

A CASE HISTORY IN RETROGRADE EVOLUTION: THE ONCA LINEAGE IN ANOLINE LIZARDS. II. SUBDIGITAL FINE STRUCTURE

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ABSTRACT. *Anolis annectens* is a presumed intermediate between the padless anole *A. onca* and more typical *Anolis* with adhesive toe pads. This study uses scanning electron microscopy to compare adult *A. annectens* with adult and juvenile *A. onca* and two species, *A. chrysolepis* and *A. auratus*, that were considered (Williams, 1974) to show stages in "retrograde" evolution of the anoline subdigital pad. Differences are found in scale shape, in scale contouring, and in the fine structural series. The fine structural series begins with short hook-like spines and terminates with setae which have a long stalk and a triangular tip. In generalized anoles, setae cover the surface of the expanded lamellar scales which form the pad. The spines appear to function as prehensile devices, while the setae may combine prehensile and adhesive mechanisms. *A. auratus* parallels *A. annectens* in showing dedifferentiation of the pad (reduction in pad width, in lamellar number, and in the distinctness of the pad from the phalanx i region), but the distribution of setae is expanded in *A. auratus*, not restricted as in *A. annectens*. The subdigital specializations of *A. auratus* may reflect adaptation to the complex surface architecture of grass blades and stems. *A. annectens* and *A. onca* appear to be on a very different adaptive pathway. Short spines partly or completely replace setae, and the lamellar scales are partially or completely replaced by multicarinate scales. Comparative data from a variety of anoles, non-anole iguanids, and geckos suggest that the subdigital specializations of *A. annectens* and *A. onca* may be correlated with radiation into sandy substrates and thorn scrub vegetation. The absence of definite keels in juvenile *onca*, in contrast to

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their extreme development in adult *A. onca*, is believed to be an ontogenetic adaptation which coincidentally parallels the phyletic sequence. *A. chrysolepis*, with somewhat narrowed pads and a few subdigital keels, is a suitable structural ancestor for *A. auratus* as well as *A. annectens* and *A. onca*.

The alternative adaptive pathways leading to *A. auratus* and *A. onca* emphasize that “retrograde” is purely a descriptive term calling attention to the dedifferentiation of a typical *Anolis* digital pad, not a statement of loss of adaptive value for the end points in the “retrograde” series.

INTRODUCTION

In an earlier paper one of us (Williams, 1974) described a new species, *Anolis annectens*, whose subdigital morphology represented an intermediate between the adhesive toe pad of generalized anoles and the keeled subdigital scales of *A. (Tropidodactylus) onca*. On this basis and other comparative data, the earlier paper: 1) proposed a series of morphological stages in the loss of the subdigital adhesive pad, 2) suggested that *A. annectens* was derived from an *A. chrysolepis* “stage” of the mainland beta anoles and represented an intermediate stage in the evolution of the very specialized condition in *onca*, and 3) discussed probable

correlations of habitat and subdigital morphology.

In this paper we amplify and examine these ideas, drawing upon new and more detailed morphological data obtained by scanning electron microscopy (SEM) from *A. annectens*, *A. onca*, their probable relatives, and still other species that appear to provide insight into the morphological sequence of pad loss.

MATERIALS AND METHODS

The size, sex, and source for specimens used in the study are given in Table 1.

In the previous paper the fourth toe of the hindfoot formed the basis for interspecific comparisons (Williams, 1974). Because *Anolis annectens* is known only from the unique type, we have shifted our attention to a toe not described or figured in the original paper. All descriptions of fine structure in *annectens* and other species are based on the third toe of the hindfoot. However, except in *annectens*, we have also examined the fourth toe of each species.

Phalangeal dimensions were taken

TABLE 1. SPECIMENS EXAMINED.

		Snout-vent length (SVL)
<i>Anolis annectens</i>	*holotype FMNH 5679	68.5 mm male
<i>Anolis onca</i>	*MCZ 158248	67 mm male
	MCZ 158249	83 mm male
	MCZ 158250	77 mm female
	*MCZ 158251	69 mm male
	*MCZ 154068	26 mm (juvenile)
	MCZ 154067	25 mm (juvenile)
<i>Anolis chrysolepis</i>	*LACM 74485	62 mm male
	MCZ 43856	62.5 mm male
<i>Anolis auratus</i>	*LACM 72781	54 mm female
	MCZ 77428	47.5 mm female

* Measurements and illustrations are largely based on these animals.

Abbreviations:

FMNH Field Museum of Natural History, Chicago, Illinois
LACM Los Angeles County Museum of Natural History, Los Angeles, California
MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts

with dial calipers or an ocular micrometer. In discussing the subdigital scales we number them from claw to palm. Phalangeal number is counted in the same fashion from distal to proximal.¹

Specimens were prepared for microscopy by cutting the third and fourth toes from the foot at the metatarsal-phalangeal joint. The toes were then critical-point dried and coated with carbon followed by gold/palladium. Coatings were applied in 15–20 sec. bursts to avoid the possibility of heat damage.

Measurements of fine structure were made from photographs corrected for the magnification given by the instrument. Manufacturer's specifications suggest that the error in reported magnification may be as high as 20%, although with some care it is unlikely to be more than 10%. The *annectens* specimen was photographed twice, with eight weeks separating the sessions. Measurements of seta and scale dimensions taken from the two sets of photographs differed by 3–8%. Where photographs were taken at an undetermined angle to the plane of the structure, an angular correction is estimated, and the data are reported as approximate. More precise measures are reported as the mean of 6–20 individual measures along with the 95% confidence limit of the mean.

ANOLIS ANNECTENS MORPHOLOGY

There are 20 subdigital scales on the third toe: one over the claw base, seven under phalanx i (2–8), six under phalanx ii (9–14), and six under phalanx iii (15–

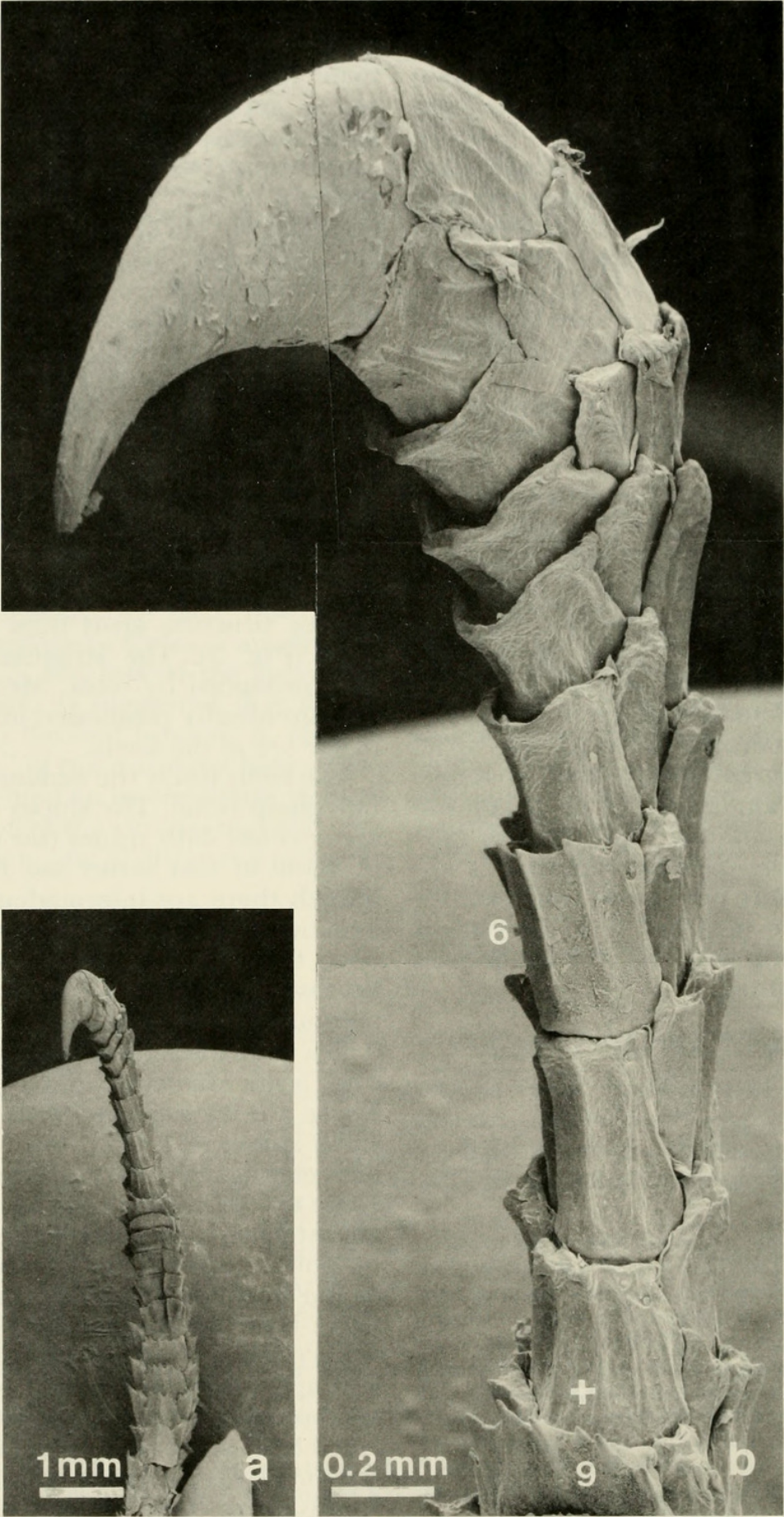
20) (Fig. 1). The subdigital scales fall into three morphological groups: a) multicarinate scales, b) lamellar or lamellar-like scales, and c) unique scales of an intermediate type.

a) Scales 1–8 (i.e., all those distal to phalanx ii) and 16–19 are multicarinate (scale 20 was cut at the palm, but presumably belongs in this group). These are relatively narrow, have robust, unfrayed distal margins studded with “mechanoreceptors” (see Schmidt, 1920; Miller and Kasahara, 1967; Hiller, 1968), and closely resemble the scales on the lateral margins of the toe.

A typical multicarinate scale has three to five keels. The keels originate near the proximal base of the scale and expand distally into large rounded bosses. The crests of the keels are bare and devoid of surface structure apart from a few striations (Fig. 3). The striations are probably produced by wear. Mechanoreceptors are usually positioned just distal and in the lee of the keels.

The keels throw the surface of the scale into sharp relief. The slopes of the keels are covered with spines (for terminology of spine to seta series see Fig. 21). Although there are intermediate sizes and variation in spine size is actually continuous, two major size classes of spines can be distinguished. The larger, more numerous spines are 0.9–1.2 μ tall and 0.5–0.75 μ in diameter near their base (Fig. 3). They occur in a density of 1.75 spines/sq μ . These are interspersed with nubbin-like small spines (0.1–0.5 μ tall; 0.2–0.3 μ in diameter near the base). The shape of the spine tip varies from sharply recurved to almost straight. Recurved spines with the tip pointing distally and toward the crest of the keel are the most common. The spine bases are formed by buttresses or struts (Ruibal, 1968), so that the scale surface appears to be pinched or pulled up into spines. The centers of the spines are 0.6–0.8 μ apart, and regions like that shown in Fig. 3c have a density of 2.0 spines/sq μ . The spines are separated

¹ Numbering the phalanges from distal to proximal and ignoring the claw has been the convention in taxonomic descriptions of *Anolis* since at least Boulenger (1885). It has therefore been used here, as it was in Williams (1974). Morphologists, since they emphasize the number of phalanges in each digit, have preferred to count from proximal to distal (e.g., Russell, 1975). We have preferred consistency within this series and within taxonomic literature to congruence with the morphological literature. The discrepancy is radical, but in each case context should make the usage clear.



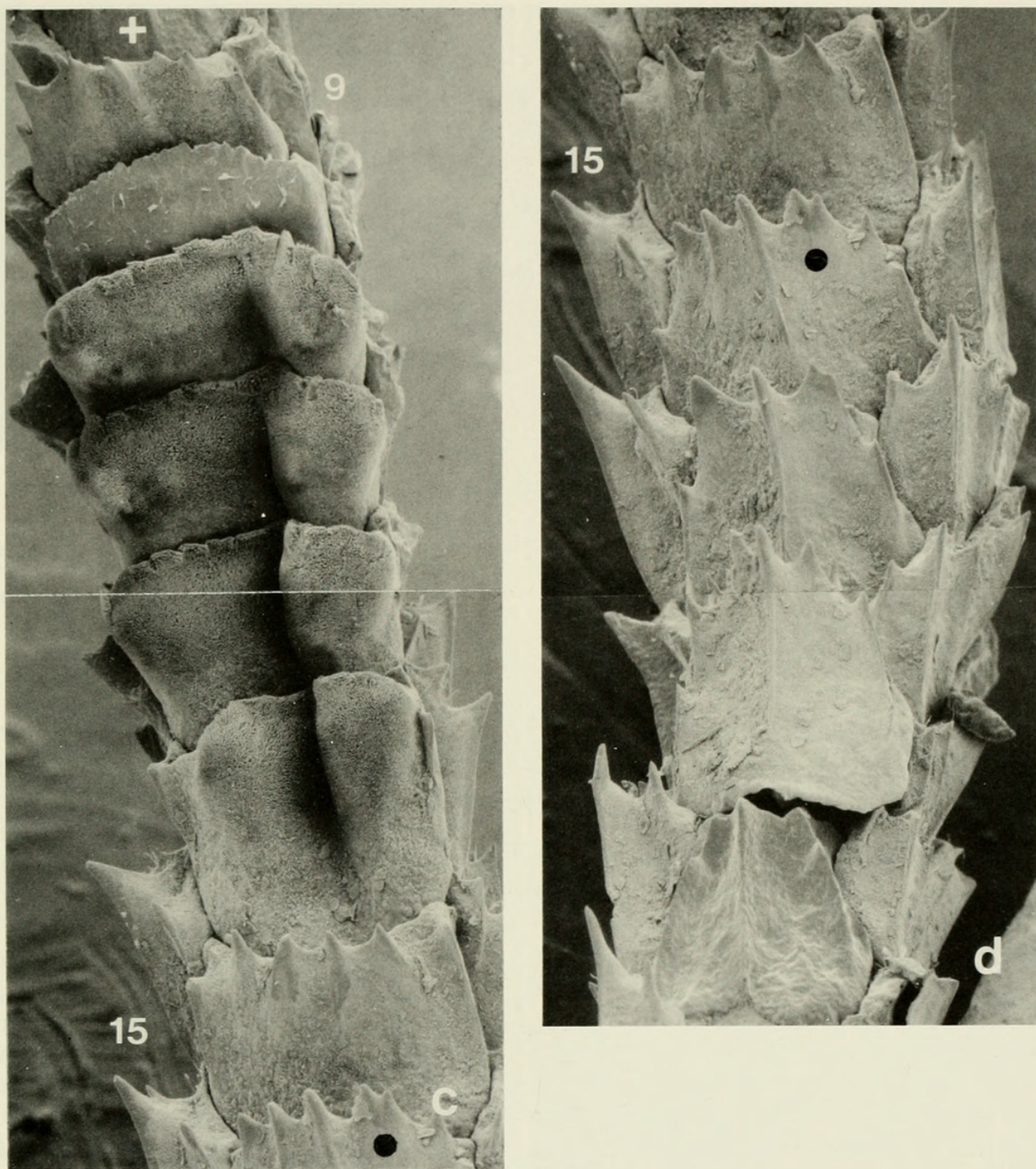


Figure 1. The third toe of *A. annectens*. a) Shows an overall view. Phalanx i(b), ii(c), and iii(d) scales are shown as montages; (b) and (c) match at "+" and scale 9; (c) and (d) match at the "●" and scale 15. Scales are numbered from the claw.

into irregularly shaped fields by narrow ($0.6\ \mu$) "trackways." The trackways presumably represent the borders of the epidermal cells (Ruibal, 1968).

The general pattern described above is modified slightly in the proximal portion of the scales of phalanx iii. In these regions the scale surface is slightly contoured into low "hillocks" (Figs. 1, 3)

which appear to correspond to a single epidermal cell as each is completely bounded by a trackway (see also Figs. 6 and 7 of adult *A. onca*). The density of spines increases slightly between the trackway boundary and the crest of the hillock. This variation also occurs on the lateral digital scales.

b) Subdigital scales 10–14 resemble la-

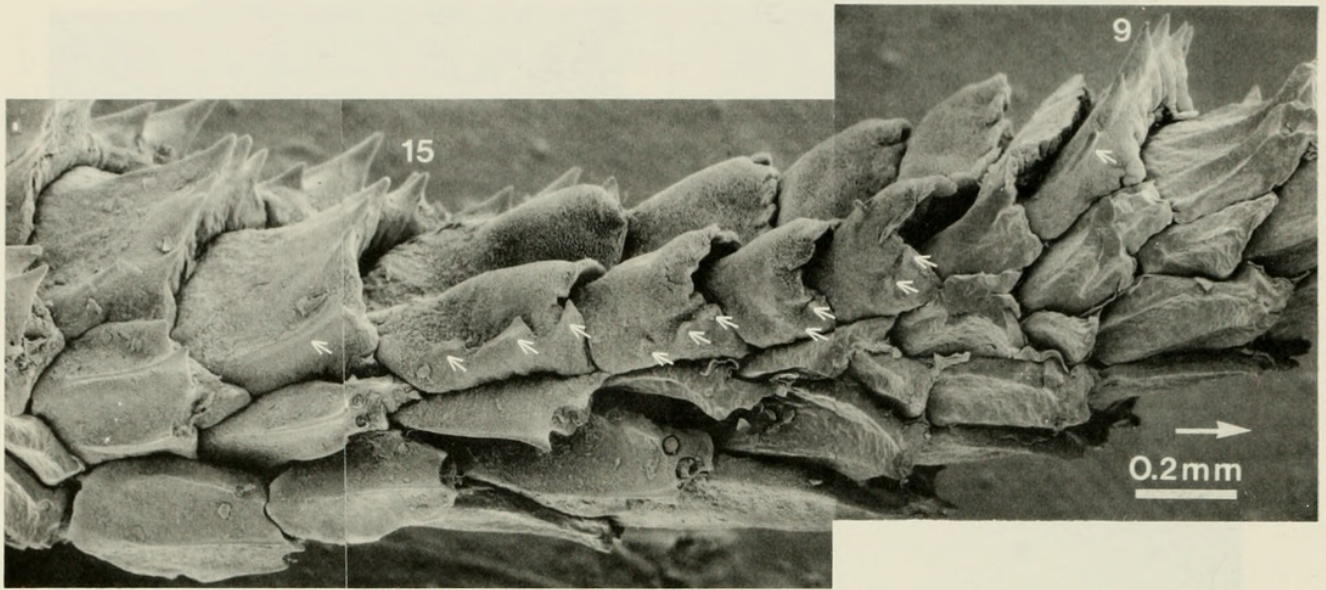


Figure 2. Oblique view of the phalanx ii scales of the third toe in *A. annectens*. The keels and bosses on the lamellae and intermediate scales are indicated by small arrows. Note the relief of the keels and bosses on scales 9, 14, and 15. The arrow adjacent to the dimensional scale indicates the direction of the claw (distal). This convention is used in subsequent figures.

mellae in having a distinct, thin, frayed free margin and in being laterally expanded to form a pad.¹ They differ from typical *Anolis* lamellae in having small bosses or keels along their lateral margins (Fig. 2). The surface architecture of the bosses is similar to that of the keels on the multicarinate scales.

The central portion of each of the lamellar scales is covered with setae (Fig. 4). The setae are about $20\ \mu$ tall (shorter near the base of the scale and margins), have a terminal "spatula," and occur with a spacing of about $1\ \mu$ (density of 1–2 setae/sq μ). Midway between the spatula and the scale surface, the shaft of the seta is round in cross section and $0.48 \pm 0.08\ \mu$ in diameter. The shaft tapers slightly (to 0.35 – $0.45\ \mu$ in diameter) toward the spatula. At about $1.4\ \mu$ proximal to the spatula the setae are usually inflected slightly toward the claw and the shaft becomes oval in cross section (dimensions are about 0.25 – $0.35\ \mu$ by $0.2\ \mu$). Just proximal

to the spatula the shaft is constricted and bent toward the metatarsal-phalangeal joint. The two inflections in the shaft are responsible for orienting the spatula so that its free distal margin faces the metatarsal-phalangeal joint, and its expanse is 30° – 90° from the vertical plane of the shaft (orientation varies significantly). The distal margin of the spatula is usually frayed, and it may be concave toward the lamellar surface. The spatula itself is shaped like an isosceles triangle with a base of $0.73 \pm 0.09\ \mu$ and a height of $0.58 \pm 0.02\ \mu$. The area of the spatula is 0.211 ± 0.022 sq μ . The morphology of the setae in *annectens* is very similar to that in generalized anoles (e.g., *A. carolinensis* and *A. sagrei* as described by Ruibal and Ernst, 1965).

c) Subdigital scales 9 and 15 (Figs. 2, 5) exhibit a blend of lamellar and multicarinate scale features.

Scale 9 is laterally expanded, but less so than the more proximal lamellar scales. Unlike the lamellae, the distal margin is quite robust, and there are eight small bosses or keels along the distal margin. One of these shelters a me-

¹ The outer keratin layer was absent on scale 10, but there are some probable "boss" sites and a relatively thin margin. We have included it with the lamellar-like scales on the basis of these characters.

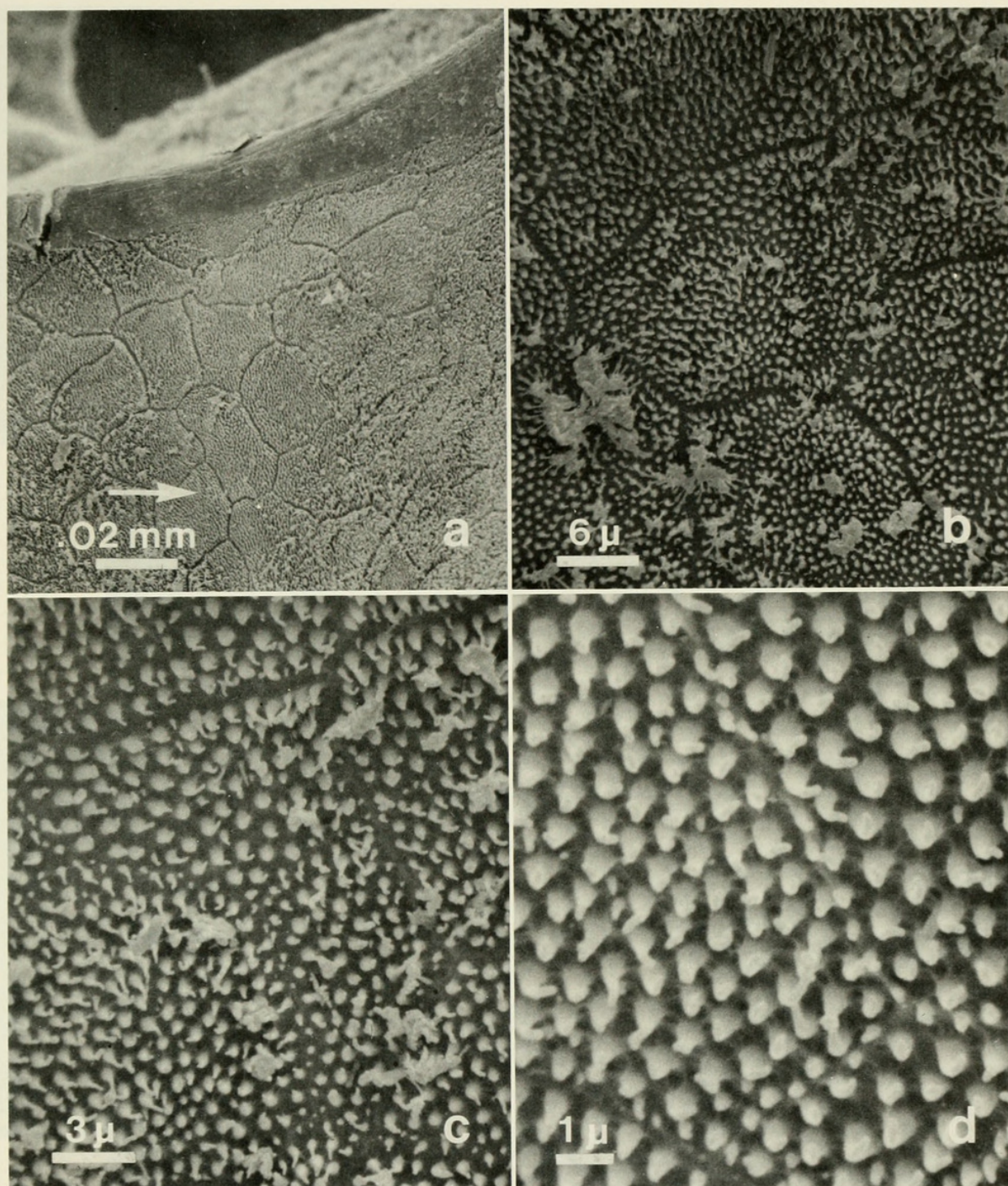


Figure 3. The fine structure of multicarinate scale 17 in *A. annectens*. a) Shows the central keel and adjacent fields of spines. b), c), and d) Are progressively higher magnifications of the spinate surface. Note the low hillocks in (b) and (c) and the presence of many small spines and knobs in (d) (compare with Figs. 21 and 22).

chanoreceptor. The surface of the scale appears "velvety," but less so than the lamellar scales. Based on gross characters it is neither a lamellar nor a multicarinate scale.

The fine structure also suggests the intermediate character of the scale (Fig. 5;

Fig. 21 for definition of types). The surface architecture of the bosses is similar to that of the keels on the multicarinate scales. In a few regions, particularly adjacent to the central keels, there are fields of small spines ($0.2\text{--}0.3\ \mu$ diameter at the base; a density of $2.2\ \text{spines/sq}\ \mu$).

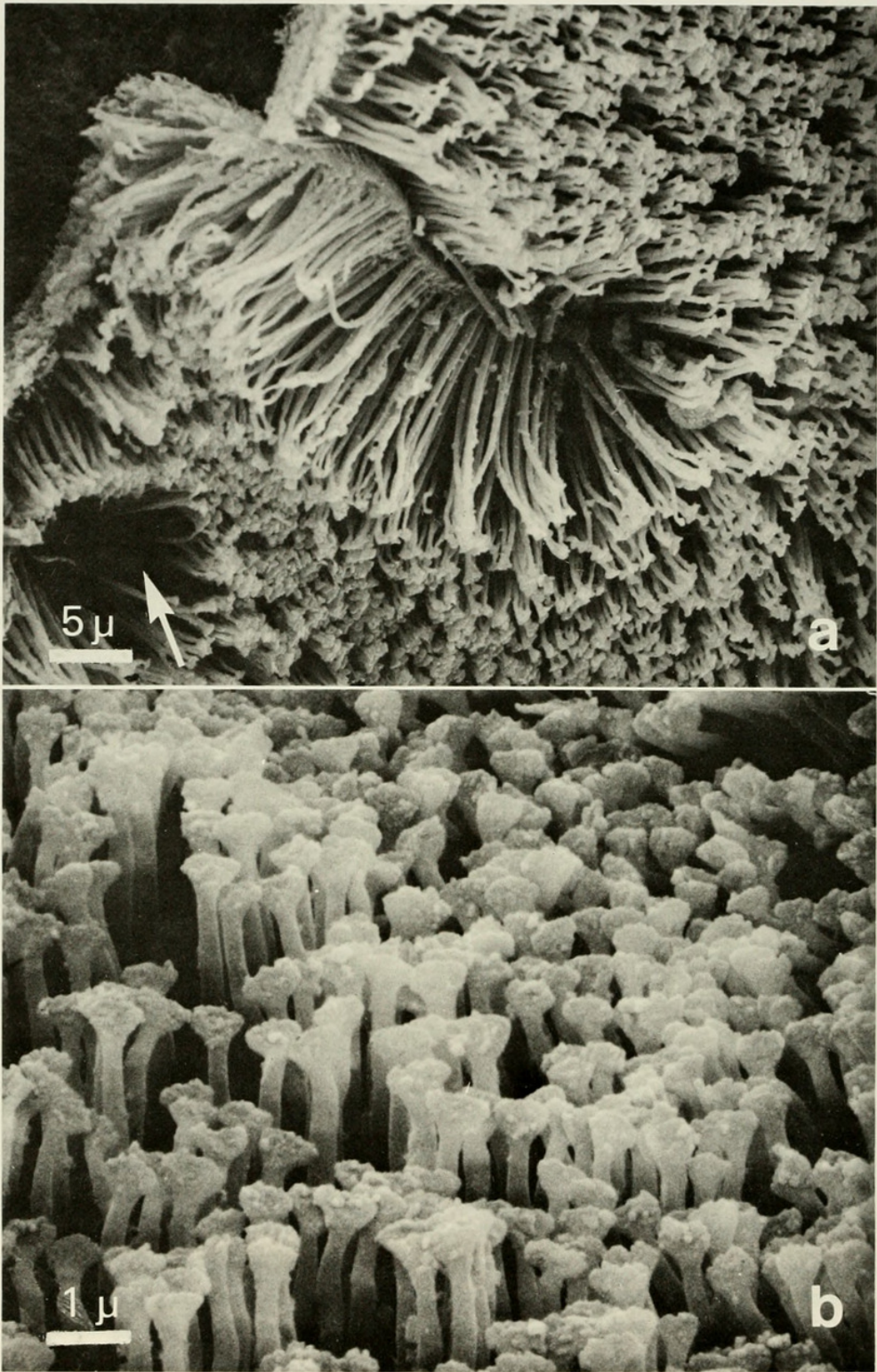


Figure 4. The setae on scale 12 (lamella 3) in *A. annectens*. a) Shows setae along the distal margin of the lamella. b) Is a view of the spatulae as seen from the claw.

These are taller, but otherwise similar to the small spines on the multicarinate scales. The zones of small spines are bounded by regions of somewhat larger

spines (Fig. 5b and lower left and center top of Fig. 5c). These spines have the diameter ($0.55\ \mu$ at the base) and spacing characteristics of the larger spines on the

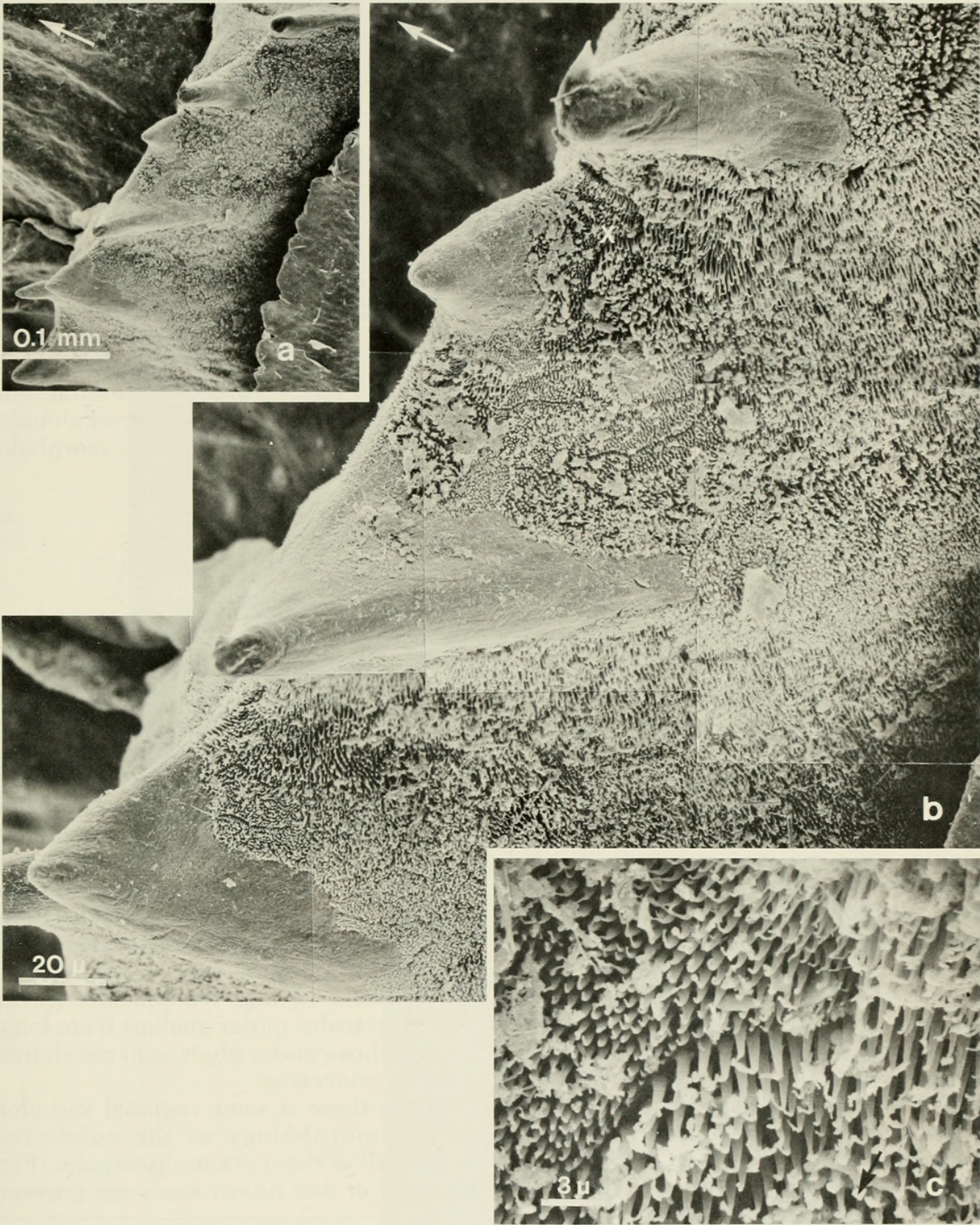


Figure 5. The morphology of scale 9 in *A. annectens*. a) Shows an overall view. b) A montage of half the scale surface illustrates the heterogeneous fine structure and relationship of the keels and spine/spike/seta series. The region indicated with an "x" is shown in higher magnification in (c). Note the spines to the left of (c), the abrupt transition from spines to prongs along the bottom of (c), and the gradual transition from spines to spikes to prongs along the top of (c). A few seta shapes occur to the lower right (black arrow).

multicarinate scales, but grade up to $5\ \mu$ in height (by definition; see below). Most of the scale, however, is covered by even taller, more robust "spine-like" forms which grade through a variety of shapes into a few setae. The much taller (above $5\ \mu$) and thicker ($0.7\text{--}0.8\ \mu$ at the base; $0.5\ \mu$ midpoint diameter) structures with strongly tapered, needle-like tips we refer to as spikes (Fig. 5 center top; Figs. 21, 22). The gradation from spines to spikes may be abrupt, as along the center of Fig. 5c, or very gradual, as along the top of Fig. 5c. The spikes in the lower and right portions of the figure are interspersed with structures, here called "prongs," which have a straight or recurved tip which is less tapered than the spike (see also Figs. 21, 22). There are seta shapes (defined by the expanded triangular tip) in the lower left of the figure (note black arrow; see also Fig. 21). Setae are rare compared to spikes and prongs. In just a few areas adjacent to the "bosses" and over the central portion of the scale, spikes and prongs grade into setae. The dimensions of the spatula on these setae are comparable to those of spatulae on the lamellar scales, and the midpoint diameter of the stalk is also similar. Setae on scale 9 differ only in their shorter stalk ($6\text{--}7\ \mu$ compared to about $20\ \mu$ for the lamellar setae). Although we have not encountered setae this short elsewhere, height is probably not a reasonable basis for differentiating them from the setae on the lamellar scales because 1) a few of the setae from the marginal and proximal areas of the lamellar scales are almost this short (about $10\ \mu$), and 2) stalk height is a variable character within and between anole individuals and species (Peterson and Williams, unpublished data).

Scale 15 is quite similar to scale 9, although there are more definite keels along its lateral margins (Figs. 1, 2). These are almost certainly serially homologous with those on multicarinate scale 16 and lamellar scale 14. The adjacent multicarinate scales have a dominant central keel which is missing on scale 15. The fine structure of scale 15 was difficult to examine thoroughly because of the debris on its surface. There are spines grading into spikes, as on scale 9, but we were unable to confirm that setae are present. Scales 9 and probably 15 combine the features of lamellar and multicarinate scales and suggest a model for evolutionary intermediate morphology.

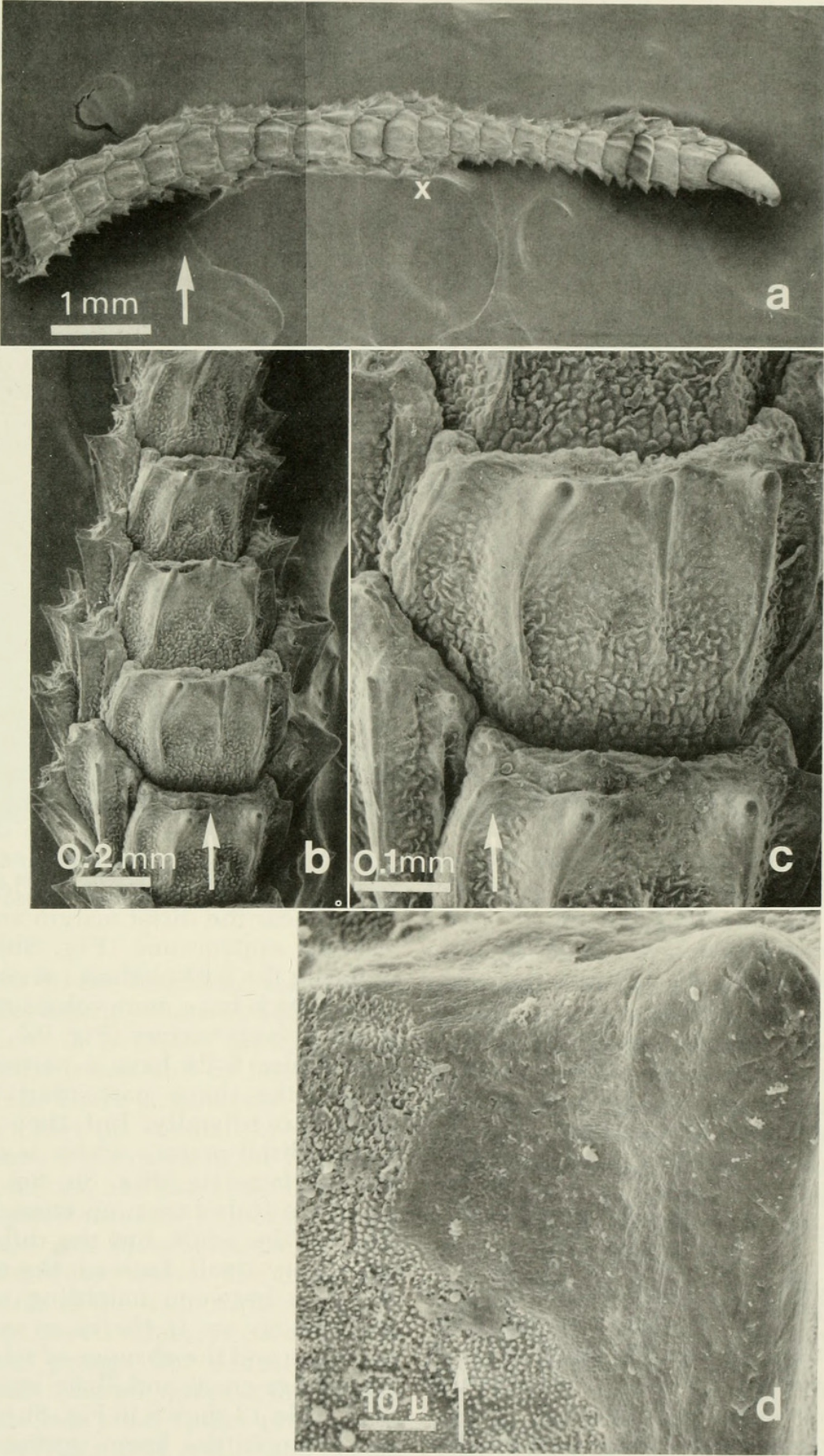
COMPARISON WITH *ANOLIS* (*TROPIDODACTYLUS*) *ONCA*

Adult Morphology

There are more subdigital scales in *A. onca* than in *A. annectens* (24 rather than 20, Figs. 1, 6). This reflects a) the longer phalanges in an *onca* of approximately the same snout-vent length as the *annectens* type (phalanges ii and iii are 2.3 mm and 2.8 mm compared to 1.4 mm and 2.4 mm, respectively, in *annectens*), and b) differences in the size of the scales in some regions. The distribution of scales relative to the phalanges in *onca* versus *annectens* is: 1/1 claw base; 9/7 phalanx i; 6/6 phalanx ii; and 8/6 phalanx iii. In *onca* the scales under phalanx ii are longer, and those under phalanx iii are shorter than in *annectens*.

While there is some regional variation in the morphology of the subdigital scales, all of them are multicarinate (Fig. 6). Four or five robust keels are present,

Figure 6. The third toe of *A. onca*. a) Only the distal 22 scales are shown. The "x" indicates the scale shown in (b) center. b) Shows multicarinate scales 8, 9, 10, 11, and 12 at the i/ii interphalangeal joint. Note the more prominent median keel on scale 11, the asymmetry of the keels, and the great relief of the keels on the lateral digital scales. c) Shows the structure of an individual scale. Hillocks occur toward the base of the scale, and the two pairs of lateral keels are most prominent. d) Illustrates the bare surface of the keel and junction with adjacent spinate areas. Note the "wear striations" along the crest and proximal slopes of the keel.



and the distal margins of the scales have additional bosses. The distal margin is definitely not thin or frayed, and numerous mechanoreceptors occur in the lee of the keels and bosses. The regions between the keels and toward the base of the scale are somewhat velvety in appearance and heavily contoured into hillocks (Figs. 6, 7). The subdigital and lateral scales have very similar gross morphology.

All the subdigital scales in *onca* resemble the multicarinate series (scales 1–8, 16–20) in *annectens*. There is a difference, however, in the prominence and placement of the keels. The pattern in both animals is based on five possible keels: a median keel, a pair of lateral keels, and a pair of far lateral keels. In *onca* the four lateral keels are consistently well developed with the lateral pair being the most robust and prominent, while the fifth or median keel is conspicuous only adjacent to the interphalangeal and metatarsal-phalangeal joints (Fig. 6). This differs from the condition in *annectens* in which the median keel is always well developed and the most prominent of the five keels.

The fine structure of the keels in *onca* appears similar in every respect to that of the keels in *annectens* (Fig. 6).

The areas between the keels are covered with spines. Distally on the scale where hillock contouring is not well developed, the spines are relatively uniform (Fig. 7c). They are 0.8–1.2 μ tall and 0.3–0.45 μ in diameter near the base (0.1–0.2 μ in diameter at their midpoint) and occur in a density of about 1.2 spines/sq μ . The tips are sharp and recurved, usually toward the crest of the keel.

Most of the scale surface, however, is heavily contoured, and in these areas the spines are more varied in morphology and spacing (Fig. 7d). The range of spine height becomes 1.0–1.8 μ , and there is marked variation in robustness. While some spines resemble those near the dis-

tal margin, others have extremely large buttresses or struts, so that their diameter at the base (0.8 μ) is as much as half their height. Spacing between the center of the spines ranges from 0.7 μ near the crests of the hillocks where the buttresses of adjacent spines interdigitate to more than 3 μ in the depths of the valleys between the crests.

The spinose regions of the scale in *onca* differ from those in *annectens* only in a) the scarcity of small spines (these are present, but rare), and b) the more extreme development of contouring and associated spine variation.

Juvenile Morphology

Juvenile *onca* have a different subdigital morphology from that of the adults (Maderson and Williams, 1978). The number (24) and distribution of the subdigital scales relative to the phalanges do agree with the condition in the adults. But, in contrast to the adults, none of the scales are strictly multicarinate (Fig. 8a). There are two poorly differentiated series: a) scales in the phalanx ii and iii regions (scales 10–24) and the distal and proximal scales in the phalanx i region (scales 1, 8, 9), which have less robust ridges near the distal margin and a more velvety appearance (Fig. 8b), and b) scales in the mid-phalanx i region (scales 2–7), which have more robust ridges and a less velvety texture (Fig. 9a).

a) Scales 8–24 have a narrow but lamellar-like shape particularly because they flare distally, but they lack the frayed distal margin which is characteristic of lamellae (Fig. 8b, 8c). In most cases the scales are proportionally wider than in the adult, but the difference is often very small. Instead, the major differences between hatchling and adult morphology are in the more velvety appearance and the absence of robust keels with sharp crests and “bare areas” (compare scale 13 shown in Fig. 8b with scale 11 shown in the lower portion of Figs.

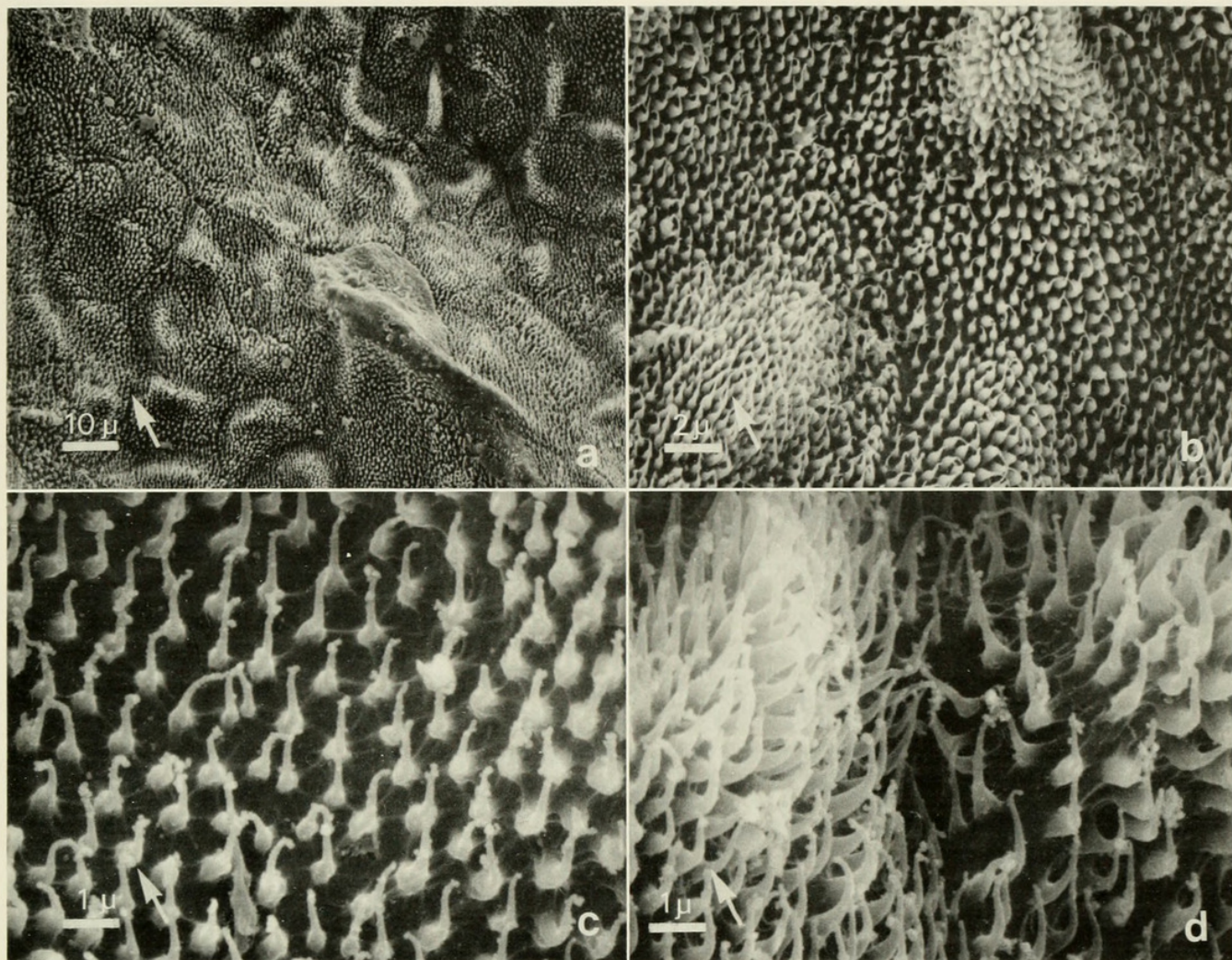


Figure 7. The third toe of *A. onca*. a) Shows detail of the surface of scale 7. A small keel occurs in the lower right. b) Shows detail of the hillocks. c) Is taken on scale 7; d) is from scale 11. c) and d) illustrate the differences in spine morphology between countoured and uncountoured regions.

6b and 6c). In the hatchling, the surface of the scales is gently contoured into ridges which occur in positions corresponding to the robust lateral and far lateral keels of the adult. There is, however, no ridge that anticipates the median keel. Mechanoreceptors often occur in the lee of the lateral contours, and the scale bases are also contoured into low hillocks.

Setae are not present on any of the third or fourth toe scales. The distal half or two-thirds of the scale surface, including the contoured ridges, is covered with spikes and prongs (for definitions see Figs. 21, 22). Shorter spikes at the margin itself grade into taller spikes proximal to the margin ($7.2 \pm 0.51 \mu$ tall; 0.56 ± 0.08

μ in diameter). In some areas the spikes grade into forms with a more robust prong-like tip (in Fig. 8d spikes in the upper left are shown grading into prongs in the lower right). Between the contoured ridges as well as proximally, the scale surface is covered with spines (Fig. 9b). There is continuous variation in spine height from about 0.75μ up to the spike morphology at 5μ .

Although its shape is quite different, scale 1 is included in this series because its contouring and fine structure are comparable to those of scales 8–24. The surface of the scale is covered with spikes and prongs 5–7 μ tall.

b) Scales 2–7 in the juvenile have a

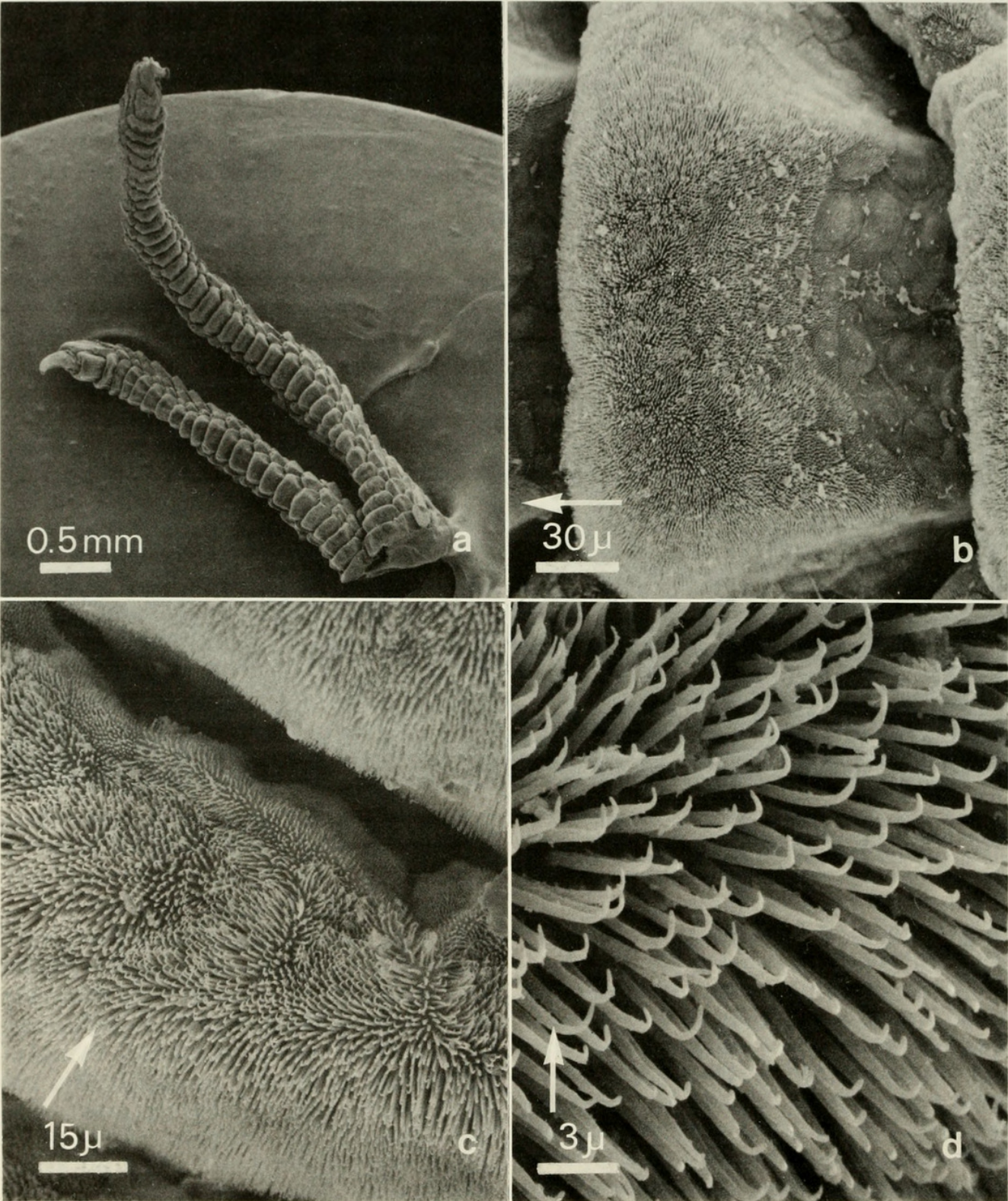


Figure 8. The third and fourth toes of juvenile *A. onca*. a) Shows an overall view. b) Shows scale 13; the lamellar-like scales in the phalanx ii region of the third toe have contours in the position of the lateral keels. c) Shows a robust distal scale margin. d) The surface of the scale is covered with spikes (upper left portion) and prongs (lower right portion).

gross shape similar to their homologues in the adult, and the position of the ridges in most cases anticipates the position of keels in the adult.

The scale surface adjacent to the distal margin and that over the distal portion of the ridges is covered with spines (Fig. 9a). On scale 6, spines in the distal region

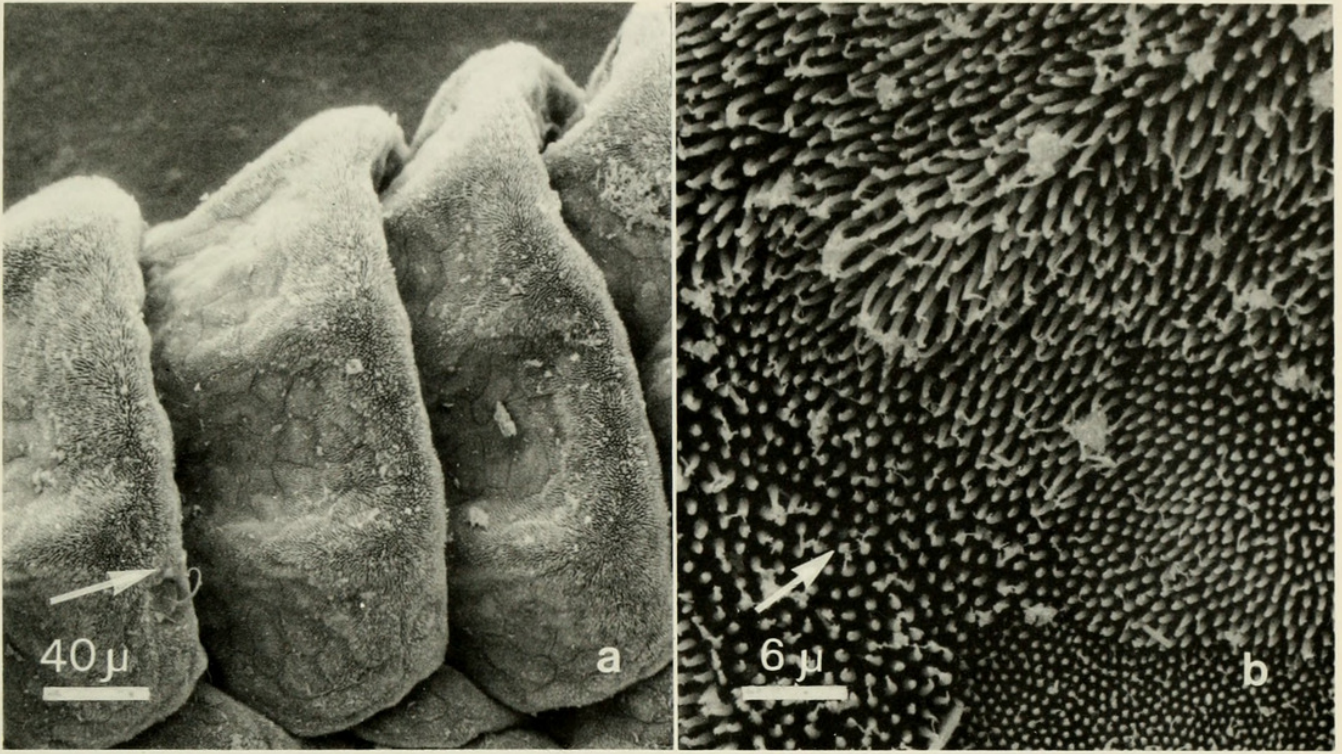


Figure 9. The second, third, fourth, and fifth scales of the third toe (phalanx i region) of juvenile *A. onca*. a) Shows 3–4 μ tall spines along the distal margin and over the ridges. The region between the contours and toward the base of the scale is covered with shorter spines. b) Illustrates the border between the distal and proximal spines on scale 5.

are $3.37 \pm 0.75 \mu$ tall and $0.47 \pm 0.08 \mu$ in diameter (see the top portion of Fig. 9b). These grade more or less abruptly into spines which are more comparable to those of the adult (1–2 μ tall; 0.5 μ diameter at the base; and a range of densities of 0.7–1.2 spines/sq μ ; see the lower portion of Fig. 9b). In some proximal areas fields of still smaller spines occur (0.5 μ tall; 0.3 μ diameter at the base; and 2 spines/sq μ ; see the lower right corner of Fig. 9b).

Scales 7 and 8 at the boundary between the series are not very different in shape, contouring, or fine structure. The “spines” on scale 7 are 4–5 μ tall, while the spikes on scale 8 are 6–7 μ tall. The subdigital scales are regionally differentiated more than in the adult, but much less than in *annectens* or *chrysolepis*.

Some of the lateral digital scales have robust keels with bare areas, but most of the scales immediately adjacent to the subdigital series have ridges (Fig. 9a) rather than keels as in the adult (Fig. 7b).

COMPARISON WITH *ANOLIS CHRYSOLEPIS*

A. chrysolepis has 29 subdigital scales (a second specimen has 27; Fig. 10). The distribution of these scales relative to the phalanges in *chrysolepis* versus *annectens* is: 1/1 claw base; 10/7 phalanx i; 11/6 phalanx ii (9/6 in the second specimen); and 7/6 phalanx iii. The differences in distribution reflect smaller scales over phalanges ii and iii in *chrysolepis* and a longer second phalanx in *chrysolepis* (2.1 mm compared to 1.4 mm in *annectens*; phalanx iii is 2.3 mm in *chrysolepis* and 2.4 mm in *annectens*).

The subdigital scales of *chrysolepis* include a) lamellae (scales 13–22), b) generalized subdigital scales which are defined as non-lamellar and unkeeled (scales 10–12, 22–29), and c) scales with small keels or boss-like areas (scales 1–9; Fig. 12).

a) The lamellar scales lie under phalanx ii, form a pad, and resemble the la-

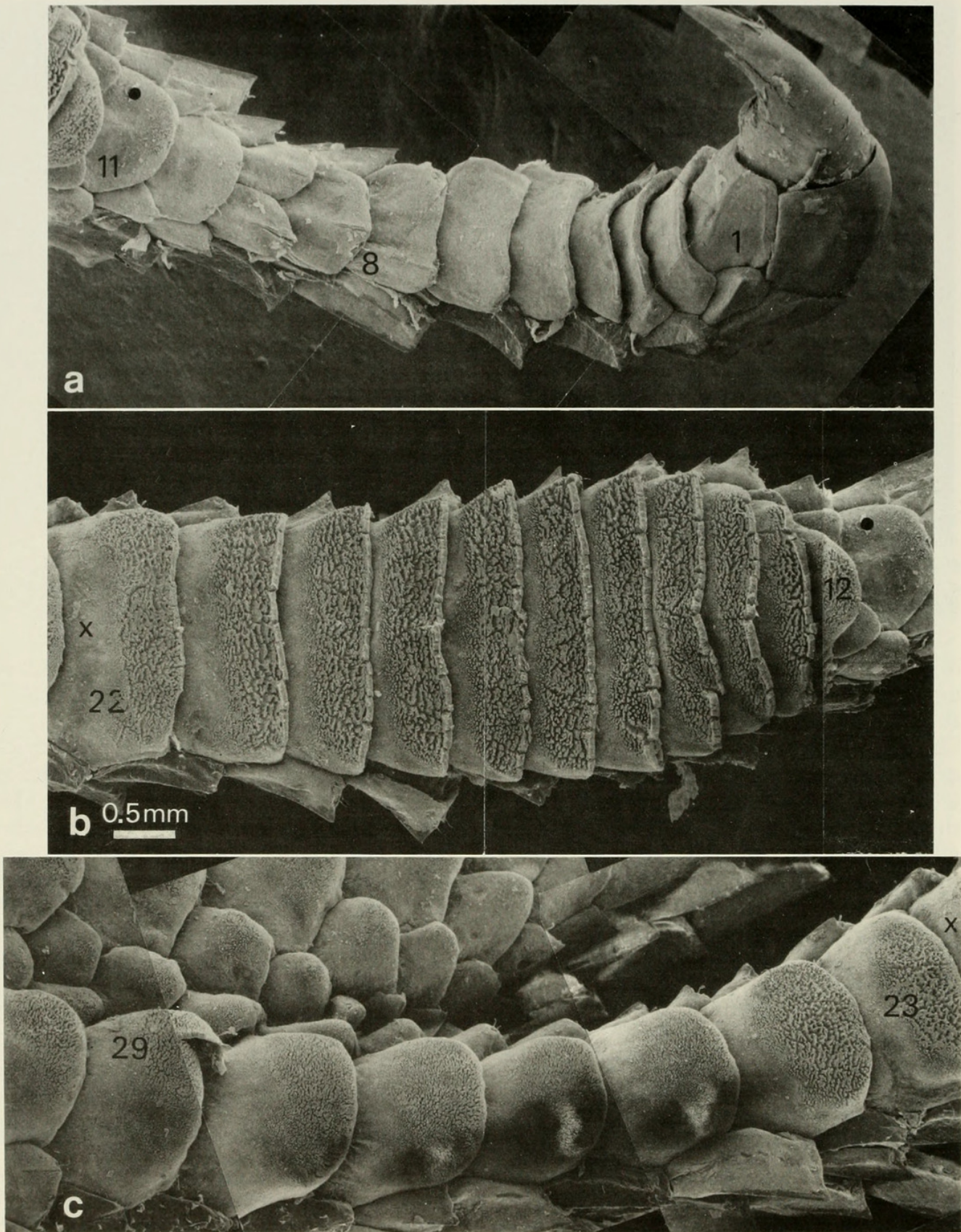


Figure 10. Composite of the third toe in *A. chrysolepis*. The distal scale series (a) fits with the pad series (b) at the "●"; the proximal series (c) matches (b) at "x."

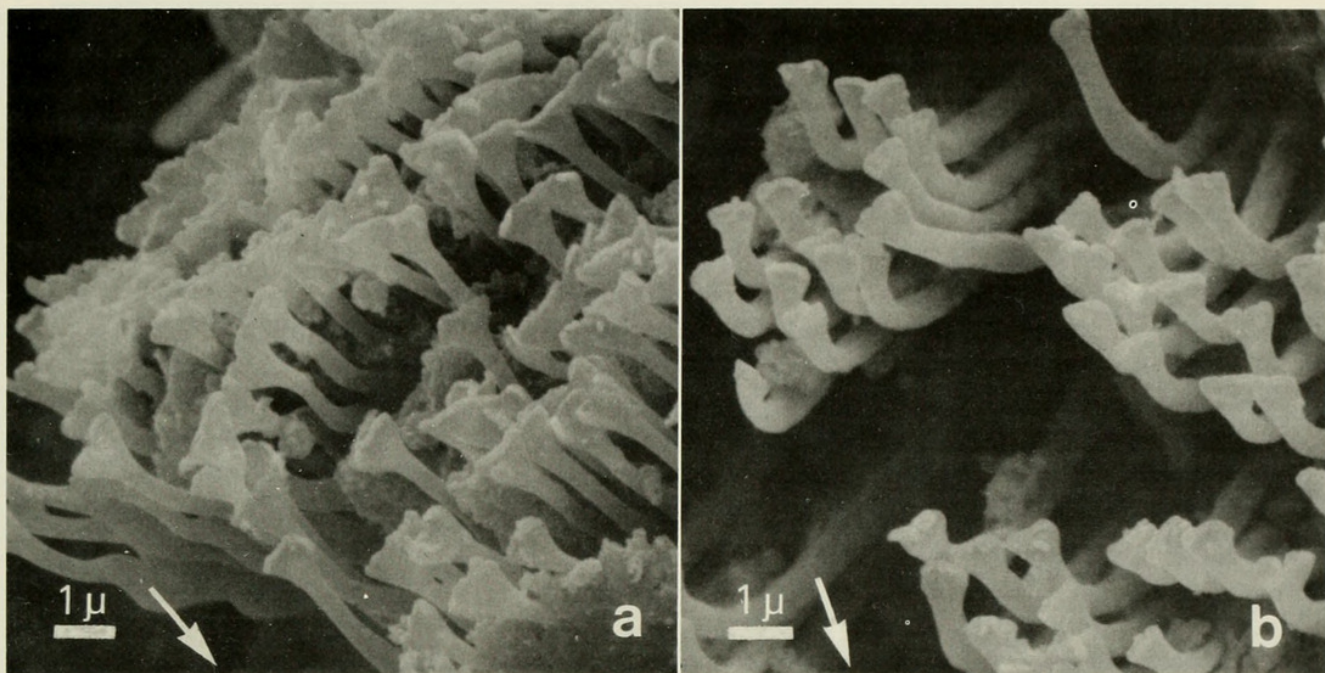


Figure 11. The setae in *A. chrysolepis*. a) Is taken on the eighth lamellae (scale 20) adjacent to the distal margin (the material below the spatulae is debris). b) Is taken on scale 28 just distal to the metatarsal-phalangeal joint. The setae on scales 28 and 30 are slightly narrower than on the lamellar scales ($0.84 \pm 0.05 \mu$ compared to $1.01 \pm 0.07 \mu$; the height of the spatula is not different), and the stalk is less tapered and thicker just below the spatula. The difference in density of setae is an artefact of the sites chosen.

mellae of generalized anoles. There is no evidence of small keels or bosses like those of *annectens*. The surface of these scales is covered with setae (Fig. 11). The orientation and height of the setae are comparable to those of *annectens*, but the stalk diameter ($0.79 \pm 0.09 \mu$ at the midpoint) and spatular dimensions (base [width] $1.01 \pm 0.07 \mu$; height [length] $0.71 \pm 0.05 \mu$; area $0.358 \pm 0.037 \text{ sq } \mu$) are larger. The *chrysolepis* measurements are unusually large for *Anolis*. The dimensions in *annectens* are similar to those of West Indian anoles investigated by us and by Ruibal and Ernst (1965).

b) Proximal and distal to the lamellae there are unspecialized subdigital scales (Figs. 10, 12). These have a fairly robust rounded distal margin and a velvety surface texture. Mechanoreceptors occasionally occur along their distal margins. The shape of these scales is highly variable. The series of scales proximal to the pad continues beyond the metatarsal-phalangeal joint and into the sole of the foot. Scales with these gross characters occur

proximal and distal to the pad in most anoles we have examined.

There is a poor correlation between this gross morphology and the fine structure of the scale. In *chrysolepis* the scale series proximal to the pad (scales 23–29 and beyond into the sole of the foot) bears setae with well-defined spatulate tips (Fig. 11). Distal to the lamellae only one of the scales with this gross morphology bears setae. This is scale 12, which is adjacent to the lamellae and part of the raised pad. Scale 11, distal to the pad, bears tall spikes with tips which combine the shape characters of the seta and the prong (Fig. 13). The tip is flattened or compressed like the spatula, but not laterally expanded to form a triangular surface and broad distal margin (in generalized anoles this unexpanded tip shape is present in the very proximal portion of the lamella as part of the morphological grade from spines to setae; Fig. 23). The seta/prong intermediate morphology occurs over the central portion of scale 11 (the distribution is evi-

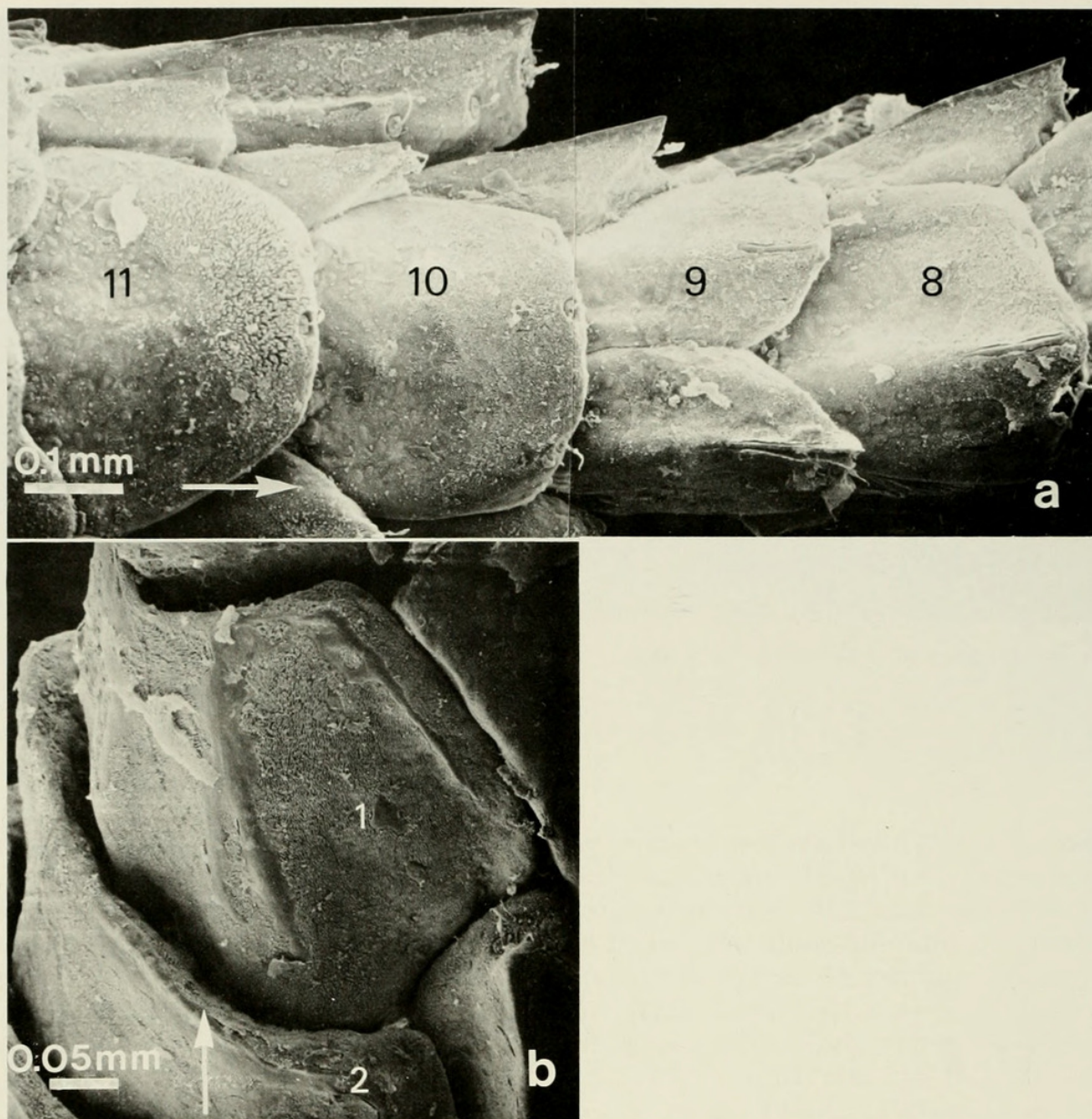


Figure 12. Scales distal to the pad in *A. chrysolepis*. a) Shows the scales just distal to the pad. b) Is an oblique view of scales 1 and 2. Ridges (scale 1), small keels (e.g., scale 8), or bare areas (e.g., scale 2) are present on the series 1–9.

dent from Fig. 13a). Toward the lateral and proximal portions of the scale the shape grades into a blunt prong and finally a short spine with a recurved tip. The spinose regions of the scale exhibit contouring similar to that seen in *annectens*.

c) The still more distal groups of scales (scales 1–9) grossly resemble scales 10 and 11 with the addition of small keels or keel-like bare areas (Figs. 12, 14). The fine structure of the keels and bare areas is similar to that of the keels on the lateral

scales and the keels in *annectens* and *onca*. The scale surface adjacent to these regions is covered by spines with needle-like tips. The spines over most regions are 1.4–1.7 μ tall, but on scales 8 and 7 they are as tall as 3.2 μ and 2.4 μ , respectively.

COMPARISON WITH *ANOLIS AURATUS*

A. auratus has 22 subdigital scales (Fig. 15). Their distribution relative to the phalanges is quite similar to that in

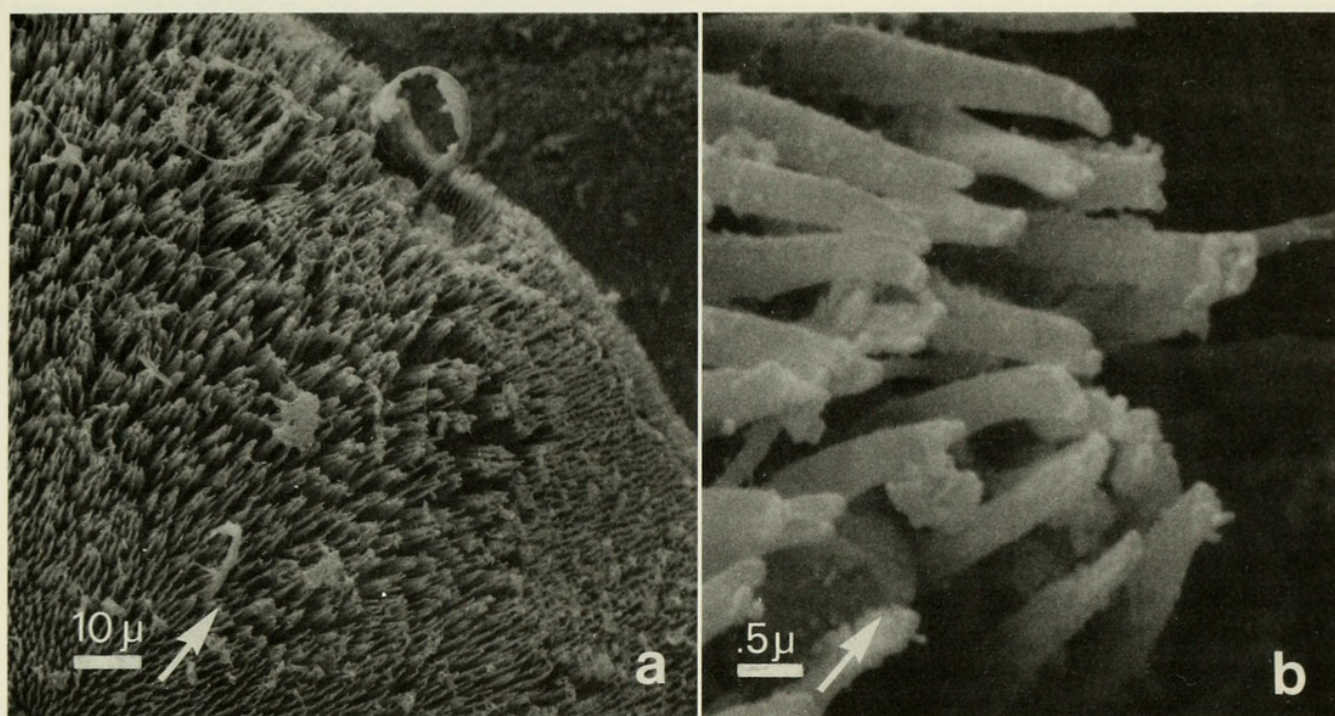


Figure 13. The morphology of scale 11 in *A. chrysolepis*. a) Shows the distal portion of the scale (Fig. 10) and the grade from spikes into the taller seta-prong intermediate morphology. b) Shows the flattened tip and frayed margin of the intermediate shape. Note that some of the tips appear to be bifurcated and not simply frayed.

A. annectens; the distribution in *auratus* versus *annectens* is: 1/1 claw base; 7/7 phalanx i; 8/6 phalanx ii; and 6/6 phalanx iii. Overall toe length, individual phalangeal lengths (phalanx ii is 1.3 mm in *auratus* and 1.4 mm in *annectens*), and scale sizes are very similar in spite of the smaller body size of *auratus* (Table 1).

The *auratus* scales include a) lamellae (scales 9–15), b) generalized subdigital scales (scales 7, 8, 16–22), and c) intermediate scales (scales 1–6).

a) The lamellae are grossly similar to those in *annectens* (apart from the absence of small lateral keels and bosses) and *chrysolepis*. The series of lamellae particularly resembles *annectens* in forming a narrower pad which is not clearly set off from the distal scale series (the “Norops” condition;¹ Figs. 1, 15, 18).

¹ The “Norops type condition” was defined by Williams (1974: 17) as “loss of distinctness of the anterior margin of the pad (that under phalanx ii) as against the scales under phalanx i” and was regarded as the third morphological stage in a sequence of “retrograde evolution.” The present study has

The lamellae are covered with setae (Fig. 16). The seta stalk is shorter than that in *annectens* (mean height over the front half of the lamella is $13.2 \pm 0.5 \mu$; maximum height is 15.7μ ; height at the distal margin is 12μ), but the orientation, stalk diameter ($0.55 \pm 0.06 \mu$), and spatular dimensions (base [width] $0.60 \pm 0.04 \mu$; height [length] $0.57 \pm 0.04 \mu$; area $0.173 \pm 0.020 \text{ sq } \mu$) are similar to those in *annectens*. The spatula is slightly less broad than that in most West Indian *Anolis*.

shown that the condition depends upon the absence of one or more small scales deep to the pad at the ii/i interphalangeal joint. These scales, when present, “raise” the first phalanx relative to the pad (*Anolis* condition *vide* Boulenger, 1885: 11); in their absence the pad is “not raised” (Norops condition *vide* Boulenger, p. 95). The two conditions are less sharply distinct than Boulenger believed, although the end points of the series are indeed conspicuously different. Also, as we shall show below, the “Norops type condition” is not, as Williams (1974) supposed, truly retrograde in the sense of any loss of adaptive or even adhesive value; it is instead an *alternative* adaptation.

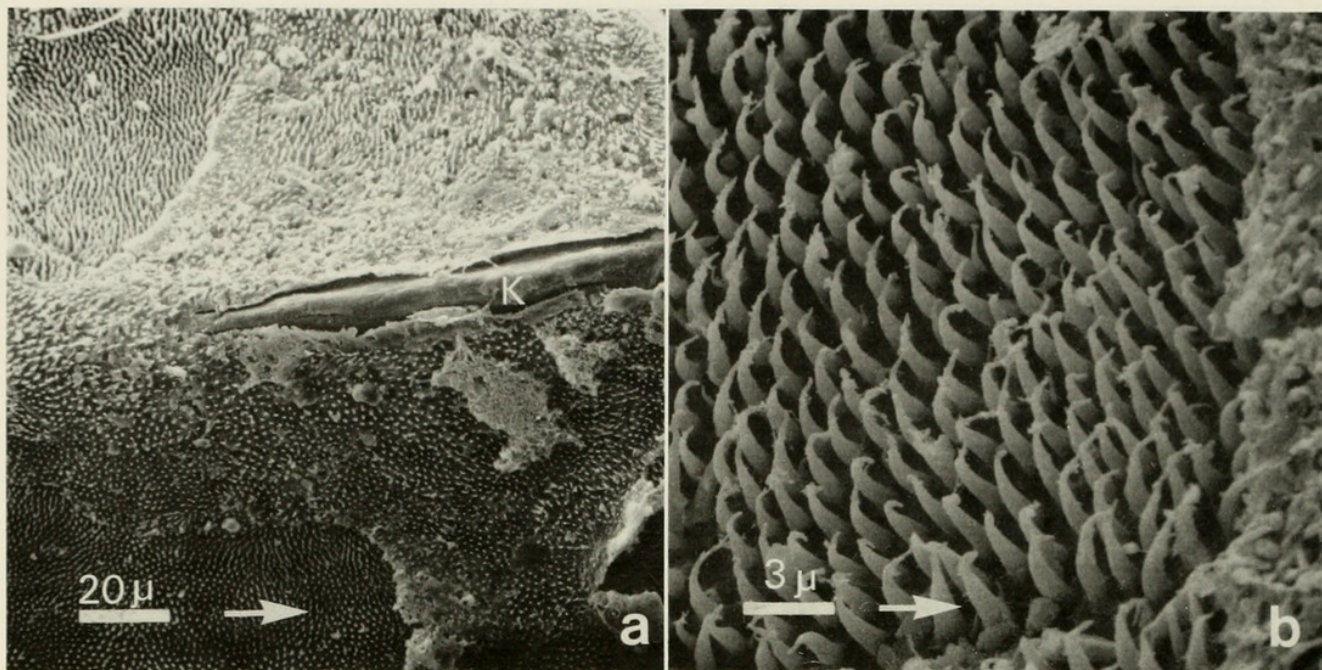


Figure 14. Scale 8 in *A. chrysolepis*. a) Shows a keel "k." b) Shows spines. This fine structure is typical of scales 1–8.

b) Scales 7, 8, and 17–22 resemble the generalized subdigital scales (non-lamellar and unkeeled) in *chrysolepis* and are unlike any of the scales in *annectens*. Scales 8 and 17 (Fig. 15) which flank the series of lamellae are more laterally expanded and could be considered lamellae except that the distal border is not thin and frayed.

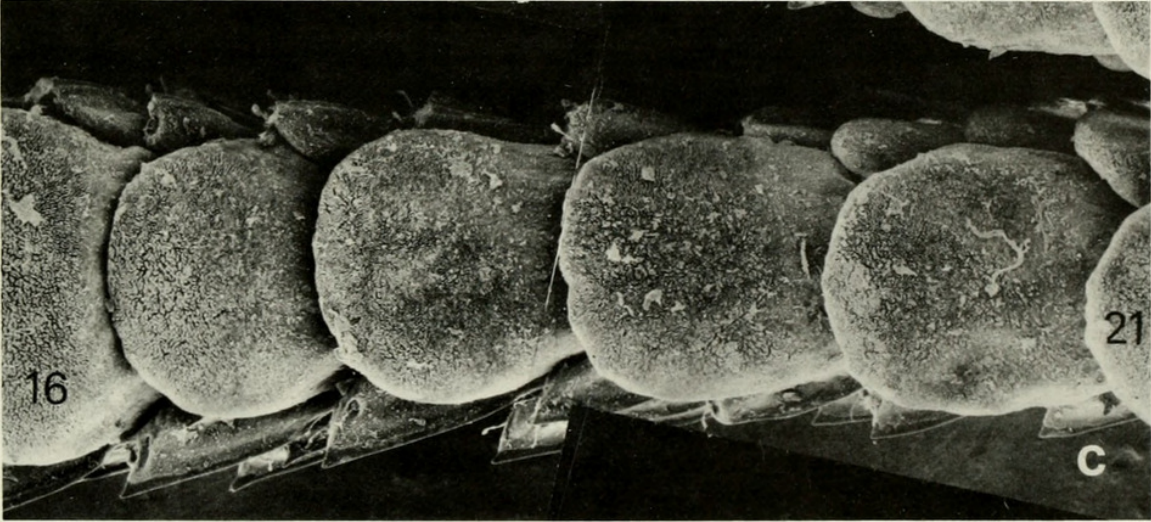
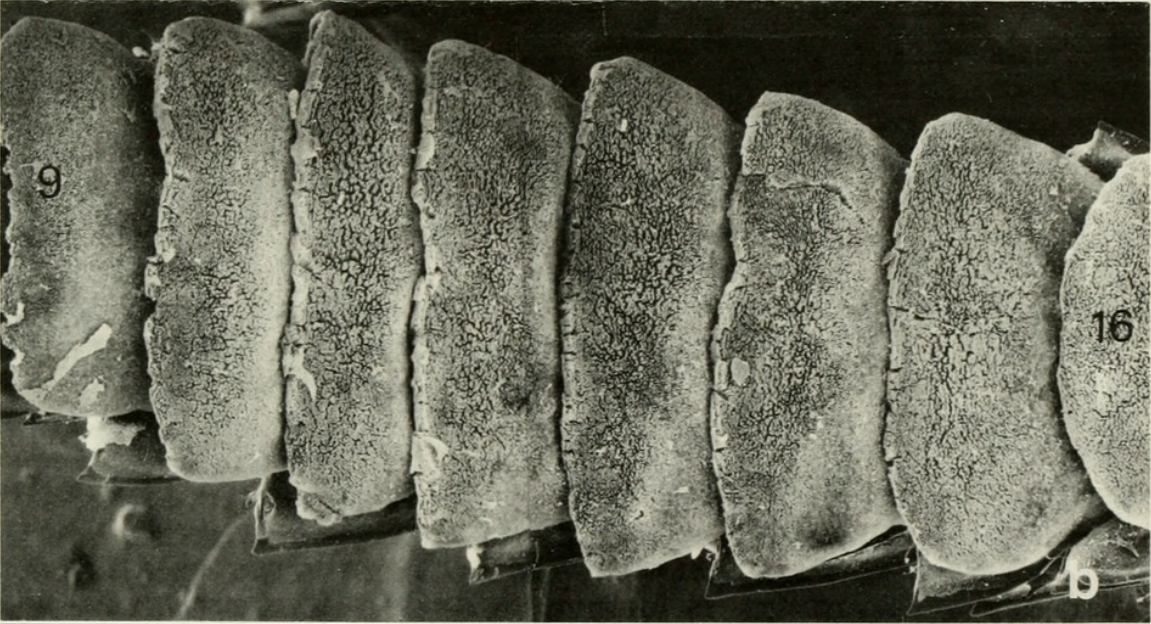
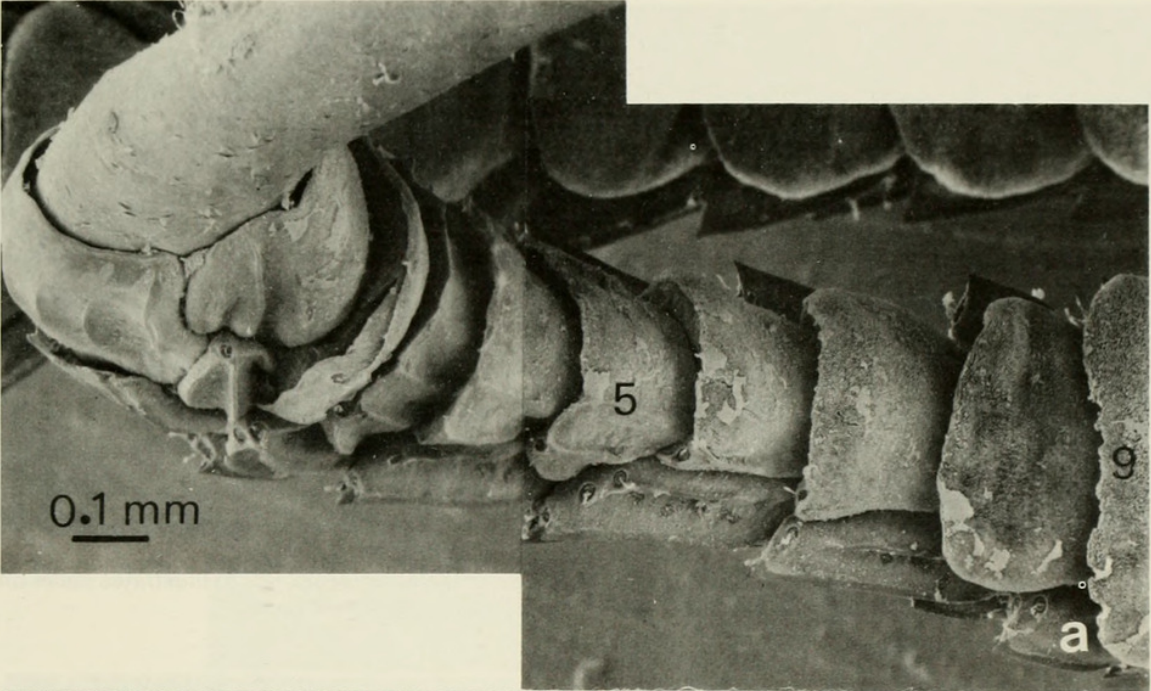
All of the scales in this group bear setae (Fig. 16). The stalk height, particularly maximum height, is less than that of setae on the lamellar scales, but the other dimensions are not different. The setae are distributed over the central and distal regions of the scale. Proximally and laterally the morphology grades into prongs, spikes, and finally spines. The fine structure of the scales is generally similar to that of the proximal scale series (scales 22–29) in *chrysolepis*.

c) *A. auratus*, like *A. annectens*, has individual scales with an unusually het-

erogeneous fine structure which combines the keels or bosses of multicarinate scales with the setae typical of lamellae. In *auratus* these intermediate scales extend from the claw almost to the pad.

Grossly, the intermediate scales (scales 1–6; Figs. 15, 18) have a fairly robust distal margin and well-developed keels. A few bosses occur over the median portion of the distal margin on scales 2, 3, and 4, but keels occur on all the scales. From one to four pairs of keels are present in median-lateral (on scale 3 only), lateral, far lateral, and extreme lateral positions (Fig. 18). The number of keels along the side of the toe is relatively constant, but their distribution on the subdigital versus the lateral digital scales differs. Excluding the median-lateral keel, the number of keels on the subdigital scales increases from proximal to distal as the subdigital scale expands around the phalanx. Proximally (e.g., scale 6) only the lateral keel

Figure 15. The third toe in *A. auratus*. The phalanx i(a) and ii(b) regions match at scale 9; the phalanx ii(b) and iii(c) regions match at scale 16. Note the difference in morphology of the distal borders of scales 15 and 16.



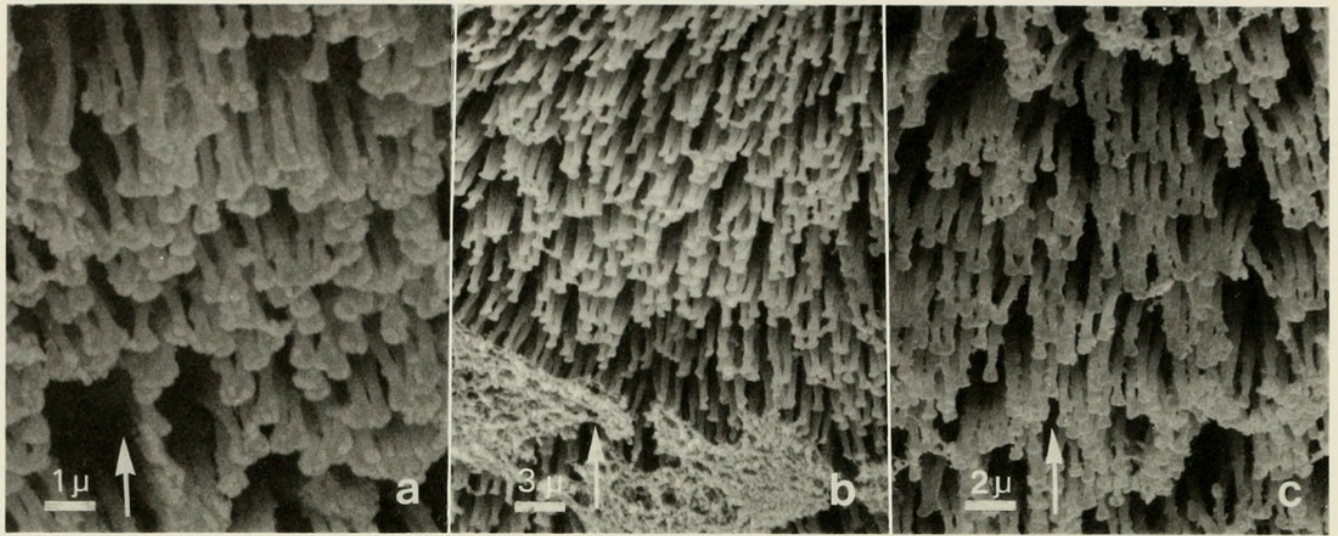


Figure 16. The setae in *A. auratus*. a) Illustrates setae on the fourth lamellae (scale 12). b) Illustrates setae on the claw base (scale 1). c) Shows setae on scale 21 just distal to the metatarsal-phalangeal joint.

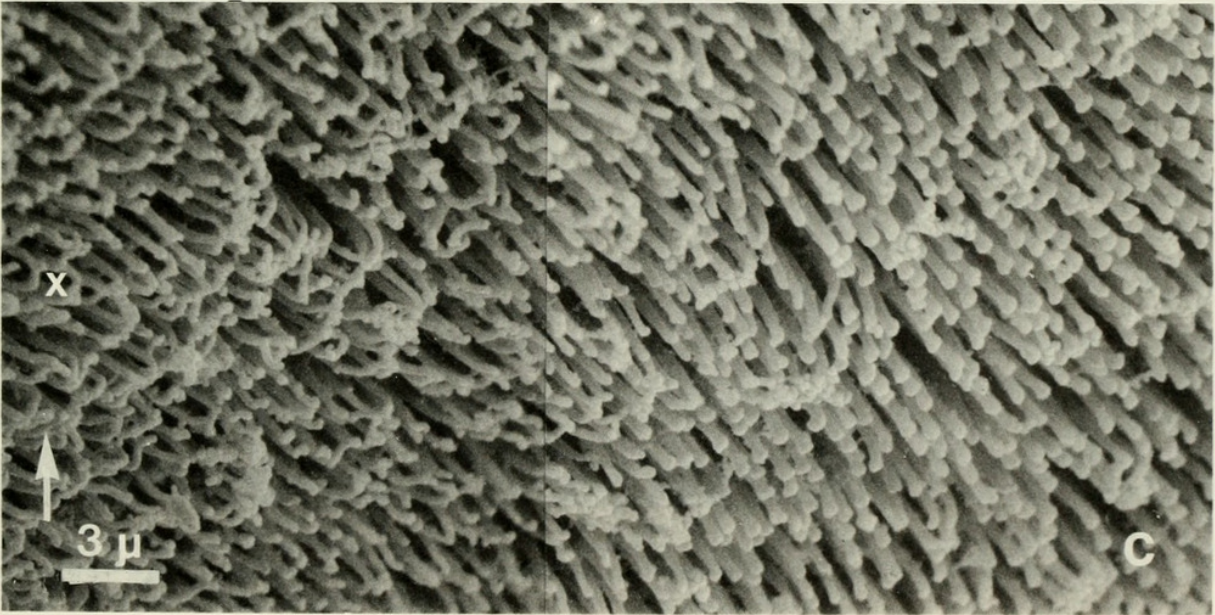
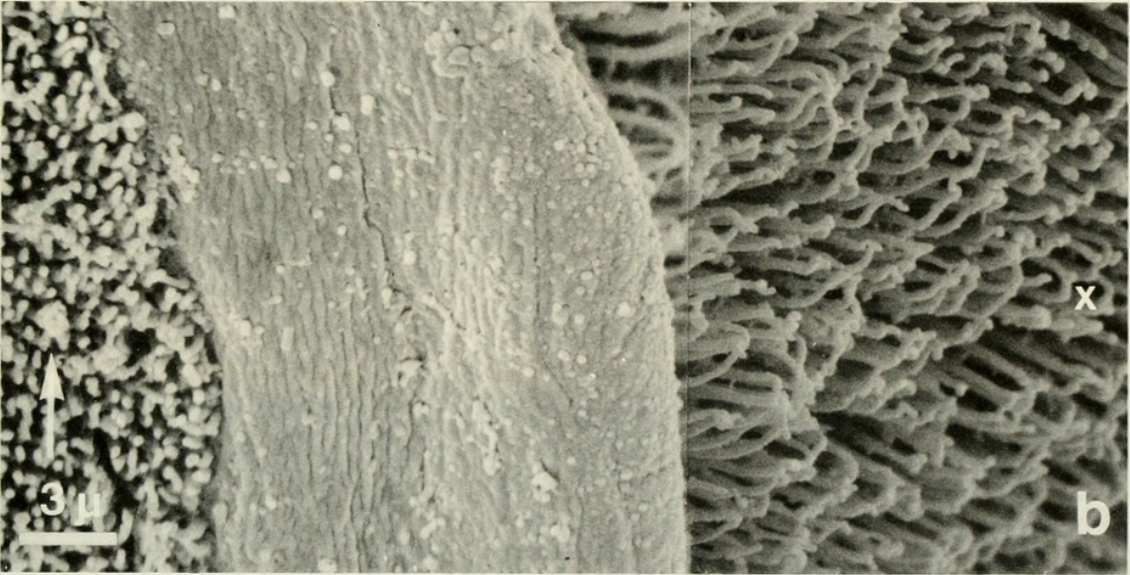
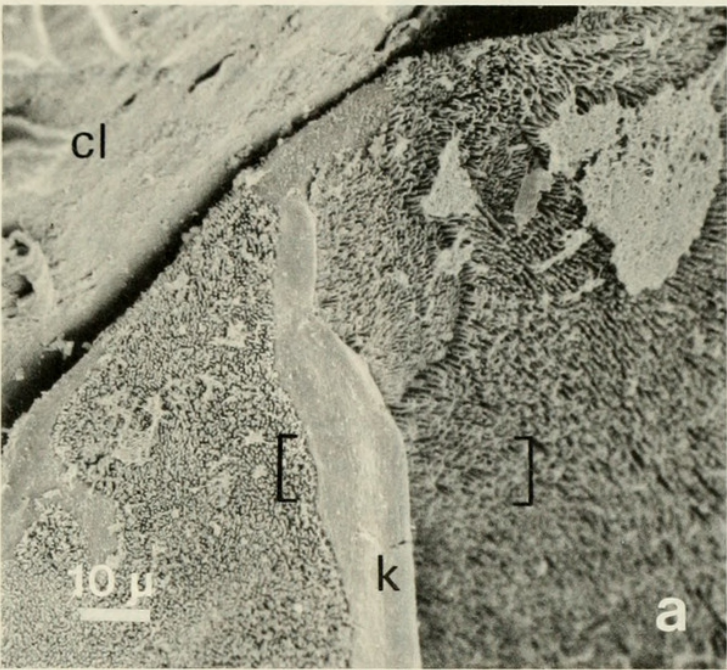
is present on the subdigital scale, while the lateral digital scale is multicarinate. Distally (e.g., scale 3) where the subdigital scale wraps 180° around the phalanx, all three pairs of lateral keels (plus an additional median-lateral keel) are present on the subdigital scale, while the lateral digital scale is small and unicarinate.

The fine structure of the subdigital keels and bosses is comparable to that in *annectens*, adult *onca*, and *chrysolepis*. But there is a major difference in keel placement. In those species, a median keel is present and often the dominant scale feature. In *auratus* the homologous central region of the scale is covered with setae (Fig. 17). The dimensions, density, and orientation of these setae are comparable to those of the lamellar setae (with the possible exception of stalk

height, which may be reduced). The setae grade into prongs and tall spikes adjacent to the lateral keel. Over the lateral region of the scale, including the zones between the keels (e.g., the lateral and far lateral keels), the scale surface is covered with spikes and prongs.

While the combination of features, particularly the grade from setae to spines to keel, is very similar to that on scale 9 in *annectens* (compare Figs. 5 and 17), there are some interesting differences. 1) In *annectens* the grade from setae to spines occurs on the medial side of numerous bosses scattered along the distal margin of the scale. The field of setae is much less coherent than in *auratus*. 2) The spikes and prongs are numerically dominant on the transitional scales in *annectens*, while in *auratus* the setae are much more common.

Figure 17. The morphological grade from spikes to setae adjacent to the keel on scale 1 in *A. auratus*. a) Illustrates an oblique view of the scale, claw "cl" and keel "k" position. The "[]'s" indicate the position of the transect which begins at the left of (b) and continues to the right through (c). The (b) and (c) sections fit together at the point indicated by the "x." Spikes and prongs are mixed through (b). At the left in (c) are prongs grading into the seta/prong intermediate shape and finally setae at the far right. The grade continues to the right of (c), toward the center of the scale, as the spatulae become broader (see Fig. 14b). The difference between morphotypes can be most readily seen by comparing regions which are far apart (e.g., the right of [b] and [c]) and using Fig. 21 as a guide. The gradation of one morphotype into another is clear in regions such as (c) center. The tip shapes in these regions are not readily classified.



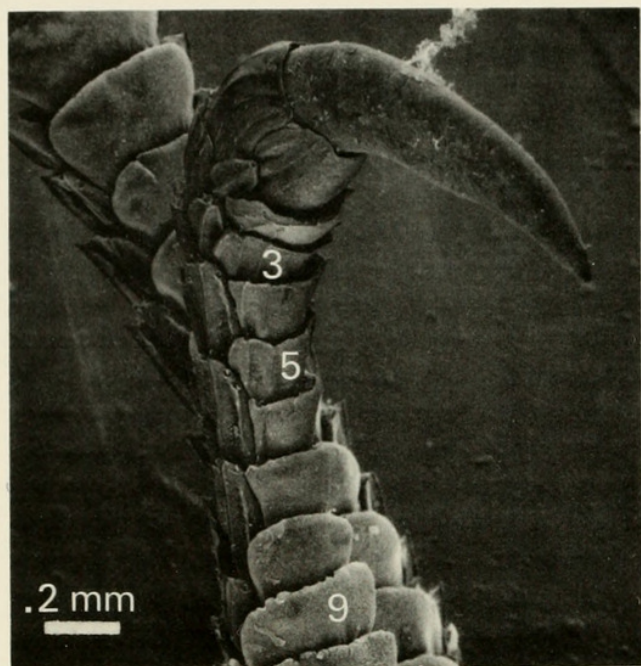


Figure 18. Distal portion of the third toe in *A. auratus*. Note the variation in keel number and placement in scales 1–7.

The lateral scales in *auratus* are multi- or unicarinate, studded with mechanoreceptors, and covered with spines. The spines occur in several sizes (Fig. 19).

DISCUSSION

Summary of the Comparative Data

The comparisons among *annectens*, adult and juvenile *onca*, *chrysolepis*, and *auratus* suggest that there are significant interspecific differences but relatively little novelty in subdigital morphology *per se*. The fine structure of setae, keels, spines, etc. is relatively similar among the species, and, in three of the species, the regional variation in structure approximates the range of interspecific variation. The dominant evolutionary pattern is change in the distribution of keels, setae, and spines relative to the phalanges.

If the species are arranged in the phylogenetic series proposed in the earlier paper (Williams, 1974), the major interspecific differences appear as trends for a) expanded setae distribution in *auratus* relative to *chrysolepis*, and b) the progressive substitution of multicarinate, spinate morphology for lamellae and setae in the *chrysolepis-annectens-onca* series (Fig. 20).

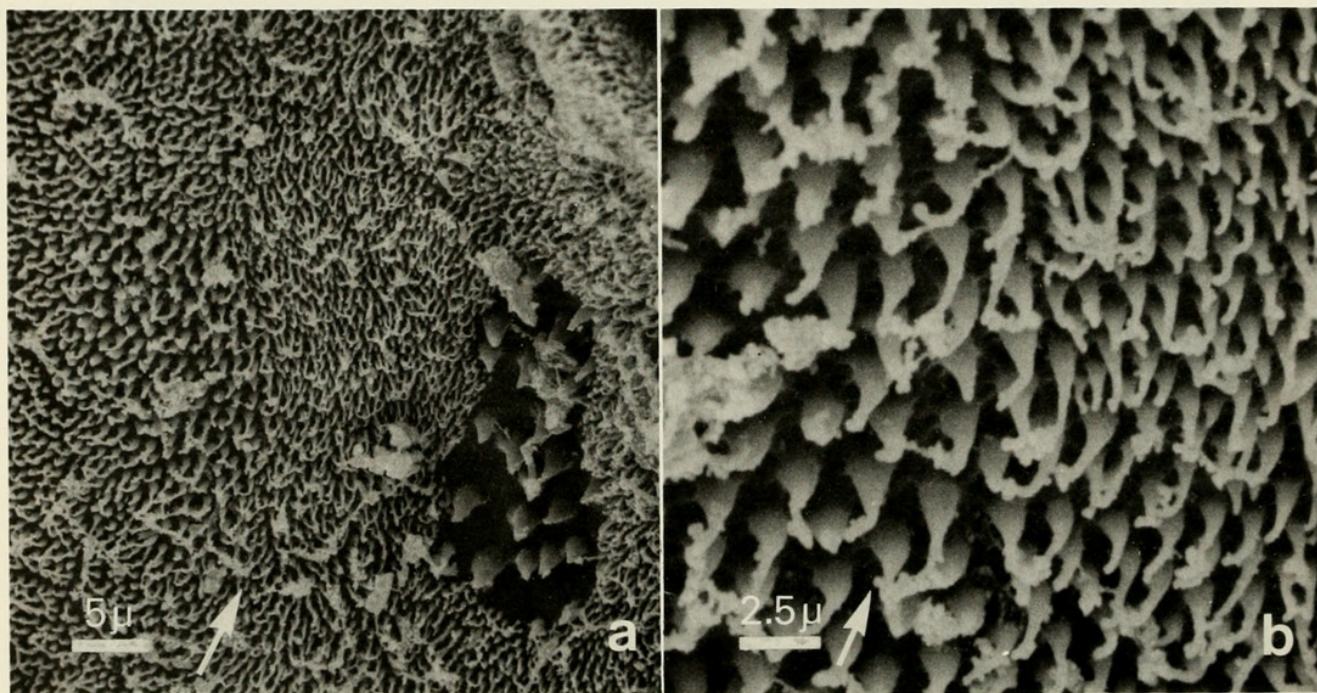


Figure 19. The diversity of spine shapes and sizes in *A. auratus*. The figures are taken on the infradigital scale adjacent to scale 5. a) Shows three spine sizes. b) Is a higher magnification view of the junction between two fields of spines.

A. onca

- phalanx i – narrow, multicarinate, spinate
 ii – narrow, multicarinate, spinate
 iii – narrow, multicarinate, spinate

↑
 SETAE OVER PHALANX ii "LOST"
 REPLACED BY MULTICARINATE FEATURES

A. annectens

- phalanx i – narrow, multicarinate, spinate
 phalanx ii – scale 9: lamellar shape, multicarinate, spines and setae
 scales 10–14: lamellae, keels or bosses, setae
 scale 15: lamellar shape, multicarinate, spines and setae (?)
 phalanx iii – narrow, multicarinate, spinate

↑
 SETAE RESTRICTED TO PHALANX ii
 INCREASED KEELING ON PHALANGES i & iii
 INTRODUCTION OF KEELS ON PHALANX ii

A. auratus

- phalanx i – shapes various, multicarinate, setae and spines
 phalanx ii – lamellae, acarinate, setae
 phalanx iii – narrow, acarinate, setae

↑
 SETAE DISTRIBUTION EXPANDED TO ALL
 SUBDIGITAL SCALES
 INCREASED KEELING ON PHALANX i SCALES

A. chrysolepis

- phalanx i – scales 1–9: narrow, ridges and bare areas on robust margin and spinate
 – scales 10, 11: narrow, acarinate and spinate
 – scale 12: narrow, acarinate and setae
 phalanx ii – lamellae, acarinate, setae
 phalanx iii – narrow, acarinate, setae

Figure 20. Summary of the comparative data.

Annectens differs from *chrysolepis* in three respects: a) the substitution of multicarinate, spinate scales on phalanx iii (scale shape is similar), b) the encroachment of multicarinate, spinate characters on the phalanx ii scales (the "lamellae" are slightly narrower, keels are present on the lateral portion of the lamellae, and the first and last "lamellae" are multicar-

inate with a surface dominated by spines and spikes), and c) the expansion of the multicarinate, spinate morphology to all the phalanx i scales.

Adult *onca* goes beyond *annectens* only in the morphology of the phalanx ii scales. The lamellar scales and setae have been replaced by narrower, multicarinate, spinate scales.

The presence of an almost pad-like scale series in juvenile *onca* along with the existence of a unique *annectens* specimen places particular importance on the similarities and differences among *annectens*, adult *onca*, and juvenile *onca*. The subdigital morphology of juvenile *onca* resembles the adult morphology in several respects: a) in the number and distribution of the scales, b) to some extent in the shape of the scales, c) in the correspondence between ridges in the juvenile and keels in the adult, d) in the absence of lamellae and setae, and e) in the poor differentiation among phalangeal regions. The morphology of the juvenile *onca* differs from that of the adult in a) the absence of definite keels, although scale contouring in some regions is pronounced, and b) the presence of tall spines, spikes, and prongs. In the first of these differences, the juvenile morphology is more conservative in terms of the proposed phylogenetic series than that of *annectens* or even *chrysolepis*, which have keeled subdigital scales. The absence of well-developed keels in juveniles may not be unique to *onca*. *A. cristatellus* adults have marked keels and bare areas in the phalanx i region while hatchling-sized (28.7 mm SVL) *cristatellus* have spine-covered ridges like those of *onca* juveniles and a few bare areas which are not associated with the ridges. Most of the contours on the lateral scales are also covered with spines as in juvenile *onca*. In the second of the differences relative to adult *onca*, the juvenile morphology is less conservative than that of *annectens* which has the complete spine to seta series and definite lamellae (see below and Fig. 21).

There is little resemblance between juvenile *onca* and *annectens*. In both forms the spine-seta series is more complete than in adult *onca*, and there is some regional differentiation in the subdigital scale series. But neither of these parallels translates into a convincing similarity between juvenile *onca* and *annec-*

tens. For example, the differentiated region in juvenile *onca* is not synonymous with any of the regional series in *annectens*.

It is highly implausible that *annectens* is an "unmetamorphosed" *onca* hatchling. Juvenile *onca* are more similar to the adult *onca* than they are to *annectens*, *chrysolepis*, *auratus*, or generalized "Norops" species (e.g., *A. tropidonotus* and *A. notopholis*).

Clearly juvenile *onca* displays still another morphology intermediate between more generalized anoles, such as *chrysolepis*, and adult *onca*. Indeed, the implications of *annectens* and juvenile *onca* for a "retrograde" sequence are contradictory. *A. annectens* morphology implies a sequence in which robust keels invade and progressively replace setae and lamellae. In contrast, juvenile *onca* morphology would appear to imply that a substantial "retrograde" shift in the spine to setae series (see below) and de-differentiation of the pad occur prior to the appearance of definite keels.

The juvenile *onca* morphology is an ontogenetic adaptation. It may or may not also represent a phylogenetically intermediate morphology in the "retrograde" sequence. We discuss these alternatives in light of additional functional and comparative considerations in the final paragraphs of the discussion.

The Morphological Series

The extraordinary diversity in subdigital scale morphology may be related to the wealth of structural intermediates and to the poor correlation among the characters. These factors result in a myriad of possible character combinations for a given scale. Setae occur not only on lamellae but also on narrow multicarinate scales. Keels occur on lamellae as well as on scales with a robust distal margin. Some "generalized subdigital scales" bear setae while others which are not otherwise different do not. This particular group of species may exhibit more

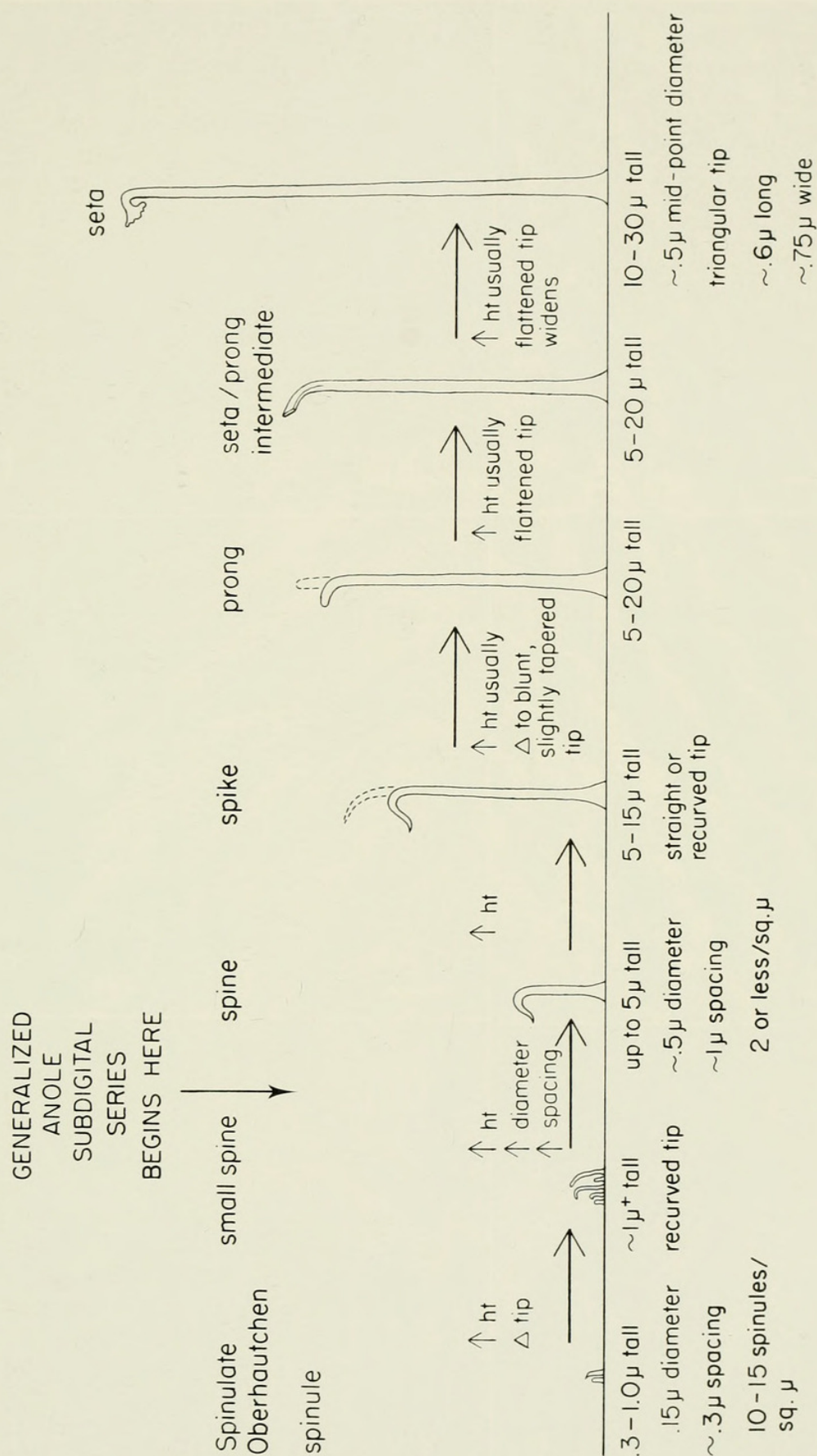
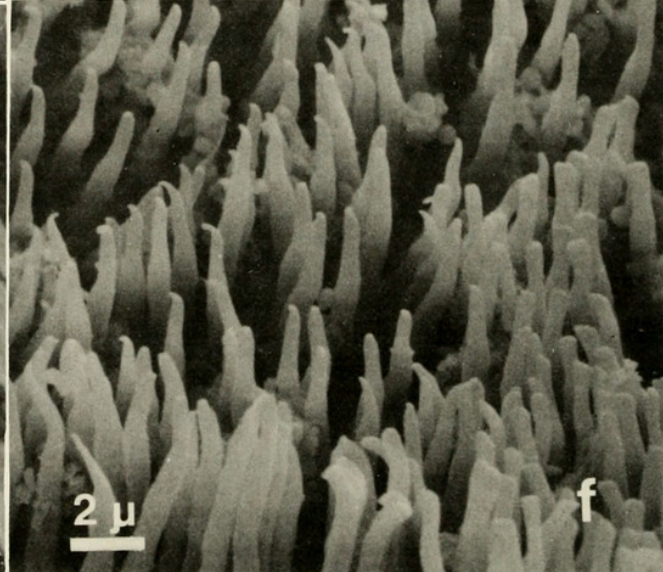
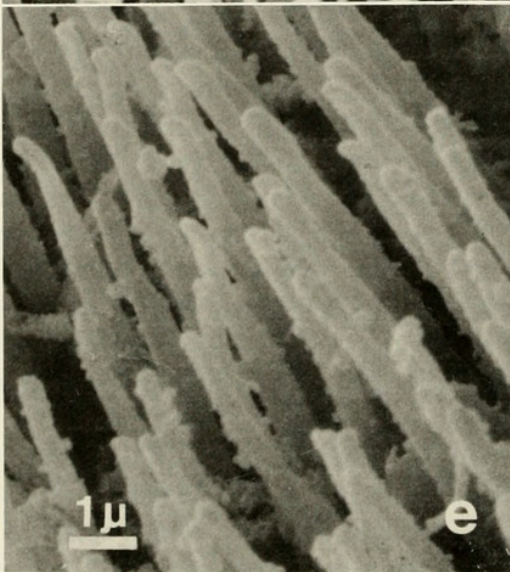
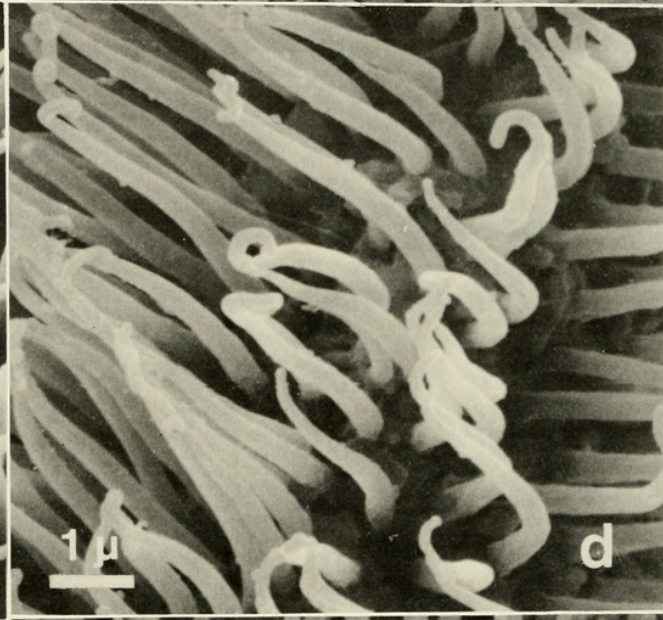
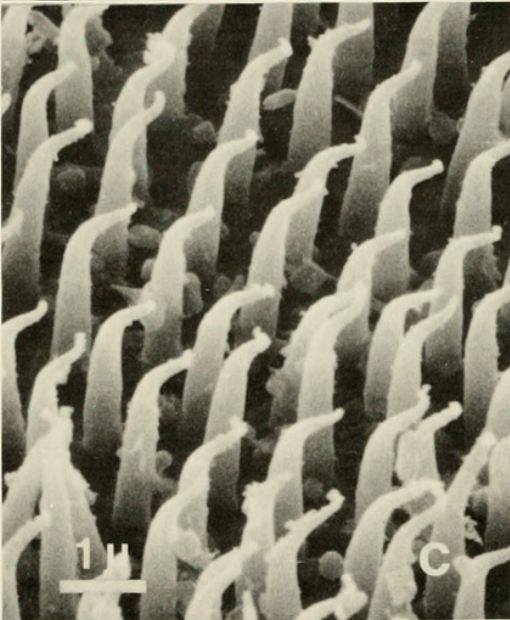
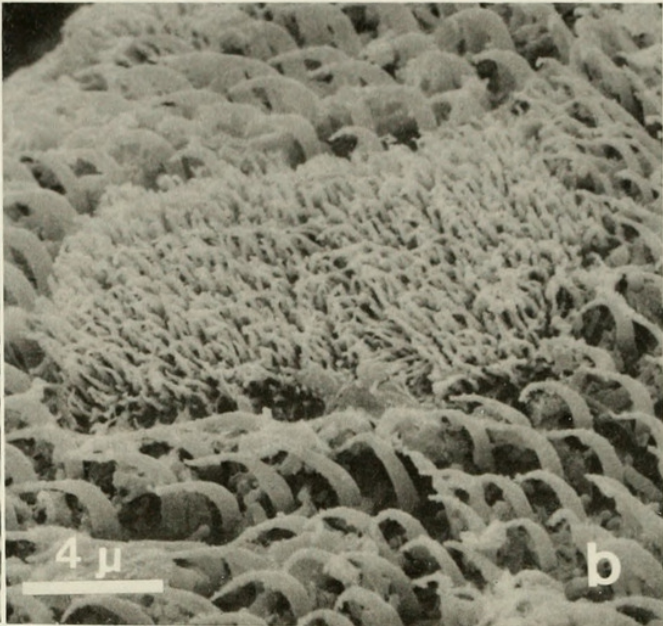
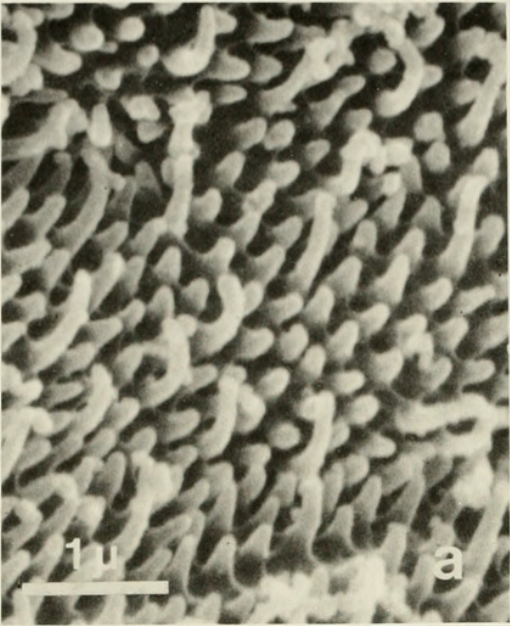


Figure 21. The morphological series of spine to seta.



“creativity” in character combinations than most anoles, but their morphology is a cogent argument for the existence of more than one morphological series or character suite in the evolution of scale morphology.

The diversity in scale morphology appears to be interpretable in terms of three semi-independent morphological series, each one operating within a different dimensional range. These are: gross scale shape, contouring of the scale surface by keels, hillocks, etc., and fine structural specialization of the Oberhautchen (i.e., the spine to seta series; see Figs. 21, 22, 23).

Gross Scale Shape

Gross scale shape is determined by the length/width dimensions of the scale, the character of the borders, the cross-sectional shape, and the junctions with adjacent scales. In the present context our concern is the differentiation between lamellar and non-lamellar scales in anoles (A. Russell informs us that lamellar morphology in geckos is different). Lamellae are highly specialized scales, but they can be defined rather simply by the presence of a frayed, thin distal border and a length/width ratio < 1 . Both features are required to characterize lamellae. Wide scales with a robust margin occur fairly frequently, particularly adjacent to the claw and interphalangeal joints (e.g., *auratus* scale 3), but with rare exceptions (e.g., the most proximal lamella in *pulchellus*) all scales with a free, thin distal border are wider than they are long.

Scale Contouring

Variation in the surface contouring of scales can be arranged in a series based on increasing elevation and extent of the raised contours. The series begins with a relatively flat surface and extends to hillocks, which involve a single epidermal cell (e.g., Fig. 7), to ridges and bosses, and finally to keels. The hillock morphology apparently occurs only over the proximal and central portion of the scale. It is not clear that the hillocks are homologous with the rest of the series. Ridges, which extend into the central portion of the scale, and bosses, which occur adjacent to the distal margin, appear to be small keels. While both these features usually have a bare, smooth surface, the ridges, at least, may be covered with spines as in juvenile *onca*.

The Fine Structural Series: Spine to Seta

The *Anolis* Oberhautchen has spinules (Fig. 22; Ruibal and Ernst, 1965; Ruibal, 1968; Maderson, 1970). Such spinules are the beginning term in a morphological series which can be described as follows (Fig. 21): a) the spinulate Oberhautchen (Fig. 22a) consists of spinules and knobs which are $0.3\text{--}1.0\ \mu$ tall, $0.15\ \mu$ in diameter and about $0.3\ \mu$ apart (or 10–15 spinules/sq μ), b) the small spine (Fig. 22b center), which differs from the spinules by greater stalk height, a curved, more tapered tip, and reduced density (only some spinules are longer; see discussion following), c) the subdigital spine (Fig. 22b, c), which is marked by the absence of an understory of spinules, increased

Figure 22. a) The spinulate Oberhautchen from a dorsal digital scale in *A. evermanni*. b) Is taken on a lateral digital scale of *A. eugenegrahami* at one-quarter the magnification of (a). The central patch of small spines with a spinule understory has the same diameter and overall density as the spinulate Oberhautchen. The adjacent larger spines illustrate the diameter and spacing features which are typical of the subdigital spine/seta series. c) Illustrates fairly tall spines in *A. pulchellus*. d) Shows the even taller spikes in *A. evermanni*. Prongs are shown in the lower right of (e), and a few seta-prong intermediates are visible in the upper center of (e). The specimen is *Anolis* sp. n. near *eulaemus*. f) Shows a heterogeneous field of spikes, prongs, and seta-prong intermediates in *A. cuvieri*.

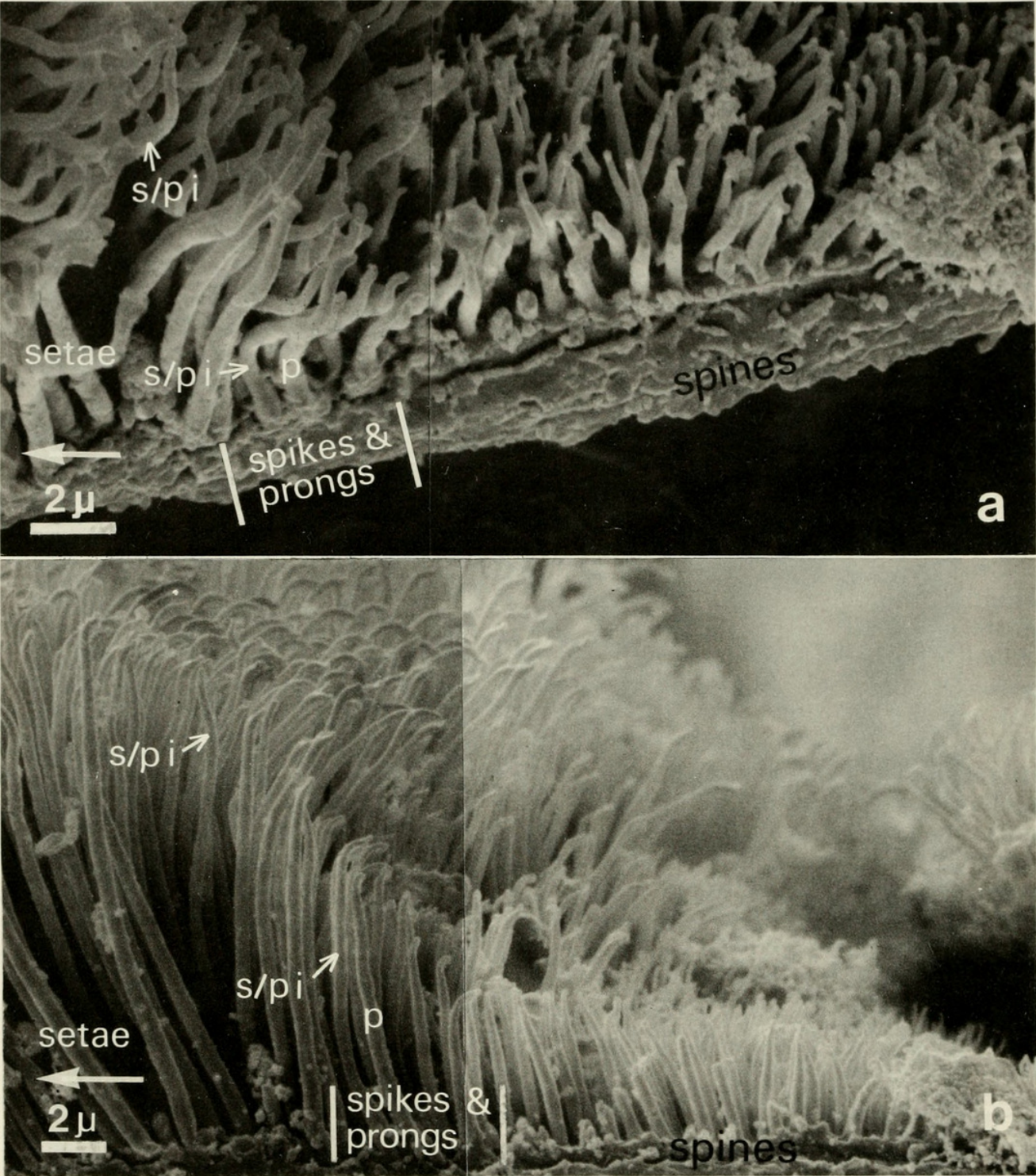


Figure 23. The subdigital spine to seta morphological series in *A. evermanni*. The figures are taken in the proximal portion of lamellae 8. The toe has been sectioned proximodistally. a) Is a ventral view at a slightly larger magnification than the lateral view (b). In this particular specimen the hook tips are not strongly recurved or highly tapered (cf. Fig. 20) so that the spike morphology is not well shown. The seta-prong intermediate "s/pi" shape is shown along the section margin and lateral to the margin (see also Figs. 13 and 20). A prong, "p," is also indicated. Setae significantly increase in height distal to the figure margin.

diameter of the stalk (about $0.5\ \mu$ at the midpoint or base, if the stalk is very short), decreased density (2 or less/ $\text{sq}\ \mu$; spacing about $1\ \mu$), and often increased height (up to $5\ \mu$), d) the spike (Fig. 22d), which differs from the spine by increased stalk height, e) the prong (Fig. 22e, f), which has a blunt or curved, but almost untapered tip, f) the seta-prong intermediate (Figs. 22e, f, 13b), in which the prong tip is dorso-ventrally compressed and stalk height is often greater, and g) the seta (e.g., Figs. 4, 11, 16, etc.), in which the flattened tip is expanded into a spatulate, triangular shape (the spatula is about $0.75\ \mu$ wide by $0.6\ \mu$ long). Several of the morphologies in this series may occur within the borders of one epidermal cell, and generalized anoles usually have all members of the series. Subdigital scales usually exhibit only the terminal (right) portion of the series (c–g). The structural series between spines (c) and setae (g) typically occurs in the proximal portion of lamellae (Ruibal and Ernst, 1965; Fig. 23). The spinule/spine portion of the series (a–c) occurs on the lateral digital and body scales, although spines with the dimensions of subdigital spines are rare except on the lateral digital and plantar/palmar scales.

The spinule (a) to spine (c) series appears to model the transition from the spinulate Oberhautchen to the subdigital series. It involves alteration in the height and diameter of the spinules and a major change in their spacing or density. The spine (c) to seta (g) series is based on variation in stalk height and tip shape. Stalk diameter and spacing or density are relatively constant between the spine or spike and the setae. Russell (1976) proposed a morphological series for the origin of gecko setae based on interspecific variation in *Cyrtodactylus* which appears to show spine-spike-seta components. Dimensions apart from height are not indicated, so it is difficult to compare the two series in detail.

The aspinulate, bare areas are typical of major scale contours, but also occur in regions with no relief (Figs. 8, 9). The relationship of this Oberhautchen specialization to the spinulate series is unclear. In fact, the surface morphology of these bare areas is unlike any of the three generalized Oberhautchen types (spinulate, lamellate, or dentate) described by Ruibal (1968) and Maderson (1970). A number of observations suggest that the morphology is not an artefact of the shedding cycle nor produced from a spinulate Oberhautchen by wear. a) The bare areas are often slightly raised or elevated relative to the plane of the adjacent spinate areas—they are not worn down. b) The immediately adjacent spines do not show excessive wear. c) The bare surface is actually striated as if by use, and these striations do not occur in specimens where the Oberhautchen has separated post-mortem. d) Limited comparisons (for West Indian species) suggest that there is consistency in the placement of these areas between individuals. The bare, smooth Oberhautchen morphology characterizes all of the subdigital scales in the primitive iguanid, *Morunasaurus groi* (Peterson and Williams, unpublished data). It is not clear whether this surface morphology is a specialization of and within the spinulate Oberhautchen series or whether it represents an even simpler and distinct Oberhautchen type. The problem is compounded by the difference and implied increase in bare areas between juvenile and adult specimens of *cristatellus* and *onca* (see Maderson and Williams, 1978, and in preparation, for discussion of *onca*).

Functional and Ecological Implications

Without actual behavioral and experimental data, discussion of the functional significance of variation within and among the three morphological series has to be limited. But we can construct and

evaluate a number of hypotheses on the basis of comparative data.

Possible Functional Significance of Lamellae

THE RELATIONSHIP BETWEEN LAMELLAE AND SETAE

The shape of a lamella appears to reflect its function in bearing adhesive hairs or setae. Given that the density of setae is constant over the exposed portion of the scale surface, the number of setae is determined by the total surface area (more extensive data regarding this are given in Peterson and Williams, in preparation). Lateral expansion of the scales which bear setae produces the characteristic lamellar shape and, at least in the West Indian ecomorphs we have examined, is a major vehicle for adjusting the number of adhesive hairs to the body weight (loading) (Peterson and Williams, in preparation). There are, however, two additional and alternative means to vary seta number: a) change in the length of the phalanges which have setae-bearing scales (varying the length of the "pad" independently of lamellar number or pad width), and b) restricting or expanding the distribution of setae relative to the phalanges. It is important to note that packing more or less lamellae into a pad of a given length and width does not significantly alter the number of setae.

The relatively narrow pad of many anoles—*chrysolepis*, *auratus*, and *annectens* among them—would itself provide for fewer setae in proportion to the animal's body weight than in the West Indian ecomorphs unless the alternative adjustments are made. In *auratus*, where the pad is particularly narrow, the phalanges are long in relation to snout-vent length, and setae occur on all the subdigital scales (i.e., two compensating adjustments are made). Crude estimates of seta number (based on seta density and seta-bearing area) indicate that these adjust-

ments more than compensate for the reduction in lamellar width. *A. auratus* has at least as many setae as an *A. evermanni* (a Puerto Rican trunk-crown ecomorph with a wide pad and many lamellae) of the same body size. The situation is rather different for *annectens*. While it is very possible that the ratio of setae/body weight might be altered without comprising essential function, the "safety factor" reflected in generalized anole ratios would have to be very great for the reduction in the *annectens* ratio not to have behavioral consequence. The restriction in pad width coupled with the short second phalanx (1.4 mm compared to 2.1 mm in a comparably sized specimen of *chrysolepis*) and the restriction in seta distribution to the second phalanx could mean that the setae would have to "cooperate" with other devices to support the animal.

Apart from the relationship with body size, the functional advantage of narrow lamellae is unclear. As suggested in the earlier paper, narrow lamellae may constitute a stage in pad reduction *per se*, but clearly they do not always imply a reduction in the number of setae (cf. again *auratus*) nor presumably decreased competence in adhesion.

Lamellar scale morphology probably also reflects adaptation for applying setae. Lamellar scales, particularly the thin distal margins, are unusually flexible and compliant. Flexibility of the scale along with the length of the seta stalk permit the spatulae to "find" the environmental surface and conform to a curved or otherwise grossly irregular substrate (Hecht, 1952, discusses lamellar shape in terms of pad flexibility; see also Hiller, 1968, and the discussion of seta function following). For a pad of a given size, an increase in lamellar number might permit the seta-bearing area to better conform to surfaces with a smaller radius of curvature. This aspect of lamellar function may partially explain the interspecific increase in lamellar number with increas-

ing perch elevation (and decreasing perch diameter) (Collette, 1955; Williams, 1974).

The lamellae of geckos (Dellit, 1934; Russell, 1975, 1976, 1979) receive the insertion of numerous tendons originating from the metatarsal-phalangeal joint capsules and plantar tendon system. Ultimately the tendons operate in series with the digital and ankle flexors. The specialized tendon arrangement coupled with the flexibility of lamellae have suggested to Hiller (1968) and Russell (1975, 1976) that lamellae have a dynamic role in applying setae. Russell (1975) argues that the subdivision of the pad into scanorial plates (i.e., lamellae) increases the effectiveness of the setae because each lamella can be individually controlled by the tendons. Once the setae tips "find" the surface, flexion of the lamellae via the tendons places the setae under tension and transmits force between the adherent epidermis and the skeleton (Russell, 1975). Hiller's (1968) hypothesis for seta function in geckos involves an initial application of the spatulae via an active flexion of the toes and lamellae. (Russell [1975] and Hiller [1968] also implicate inflation of digital venous sinuses, which are present in some geckos, in the adhesion process.)

Anole lamellae have a similar set of tendons (Peterson and Williams, unpublished data; Russell, personal communication). Given the morphology of the setae in anoles, tension exerted on the lamellae, which is produced as the foot approaches contact with the substrate and the digital flexor musculature fires to meet weight-bearing conditions, would wipe the distal edges or flattened expanse of the setae into the surface and establish the "grip" (see discussion of seta function). Once the "grip" is established, tensile stress can be transmitted from the setae/epidermis to the skeleton via the lamellar tendons as in geckos. If these hypotheses are correct, the internal morphology and flexibility of

lamellae are significant adaptations for applying setae and transmitting tensile forces.

The function of lamellar tendons in transmitting tensile forces may also contribute to the correlation between lamellar number and body size (Hecht, 1952; Collette, 1955; Williams, 1974). Scaling for increased tensile loads could occur by an increase in tendon diameter or by an increase in the number of tendons (by increasing the number of lamellae). Tendon robustness does vary, but, at least in the West Indian anoles, the dominant pattern is to multiply the number of tendons (and therefore the number of lamellae). This pattern maintains a relatively size-independent lamellar area/tendon relationship while scaling total tendon cross-sectional area to total seta stalk cross-sectional area. A size-correlated increase in tendon diameter by itself would scale the cross-sectional areas of the load-bearing tissues, but drastically increase the lamellar area served by each tendon. Perhaps the role of lamellae and lamellar tendons in applying setae has required criteria of scaling similarity which include lamellar area.

An interesting caveat to the argument that setae and lamellae are functionally associated is the existence of setae on non-lamellar scales (or the converse—lamellae which do not bear setae). This occurs not only in *chrysolepis* and *auratus*, but in several West Indian and Central/South American species (Peterson and Williams, in preparation). The non-lamellar setae are slightly different from typical lamellar setae. In *auratus* the stalk is shorter. In *chrysolepis* the stalk is shorter and less tapered, and the spatula is somewhat narrower. But, in each case the range of variation in lamellar setae includes these morphologies. Unless very similar seta morphology can function in a totally different fashion on lamellar and non-lamellar scales, the flexibility, compliant margin, and internal tendons of lamellae

are simply not necessary for seta function.

There are several possible, complementary explanations for the variation in distribution of setae compared to lamellae. a) Pad morphology (i.e., lamellae) might be less effective in positions adjacent to the claw or sole of the foot. In some anoles the pads extend to the sole, but lamellar morphology does not seem to occur in the phalanx i region of any anole (cf. geckos; Russell, 1976, 1979). b) If there is a necessary relationship between external lamellar morphology and internal digital tendons, the distribution of lamellae might be limited to certain phalanges by constraints on the distribution of the tendons. There are a number of potential mechanical constraints on extending tendons into the phalanx i region. For example, long tendons which are not controlled by a retinaculum or placed very deeply in the toe could act not only on their lamella of insertion, but "bowstring" or alter the more proximal pad contour and disengage setae. The arrangement in geckos (Russell, 1975, 1976) appears to avoid this problem with a deeper placement of the tendons and a more conservative (distal) branching of the tendons serving individual lamellae. But it is also interesting that the terminal and basal pads in several gecko genera are associated with separate internal tendon systems (Russell, 1976). Any of these "potential constraints" beg the question of an altered tendon origin and arrangement in anoles, but nonetheless, mechanical constraints may be operating to limit the distribution of lamellae to certain phalanges. c) Lamellar morphology may increase the effectiveness of setae by engaging more of them, but the advantage of lamellar setae may be significant only on certain environmental surfaces. Both the number of lamellae (Collette, 1955; Williams, 1974) and seta distribution relative to the lamellae (Peterson and Williams, in preparation) appear to be related to the environmental surfaces used by the

species. There is an enormous diversity in the architecture of vegetational surfaces ranging from the waxy rubble, often trichome-studded surface of deciduous leaves to the grooved and "rough" surface of grass blades, to the very gross surface relief of cork and older bark (Martin and Juniper, 1970). While the claws probably contribute most of the grip on rough bark, setae appear to be responsible for purchase on very dissimilar cuticular surfaces, e.g., on grass blades and herbaceous leaves. The grass anole, *A. auratus*, has at least as many setae for its size, fewer lamellae, and a high proportion of non-lamellar setae compared to ecomorphs which use leaf, stem, and twig vegetational surfaces. The functional association between lamellae and setae presumably is reduced in *auratus*, suggesting that lamellae may not be as advantageous on grass as on most herbaceous leaves. Considerably more data on plant cuticles, setae, and setae/lamellae distribution are required to approach this problem, but the functional advantage and significance of lamellar morphology may vary with the properties and fine structure of vegetational surfaces.

IMPLICATIONS FOR THE "RETROGRADE" SERIES

This general discussion suggests a framework for evaluating the morphological trends in the *auratus* and *annectens-onca* lineages. In both lineages the number of lamellae and pad area are reduced relative to *chrysolepis*, and the "Norops" condition appears. These morphological parallels are probably not indicative of precise parallels in behavioral and ecological specialization.

The functional significance of the "Norops" condition is unclear at this point. The distribution of the character within *Anolis* and its association with trends in fine structure are not readily interpretable. In the *annectens-onca* line the "Norops" condition is associated

with the invasion of multicarinate morphology into the phalanx ii or pad region, while in *auratus* it is associated with the expansion of pad or adhesive function into the phalanx i region. In both cases morphological differentiation of the phalanx i and ii regions is decreasing, but the effect appears to be functional divergence. The "Norops" condition, we emphasize again, is not invariably a "retrograde" change and an indication of decline in adhesive function.

While the number of lamellae and pad area in *auratus* are reduced relative to *chrysolepis*, they are comparable to those of West Indian grass anoles (e.g., *pulchellus*, where, however, the fine structure of the pad is different). Even if there were no data on the behavior and habitat preferences of *auratus* (Kiester *et al.*, 1975), there would be little basis to question the functional competence of the pad. The trends in *auratus* appear to represent body size and habitat specialization of the "adhesive" structures rather than selection for an alternative "non-adhesive" function.

The situation is different in *annectens*. If, as we have argued above, pad area is crudely indicative of the number of setae available to support the animal (in this species there are few non-lamellar setae) and lamellae variously function in applying setae, and if interspecific comparisons can be used to infer what the absolute values mean in terms of limits on adhesive behavior and vegetational habitat, then there are rather serious questions whether the *annectens* pad is functionally competent to support the animal. For its size *annectens* has fewer lamellae and less seta area than 1) grass anoles like *auratus* and *pulchellus*, 2) *chrysolepis*, which uses a wide range of vegetational surfaces close to and including the forest floor, and 3) the West Indian trunk-ground ecomorphs, such as *cratatellus* and *cybotes*, which often sleep on leaves, but climb and forage from the lower trunk (see also Kiester *et al.*, 1975). Among

these more terrestrial, but still generalized anoles, there are no parallels for *annectens*. The morphology suggests that selection for "adhesion" based on setae is diminished in *annectens* and that the range of vegetation and behavioral repertoire of the animal are altered relative to generalized anoles. *Annectens* probably is much more dependent on its claws, and surfaces which will not accept the claw, like grass blades and leaves, may not be as readily used.

Possible Functional Significance of Scale Contouring

CONTOURS AS "TRACTION" DEVICES

Scale contours which are relatively rigid and permanent are probably "traction" devices which work with moderately large (on the order of 0.5 mm–1 mm) surface irregularities (e.g., on bark) or create such irregularities in loose sand or dirt. Keels, bosses, ridges, and even the distal margins of carinate scales will interdigitate with the gross surface irregularities of bark or terrestrial substrates, and the relative rigidity of multicarinate scales permits these contacts to transmit propulsive and reaction forces. Given irregularities of the proper size or loose sand or dirt, carinate scales will increase the static frictional coefficient of the contact between the foot and environment (Gans, 1974) so that more force can be transmitted across the contact without slippage.

The keel can transmit forces applied a) parallel to the toe if the distal end of the keel is engaged by an environmental contour, and/or b) perpendicular to the long axis of the toe if the crest of the keel is braced against an environmental contour. Both probably occur, and the ostensibly parallel keels on adjacent digits are able to "find" and exploit environmental irregularities with a variety of spatial orientations because the hind limb digits (1–4) are placed at angles of 30°–110° to the direction of motion (see also Robinson, 1975). The long third and fourth toes are

nearly perpendicular to the direction of motion (there is considerably greater diversity in arboreal postural positions). The interdigitating contacts created by the keels on these toes can very effectively transmit propulsive forces applied perpendicular and parallel to the direction of motion. The proximo-distal orientation of the keels may also be advantageous in providing traction as these toes rotate about their long axis during the propulsive phase (Laerm, 1973 describes this rotation for *Basiliscus*, but it occurs to some degree in many lizards). Keels are rotated into contact with the substrate during limb retraction, and like caterpillar or tank tread, could "find" or create contacts which maintain a high coefficient of static friction. In many terrestrial cursors (e.g., *Dipsosaurus*) and some forms that combine scansorial and terrestrial habits (e.g., *Enyalioides*) keel shape, placement, and relief often display a preaxial/postaxial asymmetry that is probably related to the long-axis rotation of the digits during the propulsive phase.

THE EVOLUTION OF MULTICARINATE SCALES IN *ANOLIS*

An evolutionary trend to substitute contoured, multicarinate scales for uncontoured scales may represent adaptation for using environmental surfaces which would have low coefficients of static friction to a smooth scale. Low coefficients of static friction might arise for a smooth scale if the environmental surface is formed a) by particles with low cohesion (e.g., sand) or b) by rigid irregularities which offer too little contact area for the scale. The latter situation might occur on tree bark or branches. Whether it does or not depends on the relationship between the spacing of the surface irregularities and the dimensions of the digits. Keels and other contour features would appear to be advantageous for locomotion on bark surfaces where the distance between irregularities is somewhat less than the width of the digit or on sand.

Keels may also represent adaptation for behaviors which rely on the rapid application of large forces, e.g., running. From these hypotheses one would predict that keels and related scale contours would characterize climbing, trunk-dwelling, and terrestrial species, but not those specializing in twig or smooth leaf surfaces. Among the West Indian anole ecomorphs, subdigital keels occur on some scales in the phalanx i region in the trunk-ground ecomorphs (i.e., *A. cristatellus*, *A. lineatopus*, and *A. cybotes*); in these species the other phalanx i scales have striated, bare areas along the robust curved margins of the scales. The keels and bare areas have somewhat more relief, but are generally similar to those in *chrysolepis* (Fig. 10). Both morphologies are absent in twig anoles, e.g., *A. valencienni* and *A. occultus*. The anole ecomorphs which use the trunk and large diameter branches, e.g., *A. distichus* and *A. stratulus*, lack subdigital keels, but have prominent bare areas on the phalanx i scales similar to those in *chrysolepis* and *cristatellus*. These contoured margins may be able to function like keels in increasing traction relative to forces applied parallel to the toe (e.g., digital flexion in a leap), but scale contouring appears to be less prominent in the more strictly trunk-dwelling species than in the trunk-ground ecomorphs. Keels are not present in the West Indian grass anole species we have examined (*A. pulchellus*, *A. poncensis*, *A. olssoni*, and *A. semilineatus*) although "bare areas" occur on some of the phalanx i scales.

Subdigital keels or marked scale contouring into ridges appear in several Central and South American anole species (e.g., *A. notopholis*, *A. tropidonotus*, *A. nebuloides*, *A. nebulosus*, *A. quercorum*, *A. liogaster*, and *A. dollfusianus*) which combine terrestrial substrates with perches close to the ground. The keels are confined to the phalanx i region and are comparable to those in *cristatellus* in

relief (the position of the keels on the scale and the distribution of multicarinate scales within the phalanx i area are quite variable).

The available intergeneric comparisons largely corroborate the pattern in *Anolis*. Multicarinate subdigital scales occur in many (e.g., *Agama agama*, *A. stellio*, *Dipsosaurus*, *Phrynosoma*, *Crotaphytus*, *Morunasaurus*, *Sceloporus*, *Enyalioides*, *Tropidurus*, and *Iguana*), but not all (e.g., *Diplolaemus* and *Lacerta viridis*), the terrestrial and terrestrial/scansorial lizards. The subdigital scales are acarinate in *Chamaeleo* and *Phenacosaurus*, which are slow moving and characteristically use small diameter, smoother surfaces similar to those used by *A. valencienni*. However, *Polychrus* shares these behaviors and habitat preferences and has subdigital scales which are crowded with low bosses and keels (Peterson and Williams, unpublished).

Although there are exceptions and the character of bark and terrestrial substrates is more complex than we can consider, the distribution of multicarinate scales is generally consistent with their role as a "traction" device and with adaptation for locomotion on surfaces which have a low coefficient of friction because of gross surface irregularity or the low cohesion of surface particles. Within *Anolis*, keels occur in species which use terrestrial substrates, but not in the more strictly scansorial or grass-dwelling forms (*A. auratus* appears to be an exception in possessing keels). The distribution of keels within the genus suggests that the trunk-ground structural habitat (broadly defined to include forms such as *chrysolepis*) might be the starting point for the elaboration of multicarinate features in the *annectens-onca* lineage.

It is interesting that trunk-ground anoles have limited keels and an adhesive pad while most other scansorial/terrestrial iguanids have multicarinate subdigital scales. The smaller body size of trunk-ground anoles permits them to use a broader range of vegetational surfaces

than most of these iguanids. Leaves, twigs, and other grossly smooth vegetational surfaces are often used as sleeping sites or rarely as auxiliary perches. This greater repertoire of surfaces may make it advantageous to maintain the pad and introduce keels in only a limited area adjacent to the claw. The trunk-ground structural niche might begin to approximate the iguanid scansorial/terrestrial habitat with an increase in body size or in extreme xeric areas where a) the vegetation may be deciduous and the leaves are often too narrow and small to support the animals, and b) the presence of loose, sandy soil might increase selection for scale contours as "traction" devices. Body size is generally conservative among trunk-ground forms, but the West Indian ecomorphs offer two cases to examine whether scale contour features are exaggerated and the pad characters reduced when trunk-ground forms radiate into arid regions. These are: the radiation of Puerto Rican *cristatellus* stock into scrub forest as *A. cooki* and the radiation of Hispaniolan *cybotes* stock into thorn scrub forest as *A. whitemani* (Williams, 1963).

Comparison of *A. cristatellus* and *A. cooki* indicates no marked difference in the contour features of the phalanx i region and no contour features present in the phalanx ii and iii regions, although lamellar number and pad width appear to be reduced in *cooki*. Comparison of *A. cybotes* and *A. whitemani* reveals that some *A. whitemani* individuals have three or more robust keels on all the phalanx i scales while *cybotes* has laterally compressed scales with robust distal margins distally and two or three keeled scales proximally. *A. whitemani* shows no expansion of keels into the phalanx ii or iii regions, and there is no indication of reduction in lamellar number or pad size.

The multicarinate scales in *A. whitemani* combine the features of *annectens* and *onca*. Scale shape resembles the *onca* phalanx i scales rather than the long

cylindrical scales of *annectens* (Fig. 1b). The relief of the keels is less than that in *onca* and comparable to that of most *annectens* keels, but the lateral digital scales have many sharp, protruding keels as in *onca*. Hillock contouring between the keels and toward the base of the scale is comparable to that in *annectens*. The positions and relative development of the keels show no consistent resemblance to *annectens* or *onca*. The more proximal phalanx i scales have a dominant median keel and a pair of lateral keels. This is similar to the *annectens* phalanx iii pattern or *onca* scales at the interphalangeal joints. Midway between the claw and the pad the pair of lateral keels are dominant, and a second pair of lateral keels may be added. This is similar to *onca* scales in the mid-phalangeal regions. The most distal scales are similar in all three species.

A. whitemani occurs over a range of arid habitats. It can occur in the same general localities as *A. cybotes*. In these areas *cybotes* is found in small oases of trees adjacent to springs, while *A. whitemani* occurs in surrounding open dry scrub and out into sparsely vegetated areas (Williams, 1963). Extreme *whitemani* habitat is similar to that of *onca*. Unfortunately, our series of *whitemani* specimens is too small to examine the individual variation in subdigital keels in terms of habitat variation, but the appearance of robust keels in at least some specimens of a species which has radiated into sandy, extreme xeric habitat comparable to that of *onca* is striking.

The results of the two comparisons are inconsistent: each case is unique, and there are too few behavioral and ecological data to interpret their differences. But each appears to exhibit nascent trends which parallel the *annectens-onca* lineage: a) reduction in lamellar number and pad width in *cooki*, and b) an increase in the number and robustness of the keels in some specimens of *whitemani*.

It is, however, the coincidence of these trends which characterizes the *annectens-onca* lineage, and, to our knowledge, the *annectens-onca* lineage is unique among anoles in the combination of trends for pad reduction and marked expansion of multicarinate scales. If we view this combination of trends as an extreme in the spectrum of adaptation, rather than as a truly unique evolutionary pattern, the comparisons among anoles suggest the following interpretation of the evolutionary sequence in keel elaboration. a) A few low subdigital keels occur in the phalanx i region of a substantial number of anole species which use terrestrial substrates. These less "arboreal" or trunk-ground species also evidence narrower pads and/or reduction in lamellar number compared to trunk and canopy species of the same body size. Grass anoles may parallel the trend in pad reduction, but keels are infrequent. If, as is suggested by juvenile *onca* morphology, the "retrograde" sequence begins with pad dedifferentiation, then either grass or trunk-ground species might be the starting point for the radiation. But if, as is suggested by the *annectens* morphology, the "retrograde" sequence involves the progressive expansion of multicarinate features into seta-bearing areas, then the most probable starting point for the *annectens-onca* lineage is a trunk-ground habitat (broadly defined). b) To our present knowledge, multicarinate features are elaborated in only three anole species: *whitemani* (some individuals), *annectens*, and *onca*. In the cases where the general habitat associated with this shift is known, it is a xeric region. Although our survey has not been exhaustive, we have seen no evidence of keel elaboration in trunk-ground species with other habitat associations. *A. notopholis*, a mesic trunk-ground species, comes the closest to being an exception. In *notopholis* all but one of the phalanx i scales have long low keels. Keel position and relief is compa-

able to that in *auratus*, and relief is much less than that in the *whitemani* specimens described above. Other ecomorphs, particularly grass (e.g., *auratus*, *poncensis*, and *olssoni*) and trunk (e.g., *brevirostris*) anoles, also radiate into xeric areas. With the exception of *auratus*, multicarinate scales do not seem to appear in xeric grass or trunk forms. Elaboration of multicarinate features in anoles is not always (e.g., *cooki*) or perhaps exclusively (e.g., *notopholis*) associated with the invasion of xeric regions by trunk-ground species, but there does appear to be some relationship among the habitat, ecomorph, and subdigital keels. c) Presumably the invasion of xeric areas translates into diminished selection for an "adhesive pad" (see the section on behavioral ecology of *onca*) and selection for scale contours which are more effective on lower friction surfaces like sand and rough bark. Continued or extreme selection for locomotion on these substrates might be correlated with the encroachment or substitution of multicarinate scales for seta-bearing lamellae in *annectens* and *onca*.

THE EVIDENCE FROM NON-ANOLE IGUANIDS AND GECKOS

Subdigital keels are relatively uncommon in anoles, but quite common in non-anoles. Some insight into the habitat and behavioral correlates of keels can be gathered from the non-anoles if we examine not the origin or appearance of keels, but the interspecific variation in keel shape and position. The comparisons among non-anoles iguanids can be constructed to evaluate whether a) variation in keel shape and position is correlated with habitat differences similar to those implicated by the examination of anole species, and b) whether the multicarinate scales of *onca* and *annectens* are convergent on those of desert-dwelling iguanids. A complete survey is beyond the scope of this paper, but the

comparisons which we have constructed as "test cases" proved quite interesting.

Enyalioides microlepis and *E. heterolepis* are mesic forest species which differ in the proportion to which they use bark and forest floor substrates (K. Miyata, personal communication). Keel shape and position are very similar in the two species.

The pattern of keel placement is also similar in two scansorial *Tropidurus* species: *T. torquatus*, from mesic open areas (Rand and Rand, 1966) and *T. occipitalis* from xeric coastal Peru (Dixon and Wright, 1975). Both species have a dominant median keel flanked by subsidiary lateral keels similar to the pattern in the *Enyalioides* species and on the phalanx iii scales of *annectens*. The xeric species, *occipitalis*, however, does differ from *torquatus* in several other features: a) the keel tips and crests are sharper, and b) keels on the lateral digital scales have more relief. These features and the morphology of the phalanx i region are convergent on *annectens*.

Scale shape and keel development are different in *Tropidurus peruvianus*, a xeric Peruvian coastal species which is predominantly terrestrial and lives on beaches, sand dunes, and boulders (Dixon and Wright, 1975). Keel asymmetry is marked in *peruvianus*, but there is a pair of dominant keels (probably the median and postaxial lateral) except at the interphalangeal joints where three robust keels (the median and the pair of lateral keels) are present. While the asymmetry and probable homologies of the keels are different, the emphasis on two robust keels rather than a single dominant median keel is similar in *onca* and *peruvianus*.

The more terrestrial, sand-dwelling iguanids which we have examined (*Crotaphytus wizlizeni*, *C. collaris*, *Dipsosaurus dorsalis*, *Phrynosoma* sp. and *Callisaurus*) resemble *T. peruvianus* and *onca* in having two, or usually more, relatively equal keels in lateral positions

rather than a dominant median keel (the homologies of the lateral and far lateral keels are not particularly clear because of torsion and asymmetry in the scales, e.g., *C. wizlizeni* has four or more keels all on the postaxial side of the scale).¹ In contrast, *Basiliscus vittatus*, a mesic cursorial/scansorial form, has a single keel that is asymmetrical in orientation. *Sceloporus olivaceus*, a xeric climber, has a robust median keel, although on some scales the pair of lateral keels are as large as the median. In *Iguana*, there are two relatively equal keels placed so close together in the median plane that they might well operate as a single keel.

The xeric terrestrial iguanids appear to have a larger number of keels and more robust keels in the lateral portion of the scale than the terrestrial forms in mesic habitats or than the more scansorial forms, which as a group emphasize a medially placed keel. This provides some corroboration of the relationship between elaboration of keeled scales and xeric habitats in *Anolis*. Presumably the aspect of xeric habitats which is functionally significant for subdigital scales is sandy or loose soil substrates. It is possible that the increased number and lateral placement of the keels are more effective in stabilizing sand to apply propulsive force while a single median keel is more effective on a curved surface or in working into bark crevices (a large number of keels acting

on a rigid irregular surface would probably decrease the coefficient of friction by decreasing the area of contact or preventing keels from projecting into crevices). The xeric scansorial forms (*Sceloporus olivaceus* and *Tropidurus occipitalis*) utilize terrestrial substrates for foraging (Blair, 1960; Dixon and Wright, 1975), and both display an increase in keel number or robustness compared to mesic forms. This could be related to foraging on sand, but there may be other habitat differences, and the relationship is likely to be more complex.

The difference in keel placement between *annectens* and *onca* is mirrored in the difference between *Tropidurus occipitalis* and *T. peruvianus*, and the differences in subdigital scales between *occipitalis* and *torquatus* are generally convergences between *occipitalis* and *annectens*. The resemblance and comparative data are not complete enough to suggest a probable habitat and behavior for *annectens*. But the difference in keel placement and shape between *annectens* and *onca* appears to be significant in light of data from the non-anole iguanids. Quite apart from the difference in pad retention, the morphology of the multicaudate scales suggests that *annectens* may be adapted for a somewhat different structural habitat than *onca*. Both pad retention and the morphology of the keels in *annectens* appear to indicate a more traditional anole structural habitat.

The most striking parallel for the substitution of a keeled surface for the adhesive pad may come from geckos. Russell (1976, 1979) describes the reduction or loss of subdigital pads in two groups of geckos which have radiated into xeric, sandy habitats. In these cases the pad is replaced by small, erect granular scales covered with spines similar to those in primitively padless, sand-dwelling forms (Russell, 1979). It is possible that the small, erect scales behave like individual keels and stabilize sand under the foot as propulsive forces are applied. Although

¹ Fringe-toed lizards such as *Uma scoparia*, *Acanthodactylus scutellatus*, and *Aporosaurus anchietae* are apparent exceptions to the generalization of greater keel numbers in sand-dwelling species. The subdigital scales in these forms are laterally compressed with a single median or median preaxial keel and subsidiary keels are absent. *Tropidurus thoracicus*, a relative of *T. peruvianus*, which even "sand swims" has similar subdigital morphology (Dixon and Wright, 1975). Presumably this morphology is adapted to trap sand between the "fringe" on the lateral digital scales and the subdigital keel.

Apparently there are a number of alternative adaptations which will increase the coefficient of sliding friction between the animal and a loose sand substrate (see also sidewinding [Gans, 1974]).

little is known of the behavior of these animals (they appear to be more terrestrial than *onca*, see Werner and Broza, 1969), the parallel reduction in adhesive structures in sand-dwelling geckos and anoles is striking. It is possible that sand injures or clogs the setae (Underwood, 1954, makes a comparable argument for forest floor geckos), but anoles in captivity do not appear to have any difficulty in climbing after walking or running over sand, and pad retention in the xeric trunk-ground species would suggest that sandy substrates do not strongly select against a pad and setae in anoles. We would interpret the trend in *Anolis* in terms of a) diminished selection for pad morphology in arboreal/climbing behaviors (also discussed in the subsequent section), and b) enhanced selection for keels and "traction" devices which are effective in loose sand or dirt.

Possible Functional Significance of the Spine to Seta Series

THE SPINE TO SETA SERIES: ADHESION OR PREHENSION

The morphological series in fine structure is remarkably continuous and almost certainly reflects the interface of developmental processes and function. In order to develop functional hypotheses for the differences reflected in the series, we will assume, for the present, that the morphological series is also a phylogenetic one and that the spinule morphology is a "starting point" for the subdigital series.

There appear to be two distinct portions of the series: the first involves the transition from the generalized Oberhautchen spinules to the subdigital spine-seta series (Figs. 21, 22), and the second comprises variation within the subdigital series (Figs. 21, 23).

The functional significance of the spinulate Oberhautchen is not well understood. The spinules may represent adaptation for protection from physical

abrasion (Ruibal, 1968), the diffusion of some wave lengths of radiant energy (Porter, 1967), facilitation of shedding (Maderson, 1970), and/or some yet unappreciated factor.

The transition from the spinules to the subdigital spine-seta series might have occurred in response to selection for greater abrasion resistance, but this would not seem to explain the acquisition of a recurved tip. It is more likely that selection for purchase or grip is responsible. Initially, the spinulate surface itself might in some fashion interdigitate with the environmental surface and increase the frictional coefficient of the contact. The longer spinules (see Fig. 22a) might even be able to engage environmental irregularities like small hooks (the "velcro" principle). Selection to augment the microscopic prehension or interdigitation of some of the spinules could result in exaggeration of the stalk height and acquisition of a recurved, more hook-like tip (e.g., the small spine morphology shown in the central portion of Fig. 22b; note in the figure that not all the spinules have been exaggerated into small spines: there is an understory of very short spines and knobs similar to those shown in Fig. 22a). Presumably the height increase is selectively advantageous because a consistent increase in stalk height would produce too dense a "pile" for the tips to function. The selective increase in height establishes or aggravates a functional differentiation between spinules in the understory which do not function in prehension and small spines which do, and it alters the functional density. The spinules in Fig. 22a occur in a density greater than $10/\text{sq } \mu$; the small spines (excluding the understory in Fig. 22b) are about half as dense. Continued selection for prehensile, microscopic hooks could then result in increased stalk height to augment the effective range of the hook and in increased diameter to tolerate larger tensile loadings. The increase in stalk diameter is

necessarily linked with reduction in density and occurs at the expense of the spinules in the understory. The generalized subdigital spine morphology is reached with a height of at least $1\ \mu$ (usually greater, see Figs. 22, 23), a diameter close to $0.5\ \mu$ near the base, and a density of 2 or less/sq μ .

The collective alterations involved in the shift from spinules to subdigital spines could create a "prehensile" scale surface capable of augmenting the claw. It might augment the claw in such a way as to permit acrobatic and perch-walking maneuvers over a wider range of substrates. The effect of a "prehensile" scale surface would presumably be least on the tree trunk and greatest in the bush/canopy branch and twig zones where the surfaces accept the claw less well and the radius of curvature of the perch is small. Some of the foot positions which anoles use in acrobatic maneuvers on small perches would not be possible unless some grip independent of the claw were permitted. If spine-covered subdigital scales, like the series of phalanx i and iii scales in many anoles, could contribute to grip, the shift from spinules to the subdigital spine series would have significant impact on the range of vegetational surfaces and the repertoire of behaviors.

Hiller (1968) argues that, while the spine tip might behave like a microscopic hook, the behavioral significance of spines is negligible. His argument is largely based on experiments with geckos adhering to a series of artificial surfaces which are much smoother than twigs or branches, and probably too smooth for the small number of spines present to develop much gripping force (these experiments are discussed in more detail below). Sanding of the surface to roughen it resulted in a slight increase (value not reported) in the gripping force (Hiller, 1968). It is simply not clear that Hiller's (1968) objection would hold for natural surfaces or if major portions of the

subdigital surface were studded with spines.

Within the anole subdigital series there are two trends operating to create the different morphologies: one in stalk height and one in tip shape.

1) The variation in stalk height is continuous and not closely correlated with tip shape (e.g., the sharp, recurved tip and spatula occur over a significant range of stalk heights). Stalk height affects the independence of the tip from the scale surface. A longer stalk permits the tip a greater range of positions and increases the odds that the tip will contact the environmental surface. Because the stalks are stressed in tension, variation in their length does not alter their strength nor require a compensatory change in diameter (Peterson *et al.*, in preparation). While there is no purely mechanical disadvantage or cost associated with increasing stalk length, presumably there is a developmental and material cost. Exceptionally long stalks would also be more likely to tangle and trap debris, and the properties of the keratin would have to be such as to maintain the tip orientation relative to the scale surface regardless of stalk length.

The longest stalks generally occur on lamellar setae (there is significant interspecific and regional variation in setae stalk height; Peterson and Williams, in preparation). The length of the stalk coupled with the flexibility of the lamellae permit the spatulate tips to reach surfaces which have a small radius of curvature or are irregular at the ultrastructural level (see discussion of tip function following). This is an extremely important aspect of seta function in anoles because the total number of spatulate tips is not particularly high (cf. the branched setae of geckos) and the total area of the spatulae is actually less than that of the underlying lamellae (Peterson and Williams, in preparation). The advantage of setae regardless of their mechanism is not exclusively in

the area or number of tips which they offer to the environment, but in the ability of those tips to "find," mold to, and engage the substrate, and this substantially depends on the dimensions and properties of the stalk.

Short stalks occur in narrow zones on the periphery of seta, prong, or spike-covered areas (Fig. 23), often where the scale surface is shadowed by another scale, and occur widely over the surface of more rigid, often contoured scales. The tips on stalks along contour slopes and valleys will contact the environmental surface if a) the contour interdigitates with a permanent irregularity of the substrate, or b) the substrate molds to the scale contour. But given scale relief an order of magnitude greater than the maximum observed stalk length, "finding" the substrate does not depend on stalk length. Possibly the fine structure of contoured scales is not selected to "find" the substrate as setae do, but to interact with particular portions of the substrate which "find" the stalks by offering resistance or purchase to the scale contours. Short stalks, regardless of the associated tip shape, may be functionally advantageous on multicarinate scales if, by "roughening" the keel slopes, the stalks increase the frictional coefficient of the scale surface.

2) Although the variation in tip shape is continuous, there are two basic and numerically dominant shapes, the hook and spatula (Fig. 21). The hook tip on spines and spikes (and even prongs) functions like a microscopic hook to engage irregularities of the environmental surface (see above and Hiller, 1968). There is a variety of hypotheses on spatular mechanisms (see Russell, 1975 and Hiller, 1968 for review), but two seem most likely for anoles. Compression and lateral expansion of the hook tip into a spatula could be an adaptation a) to shift from a prehensile mechanism to an adhesive one (Hiller, 1968 for geckos), or b) to add

the option of an adhesive mechanism to the existing prehension. In either case, the difference between the hook and the spatula seems to be adhesion. An adhesive gripping force depends a) on the surface energy or tension of the environmental surface and of the seta keratin, and b) on the area of contact between them. Given that the seta keratin itself is preadapted for adhesion, selection might increase the area of contact of the tip in the following sequence (Fig. 21): a) reduction in the stalk taper to yield a thicker, larger tip—the prong, b) compression of the round or oval prong to form a planar surface and increase the effective area—the seta-prong, and c) expansion of the flattened surface—the seta. The prong and seta-prong shapes are very rare in generalized anoles (Fig. 23) and appear to represent developmental and evolutionary transitions linking the hook and the spatula.

There is no direct evidence for an adhesive nor for a prehensile mechanism in anoles. Hiller (1968) argues strongly for an adhesion mechanism based on the morphology of the spatula and on experiments measuring the clinging force of geckos on a series of artificial surfaces. The force required to dislodge a gecko from a horizontal surface was directly proportional to the surface tension of the material (Hiller, 1968). Considerable force was required to dislodge the animal from glass which has high surface tension (contact angle of water droplet with glass is 0°), while the animal had little or no adhesive strength on certain plastics of low surface tension (water-drop contact angles of 80° or more). Hiller (1968) argues that "velcro"-like prehensile mechanisms can be excluded because a) roughening the surface of a low surface tension material results in only a slight increase in gripping force, and b) pulling the animal perpendicular rather than parallel to low ridges on the unroughened surface of a low surface tension material

resulted in only a slight increase in gripping force (values were not reported in either case). In Hiller's adhesion hypothesis whole animal adherence occurs as the spatula is brought into intimate contact with a flat, high surface tension substrate. Surface roughness or ultramicroscopic irregularities will interfere with this process so that the animal is unable to cling to such surfaces without its claws. Russell (1976) augments Hiller's argument with the hypothesis that the waxy secretions on leaves and smooth bark provide the initial advantage to seta-bearing geckos.

There are two major difficulties in accepting or extending the adhesion hypotheses to anoles. 1) The surface properties of vegetation suggest that, if an adhesive mechanism alone is possible, anoles could not use some of the substrates they clearly thrive on. The majority of plant surfaces appear to have lower surface tension than Hiller (1968) found was required in geckos (contact angles of 80° or less were required for even modest adhesive force). The common chemical constituents of plant waxes have (water drop) contact angles from 94° – 108° ; the isolated smooth surfaces of the native waxes yield angles between 80° and 108° (Martin and Juniper, 1970). The accumulated SEM data on leaf and stem surfaces (see review in Martin and Juniper, 1970) indicate that the surfaces are also highly irregular and rough in the dimensional scale of the spatulae: waxes commonly exist in projecting rods or semi-crystalline excrescences; the epidermis may be grooved or the individual cells convex or granular; trichomes often project from the surface of leaves; stems and twigs have cracks, ridges, rough scars, and considerable debris. Only a portion, and often a small portion (e.g., 28% on corn leaves, Martin and Juniper, 1970), of the leaf or bark area is flat and smooth enough to make close and complete contact with the spatula. Fine structural irregularity raises the contact angle of

many surfaces to better than 110° ; in Holloway's (1969) study of the leaf surfaces of 40 common plant species, 24 have contact angles greater than 110° , and an additional 6 have contact angles between 90° and 110° . Presumably the small size and active application of setae will permit the spatulae to "find" the smooth portions of the surface better than a water droplet which rides on the peaks of the irregularities, so that the contact angles in excess of 110° may not themselves be relevant. But, major portions of common vegetational surfaces (leaves, young bark, stems, and particularly grass blades) are unsuitable for adhesion. They have been selected for surface irregularity and low surface tension to inhibit the adhesion of water droplets (Martin and Juniper, 1970). 2) There is little indication that anoles in natural habitats are selecting particular plant species or surfaces which might have high surface tension and low surface irregularity (but see Kiester *et al.*, 1975 for *auratus*). In the laboratory, anoles will adhere to smooth, high surface tension glass and waxy, low surface tension leaves (neither surface will accept the claw). The discrepancy among Hiller's findings, the properties of natural surfaces, and the behavior of anoles need to be addressed directly with adhesive force experiments on natural surfaces, but provisionally we would suggest that spatular morphology permits coexisting adhesion and prehension mechanisms. The eccentric attachment of the spatula to the stalk and the broad leading margin could permit the setae to function as a hook. It seems to us possible that the foot and lamellar movements wipe the spatulae over the environmental surface until the leading edge of the spatula catches on a wax rod/crystal or cuticular irregularity or until the spatular surface finds a smooth, high surface tension area of cuticle. Either would establish the grip and, since most leaf and twig surfaces are rough/smooth mosaics, even adjacent setae might exhibit different gripping

mechanisms. Anole setae probably represent an adaptation for this mosaic surface structure and a variety of surface tensions.

IMPLICATIONS FOR THE "RETROGRADE" SERIES

This general discussion of the spine-seta series provides a context within which to evaluate the trends in the *annectens-onca* and *auratus* lineages. The two lines offer an extraordinary contrast, not in the morphology of members of the series, for all but *onca* have quite similar representatives of all stages, but in specialization for long or short stalks and for hook or spatulate tips. In generalized anoles the subdigital surface is covered with spatulate and hook tips in about the proportions 60/40 or 70/30, depending on body size and ecomorph. In *auratus* the series is shifted even further toward the spatula and relatively long stalks. All the subdigital scales bear setae, and spines are quite rare. In the *annectens-onca* line, the series is shifted in the opposite direction, until in adult *onca* only spines are present. The functional significance of this divergence is at least in part related to the substrate features.

A. auratus and Grass Surfaces

The characteristic substrates of *auratus*, grass blades, sheaths, and stems (culms), will not accept the claw, and most of the surface irregularities are too small for scale contouring to be effective. Purchase largely, if not entirely, depends on adaptations of the spine-seta series. Substrate selection should favor long stalks to permit the tips to "find" the surface, since grass is too rigid to comply and "find" the tips, and either a hook (spike) or spatulate (seta) tip, depending on surface tension and irregularity. The surface characteristics of the Panamanian grasses are not known, but the available data suggest that most Gramineae have a) ribs or keels on stems, sheaths, and

blades, b) prominent surface corrugations or groove/ridge contours between the ribs on the blades, c) trichomes, and d) a coating of surface wax (Martin and Juniper, 1970; Challen, 1960; personal observation). Challen (1960) found contact angles of 135° and 110° on two temperate grasses (*Agropyron repens* and *Festuca pratensis*). Removing the surface wax reduced the angles to about 67° and 77°, respectively (Challen, 1960). The common Panamanian grasses (*Paniculum pilosum*, *Paspalum conjugatum*, and *P. paniculatum*; Croat, 1978) probably used by *auratus* have surface ribs and corrugations at least as prominent as those of the species investigated by Challen (1960). The surfaces *auratus* uses are clearly "rough" in the dimensional scale of the tips and probably have a relatively low surface tension. Systematic descriptions, however, indicate regional variation in some of the sources of surface roughness (e.g., the stem may lack trichomes while the sheath or blades are pubescent; Croat, 1978). Although a non-adhesive mechanism appears to be required and dominant, there is sufficient variation among the regions of the grass plant and on an ultrastructural level (e.g., smooth, moderate surface tension cuticle exposed between wax crystals and adjacent to the ribs) to permit the possibility of supplemental or occasional adhesive contacts. If these adhesive contacts are behaviorally significant and if anole setae can function in either prehension or adhesion, selection related to grass substrates would favor setae or a combination of setae and tall spikes. The West Indian grass anole, *A. pulchellus*, exhibits the second condition: setae and large numbers of spikes occur on a well-developed pad. In *auratus*, the seta spatula is somewhat narrower, but setae cover almost all of the subdigital surface. The distribution of setae to all phalanges is apparently correlated with the absence of an expanded phalanx ii pad and with dimensions and density parameters within the spike to

seta series (see discussion of lamellar scale shape). The *auratus* morphology represents adaptation for the use of grass or grossly smooth vegetational surfaces and for a narrow pad region. The differences between *auratus* and *pulchellus* in pad width and in the specialization for setae versus the combination of spikes and setae are major, but we cannot yet interpret their functional significance. It does seem reasonably clear, however, that if the environmental surface is grossly smooth, and fine structure is responsible for whole animal adherence, setae or the spike-seta portion of the morphotypic series is selectively advantageous.

A. *onca* and Diminished Selection for Setae

While *onca* (and presumably *annectens*) climb, setae would not necessarily be appropriate or advantageous, given the climbing behavior and vegetation (see Williams, 1974; Collins, 1971). The vegetation in *onca* habitat is unusual for an anole; there are no broad leaf plants and few trees. Fence posts and the dense maze of thorn scrub bushes are readily negotiated with claws. The thorn scrub branches are used in combination (two or more perches support the animal) so that foot positions can be chosen to take advantage of the claws and even opposing combinations of digits. *Dipsosaurus*, a predominantly terrestrial iguanid that also clambers into sage and other scrub bushes, exhibits very similar "climbing" behavior. In captivity *onca* climb bark and apparently "rough" surfaces and "walk" through a closely spaced mesh of small diameter perches as well as any other anole. If *onca* are placed in a generalized anole habitat—the more open, arboreal network of perches or a trunk-ground interface—they do not seem to display the repertoire of fast acrobatic and single perch maneuvers which most other anoles have. When the distance between perches is greater than a comfortable step or a short hop, they usually drop

from the perch rather than leaping. Although the scrub bush is superficially like the arboreal habitat where anoles obviously depend on seta/pad function, the mesh of perches is dense relative to adult *onca* body size, and there is a meter or more distance between bushes. These factors effectively preclude the single perch and fast acrobatic behavioral strategies of generalized trunk-ground anoles. The vegetational structure permits *onca* (and *Dipsosaurus*) to use climbing behaviors that require precise foot placement but are not otherwise very different from those used in terrestrial locomotion. Given the character of the vegetational/structural habitat and the behavioral strategies of anoles, it is likely that habitat selection for seta/pad function is diminished in adult *onca*.

Juvenile *onca* are found in thorn bushes and the dense dry grass at the base of the bush (K. Miyata, personal communication). Sandy areas surrounding the thorn bush islands seem to be rarely encountered, and this could reduce the selection for multicarinate features in hatchlings. Also, the body size range over which the juvenile morphology occurs is about half that of the adult (Maderison and Williams, in preparation), so that the relationship between body size and perch/perch matrix dimensions is more like that of a grass anole than that of adult *onca*. It is not known whether juvenile *onca* utilize the behavioral strategies of generalized grass or trunk-ground anoles, but it seems feasible for juveniles to perch on a single twig, grass blade, or thorn bush leaf while it does not seem feasible for the adults. The surface properties of these substrates might permit adhesion, so that it is not clear that the advantage of setae would be diminished for the juvenile to the same degree as it appears to be for the adult. But, grass, twigs, and probably the available leaf surfaces would almost certainly provide microscopically rough substrates which would be engaged by

the prehensile elements of the fine structural series (prong/spike/spine). Robust keels like those of the adult would probably be less effective in dealing with this range of substrates than setae or the prehensile forms in the fine structural series.

Juvenile *onca* morphology underlines the argument that diminished selection for setae is not by itself an adequate argument for the substitution of multicarinate scales and the convergence toward sand-dwelling iguanids demonstrated by the adult *onca* morphology. If lamellae and setae are developmentally expensive (Williams, 1974) and not particularly advantageous in locomotion, it is naively reasonable to expect the substitution of spine/spike-covered generalized subdigital scales like those in the phalanx iii region of many anoles or in juvenile *onca* or in some of the para-anoline genera (Peterson and Williams, in preparation). A number of semiaquatic, streamside anole species retain the pad and gross characters of generalized anoles, but spikes and prongs have completely replaced setae on the subdigital scales (Peterson and Williams, in preparation).

Adult *onca* morphology reflects a parallel but more extreme "retrograde" shift in the spine-seta series coupled with a trend to contour the scales. It appears that this is related to the combination of sand and bark substrates. The surface irregularity which dominates bark or must be created in sand is at least an order of magnitude larger than that on grass blades. Purchase and traction on bark and sand depend on adaptations—claws, scale shape, and keels—at a larger dimensional scale than spikes and setae. The subdigital surface may be selected for short stalks and hook tips to increase the frictional coefficient of the keel slopes or even to contribute some grip by prehension, but much of the propulsive force is probably transmitted independent of the spines.

The comparatively reduced significance of the spine-seta series in actual

grip may be indicated by the *onca* spine morphology itself. Except where the spines are associated with a contour, as on a hillock or adjacent to a keel, their height and diameter are less than those of generalized subdigital spines. With a diameter of $0.3\text{--}0.45\ \mu$ and a density of $1.2\text{ spines/sq }\mu$, most of the scale surface is bare. By itself, the reduced size of the spines suggests a simple retrograde shift toward Oberhautchen spinules, but the combination of low spine density and small individual spines appears to indicate a general trend toward repression of the spine-seta series and a completely bare contoured surface similar to that of multicarinate scales in some iguanids, e.g., *Dipsosaurus*.

A. annectens and Juvenile *onca* as Alternative Models for the "Retrograde" Series

The earlier paper outlined a five-stage sequence in the "retrograde" evolution from the typical anoline pad morphology to the keeled subdigital surface in *annectens* and *onca* (Williams, 1974). Through the first three steps—narrowing of the lamellae, reduction in the number of lamellae, and loss of the raised character of the pad—the pad dedifferentiates from the adjacent phalanx i and iii scales. If phalangeal length is constant, narrowing of the pad and reduction in the number of scales convert the lamellar scale shape into that of generalized subdigital scales. Pad dedifferentiation characterizes a variety of "Norops" species, including *auratus*, and is approached by *A. chrysolepis*. The fourth and fifth steps in the sequence comprise the shift from generalized subdigital scales to multicarinate scales. Keels are introduced into the phalanx iii series in *annectens* (step four), and in *onca* the entire series of subdigital scales is multicarinate (step five).

The additional comparisons and fine structural data alter our view of the sequence in several ways. 1) It is no longer

clear that *auratus*, as an example of a "Norops" species, is an appropriate model for the early stages in the sequence. The expanded seta distribution in *auratus* demonstrates that dedifferentiation of the pad is not necessarily linked to a decrease in the seta-bearing area nor to the substitution of multicarinate scales. 2) There appear to be two alternative sequences.

If juvenile *onca* morphology is used to model the intermediate stages, the sequence might a) begin with a trunk-ground or even more probably a grass anole with gross morphology similar to that of *auratus*, b) progress by more extreme dedifferentiation of the pad region (including loss of the frayed lamellar border and extreme narrowing of the lamellae) combined with the replacement of setae by spikes, prongs, and spines to yield the gross morphology of the *onca* juvenile, and c) culminate with keels and marked contour features throughout the series of subdigital scales (the *onca* condition). In this scheme *A. annectens* would represent a parallel lineage independent of that of *onca* after the first step in the sequence.

If, on the other hand, *A. annectens* morphology is considered representative of the intermediate stages, the "retrograde" sequence could a) begin with a trunk-ground anole (broadly defined) not unlike *A. chrysolepis*, i.e., perhaps with narrow lamellae, but a defined pad region and a few phalanx i keels, b) continue with elaboration of the keel features in the phalanx i region (the *A. whitemani* variant morphology), c) follow this by invasion of keels into the phalanx iii region of generalized subdigital scales (the *A. annectens* morphology), and d) finally substitute multicarinate scales for lamellae and setae in the phalanx ii region (the *onca* condition). In this scheme the "Norops" condition may arise at any point before the substitution of keels for lamellae and setae in the phalanx ii region, and the juvenile *onca* morphology would

be considered an ontogenetic adaptation with no relationship to the phylogeny of adult morphology.

The critical difference between these sequences is whether the adhesive pad dedifferentiates prior to the appearance of multicarinate scales or whether multicarinate scales progressively encroach on and replace lamellae. These different modes of origin for the multicarinate scales correspond to two possible models for transitional scales. *Onca* juvenile scales (e.g., scale 13) have the gross shape of the adult multicarinate scales and rounded contours without the bare areas which characterize keels. A "retrograde" shift in the spine to seta series has occurred over most of the scale. The central portion has prongs, a "more conservative" morphology than the spikes. The latter occur distally and laterally, suggesting that the trend progresses inward from the scale margins. But, on the whole, the scale surface is reasonably homogeneous, and adjacent scales have very similar architecture.

A. annectens scale 9 suggests a very different mode of evolution in scale architecture. Here the transitional scale shape is close to that of the lamellae, but the distal margin is robust and set with bosses or keels. The bosses are set into fields of spines, spikes, prongs, and a few rare setae. The fine structure is extraordinarily heterogeneous, apart from the distal border which is covered with spines. Compared to the morphology of scales in the *onca* hatchlings, the fine structure of scale 9 appears chaotic and disrupted. Scale 9 is also markedly different from the lamellae and multicarinate scales on either side of it. The small keels which are present on the lamellae appear to become progressively more robust toward the interphalangeal joints (at scales 9 and 15). The morphology itself suggests that the transition begins as keels invade the surface of lamellae.

It is not clear which of these two sequences or models of the transitional

morphology are correct. We cannot provide incisive arguments for or against either of them, but the second or *A. annectens* model seems somewhat more plausible.

1) If *onca* and *annectens* represent parallel lineages which have been independent from the *chrysolepis*-like stage of the sequence, it is difficult to explain the close resemblance in non-digital characters (Williams, 1974). There are marked differences in digital characters (e.g., phalangeal length, scale shape, keel placement, and the retention of lamellae and setae), but these could represent adaptation to somewhat different structural habitats.

2) Each of the model intermediates has equivocal status or relevance to the evolution of *onca*. *A. annectens* is a unique specimen which closely resembles *onca* in non-digital characters. There is the possibility it is an individual variant of *onca*. Elements of the morphology might be relevant to the sequence in this event, but the particular combination of characters on which the sequence is based could as readily reflect developmental patterns as the phylogenetic sequence. The juvenile *onca* morphology may, on the other hand, imply the phylogenetic sequence or reflect ontogenetic adaptation for a smaller body size and different habitat and behavior. There are two critical features on which the juvenile morphology makes any claim as an intermediate between generalized anoles and *onca*: the absence of definite keels and the presence of spikes and prongs. The absence of definite keels on the subdigital scales in the hatchling of another anole species (*A. cristatellus*) suggests that this character is not restricted to *onca* juveniles. It may be a feature of juvenile anoles and an ontogenetic adaptation which coincidentally parallels the phylogenetic sequence. The presence of well-developed contours usually in the position of the adult keels and on all the subdigital scales also suggests a very de-

rived status in terms of keel elaboration. Juvenile *cristatellus* have setae and the same fine structural series as the adults, but with decreased stalk height. The opposite difference—increased stalk height—in the juvenile *onca* appears to be a feature that is unique to *onca* juveniles. If the *onca* juvenile morphology is converted into a hypothetical adult by the addition of bare areas to the contours to form keels, the result is a form which is very similar to *onca* and an apparently later member of the transitional series than *annectens*. If the hypothetical adult/juvenile *onca* is used as the basis of a revised “retrograde” sequence, it suggests very little about the early stages of the lineage, particularly about keel origin and expansion, so that a number of sequences are possible, including the early part of the *annectens* sequence. Any of the juvenile *onca* sequences and the *annectens* sequence differ markedly on the issue of a sequential versus a simultaneous shift to multicarinate scales in the phalanx ii and iii regions. Even the hypothetical adult version of the juvenile *onca* morphology still leaves the two model intermediates as mutually exclusive forms in the *onca* lineage.

3) The alternative sequences and models for transitional scale types can also be compared in terms of circumstantial support from the comparative data.

a) The pattern of transitional scales based on the *onca* juvenile morphology has some comparative support although it is unique in most features. In the *lionotus* species group there is a general trend to replace setae with spikes, and on several lamellae in *A. lionotus* only the central portion of the scale has setae while the surrounding areas are covered with spikes. The “retrograde” shift in fine structure appears to occur from the lateral and distal portions of the scale inward, but, in this case, the shift occurs on a lamellar scale and there are no contours present. The *annectens* scale 9 fine structure is to our knowledge unique, but

apart from *annectens*, there are no examples of keels invading lamellae. Given that keels are being added to the scale surface, the disrupted, heterogeneous fine structure is no less plausible than the more homogeneous fine structure of the *onca* juvenile.

b) The transitional scale model and sequence based on the *onca* juvenile are unusual for anoles because they imply so little regional differentiation and sequential change. The "retrograde" shift from setae to spikes in *A. lionotus* appears to have occurred in a scale-by-scale sequence beginning at the i/ii and ii/iii interphalangeal joints and progressing toward the center of the pad. This is similar to the suggested pattern of keel encroachment in *annectens* and is markedly different from the simultaneous change in two or more phalangeal regions suggested by juvenile *onca*. The expansion or retraction of setae in the phalanx ii region (the phalanx iii and iv regions of the fourth toe) of West Indian anoles also appears to occur with a sequential scale-by-scale pattern. Marked differentiation in fine structure of the phalanx i and ii regions occurs even in some extreme "Norops" species like *A. aequatorialis*, *A. notopholis*, and *A. meridionalis*. The dominant morphological and evolutionary patterns within the genus are regional differentiation and sequential change (scale-by-scale and phalangeal region-by-phalangeal region). Clearly the *onca* lineage could be exceptional in this regard, but the sequence and transitional morphology implied by *annectens* is quite consistent with the patterns we have encountered elsewhere in the genus while those suggested by the *onca* juvenile are not.

c) There is no great difficulty in deriving *A. annectens* from generalized trunk-ground forms such as *A. chrysolepis*, and parallels for the early stages in the sequence can be found among other lineages (e.g., *A. whitemani*). But it is very

difficult to find a model ancestor for the juvenile *onca* morphology. All of the prospective models with which we are familiar (e.g., *A. chrysolepis*, *A. barkeri*, *A. notopholis*, *A. tropidonotus*, *A. auratus*, *A. nebulosus*) have keels or bare areas. Based on the morphology of these more generalized related species, either keels and bare areas are lost in the early portion of the *onca* juvenile sequence and then "re-acquired" at the *onca* stage or the absence of bare areas is not descriptive of the phylogenetic intermediate. If one accepts, as is argued above, that the absence of bare areas on the contours is an ontogenetic adaptation and that the adult intermediate morphology includes keels, then any of the forms cited above could model the starting point of the *onca* lineage. The gap between any of the prospective initial morphologies and that of juvenile *onca* is so great that it simply is not clear how the sequence might start. The "Norops" condition is combined with narrow but definite lamellae in *A. notopholis* and *A. tropidonotus*, but there is no evidence of a "retrograde" shift in fine structure or conversion of phalanx ii lamellae into generalized subdigital scales. *A. auratus* exhibits the "Norops" condition, narrow lamellae and poor regional differentiation in fine structure, but the latter is associated with an expansion of setae into the phalanx i region rather than a "retrograde" shift. *A. barkeri* exhibits a "retrograde" shift in the fine structure of the phalanx ii and iii regions (prongs are present), but there is little indication of pad dedifferentiation or replacement of lamellar scales. The differences between generalized anoles and juvenile *onca* suggest that three trends occurred in the intervening stages: dedifferentiation of the pad and lamellae, a "retrograde" shift in the fine structure, and expansion of contours and keels into the phalanx ii and iii regions. But there is no real indication of the order or relative emphasis of these

trends during the early portion of the radiation.

Summary: The relative efficacy of the *annectens* and juvenile *onca* specimens as phylogenetic models for the *onca* lineage cannot be evaluated with any degree of security from the available data. The possibility that *annectens* is an aberrant version of *onca* or represents an independent radiation has to be weighed against the possibility that the differences between *onca* juveniles and adults coincidentally parallel the phylogenetic sequence. But the odds appear to be shifted slightly in favor of *annectens* as a model. 1) The similarity between *annectens* and *onca* in non-digital characters is so great that it seems unlikely that they represent as distantly related forms as the *onca* juvenile morphology would imply. 2) The individual variation we usually encounter (e.g., *whitemani*) involves a single morphological series, while that in *annectens* involves all three series plus scale number and phalangeal lengths. A. *annectens* is thus less likely to be an individual variant than if pad retention were the only character distinguishing it from *onca*. 3) Comparison with the juvenile of another anole species and consideration of the more generalized anoles related to *onca* suggest that the absence of definite keels in juvenile *onca* is an ontogenetic adaptation which coincidentally parallels the phylogenetic sequence. If this is the case, it is only the presence of longer stalks in the fine structural series which makes the case for juvenile *onca* as a model intermediate; the rest of the features are highly derived and resemble adult *onca*. 4) The models for transitional scales based on *annectens* scale 9 and *onca* juvenile scales seem equally plausible. The *annectens* sequence is more consistent with the evolutionary patterns for regional differentiation and sequential change that we have encountered elsewhere in the genus.

CONCLUSIONS

The significant differences in the subdigital morphology of *annectens*, *onca*, *chrysolepis*, and *auratus* can be described in terms of changes in three morphological series: a) scale shape, b) scale surface contouring, and c) fine structure or the spine-seta series. The series are quite similar in the different species, and the dominant evolutionary pattern is change in the distribution or relative abundance of members of the series.

There appear to be two lineages: the *chrysolepis-auratus* lineage and the *chrysolepis-annectens-onca* lineage. An alternative hypothesis is that the latter species are divergent and that the morphology of *onca* juveniles rather than that of *annectens* is the relevant model for the evolution of adult *onca* morphology.

In the *auratus* lineage there are trends for: a) pad dedifferentiation, b) limited keel elaboration in the lateral portion of the phalanx i scales, and c) expansion of seta distribution to cover not only the pad scales, but also the entire phalanx i region. In the *annectens-onca* lineage there are trends for: a) pad dedifferentiation, b) expansion in the distribution and increased size and number of keels, and c) a "retrograde" shift from setae to spines in the pad region. The combination of these trends results in the progressive substitution of multicarinate scales for lamellae and for smooth generalized subdigital scales. In *onca* this substitution has been complete. In *annectens* it has occurred in the phalanx i and iii regions and begun in the phalanx ii area, but setae and lamellae are still present.

Dedifferentiation of the pad (reduction in lamellar number and width and the absence of a raised distal border [i.e., the "Norops" condition]) occurs in both lineages, but the significance of the trend is probably different in each case. In *au-*

ratus pad dedifferentiation is associated with the expansion of setae into the phalanx i region. The seta-bearing area which is "lost" through decreased lamellar width is more than compensated for by the increased phalangeal length and expansion of setae onto the non-lamellar phalanx i scales. There is no indication that pad dedifferentiation in *auratus* is associated with decreased competence of the setae for gripping or with selection for another mechanism. In contrast, pad dedifferentiation in the *annectens-onca* lineage is associated with reduction in the seta-bearing area (relative to body size). Almost certainly, the competence of the fine structural series in maintaining grip is compromised relative to generalized anoles.

In the *annectens-onca* lineage the substitution of keels and a highly contoured scale surface for lamellae and setae appears to reflect selection for an alternative "gripping" or "traction" device. Keels probably function as "traction" devices and presumably are more effective than the fine structural series on surfaces with gross irregularity, like most mature bark, or on surfaces with low cohesion of particles, like loose sand or dirt. Within *Anolis* subdigital keels occur in the phalanx i region of species which use the trunk-ground structural niche (broadly defined) and are rare in other ecomorphs. In at least one case keels are elaborated in a trunk-ground species which has invaded habitat similar to that of *onca*. Limited comparisons among non-anole iguanids suggest that locomotion on loose sand or dirt selects for additional and larger keels. The comparative data suggest that the *annectens-onca* lineage represents a radiation of trunk-ground anoles into extreme xeric habitats where there is enhanced selection for keels and "traction" devices which are effective on the combination of bark and loose sand (see also below).

The fine structural series includes a number of morphotypes which act like

microscopic hooks in addition to setae which may alternate this prehensile mechanism with adhesion. The fine structural series is adapted to utilize a) microscopic surface irregularity, or b) high surface tension, smooth regions of a grossly smooth environmental surface like that of leaves, stems, and twigs. The trend to increase the distribution and to emphasize the fine structural series in *auratus* correlates with behavioral specialization for perching and acrobatics on single grass blades, stems, and twigs on which robust keels like those of *onca* would provide too little contact between the subdigital and environmental surfaces.

The extreme xeric habitats of *onca* offer relatively little broad leaf and grossly smooth vegetation which can be used by an animal with adult *onca* body size. Given the body size of adult *onca*, the dense maze of small diameter thorn bush twigs precludes most of the single perch and fast acrobatic behavioral strategies which select for pad function in *auratus* and generalized anoles. The character of the vegetation in *onca* habitat is such that selection for "grip" based on the fine structural series is probably diminished.

Several alternative sequences of evolutionary morphological paths toward *annectens* and *onca* are discussed. The most likely sequence, in our judgment, begins with a generalized trunk-ground form, which, like *chrysolepis*, has a narrow pad and a few keels in the phalanx i region. Radiation into a more xeric habitat in which bare soil and sand becomes the common terrestrial component of the trunk-ground structural habitat, but in which trees and large open shrubs are still present, would select for the elaboration of the keels in the phalanx i region (the variant *A. whitemani* morphology) and perhaps expansion of keeled scales into the phalanx iii region (the *annectens* morphology). Finally, multicarinate scales replace lamellae and setae in the phalanx ii region (the *onca* morphology). The

complete substitution of multicarinate scales seems to be associated with the invasion of extreme xeric habitats a) where vegetation is scarce and selection for locomotion on loose sand is even more enhanced, and b) where the residual vegetation does not offer enough smooth surfaces nor select for behaviors which would maintain the setae and spike portions of the fine structural series.

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