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No. 4

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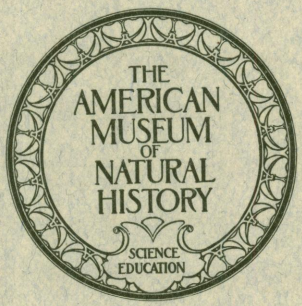

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THE BONY STRUCTURE AND PHYLETIC RELATIONS OF *SPHÆRODACTYLUS* AND ALLIED LACERTILIAN GENERA, WITH THE DESCRIPTION OF A NEW GENUS

By G. K. Noble

Sphærodactylus embraces a group of very small neotropical lizards including one species which is probably the smallest lizard in the world. It is not surprising that the osteology and closest affinities of the genus have remained until this time practically unknown. It is not my intention to give here more than a bare outline of the more important structural features of *Sphærodactylus* or to discuss points which do not add definite evidence of phyletic relations.

The various species of *Sphærodactylus* have been exhaustively studied by Dr. Thomas Barbour. He has ready for press an elaborate monograph on the group. Dr. Barbour has aided me greatly in my study of the osteology of *Sphærodactylus* and its allies. I am especially indebted to him for specimens of *Aristelliger*, *Phelsuma*, *Lathrogecko*, *Lepidoblepharis*, and *Gonatodes*. These specimens were received in exchange from the Museum of Comparative Zoology and are now incorporated in the collections of the American Museum.

Comparison of Structural Characters

Sphærodactylus possesses procœlous vertebræ. It would seem that it could no longer be ranged with the gekkonids but should be grouped with *Coleonyx* in the Eublepharidæ. A detailed study of the skeleton of *Sphærodactylus* has shown that it is not closely related to *Coleonyx*. A search for its nearest allies has involved the examination of the skeletons of many genera of gekkonids and eublepharids. Small differences have been observed in the material prepared. It has been difficult to determine the relative value of these differences. Those characters which have seemed the most important are discussed below.

Vertebræ and Ribs

The vertebræ of *Sphærodactylus* are procœlous, agreeing in detail with those of the eublepharids *Lepidoblepharis* and *Lathrogecko*, and but slightly different from those of *Coleonyx*. Two views of a single vertebra

of *Sphærodactylus* are shown in Figure 1. It will be noted that the vertebra is of a very simple type.

It was surprising to find that a cartilaginous or fibro-cartilaginous band extends in *Sphærodactylus* from about the middle of the neural arch to the angular portion of the head of the rib. The cartilaginous nature of this band and its position relative to the neural arch and rib strongly suggest that it is the last vestige of the tubercle, a character-

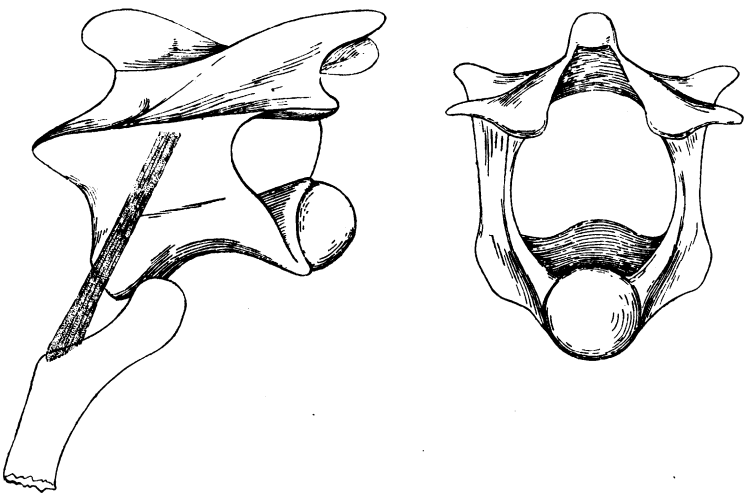


Fig. 1.—Vertebra (18th) of *Sphærodactylus macrolepis* Günther, lateral and posterior aspect. The former shows the cartilaginous tuberculum (stippled) of the rib.

istic structure of the ribs of primitive reptiles but one believed to have been entirely lost in the Lacertilia. Williston (1914, p. 33) states: "By the loss of the tubercle in lizards, the head became truly single-headed, and attached solely to the body; and this condition is characteristic of the order Squamata."

A cartilaginous tubercle, if such it may be called, is found not only in *Sphærodactylus* but also in *Lathrogecko*, *Lepidoblepharis*, and the neotropical species of *Gonatodes*. In *Coleonyx*, it is reduced, is more fibrous, and has a more anterior position than in *Sphærodactylus*. In all other lizards which I have examined, gekkonids, iguanids, teiids, xantusids, etc., this structure is represented by a ligament which is sometimes very slender and attached to the body of the vertebra near the articulation of the capitulum. In most iguanids and gekkonids, it is flattened and sometimes very difficult to distinguish.

Skull Structure

In addition to the procœlous form of the vertebræ, one other character has been used to distinguish the Eublepharidæ from the Gekkonidæ. The parietals of the eublepharids are stated to be fused into a single element in contrast to the paired parietals of the latter group. The parietals of *Sphærodactylus* remain perfectly distinct throughout life. It would seem that this was a feature indicating a close affinity to the true gekkonids. An examination of the skulls of the various gekkonids and eublepharids at hand has convinced me that the fusion of the parietals into a single element cannot be considered diagnostic of the eublepharids. Most gekkonids possess paired parietals, but there are exceptions even within a genus. Thus, I find that while all the neotropical species of *Phyllodactylus* at hand have paired parietals, there is but a single element in *P. siamensis*. The single parietal is not a constant feature of all eublepharids. It is single in *Coleonyx variegatus* (Baird) and *C. elegans* Gray, but double in *Lathrogecko xanthostigma* Noble. It was described as single in *Lepidoblepharis festæ* Peracca but it is double in *Lepidoblepharis barbouri* Noble.

Cope (1892) pointed out some differences between the skull of *Coleonyx* and that of *Phyllodactylus*. I have compared skulls of the same genera but have failed to find any marked differences. There is a reduced jugal in *Coleonyx* as well as in *Phyllodactylus*. Cope, however, did not consider those differences which he found of great importance, since in a later report (1898, p. 464) he states that the skeleton of the Eublepharidæ "is similar" to that of the Gekkonidæ "except in the procœlian vertebræ and single parietal bone."

Hyoid and Branchial Arches

Perhaps no one structure indicates the relationships of *Sphærodactylus* better than its hyoid apparatus. As shown in Figure 2*A*, the arches are very complete. The second epibranchial is well developed and is attached at both ends, a very unusual condition. The distal end is adherent to the exoccipital at the base of the paroccipital process; the proximal end is loosely attached to the second basibranchial some distance from the end. The hyoid arch is a simple bent rod. It is attached distally to the paroccipital process. The hyoid apparatus of a number of gekkonids has been figured. I have examined specimens of *Phyllodactylus* (3 species), *Thecadactylus*, *Hemidactylus*, *Aristelliger*, *Gehyra*, *Lygodactylus*, *Gekko*, *Tarentola* (2 species), *Pachydactylus*,

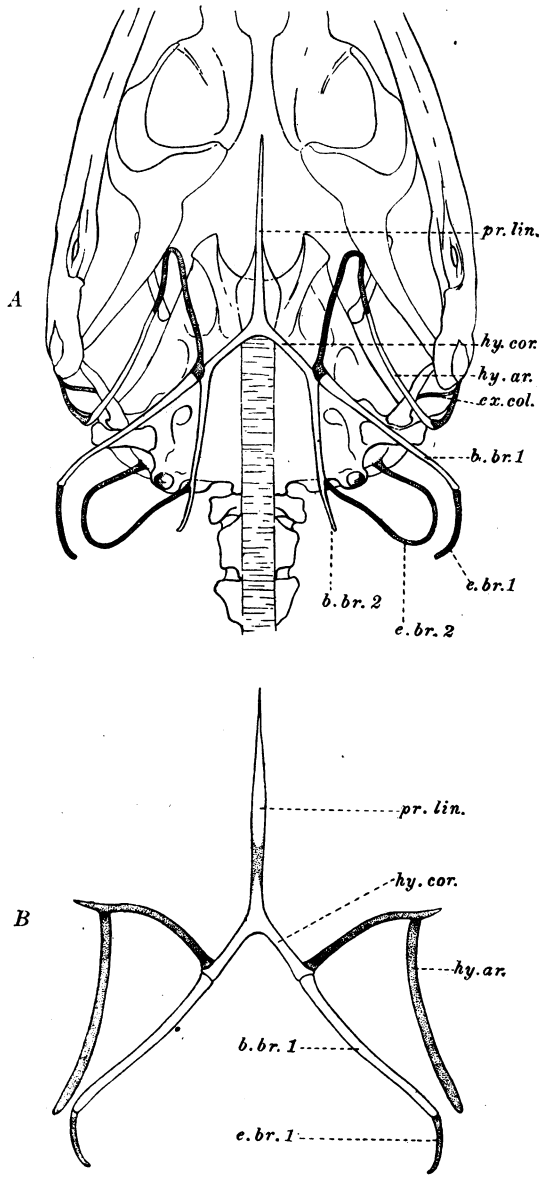


Fig. 2.—Hyoid Apparatus, ventral view. *A.—Sphærodactylus macrolepis* Günther, *in situ* to show attachments. *B.—Paragonatodes dickersoni* (Schmidt), a typical gekkonid hyoid apparatus with a specialized hyoid arch and with the second branchial arch wanting.

B.br. 1 = basibranchial I; b.br. 2 = basibranchial II; e.br. 1 = epibranchial I; e.br. 2 = epibranchial II; ex.col. = extracolumella; hy.ar. = hyoid arch; hy. cor. = body of hyoid; pr. lin. = lingual process.

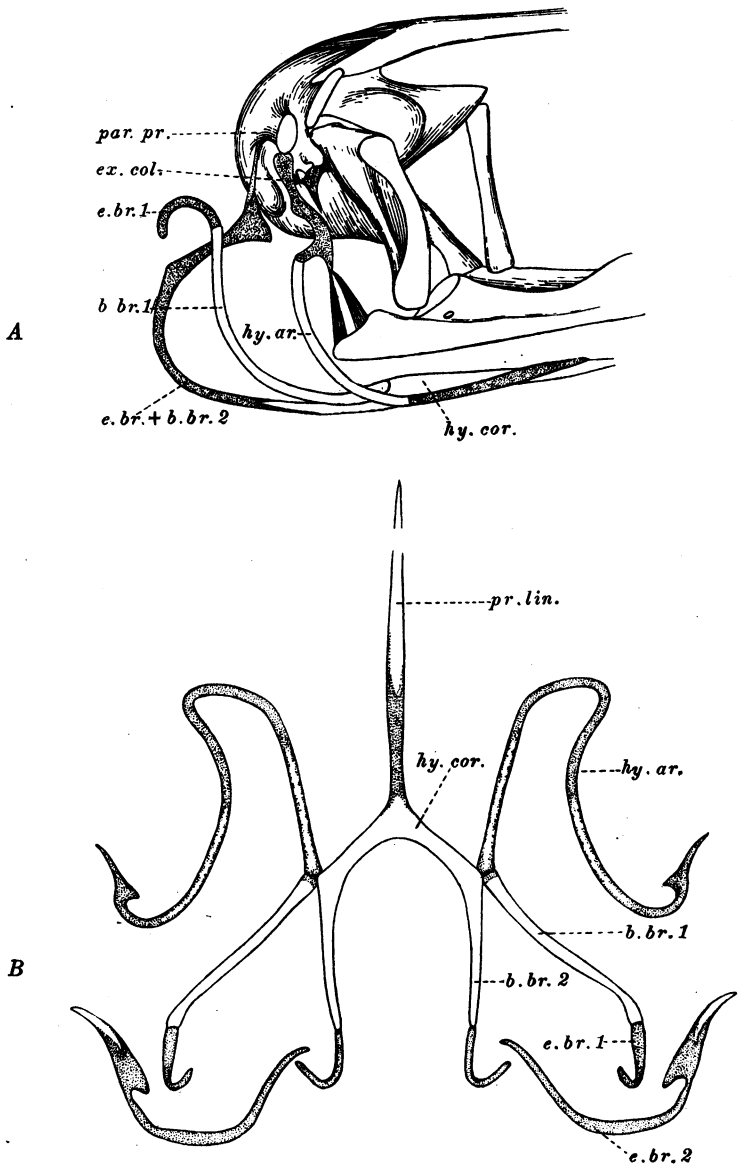


Fig. 3.—Hyoid Apparatus. *A.*—*Coleonyx variegatus* (Baird), lateral aspect of posterior part of cranium showing attachments of hyoid apparatus to skull. *B.*—*Lathrogecko xanthostigma* Noble, ventral view of the hyoid and branchial arches in their normal position.

B.br. 1 = basibranchial I; b.br. 2 = basibranchial II; e.br. 1 = epibranchial I; e.br. 2 = epibranchial II; ex.col. = extracolumella; hy.ar. = hyoid arch; hy.cor. = body of hyoid; par.pr. = paroccipital process; pr.lin. = lingual process.

Phelsuma, and *Gonatodes* (3 species). In none of these genera, except the neotropical species of *Gonatodes*, do the hyoid and branchial arches have a form and arrangement approaching the condition in *Sphærodactylus*. The arches of all gekkonids, with the exception just noted, are more or less reduced, especially the second branchial arch. The second epibranchial is generally present as a short and delicate cartilage lying free in the muscles and considerably removed from any attachment to either skull or basibranchials. In a number of specimens I could find no indication of such an epibranchial. It may not exist in the African gekkonid described by Schmidt as *Gonatodes dickersoni* (Figure 2*B*).

In the South American *Gonatodes atricucullaris* Noble and *G. annularis* Boulenger, the hyoid is very similar to that of *Sphærodactylus*. The chief difference lies in the fact that the second epibranchial, although well developed, is loosely associated with the skull and is free from the basibranchial. These two species agree with *Sphærodactylus* in the long basibranchials, extensive epibranchials, and simple hyoid arch. No gekkonids, except the neotropical species of *Gonatodes*, have been found to agree with *Sphærodactylus* in possessing a combination of these three features.

It is remarkable that such a distinctive type of hyoid apparatus as that of the neotropical species of *Gonatodes* should be found in the eublepharids *Lathrogecko* and *Lepidoblepharis*. The arches of these two genera are identical and differ from that of *Gonatodes atricucullaris* only in the slightly shorter first branchial arch and slightly larger arrow head to the second epibranchial. The distal end of the second epibranchial is not calcified in *G. atricucullaris* as it is in the several specimens of *Lepidoblepharis barbouri* and a specimen of *Lathrogecko xanthostigma* (Figure 3*B*) which I have examined. In all three forms, the distal end of the second epibranchial is loosely attached to the paroccipital process and lies closely associated with the endolymphatic sac. It seems obvious that the presence of such a well-developed hyoid in *Sphærodactylus*, *Lepidoblepharis*, *Lathrogecko*, and the neotropical forms of *Gonatodes* indicates common ancestry.

The most primitive type of lacertilian hyoid apparatus is that found in *Coleonyx*. This was not realized until very recently (Fürbringer, 1919). The figure of Cope (1892, Pl. III, fig. 8) of the hyoid apparatus of *C. variegatus* is very incorrect. *C. variegatus* and *C. elegans* have similar hyoid and branchial arches. The second epibranchial is continuous with the second basibranchial and there is no suture or break between the two parts. The distal portion of this second branchial arch is attached very

loosely to the skull by a ligament. The cartilaginous portions of both hyoid and branchial arches have a characteristic form (Figure 3*A*). This very primitive type of hyoid apparatus found in *Coleonyx* seems to indicate that the genus has no close affinity to *Sphærodactylus*. If primary importance were arbitrarily laid on the form of the hyoid and branchial arches in determining relationships, it would follow that *Sphærodactylus* is more closely related to the gekkonid *Gonatodes* than to the eublepharid *Coleonyx*. Such is probably the correct view.

Pectoral Girdle

Sphærodactylus possesses a typical gekkonid shoulder girdle, with subcruciform interclavicle and expanded, perforated clavicle. Its pectoral girdle differs radically from that of *Coleonyx* in having four instead of three ribs attached to the sternum. The other two genera of neotropical eublepharids agree with *Sphærodactylus* as regards the sternal ribs but differ in the form of the clavicle. In neither *Lepidoblepharis* nor *Lathrogecko* is the clavicle perforated.

Altogether too much emphasis has been laid on form of the clavicle as defining the larger groups of Lacertilia. It is now well known that a number of iguanids possess expanded and perforated clavicles. The expanded, perforated clavicle cannot be considered a diagnostic feature of all gekkonids. The clavicle of the neotropical species of *Gonatodes* (Figure 4*A*) is not more expanded than many so-called cylindrical clavicles.

If one considers the slightly dilated clavicle of the neotropical species of *Gonatodes* (Figure 4*A*) as the primitive type, one can readily derive from that the conditions found in the neotropical eublepharids. The clavicle of *Lathrogecko* is slightly more dilated than that of *Gonatodes*. In *Lepidoblepharis* (Figure 5*A*) it is still more expanded. In *Sphærodactylus* (Figure 5*B*), the expanded portion has become fenestrated. The series exhibited by *Gonatodes*, *Lathrogecko*, *Lepidoblepharis*, and *Sphærodactylus* illustrates beautifully how the clavicle might have been gradually expanded and in the extreme stage thinned out until a foramen was formed. There is much reason to believe that we have in this series of genera a natural group and that the expanded, perforated clavicle has been evolved from the cylindrical one.

It may be well to mention at this point that the subcruciform interclavicle is not always present in the gekkonids. I have found that the African *Gonatodes dickersoni* and the Madagascarian *Phelsuma laticauda*

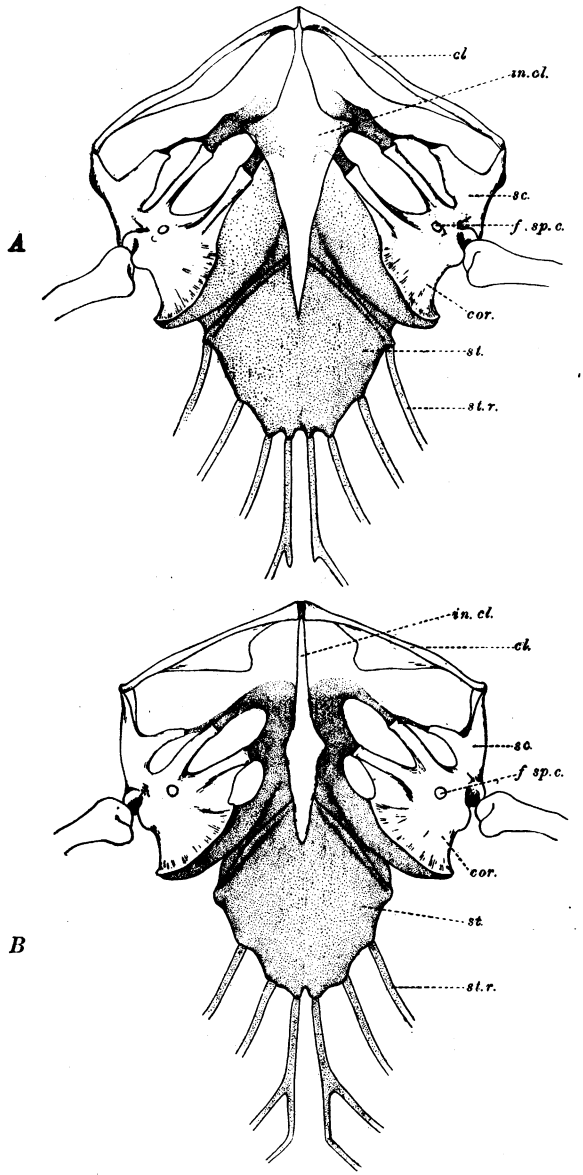


Fig. 4.—Pectoral Girdles, ventral aspect. *A.—Gonatodes atricucullaris* Noble. *B.—Paragonatodes dickersoni* (Schmidt).

Cor. = coracoid; cl. = clavicle; f.sp.c. = supracoracoid foramen; in.cl. = interclavicle; sc. = scapula; st = sternum; st.r. = sternal rib.

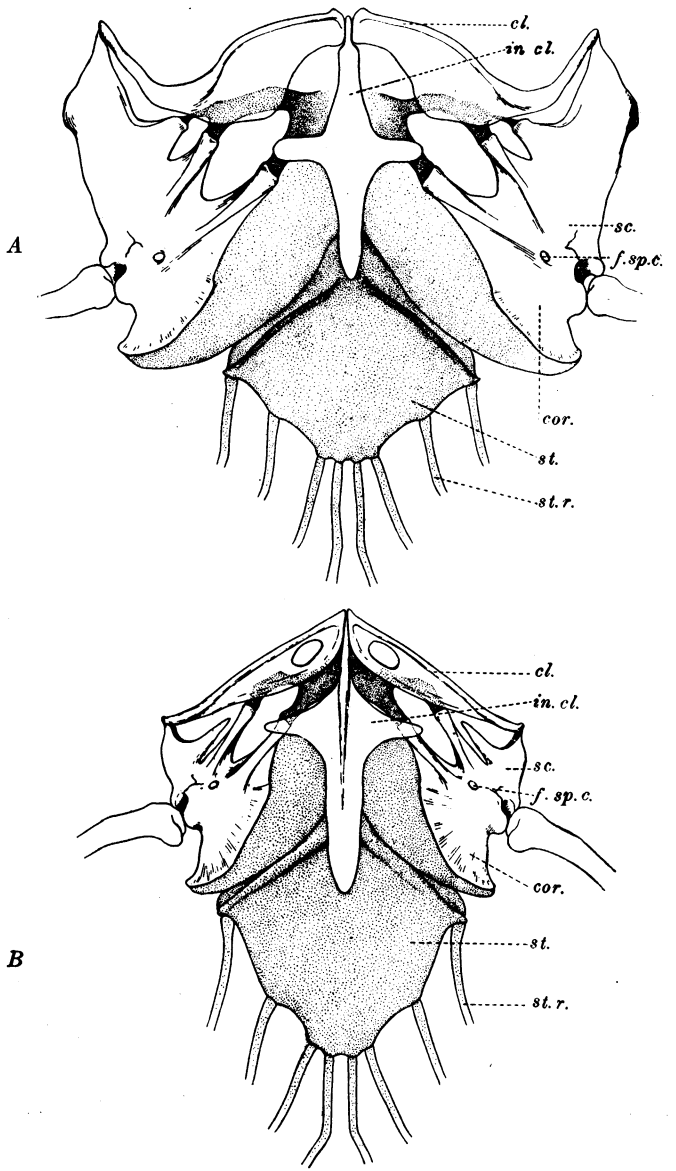


Fig. 5.—Pectoral Girdles, ventral aspect. *A.*—*Lepidoblepharis barbouri* Noble. *B.*—*Sphærodactylus macrolepis* Günther.

Cor. = coracoid; cl. = clavicle; f.sp.c. = supracoracoid foramen; in.cl. = interclavicle; sc. = scapula; st. = sternum; st.r. = sternal rib.

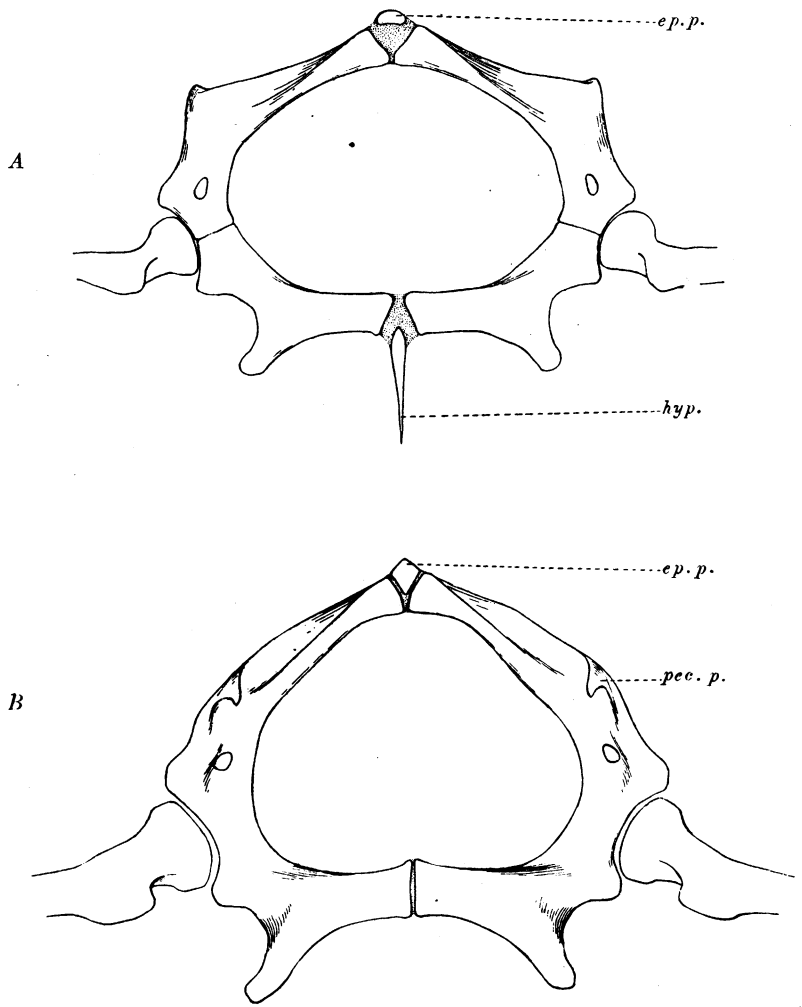


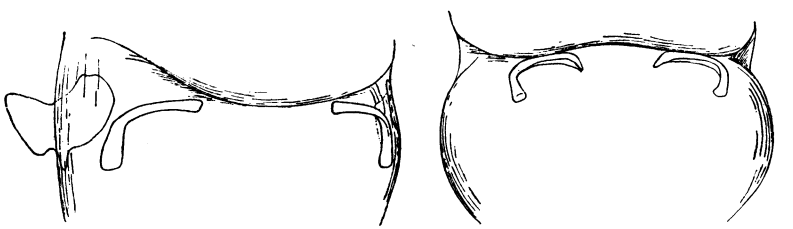
Fig. 6.—Pelves, ventral view. *A.—Paragonatodes dickersoni* (Schmidt.) *B.—Sphærodactylus macrolepis* Günther.

Ep.p. =epipubis; hyp. =hypo-ischium; pec.p =pectineal process.

have the transverse arms of the interclavicle reduced or wanting. The former species differs greatly from the neotropical species of *Gonatodes* in having only three sternal ribs (Figure 4*B*).

Pelvis and Cloacal Bones

Gonatodes dickersoni differs from the neotropical species of *Gonatodes* in the form of its pelvis (Figure 6*A*) and the presence of cloacal bones in the male. The pubis has a very small pectineal process in *G. dickersoni* and there is a well-developed hypo-ischium and epipubis. The pubis of the neotropical species of *Gonatodes* agrees with that of *Lathrogecko*, *Lepidoblepharis*, and *Sphærodactylus* in the large pectineal process directed ventrally. The hypo-ischium may be very rudimentary or wanting in *Sphærodactylus* (Figure 6*B*) and is wanting in the other genera. In *Coleonyx* there is no hypo-ischium, but there are two pairs of large cloacal bones (Figure 7*A*), one pair projecting through the skin.



A *B*

Fig. 7.—Cloacal Bones, showing relation to the cloacal slit. *A*.—*Coleonyx variegatus* (Baird). *B*.—*Paragonatodes dickersoni* (Schmidt).

Very little reference appears in the literature in regard to the cloacal bones. Lying free near the hemipenes and below the skin, they have been often overlooked. The hypo-ischium has been often called an os cloacæ. The hypo-ischium and cloacal bones should not be confused. They are neither homologous nor analogous. I find the greatest development of cloacal bones in *Pachydactylus maculatus* where, in addition to a broad fenestrated median bone lying transversely across the anterior lip of the cloaca, there is a pair of irregularly shaped bones posterior to either corner of the cloacal slit. The hypo-ischium in this species is very long. In the several species of *Phyllodactylus* which I have examined, the males are provided with cloacal bones very similar in form to those of *Gonatodes dickersoni*.

External Characters

The obvious external similarity of *Gonatodes* and *Lepidoblepharis* has been pointed out by Peracca (1897). Of the three features emphasized by Ruthven (1916) in distinguishing *Lathrogecko* from *Lepidoblepharis*, only one, that of the form of the digits, can be considered of generic importance. It is apparent from a study of both internal and external structure that *Lathrogecko* is closely allied to *Lepidoblepharis*. *Sphærodactylus* agrees with *Gonatodes*, *Lathrogecko*, and *Lepidoblepharis* in the slender form of the body, the narrowness of the head, the arrangement of labials, rostral, and nostril, and the shape of the pupil. Some species of *Sphærodactylus* agree with some species of *Gonatodes* in the pronounced sexual dimorphism and general color pattern. Still, it has been very difficult to pick out any definite external characters which demonstrate a closer relation between *Sphærodactylus* and the above genera than between *Sphærodactylus* and any other gekkonoid groups. Cope (1898) seemed prepared to believe that *Sphærodactylus* was closely allied to *Phyllodactylus*. Most other reviewers have considered that the form of the digit tips in *Sphærodactylus* warranted the placing of that genus in an isolated position in any scheme of phylogeny adopted.

A careful examination of the digits of *Sphærodactylus* will show that their terminal dilations are composed of scales having the same mutual relations as those which make up the claw sheath in *Lepidoblepharis*. It would seem that an asymmetrical enlargement of one side of the claw sheath of *Lepidoblepharis* would give exactly the condition found in *Sphærodactylus*. In *S. macrolepis* and apparently throughout the genus, this enlargement has been the outer scales of the claw sheath in the pes and the outer on all the digits of the manus except the fifth, where it has been the inner side of the original sheath which has become enlarged to form the disk.

The homology of these scales becomes much more obvious if the claw sheaths of *Gonatodes* and *Lathrogecko* are compared at the same time. It seems fairly certain when these sheaths are arranged in a series that we have before us an actual phylogenetic sequence. The claw sheath of *Lathrogecko* (Figure 8*B*) may have been derived directly from that of the neotropical species of *Gonatodes* by an enlargement of the terminal scales of the digits. The claw sheath of *Lepidoblepharis* (Figure 8*C*) could have been developed from the sheath of *Lathrogecko* by the dropping out of the second median scale. Finally, the disks of *Sphærodactylus* are understandable only if we assume that they were formed from the *Lepidoblepharis* claw sheath by the asymmetrical enlargement of the

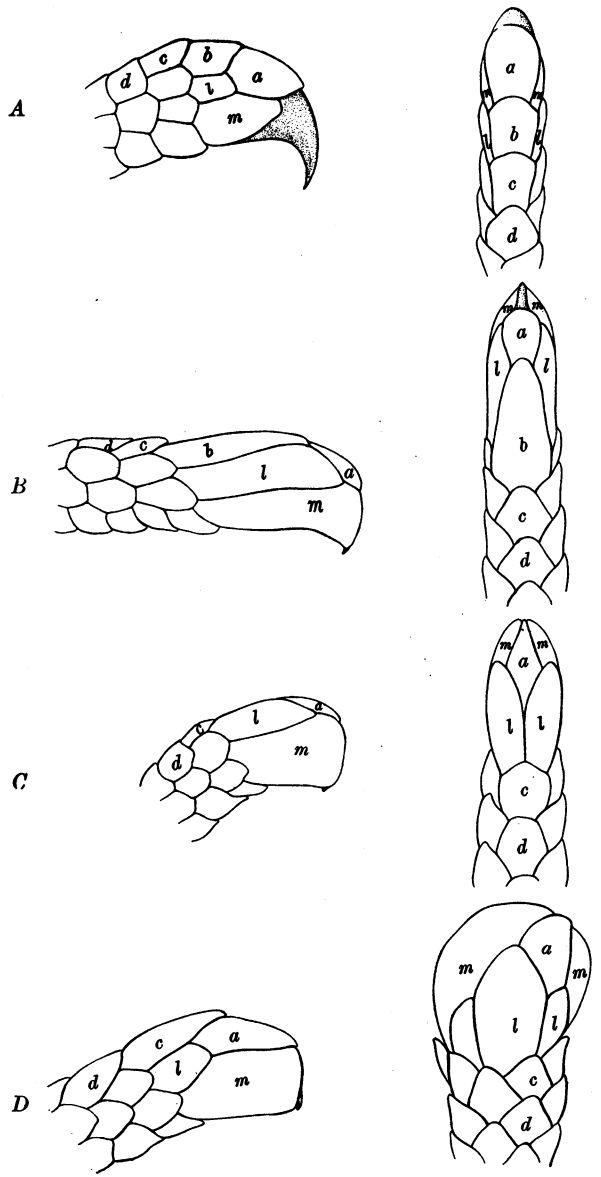


Fig. 8.—Claw Sheaths illustrating four stages in a single line of specialization. Homologous scales bear the same letters; original dorsal scales, *a–d*; laterals, *l* and *m*. *A.—Gonatodes atricucullaris* Noble. *B.—Lathrogecko xanthostigma* Noble. *C.—Lepidoblepharis barbouri* Noble. *D.—Sphærodactylus macrolepis* Günther.

scales on one side of the sheath. The steps assumed in the change from the *Gonatodes* to the *Lathrogecko* to the *Lepidoblepharis* types of sheath are not great; the step from the *Lepidoblepharis* to the *Sphærodactylus* type is less clear but no less admissible.

Phylogenetic Relations

It follows from the above résumé of distinctive characters that the eublepharids, *Sphærodactylus*, *Lepidoblepharis*, and *Lathrogecko*, are closely related to each other and to the neotropical species of the gekkonid *Gonatodes*. At least one of the Old World species of *Gonatodes*, and probably all, has no close affinity to the neotropical forms. Since the genus *Gonatodes* was based on a neotropical species, a new name will have to be proposed for Old World forms, or for at least the one species which we have studied in detail. It is probable that this new genus will embrace all three African species, less probable that it will include the East Indian forms which have until now been referred to *Gonatodes*.

Paragonatodes, new genus (Gekkonidæ)

Type.—*Gonatodes dickersoni* Schmidt. (Type locality, Medje, Belgian Congo.)

Diagnosis.—Digits slender, clawed; the distal portion of the digits slightly compressed and forming an angle with the claw; these distal portions covered beneath with a single series of scales distally, and with a double series of much smaller ones proximally (see Schmidt, 1919, fig. 6); body slender, with granules and tubercles above, with small scales below; tail cylindrical; pupil circular; eyelid distinct around eye. Hyoid apparatus reduced; no second basibranchials; no second epibranchials (Figure 2*B*); interclavicle dagger-form, no transverse arms; clavicle dilated but not fenestrated (Figure 4*B*); only three sternal ribs; pectineal process of pubis rudimentary; a well-developed hypo-ischium; male with a single pair of bow-shaped cloacal bones (Figure 7*B*); ligamentous tubercle of the ribs much reduced and proximated to the capitulum.

It seems extremely probable that *Sphærodactylus*, *Lepidoblepharis*, and *Lathrogecko*, with their procœlous vertebræ, four sternal ribs, cartilaginous tuberculum, distinctive hyoid, pelvis and cloacal regions, form a natural group of genera. These genera show closer affinity to *Gonatodes* than to any other gekkonid.

Evidence has been brought forth to show that we have in this group a natural series commencing with *Gonatodes*, and leading through *Lathrogecko* and *Lepidoblepharis* to *Sphærodactylus*. It is believed that this series represents an actual morphogenetic sequence. The more important changes which occurred in this series may be listed. (1) The vertebræ

changed from amphicœlous to procœlous, and most of the intercentra were lost. (2) The second epibranchial lost its characteristic arrow-shaped head and became attached to the exoccipital near the base of the paroccipital process. The proximal end of the second epibranchial migrated anteriorly and became loosely attached to the second basibranchial. (3) The clavicles evolved from narrow but flattened rods to broadly expanded sheets, and finally thinned out in their proximal portions to form median fenestræ. (4) The terminal scales of the digits became elongated to form six-scaled claw sheaths. The posterior dorsal of these six scales dropped out to form five-scaled sheaths. Finally, there was an asymmetrical enlargement of one side of the sheaths to form disks.

It is important to emphasize that this series of steps has only been assumed after a study of all the genera of gekkonids and eublepharids available to me; that *Gonatodes*, *Lathrogecko*, *Lepidoblepharis*, and *Sphærodactylus* have more in common with each other than can be found between *Sphærodactylus* and *Coleonyx*, or *Gonatodes* and any of the ten other genera of gekkonids at hand. In other words, it seems extremely likely that, among other things, the procœlous vertebræ have been developed in this series quite independently of similar changes in any other series. It follows that in all probability the Eublepharidæ had a polyphyletic origin and, instead of being a very ancient group as hitherto believed, they may be a very recent assemblage, even if a conservative one.

It has been suggested that the gekkonids are degenerate forms, their amphicœlous vertebræ secondary structures. There is obviously nothing primitive in the highly reduced skull of the gekkonids. *Coleonyx* with its very primitive hyoid possesses procœlous vertebræ. Xantusids with procœlus vertebræ also have primitive hyoids, and I have found that *Xantusia vigilis* retains the intermedium in the carpus as further evidence of its ancestral position among primitive Lacertilia. Why, then, should we not reverse our series and evolve *Gonatodes* from *Sphærodactylus* or at least *Lathrogecko*? This would necessitate developing intercentra again, evolving cylindrical from expanded clavicles, and changing from specialized to primitive claw sheaths. Altogether too little is known about the osteology of the Lacertilia to be entirely certain about the direction in which evolution has progressed. The view I have outlined above seems at the present time the most probable.

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