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COMPARISON OF SKULL MORPHOLOGY IN NINE ASIAN PIT VIPERS (SERPENTES: CROTALINAE)

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The relationships of nine Asian pit vipers are discussed using a comparison of skull morphology. *Protobothrops xiangchengensis* shares more characters with other *Protobothrops* species than with the other genera. It is morphologically distinct from *P. mucrosquamatus*. *Zhaoermia mangshanensis* shows many similarities with the members of the genus *Protobothrops*, supporting its close relationship with *Protobothrops*. *Ovophis monticola* is unique in several skull characters among the species examined. The relationships indicated by skull morphology between *Viridovipera stejnegeri*, *V. yunnanensis* and *Cryptelytrops albolabris* are consistent with their previous reclassification based on molecular results and hemipenial comparison.

Key words: morphometrics, snake, taxonomy, *Trimeresurus*

INTRODUCTION

Trimeresurus (*sensu lato*), which consists of over 40 species (David & Ineich, 1999; McDiarmid *et al.*, 1999; Gumprecht *et al.*, 2004), represents a major evolutionary radiation (Malhotra & Thorpe, 2000), and ranges widely over southern, eastern and south-eastern Asia (Gumprecht *et al.*, 2004). The species of this group occupy a wide range of habits and display a variety of lifestyles (terrestrial, semi-arboreal and arboreal) and reproductive modes (oviparous and ovoviviparous). Originally, all were considered to be congeneric in *Trimeresurus* (*sensu lato*). Subsequently, several new genera have been proposed (*Tropidolaemus*, Wagler, 1830; *Ovophis*, Burger in Hoge & Romano-Hoge, 1981; *Protobothrops*, Hoge & Romano-Hoge, 1983; *Triceratolepidophis*, Ziegler *et al.*, 2000; *Zhaoermia*, Gumprecht & Tillack, 2004) based on morphological studies (Burger, 1971; Gumprecht & Tillack, 2004; Hoge & Romano-Hoge, 1981, 1983; Zhang, 1993, 1998; Ziegler *et al.*, 2000). More recently, a revised taxonomy for *Trimeresurus* (*sensu stricto*) and *Ovophis* (*sensu lato*) has been published on the basis of hemipenial features and molecular phylogeny (Malhotra & Thorpe, 2004). This taxonomy is followed here.

The skull is one of the most important structures available for the taxonomy and phylogenetic analysis of pit vipers (Brattstrom, 1964; Burger, 1971; Guo *et al.*, 1999; Hoge & Romano-Hoge, 1981, 1983; Zhang, 1993; Zhang & Zhao, 1990). Although several skull morphological studies of *Trimeresurus* (*sensu lato*) have appeared in past decades, a limited number of specimens or species were included (Burger, 1971; Hoge & Romano-Hoge, 1981, 1983; Zhang & Zhao, 1990; Zhang, 1993, 1998).

In the present paper, we report on a comparative study of the skulls of nine Asian pit vipers. Our aim is to re-evaluate the relationships within *Trimeresurus* (*sensu lato*) by skull morphological comparison methods, and propose diagnostic characters for some valid genera. Although the number of specimens and species is not enough to clarify all of the relationships, it is an important step toward resolving the taxonomy and phylogeny of this group.

MATERIALS AND METHODS

Thirty-one individuals representing nine species and five genera of Asian pit vipers were examined, including four specimens of *Ovophis monticola*, one specimen of *Zhaoermia mangshanensis*, one specimen of *Protobothrops flavoviridis*, six specimens of *P. jerdonii*, five specimens of *P. mucrosquamatus*, three specimens of *P. xiangchengensis*, four specimens of *Viridovipera stejnegeri*, four specimens of *V. yunnanensis* and three specimens of *Cryptelytrops albolabris*. Detailed information on the studied specimens is listed in Appendix 1. All specimens are adults without anomalies and injuries to the head. Vernier callipers were used to measure different bones using the methods suggested by Brattstrom (1964) (Fig. 1). The descriptive methods for skull characters follow Guo *et al.* (1999). Accurate tooth counts can be obtained by counting the sockets and the teeth present, rather than by just counting the teeth present. The line drawings of skulls are based on the photographs and skull samples.

All specimens and skull samples are deposited in the Sichuan University Museum.

RESULTS

The skull structure and feature of nine Asian pit vipers is consistent with the other pit vipers; for example, they share movable maxilla, hollow fang, pit cavity. The skull of each species is not described here in detail, but rather illustrated in both ventral and dorsal view (Figs. 7–15); some single bones are also illustrated. In Table 2, some characters are compared for

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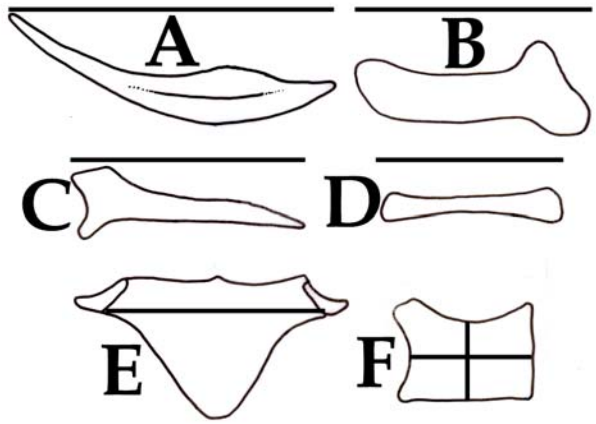

FIG. 1. Measurement of skulls (horizontal and vertical lines indicate length and width respectively). A: Pterygoid; B: Squamosal; C: Ectopterygoid; D: Quadrate; E: Lower jaw; F: Parietal.

each species. A detailed description of some bones, with variation noted, is given below. In Fig.3 to Fig. 15, the horizontal line bars indicate 0.5 cm

TEETH

In Crotalidae, teeth are found on the maxilla, pterygoid, palatine and dentary bones. The fang, which is on the maxilla, is not very different between species. Brattstrom (1964) and Zhang (1993) proposed that the fangs of various species were different in the length and curvature. However, these characters are very difficult to described and compared in practice. The number of palatine teeth varies from 0 to 5 in the specimens examined. Palatine teeth are absent in *Zhaoermia mangshanensis*, *Ovophis monticola*, *Protobothrops xiangchengensis, P. mucrosquamatus, P. flavoviridis*; 3–5 are present in *Viridovipera stejnegeri*, *V. yunnanensis* and *Cryptelytrops albolabris*. However, in *Protobothrops jerdonii*, some have one or two teeth (SCUM035028-29, SCUM035041), while in others, the palatine teeth are absent (SCUM035075, SCUM035078, SCUM035081).

Generally, the number of dentary teeth is 8–14 (10 on average), but *Ovophis monticola* has more (17–18). The pterygoid teeth vary greatly in numbers among species. *Ovophis monticola* has the greatest number of pterygoid teeth (14 on average), but *Protobothrops mucrosquamatus* has only five, *Protobothrops flavoviridis*, *V. stejnegeri*, *V. yunnanensis* and *C. albolabris* have more than 10, while the others have about eight. The positions of the first and last pterygoid teeth are very stable traits. For example, the pterygoid teeth of *Ovophis monticola* begins immediately at the articulation of the pterygoid with the palatine, and extends beyond the posterior end of the articulation of the ectopterygoid with the pterygoid; however, those of *Protobothrops mucrosquamatus* begin at a distance from the articulation of the pterygoid with the palatine, and do not extend to the anterior articulation of the ectopterygoid with the pterygoid.

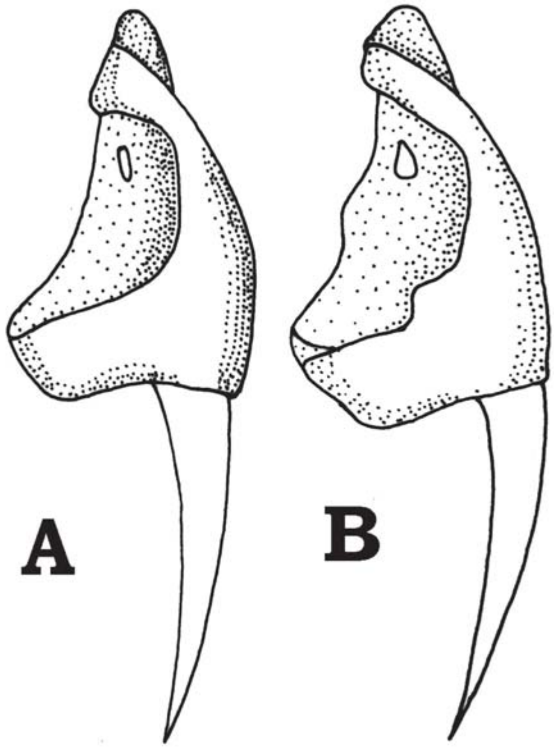

FIG. 2. Two types of maxilla. A: no projection; B: with projection.

MAXILLA

The maxilla is located in front of the prefrontal. This bone has a large lateral opening that contains the heat-sensitive facial pit. The shape of the anterior edge of the pit cavity is of some taxonomic importance (Brattstrom, 1964). Two states of this character were detected among the specimens examined (Fig. 2). Some species are smooth on the edge of the pit cavity (Fig. 2A), e.g. *Ovophis monticola*, *Protobothrops mucrosquamatus*; the others have a projection or process on the border of the pit cavity (Fig. 2B), e.g. *Zhaoermia mangshanensis*, *Protobothrops xiangchengensis*.

FRONTAL

The frontal bone, which is flat and quadrate, articulates posteriorly with the parietal (sometimes with the postfrontal), anteroventrally with the nasal and anterolaterally with the prefrontals. The shape of the frontal is constant within each species (Table 1). The frontals of four species of *Protobothrops* (*flavoviridis*, *jerdonii*, *mucrosquamatus*, *xiangchengensis*) are elongate (longer than wide); those of *Viridovipera stejnegeri*, *V. yunnanensis* and *Cryptelytrops albolabris* are square; those of *Zhaoermia mangshanensis* and *Ovophis monticola* are generally wider than long.

POSTFRONTAL

The postfrontal is present in all crotalids (Brattstrom, 1964). This bone either touches the frontal or not, and

TABLE 1. Skull comparison of nine Asian pit vipers. Abbreviations: *Zm*: *Z. mangshanensis*; *Om*: *O. monticola*; *Pf*: *P. flavoviridis*; *Pm*: *P. mucrosquamatus*; *Px*: *P. xiangchengensis; Pj*: *P. jerdonii*; *Vs*: *V. stejnegeri*; *Vy*: *V. yunnanensis*; *Ca*: *C. albolabris*. BMC: border of maxillary cavity; PR: parietal ridge; PS1: parietal shape; PTF: postfrontal touches frontal; SEBB: squamosal extends beyond the posterior end of the braincase; PS2: palatine shape; PT1: palatine teeth; DT: dentary teeth; PT2: pterygoid teeth; BP1: basisphenoid process; BP2: basioccipital process; EALP: ectopterygoid anterior lateral process; RLW: the ratio of skull length to width; RF: the ratio of frontal length to width; RQ: the ratio of quadrate length to skull length; RM: the ratio of mandible length to skull length; RE: the ratio of ectopterygoid length to skull length; RS: the ratio of squamosal length to skull length; RP: the ratio of pterygoid length to skull length.

Species	*Zm*	*Om*	*Pf*	*Pm*	*Px*	*Pj*	*Vs*	*Vy*	*Ca*
BMC	Projection	No	No	No	Projection	Projection	Projection	Projection	Projection
PR	Strong, Flanged	Moderate	Moderate	Moderate	Weak	Weak	Moderate	Moderate	Moderate
PS1	Triangle	T-shape	Triangle	Triangle	Triangle	Triangle	T-shape	T-shape	T-shape
PTF	Yes	Yes	No	Yes or no	Yes or no	Yes or no	No	Yes or no	Yes or no
SEBB	Yes	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes
PS2	Triangle	Triangle	Triangle	Triangle	Triangle	Triangle	Crescent	Crescent	Triangle
	Not forked	Forked	Not forked	Not forked	Not forked	Not forked	Forked	Forked	Forked
EALP	Not broad	Broad	Not broad	Not broad	Not broad	Not broad	Broad	Broad	Broad
BP1	Strong	Strong	Strong	Strong	Moderate	Moderate	Weak	Weak	Moderate
BP2	Strong	Strong	Strong	Strong	Moderate	Moderate	Weak	Weak	Moderate
PT1	0	4 (3–4)	0	0	0	0, 1, 2	5 (4–5)	5	4 (3–5)
DT	11	17 (17–18)	13–14	9 (8–11)	11 (10–12)	11 (10–11)	12 (10–14)	13 (11–14)	12 (11–13)
PT2	8/9	14 (13–15)	11	5 (4–7)	8 (7–9)	8 (6–9)	12 (9–14)	13 (12–14)	10 (9–11)
RLW	1.81	1.95	2.03	2.45 (2.36–2.51)	2.07 (2.05–2.10)	2.08 (1.94–2.20)	1.60 (1.52–1.65)	1.72 (1.63–1.87)	2.11 (2.11–2.14)
RF	0.93	0.93	1.34	1.50 (1.40–1.58)	1.48 (1.47–1.50)	1.25 (1.1–1.33)	1.06 (1.0–1.15)	0.97 (0.93–1.0)	1.17 (1.11–1.23)
RQ	0.59	0.44	0.45	0.47 (0.44–0.48)	0.45	0.43 (0.40–0.45)	0.44 (0.43–0.45)	0.49 (0.47–0.52)	0.52 (0.51–0.54)
RM	1.58	1.36	1.40	1.44 (1.42–1.45)	1.39 (1.37–1.41)	1.30 (1.29–1.36)	1.40 (1.35–1.43)	1.42 (1.36–1.51)	1.45 (1.43–1.47)
RE	0.72	0.57	0.66	0.69 (0.63–0.74)	0.62 (0.60–0.64)	0.63 (0.60–0.64)	0.68 (0.65–0.71)	0.68 (0.66–0.70)	0.73 (0.72–0.73)
RS	0.32	0.38	0.30	0.31 (0.29–0.33)	0.29 (0.28–0.30)	0.32 (0.28–0.34)	0.34 (0.32–0.39)	0.31 (0.30–0.32)	0.30 (0.30–0.31)
RP	1.08	1.0	0.92	0.96 (0.93–0.99)	0.96 (0.95–0.98)	0.89 (0.84–0.91)	1.02 (0.97–1.08)	0.98 (0.94–1.0)	1.0 (0.98–1.05)

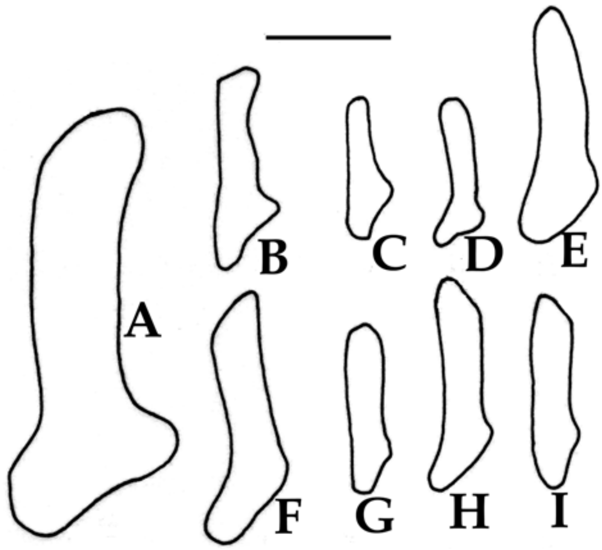

FIG. 3. Squamosals of nine Asian pit vipers (right, dorsal view). A: *Zhaoermia mangshanensis* (SCUM035024); B: *Ovophis monticola* (SCUM035030); C: *Protobothrops jerdonii* (SCUM035041); D: *P. xiangchengensis* (SCUM035043); E: *P. mucrosquamatus* (SCUM035026); F: *P. flavoviridis* (SCUM035056); G: *Viridovipera stejnegeri* (SCUM035053); H: *V. yunnanensis* (SCUM035045); I: *Cryptelytrops albolabris* (SCUM035008).

the distinction is usually considered to be taxonomically important (Brattstrom, 1964; Zhang & Zhao, 1990). The postfrontal touches the frontal in *Zhaoermia mangshanensis* and *Ovophis monticola*, and does not in *V. stejnegeri*. In the other species, both conditions (touches or not) are present within a species, even within an individual (e.g. SCUM035043).

PARIETAL

The parietal is the largest and heaviest bone of the crotalid skull. The parietal ridge is strongest in *Zhaoermia mangshanensis*, and is wing-shaped on both sides. The shape of the dorsal surface of the parietal is characteristic for each species (Figs. 7–15). It is T-shaped in *Viridovipera stejnegeri*, *V. yunnanensis*, *Cryptelytrops albolabris* and *Ovophis monticola*, but triangular in the others.

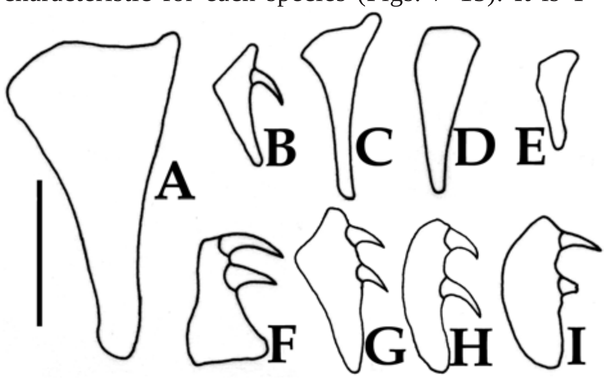

FIG. 4. Palatines of nine Asian pit vipers (side view). A: *Zhaoermia mangshanensis* (SCUM035024); B: *Protobothrops jerdonii* (SCUM035041); C: *P. flavoviridis* (SCUM035056); D: *P. mucrosquamatus* (SCUM035026); E: *P. xiangchengensis* (SCUM035043); F: *Ovophis monticola* (SCUM035030); G: *Cryptelytrops albolabris* (SCUM035008); *H: Viridovipera yunnanensis* (SCUM035045); I: *V. stejnegeri* (SCUM035053).

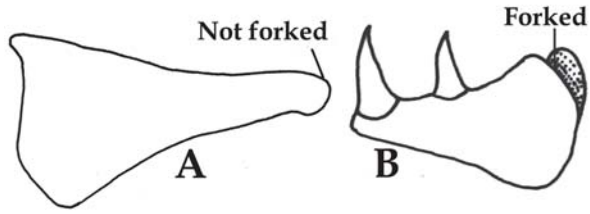

FIG. 5 . Two types of palatine (A: not forked; B: forked).

SQUAMOSAL

The squamosal is a thin, flat bone, lying on the posterolateral corner of the parietal. The shape and relative length of this bone vary for each species. In *Ovophis monticola* and *Cryptelytrops albolabris*, the squamosal has an externally lateral process at its end. In *Protobothrops flavoviridis* and *Protobothrops mucrosquamatu*s, it has a hook at its end. Some species (for example, *Zhaoermia mangshanensis*, *Protobotrops xiangchengensis*) have both the above conditions (Fig. 3).

The relative length of the squamosal to the skull is about 0.30 in most species, but that of *Ovophis monticola* is 0.38. With the exception of *Protobothrops xiangchengensis*, the squamosals of all species examined extend beyond the braincase.

QUADRATE

The shape of this bone shows little variation among the species examined. The ratio of the quadrate length to the skull is about 0.45 for most species except *Cryptelytrops albolabris* and *Zhaoermia mangshanensis* (Table 1).

PALATINE

This lies between, but does not articulate with, the medial wall of the maxilla and the lateral edge of the vomer. The shape of the palatine and whether it is posteriorly forked or not are characters of some mportance. In the four *Protobothrops* species, *Zhaoermia mangshanenis*, *Cryptelytrops albolabris* and *Ovophis monticola*, the palatines are triangular, but only the latter two are forked; those of *Viridovipera stejnegeri* and *V. yunnanensis* are crescent-shaped and forked (Figs 4 and 5).

PTERYGOID

The pterygoid is a toothed bone. It is narrow, and articulates with the palatine anteriorly and joins with the articular bone. The teeth are present anteriorly. Previous studies indicated that the shape of the posterior portion of the pterygoid, the curvature of the medial and lateral edges, the position of the ectopterygoid junction and the size and shape of the ridge on the ven-

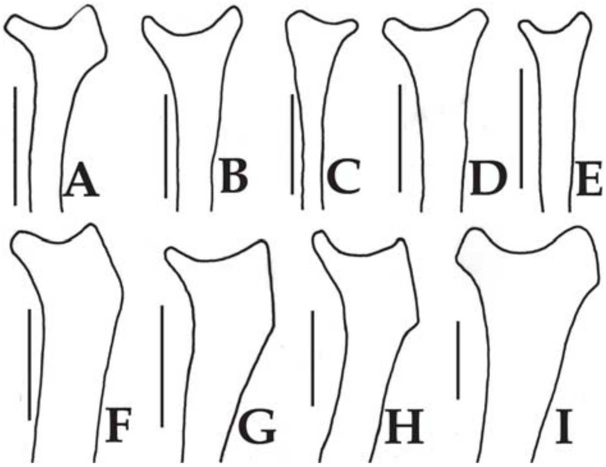

FIG. 6. Ectopterygoids of nine Asian pit vipers (right dorsal view except C). A: *Ovophis monticola* (SCUM035030); B: *Protobothrops flavoviridis* (SCUM035056); C: *P. jerdonii* (SCUM035041, left); D: *P. mucrosquamatus* (SCUM035026); E: *P. xiangchengensis* (SCUM035043); F: *Cryptelytrops albolabris* (SCUM035008); G: *Viridovipera stejnegeri* (SCUM035053); H: *V. yunnanensis* (SCUM035045); I: *Zhaoermia mangshanensis* (SCUM035024).

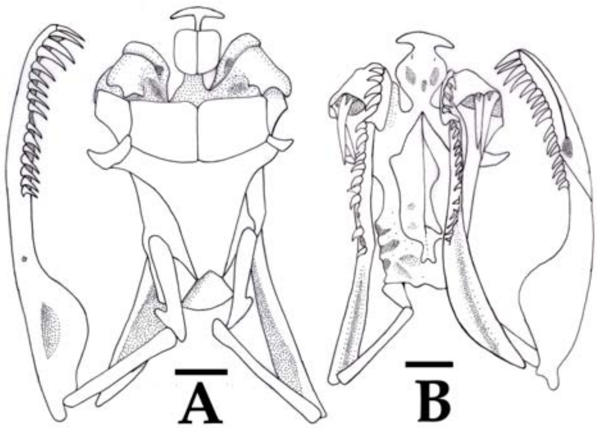

FIG. 7. The skull of *Ovophis monticola* (SCUM035083). A: dorsal view; B: ventral view.

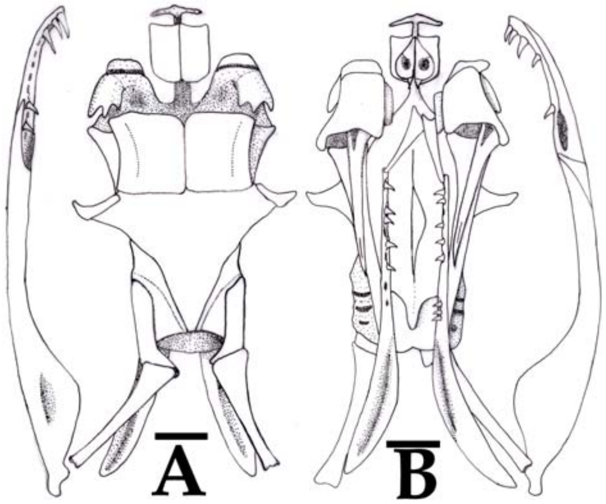

FIG. 8. The skull of *Protobothrops flavoviridis* (SCUM035056). A: dorsal view; B: ventral view.

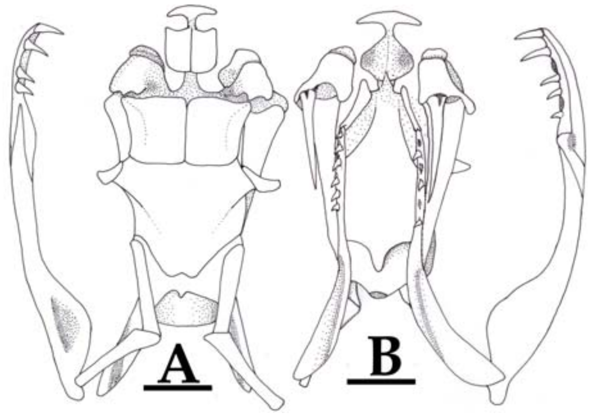

FIG. 9. The skull of *P. jerdonii* (SCUM035075). A: dorsal view; B: ventral view.

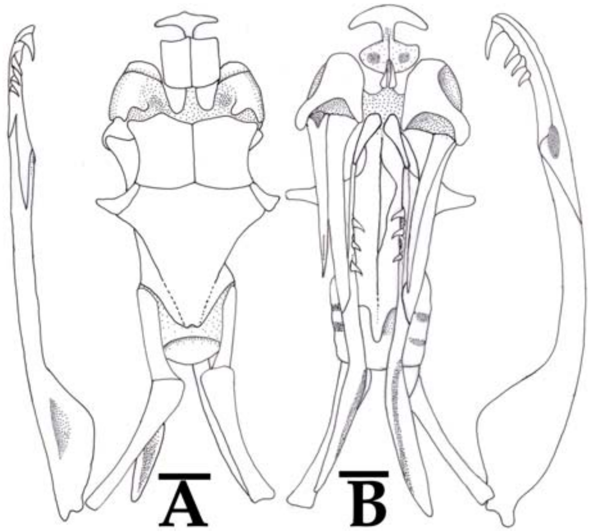

FIG. 10. The skull of *P. mucrosquamatus* (SCUM035050). A: dorsal view; B: ventral view.

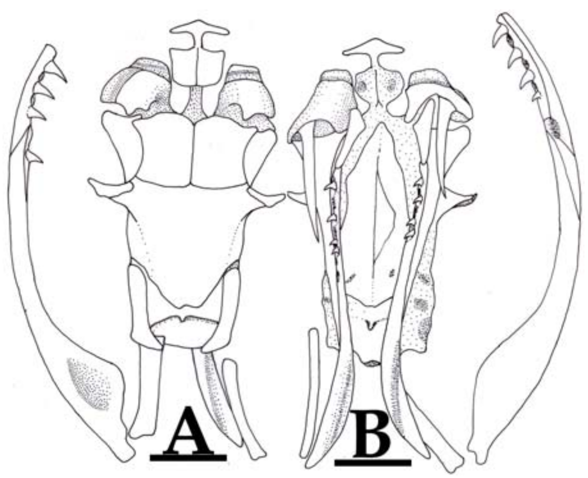

FIG. 11. The skull of *P. xiangchengensis* (SCUM035042). A: dorsal view; B: ventral view.

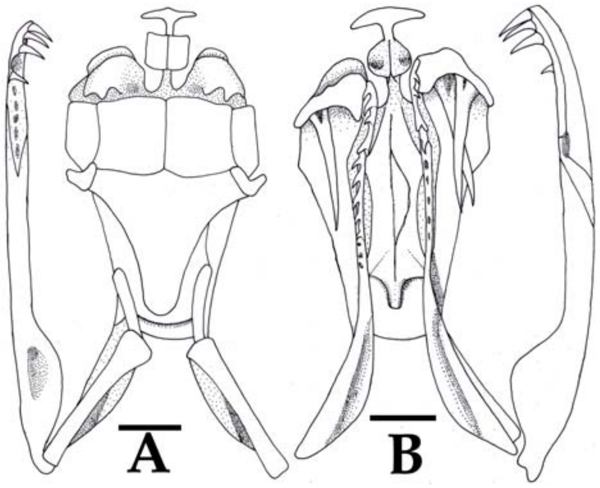

FIG. 12. The skull of *Cryptelytrops albolabris* (SCUM035009). A: dorsal view; B: ventral view.

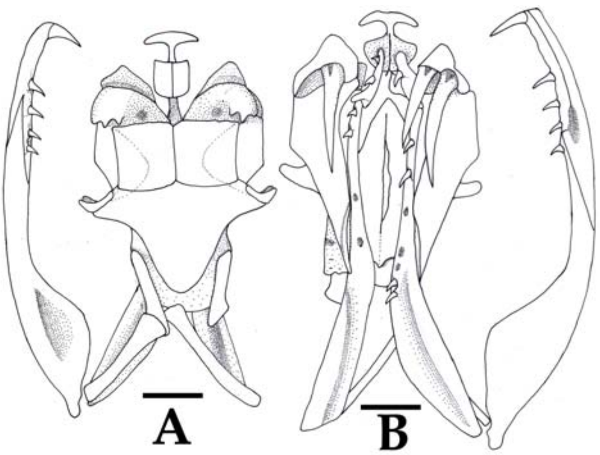

FIG. 13. The skull of *Viridovipera stejnegeri* (SCUM035079). A: dorsal view; B: ventral view.

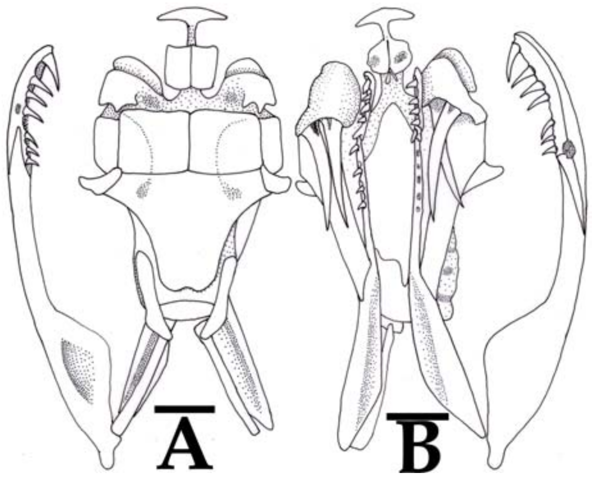

FIG. 14. The skull of *V. yunnanensis* (SCUM035045). A:

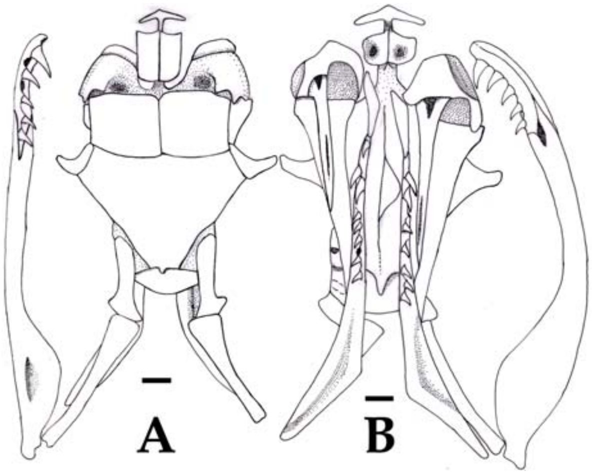

FIG. 15. The skull of *Zhaoermia mangshanensis* (SCUM035024). A: dorsal view; B: ventral view.

tral surface of the pterygoid were all quite characteristic of each species (Brattstrom, 1964). However, these characters are difficult to clarify and describe, and thus their value in determining relationships is limited.

The relative length of the pterygoid to the skull varies slightly, and in most species is about 1.0.

ECTOPTERYGOID

The ectopterygoid is usually forked anteriorly. In all species examined in this study the shape of this fork shows no variation, but the lateral process of the fork is much different among species (Fig. 6). This process is narrow in the four species of *Protobothrops* and *Zhaoermia mangshanensis*, whereas it is broad in *Ovophis monticola*, *Viridovipera stejnegeri*, *V. yunnanensis* and *Cryptelytrops albolabris*.

LOWER JAW

The lower jaw is compound, containing four bones: the angular, splenial, dentary and articular. Both the angular and splenial are located on the medial side of the lower jaw. The angular and splenial are distinctly separate in all the species examined except *Ovophis monticola*.

The ratio of the lower jaw length to the skull is between 1.30 and 1.40, but in *Zhaoermia mangshanensis* is 1.58.

BASISPHENOID AND BASIOCCIPITAL

Both bones are located in the ventral braincase. A thin ventral process is present in both. The height of the ventral process shows interspecific variation: it is lowest in *Viridovipera stejnegeri* and *V. yunnanensis*, moderate in *Protobothrops xiangchengensis*, *P. jerdonii* and *Cryptelytrops albolabris*, and highest in the other four species.

DISCUSSION

The description of some bones and the comparison of 19 characters (Table 1) indicate that (1) skull morphology differs among species, and each species can be identified by its skull features, although the degree of interspecific differentiation varies to some extent; (2) no intraspecific differences in most skull characters can be detected among the species examined with theexception of whether the postfrontal touches the frontal or not; (3) the shape of the palatine, the size of the ectopterygoid anterior lateral process and the shape of the frontal are stable characters within species, and even within genera: they are therefore important for specific identification and classification.

COMPARISON WITH PREVIOUS STUDIES OF SKULL MORPHOLOGY

The present results are consistent with most of the previous conclusions (Brattstrom, 1964; Burger, 1971; Hoge & Romano-Hoge, 1983; Zhang, 1993; Zhang & Zhao, 1990) with the exception of those described below. Zhang (1993) proposed that "the squamosal of *O. monticola* is short and narrow, its posterior end becomes thin and does not extend beyond the braincase; its length relative to skull length 0.24; the dentary teeth 11–12". However, on the basis of the four specimens of *O. monticola* studied here, the posterior end of the squamosal extends beyond the braincase, the relative length of the squamosal to the skull is 0.38, and the dentary teeth number is 17–18. 2. Based on a skull morphological comparison of six species of *Trimeresurus sensu lato*, Zhang & Zhao (1990) suggested that the postfrontals of these species touched the frontal except in *Protobothrops xiangchengensis*. However, the results presented here show that only *Zhaoermia mangshanensis*, *O. monticola*, *P. flavoviridis* and *Viridovipera stejnegeri* share the stable condition that the postfrontal touches frontal. Among other species, intraspecific variation was detected. Even in *P. mucrosquamatus* and *P. xiangchengensis*, both conditions of this character (postfrontal touches frontal or not) were found in an individual.

PROTOBOTHROPS (HOGE & ROMANO-HOGE, 1983)

The systematic position of *Trimeresurus xiangchengensis* (Zhao *et al.*, 1978), is controversial (see Guo & Zhao, 2004). Recently, based on three mitochondrial gene fragments (12S rRNA, 16S rRNA, cytochrome *b*), phylogenetic analysis indicated that *xiangchengensis* should be a member of *Protobothrops*, and that it is more closely related to *P. jerdonii* than to *P. mucrosquamatus* (Guo *et al.*, unpubl. data). In skull morphology, *Protobothrops xiangchengensis* is greatly distinct from *Viridovipera stejnegeri*, *V. yunnanensis* and *Cryptelytrops albolabris* in the shape of the palatine and the ectopterygoid anterior lateral process. However, this species shares many characters with *P. flavoviridis*, *P. jerdonii* and *P. mucrosquamatus*. These include: (1) palatine triangular, not forked, and generally edentulous; (2) ectopterygoid anterior lateral process not broad; (3) frontal rectangular (longer than wide); (4) head length twice the width. Additionally, they show some similarities in external features. Hence, the placement of *xiangchengensis* into *Protobothrops* is supported morphologically.

Among *Protobothrops* species, *P. xiangchengensis* is very different from *P. mucrosquamatus* in the following skull characters: (1) the projection on the border of the cavity is absent in *P. xiangchengsis*, but present in *P. mucrosquamatus*; (2) the squamosal of *P. xiangchengensis* does not extend beyond the braincase, but that of *P. mucrosquamatus* does; (3) *P. xiangchengensis* has many more pterygoid teeth than *P. mucrosquamatus* (eight versus five on average) and its pterygoid teeth extend beyond the anterior margin of articulation with the ectopterygoid; (4) the two species are distinct in the height of the ventral process of the basioccipital and basisphenoid, and the ratio of head length to head width. Obviously, *P. mucrosquamatus* and *P. xiangchengensis* should be considered two morphologically distinct species, which is consistent with molecular analysis (Guo *et al.*, unpubl. data).

In the description of *Protobothrops*, Hoge & Romano-Hoge (1983) proposed that a projection was absent on the border of the pit cavity. However, another state, in which a projection is present on the border of the pit cavity, was detected in *P. jerdonii* and *P. xiangchengensis* (Table 1) in this paper. Hence, the presence of a projection in the pit cavity cannot be regarded as one of the generic characters of *Protobothrops*.

Additionally, the species of *Protobothrops* share several characters that can distinguish them from the other genera; for example, the relative ratio of the frontal length to width is 1.25–1.50, and the head is clearly elongate, with its length being twice its width.

ZHAOERMIA (GUMPRECHT AND TILLACK, 2004)

Zhang (1993) proposed the genus *Ermia*, which was later replaced by *Zhaoermia* (Gumprecht & Tillack, 2004), based on external and skull features of *Trimeresurus mangshanensis*. *Zhaoermia mangshanensis* is distinct from the other species examined in its unique parietal shape (see above). The shape of the frontal and the relative length of the quadrate to the skull are also different from those of the other species examined.

Among the nine species studied, *Zhaoermia mangshanensis* shares more characters with *Protobothrops* species than with the others. First, the palatine is triangular, not forked, and generally without teeth. Second, the ectopterygoid anterior lateral process is not broad. Third, the shape of the parietal is triangular. The above similarities further strengthen the suggestion that *Zhaoermia* is closely related to *Protobothrops* (Malhotra & Thorpe, 2004; Guo *et al.*, unpubl. data).

OVOPHIS (BURGER, IN HOGE AND ROMANO-HOGE, 1981)

In his unpublished dissertation, Burger (1971) put forward *Ovophis*. Subsequently, Hoge & Romano-Hoge (1981) formally published the diagnosis of this genus. Combining Burger's (1971) work with the present study, *Ovophis monticola* shows the following characters that are distinct from other genera: (1) the maxillary does not possess a projection on the border of the cavity; (2) it has a triangular, tall, forked palatine (Fig. 4F); (3) the palatine teeth number 3–4; 4) it has many more dentary teeth (17–18) and pterygoid teeth (13–15); (5) the ectopterygoid anterior lateral process is very broad; (6) it has a T-shaped parietal. The shape of the palatine and the number of dentary and ectopterygoid teeth are unique for this species among the species examined.

TRIMERESURUS (LACEPEDE, 1804)

Viridovipera stejnegeri, *V. yunnanensis*, and *Cryptelytrops albolabris* were assigned to *Trimeresurus* (*sensu stricto*) previously (David & Ineich, 1999; McDiarmid *et al.*, 1999). Recently, taking hemipenial characters and molecular analysis results into account, Malhotra & Thorpe (2004) proposed a new genus *Viridovipera*, and revalidated *Cryptelytrops*. According to their description of the two genera, *stejnegeri* and *yunnanensis* should be placed into the former, and *albolabris* into the latter. The hemipenis of *V. stejnegeri* and *V. yunnanensis* is forked shallowly, calyculate distally and spinous proximally; but that of *C. albolabris* is long and slender, the distal third is calyculate and the remainder is papillose (Guo & Zhang, 2001; Guo, 2000; Guo *et al.*, 2006). In this study, *V. stejnegeri* shares several characters with *V. yunnanensis* relative to *C. albolabris*: (1) the palatine is crescent shaped (Fig. 4D, I); (2) a wider head (the ratio of skull length to width is 1.60 in *V. stejnegeri* and 1.72 in *V. yunnanensis*, versus 2.11 in *C. albolabris*) (Table 1); (3) a lower process on the basiocciptical and basisphenoid. The distinct morphological differences between the two species of *Viridovipera* and *C. albolabris* indicate that they should be placed in different groups, and thus support the reclassification of these three species proposed by Malhotra & Thorpe (2004).

CONCLUSION

The skulls of nine Asian pit vipers were examined, described and figured in order to re-evaluate the taxonomy of pit vipers. Most bones, such as the palatine, squamosal and parietal, are relatively constant and distinctive for each species and hence useful in identifying species, taxonomy and determining relationships. The relationships indicated by skull morphology among these nine pit vipers are mostly consistent with those proposed by molecular analyses. Although the specimens and species examined in this study are not enough to clarify all of the relationships, it is an important step toward resolving the taxonomy and phylogeny of this group.

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APPENDIX 1: SPECIMENS EXAMINED

SCUM: Sichuan University Museum.

Ovophis monticola
Huili, Sichuan: SCUM035082-83, SCUM035040. Anxian, Sichuan: SCUM035030.

Protobothrops flavoviridis
Japan: SCUM035056.

P. jerdonii
Anxian, Sichuan: SCUM035028-29. Huili, Sichuan: SCUM035041, SCUM035075. Ruoergai, Sichuan: SCUM035081. Qingling, Shaanxi: SCUM035078.

P. mucrosquamatus
Yibin, Sichuan: SCUM035026. Hongya, Sichuan: SCUM035031-32, SCUM035076. Chengdu, Sichuan: SCUM035050.

P. xiangchengensis
Jiulong, Sichuan: SCUM035042-43, SCUM035046.

Cryptelytrops albolabris
Danzhou, Hainan: SCUM035007-9.

Viridovipera stejnegeri
Qunzhong, Hainan: SCUM035013-14. Hejiang, Sichuan: SCUM035053. Guangdong: SCUM035079.

V. yunnanensis
Huili, Sichuan: SCUM035037, SCUM035045, SCUM035114. Kunming, Yunnan: SCUM035077.

Zhaoermia mangshanensis
Yizhang, Hunan: SCUM035024.