

The Structure of the Vertebral Column in the Anura *Phaneroglossa* and its Importance as a Basis of Classification. By GEO. E. NICHOLAS, D.Sc., F.L.S., Beit Memorial Fellow, Department of Zoology, King's College, London. (With 1 Text-figure.)

[Read 1st June, 1916.]

As is well known, the vertebral column of the common frog consists of nine vertebrae of which the ninth (the sacral) has a biconvex centrum. Of the eight pre-sacral vertebrae, the first seven are procelous and the eighth has a biconcave (amphicelous) centrum.

It is generally supposed that this condition prevails among the greater number of living Anura, and this type of vertebral column is commonly described (notwithstanding the condition of the eighth and ninth vertebrae) as *procelous*, in distinction to that of those few primitive Anura in which the presacral vertebrae are *uniformly opisthocelous*.

Thus Gadow states ('01, p. 19), "Procelous vertebrae exist in the overwhelming majority of the Anura: opisthocelous are those of the Aglossa, the Discoglossidae, and of some Pelobatidae." He continues (p. 20), "*the sacral vertebra, . . . in all the Anura is invariably biconcave, the eighth being biconcave in the procelous families*" (my italics).

Now this generalization which had appeared, in almost identical form, several years earlier in Boulenger's admirable work on "The Tailless Batrachians of Europe," is, as I shall presently show, by no means correct.

The accuracy of the statement, however, appears never to have been challenged, nor even the existence of exceptions recorded until recently, when I called attention ('14, pp. 420-1) to the fact that the condition of the eighth and ninth vertebrae of *Bufo* constituted a very distinct departure from this rule.

This fact had been ascertained by the examination of all of the Bufonid skeletons in the Collection of the British Museum, this material (with my own specimens) comprising more than fifty examples representing over thirty species. In this genus the centra of all of the vertebrae are alike excepting only that the convexity (for articulation with the ensuing coccyx) upon the hinder face of the ninth vertebra is doubled in the manner that is so nearly universal among the Anura.

In *Bufo*, then, there exists a third type of vertebral column which is *uniformly procelous*, and therefore perfectly distinct from that which has a biconvex sacral and a biconcave eighth vertebra but which, nevertheless, has hitherto been described as procelous. It is obvious that only to such a vertebral column as that of *Bufo* can the term "Procelous" be strictly applicable, in distinction to that of the lower Anura (Aglossa) in which the vertebral column is *opisthocelous*.

I recommend, therefore, that the term "Procelous" be restricted to vertebral columns of the Bufonid type in which *all* of the centra are hollow in front. For those vertebral columns, hitherto described as procelous, which have *only the first seven* vertebral centra hollow in front, the eighth hollow upon both faces and the ninth doubly convex, I propose that the term "*Diplasiodelous*" (which has been suggested to me by Mr. Boulenger) should be employed.

When, in 1914, I recorded the existence of a uniformly procelous condition in *Bufo*, I assumed, mistakenly as it now appears, that this type of vertebral column might be found to be confined to that genus. That such a condition could be of widespread occurrence seemed incredible in view of the authoritative statement above quoted.

Recently, however, I have been enabled, by the kindness of Mr. Boulenger, to examine practically the entire collection of Anuran skeletons in the British Museum. This material includes, in addition to some eight specimens of Aglossa (*Xenopus laevis* [4], *X. calcaratus*, *Hymenochirus boettgeri*, and *Pipa americana* [2]), nearly two hundred examples of the Phaneroglossa. To these must be added about fifty specimens representing nine species which are in the teaching collections of King's College and the Agra College and in my own possession. The vertebral columns of more than one hundred and fifty common frogs (*R. temporaria*) were also examined in this connection. In all, there were examined over four hundred vertebral columns of some fifty genera of Anura.

The Discoglossidae were represented by nearly a dozen specimens (*Discoglossus pictus* [5], *Bombinator igneus* [3], *Algytes obstetricans* [3]), and were found to be, without exception, normally opisthocelous.

Of the Pelobatidae, I have examined fourteen specimens of the genera *Megalophrys* (*M. montana* [2], *M. nasuta* [2], *M. féei*, *M. longipes*), *Pelobates* (*P. fuscus* [6]), *Scaphiopus solitarius*, *Pelodytes punctatus*, and *Palaobatrachus* sp. Of these all were uniformly procelous excepting two individuals of *Megalophrys* (*M. montana*, *M. nasuta*), which were opisthocelous.

The families Hyliidae, Bufonidae, and Cystignathidae were, without exception, characterized by the possession of a procelous (*strictu sensu*) vertebral column. The Hyliidae examined were *Hyla* (*H. venulosa* [2], *H. dohertyi* [2], *H. grisea*, *H. macrops*, *H. ichenuta*, *H. taurina*, *H. cernua* [2], *H. areia* [2], *H. faba*, *H. arborea* [3], *H. pulchella* [2], *H. macrinii*, *H. versicolor*, *H. bawilina*, *H. boani*), *Nototrema* (*N. marsupiatum* [2]), and *Phyllomedusa* (*P. decemcolor* [2] and *P. burmeisteri*). Except for a single specimen of *Nectophryne hosi*, all of the Bufonidae examined belonged to a single genus, *Bufo*. The species included *B. marinus* [3], *B. quadrivirgatus*, *B. vulgaris* [8], *B. calamita* [2],

* The numerals in [] indicate the number of specimens of each species examined.

B. leptopus, *B. asper*, *B. vittatus*, *B. dolsoni*, *B. americanus*, *B. val-leys* [2], *B. spinulosus*, *B. viridis* [2], *B. typhlonus*, *B. carens*, *B. anderssoni* [3], *B. lentiginosus* [3], *B. grandulosus*, *B. regularis*, *B. reddii*, *B. tuberosus*, *B. claviger*, *B. boreus*, *B. pentoni*, *B. latifrons*, *B. intermedius*, *B. melanostictus* [4], *B. mauritanicus*, *B. leuaticus*, *B. superciliosus*, and *B. cruxiger*. Of the Cystogathidae, on the other hand, there were representatives of no less than twelve genera and nineteen species:—*Ceratophyllus*, *Pseudis parvulus*, *Calypsocephalus gylli*, *Telmatochelys jelskii*, *Ceratophrys ornata*, *C. boiei*, *Chiropletes australis*, *C. platycephalus*, *Heleporus albopunctatus*, *H. pictus*, *Hydrolas lineatus*, *H. variiformis*, *H. fleischmanni*, *Cryptotis brevis*, *Limnodynastes tasmanicus* [2], *L. dorsalis*, *L. ornatus*, *Leptodactylus pentadactylus*, and *Hylophina silvatica*. The closely related Dendrophryniscine are represented in the British Museum Collection by a skeleton of *Batrachophryne brachydactylus*, which was also procelonous.

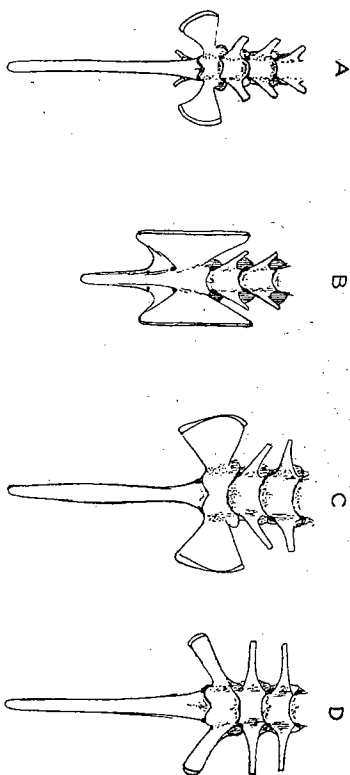
Among the forms included in the Engystomidae and Dyso-phidae, three specimens (representing two genera) were found to retain the strictly procelonous condition. These were *Rhombophryne testudo*, *Atelopus acryrhynchus* and *A. ignescens*, each represented by but a single specimen. The majority of the specimens exhibit the diplasiocelous condition, which was seen in eight genera, viz.:—*Breviceps* (*B. verrucosus*, *B. mossambicus*), *Calophryne* (*C. pleurostigma*, *C. madagascariensis*), *Scaphophryne* (*S. macmoroti*), *Cacopus* (*C. systoma*), *Calliops* (*C. doriae*), *Cathila* (*C. pulchra*), *Hypopachus* (*H. varicosus*), and *Genophryne* (*G. thomsoni*).

Among the Ranidae the diplasiocelous condition also prevails, only five specimens (referred to four species of *Rhacophorus*) being found to retain the more primitive procelonous condition. The specimens of this family which have been examined include the following:—*Hylambates* (*H. angolensis*), *Trechobatrachus* (*T. robustus*), *Gampsosteonys* (*G. batesi*), *Rana* (*R. clamata*, *R. tigrina* [35], *R. agilis*, *R. adspersa*, *R. latasini*, *R. afghana* [2], *R. montezumae* [2], *R. catshiana*, *R. galamensis*, *R. gutturalis*, *R. fusca*, *R. macrodactylus*, *R. gracilis*, *R. cyanophyllus*, *R. esculenta* [12], *R. gramineus*, *R. erythraea*, *R. malabarica*, *R. beccarii*, *R. pleurodactylus*, *R. adenopleura*, *R. jerdoni*, *R. arvalis*, *R. comeniani*, *R. greca*, *R. iberica*, *R. palustris*, *R. madagascariensis*, *R. boylii*, *R. ornatesima*, *R. lebigii*, *R. hexadactylus*, and *R. temporaria* (about 160). *Rhacophorus* (*R. maculatus*, *R. cruciger*, *R. goudotii*, *R. macrostis*, *R. robustus*, *R. schlegelii*, *R. reinwardtii* [2], *R. macinui*, and *R. madagascariensis*), *Chironomantis* (*C. petersi*), *Corrufer* (*C. corrugatus*), *Oxyglossus* (*O. levis*), *Tympanonotus* (*T. newtoni*), *Oxyphacis levis*, *Arthroleptis* (*A. variabilis*), and *Ceratobatrachus guentheri* [2].

In by far the greater number of cases, disarticulated vertebral columns were not available, but this circumstance presented no serious difficulty since the condition of the vertebral centra can,

in almost every case, be made out with ease by a careful examination of the ventral surface of the vertebral column (see text-figure). In a few specimens in the Collection of the British Museum the vertebrae were sufficiently free to admit of an actual observation of the anterior faces of the sacral and preceding vertebrae. In every such case this examination confirmed the opinion already formed from the examination of the entire vertebral column of a specimen of the species in question. A few specimens (a bare half-dozen), concerning which I could not feel absolutely certain, were referred to Mr. Boulenger, who was able to confirm, in every case, the correctness of the conclusion at which I had, provisionally, arrived.

The result of this investigation was quite unexpected, for, as has been shown, it was found that the Diplasiocelous ("procelonous") condition, which was supposed to characterize "the overwhelming majority" of Anura, is in fact confined to the Firmisternia forms!



Ventral view of the hinder part of the vertebral columns of (A) *Diplacopsus pictus*, (B) *Pelobates fuscus*, (C) *Bufo anderssoni* (all X 2), and (D) *Rana tigrina* (nat. size), to show the opisthocelous, anomocelous, procelonous, and diplasiocelous conditions.

The biconvexity of the centrum of the sacral vertebra, therefore, so far from being an "invariable" feature of the Anuran vertebral column, is in fact restricted, except for individual variation, practically to the Discoglossidae and the Firmisternia*.

On the other hand, a vertebral column in which all the centra are hollow in front (Procelonous, *strictu sensu*) is found in the Cystignathidae, Hyllidae, Bufonidae, and the Pelobatidae, i.e., the whole of the Arctera excluding only the Discoglossidae.

The Pelobatidae are known to be extremely variable in the condition of the vertebral column. They are, nevertheless, excepting

* A few opisthocelous Pelobatidae may have a biconvex ninth centrum, which is, however, easily distinguished from those of Discoglossidae or Firmisternia by its single coccygeal condyle.

for what will probably prove to be merely individual variations (*vide infra*), of the uniformly procelous type. They differ, however, from the remaining procelous families, in that the convexity upon the sacral vertebral centrum (for articulation with the coccyx) is single instead of double as in all other Anura.

It will be seen, therefore, that the Anura may be divided sharply into *five* groups, according to the structure of the vertebral column (and attached ribs).

- (i.) Sacral vertebrae always fused with coccyx; pre-sacral vertebrae seven (or fewer), opisthocelous: with ribs in development. (Aglossa.)
- (ii.) Sacral vertebra free, with biconvex centrum; pre-sacral vertebrae not less than eight, opisthocelous: with ribs. (DiscoGLOSSIDÆ.)
- (iii.) Sacral vertebra procelous, ankylosed to coccyx, or if free, with but a single condyle for articulation with coccyx; pre-sacral vertebrae eight, procelous: without ribs. (PELOBAIDÆ.)
- (iv.) Sacral vertebra free, procelous, with double condyle for the coccyx; pre-sacral vertebrae eight, procelous: without ribs. (Remaining AREIFERA.)
- (v.) Sacral vertebra free, biconvex; eighth vertebra biconcave; first seven vertebrae procelous: without ribs. (FIRMISTERNINÆ.)

DISCUSSION.

Earlier Views as to the importance of the condition of the Vertebral Centrum as a systematic character.

As is well known, a varying degree of importance has been attached, by different authors, to the condition of the vertebral centra in the Anura. Thus both Cope ('66) and Lataste ('79) laid considerable stress upon the opisthocelous or procelous character. Boulenger ('82), in his 'Catalogue of the Batrachia Salientia s. Ecaudata,' made use, principally, of the condition of the pectoral girdle and of the dentition, and pointed out that the mode of vertebral articulation appeared to be of unequal importance throughout the group.

Some three years later, Blanchard ('85, p. 588) went so far as to propose that the tailless Batrachia should be separated into two principal groups, the "Opisthoceliennes" and the "Proceliennes." His suggestion did not meet with acceptance, and subsequent writers seem to have attached less and less value to the condition of the centra as a systematic character. Thus, in 1901, Gadow wrote ('01, p. 19): "The systematic value of this pro- or opisthocelous character has been much exaggerated." He continued (p. 20), "it is not difficult to imagine that in the Anura the production of pro- or opisthocelous vertebrae depends simply upon the centra or articulating knobs happening to fuse either with the hind or the front end of the vertebrae."

In 1907 Beddard pointed out that in some species of the genus

Megalophrys, which was said to be opisthocelous, the procelous condition actually occurred, and in the following year Boulenger, referring to this point, concluded ('08, p. 408): "It is therefore clear that this character, however important it may appear at first, is worthless even as a specific character in these Batrachians."

The Infrequency of Variation in the Mode of Vertebral Articulation.

A fact, however, which lends weight to the value of the character of the vertebral centra for systematic purposes is the extraordinary rarity of the occurrence of individual variation. In not one of at least a hundred specimens of the procelous families Bufonidæ, Hylidæ, and Cystignathidæ (represented by over seventy species) did I find a case of individual variation in the character of the vertebral centra, although variation affecting the vertebrae in other ways was not infrequent! Indeed, so far as I can discover, only once has an abnormality affecting the centra been recorded in a member of these families, this being described by Cope ('66) in *Bombocrotas*. In the vertebral column of the Pelobatidæ individual variation is peculiarly frequent, but even in this family, very few cases of variation in the character of the centra have been met with outside of the genus *Megalophrys*.

Among the Diplasiocelous families, also, the occurrence of individual variation in the condition of the centra is extraordinarily rare—indeed, it is almost certainly the rarest of all abnormalities. When such variation does occur it appears invariably to take the form of a reversion to the more primitive (strictly procelous) condition. Thus, Lloyd Morgan has described one such case in the common frog, while I have myself met with two other instances of this reversion. The first of these was found in a specimen of *R. esculenta*, and the second may be seen in a specimen which is preserved in the British Museum Collection. It is labelled *Rana* sp., but is, almost certainly, *R. tigrina*. Apart from these three examples* there are, I believe, no known cases of variation in the condition of the centra in diplasiocelous forms. Moreover, I have recently examined the vertebral column of more than one hundred and fifty specimens of the common frog, and although I find that the vertebral column is variable in 8 per cent. of the specimens examined, yet there was not one which departed from the typical diplasiocelous condition of the centra.

The Character of the Vertebral Centrum not "Adaptive."

The precise manner in which the vertebral centra articulate does not appear to be related to the habits of the various forms, that is, it cannot be described as an adaptive character. There

* An abnormal vertebral column (*R. temporaria*) described by Howes ('86) had ten vertebrae all of which were procelous.

are forms which jump as powerfully or swim as strongly in the procelous Arcifera as in the diploscoelous Firmisternia, just as there are crawling, burrowing, or arboreal forms in each group. A very similar statement might be made, comparing the opisthocelous forms with the procelous. Indeed, from the standpoint of function it would appear to be a matter of little import whether the intervertebral spheres become attached to the anterior or the posterior face of an adjoining vertebra, and, as Gadow has remarked, we might imagine that the union of these intervertebral spheres with centra before or behind would be a mere matter of chance. Occasionally, as a very rare variation in the Pelobatidae, the intervertebral spheres altogether fail to unite with the centra and the amphicoelous (ancestral) condition of the embryo persists into maturity (*P. cultus*, Duges, '34; *P. fuscus*, Stannius, '54).

When, therefore, such a comparatively trivial character as this is found to occur over a wide range of genera in which there is an almost complete absence of individual variation*, we are surely justified in attaching to it considerable value as a systematic character, since its occurrence is to be explained only upon the ground of community of descent.

A division of the Phaneroglossa, based upon this character, gives us, moreover, a grouping which (while it corresponds fairly closely with that at present accepted as representing a natural classification) separates the Discoglossidae a little more widely from the remaining Arciferous forms.

The breaking-up of the Arcifera has already been proposed by Stejneger ('07). That author divided the Anura into three sub-orders:—Agllossa, Costata (the Discoglossidae), and Lingata (the remaining Phaneroglossa).

Lataste ('79) and Blanchard ('85) went still further and proposed the inclusion of both the Aglossa and the Discoglossidae in the same Sub-order (Opisthocaela).

The change which I propose in our present classification consists simply in the grouping of the families of the Phaneroglossa into four larger divisions (tribes) in place of the two series, Arcifera and Firmisternia, at present recognized.

PHANEROGLOSSA.

I. OPISTHOCERA. Sacral vertebra biconvex, free from coccyx; pre-sacral vertebrae eight, opisthocelous; with ribs.

Includes but one family, the Discoglossidae.

II. ANOMOCERA. Sacral vertebra ankylosed to coccyx or articulating therewith by a single condyle; vertebrae procelous (rarely opisthocelous); without ribs.

Includes a single family, the Pelobatidae.

* Even in the very variable Pelobatidae only two cases of *anomalous* centra (apart from the amphicoelous above mentioned) have been recorded in the procelous species. These were described by Stannius ('54) in *Pelobates fuscus* and by Boulenger ('32) in *Xenophrys monticola*.

III. PROCEA. Sacral vertebra free, articulating with the coccyx by a double condyle; vertebrae uniformly procelous.

Includes the Bufonidae, Hyliidae, and Cystignathidae.

IV. DIPLASIOCERA (= Firmisternia). Sacral vertebra biconvex, eighth vertebra biconcave; the first seven vertebrae procelous.

Includes the Ranidae and Engystomnidae.

(i.) This arrangement involves, as will be seen, the subdivision of the Arciferous forms into three groups. As already pointed out, it has long been recognized that the Discoglossidae are somewhat more widely removed than the existing classification would indicate.

(ii.) Concerning the Pelobatidae, Gadow remarks that they can be separated from the Bufonidae only by the dentition. Nevertheless he advocates that they shall be retained as a distinct family. In the condition of their vertebral articulation, however, the Pelobatidae apparently possess a distinctive character which amply justifies their separation from the Bufonidae. That both procelous and opisthocelous vertebrae occur within a single genus (*Megalophrys*) has been considered as sufficient justification for altogether discarding this character for systematic purposes. As a matter of fact, however, the whole family appears to be strictly procelous apart from this single genus. As a family, moreover, it is notable for the extremely frequent occurrence of variations in the vertebral column. Thus, Adolphi found in *Pelobates fuscus* that abnormalities in the vertebral column occurred in more than 23 per cent. of the specimens examined! As mentioned above, the two examples recorded in the Anura, in which the amphicoelous (embryonic) condition of the centra is retained in mature animals, were both examples of *Pelobates*. Nevertheless but one example (that recorded by Stannius) appears to be known of an *irregularly* abnormal condition of the centra in this genus.

In *Megalophrys*, however, variation seems frequently to extend to the centrum. In *Megalophrys parva* (*Xenophrys monticola*) Boulenger has described an anomalous arrangement of the vertebral centra comparable to the case of *P. fuscus* described by Stannius. Moreover, *M. montana* (the type species) was originally described by Cope as having opisthocelous centra, and this type of vertebra has since been recorded in two other species (*M. nasuta*, *M. longipes*). It is now known that the procelous condition is, even in these three species, at least equally frequent, while in the remaining eleven species, hitherto described, the vertebrae appear to be uniformly procelous! Thus there is little reason to regard the occurrence of the opisthocelous condition in a few specimens of these three species as other than unusually frequent cases of individual variation*.

* Concerning *Asterophrys* little seems to be recorded. Like *Megalophrys*, it has been described as opisthocelous, but its tongue is said to be entire and adherent, and Blanchard assigned it to the Discoglossidae.

Two other genera, *Cophophryne* (*C. sickimensis*) and *Ophryne* (*O. microstoma*), which are at present placed with the Bufonidae but which agree with the Pelobatidae in the character of the vertebral column, should probably be included in that family. They differ from the Pelobatidae merely in the absence of teeth and, in describing *Ophryophryne*, Boulenger remarks ('03, p. 17) that "One must regard it as on the whole nearer to the latter (Pelobatidae) than to the true toads; another instance of the over-estimation of dentition as a character by which to define families of the Batrachia."

In *Scaphiopus* and in one species of *Pelobates* (*P. fuscus*) there appears to be an invariable fusion of the sacral vertebra with the coccyx comparable to that which occurs in the Aglossa, but in both of these Pelobatidae the vertebrae are uniformly procoelous. A similar fusion appears to occur as an individual variation in some other species of the Pelobatidae (e.g. *P. cultripes*, *M. nasuta*, Boulenger, '08), but even where this variation coincides with the occurrence of opisthocelous centra there is no danger of confusion with the Aglossal condition, for, in the latter, there are never more than seven pre-sacral vertebrae.

Bombinator is the only form, outside of the Pelobatidae, in which the sacral vertebra articulates with the coccyx by but a single condyle. Like the Pelobatidae, too, it is notable for the frequency of occurrence of individual variations. The vertebral column can, however, be distinguished from even an opisthocelous specimen of the Pelobatidae by the attached ribs.

Pelodytes, which appears to lead towards the Bufonidae, forms an exception, apparently, to the rule that in the Pelobatidae the sacral vertebra has but a single condyle for the coccyx. According to Boulenger ('97) the posterior convexity of the centrum of the sacral vertebra is doubled in this genus. This is certainly true of the single specimen (1915, 9.15.5) in the British Museum Collection. There are, however, conflicting statements upon this matter, for Gadow describes ('01, p. 161) this genus as having but a single condyle, this character being made use of to distinguish *Pelodytes* from *Leptobranchium*, which is said to have two coccygeal condyles. On the other hand, Boulenger has merged *Leptobranchium* in the genus *Megalophrys*, which has but a single condyle for the coccyx. The explanation of these apparent contradictions may be that the doubling of the condyle is, in these genera, subject to some variation.

(iii.) The Bufonidae, Hyliidae, and Cystignathidae are, without exception, in the species which I have examined, distinguished from the Pelobatidae (excluding *Pelodytes*) in having the sacral vertebra provided with two coccygeal condyles. Otherwise, in the uniformly procoelous condition of the vertebra, they closely resemble the Pelobatidae and are sharply marked off from the firmisternal forms in which the diplasiocelous condition prevails. The Hemiphractidae, however, which are included by Gadow in the Cystignathidae, have been described as possessing opisthocelous

centra. Whether this is an invariable condition in that genus or whether the description was based upon the examination of a variable individual, I have no means of deciding, but the only member of this family (or sub-family) which I have examined, a specimen of *Cercolophya bubalus*, was certainly uniformly procoelous. In the former case the genus would appear to furnish a link between the Procoela and the Opisthocœla comparable to that supplied by *Megalophrys* between the Opisthocœla and the Anomœœla.

Apart, however, from this single, possibly exceptional, genus, there has been described but a single instance of the occurrence of variable centra in these three great families which comprise the majority of living Anura.*

Remarkings upon the resemblance which exists between many of the Cystignathidae and the Ranidae, Gadow says ('01, p. 210), "young Ranidae, before the firmisternal character is assumed, are indistinguishable from the Cystignathidae, and the latter would turn into Ranidae if they could be induced to consolidate their sternal apparatus." The condition of the vertebral centra, however, permits of a distinction being readily made even between these immature forms.

(iv.) The Diplasiocelous condition (which, as already pointed out, is restricted to Firmisternal forms) is likewise extremely constant, individual variations being almost unknown. The occurrence, therefore, of two or three genera at present included in the Firmisterna, in which the diplasiocelous condition has, apparently, not been attained, is a matter of considerable interest.

Thus, among the Engystomatidae which, as Gadow points out (*op. cit.* p. 143), may be connecting links between the Procoela and Diplasiocœla, I find three specimens exhibiting the uniformly procoelous condition. These are one example each of *Aleiopus uaythynthus*, *A. ignescens*, and *Rhombophryne testudo*. Having had but a single skeleton of each of these three species for examination, I am unable to say whether or no these are cases of individual variation. It is scarcely probable, however, that two specimens belonging to distinct species should both have chanced to be similarly abnormal, and it may be assumed that *Aleiopus* is normally procoelous. It is not, however, surprising that we should find in one or two genera which have become firmisternal, that there is a retention of what must be recognized as a more primitive condition of the vertebral column.

A more puzzling exception is met with in the genus *Rhacophorus*, and there can be, I think, in this case, no question of abnormality or individual variation.

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. cruentiger*, *R. macrotis*, and *R. robustus*,

* The specimen of *Bombinator* described by Cope ('66).

were diplosiocelous. The remaining specimens, *R. marinus*, *R. madagascariensis*, *R. schlegelii*, and *R. reinwardtii* [2], were uniformly procelous. Of the five specimens but one (*R. reinwardtii*) permitted of direct observation of the vertebral faces, but Mr. Boulenger, to whom I referred the question, agreed that the vertebral articulation in these specimens is as stated.

Such a condition is apparently inexplicable in view of the fact that the *Rhacophori* are generally accepted as true Ranidae. It is, however, of peculiar interest in view of the fact that the *Rhacophori* have not always been regarded as Ranidae. Originally they were placed with the Hyliidae (which are of course procelous), to which they bear a most remarkable resemblance which is, at the present time, attributed merely to convergence. How close is this resemblance may be judged from a fact recently brought to light by Stejneger ('07). This author has pointed out that the specimen originally figured by Schlegel and regarded as the type specimen of *Polydactylus* (*Rhacophorus*) *schlegelii* is actually a mere variety of *Hyla arborea* (*H. arborea japonica*)! This view, he remarks ('07, p. 17), has been confirmed by an examination of the original specimen in the Leiden Museum. He figures this variety of *Hyla* as possessing the tongue typical of the Hyliidae but as having a foot which, so Mr. Boulenger informs me, is absolutely characteristic of *Rhacophorus*!

The skeletons of the several species of *Rhacophorus* in the collection of the British Museum show the coracoids united but somewhat widely separated from the weak clavicles by conspicuous and well-calculated precoracoids.

Apart from these apparent exceptions, the whole of the remaining forms, at present grouped in the Firmisternia and which I have been able to examine, are diplosiocelous. Moreover, this character, as already pointed out, is one which, in this group as in the Procela, is exceptionally free from individual variation.

It may, nevertheless, be objected that the occurrence of exceptions renders the character of the vertebral articulation of little value for systematic purposes. The condition of the sternal apparatus is, however, open equally to such objection. Forms with sternal apparatus as diverse as those of *Rana* and of *Hemias* or of *Breviceps* and of *Caeopus* are all grouped together as Firmisternia. I have shown, too, in a recent paper ('15), that there is normally in *Rana tigrina* a very marked overlap of the coracoids rivaling that of many Arciferous forms.

It is obvious, moreover, that whereas the precise manner in which the intervertebral spheres unite with adjoining centra has no physiological importance, the consolidation of the sternal apparatus may well be of considerable physiological value and therefore be a character which might well arise independently in widely separated forms*.

* Cf. the existence of a consolidated sternal apparatus in the Aglossa.

This was apparently Cope's view, and Gadow suggests ('01, p. 143) that the Firmisternia may prove to be a polyphyletic assemblage.

Further, the Anura are known as a very modern and wonderfully plastic group. It is to be expected, therefore, that there should be found persisting forms which appear to connect the several groups. The difficulty that is experienced in attempting to draw hard and fast lines between the different families suggests that our classification is, in the main, a natural one and does not represent merely a convenient key as Gadow is prepared to believe ('01, p. 143).

Thus the Pelobatid *Megalophrys* with its occasional opisthocelous centra serves as a link with the Discoglossidae, a link which is strengthened by the invariable occurrence in the otherwise very variable *Bombinator* of but a single coccygeal condyle. On the other hand, *Pelodytes* seems to connect the Anomoeala with the Procela. *Rhombophryne* and *Atelopus*, too, may be considered either as Procela in which the consolidation of the sternal apparatus (foreshadowed in the Bufonide, *Rhinophryne*, and *Myobatrachus*) has become an accomplished fact, or as Firmisternia in which the Diplosiocelous condition has not yet been attained.

I desire to take this opportunity to express my thanks to Mr. Boulenger for directing my attention to certain of the literature, and to Professor Dendy for much valuable criticism.

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