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A new genus name for an ancient Malagasy chameleon clade
and a PDF-embedded 3D model of its skeleton

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Recent research has led to enormous progress in the understanding of chameleon phylogeny (e.g., RAXWORTHY et al. 2002, TOWNSEND et al. 2009, TOLLEY et al. 2013), and new genus names were introduced for most of the identified deep chameleon clades (*Kinyongia*, *Nadzikambia*, *Rieppoleon*), or available names were resurrected from synonymy (*Archaius*) or elevated from subgenus level (*Trioceros*). A remarkable exception is a deep lineage composed of the two morphologically distinct species *Brookesia nasus* and *B. lolontany* from Madagascar. RAXWORTHY et al. (2002) found this lineage to be the basal clade in the family Chamaeleonidae, but more recent studies regarded it (with limited support) as a sister group of all other *Brookesia* that split off in the Cretaceous (TOWNSEND et al. 2009) or Palaeocene (TOLLEY et al. 2013). Thus, the *Brookesia nasus-lolontany* clade split off much earlier than all other extant chameleon clades recognized today as distinct genera. In the present paper, we provide new data on *B. lolontany* (including an embedded 3D-PDF model of its skeleton) and a morphological diagnosis of the *B. nasus-lolontany* clade, and transfer the two species to a new genus. As already emphasized by VENCES et al. (2013), this decision results in two clearly monophyletic genera with improved morphological diagnosability.

Brookesia lolontany, previously known from the Tsaranana massif only, was found on 28 November 2012 in the cloud forest of the Sorata massif (13.6750° S, 49.4392° E, 1580 m a.s.l.) in northern Madagascar, which represents a significant extension of its known range to the north. Two specimens (female: ZSM 1679/2012, field number FGZC 3666 and male: UADBA-FGZC 3667) were collected. The hitherto undescribed male of *B. lolontany* (Fig. 1., snout–vent length 22.1 mm, total length 36.7 mm, hemipenes everted, therefore probably adult) generally resembles the male of *B. nasus*, but is much smaller, has a more tubercular skin and a relatively long (1.1 mm), single, dermal lobe on the tip of the snout. This lobe is longer than in the female (0.8 mm) and longer than the paired tiny lobes present in *B. nasus*. Another

sexually dimorphic character is the wave-like dorsal crest of the *lolontany* male, which is, however, less developed than in *B. nasus* males. Both *B. lolontany* specimens were found after dusk, roosting on low vegetation (male ca. 40 cm, female ca. 60 cm above the ground). An X-ray computed tomography (CT) scan of the female (Fig. 2 with embedded 3D model, performed with a nanotom m [phoenix|x-ray] at 160 kV and 40 µA, skeleton segmented using AMIRA) revealed a long and pointed snout, long dorsal vertebral processes, and a single well-developed egg in its body (details are intended to be described elsewhere). Both the male and female displayed distinct death-feigning behaviour when handled, including falling on their sides, pulling the limbs close to the body, and – in more extreme cases – assuming a convex body posture with closed eyes and a slightly open mouth. In contrast to other chameleons, *Brookesia* spp. place the tip or the dorsal end of the tail on the substrate when walking, thus improving stability (MÜLLER & HILDENHAGEN 2009, BOISTEL et al. 2010). This behaviour is even visible in many photographs. We did neither observe this behaviour in *B. nasus* and *B. lolontany* nor find any clear indications for it in photographs of these species. It remains to be clarified, though, whether this is a behavioural difference between *Brookesia* and the new genus described below.

Molecular data (e.g., TOWNSEND et al. 2009) revealed that *B. nasus* and *B. lolontany* form a clade clearly separated from all other *Brookesia*. The morphological, osteological and behavioural data provided in the present paper confirm this result, and we therefore include both species in a new genus, which is described as

***Palleon* gen. n.**Type species: *Brookesia nasus* BOULENGER, 1887

Content: *Palleon nasus nasus* (BOULENGER, 1887), *Palleon nasus pauliani* (BRYGOO, BLANC & DOMERGUE, 1972), *Palleon lolontany* (RAXWORTHY & NUSSBAUM, 1995).



Figure 1. First published colour photograph of *Palleon lolontany* in life (male from the Sorata massif, a new locality for this species).

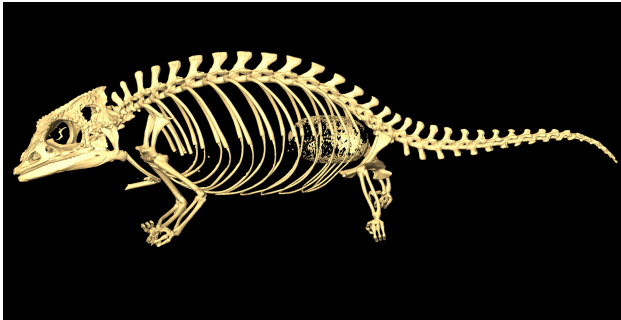


Figure 2. Skeleton of an adult female of *Palleon lolontany* from the left (ZSM 1679/2012, snout–vent length 33.4 mm, total length 52.9 mm) with 3D model in the PDF version. Click on image in Adobe Acrobat or Reader to activate the model!

Distribution: Humid forests in southeastern and northern Madagascar, from close to sea level to 2050 m a.s.l.

Diagnosis: Small, brownish chameleons (snout–vent length 22–49 mm, total length 37–87 mm) with a relatively short tail, long snout, laterally compressed body, strongly convex dorsal ridge, at least one dermal appendage on snout tip, and a moderately developed wave-like dorsal crest in males. No pelvic shield or series of vertebral spines (some irregular tubercles may be present). The two species of *Palleon* differ from all *Brookesia* species by (1) a long and pointed head versus very short head, (2) a single dermal lobe (*P. lolontany*) or pair of small pointed lobes (*P. nasus*) on snout tip (absent in all *Brookesia*), (3) the presence of a strongly convex dorsal ridge (dorsal ridge in *Brookesia* mostly absent, if present, it will be almost straight [RAXWORTHY & NUSSBAUM 1995]: *B. superciliaris*, *B. therezieni*, and *B. bekolosi*), (4) presence of a wave-like dorsal crest in males (dorsal crest entirely absent in all *Brookesia*), (5) absence of a regular series of vertebral spines or tubercles (present in most *Brookesia*), (6) very distinct genetic divergence (TOWNSEND et al. 2009, TOLLEY et al. 2013).

Palleon most closely resembles several species of the mainland African genus *Rhampholeon* by sharing with these a long and pointed head, small size, presence of dermal lobe(s) on snout tip, presence of a convex dorsal ridge,

occurrence of wave-like dorsal crests, absence of a regular series of vertebral spines or tubercles, and a predominantly brownish colouration (see TILBURY 2010), but the genetic differences between the two genera are very strong (e.g., TOWNSEND et al. 2009). *Palleon* differs from *Rieppeleon* by its longer snout and tail (except *R. kerstenii*) and from all remaining chameleon genera by its much smaller size, the generally shorter relative tail length, absence of any colourful markings, and strong genetic divergence (TOWNSEND et al. 2009, TOLLEY et al. 2013).

Etymology. The new genus name *Palleon* is derived from the Greek word “*Palae-*” (meaning “old”) and the Greek word “*leon*” (meaning “lion”; as used for other chameleon genera), referring to the very early separation of this clade. The resulting composite *Palae-o-leon* is shortened to *Palleon* for simplified pronunciation. The gender of the genus is masculine.

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