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On *Atopophrynus*, a Recently Described Frog Wrongly Assigned to the Dendrobatidae

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ABSTRACT

In 1982 Lynch and Ruíz-Carranza named a new genus and species of small Andean frog, *Atopophrynus syntomopus*, based on three specimens from the Cordillera Central in northern Colombia. They assigned it to the Dendrobatidae without explanation, but reexamination of the two paratopotypes (one cleared and stained) clearly contradicts a dendrobatid relationship. There are numerous differences and no significant points of similarity. The taxon is redescribed and its familial assignment reconsidered. *Atopophrynus* might be comfortably accommodated in the Bufonidae, but additional specimens are needed for determining presence or absence of the synapomorphic Bidder's organ and other bufonid apomorphies.

Two possible synapomorphies (long and slender

paired anterior processes on each hyale of the hyoid, and internal concealment of first toe) seem to unite *Atopophrynus* with *Geobatrachus*, a monotypic genus endemic to the Sierra Nevada de Santa Marta—an isolated block of the Cordillera Central some 500 km from the type locality of *Atopophrynus syntomopus*. A sister-group relationship is suggestive, although marked differences in jaw musculature and other features are not explained. *Geobatrachus* is a presumptive member of the Leptodactylidae. Therefore, *Atopophrynus syntomopus* is placed in the same family as *Geobatrachus*. This assignment can only be provisional, since the Leptodactylidae are a family that is defined on the basis of primitive characters. Be that as it may, *Atopophrynus* is not a dendrobatid.

INTRODUCTION

Lynch and Ruíz-Carranza (1982) named *Atopophrynus syntomopus* as a new genus and new species of "poison-dart frog" from the

central Andes of northern Colombia. These authors did not state why they attributed *Atopophrynus* to the family Dendrobatidae, al-

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FIG. 1. *Atopophrynus syntomopus* Lynch and Ruíz-C., 1982. Dorsal and ventral views of one of the three known specimens, a paratopotype (ICN 8612), $\times 2.9$.

though they pointed out some fundamental anatomical differences between it and dendrobatids as previously known. Myers and Daly (1983) had learned of the description in time to mention *Atopophrynus* among the several other recognized genera of dendrobatids, but Maxson and Myers (1985) commented in passing that the familial placement of the genus is uncorroborated.

Atopophrynus syntomopus is known only from the holotype and two paratopotypes, but through the courtesy of the original authors we have been able to study the paratypic specimens. If we could have confirmed *Atopophrynus* as a dendrobatid, the reexamination of these specimens would have contributed data to our ongoing analyses of phylogeny within that family. We are forced to conclude, however, that *Atopophrynus* is not a dendrobatid and that its relationship lies instead within either the Bufonidae or Leptodactylidae. The following description and illustrations are intended to supplement Lynch and Ruíz-Carranza's paper and to provide a basis for our discussion of possible

relationships and recommendation for familial reassignment.

ACKNOWLEDGMENTS

We are grateful to Prof. Pedro M. Ruíz-Carranza for authorizing the loan of specimens belonging to the Instituto de Ciencias Naturales (ICN), Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá, and to Prof. John D. Lynch for effecting transfer of the loan from the School of Life Sciences, University of Nebraska. Mr. Guido Dingerkus, in the American Museum's Department of Ichthyology, kindly demonstrated his new technique for staining cartilage in cleared specimens already stained for bone. We thank Drs. David C. Cannatella, Linda Trueb, and Richard G. Zweifel for their interest and for comments on the manuscript.

EXTERNAL MORPHOLOGY

Atopophrynus syntomopus is a small-bodied earless frog approaching 20 mm from snout to vent, with disproportionately large

forelimbs and with large webbed feet that have only four externally visible toes (fig. 1). The sole alcoholic specimen seen by us is ICN 8612,³ measuring 19.6 mm snout-to-vent length (SVL) and determined by dissection to be an adult female. A lateral incision into the body cavity revealed a small number of closely packed unpigmented (yellow) ova that are quite large, with diameters roughly in the range of 1.0–1.5 mm (largest ova were 1.8–2.0 mm in another specimen, ICN 8613, fide Lynch and Ruiz-Carranza).

Skin of dorsum nearly smooth in preservative, with a few barely discernible small smooth warts or tubercles in sacral region; a few small tubercles on upper lip. Venter nearly smooth, but with weakly defined broad granules, some of which bear white spots (fig. 1). Head wider than long and narrower than body; greatest head width (between angles of jaws) 82 percent of greatest body width, 35 percent of SVL. Head width between outer edges of upper eyelids about 80 percent of head width between angles of jaws. Head strongly sloping in profile, as well shown in drawing of holotype in original description; snout broad, with tip slightly pointed in dorsal (fig. 1) and ventral view, protruding in profile. Nares situated well behind tip of snout and directed posterodorsally (not “anterolaterally” as in original description); nares visible from above and from in front, but only the narial protuberances (and not the posterodorsally directed openings) are visible from below. Canthus rostralis rounded; loreal region slightly concave, sloping outward to lip. Interorbital distance about twice the width of an upper eyelid. Length of snout shorter than eye length (snout/eye = 0.81; center naris–edge eye/eye = 0.54). Tympanum absent.

Hand large, its length (proximal edge outer metacarpal tubercle to tip longest finger) 91 percent of greatest head width, 32 percent of SVL. Relative length of appressed fingers $3 > 4 > 2 > 1$; all digits except first broad and flat, with fleshy basal webbing (fig. 2). Finger 1 short and distally narrowed, without disc or pad; fingers 2–4 with broad, rounded, flat

discs bearing subdigital pads⁴ that are wider than long. Disc of third finger 1.4 times wider than finger (penultimate phalanx). A moderate-size circular outer metacarpal tubercle on median base of palm, and a smaller oval tubercle on base of first finger; these tubercles are distinct although low and rounded. No other tubercles on hand except for barely discernible subarticular swellings. *No scutes atop discs of fingers or toes* (despite claim in original description of paired scutes on fingers; see figs. 2, 7).

Hind limbs of moderate length, with heel of appressed limb reaching eye; heels fail to touch when tibia are parallel to thighs positioned at right angles to body; tibia 47 percent of SVL. Bones of first toe concealed within a flange on medial edge of second toe—only four toes present externally, with relative length of $4 > 5 > 3 > 2$ when appressed; toes broad, distally flattened and apically rounded, with the apical disc of all except outermost (“fifth”) toe wider than penultimate phalanx; subdigital pads wider than long. Feet extensively webbed (fig. 1; see also drawing in original description). A small protuberant outer metatarsal tubercle, and an oval nonprotuberant inner metatarsal tubercle at base of the medially protuberant flange within which is concealed the first digit. Subarticular tubercles barely discernible. No tarsal tubercle or tarsal fold.

In life, “dorsum red with green markings overlain with white flecks” and “posterior surfaces of thighs olive-green” (Lynch and Ruiz-Carranza, 1982). In preservative the dorsum of ICN 8612 is obscurely mottled blackish brown on light brown, with a pair of pale brown divergent spots on the middle of the back (fig. 1); the limbs, including posterior thigh surfaces, are colored like the body, with a weak banded pattern. (The original description mentions a dark interorbital bar and scapular and sacral markings which are not obvious on this paratype.) In life, “undersides pale olive with blue-white spots edged with brown,” whereas in preservative

³ Through the courtesy of Prof. Ruiz-C. and the Instituto de Ciencias Naturales, this specimen has been exchanged to the American Museum (AMNH 122260).

⁴ The term *pad* is here given a normal anatomical meaning. The terms *disc* and *pad* are reversed in Lynch and Ruiz-Carranza (1982) following the customary usage of the first author (but see Lynch and Myers, 1983, p. 489n).



FIG. 2. Left and right hands of *Atopophrynus syntomopus* (ICN 8612) in dorsal view, $\times 12$.

the ventral surfaces are "cream, blotched with white and flecked with brown; pair of brown blotches on breast" (op. cit.). The midline of the venter is nearly unpigmented, and the white spots extend ventrolaterally onto the lower sides. The iris was "bright copper" in life.

MEASUREMENTS (IN MM): The total length of ICN 8612, an adult female, was measured with dial calipers; other measurements were made with an ocular micrometer in a dissecting microscope. Length from snout to vent 19.6; tibia length from heel to top of knee (with limb segments at right angles) 9.2; greatest width of body 8.4; greatest head width (between angles of jaws) 6.9; head width between outer edges upper eyelids 5.5; approximate interorbital distance at midorbit 2.5; head length (oblique) from tip of snout to angle of jaws about 4.5 (jaws had been cut on both sides); tip of snout to center of naris (lateral plane) 0.7; center of naris to anterior corner of eye 1.4; distance between centers of nares 2.7; eye length from anterior to posterior corner 2.6; hand length from proximal edge of large medial palmar tubercle to tip of longest (third) finger 6.3; width of disc of third finger 1.3; width of third finger (penultimate phalanx) below disc 0.9; width of disc of second visible toe (=third) 1.0; width of second visible toe (penultimate phalanx) below disc 0.9; width of disc of third visible toe (=fourth) 1.1; width of phalanx below disc of this toe 0.8.

MYOLOGY

The original description of *Atopophrynus* contains no mention of musculature although one of the paratypes (ICN 8613) had been skinned prior to clearing and staining. The muscle tissue of this specimen, however, had not been completely cleared to transparency, and some of the slightly opaque muscles could be examined before the frog was subjected to further clearing and restaining (see Osteology).

JAW MUSCLES: The massive m. depressor mandibulae originates entirely from the long (1.3 mm) otic ramus of the squamosal; none of its fibers could be traced to an origin from the dorsal fascia. Both the m. adductor mandibulae externus superficialis and the deeper m. adductor mandibulae posterior subexternus seem to be present. As confirmation, on each side after cutting and reflecting the first muscle, a fine fiber was found that appeared to be the mandibular branch of the trigeminal nerve passing between these two adductor muscles.

THIGH MUSCLES: The m. tensor fasciae latae is a narrow muscle originating on the rear (i.e., on posterior one-third) of the ilium and inserting on the cruralis at about midthigh. The m. sartorius is rather broad (relatively wider than in *Atelopus zeteki*) but it is thin and had been partially destroyed on both legs, probably during skinning. With the sartorius removed, the insertion tendon of the m.

semitendinosus is clearly visible without displacing any part of the mm. gracilis complex. The long tendon of the deep semitendinosus muscle emerges to pass ventrally over that of the mm. gracilis complex prior to insertion.

OSTEOLOGY

One of the paratypes, an adult female (ICN 8613), had been previously skinned, partially cleared in KOH, and the bones weakly stained with alizarin red. After we examined several of the slightly opaque muscles (see above), the flesh of this specimen was cleared to transparency, the cartilage stained with alcian blue, and the bones stained a darker red.⁵ The specimen was then compared with 38 species of cleared and stained dendrobatids (19 *Colostethus*, 16 *Dendrobates*, 3 *Phyllobates*).

SKULL

The skull of *Atopophrynus* is poorly ossified (fig. 3). The bones are thin and many are relatively small. They are generally nonoverlapping or make only slight contact.

NASALS: These bones are small and arc shaped. They are dorsolateral to the nasal capsule; therefore most of the nasal organ is unprotected and unroofed by bone. A small fragment of the right nasal is separated from the rest of the bone.

SEPTOMAXILLAE: These are tiny U-shaped bones situated anterior and deep to the nasals.

SPHENETHMOID: Dorsally this bone is shallow medially, extends posteriorly one-third of the length along the lateral margin of the brain, but is minimally overlapped by the frontoparietals. Expansion anterior to the brain is minimal and does not reach the nasal capsules. Ventrally, the sphenethmoid is medially divided and does not come in contact

⁵ We are grateful to Guido Dingerkus for demonstrating his new and still unpublished technique for staining cartilage in specimens that already have been stained for bone. Cartilage in such specimens does not stain as darkly as in those differentially stained in one continuous process (Dingerkus and Uhler, 1977), but the ability to reveal cartilage in some alizarin-stained specimens is a decided advance.

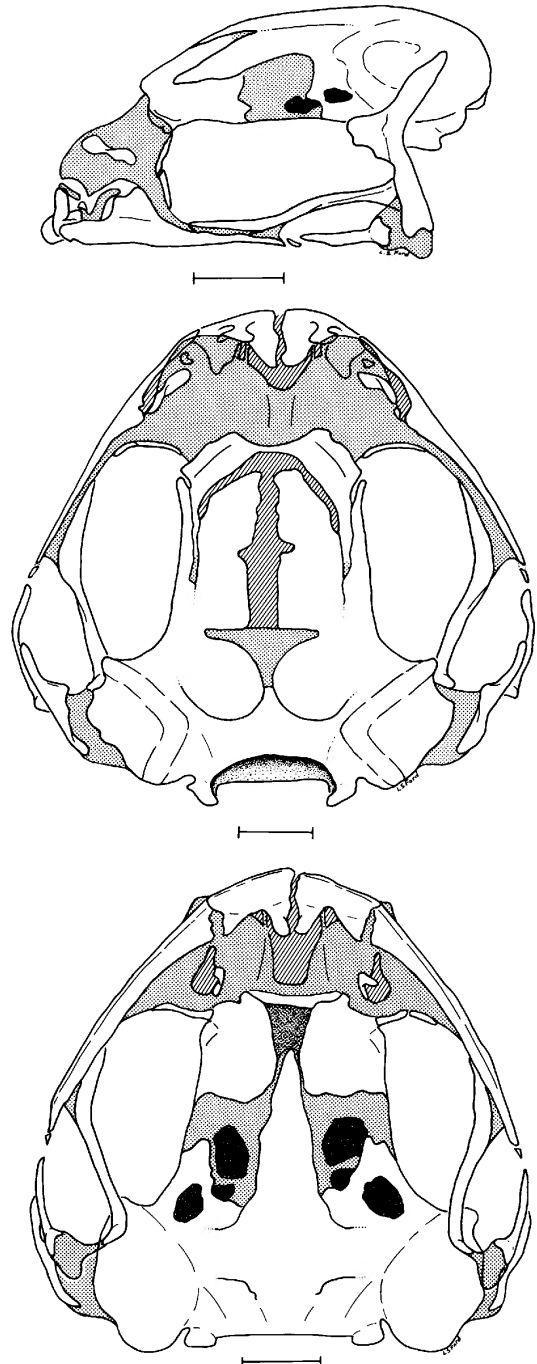


FIG. 3. Skull of *Atopophrynus syntomopus* (ICN 8613, paratopotype) in lateral, dorsal, and ventral views. Cartilage gray; some open areas atop skull and in snout region represented by hatched pattern. Lines = 1 mm.

with the parasphenoid; the two halves of the sphenethmoid are separated by calcified car-

tilage. Ventrolaterally, this bone extends posteriorly for one-third of the length of the brain.

FRONTO-PARIETALS: These are large relative to the other dermal roofing bones, with thin to incomplete ossification and minimal contact with surrounding bones. Anteriorly, each is forked along the lateral margin, and only slightly overlaps the sphenethmoid; medially they are not in contact, resulting in an asymmetric, long, narrow exposure of the underlying frontoparietal fontanelle. Posteromedially, the frontoparietals cover the parietal fontanelles, but do not cover the taenia tecti medialis and transversum; posterolaterally, the sutures are indistinguishable and the bones may be fused to the prootic.

PROOTIC/EXOCCIPITAL: The prootic and exoccipital are completely fused. As noted above, the frontoparietals seem to be partially fused to the prootic. The anterior margin of the epiotic eminences extends past the surrounding prootic. Ventrally, the prootic extends anteriorly two-fifths of the length along the lateral margin of the brain; moderate-size prootic foramina are present for the passage of nerves V–VII. No trochlear foramina are detectable in this specimen; therefore nerve IV presumably exits through the optic foramen in the orbital cartilage with nerve II (Duellman and Trueb, 1985, p. 394). Laterally, the prootic and exoccipital are widely separated from the otic ramus of the squamosal because of incomplete ossification over the crista parotica. Occipital condyles are widely separated, and columellae are lacking.

PREMAXILLAE: These bones are edentate, narrowly separated medially, and overlapped by the maxillae at the posterolateral edge of the palatine process. The palatine process is prominent with an indentation at the midsection that extends to the alary process. The alary process flares dorsally (as opposed to “anterodorsally” in the original description) and curves laterally to contact the medial margin of the alary cartilage that forms the anterior portion of the nasal capsule.

MAXILLAE: As noted above, the maxilla minimally overlaps the premaxilla; it is narrowly separated from the quadratojugal and is edentate. The posterior tip of the maxilla in this specimen is fractured on both sides. Anteriorly, the pars palatina flares to the width of the palatine process of the premaxilla and

narrows posteriorly. The pars facialis is low, except for a prominent preorbital process.

QUADRATOJUGALS: These bones are thin, narrow anteriorly, and expand posteriorly at the articulation with the quadrate. They do not articulate with the maxillae or squamosals.

SQUAMOSALS: The squamosals are almost vertically oriented, triradiate bones. The uniform ventral ramus forms an 82° angle with the maxillary arch. The otic ramus is long (=1.3 mm) but does not overlap the ossified portion of the crista parotica; the ramus lies laterally adjacent to it. The anteriorly directed zygomatic ramus is short and extends one-fifth the distance to the maxillary arch, but it is as wide at the base as long.

PTERYGOIDS: These bones are sigmoid in shape and lack a medial ramus. The anterior ramus is in broad contact with the palatine shelf of the maxilla, and tapers to a fine point anteriorly, but does not extend to the anterior edge of the orbit. Posteriorly the anterior ramus angles medially to overlap the otic capsule. The posterior ramus is short, directed posterolaterally, and articulates with a medial extension of the quadrate.

VOMERS: These bones are small, C-shaped, and support the medial margin of the choanae. They are oriented almost vertically relative to the ventral plane of the skull and are closely placed to the anterior margins of the palatines and ossified portion of the sphenethmoid.

PALATINES: These small, thin slivers of bone are in minimal contact with the lateral margin of the sphenethmoid, and are widely separated from the maxillae. The left palatine is broken.

PARASPHENOID: This bone is triradiate and prominent on the ventral side of the braincase. The cultriform process extends anteriorly to three-fourths the length of the orbit and lies adjacent to the sphenethmoid. Most of the lateral alae and posterior edge are fused to the prootic and exoccipital.

CHONDROCRANIUM

NASAL CARTILAGES: Dorsally, the nasal region is shielded by very little bone, and furthermore there is no ossification of the nasal cartilages. Protection of this region is achieved

predominantly by extensive oblique cartilages. The nares are directed laterally; the opening is supported dorsally and posteriorly by the oblique cartilage and anteriorly by the alary cartilage, which extends laterally past the oblique cartilage. The septum nasi is expansive and widely separates the nasal capsules.

CARTILAGES OF THE BRAINCASE: The orbital cartilages cover the midsection of the brain that is not protected by the sphenethmoid, prootic, frontoparietal, or parasphenoid bones. Ventrally, optic and oculomotor foramina are barely detectable (because the cartilage is lightly stained) for the passage of nerves II and III, respectively; because no trochlear foramen was found in the prootic, nerve IV probably exits through the optic foramen with nerve II. The taenia tecti medialis and transversum are present and not covered by the frontoparietals.

MANDIBLE

MENTOMECKELIAN BONES: These are cylinders of ossification at the anterior end of Meckel's cartilage. They do not articulate medially but are fused anteriorly and laterally with the overlapping dentaries.

DENTARIES: These are slender, fused to the mentomeckelian bones, and extend posteriorly on the lateral side of Meckel's cartilage for one-half the length of the mandible.

ANGULOSPLENIALS: These lie medial to Meckel's cartilage. Anteriorly they are slender and do not articulate with the mentomeckelian bones. Posteriorly they expand until they medially cover Meckel's cartilage at the level of the articulation of the jaw.

HYOLARYNGEAL SKELETON

HYOID: The hyalia (fig. 4) are long and slender, angling posterolaterally to the jaw attachments. Each hyale bears two slender and relatively long processes that extend directly anteriorly; in each pair, the tips of the anterior processes curve toward one another but remain well separated. The two medialmost anterior processes form a deep hyolaryngeal sinus. Both the alary and posterolateral processes of the hyoid plate are crescent-shaped and directed anterolaterally. The postero-

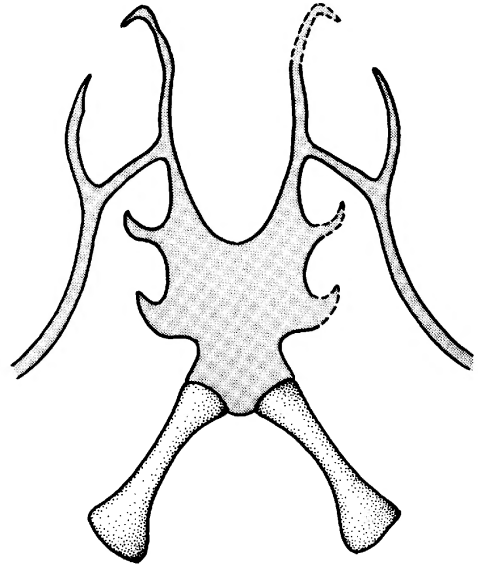


FIG. 4. Hyoid apparatus of *Atopophrynus syntomopus* (ICN 8613) in ventral view, $\times 14.6$. Cartilage gray.

medial processes are ossified and directed posterolaterally.

LARYNX: The cricoid ring seems complete. The dorsal aspect is obscured slightly owing to the lightly stained cartilage and the delicate condition of the specimen. However, the ring seems to be complete and is directed posteriorly in a V-shape. Ventrally, the bronchial processes are long. There are no cardiac processes, and the lateral processes are directed anterolaterally. The configuration of the pair of arytenoid cartilages is funnel-shaped; dorsally, the pair of cartilages are slightly separated and they extend and expand posteriorly to form the mouth of the funnellike configuration. Ventrally, the cartilages are widely separated but are short and do not expand posteriorly.

AXIAL SKELETON

There are eight procoelous vertebrae; the first two are fused. The neural arches are not imbricate. The transverse processes of presacral vertebra II are directed anteriorly at a 29° angle with the longitudinal axis of the vertebral column; processes of vertebrae III–VI (III is the largest) are directed posteriorly at 19° , 28° , 30° , and 25° angles, respectively. Processes of vertebrae VII–VIII are directed

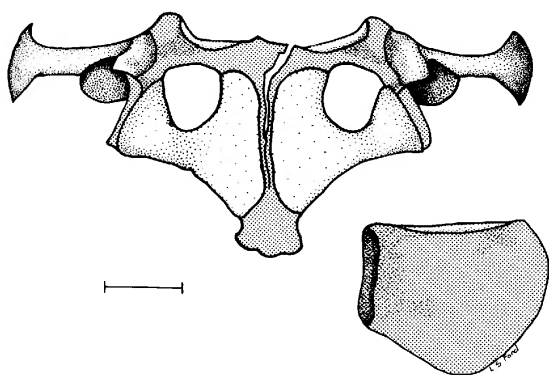


FIG. 5. Pectoral girdle of *Atopophrynus syntomopus* (ICN 8613) shown in ventral view, except lower right (suprascapula and cleithrum) is in dorsal perspective. Cartilage gray (anterior split in procoracoid-epicoracoid cartilages is an artifact). Line = 1 mm.

laterally. The formula for the relative lengths of the transverse processes (II–VIII) and sacrum (S) is III > S = IV > V = VI = VII = VIII > II. The articulation between the sacrum and coccyx is bicondylar. The shaft of the coccyx is slender, and the ends are wider than the shaft; the posterior end of the coccyx is two-thirds as wide as at the articulation. The dorsal coccygeal ridge begins at the articulation and continues slightly past one-half the length of the coccyx; a small process at the point of articulation extends anteriorly past the coccyx and overlaps the sacrum.

PECTORAL GIRDLE

The pectoral girdle (fig. 5) is firmisternal and is narrow (width between glenoid fossae) in relation to the size of the specimen. The coracoids are large, obliquely oriented to form a 61.5° angle with the longitudinal midline axis of the body, and as wide as they are long. The medial margins of the coracoids are expansively widened and border the medial edge of the pectoral fenestrae; less prominent lateral expansions form most of the medial glenoid cavity. The clavicles are short, slender, and curved anterolaterally at the distal ends. They are not in contact with the coracoids or scapulae, and are widely separated medially. An omosternum is absent. The broad, truncate, posteromedial body of cartilage in the pectoral girdle is presumably the sternum,

based on its position and size. It is indistinguishable from the epicoracoid cartilage; however, all the cartilages (epicoracoids, procoracoids) in the girdle are fused. The epicoracoid cartilages, which have no detectable posterior horns (sensu Griffiths, 1963, pp. 264–265), fuse to form a slender strip of cartilage between the coracoids and are indistinguishable from the procoracoid cartilages anteriorly. Anteriorly the bulk of the pectoral girdle is composed of the fused procoracoid cartilages, which expand from midline to the scapulae, where they overlap and form the anteromedial corner of the glenoid cavities. Small patches of endochondral ossification are found in these cartilages. A split in the fused cartilage from the anterior edge of the procoracoids continues through the epicoracoids between the coracoid bones, but this seems to be an unnatural separation that probably occurred during the preparation of the specimen (both humeri are broken also). The scapulae are not in contact with the clavicles or coracoids; they form most of the anterior glenoid cavity and articulate dorsally with the suprascapulae. The suprascapulae are predominantly cartilaginous with small areas of endochondral ossification. The cleithra are small and slender.

PELVIC GIRDLE

Anteriorly, the ilia loosely articulate with the sacral diapophyses and overlap balls of cartilage at the ends of the diapophyses. The iliosacral articulation is similar to “type IIB” (Emerson, 1979); the ligament scars are situated near the distal end of the posterolaterally oriented sacral diapophyses and there is a small nongrooved cartilaginous tip on the diapophysis. But it differs from Emerson’s type IIB in that the diapophyses are somewhat expanded rather than narrow (fig. 6); the iliolumbaris muscle and the sesamoid cartilage could not be examined in this specimen. The ilia are bowed laterally and lack detectable crests. The distance between the ilia at the sacral articulation is three-fourths the length of the ilia (as measured from the point of sacral articulation to the anteromedial point of the ilial articulation). The articulation between the individual ilia projects slightly anteriorly. The preacetabular angle of

each ilium is 90°. Posteriorly, a simple dorsal ilial prominence is broad, low, and projects dorsolaterally. The distance between the posterior rims of the acetabula is one-half the distance between the individual dorsal prominences. The ischium is ossified, and the pubis is cartilaginous. The postacetabular rim of the ischium and pubis is smooth and semi-circular in shape.

APPENDAGES

FORELIMBS: The humeri are stocky; the deltoid crests are prominent and the relative diameter of the bone seems large for the overall size of this female frog. The proximal and distal condyles of articulation are large; the proximal end expands to the diameter of the bone including the deltoid crest, and the distal end is twice the diameter of the shaft. There are five distinct carpal bones as defined by Jarošová (1973): radiale, ulnare, preaxiale centrale, postaxiale centrale, and distale carpal II. The preaxiale centrale and distale carpal II are partially fused, this fusion being better developed in the left carpus. The postaxiale centrale is large; based on its distal position, it seems to be a composite fusion involving the postaxiale and distale carpales III and IV. The prepollex consists of one bony element. The phalangeal formula is 2-2-3-3; the phalanges of the first digit are extremely reduced. Except for the reduced first digit, the terminal phalanges are prominently T-shaped. The terminal phalanx (stem of the T) is long in digits II-IV, resulting in the distal transverse process (top of the T) being positioned more than halfway toward the distal margin of the finger disc. The distal transverse process of a terminal phalanx is long, at least twice the width of a penultimate phalanx at midpoint.

HIND LIMBS: The femur and tibiofibula are long and unremarkable. The astragalus and calcaneus are fused at proximal and distal ends only. One heterotopic element is present; the cartilago sesamoides is found at the tibiofibular-tarsal joint (Nussbaum, 1982). There are three tarsal bones; the medial one is cartilaginous. All three prehallical elements are cartilaginous. The phalangeal formula is 2-2-3-4-3 and the first digit is extremely reduced. The terminal phalanges are promi-

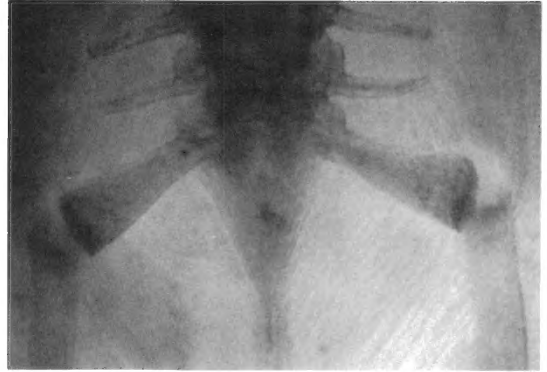


FIG. 6. Dilated sacral diapophyses of *Atopophrynus syntomopus* (ICN 8613), $\times 12$.

nently T-shaped, except that digit I is claw-shaped. The terminal phalanx (stem of the T) is long in digits II-IV, resulting in the distal transverse process (top of the T) being positioned over halfway toward the distal margin of the toe disc. The distal transverse process of a terminal phalanx is long, at least twice the width of the penultimate phalanx at midpoint.

COMPARISON WITH DENDROBATIDS

We find no support for Lynch and Ruiz-Carranza's (1982) claim that *Atopophrynus syntomopus* is a member of the Dendrobatidae. Curiously, they gave no reason for this familial placement. The firmisternal condition of the pectoral girdle, T-shaped terminal phalanges, and paired scutes atop the finger discs were the only characters given in the original description that possibly seem to suggest such a relationship. But our examination of the paratypic material shows that (1) the purported digital scutes are absent rather than simply "ill-defined," (2) the firmisterny seems not to be homologous with the dendrobatid condition, and (3) there even are proportional differences in the terminal phalanges. Major points of comparison between *Atopophrynus* and dendrobatids are discussed below.

EXTERNAL MORPHOLOGY: The vast majority of dendrobatid frogs share a surprisingly uniform morphology, with which *Atopophrynus* agrees in no particular detail. It is a terrestrial or semiaquatic frog with arms and

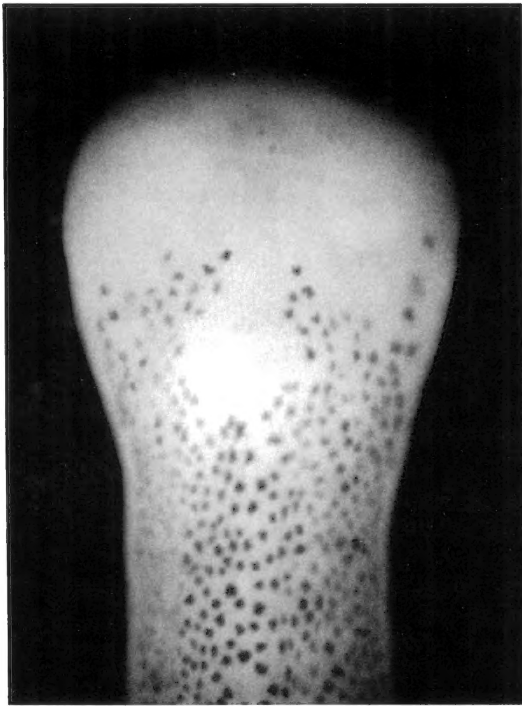


FIG. 7. Third finger of right hand (fig. 2) of *Atopophrynus syntomopus* (ICN 8612) in dorsal view, $\times 40$. The T-shaped terminal phalanx is visible through the unpigmented digital tip, which lacks dorsal scutes.

hands disproportionately large for the head and body (fig. 1); hand length/head width = 0.91, and a ratio this large would be expected only in an arboreal *Dendrobates*. The flattened digits of the hands and feet are relatively broader than in dendrobatids or most other frogs, and, based on the one alcoholic paratype, there are no scutes atop either finger or toe discs. Although we have not examined the holotype nor did we see the other paratype before it was skinned and partially cleared, we voice a reasonable doubt that either specimen has or had an "ill-defined pair of scutes on tops of pads [=discs] on fingers II-IV." The presence of dorsal digital scutes implies a tissue thickening, whereas the digital-tip skin is so thin in *Atopophrynus* that the terminal phalanx is visible in the absence of melanophores (fig. 7). The tops of some digits (fig. 2) bear a poorly defined pair of spots formed by the absence of melanophores, and we suspect that it was these which were mistaken for paired scutes.

As realized by Lynch and Ruíz-Carranza, the concealed first toe of *Atopophrynus* has no parallel in the Dendrobatidae. They erred in a minor way, however, in stating (pp. 557, 561) that the extensively webbed feet and lack of a tarsal fold or tubercle separate *Atopophrynus* from all dendrobatids, although these character states are indeed uncommon in that group. The hind foot webbing, however, seems thicker and less membranous than in those dendrobatids that have webbed feet.

Much of the characteristic appearance of dendrobatids is vested in the head. The eyes are protuberant, and head width between the outer edges of the upper eyelids often approaches or equals head width between the angles of the jaws. The snout slopes gently forward but the loreal region is more often vertical than sloping. The posterolaterally directed nares are situated close to the tip of the snout, which is rounded to truncate in dorsal view. The tympanic ring is concealed posterodorsally owing to a synapomorphic arrangement of the depressor mandibulae muscle (see below). The head of *Atopophrynus* differs in all these particulars, and the complete absence of the ear is unknown in the Dendrobatidae.

The Dendrobatidae are renowned for variability of coloration but normally there is a well-defined pattern, and the vague red-and-green dorsal coloring of *Atopophrynus* would be unusual in the family. Thus there is not a single external feature of *Atopophrynus syntomopus* that is reminiscent of the Dendrobatidae generally, and only a few scattered features are shared by the occasional dendrobatid species (e.g., sloping loreal region, lack of tarsal tubercle, extensively webbed feet).

JAW MUSCLES: A dendrobatid synapomorphy is that the posterodorsal part of the tympanum is subcutaneously tilted under the anterior edge of the massive superficial slip of the m. depressor mandibulae. The superficial slip is the major part of this muscle and it originates from the dorsal fascia; it conceals a smaller, deeper slip that always originates from the otic ramus of the squamosal bone; there may be a still smaller third slip originating from the tympanic ring, but sometimes the few fibers having a tympanic attachment cannot otherwise be separated from

the second slip (Myers et al., 1984, p. 8). Thus the tympanic ring plays only a minor, albeit variable, role in the origin of the depressor mandibulae muscle of dendrobatids, and it is not evident that the complete loss of the ear (as in *Atopophrynus*) should cause a major realignment of this muscle. But in *Atopophrynus*, the m. depressor mandibulae apparently forms a single massive slip that seems to originate *entirely* from the long otic ramus of the squamosal bone. No fibers could be traced to the dorsal fascia of paratype ICN 8613 (although myological study of a partially cleared and stained specimen does leave something to be desired).

So far as is known, dendrobatids lack the m. adductor mandibulae externus, although this muscle appears to be present in *Atopophrynus*.

THIGH MUSCLES: In all dendrobatids so far reported in the literature or examined by us, the synapomorphic condition is that the tendon of the m. semitendinosus pierces the tendon of the mm. gracilis complex prior to insertion. In *Atopophrynus*, however, the insertion of the semitendinosus is the bufonoid type, with the tendon passing ventrally to the gracilis tendon.

SKULL: The skulls of dendrobatids and *Atopophrynus* exhibit conflicting character states. Those for dendrobatids are listed with the state in *Atopophrynus* following in parentheses. In dendrobatids the alary processes of the maxillae are tilted anterolaterally (directed dorsally [not "anterodorsally" as in original description]); the palatines are absent except in a few *Colostethus* species (present); nasals very large (small); sphenethmoid expansive posteriorly over braincase and anteriorly toward the nasal capsule (no anterior expansion and dorsally the posterior expansion is limited to lateral sides of the braincase); the ventral ramus of the squamosal and maxillary arch form a 45–65° angle (angle is 82°); the medial ramus of the pterygoid is present (absent); a retroarticular process on the mandible is present (absent).

The nasal capsules are unusually widely separated in *Atopophrynus* by an expansive septum nasi cartilage, but they are closely set in dendrobatids. The taenia tecti medialis and transversum are present in *Atopophrynus* but are absent in dendrobatids. The oculomotor

foramen and most of the optic foramen are enclosed in bone in dendrobatids. Prominent orbital cartilage surrounds these foramina in *Atopophrynus*, but generally is not present in dendrobatids; it is found in several *Colostethus* (*C. inguinalis*, *C. talamancae*, *C. trinitatis*), but is restricted to the anterior margin of the optic foramen.

HYOLARYNGEAL SKELETON: In dendrobatids, each of the two hyalia of the hyoid bears a single long anterior process, whereas *Atopophrynus* is odd in that each hyale bears two long anterior processes. Also the posterolateral process of the hyoid plate in *Atopophrynus* may be unique among frogs because it is directed anterolaterally (fig. 4).

AXIAL SKELETON: There is less size deviation among the transverse processes and between the processes and the sacrum in dendrobatids than in *Atopophrynus*. Also, in dendrobatids the length of the sacrum is approximately equal to or slightly larger or smaller than most of the processes (III–VIII), whereas in *Atopophrynus* the sacrum is one-fourth as long as the processes. The sacral diapophyses in *Atopophrynus* are dilated (fig. 6) as opposed to being usually rounded in dendrobatids. The anterior projection of the coccygeal ridge that overlaps the sacrum in *Atopophrynus* is absent in dendrobatids.

PECTORAL GIRDLE: Firmisterny is a character that, when loosely defined, unites other groups of anurans as well as dendrobatids (see below under Comparisons with Other Frogs). When the pectoral girdle is analyzed as a complex of characters, however, *Atopophrynus* deviates from the dendrobatid condition. In *Atopophrynus* the fused procoracoid cartilage is massive and completely supports reduced clavicles that are anterolaterally directed at the distal ends and that are not in contact with the scapulae or with each other. The sternum is short, truncate, and fused to the epicoracoid cartilages, which are fused to each other and to the fused procoracoid cartilages. An omosternum is absent in *Atopophrynus* but present in the majority of dendrobatids. Dendrobatid pectoral girdles are generally completely ossified and fused. The procoracoid cartilages of dendrobatids are extremely small and as narrow in width as the clavicles, which are laterally oriented and in contact with the scapulae and almost in

contact with each other at the midline. The sternum in dendrobatids is posteriorly pointed, never broadly rounded as in *Atopophrynus*; it usually is distinguishable from the epicoracoid cartilages and is often ossified.

Some of these characters can be argued to be paedomorphic in *Atopophrynus* (incomplete ossification, small clavicles), but other characters suggest derived status (complete fusion between cartilages, massive coracoids and procoracoid cartilage).

PELVIC GIRDLE: The ilia in dendrobatids are perfectly V-shaped and the shafts are straight to the sacral articulation. In *Atopophrynus*, they are laterally bowed and the anteromedial point of contact between the individual ilia projects slightly anteriorly between the shafts.

APPENDICULAR SKELETON: The reduction in digit I of the *Atopophrynus* foot is accomplished by the overall miniaturization of each of the individual phalangeal bones that compose that digit. This mode of reduction differs from the distal-proximal loss of bones reported by Alberch and Gale (1985).

Both *Atopophrynus* and dendrobatids have T-shaped terminal phalanges; however, this character is also found in other groups of anurans (hylids, centrolenids, some bufonids, leptodactylids, microhylids). On closer examination, the terminal phalanges are proportioned somewhat differently in *Atopophrynus* than in most dendrobatids. Most dendrobatids have a relatively short terminal phalanx, which places the distal transverse process in the proximal half of the disc, and the transverse process tends to be fairly short, approximately equal to the width of the penultimate phalanx at its midpoint; in large-disced *Dendrobates*, however, the terminal phalanx is better developed and its transverse process lies at about the middle of the disc. In *Atopophrynus*, each T-shaped terminal phalanx is relatively long, placing its distal transverse process into the distal half of the finger or toe disc; and the transverse process is at least twice the width of the penultimate phalanx at midpoint. Possibly, however, the differences are a simple corollary of added support for larger discs.

COMPARISON WITH OTHER FROGS

The original assignment of *Atopophrynus* to the Dendrobatidae seems likely to have

been made principally on the basis of the firmisternal nature of the pectoral girdle. Firmisterny, however, also characterizes other groups of Neotropical frogs—including (but not limited to) the Microhylidae and some genera of the Bufonidae and Leptodactylidae, which are the families that we first considered as most likely to contain the nearest relatives of *Atopophrynus*.

The Microhylidae seem to be definable by a synapomorphy involving the mandible—namely the presence of posteriorly directed processes of the mentomandibulars, in association with a strip of connective tissue intervening between the mentomandibular and the dentary (Pentz, 1943, pp. 206–207, fig. 8; R. G. Zweifel, personal commun.). Most microhylids also have two or three pharyngeal folds across the palate in front of the pharynx (Parker, 1934, p. 6), and the insertion of the semitendinosus muscle is of the ranoid type (i.e., dorsal to the gracilis). These structures are lacking in *Atopophrynus*, and it has the bufonoid type of semitendinosus insertion.

Lynch and Ruíz-Carranza (1982, p. 561) stated that “Neither the peculiar modification of the hind foot of *Atopophrynus* nor its loss of the ear is presaged elsewhere in the family” (i.e., in the Dendrobatidae). Such conditions are, however, not at all unknown in the Bufonidae, in which various degrees of firmisterny, earlessness, digit reduction, and even T-shaped terminal phalanges are documented (see especially McDiarmid, 1971). In addition to these, a number of other character states in *Atopophrynus* are at least consistent with the possibility of a bufonid relationship, including the presence of the external adductor mandibulae, the single (squamosal) origin of the depressor mandibulae, the method of insertion of the semitendinosus muscle, the lack of teeth, the absence of an omosternum, and the dilated sacral diapophyses. Certainly *Atopophrynus* more comfortably fits into the variation of this family than in the Dendrobatidae, but presence of Bidder’s organ would seem to be the best confirmation of a bufonid relationship at present.⁶ Examination for this synapo-

⁶ Other possible synapomorphies of the Bufonidae are not as well elucidated, but the nonunique absence both of pulvinaria vocalia and the m. constrictor laryngis pos-

morphic structure should be a matter of priority when additional specimens become available, especially males since the structure is often or usually lacking in adult females (Davis, 1936, p. 117). The alcoholic paratype seen by us is a female packed with large ova, and destructive dissection of this small frog was unwarranted.

The family Leptodactylidae is loosely defined on primitive characters (Lynch, 1971, pp. 20, 70) and can thus accommodate virtually any "bufonoid" genus not clearly assignable to another family.⁷ *Atopophrynus* deserves serious comparison with the presumptive leptodactylid *Geobatrachus walkeri*. Like *Atopophrynus*, *Geobatrachus* is a high-elevation (1700–3000 m) monotypic genus of the northern Andes; it is endemic to the Sierra Nevada de Santa Marta, a structurally isolated block of the Cordillera Central (Gansser, 1973, p. 110) about 500 km northeast of the type locality of *Atopophrynus*

terior may distinguish bufonids from leptodactylids (Trewavas, 1933; Griffiths, 1959). The Bufonidae seem to be rich in other laryngeal apomorphies that are informative at the intergeneric level even if not synapomorphic for the family (Martin, 1972, pp. 283–287).

⁷ In Lynch's view (supra cit., p. 20): "The Leptodactylidae are regarded as the basal stock from which all other families of Bufonoidea [i.e., Bufonidae including Atelopodidae *auct.*, Centrolenidae, Dendrobatidae, Hyliidae, Pseudidae, and Rhinodermatidae] have evolved. . . . The Leptodactylidae are defined as the remaining bufonoid frogs. All lack an organ of Bidder, intercalary phalangeal element (cartilages or bone), and have an arciferal or modified arciferal pectoral girdle (the epicoracoidal horns are visible near the posterior edge of the sternum)." Such symplesiomorphy does not by itself mean that the family is nonmonophyletic, but it does mean that one cannot readily confirm or reject inclusion of genera with nonunique apomorphies (e.g., firmisternal pectoral girdles).

In a paper published two years later (1973), Lynch geographically restricted the Leptodactylidae to Neotropical genera. The 1973 paper already was in press in 1971, however, and Lynch's equivocal discussion (1971, p. 204n) of it does not say which of two diagrammed hypotheses of relationships he considered the most current (i.e., 1971, fig. 127, or 1973, fig. 3.6). But neither of the internally inconsistent schemes offered any evidence of monophyly for the family, which is shown in the 1973 cladogram as being either polyphyletic (the distant Ceratophryinae are retained in the restricted family fide p. 172) or else severely paraphyletic, depending on definitions.

syntomopus. Lynch (1971, pp. 69, 223) excluded *Geobatrachus* from the Leptodactylidae on advice of the late Charles F. Walker and tentatively assigned it to the Microhylidae. But *Geobatrachus* lacks the mento-mandibular processes and other microhylid characters (see above); Ardila-Robayo (1979) placed it back into the Leptodactylidae, in the tribe Eleutherodactylini.⁸

Geobatrachus superficially resembles *Atopophrynus* in being a small (15–24 mm SVL) frog with sloping loreal region and similarly placed nostrils. But *Geobatrachus* has much smaller hands and feet, and the narrower digits are pointed, discless, and not joined by webbing (as befitting a semifossorial frog). Also there are internal differences in foot structure: In *Geobatrachus* the heavily ossified astragalus and calcaneum are fused over their entire length (a condition otherwise only known in the Centrolenidae and Pelodytidae), the prehallical elements are ossified, and the reduced first digit is composed of a shortened metatarsal and nub of the penultimate phalanx. In contrast, in *Atopophrynus* only the ends of the astragalus and calcaneum are fused, the prehallical elements are cartilaginous, and the small size of the first digit is due to the miniaturization of the metatarsal and two phalanges (rather than to shortening and loss). Despite these differences, however, there are a few pronounced similarities: The terminal phalanges are T-shaped and *Atopophrynus* and *Geobatrachus* both have the first toe similarly concealed within the foot and externally indicated by a swelling. The latter condition is unusual among frogs, even more so as a similarity shared by geographic neighbors of such different habits, for which reasons synapomorphy seems likely.

Among other osteological differences, the skull of *Geobatrachus* is more ossified, as might be expected from its semifossorial habits, and it retains teeth. *Geobatrachus* also retains the ear, although the tympanum lies under the skin. The firmisternal pectoral gir-

⁸ Our comments on *Geobatrachus walkeri* are mainly based on two cleared and double-stained specimens (AMNH 88613, MCZ 20252) and on Ardila-Robayo's (1979) admirable monograph. Like *Atopophrynus*, *Geobatrachus* originally was described as a genus of Dendrobatidae (Ruthven, 1915); Griffiths (1959, p. 481) associated it with the Leptodactylidae.

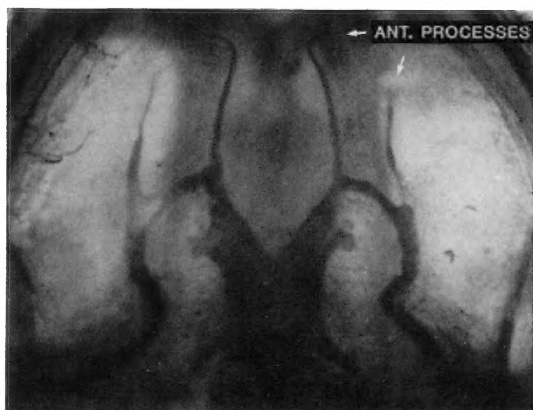


FIG. 8. Hyoid of *Geobatrachus walkeri* (AMNH 88613) in ventral view, showing the slender, paired processes that project anteriorly from each of the hyalia, $\times 14.6$. Compare with *Atopophrynus* (fig. 4).

dles differ in several details (compare fig. 5 with Ardila-Robayo, 1979, fig. 17), although the differences are not as great as when either genus is compared with dendrobatids.

There is a pronounced similarity and possible synapomorphy in the hyoid: both frogs have two long and slender processes extending anteriorly from each of the hyalia, as can be seen by comparing figures 4 and 8 (also drawing in Ardila-Robayo, 1979, p. 419). This condition is unusual and nothing like it is seen in the many figures of the hyoid presented by Trewavas (1933). The hyalia of most frogs either lack anterior processes or have but one on each side. Two anterior processes do occur in some Hyperoliidae, but, in this Ethiopian family (southern Africa, Madagascar, and Seychelles), the processes are short and thick and their variable configurations are usually quite different from those of *Atopophrynus* and *Geobatrachus* (Trewavas, 1933, fig. 58; Hoffman, 1942, fig. 13; Drewes, 1984, figs. 4–5). *Atopophrynus* differs from *Geobatrachus* and may be unique among frogs in having the posterolateral processes of the hyoid plate directed anteriorly (fig. 4).

The m. depressor mandibulae (based on dissection of AMNH 88613) originates differently from that of *Atopophrynus*. It rises as a broad superficial sheet from the dorsal fascia + the posterior and ventral edge of the tympanic ring; posterodorsally, the origin of this muscle completely overlaps the origin of

the m. latissimus dorsi; a deeper slip of the depressor mandibulae originates from a long otic ramus of the squamosal bone. *Geobatrachus* also differs in lacking the external adductor mandibulae. The semitendinosus muscle has the same insertion pattern. Other aspects of musculature deserve careful comparison when adequate material of *Atopophrynus* becomes available.

CONCLUSIONS

Atopophrynus is not a member of the Dendrobatidae. The original assignment to this family is supported neither by synapomorphy nor even by misleading plesiomorphy, since *Atopophrynus syntomopus* looks nothing like a dendrobatid and differs in nearly all points of comparison. The genus quite possibly belongs in the Bufonidae, but this can be neither confirmed nor adequately rejected until there is a thorough examination for the presence or absence of Bidder's organ and other bufonid apomorphies.

Despite obvious morphological differences, a few of which seem correlated with life-style (semiaquatic vs. semifossorial), *Atopophrynus syntomopus* shares a few impressive resemblances with a presumptive leptodactylid, *Geobatrachus walkeri*. The manner of concealment of the first toe, and, especially, the pair of slender anterior processes on each hyale of the hyoid are conditions unusual enough to suggest synapomorphy. We therefore suggest that *Atopophrynus* and *Geobatrachus* may be sister groups, for which reason we place *Atopophrynus syntomopus* in the Leptodactylidae. This assignment is necessarily provisional, owing partly to incomplete anatomical information on *Atopophrynus* and partly because current definitions of the family are based on symplesiomorphy.

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