An investigation of the cranial evolution of Asian pitvipers (Serpentes: Crotalinae), with comments on the phylogenetic position of *Peltopelor macrolepis*

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Abstract

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We investigated the evolution of 12 cranial characters of 31 species of Asian pitvipers by examining the character state changes on a consensus tree modified from broadly consistent molecular results. We found that these characters appear stable with only one intraspecific polymorphism. Nine of the 12 characters form useful synapomorphies, whereas three are ambiguous and evolutionarily plastic. Clades that are supported with numerous apomorphies are the *Trimeresurus* group [consisting of the recently defined genera *Trimeresurus sensu* Malhotra and Thorpe (2004), *Parias*, *Popeia*, *Viridovipera*, *Himalayophis*, and *Cryptelytrops*] and the genera *Protobothrops*, *Parias*, and *Viridovipera*. Two species previously considered as congeners but now known to be distantly related, *Ovophis monticola* and '*Ovophis*' *okinavensis*, have nearly identical character states, demonstrating substantial convergence in cranial characters. Finally, we attempt to infer the phylogenetic position of *Peltopelor macrolepis* by comparing its cranial features with that of other pitvipers.

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Introduction

Asian pitvipers are a diverse group of more than 70 terrestrial, arboreal, and semi-aquatic species, which live in nearly every available habitat (David and Ineich 1999; Gumprecht *et al.* 2004; Vogel 2006). Because of their medical importance, the systematics, morphology, ecology, and evolution of this group have been widely studied. Using molecular phylogenetics and morphological comparisons, much of the evolutionary history and phylogenetic relationships of Asian pitvipers have been elucidated (e.g. Herrmann *et al.* 2004; Malhotra and Thorpe 2004; Castoe and Parkinson 2006; Creer *et al.* 2006; Sanders *et al.* 2006; Guo *et al.* 2009). Malhotra and Thorpe (2004) underscored the importance of finding diagnostic morphological characters to enhance taxonomic accuracy of pitvipers, even with the existence of strongly supported molecular phylogenies.

In pitvipers, investigations of skull anatomy have provided informative character data on taxonomy (Brattstrom 1964;

Cundall 1981; Guo and Zhao 2006; Guo *et al.* 2009) and morphological phylogenetics (Marx and Rabb 1972; Werman 1992; Gutberlet 1998). In this study, we investigate the evolution of 12 osteological characters in 31 species of Asian pitvipers from a phylogenetic perspective. In addition, we hypothesize the relationship of the enigmatic southern Indian species, *Peltopelor macrolepis*, the phylogenetic position of which has not yet been assessed, with other Asian pitvipers by comparing its cranial features with that of other Asian pitvipers.

Materials and Methods

We investigated the states of 12 discrete osteological characters using 88 osteological preparations (Appendix I) of 31 species of Asian pitvipers, representing nine currently recognized genera (Malhotra and Thorpe 2004; Guo *et al.* 2007). Whenever possible, multiple osteological preparations of a single species were examined to investigate the polymorphism of

osteological characters within a single species. All characters were previously described in Guo and Zhao (2006) and Guo *et al.* (2009). Because these characters were not included in a phylogenetic analysis, polarization was unnecessary and ancestral character states were not assumed.

1. The dorsal process of the dentary (0) does not reach, (1) just reaches, (2) extends further posteriorly than, the ventral process.
2. The shape of the anterior end of the ectopterygoid: (0) narrow, (1) broad (Fig. 1).
3. Thin flap on the posterior ventrolateral edge of the lower jaw: (0) absent, (1) present.
4. The shape of the palatine: (0) not forked, (1) forked.
5. Length of the postfrontal is: (0) less than, (1) more than the distance between the posterior end of the postfrontal and the posterior corner of the frontal.
6. Projection on border of maxillary cavity: (0) absent, (1) present.
7. Shape of the parietal ridge: (0) triangular, (1) T-shaped, (2) diamond shaped.
8. Pterygoid teeth: (0) do not extend to, (1) extend to, posterior margin of articulation with ectopterygoid.
9. Squamosal (0) does not, (1) does, extend beyond the posterior end of the braincase.
10. Splenial and angular: (0) separated, (1) fused.
11. Second lateral expansion in the parietal: (0) absent, (1) present.
12. Maxillary cavity is: (0) closed, (1) open.

A consensus phylogeny (Fig. 2), modified from several consistent molecular studies (Malhotra and Thorpe 2004; Castoe and Parkinson 2006; Creer *et al.* 2006; Guo *et al.* 2006; Dawson *et al.* 2008), was constructed for 30 pitviper species to examine character state changes among clades. No phylogenetic hypothesis exists for *Peltopelor macrolepis*, although this species was formerly placed in the large genus *Trimeresurus*. In this study, we compared its osteological
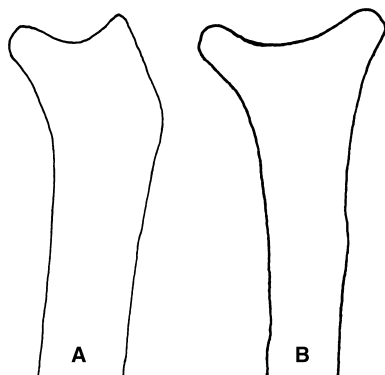

Fig. 1—The shape of the anterior end of the ectopterygoid (**A**: broad; **B**: narrow) (modified from Guo and Zhao 2006).

similarities with that of other pitviper species to predict its phylogenetic position.

Results and Discussion

An examination of the cranial evolution on the consensus tree shows that most of the major clades are supported by one or more synapomorphies. Below we report the apomorphies and state changes for each clade.

Trimeresurus *group*

The genus *Trimeresurus* has had several definitions during its long history. In this study, we use the term *Trimeresurus* group to refer to the clade formed by most members of the former genus *Trimeresurus* [*sensu lato*; e.g. Gumprecht *et al.* (2004)] prior to its split into separate genera (i.e. *Cryptelytrops*, *Himalayophis*, *Parias*, *Popeia*, *Trimeresurus sensu stricto*, *Peltopelor*, and *Viridovipera*) by Malhotra and Thorpe (2004). However, we only include genera which are known to form part of this monophyletic radiation and therefore do not include *Peltopelor*, the phylogenetic relationships of which are currently unknown. *Trimeresurus sensu stricto* will be used to refer to the narrowest definition of that genus, restricted by Malhotra and Thorpe (2004) to species found in the Indian Peninsula and the Indo-Malayan archipelago.

The primary synapomorphy for the *Trimeresurus* group is the possession of a dorsal process that barely reaches the ventral process (1:1 → 0). With the exception of *Parias mcgregori*, the projection on the border of the maxillary cavity is present (6:0 → 1) in all species examined. The parietal ridge is T-shaped in all species except *Himalayophis tibetanus*, where it is diamond shaped (7:1 → 2). The maxillary cavity is open (12:0 → 1) in *H. tibetanus* and closed in other species of the *Trimeresurus* group. The splenial and angular of the dentary bone is fused (10:0 → 1) in all species of the group, except *Parias mcgregori* where it is separated.

Within the *Trimeresurus* group, the clades *Parias* and *Viridovipera* are both supported by the presence of a thin flap on the posterior ventrolateral edge of the lower jaw (3:0 → 1), except for *Parias mcgregori* where it is absent. *Trimeresurus malabaricus* and the genus *Popeia* have also evolved the presence of the flap, whereas only one species outside the *Trimeresurus* group, *Protobothrops flavoviridis*, has evolved this flap.

Trimeresurus sensu stricto is supported by having a postfrontal with a length which is less than the distance between the posterior end of the postfrontal and the posterior corner of the frontal (5:1 → 0). Other species in the *Trimeresurus* group that share this state are *Parias mcgregori* and three species of *Cryptelytrops*.

The most plastic character in the *Trimeresurus* group is the presence or absence of a second lateral expansion of the parietal bone. This character is present (11:0 → 1) in the *Himalayophis–Popeia* clade, *Viridovipera*, *Cryptelytrops insularis*, *Cryptelytrops macrops*, and *Parias sumatranus*, and absent in
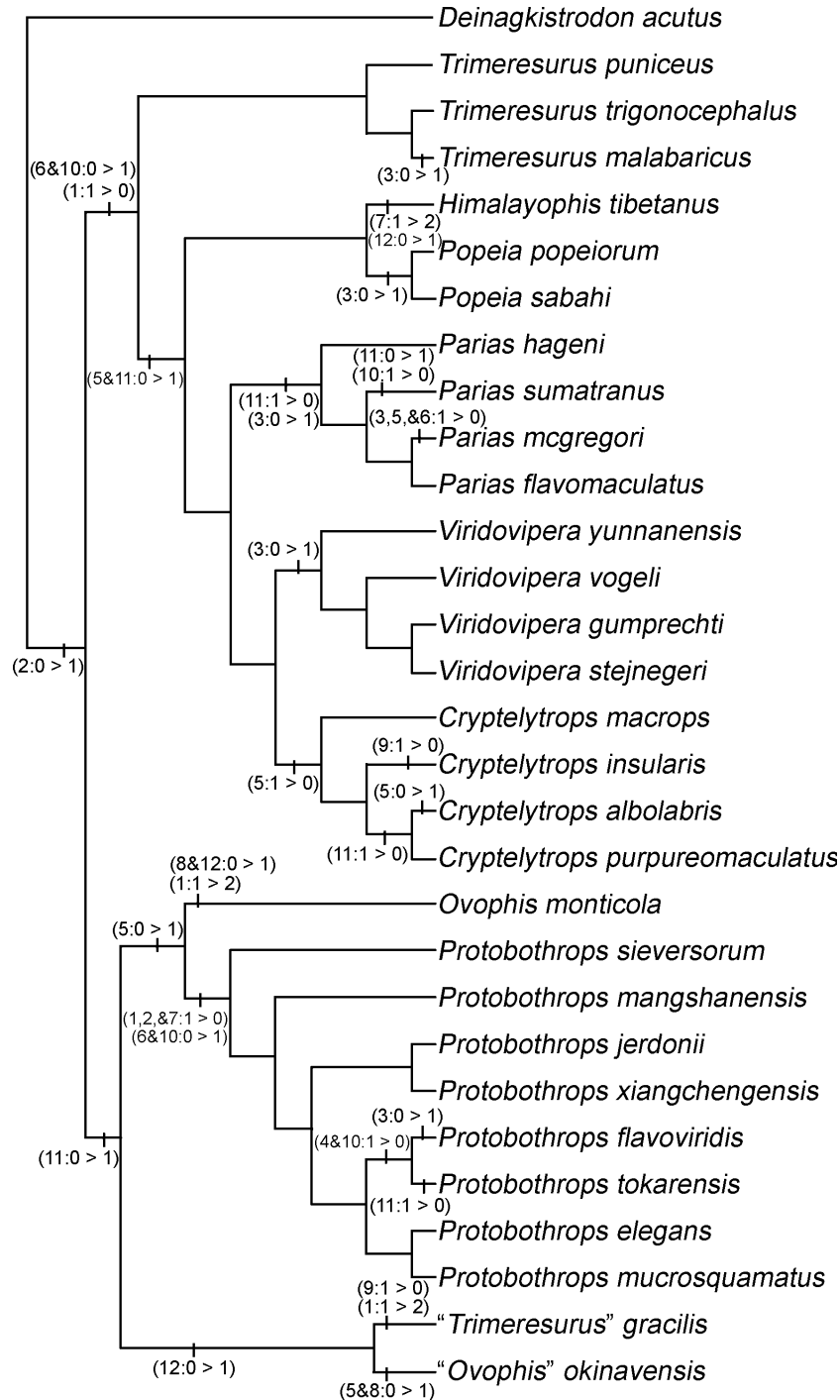
Fig. 2—Consensus phylogeny of 30 species of Asian pitvipers based on the molecular phylogenies (Malhotra and Thorpe 2004; Castoe and Parkinson 2006; Creer *et al.* 2006; Guo *et al.* 2006; Dawson *et al.* 2008). A symbol such as (2:0 → 1) denotes that character 2 is changing at that branch from state 0 to state 1.

Trimeresurus sensu stricto, *Cryptelytrops albolabris*, *Cryptelytrops purpureomaculatus*, and the remaining species of *Parias*.

The isolation of *Parias mcgregori* on the Philippines' northernmost Batanes island group may have led to the reversal or convergence of several characters independent of the other species of *Parias*. The cranial data presented in this study help distinguish this species from *Parias flavomaculatus* as an independently evolving species, which is not

recognized in some literature (e.g. McDiarmid *et al.* 1999; Uetz *et al.* 2009).

Protobothrops

A recent molecular phylogenetic study and morphological comparison between a rare species, *Protobothrops kaulbacki*, and related taxa concluded that the monotypic genera *Triceretolepidophis* and *Zhaoermia* should be synonymized with *Protobothrops* (Guo *et al.* 2007). This clade is further supported by several osteological synapomorphies investigated in this study, such as having a dorsal process that does not reach the ventral process (1:1 → 0), an anterior end of the ectopterygoid which is narrow (2:1 → 0), a projection on the border of the maxillary cavity (6:0 → 1), a triangular parietal ridge (7:1 → 0), and a closed maxillary cavity (12:1 → 0). An apomorphy supporting the *Protobothrops–Ovophis monticola* clade is a postfrontal that has a length which is more than the distance between the posterior end of the postfrontal and the posterior corner of the frontal (5:0 → 1).

Within *Protobothrops*, synapomorphies supporting the *Protobothrops flavoviridis–Protobothrops tokarensis* clade are a palatine bone that does not fork (4:1 → 0), which is forked in all other species examined in this study. The splenial and angular are also separated (10:1 → 0), which are fused in all other congeneric species. With the exception of *Protobothrops tokarensis*, all species in *Protobothrops* and the 'Ovophis' okinavensis–'Trimeresurus' gracilis clade have a second lateral expansion in the parietal bone (11:0 → 1). However, a number of other species (including the very large New World radiation) have uncertain affinities with *Protobothrops* and *Ovophis*, and have not been included in this study.

Ovophis monticola *and* 'Trimeresurus' gracilis–'Ovophis' okinavensis

Although strong molecular evidence suggests that *O. monticola* and 'O.' okinavensis are not closely related (Malhotra and Thorpe 2004; Castoe and Parkinson 2006), they not only greatly resemble one another externally but also share nearly identical cranial features (i.e. characters 2–12). The osteological features of these two species show significant convergence, consistent with the interpretation of Guo *et al.* (2009). As a consequence, most apomorphies between the species in the clade containing 'O.' okinavensis, which are defined in all molecular analyses to date (i.e. 2–4, 6, 7, 10, and 11), are also shared by *O. monticola*. The only unambiguous cranial synapomorphy supporting the relationship of 'T. gracilis–'O. okinavensis is an open maxillary cavity (12:0 → 1), a state also shared by *Himalayophis tibetanus* as well as *O. monticola*. Many seemingly evolutionarily stable characters (i.e. 1, 8, and 9) differ between 'T.' gracilis and 'O.' okinavensis. Therefore, although molecular evidence strongly suggests that these two species form a clade (Malhotra and Thorpe 2004; Castoe and Parkinson 2006;

Creer *et al.* 2006), cranial evidence suggests much dissimilarity between them.

Peltopelor macrolepis

Peltopelor (*Pel.*) is a monotypic genus found in the mountains of southern India. The species *Pel. macrolepis* is identified by enlarged head scales and a long calyculate hemipenis (Malhotra and Thorpe 2004). Based on hemipenial morphology, Malhotra and Thorpe (2004) stated that *Pel. macrolepis* was probably closely related to *Popeia*. However, the cranial characters presented in this study are inconsistent with their hypothesis. We find more similarities of *Pel. macrolepis* to either *Trimeresurus sensu stricto* or *Cryptelytrops*. Although *Pel. macrolepis* shares most characters with *C. macrops*, the states of several characters (i.e. 5, 9, and 11) within *Cryptelytrops* vary and seem quite plastic, likely causing confusion. Character states within *Trimeresurus sensu stricto* are more stable and these three species share 10 characters with *Pel. macrolepis* (Table 1). We suggest that *Pel. macrolepis* is sister to *Trimeresurus sensu stricto*; however, it could be possible that *Pel. macrolepis* is at the base of the *Trimeresurus* group, and that the long calyculate hemipenis represents the ancentral hemipenis of this group. This potentially explains why *Pel. macrolepis* shares several characters with so many genera. Further studies, particularly molecular phylogenetic studies, should clarify this.

Osteological characters

Only one character (number 1) of one species (*Peltopelor macrolepis*) was found to reveal intraspecific polymorphism, exhibiting a dorsal process that either does not or just barely reaches the ventral process (states 0 and 1, respectively), but that does not reach further. Characters 3, 5, and 11 appear to be evolutionarily plastic, having arisen and/or reversed in many lineages. In a phylogenetic context, these characters may provide a signal for intrageneric relationships, whereas more evolutionarily stable cranial features (e.g. characters 2, 6, and 7) may provide more signal at the intergeneric level.

Autapomorphies that occur in the species examined are: the dorsal process of *O. monticola* and 'T.' gracilis reaches further than the ventral process (1:1 → 2), the pterygoid teeth of *O. monticola* and 'O.' okinavensis extend to the posterior margin of articulation with their ectopterygoid (8:0 → 1), and the squamosals of *Cryptelytrops insularis* and 'T.' gracilis do not extend beyond the posterior end of the braincase (9:1 → 0).

Although the number of molecular phylogenetic studies now greatly exceed those based on morphology, anatomical data continue to provide important phylogenetic information (e.g. Werman 1992; Gutberlet 1998; Gutberlet and Harvey 2004; Malhotra and Thorpe 2004) and our cranial data can be used for future phylogenetic studies. Recently, Guo *et al.* (2009) conducted a cranial morphometric analysis among 24 species of Asian pitvipers and evaluated the systematic value

Table 1 Data matrix of cranial character states used in this study. All characters are discrete and the numbers correspond to those listed in the Materials and Methods

Species	Characters											
	1	2	3	4	5	6	7	8	9	10	11	12
Cryptelytrops albolabris	0	1	0	1	1	1	1	0	1	1	0	0
Cryptelytrops insularis	0	1	0	1	0	1	1	0	0	1	1	0
Cryptelytrops macrops	0	1	0	1	0	1	1	0	1	1	1	0
Cryptelytrops purpureomaculatus	0	1	0	1	0	1	1	0	1	1	0	0
Deinagkistrodon acutus	1	0	0	1	0	0	1	0	1	0	0	0
Himalayophis tibetanus	0	1	0	1	1	1	2	0	1	1	1	1
'*Ovophis*' *okinavensis*	1	1	0	1	1	0	1	1	1	0	1	1
Ovophis monticola	2	1	0	1	1	0	1	1	1	0	1	1
Parias flavomaculatus	0	1	1	1	1	1	1	0	1	1	0	0
Parias hageni	0	1	1	1	1	1	1	0	1	1	0	0
Parias mcgregori	0	1	0	1	0	0	1	0	1	1	0	0
Parias sumatranus	0	1	1	1	1	1	1	0	1	0	1	0
Peltopelor macrolepis	0–1	1	0	1	0	1	1	0	1	1	1	1
Popeia popeiorum	0	1	1	1	1	1	1	0	1	1	1	0
Popeia sabahi	0	1	1	1	1	1	1	0	1	1	1	0
Protobothrops elegans	0	0	0	1	1	1	0	0	1	1	1	0
Protobothrops flavoviridis	0	0	1	0	1	1	0	0	1	0	1	0
Protobothrops jerdonii	0	0	0	1	1	1	0	0	1	1	1	0
Protobothrops mangshanensis	0	0	0	1	1	1	0	0	1	1	1	0
Protobothrops mucrosquomatus	0	0	0	1	1	1	0	0	1	1	1	0
Protobothrops tokarensis	0	0	0	0	1	1	0	0	1	0	0	0
Protobothrops xiangchengensis	0	0	0	1	1	1	0	0	1	1	1	0
Protobothrops sieversorum	0	0	0	1	1	1	0	0	1	1	1	0
'*Trimeresurus*' *gracilis*	2	1	0	1	0	0	1	0	0	0	1	1
Trimeresurus malabaricus	0	1	1	1	0	1	1	0	1	1	0	0
Trimeresurus puniceus	0	1	0	1	0	1	1	0	1	1	0	0
Trimeresurus trigonocephalus	0	1	0	1	0	1	1	0	1	1	0	0
Viridovipera gumprechti	0	1	1	1	1	1	1	0	1	1	1	0
Viridovipera stejnegeri	0	1	1	1	1	1	1	0	1	1	1	0
Viridovipera vogeli	0	1	1	1	1	1	1	0	1	1	1	0
Viridovipera yunnanensis	0	1	1	1	1	1	1	0	1	1	1	0

of cranial morphology. Their results indicated that cranial morphology can contribute to an overall understanding of pitviper evolution and taxonomy; however, care should be taken when constructing phylogenetic relationships, as cranial phenotypes contain homoplastic information.

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Appendix I: Specimens Examined

Institutional abbreviations used are as follows: BMNH: British Museum (Natural History), London; CAS: California Academy of Science, San Francisco; FMNH: Field Museum of Natural History, Chicago; KUZ: Zoological Collection, Kyoto University Museum, Japan; PNNP: Phong Nha-Ke Bang National Park, Quang Binh, Vietnam; USNM: United States National Museum of Natural History, Smithsonian Institute, Washington; SCUM: Sichuan University Museum, China; YBU: Yibin University, China; ZMB: Museum für Naturkunde, Humboldt-Universität, Berlin. AM, AFS, and RTV are personal catalog numbers of Anita Malhotra.

Cryptelytrops albolabris, Danzhou, Hainan: SCUM035007–09. *Cryptelytrops venustus*, South Thailand: AFS 06.41. *Cryptelytrops insularis*. West Timor: RTV 16B; Indonesia: AFS 06.44. *Cryptelytrops macrops*, Thailand: FMNH 180271, BMNH 1988.1055–56, AM 04. *Cryptelytrops purpureomaculatus*, Ayeyarwade, Myanmar: CAS 212242, CAS 212244. *Deinagkistrodon acutus*, Huangshan, Anhui: YBU0801. *Himalayophis tibetanus*, Bagmati, Nepal: ZMB 65639. 'Ovophis' okinavensis. Japan: CAS 21927, FMNH 45074, KUZ R19071, KUZ R19248. *Ovophis monticola*. China: AFS 06.30; Nepal: AFS 06.49; Huili, Sichuan: SCUM035082-83, SCUM035040; Anxian, Sichuan: SCUM035030. *Parias flavomaculatus*, Luzon Is., Philippines: AFS 06.35, BMNH 2002.26, BMNH 2002.31. *Parias hageni*, Malaysia: AM 01; Sumatra: RTV 35, AM 06. *Parias mcgregori*, Batane Is., Philippines: AFS 06.52, BMNH 2005.5, BMNH 2005.11. *Parias sumatranus*, Sumatra: AFS 06.19, AFS 06.31. *Peltopelor macrolepis*, S. India: BMNH 1955.1.3.86–87. *Popeia popeiorum*, Chiang Mai, Thailand: AFS 06.28. *Popeia sabahi*, Selangor, West Malaysia: AM 03; Sumatra: AFS 06.33; Fraser's Hill, Thailand: AFS 06. 57. *Protobothrops elegans*. Japan: USNM 133984, CAS 21944, CAS 21946, KUZ R1108, KUZ R33011. *Protobothrops flavoviridis*. Japan: KUZ R48345, FMNH 72584, SCUM035056. *Protobothrops jerdonii*, Anxian, Sichuan: SCUM035028-29; Huili, Sichuan: SCUM035041, SCUM035075; Ruoergai, Sichuan: SCUM035081; Qingling, Shaanxi: SCUM035078. *Protobothrops mangshanensis*, Yizhang, Hunan: SCUM035024. *Protobothrops mucrosquamatus*, Yibin, Sichuan: SCUM035026; Hongya, Sichuan: SCUM035031–32, SCUM035076; Chengdu, Sichuan: SCUM035050. *Protobothrops sieversorum*. Vietnam: PNNP 00220. *Protobothrops tokarensis*. Japan: KUZ R21123. *Protobothrops xiangchengensis*, Jiulong, Sichuan: SCUM035042-43, SCUM035046. *Trimeresurus puniceus*, Indonesia: AFS 06.45, AM 02, AM 05. *Trimeresurus trigonocephalus*, Sri Lanka: AFS 06.36–37, AFS 06.47. *Trimeresurus malabaricus*, India: FMNH 217679, BMNH 1955.1.3.72–73. 'Trimeresurus' gracilis. Taiwan, China: USNM 134034. *Viridovipera gumprechti*, Loei, Thailand: AFS 06.27, AM 08, AM 09. *Viridovipera stejnegeri*, Qunzhong, Hainan: SCUM035013–14; Hejiang, Sichuan: SCUM035053; Guangdong: SCUM035079. *Viridovipera vogeli*, Nakhon Ratchasima, Thailand: AM 07, FMNH 180269, RTV 10. *Viridovipera yunnanensis*, Huili, Sichuan: SCUM035037, SCUM035045, SCUM035114. Kunming, Yunnan: SCUM035077.