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Dorsal scale microstructure of *Xenopeltis unicolor* (Serpentes, Xenopeltidae): description and position among the ophidian microdermatoglyphic patterns

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The microstructure of the dorsal scales of the Oriental Sunbeam Snake, *Xenopeltis unicolor* Boie, 1827 was studied by Scanning Electron Microscopy. *Xenopeltis* has a papillate pattern, like that seen in the Booidea (including *Calabaria* Gray, 1858) and Anilioidea (notably *Loxocemus* Cope, 1861). The papillate pattern was compared with other major ophidian microdermatoglyphic patterns. A preliminary interpretation of the evolutionary placing of the various lamellate patterns is offered; the papillate pattern is considered to be primitive within the lamellate patterns.

INTRODUCTION

The phyletic relationships of the snake genus *Xenopeltis* Boie, 1827[1], widely distributed in Southeast Asia and the Indo-Malay Archipelago, are controversial. Along with the Central American *Loxocemus*, it was placed in the subfamily Xenopeltinae of

[1] For the authorship of the specific epithet, that authors usually credited to REINWARDT, we follow the nomenclatural correction of DAVID & VOGEL (1996), who referred it to BOIE.

the Boidae Gray, 1825 by UNDERWOOD (1976), DOWLING (1975) and DOWLING & DUELLMAN (1978), and these latter authors also included the African genus *Calabaria* in this subfamily. MCDOWELL (1987) regarded the genera *Xenopeltis* and *Loxocemus* as sufficiently distinct from all other snakes, and from each other, to warrant their placing in their own families Xenopeltidae Bonaparte, 1845 and Loxocemidae Cope, 1861, within the superfamily Anilioidea Stejneger, 1907. MCDOWELL (1987) placed *Calabaria* in the Pythonidae Fitzinger, 1826 within the superfamily Booidea. These allocations were based on meristic, visceral, muscular, hemipenial and osteological characters.

We compared the microstructure of the dorsal scales of *Xenopeltis* with those found in representatives of other snake groups (including the Typhlopidae Gray, 1825), in order to provide one more character for comparison with its presumed relatives, and to insert its microstructural pattern within a hypothetical evolutionary arrangement of all currently known major types of dorsal scale patterns in snakes.

Among the various microscopic reliefs that can be observed at the surface of snake scales, in this study we decided to focus on the repeating waved pattern (lamellate oberhautchen, sensu IRISH et al. [1988, see their figure 5 B]; for a recent review on oberhautchen studies see MADERSON et al., 1998) with special reference to its variation along the scale and among taxa. The histological units to which the lamellae observed on the oberhautchen of most snakes correspond are not always easy to interpret, as it is sometimes not clear whether they represent cell delimitations or within-cell surface ornamentation (see discussion by IRISH et al., 1988: 115).

ABBREVIATIONS

BMNH: The Natural History Museum, London, United Kingdom.
IRSNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.
MNHN: Muséum National d'Histoire Naturelle, Paris, France.
ULB: Université Libre de Bruxelles, Brussels, Belgium.

MATERIAL AND METHODS

A skin sample was removed from a specimen of *Xenopeltis unicolor* (MNHN 1997.4300) which had been fixed in 4 % formalin and stored in 70 % vol. ethanol. The sample was taken from the mid-dorsal region in mid-body, a point defined as halfway along the series of ventral scales. The sample was dehydrated in absolute ethanol, dried at critical-point, and coated with gold in a supter coater Balzers (BAE 301 with BAE 014) in two consecutive periods of 10 seconds. We worked at the ULB on a ISI DS 130 scanning electron microscope under accelerating voltages of 20 kV. The pictures were taken using Ilford Pan F 50 film.

For comparison, we also studied the microstructure of similar scales from *Ramphotyphlops braminus* (Daudin, 1803) (MNHN 1997.2797), *Pseudohaje goldii* (Boulenger, 1895) (IRSNB 3759a) and *Trimeresurus albolabris* (Gray, 1842) (MNHN 1988.2105 and MNHN 1998.0569) under the same conditions.

The terminology describing the microstructure patterns mostly follows that given by PRICE (1982) and PRICE & KELLY (1989).

RESULTS

To the naked eye, the scale surface of *Xenopeltis unicolor* appears completely smooth (Pl. 1, fig. 1). High magnification reveals a regular microstructure, composed of transverse, subparallel ranks (lamellae). No polygonal cell borders are superimposed on the lamellate pattern of the ranks. The ranks present a dense alignment of indentations (the *denticules* of GASC & RENOUS, 1980), separated by smooth inter-rank spaces (i.e., the free surface of the oberhautchen cells). At the anterior extremity of the scale, these indentations are short; their length, less than one micron, being less than the inter-rank distance (Pl. 1, fig. 2). Towards the posterior part of the scale, the indentations progressively lengthen, reducing the inter-rank free surface (Pl. 1, fig. 3). At the posterior extremity of the scale, the indentations are about 1.3 microns long, so that they meet those of the next rank, nearly covering the inter-rank space (Pl. 1, fig. 4). Globally, the structural modification across the scale is very slight in this typical *papillate* pattern.

The scale surface of *Pseudohaje goldii* is completely covered with a regular microstructure composed of transverse, subparallel ranks (lamellae) with a dense alignment of indentations (Pl. 2, fig. 1; Pl. 3, fig. 2). At the anterior part of the scale, these indentations nearly reach the bases of the indentations of the next rank, and their length is about 3 microns. Towards the posterior part of the scale, the indentations progressively lengthen, covering at least the bases of the indentations of the next rank, and reaching a length of about 4 microns. Punctuations are visible on the inter-rank spaces. No polygonal cell borders are superimposed on the lamellate pattern. This arrangement corresponds to the *echinate* pattern as defined by PRICE (1982).

At high magnification, the scale surfaces of *Ramphotyphlops braminus* show a simple uniform pattern of brachylamellate, juxtaposed oberhautchen cells. The width of these cells (transverse to the scale length) is approximatively 50 microns; their length about 10 microns. There are neither discernible ranks of indentations (lamellae) nor punctuations (Pl. 2, fig. 2-3).

Trimeresurus albolabris has an irregular pattern of polygonal, sharply delimited oberhautchen cells (Pl. 2, fig. 4; Pl. 3, fig. 5). Most cells have a more or less elevated, sometimes offset, hummock. The cell surface is covered with numerous, narrow circular punctuations producing a very dense, sponge-like structure in the anterior part of the scale; these punctuations progressively stretch and turn up backwards into a dense net of thin, heavily intertwined, fiber-like structures. The length of the cells is about 25 microns; their width about 20 microns. No lamellate pattern is detectable.

DISCUSSION

The patterns of *Xenopeltis* and *Pseudohaje*, although differing notably in the size of their indentations, are globally similar. They have units which correspond to transversal lamellae ornamenting the surface of oberhautchen cells whose outlines are not discernible. The other two patterns (i.e., those of *Ramphotyphlops* and *Trimeresurus*) are very different in that they have clearly delimited units which correspond to cell outlines.

The microstructure of *X. unicolor* corresponds to the papillate dorsal microdermatoglyphic pattern defined by PRICE (1982). This author, as well as PRICE & KELLY (1989), found this pattern in the Anilioidea (i.e., *Anilius* and *Loxocemus*), and in the Booidea (*Calabaria*, *Charina* Gray, 1849, *Liasis* Gray, 1842, *Morelia* Gray, 1842, and *Python* Daudin, 1803) (both superfamilies sensu MCDOWELL, 1987). This is also the pattern that can be identified on the illustration of the facial sensilla given by POVEL & VAN DER KOOIJ (1997) for *Cylindrophis* Wagler, 1828 (Anilioidea) and *Xenopeltis* Boie, 1827.

PRICE & KELLY (1989) explained how the microstructural pattern could vary from the anterior to the posterior part of the scale: anteriorly the scale has a basal morphotype that becomes more complicated along a transition zone resulting in an apical/posterior morphotype. We agree with these authors, who stated that basal/anterior patterns may represent a primitive condition of the apical/posterior pattern on a given scale. However, unlike these authors, we do not interpret lamellae in the lamellate patterns (i.e., *canaliculate*, *echinate*, *fimbriate*, *papillate*, *plicate* and *reticulate*) as being whole cells, but as lamellar ornamentations on the surfaces of oberhautchen cells.

To our knowledge, the papillate pattern does not occur outside the Booidea and Anilioidea. It could be interpreted as a simplified form of the echinate pattern which is widespread in the Colubroidea Oppel, 1811. In the echinate pattern, the microstructure varies to a greater degree along the scale length, with the indentations lengthening, their pointed apical extremity covering at least the bases of the indentations of the next rank.

PRICE (1982) and PRICE & KELLY (1989) found the echinate pattern in snakes belonging to various genera including *Atractaspis* Smith, 1849 (Atractaspididae), *Chilomeniscus* Cope, 1860, *Chionactis* Cope, 1860, *Coniophanes* Hallowell *in* Cope, 1860, *Diadophis* Girard *in* Baird & Girard, 1853, *Dinodon* Duméril, Bibron & Duméril, 1854, *Dromicodryas* Boulenger, 1893, *Elaphe* Fitzinger *in* Wagler, 1833, *Enhydris* Latreille *in* Sonnini & Latreille, 1801, *Farancia* Gray, 1842, *Lampropeltis* Fitzinger, 1843, *Prosymna* Gray, 1849, *Rhadinaea* Cope, 1863, *Seminatrix* Cope, 1895, *Sonora* Girard *in* Baird & Girard, 1853, *Stegonotus* Duméril, Bibron & Duméril, 1854, *Tantilla* Girard *in* Baird & Girard, 1853 (Colubridae), *Boulengerina* Dollo, 1885, *Elapsoidea* Bocage, 1866, *Pseudohaje* Günther, 1858, *Pseudonaja* Günther, 1858, *Suta* Worrell, 1961 and *Walterinnesia* Lataste, 1887 (Elapidae). The microstructure of *Drymarchon* Fitzinger, 1843 (Colubridae) described by MONROE & MONROE (1967), and that of *Leimadophis* Fitzinger, 1843 (now *Liophis* Wagler, 1830) (Colubridae) illustrated in RENOUS & GASC (1989) clearly correspond to the echinate pattern. ROZE (1996) represented typically echinate microstructures of several species of *Leptomicrurus* Schmidt, 1937, *Micruroides* Schmidt, 1928, and *Micrurus* Wagler *in* Spix, 1824 (Elapidae).

According to the species, scales possess various apical/posterior morphotypes, more or less complex than, and more or less modified from, their basal/anterior morphotype. This generalization permits understanding of the transition between the several major patterns defined in PRICE (1982), as suggested by PRICE & KELLY (1989). Notably, a variety of echinate subpatterns can be seen in *Psammophis* Boie *in* Fitzinger, 1826 (Colubridae), from a dense network of contiguous indentations (*P. angolensis* (Bocage, 1872), see BRANDSTÄTTER, 1995: 426; *P. sibilans* (Linné, 1758), see BRANDSTÄTTER, 1996: 24) to a spaced out network where the indentations are laterally separated by a distance larger than their base (e.g. *P. jallae* Peracca, 1896, see BRANDSTÄTTER, 1995: 431). In some species (e.g. *P. leightoni* Boulenger, 1902, see BRANDSTÄTTER, 1995: 433; *P. subtaeniatus* (Peters, 1882), see LILLYWHITE & MADERSON, 1982: 407), the inter-rank space increases and the pattern exactly corresponds with the *canaliculate* pattern of PRICE (1982: 300). PRICE (1982, 1983, 1990) reported the canaliculate pattern for the colubrid genera, *Dispholidus* Duvernoy, 1832, *Langaha* Bonnaterre, 1790, *Natrix* Laurenti, 1768, *Nerodia* Baird *in* Baird & Girard, 1853, *Oxybelis* Wagler, 1830 (also illustrated and commented in RENOUS & GASC, 1989*a-b*), *Regina* Baird *in* Baird & Girard, 1853 and *Thelotornis* Smith, 1849. Illustrations of canaliculate patterns in *Thamnophis* Fitzinger, 1843 and *Nerodia* are also given by CHIASSON & LOWE (1989).

On the anterior portion of the scales of *Psammophis sibilans*, longitudinal ranks are visible, but the indentations are not developed (BRANDSTÄTTER, 1995: 423). When the indentations are particularly short in this location (BRANDSTÄTTER, 1995: fig. 28), the pattern is quite similar to the plicate pattern shown by PRICE (1982, 1983) for *Helicops angulatus* Linné, 1758, *Regina alleni* (Garman, 1874) and *R. rigida* (Say, 1825) (Colubridae).

When the free surface of the cell in the echinate pattern splits (see BRANDSTÄTTER, 1995: fig. 42 for *P. condanarus indochinensis* Smith, 1943, and fig. 90 *Hemirhagerrhis nototaenia* (Günther, 1864), it forms a pattern very comparable to the reticulate pattern of PRICE (1982: 301).

Transitions between the echinate and canaliculate patterns can be observed in the illustrations given by BRANDSTÄTTER for the genus *Hemirhagerrhis* Boettger, 1893. Although the picture of *H. kelleri* Boettger, 1893 (BRANDSTÄTTER, 1995: fig. 89) shows a typically echinate pattern, that of *H. viperinus* (Bocage, 1873) (BRANDSTÄTTER, 1995: fig. 91-92) is typically canaliculate. Similarly, the pattern shown for *Malpolon m. monspessulanus* (Hermann, 1804) (BRANDSTÄTTER, 1995: fig. 93-94) is echinate; that of *M. monspessulanus insignitus* (Geoffroy Saint Hilaire, 1827) (BRANDSTÄTTER, 1995: fig. 95) is intermediate echinate-canaliculate, and that of *M. moilensis* (Reuss, 1834) (BRANDSTÄTTER, 1995: fig. 96) is canaliculate. Illustrations of patterns intermediate between the echinate and the reticulate patterns can also be identified in DOWLING & PRICE (1988).

A *fimbriate* pattern is indicated when the indentations are erect, rather than flat as in the echinate pattern. The rare fimbriate pattern was found in the colubrids *Tropidodryas serra* (Schlegel, 1837) and *T. striaticeps* (Cope, 1870) by THOMAS & DIXON (1977) and *Boiga blandingi* (Hallowell, 1844) by PRICE (1982).

Among the other patterns defined by PRICE (1982), the very close *foveate*, *cristate* and *verrucate* apical patterns, found in crotalids and viperids (with the notable exception of *Azemiops* Boulenger, 1888, which has a typical echinate pattern, PAUWELS, unpublished data), are here united under the term *tessellate*. Unlike the lamellae of the lamellate patterns, in our opinion the units of the tessellate pattern really correspond to single oberhautchen cells. Although PRICE and KELLY (1989) offer a number of names for microstructural patterns in the Viperoidea, we interpret nearly all of them as tessellate. The microstructures of *Atheris nitschei*[2] Tornier, 1902, *Adenorhinos barbouri* (Loveridge, 1930) and *Montatheris hindii* (Boulenger, 1910) shown in BROADLEY (1996) are tessellate, as are those of *Causus* Wagler, 1830, *Pseudocerastes* Boulenger, 1896, and *Vipera* Laurenti, 1768, as shown by PRICE (1987). The illustrations of

[2]The patterns of *Bitis caudalis* Smith, 1849 and *Atheris squamigera* (Hallowell, 1854) were considered by PRICE (1982) to be respectively cristate and foveate; both were called reticulate by GROOMBRIDGE (1986), who did not cite PRICE (1982).

PICADO (1931), while made at low magnification and with a light microscope, seem to reveal such a pattern in *Bothrops* Wagler, 1824. The drawings by POCKRANDT (1937), made from observations with light microscope, seem to show a tessellate pattern for at least *Crotalus horridus* Linné, 1758, *Echis carinatus* (Schneider, 1801), and *Tropidolaemus wagleri* Wagler, 1830. The same is true for the illustrations of *Echis carinatus* obtained by KIMMICH & BLANEY (1973) with S.E.M. at low magnification, that of *Crotalus durissus* Linné, 1758, illustrated by RENOUS & GASC (1989) and the patterns shown for *Gloydius caliginosus* (Gloyd, 1972), *Ovophis okinavensis* (Boulenger, 1892) and *Protobothrops* Hoge & Romano-Hoge, 1983 by KIKUCHI et al. (1981*a-b*, 1982). Within the genus *Vipera* an apical tessellate pattern is sometimes absent, as we can see in BEA (1978, 1986, 1987) and BEA & FONTARNAU (1986), but rather there is a canaliculoreticulate pattern (PRICE & KELLY, 1989).

CONCLUSION

We have shown that the dorsal scale papillate microstructure of *Xenopeltis* is shared with other genera of the superfamilies Anilioidea and Booidea. This character alone does not support a familial distinction of Xenopeltidae with respect to other groups of the Anilioidea.

Among the lamellate patterns, the papillate pattern seems to be primitive, indicating that snakes having such could belong to an ancestral stock. This pattern, with its little developed indentations (Pl. 3, fig. 1), could represent an ancestral stage of the echinate pattern (Pl. 3, fig. 2) and the derived canaliculate (Pl. 3, fig. 3-4), fimbriate and reticulate patterns.

We believe that the detail observable on the scale surface of *Ramphotyphlops* (Pl. 2, fig. 2-3) represents the delimitations of elongate oberhautchen cells. Their absolute size, and their periodicity preclude their interpretation as lamellar ornamentation on the surface of cells (the delimitations of which are undetectable).

It is important to keep in mind that the visible units in the lamellate patterns (i.e., lamellae) and those of the tessellate patterns are not homologous, because the former are lamellar ornamentations on the surfaces of oberhautchen cells, while the latter are cell outlines. In some cases, identifying the observed units is difficult, as is the case in the microstructure of *Ramphotyphlops braminus*.

Snake scale surfaces rarely offer a visible superimposition of polygonal cell delimitations (these latter being those of the oberhautchen cells or of the clear layer cells, IRISH et al. 1988) over the lamellae. Booidea and Anilioidea seem to be characterized by a lamellate pattern in which polygonal cells can not be detected at all, with little developed indentations and no imbrication of the ranks (papillate pattern). The indentations of the papillate pattern seem to vary little along the scale and among the taxa. Colubroidea (Atractaspididae, most Colubridae, Elapidae, and *Azemiops*) have developed, to hyperdeveloped, indentations causing a slight to major imbrication of the ranks, with or without punctuations, with a high morphological variation of the indentations along the scale and among taxa. Viperidae very rarely present lamellae, but rather have a tessellate pattern with clearly delineated oberhautchen cells showing a complex microornamention composed of circular punctuations and stretched punctuations (Pl. 3, fig. 5), and sometimes hummocks, varying along the scale length, and with a high generic to specific variability. In the Colubroidea and Viperoidea, the documented interspecific variability in scale microstructure still holds promise as a taxonomic character.

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Plate 1: dorsal scales microstructure of *Xenopeltis unicolor*. MNHN 1997.4300.

Fig. 1: general view of the entire scale. 40 ×.

Fig. 2: microstructure at the anterior extremity of the scale. 4050 ×.

Fig. 3: microstructure at the mid-length of the scale. 5950 ×.

Fig. 4: microstructure at the posterior extremity of the scale. 5840 ×.

(Each figure is oriented with the anterior part of the scale on the left).

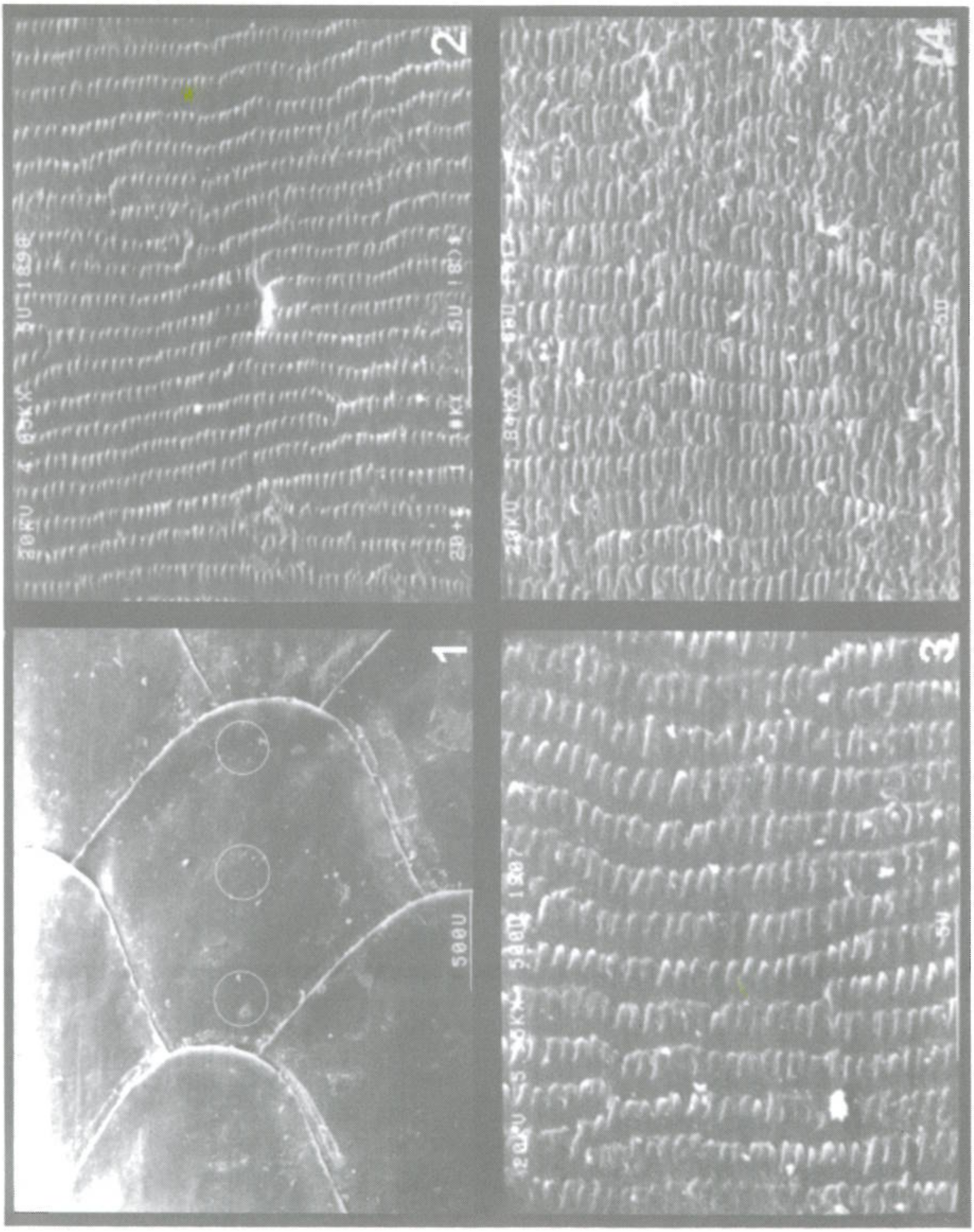

Plate 2.

Fig. 1: dorsal scale microstructure of *Pseudohaje goldii*. IRSNB 3759a. 4170 ×.

Fig. 2: dorsal scale microstructure of *Ramphotyphlops braminus*. MNHN 1997.2797. 2290 ×.

Fig. 3: posterior part of scale of *Ramphotyphlops braminus*. MNHN 1997.2797. 900 ×.

Fig. 4: posterior part of scale of *Trimeresurus albolabris*. MNHN 1998.0569. 425 ×.

(Each figure is oriented with the anterior part of the scale on the left).

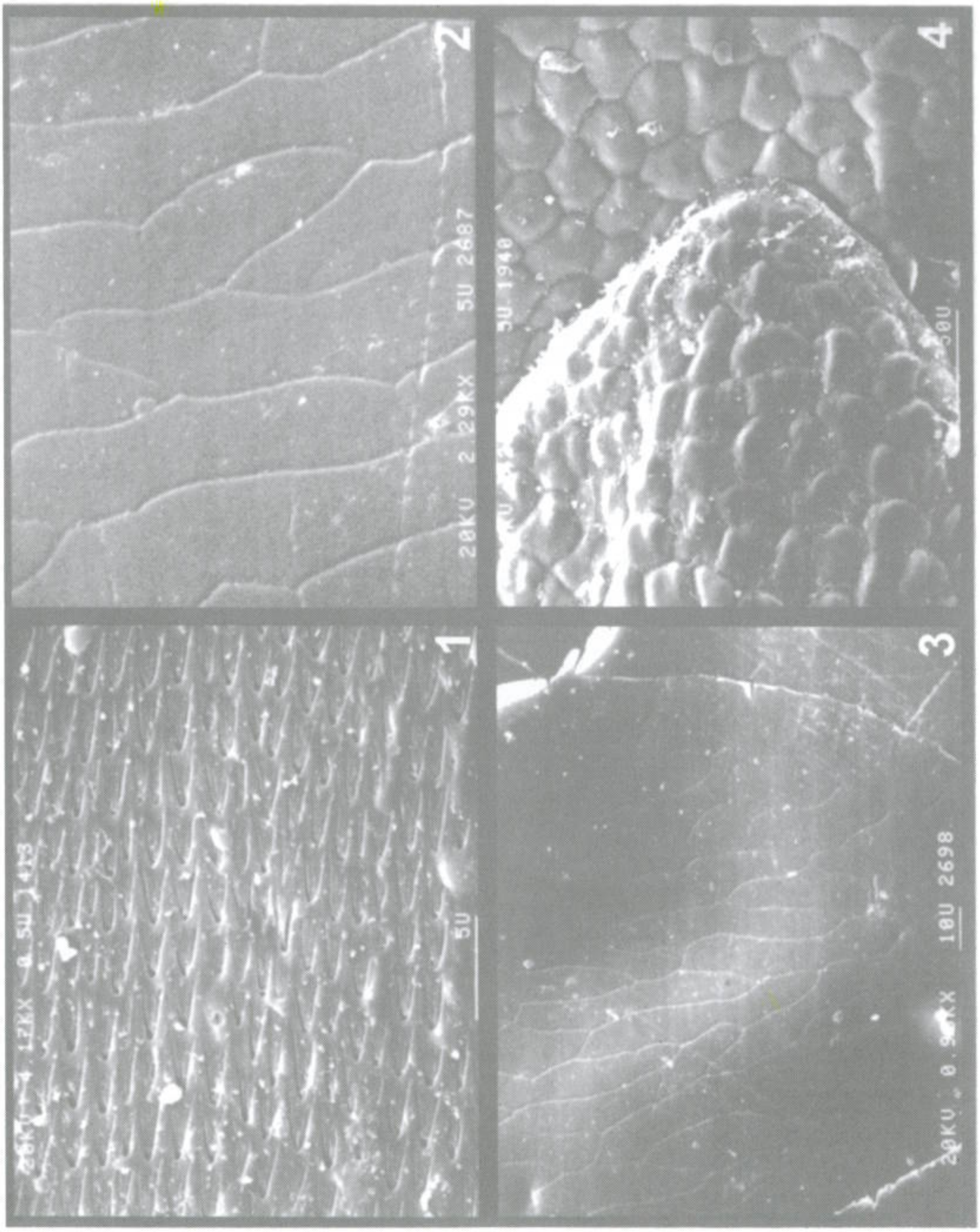

Plate 3.

Fig. 1: papillate pattern (*Xenopeltis unicolor.* MNHN 1997.4300): detail of the indentations

Fig. 2: echinate pattern (*Pseudohaje goldii.* IRSNB 3759a): detail of the indentations

Fig. 3: echinate-canaliculate pattern (*Psammophis notostictus*, adapted from photo. 54 in BRANDSTÄTTER, 1995): detail of the indentations

Fig. 4: canaliculate pattern (*Psammophis tanganicus*, adapted from photo. 77 in BRANDSTÄTTER, 1995): detail of the indentations

Fig. 5: tessellate pattern showing juxtaposed cells without lamellae (*Trimeresurus albolabris.* MNHN 1988.2105)

(Each figure is oriented with the anterior part of the scale on the top).