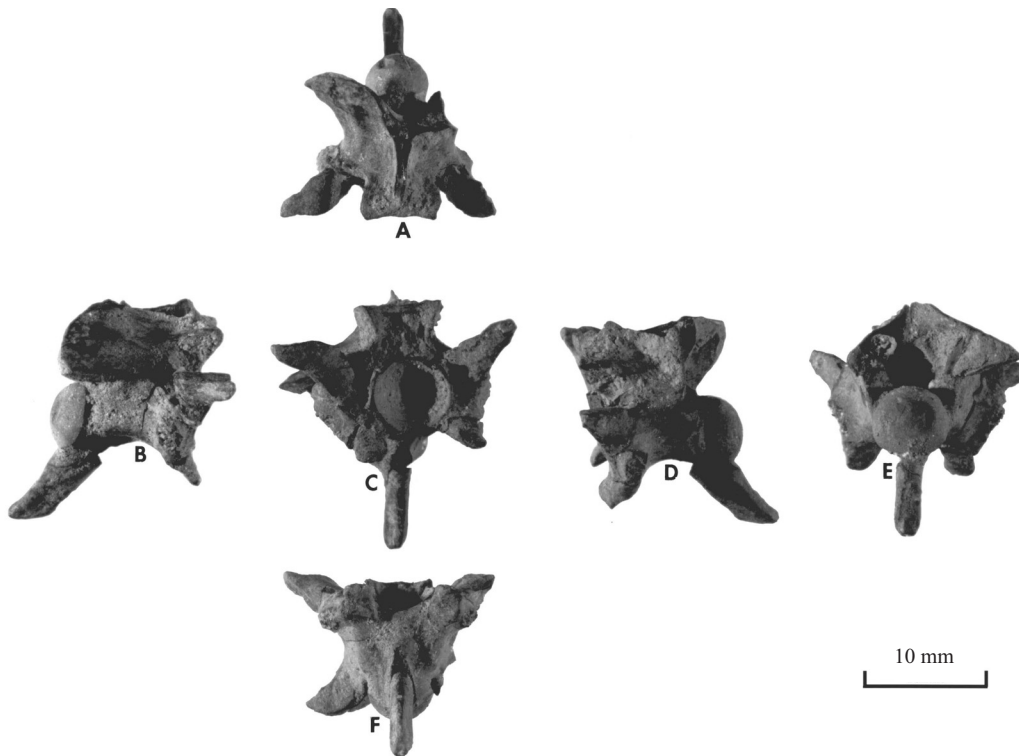
Fig. 2. Photographic image of cf. *Trimeresurus* sp. indet. (MFM 17851) from the late Early Miocene of central Japan. A – dorsal view; B – right lateral view; C – anterior view; D – left lateral view; E – posterior view; F – ventral view. The scale bar applies to all figures.

II. SYSTEMATIC PALEONTOLOGY

The systematic arrangement below follows MCDIARMID et al. (1999) which was adopted as the standard reference to snake nomenclature at the 10th Meeting of the Conference of the Parties to the Conventions on International Trade in Endangered Species of Wild Fauna and Flora (CITES) 9-20

June l997, Harare, Zimbabwe. Consistent with the modern trend that exists because of the present taxonomic instability of snakes, Linnaean catagories (e.g. class, order, suborder, superfamily etc.) are not used (see MCDIARMID et al., 1999, pp 10-11). Terminology for snake vertebral structures are from HOLMAN (2000). All measurements are in millimeters (mm). The fossil vertebra resides in the Mizunami City Fossil Museum (MFM) as number 17851.

Reptilia LAURENTI, 1768

Squamata OPPEL, 1811

Serpentes LINNAEUS, 1758

Caenophidia HOFFSTETTER, 1939

Colubroidea OPPEL, 1811

Viperidae OPPEL, 1811

Crotalinae OPPEL, 1811

cf. *Trimeresurus* LACÉPÈDE, 1804

cf. *Trimeresurus* sp. indet.

(Figs 2 and 3)

D e s c r i p t i o n. In dorsal view: vertebra wider than long; anterior border of zygosphene slightly concave; prezygapophyseal articular facets ovoid; neural spine moderately thick; moderately small epizygapophyseal spine present; hypapophysis thick and spatulate in shape. In anterior view: neural arch moderately vaulted; roof of zygosphene almost straight, with its lateral edges not sharply tilted upward; sides of zygosphene slightly concave; neural canal rectangular and smaller than moderately excavated, round cotyle; hypapophysis tapering slightly into rounded apex; parapophyses robust and wide; tip of right hypophysis truncated, left hypapophysis missing.

In ventral view: vertebra shorter than wide; parapophyses well-developed and relatively short and wide, their apices truncated; anterior edge of left prezygapophyseal articular process moderately pointed; hypapophysis thick, tapering slightly to a rounded apex ; bottom of centrum tapering moderately from anterior to posterior; subcentral grooves present, but rather weakly excavated; small, elongate depression in middle of anterior-posterior extent of left subcentral groove may indicate site of left subcentral foramen. In right and left lateral views: vertebra moderately short; neural spine represented only by small portion at anterior end of vertebra; condyle short and posteriorly rounded, separated from centrum by short, slightly constricted neck; hypapophysis long and straight, not markedly backswept, tapering very slightly downward to anteriorly beveled apex; parapophyses robust; both diapophyses broken. In posterior view: vertebra moderately vaulted; left postzygapophyseal area broken away, right postzygapophyseal facet tilted upward; neural canal roughly rounded, much smaller than condyle which is large and rounded; hypapophysis thick, but about same width throughout its length, its apex rounded; parapophyses robust, short and wide, terminally truncated.

Measurements in mm are: greatest anterior width of vertebra through prezygapophyses, 14.0; greatest anterior width through parapophyses 7.6; greatest width of cotyle, 4.8; greatest width of zygosphene, 4.8; greatest length of vertebra through pre and postzygapophyses, 9.6; greatest width of condyle, 4.2.

I d e n t i f i c a t i o n. We are unable to distinguish the Japanese Miocene cf. *Trimeresurus* from living and Pleistocene *Trimeresurus flavoviridis* (HALLOWELL,1861) (see Figs. 2 and 3 and compare with MANABE and HASEGAWA 1985: fig. p. 149; OSHIRO 1987: fig. p. 88; and SZYNDLAR
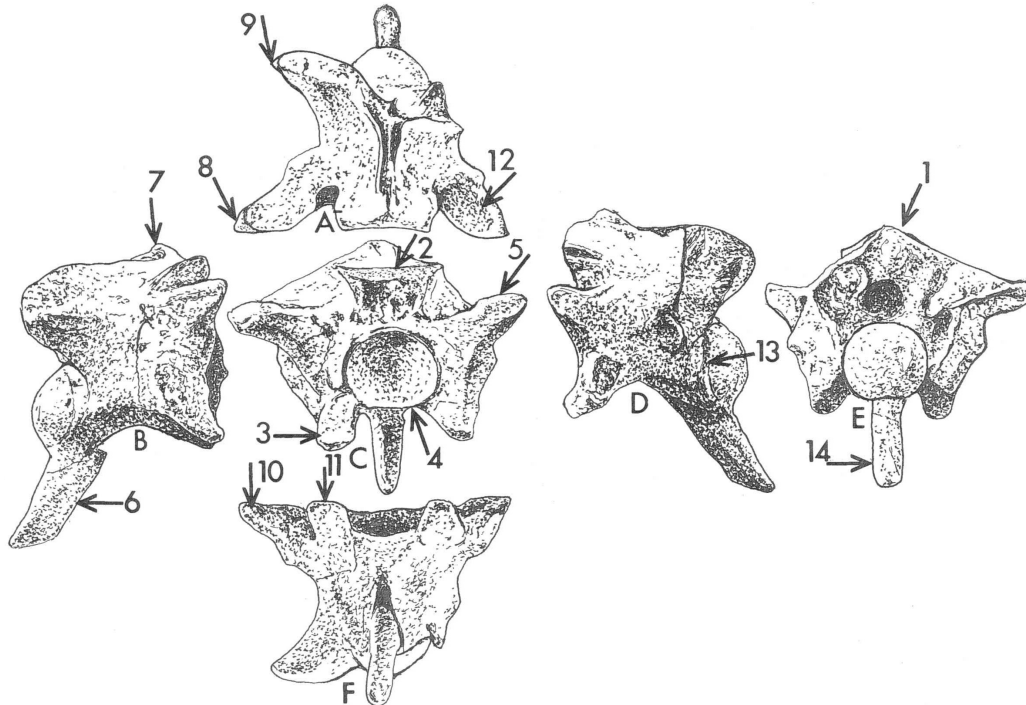
Fig. 3. Drawing of cf. *Trimeresurus* sp. indet. (MFM 17851) indicating important vertebral structures in Fig. 2. 1 – neural arch in posterior view; 2 – roof of zygosphene in anterior view; 3 – right parapophysis in anterior view; 4 – cotyle; 5 – left prezygapophysis in anterior view; 6 – hypapophysis in right lateral view; 7 – anterior remnant of neural spine in right lateral view; 8 – right prezygapophyseal accessory process in dorsal view; 9 – epizygapophyseal spine; 10 – right prezygapophyseal accessory process in ventral view; 11 – right parapophysis in ventral view; 12 – left prezygapophyseal articular facet in dorsal view; 13 – condylar neck; 14 – hypapophysis in posterior view.

1991: Fig. 8D, p. 244). Trenchant characters, among others (see SZYNDLAR, 1991), that occur in the Japanese fossil and in *Trimeresurus flavoviridis* are that both have a hypapophysis that is very long, straight, and anteriorly bevelled at its ventral end; and both have only a moderately vaulted neural arch.

In comparing the Japanese Miocene cf. *Trimeresurus* with the vertebral groups of the subfamily Viperinae of SZYNDLAR and RAGE (1999), one finds that the *Vipera berus* species group has a short, posteriorly directed hypapophyses whereas the Japanese cf. *Trimeresurus* has its hypapophysis longer and more anteriorly directed as in *T. flavoviridis*. In the *Vipera aspis* vertebral species group, we find that the Japanese cf. *Trimeresurus* still has a longer, more anteriorly directed neural spine than in that group, but that this difference is not as pronounced as in the *V. berus* group.

SZYNDLAR (1991) points out that *Trimeresurus* shares some characters with the Oriental Viper group. *Vipera platyspondyla* of the Late Early Miocene of Dolnice, Czech Republic (the oldest representative of the Oriental vipers in East Europe) and *Vipera* sp. of the Late Early Miocene of Langenau, Germany and Artenay, France are superficially similar to *Trimeresurus*. The Japanese cf. *Trimeresurus* differs from *V. platyspondyla* and is similar to cf. *Trimeresurus* sp. above in having the neural arch less flattened and the zygosphene (in anterior view) straighter and with its lateral borders not sharply tilted upward. But it differs from cf. *Trimeresurus* sp. above in having the parapophyses shorter, wider, and with more truncated apices; the cotyle more rounded; and the prezygapophyses more sharply tilted upward. The Japanese fossil differs from both of these taxa in having well-defined epizygapophyseal spines.

Compared with the only form of the subfamily Crotalinae that presently lives in Japan, namely *Gloydius blomhoffii blomhoffii,* the vertebra of the Japanese fossil is much larger, is shorter and wider, and the prezygapophseal accessory processes are relatively larger. Moreover, the condyle is round whereas it is depressed in *G. b. blomhoffii*; the parapophyses are longer and more massive, and the hypapophysis is thicker than in *G. b. blomhoffii*.

Compared to the Crotalinae of the New World, the Japanese cf. *Trimeresurus* differs from North American *Agkistrodon* (*A. bilineatus*, *A. contortrix,* and *A. contortrix*) and many species of *Crotalus* observed by J.A.H. in lacking the large paracotylar foramina that are characteristic of both of these genera. Moreover, the Japanese fossil differs in having the prezygapophyseal accessory processes wide and terminally rounded rather than narrow as in NA *Agkistrodon*; and in having the condyle and cotyle rounded rather than oval as in NA *Agkistrodon*. The Japanese cf. *Trimeresurus* strongly differs from *Sistrurus catenatus* in having the neural arches less vaulted, the paracotylar foramina less well developed, the hypapophyses not constricted at their bases, the prezygapophyseal accessory processes more highly developed, and in having a wider vertebral form.

III. DISCUSSION

Based on the fact that only a single vertebra of cf. *Trimeresurus* is known from the late Early Miocene of central Japan, we defer the identification of this specimen to a more specific level until more material is available. Nevertheless, the probable presence of this modern crotaline genus in Japan is quite noteworthy. The phylogenetic relationships of the Miocene Japanese cf. *Trimeresurus* to the numerous modern species of the genus (see MCDIARMID et al. 1999) obviously remains to be seen.

To that effect, we should mention that the genus *Protobothrops* HODGE and ROMANO-HODGE 1983 was erected for *Trimeresurus flavoviridis* (HALLOWELL, 1861), *T. jerdonii* GÜNTHER, 1875, and *T. mucrosquamatus* (CANTOR, 1839). Recognition of this genus has not been widely accepted (MCDIARMID et al. 1999), thus these authors decided to treat all *Trimeresurus, sensu lato,* as a single genus with the recognition that another monophyletic clade is likely to be found within this genus. It is possible that more abundant material of the Japanese Miocene cf. *Trimeresurus* might ultimately bear on the *Trimeresurus-Protobothrops* problem.

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