

History and Function of Scale Microornamentation in Lacertid Lizards

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ABSTRACT Differences in surface structure (oberhautchen) of body scales of lacertid lizards involve cell size, shape and surface profile, presence or absence of fine pitting, form of cell margins, and the occurrence of longitudinal ridges and pustular projections. Phylogenetic information indicates that the primitive pattern involved narrow strap-shaped cells, with low posteriorly overlapping edges and relatively smooth surfaces. Deviations from this condition produce a more sculptured surface and have developed many times, although subsequent overt reversals are uncommon. Like variations in scale shape, different patterns of dorsal body microornamentation appear to confer different and conflicting performance advantages. The primitive pattern may reduce friction during locomotion and also enhances dirt shedding, especially in ground-dwelling forms from moist habitats. However, this smooth microornamentation generates shine that may compromise cryptic coloration, especially when scales are large. Many derived features show correlation with such large scales and appear to suppress shine. They occur

most frequently in forms from dry habitats or forms that climb in vegetation away from the ground, situations where dirt adhesion is less of a problem. Microornamentation differences involving other parts of the body and other squamate groups tend to corroborate this functional interpretation. Microornamentation features can develop on lineages in different orders and appear to act additively in reducing shine. In some cases different combinations may be optimal solutions in particular environments, but lineage effects, such as limited reversibility and different developmental proclivities, may also be important in their genesis. The fine pits often found on cell surfaces are unconnected with shine reduction, as they are smaller than the wavelengths of most visible light. *J. Morphol.* 252:145–169, 2002. © 2002 Wiley-Liss, Inc.

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Phylogenetic information may permit the history of morphological features that vary complexly through a clade to be at least partly reconstructed. The history can then be used to explore the evolutionary origins of the variation, in particular by enabling correlations between the appearance of particular traits and changes in selective regime to be recognized. This approach is applied here to the fine surface structure of the scales of lacertid lizards.

The scales of squamates (lizards and snakes) have a rigid outer epidermal layer of β -keratin, the β -layer, which is underlain by the mesos and then the α -layers. All these are formed from cells produced by the living basal layer of the epidermis, the stratum germinativum. The β -layer is covered by the oberhautchen (the anglicized form of the original German Oberhäutchen, recommended by Irish et al., 1988). By the time the β -layer and oberhautchen mature, coherent cell boundaries are not apparent within them (Maderson et al., 1998). There are often cell-like enclosures visible on the surface of the oberhautchen, although it is not certain that these are always derived from individual cells. The surface of the oberhautchen frequently exhibits a complex, microscopical, three-dimensional structure first noted by Leydig (1872, 1873), which usually includes fea-

tures additional to the cell-like enclosures. Also, the oberhautchen and underlying layers may all be rucked to produce ridges on the scale surface (Harvey, 1993). The overall structure of features of the oberhautchen surface and epidermal folding is referred to here as microornamentation (Ruibal, 1968) but has also been termed ultradermatoglyphics (Larsen et al., 1973), dermatoglyphics (Burstein et al., 1974), microdermatoglyphics (Dowling et al., 1972), microstructure (Perret and Wuest, 1983), and microarchitecture (Peterson, 1984a).

Squamate microornamentation is easily studied by scanning electron microscopy (SEM) and there is now a substantial literature on the subject. For instance, publications dealing with dorsal body scales include: Bryant et al. (1967), Monroe and Monroe (1967), Ruibal (1968), Stewart and Daniel (1972, 1973, 1975), Burstein et al. (1974), Cole and van

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Devender (1976), Sammartano (1976), Gans and Baic (1977), Gasc and Renous (1980), Groombridge (1980), Perret and Wuest (1982, 1983), Price (1982, 1983, 1989), Peterson (1984a,b), Peterson and Bezy (1985), Renous et al. (1985), Bea (1986), Bowker et al. (1987), McCarthy (1987), Stille (1987), Bezy and Peterson (1988), Irish et al. (1988), Vaccaro et al. (1988), Chiasson and Lowe (1989), Lang (1989), Price and Kelly (1989), Renous and Gasc (1989), Harvey (1993), and Harvey and Gutberlet (1995).

In spite of these extensive studies, no broad assessment of the evolutionary factors that may cause the development of different patterns of microornamentation has been made. Although convincing functional interpretations have been put forward in restricted instances (see Factors That May Cause Evolutionary Change, below), microornamentation does not in general correlate closely with known environmental parameters (Price, 1982; Peterson, 1984a,b). Nor does it seem to be a particularly good general indicator of relationship, although it may include some phylogenetic signal (see, for instance, Harvey and Gutberlet, 1995, on cordylid and gerrhosaurid lizards).

Although microornamentation has sometimes been surveyed across whole taxonomic groups (e.g., Peterson and Bezy, 1985; Lang, 1989; Harvey and Gutberlet, 1995), sampling is often limited or the assemblage concerned is small, relatively uniform in ecology, or both. Lacertid lizards exhibit substantial variation in microornamentation and, with some 23 genera and 250 species spread over a wide range of environments, they provide an opportunity to explore this variation more fully in a historical and functional context. As only a few published descriptions of lacertid microornamentation are available (for instance, *Lacerta vivipara* [Bryant et al., 1967]; *Lacerta viridis* [Sammartano, 1976; Peterson, 1984a]; *Podarcis hispanica* [Bowker et al. 1987]), a systematic survey was undertaken as the first stage of the investigation.

MATERIALS AND METHODS

Areas of Body Examined

Differences in squamate scale microornamentation occur not only between taxa but also on different parts of the body of individual animals and even on individual scales (Cole and Van Devender, 1976; Peterson, 1984b). In consequence, the survey conducted here has been restricted to specified areas of the skin. Most observations were made on the paravertebral mid-dorsal surface of the posterior body, as this is often typical of a large area of the trunk dorsum, but a smaller number involve the dorsal tail base and the belly.

Specimens and Their Examination

Material was obtained from alcohol-preserved specimens in the permanent reptile collection of the

Natural History Museum, London. At least three specimens of each species were examined.

The β -layer of the epidermis of individual scales was removed with forceps, washed in 80% alcohol, and, in a few cases where it was necessary, cleaned further by brief ultravibration in chloroform. The samples were then dried and mounted with Araldite on scanning electron microscope stubs. After coating with gold, the scales were examined using a Hitachi 2500 scanning electron microscope at 15 kV and at magnifications from $\times 35$ to $\times 10,000$. Dorsal scales of 95 species were examined (Table 2) as well as basal caudal scales of 20 species and belly scales of 15. Estimates of cell size were made by measurement of individual cells on micrographs of scale surfaces enlarged $\times 5,000$. Micrographs of the examined scales, together with the accession numbers of the individual lizards from which they came, are deposited in the library of the Reptile and Amphibian section of the Natural History Museum.

Experimental Assessment of Dirt-Shedding Ability and Reflectivity

The relative ability of different microornamentation patterns to shed dirt was tested by painting dry detached scales of large-scaled species of lacertids with fine wet silt, produced by differential flotation of garden soil in water. This was allowed to dry and the scale then subjected to controlled gentle wiping with a truncated primary feather of a house sparrow (*Passer domesticus*), the number of strokes necessary to clean the scale giving some idea of its tendency to retain dirt. Light scattering by microornamentation was assessed by directing a narrow parallel beam of light at various angles at the external surfaces of detached scales of large-scaled lacertids, which had been glued flat onto a plane surface with Araldite, and noting the degree of dispersal of the reflected beam and whether coherent shine was produced.

Approach to Data Analysis

The very wide range of microornamentation encountered in lacertids has a complex taxonomic distribution. It is analyzed as follows. 1) Beginning with the microornamentation of the dorsal scales, variable features are identified and separated into characters with two or more states; the distribution of the states of each character is then plotted on the phylogeny of the family. 2) The history of the individual characters is assessed, including the direction and stages of their evolution and the frequent multiple origin of derived states. 3) Possible correlations with features of the microornamentation of dorsal scales are looked for. These correlations may include other aspects of microornamentation, other intrinsic aspects of the species concerned, or environmental parameters. Even distinctly imperfect

correlations may be significant and do not necessarily have to apply just to derived states. Correlations with other aspects of microornamentation may involve single features or groups of them associated by some common factor; for instance, being derived rather than primitive or possessing a particular physical characteristic. 4) These various correlations are used to generate a hypothesis about the possible function of different types of dorsal body microornamentation. 5) So far as is feasible, the hypothesis is tested by simple experiment and controlled observation. 6) It is further tested by using it to make predictions about the kind of microornamentation to be expected on other areas of the body surface of lacertids living in particular situations, and then checking to see if the predictions hold. This kind of testing is also extended to other taxa. 7) Observed apparent violations of the predictions of the hypothesis are considered to see if they can be reconciled with it.

RESULTS

Dorsal Scales of Body

The variations in microornamentation encountered on lacertid dorsal body scales (Figs. 1–3) can be resolved into differences in a few main characters that often vary independently. This variation is discussed below and the characters and their different states are listed in Table 1. Differences in these features between species examined in this study are shown in Table 2.

Cell shape. As noted, boundaries on the oberhautchen surface may not necessarily represent the margins of actual cells, but units with continuous perimeters made up of welts or grooves are usually referred to by that term in discussions of microornamentation and that convention will be followed here. Such cells are frequently visible in the microornamentation of lacertids and are often narrow and strap-shaped, their longer axes running transversely to the main, approximately anteroposterior axis of the scale (Fig. 1a). In a minority of cases, the microornamentation includes a reticulation of welts or ridges enclosing polygonal areas (Fig. 1b–d) that have also frequently been termed cells (see Problems of Homology, pg. 7).

Profile of cell surface. The surface of a cell is often more or less flat (Fig. 1a) but in polygonal ones it may be centrally depressed so that it is dished (Fig. 1b,c).

Cell dimensions. Strap-shaped cells vary from 1–4 μm in the length of their shorter axes. In polygonal cells this axis is about 4–6 μm in *Heliobolus spekii*, *Pedioplanis inornata*, *P. namaquensis* and *Ophisops jerdoni*, about 10 μm in *P. lineoocellata*, *P. inornata*, *P. undata*, and *O. elbaensis*, and 15–20 μm in *Ichnotropis*, *Pseuderemias mucronata*, *P. striata*, and *Pedioplanis rubens*.

Cell margins. In strap-shaped cells, the cell surface often slopes slightly upwards posteriorly and

the hind margin projects backwards to overlap the cell (or cells) behind (Fig. 1a; see also longitudinal section of *Lacerta vivipara* scale illustrated by Bryant et al., 1967, plate XI). The amount of imbrication is very variable. In some instances, the projecting margins are set at a steeper upward angle (Fig. 1e) and in these cases are also often particularly extensive. The most extreme examples of this condition, for instance, in *Poromera* (Fig. 1f) and some *Gallotia*, have the raised margins projecting almost perpendicularly from the general cell surface.

In *Nucras boulengeri* and *N. tessellata* the areas of contact between adjoining cells are depressed to form grooves (Fig. 2a). As noted above, the borders of polygonal cells in particular may be raised into welts or ridges, for example in *Heliobolus spekii*, *Ichnotropis* (Fig. 1c), *Pseuderemias* (Fig. 1d), some *Pedioplanis*, and *Ophisops* (Fig. 1b).

Denticulation of posterior cell margins. The posterior borders of strap-shaped cells are sometimes rather wavy or slightly notched and, in a few cases, where the borders are steeply angled or perpendicular they are denticulated. The denticulations may be rather sparse and irregular (*Algyroides moreoticus*, Fig. 2b), or may form very distinct groups, being coordinated in succeeding cells to form tracts running mainly anteroposteriorly along the scale (*Poromera fordi*, Fig. 1f). In other cases denticulations are abundant and widespread, forming a field of spikes (*Gallotia stehlini*, Fig. 2c).

Detailed structure of cell surface. This is not always easily seen, especially where strap-shaped cells have long, almost perpendicular posterior edges. When visible, the cell surface frequently appears quite smooth (Fig. 1a.), even at magnifications of $\times 8,000$ or more, but in other cases it exhibits an array of pits that are often about 0.5 μm in diameter. In some instances these pits are shallow and scattered; for instance, in *Nucras* (Fig. 2a) and *Philochortus* (Fig. 2d), but in many taxa they are rather larger, irregular, and densely packed (Fig. 1b–d). When this is so, the surface keratin may be reduced to a filigree, with the enclosed cavities making up about half the total cell surface (Fig. 2e).

Longitudinal ridges. In scales with strap-shaped cells, the epidermal surface may be rucked to produce ridges that run essentially longitudinally, either roughly parallel to the main axis of the scale or converging posteriorly (some *Takydromus*, Fig. 3a) or diverging in this direction (vertebral scales of *Philochortus hardeggeri*, Fig. 3c). The ridges are usually quite long (Fig. 3a), but may sometimes be short (Fig. 3c) and may anastomose with each other. At lower magnifications, *Poromera* appears to have ridges arranged similarly to those in *Takydromus* (Fig. 3a,b), but in reality these are tracts of denticulations (Fig. 1f).

Pustular projections. Strap-shaped cells may be interrupted by large pustular projections, a fea-

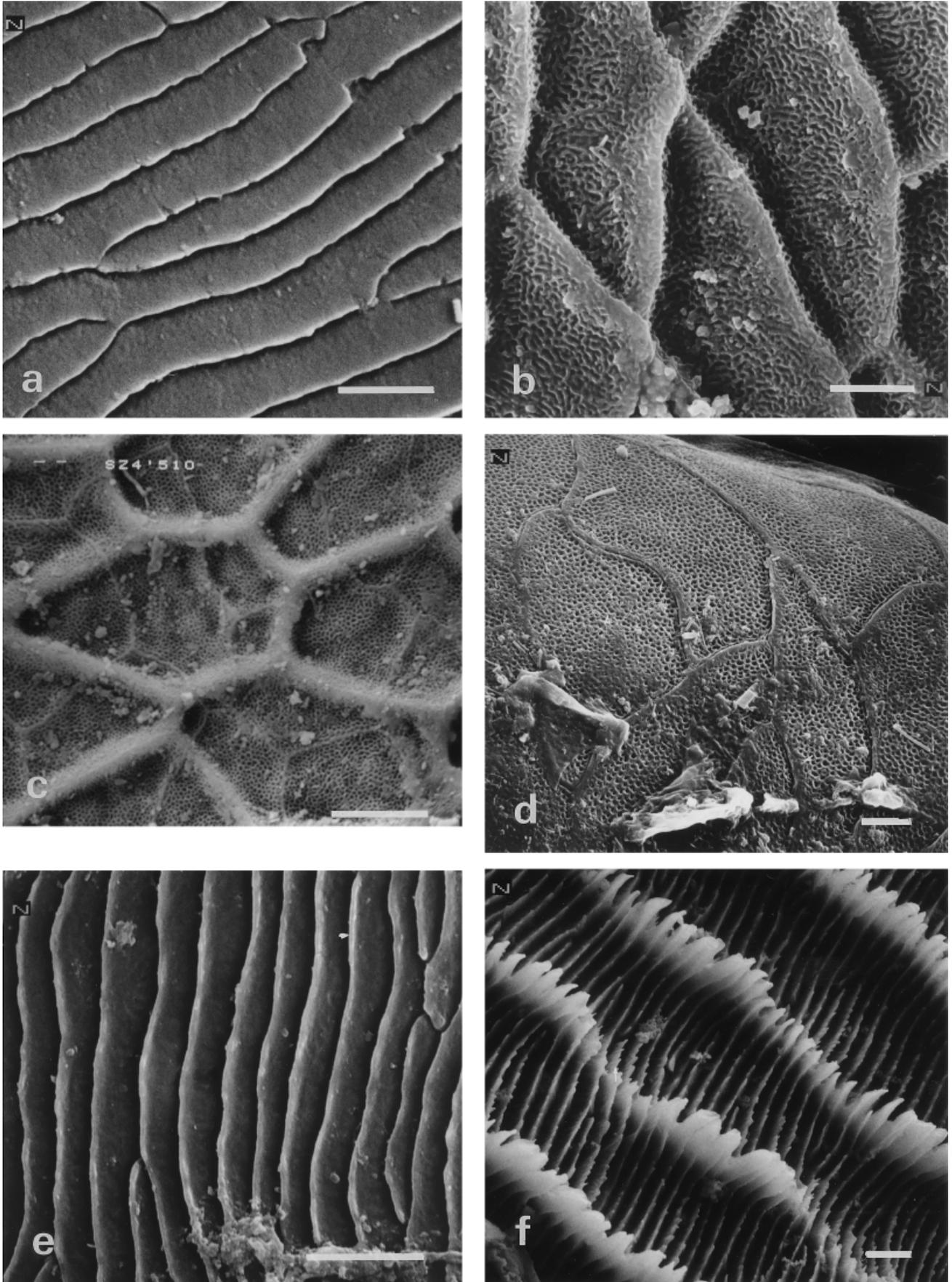


Fig. 1. Microornamentation on dorsal scales of lacertid lizards. **a:** *Lacerta monticola cantabrica* ($\times 4,000$). **b:** *Ophisops jerdoni* ($\times 3,500$). **c:** *Ichnotropis capensis* ($\times 4,000$). **d:** *Pseudieremias mucronata* ($\times 2,000$). **e:** *Tropidosaura montana* ($\times 5,000$). **f:** *Poromera fordii* ($\times 2,000$). Anterior of scale is in the direction of upper left corner of photograph **a**, to the right in **e**, and to the left in the remainder. Scale bar = 5 μm .

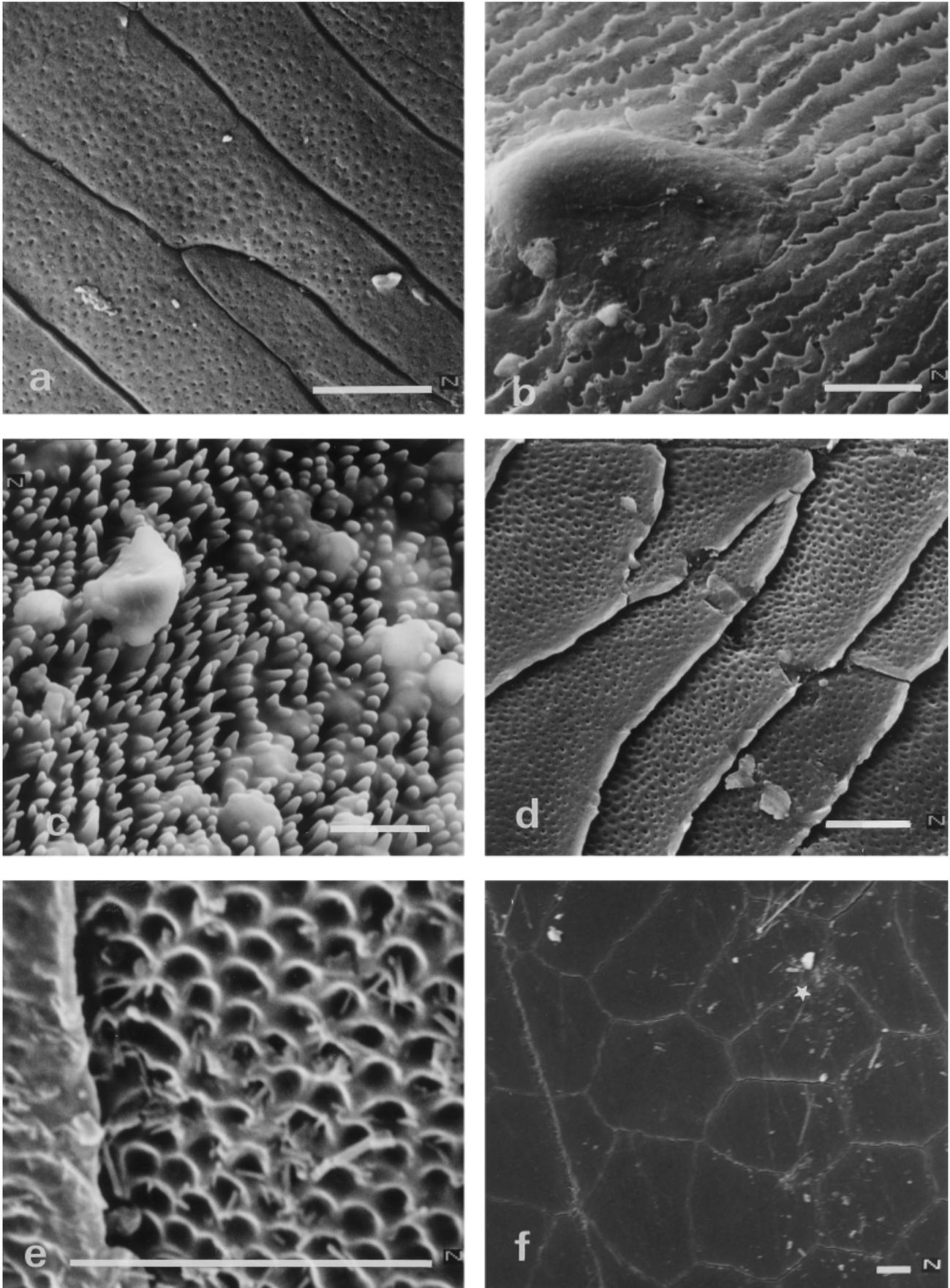


Fig. 2. Microornamentation on scales of lacertid lizards; **a**, **b**, **d**, and **e** show dorsal body scales. **a**: *Nucras boulengeri* ($\times 5,000$). **b**: *Algyroides moreoticus* ($\times 4,000$). **c**: *Gallotia stehlini* ($\times 4,000$), proximal tail scale. **d**: *Philochortus spinalis* ($\times 3,500$). **e**: *Pseuderemias mucronata* ($\times 15,000$). **f**: *Pseuderemias mucronata* ($\times 1,500$), ventral body scale. Anterior of scale is in the direction of the bottom left corner of photograph **a**, bottom right corner in photograph **b**, top left corner in photograph **d**, and to the left in the remainder. Scale bar = 5 μm .

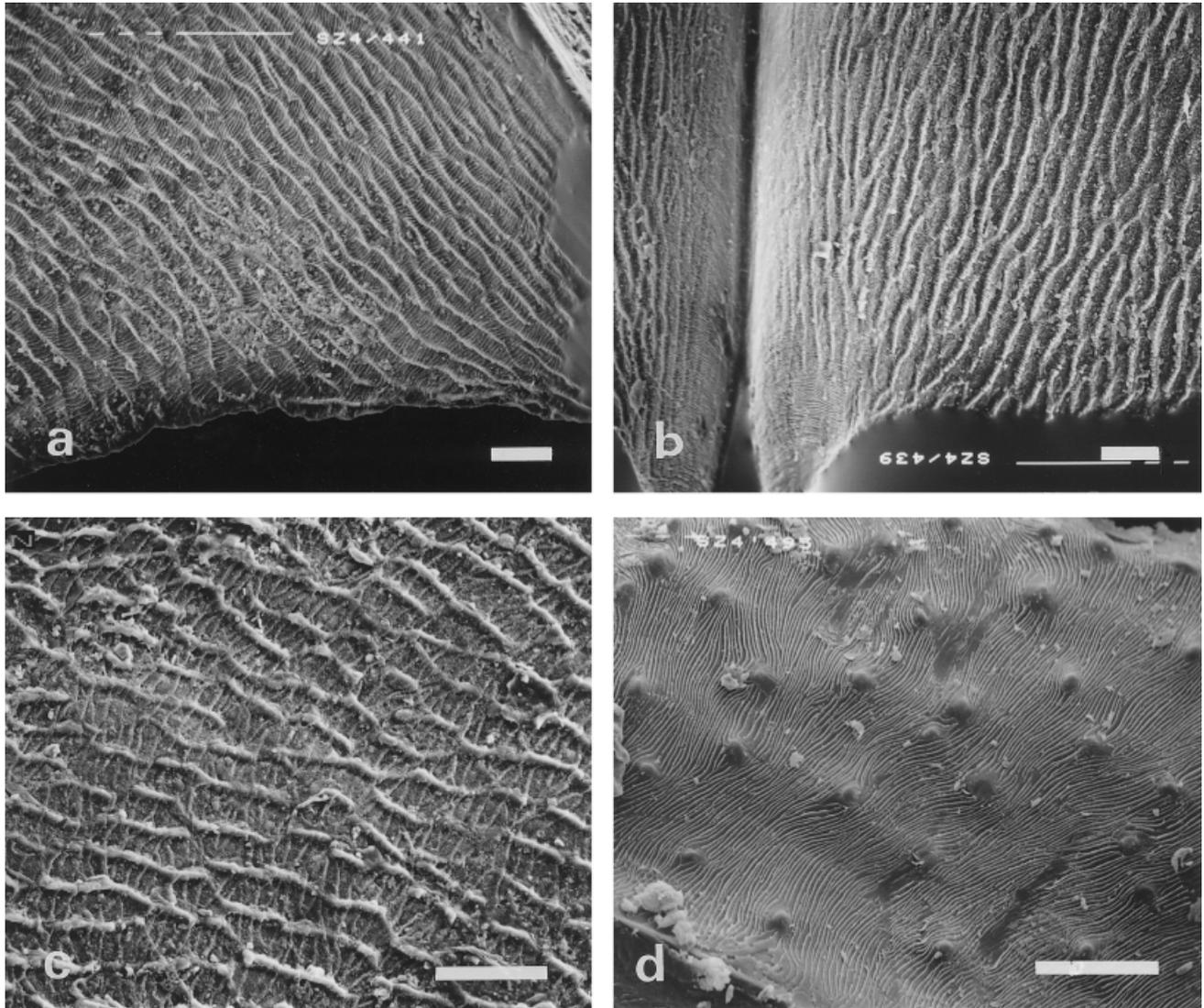


Fig. 3. Microornamentation on dorsal scales of lacertid lizards. **a:** *Takydromus septentrionalis* ($\times 200$). **b:** *Poromera fordi* ($\times 200$). **c:** *Philochortus hardeggeri* ($\times 350$). **d:** *Algyroides nigropunctatus* ($\times 400$). Anterior of scale is in the direction of top left corner of photograph, in **a** and **d** where it is towards upper margin in **b**, and towards bottom right corner in **c**. Scale bar = 50 μm .

ture only encountered in *Algyroides* (Figs. 2b, 3d) and *Adolfus africanus*.

Most derived features involve increased sculpturing and roughening of the scale surface relative to the 0 states in Table 1.

Dorsal Scales on Tail Base

Among many Lacertinae and the more basal Eremiainae (see Fig. 5), microornamentation on the large dorsal scales of the proximal part of the tail is similar to that present on the dorsal body scales. This is true in *Lacerta oxycephala*, *L. praticola*, *L. dugesii*, *Podarcis taurica*, *Adolfus africanus*, *A. vauereselli*, *Tropidosaura cottrelli*, *T. essexi*, and *Poromera fordi*. In some other forms in this assem-

blage there are differences, but these are relatively slight in the studied cases. For instance, *L. monticola* has the edges of the strap-shaped cells more raised on the tail scales than on the body, and in *Gallotia stehlini* denticulations become more florid. Similarity of the microornamentation of the scales of the dorsal body and tail also occurs in a scattering of forms among the more derived members of the Eremiainae, including *Philochortus spinalis*, *Pseudermias striata*, *Pedioplanis laticeps*, and *Acanthodactylus haasi*. However, substantial differences between body and tail scales are common here. In *Nucras boulengeri*, *N. tessellata*, *Heliobolus speki*, and *H. lugubris* the non-overlapping strap-shaped cells on the dorsal body scales are replaced on the tail by ones in which the posterior imbrications are

TABLE 1. Characters and states of dorsal body scale microornamentation in the Lacertidae

1. Cell shape. 0 = narrow, transversely strap-shaped; 1 = not narrow, polygonal.
2. Profile of cell surface. 0 = more or less flat; 1 = dished, the center lower than the edges.
3. Cell dimensions, anteroposterior length. 0 = 2–10 μm ; 1 = >10 μm ; 2 = <2 μm . States 1 and 2 appear to be independently derived from state 0.
4. Cell margins. 0 = hind margins posteriorly imbricate with at most a shallow upward angle; 1 = hind margins posteriorly imbricate with steep upward angle; 2 = no clear imbrication, borders between cells are grooves; 3 = no clear imbrication, borders forming raised welts. States 1, 2, and 3 appear to be independently derived from state 0.
5. Denticulation of posterior cell margins. 0 = margins more or less smooth; 1 = margins with some denticulation; 2 = denticulation abundant and widespread, forming tracts or a field of spikes.
6. Detailed structure of cell surface. 0 = smooth; 1 = scattered pits; 2 = pits densely packed, often comprising around half the scale surface.
7. Longitudinal ridges. 0 = absent; 1 = present.
8. Pustular projections. 0 = absent; 1 = present.

0 usually indicates the primitive state within the family based on its distribution in the family itself and in outgroups.

strongly raised and there is increased pitting on the scale surfaces. In *Pedioplanis namaquensis* and *P. rubens*, polygonal cells are present on the tail as well as the body, but are concave rather than convex in this situation. An increase in cell concavity also occurs on the tail of *Ophisops elbaensis*. In *Acanthodactylus micropholis* and *A. robustus*, the imbricate posterior edges of the strap-shaped cells are more raised on the tail scales.

Belly Scales

The large, smooth, shiny belly scales of most lacertids are often heavily scratched and no cell margins may be apparent on their surface. However in *Takydromus* and some Lacertinae and basal Eremiainae, the pattern common on dorsal scales of strap-shaped cells with low overlapping posterior borders and smooth surface is also present on the belly scales, the cells having an anteroposterior length of about 2–5 μm . This was observed in *Takydromus kuehnei*, *Gallotia galloti*, *Lacerta monticola*, *Adolfus africanus*, and *Tropidosauro cottrelli* and is also reported in *Podarcis hispanica* (Bowker et al., 1987). In contrast, several of the more terminal members of the Eremiainae have a pattern on the main surface of the ventral scales, consisting of large polygonal cells with simple abutting margins. It is found in *Pseudereimias mucronata* (Fig. 2f), *Acanthodactylus scutellatus*, and *Ophisops elegans* and also occurs in *Latastia boscai*, where the cells are less expanded anteroposteriorly than in other cases and are lightly pitted. Polygonal cells on lacertid ventral scales are about 10 μm in length anteroposteriorly in *Latastia boscai* and around 20 μm in the other species exam-

ined. In *Ichnotropis capensis* and *Pedioplanis husabensis* the main surface of the scale is quite smooth, without visible cell boundaries.

Surface structure may be different on the anterior, basal region of a ventral scale and sometimes also on the posterior margin of the scale where it curves upwards. *Ichnotropis capensis* and *Pedioplanis husabensis* have polygonal cells in the basal region and *Ophisops elegans* strap-shaped, overlapping ones.

DISCUSSION

Problems of Homology

Harvey 1993, and Harvey and Gutberlet 1995; gives reasons why strap-shaped cells in squamate microornamentation may not be homologous with the polygonal units that are also often called cells but that he terms “macro-honeycomb.” This author points out that in some xenosaurid lizards, where the borders of the polygonal units are raised and the units themselves dished, the ridge-like borders involve not only the oberhautchen but also the β -, mesos, and α -layers of the epidermis underlying it. Furthermore, in *Xenosaurus grandis agrenon* strap-shaped cells overlie a larger polygonal pattern of ridges. In this case the two elements thus appear to fail the conjunction test for homology (Patterson, 1982).

In lacertids, no cases have been encountered of discrete strap-shaped cells and polygonal structures being superimposed, and intermediate conditions occur between strap-shaped cells and deeply dished polygonal units. In some species there may be gradation on the same body scales from relatively strap-shaped cells to polygonal ones (*Pedioplanis namaquensis*), and from flat polygonal units on the dorsal body to dished polygonal units on the dorsal tail base (*P. rubens*). The fact that, where the borders of polygonal units are raised into ridges, other deeper layers of the epidermis may be involved does not automatically negate homology with borders where this is not the case, especially if there are intermediates between the two conditions. Because of this, strap-shaped and polygonal units in lacertid lizards are regarded here as provisionally homologous. In *Ichnotropis squamulosa* (Fig. 1c) the polygonal network of raised ridges is accompanied by a staggered polygonal system of thin, unraised lines. Similar patterns of thin lines in other lizards have been interpreted as resulting from the cell borders of the clear layer that separates the oberhautchen from the previous exuvium during development (Stewart and Daniel, 1972; see also discussion by Irish et al., 1988).

History of Dorsal Microornamentation

Relationships within Lacertidae. Recent investigations of the morphology (Arnold, 1989a,b, 1991) and mitochondrial DNA sequence (Harris et

TABLE 2. Variation in microornamentation in 95 species of lacertid lizards

	1	2	3	4	5	6	7	8	9
	Cell shape	Cell profile	Cell size	Cell margins	Denticulate	Cell texture	Long. ridges	Pustules	Scale size
<i>Psammmodromus hispanicus</i>	0	—	2	1	1	—	0	0	?
<i>Psammmodromus algirus</i>	0	—	0	1	0	1	1	0	1
<i>Gallotia atlantica</i>	0	—	2	1	1	0	0	0	0
<i>Gallotia galloti</i>	0	—	2	1	1	—	0	0	0
<i>Gallotia stehlini</i>	0	—	2	1	2	—	0	0	0
<i>Lacerta vivipara</i>	0	0	0	—	0	—	0	0	1
<i>Lacerta lepida</i>	0	0	0	0	0	0	0	0	0
<i>Lacerta princeps</i>	0	0	0	0	0	0	0	0	0
<i>Lacerta agilis</i>	0	0	0	0	0	0	0	0	0
<i>Lacerta monticola</i>	0	0	0	0	0	0	0	0	0
<i>Lacerta mosorensis</i>	0	0	0	0	0	0	0	0	1
<i>Lacerta oxycephala</i>	0	0	0	0	0	0	0	0	0
<i>Lacerta brandti</i>	0	0	0	0	0	1	0	0	0
<i>Lacerta praticola</i>	0	0	0	0	0	0	0	0	0
<i>Lacerta graeca</i>	0	0	0	0	0	0	0	0	0
<i>Lacerta cappadocica</i>	0	0	0	0	0	1	0	0	0
<i>Lacerta laevis</i>	0	0	0	1	0	0	0	0	0
<i>Lacerta fraasi</i>	0	0	2	0	0	0	0	0	0
<i>Lacerta parva</i>	0	0	2	1	0	0	0	0	0
<i>Lacerta andreanszkii</i>	0	0	2	0	0	0	0	0	0
<i>Lacerta dugesii</i>	0	0	0	0	0	0	0	0	0
<i>Podarcis hispanica</i>	0	0	0	0	0	0	0	0	0
<i>Podarcis melisellensis</i>	0	0	0	0	0	0	0	0	0
<i>Podarcis taurica</i>	0	0	0	0	0	0	0	0	0
<i>Algyroides nigropunctatus</i>	0	—	2	1	0	0	0	1	1
<i>Algyroides moreoticus</i>	0	0	2	1	1	0	0	1	1
<i>Algyroides fitzingeri</i>	0	—	2	1	0	0	0	1	1
<i>Algyroides marchi</i>	0	0	2	1	0	0	0	1	1
<i>Takydromus amurensis</i>	0	—	2	1	0	—	1	0	1
<i>Takydromus septentrionalis</i>	0	0	0	1	0	?	1	0	1
<i>Takydromus sexlineatus</i>	0	0	0	1	0	2	1	0	1
<i>Takydromus kuehnei</i>	0	0	0	1	0	—	1	0	1
<i>Takydromus toyamai</i>	0	0	0	0	0	0	1	0	1
<i>Australolacerta australis</i>	0	0	0	0	0	1	0	0	0
<i>Omanosaura cyanura</i>	0	0	0	0	0	0	0	0	0
<i>Omanosaura jayakari</i>	0	0	0	0	0	1	0	0	0
<i>Adolfus jacksoni</i>	0	0	0	0	0	0	0	0	0
<i>Adolfus alleni</i>	0	0	0	1	0	1	0	0	1
<i>Adolfus africanus</i>	0	0	0	1	0	1	0	1	1
<i>Adolfus vauereselli</i>	0	0	2	0	0	0	0	0	1
<i>Holaspis guentheri</i>	0	0	0	0	0	0	0	0	1
<i>Gastropholis echinata</i>	0	0	0	1	0	1	1	0	0
<i>Gastropholis tropidopholis</i>	0	0	0	0	0	1	1	0	1
<i>Gastropholis vittata</i>	0	0	0	0	0	1	1	0	1
<i>Tropidosaura montana</i>	0	—	2	1	0	0	0	0	1
<i>Tropidosaura gularis</i>	0	0	2	1	0	0	0	0	1
<i>Tropidosaura cottrelli</i>	0	0	2	1	0	0	0	0	1
<i>Tropidosaura essexi</i>	0	0	2	1	0	0	0	0	1
<i>Poromera fordii</i>	0	—	2	1	2	0	?	0	1
<i>Nucras boulengeri</i>	0	0	0	2	0	1	0	0	0
<i>Nucras tessellata</i>	0	0	0	2	0	1	0	0	0
<i>Nucras lalandei</i>	0	0	0	0	0	1	0	0	0
<i>Philochortus hardeggeri</i>	0	0	0	0	0	1	1	0	1
<i>Philochortus spinalis</i>	0	0	0	0	0	2	0	0	0
<i>Latastia longicaudata</i>	0	0	—	0	0	—	0	0	0
<i>Latastia johnstoni</i>	0	0	0	0	0	2	0	0	0
<i>Latastia neumanni</i>	0	0	0	0	0	2	0	0	0
<i>Heliobolus nitida</i>	0	0	0	0	0	2	0	0	0
<i>Heliobolus speki</i>	1	0	0	3	0	2	0	0	0
<i>Heliobolus lugubris</i>	0	0	0	0	0	2	0	0	0
<i>Ichnotropis capensis</i>	1	1	1	3	0	2	0	0	1
<i>Ichnotropis squamulosa</i>	1	1	1	3	0	2	0	0	1
<i>Pseuderemias mucronata</i>	1	0	1	3	0	2	0	0	0
<i>Pseuderemias striata</i>	1	0	1	3	0	2	0	0	0
<i>Meroles knoxi</i>	0	0	0	0	0	—	0	0	0
<i>Meroles suborbitalis</i>	0	0	0	0	0	1	0	0	0
<i>Meroles ctenodactylus</i>	0	0	0	0	0	1	0	0	0

TABLE 2. (Continued)

	1	2	3	4	5	6	7	8	9
	Cell shape	Cell profile	Cell size	Cell margins	Denticulate	Cell texture	Long. ridges	Pustules	Scale size
Pedioplanis lineocellata	1	1	1	3	0	2	0	0	0
Pedioplanis breviceps	0	0	0	0	0	1	0	0	0
Pedioplanis burchelli	0	0	0	0	0	1	0	0	0
Pedioplanis laticeps	0	0	0	3	0	1	0	0	0
Pedioplanis inornata	1	0	0	3	0	2	0	0	0
Pedioplanis namaquensis	1	0	0	0	0	2	0	0	0
Pedioplanis rubens	1	0	1	3	0	2	0	0	0
Pedioplanis undata	1	0	—	3	0	—	0	0	0
Eremias velox	0	0	0	0	0	0	0	0	0
Eremias fasciata	0	0	0	0	0	1	0	0	0
Eremias grammica	0	0	0	0	0	1	0	0	0
Acanthodactylus boskianus	0	0	0	1	0	—	0	0	?
Acanthodactylus micropholis	0	0	0	0	0	1	0	0	0
Acanthodactylus schmidti	0	0	0	0	0	2	0	0	0
Acanthodactylus tilburyi	0	0	0	0	0	1	0	0	0
Acanthodactylus haasi	0	0	0	0	0	1	0	0	0
Acantho. gongrorhynchatus	0	0	0	0	0	1	0	0	0
Acanthodactylus robustus	0	0	0	0	0	0	0	0	0
Acanthodactylus erythrurus	0	0	0	0	0	1	0	0	0
Acanthodactylus pardalis	0	0	0	0	0	—	0	0	0
Acanthodactylus scutellatus	0	0	0	0	0	1	0	0	0
Mesalina balfouri	0	0	0	0	0	1	0	0	0
Mesalina rubropunctata	0	0	0	0	0	1	0	0	0
Ophisops elegans	0	0	2	1	0	0	0	0	1
Ophisops leschenaulti	0	0	0	1	0	—	1	0	1
Ophisops elbaensis	1	1	1	3	0	2	0	0	1
Ophisops jerdoni	1	1	1	3	0	2	0	0	1
Ophisops minor	0	0	2	1	0	—	1	0	1
Teiids	1	0	2	3	0	?	?	?	?

States of characters given in columns 1–8 are listed in Table 1. Column 9 indicates size of dorsal scales (0 small, 1 large, see section on Nonancestral Resemblance). Dashes indicate lack of data. Data for *Holaspis* and *Philochortus*, refer to the enlarged vertebral body scales.

al., 1998) of lacertid lizards indicate that principal relationships within the family are as shown in Figure 5. The Gallotiinae occur in the West Mediterranean area and the Canary Islands, the Lacertinae principally in the West Palaearctic, and the Eremiainae mainly in the Afrotropical region, but with four terminal genera in North Africa and southwest and central Eurasia. The precise position of *Takydromus* of East Asia relative to the last two groups is unresolved. Many species occur in generally mesic habitats but *Psammotromus* and the more derived members of the Eremiainae (*Nucras* and its apparent sister group) are mainly found in more arid situations.

Phylogenetic distribution. The MacClade program (Maddison and Maddison, 1996) was used to estimate character states on internal branches of the lacertid phylogeny by parsimony (see Figs. 4–9). This indicates that many states were derived within the family, including polygonal cells, cell dishing, large cell size, borders consisting of grooves or welts, high levels of pitting, longitudinal ridges, and pustular projections.

With some other traits, it is not clear from their distribution in the Lacertidae that they always arose within the family, although they did so on occasion and are also usually minority states. Nor do

conditions in outgroups clearly resolve the polarity of these features, which include small cell size, posterior cell edges markedly raised, and these edges denticulated. This is because microornamentation is very varied in some of the Scleroglossan groups concerned and not all the interrelationships of these groups are unequivocally resolved; for instance, the schemes of Estes et al. (1988) and of Lee (1998) exhibit significant differences. It is, however, generally agreed that the sister-group of the Lacertidae is the Teiioidea, which often exhibit large cell size and posterior cell edges that are not markedly raised or denticulated (Stewart and Daniel, 1975; Peterson, 1984a; Peterson and Bezy, 1985; Vaccaro et al., 1988). The last two features are uncommon in Scleroglossans as a whole, although they are frequent in the Scincidae. Given that pitting occurs in the Teiioidea, it is most parsimonious to consider low levels of pitting as the primitive state in the Lacertidae if detailed structure of the cell surface is treated as an ordered character, while polarity is unresolved if it is not.

It appears from these considerations that the primitive dorsal microornamentation pattern for the Lacertidae is likely to be a combination of strap-shaped cells of intermediate size with imbricate posterior bor-

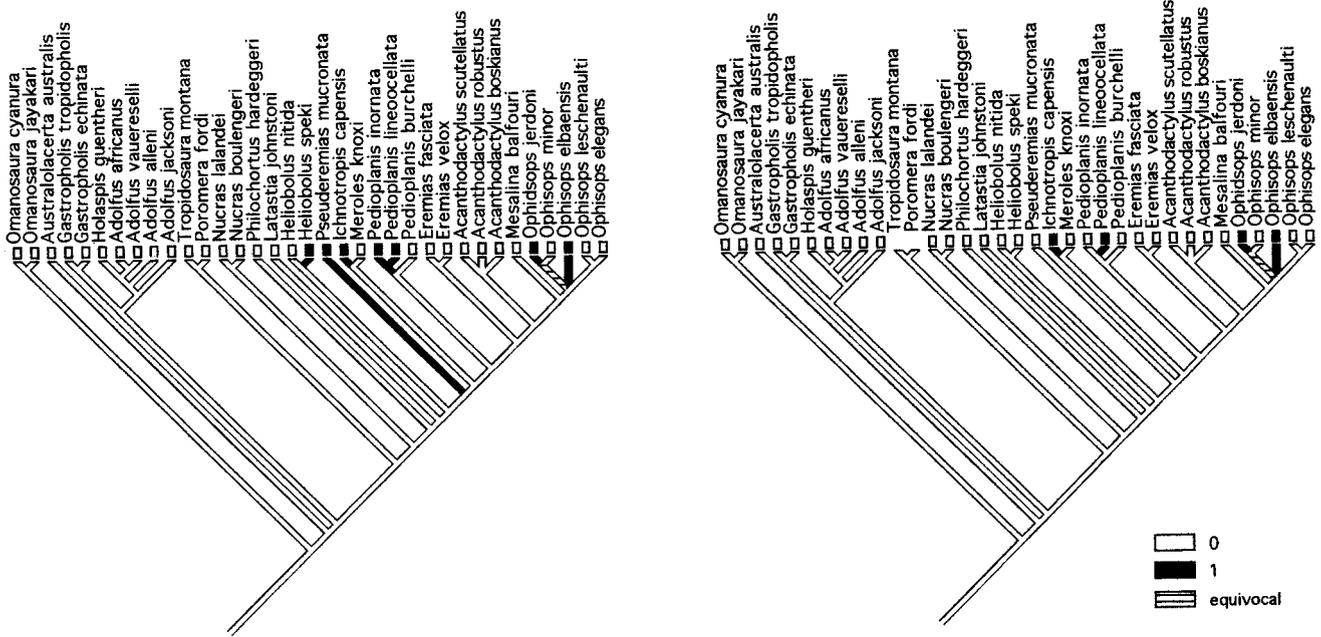


Fig. 4. Left. Phylogenetic distribution of strap-shaped cells (0) and polygonal cells (1). Right. Phylogenetic distribution of dished cell surfaces (1). Here and in Figures 5–9, 12 and 13 not all the species in Table 2 are included.

ders that are not sharply raised, and lightly pitted or smooth cell surfaces in which denticulation, large ridges, and pustules are absent (Fig. 1a).

The primitive lacertid pattern also occurs widely, although sporadically, in other lizards, being found in basal xantusiids (Stewart and Daniel, 1975; Peterson and Bezy, 1985), gerrhosaurids, the cordylid *Platysaurus* (Harvey and Gutberlet, 1995), and some anguids (*Gerrhonotus multicarinatus* [Stewart and Daniel, 1973]). Scale microornamentation of *Sphenodon*, the living outgroup of the squamates, is also reported to be similar (Peterson, 1984a), although this has been disputed (Maderson et al., 1998).

Use of MacClade also helped determine transformation series in multistate characters (Table 1). Especially large and especially small cells appear to have arisen from the more widespread intermediate condition occurring in the primitive microornamentation. Similarly, raised imbricate posterior cell margins, grooves between cells, and borders forming ridges or welts between deeply dished cell surfaces all seem to have been derived independently from the primitive condition. In these cases decisions were supported by other clues as to proximity of states in transformation sequences, including relative similarity of states and their occurrence together, often with intermediates, in the same individuals.

Nonancestral Resemblance in Dorsal Body Microornamentation

It can be seen from Figures 4–9 and Table 3 that most of the derived features of microornamentation

found in lacertids have evolved more than once and often on several occasions. For instance, if the polarities assumed for the Lacertidae are accepted, strong pitting of cell surfaces has originated 3–4 times, small cells 8–10, and raised posterior cell edges 9–12. For the 13 different forward transformations listed in Table 1, there are a total of 43–61 independent cases. In the more restricted context of the Eremiinae, where polarity for most features can be determined without recourse to groups outside the Lacertidae, high levels of parallelism are again apparent (Table 3).

Given that only minimal numbers of origins can be estimated (since estimates are based on a parsimony analysis and not all lacertid taxa are included), this degree of parallelism is very striking. It suggests that, in developmental terms, the features may be quite easily produced. This could be partly a characteristic of small-scale structures, where there is a high degree of self-organization, and possible developmental paths are quite limited. Perhaps the different derived features may be “switched on” by natural selection if they promote performance advantage in particular situations, but there seem to be limits to the variations that can be produced.

Although conditions on some internal branches are equivocal, with parallelism and reversal both being possibilities, in the great majority of microornamentation features there is no overt evidence of reversal to primitive states taking place within the Lacertidae. The principal exception is the presence of strong pitting on the scale surface, for which parsimony indicates at least one reversal leading to

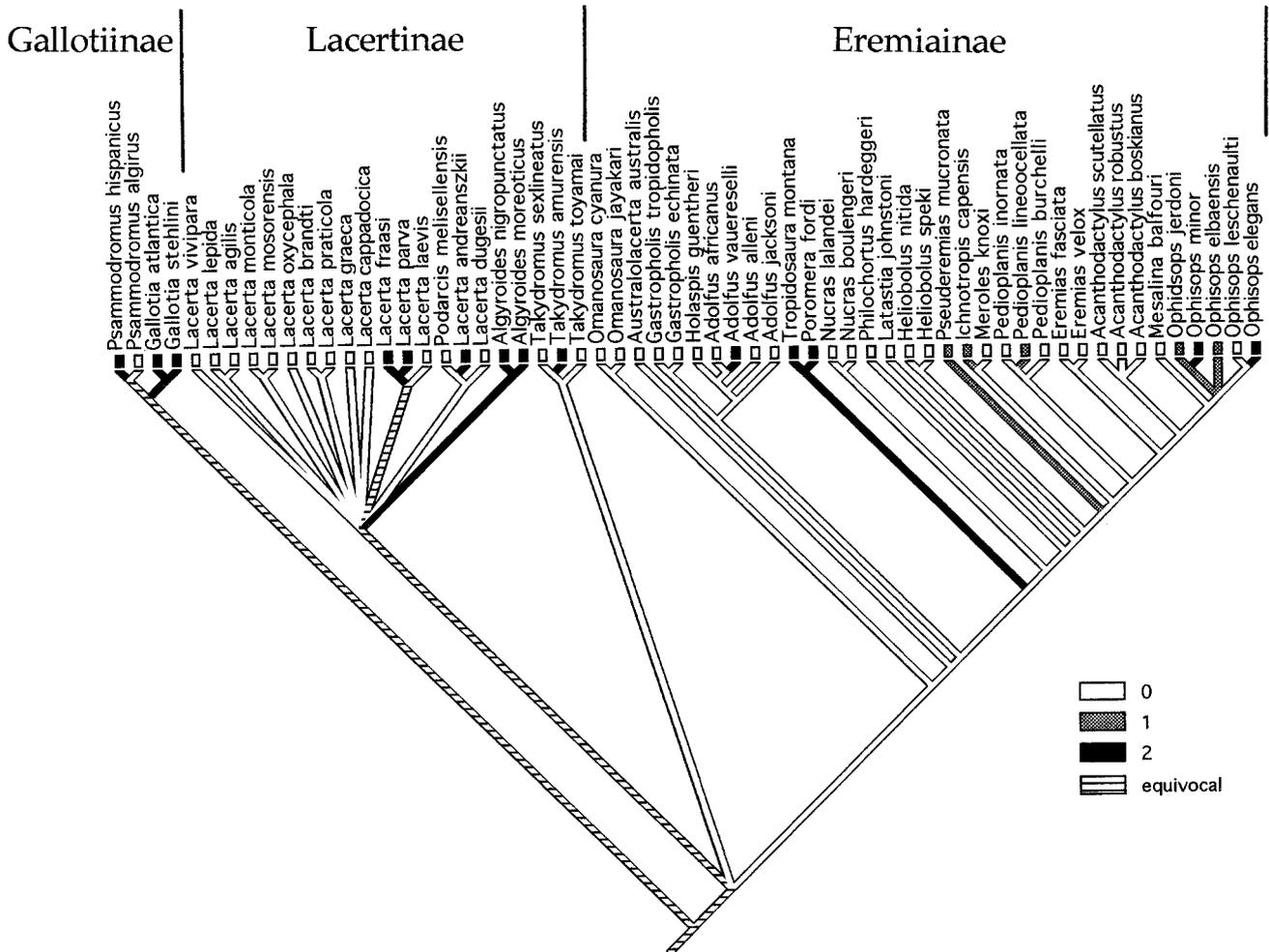


Fig. 5. Phylogenetic distribution of large (1) and small (2) cells. Allocation of taxa to the three subfamilies of the Lacertidae is also shown.

more primitive states in one or more members of *Pedioplanis*, *Eremias*, *Acanthodactylus*, *Mesalina*, and *Ophisops* (Fig. 8). Reversal may possibly also occur in the development of dished cell surfaces (see Lack of reversal after loss of function?, below). Such an asymmetry in frequency between parallelism and reversal may also occur outside the Lacertidae, as absence of reversal in microornamentation has been suggested in the phrynosomatid genus *Sceloporus* (Burstein et al., 1974).

In spite of the rarity of overt reversal, the high incidence of homoplasy that exists makes microornamentation overall a poor indicator of relationship among lacertids, at least at higher taxonomic levels, as is true in other taxa. Sometimes, however, particular groups of lacertids are characterized by relatively rare features that distinguish the assemblages concerned from their closer relatives. Such cases include substantial denticulation of posterior cell margins in *Gallotia* and the presence of pustules in *Algyroides*.

Among main squamate clades there may be general trends in microornamentation. Thus, iguanians and gekkotans typically have polygonal cells, while strap-shaped ones are usual in scincids (Perret and Wuest, 1982, 1983). But even at this taxonomic level, there may be striking parallels across large systematic distances. The microornamentation pattern found in *Ichnotropis* (Fig. 1c) is very similar to that occurring in some iguanians, such as *Polychrus* (Peterson, 1984b; Fig. 1c). Subdigital setae, which are another form of microornamentation, are widespread in gekkotans but also occur in the iguanian genus *Anolis* and in one species of the autarchoglossan scincid lizard genus *Prasinohaema* (Williams and Peterson, 1982). Such close derived resemblances among very distant relatives supports the hypothesis that developmental pathways for microornamentation may be restricted, and the discovery of just one case of digital setae among the 1,700 or so species of the autarchoglossan lizards warns against making sweeping statements about the limits to the

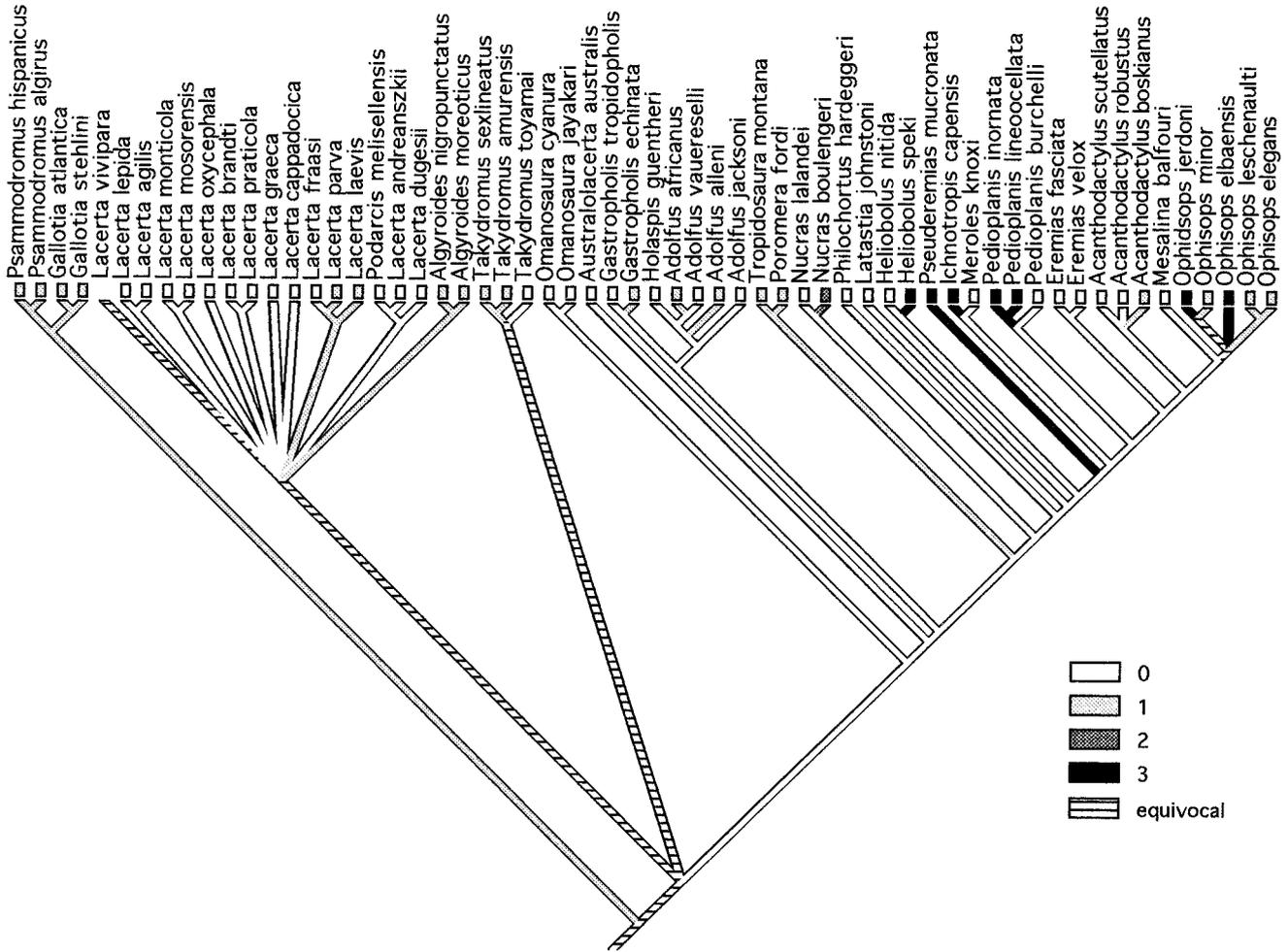


Fig. 6. Phylogenetic distribution of raised posterior cell margins (1), groove-like cell borders (2), and welt- or ridge-like borders (3).

kinds of microornamentation that can occur in particular groups.

Patterns of Association and Order of Change in Dorsal Body Ornamentation

The principal derived features of lacertid microornamentation occur together in two main groupings (Fig. 10). In one, microornamentation may include small cell size, raised posterior cell edges, denticulation, longitudinal ridges, and pustules. In the other, possible components are polygonal cells, dished cell surfaces, large cell size, welt-like borders and dense pitting.

Derived features of up to five characters of lacertid microornamentation may sometimes occur together. If derived features in general were assembled in a fixed order during evolution, it would be possible, given the degree of homoplasy present, to recognize repeated linear sequences of varying length resulting in increasingly complex microornamentation. In fact, this is not the case

and the different derived features may appear in a range of sequences (see Fig. 11). In some instances, one feature may occur before another on a particular lineage, while appearing after it on another one. The lack of a simple pattern of order of change in the features of microornamentation indicates that they are developmentally substantially independent.

Comments on Microornamentation of Dorsal Tail Base and Belly

In general, the widespread primitive pattern of microornamentation of the dorsal body scales is also found on the dorsal tail scales of many of the more basal forms of the Lacertinae, while *Gallotia* and members of the Eremiinae have more derived conditions on the tail. Where it is different from the microornamentation on the dorsal body scales, that on the tail base may be more derived or less so. It is more derived where the edges of strap-shaped cells are raised in *Lacerta monticola* and *Acanthodacty-*

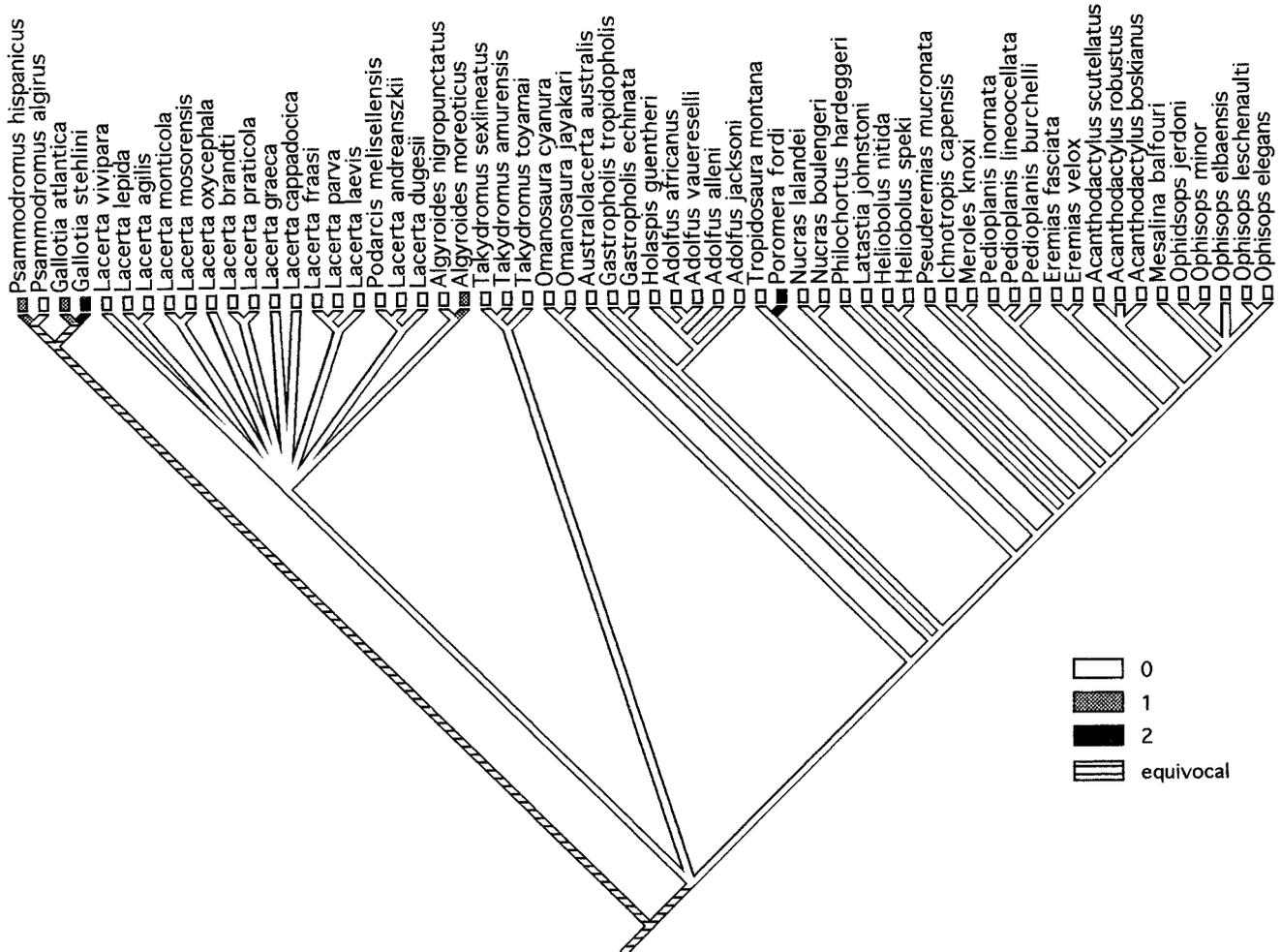


Fig. 7. Phylogenetic distribution of denticulated raised posterior cell margins: weak (1) and strong (2).

lus and where the edges are more denticulated, as in *Gallotia stehlini*. In contrast, it is more primitive in the species of *Nucras*, *Heliobolus*, and *Pedioplanis* examined. In all these cases where microornamentation on the tail scales is different from that on the body, it is also more sculptured and three-dimensional.

Distinctive ornamentation at the base of the belly scales found in some lacertids has also been noted on the dorsal scales of snakes (McCarthy, 1987; Price and Kelly, 1989). In adult snakes, the basal pattern is often more primitive than that on the greater part of the scale and, in cases where there is ontogenetic change in the latter region, the basal area tends to remain more similar to the condition in neonates (Price and Kelly, 1989). It is not known whether the latter phenomenon is found in lacertid ventral scales but, in the few cases where a different basal pattern has been observed, it is indeed primitive relative to that found on the main surface of the scale. Thus, the scale base has overlapping strap-shaped cells in cases where those on the main surface are polygo-

nal, and polygonal ones where the main surface is featureless. The basal areas of ventral scales are less exposed to the environment than the main surface, since they are protected by the posterior imbrication of the edges of the scales lying immediately in front of them. They are therefore presumably likely to be under less pressure to change in response to alterations in external aspects of the selective regime.

Frequently, the predominant microornamentation on the ventral scales is different from that of the dorsals, being often simpler and smoother. However, in *Lacerta monticola* and *Gallotia galloti* the primitive lacertid pattern of microornamentation that occurs on their dorsal scales is also present on the ventrals and, in a few forms where the dorsal scales have complex derived microornamentation, this too is repeated on the belly scales, something that occurs in *Poromera fordi*, some *Takydromus*, and *Gastropholis tropidopholis* (see below).

Dorsal and ventral scale microornamentations can clearly evolve independently of each other. Dor-

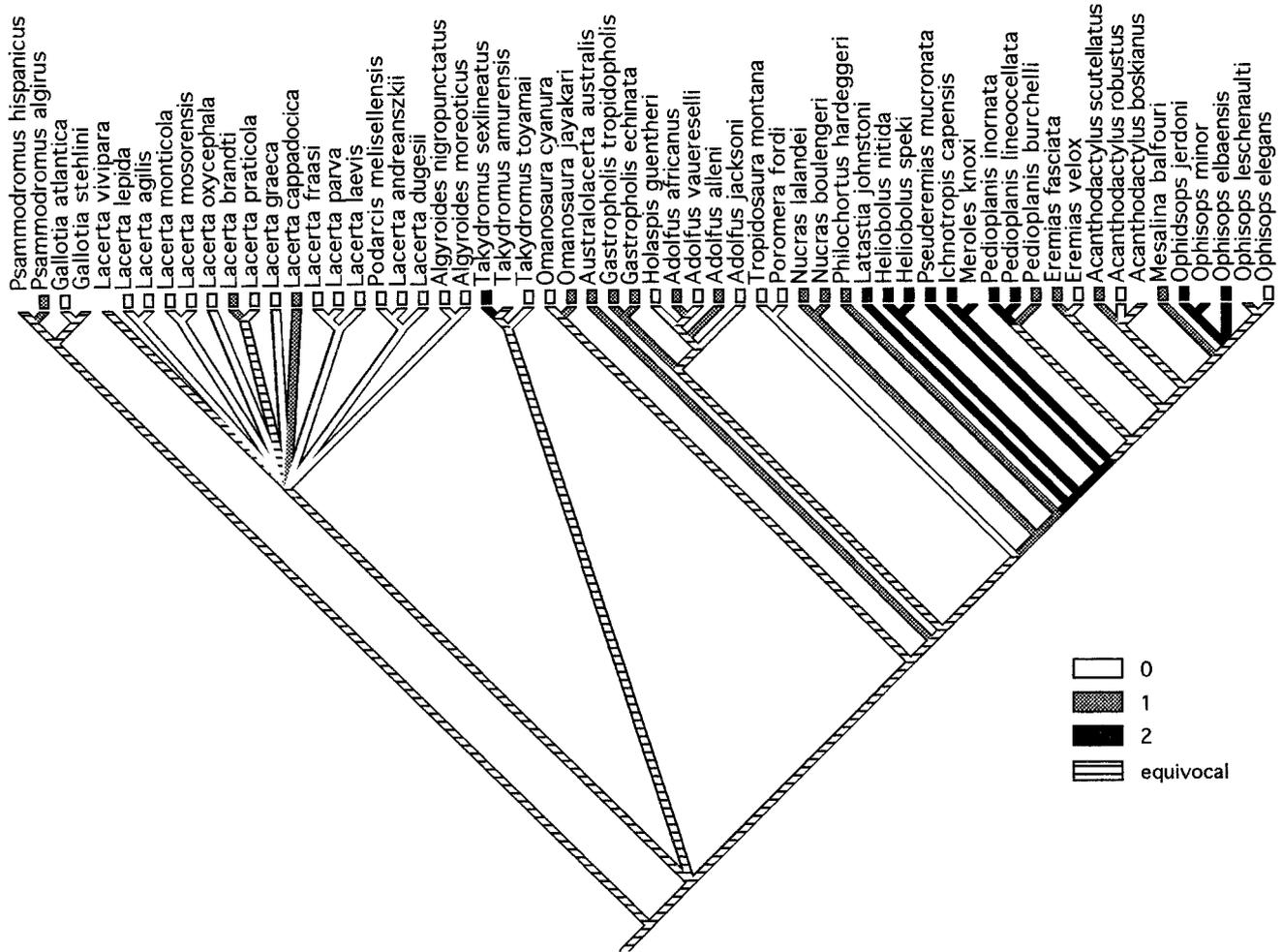


Fig. 8. Phylogenetic distribution of lightly pitted (1) and heavily pitted (2) cell surfaces. The primitive condition may be either lightly pitted or smooth surfaces.

sal microornamentation is more derived than ventral in *Takydromus kuehnei*, *Psammodromus algirus*, *Adolpus africanus*, *Tropidosaura essexi*, and *Pseudieremias mucronata*, while the pattern most widely distributed on each ventral scale is more advanced than that on the dorsals in *Latastia boscai*, *Ichnotropis capensis*, *Pedioplanis husabensis*, and *Ophisops elegans*. In some cases where dorsal and ventral microornamentation is similar, phylogenetic information indicates that they have reached their final condition at different times. This can be seen in the genus *Takydromus* (phylogeny discussed by Arnold, 1997). As noted above, dorsal microornamentation is more derived than that on the ventral scales in *Takydromus kuehnei*, a relatively primitive member of its genus, but ventral microornamentation has advanced to match that on the dorsal scales in more terminal members of the group, such as *T. toyamai*, *T. sauteri*, and independently in the lineage leading to *T. sexlineatus*. The same phenomenon is also found in *Gastropholis*, where the ventral microornamentation matches the

advanced pattern on the dorsal scales in *G. tropidopholis*, but not in other members of the genus, including the more basal *G. echinata* (relationships discussed by Arnold, 1989b).

Anatomical and Environmental Correlations

Association with large scale size. Distribution of various aspects of microornamentation was compared with that of scale size. Where dorsal scaling is homogeneous in lacertids, the number of scales in a transverse row at mid-body is roughly correlated with relative scale size. Low mean transverse counts of about 18–40 were therefore taken as indicating large scales. In other cases, like *Holaspis* and *Philochortus*, where the scales of the vertebral region are much bigger than the remaining more lateral dorsals, large size was judged by direct inspection. Distribution of large scale size in the Lacertidae is shown in Figure 12 and the number of cases where particular derived scale ornamentation features are associated with large scale size in Table 3.

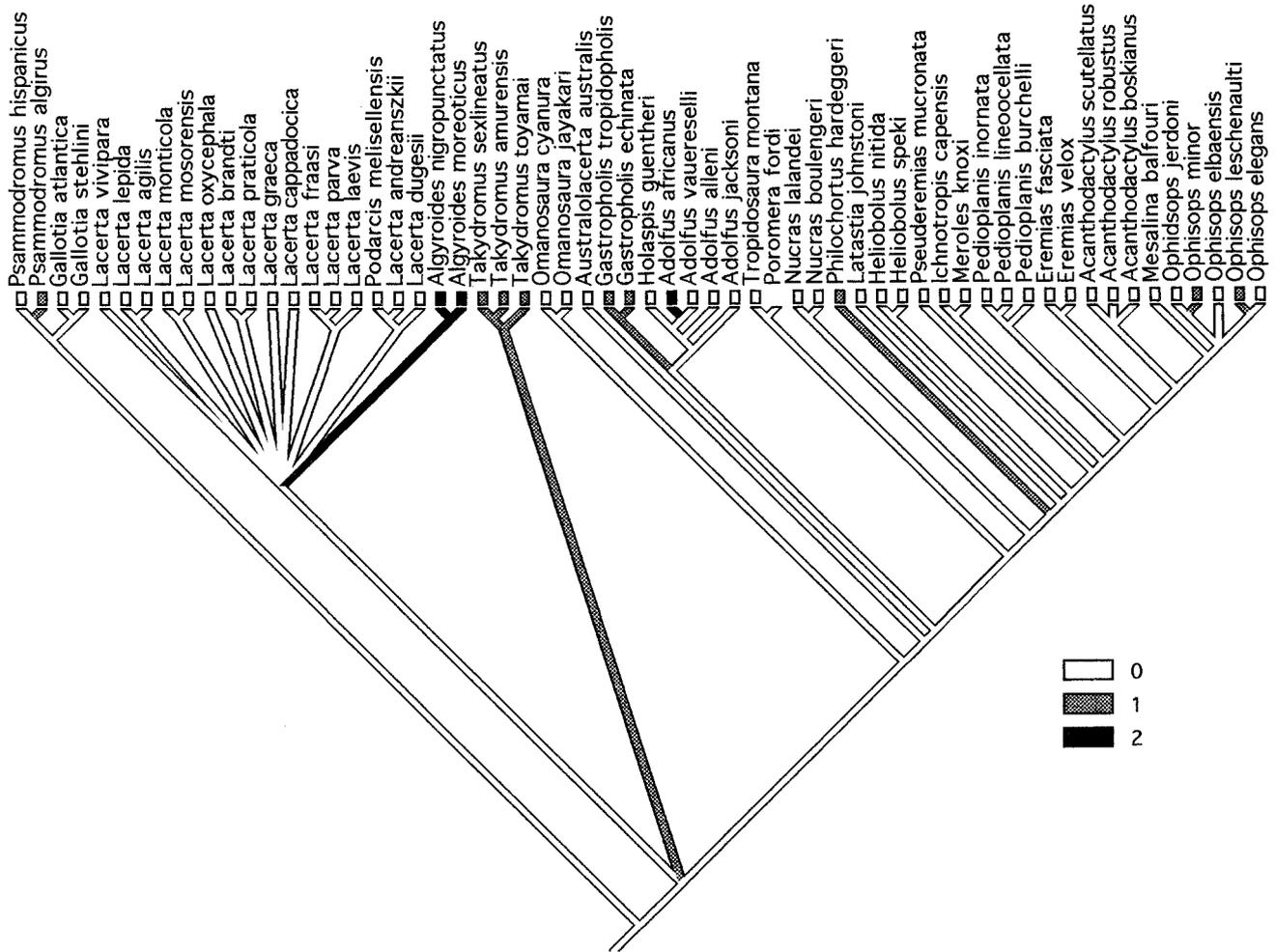


Fig. 9. Phylogenetic distribution of longitudinal ridges underlying microornamentation (1) and of pustular projections (2).

Concentrated changes tests were carried out using the MacClade program (Maddison and Maddison, 1996) to assess the association between the appearance of derived microornamentation features

and large scale size on internal branches of the lacertid phylogeny. The test can give only a rough relative idea of the likelihood of correlations being due to chance because not all lacertids could be

TABLE 3. Number of instances in which particular derived microornamentation features have apparently evolved separately

	Number of separate origins		Number overtly arising with or after large scale size
	Lacertidae	Eremiainae	
1. Cells polygonal (Fig. 4)	2-7	2-7	2-3
2. Cell surface dished (Fig. 4)	3-4	3-4	2-3
3. Cells dimensions (Fig. 5)			
large	4	4	2-3
small	8-10	4	6
4. Cell edges (Fig. 6)			
raised posteriorly	9-12	6-7	6
forming grooves	1	1	0
forming welts	2-7	2-7	2-3
5. Cell edges denticulated (Fig. 7)	3-4	1	2
6. Cell surfaces strongly pitted (Fig. 8)	3-4	2-3	1-2
7. Longitudinal ridges (Fig. 9)	6	4	6
8. Pustules (Fig. 9)	2	2	2

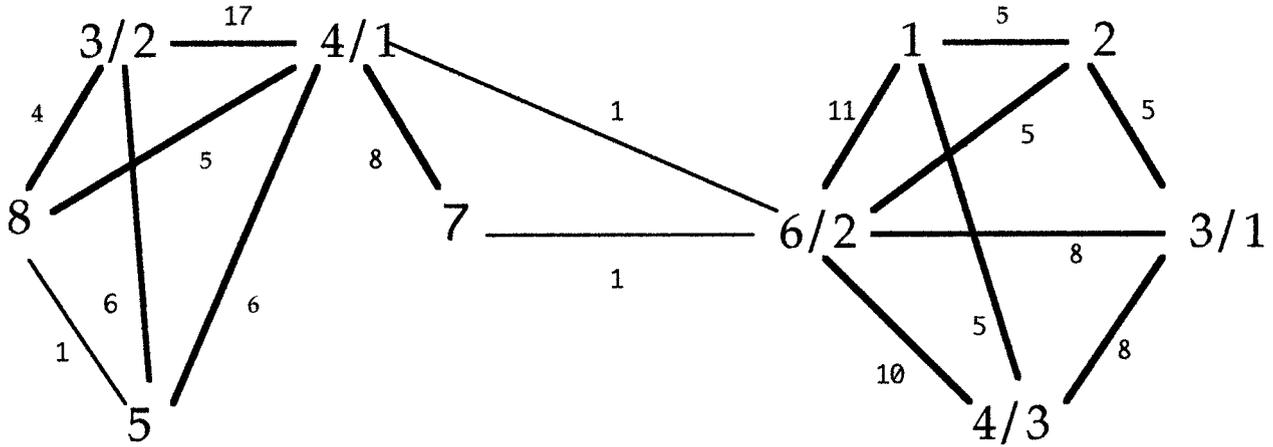


Fig. 10. Association of derived states in microornamentation. Thick lines join two states that occur together in at least five or more cases, thin lines there that occur in just one or two. Small figures show number of instances. States mainly associate in two groups: left group includes small cell size (3/2), raised posterior cell edges (4/1), denticulation (5), longitudinal ridges (7), and pustular projections (8); right group includes polygonal cells (1), dished cell surfaces (2), large cell size (3/1), welt- or ridge-like borders (4/3), and heavy pitting (6).

included in the test. Also, because the test cannot be carried out when there are polytomies in the phylogeny, these had to be arbitrarily resolved.

Bearing these limitations in mind and including the species shown in Figures 5–9, the probability of chance correlation with large scale size is <0.02 for small cells, raised edges, and longitudinal ridges, and <0.1 for dished cell profile, large cells, denticulation of posterior cell margins, strong surface pitting, and pustular projections. The rather greater probability of chance correlation in these latter cases may partly result from the features concerned having relatively few origins. The probability of chance correlation was substantially greater in the case of polygonal pits cell shape and welt-like cell margins.

The notional probability of chance correlation with large scale size was also assessed for cases in which a number of derived microornamentation features have evolved (Fig. 13). For four or more features, three or more, and two or more, the probabilities are <0.02. This indicates that there may well be a correlation between more derived microornamentation and scale size in lacertids. An association between complex derived patterns of microornamentation and large scale size has also been noted informally in xantusiid lizards (Bezy and Peterson, 1988).

Association with environment. Apparent correlations also occur between dorsal patterns of microornamentation and the general nature of the habitats occupied by the species concerned. The

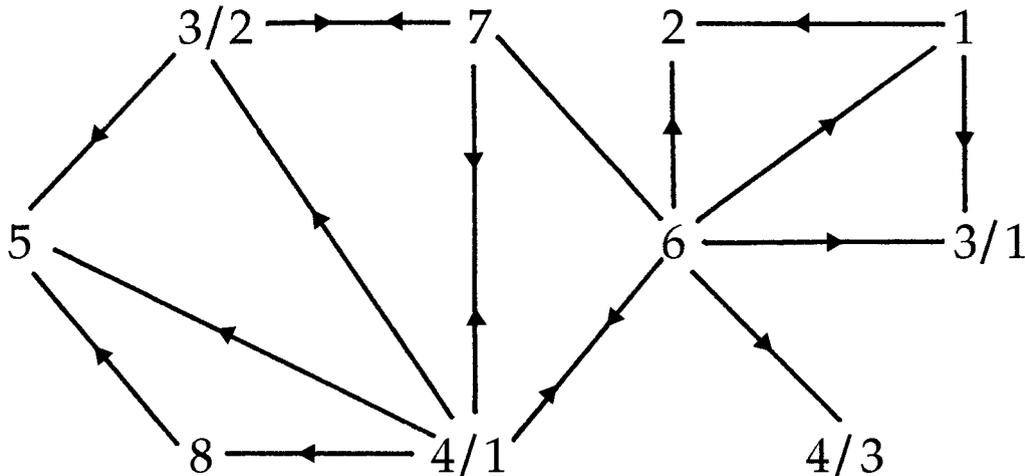


Fig. 11. Order of origin of derived states in microornamentation. Lines connect derived states that appear sequentially on at least one lineage; arrows point towards the state that arises later. Clearly, there is no single sequence of state assembly. Derived states: cells polygonal (1), cell surfaces dished (2), cell size large (3/1), cell size small (3/2), posterior cell margins raised (4/1), posterior cell margins welt- or ridge-like (4/3), denticulation (5), heavy pitting (6), longitudinal ridges (7), pustules (8).

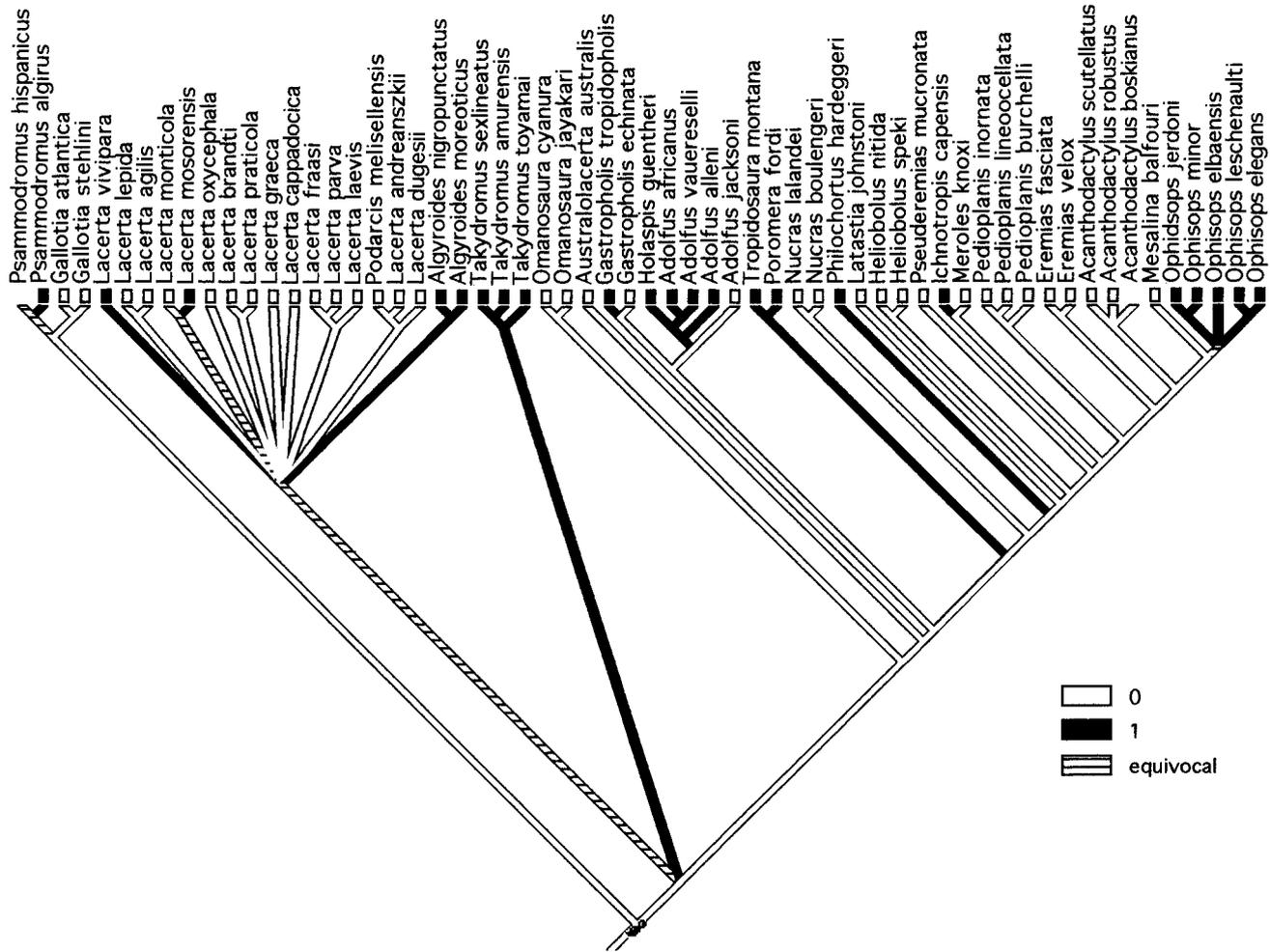


Fig. 12. Phylogenetic distribution of large dorsal scales (1). (see Nonancestral Resemblance in Dorsal Body Microornamentation).

primitive pattern is predominant in the essentially mesic habitats of the Palaearctic and in the less arid parts of Africa, although it also occurs at lower frequencies elsewhere. Among derived states, strongly raised posterior cell edges, their denticulation, longitudinal ridges, and pustules are all found in lizards occupying relatively mesic situations with some vegetation, particularly in climbing forms. The two occasions where pustules have evolved, in *Agyroides* and *Adolfus africanus*, are associated with occupation of forest-floor habitats (Arnold, 1987, 1989b). The remaining derived states are typical of more xeric conditions. Because no objective classification of lacertid habitats exists, it is not possible at present to formally test these associations.

Factors That May Cause Evolutionary Change

A range of hypotheses about possible benefits of microornamentation have been put forward. It has

been suggested that interdigitation between the sculptured surface on the newly matured β -layer and the clear layer above it may be beneficial in preparing the old overlying epidermis for shedding and in holding the immature epidermis together while it is developing (Maderson, 1966, 1970; Maderson et al., 1998). As all squamates shed their previous epidermis, such a hypothesis would not explain the extensive interspecific variation found in microornamentation. In fact, this particular suggestion is not fully tenable as a general functional explanation of microornamentation because ecdysis takes place successfully even where the epidermal surface is very smooth, such as on the body scales of laticaudine sea snakes (McCarthy, 1987) and on large areas of the belly scales of some lacertids. It has also been proposed that some aspects of lizard microornamentation may increase the mechanical strength of the β -layer or parts of it (Ruibal and Ernst, 1965; Maderson et al., 1998) and that it functions as an aid to capturing, dispersing, and retain-

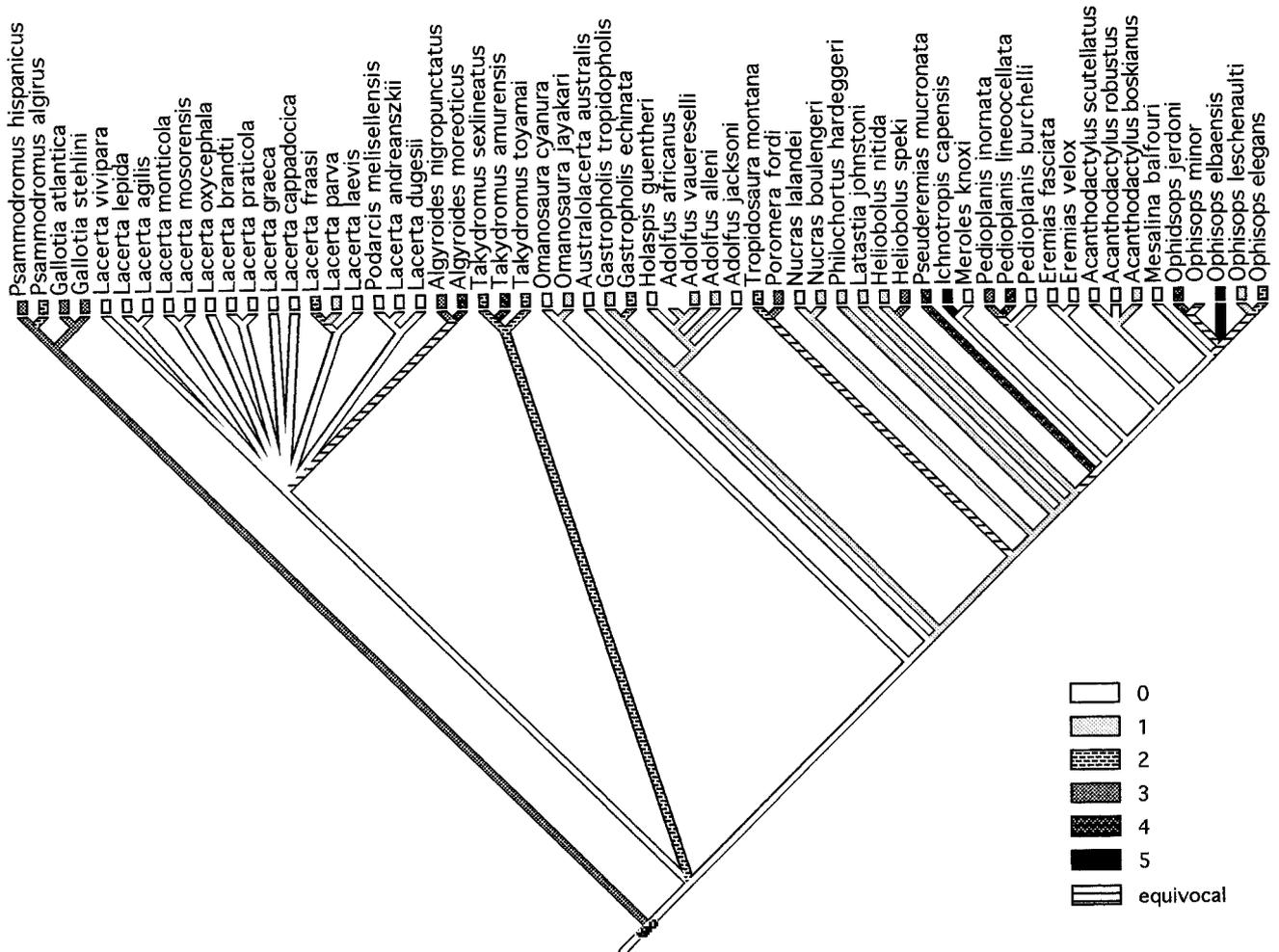


Fig. 13. Phylogenetic distribution of microornamentations with different numbers of derived features.

ing pheromones (Smith et al., 1982). Again, these hypotheses do not explain the great variability in structure involved.

Taxonomically more restricted performance advantages of squamate microornamentation patterns have been suggested and, in some cases, demonstrated. Particular patterns were thought to encourage transport of water contacting the skin towards the mouth in the agamid, *Moloch* (Bentley and Blumer, 1962) but movement was subsequently found to take place in capillary channels between the scales (Gans et al., 1982). The smooth scales of laticaudine sea snakes may reduce the possibility of the skin being colonized by marine algae and other organisms (McCarthy, 1987) and the very rough scale surfaces on the tail of uropeltid snakes encourages the accumulation of a plug of earth which helps prevent predators following the snakes into their burrows (Gans and Baic, 1977). Some partly aquatic natricine snakes in the genera *Nerodia* and *Thamnophis* have pores on their dorsal body scales that exude lipids that collect in hollows in the scale mi-

croornamentation, perhaps helping to make the skin waterproof (Chiasson and Lowe, 1989). Digital setae in many geckoes and some other lizards facilitate adhesion while climbing. No such very specialized uses of microornamentation are apparent in the Lacertidae. As they have limited distributions in squamates as a whole, and are sometimes also confined to restricted areas of the body, these uses do not explain the bulk of variation in the surface structure of scales.

In most studies involving varied microornamentation, no obvious broad correlations with environmental parameters have been discerned that would suggest function. Such lack of simple correlations does not, of course, imply absence of performance advantage for the different patterns. All sorts of factors, singly or together, may prevent such associations making themselves apparent. The precise microornamentation pattern may be influenced by historical factors and possible cases are discussed below, but previous events are unlikely to be responsible for the changes themselves. Alteration may

sometimes possibly be caused by particular occurrences, but patterns may persist even though the factors that caused their appearance no longer act. Again, different factors may conflict, with some of them being more important in some situations than in others, so that none of them show simple correlation with environmental parameters or particular features of the animals concerned, and there may also be hierarchies of priority. Finally, a particular morphology may confer advantages in more than one very different way, so it appears in very different situations.

In fact, the range of possible performance advantages for different patterns of microornamentation that has been broadly considered in the literature is quite small and discussion is often limited to restricted taxonomic groups. Two factors that deserve more consideration are the frictional and light-reflecting properties of the epidermal surface, the former being potentially significant in locomotion and dirt-shedding and the latter in the control of shine, as a means of enhancing camouflage. It is proposed here that these factors are of substantial importance in determining microornamentation patterns in lacertid lizards and at least some other squamates.

Locomotion. Some patterns of surface structure are likely to enhance locomotory capacity of squamates either in increasing purchase, for instance, by providing attachment points, or by reducing friction. Thus, while gecko setae permit adhesion of the toes, the very smooth body scales of uropeltid snakes probably minimize friction when burrowing (Gans and Baic, 1977) and the smooth belly scales of many other snakes and lizards, including most lacertids, may serve the same role in surface locomotion. Conversely, complex microornamentation on the body and tail is potentially likely to increase locomotory friction.

The benefits of friction reduction in locomotion may also explain the observation that lizard dorsal body scales that project from the skin are often smoother in their more exposed areas than elsewhere, something that is not caused by wear (Irish et al., 1988; Maderson et al., 1998). Such distal smoothness is apparent in lacertids: whatever the general microornamentation, the tips of scales and any strongly raised keels on them are nearly always much smoother than other scale regions (Fig. 3b).

As strong microornamentation is absent on the most exposed parts of the body scales of lacertids, it is unlikely to have much importance in gaining purchase, something not unexpected in these lizards, in which locomotion mainly involves the limbs. However, general smoothness may permit significant reduction in friction when passing through vegetation or through narrow cavities. Lizards in other groups that habitually make close lateral or dorsal contact with their environment during locomotion do often have relatively smooth scale surfaces. This is true of

most skinks and of gerrhosaurids, and also of the cordylid *Platysaurus* (Harvey and Gutberlet, 1995), which frequently retreats into very narrow crevices. The primitive microornamentation pattern in lacertids would be expected to limit friction, too, at least in forms that use narrow spaces. For example, *Holaspis guentheri*, which regularly enters cracks in wood and under bark (Arnold, 1989b), where its very big vertebral scales usually contact the internal surface of such crevices, is one of the few lacertids with very large dorsal scales that retain the smooth primitive lacertid pattern of microornamentation on them. Other crevice-using forms with fairly large scales, such as *Lacerta mosorensis*, also show this feature.

Dirt shedding. Most but by no means all lacertids spend a lot of time in close contact with the soil and are at potential risk of picking up dirt on their scales. This is likely to sometimes obscure cryptic coloring and markings used in intraspecific communication. Dirt may also clog the scales and the interstices between them, reducing ease of movement and, in small lizards, which have a large surface area relative to their volume and muscle mass, it may weigh them down, reducing pursuit and escape speeds. Lizards, of course, cast off all dirt when they shed their skins, but this is a relatively infrequent event and will not maintain a clean surface between sheddings.

Soiling is a problem especially in moist situations where water facilitates the spread of dirt particles over the skin surface. As the liquid evaporates, surface tension brings the small particles into very close and extensive contact with the skin, increasing adhesion by weak molecular forces and tending to pull particles into any concavities that may be present. A relatively smooth, even scale surface limits such adhesion and permits dirt to be easily wiped off the scales as the lizard brushes against objects in its environment. In contrast, dirt particles are likely to become lodged in the concavities of complex microornamentation, where their surface contact may be increased and their displacement by objects sweeping across the scale surface during locomotion is less likely.

When detached scales of large-scaled lacertids with different microornamentations were coated with fine silt, this could be easily wiped away in the case of lizards with smooth ornamentation, such as *Adolfus alleni* and *Holaspis*. In contrast, where microornamentation is more complex and three-dimensional, as in *Psammotromus algirus*, *Ichnotropis*, and *Ophisops*, some of the silt persisted through several wipings, leaving numerous particles still lodged on the scale. It is consequently not surprising that most lacertids that spend time close to the soil in moist places retain the primitive pattern of smooth microornamentation on their dorsal scales and most shifts to derived states occur in dry situations, where dirt is likely to adhere less tenaciously,

or in habitual climbers in vegetation, where exposure to soil and other kinds of dirt is considerably less.

Reflection of heat and light. The skin is important in both absorbing and reflecting electromagnetic radiation and there are interspecific variations in infrared reflectivity that could be significant in thermoregulation (Porter, 1967; Bowker, 1985). It has also been suggested that projections of the oberhautchen may reduce the amount of visible and ultraviolet radiation penetrating the body cavity, where it may damage the viscera. Refraction within projections of the microornamentation has been hypothesized to lengthen the path of radiation passing through the body wall, thus increasing its absorption before it reaches the visceral cavity (Porter, 1967). However, such possible effects are still largely uninvestigated and discussion here will be almost entirely confined to the effects of scale microornamentation on the appearance of lizards.

The squamate epidermis absorbs some visible light but is largely transparent to it, permitting transmission to the upper dermis, where a proportion is reflected back through the epidermis by chromatophores. Some light, however, may be reflected directly from the oberhautchen, something which is most obvious when it strikes obliquely. The combination of transmission and reflection by the epidermis is directly analogous to the way a sheet of glass not only transmits oblique light but also reflects some of it from its upper surface. Reflection involving some kinds of relatively fine microornamentation occasionally contributes to interference colors on the scales of snakes, for instance, in the colubrid snake, *Drymarchon* (Monroe and Monroe, 1967) and in uropeltid snakes (Gans and Baic, 1977), although such colors may at least sometimes be an incidental effect of selection for mechanical performance advantages (Gans and Baic, 1977).

More frequently, reflection of the sky and especially the sun may produce shine, where a smooth surface gives rise to coherent reflection rather than scattering the light rays in many directions. Together with shape, color, and shadows cast, shine is acknowledged in military and other contexts to be one of the factors likely to attract attention and needing to be hidden or suppressed if camouflage is to be achieved. Shine is sometimes quite striking in lizards, for instance, in many scincids, and may significantly reduce crypsis in forms that are otherwise camouflaged by their coloring and sometimes body form. Components of many common lizard habitats, such as most earth, sand, and bark, and sometimes rocks and leaves of plants, too, have matte surfaces and substantial shine on the skin of lizards occurring on such backgrounds is likely to attract the attention of predators. Such coherent reflection also often provides a clear visual cue that an inconspicuous, perhaps countershaded, object is in fact three-dimensional. Shine is especially noticeable when it

suddenly appears or disappears as an animal moves. For example, it is common in Arabia to glimpse an abrupt glint of light caused by the sun reflecting off a Sand skink (*Scincus mitranus*) as it dives into the slip-face of a dune. Similar disruption of camouflage may occur when a hunting predator, such as a cruising raptor, moves relative to its potential prey, even when this is static; shine may be intermittently seen by the predator as the positions of one or both animals change with respect to the sun. It would consequently not be surprising if, in many circumstances, there were benefits in suppressing epidermal shine and particular microornamentation patterns may be one of the means of accomplishing this, rather as the shiny surface of glass can be frosted by etching it to produce a fine-scale three-dimensional structure.

Importance of gross scale shape. In lizards with strongly reflective scale surfaces, the extent of shine that may be visible, to an observer situated on the other side of the lizard from the sun, is determined partly by scale size and form. This may be a largely unconsidered selective factor in determining the shape of squamate dorsal scales; for instance, whether they are flat or raised, smooth or keeled. Small strongly convex scales are potentially shiny over their whole surface but, when they are illuminated by the parallel rays of the sun, light is scattered in different directions by the areas of curvature (Fig. 14b). Consequently, shine will only be produced from the very small area of a convex scale that reflects light directly to an observer. Because of this, there is no continuous area of bright reflection on the skin, just a stipple of small shining spots which is not usually very conspicuous. This phenomenon can be seen in such lacertids as *Heliobolus lugubris* and *Eremias arguta*. Strongly carinate small scales also produce a discontinuous shine that is largely confined to the scale keels. In contrast, sunlight is reflected off large, flat scales as parallel rays that are likely to be perceived as a large area of shine (Fig. 14a). If some patterns of microornamentation reduce shine, it may be no accident that most derived states of this are often found in species with such scales.

The distribution of different scale shapes on the bodies of squamates also reflects the requirements of camouflage. Some lacertid lizards, such as *Lacerta agilis*, *L. viridis*, and *L. praticola* have keeled scales on their upper surfaces that limit shine, but scales are smoother on the sides of the body, which are less visible from above, and smoothness is even more marked on the belly, which is usually concealed. A similar distribution of scale types occurs in many snakes.

Effect of microornamentation on shine. Examination of living lacertids and other lizards, and of alcohol-preserved ones in which the skin surface has been allowed to dry, indicates that microornamentation does affect the amount and intensity of shine.

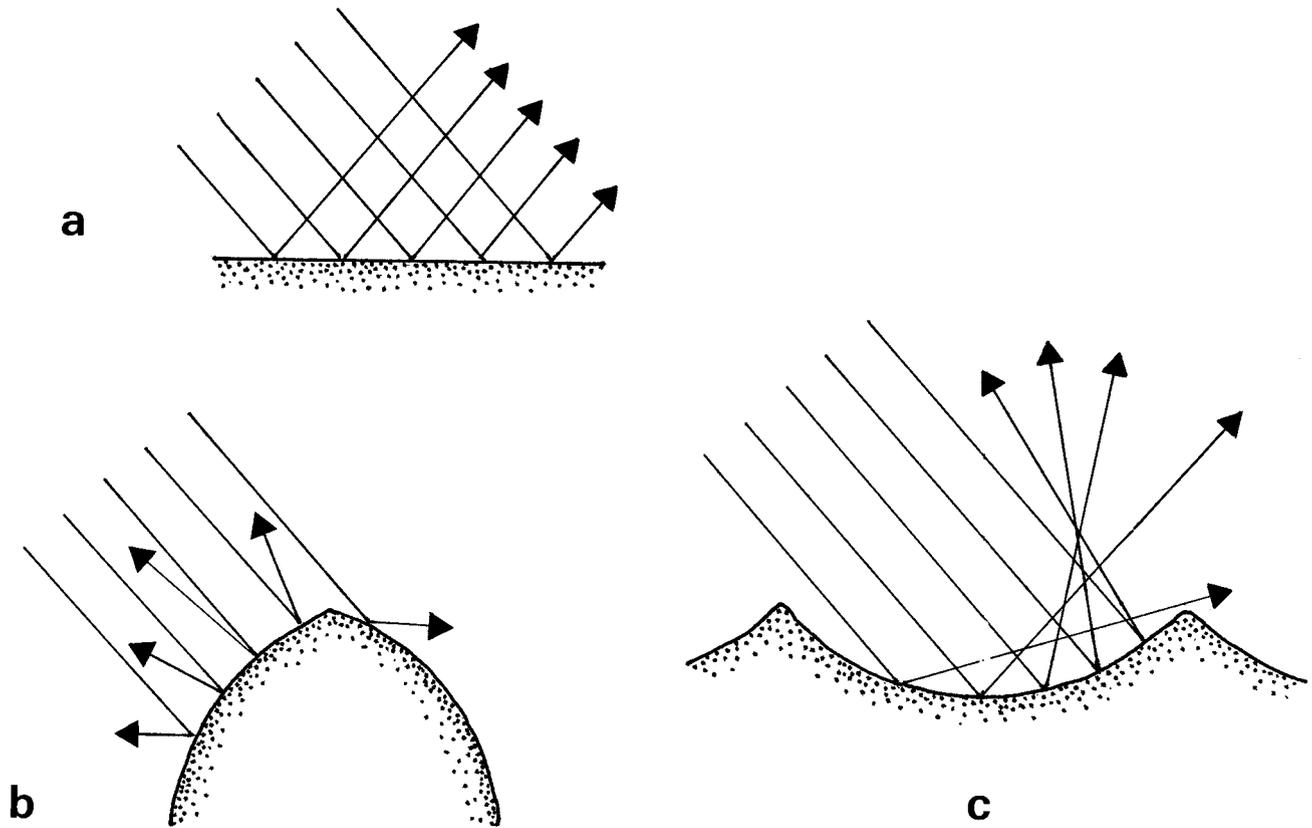


Fig. 14. Effect of curvature of reflective surfaces on light scattering. **a**: Sunlight is reflected off flat scale surfaces to produce parallel rays that are often perceived as a large area of shine. **b**: Convex scales scatter parallel light rays in different directions, so shine is only perceived from a very small area. **c**: Dished microornamentation also scatters light, restricting or eliminating shine.

As expected, shine is very marked on smooth belly scales and, among forms with relatively large dorsal scaling, it is conspicuous in species that have the primitive lacertid pattern of microornamentation, where cell surfaces are largely smooth and their imbricating posterior margins are not angled upwards. For example, this can be seen in *Lacerta vivipara*, *L. mosorensis*, and particularly *Adolfus alleni*, where the scales are especially big. In the latter species, shine is relatively subdued when light strikes the skin and, is reflected from it, at steep angles, but more conspicuous when the angles are shallower.

In forms with strap-shaped oberhautchen cells where the posterior borders are turned obliquely upwards, such as *Tropidosaura*, shine is present but tends to be reduced compared with forms with primitive microornamentation. Again, this reduction is greater at steeper angles of incidence and observation. Even if scales are still shiny at shallow angles, there are likely to be real benefits in reducing shine at steeper ones, as in many situations this is how many predators view lizards. Presumably there is less shine at steeper angles because some of the light falls into the gaps between the raised cell edges and is absorbed or reflected directly back toward the

light source. However, perceived shine will not be wholly suppressed because some normal reflection still takes place from the raised edges themselves.

Other microornamentation features often associated with raised edges reduce coherent reflection further. Thus, the pustules of *Algyroides* also interfere with coherent reflection from the scale surface. Denticulations have the same effect and, where they are particularly developed and abundant, as on the dorsal scales of the tail base of *Gallotia stehlini* (Fig. 2c), they absorb light in their interstices rather like velvet or plush does.

Large ridges contribute to light scattering by varying the orientation of different parts of the scale surface, and the combination of raised posterior edges of cells and large ridges on the scale surface is particularly effective in reducing coherent reflection, as, for instance, on the large scales of many *Takydromus* (Arnold, 1997). The combination of raised cell edges and ridge-like tracts of denticulations in *Poromera* (Fig. 3b) acts similarly. Finally, the large dished cells of *Ichnotropis* and some *Ophisops* appear to represent a different means of preventing coherent reflection by scattering light (Fig. 14c).

Conflicting benefits. The above factors suggest that lacertid microornamentation is controlled by conflicting benefits. Relatively smooth scales with low-friction characteristics may aid locomotion and dirt shedding, while reduction of shine through matte surfaces enhances camouflage. The two properties cannot be combined, for low-friction surfaces tend to shine and matte surfaces produce high levels of friction, but some situations select one property over the other. The smooth primitive pattern of microornamentation is apparently selected in forms that often live on the ground in moist places, where soiling is a particular problem, or which use narrow crevices, where friction would impede movement. Conversely, more matte surfaces are generally selected in forms with large dorsal scales that are inclined to shine. In situations where these factors conflict, low-friction considerations appear to prevail. Large-scaled forms develop matte ornamentations in dry habitats or when they live away from the ground, both situations where soiling is unlikely to be a great problem, but this does not occur in large-scaled forms that would benefit from low friction. For instance, this is true for *Adolfus alleni*, which is ground-dwelling in moist habitats and, as noted above, for crevice-using *Holaspis guentheri*.

Natural tests of performance advantage. The hypothesis that smooth microornamentation of dorsal body scales is functionally important in reducing dirt adhesion and friction during locomotion and that three-dimensional microornamentations reduce shine can be tested further. Other areas of the body where these selective pressures are also likely to occur but with different levels of severity can be examined to see if their microornamentation varies in ways predicted by the hypothesis. Thus, the belly of most lacertids is in much more extensive contact with soil than the dorsum is, when lizards are resting and during slow locomotion, and is largely out of the sight of predators. As might be expected from this, the belly microornamentation is usually either of the primitive pattern or even smoother (see Comments on Microornamentation of Dorsal Tail Base and Belly, above). There are, however, four independent cases where the smooth ventral surface has been lost and replaced by a complex microornamentation like that on the dorsum. This has occurred in the more terminal members of the two main lineages of *Takydromus* (Arnold, 1997), in *Gastropholis tropidopholis*, and in *Poromera*. All these forms climb extensively in vegetation matrixes and are likely to be out of contact with the ground much of the time and, because they are not regularly close to the substrate, their bellies are also potentially much more visible than is usual.

Flanks are somewhat intermediate between dorsum and belly in the extent of their visibility and contact with habitat. Consequently, there is a shift in the balance between the advantages of reducing shine and having low friction and this may be ac-

companied by an appropriate change in microornamentation. Thus, although the sculptured derived dorsal patterns of *Psammodromus algirus* and *Ichnotropis capensis* are still present on the flanks, they are attenuated. This parallels what happens with general scale architecture (see Importance of Gross Scale Shape, above).

The relationship between more three-dimensional, usually derived, microornamentation patterns and large scale size is corroborated by its development on the large scales of the tail of forms with small body scales that otherwise lack sculptured microornamentation. A further indication that smooth microornamentation may be important in making scale surfaces easily cleaned is that, even in forms with generally matte surfaces, like *Poromera*, the scales bordering the mouth, which are regularly smeared with prey residues, retain the primitive smooth pattern.

Observations on other squamate groups. Microornamentation reduces reflection in many other squamate groups, thus improving camouflage. This is particularly so in the production of the strikingly matte and velvety dorsal surfaces of geckos and of vipers; for instance, in the genera *Bitis* and *Bothrops*. Indeed, the Fer de Lance (*Bothrops atrox*) is called Terciopelo (=velvet) in Spanish. In these cases the dense perpendicular projections of the microornamentation act exactly like velvet in enabling light to be absorbed and to some extent randomly reflected without producing any coherent shine. In other groups, the more three-dimensional microornamentations also tend to reduce coherent reflection. This can be seen in the Mauritian skinks of the genus *Gongylomorphus*. *Gongylomorphus bojeri*, with smoother microornamentation, is very shiny, while *G. fontenayi*, in which there are stronger raised and denticulated projections from the cell edges, is more matte (pers. obs.).

Other groups also show the same kind of regional differences over the body encountered in lacertids. Thus, many snakes have greater ornamentation on the dorsum than the flanks and little if any on the belly. Again, these shifts repeat on a microscopic scale those often seen in general scale morphology.

Apparent Contraventions of the Functional Hypothesis

Although the distribution of the various kinds of microornamentation fits quite well with the hypothesis, that patterns confer different advantages in terms of smoothness and reducing shine, with smoothness having precedence in cases on conflict, there are still a number of aspects that require further explanation.

Pitting. As noted, many lacertids have minute pits on the surface of scales that may take up around half the surface area. These might be thought of as yet another means of reducing reflection. However, unlike most other kinds of potential reflection spoil-

ers, pitting in general is not strongly associated with the large scales that are likely to produce the most extensive shine. Indeed, even densely pitted scales with otherwise smooth surfaces are often shiny. This is true of *Pseuderemias* and the *Pedioplanis undata* group (including, among others, *P. undata* itself, *P. inornata*, *P. namaquensis*, and *P. rubens*) Here, although overall shine is greatly reduced by the convex shape of the small scales, these are actually quite glossy when examined closely.

In fact, pits are very small, often being only about 0.5 μm across. As such, their diameter is less than the wavelength of most visible light (0.4–7.0 μm), which means that, in the context of light reflection, such pitted surfaces are likely to act as if they were entirely smooth. Consequently, large relatively matte scales bearing pits probably get their dull finishes from the grosser features of microornamentation that they bear, such as raised cell borders, large ridges, and dished surfaces. Dense pitting is most common in dry habitats, and 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. What positive benefit pitting may confer is unclear. Perhaps it simply makes epidermis cheaper to produce by reducing the amount of β -keratin needed.

Different solutions in different situations?

Within the homogeneous genus *Ophisops*, there are two different microornamentation patterns. Members of one clade have strap-shaped cells that are small with raised posterior borders, while dished polygonal cells with ridge-like margins have arisen in other species, perhaps even twice. Both arrangements reduce coherent reflection and do not differ obviously in the extent to which they suppress shine, something that also probably applies to frictional properties. One possible explanation for the existence of these two different methods of reducing shine is that they may have different countervailing costs that may be more important in some habitats than others; for instance, those costs involving the absorption of electromagnetic energy. Visible light is converted to heat when absorbed and must contribute to the heat load of lizards and snakes. Such costs may not be important in vegetated habitats where temperatures are lower as a result of shade and evaporation from the plants, but they are likely to be more significant in dry open situations, where vegetation is sparse. Perhaps this is reflected in the kind of derived pattern of microornamentation that reduces shine. Arrays of densely packed ridges or denticulations that limit reflection partly by directing light inwards are more likely to result in light absorption and consequent heating than dished polygonal cells, where coherent reflection is limited by scattering the light by reflection. It is perhaps no accident that in other lacertid genera dished polygonal cells occur in species living in open situations. Unfortunately, not enough is known about the de-

tailed habitats of the *Ophisops* species involved to tell if this explanation is likely to apply to them.

Lack of reversal after loss of function? Although a shift to polygonal cells that are separated by welts is understandable in terms of light scattering when the cells are dished, there are cases where such dishing is not apparent. Nor are such instances associated with large matte scales, the scales concerned being small and shiny. This occurs in *Heliobolus spekii*, *Pseuderemias mucronata*, and *P. striata* and in most members of the *Pedioplanis undata* group. It is most parsimonious to assume that dishing arose after this situation, but such a sequence would be difficult to understand in functional terms. An alternative, less parsimonious, possibility is that the pattern of polygonal cells with raised borders did in fact arise in association with dishing in the context of reducing shine on large scales, but later lost this role with change in scale size and shape. Dishing then disappeared but polygonal cells and raised borders remained, not reversing to the primitive condition in spite of loss of function.

Pedioplanis provides some evidence that this may have been the case. *Pedioplanis lineocellata* has somewhat enlarged dorsal body scales that have dished polygonal cells with raised edges. An estimate of phylogeny based on 35 morphological characters places this species basal to all other members of the genus (Arnold, 1991). However, this hypothesis of relationship is not very robust and, when five variable microornamentation characters (1–4 and 6 in Table 1) are also included in the phylogenetic analysis, *P. lineocellata* shifts to become basal to the *P. undata* group alone (although admittedly this arrangement too is not strongly substantiated). Members of the *P. undata* group may consequently have passed through a stage with relatively large scales that had dished cell surfaces. Although dished cells do not occur on the dorsal body scales of the *P. undata* group, they are present on the tail of at least one of its members, *P. rubens*.

Retention of a derived microornamentation pattern in situations where it does not necessarily confer its original benefit may occur elsewhere. *Ophisops microlepis* retains the steeply angled posterior cell borders that reduce gloss in large-scaled species of its genus, but it itself has secondarily developed small dorsal scales which do not seem to merit reduction of shine.

Why are there so many derived states? If derived patterns of microornamentation are generally important in producing matte surfaces on large scales, why are there so many different “solutions”? One reason is simply that lacertid epidermis appears capable of producing a wide range of structures. Also, as noted in *Ophisops*, different patterns may sometimes possibly represent adaptations to different environmental conditions. The various derived states may also act in an additive way to

reduce shine and additional derived states are frequently incorporated into microornamentation on lineages (see Patterns of Association and Order of Change in Dorsal Body Ornamentation, above).

Lineage effects other than lack of reversal after loss of function may also have influenced outcome. For instance, *Takydromus* and *Poromera* have both evolved strikingly similar microornamentations at middle magnifications (Fig. 3a,b) and both have longitudinal arrays of apparent ridges. However, in *Takydromus* the ridges are in the scale itself and underlie the surface cells, whereas in *Poromera* they are made up of tracts of denticulations produced from the free posterior edges of the cells (Fig. 1f). Presumably, the latter option is open to animals that have some capacity to produce denticulation (a rare feature) and might substitute for the generally more frequently produced ridges.

CONCLUSION

The pattern of epidermal microornamentation found in particular lacertid lizards appears to result from a complex system of influences. Evolutionary changes occur in a variety of components that appear largely independent of each other. Particular changes may take place many times in the Lacertidae, but rarely reverse. Consequently, it seems that microornamentation involves a number of developmental pathways that are substantially unidirectional. Natural selection appears to control such changes but more than one selective factor is involved. The benefits of low friction in locomotion and dirt-shedding promote the selection of primitive smooth microornamentations, while the benefits of reduction in reflection in camouflage elicit more three-dimensional derived ones that can be achieved in different ways. Effective compromise between the two basic kinds of micromorphology is not possible and, where selective forces conflict substantially, low-friction structure prevails. The balance of the main selective factors varies not only between species and populations, but also on different areas of the skin of the same individual. Some microornamentation features, like fine pitting, are not controlled by these selective factors and different ways of producing three-dimensional microornamentations may carry different incidental costs. It is likely that the epidermal microornamentation of other squamates is also a product of these varied factors.

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LITERATURE CITED

- Arnold EN. 1987. Resource partition among lacertid lizards in southern Europe. *J Zool Lond B* 1:739–782.
- Arnold EN. 1989a. Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-world family of lizards derived from morphology. *Bull Br Mus (Nat Hist) Zool* 55:209–257.
- Arnold EN. 1989b. Systematics and adaptive radiation of equatorial African lizards assigned to the genera *Adolfus*, *Bedriagaia*, *Gastropholis*, *Holaspis* and *Lacerta* (Reptilia: Lacertidae). *J Nat Hist* 23:525–555.
- Arnold EN. 1991. Relationships of the South African desert lizards assigned to *Aporosaura*, *Meroles* and *Pedioplanis* (Reptilia: Lacertidae). *J Nat Hist* 25:783–807.
- Arnold EN. 1994. Investigating the origins of performance advantage: adaptation, exaptation and lineage effects. In: Eggleton P, Vane-Wright RI, editors. *Phylogenetics and ecology*. London: Academic Press. p 123–168.
- Arnold EN. 1997. Interrelationships and evolution of the east Asian grass lizards *Takydromus* (Squamata: Lacertidae). *Zool J Linn Soc* 119:267–296.
- Bea A. 1986. A general review of the dorsal scales' microornamentation in *Vipera* species (Reptilia: Viperidae). In: Roček Z, editor. *Studies in herpetology, Proc 3rd Ordinary General Meeting of the Societas Europaea Herpetologica*. Prague: Charles University. p 367–372.
- Bentley PJ, Blumer WFC. 1962. Uptake of water by the lizard *Moloch horridus*. *Nature* 194:699–700.
- Bezy, RL, Peterson JA. 1988. The microstructure of scale surfaces in the xantusiid lizard genus *Lepidophyma*. *Herpetologica* 44: 281–289.
- Bowker RG. 1985. The infrared reflectivity of the desert lizards *Cnemidophorus velox* and *Sceloporus undulatus*. *J Thermal Biol* 10:183–185.
- Bowker RG, Spindler HS, Tilden A, Bairos VA, Murray R. 1987. Reflections on lizard skin: the ultrastructure of the scales of *Cnemidophorus exsanguis* and *Podarcis bocagei*. In: Van Gelder JJ, Strijbosch H, Bergers PJM, editors. *Proc 4th Ordinary General Meeting of the Societas Europaea Herpetologica*. Nijmegen: Societas Europaea Herpetologica. p 83–86.
- Bryant SV, Breathnach AS, Bellairs A d'A. 1967. Ultrastructure of the epidermis of the lizard (*Lacerta vivipara*) at the resting stage of the sloughing cycle. *J Zool Lond* 152:209–219.
- Burstein N, Larsen KR, Smith HM. 1974. A preliminary survey of dermatoglyphic variation in the lizard genus *Sceloporus*. *J Herpetol* 8:359–369.
- Chiasson RB, Lowe CH. 1989. Ultrastructural scale patterns in *Nerodia* and *Thamnophis*. *J Herpetol* 23:109–118.
- Cole CJ, Van Devender TR. 1976. Surface structure of fossil and recent epidermal scales from North American lizards of the genus *Sceloporus* (Reptilia, Iguanidae). *Bull Am Mus Nat Hist* 156:451–513.
- Dowling HG, Gilboa I, Gennaro JF, Gennaro AL. 1972. Microdermatoglyphics: a new tool for reptile taxonomy (Abstract). *Herpetol Rev* 4:200.
- Estes R, de Queiroz K, Gauthier J. 1988. Phylogenetic relationships within Squamata. In: Estes R, Pregill G, editors. *Phylogenetic relationships of the lizard families*. Stanford: Stanford University Press. p 119–281.
- Gans C, Baic D. 1977. Regional specialisation of reptile scale surfaces: relation of texture and biologic role. *Sci NY* 195:1348–1350.
- Gans C, Merlin R, Blumer WFC. 1982. The water-collecting mechanism of *Moloch horridus* re-examined. *Amphibia-Reptilia* 3:57–64.
- Gasc J-P, Renous S. 1980. Les reliefs microscopiques de l'épiderme des squamates (Reptiles) et le mode de locomotion. 105e Congrès national des Sociétés savantes, Caen. *Sciences* 3:23–33.
- Groombridge BC. 1980. A phyletic analysis of the viperine snakes. PhD Thesis. London: Council for National Academic Awards.

- Harris DJ, Arnold EN, Thomas, RH. 1998. Relationships of lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology. *Proc R Soc Lond B* 265: 1939–1948.
- Harvey MB. 1993. Microstructure, ontogeny and evolution of scale surfaces in xenosaurid lizards. *J Morphol* 216:161–177.
- Harvey MB, Gutberlet RL. 1995. Microstructure, evolution and ontogeny of scale surfaces in cordylid and gerrhosaurid lizards. *J Morphol* 226:121–139.
- Irish FJ, Williams EE, Seling E. 1988. Scanning electron microscopy of changes in epidermal structure occurring during the shedding cycle in squamate reptiles. *J Morphol* 197:195–206.
- Lang M. 1989. The morphology of the Oberhautchen with the description and distribution of scale organs in basiliscine iguanians. *Amphibia-Reptilia* 10:423–434.
- Larsen KN, Burstein N, Smith HM. 1973. Phylogenetic trends in the ultradermatoglyphics of the lizard genus *Sceloporus*. *HISS News* 1:12.
- Lee MSY. 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of relationships. *Biol J Linn Soc* 65:369–453.
- Leydig F. 1872. Die in Deutschland lebenden Arten der Saurier. Tübingen: Laupp.
- Leydig F. 1873. Über die äusseren Bedeckungen der Reptilien und Amphibien. *Arch Mikrosk Anat Entwickl* 9:753–794.
- Maderson PFA. 1966. Histological changes in the epidermis of the Tokay (*Gekko gekko*) during the sloughing cycle. *J Morphol* 119:39–50.
- Maderson PFA. 1970. Lizard glands and lizard hands: models for evolutionary study. *Forma Functio* 3:179–204.
- Maderson PFA, Rabinowitz T, Tandler B, Alibardi L. 1998. Ultrastructural contributions to an understanding of the cellular mechanisms involved in lizard skin shedding with comments on the function and evolution of a unique lepidosaurian phenomenon. *J Morphol* 236:1–24.
- Maddison WP, Maddison DR. 1996. MacClade 3.06. Sunderland, MA: Sinauer Associates.
- McCarthy CJ. 1987. Sea snake puzzles. In: Van Gelder JJ, Strijbosch H, Bergers PJM, editors. *Proc 4th Ordinary General Meeting of the Societas Europaea Herpetologica*. Nijmegen: Societas Europaea Herpetologica. p 279–284.
- Monroe EA, Monroe SE. 1967. Origin of iridescent colours on the indigo snake. *Sci NY* 159:97–98.
- Patterson C. 1982. Morphological characters and homology. In: Joysey K, Friday AE, editors. *Problems of Phylogenetic Reconstruction*. Systematics Association special volume 21:21–74.
- Perret J-L, Wuest J. 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-L, Wuest J. 1983. La microstructure des écailles de quelques Scincidés africains et paléarctiques (Lacertilia), observée au microscope électronique à balayage, II. *Rev suisse Zool* 90:913–928.
- Peterson JA. 1984a. The scale microarchitecture of *Sphenodon punctatus*. *J Herpetol* 18:40–47.
- Peterson JA. 1984b. The microstructure of the scale surface in iguanid lizards. *J Herpetol* 18:437–467.
- Peterson JA, Bezy RL. 1985. The microstructure and evolution of scale surfaces in xantusiid lizards. *Herpetologica* 41:298–324.
- Porter WP. 1967. Solar radiation through the living body walls of vertebrates with emphasis on desert reptiles. *Ecol Monogr* 37: 273–296.
- Price RM. 1982. Dorsal snake scale microdermatoglyphics: ecological indicator or taxonomic tool? *J Herpetol* 16:294–306.
- Price R. 1983. Microdermatoglyphics: the *Liodytes-Regina* problem. *J Herpetol* 17:292–294.
- Price R. 1989. A unified microdermatoglyphic analysis of the genus *Aghkistrodon*. *Snake* 21:90–100.
- Price RM, Kelly P. 1989. Microdermatoglyphics: basal patterns and transition zones. *J Herpetol* 23:244–261.
- Renous S, Gasc J-P. 1989. Microornamentations of the skin and the spatial position of the Squamata in the environment. *Fortschr Zool* 35:597–601.
- Renous S, Gasc J-P, Diop A. 1985. Microstructure of the integumentary surface of the Squamata (Reptilia) in relation to their spatial position and their locomotion. *Fortschr Zool* 30:487–489.
- Ruibal R. 1968. The ultrastructure of the surface of lizard scales. *Copeia* 1968:698–703.
- Ruibal R, Ernst V. 1965. The structure of the digital setae of lizards. *J Morphol* 117:271–294.
- Sammartano F. 1976. Microornamentazioni delle scaglie di alcuni sauri. *Animalia* 3:195–205.
- Smith HM, Duvall D, Graves BM, Jones RE, Chizar D. 1982. The function of squamate epidermatoglyphics. *Bull Phil Herpetol Soc* 30:3–8.
- Stewart GR, Daniel RS. 1972. Scales of the lizard *Gekko gekko*: surface structure examined with the scanning electron microscope. *Copeia* 1972:252–257.
- Stewart GR, Daniel RS. 1973. Scanning electron microscopy of scales from different body regions of three lizard species. *J Morphol* 139:377–388.
- Stewart GR, Daniel RS. 1975. Microornamentation of lizard scales: some variations and taxonomic correlations. *Herpetologica* 31:117–130.
- Stille B. 1987. Dorsal scale microdermatoglyphics and rattlesnake (*Crotalus* and *Sistrurus*) phylogeny (Reptilia: Viperidae: Crotalinae). *Herpetologica* 43:98–104.
- Vaccaro O, Uriondo A, Filipello AM. 1988. Microornamentaciones de las células de Oberhäutchen en *Tupinambis teguixin* (Linné, 1758) y *Tupinambis rufescens* Günther, 1871 (Sauria, Teiidae). *Iheringia Sér Zool* 67:65–75.
- Williams EE, Peterson JA. 1982. Convergent and alternative designs in the digital adhesive pads of scincid lizards. *Sci NY* 215:1509–1511.