

Microstructure, Evolution, and Ontogeny of Scale Surfaces in Cordylid and Gerrhosaurid Lizards

MICHAEL B. HARVEY AND RONALD L. GUTBERLET, JR.
*Department of Biology, Box 19498, University of Texas at Arlington,
 Arlington, Texas 76019-0498*

ABSTRACT The distal oberhautchen and proximal beta layer of 41 species and every genus of cordylid and gerrhosaurid lizard were examined with a scanning electron microscope. Scale organs in these families are concentrated on the face, and scale organs occur singly or in pairs below the keel on the dorsals of cordylids but not gerrhosaurids. Most species examined possess primitive, lenticular scale organs. Unique and previously unknown, projecting scale organs occur in two species of *Cordylus*. Scale organs appear to be absent in species of *Chamaesaura*. The scale surfaces of cordylids are covered in macrohoneycomb. Individual compartments of cordylid macrohoneycomb are not intracellular structures but may be overlain by apparent oberhautchen cells. In some cordylid species, part of each cell is free and projects away from the scale surface as a pointed flap. Gerrhosaurids lack macrohoneycomb. Instead, their scale surfaces are covered in lamellae without dentate borders, 50–100 times as long as wide. The epidermis of *Platysaurus* is unique among cordylids in possessing lamellae 1–8 times as wide as long that overlap macrohoneycomb in some regions of the body. The scale surfaces of *Cordylus cordylus* undergo an ontogenetic change similar to that recently described for the xenosaurid genus *Shinisaurus*. Phylogenetic analysis of scale surface features allows the partitioning of *Cordylus* into three species groups and *Chamaesaura* into two species groups. Synapomorphies of the species of *Chamaesaura*, the species of *Platysaurus*, and the genera of the gerrhosaurids are also described. © 1995 Wiley-Liss, Inc.

Researchers have long known about the presence of sensory scale organs and unique microstructural features on the surfaces of lepidosaurian scales (see Leydig, 1872, 1873; Picado, '31, for some of the earliest descriptions). Only recently, with the advent of scanning electron microscopy has the impressive amount of variation in these features and their promising utility (Williams, '89) in systematics been realized. Characteristics of the epidermis provide valuable phylogenetic information because they are often relatively conservative at high taxonomic levels (Harvey, '93). At least some epidermal features, such as microornamentation patterns, reflect phylogenetic relationships rather than ecological specializations (Price, '81, '82). The scale surfaces of representative species from most lizard families have been described, although many families, such as the Cordylidae and Gerrhosauridae, remain poorly known.

Most frequently, two types of characters have been used in phylogenetic analyses of scale surface morphology: epidermal cell shape and subcellular microornamentation. Among lizards, microornamentation rarely consists of structures other than pits or spinules (see especially Peterson, '84), although other forms of microornamentation are observed, such as the "teeth" at the edges of lamellae in many scincids (Ruibal, '68; Stewart and Daniel, '75; Gasc et al., '82; Perret and Wuest, '82, '83), ridges in the lacertid *Poromera* (Limberger, '85), and apparently subcellular lamellae in the scincid *Emoia mivarti* (Irish et al., '88). Cell shapes have been classified as lamellate, polygonal, and polygonal with raised margins. The latter are most commonly referred to as macrohoneycomb (Peterson, '84).

Address reprint requests to Michael B. Harvey, Department of Biology, Box 19498, University of Texas at Arlington, Arlington, TX 76019-0498.

Lacking from most descriptions of scale surface morphology are studies of the histology of the epidermis: a shortcoming that has led to the incorrect definition of some character states (Harvey, '93). The histology of lepidosaurian scales is complex although well studied for a handful of species. Recent reviews summarize the histological, ultrastructural, biophysical, and functional characteristics of the six basic cell types (Landmann, '79; Maderson, '85) and diverse scale organs (Landmann, '75; von Düring and Miller, '79) of the lepidosaurian epidermis. Particularly germane to this study is the bilayered nature of epidermal keratin.

In lepidosaurians, but no other vertebrates, rigid layers of beta keratin overlie pliable layers of alpha keratin. The relative thickness of these layers and the degree to which they invest topographic features on the surface varies among taxa and is phylogenetically informative. Using scanning electron microscopy (SEM) and recently described techniques (Irish et al., '88; Harvey, '93), these deeper epidermal layers can be studied at the same time as surface features. The simultaneous study of several epidermal layers is more likely to result in the correct identification of homologous characters. New data (Harvey, '93) derived from examination of the medial surface of the β -keratin layer and distal α -keratin layer demonstrate that macrohoneycomb and lamellae are not homologous structures and should not be treated as alternative states for a single character in phylogenetic analysis. At least four tissue layers comprise the ridges of macrohoneycomb, and lamellae overlap these structures on the scale surfaces of some scleroglossans.

The scale surfaces of cordylids and gerrhosaurids have yet to be described in any detail. Photographs of scales taken from two or three species have been published (Gasc et al., '82). Unfortunately, poor photographs (Gasc et al., '82, their plate 2) of the scales of *Chamaesaura anguina* and *Gerrhosaurus flavigularis* are not properly referenced in the figure legend or the text leaving the reader unable to determine which photograph corresponds to which species. Similarly, the figure legend for their plate 1A states "motifs épidermiques des cordyloïdes et varanidés." Thus, their figure 1A could be any one of three cordylids examined or a species of *Varanus*. In a separate study (Peterson and Bezy, '85), a short paragraph was devoted to the description of scales taken from *Gerrhosaurus nigro-*

lineatus. The authors provided no photos but noted that the scales of this species are covered in pitted lamellae with unornamented free margins.

Phylogenetic techniques coupled with new data have recently been used to provide support for the monophyly of the Cordylidae + Gerrhosauridae (Rieppel, '80; Estes et al., '88; Lang, '91, and citations therein). The two taxa remain very distinct, and, although unlikely, one or the other may be more closely related to the Scincidae. A recent study proposed the superfamily Cordyliformes to accommodate the two families (Lang, '91). Within the Cordylidae and Gerrhosauridae, the phylogenetic relationships of the genera have been elucidated (Lang, '91). However, intrageneric relationships have not been subjected to rigorous analysis and the only hypothesized relationships are based on few characters and are precladistic (Loveridge, '44). As has been pointed out previously (Mouton, '86; Jacobsen and Newbery, '87), disagreement exists regarding the taxonomic status of many forms, particularly as to whether taxa should be treated as subspecies or full species.

The primary goals of this study are to address many of the questions raised in an earlier study (Harvey, '93) regarding ontogeny, distributional variation of microstructural characters, the identity of microstructural features of the distal oberhautchen, and the phylogenetic signal of macrohoneycomb in noniguanian lineages. Herein the distribution and morphology of different types of scale organs and epidermal microornamentation are described for representative species of gerrhosaurids and cordylids. Additionally, we describe the ontogeny of scale surfaces in one species of *Cordylus* and determine if deeper epidermal layers of cordylid macrohoneycomb and juvenile epidermal morphology are like those observed in xenosaurids (Harvey, '93). Characteristics of the epidermis of cordylids and gerrhosaurids are discussed in a phylogenetic framework. Finally, for species of *Cordylus* we identify three character states that may help resolve systematic problems among this speciose radiation of poorly known lizards.

MATERIALS AND METHODS

Scale surface morphologies were studied in 153 specimens representing 41 species of cordyliform lizards (Appendix). Variability of the characters reported was determined by examining scales of large series of some spe-

cies: *Cordylus cataphractus*, *C. cordylus*, *C. niger*, *C. tropidosternum*, and *C. vittifer*. For most other species, two specimens were examined.

Scales taken from museum specimens were dehydrated in an ethanol series, sonicated to remove debris, and air-dried in acetone or critical point-dried in a Samdri PVT-3B critical point dryer. The samples were then affixed to EM stubs with double-stick tape and coated with 200–300 nm of a gold–palladium mixture in a Hummer VI sputter coater. The scales were examined under a JEOL JSM 35C SEM.

Descriptions of most scale surface features are based on β -keratin-containing layers, removed by pushing on the surfaces of scales with a dissecting needle (methodology of Irish et al., '88). This technique results in the splitting of the mesos layer, perhaps weakened by the leaching of its lipid sheets by the ethanol in which specimens are stored. For most cordylid species, the β -keratin layers were removed from the parietal and one or more dorsal body, dorsal tail, ventral body, and supralabial scales. Only dorsal body scales were prepared for most gerrhosaurid species.

Most of the dorsals were mounted with the distal surface of the oberhautchen facing up. However, the proximal surface of the β layer was also prepared by mounting one dorsal scale upside down for each species. For specimens of *Cordylus cataphractus*, *C. cordylus*, *C. giganteus*, *Chamaesaura anguina*, *C. macrolepis*, *Pseudocordylus melanotus*, *Gerrhosaurus major*, and *G. flavigularis* the distal surface of the α layer was prepared by mounting an intact scale with the β -keratin-containing layers removed.

The β -keratin-containing layers of cordylid scale organs are extremely thin relative to those covering the surrounding scale. For this reason, removal of these layers using a dissecting needle results in loss of the β -keratin layers over the scale organ. Description of scale organ morphology is here restricted to only a few species (*Cordylus cataphractus*, *C. cordylus*, *C. warreni*, *Pseudocordylus melanotus*) from which entire scales could be removed. Intact scales were always critical point dried rather than air-dried before being examined.

Cladistic philosophy (Hennig, '66; Wiley, '81) was applied to interpret the phylogenetic signal of scale surface features. The most comprehensive cladistic study of the Squamata was undertaken by Estes et al. ('88).

For a hypothesis of outgroup relationships, we used the results of that study, taking into account Kluge's ('89) critique of the methodology employed. Kluge, using the computer program Hennig 86 (Farris, '88) and the data of Estes et al. ('88), generated two most parsimonious hypotheses of squamate relationships when he repolarized several characters and treated multistate characters as unordered (Kluge, '89: pp. 372–373). The two hypotheses are as follows: (Iguania (Anguimorpha (Gekkota (Lacertoidea (Scincidae (Cordylidae, Gerrhosauridae))))), and (Iguania (Anguimorpha (Lacertoidea (Gekkota (Scincidae (Cordylidae, Gerrhosauridae))))). The first of these hypotheses is the same as that of Estes et al. ('88), their figure 5A. We use Iguania, Anguimorpha, Lacertoidea, and Scincidae in the sense of Estes et al. ('88), Gekkota in the sense of Kluge ('87), and Cordylidae and Gerrhosauridae in the sense of Lang ('91).

Derived character states identified by outgroup comparisons were mapped onto previously proposed tree topologies (Kluge, '89; Lang, '91) or, where appropriate, were used to partition terminal taxa into groups. The almost complete lack of homoplasy among the characters identified made parsimony analysis straightforward, obviating the use of computer algorithms.

RESULTS

Scale organs

Among cordylids and gerrhosaurids, large numbers of tactile scale organs occur on the head (Fig. 1) and are most numerous on anterior regions of the face and dorsal surfaces of the snout. Most gulars, postmentals, and ventrals lack scale organs. In cordylids and gerrhosaurids, numbers of scale organs on specific scales are often different on opposite sides of the head and vary considerably among individuals. By way of example, loreals in *Cordylus cataphractus* have 3–8 scale organs ($n = 10$, $X = 5$, $s^2 = 2.23$), and second infralabials have 3–9 scale organs ($n = 12$, $X = 6$, $s^2 = 3.54$). Almost the complete range of counts for these scales occurs in a single specimen: 5/8 scale organs on the loreals of UTA 25131; 3/7 organs on the second infralabials in UTA 25129.

Rarely do squamates completely lack tactile scale organs. Although scale organs were clearly visible under a dissecting microscope in other cordylids, none could be found anywhere on specimens of *Chamaesaura*. The absence of scale organs in this genus was

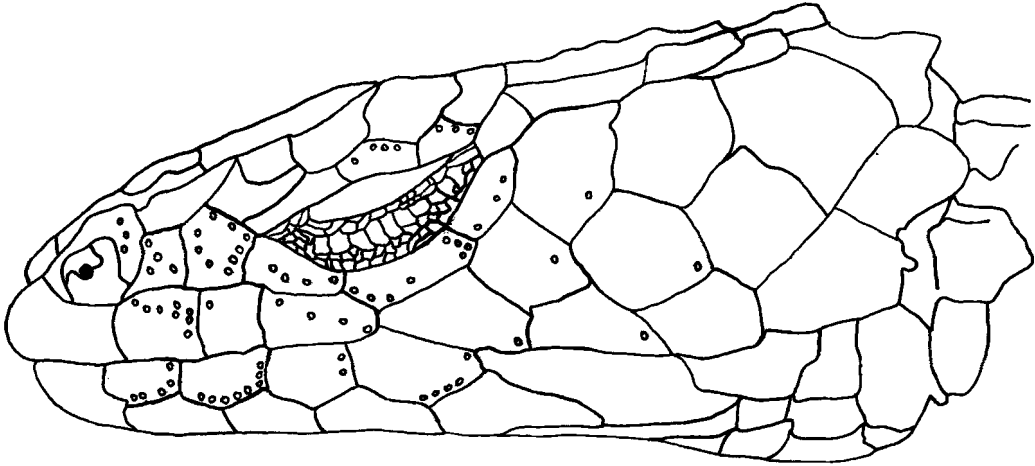


Fig. 1. *Cordylus cataphractus* (UTA 25130). Distribution of scale organs on the facial scales.

later confirmed by examination of SEM preparations of the distal oberhautchen and proximal β layer of labials, dorsals, and ventrals.

Cordylid and gerrhosaurid tactile scale organs exhibit considerable variation in shape but share extremely thin beta keratin containing layers less than $1\ \mu\text{m}$ thick (Figs. 2D, 4C–D). In preserved specimens, the β layers of cordylid and gerrhosaurid scale organs are wrinkled, perhaps as an artifact of preparation or preservation. Neither lamellae nor macrohoneycomb cover the surfaces of tactile scale organs in cordylids or gerrhosaurids. Lamellae, however, do traverse the collars and extend up onto the vertical edges of scale organs in *Gerrhosaurus* (Fig. 2).

The simplest scale organs project only slightly above adjacent scale surfaces (Figs. 2, 3F) and were observed in *Gerrhosaurus flavigularis*, *G. major*, *Zonosaurus laticaudatus*, and *Pseudocordylus melanotus*. In these species the α layer is dome shaped and resembles those described for other scincomorph and anguimorph squamates (Harvey, '93; Landmann, '75). More complex scale organs occur in *Cordylus cataphractus* and *C. cordylus* (Figs. 3A–E, 4A–D). In these species, scale organs project up to $120\ \mu\text{m}$ above the adjacent scale surface compared to less than $15\ \mu\text{m}$ in *Gerrhosaurus*. Moreover, the alpha layers possess lateral expansions (arrows, Fig. 4A) that fit into grooves (arrow, Fig. 4C) in the flanking β -keratin layers.

Excluding the scales of the head and venter, single or paired scale organs (Fig. 4E,F) appear on most scales in all cordylids except *Chamaesaura* but in no gerrhosaurid examined. Unlike scale organs on the head, these

scale organs do not project substantially above the adjacent scale surface. Moreover, whenever β -keratin layers were removed, the scale organs on dorsals were lost, leaving a hole through the β -keratin layers where they occurred. These scale organs appear to be associated with the keel and may function thigmotactically in these crevice-dwelling lizards.

Scale surface microstructure

Lamellae cover dorsal body scales of all the gerrhosaurid species examined (Fig. 5A,B). Although scales other than mid-dorsals were not prepared for most gerrhosaurids, lamellae also cover ventrals, parietals, labials, and caudals of *Gerrhosaurus major*, *G. flavigularis*, and *Zonosaurus laticaudatus*. Among cordylids, narrow¹ lamellae characterize the oberhautchen of *Platysaurus* (Fig. 5C,D), where they often overlap macrohoneycomb and occur on scales from all the body regions mentioned above.

As in many scincomorphans and anguids (Stewart and Daniel, '75; Peterson and Bezy, '85), gerrhosaurid lamellae are anywhere from 50 to more than 100 times as wide as

¹One study (Peterson and Bezy '85) described the shape of lamellae with reference to a proximodistal axis of each scale and defined length as the dimension of lamellae along this axis and width as the dimension perpendicular to this axis. For scales with concentric lamellae, a different system was employed: "the proximodistal axis is expanded into a set of minimum length radii connecting the apex and the margin of the scale. Cell length is measured parallel to the 'radii' through the cell." Under both systems "width" became the longer dimension of a lamella and "length" the shorter. Herein, this convention is followed without reference to any body or scale axis. Neither of the two systems described above could be applied satisfactorily to scales on the head or on most dorsals where more anterior lamellae do not overlap more caudal lamellae.

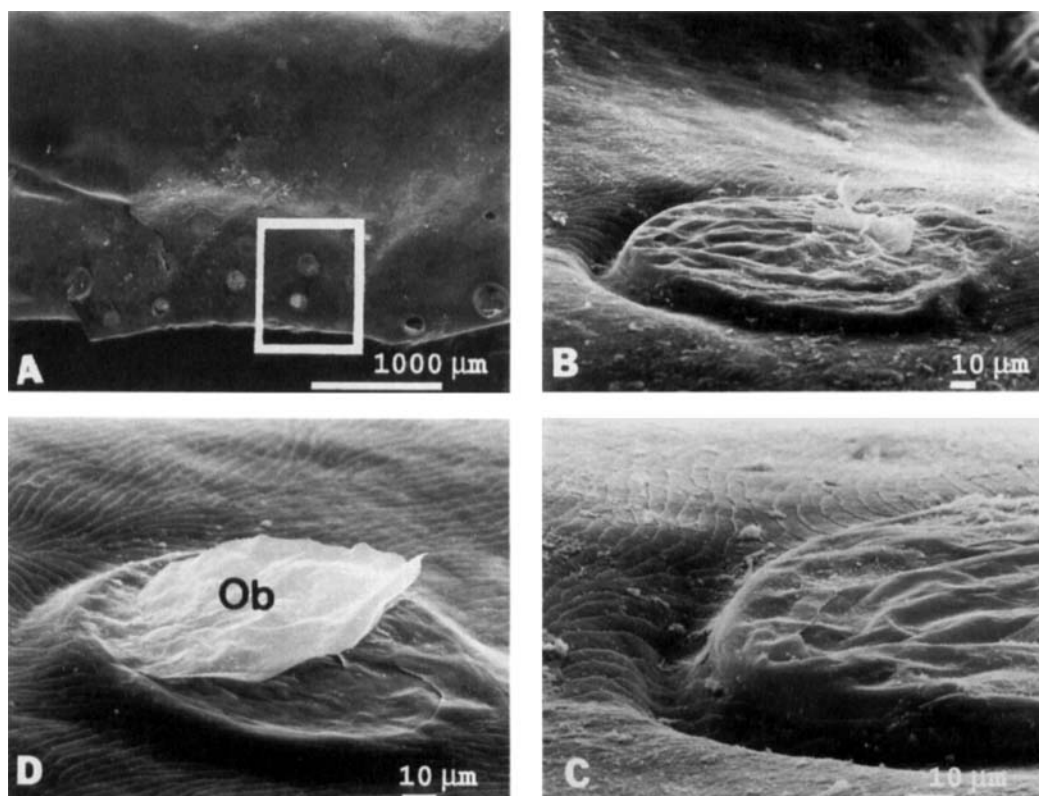


Fig. 2. *Gerrhosaurus major*. Lenticular scale organs. **A:** Intact labial with frame around two scale organs enlarged in B–D. **B,C:** Distal oberhautchen of a lenticular scale organ. Lamellae extend up onto the medial wall

of the scale organ but the dorsal surface lacks lamellae. **D:** β -keratin containing layers (Ob) displaced from the surface of a lenticular scale organ.

they are long; they bear numerous pits with diameters ranging from $0.1\ \mu\text{m}$ to $0.3\ \mu\text{m}$; the terminus of the longer axis of each lamella is most commonly interpolated between more anterior and posterior lamellae but also juxtaposed in some places; and each lamella bears a narrow free margin less than $0.3\ \mu\text{m}$ wide. The lamellae of both gerrhosaurids and *Platysaurus* lack the dentate margins characteristic of scincids.

The orientation of lamellae is not only dependent on the axis of the body, but also macroscopic features of the scales. In general, more anterior lamellae overlap more caudal lamellae. On the dorsal pictured in Figure 5A, lamellae curve to the left in the direction of a central keel and to the right in the direction of an accessory keel. Between the two keels, lamellae maintain anterior over posterior imbrication until they reach the caudal edge of the scale. There, lamellae imbricate in the opposite direction or at right angles to the body axis.

Unlike the lamellae of gerrhosaurids, the pitted lamellae of *Platysaurus* are sublip-soid or rectangular and are 1.5–8 times as wide as long. They are unlike lamellae of most scleroglossans and may actually be oberhautchen cells. As in gerrhosaurids, the orientation of the lamellae of *Platysaurus* follows scale morphology. Lamellae radiate out from the center of dome-shaped granular scales of the dorsum (Fig. 5C) with more proximal lamellae overlapping more distal lamellae. Their margins may be juxtaposed as in Figure 5D or interpolated between imbricating lamellae such as those in Figure 9. As in gerrhosaurids, the lamellae of *Platysaurus* possess free margins less than $0.3\ \mu\text{m}$ long.

Macrohoneycomb is a highly variable scale surface feature resembling the honeycombs of hymenopteran insects. All cordylid species examined thus far possess some form of macrohoneycomb while all gerrhosaurid species examined lack macrohoneycomb. On the surface of scales, macrohoneycomb consists of a

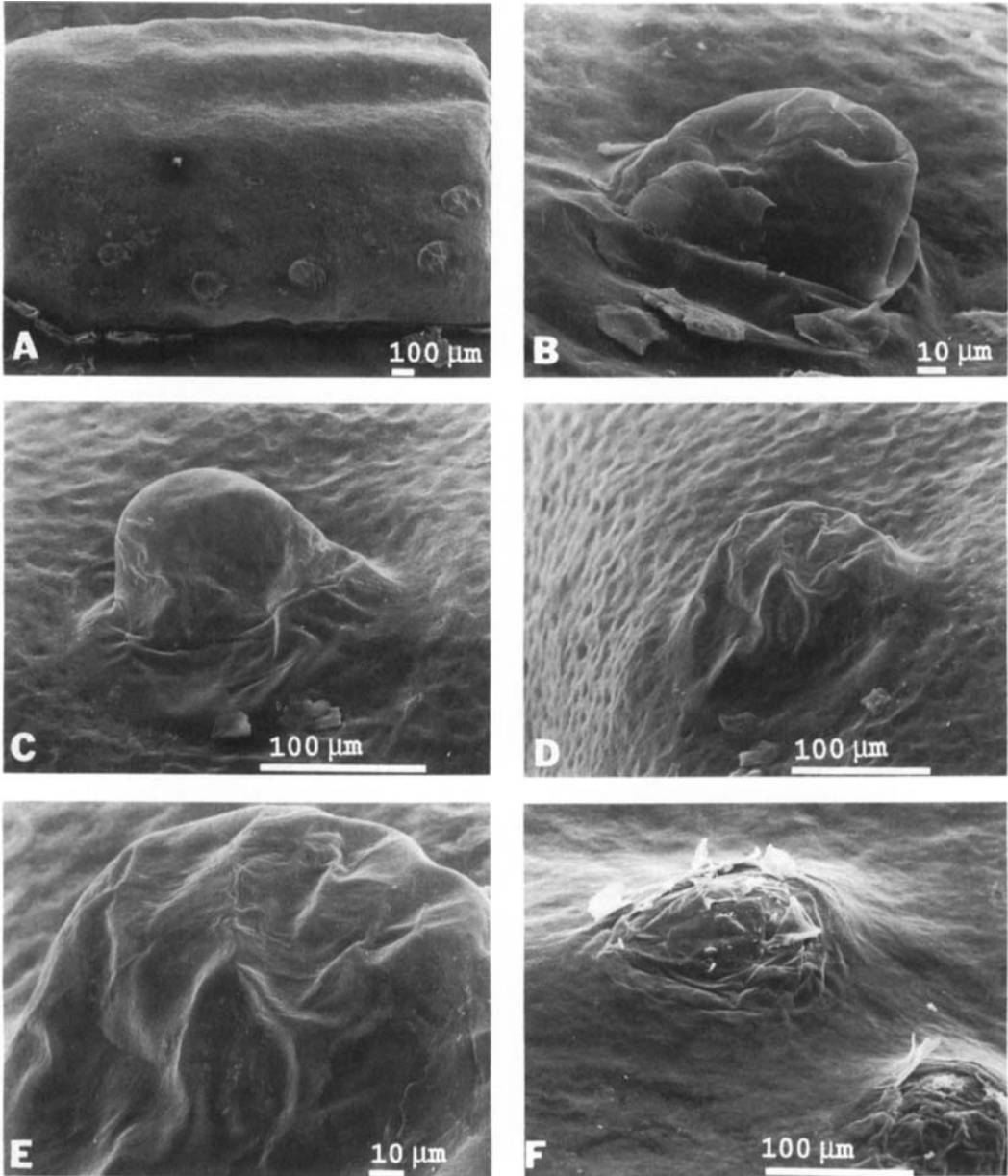


Fig. 3. *Cordylus cataphractus* **A**: Distal oberhautchen of an intact supralabial with a row of projecting scale organs positioned along the scale's edge. **B–E**: Lateral aspect of three projecting scale organs from the same

scale. *Pseudocordylus melanotus*. **F**: Scale organs on a supralabial. The oberhautchen and beta layers have been displaced over the scale organ. Remnants of the mesos layer are visible as loose, irregular sheets of tissue.

network of ridges enclosing chambers 15–30 μm in diameter. Ridges vary in height and thickness reaching 15 μm in height and 3 μm thick among *Chamaesaura* and some *Cordylus*. The other extreme typifies species of

Platysaurus, where ridges are typically less than 3 μm in height and up to 0.5 μm thick.

Like xenosaurid macrohoneycomb, the polygonally arranged ridges on the surfaces of cordylid scales are composed of more than

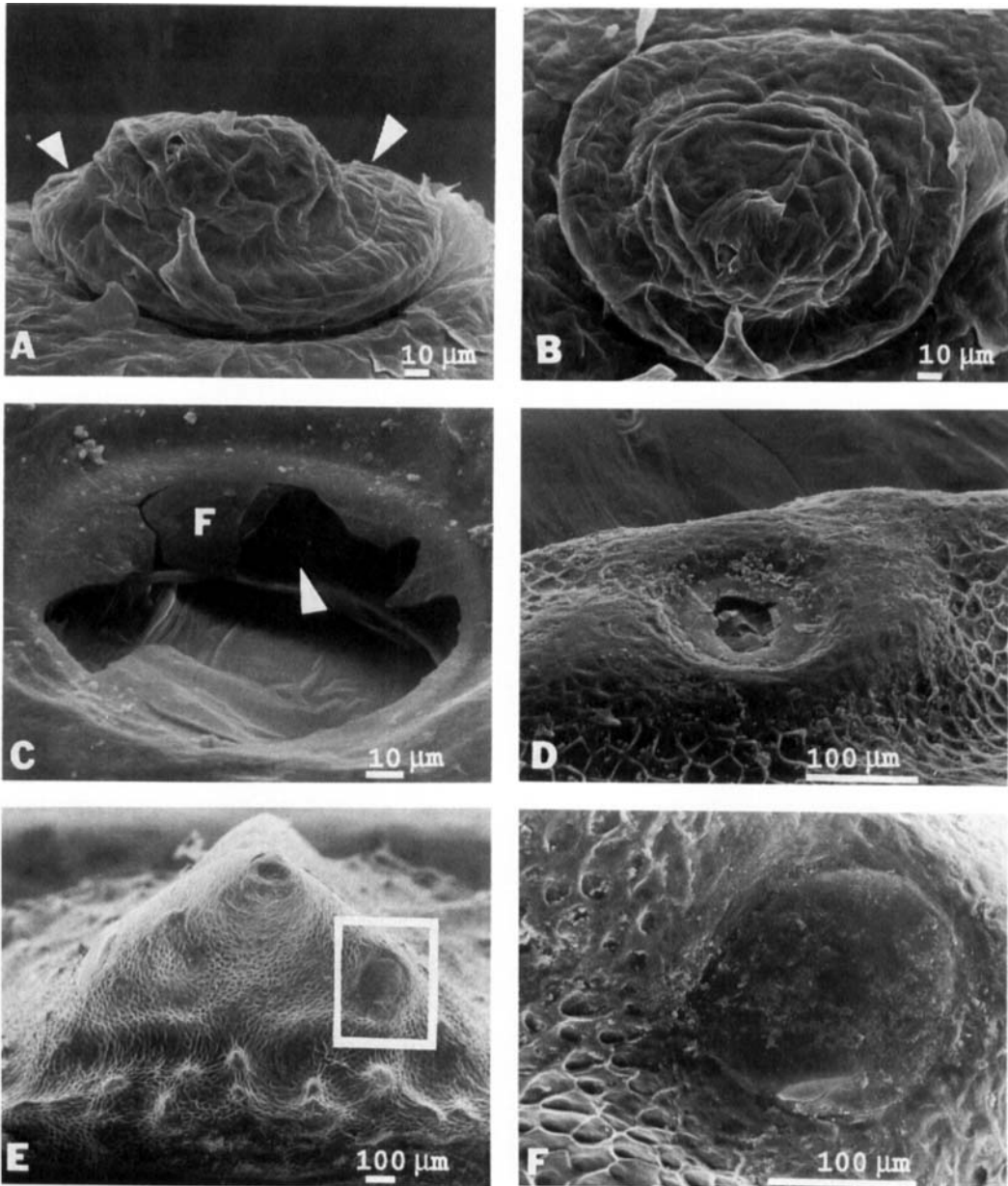


Fig. 4. *Cordylus cataphractus*. **A,B**: a layer of a labial scale organ. Arrows, tabs that interdigitate with the surrounding β layer. Irregular sheets of tissue on the scale organ surface are remnants of the mesos layer. *Cordylus cordylus*. **C,D**: Oberhautchen and β layers removed from a supralabial. Most of the β layers that

originally covered the scale organ have been lost leaving some thin flaps (**F**) at the edge of the opening. Arrow, groove into which tabs like those in **A** fit. *Cordylus warreni*. **E,F**: Caudal aspect of a dorsal body scale. Frame encloses a thigmotactic scale organ enlarged in 4**F**.

one tissue layer and are not intracellular structures. Examination of deeper layers demonstrates that each ridge consists of a fold extending through the oberhautchen, β

(Fig. 7**E,F**), α , and mesos layers. Unlike the epidermis of xenosaurids, structures resembling cell margins overlap the macrohoneycomb of cordylids. Moreover, the apparent

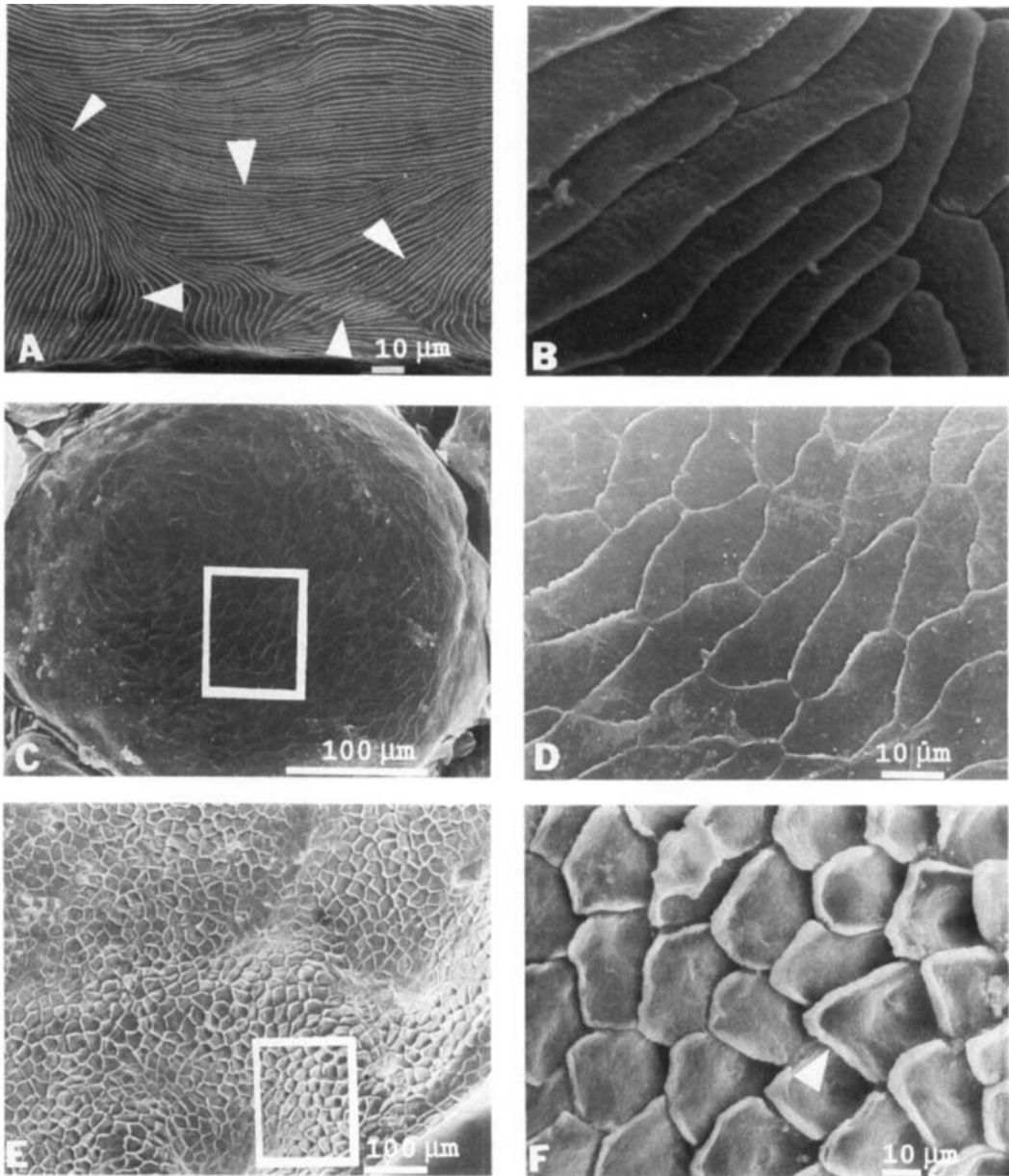


Fig. 5. *Gerrhosaurus flavigularis*. **A**: Lamellae at the caudal end of a dorsal body scale. Arrowheads, direction in which lamellae overlap one another. **B**: Enlargement of lamellae showing imbrication and pitting. *Platysaurus imperator*. **C**: Dorsal granular scale. Frame indicates region enlarged in **D** showing rectangular lamellae. *Cordylus*

cordylus. **E**: Lateral edge of a parietal scale. Frame encloses region of scale enlarged in **F**. **F**: Cell-ridge system. Cells to left are flat where they cover one of the macroscopic spines on the surface of the scale. To the right, the cells lie atop low macrohoneycomb. Arrowhead, flap of free tissue.

cell margins cannot be explained as mere cracks like the lines along macrohoneycomb ridges in *Xenosaurus newmanorum* (Harvey, '93). Along the margin of an interparietal

taken from *Cordylus cordylus* (Fig. 5E,F), macrohoneycomb is not visible although overlapping "cells", roughly diamond-shaped, are seen. Just medial to the edge of the scale,

ridges are present and overlain by "cells." In this species, each "cell" is the same size and shape as the chamber it covers, and its margins lie atop the ridges. Additionally, the caudal tips of these "cells" are raised slightly to form flap-like free margins 2–15 μm long (see also Figs. 8, 10). Finally, the imbrication of the "cells" is maintained when macrohoneycomb is present. The point must be stressed that no evidence other than external appearance exists to confirm that the structures on these scales are cells. Realizing that we may be incorrectly identifying these structures, we hereafter refer to these apparent cells and the associated macrohoneycomb as the cell-ridge system.

Most commonly in *Cordylus*, cell margins lie directly above ridges although this is not always the case. Over most of the epidermis of *C. polyzonus*, the cell margin-ridge overlap of *C. cordylus* is observed. In that portion of the interparietal covering the parietal eye, the cells and chambers are about the same size, but many of the cells appear to overlap parts of more than one chamber (Fig. 6E). As mentioned above, the lamellae of *Platysaurus* are much narrower than those in other scleroglossans and may be oberhautchen cells. As in *C. polyzonus*, each cell (=lamella) overlaps more than one chamber in species of *Platysaurus* (Fig. 6F). The chambers of *Platysaurus* are the same shape as those in other cordylids, but the cells are not, being subellipsoid to rectangular, rather than square to diamond-shaped. Thus, cell margins may lie directly above ridges as in *C. cordylus*, be shifted to lie in the middle of chambers as in the parietal region of *C. polyzonus*, or be a different shape than the underlying ridges as in species of *Platysaurus*.

Among cordylids, flap-like margins are unique to some species of *Cordylus*, and these are the only species other than *Platysaurus* for which apparent cell margins can be discerned. Macrohoneycomb lacking flaps was observed in *Cordylus*, *Pseudocordylus*, *Platysaurus*, and *Chamaesaura* (Fig. 7).

In addition to flaps and the elongate cells of *Platysaurus*, three other modifications of the cell-ridge system were observed in some cordylid lineages. In each of the three species of *Chamaesaura*, the chambers are oval rather than diamond shaped and deeply indented by a near-circular pit 7–15 μm in diameter. Several species of *Cordylus* possess short ridge-like projections (Figs. 6E, 8) 1–6 μm long and the same height as the surround-

ing ridges but not as high as the flap-like margins. They are located in the center of some of the macrohoneycomb chambers and show no consistent orientation to the long or short axis of the cell or any axis of the scale or body. Like similar, though taller (up to 13 μm) and more regular "tubercles" observed in the centers of cells in *Lepidophyma* species (Peterson and Bezy, '85), these projections typically are curved with a convex and a concave side. Unlike the tubercles of *Lepidophyma*, approximately 20% are tripartite (Fig. 8). Central ridge-like projections were observed only among species possessing flaps.

Among cordylids, most differences in macrohoneycomb distribution and morphology exhibit varying degrees of intraspecific variation. On dorsal scales of the same species, macrohoneycomb may cover the entire scale or be absent along macroscopic ridges, spines, or other features. The central keel of adult cordylid body and tail scales is always smooth. Other than the central keel, macrohoneycomb may uniformly cover the dorsal scales, occur in patches, or be restricted to the hinge region. The dorsals of *Platysaurus* lack macrohoneycomb entirely.

Wherever macrohoneycomb occurs on dorsal body and tail scales, the ridges are prominent. However, perhaps as a consequence of a thinner epidermis, macrohoneycomb on the labials and over the parietal eye is reduced or absent. Flap-like margins are almost never visible on labial scales but were observed there in some specimens of *Cordylus cordylus*. In species of *Platysaurus*, only lamellae were visible over the parietal eye, whereas macrohoneycomb covered the rest of the interparietal (Fig. 9). As with other characteristics of microornamentation distribution, the presence or absence of macrohoneycomb on the labials or over the parietal eye varies within species, and even within the same population.

On the ventrals of most cordylids, macrohoneycomb was observed only in the hinge region. The ventrals of *Platysaurus* lack macrohoneycomb. Macrohoneycomb is restricted to the hinge region leaving most of the ventral surface smooth in *Chamaesaura aenea*. However, in the other two species of this genus, low macrohoneycomb covers the entire scale surface of ventrals.

Ontogeny

The cell-ridge system of juvenile *Cordylus* (Fig. 10) shows some similarity to that of adults, but exhibits some striking structural

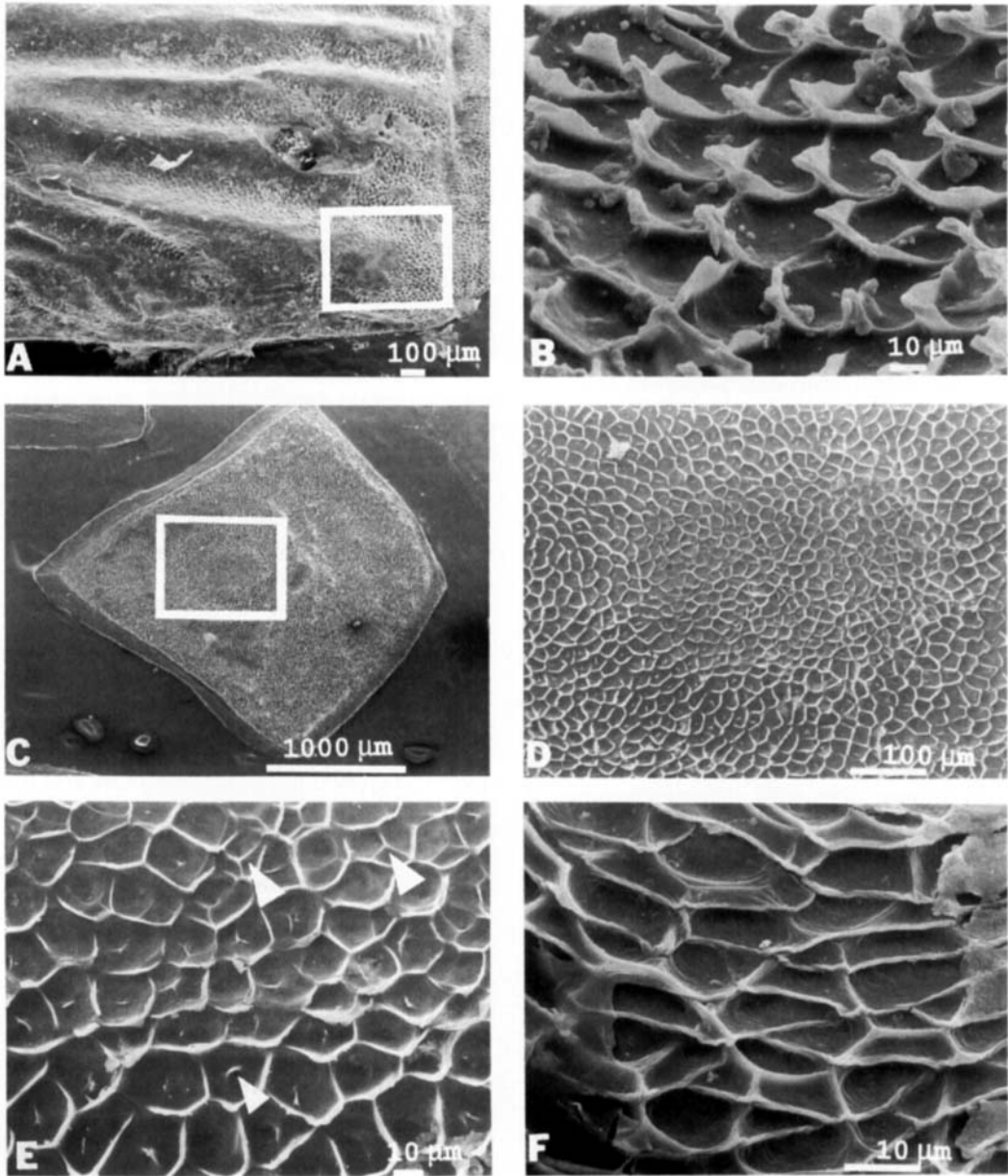


Fig. 6. *Cordylus cordylus*. **A**: Macrohoneycomb covering a dorsal tail scale. Frame encloses region enlarged in **B**. **B**: Lateral view of the cell-ridge system showing elevated flaps of tissue. *Cordylus polyzonus*, interparietal. **C**: Frame encloses region of scale enlarged in **D**, **E**. **D**: Macrohoneycomb from region of the parietal eye. **E**: Enlargement of macrohoneycomb over the parietal eye. Macrohoneycomb in lower half of figure is like that

elsewhere on the body. In top half, macrohoneycomb over the parietal eye shows an uncoupling of the cell-ridge system. Two arrowheads (top half), macrohoneycomb ridges positioned within cell boundaries. Arrowhead (lower half), a short, centrally positioned, ridge-like projection characteristic of the *Cordylus niger* species group. *Platysaurus guttatus*. **F**: Cell-ridge system.

differences. Unlike adult specimens, tubercles cover the keels of embryonic and juvenile dorsal scales (Fig. 10C). Faint lines occur between these tubercles (Fig. 10C) and may

represent cell margins. The tubercles grade into flaps that become progressively elevated nearer the scale margins (Fig. 10D–F). The flaps are considerably thicker, have a more

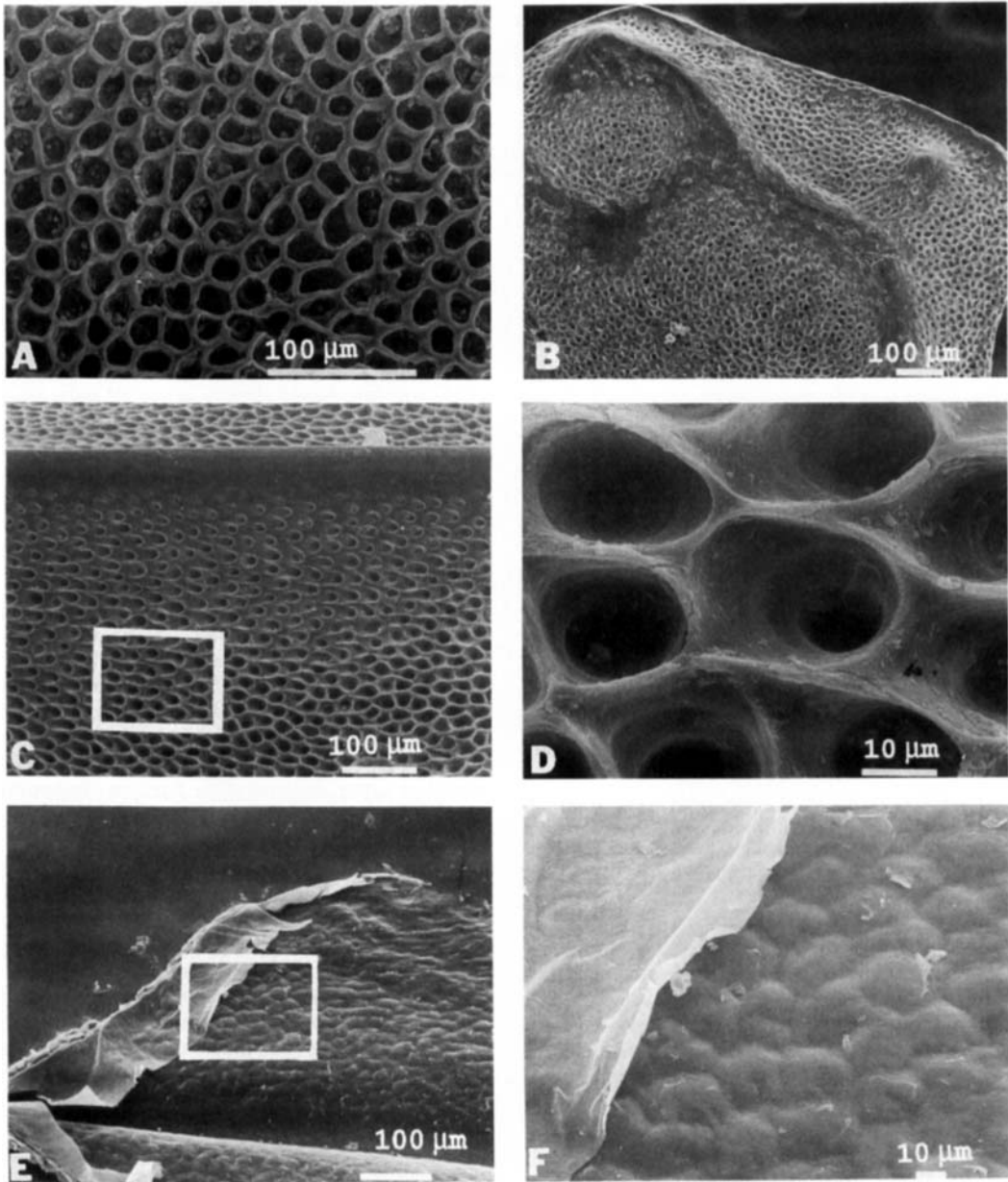


Fig. 7. Macrohoneycomb lacking flaps or noticeable cell margins: *Cordylus tropidosternum*. **A:** Macrohoneycomb from a supralabial. *Cordylus coeruleopunctatus*. **B:** A parietal scale. *Chamaesaura anguina*. **C:** Macrohoneycomb alongside a smooth keel. Frame encloses region of scale enlarged in **D**. **D:** Oval-shaped and deeply pitted

macrohoneycomb. **E:** Proximal surface of the beta layer of a dorsal scale. Flap of tissue to the left is the distal oberhautchen from the proximal surface of the scale. Frame encloses region of β layer enlarged in **F**. **F:** Folds in the proximal surface of the beta layer.

irregular shape, and are considerably more prominent in embryos and juveniles than in adults. As in the adult, apparent cell margins lie atop ridges (Fig. 10D,E) of the underlying macrohoneycomb. Examination of the under-

surface of the β layer reveals that these ridges have the same morphology as in the adult and extend through more than one tissue layer. However, α layer tissue does not project into the flaps.

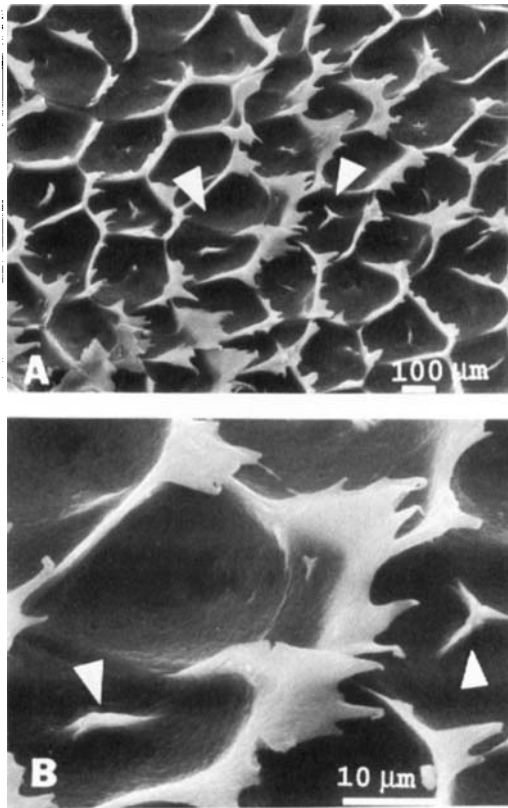


Fig. 8. *Cordylus polyzonus*. Central ridge-like projections (arrowheads, B) and frayed flaps. Arrowheads (A), two macrohoneycomb chambers (enlarged in B). Both photos were taken from the interparietal scale in Figure 6C.

The distribution of flaps in the epidermis of juvenile *Cordylus* is the same as the distribution of macrohoneycomb in adults. In the two specimens examined, flaps covered labials, dorsals, and caudals; they were absent over the parietal window and restricted to the hinge region of ventrals.

DISCUSSION

The subcellular bristles of iguanians and gekkotans have been the subject of considerable interest and show remarkable morphological diversity (Scortecci, '41; Bauer and Russell, '88; Williams, '88; Ananjeva et al., '91; and numerous citations therein). They share two characteristics: a lenticular base and some form of rigid projecting structure usually positioned in the center of the base. Morphologically, they are quite unlike the projecting scale organs that have evolved independently in *Shinisaurus* (Harvey, '93) and

Cordylus. The dissimilarity of these two classes of scale organs is explained by their apparent evolutionary histories. Examination of outgroups shows that, in each case, ancestral scale organs were lenticular, resembling the scale organs illustrated for *Gerrhosaurus major* (Fig. 2). Bristled scale organs probably evolved through modifications of existing hair-like structures, or spinules, that cover the epidermis in gekkotans and many iguanians (Schmidt, '20; Joger, '84). No evidence suggests that such protoadaptive structures were present in the ancestors of either *Shinisaurus* or *Cordylus*. In these species, a projecting structure most likely formed through the distal attenuation of an ancestral lenticular scale organ. The resulting scale organs lack any remnant of a lenticular base, but project directly from the scale surface or just medial to a narrow, encircling furrow. The scale organs of *Shinisaurus* were further modified through the thickening of the β and oberhautchen to form a rigid spike resembling scale organs shown to function like a lever arm in *Calotes* (Hiller, 1978). In *Cordylus*, the beta and oberhautchen of the facial scale organs remained thin, and the organs were modified through the lateral expansion of the α layer into the adjacent β layer.

Examination of the proximal β layer and distal α layer of cordylids further supports earlier findings (Harvey, '93) that macrohoneycomb ridges are folds extending through several tissue layers and are not restricted to the oberhautchen. Thus, oberhautchen cell shape and macrohoneycomb chamber shape are separate entities. Moreover, this study reveals that the ridges of macrohoneycomb do not always demarcate cell boundaries. In many lizards, no cell margins are visible when macrohoneycomb is present. Based on the findings of this study, the shape of oberhautchen cells should not be inferred from the shape of macrohoneycomb chambers.

Ontogenetic change in the epidermis of squamates has been poorly documented for most groups. Among all snakes examined, a recognizable neonatal microornamentation pattern is replaced by an adult pattern after the first shed over most of the scale (Price and Kelly, '89; M.B. Harvey and R.L. Gutberlet, Jr., personal observation). These findings reversed the previously held notion, that microornamentation patterns did not change during maturation (Picado, '31). Among other squamates, the ontogeny of microornamentation patterns has been well documented only

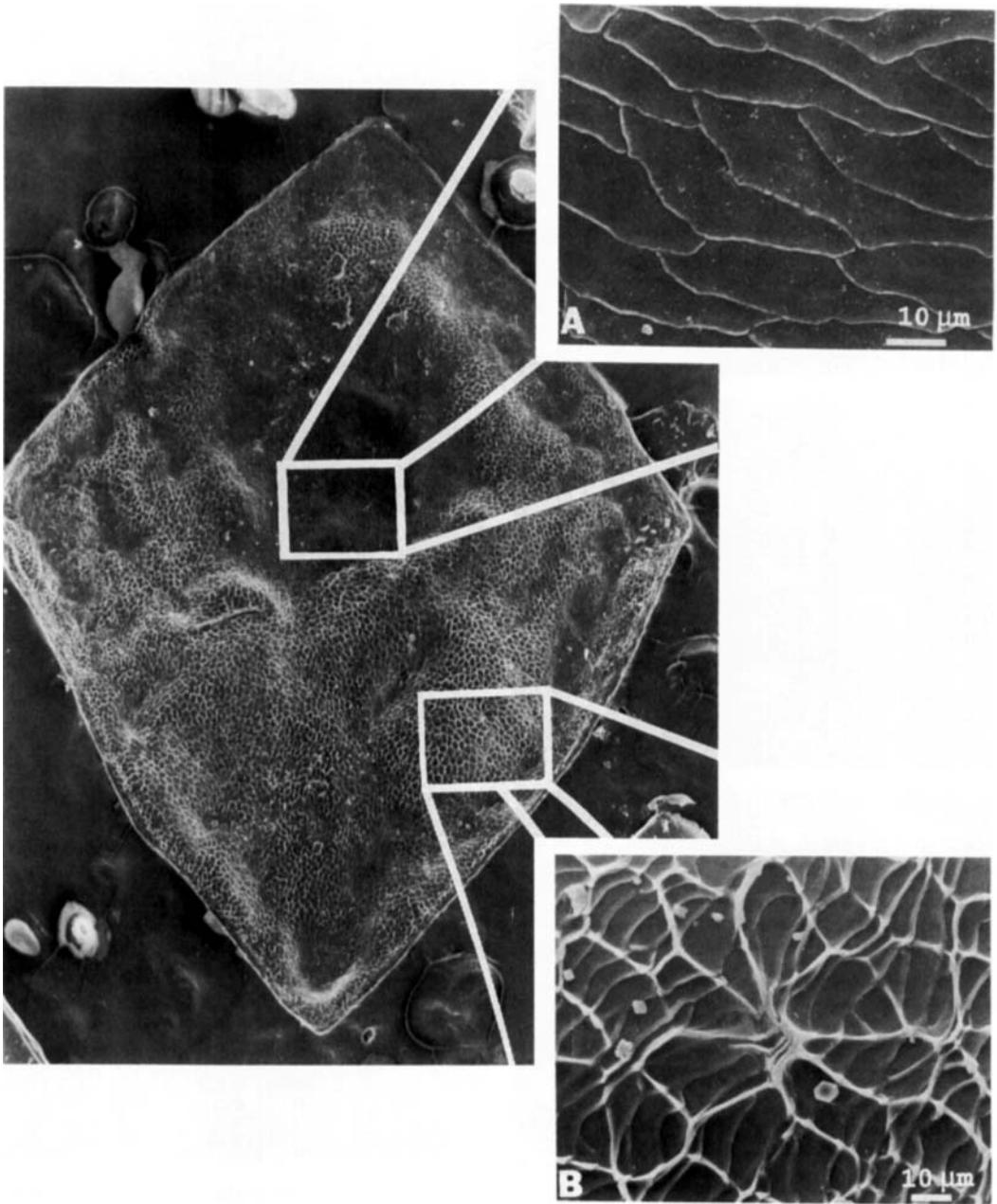


Fig. 9. *Platysaurus capensis*, interparietal. **A:** Lamellae from modified region of scale covering the parietal eye. **B:** Cell ridge system from region of scale lateral to parietal eye.

for xenosaurids. Species of *Xenosaurus* possess the same microornamentation patterns as an embryo, juvenile, and adult; whereas, *Shinisaurus* undergoes dramatic ontogenetic changes (Harvey, '93). The exaggerated

flaps on the epidermis of juvenile and embryonic *Cordylus cordylus* show some resemblance to the flaps on the surfaces of immature *Shinisaurus*. Furthermore, the transformational series from tubercles on the keel to flaps

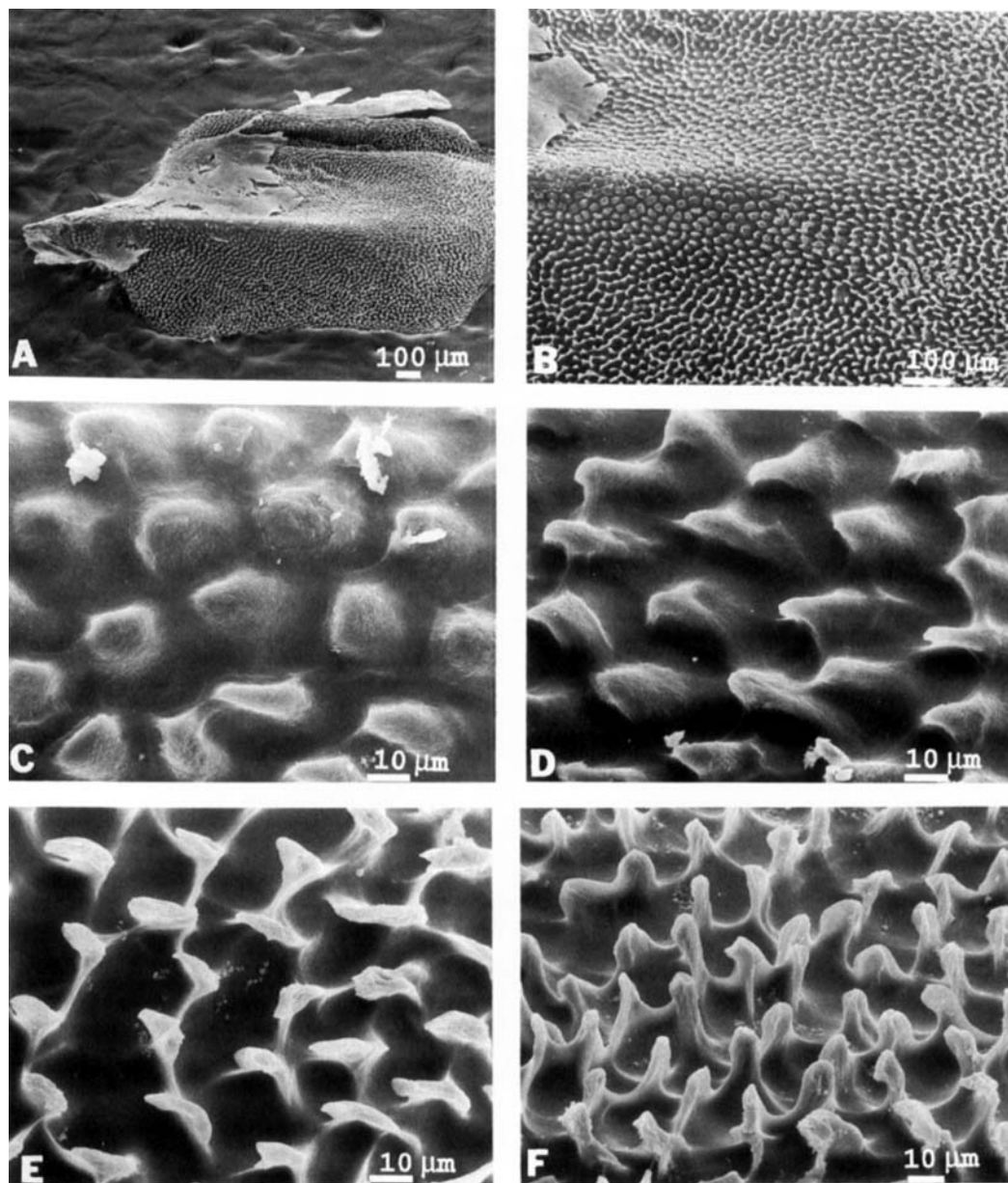


Fig. 10. *Cordylus cordylus*, neonatal scale morphology (cf. Figure 6A,B). **A**: Scale taken from the dorsal surface of the tail. **B**: Anterior (hinge) region of scale pictured in A, showing (C) tubercles from keel, (D) emer-

gent flaps from anterior (right) edge of keel, and (E,F) exaggerated flaps from the hinge region and regions of scale lateral to the keel.

elsewhere on the scale is reminiscent of the transformational series observed on the keeled venter of *Shinisaurus* (Harvey, '93, his figure 5). However, flaps in the two species are quite

different morphologically. The flaps of immature *C. cordylus*, like those of the adult, are composed solely of beta keratin, while in *Shinisaurus* the flaps are composed of layers of α - and

β -keratin. Furthermore, the exaggerated flaps of *C. cordylus* are probably free oberhautchen cell margins, while the flaps of *Shinisaurus* clearly are not intracellular structures of the oberhautchen.

Phylogenetic signal of cordylid and gerrhosaurid scale features

Our polarity decisions for characters in the ingroup Cordyliformes are the same for both of Kluge's ('89) hypotheses (see methods). During the course of the study, 10 phylogenetically informative characters were found:

1. *Macrohoneycomb*: (0) absent; (1) present. The most parsimonious hypothesis of this character's evolution is that macrohoneycomb has arisen independently within four major squamate lineages: iguanians, anguimorphans, lacertoids, and scincoids. Within the context of current hypotheses (Kluge, '89; Lang, '91), the presence of macrohoneycomb is a synapomorphy of the Cordylidae.
2. *α layer of scale organs (Figs. 2-4)*: (0) dome shaped, without tabs that interdigitate with the β layer; (1) dome-shaped with tabs. Although the α layers of many members of the outgroups to *Cordylus* have not been described, tabs have not been previously reported in any other lepidosaurian and may be unique to species of *Cordylus*.
3. *Tactile scale organs*: (0) present; (1) absent. This character is a synapomorphy of *Chamaesaura*. All other gerrhosaurids and cordylids primitively possess scale organs.
4. *Scale organs on scales of the body (Fig. 4E,F)*: (0) present; (1) absent. This character may be a synapomorphy of the Gerrhosauridae. Scale organs occur on scales of the body in cordylids other than *Chamaesaura*, all scincids we have examined, other scleroglossans, and gekkotans.
5. *Lamellae (Fig. 5)*: (0) edentate, 50-100 times as wide as long; (1) edentate, 1.5-8 times as wide as long. Lamellae similar to those observed in gerrhosaurids are widespread among scleroglossans other than gekkotans. The lamellae of *Platysaurus* are unknown in other squamates and appear to be a synapomorphy of the species of that genus.
6. *Flap-like free margins associated with the cell-ridge system (Figs. 6,7)*: (0) absent; (1) present; (2) present and frayed. Although, macrohoneycomb appears in some scleroglossan lineages such as the Lacertidae (Limberger, '85) and Scincidae (personal observation), we have found flaps in only one scincid genus and some members of *Cordylus*. Their presence, represents a synapomorphy of *C. cordylus*, *C. campbelli*, *C. lawrenci*, *C. macropholis*, *C. mclachlani*, *C. minor*, *C. niger*, *C. polyzonus*, and *C. vittifer*. Frayed flaps were observed only in *C. polyzonus* but may also occur on the interparietal of *C. campbelli*, *C. lawrenci*, or *C. minor*. Interparietals for these three species were not examined. The flap-like free margins mentioned above have not been previously reported in published descriptions of scale surface morphology. Macrohoneycomb without flaps (Fig. 7) occurs in many cordylids, all xenosaurids (Harvey, '93), many varanids (Gasc et al., '82; and personal observation), and some lacertids (Limberger, '85) and iguanians (Peterson, '84).
7. *Short ridge-like projections in the center of oberhautchen cells (Fig. 6E)*: (0) absent; (1) present. Elevated structures located in the centers of apparent oberhautchen cells have been reported in species of *Lepidophyma* (Peterson and Bezy, '85), and observed in some varanids (personal observation). However, the narrow central ridges of some *Cordylus* are unknown in other squamates and appear to be a synapomorphy of *C. campbelli*, *C. mclachlani*, *C. minor*, *C. niger*, and *C. polyzonus*.
8. *Shape of macrohoneycomb chambers (Fig. 7)*: (0) diamond-shaped, without deep indentations; (1) oval with deep indentations. The oval and deeply indented chambers of the macrohoneycomb of *Chamaesaura* are unknown in other squamates and appear to represent a synapomorphy of the species of that genus.
9. *Ventral scale surfaces*: (0) with macrohoneycomb restricted to the hinge region; (1) with low macrohoneycomb covering the entire scale. In scleroglossan lizards possessing macrohoneycomb, the ventrals either lack macrohoneycomb or have macrohoneycomb restricted to the

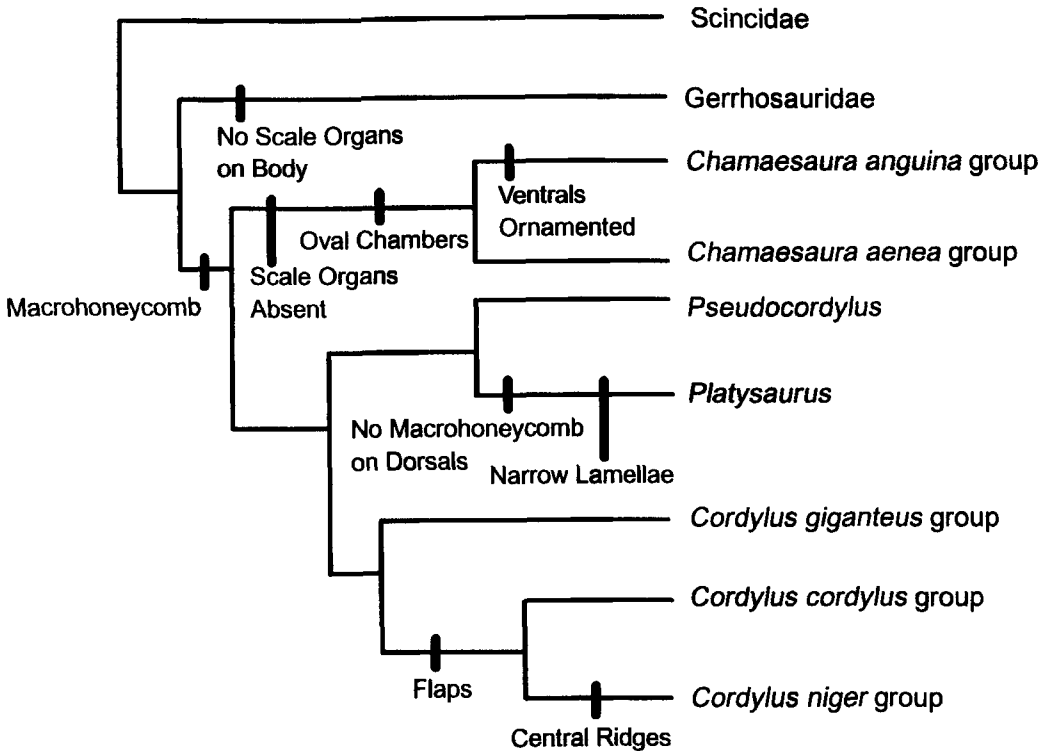


Fig. 11. Evolution of scale surface characters and the partitioning of *Cordylus* into three and *Chamaesaura* into two species groups. Phylogenetic relationships of genera and families is that of Lang ('91).

hinge region. Two exceptions are the species of *Chamaesaura* with absent or reduced forelimbs, *C. anguina* and *C. macrolepis*. In the third species, *C. aenea*, macrohoneycomb is restricted to the hinge region of ventrals.

10. *Dorsal scale surfaces*: (0) with macrohoneycomb at least in the hinge region (1) lacking macrohoneycomb. This character probably does not represent a true reversal to the gerrhosaurid condition which would be expected to result in the loss of macrohoneycomb over the entire body. (Dorsal scales from *Platysaurus ocellatus* and *P. mitchelli* were not available for study.)

As has been pointed out (Lang, '91), few and weak synapomorphies of the Cordylidae + Gerrhosauridae were presented in an earlier phylogenetic analysis (Estes et al., '88). The former study reviewed new evidence based on hemipenial morphology, my-

ology, and karyotypes that further supports the monophyletic relationship of these two families.

Scale morphology does not provide evidence for the monophyly of Cordyliformes. The lamellae of gerrhosaurids and *Platysaurus* are most likely not homologous and are not a shared characteristic of cordylids and gerrhosaurids. Although gerrhosaurids and scincids both possess lamellae, this character is plesiomorphic within the Scincoidea. Scincids rather than gerrhosaurids possess a derived modification of lamellae, the dentate borders. In contrast to gerrhosaurids, cordylids possess macrohoneycomb, which they share with some scincids.

Synapomorphies of the species of *Chamaesaura*, the species of *Platysaurus*, and the genera of the Gerrhosauridae were found (Fig. 11). Justification for recognizing three groups within *Cordylus* and two groups within *Chamaesaura* was also demonstrated:

- Chamaesaura aenea* group (1 species)
C. aenea
- Chamaesaura anguina* group (2 species)
C. anguina
C. macrolepis
- Cordylus niger* group (5 species)
C. campbelli
C. mclachlani
C. minor
C. niger
C. polyzonus
- Cordylus cordylus* group (4 species)
C. cordylus
C. lawrenci
C. macropholis
C. vittifer
- Cordylus giganteus* group (6 species)
C. cataphractus
C. coeruleopunctatus
C. giganteus
C. namaquensis
C. tropidosternum
C. warreni

Macrohoneycomb covers the ventral scales of both *Chamaesaura anguina* and *C. macrolepis* thus uniting these two taxa in a *C. anguina* group. No phylogenetic hypothesis of *Cordylus* exists. All the members of a *C. niger* group share a central ridge-like projection positioned within their oberhautchen cells. Two additional groups may be paraphyletic: the *C. cordylus* group which possesses flaps but no central ridges and the *C. giganteus* group which lacks both characters. The presence of frayed flaps in *C. polyzonus* may further partition the genus. The species is left in the *C. niger* group because, for some species, interparietals were unavailable for inspecting the condition of the flaps. When interparietals of the other species become available, recognition of a fourth group containing *C. polyzonus* may be justified. *Cordylus cataphractus* and *C. cordylus* share derived scale organs. As this study did not ascertain the condition of the scale organs for most cordylids, the level at which this character is informative is not yet apparent.

ACKNOWLEDGMENTS

Access to the UTA electron microscopy laboratory was graciously provided by H.J. Arnott. We thank H.J. Arnott, L. Bragg, and

L. Lopez for their kind guidance and patience during the course of this study. We thank J.E. Cadle, W.E. Duellman, A.G. Kluge, and H.K. Voris for the loan of specimens and for allowing us to remove the beta keratin containing layers from scales. D. Frost and J.A. Campbell kindly provided us with working space and allowed us to remove scales from specimens at the American Museum of Natural History and the University of Texas at Arlington Collection of Vertebrates.

APPENDIX

Specimens examined during the course of this study are housed in the American Museum of Natural History, New York (AMNH), the Field Museum of Natural History, Chicago (FMNH), the Museum of Natural History at the University of Kansas, Lawrence (KU), the Museum of Zoology at the University of Michigan, Ann Arbor (UMMZ), and the Collection of Vertebrates at the University of Texas at Arlington (UTA).

Specimens

Cordylidae. *Chamaesaura aenea* (1): FMNH 17465. *Chamaesaura anguina* (3): AMNH 18220, FMNH 168843-44. *Chamaesaura macrolepis* (4): AMNH 57629, FMNH 154741-42, UTA 34959. *Cordylus campbelli* (1): MCZ 46824. *Cordylus cataphractus* (14): FMNH 57648, 187011, 204850, 206533-36, UTA 6300, 7860, 25128-31. *Cordylus coeruleopunctatus* (5): FMNH 186970-74. *Cordylus cordylus* (17): FMNH 17467, 17484-85, 186917-19, 186928-29, 187180-81, 204844 (embryo), UTA 6692, 6763 (juvenile), 29665, 34061-63. *Cordylus giganteus* (9): UTA 6717, 7659, 8025, 8041, 31971, 34493-95, 34545. *Cordylus lawrenci* (1): MCZ 159177. *Cordylus macropholis* (2): FMNH 187016-17. *Cordylus mclachlani* (1): KU 207964. *Cordylus minor* (2): KU 207969-70. *Cordylus namaquensis* (1): MCZ 46840. *Cordylus niger* (16): FMNH 186934-38, 186947, 186949-56, UMMZ 61461, 62507. *Cordylus peersi* (2): FMNH 186966-67. *Cordylus polyzonus* (3): FMNH 187004-05, UTA 34964. *Cordylus tropidosternum* (6): FMNH 58294, 78157, 129601-03, AMNH 16820. *Cordylus vittifer* (18): FMNH 17477, 17479, 204852, 219776, 219778, 220041-43, 220045, 220048-52, 220209, 220211, 220260, UTA 9074. *Cordylus warreni* (2): AMNH 107313, UTA 10507. *Platysaurus capensis* (2): FMNH 187031,

206530. *Platysaurus guttatus* (2): FMNH 17323-24. *Platysaurus imperator* (1): AMNH 90176. *Platysaurus intermedius* (2): FMNH 187029-30. *Platysaurus mitchelli* (1): AMNH 90178. *Platysaurus ocellatus* (1): AMNH 90177. *Pseudocordylus capensis* (2): FMNH 186916, UTA 34951. *Pseudocordylus melanotus* (2): UTA 6302, 8246. *Pseudocordylus microlepidotus* (3): AMNH 5888, FMNH 187014-15.

Gerrhosauridae. *Angolosaurus skoogi* (1): FMNH 204849. *Cordylus subtesellatus* (2): FMNH 74082-83. *Gerrhosaurus flavigularis*: UTA (6) 29666-69, 34956-57. *Gerrhosaurus major* (2): UTA 29670, 34096. *Gerrhosaurus multilineatus* (2): FMNH 17288-89. *Gerrhosaurus nigrolineatus* (2): FMNH 129717-18. *Gerrhosaurus validus* (2): 74080-81. *Tetradactylus seps* (2): FMNH 206569-70. *Tetradactylus tetradactylus* (2): FMNH 206571-72. *Tracheloptychus madagascariensis* (2): FMNH 75636-37. *Zonosaurus laticaudatus* (2): UTA 9370-71. *Zonosaurus maximus* (2): FMNH 75642-43. *Zonosaurus ornatus* (2): FMNH 73077-78.

LITERATURE CITED

- Ananjeva, N.J., M.E. Dilmuchamedov, and T.N. Matveyeva (1991) The skin sense organs of some iguanian lizards. *J. Herpetol.* 25:186-199.
- Bauer, A.M., and A.P. Russell (1988) Morphology of gekkonid cutaneous sensilla with comments on function and phylogeny in the Carphodactylini (Reptilia: Gekkonidae). *Can. J. Zool.* 66:1583-1588.
- Estes, R., K. de Queiroz, and J. Gauthier (1988) Phylogenetic relationships within squamata. In R. Estes and G. Pregill (eds): *Phylogenetic Relationships of the Lizard Families*. Stanford: Stanford University Press, pp. 119-281.
- Farris, J.S. (1988) Hennig86 Reference, Ver. 1.5. Privately printed.
- Gasc, J., S. Renous, and A. Diop (1982) Configuration des motifs microscopiques et topographie régionale de la peau chez les reptiles squamates. 107 Congrès national des Sociétés savantes, Brest, 1982, Sci. fasc. II:73-88.
- Harvey, M.B. (1993) Microstructure, ontogeny, and evolution of scale surfaces in xenosaurid lizards. *J. Morphol.* 216:161-177.
- Hennig, W. (1966) *Phylogenetic Systematics*. Urbana: University of Illinois Press.
- Hiller, U. (1978) Morphology and electrophysiological properties of cutaneous sensilla in agamid lizards. *Pflügers Arch.* 377:189-191.
- Irish, F.J., E.E. Williams, and E. Seling (1988) Scanning electron microscopy of changes in epidermal structure occurring during the shedding cycle in squamate reptiles. *J. Morphol.* 197:105-126.
- Jacobsen, N.H.G. and R.E. Newbery (1987) The genus *Platysaurus* A. Smith 1844 in the Transvaal. *Herp. Assoc. Afr.* 36:51-63.
- Joger, U. (1984) Morphologische und biochemisch-immunologische Untersuchungen zur Systematik und Evolution der Gattung *Tarentola* (Reptilia, Gekkonidae). *Zool. Jahrb. Anat.* 112:137-256.
- Kluge, A.G. (1987) Cladistic relationships among the Gekkonoidea. *Misc. Publ. Mus. Zool. Univ. Mich.* 173: i-iv + 1-54.
- Kluge, A.G. (1989) Progress in squamate classification. *Herpetologica* 45:368-379.
- Landmann, L. (1975) The sense organs in the skin of the head of Squamata (Reptilia). *Isr. J. Zool.* 24:99-135.
- Landmann, L. (1986) Epidermis and dermis. In J. Bereiter-Hahn, A.G. Matoltsy, and K.S. Richards (eds): *Biology of the Integument, Vol. 2: Vertebrates*. Berlin: Springer-Verlag, pp. 150-187.
- Lang, M. (1991) Generic relationships within Cordyliformes (Reptilia: Squamata). *Bull. Inst. R. Sci. Nat. Belg. Biol.* 61:121-188.
- Leydig, F. (1872) Die in Deutschland lebenden Arten der Saurier. Laupp: Tübingen.
- Leydig, F. (1873) Über die äusseren Bedeckungen der Reptilien und Amphibien. *Arch. Mikrosk. Anat. Entwicklungsmech.* 9:753-794.
- Limberger, P.L. (1985) A preliminary study of the microornamentation of the Old World lizard family Lacertidae: its variation and systematic implications. M.A. thesis. Fullerton: California State University.
- Loveridge, A. (1944) Revision of the African lizards of the family Cordylidae. *Bull. Mus. Comp. Zool. Harvard* 95:1-118.
- Maderson, P.F.A. (1985) Some developmental problems of the reptilian integument. In C. Gans, F. Billett, and P. Maderson (eds): *Biology of the Reptilia*. New York: Wiley, pp. 523-598.
- Mouton, P. le F.N. (1986) Description of a new species of *Cordylus* Laurenti (Reptilia: Cordylidae) from the southwestern Cape, South Africa. *S. Afr. J. Zool.* 21: 319-324.
- Perret, J., and J. Wuest (1982) La structure fine des écailles de quelques Lygosominae africains (Lacertilia, Scincidae), révélée par le microscope électronique à balayage. *Rev. Suisse Zool.* 89:269-280.
- Perret, J., and J. Wuest (1983) La microstructure des écailles de quelques Scincides africains et paléarctiques (Lacertilia), observée au microscope électronique à balayage. II. *Rev Suisse Zool.* 90:913-928.
- Peterson, J.A. (1984) The microstructure of the scale surface in iguanid lizards. *J. Herpetol.* 18:437-467.
- Peterson, J.A., and R.L. Bezy (1985) The microstructure and evolution of scale surfaces in xantusiid lizards. *Herpetologica* 41:298-324.
- Picado, C. (1931) Epidermal microornaments of the Crotalinae. *Bull. Antivenin Inst. Amer.* 4:104-105.
- Price, R.M. (1981) Analysis of the ecological and taxonomic correspondence of dorsal snake scale microdermatoglyphics. Doctoral dissertation. New York University.
- Price, R.M. (1982). Dorsal snake scale microdermatoglyphics: Ecological indicator or taxonomic tool? *J. Herpetol.* 16:294-306.
- Price, R.M., and R. Kelly (1989) Microdermatoglyphics: Basal Patterns and Transition Zones. *J. Herpetol.* 23: 244-261.
- Rieppel, O. (1980) The trigeminal jaw adductor musculature of *Tupinambis*, with comments on the phylogenetic relationships of the Teiidae (Reptilia, Lacertilia). *Zool. J. Linn. Soc. Lond.* 69:1-29.
- Ruibal, R. (1968) The ultrastructure of the surface of lizard scales. *Copeia* 1968:698-704.
- Schmidt, W.J. (1920) Einiges über die Hautsinnesorgane der Agamiden insbesondere von *Calotes*, nebst Bemerkungen über diese Organe bei Gekkonidae und Iguanidae. *Anat. Anz.* 53:113-139.

- Scortecchi, G. (1941) I recettori degli Agamidi. *Mem. Soc. Ital. Sci. Nat.* 10:207-326.
- Stewart, G.R., and R.S. Daniel (1975) Microornamentation of lizard scales: Some variations and taxonomic correlations. *Herpetologica* 31:117-130.
- von Düring, M., and M.R. Miller (1979) Sensory nerve endings on the skin and deeper structures. In C. Gans, R.G. Northcutt, and P. Ulinski (eds): *Biology of the Reptilia*. Vol. 9. New York: Academic Press, pp. 407-441.
- Wiley, E.O. (1981) *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. New York: Wiley.
- Williams, E.E. (1988) A new look at the Iguania. In P.E. Vanzolini and W.R. Heyer (eds): *Proceedings of a Workshop on Neotropical Distribution Patterns*. Rio de Janeiro: Academia Brasileira de Ciencias, pp. 429-488.
- Williams, E.E. (1989) Review of phylogenetic relationships of the lizard families. *Essays Commemorating Charles L. Camp. Copeia* 1989:1108-1117.