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On the Phylogeny of Hair

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The phylogenetic origin of the hair of mammals has puzzled comparative anatomists for a century. Many structures of lower vertebrates have been suggested as ancestral to the hair. Among them were certain tactile organs of fishes, amphibians, and reptiles; reptilian scales and birds' feathers were also suggested.

Reviews of these opinions have been presented by Oppenheimer (1895), Botezat (1914) and Pinkus (1927).

During a survey of elevations in the amphibian skin by Elias and Shapiro (1957), certain structures were found that resemble hairs. These recently found structures, when related appropriately to those previously described, seem to fill the remaining gap in our understanding of evolution of the scale of the Amniota and of the hair.

The feather, most probably a descendant of the scale, constitutes a phylogenetic side branch. It is not considered in the present discussion.

Let us first define the terms "scale" and "hair."

The scale of the Amniota (fig. 1) is a flat, slanting projection of the corium above the general level of the skin, covered by epidermis.

The hair (fig. 2) consists of a downward thickening of the epidermis into the lower end of which a corium papilla projects. From this downward thickening an extremely long and acute cone of epidermis projects above the general level of the skin; this projecting cone is surrounded by a ditch. The organ is innervated and can serve for the perception of pressure, but serves particularly for the perception of lateral displacement of its freely projecting part. Thus the mammalian hair functions as a sen-

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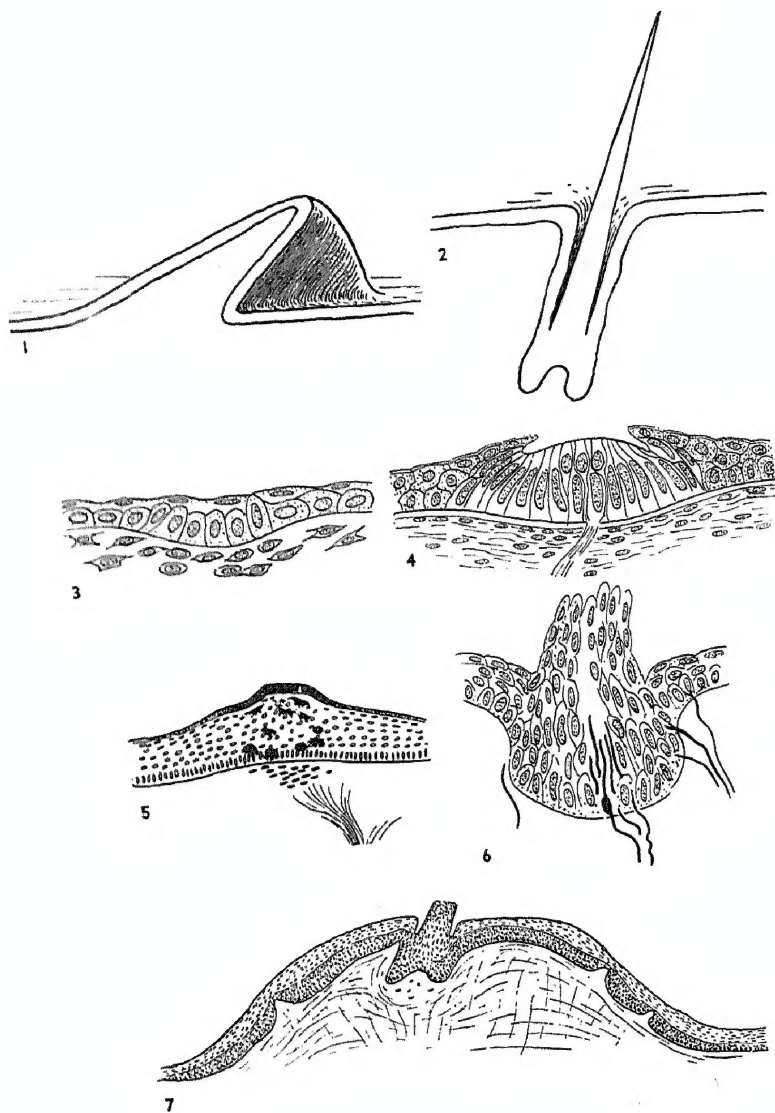


FIG. 1. Diagram of a scale of the Amniota.

FIG. 2. Diagram of a hair.

FIG. 3. "Nervous end hill" of trout, redrawn from Maurer (1892, fig. 23).

FIG. 4. "Nervous end hill" of *Squalus acanthias*, redrawn from Maurer (1892, fig. 29).

FIG. 5. "Tactile hill of frog," redrawn from Merkel (1880, pl. 9, fig. 5).

FIG. 6. "Sensory bud" of *Triton cristatus*, redrawn from Maurer (1892, fig. 29).

FIG. 7. "Sensory bud" on top of a wart of *Cryptobranchus allegheniensis*, redrawn from Maurer (1892, fig. 19).

sory organ which can detect objects located at a certain distance from the body surface as well as the direction of movements of substances such as soil, weeds, water, and air.

Organs of similar structure and function have been named as homologous to hairs. But the relation of hairs to scales (as it occurs in some mammals) has not yet been clarified.

Problems of phylogeny are essentially speculative in nature. Even speculation is hampered by the fact that it is not possible to examine the skin of the entire series of our direct ancestors. Therefore we must look for homologues among species that are more or less remote from the direct line of our ancestry. In these forms we may find vestiges of organs descended from their ancestors. These vestiges can be assigned a logical sequence of occurrence which may very well parallel the actual course of phylogeny.

As we can now add, to the data obtained by Merkel (1880), Maurer (1892), Oppenheimer (1895) and Schmidt (1920), our observations on the genera *Scaphiopus*, *Pipa*, and *Bufo*, we are able to present a fairly complete series of evolutionary stages of the forerunners of hair.

Again, because our direct ancestral lineage is no longer accessible for histological investigation, the series of hypothetical stages is not one of taxonomic succession.

A HYPOTHESIS ON THE EVOLUTION OF HAIR

A forerunner of the hair may be called a protothrix (plural: proto-triches).¹

The simplest prototriches are downward thickenings of the epidermis as found by Maurer in the trout (fig. 3) and in the shark and by Oppenheimer in *Sphenodon* (= *Hatteria*). These very simple prototriches are innervated by afferent nerves. They resemble the earliest primordium of a hair in a mammalian embryo.

In the skin of a frog, Merkel (1880) found epidermal thickenings which project above the level of the skin only (fig. 5). This would be called, in the nomenclature introduced by Elias and Shapiro (1957) for amphibian skin elevations, a "verruca epithelialis." With some reservations it may be suggested that it is homologous to the shaft of a hair.

A primitive form of protothrix which combines downward epithelial thickening, upward projection, and a peripheral ditch is a sensory organ found by Maurer in the shark and reproduced here as figure 4. This organ is a lens-shaped, epidermal thickening which projects only slightly

¹ πρωτότος = original, earliest; θρίξ, τριχός = hair.

downward and upward. It is surrounded by a sharp, low rim which produces a peripheral ditch.

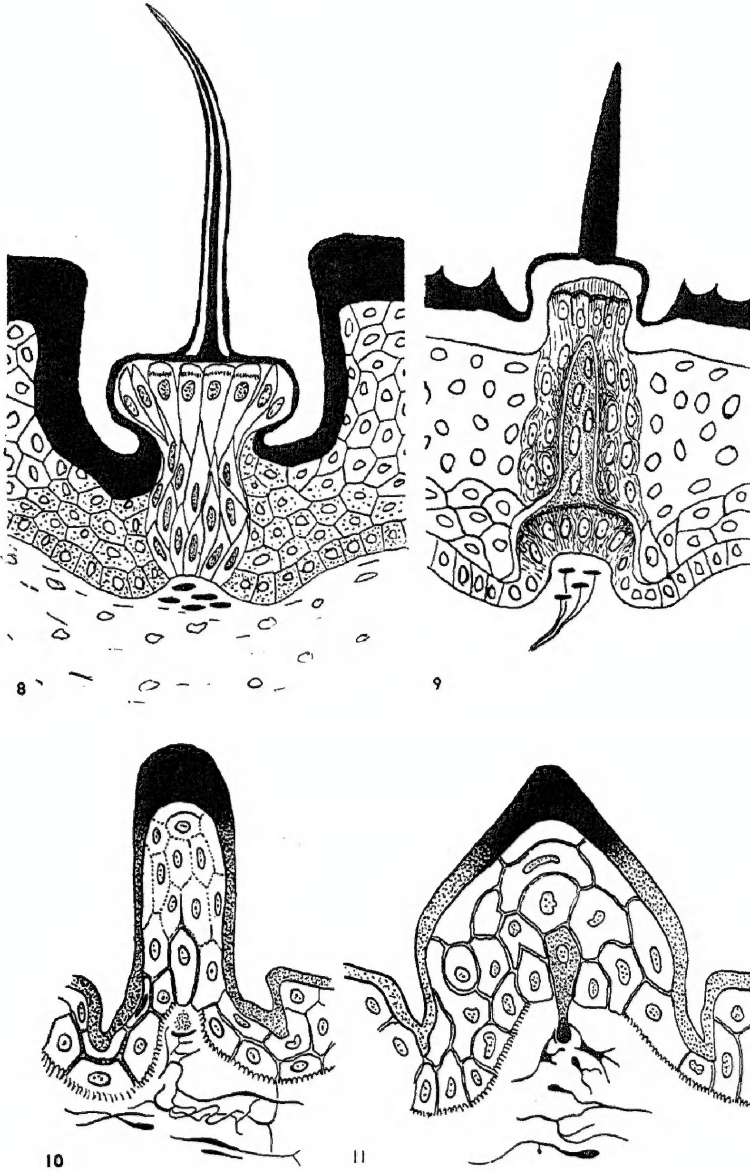
Next in the advancing series of prototriches appear sensory organs in the skin of tailed amphibians such as *Triton cristatus* (fig. 6). This organ resembles a hair much more than do the preceding ones. It consists of a rather large downward projection of the epidermis reaching three to four layers of columnar cells into the corium and of a cylindrical upper portion projecting three layers of columnar cells above the skin surface. The upper cylinder is surrounded by a sharp ditch.

A still more hair-like organ was found, again by Maurer, in another caudate amphibian, *Cryptobranchus*. One of them is shown on the top of a wart in figure 7. This "sensory bud" might be regarded as a diagrammatically shortened hair. Its "follicle" is a downward projecting cylinder which is indented at its lower end by a small corium papilla. Its outward projecting cylinder, being thinner than the deep portion of the organ, is surrounded by a sharply pronounced ditch.

Also in the skin of reptiles, sensory organs have been found which have the above specified character of hairs, though they are not so long in either direction. Such prototriches have been described by Schmidt; his most striking prototrix, found in the lizard *Agama colonorum*, is shown in our figure 8. Preiss (1922) showed similar prototriches, "tactile bristles" (fig. 9), in other members of the Agamidae and showed that these bristles are replaced in a manner very similar to the mode of mammalian hair replacement.

Revealing conditions are found in some toads, and especially in the primitive genus *Scaphiopus* (spadefoot toads).¹ We are indebted for specimens of this important group to Dr. Arthur N. Bragg of the University of Oklahoma, Dr. Albert P. Blair of the University of Tulsa, and to Mr. Charles M. Bogert of the American Museum of Natural History. The spadefoot toads bear projections on the skin which are capped by a thickened, blackened stratum corneum, frequently of spike-like acuity (fig. 12). Each is surrounded by a ditch (figs. 10, 11, and 12). Beneath the ditch, the epidermis may project a little downward. There is always a corium papilla projecting into the organ from below. This papilla contains a tactile corpuscle of the Meissner type (figs. 12, 14, 15, and 18). In some specimens (especially *S. hurteri*) flask-shaped cells occur in the basal layer of the epidermis, the "neck" projecting downward into the

¹ The approximate number of *Scaphiopus* specimens examined is as follows: *S. hammondi*, three or four; *S. hurteri*, 10 to 11; *S. couchi*, two; *S. bombifrons*, three; *S. holbrooki*, 15 to 20.



FIGS. 8, 9. *Agama colonorum*. 8. "Sensory organ," redrawn from Schmidt (1920, fig. 11). 9. "Tactile bristle," showing replacement similar to hair replacement, redrawn from Pinkus (1927, fig. 2, after Preiss, 1922).

FIGS. 10, 11. *Coni circumfossati* of *Scaphiopus hurteri*. 10. With tactile corpuscle. 11. With flask cell (gold chloride impregnation).

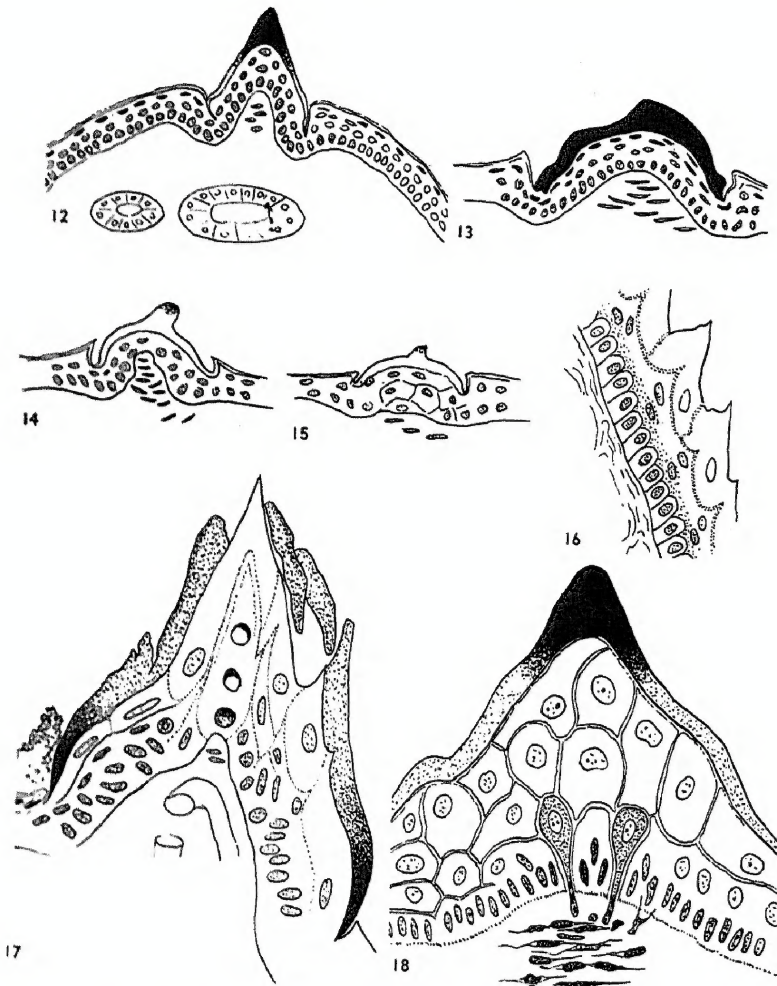


FIG. 12. Conus circumfossatus of *Scaphiopus couchi*.

FIGS. 13-15. Coni circumfossati. 13. *Scaphiopus hurteri*. 14, 15. *Scaphiopus bombifrons*.

FIG. 16. Verrucae unicellulares on sloping surface of a large conus circumfossatus of *Pipa pipa*.

FIG. 17. Conus circumfossatus of *Pipa pipa (americana)*.

FIG. 18. Verruca epithelialis of *Bufo americanus*, with conus apicalis, flask cells, and tactile corpuscle (gold chloride impregnation).

corium papilla (fig. 11, and fig. 10 in tangential section), and this long neck of the flask cell is in contact with the terminal arborizations of nervous elements (fig. 11). Obviously, these organs must be capable of perceiving stimuli of pressure and of lateral displacement. Within a general classification of various kinds of skin thickenings of Salientia, they were named "coni circumfossati"¹ (Elias and Shapiro, 1957). Because of their

¹ *Fossa* = ditch.



FIGS. 19, 20. Tangential view of skin. 19. *Scaphiopus hammondi*. 20. *Scaphiopus bombifrons*.

resemblance to hairs in structure and probable tactile function, the conical circumfossate of spadefoot toads are considered among the prototriches.

When one reads the enlightening account by Bragg (1944) on the mode of life of the spadefoot toads, it becomes obvious that these animals, who spend the day underground and emerge only at night, would be greatly benefited by a tactile apparatus of this kind.

Within the genus *Scaphiopus* the conical circumfossate undergo certain changes. The most constant and perfect structure of the prototriches (conical circumfossate) is found in *S. hammondi* (fig. 19), and to a lesser degree of perfection in *S. couchi* (fig. 12) and in *S. holbrooki* (fig. 11). In *S. hammondi* the prototriches have the shape of sharply pointed cones. In *S. couchi* and *S. holbrooki* they are less sharp. In *S. hurteri* a great variety of shapes of prototriches can be found among various individuals of the same species and sometimes even in the skin of a single specimen. The prototriches of this species may be perfect cones, as those of *S. hammondi*, *S. couchi*, and *S. holbrooki*, or they may be long cylinders, similar to hairs, with rounded apices (fig. 10). They may have the shape of

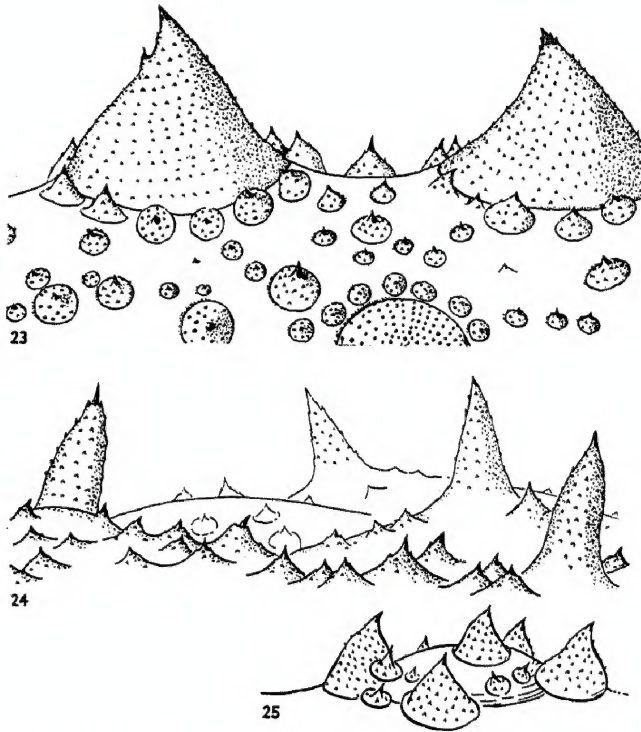


FIGS. 21, 22. Tangential view of skin. 21. *Scaphiopus hurteri*. 22. *Scaphiopus holbrooki*.

hemispheres or of flat disks, occasionally with a slight, central depression (fig. 21), or they may have an irregular surface (fig. 12). In *S. bombifrons*, the prototriches undergo a reduction to a very low hemisphere, sometimes scarcely projecting above the skin, with a central, nipple-shaped apex (figs. 14, 15).

However these prototriches of *Scaphiopus* are shaped, they all possess a considerably thickened and often blackened stratum corneum, and they all are surrounded by conspicuous ditches. Especially in the prototriches of *S. hurteri*, in which the apices are obtuse, the stratum corneum reaches with a sharp edge to the bottom of the ditch, suggesting that its pressure may be perceived by free nerve endings in the epidermis below the ditch (fig. 13). A specific regularity of arrangement of prototriches in relation to warts is a typical characteristic of each species.

The largest prototriches are macroscopically visible cones of *Pipa pipa*. Specimens of that interesting South American toad were obtained



FIGS. 23-25. *Pipa pipa*. 23. Dorsal skin. 24. Ventral skin. 25. Oblong wart on the lateral line showing five large coni circumfossati associated with this wart in typical arrangement.

through Mr. Charles M. Bogert. The core of these cones consists chiefly of connective tissue. The largest cones of the dorsum also contain glands. Their walls are studded with sharp, unicellular projections (verrucae unicellulares, fig. 16). At their apices they bear a sharp spine of stratum corneum (figs. 23, 24); they are surrounded by a ditch (fig. 17), and there is a slight downward thickening of the epidermis below the ditch. Obviously, these warts, some of which are macroscopic but many more of which are microscopic, are coni circumfossati. It is further evident from some features of their arrangement that these large and small cones of *Pipa* are homologous to the small prototriches of *Scaphiopus*. While the macroscopic cones are irregularly and rather evenly distributed over the entire body, some are related to large, compound warts. Oval warts are located in linear arrangement along a lateral and a dorsolateral line. The base line of each compound wart is an ellipse, the long axis directed parasagittally, the short axis transversely. On the apex, there is located a medium-sized, macroscopic conus circumfossatus (fig. 25). Four larger

cones are located at ends of the main axes of the ellipse. Between these large cones are many microscopic ones. Many of the large cones on the general skin are surrounded by a neat circle of microscopic cones (fig. 23).

Through their structure, they appear to be well formed for perception of tactile stimuli. Pressure stimuli can probably be transmitted by the sharp edges of the heavy stratum corneum upon the bottom of the ditch (fig. 17). Lateral displacement of these warts by external objects is facilitated by the keratinized spine at the apex and by the numerous microscopic, horny papillae unicellulares with which the sides of the warts are studded. When lateral displacement occurs, it can be expected that the edge of the stratum corneum in the ditch exerts unilateral pressure, facilitating the perception of the direction of the lateral displacement.

While the conical ones on the dorsum are broad cones (fig. 23), the large ones at the ventral surface, particularly in the cervical region, are tall and towering (fig. 24). One might safely venture that the animal can orient itself by means of these projections. (Unfortunately, the toads that we obtained from the American Museum were not preserved in such a way that nerves could be demonstrated.)

Finally, we must consider the "conical apical," i.e., horny spines, that are found on the tops and walls of warts among the Bufonidae. The European toad, *Bufo vulgaris*, was at one time called *B. spinosus* because of their presence. But the American toad, *Bufo americanus*, is no less spinous than its European counterpart. In *B. fowleri* the apical cones of the warts are pointed but form only obtuse angles. The warts of *Bufo americanus* are very varied in their internal structure. Our figure 18 shows a medium-sized verruca epithelialis. The apices of these warts in *Bufo* are innervated by free nerve endings in the epidermis. Some contain flask cells as described for *Scaphiopus hurteri*; others are provided with a thin, apical corium papilla containing a tactile corpuscle. The wart shown in figure 18 has both.

These conical apical ones of *Bufo* are not surrounded by a ditch and would have eluded consideration as homologous to hairs were it not for their resemblance to the conical circumfossate ones of *Scaphiopus* and *Pipa*.

RELATIONSHIP OF AMPHIBIAN WARTS AND PROTOTRICHES TO SCALES OF AMNIOTA AND TO HAIRS

The conical apical ones of *Bufo*, though homologous to hairs, are not classed among the prototriches, because they are not circumfossate. Yet they hold the key to an understanding of the relationship of scales to hairs. Quite characteristically, in *Bufo americanus* and *B. fowleri* every wart,

regardless of size and internal structure, is crowned by a sharp and thick cone of blackened stratum corneum, the conus apicalis.

In *Scaphiopus hammondi* (fig. 19) and *S. couchi* every wart is crowned by a protothrix larger and more darkly colored than the other prototriches. In some specimens of *S. hurteri* a very similar arrangement, slightly modified, can be observed: the rounded top of the wart bears a relatively large and dark protothrix, and there is a gradual diminution in size and degree of darkness among the prototriches from the top of the wart to the valleys between warts.

One will also observe that each apical protothrix of *S. hammondi* is surrounded by a circular area free from prototriches and free from melanophores. The same can be observed in *S. couchi* (Elias and Shapiro, 1957, fig. 9).

This condition, we venture, is the original, primitive condition of the Scaphopodidae. It is an arrangement of strict regularity. The slightly larger and darker apical protothrix is obviously homologous to the generally single conus apicalis of *Bufo*.

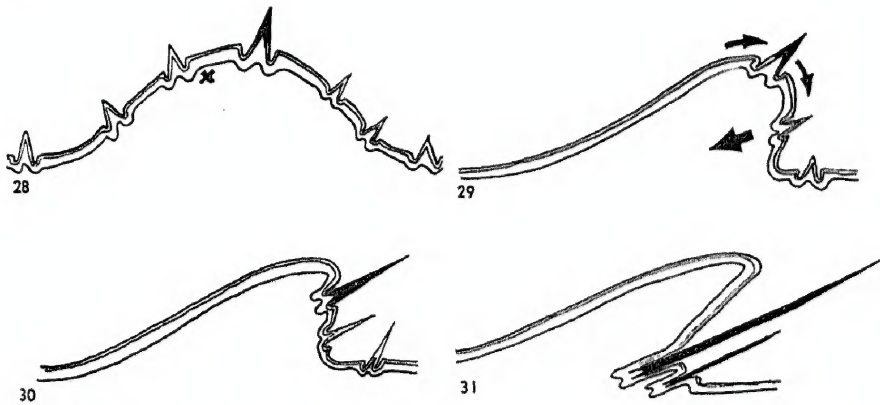
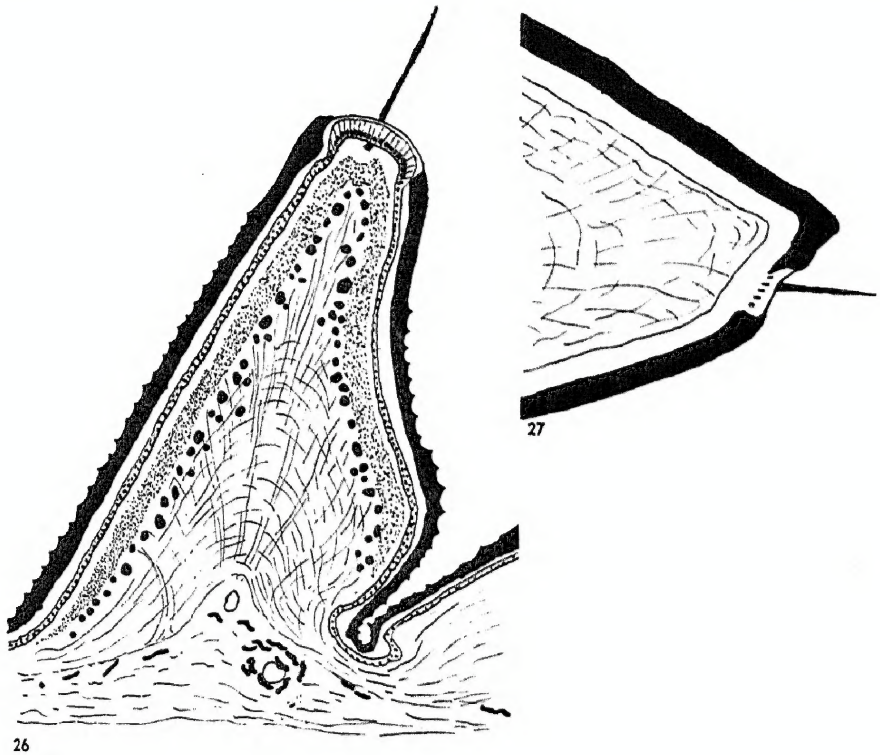
In *S. hurteri* we find a loss of this strict regularity. Even in the most conservative specimens, the protothrix-free halo around the apical protothrix has been lost. There is an almost even distribution of prototriches. In other specimens of the same species, the strictly conical shape of the prototriches is lost; and, though the apical protothrix is still the largest, there is a great and irregular variety of shapes (fig. 21).

In *S. bombifrons* (fig. 20) the apical protothrix has become very greatly enlarged and flattened and has acquired a rough surface, and the non-apical prototriches have become reduced in prominence, but the free halo surrounding the apex is well developed.

Finally, in *S. holbrooki* (fig. 22) the apical protothrix is almost fully degenerated. It is reduced to a dark, round patch in the stratum corneum, only occasionally slightly thickened. This apical spot is surrounded by a circular area devoid of melanophores and prototriches. The remaining prototriches, sharp coni circumfossati with tactile corpuscles, are evenly distributed over the entire skin, avoiding only the apical patch and halo of each wart.¹

Returning now to Schmidt's observations on Agamidae we find, among

¹ This arbitrary sequence suggests a specific phylogenetic arrangement. It is not identical with the phylogenies of the Scaphiopodidae suggested by others, as presented and modified in Bragg's review (1945). Skeletal structure, behavior, and skin structure each suggests a different line of evolution. It might be that the recent species of this family are not descendants one of another, but that each now existing species arose through cross breeding of several varieties of species now extinct.



FIGS. 26, 27. Scales of *Calotes*. 26. With apical, sensory bristle, redrawn from Schmidt (1920, fig. 15). 27. With subapical, sensory bristle, redrawn from Schmidt (1920, fig. 9).

FIGS. 28-31. A hypothetical sequence explaining the evolution of the mammalian scale with retrosquamous hairs (fig. 31) from the wart and prototriches (fig. 28).

his figures of scales of *Calotes jubatus*, scales which, except for a slight slant, resemble very much the warts of *Pipa pipa*.

One of these scales of *Calotes* is reproduced in our figure 26. It bears a sensory bristle at the apex, very similar to the spine (conus apicalis) of *Bufo*. Its side walls are lined with a jagged stratum corneum, as are the cones of *Pipa*.

Because the core of this scale consists of connective tissue, it may be homologous to an amphibian verruca syndesmica with conus apicalis. If this is so, then this scale should be homologous also to a wart with apical protothrix of *Scaphiopus*.

Another scale of *Calotes* with an almost apical sensory bristle, but located slightly below and behind the apex of the slanting scale, was demonstrated by Schmidt (our fig. 27). There is no reason to assume that this bristle, because it is not located exactly at the apex of the scale, should not be considered homologous to one at the exact apex.

If we find, in mammals, hairs that are located behind scales, it is not unreasonable to imagine that these also are homologous to the original, apical conus of *Bufo* and of *Scaphiopus*. We usually find, in scaled mammals, a group of three or more hairs placed behind each scale. The central hair is larger than the lateral ones. It may be suggested that the central hair is homologous to the apical protothrix, while the accompanying smaller hairs are homologous to smaller prototriches growing on the slopes of amphibian warts.

Figures 28 to 31 show the hypothetical course of evolution of scales from warts and of retrosquamous hairs from prototriches. Figure 28 shows a verruca syndesmica of the *Scaphiopus hammondi* type. This verruca is caudally inclined in figure 29, and the cranial prototriches have disappeared. It resembles the scale of *Calotes* shown in figure 26. As the wart inclines more (fig. 30), the apical protothrix appears to have moved back and downward until, in the mammals, the hair (thrix) occupies a position behind the scale (fig. 31). However, a movement of a structure from one place to another is phylogenetically unacceptable. It seems more conservative to assume that a kind of uneven "growth" has taken place during the course of evolution in such a way that the connective tissue under the caudal slope has undergone atrophy so that a "vacuum" has been created at this location, exerting a cranially directed negative pressure upon the surface of the wart. In this manner, the epidermis has gradually slipped into the caudal depression thus created. The former apex of the wart has thus become drawn into the retrosquamous sulcus, while a point (marked with an x in figure 28) previously located on the cranial slope of the wart has become the new apex of the scale.

There are also mammals with grouped hairs but without scales. The evolution of their hair arrangement can be explained as follows. The warts of *Scaphiopus hammondi* are quite flat (fig. 13). In a different line of evolution it may be assumed that the warts disappeared completely, but that the prototriches remained in their original grouping which was based on their location on warts. The circular grouping of small circumfossated cones around a large one as seen on flat skin surfaces of *Pipa* (fig. 23) may be the result of an identical evolutionary process.

Finally, there are mammals in which the hairs are irregularly distributed over large areas.

Such even and irregular distribution is found in the interverrucal areas of all spadefoot toads (figs. 19-20) and also among many of the large as well as small cones of *Pipa*.

SUMMARY

Thickenings of the epidermis that project downward and upward, the outward projections of which are surrounded by circular ditches, and that perform a mechanico-sensory function are considered forerunners of hairs (prototriches).

Findings of previous observers on such structures in fishes, tailed amphibians, and reptiles are combined with new observations on skin projections of some Salientia to devise a theory of hair and scale evolution. The most primitive prototriches are simple downward thickenings of the epidermis (fishes). In the next stage, a small corium papilla pushes into the epidermal downward thickening and a slight external elevation is added (tailed amphibians). Further phases involve keratinized, sharp, conical projections with circular ditches (coni circumfossati) in spadefoot toads.

In some reptiles sensory bristles of similar structure present another phase.

The prototriches in tailless amphibians are arranged in characteristic patterns on the warts.

Transitional phases between protothrix-studded warts and scale-hair combinations can be shown.

The theory is advanced that while the hairs derive from the prototriches, the scales of Amniota derive from warts of amphibians.

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