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Revalidation of *Pyxicephalus angusticeps* Parry, 1982 (Anura: Natatanura: Pyxicephalidae), a bullfrog endemic to the lowlands of eastern Africa

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Abstract

Pyxicephalus currently contains three recognized species, viz. *P. adspersus*, *P. edulis* and *P. obbianus*, the former two of which have a long history of confusion. Parry (1982) described *P. adspersus angusticeps* from Beira, Mozambique, which was synonymized with *P. edulis*. We re-examine the taxonomic status of *Pyxicephalus* taxa from Mozambique, examining the types and contrasting them to congeners throughout Africa. Morphological characters previously used to delimit species in *Pyxicephalus* are examined, and problems with some identified. Additional diagnostic characters and their variation in *Pyxicephalus* are discussed, and a revised key is provided. Confusion among species in the genus, type localities, literature and folklore led to *P. adspersus angusticeps* being incorrectly synonymized with *P. edulis*. We formally revalidate *P. angusticeps*, and designate a lectotype for *P. edulis*. The identity of voucher specimens from previous work suggests that the breeding ecology of *P. angusticeps* is distinct from that of *P. adspersus* and *P. edulis*, and that the advertisement call of *P. angusticeps* was used as part of the evidence for elevating *P. edulis* out of synonymy with *P. adspersus*. The previous confusion of *P. adspersus* and *P. edulis* does not affect the recognition of *P. angusticeps*. The wider implication of the previous misidentification of *P. angusticeps* as *P. edulis* is that most of the museum material labeled as *P. adspersus* from East Africa is *P. edulis*, and most of the museum material labeled as *P. edulis* from East Africa is *P. angusticeps*. This conclusion has been confirmed from East African museum material thus far examined.

Key words: *Pyxicephalus obbianus*, *Pyxicephalus edulis*, *Pyxicephalus adspersus*, *Pyxicephalus angusticeps*, allopatry, vocalizations, Mozambique, Kenya, Tanzania, niche separation

Introduction

The African bullfrog genus *Pyxicephalus* is among the most charismatic of African Anura. In southern Africa, two species are currently recognized, viz. the giant African bullfrog, *P. adspersus* Tschudi, 1838 and the edible African bullfrog, *P. edulis* Peters, 1854. A third poorly known species, *P. obbianus* Calabrezi, 1927 occurs in Somalia. Species boundaries in *Pyxicephalus* are poorly understood, particularly those between *P. adspersus* and *P. edulis*. Despite their obvious morphological differences, *P. edulis* was twice synonymized with *P. adspersus* and twice removed from synonymy with *P. adspersus* (Boulenger 1882; Loveridge 1936, 1950; Poynton 1964; Channing *et al.* 1994). Parry (1982) revised the genus in southern Africa, examining most of the holdings of southern African museums, and described the subspecies *Pyxicephalus adspersus angusticeps* Parry, 1982 from Mozambique. In a review of the status of *Pyxicephalus* in southern Africa, Channing *et al.* (1994) provided detailed accounts of the breeding biology and vocalizations of *P. adspersus* from Bloemfontein, and a species of *Pyxicephalus* from Beira, Mozambique, concluding that they were not conspecific and that two species of bullfrogs occurred in southern Africa. Channing *et al.* (1994) elevated *P. adspersus edulis* to species rank, at the same time synonymizing the

described taxon from Beira (*P. a. angusticeps*) with *P. edulis*. Channing *et al.* (1994) did not present data for the voucher specimens examined other than the snout-vent length, head width and museum accession numbers of the types of *P. edulis*. There is no mention of the types of *P. a. angusticeps* being examined, although material from Beira, the type locality of *P. a. angusticeps*, was examined.

We re-assessed the taxonomic status of *Pyxicephalus edulis* and *P. a. angusticeps*, both of whose type localities are in Mozambique, based on the examination of museum material. We compared the types of both taxa with congeners from throughout Africa, discussing the characters reported as diagnostic to species in previous literature, and proposing others. The breeding biology from literature reports and the distribution of *Pyxicephalus* on the Mozambique plain are also discussed.

Material and methods

Museum acronyms follow Frost (2011). All type and non-type material of *P. a. angusticeps* in NMP and NMZB were examined. Six existing adult specimens presumed to be the type series of *P. edulis*, housed at the ZMB, were examined from high resolution photographs; two were loaned. Additional non-type material of *Pyxicephalus* was examined from the collections of the above-mentioned institutions, as well as AMNH, BMNH, CAS, NMK, MNHNP, MVZ, MZUF, TMP and the amphibian collections of Alan Channing (AC), Martin Pickersgill (MP) and Elizabeth Scott-Prendini (ESP). Comparative material of *Pyxicephalus* from throughout Africa examined during the study is listed in Appendix 1. A dissecting microscope was used to compare colouration patterns, secondary sexual features, skin glands, dorsal ridge patterns and other features, as listed in Table 1. Head width to SVL ratios and tympanum distance from the eye were not used as characters to determine sex or species. Sex of the specimens was determined from examination of the gonads of dissected material (where possible, dissection was performed). Presence of nuptial pads was used together with the presence of sex-specific coloration patterns, notably of the gular and chest regions, to sex non-dissected material.

In general, the pattern of dorsal ridges is extremely complex in *Pyxicephalus*. Field studies (C.A. Yetman, pers. obs.) and museum studies of large series collected from single localities during single collection events (E. Scott, pers. obs.) indicate that there is some individual variation in the degree of dorsal ridge development within populations, similar to the unique stripe pattern observed on individual zebras (e.g. Petersen 1972). However, the absolute presence or absence of particular series of the dorsal ridges is species-specific, and we use these in the descriptions. Three pairs of strongly developed and continuous (or nearly so) primary dorsal ridges is the general (basic) condition in *Pyxicephalus* (see character 173 of Scott 2005). Variation in presence or absence of this general number of ridges (excluding their completeness and nature) was observed between species. There is usually a shorter additional set of lateral ridges on the flanks of *Pyxicephalus*, which we term 'lateral ridges'. Sometimes an additional clear series of continuous (or near-continuous) 'secondary dorsal ridges' are present, which are then positioned between Primary Dorsal Ridge Series 1 and 2 (i.e. the two dorsal-most sets of primary dorsal ridges), and occasionally also between Primary Dorsal Ridge Series 2 and 3 (i.e. the median and outer sets of primary dorsal ridges). Primary Dorsal Ridge Series 2 usually runs from directly behind the eyes, serving as a reference point to identify the other ridges. All these ridges may be continuous or nearly so, or be long aligned series of ridge-like elongated warts. These also vary in thickness, waviness and may have small broken patches of white colouration crossing or upon them (see Table 1).

Digits of the hand are numbered in accordance with the interpretation of digit ontogeny outlined by Fabrezi & Alberch (1996), *viz.* the innermost finger is termed Digit II, considering the first digit to have been lost and not homologous with the prepollex. Calls used by Channing *et al.* (2004) were obtained from A. Channing, and re-analysed to produce audio spectrograms in Raven Pro 1.4. (Cornell Bioacoustic Research Group, Ithaca, NY), using a Discrete Fourier Transform (DFT) filter of 256 points. Distribution data for *Pyxicephalus* were collated from specimen labels or museum catalogue data. Point locality co-ordinates (in decimal degrees) were calculated from the collector's notes where possible, gazetteers and the official 1:250 000 and 1:500 000 topocadastral maps of South Africa and neighbouring countries published by the Government Printer (mostly collated in the Reader's Digest Illustrated Atlas of Southern Africa 1984, 1994). Many locality records were traced using the Fuzzy Gazetteer (<http://www.isodp.hof-university.de/fuzzyg/query/>) or the GEONet Names Server (GNS) (http://164.214.2.59/gns/html/cntry_files.html). These were mapped in ArcView 3.2 (ESRI, Redlands, CA).

TABLE 1. Definitions of morphological characters used to evaluate variation in *Pyxicephalus*.

1. Tibia tubercles and asperites: (0) irregularly dispersed; (1) some arranged into lines.
2. Dorsal Ridges, degree of development: (0) smooth or light ridges; (1) medium ridges; (2) heavy ridges and warts; (3) oval warts only.
3. Dorsal Ridges, width: (0) thick; (1) medium; (2) thin; (3) absent.
4. Dorsal Ridges, primary series: (0) absent; (1) only second present, running from behind eyes, weakly developed and incomplete; (2) first and second present, basically complete.
5. Dorsal Ridges, secondary series: (0) absent; (1) single ridge present between two dorsal primary ridges.
6. Darker speckles or stippling between larger mottled patches: (0) present; (1) absent.
7. Pale cross-bar dorsally above eyes in adults: (0) present, complete; (1) absent; (2) some spots but incomplete (**state 0 additionally diagnostic for *P. edulis***).
8. Barring on upper jaw, between eye and upper lip, adult male: (0) present; (1) absent; (2) white blotches, not complete bars; (3) faint but complete bars in washed out upper lip region (**state 1 characteristic of *P. adspersus*, used in key**).
9. Upper lip colour: (0) as between eye and upper lip; (1) light or unpigmented.
10. Odontoids (adults): (0) small, under-developed, usually wider than long; (1) as wide as long, triangular; (2) longer than wide (**state 0 diagnostic for *P. angusticeps*, used in key**).
11. Light spot on tympanum in adults: (0) absent; (1) present, thick blob or crescent; (2) present, thin line or crescent.
12. Tympanum width compared to eye width (adult males): (0) tympanum width less than or equal to eye width; (1) tympanum width greater than eye width (**state 1 diagnostic for *P. obbianus*, used in key**).
13. Tympanum, distance from eye: (0) greater than or equal to one eye width in distance from eye; (1) less than one eye width in distance from eye (**Traditional form of this character**).
14. Tympanum distance from eyes: (0) more than one tympanum width in distance from eye; (1) less than or equal to one tympanum width in distance from eye (**Advocated form of this character**).
15. Nuptial pads, breeding adult males: (0) absent; (1) present on Digit II only; (2) present on Digits II and III only; (3) present on Digits II, III and IV, sometimes wrist also (**state 1 distinguishes *P. angusticeps* and *P. obbianus* from *P. adspersus* and *P. edulis***).
16. Mid dorsal (vertebral) stripe in adults: (0) present, thick, margins diffuse; (1) present, thin, well-defined; (2) absent; (3) on snout only (**state 3 additionally diagnostic for *P. obbianus***).
17. Mid dorsal (vertebral) stripe, if present (even in subadults): (0) coppery-orange or reddish; (1) yellow, white or light green (**state 0 characteristic of *P. angusticeps***).
18. Creamy light-coloured mottling on flanks (laterally): (0) present; (1) absent.
19. White coloration on ridges (adults): (0) absent; (1) present.
20. Toe webbing: (0) moderate; (1) rudimentary, maximum up to first tubercle only (**state 0 diagnostic in *Pyxicephalus* for *P. obbianus*, used in key**).
21. Enlargement of head in breeding males: (0) not observed; (1) present (**state 0 characteristic of *P. angusticeps***).
22. Lekking behaviour during spawning: (0) not observed; (1) observed (**state 0 probably only in *P. angusticeps***).
23. Breeding activity time: (0) nocturnal; (1) diurnal.

Results

Characteristics examined and their coding within populations from broad geographical regions are given in Tables 1 and 2. Based on our re-evaluation of taxonomic characters, we present a revised key to the species of *Pyxicephalus*. We argue that *P. a. angusticeps* has been confused with *P. edulis*, and elevate *P. angusticeps* New Status to species level. A distribution map of *P. angusticeps* New Status is presented in Fig. 1, showing that this species extends northwards as far as Kenya. The holotype male of *P. angusticeps* New Status is shown in Fig. 2, while two adult males and an adult female collected at or near the type locality (Mozambique) are shown in Fig. 3. Two adult males and an adult female from near the northern extent of the known range of *P. angusticeps* (viz. coastal regions of Tanzania and Kenya) are shown in Fig. 4. We designate a lectotype for *P. edulis* (Fig. 5), but one paralectotype of *P. edulis* (Fig. 6) is determined by us to be *P. angusticeps* New Status. Comparative figures are presented of well-preserved *P. edulis* (Fig. 7), *P. obbianus* (Fig. 8) and *P. adspersus* (Fig. 9), a comparative dorsal and ventral overview of adult males (Fig. 10), metamorphs (Fig. 11) and mandibular odontoids (Fig. 12) of recognized *Pyxicephalus* species. We found no evidence from museum specimens (Appendix 1) or advertisement calls (Fig. 13) that *P. edulis* and *P. adspersus* are sympatric, or that *P. adspersus* occurs on the Mozambique plain.

TABLE 2. Matrix of characters observed in *Pyxicephalus* across its range, indicating levels of variation. Terminals represent species or populations from broad geographic regions, as indicated. Character states are scored 0–3, ? (unknown), - (inapplicable), A (polymorphic 0/1), B (polymorphic 1/2). Refer to Table 1 for character descriptions. ZA = South Africa; Zim = Zimbabwe. See Appendix 1 for material examined.

| | 1 | 6 | 11 | 16 | 21 |
|--|-------|-------|-------|-------|-----|
| <i>P. angusticeps</i> (Mozambique; <i>n</i> = 18) | 13300 | 01010 | 00111 | 00101 | 000 |
| <i>P. angusticeps</i> (Tanzania + Kenya; <i>n</i> = 44) | 00110 | 01A00 | A0111 | 10101 | 0?? |
| <i>P. adspersus</i> (Namibia; <i>n</i> = 13) | 02021 | 021A2 | 00003 | B1101 | 111 |
| <i>P. adspersus</i> (ZA + Zim; <i>n</i> = 37) | 02021 | 11102 | 0000? | B1111 | 111 |
| <i>P. “adspersus”</i> (Tanzania + Kenya, adults; <i>n</i> = 9) | 02021 | 10302 | 10003 | B1001 | 1?? |
| <i>P. edulis</i> (Tanzania + Kenya, subadults; <i>n</i> = 21) | 01121 | 00002 | 1011? | 11001 | 1?? |
| <i>P. edulis</i> (ZA + Zim + Mozambique; <i>n</i> = 162) | 01120 | 00002 | 10003 | 11011 | 111 |
| <i>P. edulis</i> (West Africa; <i>n</i> = 24) | 12221 | 100A1 | 20113 | 11101 | 1?? |
| <i>P. obbianus</i> (Somalia; <i>n</i> = 35) | 03100 | 12001 | 01111 | 3-000 | 1?? |

Key to the species of *Pyxicephalus*

- 1.a. Odontoids wider than long *P. angusticeps* New Status
- 1b. Odontoids longer than wide 2
- 2.a. Upper jaw free of barring in adults *P. adspersus*
- 2b. Upper jaw barred in adults 3
- 3.a. Tympanum hypertrophied (width greater than eye diameter), and positioned less than one half eye diameter in distance from eye; toes with moderate webbing *P. obbianus*
- 3b. Tympanum not hypertrophied (width less than or equal to eye diameter), and positioned more than one half eye diameter in distance from eye; toes with rudimentary webbing *P. edulis*

Systematic account

Pyxicephalus angusticeps Parry, 1982 New Status

Figs 1–4, 6, 10G–H, 11A–C, 12B, 13E.

Pyxicephalus adspersus angusticeps Parry 1982: 281–292, figs 1, 4, 5, 7, table 1. Poynton & Broadley 1985: 123–124.

Pyxicephalus edulis: Channing, Du Preez & Passmore 1994: 141–148, fig. 1b, plate 1b, synonymized *P. adspersus angusticeps*.

Channing 2001: 349–351, figs 22.5, 281. Channing & Howell 2006: 322–323, fig. 22.6.

Pyxicephalus edulis: Pickersgill 2007: 105–108 (part), figs 45, 46.

Type material. Holotype: Adult ♂, NMSA 1992 (UNP 3099, NMSA Type number 2581), from Beira, Mozambique (Fig. 2). Paratypes: One adult ♂, NMSA 1991 (UNP 3098), and two subadults, NMSA 1990 (UNP 3063), NMSA 1993 (UNP 3100) with same data as the holotype; twelve subadult paratypes NMZB-UM 6451 (two specimens), NMZB-UM 7516 (five specimens), NMZB-UM 19774 (four specimens; no. A shown in Figs 11A–C) and NMZB-UM 23374, from Beira, Mozambique.

Diagnosis. This species is assigned to the genus *Pyxicephalus* by the combination of presence of mandibular odontoids (outgrowths of the dentary), femoral glands, cranial exostosis on the frontoparietals and nasals, hypertrophied inner metatarsal tubercle, and supraorbital flanges on the frontoparietals (see Scott 2005 for comparisons of these characters in other genera of ranoid frogs). *Pyxicephalus angusticeps* can be distinguished from *P. obbianus* (Figs 8, 10C–D, 11D–F) by the: (1) rudimentary webbing between the toes (more extensive in *P. obbianus*; Fig. 8F); (2) tympanum width less than eye diameter (more than one and one half times eye diameter in adult male *P. obbianus*; Figs 8A, 8C), positioned approximately one tympanum width or slightly less from eye (less than half the tympanum width in *P. obbianus*; Fig. 8C); and (3) vertebral stripe running most of the length of body (restricted to the snout in adult *P. obbianus*; Figs 8A, 8D).

Pyxicephalus angusticeps can be distinguished from *P. edulis* (Figs 5, 7, 10 E–F, 12C–D) and *P. adspersus* (Figs 9, 10A–B, 12A) by: (1) nuptial pads present only on innermost finger (Digit II) of breeding males (as in *P. obbianus*, but present on Digits II–IV in *P. adspersus* and *P. edulis*); (2) head of breeding males less proportionately

enlarged (see Fig. 10), particularly in width, than in *P. adspersus* and *P. edulis*; (3) distinct subadult gular colouration (Fig. 11C), which is darkly marbled and more persistent in the adult female (Fig. 3F) than in *P. adspersus* and *P. edulis*; (4) small, triangular, pointed odontoids, not longer than wide (Fig. 12B in *P. angusticeps* vs. Figs 12C–D in *P. edulis*; Fig. 8D in *P. obbianus*), whereas odontoids are large and well-developed in all other species of *Pyxicephalus*; (5) presence of at most poorly-developed dorsal ridges, usually the most distinct running from behind eyes (dorsum of type material covered only by weakly or strongly developed oval or round warts), whereas these are thick and highly developed in *P. adspersus* (Fig. 10A); and narrower, finer and often continuous in *P. edulis* (Figs 5A, 10E); (6) vertebral stripe wide, pale (coppery-orange in preservation) and diffuse, formed by pale background colour visible between densely-packed, dark dorsal blotches, which are absent medially, with fine, dark stippling present elsewhere between dark dorsal blotches (Figs 3, 4), whereas the vertebral stripe is absent in adults of *P. adspersus*, and variably (but usually) present, thin and pale green-yellow in *P. edulis* (Figs 7A, 10); (7) femoral glands well-developed and relatively larger and more conspicuous than in all other species of *Pyxicephalus*.

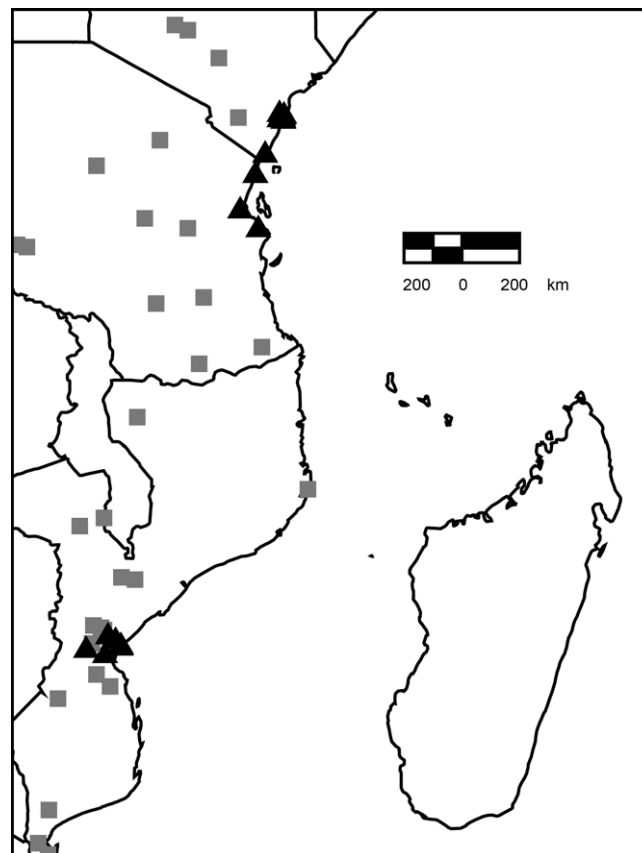


FIGURE 1. Distribution of *P. angusticeps* Parry, 1982 New Status (black triangles) and *P. edulis* Peters, 1854 (grey squares) in east Africa. Localities of juvenile specimens are not included.

Redescription of the holotype. Adult male, NMSA 1992 (field number UNP 3099, NMSA Type Number 2581, Fig. 2), collected at Beira, the swamp beyond Estoril [$19^{\circ}50'37''S$, $34^{\circ}50'20''E$]: Jan. 26, 1959, Nyasaland-Mozambique Expedition [of the University of Natal, Pietermaritzburg].

Head. Tympanum visible, subcircular (oval) in shape, slanted slightly anteriorly. Tympanum width smaller than that of eye. Tympanum positioned approximately its own width in distance from eye (i.e. less than one times width of eye away from eye). White spot or marking absent from right tympanum, but minute white spot present on left tympanum (Fig. 2C). Upper lip with thin rim of light colouration. Upper jaw with four pale coppery-orange brown bars on each side; posterior two broader than anterior two. Two anterior-most bars on upper jaw on each side of face meet anterior to eyes. Gular region pale with diffuse brown colouration laterally. Light irregular spots (not a complete crossbar) across head above eyes. Head narrow, not as wide as body at level of sacrum, not disproportionately wide. Odontoids in lower jaw weakly-developed, triangular. Tongue notched, typically ranid, no mid-lingual papilla. Nostrils large, situated slightly closer to eyes than tip of snout.



FIGURE 2. Holotype of *Pyxicephalus angusticeps* Parry, 1982 New Status: NMSA 1992, adult ♂ from Beira, Mozambique. **2A.** Dorsal view. **2B.** Ventral view. **2C.** Lateral view, left. **2D.** Frontal view. **2E.** Hand. **2F.** Foot. Scale bar = 1 cm.

Secondary sexual characteristics. Nuptial pads visible only on Digit II (inner finger) of hand, covering most of dorsal and lateral surfaces of these digits, including side of thenar tubercle. Forearms only slightly thickened, indicating youth. Testes large, elongated, dark yellow in preservation with blackened mesenteric tissue above.

Limbs. A gracile, slender-bodied animal. Toes slightly webbed, web extending to half length of longest toe (approximately to level of proximal subarticular tubercle), such that three phalanges of longest toe free of webbing; remaining length of toes with slight paler lateral flanges. Inner metatarsal tubercle hypertrophied, spade-like; outer metatarsal tubercle absent. Digits of hand elongated, tapering, with slight paler lateral flanges. Ventral surface of hands lighter, dorsal side brown. Digit II (inner finger) longer than Digit III (second finger) and Digit V (fourth finger), Digit IV (third finger) longest. Subdigital tubercles present, large and rounded. Subarticular tubercles present on Digit IV, inconspicuous on other fingers. Thenar tubercle large and bilobed (not divided completely), palmar tubercle present. Palms of hands otherwise smooth. Digit tips unexpanded, rather narrowing distally, with a paler hardened tip.

Dorsal and dorso-lateral surfaces of thighs, calves and along margin of tarsus with small white asperites, arranged loosely into lines on weak skin ridges on dorsal surfaces of calves. White asperites present on posterior third of dorsum, set on small raised tubercles, most densely arranged around cloaca. White asperites absent from ventral surfaces of limbs. Femoral granules present around cloaca, and on posterior-dorsal surface to half length of thighs.

Ventral colouration. Colouration of dorsal surface of calves extending onto ventral surface of calves. Flanks and underside of limbs lightly stippled with diffuse brown pigment. Abdomen off-white, granular. Pectoral region with two medially directed triangular ‘waistcoat’ scars¹ on each side, interior of which is coloured with diffuse light brown stippling.

Glands. Pectoral glands present, small, elongate, triangular and inconspicuous. Femoral glands large, elongate, oval, brown, inconspicuous, set within pigment horizon of ventral thighs, which is indistinct, grading into ventral colouration. Femoral glands positioned closer to knee than cloaca, confined to distal two-fifths of length of thighs.

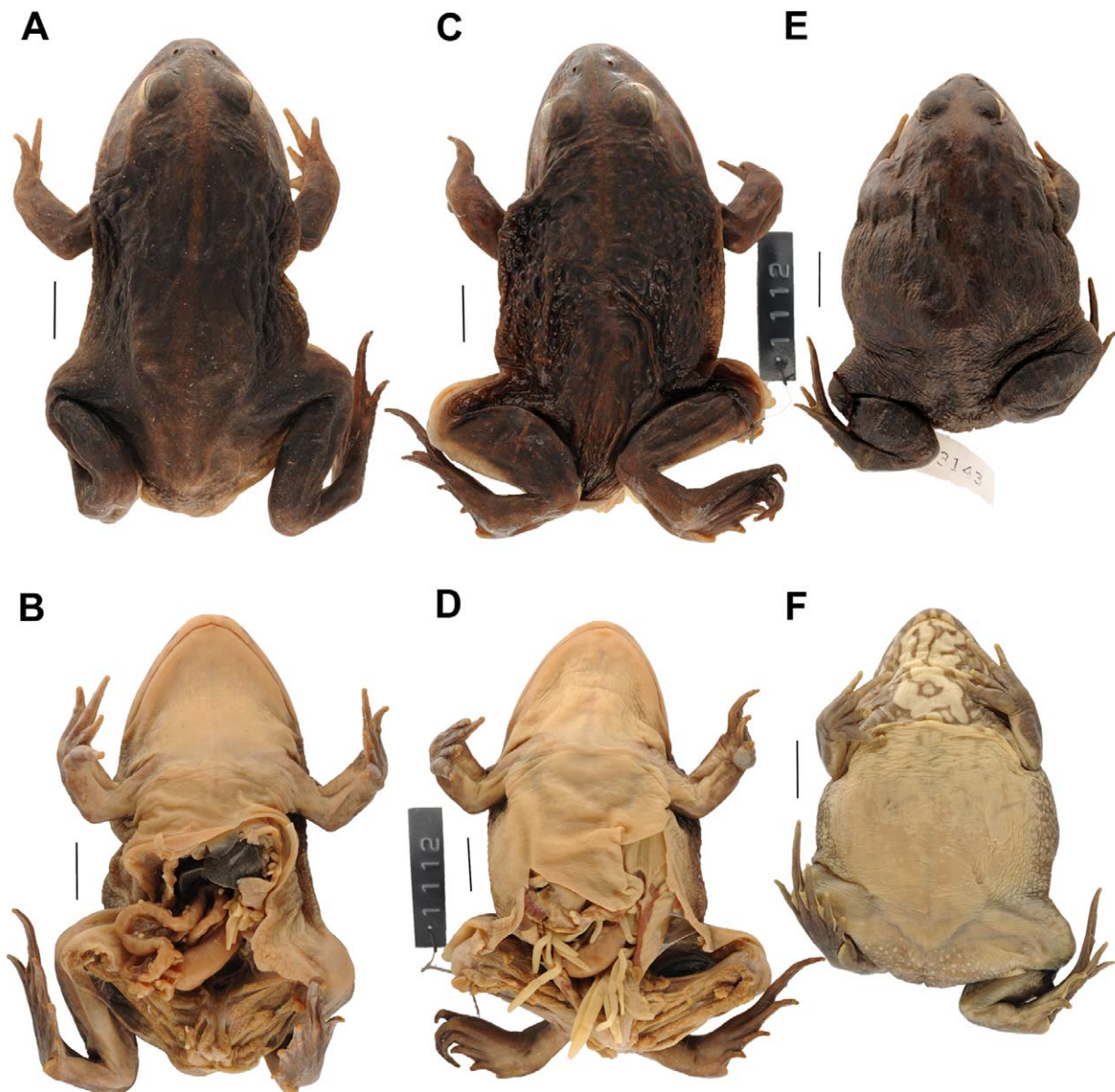


FIGURE 3. *Pyxicephalus angusticeps* Parry, 1982 New Status. **3A, 3B:** AC 1104, adult ♂ from Beira, Mozambique, dorsal and ventral views. **3C, 3D:** AC 1112, adult ♂ from Beira, Mozambique, dorsal and ventral views. **3E, 3F:** MP 3143, adult ♀ from Dondo, Mozambique, dorsal and ventral views. Scale bar = 1 cm.

1. These triangular ‘waistcoat’ patterns are commonly observed in *Pyxicephalus*, and may be relictual scars from the emergence of forelimbs.

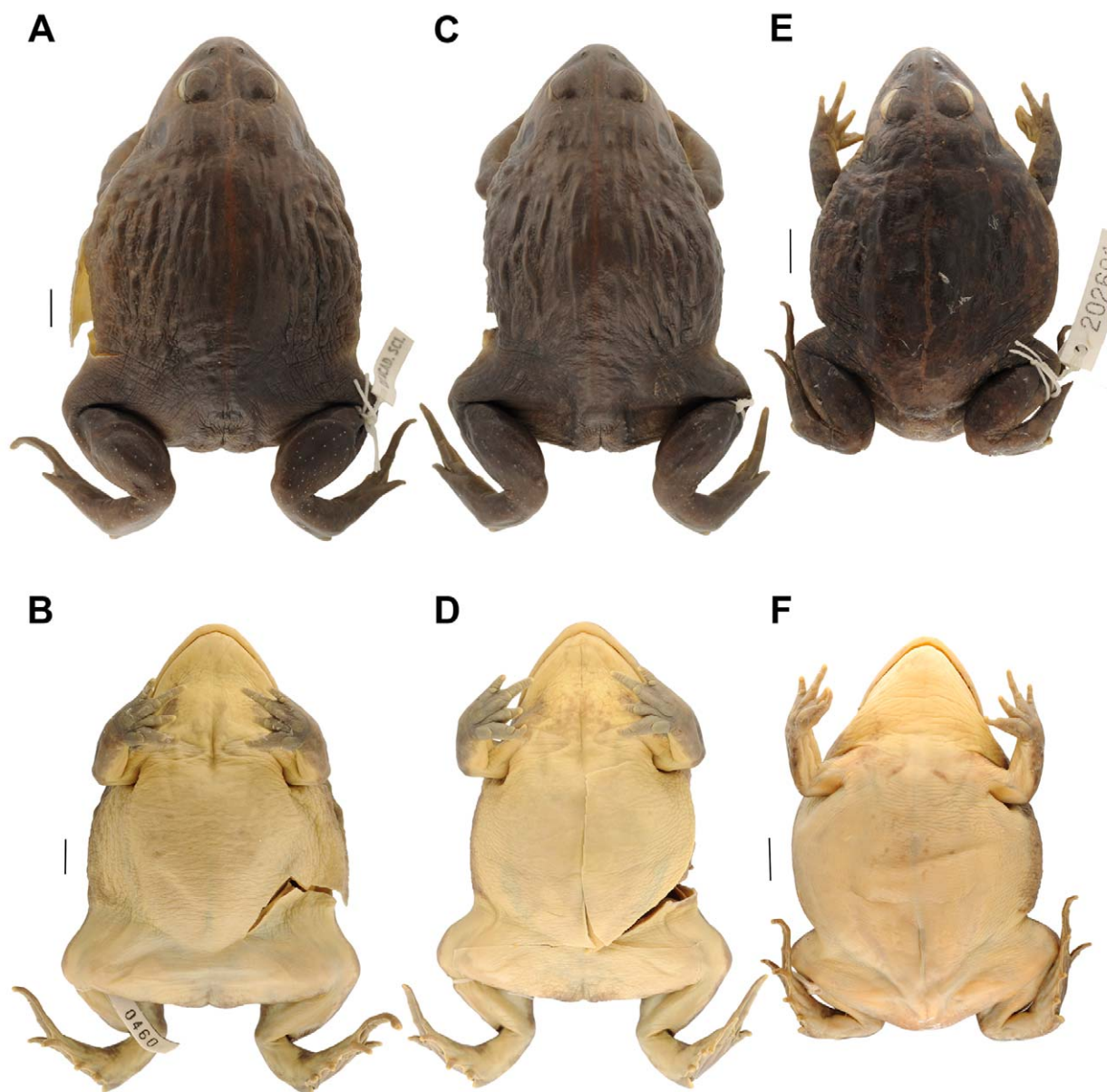


FIGURE 4. *Pyxicephalus angusticeps* Parry, 1982 New Status. **3A, 3B:** CAS 164712, adult ♂ from Malindi-Mombasa road, Kenya, dorsal and ventral views. **3C, 3D:** CAS 164708, adult ♂ from Malindi-Mombasa road, Kenya, dorsal and ventral views. **3E, 3F:** CAS 202691, adult ♀ from Zaraninge [Kiono] Forest Reserve, Tanzania, dorsal and ventral views. Scale bar = 1 cm.

Dorsal colouration. Dorsum dark brownish-grey in preservation. Small rounded darker dorsal blotches visible anteriorly, indistinct posteriorly. No symmetrically arranged (opposite or alternate) blotches visible over urostyle region. Vertebral stripe broad, coppery-orange brown, the edges formed by irregularly-positioned, dark rounded dorsal blotches; vertebral stripe extending to tip of snout, but narrowing anteriorly from approximate level of eyes, and indistinct from approximate level of sacrum posteriorly. Small patches of mottling and stippling apparent anteriorly against pale base colour of dorsum, becoming less conspicuous posteriorly.

Dorsal ridges and warts. Primary Dorsal Ridge Series 2 broken and only partially visible on right side, not extending full length of dorsum. Primary Dorsal Ridge Series 1 and 3 are greatly reduced to few weakly-developed warts. Lateral ridge absent on left, weakly present on right. Numerous conspicuous but narrow, raised oval warts present on flanks. Dorsum otherwise relatively smooth, with few slightly raised warts. Weak supratympanic ridge of warts apparent.

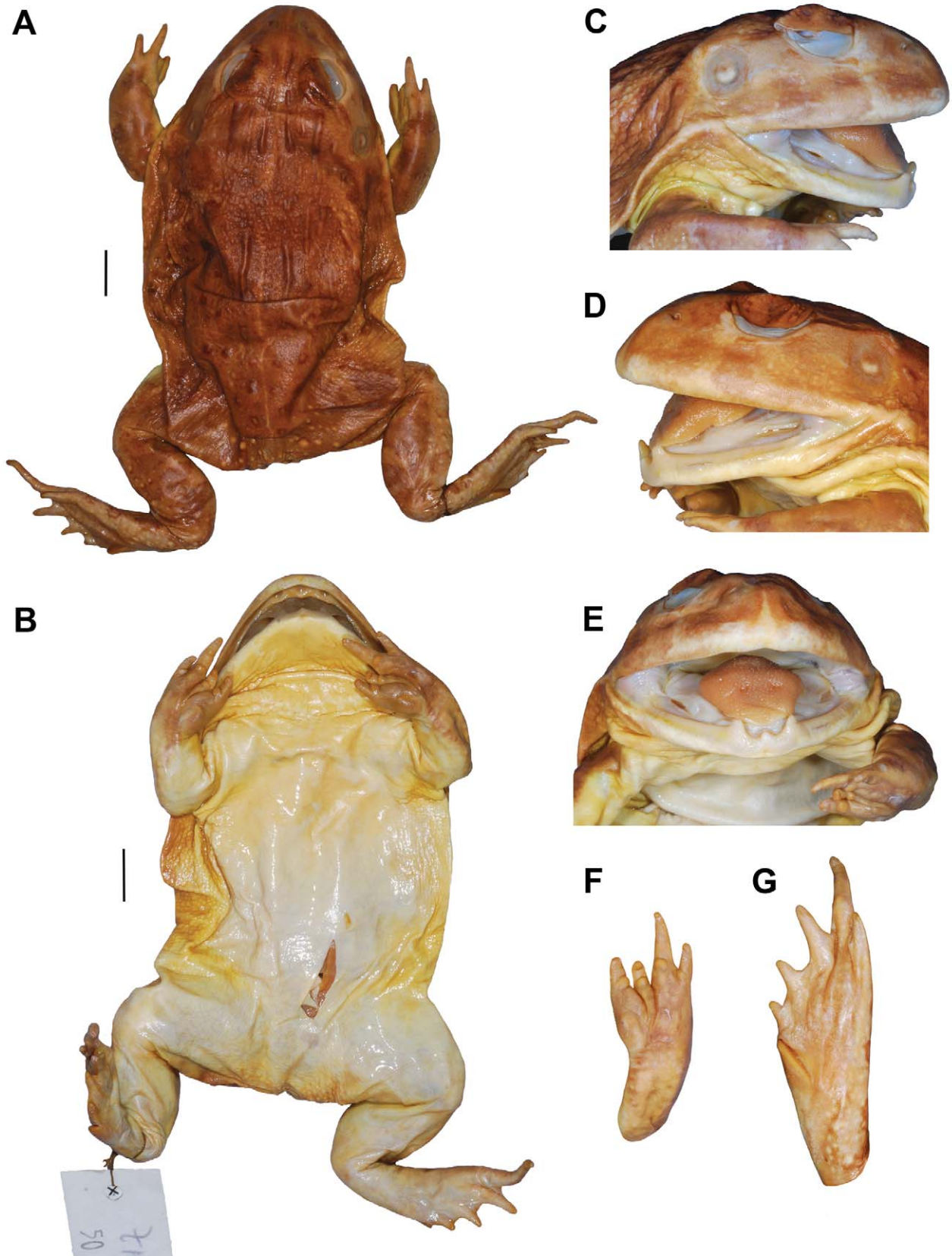


FIGURE 5. Lectotype of *Pyxicephalus edulis* Peters, 1854: ZMB 50301 (formerly one of two specimens accessioned under ZMB 10056), adult ♂ from Tete, Mozambique. **5A.** Dorsal view. **5B.** Ventral view. **5C.** Lateral view, right. **5D.** Lateral view, left. **5E.** Frontal view. **5F.** Hand. **5G.** Foot. Scale bar = 1 cm.

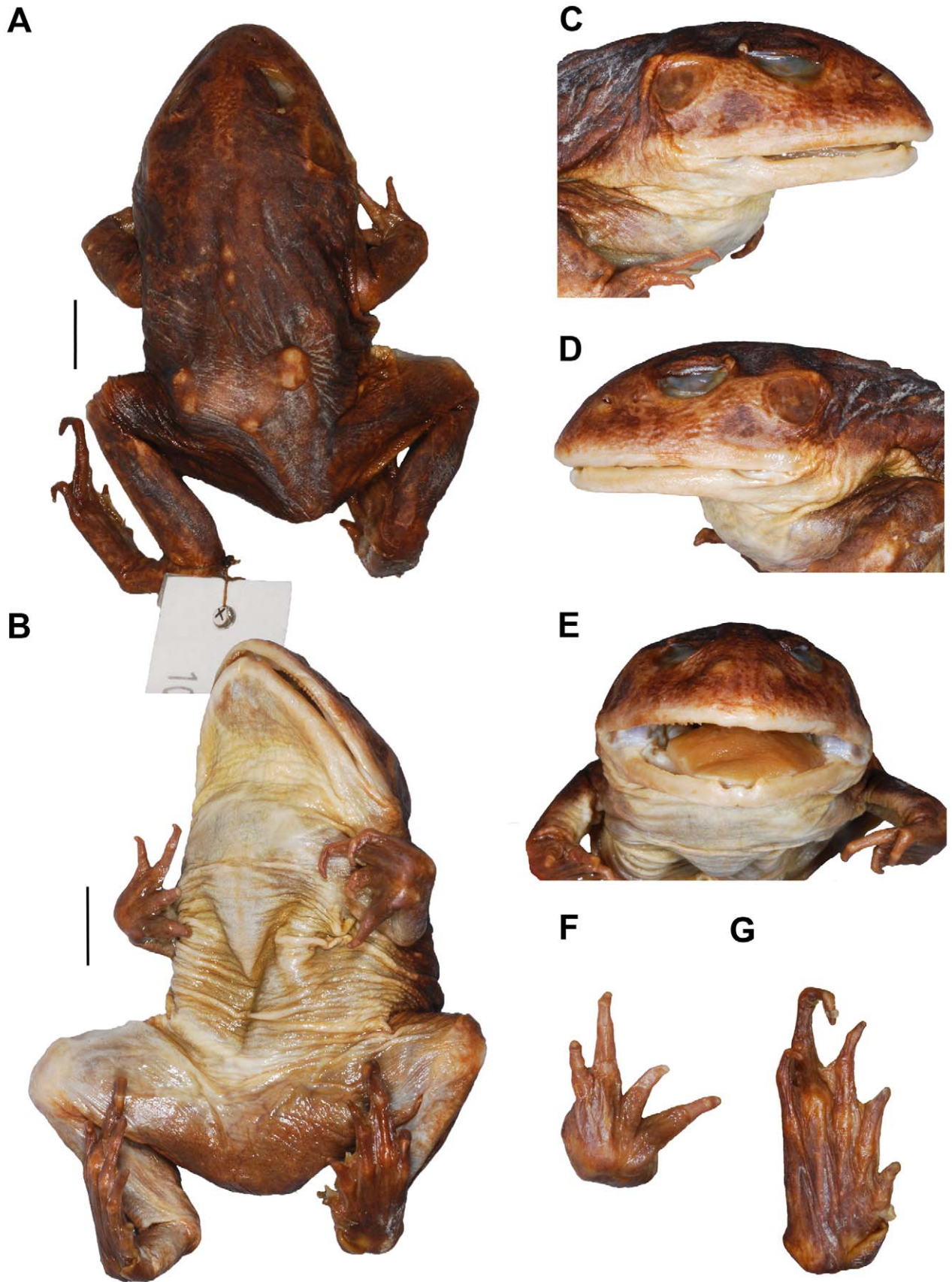


FIGURE 6. Paralectotype of *Pyxicephalus edulis* Peters, 1854: ZMB 10056, determined here to be *P. angusticeps* Parry, 1982 New Status, adult ♂ from Tete, Mozambique. **6A.** Dorsal view. **6B.** Ventral view. **6C.** Lateral view, right. **6D.** Lateral view, left. **6E.** Frontal view. **6F.** Hand. **6G.** Foot. Scale bar = 1 cm.

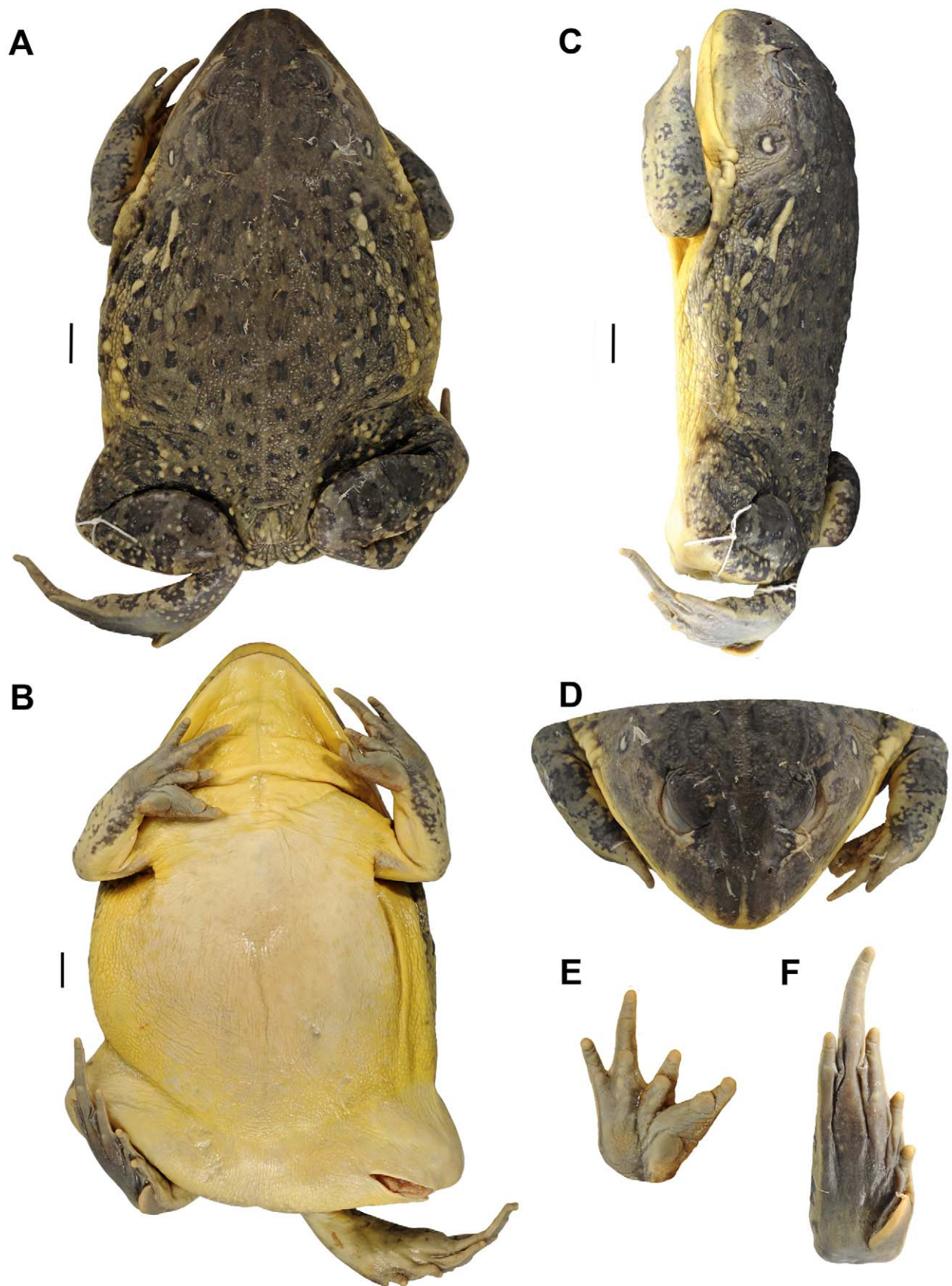


FIGURE 7. *Pyxicephalus edulis* Peters, 1854: MNHNP 2010.0153, adult ♂ from Nhica do Rovuma, Mozambique. **7A.** Dorsal view. **7B.** Ventral view. **7C.** Lateral view, left. **7D.** Frontal view. **7E.** Hand. **7F.** Foot. Scale bar = 1 cm.

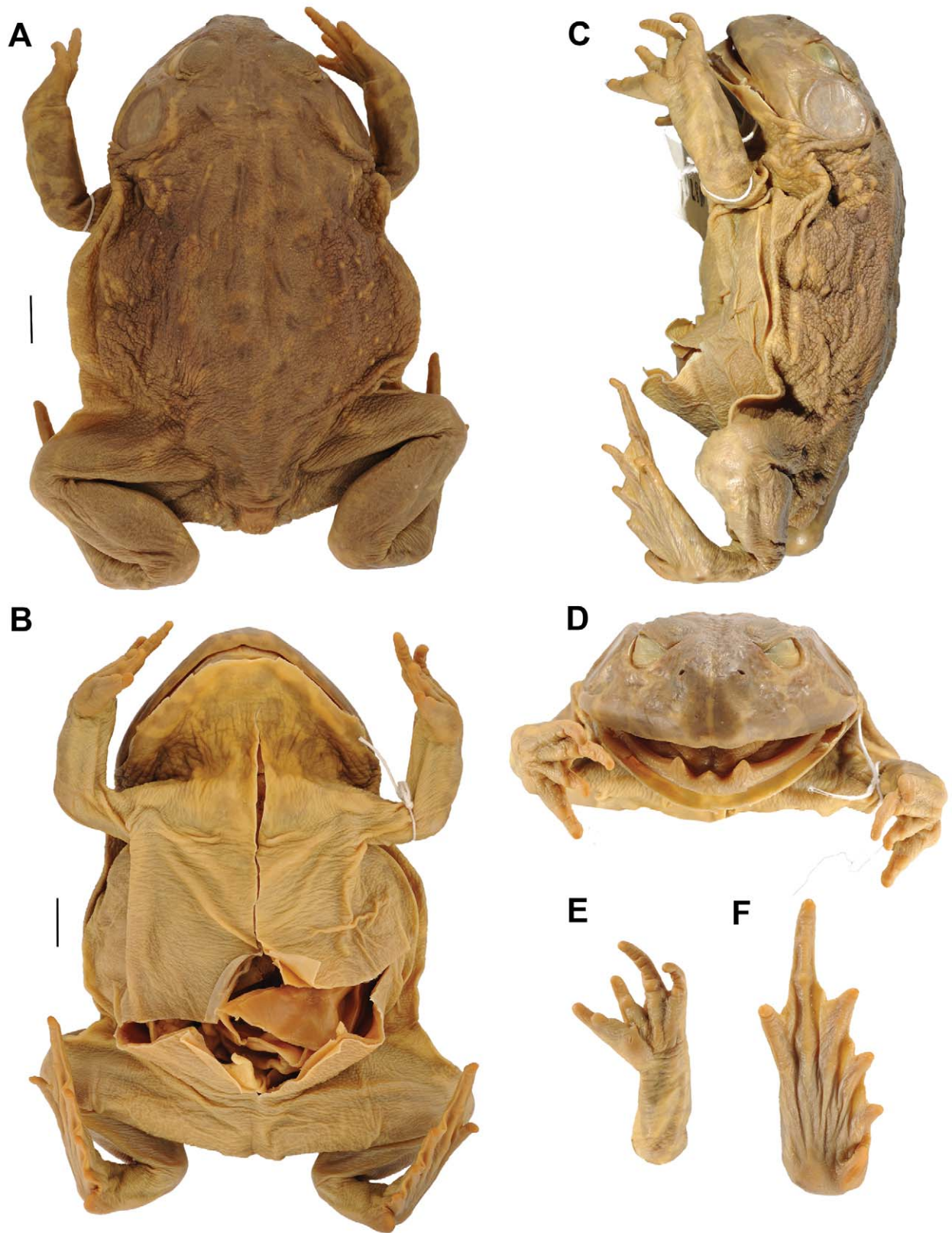


FIGURE 8. *Pyxicephalus obbianus* Calabrezi, 1927: MZUF 10337, adult ♂ from Òbbia, ca. 100 km NW of, along track Òbbia to Galcàio, Somalia. **8A.** Dorsal view. **8B.** Ventral view. **8C.** Lateral view, left. **8D.** Frontal view. **8E.** Hand. **8F.** Foot. Scale bar = 1 cm.

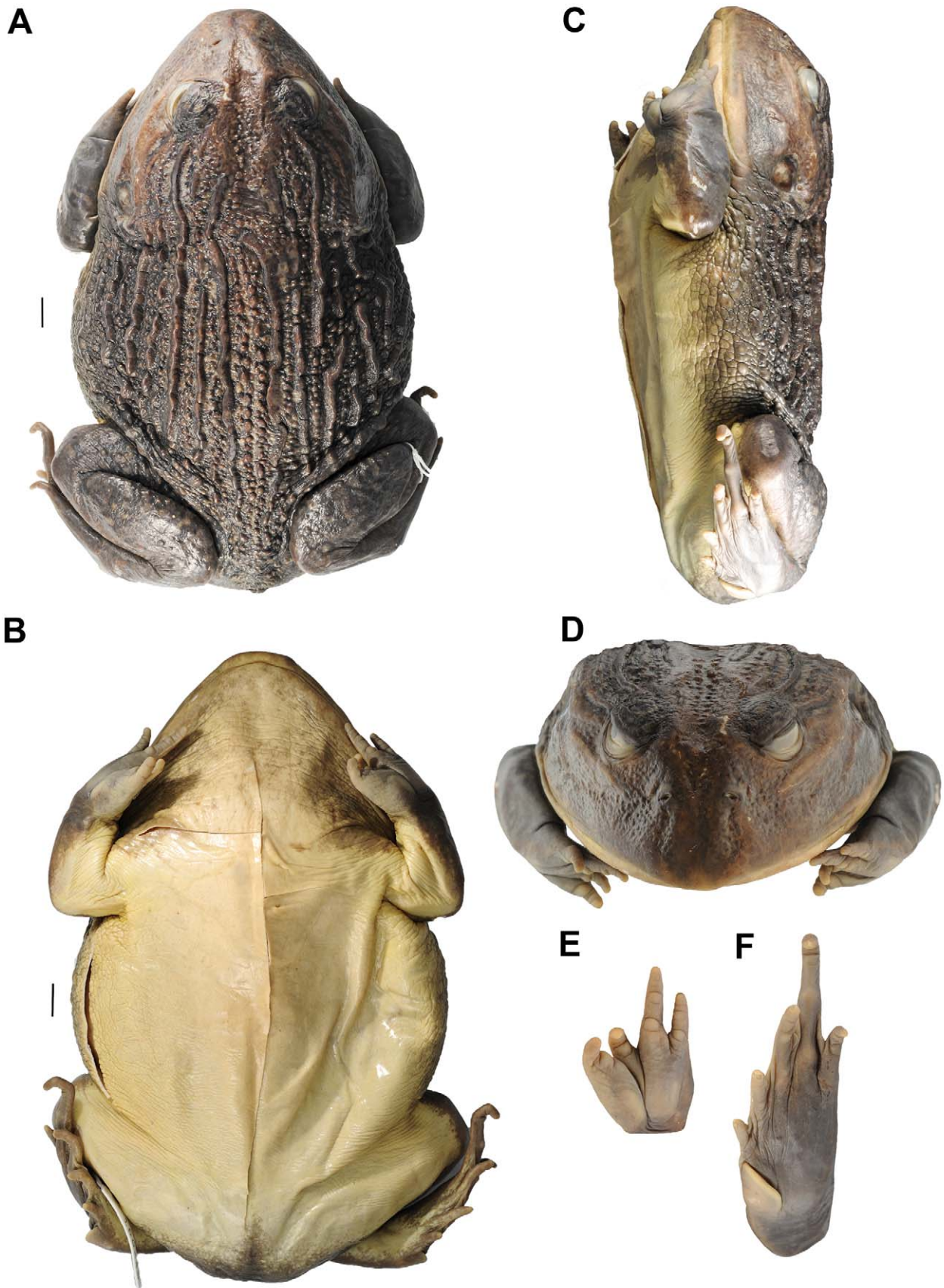


FIGURE 9. *Pyxicephalus adspersus* Tschudi, 1838: CAS 160245, adult ♂ from Katima Mulilo, Namibia. **9A.** Dorsal view. **9B.** Ventral view. **9C.** Lateral view, left. **9D.** Frontal view. **9E.** Hand. **9F.** Foot. Scale bar = 1 cm.

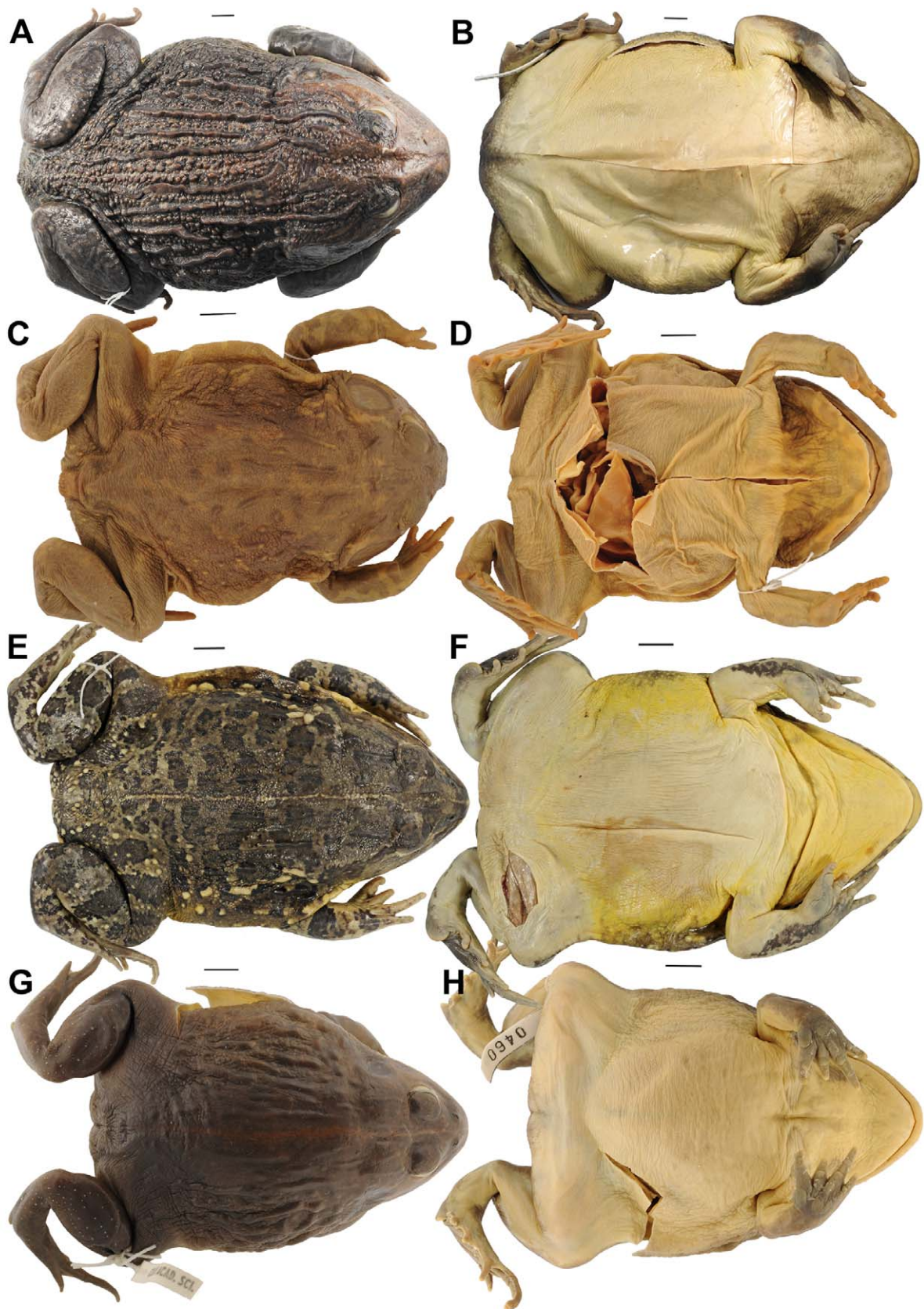


FIGURE 10. Comparison of adult males of *Pyxicephalus* Tschudi, 1838. **10A, 10B.** *Pyxicephalus adspersus* Tschudi, 1838: CAS 160245, Katima Mulilo, Namibia. **10C, 10D.** *Pyxicephalus obbianus* Calabrezi, 1927: MZUF 10337, Òbbia, ca. 100 km NW of, along track Òbbia to Galcàio, Somalia. **10E, 10F.** *Pyxicephalus edulis* Peters, 1854: MNHNP 2010.0153, Nhica do Rovuma, Mozambique. **10G, 10H.** *Pyxicephalus angusticeps* Parry, 1982 New Status: CAS 164712, Malindi-Mombasa road, Kenya. Scale bar = 1 mm.

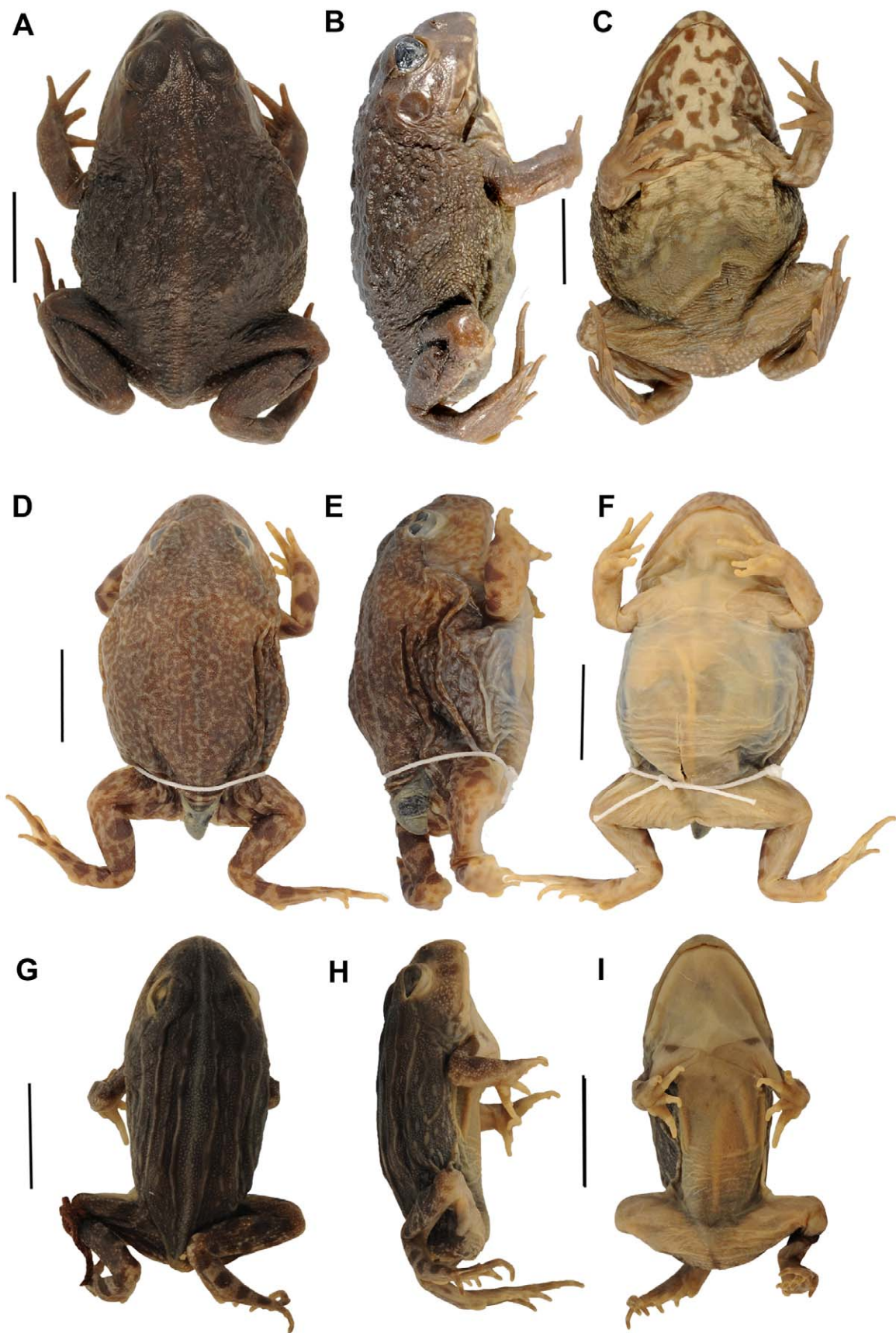


FIGURE 11. Subadult and metamorphs of *Pyxicephalus* Tschudi, 1838. **11A, 11B, 11C.** Paratype of *Pyxicephalus angusticeps* Parry, 1982 New Status: NMZB-UM 19774A, subadult, dorsal, lateral and ventral views. **11D, 11E, 11F.** *Pyxicephalus obbianus* Calabrezi, 1927: MZUF 10446, metamorph, dorsal, lateral and ventral views. **11G, 11H, 11I.** *Pyxicephalus adspersus* Tschudi, 1838: MP 4600, metamorph, dorsal view. Scale bar = 1 cm.

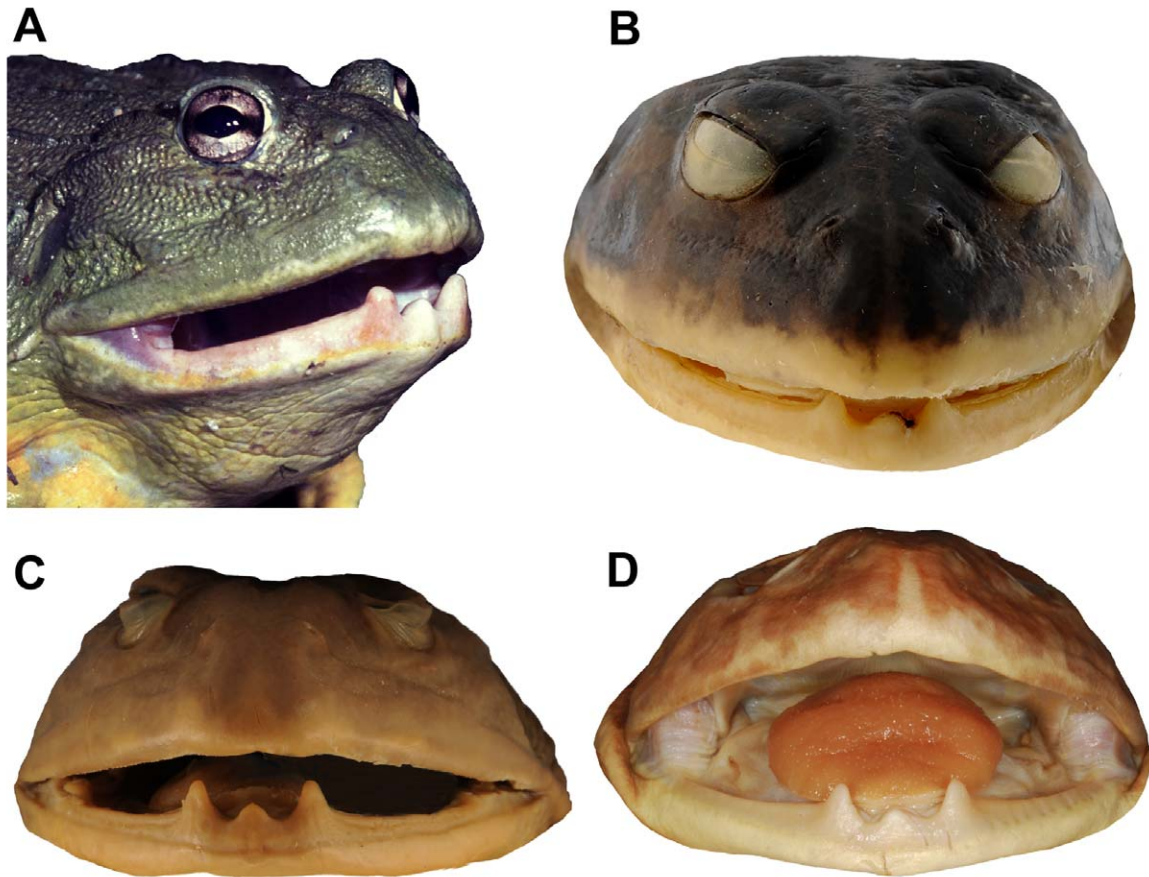


FIGURE 12. Odontoids of *Pyxicephalus* Tschudi, 1838. **12A.** Unvouchered live adult ♂ specimen of *P. adspersus* Tschudi, 1838. **12B.** *Pyxicephalus angusticeps* Parry, 1982 New Status: CAS 164711, adult ♂, Malindi-Mombassa road, Kenya. **12C.** *Pyxicephalus edulis* Peters, 1854: CAS-SUA 18321, adult ♂, Livalr District, Tanzania. **12D.** Paratype of *P. edulis* Peters, 1854: ZMB 3349, adult ♂, from Mozambique.

Variation. Adult material from the coastal lowlands of Kenya and Tanzania (Fig. 4, Appendix 1) differs from typical Mozambican material of *P. angusticeps* (Figs 2, 3) in the following respects. The vertebral stripe is narrower, better defined and a darker orange-red colour in preservation. The dorsum may present more, but poorly-defined and wider broken ridges, and have more distinct dark dorsal blotches. Barring is occasionally absent between the upper lip and the eye. Adults are larger than those from Beira. The asperites on the dorsal surface of the tibia are more irregularly arranged.

Metamorphs and subadults. The metamorphs of *P. angusticeps* can be distinguished from both *P. adspersus* and *P. edulis* on at least three external characters. The adult pattern of fewer ridges and conspicuous oval warts is also evident in metamorphs and subadults of *P. angusticeps* (Figs 11A–C). There are only a few broken ridges in place of Primary Dorsal Ridge Series 2, and the dorsum is covered in conspicuous oval warts, usually more pronounced laterally, in metamorph material (with tail vestiges) from NMZB that we assigned to *P. angusticeps* based on occurrence at the same locality as the distinctive subadult paratypes. These evenly-spaced warts in metamorphs and sub-adults of *P. angusticeps* are absent from the dorsum in metamorphs of *P. adspersus* (Figs 11G–I), *P. edulis* and *P. obbianus* (Figs 11D–F), and conform in appearance to those observed in the warty adult individual illustrated by Channing (2001, fig. 22.5), Channing *et al.* (1994, plate 1b), and Channing & Howell (2006, plate 22.6). They resemble dorsal warts observed in the pyxicephaline genus *Poyntonia* Channing & Boycott, 1989. The metamorphs of *P. obbianus* also differ markedly in colouration from their congeners, being finely vermiculated over the entire dorsum, with larger blotches present only on the limbs, and in having immaculate abdomens. A primary series of six ridges develop in late-stage *P. adspersus* and *P. edulis* larvae, and are pronounced by the time metamorphosis is complete (Figs 11G–I); these ridges are lacking in metamorphs of *P. obbianus* (Figs 11D–F).

Larvae. Tadpoles listed in the account of Pickersgill (2007 fig. 47, top, viz. MP 2155) from Tica, Mozambique, are typical of *P. edulis* (according to information presented in Du Preez & Carruthers 2009: 414–417), in having the labial tooth row formula 5(3-5)/3. The tadpole of *P. angusticeps* is unknown.

Distribution. Parry (1982) suggested that *P. angusticeps* was probably isolated from the western populations of *P. edulis* by the old course of the Zambezi River, which reached the sea south of Beira. He predicted that the range of *P. angusticeps* would include the area north to the Zambezi River and west to the Urema Trough. Although the southern limit of the known distribution of *P. angusticeps* appears to be the type locality, Beira in Mozambique, the species probably extends northwards through the lowland plains of East Africa, as far as Kakuyuni in Kenya (Appendix 1). A distribution map of *P. angusticeps* in East Africa is presented in Fig. 1, and is similar to that presented for *P. edulis* in fig. 252 of Channing & Howell (2006). There is, however, a substantial disjunction between known records from Mozambique and those from Tanzania and Kenya, which may be due to poor collecting effort in the intervening lowlands. Few herpetological surveys have been undertaken in Mozambique, and even those conducted in areas where *Pyxicephalus* should occur (e.g. Jacobsen *et al.* 2010) may not detect these frogs, due to their prolonged periods of inactivity. We have used the distinctive characteristics of the metamorphs (discussed above) to assign some metamorphs without associated adult material from two additional localities to *P. angusticeps*. Jorge (1933DD) is on the Buzi River, about 120 km upstream from its confluence with the Pungwe River estuary. Alvez de Lima (2034AB) was a safari camp ca. 50 km south-west of Beira, far from any major rivers. According to unpublished ecological modeling results (C.A. Yetman), areas in northern Mozambique with potentially suitable habitat for *P. angusticeps* include parts of north-central Manica Province, south-west of Quelimane on the coast in Zambezia Province, and along the Limpopo River in central Gaza Province.

Conservation status. Additional survey work is required to accurately assess the range and conservation status of *P. angusticeps*, which may be more widespread in East Africa. Currently, it is best considered as ‘Data Deficient’ (IUCN 2011).

Discussion

Type localities and Lectotype designation for *Pyxicephalus edulis*

Peters’ (1854: 626) original description gives the type localities for *P. edulis* as “Mosambique, Boror, Tette”. Specimens from these three localities labeled as types in the Museum für Naturkunde in Berlin (ZMB), underlined in red in the catalogue and marked with an asterisk, were collected before Peters’ (1854) description. The ZMB accession numbers were presumably added later. Much of Peters’ type material at ZMB is simply labeled “Mosambique”, including four type specimens of *P. edulis*. Some of the actual localities are listed in his publications. Peters (1882: 153) mentions “der Insel Mossambique” in his later account of *P. edulis*, suggesting that the exact locality of the four ZMB type specimens labeled as “Mosambique” is either Mozambique Island, where Peters was based, or the mainland opposite this. Channing *et al.* (1994) listed Sena and Cabaçeira as type localities of *P. edulis*, and stated that two type specimens were collected from Sena (ZMB 10057), but the type specimen(s) from Cabaçeira could not be traced. The Cabaçeira specimens (ZMB 10058, originally two specimens; the second now moved to ZMB 77320) were recently located. However, Peters (1854: 626) mentioned neither Cabaçeira by name, nor Sena in his original description of *P. edulis*, although he mentioned all five localities in his subsequent treatment of this species (Peters 1882). The specimens from Sena are underlined in a different red pen from that used to underline the original types in the ZMB catalogue, and listed as types therein, but the numbers from Cabaçeira are not underlined. We do not consider the specimens from Sena or Cabaçeira as part of the type series.

Loveridge (1950) restricted the type locality of *P. edulis* to one of the three localities mentioned by Peters (1854), viz. Tete, which is relatively distant (ca. 400 km NNW) from the type locality of *P. angusticeps*, i.e. Beira. To avoid future confusion regarding the identity of *P. edulis*, we hereby designate an adult male ZMB 50301 [old number ZMB 10056] (Fig. 5, see Appendix 1) from Tete as the lectotype of *P. edulis*. Tete is the only unambiguous locality for the type specimens mentioned in Peters’ (1854) original description from which specimens still exist, and Loveridge (1950) also regarded Tete as the type locality of *P. edulis*. Peters’ remaining specimens from the three localities mentioned in the description are hereby designated as paralectotypes of *P. edulis*. Three of the four adult ZMB paralectotype specimens and Peters’ two ZMB adults from Sena that we examined are typical of the

large *Pyxicephalus* widespread in Mozambique (Fig. 5), and precisely match the habitus figure XXIII and skull figure XXVI published by Peters (1882). This form is hereafter considered typical *P. edulis*. The remaining adult paralectotype examined, ZMB 10056 (Fig. 6) reportedly originating in ‘Tette’, is conspecific with *P. angusticeps*, as assessed from its small odontoids that are wider than long, lack of white tympanic markings, relatively smooth dorsum, brownish colouration on areas of the ventral surface, large femoral glands (not shown) and narrower head width than Peters’ other specimens of *P. edulis* (which are all as in Fig. 5). We assume that the locality data for ZMB 10056 may be erroneous; no other specimens of *P. angusticeps* have been collected near Tete, despite numerous other collections, including recent survey effort, from the area (see Appendix 1).

Taxonomic characters of adult *Pyxicephalus*

The discussion below refers to character states described in Table 1, with levels of variation observed between populations from major geographical regions of Africa documented in Table 2.

Head width. Male *Pyxicephalus*, with the exception of *P. angusticeps*, develop a disproportionately enlarged head as they mature. This is part of a suite of complex, highly specialized, correlated morphological characters associated with the specialized breeding system found in most species of *Pyxicephalus* (Scott 2005), which appears to have evolved convergently in the ‘fanged ranids’ of Asia (*sensu* Emerson & Ward 1998). The main diagnostic characteristic of *P. a. angusticeps* presented by Parry (1982) was the comparatively narrower head width (see Fig. 10). Poynton & Broadley (1985: 122) stated “the three forms recognised by Parry [from southern Africa] can be distinguished at all ages on the basis of skull width...”, in that *P. a. angusticeps* displays a head width less than 41% of SVL.

Relative head width as a diagnostic character in *Pyxicephalus* was dismissed by Channing *et al.* (1994), because their own measurements showed wide, and similar, variation within *P. adspersus* and *P. edulis*. These authors found that Parry’s (1982) measurements of *P. a. angusticeps* fell within the variation they observed in *P. edulis*, including the two ZMB types from Tete, one of which is now known to be conspecific with *P. angusticeps*. However, neither Parry (1982) nor Channing *et al.* (1994) considered meristic differences among semaphoronts. It is not surprising that the averages for the meristic data presented by Channing *et al.* (1994) are uninformative, and that the standard errors of Parry’s (1992) morphometric analysis overlap, because the data for both sexes and all stages were pooled. However, Channing & Howell (2006: 322) state that the taxon they consider as *P. edulis* can be distinguished from *P. adspersus* on the basis of a narrower head (see Figs 10G–H vs. Figs 10A–F).

Colouration. *Pyxicephalus angusticeps* does not exhibit the wide cream-coloured lateral stripes and creamy-coloured vermiculations laterally on the flanks that is often present in subadult *P. adspersus*, which are typical of *P. edulis* from Mozambique and *P. obbianus* from Somalia. The dorsal and lateral skin of preserved *P. angusticeps* is dark brown with darker blotches that are barely evident. A coppery-orange vertebral stripe is clearly visible in *P. angusticeps* from Mozambique, formed by the absence of dorsal blotches allowing the base colour to be apparent. The vertebral stripe is thus less sharply defined in *P. angusticeps*, and is wider than that observed in typical *P. edulis*. Fine stippling is visible in the base colour of type material from Beira. The upper jaw of *P. angusticeps* adults is barred, as in *P. edulis* from throughout Africa and *P. obbianus* from Somalia, but not as in adults of *P. adspersus* (Parry 1982; Poynton & Broadley 1985; Lambiris 1989; Du Preez & Carruthers 2009).

Gular pattern. A striking feature of subadult paratypes of *P. angusticeps* (NMZB-UM 19774A, Figs 11B–C), noted by Parry (1982) and Poynton & Broadley (1985), is the distinct darkly marbled colouration of the gular region. This general pattern is observed in other members of the genus and other pyxicephaline genera, e.g. *Amietia* Dubois, 1986. The mottling appears to fade in adult *Pyxicephalus*, particularly males, whereas females usually retain a few more spots or mottles, sometimes concentrated laterally. Male *P. adspersus* may display a densely spotted or blotched gular and chest region; in life, dark green or yellow spots are visible, fading to grey in preservative. The postero-lateral areas of the gular region and often the anterior chest region of males of *P. angusticeps* and *P. edulis* may be uniform grey, or coloured as the rest of the ventrum. However, as noted by Parry (1982) and Poynton & Broadley (1985), the mottling is considerably darker, with fine, strongly-developed vermiculations which are more persistent in adult females of *P. angusticeps* (Fig. 3F) than in other species of the genus, including *P. adspersus* (we have no information for female *P. obbianus*).

Dorsal ridge pattern. Based on an examination and measurements of snout-vent length (SVL) and head width of the ZMB types of *P. edulis* by a third-party, Channing *et al.* (1994) assumed that *P. edulis* was equivalent to *P. angusticeps*, and stated (p. 145), “The smoother dorsum [compared to *P. adspersus*] of the breeding males at Beira is also characteristic of Peters’ types of *P. edulis*. The name *P. edulis* is therefore valid”. However, both *P. edulis* and *P. angusticeps* have less well-developed dorsal ridges than *P. adspersus*, so this holds true for both taxa in comparison to *P. adspersus*. There is a noticeable distinction between the development of ridges of *P. edulis* and *P. angusticeps*. Photographs of the types of *P. edulis* show distinct well-developed ridges on the dorsal surfaces (Fig. 5A), the single exception being the specimen of *P. angusticeps* in the type series of *P. edulis* (Fig. 6A), which has a smooth dorsum.

Pyxicephalus angusticeps either has no ridges, or only Primary Dorsal Ridge Pair 2 (the central pair of the three basic primary dorsal ridges) is distinct. If present in *P. angusticeps*, Primary Dorsal Ridge Pair 2 runs longitudinally, aligned behind the eyes, and is reduced anteriorly and posteriorly. The dorsum in adults of *P. angusticeps* is otherwise relatively smooth, but may have evenly spaced, rounded or elongated oval warts thereon. The flanks of *P. angusticeps* are covered in small, evenly-spaced, conspicuous, round or oval warts. These warts are also usually seen in *P. adspersus* and *P. edulis*, but in these taxa, they are usually well-developed, elongated and may form a set of lateral ridges in addition.

Tympanum colouration. An obvious difference between *P. angusticeps* and *P. edulis* is the absence of the light coloured spot or crescent on the tympanum in the former. This white marking was considered diagnostic of *P. edulis* by Lambiris (1989) and Du Preez & Carruthers (2009). Channing *et al.* (1994) noted that the light tympanic marking is absent in material from Beira, and Parry (1982) did not report its presence in his description of the holotype of *P. angusticeps* (NMSA 1992, Figs 2A, 2C, 2D). The light tympanic marking is consistently absent in *P. angusticeps* from Mozambique, but is consistently present in type and non-type material of *P. edulis* from throughout Africa, although its shape may vary geographically, e.g. it is present only as a thin cream-coloured crescent in West African material. There is no light spot on the hyper-enlarged tympanum of *P. obbianus*, although the *pars externa plectri* are prominent (Fig. 8C).

Tympanum size and position. The character used to separate *P. adspersus* from *P. edulis* in the key of Channing (2001), i.e. distance from tympanum to eye is less than one eye diameter in *P. edulis*, and more than one eye diameter in *P. adspersus* is unreliable in adults and fails in juveniles. This ratio does not appear to be a fixed value as males grow into the largest size classes, as assessed among individuals within populations from single localities, but appears to be contingent on the extent of development of the squamosal (unpublished CT scan data, and suspected by Pickersgill 2007: 105). Particularly in males of both *P. adspersus* and *P. edulis*, the tympanum appears to displace backwards as the skull thickens in older larger individuals. The use of this character offers some explanation as to why large individuals of *P. edulis* are often incorrectly assigned to *P. adspersus*, and why juveniles and smaller adults are more often assigned to *P. edulis*. Furthermore, the character does not hold true in the type series and fresh material of *P. edulis* from Mozambique, in which the tympanum is at least one eye diameter from the eye, often further away, as in *P. adspersus* from Malawi, Namibia and South Africa. The tympanum is hypertrophied and positioned right next to the eye, by virtue of its large size, in *P. obbianus*. However, in *P. angusticeps*, the tympanum is much less than one eye diameter from the eye, usually around one tympanum width from the eye. Using the tympanum width against the distance of the tympanum from the eye appears to yield more accurate, consistent results within populations and between species than using the eye diameter, but still may not account for allometric growth changes that occur in larger individuals when the skull widens and thickens. This phenomenon is under further investigation using Geometric Morphometric methods.

Odontoids. All species of *Pyxicephalus* have well-developed odontoids in the lower jaw, but these are much smaller and differ in shape in *P. angusticeps* (Fig. 12B). Channing & Howell (2006: 319) used the character ‘longer than wide’ versus ‘as long as wide’ odontoids to distinguish *P. adspersus* from their concept of *P. edulis*. We regard this as a diagnostic character separating *P. angusticeps*, wherein the visible section of the odontoids appear small and triangular, and are about as long as their bases are wide, from other species of *Pyxicephalus*, which all have substantially larger, longer odontoids. In *P. adspersus* (Fig. 12A) and *P. edulis* (Figs 12C–D), odontoids are longer than wide, and in *P. obbianus* (Fig. 8D) they are large but appear more triangular.

Femoral glands. These glands are present in all species of *Pyxicephalus* (Parry 1982; Ohler 1996; Crnkovic 2003; Scott 2005 character 140; Oliver & Scott-Prendini 2011) and its sister-genus, *Aubria* Boulenger, 1917 (Ohler 1996; Scott 2005). Femoral glands are confined to the distal two-fifths of the inner thigh in *P. angusticeps*, but tend

to be relatively larger, especially in subadults, than in *P. adspersus*, *P. edulis* and *P. obbianus*. They may have an irregular white pattern in subadults of *P. angusticeps*, which Parry (1982: 290) noted as “very faintly marked with light area”.

Dorsal asperites. The dorsal surfaces of the calves and thighs have small white asperites in breeding adult *Pyxicephalus*, which tend to merge into lines on slightly raised ridges in *P. angusticeps* (not observed in *P. adspersus*, *P. edulis* and *P. obbianus*).

Nuptial pads. Nuptial pads are restricted to the thumb (i.e. Digit II of hand *sensu* Fabri & Alberch 1996) of *P. angusticeps* and *P. obbianus*, whereas they are present on the thumb and next two fingers (Digits II–IV) of *P. adspersus* and *P. edulis* from throughout Africa.

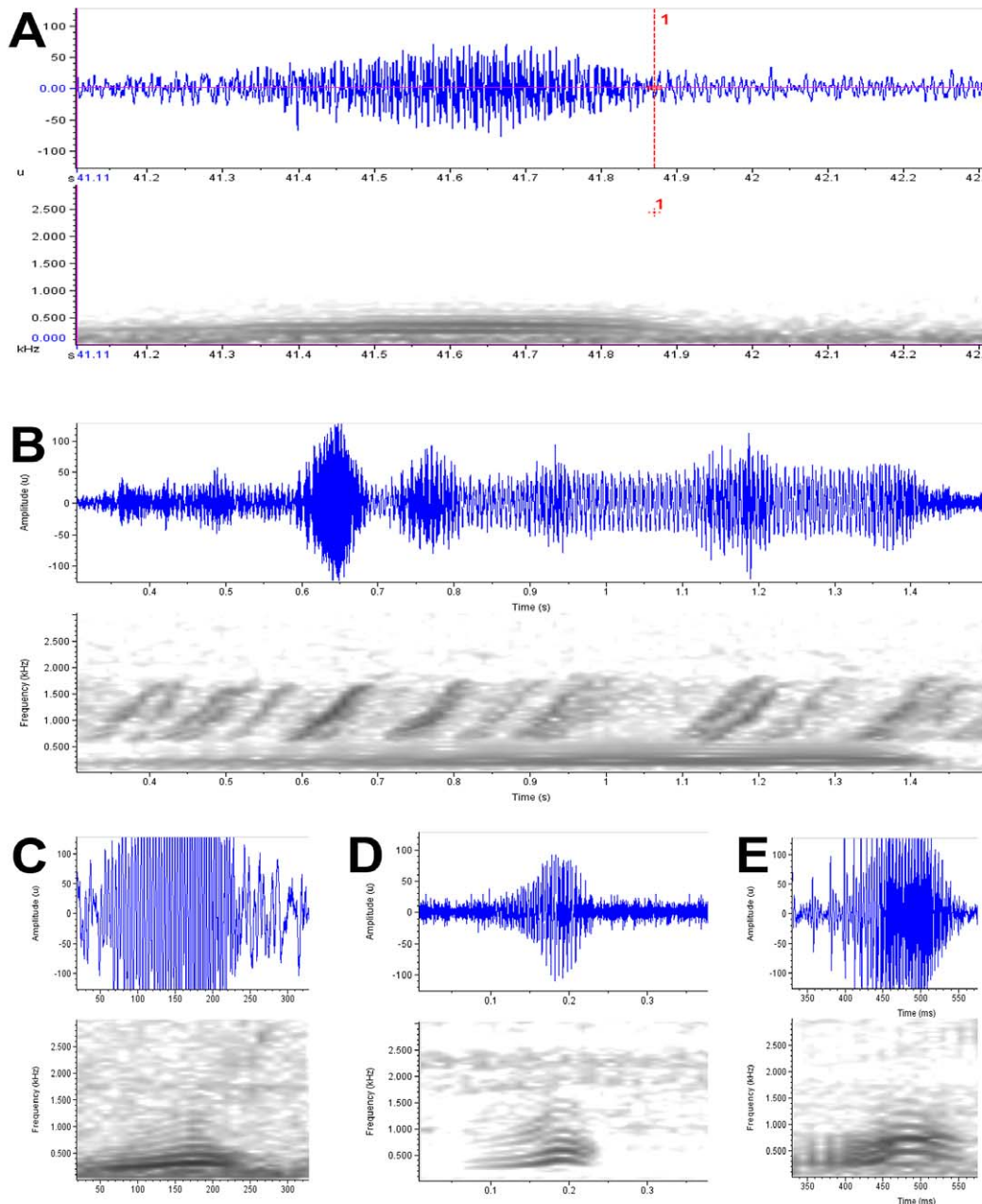


FIGURE 13. Spectrograms of *Pyxicephalus* Tschudi, 1838 produced via a DFT filter of 256 points. **13A.** *Pyxicephalus adspersus* Tschudi, 1838 from Bloemfontein, South Africa (recorded by Louis du Preez). **13B.** *Pyxicephalus adspersus* Tschudi, 1838 from Naboomspruit, South Africa (from collection of Alan Channing), with numerous calls of *Kassina senegalensis* Duméril & Bibron, 1841 visible above [published in Channing *et al.* 1994]. **13C.** *Pyxicephalus edulis* Peters, 1854 from ‘Transvaal’ (from collection of Alan Channing). **13D.** *Pyxicephalus edulis* Peters, 1854 from Tschaneni, Swaziland (recorded by Vincent Carruthers). **13E.** *Pyxicephalus angusticeps* Parry, 1982 New Status from Beira, Mozambique (recorded by Alan Channing) [published in Channing *et al.* 1994].

Advertisement calls

Channing *et al.* (1994) based their recognition of *P. edulis* predominantly on the difference between the shorter call of the taxon they considered as *P. edulis* and the longer call of *P. adspersus*, stating (p. 145): “The distinctive advertisement call described below confirms that a second species of bullfrog is present in southern Africa. This call was recorded from a number of localities, including Beira, near the type locality of *P. edulis*”. Channing *et al.* (1994: 144) presented a spectrogram, alleged to be *P. edulis*, as their fig. 1b. Although the locality at which this recording was made was not stated by Channing *et al.* (1994), the original sound file which produces this particular spectrogram is labeled as Beira (Fig. 13E). The voucher specimens collected from the locality at which this recording was made (AC 1104, Figs 3A–B; and AC 1112, Figs 3C–D) are conspecific with the holotype of *P. angusticeps* (Fig. 2). The calls recorded from Dondo (ca. 30 km NNW of Beira) by Pickersgill (2007) are similarly assigned to *P. angusticeps* based on the identity of the voucher specimens collected there (MP 3143, Figs 3E–F; and MP 3144).

Further work is required to accurately determine whether differences exist between the calls of *P. angusticeps* and *P. edulis*, because the number of individual calls, length and quality of the available recordings are inadequate to compare them statistically. However, the known calls of both species appear to be substantially shorter in length than those of *P. adspersus* (Figs 13A–B). The call of *P. angusticeps* (Fig. 13E) appears to differ from that of *P. edulis* (recorded from the Limpopo and Mpumalanga Provinces of South Africa, Figs 13C–D), being slightly shorter, with a higher dominant frequency (as generally expected from smaller size), and with greater frequency modulation (the dominant frequency raises and falls again during the call), than the other calls referred to *P. edulis* by Channing *et al.* (1994), which are flatter in dominant frequency, as in the spectrogram of *P. edulis* presented in Du Preez & Carruthers (2009: 479).

Breeding biology of *P. angusticeps*

On the basis of the identity of the aforementioned voucher specimens from Beira (Figs 3A–D), we consider that the account of the breeding biology of *Pyxicephalus* from Beira refers to *P. angusticeps*. Channing *et al.* (1994: 145) noted distinct breeding differences between the *Pyxicephalus* they observed in Beira (which they considered as *P. edulis*) and their own observations of *P. adspersus* from Bloemfontein. These observations from Beira differ markedly from the published literature for *P. adspersus* (Balinsky & Balinsky 1954; Clauss & Clauss 2002; Cook & Minter 2004; Passmore & Carruthers 1996; Du Preez & Carruthers 2009), but also from other published observations of *P. edulis*, in the following ways.

Response to rainfall. Channing *et al.* (1994: 145) described the breeding of *Pyxicephalus* from Beira (under *P. edulis*) as being similar to that of *Rana* [*Amietia*] *angolensis* Bocage, 1866. Channing (2001: 350) stated that males of *P. edulis* call “after even light rain early in the [rainy breeding] season”; this is re-iterated in Channing & Howell (2006). Based on our unpublished observations, and as reported by Cook & Minter (2004), Braack & Maguire (2005) and Du Preez & Carruthers (2009), the breeding biology of *P. edulis* is similar to that of *P. adspersus*, and spawning is triggered in both species by heavy rain, considered a minimum of 65 mm in a 48 hour period for *P. adspersus* by Channing (2001).

Egg laying. Channing *et al.* (1994) state that eggs of *Pyxicephalus* from Beira (i.e. *P. angusticeps*) appeared to be laid in the typical *Rana* [*Amietia*] fashion, whereas Du Preez & Carruthers (2009) documented that the amplexing pair’s cloacas are lifted out of the water during egg laying in both *P. adspersus* and *P. edulis*.

Lekking behavior and diel activity. Channing *et al.* (1994) and Channing & Howell (2006) state that the species they consider as *P. edulis* lays eggs at night throughout various parts of the breeding ponds. Diurnal breeding, during which ‘leks’ are formed by concentrations of males, have been recorded for both *P. adspersus* and *P. edulis* (Du Preez & Carruthers 2009).

Aggression. Channing *et al.* (1994) reported that no inter-male aggression during breeding was observed in the *Pyxicephalus* from Beira. Aggression during breeding is well-documented for both *P. adspersus* and *P. edulis*. Cook & Minter (2004) noted that the populations of *P. edulis* from Mpumalanga Province, South Africa (geographically proximate to Mozambique), differ in aggression and breeding from the account from Beira, Mozambique, given by Channing *et al.* (1994). Aggression during breeding in *P. edulis* has also been documented

by Braack & Maguire (2005), from the Hans Merensky Nature Reserve in Limpopo Province, South Africa. Braack & Maguire (2005) stated that their observations corroborate those of several farmers in the Phalaborwa and Hoedspruit districts of Mpumalanga Province, South Africa, as well as those of L. Minter in the Kruger National Park. The generic account for *Pyxicephalus* in Du Preez & Carruthers (2009) does not note any differences in breeding biology between *P. adspersus* and *P. edulis*. It is unlikely that these above-mentioned accounts include material of *P. angusticeps*, due to the species apparent absence from Botswana, Lesotho, Namibia, South Africa, Swaziland, Zambia and Zimbabwe (as assessed from available museum specimens, Appendix 1). However, the importance of providing voucher specimens to affirm literature accounts is underscored here; without listing voucher specimens, identifications cannot be verified *post hoc*.

Sympatry of *Pyxicephalus* species

According to Channing *et al.* (1994) and Channing (2001), *P. adspersus* and *P. edulis* both occur on the Mozambique coastal plain, and local inhabitants reportedly eat the smaller species early in the rainy season, and the larger species after very heavy rainfall in February. Channing (2001: 351) notes that local tribesmen in Mozambique even prepare them for consumption differently. Channing (2001) also mentions that the local people believe the small animals from early in the season grow into the large animals, which are only found later in the season after heavy rains. This is unlikely, because skeletochronological research on *P. adspersus* indicates that it takes at least 3–4 years for a male to reach breeding size (Yetman *et al.* 2012).

These field observations and folklore are consistent with the occurrence of two phenologically distinct species of *Pyxicephalus* on the Mozambique plain. However, we suggest that these two species, one larger and the other smaller, are in fact *P. edulis* and *P. angusticeps* respectively; not *P. adspersus* and *P. edulis*, as interpreted by Channing *et al.* (1994). It is important to recognise that *P. edulis* is not a small species, and male specimens may attain considerable size. Parry (1982) reports that males of *P. edulis* average 100 mm. Our unpublished data indicate that typical *P. edulis* males from Mozambique can reach 138 mm SVL (recorded for MNHNP 2010.0153, Fig. 7), but are not as large as the largest *P. adspersus* (maximum 191 mm SVL recorded for AMNH-A 23621). Misidentifications of *P. edulis* as *P. adspersus* that appear to be based on size are common in museum collections. Furthermore, no characters reliably distinguish the metamorphs of *P. adspersus* from *P. edulis* until a fairly large size class is reached (hence our list of ‘indeterminate’ metamorphs in Appendix 1). A large proportion of museum material of *Pyxicephalus* comprises small metamorphs, which emerge in large numbers and are easily collected, but often poorly preserved. This material has generally been variously assigned to *P. adspersus* or *P. edulis*. The erroneous sympatric distribution reported for *P. adspersus* and *P. edulis* appear to be due largely to size-based museum determinations, together with random determinations of juveniles, compounded by general confusion arising from failure of some traditional characters to adequately diagnose these two taxa (see revised key). Parry (1982) misidentified some large individuals of *P. edulis* from Botswana as *P. adspersus* (asterisks in Appendix 1). Specimens from Botswana have previously been difficult to identify. Parry (1982) and Poynton & Broadley (1985) mention ‘introgression’ of *P. adspersus* and *P. edulis* characteristics in material from Botswana. However, Parry (1982) did not misidentify any adult material from Mozambique as *P. adspersus* (see Appendix 1). Our revised distribution data for re-examined adult museum specimens from Mozambique corroborates the studies of Parry (1982) and Poynton & Broadley (1985), neither of which listed any specimens of *P. adspersus* from the Mozambique plain, despite examining all material available in several major collections. Based on this evidence, we conclude that *P. adspersus* does not occur on the Mozambique plain.

We agree with Pickersgill (2007) that the apparent sympatry of *P. adspersus* and *P. edulis* mentioned by Channing *et al.* (1994), on the basis of an unspecified recording from Naboomspruit (Limpopo Province, South Africa) wherein both species were allegedly present, remains to be verified. The only available published sonograph from the locality (see Fig. 13B) indicates only the long call. This also applies to Channing’s (2001: 350) statement that both species occur together at Nylsvlei (near Naboomspruit) and at Beira in Mozambique. The recording(s) and/or sonographs which form the basis of these statements of sympatry need to be re-examined. In the absence of adult voucher specimens of both *P. adspersus* and *P. edulis* from these localities, and given the apparent confusion of *P. edulis* and *P. angusticeps* documented above, it is more parsimonious to assume that *P. adspersus* and *P. edulis* are allopatric.

We suggest that *P. angusticeps* and *P. edulis* may be sympatric on the Mozambique plain, although these two species have not yet been observed in the same microhabitat. If syntopy were the case, other isolating mechanisms must be in force separating *P. edulis* and *P. angusticeps*, e.g. differences in breeding phenology, diet and/or male vocalizations. Channing *et al.* (1994) documented differences in breeding phenology between the two species on the Mozambique plain (discussed earlier), but clear differences in calls between these two taxa have not rigorously been established yet, requiring further investigation. Larger general size in concert with a wider gape in *P. edulis* could theoretically be responsible for ecological niche differentiation in diet between adults of this species and *P. angusticeps*. Lynch (1975) mentioned that wide gape of the wide-headed *Pyxicephalus* of Africa could be correlated with the specialized habit of predated on other frogs. Lynch (1975) restated the views of Hutchinson (1959) that greater head width and concomitant gape size in frogs seems to be a means of affecting niche separation without having to become larger. *Pyxicephalus angusticeps* is not as squat as its congeners, with relatively thin, long fingers and a slight increase in toe webbing, compared to *P. edulis*. The narrower head, more gracile body form, slight increase in webbing and longer digits of *P. angusticeps*, as compared with *P. edulis*, suggest a more aquatic lifestyle. *Pyxicephalus angusticeps* may require more swamp-like habitats or flooded grasslands, based on the habitats (e.g. flooded rice paddies) in which it has predominantly been collected in Mozambique.

Conclusion

The confusion and mistaken synonymy of *P. angusticeps* with *P. edulis* originates primarily from the decision of Channing *et al.* (1994) to compare *P. adspersus* to what they thought was *P. edulis* material from Beira. These authors synonymized the described *Pyxicephalus* taxon from Beira, at the same time concluding that *P. edulis* is specifically distinct from *P. adspersus*. Channing *et al.* (1994) used distinct call differences between the long call of *P. adspersus* from Bloemfontein and the form(s) with shorter calls, including *P. angusticeps* material from Beira, as evidence. Channing *et al.* (1994) dismissed Parry's (1982) main diagnostic character of *P. angusticeps*, *viz.* a narrower head width. However, Channing & Howell (2006) use a narrower head width to diagnose their concept of *P. edulis* (which we consider as *P. angusticeps*) from the larger species present in the lowlands of East Africa.

The presence of two species of *Pyxicephalus* on the Mozambique plain is confirmed by examination of museum specimens and literature. This supports our opinion that *P. angusticeps* and *P. edulis* may be sympatric on the Mozambique plain. It does not support the distinction of *P. adspersus* and *P. edulis*, as presented by Channing *et al.* (1994). Channing *et al.* (1994) made important observations regarding the distinct breeding biology and call of the *Pyxicephalus* from Beira, which show that it is specifically distinct from *P. adspersus*, and provided other ecological information which, in retrospect, distinguishes *P. angusticeps* from *P. edulis*. These distinctive differences merit further investigation, particularly with regard to aestivation strategies, temporal activity in response to rainfall, and possible differences in ecological niche compared to *P. edulis*. Although notable taxonomic difficulties remain in *Pyxicephalus*, particularly in distinguishing *P. adspersus* and *P. edulis* from throughout all regions of Africa, this issue does not affect the recognition of *P. angusticeps*, the type material of which is distinct from *P. adspersus*, *P. obbianus*, and the type material of *P. edulis*. We thus consider *P. angusticeps* as valid. A full generic revision, based on DNA sequence data, advertisement calls, morphometrics, external morphology and osteological data, will clarify outstanding issues in the taxonomy of *Pyxicephalus*.

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APPENDIX 1

Material of *Pyxicephalus* Tshudi, 1834 examined from throughout Africa. Museum abbreviations are: American Museum of Natural History, New York (AMNH); The Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CAS); Ditsong Natural History Museum (formerly Transvaal Museum, Pretoria: TMP); Natal Museum, Pietermaritzburg (NMP); National Museum of Kenya, Nairobi (NMK); Natural History Museum of Zimbabwe, Bulawayo (NMZB, incorporating the collections of the former National Museum of Southern Rhodesia [NMSR], Umtali Museum [UM] and Queen Victoria Museum [QVM]); Museum für Naturkunde (formerly Zoologische Museum, Berlin: ZMB); Muséum national d'Histoire Naturelle, Paris (MNHN); Museo di Storia Naturale, Firenze (MZUF); and the amphibian collections of Alan Channing (AC), Martin Pickersgill (MP) and Elizabeth Scott-Prendini (ESP). Co-ordinates, original collector's numbers and corrected or interpreted data are given in brackets. Specimens examined by Parry (1982) but determined differently in this study are marked as follows: * = Parry (1982) determined as *P. adspersus*; ** = Parry (1982) determined as *P. edulis*. ? = catalogued as *P. adspersus*.

Pyxicephalus adspersus Tshudi, 1838

Material examined: No Locality: 2 ♂s (TMP 65955, 84824), 2 ♀s (NMZB 7182, 72741). **BOTSWANA:** Totten[g] [20°23'S 22°57'E]: Feb. 6, 1965, R.N.H. Smithers, 1 ♂ (NMZB-UM 10531). **NAMIBIA:** 1 ♂ (CAS 162045). “German Southwest Africa”: 1 ♂ (AMNH-A 23621). Oshakati, 60 km W of, crossing road in dry savanna [17°35'S 15°09'E]: Feb. 12, 2007, M. Pickersgill, 1102 m, 2 metamorphs (MP 4600, 4601). Ruacana, E of [17°25'S 14°32'E]: Feb. 12, 2007, M. Pickersgill, 1107 m, batch metamorphs (MP 4626). Rundu, Kavango floodplain [17°54'S 19°46'E]: M. Pickersgill, 1063 m, batch metamorphs (MP 4630). **Caprivi Region: Katima Mulilo District:** Katima Mulilo [17°32'S 24°15'E]: Oct. 22, 1970, W.D. Haacke, 1 ♂ (TMP **39321); Feb 1986, A. Channing, 1 ♂ (CAS 160245). **Kunene: Opuwo District:** Van Zyl's cutting: Apr. 1930, V. Fitzsimons, 1 ♂ (TMP 14752). **Otjozondjupa Region: Omatako District:** Klein Hamakari, Waterberg [20°40'S 18°00'E]: Dec. 3, 1988, A. Channing, (TMP 84440 [AC 500]). **Ovamboland:** Itota dune: June 1937, V. Fitzsimons, 2 ♂s (TMP **17139, **17140). **SOUTH AFRICA: Eastern Cape Province:** Queenstown: 5 metamorphs (NMP 5501, 5502, 5503, 5504, 5505). Transkei, near Umtata [31°35'S 28°47'E]: Jan 11, 1970, E.J. Morris, 1 ♀ (CAS 135127). **Free State Province:** Sasol Mine: 2 metamorphs (NMP 2006, 2007). **Odendaalsrus District:** Allanridge, Odendaalsrus [27°45'S 26°38'E]: May 1960, Prozesky, 1 metamorph (TMP 26429). **Gauteng Province: Pretoria District:** Halfway House, Midrand: Mar 1972, K.H. Switak, 1 ♀ (CAS 135194). Kameeldrift: Nov. 7, 1989, Zoigt, 1 ♂ (TMP 68884). Pretoria, Zoo Hill: Nov. 25, 1910, 1 ♀ (TMP 6996). Pretoria [25°42'25"S 28°13'46"E]: W.L. Distant, 1 ♂ (BMNH 91.12.7.15), 2 subad. (91.12.7.16–17), 2 ♂s (BMNH 98.5.4.16–17). **North-west Province: Bloemhof District:** Bloemhof: Nov. 28, 1980, N.H.G. Jacobsen, 1 ♂ (TMP 74409). **Christiana District:** Farm Christiana: Nov. 27, 1980, N.H.G. Jacobsen, 1 ♀ (TMP 74401). **Schweizer Reneke District:** Farm Lot 43: Nov. 28, 1980, N.H.G. Jacobsen, 1 ♀ (TMP 74414). **Ventersdorp District:** Orkney, dorpsgebied [town centre]: Feb. 24, 1981, N.H.G. Jacobsen, 1 ♀ (TMP 74417). **Vryburg District:** Farm Villa Franca: Nov. 24, 1977, De Jager, 1 ♂ (TMP 50666). **ZIMBABWE: Rusape (Manda) [18°32'S 32°07'E]:** 1 ♂ (NMZB-UM 22131). Saffron Walden, Ha-am: 1 ♀ (NMZB-NMSR 4450). **Harare Municipal Province:** Epworth, Salisbury [Harare] [17°53'24"S 31°08'51"E]: 1 ♂ (NMZB-UM 33292). Mabelreign, Salisbury [Harare] [17°47'26"S 31°00'05"E]: 1 ♂ (NMZB-QVM-A 500), Feb. 19, 1972, P.R. Muller, (NMZB-UM 32422), 1 ♂ (NMZB-QVM-A 501). Salisbury [Harare]: D.K. Blake, 3 metamorphs (NMZB-UM 2629). Warren Hills, Salisbury [Harare]: Jan. 18, 1972, 2 ♂s (NMZB-UM 28426 [JPL 1133], 28427 [JPL 1134]). **Bulawayo Municipal Province:** Bulawayo: 2 ♂s (NMZB-NMSR 2735, 2742), 2 ♂s (NMZB 12505, 6263), 1 subadult (NMZB 2736), 1 metamorph (NMZB 2740). Bulawayo, Hillside Dam: 1 ♀ (NMZB 7182).

Pyxicephalus angusticeps Parry, 1982 New Status

Holotype: MOZAMBIQUE: Sofala Province: Dondo District: Beira, the swamp beyond Estoril [19°50'37"S, 34°50'20"E]: Jan. 26, 1959, Nyasaland-Mozambique Expedition [of the University of Natal, Pietermaritzburg], 1 ♂ (NMP 1992 [UNP 3099]; NMP Type Number 2581).

Paratypes: MOZAMBIQUE: Sofala Province: Dondo District: Beira, the swamp beyond Estoril [19°50'37"S, 34°50'20"E]: Jan. 26, 1959, Nyasaland-Mozambique Expedition [of the University of Natal, Pietermaritzburg], 1 ♂ (NMP 1991 [UNP 3098]), 2 subadults (NMP 1990 [UNP 3063], 1993 [UNP 3100]). Beira: 2 subadults (NMZB-UM 6451), 5 subadults (NMZB-UM 7516), 4 subadults (NMZB-UM 19774), 1 subadult (NMZB-UM 23374).

Additional Material Examined: MALAWI: Shiré Highlands [plateau]: S. Elliot, 1 subadult (BMNH 95.4.17.34) [possible erroneous locality]. **MOZAMBIQUE: Manica Province: Sussundenga District:** Jorge [19°55'11"S 33°49'37"E]: 3 metamorphs (NMZB-UM 27574). **Sofala Province: Buzi District:** Alves de Lima [20°05'S 34°25'E]: 1 metamorph (NMZB-UM 3085 [JPT 2182]). **Dondo District:** Beira: Dec. 1991, A. Channing, 2 ♂s (AC 1104, 1112) {to be accessioned at AMNH}. Beira, inundated rice paddies on road to airport [19°47'36"S 34°55'08"E]: Feb. 9, 1997, M. Pickersgill, 3 m, 1 ♂ (MP 2796). Dondo, in flooded grass near railway station [19°37'01"S 34°44'48"E]: Feb. 10, 1997, M. Pickersgill, 52 m, 2 ♀s (MP 3143, 3144). **Nhamatanda District:** Ponte do Pungué [Pungwe] [19°28'29"S 34°31'09"E]: 1 ♂ (NMZB-UM 31071). **Tete Province: Moatize District:** Tette [Tete] [27°07'S 32°15'E, 1633BA]: 1 ♂ (ZMB 10056) [Paralectotype of *P. edulis*; misidentified as *P. edulis*; considered an incorrect locality record]. **KENYA: Coast Province: Kilifi District:** Malindi-Mombasa Rd, 3 km S of Watamu junction, 1 km W of, on dirt road [03°19'S 39°59'E]: Aug 24, 1987, R.C. Drewes, S. Ashe & J.V. Vindum, 1 ♂ (CAS 164708 [JVV 286]), Aug 27, 1987, R.C. Drewes & J.V. Vindum, 3 ♂s (CAS 164711 [JVV 459], 164712 [JVV 460], 164713 [JVV 461]). Kakuyuni [03°13'S 40°00'E]: Jul. 7, 1979, M.S.E. Easterbrook, 2 subads (NMK-A 1209/1, 1209/2), Jul. 21, 1979, M.S.E. Easterbrook, 1 ♀ (NMK-A 1213/1), Aug. 10, 1979, M.S.E. Easterbrook, 1 ♀ (NMK-A 1240/3), 1 subad. (NMK-A 1240/1), Aug. 25, 1979, M.S.E. Easterbrook, 2 ♀s (NMK-A 1253/1, 1253/3), Sept. 23, 1979, M.S.E. Easterbrook, 1 ♂ (NMK-A 3374/1), 1 ♀ (NMK-A 3374/2). Mida Creek [03°22'S 39°58'E]: 2 ♀s (NMK-A 1251/1, 1251/3). Mida, Mida Creek: Oct. 1990, M. Poggesi & M. Borri, 1 ♂ (MZUF 20360), 2 subad. (MZUF 20361, 20362). Kabateni, near Vitengeni [03°19'S 39°51'E]: Sept. 2, 1979, M.S.E. Easterbrook, 2 ♂s (NMK-A 1260/1, 1260/2). **Malindi District:** Arabuko Sokoke National Park [03°20'S 39°52'E]: May 1996, A. Espira, 1 ♂ (NMK-A 3132/2), 2 ♀s (NMK-A 3132/1, 3137). **TANZANIA:** Kivukoni [04°33'S 38°37'E]: Mar. 11, 1963, Rees, 1 metamorph (BMNH 1969.1401), 2 ♂s (BMNH 1969.1399 [662], 1969.1400[577]). Mahenge [Mahenge?] [04°46'S 34°20'E]: Mar. 10, 1963, Rees, 2 metamorphs (BMNH 1969.1402–1403). Kilombero Valley [08°34–36'S 36°27–30'E]: 270 m, K.M. Howell, 1 subad. (BMNH 2000.400). Ruwu South Forest Reserve [06°56'S 38°52'E]: 190 m, K.M. Howell, 1 subad. (BMNH 2002.437). Taru, East Africa [05°13'S 35°02'E]: C.S. Belton, 2 subad. (BMNH 98.1.8.21–22). Ubungo, near University campus [06°46'S 39°12'E]: May 21, 1997, M. Pickersgill, 30 m, 1 subadult (MP 2221). Zaraninge Depression [Kiono Depression] [06°10'S 38°38'W]: Apr. 19, 1995, C.A. Msuya, Pitfall trapped, 1 ♀ (CAS 202692 [CAM 557]); May 27, 1995, 1 ♀ (CAS 202691 [CAM 556]).

Pyxicephalus edulis Peters, 1854

Lectotype: MOZAMBIQUE: Tete Province: Moatize District: Tette [Tete] [27°07'S 32°15'E, 1633BA]: 1 ♂ (ZMB 50301 [formerly in ZMB 10056]).

Syntypes: MOZAMBIQUE: “Mosambique”: 2 ♂ (ZMB 50260 [formerly in ZMB 3349], 3349).

Additional Material Examined: BOTSWANA: Francistown, 40 mi NW of: 1967, D.G. Broadley, 1 ♂ (DGB 511). Kangyane Pan: D.G. Broadley, 1 ♀ (NMZB-UM *12959 [ex DGB 561]). Kanye, pan 50 km W of: Mar. 3, 1961, R.N.H. Smithers, 2 subadults (NMZB-UM 5663). Mabua Sehubi Pan [Mabuasehube Pan *sensu* Parry]: 1 ♀ (NMZB-UM *12960). Plumtree to Francistown: 1 ♀ (NMZB-NMSR 2799). Serowe, 40 mi [66 km] NNW of: 1 ♂ (NMZB-UM 14765), 1 subadult (NMZB-UM 14766). Tsangara Pan: 1 ♂ (NMZB-UM 8957). **Gaborone:** Metsimahaba [Metsimaclaba] River: Mar. 1930, V. Fitzsimons, 1 subadult (TMP 14749). Metsmathlabe [Metsimaclaba] River, near Thamago, approx. 40 km W of Gaberone [24°41.202'S 25°34.153'E]: Nov. 21, 1998, E. Scott & L. Prendini, 1 ♀ (TMP 84415 [ESP 200]). **Kweneng:** Khutse Pan: Mar. 1930, V. Fitzsimons, 2 metamorphs (TMP *14750, *14751). **Makarikari:** Nata: Jan. 15, 1978, C. Scholtz, 1 subadult (TMP *50855). Nata River junction [delta], Makgadikgadi Pan: Aug. 1930, V. Fitzsimons, 1 ♀ (TMP 14756). **Ngamiland:** Mabeleapodi [Mabeleapodi *sensu* Parry]: May 1930, V. Fitzsimons, 1 subadult (TMP *14755), 1 metamorph (TMP *14754). **Ghanzi:** Gemsbok Pan: Mar. 1930, V. Fitzsimons, 1 subadult (TMP *14753). **BURKINA FASO:** Fabre, 17 km N of: May 5, 1970, Father Terrible, 1 ♂ (MNHNP 1989.4058), 1 ♀ (MNHNP 1989.4059). Garango near Teukodogo [11°48'N 00°34'W]: June 18, 1962, 1 ♀ (MNHNP 1989.4062). Lay [12°31'45"N 01°46'28"W]: Aug. 6, 1966, 1 ♀ (MNHNP 1994.5527); Aug. 16, 1966, 2 ♂s (MNHNP 1994.4508), 1 ♀ (MNHNP 1994.4511), 2 subadult ♂s (MNHNP 1994.4509, 1994.4510). Ouagadougou [12°22'13"N 01°31'29"W]: 1 metamorph (MNHNP 1993.1497). Samba [12°40'N 02°23'W]: 2 subadults (MNHNP 1985.2688, 1985.2689), 1963, 1 ♀ (MNHNP 1985.2686). **CHAD:** Bongor: Nov. 1973, 1 ♀ (MNHNP 1989.4063). Farcha N'djamena [12°07'N 15°03'E]: Aug. 30, 1964, 1 ♂ (MNHNP 1989.4060). Gounou Gaya [09°38'N 15°31'E]: June 1974, Sister Gordon, 1 ♂ (MNHNP 1989.4061). Kousri (Chari River) [12°32'N 17°18'E]: 1 metamorph (MNHNP 1904.0217), 2 ♂s (MNHNP 1904.0215, 1904.0216). **KENYA:** Jjara, 2.5 mi SW of: May 16, 1960, A. Channing, 250 ft, 1 subadult (AMNH-A 68409). **MALI:** Yélimané [15°08'N 10°34'W]: Sep. 29, 1895, Knight, 1 ♂ (MNHNP 1895.0470), 1 ♀ (MNHNP 1895.0469). **MOZAMBIQUE: Lelui District:** 1 metamorph (MNHNP 276). **Cabo Delgado Province:** Camp of Nhica do Rovuma, route du camp au village Nhica [10°45'19"S 40°13'00"E]: Nov. 26, 2009, A. Ohler, 122 m, 6 ♂s (MNHNP 2010.0153, 2010.0154, 2010.0156, 2010.0157, 2010.0158, 2010.0159), 3 ♀s (MNHNP 2010.0151, 2010.0152, 2010.0155). **Gaza Province: Massagena District:** Massangena, Save River (Falcon College): 1 ♀ (NMZB-UM 29283). **Inhambane Province: Govuro District:** Vila Franca do Save [21°08'29"S; 34°33'59"E], 15 km SE of: 1 ♂ (NMZB-UM 28454), 2 ♀s (NMZB-UM 28455, 28543). **Maputo Province: Matutuine District:** Matchova [26°24'42"S 32°37'50"E]: 1 ♀ (NMZB-UM 28850 [JPT 1279]). **Sofala Province: Buzi District:** Grudja [19°48'30"S 34°00'59"E]: Aug. 1965, C.R. Owen, 1 ♂ (NMZB-UM 9262). **Caia**

District: Caia [17°50'S 35°14'E]: H.B. Cott, Feb. 14, 1927, 2 subadults (BMNH 1929.12.20.10–11). Sena [17°45'S 34°55'E]: 2 ♂s (ZMB 10057, 50290 [formerly in ZMB 10057]) [underlined in red and listed as types in ZMB catalogue, but locality not mentioned in original description, therefore not considered types here]. Villa Fontes [17°49'13"S 35°20'39"E]: 1 ♂ (NMZB-UM 19422). **Chibabava District:** Madassipo, crossing the road in open bush country [20°47'S 34°09'E]: Feb. 5, 1997, M. Pickersgill, 4 metamorphs (MP 3101, 3115, 3116, 3117). **Nhamatanda District:** Lamego [19°19'08"S 34°17'07"E]: 1 subadult (NMZB-UM 31082). Muda -[to] Lamego: 1 ♂ (NMZB-UM 26244), 1 ♀ (NMZB-UM 26245), 2 subadults (NMZB-UM 26246, 26247), 1 subadult (NMZB-UM 26244). Tica, beside railway station [19°23'S 34°25'E]: Feb. 11, 1997, M. Pickersgill, batch metamorphs (MP 2155). Xiluvo [19°14'56"S 34°02'54"E]: 4 ♂s (NMZB-UM 26311, 26312, 26313, 26314), 2 ♀s (NMZB-UM 26315, 26316). **Tete Province: Moatize District:** Tete [27°07'S 32°15'E]: Jan. 15, 1959, Nyasaland-Mozambique Expedition [of the University of Natal, Pietermaritzburg], 1 ♂ (NMP 1997 [UNP 2755]). Tete, 72 km (45 mi) ENE of: Dec. 2, 1962, 2 ♂s (NMZB-UM 4082, 4083). **Zambezi Province:** L. [Lake] Mutarara: Apr. 1, 1927, H.B. Cott, 3 metamorphs (BMNH 1929.12.20.12–14). **SENEGAL: Saint-Louis Region:** Richard Toll [16°28'N 15°41'W]: Aug. 30, 1969, 2 metamorphs (MNHP 1994.5530, 1994.5531), 1 metamorph (MNHP 1993.1498). **SOUTH AFRICA: KwaZulu-Natal Province: Hhluwe District: Bonamanzi Nature Reserve:** [28°4'22.2"S 32°17'1.9"E]: Jan. 7, 2011, E. Scott, J. Marais & H. Heinz, 218 m, 3 ♂s (ESP 1101, 1105, 1106), 3 ♀s (ESP 1102, 1103, 1104). **Gauteng Province: Pretoria:** Pretoria: 1 ♂ (TMP 8127) {considered an imprecise locality}. **Limpopo Province: Gazankulu District: Manyeleti Nature Reserve (MNR):** MNR, Farm Andover [24°34'S 31°12'E]: Dec. 16, 1987, G. Haagner, 1 ♀ (TMP 67097). MNR [24°36'S 31°27'E]: Dec. 10, 1986, G. Haagner, 1 ♂ (TMP 65761); Dec. 29, 1986, 1 ♀ (TMP 65727). MNR [24°39'S 31°34'E]: Dec. 17, 1986, G. Haagner, 1 ♀ (TMP 65763). MNR [24°42'S 31°31'E]: Feb. 28, 1988, G. Haagner, 1 ♀ (TMP 67778). MNR, Main camp [24°38'S 31°28'E]: Dec. 15, 1987, Van Rhyn, 1 ♀ (TMP 67078); Dec. 27, 1986, G. Haagner, 1 ♀ (TMP 65762); Mar. 2, 1987, 1 ♂ (TMP 65970). MNR, Sarabank [24°37'S 31°33'E]: Dec. 6, 1987, G. Haagner, 1 ♂ (TMP 67054). **Giyan District:** Dzumeri: Dec. 21, 1979, N.H.G. Jacobsen, 1 ♂ (TMP 74422). Ka Kheyi: Dec. 19, 1979, N.H.G. Jacobsen, 1 ♂ (TMP 74425). **Letaba 2 District:** Griffin Mine, Leydsdorp: Jan. 1915, Van Dam, 1 ♂ (TMP 6990). **Mhala District:** Farm Rolle 235: Feb. 2, 1981, N.H.G. Jacobsen, 1 ♀ (TMP 74421). **Phalaborwa District:** Farm Ross: Nov. 28, 1980, N.H.G. Jacobsen, 1 ♀ (TMP 74419). **Kruger National Park (KNP):** KNP, Dzundweni Waterhole [22°45' 31°09'E]: Mar. 26, 1960, Brain, 25 metamorphs (TMP 26391). KNP, Satara & Tshokwane, 30km, KNP: Dec. 22, 1973, Scholtz, 1 subadult (TMP 50231). KNP, Shingwedzi: Nov. 15, 1959, Coetzee, 1 ♂ (TMP 26390). **Thabazimbi District:** Farm Verpoort 161: Mar. 2, 1980, N.H.G. Jacobsen, 1 ♀ (TMP 74402). **Mpumalanga Province: Barberton District:** Farm Helena 400: N.H.G. Jacobsen, 1 ♂ (TMP 74415). Ngwenya Lodge, 10 km NW of Komatiport: Jan. 19, 1996, M. Whiting, 1 ♀ (TMP 80189). **Pilgrim's Rest District:** Farm Dublin 218, on Olifants River [24°33'S 30°38'E]: Nov. 1, 1927, Lang, 1 ♂ (TMP 12834). **North-west Province: Bloemhof District:** Farm Gezicht 265: Mar. 23, 1981, N.H.G. Jacobsen, 1 subadult (TMP 74413). **Christiana District:** Farm Kameelpan: Nov. 29, 1980, N.H.G. Jacobsen, 1 subadult (TMP 74404). **Rustenburg District:** Farm Kameellaagte 61: Jan. 10, 1980, N.H.G. Jacobsen, 1 ♂ (TMP 74398). **Schweizer Reneke District:** Farm Kareelaagte 70: Nov. 29, 1980, N.H.G. Jacobsen, 1 ♀ (TMP 74423). Farm Uitvalskop: Dec. 2, 1980, N.H.G. Jacobsen, 1 ♀ (TMP 74400). **Wolmaransstad District:** Farm Boschrand 158: Mar. 20, 1981, N.H.G. Jacobsen, 1 subadult & 1 metamorph (TMP 74399). **SWAZILAND:** Lavumisa, 10 km N of [27°13'35"S 31°54'06"E]: Feb. 7, 1991, R.C. Boycott, 1 ♂ (TMP 71724), 1 ♀ (TMP 71725). Maloma, 4.5 km E of [26°59'54"S 31°41'45"E]: Jan. 11, 1991, R.C. Boycott, 1 subadult (TMP 71719, roadkill). Maphiveni, 10 km NW of [26°07'S 31°53'31"E]: Nov. 19, 1995, R.C. Boycott, 1 subadult (TMP 80113). Matsamo to Balegane road, Jan. 8, 1989, R.C. Boycott, 1 ♂ (TMP 69397). Tunzini Citrus Estate [25°57'24"S 31°44'43"E]: Dec. 30, 192 m, La Croix (TMP 80087). Tunzini Citrus Estate [25°57'25"S 31°43'43"S]: Nov. 15, 1991, R.C. Boycott & La Croix, 1 ♂ (TMP 71734). Tunzini Citrus Estate [25°57'28"S 31°43'43"S]: Nov. 14, 1991, R.C. Boycott & La Croix, 1 ♀ (TMP 71733). Tambuti Guest lodge, 2 km outside, on road to Big Bend [26°43'49.8"S 31°48'43.4"E]: Jan. 5, 2011, E. Scott, J. Marais & H. Heinz, 200 m, 1 ♂ (ESP 1079). Tshaneni: 2 subadults (NMZB-UM 32773, 32774). Tshaneni / Bordergate road, Dec. 5, 1989, R.C. Boycott & Culverwell, 2 ♀s (TMP 69403, 69404). **TANZANIA:** Kizumbe [05°13'S 38°46'E]: Dec. 28, 1928, 1 ♂ (AMNH-A 59395). Mawere Shamba, 40 mi S of Tabora: Dec. 1934, 2 ♂s (AMNH-A 59506, 59507). Mikindani, East Africa: 1910, 1 ♀ (AMNH-A 23758). Mikindans: Apr. 10, 1939, Loveridge, 1 ♂ (TMSA 35986). Rumgwa, Mpanda [07°21'S 31°40'E]: 1 ♀ (NMZB-UM 19269). Sonta, Rukwa: 1 ♂ (NMZB-UM 25779 [FN 17993]). Southern Region Livalr District [09°46'S 37°55'60"W]: Charles, 1 ♂ (CAS-SUA 18321 [B 321]). Tanga, flooded rice paddies to the north of town [05°03'58"S 39°05'20"E]: May 28, 1997, M. Pickersgill, 9 m, 1 subadult (MP 3535). **Tarangire National Park:** Bwawa Mbili [03°58'51"S 35°58'52"E]: Mar. 21, 1995, M.W. Klemens, 1170 m, 1 subadult (AMNH-A 154614); Silale Mbuga, E side of [04°14'S 36°08'13"E]: Mar. 24, 1995, M.W. Klemens, 1140 m, 11 subadults (AMNH-A 154619, 154620, 154621, 154623, 154624, 154625, 154626, 154627, 154628, 154629, 154630); Mar. 26, 1995, 3 subadults (AMNH-A 154631, 154633, 154634); Mar. 27, 1995, 1 subadult (AMNH-A 154632). Silale Mbuga, W side of [04°00'S 36°00'E]: Mar. 18, 1995, M.W. Klemens, 1 subadult (AMNH-A 154615), 1 subadult (AMNH-A 154616); Mar. 23, 1995, M.W. Klemens, 2 subadults (AMNH-A 154617, 154618). **ZAMBIA:** Lochinvar, Mazabuka: 1 ♂ (NMZB 3179). Mazabuka: 1 ♀ (NMZB 11043), 1 subadult (NMZB-UM 257780) [tanned]. Mulanga, Kalomo: 1 ♂ (NMZB-NMSR 3178 [BLM 428]). Nkala Stream, Ngoma [15°55'S 25°57'E]: Jan. 24, 1969, D.D.H. Day, 3500 ft, 2 subadults (NMZB-UM 19889, 19892). Kafue National Park: Chunga: 1 ♂ (NMZB-UM 30093) [tanned]. Nkaka: 1 ♂ (NMZB-NMSR 2641). **Barotseland:** Kalabo: 1 ♀ (NMZB-UM 21205). **Eastern Province:** Chikowa: 1 ♂ (NMZB 16961 [VJW 779]). Luembe, Luangwa River: 1 subadult (NMZB 16964 [VJW 1223]). Sayiri Court: 2 ♂s (NMZB 16962 [VJW [859-61], 16975 [VJW [859-61]]), 1 ♀ (NMZB 16963 [VJW [859-61]]). **ZIMBABWE:** Beitbridge, 20 km NNW of: 1 ♂ (NMZB 5703). Birchenough Bridge: 1 ♂ (NMZB 13130). Chipangani River Bridge: 1 subadult (NMZB-UM 28100). Chiredzi [21°03'S 31°40'E]: 2 ♀s (NMZB-UM 23738, 23739). Doddieburn Ranch: 2 ♀s

(NMZB 8035, 8036). Goku(w)e-San(h)yati C. Hunting Area: Feb. 1965, N.H.G. Jacobsen, 1 ♀ 1 metamorph (NMZB-UM 12598). Majinji Pan, S. bank of Nuanetsi River, 3 mi below Malipati Drift: 1 ♀ (NMZB-UM 27388), 1 subadult (NMZB-UM 27389). Mana Pools: 1 ♂ (NMZB-UM 27047). Marhumbini: 1 ♀ (NMZB-UM 17676). Mount Selinda: Dec. 20, 1937, V. Fitzsimons, 2 ♂s (TMP 19202, 19203). Mtoko, 50 km NE of: 1 ♂ (NMZB-NMSR 4908). Mukwasini/ Sabi [River] Confluence, 10.5 km SW of: 1 subadult (NMZB 14184). Nuanetsi: 1 ♂ (NMZB-UM 20238), 2 ♀s (NMZB-UM 20225, 20239). Runde T.T.L. [Tribal Trust Lands]: 1 metamorph (NMZB-UM 26714). Gwanda: Makado, Gwanda: 1 ♂ (NMZB 5711), 1 ♀ (NMZB 5710). Sengwe C.L. [conservation lands?]: Pukupela Dip: 3 ♂s (NMZB 16263, 16264, 16265), 1 subadult (NMZB 16262). **Guruve:** Kadzi River Bridge: 2 subadults (NMZB 15215, 15216). Mururuzi River Bridge: 1 ♂ (NMZB 15128), 1 subadult (NMZB 15127). **Lupane District:** Karna Block [18°34'S 27°23'E]: 1 subadult (NMZB 17644). Lupane, 10 km WNW of: 2 subadults (NMZB 14634, 14635), 1 subadult (NMZB 14721). **Mashonaland West Province: Mana Pools National Park:** Nyakasikana: 1 ♂ (NMZB 7648), 2 ♀s (NMZB 7651, 7653). **Matabeleland North Province:** Igusi [Iguesi/ Igelesi/Igeusi], Matabeleland: G.A. Boulenger, 1 subadult (BMNH 1905.10.18.12). **Hwange District:** Kazuma Depression (east): 1 ♀ (NMZB 9184). Kazuma Depression (west) [18°24'30"S 25°33'E]: 1 subadult (NMZB 9020). Kazuma Forest Land: 1 ♀ (NMZB 9287). Kazungula: 2 ♀s (NMZB-UM 1914, 1917). **Hwange (Wankie) National Park (HNP):** HNP, Limpandi Dam: 1 ♀ (NMZB 13406). HNP, Ngweshla Pan: 1 metamorph (NMZB 11897). **Victoria Province: Gona-re-zhou Game Reserve:** Sazale Pan: 1 ♂ (NMZB-UM 12339).

***Pyxicephalus obbianus* Calabrezi, 1927**

Holotype: SOMALIA: Dolobscìò [05°35'N 48°05'E]: 1924, G. Stefanini & G. Puccioni Expedition [of MZUF], 1 ♂ (MZUF 302 [M 4718]).

Paratype: SOMALIA: Stag[n]gno di Dolobiscìò (zona di Òbbia): 1923, G. Stefanini & G. Puccioni Expedition [of MZUF], 1 ♂ (MZUF 10376 [4718]) [Listed by MZUF as a paralectotype].

Additional Material Examined: SOMALIA: "British Somaliland": W.A. MacFayden, 1 subadult, 6 metamorphs, 4 tadpoles with legs and 10 tadpoles (BMNH 1949.1.3.22–42). El Bur [04°41'N 46°37'E]: Aug. 7, 1959, S.B.S. [Expedition Biological to Somalia of MZUF], 1 ♂ (MZUF 1286 [4894]), skin, partial skeleton and skull; Dec. 5, 1982, S.B.S. [Scientific Expedition of Somalia], 1 subad. (MZUF 14179). Galcàio, ca. 70 km SE of, along track to Òbbia-Galcìào [05°35'N 48°05'E], in pond on side of road: Nov. 3, 1957, G. Scortecci, 13 metamorphs (MZUF 10441–10443, 10445–10447, 10449, 10450, 104552–10456). Hand [08°20'N 46°00'E]: R.H.R. Taylor, 2100 ft, 1 ♂ (BMNH 1976.2194 [211]). Òbbia, ca. 100 km NW of, along track Òbbia to Galcàio: Nov. 1957, 1 ♂ (MZUF 10377).

Pyxicephalus* metamorphs and subadults, indeterminate, either *P. edulis* or *P. adspersus

Material Examined: BOTSWANA: Kwebe Hills, 15 km N of: Feb. 12, 1965, R.N.H. Smithers, 1 metamorph (NMZB-UM *10546). Lothlekane Well, pan 15 km N of: 1 metamorph (NMZB *2800). Mabua Sehubi Pan [Mabuasehube Pan *sensu* Parry]: Feb. 23, 1963, R.C. Bigalke, 3 metamorphs (TMP *34654, *34655, *34656). Maun, 100 mi [166 km] E of: Dec. 10, 1962, R.N.H. Smithers, 1 metamorph (NMZB-UM *4666). Otse, 5 km S of: 1 metamorph (NMZB 8763 [CAS field 5331]). **MOZAMBIQUE: Gaza Province: Massagena District:** Massagena, Save River: Feb. 1964, W.D. Haacke, 1 metamorph (TMP **29539). **Inhambane Province: Vilanculos District:** Muabsa [22°13'54"S 34°46'51"E]: 1 metamorph (NMZB-UM 30849). **Maputo Province: Magude District:** Magude: Oct. 1918, C.J. Swierstra, 3 metamorphs (TMP **6995, **6997, **7003). Magude, 15 km SW: Feb. 1964, R.E. Cole, 1 metamorph (TMP **29597). Mapulunguene [Mapulanguene], 8 km E: Feb. 1964, W.D. Haacke, 1 metamorph (TMP **29610). **Sede District:** Boane [26°02'30"S 32°19'31"E]: Mar. 1964, W.D. Haacke, 3 metamorphs (TMP **29530, **29531, **29532). **Tete Province: Changara District:** Kasumbadeza: Jan. 27, 1949, A. Loveridge, 1 metamorph (TMP 35987). **NAMIBIA:** Namutoni, 120 km N of: May 27, 1937, V. Fitzsimons, 2 metamorphs (TMP 16995, 16996). Ondonga Pan: June 1937, V. Fitzsimons, 3 metamorphs (TMP 17120, 17125, 17126). Oshikango [17°24'S 15°53'E]: Apr. 19, 1970, W.D. Haacke, 2 metamorphs (TMP **38578, **38579). Otjikoto–Nakusib, between: May 22, 1937, V. Fitzsimons, 1 subadult (TMP 16952). **SOUTH AFRICA: Gauteng Province: Pretoria District:** Pretoria: 1 ♂ (TMP **7001) [poor condition]. **KwaZulu-Natal Province: Ngotshe District:** Farm Nooitgedacht 614: Feb. 22, 1984, Peterson, 1 metamorph (TMP 74431). **Limpopo Province: Letaba 2 District:** Griffin Mine, Leydsdorp: Jan. 1915, Van Dam, 1 metamorph (TMP **7014). **Phalaborwa District:** Farm Argyle 46: Jan. 26, 1981, N.H.G. Jacobsen, 1 metamorph (TMP 74427). Farm Ross: Jan. 26, 1981, N.H.G. Jacobsen, 1 metamorph (TMP 74407). **Mpumalanga Province: Standerton District:** Beerlaagte: Mar. 10, 1915, Van Dam, 1 metamorph (TMP *7000). **ZIMBABWE:** Chibuwe, Sabi River: Jan. 6, 1965, D.C.H. Powers, 2 metamorphs (NMZB-UM **7426). Chizwinigwi Settlement, 6 km NSW Sabi School, S.E. lowveld: 1 metamorph (NMZB 14175). Delvillewood Farm, Que Que: 2 metamorphs (NMZB-UM *32789). Kamashoboya [Kamashobody]–Lutope [rivers] confluence: Feb. 1966, N.H.G. Jacobsen, 2 metamorphs (NMZB-UM **12654). Machaniwa [Machinawa] Pan, Marhumbini: 1 metamorph (NMZB-UM **17633). **Guruve District:** Dande Safari Area (East): 1 metamorph (NMZB 15193). **Nuanetsi District:** Neshura, Matibi One T.T.L. [Tribal Trust Land]: Feb. 11, 1971, P. Taylor, 1 metamorph (NMZB-UM **27385). **Mashonaland East Province: Harare District:** Mabelreign, Salisbury [Harare]: Jan. 23, 1965, B.H. Balarin, 1 metamorph (NMZB-UM 7542). **Matabeleland North Province: Bulawayo District:** Cement, Bulawayo [20°06'50"S 28°41'08"E]: 2 metamorphs (NMZB-UM *137). Craigleigh, Bulawayo: 1 metamorph (NMZB 6309). **Hwange District: Hwange (Wankie) National Park (HNP):** HNP, Jalopi River: Mar. 8, 1961, D.G. Broadley, 1 metamorph (NMZB-UM **159); HNP, Robins Camp: 2 metamorphs (NMZB 12892); HNP, Shapi Pan: 3 metamorphs (NMZB-UM 29201); Wankie [Hwange]: Feb. 22, 1932, B. Levy, 1 metamorph (TMP 14378).