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TWO NEW CHAMELEONS OF THE GENUS *CALUMMA* FROM NORTH-EAST MADAGASCAR, WITH OBSERVATIONS ON HEMIPENIAL MORPHOLOGY IN THE *CALUMMA FURCIFER* GROUP (REPTILIA, SQUAMATA, CHAMAELEONIDAE)

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During herpetological surveys in N.E. Madagascar two new species of *Calumma* chameleons belonging to the *C. furcifer* group were found and are described here. The first species, *Calumma vencesi* n. sp., was found at three rainforest sites: Ambolokopatrika (corridor between the Anjanaharibe-Sud and Marojejy massifs), Besariaka (classified forest south of the Anjanaharibe-Sud Massif), and Tsararano (forest between Besariaka and Masoala). This species is related to *C. gastrotaenia*, *C. guillaumeti* and *C. marojezensis*. *C. vencesi* n. sp. differs in having a larger size, a dorsal crest, and – in females – a typical green coloration with a network of alternating dark and light semicircular stripes. Furthermore, it is characterized by a unique combination of hemipenis characters: a pair of sulcal rotulae anteriorly bearing a papillary field; a pair of asulcal rotulae showing a double denticulated edge; and a pair of long pointed cylindrical papillae bearing a micropapillary field on top. The second species, *Calumma vatosoa* n. sp., found in ericoid habitat on the summit of the Tsararano Chain, is conspicuous due to its bright greenish coloration, with a longitudinal midlateral whitish band, and a yellowish spot in the middle of each flank. The hemipenis ornamentation includes a feature exclusive to this species which has not been described in any other species of the genus *Calumma*: the coexistence of three pairs of rotulae. This species is perhaps related to *C. peyrierasi*. The distribution of the species belonging to the *C. furcifer* group is also discussed from the point of view of biogeographic patterns and refuge massifs.

Key words: *Calumma*, Madagascar, chameleon, hemipenial morphology

INTRODUCTION

According to the revision of the family Chamaeleonidae proposed by Klaver & Böhme (1986, 1997) and complementary studies (Hofman *et al.*, 1991), two genera endemic to Madagascar and neighbouring islands are ascribed to the subfamily Chamaeleoninae: *Furcifer* and *Calumma*. Whereas most *Furcifer* species are typical inhabitants of deciduous habitats with a marked dry season – including degraded areas of this type – the *Calumma* species seem to be restricted to rainforests within the eastern region of Madagascar. Most of the latter exclusively occur in mid- and high-altitude rainforests, thus showing a rather narrow range of microthermal preferences: the highest elevational record belongs to *Calumma tsaratananensis*, collected at about 2500 m on the Tsaratanana Massif (Brygoo & Domergue, 1968). A phenetic classification based on external morphology proposed by Brygoo (1971) and reviewed by Glaw &

Vences (1994) identified five species groups within the genus *Furcifer* and four within the genus *Calumma*. The *Calumma furcifer* group has been recently reviewed by Böhme (1997), giving evidence for the elevation to full species status of the taxa formerly regarded as *C. gastrotaenia* subspecies: *C. guillaumeti*, *C. marojezensis* and *C. andringitraensis*. The description of *C. glawi* by Böhme (1997) made the *C. furcifer* group the richest species assemblage within the genera *Calumma* and *Furcifer*, with seven species.

During recent survey work in northern Madagascar, we had the opportunity to find several new species of amphibian and reptile and to obtain new records for others (e.g., Andreone *et al.*, 1998; Nussbaum *et al.*, 1998; Jesu *et al.*, 1998; Mattioli, 1998), thus stressing the importance of this geographic area. In particular, we collected two chameleons that did not fall into any known taxon, and therefore are regarded as new species. In this paper we describe them and summarize information on their distribution and phenetic relationships. Furthermore, we provide data on the hemipenis morphology and a preliminary key to the identification of the males of all the known species of this group.

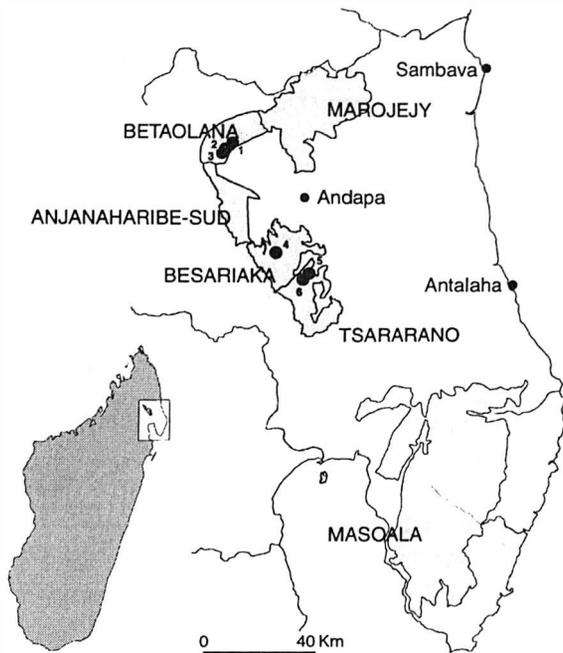


FIG. 1. Map of N.E. Madagascar with sites where some taxa belonging to the *Calumma furcifer* group were found during field surveys. 1-3, campsites 1-3 at Ambolokopatrika Corridor (collecting localities of *Calumma vencesi* n.sp.); 4, campsite 1 at Forêt de Besariaka (Betaolana Ridge) (collecting locality of *C. vencesi* n. sp.); 5, campsite 1 at Forêt de Tsararano (collecting locality of *C. vencesi* n.sp.); 6, campsite 2 at Forêt de Tsararano (collecting locality of *C. vatosoa* n. sp.). Area borders refer to the political boundaries of protected areas (PN de Marojejy, RS d'Anjanaharibe-Sud, PN de Masoala) and classified forests (Forêt de Besariaka, Forêt de Tsararano). Based upon FTM (Foiben-Taosarintanin'I Madagasikara/Institut Géographique et Hydrogéographique National) maps and a digital elaboration of GIS Service at WWF Madagascar.

MATERIALS AND METHODS

STUDY SITES AND PERIODS

The sites where the two new species were found are described below, and a map is given in Fig. 1. Latitudes and longitudes were given according to GPS prospecting, maps and IUCN/UNEP/WWF (1987). A more detailed description of these sites is given by Andreone *et al.* (2000).

(1) *Ambolokopatrika*. This forest is situated northwest of the Andapa Basin, between the Anjanaharibe-Sud and Marojejy massifs (Betaolana Ridge). The vegetation of the forest belongs to the domains of East and Central Madagascar (Humbert, 1955). Due to human activity, the Ambolokopatrika corridor is currently a mosaic of fairly intact forest, "savoka" (a degraded vegetational formation mainly constituted of herbaceous species) and secondary forest. At Ambolokopatrika three study sites were chosen, all within the Andapa Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), "Andemakatsara" (Campsite 1), 14°31.8'S, 49°26.5'E, 810-875 m (27 May - 3 June 1997); "Andranomadio" (Campsite 2),

14°32.4'S, 49°26.3'E, 860-910 m (4-12 June 1997 and 29 November-8 December 1997); "Antsinjorano" (Campsite 3), 14°32.6'S, 49°25.8'E, 950-1250 m (9-20 December 1997). The forest around Campsites 1 and 2 is a mid-altitude rainforest, while at Campsite 3 it is transitional between lowland and mid-altitude rainforest; at all sites there are patchworks of, on the one hand, fairly rather intact, and on the other, somewhat altered rainforest.

(2) *Besariaka*. This classified forest is about 60 km south of Andapa. It is delimited to the north by the RS d'Anjanaharibe-Sud, and to the south by the Tsararano Chain. The elevational range is 470-1232 m. Capture of the first newly described species occurred at "Ambinanin'ny miaka-midina" (Campsite 1), 14°50.8'S, 49°35.7'E, 940-995 m (4-15 June 1996). This campsite is within the Andapa Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province). There the forest is rather degraded, especially in parcels far from streams. This is apparently due to several reasons, among which are the use of forest areas for cattle, the cutting of trees by villagers, and the use of well established path systems to search for "bilahy" bark (used to make the local alcoholic beverage named "betsabetsa"), and for hunting.

(3) *Tsararano*. This chain, formed by several hills (altitude 400-1269 m) and the forest of the same name lie south of the Andapa Basin, midway between the Anjanaharibe-Sud Massif and the Masoala Peninsula. The collections were made at two sites: "Antsarahany tsararano" (Campsite 1), 14°54.4'S, 49°41.2'E, 700-850 m (29 November - 7 December 1996), and "Andatony anivo" (Campsite 2), 14°54.8'S, 49°42.6'E, 600-750 m (8-18 December 1996). Both of the campsites are included within the Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province). The forest of Tsararano appears to be quite intact, most likely due to its distance from large sized villages. As elsewhere, paths are being cut for the collection of local products and for the hunting of lemurs.

According to Goodman & Lewis (1998) the Andapa region is characterized by a humid and tropical climate. The mean temperature ranges from 18°C in July to 25°C in February. The relative humidity is about 87%, but reaches 97% in March and April. The annual precipitation is slightly more than 2000 mm. On average it rains 271 days per year. The "dry" season lasts about two months (September and October), with 41.1 mm and 52.6 mm of rain distributed throughout 14.7 and 15.1 days respectively.

CAPTURE AND PRESERVATION TECHNIQUES

Chameleons were captured by hand during the night when they are paler and more visible, with the aid of battery powered torches. Some specimens were photographed to obtain information on their natural coloration. Later they were euthanased, fixed in 10% formalin or in 90% ethanol, and preserved in a final so-

lution of 75% ethanol. The voucher specimens are now housed at the Museo Regionale di Scienze Naturali (Torino), and Parc Botanique de Tsimbazaza (Antananarivo).

ACRONYMS, MORPHOMETRY AND HEMIPENIS TERMINOLOGY

Throughout the text the following acronyms have been used: BM(NH), Natural History Museum, London (formerly the British Museum of Natural History); MNHN, Muséum national d'Histoire naturelle, Paris; MRSN, Museo Regionale di Scienze Naturali, Torino; MZUT, Museo di Zoologia dell'Università di Torino (collection now housed at the MRSN); MSNG, Museo Civico di Storia Naturale "G. Doria", Genova; PBZT-FN, Parc Botanique et Zoologique de Tsimbazaza, Antananarivo; ZFMK, Zoologisches Forschungsinstitut und Museum "Alexander Koenig", Bonn; PN, Parc National (National Park); RNI, Réserve Naturelle Intégrale (Strict Nature Reserve); RS, Réserve Spéciale (Special Reserve). Some specimens quoted in the species description (paratypes), and marked with an asterisk (*) currently bear the MRSN acronym, but will be later housed at PBZT. We also analysed several specimens belonging to the species of the *Calumma furcifer* group. All morphological measurements (Tables 1-2) were taken by one of us (F. Mattioli) with a dial calliper (precision at 0.1 mm): head length (HL), head depth (HD), head width (HW), socket diameter (SD), snout-vent length (SVL), tail length (TL), axilla-groin distance (AGD). For hemipenis morphology, we followed the terminology proposed by Klaver & Böhme (1986) and Böhme (1988).

The drawings of the external morphology of heads and hemipenes were made by tracing pictures obtained from slides in order to maintain the correct proportions; these were then enhanced with details gathered from direct observations using a binocular microscope.

On the basis of a few dissected specimens which all showed completely developed gonads, we assumed that all other specimens of a similar size were adults. The only exception was represented by the specimen MRSN R11682.2: in this case the dissection revealed the presence of incompletely developed ovaria, thus indicating that it had not reached maturity.

RESULTS

CALUMMA VENCESI NEW SPECIES

Diagnosis. A medium-sized chameleon (snout-vent length up to 73 mm), included in the *Calumma furcifer* group (*sensu* Glaw & Vences, 1994) by virtue of the absence of occipital lobes, absence of gular and ventral crest, markedly acute rostral profile and greenish coloration. This new species differs from all the others in the group in the following combination of morphological features: homogeneous scalation, divided canthi rostrales, absence of rostral appendage, evident lateral crests, evident nuchal fold, markedly oblique parietal

profile, double longitudinal ventral white line, weakly developed dorsal crest, rings made by 1-2 rows of white scales on upper surfaces of fingers [described as "*bagues au niveau des doigts*" by Brygoo (1978) in regard to *Calumma marojezensis*, formerly *Chamaeleo gastrotaenia marojezensis*]. Concerning the hemipenis ornamentation, it differs in that (1) a pair of sulcal rotulae anteriorly bear a papillary field, and (2) a pair of asulcal rotulae showing a double denticulated edge and a pair of long pointed cylindrical papillae bear a micropapillary field on top.

Holotype. MRSN R1690, Forêt d'Ambolokopatrika (Campsite 2), 870 m, 14 December 1997, leg. F. Andreone, G. Aprea and J. E. Randrianirina.

Paratypes. MRSN R1703.1-2, Forêt de Besariaka (Campsite 1), 950 m, 7 May 1996, leg. J. E. Randrianirina; MRSN R1681, Forêt de Besariaka (Campsite 1), 945 m, 9 June 1996, leg. F. Andreone and J. E. Randrianirina; MRSN R1682.1-2*, Forêt de Besariaka (Campsite 1), 970 m, 12 June 1996, leg. F. Andreone and J. E. Randrianirina; MRSN R1683.1-2, Forêt de Tsararano (Campsite 1), 700 m, 20 October 1996, leg. J. E. Randrianirina; MRSN R1684, Forêt de Tsararano (Campsite 1), 730 m, 28 November 1996, leg. F. Andreone and J. E. Randrianirina; MRSN R1685*, Forêt de Tsararano (Campsite 1), 730 m, 2 December 1996, leg. F. Andreone and J. E. Randrianirina; MRSN R1686.1 and R1686.2*, Forêt d'Ambolokopatrika (Campsite 2), 875 m, leg. F. Andreone, G. Aprea and J. E. Randrianirina 30 November 1997; MRSN R1687.1-2, Forêt d'Ambolokopatrika (Campsite 2), 860 m, 4 December 1997, leg. F. Andreone, G. Aprea and J. E. Randrianirina; MRSN R1688, Forêt d'Ambolokopatrika (Campsite 2), 865 m, 12 December 1997, leg. F. Andreone, G. Aprea and J. E. Randrianirina; MRSN R1689.1-3, Forêt d'Ambolokopatrika (Campsite 3), 960 m, 11 December 1997, leg. F. Andreone, G. Aprea and J. E. Randrianirina; PBZT-FN 6661 [specimen not measured], Forêt d'Ambolokopatrika (Campsite 1), 850 m, 29 May 1997, leg. F. Andreone and J. E. Randrianirina; PBZT-FN 6662 [specimen not measured], Forêt d'Ambolokopatrika (Campsite 1), 850 m, 29 May 1997, leg. F. Andreone and J. E. Randrianirina; PBZT-FN 6690 [specimen not measured], Forêt d'Ambolokopatrika (Campsite 1), 850 m, 2 June 1997, leg. F. Andreone and J. E. Randrianirina.

DESCRIPTION OF THE HOLOTYPE

External morphology. Adult male in a good state of preservation with fully everted hemipenes. Scales homogeneous, except on vicinity of cranial crests and parietal region (upper side of the cranium), in which they are a little bit larger. Head (Fig. 2) shows slightly developed orbital and parasagittal crests and rather developed lateral crest. The parasagittal crests joined at occiput apex. Absence of occipital lobes and gular crest. Canthi rostrales divided and rostral appendage

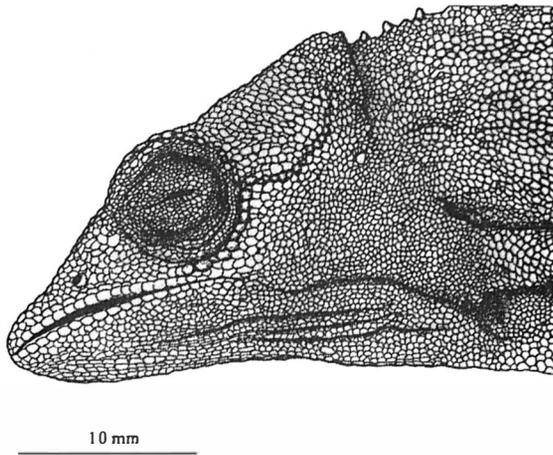


FIG. 2. Lateral view of the head of *Calumma vencesi* n. sp. (MRSN R1690, male, holotype).

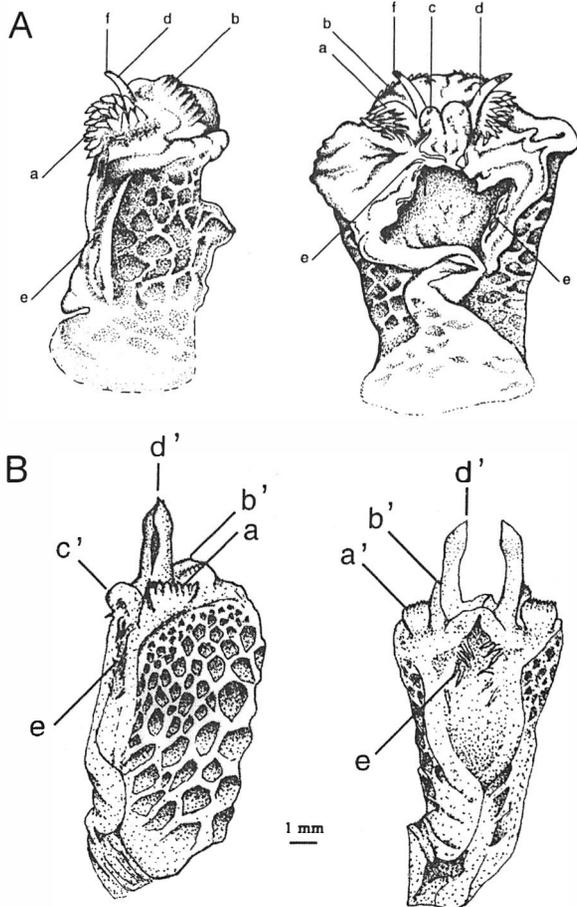


FIG. 3. Hemipenis morphology (lateral and sulcal view) of *Calumma vencesi* n. sp. (MRSN R1690, male, holotype) (A), compared with *Calumma marojezensis* (MRSN R1701) (B). Main ornamentations: sulcal rotulae bearing papillary field (a); asulcal rotulae bearing a double denticulated edge (b); pair of hypertrophic papillae (c); pair of long pointed cylindrical papillae (d); double row of pointed papillae on sulcal lips (e); micropapillary field (f); sulcal rotulae (a'); asulcal rotulae (b'); two hypertrophic papillae joined together (c'); pair of long pointed cylindrical papillae enlarged on top (d'). Same letters mark presumably homologous structures.

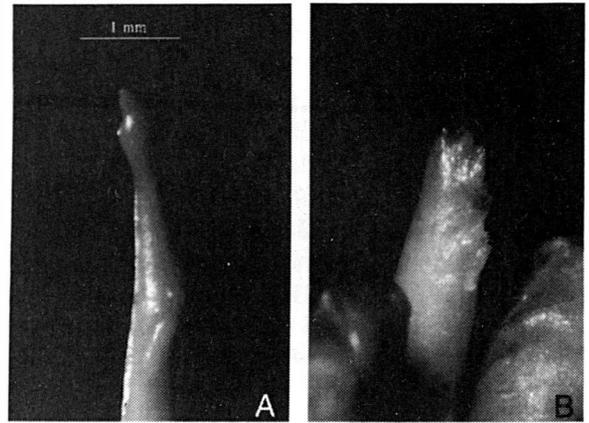


FIG. 4. Comparison between the tips of the cylindrical papillae of *C. marojezensis* (A) and the tips of the cylindrical papillae of *C. vencesi* n. sp. bearing a micropapillary field (B).

absent. Scales enlarged around nostrils. Markedly acute rostral profile and oblique parietal profile. At nape level a dermal fold extends on back for 2 mm. Occiput apex slightly raised forming a pointed helmet. Dorsal crest consisting of ten spines with different degrees of development distributed along the whole body length, but absent on tail. Deep axillary pockets. Number of scales at widest point of flanks: 58. Absence of ventral crest. Evident rings – often joined to each other – consisting of 1-2 rows of white scales on upper surfaces of fingers.

Hemipenial morphology. Hemipenis (Fig. 3) clavate, calcified, capitate, slightly flattened on sulcal plane. Sulcal lips markedly divergent. Sulcus with ridges and distally limited by a fleshy outgrowth sited at the point at which the sulcal lips join each other. Caput ornamentation consists of: (1) a pair of large sulcal rotulae bearing a papillary field on sulcal side; (2) a pair of smaller asulcal rotulae showing a double denticulated edge; (3) a pair of rounded hypertrophic papillae in sulcal central position; (4) a pair of long pointed cylindrical papillae – longer than any other ornamentation structures – bearing a micropapillary field on top (Fig. 4), sited between the pair of sulcal rotulae and the pair of central papillae; (5) a double row of twelve pointed thin papillae of various sizes respectively starting on left and right of the pair of central papillae and descending along the sulcal lips. Hemipenis length around 10 mm, i.e. 13.7% of snout-vent length.

Coloration in life. The male holotype (Fig. 5, photographed during the night) is characterised by a rather light green coloration on the back. Small scattered darker spots are also evident. A thin, pale line runs midlaterally from the head (at the level of the occiput indentation) to the hindlegs. Two light spots surrounded by a darker border are also visible along this line. Belly light green-whitish, with a double whitish longitudinal stripe bordered by reddish lines (like in most *C. gastrotaenia*). This light and reddish coloration

is also visible around the cloaca. A thin reddish stripe continues also on to the lower part of the tail-base.

Coloration in preservative. Predominantly greyish-blue, with many fine black spots on truncus, limbs and tail. Head blue with the exception of a few whitish areas on temporal region and throat (the latter sprinkled with black single scale-sized spots). Dorsum dark bluish shading into lighter tonalities approaching the ventral region, a few whitish areas above the limb insertions. Three white spots in longitudinal alignment running along mid-flanks. Axillary pockets white. Two longitudinal, ventral, white lines, separated by a thin medio-ventral dark blue line, originating at the proximal ends of arms and running all along the venter; a single longitudinal, ventral, white line running all along the tail.

Variation. The analysis of paratypes, belonging to three different populations (Ambolokopatrika, Besariaka, Tsararano), permits a first assessment of intraspecific variability, which can be summarized as follows: the mean total length in females is significantly smaller than in males [respectively 119.6±9.58 mm (mean±SD) compared to 135.8±4.79 mm; $t=4.48$, $df=15$, $P<0.05$], while there is no significant difference in mean SVL (respectively 62.9±7.57 mm compared to 68.9±3.14 mm; $t=2.19$, $df=15$, $P>0.05$); the female paratypes belonging to the Besariaka population (MRSN R1703.2, R1681, R1682.1) show a significantly larger size than all the other females (respectively 129.00±6.24 mm compared to 114.00±5.96 mm; $t=3.39$, $df=6$, $P<0.05$); the occiput apex is not heightened, thus meaning that the helmet is flattened, in most paratypes (MRSN R1703.1-2, R1681, R1682.1, R1682.2, R1683.1, R1683.2, R1684, R1685, R1686.1-2, R1687.1, R1688, R1689.1, R1689.3); a few specimens (MRSN R1689.1-2) show a reduced nuchal fold. The number of spines forming the dorsal crest is variable (1-4 in females, 2-13 in males), while its mean value, although higher in males than in females (males: 8.44±4.67; females: 3.5±0.93) is not significantly different (Mann-Whitney $U=16$, $P>0.05$); the dorsal keel is wavy and the rostral profile is extremely acute in the male paratype from Besariaka (MRSN R1703.1); the rings on the upper surfaces of the fingers are often joined together. The cylindrical papillae on the hemipenis apex may be much less developed (probably due to incomplete evagination); the number of pointed papillae forming the double row running along the sulcal lips is variable, but never smaller than ten; the white spots on the flanks may be less than three or absent, but always on the same line; the fine black spots on the flanks are found on all paratypes, even if their density may differ greatly from specimen to specimen. In life the coloration of females is very conspicuous (Fig. 6): the back and the flanks are light green shading to yellowish, with a network of darker irregular stripes that create a type of semicircular banding – rather interconnected (in the depicted

specimen this delineates something of a midlateral clear band), two brownish darker spots are situated on each flank overlapping the light band, scattered spots are visible more than in males and are more contrasted when lying upon the yellowish light coloration, the head is somewhat darker than the rest of the body especially on the parietal region, the eyes are brownish, the pupil is blackish with a light surround, as in males the belly is lighter with a whitish median longitudinal band internally bordered by two thin reddish lines; three females (MRSN R1683.1-2, R1684) belonging to Tsararano population show the dark stripes on the flanks even in preservative, this feature being less evident in the specimen MRSN R1684. MRSN R1682.2 turned out to be much smaller than all the other paratypes (SVL=45.0 mm; T=30.0 mm), and is therefore considered a young female, as confirmed by its dissection.

Etymology. We wish to dedicate this new species to Miguel Vences (Cologne, Germany), in recognition of his outstanding research activity on Malagasy herpetofauna.

Habitat and habits. *Calumma vencesi* n. sp. was found at the three forests between 700 and 960 m, thus showing an altitudinal range of about 260 m. It is, however, likely that the minimum altitudinal limit is lower, at about 600 m, while the maximum altitude be as much as 1000 m. This appears to be consistent with what is known for the various species belonging to the *Calumma gastrotaenia* complex, which usually have a narrow altitudinal distribution. At all the sites *C. vencesi* n. sp. appears to prefer rather intact parcels of forest. At Besariaka it was never found in cleared areas. As with other species in this group, it has been found almost homogeneously throughout the forest, without showing a clear preference for the riverine habitats (= forest at a distance lower than 20 m from the river). At the sites where it has been found *C. vencesi* n. sp. turned out to be rather abundant, and within a single search period (about 4 hours) we usually found between three and 10 specimens. At some locations, it seemed to be more common, although the reasons for this were not clear. Despite our intensive survey activity we never detected individuals during the day. Almost all the specimens were found at an elevation of 10-90 cm from the ground, usually hanging on to a leaf and having the head oriented upwards. We never observed phenomena of territoriality or other aggressive interactions.

CALUMMA VATOSOA NEW SPECIES

Diagnosis. A medium-sized chameleon (snout-vent length 60 mm), ascribed to the *Calumma furcifer* group (see later) due to the following characters: absence of occipital lobes, absence of gular and ventral crest, markedly acute rostral profile and greenish coloration. Assignment to the other *Calumma* group including medium-sized chameleons (*C. nasuta* group) cannot be supported because of the absence of the soft dermal

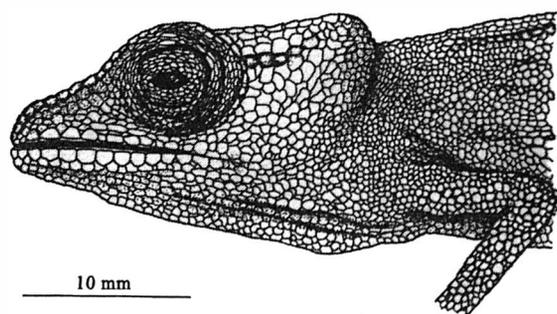


FIG. 7. Lateral view of the head of *Calumma vatosoa* n. sp. (MRSN R1628, male, holotype).

rostral appendage and the completely different hemipenis ornamentation. This new species differs from all the others of the group for the following combination of external morphological features: heterogeneous scalation, canthi rostrales joined at snout tip, absence of rostral appendage, evident lateral crests, flattened helmet, absence of dorsal crest and presence of axillary pockets. In terms of hemipenis ornamentation, there is a feature exclusive to this species which has not been described in any other species of the genus *Calumma*: the coexistence of three pairs of rotulae.

Holotype. MRSN R1628, adult male, Forêt de Tsararano (Campsite 2), 665 m, 14 December 1996, leg. F. Andreone and J. E. Randrianirina.

DESCRIPTION OF HOLOTYPE

External morphology. Adult male in good state of preservation. Hemipenes fully everted. Scalation heterogeneous: scales are uniformly small along the flanks, but significantly larger on head, limbs, dorsal keel and tail. Scale shape rounded on throat and limbs. Head (Fig. 7) shows slightly developed parietal and sagittal crests joined at mid length of parietal crests, rudimental orbital crests and lateral crests starting at

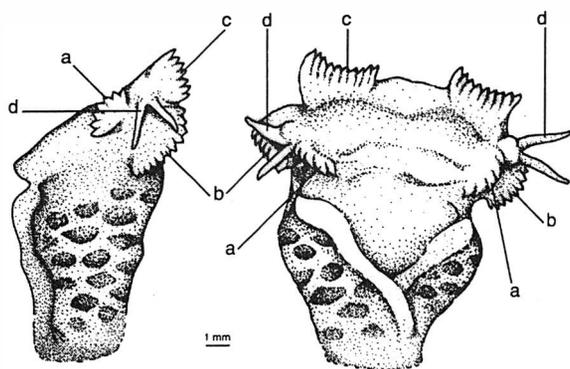


FIG. 8. Hemipenis morphology of *Calumma vatosoa* n. sp. (MRSN R1628, holotype): lateral view on the left, sulcal view on the right. Main ornamentations: sulcal rotulae (a); asulcal rotulae (b); large apical rotulae (c); pairs of papillae in latero-sulcal position (d).

mid orbit and approaching occiput following helmet profile. Absence of occipital lobes and gular crest. Canthi rostrales joined at snout tip. Acute rostral profile. Flattened helmet extends on dorsum for 2 mm. Absence of dorsal crest. Evident axillary pockets. Forty-nine scales at widest point of flanks.

Hemipenial morphology. Hemipenis clavate, calculated, capitate, considerably flattened on sulcal plane (Fig. 8). Sulcal lips markedly divergent. Caput ornamentation consists of the following: a pair of tiny sulcal rotulae (similar to auriculae) parallel to the sulcal plane; a pair of large apical rotulae, slightly concave on asulcal side; a pair of large asulcal rotulae in lateral position; two pairs of papillae in latero-sulcal positions, each of them with a shorter external papilla. Hemipenis length around 4.4 mm, i.e. 7.3% of snout-vent length.

Coloration in life. The single collected specimen possessed unusual coloration, until now unique among the *Calumma* chameleons (Fig. 9). Flanks and back have a greenish background, which – depending on the light exposure – varied from light to dark green. Warty scales of the flanks appear darker at their tip. A midlateral white stripe runs from the upper lip, past the front edge of the eye, to a position a few millimetres behind the hindlimbs. This band is wider towards the anterior end, and thinner posteriorly. The flanks are therefore divided by this white band: on the upper and lower sides a network of blackish lines is visible, more evident on the hind part of the back and on the tail. These lines are almost parallel (except for the lower “branches”) and run diagonally towards the anterior part of the body. At mid flank the greenish coloration becomes almost yellowish-orange, forming an irregular wide spot. A more or less yellowish area is also visible in the first half of the tail. The superior part of the head and the helmet are dark greenish-brown, with a darker line which passes throughout the eye and stops at the helmet’s posterior edge. Except for this dark stripe the eyelids are turquoise with a thin yellowish area just around the pupil. The coloration of the legs is similar to that of the back, although they appear a little darker, with the tubercles clearly visible and generally lighter than the background. The belly is much lighter than the rest of the body and is almost greyish-yellow, but without any well-delineated stripe. At the level of the axillae the coloration is lighter, almost whitish.

Coloration in preservative. In preservative the holotype faded, and the green coloration almost disappeared, changing to a dark bronze with shades through to black. The throat and venter were paler than in life. Conspicuous spots absent, unless due to scale wear.

Etymology. The Malagasy word “vatosoa” is a compound of “vato” (meaning stone), and “soa” (meaning beautiful), and in general it is used to indicate a crystal, jewel or precious stone. We assign this name to the new chameleon from Tsararano for its wonderful live coloration, which could indeed be a symbol for Malagasy beauty and for herpetological conservation. In addition,

Franco Andreone wishes to dedicate this new species to his daughter, Serena Crystal Vatosoa, with much love and hope of endless happiness.

Habitat and habits. At the place where the holotype was found (Tsararano, 665 m) the forest appears to be a mixture of typical rainforest with small patches of *Philippia* [= *Erica*] ericoid heathland. This vegetation is present here at a lower altitude than at other sites (e.g. at Marojejy it appears to be confined to altitudes higher than 1800 m: Nicoll & Langrand, 1988). *Calumma vatosoa* n. sp. seems to be a chameleon closely tied to this habitat. The holotype was found during the day about 110 cm from the ground.

JUSTIFICATION OF THE TWO NEW SPECIES AND OBSERVATIONS ON HEMIPENIS MORPHOLOGY

Calumma vencesi n. sp. shows general external morphological features that led us to include it in the *C. furcifer* group, which has until now comprised the following species: *C. furcifer*, *C. gastrotaenia*, *C. peyrierasi*, *C. guillaumeti*, *C. marojezensis*, *C. andringitraensis* and *C. glawi*. Nevertheless, remarkable differences allow identification of the new species, which differs from *C. furcifer* in the absence of the forked rostral appendage in males; from *C. peyrierasi* in terms of its larger size and the double longitudinal, whitish ventral lines; from *C. gastrotaenia* and *C. guillaumeti* in terms of the larger size of males, reduced or absent dorsal crest, nuchal fold and rings on

fingers; from *C. andringitraensis* by the larger size of males, nuchal fold, rings on fingers; from *C. glawi* by the larger size of males and reduced dorsal crest; from *C. marojezensis* in terms of the nuchal fold and markedly oblique parietal profile (subhorizontal in *C. marojezensis*). The obvious differences from *C. vatosoa* n. sp. are discussed at the end of this section.

Moreover, in accordance with Klaver & Böhme (1986, 1997), Böhme (1997) and Ziegler & Böhme (1997), we assume that the hemipenis morphology plays a fundamental role in specific recognition of chameleons, in particular within the *C. furcifer* group, in which morphological differences are less obvious than in other groups. The comparison of the hemipenis structure of *C. vencesi* n. sp. with that already described for the other taxa belonging to the *C. furcifer* group shows evidence for the presence of some ornamentation structures exclusive to this new species: (1) the papillary field on each sulcal rotula; (2) the double denticulated edge of each asulcal rotula; (3) the pair of pointed cylindrical papillae bearing a micropapillary field on top (Fig. 4). The double row of pointed papillae descending along the sulcal lips is not a feature exclusive to *C. vencesi*, since we observed the same ornamentation (Fig. 3) also in all the examined males of *C. marojezensis* (two from Marojejy and five from Masoala). This feature was overlooked by Brygoo *et al.* (1970a), when they described the peculiar hemipenis morphology of *C. marojezensis* in examining the

TABLE 1. Biometric measurements (in mm) of the type specimens of *Calumma vencesi* n. sp. and *C. vatosoa* n. sp. M, male; F, female; J, juvenile; SVL, snout-vent length; TL, tail length; HL, head length; HD, head depth; HW, head width; SD, socket diameter; AGD, axilla-groin distance.

Species	Status	Sex	Locality	SVL	TL	HL	HD	HW	SD	AGD
<i>Calumma vencesi</i> n. sp.										
MRSN R1690	Holotype	M	Ambolokopatrika	73.0	72.0	19.0	14.2	11.0	5.6	38.0
MRSN R1686.1	Paratype	M	Ambolokopatrika	70.0	64.0	18.0	13.0	9.6	5.8	39.0
MRSN R1686.2	Paratype	M	Ambolokopatrika	73.0	64.0	19.3	10.5	10.0	6.0	40.0
MRSN R1687.1	Paratype	M	Ambolokopatrika	68.0	67.0	18.0	12.0	10.5	5.6	38.0
MRSN R1687.2	Paratype	M	Ambolokopatrika	69.0	62.0	19.0	13.0	10.6	6.3	40.0
MRSN R1688	Paratype	M	Ambolokopatrika	70.0	68.0	19.8	12.0	10.6	5.2	38.0
MRSN R1689.2	Paratype	M	Ambolokopatrika	63.0	67.0	17.0	11.0	9.8	5.0	32.0
MRSN R1689.1	Paratype	F	Ambolokopatrika	60.0	56.0	17.3	10.0	9.4	5.4	30.0
MRSN R1689.3	Paratype	F	Ambolokopatrika	52.0	54.0	15.4	9.3	8.7	4.5	27.0
MRSN R1703.1	Paratype	M	Besariaka	67.0	73.0	21.5	11.5	9.9	6.0	33.0
MRSN R1703.2	Paratype	F	Besariaka	67.0	55.0	20.0	12.0	9.0	5.9	29.0
MRSN R1681	Paratype	F	Besariaka	71.0	63.0	19.5	11.0	10.0	6.0	36.0
MRSN R1682.1	Paratype	F	Besariaka	72.0	59.0	21.0	12.0	10.5	6.0	37.0
MRSN R1682.2	Paratype	J	Besariaka	45.0	30.0	13.5	8.5	7.5	4.0	21.0
MRSN R1685	Paratype	M	Tsararano	67.0	65.0	17.0	11.0	9.6	6.1	32.0
MRSN R1683.1	Paratype	F	Tsararano	56.0	55.0	16.8	10.2	9.0	5.0	27.0
MRSN R1683.2	Paratype	F	Tsararano	57.0	58.0	17.0	11.7	9.5	5.6	30.0
MRSN R1684	Paratype	F	Tsararano	68.0	54.0	17.0	10.7	9.4	5.5	42.0
<i>Calumma vatosoa</i> n. sp.										
MRSN R1628	Holotype	M	Tsararano	60.0	66.0	18.0	9.0	7.5	6.4	36.0

holotype (MNHN 1993.0160). We noticed the occurrence of this ornamentation both in the holotype and in the only paratype showing everted hemipenes (MNHN 1989.2873). In this respect, we consider it helpful to redescribe the hemipenis structure of this species using for the first time the terminology introduced by Klaver & Böhme (1986). The following description deals with the ornamentations observed in the specimen MRSN R1701: hemipenis (Fig. 3) clavate, calculated, capitate, sulcal lips divergent, caput ornamentation consists of: (1) a pair of sulcal rotulae; (2) a pair of asulcal rotulae; (3) a pair of rounded hypertrophic papillae in sulcal central position joined together to form a unique structure; (4) a pair of very long, pointed cylindrical papillae slightly enlarged on top, sited between the pair of sulcal rotulae and the pair of central papillae; (5) a double row of fifteen pointed, thin papillae of various sizes respectively starting on the left and the right of the pair of central papillae, and descending along the sulcal lips. Hemipenis length around 14 mm, i.e. 22% of SVL. Within the caption of Fig. 3, which compares hemipenis ornamentations of *C. vencesi* n. sp. and *C. marojezensis*, the identification of presumably homologous structures has been suggested following the guidelines already proposed by Klaver & Böhme (1986). In this context, we consider homologous the pair of hypertrophic papillae with the unique structure made by their fusion, and the respective pairs of sulcal rotulae, asulcal rotulae, and pointed cylindrical papillae. In terms of the double row of pointed papillae on the sulcal lips occurring in *C. vencesi* n. sp. and *C. marojezensis*, it appears that this is a structure maintained in a very conservative way in both species. It is difficult to establish whether all these characters might be considered as plesiomorphic, and whether the long and pointed papillae in *C. vencesi* n. sp. are apomorphic characters. Further studies and comparative analyses in this area are badly needed.

Whereas the absence of the rostral appendage in *Calumma vatosoa* n. sp. and the double, ventral white lines makes it unlikely that the species would be confused with *C. furcifer*, it is clearly different from *C. gastrotaenia*, *C. marojezensis*, *C. guillaumeti*, *C. andringitraensis* and *C. glawi* due to different head morphology and, again, the absence of the double ventral white line. The general morphology apparently shares some similarities with *C. peyrierasi*, this being confirmed by some affinities in hemipenis ornamentation (a pair of large apical rotulae; a pair of asulcal rotulae in lateral position; two pairs of papillae in latero-sulcal position, each of them showing the external one as shorter). The description and the drawings of the hemipenis structure of *C. peyrierasi* are reported by Brygoo *et al.* (1974). Nevertheless, *C. vatosoa* n. sp. reaches a larger size than *C. peyrierasi* (126 mm compared to 110 mm), and has a flattened helmet extending caudally (the occiput is heightened in *C. peyrierasi*), canthi rostrales which – even though joined at snout tip

– do not limit a depressed area, and no dorsal crest. Finally, a comparison with *C. vencesi* n. sp. reveals obvious differences: the holotype of *C. vatosoa*, besides lacking ventral lines, dorsal crest and rings on fingers, is in fact characterised by heterogeneous scalation and joined canthi rostrales. Further evidence for treating MRSN R1628 as a new taxon comes from the comparison of hemipenis ornamentation: the third pair of rotulae observed in this specimen has not been found in any other *Calumma* species so far described.

MORPHOMETRIC OBSERVATIONS

Within *Calumma vencesi* n. sp., males are in general larger than females (Table 1). The adult specimens of the typical series showed that males and females have a mean SVL±SD of 68.9±3.1 mm and 62.9±7.6 mm respectively. These values are significantly different ($t=2.19$; $df=15$, $P<0.05$). The same significance was found for other biometric parameters, such as tail length, head depth and axilla-groin distance. Conversely, we did not find any significant difference in biometric ratios, although these are usually higher in males. This suggests, at least according to the limited number of specimens examined, that in this species males differ from females mainly in general body size, rather than in development of the morphometric characters analysed. Most likely a different body size, associated with behaviour and coloration, are sufficient to ensure male-female recognition in the wild.

Calumma vencesi n. sp. appears to be the largest member of the *C. furcifer* group analysed by us, with a maximum SVL of 73.0 mm (Table 2). In terms of body length, *C. vencesi* n. sp. is followed by *C. marojezensis*, *C. gastrotaenia*, *C. andringitraensis* and *C. guillaumeti*. *Calumma furcifer* has been reported (Glaw & Vences, 1994) to reach a total length of 150 mm, which represents the highest value ever recorded in any species belonging to the *C. furcifer* group. *C. andringitraensis* and *C. guillaumeti*, as already stated, are typical high altitude taxa, therefore their small SVL may be related to their elevational preference. Almost nothing is known about the size range of either *C. vatosoa* n. sp. or *C. peyrierasi*, of which only two specimens are known.

Differences between the males of *C. vencesi* n. sp. and *C. marojezensis* concern the SVL, which is significantly different ($t=3.29$, $df=16$, $P<0.01$) and the head depth/head length ratio ($t=2.16$, $df=16$, $P<0.05$). *C. vencesi* n. sp. is also larger than *C. gastrotaenia* (68.9±3.1 versus 60.4±8.5 mm; $t=2.77$, $df=14$, $P<0.05$), while no other significant differences are found for the other parameters. The comparison between *C. vencesi* n. sp. and *C. guillaumeti* (three measured specimens) shows significant differences regarding all the lengths, which seems obvious taking into account the remarkable diversity between these two taxa (*C. guillaumeti* has a mean SVL which more or less corresponds to 77% of *C. vencesi* n. sp.).

Females of *C. gastrotaenia* are smaller in SVL (49.0 ± 4.35 mm) than females of *C. vencesi* n. sp. (62.9 ± 7.6 mm; $t=2.94$, $df=15$, $P<0.05$), which differ also for the socket diameter / SVL ratio (0.10 ± 0.01 versus 0.09 ± 0.01 ; $t=3.25$, $df=9$, $P<0.01$). Conversely, female *C. marojezensis* and *C. vencesi* n. sp. do not differ in general lengths, while they show significant differences in the axilla-groin distance (37.6 ± 2.8 mm versus 32.3 ± 5.5 mm; $t=2.56$, $df=15$, $P=0.05$) and in axilla-groin / SVL ratio (0.58 ± 0.03 versus 0.51 ± 0.05 ; $t=3.45$, $df=15$, $P=0.01$).

It therefore appears that, with a few exceptions, differences between sexes and species lie mainly in size. The group appears to be extremely conservative in terms of coloration, ecology and morphology, and – for this reason – identification in the field is somewhat difficult. Thus, we can reasonably hypothesize that other undescribed taxa remain to be discovered within the *C. furcifer* group, especially in the territories of central and south-eastern Madagascar.

KEY TO THE MALES OF THE *CALUMMA* *FURCIFER* GROUP

Here we provide an identification key to the males of the *Calumma furcifer* group, based mainly on the external morphology (thus excluding hemipenial characters), coloration, and provenience. The females of this groups are substantially similar, and it is extremely difficult to identify diagnostic characters. Furthermore for many species they are still unknown.

1. Bifid rostral appendage..... *Calumma furcifer*
No rostral appendage..... 2
2. One longitudinal stripe or no stripes at all at mid-venter.....3
Two parallel white longitudinal stripes at mid-venter5
3. Nuchal fold..... *C. glawi*
No nuchal fold.....4
4. Dorsal crest well developed.....*C. peyeriasi*
No dorsal crest.....*C. vatosoa* n. sp.
5. Dorsal crest well developed at least on the anterior two-thirds of the body.....6
Dorsal crest absent, or if present, slightly developed and not exceeding the anterior two-thirds of the body.....7
6. Helmet well developed and swollen on the occiput, white spots on the flanks usually arranged in one row, under 1100 m altitude, probably central-eastern Madagascar.....*C. gastrotaenia*
Helmet normally developed and flattened on the occiput, white spots on the flanks usually arranged in two or more rows, between 1200 and 1700 m altitude, likely only in N. Madagascar (complex Tsaratanana-Marojejy-Anjanaharibe-Sud).....
.....*C. guillaumeti*
7. Very distinct mid-ventral white stripes starting at the tip of the chin (Andringitra Massif, 1500 m).....
.....*C. andringitraensis*

Mid-ventral white stripes slightly distinct anteriorly to the insertion of forelegs, well distinct posteriorly to it.....8
8. Nuchal fold present, body comparatively well-developed vertically; oblique parietal profile.....*C. vencesi* n. sp.

No nuchal fold, body comparatively slender, sub-horizontal parietal profile..... *C. marojezensis*

DISCUSSION

The description of two new species of *Calumma* chameleon emphasizes, once again, how the Madagascan herpetofauna, although considerably diverse in species (182 amphibians and 333 reptiles according to Glaw & Vences, 2000) is still poorly known. Indeed, other species await discovery: producing descriptions is therefore a race against time, as species are habitat-specific, and the implacable deforestation affecting Madagascar makes it likely that many species will disappear before they are known to science.

The biogeographical importance of northern Madagascar is also confirmed by several other findings, including some dwarf *Brookesia* chameleons (Raxworthy & Nussbaum, 1995), skinks of the genus *Mabuya* (Nussbaum & Raxworthy, 1998), treefrogs of the genus *Boophis* (Andreone, 1996), a new *Pseudoxyrhopus* snake (Nussbaum *et al.*, 1998), and the second known specimen of the colubrid *Brygophis coulangesi* (Andreone & Raxworthy, 1998). This richness in species diversity is most likely due to several different causes, including (1) presence of many ecosystems, including rainforests and dry deciduous areas; (2) presence of many massifs (such as Anjanaharibe-Sud, Marojejy, Manongarivo, Tsaratanana, Montagne d'Ambre) which act as biogeographic refuges; and (3) the active survey work carried out by several teams in the last years.

The two new chameleons have been included in the *Calumma furcifer* group, which appears to be composed of two different phenetic clusters. The first is represented by the “*Calumma gastrotaenia*-like” species, which include the former subspecies of *C. gastrotaenia* (*C. gastrotaenia*, *C. guillaumeti*, *C. marojezensis*, *C. andringitraensis*), *C. glawi*, *C. vencesi* n. sp., and possibly, *C. furcifer*. All these chameleons are green coloured, live mainly in primary rainforests (or in mature secondary rainforests), and generally show limited capacities to adapt to disturbed environments. The only possible exception to this ecological preference is represented by *C. gastrotaenia*, which has sometimes recorded even on shrubby vegetation along asphalted roads and in areas in where selective logging has taken place (L. Brady, pers. comm.; F. Andreone pers. obs.). Moreover, with the exception of *C. furcifer*, these species do not have dermal appendages, and possess a body almost flattened laterally yet rather well-developed vertically. All the species exhibit overall similar ecological preferences, and occupy apparently analogous spatial, temporal, and trophic niches. They are often vicariant, either in terms of geo-



FIG. 5. Holotype (MRSN R 1690, male) of *Calumma vencesi* n. sp. from Ambolokopatrika, N.E. Madagascar.

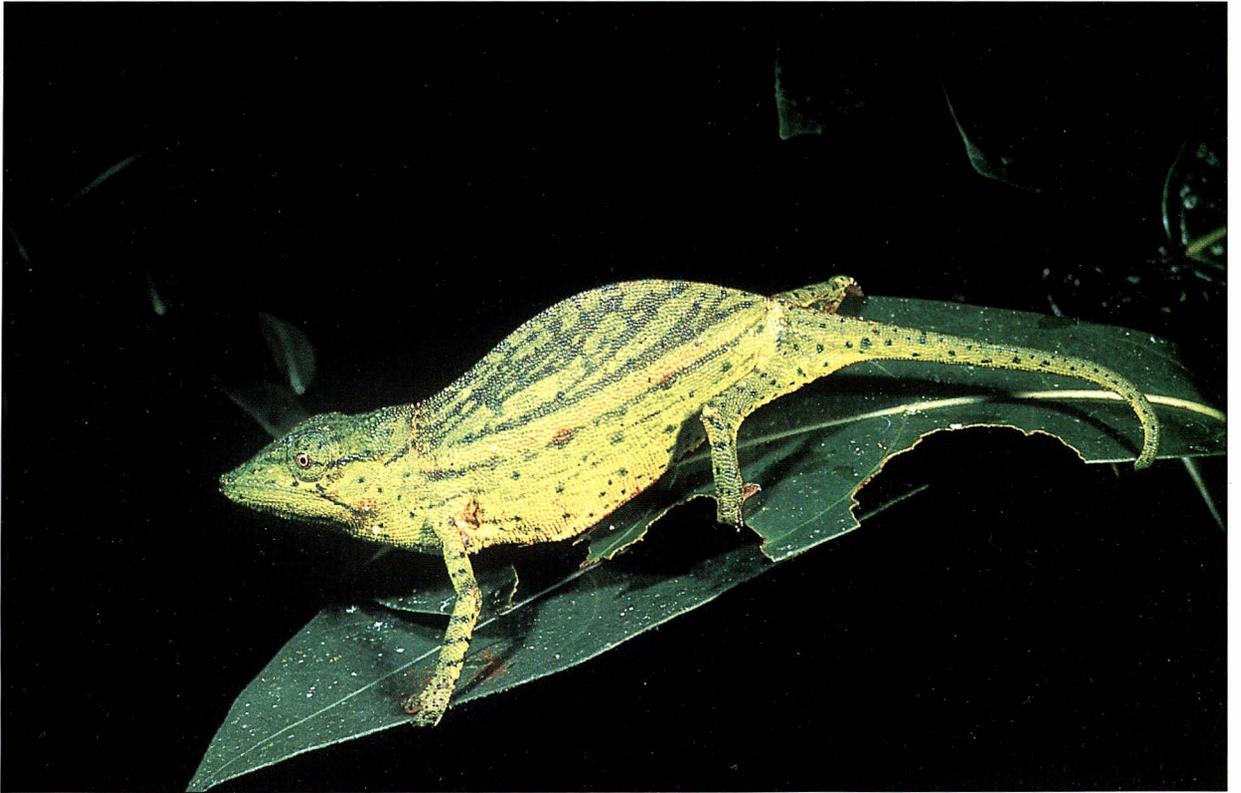


FIG. 6. *Calumma vencesi* n. sp. (PBZT-FN 6690, female) from Ambolokopatrika, N.E. Madagascar.



FIG. 9. Holotype (MRSN R1628, male) of *Calumma vatosoa* n. sp. from Tsararano, N.E. Madagascar.

graphical distribution or elevation. According to our knowledge, *C. gastrotaenia* is present in the central eastern rainforests, at low and mid-altitudes (Andreone, 1991a,b; Glaw & Vences, 1994; Brady & Griffiths, 1999). It is possible, on the other hand, that some *C. gastrotaenia* records belong to other taxa that yet have to be described. As an example, the recent works by Nussbaum *et al.* (1999) at Andohahela (S.E. Madagascar) provided evidence for the presence of *C. gastrotaenia*. Anyhow, it is not clear whether these authors follow Böhme's (1997) suggestion to consider former subspecies of *C. gastrotaenia* as full species. If this was the case, the *C. gastrotaenia* from Andohahela would correspond to the "old" *C. g. gastrotaenia*.

Apart from *C. gastrotaenia* (which has a wide distribution), the other members of this group from central-eastern Madagascar are *C. andringitraensis*, which is known for Andringitra Massif (Rasolonandrasana & Goodman, 2000), and *C. glawi*, from the Ranomafana area (Böhme, 1997). *C. glawi* is the only taxon known to occur in sympatry (likely in syntopy) with another species of the same group (namely *C. gastrotaenia*: L. Brady, pers. comm.). Observations of *C. glawi* at Ranomafana indicate that it is generally allotopic with *C. gastrotaenia*. Brady and co-workers (pers. comm.) observed both species at several locations within this national park. At Vatoharanana (the study area detailed by Jenkins *et al.*, 1999), only *C. glawi* was observed. However, at nearby Vohiparara both species occur together and are therefore syntopic.

All the other species are apparently restricted to N. Madagascar. According to current information,

Calumma guillaumeti is a high altitude species, which was found at 1200-1675 m on three massifs: Marojejy (Brygoo *et al.*, 1974; Raselimanana *et al.*, 2000), Anjanaharibe-Sud (Raxworthy *et al.*, 1998) and Tsaratanana (Jesu *et al.*, 1998; Mattioli, 1998). These findings suggest that the current distribution is due to the restriction of this species to refuge massifs. The hemipenis morphology of *C. guillaumeti* is different from that observed in the other taxa closely related to *C. gastrotaenia*. Interestingly, another species, *C. andringitraensis*, exhibits morphological and hemipenial characters which appear to make these two species very similar (Glaw & Vences, 1994; Mattioli, 1998). Like *C. guillaumeti*, *C. andringitraensis* has been found only at rather high altitudes (up to 1680 m on the Andringitra mountains; Raxworthy & Nussbaum, 1996). We are inclined to consider *C. guillaumeti* and *C. andringitraensis* as sister species, with a north-south vicariant distribution. In this sense they are similar to other taxa having this kind of distribution, such as the snakes *Pseudoxyrhopus sokosoko* and *P. heterurus* (Raxworthy & Nussbaum, 1994), the green treefrogs *Boophis jaegeri* and *B. andohahela*, the dwarf chameleons *Brookesia lolontany* and *B. nasus* (Raxworthy & Nussbaum, 1995).

Another species of this group, *C. marojezensis*, is restricted to northern Madagascar, but appears to be a lowland taxon. Up to now it has been recorded at Marojejy, Masoala, Anandrivola and, possibly, Anjanaharibe-Sud. Actually the last record, reported by Raxworthy *et al.* (1998), needs confirmation, since the re-examined specimens currently conserved at Torino

TABLE 2. Biometric measurements (precision at 0.1 mm) of adult males and females (juveniles are excluded) of the species belonging to the *Calumma furcifer* group, including the newly described *C. vencesi* n. sp. and *C. vatosoa* n. sp. For each taxon the mean \pm SD (1st row), and range (minimum and maximum values, 2nd row, in parentheses) are given. Abbreviations are given in Table 1.

Taxon	Number	SVL	TaL	HL	HD	HW	SD	AGD
<i>C. andringitraensis</i>	2MM	56.0 \pm 8.5 (50.0-62.0)	65.0 \pm 12.7 (56.0-74.0)	16.1 \pm 3.8 (13.4-18.7)	11.7 \pm 3.0 (9.5-13.8)	8.6 \pm 1.8 (7.3-9.8)	5.7 \pm 1.6 (4.5-6.8)	29.5 \pm 5.0 (26.0-33.0)
<i>C. furcifer</i>	1M	72.0	76.0	23.1	11.7	10	5.5	37.0
<i>C. gastrotaenia</i>	7MM	60.4 \pm 8.5 (46.0-73.0)	63.1 \pm 8.4 (48.0-74.0)	17.9 \pm 1.1 (16.6-19.4)	12.2 \pm 2.8 (7.5-15.0)	9.3 \pm 1.4 (6.6-10.5)	5.4 \pm 4.5 (4.8-6.0)	32.4 \pm 6.0 (22.0-42.0)
	3FF	49.0 \pm 4.4 (46.0-54.0)	46.0 \pm 1.0 (45.0-47.0)	14.7 \pm 1.5 (13.0-15.6)	9.3 \pm 1.3 (8.0-10.6)	7.1 \pm 0.8 (6.4-7.9)	5.0 \pm 0.6 (4.3-5.4)	28.0 \pm 5.3 (24.0-34.0)
<i>C. glawi</i>	1F	56.0	59.0	15.5	9.3	7.9	4.6	29.0
<i>C. guillaumeti</i>	3MM	53.3 \pm 4.2 (50.0-58.0)	53.7 \pm 5.9 (47.0-58.0)	15.9 \pm 2.2 (13.7-18.0)	10.1 \pm 1.5 (8.4-11.4)	8.0 \pm 0.8 (7.1-8.6)	4.6 \pm 0.3 (4.3-4.8)	27.0 \pm 2.6 (24.0-29.0)
	1F	56.0	52.0	16.0	10.5	8.0	4.5	25.0
<i>C. marojezensis</i>	9MM	63.6 \pm 3.7 (60.0-71.0)	63.0 \pm 5.8 (55.0-72.0)	16.9 \pm 1.7 (15.0-20.5)	9.6 \pm 0.7 (9.0-10.7)	9.1 \pm 4.5 (8.5-9.7)	5.8 \pm 0.9 (5.0-7.2)	35.1 \pm 4.1 (29.0-42.0)
	8FF	64.4 \pm 5.3 (55.0-72.0)	55.8 \pm 5.2 (47.0-61.0)	17.6 \pm 0.9 (16.5-19.0)	10.9 \pm 1.0 (9.2-12.5)	9.6 \pm 0.6 (8.8-10.7)	5.6 \pm 0.9 (4.7-7.4)	37.6 \pm 2.8 (33.0-41.0)
<i>C. vencesi</i> n. sp.	9MM	68.9 \pm 3.1 (63.0-73.0)	66.9 \pm 3.7 (62.0-73.0)	18.7 \pm 1.4 (17.0-21.5)	12.0 \pm 1.2 (10.5-14.2)	10.2 \pm 0.5 (9.6-11.0)	5.7 \pm 0.4 (5.0-6.3)	37.1 \pm 3.8 (32.0-42.0)
	8FF	62.9 \pm 7.6 (52.0-72.0)	56.8 \pm 3.1 (54.0-63.0)	18.0 \pm 1.9 (15.4-21.0)	10.9 \pm 1.0 (9.3-12.0)	9.4 \pm 0.6 (8.7-10.5)	5.5 \pm 0.5 (4.5-6.0)	32.3 \pm 5.4 (27.0-42.0)
<i>C. vatosoa</i> n. sp.	1M	60.0	66.0	18.0	9.0	7.5	6.4	36.0
<i>C. peyrierasi</i>	1M	49.0	61.0	15.0	11.4	7.0	4.9	24.0
	1F	50.0	37.0	14.3	10.2	8.0	5.0	29.0

actually all belong to *C. guillaumeti*, while specimens from lower altitudes are missing. Also the designation of *C. marojezensis* for Anandrivola (475-625 m) given by Raxworthy (1988) needs careful investigation, since this record apparently occurs within the distribution area of *C. gastrotaenia*.

The finding of a new species, *C. vencesi*, in the mountainous area around Andapa deserves more detailed comments. According to our data it is a mid-elevation taxon, present at Ambolokopatrika, Besariaka, and Tsararano. Since Anjanaharibe-Sud lies just midway between Ambolokopatrika and Besariaka, it is likely that the low altitude areas of this massif are inhabited by this species. Recent data for Marojejy by Raselimanana *et al.* (2000) indicate the presence of *C. marojezensis* at two lower transects (below 850 m), with *C. guillaumeti* from 1250 to 1675 m. In their survey there is a gap between 850 and 1250 m, due to the absence of study sites.

It is not unlikely, therefore, that the rainforests within this mid-altitude elevational range are occupied by *C. vencesi* n. sp. An alternative explanation could interpret this as a real absence, and in this case we may hypothesize that it might be due to a barrier effect

played by the Marojejy Massif. Indeed, this is similar to the case observed by Vences *et al.* (1999) and Andreone *et al.* (2000) for the dwarf *Zonosaurus* species: these authors found *Z. brygooi* in forests west of Marojejy – this species seems to be absent at Marojejy, where it is apparently replaced by *Z. rufipes* and *Z. subunicolor*. Further surveys are badly needed to confirm this hypothesis, especially with respect to the western slopes of Marojejy.

The second species cluster within the *C. furcifer* group is represented by *C. peyrierasi* (an apparently rare taxon endemic to Marojejy) and *C. vatosoa* n. sp. They are two obviously related species, yet rather different from the *C. gastrotaenia* cluster. In particular, *C. peyrierasi* and *C. vatosoa* n. sp. differ from these species in: (1) being not predominantly greenish in coloration; (2) having a body profile not particularly high; (3) being almost exclusive to the ericoid bush habitat of mid-high altitudes; (4) lacking a clearly defined double white belly line; (5) showing a very peculiar hemipenis morphology (especially *C. vatosoa*, which represents the only *Calumma* species exhibiting three pairs of rotulae). Although more detailed analyses are needed, we believe that *C. peyrierasi* and *C.*

vatosoa n. sp. are not so closely related to the species of the *C. gastrotaenia* complex, and possibly they should be included in a different phenetic group.

In terms of conservation, it is worth stressing that the presence of three species of the *C. gastrotaenia* complex, and of *C. peyrierasi*/*C. vatosoa* n. sp., in the massifs surrounding Andapa makes the north-east of Madagascar one of the most important geographic areas in terms of chameleon biodiversity. Parts of Anjanaharibe-Sud and Marojejy massifs are currently managed as protected areas (see Berner, 1995), and therefore this fact should assure some degree of protection to *C. guillaumeti*, *C. marojezensis* and *C. peyrierasi*. On the other hand, the two newly described species were found only outside these protected forests. As has already been suggested by Andreone *et al.* (2000), some protection should be given to Ambolokopatrika, Besariaka, and Tsararano forests. In particular, Ambolokopatrika appears to still retain good habitat (although "tavy" - i.e. "slash and burn" agricultural practice seems to be widespread), and it would be advisable to include it in the Anjanaharibe-Sud/Marojejy complex as the natural bridge between these massifs. This would give some protection to some of the *C. vencesi* n. sp. populations. Moreover, the importance of the Besariaka and Tsararano complex is due to the fact that, apart from the presence of both *C. vatosoa* n. sp. and *C. vencesi* n. sp. at Tsararano, these forests are also part of the important corridor which connects the Marojejy and the Anjanaharibe-Sud massifs to the large Masoala Forest. Conservation of these forests would also ensure the survivorship of the diverse faunas, floras and biotopes of the largest rainforest complex in Madagascar.

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APPENDIX: Specimens Examined

Calumma andringitraensis (Brygoo, Blanc and Domergue, 1972): MNHN 1993.0330-1 (626-7 C; A 330-1), holotype and paratype (MM), Ampanasana, 1530 m, Andringitra Massif, Fianarantsoa Faritany (Province), 17 January 1971, leg. C. P. Blanc.

Calumma furcifer (Vaillant & Grandidier, 1880): MNHN 1992.4410, Andekaleka, Toamasina (Tamatave) Faritany (Province), leg. F. Leberre; ZSM 314 2000, Vohidrazana, Toamasina (Tamatave) Faritany (Province), 10 April 2000, leg. F. Glaw; ZSM 315 2000, Vohidrazana, Toamasina (Tamatave) Faritany (Province), 10 April 2000, leg. F. Glaw.

Calumma gastrotaenia (Boulenger, 1888): MNHN 1899.0416, next to Suberbievilla, Boina, 23 October 1899, leg. J. L. Guillaumet and M. A. Grandidier; MNHN 1970.0382, Madagascar, leg. J. Arnoult; MNHN 1974 1081, Natural Reserve XII, West Marojejy, 1140 m, Sambava, Antsiranana (Diégo Suarez) Faritany (Province), leg. P. Soga; MNHN 1996.0007, don. F. Girard; MRSN R1191, Périnet-Analamazoatra, 18°56'S, 48°25'E, about 900 m, Fivondronana Moramanga, Toamasina (Tamatave) Faritany (Province), 1 May 1990, leg. F. Andreone and J. E. Randrianirina; MRSN R1702, Périnet-Analamazoatra, 18°56'S, 48°25'E, about 900 m, Fivondronana Moramanga, Toamasina (Tamatave) Faritany (Province), 21 July 1998 leg. F. Andreone and J. E. Randrianirina. MZUT R660.1-2, "Umbi Valley", Andrangoloaka, 47°55'S, 19°02'E, 1386 m, Fivondronana Moramanga, Toamasina (Tamatave) Faritany (Province), leg. G. Pittarelli (?), don. M.G. Peracca; ZFMK 59810, (M), RS d'Ambositantely, Ankazobe Fivondronana, about 1500 m, Antananarivo (Tanarive) Faritany (Province), 7 April 1995, leg. F. Glaw and D. Vallan; ZFMK 60143 (F), RS d'Ambositantely, Ankazobe Fivondronana, Antananarivo (Tanarive) Faritany (Province), 7 April 1995, leg. F. Glaw and D. Vallan; ZFMK 50634,

Andasibe (likely Périnet-Analamazoatra), 18°56'S, 48°25'E, about 900 m, Fivondronana Moramanga, Toamasina (Tamatave) Faritany (Province), leg. F. W. Henkel, W. Schmidt & V. Müller, May 1989; ZFMK 48190, Andasibe (likely Périnet-Analamazoatra), 18°56'S, 48°25'E, about 900 m, Fivondronana Moramanga, Toamasina (Tamatave) Faritany (Province), leg. F. W. Henkel & R. Seipp, April 1988; ZFMK 69998, Andraha (likely Mandraka);

Calumma marojezensis (Brygoo, Blanc and Domergue, 1970): MNHN 1989.2873 (529 C, 713), paratype (M), 14°26'S, 49°45' 40'E, about 700 m, Marojejy Massif, Sambava Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 30 December 1968, leg. C.P. Blanc; MNHN 1993.0160-2 (531 C, 712 and 714; A 160-2), holotype (M) and two paratypes (M and F), 14°26'S, 49°45' 40'E, about 700 m, Marojejy Massif, Sambava Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 30 December 1968, leg. C. P. Blanc; MRSN R1693.1-3, Forêt de Beanjada, 15°16.8'S, 49°59.8'E, 620 m, PN de Masoala, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 22 November 1998, leg. F. Andreone and J. E. Randrianirina; MRSN R1694, Forêt d'Andasin'i Governera, 15°18.5'S, 50°01.4'E, 620 m, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 9 December 1998, leg. F. Andreone and J. E. Randrianirina; MRSN R1695, Forêt d'Andasin'i Governera, 15°18.5'S, 50°01.4'E, 620 m, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 3 December 1998 leg. F. Andreone and J. E. Randrianirina; MRSN R1696, Forêt d'Andasin'i Governera, 15°18.5'S, 50°01.4'E, 620 m, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 2 December 1998, leg. F. Andreone and J. E. Randrianirina; MRSN R1700, Forêt de Beanjada, 15°16.8'S, 49°59.8'E, 620 m, PN de Masoala, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 22 November 1998, leg. F. Andreone and J. E. Randrianirina; MRSN R1697, Corridor d'Ambatoledama, 15°17.00'S, 50°01.3'E, 450 m, PN de Masoala, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 16 November 1998, leg. F. Andreone and J. E. Randrianirina; MRSN R1698, Corridor d'Ambatoledama, 15°17.00'S, 50°01.3'E, 450 m, PN de Masoala, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 17 November 1998, leg. F. Andreone and J. E. Randrianirina; MRSN R1699, Corridor d'Ambatoledama, 15°17.00'S, 50°01.3'E, 450 m, PN de Masoala, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 19.XI.1998, leg. F. Andreone and J. E. Randrianirina; MRSN R1701, Forêt d'Andasin'i Governera, 15°18.5'S, 50°01.4'E, 620 m, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 2 December 1998, leg. F. Andreone and J. E. Randrianirina; MRSN R1704.1-2, Corridor d'Ambatoledama, 15°17.00'S, 50°01.3'E, 500 m, PN de

Masoala, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 3-9 September 1998, leg. J. E. Randrianirina; ZFMK 59795 (F), Marojejy above Camp 1 (about 300 m), Antsiranana (Diégo Suarez) Faritany (Province), 1 March 1995, leg. F. Glaw and O. Ramilison.

Calumma guillaumeti (Brygoo, Blanc and Domergue, 1974): MRSN R1691, Anjanaharibe-Sud, Campsite W1, 14°44'S, 49°25'E, 1000-1100 m, Befandriana Fivondronana, Mahajunga (Majunga) Faritany (Province), 25 January – 3 February 1996, leg. F. Andreone, J. E. Randrianirina and H. Randriamahazo; MRSN 1692.1-2, Anjanaharibe-Sud, Campsite W2, 14°46'S, 49°30'E, 1200-1600 m, Befandriana Fivondronana, Mahajunga (Majunga) Faritany (Province), 5-11 February 1996, leg. F. Andreone, J. E. Randrianirina and H. Randriamahazo;

MSNG 49104, Manarikoba Forest, WP 14, 14°02.4'S, 48°47.3'E, 1,300 m, RNI de Tsaratanana, Antsiranana (Diégo Suarez) Faritany (Province), 22 February 1997, leg. R. Jesu and G. Schimmenti.

Calumma peyrierasi (Brygoo, Blanc and Domergue, 1974): MNHN 1973.0440 (689 C), holotype (M), 1900-2000 m, Marojejy Massif, Antsiranana (Diégo Suarez) Faritany (Province), 30 November 1972, leg. C. P. Blanc; MNHN 1973.0441 (699 C), paratype (F), 1900-2000 m, Marojejy Massif, Antsiranana (Diégo Suarez) Faritany (Province), 30 November 1972, leg. C. P. Blanc.

Calumma glawi (Böhme, 1997): ZFMK 62882, paratype (F), Vohiparara, about 1000 m, Ambohimahasoa Fivondronana, Fianarantsoa Faritany (Province), 27 February 1996, leg. F. Glaw, D. Rakotomalala and F. Ranaivojaona.