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Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany

Systematic revision of the genus *Aglyptodactylus* Boulenger, 1919 (Amphibia: Ranidae), and analysis of its phylogenetic relationships to other Madagascan ranid genera (*Tomopterna*, *Boophis*, *Mantidactylus*, and *Mantella*)

F. GLAW, M. VENCES and W. BÖHME

Abstract

Recent field studies revealed two new species of the genus *Aglyptodactylus* (Amphibia: Anura: Ranidae), which was hitherto considered as monotypic and confined to humid eastern Madagascar. Both new species, *Aglyptodactylus laticeps* sp. *n.* and *Aglyptodactylus securifer* sp. *n.*, occur syntopically in the deciduous dry forest of Kirindy in western Madagascar. In comparison to *Aglyptodactylus madagascariensis* from eastern rainforests, the new species *A. laticeps* shows a remarkable morphological divergence, which may be partly due to adaptations to burrowing habits in dry environments. Despite of the morphological differentiation, advertisement calls and osteology indicate that all three species of *Aglyptodactylus* are closely related. A phylogenetic analysis of the Madagascan ranid genera *Aglyptodactylus*, *Mantella*, *Mantidactylus*, *Boophis*, and *Tomopterna* (the latter including species from Madagascar, Africa, and Asia) strongly supports a sister group relationship of *Aglyptodactylus* with the ranine genus *Tomopterna*. We therefore transfer *Aglyptodactylus* from the Rhacophorinae to the Raninae and discuss implications of this rearrangement for ranoid systematics. The existence of the endemic genus *Aglyptodactylus* in Madagascar as well as its close phylogenetic relationships to *Tomopterna* confirm that the Raninae were already present on the Madagascan plate before its separation from Africa. The Madagascan *Tomopterna labrosa* shows several important differences both to Asian and to African species of the genus, and is therefore transferred from the subgenus *Sphaerotheca* (now restricted to Asia) to a new subgenus *Laliostoma* subgen. *n.*

Key words: Amphibia – Anura – Ranidae – Rhacophorinae – *Aglyptodactylus* – *A. laticeps* sp. *n.* – *A. securifer* sp.*n.* – *Boophis* – *Mantidactylus* – *Mantella* – *Tomopterna* – *Laliostoma* subgen. *n.* – Madagascar – systematics – phylogeny – biogeography

Introduction

Madagascar has a very diverse anuran fauna. All of the currently 175 recognized species have a firmisternal shoulder girdle and are classified in the suborder Neobatrachia, superfamily Ranoidea (*sensu* Dubois 1992). Apart from the families Microhylidae and Hyperoliidae, ranoid frogs are represented in Madagascar by the following groups:

1. The endemic Mantellinae is considered either a subfamily of the Ranidae (Blommers-Schlösser 1993) or a subfamily of the Rhacophoridae (Channing 1989). Two genera are currently accepted: the well-defined, monophyletic *Mantella*, and the speciose *Mantidactylus* which is divided into 12 subgenera (Glaw and Vences 1994; Vences et al. *in press*).
2. The subfamily Raninae contains the only non-endemic Madagascan anuran species and genera: the introduced Asian *Hoplobatrachus tigerinus*, the non-endemic African *Ptychadena mascareniensis*, and the endemic species *Tomopterna labrosa*. The distribution of *Tomopterna* is very disjunct; the genus currently includes six species in Africa, one species in Madagascar and two (Dubois 1992) or six (Frost 1985; Dutta and Manamendra-Arachchi 1996) in Asia.
3. The rhacophorines are considered a subfamily of the Ranidae by Blommers-Schlösser (1993). According to this author, rhacophorines are represented in Madagascar by two endemic genera, the mainly arboreal *Boophis* and the monotypic and terrestrial *Aglyptodactylus*.

Aglyptodactylus madagascariensis (Duméril, 1853) was among the first five anuran species described from Madagascar. Originally named *Limnodytes madagascariensis*, the species was transferred to *Mantidactylus* by Mocquard (1902), when he noted the presence of an intercalary element (*'phalange additionelle'*). Boulenger (1919) recognized that (in contrast to *Mantidactylus*) the digital terminal expansions of this species are not completely grooved, and therefore created the monotypic genus *Aglyptodactylus* [*a* (Greek) = non; *glyptos* (Greek) = groove; *dactylos* (Greek) = finger].

Since then, authors have stressed several differences of *Aglyptodactylus* to *Mantidactylus* and to *Boophis*, confirming the validity of the genus (Guibé 1978; Blommers-Schlösser 1978, 1979a, 1979b). However, its systematic and phylogenetic relationships are still controversial, and the corresponding discussion largely reflects the lack of consensus in the classification of mantelline and rhacophorine frogs. Blommers-Schlösser (1993) regarded both the Mantellinae and the Rhacophorinae as sister groups within the family Ranidae. She classified *Aglyptodactylus* with the rhacophorines, relying on previous works (Blommers-Schlösser 1979a); this arrangement, however, was largely based on symplesiomorphic characters related with breeding biology, and on non-polarized osteological characters. On the other hand, Channing (1989) considered *Aglyptodactylus* a sister group of *Mantidactylus* in the subfamily Mantellinae.

Since its creation, the genus *Aglyptodactylus* was considered monotypic and restricted to the eastern rainforest belt of Madagascar (see map in Blommers-Schlösser and Blanc 1991). We recently discovered two new species of the genus in arid western Madagascar which are described below. The surprising morphological differences of one of the new species from *A. madagascariensis* and its similarity to *T. labrosa* led us to reconsider the phylogeny of Madagascan ranids by analyzing the relationships of *Aglyptodactylus* to *Boophis* (Rhacophorinae), *Tomopterna* (Raninae), and the Mantellinae (*Mantidactylus* and *Mantella*).

Material and methods

Specimens were captured by opportunistic night searching and by locating calling males. Field observations, unless otherwise stated, were made by F. G. Vocalizations were recorded with a portable Tensai tape

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recorder (model RCR-3222) and an external microphone (Vivanco EM 238). Bioacoustic measurements were done by F. G. with the sound analyzing system MEDAV Spektro 3.2.

Morphometric measurements were carried out by M. V. with a precision calliper to the nearest tenth of millimetre. Measurements taken were snout-vent length (SVL), head width behind the eyes (HW), head length from posterior maxillary commissure to snout tip (HL), horizontal eye diameter (Eye), horizontal tympanum diameter (Tym), distance from eye to nostril (Eye-Ns), distance from nostril to snout tip (Ns-St), distance between nostrils (Ns-Ns), foot length (FoL), foot length including tarsus (FoTL), hindlimb length from anus to tip of longest toe (HiL), forelimb length from axil to tip of longest finger (ForL), length of fingers 1–3 (F1, F2, F3), hand length (HaL), length, width and height of inner metatarsal tubercle (IMTL, IMTW, IMTH). Definitions of morphological measurements used in this paper are described in Glaw and Vences (1994). To allow better comparisons, the webbing formulae follow the system which was first applied to Madagascan frogs by Blommers-Schlösser (1979a, 1979b) and continued by most subsequent authors.

Morphometric data were processed statistically with the software package SPSS for Windows. Species were pairwise compared for each variable by analyses of covariance (ANCOVA), using SVL as covariable to eliminate the size factor. Data were transformed logarithmically (log$_{10}$) to render relationships between them linear. A Multiple Group Principal Component Analysis (MGPCA) was carried out using the log$_{10}$-transformed data. Cladistic analysis was performed with Hennig86 software (Farris 1988).

Allozyme electrophoresis followed standard techniques; a detailed description of the used method (vertical starch gel electrophoresis) and data sources for buffer and stain protocols are provided by Hille and Meinig (1996). Electromorphs were assigned to alleles and coded from a to f with increasing anodal mobility. Analyzed enzyme systems were glyceraldehyde-3-phosphate dehydrogenase (Ga3pdh), alpha-glycerophosphate dehydrogenase (Gpdh), lactate dehydrogenase (Ldh-2), isocitrate dehydrogenase (Idh-1, Idh-2), phosphoglucomutase (Pgm), as well as two unidentified serum proteins.

Osteological data were taken from the following alizarin/alcian blue stained specimens (method modified after Dingerkus and Uhler 1977; see Plösch 1991): *Aglyptodactylus madagascariensis* (ZFMK 18954 from Moramanga, ZFMK 52682 from Maroantsetra); *A. laticeps* sp. *n.* (ZFMK 59970, paratype); *A. securifer* sp. *n.* (ZFMK 59976, paratype); *Boophis microtympanum* (ZFMK 53660 from Ankaratra); *Mantidactylus luteus* (ZFMK 52712 from Nosy Boraha); 13 species of *Mantella* (for reference specimens see Vences et al. *in press*); *T. labrosa* (ZFMK 8890 from Toliara, ZFMK 52755 from Berenty, ZFMK 59965 and 59967 both from Kirindy); *Tomopterna delalandii* (ZFMK 44598 from Molepolole Gorge, Botswana); *Tomopterna natalensis* (ZFMK 33164 from Durban, South Africa); *Tomopterna breviceps* (ZFMK 13796 from India; without specific locality).

Colour slides of living specimens were made in the field to record natural colouration. Museum acronyms are used as follows: BM, Natural History Museum, London; MNHN, Muséum National d'Histoire Naturelle, Paris; ZMB, Zoologisches Museum, Berlin; ZFMK, Zoologisches Forschungsinstitut und Museum Koenig, Bonn.

Distribution of *Aglyptodactylus* in western Madagascar and description of two new species

Until recently the distribution of *Aglyptodactylus* was considered to be restricted to the humid eastern parts of Madagascar, from the area around Tolagnaro (i.e. Fort Dauphin) in the southeast to the north and the Sambirano region (Blommers-Schlösser and Blanc 1991). Bachmann and Blommers-Schlösser (1975) mentioned *Aglyptodactylus* among frogs occurring in western Madagascar, but neither in their study nor in Blommers-Schlösser (1979) nor Blommers-Schlösser and Blanc (1991) has any evidence of such occurrence been published. Guibé (1978) provided only the general information that *A. madagascariensis* is a common species which can be found in all forested regions of Madagascar. Hallmann et al. (personal communication) photographed a frog in the area around Antsalova in western Madagascar, which was identified by us as *A. madagascariensis*. This was apparently the first reliable record of the genus in western Madagascar and was quoted in Glaw and Vences (1992b). Subsequently, Emanueli and Jesu (1995) found *A. madagascariensis* in the western Nature Reserve Tsingy de Bemaraha.

In 1994 we received several photographs of frogs taken in the Kirindy Forest by T. Hafen, among them a couple of an unusually broad-headed *Aglyptodactylus*, which were pictured in Glaw and Vences (1994: 83, Fig. 229) as *A. madagascariensis*. Kirindy is a deciduous dry forest situated about 60 km north of Morondava near the west coast of Madagascar. Mean temperature around the year is 25 °C, annual rainfall during the rainy season (December to March) is 300–1400 mm; during the dry season, generally no rainfall occurs and three-quarters of the tree species lose their leaves (Ganzhorn 1992).

During two visits to Kirindy, from 5–8 January and on the 21 January 1995, specimens belonging to two different species of *Aglyptodactylus* were found which both differ from *A. madagascariensis* from the eastern rainforests:

Aglyptodactylus laticeps sp. *n.* (Figs 1 and 3)

Holotype

ZFMK 59972, adult male, collected 21 January 1995 in the Kirindy Forest (20°03′S, 44°39′E; at less than 100 m above sea level), western Madagascar, by F. Glaw.

Paratypes

ZFMK 59969–59971 (three adult males, ZFMK 59970 cleared and stained), 59973, 59974, 64135 (three juveniles), collected 21 January 1995 in the Kirindy Forest by F. Glaw. ZFMK 59968 (adult female) collected 6 January 1995 in the Kirindy Forest by F. Glaw, N. Rabibisoa and O. Ramilison.

Additional material

Several specimens (same locality and collecting dates as the type material) are deposited in the herpetological collection at the University of Antananarivo, Madagascar.

Diagnosis

A member of the genus *Aglyptodactylus* based on (a) presence of an intercalary element between terminal and subterminal phalanges of fingers and toes (b) large sphenethmoid (c) sternum unforked and longer than omosternum (d) digital terminal expansions not completely grooved (e) presence of amplexus during mating (f) black inguinal spots (g) second finger shorter than first finger (h) two free distal tarsals. The new species differs distinctly from *A. madagascariensis* (including its junior synonyms *Rana inguinalis* Günther, 1877 and *Mantidactylus purpureus* Ahl, 1929) by (a) broader head (see Figs 1 and 2, and Table 1; mean ratio HW/HL 1.06 vs. 0.92) (b) shorter hindlimbs (Table 1; mean ratio HiL/SVL 1.42 vs. 1.96) (c) shorter hands (Table 1; mean ratio HaL/SVL 0.26 vs. 0.30) (d) partly connected lateral metatarsalia (e) less webbing (Table 2) (f) a larger inner metatarsal tubercle (Table 1; mean ratio IMTH/FoL 0.055 vs. 0.025) (g) presence of very distinct subarticular tubercles (h) relative finger and toe length (Table 2) (i) colouration of the tympanic region. Additional differences (not verified in the types of *A. madagascariensis* and its synonyms) are (j) fusion of prehallux elements, and (k) advertisement calls.

Morphology of holotype

Body stout; head broader than body; snout slightly triangular in dorsal view; nostrils directed dorsolaterally, slightly pro-

Fig. 1. *Aglyptodactylus laticeps*, from Kirindy, frontal view of head

Fig. 2. *Aglyptodactylus madagascariensis*, from Nahampoana, frontal view of head

tuberant, nearly equidistant from tip of snout and eye; canthus rostralis straight and distinct; loreal region weakly concave; tympanum distinct, medium sized, oval, its horizontal diameter about 2/3 of eye diameter; distinct supratympanic fold; single subgular vocal sac; tongue ovoid, distinctly bifid posteriorly; vomerine teeth small but distinct. Arms slender; fingers with very distinct and single subarticular tubercles; outer metacarpal tubercle rounded, inner metacarpal tubercle elliptical-triangular, both well developed; fingers without webbing; comparative finger length $2 = 4 < 1 < 3$; slightly developed terminal finger disks without circummarginal grooves. No black nuptial pads recognizable on the inner fingers. Legs moderately developed; tibiotarsal articulation reaches between tympanum and eye; feet with an elongated inner metatarsal tubercle, no recognizable

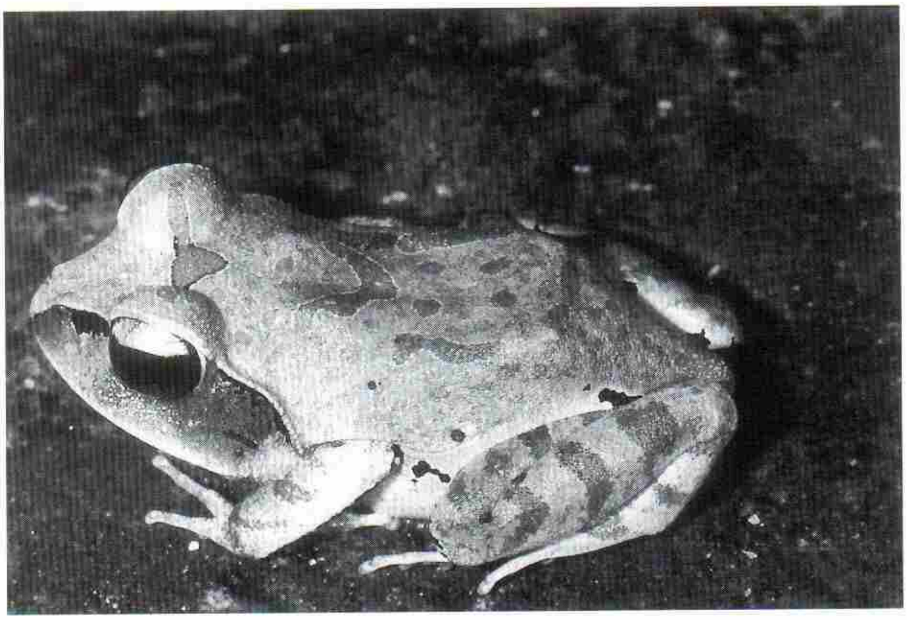

Fig. 3. *Aglyptodactylus laticeps*, from Kirindy, dorsolateral view

Table 1. Morphometric ratios (mean ± SD and range) in *Aglyptodactylus madagascariensis*, *A. securifer*, *A. laticeps*, and *Tomopterna labrosa*. Calculated from original data in Table 3.

	Aglyptodactylus madagascariensis	*Aglyptodactylus securifer*	*Aglyptodactylus laticeps*	*Tomopterna labrosa*
HaL/SVL	0.297 ± 0.018 0.267–0.341	0.251	0.258 ± 0.029 0.225–0.285	0.243 ± 0.011 0.231–0.250
HiL/SVL	1.954 ± 0.093 1.824–2.195	1.686	1.415 ± 0.105 1.296–1.510	1.503 ± 0.085 1.427–1.595
HW/HL	0.915 ± 0.043 0.842–0.994	0.977	1.058 ± 0.029 1.017–1.078	0.962 ± 0.023 0.945–0.987
Ns-Ns/HW	0.249 ± 0.016 0.221–0.290	0.209	0.199 ± 0.010 0.186–0.209	0.209 ± 0.041 0.162–0.242
Tym/Eye	0.649 ± 0.080 0.475–0.781	0.643	0.602 ± 0.046 0.544–0.642	0.622 ± 0.108 0.500–0.704
Ns-St/Eye-Ns	0.931 ± 0.108 0.750–1.233	0.929	1.008 ± 0.086 0.914–1.116	1.273 ± 0.046 1.242–1.326
IMTH/FoL [*10]	0.246 ± 0.070 0.137–0.412	0.500	0.552 ± 0.098 0.428–0.659	0.615 ± 0.191 0.404–0.777

outer metatarsal tubercle; subarticular tubercles very distinct, single, rounded; toe disks slightly developed; lateral metatarsalia partly connected; comparative toe length 1 < 2 < 5 < 3 < 4, toe 4 of the left foot is shortened, probably by an earlier injury. Skin on the upper surface smooth, throat and anterior venter smooth, posterior venter and ventral surface of femur slightly granular. For morphological measurements see Tables 2 and 3.

Colour of holotype in preservative (*after 20 months in alcohol*)
Head and anterior dorsum light greyish becoming brownish posteriorly. A triangular, symmetrical, greyish marking between the eyes, pointed posteriorly and extended onto the eyes. The marking is partly bordered by a very fine dark line. A white vertebral line from the anus to the anterior border of this marking. Small brownish rounded and some elongated spots on the whole back. On each side of the dorsum one elongated brownish spot from the posterior head converging to (but not reaching) the vertebral line in the middle of the back, forming a pseudo-V-like pattern. In the middle of each branch of the pseudo-V, an additional brownish marking starts running dorsolaterally to the inguinal spots. The inguinal spots (a distinct one on each side) are more or less vertical and blackish, anteriorly desintegrating in small dark lateral spots which continue irregularly anteriorly. The whole dorsal pattern are roughly symmetrical to both sides of the vertebral column. Loreal and temporal region including tympanum brownish. The supratympanic fold is ventrally bordered by a black line. A blackish band between eye and nostril becoming nearly triangular near the nostril. A dark spot between nostril and tip of snout. Upper lip white. Dorsal surface of legs and feets light brown, femur and tibia with three distinct (and one less distinct) dark brown crossbands. Two less distinct crossbands on the feet. Forearms light brown, with three bands on the left and one distinct band on the right arm. Iris blackish, pupil white. Belly white, throat grey, anterior venter and ventral surface of arms and femurs yellowish. The lateral border between dorsal surface and ventral surface of lower arm, elbow, femur, knee, tibia, tarsus and foot dark blackish-brown.

Colouration in life (*based on photographs of several specimens*)
In general the colouration in life is similar to that in preserved specimens. Head, anterior dorsum, flanks, and upper surfaces of arms beige, brown or reddish brown, becoming more greyish

Table 2. Foot webbing, relative toe and finger length, and relative hindlimb length of the studied specimens of *Aglyptodactylus madagascariensis*, *A. securifer*, *A. laticeps*, and *Tomopterna labrosa*. Relative hindlimb length is given as the point that the tibiotarsal articulation reaches when the hindlimb is adpressed along the body. Status: HT = holotype, PT = paratype, ST = syntype. Ri, Mp = *Rana inguinalis*, *Mantidactylus purpureus* (junior synonyms of *Aglyptodactylus madagascariensis*)

			Foot Webbing											
	Sex	Status	1	2i	2e	3i	3e	4i	4e	5	Finger length	Toe length	Tibiotarsal articulation reaches
Aglyptodactylus madagascariensis													
MNHN 4574	F	HT	1	1,5	0,5	2	0,5	2	1,5	0	$2 < 4$	$3 < 5$	clearly beyond snout
BM 1947.2.26.54	M?	HT (Ri)	0,5	1	0	2	0	2	1,5	0	$2 < 4$	$3 \leqslant 5$	clearly beyond snout
ZMB 30505	F	ST (Mp)	1	1,5	0,5	2	1	2	1,5	0,5	$2 < 4$	$3 < 5$	clearly beyond snout
ZMB 53728	F	ST (Mp)	1	1,5	0,5	2	1	2	1,5	0	$2 < 4$	$3 < 5$	clearly beyond snout
ZMB 53729	F?	ST (Mp)	1	1,5	0,5	2	0,5	2	1,5	0	$2 < 4$	$3 < 5$	clearly beyond snout
ZMB 53730	M?	ST (Mp)	0,5	1	0,5	2	0,5	2	1,5	0	$2 < 4$	$3 \leqslant 5$	clearly beyond snout
ZMB 53731	J	ST (Mp)	1	1	0,5	2	0,5	2	1,5	0	$2 < 4$	$3 < 5$	clearly beyond snout
ZMB 53732	J	ST (Mp)	1	1	0,5	2	0,5	2	1,5	0,5	$2 < 4$	$3 < 5$	beyond snout
ZFMK 17611	M?		1	1,5	0,5	2	0,5	2	2	0,5	$2 < 4$	$3 < 5$	clearly beyond snout
ZFMK 18951	?		1	1,5	0,5	2	1	2	2	0	$2 < 4$	$3 < 5$	beyond snout
ZFMK 53612	M?										$2 < 4$		clearly beyond snout
ZFMK 60032	F?		0,5	1	0,5	1,5	0,5	2	1,5	0	$2 < 4$	$3 < 5$	clearly beyond snout
ZFMK 62290	F?		0,5	1	0,5	1,5	1	2	1,5	0	$2 < 4$	$3 < 5$	beyond snout
ZFMK 59823	M		0,5	1,5	0,5	2	0,5	2	1,5	0,5	$2 < 4$	$3 < 5$	clearly beyond snout
ZFMK 64106	F		1	1	0,5	2	0,5	2	1,5	0	$2 < 4$	$3 < 5$	beyond snout
ZFMK 64137	J										$2 < 4$		clearly beyond snout
MNHN 1893–239	?		1	1,5	0,5	1,5	0,5	2	1,5	0	$2 < 4$	$3 < 5$	clearly beyond snout
MNHN 1883–582	F		0,5	1	0,5	1,5	0,5	2	1,5	0	$2 < 4$	$3 < 5$	clearly beyond snout
Aglyptodactylus securifer													
ZFMK 59975	M	HT	1	1,5	0,5	2	1	2,5	2	0,5	$2 = 4$	$3 < 5$	between nostril and snout tip
Aglyptodactylus laticeps													
ZFMK 59968	F	PT	1	1,5	1	2,5	2	3,5	3,5	1,5	$2 = 4$	$3 > 5$	tympanum
ZFMK 59969	M	PT	1	2	1	2,5	2	3,5	3,5	1,5	$2 = 4$	$3 > 5$	eye
ZFMK 59971	M	PT	1	2	1	2,5	2	3,5	3,5	1,5	$2 > 4$	$3 > 5$	eye
ZFMK 59972	M	HT	1	2	1	3	2	3	3	1,5	$2 > 4$	$3 > 5$	between tympanum and eye
ZFMK 64135	J	PT											between eye and nostril
Tomopterna labrosa													
ZFMK 53713	?		0	1	0,5	1,5	0,5	2	2	0,5	$2 = 4$	$3 = 5$	between eye and nostril
ZFMK 59964	F		0	1	0,5	2	1	1,5	1,5	1	$2 < 4$	$3 < 5$	eye
ZFMK 59966	M		0	1	0,5	1,5	1	2,5	2,5	1	$2 = 4$	$3 = 5$	eye

Table 3. Morphometric measurements (in mm) of the studied specimens of *Aglyptodactylus madagascariensis*, *A. securifer*, *A. laticeps*, and *Tomopterna labrosa*. Abbreviations of measured variables are explained in the Material and methods chapter. Other abbreviations as in Table 2

	Sex	Status	SVL	HW	HL	Eye	Tym	Eye-Ns	Ns-St	Ns-Ns	ForL	HaL	F1	F2	F3	HiL	FoTL	FoL	IMTW	IMTL	IMTH
Aglyptodactylus madagascariensis																					
MNHN 4574	F	HT	47,8	16,2	18,4	5,6	4,2	4,4	3,3	4	32,8	14	8,4	6,2	9,3	94,4	40,6	28,2	0,9	1,8	0,7
BM 1947.2.26.54	M?	HT (Ri)	33,4	11,2	13,3	4,6	2,6	3	2,7	2,9	22	10,5	5,5	4,1	7	64,8	28,3	18,7	0,7	1	0,6
ZMB 30505	F	ST (Mp)	42,5	16,9	17	5,2	3,2	3,8	3,7	4	33,6	14,5	7,9	6,3	10,2	93,3	42,2	27,9	1	2,2	0,6
ZMB 53728	F	ST (Mp)	54,1	18,7	19,8	6,4	3,8	4,7	4,4	4,7	35,7	15,9	8,7	6,7	11,2	107	42,1	32,9	1,3	2,5	1
ZMB 53729	F?	ST (Mp)	46,9	16,4	17,3	5,1	3,4	4	3,4	4,3	31,7	14	8,1	6,3	9,7	93,5	40,9	27,5	1	1,8	0,9
ZMB 53730	M?	ST (Mp)	36,2	12,5	13,9	4	3	2,9	2,8	3,1	23,9	10,3	4,7	4,1	6,8	72	30,4	20,8	0,7	1,6	0,5
ZMB 53731	J	ST (Mp)	32,7	12,2	13	4,2	2,4	2,8	2,8	2,7	22,4	10,5	5,9	4,5	7	65,5	28,1	19,2	0,7	1,6	0,5
ZMB 53732	J	ST (Mp)	29,8	11	11,7	4	1,9	2,5	2,3	2,9	18,5	8,4	3,7	3,3	5,5	56,7	23,7	16,1	0,5	1,3	0,3
ZFMK 17611	M?		40,1	14,6	15,8	4,5	3,2	3,7	3	3,8	24,5	11,6	6	4,5	7,6	82,2	36,1	24,1	1	1,7	0,4
ZFMK 18951	?		28,8	10,7	12,4	3,3	2	2,4	2,3	2,6	18	7,7	3,6	3,1	5	52,8	21,8	14,6	0,6	0,9	0,2
ZFMK 53612	M?		34,7	13,2	14,2	4,1	3,2	3,3	2,6	3,4	22,9	9,6	5	3,3	5,7	62					
ZFMK 60032	F?		36,4	12,7	15	4,7	3	3,2	3	3,1	22,4	10,4	5,4	4,1	7	66,4	29,8	19,4	0,7	1,5	0,5
ZFMK 62290	F?		53	19,1	21,7	6,4	4,1	4,5	4,4	4,7	32	15	8	6,2	9,5	99,2	43,8	30,8	1,2	2	0,8
ZFMK 59823	M		41,3	14,5	15,8	5,2	3,3	3	3,7	4,2	24,4	12,2	6,6	5,5	8,5	79,9	35,4	24,3	1,1	2	1
ZFMK 64106	F		59,3	21,6	23,2	6,4	5	4,5	4,4	5	35,9	16,7	9,1	6,9	11,1	116	48,6	35	1,4	2	0,7
ZFMK 64137	J		41,8	14,6	15,3	4,6	3,6	3,3	3	3,4	26,8	12	6,6	5	8	70,7			0,8	1,7	0,5
MNHN 1893–239	?		33,1	12,3	12,7	4,3	3	2,8	2,5	3	22	10	4,7	4,2	6,9	60,8	26,1	17,8	0,7	1,3	0,4
MNHN 1883–582	F		48	17,6	19,2	6	4,1	4,4	3,6	4,2	32,7	15	7,8	6,7	10	94,8	41,6	28,7	1	2	0,5
Aglyptodactylus securifer																					
ZFMK 59975	M	HT	35	12,9	13,2	4,2	2,7	2,8	2,6	2,7	21,6	8,8	5,8	3,9	5,8	59	25,7	18	0,9	1,7	0,9
Aglyptodactylus laticeps																					
ZFMK 59968	F	PT	60,4	24,7	24,3	7,9	4,3	4,3	4,8	4,6	33,5	13,6	7,3	4,7	8,6	78,3	33,8	23,8	1,4	3,4	1,4
ZFMK 59969	M	PT	45,4	18,3	17	5,8	3,4	3,3	3,4	3,6	26,4	11	6,2	4,4	7,7	61,6	26	18,8	1,4	2,6	1
ZFMK 59971	M	PT	40,3	18	16,7	5,2	3,3	3,5	3,2	3,7	25,3	11,2	5,7	4,9	7,4	60,3	24,5	18,7	1,9	2,7	0,8
ZFMK 59972	M	HT	38,6	18,7	17,6	5,3	3,4	3,5	3,4	3,9	26,4	11	6,2	4,8	7,7	58,3	35,3	18,2	1,2	2,8	1,2
ZFMK 64135	J	PT	27,4	11,4	10,9	3,7	2,2	2,7	2	2,6											
Tomopterna labrosa																					
ZFMK 53713	?		40	15,3	16,2	5,6	2,8	3,3	4,1	3,7	22,5	10	5,4	4,4	6,8	63,8	28,3	19,8	0,7	2,5	0,8
ZFMK 59964	F		66,3	23,4	23,7	6,8	4,5	4,6	6,1	3,8	34	15,3	7,6	6	9,4	94,6	43,4	30,9	1,1	3,7	2,4
ZFMK 59966	M		44,3	16,2	17	5,4	3,8	3,2	4	3,6	22,7	11	5,2	4,2	6,9	65,9	29,5	21,1	0,8	2,7	1,4

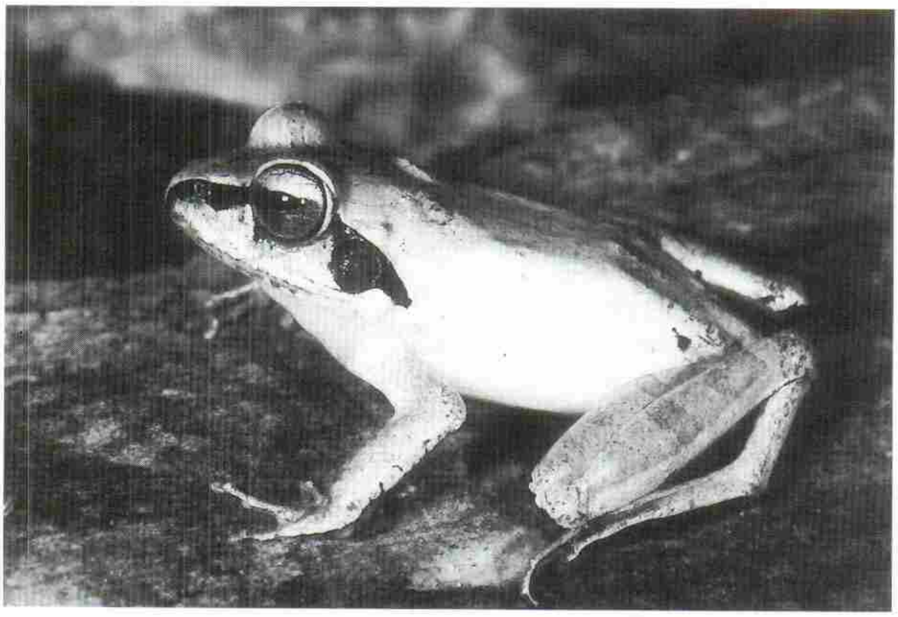

Fig. 4. *Aglyptodactylus securifer*, holotype, dorsolateral view

posteriorly. The triangular marking between the eyes and the markings on the back are grey or brown. The vertebral line (if present) is yellowish white. Upper surfaces of legs grey. Crossbands on legs and arms dark grey. Inguinal spots and spots along the flanks black, tympanic region brown, dark spot in the loreal region black. Iris golden on the dorsal half, dark on the ventral half, pupil black. Throat completely white or white with grey along the margin of lower jaw, venter nearly uniformly white. Ventral surface of femur and (less distinct) of tibia and arms purple.

Variation

For measurements of type specimens see Tables 2 and 3. Three males measure 64–75% of the female SVL. The size of the juveniles ZFMK 59973 and 59974 (27.7 and 23.5 mm SVL) indicate that they are probably the offspring from the rainy season of the preceding year. Morphological characters of the paratypes are similar to the holotype. All type specimens have generally similar colour pattern. However, the pattern of elongated spots on the back differ individually, being often more irregular than in the holotype. A light vertebral line is completely absent in ZFMK 59971 and 59974, but at least partially present in the other type specimens. Blackish nuptial pads are only recognizable on the inner finger of the right hand of ZFMK 59969, although they were present on most males captured 21 January 1995. Since the specimens were not preserved immediately, the nuptial pads were obviously lost.

Osteology (after cleared and stained paratype ZFMK 59970)

Frontoparietals divided along their whole length, anteriorly not reaching the palatines, widely separated from nasals. Along their whole length of more or less rectangular shape except the anterior edge, which is laterally pointed, reaching clearly further to the front laterally than medially. Thus anterior edge of the whole frontoparietal complex appearing with a large central notch. Nasals small, more or less triangular, with long posteroventral processes. Sphenethmoid relatively large, reaching anteriorly the height of centers of nasals, and overlapping distinctly with nasals and frontoparietals. Teeth present on maxillae and premaxillae. Vomers relatively small, fragmented (perhaps an exceptional state of the examined specimen; all other examined *Aglyptodactylus* had well-ossified, continuous vomers) into two elements. The outer fragments have two spine-like dorsolaterally directed processes. Vomer posteriorly not reaching palatines. Dentigerous process with few ventrally directed teeth, not as postero-ventrally directed comb-like structure. Palatines present. Central processus of parasphenoid reaches anteriorly as irregular, fibrous structure nearly to the palatines. Squamosal with distinct zygomatic and posterior processes; zygomatic process shorter than posterior process. Cervical atlantal cotyles kidney-shaped, narrowly separated.

There are eight presacral vertebrae. Transversal processes of 2., 3., and 4. vertebrae enlarged, those of 3. and 4. vertebrae, especially distally, larger than the (only slightly enlarged) sacral diapophyses.

Omosternum largely ossified, short, distinctly forked at the base. Sternum largely ossified, conical, clearly longer than omosternum, not distinctly forked on its base. Ilium with a distinct posterolaterally directed dorsal protuberance. Intercalary element between terminal and subterminal phalanges of all fingers and toes present. Terminal phalanges more or less triangular in dorsal view, distally becoming narrower, ending roundish, knob-like. Elements of the prehallux fused to a single axe-shaped structure which obviously functions as bony support of the enlarged metatarsal tubercle. There are two free distal tarsal elements.

Habitat and habits

Calling males were observed in the evening and night of the 21 January 1995, after heavy rain in the afternoon. They were abundantly sitting on the ground just at the edge of temporary puddles. Only a few specimens were found around larger pools. Calling activity started at dusk and was continued until much after midnight. Females and juveniles were active on the ground after sunset during quite dry evenings from 6 to 8 January 1995, crossing the small trails in the forest. Beside *A. laticeps* we found the following anuran species in the Kirindy Forest: *Aglyptodactylus securifer* sp. n. (see below and Fig. 4), *Boophis tephraeomystax*, *Boophis xerophilus*, *Dyscophus insularis*, *Heterixalus luteostriatus*, *Mantella betsileo*, *Ptychadena mascareniensis*, *Scaphiophryne brevis*, *S. calcarata* and *Tomopterna*

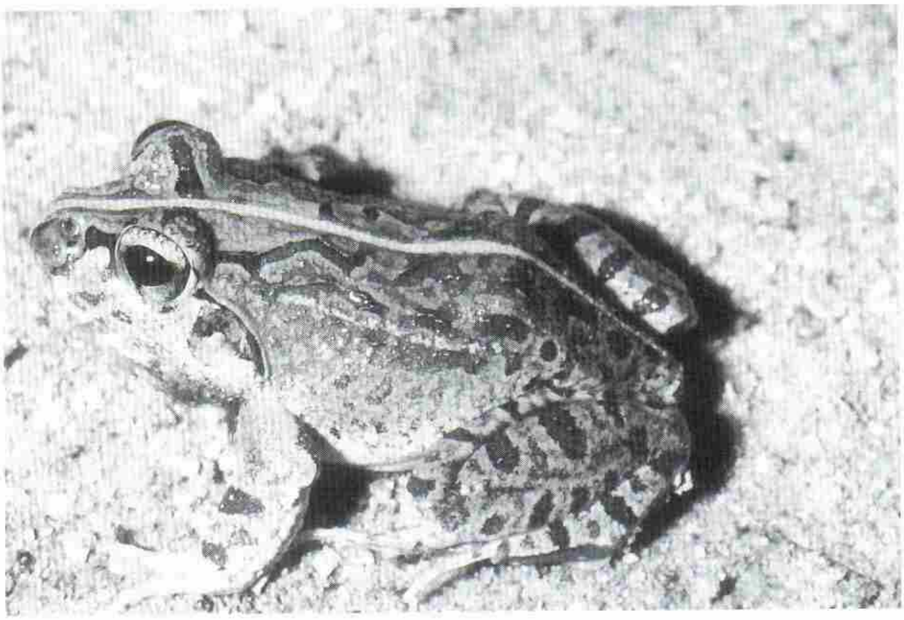

Fig. 5. *Tomopterna labrosa*, from Toliara, dorsolateral view

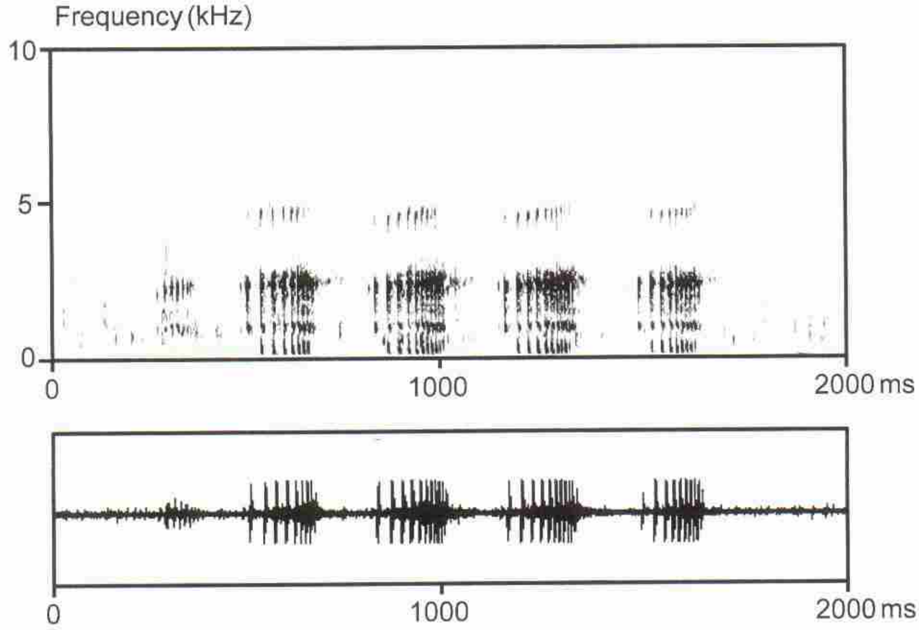

Fig. 6. Sonagram and oscillogram of a call of *Aglyptodactylus laticeps*

labrosa (Fig. 5). Except for *Mantella betsileo*, which was only found along a brook, all other species were observed in close syntopy with *A. laticeps*.

Reproduction

As with most other frogs found at Kirindy, *A. laticeps* is obviously an explosive breeder which starts breeding after heavy rain at the beginning of the rainy season. This characteristic is shared with *A. madagascariensis* from the eastern rainforests (see Glaw and Vences 1994). No couple in amplexus was observed by us, but, as indicated by a photograph of T. Hafen (see Glaw and Vences 1994), the amplexus is axillary. The female paratype (ZFMK 59968) contained 4130 eggs of about 1 mm diameter with a black and a white pole.

Food

The stomach of the female paratype contained the remains of an orthopteran insect. In its intestine the remains of strong arthropod mandibles were found, indicating that the species may consume large prey.

Parasites

A white nematode of about 35 mm length and 1 mm diameter was found in the paratype ZFMK 59970. It was situated in an enrolled position just in front of the pectoral girdle between dermis and musculature. Blommers-Schlösser and Blanc (1993: 457–458) reviewed the occurrence of parasites in Madagascan frogs but did not mention any records of parasites in the genus *Aglyptodactylus*.

Vocalization (recorded on 21 January 1995 at 25°C air temperature; Fig. 6.)

Calls consist of a series of 3–5 (mean 4, $n = 9$) unharmonious notes. Note duration is 121–285 ms (mean 215 ms, $n = 18$), intervals between notes are 31–133 ms (mean 82 ms, $n = 14$), note repetition rate is 3.4–3.9 per second, call duration is 774–

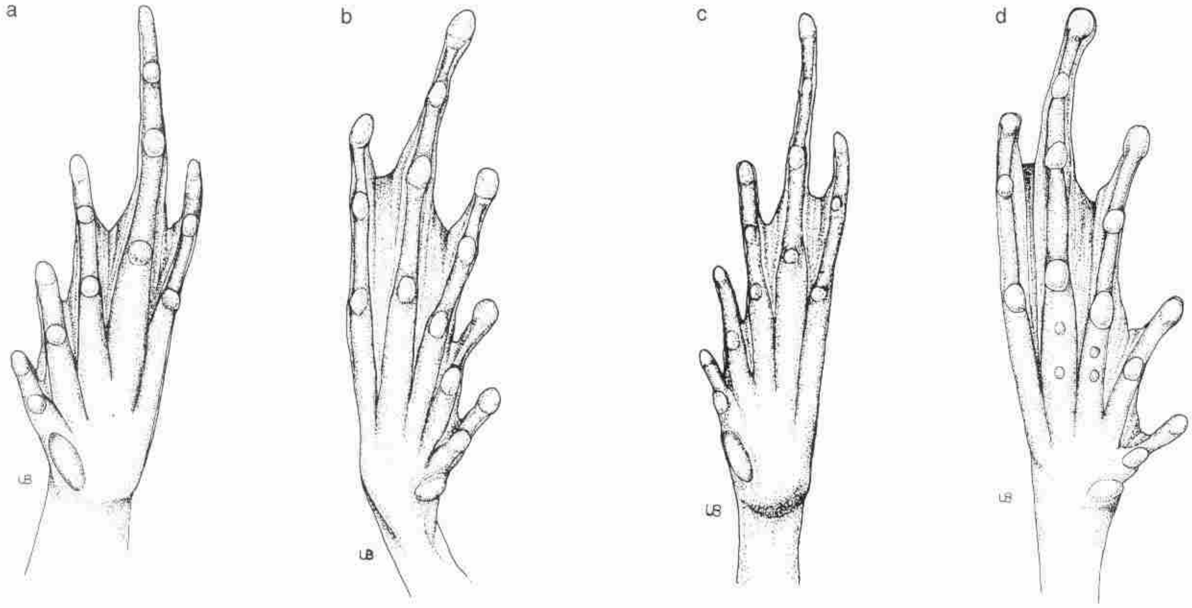

Fig. 7. Ventral view of left, respectively, right foot of a) *Tomopterna labrosa* (ZFMK 53713), b) *Aglyptodactylus madagascariensis* (ZFMK 62290), c) *A. securifer* (ZFMK 59975), and d) *A. laticeps* (ZFMK 59968). Not to scale

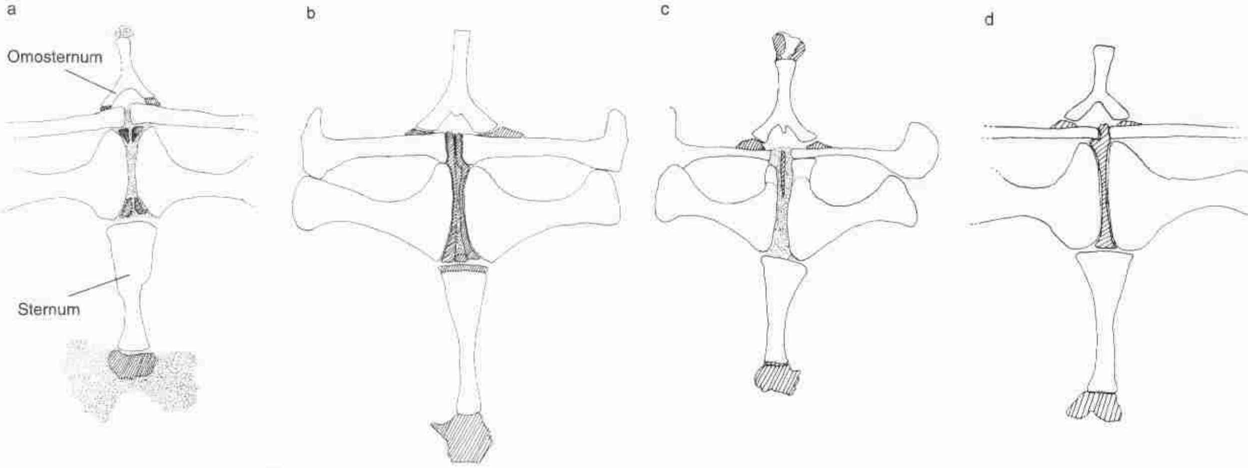

Fig. 8. Shoulder girdles of (a, b) *Tomopterna labrosa* (ZFMK 59967 and 59965), c) *Aglyptodactylus madagascariensis* (ZFMK 52682) and d) *A. laticeps* (ZFMK 59970) in ventral view. Spotted: cartilage; shaded: calcified cartilage. Not to scale

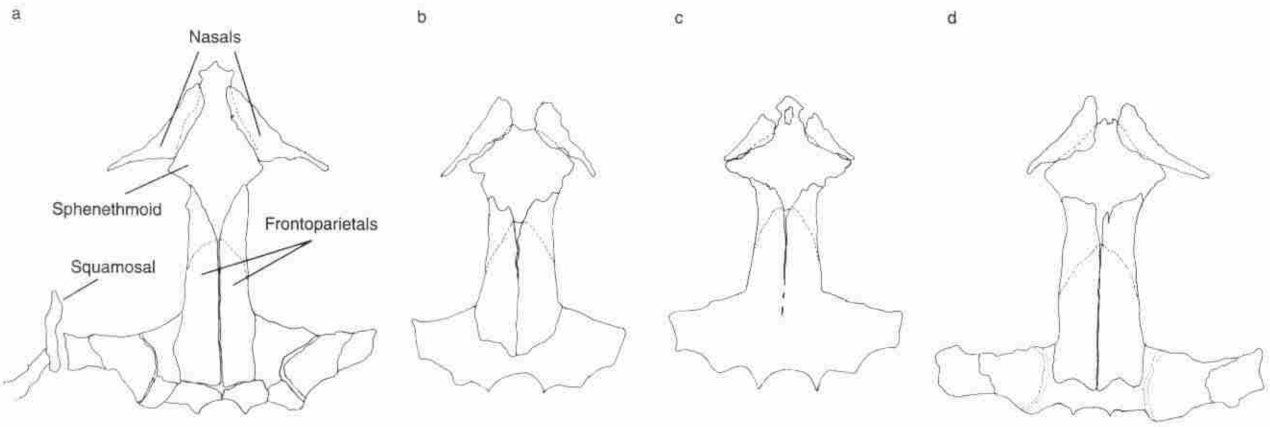

Fig. 9. Dorsal skull elements of a) *Tomopterna labrosa* (ZFMK 59967), b) *Aglyptodactylus madagascariensis* (ZFMK 52682), c) *A. securifer* (ZFMK 59976), and d) *A. laticeps* (ZFMK 59970). Note posterior fusion of frontoparietals in *A. securifer*. Not to scale

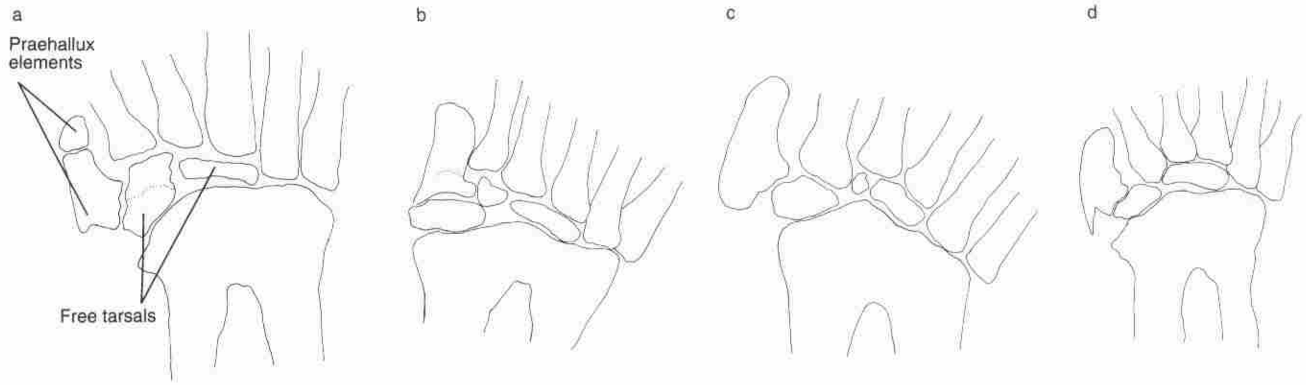

Fig. 10. Partial dorsal view of foot skeleton of a) *Tomopterna labrosa* (*ZFMK* 59967), b)*T. breviceps* (ZFMK 13796), c), *T. natalensis* (ZFMK 33164), and d) *Aglyptodactylus laticeps* (ZFMK 59970). Note number of free tarsals and unfused prehallux elements in *T. labrosa*. Not to scale

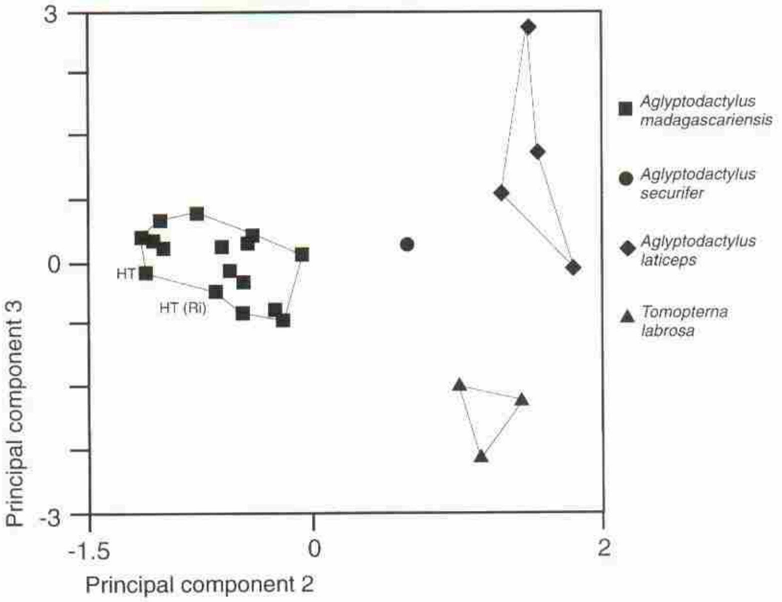

Fig. 11. Scatterplot of studied adult specimens of *Aglyptodactylus madagascariensis*, *A. securifer*, *A. laticeps*, and *Tomopterna labrosa* along the second and third principal components of MGPCA analysis of data in Table 3. HT = holotype of *A. madagascariensis*; HT (Ri) holotype of *Rana inguinalis* (junior synonym of *A. madagascariensis*)

1478 ms. Calls are generally arranged in series. Intervals between the calls of a call series are 1284–1915 ms (mean 1588 ms, $n = 8$). Each note consists of 8–12 pulses. Pulse repetition rate is 49–58 per second ($n = 9$). Frequency ranges from 0.8–3.4 kHz, dominant frequency is between 2.2 and 2.5 kHz. The call of *A. laticeps* much resembles that of *A. madagascariensis* from eastern Madagascar (see Glaw and Vences 1994 for data), but the mean pulse repetition rate is only about the half in *A. laticeps*.

Morphometry

A statistical comparison of *A. laticeps* with *A. madagascariensis* (ANCOVA with SVL as covariate) demonstrated significant differences in most morphometric variables: F1, F2, F3 ($p < 0.05$); Eye, FoTL, HaL ($p < 0.005$); FoL, HiL, HW, IMTL, IMTH, IMTW ($p < 0.001$). The three species *A. madagascariensis*, *A. laticeps* sp. *n.*, and *T. labrosa* were easily separated by principal component analysis. After removal of the first principal component (equivalent to the size or growth factor), the second and third principal components (equivalent to the most important shape factors) were plotted in Fig. 11.

Etymology

The name *laticeps* is derived from *latus* (Latin) = broad, and *ceps* (Latin) = belonging to the head (*caput*); it refers to the large head of the new species.

Electrophoresis

In a preliminary study, we compared the electrophoretic mobility of several allozymes of one *A. laticeps* male from Kirindy to those of one *A. madagascariensis* male from Andasibe. Data are available for eight loci (see Table 4). Regarding the low sample size and low number of scored loci, definite conclusions can not be drawn from the electrophoretic data. They can, however, be seen as additional evidence of the distinctness between both species. In three out of seven scorable loci (43%) *A. madagascariensis* and *A. laticeps* had different alleles. However, due to the small sample size we cannot estimate whether the identified alleles constitute fixed and thus diagnostic characters.

Ecological correlates of characters

The morphological divergence between *Aglyptodactylus madagascariensis* and *A. laticeps* may be partly correlated with

Table 4. Alleles identified in Madagascan anurans by allozyme electrophoresis

Enzyme	*Aglyptodactylus laticeps*	*Aglyptodactylus madagascariensis*	*Mantidactylus biporus*	*Mantella* spp.
Ga3pdH	a,b	a	–	c,d
Prot-1	a	a	a	a
Prot-2	a	b	b	c,d
GpdH	b	c	b	a,b,c
Ldh-2	c	c	–	a,b
Pgm	c	d	a,b	c,e,f
Idh-1	c	c	–	a,b
Idh-2	–	d,e	–	a,b,c

different habitats and habits of both species. This applies to the reduced lengths of external fingers and toes, the clumsy body shape with short limbs, the reduced webbing, the enlarged inner metatarsal tubercle, and the partly connected lateral metatarsalia of *A. laticeps*. All these characters may be adaptive by enhancing burrowing ability (which is advantageous in seasonal arid environments), and/or reduce body surface and thus evaporative water loss. The broad head of *A. laticeps* may be correlated with different prey preferences. Frogs eating large prey often have relatively wider skulls than other confamilial species (Emerson 1985).

***Aglyptodactylus securifer* sp. n. (Fig. 4)**

Holotype

ZFMK 59975, adult male, collected 6 January 1995 in the Kirindy Forest (20°03′S, 44°39′E), at less than 100 m above sea level, about 60 km north of Morondava, western Madagascar by F. Glaw, N. Rabibisoa and O. Ramilison.

Paratype

ZFMK 59976, adult specimen (cleared and stained), same locality and collecting data as holotype.

Diagnosis

A member of the genus *Aglyptodactylus* based on the same characters as listed in the diagnosis of *A. laticeps* (character e not verified; refer to Table 1 for differences in morphometric ratios). The differences of *A. securifer* to *A. madagascariensis* (including its junior synonyms) are as follows: (a) shorter hindlimbs (Table 1; mean ratio HiL/SVL 1.69 vs. 1.95) (b) less webbing (Table 2) (c) larger inner metatarsal tubercle (Fig. 7; Table 1; mean ratio IMTH/FoL 0.05 vs. 0.025) (d) tympanum round (vertically ovoid in *A. madagascariensis*) (e) diameter of group of vomerine teeth distinctly smaller than diameter of choanae (diameter of vomerine teeth group and tympanum is generally similar in *A. madagascariensis*) (f) finger 2 of same length as finger 4 (Table 2). Several osteological differences were also noted (not verified in type specimens of *A. madagascariensis* and its synonyms): (g) fusion of the bony elements of the prehallux to a large axe-shaped structure (h) generally stronger ossification (posterior fusion of frontoparietals, very large ossification of the suprascapula, larger sphenethmoid). Most differences of *A. laticeps* to *A. madagascariensis* (listed in the diagnosis of the former as a, b, c, d, e, f, g) also hold for a distinction between *A. laticeps* and *A. securifer*.

Morphology of holotype

Adult male, as indicated by brown nuptial pads on the first finger. Body slender; head slightly broader than body; snout triangular in dorsal view, nostrils directed dorsolaterally, slightly nearer to snout tip than to eye; canthus rostralis slightly concave and distinct, loreal region weakly concave, tympanum distinct, round, its horizontal diameter 2/3 of eye diameter; distinct supratympanic fold; tongue ovoid, distinctly bifid posteriorly; vomerine teeth small but distinct, the diameter of the group of vomerine teeth distinctly smaller than diameter of choanae. Arms slender, fingers with distinct single subarticular tubercles, outer metacarpal tubercle rounded, inner metacarpal tubercle elliptical, both moderately developed; fingers without webbing; comparative finger length $2 = 4 < 1 < 3$, slightly developed terminal finger disks, without circummarginal grooves; legs slender, tibiotarsal articulation reaches between nostrils and snout tip, feet with an elongated inner metatarsal tubercle, no recognizable outer metatarsal tubercle, subarticular tubercle moderately distinct, single, rounded; toe disks slightly developed, lateral metatarsalia separated, comparative toe length $1 < 2 < 3 < 5 < 4$. Skin on the upper surface smooth, throat and anterior venter smooth, posterior venter slightly granular. For morphological measurements see Tables 2 and 3.

Colouration of holotype in preservative (after 20 months in alcohol)

Head and dorsum light greyish. Small dark irregular markings and spots on the back. Dark inguinal spots present, more or less vertical and blackish. Tympanic region brownish. The supratympanic fold is ventrally bordered by a black band. A dark brown spot in the loreal region behind the nostrils. Dorsal surface of legs and feet light brown. Femur and tibia with three dark crossbands. Arms light brown with three crossbands. Venter and throat white. Ventral surfaces of arms and femurs slightly yellowish. The lateral border between dorsal surface and ventral surface of lower arm, elbow, knee, tibia, tarsus and foot dark blackish brown.

Colouration of holotype in life

Head, dorsum, flanks, upper surfaces of legs and arms silvery-grey to beige. Crossbands on legs and arms grey. Inguinal spot blackish, tympanic region and dark spot in the loreal region dark brown. Iris golden, pupil black. Throat and ventral parts of arms yellow. Belly white in the center, yellow towards the flanks. Ventral surface of legs yellowish.

Osteology (after cleared and stained paratype ZFMK 59976)

Frontoparietals separated along their anterior half, largely fused along their posterior half, rectangular except notched, concave anterior edge. Anteriorly not reaching the palatines, widely separated from nasals. Nasals small, triangular with long posteroventral processes. Sphenethmoid dorsally very large (divided ventrally), reaching anterior edges of nasals and overlapping distinctly with nasals and frontoparietals. Teeth present on maxillae and premaxillae. Vomer well developed, with four lateral spiny processes, and a small posteriorly directed dentigerous process. Vomerine teeth small. Palatines present. Central processus of parasphenoid anteriorly irregularly fibrous, not reaching palatines. Zygomatic process of squamosal shorter than posterior process. Eight presacral vertebrae. Transversal processes of 2., 3., and 4. vertebrae enlarged, those of 3. and 4. vertebrae at their distal ends larger than the sacral diapophyses. Omosternum largely ossified, distinctly but narrowly forked at the base. Sternum largely ossified, slightly longer than omosternum, unforked. Ilium with a distinct posterolaterally directed dorsal protuberance. Intercalary elements present. Terminal phalanges ending knob-like. Suprascapula very strongly ossified, including all generally cartilaginous structures. Elements of the prehallux fused to a single axe-shaped structure which obviously functions as bony support of the enlarged metatarsal tubercle. Two free distal tarsal elements.

Habitat and habits
Both specimens were found actively on the ground after sunset, crossing small trails in dry forest. No data are available on reproduction, food, and vocalization.

Morphometry
A statistical comparison of the morphometric differences is not possible due to the low sample size (one individual) in the new species. However, the holotype clustered relatively far away from all *madagascariensis* specimens in the principal component analysis (Fig. 11)

Etymology
The name *securifer* is derived from *securis* (Latin) = hachet, axe, and *-fer* (Latin) suffix derived from *ferre* = to carry. Named after the axe-shaped prehallux.

Characters used for phylogenetic analysis

In the following sections we compare characters of *Aglyptodactylus* species with those found in representatives of four other ranid genera from Madagascar (*Tomopterna*, *Boophis*, *Mantidactylus* and *Mantella*). The data presented are mainly based on our own results; osteological characters refer to specimens listed in the material and methods section. When available we give also comparative data from other authors; in these cases the data sources are always mentioned. Regarding osteological characters we included data of Guibé (1978), Clarke (1981), Blommers-Schlösser and Blanc (1991), Blommers-Schlösser (1993) and Cadle (1995).

According to Blommers-Schlösser (1993), the Ranidae are defined by the synapomorphic characters of an ossified sternum (present in all Malagasy ranids according to our data), carpal reduction and presence of the musculus cutaneus pectoris (characters not included in our study). The arthroleptid/hyperoliid lineage forms the sister group of the Ranidae (Blommers-Schlösser 1993). This lineage was therefore chosen as outgroup for the phylogenetic analysis. Character states were coded in arabic numbers. To make reading of character states und presumed state transitions easier, we consistently coded the outgroup state as '0'. Outgroup data for several characters were either contradictory, lacking or insufficient. We coded the states of these characters with capital letters, to allow their immediate recognition. These characters were included without outgroup data in the phylogenetic analysis. Character numbers correspond to those in Table 5.

Cervical atlantal intercotylar distance (1)
We identified two different states: In species of *Tomopterna* and *Aglyptodactylus* the cotyles are rather large, kidney-shaped, and the distance between their inner edges is slightly less than their height. In species of *Boophis*, *Mantidactylus* and *Mantella* the cotyles are smaller, rounded, widely separated, their distance being larger than their height (*Mantidactylus luteus*: personal observation; *M. grandidieri*, *M. femoralis*, *M. opiparis*, *M. betsileanus*, *M. asper*, *M. depressiceps*, *M. bicalcaratus*, *M. liber*, *M. blommersae*, *Mantella aurantiaca*, *Boophis goudoti*, *B. madagascariensis*, *B. tephraeomystax*: Blommers-Schlösser 1993). Widely separated cotyles are found in nearly all taxa of the outgroup (except some astylosternines; Blommers-Schlösser 1993). States: (0) wide separation (1) narrow separation. For drawings of these states refer to Lynch (1971).

Free distal tarsals (2)
Blommers-Schlösser (1993) found three free distal tarsals in mantellines and ranines and two free tarsals in rhacophorines (including *Aglyptodactylus madagascariensis*). Our data agree in that species of *Mantidactylus* and *Mantella* (species and references as in section of character 1) have three free tarsals (although the third may be extremely small and hard to recognize, e.g. in *Mantidactylus luteus*). Representatives of *Boophis* (*B. microtympanum*: personal observation; *B. goudoti*, *B. madagascariensis*, *B. tephraeomystax*: Blommers-Schlösser 1993), *Aglyptodactylus* (ascertained in all three species) and *Tomopterna labrosa* have two free tarsals, whereas a distinct third free tarsal was found in *Tomopterna breviceps* and *T. natalensis* (Fig. 10). All representatives of the arthroleptid-hyperoliid lineage have three free tarsals (Blommers-Schlösser 1993). States: (0) three free tarsals (1) two free tarsals.

Nasals and sphenethmoid (3)
Nasals of *Aglyptodactylus* and *Tomopterna* species are characteristically triangular, with a posterolateral process in most specimens (Fig. 9). This configuration occurs also in some *Boophis* (*B. tephraeomystax* and *B. goudoti*, see drawings in Guibé 1978), but other *Boophis* (*B. luteus*: Guibé 1978; *B. microtympanum*: personal observation) have very small, widely separated nasals. On the other hand, in species of *Mantidactylus* and *Mantella* the nasals generally resemble a rounded plate with a posterolateral process (all known species of *Mantella*: Vences et al. *in press*; *Mantidactylus luteus*, *M. albofrenatus*, *M. blommersae*: personal observation; *Mantidactylus lugubris*, *M. ulcerosus*, *M. madecassus*, *M. betsileanus*, *M. elegans*, *M. boulengeri*, *M. pulcher*: Guibé 1978). We found no significant differences in nasal shape between the three *Aglyptodactylus* species. The sphenethmoid is relatively large and overlaps distinctly with the nasals in all studied adult specimens of *Aglyptodactylus* and *T. labrosa*. This is not the case in one subadult *A. madagascariensis* (ZFMK 18954) and one subadult *T. labrosa* (ZFMK 52755). These specimens have only a rudimentary sphenethmoid, indicating that ossification of this element occurs only late in individual development. Except for these two specimens all *Aglyptodactylus* and *T. labrosa* specimens are characterized by the anterior extension of the sphenethmoid, which reaches at least the longitudinal center of the nasals, agreeing with the drawing in Guibé (1978). In *A. securifer* the sphenethmoid is much larger, as in one *T. labrosa* (ZFMK

Table 5. States identified in the studied anuran groups regarding 20 characters used for phylogenetic analysis. Chosen outgroup is the hyperoliid/arthroleptid lineage. For several characters, the states found in the (large) outgroup are not sufficiently known. Explanation of character numbers see text. For most characters, states are not known for all species of the respective genera; see corresponding text sections for species lists

Character	*Mantella*	*Mantidactylus*	*Boophis*	*Aglyptodactylus*	*Tomopterna labrosa*	African *Tomopterna*	*Tomopterna breviceps*	Outgroup
1	0	0	0	1	1	1	1	0/(1)
2	0	0	1	1	1	0	0	0
3	B	B	B	A	A	A	A	?
4	B	B	B	A	A	A	A	?
5	1	0	0	0	0	0	0	0
6	A	A	A	A	B	B	B	?
7	A	B	A	A	B	A	A	?
8	1	1	1	1	0	0	0	0/1
9	1	1	1	0	0	0	0	0
10	A/B	A/B	B	B	B	B	B	?
11	A	A/B	B	A	A	B	A	?
12	A	A	B	B	B	B	B	?
13	0	0	0	0	1	2	1	0
14	A/D	C/D	B	D	?	?	?	?
15a	1	1	0	0	?	?	?	0
15b	1	1	0	0	0	0	0	0
15c	B	B	A	?	?	?	?	?
16	1	1	0	0	0	0	0	0/1
17	0	0/1	0	0	0	0	0	0
18	B	B	B	A	A	A	A	?
19	B	B	B	A	A	A	A	?
20	0	0	0	1	1	?	?	0

59967) in which there is even a poorly ossified part of the sphenethmoid (calcified cartilage?) reaching further than nasals. Interestingly, the sphenethmoid is smaller and not overlapping with nasals in *Tomopterna delalandii*. In none of the *Boophis* and *Mantidactylus* described in the literature (see above) has the sphenethmoid an anterior expansion as in *Aglyptodactylus*. Of the species studied by us, the sphenethmoid is fragmented into two rudiments in *B. microtympanum*, nearly completely reduced in *Mantidactylus albofrenatus*, relatively large but reaching less far anteriorly in *M. luteus*. In some *Mantella* (especially *M. baroni*) the sphenethmoid is very large and similar to the state in *Aglyptodactylus* species and *T. labrosa*; in these species, however, nasal shape is different. There are no comprehensive outgroup data regarding this character.

States: (A) Sphenethmoid large, reaching anteriorly to the longitudinal center of nasals or further; nasals triangular and longitudinally directed, generally overlapping with sphenethmoid; (B) different state; generally sphenethmoid smaller, and nasals not triangular and directed longitudinally.

Frontoparietals (4)
The frontoparietals are divided along their whole length in all species studied except *A. securifer*. A difference of all species of *Aglyptodactylus* and *Tomopterna* to representatives of the restant genera seems to be the shape of the anterior edge of the frontoparietals (Fig. 9). Each frontoparietal reaches laterally further than medially, resulting in a distinct concave central notch. Although such a notch may be present – but generally less distinct – in some *Mantidactylus* and *Boophis* (*M. madecassus*, *M. betsileanus*, *M. curtus*, *B. goudoti*, see drawings in Guibé 1978; more distinct in *Boophis albilabris*, see drawings in Cadle 1995), the typical shape in representatives of these genera (remaining species listed in the section of character 3; Guibé 1978; personal observation) and in *Mantella* (all known species; Vences et al. in press) is an anteriorly rounded, convex anterior edge. There are no comprehensive outgroup data regarding this character. States: Frontoparietals (A) anteriorly with a distinct concave notch (B) generally rounded, convex.

Maxillary teeth (5)
Species of *Aglyptodactylus*, *Tomopterna*, *Mantidactylus*, and *Boophis* have maxillary teeth which are absent in *Mantella*. These states were ascertained in all species of *Mantella* (Vences et al. *in press*) and in all species of the remaining genera studied by us (personal observation). They also form part of the corresponding generic diagnoses in Guibé (1978) and Blommers-Schlösser and Blanc (1991). The loss of teeth is to be considered as synapomorphy of all *Mantella* species and as part of an etho-morphological character complex related to microphagy (Vences et al. *in press*). Maxillary teeth are present, as far as known, in all outgroup taxa. States: Maxillary teeth (0) present (1) absent.

Maxilla-preorbital process of pars fascialis (6)
In species of *Aglyptodactylus*, *Mantidactylus*, *Boophis* and *Mantella* studied by us this process is anteriorly reduced, although in *Aglyptodactylus* the maxilla is deeper at the anterior edge. In *Tomopterna* the anterior edge is very deep, resulting in a second dorsal process which in *T. labrosa* reaches dorsally nearly as far as the alary process of the premaxilla. There are no comprehensive outgroup data regarding this character. States: (A) preorbital process of maxilla not reduced (B) anteriorly reduced.

Squamosal (7)
In all three *Aglyptodactylus* species the zygomatic process of the squamosal is shorter than the posterior (otic) process. The same state is found in African *Tomopterna* (see also Clarke

1981) and in *T. breviceps*, whereas in most *T. labrosa* the zygomatic process is longer than the otic process. In *Mantidactylus* species the zygomatic process seems either to be longer or of similar length as the posterior process after the drawings in Guibé (1978) which correspond to the species listed in the section of character 3. It was longer than the posterior process in the specimen of *M. luteus* studied by us, and shorter in the specimen of *M. albofrenatus*. In all *Mantella* species it is very short, probably being adaptive in the context of an etho-morphological character complex related to microphagy (Vences et al. *in press*). In *Boophis* species it is generally shorter than the posterior process (personal observation; drawings in Guibé 1978 corresponding to *B. laurenti*, *B. tephraeomystax*, *B. goudoti*, *B. luteus*). There are no comprehensive outgroup data regarding this character. States: Zygomatic process of the squamosal (A) shorter (B) longer or of similar length as posterior process.

Intercalary element (8)
Intercalary, calcified cartilage between terminal and subterminal phalanges of all fingers and toes is universally present in all studied species of *Boophis*, *Mantidactylus*, *Mantella* and *Aglyptodactylus* (personal observation on species studied by us; all known *Mantella*: Vences et al. *in press*; species listed in section of character 1: Blommers-Schlösser 1993; also mentioned in the corresponding generic diagnoses of Guibé 1978), but absent in representatives of *Tomopterna*. Within the outgroup, intercalary elements are present in the Hyperoliidae and absent in the Arthroleptidae. In a preliminary way, we here follow Blommers-Schlösser (1993) who regarded the intercalary elements of hyperoliids as convergently derived. This is also corroborated by the interpretation of Drewes (1984), who considered the intercalary elements composed of juvenile cartilage, as found in primitive hyperoliids (*Leptopelis*), as precursors on the way towards the calcified elements of derived hyperoliids. States: Intercalary element (0) absent (1) present.

Terminal phalanges (9)
The terminal phalanges of *Tomopterna* and *Aglyptodactylus* species have a very similar shape, triangular with a knob-like ending, whereas those of the representatives of *Mantidactylus*, *Mantella*, and *Boophis* were more or less Y-shaped (personal observation on species studied by us; all known *Mantella*: Vences et al. *in press*; species listed in section of character 1: Blommers-Schlösser 1993). This Y-shape was often (but not always) more distinct in species with broadly expanded fingertips, whereas in species with only slightly enlarged fingertips it was merely recognizable as a notch. Y-shaped phalanges are unknown in the outgroup (Blommers-Schlösser 1993), whereas knob-like phalanges occur at least in the Hyperoliidae (Drewes 1984). States: Terminal phalanx of third finger (0) knob-like (1) Y-shaped.

Sternum (10)
The sternum is ossified in all species considered. It is forked at its base in several *Mantella* and *Mantidactylus* (all known *Mantella* species except those listed below: Vences et al. *in press*; *Mantidactylus depressiceps*, *M. pulcher*, *M. decaryi*, *M. boulengeri*, *M. bertini*: Guibé 1978; Blommers-Schlösser 1979a), unforked in other species of these genera (*Mantella baroni*, *M. cowani*, *M. nigricans*, *M. bernhardi*: Vences et al. *in press*; *Mantidactylus redimitus*, *M. madecassus*, *M. klemmeri*, *M. guibei*, *M. guttulatus*, *M. ulcerosus*, *M. albofrenatus*, *M. aglavei*, *M. asper*, *M. wittei*: Guibé 1978; Blommers-Schlösser 1979a; *M. luteus*: personal observation) and in all *Boophis*, *Aglyptodactylus* and *Tomopterna* so far studied (*B. tephraeomystax*, *B. goudoti*, *B. luteus*: Guibé 1978; *B. microtympanum*: personal observation; *Aglyptodactylus madagascariensis*, *A. laticeps*, *A. securifer*, *Tomopterna labrosa*, *T. delalandii*, *T. breviceps*: personal observation; *Tomopterna cryptotis*, *T. krugerensis*, *T. marmorata*, *T. natalensis*, *T. tuberculosa*: Clarke 1981). There are no outgroup data regarding this character since in arthroleptids and hyperoliids an ossified sternal style is generally absent (Blommers-Schlösser 1993). States: Sternum (A) forked (B) unforked.

Omosternum (11)
The omosternum is distinctly forked in all specimens of *T. labrosa* and *Aglyptodactylus* studied by us, as well as in *Tomopterna breviceps*. It is unforked or slightly forked in African *Tomopterna* (unforked in *T. delalandii*, slightly forked in *T. natalensis*: personal observation; species listed in section of character 10: Clarke 1981). It is generally unforked in *Boophis* species (species listed in section of character 10 and *B. madagascariensis* and *B. albilabris*: personal observation; Guibé 1978; Blommers-Schlösser 1993; Cadle 1995). Cadle's (1995) statement of a forked omosternum in *Boophis goudoti* and *B. madagascariensis* is due to a erroneous citation of Blommers-Schlösser's (1993) data. The omosternum is forked in most *Mantidactylus* (species listed in section of character 10), although it is totally or nearly unforked in several species of that genus (*M. webbi*, *M. leucomaculatus*, young *M. microtympanum*: Glaw and Vences 1994). There are no comprehensive outgroup data regarding this character. States: Omosternum (A) distinctly forked (B) not or very slightly forked.

Relative omosternum length (12)
The ossified part of the omosternum is of similar length or longer than the ossified part of the sternum in the studied species of *Mantidactylus* and *Mantella*; it is generally (at least slightly) shorter in representatives of the other studied genera (species and references as in section of character 10; see also Guibé 1978; Blommers-Schlösser and Blanc 1991). There are no outgroup data regarding this character since in arthroleptids and hyperoliids an ossified sternal style is generally absent. States: Omosternum (A) longer than sternum or of same length (B) shorter than sternum.

Ilium (13)
This character was used by Clarke (1981) to separate African (derived state) from Madagascan and Asian *Tomopterna*. We distinguish three states: (0) Species of all included genera except *Tomopterna* have a posterolaterally directed distinct oval protuberance (no literature data; ascertained in species studied by us) (1) *T. labrosa* and *T. breviceps* have a faintly developed thickened bony area but no real protuberance (personal observation) (2) African *Tomopterna* have a distinct anterodorsally directed prominence (*T. delalandii*, *T. natalensis*:, personal observation; *Tomopterna cryptotis*, *T. krugerensis*, *T. marmorata*, *T. natalensis*, *T. tuberculosa*: Clarke 1981). There are no comprehensive outgroup data regarding this character, but one examined hyperoliid (*Heterixalus madagascariensis*; ZFMK 52574) had clearly expressed state 0 (personal observation). Since this corresponds with the polarization of Clarke (1981), we here accept it in a preliminary way, but the character should

be studied in more outgroup taxa for future analyses. Refer to Clarke (1981) for drawings of the character states 0 and 2.

Hyoidal apparatus (14)
Unfortunately not recognizable in our specimens of *Tomopterna*, *A. laticeps* and *A. securifer* due to poor alcian blue staining. The hyoid of *A. madagascariensis* was described by Guibé (1978); our data on ZFMK 18954 correspond well with his data. We have own data on *Mantidactylus albofrenatus*, *Boophis microtympanum*, and several *Mantella* (generally corresponding with other species of their respective genera; see drawings in Guibé 1978). We identified different states: In species of *Mantella* the anterior process of the hyale curves backwards, fusing again with the hyale, forming a complete arch (intraspecific variation regarding this character was found). In *Boophis*, there are only data for *B. goudoti* (Guibé 1978), *B. albilabris* (Cadle 1995) and *B. microtympanum* (personal observation), but these seem to indicate that the lack of the anterolateral hyoidal process is a shared state at least of representatives of several *Boophis* species groups. Several *Mantidactylus* have a reduced posterolateral hyoidal process (*M. pulcher*, *M. boulengeri* according to Guibé 1978). There are no comprehensive outgroup data regarding this character. States: Hyoidal apparatus (A) with anterior process of hyale forming a complete arch (B) with reduced anterolateral process (C) with reduced posterolateral process (D) without any of these modifications. Refer to Guibé (1978) for drawings of the character states.

Amplexus (15a)
The presence of a strong amplexus during mating is the primitive condition in anurans, which has been lost several times independently, e.g. in the Dendrobatidae and the Mantellinae which retain a loose amplexus in male–male combats (Blommers-Schlösser 1993; personal observation). According to this author, only mantellines share a lack of mating amplexus within ranoid frogs, but it may be possible that several petropedetines with femoral glands also share this state (Daly et al. 1996: 5). A strong axillary amplexus during mating is present in species of *Aglyptodactylus* (personal observation), *Boophis* (Glaw and Vences 1997) and probably *Tomopterna* (no explicit statements found in the literature), but absent in species of *Mantidactylus* and *Mantella* (according to our observations inter- and intrasexual amplexus between *Mantella* specimens was associated with aggressive interactions). As far as known, a strong mating amplexus is present in hyperoliids (e.g. Drewes 1984; Glaw and Vences 1994: Fig. 222). Character states: Strong amplexus during mating (0) present (1) absent.

Nuptial pads (15b)
Nuptial pads on the inner fingers of males are a plesiomorphic character in anurans and closely associated with a strong amplexus during mating. Species of *Mantella* and *Mantidactylus* have no recognizable nuptial pads (personal observation on virtually all known species of these genera), which is probably correlated with the loss of strong mating amplexus. In *Boophis* species, nuptial pads are generally recognizable but not strongly developed (known for nearly all species of the genus; see Glaw and Vences 1994). Mostly they are whitish and rather indistinct, in *Boophis albilabris* distinct, black pads are known. Distinct black pads during the reproductive period are typical for *Tomopterna labrosa* (Blommers-Schlösser and Blanc 1991: 128), and the three species of *Aglyptodactylus* (personal observation). Nuptial pads were also found in the Asian *Tomopterna rolandae* (Dubois 1983), but it is not clear whether they are as distinct and blackish as in *Aglyptodactylus* species. We are not aware of any record of distinct, blackish nuptial pads in African *Tomopterna*. Specimens examined by us did not show distinct pads, whereas Salvador (1996) states that males of *T. cryptotis* have *'keratinized ridges on first and second finger'*. Nuptial pads are present in at least some outgroup taxa (Drewes 1984), as they are generally in anurans. States: Nuptial pads (0) present (1) absent.

Release calls (15c)
Release calls are probably associated with strong mating amplexus and we therefore consider them as ancestral. They are known from several *Boophis* (e.g. *B. jaegeri*, *B. guibei*: Glaw and Vences 1992a, 1994). No observations are available for *Tomopterna* and *Aglyptodactylus* species. Release calls were never found in species of *Mantidactylus* and *Mantella* (Glaw and Vences 1994; personal observation). We are not aware of outgroup data regarding this character, but release calls are known from most groups of frogs (Duellman and Trueb 1986), and we strongly suspect their presence in at least some outgroup taxa. States: Release calls (A) present (B) absent.

Egg deposition (16)
Among Madagascan ranid genera, only species of *Mantella* and *Mantidactylus* are known to share the mode of egg deposition outside of the water (Glaw and Vences 1994). States: Egg deposition (0) inside water (1) outside water. Both states occur in the outgroup, but egg deposition outside the water in outgroup taxa is mostly associated with special leaf-folding or nest-constructing behaviour (at least in hyperoliids; see Drewes 1984). Terrestrial egg deposition has evolved many times convergently among anurans (Duellman and Trueb 1986). We suggest that the state found in some outgroup taxa is not homologous to the state found in mantellines, and thus consider the latter as derived within the Ranidae.

Femoral glands (17)
Distinct femoral glands are present in males of most *Mantidactylus* subgenera (absent or indistinct in *Guibemantis*). Sometimes reduced glands are also present in females (refer to Glaw and Vences 1994 for pictures of femoral glands). Granular skin on the ventral parts of the femur in species of the *Mantidactylus* subgenus *Guibemantis* and in some *Mantella* (especially in *M. madagascariensis*) are probably a plesiomorphic state (personal observation; see also Daly et al. 1996). They may or may not be homologous with femoral glands in *Mantidactylus* species. No femoral glands are recognizable in representatives of *Aglyptodactylus*, *Tomopterna*, and *Boophis* (personal observation) as in most other ranoid frogs. Femoral glands do not occur in the outgroup (Blommers-Schlösser 1993). States: Femoral glands (0) absent (1) present.

Relative finger length (18)
A conspicuous feature of *Aglyptodactylus* species and *T. labrosa* is that the second finger is shorter than the first finger. The same is true for Asian and African *Tomopterna* (verified in ZFMK specimens of *T. breviceps*, *T. delalandii*, *T. cryptotis*, *T. marmorata*, *T. natalensis*). In all *Boophis* and in most *Mantidactylus*, the second finger is longer than the first finger (Blommers-Schlösser and Blanc 1991; personal observation); only in species of the *Mantidactylus* subgenus *Brygoomantis* both fingers are of similar length. In *Mantella* species the second finger is slightly

longer or of similar length than the first finger (Blommers-Schlösser and Blanc 1991; personal observation). There are no comprehensive outgroup data regarding this character. States: (A) second finger shorter than first finger (B) second finger not shorter than first finger.

Circummarginal groove (19)
As noted by Boulenger (1919), the terminal expansions of fingers and toes are not grooved in *A. madagascariensis*. The same is true for *A. laticeps* and *A. securifer*. A circummarginal groove is present in species of *Mantella*, *Mantidactylus* and *Boophis*, but lacking in species of *Tomopterna* (personal observation). Both grooved (species of *Hyperolius*, *Tachycnemis*, *Leptopelis*) and ungrooved (species of *Kassina*, *Arthroleptis*) finger expansion occur in the outgroup (personal observation). States: Ventral circummarginal groove of digital pad (A) absent (B) present.

DNA content (20)
Bachmann and Blommers-Schlösser (1975) investigated DNA content of 40 Madagascan anuran species. Only three of these had less than 7 pg/cell, differing largely from the modal value found in anurans. These species were *A. madagascariensis* (6.1 pg), *T. labrosa* (6.5 pg) and *P. mascareniensis* (6.7 pg). Low DNA content may be correlated with rapid development (see King 1990: 116–117 for an extensive discussion and references) and thus allow anurans to inhabit arid regions, where the temporary water bodies dry out soon. However, this does not exclude that the origin of this state was due to phylogenetic relationships. At least some outgroup taxa (four species of *Heterixalus* and one species of *Hyperolius*; King 1990) have a DNA content around the modal value. States: Nuclear DNA content (0) around modal value (1) reduced (<0.7 pg/cell).

Characters not used for phylogenetic analysis

Several characters studied were not analysed phylogenetically by one of three reasons: (a) they were highly variable within genera (b) a convincing character delimitation was not possible, or (c) they were not variable between examined individuals, but differences to pertinent literature were found. These characters are discussed in the present section.

Palatines
We identified similar palatines in all specimens studied. We did not recognize a sigmoid shape of the palatines in the studied *Mantidactylus*. This state was figured by a drawing of Laurent (1943) for *Mantidactylus curtus* and given by Blommers-Schlösser and Blanc (1991) as diagnostic for the genus, but is recognizable in none of the drawings of Guibé (1978) and was not considered further by Blommers-Schlösser (1993). We therefore conclude that this shape is either an exceptional state found in the specimens studied by Laurent, and thus not diagnostic for *Mantidactylus*, or is more difficult to recognize than could be expected from Laurent's drawing. In the latter case it may well be possible that also representatives of other genera have a sigmoid palatinum, and that this character was overlooked in recent studies.

Parasphenoid shape
A pointed cultriform anterior process of the parasphenoid was considered apomorphic for *Tomopterna* by Clarke (1981). We found such a process in *T. natalensis* and *T. delalandii*, but *T. labrosa* had a slender process with an irregular fibrous ending, as it was found in *Aglyptodactylus*, whereas *T. breviceps* had a slender process with a slightly notched end. There was considerable variation of this character within *Mantella* and *Mantidactylus*.

Prehallux
In two *Aglyptodactylus* (*A. laticeps* and *A. securifer*) the elements of the prehallux are fused to an axe-shape structure which may constitute a bony support of the metatarsal tubercle (and is therefore probably useful for digging). *A. madagascariensis* had always two unfused prehallux elements. In *T. labrosa* two unfused elements were found. In *T. natalensis*, *T. delalandii* and *T. breviceps* we observed a fusion, although the prehallux was less axe-shaped than in *Aglyptodactylus*. A fused prehallux can probably be considered as derived, but due to the adaptive nature of this character the states in species of *Tomopterna* and *Aglyptodactylus* are possibly not homologous.

Eggs
The high number of eggs (4130 in a female) and the small egg diameter found in *Aglyptodactylus laticeps* are unique among Madagascan frogs. In comparison, a female of *A. madagascariensis* from Andasibe (65 mm SVL) deposited about 1600 eggs measuring 1.2–1.5 mm in diameter (Glaw and Vences 1994). No data on egg number and egg size of *T. labrosa* is available. A large number of small eggs were present in an African *T. delalandii* (personal observation). A moderately high egg number (up to 1103) and a variable egg diameter (1.5–3.5 mm) was found in gravid *Boophis* (Glaw and Vences 1997). Clutches of *Mantidactylus* and *Mantella* generally do not consist of more than 150 eggs (personal observation, Glaw and Vences 1994). In the classical scheme of r-strategists and K-strategists, *Aglyptodactylus* (and especially *A. laticeps*) range clearly among r-adapted species.

Lateral metatarsalia
The lateral metatarsalia are generally separated in species of *Boophis* and connected in *Mantella* species. In representatives of *Mantidactylus* there is a wide variety of states, with distinct differences even between sibling species (e.g. in the *M. wittei* complex; see Glaw and Vences 1994). The differences between species of *Aglyptodactylus* (partly connected in *A. laticeps*, separated in *A. madagascariensis* and *A. securifer*) provide an additional example that the state of the lateral metatarsalia connection is not useful to distinguish between genera as it was done in the past (e.g. genera *Gephyromantis* and *Mantidactylus* as defined by Guibé 1978).

Karyotype
Chromosome morphology of Madagascan ranoids has been studied by Blommers-Schlösser (1978). Most Madagascan ranoids have a chromosome complement of 2n = 26. A reduced set of 2n = 24 is present in several *Mantidactylus* (subgenus *Brygoomantis* and *Mantidactylus aglavei*), *Ptychadena mascareniensis*, and *Heterixalus*. Other *Mantidactylus* are characterized by the presence of one or several acrocentric chromosomes. Typical for species of *Mantidactylus* and *Boophis* is a distinct size difference between 5 pairs of larger chromosomes and 8 pairs of smaller chromosomes. This situation is not found in *T. labrosa*, in which there are 6 pairs of large and 7 pairs of small chromosomes (Blommers-Schlösser and Blanc 1991). In the African *T. delalandii* (the type species of *Tomopterna*) diploid and tetraploid karyotypes have been described by Bogart

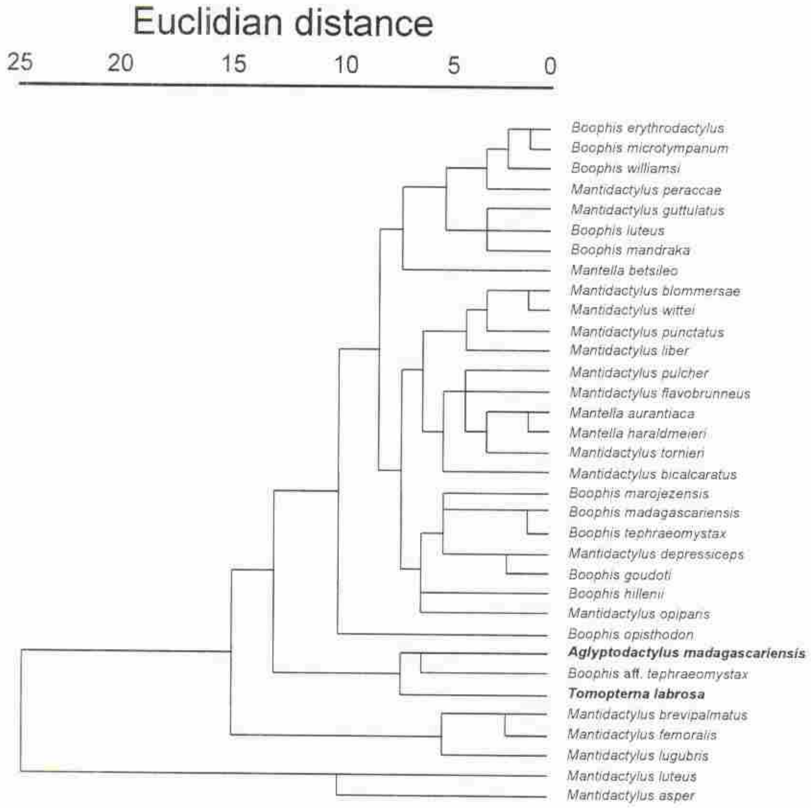

Fig. 12. Phenetic relationships between Madagascan ranid frogs based on chromosome morphology. The UPGMA-dendrogram of species with a chromosome complement of $2n = 26$ is based on squared euclidian distances calculated with relative chromosome lengths and centromer indices of Blommers-Schlösser (1978). Specific names were modified according to Blommers-Schlösser (1979a, b) and own unpublished data

and Tandy (1976, 1981) who therefore suggested the existence of a cryptic undescribed species.

We compared the original data of Blommers-Schlösser (1978) regarding species with $2n = 26$ in a phenetic analysis. Relative lengths and centromer indices of all chromosome pairs were used, giving a total number of 26 characters. Centromer indices (ci) were multiplied by 10, in order to make them comparable in relative weight to the relative lengths (rl). Euclidian distances between all taxa were calculated, and used to construct a phenetic UPGMA-dendrogram (Fig. 12). The analysis first clusters two groups of *Mantidactylus* with acrocentric chromosomes away from the other taxa, with a distinction between a cluster containing representatives of the subgenus *Gephyromantis*, and a second cluster containing representatives of the subgenera *Hylobatrachus*, *Chonomantis* and *Ochthomantis*. A third cluster is formed by *T. labrosa*, *A. madagascariensis* (from Ranomafana, eastern Madagascar) and one *Boophis* which was named *B.* aff. *tephraeomystax* by Blommers-Schlösser (1978). Phenetic distances between the remaining taxa are relatively low, reflecting the low differences in chromosome morphology within and between *Mantella*, *Mantidactylus* and *Boophis*. Regarding *Aglyptodactylus*, chromosome morphology therefore supports close affinities to *T. labrosa*. The status of *Boophis* aff. *tephraeomystax* (from eastern Madagascar) remains enigmatic, since its chromosome morphology differs distinctly from that of other *Boophis*, and even from that of *B. tephraeomystax* from Toliara in south-western Madagascar (Blommers-Schlösser 1978). On the other hand, *B. tephraeomystax* from several localities in western and eastern Madagascar were found to be similar morphologically and bioacoustically (Glaw and Vences 1994; personal observation).

Electrophoresis

In five out of eight loci (63%) the alleles that we identified in both *Aglyptodactylus* species were not found in species of *Mantella*, the type genus of the Mantellinae. This result can be seen as significant due to the large number of *Mantella* analyzed (about 120 specimens belonging to 13 species), and does not support close relationships between both genera. The single species of *Mantidactylus* (*M. biporus*) differed from *Aglyptodactylus* in only 25% of the loci, but this can not be taken as evidence for closer relationships, especially due to the low number (4) of comparatively scorable loci in *M. biporus*.

Phylogenetic analysis

The phylogenetic analysis, based on 20 characters, results in three equally parsimonious cladograms. A strict consensus cladogram of these is presented in Fig. 13. *Aglyptodactylus* and *Tomopterna* form a clade, but relationships between the three *Tomopterna* groups (Africa, Madagascar, Asia) are not resolved. *Mantella* and *Mantidactylus* also are a monophyletic unit, supporting the clade Mantellinae which is currently composed of only these two genera. Relationships between *Boophis*, the Mantellinae, and the *Aglyptodactylus*/*Tomopterna* clade are not resolved, resulting in a basal trichotomy of the cladogram.

Discussion and conclusions

Subfamilial placement of *Aglyptodactylus* and biogeographical implications

Our data provide clear evidence that the genera *Tomopterna* and *Aglyptodactylus* are parts of a monophyletic lineage when compared with *Boophis*, *Mantidactylus* and *Mantella*. This result of the phylogenetic analysis is further supported by the phenetic comparison of chromosome complements. Additional similarities in external morphology and ecology may be due to selective pressures in arid environments, but can also have phylogenetic origin. Among these are the similar general appearance of *T. labrosa* and *A. laticeps*, the (at least partly)

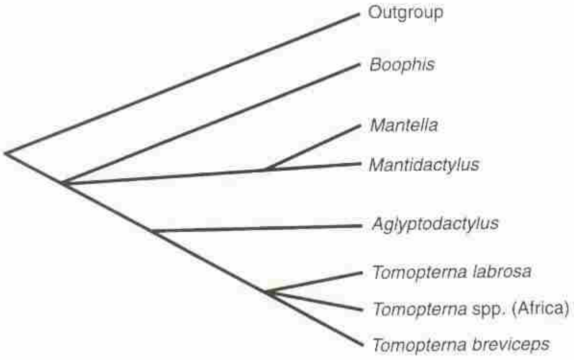

Fig. 13. Strict consensus tree of three equally parsimonious cladograms (consistency index 82, retention index 82) obtained by analysis of characters presented in Table 5. For the phylogenetic analysis groups with multiple states were coded as follows: character 10, *Mantella* A, *Mantidactylus* A; character 11, *Mantidactylus* A, *Boophis* B (states occurring in most examined species, respectively); character 14, *Mantella* A, *Mantidactylus* C (autapomorphies occurring within the mentioned genera); character 19, *Mantidactylus* 1 (autapomorphy of a group of most subgenera). Characters 15a, 15b, and 15c are considered as components of a character complex related with reproduction and considered as one character only. Multiple states were included as unordered transformation

connected lateral metatarsalia of both, the laterally blackish throat, and the distinct black nuptial pads. The latter probably represents a plesiomorphic state, but in this they stand against close relationships between *Aglyptodactylus* and *Boophis*, in which only *B. albilabris* is known to have distinct black pads. We also expect that a large clutch size and small egg diameter is a shared character of *Aglyptodactylus* and *T. labrosa* although data on the latter species are not available.

It still is true that 'the systematics of ranoid frogs is in a state of chaos' (Duellman and Trueb 1986). New classifications which recently have been suggested (Dubois 1992; Blommers-Schlösser 1993) differ largely from each other, even regarding the arrangement of genera into subfamilies. The osteological study of Clarke (1981) was restricted to African ranoids, Blommers-Schlösser (1993) did not focus on generic but on subfamilial relationships, and our analysis is restricted to genera occurring in Madagascar. Thus no comprehensive study of relationships of ranid genera exists. The validity of the *Aglyptodactylus-Tomopterna* clade will be tested in future studies including all ranid genera.

We can state, however, that *Aglyptodactylus* is neither closely related to the Mantellinae nor to the Rhacophorinae. When using only the data of Blommers-Schlösser (1993), who included *Aglyptodactylus* in the Rhacophorinae, three transformations must be assumed: one convergence (cervical cotyles) and two reversals (shape of terminal phalanges, circummarginal groove of digital pads). On the contrary, only two transformations (convergences) would be necessary (using the same data) by inclusion of *Aglyptodactylus* in the Raninae (intercalary element, tarsals).

Beside the suggestive strength of the occurrence in Madagascar, where the main groups of ranoid frogs are rhacophorines and mantellines, the presence of an intercalary element was the main argument to group *Aglyptodactylus* with one of those. Liem (1970: 1) states that Old World treefrogs (including rhacophorines and mantellines *sensu* Blommers-Schlösser 1993) 'differ from the Ranidae only in the presence of the intercalary cartilage'. However, the intercalary element clearly has evolved several times among anurans (at least once in the hylid/centrolenid lineage and once in the ranoid lineage; see Duellman and Trueb 1986). Laurent (1991) even states that he 'would not even be surprised if it proved to have appeared three times or even more' within the ranoid lineage. We suggest that the intercalary element evolved once more convergently within ranoids, i.e. in *Aglyptodactylus*.

It must also be stressed that it is not completely clarified whether the intercalary element is a derived or primitive state within the Ranidae, since the outgroup (hyperoliids and arthroleptids) includes both species with and without intercalary elements. Assuming that the intercalary element is an ancestral state in the whole hyperoliid/arthroleptid/ranid lineage, with a convergent loss in several clades, may even result in a more parsimonious phylogenetic hypothesis than the current schemes.

The genera *Tomopterna* and *Aglyptodactylus* are parts of a monophyletic lineage according to our analysis. This conclusion is supported by one synapomorphic character (reduced DNA content; character 20) and four unpolarized characters (arrangement of nasals and sphenethmoid, arrangement of frontoparietals, comparative finger length, circummarginal groove; characters 3, 4, 18 and 19). *Tomopterna* is generally considered to belong to the ranid subfamily Raninae (e.g. Blommers-Schlösser 1993). Dubois (1992) included the genus in a separate subfamily Tomopterninae, based on Clarke's (1981) osteological data on African species. The differences which we found within *Tomopterna* (see below) show a more complex situation, indicating that a subfamily Tomopterninae is not warranted at present. We therefore transfer the genus *Aglyptodactylus* from the Rhacophorinae (Blommers-Schlösser 1979, 1993), respectively, from the Mantellinae (Channing 1989) to the Raninae.

Blommers-Schlösser and Blanc (1993) hypothesized that the biogeographic origin of *Tomopterna* in Madagascar was 'vraisemblablement [...] la même' as that of mantellines, i.e. that *T. labrosa* was descendant of an ancient ranine stock that populated eastern Gondwana. The existence of the endemic ranine genus *Aglyptodactylus* in Madagascar as well as the close phylogenetic relationships between *Aglyptodactylus* and *Tomopterna labrosa* strongly confirm the biogeographical implication that the Raninae were already present on the Madagascan plate when it broke off from continental Africa. Later drift waifing of *Tomopterna* from Africa to Madagascar is therefore unlikely. Oceanic islands are generally not populated by autochthonous amphibians, indicating that drift waifing is a very uncommon dispersal mode in this group of vertebrates.

Status and relationships of the Rhacophorinae

In Blommers-Schlösser's (1993) phylogenetic hypothesis the Rhacophorinae and Mantellinae are sister groups within the family Ranidae. This contrasts with the opinion of many previous workers who considered the former group as family Rhacophoridae. Our data confirm Blommers-Schlösser's opinion in that differences between rhacophorines, mantellines and ranines are weak, and that this situation is best reflected by a subfamilial status of the rhacophorines. However, some doubts remain on the sister group relationship of the Rhacophorinae and Mantellinae, which is not corroborated by our cladogram. A closer look at Blommers-Schlösser's data shows that this hypothesis is only supported by the presence of an intercalary element in both groups. The need to include *Aglyptodactylus* in the Raninae reduces the significance of this character for phylogenetic analysis and suggests its convergent evolution within the Raninae. There is one other character in Blommers-Schlösser's data set, the shape of the terminal phalanges, in which a derived state (Y-shape) is shared by the Mantellinae and Rhacophorinae, and by only one additional group, the Indiraninae. We can not evaluate the importance of this character state, which was characterized by Daly et al. (1996: 8) as widespread, but we conclude that the sister group relationship Mantellinae-Rhacophorinae is in need of evidence. This is especially the case since, according to Blommers-Schlösser (1993), this relationship assumes one reversal (loss of femoral glands) in the Rhacophorinae. The character 'femoral glands' is poorly defined and not recognizable in all Mantellinae (Daly et al. 1996; personal observation). They probably must be seen in the context of a derived mating behaviour of mantellines (loss of amplexus; see Blommers-Schlösser 1993), but the mating behaviour of petropedetines with femoral glands seems to be unknown (Daly et al. 1996). Future studies should (a) compare histologically femoral gland structures to determine their homology and phylogenetic significance (b) search for additional synapomorphic and autapomorphic characters of the Rhacophorinae and Mantellinae (c) evaluate the phylogenetic importance of Y-shaped terminal phalanges, and (d) clarify the mating behaviour of petropedetines with femoral glands.

Intrageneric relationships of *Tomopterna*

Dubois (1987, 1992) classified *Tomopterna* into two subgenera, *Tomopterna* and *Sphaerotheca*. In the former he included the species from continental Africa, whereas in the latter he grouped *T. labrosa* from Madagascar and two species from India and Sri Lanka (*T. breviceps* and *T. rolandae*). This classification was based on Clarke's (1981) observation of a derived ilium protuberance in the African species.

Glaw and Vences (1994) stated that by tadpole morphology (number of keratodont rows), the Madagascan *T. labrosa* is more similar to African species than to the Asian *T. breviceps*. The advertisement calls of many *Tomopterna* species have been described: *T. breviceps* (Kanamadi et al. 1994), five of six African species (Passmore and Carruthers 1995), and *T. labrosa* (Glaw and Vences 1994). However, structural similarities of advertisement calls are only obvious between the five South African species. Their calls consist of series of short notes arranged in two frequency bands suggesting monophyly. Morphological differences between them are small, and the call is the most reliable character for species identification (Passmore and Carruthers 1995: 292).

The classification of Madagascan and Asian *Tomopterna* in one subgenus, *Sphaerotheca*, is therefore only based on one symplesiomorphic character. Nevertheless, Blanc and Paulian (1996) state that 'les espèces asiatiques et malgache sont nettement plus primitives que les formes africaines.' The present classification is further misleading in that it implies close biogeographic relationships between Madagascar and India. We did not find any unique synapomorphic character of *T. breviceps* and *T. labrosa*. However, derived states which define at least the Madagascan and the African intrageneric lineage as monophyletic do exist. *T. labrosa* is defined by having two free tarsals, as far as known a state that in the whole subfamily Raninae (sensu Blommers-Schlösser 1993) is only shared by species of *Aglyptodactylus*. This situation is best served by removing *T. labrosa* from *Sphaerotheca* to a separate subgenus. Since no generic name is available, we here describe the new subgenus.

Laliostoma subgen. *n.*
Type species
Tomopterna labrosa Cope, 1868.

Etymology
Derived from *lalia* (Greek) = chat, and *stoma* (Greek) = mouth. In arid regions of Madagascar, the call of *T. labrosa* is a very conspicuous sound during its short breeding season.

Diagnosis
Distinguished from both African and Asian species of *Tomopterna* (subgenera *Tomopterna* and *Sphaerotheca*, respectively) by (a) two free tarsals (b) long zygomatic squamosal process (c) unfused prehallux (d) larger size (e) call structure. Additionally distinguished from African species by (a) lack of a dorsal ilium protuberance (b) a distinctly forked omosternum (c) a different shape of the anterior parasphenoid process, and from Asian species by number of tadpole keratodont rows (see Glaw and Vences 1994).

Included species
Tomopterna (*Laliostoma*) *labrosa*

Distribution
Madagascar

The recognition of three subgenera within *Tomopterna* clearly reflects better the intrageneric phylogeny than the previous situation. In our phylogenetic hypothesis (in which no character weighting was employed) the three subgenera cluster as monophyletic unit, supported by one unpolarized character (maxilla-preorbital process of pars facialis; character 6) and absence of the intercalary element, (character 8). However, it should be stated that this evidence is rather weak since lack of an intercalary element is widespread among the Ranidae (see above), and a well developed maxilla-preorbital process also occurs in several other ranids, e.g. representatives of the genera *Aubria*, *Pyxicephalus*, and *Rana* (Clarke 1981). Thus, it can not be excluded that the genus is in fact a para- or polyphyletic assemblage. The derived tarsal reduction in the three species of *Aglyptodactylus* and in *T. labrosa* may indicate that these taxa form a monophyletic lineage.

Current evidence, however, is too weak to support a generic partition of *Tomopterna*. The phylogeny of the genus, which is extremely interesting considering its potential implications on historical biogeography and plate tectonics in the Indian Ocean (see Duellman and Trueb 1986), is far from being resolved. Comprehensive studies, including more genera and molecular techniques, are necessary to address this question.

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Zusammenfassung

Revision der Gattung Aglyptodactylus *Boulenger, 1919* (*Amphibia: Ranidae*), *und Analyse der phylogenetischen Beziehungen zu anderen madagassischen Gattungen der Ranidae* (Tomopterna, Boophis, Mantidactylus *und* Mantella)

Aglyptodactylus galt bislang als monotypische Gattung, deren Verbreitung auf humide Regionen Ostmadagaskars beschränkt ist. Unsere Freilandbeobachtungen ergaben, daß im Trockenwald von Kirindy (Westmadagaskar) zwei neue *Aglyptodactylus*-Arten syntop vorkommen: *A. laticeps* sp. *n.* und *A. securifer* sp. *n.* Im Vergleich zu *A. madagascariensis* aus den östlichen Regenwaldgebieten zeigt *A. laticeps* sp. *n.* auffällige morphologische Unterschiede, die teilweise als Anpassungen and trockenes Klima und grabende Lebensweise gedeutet werden können. Trotz dieser morphologischen Differenzierung weisen bioakustische und osteologische Daten darauf hin, daß alle drei *Aglyptodactylus*-Arten nahe miteinander verwandt sind.

Eine phylogenetische Analyse der madagassischen Gattungen der Familie Ranidae (*Aglyptodactylus, Mantella, Mantidactylus, Boophis* und *Tomopterna*; letztere mit Vertretern in Madagaskar, Afrika und Asien) resultierte in einem Schwestergruppenverhältnis zwischen *Tomopterna* (Unterfamilie Raninae) und *Aglyptodactylus*. Aus diesem Grund gliedern wir *Aglyptodactylus* aus der Unterfamilie Rhacophorinae aus, stellen die Gattung in die Unterfamilie Raninae und diskutieren die Implikationen dieses Schrittes für die Systematik ranoider Frösche. Da mit *Aglyptodactylus* eine endemische Gattung der Raninae auf Madagaskar existiert, kann angenommen werden, daß diese Unterfamilie Madagaskar bereits vor der endgültigen Trennung von Afrika besiedelte. Die madagassische Art *Tomopterna labrosa* zeigt mehrere wichtige Unterschiede sowohl zu afrikanischen als auch zu asiatischen Vertretern der Gattung und wird daher aus der Untergattung *Sphaerotheca* (die damit auf Asien beschränkt ist) ausgegliedert und in eine neue Untergattung *Laliostoma* subgen. *n.* gestellt.

References

Ahl, E., 1929: Beschreibung neuer Frösche aus Madagaskar. Mitt. zool. Mus. Berlin **14,** 469–484.

Bachmann, K.; Blommers-Schlösser, R., 1975: Nuclear DNA Amounts of the Frogs of Madagascar. Zool. Anz. **194,** 13–21.

Blanc, C. P.; Paulian, R., 1996: Originalité biogéographique de la faune du sud malgache. In: Lourenco, W. R. (ed.), Actes du Colloque International Biogéographie de Madagascar. Paris: Société de Biogéographie – Muséum – ORSTOM. pp. 245–258.

Blommers-Schlösser, R. M. A., 1978: Cytotaxonomy of the Ranidae, Rhacophoridae, Hyperoliidae (Anura) from Madagascar with a note on the karyotype of two amphibians of the Seychelles. Genetica **48,** 23–40.

–, 1979a: Biosystematics of the Malagasy frogs. I. Mantellinae (Ranidae). Beaufortia **29,** 1–77.

–, 1979b: Biosystematics of the Malagasy frogs. II. The genus *Boophis* (Rhacophoridae). Bijdr. Dierk. **49,** 261–312.

–, 1993: Systematic relationships of the Mantellinae Laurent 1946 (Anura Ranoidea). Ethol. Ecol. Evol. **5,** 199–218.

Blommers-Schlösser, R. M. A.; Blanc, C. P., 1991: Amphibiens (première partie). Faune de Madagascar, Paris **75** (1), 1–379.

–; –, 1993: Amphibiens (deuxième partie). Faune de Madagascar, Paris **75** (2), 385–530.

Bogart, J. P.; Tandy, M., 1976: Polyploid amphibians: three more diploid-tetraploid species of frogs. Science **193,** 334–335.

–; –, 1981: Chromosome lineages in African Ranoid frogs. Mon. Zool. Ital. (N.S.) **15** (suppl), 55–91.

Boulenger, G. A., 1919: On the Madagascar Frogs of the Genus *Mantidactylus* Blgr. Proc. Zool. Soc. London **19,** 257–261.

Cadle, J. E., 1995: A new species of *Boophis* (Anura: Rhacophoridae) with unusual skin glands from Madagascar, and a discussion of variation and sexual dimorphism in *Boophis albilabris* (Boulenger). Zool. J. Linn. Soc. **115,** 313–345.

Channing, A., 1989: A re-evaluation of the phylogeny of Old-World treefrogs. S. Afr. J. Zool. **24,** 116–131.

Clarke, B., 1981: Comparative osteology and evolutionary relationships in the African Raninae (Anura Ranidae). Monit. zool. ital. (N.S.) **15** (Suppl), 285–331.

Cope, E. D.; 1868: Second supplement on some new Raniformia of the old World. Proc. Acad. Nat. Sci. Philadelphia **20,** 138–139.

Daly, J. W.; Andriamaharavo, N. R.; Andriantsiferana, M.; Myers, C. W., 1996: Madagascan Poison Frogs (*Mantella*) and Their Skin Alkaloids. Am. Mus. Novitates **3177,** 1–34.

Dingerkus, G.; Uhler, L. D., 1977: Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Technol. **52,** 229–232.

Drewes, R. C., 1984: A phylogenetic analysis of the Hyperoliidae (Anura): Treefrogs of Africa, Madagascar, and the Seychelles Islands. Occ. Pap. California Acad. Sc. **139,** 1–70.

Dubois, A., 1983: Note preliminaire sur le groupe de *Rana* (*Tomopterna*) *breviceps* Schneider, 1799 (Amphibiens, Anoures), avec diagnose d' une sous-espece nouvelle de Ceylan. Alytes **2,** 163–170.

–, 1987: Miscellanea taxinomica batrachologica (I). Alytes **5,** 7–95.

–, 1992: Notes sur la classification des Ranidae (Amphibiens Anoures). Bull. mens. Soc. linn. Lyon **61,** 305–352.

Duellman, W. E.; Trueb, L., 1986: Biology of Amphibians. New York: McGraw-Hill.

Duméril, A.; 1853: Mémoire sur les Batraciens anoures de la famille des Hylaeformes ou Rainettes, comprenant la description d'un genre nouveau et de onze espèces nouvelles. Ann. Sci. nat. Paris (3, Zool.) **19,** 135–179.

Dutta, S. K.; Manamendra-Arachchi, K., 1996: The amphibian fauna of Sri Lanka. Colombo: Wildlife Heritage Trust of Sri Lanka.

Emanueli, L.; Jesu, R., 1995: The herpetofauna of the World Heritage Site 'Tsingy de Bemaraha' (Western Madagascar). In: Llorente, G. A. et al. (eds), Scientia Herpetologica 1995, pp. 341–348.

Emerson, S. B., 1985: Skull shape in frogs – correlations with diet. Herpetologica **41,** 177–188.

Farris, J. S., 1988: Hennig. Hennig86 reference, version 1.5.

Frost, D. R. (ed.), 1985: Amphibian species of the world: A taxonomic and geographical reference. Lawrence: Allen Press and ASC.

Ganzhorn, J. U., 1992: Fallstudie zur integrierten Nutzung von Trockenwäldern. In: A. Bittner (ed.), Madagascar – Mensch und Natur im Konflikt. Basel, Switzerland: Birkhäuser pp. 183–190.

Glaw, F.; Vences, M., 1992a: Zur Kenntnis der Gattungen *Boophis, Aglyptodactylus* und *Mantidactylus* (Amphibia: Anura) aus Madagaskar, mit Beschreibung einer neuen Art. Bonner zool. Beitr. **43,** 45–77.

–; –, 1992b: A Fieldguide to the Amphibians and Reptiles of Madagascar. Köln: Vences and Glaw.

–; –, 1994: A Fieldguide to the Amphibians and Reptiles of Madagascar, 2nd edn, including mammals and freshwater fish. Köln: Vences and Glaw.

–; –, 1997: Neue Ergebnisse zur *Boophis goudoti*-Gruppe aus Madagaskar: Bioakustik, Fortpflanzungsstrategien und Beschreibung von *Boophis rufioculis* sp. nov.- Salamandra **32,** 225–242.

Guibé, J., 1978: Les Batraciens de Madagascar. Bonner Zool. Monogr. **11,** 1–140.

Günther, A., 1877: Descriptions of some new species of reptiles from Madagascar. Ann. Mag. Nat. Hist., Ser. **4,** 313–317.

Hille, A.; Meinig, H., 1996: The subspecific status of European populations of the striped field mouse *Apodemus agrarius* (Pallas, 1771) based on morphological and biochemical characters. Bonner Zool. Beitr. **46,** 203–231.

Kanamadi, R. D.; Hiremath, C. R.; Schneider, H., 1994: Advertisement calls of two anuran amphibians, *Rana tigrina* and *Tomopterna breviceps.* J. Biosc. **19,** 75–80.

King, M., 1990: Amphibia. Animal Cytogenetics. 4. Chordata 2. Stuttgart: Borntraeger.

Laurent, R. F., 1943: Sur la position systématique et l'osteologie du genre *Mantidactylus* Boulenger. Bull. Mus. r. Hist. Nat. Belg. **19,** 1–8.

–, 1991: Classification and phylogeny of ranoid frogs. Circalytes **5,** 1–7.

Liem, S. S., 1970: The morphology, systematics and evolution of Old

World treefrogs (Rhacophoridae and Hyperoliidae). Fieldiana Zool. **57,** 1–145.

Lynch, J. D., 1971: Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. Mus. Nat. Hist., University of Kansas Misc. Publ. **53,** 1–238.

Mocquard, M. F., 1902: Sur une collection de reptiles et de batraciens recueillis par M. Alluaud dans le sud de Madagascar. Bull. Soc. philomath., Paris, Ser **9,** 5–25.

Passmore, N. I.; Carruthers, V. C., 1995: South African Frogs. A Complete Guide. Revised edn, Johannesburg: Southern book publishers, Witwatersrand University Press.

Plösch, T., 1991: Die Alizarin-/Alcianblau-Färbung nach Dingerkus and Uhler. DATZ **44,** 252–254.

Salvador, A., 1996: Amphibians of northwest Africa. Smithsonian Herpetological Information Service **109,** 1–43.

Vences, M.; Glaw, F.; Böhme, W.; Mausfeld, P., in press: Comparative osteology of Malagasy poison frogs of the genus *Mantella* (Amphibia: Anura: Mantellinae). Bonner Zool. Beitr.

Authors' address: Frank Glaw, Zoologische Staatssammlung München, Münchhausenstr. 21, D-81247 München, Germany; Miguel Vences, Wolfgang Böhme, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany.