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A new chameleon of the *Trioceros affinis* species complex (Squamata, Chamaeleonidae) from Ethiopia

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Abstract

A new species of chameleon, *Trioceros wolfgangboehmei* **sp. nov.**, inhabiting the northern slopes of the Bale Mountains in Ethiopia, is described. It differs from its Ethiopian congeners by a combination of the following features: presence of a prominent dorsal crest with a low number of enlarged conical scales reaching along the anterior half of the tail as a prominent tail crest, a casque raised above the dorsal crest, heterogeneous body scalation, long canthus parietalis, rugose head scalation, high number of flank scales at midbody and unique hemipenial morphology. Based on morphological characteristics, phylogenetic discordances of previous studies and biogeographical patterns, this new species is assigned to the *Trioceros affinis* (Rüppell, 1845) species complex. An updated comprehensive key to the *Trioceros* found in Ethiopia is provided.

Key Words

Introduction

Chameleons can be considered as one of the most fascinating groups of squamate reptiles, not only due to their exceptional locomotion, behaviour or anatomical adaptations, but also because of their extraordinary species diversity and radiations (Raxworthy et al. 2002; Tolley et al. 2008, 2011). The more than 215 described species of the family Chamaeleonidae are distributed from Africa (including Madagascar), Southern Europe and the Middle East to parts of South Asia (Nečas 2004; Tilbury 2010; Uetz et al. 2020). Apart from the fact that Madagascar is a well-known hotspot of chameleon diversity (Townsend et al. 2009; Gehring et al. 2012; Prötzel et al. 2018), it was hypothesised that this family originated in mainland Africa (Tolley et al. 2013; Čerňanský et al. 2020).

The African continent harbours not only a broad variety of morphologically and ecologically distinct chameleon species, but, in particular, also a high number of montane endemics that are restricted to single mountains or mountain ranges. Examples include the genus *Kinyongia* (Menegon et al. 2002, 2009; Nečas et al. 2009; Hughes et al. 2017), but also several recently described species of the genus *Trioceros* like *T. hanangensis* (Mt. Hanang) from Tanzania (Krause and Böhme 2010) or *T. kinangopensis* (Kinangop Peak, Aberdare Mountains), *T. narraioca* (Mt. Kulal), *T. ntunte* (Mt. Nyiru) and *T. nyirit* (Mtelo Massif) from Kenya (Nečas et al. 2003, 2005; Stipala et al. 2011, 2012).

This Eastern Afromontane region (EAR) exhibits an outstanding level of species richness, endemism and diversification (Mittermeier et al. 2011; Demos et al. 2014; Mairal et al. 2017) and can be also considered an extraordinary biogeographical unit for chameleon diversity (Mariaux and Tilbury 2006; Ceccarelli et al. 2014; Menegon et al. 2015; Hughes et al. 2018). The geographical

uniqueness of this region is shaped by the Great Rift Valley, a geological longitudinal split between the Somalian and Nubian Plate, running nearly 5,000 km through the African Plate from the Red Sea to Mozambique (Chorowicz 2005). These topographical and, consequently, biogeographical patterns are not only present along the tropical East African Great Rift in Tanzania or Kenya, where many endemic *Trioceros* species live. They can also be found in the Ethiopian Highlands, another biodiversity hotspot at the Horn of Africa (Mittermeier et al. 2011).

This northern part of the Great Rift System is located south of the Afar Depression between the Abyssinian and the Harrar Massif within the Ethiopian Highland Plateau. Species differentiation is also common in this part of the Rift and numerous examples of plants, insects and vertebrates have been described in the past (Mairal et al. 2017; Manthey et al. 2017). Particularly, for several mammals and amphibians, e.g. for the Ethiopian wolf (Gottelli et al. 2004), the gelada baboon (Belay and Mori 2006) or anurans (Evans et al. 2011; Freilich et al. 2014, 2016), phylogeographic disjunctions across the Ethiopian Rift were shown.

The Ethiopian Chameleon *Trioceros affinis* (Rüppell, 1845) is a small chameleon species, endemic to the Ethiopian highlands, where it is widely distributed in altitudes higher than 1,600 m above sea level (Nečas 2004; Largen and Spawls 2010). However, its distribution range within the Ethiopian region includes multiple populations isolated in high-altitude forest patches (Ceccarelli et al. 2014). Since some of these populations are particularly isolated and additionally located both west and east of the Ethiopian Rift, the separation by this geological trench might have acted as a long-term dispersal barrier as it also does in other taxa (Mairal et al. 2017). This variation of *T. affinis* populations across the Ethiopian Highlands was already indicated by Neumann (1905) based on differences in the shape of the cranial crests and granularity of the body scalation. Nečas (1994, 2004) stressed the possible existence of various distinct and geographically separated forms currently assigned to *T. affinis* as well. Subsequently, it was shown that considerable genetic divergence between western and eastern populations separated by the Rift is present and that *T. affinis* actually should be referred to as a species complex (Ceccarelli et al. 2014). Despite limited sampling, Ceccarelli et al. (2014) were able to identify two lineages, one west of the Rift around Addis Abeba and another one based on material from Goba and Dinsho, which diverged during the Pliocene (4 mya) and suggested their distinctness at species level.

Rüppell (1845) separated *Trioceros affinis* from *Chamaeleo senegalensis* based on the lack of a gular crest and referred to 'Abyssinia' as a type locality. This reference to an uncertain and broad locality description may not reflect the actual diversity and divergence of this chameleon. Unfortunately, it is not possible to narrow down the type locality based on further or more detailed locality data from other herpetological examinations of Rüppell's material and descriptions (von Heyden 1827). In later treatises by Gray (1864) only additional morphological characteristics of *T. affinis* are described but no

specific remarks concerning its distribution are given. Finally, when assigning lectotype material for this species (Fig. 1), Mertens (1967) also had no evidence for further concrete specifications of the locality likewise and had to refer to the vague and imprecise term 'Abyssinia' again. Considering the shown genetic discordance and possible additional taxonomic assessments, a restriction of the type locality for *T. affinis* might be possible in future.

In the context of northern Eastern Afromontane biodiversity hotspots, the Bale Mountains are an extraordinary biogeographical unit within the Ethiopian Highlands (Hillmann 1988). This extensive south-central Ethiopian high-elevation plateau and massif above 3,000 m is a remarkable centre of endemism: Numerous endemic species are restricted to this area, e.g. several rodents, like *Arvicanthis blicki*, *Dendromus lovati*, *Lophuromys melanonyx* or *Stenocephalemys albocaudata* (Lavrenchenko et al. 1997), frogs, like *Altiphrynoides malcolmi*, *Balebreviceps hillmani*, *Ericabatrachus baleensis* or *Spinophrynoides osgoodi* (Largen and Spawls 2011; Gower et al. 2013), or the Bale Mountains Adder *Bitis harenna* (Gower et al. 2016), and also the endangered Mountain Nyala *Tragelaphus buxtoni* occurs in this area (Refera and Bekele 2004).

Two *Trioceros* species endemic to this area are already known: *T. balebicornutus* (Tilbury 1998) and *T. harennae* (Largen 1995). In specimens assigned to *T. affinis* from the museum collections of the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany (SMF) and the Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK), individuals from northern regions of the Bale Mountains could be identified by the first author. Examination of collection material from this centre of endemism on the one hand, and in biogeographical separation across the Ethiopian Rift from other populations, on the other, revealed the presence of a cryptic species within the *Trioceros affinis* species complex in this region. In the following, we describe it as a new species and provide a re-description of the lectotype material.

Material and methods

Morphological analysis

We examined a total of 66 specimens preserved in 70% ethanol obtained from the museum collections of the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany (**SMF**) and the Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (**ZFMK**).

Scale counts were made using a stereo microscope and morphological measurements were taken with a vernier caliper to the nearest 0.1 mm. Morphometric features for the morphological analyses were selected based on previous taxonomic studies of chameleons (Nečas 1994; Nečas et al. 2005; Barej et al. 2010; Stipala et al. 2011; Greenbaum et al. 2012). In addition to these meristic and quantitative mensural characters, we added three qualitative morphological features in order to account for the presence and characterisation of the prominent, distinctive

patterns of the head, body and dorsal crest scalation. These are the enlarged dorsal crest scales (**EDCS**), heterogeneous body scalation (**HBS**) and rugose head scalation (**RHS**) (detailed explanations provided below). For all specimens examined, we determined sex and measured the following 26 morphometric features (see Table 1 and Suppl. material 2: Individual mensural and meristic measurements): **SVL** – snout-vent length, from the snout tip to the frontal margin of the cloacal fissure; **TaL** – tail-length, from the frontal margin of the cloacal fissure to the tail tip; **TL** – total length as a sum of SVL + TaL; **HL** – head length from superior tip of casque to snout tip; **HW** – head width, measured at widest point just posterior to eyes; **ML** – mouth length, from tip of rostral to jaw commissure; **CH** – casque height, from commissure of jaw to superior tip of casque; **CN** – casque exceeding neck, distance between top of casque and level of the dorsal crest on neck; **CE** – casque-eye length, measured diagonally from posterior margin of orbit to superior tip of casque; **SL** – snout length, from tip of snout to anterior margin of orbit; **ED** – eye diameter, measured horizontally at centre of eye; **IOS** – number of inter-orbital scales, number of scales between supra-orbital crests, including crests scales; **PCL** – length of parietal crest, from superior tip of casque to rostral border of parietal crest; **CC** – cranial crest gap, measured across the crown between raised supraorbital crests at mid-eye; **IL** – inter-limb length, from axillary to inguina; **FLL** – forelimb length, from elbow to wrist; **LHLL** – lower hindlimb length, from knee to heel; **UL** – number of supralabials to posterior margin of orbit; **LL** – infralabials to posterior margin of orbit; **SEH** – number of scales between eye and posterior margin of head; **FSM** – flank scales at midbody; **SDC** – enlarged (more than twice the size of the surrounding dorsolateral scales) and conical scales forming dorsal crest, from head to frontal margin of the cloacal fissure; **SCP** – scales forming parietal crest; **EDCS** – presence of significantly enlarged (more than twice the size of the surrounding dorsolateral scales) conical dorsal crest scales; **HBS** – presence of a prominent heterogeneous body scalation; **RHS** – presence of a rugose head scalation consisting of enlarged (more than 1.2 times the size of the surrounding dorsolateral scales) and slightly conical scales.

The following eight ratios were calculated: **TaL/SVL** – tail length/snout-vent length ratio; **RTL** – relative tail length, tail length/total length ratio; **HW/HL** – head width/head length ratio; **RCH** – relative casque height, CH/ML; **RCN** – relative length of casque exceeding neck, CN/ML; **ED/HW** – eye diameter/head width ratio; **FLL/SVL** – forearm length/snout-vent length ratio; **LHLL/SVL** – lower hindlimb length/snout-vent length ratio.

Furthermore, colouration and patterns were recorded for the preserved individuals examined (see Suppl. material 2: Individual mensural and meristic measurements).

For obtaining information on hemipenial morphology, hemipenes of *Trioceros affinis* (ZFMK 54264) (Fig. 4A–C) and *Trioceros* sp. nov. (ZFMK 84811, holotype) (Fig. 4D–F) were scanned with a Skyscan 1173 μ-computer-tomograph (μ-CT) (Bruker, Billerica / USA)

at the Museum Koenig in Bonn Germany. Hemipenes preparation was modified after Ziegler and Böhme (1997) and Zaher (1999): For each specimen the already everted left hemipenis was removed, submerged in a solution of 3% KOH for around 15 minutes until it became flexible and finally inflated with coloured petroleum jelly. For increasing X-ray absorbance, all samples were stained with iodine for two days following Prötzel et al. (2015). The scans were performed with the following parameters: 30 kV for *Trioceros affinis* and 31 kV for *Trioceros* sp. nov., 133 μA, 1000 ms exposure time for *Trioceros affinis* and 1100 for *Trioceros* sp. nov., 0.3° rotation steps over 360° for *Trioceros affinis* and 0.35° over 360° for *Trioceros* sp. nov., frame averaging of 7 for *Trioceros affinis* and 8 for *Trioceros* sp. nov., random movement of 15, image pixel size 8.1627 μm for *Trioceros affinis* and 6.0343 for *Trioceros* sp. nov. Both scans are deposited in the collection of the Museum Koenig in Bonn and can be downloaded at Morphobank (https://morphobank.org) under project number P3948. The scans were reconstructed with the software NRecon (Bruker, Billerica / USA). Segmentation of the resulting scans was performed with Amira 5.3 (Thermofisher, Waltham / USA). Subsequent volume rendering was done with VG Studio 3.3.4 (Volume Graphics, Heidelberg / Germany). Final images and plates were edited with Adobe CS6 (Adobe, San Jose / USA). Terminology describing hemipenial structures follows Klaver and Böhme (1986) and Prötzel et al. (2015, 2018).

Principal component analysis of morphological data

A principal component analysis (PCA) of chosen mensural and meristic characters (indicated in Table 1; ratios and TL as a cumulative character were not included in the principal component analysis in order to avoid the double use of characters and resulting bias) was conducted using the Ade4 package (Dray and Dufour 2007) for the software R (R Development Core Team 2012). Regression residuals of continuous variables were calculated. The analysis was performed by using mixed variables. We applied the Broken Stick analysis using the "evplot" function from the package "lmom" in R to calculate the number of the meaningful components. Based on both quantitative and categorical variables, the first two principal components (PCs) are visualised in Fig. 5.

We applied a non-parametric MANOVA (Per-MANOVA) on the first 3 principal components (obtained through Broken Stick analysis) using the software package PAST (Hammer et al. 2001) in order to investigate if the specimens from the northern Bale region (Goba and Dinsho) significantly differ from those of other examined populations of *Trioceros affinis* . We tested our meaningful components for normal distribution, however since there are more dependent variables than sampling units included in the analysis, we used the non-parametric MANOVA test (Per-Manova) over the parametric one (Anderson 2001; Kean et al. 2015).

Results

Re-description of the lectotype of *Trioceros affinis* (Rüppell, 1845)

Systematics
Chamaeleonidae Werner, 1902
***Trioceros* Swainson, 1839**

***Trioceros affinis* (Rüppell, 1845)**

Material examined. *Lectotype*: SMF 16402, adult male; origin: 'Abyssinia'; collected by E. Rüppell, 1834; designated by Mertens (1967) (Fig. 1A–C).

Paralectotype: SMF 16403, adult female, same collection data as the lectotype (Fig. 1D–F).

Re-description of the lectotype. The adult male lectotype (SMF 16402) of *Trioceros affinis* is a small-sized and slender chameleon without outstanding ornamentation on the body and head. It has a total length of 148.3 mm (snout-vent length of 68.9 mm and a tail length of 79.4 mm) (Fig. 1A). The tail is slightly longer than the rest of the body (RTL 0.54), heavily thickened at the base due to the presence of hemipenes situated in their pockets. The extremities are thin, the hind legs are slightly wider in diameter but equal in length.

The head is relatively short and blunt (HW/HL 0.52) with a low casque (RCH 0.85) merely exceeding the level of the neck (RCN 0.2). The head surface is covered with slightly enlarged flattened scales, which are more convex and slightly rugose between the canthi rostrales (Fig. 1B, C; see Suppl. material 3: Dorsal head views). The head crests, typical for the genus *Trioceros*, are well developed and ornamented with slightly enlarged, convex scales. The canthus lateralis is well developed in all its parts. It starts with two paramesial scales on each side of the head, builds a margin of the low casque, continues as slightly less expressed supra-ocular crest with a more warty appearance on the canthus rostralis, which conjoin just above the tip of the snout forming a low ridge. The parietal crest consists of 5 scales merely larger than the surrounding ones, building a faint yet sharp medial ridge on the top of the casque. The temporal crest, consisting of 6 enlarged scales is expressed as a lateroventral emargination of a rugose triangular field below the lateral crest just behind the orbit and posterodorsally from it. It reaches the canthus lateralis proprius at about half of its length where it fuses with it. There are 16 upper labials and 16 lower labials on both sides of the head. The eye turrets are covered with a granular homogeneous scalation. The nostril is situated at half distance between the tip of the snout and rostroventral margin of the orbit. The body is covered with subhomogenous scalation, the standard scales are convex, not flat, of sub-circular or sub-oval form and of approximately same size all over the body, tail and extremities, with a tendency to become smaller ventrally towards the midventral line and on the distal part of the tail towards the tail tip. On the flanks, they are ordered in more or less longitudinal or diagonal long fields (running in craniodorsal-caudoventral orientation) that are grouped in rows of two (rarely three) scales. Here no interstitial skin is exposed, with the exception of the gular region, where lateroventrally, an inconspicuous groove can be observed between the slightly enlarged, spindle-shaped scales. There is one irregular, interrupted line of 8 significantly enlarged lenticular scales (the largest ones are about 3 times longer and 2 times wider than the surrounding standard scales). These scales are separated from each other by 3–7 standard scales, oriented longitudinally at about 2/3 of the body height and range from the shoulder to the pelvic region.

Anteriorly, the dorsal crest runs posteriorly of the casque, extending as a continuous well-developed, but low, crest consisting of conical scales of about double width and double height compared to the surrounding standard scales. The dorsal crest reaches in its described form the level of the groin, decreasing in height and formed by smaller subconical scales up to the first 1/4 of the tail with a more inconspicuous appearance. Dorsolaterally on both flanks, the first line of scales bordering the dorsal crest is slightly enlarged.

The gular crest is absent, instead, a rather narrow triangular field scattered with significantly smaller granular scales is present and ranges from the mentum to the arch of the hyoid. The ventral crest consists of a slightly enlarged, midventral line of scales ranging from the shoulder to the frontal margin of the cloacal fissure, which is separated into two parallel rows just along the umbilical scar, and ends at the ventral part of the tail.

Detailed meristic and mensural measurements of the lectotype are given in Table 1 and in the Suppl. material 2: Individual mensural and meristic measurements.

Coloration in preservative. The animal is more or less uniformly greyish beige all over the body without any conspicuous pattern. Only a slight yellow hue can be found midventrally on the body, tail and the soles. The top of the head is slightly brownish. The claws are brownish yellow. Some prominent scales in the head region have a blackish centre, probably as a result of a mechanical bruise.

Variation. The adult gravid female paralectotype (SMF 16403) (Fig. 1D–F) shows only minor morphological differences compared to the male lectotype. It has a lower total length (TL 146.0 mm) and longer tail (RTL 0.50). Also, it has a relatively higher casque (RCH 0.89) (Fig. 1E, F). Both for the upper and lower labials 19 are present. 56 flank scales at midbody are present (vs. 54 in the lectotype) and a slightly lower number of scales forming the dorsal crest can be found (49 vs. 53 in the lectotype). The canthus parietalis is formed by only 3 scales. In contrast to the lectotype, the entire head region is coloured whitish without any brownish hue.

Detailed meristic and mensural measurements of the paralectotype are given in Table 1 and in the Suppl. material 2.

Based on our comparative examination of *T. affinis* specimens from different regions of Ethiopia, the lecto-

Figure 1. The preserved male lectotype (SMF 16402) (**A.**) and female paralectotype (SMF 16403) (**B.**) of *Trioceros affinis* collected by E. Rüppell 1834 and designated by Robert Mertens. Head morphology: Head of the lectotype in left (**C.**) and right (**D.**) view and of the paralectotype in left (**E.**) and right (**F.**) view. Scale bars represent 1 cm. Photos by Morris Flecks.

type material can be clearly assigned to populations west of the Ethiopian Rift. Individuals from south-western Ethiopia showed a lower body length compared with the

lectotype material. Compared to the lectotype material, single individuals from Addis Abeba showed a more heterogeneous scalation on parts of the flanks by having sin-

gle lateral scales that are enlarged more than 1.5 times compared to the surrounding scales. However, this heterogeneous scalation is not as prominent and extensive as in individuals of the northern Bale region. Actually, the latter were clearly distinct from other *T. affinis* specimens, which in the following is shown by significant statistical support and conspicuous differences in other diagnostic characters.

Justification for a new species of *Trioceros* based on statistical analyses. According to our PCA analysis based on the morphological examination of the lectotype material of *T. affinis* as well as *T.* cf. *affinis* specimens from various localities in Ethiopia the first three components (those obtained through Broken Stick analysis) explained 24%, 17%, 10% of the total variation respectively). The first component was clearly discriminative between the species (Fig. 5; see Suppl. material 4: PCA Axis 1 vs. Axis 3 and PCA Axis 2 vs. Axis 3). The highest loadings for the first component referred to the continuous variables SDC, PEL, SCP and the categorical variables EDCS, HBS and RHS (Suppl. material 1: PCA loadings). Based on this component the new species has a lower number of SDC, a longer PEL and a higher number of SCP than *T. affinis*. Also, the new species has the exclusive characters EDCS, HBS and RHS, while none of the *T. affinis* individuals did. The first axis did not separate different sexes in any of the species. The lectotype and paralectotype of *T. affinis* show no significant differences to individuals of other populations included in our statistical analyses. Even though only the first principal component showed clear shape separation among the studied species, we still used all 3 meaningful components in the Per-MANOVA analysis. Based on Per-MANOVA the two species were significantly different from each other (F = 43.7, *p* = 0.0001).

According to the extensive morphological investigation of both the lectotype material of *Trioceros affinis* sensu stricto and individuals of *T. affinis* from other locations in Ethiopia, and the significant statistical distinctness of our new species from all the other *T. affinis*, we here formally describe *Trioceros wolfgangboehmei* sp. nov.

Systematics
Chamaeleonidae Werner, 1902
***Trioceros* Swainson, 1839**

***Trioceros wolfgangboehmei*, sp. nov.**

http://zoobank.org/20A1D4E2-40E5-49C1-8F4D-1580EAD87531

Suggested common English name: Wolfgang Böhme's Ethiopian Chameleon

Material examined. *Holotype*: ZFMK 84811, adult male, Dinsho (3,130 m a.s.l. / 7°06'10"N, 39°47'25"E), Bale Mountains, Ethiopia, collected by Petr Nečas on the 6. August, 2004 (Fig. 2A, C, D).

Paratypes: ZFMK 84812, adult female, with the same locality and collecting data as the holotype; ZFMK 84813, adult female, Goba (2,740 m a.s.l. / 7°00'36"N, 39°57'28"E), Bale Mountains, Ethiopia collected by Petr Nečas on the 7. August, 2004 (Fig. 2B, E, F); ZFMK 63063, adult female, 10 km from Goba (2700 m a.s.l.), Bale Mountains, Ethiopia collected by Colin Tilbury in October 1996.

Diagnosis. *Trioceros wolfgangboehmei* sp. nov. is a small-sized chameleon of the *Trioceros affinis* species complex (sensu Ceccarelli et al. 2014). It can be distinguished from all other members of the same species complex by the following combination of characters:

(1)　presence of a prominent and well-developed dorsal crest consisting of a relatively low number of significantly pointed and enlarged conical scales, forming a single row and reaching along the anterior half the tail;
(2)　top of the casque posteriorly raised above the dorsal crest;
(3)　heterogeneous body scalation with both small scattered standard scales and enlarged flattened platelike scales;
(4)　long canthus parietalis formed by 9–12 slightly enlarged scales;
(5)　rugose head scalation consisting of enlarged scales forming the cranial crests that fill the area between the lateral and temporal crest and the posterior rim of the orbit;
(6)　relatively high number of flank scales at midbody (53–59);
(7)　relatively short snout-vent length (up to 66 mm);
(8)　a unique hemipenial morphology including shallow calyces with smooth margins on the truncus, four pairs of thick, pointed and thorn-like papillae and two pairs of non-serrated rotulae.

Description of the holotype. The adult male holotype (ZFMK 84811) of *Trioceros wolfgangboehmei* sp. nov. is a small-sized chameleon with a total length of 156.3 mm (snout-vent length of 65.3 mm and a tail length of 91.0 mm) (Fig. 2A). The head is relatively short, 18.9 mm long (HW/HL 0.54). The head scalation is rugose consisting of enlarged scales forming the cranial crests and filling the area between the lateral and temporal crest and the posterior rim of the orbit (Fig. 2C, D; see Suppl. material 3: Dorsal head views). The top of the casque is raised posteriorly above the dorsal crest. Nine convex, enlarged and tubercular scales form the parietal crest. The casque is 11.7 mm high (RCH 0.91) and exceeds the dorsal crest on the neck by 3.2 mm (RCN 0.25). The parietal crest is 9.2 mm long. The temporal region is covered by prominent enlarged scales of larger size than the standard scales on flanks and limbs. The gular crest is absent in preserved specimens – in life, it is visible as two parallel paramesial skin folds on the throat. The temporal crest is

Table 1. Mensural and meristic measurements of type specimens of *Trioceros wolfgangboehmei* sp. nov. and male, female and juvenile individuals of *T. affinis* examined (including the lectotype material). For the specimens of *T. affinis* linear measurements (in mm) and scale counts are given as mean values (Mean) ± standard deviation (SD) and sample size (N), minimum (Min) and maximum (Max) are shown. Presence (present) and absence (–) of characters are indicated. Characters used for statistical analysis are marked with a star (*). See Materials and Methods for explanation of the single character abbreviations.

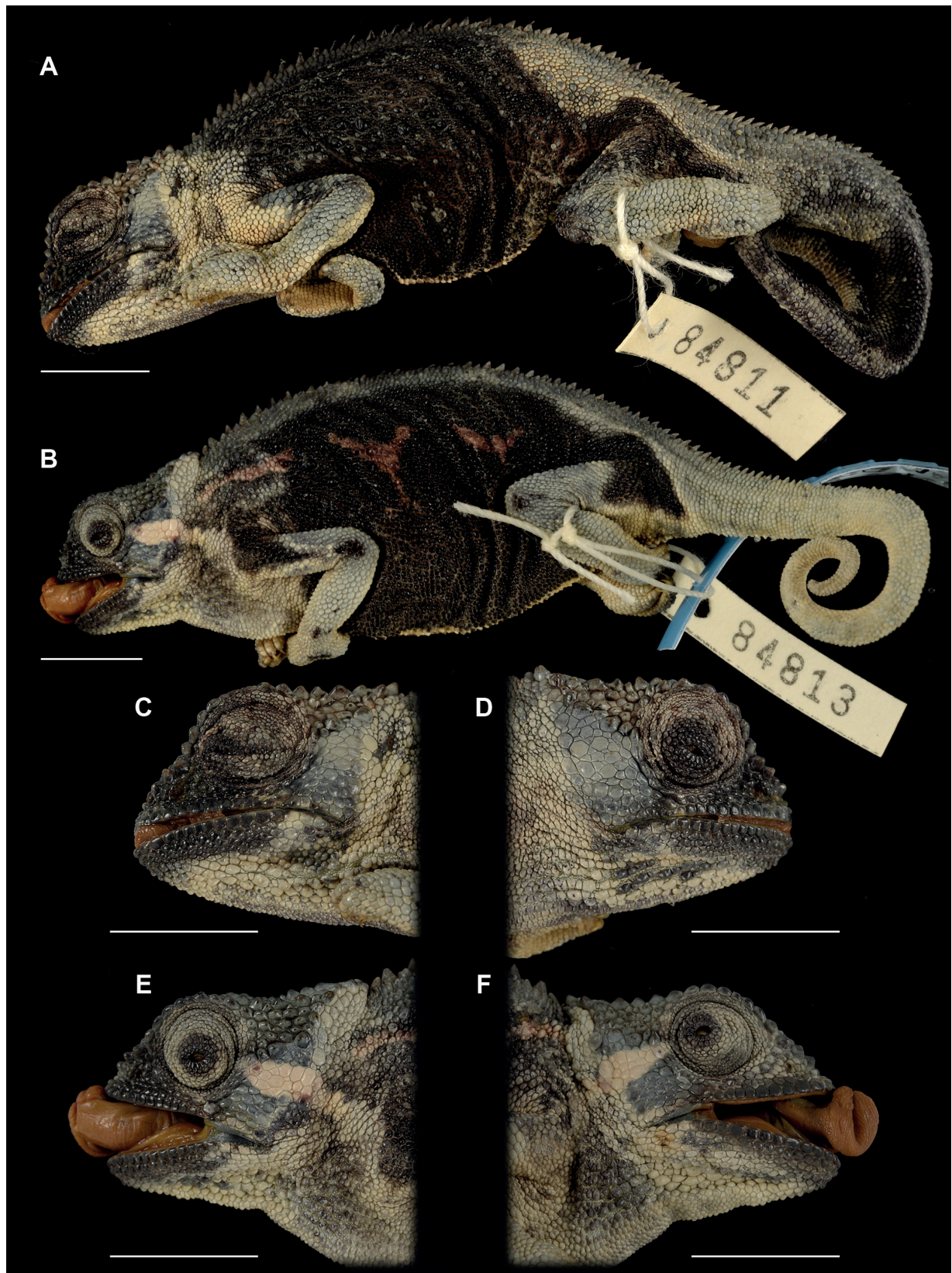| Species	*Trioceros wolfgangboehmei* sp. nov.						*Trioceros affinis*								
Sex	male	female	female	female	male	female	male			female			juvenile		
Locality	Dinsho	Dinsho	Goba	Goba	Abyssinia	Abyssinia	Ethiopia			Ethiopia			Ethiopia		
							N = 26			N = 32			N = 4		
	holotype ZFMK 84811	paratype ZFMK 84812	paratype ZFMK 84813	paratype ZFMK 63063	lectotype SMF 16402	paralectotype SMF 16403	Mean ± SD	Min	Max	Mean ± SD	Min	Max	Mean ± SD	Min	Max
SVL*	65.3	65.8	60.3	59.7	68.9	73.3	74.73 ± 4.57	67.6	84.6	77.95 ± 6.31	63	88.3	51.88 ± 2.87	48.2	55.2
TaL*	91.0	81.4	72.0	77.3	79.4	72.7	89.87 ± 7.66	77.2	110.2	80.33 ± 7.41	62.1	92.4	60.83 ± 1.90	58.1	62.5
TL	156.3	147.2	132.3	137	148.3	146.0	164.60 ± 10.50	145.8	183.1	158.28 ± 12.46	133.2	178.4	112.70 ± 4.41	106.3	116.4
HL*	18.9	20.3	17.9	18.1	18.8	20.2	20.37 ± 1.25	18	22.7	20.70 ± 1.25	18.2	22.7	15.90 ± 0.62	15.4	16.8
HW*	10.2	10.8	9.1	9.5	9.7	10.6	10.05 ± 1.13	8.5	13.9	10.20 ± 0.88	8.2	11.9	8.43 ± 0.48	8	9.1
ML*	12.9	15.4	12.7	12.4	13.6	14.8	14.62 ± 0.81	13.5	16.4	15.19 ± 1.26	13	17.2	11.30 ± 0.38	11	11.8
CH*	11.7	12.6	12.2	11.2	11.6	13.1	12.27 ± 0.96	10.2	14.2	12.76 ± 0.91	11	14.1	9.63 ± 0.67	8.9	10.5
CN*	3.2	4.6	4.1	3.0	2.7	3.3	3.17 ± 0.56	2.2	4.8	3.21 ± 0.59	2.3	4.9	2.20 ± 0.35	1.9	2.7
CE*	8.3	8.8	8.4	8.9	8.3	9.4	8.88 ± 1.00	6.5	10.8	8.77 ± 0.81	6.9	10.4	6.48 ± 0.53	5.7	6.9
SL*	5.4	6.3	5.0	5.7	6.3	7.6	6.48 ± 0.61	5.4	7.7	6.98 ± 1.89	5.2	15.7	4.60 ± 0.48	3.9	5
ED*	6.1	5.8	5.2	4.9	6.5	5.4	6.50 ± 0.53	5	7.4	6.56 ± 0.45	5.7	7.5	5.60 ± 0.56	4.9	6.1
IOS*	12	11	11	11	13	12	13.08 ± 1.02	11	15	13.23 ± 1.11	11	15	12.50 ± 0.58	12	13
PCL*	9.2	12.6	10.1	9.2	4.1	3.8	4.81 ± 1.14	3.1	7.9	4.60 ± 0.94	2.4	7.6	3.60 ± 0.83	3	4.8
CC*	8.5	8.4	7.6	7.6	7.6	8.1	8.34 ± 0.59	7.4	9.4	8.33 ± 0.74	7.1	9.9	6.65 ± 0.53	6	7.3
IL*	39.2	36.4	34.1	31.9	37.8	43.9	41.10 ± 3.70	34.6	49	45.07 ± 4.99	34.9	55.2	27.35 ± 3.40	22.4	30
FLL*	11.9	11.8	10.7	9.5	14.9	15.4	13.64 ± 1.37	11.1	16.2	13.60 ± 1.46	11.2	16.8	10.53 ± 0.71	9.8	11.5
LHLL*	10.8	11.4	11.2	11.2	14.0	15.8	13.36 ± 1.10	10.4	15	13.36 ± 1.25	11.7	16.9	10.03 ± 0.83	9.3	11.2
UL*	16	16	15	16	14	15	16.27 ± 1.64	13	19	16.62 ± 1.60	13	19	14.50 ± 1.29	13	16
LL*	17	15	15	15	14	15	15.27 ± 1.12	12	17	14.92 ± 1.26	12	18	15.00 ± 1.15	14	16
SEH*	6	7	7	7	7	7	8.00 ± 1.17	6	11	8.15 ± 0.97	6	10	6.50 ± 0.58	6	7
FSM*	53	58	59	53	54	56	60.15 ± 5.30	48	69	62.69 ± 4.03	56	69	52.50 ± 1.29	51	54
SDC*	37	33	35	38	53	49	62.31 ± 8.00	47	78	64.38 ± 5.07	56	76	49.75 ± 5.68	46	58
SCP*	10	12	9	11	5	3	4.42 ± 1.14	3	7	4.35 ± 1.16	1	6	3.75 ± 0.96	3	5
EDCS*	present	present	present	present	–	–	–	–	–	–	–	–	–	–	–
HBS*	present	present	present	present	–	–	–	–	–	–	–	–	–	–	–
RHS*	present	present	present	present	–	–	–	–	–	–	–	–	–	–	–
TaL/ SVL	1.39	1.24	1.19	1.29	1.15	0.99	1.20 ± 0.10	1.07	1.51	1.03 ± 0.08	0.87	1.17	1.17 ± 0.05	1.11	1.21
RTL	0.58	0.55	0.54	0.56	0.54	0.50	0.55 ± 0.02	0.52	0.60	0.51 ± 0.02	0.47	0.54	0.54 ± 0.01	0.53	0.55
HW/HL	0.54	0.53	0.51	0.52	0.52	0.52	0.49 ± 0.05	0.45	0.66	0.49 ± 0.02	0.44	0.53	0.53 ± 0.01	0.51	0.54
RCH	0.91	0.82	0.96	0.90	0.85	0.89	0.84 ± 0.07	0.71	0.99	0.84 ± 0.06	0.70	0.96	0.85 ± 0.07	0.75	0.92
RCN	0.25	0.30	0.32	0.24	0.20	0.22	0.22 ± 0.04	0.15	0.34	0.21 ± 0.04	0.16	0.30	0.20 ± 0.04	0.16	0.25
ED/HW	0.60	0.54	0.57	0.52	0.67	0.51	0.65 ± 0.07	0.53	0.79	0.65 ± 0.06	0.55	0.76	0.66 ± 0.05	0.60	0.71
FLL/ SVL	0.18	0.18	0.18	0.16	0.22	0.21	0.18 ± 0.02	0.15	0.22	0.18 ± 0.02	0.15	0.22	0.20 ± 0.02	0.18	0.22
LHLL/ SVL	0.17	0.17	0.19	0.19	0.20	0.22	0.18 ± 0.02	0.15	0.20	0.17 ± 0.02	0.14	0.21	0.19 ± 0.02	0.18	0.22

Figure 2. The preserved adult male holotype (ZFMK 84811) from Dinsho (**A.**) and adult female paratype (ZFMK 84813) from Goba (**B.**) of *Trioceros wolfgangboehmei* sp. nov. Head morphology: Head of the holotype in left (**C.**) and right (**D.**) view and of the paratype in left (**E.**) and right (**F.**) view. Scale bars represent 1 cm. Photos by Thore Koppetsch.

weakly expressed; it is present merely as the caudodorsal emargination of the triangular temporal field of enlarged scales, described above. No gular grooves are present on the throat. The scalation on the eye turrets consists of granular scales, gradually slightly enlarged towards the eye opening. The supraorbital crest is formed by a
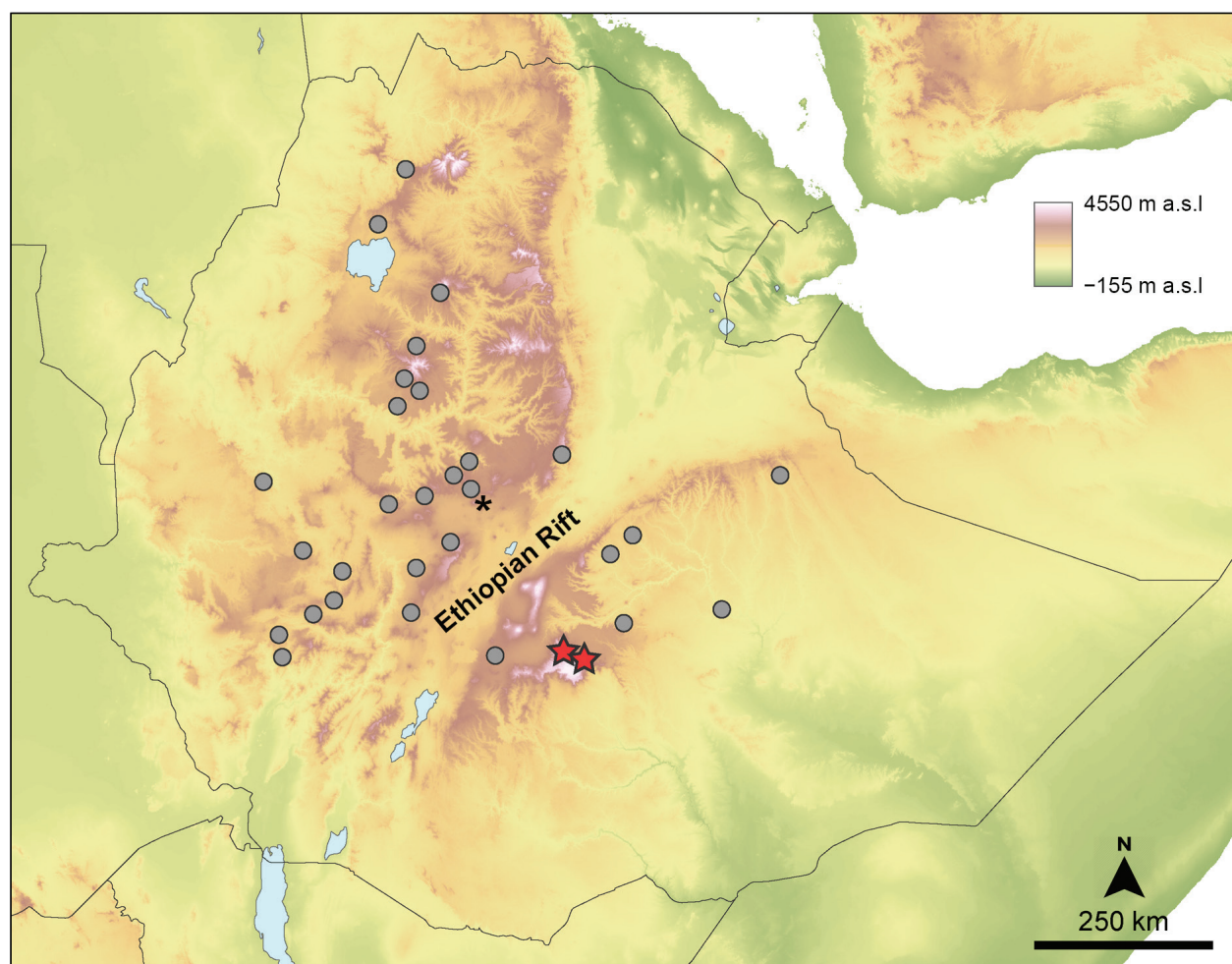
Figure 3. Digital elevation map of Ethiopia (generated by using the geographic information system ArcGIS 10.0; elevation in m a.s.l) indicating the currently known distribution of *Trioceros wolfgangboehmei* sp. nov. east of the Ethiopian Rift in the northern Bale Mountains (red stars; left star: Dinsho, right star: Goba). Black star: Addis Abeba. Grey dots show records of *T. affinis* based on distributional data after Largen and Spawls (2010) and Ceccarelli et al. (2014). The status of these different Ethiopian populations of *T. affinis* will be investigated in more detail in further ongoing studies.

single row of enlarged, pointed and sub-conical scales. Supralabials 16, infralabials 17. Between the supra-orbital crests, 12 inter-orbital scales, including crest scales, are present.

The prominent and well-developed dorsal crest consists of a relatively low number (37) of significantly pointed and enlarged conical scales, forming a single row and reaching along the anterior half of the tail as a prominent tail crest. The size of the dorsal crest scales is gradually decreasing posteriorly. The ventral crest is indicated by slightly enlarged conical scales forming a white midventral line.

The body scalation is heterogeneous and consists both of small scattered standard tubercular scales and, across the flanks, but especially dorso-laterally, enlarged flattened lenticular scales. The ventral regions of limbs and tail are covered by a fine granular sub-homogeneous scalation. No tarsal spurs are present on the hind-feet, toes terminate in a single, white claw and the soles of the extremities are smooth.

The hemipenes are everted and illustrated in asulcal, lateral and sulcal view with the apex on top (Fig. 4D–F).

On the asulcal side of the truncus, shallow calyces with smooth margins are present. The most prominent calyces are located on the distal aspect of the asulcal side. The sulcal lips covering the sulcus spermaticus are partially relatively smooth. Two pairs of unserrated rotulae are located on the apex, with the asulcal pair being of slightly larger size. On the sulcal side, four pairs of thick pointed and thorn-like papillae are arranged in a row between the rotulae. The papillae distally to the rotulae are the largest, the proximal ones are the smallest. Mensural and meristic data on the holotype are shown in Table 1.

Colouration in life. The ground body colour of living specimens of *Trioceros wolfgangboehmei* sp. nov. is yellowish, brownish or even bright green and varies in different individuals (Figs 6, 7). Most specimens show a prominent bright white temporal spot posterior of the orbit formed by enlarged flattened scales (Figs 6, 9). A dorso-lateral bright white or slightly orange longitudinal stripe can be found in many individuals. This dorsolateral stripe often is continuous, spreading along
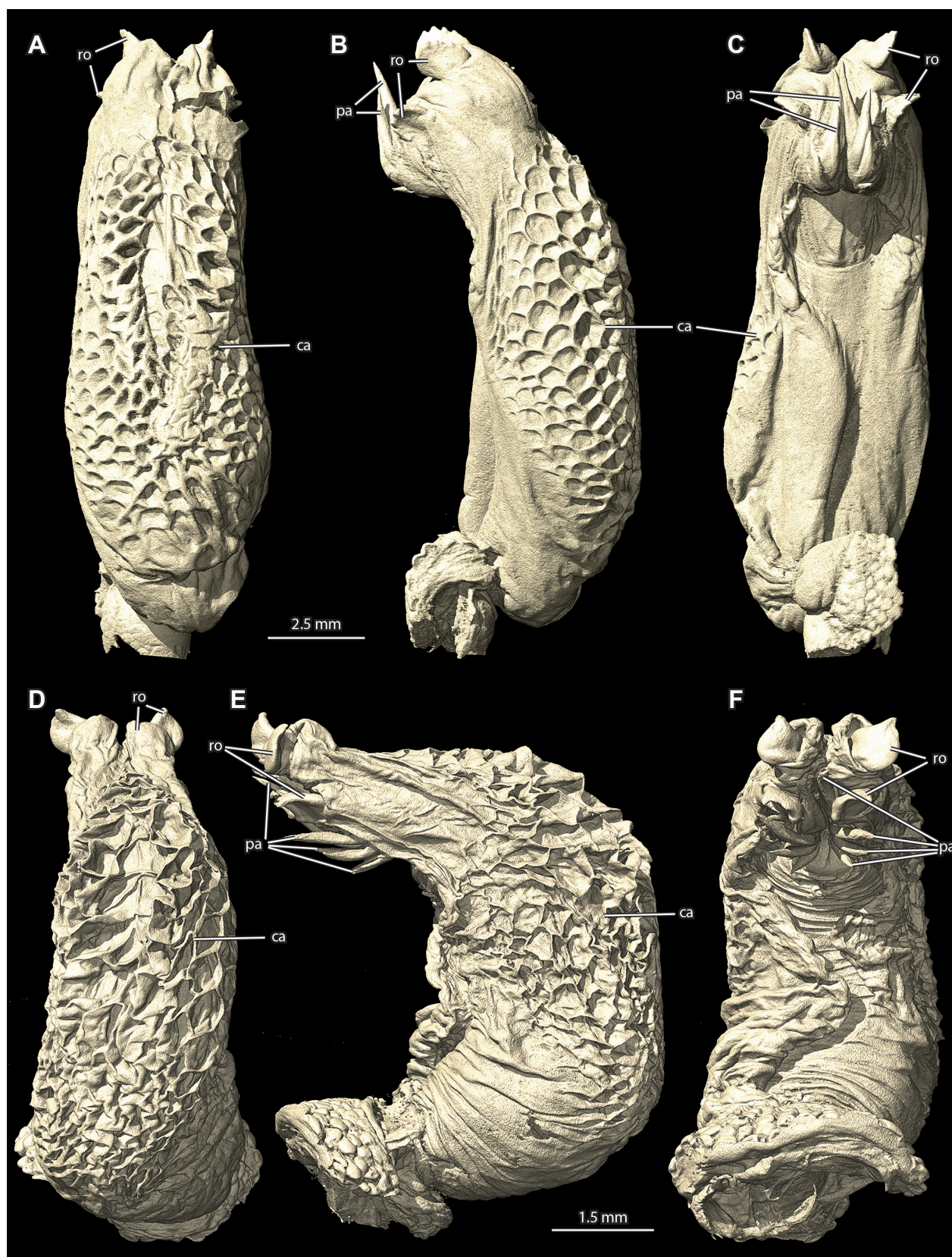
Figure 4. Volume renders of the µCT scans of the hemipenes of *Trioceros affinis* (ZFMK 54264) (**A–C.**) and the holotype of *Trioceros wolfgangboehmei* sp. nov. (ZFMK 84811) (**D–F.**) in asulcal (left), lateral (middle) and sulcal view (right) with the apex on top. ro – rotulae; pa – papillae; ca – calyces.

the flanks, but can be interrupted and form a Y-shaped pattern laterally (Fig. 8). This dorso-lateral pattern is corresponding with the occurrence of enlarged and flat-tened scales. The colour of the dorsal crest only slight-ly differs from the background colouration by being a little bit darker or brighter. A white stripe is present on
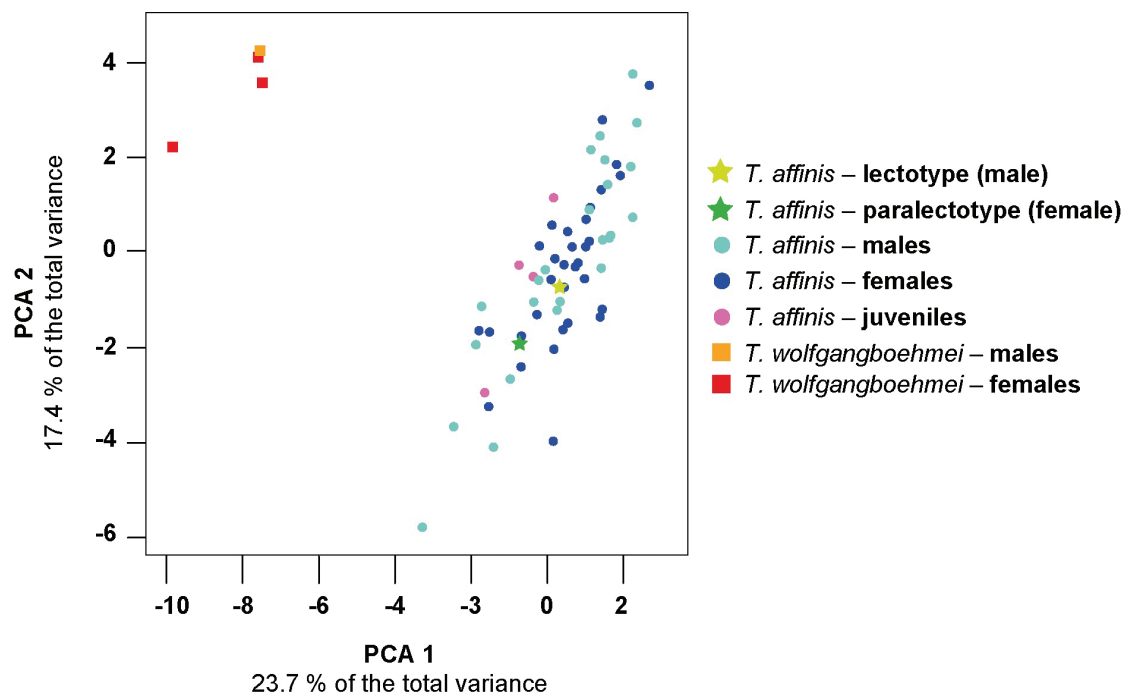
Figure 5. Principal component analysis (PCA) of morphological differences between *Trioceros affinis* (lectotype/paralectotype/males/females/juveniles) and *T. wolfgangboehmei* sp. nov. (male/females). Principal component axes refer to the first two principal components.
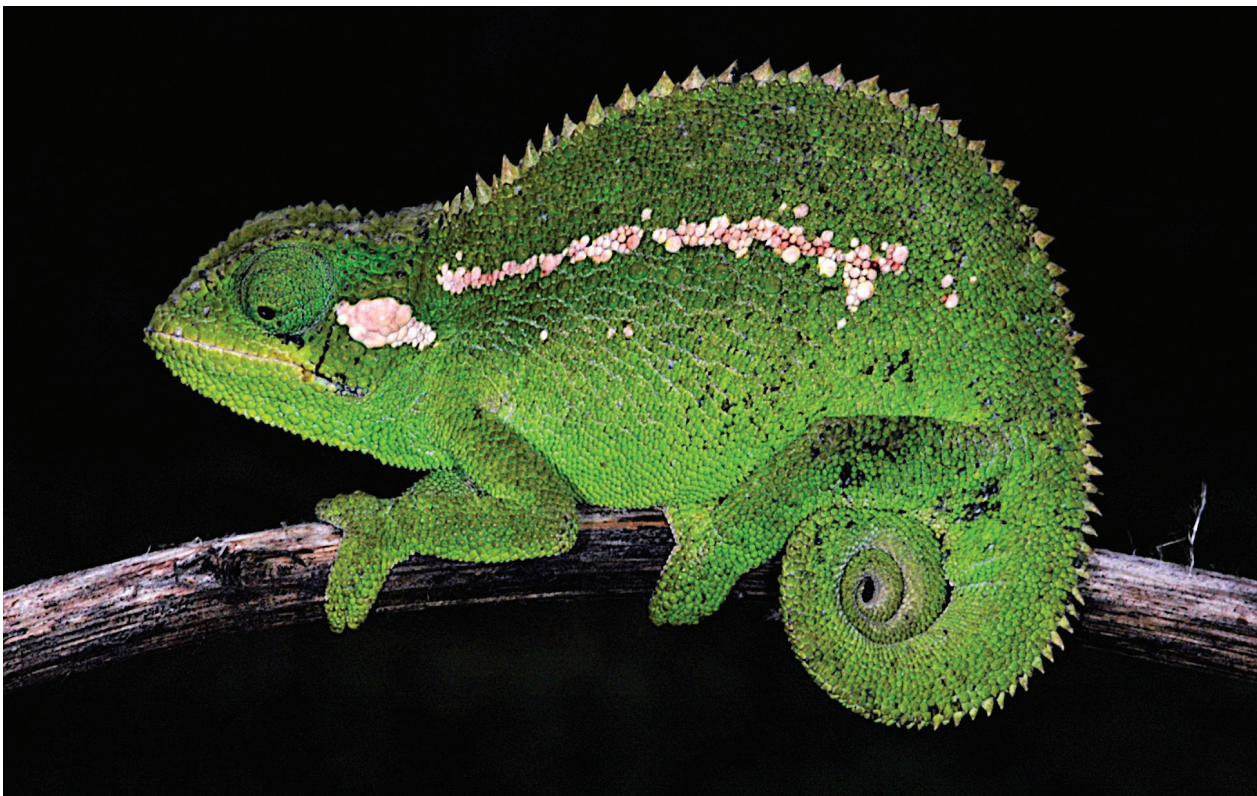

Figure 6. Living individual of *Trioceros wolfgangboehmei* sp. nov. from Dinsho, Ethiopia showing a prominent white temporal spot and dorsolateral longitudinal stripe. Photo by Petr Nečas.

the weakly expressed ventral crest. The throat region is usually of lighter colour in comparison to the ground colour. In some specimens, a beige ground pattern with slight reddish stripes can be found in the head region around the orbit. It ranges from dorsal to the nostrils around the entire eye turret to the casque and is bordered posteriorly by the temporal crest (Fig. 7). The limbs exhibit the same colour as the body, though they are coloured beige or yellowish medially.

Colouration in preservative. The male holotype shows a dark, blackish body colouration, except on fore- and

Figure 7. Living individual of *Trioceros wolfgangboehmei* sp. nov. from Goba, Ethiopia, showing a beige ground pattern with slight reddish stripes in the head region around the orbit. Photo by Petr Nečas.

hindlimbs, the dorsal part of the tail, the posterior head region and the throat, which are of pale whitish colour (Fig. 2A). A white midventral crest reaches from the throat to the cloaca. In the female paratypes, the more or less interrupted, sometimes Y-shaped, dorsolateral stripe is coloured orange, and also a whitish temporal spot or at least indistinct whitish colouration beyond the orbit can be recognised (Fig. 2B).

Variation. Variation in mensural and meristic characters for the adult type series is shown in Table 1. The female paratypes of *Trioceros wolfgangboehmei* sp. nov. show only slight differences in snout-vent length (ranging from 59.7 mm to 65.8 mm vs. 65.3 mm in the male holotype). Females show a slightly lower relative tail length (ranging from 0.54 to 0.56 vs. 0.58 in the male holotype) as well as a lower head width/head length ratio (ranging from 0.51 to 0.53 vs. 0.54 in the male holotype). In the female paratypes, only 11 (vs. 12 in the holotype) inter-orbital scales between the supraorbital crests are present. Some female specimens show a longer parietal crest (PCL/SVL ranging from 0.15 to 0.19) compared to the male holotype (PCL/SVL 0.14).

The female paratypes show a variable dorsolateral colouration (Fig. 2B) by having an orange coloured, more or less interrupted, sometimes Y-shaped, dorsolateral stripe (Fig. 8). In addition, the temporal light spot is more prominent and coloured white or orange (Figs 6, 9).

Field observations of juvenile specimens around Goba show that the characteristic heterogeneous body scalation of adults (Fig. 8) can be clearly recognised already at early age (Fig. 10). Juveniles are uniform reddish brown with a slightly lighter gular and ventral regions.

Comparisons. *Trioceros wolfgangboehmei* sp. nov. can be distinguished by a unique combination of morphological

Figure 8. Lateral detail of a living *Trioceros wolfgangboehmei* sp. nov. from Goba, Ethiopia, showing the heterogeneous body scalation with both small scattered tubercles and enlarged flattened plate-like scales. In this individual the dorsolateral stripe is interrupted and forms a Y-shaped pattern on the flanks. Photo by Petr Nečas.

Figure 9. Head of a living *Trioceros wolfgangboehmei* sp. nov. from Goba, Ethiopia. Photo by Petr Nečas.

Figure 10. Living juvenile of *Trioceros wolfgangboehmei* sp. nov. from Goba, Ethiopia. Photo by Petr Nečas.

features from the other representatives of the genus *Trioceros* occurring in Ethiopia (see the key to the Ethiopian *Trioceros* provided below). It can be separated from *T. bitaeniatus* by lacking a midventral gular crest composed of conical scales; the absence of a dorsal crest with isolated groups of 3–5 enlarged scales; the lack of a low but prominent parietal crest and in not showing two longitudinal rows of enlarged flattened scales on the flanks forming a pair of lateral stripes differentiated in colour. Also, *T. harennae* differs from the newly described species by possessing a single gular crest that is conspicuously well-developed and formed by long, sometimes even laterally flattened scales. *T. balebicornutus* can be distinguished by a conspicuous gular crest and the shape and arrangement of the rostral scales. Males have a pair of rostral horns, while females show a pair of rostral pointed conical scales (or rugose and prominently enlarged warty scales in some females).

The new chameleon *Trioceros wolfgangboehmei* sp. nov. shows the closest morphological resemblance to *T. affinis* and is considered as a member of the *T. affinis* species complex (sensu Ceccarelli et al. 2014). Also, previous phylogenetic analyses revealed that populations of *T. affinis* from Addis Abeba show about 5% sequence divergence in the genetic marker ND4 (NADH dehydrogenase subunit 4) compared to individuals from the type locality of *T. wolfgangboehmei* sp. nov. (Ceccarelli et al. 2014).

T. affinis sensu stricto, as defined by the lectotype specimen (Fig. 1), differs from *T. wolfgangboehmei* sp. nov. by having a less prominent dorsal crest consisting of a relatively higher number of smaller conical scales

reaching to the base of the tail, a flat casque not raised above the level of the dorsal crest, no rugose and only slightly enlarged scales on the head and by showing a shorter canthus parietalis formed by a lower number of slightly enlarged scales. Although the new species shares single characters, but not in combination with each other or the exclusive scalation patterns described above, with some *T. affinis* populations e.g. from south-western Ethiopia, like a heterogeneous body scalation, relatively high number of flank scales at midbody and a relatively short snout-vent length, these characteristics are useful when distinguishing between new species and *T. affinis* specimens without precise indication of origin.

Concerning its hemipenial morphology, *Trioceros wolfgangboehmei* sp. nov. is distinct from *T. affinis*, which shows serrated rotulae (also present in *T. balebicornutus*) and slightly deeper calyces (Fig. 4).

Etymology. The specific epithet honours Wolfgang Böhme, senior herpetologist at the Zoological Research Museum Alexander Koenig in Bonn, Germany, for his numerous contributions to research on chameleons, for his outstanding and ongoing herpetological research in general, and, last but not least, for his continuously generous support of the first as well as second author and numerous junior zoologists. The species epithet is a noun in the genitive case.

Distribution and natural history. *Trioceros wolfgangboehmei* sp. nov. is only known from the region around

Dinsho and Goba in south-central Ethiopia. Those two villages are located directly in the Bale Mountains. The new species appears to be restricted to this area and can be considered as another endemic for the Bale Mountains. *Trioceros wolfgangboehmei* sp. nov. is not occurring syntopically with the two other *Trioceros* species distributed in the Bale Mountains, *T. harennae* or *T. balebicornutus*, which are confined to their southern slopes.

Trioceros wolfgangboehmei sp. nov. naturally occurs on the northern and north-eastern slopes of the Bale Mountains, Ethiopia. It was found at 3,130 m a.s.l. (Nečas, pers.obs.) as well as at altitudes around 2,700 m (Tilbury 1998), but they might well climb higher within the National Park areas, and, they drop lower, living in the city centres of Goba (2,750 m a.s.l.) and Robe (2,500 m a.s.l.) and even in the northern suburbs of Robe around 2,400 m a.s.l. (Nečas, pers. obs.). They are typical forest-edge inhabitants, not entering continuous forest zones. The perch height was recorded to reach from 0.7 m to 2.1 m above ground for the adults, with the majority of animals found at 1 to 1.5 m height, despite the possibility to climb higher. Juveniles tend to stay lower; they were recorded between 0.3 and 1 m high. Two predation records were made, a domestic cat and Somali Shrike (*Lanius somalicus* Hartlaub, 1859) (Nečas, pers. obs.).

Trioceros wolfgangboehmei sp. nov. prefers to live on small trees and bushes; juveniles can be found in grass, but always adjacent to trees and bushes. They are absent from large monoculture fields, while they form quite dense populations in traditional small fields and gardens. Based on field surveys and observations, the population density was estimated in 2004 to be even lower in the natural habitats within the National park (ca. 20–40 individuals per hectare) compared to surrounding gardens and local farms areas (ca. 80–110 individuals per hectare) (Nečas, pers. obs.). The reason for higher densities in disturbed habitats is, that the living fences between fields and gardens are actually simulating the natural habitat: forest edge in much higher density, than under natural conditions, where they seem to be confined either to the real forest edge or microbiotopes at clearings, along water streams etc. This phenomenon is common for some other Afromontane species, confined to forest edge.

Conservation status. The currently known distribution range of *Trioceros wolfgangboehmei* sp. nov. is restricted to a small region on the northern slopes of the Bale mountains. A part of the population is well protected within the Bale Mountains National Park, but another part is living outside, in the agriculturally used areas and even in gardens and remnants of vegetation in the local villages (Nečas, pers. obs.). The man-modified landscape and a traditional way of agricultural land usage can have a positive impact on the abundance of chameleon populations, with occasionally higher densities in rural than in pristine areas. Their dependence on the forest is indirect, as they are evidently a forest edge species. Habitat destruction and fragmentation might be caused particularly by urbanisation, fires, monocultures, deforestation, aridisation and, in urban areas, increased predation by carnivores such as domestic cats. Chameleons, in general, are especially threatened by transformation of their habitats since their dispersal abilities to access and spread in new areas are limited and often they are highly adapted to well-defined ecological and climatic conditions. Due to its small distribution range and restricted area of occupancy on the one hand, but partially profiting from human-induced habitat changes on the other, it is likely that *Trioceros wolfgangboehmei* sp. nov. would be threatened. However, the species and its distribution remain insufficiently known, since – apart from our field observations – robust data concerning its conservation status are missing.

Key to the *Trioceros* of Ethiopia

1 Presence of a well-developed prominent gular crest with pointed gular crest scales at least twice the size of the surrounding midventral scales.. 2

– Absence of such a well-developed prominent gular crest.. 4

2 A pair of rostral horns in male, a pair of rostral pointed conical scales in females (or rugose, upraised and prominently enlarged warty scales in some individuals) ....*T. balebicornutus*

– No rostral appendage.. 3

3 Dorsal crest formed by groups of 3–5 consecutively enlarged scales therein; two longitudinal rows of enlarged lenticular scales on each flank, usually placed within a distinctly coloured (mostly whitish) lateral stripe ....*T. bitaeniatus*

– Conspicuous well-developed gular crest formed by long, laterally flattened conical scales; absence of two longitudinal lateral rows of enlarged flattened scales differentiated in colour on each flank .... *T. harennae*

4 Flat casque with a parietal crest not (or slightly) raising above the level of the dorsal crest; homogeneous body scalation with only very few enlarged scales; in some west Ethiopian populations no rugose and only slightly enlarged scales on the head and higher number of small conical dorsal crest scales.. *T. affinis*

– Top of the casque posteriorly raised above the dorsal crest; heterogeneous body scalation with both small scattered tubercles and enlarged flattened scales; presence of a prominent and well-developed dorsal crest consisting of a relatively low number of pointed and enlarged conical scales, also reaching along the anterior half of the tail as a prominent tail crest .... *T. wolfgangboehmei* sp. nov.

Discussion

Trioceros wolfgangboehmei sp. nov. can be recognised as a distinct taxon within the *T. affinis* species complex based on our morphological examinations, the genetic disparities with *T. affinis* in western Ethiopia proven by Ceccarelli et al. (2014) and the biogeographical segregation caused by the Great Rift Valley. Accordingly, the population level relationships within the *T. affinis* complex might be considered analogous to previous estimations of the *T. bitaeniatus* species complex or at least subgroups like the *T. rudis* group (Rand 1963). Resulting from detailed comparative and extensive examinations of those groups and complexes, various taxa are treated now as species (Tilbury 1991; Nečas et al. 2003, 2005; Krause and Böhme 2010; Stipala et al. 2011). Phylogenetic divergence within the *T. affinis* complex, but also other taxa, e.g. *T. deremensis*, *T. werneri* or *T. tempeli*, indicate the presence of further unresolved species complexes, and an underestimated species diversity for *Trioceros* in general (Ceccarelli et al. 2014).

Some of the morphological differences between *T. affinis* and *T. wolfgangboehmei* sp. nov. resemble characteristics that are also diverging within the *T. bitaeniatus* or *T. rudis* complexes. Sternfeld (1912) noted that the development of the dorsal crest and the shape and counts of its scalation differs within those groups. Similar to our new species, the size variation and degree of enlargement in dorsal crest scales is in these species also associated with the uniformity of the dorsal crest scales or the scalation pattern. Thus, the shape of the dorsal crest also affects the general appearance of a chameleon. When chameleons occur in sympatry, those characters might also contribute directly or indirectly to species recognition, intra-specific communication or interspecific ethological barriers (Rand 1961; Nečas 2004; Stuart-Fox et al. 2007).

Also our statistical analyses clearly differentiated *T. wolfgangboehmei* sp. nov. from *T. affinis* sensu stricto. Despite only a comparable lower number of specimens of the new species being available, its significant distinctness was shown (Fig. 5).

Concerning hemipenial morphology, the function of minor differences (serration of rotulae or depth of calyces) as a pre-zygotic barrier between species is not completely understood until now. However, it can be speculated that reinforcement of allopatric speciation is specifically shaped by geographical separation, like here by the Great Rift Valley. Also, Ceccarelli et al. (2014) suggested that phylogenetic disjunctions between western populations of the *T. affinis* complex and the eastern populations in the northern Bale region, here assigned to *T. wolfgangboehmei* sp. nov., are clearly associated with the presence of the Ethiopian Rift. Similar patterns shaped across this biogeographical barrier are also present in species complexes of other animal groups, e.g. in rodents (Šumbera et al. 2018) or frogs (Freilich et al. 2014).

T. affinis is reported to be associated with both grassland and forest habitats ranging from high to moderate elevations within its wide range of distribution in the Ethiopian highlands (Largen 1995). It is thus possible that further cryptic taxa within the *T. affinis* species complex can be expected also in populations west of the Ethiopian Rift. However, resolving the systematics within this species complex is impeded as the locality designated for the lectotype of *T. affinis* sensu stricto does not allow any clear conclusion to be drawn concerning the exact origin of this specimen. Based on our comparative examination of *T. affinis* specimens from different regions of Ethiopia, the lectotype material can be clearly assigned to populations west of the Ethiopian Rift. However, the verification of a precise allocation and possible need of restricting the type locality will be investigated in more detail in further ongoing studies.

Next to *T. balebicornutus* and *T. harennae*, *T. wolfgangboehmei* sp. nov. is the third chameleon species endemic to the Bale Mountains. Nevertheless, those species apparently do not occur syntopically. Thus, the present paper corroborates the already recognised uniqueness of the Bale Mountains concerning their species richness and endemism. Particularly, the diversity of lizards restricted to this region appears to be relatively low (Largen and Spawls 2011), for instance compared to the presence of three frog genera endemic to this area (Gower et al. 2013), so that an overlooked endemism might also be expected also for other taxa, e.g. skinks. Apart from numerous new and only recent discoveries of vertebrate diversity across the Ethiopian Highlands (Konečný et al. 2020; Koppetsch 2020; Levin et al. 2020; Mizerovská et al. 2020), our new species highlights that particularly the Bale Mountains are a unique centre of endemism and still unknown diversity. In light of ongoing conflicts between human and wildlife in this region (Mekonen 2020) we want to emphasise the need for a long-termed and sustainable preservation and extensive habitat conservation.

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Appendix I

Material examined

Trioceros affinis: Ethiopia: Abyssinia (SMF 16402, lectotype; SMF 16403, paralectotype); Shoa (ZFMK 57538–57543); Shoa: Addis Abeba (ZFMK 2739; ZFMK 57158; ZFMK 57546; ZFMK 57695; ZFMK 63064); Shoa: Gololtscha (ZFMK 2740–2741); Illubabor: Bedele (ZFMK 54264–54275; ZFMK 55439–55481; ZFMK 56587–56589; ZFMK 57159; ZFMK 57162; ZFMK 60539); Illubabor: Bonga (ZFMK 63065); Lake Abaya: Chencha (ZFMK 84817–84818)

Trioceros wolfgangboehmei sp. nov.: Ethiopia: Bale Mountains: Dinsho (ZFMK 84811, holotype; ZFMK 84812, paratype); Bale Mountains: Goba (ZFMK 63063, paratype; ZFMK 84813, paratype)

Supplementary material 1

PCA loadings

Authors: Thore Koppetsch, Petr Nečas, Benjamin Wipfler
Data type: xls spreadsheet
Explanation note: Loadings of the first seven components (Eigenvalues ≥ 1) of the principal component analysis (PCA).
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow us-ers to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/zse.97.25297.suppl1

Supplementary material 2

Individual mensural and meristic measurements

Authors: Thore Koppetsch, Petr Nečas, Benjamin Wipfler
Data type: xls spreadsheet
Explanation note: Individual mensural and meristic mea-surements of type specimens of *Trioceros wolfgang-boehmei* sp. nov. and male, female and juvenile indi-viduals of *T. affinis* examined (including the lectotype material).
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow us-ers to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/zse.97.25297.suppl2

Supplementary material 3

Dorsal head views

Authors: Thore Koppetsch, Petr Nečas, Benjamin Wipfler
Data type: .docx file
Explanation note: Dorsal view of the head male lecto-type (SMF 16402) (A) and female paralectotype (SMF 16403) (B) of *Trioceros affinis* and of the male holo-type (ZFMK 84811) (C) and female paratype (ZFMK 84813) (D) of *Trioceros wolfgangboehmei* sp. nov.

Link: https://doi.org/10.3897/zse.97.25297.suppl3

Supplementary material 4

PCA Axis 1 vs. Axis 3 and PCA Axis 2 vs. Axis 3

Authors: Thore Koppetsch, Petr Nečas, Benjamin Wipfler
Data type: .docx file
Explanation note: Principal component analysis (PCA) of morphological differences between *Trioceros affinis* (lectotype/paralectotype/males/females/juveniles) and *T. wolfgangboehmei* sp. nov. (male/females). Principal component axes refer to the first and third principal components.

Link: https://doi.org/10.3897/zse.97.25297.suppl4