LIZARD

by Anthony P. Russell

Lizard

The family Gekkonidae is distributed circumglobally between 50°N and 50°S, and its more than 650 species are currently arranged in four subfamilies. Three of these include members with digits remarkably modified for climbing. The digits have expanded pads bearing setae on the ventral surface. These minute, hairlike outgrowths (Figs. 1*k* and 4) are epidermal derivatives and thus part of the skin. They are composed of β-keratin (a tough protein substance also found in feathers) and produce the bond between organism and locomotor surface. Research has indicated that these climbing pads have been developed independently in the different groups of geckos, providing a good example of parallel evolution. Recent interest has centered upon complex internal modifications associated with the external structures and aspects of the adhesive process.

External form of digits. The pads are expansions beneath various parts of the digit, depending upon the genus (Fig. 1). The expansions are, in essence, modified scales but also possess some deeper components. The pads are composed of lamellae (Fig. 2*c*) numbering from a single terminal pair to from two to many divided or undivided overlapping plates (Fig. 1). The setae, which cover the pad surfaces, have spatulate terminal tips (Figs. 1*k* and 4) and may be branched. Typical dimensions of these setae are 0.5–5.0 μm in diameter at the widest point of the shaft, 0.2–0.75 μm in width across the spatula, and 12–100 μm in length, depending on the species and the degree of branching (Fig. 1*k*). In the tokay gecko, a well-known species from southeastern Asia, it has been estimated that there are about a million setae on all 20 digits combined. With the profuse branching of the setal tips (Fig. 1*k*) this gives rise to many millions of spatulae potentially able to make contact with the locomotor substratum.

The setae are elaborations of the fine spinules that are present over the entire body surface of geckos (Fig. 4*e*). The spinules are visible with the scanning electron microscope, and they are generally less than a micrometer in height. The setae, being larger, are fewer in number per unit area than the spinules. Almost all other lizards have a nonspinulate epidermis. An exception is the anoline lizards (family Iguanidae), which have both a spinulate epidermis and climbing pads (Fig. 4*f*) that are structurally and mechanically very similar to those of geckos. In this respect geckos and anoles represent a major example of convergent evolution.

Other epidermal modifications, in the form of

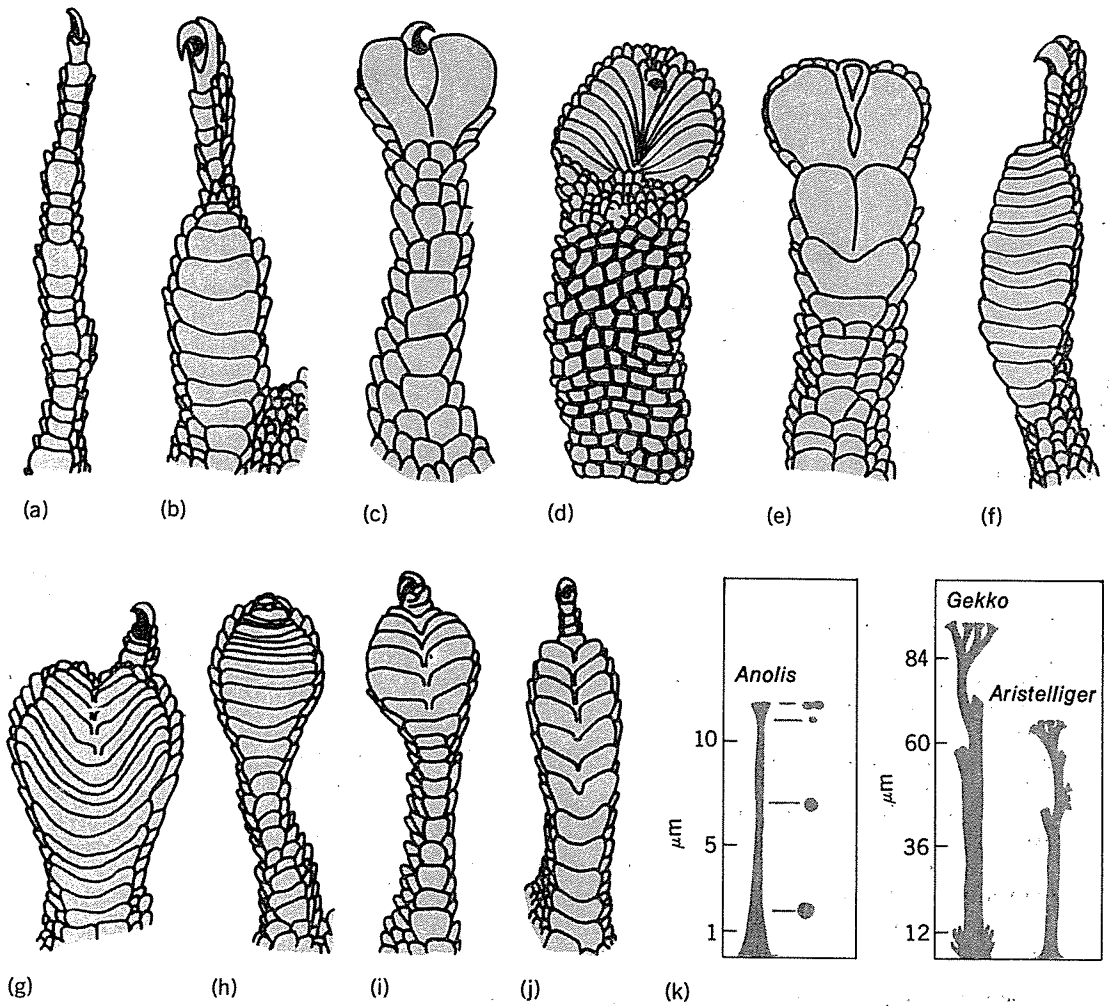

Fig. 1. Variation in the external form of the digits of geckos (subfamily Gekkoninae); digits are not drawn to scale, and all represent the fourth toe of the hindfoot (*a. b, d, e, f, h,* and *i* from the left side; *c, g,* and *j* from the right). *(a) Pristurus carteri; (b) Cyrtodactylus brevipalmatus; (c) Phyllodactylus marmoratus; (d) Uroplatus ebenaui; (e) Afroedura transvaalica; (f) Aristelliger lar; (g) Perochirus articulatus; (h) Phelsuma barbouri; (i) Lygodactylus bonsi; (j) Hemidactylus garnotii.* (*k*) Relative size and complexity of setae from two geckos and an anole.

setalike mechanoreceptors (Fig. 4*d*, *e*), are also present on the scales subtending the lamellae, and the digits are unusually sensitive to pressure, vibration, and foreign material.

Internal modifications of limbs and feet. A number of modifications of the dermal, muscular, skeletal, and circulatory systems of the limbs and feet aid in the gecko's effective use of the setae. When functioning as adhesive mechanisms, the setae are under tensile stress and such stress must be transmitted to a resistant area. The dermis (deep layer of the skin) of the ventral surface of the lamellae is modified so that the epidermis sits directly on a tightly knit collagenous layer rather than on a loose network typical of the outer dermal portion of most reptilian scales. This collagenous layer links up with stout lateral tendons which follow the contours of the pad and link up with the skeleton at the joint capsule between the metacarpal/tarsal and the first phalanx of that digit. Thus, tensile stresses are passed from setae to collagen to tendon to skeleton via a joint capsule. The linkage system is governed by sets of muscles in the foot and lower limb and also via the joint capsules. This control system permits varying load-bearing conditions to be met and ensures adequate contact with the locomotor surface. The flexor muscles, by way of this linkage system, pull the lamellae onto the surface when contact is made, and various check ligaments ensure that such pull is optimal. The lamellar system (Fig. 2*c*) permits individual control over relatively small fields of setae, and the inherent problems of application and removal of a continuous sheet of such structures are thus overcome.

The skeleton of the feet and digits is specialized in a number of ways. The arrangement of the carpal and tarsal elements has given rise to a secondarily symmetrical foot (Fig. 2*a*) with digits radiating around a semicircle. This contrasts with the markedly asymmetrical feet of most other lizards (Fig. 2*b*). The phalanges (finger bones) also have a much modified form, being broad and flattened dorsoventrally, rather than cylindrical. The joints between the phalanges are extremely mobile and play an important role in the application of the lamellae and their removal from the substratum. The digital muscles are also markedly developed in

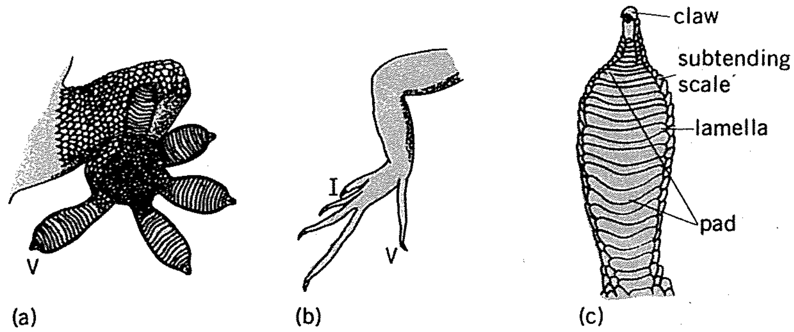

Fig. 2. Digit and foot modifications. *(a)* Ventral view of the left hindfoot of the tokay (*Gekko gecko*) showing the digital lamellae and the secondary symmetry of the foot. *(b)* Dorsal view of the left hindfoot of *Uta stansburiana*, an iguanid lizard, showing the more typical asymmetrical nature of the hindfoot in lizards (digits numbered I–V). *(c)* Ventral view of the fourth digit of the left hindfoot of the tokay (*G. gecko*); the pad consists of a series of lamellae.

many species, the extensor set traversing all of the phalanges as far as the claw instead of terminating at the base of the digits. Combined modifications of the phalanges and muscles permit the phenomenon of hyperextension of the digits.

Another significant feature of the digits is seen in the enormous proliferation of the blood system. Previous work often emphasized the importance of digital blood sinuses, but recent investigations indicate that these are only a small part of a much more extensive blood lacunar system which ramifies the core of each lamella. The blood system of the pads acts as a hydrostatic skeleton and enhances the ability of the lamellae to conform with the substratum and each other.

Behavioral modifications. Certain aspects of locomotor behavior have been mentioned above, especially the phenomenon of digital hyperextension. In lizards that climb without the aid of pilose pads, the claws and certain inflections of the digits are of great importance in maintenance of the grip. First the claws contact the surface and create the grip, which is maintained until the moment of release. The digits are often considerably contorted as the force stroke of the limb cycle reaches its conclusion. When the claws are finally released, the limb is carried rapidly through its recovery cycle for placement of the claws again.

In geckos with pads, a dramatic difference is evident. The digits are carried through the recovery cycle in a hyperextended state (that is, rolled back on themselves) and are placed onto the substratum by unrolling from base to tip, with the claw being the last part of the digit to make contact. The force stroke of the limb proceeds without any notable distortion of the digits, which are finally released in a direct reversal of their placement pattern, being rolled up from tip to base. The claw is thus the first part of the digit to lose contact.

Such behavioral modifications, in association with the functioning of the setae, have led to some remarkable occurrences. Some genera of geckos have lost their claws totally, and thus rely for grip on the setae alone (Fig. 1*h*). These are the only instances in lizards of claws being forsaken. The efficiency of the system has also enabled locomotor gaits typical of terrestrial lizards to be employed on vertical surfaces (Fig. 3).

Theories of adhesion. One of the most active lines of research with respect to these modifications has been investigation into the mechanism of adhesion. A wide array of theories have been put forward intimating a number of physical phenomena. Early theories attempted to explain the process of adhesion as resulting from secretions, but there is no evidence of any glands on the subdigital surfaces. Later theories, advanced around the turn of the century, proposed that negative pressure was involved, either by air being driven out from between the lamellae or by the setae forming minute suction cups. The latter idea was briefly revived in the late 1960s following a study with the scanning electron microscope. Previous and subsequent

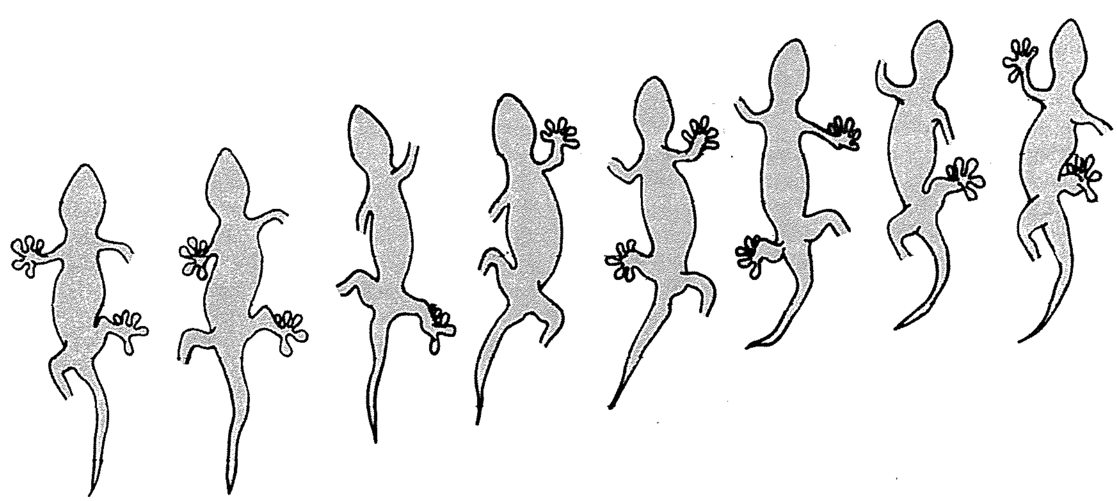

Fig. 3. Stages in the locomotion (from left to right) of *Gekko gecko* on a vertical glass surface. Only the feet in contact with the substratum are shown; those limbs in which the foot is not shown are undergoing their recovery stroke. This represents a complete locomotor cycle of all four limbs, which in life takes about 0.166 second. *(From A. P. Russell, A contribution to the functional analysis of the foot of the tokay,* Gekko gecko *(Reptilia: Gekkonidae), J. Zool. London, 176:437–476, 1976)*

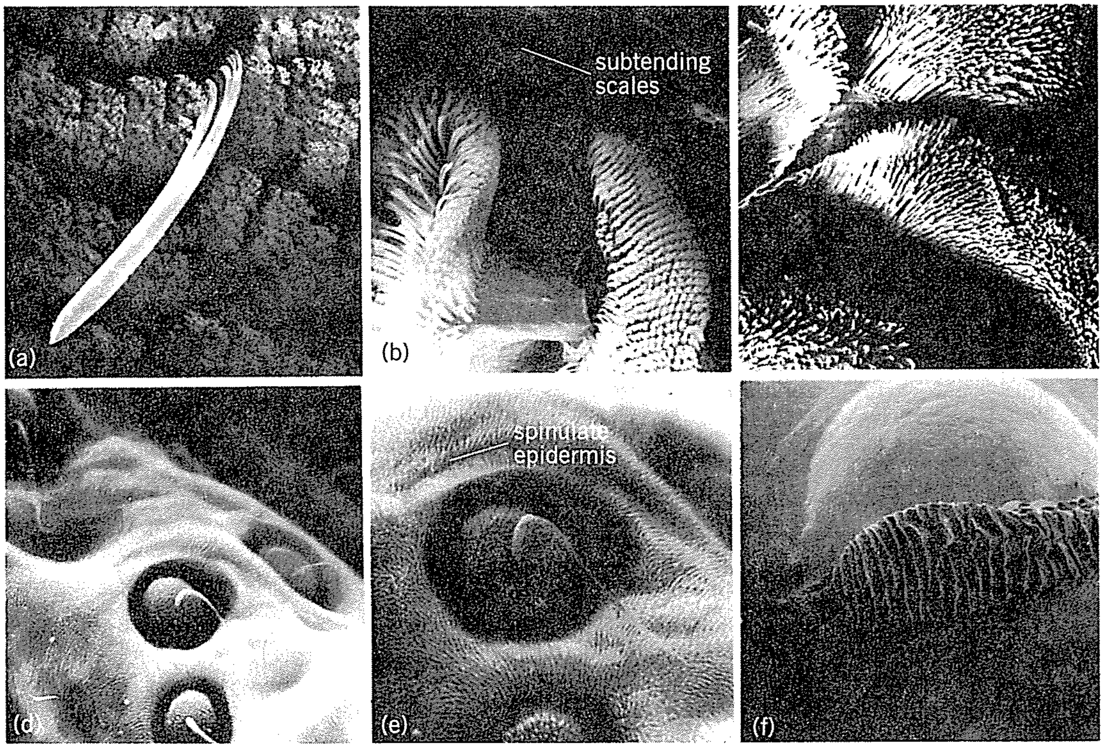

Fig. 4. Scanning electron micrographs of aspects of digital structure. *(a)* A detached seta of *Gekko gecko* above a field of setae still attached to lamellae *(from A. P. Russell, A contribution to the functional analysis of the foot of the tokay, Gekko gecko (Reptilia: Gekkonidae), J. Zool. London, 176:437–476, 1976)*. *(b)* Two lamellae of *G. gecko* with associated setae. Subtending scales with mechanoreceptors can be seen at the top. *(c)* Fields of setae on the divided lamellae of *Hemidactylus brooki*. *(d)* Hairlike mechanoreceptors of *G. gecko* on a subtending scale. *(e)* A hairlike mechanoreceptor and surrounding spinulate epidermis typical of the general body surface. *(f)* Subdigital lamellae of the iguanid *Anolis carolinensis* showing the structural similarity to the foot pads of geckos.

work indicating that gecko feet can adhere quite effectively in a vacuum, however, lend little credence to these ideas. Other theories in the early part of this century proposed electrostatic and frictional forces.

Current understanding of the mechanism of adhesion is the result of a synthesis of several approaches, and it is becoming apparent that a combination of factors may be involved. From 1934 to the present, a growing body of information has been accumulating based on anatomical and experimental approaches. Recent work has concentrated upon the types of surfaces used in nature rather than on the artificial substrata employed in the laboratory. In the late 1960s considerable experimental work indicated that high free-surface energy (surface tension) is conducive to adhesion. Experiments leading to this conclusion were based on testing the grip of animals on polyethylene sheeting subjected to different levels of coronal discharge—the higher the charge, the better the adhesive ability. Correlating these data with field data, however, leads to some problems. It appears that in nature setae may largely be employed on leaf surfaces. The waxy cuticles covering these have very low free-surface energy, yet adhesion is effective. Such conflicts have led to reassessment and compromise, and it is now being suggested that both free-surface energy and the catching of setae on minute irregularities (frictional forces) may play a part at different times. Thus setae may have a dual mode of functioning. This area is still one of open debate, and further research into the nature of surfaces and β-keratin, as well as further behavioral observations, is required.

Summary. The foot pads of gekkonid lizards (and the similar structures of anoline lizards) are aids to climbing on a variety of natural and artificial surfaces. The ultimate agents in the adhesive process are microscopic setae borne on the underside of subdigital lamellae. The setae are composed of β-keratin, and mechanical connection to the skeleton is accomplished via the rest of the epidermis, dermal collagen, tendons, and joint capsules. Many modifications of the skeleton, blood system, and musculature of the feet, and locomotor behavior enable the setae to be employed effectively. The actual mechanism of adhesion remains somewhat enigmatic, but recent evidence suggests that both free-surface energy and microscopic interdigitation may be involved at different times, or simultaneously at different contact points on a heterogeneous substratum.

For background information *see* GECKO; SQUAMATA in the McGraw-Hill Encyclopedia of Science and Technology.

[ANTHONY P. RUSSELL]

Bibliography: U. Hiller, *Morphol. Tiere*, 62: 307–362, 1968; P. F. A. Maderson, *Forma et Functio*, 3:179–204, 1970; A. P. Russell, *Copeia*, 1979: 1–21, 1979; A. P. Russell, *J. Zool. London*, 176: 437–476, 1975.