

ANURANS FROM THE EARLY
TERTIARY OF PATAGONIA

BOBB SCHAEFFER

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INTRODUCTION

THE SOUTH AMERICAN CONTINENT has thus far yielded a small number of fragmentary fossil anurans. *Teracophrys* (*nomen nudum*) was listed by Ameghino (1901) from the Upper Oligocene of Patagonia. The specimens, apparently referable to the Leptodactylidae, cannot be located in the Ameghino Collection of the Museo Argentino de Ciencias Naturales (Miss Noemí Cattoi, personal communication). *Ceratophrys prisca* has been described by Ameghino (1899) and Rovereto (1914) from the Upper Pliocene of Monte Hermoso, Argentina, and *C. ensenadensis* by Rusconi (1932) from the Pleistocene (Ensenadan) near Buenos Aires.

Both Noble (1928) and Dunn (1931) have emphasized the importance of paleontological discovery in determining the approximate times and routes of anuran dispersal. They have also pointed out the danger of assuming that the failure to discover fossil anurans belonging to particular groups is proof that such groups never existed in a given area. Dunn wisely states (*ibid.*, p. 118), "... great weight should be given to positive evidence, and very little to negative evidence." It is of course true that in the absence of fossil data certain reasonable conclusions can be drawn on the basis of the distributional pattern of the present day faunas. There is, for instance, good reason for believing that the Discoglossidae never entered North America and that the Pelobatidae did not invade South America. The pelobatids were present in North America by the Pliocene (Taylor, 1937) but apparently have migrated no farther south than Mexico.

The main taxonomic subdivisions of the Anura now generally recognized are based on the five different types of vertebral column occurring within the order (Nicholls, 1916; Noble, 1922, 1931). The smaller categories are usually defined on suites of characters involving the skull (particularly the prevomer, the presence or absence of teeth, and the middle ear), the shoulder girdle, the nature of the terminal phalanges, the tongue, the thigh musculature, the parotid gland, the presence or absence of Bidder's organ, and certain external features and proportions.

From this incomplete but representative list it is evident that relatively few characters are actually available in working out the affinities of a fossil anuran. The nature of the vertebrate column can often be determined, as well as a few skull characters, unfortunately rarely including the structure of the prevomer. By using the criteria mentioned by Noble (1930), it may be possible to postulate an arciferal or firmisternal condition for the shoulder girdle. The terminal phalanges may or may not be present. Thus the opportunity for exact identification is dependent upon the nature and completeness of preservation and on the possibility of making such identification without recourse to structures usually not fossilized.

Parker (1940) has pointed out the difficulties associated with the interpretation of fossil anuran material, and it is obvious that a conservative approach in the matter of taxonomic relationship is desirable unless a positive identification can be made, as in the case of the *Calyptocephalella* described in this paper. It might be pointed out that detailed information on the osteology of the modern anurans is widely scattered and far from complete. Herpetologists could render paleontology (and possibly themselves) a great service by making comprehensive studies available. A single fossil discovery may be of the greatest importance in working out the ramifications of anuran evolution and in determining routes of dispersal, providing a reasonably accurate identification can be made. This is too often not possible and, as a survey of the literature indicates, has led to many differences of opinion among competent students of the subject.

The present study is based on a collection of lower Eocene and Middle and Upper Oligocene anurans obtained by Dr. George Gaylord Simpson in 1930 and 1934 while on the First and Second Scarritt Patagonian Expeditions. The specimens consist of crushed and mostly dissociated skeletons embedded in very fine lacustrine or fluvial sediments.

The writer is greatly obligated to Dr. E.

R. Dunn for a number of helpful suggestions and for reading the manuscript. He is likewise indebted to Mr. K. P. Schmidt, Mr. Arthur Loveridge, Mr. C. M. Bogert, and Dr. J. A. Oliver for the loan of Recent specimens for comparative purposes. Dr. Simpson

supplied important information from his field books and from preliminary notes made on this collection. The drawings were prepared by Dorothea Kay Barlow and the photographs were taken by Elwood Logan.

SYSTEMATIC DESCRIPTIONS

FAMILY ?LEPTODACTYLIDAE

EOPHRACTUS, NEW GENUS

GENOTYPE: *Eophractus casamayorensis*, new species.

GENERIC DIAGNOSIS: An anuran of leptodactylid or possibly hylid affinities. Outer surface of known dermal bones of skull covered with deep rounded depressions which are surrounded by narrow, sharp, connecting ridges. Portion of nasal bone between orbit and nares wide; nasals in contact along mid-dorsal line. Anterior and median border of

describes the "Bird Clay" in his field notes as a "hard, massive, bright green clay with intercalated bands of white tuff." This lacustrine deposit is exposed at the south end of Cañadón Hondo near Paso Niemann, Territory of Chubut, Argentina (see locating diagram, Schaeffer, 1947). The anuran fragments were found in the white tuff.

SPECIFIC DIAGNOSIS: Same as for genus.

DESCRIPTION: These fragments, consisting of the associated elements representing the type and in addition a second partial maxillary and a single vertebra (A.M.N.H. No.

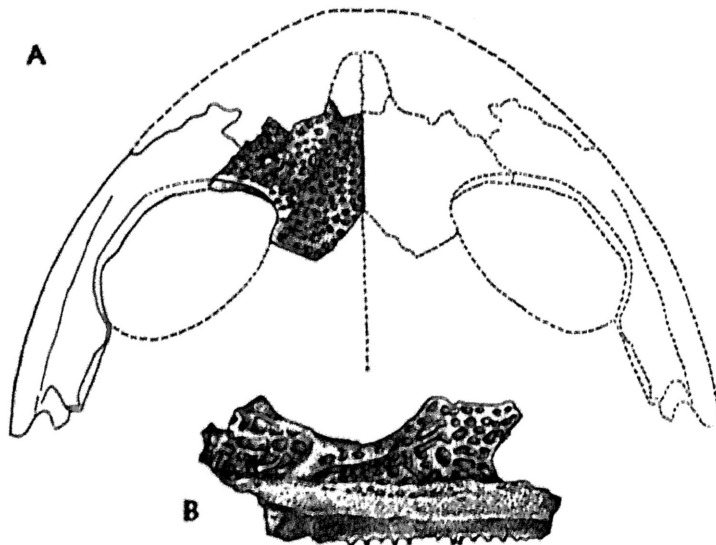


FIG. 1. *Eophractus casamayorensis*, new genus and species. A.M.N.H. No. 3165, type specimens. A. Dorsal view of isolated left nasal in articulation with associated maxillary illustrated below. Probable shape of front part of skull indicated. B. Lateral view of incomplete left maxillary. $\times 3/2$.

orbit elevated. Maxillary deep, with teeth; ascending process of maxillary robust, indicating at least partial roofing of the temporal area, and separated from thickened dentigerous portion by shallow groove. Single known vertebra procœlous, with cylindrical centrum.

Eophractus casamayorensis, new species

TYPE: A.M.N.H. No. 3165, associated left nasal and left maxillary.

HORIZON AND LOCALITY: "Bird Clay," Casamayoran Stage, Lower Eocene. Simpson

3164), represent the oldest known anuran remains from South America. The few really diagnostic characters observable indicate affinity with either the Leptodactylidae or the Hylidae. Of the six anuran families represented in South America having an entirely or partly procœlous vertebral column, the tendency towards a secondary deposition of dermal bone over the temporal area occurs only in the two just mentioned. The ascending process on the *Eophractus* maxillary is broad and high and may possibly have an articular surface for the squamosal, but this is not

certain. In any case, at least partial roofing of the temporal area is clearly indicated. The size and depth of the maxillary and the form of the ascending process are very similar to the condition in *Calyptocephalella*, the only Recent South American leptodactylid with a roofed temporal region. The Australian *Cyclorana* has a similar broad articulation between the maxillary and squamosal (Parker, 1930). Among the Neotropical Hemiphractinae there are various degrees of roofing, ranging from *Amphignathodon* with none to *Hemiphractus* in which the temporal area is completely covered.

The nature of the dermal bone sculpturing is highly variable in both the Leptodactylidae and the Hyliidae, although it does appear to be constant within a genus. The pitted ornamentation of *Eophractus* is somewhat similar to that occurring in very small subadults of *Calyptocephalella* (Reinbach, 1939) but is very different from the fully adult denticulated pattern. It agrees most closely with the sculpturing of *Amphignathodon* sp. from the Oligocene and Miocene of France (Piveteau, 1927) and *A. guentheri* from Ecuador.

The elevation of the orbital rim is characteristic of the hylids rather than the leptodactylids, as is the groove on the outer surface of the maxillary. A broad contact between the nasals occurs in various genera of both families (e.g., *Calyptocephalella*, *Hemiphractus*).

The skull of *Eophractus* was heavily ossified and in general appearance and proportions must have resembled that of *Calyptocephalella* very closely. It is thus very tempting to consider that the two genera are closely related, particularly since the Oligocene *Calyptocephalella canqueli*, to be described next, has a wide nasal bridge. There is no proof for such an assumption, however, and the true affinities of *Eophractus* must await the recovery of additional specimens.

HYPODIGM: The type and A.M.N.H. No. 3164, partial left maxillary and single precocious vertebra.

FAMILY LEPTODACTYLIDAE

CALYPTOCEPHALELLA STRAND

Calyptocephalus DUMÉRIL AND BIBRON, 1841, *Erpétologie générale*, p. 450.

Calyptocephalella STRAND, 1926, *Arch. Naturgesch.*, div. A, vol. 92, no. 8, p. 55 (new name for *Calyptocephalus* Duméril and Bibron, 1841, preoccupied).

GENOTYPE: *Calyptocephalus gayi* Duméril and Bibron.

Calyptocephalella canqueli, new species

TYPE: A.M.N.H. No. 3429, partial skeleton consisting of crushed skull, right half of pectoral girdle, right fore limb, and first three vertebrae, also isolated vertebrae and limb fragments belonging to same individual.

HORIZON AND TYPE LOCALITY: Sarmientan Group, Deseadan Stage, Lower Oligocene. Scarritt Pocket, southwest portion of Rinconada de los Lopez, west side of Sierra Canquel, central Chubut, Argentina.

SPECIFIC DIAGNOSIS: Very close to *Calyptocephalella gayi* in all observable characters, but differing from the Recent species in the greater width of the nasal bone between the orbit and the nares, the shape of the orbit in adult individuals, which is narrower in relation to length, and the shape of the posterolateral projection of the squamosal that is relatively larger and more rounded in *C. gayi*.

DESCRIPTION: The most striking similarity between the fossil and the recent species is the ornamentation of the cranial roof. Reinbach (1939) has pointed out that in subadults of *C. gayi* the surface of the dermal bones is covered with shallow depressions which are separated from one another by rather sharp and narrow ridges. With increase in age, denticles develop on the ridges which gradually encroach upon the depressions and finally obliterate them. The skull roof of *C. canqueli* is completely denticulated as is the skull of a specimen of *C. gayi* of approximately the same size.

The only preserved skull of *C. canqueli* lacks the premaxillaries, excepting for the ascending processes, and also the left maxillary. The ascending processes are relatively broad as in *C. gayi*. The denticigerous right maxillary has a more extended articulation with the nasal than the Recent species, while the contact with the squamosal is of about the same length. As pointed out above, the nasal bridge between the orbits and the nares is wider in the fossil form, a character as-

sociated with the longer naso-maxillary articulation. A logarithmic plotting of the length of the nasal along the middorsal line to the

The shape of the orbit in *C. canqueli* and in *C. gayi* is related to the length of the contact between the frontoparietal and the

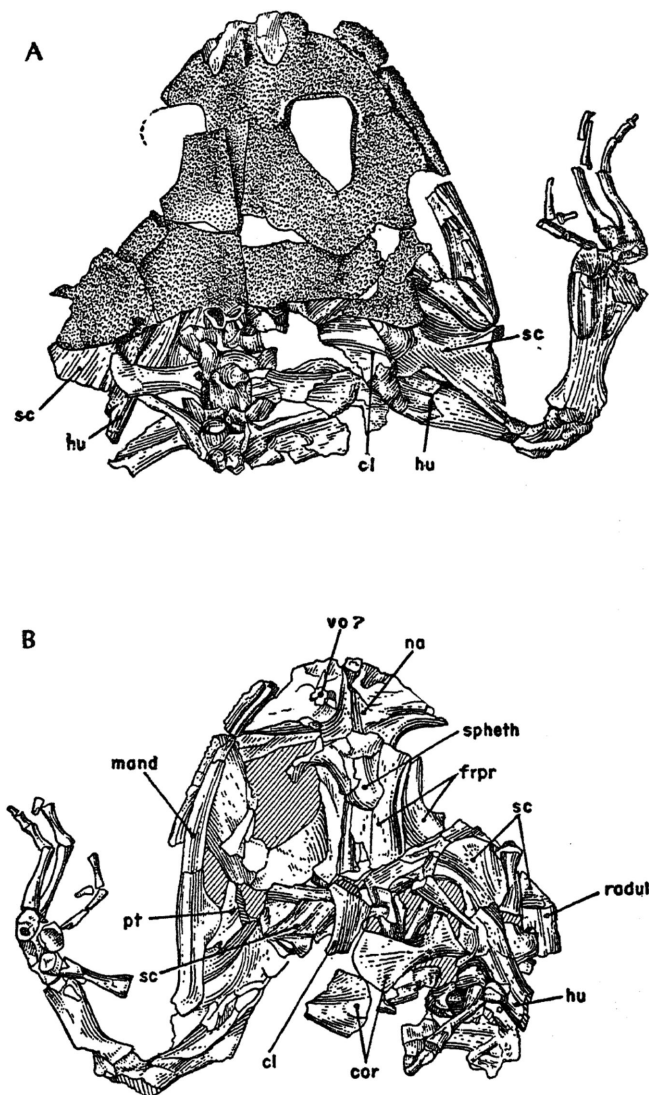


FIG. 2. *Calyptocephalella canqueli*, new species. A.M.N.H. No. 3429, type specimen. A. Dorsal view. B. Ventral view. Abbreviations: cl, clavicle; cor, coracoid; frpr, frontoparietal; hu, humerus; mand, mandible; na, nasal; pt, pterygoid; radul, radio-ulna; sc, scapula; spheth, sphenethmoid; vo?, vomer. $\times 1/1$.

width of the nasal bridge for five skulls of *C. gayi* of different sizes and for the single specimen of *C. canqueli* (fig. 3A) further suggests that the nasal of the latter exhibits a slightly different relative growth pattern.

squamosal. When this suture is relatively short, the posterior rim of the orbit is extended backwards. As the logarithmic plotting of orbit length to orbit width in *C. gayi* demonstrates, the orbit increases in width

more rapidly than in length with increase in skull size. The single record for *C. canqueli* suggests a slower width increase, although this obviously cannot be proved on the basis of a single point. In any case, the shape of the orbit and the narrower frontoparietal-squamosal contact in *C. canqueli* are very similar to the condition found in small sub-adults of *C. gayi*.

The frontoparietals and squamosals are of

about the same relative size in the Oligocene and Recent species. The posterolateral corner of the squamosal in *canqueli* is neither extended posteriorly nor rounded as in *C. gayi* but is more angular and has a slight lateral extension. In this respect, *canqueli* again agrees with the young adult condition in *C. gayi*. The arm of the squamosal articulating with the quadrate, with due allowance for crushing, is of the same length and robustness

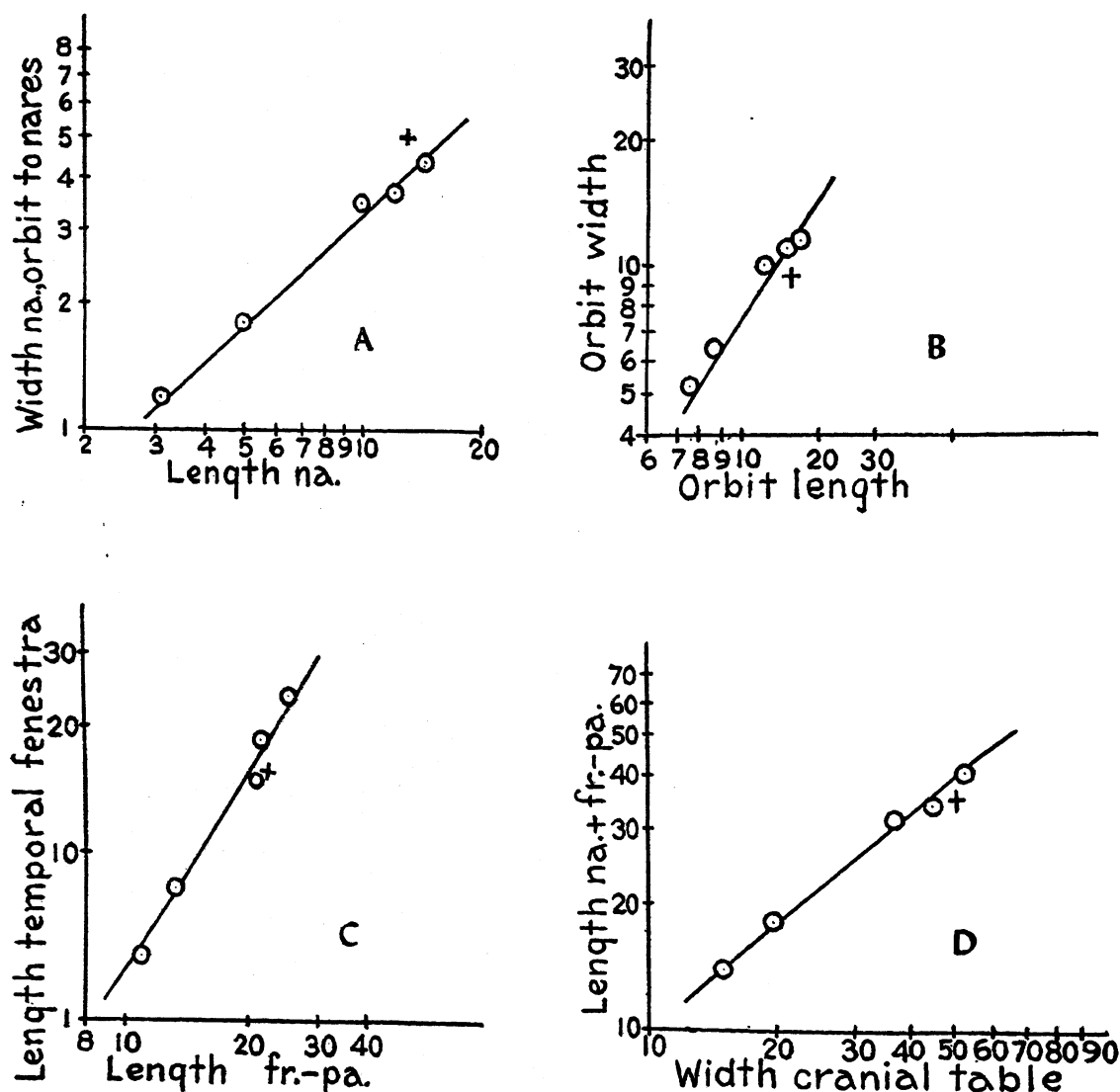


FIG. 3. Logarithmic graphs illustrating growth changes for the indicated skull characters in *Calyptcephalella gayi*. The crosses represent determinations for the skull of *C. canqueli*. Regression lines determined by method of least squares.

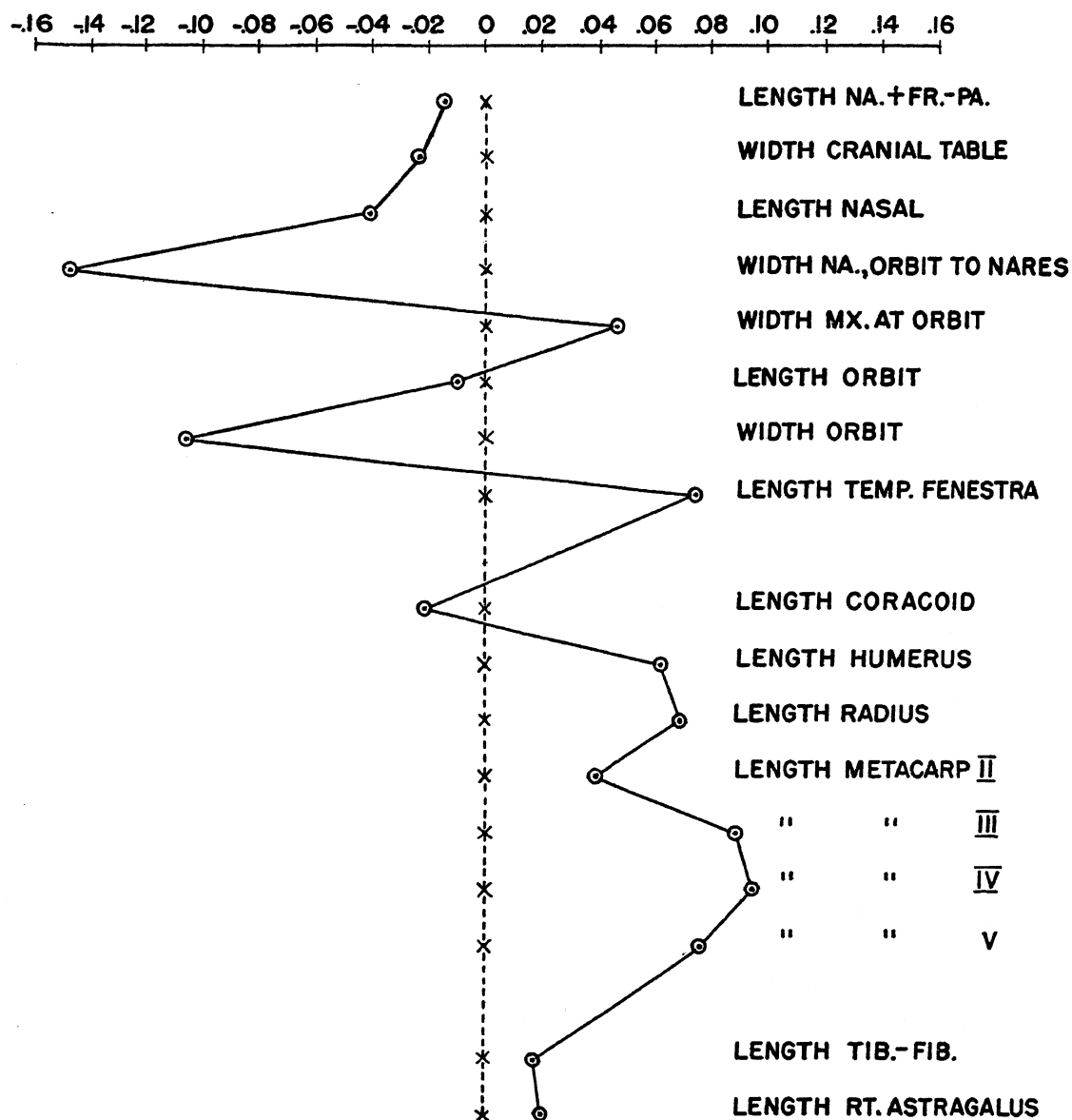


FIG. 4. Ratio diagram comparing various measurements of *Calyptocephalella canqueli* (dotted line) and *Calyptocephalella gayi* (solid line).

as in *C. gayi*. The temporal fenestra appears to be somewhat shorter than in the Recent species (in relation to the length of the frontoparietal) in spite of some crushing in this area (fig. 3C).

The cranial table is gently convex in *C. gayi*. The difference in the width of the table when arched and when flattened is about 2 mm. After such an allowance for crushing in

C. canqueli is made, it is found that the width along the posterior border of the table is about the same as in *C. gayi* in relation to the length of the nasal plus the frontoparietal (fig. 3D) as measured along the middorsal line.

A portion of the right vomer is preserved, but it is badly crushed and reveals no important characters. The palatines appear

identical in shape and extent with those of *C. gayi*, although they are likewise obscured by crushing. The sphenethmoid is completely ossified. The posterior portion of the parasphenoid, and the otic and occipital regions are obscured by the remains of the pectoral girdle and left fore limb.

The mandible is edentulous. The coronoid process of the angulosplenial is larger and more clearly defined than in *C. gayi*, but otherwise the similarity with the Recent species is again very close.

The vertebrae are clearly procoelous but are otherwise too poorly preserved for detailed description or comparison. The first two presacral vertebrae in the type have been compressed between the skull and the third presacral. The transverse processes of the third are robust and of about the same relative length as in *C. gayi*.

The left coracoid and the right scapula are well preserved in the type specimen and again are not distinct from these elements in *C. gayi*. The clavicles are badly broken and comparison is not possible. The humerus and radio-ulnar are of similar relative length in both species. The metacarpals are somewhat shorter and more delicate in *C. canqueli*. The distal phalanges agree in having slightly bulbous tips.

The pelvic girdle and hind limbs are preserved in a referred specimen (A.M.N.H. No. 3427). Although the skull is missing, the specimen may be confidently assigned to *C. canqueli*. The sacral diapophyses are moderately dilated as in *C. gayi*. The coccyx has two condyles and a strongly developed dorsal ridge. The hind limbs offer no additional differentiating characters.

The logarithmic regressions tend to demonstrate the close similarity of *C. canqueli* and *C. gayi*, while the ratio diagram (fig. 4) emphasizes such differences as do exist. Although the differences may appear hardly worthy of specific separation, they are consistent within the limits of the available adult material, both fossil and Recent. The ontogenetic series of *C. gayi* skulls shows a number of interesting changes in proportion with increase in size, the most obvious being the relative increase in orbit width and the length of the temporal fenestra. Apparently, adults of *C. canqueli* retained some of these

subadult skull characters such as orbit shape and a slightly shorter temporal fenestra, in addition to possessing features that appear to be unaffected by relative growth changes such as the wider nasal bridge. The fore limb elements are consistently longer in *C. gayi* than in *canqueli*.

Although the fossil remains just described have been compared with other recent leptodactylids, the characteristic skull ornamentation and the secondary deposit of bone on the skull immediately suggest close affinity with *Calyptocephalella*, and this appears to be confirmed on the basis of the available fossil specimens. The difficulty with which a number of the Tertiary anurans are separated from Recent species on an osteological basis suggests that many species may actually extend back well into the Tertiary. The very close resemblance between *C. gayi* and *C. canqueli* would appear further to support this thesis.

MEASUREMENTS IN MILLIMETERS

	<i>Calyptocephalella gayi</i> M.C.Z. No. 447	<i>Calyptocephalella canqueli</i> A.M.N.H. No. 3429
Length of nasal + frontoparietal	34.2	35.0
Width of cranial table	44.9	51.0
Length of nasal	12.3	13.0
Length of frontoparietal	22.0	23.0
Width of nasal, nares to orbit	3.7	5.0
Length of orbit	12.7	13.0
Maximum width of orbit	11.0	9.5
Length of temporal fenestra	19.1	16.0
Length of coracoid	14.0	14.7
Length of humerus	31.0	26.8
Length of radio-ulna	20.8	17.7
Length of tibiofibula	41.8	40.2
Length of right astragalus	21.5	20.5

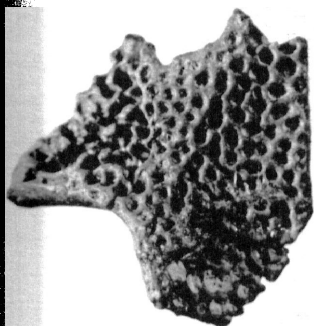
REFERRED SPECIMENS

From same horizon and locality as the type specimen:

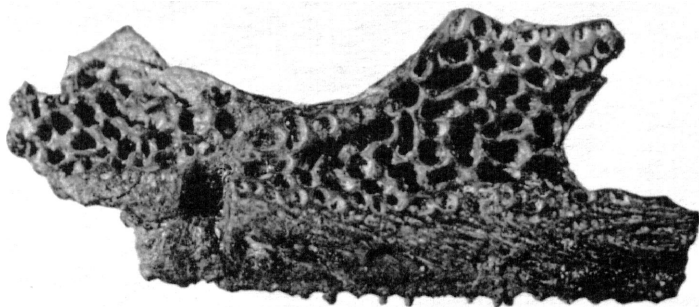
A.M.N.H. No. 3400, dissociated lower jaw and limb fragments

A.M.N.H. No. 3427, partial skeleton showing coccyx, pelvis, and hind limbs

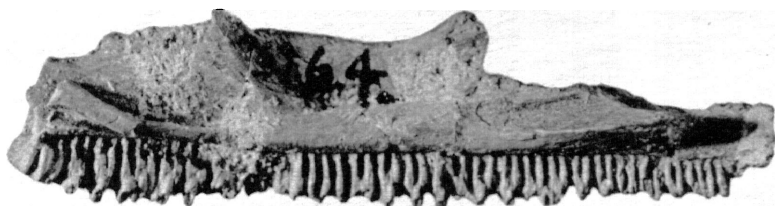
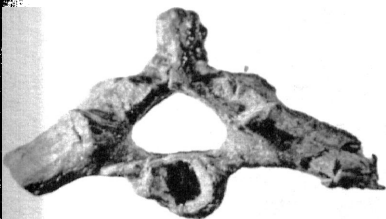
From upper portion of Sarmientan Group, Colhuehuapian Stage, Upper Oligocene. South end of Lago Coli-Huapi, 15 kilometers



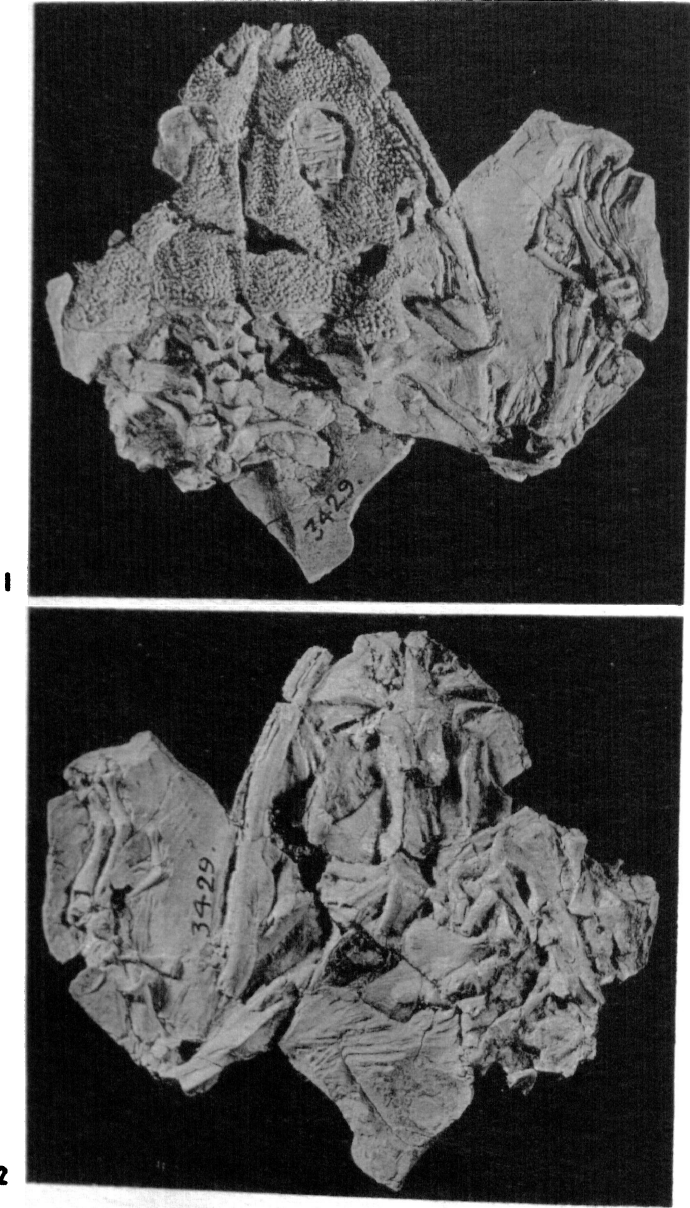
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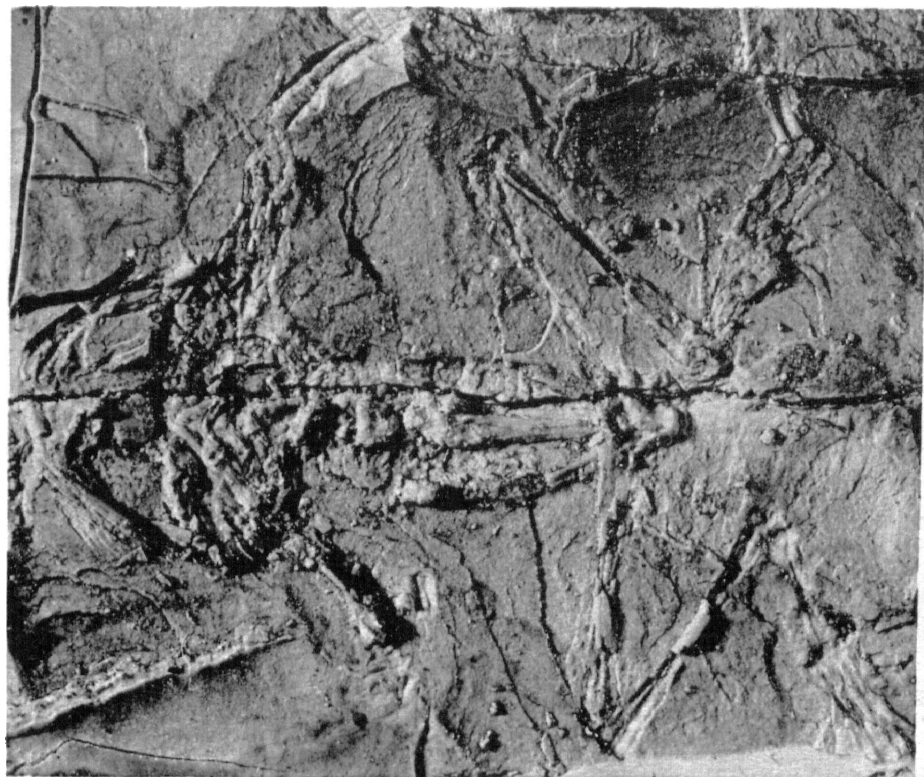
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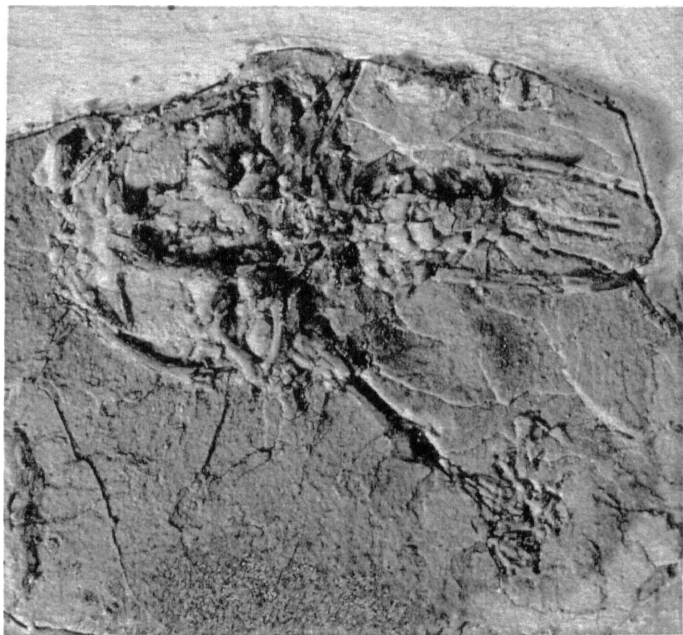
Eophractus casamayorensis, new genus and species. 1. A.M.N.H. No. 3165, type specimen. Dorsal aspect of incomplete left nasal bone on left, lateral aspect of incomplete left maxillary on right. 2. A.M.N.H. No. 3164. Anterior aspect of presacral vertebra on left, median aspect of incomplete right maxillary on right. $\times 3/1$



Calypptosphaella canqueli, new species. A.M.N.H. No. 3429, type specimen. 1. Dorsal view. 2. Ventral view. $\times 1/1$

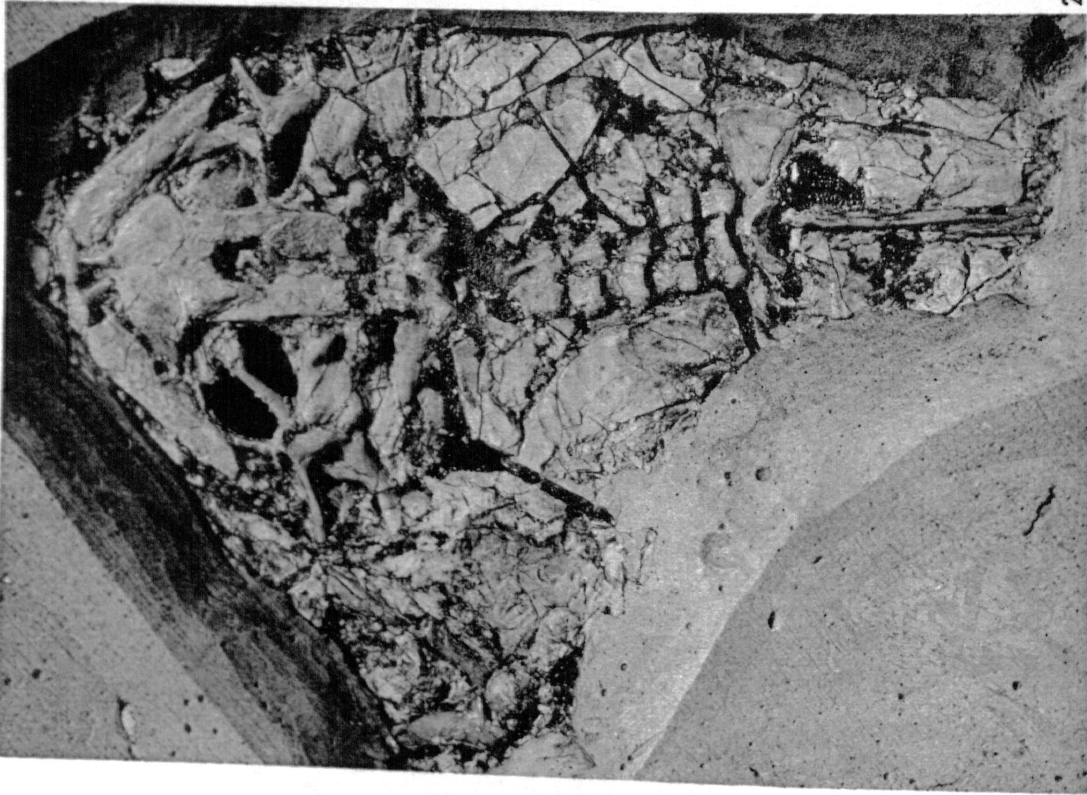


2



1

Eupsophus sp. 1. A.M.N.H. No. 3422, dorsal view. $\times 3/1$. 2. A.M.N.H. No. 3407. Almost complete but badly crushed specimen preserved in ventral aspect. $\times 3/1$



Neoprocode edentatus, new genus and species. A.M.N.H. No. 3428, type specimen. 1. Dorsal aspect. 2. Ventral aspect. $\times 2/1$

southwest of Casa Ramos, central Chubut, Argentina. These fragments may be definitely assigned to *Calyptocephalella* and, so far as can be determined, show no specific differences from *C. canqueli* in spite of the time interval involved.

A.M.N.H. No. 3236, fragments of maxillary

A.M.N.H. No. 3237, fragments of maxillary

A.M.N.H. No. 3238, isolated sphenethmoid

A.M.N.H. No. 3239, isolated sphenethmoid and fragment of right ilium

A.M.N.H. No. 3241, maxillary fragments, portions of skull roof, and two presacral procoelous vertebrae

FAMILY LEPTODACTYLIDAE

EUPSOPHUS FITZINGER

Cystignathus DUMÉRIL AND BIBRON (in part), 1841, *Erpétologie général*, vol. 8, p. 392.

Borborocoetes BELL, 1843, *The zoology of the voyage of H.M.S. Beagle*, pt. 5, reptiles, p. 34.

Eupsophus FITZINGER, 1843, *Systema reptilium*, p. 31. (For discussion of generic synonymy, see Parker, 1932, *Ann. Mag. Nat. Hist.*, ser. 10, vol. 10, p. 342.)

GENOTYPE: *Cystignathus roseus* Duméril and Bibron.

Eupsophus sp.

HORIZON AND LOCALITY: Sarmientan Group, Deseadan Stage, Lower Oligocene. Scarritt Pocket, southwest portion of Rinconada de los Lopez, west side of Sierra Canquel, central Chubut, Argentina.

DESCRIPTION: A small leptodactylid not separable from *Eupsophus* on the basis of available specimens. The maxillaries are shallow, with teeth. The nasals are relatively large and possibly in contact. A frontoparietal fontanelle is present. The vertebrae are procoelous, the sacral articulation is double in some specimens, the sacral diapophyses are moderately expanded, and there is a double condyle on the coccyx. The hind limbs are elongated as in Recent species of this genus.

The observable characters of the skull and postcranial skeleton indicate relationship with *Eupsophus* or *Hylorhina*. The osteological characters separating these genera, such as the presence of a bony sternum in *Hylorhina*, cannot be distinguished in any of the fossil specimens. A comparison of the skulls, however, does suggest closer affinity with

Eupsophus. The greatly elongated hind limbs, particularly the feet, appear very similar in their proportions to the limb segments of *Hylorhina*. Actually, the differences in the relative lengths of the limb elements in *Hylorhina silvatica*, *Eupsophus grayi*, and the form here described are hardly great enough to be of much taxonomic significance. The total length of the hind limb compared with the length of the axial skeleton in *H. silvatica* is about 1.9, while in both *E. grayi* and the form here described it is no more than 1.8. Ratios of the hind limb segments on the basis of a femoral length of two units indicate the following (figures represent: femur, tibiofibula, astragalocalcaneal segment, fourth digit): *H. silvatica*, 2, 2.3, 1.3, 2.5; *E. grayi*, 2, 2.2, 1.2, 2.2; *E. sp.*, 2, 2.1, 1.0, 2.3.

The nasals are well ossified and are of the same relative size as in *E. grayi*. In contrast to the condition in this species, however, these elements are in contact, which may or may not be a consequence of crushing. The frontoparietals are separated for most of their length, but the details of their extent and of the size of the fontanelle cannot be determined. One skull preserved in ventral aspect (A.M.N.H. No. 3407) demonstrates that the portion of the sphenethmoid anterior to the prevomers is ossified as in *E. grayi*. The presence of prevomers is indicated, but no details are preserved.

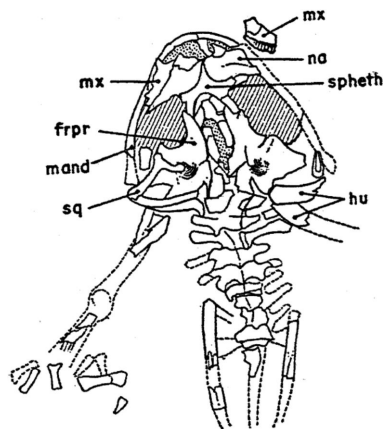


FIG. 5. *Eupsophus* sp. A.M.N.H. No. 3422. Partial skeleton preserved in dorsal aspect. Abbreviations: frpr, frontoparietal; hu, humerus; mand, mandible; mx, maxillary; na, nasal; spheneth, sphenethmoid; sq, squamosal. $\times 2/1$.

MEASUREMENTS IN MILLIMETERS

	<i>Eupsophus grayi</i>	<i>Eupsophus</i> sp.			
	A.M.N.H. No. 22104	A.M.N.H. No. 3407	A.M.N.H. No. 3424	A.M.N.H. No. 3426	A.M.N.H. No. 3430
Length of skull	12.0	9.60	—	—	—
Width of skull	14.3	—	—	—	—
Length of vertebral column (including urostyle)	23.5	17.5	—	—	—
Length of humerus	10.5	8.0	—	9.5	—
Length of radio-ulna	7.5	—	—	6.5	—
Length of femur	17.5	13.3	—	12.2	13.0
Length of tibiofibula	19.0	14.0	14.0	14.0	14.3
Length of astragalocalcaneal segment	10.5	6.0	6.5	6.0	7.0
Length of fourth digit	19.0	—	15.4	15.2	16.5
Total length of pes	28.7	—	21.4	—	23.5

There are nine procoelous vertebrae which might be distinguished from those of *E. grayi* only by a somewhat stronger development of the neural spines, actually merely longitudinal ridges, on the fifth through seventh vertebrae. It is reasonable to suppose, however, that the size of these ridges is subject to at least this much variation. Two specimens (A.M.N.H. Nos. 3422 and 3426) appear to have a double sacral articulation. The diapophyses of the ninth vertebra are moderately expanded, while those of the eighth, which are in contact with the ends of the ilia, are of uniform width. This condition may be associated with a relatively shorter coccyx than in *E. grayi*. A double articulation between the sacral vertebra and the coccyx is evident in one specimen (A.M.N.H. No. 3407).

The elements of the pectoral girdle cannot be observed in any of the specimens. The fore limbs and, as pointed out above, the hind limbs are similar in their proportions to those of the Recent species with the exceptions noted.

Assignment to *Eupsophus* is indicated by all the observable characters. The poor preservation precludes detailed description and the determination of specific differences, if any are actually present, between this form and *E. grayi*.

REFERRED SPECIMENS

A.M.N.H. No. 3407, complete skeleton, skull badly crushed

A.M.N.H. No. 3415, pelvis and hind appendages of small individual
A.M.N.H. No. 3420, skull fragments and hind appendages
A.M.N.H. No. 3422, crushed skull, left forearm, and vertebral column

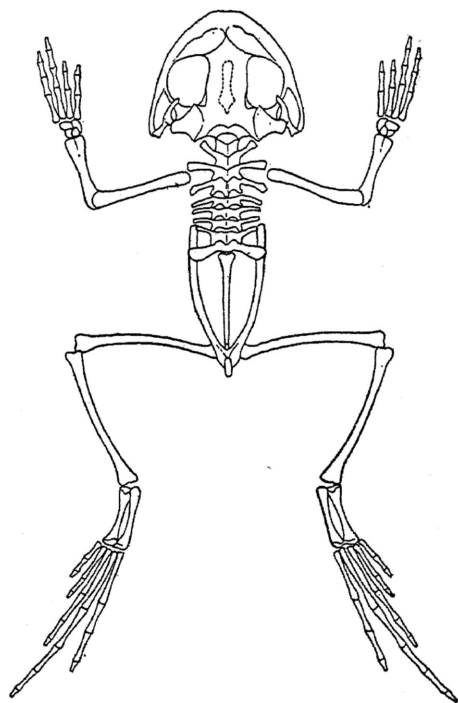


FIG. 6. Tentative restoration of *Eupsophus* sp. based on all available specimens to show proportions of axial skeleton and limb segments. Approximately $\times 3/2$.

- A.M.N.H. No. 3424, hind appendages
 A.M.N.H. No. 3425, anterior portion of skull
 A.M.N.H. No. 3426, postcranial skeleton
 A.M.N.H. No. 3430, two partly superimposed
 and crushed skeletons

FAMILY LEPTODACTYLIDAE

NEOPROCOELA, NEW GENUS

GENOTYPE: *Neoprocoela edentatus*, new species.

GENERIC DIAGNOSIS: A presumed leptodactylid with several primitive, criniid-like

Group, Deseadan Stage, Lower Oligocene. Scarritt Pocket, southwest portion of Rinconada de los Lopez, west side of Sierra Canquel, central Chubut, Argentina.

SPECIFIC DIAGNOSIS: Same as for genus.

DESCRIPTION: In a number of respects this is the most interesting form in the collection, and it is unfortunate that it is represented only by the type specimen. The large fontanelle, edentulous upper jaw, wide maxillary, and dilated sacral diapophyses suggest relationship with the Australian leptodactylids.

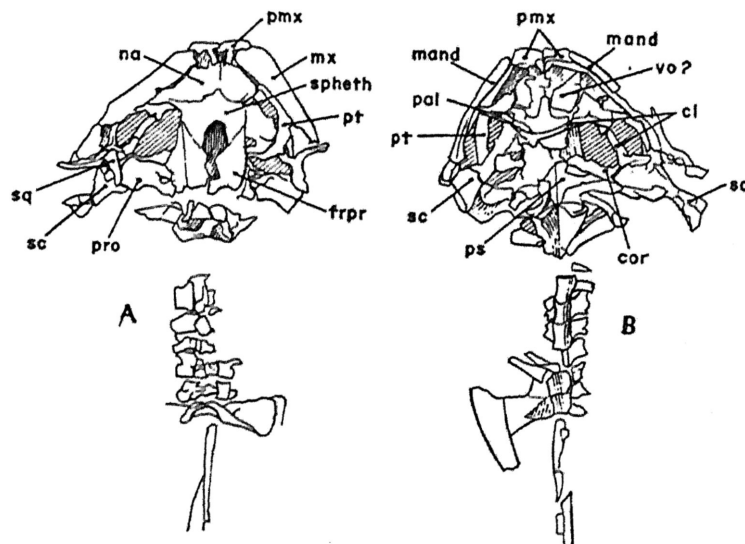


FIG. 7. *Neoprocoela edentatus*, new genus and species. A.M.N.H. No. 3428, type specimen. A. Dorsal view. B. Ventral view. Abbreviations: cl, clavicle; cor, coracoid; frpr, frontoparietal; mand, mandible; mx, maxillary; na, nasal; pal, palatine; pmx, premaxillary; pro, prootic; ps, parasphenoid; pt, pterygoid; sc, scapula; spheth, sphenethmoid; sq, squamosal; vo?, vomer. $\times 1/1$.

features. Premaxillaries T-shaped, edentulous. Maxillaries broad, edentulous, with long pterygoid articulation. Nasals completely ossified and in contact. Fontanelle present, with frontoparietals widely separated. Sphenethmoid ossified and entire. Vertebrae procoelous, intervertebral condyle fused with centrum; sacral diapophyses dilated, triangular in shape; coccyx probably not fused to sacrum. Shoulder girdle as in *Eupsophus*.

Neoprocoela edentatus, new species

TYPE: A.M.N.H. No. 3428. Partial skeleton consisting of skull, vertebral column, and proximal portion of left forearm.

HORIZON AND LOCALITY: Sarmientan

All the Australian genera but two, however, have an incompletely fused vertebral condyle (Parker, 1940), and this is the condition in the Eocene *Indobatrachus* (Noble, 1930). In *Neoprocoela* there is complete fusion of the vertebral condyles. It may be concluded on the basis of available evidence that *Neoprocoela* is a true leptodactylid retaining several primitive leptodactylid features. The toothless condition was probably an independent development, as must be the case with many of the Australian genera and for that matter with the Neotropical *Batrachophrynus*.

Although many of the characters of *Neoprocoela* suggest relationship with other

families of procoelous anurans, these groups appear to be ruled out on the basis of other more specific or diagnostic characters. There is, for instance, a marked resemblance in skull structure to that of *Bufo*, the principal difference being the presence of the fontanelle in *Neoprocoela*. To consider this Oligocene form as a specialized *Bufo*, however, would require the presence of the Bufonidae (*sensu stricto*) in South America by no later than the early Oligocene, an occurrence which is not supported by the known paleontological facts.

The general nature of the skull thus supports affinity with the more generalized South American leptodactylids such as *Telmatobius* or its edentulous derivative, *Batrachophrynus*. The nasals are in contact in the latter, the maxillary is broad, the articulation between the maxillary and pterygoid is extended, and a fontanelle is present, although it is smaller than in *Telmatobius*. The fontanelles of *Neoprocoela* and of *Telmatobius* are of about equal size, separating the frontoparietals for most of their length.

The fragmentary prevomers show no indication of teeth, a condition commonly correlated with an edentulous upper jaw. The other palatal structures show no unusual characters. The sphenethmoid is well ossified, the bony portion ending at the level of the prevomers. The squamosals are small with delicate anterior processes of unknown length.

The left shoulder girdle is completely preserved, consisting of a narrow, rod-like clavicle, somewhat wider coracoid, and typical leptodactylid scapula. The clavicle and coracoid are preserved in a divergent position, and the left clavicle, which is also present, shows evidence of being slightly arched. This suggests the arciferal pectoral girdle as pointed out by Noble (1930). Scat-

tered elements of the left manus were closely associated with the posterior portion of the parasphenoid. While these bones and the surrounding matrix were being removed, in order to expose fully the palatal area, a single terminal phalanx was uncovered. This element shows no appreciable dilation at its distal end.

The procoelous vertebrae, nine including the sacral, have cylindrical centra that are longer than wide. The dilated, triangular sacral diapophyses present a difficult problem, as they are characteristic of *Indobatrachus* and the Australian leptodactylids as well as the Hylidae, Brachycephalidae, and Brevicipitidae (Microhylinae) but not of the Recent South American leptodactylids. In spite of this fact, the weight of the observable characters, as pointed out above, indicates that *Neoprocoela* is a true but primitive leptodactylid with the edentulous upper jaw as its principal specialized divergence.

The absence of the centrum of the sacral vertebra and the poor preservation of the coccyx make it impossible to determine the nature of the sacrococcygeal articulation. The dilation of the proximal end of the coccyx suggests that a double condyle was present, but this is not certain. Furthermore, fusion between the sacral vertebrae and the coccyx cannot be definitely ruled out. As will be pointed out in the discussion, there are a number of resemblances to the Atelopodidae which cannot at present be properly evaluated.

MEASUREMENTS: The fragmentary nature of the single known specimen makes it impossible to take accurate or meaningful measurements.

HYPODIGM: Type specimen only.

DISCUSSION

ANURAN DIFFERENTIATION

A GENERAL TREATMENT of the origin of the Neotropical anuran fauna including consideration of the more recently discovered fossil evidence has not been attempted since the pioneer studies of Noble (1925 and 1931) and Dunn (1931). Not being an anuran specialist, the writer embarks on such an effort with even more hesitation than did Dunn, but in the hope that the recently accumulated paleontological data will throw some additional light on the problem.

There is still no general agreement among herpetologists regarding the phylogeny and composition of many of the families of Salientia. The list included in table 1 is based for the most part on the most recent opinions of Davis, Dunn, Noble, and Parker for the modern families and of Watson, Piveteau, and Romer for the extinct ones. In order to give the Neotropical fauna its proper setting and to present recently discovered fossil data supporting a Holarctic origin for the stocks from which the Neotropical fauna was derived, the probable origin and dispersal of all the families listed in table 1 will be briefly discussed.

The recent work of Watson (1941) has rather clearly demonstrated that the Salientia evolved from the labyrinthodonts. In the Pennsylvanian genera *Amphibamus* and *Mio-batrachus*, which are grouped in the family Amphibamidae, there are already changes in the skull and vertebrae in an anuran direction. In the Triassic *Protobatrachus*, the only known member of the Protobatrachidae, this trend is carried still further with a more anuran-like skull and an elongated ilium (Piveteau, 1939). With the Amphibamidae known only from one locality in North America and the Protobatrachidae only from Madagascar, there is as yet no clue as to a center of origin for the Salientia. This evidence does indicate, however, that the group must have reached its distinctive status by no later than the early Jurassic.

AMPHICOELA: The Amphicoela were possibly a distinct group by Upper Jurassic time. The single known vertebra of *Eobatrachus* (Moodie, 1914) appears to be amphi-

coelous, and the coccyx has a double condyle. Romer (1945) has tentatively placed this genus, together with *Montsechobatrachus* (Vidal, 1902) from the Upper Jurassic of Spain and *Siremmia* of the same age from East Africa, in the family Montsechobatrachidae as a subdivision of the Amphicoela. As these genera are known only from fragmentary remains and impressions, the family is very possibly not a natural one. They do demonstrate the presence of definitive anurans at this time and testify to a world-wide distribution in the Upper Jurassic.

The other amphicoelous family, the Liopelmidae, includes two Recent genera with a well-known disjunctive distribution. *Liopelma* occurs in New Zealand and *Ascapus* in the northwestern United States. As Noble and others have pointed out, this distribution also suggests a former world-wide or at least Holarctic distribution of a generalized, primitive amphicoelous stock.

OPISTHOCOELA: This suborder, which is characterized by possessing opisthocelous vertebrae and free ribs in the larval or adult stage, has a thigh musculature which, according to Noble, closely resembles that of the Amphicoela. Of the two families included in the Opisthocoela, the Discoglossidae and the Pipidae, the former is presumably the more primitive with free ribs in the adult. The discoglossids are first known from the Upper Oligocene of France with the description of *Prodiscoglossus* by Friant (1944). It appears to combine certain characters of *Bombina*, *Discoglossus*, and *Alytes*. The modern genera *Discoglossus* and *Alytes* occur also in the Lower Miocene of France and the Middle Miocene of Germany. Two extinct genera, *Pelophilus* and *Latonia*, have been found in the Upper Miocene of Germany. The discoglossids thus give every appearance of being primarily an Eurasiatic group that was differentiated in the early Tertiary about as completely as it is today. During the Tertiary *Bombina* spread from some unknown center of origin until it covered most of Eurasia. *Discoglossus* reached Africa but

TABLE 1
FIRST KNOWN APPEARANCE OF THE FAMILIES OF SALIENTIA

		Eurasia	Australia	N. Zealand	Africa	Madagascar	N. America	S. America
Eoanura	Amphibamidae	—	—	—	—	—	Penn.	—
Proanura	Protobatrachidae	—	—	—	—	L. Trias.	—	—
Amphicoela	Montsechobatrachidae Liopelmidæ	U. Jur. —	— —	— R.	U. Jur. —	— —	U. Jur. R.	— —
Opisthocoela	Discoglossidae Pipidae	U. Olig. —	— —	— —	— L. Tert.	— —	— —	— R.
Anomocoela	Pelobatidae Pelodytidae	U. Olig. M. Eoc.	— —	— —	— —	— —	U. Plioc. M. Mioc.	— —
Procoela	Palaeobatrachidae	Mioc. Eoc.	—	—	—	—	—	—
	Leptodactylidae	—	R.	—	R.	—	—	—
	Rhinodermatidae	—	—	—	—	—	—	—
	Dendrobatidae	—	—	—	—	—	—	—
	Atelopodidae	R.	—	—	—	—	—	—
Diplasiocoela	(= Brachycephalinae)	Olig. Olig.	—	—	—	—	—	—
	Bufonidae	—	R.	—	R. R.	—	U. Plioc. R.	R. R.
	Hylidae	—	—	—	—	—	—	—
	Ranidae	U. Mioc. R.	R.	—	R. R.	—	U. Plioc.	R.
	Rhacophoridae (= Polypedatidae)	—	—	—	—	R.	—	—
	Microhylidae	R.	—	—	R.	R.	R.	R.
	Phrynomeridae	—	—	—	—	—	—	—

possibly not Asia. *Alytes* presumably differentiated in Europe and remained there. A single genus, *Barbourula*, unknown in the fossil state, reached or was differentiated in the Philippines. This primitive anuran family, on the basis of both fossil and Recent evidence, had a relatively restricted and slow dispersal.

The Pipidae were already distinct from the discoglossid stock by the early Tertiary. The problematical *Eoxenopoides* (Haughton, 1931) from Lower Tertiary clays in Namaqualand, South Africa, appears to be a member of this family. Its systematic position is not definite, however, mainly because of the surprising variation in the nature of the sacral articulation. *Xenopus stromeri* (Ahl, 1926) has been described from the Miocene of southwest Africa. Although the differences between the South American and African pipids are not great (E. R. Dunn, personal communication), those that do exist appear to be consistent. The African occurrences strongly indicate a late Mesozoic dispersal from some unknown Holarctic center, with a *Protopipa*-like form reaching South America from the north prior to the break in the Panamanian bridge. One other tempting hypothesis, for which there is no convincing morphological evidence, suggests an independent origin of the African and South American pipids from a primitive Eurasian discoglossid stock.

ANOMOCOELA: The Anomocoela, according to Noble (1924), evolved from the primitive Discoglossidae by a fusion of the intervertebral cartilages resulting in a procoelous condition, a reduction in the number of presacral vertebrae to eight, loss of ribs, appearance of an acromion process, and expansion of the sacral diapophyses. Although this suborder was formerly considered to include but one family, the Pelobatidae, Taylor (1941) has recommended the recognition of an additional family, the Pelodytidae (originally employed by Cope in a less restricted sense).

The oldest known member of the Pelobatidae, *Macropelobates*, occurs in the late Oligocene of Mongolia (Noble, 1927). *Eopelobates*, from the Miocene of Germany, is considered by Parker (1929) to represent a structurally earlier stage than the Oligocene form. *Macropelobates* is apparently a typical pelobatid with an enlarged prehallux, while

Eopelobates only lacks this increase in size. *Scaphiopus* and the related extinct genus *Neoscapthiopus* have been described by Taylor (1942) from the Upper Pliocene of Kansas.

The Pelodytidae are characterized, following Taylor, by an unornamented skull, no palatine bone, prehallux not forming a spade, coccyx articulating with the sacral vertebra by a double condyle, astragalus and calcaneum more or less fused throughout their length. The family may be represented in the Middle Eocene of Germany by *Propelodytes* (Weitzel, 1938), a form with procoelous vertebrae and sacrococcygeal joint not fused. The astragalus and calcaneum are fused, however, only at their proximal and distal ends, which may or may not represent an incipient stage towards more complete fusion. A form named *Miopelodytes* which is very similar to the European *Pelodytes* has been described by Taylor (1941) from the Middle Miocene of Nevada. It has the astragalus and calcaneum fused throughout their length.

Both families of the Anomocoela clearly had a Holarctic distribution with representatives reaching North America no later than the middle of the Tertiary. There is no evidence, Recent or fossil, that the Pelobatidae or the Pelodytidae entered South America or Africa.

PROCOELA: The early Eocene Intertrappean beds of India have yielded one of the oldest representatives of the Procoela in the form of a leptodactylid bearing many characters in common with the Recent Australian Leptodactylidae. *Indobatrachus* (Noble, 1930) may possibly belong to the subfamily Myobatrachinae (Parker, 1940). This occurrence indicates a southern Holarctic origin for the Procoela, a conclusion not opposed by the presence, in the Miocene of Europe, of two procoelous genera, *Palaeobatrachus* and *?Protopelobates*, which are placed in the separate family Palaeobatrachidae. The relationships of this family, which may very well be an unnatural assemblage, are not clear (see Wolterstorff, 1929).

Most herpetologists have not followed Noble's practice of lumping the Leptodactylidae with the Bufonidae. The two families are practically indistinguishable from the standpoint of osteology and myology, particularly since toothless leptodactylids have

been described. Davis (1936) has pointed out, however, that Bidder's organ is present in the Bufonidae but absent in the Leptodactylidae, and he presents a logical thesis for believing that this structure first appeared in the Bufonidae. He concludes on this and other evidence that the Leptodactylidae and Bufonidae are natural groups with a common origin, a concept that is certainly not in opposition to the paleontological record. Their separation may have taken place some time in the Cretaceous.

The Leptodactylidae must have had a wide Holarctic distribution in the late Mesozoic and probably extended into Australia prior to its isolation in the Upper Cretaceous. Although the systematic position of several of the forms described in this paper is not definite, the evidence clearly indicates that representatives of this family entered South America before that continent was isolated at the beginning of the Tertiary. Dispersal into Africa presumably occurred sometime during or before the Tertiary, although the fossil evidence is still lacking for this assumption.

The Bufonidae (*Bufo*) are first known from the Oligocene of Europe (Filhol, 1877), and remains of *Bufo* have also been described from the Upper Pliocene of Kansas (Taylor, 1937). The center of dispersal must have been somewhere in Eurasia, with *Bufo* only reaching North America during the Tertiary and entering the Neotropical region either by a sweepstakes route before the Middle Pliocene or by the Panamanian bridge after that time. The failure of the bufonids to reach Australia suggests a later radiation than occurred in the case of the leptodactylids. The bufonids occurring in Africa and the Indo-Malayan region present no particular dispersal problem.

The Brachycephalidae were considered by Noble (1931) to be a composite family, and Davis (1935) divided the group into three families, the Rhinodermatidae, Dendrobatidae, and Atelopodidae. The Rhinodermatidae and Dendrobatidae are probably endemic to South America, being derived from leptodactylid types close to *Syrrhophus* and *Crosodactylus*, respectively, during the Tertiary (Noble, 1931). Davis has demonstrated,

however, that the East Indian genus *Cacophryne* belongs to the Atelopodidae, indicating that this family must have formerly been rather widely distributed in the Holarctic area. The time of migration into South America is difficult to conjecture. It might be considered as having occurred in the late Tertiary except for certain disturbing resemblances to *Neoprocoela* such as the dilated sacral diapophyses and edentulous maxillary. The presence or absence of a firmisternal pectoral girdle in fossil Anura cannot be definitely determined in most cases. The single specimen of *Neoprocoela* lacks the sacrococcygeal articulation, and it is possible that fusion did actually exist. The fontanelle in this species may be a primitive leptodactylid character which could have been lost in certain of its descendants. If *Neoprocoela* is, in fact, a true atelopodid, this family must have then entered South America in the Paleocene.

On the basis of available evidence, it is reasonable to conclude that the Hylidae evolved from some primitive leptodactylid-like stock in the late Mesozoic. The two hylid subfamilies recognized by Noble, the Hemiphractinae and the Hylinae, are possibly not valid, and fossil remains cannot be assigned to either subfamily on the basis of osteology unless reference to a Recent genus is possible. One of the most unexpected discoveries in the paleontology of the Salientia is the presence of remains assigned to the genus *Amphignathodon* in the late Oligocene and early Miocene of France (Piveteau, 1927). This specialized member of the Hemiphractinae, the only definitive anuran with mandibular teeth, is confined at the present time to Ecuador. The other members of this subfamily, which are all Neotropical and have no known fossil representatives, are in some respects less specialized, in others almost equally so. They all appear to be derived from a *Hyla*-like ancestral stock which undoubtedly had a Holarctic dispersal. Furthermore, the possible occurrence in Europe of *Amphignathodon* by the late Oligocene and of *Hyla* by the Lower Miocene (Noble, 1928) indicates that possibly both subfamilies of the Hylidae were well differentiated in the Northern Hemisphere. The

Hemiphractinae presumably entered North America in the Tertiary and South America either by a sweepstakes route during the isolation period or after the bridge was re-established. Tree frogs might be quite readily transported on floating logs and other vegetation. The presence of *Amphignathodon* in Europe presents a problem regarding the place of origin of the other hemiphractid genera now confined to South America. This genus is clearly not ancestral to the other hemiphractids, and it may be reasonably concluded that at least one other type, possibly resembling *Gastrotheca*, entered from the north which subsequently gave rise to *Gastrotheca* itself, as well as *Hemiphractus* and *Cryptobatrachus*. Any of these genera may also have occurred in the Northern Hemisphere.

The great diversification of the Hylinae in South America might suggest the Neotropical area as their place of origin. The occurrence of *Hyla* in the European Tertiary, the relic survival pattern of the entire group, and the parallelism and endemism of the African and Oriental species indicate a former wide dispersal in the Holarctic. Migration into South America of some *Hyla*-like types, but not necessarily *Hyla* itself, must have occurred in the early Tertiary. *Hyla*, like *Bufo*, might have reached the Neotropical area in the late Tertiary, although there is no real evidence opposing an early Tertiary arrival. Much additional fossil evidence is needed before the complicated picture of the radiation and dispersal of the Hylidae is well understood.

DIPLASIOCOELA: The Diplasiocoela were probably derived sometime in the late Mesozoic from some primitive group of the Procoela. The taxonomic history of this suborder is complicated but has been greatly clarified by Parker (1934). It appears that four families must now be recognized: the Microhylidae, the Phrynomeridae, the Ranidae, and the Phacophoridae. The Brevicipitidae, as defined by Noble, is thus considered to be an unnatural assemblage with many of its subfamilies now included by Parker in the Microhylidae, while others are considered to be of uncertain position but probably inde-

pendently descended from the Ranidae (i.e., Hemisinae and Cacosterninae).

Parker considers the Microhylidae to be an ancient offshoot from a primitive firmisternal stock and the Phrynomeridae to be derived from the same general line. He believes that this same stock at a later date gave rise to the Ranidae in the Holarctic realm and the Rhacophoridae (= Polypedatidae) in the Ethiopian region. This subdivision must have been well under way by the beginning of the Tertiary. The Microhylidae are unknown as fossils. They apparently had an early Tertiary radiation in Asia extending into Africa and North America. Only one subfamily, the Microhylinae, reached South America, probably relatively late in the Tertiary. The Phrynomeridae, containing the single African genus *Phrynomerus*, must have evolved from the microhylid stock early in the Tertiary if its degree of specialization be considered as an index of antiquity.

The Ranidae, like the Microhylidae, almost certainly became differentiated before the beginning of the Tertiary. The nearly universal distribution of *Rana*, including Australia, and the great diversification of the family in Africa and South Asia suggest a possibly late Cretaceous dispersal of the Ranidae over much of Eurasia with migration into Africa at least by the early Tertiary. *Rana* occurs in the Upper Miocene and later formations of Europe and in the Tertiary of Mongolia and China (Schlosser, 1924; Young, 1936). *Ranavus* (Portis, 1885) and *Aspherion* (Von Meyer, 1847, p. 192), two genera rather similar to *Rana*, are found also in the Miocene of Europe. *Rana* reached North America by no later than the Upper Pliocene (Taylor, 1942) and presumably entered South America over the Panamanian bridge. The Phacophoridae (= Polypedatidae), derived from the ranid stock, presumably remained much closer to their center of radiation, the limits of their range being Japan, southern Asia, the East Indies, and into Africa and Madagascar. The occurrence on Madagascar indicates a long existence in Africa, with arrival on this island either over a land bridge at the beginning of the Tertiary or by a sweepstakes route sometime later.

ANURAN DISPERSAL

On the basis of available paleontological evidence it is very tempting to consider southern Asia as the primary center of dispersal for the modern anuran families that can be traced to the beginning of the Tertiary.¹ The role that Africa has played, however, is difficult to evaluate. Parker (1929) believes that the Rhacophoridae (= Polypedatidae) are of African origin, and there is some support for such a conclusion on the basis of the distribution of modern genera. Paleontological evidence is, however, completely lacking. In any case, that continent must have had a rather diversified anuran fauna very early in the Tertiary or more probably in the late Mesozoic.

The factors affecting the extent and rate of dispersal of the Salientia are largely unknown, particularly in regard to migration across an entire continent, or from one continent to another across a land bridge. The discoglossids apparently expanded their range very slowly across Eurasia during the Tertiary but for some reason never reached North America. As Simpson (1940) has pointed out in the case of certain mammalian groups, the age and area theory requires that the Discoglossidae be a family of relatively recent origin. This is obviously not the case. The Pipidae, which are probably not so ancient as the Discoglossidae and may have evolved from the discoglossid stock, had a rapid expansion which carried them into Africa and South America at the beginning of the Tertiary. The Leptodactylidae, and possibly the Atelopodidae and Hylidae, also fall into this category, with an early Tertiary or even a late Cretaceous dispersal.

Although both the Pelobatidae and the Pelodytidae entered North America during the Tertiary, there is as yet no evidence that they reached South America. A filter-bridge

action is even more striking in the case of single genera that migrated into North America from Asia and finally into South America towards the end of the Tertiary. *Bufo* and *Rana* are the only members of their respective families to reach the New World, while the appearance of *Hyla* may have represented a second migration wave within this family. Taylor (1942) has erected the genus *Anchylorana* for some Upper Pliocene remains from Kansas, which are apparently close to *Rana* but possibly distinguished from it by the fusion of the eighth and ninth vertebrae. If such fusion is not within the range of variation of the vertebral column of *Rana*, although the evidence cited by Taylor indicates it may be, the presence of a genus allied to *Rana* in North America suggests some Tertiary differentiation of the *Rana* stock which subsequently became extinct.

The paleogeographic factors affecting the introduction of a terrestrial fauna into South America have been considered by Simpson (1943). Adopting his categories, which were devised for Neotropical land mammals but which should apply with equal validity to the Salientia, the following may be recognized:

A. Anurans that entered South America prior to its isolation in the early Tertiary and evolved there during this isolation: Pipidae, Leptodactylidae, ?Atelopodidae, Hylidae (possibly but not necessarily excluding *Hyla*).

B. Those that arrived during the period of isolation by some sweepstakes route: ?Bufonidae (*Bufo* only).

C. Those that entered South America after the connection with North America was reestablished at the end of the Pliocene: Hylidae (*Hyla* only, but possibly an early Tertiary arrival), Microhylidae (Microhylinae), Ranidae (*Rana* only).

D. Those that were differentiated in South America, but were originally derived from forms that arrived prior to the isolation: Rhinodermatidae, Dendrobatidae.

The accumulated evidence, fossil and Recent, indicates that the distributional pattern of the Salientia can be adequately explained on the basis of dispersal involving only the

¹ The important study by P. J. Darlington, Jr., on "The geographical distribution of cold-blooded vertebrates" (Quart. Rev. Biol., 1948, vol. 23, no. 1, pp. 1-26; no. 2, pp. 105-123) appeared too late for proper consideration here. In regard to the existing anuran families, the author concludes that they probably originated in the Old World tropics and have dispersed by northern routes, a thesis that is not at variance with the conclusions reached in this paper.

Bering and Panamanian land bridges. As far as the Neotropical anuran fauna is concerned, it appears manifestly unnecessary to agree with Joleaud (1939) that the "cystignathids"

migrated between Australia and South America via Antarctica or that the pipids and (?) dendrobatids employed a South Atlantic bridge.

TRENDS IN ANURAN EVOLUTION

With the possible exception of the Amphicoela, which may have been differentiated as early as the Upper Jurassic, the modern anuran suborders and, in fact, most of the modern families appear abruptly in the early Tertiary. This circumstance, together with the presence of definitive anurans in the Upper Jurassic, implies that the major salientian radiation occurred during the Cretaceous. As this period had a duration of roughly 65 million years, it is not possible to determine the tempo and mode of this radiation, particularly since Cretaceous anurans are completely unknown. It is evident, however, that the rate of evolution during the Tertiary, representing an almost equivalent time interval, was relatively very much slower.

The amphibamids and *Protobatrachus* indicate, as Romer (1945) has pointed out, that the skull evolved more rapidly in an anuran direction than the postcranial skeleton. By the end of the Jurassic, however, the entire skeleton must have approached the biomechanical limit of salientian specialization. The subsequent modifications in the skull, vertebral column, pectoral girdle, and relative length of the limb segments were relatively minor refinements superimposed on an already highly specialized skeletal design.

One of the most striking features of the anuran skeleton is its capacity for variation at both the intraspecific and supraspecific levels. Among the many possible examples of intraspecific variation, an interesting one is that occurring in the sacral articulation of the early Tertiary ?pipid *Eoxenopoides remingi* described by Houghton (1931). He divides the sacral variants into five "morphological stages." More than 50 specimens, representing an exceptionally large sample for fossil anurans, were found scattered through a very localized clay deposit over 100 feet in thickness. There is no evidence that

a single variant was confined to a particular level, but rather that all or most of the stages existed simultaneously throughout the time interval represented by the deposit. The stages can be arranged in a sequence illustrating a progressive forward shift in the sacral articulation from one in which the diapophyses of the first four coccygeal vertebrae (typically fused but with well-developed transverse processes) are involved to one in which only the diapophyses of the last presacral vertebra articulate with the ilia. There is still another type in which a diapophysis of the first coccygeal vertebra and the opposite one of the last presacral make up the sacral articulation. All these variations must have permitted essentially normal locomotion, as adequate support in the sacral region is indicated in every type. *Ateolepus varius* exhibits a similar but less extreme variation (Noble, 1931). The six species of *Rana* (Taylor, 1942) in the Upper Pliocene Rexroad fauna of Kansas, described on the basis of slight differences in the morphology of the sacral vertebra, may actually represent variants of a much smaller number of species.

At the supraspecific level, the variation in characters usually considered to be of ordinal, familial, or generic significance may be very disconcerting. Although the Microhylidae are included in the Displasiocoela, Parker (1934) has pointed out that three of the eight recognized subfamilies have uniformly procoelous vertebrae, while a fourth subfamily includes some genera with a procoelous column and others with a diplasiocoelous. Other examples of this type are further discussed by Parker (1932), such as the presence or absence of teeth in the upper jaw as in the Leptodactylidae, the variation in the vomero-palatine region, in the degree of dilation of the sacral diapophyses, and in the ornamentation of the skull roof.

While intraspecific variation may indicate weak selection towards structural uniformity,

supraspecific variation implies selection towards some sort of constant morphological and biomechanical pattern at some particular taxonomic level. Why some genera of the microhylid subfamily Microhylinae are procoelous and others diplasiocoelous is unknown. There appears to be no direct environmental correlation although such, however subtle, probably exists. In spite of interesting experiments by Fick and others, there is still no satisfactory basic functional explanation for the different types of vertebral articulation.

With the small samples of fossil anurans that are usually available, it is very difficult to consider variation properly, or to distinguish between the two types just discussed. In connection with the frogs described in this paper, a number of such problems are evident, such as the significance of the skull ornamentation in *Eophractus*, the increased width of the nasal bridge in *Calyptocephalella canqueli*, and the edentulous condition and dilated sacral diapophyses of *Neoprocoela*.

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