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Triceratolepidophis sieversorum, A NEW GENUS AND SPECIES OF PITVIPER (REPTILIA: SERPENTES: VIPERIDAE: CROTALINAE) FROM VIETNAM

Thomas Ziegler,[1] Hans-Werner Herrmann,[2] Patrick David,[3] Nikolai L. Orlov,[4] and Olivier S. G. Pauwels[5]

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A new genus and species of pitviper from the Annam Mountain Range, Quang Binh Province, Vietnam are described. The description is based on a single male specimen. This member of the *Trimeresurus* group is characterized by the presence of raised horn-like multiple supraoculars and by having the unique structure of the dorsal scales showing a keel consisting of three horn-like upraisings as well as the unique microdermatoglyphic pattern of the Oberhäutchen, which is tessellate fimbriate. First notes on its biology are provided and possible relationships of this new and striking taxon are discussed.

Key Words: Reptilia, Squamata, Serpentes, Viperidae, Crotalinae, *Triceratolepidophis* genus nov., *Triceratolepidophis sieversorum* species nov., Phong Nha Nature Reserve, Vietnam.

INTRODUCTION

Within the last 25 years, the snake fauna of Vietnam has been the subject of a renewal of interest from both native and foreign herpetologists. Although it is still imperfectly known, the number of recorded species has increased considerably. One striking example may be obtained in merely comparing two overviews of the fauna of a herpetologically well known area, the Tam Dào ridge in Northern Vietnam, which appeared in Bourret (1935) and Orlov et al. (2000), respectively. The number of recognized species has increased during this period from about 43 to 87 species. With consideration that many parts of Vietnam, especially in the center of the country, have not yet received attention from herpetologists, it is obvious that a good number of reptile taxa are yet to be discovered.

In the progress of current field studies in the Phong Nha Karst Forest Nature Reserve in the Quang Binh Province (Ziegler and Herrmann, 2000; Herrmann and Pagel, 2000), a remarkable horned crotaline snake was discovered. According to David and Ineich (1999), 11 species of crotaline snakes are currently recognized for Vietnam, namely *Calloselasma rhodostoma* (Boie, 1827), *Deinagkistrodon acutus* (Gunther, 1888), *Ovophis monticola* (Gunther, 1864), *O. tonkinensis* (Bourret, 1934), *Protobothrops jerdonii* (Gunther, 1875), *P. mucrosquamatus* (Cantor, 1839), *Trimeresurus albolabris* (Gray, 1842), *T. cornutus* Smith, 1930, *T. macrops* Kramer, 1977, *T. popeiorum* Smith, 1937, and *T. stejnegeri* Schmidt, 1925 (see also Nguyên and Hô, 1996; Orlov, 1998; Orlov et al., 2000). Furthermore, Bourret (1936) and Nguyên and Hô (1996) listed from South Vietnam the Indo-Malayan pitviper *Tropidolaemus wagleri* Wagler, 1830 (as *Trimeresurus wagleri*, see also Orlov, 1999).

Among all these species, *Trimeresurus cornutus* Smith, 1930 is the sole species to possess distinctly raised, horn-like enlarged supraoculars (Pope, 1935:404; Bourret, 1936:475; Smith, 1943:514). Due to this striking morphological feature, and according to the key provided by David and Tong (1997), the single collected specimen from Phong Nha was pro-

[1] Staatliche Naturhistorische Sammlungen Dresden, Museum für Tierkunde, A. B. Meyer-Bau, Königsbrücker Landstraße 159, D-01109 Dresden, Germany. E-mail: ziegler@snsd.de

[2] Kölner Aquarium am Zoo, Riehler Straße 173, D-50735 Köln, Germany. E-mail: hwherrmann@zoo-koeln.de

[3] Laboratoire des Reptiles et Amphibiens, Muséum National d'Histoire Naturelle, 25 rue Cuvier, F-75005 Paris, France. E-mail: pdavid@mnhn.fr

[4] Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St. Petersburg 199034, Russia. E-mail: agama@NA4755.spb.edu

[5] Department of Recent Vertebrates, Institut Royal des Sciences naturelles de Belgique, 29 rue Vautier, B-1000 Brussels, Belgium. E-mail: osgpauwels@hotmail.com

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visionally assigned to *Trimeresurus cornutus* by Ziegler and Herrmann (1999:252 – 253) in the Programme and Abstracts Volume of the 10th Ordinary General Meeting of the Societas Europaea Herpetologica (SEH). *T. cornutus* is a very rare species endemic to Vietnam, of which only three specimens are known. Two were collected in North Vietnam, including the holotype (BMNH 1946.1.19.25, formerly BMNH 1930.11.16.2; from "Fan-si-pan Mts., Tonking," now Mt. Fan Si Pan, Lai Châu Province). A further specimen was collected in the 1940's from the resort station of Bach Ma, Thua Thien-Hue Province, southern Vietnam, and was reported in Campden-Main (1970), Trân et al. (1992), Nguyên and Hô (1996), Orlov (1998), and McDiarmid et al. (1999). Although this specimen is now lost, its existence and description were recently confirmed to P.D. (J. Vidal, personal communication, June 2000).

However, as stated in Ziegler and Herrmann (2000:56 – 57), a more detailed comparison between the horned crotaline specimen from Phong Nha Nature Reserve with the original description of *T. cornutus* (Smith, 1930) showed distinct differences in the scalation and pattern of the two forms. Such distinctions were subsequently confirmed by comparisons with the holotype of *Trimeresurus cornutus* and the second known specimen of *T. cornutus* (MNHN 1937.35).

Moreover, comparisons of morphological features with representatives of all other crotaline snakes of that region clearly confirmed the unique taxonomic status of the Phong Nha specimen. Its distinctive dorsal scale morphology thus compelled us to assign this snake to a new species and genus, which are described below. The unique macroscopic structure of dorsal scales led us to examine the microdermatoglyphic pattern of these scales by Scanning Electron Microscopy (SEM), a tool which proved to be useful in snake taxonomy (Pauwels et al., 2000). Possible relationships of this new and striking taxon are discussed and some data on its biology are provided.

MATERIAL AND METHODS

This study is based both on morphological data and SEM analysis of microdermatoglyphic patterns of dorsal scales. Because of the uniqueness of the available specimen, we refrained from attempting to remove and examine any part of the skull, especially the maxilla, or skeleton, such as the vertebrae, in spite of the importance of these elements. The results of currently prepared x-ray photographs will be published elsewhere.

Measurements on preserved specimens were taken with a slide-caliper to the nearest 0.05 mm. Head morphometric data were taken only on adult specimens to avoid biased results due to the proportionally larger head and eyes in juveniles. Abbreviations of measurements (in mm) used in the text and tables are as follows: **SVL**) snout-vent length, from snout tip to cloaca; **TaL**) tail length, from cloaca to tail tip; **TL**) total length (**SVL** + **TaL**); **HL**) head length, from snout tip to rear of maxilla. Abbreviations of meristic characters are: **Ven**) ventral scales; **SubC**) subcaudal scales; **Co(m)**) dorsal scale rows at midbody (see below); **SpL**) supralabials. Other abbreviation: **a.s.l.**) above sea level. Terminology of genital morphology follows Ziegler and Böhme (1997).

The number of ventral scales is counted after Dowling (1951). Preventrals, as understood here, are the scales wider than long but not in contact with the first row of dorsals. The number of subcaudals does not include the terminal scute. The numbers of dorsal scale rows are counted at one head length behind head, at midbody (i.e., at the level of the ventral plate corresponding to a half number of the total ventrals), and at one head length before vent, respectively. Values for symmetric head characters are given in left/right order.

The SEM was conducted following the procedure described in Joger and Courage (1999). An array of scales from the left lateral body side (between ventral 106 and 109, between dorsal 5 and 9 counted from the first dorsal bordering the ventral "paraventral" on the left body side) of the alcohol-preserved holotype exhibiting an intact Oberhäutchen (*supra epidermis*) was taken. This skin fragment was attached to a metal plate and coated with gold. The scanning electron microscope used was a Hitachi S-530 with 25 cm distance to the object and a voltage of 25 kV. Photographs were taken from several angles with magnifications ranging from 20 to 3000 times on Ilford Pan F 6 × 6.

A list of examined specimens in the framework of this paper is given in the Appendix. Museum abbreviations are as follows: **BMNH**) The Natural History Museum, London; **CIB**) Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu, China; **MNHN**) Muséum National d'Histoire Naturelle, Paris; **ZFMK**) Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.

RESULTS

The specimen from the Phong Nha area presents the typical external morphological characters of Asian crotaline members of the *Trimeresurus* group, as defined by Brattstrom (1964) and Burger (1971): the presence of a loreal pit, a nostril in the center of the nasal scale, the presence of a nasal pore in the posterior wall of the nostril, small, irregular fragmented upper cephalic scales, the presence of two upper preoculars and one lower preocular bordering the loreal pit, smooth scales covering upper snout surface, unkeeled chin and gular scales, and a single anal plate. On another hand, it shows such an unusual combination of morphological features that we assign it to both a new genus and species, which we herein successively name as:

Triceratolepidophis genus nov.
(Figs. 1 – 8)

Type species. *Triceratolepidophis sieversorum* sp. nov. herein described.

Diagnosis. A genus of Asian pitviper belonging to the *Trimeresurus* group, characterized by a large size, reaching at least 1255 mm; elongated head and body; the presence of a nasal pore; strongly keeled dorsal scales, bearing an elongated longitudinal keel covering at least two thirds of the length of the scale, made of a series of three consecutive horns or crests, high and wide, rising progressively from front to back, separated by two lower but distinctively elevated parts (Fig. 7*a* – *d*), producing very strongly keeled dorsal scales; a tessellate fimbriate microdermatoglyphic pattern of dorsal scales with distinctly raised fimbriae; raised, horn-like multiple supraoculars; cephalic scales on upper head surface between supraoculars distinctly keeled for a part, all becoming progressively strongly keeled towards the occipital region; and a grayish brown ground color with a blotched dorsal pattern.

Triceratolepidophis, although sharing several morphological similarities with other members of the genera *Trimeresurus* and *Protobothrops*, such as the ground color, blotched dorsal pattern, the upraised supraoculars and head scalation, differs from all other Asian crotaline genera currently recognized in David and Ineich (1999), namely *Calloselasma* Cope, 1860, *Deinagkistrodon* Gloyd, 1979, *Ermia* Zhang, 1993, *Gloydius* Hoge and Romano Hoge, 1981, *Hypnale* Fitzinger, 1843, *Ovophis* Burger *in* Hoge and Romano Hoge, 1981, *Protobothrops* Hoge and Romano Hoge, 1983, *Trimeresurus* Lacepède, 1804, and *Tropidolaemus* Wagler, 1830, by the unique autapomorph scale structure as well as the unique microdermatoglyphic pattern of the Oberhäutchen, which is tessellate fimbriate due to the upraising of the fimbriae. This structure is unique in the *Trimeresurus* group, in which other species have only the tessellate pattern typical of the Crotalinae and is further discussed below.

Distribution. At present known only from Vietnam, at the type locality of the sole included species, although its occurrence in eastern Laos is likely.

Etymology. The generic nomen *Triceratolepidophis* is derived from the Greek words tri meaning "three," keras meaning "horn," lepis meaning "scale," and ophis, meaning "snake." It describes the unique structure of the dorsal scales, ornated with a strong keel composed of three consecutive horn/crest-like ornamentations, found in different degrees of pronounciation in all dorsal parts of the body except the head and the neck region. This generic nomen is masculine in gender. We suggest the following common generic names in English/French/German respectively: Three horned-scale pitvipers/Triceratolépidophides/Dreihornschuppen-Grubenottern.

Contents. This genus at present contains only one species, *Triceratolepidophis sieversorum* sp. nov., the description of which is given as:

Triceratolepidophis sieversorum species nov.
(Figs. 1 – 8)

Holotype. ZFMK 71262, adult male, from Phong Nha (village), Phong Nha Nature Reserve, Quang Binh Province, Vietnam, ~100 m a.s.l.; collected by a local "medicine man" during the first half-year of 1999.

Diagnosis. An Asian pitviper of the *Trimeresurus* group, characterized by the main diagnostic features given above for the genus, namely a large size, at least up to 1255 mm; elongated head and body; strongly keeled dorsal scales due to the presence on most of them of an elongated longitudinal keel made of a series of three consecutive, high and wide horn/crest-like summits, rising progressively from front to back, separated by two lower but distinctively elevated parts (Fig. 7*a* – *d*); the tessellate fimbriate microdermatoglyphic pattern of dorsal scales; raised, horn-like multiple supraoculars; cephalic scales between supraoculars keeled for a part and becoming progressively strongly keeled backwards on the occipital region; and an overall grayish ground color. Other diagnostic characters include the following features: 23 dorsal scale rows at midbody; high

numbers of ventral and subcaudal plates, 228 and 82 respectively; 8 – 9 supralabials, first totally separated from nasal, the longest being numbers 4 and 5; upper preocular divided into 3 consecutive small scales, from front to back one large and two small; a single true loreal; 5th supralabial approximately as high and wide as the 4th; and a lower row of temporals much larger than upper rows.

This species is distinguishable from all other Asian pitvipers by the unique macro- and microstructures of the dorsal scales. The combination of other morphological characters are also sufficient to separate this species from all other known Asian pitvipers. However, the ground color and horn-like supraoculars make it superficially similar to some other members of the genus *Trimeresurus*, namely *T. cornutus* and *T. puniceus*. Nevertheless, general habitus, color and pattern as well as meristic characters are shared by several species of the genus *Protobothrops*, especially *P. mucrosquamatus.*

From the other horned species of the *Trimeresurus* group, *Triceratolepidophis sieversorum* is immediately distinguished by the strongly and uniquely keeled dorsal scales; furthermore, the structure of the supraoculars is different from *T. cornutus*, in which the 3 or 4 horns are convergent and confluent at their tips, whereas they are divergent and free in the new species. From the Indo-Malayan *T. puniceus*, it differs by the diagnostic characters given above, and much higher numbers of ventral and subcaudal plates. Other Indo-Malayan horned species, *T. borneensis* Peters, 1872 and *T. brongersmai* Hoge, 1969, also exhibit much lower numbers of ventral and subcaudal plates, and a strongly projected spatulate nose.

From *Protobothrops mucrosquamatus*, to which superficially it is quite similar, this new taxon differs by the keels of the dorsal scales as well as a completely different microdermatoglyphic pattern, which is typically tessellate in *P. mucrosquamatus*, but also by the presence of raised supraoculars and an upper preocular divided into 3 scales instead of two as in *P. mucrosquamatus*. However, the morphological similarities of these two species deserve more attention and are dealt with at length in the Discussion.

Description of the holotype (Figs. 1 – 8). The specimen, although in good condition, is injured on the head posteriorly, at the neck and at mid body. Furthermore the tail is almost completely disrupted from the body about 10 mm posterior from the cloaca. The missing rectangular piece of skin visible in Fig. 1 was removed for the purpose of SEM analysis.

Morphology. Body rather elongate for a member of the *Trimeresurus* group, cylindrical but distinctly laterally compressed; head triangular, large, flattened, rather short, only 3.9% of SVL, 1.9 times as long as wide, clearly distinct from the neck; snout elongate, accounting for 24.2% of total head length, 2.2 times as long as diameter of eye, flattened, rounded when seen from above, rather rectangular when seen from lateral side, with a very distinct and sharp canthus rostralis; eye rather small, eye diameter/distance between lower margin of eye and upper lip border ratio 0.74 (mean value of both sides); nostril-loreal pit distance/nostril-eye distance ratio 0.48 (mean value of both sides); tail quite short, cylindrical, tapering, not prehensile.

Measurements. SVL: 1045 mm; TaL: 210 mm; TL: 1255 mm; HL: 41.90 mm; ratio TaL/TL: 0.17.

Body scalation. Ven: 228 (+ 2 preventrals); SubC: 82, paired, plus one terminal scale; anal entire.

Dorsal scales. 33-23-17 scales, rhomboid, strongly keeled throughout, including the outermost row, due to the presence of the elongate longitudinal keel made of three consecutive horns or crests, high and wide, separated by two lower parts; first dorsal row enlarged, while others, including the vertebral row, are similar in size.

Dorsal scale row reductions, from 23 to 17 rows, are as follows (23 rows at Ven 30; reductions before ventral 30 were not considered):

3+4 (Ven 129)	4+5 (Ven 136)	3+4 (Ven 156)	(right)
23	21	19	17
4+5 (Ven 132)	4+5 (Ven 138)	3+4 (Ven 151)	(left)

Macrostructure. The unique scale structure, characterized by the elongated longitudinal keel from which emerges a series of three consecutive crest-like high and wide horns, separated by lower but yet elevated parts, producing very strongly keeled dorsal scales, is clearly present on all dorsal scales from the level of the 30th ventral onwards, except for the vertebral row which is smooth. This structure is also absent from preventrals, ventrals, anal and subcaudals. On the tail, the three crests are connected, forming a serrated, three tipped keel, with the keeling becoming less pronounced towards the end of the tail. This unique scale structure gives the snake a somewhat rough or abrasive appearance, especially pronounced in the region of midbody.

Microstructure. Perpendicular to the scale central axis bearing the peculiar triple crests, the scale shows shallow furrows (Fig. 7*e*) which are observable on the specimen through a standard microscope. At higher magnifications by SEM (Fig. 7*f*), the scale

surface appears covered with clearly delimited polygonal Oberhäutchen cells, the whole surface of which is bulged. As can be seen in Fig. 7*e*, the microdermatoglyphic relief is attenuated on the surface of each of the three horns of the keels. In Fig. 7*g*, one can detect the superimposition of the staggered delimitations of clear-layer cells and Oberhäutchen cells. The highest magnification (Fig. 7*h*) reveals a fimbriate microdermatoglyphic pattern (sensu Price, 1982:296) with long, erect fimbriae.

Head morphology and scalation. Nasal pore present on posterior wall of nostril; rostral 1.6 times broader than high, triangular, visible from above; nasal rectangular, elongated, with the anterior part larger than posterior half and turning up onto the *canthus rostralis*; 1.3 or 1.4 times as long as high, vertically divided in totality, with large nostril in its middle; one pair of much enlarged and elongated, rectangular internasals, 2.5 times as wide as deep, approximately 2.5 times as long and 1.2 times as wide as the adjacent upper snout scales, separated by two small, triangular scales, slightly larger than adjacent snout scales; 9 small scales on the snout on a line between the scales separating internasals and a line connecting the anterior margin of the eyes, not enlarged and of same sizes as cephalic scales; 5/5 subequal canthal scales bordering the *canthus rostralis* between internasal and corresponding supraocular, slightly enlarged compared with adjacent snout scales; 1/1 loreal located between the foremost upper preocular and nasal (see *Discussion*); 3 preoculars, the upper one divided into 3 consecutive small scales, the rearmost much enlarged and irregularly subrectangular, two foremost ones short and small, the first one being in contact with the loreal (see *Discussion*); central preocular elongated and in contact with the loreal; lower preocular forming lower margin of loreal pit; 3/3 postoculars; 2 supraoculars on each side, rather small, triangular but vertically raised and divergent, projecting slightly beyond the border of the head, each about 2 – 3 mm high, much wider than the adjacent upper head scales but only 0.8 times as wide as internasals, indented by upper head scales, bordered by enlarged and keeled flat cephalic scales; scales on upper surface of head and snout relatively small, rounded or irregular in shape, unequal, flat, smooth on the middle of the head, keeled on its margin, all becoming progressively keeled backwards, strongly keeled and swollen on the occipital region; 15 scales on a line between supraoculars; temporals very unequal, in 3 rows: lower row smooth, much enlarged, distinctly larger than posterior supralabials, 2nd row enlarged, slightly keeled, and upper row small but very strongly keeled; 1/1 thin, elongated, crescent-like subocular; 9 (left)/8 (right) SpL; 1st SpL short, longer than high, totally separated from nasal on both sides; 2nd SpL high, entire at right, partly divided by a transversal suture at left but forming on each side the anterior border of loreal pit, separated from the nasal by 2 small irregular scales on each side; 3rd SpL enlarged, approximately 1.5 times as long as high, separated from the subocular by 2 scales on each side; 4th SpL shorter (about 80%) than 3rd but slightly longer, separated from subocular by 4 scales at right and 3 scales at left; 5th SpL of about same size as 4th; other posterior supralabials slightly smaller than 4th, separated from subocular by 4 rows of scales of similar size and in contact with first row of temporals; 14 (left)/13 (right) infralabials, first pair in contact with each other, first and second pairs in contact with chin shields; 9/9 rows of smooth gular scales; chin shields smooth, irregularly arranged. The elongated, narrow, slightly back-curved left solenoglyphous fang exhibits a total length of 12 mm.

Genital morphology. The everted left hemipenis is 23.5 mm long. It bears two lobes with the sperm groove forked at the truncus and from there extending straight to the lobe's ends. The truncus is partly covered with microspines. A large spine can be found laterally before the beginning of each lobe, followed above by medium and, especially on the inner sides of the lobes and around the sulcus spermaticus, by small spines. At the lobe's ends the spine ornamentation changes into a calyces ornamentation (see Fig. 8).

Coloration. In alcohol, the dorsal surface is light grayish brown, with a pattern running from the neck to the tail tip of large, irregular or rhomboedric dark grayish brown to almost black dorsal blotches, anterior and posterior more or less bordered black (Fig. 1); these blotches are either alternating along the vertebral line, sometimes confluent with their immediate neighbors on the same side, or more or less confluent and in opposition each with the other on each side of the vertebral line, producing larger blotches unconnected with those immediately forwards and backwards; a series of medium sized dark grayish brown lateral blotches (Fig. 6), partly edged with black, elongated and oval-shaped, located just below dorsal blotches but smaller than and unconnected with them, running from neck to the last two thirds of the tail; on approximately the last five centimeters of the tail these blotches are fused to build

Fig. 1. Dorsal view of the holotype of *Triceratolepidophis sieversorum*. Photograph by T. Ziegler.

Fig. 2. Ventral view of the holotype of *Triceratolepidophis sieversorum*. Photograph by T. Ziegler.

Fig. 3. Lateral view of the head of the holotype of *Triceratolepidophis sieversorum*. Photograph by T. Ziegler.

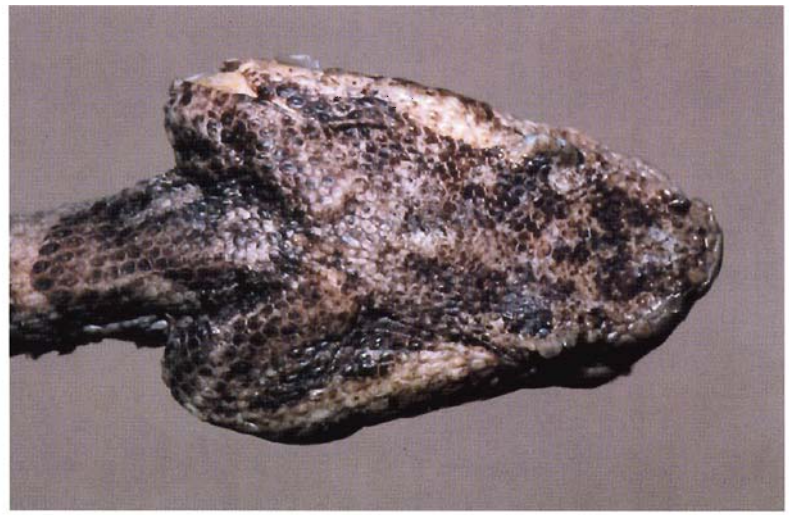

Fig. 4. Dorsal view of the head of the holotype of *Triceratolepidophis sieversorum*. Photograph by T. Ziegler.

Fig. 6. Lateral view of the body of the holotype of *Triceratolepidophis sieversorum*. Photograph by T. Ziegler.

Fig. 5. Ventral view of the head of the holotype of *Triceratolepidophis sieversorum*. Photograph by T. Ziegler.

larger dark areas, a few scales wide, which are separated by only a few light (beige or yellow) rings.

Upper head surface pale gray brown, patterned with dark brown markings (Figs. 3 – 4); lateral head surface beige to pale grayish brown, marked with dark brown vertical bars on infralabials and front supralabials; a broad dark brown stripe runs from eye to the respective mouth corner, topped above by another beige to light brown stripe.

Venter yellowish brown to beige, spotted in parts with gray brown (Fig. 2); outermost tips of ventral plates marked with large dark brown blotches; on the subcaudal plates, these blotches fuse with the lateral-dorsal dark pattern forming dark closed rings in the last two thirds of the tail. The dark marginal pattern of the ventrals and subcaudals increases in intensity from the neck to the tail; chin, infralabials and throat uniformly pale gray, with the exception of dark infralabial bars and some small dark spots (Fig. 5).

By analogy with species of the *Protobothrops* genus, especially *P. mucrosquamatus*, one may consider that the color and pattern in life are similar.

Etymology. The specific name is dedicated to Moritz and Julian Sievers (Bönningstedt) in recognition of the efforts of their father Dr. J.-H. Sievers in financially supporting zoological research and nature conservation in the Phong Nha Nature Reserve, Vietnam.

For this species, we suggest the following common specific names in English/French/German respectively: Sievers' three horned-scale pitviper/Triceratolépidophide des Sievers/Sievers Dreihornschuppen-Grubenotter.

Distribution. *Triceratolepidophis sieversorum* is currently known only from the type locality (see Fig. 9), in Quang Binh Province, Vietnam. This locality was described in detail in Ziegler and Herrmann (2000), to which we refer the reader for detailed information. To summarize, the Phong Nha Nature Reserve (Fig. 10), together with the adjacent limestone forest area Ke Bang, located on the eastern slopes of the Annam Mountain Range, cover a total of 148,000 ha and are one of the largest contiguous karst mountain areas in Vietnam. The elevation ranges from less than 100 m to ~1000 m a.s.l. The climate is tropical and the vegetation is dominated by primary and secondary limestone forest.

However, this complex karst massif is located immediately east to the border of Laos, into which it extends considerably westwards. It is likely that the new species also occurs in karstic regions of Laos, especially in the Hin Namno National Biodiversity

Conservation Area, a protected forested area of 86,500 ha lying in the Laotian part of the Annam mountains (Duckworth et al., 1999).

Biologically speaking, the Phong Nha – Ke Bang limestone area is a very rich region, with nearly 100 recorded species of amphibians and reptiles (Ziegler and Herrmann, 2000). The extremely high biodiversity and conservation value of the studied area is shown by the fact that more than 20% of the recorded species, among them ten snakes, are listed in the Red Data Book for Vietnam (Trân et al., 1992).

Remarks. In a recent report on the primary forest of the Phong Nha – Ke Bang area in Quang Binh Province ("Herpetological investigations") by Boris D. Vassiliev, a viperid specimen is listed in the "Crotalidae" as "*Trimeresurus cornutus* (?) or *Daboia* sp. (?)." According to the information given to one of the authors (Nikolai L. Orlov) such a specimen does in fact not exist.

The horned viperid specimen cited as *Trimeresurus cornutus* in Campden-Main (1970:100) from South Vietnam seems to refer indeed to *T. cornutus*, on the basis of a detailed oral description of this specimen, now lost, given to Patrick David by Dr. J. Vidal (personal communication, June 2000), who had this specimen in hand around 1940. The convergent, united raised supraoculars of this specimen, unambiguously described by Dr. Vidal, are typical of *T. cornutus*, and different from the divergent supraoculars of *Triceratolepidophis sieversorum*. Dr. Vidal reported that this specimen was collected at about 1400 – 1500 m a.s.l. in the high altitude resort station, located in the wet montane forest of the Bach Ma National Park. The snake was discovered inside a pile of firewood close to the chalets of the station.

Field notes. The sole known specimen was not observed alive. It was discovered by H.-W. Herrmann and T. Ziegler in the collection of a local "medicine man," where it was preserved in rice liquor. According to the collector, the snake was caught during the first half of 1999 inside a chicken stable in the village of Phong Nha, near the border of the karst forest. It is not known whether this snake, the stomach of which was empty, was attracted by the chickens or by the rats usually abundant around human settlements.

Protobothrops mucrosquamatus, an opportunistic species, both terrestrial and arboreal, is also known to visit chicken stables and human settlements where it feeds on mammals and birds, among other prey. Although not yet recorded for the Phong Nha Nature Reserve, within Vietnam *P. mucrosquamatus* is known from the central and northern parts (e.g., Bourret, 1936; Nguyên and Hô, 1996; Szyndlar and Nguyên, 1996; Hoang et al., 1997; Orlov, 1997; 1998).

DISCUSSION

This unique pitviper exhibits peculiar features, making it totally isolated within the *Trimeresurus* group. As stated above, this new genus and species present two diagnostic features which have not been observed in any other specimen, namely the three-keeled dorsal scales and the microdermatoglyphic pattern, which we discuss in detail.

Although we examined several hundreds of specimens of *Trimeresurus* sensu lato, belonging to all currently known species, we encountered the state of divided dorsal scale keels only in several specimens of a rare Chinese species, tentatively placed in the genus *Protobothrops*, *Protobothrops xiangchengensis* (Zhao, Jiang and Huang, 1978), which shows keels made of two or three consecutive parts. However, these keels, narrow and long, are by no way similar to the irregular keel made of three crests progressively uplifted from front to back encountered in *Triceratolepidophis sieversorum*. *Protobothrops xiangchengensis* differs from the latter species by numerous morphological features, including the macro- and microstructure of dorsal scales, a distinct dorsal pattern, a smaller size with a maximum of 889 mm (Zhao et al., 1998), a much lower number of ventral plates (175 – 194) and subcaudal plates (44 – 66) (Zhao et al., 1998; unpublished data), 25 scale rows at midbody, a longer head (4.7 – 5.1% [mean 4.9] of SVL), upper preocular divided into two scales, the anterior one much smaller than the posterior, 5th SpL much shorter and smaller than 4th, and very wide, single, flat supraocular scales; it is also a strict montane species, currently not known below 2750 m. All other examined specimens of any other species belonging to the *Trimeresurus* group which have keeled dorsal scales exhibit a single, elongated and narrow keel.

The microdermatoglyphic pattern is also unique within the *Trimeresurus* group. Although the pattern of all known species has not yet been examined, David and Pauwels (2000; in preparation) investigated the microstructure of ten species belonging to all subgroups recognized by Brattstrom (1964). In all of them, the structure is typically flat or slightly bulged tessellate. In *Triceratolepidophis sieversorum*, the structure is markedly tessellate fimbriate, with distinctly erected fimbriae. Although a tessellate pattern

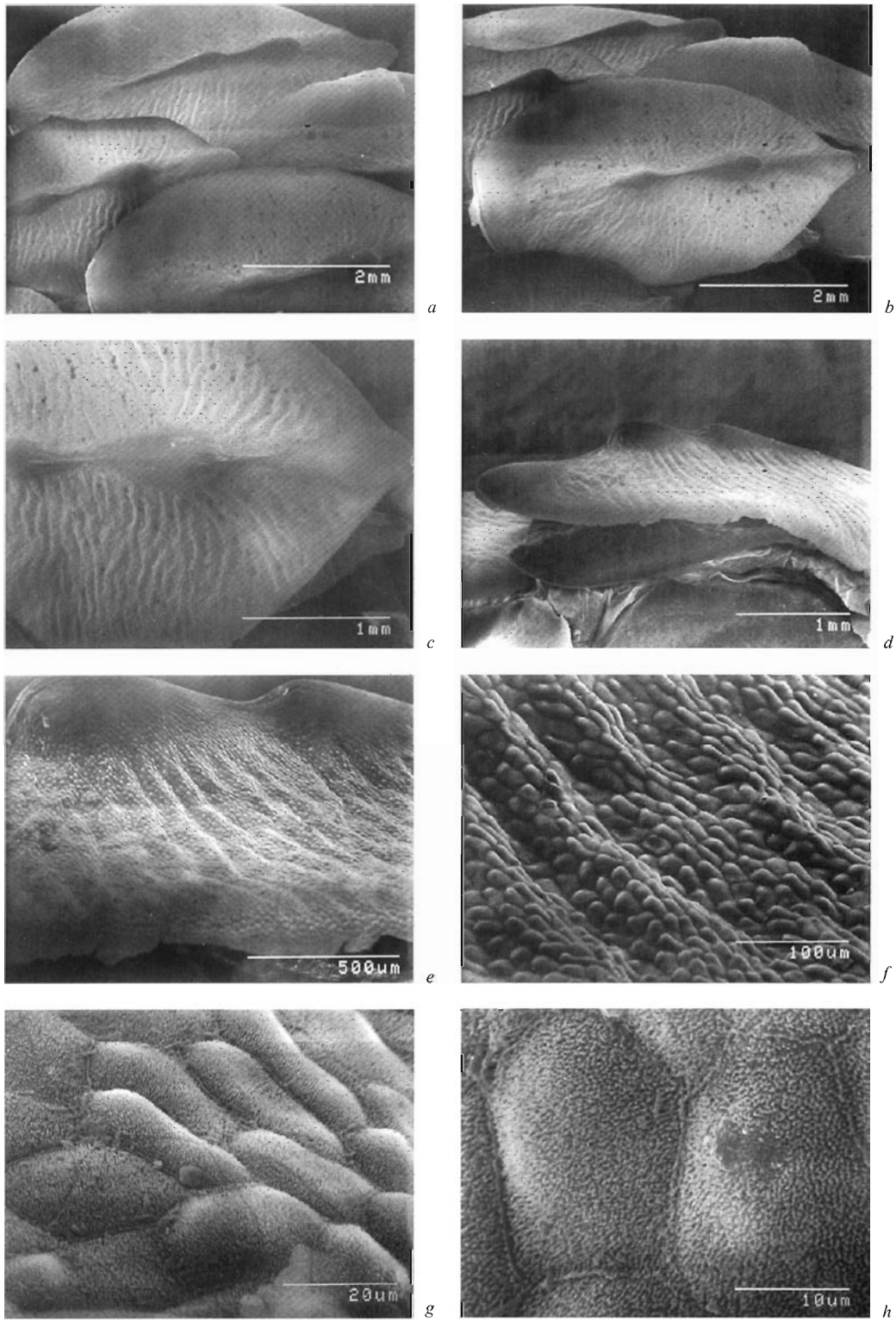

Fig. 7. SEM photographs of dorsal scales of the holotype of *Triceratolepidophis sieversorum* (see text for detailed information). Photographs by L. Beck.

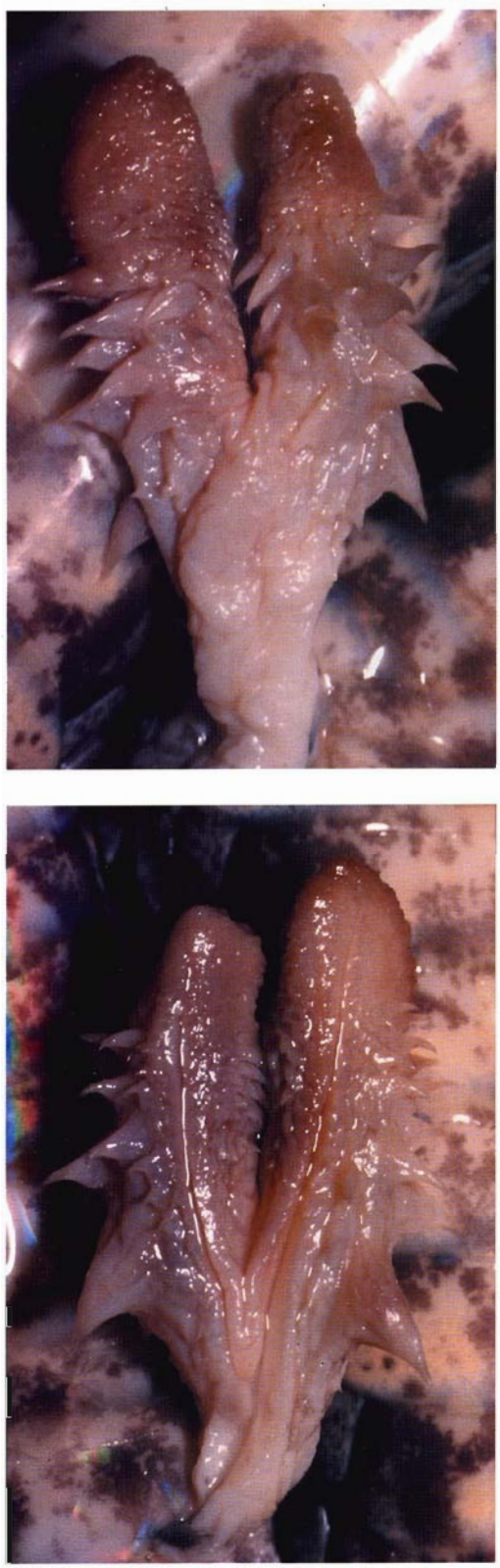

Fig. 8. Everted left hemipenis of the holotype of *Triceratolepidophis sieversorum*; left sulcal, right asulcal view. Photographs by T. Ziegler.

(sensu Pauwels et al., 2000) is a normal condition in the Crotalinae, the present microstructure differs from all other microstructures observed to date in the genera *Calloselasma*, *Ovophis*, *Protobothrops*, *Trimeresurus*, and *Tropidolaemus*, notably all species examined by David and Pauwels (2000), by its combination with a fimbriate pattern. The fimbriate pattern is quite uncommon among snakes (Pauwels et al., 2000), and the superposition of a tessellate and a fimbriate pattern is very rare. It is known for instance in the African genus *Causus* Wagler, 1830 (see illustrations in Price, 1981, 1987), in which the microdermatoglyphic pattern is strikingly similar to that of our new taxon (with the exception of the triple keels and the transversal furrows which seem to be unique in the new genus). At the cell level, it is also comparable to some extent to patterns shown by some members of the genus *Crotalus* (see illustrations in Stille, 1987), although the fimbriae are much shorter in this latter genus.

On the basis of osteological and morphological features, including the microdermatoglyphic pattern, Hoge and Romano Hoge (1983) described the genus *Protobothrops* to accommodate long-bodied species related to *Trimeresurus flavoviridis* (Hallowell, 1861). Their new genus was partly based on the peculiar microdermatoglyphic pattern which these authors observed in *Protobothrops jerdonii* Gunther, 1875, namely a striated pattern totally different from the one seen in *T. albolabris* (Gray, 1842), *T. gramineus* (Shaw, 1802), *Ovophis okinavensis* (Boulenger, 1892), and *Tropidolaemus wagleri* Wagler, 1830. We unfortunately did not observe the structure of *P. jerdonii*, but it is certainly not present in *P. mucrosquamatus* and *P. flavoviridis* (David and Pauwels, in preparation), nor in *Triceratolepidophis sieversorum*. However, as Hoge and Romano Hoge (1983) did not detail their method, comparisons with our own results may prove to be difficult.

If we compare the other morphological features of *Triceratolepidophis sieversorum* with those of other members of the *Trimeresurus* group, its gray brown dorsal color makes it immediately different from green members of the genus *Trimeresurus*, placed in the subgroups of *T. albolabris*, *T. stejnegeri* and *T. gramineus* (Malhotra and Thorpe, 2000). However, species of the *Trimeresurus* group displaying a gray or brown dorsal ground color with a dorsal pattern made of darker blotches are numerous. They are placed in the genera *Ovophis*, *Trimeresurus*, *Ermia*, and *Protobothrops*, which are now examined in this order.

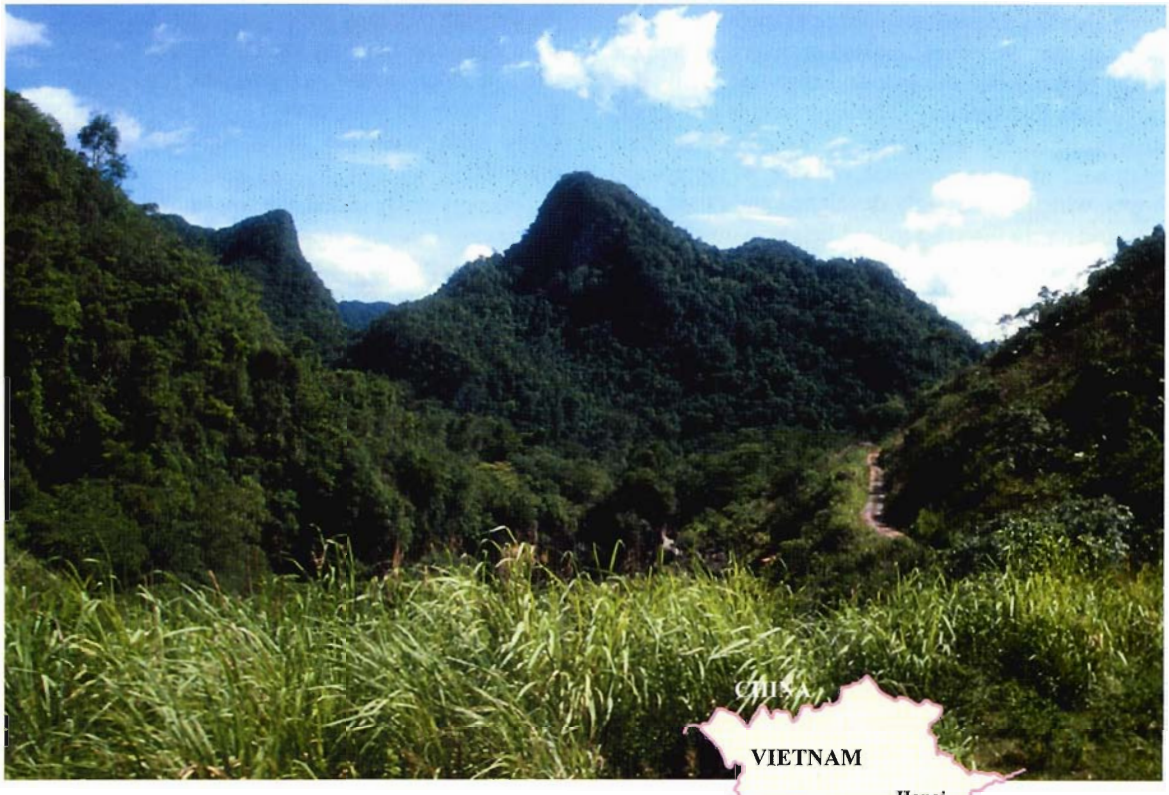

Fig. 10. Phong Nha Nature Reserve near Phong Nha village. Photograph by T. Ziegler.

Fig. 9. Map of Vietnam showing Phong Nha village within Quang Binh Province, the type locality of *Triceratolepidophis sieversorum*.

In addition to its three-keeled dorsal scales and the microdermatoglyphic patterns, the new species is distinguished from members of the genus *Ovophis*, which also have a grayish-brown ground color, and especially the wide ranging mainland species *O. monticola*, by the combination of a larger size, much more elongated head and body, larger eye, longer snout, different shape of dorsal blotches, a much higher number of ventrals, which does not exceed 169 in *O. monticola*, 176 in *O. zayuensis*, more prominently keeled dorsal scales, keeled cephalic and occipital scales, and the presence of divided, uplifted supraoculars, which are always flat and most often entire in *Ovophis*. Members of the genus *Ovophis* present the typical flat tessellate pattern of the genus *Trimeresurus* (David and Pauwels, 2000; in preparation).

Within the genus *Trimeresurus* sensu stricto (following Malhotra and Thorpe, 2000), there are also several gray or brown species, of which three are horned, namely *T. brongersmai*, *T. cornutus*, and *T. puniceus*. Closely related to *T. puniceus*, *T. borne-*

ensis also has divided, swollen or granular supraoculars, but they are never upraised or divergent, and the shape of the snout, bilobate and spatulate, easily distinguishes this species. *T. brongersmai* is also easily distinguished by the shape of its snout, strongly spatulate, and the presence of 3 or 4 supraocular horns, which are strongly developed and raised, narrow and partly fused up to mid-height, a much different dorsal pattern with vertically elongated dorsolateral blotches, 19 scale rows at midbody, and much lower number of ventrals, not exceeding 150 (Hoge and de Lemos Romano, 1974; unpublished data). Furthermore, the microdermatoglyphic pattern of *T. borneensis* is typical for the genus *Trimeresurus* (David and Pauwels, in preparation).

Trimeresurus puniceus and *T. cornutus* have a typical, not projected nor spatulate crotaline snout and upraised supraoculars. *T. puniceus*, an Indonesian taxon not known from the Asian mainland, is distinguished, among other characters, by its different dorsal pattern (see Hoge and de Lemos Romano, 1974), the presence of 3 or 4 short, thick, triangular uplifted supraoculars, quite low and more uplifted outwards than truly upraised, a longer head (5.9 – 7.6 [mean 6.5]% of SVL), a longer snout, from 2.4 to 3.0 times (mean 2.6 times) the diameter of the eye, a smaller eye (ratio eye diameter/ distance eye-lower margin of lip between 0.5 and 0.7), a lower number of ventrals, not exceeding 176, a single upper preocular, a 2nd supralabial very short, not bordering the loreal pit and topped by a prefoveal scale, and 2 consecutive loreals. Under the term "loreal," it must be understood as the scale present between the preocular(s) and the nasal. In the case of *Triceratolepidophis sieversorum*, the upper preocular is divided into 3 scales, so the two foremost scales might also be counted as loreals, as along with the true loreal, they separate the scale in contact with the eye from the nasal. However, these two scales obviously result from the division of a long upper preocular, and we refrain from counting them as loreal, by opposition to the two true loreals found in *T. puniceus* (and related species), which are independent scales in contact posteriorly both with the upper (entire) and middle preoculars.

As previously stated, the sole known specimen of *Triceratolepidophis sieversorum* was at first identified as a new specimen of *Trimeresurus cornutus*. There are some similarities between the two taxa, such as the presence of raised supraoculars, the divided upper preoculars, the dorsal color, and the beige venter spotted with gray brown, but they are separated by numerous characters. *T. cornutus* is characterized by a different dorsal pattern made of vertically elongated dorsolateral blotches, a lower number of ventrals (193 – 197) and dorsal scale rows (21 at midbody), a much higher ratio TaL/TL, with 0.182 and 0.180 in the two known females, a longer head (5.3 – 5.6 [mean 5.4]% of SVL), a greater eye (ratio eye diameter/distance eye-lower margin of lip between 0.85 and 0.95), first 3 pairs of infralabials vs. first two pairs in contact with the chin shield in the new species, and different supraocular horns: among the 4 or 5 supraocular scales, the two or three central ones, triangular and thick, are both strongly raised and convergent, being united in their upper part instead of being divergent, giving the appearance of a high (more than 2 mm) single horn made of 2 or 3 intertwined scales. Moreover, it seems that *T. cornutus* is a rather small species, with a maximal size of 588 mm, but the number of known specimens is too low to draw conclusion on this point. Keels of its dorsal scales, are single, very narrow, quite low and entire, and also very different from those encountered in *P. mucrosquamatus* (see below), whereas its cephalic scales are smooth. Lastly, the hemipenis structure of *T. cornutus* is unknown, as only two females are available. Its microdermatoglyphic pattern has not

TABLE 1. Comparison of the Morphology between *Triceratolepidophis sieversorum* (*T.s.*) and *Protobothrops mucrosquamatus* (*P.m.*)

Taxon	Max. size, mm	TaL/TL (males)	HL/SVL (×100)	Co(m) keels	Micro-dermat.	Co(m)	Ven (males)	SubC (males)
T.s.	**1255**	0.17	**4.0**	**triple**	**fimbriate**	23	**228**	82
P.m.	**1174**	0.16 – 0.24	**4.3 – 4.7**	**single**	**afimbriate**	23 – 27	**198 – 222**	78 – 100
Taxon	SpL	Preoc. Div.	InN separ.	SupOc	Cep	Cep keels	Color	Pattern
T.s.	8 – 9	**3**	2	**horns**	15	**yes**	gray brown	dorsal blotches
P.m.	9 – 12	**2**	2 – 5	**flat**	11 – 18	**no**	gray brown	dorsal blotches

Abbreviations (see also *Material and Methods*). Microdermat.: **Co(m) keels**) status of the keel of dorsal scales at midbody; **Microdermat.**) dorsal microdermatoglyphic pattern, at midbody; **Preoc. div.**) division of the upper preocular; **InN separ.**) number of scales separating the internasals; **SupOc**) supraoculars; **Cep**) number of cephalic scales on a line between supraoculars; **Cep keels**) presence of keels on cephalic scales, between supraoculars.

yet been investigated, but even under a binocular lens, it is possible to distinguish a tessellate pattern made of numerous rounded, flat and juxtaposed cells, typical of crotalines. The biology of the two species seems also to be much different, as the two specimens of *T. cornutus* for which some data are available were collected at 1400 m in a wet montane forest (Bach Ma) and at 2000 m on the Mt. Fan Si Pan (Trân et al., 1992).

Ermia mangshanensis (Zhao *in* Zhao and Chen, 1990) is a very large species, at least up to 2100 mm, currently known only from a small region of montane forests of the Hunan Province, in the south of China (Zhao et al., 1998). This impressive species was first described in the genus *Trimeresurus*, then referred to the new genus *Ermia* Zhang, 1993 on the basis of distinct characters of its skull and head musculature (Zhang, 1993; 1998). It differs from *Triceratolepidophis sieversorum* by its dorsal pattern, best described as lichen-like blotches, a rather thick body, a lower ratio TaL/TL (between 0.13 to 0.15, on our small sample), longer head, a much lower number of ventrals (187 – 198) and subcaudals (60 – 67), 25 dorsal scale rows at midbody, of which the outermost is much enlarged, the presence of large, entire supraocular, a single loreal, internasals in contact, only 6 – 8 cephalic scales between the supraoculars, and a second SpL very short, not bordering the loreal pit and topped by a prefoveal scale.

Our new species most strongly presents the general morphology of some species of the genus *Protobothrops* Hoge and Romano Hoge, 1983. Although the contents of this genus are still not well defined, it includes an informal group of large, usually more than one meter long, elongated, terrestrial species, which includes *P. flavoviridis* and two other closely related Japanese species, and *P. mucrosquamatus*, *P. jerdonii*, and probably *P. kaulbacki* (Smith, 1940) and *P. xiangchengensis* discussed above (David and Ineich, 1999; Malhotra and Thorpe, 2000). Among them, only *P. mucrosquamatus* and *P. jerdonii* are currently known from Vietnam. The latter species is easily distinguished from *Triceratolepidophis sieversorum* by its dark ground coloration bearing an erratic pattern of yellow blotches and spots, or large rusty ovoid blotches, and body and head scalation (see Zhao et al., 1998).

To the contrary, *Triceratolepidophis sieversorum* bears an overall strong similarity with *Protobothrops mucrosquamatus*, with which it shares several morphological features. A thorough comparison between these two species is given in Table 1. Diagnostic characters appear in **bold**. Values usually bearing a sexual difference, such the maximal size, numbers of ventrals, subcaudals and the ratio TaL/TL, are given only for the males of *P. mucrosquamatus*. Data on these latter species are largely based on Zhao et al. (1998) and our unpublished data.

The maximal size reported for *P. mucrosquamatus* is 1280 mm (SVL 998 mm, TaL 282 mm) for a female, which according to Zhao et al. (1998) are in this species larger than males.

Other differences between these two species include the proportional size of the eye, greater in *P. mucrosquamatus*, with a ratio eye diameter/distance eye-lip between 0.85 – 0.95 in three Vietnamese specimens vs. 0.74 in *T. sieversorum*; usually a greater number of scales separating the internasals (generally 3 to 5, but sometimes 1 or 2). To the contrary, aside from the ground coloration and the general pattern, similarities include: a large nostril; the presence of comparatively very small scales on upper snout and head surfaces; a 5th supralabial nearly as high as the 4th, a condition also found in *P. mucrosquamatus* and the contact of the first two pairs of infralabials with the chin shield.

Concerning outer genital morphology, there seem to be only slight differences between the hemipenes of *Triceratolepidophis sieversorum* and *Protobothrops mucrosquamatus* (compare with Maki, 1931 *in* 1931-33; Pope, 1935; Mao et al., 1984).

Although the structure of the keels of the dorsal scales in these two species is beyond doubt different, some similarities may be found in the relative width of the keels. In *P. mucrosquamatus*, although they were always undivided in the multiple specimens which we examined, the keel is comparatively very wide, high, triangular or trapezoidal in section, covering a significant part of the width of the scale. It is much different from the narrow, wall like or nearly blade-like, and high keels found in *T. stejnegeri*, *T. puniceus*, or *T. cornutus*. In *Triceratolepidophis sieversorum*, the three elevations or horns emerging upwards from the keel are also comparatively wide (see Fig. *7b – d*), although they are not as regularly raised upwards and do not have as steep slopes as in *P. mucrosquamatus*.

Based on the single available specimen of *Triceratolepidophis sieversorum*, it is difficult to ascertain the relationships of this species with such unique, isolated characters. Not withstanding the macro- and microstructures of the dorsal scales, we, on the basis of purely morphological characters, would tentatively suggest some kind of affinity with members of

the genus *Protobothrops*. Molecular analyses will undoubtedly prove necessary to determine the position of this genus in the phylogeny of the *Trimeresurus* group. Currently, emphasis is put on green species (Malhotra and Thorpe, 2000), but investigations in the group of the elongated, terrestrial species of montane regions of China, Myanmar and the Indochinese Peninsula, will undoubtedly reveal new taxa and a better understanding of the relationships among the *Trimeresurus* group.

Further records of *Triceratolepidophis sieversorum* and detailed observations on its biology are necessary. For example, the strongly developed keels of the dorsal scales suggest some kind of morphological functionality. In viperid snakes, serrated lateral scale keels are known from the genera *Echis*, *Cerastes*, and certain species of the genus *Atheris*, as well as from the colubrid genus *Dasypeltis* (Joger and Courage, 1999). In all these cases the serrated keels play an important functional role in the production of a special defensive "rattling noise." While that character seems to be a shared autapomorphy in the three monophyletic viperid genera mentioned above, the serrated keels in *Dasypeltis* are a convergence. Relative to the here described *Triceratolepidophis sieversorum*, the function of the unique scale structure is not known due to the lack of living specimens. Whether this structure plays a role in defensive behavior, enhances climbing abilities or possibly has another function in *Triceratolepidophis* must remain unresolved until live specimens become available.

Nevertheless, the discovery of this unexpected and totally new taxon reinforces the necessity of further investigation in remote parts of Southeastern Asia, especially in the Indochinese region, and, also, the absolute priority to protect as many as possible still undisturbed, forested areas, such as the limestone forests of the Annam Mountain Range in Vietnam and Laos.

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APPENDIX
Specimens examined

***Ermia mangshanensis*:** CIB 8900, CIB 8902, CIB 8910, all from Yizhang, Mang Shan (Mt. Mang), Hunan Province, People's Republic of China.

***Protobothrops mucrosquamatus*:** MNHN 1897.100, "Iles Norway, Baie d'Along près d'Haï-Phong, Tonkin," now Long Châu Dao (Islands), Hai Phong Province, Vietnam; MNHN 1935.118, "Tam-Dao: 60 km N. d'Hanoï, Tonkin," now Tam Dáo Hill Station, Vinh Phú Province, Vietnam; MNHN 1948.108, "Mt. Bavi, 1250 m, près de Hanoï," now Ba Vi Mt., Hà Tây Province, Vietnam.

***Protobothrops xiangchengensis*:** CIB 725048, Xiangcheng, Qianjin County, Sichuan Province, 3000 m, China; CIB 725049 – 725050, Xiangcheng, Qianjin County, Sichuan Province, 3100 m; CIB 725051 – 725052, Xiangcheng, Qianjin County, Sichuan Province, 3200 m; CIB 725055, Xiangcheng, Qianjin County, Sichuan Province, 3100 m.

***Trimeresurus cornutus*:** BMNH 1946.1.19.25, "Fan-si-pan Mts., Tonking," now Mt. Fan Si Pan, Lai Châu Province, Vietnam; MNHN 1937.35, "Tonkin," northern Vietnam.

***Trimeresurus puniceus*:** RMNH 1557, "Java"; RMNH 1558a-b, "Java";– RMNH 7259A, "Kali Baroe, Banajoewangi, Java," now Kalibaru, near Banyuwangi, Jawa Timur Province; RMNH 8504, "Wonosobo, ±1000 m," Jawa Tengah Province; RMNH 8988, "Nongkodjadjar, ±1200 m, O. Java" Jawa Timur Province; RMNH 8990, "Ungebung von Bandoeng, W. Java" now Bandung, Jawa Barat Province; RMNH 8991, "Poentjak Pass, ±1400 m, W. Java" Jawa Barat Province; RMNH 11408, "Wonosobo, ±1000 m, M. Java" Jawa Tengah Province, all from Java Island, Indonesia.