JOURNAL OF MORPHOLOGY 258:249–268 (2003)

Scale Microornamentation of Uropeltid Snakes

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ABSTRACT Microornamentation was examined on the exposed oberhautchen surface of dorsal, lateral, and ventral scales from the midbody region of 20 species of the fossorial snake family Uropeltidae and seven species of fossorial scolecophidian and anilioid outgroups. No substantial variation was observed in microornamentation from the different areas around the midbody circumference within species. All oberhautchen cells were flat and exhibited no major surface features other than occasional posterior margin denticulations, small pores/pits, and narrow, low ridges. This is largely consistent with the hypothesis that friction reduction and dirt shedding are the main selective pressures on microornamentation, given that reducing shine is not of key importance in fossorial animals. Variations among taxa were observed in the shape and size of oberhautchen cells, in the presence of pores/pits, in the presence and size of denticulations on posterior cell margins, and in the level or imbricate nature of cell borders. Six microornamentation characters were formulated, scored, and plotted onto a selected phylogeny. Character evolution and phylogenetic signal were explored, accepting the incomplete understanding of intraspecific variation and of uropeltid interrelationships. There is evidence that all but one of these characters evolved homoplastically, probably by multiple independent origin. There is no clear evidence for character state reversal, but greater phylogenetic resolution is required to test this further. Phylogenetic signal appears to exist in some instances, including possible microornamentation synapomorphies for Uropeltidae and *Melanophidium*. These derived character states are found elsewhere within Squamata. A microornamentation of narrow, finely, and regularly spaced ridges is associated with scale iridescence. These ridges, and possibly pores/pits, are also associated with scales that are less wettable, and that therefore might be expected to be better at shedding dirt in moist conditions. Testable hypotheses are presented that might explain minor variations in the form of ridges and pits among uropeltids. J. Morphol. 258:249–268, 2003.

KEY WORDS: Serpentes; Anilioidea; Uropeltidae; SEM; evolution; phylogeny

The scales of squamate reptiles are composed of several histologically discrete layers formed from cells of a living basal layer, the stratum germinativum. The outermost epidermal layer is rigid and composed of β-keratin, and this is overlain by the oberhautchen (see Irish et al., 1988). The outer surface of the oberhautchen is in direct contact with the environment. It is often composed of cell-like divisions that may bear complex three-dimensional features. The overall arrangement of these cells and their surface features are termed microornamentation (Ruibal, 1968; Arnold, 2002a), and these features are readily studied with scanning electron microscopy.

There have been several studies of microornamentation in various groups of squamates (see Arnold, 2002a, and literature cited therein). An early concern of this research was whether taxonomic variations in microornamentation were associated with systematics or ecology; that is, whether taxonomic patterns are determined more by phylogenetic history or by functional requirements. Earlier works often considered one of these factors over the other. Strong correlation between microornamentation and general ecology was not found (e.g., Price, 1982; Peterson, 1984; Peterson and Bezy, 1985) and some phylogenetic utility was advocated (e.g., Harvey, 1993; Harvey and Gutberlet, 1995), so that history was often considered the most important factor. For example, Burstein et al. (1974:359) stated that "Since the ultrastructural features of scales may be relatively free from selection as a result of direct adaptational pressures, they could well be more reliable indicators of interspecific relationships," and Price (1982:294) noted that microornamentation "patterns reflect phylogenetic relationship rather than ecological or habitat factors" and that (p. 297) "there is no case to make for a correlation between ecology or habitat and [microornamentation]."

On the other hand, functional requirements that were considered to be associated with certain forms of microornamentation were varied and included adaptations associated with the sloughing cycle (e.g., Maderson, 1966), mechanical strength (e.g., Ruibal and Ernst, 1965), reduction of friction with the substrate/adjacent scales (e.g., Stewart and Daniel, 1972, 1975), light penetration (e.g., Porter, 1967), dirt shedding (e.g., Gans and Baic, 1977), locomotion

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DOI: 10.1002/jmor.10147

(e.g., Renous et al., 1985), pheromone movement (Smith et al., 1982), and anti-fouling (McCarthy, 1987). In some cases functional links are clear; for example, in the sharp distinction between microornamentation of dirt-shedding body scales and dirt-trapping tail shield scales of uropeltid snakes (Gans and Baic, 1977), and the specialized setae on the digits of many climbing lizards.

Despite this conflict, there was an understanding that both history and function had a bearing on the taxonomic patterns observed (e.g., Stewart and Daniel, 1975; Renous and Gasc, 1989), although studies that teased apart these factors were largely not forthcoming. Recently, Arnold (2002a) applied a thorough, explicit approach to the understanding of microornamentation in lacertid lizards by attempting to explain variations in morphology through an integrated historical (phylogenetic) and functional analysis. For lacertids, a broad correlation between microornamentation and general habitat was found. Arnold concluded that the apparently ancestral, smooth microornamentation is more efficient at shedding dirt, but that it also generates shine by reflecting light and that this may compromise cryptic coloration. Arnold used this to explain derived patterns in which microornamentation becomes more elaborate in species and morphological regions (e.g., dorsal surface of the body) that are not in contact with particularly moist substrates. Mapping features onto a phylogeny and reconstructing states for internal branches indicated that lineage effects were probably important because reversals in microornamentation appeared to be extremely limited, but also that many of the derived patterns had evolved many times independently, and that (p. 154) "there seem to be limits on the variations that can be produced."

Examples of intraorganismal diversity and relatively sharp transition zones in morphologies suggest that there is a strong selective regime operating on at least some aspects of scale microornamentation (e.g., Gans and Baic, 1977; Arnold, 2002a). Given that shine control and dirt shedding plus friction reduction appear to entail opposing structural solutions, yet are of "substantial importance" (Arnold, 2002a:163), it is of interest to consider microornamentation in predominantly fossorial squamates in which shine control can be expected to be of little or no concern, and dirt shedding to be of great importance.

In this article I present a preliminary survey of body scale microornamentation in uropeltid snakes and some proximate outgroups. Uropeltidae is endemic to peninsular India and Sri Lanka, where individuals of the constituent species burrow in generally moist soils, mostly in upland, forested areas (e.g., Rajendran, 1985). Given our current understanding (Arnold, 2002a, and references therein), several predictions might be made about the microornamentation of a clade of limbless, burrowing squamates, namely: 1) that microornamentation will not vary around the circumference of the body; 2) that microornamentation will be conserved within the group, such that scales are generally smooth to reduce friction and to shed dirt; and 3) that similarities in generally minor variations in microornamentation among taxa can be attributed to recency of common ancestry and/or shared biology and habitat.

MATERIALS AND METHODS

Examination of Specimens

Material was obtained from specimens stored in industrial methylated spirits and ethanol in the reptile collection of the Natural History Museum, London (BMNH), the Department of National Museums, Colombo, Sri Lanka (DNM field tags with MW prefix), and the Department of Zoology, University of Kerala (field tags with MW prefix). Scales were not cleaned prior to examination. In some cases, multiple specimens were examined when some were too dirty for microornamentation to be properly viewed. Ultimately, microornamentation of only a single specimen was examined for most species, although two specimens were examined for some species. A list of the material examined is given in the Appendix. The aim of this preliminary survey of uropeltid microornamentation was to focus more on taxonomic breadth rather than make a detailed assessment of intraspecific and overall intraorganismal variation. In addition, several of the taxa under consideration are generally represented by only a few specimens in museum collections. Including previously published studies (of the uropeltid *Rhinophis drummondhayi* by Gans and Baic, 1977; and the aniliid *Anilius scytale* by Price and Kelly, 1989), the taxonomic coverage incorporated one species from each of the three scolecophidian families and representatives of all major groups within the Anilioidea. Anilioid samples comprised two of the eight species of the monotypic Cylindrophiidae, one species of the monotypic Anomochilidae, the only known extant species of the Aniliidae, and 20 species of uropeltids (known diversity 47 species, McDiarmid et al., 1999), including at least one species from each of the eight known genera.

All examined scales were from the midbody region and identified as dorsal, ventral, or lateral. At least one scale from each of these three regions around the circumferential perimeter of the body was examined for each specimen. The β-layer of the epidermis of single scales was removed with forceps, briefly air-dried, and mounted on scanning electron microscope stubs with a thin veneer of Araldite glue. Stubs were coated with gold and examined using Hitachi 2500 and Phillips XL30 scanning electron microscopes, almost entirely at 2–5 kV, and at magnifications of up to ×10,000.

Data Collection and Analysis

Dimensions of microornamentation features were measured from scanning electron micrographs taken at magnifications of ×800 to ×10,000. Where the measured features are consecutive and aligned, such as the length of consecutive cells (aligned longitudinally) and the spacing of denticulations on the posterior cell margins (aligned transversely), generally the maximum of a set of means were recorded from measures of at least 10 of the units under consideration. For dimensions that are not spatially consecutive, such as the length of posterior denticulations, between 10 and 20 individual measures of individual units were taken from each micrograph.

Features that were deemed to be reasonably constant within species but that varied to some extent among species were formulated into characters of two or more states. The states of these characters were recorded for each species examined. The software package MacClade 3.01 (Maddison and Maddison, 1992) was used

TABLE 1. Form and dimensions of midbody scale microornamentation features in scolecophidian and anilioid snakes (see Appendix for details of material examined)

Taxon	Distribution	Body scale	Cell shape	Cell borders	Maximum cell length	Denticulations	
						Max. length	Mean spacing
Leptotyphlops macrolepis		V	S	O	4.4–6	0.7–0.8	0.5
Liotyphlops ternetzii		V	S	O	4.4–8.1	0.4–0.5	0.3–0.4
Typhlops mirus		V	RP	L	22.8–28.8	—	—
Anomochilus leonardi		D, V	S	O	2.2–2.4	1.3–1.7	0.5
Cylindrophis maculatus		D, L, V	S	O	1.6–2.3	1.0–1.5	0.4–0.5
Cylindrophis ruffus		D, V	S	O	1.6–1.7	1.1–1.3	0.4–0.5
Anilius scytale[1]		D	S	O	1.6	0.9–1.2	0.3
Melanophidium bilineatum	India	D, L, V	RP	L	18.7–38.6	—	—
Melanophidium punctatum	India	L	RP	L	29	—	—
Melanophidium wynaudense	India	D	RP	L	30.7–37	—	—
Teretrurus sanguineus	India	D, L	S	O	2.9–3	1.6–1.9	0.5–0.6
Brachyophidium rhodogaster	India	L, V	S	O	1.8–3.3	up to 3.7	0.4–0.6
Plectrurus perrotetii	India	D, V	S	O	8.8–11.9	0.5–0.8	0.5
Platyplectrurus trilineatus	India	D, V	S	O	2.4–3	1.9–2.7	0.6–0.7
Pseudotyphlops philippinus	Sri Lanka	D	S	L	8.2–8.5	0.6–0.7	0.6
Rhinophis sanguineus	India	D	S	O	3.8–4.8	1.1–1.3	0.6
Rhinophis travancoricus	India	D, L	S	O	2.5–3.2	0.8–1	0.5
Rhinophis drummondhayi[2]	Sri Lanka	D	S	L	?	0.8	0.5
Rhinophis oxyrhynchus	Sri Lanka	D, V	S	O	4.3–5.1	0.8	0.5–0.6
Rhinophis philippinus	Sri Lanka	D, L	S	L	4.2–6.8	0.7–1	0.4–0.5
Rhinophis blythii	Sri Lanka	D	S	L	6.5–7.2	0.8–0.9	0.5–0.6
Rhinophis homolepis	Sri Lanka	D, V	S	O	5.2–6.1	0.7–0.9	0.5
Uropeltis phillipsi	Sri Lanka	L, V	S	O	5.8–6.6	0.7	0.5
Uropeltis melanogaster	Sri Lanka	D, L	S	O	6.7–7.4	0.7–0.8	0.5
Uropeltis phipsonii	India	L, V	S	O	4.3–4.7	2.4–3.1	0.5–0.9
Uropeltis ellioti	India	D, L, V	S	O	4.7–6.2	1.7–2.1	0.5
Uropeltis ceylanica	India	L	S	O	3.6–6.6	2.7–2.9	0.6–0.8

Distributional data are given for uropeltids. For each species, dimensions (μm) were measured from micrographs taken of dorsal (D), lateral (L), and/or ventral (V) scales. Oberhautchen cells were either strap (S) or rounded polygon (RP) shaped, and with overlapping (O) or level (L) borders.
[1]Data recorded from Price and Kelly (1989: fig. 8B).
[2]Data recorded from Gans and Baic (1977: fig. 2H).

to explore microornamentation character evolution on a selected phylogenetic hypothesis (see Discussion) using parsimony.

RESULTS

The dimensions of microornamentation features for the taxa observed are presented in Table 1. Aspects of microornamentation are described in the following section.

Outgroups

The three scolecophidian species examined from the three known families showed no notable intraspecific variation in the microornamentation of dorsal, lateral, and ventral midbody scales. In the leptotyphlopid *Leptotyphlops macrolepis* (Fig. 1a) and the anomalepidid *Liotyphlops ternetzii* (Fig. 1b), the cells are strap-shaped and have overlapping posterior borders with short denticulations. That this pattern is not common to all scolecophidians is demonstrated by the much longer, rounded polygonal cells with level, nonoverlapping, nondenticulate borders in the typhlopid *Typhlops mirus* (Fig. 1c).

The two species of cylindrophiid examined, *Cylindrophis maculatus* (Fig. 1e) and *C. ruffus* (Fig. 1f), also showed no notable intraspecific microornamentation variation with respect to the position of midbody scales. Both species share a similar microornamentation, with relatively short strap-shaped cells with overlapping posterior boundaries. These overlapping boundaries have denticulations that are much longer than in the scolecophidians examined. There are no signs of pores, but the occasional presence of matrix lying within larger pores/pits in uropeltids (see below; Gans and Baic, 1977) means that the presence of very small and/or diffuse pores/pits cannot be discounted.

The single anomochilid examined, *Anomochilus leonardi* (Fig. 1d), has a very similar microornamentation to that of *Cylindrophis* in terms of observable features and their dimensions. The microornamentation observed in *Cylindrophis* and *Anomochilus* is similar to that shown for a dorsal scale of the only known aniliid anilioid, *Anilius scytale,* by Price and Kelly (1989: fig. 8B). Shared similarities include the lack of obvious pores, the size of the strap-shaped

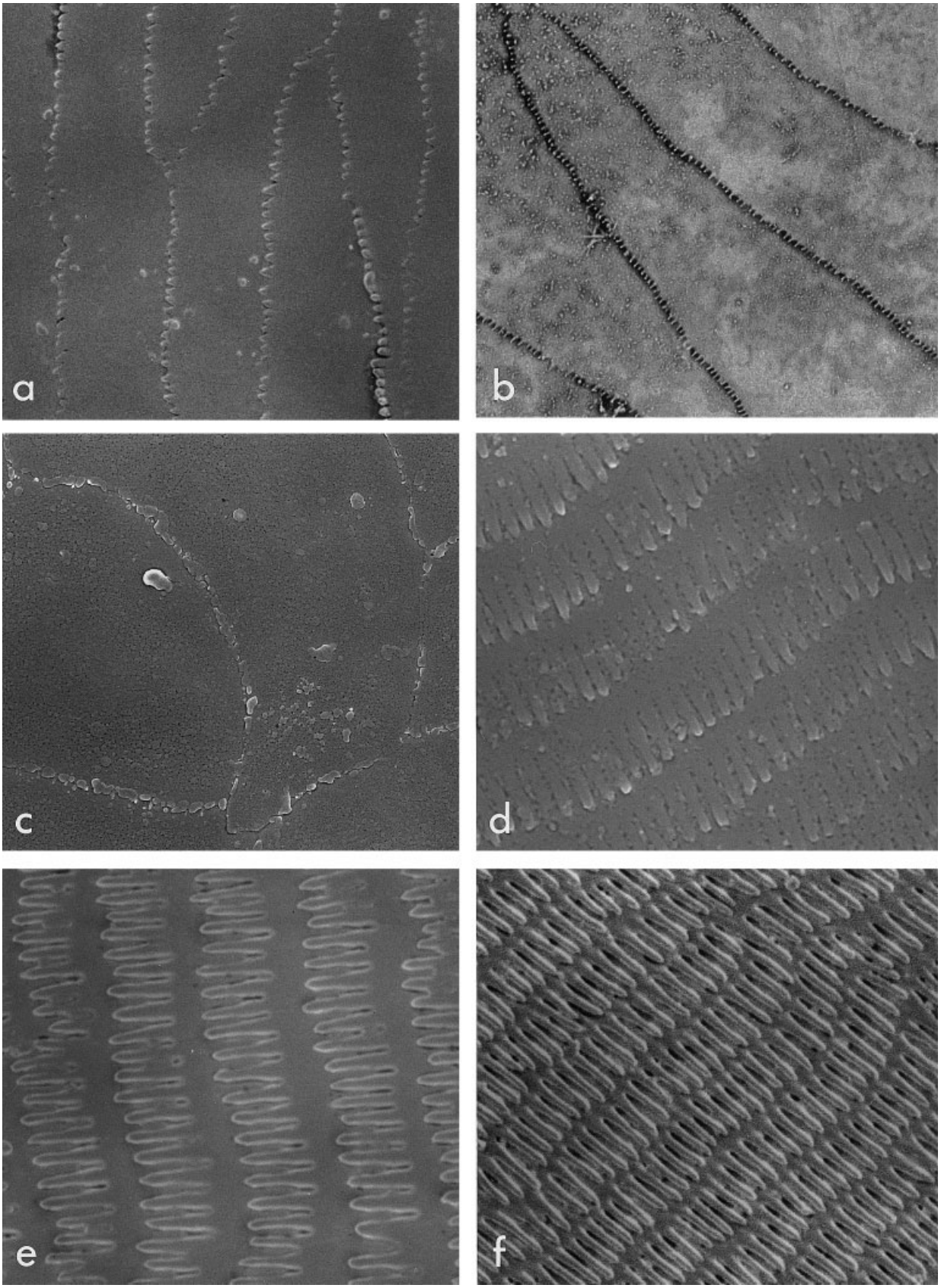

Fig. 1. Microornamentation of midbody scales of fossorial scolecophidian and anilioid snakes. **a:** Ventral scale of *Leptotyphlops macrolepis* (×3,500), 17.5 mm = 5 μm. **b:** Ventral scale of *Liotyphlops ternetzii* (×2,000), 10.5 mm = 5 μm. **c:** Ventral scale of *Typhlops mirus* (×2,500), 12.5 mm = 5 μm. **d:** Ventral scale of *Anomochilus leonardi* (×6,500), 33 mm = 5 μm. **e:** Ventral scale of *Cylindrophis maculatus* (×8,000), 11.5 mm = 2 μm. **f:** Ventral scale of *Cylindrophis ruffus* (×6,500), 33 mm = 5 μm. Anterior of scale is in the direction of right of photographs **a,e**, the upper right of **b,c**, and upper left of **d,f**.

cells, and posterior denticulations on the overlapping cell boundaries.

None of these outgroup taxa exhibits any substantial elaboration of their flat oberhautchen surfaces, such as ridges or pustular projections. Pits or pores are absent or very small.

Melanophidium

In common with the scolecophidians and other anilioids examined, the oberhautchen cells in *Melanophidium* (Fig. 2) are flat. As with other uropeltids (see below), the oberhautchen surface is more textured than in scolecophidians and non-uropeltid anilioids. However, all three currently known species of *Melanophidium* share a common microornamentation that is markedly different from that seen in any other anilioid. Most notably, the cells are not strap-shaped but are instead rounded polygons. They are longer than they are wide, with a longitudinal dimension that is much greater than other anilioids and greater than in some other uropeltids by an order of magnitude. In contrast to other anilioids, the oberhautchen cell posterior margins lack denticulations. Cell borders are not overlapping. The oberhautchen surface is covered by low, narrow, and finely spaced longitudinal ridges. These mostly extend across the length of a cell without breaking or merging with other ridges. They are low and thus do not continue across cell borders, but they are generally aligned with ridges on the adjacent posterior and anterior cells. Regularly sized pits/pores are closely packed in single lines between the ridges. There is no substantial variation in microornamentation around the midbody circumference.

Brachyophidium, Teretrurus, Platyplectrurus

Brachyophidium and *Teretrurus* are monotypic genera. *Brachyophidium rhodogaster* (Fig. 3a), *T. sanguineus* (Fig. 3c), and the single species of *Platyplectrurus* examined, *P. trilineatus* (Fig. 3b), all possess flat, strap-shaped oberhautchen cells, with no substantial variation in microornamentation around the midbody circumference. The cells are of a not dissimilar length in the three genera and all three species examined have cells with fairly long posterior denticulations that overlap the bordering cells. The denticulations in *B. rhodogaster* are more slender than those in the other two genera and they are so long relative to the cell length that the exposed oberhautchen surface is almost entirely composed of denticulations (Fig. 3a). There are no ridges on the oberhautchen surface in these three species. There are relatively large, oval-shaped pits/pores. Their shape and distribution are more irregular than in, e.g., *Melanophidium*, and some occur on the proximal ends of the denticulations.

Plectrurus perrotetii

The oberhautchen cells are flat and strap-shaped (Fig. 3d), with no substantial variation in microornamentation around the midbody circumference. The maximum length of measured cells is longer than in any other genus of uropeltid examined except *Melanophidium*. The posterior margins of the cells have small denticulations and they overlap the bordering cells. Relatively large, oval-shaped pits/pores are distributed in single-file lines that are approximately parallel with the longitudinal axis of the scale. The areas between lines of pores/pits do not appear to form clear, raised ridges. The lines of pores/pits and narrow regions between them tend to become less clearly defined towards the posterior border of each cell.

Rhinophis

The seven species of Indian and Sri Lankan *Rhinophis* examined (Fig. 4) share a number of features. They all have flat, strap-shaped oberhautchen cells, with no substantial variation in microornamentation around the midbody circumference. While there is a fairly narrow range of maximum cell lengths (Table 1), the two Indian species (*R. sanguineus* and *R. travancoricus*) are at the lower end of this spectrum. The posterior margins of the cells in all examined species have small denticulations, shorter than 1.5 μm. All examined species have relatively large, oval-shaped pores/pits that are mostly regularly distributed in lines parallel to the long axis of the scale. Each aligned row of pores/pits is bordered on each side by a smooth surface that may form very low ridges. Against this common pattern, many of the features of which are found in species in other genera, there are a few variations in microornamentation among species of *Rhinophis*. While most variations are subtle, the most notable one is whether the posterior margins are overlapping (*R. sanguineus, R. travancoricus, R. oxyrhynchus, R. homolepis*) or level (*R. philippinus, R. blythii, R. drummondhayi*). There may be a small amount of variation in how clearly defined the ridges between lines of pores/pits are, being apparently lower and less regular in, for example, *R. sanguineus,* and apparently higher and more regular in, for example, *R. blythii* (Fig. 4c) and *R. philippinus* (Fig. 4d; Gans and Baic, 1977: fig. 2G). There is also variation in the shape and packing of the posterior denticulations; compare, for example, *R. sanguineus* (Fig. 4a) with *R. travancoricus* (Fig. 4b).

Pseudotyphlops philippinus

The oberhautchen cells of *Pseudotyphlops philippinus* (Fig. 5a) are flat and strap-shaped, with lengths at the upper range of uropeltids other than *Melanophidium* (Table 1). The posterior margins of

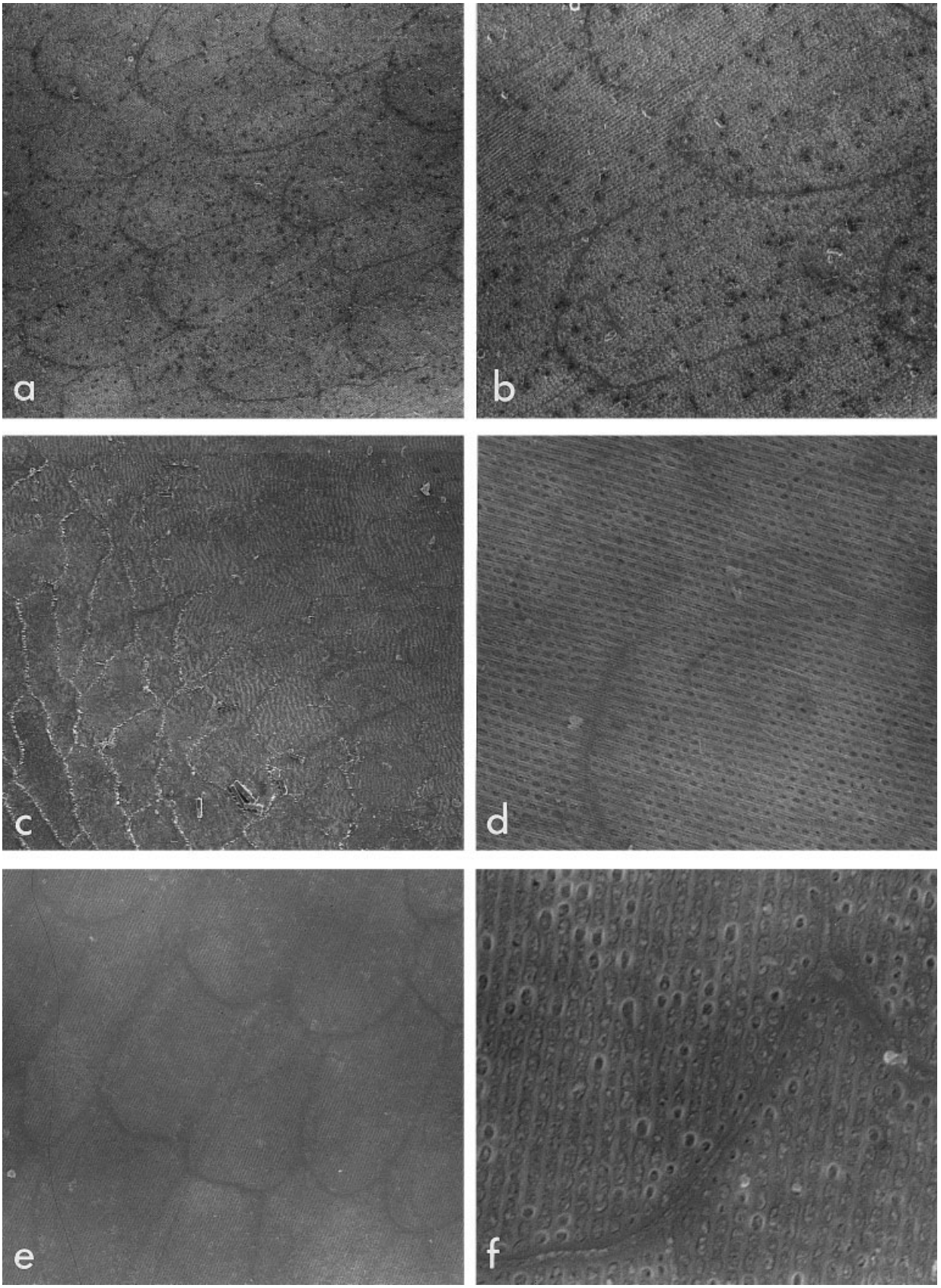

Fig. 2. Microornamentation of midbody scales of the uropeltid snake *Melanophidium*. **a:** Dorsal scale of *Melanophidium bilineatum* (×1,000), 10.5 mm = 10 μm. **b:** Dorsal scale of *Melanophidium bilineatum* (×2,000), 10.5 mm = 5 μm. **c:** Basal region of lateral scale of *Melanophidium punctatum* (×500), showing transition from short, strap-shaped to long, rounded cells, 25.5 mm = 50 μm. **d:** Lateral scale of *Melanophidium punctatum* (×5,000), 25.5 mm = 5 μm. **e:** Lateral scale of *Melanophidium wynaudense* (×1,500), 30.5 mm = 20 μm. **f:** Ventral scale of *Melanophidium wynaudense* (×8,000), 16.5 mm = 2 μm. Anterior of scale is to lower left of photographs **a,b,c,e**, to upper left of **d**, and bottom of **f**.

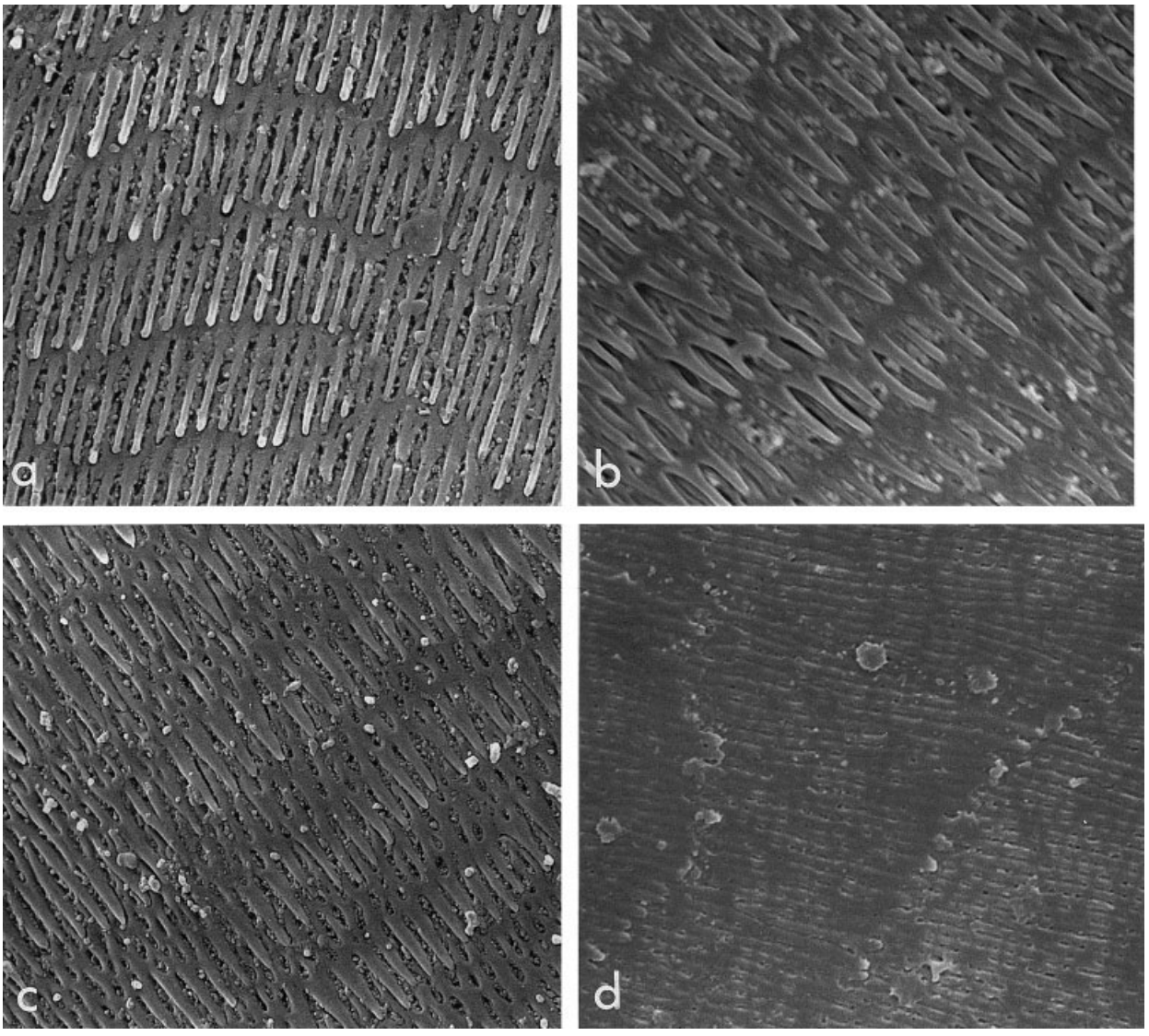

Fig. 3. Microornamentation of midbody scales of uropeltid snakes. **a:** Ventral scale of *Brachyophidium rhodogaster* (×6,500), 33 mm = 5 μm. **b:** Dorsal scale of *Platyplectrurus trilineatus* (×6,500), 33 mm = 5 μm. **c:** Lateral scale of *Teretrurus sanguineus* (×6,500), 33 mm = 5 μm. **d:** Dorsal scale of *Plectrurus perrotetii* (×5,000), 21.5 mm = 5 μm. Anterior of scale is to upper right of photograph **a**, to upper left of **b,c**, and to left of **d**.

each cell bear short, irregular denticulations. The cell borders are level rather than overlapping. There is a high density of relatively large (though small relative to the wavelength of most visible light, see Discussion) pores/pits. These are generally a little longer than they are wide and their long axes are generally aligned with the long axis of the whole snake. This alignment of pores/pits gives an initial impression that each line is bordered on either side by low, longitudinal ridges, and this is especially so in areas where matrix fills the pores/pits without covering the thin areas between them (see upper central part of Fig. 5a). However, although the areas between the sides of the pores/pits appear to be slightly higher than those between the ends (approximately anterior and posterior, relative to the long axis of the body) of the pores/pits, these areas do not appear to be raised above the level of the cell borders, and so form nothing more than very low ridges. There is no substantial variation in microornamentation around the midbody circumference.

Indian *Uropeltis*

The three Indian species of *Uropeltis* examined have a very similar scale microornamentation (Fig. 5d–f). The oberhautchen cells are flat, strap-shaped, and of a similar length (Table 1). There are no substantial variations in microornamentation around the midbody circumference in any of these species. The posterior cell margins overlap the adjacent cells

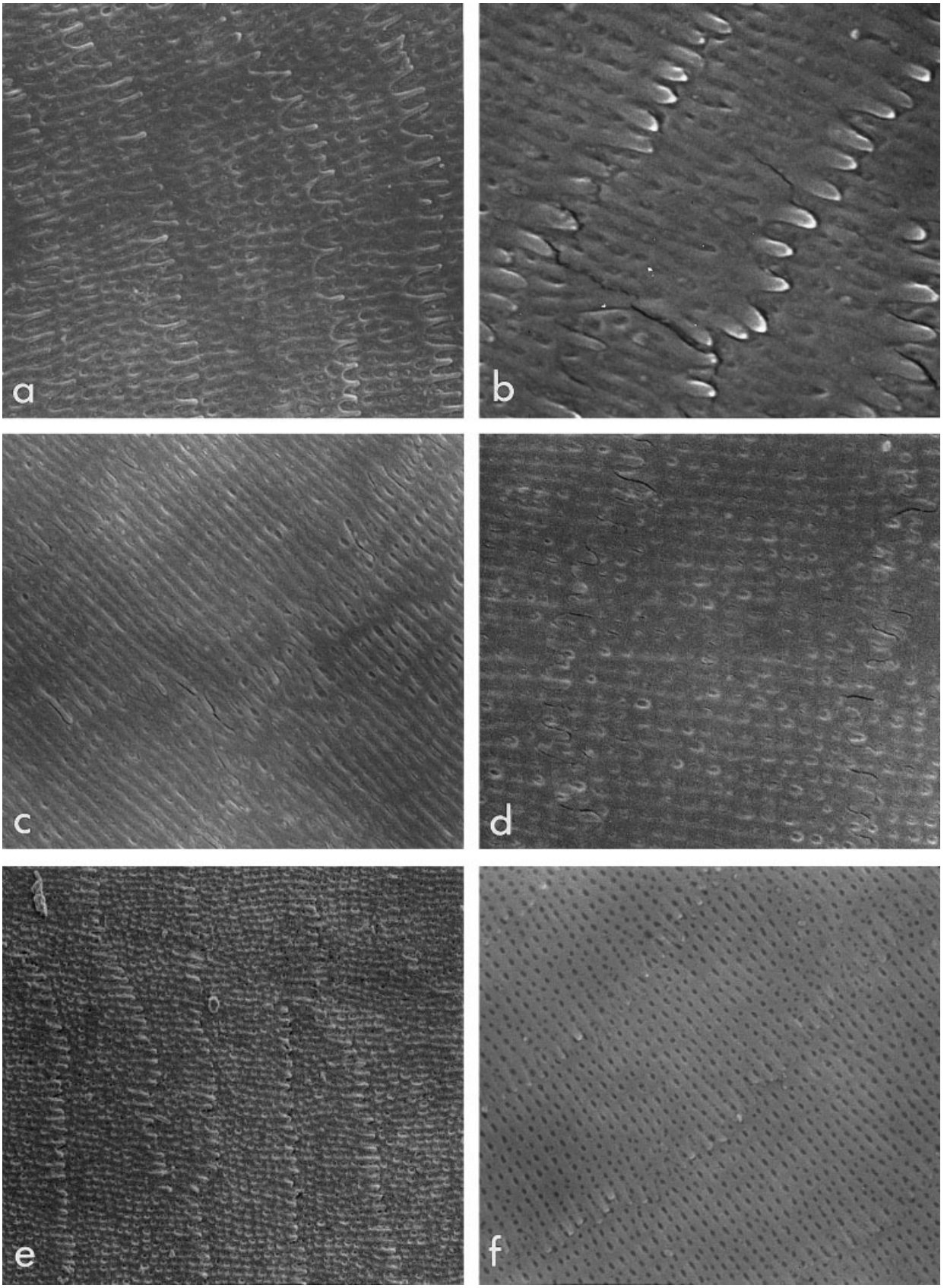

Fig. 4. Microornamentation of midbody scales of uropeltid snakes. **a:** Dorsal scale of *Rhinophis sanguineus* (×5,000), 26.5 mm = 5 μm. **b:** Lateral scale of *Rhinophis travancoricus* (×10,000), 30.5 mm = 3 μm. **c:** Dorsal scale of *Rhinophis blythii* (×6,500), 33 mm = 5 μm. **d:** Dorsal scale of *Rhinophis philippinus* (×8,000), 16.5 mm = 2 μm. **e:** Dorsal scale of *Rhinophis oxyrhynchus* (×3,500), 18 mm = 5 μm. **f:** Dorsal scale of *Rhinophis homolepis* (×5,000), 25.5 mm = 5 μm. Anterior of scale is to lower left of photograph **a**, to upper left of **b,c,f**, and left of **d,e**.

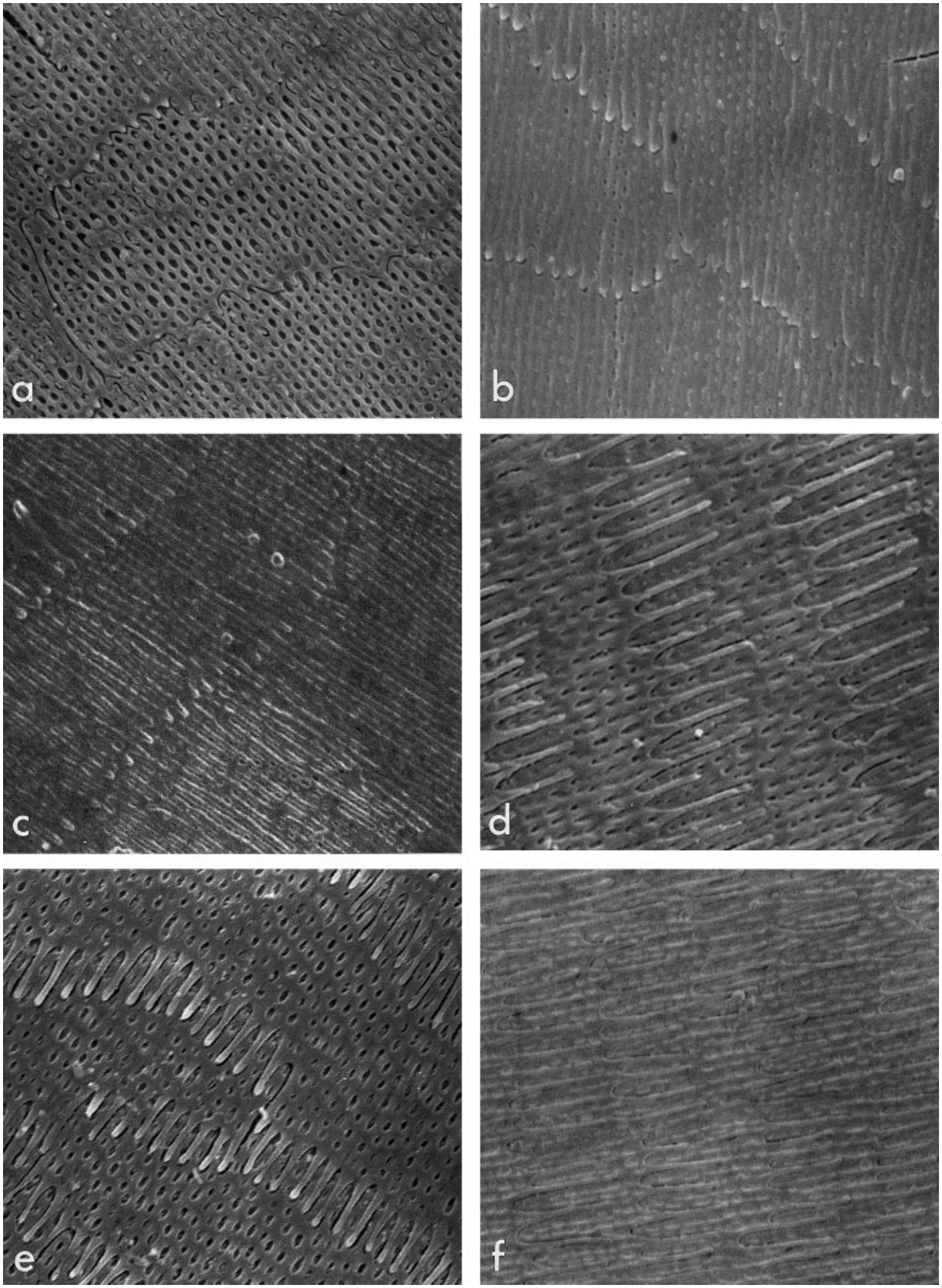

Fig. 5. Microornamentation of midbody scales of uropeltid snakes. **a:** Dorsal scale of *Pseudotyphlops philippinus* (×5,000), 25.5 mm = 5 μm. **b:** Ventral scale of *Uropeltis phillipsi* (×6,500), 33 mm = 5 μm. **c:** Ventral scale of *Uropeltis melanogaster* (×5,000), 26.5 mm = 5 μm. **d:** Ventral scale of *Uropeltis phipsonii* (×8,000), 11.5 mm = 2 μm. **e:** Ventral scale of *Uropeltis ellioti* (×6,500), 34 mm = 5 μm. **f:** Lateral scale of *Uropeltis ceylanica* (5,000), 25.5 mm = 5 μm. Anterior of scale is to upper left of photographs **a,c**, top of **b**, lower left of **d**, upper right of **e**, and left of **f**.

and they bear long, slender denticulations. These are longer in all three species than in any species of *Rhinophis* examined. They are a little longer and more slender in *U. phipsonii* (Fig. 5d) and *U. ceylanica* (Fig. 5f) than in *U. ellioti* (Fig. 5e). There are relatively large, oval-shaped pores/pits arranged in approximately longitudinal rows and separated by smooth, low ridges. The pores/pits appear to be more irregular in size and shape, and less densely packed, than in species of, for example, *Melanophidium*.

Sri Lankan *Uropeltis*

Two Sri Lankan species of *Uropeltis* were examined, *U. phillipsi* (Fig. 5b) and *U. melanogaster* (Fig. 5c). Both species have flat, strap-shaped cells of similar size, with short posterior denticulations, and with no substantial variation in microornamentation around the midbody circumference. There are longitudinal rows of relatively large, oval-shaped pores/pits separated by low ridges. The microornamentation of *U. phillipsi* and *U. melanogaster* is much more similar to that of the species of *Rhinophis* examined than to that of the Indian species of *Uropeltis*.

Summary of Taxonomic Variation

The microornamentation of midbody scales of these fossorial snakes is low in diversity and essentially homogenous around the midbody circumference. All oberhautchen cells are flat and they lack raised borders and prominent elaboration of their surface into, for example, prominent projections. The mean distance between denticulations (= transverse distance along posterior cell margin divided by number of denticulations) does not vary widely within uropeltids (0.4–0.9 μm), within the outgroup taxa examined (0.3–0.5 μm), or among both groups. Among uropeltids, there is a close approximation between the number of posterior denticulations and, where discernible, the number of longitudinal lines of pores/pits and ridges. In no species examined do the number of denticulations outnumber the ridges or lines of pores/pits, and the maximum width of the pores/pits and ridges are less than the mean distance between denticulations. There is some variation in the slenderness of the denticulations among taxa, so that in some species (e.g., *Uropeltis phipsonii*, Fig. 5d) the spaces between denticulations are clearly larger in area than the denticulations themselves, while in other species (e.g., *Anomochilus leonardi*, Fig. 1d) the reverse is true. This feature was not formally scored for each species examined in this study because of cases where the relationship is unclear or variable (e.g., Figs. 4b, 5b). In those species where denticulations are relatively long, they appear more regular in size on any given scale than in species with short denticulations. Greater denticulation regularity also appears in those taxa with overlapping cell boundaries.

TABLE 2. Characters and states of midbody scale microornamentation in Uropeltidae and outgroups

Taxon	Character 1	2	3	4	5	6
Leptotyphlops macrolepis	0	1	0	2	1	1
Liotyphlops ternetzii	0	1	0	2	1	1
Typhlops mirus	1	0	0	2	0	0
Anomochilus leonardi	0	1	0	0	1	2
Anilius scytale	0	1	0	0	1	2
Cylindrophis maculatus	0	1	0	0	1	2
Cylindrophis ruffus	0	1	0	0	1	2
Melanophidium bilineatum	1	0	1	2	0	0
Melanophidium punctatum	1	0	1	2	0	0
Melanophidium wynaudense	1	0	1	2	0	0
Teretrurus sanguineus	0	1	1	0	2	2
Plectrurus perrotetii	0	1	1	1	1	1
Brachyophidium rhodogaster	0	1	1	0	2	3
Platyplectrurus trilineatus	0	1	1	0	2	3
Pseudotyphlops philippinus	0	0	1	0	1	1
Rhinophis sanguineus	0	1	1	0	1	1
Rhinophis travancoricus	0	1	1	0	1	1
Rhinophis drummondhayi	0	0	1	?	1	1
Rhinophis blythii	0	0	1	0	1	1
Rhinophis philippinus	0	0	1	0	1	1
Rhinophis oxyrhynchus	0	1	1	0	1	1
Rhinophis homolepis	0	1	1	0	1	1
Uropeltis phillipsi	0	1	1	0	1	1
Uropeltis melanogaster	0	1	1	0	1	1
Uropeltis phipsonii	0	1	1	0	2	2
Uropeltis ellioti	0	1	1	0	2	2
Uropeltis ceylanica	0	1	1	0	2	2

See text for description of characters and character states.

Microornamentation Characters

Six characters were formulated from variation in microornamentation features. The distribution of the observed character states among the taxa examined is given in Table 2. There are often multiple possible approaches to character construction, and these can have important implications for phylogenetic analysis and studies of character evolution (e.g., Wilkinson, 1995; Harris et al., 2003). Although some of the characters formulated here fell into discrete states, those based on dimensions were divided into potentially arbitrary states.

1. Cell shape. Cells were scored as either wider than long and strap-shaped (0), or longer than wide and polygonal (1). There have been questions raised about the homology of various shaped and sized enclosures visible on the surface of squamate scales (Harvey, 1993; Harvey and Gutberlet, 1995), but I follow Arnold (2002a) in considering, for example, the large polygons of *Melanophidium* and *Typhlops mirus* homologous with the strap-shaped cells of

other scolecophidians and anilioids. Support for this also comes from the rapid but gradual transition from a basal microornamentation with strap-shaped cells to a more apical one with rounded, polygonal cells in *M. punctatum* (Fig. 2c).

2. Cell borders. The contact between oberhautchen cells was scored as either imbricate (0), or level (1). In state 1, posterior denticulations (where present) interdigitate with adjacent cells.

3. Pores/pits. Microornamentation was characterized as having either no or very small pores/pits, such that the oberhautchen surface appears unperforated at magnifications of up to ×10,000 (0), or as having clear pores/pits at this and lower magnifications (1).

4. Cell length. The range of maximum cell lengths (Table 1) was divided into three discrete character states: less than 10 μm (0), more than 10 μm but less than 20 μm (1), or more than 20 μm (2). This character was ordered 0-1-2 following the reasoning given by Wilkinson (1992).

5. Denticulations and their length. The presence and range of lengths of denticulations was divided into three discrete, ordered character states: absent (0), present and less than 1.7 μm (1), or up to lengths of 2 μm and longer (2).

6. Denticulation length: cell length. Two alternative formulations of ordered characters based on this relationship were explored. Formulation 6A has three states: denticulations absent (0), <50% of cell length (1), or = 50% of cell length (2). Formulation 6B has four states: denticulations absent (0), <50% of cell length (1), 51–80% of cell length (2), or >80% of cell length (3). The different formulations had no bearing on the reconstruction of character states on internal branches, and so only version 6B is used here (Table 2). This character is logically linked to the two characters (4 and 5) describing variation in the absolute length of cells and denticulations.

DISCUSSION

Variation

Previous studies of microornamentation in squamates have found intraspecific variation associated with ontogeny, body region, scale size and structure, position on scale, and sloughing cycle (e.g., Stewart and Daniel, 1972, 1975; Peterson and Bezy, 1985; Bea, 1986; Irish et al., 1988; Bezy and Peterson, 1988; Price and Kelly, 1989; Harvey, 1993). A major limitation of this study is that detailed explorations of intraspecific variation were not carried out. However, some variations were noted. Other than dimensions of measured features (Table 1), variations were observed in microornamentation along the length of any given scale. In general, the morphology of the basal part of any given scale was notably different from that on the more distal parts of the scale that are not overlapped by the preceding scale. Even in taxa recorded here as having polygonal cells, such as *Melanophidium* spp., the cells at the very basal (proximal) end of the examined scales were lenticular to strap-shaped, with the transition to polygonal cells occurring over a very short distance (e.g., *Melanophidium punctatum*, Fig. 2c). The focus of this study is microornamentation of scale surfaces in contact with soil in burrowing snakes, but these basal regions and the transition to a more apical microornamentation are clearly worthy of investigation (e.g., Price and Kelly, 1989).

Arnold (2002a:157) found for lacertids that "Dorsal and ventral scale microornamentation can clearly evolve independently of each other," but in this study no major variations in microornamentation were found with the position of scales around the midbody circumference. Microornamentation of scales from other regions of fossorial snakes is also worthy of future investigation.

The most obvious variation possibly associated with the sloughing cycle (although this variable was not directly assessed for the material examined) was in the amount of scratching of the oberhautchen surface, presumably caused by mechanical wear. In the *Plectrurus perrotetii* examined, the posterior cell denticulations almost all overlap with adjacent cells, but this is less clear in some small regions where the cell borders appear level (Fig. 3d). In some other species, such as *Cylindrophis maculatus*, the extent to which the denticulations are flat against, or slightly raised from, the surface of the adjacent cells was seen to vary. It might be that the overlapping becomes developed or increases as the oberhautchen surface ages.

Correlation occurs among some characters. For example, all the species observed with polygonal cells (*Typhlops mirus* and the three species of *Melanophidium*) were also the only species with very long (>20 μm) cells that lack denticulations on the posterior cell margins. They were also among the species with level, rather than imbricate cell borders. Some previous studies have found correlation between scale size and certain, usually complex, derived microornamentation features in squamates (e.g., Bezy and Peterson, 1988; Arnold, 2002a). Scale size has not been quantified for the species examined here, but there is variation among taxa. For example, species of *Melanophidium* have large ventral scales compared with other uropeltids and counts of midbody scale rows (15) at the lower end of uropeltid variation. However, that the distinctive microornamentation of these species and their relatively large scales are not completely correlated is demonstrated by a very similar number of scale rows in some other uropeltid genera (*Brachyophidium, Platyplectrurus, Plectrurus, Teretrurus*) and microornamentation character states shared with small (and small scaled) scolecophidians.

Uropeltid Microornamentation

In life, the bodies of uropeltids are smooth and give off an iridescent shine (Gans and Baic, 1977; pers. obs.). While shine might have been expected to be caused by essentially flat, smooth scale microornamentation with features generally smaller than the wavelength of most visible light (0.4–7.0 μm; see Arnold, 2002a), this had only been shown previously for a couple of species by Gans and Baic (1977). The survey presented here confirms that body scale microornamentation in uropeltids is flat, with generally very low and regular, narrow ridges parallel with the long axis of the body, and pores/pits. Pores/pits were also observed by Gans and Baic (1977), who considered them to be randomly spaced in the few species they examined. The regularity of the pores/pits varies among the taxa surveyed in this study with the pattern in, for example, *Melanophidium* being decidedly regular. The association between shine and flat, relatively smooth oberhautchen cells also holds for scolecophidians and at least *Cylindrophis* (pers. obs.).

The main variations in microornamentation among uropeltids (and the outgroups examined here) are confined to cell size and shape, cell posterior margins (presence and form of denticulations), and cell borders (overlapping or level). Gans and Baic (1977) stated that microornamentation patterns in uropeltids were species-specific. This current survey shows that some different species within genera may differ in their microornamentation to only a very minor degree, and more detailed study is required to ascertain whether species specificity is universal among uropeltids.

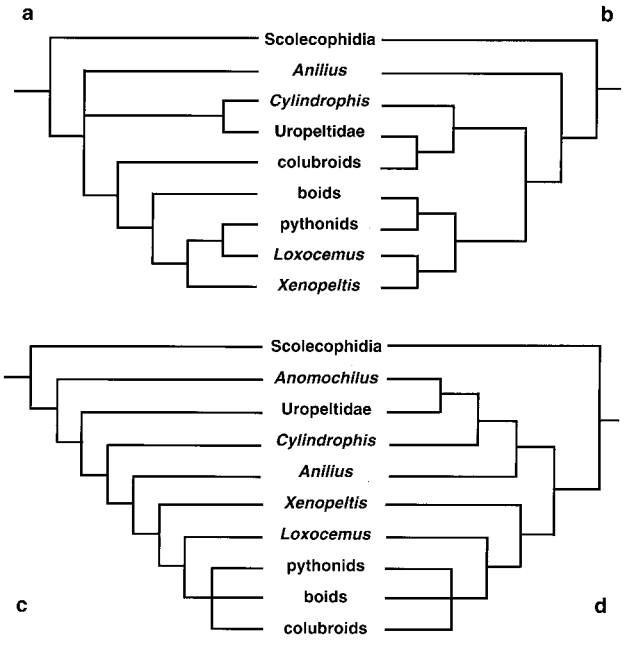

Fig. 6. Higher-level snake phylogeny. **a:** From Slowinski and Lawson's (2002) analysis of nuclear and mitochondrial DNA sequence data. **b:** From Wilcox et al.'s (2002) analysis of mitochondrial DNA sequence data. **c:** From Cundall et al.'s (1993) analysis of morphological data. **d:** From Tchernov et al.'s (2000) analysis of osteological data.

History

Phylogeny. The present study is an insufficient basis to conduct an independent phylogenetic analysis. For the purposes of exploring the potential phylogenetic signal of microornamentation characters in the sampled taxa, and for examining possible patterns of character evolution, an incompletely resolved phylogenetic hypothesis was selected (Figs. 8–13). Monophyly of Uropeltidae is assumed (e.g., data presented by Underwood, 1967; Rieppel, 1977) and the relationships of this clade to the outgroups is a strict consensus of the recent hypotheses (Fig. 6) presented by, for example, Cundall et al. (1993), Tchernov et al. (2000), Slowinski and Lawson (2002), and Wilcox et al. (2002). The relationships within Uropeltidae are compiled from various sources, although only two explicit phylogenetic analyses have been published, using largely nonoverlapping sets of taxa (Cadle et al., 1990; Rieppel and Zaher, 2002; see Fig. 7). The monophyly of *Melanophidium* is tentatively entertained (despite the findings of Rieppel and Zaher, 2002), and its position as sister taxon to all other uropeltids follows morphological evidence presented by Underwood (1967), Rieppel (1977), and Rieppel and Zaher (2002). The monophyly of Sri Lankan uropeltids and their sister relationship to Indian *Rhinophis* partly follows Cadle et al.'s (1990) phylogeny estimated from immunological and electrophoretic data. The same study forms the basis of the provisional acceptance of the monophyly of Indian *Uropeltis* and their sister relationship to *Teretrurus*. The relationships of *Brachyophidium, Plectrurus,* and *Platyplectrurus* are left unresolved within uropeltids other than *Melanophidium*. Clearly, hypotheses of relationships of many uropeltids are yet to stabilize, and the framework hypothesis used here will need to be reassessed.

Character evolution. Character states shown in Table 2 were used to reconstruct states on internal branches of the selected phylogenetic hypothesis (Figs. 8–13). The ancestral microornamentation for several groups of squamates has been considered to comprise generally smooth, flat, strap-shaped oberhautchen cells (see Arnold, 2002a), and this may hold true for snakes also (although this morphology is not present in the scolecophidian *Typhlops mirus)*. Homoplasy is implied for all but one of the characters generated here when mapped onto the phylogeny. Parsimonious optimization of character 3 (Fig. 10) suggests that at least relatively large pores/pits were acquired once and were present in the ancestral uropeltid. All but one of the character states

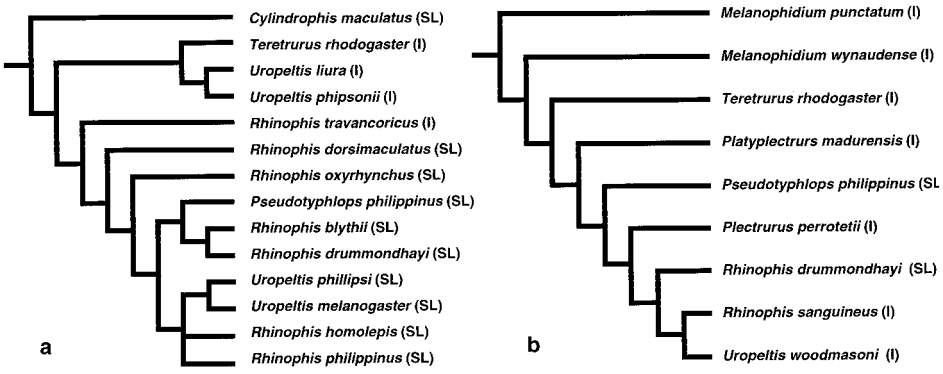

Fig. 7. Lower-level phylogeny of uropeltid snakes following the only existing numerical, explicit analyses published to date. **a:** Cadle et al.'s (1990) preferred hypothesis derived from electrophoretic and albumin immunological data. **b:** Rieppel and Zaher's (2002) hypothesis derived from (largely cranial) osteological data. Taxonomic nomenclature follows McDiarmid et al. (1999), except for "*Teretrurus rhodogaster*" which is likely to be *T. sanguineus* or *Brachyophidium rhodogaster*, the only currently recognized species in these two monospecific genera. Indian (I) and Sri Lankan (SL) species are indicated.

seen in *Melanophidium* are found in other taxa considered here, particularly one or more of the scolecophidian outgroups, and probably represent multiple origins. Some of the probable instances of independent origins, such as a level cell border in *Melanophidium* and some Sri Lankan uropeltids (Fig. 9), require increased phylogenetic resolution to ascertain the number of times this may have occurred independently.

The order of change in lineages with derived states has not been explored in detail because of a lack of phylogenetic resolution, equivocal character state reconstructions, and covariation in several characters. Concerning *Melanophidium*, for example, characters with derived states covary completely in their distribution, and reconstructed character states for the branch by which this clade is subtended to the rest of the tree are equivocal for all but character 3 (Fig. 10).

Some previous studies of microornamentation in other groups of squamates have concluded that reversals in microornamentation character states are

Fig. 8. Distribution of cell shape character states, with internal branches reconstructed by parsimony using MacClade 3.01: wider than long and strap-shaped (0) and longer than wide and rounded/polygonal (1).

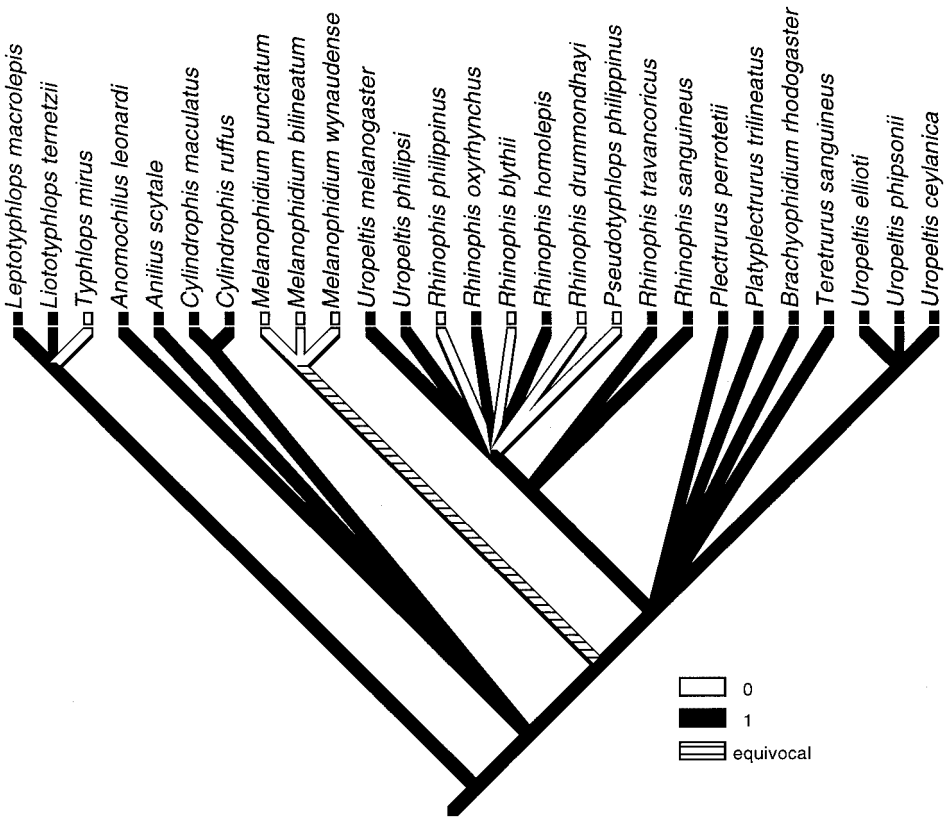

Fig. 9. Distribution of character states describing cell borders, with internal branches reconstructed by parsimony using MacClade 3.01: imbricate (0) and level (1).

uncommon (Arnold, 2002a) or even that microornamentation characters might be unidirectional (Burstein et al., 1974) in their evolution. Potential character state reversals in microornamentation of the taxa studied here require a more fully resolved phylogeny for confirmation. This includes, for example, the possible reversal back to relatively long denticulations in Indian *Uropeltis, Teretrurus, Brachyophidium,* and *Platyplectrurus* (Fig. 13). Evidence for reversal to a smooth microornamentation in other groups of snakes is contained in McCarthy's (1987) report of smooth scales in sea snakes, but ridged scales among some terrestrial elapids that probably constitute the proximate outgroups.

Phylogenetic signal in microornamentation. All the characters explored are congruent with the monophyly of *Melanophidium*, and all but character 3 (pores/pits) support this monophyly, although these are all homoplastic across the tree as a whole. All characters are congruent with the hypothesis that *Teretrurus* is more closely related to Indian *Uropeltis* than to Sri Lankan *Uropeltis* and *Rhinophis*. Characters 5 and 6, describing the variation in the absolute and relative length of denticulations, support the hypothesis that *Brachyophidium* and *Platyplectrurus* are more closely related to Indian *Uropeltis* (and *Teretrurus*) than to *Rhinophis* (and Sri Lankan *Uropeltis*).

In the absence of any recent taxonomic revision and a well-resolved and robust phylogeny for Uropeltidae, assessment of potential phylogenetic signal in variations in scale microornamentation is necessarily limited. Uropeltid phylogeny needs to be investigated further with an expanded dataset. The strongest potential signal in uropeltid microornamentation comes from the putative synapomorphies of *Melanophidium*, but the monophyly of this genus requires further testing. In other squamates, microornamentation has generally been found to be homoplastic at higher levels, but also to contain some phylogenetic signal, especially at relatively low taxonomic levels (e.g., Harvey, 1993; Harvey and Gutberlet, 1995; Arnold, 2002a).

Function

Shine and iridescence. Gans and Baic (1977) concluded that iridescence of uropeltid body scales resulted from interference colors generated by reflection off regularly and finely spaced microornamentation ridges. They also concluded that iridescence was a by-product of a microornamentation selected for its dirt-shedding capability and is not itself necessarily adaptive. Iridescence occurs in many organisms, where interference colors (e.g., Nelkon, 1958) are usually generated by reflection from regular ridges or multiple stacked layers (equivalent to thin films). It has been considered functional in several groups of organisms; for example, in visual communication (e.g., butterfly wing

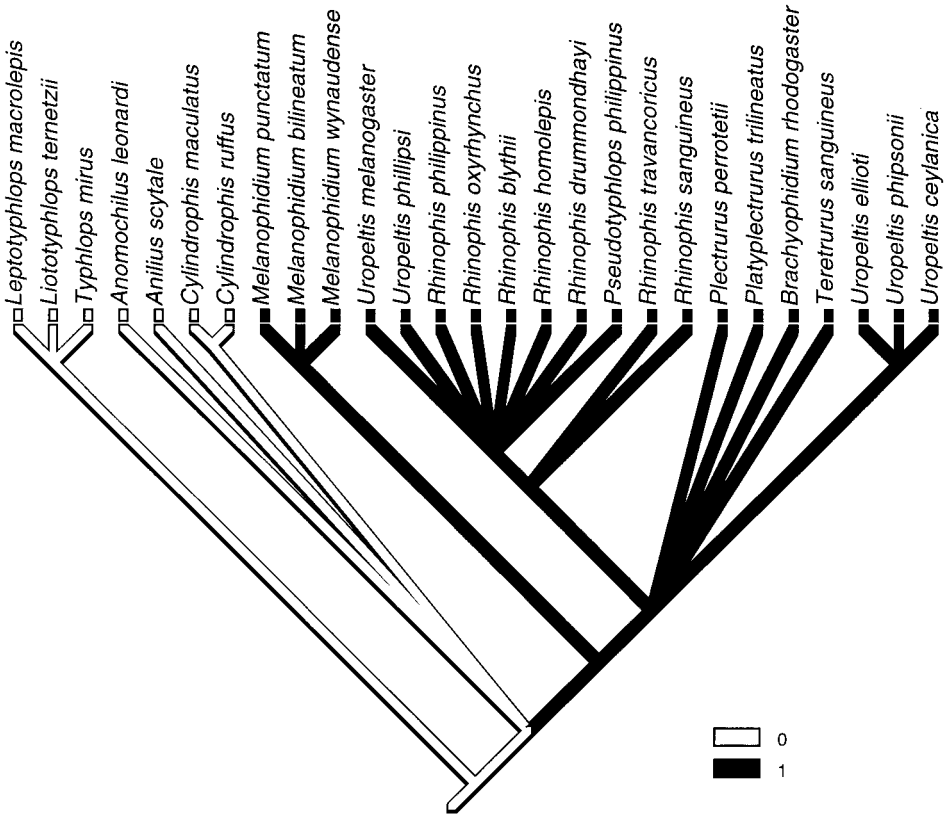

Fig. 10. Distribution of character states describing pores/pits, with internal branches reconstructed by parsimony using MacClade 3.01: pores/pits absent or very small (0) and present, clearly visible at magnifications of <10,000 (1).

scales: Vukusic et al., 1999; spines of the sea mouse *Aphrodita*: Parker et al., 2001) and potentially in thermoregulation (solar collectors in butterfly wings: Miaoulis and Heilman, 1998; but see Koon, 1999). No plausible adaptive explanations have been forwarded for scale iridescence in snakes that spend most of their time in soil. However, Gans and Baic's (1977) understanding that finely and regularly spaced ridges assist dirt-shedding has also yet to be fully explained or demonstrated. Iridescent scales are present in several independent lineages of fossorial or semifossorial snakes, including the Old and New World sunbeam snakes *Loxocemus bicolor* and *Xenopeltis* (e.g., Greene, 1997), respectively, and colubroids such as the south Asian *Xylophis* and *Aspidura* (pers. obs.) and the North American mudsnakes *Farancia* (e.g., Werler and Dixon, 2000). These snakes might also be expected to have narrow and finely and regularly spaced ridges formed either on the main body of oberhautchen cells or by overlapping, slender denticulations on their borders.

No attempt was made to quantify iridescence in the species examined for this study, although some variations among taxa were noted. For example, body scales of species of *Melanophidium* are highly iridescent and appear to be more so than for species of *Uropeltis* and *Rhinophis*. Interestingly, species of *Melanophidium* appear also to have the most complete and regularly arranged microornamentation ridges of the species surveyed. Some species without any sign of microornamentation ridges whatsoever, such as *Anomochilus* (e.g., Zug et al., 2001: fig. 21.6) and *Cylindrophis* spp. (pers. obs.), are also iridescent. However, they do have long overlapping denticulations that effectively form incomplete ridges, and these are perhaps sufficient to effect interference colors upon reflection of light. Much smoother microornamentation is associated with shiny, but not iridescent scales, such as in *Typhlops mirus*. Smooth microornamentation has also been reported for dorsal body scales of the fossorial, limbless lizard *Anniella pulchra* (Stewart and Daniel, 1973), the amphisbaenian *Loveridgea ionidesi* (Irish et al., 1988), and the fossorial, limbless skink *Typhlosaurus* (Renous and Gasc, 1989). A brief examination of individuals of these taxa showed the body scales to be shiny but not iridescent (pers. obs. of BMNH material preserved in industrial methylated spirits).

Oberhautchen ridges and overlapping denticulations. The presence of narrow, regular ridges in independent lineages of fossorial taxa (predicted from scale iridescence in some instances) suggests that this microornamentation may offer performance advantages for life in soil, perhaps most by aiding in dirt shedding. Passive reduction of the adhesion of moist substrate onto scales requires a low energy surface, and one possibility is that the ridges are associated with this. It has been shown that insect wings (Wagner et al., 1996) and plant leaves (Barthlott and Neinhuis, 1997) with a micro-

Fig. 11. Distribution of ordered character states describing cell length, with internal branches reconstructed by parsimony using MacClade 3.01: <10 μm (0), >10 μm but <20 μm (1), and >20 μm.

relief (of papillae or regular ridges) are less wettable and more able to shed dirt than smooth wings/leaves. Based on data and theory from surface chemistry (see Wagner et al., 1996; Barthlott and Neinhuis, 1997, and references therein), it is thought that dirt particles are cleaned from a non-wettable solid surface by water if the adhesion between the particles and water is greater than between particles and the surface. This is more probable if the surface has a microrelief finer than the size of most particles, so that it is the size and spacing of three-dimensional microornamentation features as well as their presence that is of importance. The microrelief features on insect wings reported by Wagner et al. (1996) are mostly small papillae 0.3–0.5 μm apart, and this is similar to the spacing of ridges measured here for uropeltid snakes.

Wetting of a solid surface (such as scale oberhautchen) occurs when the molecules of a liquid (water) have a stronger attraction to the molecules of the surface than to each other, such that the forces of adhesion are stronger than those of cohesion. This can be assessed experimentally by measuring the contact angle of a drop of water on the oberhautchen. Smaller contact angles occur on more wettable surfaces. Generally, a contact angle of >90° is found on non-wettable surfaces, while much lower angles of <20° are found on the most wettable surfaces. A preliminary investigation of the contact angle of tap water on body scales was carried out for a few species on preserved specimens that were temporarily removed from industrial methylated spirit and superficially dried. This angle was found to be clearly >90° for *Melanophidium wynaudense, Uropeltis* spp., *Rhinophis philippinus*, and *Cylindrophis maculatus*. The angle is close to, but <90° for *T. mirus* and *T. reticulatus* (BMNH uncatalogued specimen), the latter being a larger species of typhlopid than *T. mirus*, but one that also has shiny, non-iridescent scales. This is a promising avenue for future research, but more data are required and fresh and preserved material needs to be compared (see below).

The functional significance of variations in the oberhautchen ridges and denticulations of uropeltids, if any, is difficult to ascertain. There are virtually no data on the relative dirt-shedding or burrowing ability and locomotory mechanics among different uropeltids, and very little data on their environmental preferences. Despite this, testable hypotheses can be forwarded. It may be that ridges on the main body of the oberhautchen cells, and overlapping denticulations are simply different ways of achieving a regularly ridged surface (that may assist dirt shedding), and that variations correspond to different environmental conditions experienced during the acquisition of these microornamentations. Additionally or alternatively, species with long overlapping denticulations on the posterior borders of cells might be expected to have more

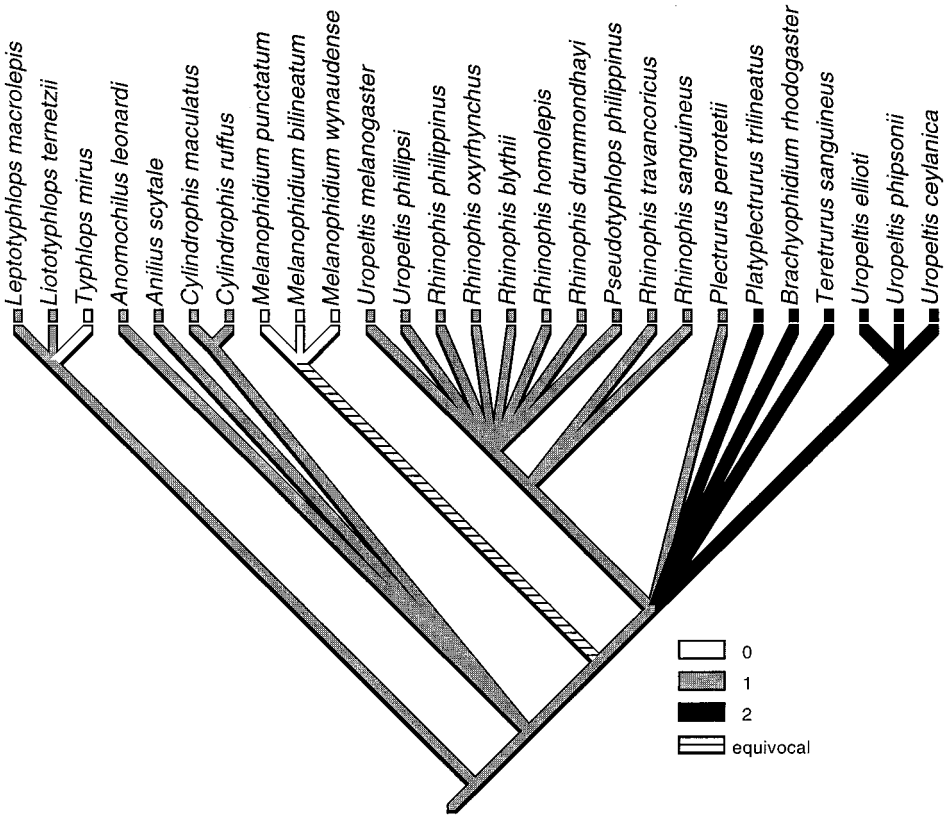

Fig. 12. Distribution of ordered character states describing cell posterior denticulations and their length, with internal branches reconstructed by parsimony using MacClade 3.01: absent (0), present and <1.7 μm (1) present and up to lengths of 2 μm and longer (2).

frictional resistance in a posterior to anterior direction than in those taxa lacking denticulations and/or having level, nonimbricating cell boundaries (see also Arnold, 2002a: 163). This conceivably might be associated with a particular mode of burrowing locomotion (see also Renous et al., 1985) and/or improved burrowing performance in particular substrate types. This can be tested experimentally on living material. Gans et al. (1978) reported ultrastructural and enzymatic differentiation in axial musculature along the length of the trunk of species of *Rhinophis* and Sri Lankan and Indian *Uropeltis*, and associated this with a particular mode of burrowing. Interestingly, Gans did not find this feature in *Pseudotyphlops* or *Teretrurus*, and thus it does not covary neatly with the scale microornamentation characters assessed here.

It should be borne in mind that information on the current habitat of species in the absence of experimental data is not necessarily a reliable indicator of the performance of ridged and smooth microornamentations in shedding dirt, because taxa with a range of microornamentations can be found in the same place (e.g., different species of uropeltids, Rajendran, 1985; scolecophidians and *Cylindrophis,* Presswell et al., 2002).

Oberhautchen pores/pits. Uropeltid body scale surfaces are not completely smooth, even between the ridges, but instead have pits/pores on their surfaces. These features are too small to substantially affect the reflection of light, but it is unclear how they affect dirt-shedding (as well as friction reduction). Closely packed pores or pits might serve to increase the non-wettability (and therefore increase the dirt-shedding ability) of the oberhautchen surface by reducing further the area of contact between water and the solid surface (see Barthlott and Neinhuis, 1997).

Arnold (2002a:167) found that a heavily pitted oberhautchen in lacertid lizards was generally found in forms inhabiting dry habitats and that "possibly it can only be sustained in such situations where adhesion is less of a problem, because pitted surfaces are perhaps more prone to hold dirt." However, considerations of surface chemistry (see above) mean that this may not necessarily be the case. In searching for a possible benefit of pitting, Arnold considered that pitted epidermis is cheaper to construct in terms of the amount of β-keratin required. For uropeltids, one other possibility is that the pits/pores enable substances to be released onto, or held on, the oberhautchen surface, and that this facilitates dirt shedding, and perhaps friction reduction. One problem with this hypothesis is that the possible pores in uropeltids are perhaps too small to allow even the thinnest of liquids to be extruded. Chiasson and Lowe (1989) speculated that depressions on the oberhautchen surface of aquatic colubrid snakes may hold possibly waterproofing oils, and this was supported by the discovery of the esters of at least

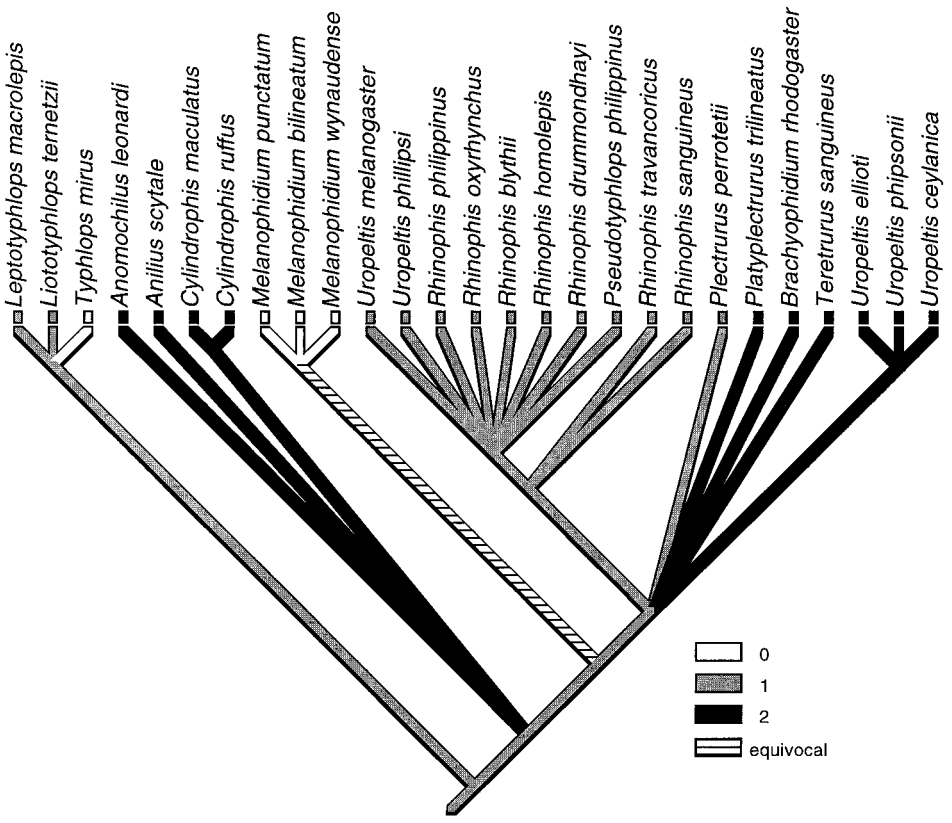

Fig. 13. Distribution of ordered character states describing relationship between length of denticulations and length of cells, with internal branches reconstructed by parsimony using MacClade 3.01: denticulations absent (0), <50% of cell length (1), and = 50% of cell length (2).

two fatty acids in material covering the surface of scales of these snakes, and by the fatty nature of the underlying mesos layer in squamates. In this context, it might also be noted that the European colubrid *Malpolon monspessulanus* is known to wipe a liquid secretion from a pair of snout glands over its body (e.g., Arnold, 2002b) but, as far as I am aware, its scale microornamentation has not been investigated.

The hypothesis that substances are released onto or held on the oberhautchen surface in uropeltids is open to testing. If it has some basis, it might explain the origin of the matrix revealed by scanning electron microscopy to be seen held by some of these pits/pores (Gans and Baic, 1977; this study). That dirt shedding by uropeltid scales might not be achieved only by passive, mechanic properties of microornamentation perhaps receives support from the observation that some (perhaps damaged) patches of live uropeltids occasionally may have dirt attached to them (pers. obs.). Evidence inconsistent with the hypothesis that all oberhautchen pores/pits in uropeltids transmit/hold substances that aid in dirt shedding comes from the observation that pores/pits are present on the scales of the dirt-trapping tail shield of at least some species (Gans and Baic, 1977). Future work might conduct experiments to assess the dirt-shedding ability of scales of fresh and preserved material.

CONCLUSION

As predicted from background data, scale microornamentation in scolecophidian and anilioid snakes that are dedicated burrowers in generally moist soil does not vary substantially around the circumference of the midbody region. Further, and in association with scale shine, these taxa either have a smooth microornamentation or have oberhautchen features that are smaller than the wavelength of most visible light. Iridescence is associated with narrow, finely, and regularly spaced ridges either on the main body of oberhautchen cells or formed by their overlapping posterior denticulations. A ridged microornamentation is apparently associated with a reduced surface wettability that is expected to improve dirt shedding. Pores/pits may contribute to this further. Among uropeltids, there is an unexpected diversity in the size, shape, posterior margins, and borders of oberhautchen cells. Some of these variations are congruent with some phylogenetic hypotheses, but a more resolved and robust phylogeny is required. Ecological data are currently too scant to test possible functional hypotheses, and major caveats in interpreting this survey are the superficial assessment of intraspecific and intraorganismal variation and the lack of a robust, resolved phylogenetic hypothesis for uropeltids. However, it is apparent that "basal" fossorial snakes did not evolve and maintain only a single

form of scale microstructure adapted for a burrowing lifestyle. Whether this indicates independent origins of fossoriality, a strong performance advantage of minor microornamentation variants with variations in function and/or environment, or something else, is as yet unclear.

ACKNOWLEDGMENTS

I thank Jonathan Ablett (supported by an NHM vacation studentship), who prepared specimens and conducted a substantial part of the SEM work. For practical help and advice, ideas, literature, critical discussion, and reviews of manuscript drafts, I thank Nick Arnold, Alex Ball, Jon Gower, Simon Harris, Frederick Harrison, Chris Jones, K.G. Lalith, K. Kariyawasam, Sharath Krishna, Simon Loader, Yasantha Mapatuna, Colin McCarthy, Oommen V. Oommen, Dinarzarde Raheem, S.R.M. Swarnapali Samaradiwakara, Gill Sparrow, Garth Underwood, K.A.S. Ravindra Wickramanaike, and Mark Wilkinson. This work was supported, in part, by a Leverhulme Trust pilot research grant.

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APPENDIX
Material Studied

Here, only those specimens that yielded clean scales are listed. The taxonomy of some of these taxa, and of uropeltids in particular, is unstable and is likely to be substantially revised in future. Nomenclature follows McDiarmid et al. (1999).

Scolecophidia
Leptotyphlopidae
Leptotyphlops macrolepis: BMNH 1913.9.10.2
Anomalepididae
Liotyphlops ternetzii: BMNH 1956.1.16.34
Typhlopidae
Typhlops mirus: DNM (MW) 1727
Alethinophidia
Anilioidea
Anomochilidae
Anomochilus leonardi: BMNH 1946.1.17.4
Cylindrophiidae
Cylindrophis maculatus: DNM (MW) 1762, DNM (MW) 1797
Cylindrophis ruffus: BMNH 97.12.28.50
Uropeltidae
Melanophidium bilineatum: BMNH 74.4.29.698
Melanophidium punctatum: BMNH 1946.1.4.37
Melanophidium wynaudense: MW 1458
Teretrurus sanguineus: BMNH 68.8.12.4
Brachyophidium rhodogaster: BMNH 1923.12.13.32, BMNH 1936.6.11.3
Plectrurus perrotetii: BMNH 1922.5.25.9
Platyplectrurus trilineatus: BMNH 85.3.21.5
Pseudotyphlops philippinus: BMNH 1955.1.9.60
Rhinophis sanguineus: MW 1609
Rhinophis travancoricus: MW 219
Rhinophis oxyrhynchus: BMNH 223-5
Rhinophis philippinus: DNM (MW) 1739
Rhinophis blythii: DNM (MW) 1718
Rhinophis homolepis: DNM (MW) 1796
Uropeltis phillipsi: DNM (MW) 1757
Uropeltis ceylanica: BMNH (number not recorded)
Uropeltis melanogaster: BMNH 1969.2743-54 no.4
Uropeltis phipsonii: BMNH 1937.9.7.2
Uropeltis ellioti: BMNH 91.11.27.8