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DISTINGUISHING FEATURES OF THE SUB-SAHARAN FROG GENERA *ARTHROLEPTIS* AND *PHRYNOBATRACHUS*: A SHORT GUIDE FOR FIELD AND MUSEUM RESEARCHERS

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ABSTRACT. Typically small body size and similar external anatomy have made it difficult for researchers to distinguish between species of two distantly related, but often sympatric, African ranoid frog genera: *Arthroleptis* (Arthroleptidae) and *Phrynobatrachus* (Phrynobatrachidae). We define a suite of external morphological characters, extending beyond the traditionally used secondary sexual characteristics, that can be used to definitively distinguish between adult *Arthroleptis* and *Phrynobatrachus*. Photographs comparing absence, presence, and variation of morphological characters are included for clarification. Significant differences between body proportions (head width/snout–vent length) are also observed between these genera. Although smaller species might be more difficult to identify, larger species (> 30 mm snout–vent length) of *Arthroleptis* can be distinguished from *Phrynobatrachus* because of their relatively wider heads. We intend this to serve as a heuristic guide for both field- and museum-based researchers.

KEY WORDS: Africa; Amphibia; Arthroleptidae; identification; Ranoidea; Phrynobatrachidae

INTRODUCTION

Nearly every herpetologist is familiar with the overwhelming diversity of "little brown frogs." Many leaf litter anurans are small, generally drab in color, and morphologically similar, and this has hampered both systematic research and identification in the field and in museum collections. Within sub-Saharan Africa, two such genera, *Arthroleptis* Smith 1849 and *Phrynobatrachus* Günther 1862, have been confused for more than a century (i.e., Boulenger, 1882). On the basis of studies of skeletal morphology (e.g., Laurent, 1940, 1941a, b; Scott, 2005) and the results of molecular phylogenetic analyses (e.g., Bossuyt *et al.*, 2006; Frost *et al.*, 2006; Roelants *et al.*, 2007), it is now very clear that these genera, although externally similar, are only distantly related. In our

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experience, many researchers are unaware of the numerous external morphological characters that can be used to distinguish between each genus. *Arthroleptis* and *Phrynobatrachus* continue to be confused in the field and in museum collections, which can then confound further research such as molecular phylogenetic analyses (see Discussion for an example). Thus the external morphological differences between these two genera warrant a thorough treatment to improve the efficacy of identification.

Squeakers (*Arthroleptis sensu* Frost, 2007) are generally small (16–54 mm snout–vent length), terrestrial, leaf litter anurans, and all of the approximately 37 species are believed to have lost the free-living, feeding tadpole stage (i.e., direct development). The smallest *Arthroleptis* species were previously placed in *Schoutedenella* (Laurent, 1954); Frost *et al.* (2006) synonymized *Schoutedenella* with *Arthroleptis* on the basis of the results of their molecular phylogenetic analysis. An analysis of the relationships within *Arthroleptis* and its putative sister taxon *Cardioglossa* is currently in preparation (Blackburn, unpublished).

Puddle frogs (*Phrynobatrachus*) comprise a lineage of approximately 75 species found in diverse terrestrial habitats across sub-Saharan Africa (Frost, 2007). *Phrynobatrachus* has been a long-standing source of confusion to systematists because of extensive geographic and intrapopulation variation accompanied by only slight morphological differences among species (Largen, 2001; Rödel, 2000; Stewart, 1974). Molecular data from mitochondrial and nuclear markers indicate that both *Dimorphognathus* and *Phrynodon* might be embedded within *Phrynobatrachus*, thus rendering the genus paraphyletic (Frost *et al.*, 2006; Scott, 2005). Both Scott (2005) and Frost *et al.* (2006) argued for synonymizing these genera with *Phrynobatrachus*. Whereas *Dimorphognathus africanus* is embedded deeply within *Phrynobatrachus*, supporting the synonymization of this monotypic genus, the placement of *Phrynodon sandersoni* within *Phrynobatrachus* is more controversial because of its basal position within the lineage; the synonymy of *Phrynodon* with *Phrynobatrachus* is currently being examined as part of a phylogenetic study of the Phrynobatrachidae (*sensu* Frost, 2007; Zimkus, unpublished).

The long taxonomic history linking *Arthroleptis* and *Phrynobatrachus* contributes to the present difficulties resolving the identifications of these distantly related frog genera (e.g., Boulenger, 1882). Many species originally described as *Arthroleptis* have been since transferred to other genera, including 21 species that are currently considered valid species of *Phrynobatrachus* (Frost, 2007). In part on the basis of the work of Deckert (1938), Laurent (1940, 1941a, b) used osteological characters to separate species into two genera, *Arthroleptis* and *Phrynobatrachus*, which he believed were not closely related. The morphological differentiation of these genera is further supported by recent molecular phylogenetic studies (e.g., Bossuyt *et al.*, 2006; Frost *et al.*, 2006; Roelants *et al.*, 2007), which show that *Arthroleptis* and *Phrynobatrachus* belong to different radiations within ranoid frogs.

The purpose of this study is to clearly determine those external morphological characters that can be used to discriminate between *Arthroleptis* and *Phrynobatrachus*. We also document characters that could be useful for identification but vary within these genera. Because we have found that written descriptions of these characters are often unclear, we provide photographs to illustrate the more important characters. Although this information might not be entirely novel for tenured African amphibian biologists, we hope that those not familiar with these genera will find this to be a useful guide.

METHODOLOGY

Using the taxonomic, systematic, and faunal literature as our guide, we examined museum specimens for characteristics reportedly useful in differentiating between *Arthroleptis* and *Phrynobatrachus*. We focused solely on external characteristics to make our observations equally useful to researchers conducting field surveys or sorting specimens in museum collections. A total of 15 morphological characters were investigated; six of these are male secondary sexual characters. Characters are provided in Appendix 1, and Appendix 2 comprises a data matrix in which all species examined are coded for these characters.

The results of this work are based on our study of specimens from museum collections, as well as our respective experiences in the field. Museum abbreviations correspond to those of Leviton *et al.* (1985), with the exception of MMB (Museums of Malawi, Blantyre). The allocation of species to either *Arthroleptis* or *Phrynobatrachus* follows Frost (2007). High-resolution images were obtained with a JVC 3-CCD digital camera using AutoMontage Pro 5.0 (Synoptics). Images were saved as TIFF files, cropped, and contrast-adjusted with Adobe Photoshop 7.0 for Macintosh. We gathered meristic data from 280 adult specimens representing 27 species of *Arthroleptis* and 246 adult specimens representing 31 species of *Phrynobatrachus* (Online Supplement: Appendix 1).

Arthroleptis and *Phrynobatrachus* appear to generally exhibit different body shapes, with *Arthroleptis* having relatively wider heads. To test whether this difference is significant, we took measurements (± 0.1 mm) of snout–vent length (SVL) and head width (HdWd) with digital calipers (Online Supplement: Appendix 1). We used an analysis of covariance to test for significant difference in the slope of the regression lines in which HdWd is the dependent variable and SVL is independent. To take into account variation in both HdWd and SVL, reduced major axis regression was used. Statistical significance was evaluated for $\alpha = 0.05$.

RESULTS

The characters examined and evaluated in this study are summarized in Table 1. Nearly all characters reported to differentiate *Arthroleptis* and *Phrynobatrachus* were found to vary both within and between species in each genus (Table 1). Only two external morphological characters definitively differentiate these genera:

1. the presence of a tarsal tubercle and
2. the presence of an outer metatarsal tubercle.

However, among African anurans, only the presence of a tarsal tubercle is unique to *Phrynobatrachus*.

In general, *Arthroleptis* have relatively wider heads than *Phrynobatrachus*. The coefficients (β) of linear regression of HdWd on SVL are significantly different between these two genera (*Arthroleptis*: $\beta = 0.461$, SE $= 0.006$; *Phrynobatrachus*: $\beta = 0.348$, SE $= 0.005$; $P < 0.0001$, $F = 64.39$). Although highly significant, in practice it is very difficult to discriminate between these genera on the basis only of these data if specimens are less than 30 mm SVL (Fig. 1). The difference in relative head width is only obvious for specimens more than 30 mm SVL (HdWd/SVL: 40% vs. 34%).

DISCUSSION

In this study, we examined a suite of morphological characters believed to be useful in distinguishing between adults of *Arthroleptis* and *Phrynobatrachus*. The most

TABLE 1. EXTERNAL MORPHOLOGICAL CHARACTERS USEFUL FOR DIFFERENTIATING BETWEEN *ARTHROLEPTIS* AND *PHRYNOBATRACHUS*.

Character	*Arthroleptis*	*Phrynobatrachus*	References
Tarsal tubercle	absent	present	Blackburn, 2005; Channing and Boycott, 1989; Drewes and Perret, 2000; Scott, 2005
Outer metatarsal tubercle	absent	present	Deckert, 1938
Heel tubercle (located on the proximal end of the tarsus)	absent	variable	Scott, 2005
Circummarginal groove on terminal phalanx	absent	variable	Blackburn, 2005; Scott, 2005
Pedal webbing	absent	variable	Schmidt and Inger, 1959; Stewart, 1967
Median dorsal skin raphe	present*	absent	Drewes and Perret, 2000; Laurent, 1957; Scott, 2005
Hourglass or triple diadem pattern on dorsum	variable	absent	Scott, 2005
Chevron-shaped glands in scapular region	absent	variable	Scott, 2005; Stewart, 1974
Eyelid cornicle or spur	absent	variable	Perret, 1988; Rödel, 2000
Sexually mature males			
Elongate third finger	variable	absent	Blackburn, 2005; Noble, 1931
Dermal digital spines	variable	absent	Noble, 1931; Schmidt and Inger, 1959
Inguinal spines	variable	absent	Blackburn, unpublished
Nuptial excrescence (thickened pad of skin) on first finger	absent	variable	Scott, 2005; Stewart, 1967
Femoral gland	absent	variable	Blackburn, 2005; Parker, 1935; Stewart, 1967
Lateral vocal folds	absent	variable	Stewart, 1967

*Variation is the result of preservation, desiccation, or both.

definitive characteristic that can be used to differentiate between these two genera is the presence of both an outer metatarsal tubercle and a tarsal tubercle in *Phrynobatrachus* (including the previously synonymized *Dimorphognathus* and *Phrynodon*) (Fig. 2B). *Arthroleptis* (including *Schoutedenella*) only exhibits an inner metatarsal tubercle, which is also found in *Phrynobatrachus*. Although Drewes and Perret (2000) found *Phrynobatrachus* (*Dimorphognathus*) *africanus* and *Phrynobatrachus* (*Phrynodon*) *sandersoni* to lack a tarsal tubercle, we found the tarsal tubercle present in both taxa, albeit rather reduced in size in the latter species.

Numerous morphological characters examined in this study are present in other

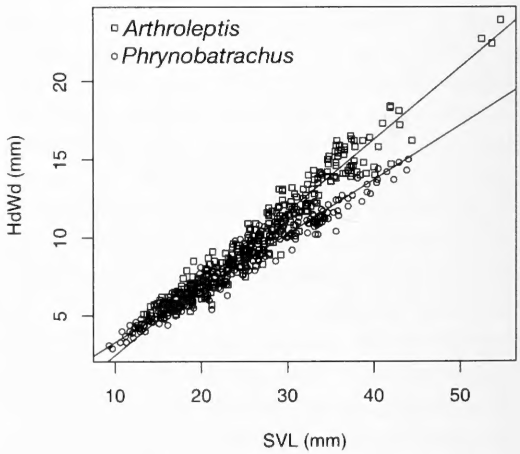

Figure 1. Head width (HdWd) plotted against snout–vent length (SVL) for *Arthroleptis* (squares) and *Phrynobatrachus* (circles).

African frogs, but the presence or combination of particular characters can be useful in distinguishing between adult *Phrynobatrachus* and *Arthroleptis*. Expansion of the terminal phalanx of manual and pedal digits is found in both genera, but circummarginal grooves are found only in some species of *Phrynobatrachus* (Blackburn, 2005; Scott, 2005; Fig. 2E). *Phrynobatrachus* differs from *Arthroleptis* by the presence of pedal webbing in many species of the former (Schmidt and Inger, 1959). Webbing ranges from absent or rudimentary in numerous smaller species such as *P. minutus*, *P. parvulus*, and *P. ukingensis* to extensive in the majority of larger, rheophilic species such as *P. acutirostris, P. krefftii*, and *P. versicolor* (Fig. 2C, D). Five species of *Phrynobatrachus*, including *P. annulatus*, *P. calcaratus*, *P. cornutus*, *P. taiensis*, and *P. villiersi*, possess a single spinelike dermal tubercle on the upper eyelid (Rödel, 2000), a character that can be used to distinguish *Phrynobatrachus* from *Arthroleptis* (Perret, 1988), as well as other African anurans.

A number of external morphological characters vary both within and between species in each genus, and this variation is due to either natural variation within or between populations or the condition of preserved specimens. Chevron-shaped glands in the scapular region of *Phrynobatrachus* and a dorsal triple diadem pattern in *Arthroleptis* can both be used to identify species of these genera (Scott, 2005; Stewart, 1974). However, these are not always prominent in all members of a species or may be completely lacking in some species. The size and shape of the chevron-shaped glands of *Phrynobatrachus* are quite variable and can originate and terminate in the scapular region or instead extend almost the entire length of the body (Fig. 2H). The median dorsal skin raphe of *Arthroleptis* can be a difficult character to visualize, especially in poorly preserved specimens (Fig. 2G); however, the presence of this character can be used to accurately identify *Arthroleptis*. Finally, some species of *Phrynobatrachus* exhibit circummarginal grooves on the manual or pedal digit tips; in some species, these furrows are found only on the longest digits. In addition, the presence of circummarginal grooves could be difficult to determine because of desiccation of preserved specimens. However, if circummarginal grooves are present, this character can be used to differentiate *Phrynobatrachus* from *Arthroleptis*, because it is lacking in the latter, but not necessarily from other African frog genera (Blackburn, 2005; Scott, 2005; Fig. 2E).

The presence of male secondary sexual characters can lead to the most straightforward identifications of specimens as *Arthroleptis* or *Phrynobatrachus*. An elongate third finger is found in many male *Arthroleptis*, as well as most species of *Cardioglossa,* the putative sister genus of *Arthroleptis* (Blackburn, in press; Fig. 3A, B). This sexual dimorphism is not found in *Phrynobatrachus* or any other anurans. Males of nearly all *Arthroleptis* species have dermal spines lining the medial surface of the elongate third finger and are also sometimes found on the lateral, medial, or both surfaces of the second finger (Fig. 3B). In some species, the presence of spines can vary seasonally (e.g., Schmidt and Inger, 1959). Males of some species of *Phrynobatrachus* possess a nuptial excrescence or thickened pad of skin on the medial and dorsal surface of the first finger, which was hypothesized by Parker (1940) to be an adaptation to aquatic amplexus. In *P. africanus*, this pad is greatly hypertrophied and covers much of the dorsal surface of the hand (Fig. 3C). The presence of an elongate ovoid femoral gland, which is most evident in life because it often can be hardened and yellow in color, allows the

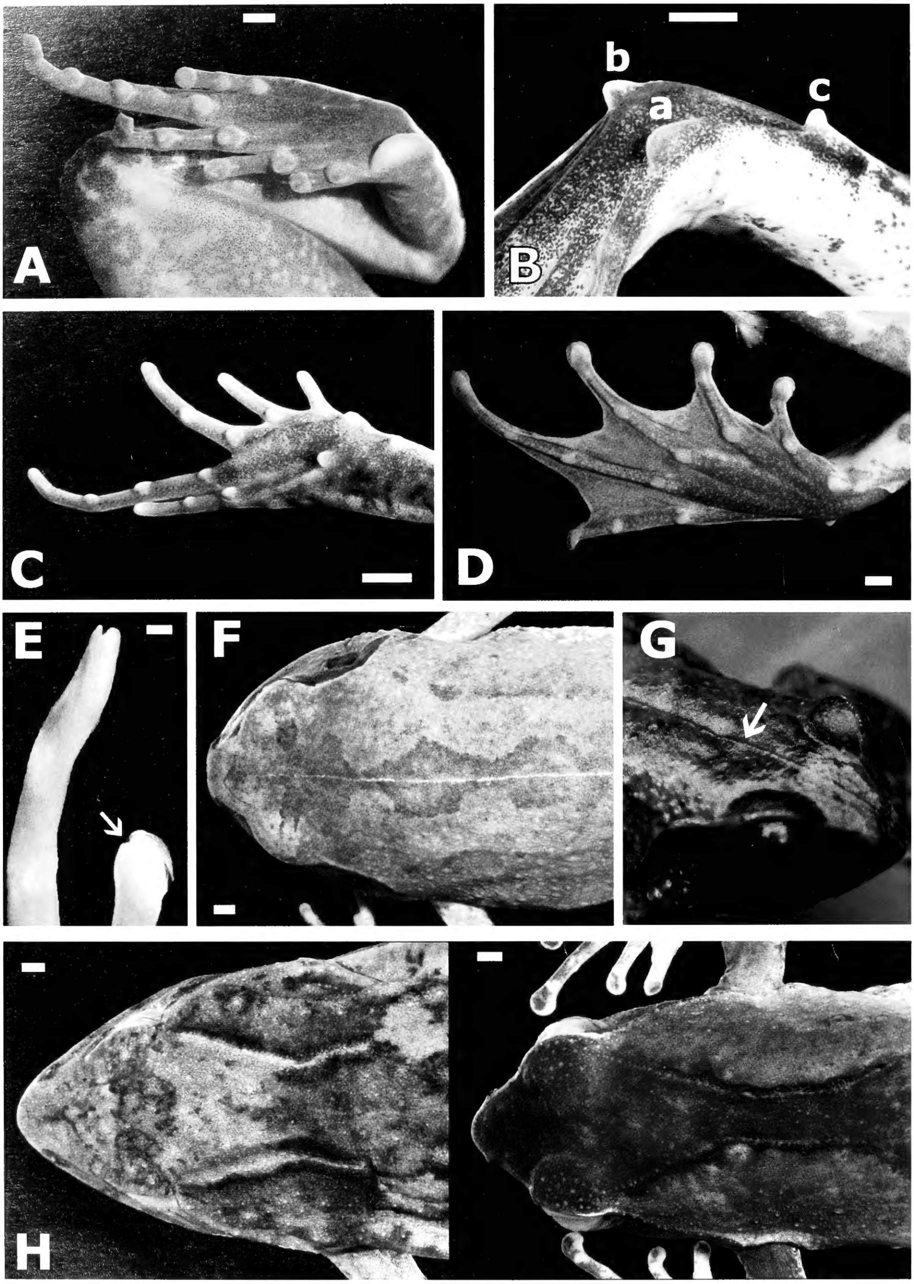

Figure 2. Morphological characters useful in distinguishing between *Arthroleptis* and *Phrynobatrachus*. A, Left foot of *A. stenodactylus* (MCZ A-137060) in ventral view illustrating inner metatarsal tubercle and lack of webbing. B, Left foot of *P. natalensis* (MCZ A-138084) in ventral view illustrating inner metatarsal tubercle (a), outer metatarsal tubercle (b), and tarsal tubercle (c). C, Left foot of *P. parvulus* (MCZ A-137121) in ventral view illustrating absent or rudimentary webbing. D, Right foot of *P. steindachneri* (MCZ A-136907) in ventral view

identification of breeding *Phrynobatrachus* males (Blackburn, 2005; Stewart, 1967). However, in most species, this gland might be difficult to identify after preservation. Breeding *Phrynobatrachus* males have a single subgular vocal sac, which, when not distended, forms one or multiple folds, roughly parallel to the lower jaw, on the lateral margins of the throat (Stewart, 1967; Fig. 3E). Although the gular region of *Arthroleptis* can be distended and wrinkled, prominent gular folds are not present (Fig. 3D).

For many field biologists that regularly collect *Arthroleptis* and *Phrynobatrachus*, it is obvious that the body proportions of these frogs generally differ. Indeed, we find that *Arthroleptis* have heads that are relatively wider than *Phrynobatrachus*. Meristic data collected in this study illustrate that the linear regression coefficients differ significantly between these two genera. However, in general, the difference in body proportions is only obvious in large specimens (> 30 mm SVL). Thus, at least for larger specimens, the relative width of the head could be a useful quick diagnostic feature, especially if used in concert with other morphological characters discussed herein (Table 1).

It is also important to note that numerous nonmorphological characters such as call structure, breeding biology, and habitat preference can also be used in the field to assist in the identification of *Arthroleptis* and *Phrynobatrachus*. All *Arthroleptis* are believed to have direct development, in which froglets hatch from a small clutch of terrestrially deposited eggs. In contrast, most *Phrynobatrachus* species deposit hundreds to thousands of eggs in ponds, streams, or pools, and a small number of species deposit small clutches of eggs in stagnant water found in tree holes, in empty fruit capsules, within snail shells, or terrestrially (Rödel, 1998; Rödel and Ernst, 2002). Species exhibiting these alternative reproductive modes include *P. dendrobates, P. guineensis, P. krefftii, P. phyllophilus, P. sandersoni*, and *P. tokba*, although all have free-living tadpoles (Amiet, 1981; Rödel, 1998; Rödel and Ernst, 2002). Although few advertisement calls of these genera are published, those currently available will undoubtedly assist in distinguishing *Phrynobatrachus* from *Arthroleptis* (e.g., Drewes and Perret, 2000; Rödel, 2000; Schiøtz, 1964).

Although we demonstrate in this study that it is possible to distinguish adult *Phrynobatrachus* and *Arthroleptis* with the use of morphological characters, the identification of juvenile and subadult *Arthroleptis* and *Phrynobatrachus* continues to be challenging, even occasionally for the authors of this study. Fortunately, the identification of numerous taxa has been greatly facilitated by the recent use of DNA barcoding (e.g., Hebert *et al.*, 2003; Moritz and Cicero, 2004; Vences *et al.*, 2005). The use of the mitochondrial 16S ribosomal RNA (rRNA) gene has proven to be particularly successful in amplification of amphibian DNA (Vences *et al.*, 2005). We have found that the

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illustrating extensive webbing. E, Tips of left pedal digits III and IV of *P. tokba* (MCZ A-26905) illustrating expansion of digit tip and circummarginal grooves. F, Dorsal surface of *A. stenodactylus* (MCZ A-137060) illustrating the hourglass (i.e., triple diadem) pattern. G, Dorsal surface of *A.* sp. nov. (MCZ A-137978), in life, illustrating the median dorsal skin raphe. H, Dorsal surface of *P. steindachneri* (MCZ A-136907) on left and *P. auritus* (MCZ A-138095) on right illustrating variability in chevron-shaped glands. Scale bar 1 mm in 2A–D, F–H; 0.1 mm in 2E.

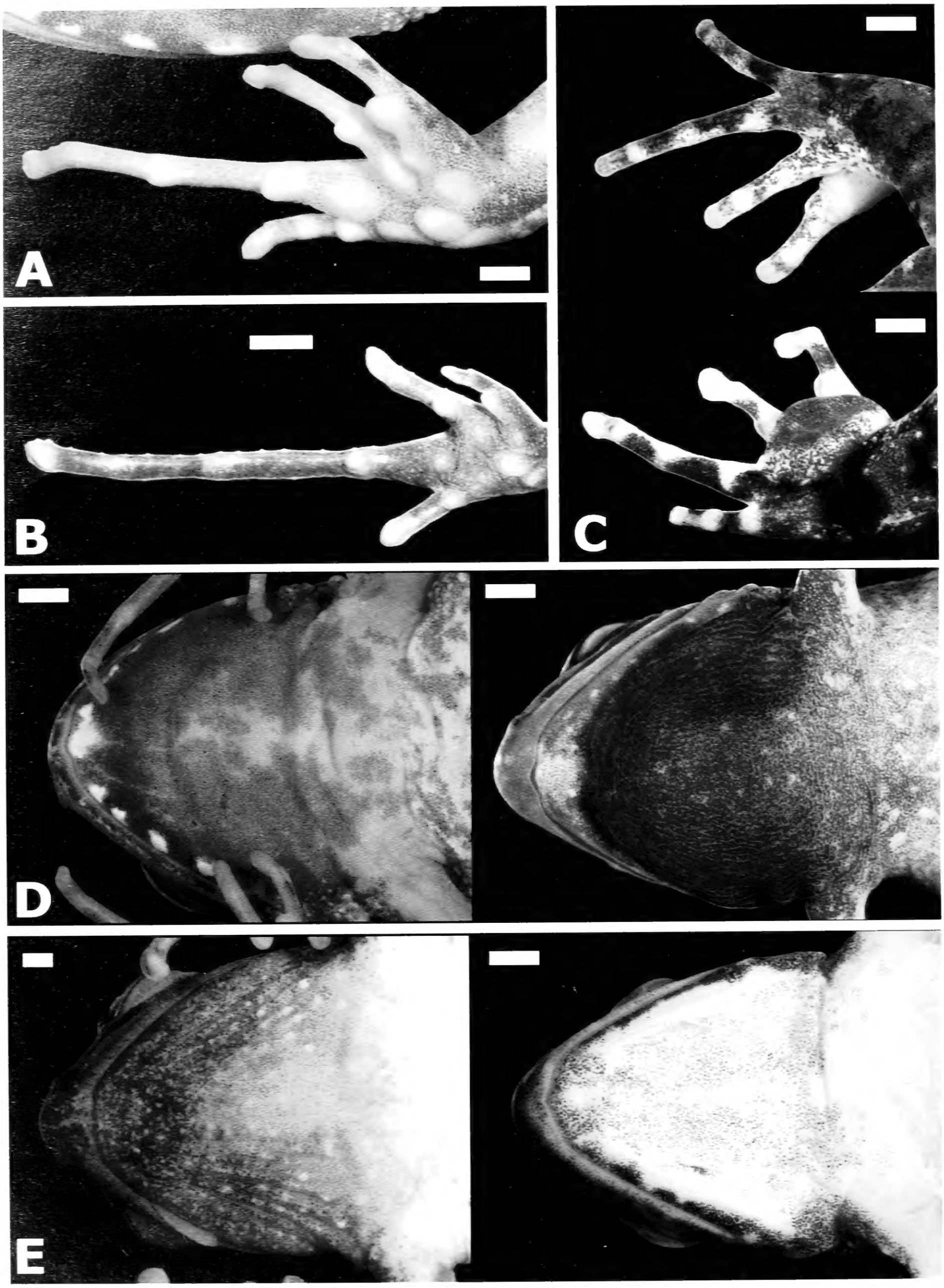

Figure 3. Secondary sexual characters of males useful in distinguishing between *Arthroleptis* and *Phrynobatrachus*. A. Right hand of *A. stenodactylus* (MCZ A-137060) in ventral view showing elongate digit III. B. Fingers II and III of male *A. schubotzi* (CAS 201717) in ventral view illustrating dermal spines. C. Right hand of male *P. natalensis* (MCZ A-138084), above, and left hand of male *P. (Dimorphognathus) africanus* (MCZ A-136757), below, in dorsal view illustrating nuptial excrescence (pad) on digit I. D. Throat of male *A. schubotzi* (CAS 201717), left, and *A. stenodactylus* (MCZ A-137061), right, illustrating lack of vocal folds. E. Throat of male *P. auritus* (MCZ A-138095) and *P. (Phrynodon) sandersoni* (MCZ A-136790) illustrating visible vocal folds. Scale bar 1 mm.

amplification of this gene is effective in identifying tadpoles, juveniles, and subadults of numerous African ranoid frogs, including *Phrynobatrachus* and *Arthroleptis*. However, molecular data and analyses can be confounded by the misidentification of voucher specimens. For instance, nucleotide BLAST searches against GenBank sequence data for the *Arthroleptis* specimens for which Vences *et al.* (2003) amplified the 16S rRNA gene reveals that these specimens are misidentified (GenBank sequences AF215139–40). Although Vences *et al.* (2003) attribute the unusual paraphyly of *Arthroleptis* 16S genes to uncertainties in their sequence data, this result is easily explained: These sequences have high similarity to *Phrynobatrachus* and thus are misidentified at the genus level. We advocate DNA identification of specimens only to the level of genus because of the difficulty in accurately identifying species of either genus. Thorough taxonomic study in combination with molecular data will be necessary before DNA identification can be used confidently to identify species of these two genera.

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APPENDIX 1. MORPHOLOGICAL CHARACTERS EXAMINED.

External Morphology

1. Tarsal tubercle: (0) absent; (1) present.
2. Outer metatarsal tubercle: (0) absent; (1) present.
3. Heel tubercle (located at the proximal end of the tarsus): (0) absent; (1) present.
4. Circummarginal groove at manual and/or pedal digit tips: (0) absent; (1) present. In some species, this groove is present only on the tips of the longest digits. Variation in museum specimens might be the result of preservation, desiccation, or both.
5. Pedal webbing: (0) absent or rudimentary with more than two distalmost phalanges of digit IV unwebbed; (1) moderate to extensive with no more than the two distalmost phalanges of digit IV unwebbed.
6. Median dorsal skin raphe: (0) absent; (1) present.
7. Hourglass or triple diadem pattern on dorsum: (0) absent; (1) present.
8. Chevron-shaped glands in scapular region: (0) absent; (1) present. These ridges of skin can be short or can extend the entire length of the body when present.
9. Eyelid cornicle or spur: (0) absent; (1) present.

Secondary Sexual Characteristics

10. Sexually mature males, third finger relatively longer than in females: (0) absent; (1) present.
11. Sexually mature males, dermal spines on fingers: (0) absent; (1) present.
12. Sexually mature males, inguinal spines: (0) absent; (1) present.
13. Sexually mature males, nuptial excrescence (thickened pad of skin that can appear velvety) on first finger: (0) absent; (1) present.
14. Sexually mature males, femoral glands: (0) absent; (1) present. Most often the

femoral glands of *Phrynobatrachus* are located on the posterior thigh. However, glands can be situated closer to either the knee or vent. These glands are most easily seen in living specimens because they are usually bright yellow.

15. Sexually mature males, lateral vocal folds: (0) absent; (1) present. When present, folds run roughly parallel to the lower jaw, at the lateral margins of the throat, and form one or multiple creases.

APPENDIX 2. DISTRIBUTION OF MORPHOLOGICAL CHARACTERS AMONG SPECIES OF *ARTHROLEPTIS* AND *PHRYNOBATRACHUS*. ALL CHARACTER STATES ARE BINARY (0, 1). MISSING DATA ARE CODED AS "?"; 0.1 DENOTES POLYMORPHISM. REFER TO APPENDIX 1 FOR CHARACTER DESCRIPTIONS.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Arthroleptis adelphus	0	0	0	0	1	1	0.1	0	0	1	1	1	0	0	0
A. adolfifriederici	0	0	0	0	1	1	0	0	0	1	1	1	0	0	0
A. affinis	0	0	0	0	1	1	0.1	0	0	1	1	0	0	0	0
A. brevipes	0	0	0	0	1	?	0	0	0	?	?	?	0	0	0
A. crusculum	0	0	0	0	1	1	0.1	0	0	1	1	1	0	0	0
A. francei	0	0	0	0	1	1	0.1	0	0	1	1	1	0	0	0
A. hematogaster	0	0	0	0	1	1	0	0	0	?	?	?	0	0	0
A. lameerei	0	0	0	0	1	1	0.1	0	0	1	0	0	0	0	0
A. nikeae	0	0	0	0	1	1	0	0	0	?	?	?	0	0	0
A. nimbaensis	0	0	0	0	1	?	0.1	0	0	1	1	1	0	0	0
A. "poecilonotus"	0	0	0	0	1	1	0.1	0	0	1	1	1	0	0	0
A. pyrrhoscelis	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0
A. reichei	0	0	0	0	1	1	0.1	0	0	1	1	1	0	0	0
A. schubotzi	0	0	0	0	1	1	0.1	0	0	1	1	1	0	0	0
A. stenodactylus	0	0	0	0	1	1	0.1	0	0	1	1	1	0	0	0
A. sylvaticus	0	0	0	0	1	1	0.1	0	0	1	0.1	1	0	0	0
A. taeniatus	0	0	0	0	1	1	0	0	0	1	1	1	0	0	0
A. tanneri	0	0	0	0	1	1	0	0	0	1	1	1	0	0	0
A. troglodytes	0	0	0	0	1	1	0.1	0	0	?	1	1	0	0	0
A. tuberosus	0	0	0	0	1	1	0.1	0	0	1	1	1	0	0	0
A. variabilis	0	0	0	0	1	1	0.1	0	0	1	1	1	0	0	0
A. wahlbergii	0	0	0	0	1	1	0.1	0	0	1	1	1	0	0	0
A. xenochirus	0	0	0	0	1	1	0.1	0	0	1	1	1	0	0	0
A. xenodactyloides	0	0	0	0	1	1	0.1	0	0	1	1	1	0	0	0
A. xenodactylus	0	0	0	0	1	1	0	0	0	1	1	1	0	0	0
A. zimmeri	0	0	0	0	1	?	?	0	0	?	?	?	0	0	0
Arthroleptis sp. nov.	0	0	0	0	1	1	0	0	0	?	?	?	0	0	0
Phrynobatrachus acridoides	1	1	0.1	1	1	0	0	1	0	0	0	0	1	1	1
P. acutirostris	1	1	1	1	1	0	0	1	0	0	0	0	1	0	1
P. africanus	1	1	0.1	1	0	0	0	1	0	0	0	0	1	0	1
P. auritus	1	1	1	1	1	0	0	1	0	0	0	0	0	1	1
P. batesii	1	1	0	1	0	0	0	1	0	0	0	0	?	?	?
P. bequaerti	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0
P. bullans	1	1	1	0	1	0	0	1	0	0	0	0	1	1	1
P. calcaratus	1	1	0.1	1	0	0	0	1	1	0	0	0	0	0	1

APPENDIX 2. Continued.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
P. cornutus	1	1	0	1	0	0	0	1	1	0	0	0	?	?	?
P. cricogaster	1	1	1	1	1	0	0	1	0	0	0	0	1	0	0
P. cryptotis	1	1	0,1	0	0	0	0	1	0	0	0	0	0	0	1
P. dendrobates	1	1	0	1	0	0	0	1	0	0	0	0	1	0	1
P. francisci	1	1	0	0	1	0	0	1	0	0	0	0	?	?	?
P. inexpectatus	1	1	0	0	0	0	0	0,1	0	0	0	0	0	1	1
P. keniensis	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1
P. kinangopensis	1	1	0,1	0	1	0	0	1	0	0	0	0	1	0	1
P. krefftii	1	1	0	1	1	0	0	1	0	0	0	0	1	1	1
P. mababiensis	1	1	0,1	0	0	0	0	1	0	0	0	0	?	?	?
P. manengoubensis	1	1	0	1	0	0	0	1	0	0	0	0	0	1	1
P. minutus	1	1	0	0	0	0	0	1	0	0	0	0	?	?	?
P. natalensis	1	1	0,1	0	1	0	0	0,1	0	0	0	0	1	1	1
P. pakenhami	1	1	0	1	1	0	0	0,1	0	0	0	0	0	1	1
P. parvulus	1	1	0	0	0	0	0	1	0	0	0	0	1	1	1
P. plicatus	1	1	0	1	1	0	0	1	0	0	0	0	0	0	1
P. rungwensis	1	1	1	1	0	0	0	1	0	0	0	0	1	1	1
P. sandersoni	1	1	1	1	1	0	0	1	0	0	0	0	1	1	1
P. scheffleri	1	1	1	0	0	0	0	1	0	0	0	0	?	?	?
P. steindachneri	1	1	0,1	1	1	0	0	1	0	0	0	0	1	1	0
P. stewartae	1	1	?	0	1	0	0	1	0	0	0	0	1	1	1
P. ukingensis	1	1	0,1	1	0	0	0	0,1	0	0	0	0	1	1	1
P. versicolor	1	1	0	1	1	0	0	1	0	0	0	0	1	0	1

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