SOME ASPECTS OF THE ANATOMY OF ANURA
(AMPHIBIA)—A REVIEW*

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* Based on the published papers of the author and accepted for the Doctor of Science Degree of the University of Madras, March 1938.
I. Introduction

At the outset, it must be pointed out that under the title of anatomical studies of Indian and some extrapeninsular Anura, I have examined the cranium and larynx by the method of sections and also by gross study, and the morphological features of the vertebral column of some Indian anuran species by the latter method. It may be remarked here, that the study of cranial morphology by the method of sections revived at the incentive, given by Dr. de Villiers of South Africa, is still young. The various internal anatomical characters exhibited by the anuran species have to be examined comparatively and then only we can embark upon any generalizations. As we go on working, the only procedure can be, therefore, to correlate and compare such features as become manifest in the several families and subfamilies and then try to assess their usefulness from the viewpoint of taxonomy. In trying to correlate these characters, we have to bear in mind that the environmental conditions may have a profound influence upon the organization of individuals, and that secondary modifications in response to changed surroundings are often largely developed.

I have examined the cranial morphology of adult specimens of the following species and in many cases more than one specimen has been utilised for this purpose (author, 1932, 1932a, 1934, 1935, 1935a, 1937):

1. Microhylidae.
   - Microhyla ornata Dum. & Bibr.
   - Kaloula pulchra Günth. part (K. pulchra taprobanica Parker, 1934)
   - Uperodon systoma Schneid (Cacopus systoma Schneid).
   - Glyphoglossus molossus Günth.

2. Ranidae.
   - Rana hexadactyla Less.
   - Rana cyanophlyctis Schneid.
   - Rana curtipes Jerdon.

3. Rhacophoridae (Polypedatidae).
   - Rhacophorus maculatus Blgr.
   - Rhacophorus microtyympanum Günth.
   - Philautus petersi Blgr.
   - Philautus chalazodes Günth.
   - Philautus oxyrhynchos Günth.
4. **Bufonidæ.**

*Bufo melanostictus* Schneid.
*Bufo parietalis* Blgr.
*Bufo hololius* Günth.
*Bufo beddomii* Günth.
*Nectophryne misera* Mocq.

5. **Pelobatidæ.**

*Megophrys major* Blgr. (*M. gigas* Jerd. = *major* Blgr.).
*Scaphiopus holobrookii* Harlan.

The descriptions of the sections of the larynx of *Uperodon systoma* Schneid, *Kaloula pulchra* Günth. part (*K. pulchra* taprobanica Parker) and *Microhyla ornata* Dum. and Bibr. (author, 1932 b) are given; and morphological accounts of the larynx of *Megophrys major* Blgr. and *Scaphiopus hammondii* (author, 1935 b) and of the hyoid of these and of the South Indian Microhylid forms named above are described.

The morphology of the adult vertebral column in the following species is described (author, 1933):

1. **Rhacophoridae (Polypedatidæ).**

*Rhacophorus maculatus* Blgr.
*Rh. eques* Günth.
*Rh. microtympanum* Günth.
*Philautus chalazodes* Günth.
*Ph. sylvaticus* Rao.†
*Ph. nasutus* Günth.
*Ph. oxyrhyynchus* Günth.
*Ph. sp.* (marked B in the Central College Museum collection).

2. **Ranidæ.**

*Micrixalus saxicola* Jerd.
*Micrixalus* sp. (marked A in the Museum collection).
*Nyctibatrachus major* Blgr.
*N. pygmaeus* Blgr.
*N. sanctipalustris* Rao (1920).
*Nannobatrachus hempholeyensis* Rao (1937).
*Rana beddomii* Günth.
*R. bhagmandalensis* Rao (1922).

† This form has been since discovered to be a new species of *Nyctibatrachus* by Rao (1937), and is therefore, treated as *Nyctibatrachus sylvaticus* Rao.
The occurrence of a Bursa angularis oris or Mundwinkeldrüse is reported by me (1933 a) in Glyphoglossus molossus Günth., Uperodon systoma Schneid, Microhyla ornata Dum. and Bibr. Kaloula pulchra Günth (K. pulchra taprobanica Parker) and in Rhacophorus maculatus Blgr. The Apodan genera Ichthyophis and Uraotyphlus were also investigated in this connection.

With regard to the Microhylid species investigated by me, the genus Kaloula Gray has been subsequently split into two, Kaloula Gray and Ramanella Rao by Parker (1934) and this splitting is based on the difference in the nature of the prevomer. Rao (1925) described a new genus of Microhylid frog from South India which he called Ramanella symbiotica and he makes no reference to the exact nature of the prevomer in this species. This form, however, was later discovered to be none other than a species of Kaloula, K. variegata Stoliczk. But Parker (1934) retains the generic name Ramanella for accommodating five species which were originally included under Kaloula Gray and according to him the difference between Kaloula Gray and Ramanella Rao is that in the latter, the prevomer is reduced and broken up. My descriptions of K. pulchra were drawn up from a specimen of the race which Parker subsequently described as K. pulchra taprobanica (1934).

As regards the other genera, I included Rhacophorus (Polypedates) under the family Ranidæ following the observations of Gadow (1901) and
Boulenger (1882 and 1890). But Noble (1927 and 1931) has dissociated *Rhacophorus* from the Ranidae and erected a new family Polypedatidæ, in which he includes *Rhacophorus* (Polypedates), *Philautus* and some other genera. Moreover, the genus *Rana* itself has been split into nine subgenera by Boulenger (1920), viz., *Rana*, *Tomopterna*, *Hildebrandia*, *Ptychadena*, *Aubria*, *Hylorana*, *Discodèles*, *Nanorana* and *Pyxicephalus*. The two species *R. hexadactyla* and *R. cyanophlyctis* come under the subgenus *Rana* s. str., while *R. curtipes* is included under the subgenus *Hylarana*. This splitting is very well supported by my anatomical observations.

In describing the Bufonid head (author, 1937), I have remarked in the introduction that *Notaden* is a member of the family Bufonidae. I have followed Gadow (1901) and Noble (1931) in this, and Noble (1931) correctly points out that neither *Notaden* nor *Myobatrachus* shows any "affinity to bufonids found to-day outside Australia" and insists that they do not belong to the subfamily Bufoninae which according to Parker (in litt.) is approximately equal to Bufonidae of Gadow and Boulenger. With regard to the other genus *Nectes*, it was placed as a synonym of *Pseudobufo* by van Kampen (1923) and this nomenclature is followed by Smith (1930). Further the Bufonid genus *Cophophryne* of Boulenger is treated by Noble (1931) under the family Pelobatidæ.

In connection with the vertebral column, I have examined members belonging to the two families Ranidæ and Rhacophoridae (Polypedatidæ). Subsequent to the publication of a note on the procœlous nature of the 8th and 9th vertebrae in *Rhacophorus maximus* by Mookerjee (1932), it occurred to me that "if it could be shown that the vertebrae are uniformly procœlous in this genus *Rhacophorus*, then its inclusion under the family Ranidæ, becomes a questionable procedure". I have examined four species of *Rhacophorus* of which one (*R. maculatus*) confirms the observations of Nicholls (1915–16) in being diplasiocœlous.

II. Literature Selected

In referring to previous work I have largely restricted myself to recent workers who have studied the skull of anuran species by the method of sections. This does not necessarily mean that I have ignored the morphological descriptions of other authors, and in some cases I have not been able to secure the necessary literature, and therefore, my bibliographical list may not be exhaustive.

III. Review

(a) Narial region.—The very first structure that we meet with in the rostral end of the anuran examples studied is the prenasal cartilage
associated with the premaxilla. In the Microhylid examples studied, it is noticed that *Uperodon* and *Glyphoglossus* possess both the prenasal cartilages (prenasalis superior and inferior) while their congeners *Microhyla ornata* and *Kaloula pulchra* (*K. p. taprobanica*) possess only the superior cartilage. On p. 2 of my paper on the *Glyphoglossus* head (author, 1932 a) I have said, "At the outset it must be pointed out that *Glyphoglossus* stands apart from the other members of the group Engystomatidæ in very many features. Both the prenasal cartilages, the superior and inferior, are present and support the premaxillæ." This gives an idea that the Microhylid (Engystomatid) examples examined possess only one prenasal cartilage; the sentence ought to read "*Glyphoglossus* possesses both the prenasal cartilages and in this feature it resembles *Cacopus*, but in many other characters it differs from the other members of the same family with which it has been compared". In the Ranid forms (*R. hexadactyla*, *R. cyanophlyctis*, *R. curtipes*) and the Rhacophoridae (Polypedatidæ), (*Rh. maculatus* and *R. microtympanum*, *Philautus petersi*, *P. chalazodes*, *P. oxyrhynchus*) and the Bufonid examples (*B. melanostictus*, *B. parietalis*, *B. hololius*, *B. beddomii* and *Nectophryne misera*) both the prenasal cartilages are present.

*Previous work.*—In the forms examined by de Villiers (*Phrynomerus* 1930 a, *Cacosternum* 1931, *Anhydrophryne* 1931 c, *Ascaphus* 1934, *Rhombocephryne* 1934 a, *Microbatrachella* 1934 b) the prenasal cartilages are double, while in *Breviceps fuscus* (1931 d), the superior is reduced, in *Hemisus* (1931 b), the inferior is absent. In *Bufo* (Schoonees, 1930), *Phrynobatrachus* (G. du Toit, 1933), *Liopelma* (Wagner, 1934), *Dana* and *Crinia* (C. du Toit, 1933 ; 1934) and *Spelaeophryne* (de Vos, 1935) the prenasal cartilages are normally disposed.

The cartilaginous tectum of the nasal capsule gives rise anteriorly to the cartilago alaris and cartilago obliqua. The alary cartilage gives attachment to the superior prenasal cartilage, while from the cartilago obliqua, depends into the nasal chamber, a plica. In *Rana* the plica (Bruner, 1902) is described as a connective tissue projection into the nasal chamber depending from the tectal cartilage. But in the forms examined by me (Microhylidæ, *viz.*, *Uperodon systoma*, *K. pulchra* (*K. p. taprobanica*) and *Microhyla ornata* (1932), *Glyphoglossus mollusus* (1932 a), *Ranidæ* (1935), *Pelobatidæ* (1935 a) and *Bufonidæ* (1937), the plica depends from the cartilago obliqua and not from the tectum. In Rhacophoridæ (Polypedatidæ) (author, 1934) the plica may depend from the tectum (examined species of *Philautus*) or from the cartilago obliqua (*Rhacophorus maculatus* and *R. microtympanum*).
Previous work.—According to de Villiers the oblique suspension is noticed in *Phrynokerus* (1930 a), *Cacosternum* (1931), *Anhydrophryne* (1931 c), *Rhomboophryne* (1934 a), *Microbatrachella* (1934 b), and by C. du Toit in *Rana grayi* (1933). Similarly in *Phrynobatrachus* (G. du Toit, 1933), *Bufo* (Schoonees 1930) and *Spelaophryne* (de Vos, 1935). However in *Liopelmidae* (Wagner, 1934), *Crinia* (C. du Toit, 1934) and *Breviceps fuscus* (de Villiers, 1931 d), the plica depends from the tectum.

The nasal chamber referred to above is disposed in the form of three sacs—the cavum principale, cavum medium and cavum inferius. It is noticed that posteriorly, the cavum principale opens into the buccal cavity by means of the choana. The cavum medium gives rise to the ductus nasolacrimalis on its external aspect which opens below the eye normally by a single opening. In *Scaphiopus holbrooki*, the cavum medium is comparatively diminished in size. The cavum inferius, it may be noted in passing, is differentiated into a recessus medialis towards the septum where it is surrounded by glands in all the forms examined. Now, this recessus medialis is considered to represent the Organ of Jacobson so commonly met with in Reptiles and other examples. Lapage (1928) homologises the cavum inferius with the Organ of Jacobson and Howes (1891) is inclined to believe that the supposed Organ of Jacobson in Amphibia is a maxillary sinus. Gaupp, however, notes the recessus medialis as Jacobson's Organ. I have followed the descriptions of Gaupp and labelled the thickened internal part of the cavum inferius as recessus medialis.

(b) Prechoanal sac.—Another important feature one meets with in the sectional views of the narial region of *Uperodon systoma*, *Microhyla ornata* and *Kaloula pulchra* (*K. p. taprobanica*) is the occurrence of a prechoanal sac. In *Uperodon systoma* anterior to the choanal opening, there appears a vestigial sac in the roof of the mouth—the prechoanal sac. In *M. ornata* and *K. pulchra* (*K. p. taprobanica*) the cavum principale opens on either side into a prechoanal sac and these two sacs open into the buccal cavity. However, in the larval forms of one of these examples (*M. ornata*) no prechoanal sac is noticed, though in the case of *U. systoma*, the choanae of the tadpole enter into a spacious prechoanal sac which opens into the buccal cavity posteriorly. I have not examined the larval forms of *Kaloula* since I was not able to secure the tadpoles. Now, with regard to the morphological significance of the prechoanal sac found in the adult of *M. ornata* or *K. pulchra* (*K. p. taprobanica*), I noticed that a similar state of affairs is met with in *Phrynokerus* (de Villiers, 1930 a). He notes that “it is
more than probable that the sacs referred to above are vestiges of the Organ of Jacobson”. Then if this view is accepted, is it that the narial part of the Jacobson’s Organ is represented by the recessus medialis of the cavum inferius and the buccal division in Microhyla and Kaloula by the prechoanal sacs? In the other examples investigated by me, a prechoanal sac is absent from Gluphoglossus (author, 1932 a), Rhacophorus microtympanum, Philautus petersi, P. chalazodes, P. oxyrhynchus (author, 1934), Rana hexadactyla, R. cyanophlyctis, R. curtipes (author, 1935), Scaphiopus holbrookii (author, 1935 a), Bufo parietalis, B. hotolius, B. beddomii, Nectophryne misera (author, 1937) while in Rhacophorus maculatus (author, 1934) and Megophrys major (author, 1935 a), it is present.

Previous work.—I will only refer to those forms where a prechoanal sac is noticed. Phrynomerus (de Villiers, 1930 a) has a paired prechoanal sac. Cacosternum (de Villiers, 1931 a) has an unpaired one; similarly in Breviceps and Probreviceps (de Villiers, 1932 a), Hemisus (de Villiers, 1931 b), Speleoophryne (de Vos, 1935) and Rana grayi (C. du Toit, 1933).

(c) Septomaxilla.—Associated with the narial cartilages, viz., lamina superior crista intermediae and lamina inferior crista intermediae, the septomaxilla (internasal of Gaupp) makes its appearance. This bone, possessing posteriorly diverticula or limbs, is noticed to embrace the recessus saciformis or the infundibulum (the passage between the cavum principale and cavum medium). In the case of Rana (author, 1935) the posterior portion of the septomaxilla is triradiate; this arrangement is not seen in the case of Scaphiopus holbrookii (author, 1935 a). It is noticed in the latter example that after the fusion of the two limbs (the superior laminal and inferior laminal) of the septomaxilla as in Rana, the bone again appears as two investments of the planum and continues to be so till it finally disappears, thus differing from the Ranid type where the bone is noticed to delimit the anterior extremity of the planum. Now, in the Bufonidæ (author, 1937) the bone follows the common plan in the examined species of Bufo while in Nectophryne misera the disposition is slightly different. At any rate, there is a common feature between the two genera; a limb of the bone appears below the plica in Bufo and slightly behind the plica in Nectophryne misera—a feature not met with in the Ranidæ and Rhacophoridae (PolyPEDATIDÆ). In the latter family (author, 1934) the arrangement of the bone is Ranid in nature. The minor variations noticed are not of great significance but it is to be noted, however, that the nature of the bone itself has been interpreted in two ways. According to Lapage (1928) the bone is considered as “originally a cartilage
bone" and one of the criteria in determining this is "in certain places for example, where the septomaxillary is in contact with the lamina superior of the crista intermedia, these cartilages seem to be continuous with the septomaxillary—a fact which further supports the view that the septomaxillary arises in the cartilage" (p. 413). Now in the case of the examples studied by me, in certain regions of the laminal cartilage of *Uperodon systoma*, *Kaloula pulchra* (*K. p. taprobanica*) and *Microhyla ornata*, the bone is actually in contact with the cartilage thereby supporting Lapage’s theory. This, in fact, is really very pronounced in *K. pulchra* (*K. p. taprobanica*). Therefore, concluded at the time that in these examples the bone was of cartilaginous origin which, of course, was not supported by embryological evidence. Subsequent study has convinced me that in a large majority of forms like *Rana, Rhacophorus* (*Polypedates*), *Philautus, Bufo, Nectophryne, Megophrys* and *Scaphiopus*, the bone is separated from the cartilage by connective tissue; and, more than that, "the attachment and apparent continuity of one end of the bone with that part of the cartilage of the nasal capsule does not mean that the bone was preformed in cartilage" (de Beer, 1937). A study of the development of the bone will finally settle the matter and till then it may be treated as a membrane bone.

**Previous work.**—W. K. Parker (1881) describes a large number of forms without a septomaxilla, and it has been shown that his observations are inaccurate in some cases. De Villiers and his school describe it as a membrane bone.

(d) **Eminentia olfactoria.**—Both anteriorly and posteriorly to the choana, the solum may give rise to an elevated cartilage into the cavum principale which is called the eminentia olfactoria. Such an elevation is remarkably well developed in the fossorial *Uperodon systoma*, *Microhyla ornata* and *Kaloula pulchra* (*K. p. taprobanica*). *Uperodon* is found to live several feet below the earth, while *Microhyla* lives under loose sand and *Kaloula* under rocks and the bark of trees. Further, in the case of *Scaphiopus holbrookii* (author, 1935 a), *Bufo* (author, 1937), *Glyphoglossus* (author, 1932 a), *Rana hexadactyla* and *R. cyanophlyctis* and (author, 1935), the eminentia is elevated. In the other examples investigated, *viz.*., *Rhacophorus* (*Polypedates*), *Philautus, Rana curtipes*, *Megophrys major* and the arboreal *Nectophryne misera*, the eminentia is flat and not elevated. The African School of anatomists headed by de Villiers put forward a theory that the elevation of the eminentia is closely correlated with the fossorial mode of existence of these animals. De Villiers (1932 a) significantly remarks in this connection that "...increase in the area of the eminentia olfactoria
represents a purely physiological phenomenon, associated with adaptation
to terrestrial life and has been independently evolved in Bufonidae, Ranidae
and Brevicipitidae”’. This view fitted in extremely well when I worked out
the Microhylid examples but when I investigated the Ranid forms like
R. hexadactyla and R. cyanophlyctis and R. curtipes, I was rather struck by
the variation noticed in the nature of the eminentia. It is elevated in
R. hexadactyla and R. cyanophlyctis while in R. curtipes it is flat. It
is very well known that the former two examples are completely aquatic
forms, and therefore, the occurrence of an elevated eminentia does not very
well fit in with the theory that the elevated eminentia is closely correlated
with a fossorial mode of existence even though it may have been evolved
independently. If the two Ranid genera were terrestrial, the independent
evolution of the elevated eminentia would have amply borne out but since
they are aquatic, I pointed out (1935, p. 6) that “the elevation of the emi-
nentia has probably nothing to do with terrestrial adaptations of the Anura.
It may, however, be said that the structure increases in area purely in
response to the sensory requirements of the individual”. Probably experi-
mental zoology may be able to clear this difficulty.

Previous work.—The occurrence of an elevated eminentia is noticed in
Phrynomerus (de Villiers, 1930 a), Breviceps (de Villiers, 1931 d), Pro-
breviceps (de Villiers, 1932 a) and Spelæophysyne (de Vos, 1935) and no
reference is made to it in Rhombophryne (de Villiers, 1934 a). In
Bufo angusticeps, Schoonees (1930) records an elevated eminentia.

e) The sphenethmoid bone (Os en Ceinture Cuvier).—This bone
occurring in the ethmoid region is known as the girdle-shaped bone since it
forms a girdle round the brain. It appears in the anterior sections on the
lateral aspects of the brain and posteriorly extends ventrally also and in
some examples a piece of trabecular cartilage is left unossified midventrally,
when the bone is said to be distinctly paired. Such a feature is noticed in
Uperodon systoma, Microhyla ornata, Kaloula pulchra (K. p. taprobanica),
Rh. microlymanum and Philautus chalazodes. In the last two species the
sphenethmoid is feebly developed. However, in Rana hexadactyla, R. cyanop-
hyctis, Megophrys major, Scaphiopus holbrookii, Philautus oxyrhynchus and
P. petersi, there is no ventral trabecular piece and the bone is one complete
girdle. In P. petersi the bone originates far anteriorly in the septum nasi.
In Rhacophorus microlymanum a feeble sphenethmoid is seen and in Rana
curtipes in the sphenethmoid region, no ossification is noticed.

(f) Subethmoidal cartilage.—There is a remarkable feature noticed in the
case of Rana cyanophlyctis in the ethmoid region. In the anterior region of
the sphenethmoid, disposed between it and the parasphenoid, is a cartilage which has been called the subethmoidal cartilage, also noticed in *Rana grayi* (C. du Toit, 1933). What exactly is the significance of this cartilage, I am unable to say.

Previous work.—W. K. Parker's monograph (1881) on the Anuran skulls gives us an account of the sphenethmoid but unfortunately the double nature is not disclosed in many forms. The paired nature of the bone is described by de Villiers in *Phrynomerus* (1930 a), *Rhomobryphryne* (1934 a), by C. du Toit in *Crinia* (1934), by G. du Toit and de Villiers in *Hyperolius* (1932), by Wagner in *Liopelma* (1934). In the other forms whose cranial anatomy has been studied variations are met with. In *Cacosternum*, the sphenethmoid is noticed posteriorly (de Villiers, 1931 ; 1931 a), the bone is completely girdle-shaped in *Phrynobatrachus* (G. du Toit, 1933) and in *Rana grayi* (C. du Toit, 1933) and in *Bufo angusticeps* (Schoonees, 1930) portions of cartilage are discovered in the bone. In *Breviceps* and *Probreviceps* (de Villiers, 1932 a) and in *Spelaeophryne* (de Vos, 1935), the bone is wanting. In *Ascaphus* (de Villiers, 1934) an orbitosphenoid is described and in 'Liopelmidæ' Wagner (1934) describes the sphenethmoid as paired. Peculiarly in *Hemisus* (de Villiers, 1931 b) the bone has fused with the nasals above. Representatives of 58 genera have been examined by Parker (1934) and the normal condition in these is that the sphenethmoid is single; however, variations in few cases were also met with.

(g) Maxillae.—The premaxillae and maxillae do not show many variations. However, it may be remarked that in the Microhylid species examined by me, *viz.*, *U. systoma*, *M. ornata* and *K. pulchra* (*K. p. taprobanica*), the maxillae (and also the prevomers) are edentulous. Now it has been long established that no stress need be laid on the dentigerous or edentulous nature of the bones, for in the same family, members possessing teeth (*e.g.*, Microhylid Dyscophinæ) and also without them are found. Again in *Bufo* and *Nectophryne* (author, 1937) the maxillæ and prevomers are edentulous while in *Ranidae* (the author 1935) and *Rhacophoridae* (Poly-pedatidae) (author, 1934), the maxillæ are dentigerous. Therefore, this character cannot be utilised for systematic purposes especially with reference to the Microhylid family.

Previous work.—W. K. Parker (1881) describes a large number of forms with and without teeth on the maxillæ. In describing the maxillary bones, de Villiers (1931) also notes that "Noble has repeatedly
maintained that no great systematic value can be attached to the absence or presence of teeth”. In describing the cranial morphology of *Cacosternum* (1931, 1931 a) he notes that the species of this genus behave rather differently; *C. börigeri* and *C. capense* possess pre-maxillary teeth while *C. namaquense* does not but the maxillæ are dentigerous. Peculiarly, the Microhylid genera, *Breviceps* and *Probreviceps* (de Villiers, 1932 a), *Rhomobophryne* (de Villiers, 1934 a) and *Spelæophryne* (de Vos, 1935) possess edentulous maxillæ. *Phrynomerus* (de Villiers, 1930 a) which is treated as a genus under the family *Phrynomeridae* by Parker (1934) also possesses, like the Microhylid genera referred to above, edentulous maxillæ.

*(h) Prevomer* (Broom).—The topographical disposition and the nature of this bone is largely used in Anuran taxonomy. In the species that I have examined of the Microhylid family, *viz.*, *U. systoma*, *M. ornata*, *K. pulchra* (*K. p. taprobanica*) and *Glyphoglossus molossus*, the disposition of the prevomer is based on a common plan. In *U. systoma*, the prevomer appears divided anterior to the choana, is edentulous and there is a small bone posterior to the choana, which I have called the degenerate palatine in consonance with the nomenclature adopted in labelling the bone occurring in this region in other anuran genera on purely topographical evidence. In the second species of *Uperodon*, *U. globulosum*, the prevomer embraces the choana (Parker, 1934) and a palatine is wanting. Now, since the palatine is absent in this species, it is thought that in other species *U. systoma* also, a true palatine is absent and the degenerate bone that is present postchoanally [palatine according to me (1932) and Devanesan (1922)] may be the posterior portion of the prevomer. If, however, it is proved that *U. systoma* is more primitive and possesses a prechoanal prevomer and a degenerate palatine, then the condition noticed in *U. globulosum* should be interpreted as one in which a fused prevomeropalatine bone is noticed. My slides of the head of *U. systoma* do not provide any clue to this problem. In *K. pulchra* (*K. p. taprobanica*) the prevomer is large and edentulous and in the alizarin preparations that I have examined of *K. pulchra* (*K. p. taprobanica*), the prevomer is well developed and the postchoanal portion is associated with the well-developed palatine. I have already remarked that according to Parker (1934), the genus *Kaioula* Gray is split into two genera *Kaloula* Gray and *Ramanella* Rao, based on the nature of the prevomer, and since I have not described any species belonging to *Ramanella* in these two papers (author, 1932; 1932 a), I shall not discuss the prevomerine condition in the latter genus. On p. 11 of my paper (author, 1932), I have said that “The
vomer does not form a vomeropalatine and in Kaloula the vomer is super-imposed by the palatine". It ought to read that the palatine is super-imposed by the vomer. Now in M. ornata, the prevomer is poorly developed and a limb of it extends intrachoanally as in Phrynomerus (de Villiers, 1930 a) but this does not embrace the choana posteriorly. I have clearly stated this point in my paper on Rhacophoridae (Polypedatidae) (author, 1934, p. 84): "The occurrence of this intranasal prolongation of the vomer (prevomer) is also noticed in one of the South Indian Engystomatid examples Microhyla and in a large number of foreign forms [see Phrynobatrachus (G. du Toit, 1933) and Phrynomerus (de Villiers, 1930)]." In my specimen of Glyphoglossus molossus (author, 1932), the prevomer is small and there is no intrachoanal prolongation as much as we see in M. ornata. But in a figure drawn by Parker (1934, p. 72) of the ventral aspect of the cranium of G. molossus, a prevomer which embraces the choana is shown. I am unable to make out the palatine as an independent bone in the figure and in the description we read "Prevomer undivided, the postchoanal portion overlying the palatine region and bearing, mesially, one or two knob-like prominences (Fig. 30)". The figure suggests that a prevomeropalatine arrangement is present. My description of the prevomer in Glyphoglossus (author, 1932 a) is that "at the base of the solum nasi the prevomer makes its appearance and unlike the Brevicipitidae and Microhyla, no extension of the prevomer seems to embrace the choanae in Glyphoglossus". What I mean by "embrace" is an intranasal prolongation of the prevomer as in Microhyla, and not a post-choanal extension as seen in U. globulosum. As already noted above, I have made this point clear in my paper on Rhacophoridae (Polypedatidae) (author, 1934, p. 84, vide supra). Further my slides do not disclose 'the postchoanal portion overlying the palatine region' in Glyphoglossus as described by Parker (1934, p. 72). This is due to the fact that my observations were made on an immature specimen. In this, the bone investing the ventral aspect of the antorbital cartilage which I called the palatine is separate, and there is a prechoanal prevomer. When the adult condition is reached, the prevomer and the palatine (if it is a palatine) obviously fuse together (Parker in litt.) and a prevomeropalatine arrangement is noticed; or it may be that the palatine really represents the postchoanal portion of the prevomer. Then, the figure drawn by Parker (1934, p. 72), represents a prevomer with a postchoanal portion or it may be a prevomeropalatine bone. Further, Parker points out that this genus Glyphoglossus "ought, perhaps, to be united with Uperodon. Uperodon globulosum is almost exactly intermediate between the type species of Uperodon and Glyphoglossus". In adult U. systoma, then, there is a pre-
choanal prevomer and a postchoanal prevomer or palatine; in *G. molossus*, the juvenile specimens show a prevomer and a postchoanal prevomer or palatine and in the adult, the prechoanal and postchoanal portions fuse representing either a prevomer or a prevomeropalatine. Similarly in *U. globulosum*, the bone may be a prevomeropalatine or a true prevomer with a postchoanal limb. Now, in the Rhacophorid (Polypedatid) family examined (author, 1934), the prevomer is rather interesting. According to Boulenger (1890), the difference between *Rhacophorus* (*Polypedates*) and *Philautus* (*Ixalus*) consists in the presence of prevomerine teeth in the former and their absence from the latter. I have noted in that paper (author, 1934, p. 82) that 'This may not be so very safe and stable criterion of enough systematic importance since Boulenger himself is doubtful about the existence of vomerine teeth in *Rhacophorus dubius*'. Noble (1927, 1931) at any rate, distinguishes *Rhacophorus* (*Polypedates*) from *Philautus* by the absence of vomerine teeth in the latter and he points out that the genus is derived from *Rhacophorus* by a 'loss of the vomerine teeth'. However this may be, the family Rhacophoridae (Polypedatidae) according to the same author (1931), is a natural group possessing cylindrical sacral diapophyses, intercalary cartilages and a diplasiocelous vertebral column, and further confirms his statement by saying that 'the anatomical evidence at present available points toward the Polypedatidae as being a natural group' (p. 525). Within the family, since *Philautus* has arisen from *Polypedates* by the loss of vomerine teeth, Noble is inclined to believe that *Philautus* is not a natural genus but a polyphyletic one. The sectional views of the prevomer reveal that the bone is dentigerous in *Rhacophorus maculatus*, *Philautus chalazodes* and *P. oxyrynchus* while in *P. petersi* and *Rhacophorus microtympanum*, it is edentulous. Thus, both among *Rhacophorus* and *Philautus*, there are species with and without prevomerine teeth and it becomes apparent how futile it is to utilise this character for purposes of further classification of these two genera. If we accept Noble's dictum that the genus *Philautus* represents a polyphyletic assemblage, then we are not justified in retaining it as a single distinct genus; we may have to merge the several species of *Philautus* under those of *Rhacophorus*. This view is very well supported by my observation of the prevomerine teeth for, both genera *Rhacophorus* and *Philautus* possess species with and without prevomerine teeth. But the other aspects of cranial anatomy as reported by me (author, 1934) do not warrant this, and therefore, it is very unlikely that *Philautus* is, as Noble thinks, polyphyletic, unless it be that the other characters, too, have been developed independently on more than one occasion (Parker in litt.). In the Ranid examples studied, *viz.*, *R. hexadactyla*, *R. cyanophlyctis* and
R. curtipes, the prevomer is normally disposed with no postchoanal portion, is dentigerous and resembles that in R. temporaria (Gaupp, 1904). In the Pelobatid examples studied Megophrys major and Scaphiopus holbrookii (author, 1935 a), the prevomer is single on either side and possesses two limbs posteriorly. In M. major (author, 1935, p. 72, Fig. 5) "on the ventral aspect of the eminentia the prevomer is noticed and posteriorly, it is divided into two between which the Rachendrüse are present (Fig. 5 a) and more posteriorly the internal limb (Fig. 5 b) is present and this is the intrachoanal portion of the prevomer," which, however, disappears posteriorly. In S. holbrookii, 'Disposed at the tip of the bony eminentia is the large vomerine bone' (p. 72). "The vomer (prevomer) (Figs. 4 and 6 v) in Scaphiopus underlies the large bony eminentia and, as in Megophrys, in posterior regions the bone is present in the form of two parts with loose connective tissue and the Rachendrüse in between" (pp. 73 and 74). Posteriorly, the maxillary limb of the prevomer alone persists and this also disappears after cutting through some or more sections posteriorly. In Bufo and Nectophrynine misera (author, 1937), the prevomer is small and edentulous. It does not extend postchoanal. In my introductory chapter on the Morphology of the Bufonid head, I have remarked about 'the absence of the teeth from the jaws (except Notaden)..' and this implies that Notaden possesses dentigerous jaws. The implication was not intended; Notaden also lacks teeth in the jaws, but prevomerine teeth are present. In passing, it may be noted that the systematic position of Notaden is changed now, and I am not in possession of the literature referring to it (see, however, Noble, 1931, p. 498).

Previous work.—W. K. Parker (1881) depicts the prevomer in a large number of forms and he draws figures of the skulls of two species of Microhyla under the name of Diplopelma and also that of Callula pulchra. H. W. Parker (1934) describes, amongst other Microhylidae, the disposition of this investing bone in Uperodon, Kaloula, Ramanella, Microhyla and Glyphoglossus. In Uperodon, 'Prevomer entire or divided (Fig. 31 and 32), the postchoanal portion overlying the palatine region and sometimes bearing a raised knob at its mesial end'; in Kaloula 'prevomer undivided, the postchoanal portion overlying the palatine region and raised into a strong, sometimes crenulate ridge (Fig. 33)'. However, Smith (1930) draws a palatal aspect of K. pulchra (Fig. 10, p. 121) and in the description he says 'vomer forming a sharp transverse ridge behind the choana; palatine much reduced, its inner extremity underlying the vomer'. In Phrynomerus (de Villiers, 1930 a), a vomeropalatine arrangement is
seen; in *Cacosternum* (de Villiers, 1931a), vomer is edentulous and large; in *Breviceps* (de Villiers, 1931d), there is an intranasal prolongation which is absent in *Proreviceps* (de Villiers, 1932a); in *Hemisus* (de Villiers, 1931b), the vomer is absent; in *Rhomboophryne* (Noble and Parker, 1926; de Villiers, 1934a), it is disposed in two parts; in *Asca-
phus* (de Villiers, 1934), there is a toothed prevomer with the rostral portion edentulous; in *Spelæophryne* (Parker, 1934; de Vos, 1935), the prevomer is edentulous; in *Crinia* (C. du Toit, 1934), a divided prevomer is present; in *R. grayi* (C. du Toit, 1933), it is simple and undivided; in *Phrynobatrachus* (G. du Toit, 1933), the edentulous prevomer fringes the choana and in *Bufo* (Schoonees, 1930), the bone is edentulous. Also in *Hyperolius* (G. du Toit and de Villiers, 1932) the vomer is without teeth.

(i) Palatine bone.—In the Anura, the palatine bone shows considerable variation. Forms with and without, or with degenerate palatine or with a prevomeropalatine are not uncommon. Among the forms studied by me, in the Microhylid genera, 'the palatine observes a sequence in reduction'. *Kaloula* has a comparatively well-developed palatine; *Uperodon systoma* a vestigial one (see below) while *M. ornata* has lost it. Smith (1930) remarks that in the case of *K. pulchra* (*K. p. taprobanaica*), there is a 'reduced palatine' and when we compare this with the other two South Indian Microhylid examples, it must be said that the palatine is comparatively well developed. In the case of *U. systoma*, a bone on the ventral aspect of the quadratoethmoidal commissure has been labelled by Devanesan (1922) as palatine and I have also followed the same nomenclature. Whether it is a true palatine or only a postchoanal portion of the prevomer is rather difficult to say and the probabilities have been discussed on pp. 53-54. With regard to *Microhyla*, I have noted that the palatine is absent (author, 1932, p. 11) and that 'Parker (23) finds that among the species of *Microhyla* an orthogenetic series could be established, ranging from forms having a palatine to forms completely devoid of it'. As early as 1881, W. K. Parker figured two species of *Microhyla* under the name of *Diplopelma* where he has drawn a well-developed palatine. Obviously, the genus contains species both with and without a palatine bone. H. W. Parker (1928) as stated above, had studied all the species of the genus *Microhyla* and had come to the same conclusion. He draws an interesting correlation when he says that 'only rarely does it persist when the post-choanal portion of the prevomer is absent'. In the Ranid and Rhacophorid (Polypedatid) forms examined (author, 1934, 1935), the palatine is normally disposed on the ventral aspect of the antorbital cartilage.
In *Megophrys major* a single specimen of which I secured from the Indian Museum at the time I reported, I have noted (author, 1935 a) that the palatine is absent and investing the ventral aspect of the quadratoethmoidal commissure is a projection of the maxilla. This projection forms the posterior boundary of the choana. However, after examining a large number of species of *Megophrys*, including *M. major*, Parker informs me (in litt.) that a palatine is normally present and therefore, my specimen does not represent the normal condition. Subsequently I examined another specimen of *M. major* and also discovered the same feature noticed in the first one with regard to the palatine. Mr. H. W. Parker of the British Museum has examined my second specimen. It is to be noted that the bony extension of the maxilla described by me (author, 1935 a) as forming the posterior boundary of the choana which I propose to call maxillo-palatine, is topographically identical with the palatine of other *Anura* and therefore, Parker (in litt.) is inclined to label this merely as palatine bone. Further he states that if it is to be regarded as a maxillo-palatine, one of the two assumptions have to be made, viz., that it is a bone not foreshadowed in any frog and appears for the first time here or that the processus frontalis of the maxilla has grown ventrally to the antorbital cartilage. If, however, following Parker, it is labelled as palatine, the union of the maxilla and palatine in this region is lost sight of and probably this is the first anuran where such a condition of fusion has appeared.

In *S. holbrooki*, the palatine is wanting. Further, in the same paper (1935 a, p. 75) it is noted that ‘in all the examined species of *Microhyla* (H. W. Parker, 1928) the palatine is wanting....’ This is not correct, and therefore, it should be re-stated that in the examined species of *Microhyla*, the palatine may be present or absent. In *Bufo* (author, 1937), the palatine is normally disposed while in *Nectophryne misera*, the bone is wanting. On p. 1163, I have noted in my paper on the morphology of the Bufonid Head (1937) that ‘Peculiarly, however, in the arboreal *Nectophryne*, the palatines are wanting. This, I am informed, gives an impression that in all the species of the genus *Nectophryne*, the palatine is wanting which of course is not what I mean; my idea is that in the examined species of *Nectophryne*, the bone is wanting, which I have clearly pointed out in the summary of that paper.

Previous work.—W. K. Parker (1881) draws the disposition of the palatine in a large number of forms described by him like *Callula pulchra* and two species of *Microhyla*, which he describes under the name of *Diplopelma, D. ornatum vel rubrum* and *D. Berdmorei (?).
The description of Parker of these two species are as follows: "In *D. ornatum vel rubrum*, the lateral rudiments of the girdle bone are less and run into their own alæ partially; yet an endosteal deposit, with scarcely any perichondrial bone (ectosteal palatine) runs up to the cheek." He further mentions the presence of a postpalatine being separated from the pterygoid. In *D. Berdmorei*, the palatine is feebly developed. There is no girdle bone and in both species Parker has figured a prevomer. I have not been able to secure H. W. Parker's paper (1931) where an account of the prevomer and palatine of *Uperodon* is given. The same author (1934) also describes the palatal bones in a large number of Microhylidae. In *Phrynomerus* (de Villiers, 1930a), a prevomeropalatine is formed; similarly in *Liopelma* (Wagner, 1934); in *Cacosternum* (de Villiers, 1931), *Crinia* (C. du Toit, 1934) and *R. grayi* (C. du Toit, 1933), *Bufo* (Schoonees, 1930), the bone is normal. In *Hemisus* (de Villiers, 1931b), *Breviceps* and *Probreviceps* (1932a), *Ascaphus* (de Villiers, 1934) and *Spelaeophryne* (de Vos, 1935), a palatine is wanting. In *Rhombocephryne* (Noble and Parker, 1926; de Villiers, 1934a), the posterior portion of the prevomer overlies the palatine. According to W. K. Parker (1881) in *B. melanostictus*, there is a lopsided variation in the development of the palatine which, however, is not seen in my specimens.

(j) The Nasal, Frontoparietal, Squamosal (paraquadrate Gaupp), Pterygoid, Quadratojugal (quadratomaxillary Gaupp) and Parasphenoid.—The variations noticed in these investing bones are minor and present no great morphological significance. The nasals may be so situated that the sphenethmoid is exposed between them and the frontoparietals, or as in *Nectophryne misera* and *Megophrys major*, the nasals may be separated anteriorly where the ossified tectum can be seen. The frontoparietals extend as far as the nasals anteriorly and posteriorly they cover the synotic region. I have not noticed any co-ossofication between the frontoparietals and the exoccipitals, but in *Philautus petersi*, the frontoparietals are united mesially and in *P. oxyrhynchus*, the frontoparietals of either side unite with the pro-otic bone. Both in *Megophrys major* and *Scaphiopus holbrookii*, the nasals and frontoparietals are studded dorsally with bony asperites, while in the other examples, the bones are smooth. With regard to the parasphenoid, the anterior end may show a divided appearance in some examples (*Scaphiopus holbrookii* and *Philautus petersi*).

The squamosal (paraquadrate Gaupp) in *Rana* is a triradiate bone according to Gaupp with an anterior, posterior upper and lower arms. In
the Microhylid examples studied by me, viz., U. systoma, M. ornata and K. pulchra (K. p. taprobanica), a gradual reduction in the development of the arms could be studied and the sequence of reduction being in the order, Kaloula, Microhyla and Uperodon. The posterior arm is reduced in Kaloula and Microhyla while it is absent from Uperodon (Devanesan, 1922). In Glyphoglossus molossus, it is not reduced. In the Ranid, Polypedatid, Bufonid and Pelobatid genera examined by me, the bone is typically Ranid in nature and these are, therefore, of no great significance.

In discussing the suspensorial region of U. systoma, K. pulchra (K. p. taprobanica) and M. ornata, I have said (author, 1932, p. 67) that “In Kaloula the processus quadratus becomes one with the processus pterygoideus and thus all the three, quadratomaxillary, paraquadrate and pterygoid invest this cartilage, while in Rana only the quadratomaxillary invests it”. In all the Microhylid species examined and also in Rana, it is only the quadratojugal that invades the processus quadratus, while the squamosal and pterygoid invest it.

Now, in the descriptions of the cranium of the several Anura studied by me, I have designated the squamosal bone as the paraquadrate bone following Gaupp and de Villiers. According to the latter author (1936), ‘the paraquadrate in the Anura is not an investing bone of the otic capsule and as such cannot be a squamosal’. Further, he points out that it is typically a membrane bone of the palatoquadrate, and adduces embryological evidence from the study of Urodela and describes a quadrato-maxillary in the apodan Boulengerula (1936). A year prior to the publication of this paper, Brock (1935) having studied the temporal bones in Lizards, Birds and Mammals, pointed out that, “There is no need for Gaupp’s term ‘paraquadrate’ for the reptiles and amphibia, since it is merely a synonym for squamosal, a bone which may be defined as a membrane bone primarily associated with the lateral surface of the quadrate; with the migration of the quadrate (incus) into the tympanic cavity, the squamosal of the mammal secondarily becomes a bone of the otic capsule”. Probably, de Villiers was not aware of this work (?) or at any rate, he does not refer to it. In the latest book on the development of the vertebrate skull, de Beer (1937) has pointed out that since Gaupp was not able to discover in Amphibia a squamosal of the type seen in Birds and Mammals, he called it a ‘paraquadrate’. This view becomes untenable when we realise that ‘the living Amphibia with their large quadrate cartilages are highly specialised, and that with the reduction of the quadrato to the incus which becomes protected by the tegmen tympani, the squamosal which covered the quadrato in the lower vertebrates, becomes a covering
bone of the auditory capsule in the higher forms....'. Thus, it becomes unnecessary to introduce the term paraquadrate for describing the squamosal.

It may not be out of place here to remark that de Villiers (1936) has also discussed Gaupp’s denomination of the quadratojugal as the quadratomaxillary. He points out that this is not a sesamoid bone and is represented by a quadrate squame in Gymnophiona where it is described as being absent. According to him, ‘Gaupp’s nomenclature is followed in preference to what might be called a purely topographic one’. Brock (1935) does not make a critical reference to this bone nor does de Beer (1937), though in describing the osteocranium of Amphibia, the latter author retains the term quadratojugal and treats it as a synonym of Gaupp’s quadratomaxillary.

Previous work.—I am only making a brief reference to these investing bones in the other forms that have been studied; the frontoparietals, nasals and the parasphenoid are not always normally disposed; in Hemisus (de Villiers, 1931 b), the sphenethmoid fuses with the nasals. In Phrynomerus (de Villiers, 1930 a), there is a large frontoparietal fontanelle; in Cacosternum (de Villiers, 1931; 1931 a), these and the pterygoid and squamosal are Ranid in disposition, but the frontoparietals are poorly developed. In Hemisus (op. cit.) the pterygoid is normal while the anterior process is absent from the squamosal. The frontoparietals are fused together and is disposed over the nasoethmoid. In Breviceps (de Villiers, 1932 a), the frontoparietals are separate while in Probreviceps the nasals and frontoparietals fuse together. In all the three genera (Hemisus, Breviceps and Probreviceps) the quadratojugal is absent, and probably on account of this, de Villiers notes that the squamosal and pterygoid have fused together. In Ascaphus (de Villiers, 1934), the nasals and frontoparietals are separate; similarly the pterygoid and squamosal. In Rhombophryne (de Villiers, 1934 a), the disposition of these bones is Ranid. In Spelæophryne (de Vos, 1935), the squamosal is reduced; the quadratojugal is absent and in the pterygoid and squamosal have fused and the frontoparietals are narrow bones. In the other examples (Crinia, Rana grayi, C. du Toit, 1934 and 1933 respectively) and Bufo (Schoonees, 1930), the bones are normally disposed.

IV. The Middle Ear Region

In sectional views the relationship of the pterygoid and squamosal to the middle ear and to the sound conducting apparatus is clearly made out. I shall now describe the sound conducting apparatus in brief. This consists of columella and stapes. According to Gaupp, the columella is
composed of three parts; a cartilaginous pars externa plectri (extrastapedial of Parker) which abuts on the internal aspect of the tympanic membrane; a pars media plectri (mediostapedial of Parker) which is bony and an internal pars interna plectri (interstapedial of Parker) which plugs the anterior region of the fenestra where the cartilaginous operculum (stapes of Parker) closes or fits into the foramen ovale. In the Ranid forms (Gaupp) from the pars externa plectri arises a dorsal process (commonly met with in Reptilia) called the processus or pars ascendens plectri or laterohyal (suprastapedial of Parker) which gains attachment with the crista parotica. The tympanic membrane or tympanum, a modified region of the skin in that region is held taut by means of an annulus tympanicus cartilage. In some examples, the tympanum is 'hidden' being covered over by the unmodified skin. In the Microhylid examples studied by me, the tympanum is not externally visible or in other words the skin in this region is not modified to cover the tympanum. By 'hidden' we mean, therefore, the condition noted above. Günther, as early as 1858, described in detail the classification of Anurous Batrachians depending mainly on external and readily ascertainable characters, in which the question of "hidden tympanum" as described by Prashad (1918) and Boulenger (1920) is also discussed. Mivart (1869) in a paper "On the classification of Anurous Batrachia" utilises certain osteological characters some of which are drawn from Cope's studies. With regard to the ear, Mivart points out that he agrees with Günther, in that "the Batrachians with imperfectly developed ear would form together an unnatural group and would be separated too far from other allied forms". He divides, therefore, Anura, with reference to teeth, tongue and perfect or imperfect ear. Baini Prashad (1918) writing on the middle ear of Anura, introduced a new terminology, and on looking through his bibliography list, I find no reference to Günther (1858) and Mivart (1869). According to him, the 'tympanic area' is the name given "to the area of skin situated on the temporal patch on the side of the head. This area is continuous with the skin...." Further, the tympanic membrane "is quite a distinct structure lying immediately underneath the so-called tympanic membrane of authors. It can be easily separated from the skin covering it". It is obvious that it is unnecessary to use this fresh terminology, for Boulenger (1897, 1920) after referring to the previous workers, has remarked that, 'The tympanum, or drum of the ear, is absent in Bombinator and Pelobates. When present it may be concealed under the skin, as in some specimens of Discoglossus, Pelodytes and Bufo vulgaris, or appear on the temple behind the eye as a round or oval disc covered with thin skin'. Rightly does de Villiers (1930 a, p. 689) point out in this connection that
"A 'hidden tympanum,' is in any case a dangerous cliché, for it is never anything but hidden, whether the superficial ectoderm is thin and transparent or thick and undifferentiated."

Now, with regard to the plectrum, it is noticed that in none of the Microhylid examples studied is a suprastapedial process developed. Further, the pars externa plectri expands into an oval cartilage on the inner aspect of the skin within the annulus tympanicus and on account of its expanded nature and its suspension from the end of the pars externa, it is not like the Ranid pars externa plectri, where the pars media attaches itself to the middle of the pars externa. This cartilage is therefore, composed of pars externa plectri plus the extraplectral cartilage. Whatever this difference may be, the plectral apparatus of the Anura can be homologised with the similar one noticed in Reptiles (Abel, 1929); if this view is not accepted by all, then there is no point in calling the cartilage extrastapedial, for the whole pectral apparatus is external to the operculum. Therefore, I have followed the terminology used by de Villiers and called it the "extrapectral" cartilage. A brief reference may be made to the operculum. According to Versluys (1924) this structure is developed in response to the needs of a terrestrial life. In the terrestrial forms like *U. systoma*, *M. ornata*, *K. pulchra* (*K. p. taprobanica*) and *Glyphoglossus molossus*, the operculum is well developed and possesses a knob on the exterior aspect for the attachment of an opercular muscle. An operculum is also noticed by me in aquatic forms like *Rana hexadactyla*, *R. tigrina*, *R. curtipes*, and Rhacophorid (Polypedatid) examples and in the terrestrial forms like the species of *Bufo* and in the arboreal *Nectophryne misera*. It would, therefore, be extremely interesting to make a comparative study of the development of this structure in these forms and examine if the statement which Parker (1934) makes with reference to the Microhylidæ that 'the operculum is normal in the family and retains its muscular connection with the scapula' is applicable to the other families also.

**Previous work.**—I have already referred to the classificatory importance of the ear region as discussed by Mivart (1869). The occurrence of a normal middle ear, eustachian passage and plectral apparatus is described in *Phrynomerus* (de Villiers, 1930 a), *Cacosternum* (de Villiers, 1931), *Anhydrophryne* (de Villiers, 1931 c), *Microbatrachella* (de Villiers, 1934 b), *Rana grayi* (C. du Toit, 1933), *Crinia* (C. du Toit, 1934) and *Spelaeophryne* (de Vos, 1935). In *Hemisus* (de Villiers, 1931 b) the middle ear, tympanic membrane, annulus tympanicus, eustachian passage and plectral apparatus are absent. Parker (1934)
also notices the same feature in *Melanobatrachus, Hoplophryne* (and presumably *Parhoplophryne* also). Similarly in *Liopelminidae* (Wagner, 1934). While the plectrum and middle ear are developed in *Aglossa* (de Villiers, 1932), the eustachian tubes enter the buccal cavity by a median opening. The division of the tympanic cavity in *Probreviceps* is complete while in *Breviceps* (de Villiers, 1932 a) it is incipient. Further, in the former species an opercular portion of the *M. levator* scapulae superior is differentiated while the muscle and processus opercularis are absent from *Breviceps* and *Phrynomerus* (de Villiers, 1931d). In this feature, these two examples differ considerably from the Microhylid character enumerated above and it may be noted here again that Parker (1934) has created a separate family for the accommodation of *Phrynomerus*. He also refers to the taxonomic importance of the ear region.

**V. (a) The Pterygoquadrate and its Attachments**

In the larval condition of the Anura, it is noticed that the pterygoquadrate gains cartilaginous attachment with the cranium in three regions normally. The first is the quadratocranial commissure and in the majority of cases a quadratoethmoidal commissure is also formed and is anterior to the quadratocranial one. The quadrato-ethmoidal commissure connects the processus maxillaris posterior of the lamina-orbitalis and the processus pterygoideus of the quadrate. Next comes the processus ascendens which gains attachment with the pila antotica (or the orbital cartilage). Now, in some cases it is noticed that the pterygoquadrate may also give rise to a process in this region, which may articulate with the ventral wall of the cranium; if this palatobasal articulation is anterior to the palatine nerve (VII), it is described as the true basal articulation. In Anura generally, this process is posterior to the palatine branch of the seventh cranial nerve, and therefore, it is called the pseudobasal process and the articulation is similarly known as the pseudobasal articulation. In *Rana* (de Beer, 1937), a larval pseudobasal connection is formed and this is replaced by a pseudobasal articulation when the tadpole metamorphoses into the adult. Now, the last connection in anuran larvae is the processus oticus which unites the pterygoquadrate with the otic capsule over the carniocaudate passage. This process lies laterally to the head vein and anterolaterally to the hyomandibular branch of facial nerve. Exceptions to what has been described above with regard to the pseudobasal process and the processus oticus are also found. When the tadpole undergoes metamorphosis, the larval quadratocranial commissure is lost and is
replaced by the quadratoethmoidal commissure; the processus ascendens disappears completely; the adult oticus connection is formed by the rotation of the processus muscularis and its subsequent fusion with the crista parotica. A pseudobasal articulation is found in Rana (incompletely autosystylic) while in Bufo, it is completely autosystylic. With this adult arrangement of the pterygoquadrate as the background, if we examine the Microhylid, Rhacophorid (Polypedatid), Ranid, Bufonid and Pelobatid genera studied, it is noticed that in all these, a pseudobasal process is developed. This articulates with the subocular shelf (there being no basitrabecular process) posteriorly to the palatine nerve and is ventral to the vena capitis lateralis. It is obvious from a review of the previous literature on this topic, that morphologists have followed Gaupp's nomenclature and called it the processus basalis, and it was de Beer (1926) who pointed out the difference between the true and pseudobasal processes. In all the forms examined by me [Microhylidæ, 1932, 1932 a; Rhacophoridæ, 1934 (Polypdeatidæ), Ranidæ (1935), Pelobatidæ (1935 a) except Bufonidæ (author, 1937)] there is an incomplete autosystyly; however, in Rhacophorus maculatus (author, 1934, Plate, IX, Fig. 5), there is a slight fusion of the internal end of the pseudobasal process with the ventral part of the otic capsule. Until the tadpoles of this species are examined, the significance of this connection is difficult to ascertain. At any rate, this is not like the one noticed in Bufonidæ where the entire pseudobasal process fuses with the ventral wall of the otic capsule. An antorbital and an oticus connection are uniformly noticed in the forms examined by me.

Previous work.—A pseudobasal process is described in all the species examined by de Villiers [except in Ascaphus (1934) where a true basal process is present] and by C. and G. du Toit, de Vos and Schoonees in the forms examined by them. The last author describes a complete autosystyly in Bufo angusticeps. In Hemisus (de Villiers, 1931 b), the absence of a "basal" process is noted.

V. (b) Arteria Carotis Interna

In describing the orbito-temporal and posterior region of the cranium, a brief reference may be made to the disposition of the arteria carotis interna. In the larval Anura (Gaupp, 1893; de Beer, 1937) it is noticed that the carotid artery becomes intramural after entering through the carotid foramen. Here it gives rise to the ophthalmica magna artery which gains exit through the metoptic foramen and the anterior and posterior cerebral arteries. The intracranial palatine artery which is also given off by the carotid gets out through the craniopalatine foramen. Now, when the tadpole undergoes
metamorphosis, the trabecular portion separating the metoptic foramen and the carotid artery breaks down, so much so that the vessels (ophthalmica magna and internal carotid arteries) look as though they enter the cranium through the oculomotor foramen. An anomalous condition, analogous to, though different from this is also noticed in some fishes like Amiurus, etc. In the Ranid forms examined by me, a similar disposition is also seen and I am examining the larvae of these and also of the other genera to note if this phenomenon also occurs.

VI. Bursa angularis oris (Fuchs, 1931) or the Mundwinkeldrüse

The occurrence of this gland (?) was first described under the name of 'Mundwinkeldrüse' by de Villiers in Anhydrobryne (1931c). It was later found to be present in some Amniote examples also and since the name Mundwinkeldrüse was preoccupied, Fuchs (1931) introduced the phrase 'Bursa angularis oris' to describe it. This is a lymphocytic accumulation occurring in the angle of the mouth of frogs between the maxillary and pterygoid bones. In my study of this gland (1933 a), I have noticed that it uniformly occurs in all the four Microhylid examples, U. systoma, M. ornata, K. pulchra (K. p. taprobanica) and Glyphoglossus molossus; further, it is also present in the Ranid and Rhacophorid (Polypedatid) genera examined. It is, however, wanting in Pelobatid and Bufonid examples studied by me. I have remarked that the exact function of the gland is not yet known and Müller (1932) has gone to the extent of questioning the glandular nature of it. The gland is ill-developed in Glyphoglossus molossus (young specimen) but well-formed in Uperodon systoma, M. ornata, K. pulchra (K. p. taprobanica) and Rhacophorus maculatus. At the time I reported, I suggested that the probable line of evolution may have proceeded with Glyphoglossus as the starting point and the type seen in Rhacophorus as having taken its origin and proceeded on one side while that seen in Kaloula, Microhyla and Uperodon, on the other. This, according to me, is intended mainly to give an idea of the interrelationship of the Microhylid examples investigated by me. At the same time, I have cautioned that this is of no phyletic significance and particularly when we know that Breviceps fuscus lacks one and de Villiers (1933 a) himself is not quite sure if the other species of the genus Breviceps are devoid of it. This should not cause surprise for B. fuscus exhibits a series of peculiar features, as e.g., the reduced superior prenasal cartilage, absence of palatine, sphenethmoid, quadrato-jugal bones and of an opercular muscle; the fusion of the cartilago obliqua posteriorly with the septum, the fusion of the pterygoid and squamosal bones and the absence of a "basal" process.
Previous work.—The gland has been described in *Anhydrophryne* (de Villiers, 1931c), *Probreviceps* (1932a), *Rhomboxphryne* (de Villiers, 1934a), *Spelæophryne* (de Vos, 1935), *Rana grayi* (C. du Toit, 1933) and *Crinia* (C. du Toit, 1934). In *Phrynomerus*, *Cacosternum* and *Hemisus*, de Villiers does not mention about the gland while in *Breviceps fuscus*, de Villiers (1931d) notes the absence of the gland even though it is closely related to *Probreviceps* (de Villiers, 1932a). Schoonees (1930) notes its absence in *B. angusticeps*.

VII. The Lower Jaw

The lower jaw is characterised uniformly in the Anura by the possession of the two membrane bones, *viz.*, the angular and the dentary and a single cartilage bone—the mentomandibular. The membrane bones are investments of Meckel's cartilage. The dentary is only met with in the anterior sections of the lower jaw. In the Microhylid examples studied, *viz.*, *U. systoma*, *M. ornata*, *K. pulchra* (*K. p. taprobanica*) and *G. molossus*, there is a Meckelian epiphysis which projects postero-internally (author, 1932b) parallel to the jaw on either side. The presence of this was first noticed by Devanesan (1922) in *U. systoma*. In the foreign Phrynomeridae and Microhylidae studied by de Villiers, its occurrence is also noticed (*Phrynomerus* 1930a, *Breviceps* 1931d; *Probreviceps* 1932a, *Rhomboxphryne* 1934a, and by de Vos in *Spelæophryne*, 1935). In *Cacosternum* and *Hemisus* (de Villiers, 1931 and 1931b respectively) it is absent and therefore, they do not show this Microhylid affinity. It may be pointed out here that in the Ranid, Rhacophorid (Polypedatid) and Bufonid examples studied by me, the epiphysis is absent. Further, de Villiers (1934b) discovered the absence of it in *Microbatrachella*, and therefore, excluded it from the Microhylidae; he notes (p. 414) "I agree with Ramaswami (1932b) that 'it is a lateral epiphysis of Meckel's cartilage uniformly occurring in the Engystomatidae'. The absence of this process in *Microbatrachella* definitely excludes the genus from Brevicepitidae....". From the same point of view, *Cacosternum* and *Hemisus* cannot be included under Microhylidae and rightly does Parker (1934) omit these two from the Microhylid family. Thus, this character of the possession of Meckelian epiphysis will be very useful in discussing the affinities of the Microhylid genera.

VIII. The Hyolaryngeal Apparatus of Microhylidae and Pelobatidae

As already pointed out, I have studied the sectional views of the larynges of both sexes of *U. systoma*, *M. ornata* and *K. pulchra* (*K. p. taprobanica*) and the gross anatomy of the larynges of various Ranid and Rhacophorid (Polypedatid) species. With regard to the Microhylid hyolaryngeal
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apparatus, I have recorded certain interesting features, everyone of which has been confirmed by the later worker Trewavas (1933) and in a personal communication, she has stated that my paper (author, 1932 b) was unfortunately not available to her at the time. I have also studied the gross anatomy (1935 b) of the hyolaryngeal apparatus of Pelobatidæ, and noted that there is considerable variation with regard to the cricoid element. With regard to the hyoid apparatus, I have shown that a demarcation line could be drawn between the subfamilies Megophrynæ and Pelobatinæ. In the case of the Megophryne hyoid apparatus, a lateral foramen is absent while in the Pelobatinæ, it is well developed. There is, however, one exception. In the case of Megophrys feæ (Beddard, 1911) the occurrence of a lateral foramen is noted, and this escaped my attention when I wrote my paper. Further, in the case of Pelobates fuscus, W. K. Parker (1881) does not depict a lateral foramen, though according to the observation made above, the hyoid of Pelobatinæ must possess a lateral foramen. Probably, Parker’s delineation is incorrect, or it is an individual variation, for it is noticed that in his paper on the development of the hyoid apparatus of Pelodytes, Ridewood (1897, Fig. 12) draws, for comparison, a figure of the hyoid of Pelobates fuscus, where a lateral foramen is clearly shown. Thus, so far as is known to me, the Pelobatine hyoid apparatus possesses a lateral foramen while in the case of Megophrys (except M. feæ) the lateral foramen is absent and M. feæ may be treated as a connecting link between the two.

Now, with regard to the hyolaryngeal apparatus of the Microhylid examples studied (author, 1932 b), the following important points are noted:

(1) The hyoid plate has a cartilaginous or bony, beak-like portion between the postero-medial processes. This feature was already noticed by W. K. Parker (1881) in Callula pulchra and two species of Microhyla which he described under the name of Diplopelma, D. ornatum vel rubram, and D. Berdmorei (?). It is rather unfortunate that neither Trewavas (1933) nor myself referred to Kaloula and Microhyla, though Trewavas did refer to Gastrophryne of Parker (1881). With regard to Microhyla, the difference in nomenclature is responsible.

(2) An extra-hyal associated with the anterior cornu is well represented. Parker (1881) does not draw the occurrence of an extra-hyal in his specimen of Callula pulchra. Trewavas (1933) notes its presence. In Microhyla okinavensis, an extra-hyal is absent according to Frazier (1924).
(3) A cartilage of Santorini (cartilago apicalis Gaupp) is absent.

(4) The cricoid annulus does not possess an oesophageal process (spina oesophagea Gaupp). This process is commonly met with in the female specimens of the Ranid species studied by me. However, in only two examples of Ranids, *viz.*, *Rana tigrina* and *R. breviceps*, the male may also possess this process though this feature is not uniformly noticed. Therefore, this is an erratic variation and no importance need be attached to it. Thus, since the oesophageal process was noticed in all the Ranid females examined by me, it may well be used as a sex determiner.

(5) The broncheal processes are long and embrace the root of the lung as expanded plates.

And to these characters Trewavas (1933) adds five more, four of which are with regard to the musculature of the hyolaryngeal apparatus and the other with reference to the postero-medial processes of the hyoid apparatus. These characters taken together exclusively distinguish the Microhylid hyolaryngeal apparatus from that of the others.

I have mentioned on p. 40 of my paper (1932 b) that *Microhyla* and *Kaloula* are devoid of a vocal sac, an observation made on insufficient material. I have since examined the male members and have discovered the presence of a small vocal sac, and as early as 1882, Boulenger reported the occurrence of a vocal sac in the South Indian Microhylid genera. Parker (1934), who has described these forms, also notices the presence of vocal sac in *Kaloula* and *Microhyla*. In *Uperodon systoma*, Devanesan (1922) also draws attention to the occurrence of a large vocal sac.

Previous work.—Trewavas (1933) gives us an exhaustive account of previous workers on this subject. However, she does not refer to some of Blume’s papers, and they are W. Blume (1931, 1932 and 1933).

IX. The Vertebal Column

The examination of the vertebral centrum in the Ranid and Rhacophorid (Polypedatid) families has revealed some important variations. At the time of writing my paper (1933), I was not able to secure Nicholls’ paper (1915–16) which deals with the classificatory importance of the vertebral column in Anura. I have noted that in the case of *Rhacophorus* (Polypedates) *dubius* and *R. microtympanum*, the 8th vertebra is procœlous, while in *R. maculatus* and *R. eques* it is diplasiocœlous,—a term invented to represent the double concave nature of the centrum by Boulenger. I have
confirmed Nicholls' observation (1915-16) of the diplasiocelous nature of the centrum in *Rhacophorus maculatus*. Mookerjee's observation (1932) on *Rhacophorus maximus* was already anticipated by Nicholls. And with regard to the genus *Rhacophorus* (*Polypedates*), I have stated (author, 1933) that so far as the characters of the 8th and 9th vertebrae are concerned, it could be split into two. Under the procœlous Rhacophoridæ (*Polypedatidæ*), we have to treat probably the procœlous species of *Philautus* examined (*Philautus chalazodes, P. nasutus* and *P. oxyrhynchus*) and if more species are discovered with pro- or diplasiocelous type of centrum of the 8th vertebra, then, this would be another feature, besides the prevomerine teeth and sphenethmoid, to support Noble's view that *Philautus* is not a single distinct genus but a polyphyletic assemblage. In passing, it may be noted, that from the view-point of cranial anatomy, there is a vast body of evidence disproving Noble's dictum that *Philautus* does not represent a natural genus. In the family Ranidæ, a large number of species exhibits the diplasiocelous 8th vertebra. With regard to the genus *Micrixalus*, I have stated (author, 1933) that in the possession of diplasiocelous (incorrectly stated as procœlous, p. 1, column 2, line 27) 8th vertebra, "*Micrixalus* is Ranid in every respect". The three species of *Nyctibatrachus*, the majority of the species of *Rana* (except *Rana curtipes* Jerd., and *R. tenuilingua* Rao) examined by me are diplasiocelous. In *R. curtipes*, however, the 8th and 9th vertebrae are fused and there is a single centrum and the zygaphyses are a pair in number (anterior). The transverse processes are Ranid in character, but in one specimen of *R. curtipes*, the right transverse process of the 9th vertebra is absent and the ilium gains attachment with the transverse process of the 8th vertebra. The fusion of the 8th and 9th vertebrae is noticed in all the specimens of *R. curtipes* examined by me, so much so that it is a distinguishing character of this species and the position of this with reference to the other genera where fusion of the vertebral elements occurs, is discussed in my paper (author, 1933).

When Nicholls discovered the diversity in the vertebral column of the genera *Rana* and *Rhacophorus* of the family Ranidæ [the Rhacophoridæ (*Polypedatidæ*) being included under it], he noticed the difficulty of including the genus *Rhacophorus* under the family Ranidæ. He says, "The genus is one in which Boulenger has merged the genus *Polypedates*, and it is represented in the British Museum collection of skeletons by nine specimens. Of these, four belonging to the species *R. maculatus, R. cruciger, R. macrotis* and *R. robustus* were diplasiocelous. The remaining specimens *R. maximus, R. madagascariensis, R. schlegelii* and *R. reinwardtii* were uniformly procœlous". Noble (1931, p. 514) has treated the suborder diplasiocelae
(the true frogs, Ranids; old world tree frogs, polypedatids and narrow-mouthed toads, brevicipitids) as comprising three families, *viz.*, Ranidæ, Rhacophoridae (Polypedatidæ) and Brevicipitidæ. The Rhacophoridae (Polypedatidæ) are differentiated from the Ranids by the presence of an intercalary cartilage between the distal and penultimate phalanges. Under the subfamily Raninæ come the species of *Rana*, *Nyctibatrachus* and *Nannobatrachus* and under the subfamily Cornuferinae, is treated *Micrixalus*. With regard to the two genera *Philautus* (*Ixalus*) and *Micrixalus*, Noble (1931) states that "*Philautus* has arisen from *Polypedates* in many parts of its range by the oft repeated process, a loss of vomerine teeth" and treats this under the family Rhacophoridae (Polypedatidæ). I have shown elsewhere (author, 1934) that cranial anatomy does not support the merging of *Philautus* with *Rhacophorus* except when the dentition of the prevomers, the sphenethmoid and the nature of the vertebral centra of 8th and 9th are taken into consideration (see p. 69). *Micrixalus* is described by Noble (1931) as a group of small species of *Hylarana* lacking vomerine teeth. Thus both these genera *Micrixalus* and *Philautus* while possessing digital expansions lack vomerine teeth; but *Philautus* is a Rhacophorid (Polypedatid) with intercalary phalanges, and *Micrixalus* a Ranid without them. Therefore, the view "that the separation of *Micrixalus* from *Ixalus* is based on arbitrary grounds and possibly when a large number of species is examined the diagnostic characters of the two genera may be found to be too slender for erecting two genera for their reception" (author, 1933) is not tenable.

**IX. The Vertebral Column of Megophrys major** (author, 1935 a)

In the preparation that I have of the vertebral column of *M. major*, the 1st and 2nd vertebrae are fused, and therefore, I have stated that it differs from the ancestral form, the Liopelmidæ. The ancestral forms possess ten vertebrae and the first forms of Pelobatidæ to be derived from these are the Megalophrynæ (Megalophrynæ) and one of the species of this group *M. major* examined by me, therefore, differs from the ancestral stock in the possession of only 8 vertebrae. I have now examined another specimen of the same species and have discovered that the 1st and 2nd vertebrae are not fused, and therefore, the normal form differs from the ancestral stock in possessing 9 vertebrae. The one with fused 1st and 2nd vertebrae shows therefore, a variation. Further, in my 1st specimen, the coccyx is partially united with the sacrum though Boulenger finds it immovably united in his specimen of *M. major*. Parker, after an examination of a large number of species of Megalophrys including *M. major*,
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informs me (in litt.) that in normal cases of *M. major*, a small subcircular cartilaginous omosternum is present. He also points out that in his specimen of *M. major*, the coccyx is incompletely fused with the sacrum as in mine and unlike that of Boulenger's. Probably Boulenger failed to see the non-fusion.

In discussing the ancestry of Pelobatidæ, I have followed the observations of Noble (1924, 1931). According to him, the Liopelmidæ are the most primitive Anurans. This group has given rise on the one hand to the Discoglossidæ and on the other to the Pelobatidæ, and cranial morphology supports this origin of the Pelobatidæ from the Liopelmid stock in 4 features. They are the absence of a recessus sacciformis, of a Bursa angularis oris and the presence of a septomaxillary and the fusion of the mentomandibular with the dentary. It is true that any one of these features may be found in any other Anuran family but when we take all these four features together, Noble's hypothesis is amply borne out by cranial anatomical studies.

X. Summary and Conclusions

It has been known from a long time that Anuran families cannot be distinguished systematically from one another by a single character but by a set of features. With this in mind, we shall now proceed to examine the various features that the cranial morphological investigations have revealed:

1. The cartilago prenasalis superior and inferior are uniformly met with in the Anura. Exceptions, however, are very few where either the superior is reduced (*Breviceps fuscus*) or the inferior cartilage is absent (*Hemisus*). Thus, this character is of no diagnostic importance.

2. The cartilago obliqua is a lateral extension in the anterior narial region from the tectum and from this a connective tissue projection—the plica obliqua depends into the cavum. Gaupp who studied *Rana fusca* (*S. temporaria*) noticed that it depended from the cartilaginous roof and not from the cartilago obliqua and the same feature as reported for *Rana fusca* is also seen in *Breviceps fuscus*. Now, in the Rhacophorid (*Polypedatid*) forms examined by me, it is noticed that in three species of *Philautus*, the plica depends from the tectum, while in the species of *Rhacophorus* (*Polypedates*), it depends from the cartilago obliqua. In the Ranids, Bufonids and Pelobatids examined by me and in the forms studied by the South African anatomists (with the exception mentioned on pp. 46 and 47), the plica depends from the cartilago obliqua. While the nature of the dependence of the plica cannot be made use of for classificatory purposes in other families, at any rate in the Rhacophoridae (*Polypedatidæ*), it
appears to be useful in the present state of our knowledge, in distinguishing \textit{Philautus} from \textit{Rhacophorus} (Polypedates).

3. The prechoanal sac which may occur as two sacs in the anterior region into which the choanae open or as a single sac (\textit{Rhacophorus maculatus} and \textit{Megophrys major}) or as a vestigial structure (\textit{Uperodon systoma}) into which the choanae do not open, is also noticed in other forms like \textit{Phrynomerus} (double), \textit{Probreviceps}, \textit{Breviceps}, \textit{Spelæophryne}, \textit{Rhombophryne} and \textit{Rana grayi}. It is absent from \textit{Glyphoglossus molossus}, examined species of \textit{Rhacophorus} (except \textit{R. maculatus}) and \textit{Philautus}, \textit{Bufo}, and from \textit{Scaphiopus holbrooki} and \textit{Nectophryne misera}. Since the occurrence of this is noticed in genera, of different families, it is probably of independent origin and does not show, therefore, any relationship. Obviously, this cannot be used in systematic study.

4. The septum nasi which is either cartilaginous or is posteriorly ossified gives rise to the tectum or the roof and the solum or the floor. The solum is noticed to give rise to an elevated eminencia in a large number of forms comprising Microhylidae, Ranidae, Bufonidae and Pelobatidae. It was theorised by the South African anatomists that the occurrence of an elevated eminencia was closely correlated with a terrestrial mode of life. This is true in the case of forms like \textit{Uperodon systoma}, \textit{Microhyla ornata}, \textit{Kaloula pulchra} (\textit{K. p. taprobanica}), \textit{Glyphoglossus molossus}, \textit{Breviceps}, \textit{Probreviceps}, \textit{Spelæophryne} and other forms like \textit{Bufo} and \textit{Hemisus}. The appearance of this structure in different forms can only be explained as due to independent development. If only the terrestrial forms developed this structure, of course the theory advanced would not have been found fault with. In two typically aquatic forms of South India, \textit{Rana hexadactyla} and \textit{Rana cyanophlyctis}, an elevated eminencia is met with, and it is therefore thought, that the elevation is purely in response to the sensory needs of the animal. Whatever this aspect of the question may be, it is interesting to note that the Microhylid genera so far studied, viz., \textit{Microhyla}, \textit{Uperodon}, \textit{Kaloula}, \textit{Ramanella}, \textit{Breviceps}, \textit{Probreviceps}, \textit{Spelæophryne} and \textit{Rhombophryne} (?), the elevated eminencia uniformly occurs and this character therefore, can be utilised along with other features in distinguishing the Microhylids.

5. The sphenethmoid bone: It has been noticed that in some examples this bone is divided by means of a trabecular cartilage into a right and left portions when the bone is described as paired. A complete sphenethmoid is seen in \textit{Rhacophorus maculatus}, \textit{Philautus petersi}, \textit{P. oxyrhynchus}, \textit{Rana cyanophlyctis}, \textit{R. hexadactyla}, \textit{Megophrys major} and \textit{Scaphiopus holbrookii}
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while in *U. systoma, K. pulchra (K. p. taprobanica), M. ornata, G. molossus, Rhacophorus microtympanum, Philautus chalazodes, Phrynomerus* and *Rhombophryne* it is paired; in some, it may be absent like *Speleophrine, Ascaphus* and *Rana curtipes*, etc. We find that in the case of all Microhylid examples so far studied, it is either paired or is absent (*Speleophrine, Breviceps, Probreviceps, Kalophrynus, Callulina, etc*). In the Ranidae, it may be absent or it may be single or paired [though Parker (1934) says that the ethmoid is single] and we meet with the same state of affairs in Rhacophoridæ (Polypedatidæ). Hence, this character of the paired nature of the sphenethmoid can be conveniently utilised with others in describing the family characters of the Microhylidæ, till we find other exceptions. With regard to the Ranidæ and Rhacophoridæ (Polypedatidæ), the sphenethmoid can be described as either single or paired or absent (some Ranidæ). More examples should be studied before we can come to any conclusion with regard to the sphenethmoid of the Bufonid and Pelobatid families.

6. The maxillae and premaxillæ are not of great importance to us in systematic study of the genera examined by me.

7. The prevomer, in the Ranid and Rhacophorid (Polypedatid) families does not embrace the choana posteriorly and is not flat. This observation is supported by *Rhacophorus maculatus, R. microtympanum, Philautus chalazodes, P. oxyrhynchus, P. petersi and Rana hexadactyla, R. curtipes and R. cyanophlyctis*. In the Microhylid forms studied by me, *U. systoma* exhibits a well-developed prevomer and a degenerate palatine (?); in *M. ornata*, the choana is not embraced posteriorly by the prevomer, while in *K. pulchra (K. p. taprobanica)*, the posterior portion of the prevomer overlies the palatine. In *G. molossus*, there is a postchoanal portion (prevomer or prevomeropalatine). Thus, in the Microhylid family, we meet with conditions where the choana may be completely or incompletely (*Kaloula, Glyphoglossus, Rhombophryne, Speleophrine, Breviceps, Probreviceps*) or may not be surrounded by the prevomer as in *Microhyla*. Therefore, the nature of the prevomer is not only useful in distinguishing the family but also in classifying the genera within it. Whether the statement can be applied to the Bufonidæ and Pelobatidæ can only be settled after examining some more genera.

8. The palatine bone is not so useful as the prevomer. This may be degenerate (*U. systoma*? for the bone may also be described as a postchoanal prevomer), or absent (*M. ornata*) or a pre-vomeropalatine arrangement may be seen. Generally in the Ranidæ, Rhacophoridæ (Polypedatidæ), Bufonidæ and Pelobatidæ, the bone is present; however exceptions are not
uncommon. *Nectophryne misera* and *Scaphiopus holbrookii* can be mentioned as instances. Among the several species of *Microhyla*, some possess it, while others do not. Thus, the nature or the disposition of this bone cannot be utilised in taxonomy.

9. The septomaxilla is noticed to occur uniformly in all the forms examined by me. This is not, therefore, of great systematic importance except in one case. In *Bufonidae*, a limb of the septomaxilla appears in the plica, a feature in which this family stands apart from the others. I am aware of an exception to this; in *Bombinator*, Brüner describes a limb of the septomaxilla in the plica. Barring this exception, it will be found useful to introduce this feature of the septomaxilla in describing the family characters of the *Bufonidae*.

10. The middle ear and associated structures: It is very well known that in widely different forms, the disappearance of the middle ear, eustachian passage, tympanum and plectral apparatus may occur, as in *Liopelma, Ascaphus, Hemisus, Pelobates*, etc. This may not establish any genetic affinity and therefore, the disappearance of these structures fully or otherwise should be considered secondary. Overlooking these genera, there is a common plan on which the middle ear region with its associated structures is built. The attachment of the columella (pars media plectri) to the dorsal rim of the extraplectral (pars externa plectri plus extraplectral) cartilage in the *Microhylid* examples examined by me, associated with a sickle-shaped annulus tympanicus, is certainly different from the median attachment of the columella with the pars externa noticed in *Ranidae, Rhacophoridae* (Polypedatidæ) and *Pelobatidae*. Since this feature is not uniformly noticed in the other species of the *Microhylid* family, it cannot be used as a safe criterion. The pars ascendents plectri deserves to be mentioned. Gaupp described this commissural cartilage (laterohyal) in *Rana*, but this has not been confirmed by me in all the species of *Rana* examined or in the *Rhacophoridae* (Polypedatidæ) species studied. In *Bufonid* species (except *Bufo vulgaris*), a laterohyal is noticed, and this internal character can therefore be utilised in describing the family characters. It may be said that *Bufonids* generally posses a laterohyal.

11. The pseudobasal joint: In the Anura, the pseudobasal joint between the subocular shelf and the pseudobasal process (except in *Ascaphus*) of the pterygoquadrate is common. In the *Ranidae, Rhacophoridae* (Polypedatid) and *Pelobatid* families, the pseudobasal articulation is found while in *Bufonid* species studied, there is a definite pseudobasal connection. This is a distinguishing feature of the *Bufonidae*. Whether it is
an articulation or a connection it always lies posterior to the palatine branch of the facial nerve and is ventral to the head vein. In describing the family characters of Bufonidae, the possession of a complete autosystyly should also be included.

12. The Bursa angularis oris or Mundwinkeldrüse is noticed in Microhylidae (except Breviceps fuscus), Ranidae and Rhacophoridae (Poly PEDATIDAE) and is generally absent from Bufonidae and Pelobatidae. In describing, therefore, the family characters of the first three, the presence of the Bursa may also be included.

13. The occurrence of a bony or cartilaginous beak between the posteromedial processess of the hyoid (called basi-branchial by Parker, 1881) is uniformly noticed in the South Indian Microhylid examples, but in the foreign forms Breviceps, Probreviceps, Speleophryne and Rhombophryne, this is not present; all the same, Trewavas considers this as a distinguishing character of the Gastrophryne group of the Brevicipitidae. This feature is of no great systematic value in general but is of sufficient importance to demarcate the examined Indian genera. To this may be added, the absence of an omohyoid and the presence of only two petrohyoidus muscles (Trewavas) and these three characters are very useful in distinguishing the Microhylidae. The larynx of the Microhylidae exhibits two important diagnostic features, viz., the absence of an independent apical cartilage and of an oesophageal process from the cricoid annulus of both sexes. With regard to the Pelobatidae, the presence of a lateral foramen in the Pelobatineæ would distinguish the Megophrynae (except M. fœæ, where also a lateral foramen is present). Following Trewavas, the diagnostic features of the Pelobatid family would be as follows:—

(a) The occurrence of an arytenoid without an apical cartilage,
(b) cricoid ring incomplete dorsally [except in Scaphiopus hammondii (male) where it is complete] (author, 1935 a), and
(c) hyalia more or less reduced.

14. The occurrence of a Meckelian epiphysis is so characteristic of Microhylidae that it ought to be included as a taxonomic feature. However, we note the occurrence of a Meckelian epiphysis in Phrynomenus, which has been treated as belonging to the subfamily Phrynomerinae under Brevicipitidae by Noble (1931). Besides, Phrynomenus also shows other Microhylid affinities, as dilated sacral diaphysis, prechoanal prevomer (Parker, 1934) as in Microhyla (but de Villiers (1930 a) describes the formation of a prevomeropatalatine in (Phrynomenus), divided ethmoid, etc. In spite of all these features common with the Microhylidae, Noble says that, “The
African *Phrynomerus* is not closely related to any other breviceptid". Whatever may be the number of similarities between this genus and the other genera of Brevicipitidae of Noble, there is one important distinguishing feature and that is, the presence of intercalary phalanges. No Microhylid possesses these, and therefore, Parker (1934) has erected a new family Phrynomeridae for accommodating this genus.

15. The nature of the centrum of the vertebrae has been utilised largely in taxonomy. Within the family Ranidae and Rhacophoridae (Polypedatidae), I have shown that both the procôelous and diplasiocôelous type of centrum for the 8th vertebra occur. Therefore, in distinguishing families this may not be a safe criterion, and it must be said that the propriety of using the nature of the vertebra has been questioned from the time of Gadow since the variations noticed have been largely fortuitous. At any rate, I have no hesitation in following Parker (1934) for using the nature of the centrum in the diagnosis of groups of genera within the families.

*Conclusions*

The study of cranial morphology and of the hyolaryngeal apparatus and the vertebral column reveals the following features which can safely be utilised along with others (Parker, 1934) in the classification of Anuran families and subfamilies:

**Ranidae**:
(a) Vertebral column diplasiocôelous or procôelous.
(b) Ethmoid entire or paired or absent.
(c) Eminentia generally flat except in *Rana hexadactyla* and *Rana cyanophlyctis*.
(d) A Bursa angularis oris is present.
(e) A pseudobasal articulation is noticed.

**Rhacophoridae (Polypedatidae)**:
(a) Vertebral column diplasiocôelous or procôelous.
(b) A Bursa angularis oris is present.
(c) A pseudobasal articulation is noticed.

**Microhylidae**:
(a) Eminentia is invariably elevated.
(b) A Bursa angularis oris is present.
(c) A Meckelian epiphysis is present on either side in the lower jaw.
(d) An independent cartilago apicalis is absent from the arytenoid cartilage.
(e) An œosphageal process is absent from the cricoid annulus.
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**Bufonidae**:

(a) Invariably a limb of the septomaxilla is seen in the plica obliqua.
(b) A Bursa angularis oris is absent.
(c) A pseudobasal connection is present.
(d) A laterohyal is invariably present.

**Pelobatidae**:

(a) A Bursa angularis oris is absent.
(b) A pseudobasal articulation is present.
(c) The cricoid annulus is complete or incomplete.
(d) The hyoid of the subfamily Pelobatinae possesses a lateral foramen while in Megophrynae, it is wanting except in *M. feae*.

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