

A new cryptic frog species of the *Mantidactylus boulengeri* group with a divergent vocal sac structure

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Abstract. We describe a new frog species of the *Mantidactylus boulengeri* group (Amphibia: Anura: Mantellidae) in the subgenus *Gephyromantis* from south-eastern Madagascar. It is morphologically similar to *M. eiselti* and *M. thelenae* but differs in its advertisement calls with a distinctly shorter note duration, and in its bilobate (not single) subgular vocal sac. Like *M. eiselti* and *M. thelenae* the new species *Mantidactylus enki* is predominantly diurnal and calling males do not aggregate close to water bodies, indicating direct development as it has been demonstrated previously in *M. eiselti*. The advertisement calls of all three species are described in detail. A comparison with a further pair of cryptic species with bilobate vs. single subgular vocal sac (*Mantidactylus tschenki* — *M. cornutus*) did not reveal any consistent pattern of call variation correlated with vocal sac structure. Therefore, sexual selection may also be considered to explain differences in the colour and external structure of vocal sacs among closely related species.

Introduction

Recent research demonstrated that the anuran fauna of Madagascar contains many species which are distinguished mainly by their advertisement calls but have very low morphological differentiation (Glaw and Vences, 2000b). The available data indicate that generally these cryptic species are genetically well defined entities (Vences and Glaw, 2001) as is also known from other anuran groups (Estrada and Hedges, 1997). Recently, Glaw and Vences (2001) noted that two morphologically otherwise indistinguishable cryptic species in the genus *Mantidactylus* differed in vocal sac structure: while *Mantidactylus cornutus* Glaw and Vences, 1992, had a subgular vocal sac which in inflated state was clearly single and rounded, the sac of *M. tschenki* Glaw and Vences, 2001 was bilobate. The ecological and morphological correlates of advertisement call structure in anurans are poorly under-

stood and the study of sibling species may therefore shed light on the factors involved in modifications of the structure of vocalizations and morphology of vocal sacs.

The *M. boulengeri* group (subgenus *Gephyromantis*) contains a number of diurnal species that call away from water bodies and probably lack free-swimming larval stages. Two of the included species are morphologically very similar to each other and occur syntopically in the area of Andasibe in central eastern Madagascar: *Mantidactylus eiselti* (Guibé, 1975) and *M. thelenae* Glaw and Vences, 1994. Recent fieldwork in the area of the Parc National de Ranomafana in south-eastern Madagascar resulted in the discovery of a new species which is morphologically similar to *M. eiselti* and *M. thelenae*. In this paper we describe the new species and discuss possible correlates of its divergent advertisement calls and external vocal sac morphology.

Materials and Methods

Frogs were collected during the day, mainly by localizing calling males. They were sacrificed using chlorobutanol, fixed in 90% ethanol and preserved in 70% ethanol. Specimens studied in this paper are deposited in the herpetological collections of the Muséum National d'Histoire Naturelle, Paris (MNHN), Zoologische Forschungsinstitut und Museum A. Koenig, Bonn (ZFMK), and Zoologische Staatssammlung, München (ZSM).

Morphological measurements were taken by M. V., using calipers, to the nearest 0.1 mm: SVL (snout-vent length), HW (head width), HL (head length), ED (horizontal eye diameter), END (eye-nostril distance), NSD (nostril-snout tip distance), NND (nostril-nostril distance), TD (horizontal tympanum diameter), HAL (hand length), FORL (forelimb length), HIL (hindlimb length), FOL (foot length), FOTL (foot length including tarsus), IMTL, IMTH (length and height of inner metatarsal tubercle).

Advertisement calls were recorded with different tape recorders using external microphones. They were analysed with a MEDAV sound analysing system using the software Spektro 3.2. Temporal and metric measurements are given as range, with mean \pm standard deviation and number of measured units in parentheses.

Mantidactylus enki sp. n. (figs 1-2)

Holotype. ZFMK 62293, adult male, collected by F. Glaw, D. Rakotomalala and F. Ranaivojaona on 28 February 1996 at Ambatolahy (between Vohiparara and Ranomafana), south-eastern Madagascar, 21°15'S/47°24'E, at ca. 800 m above sea level.

Paratypes. ZSM 1083/2001 (originally ZFMK 62274), adult male and ZFMK 62289, adult female, collected by F. Glaw, D. Rakotomalala and F. Ranaivojaona on 3-4 March 1996 at Vohiparara (close to Ranomafana), south-eastern Madagascar, 21°13'S/47°22'E, at ca. 1050 m above sea level.

Diagnosis. A species of *Mantidactylus* as recognizable by the absence of nuptial pads and presence of femoral glands (though indistinct) in males. Assigned to the *Mantidactylus boulengeri* group in the subgenus *Gephyromantis* by (a) small body size (male SVL 20 mm, female SVL 21 mm), (b) blackish folds along the lower jaw in males, corresponding to the vocal sacs, (c) absence of webbing between toes, (d) totally connected lateral metatarsalia, (e) diurnal calling, not concentrated around water bodies and (f) morphological similarity

to *M. eiselti* and *M. thelenae*. Distinguished from the latter two species by its vocal sac structure when inflated (distinctly bilobate vs. single subgular) and advertisement calls (figs 3-5): series of short melodious notes vs. longer melodious notes in *M. eiselti* (note duration 31-34 ms in *M. enki* vs. 158-186 in *M. eiselti*) and still much longer and unmelodious notes in *M. thelenae*. Furthermore distinguished from the available material of *M. eiselti* and *M. thelenae* by slightly smaller body size (male SVL 20 mm vs. 21-23 mm; table 1), a slightly more granular belly skin, a larger tympanum (62-64% of eye diameter, vs. 47-55%, except one *M. thelenae* with 67%), and a more distinct light median stripe on throat and chest.

Distinguished from *Mantidactylus blanci* (Guibé, 1974), *M. boulengeri* (Methuen, 1920) and *M. leucocephalus* (Angel, 1930) by smaller body size (male SVL 20 mm vs. 21-29 mm), complete absence of webbing (vs. presence of rudiments). Further distinguished from these and all other species in the *M. boulengeri* group by advertisement call structure.

Etymology. Enki is the name of a Sumerian god and means “Lord of the Soil”. The name is used as invariable noun in apposition to the generic name.

Description of the holotype. Specimen in excellent state of preservation. SVL 19.9 mm. For measurements see table 1. Body slender; head distinctly longer than wide, not wider than body; snout slightly pointed in dorsal view, rounded in lateral view; nostrils directed posterolaterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis indistinct, rounded; loreal region concave; tympanum distinct, rounded, 62% of eye diameter; supratympanic fold distinct and straight; tongue ovoid, posteriorly bifid; maxillary teeth present; vomerine teeth absent; choanae rounded. Arms slender, distinct single subarticular tubercles; inner and outer metacarpal tubercles indistinct but visible; fingers without webbing; relative length of fingers 1 < 2 < 4 < 3, fourth finger clearly longer than second finger; finger discs distinctly enlarged; nuptial pads absent. Hindlimbs slender; tibiotarsal articulation reaches nostril when hindlimb is adpressed along body; lateral metatarsalia strongly connected; inner and outer metatarsal tubercles distinct; webbing between toes absent; relative length of toes 1 < 2 < 5 < 3 < 4; fifth toe slightly shorter than third toe. Skin on the dorsal surface smooth, with clearly visible dorsolateral folds. Ventral skin smooth on throat, chest and limbs, granular on central and posterior belly, and coarsely granular on lateral belly. Femoral glands indistinct in external view.

After five years in preservative, dorsally uniformly greyish brown with few dark spots on head surface forming an interrupted line between eyes. Dorsal colour gradually fades into light ventral colouration on flanks. Tympanic area dark brown, dorsally sharply limited by supratympanic fold and ventrally by a white line which runs from snout tip to forelimb insertion, and partly continues on upper arm. Another dark brown line running from nostril to eye along canthus rostralis limits this white stripe, which makes up most of head sides including upper lip, in anterior head region. Along upper lip few small dark spots, which do not form a regular alternating brown-white pattern. Very faint greyish crossbands on

Table 1. Morphometric measurements (all in mm) of available specimens of *Mantidactylus enki*, *M. eiselti* and *M. thelenae*. For abbreviations of measured variables, see Materials and Methods; further abbreviations used: M (male); F (female); HT (holotype); PT (paratype); RHL (relative hindlimb length: point reached by tibiotarsal articulation when the hindlimb is adpressed along the body).

Specimen	Sex	Status	SVL	HW	HL	TL	ED	END	NSD	NND	HAL	FORL	HIL	FOTL	FOL	IMTL	IMTW	RHL
<i>Mantidactylus enki</i>																		
ZSM 1083/2001	M	PT	20.4	6.7	7.5	1.6	2.5	2.0	1.4	2.0	5.9	13.3	36.4	16.0	10.0	1.0	0.4	snout tip
ZFMK 62293	M	HT	19.9	6.8	7.8	1.6	2.6	2.0	1.2	2.1	5.7	12.7	34.8	15.9	10.1	0.9	0.3	nostril
ZFMK 62289	F	PT	20.9	6.4	7.8	1.7	2.7	1.9	1.5	1.9	6.2	13.5	37.2	16.9	10.2	0.8	0.3	nostril
<i>Mantidactylus eiselti</i>																		
MNHN 1975.2	M	HT	21.3	6.5	7.7	1.6	2.8	1.9	1.7	2.2	6.7	14.0	35.8	16.3	10.8	1.2	0.6	between nostril and snout tip
ZFMK 53696	M	-	22.2	6.7	7.6	1.3	2.7	2.0	1.5	2.2	6.6	14.6	37.8	16.4	10.4	1.0	0.4	nostril
ZFMK 53697	M	-	21.8	6.7	8.2	1.6	3.0	1.9	1.5	2.4	6.3	13.8	34.7	15.7	9.4	1.2	0.4	between eye and nostril
ZFMK 57421	M	-	21.2	6.9	7.8	1.4	2.9	1.7	1.3	2.0	6.4	14.1	36.7	16.9	10.2	0.8	0.4	nostril
ZFMK 59874	M	-	22.0	6.7	8.4	1.4	3.0	2.1	1.4	2.2	6.3	13.2	38.0	16.7	10.2	1.1	0.4	nostril
<i>Mantidactylus thelenae</i>																		
ZFMK 57422	M	HT	22.9	7.5	8.7	1.6	2.9	2.5	1.3	2.5	7.0	14.5	37.8	16.6	10.4	1.0	0.6	nostril
ZFMK 57423	M	PT	22.8	7.7	8.4	1.8	2.7	2.2	1.5	2.5	7.1	14.5	37.7	16.7	10.6	1.2	0.5	between eye and nostril
ZFMK 57424	M	PT	22.8	7.4	8.6	1.6	3.2	2.2	1.5	2.5	7.1	14.7	37.5	17.2	11.3	0.9	0.5	between eye and nostril

limbs. Ventrally, dirty yellowish, with some dark mottling on shanks and thighs. A white median band, bordered by dark, runs along throat and chest, which also has some additional white pigment. Lower lip ventrally with distinct alternating brown-white pattern. Blackish folds along lower jaw in males, corresponding to vocal sac. Anterior belly with some white pigment.

Variation. The male paratype (ZSM 1083/2001) agrees well with the holotype in morphology and colouration. The alternating dark-light pattern is totally absent from the upper lip and only indistinct ventrally on the lower lip. The female paratype (ZFMK 62289) is slightly larger than the males: mean male SVL is 96% of female SVL. The white stripe on the throat is less marked than in the males; instead, the whole throat appears whitish with darker mottling. The female, furthermore, has, dorsally, a light median stripe and a light thin line on the posterodorsal surface of hindlimbs. Its head surface is reddish brown; this colour ends posteriorly triangular and thus forms a well-delimited rhomboid marking. In ZSM 1083/2001, the femoral gland in internal view (after dissection and reflection of thigh skin) is a very indistinct patch of 3-5 similarly sized granules.

Natural history. Calling males were observed during the day in primary rainforest as well as in degraded vegetation, on the ground and up to 1 m high in shrubs. They were not concentrated around water bodies. It is therefore likely that *M. enki* has a reproductive mode of direct development without free-swimming larval stages as has been demonstrated for *M. eiselti* (Glaw and Vences, 1994).

Advertisement calls. Recorded on 26 February 1996 at Ranomafana. Regular series of short melodious notes (fig. 3). Each note corresponded to one expiration. One analysed call had a duration of 16.4 s and consisted of 37 notes. Note duration was 31-34 ms (33 ± 1 ms, $n = 18$), duration of inter-note intervals was 371-466 ms (401 ± 28 ms, $n = 17$), note repetition rate was 2.2-2.3/s. Fundamental frequency was 2150-2650 Hz, dominant frequency 4300-5600 Hz. The inflated vocal sac had a bilobate shape.

New data on *Mantidactylus eiselti* and *M. thelenae*

Calls of Mantidactylus eiselti. Calling males were observed 20-50 cm high in dense vegetation, not concentrated around water bodies. Fewer specimens were heard in primary rainforest than in degraded fern vegetation. Calling activity was mainly diurnal, but single calls were also recorded at night (at least until 01:30 a.m.). The inflated vocal sac was single subgular (not bilobate). Calls were series of 7-21 melodious notes (fig. 4). Call parameters in recordings from Andasibe (on 28 February 1994 at 24.2°C air temperature) were as follows: note duration 158-186 ms (174 ± 8 ms, $n = 13$), inter-note interval duration 321-499 ms (413 ± 50 ms, $n = 12$), note repetition rate 1.6-2.3/s, dominant frequency 3900-4100 Hz with harmonics at 7950-8150 Hz. Alternating calls between two males occasionally occurred; in these cases, inter-note intervals had longer durations.

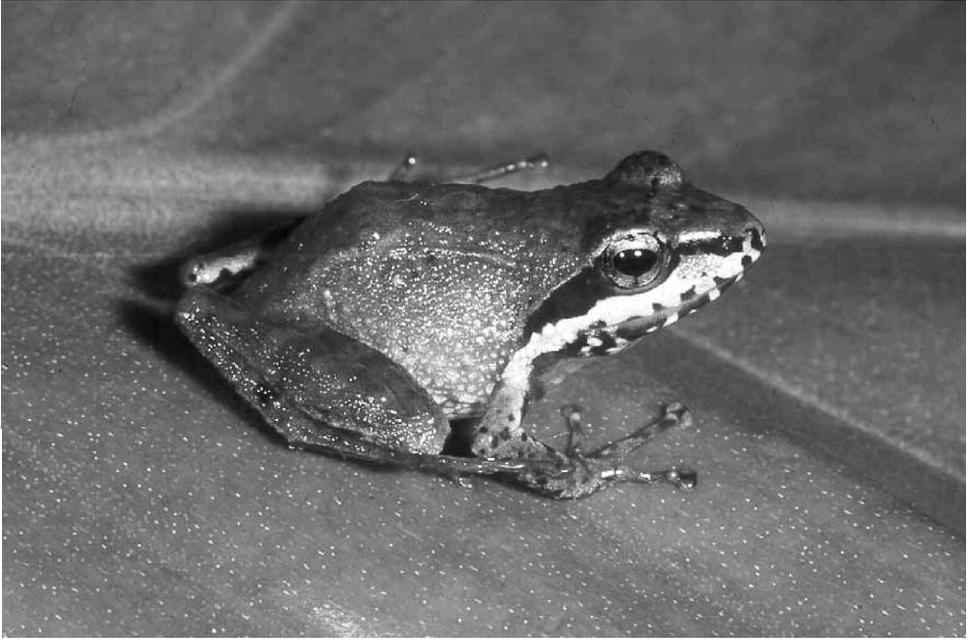


Figure 1. *Mantidactylus enki*, male holotype (ZFMK 62293) in life.

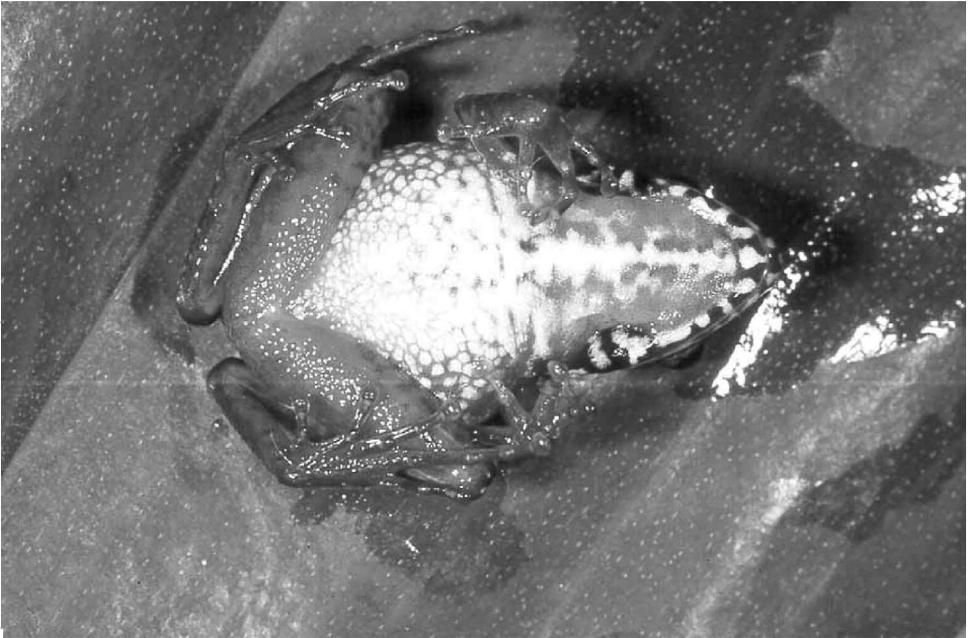


Figure 2. *Mantidactylus enki*, male holotype (ZFMK 62293) in ventral view.

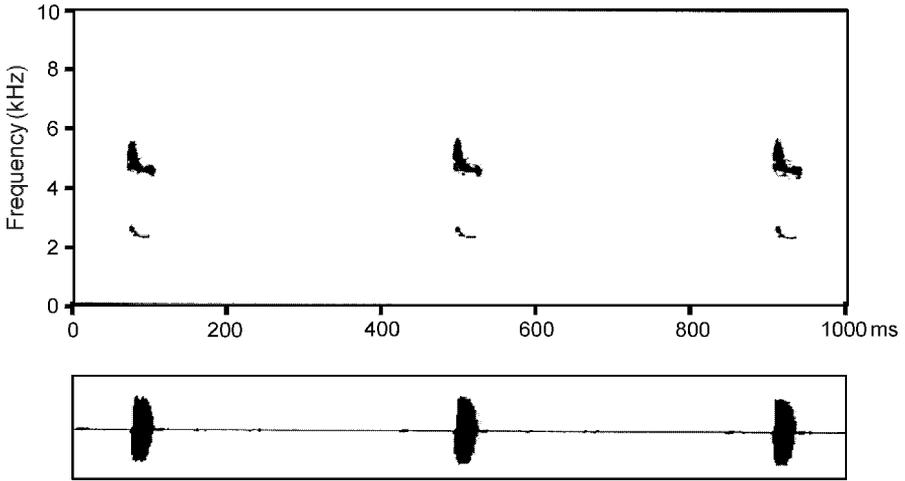


Figure 3. Sonagram and oscillogram of three notes of a call of *Mantidactylus enki* from Ranomafana.

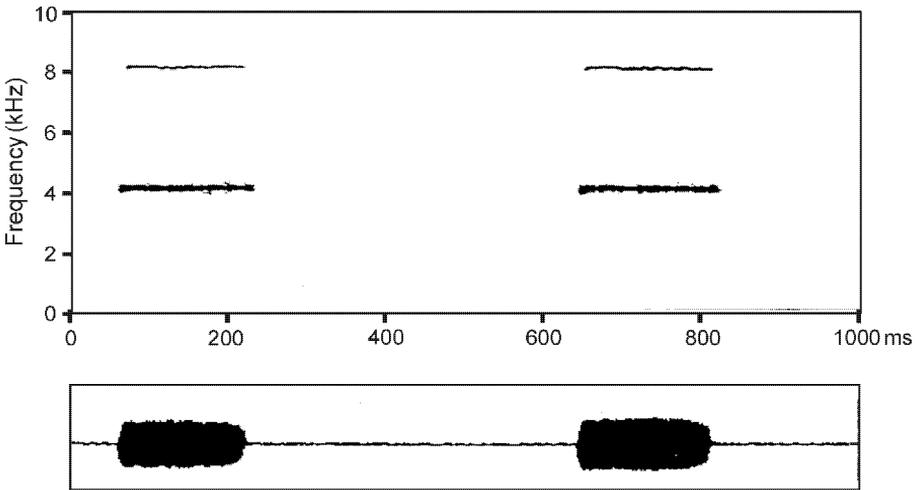


Figure 4. Sonagram and oscillogram of two notes of a call of *Mantidactylus eiselti* from Andasibe.

Calls of Mantidactylus thelenae. Calling males were heard during the day in secondary fern vegetation (Andasibe) as well as primary rainforest (Mantady) and were never aggregated around water bodies. At Mantady syntopic occurrence of *M. thelenae* and *M. eiselti* was observed: *M. thelenae* occupied almost exclusively the foot of a hill; ascending the hill, *M. thelenae* calls became rarer whereas *M. eiselti* became more common and was the only species on the hilltop. The inflated vocal sac of *M. thelenae* was single subgular (not bilobate). Calls were series of 5-8 unharmonious pulsed notes (fig. 5). Each note corresponded to one expiration. Call parameters were as follows. In recordings

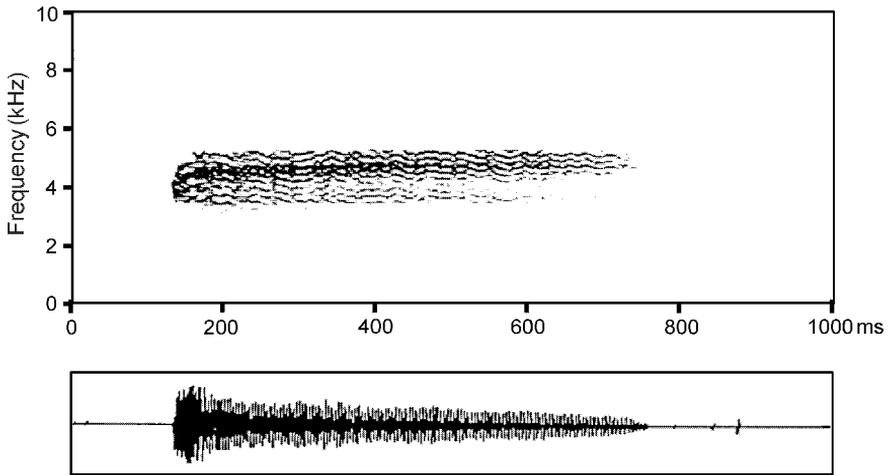


Figure 5. Sonogram and oscillogram of one note of a call of *Mantidactylus thelenae* from Andasibe.

from Andasibe (28 February 1994, 11:00 a.m., 24°C air temperature), note duration was 482–684 ms (577 ± 54 ms, $n = 21$), inter-note interval duration was 1027–1837 ms (1405 ± 221 ms, $n = 15$), pulse repetition rate within notes was 250/s, frequency was 2850–5200 Hz, dominant frequency 3600–4700 Hz. In recordings from Mantady (10 February 1996), note duration was 540–610 ms (587 ± 33 ms, $n = 4$), inter-note interval duration was 1110–1431 ms (1290 ± 164 ms, $n = 3$), frequency 2550–3700, dominant frequency 3600–4650 Hz.

Distribution of M. eiselti, M. thelenae, and M. enki. Blommers-Schlösser and Blanc (1991) mention the locality Soavala in far south-eastern Madagascar for *M. eiselti*, whereas Raxworthy and Nussbaum (1996) recorded the species from the Andringitra massif, Ranomafana (900–1050 m altitude) and the Anosy massif. We re-examined the material in the Paris museum, which was the basis for the distribution information in Blommers-Schlösser and Blanc (1991). Specimens labelled as *M. eiselti* from the Chaînes Anosyennes (= Anosy Massif; comprising Soavala, and located in the same area as Andohahela) belong to a large series of frogs originally catalogued as *M. boulengeri* (e.g., MNHN 1972.1842–2069, collected by Ch.P. Blanc). They could not be morphologically distinguished from other specimens in the same series of less uniform colouration.

To clarify the specific identification of these individuals, we re-examined all specimens of the *M. boulengeri* group available to us. Based on examination of more than 200 specimens (see appendix), and in addition to *M. eiselti*, *M. thelenae*, and *M. enki*, we distinguish the following species with blackish folds along the lower jaw in males, corresponding to the vocal sacs: (1) *Mantidactylus decaryi* (Angel, 1930), characterized by distinct dorsal ridges (see Glaw and Vences, 2000a); (2) *M. klemmeri* (Guibé, 1974) from Marojejy in north-eastern Madagascar, characterized by white upper lips, absence of dorsolateral folds

and a smooth dorsum (Vences et al., 1997); (3) *M. blanci*, characterized by a white upper lip, continuous dorsolateral folds, a relatively small pigmented inner metatarsal tubercle, and rudimentary webbing (reaching closer to second than first subarticular tubercle of fifth toe), (4) *M. leucocephalus*, characterized by absence of uniform white colour of upper lip and of continuous dorsolateral folds, a relatively large unpigmented inner metatarsal tubercle, and more extended webbing (reaching closer to the first than second subarticular tubercle of fifth toe); and (5) *M. boulengeri*, characterized by absence of uniform white colour on upper lip and of dorsolateral folds, a relatively small pigmented inner metatarsal tubercle, and a reduced webbing.

Following these definitions, the specimens from the Chaînes Anosyennes catalogued as *M. eiselti* can clearly be attributed to *M. blanci*. Their belonging to *M. eiselti* could be excluded by their larger size, and by the presence of distinct femoral glands in the single male. Voucher numbers and their corresponding SVL are as follows: MNHN 1972.631 (Soavala; female, SVL 26.0 mm); MNHN 1972.1848 (female, SVL 26.6 mm), 1972.1877 (female, SVL 24.8 mm), 1972.1888 (female, SVL 25.2 mm), 1972.1971 (female, SVL 24.0 mm), 1972.2015 (male, SVL 23.6 mm) (all from Chaînes Anosyennes).

In conclusion, the occurrence of *M. eiselti* and *M. thelenae* in south-eastern Madagascar is in strong need of confirmation. The same applies to records from Andringitra, while findings of *M. eiselti* in Ranomafana (Raxworthy and Nussbaum, 1996) probably refer to *M. enki*. Revision of MNHN material further led us to confirm that the paratypes of *Mantidactylus eiselti* (MNHN 1975.3-4, two females) do not belong to that species but to *Mantidactylus blommersae* (see Blommers-Schlösser and Blanc, 1991).

After exclusion of doubtful records, the localities of *M. eiselti*, *M. thelenae* and *M. enki* are as follows. *Mantidactylus eiselti*: (1) type locality Andasibe (=Perinet); (2) Analamazotra (Glaw and Vences, 1994); (3) Mandraka (Glaw and Vences, 1994); (4) Ankeniheny (Glaw and Vences, 1994); (5) Vohidrazana (call record); (6) Mantady (call record). *Mantidactylus thelenae*: (1) type locality Andasibe; (2) Mantady (call record). *Mantidactylus enki*: (1) type locality Ambatolahy; (2) Vohiparara; (3) Ranomafana (call record).

Discussion

Mantidactylus enki adds a new species to the phenetic *Mantidactylus boulengeri* group which so far contained nine species. While there remains no doubt that *M. eiselti*, *M. thelenae* and *M. enki* are closely related because of their extremely similar morphology, their relationships to other species are less evident. Three species of the *M. boulengeri* group occur associated with brooks and possibly do not have direct development: *M. webbi* (Grandison, 1953) which has white folds along the lower jaw in males, as well as *M. rivicola* Vences, Glaw and Andreone, 1997 and *M. silvanus* Vences, Glaw and Andreone, 1997 which are characterized by a large and prominent inner metatarsal tubercle

which is lacking in the other species of the group (Vences et al., 1997). The remaining species, *M. blanci*, *M. boulengeri*, *M. leucocephalus*, *M. decaryi* and *M. klemmeri* all have blackish folds along the lower jaw in males and diurnal calling behaviour far from water. It is likely that these species form a monophyletic lineage that also includes *M. eiselti*, *M. thelenae* and *M. enki*. All these taxa are characterized by calls consisting of a single note type which is emitted in series. It is remarkable that a transformation series can be drawn from the short and melodious notes of *M. enki* through the longer melodious notes of *M. eiselti* and the still longer unharmonious and pulsed notes of *M. thelenae* to the notes of *M. klemmeri* with widely spaced pulses (see Vences et al., 1997 for call description of the latter species). Whether this series actually corresponds to an evolutionary trend in the group cannot be ascertained without a well founded phylogenetic reconstruction, but it may constitute a model to understand how pulsed notes can evolve out of melodious notes by an increase of note duration.

Mantidactylus enki from the Ranomafana area has a bilobate vocal sac when inflated while *M. eiselti* and *M. thelenae* from Andasibe have a single sac. A similar difference is found between *M. tschenki* and *M. cornutus* (Glaw and Vences, 2001). However, no concordant associated pattern of differences in call structure is obvious from the available data: comparing *M. enki* to *M. eiselti* which agrees in general (melodious) call structure, both taxa have rather loud calls that can be heard at large distances; *M. enki* (bilobate sac) is characterized by a shorter note duration and higher dominant frequency than *M. eiselti* (single sac). *Mantidactylus tschenki* (bilobate sac) has a rather loud call, while that of *M. cornutus* (single sac) appears to be less intense. Notes in *M. tschenki* are longer and have a lower pulse repetition rate and higher dominant frequency. The only concordant pattern is thus a higher dominant frequency in the species with bilobate sacs, but this may be caused by their smaller body size. Differences in vocal sac structure between closely related frog species have been known for long (Liu, 1935) but, to our knowledge, functional correlations have not been documented. As inflated vocal sacs have an obvious relevance for short-distance visual signalling, it is well possible that their shape and colour are under influence of sexual selection, especially in diurnal species such as *M. eiselti*, *M. thelenae* and *M. enki*.

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Appendix: Comparative material examined

Mantidactylus blanci

MNHN 1972.183 (holotype) and MNHN 1972. 184-189 (paratypes) (Ambalamarovandana); MNHN1933.231 (Ruisseau Iorantjatsy); MNHN 1953.120 (Andringitra, forêt Fivahona); MNHN 1972.641-642 (Ambalamarovandana); MNHN 1972.643-644 (Andrianony); MNHN 1972.1846-1847, 1972.1849-1851, 1972.1853-1857, 1972.1859-1860, 1972.1862-1864, 1972.1871-1874, 1972.1876, 1972.1878, 1972.1880-1887, 1972.1889-1893, 1972.1897, 1972.1901, 1972.1905-1906, 1972.1908, 1972.1910-1917, 1972.1919-1920, 1972.1922-1923, 1972.1926-1928, 1972.1931-1934, 1972.1936, 1972.1938-1939, 1972.1942-1944, 1972.1946-1948, 1972.1950, 1972.1952, 1972.1954, 1972.1956, 1972.1958, 1972.1962-1963, 1972.1967-1970, 1972.1972, 1972.1975-1977, 1972.1979, 1972.1987, 1972.1991-1993, 1972.1995-1997, 1972.1999-2000, 1972.2009, 1972.2013, 1972.2034, 1972.2054, 1972.2061, 1972.2063, 1972.2065, 1972.2069 (Camps III, IV and V, Chaînes Anosyennes); MNHN 1975.769 (ex 1953.120?, probably Andringitra); MNHN 1975.780 (Nosiarivo; possibly erroneous); ZFMK 57426-57427 and 59829-59830 (Andringitra).

Mantidactylus boulengeri

MNHN 1953.124 (Ambila); MNHN 1975.955 (Fenerive, juvenile); ZFMK 52721, 53692 and 56164 (Andasibe); ZFMK 52722 (Nosy Boraha); ZFMK 52723-52724 and 66672 (Nosy Mangabe).

Mantidactylus decaryi

MNHN 1930.435 (lectotype, Midongy du Sud); MNHN 1930.437 (paralectotype, Pic d'Ivohibe); MNHN 1930.438 (paralectotype, Midongy du Sud); ZFMK 62294 (Ranomafana); ZFMK 62279 (next to Vohiparara).

Mantidactylus eiselti

MNHN 1975.2 (holotype, Andasibe); ZFMK 53696-53697, 57421 and 59874 (Andasibe).

Mantidactylus klemmeri

MNHN 1973.955-963 (holotype and paratypes, Marojejy); ZFMK 59942-59944 (Marojejy).

Mantidactylus leucocephalus

Remark: This taxon was considered as of uncertain status by Glaw and Vences (1994) or as subspecies (Andreone and Randriamahazo 1997). Based on differences in advertisement calls (Glaw and Vences 1994), distinct morphology (see Results herein) and reanalysis of types which share states of webbing, dorsal integument and inner metatarsal tubercle with other specimens assigned to this taxon previously, we herein treat it as full species.

MNHN 1930.441-442 (syntypes of *Gephyromantis decaryi leucocephala* Angel, 1930; Midongy du Sud and Befotaka); MNHN 1935.152 and 166 (Isaka-Ivondro); MNHN 1972.1842-1845, 1972.1852, 1972.1858, 1972.1861, 1972.1867-1870, 1972.1879, 1972.1895-1896, 1972.1898-1900, 1972.1902-1903, 1972.1907, 1972.1909, 1972.1918, 1972.1921, 1972.1924, 1972.1929-1930, 1972.1935, 1972.1937, 1972.1940-1941, 1972.1945, 1972.1949, 1972.1951-1953, 1972.1955, 1972.1957, 1972.1959-1960, 1972.1964-1966, 1972.1973-1974, 1972.1978, 1972.1981-1972.1986, 1972.1988-1990, 1972.1994, 1972.1998, 1972.2001-2008, 2010-2012, 1972.2014, 1972.2017-2027, 1972.2029-2030, 1972.2032-2033, 1972.2037, 1972.2039-2043, 1972.2046-2053, 1972.2055, 1972.2057-2060, 1972.2062, 1972.2064, 1972.2066-2067 (Chaînes Anosyennes); MNHN 1972.633 (Soavala, Chaînes Anosyennes); MNHN 1975.634-635 (Ambana-Bekazaha, Chaînes Anosyennes); MNHN 1975.782 (St. Luce); ZFMK 52717-52729 and 53693-53695 (Nahampoana).

Mantidactylus thelenae

ZFMK 57422-57424 and ZSM 580/1999 [originally ZFMK 57425] (holotype and paratypes, Andasibe).

Uncertain determination

MNHN 1930.439 (Befotaka, possibly *M. leucocephalus*); MNHN 1930.440 (Vondrozo); MNHN 1930.443-444 (syntypes of *Gephyromantis verrucosus* Angel, 1930, Fort Carnot, 600 m altitude, probably *M. boulengeri*); MNHN 1953.125 (Bas Sambirano, probably *Mantidactylus pseudoasper*); MNHN 1975.788 (Bas Manongarivo, probably *M. pseudoasper*); MNHN 1975.955-956 (Fenerive, juveniles, possibly *M. boulengeri*). Vouchers for other localities given in Blommers-Schlösser and Blanc (1991) were not found in the MNHN collection.

