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A CONTRIBUTION TO OUR KNOWLEDGE OF THE ANATOMY OF CHAMAELEONS.

By Paul A. Methuen, M.A. (Oxon), and John Hewitt, B.A. (Cantab).

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Introduction.

In this paper we record the results of some investigations which commenced with the examination of the lungs of the various species of Chamaeleon found in South Africa, but which eventually led to an attempt to determine the morphological position of the various forms in general.

The preliminary examination of one character alone furnished data which induced us to make a critical survey of various structural characters; and it soon became apparent that the group which included the viviparous *C. pumilus* and its allies was in several respects more generalized than the group of oviparous Chamaeleons, namely, *C. dilepis* and allies, but that to what extent these two groups might be sharply separated and how far the simplicity of structure in the *pumilus* section might be primitive or secondary could only be ascertained by an examination of all the main types of the family. A survey as comprehensive as this has not been possible, but sufficient material from Madagascar (as recorded in Ann. Trans. Mus., vol. iii., 1913, p. 190) and from South Africa has been available to enable us to place the more important groups of the family in their respective positions with regard to structure, and to point out the primitive forms with fair degree of probability.

This account is therefore not intended to deal exhaustively with any morphological character herein considered, but merely to compare the several structures concerned as they are found in the various species.

The Lungs.

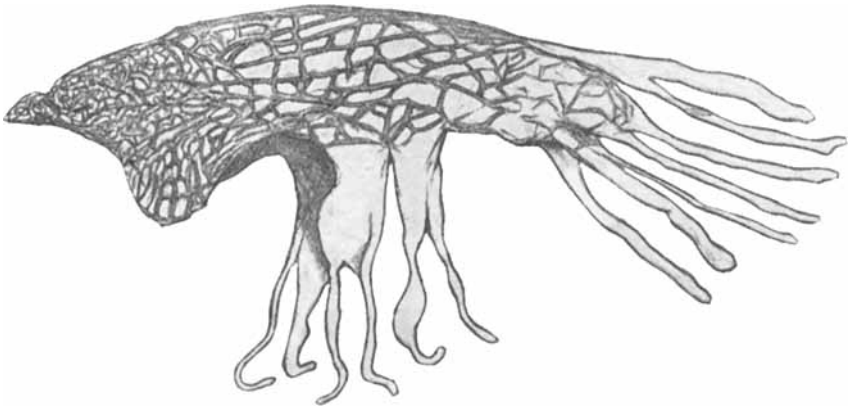
The peculiar features of the lungs of the common Chamaeleon (*C. vulgaris*) have often been figured and briefly described in the various text-books of comparative anatomy; but as was pointed out long ago by Cuvier, and recently emphasized by Mr. F. E. Beddard (P.Z.S. 1907, p. 35), such features are not found in all species, and it has been shown that the small Cape Chamaeleon (*C. pumilus*) possesses lungs which are in no way anomalous amongst Lacertilia. Beddard's paper includes an excellent account of the lungs of the latter species and of several others.

If the lungs of *Chamaeleon vulgaris* be examined, it will be seen that the organ is produced into a number of elongated sacs or diverticula which in structure differ from the lung itself in that these processes are not supplied with a reticulum of blood-vessels. The function of these diverticula

is at present unknown. They are capable of expansion and contraction. Their position is generally in the posterior part of the body, and ventrally lying over and between the intestines.

In the common Transvaal Chamaeleon, *Ch. quilensis*, these peculiar structures are also very well developed as posterior and ventral diverticula of some considerable length (*vide* Text-fig. 1). The figure is based on the lung of a fresh individual drawn *in situ*; the general position of the outgrowths has been delineated as in life. However, a good length of each sac must be imagined as tucked away and twisted between the intestines.

Mr. Beddard has given a figure of the lung of *Ch. dilepis* with very short diverticula. Though we have examined several specimens of this species we have found the sacs to be short only when much contracted. Indeed, we have been quite unable to detect any difference between the



TEXT-FIG. 1.—LEFT LUNG OF *C. quilensis*.

lungs of *dilepis* and those of *quilensis*, though Beddard, who had much less material at his disposal, regarded them as essentially different This is a point of some importance, seeing that some authorities, including Boulenger, regard *dilepis* and *quilensis* as distinct species, whilst Tornier and Werner believe them to be merely forms of the same species. We are in favour of the latter view.

In South Africa the genus *Chamaeleon*, as defined by Boulenger, is represented by about nine species, which, according to their external characters, are arranged into three sections: (1) that of *dilepis* and its variety *quilensis*, (2) that of *namaquensis*, and (3) the *pumilus* section which includes all the species so characteristic of southern and eastern Cape Colony with outliers in Natal and the Transvaal. Of *namaquensis* we have been able to examine two specimens. The lungs were found to have several long diverticula distally and ventrally, but they were not so numerous as in *dilepis*. We may add that *namaquensis* shows a further

resemblance to *dilepis* rather than to the *pumilus* section in the total absence of pigmentation on the peritoneum, which is black in *damaranus*, *ventralis*, etc. We have examined several specimens each of *pumilus*, *ventralis*, and *damaranus*,* in every case finding no trace of diverticula. As the *pumilus* section is fairly homogeneous in external characters, we assume that the absence of diverticula is characteristic of the whole section. Further, *Brookesia* of Madagascar is in agreement with the *pumilus* section in this respect. It would be of great interest to know what are the lung characters of the genus *Rhampholeon* of tropical Africa, but unfortunately no material is available. We venture to surmise, however, that it will prove to be similar to *Brookesia*. *Chamaeleon tigris* of the Seychelles also seems to be allied to the *pumilus* section, but we do not know its lung characters.

(Through the courtesy of Mr. G. A. Boulenger, F.R.S., we have been enabled to examine a specimen of *Rhampholeon spectrum* (Oban, Calabar) and two specimens of *Chamaeleon tigris* (Silhouette Is., Seychelles) in the British Museum collection.

The lungs of *Rhampholeon* were found to be simple, without trace of diverticula. Both the specimens of *Chamaeleon tigris* showed that the lungs were without diverticula such as those described below for other species of *Chamaeleon;* but the lungs in both had ventrally and at a point about two-thirds the length of the organ distally a rounded lobe supplied with blood-vessels. In the absence of true diverticula *C. tigris* resembles the *pumilus* section of the Cape; on the other hand, the examination of a rather badly preserved skull of this species inclines us to the view that it is in all probability an isolated form, related most nearly perhaps to some of the Madagascar species.) †

Undoubtedly the primitive scheme of lung of the Rhiptoglossa is that which conforms to a great extent to that of other Lacertilia; and for this reason in the genus *Chamaeleon*, the Cape species, *C. pumilus*, *ventralis*, *damaranus*, etc., seem to be (they may be degraded) nearer the primitive Rhiptoglossan stock than the Malagasy and other species of this genus (cf. Beddard, *loc. cit.* p. 41, line 44), and similarly the genus *Brookesia* must rank as the Malagasy representative of that primitive stock, though it is now in some respects a highly specialized creature.

The variation which obtains in the peculiar type of lung as presented by the common Chamaeleon and by *C. dilepis* may be illustrated by reference to the following species :—

Chamaeleon dilepis, Leach, var. *quilensis*, Boc. (Text-fig. 1).—A good deal of variation obtains, and even in the same individual the number of

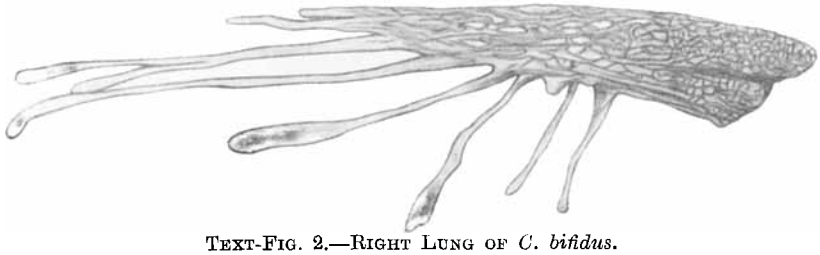
* Our specimens of *damaranus* came from Knysna. It is highly improbable that the original locality record for this species, "Damaraland," can be correct.

† Inserted April, 1914.

diverticula may be different on the two sides. The size of the sacs varies. Further, some may be simple, but the majority are generally bifid. In one specimen examined four simple and four bifid outgrowths existed; in another (*vide* Text-fig. 1) one simple and six bifid. In the latter case the outgrowths were much expanded at their bases, and generally thin and tubular in their distal parts.

Specimens from Pretoria.

C. bifidus (Text-fig. 2).—The lung figured was much contracted, but the diverticula had retained their normal condition. As outgrowths from the posterior portion of the lung two small processes had been developed: also two long processes—one of them bifid—and four of moderate length

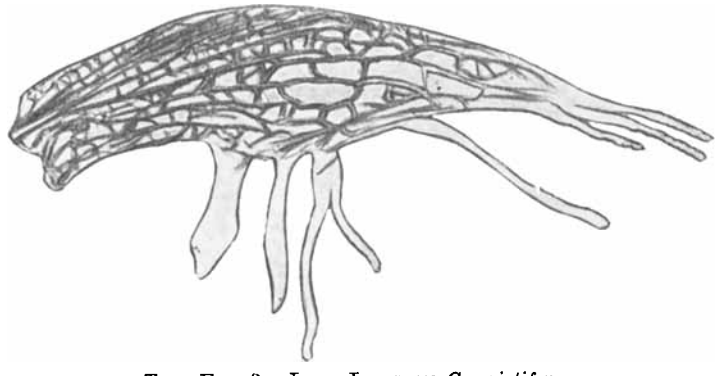


TEXT-FIG. 2.—RIGHT LUNG OF *C. bifidus*.

were noticed. Another outgrowth is indicated in the figure (it was probably broken during dissection).

Specimen, an adult male from Ambilo, district of Andevoranto, east coast of Madagascar.

C. parsonii, Cuv., var. *cristifer*, Mthn. and Hew. (Text-fig. 3).—In the specimen chosen for dissection several of the sacs were much contracted.

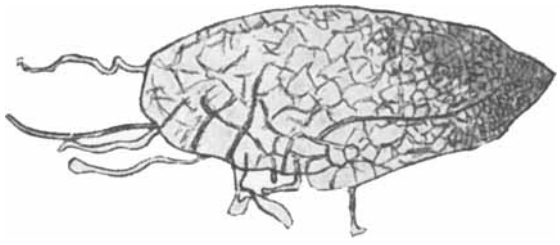


TEXT-FIG. 3.—LEFT LUNG OF *C. cristifer*.

Seven processes were detected. It will be noticed that the anterior process is much swollen.

Specimen from Analamazotra, east region of Madagascar.

C. lateralis, Gray (Text-fig. 4).—The diverticula, though fairly numerous, are insignificant structures if compared with those of the foregoing species. The figure shows one posterior and four basal diverticula, and

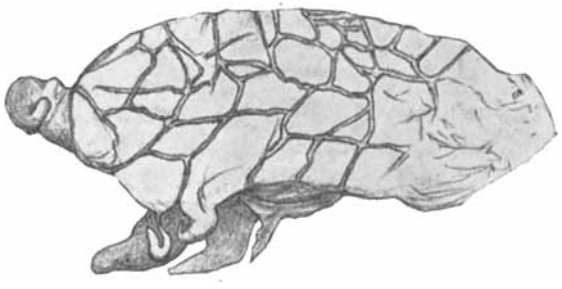


TEXT-FIG. 4.—LEFT LUNG OF *C. lateralis*.

on the inner side of the lung (seen through the organ) one fairly large and two smaller diverticula.

Specimen from Analamazotra.

C. malthe, Gthr. (Text-fig. 5).—The outgrowths consist of a swollen posterior and two enlarged ventral sacs; also three ventral processes.



TEXT-FIG. 5.—RIGHT LUNG OF *C. malthé*.

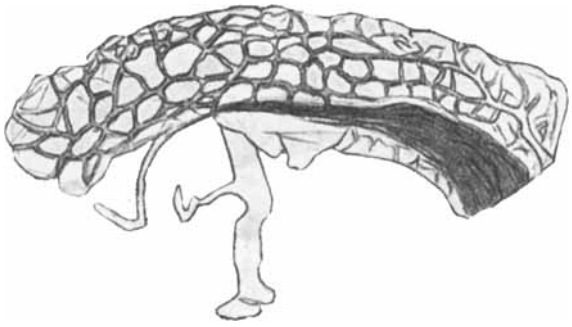
Specimen from Analamazotra.

C. brevicornis, Gthr. (Text-fig. 6).—A great reduction as regards the outgrowths is apparent. One large diverticulum with a small elongated process directed in a posterior direction; posterior to this a long, thin outgrowth; and partly anterior to these two ill-developed sacs.

C. nasuta, D. and B. (Text-fig. 7*a*), and *C. gastrotaenia* (Text-fig. 7 *b*). —In both these small Malagasy species the development of the outgrowths is very feeble, but the sacs are to be recognized readily.

Specimens from the eastern parts of Madagascar.

In no species of *Chamaeleon* from Madagascar have we found simple lungs.

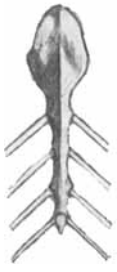


TEXT-FIG. 6.—RIGHT LUNG OF *C. brevicornis.*

TEXT-FIG. 7.—*a*, LEFT LUNG OF *C. nasuta*, and *b*, RIGHT LUNG OF *C. gastrotaenia.*

THE STERNUM AND RIBS.

In the nature of the sternal apparatus and attachment of the ribs we have a further structural character which can be utilized to some extent



TEXT-FIG. 8.—ABNORMAL ARRANGEMENT OF STERNAL RIBS IN *C. quilensis.*

TEXT-FIG. 9.—ABNORMAL ARRANGEMENT OF STERNAL RIBS IN *C. damaranus.*

in determining the morphological position of the various groups of Chamaeleons.

Normally in all the groups which we have examined three pairs of ribs are attached to the sternum. In exceptional cases four pairs may become attached (Text-fig. 8), or three on one side, four on the other (Text-fig. 9). The remaining ribs form continuous hoops behind the sternum.

The simplest arrangement appears to be in *Brookesia*. The anterior part of the sternum in *B. superciliaris* (Text-fig. 10) is well developed. The manubrium, which is comparatively short, is broad at the base and slender posteriorly. There is no xiphoid process. The first post-sternal

TEXT-FIG. 10.—STERNAL ARRANGEMENT IN *Brookesia*.

TEXT-FIG. 11.—TYPICAL ARRANGEMENT OF STERNAL RIBS IN *C. ventralis*.

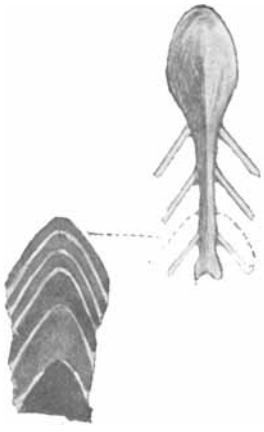
hoop is placed a little way behind the sternal ribs. Siebenrock has also figured the sternum of *Brookesia* (Sitz. Akad. Wiss. Wien, 1893).

C. ventralis (Text-fig. 11).—The manubrium is fairly long, is more clearly differentiated than in *Brookesia*, and possesses a slender xiphoid process which is underlain by the first or, in addition, the second pair of abdominal hoops. In *C. damaranus* much the same arrangement is to be seen, though abnormally four pairs of ribs on one side, three on the other, may articulate with the sternum (Text-fig. 9). In the figure the first hoop is in reality underlying the xiphoid process and is not intimately attached to it.

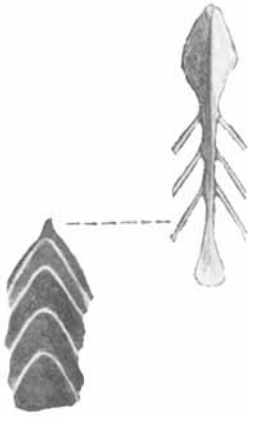
In the Malagasy species of the genus *Chamaeleon* the sternal apparatus conforms more or less to that of the *pumilus* section just considered, but a certain specialization has come about. The xiphoid process is better developed, and is variously shaped. Generally three if not four abdominal hoops underlie the xiphisternum, a strong membrane attaching the first hoop to the tip of the xiphoid process. The first three or four hoops are connected by muscles to the anterior part of the sternum.

Text-fig. 12 shows the arrangement in *C. brevicornis*, and a similar condition obtains in *C. bifidus* and in *C. parsonii cristifer*, though in the last a small bilobed cartilage articulating with the extremity of the xiphi-

sternum serves as an attachment for the membrane which is connected to the first pair of abdominal hoops.



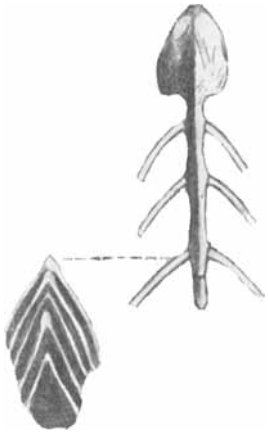
TEXT-FIG. 12.—STERNAL ARRANGEMENT IN *C. brevicornis.*



TEXT-FIG. 13.—STERNAL ARRANGEMENT IN *C. lateralis.*

Text-fig. 13 shows the sternum of *C. lateralis ;* it is chiefly peculiar in the length and breadth posteriorly of the xiphoid process.

The highest specialization appears to take place in the *dilepis* group, as exemplified in this paper by *C. quilensis* and *C. dilepis.* Normally (Text-



TEXT-FIG. 14.—TYPICAL ARRANGEMENT OF STERNAL RIBS IN *C. dilepis.*

fig. 14) three pairs of ribs are attached to the sternum, but sometimes there are four. The xiphisternum is rather small. A membrane attaches

this process to the first four hoops, which are bunched closely together; whereas in the *pumilus* group, as exemplified in *C. ventralis*, the corresponding hoops are not thus bunched together, but occupy positions more or less equidistant from one another, just like the hoops more posteriorly situated.

Ribs.—Chamaeleons are remarkable amongst reptiles, excluding snakes and serpentiform lizards, in that most of the post-sternal ribs form complete hoops. According to Werner there are eight of these hoops in *Chamaeleon*, but only six in *Brookesia* and *Rhampholeon*. However, the total number of rib-bearing vertebrae is also greater in Chamaeleons, for Werner cites fifteen in *Chamaeleon*, twelve in *Rhampholeon*, and nine in *Brookesia*. As a matter of fact, the number of rib-bearing vertebrae varies considerably within the genus *Chamaeleon*. We find that there are fourteen in *C. pumilus* and *C. ventralis*, sixteen or seventeen in *C. dilepis* or *C. quilensis*, whilst the small species, *C. gastrotaenia* and *C. nasuta*, have only thirteen rib-bearing vertebrae. The smaller numbers most probably represent the more primitive conditions.

Skull.*

The various published descriptions and figures of the Chamaeleon skull relate mostly to *C. vulgaris*, which, it may be noted, is one of the most specialized members of the family. In an important pioneer paper W. K. Parker has dealt at great length with the skulls of *C. vulgaris* and of *C. pumilus*, but in our judgment his account is in several respects misleading or inaccurate; unfortunately his errors have been repeated in the text-books. So far as we know a really good account of the Chamaeleon skull has not been published: Siebenrock, however, has given a careful description of the skull of *Brookesia*. We have therefore been obliged to depart somewhat from our original intention of merely comparing together the various types, since in indicating the homologies of particular bones it seemed advisable to point out clearly in what respects the views of other authors were in conflict with our own.

Squamosal and prosquamosal.†—In applying these terms to the inner

* The following account of Chamaeleon skulls is based on external examination, not on sections.

† Since this account was written, Dr. Broom has kindly sent us a copy of his paper "On the Squamosal and Related Bones in the Mosasaurs and Lizards" (Bull. Amer. Mus. Nat. Hist., vol. 32, art. 32, pp. 507–508, publ. Oct., 1913), in which he adduces reasons for changing his previously expressed views on the homologies of the bones here considered. He is now of opinion that the outer bone in Mosasaurs and Lizards is the squamosal, and the inner one the tabulare. He remarks that the inner bone in Mosasaurs is "apparently not a bone of the temporal roof at all, except to some slight extent secondarily": it is "more of an occipital element than an element of the temporal roof."

It appears to us that the identity of the outer bone with the mammalian squamosal is still undecided.

and outer elements respectively of the "supratemporal" arch of a lizard's skull we do so on the recommendation of Drs. Broom and Gadow, to each of whom we are greatly indebted for information regarding the probable homologies of these elements in general. However, we are limiting the present question to a brief comparison between the various forms of Chamaeleons and some other lizards in respect to these bones. In the posterior part of the supratemporal arch of the common Chamaeleons (*C. vulgaris* or *C. quilensis*) two bones are found, a larger one extending the whole distance from the tip of the parietal to the postfrontal and jugal, and a small inconspicuous sheathing bone only seen in hind view and stretching but a short distance above the quadrate. Comparing these with the bones of a typical lacertilian, such as *Varanus*, we believe that the larger one is homologous with the bar (the *prosquamosal*) which in *Varanus* connects the quadrate with the postfrontal; whilst the very small bone is the homologue of the inner element (the *squamosal*) which passes from the quadrate to the lateral part of the parietal. This view of their homology does not appear to have been held by some other writers on Chamaeleons. Owen spoke of the large bone as the mastoid, implying its homology with the inner bone of *Varanus*. Boulenger, in the British Museum Catalogue of Lizards, calls this same bone the "supratemporal," a term which he uses in the same work for the inner bone in other lizards. Huxley seems to have held the same view of its homology. On the other hand, in W. K. Parker's account of the structure of the skull in Chamaeleons (Trans. Zool. Soc., xi., p. 77 *et seq.*), in C. K. Hoffmann's work (Bronn's, Tierreich), and in Werner's monographs (Das Tierreich, 1911, and Zool. Jahrbuch, Sept., 1902, vol. xv.) the large bone is styled the squamosal, all these authors using that term in other lizards for the bone which we are now calling the prosquamosal. Dr. Gadow, in a short account of the Chamaeleon skull (Camb. Nat. Hist., p. 568), describes the two bones as partially fused, and is not clear regarding their homologies, for he says, "the parietal bones united into one, extends backwards far beyond the occiput, and the tip of this projection is met by a much-elongated supratemporal bone which, partly fused with the squamosal, helps to enclose a huge supratemporal fossa"; but in his accompanying figure the much elongated bone is simply labelled the squamosal.

The prosquamosal and the much reduced squamosal show various degrees of development in different members of the family of Chamaeleons. The prosquamosal is largest in the *dilepis* group: in these species it stretches from the tip of the parietal to the orbital region, where it forms sutures both with the postfrontal and the jugal. A similar arrangement is found in the Malagasy species, *C. lateralis*, *C. nasuta*, and *C. brevicornis*. In a single specimen of *C. gastrotaenia* examined, the prosquamosal does

not reach the jugal. In the several Cape species belonging to the *pumilus* group, the prosquamosal does not reach to the tip of the parietal, but is met by a descending lateral process of that bone, whilst anteriorly it forms a suture with the postfrontal, but does not reach the jugal. In this latter respect the *pumilus* condition resembles that in *Varanus*, whilst the *dilepis* condition is like that in *Agama*. According to W. K. Parker's figures, the prosquamosal of a juvenile *C. vulgaris* does not reach the jugal, whilst in the adult of that species, as in *dilepis*, it forms a fairly broad suture therewith. In *Brookesia* (and apparently also in *Rhampholeon*) the prosquamosal is completely separated from the jugal. Assuming the accuracy of Parker's figure and statement concerning the young of *C. vulgaris* it would appear that the primitive condition is that of *C. pumilus* and *Brookesia*.

The squamosal, though small, is quite distinct both in the *dilepis* and in the *pumilus* group, and indeed in all species of the large genus *Chamaeleon* examined by us, being best developed in *C. dilepis* and allies. In *C. ventralis* the outer surface of the squamosal occupies a hollow between the prosquamosal and the exoccipital, and by the growth of these two bones the squamosal is squeezed to the interior. In *Rhampholeon* it is said to be absent. In *Brookesia* the bone is exposed only to a very slight extent in external view, appearing at the base of the prosquamosal, and resting on the quadrate: if the prosquamosal be removed, the squamosal can be seen to extend upwards for a considerable distance.

The presence of both prosquamosal and squamosal in a reptilian skull is generally considered the more primitive condition, yet *Sphenodon* has only one bone. In *Sphenodon* that bone is often stated to be the homologue of the mammalian squamosal, in which case if the inner bone of a *Varanus* skull is correctly homologized with the squamosal of mammals it would appear that the single bone found in *Rhampholeon* (or the larger one in *Brookesia*), though occupying precisely the same position relative to the other bones of the skull, is nevertheless not homologous with the single bone of *Sphenodon*. To us it would seem just as probable that the single element in *Rhampholeon* (one of the most primitive of Rhiptoglossa) and of *Sphenodon* are homologues; from this it would follow that either this element in *Sphenodon* is a prosquamosal, or the outer element in *Varanus* and lizards in general is a true squamosal.

We are not, however, in a position to determine this point, and we doubt if it ever will be possible to determine with certainty the lacertilian homologue of the single bone in *sphenodon*. The enlargement of the prosquamosal and the accompanying reduction of the squamosal is probably not due to the formation of the casque, as might perhaps have been suspected from consideration of *C. quilensis* or of *C. vulgaris*,

since the same conditions obtain for *Brookesia*, which, judging from our specimens of *B. superciliaris*, practically has no casque: this, however, involves the assumption that *Brookesia* is not a degraded type.

Parietal.—The parietal is single, forming in *C. quilensis* and *C. vulgaris* a much-narrowed and compressed style, whereas in *C. pumilus* and allies it takes the form of a broad plate with a descending process on either side which meets the prosquamosal. In *C. brevicornis* and some other Malagasy Chamaeleons the parietal, though it expands a little posteriorly, never forms a broad plate, nor has a descending process postero-laterally. The descending process of the parietal, which in the genus *Chamaeleon* is found apparently only in the *pumilus* group, corresponds no doubt with the crescentic horn at the hind angle of the parietal of *Varanus* or *Agama*. The plate-like parietal in the skull of *Brookesia* is, however, still more typically lacertilian than that of *C. pumilus*, as it is not prolonged backwards beyond the occipital region (Siebenrock, however, dealing with *B. superciliaris*, figures a backwardly projecting parietal); and, further, it has retained on either side anteriorly a descending process which is attached to the prootic region; it has also the descending postero-lateral process. *Rhampholeon* is stated to have no such lateral process to its parietal. According to W. K. Parker, in his detailed account of *C. vulgaris*, the bone which we are referring to as the parietal is really an interparietal, the true parietals having more or less completely fused with the prosquamosals. He describes and figures a suture in the prosquamosal which marks the junction of these two bones, but we have found no trace of such a suture in any Chamaeleon, and Parker himself was unable to detect any indication of distinct parietals and interparietals in *C. pumilus*.

Mr. Boulenger, in the British Museum Catalogue of Lizards, describes what would appear to be a similar state of affairs as follows: "Parietal single, often much narrowed and compressed, forming a crest and meeting posteriorly the extremities of a pair of bones the supratemporals, which on each side connect it with the squamosal. In some species the parietal in the adult may be much expanded *and form a bony slab, from which the supratemporals are no longer to be distinguished.*" We are unable to comprehend the meaning of the latter sentence, and we believe that the bone we call parietal is homologous throughout the family.

Frontal.—The frontal is generally stated to be single in Chamaeleons. According to W. K. Parker there are two frontals in the skull of a newly hatched *C. vulgaris*. In young skulls of *C. ventralis* we have found no indication whatever of a paired condition.

Pre- and Post-frontals.—These bones in *Brookesia* (and in *Rhampholeon*) are separated by the frontal, as in the case of *Varanus* or *Agama*. In *C. dilepis* and *vulgaris* they meet on each side to form the upper

boundary of the orbit: in the *pumilus* group, however, they do not meet. This character is not absolutely constant in the genus *Chamaeleon* even apart from the *pumilus* section, since *C. nasutus* and *C. gastrotaenia* exhibit the *pumilus* condition; whilst *C. lateralis* has the pre- and post-frontals connected by a membrane external to the frontal, *C. brevicornis* agrees with the condition found in *dilepis*. There can be little doubt but that the *dilepis* condition is secondary.

Lachrymal.—*C. dilepis* has a distinct lachrymal bone like most lizards, but no such bone is to be found in *Brookesia* (and in *Rhampholeon*) and in the *pumilus* group. It is also absent in *C. brevicornis* and *C. lateralis*.

Nasal.—The nasal bone in the skull of *Brookesia* is a large unpaired plate bordering the nasal opening. In all species of Chamaeleon the nasal bones are small and paired and do not border the nasal opening, being cut off therefrom by a forward prolongation of the prefrontals. In the adult skull the large prefrontal fontanelle is bordered internally by the nasals, and is thus entirely separated from the nasal opening; but in the young of *ventralis* the prefrontal fontanelle and the nasal opening are in open connection—a condition which, according to Parker, is exhibited also in the case of the newly hatched young of *C. vulgaris*, and according to Werner in the adult of *Rhampholeon*. This latter genus is said to have small paired nasals. In one species of the *pumilus* group, namely in *C. damaranus* the nasal has a transverse process passing to the prefrontal and then completely dividing the prefrontal fontanelle into two; otherwise the *pumilus* group shows in this respect no important difference from *quilensis* or *vulgaris*.

Parasphenoid.—According to Parker a parasphenoid bone occurs in the skull of *C. pumilus*, but is absent from that of *C. vulgaris*. Siebenrock further describes and figures this bone in *Brookesia*. We have not been able to find any trace of the bone in *C. ventralis*: in this species the interorbital septum is thickened at the base, but shows no ossification whatever.

Vomer.—An unpaired vomer is found in the *pumilus* group and in *C. quilensis*. In *C. pumilus* it is notched at both ends, but otherwise shows no indication of a paired origin even in young skulls. It is absent in *Brookesia* and *Rhampholeon*. The single vomer of *Chamaeleon* is no doubt homologous with the paired elements of lizards to which Dr. Broom has assigned the name "Prevomers," as they are suspected to be different from the mammalian vomer.

Columella cranii.—Mr. Boulenger states that Chamaeleons have a small columella, and Dr. Gadow says that this bone is present in a much-reduced state, partly imbedded in the interorbital septum. We have not been able to find any trace of the bone, and Parker noted its complete absence.

Conclusions.

The genus *Brookesia* approximates to the normal lacertilian type in so many respects that we may safely regard it (and *Rhampholeon* probably) as the most generalized of living Chamaeleons. The *pumilus* section is in several respects the least specialized division of the large genus *Chamaeleon* and the *dilepis* section is the most advanced of the whole family. Mr. Beddard comments on his lung investigations as follows : "The simplicity of structure which is often associated with small sized forms as compared with their allies of larger size is well seen in the two small species of Chamaeleons, viz., *C. pumilus* and *C. taeniobronchus* where the lungs have no diverticula and the intestinal tract is nearly straight." This is only partially correct : it is certainly correct that all the largest species belong to the advanced group, but some of the Malagasy species (*e.g.*, *C. lateralis*) which are smaller than *C. pumilus* or *C. ventralis*, must also be included amongst the most specialized forms. Although Mr. Beddard does not thus explain the facts, some might infer that smallness of size is accompanied to some extent by degradation in structure giving a false appearance of simplicity ; and while admitting the possibility of such degradation in *Brookesia* and *C. pumilus* with respect to some characters (*e.g.*, the reduction of the squamosal and absence of lachrymal), we think it highly improbable that this can be the explanation of the simplicity of those types in respect to so many characters. Indeed, the fact that the *vulgaris* and *dilepis* section show in immature specimens some of the characters which belong to the adult stage in *C. pumilus*, *Brookesia*, or *Rhampholeon*, whilst, on the other hand, *C. ventralis*, at any rate, does not pass through a stage reminiscent of the higher types in its young, is decidedly against that view.* Further, our opinion with regard to the primitive nature of *Brookesia* is in some degree supported, we think, by the fact that Madagascar is known to be the home of primitive animals in various groups (cf. especially the primitive Colubrine snakes of that island) ; however, we do not desire to lay stress on this argument, as it cannot be said that the whole Malagasy fauna is primitive.

It is important to note that the one or two widespreading Mediterranean and Indian species are included amongst the most advanced section which, moreover, has its headquarters in Africa. We are probably justified in assuming therefrom that the extra-Ethiopian species are outliers which have spread in comparatively recent times to the places they now inhabit, and there is no reason to suspect that they are relict forms indicating a former much wider distribution for the family. On the other hand, Chamaeleon

* Fully to substantiate this argument, more complete embryological data than is now available will be required. By tracing the development of the skull and of the lungs in the embryos of *Brookesia* and various species of *Chamaeleon*, the problem could in all probability be definitely settled.

remains have been reported from Oligocene deposits in France, but we are unable to express any opinion regarding the accuracy of the record.

Further, taking all the data of distribution * and morphology into consideration, it is difficult to avoid the conclusion that the family as we know it to-day has spread from a centre of origin situated in that portion of the Ethiopian region of which there now remains two separated components, Madagascar and the Cape Province of Sclater, for only in these areas do we find what we believe to be the more primitive members of the family. There is no evidence in favour of a northern origin for this family.

We think it advisable to restore Gray's genus *Lophosaura* to include the *pumilus* group of the genus *Chamaeleon*, as this section seems to be sharply separated from the other members of that large genus. The characters of *Lophosaura* may be described as follows: Casque made up largely of the parietal bone which is a broad plate with a lateral process on each side descending to meet the prosquamosal; prosquamosal not forming suture with jugal; pre- and post-frontals not in contact; no lachrymal bones; maxillary and prefrontal bones in contact separating the nasal bones from the nasal aperture; 14 pairs of ribs; lungs without trace of diverticula. The external characters are those given by Mr. Boulenger for the *pumilus* group, viz.: A gular crest; no ventral crest; no light line from chin to vent; no occipital lobes; no rostral appendages; no tarsal process. The members of this genus *Lophosaura* are probably all viviparous. The genus comprises all the South African species referred to the *pumilus* group and probably also *Chamaeleon tigris* of the Seychelles. As we have previously mentioned, the remaining species included in the genus *Chamaeleon* show considerable structural differences—perhaps of varying importance—and possibly will prove to be separable into a number of distinct groups, each of generic value. Unfortunately we have not sufficient material to enable us to attempt further rearrangement.

Description of a New Variety of the Genus *Lophosaura*, Gray.

Lophosaura ventralis, var. karrooica.

Description of type: No. 1789 in the Albany Museum, collected at Beaufort West, by Master Philip Whaits.

Casque feebly elevated, not quite so narrow and pointed behind as in the typical form of *C. ventralis*—var. *typicus* –(from Grahamstown or Port Elizabeth).

* For notes on the distribution of Chamaeleons see Hewitt in Transvaal Museum Annals, vol. ii., p. 67, and for detailed accounts Werner in Zoologische Jahrbuch, 1902, and Das Tierreich, 1911.

Crests of head are similar to those of *ventralis typicus*. The upper surface of head between and somewhat in front of the eyes is concave, but there is no deep depression such as occurs in *C. pumilus*, Daud., just anterior to the eyes. Scales on back and sides granular, intermixed with rather small subconical tubercles which become flattened in the region of the groin; the tubercles are more or less regularly arranged in interrupted longitudinal rows; the smallest tubercles are those which occur on the back, the largest occurring on the flanks. A dorsal crest as in *ventralis typicus*: ventral scales practically equal (in *ventralis typicus* they are often very unequal). Throat with rather small subconical tubercles; gular crest composed of elongated scaly lobules, none of which are as broad as long, the anterior ones largest (in *ventralis typicus* the anterior gular lobes are considerably broader than long and overlap each other anteriorly).

Tail shorter than head and body, the lateral caudal tubercles slightly smaller than the larger tubercles on the flanks.

Notes on Co-types.—In 3 specimens, 2 from the same locality, and 1 from Jansenville, the tubercles occupying two middle rows on the flanks are larger than those on the rest of the body; in 2 specimens (1713) and (1732) all the gular lobes are sharply pointed.

The example from Jansenville shows an approach to the *C. ventralis typicus* condition, in that the anterior gular lobes overlap and the first lobe is only very slightly longer than broad, all the other larger lobes being however considerably longer than broad. We may mention that a Beaufort West specimen has been referred by Mr. Boulenger to *C. pumilus* (Ann. S. Af. Mus., v., p. 492). It may be doubted, however, if two species actually occur in that locality.