

Specific distinctness and biogeography of the dwarf chameleons *Brookesia minima*, *B. peyrierasi* and *B. tuberculata* (Reptilia: Chamaeleonidae): evidence from hemipenial and external morphology

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Abstract

In a recent paper Raxworthy & Nussbaum (1995) included the Madagascan dwarf chameleons *Brookesia peyrierasi* and *B. tuberculata* in the synonymy of *B. minima*, regarding known hemipenial differences between *B. tuberculata* and *B. peyrierasi* as artefacts. Our studies demonstrate that the hemipenis description of *B. tuberculata* by Brygoo & Domergue (1975) was largely correct and referred to unusual but real structures. The enormous differences in the hemipenis morphology of *B. tuberculata* (hemipenes of six specimens examined) and *B. peyrierasi* (hemipenes of five specimens examined) strongly suggest that they are not conspecific. Furthermore, morphological differences in the arrangement of head crests and expression of supraocular spines were noted between these two taxa and *B. minima*. The differentiation of the three taxa is furthermore corroborated by both univariate and multivariate analyses of morphometric data. We therefore propose to consider *Brookesia minima*, *B. peyrierasi*, and *B. tuberculata* as distinct species. This conclusion corroborates the validity of biogeographic regions as suggested from the analysis of distribution patterns of other *Brookesia* species.

Key words: Reptilia, Chamaeleonidae, *Brookesia minima* group, systematics, genital morphology, external morphology, biogeography

INTRODUCTION

In his monograph on the dwarf chameleons of the genus *Brookesia*, endemic to Madagascar, Brygoo (1978) listed five very small species (total length up to 45 mm) which were characterized by the absence of a continuous row of dorso-lateral spines, and by the absence of a pelvic shield: *Brookesia dentata*, *B. minima*, *B. peyrierasi*, *B. ramanantsoai* and *B. tuberculata*. Brygoo & Domergue (1975) created a *Brookesia minima* group to accommodate these species. Each was only known from a single or few localities, and in no instance syntopic occurrence of two species of the group was recorded (Brygoo, 1978). According to Brygoo & Domergue (1975) and Brygoo (1978), species distinction within the group was mainly based on genital morphology; hemipenes were found to be largely different between *B. peyrierasi* (Brygoo & Domergue, 1975) (type locality Nosy Mangabe), *B. tuberculata* (Mocquard, 1894) (type locality Montagne d'Ambre) and *B. ramanantsoai* (Brygoo & Domergue, 1975) (type locality 'forêt d'Ambohiboataba' according to the original description, resp. 'forêt d'Ambohiboatavo' according to

Brygoo, 1978) but remained unknown for *B. minima* (Boettger, 1893) (type locality Nosy Be) and *B. dentata* (Mocquard, 1900) (type locality Suberbierville). *Brookesia dentata* and *B. ramanantsoai* were distinguishable from the other three species by having three pairs of dorso-lateral spiny tubercles.

In 1995, Raxworthy & Nussbaum published an extensive review of the *Brookesia* species of northern Madagascar. Beside the description of six new species, five taxa were synonymized: both *B. tuberculata* and *B. peyrierasi* were included in the synonymy of *B. minima*, *B. ramanantsoai* was included in the synonymy of *B. dentata*, *B. antoetrae* was included in the synonymy of *B. thieli*, and *B. legendrei* was included in the synonymy of *B. ebenau*.

Recently, some authors have raised doubts as to the justification of some of these synonymizations. Brady *et al.* (1996) continued considering *B. antoetrae* as a valid species. Schimmenti & Jesu (1996) described a new species of the *minima* group (*B. exarmata* from the Tsingy de Bemaraha in western Madagascar) and resurrected *B. peyrierasi* and *B. tuberculata* based on several morphological differences.

In the present paper we present strong evidence for the specific distinctness of *B. tuberculata* and *B. peyrierasi* based on hemipenis morphology. We also discuss evidence for the validity of all three taxa (*B. minima*, *B. peyrierasi*, and *B. tuberculata*) based on differences in external morphology and provide considerations on the biogeography of *Brookesia* in northern Madagascar.

MATERIAL AND METHODS

Eversion of hemipenes in fresh specimens was first done by finger pressure on the hemipenial pockets at the ventral tail base in cranial direction, subsequently by injecting the organs with 70% alcohol, in order to get the maximum turgidity (see also Böhme, 1988). Only partially everted hemipenes of already fixed and preserved specimens were brought to full eversion by using a fine forceps for further inserting the retractor muscle into the not fully everted organs (see also Ziegler & Böhme, 1997). The method recently applied by Pesantes (1994) and Ziegler & Böhme (1997) for eversion of the inverted hemipenes of already fixed and preserved specimens was not successfully used due to the delicateness of the genital organs. Terminology of genital morphology follows Klaver & Böhme (1986) and Böhme (1988): the proximal part of the hemipenis is termed pedicel, followed by the truncus (mesial part) and the apex (distal part). HPL is used as abbreviation for hemipenis length, measured from cloacal base-point to tip of apex. Museum abbreviations used are as follows: MNHN = Muséum National d'Histoire Naturelle, Paris; MRSN = Museo Regionale di Scienze Naturali, Torino; SMF = Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt; UMMZ = University of Michigan, Museum of Zoology, Ann Arbor; ZFMK = Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; ZSM = Zoologische Staatssammlung, München.

Of the total of 70 examined specimens, we took morphometric measurements in a total of 61 specimens; six juveniles and two females from Sambava, because no conclusive *a priori* evidence existed for the specific attribution of this population, were excluded from further analysis; morphometric comparisons were carried out using 53 adult specimens. Variables measured were TL = total length; TaL = tail length; HW = head width; HH = head height; Eye = horizontal diameter of eye; ArmL = arm length; body length (BL) was calculated by subtraction of TaL from TL. All measurements were made by the same person (M. V.).

Data were processed with the software package SPSS for Windows; we carried out analyses of covariance (ANCOVAs) on the measurements of adult specimens. BL was used as covariate to eliminate the size factor. Males and females were analysed separately. We also performed a multivariate discriminant analysis, comparing males and females both separately and together.

Collectors are given for the type specimens only; collecting dates only for those specimens for which the

corresponding collection catalogues and labels contained unequivocal information; more detailed data on the other specimens are available in the MNHN, MRSN, SMF, and ZFMK catalogues, and on request from the authors. The following specimens were examined:

Brookesia minima

SMF 16512 (lectotype), SMF 16513 (paralectotype), and ZSM 17/1921 (paralectotype), all from Nosy Be, collected by C. Ebenau and A. Stumpff, 1880–1885; SMF 16514 (Nosy Be); MNHN 1884.582 and 1886.25 (Nosy Be); ZFMK 48215–48222, 51390, 51525, and 60664 (all from Nosy Be); ZFMK 53965–53969 (Nosy Be, collected on VII. 1993).

Brookesia tuberculata

MNHN 1893.183 (holotype) from Mararaomby, Montagne d'Ambre, collected by Alluaud and Belly; MNHN 1986.870, 871, and 873 (all from Montagne d'Ambre, collected on 10. VI. 1972); MNHN 1986.874 (locality given as 'Diego' [=town near Montagne d'Ambre]; MRSN R1640 (Montagne d'Ambre, collected on IV. 1990); ZFMK 61242 and 62194–62195 (all from Montagne d'Ambre, collected on 25. XI. 1995).

Brookesia peyrierasi

MNHN 1968.190 (holotype), 1968.184, 1968.186–189, and 1968.191 (paratypes), all from Nosy Mangabe, collected by A. Peyrieras on I. 1968; MNHN 1974.236–247 and 1974.249–250 (all from Nosy Mangabe); MNHN 1989.3748 (Nosy Mangabe according to attached label); MNHN 1974.251–252 (Sambava, collected on XI. 1968); MNHN 1986.875 (forêt de Fantanendra, north of Maroantsetra, collected on 21. II. 1969); SMF 65898–65901 (Nosy Mangabe); ZFMK 52477–52478 (Nosy Mangabe), ZFMK 60753–60756 and 61242 (all from Nosy Mangabe, collected on 16. VI. 1995); MRSN R1641.1–2 (Nosy Mangabe, collected on IV. 1990).

RESULTS

Descriptions of hemipenes

Brookesia peyrierasi (SMF 65899; Fig. 1). HPL: 4–5 mm (partly everted in the fresh specimen; terminal structures brought to maximum eversion posterior to fixation). Hemipenes strong and slightly elongate. Sulcus spermaticus distinctly forked at the base of the apex, its branches surrounding the distal lobes. Sulcal lips broad. Apex consists of two semicircular lobes, each showing



Fig. 1. Sulcal view of the left hemipenis of *Brookesia peyrierasi* (SMF 65899); scale: 1.5 mm.

four mineralized cones at its terminal end. The inner cones insert more on the asulcate surface of the respective lobe, slightly separated from each of the outer three cones, which are connected at their base.

Additionally, genital preparations of four specimens of *B. peyrierasi* were available: MNHN 1986.875 (Fig. 2), MNHN 1968.190 (holotype of *B. peyrierasi*; HPL 4.5 mm; Fig. 3), MNHN 1974.236 (HPL 5 mm) and ZFMK 60756. The (left) hemipenis of ZFMK

60756 was only partially everted and was brought to full eversion posterior to fixation. Hemipenes of the specimens correspond excellently to the everted genital organs of SMF 65899. On each lobe of the hemipenes four cones were recognized; only the lobes of the right hemipenis of MNHN 1974.236 bear a very small fifth cone. In one further specimen (MNHN 1974.242), the tip of the hemipenis (less than one mm) can be seen outside the cloaca; even in this virtually uneverted organ, the mineralized cones of one lobe are visible.

Brookesia tuberculata (ZFMK 61242; Figs 4 & 5). TaL: 14 mm; HPL: 4–5 mm (freshly everted). Hemipenes strong and curved towards the central axis of the specimen. Pedicel slender, truncus with conspicuous lateral bulges. Sulcus spermaticus distinctly forked at the base of the apex, its branches laterally leading to the end of the apex. Outer sulcal lip slightly stronger than inner sulcal lip. Apex laterally enlarged, consisting terminally of two slight bulges and a hardened, possibly mineralized crown-like structure at the centre of the asulcate surface. Both terminal bulges comprise an elongate siphon-like structure. The crown-like structure, which is open towards the sulcate surface, consists of few rounded tips. Both crown-like and siphon-like structures (Figs 4 & 5) are connected with the retractor muscle. There are no mineralized cones.

Additionally, everted hemipenes of five specimens from the same area were available: ZFMK 62194 (HPL 3 mm), MNHN 1986.870 (HPL 5.5 mm), MNHN 1986.871 (HPL 5.5 mm), MNHN 1986.873 (HPL 5 mm; Fig. 6), and MNHN 1986.874 (HPL 5.5 mm). Because of the partly poor preparations (no maximum turgidity in the genital preparations of ZFMK 62194 and MNHN 1986.870, 871 and 873; distended and partly destroyed apex in those of MNHN 1986.871 and 874) the hemipenes partly appear only slightly curved and conspicuously slender and elongate with very slight lateral bulges at the truncus. However, both the elongate siphon-like structures within the terminal bulges, as

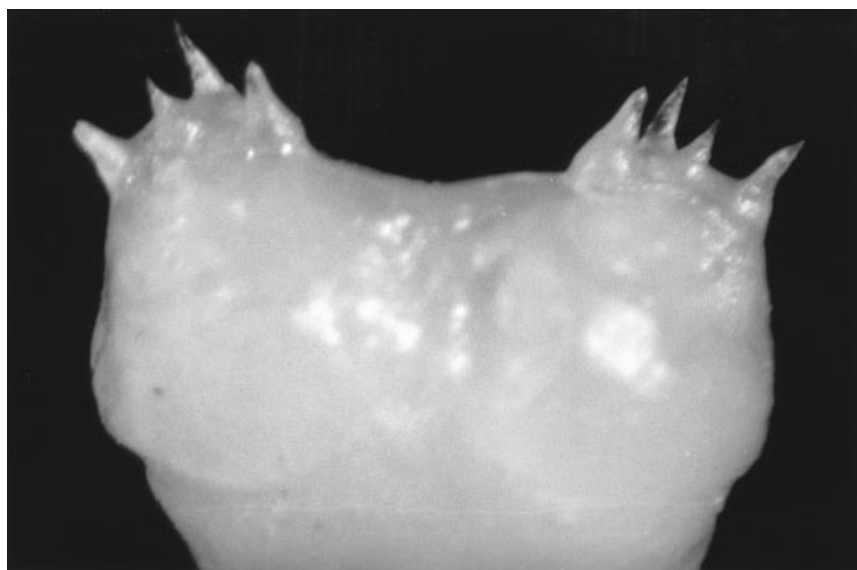


Fig. 2. Asulcal view of the apex of the hemipenis of *Brookesia peyrierasi* (MNHN 1986.875). Photograph by R. Kernchen.

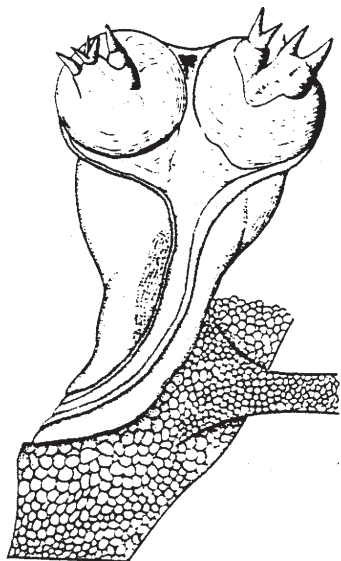


Fig. 3. Sulcal view of the hemipenis of *Brookesia peyrierasi* (holotype MNHN 1968.190) after Brygoo & Domergue (1969); scale: 1.5 mm.

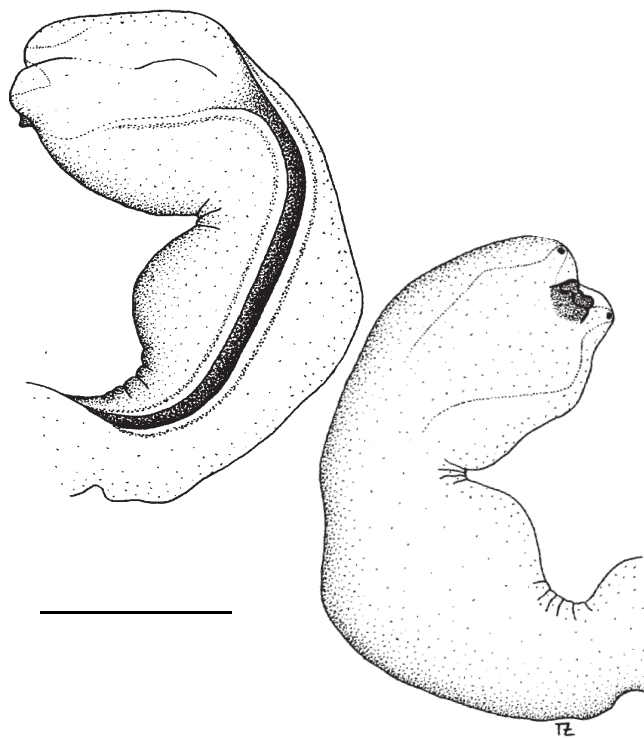


Fig. 5. Left hemipenis of *Brookesia tuberculata* (ZFMK 61242); scale: 1.5 mm. Left sulcal, right asulcal view. Due to a slightly different perspective as compared to Fig. 4, not all terminal tips of the crown-like structure are discernible. External openings of siphon-like structures are symbolized by a black spot (compare Fig. 4). Drawing by T. Ziegler.

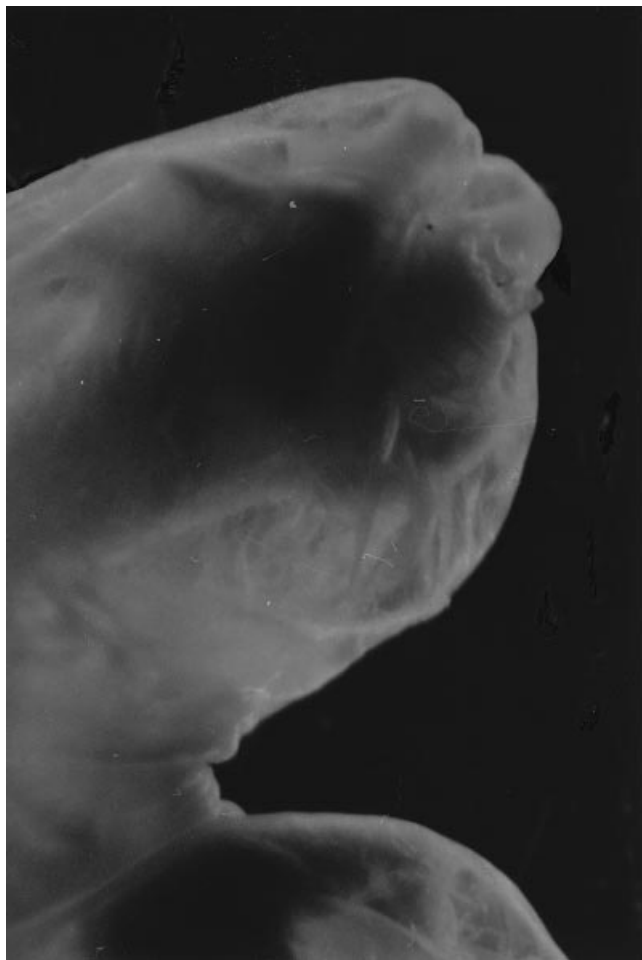


Fig. 4. Asulcal view of the apex of the left hemipenis of *Brookesia tuberculata* (ZFMK 61242).

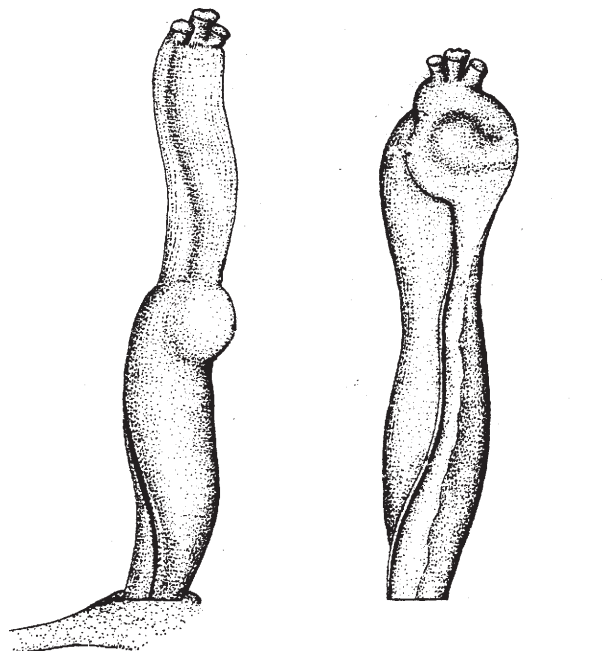


Fig. 6. Right and left hemipenes of *Brookesia tuberculata* (MNHN 1986.873) after Brygoo & Domergue (1975); scale: 1.5 mm. Left asulcal, right sulcal view.



Fig. 7. Adult male of *Brookesia peyrierasi* from Nosy Mangabe.



Fig. 8. Mating couple (male above) of *Brookesia minima* from Nosy Be. Note the slender body and the thin legs of both specimens, and the lack of supraocular spines in the male. Photograph by Wolfgang Schmidt.

well as the crown-like structure at the terminal asulcate surface are well recognizable. The crown-like structures consist of several small and rounded tips. The main structures thus correspond well to the genital preparations of ZFMK 61242.

External morphology

Careful examination of the available material of the three taxa considered yielded several characters which can be used for their distinction.

(a) *Brookesia peyrierasi* (Fig. 7) is significantly larger

(Table 2) and has a more spiny head and body ornamentation than *B. minima* and *B. tuberculata*.

(b) *Brookesia minima* (Fig. 8) differs from the remaining two taxa by details of head ornamentation; the ridge system which is found dorsally on the head has a symmetrical, rather complex but regular pattern in *B. tuberculata* and especially in *B. peyrierasi*, but is largely reduced in *B. minima* (Fig. 9). Especially transversal patterns are lacking in most specimens of *B. minima*, the ridge systems being confined to irregular elements arranged longitudinally. The inner longitudinal ridges are mostly confluent to the supraocular crest in *B. minima*, whereas in *B. tuberculata* and *B. peyrierasi* they

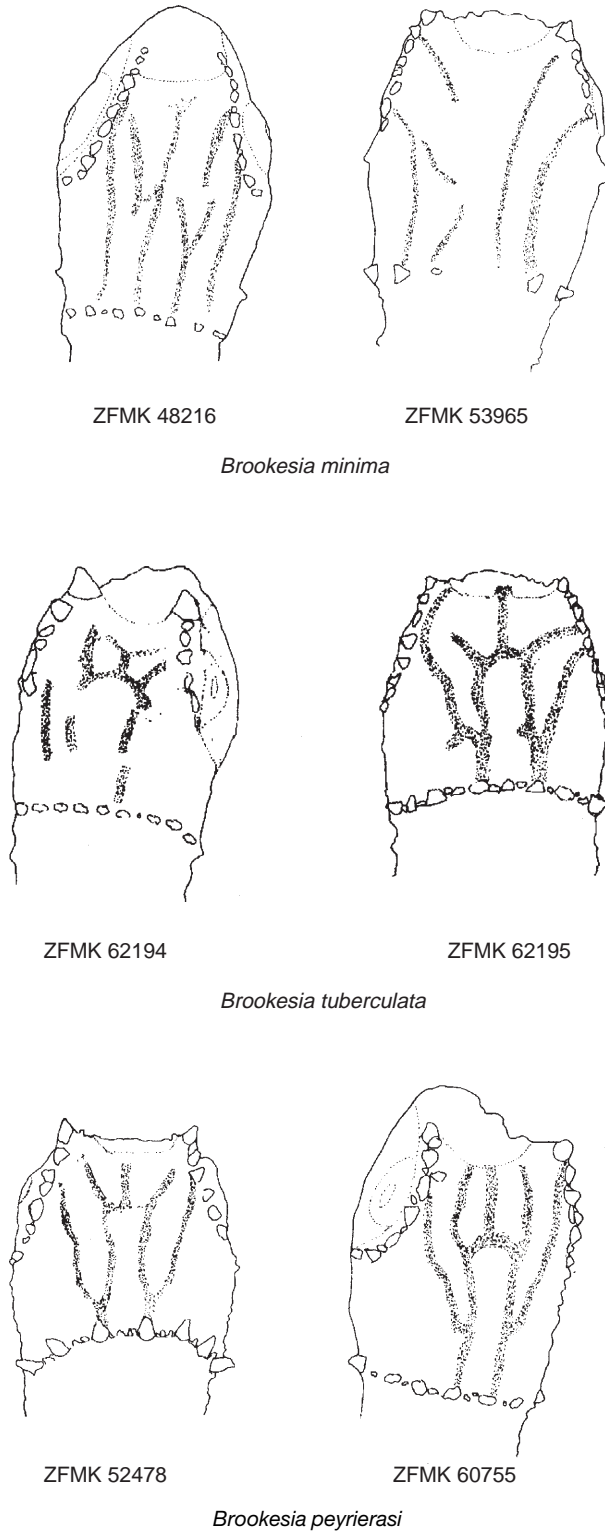


Fig. 9. Schematic drawings of typical structures of dorsal head surface in *Brookesia minima*, *B. peyrierasi* and *B. tuberculata*. Shaded lines represent elevated ridge structures. Scales and tubercles are only shown along supraocular crest and neck. Not to scale.

Table 1. Morphometric measurements (in mm) of examined specimens of *Brookesia minima*, *B. tuberculata* and *B. peyrierasi*. Used abbreviations: M = male, F = female, J = juvenile; TL = total length; TaL = tail length; HW = head width; HH = head height; Eye = horizontal diameter of eye; ArmL = arm length

	Sex	TL	TaL	HW	HH	Eye	ArmL
<i>Brookesia minima</i>							
ZFMK 51525	M	28.6	11.8	2.8	2.5	1.7	5.5
ZFMK 53966	M	30.3	12.0	3.0	3.0	1.7	6.4
ZFMK 53969	M	26.0	11.0	2.9	2.7	1.7	5.1
MNHN 1884.582	F	29.0	11.5	2.9	2.7	1.6	6.0
MNHN 1886.25	F	26.0	10.5	2.7	2.4	1.4	5.2
SMF 16512	F	31.5	11.9	3.3	2.8	1.7	6.5
SMF 16513	F	27.8	11.5	2.7	2.5	1.5	5.6
SMF 16514	F	31.8	12.9	3.3	3.1	1.7	6.7
ZFMK 48215	F	31.3	12.0	3.0	3.0	1.5	6.8
ZFMK 48216	F	33.8	12.7	3.3	3.0	1.4	6.1
ZFMK 51390	F	29.7	11.0	3.2	3.0	1.7	6.2
ZFMK 53965	F	32.3	12.1	3.2	3.2	1.6	6.5
ZFMK 53967	F	33.8	14.5	3.3	3.1	1.8	6.1
ZFMK 60664	F	30.0	11.7	3.0	3.0	1.6	6.3
ZFMK 48217	J	24.9	10.0	2.6	2.2	1.4	5.4
ZSM 17/1921	F	33.6	12.7	3.2	3.1	1.8	6.7
<i>Brookesia tuberculata</i>							
MNHN 1893.183	M	30.2	12.7	3.7	3.0	1.7	5.8
MNHN 1986.870	M	32.8	14.7	3.6	2.9	1.6	5.5
MNHN 1986.871	M	32.6	14.8	3.6	2.8	1.6	6.2
MNHN 1986.873	M	34.8	16.2	3.7	2.9	1.7	5.8
MNHN 1986.874	M	31.5	13.0	3.4	3.1	1.8	5.7
MRSN R1640	M	32.7	15.3	3.6	2.9	1.4	5.8
ZFMK 62194	M	25.2	10.8	3.0	2.7	1.4	4.8
ZFMK 62195	F	29.9	10.8	4.0	3.8	1.7	4.7
<i>Brookesia peyrierasi</i>							
MNHN 1968.188	M	36.6	15.7	3.8	3.4	1.8	7.1
MNHN 1968.189	M	37.1	16.4	3.9	3.4	1.9	6.9
MNHN 1968.190	M	38.0	16.5	4.2	3.6	1.9	7.4
MNHN 1974.236	M	39.2	17.1	4.2	3.4	1.6	7.6
MNHN 1974.242	M	34.9	12.6	4.0	3.6	2.0	7.8
MNHN 1974.243	M	36.1	16.4	3.7	3.3	1.9	7.4
MNHN 1974.244	M	39.3	17.7	4.3	3.7	1.8	7.8
MNHN 1974.246	M	39.8	17.4	3.9	3.6	1.8	7.6
MNHN 1974.247	M	35.3	15.5	3.8	3.4	1.8	6.8
MNHN 1974.249	M	36.8	16.9	3.9	3.7	1.8	7.5
MNHN 1986.875	M	38.8	17.7	3.8	3.5	1.8	7.3
MNHN 1989.3748	M	38.5	17.6	4.1	3.7	1.8	7.7
SMF 65899	M	37.8	18.1	4.1	3.5	2.0	7.5
ZFMK 60755	M	36.4	15.7	3.9	3.5	1.8	7.3
ZFMK 60756	M	36.4	16.3	4.2	3.6	2.0	7.2
MNHN 1968.184	F	36.1	14.9	4.2	3.6	1.7	7.1
MNHN 1968.186	F	36.9	13.8	4.5	4.0	1.8	7.4
MNHN 1968.187	F	39.2	15.4	4.1	3.7	1.9	7.8
MNHN 1968.191	F	41.8	16.8	4.7	4.2	2.1	8.0
MNHN 1974.237	F	39.6	16.5	3.8	3.6	1.8	7.9
MNHN 1974.240	F	38.9	15.3	4.5	3.9	2.1	7.5
MNHN 1974.241	F	34.7	14.3	4.0	3.9	1.8	7.8
MNHN 1974.245	F	35.9	14.0	3.9	3.8	1.7	7.9
MNHN 1974.250	F	34.5	14.2	4.1	3.8	1.8	7.7
MNHN 1974.251	F	43.6	16.2	4.4	3.9	2.0	9.0
MNHN 1974.252	F	41.0	15.4	4.6	4.2	2.0	8.3
MRSN R1641.1	F	38.8	15.8	4.6	4.1	1.9	7.8
MRSN R1641.2	F	32.2	13.1	3.9	3.5	1.9	7.7
SMF 65898	F	39.8	15.8	4.4	4.5	2.0	7.7
ZFMK 60753	F	39.0	15.1	4.6	4.3	2.1	7.5
ZFMK 60754	F	41.0	16.3	4.1	3.9	2.0	8.3
ZFMK 52478	F	42.0	17.7	4.5	4.1	2.0	8.1
MNHN 1974.238	J	29.5	11.5	3.6	3.2	1.6	7.3
MNHN 1974.239	J	27.1	11.3	3.3	2.9	1.7	6.3
SMF 65900	J	31.9	14.0	3.6	3.5	1.9	5.9
SMF 65901	J	25.0	10.2	3.1	3.0	1.4	5.5
ZFMK 52477	J	30.1	12.9	3.5	3.2	1.5	6.3



Fig. 10. Adult male of *Brookesia tuberculata* from Montagne d'Ambre. Note the distinct supraocular spines, the clumsy body shape and the thick legs.

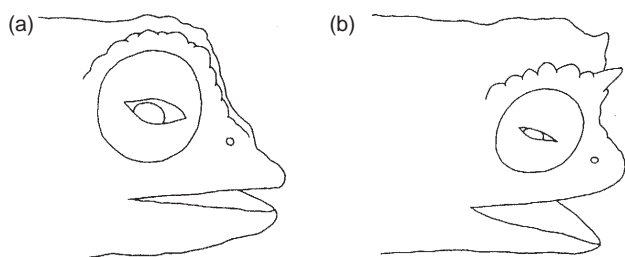


Fig. 11. Drawings of head profiles: (a) *Brookesia minima* male (ZFMK 53966); (b) *B. tuberculata* male (ZFMK 62194), showing supraocular spine.

generally curve anteriorly towards the centre. No *B. minima* specimen was observed with the regular and distinct head crest ornamentation pattern typical for *B. tuberculata* and *B. peyrierasi* as shown in Fig. 9. About one-fifth of the *B. peyrierasi* specimens (mostly males) show a weak expression of this pattern, but all *B. tuberculata* and all except one *B. peyrierasi*, had either recognizable transversal elements or longitudinal crests which at the front curve towards the centre. One single *B. peyrierasi* specimen (MNHN 1974.247) could not be distinguished from *B. minima* by head crest ornamentation alone.

(c) *Brookesia tuberculata* males (Fig. 10) differ in having one distinct, protruding spine on each supraocular crest (Fig. 11; absent in females), which are clearly shorter in *B. peyrierasi* and much shorter in *B. minima*. Additionally, *B. tuberculata* differs from *B. minima* by more robust and clumsy body shape and thicker legs (see Figs 8 & 10). The thicker constitution of the legs is

obvious in all photographs of live specimens available to us, and was verified in additional specimens observed in the field. However, due to the extremely small size of the species, this difference is very difficult to be reliably measured in preserved specimens.

Morphometrically, there are significant differences between the three taxa. Table 1 shows measurements of studied specimens, whereas differential characters are summarized in Table 2.

Brookesia peyrierasi differed from the remaining taxa by a constantly larger size, without overlap in BL values in males, and very little overlap in female values (Table 2). Size differences of males and females of *B. peyrierasi* were significant (sexes tested separately; *t*-test; $P < 0.001$) to those of *B. minima* and *B. tuberculata* except in the female comparison *B. peyrierasi*–*B. tuberculata* (only one female of the latter available; $P < 0.07$).

By pairwise ANCOVA comparisons, differences between males were as follows: *B. minima* differed from *B. tuberculata* by a relatively narrower head ($P < 0.005$), and relatively shorter tail ($P < 0.01$). *Brookesia minima* differed from *B. peyrierasi* by a relatively narrower and lower head ($P < 0.005$), shorter arms ($P < 0.05$) and tail ($P < 0.005$), and larger eyes ($P < 0.05$). *Brookesia tuberculata* differed from *B. peyrierasi* by relatively shorter arms ($P < 0.001$) and lower head ($P < 0.001$).

Differences between females were as follows: *B. minima* differed from *B. tuberculata* by a relatively narrower and lower head ($P < 0.001$), and relatively longer arms ($P < 0.005$). *Brookesia minima* differed from *B. peyrierasi* by a relatively narrower and lower head ($P < 0.001$), and shorter arms ($P < 0.001$) and tail ($P < 0.05$). *Brookesia tuberculata* differed from *B. peyr-*

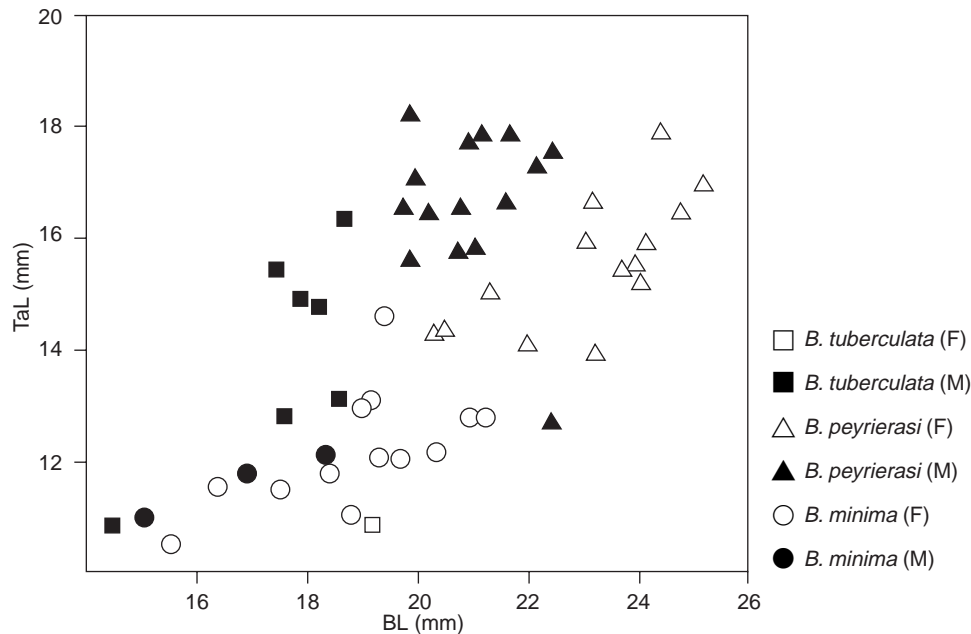


Fig. 12. Scatterplot of tail length TaL and body length BL in *Brookesia minima*, *B. tuberculata* and *B. peyrierasi*. Closed symbols, males; open symbols, females.

Table 2. Morphology and differential characters in *Brookesia minima*, *B. tuberculata* and *B. peyrierasi*. Measurements and ratios are given as mean SD and range (in parentheses). Morphometric values calculated from data in Table 1 (juveniles excluded from analysis). Body length (BL, in mm) calculated as TL, TaL

	<i>B. minima</i> (3 males, 12 females)	<i>B. tuberculata</i> (7 males, 1 female)	<i>B. peyrierasi</i> (15 males, 15 females)
BL (males)	16.7 (15.0–18.3)	17.5 (14.4–18.6)	20.9 (19.7–22.4)
BL (females)	18.8 (15.5–21.1)	19.1	22.8 (19.1–25.0)
TaL/BL (males)	0.70 (0.66–0.73)	0.80 (0.70–0.88)	0.79 (0.57–0.92)
TaL/BL (females)	0.65 (0.59–0.75)	0.57	0.67 (0.60–0.73)
ArmL/BL (males)	0.34 (0.33–0.35)	0.32 (0.30–0.35)	0.35 (0.33–0.38)
ArmL/BL (females)	0.33 (0.29–0.36)	0.25	0.34 (0.31–0.40)
HW/BL (males)	0.17 (0.16–0.19)	0.20 (0.18–0.21)	0.19 (0.17–0.21)
HW/BL (females)	0.17 (0.15–0.18)	0.21	0.19 (0.17–0.20)
HH/BL (males)	0.16 (0.15–0.18)	0.17 (0.16–0.19)	0.17 (0.15–0.19)
HH/BL (females)	0.16 (0.14–0.16)	0.20	0.17 (0.16–0.19)
Supraocular spine in males	Small	Large	Small
Dorsal head ridges	Indistinct; transversal elements reduced	Distinct, regular pattern with transversal elements	Distinct, regular pattern with transversal elements
Tubercles and spines on body	Indistinct	Indistinct	Distinct
Pelvic spine	Absent	Absent	Often present
Hemipenis	Unknown	Crown-like and siphon-like structures; no cones	Two cone-bearing lobes

ierasi by relatively shorter arms ($P < 0.001$) and tail ($P < 0.05$).

Within taxa, intersexual differences were found in *B. tuberculata* (ArmL, $P < 0.05$; HH, $P < 0.005$; TaL, $P < 0.05$) and *B. peyrierasi* (HH, $P < 0.01$; TaL, $P < 0.005$). One constant sexually dimorphic pattern found in all three taxa (although not statistically significant in *B. minima*) was relative tail length. Tails were relatively shorter in females (Fig. 12) except for one male specimen of *B. peyrierasi* (MNHN 1974.242) which possibly had a mutilated tail. Females were

generally larger than males, although this difference tested only significant in *B. peyrierasi* (BL, t -test, $P < 0.005$).

A multivariate discriminant analysis using data in Table 1 grouped specimens of all three taxa widely separated. Similar results were achieved both for males and females when analysed separately (Fig. 13), and for a combined analysis of both sexes, indicating that the interspecific differences are more important than sexual dimorphism. Standardized canonical discriminant function coefficients are given in Table 3. Discriminant

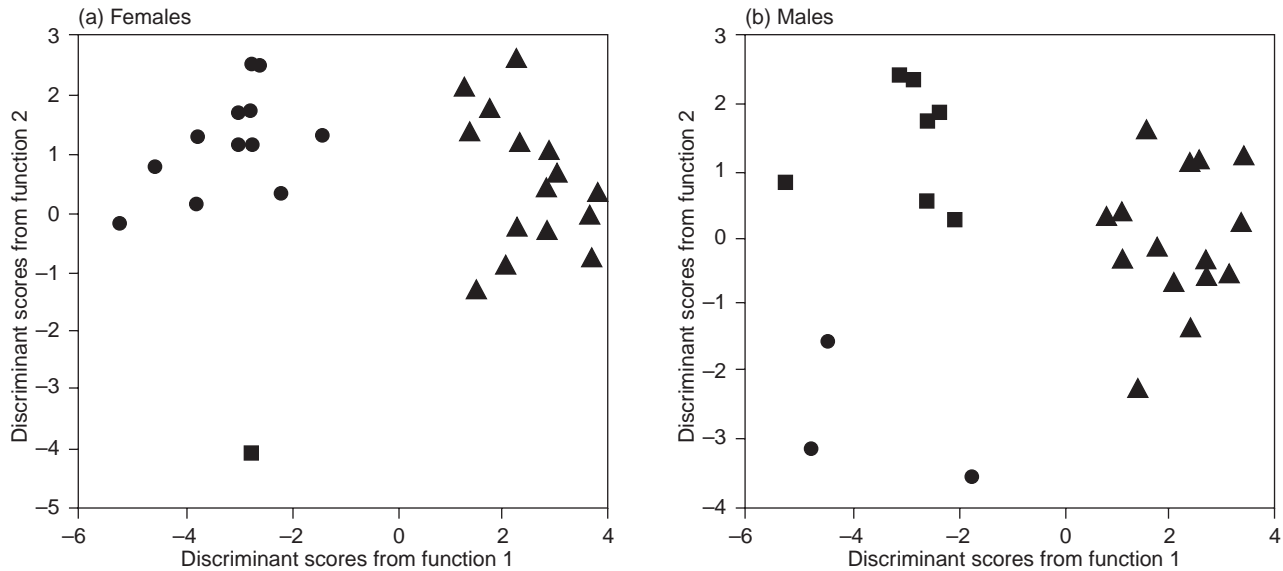


Fig. 13. Scatterplot of the first and second discriminant function in *Brookesia minima* (●), *B. tuberculata* (■) and *B. peyrierasi* (▲) females (a) and males (b), based on a multivariate discriminant analysis of data in Table 1.

Table 3. Standardized canonical discriminant function coefficients from a multiple discriminant function analysis of measurements in Table 1 for *Brookesia minima*, *B. tuberculata* and *B. peyrierasi*. Data are given for separate analyses of males and females. The two characters with the relatively greatest discriminating power for the first two discriminant functions (DFs) in each analysis are marked by a superscripted ranking

	DF 1	DF 2
Males		
ArmL	0.467 ²	-0.975 ²
Eye	0.131	-0.429
HH	0.603 ¹	0.159
HW	-0.031	1.130 ¹
SVL	-0.092	0.137
TaL	0.229	0.021
Females		
ArmL	0.994	-0.758 ²
Eye	-0.431	-0.090
HH	-0.145	0.962 ¹
HW	1.255 ¹	0.260
SVL	-1.036 ²	-0.186
TaL	0.394	-0.166

analysis predicted correctly group membership for all males with a probability > 99.99%, and for all females with a probability > 99.999% when sexes were separately analysed.

DISCUSSION

Hemipenial differentiation

Raxworthy & Nussbaum (1995) regarded *Brookesia peyrierasi* and *B. tuberculata* as synonyms of *B. minima* due to the presumed lack of differential characters, concluding that 'there is no evidence to diagnose more

than one *minima* group *Brookesia* in northern Madagascar...'.

However, Brygoo & Domergue (1969, 1974) had provided a diagnosis of both taxa based on genital morphology. Raxworthy & Nussbaum (1995: 528) quoted the published differences as follows: 'The hemipenis of *Brookesia tuberculata* from Montagne d'Ambre has a single apex bearing three short horns (Brygoo & Domergue, 1975), while the hemipenis of *B. peyrierasi* from Nosy Mangabe and Fantanendra (north of Maroantsetra) has a bi-lobed apex each bearing a papillate crest of 4–6 papillae (Brygoo & Domergue, 1970)'.

In the hemipenes of their material (specimens UMMZ 203617-8 and 203622, from the eastern localities Marojejy and Masoala, respectively), they observed similarities to the hemipenes of *B. peyrierasi*. On the contrary, they disregarded the differences to the hemipenes of *B. tuberculata* as they were described by Brygoo & Domergue (1975), stating that the organs of the pertinent specimens (MNHN 1986.871–872) are 'badly deformed and do not appear to be fully everted'. The unusual structures of the hemipenis of *B. tuberculata* had previously been discussed by Brygoo & Domergue (1975) and Klaver & Böhme (1986) who also considered the possibility that they constitute artefacts.

The new material described in the present study allows for the first time definitive clarifications about the genital morphology of *B. tuberculata*. The hemipenis preparations of ZFMK 61242 are totally everted and fully developed, whereas those described by Brygoo & Domergue (1975) are obviously slender and not completely turgid (MNHN 1986.873). Nevertheless, the most important structural characters are clearly recognizable in the latter (Fig. 6), and were largely correctly described and figured by Brygoo & Domergue (1975). This

regards the lateral truncal bulges ('renflement hémisphérique'), the two terminal siphon-like structures, and the crown-like structure at the centre of the terminal asulcate surface ('une zone apicale, confusément divisée en trois éléments dont le médian est légèrement découpé en trois denticules'). A difference is that in the hemipenes of ZFMK 61242 the crown-like structure shows a few more rounded tips than in Brygoo & Domergue's (1975) figure. This may reflect real individual differences, whereas the elongate general appearance ('le corps...c'est un cylindre irrégulier') and the relatively strongly projecting terminal structures of the hemipenes of MNHN 1986.873 and ZFMK 62194 are probably artefacts due to the lack of turgidity. The left hemipenis of MNHN 1986.873 as figured by Brygoo & Domergue (1975) shows an apical swelling not recognizable in ZFMK 61242 which may be an artefact as often occurs when liquid is directly injected into the tail base without prior manual eversion of the organs (Ziegler & Böhme, 1997); the swelling may also represent the apically shifted lateral bulges.

The detailed description of the hemipenes of *B. peyrierasi* (Brygoo & Domergue, 1969; Fig. 3) is largely corroborated by our observations except for the number of terminal cones: 'chacun d'eux porte deux groupes d'ergots épineux issus d'une base commune; le demi-ergot sternal le plus développé, est composé de trois ou quatre épines verticales, le demi-ergot tergal n'en a qu'une ou deux, également verticales'. According to the data presented herein, each lobe generally bears four mineralized cones. Only in one exceptional case, we observed a very small fifth cone on both lobes of one hemipenis (MNHN 1974.236).

Summarizing, there are very distinct hemipenial differences between *B. peyrierasi* and *B. tuberculata*. The hemipenes of *B. peyrierasi* are apically largely characterized by two semicircular lobes with mineralized cones at their terminal ends, whereas those of *B. tuberculata* show terminal siphon-like structures within both terminal bulges, and a crown-like structure at the centre of the terminal asulcate surface.

It also can be excluded that the observed differences may be due to seasonal variation. Material studied includes *B. peyrierasi* specimens collected in the dry season (June: ZFMK 60756) and in the rainy season (January: holotype MNHN 1968.190; February: MNHN 1986.875). Same regards *B. tuberculata* (June: MNHN 1986.870, 871 and 873; November: ZFMK 62194 and 62195). An explanation of the observed differences by seasonal variation is also not probable due to the existence of hardened, very probably mineralized or calcified structures on the hemipenis of *B. peyrierasi* (terminal cones) and probably also *B. tuberculata* (crown-like structure). Seasonal variation, as sometimes observed in the family Chamaeleonidae and in other saurians, has so far only been demonstrated to affect fleshy or horny outer genital structures (Böhme, 1988) whereas occurrence of seasonal modifications of mineralized or calcified structures is not probable (see also Ziegler & Böhme, 1997).

According to Klaver & Böhme (1986), 'the apical ornamentation of Malagasy [*Brookesia*] species consists of two papillate or denticulate crests or crested lobes, somewhat unequal in size'. Hence, *B. peyrierasi* fits well into the observed variation within the genus, whereas the unusual structures of *B. tuberculata* may represent a derived state.

Morphological differentiation

It is a general problem in *Brookesia* systematics and specific diagnosis that morphological differences between species are often low and moreover sometimes difficult to describe. In the tiny species of the *B. minima* group, many characters are largely reduced which in larger *Brookesia* can be used for species identification (dorsolateral spines, pelvic shield, head structures).

One peculiarity of many tetrapod species at the lower size limit is the retainment of paedomorphic features, which often results in a reduced development of external characters such as fingers and toes (Hanken & Wake, 1993). With up to 34 mm resp. 35 mm total length (Table 1) *B. minima* and *B. tuberculata* range among the smallest reptile species in the world (Glaw & Vences, 1994). The lack of dorsolateral spines, pelvic shield and distinct head crests in the *B. minima* group species can be seen as retained paedomorphic features. In fact, *Brookesia* species with distinct body and head ornamentations show a less distinct expression of adult characters in their juvenile state (F. Glaw, pers. obs. for *B. stumpffi*). This is reflected by the fact that in two cases, specimens belonging to the *B. minima* group may have been mistaken with juveniles of larger species: Glaw & Vences (1994) stated that one paratype of *B. karchei* (MNHN 1993.159) possibly belongs to a species of the *B. minima* group, and Raxworthy & Nussbaum (1995) found that one paratype of *B. thieli* (MNHN 1968.139) is in fact a specimen of *B. dentata*.

Increased maintenance of paedomorphic characters may explain why the small *B. minima* shows less distinct head ridges than *B. peyrierasi*, and the larger expression of spines and tubercles in *B. peyrierasi* may in this scheme be related to its larger size. However, the large supraocular spines of *B. tuberculata* (not found in the larger *B. peyrierasi*) contradict this explanation and indicate that maintenance of paedomorphic characters has affected the three taxa in a different way.

This also points to another fact which may be considered in the context of the large hemipenial differences between *B. peyrierasi* and *B. tuberculata*. Until present no attempt of a phylogenetic analysis of the genus *Brookesia* has been published, and no derived characters except the small size are known which would support a monophyletic origin of the *B. minima* group. Hence, although improbable, it can not be excluded that some species of the group evolved independently from larger ancestors by retainment of paedomorphic features, as has already been demonstrated in minute animals (Hanken & Wake, 1993).

Taxonomy

The differences in hemipenial morphology of *Brookesia peyrierasi* and *B. tuberculata* clearly indicate specific distinctness of both taxa. This example confirms the results of many other studies which have demonstrated that genital morphology can contribute important data to taxonomy of squamate reptiles (e. g. Ziegler & Böhme, 1997), especially in groups with conspicuous interspecific differences of hemipenial structures (often groups with absence of femoral pores as chameleons, geckos of the genus *Uroplatus*, varanids, snakes, and others). Unfortunately, no hemipenial data of material from Nosy Be, the type locality of *B. minima*, are available. Since *B. minima* was historically the first species of the group to be described, this name is clearly valid based on priority, whereas either *B. tuberculata* or *B. peyrierasi* could be synonymous with *B. minima* considering hemipenial argumentation alone.

Our investigations on Malagasy anurans (e. g. Glaw & Vences, 1994) have shown that a significant number of (often syntopic) species are nearly indistinguishable when preserved, although their specific distinctness is evident by differences in advertisement calls, life colouration and habits. A similar situation may be present in several groups of Malagasy reptiles, in which morphological differences are weak, as in some species of the *Zonosaurus aeneus* group (Vences *et al.*, 1996). Considering the differential characters presented in Table 2, and the morphometric differences as revealed by discriminant analysis (Fig. 13), we conclude that a specific status of all three taxa is currently the most plausible hypothesis, although additional data are required to determine the extent of differentiation of *B. minima* to the other two taxa. We therefore reject the synonymizations applied by Raxworthy & Nussbaum (1995) and regard all three taxa *B. minima*, *B. tuberculata* and *B. peyrierasi* as distinct species. Due to the very small size and lack of prominent external characters of the species, a reliable diagnosis of single specimens is rather difficult. However, in the material that we examined, it is possible to correctly identify all male specimens and most female specimens (except a few smaller, possibly subadult *B. peyrierasi*) using the following identification key:

1a Larger species (male BL > 19 mm; female BL 19–25 mm); pelvic spine mostly present → *B. peyrierasi*

1b Smaller species (male BL < 19 mm; female BL 16–21 mm); pelvic spine always absent → 2

2a Slender species with thin extremities (see Fig. 8); dorsal head ridges as irregular pattern without distinct transversal elements (see Fig. 9); male without supraocular spine (see Fig. 11) → *B. minima*

2b Stout species with rather thick extremities (see Fig. 10); dorsal head ridges as regular pattern with distinct transversal elements (see Fig. 9); male with distinct supraocular spine (see Fig. 11) → *B. tuberculata*

The synonymization of *B. ramanantsoai* with *B. dentata* by Raxworthy & Nussbaum (1995) also needs comments. While the native forest in the region

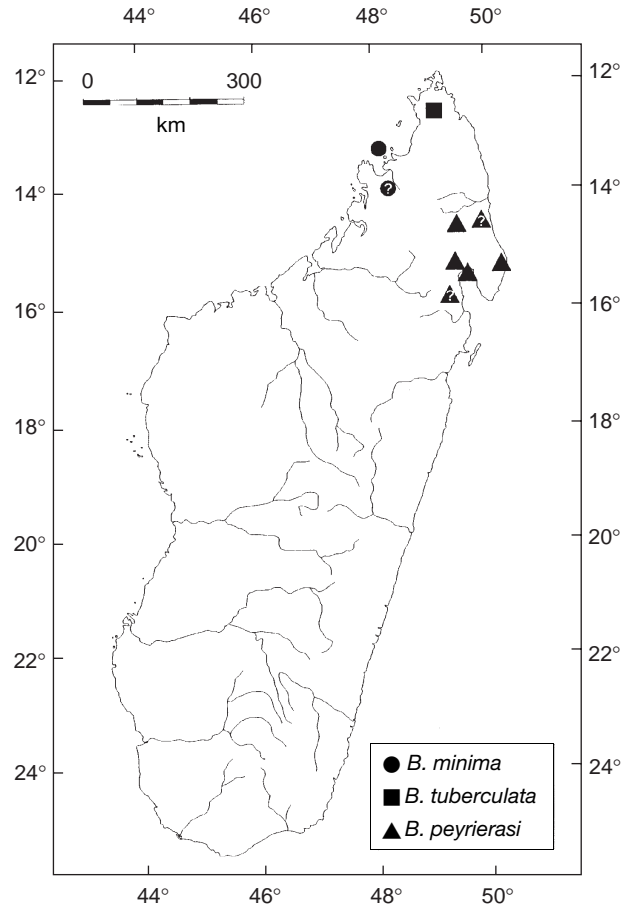


Fig. 14. Distribution of *Brookesia minima*, *B. tuberculata* and *B. peyrierasi* on Madagascar. Localities are listed and discussed in the text.

of the type locality of *B. dentata* is dry deciduous forest (Raxworthy & Nussbaum, 1995) the type locality of *B. ramanantsoai* (Ambohiboataba forest; altitude 1300 m) and other localities like Andasibe (altitude ca. 900 m) are in the area of mid-altitude rainforest. Currently there is no other known species of *Brookesia* which occurs in rainforest areas as well as in deciduous dry forest (except, perhaps, *B. stumpffi*). It should therefore be investigated whether *B. dentata* and *B. ramanantsoai* represent closely related sibling species rather than synonyms.

Biogeographical considerations

Although new data are necessary to clarify definitely the distribution of *Brookesia minima*, *B. peyrierasi* and *B. tuberculata*, at current state (Fig. 14) the known localities (after Glaw & Vences, 1994 and Raxworthy & Nussbaum, 1995) can be assigned as follows to the taxa: *B. minima*: Nosy Be, and possibly Manongarivo. *B. tuberculata*: Montagne d'Ambre. *B. peyrierasi*: Nosy Mangabe, Fantanendra, Masoala, Marojezy, and possibly Sambava and Anandrivola. The specimen from Fantanendra belongs to *B. peyrierasi* based on the

hemipenial data presented herein; those from Masoala and Marojezy are hemipenially similar according to Raxworthy & Nussbaum (1995), and therefore are here assigned to *B. peyrierasi*. Specimens from Sambava agree in size and morphometry with *B. peyrierasi*.

Raxworthy & Nussbaum (1995) defined areas of endemism in northern Madagascar based on the biogeography of *Brookesia*. They identified five different biogeographic regions: Northwest, Montagne d'Ambre, Tsaratanana, North-east and East. According to their data (Raxworthy & Nussbaum, 1995: map in their fig. 3), eight species of *Brookesia* are restricted to a single region. The same applies to *B. griveaudi* (restricted to the region North-east), although this species is erroneously reported on the map 'Distribution of *Brookesia* known from multiple regions'.

The remaining six species occur in two of the regions of northern Madagascar (*B. ebenau*, *B. betschi*, *B. superciliaris*, *B. stumpffi*, some of them additionally elsewhere) or in one region of northern Madagascar and elsewhere (*B. thieli*). Only *B. minima* (including *B. tuberculata* and *B. peyrierasi* as synonyms) is suggested to occur in four of the five regions proposed in northern Madagascar (all except Tsaratanana).

Recognition of *B. minima*, *B. peyrierasi* and *B. tuberculata* as distinct species, and their distribution patterns as shown in Fig. 14, largely confirm the biogeographic regions proposed by Raxworthy & Nussbaum (1995). Using their definitions of biogeographic regions, *B. minima* is restricted to the North-western region, *B. tuberculata* to the Montagne d'Ambre region, and *B. peyrierasi* occurs in the Eastern and North-eastern regions.

Another aspect of interest is the altitudinal range of *Brookesia* species. Raxworthy & Nussbaum (1995) state that 'almost all the northern *Brookesia* species are restricted to rainforest and occupy a relatively narrow elevational range'. This restriction to narrow elevational ranges may reflect the real situation, but it should be noted that there are significant inconsistencies in Raxworthy & Nussbaum's data.

For *Brookesia stumpffi*, Raxworthy & Nussbaum (1995: 552) indicate an altitude range between 0 and 700 m above sea level whereas in their 1994 paper (page 67) the same authors give 650–1200 m as the altitude range for the same species in Montagne d'Ambre National Park. A similar discrepancy applies to *Brookesia ebenau* (0–700 m in Raxworthy & Nussbaum, 1995; 650–800 m in Raxworthy & Nussbaum, 1994: 67). *Brookesia* sp. nov. 1 in Raxworthy & Nussbaum (1994) probably

Table 4. Number of forest dwelling amphibian and reptile species recorded at the type localities of *Brookesia minima* (Nosy Be), *B. tuberculata* (Montagne d'Ambre) and *B. peyrierasi* (Nosy Mangabe), and number of species not known from the other two localities (in parentheses)

Locality	Amphibians	Reptiles	Total
Nosy Be	16 (9)	34 (17)	50 (26)
Montagne d'Ambre	24 (14)	48 (27)	72 (41)
Nosy Mangabe	22 (18)	16 (8)	38 (26)

refers to *B. antakarana* which was described in Raxworthy & Nussbaum (1995), as can be concluded by the similar range (650–1200 m) of both. The range of *Brookesia* sp. nov. 2 (equals *B. ambreensis*) is given as 650 m in Raxworthy & Nussbaum (1994) and as 650–1150 m in Raxworthy & Nussbaum (1995). Still another discrepancy regards *B. valerieae*: Raxworthy (1991: 17) stated that the holotype was found at an altitude of 350 m; Raxworthy & Nussbaum (1995) corrected this statement and gave an elevational range between 500 and 700 m for the species. Regardless of such indiscrepancies it seems evident that *B. minima* (sensu Raxworthy & Nussbaum, 1995) is among the species with the largest elevational range (0–900 m), occurring in habitats of significantly different climate. Recognition of *B. tuberculata* and *B. peyrierasi* as valid species changes this situation, each species of the *B. minima* group being restricted to a more limited altitudinal range as typical for *Brookesia*.

Raxworthy & Nussbaum (1995) state that 'almost all the northern *Brookesia* species are restricted to rainforest'. This may be partially true, although we observed specimens of the *Brookesia minima* group in plantation-like secondary forest around Sambava, and found the highest densities of *B. stumpffi* in similar habitats at Nosy Be (Glaw & Vences, 1994). Brygoo (1978) reported *Brookesia ramanantsoai* from eastern Madagascar (Andasibe) in degraded eucalypt forest. If a general restriction of the *B. minima* group to forested areas is true, fragmentation of forest due to climatic changes in the past could have constituted a significant reinforcement of speciation, and would provide an explanation of specific distinctness of the *B. minima* group taxa occurring in different biogeographic regions of northern Madagascar.

The three *Brookesia* taxa considered in the present study (*B. minima*, *B. peyrierasi*, *B. tuberculata*) were described from well defined localities which all consti-

Table 5. Similarity coefficients between the forest herpetofaunas of the type localities of *Brookesia minima* (Nosy Be), *B. tuberculata* (Montagne d'Ambre) and *B. peyrierasi* (Nosy Mangabe). Based on species numbers in Table 4

Comparison	Amphibians			Reptiles			Amphibians and reptiles		
	N_{1+2}	C	S	N_{1+2}	C	S	N_{1+2}	C	S
Nosy Be–Ambre	34	7	0.21	68	14	0.21	102	21	0.21
Nosy Be–Nosy Mangabe	38	0	0	44	6	0.14	82	6	0.07
Ambre–Nosy Mangabe	43	3	0.07	59	5	0.09	102	8	0.08

tute protected areas in the present (Nosy Be, Montagne d'Ambre, Nosy Mangabe); as mentioned above, these localities are referable to three different biogeographical regions as proposed by Raxworthy & Nussbaum (1995). We compared the forest dwelling amphibian and reptile species communities from these localities (data from Glaw & Vences, 1994 and unpublished; Raxworthy & Nussbaum, 1994). The numbers of species known from each locality are summarized in Table 4. Coefficients of similarity ($S = C/N_{1+2}$; where C is the number of species in common and N_{1+2} is the total number of species found at both localities; see Raxworthy & Nussbaum, 1996) shows that the herpetofaunas of Montagne d'Ambre and Nosy Be have much closer similarities than each to the herpetofauna of Nosy Mangabe (Table 5). It should be tested in the future whether this pattern may also be reflected in closer relationships between *B. minima* and *B. tuberculata* than between *B. minima* and *B. peyrierasi*, or between *B. tuberculata* and *B. peyrierasi*. However, each of the three localities has a relatively large number of species not occurring at the other localities (> 50%).

MISCELLANEOUS NOTES

1. In their *Brookesia* review Raxworthy & Nussbaum (1995) used the spelling Chamaeleontidae as family name for chameleons. The same spelling is used in the Zoological Record. We here refer to the etymology provided by Klaver & Böhme (1997) and consider Chamaeleonidae as correct family name for chameleons.
2. According to Brygoo (1978), Glaw & Vences (1994), Raxworthy & Nussbaum (1995), and Klaver & Böhme (1997), *Brookesia peyrierasi* was described in Brygoo & Domergue (1975). However, already in their 1969 publication, these authors had proposed the name for the Nosy Mangabe specimens, to be used if these would be recognized as distinct species in the future. Since this proposal was not accompanied by a differential diagnosis nor by a type designation, *Brookesia peyrierasi* Brygoo & Domergue, 1969 is to be seen as nomen nudum. Brygoo & Domergue (1975) must be considered the source for the original description of the species (not as designation of a new name as wrongly stated by the authors by usage of the abbreviation *nom. nov.*).
3. *Brookesia minima* was described by Boettger (1893: 123) based on three specimens from Loucoubé (= nature reserve Lokobe) on the island Nossibé (= Nosy Be) which were donated by C. Ebenau and A. Stumpff in 1880 and 1885. Mertens (1967) designated SMF 16512 as lectotype. Brygoo (1978: 49) gives the following (somewhat confusing) information: 'Types: récoltes de C. Ebenau et A. Stumpff, 3 spécimens au Natur-Museum Senckenberg 16.513' and also figured 'paratype SMF 16.514 Senck. Mus.'. However, on page 50 he states that he has examined the paratype 16.513 from Nosy Be and another specimen (16.514) from the same locality collected by A. Voeltzkow. Since in the original description Boettger (1893) only mentioned Ebenau and

Stumpff as donators of the type specimens, SMF 16514 is neither paratype nor paralectotype. However, we recently discovered a specimen in the 'Zoologische Staatssammlung München' (ZSM 17/1921) which was received from the SMF in 1921 (probably in exchange). The specimen is labelled as cotype and its origin is given as 'Insel Nossibé bei Madagascar, 1880, C. Ebenau leg.' We conclude that the three type specimens of *Brookesia minima* are as follows: SMF 16512 (lectotype), SMF 16513 (paralectotype) and ZSM 17/1921 (paralectotype).

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