A revision of southern African Pyxicephalus Tschudi (Anura : Ranidae)

by

C. R. Parry

(Department of Zoology, University of Witwatersrand, Johannesburg)

SYNOPSIS

The status and variation of Pyxicephalus adspersus Tschudi is examined, the area considered includes Botswana, South Africa, South West Africa, Swaziland, Malawi, Zambia and Zimbabwe. The following forms are recognised: Pyxicephalus adspersus adspersus Tschudi is a large form generally restricted to higher altitudes. It has a temperate transitional distribution. Pyxicephalus adspersus edulis Peters is considered a valid subspecies of adspersus. It has a tropical distribution and is mainly confined to low altitudes. Pyxicephalus adspersus angusticeps ssp.n. is at present known only from material collected at Beira, Mozambique, apart from one adult that is probably from the periphery of its range.

INTRODUCTION

The confusion over the size difference of adspersus and edulis has led many authors to conclude that material described as edulis is juvenile adspersus (Poynton 1964). The lack of a ‘clear taxonomic character’ such as webbing and the variety of colour phases (including the similarity of juveniles of both forms) has compounded the confusion and difficulty in separation. Pyxicephalus adspersus angusticeps appears to differ from adspersus and edulis in both the adult and juvenile phases, and in having the most narrow head. Further material is required from the limits of its range, especially the northern limits, to determine what happens if and when its range meets that of edulis.

MATERIALS AND METHODS

This review is restricted to southern Africa including Angola, Botswana, South Africa, South West Africa, Malawi, Zambia and Zimbabwe. A small amount of extralimital material was examined from Tanzania. The following characters were decided upon and examined from each specimen: presence or absence of an interorbital bar, facial markings on the upper jaw and clarity in relation to the size of the specimen, the coloration of the dorsum and the presence or absence of small spinae (Elias & Shapiro 1957) on the lower dorsum and thighs. Where specimens were of a suitable size, and not distorted in preservation, three measurements were taken: snout–vent length, jaw width at widest point, and skull width above the tympanum.

Under ‘Localities’ for each taxon the museum catalogue numbers are listed for specimens examined, the following abbreviations for institutions being used:

AMA — Albany Museum, Grahamstown, South Africa.
AMN/H — American Museum of Natural History.
CRP/A — Private collection C. R. Parry.¹
DM — Durban Museum, Durban, South Africa.
KM — Kaffrarian Museum, King William’s Town, South Africa.
NKW — Kruger National Park Museum, Skukuza, South Africa.
NM — Natal Museum, Pietermaritzburg, South Africa.
PEM — Port Elizabeth Museum, Humewood, South Africa.
SAM — South African Museum, Cape Town, South Africa.
TM — Transvaal Museum, Pretoria, South Africa.
QVM/A — Queen Victoria Museum, Harare, Zimbabwe.¹
UM — Umtali Museum, Mutare, Zimbabwe.¹
VJW — Collection made by V. J. Wilson, incorporated into Bulawayo Museum Col.

If more than one specimen is catalogued under the same number, the number of specimens is shown in parentheses after the museum catalogue number. The appropriate quarter-degree grid reference is also given in parentheses.

CHARACTER ANALYSIS

Size and Proportions

_Pyxicephalus adspersus edulis_ differs from _adspersus_ in its much smaller size, and narrower head (Table 1). Adults rarely attain a snout–vent length exceeding 120 mm, while _adspersus_ commonly attains a snout–vent length of 140 mm or more. Large _edulis_ are not as robust as adult _adspersus_, most of the largest specimens of _edulis_ also show an introgression of _adspersus_ characters such as reduced mottling and facial markings. _P. a. angusticeps_ differs from _edulis_ and _adspersus_ in having narrower head proportions (Fig. 1, Table 1).

Colour

_P. a. edulis_ is characterised by having a dorsal pattern which may consist of regular large dark blotches against a lighter background, or merely a series of small dark irregular blotches. A clear vertebral stripe is present and a tympanic spot or inverted crescent is a common feature (Fig. 3). The head and facial markings provide another diagnostic feature (Fig. 6). A clear interorbital bar is present and the facial markings are formed from the basic pattern of a pair of inverted ‘Y’s’ extending from below each eye, the anterior ‘Y’ being the most persistent element when markings are obscured. _P. a. edulis_ is highly variable, even in areas where no introgression of _adspersus_ characters occur. Central and southern Mozambique specimens show exceptionally bright markings. A dull brown phase in which the dorsal and facial markings are obscured may be rarely encountered throughout the distribution of _edulis_. This is not a distinct form but a semi-permanent colour phase, as a frog of this type was found to exhibit clear _edulis_ markings after dying in captivity. However a large number of spinae (Elias & Shapiro 1957) on the ventral surface of the thighs and posterior dorsal region

¹ Held at Bulawayo Museum.
Fig. 1. Analysis of head measurements. *Pyxicephalus adspersus adspersus* is represented nearest the axis, *P. a. edulis* is central and *P. a. angusticeps* is farthest from the axes. Single lines represent the range and intercept at the mean. Rectangles represent two standard errors on either side of the mean. Three measurements were taken: (1) snout-vent length (2) skull width above tympanum and (3) jaw width at widest point. The log of the ratio of 1:2 and 1:3 was determined in order to normalise the distribution.

Table 1. Data represented in Fig. 1.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>log 1:2</th>
<th>log 1:3</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. a. adspersus</em></td>
<td>38</td>
<td>( \bar{x} = 0.318 )</td>
<td>( \bar{x} = 0.426 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \sigma = 0.024 )</td>
<td>( \sigma = 0.0314 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>std error 0.004</td>
<td>std error 0.005</td>
</tr>
<tr>
<td><em>P. a. edulis</em></td>
<td>49</td>
<td>( \bar{x} = 0.358 )</td>
<td>( \bar{x} = 0.456 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \sigma = 0.0210 )</td>
<td>( \sigma = 0.0210 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>std error 0.003</td>
<td>std error 0.003</td>
</tr>
<tr>
<td><em>P. a. angusticeps</em></td>
<td>7</td>
<td>( \bar{x} = 0.410 )</td>
<td>( \bar{x} = 0.521 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \sigma = 0.0440 )</td>
<td>( \sigma = 0.0425 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>std error 0.017</td>
<td>std error 0.017</td>
</tr>
</tbody>
</table>

may aid in recognising this phase of *edulis*. The spinae are variable characters within any *edulis* population, but are not present in pure *adspersus* and are reduced in forms showing an introgression of *edulis*.

In regions where introgression is more common due to the two forms not being separated by altitude differences, as in Botswana, it becomes increasingly more difficult to separate the two forms, especially if one is not familiar with the local characteristics of both.

Juvenile *adspersus* material often clearly shows traces of the facial pattern, but this is obscured by light stippling, producing a blurred outline. Care is required, as preservation may enhance the facial pattern. A clear vertebral stripe is present. The bright green newly metamorphosed frog attains a brown hue on the mid-dorsum, the flanks remain green. As size increases to approximately 100 mm the colour becomes uniform green dorsally, a cream to yellow ventrally and bright orange under the armpits. This may change to a dark olive dorsum with small bright yellow spots on the rugose integument and bright yellow feet and ventral surface, when active or distressed, or to a pale yellow ventral surface and completely uniform dull light green dorsum (Fig. 2), when inactive or forming a cocoon (Parry & Cavill 1978). Sometimes if an inactive frog is disturbed a clear regular blotched pattern can be discerned. This is an uncommon ‘mood’ state of the frog and does not last long. It does not appear to be maintained in preservation. The vertebral stripe may be discerned in the adult, especially in the ‘mood’ states described.

*P. a. angusticeps* has a similar facial marking (Fig. 7) with a pair of inverted ‘Y’s’ with light stippling in the juvenile that extends over the whole body. In the adult the dorsum is dark with circular patterning in preservative (Fig. 4). The juveniles are brightly coloured in life (N. H. G. Jacobsen pers. comm.)
SYSTEMATIC ACCOUNT

Pyxicephalus Tschudi


A key to the genus *Pyxicephalus*

1 Clearly mottled or blotched dorsal surface; interorbital bar represented by light cross bar and/or dark interorbital bar posteriorly; series of 2–3 dark marks on upper jaw alternating with light areas, both of which may border the eye .............................................................. 2
   – Dorsal surface uniform; no interorbital bar present; no clear pattern on upper jaw, or if present, blurred by light stippling ............. *P. a. adspersus*

2 Dorsal surface with pattern of round blotches; facial markings clear, but may be covered with faint stippling extending over the whole body; throat with dark marbling (sharply defined in juveniles); marbling generally extends at least to pectoral girdle .............................................................. *P. a. angusticeps*
   – Throat immaculate or with dark spots around edge; sometimes dark patches extending down from articulation of jawbone; no distinct marbling ........... *P. a. edulis*

Pyxicephalus adspersus adspersus Tschudi

Pyxicephalus adspersus Tschudi, 1838, *Clasif. Batr.*, 46, 84: 'Promontorium Bonae Spei'; Boulenger, 1910, 529 (part); Hewitt & Power, 1913, 169 (part); Power, 1927c, 411; Ahl, 1934, 333 (?); Hewitt, 1937a, 90, pl. 22; FitzSimons 1938, 207 (part); Balinsky & Balinsky, 1954, 55; Poynton, 1964, 93 (part); Van Dijk, 1966, 245; 1971, 121; Grobler, 1972, 1; Stevens, 1974, 1. (part ?); Carruthers, 1976, 33, pl. 5. (part); Loveridge, J. 1976, 319; Parry & Cavill, 1978, 55.


*Pyxicephalus adspersus* adspersus Tschudi. Mertens, 1971, 17 (part).

Description: Body robust, generally with several longitudinal folds running down back. Colour of dorsum generally uniform green in adult, faint mottling apparent when in distressed 'mood'. Underside cream to yellow with yellow-orange arm-pits. In juvenile dorsum varies from bright green in newly metamorphosed frogs, to green with brown on the central dorsum and dark spots coinciding with the rugose integument forming a rough series of lateral bands. Vertebral stripe generally present in juveniles. Series of facial markings in juvenile obscured by light stippling over dark marks, often blurring the edges, this feature does not persist into adulthood.
Size: Largest (CRP/A/264 Salisbury, Zimbabwe) 207 mm (snout–vent).

Habitat: Breed in temporary ponds in vleis, disperse, presumably to spend the remainder of the year buried in cocoons (Parry & Caville, 1978).

Distribution: Central and northern Botswana, mainly along the central watershed in Zimbabwe, across the highveld of Transvaal and the Orange Free State and into the northern and eastern Cape Province, throughout South West Africa, except for northern and southern limits.

Localities: BOTSWANA: Gemsbok Pan, Ghanzi dist. (2121DA) TM 14753; Kangyane Pan (2322CD) UM 12959; 70 km W. of Kanye (2423DC) QVM/A/258; Khutse Pan, S.E. Kalahari (2324BC) TM 14750–1; 27 km N. of Kgwebe Hills (2023AC) UM 10546–7(3); 16 km S. of Lethekane Well (2125BC) NMSR/2800; Mabeleapudi, S. Ngamiland (2022DC) TM 14754–5; Mabuaschube Pan (2522AA) TM 34654–6, UM 12960; 166 km E. of Maun (1924DD), UM 4664(3)–5(3)–6; Nata (2026AA) TM 50855; Shorobe (1923DD) UM 20145; Toteng (2022BD) UM 10531; Van Zyl's Cutting (2122AA) TM 14752. SOUTH AFRICA (including Homelands): Allenridge, O.F.S. (2726DA/C) TM 26429–30; Beaufort West, C.P. (3222BC) SAM/18354(3); Beerlaagte, Heidelberg dist., Tvl. (2627DD) TM 7000; Carlton Dordrecht (3127AC) AMA 312/207; Committees (3326BB) AMA 116(7); Dordrecht, C.P. (3127AC) KM 22–26; Grahamstown, C.P. (3326AD) AMA 312/416, 312/6430, 312/8529; Indwe, C.P. (3127AD) PEM 1472/69A; Johannesburg (2628AA) TM 51026; Middelburg, Tvl. (2529CD) AMA 312/218; Pietersburg, Tvl. (2329CD) TM 7012–13; Port Elizabeth, C.P. (3325DC) AMA 117(3); Pretoria, Tvl. (2528CA) TM 6991, 6994, 6996, 7016, 12656, 13652, 14981; Queenstown, C.P. (3126DD) KM 148 (15), NM 5501–5; Sasol mine, O.F.S. (2627DD) NM 2006–7; Vryburg dist., C.P. (2624DD) TM 50666; Wakkerstroom, E. Tvl. (2730AC) TM 11179. SOUTH WEST AFRICA: Grunewald, Etosha Park (1915BA) TM 28186; Maltahohe (2416DD) TM 17581; Muyako, Lake Liambezi, Caprivi Strip (1724CD) TM 46359, 46361–2; Okahandja (2116DD) SAM 19807(2); 50 km W. of Outjo (2016AA) TM 28187–91; Otjiwarongo dist. (2017AB) TM 48512–13; Quickborn, Otjiwarongo dist. (2016BB) TM 6993; 15 km S. of Sandfontein (2219BD) TM 37309. ZAMBIA: Mfuwe, E. Province (1331BB) VJM 1248. This specimen was poorly preserved and the identification is in doubt. It has been excluded from the discussion. ZIMBABWE: Bulawayo (2028BB) NMSR/2735–42, Cement UM 137; 16 km S.S.E. Chakari (1829BB) AJL 1154–7; Heany (2028BB) NMSR/5142; Hunyani (1730AC) TM 6989; Matopos (2028AD) TM 22950; Mt. Hampden (1730DB) NMSR/1794; Ngamo Pans (1927AB) UM 20328; Que Que (1829DC, 1829DD) AJL 918–22, UM 32789(2); Rasape (Manda) (1832CA) UM 22131; Saffron Walden, Salisbury. (1730DD) NMSR 4450; Salisbury (1731CA, 1731CC) AJL 108, 405, 415, 426–30, 699, 780–1, UM 2629(3), 2846–7, CRP/A/78–9, 262–4; 23,5 km W. of Salisbury (1720DD) AJL 900.

*Pyxicephalus adspersus edulis* Peters

Pyxicephalus adspersus Tschudi. Boulenger, 1910, 528 (part); Hewitt & Power, 1913, 169 (part); Ahl, 1934, 333 (part ?); FitzSimons, 1938, 207 (part); 1939, 40; Pienaar, 1963, 80; Poynton, 1964, 93 (part); Stevens, 1974 I (part ?); Carruthers, 1976, 33, fig. 8 (part); Pienaar et al., 1976, 32, figs 11, 12.

Rana adspersa (Duméril & Bibron). Boulenger, 1908, 222; Barbour & Loveridge, 1929, 200 (?). Loveridge, 1933, 359.

Rana adspersa (Tschudi). Parker, 1931, 897; Mertens, 1971, 17 (part ?).

Rana edulis (Peters). Loveridge, 1936, 408; 1942, 419.


Rana adspersa adspersa (Tschudi). Mertens, 1955, (part ?).


Pyxicephalus adspersus edulis Peters. Gans et al., 1965, 18 (?).

Description: Body robust, but not as heavily built as *adspersus*. Rugose integument highly variable, markings tending not to coincide with ridges. Dorsum generally with olive green markings on pale yellow to cream background, varying from bright contrasting markings to more subdued pattern, depending on locality. A uniform brown phase may also be encountered. Interorbital bar present, vertebral stripe present. Clear facial pattern. Spinae may be present on lower dorsum and thighs, sometimes extending over most of dorsal surface.

Size: Largest (TM 39321—Katima Mulilo, E. Caprivi Strip) 174 mm (snout-vent), female showing clear signs of *adspersus* introgression, next largest 160 mm (TM 17140 Itota Dune, Ovamboland, S.W.A.) a male. This form generally does not exceed 100 mm, gravid females around 80–85 mm noted.

Habitat: Although found in areas where vleis do not occur, presumably they utilise other temporary ponds to breed in. No data is available to confirm whether they have a ‘seasonal’ appearance similar to *adspersus*, but as several *edulis* (one from Zululand region, three from Zimbabwe) were induced to form cocoons, it is probable that they also remain buried for most of the year.

Distribution. Essentially a tropical form (Poynton 1964), widespread throughout Mozambique, extending along the Shiré and Zambezi valleys into Malawi and Zambia, widespread in the lowveld in Zimbabwe continuing into Botswana and across to South West Africa. Extends west up the Limpopo River into Zimbabwe and Botswana and into the Transvaal lowveld, reaches south into Zululand. Specimens also examined from Tanzania.

Localities: ANGOLA. 23 km N.W. Pereira d'Eca, Racadas. (1715BB) TM 40070–2. BOTSWANA: Lake Xau (2124BC) UM 7482; Between Francis-town and Plumtree (2027DA) NMSR 2799; 66 km N.W. of Francis-town (2027CC) UM 12958; Pan 53 km W. of Kanye (2322CD) UM 5663; Khunwane borehole, Kwenengolong (2324DA) TM 41456; Mochudi (2426AC) SAM 13637(3), 14019; Nata (1925CD) UM 8957, 8 km S. of Nata (1926DC) UM 7476–7, 7481, N.E. of Nata (2026AA) UM 16154; Metsimaclaba River (2425DB) TM 14749; Nata River delta, Makgadikgadi Pan (2026AC) TM 14756; 66 km N.N.W. of Serowe (2126CD) UM 14765–6. MALAWI: Lilongwe (1333DD) UM 24939; Mchenga, Lake Chilwa (1535BC) UM 26040–1. MOZAMBIQUE: Boane (2632AB) TM 29530–3; Grudja (1934CC) UM 9262; Jorge (1933DD) UM 27574 (3); Kasumbadedza (1633BA) TM 35987; Lamego (1934AD) UM 31082–4, 26244–7; Magude (2532BA) UM 6995, 6997, 6999, 7003, 15 km S.W. of Magude TM 29597; 8 km E. of Mapulanguene (2432AC)
TM 29610; Massangena (2132DB) TM 29283, TM 29539; Matchova (2233CA) UM 28850; Matundo (1633BA) UM 4419; Tete (1633BA) NM 1994–8; Vila Fontes (1735AD) UM 19422; 15 km S.E. of Vila France do Save (2134BA) UM 28455–6; Xiluvo (1934AA) UM 26311–16. SOUTH AFRICA (including Homelands): Dakamila (2321AD) NKW 359; Dublin farm on Olifants River, E. Tvl. (2430BC) TM 12834; Ellisras (2327DA) TM 44453; Griffon mine, Leydsdorp (2330CD) TM 6990, 7004, 7010–11, 7014; Hluhluwe Station, Zululand (2832AA) NM 1504–6; Klopperfontein Dam (2231CA) NKW 98; Kruger Nat. Park, Beacon 7 E. Boundary (2231CD) NKW 358; Makowe, Zululand (2732CC) DM 403; Malonga (2231DB) NKW 360; Manaba Station, Zululand (2732AD) TM 13761; Maputa, Zululand (2632DC) NM 6044(3); Mariepskop slopes, E. Tvl. (2430DB) NM 1415–16; Masambela picket (2231CD) NKW 357; Nkala stream, Ngombo (1525DD) UM 19889, 19892; Sayiri Court, E. Province (1332CD) VlW 859–61. ZIMBABWE: Binga (1727CB) NMSR 3848; Chewore–Zambezi confluence (1529DB) UM 5676; Chiredzi (2131BA) UM 23738–9; 25655, 27386; Chitza, Sabi-Lundi confluence (2132AD) UM 18599; Gatooma (1829BD) AJL 1174; Gokwe-Sanyati C.H.A. (1728BD) UM 12598(2); Jalopi River, Wankie (1826BC) UM 159; Kamashobody–Lutope confl. (1828AA) UM 12654(3); Kazuma Pan, Wankie (1825BC) UM 26995; Kazungula (1725CD) UM 1914–15, 1917–18; Malaguwe Pan, Gonarezhou (2131DB) UM 12341(3); Mana Pools (1529CB) UM 27047–8; Majinji Pan (2231AB) OVM/A/6–10, 18, UM 27387–9; Marumbini (2132AD) UM 17675–7; Machinawa Pan (2132AD) UM 17633(2); Mount Selinda (2032BC) TM 19202–3; Msoro, Mtoko (1632DC) NMSR 4789; Mukumbura (1631BA) CRP/A/237; Neshuru, Matibi T.T.L. (2030DC) UM 27385; Nuanetsi (2130BC) UM 20225–6; Nyamandhlovu Pan, Wankie (1826DD)
Pyxicephalus adspersus angusticeps ssp. n.

Pyxicephalus adspersus Tschudi. Poynton, 1964, 93 (part).


Paratypes: One adult NM 1993 and two juveniles NM 1990–1 with the same data as the holotype. Twelve juveniles UM 6451(2), 7516(5), 19774(4), 23374 deposited in the Umtali Museum.

Diagnosis: Snout tending to be more elongate than adspersus and edulis (Table 1), colour tending to be dark with circular markings on dorsum. Juvenile throat with distinctive marmorate pattern, well defined and reaching to or beyond pectoral girdle (Fig. 5). Facial markings tending to be obscured by light stippling that may extend over whole body. Brightly coloured in life. (N. H. G. Jackobsen pers. comm.)

Description of Holotype (NM 1992)

Adult male. Snout–vent length (projected) 76 mm. Interorbital distance sub-equal to internarial distance.

Dorsum with slight rugose integument. Lateral small warty protuberances present. Dorsum evenly dark. Posterior surface of tibia shows signs of small white-tipped spinae. Enlarged spinae present in vent region. Metatarsal tubercle well developed. Sole very fleshy. Webbing leaving the following phalanges free: I–1; II–1,5; IIe–1; III–2,4; IIIe–2(1); 1,7(R); IV–3; IVe–3; V–1,7. Subarticular tubercle present in the following toes: I–0; II–1; III–3; IV–3; V–2. Fingers blunt
and rounded, second, fourth and first subequal, first reaching to articulation of second phalange of third finger.

Throat with lateral dark blurred patches. Transverse hour-glass marking across pectoral girdle extending on to arms but not joined centrally. Ventral surface slightly maculate with darkening in groin and vent region.

Vertebral stripe faint originating on snout with maximum width in interorbital zone. Not distinct in posterior region. Inverted light ‘V’ originating on anterior edge of lower eyelid, one branch extending forward below nares to end as a faint highlighted mark in upper jaw, other extending downward ending with a similar faint highlight. Light mark originating below eye extending downwards, with posterior slant to jaw. Further light band extending from posterior corner of eye, slanted posteriorly downward, abutting on margin of tympanum to jaw. Upper jaw with light edge. Band extends posteriorly on to maxilla and then downwards with a further downward branch across the corner of mouth extending into throat blurring. Cutaneous gland situated posteriorly on lower third of thigh partly visible below tibia when leg is folded into normal position but foot extended. Very faintly marked with light area.


ZOOGEOGRAPHY

The terms referred to here are those used by Poynton (1964), and reference is made to his map of the zoogeographic distribution of southern African amphibia.

Pyxicephalus adspersus adspersus is essentially a transitional form with the greater part of its range being bounded by the 13 °C mean July isotherms. P. a. edulis in the north east has a tropical distribution with its southern range limit on the east, corresponding to the 18 °C mean July isotherm. It has reached beyond into the lowveld in Zimbabwe and the Transvaal, and across into Botswana and South West Africa. The form angusticeps was probably isolated from the western
populations by the Zambezi River's old course which reached the sea south of Beira. Thus it is expected that the range of angusticeps will include the sector from Beira north to the Zambezi and west to the Urema trough.

ACKNOWLEDGEMENTS

I wish to thank Dr D. G. Broadley for initially suggesting this study and his continued assistance and encouragement, and for reading the manuscript. Dr J. C. Poynton also offered invaluable advice and read the manuscript. Mr J. Akester kindly photographed the specimens and Miss W. Maier reproduced the illustrations. The assistance of the Directors and Curators of the Institutions listed is gratefully acknowledged for the loan of the specimens.

REFERENCES


HEWITT, J. 1911. A key to the species of the South African Batrachia together with some notes on the specific characters and a synopsis of the little known facts of their distribution. Rec. Albany Mus. 2: 189-228.


Date received: 18 September 1981