The taxonomy and ethology of the *Afrixalus stuhlmanni* complex (Anura: Hyperoliidae)

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INTRODUCTION

*Afrixalus* is a sub-Saharan genus containing about 35 taxa. Commonly referred to as “Leaf-folding Frogs” because of the typical mode of oviposition, they occupy a range of habitats from seasonally-moist open grassland and savanna to rain forest, and from sea level to altitudes in excess of 2000 m a.s.l. The term ‘dwarf’ is loosely applied to species which seldom if ever exceed 25 mm in length. No absolute size limits are inferred. Although some species appear to have fairly rigorous habitat requirements, inter-specific competition probably plays a key role in niche selection and evidence indicates a broader tolerance in the absence of other species within the complex.

The last taxonomic treatment of eastern African *Afrixalus* (Schötz 1974) was the first attempt to synthesize knowledge of this material in a single paper. A very simple taxonomy was presented covering the eight known forms, and this provided a starting point for future work on the genus.

Pickersgill (1984) cast doubts over the identification of Schötz's two principal dwarf species *Afrixalus brachycnemis* (Boulenger 1896) and *A. pygmaeus* (Ahl 1931). Poynton & Broadley (1987) referred Schötz's *A. pygmaeus* to *A. brachycnemis*, while Schötz's *A. brachycnemis* they referred simply to “*Afrixalus* sp.” which they termed a “wastebasket category” in the sense that the correct name for this material had still to be established. The situation has remained unresolved until the present.

Work with the southern African dwarf *Afrixalus* led the author (Pickersgill op. cit.) to suggest this was a genus of superspecies with evolution along monophyletic lines, but while there is strong evidence to support this view among the dwarf *Afrixalus* in eastern and southern Africa, little has been reported of intra-generic affinities over the rest of Africa (although see Laurent 1981; 1982). The strong species group structures among eastern and southern African *Afrixalus* compared with the more westerly forms suggests the eastern African *Afrixalus* could have evolved from as few as three or four species which were stranded in refugia with the expansion of the Central African forests during Quaternary or late Tertiary climatic fluctuations. Speciation has occurred through diversification to occupy vacant niches but is of a comparatively superficial nature, which suggests a fairly recent origin. The *Afrixalus stuhlmanni* complex is one such species group. It occupies a vast range in eastern
Africa and is sufficiently unique to justify its special treatment as a distinct faunal unit. The aim of this paper is to identify the taxa within this complex and to attempt to elucidate the relationships between the taxa.

**Terminology**

The following definitions apply to taxonomic concepts used in this paper:

**Species:** The biological species concept is applied, as defined by Mayr (1977). It is usually assumed (Poynton 1964; Schiøtz 1999) that different habits, habitat or breeding strategies suggest ethological isolation while a different (vocal) mate recognition system and constant and non-overlapping morphological characters indicate genetic isolation. As a result, a characteristic of a species is that *its geographical distribution can be plotted exactly.*

**Subspecies:** Species are not homogeneous units but rather an interconnected web of relationships, populations and evolutionary trends which still happen to be genetically and ethologically compatible. When one or more of these populations within a species is taxonomically distinguishable from other populations it is often described as a subspecies, the assumption being that a) local environmental pressures have directed the evolutionary course of the population and moulded the phenotype, and b) that some restriction of gene flow either current or in the past has prevented these adaptations from being absorbed by the entire species. The rule followed here is that two or more morphologically different taxa sharing the same vocal recognition system are subspecies of the same species if there is no permanent zoogeographical barrier separating them. Since they are still genetically compatible they hybridize without restriction at points of contact and the diagnostic morphological characters break down, so according to this definition a subspecies' geographical distribution cannot be plotted exactly.

**Form/taxon:** “...A basic taxonomic unit ...” (Poynton 1964). A neutral term for any taxonomically recognizable unit.

**Complex:** A neutral term for any grouping of taxa within a genus, which can conveniently be applied to superspecies groups. A superspecies might be defined as *a monophyletic diversion of two or more species from all other representatives of the genus.* Since monophyly has not yet been formally demonstrated among the eastern dwarf *Afrixalus* they are presently excluded from this definition, and “complex” is used throughout.

**Dwarf:** Referring to the trend, rather than to any absolute size value; the animals in which paedomorphic and/or peramorphic modifications associated with the miniaturizing process are evident.

**Material examined**

Over 1100 preserved specimens from the following collections were examined in the course of this study. Abbreviations are generally the same as the specimen label prefixes except as noted:

- **AMNH** American Museum of Natural History, New York, USA
- **BMNH** Natural History Museum, London, England (labels prefixed BM)
- **CAS** California Academy of Sciences, San Francisco, USA
- **DM** Durban Natural Science Museum, Durban, South Africa
- **JV** John Visser private collection, Cape Town, South Africa (now in NM)
- **LIVM** Liverpool Museum, Liverpool, England
- **LR** LRG Raw private collection, Hilton, South Africa
- **MCZ** Museum of Comparative Zoology, Harvard, USA
- **MHNG** Museum d'histoire naturelle, Geneva, Switzerland
- **MP** M. Pickersgill collection, Leeds, England
- **NHMW** Naturhistorisches Museum in Wien, Vienna, Austria (labels prefixed NMW)
- **NKW** Kruger National Park Collection, Skukuza, South Africa (labels prefixed NKW/Amf)
- **NMP** Natal Museum, Pietermaritzburg, South Africa (labels prefixed NM)
- **NMZB** National Museum, Bulawayo, Zimbabwe (earlier labels prefixed UM, NMSR)
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PEM Port Elizabeth Museum, Port Elizabeth, South Africa
SMF Senckenberg Museum, Frankfurt, Germany (catalogue numbers pending)
TM Transvaal Museum, Pretoria, South Africa
UDSM University of Dar es Salaam collection, Dar es Salaam, Tanzania (label prefix KMH – K.M. Howell)
USNM Smithsonian Institution, Washington DC, USA
ZMB Zoologisches Museum, Berlin, Germany
ZMUC Zoological Museum, Copenhagen, Denmark

In addition, with the exception of Afrixalus schneideri (Boettger, 1899) and A. lacteus Perret, 1976, specimens of all currently recognized species in the genus were examined for comparative purposes.

The following tadpoles were compared against those of A. stuhlmanni brachycnemis, A. aureus crotalus and A. delicatus: A. brevipalma (Ahl, 1931) (Cameroon), A. fornasini (Bianconi, 1849) (Malawi and South Africa), A. morerei Dubois, 1985 (Tanzania), A. nigeriensis Schioetz, 1963 (Côte d’Ivoire), A. paradorsalis Perret, 1960 (Cameroon), A. quadrivittatus (Werner, 1907) (Congo-Kinshasa), A. septentrionalis Schioetz, 1974 (Tanzania), A. spinifrons (Cope, 1862) (South Africa), A. uluguensis (Barbour & Loveridge, 1928) (Tanzania) and A. unicolor (Boettger, 1913) (Tanzania). Tadpoles were captured in the field along with metamorphosing individuals or captive bred from known adults.

Voices were compared with those of A. stuhlmanni brachycnemis, A. aureus crotalus and A. delicatus: A. brevipalma (Ahl, 1931) (Cameroon), A. fornasini (Bianconi, 1849) (Malawi and South Africa), A. knysnae (South Africa), A. lacteus Perret, 1976 (Cameroon), A. laevis (Ahl, 1930) (Cameroon), A. morerei (Tanzania), A. nigeriensis (Côte d’Ivoire), A. osoroi (Ferreira, 1906) (Uganda), A. paradorsalis (Cameroon), A. quadrivittatus (Ethiopia, Uganda, Kenya and Congo-Kinshasa), A. septentrionalis (Kenya), A. spinifrons (South Africa), A. unicolor (Tanzania and Kenya), A. vittiger (Peters, 1876) (Sierra Leone, Côte d’Ivoire, Ghana and Nigeria), A. weidholzi (Mertens, 1938) (Côte d’Ivoire; Cameroon) and A. wittei (Laurent, 1941) (Zambia).

Methodology

Frogs: The aim at the start of this study was to discard all preconceived ideas of species parameters. Preserved material was sorted according to physiological characters while field work suggested several species based on vocal differences. In most cases morphological characters were sufficiently robust to distinguish between taxa in the absence of obvious vocal differences; in others, the primary evidence for specific isolation came from vocal analysis, although invariably material separated by this criterion subsequently showed subtle morphological differences also. A very few females and juveniles presented a problem when their tibial markings were faded. If they were part of a series of an otherwise single species and there was no evidence for other species at that location they were presumed to belong to that species.

The principal diagnostic characters in Afrixalus are largely secondary sexual characters present only in male frogs (Pickersgill 1984). For this reason, outside the species descriptions, all morphological analyses of frogs are based on sexually mature males. The characters utilized are widely and uniformly employed in anuran morphometrics so are not repeated here.

Afrixalus are often known as Spiny Reed Frogs due to the presence of minute spinules, or asperities, in the skin of most species. The primary means of detection was through a 10X or 20X hand lens, with the wet specimen held at an angle to a light source so that as the fluid evaporated from the skin the asperities pierced the surface film. Their arrangement has been found to be diagnostic in certain taxa (Pickersgill op. cit.).

Tadpoles: A number of Afrixalus species tadpoles have been described in the literature but no serious comparative morphological analyses have been undertaken. Although Van Dijk (1966) provided descriptions of all the then-known southern African anuran larvae he was unaware that several cryptic species of Afrixalus
existed in the region, so no critical comparisons were made. Tadpoles of three species of the *Afrixalus stuhlmanni* complex have been examined in detail, namely *A. delicatus*, *A. aureus crotalus* and *A. stuhlmanni brachycnemis*. For finer measurements, standardized as percentages in order to compare all stages of ontogeny, specimens were photographed at 10X magnification and measurements taken directly from the photographs. Morphometrically all three species appear identical, but a final judgment must await further extensive sampling.

For buccal comparisons large specimens (stage 35–37) were dissected and stained with iodine or methylene blue. Very few specimens were examined because of the scarcity of material so intraspecific variation was not compared. Terminology of internal oral features follows Wassersug (1980). Only two of these features are commented on in this paper:

**Postnarial papillae**: A pair of papillae just behind the internal nares on the roof of the buccal cavity.

**Lateral ridge papillae**: A pair of papillae approximately level with the median ridge on the roof of the buccal cavity.

**Voices**: Field recordings were made on Sanyo M-1119, M-1100C and Aiwa TP-510 miniature standard cassette recorders with either the built in microphone or an additional Kos M/10 unidirectional microphone. A comparison of the author’s voice on each recording preamble ensured there were no detectable variations in playback speed. Further voice recordings were provided by a number of colleagues, identified under “Acknowledgments”. A Vaisala HM34 hygrometer was used to record air temperature and relative humidity, while altitude and barometric pressure were measured on a Casio ACT1000 Altimeter/Chronometer. Actual body temperatures of recorded frogs were not taken, since these would have been affected by the prolonged handling this would inevitably entail with small frogs of 15–22 mm. Similarly, water temperatures were not considered relevant since *Afrixalus* generally vocalize from above the water. Furthermore, water temperatures can differ by as much as 2°C over the space of only a few centimetres, making precise measurements impossible.

Attempts were made to record at least 10 specimens per species from each locality; most of these specimens were subsequently caught and preserved to supply morphological data. Unfortunately some localities provided less than the desired number of specimens or recordings.

It is well-known (Gerhardt & Mudry 1980; Gayou 1984; Nevo & Capranica 1985) that temperature affects the vocal characteristics of ectothermic animals. In order to understand the range of vocal parameters in the field it was therefore necessary to identify how temperature change affects vocal output in captive *Afrixalus*.

Temperature controlled recordings (TCR) were obtained from three captive *Afrixalus stuhlmanni brachycnemis* kept in a 900 x 900 x 900 mm aquavivarium, vegetated to approximate the animals’ natural environment. An artificial 12 hour day/night regime was maintained over the course of the experiments. Temperature was carefully monitored to ensure a maximum fluctuation during recording not exceeding ± 0.5°C. Ambient, fan-assisted heating was preferred to achieve a constant and universal temperature. A Vaisala HM34 digital thermometer was placed more or less centrally in the aquavivarium, its sensor 15 cm above the substrate. Two mercury thermometers were attached to the inside of the glass above the water at the front and side of the aquavivarium. Any change in temperature over 0.5°C on the Vaisala was verbally recorded on the tape.

Recordings were obtained at night when the frogs were naturally active, and the choice of temperature for recordings on any particular night was made randomly, although efforts were made to record the same frogs at the same temperature on at least three nonconsecutive nights. Recordings were only obtained at temperatures within the range encountered under field conditions, where few species vocalize below 17°C and night time temperatures over 30°C rarely occur. Temperatures over 28°C could not be achieved under controlled conditions. Gayou (*op. cit.*) criticized the use of air temperature alone for estimating the body temperatures of calling frogs, and it is true that many factors can influence body temperature in the field while even the act of vigorous vocalizing can generate heat. Although the author had no control over the
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last factor, in the TCRs for the present experiment air temperature was constant throughout the aquavivarium. Water temperatures averaged 1.5–2º C below the air temperature, but vocalizing males called from vegetation above the water and seldom came into contact with it.

A database of TCRs was built up which included measurements of the emphasized frequency range (FI\textsubscript{min}, FI\textsubscript{max} and FI\textsubscript{mean}), call duration (DPT), number of pulses per call (PC) and pulse repetition rate per second (PPS). Intervals between calls were not measured once it was realized this was a behavioural rather than a physiologically controlled response, determined by the proximity of potential mates or even recent mating success (vocalizations were repeated much more frequently by males which had mated successfully the previous evening – compare Dyson et al 1998). Similarly the duration of “territorial” vocalizations and prefixes are affected by the proximity of other frogs and are highly variable, and therefore of little value as a diagnostic tool.

Recordings were analyzed using the Cool Edit Pro software programme developed by David Johnston of the Syntrillium Software Corporation.

As expected, the voice of A. s. brachycnemis (Fig. 1a) showed a marked positive linear correlation (R\textsuperscript{2} = 0.9), indicating that only 0.1, or 10%, of the variation in pulse rate is not attributable to temperature. A simple standardization formula $PPS_{std} = PPS + [b(T_{std} - T_{act})]$ was produced, where $b$ represents the slope of the regression line (in this instance 0.509), $T_{std}$ the temperature to which calls are to be standardized and $T_{act}$ the actual temperature. To illustrate the importance of standardization, the increase in pulse repetition rate in an individual of A. s. brachycnemis at 18º C and 28º C averaged 4.5/s.

Following the application of the standardization formula to the same data (Fig. 1b) the value of the Correlation Coefficient was reduced to a negligible R\textsuperscript{2} = 0.0116 and the value of $b = 0.005$, indicating that temperature as an influencing factor had been effectively eliminated. Differences in frequency between taxa were not analyzed. Preliminary investigations indicated there was considerable infra-taxon variation in dominant frequency. All the voices analysed show a very broad frequency range with a consequently broad inter-taxon overlap, suggesting this would be a fruitless line of inquiry. For this reason sonagrams presented in this paper are in wide band format to emphasise pulsatility rather than frequency.

Voices of members of the A. stuhlmanni complex were compared for significant differences in medians (Mann-Whitney U test). The Mann-Whitney test was preferred over the multiple sample Kruskal-Wallis test because it provides greater control over the comparison on a taxon to taxon basis, especially since the voices in this complex are structurally very similar. Results are reported under the preamble to the complex below.

Fig. 1. A. Correlation between pulse repetition rate and temperature in temperature controlled recordings of captive Afrixalus stuhlmanni brachycnemis. B. The same pulse rates standardized to 24ºC.
SYSTEMATICS AND SPECIES DESCRIPTIONS

In the following descriptions synonymies are only provided in instances where the identity of the published taxon is unambiguous, and in many instances the published specimens have been examined by the author. Subheadings in the descriptions follow the same basic format but where data are unavailable some subheadings may be merged or omitted altogether for the sake of brevity.

Key to the eastern and southern African 'dwarf' Afrixalus (primarily for determination of adult males)

1. Gular disc granular, without melanophores; light stripe along upper labium ............... 2
   - Gular disc smooth, with or without melanophores; no distinct light stripe along upper labium ....................................................... 7
2. Straight dark paravertebral stripes not terminating at eye ............................................. 3
   - Markings other than as above; dark dorsal stripes, if present, terminate in a dark patch interorbitally ............................................ 4
3. Asperities confined to head or very weak over entire dorsum; tibial asperities weak to absent ........................................... stuhlmanni
   - Asperities dense, abundant over entire dorsum................................. brachycnemis
4. Oblique transverse band or stripe across entire exposed face of tibia ......................... 5
   - Tibial marking a blotch not extending across entire exposed face of tibia .............. 10
5. Asperities ventrally, especially in pectoral region ........................................... delicatus
   - No ventral asperities except possibly on gular disc ................................ aqureus
6. Strong dorsal asperities extending onto tibia ............................................................ sylvaticus
   - Dorsal asperities very weak or confined to head; weak to absent on tibia ....  sylvaticus
7. Dorsal asperities when present visible to naked eye; ventral asperities predominantly posterior ......................................................... 9
   - Dorsal asperities extremely fine, not visible to naked eye; ventral asperities very fine, predominantly pectoral and under thighs ..... 8
8. Irregular dark middorsal streak ....................
   - Pair of irregular paravertebral stripes ......... septentrionalis
   - Aspect stocky; gular disc quite small with much distensible skin posteriorly... knysnae
9. Aspect moderate to slim; gular disc moderate to large and plate-like, with little distensible skin ................ spinifrons ssp.
10. Asperities confined to head ........... crotalus
   - Asperities over entire dorsum......................... brachycnemis

The Afrixalus stuhlmanni complex

The following forms represent an easily identified and probably monophyletic grouping of frogs within the genus.

Complex diagnosis: Snout-urostyle length under 26 mm. Aspect slender, tibia short; snout pointed, canthus rostralis straight, rounded, loreum sloping. Gular disc large, granular, without melanophores, set well forward and with little distensible skin. Fingers with rudimentary webbing, toes about 1/3 webbed. Subarticular tubercles of outer two fingers double; palmar tubercles weakly developed; weak fringing to fingers and toes. Asperities not visible to naked eye, not enlarged over snout, posterior dorsum or feet; when present ventrally, asperities better developed pectorally. No asperities under thigh except sometimes in anal region. Asperities rudimentary in females. Dark lateral band usually with light speckles, weak lower margin and weak to strong light stripe along upper labium.

Tadpoles reach a total length of 35 mm, the trunk accounting for 26.5–33.0% of the total length. The trunk is dorsally depressed and oval, although some tadpoles become very fat and the trunk expands laterally abruptly posterior to the eyes. Nostrils are situated dorsally, the internarial distance much less than the interorbital distance and slightly less than the distance from eye to nare. There is a prominent naso-ocular groove. Eyes are positioned laterally near the top of the head. Fins are of equal depth or with dorsal fin slightly the deeper, their combined depth barely or not deeper than the trunk. Dorsal fin originates
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At the base of the trunk or a little behind, and the tail terminates in an acute point. The spiracle is sinistral and prominent, visible from above and situated approximately half way between the eye and the tail insertion. The mouth is terminal, and has a single marginal row of papillae and no keratodonts. Tadpoles are carnivorous. Those raised in captivity and fed exclusively on mosquito larvae had grey-white bowels as had the wild-caught samples, suggesting the diets are similar, compared with black or brown bowels in all vegetarian tadpoles.


Although Laurent (1947) assumed it had a close relationship with the *stuhlmanni* complex, *A. orophilus* has several unique characters and does not seem to have close affinities with any other recognised species. It differs from the *stuhlmanni* complex in having extensive fringing to fingers and toes, possessing well-developed palmar tubercles, variable (either entire, divided or both) subarticular tubercles, straight canthus rostralis with loreal region almost vertical, and a more pointed snout. The dorsal integument is rather glandular with characteristic fine dark speckling, and it lacks a light labial stripe. The tadpole is unknown. *Afrixalus orophilus* and the *stuhlmanni* complex occupy completely different zoogeographical regions with consequently different habitat requirements.

The *Afrixalus spinifrons* complex has a smooth gular disc, often with scattered melanophores, and rather weak subarticular tubercles which may be entire or divided on the outermost fingers but predominantly the former. Dorsal asperities are large and visible with the naked eye, and are often as well developed in females as in males, while ventral asperities when present are most abundant over the posterior belly. Tad-

Fig. 2. At this location near Dar es Salaam University *Afrixalus delicatus* occupies the short flooded grassland in the foreground while *A. stuhlmanni sylvaticus* occurs exclusively along irrigation trenches among denser mixed vegetation and degraded forest on the other side of the road.
pole without keratodonts and with a rudimentary second row of papillae ventrally. The complex comprises *Afrixalus spinifrons spinifrons* (Cope, 1862), *A. spinifrons intermedius* Pickersgill, 1996 and *A. knysnae* (Loveridge, 1954).

The *Afrixalus septentrionalis* complex is characterized by a smooth gular disc, usually with scattered melanophores, undivided subarticular tubercles on the outer fingers, and extremely fine dorsal and ventral asperities, with the latter especially concentrated pectorally and under the thighs. Tadpole of *A. morerei* without keratodonts, and with a weak second row of papillae below the rostradonts. The complex comprises *Afrixalus septentrionalis* Schiotz, 1974 and *Afrixalus morerei* Dubois, 1985.

On the basis of its morphology *Afrixalus delicatus* is evidently a member of the *A. stuhlmanni* complex; its morphological and vocal homogeneity suggest in favour of a later evolutionary development within this complex. By contrast, there are evident morphological and vocal trends among *A. stuhlmanni* and *A. aureus*, and although on the whole their habitat range is slightly broader than in *delicatus*, the choice of niche within those habitats appears quite conservative. Whether through competition, exclusion or habitat partitioning, in all cases where the author found *delicatus* and *stuhlmanni* in sympathy the latter occupied the more restricted habitat, its populations (based on numbers estimated from vocalizations) were much smaller, and enclaving was pronounced.

At Dar es Salaam *A. delicatus* and *A. stuhlmanni sylvaticus* occur within 40 m of each other without interaction: at this location *delicatus* occupies short flooded grassland (Fig. 2) on the edge of a football field just outside the University entrance while *sylvaticus* occurs over the road along drainage trenches in a “farmbush” habitat, with much denser mixed vegetation and degraded secondary forest. On the University campus itself *delicatus* appeared to be the only dwarf species and occupied various sites including grassy seepage on a lawn, long-standing open rain pools, a lily- and reed-covered artificial pond and denser vegetation beside a spring.

Several sites in Malawi yielded both *A. delicatus* and *A. s. brachycnemis*, but the two species were never found syntopically. At Chintzulu and Chiradzulu *delicatus* occupied open sites and dense sedges over seepage while *brachycnemis* occurred at a single small pool with tall, dense grass and herbage. At Limbe where they occupied the same pond *brachycnemis* had established an enclave of approximately 8 m² of marshy ground isolated from the more catholic *delicatus* by several swiftly flowing channels, and no *delicatus* were heard vocalizing from this enclave. At the few locations (Mzuzu; Karonga; Kasungu) where *brachycnemis* appeared to be the only dwarf *Afrixalus* it occurred in both open and closed grassland, while at Zomba where only *A. delicatus* was found similar broad tolerances were observed. Similarly at Morogoro, where *A. stuhlmanni stuhlmanni* as the only dwarf species was collected from both dense matted sedges and the grassy edges of open rice paddies.

During the day at Limbe juveniles of both *delicatus* and *brachycnemis* were found in Arum lily leaf axils on the banks of a marshy pool without any apparent segregation, and it would appear habitat partitioning only occurs in adulthood.

Pickersgill (1984) reported *A. delicatus* to be sympatric with *A. aureus crotalus* at several locations between Beira and Inchope in Mozambique. This observation was based on samples in the NMZB and NM collections; in both collections, accession numbers for these specimens were randomly assigned, suggesting both taxa were collected together. The few sites the author has since personally investigated in this region yielded only one species or the other, but failure to find the two species in syntopy does not necessarily mean they do not occur *sympatrically* - that is, at the same location, since existing evidence suggests their habitat preferences tend to be mutually exclusive where ranges overlap. It is also possible that on these locations where the two species were collected sympatrically in the late 1950s, competition has resulted in the local exclusion of one or the other species.

*A. stuhlmanni stuhlmanni* and *A. s. brachycnemis* have very similar habitat preferences and voices, and in the latter *brachycnemis* falls within the variation of both *stuhlmanni* and *sylvaticus* (Fig. 3), indicating that a subspecies designation is appropriate. The voice of *crotalus* shows a general northward increase in PPS while *bra-
Fig. 3. Sonagram/oscillograms of voices. A. *Afrixalus stuhlmanni stuhlmanni* (Morogoro, 2 calls). B. *A. s. sylvaticus* (Dar es Salaam, 4 calls). C. *A. s. brachycnemis* (Karonga, 2 calls).
chycnemis shows a general southward decrease in the same characters, so that they are most distinct in southern Malawi where the two taxa almost come into contact (Fig. 4). Here crotalus occurs in the Shire lowlands while brachycnemis appears to be confined to higher altitudes on the escarpment.

As its name indicates, A. stuhlmanni sylvaticus is more sylvicoline in habitat preference and although morphologically identical its dorsal markings are very different from those of A. s. stuhlmanni. Nevertheless hybridization occurs widely where the coastal forests are being degraded through urban pressures and agriculture and many specimens are impossible to identify to subspecific level. A series from Muheza in the author's possession shows the whole range of dorsal markings from typical stuhlmanni to typical sylvaticus. Since the trend is towards continued forest degradation and therefore more widespread intergradation between the two forms may be anticipated, a subspecific designation is indicated since they are not genetically isolated the range of neither form can be plotted exactly. It also serves a more practical purpose than maintaining sylvaticus and stuhlmanni as separate species and having to treat the numerous intergrades as “sp. indet.” A. s. stuhlmanni has not been recorded from Kenya where only frogs with typical sylvaticus markings are found, and for this reason sylvaticus should be maintained as a distinct subspecies. The amount of integra-

Fig. 4. Comparison by latitude of mean pulse rates in standardized calls of Afrixalus stuhlmanni and A. aureus, showing vocal reinforcement effects at points of closest contact – in this case southern Malawi. – Circles: A. stuhlmanni ssp.; diamonds: A. aureus ssp.

Fig. 5. Typical habitat of Afrixalus aureus aureus: a shallow seasonal marsh in relatively dry Acacia savanna. Mkuze Game Reserve, South Africa.
diation with stuhlmanni might be useful as an indicator of forest degradation.

A. aureus aureus, the southernmost representative of the complex, has quite different ecological requirements with most, if not all, recorded localities having less than 800 mm of rain per annum (Pickersgill 1984), creating a dry woodland savanna habitat dominated by Acacia (Fig. 5). Wetter areas are avoided—perhaps due to competition with A. delicatus from the moist coastal lowlands. It is not known how this form interacts with A. aureus crotalus from further north, and which seems to have a broader climatic tolerance, since the northern distribution of A. aureus aureus is unknown. The voices of the two forms from well within their respective ranges are indistinguishable. For this reason, crotalus is here treated as a northern subspecies of aureus. The voice of A. aureus ssp. differs from the intra-specific variation of A. stuhlmanni ssp. (Figs. 6a, b), suggesting that a specific designation is appropriate.

Mann-Whitney U tests were performed on the voices of five of the six taxa (Table 1) taking into account the call duration (DPT), number of pulses per call (PC), pulse rate (PPS), standardized pulse rate (PPS @ 24°C) and minimum and maximum emphasized frequencies (FI_min and FI_max), and confirm a north-south divergence of the A. stuhlmanni complex into two species, apart from the vocally distinctive A. delicatus. Generally A. stuhlmanni calls have less than, and A. aureus more than 16 PPS. The significance levels vary from location to location because voices from a single locality tend to be more conservative than from the range as a whole. Samples for the analysis were made up of vocalizations from as many localities as possible in order to capture the overall inter- and intra-taxon variation. This has the effect of obscuring the sharp vocal character reinforcement effects in southern Malawi, although this is clearly illustrated in Fig. 4. A. delicatus was omitted from the analysis since its voice is so different from other members of the complex (Fig. 6c), but for a comparison of this species with A. aureus see Backwell & Passmore (1991b).

In many anurans pulse repetition rate has been found to carry much of the species-specific information, while the call frequency defines the channel on which this information is broadcast (Straughan 1973). This is borne out by studies on the dwarf Afrixalus where there is a broad overlap in frequency in the voices of all taxa, so pulse repetition rate, coupled, perhaps, with call duration must be of paramount significance in female phonotaxis and, consequently, species diagnosis.

Some of the shortest and simplest Afrixalus calls are produced by forest species, and voice evolution in the A. stuhlmanni complex may reflect a transition between forest and savanna habitation. An analysis of voices in the stuhlmanni complex shows a gradual increase in the number of pulses per call, from A. stuhlmanni sylvaticus with 2–5 pulses to the dry savanna A. aureus aureus with 4–14 pulses (Fig. 7). Savanna adaptation in this complex has reached its acme in A. delicatus which produces a prolonged rapid rattle or buzz, and variations of this type of call are common to many savanna amphibians.

Table 1: Results of Mann-Whitney U tests comparing difference in medians of vocal characteristics on a taxon to taxon basis. The significance threshold for P < 0.05 is less than 127 for samples of 20 voices and less than 105 for sylvaticus with 17 voices. Scores of around 50 or less indicate high to very high significance. NS (not significant) indicates scores of P > 0.05. DPT = call duration; PC = number of pulses per call; PPS = pulse rate; FI = emphasized frequency.

<table>
<thead>
<tr>
<th>U-test: (N = 20 except sylvaticus: N = 17)</th>
<th>DPT</th>
<th>PC</th>
<th>PPS</th>
<th>PPS 24°C</th>
<th>FI_min</th>
<th>FI_max</th>
</tr>
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<tbody>
<tr>
<td>brachycnemis/stuhlmanni</td>
<td>51</td>
<td>70</td>
<td>NS</td>
<td>39</td>
<td>NS</td>
<td>42</td>
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<tr>
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<td>80</td>
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<td>111</td>
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<tr>
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<td>45</td>
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<td>NS</td>
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<td>100</td>
<td>NS</td>
<td>NS</td>
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<td>43.5</td>
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<td>67</td>
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<td>NS</td>
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<td>NS</td>
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</table>
Fig. 6. Sonagram/oscillograms of voices. A. *Afrixalus aureus aureus* (Mkuze Game Reserve, 2 calls). B. *A. a. crotalus* (near Odzi, 3 calls). C. *A. delicatus* (Palm Beach, part of call only).
As with morphological character displacement, vocal character reinforcement is probably a purely mechanical result of hybridization events in the past: sterility of hybrid zygotes or reduced fitness in the resulting offspring over time create a “vacuum zone” where the characters utilized by both taxa die out while those least attractive to the other taxon are perpetuated and reinforced. The phenomenon arises through genetic incompatibility and in turn works to prevent continued inter-taxon hybridization. It is important to note in this respect that the interbreeding taxa are not fully compatible genetically: if they are, intergradation will continue and vocal diversity within populations will remain high.

Despite the high value placed on vocalization as a means of attracting potential mates, the chance of interception by males with less attractive vocal qualities in the free-for-all of a breeding pond is considerable. If females only paired with the male whose voice attracted them most there would be no opportunity for satellite males (Backwell & Passmore 1991b), which do not vocalize but attempt to exploit this period of vulnerability when the female crosses their path as she attempts to make contact with her chosen partner. If many males are present, the female might have to cross numerous territories and the chance of mating with the male whose voice most attracted her would actually be quite low. In such a scenario, the general trend within and between (adjacent) populations would be for rather high vocal diversity within given parameters, since as long as some voices attract conspecific females there is a chance that marginally- or even unattractive voices will also be perpetuated through opportunistic interception of females by conspecific males.

Outside those parameters, in populations where no male voices are attractive to females of another population, the chance of opportunistic interception will be eliminated and the two populations will follow different evolutionary paths.

One strategy which functions to reduce the incidence of crossbreeding is enclaving, where conspecifics are attracted by the voices of their own species into a particular area. The resulting vocal signal directs females to its source, where relatively high concentrations of conspecific males are available.

**Afrixalus stuhlmanni stuhlmanni** (Pfeffer, 1893)

Figs. 3a, 7, 8a, 9, 10.

*Megalixalus stuhlmanni* Pfeffer, 1893: 31–32.


*Hyperolius pygmaeus* Ahl, 1931a: 22–23 (new synonymy).


*Afrixalus* n. sp. – Pickersgill 1994: 83.

Syntypes:

26 syntypes (field no. 351) originally in Hamburg, none now traceable.

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**AFRIXALUS STUHLMANNI COMPLEX**

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A. stuhlmanni superspecies

Mean pulses per call

<table>
<thead>
<tr>
<th>Pulse per call</th>
<th>sylvaticus</th>
<th>stuhlmanni</th>
<th>brachycnemis</th>
<th>crotalus</th>
<th>aureus</th>
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<td></td>
<td></td>
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</tr>
</tbody>
</table>

Fig. 7. Comparison of the mean number of pulses per call with a gradual change between forest through dense grassland to savanna in the Afrixalus stuhlmanni complex, excluding A. delicatus. The black bar indicates the range. – N = 18 (sylvaticus), 33 (stuhlmanni), 104 (brachycnemis), 102 (crotalus) and 36 (aureus).
Fig. 8. Observed pattern variations. A. *Afrixalus stuhlmanni stuhlmanni*. B. A. *s. sylvaticus*. C. A. *s. brachycnemis*. 
Material examined:
96 specimens (28 males) from Tanzania: Amani (ZMUC R 077996); Amboni Estates (MCZ 25168); Dutumi (MCZ 9524/5; 9528/9; AMNH 12605/15); Jozani Forest (BM 1978.2384); Kizerui (USNM 76864/5; MCZ 13357/60); Korogwe (AMNH 73076); Liwale (MCZ 26635); Magrotto Mt. (MCZ 25169/70); Mkokotoni (MCZ 10196/7); Morogoro (MP 3201/4; 3241/2; 3659/60; 3702/4; MCZ 51661/86); Muheza (MP 2518; 2554; 2559/60; 2562; 2564; 2566; ZMUC R 073858; 077812; 77820); Mwera (MCZ 16826/7; 16829/36); Tanga (ZMB 36102); Ukami (MCZ 16805); Zanzibar (NMW 3718:1/3; NM 5623a-d).

Taxonomy and systematics
Described by Pfeffer from Zanzibar Island in 1893, this species was synonymised with A. leptosomus by Tornier four years later and subsequently “lost” to science, apart from a description (using Pfeffer's original data but including mainland A. delicatus) by Ahl (1931b) and a reference by Frost (1985). Since then the taxonomy of the eastern African dwarf Afrixalus has undergone numerous upheavals and further research into this species has been completely neglected.

Zanzibar Island (Unguja) is home to three species of Afrixalus, one of which (Afrixalus unicolor) is easily discounted as a congener for the name A. stuhlmanni due to its much larger size and different dorsal markings. Afrixalus delicatus is common on the island, and a second, striped species less so. Although all 26 type specimens of Megalixalus stuhlmanni seem to have been lost or were destroyed during World War II and all efforts to trace surviving specimens have proved fruitless, Tornier (1897) examined the type series and his remarks concerning the dorsal markings “Zwischen Megalixalus leptosomus Peters und Megalixalus stuhlmanni Pfeffer ... finde ich nur Farbenunterscheide...” (referring, as he makes clear, to stuhlmanni's silvery, rather than beige, stripes) leave one in no doubt that the name A. stuhlmanni belongs to the second, striped species, which is consequently revived in the present work.

The type of Hyperolius pygmaeus Ahl, 1931 from Tanga (ZMB 36102) is still in very good condition and shows all the characteristics of an adult male of this species. The dorsal stripes in this specimen are fragmented, a feature commonly found in intergrades with A. stuhlmanni sylvaticus. Schiøtz (1974; 1975) used the name A. pygmaeus in connection with northern material of A. delicatus, although he commented in the earlier paper that it (the pygmaeus type) “…does not quite resemble my material in pattern and morphology...”. Nevertheless, his lead was followed by many subsequent authors (Pakenham 1983; Drewes 1984; Dubois 1985; Poynton 1991; Drewes & Altig 1996).

Definition
Length males 15.2–21.1 mm (mean 18.1 mm, N = 28), females 17.2–25.0 mm (mean 20.3 mm, N = 41). Gular disc rounded to transversely oval and weakly granular, set well forward and usually with a pronounced anterior “lip”. Dorsal asperities weak, and very weak or absent on tibia. Gular disc with or without weak asperities. No ventral asperities. Dorsal pattern a pair of paravertebral dark lines or stripes continuous from

Fig. 9. Afrixalus stuhlmanni stuhlmanni (MP 3704) from Morogoro, Tanzania.
Fig. 10. Distribution of examined specimens of Afrixalus stuhlmanni stuhlmanni (white triangles), A. s. sylvaticus (black triangles), A. s. brachycnemis (grey triangles), A. aureus aureus (black spots) and A. a. crotalus (grey spots).
snout to urostyle, not coalescing in occipital region or having projections onto upper eyelid; tibia with longitudinal dark stripe along its outer face and often a dark longitudinal streak dorsally. The dorsal edge of the lateral band is straight.

**Variation**

Gular disc width 40.0–71.6% (mean 58.8%, N = 20) of tibia length, 16.6–30.9% (mean 24.6%, N = 20) of snout-urostyle length and 58.3–98.0% (mean 81.5%, N = 16) of head width; gular disc length 37.7–65.8% (mean 52.2%, N = 18) of tibia length and 15.2–26.4% (mean 21.8%, N = 18) of snout-urostyle length. Tibia length 36.9–48.1% (mean 41.5%, N = 66) of snout-urostyle length; head width 60.2–86.7% (mean 72.7%, N = 46) of tibia length, 26.0–37.1% (mean 30.5%, N = 47) of snout-urostyle length. 1.5–2 phalanges on outer side and 1–2 phalanges on inner side of toe IV free of web, toe V with 0.25–0.66 phalanx free of web; finger IV without web, or with up to 0.5 of first phalanx webbed. Dorsal pattern may be fragmented into longitudinal streaks, most notably where intergradation with *A. stuhlmanni* occurs (Figs. 8, 9).

**Voice**

A brief series of metallic clicks lasting on average 0.5s (0.2–0.9s in analyzed calls) with between 2–9 pulses. Pulse rate 10–14/s (10–13 pps when standardized to 24°C) and pulse duration varying from 16 to 27 ms. Emphasized frequency range between 3.9–5.2 kHz (mean 4.2–5.1 kHz) (Muheza and Morogoro).

**Breeding and development**

Not recorded. Gravid Nyange on 1st October (Barbour & Loveridge 1928); 17 June (Amboni Estates); 1–6 July (Magrotto Mountain).

**Sympathy**

*Afrixalus unicolor* only. See also comments on its relationship with *A. stuhlmanni sylvaticus* below.

**Habits and habitat**

Dense grassland in humid savanna. Several specimens were collected during the day from the leaf axils of maize near a rice paddy at Morogoro, and one specimen in an exposed position on the horizontal bract of a *Cyperus* growing in shallow water. Loveridge (1942) collected two specimens in wild bananas at Magrotto Mountain, and in the outer leaves of bananas at Nyange and Kizerui (Barbour & Loveridge 1928).

**Distribution**

Low to medium altitudes east of the Eastern Arc Mountains in northern and central Tanzania (Fig. 10).

*Afrixalus stuhlmanni sylvaticus* Schiotz, 1974

Figs. 3b, 7, 8b, 10, 11.


Holotype: Zoological Museum, Copenhagen (ZMUC R 073862).

Material examined: 30 specimens (22 males) from Kenya: Garsen (Tana River AMNH 90259); Kwale (ZMUC R 074006; 074008; 74010; 74012; 078105; 078107); Maken, S. of Galole (AMNH 73067); Shimba Hills F.R. (CAS 155582; 155611; 155652/4; 155947; MHNG 1454.77). – Tanzania: Dar es Salaam (MP 3293/6; 3416; 3642/4); Muheza (MP 2561; ZMUC R 074158). – Eggs from Dar es Salaam (MP 3034). – Note: MP 2564, ZMUC R 074157 and ZMUC R 073859 from Muheza and ZMUC R 077121 from Rufiji Delta are all intergrades with the nominate form, not assignable to either subspecies.

**Systematics**

Described from Kwale, Kenya, and treated as a full species by Schiotz (1974; 1975; 1999). Clarke & Dickinson (1995) found intergrades between *stuhlmanni* (as *brachycnemis*) and *sylvaticus* in Kazimzumburi Forest Reserve in Tanzania, while the author has collected a series representing the entire range of dorsal markings from typical *sylvaticus* to typical *stuhlmanni* from disturbed forest/grassland at Muheza. The voice is similar to that of the sylvicolous *A. laevis* from Central Africa. R.C. Drewes (pers. communication) recently collected a form of *A. laevis* in Uganda with a dorsal pattern virtually indistinguishable from that of *A. stuhlmanni sylvaticus* (see Schiotz 1999, fig. 66).
**Definition**

Length males 18.0–20.8 mm (mean 19.4 mm, N = 17), females 20.6–22.8 mm (mean 21.8 mm, N = 3). Schiøtz (1999) records a snout-vent length of up to 24 mm in females. Gular disc rounded. Dorsal asperities fine and weak, confined to head or at least not extending to tibiae and feet; gular disc with or without fine asperities; no ventral asperities. Dorsum silverish to yellow, usually with scattered dark spots and with up to three darker transversely oriented bands - one between the eyes, one in the pectoral region and a broader band across the lumbar region which is continuous with a broad transverse tibial band when the limb is at rest. Lateral band without clear lower margin or light labial stripe. The dorsal edge of the lateral band in some Kenyan specimens curves slightly downwards behind the eye before curving up again to form the lumbar process.

**Variation**

Gular disc width 46.1–74.4% (mean 53.9%, N = 13) of tibia length, 20.0–30.5% (mean 22.9%, N = 13) of snout-urostyle length and 63.1–92.4% (mean 70.8%, N = 12) of head width; gular disc length 40.5–57.3% (mean 47.4%, N = 13) of tibia length and 17.3–23.5% (mean 20.1%, N = 13) of snout-urostyle length. Tibia length 40.5–45.1% (mean 42.5%, N = 20) of snout-urostyle length; head width 70.6–84.0% (mean 75.4%, N = 14) of tibia length and 29.7–34.2% (mean 31.8%, N = 15) of snout-urostyle length. 1.5–2 phalanges of toe IV free of web on inside, 1–1.5 phalanges free on outer side, and up to 0.5 phalanx free on toe V; finger IV with rudiment of web, to 0.5 phalanx webbed. Transverse bands on the dorsum may be divided medially in some specimens while in others the dorsal markings are entirely broken up into scattered dark spots (Fig. 8b).

**Voice**

Almost identical to that of the nominate form, but with fewer pulses per call on average (i.e.: 2–5) at a rate of 11–15 pps at 24.6° C (little difference when standardized to 24° C). Pulse duration 14–29 ms, emphasized frequency range 3.9–4.7 kHz, mean 4.2–4.5 kHz (Dar es Salaam).

**Breeding and development**

A batch of eggs was already hatching on 5 May (Dar es Salaam). They were deposited in the usual way in a folded leaf some centimetres above still water. Another female voided eggs in the collecting container on the same day. No tadpoles were found.

**Sympathy**

Syntopic with *A. unicolor* at Dar es Salaam and Muheza, while *A. delicatus* occurred in large numbers a few metres away from the first location at a more open site. See comments regarding its relationship with *A. stuhlmanni stuhlmanni*.

**Habits and habitat**

Associated with dense forest where they sat in open situations on vegetation surrounding a forest pool (Schiøtz 1975) but also occurs in degraded forest and farmbush.

**Distribution**

Probably as relict populations along most of the Kenyan and Tanzanian coast. Intergrading with *A. stuhlmanni stuhlmanni* makes plotting an exact distribution impossible.
Afrixalus stuhlmanni brachycnemis (Boulenger, 1896)
Figs. 1, 3c, 7, 8c, 10, 12–14.

Syntypes:
Three syntypes in the British Museum (Natural History), BM 1947.2.9.77/9.

Material examined:
101 specimens (43 males) from Tanzania: Mbamba Bay (USNM 152478a/b); Mwandemeres, Rungwe Dist (MCZ 13336/7; 16847); Mwaya (MCZ 16837/46; USNM 118762); Ugano (NMW 3719). – Malawi: Chinteche (MP 3924); Chiradzulu (BM 1947.2.9.77/9; MP 3967); Deep Bay (USNM 152476); Karonga (MP 3994; 4061; 4076; USNM 152466/75); Kasungu (MP 3962/6; 3968/72; ZMB); Limbe (MP 3899/900; AMNH 56046; 90254; MCZ 27773/4); Limphasa Dambo (UM 24708; 24710/1); Lujeri Estates (UM 4325a/b; 4326a/b); Mulosa (JV 247); Mzuzu (MP 3859/70; 4029); Nkhata Bay (MP 3216/7; 3697/9; USNM 152477); Nyika Plateau (BM 97.6.9.192/7; Ruo Gorge (MCZ 27227/8; 27250). – Mozambique: Nampula (UM 19370a-h). – Zambia: Kachalola (AMNH 99716; ZMUC R 078731/2); Mbangombe (MP 3632). – Tadpoles from Mzuzu (MP 4021; 4040; 4079). – Eggs from Kasungu (MP 4016); Mzuzu (MP 4025).

Taxonomy and systematics
Simply identifying this taxon has been one of the most difficult tasks of the present study. For many years the name A. brachycnemis has been applied to virtually any dwarf Afrixalus from eastern Africa. Schiøtz (1974) revised the eastern African members of the genus and resurrected Hyperolius pygmaeus Ahl, 1931 to accommodate what is here termed A. delicatus, referring other members of the A. stuhlmanni complex (with the exception of A. s. sylvaticus) to A. brachycnemis, and this arrangement gained acceptance among taxonomists. Pickersgill (1984) cast doubts over the correctness of Schiøtz’s diagnosis without formally redefining either pygmaeus or brachycnemis, and Poynton & Broadley (1987) independently followed suit by reversing Schiøtz’s definition - i.e.: Schiøtz’s A.
pygmaeus became *A. brachycnemis* while the bulk of the material referred to *brachycnemis* by Schiøtz was treated as “Afrixalus sp.”.

This confusion arose because the syntypes of *Megalixalus brachycnemis* Boulenger are all females, showing virtually no diagnostic features. In addition the dorsal markings have all but disappeared over the years, while Boulenger’s brief original description is open to some personal interpretation. On a visit to the type locality by the author in 1997 the only *Afrixalus* collected was *A. delicatus*, and the dorsal markings in this small series conflicted with the original description of *brachycnemis* in that not one of the specimens could comfortably be described as “striped”, while apparently (as there was no mention of significant variation in the original description) all three of the syntypes were striped.

On a number of locations in Malawi in 1999 the author collected a dwarf *Afrixalus* with paravertebral stripes identical to those illustrated in Boulenger’s figure of *M. brachycnemis*. Although the evidence that this was *A. brachycnemis* was reasonably convincing, it was only when the type locality was revisited and a single male of this form (Fig. 12) was traced by its voice (in addition to large numbers of *A. delicatus*) that the author felt the problem of *brachycnemis*’ identity was truly resolved.

Schiøtz’s (1974; 1975) diagnosis of *A. brachycnemis* is thus reaffirmed, with certain restrictions, since *brachycnemis* is confined to the environs of Lake Malawi and is replaced by *A. aureus crotalus* to the south and *A. stuhlmanni stuhlmanni* to the northeast.

**Definition**

Length males 18.3–21.9 mm (mean 20.0 mm, \(N = 37\)), females 18.7–25.9 mm (mean 21.9 mm, \(N = 26\)). Gular disc rounded to oval, sometimes with a weak anterior lip. Dorsum with abundant minute asperities overall, including the tibia but not on feet. Gular disc with few very weak, unpigmented asperities. No ventral asperities.

Dorsal pattern consists of a pair of paravertebral dark lines from either side of the urostyle to or just anterior to the eyes, between which the stripes may occasionally coalesce and/or diverge onto the eyelids. Lateral band with straight upper edge and moderate lower margin, sometimes with light speckles; weak labial stripe. Tibia with dark lower margin and a longitudinally-directed dark spot or streak in the paler area (Fig. 8c).

**Variation**

Gular disc width 49.5–76.3% (mean 60.5%, \(N = 31\)) of tibia length, 20.1–32.0% (mean 25.7%, \(N = 31\)) of snout-urostyle length and 65.1–100.0% (mean 81.2%, \(N = 30\)) of head width; gular disc length 40.7–61.1% (mean 50.8%, \(N = 29\)) of tibia length and 17.2–26.8% (mean 21.6%, \(N = 29\)) of snout-urostyle length. Tibia 33.8–46.0% (mean 40.6%, \(N = 63\)) of snout-urostyle length; head width 53.5–85.2% (mean 74.8%, \(N = 38\)) of tibia length, 21.6–34.7% (mean 31.2%, \(N = 39\)) of snout-urostyle length; 1–2 phalanges of toe IV free of web on either side, and up to 0.5 phalanx of toe V free; finger IV with rudiment of web to 0.75 webbed.
Dorsal markings are highly variable, and when tibial markings are obscure some specimens may be impossible to separate from *delicatus* on this feature alone: although paravertebral dark stripes appear to be a constant feature these sometimes merge into a rudimentary head-spot, and in such specimens there is usually a projection onto the upper eyelid. Tibial markings appear to be consistently diagnostic. The ground colour occasionally intrudes into the dark stripes, a characteristic of *A. dorsalis lasciniosus* and some *A. quadrivittatus*. An adult male from Mbamba Bay (USNM) lacks ventral asperities and is presumed to belong to this form although there are no dorsal markings.

**Voice**

Very similar to the other subspecies with 3–10 pulses over 0.2–1.1 s and a pulse rate of 7–15 pps (7–14 pps when standardized to 24°C). Pulse duration from 17 to 28 ms. Emphasized frequency range between 3.1–4.83 kHz (mean 3.45–4.68 kHz) (Karonga, Limbe, Mzuzu, Chinteche, Kasungu and Chiradzulu).

**Breeding and development**

Eggs 30 January (Kasungu), 8 March (Mzuzu). Eggs are cream, 1.6 mm in diameter in a 2.5 mm capsule (Kasungu). Newly metamorphosed froglet 26 March (Mbamba Bay).

In captivity a male mated with a female *A. dorsalis* from West Africa and eggs were produced. Only one embryo survived beyond the rotation stage (Gosner stage 15) but died at stage 19.

**Tadpoles**

Tadpoles were collected at a location where only *brachycnemis* were collected; others were raised from breeding pairs in captivity (Fig. 14). They appear identical to those of other members of the complex. Greatest trunk length at stage 38 was 10.1 mm in one individual, with others representing 27.6–29.3% of total length. Light grey above with few small scattered black punctations. Weak dark canthal streak. Whitish below. Nostrils sunken, without raised margins; internarial distance 55–60% (mean 58%, N = 4) of interocular space. Marginal papillae moderately well-developed, 12–19 in number; no inframarginal papillae. No keratodonts. Internal oral features not examined (Mzuzu).

**Sympatry**

Sympatric with *A. fornasinii* at most localities. Has a complex relationship with *A. delicatus* at Limbe, Chinteche and Chiradzulu as described in the introduction to the complex above.

**Habits and habitat**

Savanna and savanna - woodland mosaic. Tends to inhabit sites with tall dense grasses in locations where it is sympatric with *A. delicatus*. A juvenile was collected in an exposed position on shrubbery during the day near Mbangombe. Otherwise does not appear to be heliophilic.

**Distribution**

Environs of Lake Malawi and westwards to at least the eastern slopes of the Luangwa Valley in Zambia. A sample purported to be from the
Nyika Plateau at 1800m (BM) has not been confirmed in subsequent reports (Stewart & Wilson 1966) and the elevation seems unlikely. The specimens have been examined: they are in poor condition and the collection consists entirely of females but almost certainly represent this form. Three specimens collected by Loveridge from the Ruo Gorge on Mulanje Mountain at 1200m (MCZ) are all very large females in poor condition. They appear to be *brachycnemis* but they could well represent a relict population of *A. quadrivittatus*, although subarticular tubercles are divided in all three and this is not normally a characteristic of that species. Several samples in a series of subadults from Nampula, Mozambique, show the interorbital expansion of dorsal lines characteristic of *brachycnemis*.

**Afrixalus aureus aureus** Pickersgill, 1984

Figs. 6a, 7, 10, 15, 16.


Holotype:

Material examined:
63 specimens (54 males) from **South Africa**: Crocodile Bridge, Kruger National Park (NKW/Amf 144); Faai Roan Camp, Kruger N.P. (NKW/Amf 308); False Bay (NM 3886/7; USNM 308724/7); Lisbon Estate, Pilgrim’s Rest (TM 57735/7); Mhlatuze Valley (ZMUC R 077769; DM 890; NMZB 7388; MCZ 106588; CAS; SMF – formerly MP 624; 633/4; 636; 1352; 1355; 1359; BM 1983.1151; LR 1910); Mkuze G.R. (MP 2104/5; 4111/8); Ndumu (NM 3896); Nsemene Windmill, KNP (NKW/Amf 130a–c); Nyalazi (DM 306/10); near Skukuza (TM 57740/1); Tshokwane, KNP (NKW/Amf 90); Zululand (PEM 1852/3; 1868/9). – **Mozambique**: Estuatane (UM 30969); Maputo (NM 39424); Ponte do Colichane (NM 3945/9). – **Swaziland**: Mafuteni (SMF – formerly MP 1345; 1347/8).

**Taxonomy and systematics**

Originally treated as *A. brachycnemis* by Poynton (1964), Wager (1965) and Passmore & Carruthers (1979). Pickersgill (1984) described it as a new species. Lambiris (1988b) criticized the validity of this species, apparently finding no difference in the voice, morphology or habitat of *A. aureus* and *A. delicatus*. Vocal evidence now suggests *aureus* and *crotalus* are subspecies of a single species, with *aureus* having page priority.

**Definition**

Length males 16.9–23.7 mm (mean 20.5 mm, N = 45), females 20.8–25.8 mm (mean 23.1 mm, N = 5). Gular disc large, squarish to semi-triangular, weakly granular. Dorsal asperities fine, confined to head (females) or scattered over entire dorsum; gular disc with fine scattered asperities;
no ventral asperities. Dorsum yellow to gold, generally with dark lumbar patch or speckling on each side which corresponds with a broad oblique transverse tibial band when the limb is at rest; sometimes a suggestion of a darker mid-dorsal line and/or a broken headspot whose arms extend onto the upper eyelids. Lateral band broad, with a straight upper edge and generally with scattered light speckles; light labial stripe moderately well defined.

Variation

Gular disc width 46.3–60.5% (mean 53.8%, N = 15) of tibia length, 19.0–24.5% (mean 22.2%, N = 15) of snout-urostyle length and 69.8–96.1% (mean 81.5%, N = 14) of head width; gular disc length 40.5–60.5% (mean 51.7%, N = 15) of tibia length and 17.8–25.0% (mean 21.4%, N = 15) of snout-urostyle length. Tibia 36.6–46.2% of snout-vent length (mean 40.7%, N = 43); head width 63.0–70.3% (mean 66.3%, N = 16) of tibia length and 25.5–30.8% (mean 27.4%, N = 16) of snout-urostyle length. 1–2 phalanges of toe IV free of web, and up to 0.5 phalanx of toe V; webbing of outermost finger from 0.2–0.75 of first phalanx. Dorsal markings are variable, but in all examined specimens there were at least indications of lumbar patches, and the tibial markings are characteristic (Figs. 15, 16).

Voice

A finite metallic rattle lasting from 0.2–0.83s and with 4–14 (mean 8) pulses per call. Pulse rate 10–20/s (13–20 pps when standardized to 24°C). Pulse duration 21–30 ms. Very broad emphasized frequency from 2.8–5.0 kHz (mean 3.4–4.7 kHz) (Mkuze G.R. and Mhlatuze Valley).

Breeding

Gravid 16 November (Nyalazi) and 9 February (Maputo); in amplexus 30 November (Mhlatuze Valley); eggs 2 December (Mkuze G.R.). Eggs are creamy white, 1.2 mm in diameter in a rather amorphous capsule of about 2.3 mm (Mkuze G.R.) enveloped in vertically folded blades of grass 4–15 cm above the water. Newly metamorphosed froglets 11.5–11.7 mm in length in February (Mhlatuze Valley and Ponte do Calichane).
Sympathy

Both *A. aureus* and *A. delicatus* have been recorded from Ndumu (NM collection, Pickersgill 1984) but further data are lacking. The Ndumu specimen is a juvenile and its identification as *aureus* may have been in error. No other recorded sympatries.

Habits and habitat

An inhabitant of drier Acacia savanna in regions of <800 mm rainfall per year. Most specimens have been collected in the vicinity of ephemeral pools and pans but this may be because permanent and semi-permanent waters in such regions are rare. At Mafuteni specimens were found sunbathing in a head-down position in exposed sites during the day. They have also been collected during the day in the leaf axils of grasses standing in shallow water.

Distribution

Drier savannas at low to medium elevations east of Eshowe in KwaZulu-Natal, through Swaziland, southern Mozambique and the Kruger National Park.

**Afrixalus aureus crotalus** Pickersgill, 1984

Figs. 6b, 7, 10, 17–19, 20a.


Holotype: National Museum of Zimbabwe, Bulawayo (UM 16815).

Material examined:

236 specimens (156 males) from Mozambique: Amatongas (UM 3796/9; 3801a-j); Beira (UM 3774b, f, h); Cavalo (UM 10026/7); Espungalbera (UM 27813/4); Garuzo (UM 26445/8); Guro (UM 26535/7); near Inchope (MP 3159/69; NM 3920/2; 3924/30; UM 27940a-b); Inhamitanga (UM 19426); Madassipo (MP 3001/5; 3111/2); Magasso (UM 3935a-b; 3936a-b); Revue Bridge (lower) (UM 27615/8); Tete (NM 3913); Vila Franco do Save (UM 28554a-e); Vila Gouveia (UM 26481/2); Vila de Manica (UM 3590/3; 3607); Xiluvo

![Afrixalus aureus crotalus](image-url) Fig. 17. *Afrixalus aureus crotalus* from (left) near Inchope, Mozambique (MP 3169) and (right) Chiromo, Malawi (MP 3933).
AFRICALUS STUHLMANNI COMPLEX

Fig. 18. Observed pattern variation in Afrixalus aureus crotalus.

(U) 23604(4). – Zimbabwe: Bikita (UM 30357); Chipinge (NMSR 2532; 2549; 2487); Chiredzi (UM 25662/4); Machinawa Pan (UM 19555); Machipanza (NM 3931/9; 3515); Makoni (UM 2600a-b; 3316a-b; 3317); Mapor Estates (MP 2633; 2980/2); Marhumbini (UM 17769/701); Mitoko (UM 4407); Mubungwase (UM 27399a-b); Mutare (UM 3940/1; 7421a-m; 22721; 21072; 32808; 33058; 33066/7); Ngorima Reserve (MHNG 1295.91; UM 16809/17; 16893/4; 1681/3; 17083; 17078; 17159/62; 17189/90); Odzi (UM 33701; 33706/8); Pungwe Bridge, Inyanga (UM 5307/14; 6193a-c); Pungwe Gorge (NM 5622a-d); Rhino Hotel (NM 3908/12); Sabi Drift (UM 22600a-b; 3316a-b; 3317); Sabi/Lundi confluence (UM 9636); Stapleford (UM 16512); Umgilizwe River, Chipinge (NMSR 2549). – Malawi: Chikwawa (MP 2128; 2185; 2172; 2195; 2284/5; 3512; 3519; 3942/50; 4031; MCZ 27229/34); Chiromo (MP 2197; 3930/41; 3996). – Tadpoles from Chikwawa (MP 2153; 4032); Madassipo (MP 3003; 3236). – Eggs from Madassipo (MP 3791).

Taxonomy and systematics

Treated as A. brachycnemis by Schiøtz (1974; 1975).

Definition

Males 16.6–22.3 mm (mean 19.8 mm, N = 157), females 16.2–25.5 mm (mean 21.2 mm, N = 54). Gular disc squarish to semi-triangular, without clear anterior ‘lip’. Dorsal asperities fine, confined to head in both sexes; fine scattered asperities over gular disc but otherwise no ventral asperities (but see under “Variation” below). Yellow to gold above, uniform apart from the lateral bands or with vague dark paravertebral and/or median lines, the latter often slightly thicker between the eyes and over the occiput; lateral band with a straight upper edge and usually with scattered light speckles; usually broad to narrow light streak along upper lip. Tibia with dark longitudinal edge along outer exposed surface and a dark blotch, streak or band dorsally which does not extend across the entire exposed face of the tibia.

Variation

Gular disc width 38.2–77.8% (mean 58.3%, N = 43) of tibia length, 16.4–30.1% (mean 24.6%, N = 43) of snout-urostyle length and 57.6–108.6% (mean 82.7%, N = 37) of head width; gular disc length 38.2–75.3% (mean 55.6%, N = 43) of tibia length and 16.6–29.2% (mean 23.4%, N = 43) of snout-urostyle length. Tibia length 36.7–50.5% (mean 41.0%, N = 192) of snout-urostyle length; head width 60.2–76.7% (mean 69.4%, N = 40) of tibia length, 24.2–33.0% (mean 29.2%, N = 40) of snout-urostyle length. 1–2 phalanges of toe IV free of web, and 0–1 phalanx of toe V free; finger IV with 0–0.8 of first phalanx webbed.

Specimens from the Shire lowlands in Malawi have a slightly faster voice than those from further south. In addition the dorsum is a clear yellow or gold above (Fig. 17), usually without additional markings. That this material represents the present form is confirmed by the arrangement of dorsal asperities and the presence of the characteristic incomplete tibial band (Fig. 18).
A single specimen (MP 3932) from Chiromo is unique in having a scattering of pectoral asperities – a feature otherwise only found in *A. delicatus*, although in all other respects it is a typical *crotalus*. On a visit to nearby Chikwawa two years earlier an *Afrixalus aureus crotalus* was heard to utter a prolonged, but still recognizably *crotalus*, rattle. The specimen when collected was a typical *crotalus*. There may have been introgression with *A. delicatus* in these southern lowlands in the recent past but the author found no evidence of this species during his several visits.

**Voice**

A finite rattle lasting 0.17–0.77s and with 3–13 pulses per call (mean 7.8 pulses). Pulse rate 13–24 pps (12.8–26 pps when standardized to 24°C). Pulse duration 15–30 ms. Emphasized frequency between 3.44 and 5.1 kHz (mean 3.8–4.95 kHz) (Madassipo, Inchope, Mapor Estates, Chiromo and Chikwawa).

**Breeding and development**

Gravid 29 November (Amatongas) and 6 December (Vila Franco do Save); eggs 5 February (Madassipo). Eggs are creamy white, deposited in folded leaves of grasses up to 30 cm above standing water. Development was too far advanced to accurately determine egg dimensions (Madassipo). Emergent froglets were 13 mm in length on 28 March (Chikwawa).

**Tadpoles**

Identification of tadpoles was based on the apparent absence of other sympatric species at the collection sites. They seem to be identical to other members of the complex. There are up to 23 weak marginal papillae which sometimes merge to form non-papillate ridges in a Chikwawa sample. Papillae were well developed in a single tadpole from Madassipo. A few tadpoles from Chikwawa have from one to three weak infra-marginal papillae medially close to the marginal row. No keratodonts. Postnarial papillae well separated from internal nares, quite long and filamentous and projecting medially. No lateral ridge papillae (Figs. 19, 20a).

**Sympatry**

Pickersgill (1984) reported sympathy with *A.
Fig. 20. Scanning electron micrographs of tadpole mouthparts. A. *Afrixalus aureus crotalus* from Chikwawa, Malawi. B. *A. delicatus* from Bububu, Tanzania.
Afrixalus delicatus at Beira and between Gondola and Inchope based on material in the NMZB and NM collections. Sympatric with A. fornasinii at Inchope.

Habits and habitat

In Mozambique and Zimbabwe, savanna and savanna-forest mosaic. In the Shire lowlands of southern Malawi, grassy savanna with sparse trees on alluvial sand. A number of specimens were found in exposed positions on grasses during the day at Madassipo (Fig. 21).

Distribution

Up to around 1200 m a.s.l. in central Mozambique and eastern Zimbabwe. Up to 50 m a.s.l. in southern Malawi. North of this it is replaced by A. s. brachycnemis in the Malawi uplands.

Afrixalus delicatus Pickersgill, 1984

Figs. 6c, 20b, 22–26.
Afrixalus Stuhlemanni Complex


Material examined: 567 specimens (318 males) from Somalia: Giuba River, Mareri (CAS 148387/91; 148393/401; 148404/5; 148407/28; 148631/3; 152832/3). – Kenya: Changamwe, Mombasa (MCZ 20595); Diani (AMNH 68522/3); Galole (MHNG 1575.80/4); Garsen (MP 2468/9; 2471/4; LIVM 1998.46.42); Golbanti (MCZ 20590/4); Kakoneni (ZMUC R 079754/81); Malindi (AMNH 68521); Mombasa (SMF – formerly MP 668/75; 677/88; LR 1639/41; CAS 154395/406; 154751/5; 154779); Mpekatoni (MCZ 20581/4); Mtwapa (MP 2525/8; 2530/53; LIVM 1998.46.40/1); Ngomeni (ZMUC R 077610; AMNH 73064; 90260/1); Shimba Hills (ZMUC R 073855; 73948/9; 077457/8); Tiwi (MP 2398/410; 2412/31; 2433/4; 2450; 2452; 2454/5; LIVM 1998.46.38/9; ZMUC R 073949; 077162/76; 077178/82; CAS 147892); Witu (MCZ 20585/9). – Tanzania: Amboni Estate (MCZ 25167); Bububu (MP 3336/68; 3374); Dar es Salaam (MP 3297; 3645/9; MCZ 13347/56; NMZB 6693/6; 6559; USNM 204901/6; 209755/6; 226763/4; KMH 2448; 2427; 2451); Jozani, near Pete (BM 1978.2384; 1983.42); Kingupira (ZMUC R 078749); Kitaya (MP 3467; 3615; MCZ 25161/2); Mahenge (BM 1969.1279/80); Mazizini (BM 1978.2374/83); Mikindani (MCZ 25163/4); Mwaya River, near Morogoro (AMNH 153275); Ngomeni (ZMUC R 077610); Ruaha River (BM 1969.1281); Siga Caves (MCZ 25165/6); Tanga (MP 2506/8; 2565; 3537). – Malawi: Cape MacClear (BM 77.7.2.16); Chinteche (MP 3913/23; 3925/6; 3997/9; 4028); Chiradzulu (MP 3997/9; 4028); Chitala River, Salima (MCZ 27226); Limphasa Dam (UM 2470; 2479; 24680; 24779/80; 24800); Liwonde (MP 2170; 2189/80; 2255/6; 3224/5); Mt Mulanje (ZMUC R 079879/8); Nkazi River (MCZ 27863/4; 56047; 90255/8); Nkhati Bay (UM 24732); Palm Beach (MP 4044; 4060); Thyolo (UM 4348; 4349a-c); Zomba (MP 3220/1; 3887/90). – Mozambique: Beira (UM 3774a, c-e, g, i-s; NM 3917/9); Chinzuia (UM 21837); Dondo (MP 3148/9; 31567; UM 21974a-f; 26181/5); Fambani River (BM 1929.12.20.424/34); Inhaca I. (UM 2338); Maputo (MP 3246); Macuti, Beira (UM 3773); Mousuril (UM 19367a-d); Praia de Tofo (MP 30127/1216/6); Pungwe River x Beira Road (NM 3914/6); Quelimane (ZMB 11015); Zavora (MP 3158; UM 28482). – South Africa: Compensation (LR 1131); Jozini (LR 1543); Kosi Bay (MP 4124/7); Kwa-Mbonamibi (NM 3888/90); Monzi (AMNH 97928/31; 308720/3); Mosquito Hill (NM 3891/4); Mount Edgecombe (NM 4663); Mputubu (DM 889; MCZ 106586;10602); Mtunzini (NM 3897/902; 3904/6); Ndumu (NM 3895; 5624; 6686); Richards Bay (SMF – formerly MP 318; 273; 639; 1392/6; 27245/5; 2829/4; 2957/8); St. Lucia (BM 1983.1150; CAS; SMF – formerly MP 716/7; 1110/2; 1409/10; 1413; ZMUC R 077768; MCZ 106587; LR 2130; NM 5626a-n); Tugela Mouth (LR 1850); Zinkwazi Beach (LR 1850). – Tadpoles from Bububu (MP 3395); Charters Creek (NM 5625); Chinteche (MP 4034); Chiradzulu (MP 3408); Dar es Salaam (MP 3636; 3781; 3784). – Eggs from Chinteche (MP 4013); Garsen (MP 2397); Zomba (MP 4027).

Taxonomy and systematics

Following Poynton (1964) this species was long treated as *A. brachycnemis* in South Africa. After preliminary work on the eastern African dwarf *Afrixalus*, Pickersgill (1984) described it as a distinct species, stating that *A. brachycnemis* did not occur south of the Zambezi River. Like Poynton & Broadley (1987) at that time the author regarded *A. brachycnemis* as the Malawian form of what is here included in *A. delicatus*. Although morphologically Malawi material resembled the southern African *delicatus* there were slight pattern differences which at that time suggested synonymy was inadvisable, and the voice had not been recorded. Field trips to the type locality of *M. brachycnemis* in 1997 and 1999 offered convincing proof that three species of dwarf *Afrixalus* are present in Malawi and that one has a voice indistinguishable from that of *delicatus*. Although one could probably justify...
treat both the Malawian and the Kenyan/Tanzanian forms as subspecifically distinct from typical *delicatus* on the basis of consistent pattern differences this would not serve the interests of taxonomists who for the most part have to work with faded or poorly marked specimens. Accordingly, the author does not recognize subspecies of *A. delicatus*.

**Definition**

Length of males 14.6–22.2 mm (mean 18.9 mm, N = 299), length of females 16.2–23.9 mm (mean 20.7 mm, N = 88). Gular disc squarish to triangular. Fine asperities confined to head (females) or uniformly over all upper surfaces, and may also be weakly present over outer edges of feet; asperities scattered over gular disc, jaws and ventrally, where they are confined to - or at least most prominent on - the chest. Pattern never forming straight, parallel lines or stripes. Straight, clear silverish lower margin to lateral band along upper lip. Upper edge of lateral band straight. Tibia with narrow to broad, unbroken oblique transverse stripe or band (Figs. 23, 24).

**Variation**

Gular disc width in males 43.7–75.7% (mean 56.5%, N = 162) of tibia length, 16.0–30.8% (mean 24.7%, N = 162) of snout-urostyle length and 59.7–110.4% (mean 82.8%, N = 151) of head width; gular disc length 39.2–74.7% (mean 53.7%, N = 161) of tibia length and 16.6–30.2% (mean 23.5%, N = 161) of snout-urostyle length. Tibia 36.9–55.5% of snout-urostyle length (mean 43.5%, N = 344); head width 57.1–82.9% (mean 68.6%, N = 186) of tibia length, 25.9–35.3% (mean 29.9%, N = 186) of snout-urostyle length. From 1 to 2.25 phalanges of toe IV free of web, and 0–1 phalanx of toe V; outermost finger with 0–1 phalanx webbed.

Eastern African material generally shows a broadening of the dorsal pattern in the lumbar region continuous with the tibial stripe when the limb is folded; when an occipital blotch (headspot) is present, this often extends onto the upper eyelids; dorsal pattern is generally bold, with markings better developed anteriorly rather than posteriorly as in Malawian material; tibial band usually broad; light speckles in lateral band usually concentrated medially. Basic colour silvery (Fig. 22).

Malawian specimens have well-developed lumbar patches which frequently project forward, converging towards the occiput, giving the dorsal pattern a posterior bias; headspot when present often extending onto upper eyelids; dorsal pattern generally bold, the basic colour usually yellow; tibial band usually broad.

Southern African specimens lack the lumbar patches, and dorsal markings are generally weakly defined or are broken up into small spots or speckles over the median portion of the dorsum. A broken mid-dorsal line is common; headspot rarely if ever extends onto orbit; light speckles in lateral band seldom have a median bias; narrow oblique transverse tibial marking. Basic colour brassy.

**Voice**

A prolonged metallic buzz, “trill” (Schiøtz 1999) or rattle of very variable duration (0.6–21.7 s in analyzed calls) with 10 to 684 pulses per call. Pulse rate 14–35/s (mean 27 pps) is still widely variable (15.3–37 pps) when standardized to 24°C. Pulse duration 12–23 ms. Emphasized frequency between 3.35 and 5.35 kHz (mean 3.95 kHz).
Fig. 24. Some of the observed pattern variation in *Afrixalus delicatus*. The markings of the two bottom right specimens are typical of southern African material.
Breeding and development

Eggs are 1.35 mm in diameter (Zomba) and creamy white, enveloped in vertically folded leaves and grass blades just under, to up to 15 cm above, the water. Gravid 14 April (near Kakonen), 12 May (Mtwapa), 19 May (Tiwi) and 30 May (near Witu); in amplexus 7 June (Kitaya); eggs laid November (St. Lucia), 12 May (near Witu); in amplexus 7 June (Kitaya); eggs laid November (St. Lucia), 12 May (near Witu); in amplexus 7 June (Kitaya); eggs laid November (St. Lucia), 12 May (near Witu); in amplexus 7 June (Kitaya); eggs laid November (St. Lucia), 12 May (near Witu); in amplexus 7 June (Kitaya); eggs laid November (St. Lucia), 12 May (near Witu); in amplexus 7 June (Kitaya); eggs laid November (St. Lucia), 12 May (near Witu); in amplexus 7 June (Kitaya); eggs laid November (St. Lucia), 12 May (near Witu); in amplexus 7 June (Kitaya); eggs laid November (St. Lucia), 12 May (near Witu); in amplexus 7 June (Kitaya); eggs laid November (St. Lucia), 12 May (near Witu); in amplexus 7 June (Kitaya); eggs laid November (St. Lucia), 12 May (near Witu); in amplexus 7 June (Kitaya); eggs laid November (St. Lucia), 12 May (near Witu); in amplexus 7 June (Kitaya); 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Fig. 26. Distribution of examined specimens of Afrixalus delicatus.
Mount Edgecombe northwards to southern Somalia (Giuba River); up to 900 m in Malawi and eastern Tanzania (Fig. 26).

Schiøtz (1975) has recorded this form from Singida, Tanzania, which is well outside its known distribution. No specimens are available and his sonagram (unpublished) shows a very high-pitched voice. The identity of this population requires verification, but it is far more likely this material represents a member of the A. septentrionalis complex.

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REFERENCES


Parker, H. W. 1930. A collection of frogs from Portuguese
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Appendix 1. Gazetteer

Amani, Tanga Region, Tanzania (05°06'S, 38°38'E)
Amatongas, Manica Province, Mozambique (19°10'S, 33°46'E)
Amboni Estates, Tanga Region, Tanzania (05°03'S, 39°03'E)
Beira, Sofala Province, Mozambique (19°50'S, 34°50'E)
Bikita, Mashonaland, Zimbabwe (20°05'S, 31°37'E)
Bububu, Uguja Island, Zanzibar, Tanzania (06°06'S, 39°13'E)

Cape Maclear, Southern Province, Malawi (14°01'S, 34°51'E)
Cavalo, Sofala Province, Mozambique (18°28'S, 34°12'E)
Changamwe, Coast Region, Kenya (04°01'S, 39°38'E)
Charter's Creek, KwaZulu-Natal, South Africa (28°15'S, 32°13'E)
Chikwawa, Southern Province, Malawi (16°03'S, 34°48'E)
Chinziuwa, Sofala Province, Mozambique (18°58'S, 35°08'E)
Chinteche, Northern Province, Malawi (11°50'S, 34°10'E)
Chipinge, Mashonaland, Zimbabwe (20°12'S, 32°37'E)
Ngorima Reserve, Mashonaland, Zimbabwe (ca. 20° 05’S, 32° 53’E)
Nkazi River, Southern Province, Malawi (ca. 14° 52’S, 35° 16’E)
Nkhata Bay, Northern Province, Malawi (11° 36’S, 34° 18’E)
Nsemene Windmill, Mpumalanga, South Africa (ca. 24° 25’S, 31° 38’E)
Nyalazi, KwaZulu-Natal, South Africa (28° 20’S, 32° 27’E)
Nyika Plateau, Northern Province, Malawi (ca. 10° 40’S, 33° 50’E)
Odzi, Mashonaland, Zimbabwe (18° 58’S, 32° 23’E)
Palm Beach, Southern Province, Malawi (14° 23’S, 35° 12’E)
Ponta do Calichane, Maputo Province, Mozambique (ca. 26° 00’S, 32° 50’E)
Praia do Tofo, Inhambane Province, Mozambique (23° 51’S, 35° 32’E)
Pungwe Bridge, Mashonaland, Zimbabwe (18° 13’S, 32° 55’E)
Pungwe Gorge, Mashonaland, Zimbabwe (18° 15’S, 32° 58’E)
Pungwe River X Beira Road, Sofala Province, Mozambique (19° 17’S, 34° 31’E)
Quelimane, Zambezia Province, Mozambique (17° 53’S, 36° 53’E)
Revue Bridge, Mashonaland, Zimbabwe - not located
Rhino Hotel, Mashonaland, Zimbabwe (20° 54’S, 30° 47’E)
Richards Bay, KwaZulu-Natal, South Africa (28° 47’S, 32° 06’E)
Ruaha River, Morogoro Region, Tanzania (ca. 07° 57’S, 37° 48’E)
Rufiji Delta, Coast Region, Tanzania (ca. 08° 02’S, 39° 15’E)
Ruo River, Mulanje Mt., Southern Province, Malawi (ca. 16° 01’S, 35° 35’E)
Sabi Drift, Mashonaland, Zimbabwe - not located
Sabi/Lundi confluence, Mashonaland, Zimbabwe (21° 15’S, 32° 15’E)
Shimba Hills, Coast Region, Kenya (ca. 04° 13’S, 39° 25’E)
Siga Caves, Tanga Region, Tanzania (ca. 05° 02’S, 38° 58’E)
Skukuza, Mpumalanga, South Africa (24° 57’S, 31° 44’E and 25° 11’S, 31° 37’E)
St. Lucia, KwaZulu-Natal, South Africa (28° 23’S, 32° 02’E)
Stapleford, Mashonaland, Zimbabwe (18° 44’S, 32° 48’E)
Tanga, Tanga Region, Tanzania (05° 04’S, 39° 06’E)
Tete, Tete Province, Mozambique (16° 09’S, 33° 35’E)
Tiwi, Coast Region, Kenya (04° 15’S, 39° 32’E)
Tshokwane, Mpumalanga, South Africa (24° 45’S, 31° 53’E)
Tugela Mouth, KwaZulu-Natal, South Africa (29° 13’S, 31° 30’E)
Thyolo (Cholo), Southern Province, Malawi (16° 04’S, 35° 08’E)
 Ugano, Ruvuma Region, Tanzania - not located
Ukami, Morogoro Region, Tanzania – not located
Umzilizwe River, Mashonaland, Zimbabwe (ca. 20° 35’S, 32° 30’E)
 Vila Franco de Save, Sofala Province, Mozambique (21° 08’S, 34° 34’E)
 Vila de Manica, Manica Province, Mozambique (18° 56’S, 32° 53’E)
 Vila Gouveia, Manica Province, Mozambique (18° 03’S, 33° 10’E)
 Witu, Coast Region, Kenya (02° 23’S, 40° 27’E)
 Xiluvo, Sofala Province, Mozambique (19° 14’S, 34° 04’E)
Zavora, Inhambane Province, Mozambique (24° 31’S, 35° 12’E)
Zinkwazi Beach, KwaZulu-Natal, South Africa (29° 10’S, 31° 30’E)
Zomba, Southern Province, Malawi (15° 23’S, 35° 20’E)