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Documenting synonymies in *Trioceros ituriensis* (Schmidt, 1929) with remarks on sexual dimorphism in chameleons (Squamata: Chamaeleonidae)

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Abstract: The synonymization of three nominal chameleonid species-group taxa with *Trioceros ituriensis* (Schmidt, 1919) is critically discussed by comparing original texts and figures with the respective type specimens. The first case seems clear since homonymy is involved but in the other two cases, despite recent allocations, the identity of the two nominal species is not unambiguously clear. Morphological differences cast some doubt on the currently accepted synonymy. One diagnostic character of *T. ituriensis*, the hornlessness and smaller size of the males as compared to the females is discussed in respect to other chameleons with a respective sexual dimorphism in contrast to their closest relatives.

Keywords: *Chamaeleon johnstoni affinis* - *Ch. laevigularis* - *Chamaeleo (Trioceros) tremperi* - D.R. Congo - Kenya - Uganda.

INTRODUCTION

The Ituri Forest Chameleon, *Trioceros ituriensis* (Schmidt, 1919), despite its small size is not identical with the “Ituri Dwarf Chameleon” = *Kinyongia adolfifriederici* (Sternfeld, 1912) (cf. Tilbury, 2010). It was first described under a preoccupied name by Sternfeld (1912). It has been given specific rank by e.g. Schmidt (1919), Laurent (1952), Nečas (1994), Klaver & Böhme (1997), Tilbury (2010, 2018), Spawls *et al.* (2018) and Behangana & Hughes (2022). Before, it was regarded as a subspecies of *T. johnstoni* (Boulenger, 1901) e.g. by Loveridge (1942), Hillenius (1963), Mertens (1966), and, by implication, also by Klaver & Böhme, 1986. It was considered to be identical with two subsequently described nominal species, viz. *Chamaeleon laevigularis* Müller, 1926 and *Chamaeleo (Trioceros) tremperi* Nečas, 1994. Tilbury (2010) examined the type specimens of both nominal species, compared them with some “typical” *ituriensis* from the collection of the Museum Koenig (ZFMK) in Bonn and stated that he could not find significant differences. This statement was still the same in the next edition of his chameleon monograph (Tilbury, 2018). It is the aim of this note to make these synonymizations visible and more comprehensive by illustrating and discussing the respective type specimens.

When dealing with the fact that males are smaller than females in *T. ituriensis*, I take also the opportunity to give some thoughts on sexual size dimorphism (SSD) in chameleons.

The institution acronyms used are as follows: AMNH – American Museum of Natural History, New York; ZFMK – Zoologisches Forschungsmuseum A. Koenig, Leibniz Institute for the Analysis of Biodiversity Change (LIB), Bonn; ZMB – Museum für Naturkunde, Leibniz-Institute for Evolutionary and Biodiversity Research, Berlin; ZSM – Zoologische Staatssammlung, München. The authorship of chameleon names mentioned herein can be found in Klaver & Böhme (1997).

THE SYNONYMS

The names *affinis* Sternfeld, 1912 and *ituriensis* Schmidt, 1929

When K.P. Schmidt (1919) described his *Chamaeleon ituriensis* (based on AMNH 11490, type locality Medje, Ituri Forest, D.R. Congo), it was “with considerable hesitation and only tentatively that Sternfeld’s subspecies *affinis* of *C. johnstoni* is referred to the present form”. Schmidt (1919) pointed on differences in body stoutness and thickness of limbs of Sternfeld’s female syntype

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(type locality “Urwald hinter den Randbergen am Nordwestufer des Tanganyika-Sees” = pristine forest behind the edge mountains on the northwestern bank of Lake Tanganyika) as compared with females collected by him (see his fig. 2 on plate XXXI) which is obvious when both figures are compared. He also noted that the canthus rostralis differed in its outline between both females, which is again comprehensible when comparing the two photographs (here combined in Fig. 1), even more distinct in the male holotype (AMNH 11490, Fig. 2). Obviously, Sternfeld’s female type specimen (ZMB 22377) has been re-prepared (by alcohol injection?) because in its current shape it looks even stouter and more voluminous than on Sternfeld’s (1912) original photograph (Fig. 3). According to Schmidt (1919), Sternfeld’s second syntype, a juvenile male from another locality (Irumu-Mavambi Forest, situated in some distance southwest of Lake Tanganyika) fitted his males from Ituri better. It is, however, considered lost today in the ZMB collection (Bauer *et al.*, 2006), thus giving ZMB 22377 a lectotype function. The synonymization of *affinis* Sternfeld, 1912 with *ituriensis* Schmidt, 1919 by the latter author was therefore termed questionable by Bauer *et al.* (2006).

In addition to his reservations synonymizing Sternfeld’s (1912) name *affinis* with his *C. ituriensis*, Schmidt (1919) was well aware of the fact that *C. j. affinis* Sternfeld, 1912 is far antedated by the Ethiopian *C. affinis* Rüppell, 1845 so that *ituriensis* should be the valid name for the eastern Congolese species.

Loveridge (1942), possibly influenced by Sternfeld’s (1912) original specific assignment of his subspecies *affinis*, regarded it again as a subspecies of *Chamaeleon johnstoni* Boulenger, 1901, irrespective of its most obvious and diagnostic characters differentiating it from *johnstoni* and leading to its re-elevation to species rank by Laurent (1952) and de Witte (1965, see also Klaver & Böhme, 1997): (1) much smaller body size, (2) reversed sexual dimorphism in size, (3) lack of rostral and preocular horns in males, (4) a white midventral line, and (5) several rows of distinctly enlarged flat tubercles along the body and 6) rows of conical tubercles on the sides of the throat (Tilbury, 2018).

A first morphology-based phylogenetic approach to chameleons by Klaver & Böhme (1986) based on lung and hemipenial characters lead to the resurrection of the genus-group name *Trioceros* Swainson, 1839 (type species *C. owenii* Gray, 1831) as a subgenus name for the African chameleons which are characterised by a peculiar lung septation pattern and the possession of annulated horns in representatives in each of its subgroups (Klaver & Böhme, 1986). This concept was widely accepted by subsequent authors (e.g. Nečas, 1994; Klaver & Böhme, 1997), meanwhile also as a full genus (Tilbury, 2010, 2018).

Trioceros ituriensis was long regarded as an endemic of the eastern Congo basin west of the Albertine Rift Valley, but has also been recorded from its eastern margin in

Uganda; first from the Kibale Forest by Vonesh (1998) in an unpublished MSc thesis, which became publicly known only 16 years later by Tolley & Plumptre (2014; see also Tilbury, 2018). Six years earlier I had received photographs of a chameleon taken on 7 April 2008 in the Budongo Forest, Uganda showing a female of *T. ituriensis* which remained also unpublished until now. According to the photographer (Katja Rembold, pers. comm.) its body length was about 100 mm, and also the leaves of the bush or tree (*Ficus exasperata*) on which it is sitting have a mean length of 10 cm (Fig. 4A; E. Fischer, pers. comm.). The gular tubercle rows were particularly distinctly visible in this specimen in a threatening colour phase (Fig. 4B). At that time, it was the second record of the species from east of the Albertine Rift Valley. Tolley & Plumptre (2014, see also Spawls *et al.*, 2018) recorded another find from western Uganda, viz. from the Bwamba or Semliki Forest, and very recently also Behangana & Hughes (2022), when summarizing the Ugandan localities of *T. ituriensis*, listed also the Budongo Forest as an *ituriensis* locality.

Considering the relatively small distance between these western Ugandan localities, one might assume that *T. ituriensis* is further distributed on the eastern side of the Albertine Rift Valley than believed so far, at least when suitable, i.e. forested, habitats are available. And in view of the obvious separation of the *ituriensis* populations west and east of the Albertine Rift Valley by this deep trench, a closer morphological and also molecular genetic examination as suggested by Tolley & Plumptre (2014) could dismantle phylogenetic differences: “This population should be investigated in a phylogenetic context” (Tilbury, 2010), as it was true for the geographically comparable case of the *Kinyongia adolfifriderici* complex (Hughes *et al.*, 2017; Tilbury, 2018).

The synonymy list of *Trioceros ituriensis* (Schmidt, 1919) comprises two more species names which have also been regarded as synonyms by some authors with hesitation. In order to check this and to make it traceable, I document these based on their original descriptions and the respective type specimens.

The name *laevigularis* Müller, 1926

Chamaeleo laevigularis Müller, 1926 was based on a single (subadult?) male (ZSM 139/1925) which was said to come from East London, South Africa. In the original description, its body and tail length was given with 48 and 60 mm. Hillenius (1963) re-measured it and gave 55 and 53 mm as the respective values, resulting in the same total length of 108 mm. A new re-measurement for this paper resulted in 53 and 52 mm, i.e. a little bit shorter total length of only 105 mm (M. Franzen, pers. comm.). Hillenius synonymized it with *Chamaeleo johnstoni* Boulenger, 1901, thus rendering the type locality wrong,

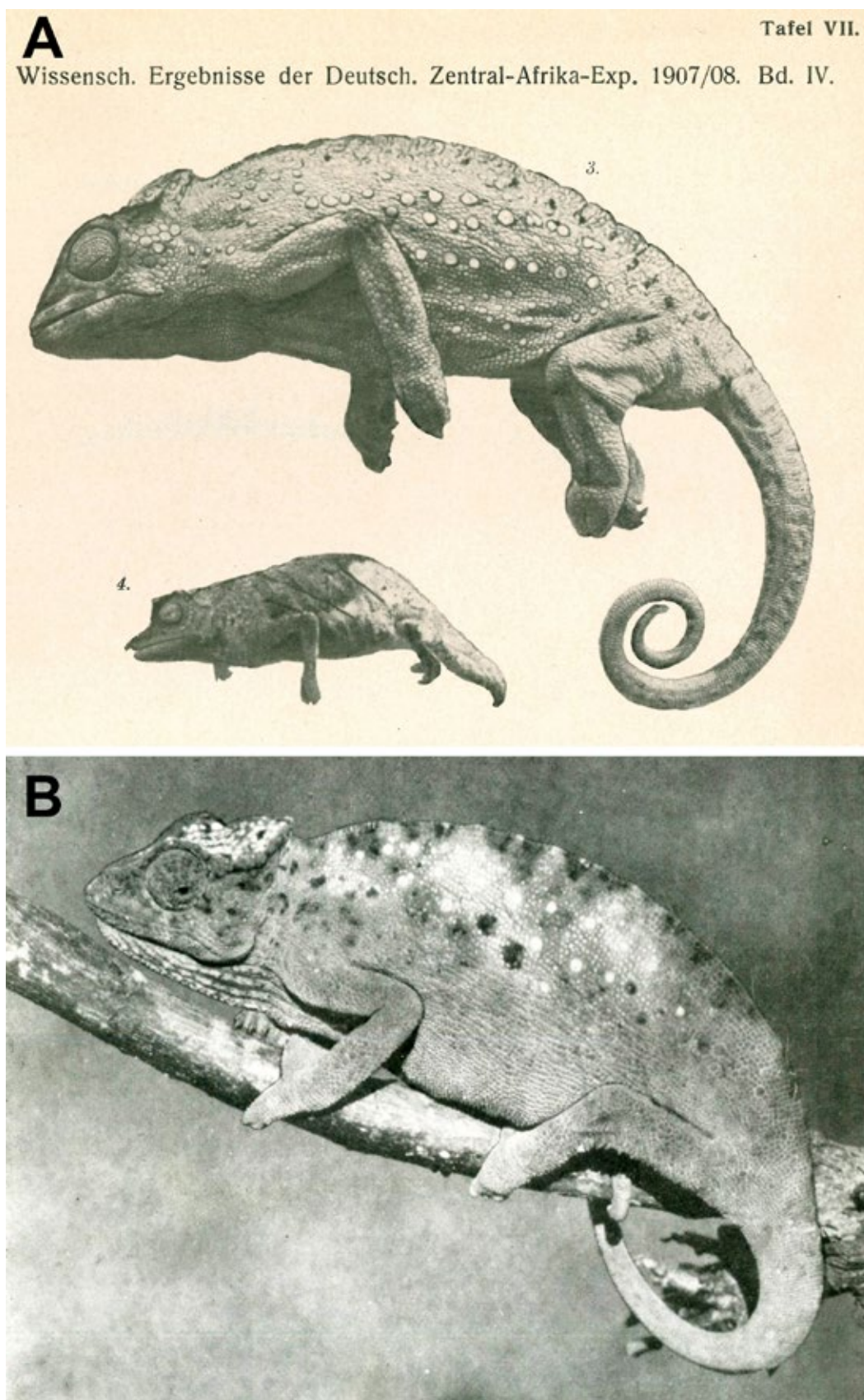


Fig. 1. *Trioceros ituriensis*. (A) Female syntype (lectotype: see text) of *Chamaeleon johnstoni affinis* Sternfeld, 1912, a homonym of *Chamaeleon affinis* Rüppell, 1843 (together with its namesake *Rhampholeon affinis* Steindachner, 1911). Photo by Frank Tillack (ZMB). (B) Female paratype of *Chamaeleon ituriensis* Schmidt, 1919 in life. From Schmidt (1919: 568, pl. XXXI, fig. 2).



Fig. 2. Male holotype of *Chaemeleon ituriensis* Schmidt, 1919, AMNH 11490. (A) lateral, (B) ventral, and (C) gular view. Photo by Lauren Vonnahme (AMNH).



Fig. 3. Female from Fig. 1A in its current shape. (A) lateral view of the entire specimen, (B) detail of head and chest region. Photo by Frank Tillack (ZMB).

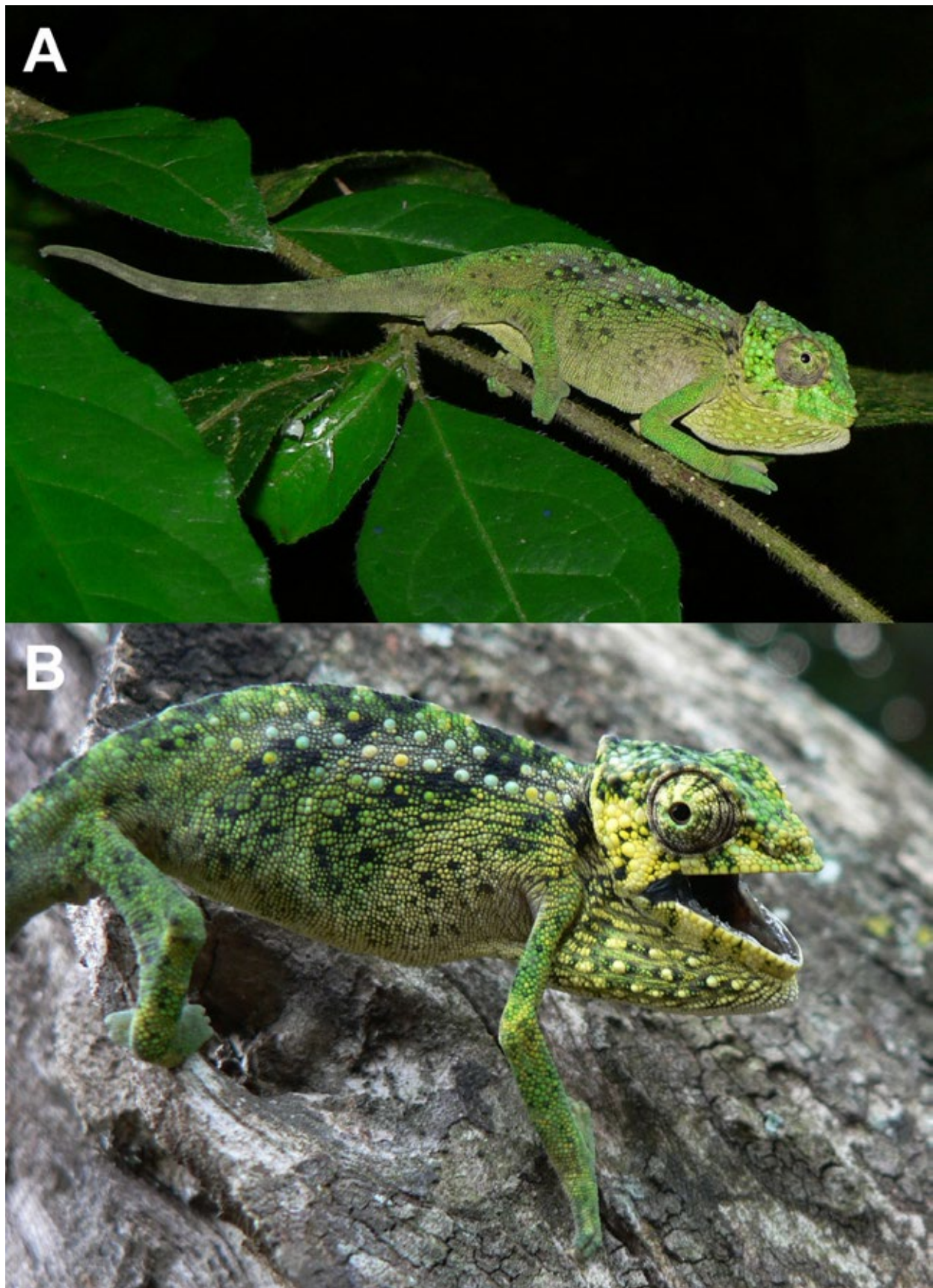


Fig. 4. Living female of *Trioceros ituriensis*. (A) on a branch of *Ficus exasperata*, Budongo Forest, Uganda, (B) the same specimen in threatening posture. Photographs by Katja Rembold, Bern.

because chameleons of the *C. johnstoni* group do not occur in South Africa. However, since it is a small hornless male, he finally suggested that it might be “still another race of hornless *Chamaeleo johnstoni* besides of *ituriensis*, of which the range is not yet known” (Hillenius, 1963).

Hillenius' (1963) synonymization with *C. johnstoni* was accepted by subsequent authors (e.g. Mertens, 1966; Klaver & Böhme, 1997) because at that time also *ituriensis* was still considered to be conspecific with the former. Synonymy with *T. ituriensis* was suggested by Tilbury (2010) who had re-examined the holotype in the Bavarian State Collection (ZSM) after Hillenius and “could find no significant differences from typical *Trioceros ituriensis*”. But because “the rediscovery of *Ch. laevigularis* is still pending, it seems expedient to leave this form as a synonym for *Trioceros ituriensis*”. This means a clear caveat.

The holotype of Müller's (1926) *Ch. laevigatus* is figured here (Fig. 5), but apart from an overall similarity at least one distinct difference in respect to an important key character of *T. ituriensis* can be seen: The gular region lacks any longitudinally arranged enlarged conical tubercles (Fig. 5A) as they are seen in Schmidt's (1919), and Witte's (1965) illustrations and also in the ZFMK specimens (Figs 6, 7) used by Tilbury (2010) for comparison, thus justifying Müller's denomination as *laevigularis* (Latin: smooth-throated). These gular rows of tubercles are typical for *T. ituriensis* and are well visible in the color photos in Tilbury (2010, 2018), Spawls *et al.* (2018), Behangana & Hughes (2022) and – particularly distinct – also in the living Budongo specimen shown in Fig. 4B.

In conclusion, both Hillenius (1963) and Tilbury (2010, 2018) were well advised to treat the synonymization of *Chamaeleo laevigularis* with some precaution.

The name *tremperi* Nečas, 1994

The second name in question is *Chamaeleo (Trioceros) tremperi* Nečas, 1994, a nominal species from western Kenya which was accepted as valid in the checklist by Klaver & Böhme (1997). Nečas (1994) placed it already into close relationships to *T. johnstoni* and *T. ituriensis* and diagnosed it against these two species by its small size, a granular body and head scalation, the shape of the torus parasagittalis (new term by him: a bulge between the parietal and lateral crest) and an enlarged, pointed scale behind the eye on the temple (see Fig. 8).

Chamaeleo (T.) tremperi was synonymized with *T. ituriensis* by Tilbury (2010) who compared the Viennese syntypes with four “typical” specimens from the ZFMK collection and found “no significant or defining characteristics to separate them”. Moreover, he pointed on several subsequent searches around the Eldama Ravine/Maji Mazuri area in Kenya which failed

to find more specimens. He concluded “since *T. tremperi* is essentially identical to *ituriensis*” that the Kenyan provenance would be most likely erroneous and that both names would consequently be synonyms, a view shared by Spawls *et al.* (2018).

There are, however, some problems connected with this conclusion. There are some discrepancies between the holotype description (which lacks any measurements) and the drawn head figure of the holotype in Nečas (1994) paper if compared with the specimen NMW 7880:1 itself (Fig. 8): The diagnostic enlarged, pointed scale behind the eye is much less prominent than in the drawing as are also the gular longitudinal rows of tubercles. Also, the “torus parasagittalis” is hardly discernible. The same is true for the description of longitudinal rows of enlarged flat tubercles along the sides of the body which are hardly distinguishable in the holotype specimen itself.

Very characteristic, in contrast, is the convex, beak-like snout tip which is very different from the rounded snout profile of the comparative ZFMK specimens (see Figs 6, 7). Here, the whole head shape looks very different from the true Congolese *ituriensis* where the profile of the canthus rostralis is clearly concave and the head much less high [see figs 2a, 6, 7 and fig. 23 in Schmidt (1919) and also fig. 40 in de Witte (1965)]. A different outline of the canthus rostralis was already observed by Schmidt (1919) between his Medje specimens and Sternfeld's (1912) type of his *affinis* (see Figs 1, 3). The prominent “torus parasagittalis” is absent in the upper view head drawings in Schmidt (1919) and de Witte (1965) and also in the ZFMK vouchers mentioned and figured above.

A last comment concerns the locality. The type series of *T. tremperi* was collected by Dr Grotte in 1904 and was sent to the Vienna museum together with a juvenile agamid lizard, collected at the same site. This agamid had a pattern of dark and light rings around its tail which is diagnostic for *Agama lionotus*, a species of the *A. agama* complex elevated to species rank by Böhme *et al.* (2005). The locality Eldama Ravine Station, southern Kenya (= Maji Mazuri, 200 km northwest of Nairobi) is situated within the distribution range of *A. lionotus* (Spawls *et al.*, 2018), but far away from the *ituriensis* localities in Uganda or in the D.R. Congo.

My conclusion is therefore that *T. tremperi* might nonetheless be a valid member of the *T. johnstoni-ituriensis* complex, a relict of a former wider distribution of the group, which might be extinct today because a forest patch may have disappeared since 1904, or that it will be rediscovered in the future because it is always much more difficult to get proof for the absence of a species than for its presence. So, the rediscovery of the provenance of this little chameleon might also be pending, as already assumed for the likewise questionable provenance of Müller's (1926) *C. laevigularis* by Tilbury (2010, 2018).

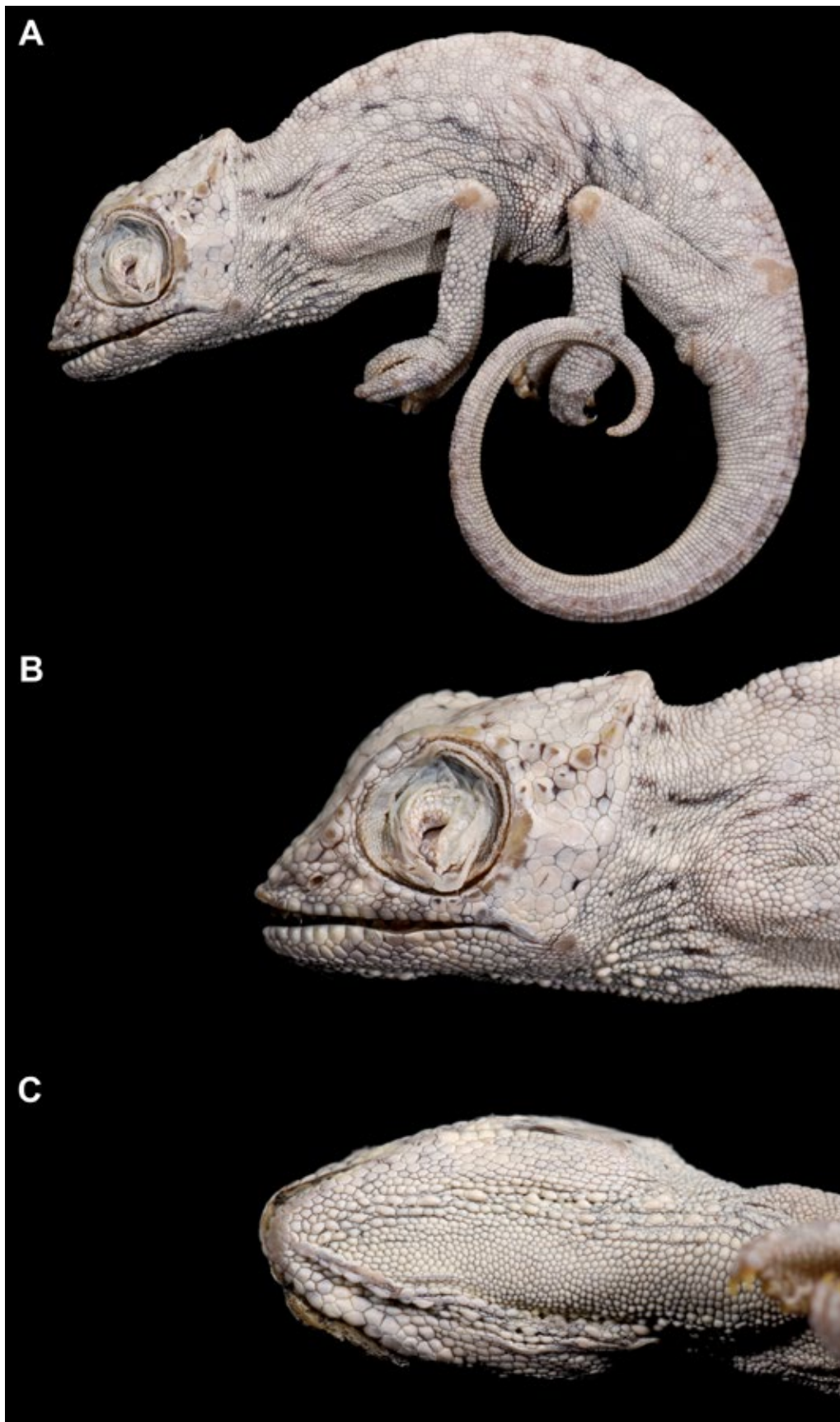


Fig. 5. Holotype of *Chamaeleon laevigularis* Müller, 1926, ZSM 139/1925. (A) lateral view of the entire specimen, (B) head and chest region, (C) gular region viewed from below. Photographs by Michael Franzen.



Fig. 6 A-C. *Trioceros ituriensis*, male from Irangi, DRC (ZFMK 46825), same views as in the foregoing picture. Photographs by Morris Flecks (ZFMK).



Fig. 7 A-C. *T. ituriensis*, female from Irangi, DRC (ZFMK 47573). Photographs by Morris Flecks (ZFMK).

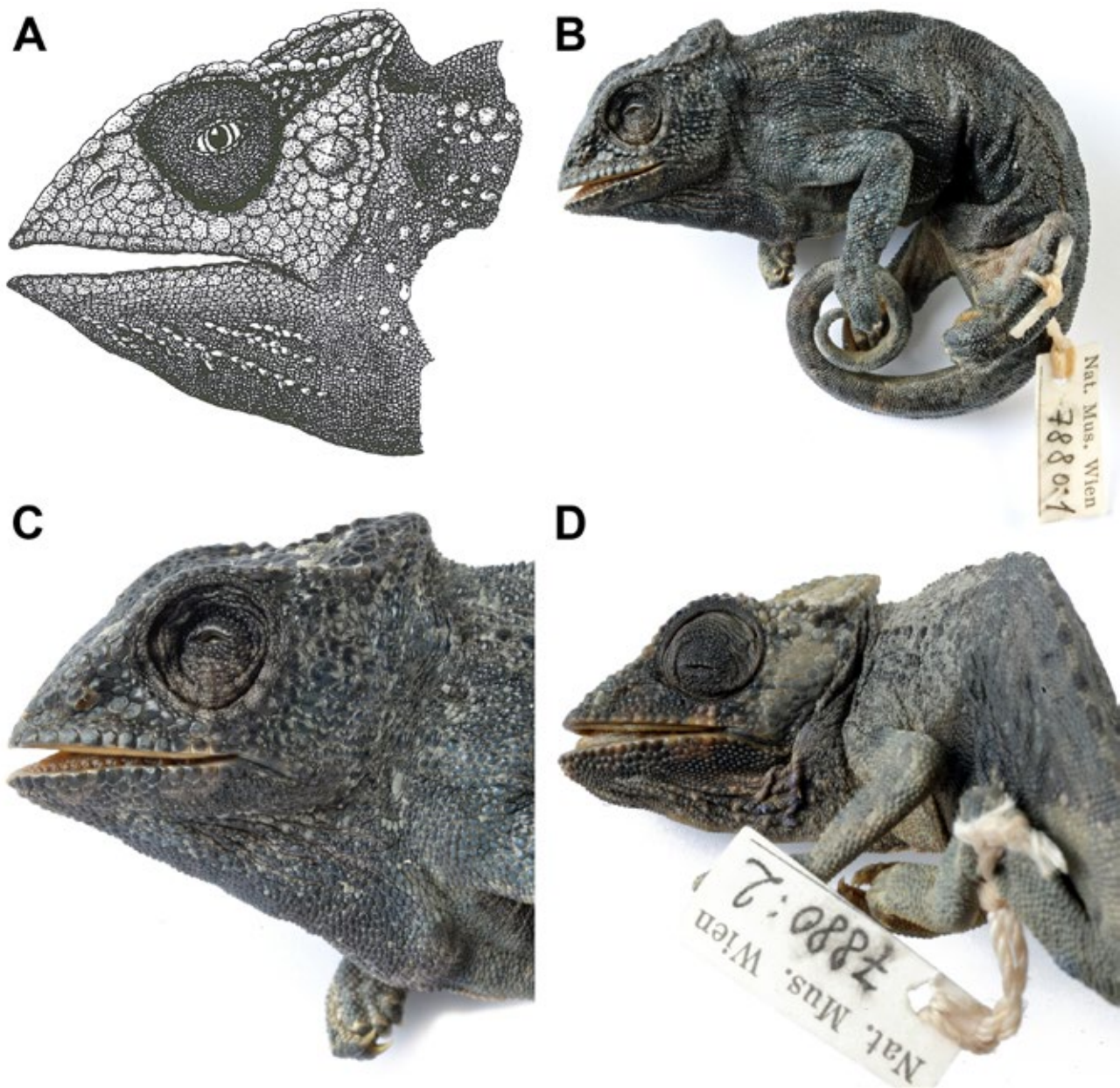


Fig. 8. Holotype of *Chamaeleo (Trioceros) tremperi* Nečas, 1994. (A) Head drawing in the original description, (B and C) lateral views of the specimen itself (NMW 78880:1), (D) male paratype (NMW 7880:2). Photographs by Alice Schumacher and Georg Gassner (NMW).

REMARKS ON SEXUAL DIMORPHISM

Two of the important characters separating *T. ituriensis* from its relative *T. johnstoni* of which it was for long considered as a subspecies (Loveridge, 1942; Hillenius, 1963; Mertens, 1966) are its reversed, female-biased sexual size dimorphism (SSD) and the accompanying lack of cephalic horns in males when compared with the latter. Whether these differences follow a rule in chameleons is discussed here.

In his big monograph on the chameleons of Africa, Tilbury (2010, 2018) mentions the sexually different

head ornaments in the genera *Trioceros*, *Kinyongia* and *Rhampholeon* but restricts his examples for a reversed, i.e., female-biased SSD to the latter genus, together with its likewise ground-dwelling relative *Rieppeleon*. According to Stuart-Fox (2014) this is also true for the Malagasy ground chameleons of the genus *Brookesia*.

In the book on chameleon biology by Tolley & Herrel (2014) one chapter, dealing with behavior and color change (Stuart-Fox, 2014), has a special paragraph on “Sexual dimorphism: Body size and ornamentation” which concerns directly the reversed SSD with males smaller than females in *T. ituriensis* as compared with

its much bigger relative *T. johnstoni* where the males are the distinctly bigger sex. Apart from the size, the most obvious difference is the possession of three cephalic horns in the *T. johnstoni* male which are used as weapons in ritual male-male combats. So the question is whether the obvious head ornamentation is directly correlated with the male-biased SSD.

But also when cephalic horns are not used as weapons in intraspecific male-male combats, they seem, together with other head and body ornaments, to play an important role in intraspecific “pre-combat” communication. Already Rand (1961) observed that among the East African chameleons where the males bear three cephalic (one nasal and two preocular) horns (*T. deremensis*, *T. johnstoni*, *T. jacksoni*, *T. fuelleborni*, *T. werneri*) there is no case of sympatry between them. This argues for a strong selection for character displacement, because the presence vs absence of horns is not mirrored by their systematic relationships, horned and hornless species occurring in the same species groups, one prominent example being the two close relatives *T. johnstoni* and *T. ituriensis*.

The lack or even loss of horns can be compensated by other ornamental structures of head and/or body and tail, such as raised cephalic helmets, enlarged gular crests, or dorsal and caudal fins supported by elongate neurapophyses of the respective vertebrae. Such a system of ornaments in a species group of West African *Trioceros* has been studied in detail by Böhme & Klaver (1981), viz. in the *T. cristatus* group, taxonomically revised by Barej *et al.* (2010). Here it was demonstrated that a two-horned species (*T. montium*), spreading from Mt. Cameroon northwards, entered the distribution range of a four-horned species (*T. quadricornis*) in two steps, first into the Rumpi Hills where the endemic *T. q. eisentrauti* reduced the cephalic horns to a small knob but enlarged its gular crest by developing little scaly skin flaps and also its dorsal and caudal sails. The subsequent dispersal into Mt. Kupe and the Manengouba Mountains forced the endemic *T. q. quadricornis* likewise to reduce the size of its four snout horns and to heighten the dorsal and caudal sails. Only the *T. quadricornis* population living on the mountains of a higher plateau of above 1500 m a.s.l. further north (*T. q. gracilior*) was not affected by an invasion of the concurring *T. montium* so that there was no need to enforce differences of the body shape in terms of character displacement. Consequently, its silhouette resembles that of the – here allopatric – *C. montium* males much more than those of the sympatric and syntopic *T. q. quadricornis* and *T. q. eisentrauti* (Böhme & Klaver, 1981).

In all these species, where the males are adorned with a cephalic and/or body/tail ornamentation, the SSD is strongly male-biased. But in this same species group, the *T. cristatus* group, are also species without such ornaments: *T. camerunensis*, *T. chapini*, *T. feae*, *T. serratus*, *T. w. wiedersheimi*, *T. w. perreti*, and in

most of them is the SSD female-biased, documented by the numerous measurement data available to Klaver & Böhme (1992). According to this paper, a female-biased SSD is also true for *T. cristatus* itself which has a distinctly heightened dorsal sail in both sexes, but no ornaments distinguishing the two sexes. And just as in our initial example of *T. ituriensis* vs. *T. johnstoni*, the hornless species with a weakly expressed SSD are also generally much smaller-sized than their ornament-bearing close relatives.

A well comparable parallel exists also in the *Chamaeleo* species. *C. calypttratus* from the southwestern Arabian peninsula with its exceedingly high parietal crest in males has a strong male-biased SSD whereas in species with low or flat parietal crests the SSD is female-biased, e.g. in the *C. dilepis* group, particularly distinct in *C. roperi*. Intermediate stages are realized in species with moderately to slightly raised parietal crests such as in *C. africanus* and *C. chamaeleon*, the size difference between the sexes is much less obvious.

According to the measurements published in Tilbury (2010, 2018), most *Kinyongia* species with unpaired or paired nasal protuberances in the males have again a marked male-biased SSD, but one of the few species with males lacking such a structure, *K. excubitor*, is data deficient in this respect. In the South African genus *Bradypodion* female-biased SSD has been reported to predominate (Stuart-Fox, 2014). In this genus, it has even been stated that the male bias in body size is correlated with habitat, males in forested biotopes being larger than their females in contrast to those in open habitats (Stuart-Fox & Moussalli, 2007; Stuart-Fox, 2014).

Although I restrict myself here to African chameleons, a similar correlation between cephalic ornamentation and sexually different body size seems to exist also in the two Madagascan chameleon genera *Calumma* and *Furcifer* whose males are often adorned with cephalic ornaments: Here “males tend to be larger than females” (Stuart-Fox, 2014, citing Nečas, 2004). Whereas this is obvious in species like *C. parsonii* and *F. oustaleti* (male-biased SSD), it does not hold true in others such as *F. lateralis* (female-biased), and has still to be worked out in more detail and demonstrated for the majority of the species of these two genera to test the above hypothesis.

A final hypothesis of an aspect of sexual dimorphism in chameleons has postulated even a correlation of male ornamentation with hemipenis structure: It was observed that males of sympatrically (syntopically) occurring chameleon species (*Trioceros quadricornis* and *T. montium*) which differ markedly in their outer appearance would have less divergent hemipenial structures than species whose males are morphologically similar (*Chamaeleo gracilis* and *C. senegalensis*) but – vice versa – have distinct structural hemipenial differences (Ziegler & Böhme, 1997: fig. 140). This hypothesis which was extended also to examples from iguanid lizards, needs further testing.

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