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Development of the Subdigital Adhesive Pads of *Ptyodactylus guttatus* (Reptilia: Gekkonidae)

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ABSTRACT Subdigital adhesive pads play an important role in the locomotion of many species of gekkonid lizards. These pads consist of integrated components derived from the epidermis, dermis, vascular system, subcuticular tendons, and phalanges. These components become intimately associated with each other during the developmental differentiation of the digits and the sequence of this integration is outlined herein in *Ptyodactylus guttatus*. The pads initially appear as paired swellings at the distal tips of the digits. Subsequently, a fan-like array of naked scansors develops on the ventral surface of each digit, at about the same time that scales differentiate over the surface of the foot as a whole. At the time of appearance of the naked scansors, the vascular sinus system of the pad also differentiates, along with subcuticular connective tissue specializations. At this stage the digits, along with the rest of the body, are clad in an embryonic periderm. Only after hatching and as the periderm is shed, do the epidermal setae and spines appear. The developmental sequence described here is consistent with predictions previously advanced about the evolutionary origin and elaboration of subdigital pads in gekkonid lizards. The paucity of available staged embryonic material leaves many questions unresolved.

The presence of subdigital pads in gekkonid lizards has been recognized for more than two centuries (Linnaeus, 1758) and the form and function of these structures have attracted considerable attention. Similar structures have been noted more recently in the anolines (Iguanidae: Peterson, '83a,b) and at least one scincid lizard (*Prasinohaema virens*—Smith, '35; Williams and Peterson, '82). Most of the consideration of these structures has been directed toward their use as systematic characters (Boulenger, 1885; Underwood '54; Kluge, '67; Russell, '76), their functional morphology (Tandler, '03; Dellit, '34; Gourvest, '60; Maderson, '64; Hiller, '68; Russell, '75, '81, '86), and their biological role in the natural setting (Hecht, '52; Collette, '61).

It is now understood that the pads are adhesive devices that permit locomotion on a variety of substrata that cannot be negotiated with the employment of claws alone. The ultimate agents of adhesion are the minute setae borne in fields on the ventral surface of the pads (Tandler, '03; Dellit, '34; Mahendra, '41; Altevogt, '54; Hiller, '68; Maderson, '70; Nachtigall, '74). A great deal of attention has been devoted to the structure of the setae, their arrangement, and the surface morphology of the scansors on which they are borne (Nicolas, 1887; Schmidt, '05; Maderson, '64; Ruibal and Ernst, '65; Ernst and Ruibal, '66; Russell, '75; Peterson, '83a,b; Stork, '83; Bauer and Good, '86; Schleich and Kästle, '86). The mechanism of deployment of the setae has been elucidated through a series of detailed anatomical investigations (Dellit, '34; Ernst and Ruibal, '66; Russell, '75, '76, '81, '86) carried out chiefly on gekkonid lizards.

We thus have a reasonable understanding of the complexity of the adhesive process and its control, and comprehend the high degree of integration of anatomical systems involved in both the establishment and release of the adhesive bond. We know little, however, of the development of the adhesive sys-

We dedicate this paper to Professor Elazar Kochva on the occasion of his 65th birthday and in recognition of his contributions to zoology.

tem and the way in which the topographical arrangement of the mechanical units (Gans, '69) is brought about. Because the scansors on which the setae are borne are more complex in structure than scales (Russell '81, '86; Russell and Bauer, '90b), and because they bear precise relationships with deeper structures (not typical of the anatomical relationships of scales), it is through a developmental study that the establishment of the integration of the component parts can be followed.

Recent reviews of limb development (Hinchliffe and Johnson, '80; Raynaud, '85) describe external form and internal organization of the manus and pes of generalized lizards, but lack information on scansors and setae. Similarly, a recent survey of the development of reptilian skin (Maderson, '85) makes little mention of the integumentary components of the adhesive system. Thus, it remains to be established how developmental events differ between padless species and those with subdigital adhesive pads.

The sloughing cycle provides some information about the potential development of setae, since these structures must be generated and elaborated each time the outer epidermal generation is shed. As part of their study of the sloughing cycle of *Anolis* and *Aristelliger,* Ernst and Ruibal ('66) described the development of setae as extensions of cells that cover the scansors of *Anolis.* Setae are interpreted to be protrusions of the distal plasma membrane that are elaborated by the Oberhäutchen cells of the inner epidermal generation and supported by the clear layer cells of the outer epidermal generation. A new generation of setae develops within the epidermis and is ready to function after shedding (Ernst and Ruibal, '66; Maderson, '70; Russell, '86). This, however, relates to renewal and does not permit an assessment of how the components that ultimately govern the control of the setae are initially integrated. To date, no attempt has been made to document the synchronous change in form of developing digits, scansors, and setae. Study of such ontogenetic integration may assist in establishing how the mechanical units (Gans, '69) develop and provide clues to the evolutionary origin of subdigital pads. The present study describes the ontogeny of digits in the gecko *Ptyodactylus guttatus* (as recognized by Heimes, '87) using scanning electron microscopy (SEM) and light microscopy.

Ptyodactylus was selected for study of the development of the adhesive pad in gekkonid lizards because it exhibits all of the major components of a multiscansorial pad in a relatively simple configuration. Russell ('76; Fig. 3e) described *Ptyodactylus* as having a multiscansorial terminal pad and outlined the mechanical units involved. The basic components of this system are: a series of scansors located beneath the penultimate phalanx only; a system of scansorial flexor tendons derived from the tendon of the m. flexor digitorum longus; a scansorial retractor system derived from the mm. interossei dorsales; and a vascular sinus system associated with the scansors (Fig. 1). Such an arrangement of parts is relatively simple when compared to that of many other pad-bearing geckos (Russell, '76: Figs. 4, 5) and avoids the additional complexities of a scansorial system involving a series of phalanges, a lateral digital tendon system associated with the scansors, the incorporation of paraphalangeal elements into the pad (Russell and Bauer, '88), and a variety of other subtle modifications (Russell, '76).

MATERIALS AND METHODS

All specimens examined in this study (except the adult examined at the Natural History Museum, London and illustrated in Fig. 1) were collected by Y.L. Werner in central Israel, fixed in Bouin's fluid, and stored in 70% ethanol. Embryos were staged according to the system of Werner ('71); specimen numbers in the GK series refer to the collection of reptiles in the Department of Evolution, Systematics, and Ecology, The Hebrew University of Jerusalem. Material used in the present study consisted of the following Werner stages: L′, N, P, Q, R, V, juvenile and adult (see Table 1 and Fig. 3a,b in Werner, '71). Serial sections of the limbs were prepared by standard histological techniques (Humason, '79) and stained with Masson's trichrome. Other specimens to be examined by SEM were critical-point dried and coated with gold-palladium in a Polaron PS3 sputter coater. Observations were made with a JEOL JSM-35CF scanning electron microscope.

RESULTS

Each of the following descriptions of adhesive pad morphology is headed by a descriptive name given to the particular developmental stage, the specimen number of the prepared material, the developmental stage designation (see Werner, '71), and appropriate figure numbers.

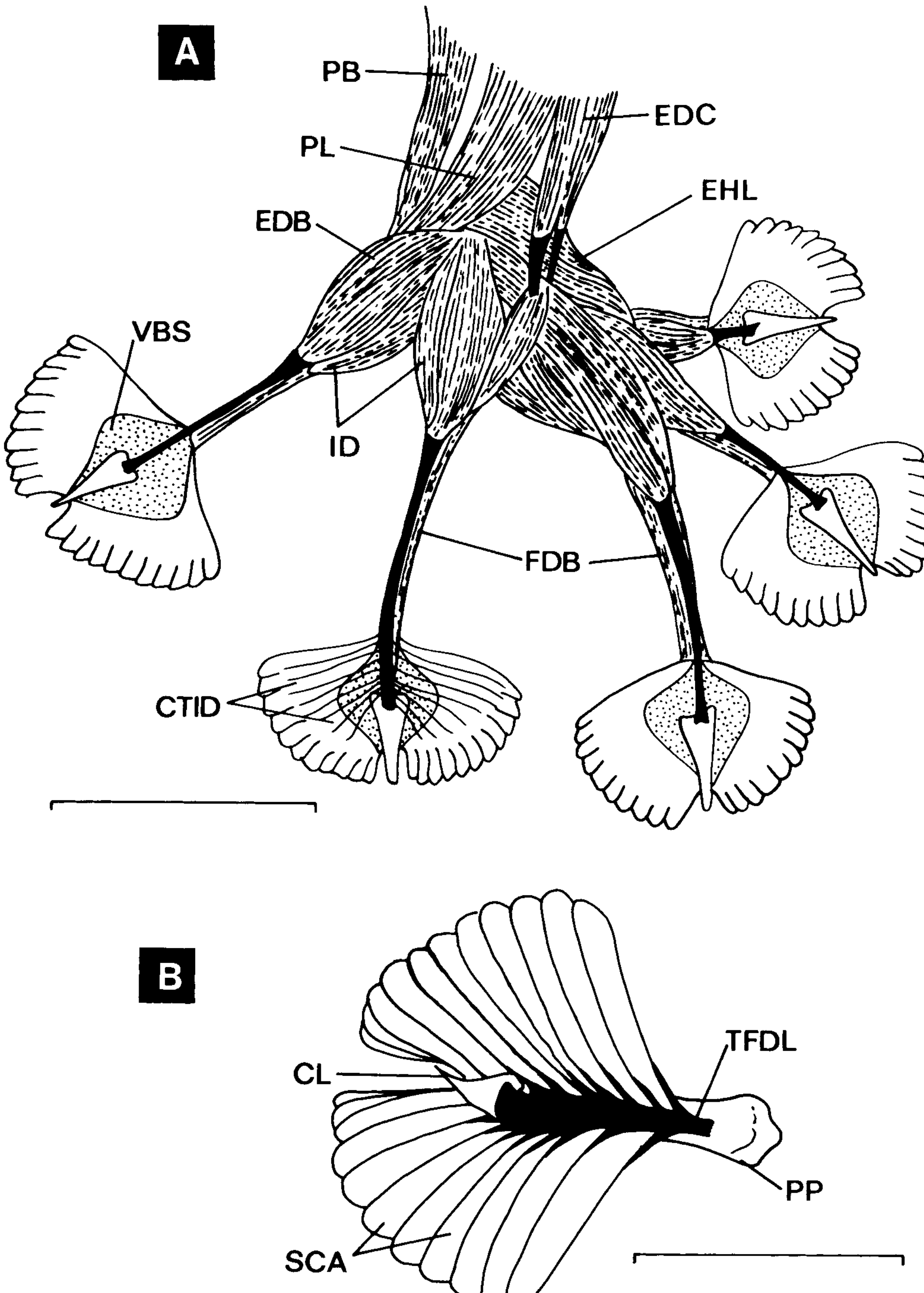

Fig. 1. *Ptyodactylus hasselquistii*. Basic morphology of the right pes showing the components of the scansorial mechanism. **A:** Dorsal aspect of BMNH 1954.1.5.40 showing extensor and flexor muscles, their tendons, and sinuses. Scale bar = 5 mm. **B:** Schematic ventral aspect with the branching tendon of the m. flexor digitorum longus superimposed. Scale bar = 2 mm. CL, claw; CTID, connective tissue strands associated with the mm. interossei dorsales that extend from the mid-line of the digit to the edges of the pad (depicted on digit IV only, but present on all digits); EDB, m. extensor digitorum brevis; EDC, m. extensor digitorum communis; EHL, m. extensor hallucis longus; FDB, accessory heads of the m. flexor digitorum brevis; ID, mm. interossei dorsales; PB, m. peroneus brevis; PL, m. peroneus longus; PP, penultimate phalanx; SCA, scansors; TFDL, tendon of the m. flexor digitorum longus; VBS, venous blood sinus.

Footplate with smooth margin (GK 98 II, Werner stage L′—Fig. 2A,C)

SEM

Dorsal and ventral surfaces are smooth and lack indications of developing digits or scales. The margin of the footplate is also smooth (Fig. 2A).

Sections

Transverse sections through the distal part of the footplate show a marginal blood vessel surrounded by a homogeneous mass of mesenchyme. Mitotic figures are clearly visible within the mass. The outermost layer of cells is slightly separated from the inner mass, resulting in a gap between the two. Sections through the more proximal portion of the footplate reveal two condensations of cells, marking the site of future carpals (Fig. 2C).

Footplate with five short projections (GK 101 IIIa; Werner stage N—Fig. 2B,D).

SEM

The surface of the footplate reflects development of five digits. The margin is clearly indented but most of the interdigital area is occupied by webbing (Fig. 2B) that is thinner than the forming digits. The epidermis is smooth and lacks indications of scales.

Sections

Cross sections of developing digits show their elliptical shape and a proximal mid-line ridge on the dorsal surface. The central axis of the distal part of each digit contains a circular aggregation of precartilage cells that are closely packed and increased in volume (Fig. 2D). Cartilage formation is more advanced proximally in the digits. A prominent blood vessel lies between the longitudinal axis of the digit and each lateral margin. The proximal parts of the digits are interconnected by a thin web. Here aggregations of mesenchyme cells with pyknotic nuclei reflect necrotic processes.

Footplate with five long projections (GK 99 II, Werner stage P and GK 75 III, Werner stage Q—Fig. 2E,F)

SEM

The digits are more fully formed and the webbing is greatly reduced. The tip of each digit has a central projection in the area of the presumptive claw. The ventral area of each digital tip contains a pair of rounded swellings marking the first external indication of the forming subdigital pad (Fig. 2E,F).

Sections

Patterns determined in earlier stages are clearly discernible. Internal structures develop along a proximal-to-distal gradient, with cartilage and presumptive muscle masses seen in proximal sections and only a circular condensation of precartilage cells in the distal sections. Serial sections indicate a change in shape of the digits along their longitudinal axis. The distal cross sections are pentagonal in outline, the intermediate sections oval, and the proximal sections circular.

Anlagen of subdigital pad and claw clearly defined (GK 185, Werner stage R—Fig. 3A–C)

SEM

The digits are elongated and lack interdigital webbing. The distal third of each digit is formed into an expanded, bilaterally rounded tip that will develop into the adhesive pad (Fig. 3A,B). However, at this stage of development, the epidermal surface is smooth and there are only the first indications of scale and scansor boundaries (see Fig. 3A, digit I). The central area of the distal tip of each digit is formed into a distinct, triangular projection that will form the claw. The ventral surface of the developing claw is continuous with the ventral surface of the developing pad. However, the base of the dorsal surface of the claw is surrounded by a U-shaped pocket.

Sections

Serial sections through the area of the developing pad indicate early differentiation of the developing claw. Thus, the primordium of the claw is a U-shaped layer that is open ventrally and surrounds the terminal phalanx (Fig. 3C). The cartilage of the terminal phalanx is laterally compressed; more proximal phalanges are roughly circular in cross section.

There are no other internal or external embryological features that can be linked to those of the adult adhesive pad. Internal cells that are ventral and ventro-lateral to the root of the claw are more concentrated than cells lateral or dorsal to the claw. The epidermis is thinnest in the dorso-lateral regions of the digit and a gap separates the epidermis from deeper layers in the lateral and ventral portions of the digit.

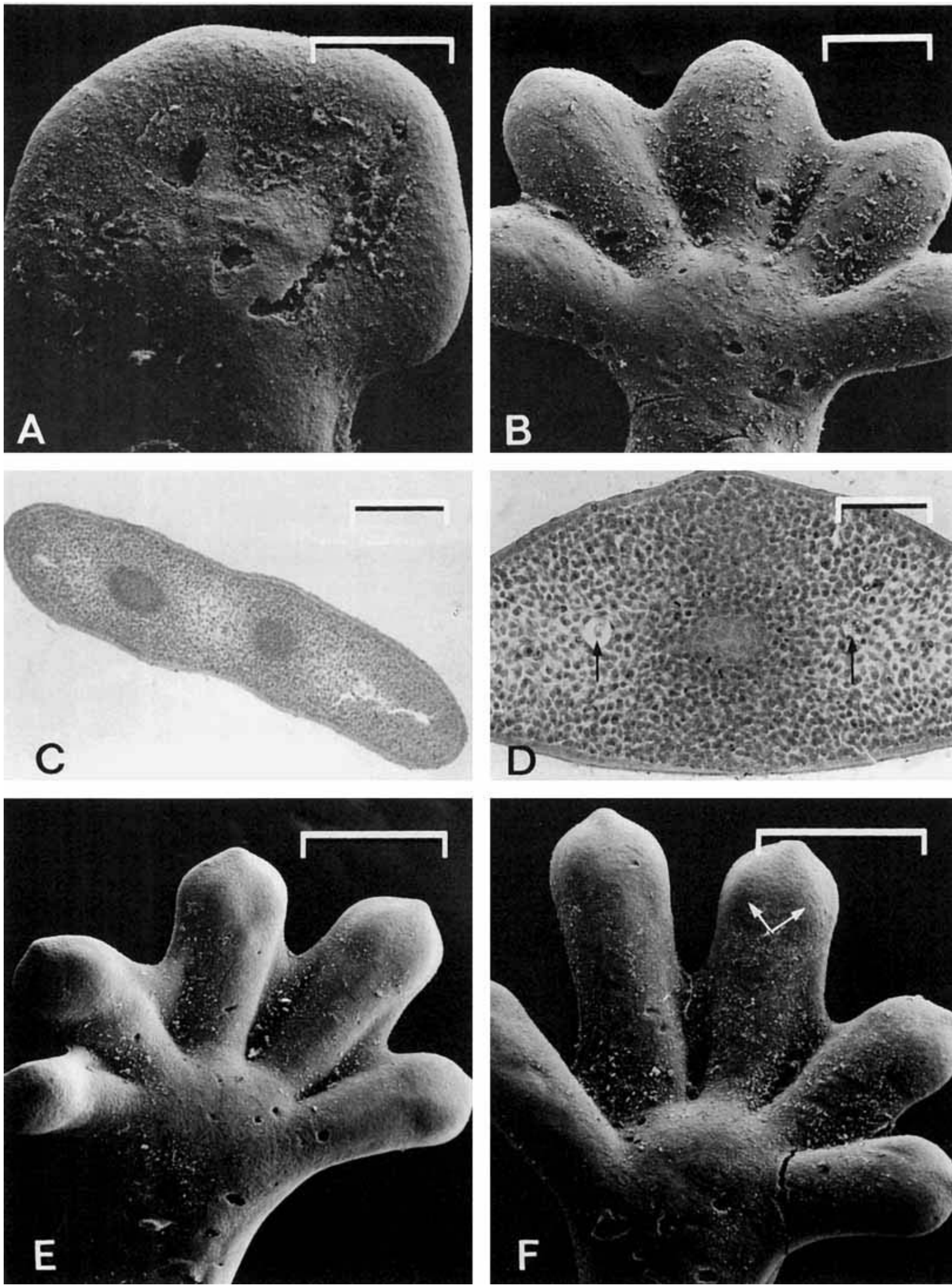

Fig. 2. *Ptyodactylus guttatus*. **A:** Werner stage L′, GK 98II, SEM showing ventral surface of footplate with smooth margin. Scale bar = 250 μm; **B:** Werner stage N, GK 101IIIa, SEM of ventral surface of early right manus showing formation of five digits. Scale bar = 250 μm. **C:** Werner stage L′, GK 98II, cross section through footplate showing two condensations of precartilage cells that will form carpals. Scale bar = 100 μm. **D:** Werner stage N, GK 101IIIa, cross section through digit showing development of central phalanx and paired, prominent vascular channels (arrows). Scale bar = 50 μm. **E:** Werner stage P, GK 99II, SEM of ventral surface of left manus showing the diminished interdigital webbing. Scale bar = 500 μm. **F:** Werner stage Q, GK 75III, SEM of ventral surface of right manus. Note the projection at the tip of each digit that will form the claw and the pair of swellings (arrows) that will form the subdigital pad. Scale bar = 500 μm.

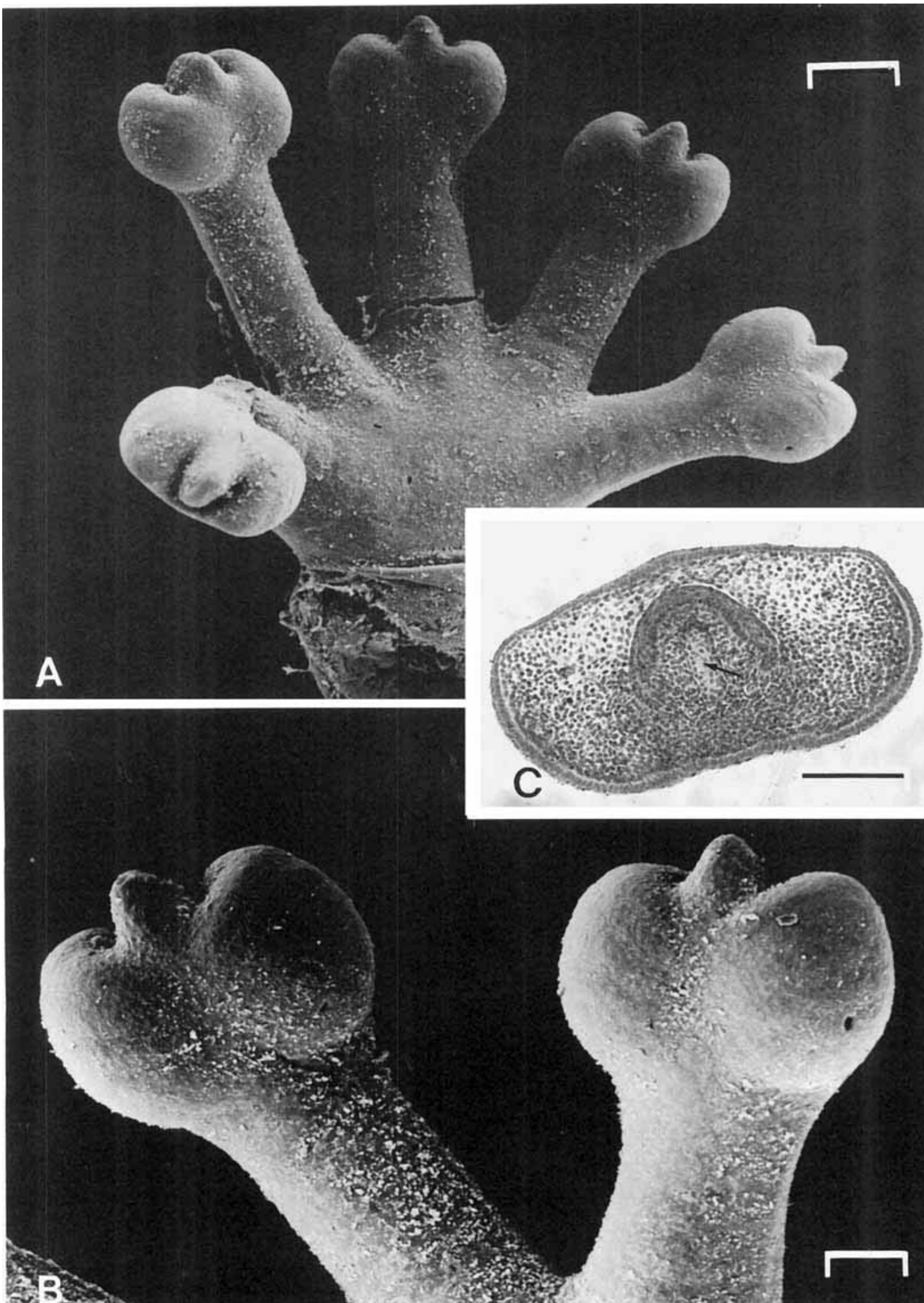

Figure 3

Subdigital pad with smooth scansors (GK 77, Werner stage V—Fig. 4A–D)

SEM

Scales cover the surface of the entire limb and the ventral surface of the pad consists of smooth scansors that lack setae. There are 11 pairs of scansors on the third digit of the manus and these are arranged in a fan-like configuration (Fig. 4B). The proximal margin of the pad is delimited ventrally by a series of small scales. Most of the ventral surface of the digit is covered with scales that are broader than they are long.

Sections

The amount of histological complexity has increased markedly at this stage of development and the entire surface of the animal is now covered with scales. The core of the digit contains a substantial cartilaginous axis and an extensive vascular sinus has developed in areas that formerly contained undifferentiated mesenchyne.

Transverse sections through the tip of the digit show the distal region of the scansors and their thickened epidermal covering (Fig. 4C). The covering shows a sequence of keratinization, with cellular detail being lost in the outermost regions of the epidermis. The pocket that surrounds the claw, and also the scales on the dorsal surface of the digit, have a thinner epidermis. There is no indication of spinules, spines, or setae associated with the superficial or deep layers of the epidermis.

Sections through the base of the claw indicate the manner in which it is closely associated with the cranial tip of the distal phalanx. The bilaterally symmetrical vascular sinus extends from the lateral surfaces of the penultimate and terminal phalanges and curves ventrally to the lateral margins of the adhesive pad. The sinus is traversed by supportive ties of connective tissue that extend wall to wall (Fig. 4D). Sinuses of the right and left side are confluent through a narrow, transverse channel that lies between the ventral surface of the phalanx and the mid-ventral surface of the adhesive pad. A prominent gap containing loose connective tissue lies between the sinus and the skin on the dorsolateral surface of the digit; the gap between the sinus and the scansors is smaller. These gaps may be an artifact of fixation, or may represent pulpal lymph sinuses (Ottaviani and Tazzi, '77).

Fig. 3. *Ptyodactylus guttatus.* Werner stage R, GK 185. **A:** SEM of ventral view of developing right manus. Note the expanded tips of the digits. Scale bar = 250 μm. **B:** SEM of digit I (to right) and digit II showing a central projection that will form the claw and a pair of bulbous swellings that will develop into the adhesive pad. The embryo is covered by a smooth periderm. Scale bar = 100 μm. **C:**Cross section through distal portion of digit showing U-shaped base of claw surrounding terminal phalanx (arrow). Mesenchyme cells are concentrated in mid-ventral and ventro-lateral regions; there is little else to indicate development of the components of the subdigital pad. Scale bar = 100 μm.

Post-hatching: juvenile has subdigital pad with scansors that bear setae (GK 195—Figs. 5A–C, 6A,B, 7)

SEM

The basic form of the manus has not changed significantly from that of the previous stage. The one major change is the appearance of densely packed setae on the scansors and spines on the more proximal scales of the mid-ventral surface of the digit. These spines have tips that are drawn out into sharp points (Fig. 6A,B) and shafts that are perpendicular to the surface of the scale. Small scales flanking the broad, mid-ventral scales are also covered with spines and some possess circular pits containing sensilla.

Setae located on the scansors are packed differently and have differently shaped tips. They are arranged along the free margin of the scansor and, thus, appear to be organized in curved rows (Fig. 5A). Most of the setae on a scansor are of approximately the same length (~49 μm), but a small proximal segment of each scansor has shorter setae and the most proximal segment of the scansor lacks them. Each seta is composed of a shaft that terminates in branched, parallel strands that have sharply truncated tips. Most of the seta is perpendicular to the surface of the scansor, but the distal end bends sharply and the tips face the mid-sagittal plane of the adhesive pad (Fig. 5B,C).

Sections

Setae are present on the ventral surface of each scansor, where they are restricted to the free margin. There is no indication of the next generation of setae even where the present generation has lifted off from its natural position. It appears that the integument of this specimen has been fixed in the resting phase of its cycle of epidermal activity (Ruibal and Ernst, '65).

An extensive system of vascular sinuses is present (Fig. 7). For the first time differenti-

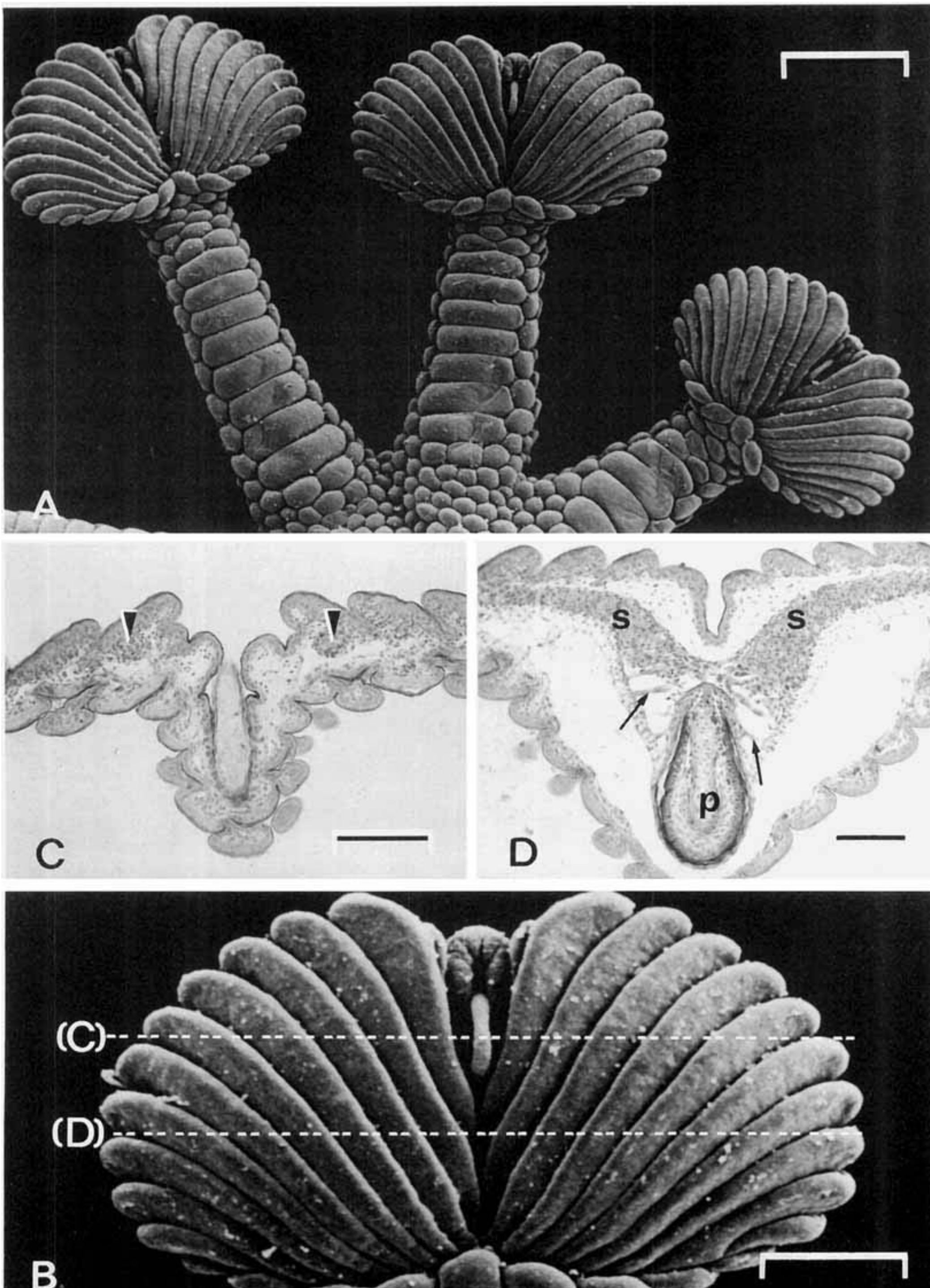

Figure 4

ated skeletal muscles are present and extend from the lateral surface of the phalanx to the medial edges of the scansors.

Post-hatching: adult has subdigital pad with scansors that bear setae (Fig. 8A–C)
SEM

The form of the subdigital adhesive pad resembles that of the juvenile. However, the central portion of the pad appears to be more highly ordered and the step-like effect caused by fields of setae having different lengths is obvious (Fig. 8A).

SEM preparations of the scales on the mid-ventral surface of the digit (Fig. 8B,C) show flaking of the surface covering, but no sign of the pointed spines seen in the juvenile stage (Fig. 6A,B). Small scales bordering the lateral margins of the scales on the mid-ventral surface of the digit each harbor several sensilla (Fig. 8B,C).

DISCUSSION

Werner stages L′, N, P, Q

These stages of embryological development, as characterized by the appearance of the autopod, are similar in most tetrapods (Hinchliffe and Johnson, '80; Raynaud, '85; Wanek et al., '89). Images derived from these four embryonic stages demonstrate that a flattened footplate develops into a pentadactyl manus. Internally are seen the development of condensations of cells that give rise to phalanges and muscles, areas of necrosis between the digits, and the simple pattern of blood vessels in loosely packed mesenchyme. The entire limb is covered by an epidermis that consists of two layers of cells: a flattened periderm lying atop cuboidal, germinal cells. In stage Q, the ventral tip of each digit bears two rounded swellings that contribute to the development of the subdigital pad.

Werner stage R

The subdigital swellings, first seen in stage Q, have expanded and altered the form of the distal end of the digit. The tips of most vertebrate digits are slightly tapered, but here the tip is greatly expanded.

Werner stage V

The ventral surface of the pad now bears an array of scansors that are symmetrically distributed on both sides of the centrally located claw and curve away from it (hence the generic name *Ptyodactylus,* meaning fan-toed). The number of pairs of scansors varies from digit to digit (Heimes, '87). There are no signs of setae or epidermal projections of any sort on the surface of the scansors or any of the scales of the digits. The previous stage lacked scales and scansors, but stage V exhibits both. The lack of preserved embryos between stages R and V prevents determining the sequence of appearance of scales and scansors (i.e., whether scales precede scansors and are their precursors, or whether both appear concurrently).

The bare scansors, unadorned by fields of setae, permit an unfettered view of the subdigital pad. The free margin of each plate follows an elongated, S-shaped curve that overlaps the base of the next more distal scansor. The longest scansors are in the middle of the right and left series, whereas the shortest lie at the two extremes of the series.

Although bare scansors resemble scales in a specialized configuration, sections through this region yield a clearer picture of the complex nature of the subdigital pad (see Russell, '81, '86). One of the most prominent features visible in sections is the bilaterally symmetrical vascular sinus, with branches occupying the expanded basal region of each scansor (Russell, '81). During loading, the confluence between right and left sinuses (Fig. 7) may be occluded as the mid-ventral surface of the penultimate phalanx presses against the mid-ventral groove of the pad. This would increase intra-sinus pressure and restrict the flow of blood into the sinus from the most lateral regions of the pad. The integrity of medial portions of the sinus system (the central reservoir, Russell, '81) is maintained by a series of transverse connective tissue ties that limit expansion of the sinus and maintain relatively high pressure. It has been

Fig. 4. *Ptyodactylus guttatus.* Werner stage V, GK 77. **A:** SEM of ventral surface showing digits I–III. Note the arrangement of scansors on the subdigital pad and scales on the remainder of the digit. Scale bar = 500 μm. **B:** SEM of ventral surface of subdigital pad on digit II. Note symmetrical arrangement of 11 pairs of scansors (most medial pair is partially hidden) and centrally located claw. Dashed lines indicate planes of sections depicted in Figure 4C,D. Scale bar = 250 μm. **C:** Cross section through claw and distal part of adhesive pad. Note overlapping scansors on ventral surface of pad near top of figure, wide central sulcus for accommodation of claw, smooth epidermal layer on scansors, and distal extensions of sinus system filling the core of each scansor (arrowheads). Scale bar = 100 μm. **D:** Cross section through distalmost phalanx (p), bilateral vascular sinus (s), and overlapping scansors at top of figure. Note the connective tissue ties (arrows) that connect walls of the sinuses. Scale bar = 100 μm.

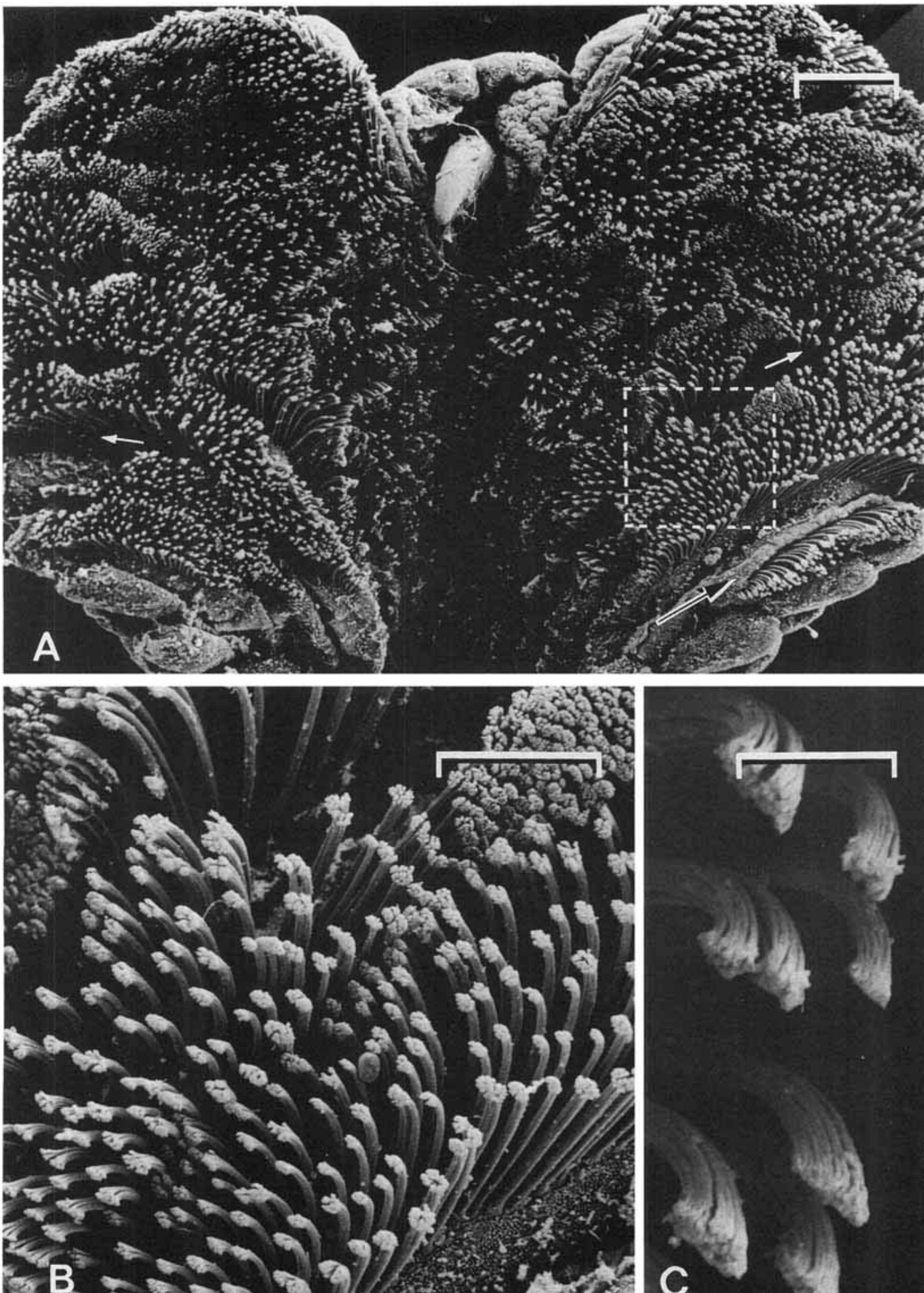

Figure 5

Fig. 5. *Ptyodactylus guttatus,* juvenile. GK 195. **A:** SEM of ventral surface of subdigital pad showing claw lying between fields of setae on scansors. The short, most lateral scansor (black arrow) is artificially separated from the adjacent scansors and clearly shows a row of setae projecting from its ventral surface. Irregular gaps separate setal fields of individual scansors (white arrows). Dashed box indicates area enlarged in Figure 4B. Scale bar = 100 μm. **B:** SEM of setae. Note orientation of shafts of setae, which lie parallel to each other and perpendicular to the ventral surface of the pad. The distal tips of the setae curve towards the mid-line of the digit. Scale bar = 50 μm. **C:** SEM of tips of setae. Note the subdivision of setae into branched tips. Scale bar = 10 μm.

postulated that the controlled bilateral flow of blood and its flow through a reticular network stiffens the bases of the individual scansors and allows the field of setae to conform to irregularities of the substrate (Russell, '81).

The developmental events outlined in Table 1 indicate the basic steps in the differentiation of the multiscansorial subdigital pad of *Ptyodactylus.* The early stages (L', N, P, Q) reveal that the integument, connective tissue, vasculature, and skeletal components of the forming pad have the same basic positional relationships to each other as is typical of the distal regions of the digits of adult lizards lacking adhesive pads (Fig. 9). These components bear distinct topographical relationships to each other, but do not exhibit the more precise integration seen in the fully differentiated digit (Russell, '76; Fig. 3e). By stage R, however, the distal tips of the digits have become expanded and the terminal phalanx has become compressed to form the core of the claw. At this stage, the distal tips of the digits have deviated markedly in form from those of primitively padless species, but the individual scansors and their control systems are not yet expressed.

Stage V reveals that scansors now have become differentiated, along with the appearance of scales on the foot as a whole. The vasculature at this stage has already expanded into a sinus system within the confines of the developing pad and has begun to become associated with the proximal region

Fig. 6. *Ptyodactylus guttatus,* juvenile. GK 195. **A:** SEM of scales on ventral surface of digit that are covered with spines and spikes (Peterson, '83a). Scale bar = 50 μm. **B:** SEM of spines with sharply tapered tips on ventral surface of digit. Scale bar = 5 μm.

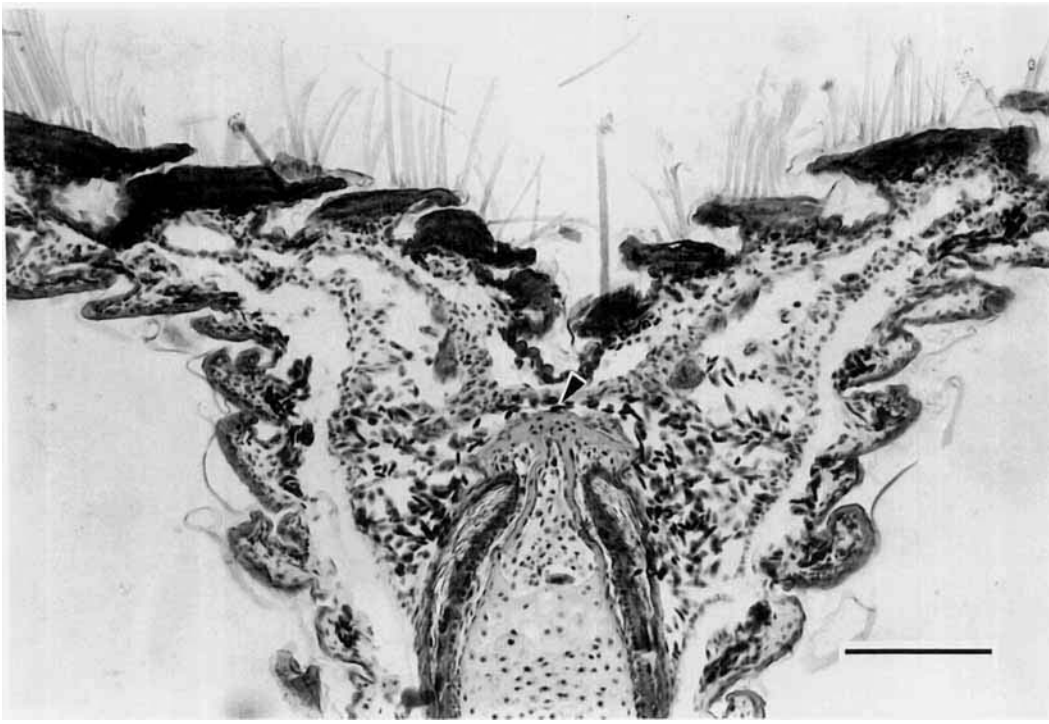

Fig. 7. *P. guttatus,* juvenile. GK 195. Cross section through subdigital pad. The right and left vascular sinuses occupy much of the core of the digit. The mid-ventral surface of the phalanx may serve as a plunger valve to occlude the vascular channel connecting the sinuses (arrowhead). Note numerous setae projecting from the free margins of the scansors. Scale bar = 100 μm.

of each developing scansor. Also at this stage, the muscles of the ventral surface of the digit have become differentiated, as have the branches of the tendon of the m. flexor digitorum longus that serve the proximoventral edge of each scansor. Thus, at this stage, the stratum compactum of the ventral surface of each scansor has become linked with the lateral branches of the tendon of the m. flexor digitorum longus to create a direct link between the flexor musculature and the scansors. It is this association that differentiates scansors from regular scales; the latter may be easily stripped away from underlying tissues, whereas the former cannot because their dermis is not free of direct integration and interconnection with underlying structures (Russell, '86). Between stages R and V, the transition between scales and scansors has occurred, indicating that the morphological changes necessary to distinguish the latter from the former take place relatively rapidly and involve considerable degrees of differentiation at a rather late stage of development. By stage V, the intricate interdigitating relationship of the venous sinus system and the flexor tendon control system (Russell, '81) has occurred. The scansors at this stage are, however, still devoid of setae, indicating that in ovo the scansorial control systems differentiate before the ultimate agents of adhesion (the setae).

Post-hatching

At the juvenile stage (after hatching has taken place), the scansorial system is fully

Fig. 8. *P. guttatus,* adult. **A:** SEM of ventral surface of central area of adhesive pad. Note the regular pattern of scansors and their corresponding rows of setae. The most proximal area of the scansor is bare, the next distal area contains short setae, and the remaining distal area contains longer setae. This produces a step-like effect. Scale bar = 250 μm. **B:** SEM of scales on ventral surface of digit just proximal to scansors (see Fig. 3A). The surface layer is fractured and partly sloughed. Note the sensilla on lateral scales (arrowheads). Scale bar = 100 μm. **C:** SEM of large plates on proximal region of digit. Note the smooth nature of the surface and see Discussion for possible explanation. Scale bar = 100 μm.

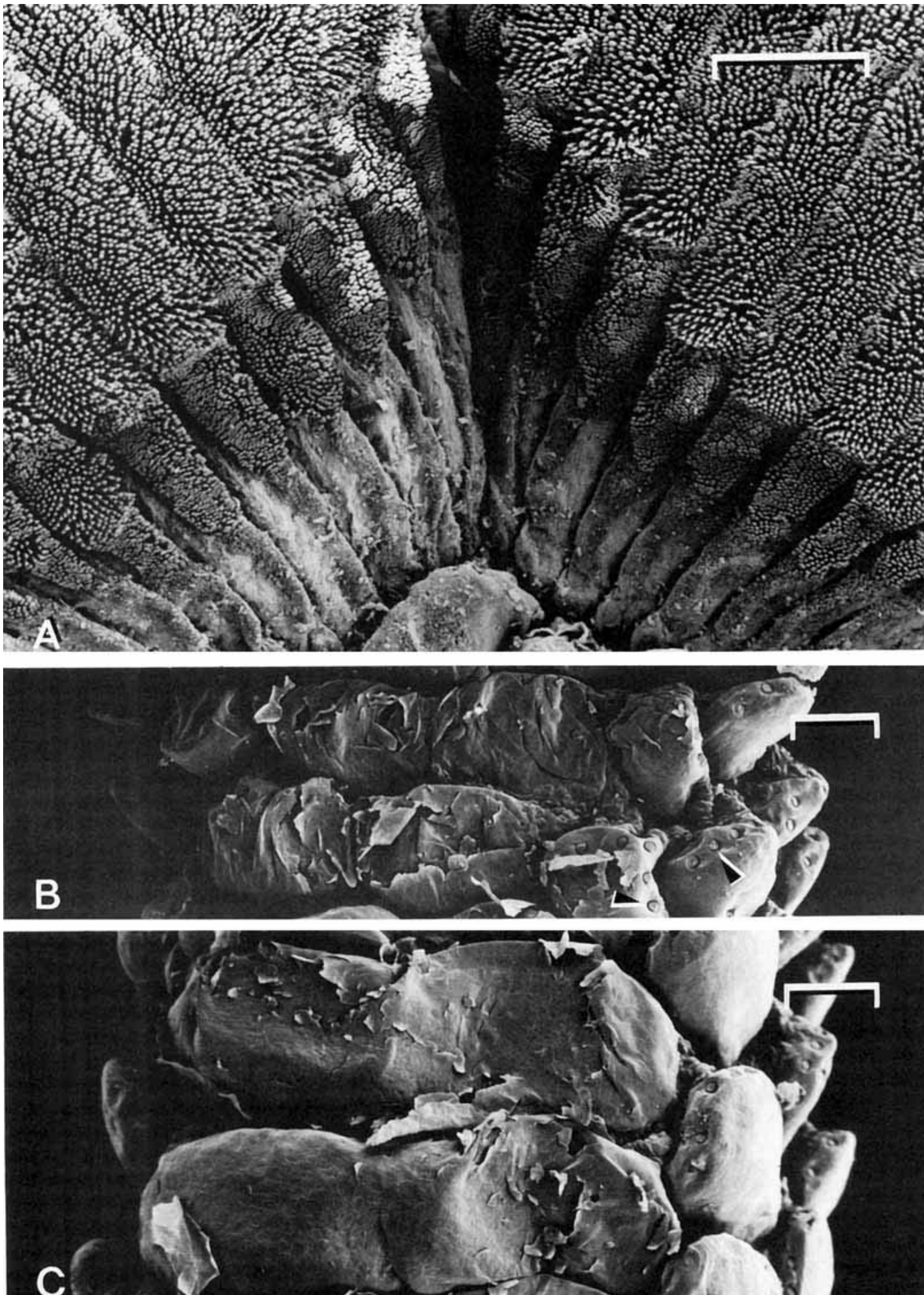

Figure 8

TABLE 1. The development of morphological components of the subdigital pad of P. guttatus

Stage	Integument	Vasculature	Connective tissue	Skeletal system
L′ (Footplate)	Smooth	Marginal vessels	Undifferentiated mesenchyne	Two proximal carpals
N (Footplate + five short digits)	Smooth	Marginal vessels	Undifferentiated mesenchyne	Condensation in center of phalanx
P, Q (Five longer digits)	Smooth + point on digital tip + pair of slight subdigital bulges	Marginal vessels	Undifferentiated mesenchyne	Condensation in center of phalanx
R (Flared digital tip)	Smooth + presumptive claw + pair of clear subdigital bulges	Marginal vessels	Undifferentiated mesenchyne + root of claw	Condensation in center of phalanx + terminal phalanx compressed
V (Subdigital pad + smooth scansors)	Scales + smooth scansors	Subdigital sinus	Tendons + muscle	Condensation in center of phalanx + terminal phalanx compressed
Juvenile (Setae present)	Scale + setae on scansors + spines on digit + sensilla	Subdigital sinus	Tendons + muscle	Condensation in center of phalanx + terminal phalanx compressed

differentiated and fully expressed, including the presence of setae. It is probable that a slough occurs at, or very soon after, hatching, in which the embryonic periderm is shed (Dhouailly and Maderson, '84) and the definitive outer epidermal generation is exposed (Maderson, '65: pp. 287, 291). This would bring about the free margin on each scansor (Russell, '81), make each scansor a fully functional unit (in the context of its adhesive properties), and reveal the sharp difference in epidermal ornamentation between the setae on the free margin of the scansors and the smaller spines and spikes elsewhere on the subdigital surface.

Figures 8B and C reveal a smooth rather than sculptured epidermis. This is probably an artifact of preservation and preparation in which the outer epidermal generation has been stripped away, revealing a smooth inner epidermal generation in the resting phase (Maderson, '70). This also is suggested by the fact that the sensilla are present as "buttons" only and lack the elongate, whiplike projections typical of such structures.

Russell ('76: Fig. 13; '77: Fig. 3) made some predictions about the evolution of adhesive pads in geckos from a primitively padless condition. These predictions were based upon morphotypic series within single genera that exhibit a wide array of foot morphology across broad geographic and ecological ranges. These morphotypic series incorporated statements about the integration of mechanical units as the transition from padless to pad-bearing digits was made. The current embryological study provides a way of testing the previously advocated hypotheses to determine whether the morphotypic and developmental sequences exhibit congruence.

Furthermore, it was emphasized that the differentiation of fully developed setae with

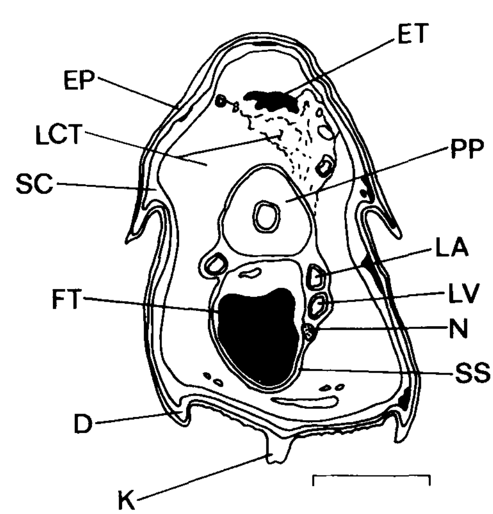

Fig. 9. *Ophisops elegans* (Lacertidae). Transverse section through the fourth toe of the left pes showing internal organization of a padless digit. D, dermis; EP, epidermis; ET, extensor tendon; FT, flexor tendon; K, keel on ventral scale; LCT, loose connective tissue; LA, lateral artery; LV, lateral vein; N, nerve; PP, penultimate phalanx; SC, subcutis; SS, synovial sheath. Scale bar = 0.2 mm.

spatulate distal tips should be preceded by hypertrophy of particular subdigital scales (Russell '76, '77). This was associated with specific modifications of the phalanges that eventually result in the possibility of digital hyperextension, modification of the extensor muscles of the digits to bring this about, and the association of the subdigital scales with branches of a flexor tendon system that establishes a firm connection between the integument and the underlying tissues. (A vascular sinus system was not incorporated as a necessary component as it is not universally present among pad-bearing geckos, although some form of cushioning of the pad is always involved. There is more than one way to bring about compliance with the substratum). The development of the digits of *Ptyodactylus* clearly is in accord with the predictions derived from the examination of morphotypic series of closely related forms and rationalizes the concept of the scale to scansor transition. In both development and phylogeny, the transition from scales to scansors is a late one and results from a series of elaborate integrations of components. The effective deployment of setae depends upon such integration (Russell and Bauer, '90a).

The developmental data presented in this study represent the first step in understanding the development of the subdigital adhesive system in gekkonid lizards. They reveal a considerable amount of detail about the relative timing of events and the way in which components become integrated to give rise to a fully functional scansorial system. Many details still remain elusive, however, due to our imperfect knowledge of gekkonid developmental biology. The only published data on gekkonid development (Werner, '71) lack details of absolute timing of events and do not provide sufficient detail in terms of the crucial stages of scansor development and differentiation. More complete series of embryos are required before the missing details can be established. The current paucity of staged (or stageable) embryonic material in herpetological collections (Alberch, '85) means that appropriate series must be assembled before such problems can be investigated further.

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