Herpetology Notes, volume 5: 335-344 (2012) (published online on 22 August 2012)

Assessing sexual dimorphism in a species of Malagasy chameleon (*Calumma boettgeri*) with a newly defined set of morphometric and meristic measurements

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Abstract. External sexual dimorphism is widespread in chameleons, with the most consistently dimorphic traits being body size, head size, ornamentation, and coloration. The *Calumma nasutum* group differs from many other Malagasy chameleons by the presence of nasal appendages in both sexes rather than in males only. Here, we compare measurements and scale counts of males and females of a population of one species of this group, *Calumma boettgeri,* from its type locality, the Malagasy offshore island Nosy Be. We found only weak evidence for a differentiation of males and females in this species which did not show significant dimorphism in body size. Univariate tests revealed differences among sexes in size-corrected length of hind limbs (longer in males), relative length of temporal edge (longer in males) and number of spines of dorsal crests (higher in males). Several measurements and scale counts proposed and defined herein might in the future be used to more efficiently delimit species in the **Calumma nasutum** group.

Keywords. Chameleonidae, sexual dimorphism, pholidosis, *Calumma nasutum* group, Madagascar, Nosy Be.

Introduction

Chameleons are unique among squamates because of their highly variable sexual dimorphism: in some genera and clades, males attain much larger body sizes than females, in others they are equal sized, and in again others, females are much larger than males (Klaver and Böhme, 1986; Böhme and Ziegler, 2009). Especially in species with male-biased size dimorphism, males often also exhibit ornaments such as rostral and/or orbital appendages, elevated helmets and tarsal spurs. Males are often highly aggressive resulting in physical combats whereat sexual traits such as horns are applied (Necas 2004; Bustard, 1958; Stuart-Fox *et al.,* 2006; Townsend and Larson, 2002). Usually, in those amphibian and reptile species in which males engage into combats, males are larger than females (e.g., Shine, 1979, 1994).

In Madagascar, chameleons are represented by three endemic genera, the ground chameleons of the genus *Brookesia* (30 species), and the arboreal chameleons of the genera *Furcifer* (21 species, plus 2 on the Comoro archipelago) and *Calumma* (32 species) (Klaver and Böhme, 1986; Glaw and Vences, 2007; and subsequent species descriptions). While the monophyly of *Brookesia* and *Furcifer* has been confirmed by numerous studies, it is currently uncertain whether the genus *Calumma* forms a clade, and the monophyly of several of the phenetic species groups within *Calumma* is also in need of confirmation (e.g., Klaver and Böhme, 1986; Townsend and Larson, 2002; Raxworthy *et al.,* 2002; Townsend *et al.,* 2011) The *Calumma nasutum* group is such a phenetic assemblage of species of untested monophyly in which both sexes have a flexible rostral appendage (Figs. 1-2), and currently contains seven nominal species, *C. boettgeri*, *C. fallax*, *C. gallus*, *C. guibei*, *C. linotum*, *C. nasutum*, and *C. vohibola*, as well as several candidate species (Gehring *et al.,* 2012). The function of the rostral appendage of these species is not entirely clarified, but several aspects indicate that it serves as a trait for intraspecific recognition and sexual selection (Parcher, 1974; Necas, 2004; Gehring *et al.,* 2011). Moreover, in some species of this group

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Note: This is after Schmidt *et al.* (2008), Randrianiaina *et al.* (2009a) and Vences *et al.* (2012) the fourth of a series of short notes produced within the yearly "Vertebrate morphology" undergraduate course at Technical University of Braunschweig, with all students of the course having contributed to the gathering and analysis of data and advised by senior scientists in the statistical interpretation and manuscript writing.

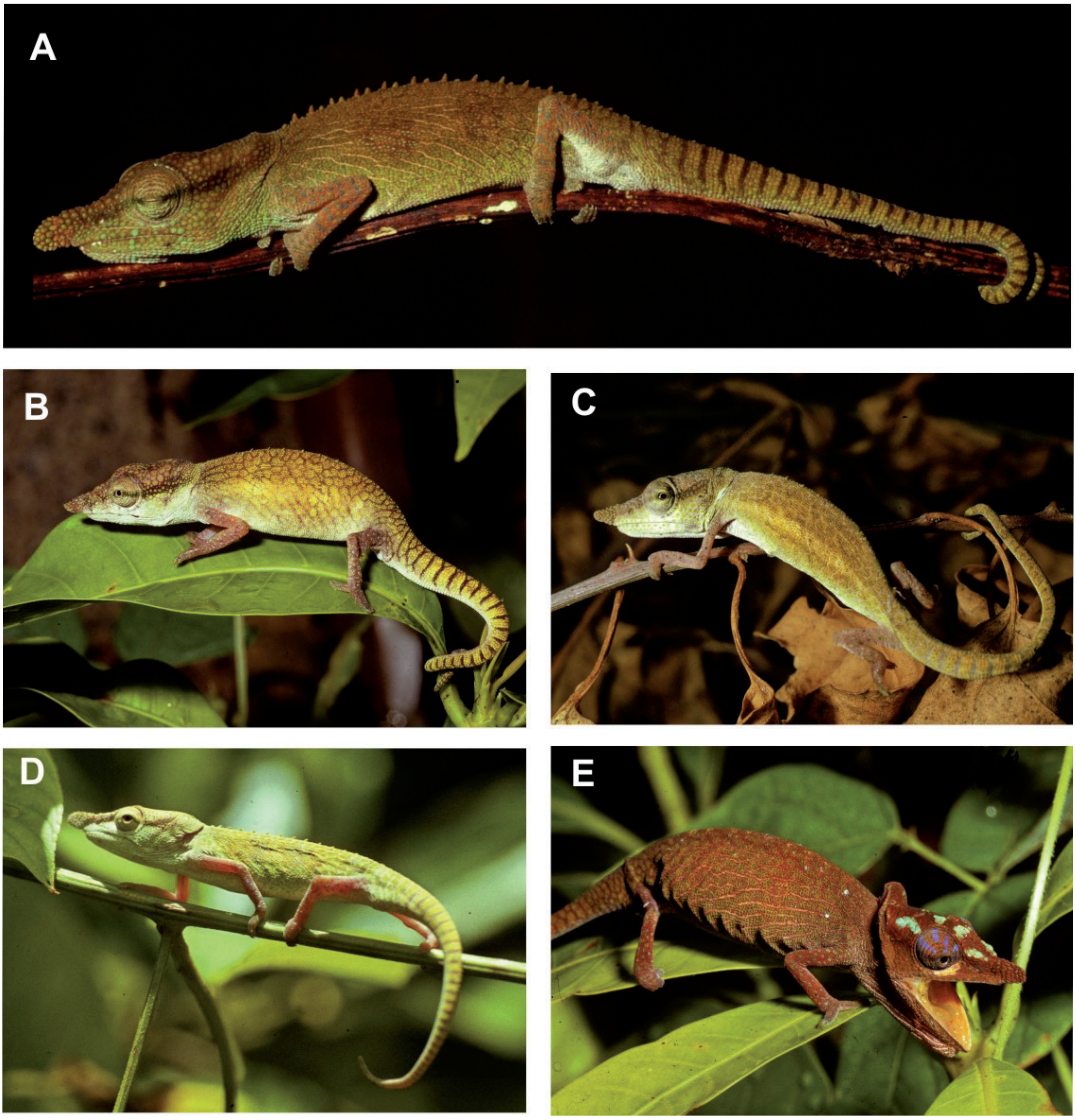

Figure 1. Specimens of *Calumma boettgeri* from Nosy Be in life (not collected). Photos A-D show different male individuals, illustrating the dark crossbands on tail, variation in the shape of the rostral appendage, and especially the variation in expression of the dorsal crest from very distinct (A) to rather indistinct (B). Photo E shows a female elevating the occipital lobes in threat posture, and with conspicuous color markings on head. All photos by F. Glaw.

(e.g. *C. boettgeri* and *C. gallus*) the rostral appendage bears a more conspicuous coloration than the rest of the head. Predominantly, these rostral appendages consist of colors in different shades of blue and red, colors that are highly reflecting in the ultraviolet spectrum and are potentially visible for the chameleons' eye (Bowmaker *et al.,* 2005; Gehring and Witte, 2007).

Morphological sexual dimorphism has never been assessed systematically in any species of the *C. nasutum* group. As a first in-depth assessment of this question, in this study we examine differences between males and females of one of its members, *C. boettgeri*, a species restricted to several localities in nothern Madagascar, for which a reasonable amount of adult specimens from a single, genetically homogeneous population (the type locality Nosy Be, Madagascar) was available.

Except for general description of morphological characters and body size, studies of chameleon morphology have rarely relied on detailed measurements or scale counts (pholidosis) (e.g. Andreone, 2001; Raxworthy and Nussbaum, 2006; Glaw *et al.,* 2009; Gehring *et al.,* 2011). Pholidosis is an established

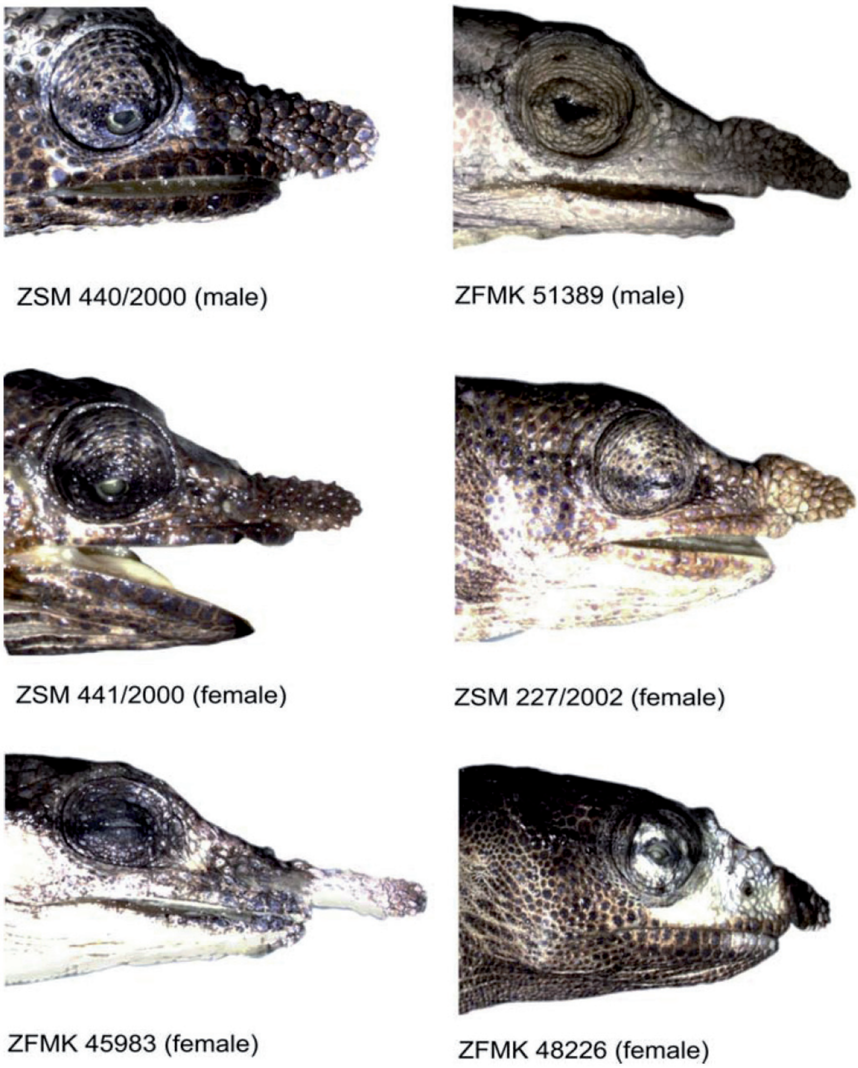

Figure 2. Lateral view of the head of selected specimen of *C. boettgeri* from Nosy Be. Males (ZSM 440-2000, ZFMK 52389) and females (ZSM 441/2000, ZSM 227/2002, ZFMK 45983, ZFMK 48226) represent different shapes of rostral appendage.

morphological feature for species diagnosis in other squamates, but the large number of small granular scales typical for chameleons make systematic counts more difficult than in many other taxa. Here, we define a set of measurements and scale counts, and use them analyze sexual dimorphism in *C. boettgeri*. We envisage that these newly defined characters might also become useful as a basis for an upcoming taxonomic revision of this group of chameleons.

Materials and Methods

The following measurements (Figs. 3-4) were taken from 21 adult specimens of *C. boettgeri* (eight males and 13 females, all from the type locality Nosy Be) with digital calipers to the nearest 0.1 mm (abbreviations as follows): HL, head length without rostral appendage; BL, body length; TAL, tail length; ED, horizontal eye diameter; FORL, forelimb length; HIL, hindlimb length; TEH, horizontal length of temporal edge; TEV, vertical length of temporal edge; OLN, depth of dorsal notch in occipital lobe connection; EHC, distance from eye center to posterior helmet cone;

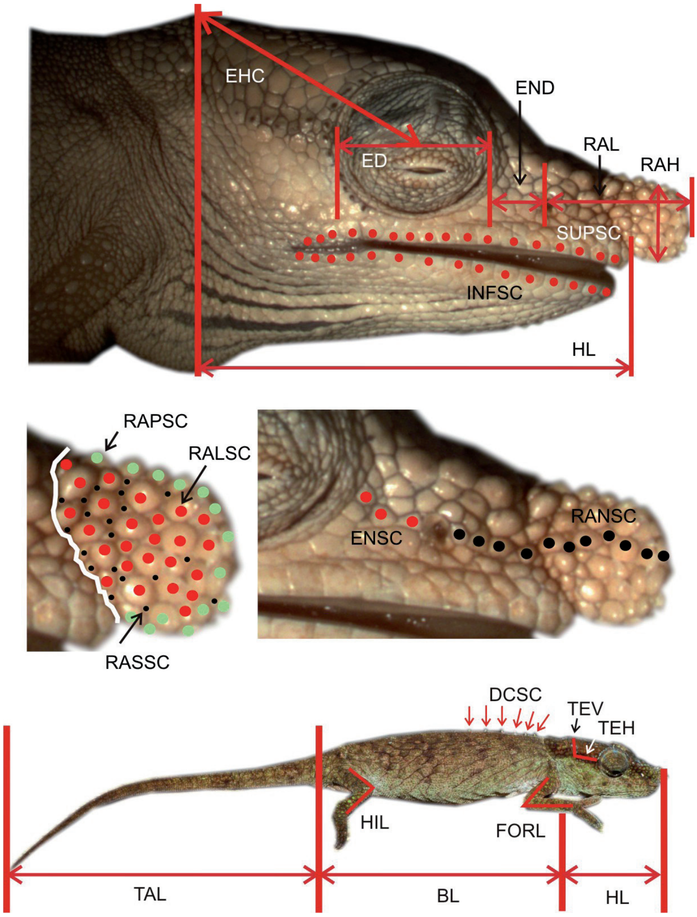

Figure 3. Landmarks for morphometric measurements and scale counts as used herein, shown in a lateral view of a *C. boettgeri* individual.

END, distance from anterior eye margin to nostril; RAL, length of rostral appendage, from nostril to tip of appendage; RAH, height of rostral appendage. Furthermore, snout-vent length (SVL) was calculated as the sum of HL+BL.

Furthermore, we assessed pholidosis by the following meristic variables (scale counts) (Figs. 3-4): RALSC, number of large scales on rostral appendage; RASSC, number of small scales on rostral appendage; RAPSC, number of peripheral scales on rostral appendage from top to bottom; RANSC, number of scales between nostril and tip of rostral appendage; ENSC, number of scales between anterior eye margin and nostril; OLPSC, number of peripheral scales of occipital lobe; OLSC, number of scales on occipital lobe; IOSC, number of interorbital scales; SUPSC, number of supralabial scales; INFSC, number of infralabial scales; DCSC, number of spines in dorsal crest. RANSC, OLPSC, OLSC, SUPSC, and INFSC were counted on both sides of the body and the mean value for each specimen was used for statistical analysis. Figs. 3-4 show the exact landmarks for measurements and scale counts. The following museum or collection abbreviations were used: ZFMK - Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; ZSM - Zoologische Staatssammlung München, Germany.

Results

In general, specimens of *C. boettgeri* are characterized by low casques and small occipital lobes that are not or at most marginally notched. Parietal crests are absent and rostral crests are rather indistinct. Lateral and temporal crests are indistinct. A rostral appendage which is flexible and dermal is present in both sexes, whereas the appendage of two females (ZFMK 45983, ZFMK 45986) seems to be amputated. Scalation is slightly heterogeneous with larger scales on the legs.

In life (Fig. 1) coloration of body and tail ranges from yellow to gray or brown. Legs are often reddish brown. On the tail there often are more than 20 dark crossbands. Most specimens show a distinct dark horizontal stripe on each side of the head, passing through the

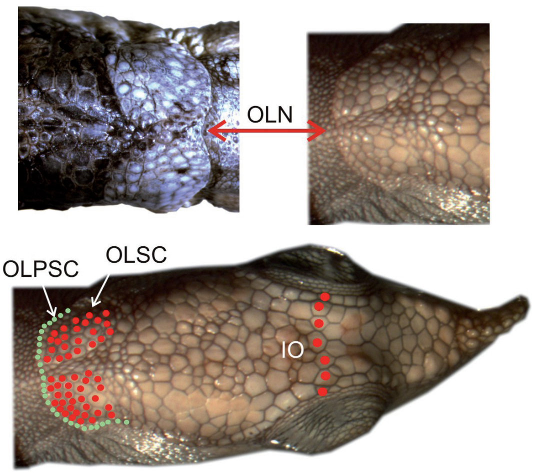

Figure 4. Scale counts as used herein, shown in a dorsal view of a *Calumma boettgeri* individual.

eyelids. A light lateral band on the flanks can be present. Displaying females show "threat spots" on the head.

Adult males can be recognized with high reliability by a thickened basis of the tail caused by the inverted hemipenes. Males tend to have rather uniform elongate and distally rounded (Fig. 2: ZSM 440-2000) or slightly lanceolate (Fig. 2: ZFMK 51389) rostral appendages, whereas in females this structure is more variable. The shape of the appendages in females ranged from short (Fig. 2: ZFMK 48226) to uniform elongate and distally rounded (Fig. 2: ZSM 441-2000), slightly lanceolate (Fig. 2: ZSM 227/2002) or relatively thin and elongate (Fig. 2: ZFMK 45983).

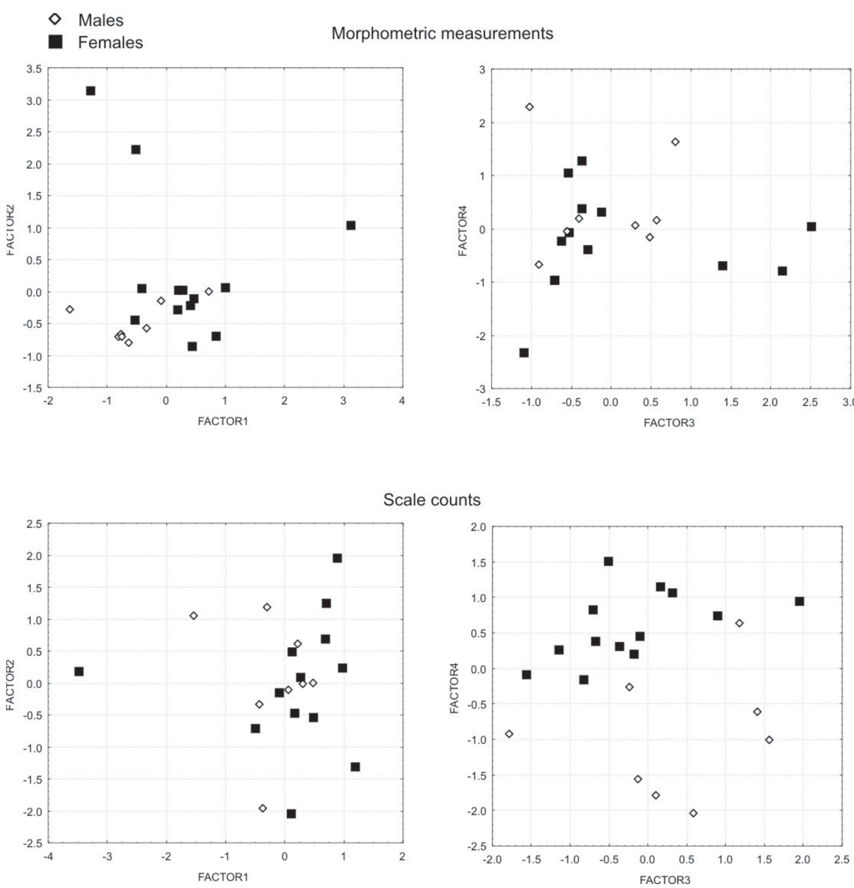

Figure 5. Scatterplots of the first four factors resulting from Principal Component Analyses based on morphometric measurements (upper graphs) and scale counts (lower graphs). Note that only factors 3 and especially factor 4 of the scale count graphs achieve a weak separation of males and females of *Calumma boettgeri*.

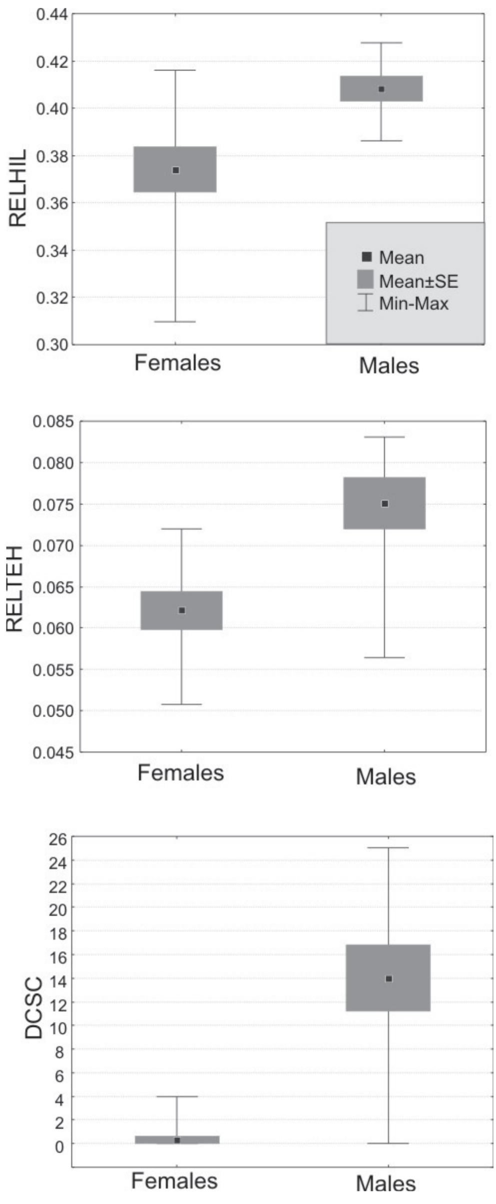

Figure 6. Plots of the three variables (relative hindlimb length, relative horizontal length of temporal edge, and number of spines in dorsal crest) in which significant differences among males and females of *Calumma boettgeri* were found in univariate comparisons (Mann-Whitney U tests; see text).

Morphometric and meristic comparisons

The morphometric data provided only weak indications for a differentiation among males and females of *C. boettgeri*. The most obvious difference between sexes of many chameleon species is size but no significant sexual dimorphism in size (SVL) was found in *C. boettgeri* (Mann-Whitney U test; P=0.238 Table 1).

Neither morphometric nor scale count variables attained a clear separation among males and females if summarized by a PCA, as visualized in the scatterplots in Fig. 5. A slight separation was achieved by factors 3 and especially 4 of the scale count variables (Fig. 5). While factor 3 reflected mainly variation in the number of supralabial and infralabial scales, factor 4 was mainly influenced by the number of spines in the dorsal crest (Table 3).

In univariate tests of relative measurements (values from Tables 1-2, divided by SVL) only relative hind limb length and relative horizontal length of the temporal edge were found to be significantly different among sexes (Mann-Whitney U tests; P=0.003 and P=0.011, respectively; Fig. 6). Similarly, the scale counts did not provide any convincing sexual difference, except a single one (number of spines in the dorsal crest; Mann-Whitney U-test, P<0.001; Fig. 6). In fact, a dorsal crest was absent in all females but one (ZFMK 45986; with the lowest number of spines in this single specimen, n=4), and present in all males but one.

Discussion

Altogether, the results presented here reveal only a weak differentiation among males and females of *Calumma boettgeri* in external morphology. We cannot exclude that with large sample sizes, additional differences could be found, but it is striking that basically no character provides an unambiguous means to differentiate among sexes of this species (except tail base length reflecting the presence of hemipenes in males, which however proved difficult to reliably measure).

The univariate tests suggested that male *C. boettgeri* have relatively longer hindlimbs (Fig. 6). In most lizards, longer hind limb length is associated with greater sprinting and and jumping ability, which has potential fitness consequences, especially in terms of escape from predators (Losos, 1990). Compared with other lizards, chameleons have weak leg musculature and rather rely on camouflage (Stuart- Fox *et al.*, 2006). The study of Stuart-Fox and Moussalli (2007) did not detect significant sexual differences in limb length in several dwarf chameleon species.

Sexes of *C. boettgeri* most convincingly differ in the number of spines in the dorsal crest. Dorsal crests are assumed to be a sexual trait that is generally more conspicuous in males or even lacks in females (Ord and Stuart-Fox, 2006). Nevertheless, our sampling includes one male (ZFMK 45987) that completely lacks a dorsal crest.

Klaver and Böhme (1986) suggested that ornamentation is a typical feature in chameleon species with male-biased body size dimorphism. *Calumma boettgeri*, and probably also other species of the *C. nasutum* group, combine rostral appendages with an absence of conspicuous body size dimorphism. These appendages occur in both sexes but do not show significant sexual differences of length or number of scales. However, such sexual dimorphism of the appendages within the *C. nasutum* group occurs at least in *C. gallus*, males possessing unique pointed rostral appendages and females shorter and rounded appendages. Other Malagasy chameleon species with rostral appendages (e.g., *Calumma furcifer*, and species of the *Calumma parsonii* group, *Furcifer rhinoceratus* group, and *Furcifer bifidus* group) show clear sexual dimorphism, the appendages typically being only present or much longer in males, and males typically attaining also larger body sizes especially in *Furcifer* (Glaw and Vences, 2007).

Several of the characters defined and used herein might be suitable to differentiate lineages or species in the *Calumma nasutum* group. For example, in the *C. guibei* complex specimens of two genetically distinct lineages show remarkable differences in the length and the number of scales on the rostral appendage and depth of the notch of the occipital lobes OLN (Gehring *et al.,* 2012; F. Eckhardt unpublished data). Branch and Tolley (2010) succesfully applied various scale count characters to define a new species in the chameleon genus *Nadzikambia*. This supports that morphometric and pholidotic characters can be useful to discern species boundaries in closely related chameleon species.

Acknowledgements. We are grateful to Wolfgang Böhme and Frank Glaw who made specimens held in their care available for examination, and for making photographs available used in Fig. 1. This work was carried out in the framework of collaborations of the author's institutions with the Université d'Antananarivo, Département de Biologie Aimale. We are indebted to the Malagasy authorities for research and export permits. PSG was supported by the Volkswagen Foundation.

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Accepted by Zoltan T. Nagy

Table 1a. Morphometric measurements in males and females of *Calumma boettgeri* from the type locality, Nosy Be. See Materials and Methods for abbreviations of variables.

Voucher	SVL	TEH	TEV	OLN	EHC	END
Males						
ZFMK 45987	50.8	3.7	5.0	0.0	18.0	4.0
ZFMK 45988	47.9	2.7	n.s	0.0	10.0	2.8
ZFMK 51389	51.7	4.2	n.s	0.5	11.0	2.1
ZFMK 51519	50.0	3.8	3.8	0.8	11.5	2.7
ZFMK 51520	50.6	4.2	n.s	0.0	11.0	2.8
ZFMK 51521	40.8	3.0	3.7	0.4	8.4	1.9
ZSM 440/2000	51.0	3.8	ns	0.3	11.3	2.4
ZSM 444/2000	49.4	4.1	3.0	0.2	11.1	2.6
Females						
ZFMK 45983	53.0	3.1	4.8	0.0	12.0	2.9
ZFMK 45984	55.2	3.3	4.6	n.a.	11.0	2.7
ZFMK 45985	48.6	2.6	4.7	0.5	9.9	1.8
ZFMK 45986	46.0	3.2	4.0	0.7	16.0	2.5
ZFMK 48226	44.6	3.1	3.7	0.3	8.1	2.6
ZFMK 48227	28.9	1.9	1.8	0.0	6.2	1.5
ZFMK 50615	44.3	n.a.	n.s	0.0	9.5	1.8
ZFMK 51516	52.5	3.6	3.9	0.0	13.0	1.5
ZFMK 51517	47.3	3.0	3.6	0.3	9.8	2.1
ZFMK 51518	48.9	n.a.	n.a.	0.3	7.5	2.5
ZSM 227/2002	47.8	2.5	2.4	0.0	8.3	1.8
ZSM 36/1913	41.1	3.0	3.7	0.0	9.8	1.8
ZSM 441/2000	45.3	2.3	2.6	0.4	10.0	1.7

Table 1b. Morphometric measurements of *Calumma boettgeri*, continued from Table 1a.

Voucher	RAL	RAH	TAL	ED	FORL	HIL
Males						
ZFMK 45987	4.9	2.3	48.5	4.7	19.2	20.9
ZFMK 45988	6.1	2.1	52.0	4.1	17.6	18.5
ZFMK 51389	5.9	2.4	48.5	4.7	18.7	20.8
ZFMK 51519	4.6	2.1	48.0	4.0	21.5	21.4
ZFMK 51520	5.6	2.3	42.1	4.6	19.8	20.4
ZFMK 51521	4.8	2.2	43.9	4.0	16.9	17.1
ZSM 440/2000	5.5	3.0	47.7	4.1	18.8	21.6
ZSM 444/2000	5.0	2.4	33.0	4.2	19.1	19.4
Females						
ZFMK 45983	6.9	1.4	44.0	4.5	16.8	17.3
ZFMK 45984	na	na	45.8	4.7	16.9	17.1
ZFMK 45985	6.0	2.2	37.9	4.5	17.4	17.9
ZFMK 45986	na	na	38.7	4.2	16.7	17.6
ZFMK 48226	4.3	1.9	42.2	3.8	18.8	17.6
ZFMK 48227	2.8	1.4	29.8	3.2	11.0	9.4
ZFMK 50615	4.0	2.3	38.2	3.7	17.4	17.9
ZFMK 51516	3.9	2.0	36.7	4.5	21.2	21.1
ZFMK 51517	5.8	2.4	41.2	4.2	16.8	17.9
ZFMK 51518	5.1	1.8	42.7	3.7	17.9	18.0
ZSM 227/2002	4.7	2.5	47.6	4.0	18.8	17.9
ZSM 36/1913	4.4	2.1	36.6	3.6	17.1	17.1
ZSM 441/2000	4.5	2.1	38.0	4.0	18.2	18.6

Table 2. Scale counts in males and females of *Calumma boettgeri* from the type locality, Nosy Be. See Materials and Methods for abbreviations of variables.

Voucher	RALSC	RASSC	RAPSC	RANSC	ENSC	OLPSC	OLSC	IOSC	SUPSC	INFSC	DCSC
Males											
ZFMK 45987	52	0	14	12/12	4	17/16	38/37	na	15/15	14/16	0
ZFMK 45988	63	18	17	16/16	4	22/22	43/36	7	19/19	16/16	12
ZFMK 51389	68	67	23	15/16	5	20/17	40/42	6	17/n.a.	16/20	19
ZFMK 51519	49	0	18	13/14	4	18/22	43/36	7	16/15	13/16	21
ZFMK 51520	70	20	17	13/12	4	20/17	42/40	8	18/20	16/16	8
ZFMK 51521	57	0	24	14/13	4	12/16	30/35	6	16/18	15/16	16
ZSM 440/2000	55	29	14	11/11	4	13/12	26/23	8	18/18	18/17	25
ZSM 444/2000	42	18	18	10/11	5	21/19	38/40	8	19/19	19/20	11
Females											
ZFMK 45983	40	10	17	11/11	4	12/14	33/45	6	19/21	15/15	0
ZFMK 45984	na	8	10	11/9	5	12/15	39/33	na	17/19	15/16	0
ZFMK 45985	41	8	15	12/14	5	15/16	39/42	7	20/18	15/16	0
ZFMK 45986	na	na	n.a.	n.a.	5	16/15	41/35	6	19/19	16/16	4
ZFMK 48226	38	0	13	12/13	5	18/23	52/48	7	18/20	18/20	0
ZFMK 48227	39	0	18	12/11	3	16/18	32/38	9	20/21	18/16	0
ZFMK 50615	48	0	17	11/12	4	24/20	45/39	7	18/18	17/17	0
ZFMK 51516	30	3	18	13/11	3	20/17	40/40	7	15/15	14/12	0
ZFMK 51517	70	4	24	11/12	4	21/20	42/34	7	15/15	15/16	0
ZFMK 51518	40	0	17	11/11	5	24/26	58/50	7	18/18	16/16	0
ZSM 227/2002	45	27	23	11/12	6	19/15	39/31	8	16/18	17/16	0
ZSM 36/1913	46	26	14	11/10	3	20/17	40/38	7	22/22	17/18	0
ZSM 441/2000	46	20	20	11/12	4	11/13	24/25	8	19/21	16/16	0

Table 3. Factor loadings, Eigenvalues and percent of explained variance of the first four factors from two Principal Component Analyses, based on morphometric variables (upper part of table) and scale counts (lower part of table). Loadings >0.7 are reproduced in bold.

Variable	Factor 1	Factor 2	Factor 3	Factor 4
TEH	0.198279	-0.264510	**0.775303**	-0.128356
TEV	-0.143733	-0.470742	**0.738770**	0.100736
EHC	**-0.736622**	0.164930	-0.297070	0.172611
OLN	-0.293686	**0.721216**	0.318128	-0.163185
RAL	-0.313259	**0.885547**	0.212216	-0.057263
RAH	-0.301403	**0.888684**	0.212432	-0.067218
TAL	-0.651844	-0.218232	0.248431	0.370298
ED	**-0.863367**	0.097407	-0.154128	-0.103591
FORL	**-0.714891**	-0.477559	-0.119127	-0.355039
HIL	**-0.819615**	-0.470459	-0.038962	-0.238353
END	-0.657801	0.003277	0.034521	0.647549
SVL	**-0.912606**	-0.088044	0.118289	-0.229761
Eigenvalue	4.496505	2.927140	1.542862	0.893670
% Total variance	37.47087	24.39283	12.85719	7.44725

Variable	Factor 1	Factor 2	Factor 3	Factor 4
IOSC	0.484953	-0.471730	-0.334281	-0.180175
RALSC	**-0.773731**	-0.023515	0.077093	0.114072
RASSC	**-0.894870**	-0.032147	-0.241344	-0.024591
RAPSC	**-0.814346**	0.060090	-0.069938	0.308110
DCSC	-0.324938	-0.049545	0.236620	**-0.818993**
ENSC	-0.394371	0.324342	-0.378699	0.069451
INFSC	-0.051427	0.013208	**-0.839913**	-0.415916
SUPSC	-0.005907	-0.318037	**-0.699068**	-0.020750
OLSC	0.209789	**0.881507**	-0.239453	0.215562
OLPSC	0.308143	**0.827340**	-0.173952	-0.131343
RANSC	-0.235835	0.417739	0.284577	-0.591708
Eigenvalue	2.756167	2.072753	1.742958	1.403838
% Total variance	25.05606	18.84321	15.84507	12.76217