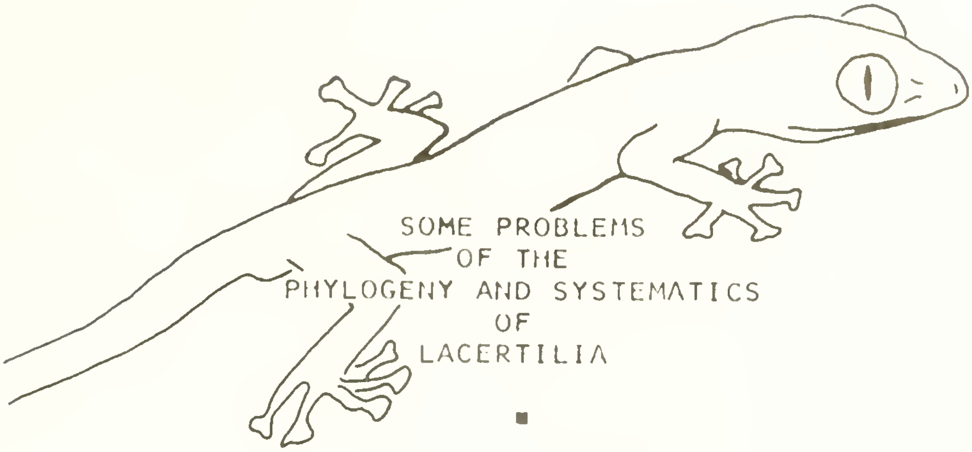

SOME PROBLEMS OF THE PHYLOGENY AND SYSTEMATICS OF LACERTILIA

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ABSTRACT

Sukhanov, V. B. SOME PROBLEMS OF THE PHYLOGENY AND SYSTEMATICS OF LACERTILIA (SEU SAURIA). Zoologicheskiy Zhurnal, vol. 40, no. 1, p. 73-83, 1961. The study of lizard musculature differentiates two strikingly different locomotor mechanisms: Scincogekkonomorphous and Iguanomorphous, both of which have tended to evolve in different directions. The locomotion of the Gekkota can also be divided into two types: Scincomorphous - crawling - and Iguanomorphous - where the body is held high above the substrate. The locomotion of gekkotan lizards, although having a more archaic appearance, shares some basic features with the locomotion of scincomorphans. Differing from the generally accepted lizard classification of Charles L. Camp (1923), the Gekkota and Scincomorpha are here suggested to be different branches of the same evolutionary lineage (division Scincogekkonomorpha). A second lineage of lizard evolution (division Iguanomorpha) possesses a greatly modified locomotor apparatus, perhaps due to their aboreality. The common ancestors of Scincogekkonomorpha and Iguanomorpha are postulated to have had a peculiar type of locomotion not found in its entirety in extant lizards: their bodies were raised high above the substrate, (as in Gekkota and Iguanomorpha), proximal parts of limbs moved nearly in a horizontal plane (as in Gekkota and Scincomorpha). The similarity of the Gekkota and Iguanomorpha results mainly from parallel or convergent evolution and not by close relationship.

TEXT

The present article discusses one of the most controversial issues concerning the phylogeny of lizards - the relationships between the Iguanomorpha (families Iguanidae and Agamidae), the Scincomorpha and the Gekkota.[1]

We find one of the first attempts to classify lizards on a phylogenetic basis in several of E. D. Cope's works (1864, 1900).[2] At the base of his tree he placed the iguanids and agamids (Pachyglossa), assuming that gekkotano (Nictisaura) descended from them by degeneration. Cope felt that the relationship of the scincids and lacertids with Pachyglossa was more remote - through the Diploglossa (Anguidae, Varanidae, etc.).

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[1]Studied: Gekkonidae - Gekko gecko, Teratoscincus scincus, Cyrtodactylus caspius; Scincidae - Eumeces schneideri, Mabuya sp.; Lacertidae - Lacerta lepida, L. agilis; Eremias grammica, E. arguta, E. velox; Agamidae - Agama agilis sanguinolenta, A. caucasica, Phrynocephalus mystaceus, P. interscapularis, P. reticulatus, P. helioscopus.

[2]References to earlier works dealing with the system of reptiles can be found in Camp (1923).

Of special interest is the system suggested by M. Fürbringer (1900) based on a study of the musculature of the shoulder area of reptiles. Fürbringer and nearly all succeeding researchers considered the gekkonids to be the most primitive group of modern lizards. Close to them are the Scincidae and Gerrhosauridae. All three of these families have a relatively high number of primitive characteristics (Fürbringer, 1900, pp. 581-582). At the same time, Fürbringer indicated the relatively isolated position of the gekkonids among all lizards by a number of characters. The phylogenetic line passes from forms resembling the scincids through the Gerrhosauridae to the Lacertidae and, possibly, the Teiidae. Throughout this line, a number of specializations is noted in the musculature. Agamids and iguanids, closely related to each other, are considered as highly specialized, aberrant forms of Lacertilia, not at all related to the gekkonids. As will become evident later, Fürbringer's views are quite similar to our views with the exception, mainly, of the evaluation of the level of differentiation of the gekkonids.

Fürbringer's ideas were not developed further. Almost all succeeding authors (Gadow, 1901; Camp, 1923) held the opinion that the Gekkota were closely related to the Iguanomorpha but not to the Scincomorpha. This point of view, most completely stated by Camp (1923), is now the most widespread. His classification of lizards is based on a number of structural details of the skull, branchial skeleton, throat and abdominal muscles, hemipenes, scutellation, etc.

However, recently more and more data have accumulated in the literature contradicting the Camp's major conclusions.[3] The relationships between the higher taxonomic groups were, evidently, constructed by Camp on the basis of a preconceived idea which prevented him from observing a number of contradictions between the classification of lizards represented in linear form and the phylogenetic tree, shown greatly abridged in Fig. 1.

According to Camp, all lizards can be divided into two basic groups (divisions): Ascalabota and Autarchoglossa. The first group, including the Gekkonomorpha, Iguanomorpha and Chameleonomorpha, unlike the Autarchoglossa (which includes the Scincomorpha group of interest to us) is characterized by high number (over four) of transverse scale rows on each body segment, a similar structure of imbricate scales (if present) with broad free edges or uniform granular scales on all parts of the body, a primitive tongue structure, calyculate hemipenes, and a primitive hyoid suspension. All these characters undoubtedly indicate a definite, although not necessarily close, relationship between these families. However, other ascalabotan characters, which Camp used as the basis of his classification, are clearly secondary, for example, the absence of m. rectus abdominis supervicialis (a character he even introduced into diagnosis) and absence of os intermedium in the wrist. Camp, referring to the embryological works of Maurer (1898), acknowledged that the presence of m. rectus abdominis superficialis is a primary characteristic, but nevertheless, felt it possible to derive the autarchoglossans possessing this muscle from the ascalabotans whose representatives have lost

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[3]Of greatest interest is the research of Malan (1944). He examined the structure of the olfactory and Jacobson's organ in the majority of lizard families. He believed it necessary to place the Gekkota between the Iguanomorpha and Scincomorpha and to combine them with the latter.

it. This is not the only contradiction in Camp's views.

In his phylogenetic tree, Camp located the Gekkota and Iguania on opposite sides of the tree. Although acknowledging the contradiction of the proposed kinship between the two, he referred to the inadequacies of a two-dimensional phylogenetic diagram, not realizing that the proximity of any groups in space reflects only convergence and not kinship. Thus, by suggesting the possibility of a secondary relationship between the Gekkota and Iguania, Camp undermined his own ideas.

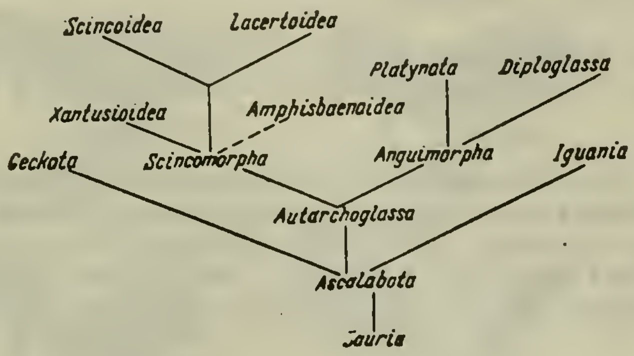

Figure 1. Phylogenetic tree of Lacertilia (after Camp)

All the differences between the Ascalabota and the Autarchoglossa, according to Camp, are due to adaptations to different habitats: the former has a strong tendency toward an arboreal mode of life, the latter, never having been adapted to climbing, lives on the ground, often with an undulatory specialization (reduction of limbs, snake-like body) in turn never observed in Ascalabota. This clearly contradicts the large number of shared characters of Gekkota and Scincomorpha which thus cannot be explained by convergence, as the habitats of these animals are different and contrarily suggests the similarity between Gekkota and Iguanomorpha may be secondary.

It seems to us that one of the main defects of Camp's classification is its dependency on static characters, characters whose developmental history has not been studied. In those cases where a character, such as m. rectus abdominis superficialis, has its own history Camp's classification begins to suffer from its own contradictions.

Before we present original material we must note that paleontology still plays a very small role in the unraveling of the phylogeny of lizards, partly because of the extremely poor knowledge of the comparative osteology of modern forms.

The main role in constructing the phylogeny of Lacertilia at present can only be played by comparative morphology and to a lesser degree by comparative embryology, thus all conclusions will be to some degree hypothetical. However, paleontology can now throw some light on the time of appearance of large groups of lizards. Iguanidae and Agamidae are found in the Upper Cretaceous (Hoffstetter, 1955; Huene, 1956) and according to some data in the Upper Jurassic (Bavarisaurus - Hoffstetter, 1953). Well differentiated representative of the Gekkonidae, Scincidae and Lacertidae are found only in the Upper Eocene. Some Upper Jurassic and Cretaceous taxa (Hoffstetter, 1953 - Yabeinosaurus, Broilisaurus) cannot currently be differentiated from the Gekkota and Scincomorpha. This indicates the possibility of the Iguanomorpha diverging early from the common trunk of lizards, perhaps in Upper Jurassic. But differentiation of the main evolutionary line of Lacertilia into Gekkota proper and Scincomorpha could hardly have occurred earlier than the Upper Cretaceous.

A study of the musculature of the locomotor apparatus of lizards shows that the Gekkota and Scincomorpha share a whole series of relatively primitive characters.

The clavicle in the majority of the Gekkonidae, Scincidae and Lacertidae is broad and perforated ventrally by a large fenestra. In the higher Scincomorpha, the clavicle becomes hook shaped because of the reduction. In the Iguania a hook-shaped clavicle is known in only three genera (Basiliscus, Laemanctus - Boulenger, 1855), Lyriocephalus (Siebenrock, 1895); all other forms have a rod-shaped clavicle. Evidently, in the higher Scincomorpha and all Iguania there is a parallel reduction of clavicles, much further advanced in the latter group, perhaps because of the greater expanse of time (Upper Jurassic to Recent). The reduction of clavicles in Scincomorpha may have begun relatively recently. In connection with the clavicular changes, there are changes in the m. deltoideus. In all representatives of the scinco-gekkonomorphic evolutionary line, some muscle fibers originate from the outer surface of the clavicle (Fig. 2, A). They extend anteriad round the front of the clavicle, join with fibers originating from the clavicle's inner surface, and extend posteriad adjacent to the fibers originating from the scapula. In the agamids (Fig. 2, B) the muscle fibers originate on the outer surface of the rod-shaped clavicle and extend directly to the scapula without curving in front of the clavicle.

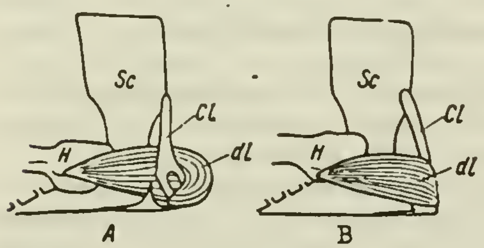

Figure 2. Illustration of the position of the m. deltoideus to the clavicle in lizards.

A - Lacerta ocellata - this type of deltoideus origin from the clavicle occurs in Gekkonidae, Scincidae and Lacertidae; B - Phrynocephalus mystaceus - this type is common in iguanids and agamids. Cl - clavicula, H - humerus, Sc - scapula, dl - m. deltoideus.

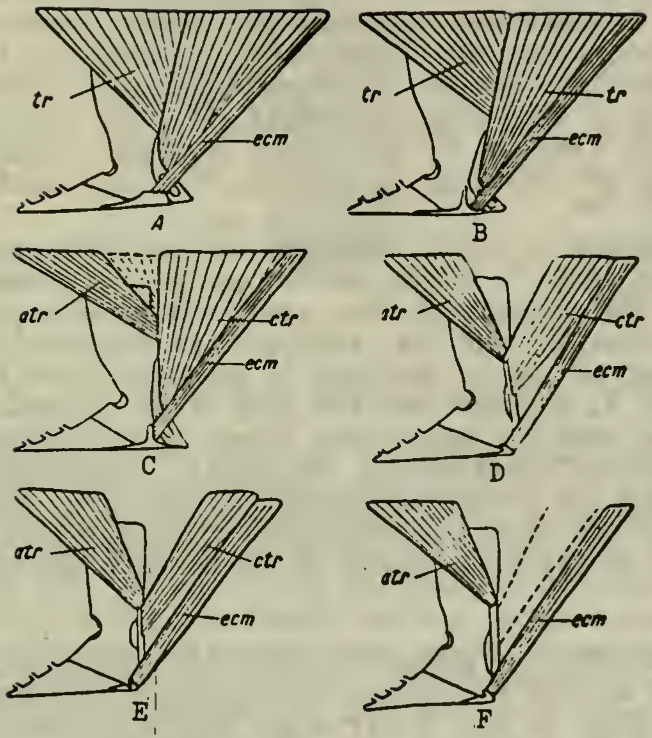

Figure 3. The development and differentiation of the m. trapezius and m. episterno-cleido-mastoideus in various lizards

A - Teratoscincus scincus, almost no traces of differentiation of either muscle. B - Eremias arguta: in m. trapezius division into two parts - one whose fibers are attached to the acromial part of the scapula and the second to the clavicle. C - Eremias grammica: both parts of m. trapezius well separated; the more cranial section of the posterior part (m. acromio-trapezius) has lost muscle fibers and become aponeurotic. D - Phrynocephalus mystaceus: m. episterno-cleido-mastoideus completely divided from m. trapezius, which in turn is divided into two independent parts - m. acromio-trapezius and m. clavotrapezius. E - Phyrnocephalus interscapularis: reduction noted in m. clavotrapezius. F - Phrynocephalus helioscopus: m. clavotrapezius has completely lost its muscle fibers, replaced by apo-neurosis, atr - m. acromiotrapezius; ctr - m. clavotrapezius, ecm - m. episterno-cleido-mastoideus, tr - m, trapezius.

The m. trapezius of gekkonids and scincids is not separated from the m. episterno-cleido-mastoideus (Fig. 3, A) nor divided into two parts, which is typical of the agamids (Fig. 3, D) ("acromiotrapezius," attached to the acromial part of the scapula, and "clavotrapezius," ending at the clavicle). In Iguanomorpha, the trapezius muscles (Fig. 3, D, E, F) are separate from the m. episterno-cleido-mastoideus and show an obvious tendency toward reduction, even to complete loss of the "clavotrapezius" (Fig. 3, F). In the lacertids, on the other hand, the m. episterno-cleido-mastoideus is very weakly divided; if the m. trapezius is reduced, it is at the expense of the posterior acromial part (Fig. 3, B, C). Thus, divergent trends are seen in the development of the m. trapezius in the lacertids and agamids.

The changes occurring in the m. anconeus are interesting. In the scincids and lacertids (Fig. 4, A) the muscle has a long "scapular" head closely connected at its origin with lig. scapulo-humeralis lateralis and lig. axillaris. In the gekkonids, the lig. axillaris is reduced,[4] but the primitive scapular head of the m. anconeus is preserved (see Fig. 7, C). In all Iguanomorpha (Fig. 4, B) there are two long heads: scapular and coracoid.[5] It is possible that the heads were formed by the divergence of fibers of the primitive "scapular" head by lig. axillaris. The scapular head, still retaining as its origin the primitive connection with lig. scapulo-humeralis lateralis, loses it in the course of evolution of Iguanomorpha. Thus, the morphological trends of the m. anconeus of the Gekkota and Iguanomorpha are contradictory.

The m. supracoracoideus of gekkonids, scincids, and lacertids is relatively small; the site of its origin is limited to the anterior edge of the bony coracoid (Fig. 5, A). A different muscle is seen in the Iguanomorpha. Agama has a much larger muscle: its origin occupies not only the bony part of the coracoid, but also its cartilaginous part, the so-called "epicoracoideum," circumscribing the coraco-scapular fenestra and even a small part of the scapula (Fig. 5, B). In Phrynocephalus, (Fig. 5, C), the cartilaginous "epicoracoideum" is reduced. As a result, the muscle is divided into two parts - a coracoid part similar in volume and form to the m. supracoracoideus of gekkonids and scincids and a scapular part of increased size; in comparison with Agama, its fibers occupy a larger area

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[4]In the relatively primitive Gekko japonicus (Sanders, 1870) a remnant of this connection is evidently still retained in the form of a tendon leading from the posterior angle of the coracoid to the m. anconeus. But it does not join with the lig. sterno-scapularis internum.

[5]The study of this taxon led to the incorrect idea that the primitive state of the m. anconeus of all reptiles is quadricipital: two long and two short heads (Romer, 1922).

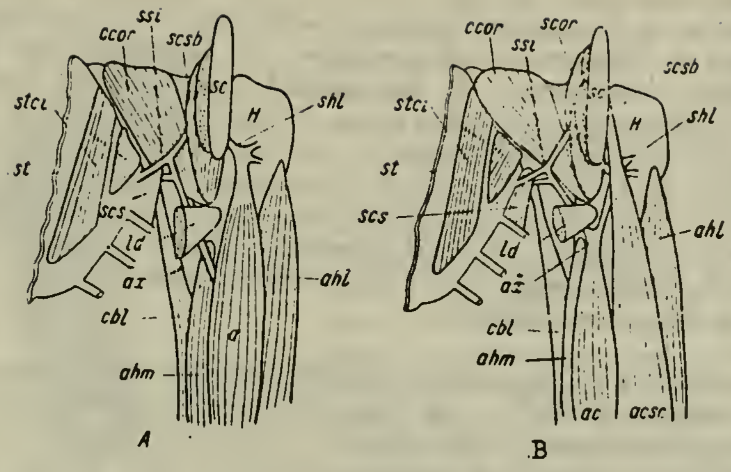

Figure 4. Two structural types of the m. anconeus in lizards.

A - Lacerta lepida has only one long "scapular" head originating from lig. axillaris and lig. scapulo-humeralis lateralis; this structural type of m. anconeus is noted in all Scinco-gekkonomorpha. B - Phrynocephalus mystaceus: primitive single long head of m. anconeus divided into two - the coracoid originating from lig. axillaris and the scapular which at its origin is completely separate from lig. axillaris and lig. scapulo-humeralis lateralis. There are two long heads of m. anconeus in all representatives of the Iguanomorphic line of evolution of lizards. St - sternum, a - long head of m. anconeus in Scincogekkonomorpha, ac - m. anconeus, caput coracoideum, acsc - m. anconeus, caput scapularis - ahl - m. anconeus, caput humerale laterale; ahm - m. anconeus, caput humerale mediale; ax - lig. axillaris, cbl - m. coraco-brachialis longus, ccor - coracoid part of coracoid head of m. subcoracoscapularis, m - latissimus dorsi, scsb - spacular head, m. subcoracoscapularis; scor - spacular part of coracoid head, m. subcoracoscapularis, scs - m. sterno-costoscapularis, shl - lig. sterno-humeralis lateralis, ssi - lig. sternoscapularis internum, stci - mm. sterno-coracoidei inertni. Other symbols explained in Figure 1.

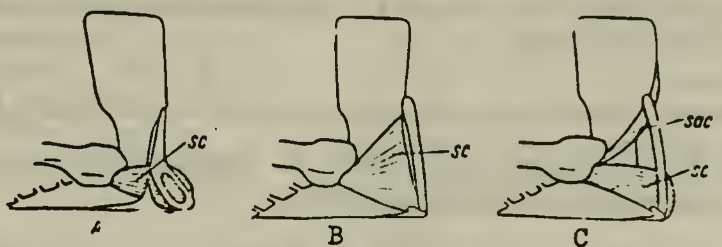

Figure 5. Three basic structural types of the m. supracoracoideus

A - Lacerta lepida, B - Agama caucasica, C - Phrynocephalus mystaceus; sac - m. supracoracoideus accessorius, sc - m. supracoracoideus.

of the scapula and part of the clavicle and extends between these bones to the inner side of the suprascapular cartilage.[6] It is still difficult to decide in which (Gekkota, Scincomorpha, or Agamidae) the m. supracoracoideus show primitive condition. If the agamid condition is primitive, then we see contradictory trends in the direction of muscle evolution in the advanced Agamidae and Scincogekkonomorpha[7]: in the first - separation of the muscle into two parts and formation of m. supracoracoideus accessorius, in the second - retention of an unicipital muscle. If the condition in the gekkonids, scincids, and lacertids is more primitive, then we must speak of its retention in the entire scincogekkonomorphic evolutionary line and continual differentiation in the Iguanomorpha.

The m. biceps of the gekkonids and scincids has only a fleshy origin ("proximal muscle belly"). In some advanced Scincomorpha (Lacerta, Ameiva, Tupinambis - Fürbringer, 1876, 1900) there is slight reduction of the proximal belly - there is a narrow tendonous part along its edge. The complete reduction of the proximal belly of m. biceps occurs in the advanced Iguanomorpha (there are numerous intermediate stages - Camp, 1923). Thus, again we see parallel development in the advanced Scincomorpha and Iguanomorpha but reduction begins much earlier in the latter group.[8]

The presence of a primitive radial complex of forearm extensors (mm. extensores antebrachii et carpi radialis), such as in tortoises (Fig. 6, A) is very typical of the gekkonids, scincids, and lacertids. In this muscle complex some fibers ("m. tractor radii" - Haines, 1939) are supplied by a branch of the flexor nerve (n. brachialis longus inferior), perforating the m. biceps and m. brachialis. A foramen ectepicondyloideus (Ribbing, 1907, 1938) for the extensor nerve, n. radialis occurs in all these families supplying the greater part of the extensor radial complex. In all Iguanomorpha (Fig. 6, B) this muscle complex is greatly reduced; the "m. tractor radii" also loses its flexor innervation. The foramen ectepicondyloideus also disappears.

The flexor ulnar complex of the forearm is greatly reduced in the Iguanomorpha: there is a progressive reduction of m. fl. antebrachii ulnaris (still observed in two iguanid genera Ctenosaura and Sceloporus - Straus, 1942) to its complete loss in advanced forms (Agama, Phyrnocephalus). In the entire Scincogekkonomorphic line, this muscle evidently does not undergo reduction. Thus, a distinct trend can be noted in the Iguanomorpha toward enlargement of the antebrachial musculature.

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[6]We called the scapular part of the m. supracoracoideus of the advanced agamids the m. supracoracoideus accessorius.

[7]Scincogekkonomorpha here refers to a taxon at a division level combining Gekkota and Scincomorpha. For contrast, we suggest the name Iguanomorpha for the group including Iguanidae, Agamidae and Chamaeleontidae.

[8]A difference in times of reduction can also be assumed.

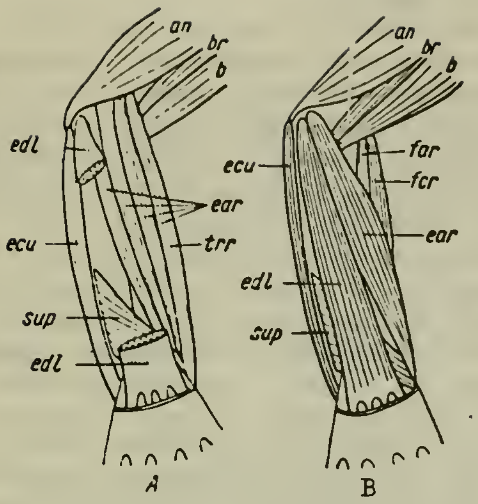

Figure 6. Two structural types of the mm. extensores antebrachii et carpi radialis

A - Lacerta lepida: primitive condition observed in the entire Scincogekkonomorphic line; muscle very strongly developed, superficially differentiated into several heads; some fibers - m. tractor radii - supplied with flexor but not extensor nerves. B - Phrynocephalus mystaceus; muscle relatively weakly developed, no differentiation, innervated only by extensor nerves; this is observed in all Iguanomorphia. an - m. anconeus, b - m. biceps, br - m. brachialis inferior, edl - m. extensor digitorum communis, ear - mm. extensores antebrachii et carpi radialis, ecu - m. extensor carpi ulnaris, far - m. flexor antebrachii radialis, fcr - m. flexor carpi radialis, sup - m. supinator manus, trr - m. tractor radii

A number of primitive characters relating the Gekkota and Scincomorpha is also observed in the musculature of hindlimbs: enlargement of the m. pubo-ischio-tibialis (in agamids, the muscle is much smaller, particularly the first part which disappears completely in Phrynocephalus); the origin of the inner head of m. gastrocnemius arises only from the tibia (in agamids, the muscle also originates from the femur; in gekkonids, on the other hand, there is a distinct trend toward the shortening of the inner head of the gastrocnemius to its complete reduction in the Caspian gecko); the m. fl. tibialis internus I is attached to both the tibia and the femur.

To supplement the aforementioned primitive characters shared by the Gekkota and Scincomorpha, we can add the primitive nature of the throat muscles, osteoderm, unfused medial skull elements (Camp, 1923), lungs (Milani, 1894), teeth, digestive system, etc. A number of these characters shared by Gekkota and Scincomorpha remain poorly studied, which makes it impossible to determine the relative degree of their evolutionary development. These are: morphology of the m. fl. tibialis internus I in comparison to the m. fl. tibialis internus II; size of the m. ilio-fibularis; relatively weak development of the outer head of the m. femoro-tibialis; origin of the accessory head of the m. il. digitorum longus from the fibula and, according to Camp, relatively greater modification of the postfrontal than the postorbital bone.

It is extremely important to note that the Gekkota and Scincomorpha are related not only by comparatively primitive characteristics, but also by a number of derived characteristics, which

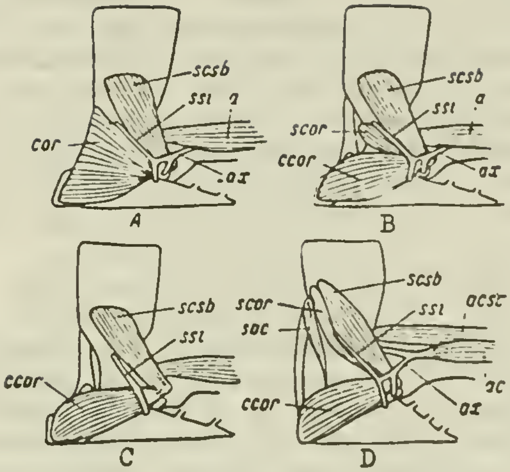

Figure 7. Structure of m. subcoracoscapularis in various lizard families

A - Scincidae (Mabuya sp); coracoid head of muscle very large. B - Lacertidae (Eremias arguta); with the disappearance of "epicoracoid" the coracoid head divided into two parts. C - Gekkonidae (Gekko gecko); scapular part of coracoid head completely reduced; also absence of lig. axillaris. D - Agamidae (Phrynocephalus mystaceus); scapular part of coracoid head very well developed; origin migrated further back, up to the scapular head proper of m. subcoracoscapularis, from which it is separated only by lig. sternoscapularis internum; cor - coracoid head of m. subcoracoscapularis. Other symbols same as Fig. 3 and 4.

evolve in the same direction in all Scincogekkonomorpha. Perhaps, this indicates that gekkonids, scincids, and lacertids, until their divergence into separate families, subfamilies and sections, evolved for a long time (possibly from Upper Jurassic to Upper Cretaceous) in the same Scincogekkonomorphic lineage.

It is in gekkonids, scincids, and lacertids that we note complex formations such as the crossing of muscle fibers in the mm. pubo-ischio-femoralis internus et externus (Sukhanov, 1957). Still small in Gekko gecko, the m. ext. iliotibialis has enlarged; the m. fl tibialis internus I is divided into several heads (not yet separated in Gekko and Eumeces, two heads in Lacerta agilis, three in L. lepida, four in Teratoscincus and Cyrtodactylus).

The changes in the m. subcoracoscapularis are extremely significant. In the scincids, the coracoid head of the muscle is very large (Fig. 7, A); it originates from the inner side of the coracoid, the "epicoracoid," and the scapula. This continuous muscle layer is triangular in shape and is separated from the scapular head by the lig. sterno-scapularis internum. The scapular head is relatively small and its fibers do not reach the outer side of the scapula. In the lacertids (Fig. 7, B) the coracoid head is divided into two parts - the scapular, partially reduced, and the coracoid. The scapular part has complete disappearance in gekkonids (Fig. 7, C). There is also partial reduction of the coracoid part proper from lacertids to gekkonids (origin of muscle occupies only the bony part of the coracoid). In the agamids studied, separation of the coracoid head into two parts was also noted but only the coracoid part is relatively reduced in size. The scapular part is, apparently enlarged and forms the anterior inner scapular head of the m. subcoracoscapularis (Fig. 6, D). In the Iguanomorpha, there is also a progressive enlargement of the external scapular head of this muscle.

Several analogous changes are observed in the m. scapulo-humeralis anterior. In scincids, the muscle in the form of a single (not separated into heads) mass originates from the outer side of the anterior part of the coracoid, the "epicoracoid," and a small part of the scapula. In the lacertids, there is a separation of the muscle into a coracoid and a slightly smaller scapular heads. In th gekkonids, the latter is completely reduced. A similar trend, evidently parallel, also occurs in the Iguanomorpha. The muscle in the agamids is quite similar to that of the scincids and the lacertids; it was weakly divided into two parts. In the advanced agamids (Phrynocephalus), the scapular head of the m. scapulo-humeralis anterior is greatly reduced, although not complete, resembling the condition observed in gekkonids.

Noting the strong similarity between the Gekkota and the Scincomorpha, we must also mention a number of characteristics which permit the differentiation of the gekkonids from other lizards (within the Scincogekkonomorpha division), unite the entire group of Gekkota, and perhaps, are slightly more advanced than in the Scincomorpha. Thus, in Gekkota, there is a reduction of the lig. axillaris; part of the fibers of the m. dorsalis scapulae spread to the inner side of the suprascapular tendon; the scapular head of the m. scapulo-humeralis anterior and the scapular part of the coracoid head of the m. subcoracoscapularis completely disappear; there is a crossing in the m. pectoralis and in the m. pubo-ischio-femoralis internus IV (Sukhanov, 1957); the inner head of the m. femoro-tibialis merges with its outer head; there is a progressive reduction of the inner head of the m. gastrocnemius to its complete reduction in the Caspian gecko; in several forms, merging of the m. fl. tibialis internus II and m. fl. tibialis externus is observed. Significant changes occur in the eyes (Underwood, 1951, 1954), and the cranial arches are reduced, etc. There is the opinion that the amphicoelous vertebrae of the gekkonids are a secondary derived condition (Underwood, 1954), but at the same time there are the facts, presented previously which indicate the extreme primitiveness of the Gekkota. Thus, this question must remain open.

From the aforementioned data, we can clearly see that there are two sharply differing types of muscle structure in the locomotor apparatus of the lizards - the Scincogekkonomorpha and the Iguanomorpha. It is interesting that the musculature of the pectoral girdle and forelimbs in the first group is definitely primitive, but that of the pelvis and hindlimbs is more advanced. In the Iguanomorpha, the relation is reversed - muscles of the pelvis are more primitive, but in the pectoral girdle there are very many specializations.

We are still far from completely understanding the role of the individual muscles or even their complexes in locomotion. The possibility of muscles of the locomotor apparatus being included in performance of functions not directly connected with locomotion (digging, displaying, etc.) makes it even harder to understand their evolution. Nevertheless, it is remarkable that we still have two basic classes of locomotion in lizards - crawling in the scincomorpha and elevated body posture during movement in the Iguanomorpha. Each type of locomotion influences all aspects of the animal (we can recall a seemingly distinct difference in body and limb proportions).

The locomotion of Gekkota outwardly resembles that of the Iguanomorpha (elevated body posture). But their upper arms move in a horizontal plane, as in the Scincomorpha, which undoubtedly is closer to the original locomotor pattern. In the Iguanomorpha, this plane is more vertical (perhaps explaining the curious similarity between such specialized forms as Phrynocephalus and mammals - the formation of a prototype of the m. supraspinatus in the form of the m. supracoracoideus accessorius (Fig. 5, C). The locomotion of terrestrial gekkonids is much slower and clumsier than that of the Iguanomorpha. This is shown both by direct measurements of the speed of the scincogekkonomorphans Phrynocephalus mystaceus and Ph. reticulatus, and the analysis of their tracks.[9]

The similar movement of forelimbs of the Gekkota and Scincomorpha may be due to the similarity in musculature. But the striking similar musculature of the pelvis and thigh of these groups is still a mystery. The crossing of the muscle fibers of the m. pubo-ischio-femoralis internus in forms with relatively short limbs (Scincomorpha) may be due to the necessity of increasing the stride during locomotion. But the hindlimbs of the Gekkota, although shorter than those of Iguanomorpha, are, nevertheless, much longer than those of the Scincomorpha and the crossing in several representatives is complex and also involves the m. pubo-ischio-femoralis externus. Moreover, according to some data, parallel crossing may appear in the Gekkota and the Scincomorpha (difference in innervation - Sukhanov, 1957).

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[9]The usual speed of the Scincogekkonomorpha does not exceed 1.0 m/sec. Maximum ground speed of a gecko escaping from an enemy is 1.2 m/sec. Tracks left in the sand at that speed differ from ordinary ones in that the imprint of the hindfoot is a round funnel. No imprints of individual toes remain. The track of the forefoot retains imprints of toes. It is interesting that this type of track is never seen under normal conditions even in the same kind of gecko during its nocturnal activity, i.e., it is evident that the ordinary demands of his movement are completely satisfied by a comparatively slow speed (to 1.0 m/sec). Phrynocephalus mystaceus and P. reticulatus show significantly greater variation in speeds in their normal "behavior." Tracks with visible impressions of the toes correspond in these two forms to speed not exceeding 1.0-1.2 m/sec. At higher speed the tracks, aside from a natural increase in the stride, change their character sharply. Both fore- and hindfeet now leave only simple funnels in the sand. Maximum noted speed for P. mystaceus running from a enemy is 2.8 m/sec, for P. reticulatus 4.0 m/sec. The usual speed of rapid running in the first varies from 1.0 to 2.5 m/sec; in the second from 1.9 to 3.0 m/sec. Such speeds are often observed under natural conditions.

It seems to us that the common ancestors of the Scincogekkonomorpha and the Iguanomorpha had a special type of locomotion, not observed in its entirely in any modern groups of lizards: they had terrestrial mode of life, while moving the the body was held high above the substrate (as in the Iguanomorpha and the Gekkota), the proximal segments of the limbs moved in an almost horizontal plane (as in Gekkota and Scincomorpha). Locomotion was slow and clumsy. The body and tail of these animals were relatively short, but the limbs comparatively long. Individual features of this original pattern of locomotion have been largely retained in extant terrestrial geckos. As a whole the Gekkota underwent specializations in parallel with the Iguanomorpha toward adaptation for climbing (an arboreal or saxicolous form of life). All Iguanomorpha in the course of evolution probably passed through an arboreal stage and only secondarily gave rise to desert terrestrial forms such as Sceloporus and Phrynocephalus. As a result of this their pectoral girdle and forelimbs were strongly modified.

The method of movement of Scincomorpha is, perhaps, the most biologically progressive among the modern lizards and arises from a locomotion pattern similar to that which is observed in terrestrial geckos.

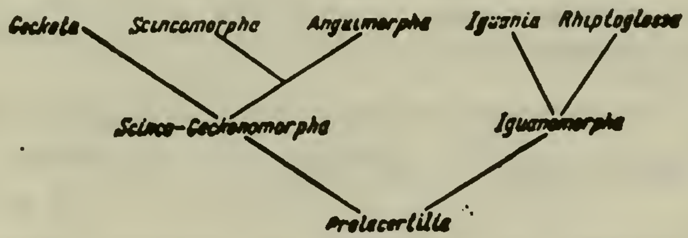

Figure 8. Phylogenetic tree (after Camp, modified by V. B. Sukhanov)

It has already been said that the above facts do not agree with Camp's classification of lizards. We feel it is necessary to modify his phylogenetic tree (Fig. 8). Dividing the lizards into the Ascalabota and the Autarchoglossa must be considered wholly artificial. The Gekkota and Scincomorpha are different branches of one evolutionary lineage (division Scincogekkonomorpha): their common ancestors possibly passed through a long evolutionary path separate from that of the Iguanomorpha (division Iguanomorpha) which represents a second evolutionary lineage of lizards. Division of the common trunk of lizards into these two groups can, probably, be dated to the Upper Jurassic and the divergency of the Gekkota and Scincomorpha to the Upper Cretaceous or Paleocene. The similarity between the Gekkonomorpha and the Iguanomorpha results principally from parallel or convergent evolution and not to close kinship.

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EDITORS' NOTES

The preceding translation is not a direct or literate one. We believed it necessary to take the translation by Scitran and modified the choice of words and phraseology to conform with current scientific English. We consistently changed the lizard group names to anglicized familial names, e.g., iguanes to iguanids, geckos to gekkonids. Similarly we changed Sukhanov's Scinco-Geckonomorpha to Scincogekkonomorpha and other such spellings to conform to current taxonomic usage. Scientific names are not italized or underlined in order to keep the single spaced typewritten copy uncluttered and, thus, more readable.

We wish to thank A. G. Kluge for bringing this important study on lizard classification to our attention and G. Jacobs for its translation.

S. Moody and G. Zug