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## THE PECTORAL GIRDLE OF THE BRACHYCEPHALID FROGS

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In recently tracing the evolution of the primary groups of frogs and toads, I found it advisable to delete the family Dendrophryniscidae. One of the two genera of this family was hardly specifically distinct from certain Andean frogs of the genus *Telmatobius*, while the other, although known to me only from descriptions, seemed to have arisen from a very different stock in eastern South America (Noble, 1922). More recently the distinguished Brazilian herpetologist, Dr. Adolfo Lutz, has sent me specimens of what he believes are referable to the latter genus *Dendrophryniscus*. These specimens have proved unusually interesting and have necessitated my restudying the development of the pectoral girdle in several families of Salientia. Very recently there has appeared a number of important contributions to our knowledge of the ontogeny of the shoulder girdle in *Rana* and *Xenopus* (de Villiers, 1922, 1924; Fuchs, 1926). My observations on the same structure in *Dendrophryniscus* and related genera are of special interest at this moment for the light they throw on the fusion process in the change from the arciferal to the firmisternal type of girdle.

Dr. Lutz's specimens of *Dendrophryniscus brevipollicatus* were collected near Rio de Janeiro, the type locality of the species. They agree closely with Espada's (1875, Pl. VI) figures of the species and also with his description (Espada, 1871). They differ in the slightly longer legs and more distinct color pattern. Miranda Ribeiro (1920) has apparently recently described the same form from the state of São Paulo under the name of *Atelopus imitator*. It has a superficial resemblance to *Atelopus* as Espada (1871) noted when originally describing *D. brevipollicatus*.

Espada (1871) distinguished *Dendrophryniscus* from *Atelopus* by its arciferal pectoral girdle and cylindrical sacral diapophyses. A binocular examination of the specimens sent by Dr. Lutz gives the impression that the pectoral girdle is actually arciferal. But the sacrum is broadly dilated. Espada did not figure the sacrum of his specimens of *D. brevipollicatus*, although he figured most of the other diagnostic structures. Espada's types are not available to me. Hence it

is impossible to check up on this character. In the meantime, we are confronted with the question of what name to apply to a frog coming from the type locality of *D. brevipollicatus*, agreeing closely with this species externally and in its apparently arciferal pectoral girdle, but on the other hand, conforming with *Atelopus*, in all external and internal characters, save the pectoral girdle. The generic relationships of this

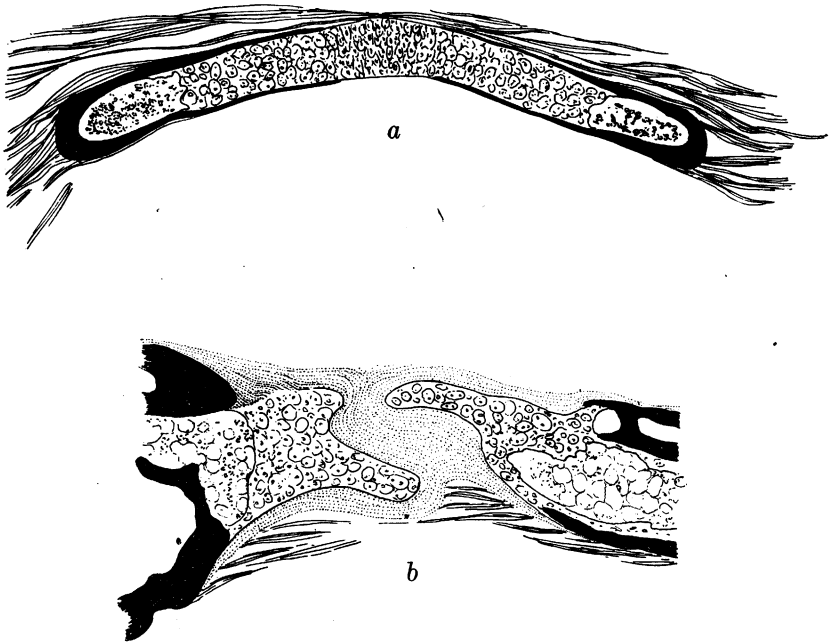


Fig. 1. Sections transverse to the body axis of the coracoid region (level *b*, Fig. 2*a*) of two brachycephalid frogs.  $\times 83$ . Ventral surface toward top of page.

*a.* *Atelopus varius* Stannius.

*b.* *Dendrophryniscus stelnzeri* (Weyenbergh).

Bone = black; cartilage = circles; connective tissue = regular stipple (or stipple lines); muscle = line; blood corpuscles = heavy clustered stipple.

genus are clearly dependent on a detailed comparison of its girdle with that of *Atelopus* and other brachycephalids.

I have studied under the high powers of the binocular the pectoral girdles of *Atelopus flavescens*, the type species of the genus, and those of *A. elegans*, *A. ignescens*, and *A. varius*. In all of these, the pectoral girdle is completely firmisternal, no suggestion of freedom being found in any part of the symphysis of the coracoid cartilages. The coracoids are very broad and the fused coracoid cartilage is reduced to a very narrow strip.

Further, I have studied sections of a young specimen of *A. varius* only 17.5 mm. in head and body length. Already at this early stage a complete fusion of the coracoid cartilages has occurred (Fig. 1a). We may conclude that the pectoral girdle of *Atelopus* is completely firmisternal, the coracoid cartilages fusing with their mates of the opposite side at an early stage.

Some time ago I showed (Noble, 1922, p. 39, footnote) that the pectoral girdle of the little Argentine frog *Atelopus stelzneri* was arciferal so far as one could determine from a binocular examination. I therefore referred the species to *Bufo*, although it differed externally from other species of the genus. The question still remained whether ordinary methods of dissection were sufficiently exact for determining the details of structure in so minute a form. There are found along the eastern part of South America a number of species closely allied to *Atelopus stelzneri*. Of these, only *A. moreiræ* is available to me, but *Oreophrynella*, the little batrachian from the top of Roraima, seems much like *stelzneri* in rugosity and proportions. It seemed advisable to restudy the pectoral girdles of these forms by more exact methods than had been done previously. I adopted both clearing and microtome methods to determine the conditions in these forms.

Cleared specimens of *A. stelzneri*, *A. moreiræ* and *O. quelchii* have revealed that these species are arciferal in the coracoid region but broadly firmisternal in the procoracoid symphysis (Fig. 2a). They are, therefore, arcifero-firmisternal as in the case of *Sminthillus* (Noble, 1922). It is difficult, however, even with the highest binocular powers to be sure of the exact point at which the coracoid cartilages are fused. I have, therefore, resorted to sections to determine this question. As shown in figures the coracoid cartilages of both *moreiræ* and *stelzneri* overlap, but in the first, the overlap is greater than in the second and the connective tissue is far less abundant. Thus, functionally, *moreiræ* is more arciferal than *stelzneri*. Tracing forward the series of sections it is found that an actual fusion of the cartilages occurs in *moreiræ* before reaching the procoracoid region. This is at level *a* in Fig. 2a. In *stelzneri*, the exact point of fusion is slightly more posterior than that of *moreiræ*. *Oreophrynella*, which I have studied only as a cleared specimen, seems to have its point of fusion at the same-level as *moreiræ*.

*Dendrophryniscus brevipollicatus* seemed on dissection to be entirely arciferal, but when sections of its pectoral girdle were cut, it was found that its coracoid cartilages were fused in the procoracoid region (level *c* in Fig. 2a). In Fig. 3a I have shown the first (most posterior) point of

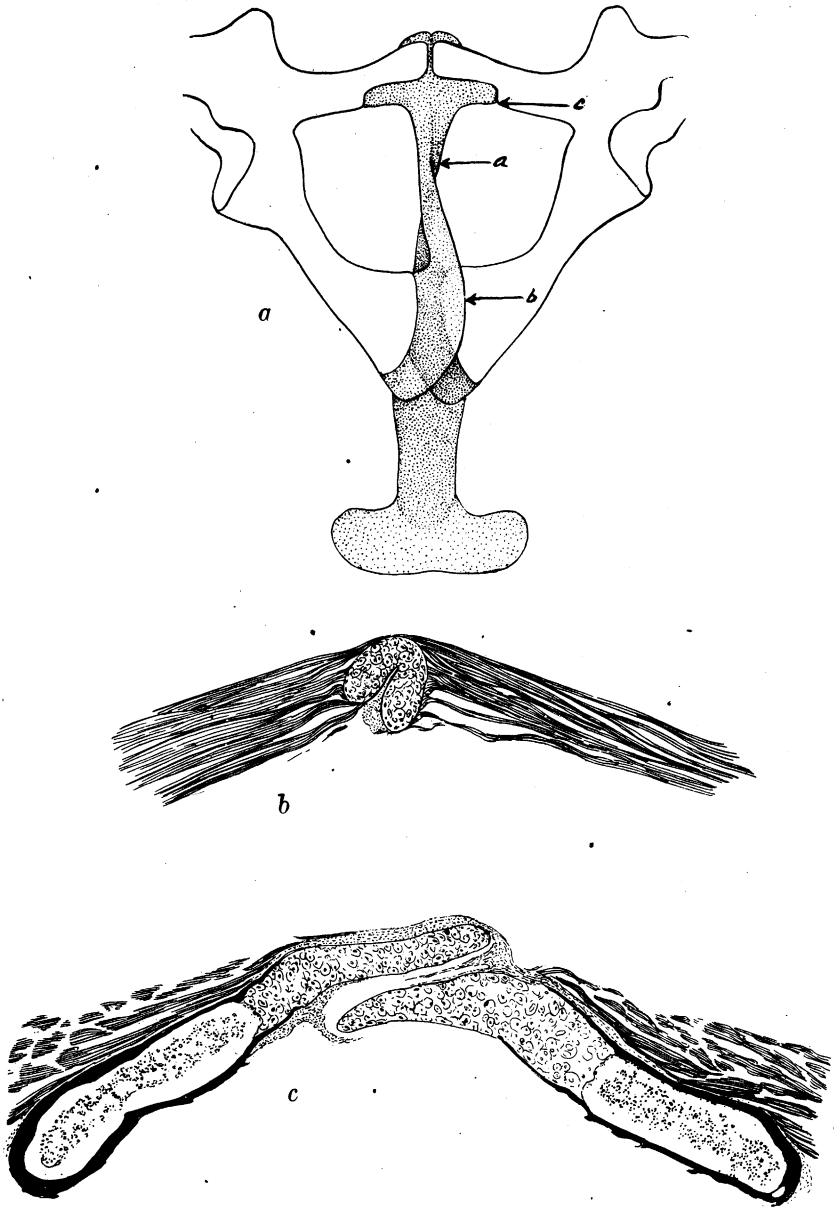


Fig. 2. Pectoral girdle of *Atelopus moreiræ* Miranda Ribeiro.

- a. Viewed from ventral surface.  
 b. Transverse section, level a.  $\times 66$ .  
 c. Transverse section, level b  $\times 66$ .  
 Schema of the sections as in Fig. 1.

fusion of the coracoid cartilages. From the amount of procoracoid cartilage present in this section as compared with a section at the fusion point of *moreiræ* (Fig. 2b), it is clear that the point lies farther anteriorly. The cartilages in the coracoid region (level b, Fig. 2a) do not overlap greatly and they are only loosely bound together by connective tissue (Fig. 3b). The pectoral girdle of *D. brevipollicatus* has advanced beyond the arciferal condition only in a partial fusion of the coracoid cartilages in

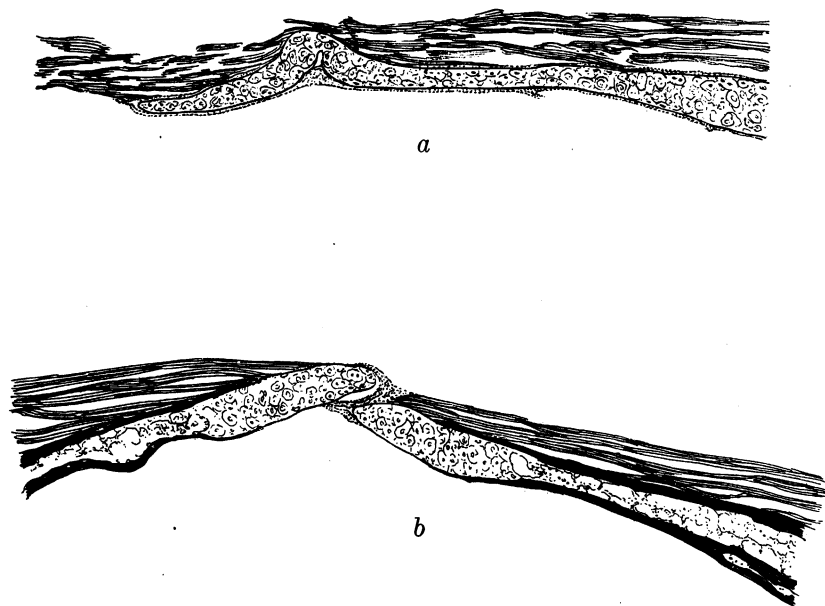


Fig. 3. Sections transverse to the body axis of the pectoral girdle of *Dendrophryniscus brevipollicatus* Espada.  $\times 91$ .

a. At level c of Fig. 2a, the most posterior point of fusion of the coracoid cartilages in this species.

b. At level b of same.

Schema as in Fig. 1.

the procoracoid region and in their tendency to barely overlap in their more posterior portions.

It would seem from these observations that there existed in eastern South America a group of brachycephalid frogs agreeing in their small size, dark and warty appearance, and in their arcifero-firmisternal girdle. *Oreophrynella* is the most specialized of this group. Not only are its feet short and broadly expanded, but its vertebral column is peculiar for its remarkable shortness. The sacrum consists of a fusion of three vertebræ

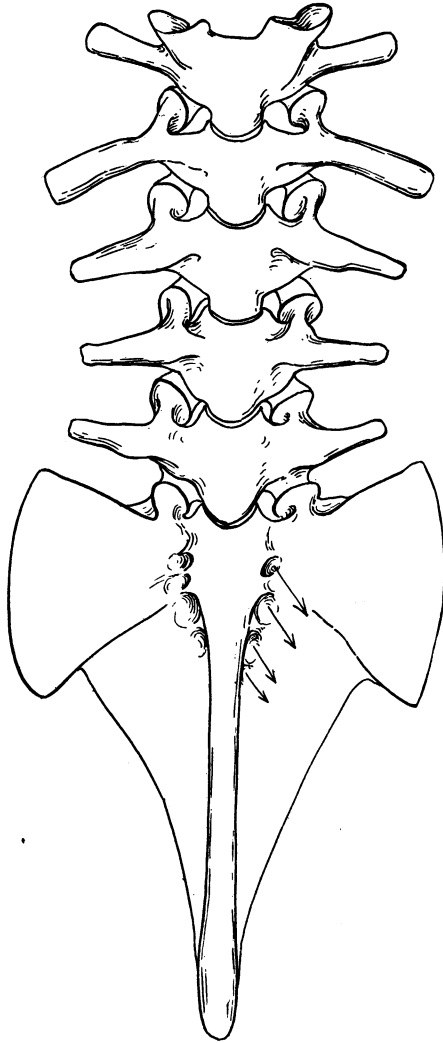


Fig. 4. Vertebral column of *Oreophrynella quelchii* Boulenger, showing the fusion of vertebrae I+II and of VII+VIII+IX+coccyx. Ventral aspect.

in addition to the coccyx (Fig. 4). Only five presacral vertebræ occur, but the first represents a fusion of two as in various other brachycephalids (Noble, 1922). *Stelzneri* and *moreiræ* are very closely allied. The most distinctive osteological feature of these two species is their complete fusion of clavicle and coracoid (Fig. 2a). These species cannot be referred to *Bufo* because their pectoral girdles are partly firmisternal. If relegated to *Atelopus*, the limits of this genus would have to be extended. This, in turn, would obscure the fact that the northern and western species represent a group distinct from the southern and eastern. There is, therefore, only one of two things to do, either to reinstate and redefine the genus *Dendrophryniscus* in order that it may include them or to establish a new genus for them. The latter course seems to me unwise in view of the great probabilities that Espada was mistaken in the form of the sacrum in the specimens before him. I, therefore, redefine *Dendrophryniscus* as a group of brachycephalid frogs differing from *Atelopus* only in the partially arciferal pectoral girdle. This genus would include, beside the type *brevipollicatus*, the well-known *stelzneri* and related species. Of the latter, I have studied only *moreiræ* and hence only this additional species can be added at this time to the list.

The brachycephalid frogs include at least three distinct groups of genera which seem to have arisen independently from bufonid ancestors. As all three, however, arose in the same general region and from the same family, I consider them a natural group. Such a procedure is in conformity with palæontological practice (Abel, 1909). The first group includes the genera just discussed. *Dendrophryniscus*, an arcifero-firmisternal stock, gave rise to partially firmisternal *Oreophrynella* and to the completely firmisternal *Brachycephalus* and *Atelopus*. Judged from osteological characters alone, it would seem that the arciferal ancestor of this group must have been closely allied to *Bufo*. But the latter genus is a recent arrival in South America and hence not a likely ancestor of such a widely dispersed and diversified group. The immediate ancestors of the group have very probably been lost.

The second group of brachycephalid frogs may be clearly traced to their bufonid ancestors. This group includes only *Hyloxalus*, *Phyllobates*, and *Dendrobates*. These genera are characterized by a pair of so-called leathery scutes on the upper surface of each digit tip. As a matter of fact, the epidermis of this region is not more cornified or stratified than elsewhere on the digits. The pad formation is due to a local thinning of the epidermis around the edges of the region and in the midline. The functional significance of the scute-like structures is unknown. The

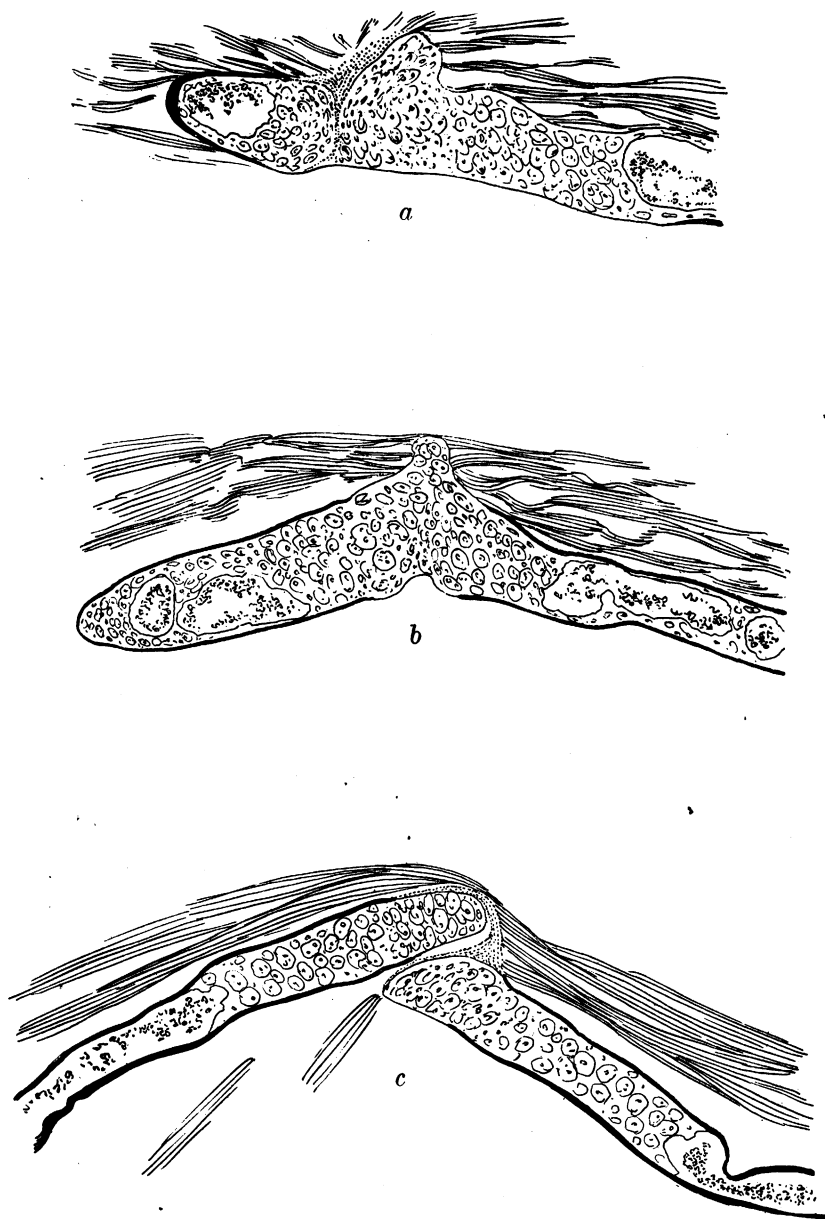


Fig. 5. Section of the coracoid cartilages of *Phyllobates subpunctatus* (Cope), transverse to the body axis.

- a. Adult, at level a of Fig. 2a, showing the incomplete fusion of the cartilages.  $\times 83$ .
- b. Adult, at the level of the coracoids (Fig. 2a level b).  $\times 83$ .
- c. Immature at the same level as b, showing the arciferous condition of the coracoids.  $\times 114$ . Schema as in Fig. 1.



immediate ancestor of this group is the bufonid *Crossodactylus* which possesses the same digital scutes. Its pectoral girdle shows an approach towards the firmisternal condition in the great reduction and slight overlap of the coracoid cartilages. *Crossodactylus* gave rise to *Hyloxalus* by merely a fusion of the coracoid cartilages. The change is only slightly greater than that which took place in the evolution of *Atelopus* from *Dendrophryniscus*. *Hyloxalus* gave rise to *Phyllobates* by a reduction of its digital webs. The latter genus evolved and is evolving directly into *Dendrobates* by a loss of its maxillary teeth. Today certain pairs of species, such as *Phyllobates inguinalis* and *Dendrobates braccatus* live side by side and seem more closely allied to one another than either species is to any other in its own genus.

The origin of the third group may be as readily recognized as that of the second. The bufonid *Syrrhophus* (or its close relative, *Eleutherodactylus*) gave rise to *Sminthillus* merely by a partial fusion of the pectoral girdle (Noble, 1922, 1925). Too little is known about the remaining genera in the family. But it seems hardly likely that *Rhinoderma* and *Geobatrachus* could have both originated from the third group with which they agree most closely structurally.

The chief point to be gathered from this hasty outline of the evolution of the Brachycephalidæ is that no group arose suddenly fully firmisternal from typically arciferal ancestors. Each group still possesses forms which are more or less intermediate. The intermediates of the first group are referable to the genus *Dendrophryniscus*, of the last to *Sminthillus*. Only the second group of genera does not show typical arcifero-firmisternal intermediates. It seemed to me possible that this discrepancy was more apparent than real and I have referred again to the microtome for exact information on the conditions in this group.

*Hyloxalus* is not represented in the collections of the American Museum by a large series. I have, however, studied the pectoral girdles of the other genera: *Crossodactylus*, *Phyllobates* and *Dendrobates*. *Crossodactylus* is completely arciferal. A recently metamorphosed specimen of *Phyllobates subpunctatus* is the same (Fig. 5c). Sexually mature specimens of the latter species are firmisternal in the coracoid region but show a trace of their youthful arciferal condition in the procoracoid region (Fig. 5a). *P. subpunctatus* normally passes through an arciferal, an arcifero-firmisternal, and a firmisternal condition in the course of its ontogeny. One difference, however, between the pectoral girdle of this form and that of their bufonid progenitors appears. In both juvenile and adult individuals, the sternal cartilage is fused to the coracoid

cartilages. No sternal leaves wedge the anterior end of the sternum between the coracoid cartilages as in the salamanders, the discoglossids and the other primitive frogs. It is possible that at still earlier stages vestiges of such leaves may occur but they are not present in my sections.

In the pectoral girdle of an adult *Dendrobates tinctorius* there is no suggestion of an arciferal condition in any of the sections. The sternum

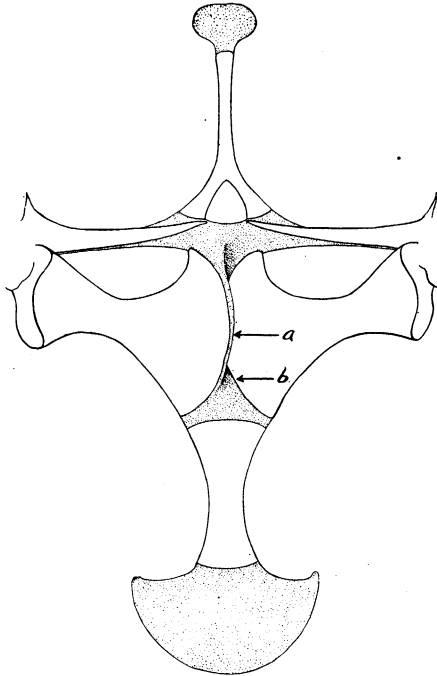


Fig. 6. Pectoral girdle of *Rana rugulosa* Wiegmann, viewed from the dorsal (cardiac) side. Adult female.

and coracoid cartilages are fused as in *Phyllobates*. It would be interesting to know if the recently metamorphosed *Dendrobates* is arciferal as in the case of *Phyllobates*.

It seemed at first glance that this arciferal stage in the ontogeny of these brachycephalids was further evidence of their non-relationship to the ranids (with which they were formerly confused) for de Villiers (1924) has recently declared that no ranid passes through such a stage in its ontogeny. I have examined several stages in the metamorphosis of the

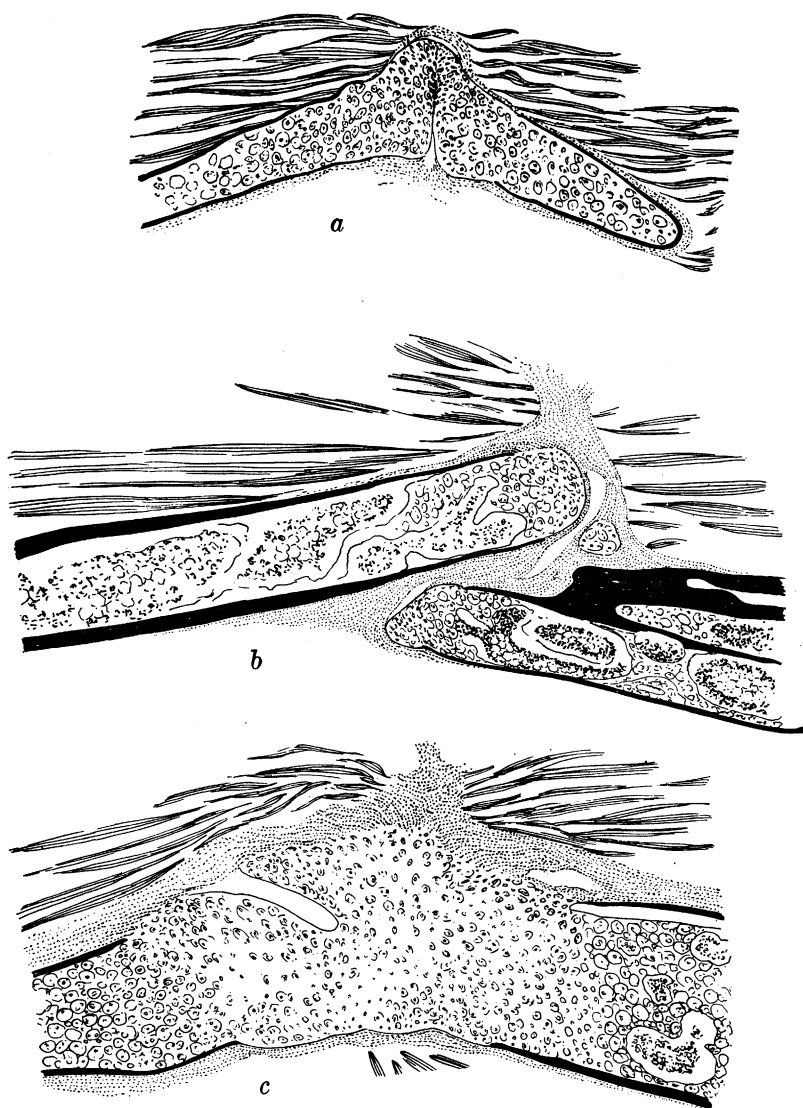


Fig. 7. Sections transverse to the body of the axis of the coracoid region of two diplasiocœlous frogs.

a. *Rhacophorus leucomystax* (Kuhl), metamorphosing larva, showing early fusion of the coracoid cartilages.  $\times 114$ .

b. *Rana rugulosa* Wiegmann, adult female, level a, Fig. 6, showing the freedom of the coracoids.  $\times 34$ .

c. Same, level b. At this point, both sternum and coracoid cartilages are fused.  $\times 34$ .

pectoral girdle of *Rana clamitans* and can confirm the statement that the two coracoid cartilages come together edge to edge and fuse without overlapping. I have also made a selection of other diplasiocœlous tadpoles and have observed similar conditions. In *Rhacophorus leucomystax* (Fig. 7a), *Philautus vittatus*, and *Microhyla pulchra* the coracoid cartilages meet edge to edge. The fusion process begins along the most ventral surface (Fig. 7a). The cartilage cells seem to migrate across the bridge of dense connective tissue cells which bind the two halves of the pectoral girdle together. This condition is readily seen in my sections of *Rhacophorus* (Fig. 7a). It may be assumed to be the typical mode of pectoral girdle fusion in the Diplasiocœla. In the Brachycephalidæ, also, the fusion occurs edge to edge, never by a juxtaposition of the flat surfaces of the coracoid cartilages, even though at certain ontogenetic and phylogenetic stages there may be a broad overlap of these cartilages. This seems to be an important feature and it raises the question of whether the first stage in the fusion of the cartilages may not always be a retreat of their borders in such a way that the edges are in a position to meet. If overlapping cartilages are unable to fuse may not one of the primary causes of arcifery in the primitive frogs be the great extent of these cartilages? Whether or not this is true it remains that the pectoral girdle of the Diplasiocœla normally do not overlap but fuse, while those of the primitive families of frogs overlap and do not fuse. If any diplasiocœlous form had coracoid cartilages which normally overlapped during ontogeny we should not, according to this theory, expect them to fuse completely.

In examining the various Diplasiocœla in the American Museum, I have found one species which immediately before metamorphosis, and for some time after this period, normally possesses a fully arciferal pectoral girdle. This species is the common Chinese frog, *Rana rugulosa* (Fig. 6). As if in direct support of the hypothesis, the coracoid cartilages, even in the fully adult female, never fuse except at their anterior and posterior ends where the two cartilages meet edge to edge. This girdle is not arciferal for the cartilages of either side are firmly fused in the midline immediately before the sternum (Fig. 7c). Just anterior to this point the cartilages are free and broadly overlapping (Fig. 7b). They are fused again in the procoracoid region. Thus *R. rugulosa* escapes being an arciferal frog only in that its coracoid cartilages are fused at both the extreme anterior and posterior ends. Adult specimens of the related *Rana tigerina tigerina* have the pectoral girdle exactly like *rugulosa*, as I have determined by dissection. The related *Rana occipitalis* of Africa, however, has only a small portion of the cartilages free. All of the procoracoid region in this form seems to be fused.

The discovery of a series of true frogs (*Rana*) tending apparently towards reverting to the arciferal condition is a very disturbing fact, for it raises the question: may not some arciferal forms have arisen from firmisternal ancestors? Fortunately, there are other checks on the phylogenetic position of the arciferal frogs besides the condition of their shoulder girdles. Perhaps the most important of these are found in the vertebral column and in the musculature (Noble, 1922). It has been my privilege to study at first hand the majority of the genera of frogs. In no case, to judge from the total number of available characters, is it probable that an arciferal form has descended from a firmisternal stock. However, it is clear from the above observations, and especially those on the Brachycephalidæ, that there are various degrees of the arciferal and firmisternal conditions. It follows that de Villiers' (1924) conclusions on the relationship of *Xenopus* based exclusively on the form of its pectoral girdle are not well founded. *Xenopus* is a pipid frog more closely allied to the Discoglossidæ than to any other family (Noble, 1922).

In conclusion, I may summarize the above observations briefly:

(1) *Dendrophryniscus* embraces a group of brachycephalid frogs differing from *Atelopus* in the arcifero-firmisternal pectoral girdle;

(2) The genus includes *brevipollicatus*, *stelzneri*, *moreiræ*, and related forms;

(3) There are three main groups of brachycephalid frogs, each having arisen independently from bufonid ancestors;

(4) The most primitive genus in each group possesses a pectoral girdle intermediate between an arciferal and firmisternal type, while the most advanced genus in each group is fully firmisternal;

(5) The fusion of the coracoid cartilages of each side always takes place edge to edge. The first stage in the change from the arciferal to firmisternal type is a reduction of the coracoid cartilages and an approach of their edges;

(6) Most Diplasiocœla are never arciferal at any stage of ontogeny, for the coracoid cartilages never overlap but fuse as they approach one another;

(7) The fusion always begins along the ventral mesial edges of the coracoid cartilages, the cartilage cells apparently migrating out into the dense connective tissue sheath of their ventral surfaces;

(8) *Rana rugulosa* is fully arciferal for some time after metamorphosis. When adult, the coracoid cartilages are fused only at their extreme anterior and posterior ends; the greater part of the coracoid cartilages are free and overlapping throughout life;

(9) The adult *Rana tigerina tigerina* appears identical to *rugulosa* in this regard. The related *Rana occipitalis* has the coracoid cartilages free in the coracoid region but fused immediately anterior and posterior to this region;

(10) There is no sharp distinction between an arciferal and a firmisternal pectoral girdle for one merges gradually into the other. No fully arciferal type, however, has arisen from a firmisternal ancestor.

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