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Systematic Status of a South American Frog, *Allophryne ruthveni* Gaige

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Gaige (1926) described *Allophryne ruthveni* as a new genus and species of diminutive bufonid from British Guiana. Noble (1931) considered *A. ruthveni* to be a toothless relative of *Centrolenella* and placed the genus in the Hylidae. Gallardo (1965) suggested that *Allophryne* is a leptodactylid of uncertain affinities. Other references to the monotypic genus have consisted only of a listing of the name or of its inclusion in a key. To date the holotype and one paratype (both females) have been reported (Gaige, 1926), and the family position of the genus remains unsettled.

A male of *Allophryne ruthveni* is among the amphibians and reptiles collected in southern British Guiana by William A. Bentley in January, 1962, and deposited in the Museum of Natural History at The University of Kansas (KU). Four additional specimens (females) are in the American Museum of Natural History; only one of the latter has definite locality data.

Acknowledgments.—We are grateful to Dr. Ernest E. Williams, Museum of Comparative Zoology (MCZ) and Dr. Richard G. Zweifel, American Museum of Natural History (AMNH) for the loan of specimens. We are further indebted to Dr. Zweifel for permission to clear and stain one specimen. Dr. William E. Duellman and Linda Trueb offered many constructive criticisms. Miss Trueb executed the drawings of the skull and finger bones. Mr. Martin Wiley provided x-ray photographs of *Allophryne*.

METHODS AND MATERIALS

Six of the seven known specimens were available for study. Measurements were taken in the manner described by Duellman (1956). One specimen was cleared and stained, using the technique of Davis and Gore (1936), in order to study the skeleton. X-ray photographs were made of another specimen for comparison.

Specimens examined.—Six, as follows: BRITISH GUIANA, *Dist. Demarara*: Marudi Creek, AMNH 44749; *Dist. Equibo*: Tumatumari, MCZ 11790 (paratype); *Dist. Rupununi (Berbice)*: Wai Wai Country, N of Acaragy Mountains, west of New River (2°N, 58°W), KU 69890. Also, 3 specimens from "probably British Guiana," AMNH 70108-10 (70110 cleared and stained).

SYSTEMATIC ACCOUNT

The availability of additional material and the new information pertaining to osteology permit an amplification of Gaige's (1926) description.

Genus *Allophryne* Gaige

Allophryne Gaige, Occas. Papers Mus. Zool., Univ. Michigan, 176:1, Oct. 14, 1926. Crawford, Annals Carnegie Mus., 21(1):29, 32, Nov. 14, 1931. Noble, The biology of the amphibia. McGraw-Hill, p. 510, 1931. Ruthven, Herpetologica, 1:3, July 11, 1936. Gallardo, Papéis Avulsos, 17:79, Jan. 1, 1965.

Type species.—*Allophryne ruthveni* Gaige.

Diagnosis and definition.—A genus of diminutive frogs; vomers, maxillae, and premaxillae edentate; skin of head strongly anchored to connective tissue on cranium; prepollical spine absent in males; disk of third finger larger than tympanum, smaller than eye; no humeral hook in either sex; ilia extending anteriorly beyond sacral expansions; adults attaining snout-vent length of 31 mm.; male having darkened external subgular vocal sac; skin of dorsum pustulate.

Allophryne ruthveni Gaige

Allophryne ruthveni Gaige, Occas. Papers Mus. Zool., Univ. Michigan, 176:1-3, pl. I, Oct. 14, 1926. Crawford, Annals Carnegie Mus., 21(1):32, Nov. 14, 1931. Ruthven, Herpetologica, 1:3, July 11, 1936. Barbour and Loveridge, Bull. Mus. Comp. Zool., 96(2):64, Feb., 1946. Peters, Occas. Papers Mus. Zool., Univ. Michigan, 539:10, Sept. 19, 1952.

Holotype.—University of Michigan Museum of Zoology 63419, adult female, from Tukeit Hill, below Kaiteur Falls, Equibo District, British Guiana; obtained in May, 1924, by E. N. Clarke.

Diagnosis.—Fingers free; toes two-thirds webbed; no supernumerary tubercles on soles or palms; no tarsal fold; elongate anal sheath, anal opening on lower surface of thighs; head broad, interorbital space 2.5 times width of upper eyelid; snout subacuminate in dorsal profile, strongly sloping in lateral profile; tympanum visible in males, concealed in females; venter areolate.

External Morphology.—(Fig. 1) *Additional features not mentioned in diagnoses:* Head wider than long, about as wide as body; supratympanic fold present; canthus rostralis rounded, loreal region slightly concave, nearly vertical; nostril at tip of snout; pupil horizontal; no teeth on maxillary, premaxillary, or vomer; tongue small, round, thick, not notched behind, free posteriorly for one-sixth of length; choanae large, only partly visible from directly below; males having darkened subgular vocal sac; vocal slits present in male.

Axillary membrane lacking or but slightly developed; no tubercles or ridge under forearm; two palmar tubercles; subarticular tubercles small, simple, round, flattened; tips of fingers slightly expanded, T-shaped, with prominent transverse groove; first finger shorter than second (stated as longer than second in diagnosis by Gaige, 1926:2); folds extending laterally from anus for a short distance, then downward to venter of thighs; no appendage on heel, no inner or outer tarsal folds or tubercles; inner metatarsal tubercle oval, about twice as long as wide; outer metatarsal tubercle nearly absent; no supernumerary tubercle on sole; subarticular tubercles on foot small, round, simple, and diffuse; toes T-shaped, slightly wider than digit; toes about two-thirds webbed (Fig. 1d).

Skin of venter coarsely areolate; skin of flanks, throat, chest, undersurfaces of arms, tibia, tarsi, dorsal surfaces of thighs, tarsi, hands, and feet smooth; skin of dorsal surfaces of tibia, forearm, back, and top and sides of head having large horny pustules (sharply spinous in male).



FIG. 1. *Altophryne ruthveni*, male (KU 69890); (a) Dorsum. (b) Thenar view of right hand. (c) Lateral profile of head. (d) Plantar view of right foot. $\times 3.5$.

Color.—Dorsum gray with irregular network of black lines and elongate blotches; flanks and labial region black with large white ocelli; dorsal surfaces of limbs gray, marked as follows: two large, elongate white spots on each thigh, concealed white spot on base of upper arm, black-edged gray transverse bars on forearms and shanks, white spot on each knee and elbow; ventral surfaces pale gray; black-edged white spot on ventral surface of thigh on each side of anal opening; chin and throat dark gray with white spots; vocal sac in male black (Fig. 1a and c).

Gaige (1926) briefly described the color, which conforms to the above in all particulars. The paratype (MCZ 11790) has lost the gray color after 40 years in preservation; now (1966) the ground-color is cream-brown, and the dorsal spotting, noted by Gaige as being black, is now brown.

The spots on the feet, tarsi, knees, thighs, flanks and upper arm are white in preservative, but in life possibly were red or yellow. These colors usually fade to white in preservative. Red or yellow spots are common aposematic colors in frogs.

Variation.—Eight measurements were taken on each specimen and four ratios were computed; these are summarized in Table 1. Gaige's illustration of the holotype shows that it has a greatly reduced pattern, whereas the para-

TABLE I.—Variation in Measurements and Proportions of *Allophryne ruthveni*. (Ranges in parentheses below means.)

Character	Male (1)	Females (5)
Snout-vent (in mm.)	20.6	23.6 (18.4–31.0)*
Tibia/snout-vent	0.43	0.43 (0.41–0.47)
Tympanum/head width	0.12	0.15 (0.14–0.16)
Eyelid/interorbital space	0.55	0.53 (0.49–0.56)
Tympanum/eye length	0.40	0.46 (0.42–0.50)

* Holotype is reported to be 31 mm. snout-vent length (Gaige, 1926). The largest measured by us was 26.2 mm. snout-vent.

type and three of the other five known specimens have relatively large and numerous spots. The male (KU 69890) and one female (AMNH 70108) have a reduced pattern intermediate between that of the holotype and the four other specimens.

The dorsal spinules are most pronounced and extensive on the male (Fig. 1) and less so in all other specimens examined. The illustration of the holotype suggests that it has equally prominent, but fewer, spinules (Gaige, 1926).

The holotype, a gravid female, is the largest known specimen (31 mm., snout-vent length). Another gravid female (AMNH 70108) has a snout-vent length of 26.2 mm.

Distribution.—All known specimens have been found in the foothills of the northeastern face of the Guiana Massif in British Guiana.

FAMILY POSITION

The following characters of *Allophryne* are those generally held to be useful in determining family relationships:

1. Presacral vertebrae procoelus, eight in number.
2. Parahyoid absent.
3. Free ribs lacking.
4. Bidder's organ absent.
5. Intercalary cartilages present in digits; phalangeal formulae 3-3-4-4 and 3-3-4-5-4.
6. Coccyx articulating with sacrum by two condyles.
7. Tarsal bones not fused.
8. Pectoral girdle arciferal.
9. Epicoracoidal horns present, free.
10. Terminal phalanges T-shaped.
11. Sacrum procoelus and diapophyses expanded.
12. Maxillae, premaxillae, and prevomers edentate.
13. Cranial roofing bones well ossified.

Griffiths (1959) accorded considerable taxonomic weight to the presence or absence of epicoracoidal horns in showing relationships among the genera placed in the Brachycephalidae [= Atelopodidae; Dendrobatidae; and Leptodactylidae (in part)] by Noble (1931). *Allophryne* possesses well-developed, free epicoracoidal horns, such as those found in the Hylidae, Centrolenidae, Leptodactylidae and Bufonidae.

The presence of intercalary elements in the digits is characteristic of the Centrolenidae, Hylidae, Phrynomeridae, Pseudidae, and the rhacophorine ranids (including the Hyperoliidae). This element is bony in the pseudids and cartilaginous in the other families. Phrynomerids and rhacophorine ranids lack epicoracoidal horns and have firmisternal pectoral girdles. Centrolenids are small, delicate, arboreal frogs having poorly ossified skulls and fused tarsal bones, but agree with *Allophryne* in having T-shaped terminal phalanges.

Only the presence of intercalary cartilages (Fig. 2) suggests relationship of *Allophryne* to the Hylidae. The T-shaped terminal phalanges suggest affinities with centrolenids, elutherodactyline leptodactylids, or certain "brachycephalid" frogs. Griffiths (1959) clearly showed that Noble's Brachycephalidae was a polyphyletic assemblage. No hylid genus is edentate, and none has either

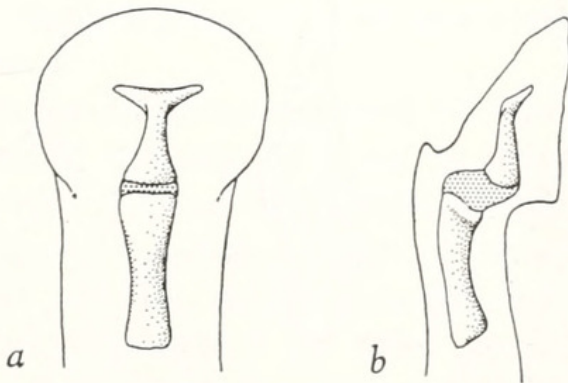


FIG. 2. Dorsal (a) and lateral (b) views of distal phalanges of third finger of *Allophryne*. $\times 40$.

T-shaped terminal phalanges or the unusual dorsal spinules. Perhaps the presence of intercalary cartilages is not indicative of relationship but instead is a parallelism (or convergence) in *Allophryne* and genera of the Centrolenidae.

CRANIAL OSTEOLOGY

The skull of *Allophryne* (Fig. 3) is distinctive among anurans; it does not closely resemble the skulls of either hylids or centrolenids, both of which have generally more delicate (except for casque-headed hylids, such as *Corythomantis*, *Diaglena*, *Osteocephalus*, *Triprion*) and generalized skulls. *Allophryne* on the other hand has a strongly ossified central region (cranial roofing bones and sphenethmoid complex) and a weak peripheral zone. The peripheral elements are reduced (maxilla, pterygoid, and squamosal) or absent (quadrate-jugal), whereas the frontoparietals, nasals, sphenethmoid, proötics, and exoccipitals form a compact central zone. An elongate frontoparietal fontanelle is present.

Dorsally (Fig. 3), the premaxillae are not visible. The proportionally gigantic septomaxillae are visible anterior to the nasals. The moderate-sized nasals are separated medially and in broad contact with the ethmoid posteriorly. The palatine process of the nasal does not meet the frontal process of the maxilla. A large frontoparietal fontanelle is evident between the frontoparietals.

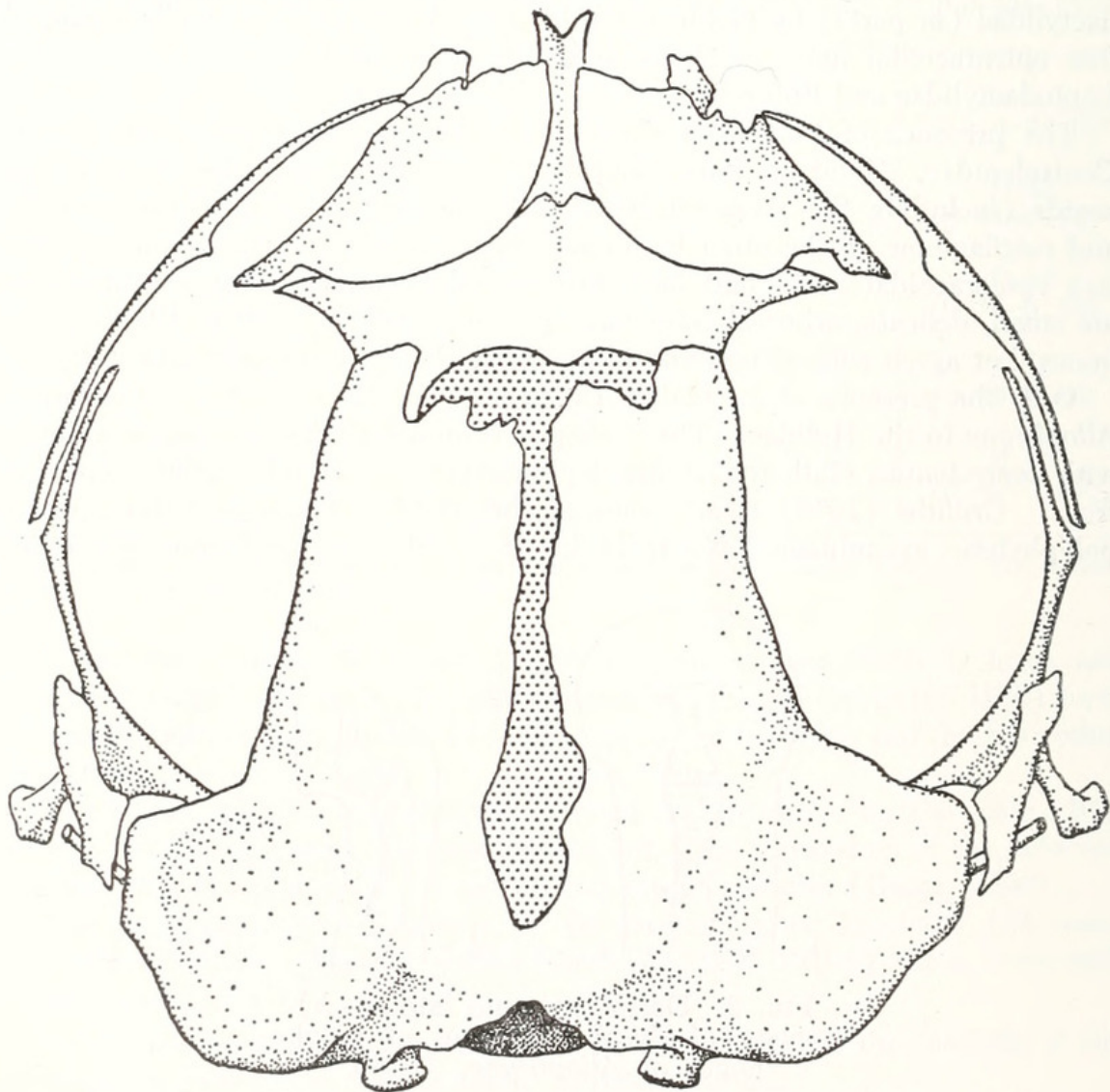


FIG. 3. Dorsal view of skull of *Allophryne* (AMNH 70110). $\times 12$.

The tegmen tympani are much reduced and maintain only cartilaginous contact with the posterior arms of the squamosals. The foramen magnum, occipital condyles, and exoccipitals show no unusual features. The *pars facialis* and frontal process of the maxilla are greatly reduced. The maxilla and premaxilla are articulated. The high, narrow alary processes of the premaxillae extend dorsally about two-thirds of the height of the snout. A cartilaginous internasal septum is illustrated (Fig. 3), but sectioning is necessary to determine the true nature and extent of this element.

Ventrally, the skull lacks palatines. The maxillae, premaxillae, and prevomers are edentate. The parasphenoid is large with relatively short, stout alary (lateral) processes. The sphenethmoid is extensive in ventral aspect and forms the major supporting structure in the anterior part of the skull. The pterygoid has a broad articulation with the maxilla, a tenuous contact with the squamosal, but is not attached to the proötic. The anterior (zygomatic) process of the squamosal is greatly reduced (only about one-third the length of the posterior process).

DISCUSSION

The skull of *Allophryne* is definitely non-hylid. Most of the postcranial features do not help to clarify relationships. *Allophryne* shares several osteological features with the Dendrobatidae: T-shaped terminal phalanges, general cranial morphology and procoelus vertebrae. But, the dendrobatids possess firmisternal pectoral girdles and lack epicoracoidal horns. Also, no dendrobatid has intercalary elements in the digits. We are, therefore, left with a taxonomic enigma. In one or more characters generally regarded as important, *Allophryne* differs from all presently defined families of frogs. The Hylidae and Dendrobatidae are the only currently recognized families in which the genus might be placed.

The function and taxonomic importance of the large septomaxillae are unknown and are probably associated with the modification of the sphenethmoid-prevomer area. A more detailed study of the cranial osteology of *Allophryne*, especially the structural relationships of the sphenethmoid-prevomer area may elucidate the relationships of *Allophryne*.

The relationships of *Allophryne* cannot be understood without a re-analysis of some of the features used as major criteria in frog classification (the nature of an intercalated cartilage; the nature of the sternal complex; the relative value of cranial osteology; the vertebral structure; and the thigh musculature). Some of these features have been investigated by other workers, most notably Griffiths, but others have not and need re-examination. A reanalysis of some of the major criteria used in frog classification is in progress (Callison, Lynch, and Trueb) and upon completion of that study we think the relationships of *Allophryne* will become apparent.

A more comprehensive study of the cranial anatomy of certain hylids, leptodactylids, dendrobatids, and atelopodids along with that of *Allophryne* is needed to clarify the relationships of *Allophryne*, and might indicate that the recognition of a fifth family is necessary.

CONCLUSION

Among currently recognized families of frogs, *Allophryne* is least different from the Hylidae although it is our opinion that inclusion of this genus in the Hylidae probably represents an unnatural classification. However, the present evidence suggesting that *Allophryne* should be in another family is less convincing than evidence suggesting it should be in the Hylidae. We tentatively place *Allophryne* in the Hylidae.

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