

## A new species of the *Acanthocercus atricollis* complex (Squamata: Agamidae) from Zambia

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**Abstract.** In the course of working on a taxonomic revision of the *Acanthocercus atricollis* complex, we discovered a population from the Luangwa and Zambezi valleys in Zambia and adjacent Malawi that is morphologically and genetically distinct from all described taxa of this complex. This population is described as a new species on the basis of morphological characters, including indistinct transverse rows of enlarged scales on the body, a large black patch on the shoulders, and a different pholidosis. It is morphologically similar to *A. a. gregorii* and *A. a. loveridgei*, but seems to be more closely related to the former.

Key words. Squamata, Agamidae, *Acanthocercus atricollis*, new species, Africa, Zambia, Malawi, Zambezi Valley, Luangwa Valley.

### Introduction

The genus *Acanthocercus* FITZINGER, 1843 is widely distributed from the southwestern corner of the Arabian Peninsula and the Horn of Africa to southern Africa. However, only a single species ranges outside Arabia and the Horn of Africa. *Acanthocercus atricollis* (SMITH, 1849) is known to occur from Ethiopia to the eastern and northern parts of South Africa. KLAUSEWITZ (1957) reviewed the species and recognized six subspecies: *A. a. atricollis* from southern Africa; *A. a. gregorii* (GÜNTHER, 1894) from coastal Kenya and Tanzania; *A. a. kiwuensis* (KLAUSEWITZ, 1957) from the area around Lake Kivu; *A. a. loveridgei* (KLAUSEWITZ, 1957) from Tanzania and northern Zambia; *A. a. minuta* (KLAUSEWITZ, 1957) from Ethiopia and Kenya; and *A. a. ugandaensis* (KLAUSEWITZ, 1957) from Uganda. However, KLAUSEWITZ (1957) failed to provide clear diagnoses, and his descriptions were published in German. Therefore, his taxonomic differentiations were often overlooked (e.g., SPAWLS et al. 2002). No other taxonomic revisions were attempted after the work of KLAUSEWITZ (1957), although some authors (e.g., LARGEN & SPAWLS 2010) recognized morphological differences between populations.

Ecologically, *A. atricollis* is a well-known species. It lives in structured colonies with one dominant male, several females and juveniles. Although generally known as diurnal, *A. atricollis* has been noted to show nocturnal activity in some situations (REANEY & WHITING 2003). Its

diet is dominated by ants and beetles, but other arthropods also play an important role (REANEY & WHITING 2002). WHITING et al. (2009) identified *A. a. atricollis* as an anthropophilic species, with higher population densities in villages than in adjacent disturbed communal rangelands or a nearby undisturbed protected area. Our observations and collection localities for *A. a. aff. atricollis*, *A. a. kiwuensis* and *A. a. ugandaensis* are consistent with the latter viewpoint.

The *Acanthocercus atricollis* group is very important in the context of a zoogeographic review of the so-called “arid corridor” that links northeastern and southwestern Africa. Zoogeographic reviews should be based on a solid taxonomy and known relations of the studied species. Therefore, the phylogenetic relationships of the complex were examined by the authors (WAGNER et al., unpubl. data), and will be published separately. This review revealed a cryptic group of related species with very similar morphology. During this review, two new species from Zambia and the Democratic Republic of the Congo were discovered. Herein, we describe the first of these new agamid species.

### Material and methods

The type material of the new species is deposited in the Zoologisches Forschungsmuseum A. Koenig (ZFMK), Bonn, and the Museum für Naturkunde, Berlin (ZMB).

It was compared with material (including types) of all *Acanthocercus atricollis* subspecies and *A. cyanogaster* from the following collections: BMNH, The Natural History Museum, London, United Kingdom; CAS, California Academy of Sciences, San Francisco, USA; MHNG, Muséum d'histoire naturelle de la Ville de Genève, Geneva, Switzerland; NMZB, Natural History Museum of Zimbabwe, Bulawayo; PEM, Bayworld (formerly Port Elizabeth Museum), South Africa; SMF, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany; UTEP, University of El Paso, Texas, USA; ZFMK, Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; ZMB, Museum für Naturkunde (formerly Zoologisches Museum Berlin), Berlin, Germany; ZSM, Zoologische Staatssammlung München, Germany.

Measurements were taken with a digital calliper under a dissecting microscope to the nearest 0.1 mm. Measurements and scale counts are consistent with KLAUSEWITZ (1957). Molecular data were collected to examine sequence variation between the new species and its closest relatives, but will be published separately (WAGNER et al., unpubl. data). The following measurements and scale counts were partly used to compare the different taxa: Snout-vent length (SVL) from tip of snout to cloaca; tail length (TL) from cloaca to tip of tail; head length (HL) from posterior end of jaw to tip of snout; head height (HH) at the highest part of head; head width (HW) at the widest part of head. Dorsal scales (D) were counted at the vertebral region from midpoint of pectoral region to midpoint of pelvic region; ventral scales (V) from midpoint of pectoral region to precloacal pores; scale rows around the body (SaM) were counted at midbody. Precloacal pores were only counted in males and maximal counts are presented here. In some cases, it was not possible to conduct scale counts because specimens were distorted or eviscerated. These specimens were used for measurements only. For material examined, see Appendix 1.

### Description of a new species

#### *Acanthocercus branchi* sp. n.

Holotype: ZFMK 88682, adult male, collected in dense Miombo woodland close to the Zambian Wildlife Authority (ZAWA) head office Chipata (approximate coordinates: -13.6053, 32.6092), Eastern Province, Zambia, by PHILIPP WAGNER on 7 September 2005.

Paratypes: ZFMK 88683, subadult male, collected opposite Manda Hill Shopping Centre (Great East Road) on a tree close to the main road in Lusaka, Lusaka Province, Zambia by PHILIPP WAGNER on 10 July 2005. ZMB 76264, adult male, collected in Lilongwe, Lilongwe District, Central Region, Malawi by VINCENZO MERCURIO on 4 November 2007. ZMB 76267, adult male, collected in the Chongoni Forest Reserve, Dedza District, Central Region, Malawi by VINCENZO MERCURIO (without collection date).

Referred specimens (17): ZFMK 88684 (head and anterior portion of body only), subadult male, collected on 23 July 2005 near Makishi Road in Lusaka, Zambia (killed by a domestic cat) by PHILIPP WAGNER. NMZB-UM 4463, "Chakwenga river [Eastern Province, Zambia]" collected by R. B. YEADON in June 1960; NMZB-UM 4622-23, "80 km ENE of Lusaka [Lusaka Province, Zambia]" collected by M. G. JEFFERIES in August 1960; NMZB-UM 4634-35, "30 km W of Katete [Eastern Province, Zambia]" collected by M. G. JEFFERIES in November 1962; NMZB-UM 32631-32, "Katete [Eastern Province, Zambia]" collected by V. J. WILSON on 8 May 1962; NMZB-UM 27143, "Kalikali Dam [Zambia]" collected by V. J. WILSON on 23 April 1962; NMZB-UM 27146-50, "Sayiri court [nr Chipata, Eastern Province, Zambia]" collected by V. J. WILSON on 20 January 1964; NMZB-UM 27151, "Petauke Old Boma [Eastern Province, Zambia]" collected by V. J. WILSON on 8 April 1964; NMZB-UM 27144-45, "[Mdala?] Chikowa [Mangochi district, Southern Region, Malawi]" collected by V. J. WILSON on 26 June 1963.

Description: A medium to large species with a maximum total length in males of 365 mm (155+210 [NMZB-UM 4634], mean 287.3 mm, n = 10), and in females of 257 mm (117+140 mm [NMZB-UM 27148], mean 241.3 mm, n = 4). Snout-vent length in males ranges between 83–155 mm (mean 121.1 mm, n = 10) and in females between 75–125 mm (mean 106 mm, n = 4). Tail short, in males 111–210 mm (mean 166.2 mm, n = 10) and in females 101–165 mm (mean 135.3 mm, n = 4), about 1.3 to 1.4 times longer than SVL (males: STL/SVL: 1.25–1.54, mean 1.37, n = 10; females: TL/SVL: 1.19–1.35, mean 1.28, n = 4).

Head distinctly broad in males, as in other species of the genus. Ear openings about the same size as the eyes, with visible tympanum. Occipital scale lacking, but a parietal shield including a pineal organ present. Nostril pear-shaped, slightly convex and situated below the canthus rostralis. Vertebral crest indistinct. Scales arranged in 103–130 (mean 115.5, n = 4) rows around midbody, and in 67–81 (mean 71.2, n = 4) longitudinal rows along the vertebrae. Matrix scales small, usually smooth and scattered with pale, enlarged and keeled scales. Enlarged scales not organized in clusters, but indistinct transverse rows present between the limbs. Vertebral scales keeled, with a higher density of enlarged scales than on the flanks, sometimes giving an impression of a margin between the vertebral area and flanks. Gular scales flat, smooth, juxtaposed and becoming smaller towards the gular fold. Ventral scales small and smooth, in 79–95 (mean 87.8, n = 4) longitudinal rows. Males usually with two rows of 21–25 (mean 22.8, n = 4) precloacal pores; it is assumed these are lacking in females, as is typical for most agamids.

Diagnosis: Because of the combination of a heterogeneous body scalation and a tail that is segmented in distinct whorls, this new species can be assigned to the genus *Acanthocercus*. The heterogeneous body scalation refers it to the *cyanogaster/atricollis* species group within this genus, and the high den-

sity of enlarged scales and the black patch on the shoulders place it in the *A. atricollis* complex. An *Acanthocercus* with a relatively short tail, and overall very similar in morphology to *A. a. loveridgei* and *A. a. gregorii*. The new species is characterized by a large black patch on the shoulder and a dorsal pattern of small matrix scales intermixed with distinctly paler, enlarged, keeled scales, forming a dotted pattern with indistinct transverse rows in adult males. The vertebral area consists of a mixture of matrix and enlarged scales, with a higher density of enlarged scales than on the flanks, sometimes giving the impression of a margin between these parts of the body. Ventral and gular scales smooth, smaller than the enlarged dorsal scales. Females with smaller and fewer enlarged keeled scales than adult males.

The new species may be distinguished from other taxa in the *A. atricollis* complex by the combination of a large black patch on the shoulders, distinctly enlarged scales on a matrix of smaller scales, and indistinct transverse rows of enlarged scales between the limbs. Specifically, the new species differs from:

(a) *A. a. atricollis* by its slightly smaller average total length, but higher maximum total length in adult males (mean 287.3 [max. 365 mm] versus 300.7 mm [max. 347 mm]), by possessing a large black patch on the shoulders (versus patch not extending to lateral parts and often not discernible in *A. a. atricollis*), the enlarged scales being very distinct from the matrix scales, by having a slightly higher number of scale rows around midbody (mean 115.5 versus 112.6) and a higher number of vertebral scales (mean 71.2 versus 50.5);

(b) *A. a. gregorii* by its larger size in adult males (total length: mean 287.3 versus mean 248.1 mm; even though maxima are similar with 365 mm versus 360 mm), by possessing a large black patch on the shoulders (smaller in *A. a. gregorii*), a lower number of scale rows around midbody (mean 115.5 versus 122), by possessing smooth gular scales versus keeled in *A. a. gregorii*, and a higher number of ventral scale rows (mean 87.8 versus 76.2);

(c) *A. a. kiwuensis* by its smaller total size in males (mean 287.3 versus 304.2 mm), but similar SVL (mean male SVL 121.5 versus 116.1 mm) and a distinctly shorter tail (TL/SVL mean 1.33 versus 1.62), by possessing a large black patch on the shoulders (versus a small black patch that is not visible from above), indistinct transverse rows of enlarged scales (versus enlarged scales arranged irregularly on the flanks, and concentrated along the vertebral line on the upper body), by having smooth gular scales (versus keeled), a higher number of scale rows around midbody (mean 115.5 versus 83.6), a higher number of ventral scale rows (mean 87.8 versus 63.9), and a higher number of vertebral scales (mean 71.2 versus 62.7);

(d) *A. a. loveridgei* by possessing a large black patch on the shoulders (versus a small black patch that is not visible from above), indistinct transverse rows of enlarged scales (versus enlarged scales arranged irregularly, and not concentrated in a specific area), a higher number of vertebral scales (mean 71.2 versus 59.3), and a slightly higher number of ventral scale rows (mean 87.8 versus 85.3);

(e) *A. a. minutus* by its larger size (total length: mean 287.3 versus 268.0 mm), by possessing a large black patch on the shoulders (versus a small black patch that is not visible from above), indistinct transverse rows of enlarged scales (versus enlarged scales irregularly arranged, usually not concentrated in a specific area), a higher number of scale rows around midbody (mean 115.5 versus 109.7), a lower number of vertebral scales (mean 71.2 versus 79.7), and a higher number of ventral scale rows (mean 87.8 versus 73.7);

(f) *A. a. ugandaensis* by its larger SVL (mean 121.1 mm versus 106 mm in spite of the similar total length in males [mean 287.3 in *A. branchi* sp. n. versus 283.1 mm in *A. a. ugandaensis*]) and a distinctly shorter tail (TL/SVL mean 1.33 versus 1.66), by possessing a large black patch on the shoulders (versus a small black patch that is not visible from above), indistinct transverse rows of enlarged scales (versus enlarged scales arranged irregularly on the flanks, and concentrated along the vertebrae on the upper body), by having smooth gular scales (versus keeled), a higher number of scale rows around midbody (mean 115.5 versus 88.4), a higher number of vertebral scales (mean 71.2 versus 60.2), and a higher number of ventral scale rows (mean 87.8 versus 65.7).

Description of the holotype: Adult male; habitus stout, with a large triangular head that is distinct from the body; tail relatively short. Nasal scale flat to faintly convex, smooth and situated slightly below canthus rostralis, pierced by round nostril in posterior part of scale, directed laterally. Scales on anterior, lateral and central parts of head large, scales are abruptly smaller from level of, and behind ear opening, only about one fourth of the size of large head scales; head scales unequal in size, not equally directed, usually smooth, sporadically heavily keeled or with an undulating structure, with free anterior margins and only sporadically with sensory pits. Twelve supralabial scales on both sides, 12 sublabial scales on the left, 10 on the right side; supraocular scales smooth, 9 on either side; parietal shield a drawn-out hexagon; pineal organ small, visible in posterior part of parietal shield. Ear opening large, about same size as eye, margin with a semicircle of 11 spinose mucronate scales; tympanum superficial. Indistinct nuchal crest present, consisting of nine erect scales. Gular scales flat, smooth, juxtaposed and becoming smaller towards gular fold. Dorsal body scales a mix of small and smooth matrix scales, sometimes giving the impression of granular scales, and scattered, pale white-edged, enlarged scales. Large scales keeled, sometimes mucronate or spinose, not arranged in clusters, but rather in four, very indistinct, transverse rows between limbs. Seventy dorsal scales along vertebral column from midpoint of pectoral region to midpoint of pelvic region. Vertebral region covered by a mix of small and large scales, but not forming a pattern distinct from rest of lateral parts of body. Large vertebral scales keeled, rarely some smaller scales feebly keeled. Ventral body scales smooth, slightly imbricate at their posterior margins, in 79 scale rows from midpoint of pectoral

region to preloacal pores. One hundred and three scale rows around midbody. Preloacal scales in two rows, 11 pores in anterior row, 10 in posterior one. Scales on upper side of forelimb unequal in size and strongly keeled, smooth on underside; upper arm scales somewhat larger than largest dorsal body scales, becoming smaller towards underside and manus. Fourth finger longest, digital length decreasing 3-2-5-1, subdigital lamellae keeled and mucronate, 20 under left 4<sup>th</sup> finger. Scales on upper side of hind

limb keeled to smooth, becoming completely smooth on underside; scales on upper thighs unequal in size, and a mix of small and scattered enlarged scales that are as large as the enlarged dorsal body scales. Fourth toe longest, digital length decreasing 3-2-5-1, subdigital lamellae keeled and mucronate, 22 under left 4<sup>th</sup> toe. Tail with whorls of four scale rings in its basal portion, whorls becoming indistinct towards tip, caudal scales keeled and mucronate. First third of tail swollen, heavily built and laterally de-



Figure 1. Male holotype of *Acanthocercus branchi* sp. n. (ZFMK 88682) from near Chipata (see text for details), Zambia.

pressed, scales extremely large and strong, feebly to heavily keeled, much larger than head plates or enlarged body scales. Tail much thinner and slightly depressed in its second third.

Measurements: snout–vent length (SVL) 115.5 mm, tail length (TL) 177.0 mm, head length (HL) 34.0 mm, head width (HW) 26.2 mm, head height (HH) 17.9 mm, left forelimb 53.9 mm, left hind limb 67.4 mm.

After four years of preservation in ethanol (see Fig. 1), head whitish to pale blue from snout to ears, and pale blue from posterior margin of ears to neck. Throat bluish at base and centre, whitish on its margins. Large black patch on

shoulders. Ground colour of dorsum brownish, enlarged scales on upper and lateral parts of body and limbs plain to dirty white. Ventral side of body, limbs and tail dirty whitish. Enlarged scales on upper side of tail base distinctly whitish, usually with a brownish margin. Scales becoming more brownish towards tail tip.

Variation: The preserved adult male holotype and adult male paratype are different from the preserved subadult male paratype in that their enlarged scales are more distinct in size and colouration (cream to dirty white versus brilliant white) from the matrix scales. However, the speci-



Figure 2. (a) Holotype of *Acanthocercus branchi* sp. n. (ZFMK 88682) in life from near Chipata (see text for details), Zambia. (b) Typical habitat of *Acanthocercus branchi* sp. n. near Chipata, Zambia.

mens are similar in other aspects of scalation and body proportions, and both exhibit the described typical characters of the new species. ZFMK 88684 lacks the lower parts of the body because it was recovered from a cat, which had partially eaten it. Therefore, it was not designated as a paratype, but it is useful for comparisons of head and anterior body characteristics.

Colouration in life: Nuptial colouration of adult males unknown. Non-nuptial males with sandy-white ground colour laterally to brownish on upper parts of body, and with a distinct large black patch on shoulders (Fig. 2a). Enlarged body scales pale sandy-whitish, distinct from ground colour. Head and throat dirty whitish. Subadult males likely show the adult female colouration (Fig. 3), similar to other taxa of the complex (e.g., KLAUSEWITZ 1953, 1957, WAGNER et al., unpubl. data): upper parts of head brownish, becoming pale bluish laterally. Upper and lateral parts of body brownish on upper parts, with black patch on shoulders and irregular transverse black lines on flanks. Some enlarged whitish scales form indistinct transverse rows. Ju-

veniles (only known from photographs, Fig. 4) brownish with a black patch on shoulders, sometimes with a pale blue head. Four dark brown, broad transverse bands between limbs, each with a diamond-shaped, whitish patch in the vertebral region, and margins of enlarged scales yellow. Upper and lateral parts of tail with brown and whitish bands. Colouration of females unknown due to the long-term preservation of the only known specimens, but they also possess an obvious large black patch on the shoulders similar to those found in males.

Distribution: The new species is known from localities within the Luangwa (Chipata, Chikowa, Sayiri Court) and Zambezi (Lusaka) valleys in Zambia. In Lusaka, it is known from several localities: Great East Road, Makishi Road, both within the city, and the Pioneer Camp about 25 km outside Lusaka on the road to Malawi, and from about 80 km ENE of Lusaka. It is also known from areas between these two regions (Katete, Petauka). In Malawi, it has been found in Lilongwe, the Chongoni Forest Reserve, southeast of Lilongwe, and Chikowa. Very recently



Figure 3. Subadult male paratype (alive) of *Acanthocercus branchi* sp. n. (ZFMK 88683) from opposite the Manda Hill Shopping Centre, Lusaka, Zambia.

(March 2012) the first author also recognized the species from Ruwa (-17.895359, 31.242528) near Harare, Zimbabwe. A specimen was seen sitting on a stump within the garden of the municipality.

**Habitat and ecology:** This new species is a tree dweller as it is typical for the *A. atricollis* complex (REANEY & WHITING 2003), although not for all subspecies (WAGNER unpubl. data). In Chipata, it was collected in dense Miombo woodland with large trees and a structured canopy. In Lusaka, it was captured on a solitary tree. At both localities, other individuals were also observed, but it was not possible to identify them as males or females. Specimens from Pioneer Camp were observed while climbing on tree trunks.

**Etymology:** This new species is named in honour of our friend and colleague WILLIAM ROY BRANCH, in recogni-

tion of his important contributions to our knowledge of African amphibians and reptiles over several decades, and in commemoration of his nominal retirement as curator of herpetology at the Port Elizabeth Museum (Bayworld).

## Discussion

Referring to sibling species, BICKFORD et al. (2006) defined cryptic species as two or more species that are or have been recognized as a single nominal species, because they are at least superficially morphologically indistinguishable. We follow this definition but suggest that, if the species are differentiated by DNA sequence data, it will often subsequently be possible to find differences in morphology or mating signals. A preliminary morphological and genetic review (WAGNER et al., unpubl. data) of the *A. atricol-*



Figure 4. Two juveniles of *Acanthocercus branchi* sp. n. of unknown sex, both from the Pioneer Camp East of Lusaka, Zambia.

*lis* complex indicated a substantial amount of cryptic diversity, and most of the constituent taxa are known to be full species, rather than subspecies. As mentioned above, the new species is similar in scale composition to two subspecies of *A. atricollis* (*A. a. loveridgei* and *A. a. gregorii*). Therefore, we decided to describe *A. branchi* sp. n. as a full species of the *A. atricollis* complex in anticipation of our pending phylogenetic study and taxonomic revision of the complex.

Many authors have pointed out that the nuptial colouration of adult males in the African agamid genera *Acantho-*

*cercus*, *Agama* and *Trapelus* is useful to identify distinct species (BOULENGER & POWER 1921, KLAUSEWITZ 1953, 1957, WAGNER 2010). Unfortunately, the nuptial colouration of adult males of the new species is unknown and a comparison with the subspecies of *A. atricollis* is therefore not possible. However, the different taxa can be differentiated by their dorsal body “scalation structure”. Indistinct transverse lines of enlarged scales are only obvious in *A. branchi* sp. n. (Fig. 5a), *A. a. gregorii* (Fig. 5c) and sometimes *A. a. loveridgei* (Fig. 5b), but *A. a. gregorii* is distinct by having fewer enlarged scales than the previous taxa. Other taxa,

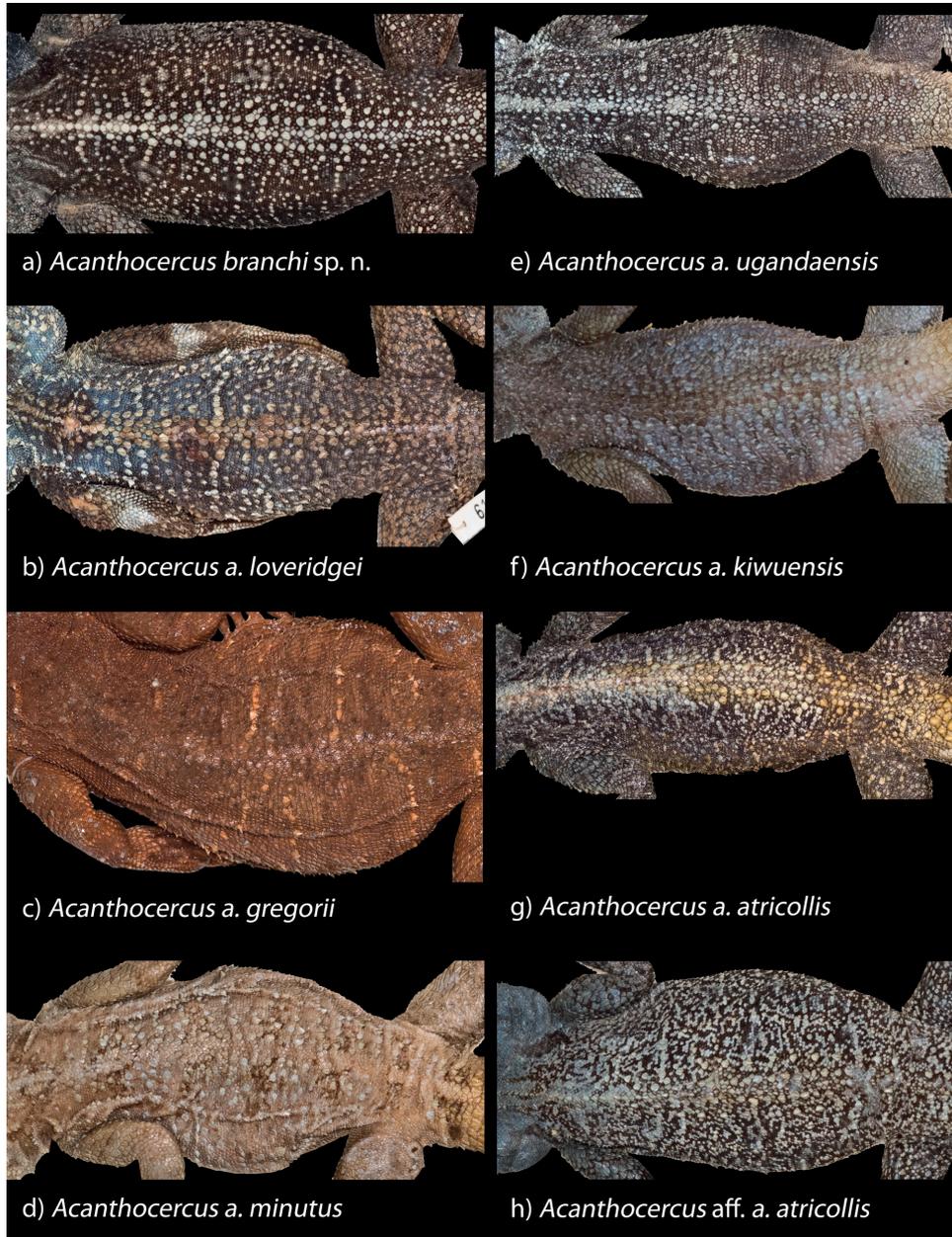


Figure 5. Comparison of dorsal body “scalation structure” of (a) *Acanthocercus branchi* sp. n. (ZMB 76264, paratype); (b) *A. a. loveridgei* (ZFMK 61662); (c) *A. a. gregorii* (MHNG 1467.86); (d) *A. a. minutus* (ZMB 29089); (e) *A. a. ugandaensis* (ZFMK 88792); (f) *A. a. kiwuensis* (ZMB 23906); (g) *A. a. atricollis* (ZFMK 41917); (h) *A. a. aff. atricollis* (ZFMK 88492).

like *A. a. kiwuensis* (Fig. 5f) or *A. a. ugandaensis* (Fig. 5e), have the enlarged scales concentrated in the vertebral area, whereas others, like *A. a. minutus* (Fig. 5d), have them irregularly scattered. *Acanthocercus branchi* sp. n. is distinct from *A. a. gregorii* by having many enlarged scales, and from *A. a. loveridgei* by having enlarged scales of various sizes. Therefore, “scalation structure” appears to be an adequate character to distinguish between taxa of the *A. atricollis* complex, which was also recognized by KLAUSEWITZ (1957) before, although not used diagnostically.

Taxa of the *A. atricollis* complex are known from several localities in Zambia. KLAUSEWITZ (1957) recognized *A. a. loveridgei* from the Bangweulu area and *A. a. atricollis* from northwestern parts of the country. Later, BROADLEY (1971) mentioned the species (as *Agama cyanogaster*) as “a common species throughout Zambia” without mentioning specific localities. From our present knowledge, KLAUSEWITZ (1957) was correct in identifying the Bangweulu population as *A. a. loveridgei*, but the northwestern populations do not represent *A. a. atricollis*, which is restricted to southern Africa. These latter populations will be treated in a review (WAGNER et al., unpubl. data) to be published in the near future, but it may be noted already at this stage that a minimum of three different taxa of the *A. atricollis* complex are represented in Zambia. As far as Malawi is concerned, the situation is poorly known. Populations from northern parts of the country should be classified as *A. a. loveridgei*, whereas those from southern parts are *A. a. atricollis* (Wagner et al., unpubl. data), but *A. branchi* sp. n. is found in-between. Therefore, there are at least three different taxa present in Malawi as well.

*Acanthocercus a. gregorii* is morphologically similar to and probably the closest relative of *A. branchi* sp. n. It is restricted to a small area of coastal Kenya and Tanzania, whereas *A. branchi* sp. n. is only known from valley systems in southern Zambia and two localities in Malawi. A possible speciation scenario is the isolation of arid-adapted species within the Luangwa Valley during climatically wet periods. During this time, the so-called arid corridor (see also POYNTON 1995, WILFERT et al. 2006, WAGNER 2010) between northeastern and southwestern Africa was interrupted by wet forest “bridges” from west to east along the Kenyan mountains and along a line from the Albertine Rift along the current border between Tanzania and Zambia (northern parts of the Luangwa Valley) (WAGNER et al. 2008). Therefore, the corridor or north-south migration route for arid-adapted species was closed, and the wet forest bridges provided a barrier to gene flow, resulting in the isolation of populations of arid-adapted species. This is supported, for instance, by the modern distribution pattern of arid-adapted reptiles (WAGNER 2010) and moreover by the fact that the Luangwa Valley harbours endemic mammal taxa like *Giraffa camelopardalis thornicrofti* (Giraffidae), *Connochaetes taurinus cooksoni* (Bovidae), and *Equus quagga crawshayi* (Equidae), indicating a geographic isolation of the valley in the past. More zoogeographic research is needed to clarify the timing and persistence of forest bridges across the arid corridor. The distribution

ranges of *A. a. gregorii* and *A. branchi* sp. n. lie more or less within this corridor and it is likely that the population was first isolated in the Luangwa Valley, and only later dispersed westward to Lusaka and eastward to Lilongwe in areas not occupied by other taxa of the complex.

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- Acanthocercus a. minuta*. Ethiopia: Dscheffedenza, Shoa (ZMB 29089); Gojam, Blue Nile Canyon (ZFMK 56655); Oromia, Didessa, a Woreda (ZFMK 56656); Shoa Province, Akaki, Modjo (ZFMK 2683–84, 2686–88); Shoa, Descheffedenza (ZMB 29089); Shoa Province, Lake Langanu (ZFMK 55356–357, 55553, 56654); Shoa Province, Nazareth, road to Wonji (ZFMK 16229–230).
- Acanthocercus a. ugandaensis*. Kenya: Kakamega Forest (ZFMK 81952–963). Rwanda: Cyamudongo (ZFMK 55710–717). Uganda: Budongo Forest (ZFMK 88792); Kilembe, Jambo Village (ZFMK 65181); Mount Ruwenzori (ZFMK 63335); Ruwenzori, Fort Portal (ZFMK 63355–359); Ruwenzori, Kasese (ZFMK 63143–145, 63275–281); Ruwenzori, Nyakalengijjo (ZFMK 63236); Ruwenzori, Semliki Forest (ZFMK 64489, 63294–295); Uganda (ZMB 11904).
- Acanthocercus branchi* sp. n. Malawi: Chongoni Forest Reserve (ZMB 76267); Lilongwe (ZMB 76264). Zambia: Chakwenga river (NMZB-UM 4463); Chikowa (NMZB-UM 27144–45); Chipata (ZFMK 88682); Kalikali Dam (NMZB-UM 27143); Katete (NMZB-UM 32631–32); 30 km W of Katete (NMZB-UM 4634–35); Lusaka (ZFMK 88683–684); 80 km ENE of Lusaka (NMZB-UM 4622–23); Petauke Old Boma (NMZB-UM 27151); Sayiri court (NMZB-UM 27146–50).

## Appendix

### Material examined

*Acanthocercus a. atricollis*. Botswana: Gabane (ZFMK 41647); Gaborone (ZFMK 41747–748, 42967–701); Otse (ZFMK 44647). Mozambique: Without detailed locality (ZFMK 41917–918). South Africa: Cape Province [in error] (ZFMK 7423–424); Durban (ZFMK 18394); “Port Natal [=Durban],” (BMNH 1946.8.28.1); Natal (ZFMK 29397); Transvaal, Gaanskuil, Rustenberg (ZFMK 2691–692).

*Acanthocercus a. gregorii*. Kenya: Mkonumbi (BMNH 1946.8.28.67). Tanzania: Serengeti, 6 km N of main Oldovai River, 8 km N Maasai Village, and 32 km N of Olobalol at bottom of N slopes of Ngorogoro foothills, 02°55′24.5″ S, 35°10′41.2″ E, 1595 m (PEM 18899); Serengeti, Naabi Gate (ZFMK 21073–086).

*Acanthocercus a. kiwuensis*. DR Congo: North Kivu, Road just north of Goma, 1160 m, S01.2043, E29.4262 (UTEP 20386); North Kivu, Kisanzi Village near Mt. Teye, Ruwenzori Mts., 1702 m, N00.56818, E29.91780 (UTEP 20364); North Kivu, Virunga NP, Kabasha Escarpment, 1202 m, S00.7453, E29.2227 (UTEP 20387); North Kivu, Virunga NP, Ndjuma lowland forest, 728 m, N00.68335, E29.67143 (UTEP 20363); Orientale, Bunia, 1248 m, N01.33869, E30.15173 (UTEP 20389); Orientale, Epulu (Ituri Forest), 740 m, N01.3985, E28.5711 (UTEP 20390); South Kivu, 100 m west of the shore of Lake Kivu in the village Isale, S01.87489, E28.98971 (UTEP 20391). Rwanda: Kibuye at Lake Kivu (ZFMK 88200); “Kissenji [=Gisenyi]” (ZMB 23906). Uganda: Kampala (ZFMK 68489, 70546–549); Rukungiri Dist., Byumba (CAS 201726–727).

*Acanthocercus a. loveridgei*. Ethiopia: Kaffa Province, Arba Minch (ZFMK 15865–866); Kaffa Province, Kambe (ZFMK 15867); Kaffa Province, Wonji (ZFMK 15868); Shoa Province, Akaki, Lake Haraironi (ZFMK 2685). Kenya: Masai Mara NP (ZFMK 41655); Narok (ZFMK 19161). Rwanda: Kibungo, Nasho (ZFMK 61662);