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An Anatomical Study of a Neotropical Tree Frog, *Centrolene prosoblepon* (Salientia: Centrolenidae)

BY

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ABSTRACT: The osteology and major features of the myology of *Centrolene prosoblepon* are described, and the position of the Centrolenidae is considered. The family appears to be an offshoot from a Neotropical group of *Hyla* in which the following characters are present: dorsal color green; forearm relatively large, especially in male; eyes large and directed about 45° forward; bones green; femur with a low posterior crest. To these features the following, distinctive of Centrolenidae, are added as specializations: fusion of tibiale and fibulare into one bone; a basal pad on the palm; T-shaped terminal phalanges (the latter independently of their occurrence elsewhere among frogs.)

INTRODUCTION

The family Centrolenidae was proposed by Taylor (1951) for a group of small Neotropical tree frogs in which the tibiale and fibulare (astragalus and calcaneum) are fused into a single bone. Usually the terminal phalanges are T-shaped, and the palm has a basal pad. In these features the family differs from Hylidae, but it resembles the latter in other respects: intercalary cartilage between terminal and penultimate phalanges; procoelous vertebral column with double condyle on sacrum, dilated sacral diapophyses; arciferal pectoral girdle. Many of the species of Centrolenidae so far known are Costa Rican (Taylor, 1952), but the family extends from Mexico to southern Brazil (Taylor and Cochran, 1953).

The general appearance of frogs in this family is shown by Fig. 1, the photograph of a male and female of *Centrolene prosoblepon*. In life they are green to cream-color dorsally, yellowish or whitish ventrally, but in alcohol the dorsal pigment becomes lavender or pink; the same is true of certain Hylidae (*Agalychnis*, *Phyllomedusa*, and a few species of *Hyla*, as *H. alleei*). In both sexes, but most

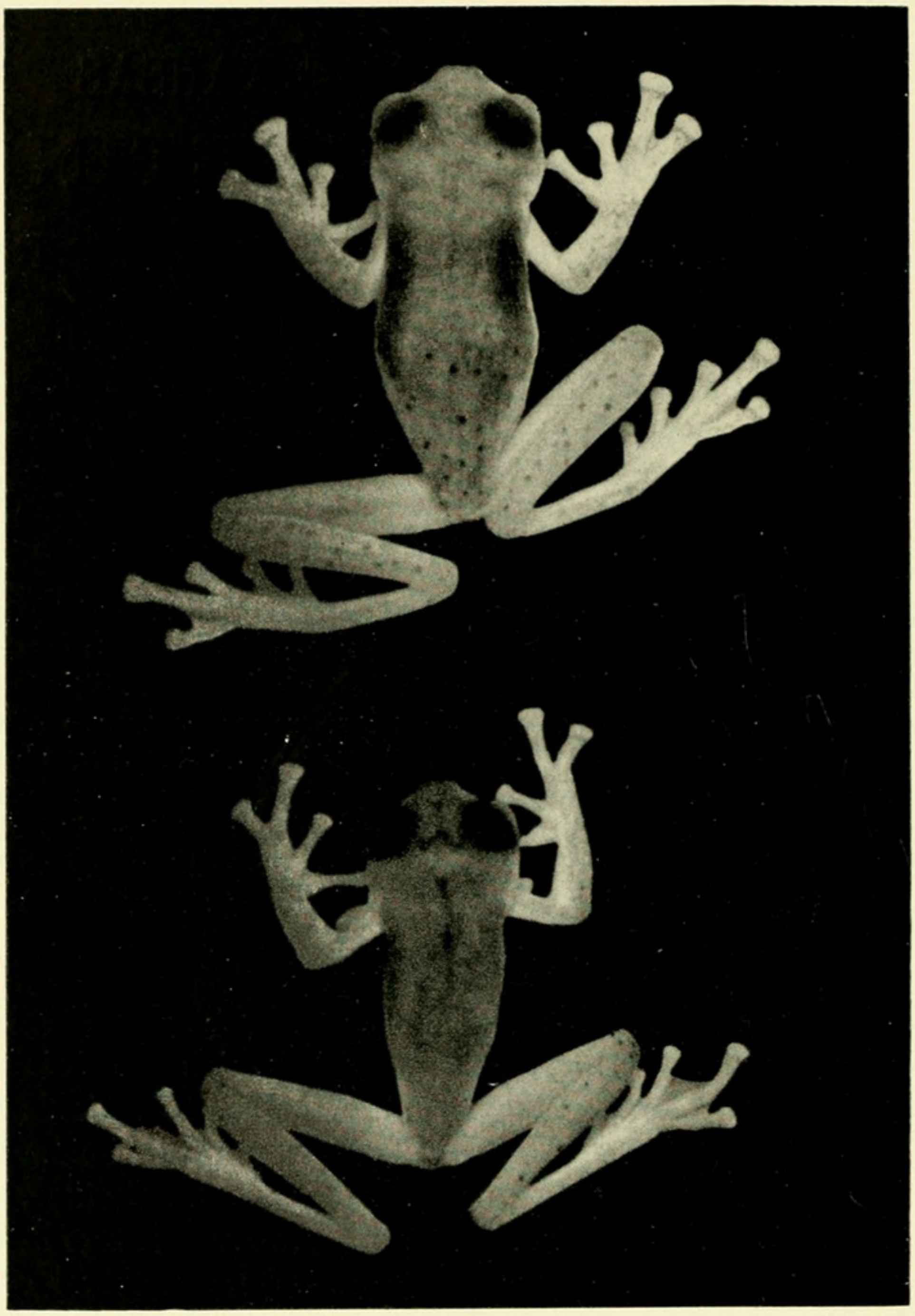


FIG. 1. Male (below) and female (above). This and all following figures are of *Centrolene prosoblepon* (Boettger). Photograph by courtesy of Professor E. H. Taylor.

obviously in the male, the forearm is massive as compared with the slim upper arm, and in preserved specimens it is difficult to force extension of the elbow without breaking the arm; this peculiarity is seen likewise in the above-mentioned Hylids. A striking feature of the Centrolenids is the nearly transparent skin, through which one may see muscles, nerves, parts of the skull, and even the brain. The bones are often green. (See Fig. 2 for details of dorsal and ventral surfaces.)

Three genera are recognized. *Centrolene,* normally with vomerine teeth, is peculiar in having a hooklike spine on the lateral face of the humerus in the males (as does the Australian *Hyla humeralis*). *C. prosoblepon* (Boettger) is the only species in Costa Rica. The males of *Teratohyla* (one species, *spinosa*) have a sharp spine on the prepollex; this may or may not project through the skin. Vomerine teeth are present but very small in *Teratohyla.* Of the Costa Rican species of *Cochranella, granulosa, albomaculata* and *pulverata* have vomerine teeth and about as much pigmentation as *Centrolene.* The remaining species, lacking vomerine teeth, tend also to reduce their pigmentation. The tympanum is still readily visible in *C. valerioi, talamancae* and *colymbiphyllum,* but is reduced and largely concealed under the skin in *chrysops* and *fleischmanni.* Evidently, then, the major group is the genus *Cochranella,* from which *Teratohyla* differs in possessing the prepollical spine, and *Centrolene* in having a humeral spine, both of these being specializations of the male.

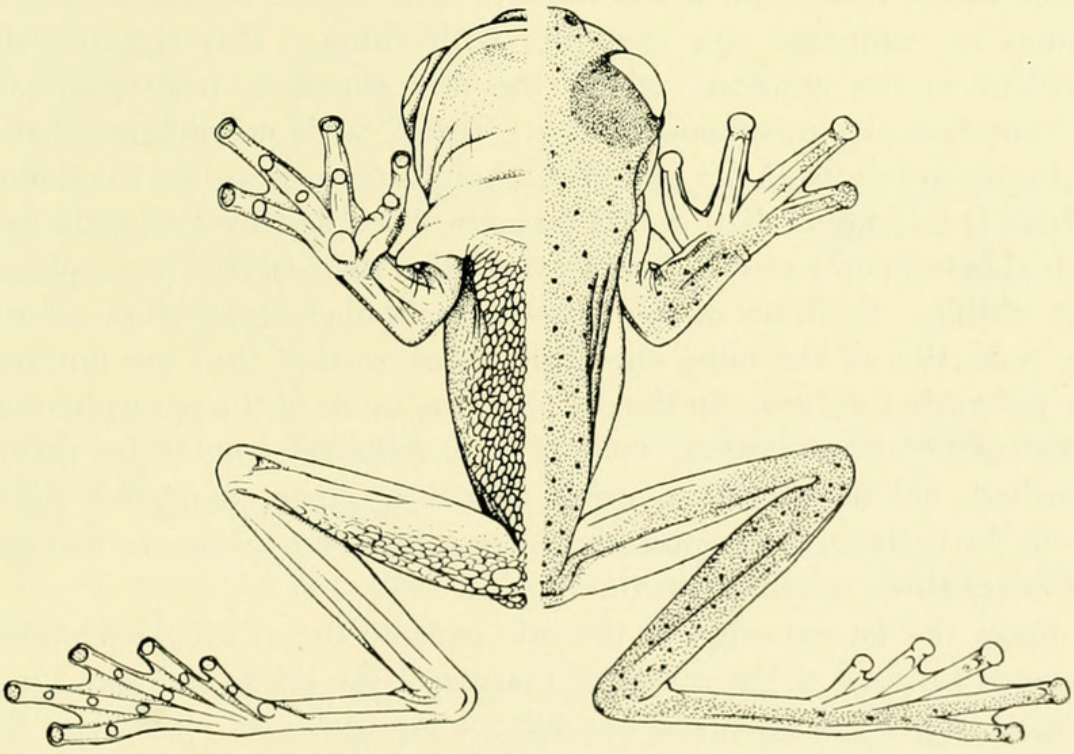


FIG. 2. Details of ventral (left) and dorsal (right) surfaces of male, K. U. catalog No. 11202. × 2.

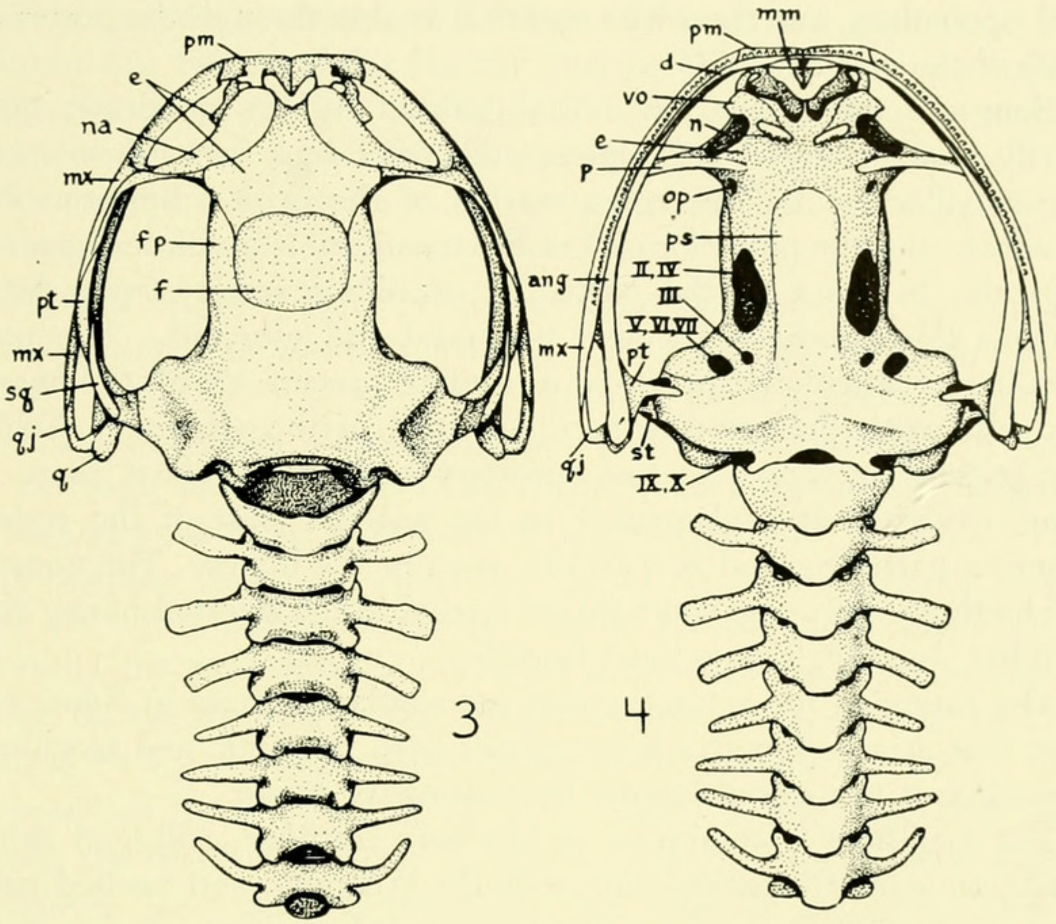
ACKNOWLEDGMENTS

To Professor Edward H. Taylor I am indebted for the opportunity to study these remarkable little frogs, including examination of all the species named above as well as certain others not yet published; also for information regarding their habits and appearance in life, and for the use of the photograph, Fig. 1. With his permission and that of John M. Legler, curator of the herpetological collections at Kansas University, I have dissected a male and female of *Centrolene prosoblepon* and examined skeletons of this and numerous species of Central American Hylidae. (Data on the dissected specimens are as follows: Male, catalog No. 37016, coll. by E. H. Taylor, Cinchona, Heredia Prov., Costa Rica, July 12, 1954. Female, catalog No. 32385, coll. by E. H. Taylor, near Pacayas, Costa Rica, July 2, 1952.) I wish to thank Professor E. Raymond Hall for use of the facilities of the Natural History Museum while I was Visiting Professor at Kansas University during the summer of 1957.

OSTEOLOGY

Skull (Figs. 3, 4). In correlation with the diminutive size of *Centrolene prosoblepon* (male snout-vent length 24.7 mm.), its skull shows reduction in the number and degree of ossification of bones as compared, for example, with *Rana*. This is especially evident in the cranium, where the otic capsules, frontoparietals, occipitals and parasphenoid all are fused, with no distinguishable sutures, and parts of the otic and ethmoid regions are cartilaginous. There is a large median dorsal fenestra, occupied by a slightly flexible sheet of connective tissue; through this the cerebral hemispheres are visible. Positions of the three semicircular canals show clearly by reduction of the bone enclosing them, so that they are outlined by protruding ridges. In the dry skull the limits of the parasphenoid, frontoparietals, palatines, vomers and ethmoid cannot be distinguished, but in dissection, using Clorox to clear connective tissue from the surface, it was possible to see some faint sutures or margins of ossification, as shown in the figures.

From the lateral edge of the otic capsule the slender squamosal extends forward to the posterior margin of the orbit, and also sends a narrow process down on the side of the quadrate. Between the squamosal and the ossified portion of the otic capsule is a zone of cartilage, not evident in the dry skull. The stapes, ossified superficially, lies just ventral to the rim of this cartilage on its posterior side, and is quite firmly fixed in the fenestra ovalis. The distal end



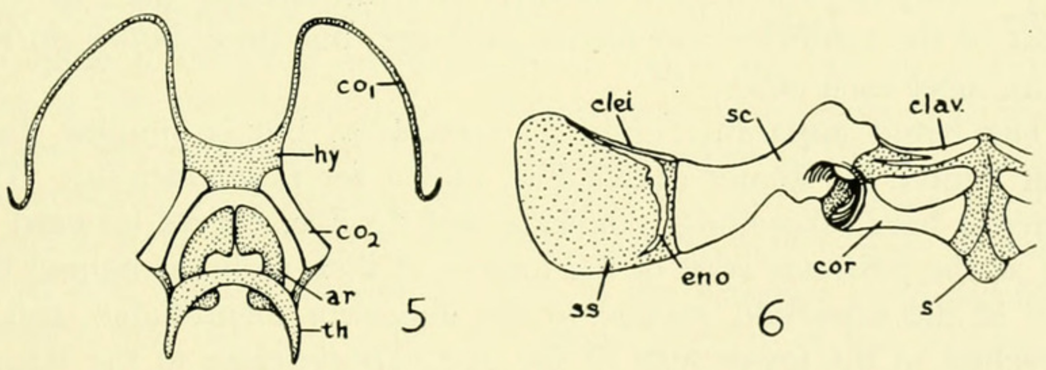


FIG. 3. Skull and first eight vertebrae of male, skeleton No. 41054, dorsal aspect, × 10.

FIG. 4. Same, ventral aspect.

FIG. 5. Hyoid apparatus of male, No. 11202, ventral aspect, × 10.

FIG. 6. Right half of pectoral girdle, shown as flattened, male, No. 11202, ventral aspect, × 10.

of the stapes reaches the dorsal margin of the tympanum rather than the center, and it seems doubtful that this bone can have much value in sound transmission. It may be on the way toward a degeneration which is reflected in the concealment of the tympanum under the skin in some species of *Cochranella*. The tympanic ring is weak and comes off with the skin in dissection. There is an ossified operculum, and the white otolith is visible through the posterior wall of the otic capsule.

Bones of the upper jaw are supported by the quadrate, only partly ossified, and by the pterygoid, extending forward to meet the maxillary along the lower margin of the orbit. Between the quadrate and the posterior end of the maxillary is a slender quadratojugal. In front of the orbit the maxillary sends a preorbital process dorsomedially to meet the nasal and ethmoid. The premaxillaries articulate by narrow ascending processes with the nasals and also with the delicate cartilage rims of the ethmoid. Teeth are present as shown in the maxillary and premaxillary; there is some evidence of replacement in the anterior part of the series, where a partial second row can be seen in the bones. The vomerine teeth are borne on short ridges medial to the internal nares, and number three or four in each fascicle.

The foramina for cranial nerves are similar to those in *Rana*, except that a large fenestra incorporates both the optic and trochlear foramina; it is covered largely by connective tissue.

The mandible is composed of Meckel's cartilage, enlarged proximally to make the articulation with the quadrate, and ossified only near the symphysis, as a small mentomeckelian bone. A thin dentary covers the cartilage anteriorly, and the angular does so over most of the posterior and medial surfaces, but these bones do not quite meet each other.

The hyoid apparatus (Fig. 5) resembles, but is simpler than, that figured by Romer (1955, Fig. 143C) for *Leptodactylus*. The anterior horn, exceedingly delicate and flexible, curves forward as far as the posterior edge of the tongue; it then recurves behind the end of the mandible, medial to the depressor mandibulae, and is attached to the lower wall of the otic capsule close to the stapes. The body of the hyoid is a thin cartilage plate receiving the posterior ends of muscle strands from the tongue. On its posterior corners are the two bony horns (first branchials). The arytenoid cartilages enclose the larynx on each side, meeting ventrally. The thyroid cartilage is a thin, delicate ventral arch ending laterally in two fairly firm horns attached to the pericardium. There is no cricoid cartilage. (In *Leptodactylus*, as cited above, a cricoid is present and the body of the hyoid bears two pairs of lateral processes.)

Vertebral Column (Figs. 3, 4, 7, 8). Little needs to be added to the details figured. There are no neural spines, and the atlas lacks transverse processes. The centra (Fig. 4) are procoelous, the sacrum has two condyles for the coccyx (Fig. 8), and the sacral diapophyses are slightly dilated. In these points and in the particular form and position of the transverse processes the Centrolenid frogs are precisely like the smaller species of *Hyla*. The figures of the pelvis (Figs. 7, 8) are self-explanatory.

Pectoral Girdle (Fig. 6). In this figure the cartilage is stippled. The sternum is a thin, fragile sheet. The cartilaginous medial ends of the coracoids overlap in the usual arciferal manner except at their anterior ends, where they fuse between the clavicles. A zone of cartilage intervenes between the ossified coracoid and scapula at the glenoid fossa, and there is a small glenoid foramen. The suprascapula bears a splinterlike cleithrum on its anterior edge, and has also a narrow irregular zone of endochondral ossification. Dorsally the suprascapula overlaps, and is fastened by connective tissue to, the tip of the first transverse process (second vertebra). This gives the pectoral girdle rigidity in the body of the frog.

Arm and Hand (Figs. 9, 10, 11). There is little difference between the male (shown in the figures) and female, except in the humerus. This bears a prominent thin spine on its lateral face in the male, so placed that it opposes the medial face of the thumb when the forearm is flexed and the hand adducted. Presumably the spine is involved mechanically in amplexus, but no observations of this have been made. The spine is occasionally present in females, normally absent. In addition, the humerus in the male has two crests on its posterior face distally (Fig. 9), the more ventral of which is for the origin of the flexor carpi radialis muscle, and the dorsal one, slightly smaller, for that of the extensor carpi radialis. Between the two crests lies the distal portion of the anconeus. These crests are faintly or not at all indicated in the female, and the associated muscles are much smaller. It should be noted that *Centrolene* is not unlike many other frogs in regard to the crests; Ritland (1955) describes a similar condition in *Ascaphus*.

On the ventral surface of the humerus there is also a conspicuous groove for the tendon of the coracoradialis muscle (Fig. 10). This muscle, with its tendon, is one of the most constant features of both frogs and salamanders. The groove is deepest and broadest near the head of the humerus; lateral to it, at the base of the spine, is a rounded ridge for the insertion of the more superficial muscles of the pectoral group.

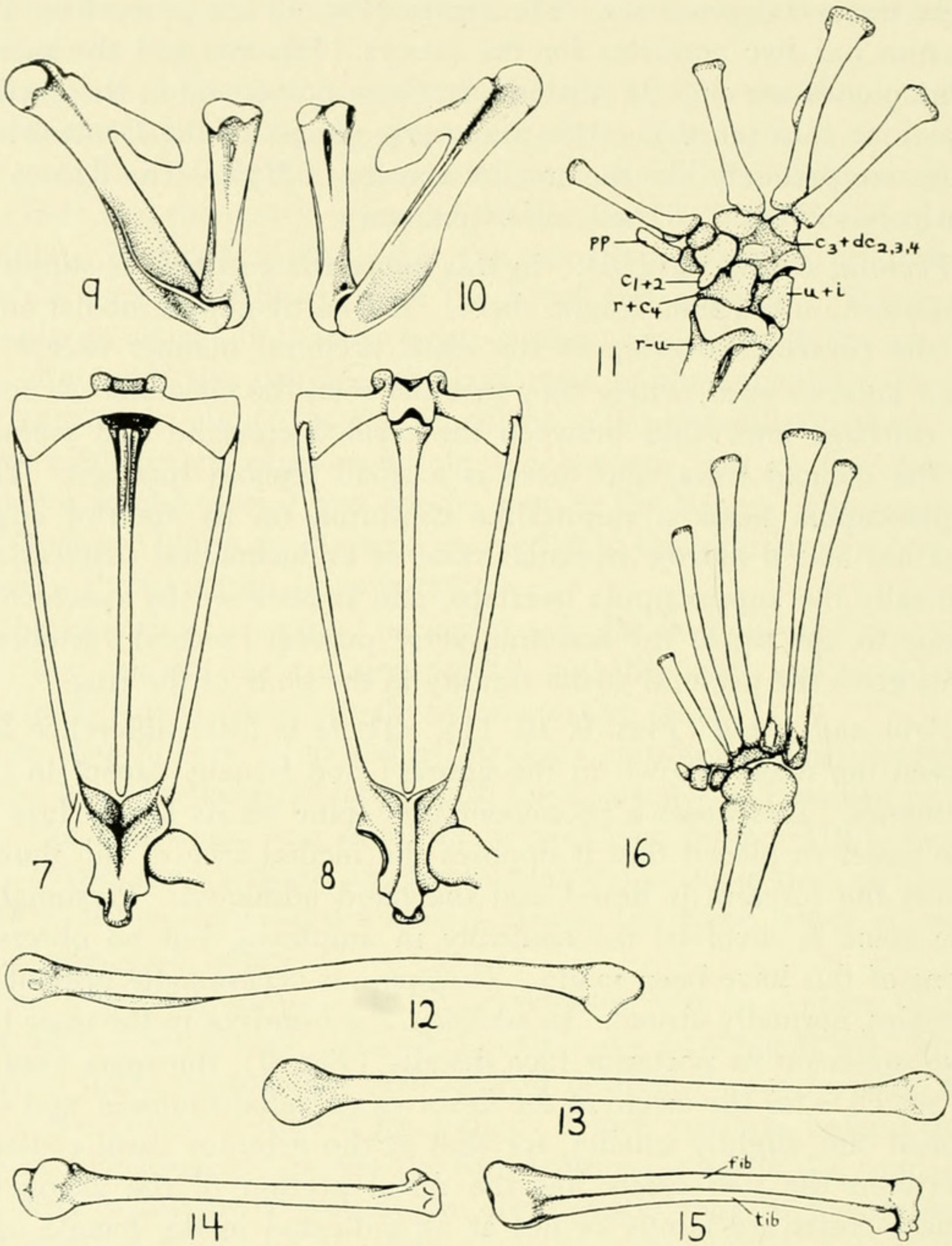


FIG. 7. Sacrum, coccyx and pelvis, male, skeleton No. 41054, dorsal aspect, × 5.

FIG. 8. Same, ventral aspect.

FIG. 9. Right humerus and radioulna, male, skeleton No. 41054, dorsal aspect, × 5.

FIG. 10. Same, ventral aspect.

FIG. 11. Right carpus, male, No. 11202, dorsal aspect, × 8.

FIG. 12. Right femur, male skeleton No. 41054, dorsal aspect, proximal end to left, posterior border down, × 5. (Figs. 13-15 are from same skeleton, same magnification.)

FIG. 13. Right tibiofibula, dorsal aspect, proximal end to left.

FIG. 14. Right tibiale-fibulare (astragalo-calcaneum), postaxial aspect, proximal end to left.

FIG. 15. Same, plantar aspect.

FIG. 16. Right tarsus, male, No. 11202, dorsal aspect, × 8.

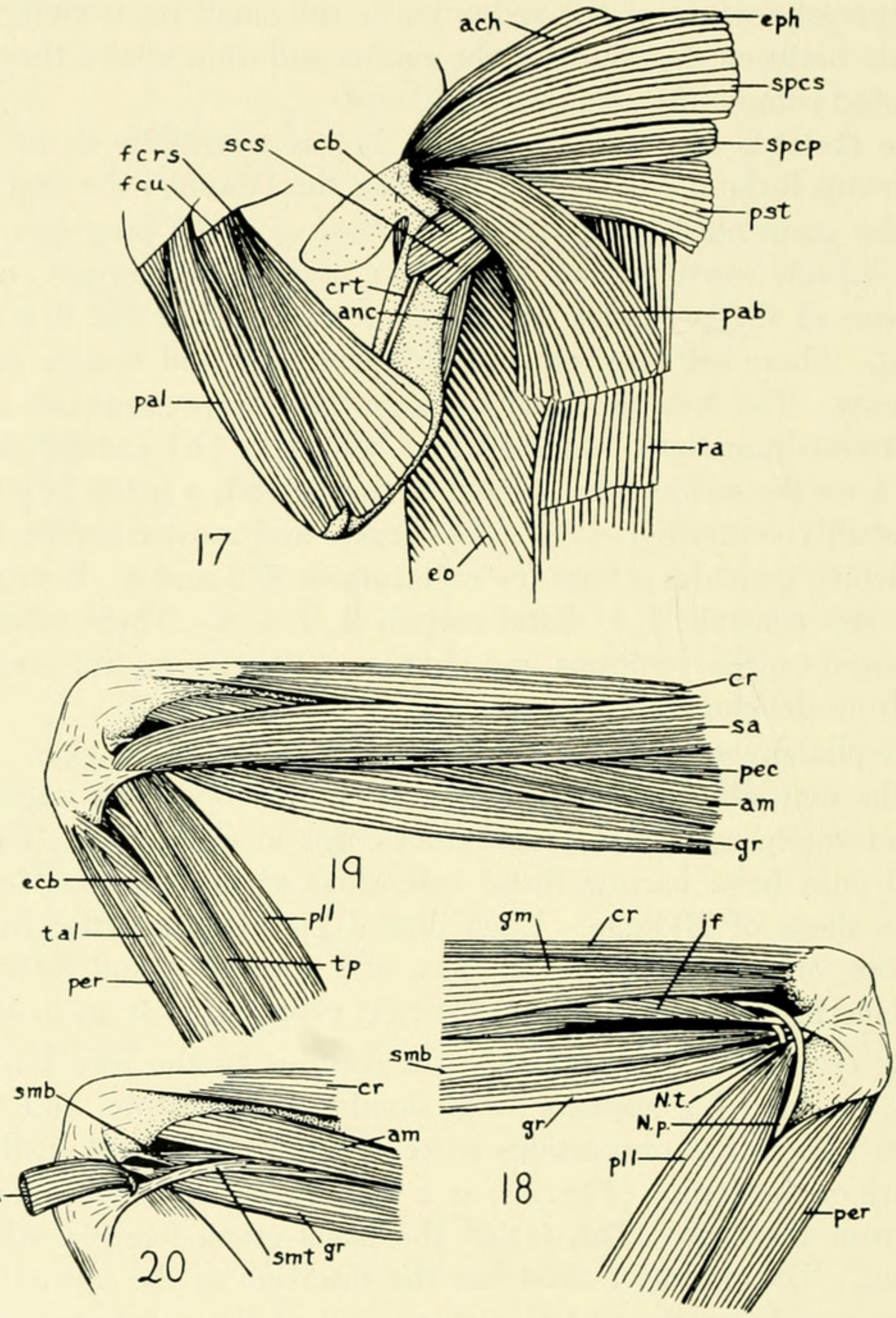
A special feature of the radioulna is the small open cleft which persists between the shafts of the radius and ulna where they have not fused completely, near the distal end.

The skeleton of the carpus (Fig. 11) is essentially as in *Rana*. Following Ritland (1955) I am calling the "thumb" the first digit, and the small bone lying against the base of it the prepollex. The only entirely cartilaginous pieces are two distal carpals, one at the base of the prepollex, the other at the base of the first metacarpal. There are four other highly irregular and mostly ossified elements. The two proximal ones probably represent (a) ulnare + intermedium fused, on the ulnar side, and (b) radiale + centrale 4, on the radial side. Distal to the latter is a piece (c) which is probably centrale 1 + 2. The largest and most complex (d) is that which provides a base for metacarpals 2, 3 and 4. It probably comprises centrale 3 + distal carpals 2, 3 + 4. These inferences are based on the positions and shapes of the pieces, but confirmation from developmental stages would be desirable.

The phalanges, not figured, number 2, 2, 3, 3 in the fingers. They, like the metacarpals, are ossified in a surface layer but apparently not internally, and have cartilaginous tips at each joint. The terminal ones have narrow distal extensions giving them a T-shape, unlike those of Hylidae. Each digital pad is supported by, and encloses, such a T-shaped phalanx, and a small round intercalary cartilage fits between that and the next proximal to it, as in Hylids.

Leg and Foot (Figs. 12-16). In contrast to the fore limb and hand the hind leg appears long, slender and delicate, and this is shown also in the proportions of the bones. The most distinctive feature of the femur (Fig. 12) is a low, thin crest on the posterior side near the base. This is not the usual crista femoris, which is lacking. The posterior crest has the insertion of the obturator externus muscle on its ventral surface, and of the quadratus femoris (more posterior) and gemellus (more anterior) on the dorsal. This crest is also present in the following small species of *Hyla*, of which I have seen skeletons: *alleei, elaeochroa, loquax, phlebodes, pseudopuma,* and *rufioculis,* all from Costa Rica, but it is lacking in a number of larger species.

The tibiofibula (Fig. 13) is nearly straight and slightly longer than the femur. The union of tibiale and fibulare into one bone (Figs. 14-16), the principal character on which the family Centrolenidae is based, might be described as a partial fusion in *Centrolene*, for the shafts are almost separate and retain their individual



Muscles of male, No. 11202, × 8.

FIG. 17. Pectoral region and arm, ventral aspect.
FIG. 18. Right knee, dorsal aspect.
FIG. 19. Right knee, ventral aspect, superficial.
FIG. 20. Same, the sartorius reflected to show tendons.

shape, while the heads are more completely fused. There remains in the tarsus proper a minute prehallux, a cartilaginous tarsal accompanying it, another tarsal also of cartilage which is associated with the first metatarsal, and a narrow crescent-shaped cartilage probably representing a fusion of tarsals 2 + 3 or 2 + 3 + 4. A ligamentum tarsi supplens is present in the position indicated by a gap in Fig. 16, but it contains no cartilage. The tips of all the metatarsals are of cartilage. The phalangeal formula in the toes is 2, 2, 3, 4, 3. Otherwise all remarks about the phalanges and digits in the hand apply also to those in the foot.

MYOLOGY

Certain portions of the muscular systems were dissected and illustrated, but time did not permit a full description of the muscles. In Fig. 17 a ventral view of the pectoral and fore limb muscles, not including the hand, shows that the humerus lacks muscles on its flexor surface, and that the only direct flexor of the forearm is the coracoradialis, acting by way of its tendon. The muscle itself is located deep on the pectoral girdle, internal to the two supracoracoidei, and covers the coracoid fenestra ventrally. Its fibers originate on the medial, cartilaginous part of the coracoid, and converge to the tendon, which then runs in its groove on the humerus and terminates at the point marked by a dot on the radio-ulna, in Fig. 10.

The greatly enlarged flexor carpi radialis superficialis and extensor carpi radialis (on dorsal aspect of forearm) are actually more important as indirect flexors of the forearm than in the functions indicated by their names, and obviously much more powerful than the coracoradialis, at least in the male. Their development is no doubt responsible for the two distal crests of the humerus already described. That this circumstance is not limited to Centrolenids and certain big-armed Hylids is shown by Ritland's (1955, p. 239) remarks on *Ascaphus* (he uses the term "antibrachial flexors" for the enlarged forearm muscles): "Mature male *Ascaphus* have tremendously enlarged forearms, primarily a result of the striking expansion of the antibrachial flexors and correlated development of broad distal wings (cristae) on the humerus for their origin. . . . The muscles of females and immature have exactly the same relative positions as those of fully grown males, but they are smaller, and since distal cristae are lacking, all originate from the humerus proper."

In the female of *Centrolene* the only differences seen in the shoulder and arm were: (1) absence of the spine and distal crests on the humerus; (2) from the ventral side, the more lateral part of the deltoid (acromiohumeralis) could be seen uninterruptedly as it went to its insertion on the shaft of the humerus; (3) the edge of the anconeus was likewise visible without interruption on its way to the proximal end of the radioulna; (4) the two "antibrachial flexors" were each no wider than the palmaris longus, although the forearm still appeared conspicuously bigger than the upper arm.

Jones (1933) gives a ventral view of the pectoral muscles of *Hyla arborea;* they are like those in the female of *Centrolene.*

Figures 18-20 are intended for comparison with Noble's (1922) illustrations of thigh muscles and their tendons in Salientia. Although he does not show any Hylids or Centrolenids, he lists 21 species of *Hyla,* 5 of *Phyllomedusa,* one each of *Agalychnis* and *Pternohyla, Centrolene geckoideum* and *Centrolenella* (now *Centrolene*) *antioquiensis,* among many others, as having the "typical bufonid tendon complex" on the ventral aspect of the knee; this is characteristic of his suborder Procoela (Bufonidae, Brachcephalidae, Hylidae, plus the recently separated Centrolenidae). The semitendinosus tendon receives on its upper edge, just before its insertion, the sartorius; the gracilis passes internally to these but at its insertion is combined with them. I have compared the thigh muscles and their tendons in *Centrolene prosoblepon* with those of *Hyla alleei* and find them so much alike that the same illustration would almost serve for both, even though among the various genera which have the "bufonid complex" there are many minor differences of detail. This, then, is to be added to the numerous features in which Centrolenidae appear directly related to *Hyla.*

CONCLUSIONS

It seems evident, in comparing the known Centrolenids with one another, that the primitive stock of this family had the following combination of characters:

(a) *Those not present in Hyla.* (1) Partial fusion of tibiale and fibulare; (2) basal pad in the palm; (3) T-shaped terminal phalanges.

(b) *Those present in some Neotropical species of Hyla.* (1) Eyes large and directed about 45° forward; (2) vomerine teeth present; (3) dorsal color green, with ample pigment, and capable of turning purplish in alcohol; (4) forearm in both sexes relatively large, with distal crests on the humerus but not a lateral spine in the male; (5) a posterior crest on the femur.

(c) *Those present in Hylidae and allied families.* (1) Procoelous vertebrae; (2) arciferal pectoral girdle; (3) characters of pectoral and thigh muscles; (4) intercalary cartilages in digits, etc.

As *Centrolene* is undoubtedly specialized in the addition of a humeral spine in the male, and *Teratohyla* in the prepollical horn, this stem-form of Centrolenidae would be a species of *Cochranella*.

The fusion of tibiale and fibulare appears to be the major specialization setting off the Centrolenids, yet it is not actually a radical change, since the two bones are easily distinguishable in *Centrolene* for most of their length. The pad on the hand and the T-shaped phalanges appear to be specializations of minor importance, occurring here independently of their development in other families. These conclusions should be qualified by the statement that the writer has not examined the anatomy of other families of arboreal frogs, such as Hyperoliidae and Rhacophoridae.

Explanation of labelling:

Roman numerals indicate foramina for cranial nerves as numbered.

ach—acromiohumeralis (deltoid)
am—adductor magnus
anc—anconeus
ang—angular
ar—arytenoid cartilage
$c_{1,2,3,4}$—centrale $_{1-4}$
cb—coracobrachialis
clav—clavicle
clei—cleithrum
$co_{1,2}$—cornua 1, 2 of hyoid
cor—coracoid
crt—coracoradialis tendon
d—dentary
$dc_{2,3,4}$—distal carpals 2-4
e—ethmoid
ecb—extensor cruris brevis
eo—external oblique
eno—endochondral ossification
eph—episternohumeralis (deltoid)
f—fenestra
fcrs—flexor carpi radialis superficialis
fcu—flexor carpi ulnaris
fib—fibulare (calcaneum)
fp—frontoparietal
gm—gluteus magnus
gr—gracilis
hy—body of hyoid
i—intermedium
if—ischioflexorius
mm—mentomeckelian bone
mx—maxillary
n—internal naris
na—nasal
N. p.—peroneal nerve
N. t.—tibial nerve
op—foramen for deep ophthalmic nerve
p—palatine
pab—pectoralis abdominalis
pal—palmaris longus
pec—pectineus
per—peroneus
pll—plantaris longus
pm—premaxillary
pp—prepollex
ps—parasphenoid
pst—pectoralis sternalis
pt—pterygoid
q—quadrate
qj—quadratojugal
r—radiale
ra—rectus abdominis
r-u—radio-ulna
s—sternum
sa—sartorius
sc—scapula
scs—subcoracoscapularis
smb—semimembranosus
smt—semitendinosus
sq—squamosal
spcp—supracoracoideus profundus
spcs—supracoracoideus superficialis
st—stapes (columella)
tal—tibialis anticus longus
th—thyroid cartilage
tib—tibiale (astragalus)
tp—tibialis posticus
u—ulnare

LITERATURE CITED

JONES, E. IDRIS

1933. Observations on the pectoral musculature of Amphibia Salientia. Ann. Mag. Nat. Hist., vol. 12, pp. 403-420, 4 figs.

NOBLE, G. K.

1922. The phylogeny of the Salientia. I. The osteology and the thigh musculature; their bearing on classification and phylogeny. Bull. Amer. Mus. Nat. Hist., vol. 46, pp. 1-87, 23 pls.

RITLAND, RICHARD M.

1955. Studies on the post-cranial morphology of *Ascaphus truei*. I. Skeleton and spinal nerves. Jour. Morph., vol. 97, pt. 1: pp. 119-174, 19 figs.

1955. Studies on the post-cranial morphology of *Ascaphus truei*. II. Myology. Jour. Morph., vol. 97, pt. 2: pp. 215-282, 10 figs.

ROMER, ALFRED S.

1955. The vertebrate body. W. B. Saunders Co., Phila. pp. i-viii, 1-644, 390 figs.

TAYLOR, EDWARD H.

1951. Two new genera and a new family of tropical frogs. Proc. Biol. Soc. Washington, vol. 64, pp. 33-40.

1952. A review of the frogs and toads of Costa Rica. Univ. Kansas Sci. Bull., vol. 35, pt. 1, no. 5, pp. 577-942, 69 figs.

TAYLOR, EDWARD H., and DORIS M. COCHRAN

1953. Frogs of the family Centrolenidae from Brasil. Univ. Kansas Sci. Bull., vol. 35, pt. 2, no. 15, pp. 1625-1656, 7 figs.