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Biosystematics of the Malagasy frogs. I. Mantellinae (Ranidae)

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ABSTRACT

A collection of frogs was made in Madagascar between November 1970 and May 1973. Observations in the field and investigations in the laboratory yielded a variety of new taxonomic characters, such as the morphology of eggs and larvae, the reproductive behaviour, the habitat and habits of both the terrestrial and aquatic stages, the mating call and the colouration in life. Karyotype studies and researches on the nuclear DNA amount of these frogs were published previously.

Because of various contradictions between the results of this study and the current classification, both these new and the more conventional morphological characters were used for a re-evaluation of the systematics of the Mantellinae Laurent, 1946. As a result, this subfamily can be considered once more a natural, probably mono-phyletic group of ranid-type frogs, primarily separated from the others by a different mating behaviour.

Of the genera *Mantidactylus* Boulenger, 1895, *Mantella* Boulenger, 1882, and *Aglyptodactylus* Boulenger, 1919, 35 species, collected by the author and representing about 70% of the known species, are treated.

The genus *Aglyptodactylus* is excluded from the Mantellinae. The genus *Gephyromantis* Methuen, 1919, is synonymized with *Mantidactylus*. The broadened genus *Mantidactylus* is divided into 10 species groups: *guttulatus* group, *ulcerosus* group, *lugubris* group, *albofrenatus* group, *aglavei* group, *asper* group, *boulengeri* group, *wittei* group, *depressiceps* group, *pulcher* group. These groups reflect the adaptive radiation within this genus.

Two new species are described: *viz.* *Mantidactylus flavobrunneus* and *M. punctatus*. Lectotypes are designated for *Rhacophorus depressiceps* Boulenger, 1882, *Rhacophorus pulcher*, Boulenger, 1882, *Rhacophorus liber* Peracca, 1893, and *Gephyromantis methueni* Angel, 1929.

The following new combinations, new synonyms and bonae species are proposed: *Mantidactylus grandidieri* Mocquard, 1895, bona species (syn. *Mantidactylus piger* (Mocquard, 1900)); *Mantidactylus opiparis* (Peracca, 1893), bona species (syn. *Mantidactylus melanopleura* (Mocquard, 1901) and *Mantidactylus frenatus* Boettger, 1913); *Mantidactylus aglavei* (Methuen & Hewitt, 1913), comb. nov. (from *Rhacophorus*); *Mantidactylus boulengeri* (Methuen, 1919), comb. nov. (from *Gephyromantis*); *Mantidactylus eiselti* (Guibé, 1975), comb. nov. (from *Gephyromantis*); *Mantidactylus blommersae* (Guibé, 1975), comb. nov. (from *Gephyromantis*); *Mantidactylus domer-*

guei (Guibé, 1974) comb. nov. (from *Gephyromantis*); *Mantidactylus peraccae* (Boulenger, 1896), comb. nov. (from *Rhacophorus*); *Mantidactylus tornieri* (Ahl, 1928), bona species; *Mantidactylus pulcher* (Boulenger, 1882) comb. nov. (from *Gephyromantis*); *Mantidactylus liber* (Peracca, 1893), comb. nov. (from *Gephyromantis*), bona species (syn. *Gephyromantis albugularis* Guibé, 1947 and *Gephyromantis variabilis* Millot & Guibé, 1951); *Mantidactylus bicalcaratus* (Boettger, 1913), comb. nov. (from *Gephyromantis*) (syn. *Gephyromantis methueni* Angel, 1929).

INTRODUCTION

Boulenger (1895) created *Mantidactylus* for the Malagasy species of the genus *Rana* Linnaeus, 1758, and *Limnodytes* Duméril & Bibron, 1841, since they possess an intercalary cartilage between the terminal phalanx (disc) and the adjacent phalanx. To this character, Mocquard (1909) added the presence of a gland on the ventral surface of the thigh (femoral gland). Methuen (1919) described the Malagasy genus *Gephyromantis* to separate the species with connected lateral metatarsalia from *Mantidactylus*. Ahl (1929) synonymized *Gephyromantis* with *Rhacophorus* Kuhl, 1822. Guibé (1945) did not accept the synonymy proposed by Ahl (1929); he gave the following definition of *Gephyromantis*: lateral metatarsalia entirely or almost entirely connected, bony style of both omosternum and sternum forked at the base, while in *Mantidactylus* the lateral metatarsalia are separated and only the omosternal style is forked. Guibé (1975a) noted, while transferring some *Rhacophorus* species to *Mantidactylus* and *Gephyromantis*, that a slightly forked sternal style exists in a few *Mantidactylus* species too. Guibé (1978) in his survey of the Malagasy frogs comments on the great diversity of characters within *Mantidactylus*: "Il est possible qu'une telle diversité soit l'indice d'hétérogénéité générique. . .".

The original purpose of this study was to supply information on the natural history, larval morphology, sound, and other features of a number of Malagasy frogs, which together with the cytogenetical data published already (Blommers-Schlösser, 1978), might help to clear up the rather confused systematics. However, it was soon felt that merely identifying the specimens was not sufficient. Consequently I have paid special attention to a number of morphological features in each species collected (and in the pertaining type specimens, as far as possible): notably, the connection of the lateral metatarsals, the bifurcation of the bony style of both sternum and omosternum, the shape of the vocal pouches, the shape of the femoral glands and the size of the finger discs.

As a result, I found that the genera *Mantidactylus* and *Gephyromantis* (sensu Guibé) overlap each other in many characters and together form a homogeneous group. It cannot be split into two clear-cut groups, but rather well into a greater number.

As a consequence, I consider the genus *Gephyromantis* a synonym of *Mantidactylus*, and I have divided the latter genus *sensu lato* in, tentatively, 10 species groups. The reasons will be discussed more fully later in this paper.

The genus *Mantidactylus* is restricted to Madagascar and contains about 45

species. It belongs together with the small endemic genera *Mantella* Boulenger, 1882, *Trachymantis* Methuen, 1919 (*Aglyptodactylus* Boulenger, 1919 was considered a subgenus of *Mantidactylus* by Laurent, 1943a) and the Asian genus *Pseudophilautus* Laurent, 1943, to the subfamily Mantellinae of the Ranidae (sensu Laurent, 1946). Liem (1970) and Guibé (1978) consider these genera not as a separate subfamily, but place them together with the Malagasy *Rhacophorus* (= *Boophis* Tschudi, 1838, sensu Laurent, 1943) and other non-endemic genera in the Rhacophoridae. However, Liem (1970) draws attention to the intermediate position of *Mantidactylus* between the Ranidae and the Rhacophoridae.

This paper is concerned with the natural history and systematics of frog species belonging to the Malagasy genera of the Mantellinae sensu Laurent. The collection on which this paper is based was assembled between November 1970 and May 1973 by the author and her husband. The number of species treated is 35, representing about 70% of those known to belong to the genera of Mantellinae occurring in Madagascar (except *Trachymantis*).

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MATERIAL AND METHODS

The material is deposited in the Zoölogisch Museum Amsterdam (ZMA). The ZMA registration numbers are given under each species with the number of specimens in parentheses. The adult specimens were compared for the greater part with type material, from the following institutes.

Muséum National d'Histoire Naturelle, Paris	MNHP
Naturhistorisches Museum, Basel	NMB
British Museum (Natural History), London	BMNH
Zoologisches Museum, Berlin	ZMB
Natur-Museum und Forschungs Institut Senckenberg, Frankfurt	SMF

Definition of measurements in the adult frog: snoutvent length — the total length of head and body; tibia length — measured on the flexed leg from the convex surface of the knee to the convex surface of the tibia-tarsal joint; foot length — the distance from the proximal edge of the inner metatarsal tubercle to the tip of the longest (fourth) toe including the disc; head length — the distance from the posterior edge of the jaw articulation to the tip of the snout; head width — taken at tympanic level; width of eyelid — the greatest width of the upper eyelid; length of hand — from the base of the palm to the tip of the third finger; length of hindlimb — from the vent to the tip of the fourth toe; lower arm length — from the elbow to the tip of the fourth toe.

Definition of characters in the adult frog: supernumerary tubercles — the small tubercles on the ventral surfaces of the digits, exclusive of the larger subarticular tubercles; palmar tubercle — one or more tubercles on the palm at the bases of the third and fourth fingers; inner metacarpal tubercle — tubercle on the ventral surface of the hand at the base of the thumb. The webbing formula: the numbers 1, 2i, 2e refer to the first toe (or finger), the inner side of the second, the outer side of the second and the numbers in parentheses refer to the number of phalanges free of web. Adpressed heels — hind legs bent at right angles to the body.

In describing larvae I have defined the stages according to Gosner (1960). Identification of the tadpoles: in the case of observed oviposition, the female was captured and preserved. In other cases, the tadpoles were reared until the young frogs were identifiable. The young resemble the adults in colour, immediately after metamorphosis.

Definition of measurements and characters in the tadpole: body length — the distance between the tip of the snout and the posteroventral edge of the body. Total length — the distance from the tip of the snout to the tip of the tail. The shape of the body is called "depressed" when the depth is clearly less than the width and "ovoid" when the depth and the width are about equal. The mouth is considered small when it is less than two thirds of the greatest width of the body. Tooth formula: the tooth rows are numbered from top to bottom both in the upper and lower lip. The separation between both lips is indicated by a double slant line. A median gap between the lateral tooth rows is marked by a plussign. The tooth formula is given from stage 28 onwards (complete).

The collecting sites (localities) are numbered (abbreviated L1, L2, etc.).

1. Midway between Ifanadiana and Mananjary ("highroad R.N. 25" Ambohimaso-Mananjary), alt. 400 m.
2. Mananjary, alt. 13 m.
3. Fort-Dauphin, alt. 44 m.
4. Ambila-Lemaitso (near Brickaville), alt. 7 m.
5. 25 km N of Tamatave, sea level.
6. Foulpointe (60 km N of Tamatave), sea level.
7. Ambodiriana (38 km NNW of Tamatave), alt. 300 m.
8. Midway between Foulpointe and Fénériver-Est, sea level.
9. Fénériver-Est, sea level.
10. Perinet ("highroad R.N. 2" at km 142), alt. 900—1100 m.
11. Mandraka-valley ("highroad R.N. 2" at km 69), rivulet Vokanatezandava and adjacent ponds, nursery garden of the city of Tananarive, alt. 1200 m.
12. Along the road from Moramanga to Anosibe at km 25, alt. 900 m.
13. Angavokely, forest station (near Carion "highroad R.N. 2" Tananarive-Tamatave at km 30), alt. 1600 m.
14. Tananarive (Zoological gardens Tsimbazaza), alt. 1300 m.
15. Ambatolampy ("highroad R.N. 7" Tananarive-Tulear at km 68), alt. 1500 m.
16. Between Ranomafana and Ifanadiana ("highroad R.N. 25"), alt. 800 m.
17. Tampoketsa d'Ankazobe, forest station ("highroad R.N. 4" Tananarive-Majunga), alt. 1600 m.
18. Manjakotompo, forest station (near Ambatolampy) Ankaratra mountains, alt. 1800—2400 m.
19. Ampijoroa ("highroad R.N. 4" Tananarive-Majunga at km 465), Ankarafantsika forest, alt. 250 m.
20. Mont Beomby, Island Nossi-Bé, alt. 300 m.

In Madagascar several quite distinct climatic areas can be distinguished; roughly the rainfall on the island decreases if one goes from East to West and from North to South. Most of the rain falls in the southern summer from November till April. Various bioclimatic areas can be distinguished (cf. Koechlin, 1972). In this respect, the collecting sites can be grouped as follows: nos. 1—9: East Area (eastern coast up to about 800 m altitude); annual precipitation exceeding 2000 mm; no dry months; *t* (temperature of coldest month) above 15°C. nos. 10—17: Centre Area (Central Plateau between 800—2000 m altitude); annual precipitation between 1500—2000 mm; 3—4 months dry season; *t* between 10° and 15°C. no. 18: High Mountains Area altitudes above 2000 m; annual precipitation exceeding 2000 mm; no dry months; *t* between 0° and 10°C. no. 19: West Area (western coast up to 800 m altitude); annual precipitation between 1500—2000 mm; 5 to 6 months dry season; *t* above 20°C. no. 20: Sambirano Area (Nossi-Bé and adjacent mainland); annual precipitation exceeding 2000 mm; 3 to 4 months dry season; *t* above 20°C.

The alkalinity of the inland waters differs widely according to soil type. In general, water is alkaline to neutral in the western and southern coastal areas, and acid in the other regions (Kiener, 1963).

Voice. — The calls of males were recorded on tape, in captivity. Sonagrams were made on a Vibralyzer (Kay Electric Co.), filter wide. For the description of the sonagrams, I have used the terminology of Duellman

(1970). The call or call-group is the entire assemblage of sound-units produced in a given sequence. A continuous note lacking an intermittent pause is said to be monophasic, whereas a note showing a brief pause is classified as diphasic. In a well-modulated note, the energy is concentrated into a number of narrow bands of frequency (called harmonics and appearing as distinct horizontal lines on audiospectrogram). Opposed to this melodious type of note is the noisy note, in which the sound is spread throughout the frequency spectrum without distinct concentrations. In the time span of a note, distinct pulsations of sound usually are noticeable; these appear as vertical marks or vertical rows of dots. The pulses can be counted in given notes. The dominant frequency is the darkest part of the note in the sonogram. The fundamental frequency is the lowest pitched harmonic.

Bachmann & Blommers-Schlösser (1975) have reported on the nuclear DNA amount, and Blommers-Schlösser (1978) on the karyotypes of Malagasy frogs. These data, being based on the same collection of frogs, are mentioned without reference throughout this paper: $2n$ is the diploid number of the chromosomes, N.F. the number of arms of chromosomes (diploid), pg = picogram (diploid).

In cases of a new synonymy, a new combination or reevaluation of a species, only relevant taxonomic references are cited. Species which are removed from previous synonymy, are called *bonae* species in the sequel. Keys for identification are used of Mocquard (1909), Boulenger (1919), Ahl (1931) and Guibé (1978).

Genus *Mantidactylus* Boulenger, 1895

Mantidactylus Boulenger, 1895: 450; Ahl, 1931 (equals *Aglyptodactylus*); Laurent, 1943a: 8 (equals *Aglyptodactylus*). Type species: *Mantidactylus guttulatus* (Boulenger, 1882) designated by Ahl, 1931: 10.

Gephyromantis Methuen, 1919: 351 (new synonymy); Ahl, 1931: 51 (in synonymy of *Rhacophorus*); Guibé, 1945: 283 (genus redefined). Type species: *Gephyromantis boulengeri* Methuen, 1919, by monotypy.

Definition. — Vertebral column pro- or diplasiocoel. Second tarsal free. Omosternum with long bony style, broadly or moderately forked posteriorly. Sternum with bony style: entire or slightly forked anteriorly. Length of style of omosternum equal or greater than that of sternal style. Maxillary teeth present. Vomerine teeth mostly present. Tongue distinctly bifid and free behind. Pupil horizontal. Intercalary cartilage present between disc and adjacent phalanx. Discs small to large, with a complete ring-shaped ventromarginal groove. Fingers free or with a small trace of web. Foot with trace of web to entirely webbed. Outer metatarsal tubercle present or absent. Lateral metatarsals separated or connected. Males lack nuptial excrescences and are slightly smaller in size than females. External vocal sacs absent or present: paired lateral subgular or single median subgular. Femoral glands (ventral surface) present in males, absent or reduced in females.

The *Mantidactylus guttulatus* group

Definition. — Omosternum moderately forked posteriorly: greatest distance between lateral arms is one and a half times the width of one arm. Sternum entire. Length of style of omosternum equal or somewhat greater than that of sternal style (fig. 42). Femoral glands small, round, elevated and solid (not granular, without notch); in females glands about half the size of those in males (fig. 52). Vocal sac not apparent externally. Lateral metatarsalia entirely separated by web. Outer metatarsal tubercle present or absent. Tibiotarsal articulation does not reach beyond tip of snout. Fingers free of web. Discs of fingers less than twice the diameter of the adjacent phalanx. Large frogs (90—120 mm). Contents: *M. guttulatus* (Boulenger, 1882), and *M. grandidieri* Mocquard, 1895.

Tadpoles: unknown.

Eggs: diameter of eggs in *M. guttulatus* 5 mm (Boulenger, 1919).

Chromosomes: *M. guttulatus*, as well as *M. grandidieri* (Blommers-Schlösser, unpublished) have $2n = 26$; N.F. = 52.

Habits and habitat: ground-dwelling frogs, living in and along brooks; in wooded areas.

Mantidactylus guttulatus (Boulenger, 1882), fig. 61.

Rana guttulata Boulenger, 1882: 21, pl. 11.

Mantidactylus guttulatus; Boulenger, 1895: 450; Boulenger, 1919: 258 (equals *piger*); Guibé, 1978: 18 (equals *grandidieri* and *piger*; in part).

Material. — ZMA 6814 (5) 1.III.73 at L 15. — ZMA 6815 (1) 24.XII.72; 6816 (1) 23.IX.72; 6817 (4) 14.XI.72; 6937 (1 young) 23.IX.72, at L 10 (900 m alt.). — ZMA 6818 (6) 15.III.73 at L 12.

Habitat. — The adults were collected in and along brooks in the forest.

Colour in life. — Back brown with small yellowish spots; venter dirty white with or without brownish spots.

Mantidactylus grandidieri Mocquard, 1895, bona species, fig. 62.

Mantidactylus grandidieri Mocquard, 1895: 105; Guibé, 1978: 18 (in synonymy of *guttulatus*).

Rana pigra Mocquard, 1900: 109 (new synonymy).

Mantidactylus piger; Mocquard, 1901: 255; Boulenger, 1919: 258 (in synonymy of *guttulatus*); Guibé, 1978: 18 (in synonymy of *guttulatus*).

Material. — MNHP 83580 one ♀ syntype, MNHP 95255 one ♂ syntype of *M. grandidieri*, East coast, Madagascar, coll. Grandidier and Humblot; MNHP 99410 the male holotype of *Rana pigra*, Ikongo forest, Madagascar, coll. Grandidier. — ZMA 7116 (1) 13.XI.72 at L 10 (1100 m alt.). — ZMA 7117 (2) 1.III.73 at L 15.

Habitat. — The adults were collected in and on the banks of brooks, in open land next to the forest.

Colour in life. — Back dark brown with small yellowish spots; venter dirty white with large blackish spots.

Taxonomy. — In my opinion, the differences apparent from the original description and figure of *Mantidactylus guttulatus* and the syntypes of *M. grandidieri* are real, because they appear consistent in our collection. Moreover, the two species are sympatric. The following differences can be found: the head of *M. guttulatus* (fig. 61) is as wide as the post-axillary region, and the skin of the back is shagreened; there is a small tubercle on the base of the fourth toe. In *M. grandidieri* (fig. 62) the head is much wider than the post-axillary region; the skin of the back is covered with numerous sharp warts; there is no tubercle on the base of the fourth toe, but there are some small tubercles on the tarsus. These differences are present in both sexes. *M. piger* agrees with *M. grandidieri* in all above-mentioned characters and is consequently synonymized with the latter species.

The *Mantidactylus ulcerosus* group

Definition. — Omosternum broadly forked posteriorly: greatest distance between lateral arms is four to five times the width of one arm. Sternum entire. Bony style of sternum distinctly shorter than style of omosternum (fig. 43). Femoral glands large, round, elevated, coarsely granular, with a central notch in males (fig. 53); in females small and flat (less than half the size of those in males). Vocal sac not apparent externally. Lateral metatarsalia entirely separated by web. Outer metatarsal tubercle present or absent. Tibiotarsal articulation does not reach beyond tip of snout. Fingers without web. Discs of fingers less than twice the diameter of the adjacent phalanx. Moderately sized frogs (30—65 mm). Contents: *M. ulcerosus* (Boettger, 1880). *M. ambohitombi* Boulenger, 1919, *M. betsileanus* (Boulenger, 1882), *M. curtus* (Boulenger, 1882), *M. alutus* (Peracca, 1893), *M. biporus* (Boulenger, 1889), *M. pauliani* Guibé, 1974.

Tadpoles: Mouth small; margin of oral disc indented laterally. Papillary border with wide dorsal gap. Tooth formula $1/2 + 2//3 - 1/4 + 4//3$. Horny beak well developed. Caudal musculature strong. Caudal dorsal fin reduced anteriorly.

Eggs: Rather large, 2.5—3.0 mm in diameter; 35—80.

Chromosomes: $2n = 24$; N.F. = 44-48 (*M. ulcerosus*, *M. curtus*, *M. biporus*, *M. betsileanus*, *M. ambohitombi*). Nuclear DNA amount 8.9—9.4 pg (*M. ulcerosus*, *M. curtus*, *M. biporus*, *M. betsileanus*).

Habits and habitat: Typically ground dwelling frogs, which spend most of their life in shallow water, rice fields, boggy meadows and roadside puddles, mostly in wooded areas. Their sound, like a creaking door, can be heard night and day. Tadpoles are found in stagnant or oozing water and they are benthonic feeders. Eggs deposited outside the water, in one mass.

Mantidactylus ulcerosus (Boettger, 1880)

Limnodytes ulcerosus Boettger, 1880: 282; Boettger, 1881: 505, pl. 4, fig. 7.

Mantidactylus ulcerosus; Boulenger, 1895: 450; Razarihelisoa, 1969: 953, fig. 7 (tadpole); Guibé, 1978: 36.

Material. — SMF 6605 the holotype of *Limnodytes ulcerosus*, Nossi-Bé, Madagascar. ZMA 6796 (13) 13.X.71; 6819 (6) 2.VIII.72; 6943 (1) 6.VIII.72; 6944 (2) 12.II.72; 6946 (2) 10.II.72; 7183 (one juv.) 13.X.71; 6993 (tadpoles) VII.72 at L 6. — ZMA 6798 (10) 16.X.71; 6947 (1) 12.II.72; 7182 (tadpoles reared from egg mass) X.71 at L 9. — ZMA 6797 (6) 22.1.73; 6945 (1) 23.IV.72 at L 19.

Habitat. — A species of shallow pools and slowly running water in marshy land or forest. The egg mass was found on a tree trunk, covered with moss, 40 cm above the water.

Colour in life. — Back light brown with dark brown markings, cream-white middorsal line often present, venter dirty white with dark brown spots.

Voice. — The males were heard calling, during day and evening, at all dates we collected them. The call consists of a short primary, low pitched, pulsed note and a long secondary note. One call group consists of 4 to 7 of these calls and the duration of the call group varies from 18.5—34 sec. The sonagram (fig. 33) made of a male (ZMA 6798) in November 1971 at 10 p.m. shows a primary note of 0.38 sec., with 8 pulses and a secondary note of 1.4 sec with 18 pulses. The dominant frequency is about 1500 Hz.

Eggs. — The egg mass of 60 eggs (each 2.5 mm in diameter) developed in the same way as observed in other species of this genus (see below: *M. wittei* group). The embryos developed in the jelly mass, having no external gills, and after seven days at room temperature, the hatchlings had wriggled free from the jelly and dropped into the water.

Tadpoles. — Thirty tadpoles in stage 25 have body lengths of 5—9 mm and total lengths of 15.5—28 mm. Average ratio of tail to body length is 1.9 (range 1.7—2.1). Six tadpoles in stages 26—30 have body lengths of 8—10 mm and total lengths of 23—31.5 mm. Seven tadpoles in stages 33—35 have body lengths of 10—11.5 mm and total lengths of 29—34 mm. Average ratio of tail to body length in stages 26—35 is 2 (range 1.9—2.1). Five metamorphosing young have body lengths of 10—12 mm. The mouth and lateral view of an entire tadpole in stage 35 (ZMA 6993) are shown in figs. 1, 2. Body depressed. Nostrils dorsal, aperture dorsolaterally situated at equal distances of eye and tip of snout. Eye situated dorsolaterally. Spiracular opening sinistral, situated at about 3/5 from snout to end of body. Cloacal tube dextral to caudal fin. Caudal musculature strong. Caudal dorsal fin reduced anteriorly. At midlength of tail, height of caudal musculature represents half of total height. Mouth small and directed anteroventrally. Margin of oral disc indented laterally. Papillary border with wide dorsal gap. Two rows of papillae present in lower lip. Tooth formula $1/3 + 3/3$, sometimes $1/2 + 2/3$. First row of lower lip often with slight median gap.

Colour of tadpole brownish in life.

In captivity the entire development took three months.

Razarihelisoa (1969) has described a tadpole as belonging to *M. ulcerosus*. This tadpole occurs in torrents in the Central Highlands, and its mouth differs slightly from the one figured here. Probably, it belongs to *M. curtus* (see below).

Mantidactylus ambohitombi Boulenger, 1919

Mantidactylus ambohitombi Boulenger, 1919: 260; Guibé, 1978: 42.

Material. — ZMA 6760 (1 ♂) 12.IX.71 at L 17.

Habitat. — The specimen was found on the bank of a clear brook, with stones on the bottom, in the forest.

Colour in life. — Back brown; venter dirty white, mottled with dark brown.

Voice. — In captivity, the male called during day and evening, often sitting in the water. The soft, low pitched, creaking call resembles the call of other species of the *M. ulcerosus* group.

Mantidactylus betsileanus (Boulenger, 1882)

Rana betsileana Boulenger, 1882: 460.

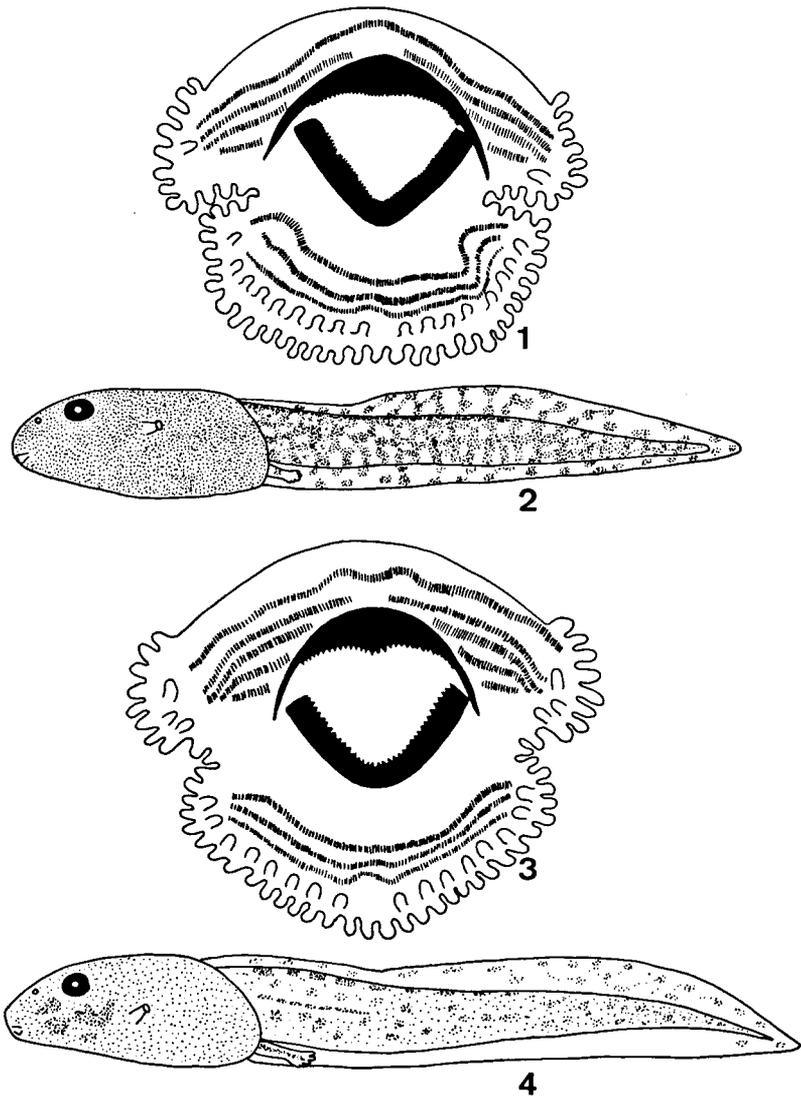
Mantidactylus betsileanus; Boulenger, 1895: 450; Arnoult & Razarihelisoa, 1967: 473 (tadpole); Guibé, 1978: 41.

Material. — ZMA 6891 (1) 17.IX.72; 6892 (2) 26.VIII.72; 6889 (1) 25.XII.70; 6885 (3) 22.VIII.71; 7024 (tadpoles) 6.I.73; 7022 (tadpoles, juveniles) 26.V.72; 7016 (tadpoles, juveniles) VIII.71; 7017 (tadpoles) 15.XI.72; 7018 (eggs and embryos) 26.XII.72; 7019 (tadpoles) VIII.72; 7025 (tadpoles and juveniles) 15.IX.72; 7026 (tadpoles) 14.III.72; 7027 (tadpoles) IX.72; 7028 (tadpoles) 22.X.71; 6873 (2) 2.IV.72; 6874 (1) 22.X.71; 6875 (1) 15.XI.72; 6876 (3) 6.XII.70 at L 11. — ZMA 6938 (2) 22.X.72; 6890 (1) 24.XII.72; 6887 (1) 12.XI.72; 6888 (juv.) 23.IX.72; 6886 (3) 4.IV.72; 6884 (2) 21.X.71; 6882 (1) 10.II.73; 7021 (tadpoles and juveniles) 14.XI.72; 6941 (1) 25.XII.70; 6940 (1) 23.IX.72; 6939 (1) 6.II.72; 7029 (tadpoles) 24.IX.72; 6880 (5) 6.XII.70; 6879 (2) 22.X.72; 6832 (1) 17.II.72; 6828 (6) 23.IX.72 all collected at L 10. — ZMA 6833 (10) 2.VII.71 at L 16. — ZMA 6883 (2) 25.IV.73; 6881 (4) 12.IX.71; 6831 (2) 30.III.72; 7023 (tadpoles) 12.IX.71 collected at L 17. — ZMA 6893 (2) 29.VIII.72; 7188 (tadpoles) 29.VIII.72; 7187 (tadpoles) 29.VIII.72; 6829 (6) 25.VIII.71 all at L 12. — ZMA 6830 (2) 1.II.73 at L 3. — ZMA 6942 (1) 30.VII.72; 7020 (tadpoles) 30.VII.72 at L 7.

Habitat. — Ordinary species in boggy places in open (degraded) forest, sometimes mixed with *M. biporus*. Tadpoles in shallow pools, often in company with those of *M. liber*. One egg mass was found fixed to a putrified leaf on the ground in sippy grassland.

Colour in life. — Back brownish, cream white middorsal line often present, flanks sometimes orange or beige; venter dirty white with or without blackish spots.

Voice. — The males were heard calling during day and evening at all our



Figs. 1—4. 1—2, *Mantidactylus ulcerosus*: 1, mouth of tadpole, ZMA 6993, x.25; 2, tadpole, ZMA 6993, x.3; 3—4, *M. betsileanus*: 3, mouth of tadpole, ZMA 7022, x.25; 4, tadpole, ZMA 7022, x.3.

visits. The call consists of a series of long, low pitched, pulsed notes, often preceded by one or more short clicks. The number of notes in one call group varies from 8 to 27. The duration of the call-group varies from 30 sec. to 2 min. 40 sec. The sonagram (fig. 34) made of a male (ZMA 6876) in October 1970 at 5 p.m. shows one note of 1.5 sec. The number of pulses in that note is 96. The duration of the notes varies from 1 to 2.2. sec. The duration of the short clicks is about 0.25 sec. The fundamental frequency is about 1000 Hz.

Eggs. — The egg mass (ZMA 7018) consisted of 35 darkly pigmented eggs of 2.5 mm in diameter. The embryonic development resembled that observed in other species (see below: *M. wittei* group); external gills did not develop. After a week, at room temperature and in a humid atmosphere, the hatchlings wriggled free and swam into the water. The hatchling measures about 8 mm, two suckers and mouth opening are present; the ratio of tail to body length is 1.8. Tadpoles from this batch in stage 25, some yolk still present, have body lengths of 4—4.5 mm and total lengths of 11—12.5 mm. The tooth formula is already complete: $1/4 + 4/3$.

Tadpoles. — The tadpoles of different localities are treated together, since we found no differences between them. Ten tadpoles in stage 25 have body lengths of 5—6.5 mm, and total lengths of 14—20.5 mm. The average ratio of tail to body length is 2.2. (range 2.0—2.4). Fifteen tadpoles in stages 26—30 have body lengths of 7—9 mm and total lengths of 22—31 mm. Twenty tadpoles in stages 31—43 have body lengths of 8.5—12 mm and total lengths of 30—40 mm. The average ratio of tail to body length in stages 26—42 is 2.3 (range 2.1—2.5). Seventeen metamorphosing young have body lengths of 10—13 mm (mean 12 mm). The mouth and lateral view of an entire tadpole in stage 36 (ZMA 7022) are shown in figs. 3, 4. Body depressed. Nostrils dorsal, aperture dorsolaterally, situated at equal distances of eye and tip of snout. Eyes situated dorsolaterally, spiracular opening sinistral, situated at equal distances of snout and end of body. Cloacal tube dextral to caudal fin. Caudal musculature strong. Caudal dorsal fin reduced anteriorly. At midlength of tail, height of caudal musculature represents half of total tail height. Mouth small and directed anteroventrally. Margin of oral disc indented laterally. Papillary border with wide dorsal gap. Two rows of papillae present. Tooth formula $1/2 + 2/3 - 1/4 + 4/3$. First row of lower lip often with slight median gap. Colour of tadpole brownish in life.

Metamorphosis was observed during the whole year. The entire development took two months in captivity, in the hot season.

This description agrees with the concise one given by Arnoult & Razarihelisoa (1967).

***Mantidactylus curtus* (Boulenger, 1882), fig. 63**

Rana curta Boulenger, 1882: 461.

Mantidactylus curtus; Boulenger, 1895: 450; Arnoult & Razarihelisoa, 1967: 477 (tadpole); Guibé, 1978: 42.

Material. — ZMA 6860 (8) 4.XI.72; 6863 (4) 19.IX.71; 6864 (9) 13.IV.72; 6865 (1) 4.XI.72; 6866 (4) 21.III.73; 6909 (1) 4.VI.72; 6911 (1) 7.XI.71; 6984 (tadpoles and juveniles) 13.IV-3.VI.72; 6985 (tadpoles) 13.IV-3.VI.72; 7072 (tadpoles) 4.XI.72; 7073 (tadpoles and juveniles) 21.III.73; 7074 (tadpoles and juveniles) 20.IX.71; 7075 (tadpoles) VIII.72; 7176 (1 young) 4.VI.72 at L 18. — ZMA 6861 (6) 17.VI.72; 6862 (4) 17.1.73, 7175 (tadpoles) 17.I.73 at L 13. — ZMA 6908 (2) 25.IV.73; 6910 (1) 12.IX.71; 6859 (2) 30.III.72 at L 17. — ZMA 7174 (1 juv.) 29.XI.70 at L 15.

Habitat. — Adults in and along streams, mainly in open areas, sometimes in the forest. They are often in company of *M. aerumnalis* and *M. alutus*, the latter only beneath altitudes of 1800 m, and by *Boophis boettgeri* (Boulenger, 1882), above 2000 m alt. The tadpoles are found in the lentic side pools (Salthe & Meham, 1974) of the same streams, also often together with tadpoles of the aforementioned species.

Colour in life. — Back light brown with dark brown markings; venter dirty white with or without brownish spots.

Voice. — The males were heard calling during day and evening at all dates, that we collected them. The call resembles the call of other species of the *M. ulcerosus* group. No records were made of this species, since in captivity it stopped calling immediately.

Eggs. — Dissected females, 3 mm in diameter, 60—80 per female.

Tadpoles. — Since the tadpoles in the different batches appeared to be similar, they are treated together. Fifty-three tadpoles in stage 25 have body lengths of 8—13 mm and total lengths of 23—38 mm. Six tadpoles in stages 26—30 have body lengths of 12—15 mm and total lengths of 34—44 mm. Sixteen tadpoles in stages 31—38 have body lengths of 15—20 mm and total lengths of 41—57 mm. The average ratio of tail length to body length is 1.9 (range 1.8—2) in stages 25—38. Eight metamorphosing young have body lengths of 17—19 mm. The mouth and lateral view of an entire tadpole in stage 34 (ZMA 6984) are shown in figs. 5, 6. Body depressed. Nostrils dorsal, aperture dorsolaterally, situated at equal distances of eye and tip of snout. Eyes situated dorsolaterally. Spiracular opening sinistral, situated at equal distances of snout and end of body. Cloacal tube dextral to caudal fin. Caudal musculature strong. Caudal dorsal fin somewhat reduced anteriorly. At midlength of tail, height of caudal musculature represents 2/5 of total tail height. Mouth small and directed anteroventrally. Margin of oral disc indented laterally. Papillary border with wide dorsal gap. Two rows of rather large papillae present, in median part of lower lip one. Tooth formula $1/4 + 4//3$, $1/3 + 3//3$, sometimes $1/2 + 2//3$. The first row of lower lip often with slight median gap. Colour in life brownish.

Metamorphosis was observed during the entire year.

Arnoult & Razarihelisoa (1967) described the tadpole of *M. curtus*. In my opinion, there is an error in their figure of the mouth, which shows a papillary border without a dorsal gap. A wide dorsal gap as found by me in

the tadpole of *M. curtus*, is a common feature of tadpoles in this group, as in almost all Ranidae.

Mantidactylus alutus (Peracca, 1893)

Rana aluta Peracca, 1893: 12.

Mantidactylus alutus; Boulenger, 1919: 258; Guibé, 1978: 38.

(Non: *Mantidactylus alutus*; Arnoult & Razarihelisoa, 1967: 484, figs. 10 and 11. (tadpole description = *Heterixalus betsileo* Grandidier, 1872).

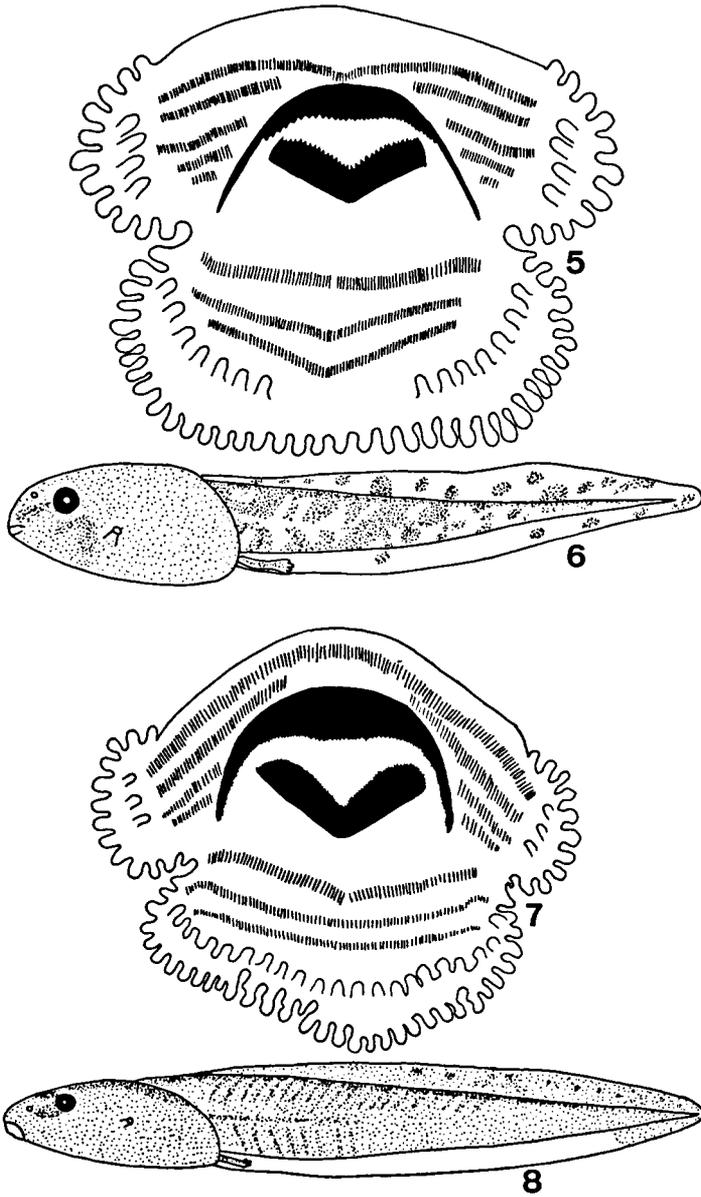
Material. — ZMA 6801 (2 juv.) 22.IX.71; 6902 (9 juv.) 4.X.71; 6905 (1) 4.XI.70; 6992 (tadpoles and juveniles) 4.X.71, at L 14. — ZMA 6903 (4) 17.I.73, at L 13. — ZMA 6904 (2) 19.IX.71, at L 18 at 1800 m alt.

Habitat. — At L 14 the frogs were collected in and along rice fields and pools, together with *Ptychadena mascareniensis* (Duméril & Bibron, 1842). The tadpoles in the nearby ditches and pools, in company with those of *P. mascareniences* and *Heterixalus betsileo* (Grandidier, 1872), a common tree frog in this area. At L 13 and L 18 the adults were found in small brooks in open land, together with *M. curtus*.

Colour in life. — Back red-brown with dark brown markings, beige middorsal line often present; venter dirty white with or without brownish spots.

Voice. — The males were heard calling during day and evening, all times of the year. The call consists of a series of low pitched, pulsed notes (5 to 14 in number). The duration of the call-group varies from 3 to 8 seconds. The sonagram (fig. 35) made of a male (ZMA 6904) in September 1971 at 9 p.m. shows that the duration of the notes varies from 0.35–0.42 sec. and the number of pulses in one note from 19–22. The latter consists of a number of harmonics, apparently of a fundamental frequency of 1000 Hz.

Tadpoles. — Eight tadpoles in stage 25 have body lengths of 7–11 mm, and total lengths of 21–34 mm. Three tadpoles in stages 26–29 have body lengths of 14–15 mm, and total lengths of 44–47 mm. Five tadpoles in stages 34–38 have body lengths of 13–18 mm, and total lengths of 42–56 mm. The average ratio of tail length to body length is 2.1 (range 2–2.3) in stages 25–38. Eight metamorphosing young have body lengths of 16–19 mm. The mouth and lateral view of an entire tadpole in stage 35 (ZMA 6992) are shown in figs. 7–8. Body depressed. Nostrils dorsal, aperture dorsolaterally, situated at equal distances of eye and tip of snout. Eyes situated dorsolaterally. Spiracular opening sinistral, situated at 3/5 from snout to end of body. Cloacal tube dextral to caudal fin. Caudal musculature strong. Caudal dorsal fin reduced anteriorly. At midlength of tail, height of caudal musculature represents 1/2 of total tail height. Mouth small and directed anteroventrally. Margin of oral disc indented laterally. Papillary border with wide dorsal gap. Two rows of rather large papillae present. Tooth formula $1/3 + 3/3$ or $1/2 + 2/3$. The first row of lower lip often with slight median gap. Colour in life brownish.



Figs. 5—8. 5—6, *Mantidactylus curtus*: 5, mouth of tadpole, ZMA 6984, x.25; 6, tadpole, ZMA 6984, x.1.5; 7—8, *M. alutus*: 7, mouth of tadpole, ZMA 6992, x.25; 8, tadpole, ZMA 6992, x.1.5.

We observed metamorphosis in January-April and September-November.

Arnoult & Razarihelisoa (1967) described a tadpole as belonging to *M. alutus*. This assignation is definitely incorrect, since the larvae considered by them belong to *H. betsileo*, as we could observe by rearing them. In fact, this tadpole resembles very much those described of African *Hyperolius* (See Wager, 1965).

Mantidactylus biporus (Boulenger, 1889)

Rana bipora Boulenger, 1889: 246.

Mantidactylus biporus; Boulenger, 1895: 450; Guibé, 1978: 35.

Material. — ZMA 6810 (6) 30.VII.72 at L 7. — ZMA 6811 (5) 31.XII.71 at L 1. — ZMA 6812 (3) 30.III.72; 6935 (1) 25.IV.73 at L 17. — ZMA 6813 (5 and 2 young) 2—4.VII.71 at L 16. — ZMA 6943 (1) 23.IX.72 at L 10, 1100 m alt. — ZMA 6936 (1) 13.X.71 at L 6.

Habitat. — A species of small, shallow, muddy pools or muddy, slowly flowing water in open land, adjacent to forest; gutter of the road, shallow water between *Raphia* palms, small pools along streams. The species was found in the company of *M. betsileanus* at all localities, except at L 6 where it was found in the company of *M. ulcerosus*.

Colour in life. — Back orange-brown with dark brown markings; venter dirty white; throat with greyish spots. Juveniles, light blue spots on the belly.

Voice. — In captivity, the males call during day and evening, mostly sitting in the water. The sound is a low pitched, softly creaking call resembling that of other species in the *M. ulcerosus* group.

Eggs. — In dissected females, 2.5 mm in diameter, 50—70 per female.

Mantidactylus pauliani Guibé, 1974

Mantidactylus pauliani Guibé, 1974: 1171; Guibé, 1978: 19.

Material. — MNHP 1972—1508, the holotype of *M. pauliani* from Nosiarivo (Ankaratra Mts.). ZMA 6803 (5) 21.III.73 at L 18 at 2200 m alt., under boulders in rapids.

Colour in life. — Back orange brown with small dark brown spots; venter dirty white.

Nothing is known about voice and tadpoles of this species.

The *Mantidactylus lugubris* group

Definition. — Omosternum broadly forked posteriorly: greatest distance between lateral arms is four to five times the width of one arm. Sternum entire. Bony style of sternum distinctly shorter than style of omosternum (fig. 45). Femoral glands large and round, elevated and coarsely granular — with a central notch in males (fig. 53); flat in females, less than

half the size of those in males. Vocal sac not apparent externally. Lateral metatarsalia entirely separated by web. Outer metatarsal tubercle present or lacking. Tibiotarsal articulation not reaching beyond tip of snout. Fingers without web. Discs of fingers at least twice the diameter of the adjacent phalanx. Moderately sized frogs (40—65 mm). Contents: *M. lugubris* (Duméril, 1853) and *M. femoralis* (Boulenger, 1882).

Tadpoles: Mouth small; margin of oral disc round. Papillary border complete. Few small teeth in lower lip. Horny beak poorly developed, reduced to a few heavy serrations. Caudal musculature strong. Caudal dorsal fin reduced anteriorly.

Eggs: 2.5—3 mm in diameter, 40—70.

Chromosomes: $2n = 26$; N.F. = 50 (*M. lugubris*, *M. femoralis*). Nuclear DNA amount 9.3—10.5 pg in the same two species.

Habits and habitat: Frogs live in dense vegetation near running water, and on stones in the water. The tadpoles are found in the lentic side pools (Salthe & Mecham, 1974) of the same streams.

Mantidactylus lugubris (Duméril, 1853)

Polypedates lugubris Duméril, 1853: 157.

Mantidactylus lugubris; 1895: 450; Guibé, 1948: 236 (equals *cowani*); Guibé, 1978: 21.

Material. — ZMA 6771 (1) 22.IV.72; 6747 (1) 24.XII.72; 6748 (2) 14.XI.72 at L 10. — ZMA 6728 (1) 12.I.73 at L 16. — ZMA 6729 (2 young) 17. — 24.IX.72 at L 11.

Habitat. — This species was always found on the banks of larger flowing currents, or on boulders in rapids, often mixed with *M. femoralis*.

Colour in life. — Back dark brown with black markings, yellow inguinal spots, venter dirty white with blackish spots. Juveniles: belly with blue spots; cross-bands on dorsal surface of limbs green with blue; discs turquoise; no yellow inguinal spots; back also blackish.

Eggs. — Diameter 3 mm (Boulenger, 1919).

Mantidactylus femoralis (Boulenger, 1882) fig. 64

Rana femoralis Boulenger, 1882: 463.

Mantidactylus femoralis; Guibé, 1948: 235; Guibé, 1978: 26.

Material. — ZMA 6906 (1) 24.IX.72; 6907 (2) 26.VIII.72; 6794 (1) 18.II.73; 6793 (2) 27.III.73; 6792 (1) 6.I.73; 6788 (2) 15.XI.72; 6990 (tadpoles and froglets reared from them) IV-VIII.72, at L 11. — ZMA 6795 (2) 3.IV.72; 6791 (1) 22.X.72 at L 10. — ZMA 6789 (1) 13.X.71 at L 6. — ZMA 6790 (1) 30.III.72 at L 17.

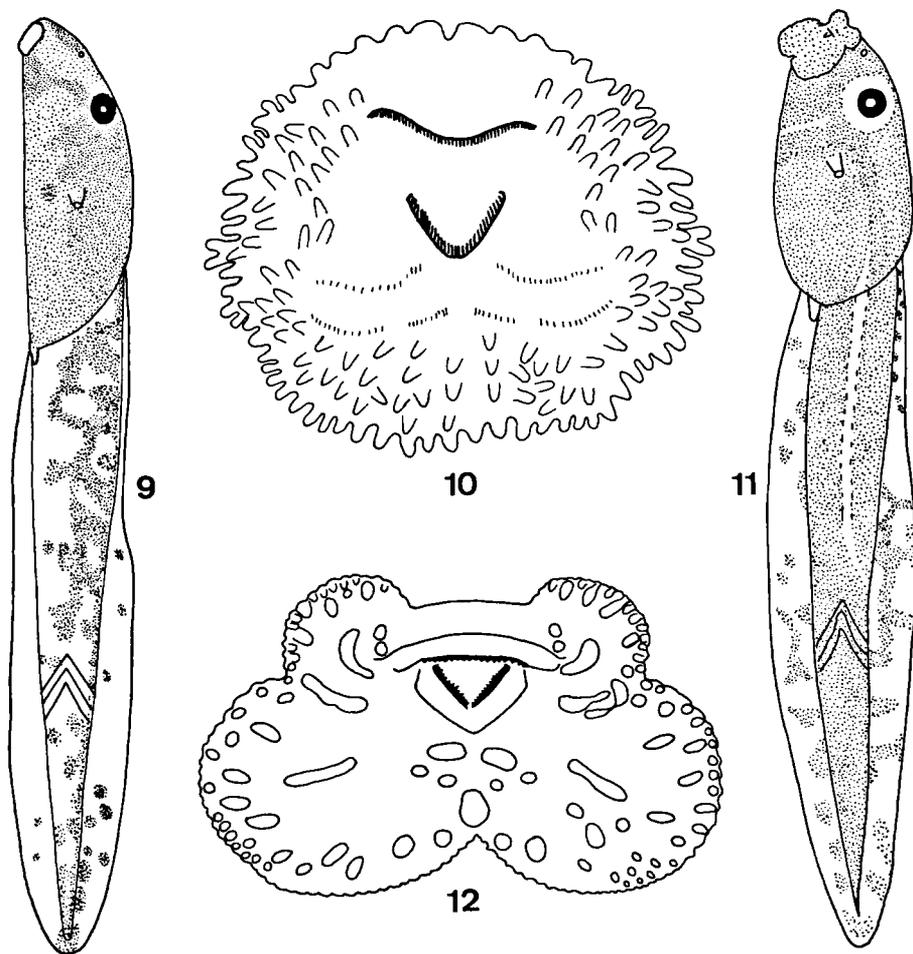
Habitat. — The adults were always found on the bottom or in shrubs, along clear forest brooks with stony bottom. The tadpoles are found in the lentic side pools of the stream.

Colour in life. — Back dark brown with black markings, yellow inguinal spots; venter dirty white with blackish spots.

Voice. — The call — a soft clattering sound — was heard in April and May in the vivarium, and in August at L 11, during day and evening.

Eggs. — In dissected females, 2.5 mm in diameter.

Tadpoles. — Twenty-eight tadpoles in stage 25 have body lengths of 8—12 mm and total lengths of 23—35 mm. The average ratio of tail length to body length is 1.9 (range 1.8—2.0). Seventeen tadpoles in stages 26—30 have



Figs. 9—12. 9—10, *Mantidactylus femoralis*: 9, tadpole, ZMA 6990, x.3; 10, mouth of tadpole, ZMA 6990, x.25; 11—12, *M. aerumnalis*: 11, tadpole, ZMA 7078, x.3; 12, mouth of tadpole, ZMA 7078, x.12.5.

body lengths of 11—14 mm and total lengths of 33—41 mm. One tadpole in stage 36 has a body length of 12 and a total length of 36 mm. The average ratio of tail to body length is 2 (range 1.9—2.1) in stages 26—36. Seven metamorphosing young have body lengths of 14—16 mm. The mouth and lateral view of an entire tadpole in stage 28 (ZMA 6990) are shown in figs. 9, 10. Body depressed. Nostrils dorsal, aperture dorsolaterally, situated at equal distances of tip of snout and eye. Eyes situated dorsolaterally. Spiracular opening sinistral, situated about halfway from snout to end of body. Cloacal tube dextral to caudal fin. Caudal musculature strong, caudal dorsal fin reduced anteriorly. At midlength of tail, height of caudal musculature represents half of total tail height. Mouth small and directed anteroventrally. Margin of oral disc round, not indented. Papillary border complete, 3 to 4 rows of small papillae present, in median part of upper lip only one row of large papillae. There are a few teeth in the lower lip of some specimens. The horny beak is also poorly developed and is armed with heavy teeth. Colour in life brownish with black spots.

The tadpoles were collected during the cool season from April to September, in which period no metamorphosis was observed. The young frogs emerged in October and November, in captivity as well as in the field. The tadpoles of this species are rather difficult to rear. Their gut contained mud.

The *Mantidactylus albofrenatus* group

Definition. — Omosternum broadly forked posteriorly: greatest distance between lateral arms is four to five times the width of one arm. Sternum entire. Bony style of sternum a little shorter than style of omosternum, or equal in length (fig. 44). Femoral glands large, round to oval, elevated, coarsely granular, with a central notch in males (fig. 53); small (less than half the size of those in males) and flat in females. Vocal sac not apparent externally. Lateral metatarsalia separated only by a groove. Outer metatarsal tubercle present or absent. Tibiotarsal articulation reaching beyond tip of snout or not. Fingers without web. Discs of fingers less than twice the diameter of the adjacent phalanx. Two dorsolateral glandular ridges, from behind eyes (not connected with tympanic fold) till end of back. Small frogs (25—40 mm). Contents: *M. albofrenatus* (Müller, 1892), *M. opiparis* (Peracca, 1893), *M. aerumnalis* (Peracca, 1893).

Tadpoles: Mouth large; margin of oral disc indented laterally, and, in median part of lower lip. Papillary border with small dorsal gap. No teeth. Horny beak reduced. Enlarged flaps around mouth opening, covered abundantly with papillae of different size. Caudal musculature strong. Caudal dorsal fin reduced anteriorly.

Eggs: 2.5—4.0 mm in diameter, 30—50.

Chromosomes: $2n = 26$; N.F. = 48—52 (*M. opiparis*, *M. aerumnalis*). Nuclear DNA amount 8.5—9.6 pg in the same two species.

Habits and habitat: Frogs active during day and evening. Living on the banks of rivulets and brooks, most frequently in dense vegetation. The tadpoles are surface feeders, found in gently running waters, often in more quiet places in the curves of brooks. They stick to the surface with the support of the tail in dense aquatic vegetation or matted dead material. Eggs are deposited outside the water in one mass.

Mantidactylus albofrenatus (Müller, 1892)

Rana albofrenata Müller, 1892: 197, pl. 3 fig. 1.

Mantidactylus albofrenatus; Boulenger, 1895: 450; Mocquard, 1902: 18 (equals *melanopleura*); Guibé, 1978: 31 (equals *opiparis*, *melanopleura*, *frenatus*; in part).

Material. — NMB 792 the ♀ holotype of *Rana albofrenata*, Madagascar. Coll. Müller. ZMA 7000 (2) 12.II.72; 7001 (8) 13.X.71; 7043 (eggs deposited by 7001 in captivity) V.72; 7044 (tadpoles) 13.X.71; 7045 (3) 23.VII—2.VIII.72, at L 6.

Habitat. — This species was found along a brook in forest during the day; the males were calling in dense vegetation. The tadpoles were found in the same brook.

Colour in life. — Back between dorsolateral ridges beige, with small red-brown spots along the ridges; flanks blackish; throat black, belly greyish with white spots.

Note. — As far as I am aware there are no synonyms for this species. For a more detailed account concerning the names that have been attributed to it see the taxonomic discussion under *M. opiparis*.

Eggs. — Diameter 2.5 mm, deposited outside the water, on the bottom of the vivarium.

Voice. — Held in the vivarium from October till June, the males were calling during the day and evening, sitting in the vegetation, often 1/2 m above the ground. The call consists of a series of low-pitched, pulsed notes (4—11), the duration of the call group varies from 1.8—5 sec. The sonagram (fig. 36) made of a male (ZMA 7001) in March 1972 at 8 p.m. shows that the duration of the notes varies from 0.19—0.21 sec. The number of pulses in one note is about 23. It consists of a series of harmonics, the fundamental frequency is about 1500 Hz. Sometimes the call starts with a few very short notes (0.02—0.07 sec.).

Tadpoles. — As the tadpoles have not been reared, only circumstantial evidence of their identity can be provided: their presence in the locality where adults were abundant and the only species present was *M. albofrenatus*. One specimen, stage 32, has a body length of 7.5 and total length of 23.5 mm, the other one in stage 34 measures 8.5 and 28.5 mm respectively. They are not different from the larvae described for *M. opiparis* and *M. aerumnalis* (see below).

Mantidactylus opiparis (Peracca, 1893), bona species

Rana opiparis Peracca, 1893: 9.

Mantidactylus opiparis; Boulenger, 1895: 450; Guibé, 1978: 32 (in synonymy of *albofrenatus*).

Rhacophorus melanopleura Mocquard, 1901: 253 (new synonymy); Mocquard, 1902: 18 (in synonymy of *albofrenatus*); Guibé, 1978: 32 (in synonymy of *albofrenatus*).

Mantidactylus frenatus Boettger, 1913: 274, pl. 23 fig. 2 (new synonymy); Guibé, 1978: 32 (in synonymy of *albofrenatus*).

Material. — MNHP 01—226, the holotype of *Rhacophorus melanopleura*, Fort-Dauphin. Coll. Alluaud. SMF 6734, the holotype of *Mantidactylus frenatus*, Moramanga. Coll. Voeltzkow. The 3 syntypes of *Rana opiparis* are unfortunately lost (Guibé pers. comm.), type locality: Andrangoloaka (near Moramanga) 48.02 E 19.06 S. Coll. Peracca. ZMA 6999 (1) 4.IV.72; 7030 (1) 17.II.72; 7036 (3) 22.X.72; 7033 (tadpoles and young reared from them) 24.IX.72; 7186 (tadpoles) 22.X.72, at L 10. — ZMA 7031 (tadpoles and young reared from them) 12.XII.71; 7032 (tadpoles and young reared from them) 15.XI.72; 7034 (tadpoles) 1.IV—26.V.72; 7035 (2) 12.XII.71; 6696 (2) 22.X.71 at L 11. — ZMA 6997 (2) 12.IX.71 at L 17. — ZMA 6998 (8) 3.VII.71 at L 16.

Habitat. — The frogs were collected in or near forest; they jump very well. The tadpoles were collected in quiet corners of rills, among debris.

Colour in life. — Back beige and sometimes red with dark brown diamond-shaped markings between the dorsolateral ridges; flanks blackish; belly greyish or blackish with white spots; throat black with a median white line.

Taxonomy. — Contrary to previous authors, I believe that the differences between the holotype of *M. albofrenatus* (Müller) and the accurate original description by Peracca of *M. opiparis* are real, because they appear to be consistent in our collection.

The ratio hind limb to body length is 1.57 in the holotype of *M. albofrenatus*, and 1.84—2.00 in the syntypes of *M. opiparis* (according to Peracca). Both the holotype of *M. melanopleura* and of *M. frenatus* agree in this respect with *M. opiparis*. In addition to these dimensions, the original description of *M. opiparis* mentions the diamond shaped figures on the middle of the back and the median white line on the throat, which are present also in the holotypes of *M. melanopleura* and *M. frenatus*, but absent in that of *M. albofrenatus*. In our collection, none of the specimens with short legs (ratio 1.45—1.60, measured in 10 specimens) shows the typical colour pattern of *M. opiparis*, which, however, is present in all specimens with long legs. This means that in *M. opiparis*, of which *M. melanopleura* and *M. frenatus* are synonyms, the adpressed hind limbs reach just beyond the tip of the snout, while the adpressed heels overlap strongly. In *M. albofrenatus* the adpressed hindlimb reaches only just beyond the eye, and the heels overlap slightly. Other differences between these two species are: The smaller size of *M. albofrenatus* (the maximum body length measured in an adult female of this species is 29 mm, compared with 40 mm in *M. opiparis*) and the third toe

is longer than the fifth in *M. albofrenatus*, while the contrary is true for *M. opiparis*.

Note: Peracca describes *M. opiparis* as having the nostrils slightly nearer to the eye than to the tip of the snout. This probably has been a slip of the pen, because the contrary is true in the aforementioned and related species.

Tadpoles. — Twenty-five tadpoles in stage 25 have body lengths of 6—9 mm and total lengths of 20.5—31.0 mm. Four tadpoles in stage 27 have body lengths of 9—10 mm and total lengths of 31—36 mm. The average ratio of tail to body length is 2.4 (range 2.2.—2.6) in stages 25—27. Seven tadpoles in stages 32—37 have body lengths of 9—12 mm and total lengths of 33—42 mm. The average ratio of tail to body length is 2.5 (range 2.4—2.7). Seven metamorphosing young have body lengths of 11—14 mm. Figs. 13, 14 show the mouth and the lateral view of an entire tadpole in stage 28 (ZMA 7031). Body depressed. Nostrils dorsolateral, aperture laterally, situated at equal distances of eye and tip of snout. Eyes situated laterally. Spiracular opening sinistral, situated at equal distances of snout and end of body. Cloacal tube dextral to caudal fin. Caudal musculature strong. Caudal dorsal fin reduced anteriorly. At midlength of tail, height of caudal musculature represents 1/2 of total tail height. Mouth large and terminal. Margin of oral disc indented laterally and in median part lower lip. Horny beak consisting of small serrations, no teeth. Papillary border with small dorsal gap. Around mouth-opening enlarged flaps, which are amply provided with papillae of different size. Colour in life brownish. The back colour and dorsal markings of the adult frog become visible already in the fully grown tadpole.

Mantidactylus aerumnalis (Peracca, 1893), fig. 65

Rana aerumnalis Peracca, 1893: 10.

Mantidactylus aerumnalis; Boulenger, 1895: 450; Guibé, 1978: 44 (equals *delormei*).

Material. — ZMA 6777 (1♂, 1♀) 19.IX.71; 6778 (1) 20.VIII.72; 6779 (1) 14.VIII.71; 6780 (1) 21.III.73; 6781 (5 young) 7.XII.71; 6782 (2) 4.XI.72; 6991 (tadpoles and young reared from them) 19.IX.71; 7078 (tadpoles) 13.IV—3.VI.72; 7079 (eggs deposited of 6777) 20.IX.71; 7080 (tadpoles) 4.XI.72; 7081 (tadpoles) VIII.72, at L 18. — ZMA 7184 A (tadpole) 17.VI.72; 7184 B (tadpoles) 17.I.73 at L 13.

Habitat. — The frogs along brooks, in forest as well as in more open areas under shrubs near forest (in August resting under tree trunks); the tadpoles in the more quiet parts of the same streams.

Colour in life. — Back brown or green with dark-brown markings, cream white middorsal line often present; venter dirty white, throat and chin often dark brown spotted with a white median line.

Eggs. — The eggmass (ZMA 7079) was deposited on land and contained 30 fertilized eggs, 3.5—4.0 mm in diameter and 8—9 mm including the capsule. Unfortunately, the embryos died after 10 days, because of extreme

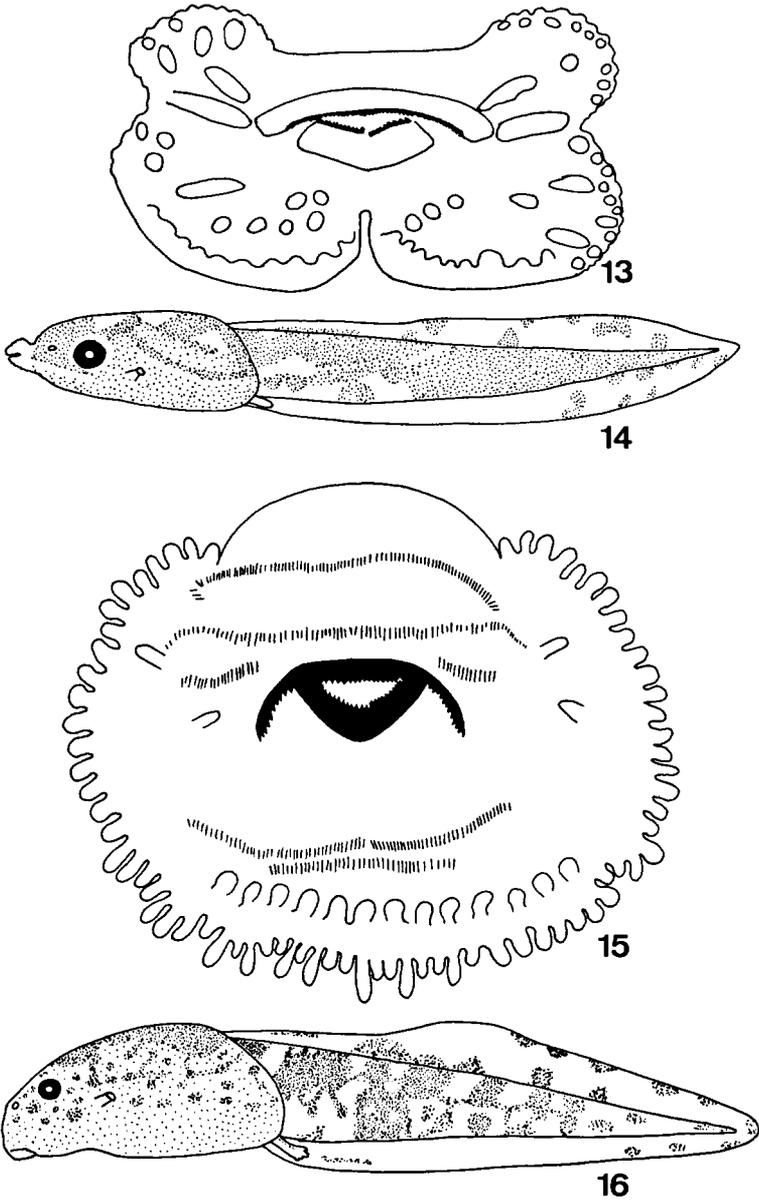
temperatures. At that time the embryos without external gills, were moving inside the mass.

Voice. — The males were heard alongside small streams, during day and evening. The call consists of a series of high-pitched, melodious notes (17—25), the duration of the call-group varies between 6—10 seconds. The sonagram (fig. 37) made of a male (ZMA 6777) at 10 p.m. October 1971 shows that the duration of the notes is about 0.08 sec. The dominant frequency is 1200 Hz.

Tadpoles. — Thirty tadpoles in stage 25 have body lengths of 5—10 mm and total lengths of 20—36 mm. Thirteen tadpoles in stages 26—30 have body lengths of 9—13 mm and total lengths of 35—50 mm. The average ratio of tail to body length is 2.7 (range 2.5—2.9) in stages 25—30. Nine tadpoles in stages 36—41 have body lengths of 13—16 mm and total lengths of 46—58 mm. The average ratio of tail to body length is 2.6 (range 2.5—2.7). Eight metamorphosing young have body lengths of 17—20 mm. The mouth and lateral view of an entire tadpole in stage 28 (ZMA 7078) is shown in figs. 11, 12. Body depressed. Nostrils dorsolateral, aperture situated laterally at equal distances of eye and tip of snout. Eyes situated laterally. Spiracular opening sinistral, situated at equal distances of snout and end of body. Cloacal tube dextral to caudal fin. Caudal musculature strong. Caudal dorsal fin reduced anteriorly. At midlength of tail, height of caudal musculature represents $\frac{2}{3}$ of total tail height. Mouth large and terminal. Margin of oral disc indented laterally and in median part lower lip. Horny beak reduced to small serrations. No teeth. Papillary border with small dorsal gap. The mouth has enlarged flaps and is richly provided with papillae of different size. Colour in life brownish.

In the late metamorphotic stages already the back shows the colour and patterns of the adult. The tadpoles feed on small particles on the surface of the water, which are collected with the extended flaps of the mouth. The tadpole keeps itself afloat by supporting itself on plants, mainly by means of its tail.

Note. — Razarihelisoa (1974b) describes the ecology and larval development of *M. brevipalmatus* Ahl, 1929. Since her collecting sites were partly the same as ours (Manjakatampo, Angavokely, Mandraka) her study concerns most probably a mixture of *M. aerumnalis* and *M. opiparis*, according to my identification. Both our descriptions are in good agreement. However, I do not know whether *M. brevipalmatus* is a valid species. According to the original description (type locality: N. W. Madagascar) it differs from *M. aerumnalis* only in the larger size of the discs. Because I have not found specimens with larger discs, I have preferred to use the name of the first described species, *aerumnalis*, the type locality of which is in the same area where we have collected.



Figs. 13—16. 13—14, *Mantidactylus opiparis*: 13, mouth of tadpole, ZMA 7031, x.25; 14, tadpole ZMA 7031, x.3; 15—16, *M. aglavei*: 15, mouth of tadpole, ZMA 6994, x.25; 16 tadpole, ZMA 6994, x.1.5.

The *Mantidactylus aglavei* group

Definition. — Omosternum broadly forked posteriorly: greatest distance between lateral arms is four times the width of one arm. Sternum entire. Bony style of sternum and omosternum equal in length (fig. 46). Femoral glands only present in males, large, oval, elevated, coarsely granular (fig. 54). Median subgular sac indicated by faint lateral foldings of the skin on the throat. Lateral metatarsalia entirely separated by web. No outer metatarsal tubercle. Tibiotarsal articulation not reaching beyond tip of snout. Fingers with rudiment of web. Discs of fingers very large, triangular. Denticulated cutaneous fold borders anterior limb from elbow to outer finger and posterior limb from heel to outer toe. Four distinct cutaneous denticulations in a transverse line at the posterior end of body, just below vent. Moderately sized frog (45—50 mm). Contents: *M. aglavei* (Methuen & Hewitt, 1913).

Tadpoles: Mouth small. Margin of oral disc round. Papillary border with small dorsal gap. Tooth formula $2/1 + 1/2$. Horny beak well developed. Caudal dorsal fin reduced anteriorly.

Chromosomes: $2n = 24$; N.F. = 48 in *M. aglavei*.

Habits and habitat: Treefrogs living in forest. Tadpoles in running waters, with dense aquatic vegetation and sandy bottom; feeding off the bottom.

Mantidactylus aglavei (Methuen & Hewitt, 1913) comb. nov., fig. 57

Rhacophorus aglavei Methuen & Hewitt, 1913: 54, pl. IX; Guibé, 1978: 62 (equals *sikorae*).

Rhacophorus sikorae Boettger, 1913: 276, pl. 23, fig. 4.

Boophis aglavei; Guibé, 1947: 439 (equals *sikorae*).

Material. — SMF 6815 the lectotype of *Rhacophorus sikorae*, Moramanga. Coll. Sikora (designed by Mertens, 1967). The holotype of *Rhacophorus aglavei*, [type locality: Analamazaotra (= Perinet)] has not been studied. ZMA 6871 (2♂) 18.II.73 at L 11. ZMA 6994 (tadpoles and young reared) 24.IX.72 at L 10, alt. 1100 m.

Habitat. — The males were found calling in a tree in the evening; the tadpoles in a shallow brook with muddy bottom and waterplants in open land near forest.

Colour in life. — Back light green with light and dark brown. The frog is coloured dazzling and hard to discover in a tree. Venter white.

Taxonomy. — The males agree with the original description and first figure of *R. aglavei*, and with the lectotype of *R. sikorae*. The presence of femoral glands and a widely bifurcated style of the omosternum places this species in the genus *Mantidactylus*.

Voice. — The voice of this species is very melodious, like the ringing of bells. The two males collected did not call in the vivarium.

Tadpoles. — Eleven tadpoles in stage 25 have body lengths of 10—15

mm and total lengths of 30—45 mm. The average ratio of tail to body length is 1.9 (range 1.8—2). Eight tadpoles in stages 30—41 have body lengths of 16—20 mm and total lengths of 47—60 mm. The average ratio of tail to body length is 2 (range 1.9—2.2). Six metamorphosing young have body lengths of 19—20 mm. One young grown during 4 months (after metamorphosis) in captivity measures 28 mm snout to vent. Figs. 15, 16 feature the mouth and lateral view of an entire tadpole in stage 35 (ZMA 6994). Nostrils dorsolateral, aperture lateral, situated nearer to eye than to tip of snout. Body is ovoid. Eyes situated dorsolaterally. Spiracular opening sinistral; situated at 2/5 from snout to end of body. Cloacal tube dextral to caudal fin. Caudal musculature strong. Caudal dorsal fin reduced anteriorly. At midlength of tail, height of caudal musculature accounts for 2/5 of total tail height. Mouth small and directed downwards. Margin of oral disc round, not indented. Papillary border with small dorsal gap. One row of rather large papillae present, in median part of lower lip two. Tooth formula $2/1 + 1/2$ or $2//2$. First row of teeth on lower lip often with a slight median gap. Colour in life brownish; a dirty white streak, in the middle of back from tip of snout and ending just before eyes, is present in all stages. Colour of the back changes to green with brown during metamorphosis. The emerging froglet resembles closely the adult in colour and shape.

Metamorphosis was observed, in the vivarium, in October and November. The tadpoles dwell above the bottom in dense aquatic vegetation in streams, holding themselves by bending the tail. It was rather difficult to rear them in captivity. Their guts contained mud and sand.

The *Mantidactylus asper* group

Definition. — Omosternum broadly forked posteriorly: greatest distance between lateral arms is four to five times the width of one arm. Sternum entire. Bony style of sternum somewhat shorter than, or equal to, omosternal style (fig. 47). Femoral glands present only in males; large, oval, elevated, coarsely granular (fig. 54). Paired lateral subgular vocal sacs, coloured black. Lateral metatarsalia entirely separated by web. Outer metatarsal tubercle present or absent. Tibiotarsal articulation reaching beyond tip of snout. Fingers without web. Discs of fingers at least twice the diameter of the adjacent phalanx. A triangular dermal appendage on heel. Moderately sized frogs (30—45 mm). Contents: *M. asper* (Boulenger, 1882), *M. luteus* Methuen & Hewitt, 1913.

Eggs: 3 mm in diameter.

Chromosomes: $2n = 26$; N.F. = 44—48; in *M. asper* and *M. luteus*. Nuclear DNA amount 8.3 pg in *M. asper*.

Habits and habitat: Frogs live in well-developed forest and dense shrubwood. They climb like tree frogs, but are also found on the ground. The breeding sites are always above the ground. *M. asper* appeared most active at dusk and in the early morning. The eggs are deposited singly or in pairs.

Mantidactylus asper (Boulenger, 1882)

Rana aspera Boulenger, 1882: 465.

Mantidactylus asper; Boulenger, 1895: 450; Guibé, 1978: 25, pl. 10 figs. 31 and 33 (equals *ceratophrys*).

Material. — ZMA 6867 (3) 13.XI.72; 6896 (1) 22.X.72; 6897 (1) 22.X.72; 7077 (deposited eggs of ZMA 6867) 13.XI.72, at L 10 at 1100 m altitude. — ZMA 6868 (3) 12.XII.71; 6894 (1) 6.XII.70; 6895 (11 young and 1 adult) 22.X.71; 7076 (eggs deposited by ZMA 6895) XI.71, at L 11.

Habitat. — This species was always encountered in dark woods, jumping over the ground, or, when calling, in trees and shrubs.

Colour in life. — Colour of back variable; light-brown with light green or with cream-white; red-brown with cream-white; belly white, throat and chin spotted with dark brown, with a median white line; vocal sacs black.

Voice. — Groups of calling males were tens of metres removed from water. They call from shrub and tree, sitting mostly about 1 m above the ground, at dusk and in the early morning in November and December. The call consists of a series of high-pitched, melodious thrills (4—10). The duration of the call group varies between 3 and 10 sec. The sonagram (fig. 38) made of a male (ZMA 6868) at 5 p.m. in December 1972, shows that the call group consists of monophasic, diphasic and triphasic notes. The duration of the notes varies from 0.18 (monophasic) to 0.45 (triphasic) sec.

Development. — On 26.XII.72, one egg was found attached to a dead branch in a brush at about 1 m above the ground at L 11, at the site where calling males were caught. Brought home and kept in a moist atmosphere, its development could be witnessed. After 14 days, we observed an embryo with black eyes, a narrow body with four stumps of extremities, a tail and still a rest of yolk. The embryo was seen turning around in the egg capsule. Unfortunately, we had to leave for a few days and, at our return, found the egg perished. Nevertheless, little doubt remains about a direct development in *M. asper*. The eggs deposited in captivity (ZMA 7076 and 7077) were attached singly or in pairs on grass blades, also outside the water. These eggs, 3 mm in diameter without the capsule and yellow with grey coloured, did not develop.

It seems that the reproductive season is limited to a few months. Although we searched the localities all the year round, this species was captured only from the end of October (start of the wet season in these places) till the beginning of January, which coincides with the period the males call. That the reproductive period is restricted to the wettest months of the year is probably correlated with the mode of reproduction; the egg needs a permanently damp atmosphere and the tiny froglet a choice of small prey, conditions only met in the rainy midsummer.

Mantidactylus luteus Methuen & Hewitt, 1913, fig. 67

Mantidactylus luteus Methuen & Hewitt, 1913: 51.

Material. — ZMA 6725 (1 ♂ and 1 juvenile) 13.X.71 at L 6.

Habitat. — The specimens were found on the forest bottom; in the vivarium they also climbed.

Colour in life. — Back yellowish with dark brown markings; venter dirty white; vocal sacs black.

The *Mantidactylus boulengeri* group

Definition. — Omosternum moderately forked posteriorly; greatest distance between lateral arms one and a half to two times the width of one arm. Sternum slightly forked anteriorly. Bony style of sternum somewhat shorter than, or equal to the style of the omosternum (fig. 48). Femoral glands present only in males: a swollen, oval part within a larger granular area (fig. 55). Lateral subgular vocal sacs, coloured black. Lateral metatarsalia half to entirely connected. Outer metatarsal tubercle present or wanting. Tibiotarsal articulation reaching beyond tip of snout, or not. Fingers free of web. Discs of fingers at least twice the diameter of the adjacent phalanx. Small sized frogs (25—40 mm). Contents: *M. boulengeri* (Methuen, 1919), *M. acuticeps* Ahl, 1929, *M. eiselti* (Guibé, 1975).

Eggs: 2.75 mm in diameter in *M. boulengeri*.

Tadpoles: unknown.

Chromosomes: $2n = 26$; N.F. = 52 in *M. acuticeps*. Acrocentric chromosomes were observed in *M. eiselti* (Blommers-Schlösser, unpublished).

Habits and habitat: Frogs of dense vegetation, especially the undergrowth of the wood. The males do not join in choruses when calling. They are widely dispersed over the forest, often tens of metres away from water and one per thicket. This behaviour might be an indication of a direct development of the egg (and parental care?). These species are particularly vulnerable, dying almost instantaneously when placed in the sun.

Mantidactylus boulengeri (Methuen, 1919) comb. nov.

Gephyromantis boulengeri Methuen, 1919: 351; Guibé, 1978: 53, pl. 28 figs. 108—113. (equals *verrucosus*).

Rhacophorus gephyromantis Ahl, 1929: 480 (substitute name).

Material. — ZMA 6967 A (1 ♀) 6.II.72 at L 10, alt. 900 m.

Habitat. — The frog was found on the forest floor.

Colour in life. — Back brown; belly dirty white, chin and throat brown with white spots and white median line.

Note. — Our female agrees with the accurate original description of *G. boulengeri* (also a female). Methuen (1919) reports that the eggs in the holotype are 2.75 mm.

Mantidactylus acuticeps Ahl, 1929

Mantidactylus acuticeps Ahl, 1929: 471.

Material. — ZMA 7142 (1♂) 13.X.72 at L 10, alt. 900 m.

Habitat. — The male was caught, calling in dense thicket in forest, far away from water, in the evening. The same calls were heard in the same wood, always at distances of 10 m or more apart, and never near the water.

Colour in life. — Back dark brown; belly dirty white, chin and throat brown with white spots and white median line; vocal sacs blackish.

Mantidactylus eiselti (Guibé, 1975) comb. nov.

Gephyromantis eiselti Guibé, 1975b: 1083, fig. 2.

Material. — MNHP 1975—2, the ♂ holotype and MNHP 1975—3 and 4, two paratypes of *Gephyromantis eiselti*, Perinet, Coll. Blommers 1971. ZMA 6967 three male topotypes 19.II.72.

Habitat. — The species was captured, while calling in brushwood in hillside forest, far away from water, during the day. While calling the males were sitting on small branches just above the ground. There, and in a few other places around Perinet, we have heard the same calls, one at a place, always meters apart, far away from open water, and only during the rainy season.

Colour in life. — Back brown, a broad dark brown band along the canthus and beneath the tympanic fold, upper and lower lip yellow; belly dirty white, chin and throat brown with white spots and white median line; vocal sacs blackish.

Remark. — Examination of the type material revealed that the paratypes of *G. eiselti* are not identical with the holotype. I identified them as *Mantidactylus blommersae*.

The *Mantidactylus wittei* group

Definition. — Omosternum broadly forked posteriorly; greatest distance between lateral arms five times the width of one arm. Sternum slightly forked anteriorly. (In *M. wittei* sternum entire or slightly forked). Bony style of omosternum distinctly longer than style of sternum (fig. 49). Femoral glands present only in males; an oval, swollen part in the middle of a larger granular area (fig. 55). Vocal sac not apparent externally. Lateral metatarsalia connected or separated. Outer metatarsal tubercle present. Tibiotarsal articulation not reaching beyond tip of snout. Fingers free of web. Discs of fingers about twice the diameter of the adjacent phalanx. Testicle black on the outside. Small sized frogs (20—30 mm). Contents: *M. wittei* Guibé, 1974, *M. blommersae* (Guibé, 1975), *M. domerguei* (Guibé, 1974).

Tadpoles: Mouth small; margin of oral disc indented laterally and somewhat in median part lower lip. Papillary border with wide dorsal gap. Tooth formula $1/4 + 4/3 - 1/5 + 5/3$. Horny beak well developed. Caudal musculature moderately developed.

Eggs: 1.2—1.7 mm in diameter, 40—100.

Chromosomes: $2n = 26$; N.F. = 52 in *M. wittei* and *M. blommersae*. Nuclear DNA amount 10.7—12.9 pg in the same two species.

Habits and habitat: Ground-dwelling frogs of forest and forest-edge, never found in water. They jump very well and mount in the lower vegetation. Egg-mass is fixed to a leaf or a similar support, at less than one metre above the water surface. Tadpoles are found in temporary pools with abundant aquatic vegetation and exposed to the sun.

***Mantidactylus wittei* Guibé, 1974, fig. 68**

Mantidactylus wittei Guibé, 1974b: 1169, fig. 1A.

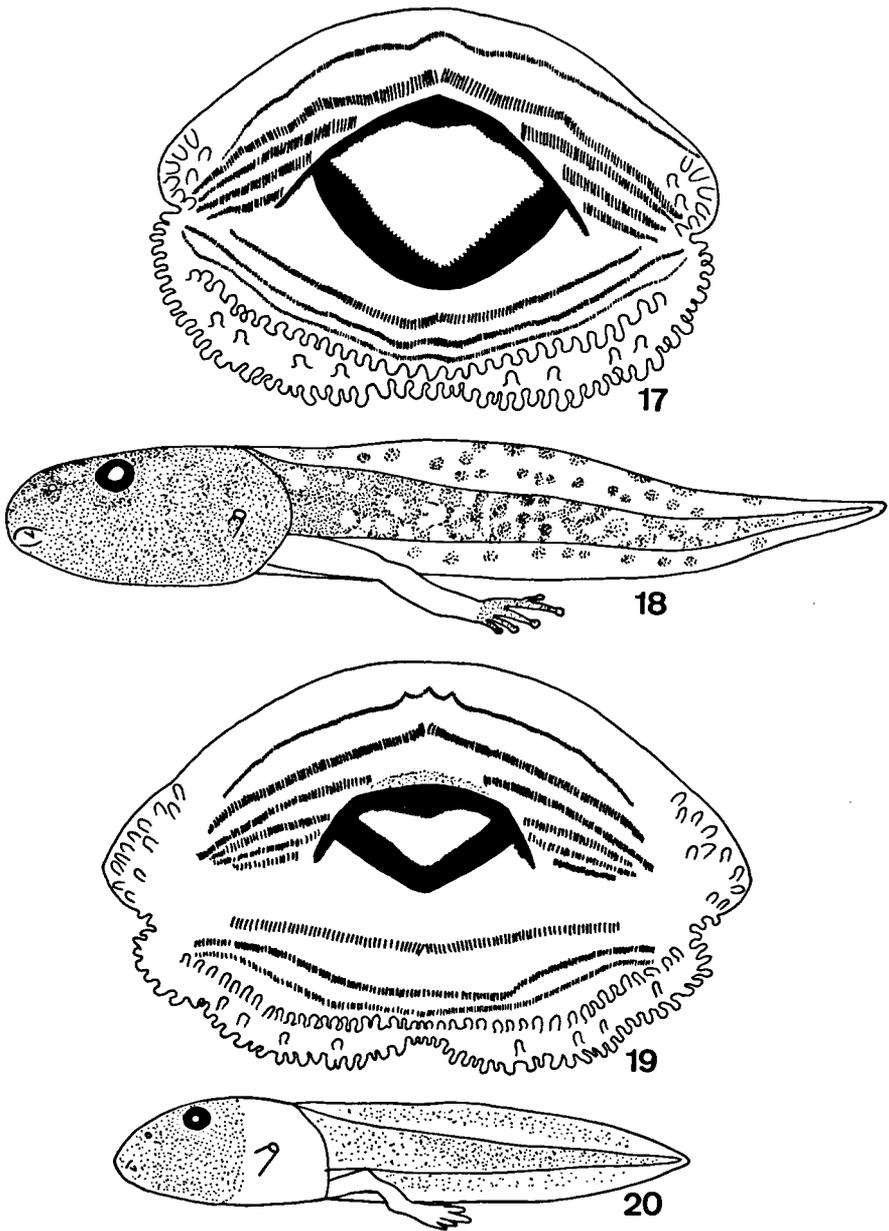
Material. — MNHP 1953—60, the holotype of *M. wittei*, type locality: near Ambanja (NW). Coll. Guibé. ZMA 6870 (4) 22.I.73; 6995 (eggs and embryos) 22.I.73; 7177 (tadpoles and young reared from them) 2.V.72; at L 19. — ZMA 7160 (2♂) 9.I.72 at L 20. — ZMA 7057 (tadpole reared from egg-mass) II.72; 7058 (2) II.72; 7059 (9) 13.II.72; 7061 (1) 6.VIII.72 at L 6. — ZMA 7060 (2) 16.X.71 at L 9.

Habitat. — The adults on the forest bottom and in low vegetation, near temporary pools, when calling. The egg-masses attached to leaves of the same vegetation, overhanging the water. The tadpoles in a sun-exposed vlei, with abundant vegetation and mixed with those of *Boophis tephraeomystax* (Duméril, 1853) and *Ptychadena mascareniensis* (Duméril & Bibron, 1842) at L 19.

Colour in life. — Back brown; venter dirty white, often mottled with brown spots.

Taxonomy. — Examination of the adult material (including the holotype) shows that the specimens from western Madagascar have less webbing than the specimens from eastern Madagascar. The formula of the webbing of the foot in the western frogs is: 1 (1), 2i (1), 2e (1), 3i (2), 3e (1), 4i (2½), 4e (2½), 5 (1). The formula in the eastern frogs: 1 (½), 2i (1), 2e (1), 3i (1½), 3e (1), 4i (2), 4e (2), 5 (0). The style of the sternum is entire, with exception of the specimens from Nossi-Bé (ZMA 7160), in which it is slightly bifurcated.

Voice. — The males were heard, at dusk, in the evening and early morning, and in rainy weather during the day in January and February. We heard them also occasionally during heavy rains near Foulpointe in July and August (cold season), but this was probably a rain-call since the breeding pools were dried up at the time. The call consists of a series of similar squeaky notes (13—16). The duration of the call group varies from 24—30



Figs. 17—20. 17—18, *Mantidactylus wittei*: 17, mouth of tadpole, ZMA 7177, x.25; 18, tadpole, ZMA 7177, x.3; 19—20, *M. blommersae*: 19, mouth of tadpole, ZMA 7055, x.34; 20, tadpole, ZMA 7008, x.3.

seconds. The sonagram (fig. 39) made of a male (ZMA 7160) at 5 p.m. on 19.I.72 shows that the duration of one note is about 0.4 sec. The call consists of a number of harmonics, apparently of a fundamental frequency of 2000 Hz.

Life history. — *M. wittei* spends the dry season in the forest, hidden under debris by day. In the rainy season they congregate, near sunlit temporary pools. The males call in large choruses, sitting on leaves overhanging the water, but in the shade of the forest. The egg-masses are deposited on the same leaves, often many of them closely together in a small stretch of vegetation. The egg mass is rectangular to slightly oval, its width about 1.5 cm and its length about 3.5 cm, containing about seventy eggs. The eggs are pale green, about 1.7 mm in diameter and the jelly is transparent. The embryo develops a tail, eyes, mouth opening and two small suckers, but no external gills. It bursts from the vitelline membrane and hangs in the liquified jelly-mass with the tails directed downwards. After about 6 days the 6—7 mm long hatchlings wriggle free from the jelly and drop into the water below. Nostrils, a spiracle, the onset of a horny beak, papillae round the mouth, an anal tube and the rudiment of two suckers are present; the gut is coiled and filled with greenish yolk. The tail is twice the body.

Tadpoles. — Thirteen tadpoles (ZMA 7177) in stages 37—41 have body lengths of 9—12 mm and total lengths of 31—39 mm. The average ratio of tail length to body length is 2.3 (range 2.3—2.5). Nine metamorphosing young (ZMA 7177) have body lengths of 13—18 mm (mean 14 mm). The mouth and lateral view in stage 39 are shown in figs. 17, 18.

Body depressed. Nostrils dorsal, aperture dorsolateral, situated at equal distances of eye and tip of snout. Eyes situated dorsally. Spiracular opening sinistral, situated at about 3/4 from snout to end of body. Cloacal tube dextral to caudal fin. Caudal musculature moderate. At midlength of tail, height of caudal musculature represents 1/3 of total tail height. End of tail very narrow. Mouth small and directed downwards. Margin of oral disc indented laterally and somewhat in median part lower lip. Papillary border with wide dorsal gap. Two rows of small papillae present. Tooth formula $1/4 + 4//3$ or $1/5 + 5//3$. First row sometimes absent in upper lip, and if present it consists of very small teeth; second row with slight median gap. First row of lower lip sometimes with slight median gap. Colour of tadpole brownish with a reddish tinge, since the blood-vessels are visible through the transparent skin.

We have kept only one tadpole alive of an egg mass collected on the East coast. It reached stage 37 after two months. Body-length of 8 mm at a total length of 25.5 mm. It does not show differences with the batch of western tadpoles described above.

***Mantidactylus domerguei* (Guibé, 1974) comb. nov.**

Gephyromantis domerguei Guibé, 1974a: 1014, figs. 7—8.

Material. — MNHP 1972—190, the holotype of *G. domerguei*, Ambalamaro-vandana 1500 m alt. Coll. Blanc. ZMA 6923 (1♀) 19.IX.71 at L 18, 1800 m alt.

Habitat. — The holotype and the ZMA specimen were found on the forest bottom near a temporary pool.

Colour in life. — Back golden; longitudinal dorsal stripes blackish; venter white.

Mantidactylus blommersae (Guibé, 1975) comb. nov.

Gephyromantis blommersae Guibé, 1975^b: 1081 fig. 1.

Material. — MNHP 1975—5, the holotype of *Gephyromantis blommersae*, 25 km south of Moramanga. Coll. Blommers. MNHP 1975 6—13, seven paratypes of *G. blommersae*, forest of Perinet. Coll. Blommers. ZMA 6841 (8) 24.XII.72; 6842 (10) 6.II.72; 6854 (10) 12.XI.72; 6855 (6) 21.X.71; 6856 (9) 12.II.72; 6958 (1) 23.IX.72; 6960 (1) 19.I.73; 6964 (9) 20.X.71; 6965 (2) 4.IV.72; 7008 (tadpoles and froglets reared from them) 4.IV.72; 7009 (eggs and embryos) 26.XII.72; 7052 (tadpoles and young reared from them) 6.II.72; 7053 (embryos and young reared from them) 6.II.72; 7054 (embryos and tadpoles reared from them) 6.II.72; 7055 (one tadpole) 6.II.72; 7056 (2 froglets) 23.IX.72, at L 10, at 900 m altitude. — ZMA 6959 (1) 25.VIII.71; 6966 (4) 29.VIII.72 at L 12 (type locality). — ZMA 6961 (2) 6.I.73; 6963 (1) 22.X.71, at L 11. — ZMA 6962 (3) 1.VII.71 at L 16.

Habitat. — The adults were collected at their breeding sites near sunlit, often temporary pools of 1 cm to 1 m deep between November and April, together with the egg-masses (attached to leaves a few feet above the water) and the tadpoles. At other times, the frogs were captured on the ground somewhere in the forest.

Colour in life. — Back brown; venter dirty white, often mottled with dark-brown.

Taxonomy. — Guibé describes entirely connected lateral metatarsalia, whereas he figures them partly connected. The latter is true. Since this species resembles *M. wittei* Guibé very much, I summarize here the main differences. *M. wittei* has entirely separated lateral metatarsalia and distinct vomerine teeth, while the third toe is slightly longer than the fifth. Vomerine teeth are absent or rudimentary and the third toe is distinctly longer than the fifth in *M. blommersae*.

Life history. — *M. blommersae* resembles *M. wittei* also in habits and habitat, but seems to replace it at higher altitudes. Gravid females and egg masses were observed during the entire wet season, with a peak in January. The males call in chorus, seated on plants. Their call is a low and soft thrill, different from *M. wittei*'s sound. It can be heard in damp weather, night and day. Oviposition takes place on rainy evenings.

One rainy night in February, we have observed what might have been a

mating attempt. A female was seated in normal position, the legs folded, on the underside of a narrow, almost perpendicularly standing, tough leaf. A male was standing (also in vertical position) over the female, clasping the edge of the leaf with its hands, and with extended legs. His thighs were touching her shoulder region, only her hindparts were visible. He was making up and down movements, but left after a while. Oviposition did not follow; perhaps our flashlight disturbed the couple, or the female was not ready. Because these contacts were similar to the mating posture observed in *M. depressiceps* and *M. liber* (see below), they represented most probably attempts to mate.

The eggs are laid in a single mass, mainly on the underside of erect, lanceolate leaves of plants, such as *Pandanus* (young) and *Crinum firmifolium* (Amaryllidaceae), generally at 50—100 cm above the water. The egg mass is rectangular to slightly oval, and transparent; 2 cm wide and 3.5 cm long. It contains 40—100 eggs, 70 in average. Since gravid females carry the same number of eggs, a female produces one egg mass at a time. The freshly laid egg is 1.2—1.4 mm in diameter; its distance to the vitelline membrane is about 0.25 mm. The eggs are pale green, but in some batches black. The development of the embryo is similar to that in *M. wittei*. The young tadpole, which drops out of the liquified jelly after a week, is in the same stage of development as in *M. wittei*.

Tadpoles. — Six tadpoles in stage 25 have body lengths of 2.0—3.5 mm and total lengths of 7—10 mm. The average ratio of tail length to body length is 2 (range 1.7—2.3). Sixteen tadpoles in stages 31—38 have body lengths of 6—10 mm and total lengths of 17—27 mm. Ten tadpoles in stages 39—41 have body lengths of 9—10.5 mm and total lengths of 24—27.5 mm. The average ratio of tail length to body length in stages 31—41 is 1.8 (range 1.6—1.9). Twenty metamorphosing young have body lengths of 8—10 mm (average 9 mm). Figs. 19 and 20 show the mouth in stage 36 (ZMA 7055) and a lateral view of a tadpole in stage 39 (ZMA 7008). Body depressed. Nostrils dorsal, aperture dorsolaterally situated at equal distances of tip of snout and eye. Eyes situated dorsally. Spiracle sinistral, opening situated at 3/4 from snout to end of body. Cloacal tube dextral to caudal fin. Caudal musculature moderately developed. At midlength of tail, height of caudal musculature accounting for 1/3 of total tail height. Mouth small and directed downwards. Margin of oral disc indented laterally, and in median part of lower lip. Papillary border with wide dorsal gap. Two rows of small papillae present. Tooth formula $1/5 + 5/3$, sometimes $1/4 + 4/3$. Second row on upper lip only slightly interrupted in the middle, first row of lower lip often slightly interrupted in the middle. First row on upper lip consists of very small teeth. Colour of tadpole brownish with a reddish tinge from the blood which shines through the transparent skin.

The tadpole feeds on micro-organisms on the surface of submersed plants, or feeds, turning upside down, on material floating at the water surface. The tadpoles are often accompanied by those of *Microhyla palmata* Guibé, 1974,

and *Boophis idae* (Steindachner, 1867). Their development takes two months in the hot season. Although spawning seems to be restricted to the rainy season (October-April), we have found metamorphosing young once in the Tampoketsa d'Ankazobe in September. Apparently, a delayed development permits tadpoles from the last clutch to survive the cold season in permanent water.

The *Mantidactylus depressiceps* group

Definition. — Omosternum broadly forked posteriorly; greatest distance between lateral arms four to five times width of one arm. Sternum slightly forked anteriorly or entire (*M. peraccae*). Bony style of sternum somewhat shorter than, or equal to style of omosternum (fig. 50). Femoral glands more diffused than in other groups; posterior ventral surface of thigh very strongly granular in both sexes (fig. 56). Median subgular sac, indicated by lateral notches in skin at sides of throat. Lateral metatarsalia entirely separated by web. Outer metatarsal tubercle present. Tibiotarsal articulation not reaching beyond tip of snout. Fingers with small trace of web. Discs of fingers at least twice the diameter of the adjacent phalanx. Testicle black on the outside (except *M. peraccae*). Moderately sized frogs (35—50 mm).

Contents: *M. depressiceps* (Boulenger, 1882), *M. tornieri* (Ahl, 1928), *M. peraccae* (Boulenger, 1896).

Tadpoles: Mouth small; margin oral disc indented laterally and also somewhat medially in lower lip. Papillary border with wide dorsal gap. Tooth formula $1/4 + 4//3 - 1/6 + 6//3$. Horny beak well developed. Caudal musculature moderately developed.

Eggs: 2.3—3 mm in diameter, 40—100.

Chromosomes: $2n = 26$; N.F. = 52 in *M. depressiceps*, *M. tornieri*, *M. peraccae*. Nuclear DNA amount 11.4—13.3 pg, in the first two species.

Habits and habitat: Treefrogs with a preference for leaf-axils near phytotelmes (stagnant water that collects in the axils and holes of some plants, see Paulian, 1961), as resting sites. We have never observed them in open water. They show often a strong positive thigmotaxis; if alarmed, they shuffle backwards, between the closely set leaves of *Pandanus*, *Ravenala* or *Typhonodorum*. The tadpoles are found in permanent, sun exposed, still water, surrounded by the plants preferred by the adults. Egg-masses are attached to a leaf or similar support, often a few metres above water level.

Mantidactylus depressiceps (Boulenger, 1882)

Rhacophorus depressiceps Boulenger, 1882: 467.

Rhacophorus mocquardi Boulenger, 1896: 402.

Boophis depressiceps; Guibé, 1947^b: 439 (equals *difficilis*).

Boophis mocquardi; Guibé, 1947^b: 439 (equals *tornieri*).

Mantidactylus depressiceps; Guibé, 1975^a: 1763 (equals *mocquardi* and *tornieri*); Guibé, 1978: 23, pl.9 figs. 27 and 28. (equals *mocquardi* and *tornieri*; in part).

Material. — BMNH 1947.2.27.50 male lectotype of *Rhacophorus depressiceps* by present designation. Type locality: East Betsileo. Coll. Cowan. BMNH 1947. 2.27.51 female paralectotype, same locality as lectotype; BMNH 1947.2.27.52—53 male paralectotypes, forest of Tsarafidy (Ambohimahaso), formerly Ankafana. Coll. Cowan. BMNH 1947.2.8.62 the male holotype of *Rhacophorus mocquardi*, Sahambendrana, Central Madagascar. Coll. Majastre. ZMA 6972 (7) 2.IV.72; 6974 (1) 18.II.73; 6976 (8) 6.I.73; 6982 (1) 15.XI.72; 6983 (1) 26.XII.72; 6980 (eggs and embryos) 6.I.73; 6981 (eggs and tadpoles reared from them) 1.72; 7114 (tadpoles) 26.V.72; 7115 (one tadpole) V.72, at L 11. — ZMA 6978 (4) 13.II.72; 6979 (1) 17.II.72; 7113 (tadpoles and young reared from them) 22.X.72; 7180 (1 juvenile) 20.X.71; 7181 (2 juveniles) 23.IX.72 at L 10 at 900 m alt. — ZMA 6973 (1) 25.VIII.71 at L 12. — ZMA 6975 (1) 2.VII.71 at L 16.

Habitat. — The frogs were captured resting in the axils of *Pandanus*, *Typhonodorum lindleyanum* (Araceae), *Musa* and tree ferns during the day and in the dry cool season. On evenings in the rainy season, they were observed on shrubs, trees and leaves, near phytotelmes, surrounding pools of 1—2 m depth. Egg masses were attached to leaves 1—2 m above ponds in which tadpoles were caught later.

Taxonomy. — We have collected two species simultaneously in Perinet at the same time, which had very different mating calls, but are hardly to distinguish morphologically. The calling males of each species were heard together and not mixed with the other species; the females of the one deposited white eggs and of the other species light green eggs. Studying type material, I found that one species agrees with *M. depressiceps* (Boulenger, 1882) and the other with *M. tornieri* (Ahl, 1928). Consequently, I do regard *M. tornieri* different from *M. depressiceps*.

Description of lectotype (BMNH 1947.2.27.50 ♂). (See Table I for metrical data). — Head as long as wide (12.5 mm); $\frac{3}{10}$ of body length. Snout subacuminate in dorsal profile and protruding in lateral profile. Snout longer than horizontal diameter of eye. Nostrils nearer to tip of snout than to eye. Distance from nostril to anterior corner of eye equals horizontal diameter of eye. Canthus distinct and angular. Loreal region slightly concave and nearly vertical. Interorbital region flat. Interorbital distance slightly wider than internarial distance. Interorbital distance about $1\frac{1}{2}$ times width of upper eyelid. Nostrils slightly protruding, opening laterally. Pupil horizontally elliptical. Dermal fold from posterior edge of eye, over tympanum curving downwards to base of forelimb. Fold covering dorsal margin of tympanum. Tympanum distinct and round. Diameter of tympanum half the horizontal diameter of eye. Distance from eye to tympanum one half diameter of tympanum. Diameter of disc third finger equals diameter of tympanum. Second finger longer than first. Subarticular tubercles small, oval and flat. Two oval flat palmar tubercles and one inner flat oval metacarpal tubercle present. Ventral surface of hand tubercular. Small rudiment of web between fingers. When limbs are laid along the side, knee and elbow overlap,

Table 1. *Mantidactylus depressiceps* and *M. tornieri*: Dimensions in mm of adult specimens.

Reg. number	sex	A	B	B/A	C	C/A	D	D/A	E	E/A	F	F/A	G	G/A	H	H/I	
<i>M. depressiceps</i>																	
BMNH 1947.2.27.50	♂	41	21	0.51	14	0.34	69	1.68	23	0.56	31	0.75	22	0.54	2.2	4.5	0.49
BMNH 1947.2.27.51	♀	39	19	0.49	13	0.33	65	1.67	21	0.54	29	0.74	20	0.51	2.1	4.2	0.50
BMNH 1947.2.27.52	♂	36	19	0.53	12	0.33	60	1.66	20	0.56	27	0.75	19	0.53	1.9	4.0	0.48
BMNH 1947.2.27.53	♂	37	19	0.52	12.5	0.34	62	1.68	20.5	0.55	28	0.76	19.5	0.53	2.0	4.2	0.48
BMNH 1947.2.8.62	♂	34	18	0.53	10.5	0.31	57	1.68	19	0.56	25	0.73	16.5	0.49	2.0	4.0	0.50
ZMA 6978	♂	37	20.5	0.55	13	0.35	64	1.73	20	0.54	27	0.72	19	0.51	2.1	4.2	0.50
ZMA 6978	♂	39	21	0.54	13	0.33	70	1.79	22	0.56	31	0.78	22	0.56	2.1	4.3	0.49
ZMA 6978	♂	40	21	0.53	14	0.35	69	1.72	23	0.58	31	0.78	22	0.55	2.1	4.3	0.48
ZMA 6978	♂	40	22	0.55	14	0.35	70	1.76	23	0.58	32	0.80	22	0.55	2.1	4.5	0.47
ZMA 6976	♀	41	22	0.54	14	0.34	70	1.71	22	0.53	31	0.76	22	0.53	2.2	4.5	0.49
ZMA 6976	♂	44	23	0.53	14.5	0.33	73	1.66	23	0.52	32	0.73	21	0.48	2.2	4.5	0.49
<i>M. tornieri</i>																	
ZMB 30533	♀	49	25	0.51	15	0.31	75	1.53	25	0.51	33	0.67	24	0.49	2	5.2	0.38
ZMA 6989	♂	48	25	0.52	15	0.31	76	1.58	25	0.52	33	0.69	23	0.48	2	5.2	0.38
ZMA 6987	♂	49	26	0.53	16	0.33	77	1.57	24	0.49	35	0.71	25	0.51	2	5.5	0.36
ZMA 6986	♂	45	23.5	0.53	15	0.33	71	1.58	22	0.49	31	0.69	23	0.51	1.9	5.0	0.38
ZMA 6988	♂	50	24	0.48	15	0.30	75	1.50	24	0.48	35	0.70	23.5	0.47	1.9	5.0	0.38
ZMA 7110	♂	45	20	0.44	11.5	0.25	61	1.36	19	0.42	27	0.60	18.5	0.41	2	4.2	0.48
ZMA 7110	♀	48	22	0.45	12.5	0.26	67	1.40	22	0.46	30	0.62	21	0.44	2	4.5	0.44
ZMA 7110	♀	48	22	0.46	12.5	0.26	65	1.35	21	0.44	29	0.60	20	0.42	2.2	4.5	0.49
ZMA 7110	♀	45	21	0.47	12	0.26	62	1.37	19	0.42	28	0.63	19.5	0.43	2	4.2	0.48
ZMA 7109	♂	45	20	0.44	12.5	0.27	62	1.38	19	0.42	27	0.60	19	0.43	2.2	4.5	0.48
ZMA 7112	♂	43	20	0.47	11	0.26	60	1.40	19	0.44	26	0.60	18.5	0.43	2	4.5	0.44
ZMA 7112	♂	44	21	0.47	12	0.27	64	1.45	19	0.44	28	0.64	20	0.45	2	4.5	0.44

A = snout to vent; B = length of lower arm; C = hand-length; D = length of hind limb; E = tibia length;

F = length of foot and tarsus; G = foot length; H = horizontal diameter of tympanum; I = horizontal diameter of eye.

adpressed heels overlap. When hind limb is adpressed, heel reaches between nostril and anterior corner of eye. Small elliptical, protruding inner metatarsal tubercle and smaller round outer metatarsal tubercle present. Subarticular tubercles small, round and flat. Discs on toes almost as large as those on the hand. Fifth toe slightly longer than third. Formula of webbing of foot: 1 (1), 2i (1), 2e ($\frac{1}{2}$), 3i (2), 3e (1), 4i (2), 4e (2), 5 (1). Ventral surface of foot tubercular, ventral surface of web glandular. Lateral metatarsalia separated by web. Anal opening, directed posteriorly at upper level of thighs. Tongue distinctly bifid and free behind. Vomerine teeth in two oblique oval groups medially behind choanae. Vocal slits small, situated in floor of mouth near angles of jaws. Skin of back finely tubercular. Skin of chin and throat smooth, of belly coarsely granular, posterior undersurface of thigh very coarsely granular, and ventral surface of limbs smooth. Upper rim palpebral membrane pigmented with brown. Brown above, loreal and temporal regions blackish, a light streak from beneath the eye to the angle of the jaw, sides of body marbled with dark brown; hindlimbs with indistinct crossbands; greyish white beneath, spotted with dark brown.

Additional ZMA material. — Sexual dimorphy: throat of male clear white (in breeding season) with faint lateral notches in skin, indicating a median subgular sac. Throat of calling male becomes about hemispherical when inflated. Venter creamy white with numerous brown spots. In female skin of throat level without wrinkles; throat and venter evenly creamy white coloured, sometimes with a few brown spots. Skin of dorsum finely tubercular in male, finely granular in female. Skin of chin and throat finely granular in male, smooth in female. In both sexes the belly and posterior ventral surface of thigh coarsely granular.

Colour in alcohol (same as in life): iris silvery grey with brown reticulation. Back greyish or brownish, red in one specimen (ZMA 6973), sometimes with a creamy white middorsal line; loreal and temporal regions blackish, flanks and posterior surface of thighs with white spots in dark brown network, ventral surface of hindlimbs and web of feet blackish. Dorsal surface of limbs with dark brown cross-bands, sometimes a narrow light beige longitudinal streak in middle of dorsal surface of thigh and shank.

Life history. — *M. depressiceps* is inactive during the day, but after sunset in the rainy season it is present on leaves, about 2 m above permanent ponds, in large groups. The males call in large choruses on rainy evenings, the call being a loud rrah, rrah, rrah. Oviposition occurs at these occasions. Egg masses were observed from December through April, with a peak in January-February.

We have observed the mating behaviour of this species, in pouring rain, in Mandraka on the 6th of January 1973, at 9 p.m. The males, present in greater numbers than the females, were calling loudly and moving over the leaves and branches of a few tall shrubs. On meeting another frog, the excited male tried to place himself over it and to rub its head and shoulder-region with the underside of his thighs. If the other was also a male, the latter violently

resisted and jumped away; however, if it was a ready female, she started oviposition almost immediately. She deposited eggs in rows, on the upper surface of a vertically hanging leaf, starting at the lower rim, each following row of eggs was placed above the former one. She finished oviposition within 10 minutes. The male did not stay with her so long, but left before she had finished oviposition and started calling again some distance away. We have collected the egg mass and observed its development. Therefore, we have little doubt that the observed quick mating act is normal for this species. Apparently, the male ejaculates the sperm on the back of the female, leaving it to find its way downwards to the eggs. A similar mating behaviour was observed in *M. liber* (Peracca, 1893) on the same evening (Blommers-Schlösser, 1975).

The egg mass of *M. depressiceps* is round to oval, measuring about 4—5 cm in diameter and containing 60 to 100 eggs. In a freshly-laid egg mass, one can observe the individual white eggs, measuring about 3 mm in diameter, surrounded by thick white jelly patches. The rain causes the jelly to swell and to become whitishly opaque (fig. 70). During the following days, the jelly becomes less viscous and the mass larger. The embryo bursts from the vitelline membrane, it develops a tail, eyes, mouth opening and two small round suckers, but no external gills. They hang in the liquified jelly mass with the tails downwards. After 8 days the hatchlings wriggle free from the jelly and drop into the water underneath. The hatchling measures 11—12 mm. Nostrils, a spiracle, the begin of a horny beak, papillae and anal tube and a rudiment of suckers are present. The gut is coiled and filled with yolk.

Tadpoles. — Four tadpoles in stage 25 (with yolk still present) have body lengths of 4 mm and total lengths of 11.5—12.0 mm. The average ratio of tail length to body length is 2 (range 1.9—2.0). Seventeen tadpoles in stage 25 (yolk disappeared) have body lengths of 5—10 mm and total lengths of 14—29 mm. Seven tadpoles in stages 26—30 have body lengths of 9—12 mm and total lengths of 25—34 mm. One tadpole in stage 38 has a body length of 15 mm and a total length of 42 mm. The average ratio of tail length to body length is 1.8 (range 1.7—1.9) in stages 25—38. Three metamorphosing young have body lengths of 16—17 mm.

Mouth (ZMA 7115) and lateral view of a tadpole (ZMA 6981) in stage 28 are shown in figs. 25, 26. Body depressed. Nostrils dorsal, aperture dorsolateral, situated at equal distances of tip of snout and eye. Eyes situated dorsolaterally. Spiracular opening sinistral, situated at about 2/3 from snout to end of body. Cloacal tube dextral to caudal fin. Caudal musculature moderate. At midlength of tail, height of caudal musculature represents about 1/3 of total tail height. Mouth small and directed downwards. Margin of oral disc indented laterally and also somewhat in median part of lower lip. Papillary border with wide dorsal gap. Two rows of small papillae present, one in median part of lower lip. Tooth formula $1/5 + 5//3$ or $1/6 + 6//3$. Second row of teeth on upper lip with slight median gap; and first row on lower lip

often with slight median gap. Colour of tadpole greyish in life. The whole development took three months in the vivarium, in the hot season.

The last eggs were found at the end of April (end of the wet summer). From then till October, we did not observe oviposition. However, we collected far developed tadpoles and metamorphosing young in October (begin hot season), which might mean that the metamorphosis is delayed in the cool season.

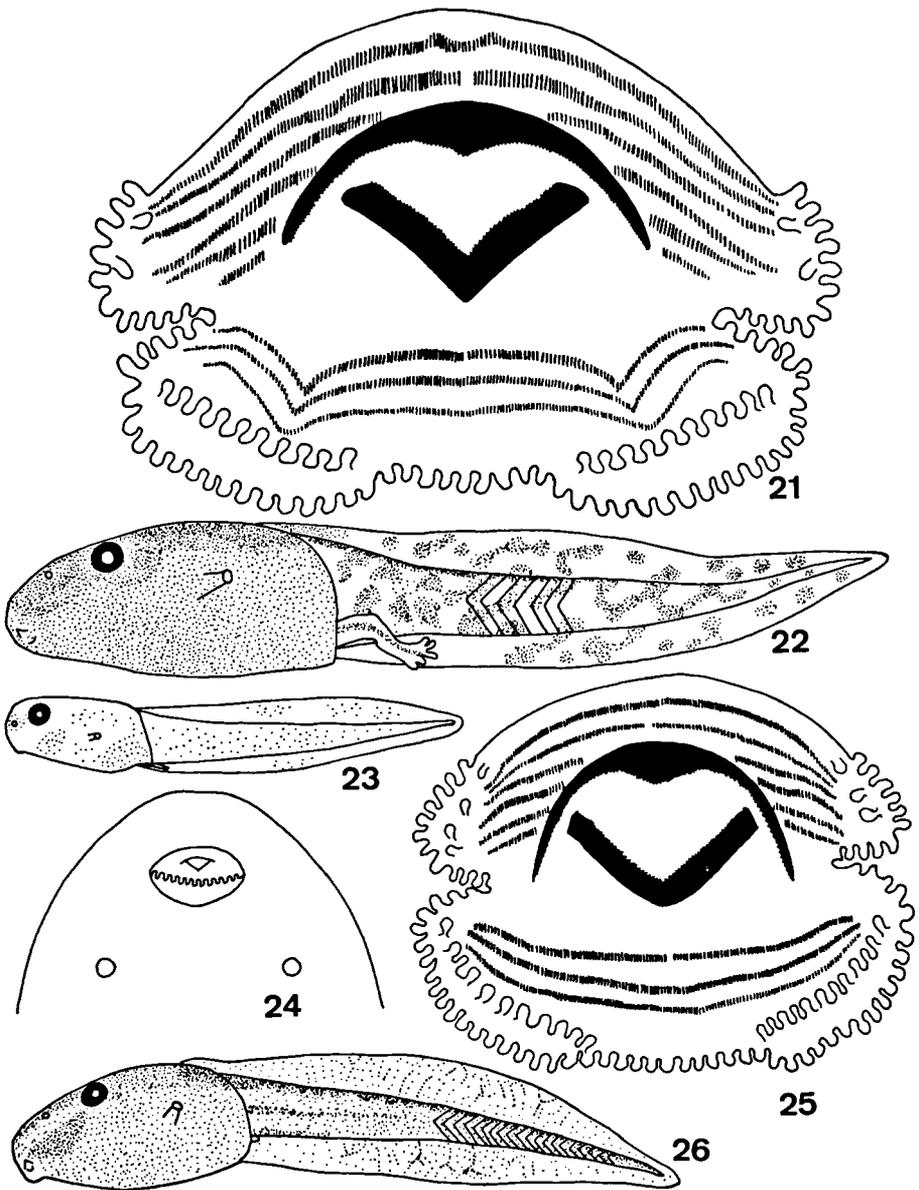
***Mantidactylus tornieri* (Ahl, 1928), fig. 69, bona species.**

Rhacophorus tornieri Ahl, 1928: 316; Guibé, 1947: 439 (in synonymy of *mocquardi*); Guibé, 1975*: 1763 (in synonymy of *depressiceps*).

Material. — ZMB 30533 the female holotype of *Rhacophorus tornieri*, Anhoraka, Sahambendrana, Central Madagascar. Coll. Braun. ZMA 6986 (1) 4.IV.72; 6987 (1) 13.II.72; 6988 (1) 20.X.71; 6989 (1) 13.XI.72, at L 10. — ZMA 7109 (1) 2.VIII.72; 7112 (2) 13.X.71; 7110 (4) 13.II.72; 7106 (tadpoles and young reared from them) VII.72; 7107 (eggs and tadpoles reared from them) VII.72; 7108 (tadpoles) VII.72; 7111 (eggs, embryos, tadpoles and juveniles reared from them) VII.72, at L 6.

Habitat. — The frogs were collected in the forest, during the day in their resting places, such as the exterior axils of *Ravenala madagascariensis* (Musaceae) and *Typhonodorum lindleyanum* (Araceae); in the evening they come out onto the leaves. Egg masses were attached on leaves 30 cm to 3 m above permanent ponds; tadpoles were found in the same pools.

Description of holotype (ZMB 30533 ♀). (See Table I for metrical data). — Head as long as wide (16 mm); one third of body length. Snout subacuminate in dorsal profile and round in lateral profile. Upper jaw slightly projecting beyond lower jaw. Snout longer than horizontal diameter of eye. Nostrils nearer to tip of snout than to eye. Distance from nostril to anterior corner of eye equals horizontal diameter of eye. Canthus distinct and angular. Loreal region slightly concave and nearly vertical. Interorbital region flat. Interorbital distance is somewhat wider than internarial distance. Interorbital distance somewhat wider than width upper eyelid. Nostrils slightly protruding, opening laterally. Pupil horizontal, elliptical. Dermal fold from posterior edge of eye, over tympanum, curving downwards to base of forelimb. Tympanum distinct and round. Diameter of tympanum about 2/5 of horizontal diameter eye. Distance from eye to tympanum 3/4 diameter of tympanum. Diameter disc third finger equals diameter of tympanum. Second finger longer than first. Subarticular tubercles, small, oval and slightly protruding. Two oval flat palmar tubercles and one inner oval flat metacarpal tubercle present. Ventral surface of hand tubercular. Small rudiment of web between fingers. When limbs are laid along the side, knee and elbow overlap slightly. When hindlimb is adpressed, heel reaches the centre of eye. Adpressed heels overlap slightly. Small, elliptical, protruding inner metatarsal tubercle, and smaller round outer metatarsal tubercle



Figs. 21—26. 21—24, *Mantidactylus tornieri*: 21, mouth of tadpole, ZMA 7106, x.25; 22, tadpole, ZMA 7106, x.3; 23, hatchling, ZMA 7111, x.6; 24, mouth of hatchling, ZMA 7111, x.25; 25—26, *M. depressiceps*: 25, mouth of tadpole, ZMA 7115, x.34; 26, tadpole, ZMA 6981, x.3.

present. Terminal discs somewhat smaller than those on the hand. Fifth toe slightly longer than third. Subarticular tubercles, small, round, slightly protruding. Formula of webbing of foot: 1 ($\frac{1}{2}$), 2i (1), 2e (0), 3i ($1\frac{1}{2}$), 3e (1), 4i (2), 4e ($1\frac{1}{2}$), 5 (0). Ventral surface of foot tubercular, ventral surface of web glandular. Lateral metatarsalia separated by web. Anal opening directed posteriorly at upper level of thighs. Tongue distinctly bifid and free behind. Vomerine teeth in two oblique oval groups medially behind choanae. Skin of back finely granular, skin of chin and throat smooth, of belly and posterior undersurface of thigh coarsely granular, and of undersurface limbs smooth. Upper rim palpebral membrane pigmented with brown. Back light brown with dark brown spots, dark brown streak between eyes, loreal and temporal region dark-brown, a cream-white streak from beneath eye to forearm. Flanks with irregular dark brown and cream-white spots. Limbs with dark brown cross-bands, cream-white longitudinal midline on upper surface of thigh and shank, post-surface of thigh cream-white with two longitudinal dark brown stripes. Belly, chin and throat dirty white, somewhat spotted with dark brown.

Additional ZMA material. — Sexual dimorphy: male with vocal slits in the floor of mouth, near commissure of jaws. Throat of male brightly white, with faint lateral notches in skin, indicating a median subgular sac. Venter cream-white with numerous brown spots. In female skin of throat level without wrinkles; throat and venter cream-white, sometimes with a few brown spots. Skin of dorsum finely tubercular in male and finely granular in female. Skin of chin and throat finely granular in males and smooth in females. In both sexes the belly and the posterior ventral surface of thigh is coarsely granular.

Colour in life: Iris silvery grey with brown spots. Back beige, sometimes with white middorsal line, continuing on thigh and shank, canthal and temporal region dark brown, often cream-white streak from beneath eye to insertion of base of forelimb; flanks: yellow spots in dark brown, dorsal surface limbs: beige with dark brown cross-bands; posterior surface of thigh: irregular yellow stripes in dark brown.

Remarks: Disc of third finger is larger than tympanum in specimens from Perinet and equal to tympanum in specimens from Foulpointe. Tibiotarsal articulation reaches the centre of eye in specimens from Perinet, but reaches posterior corner of eye in specimens from Foulpointe. The forelimbs of specimens from Foulpointe are shorter than of those from Perinet. Eye of specimens from Perinet is larger than that of specimens from Foulpointe (see Table I). It is possible, that the specimens of Foulpointe represent a subspecies, but the material is not sufficient to decide this for the moment.

Differential diagnosis. — The snout of *M. depressiceps* is in lateral profile protruding, round in *M. tornieri*. Web of fifth toe reaches base of penultimate phalanx in *M. depressiceps*, disc in *M. tornieri*. Tibiotarsal articulation reaches between nostril and anterior corner of eye in *M. depressiceps* and centre of eye or posterior corner of eye in *M. tornieri*.

Eggs of *M. depressiceps* are white; those of *M. tornieri* green. Nuclear DNA amount 11.4 pg in *M. depressiceps* and 13.3 pg in *M. tornieri*.

Life history. — *M. tornieri* is similar to *M. depressiceps*, also in habits and habitat. They prefer resting in leaf-axils. The males were calling in Perinet on rainy evenings from November through April. Their sound is like a roll of drums, a loud pomm, pomm. Egg masses were seen in Perinet in the same period, and in Foulpointe during a period of damp weather in July. The eggs form a single mass, round to slightly oval, attached to the upper surface of a vertically hanging leaf, 30 cm to 3 m above the pond. An egg mass measures about 4–5 cm in diameter and contains 40–100 eggs. The eggs are pale green, about 2.3 mm in diameter, and the jelly is transparent. The embryo develops a tail, eyes, mouth opening and two small suckers, but no external gills, it bursts from the vitelline membrane and hangs in the liquified jelly mass with the tail directed downwards. After 7 days the hatchlings wriggle free from the jelly until they drop into the water below. At that time the hatchling measures 9.5–10.5 mm. Nostrils, spiracle, begin of horny beak, papillae, anal tube and rudiment of suckers present. The green yolk mass is coiled (figs. 23, 24).

Tadpoles. — Nine tadpoles in stage 25 have body lengths of 3.5–4 mm and total lengths of 10–12 mm. One tadpole in stage 27 has a body length of 8 mm and a total length of 24 mm. Fifteen tadpoles in stages 31–40 have body lengths of 9–15 mm and total lengths of 24.5–40 mm. The average ratio of tail to body length is 2 (range 1.9–2) in stages 25–27; and 1.8 (range 1.7–1.9) in stages 31–40. Five metamorphosing young have body lengths of 13–14 mm. Figs. 21, 22 show the mouth and lateral view of a tadpole in stage 37 (ZMA 7106). Body depressed. Nostrils dorsal, aperture dorsolateral, situated at equal distances of eye and tip of snout. Eyes situated dorsolaterally. Spiracle sinistral, opening situated at 2/3 from snout to end of body. Cloacal tube dextral to caudal fin. Caudal musculature moderate. At midlength of tail, height of caudal musculature accounts for 1/3 of total height. Mouth small and directed downwards. Margin of oral disc indented laterally and indented slightly in median part of lower lip. Papillary border with wide dorsal gap. Two rows of small papillae present, in median part of lower lip one row. Tooth formulae $1/4 + 4//3$ or $1/5 + 5//3$. Second row of upper lip with slight median gap and first row of lower lip frequently with slight median gap. Colour in life greyish to brownish.

The whole development took three months in the vivarium.

***Mantidactylus peraccae* (Boulenger, 1896) comb. nov.**

Rhacophorus peraccae Boulenger, 1896: 421.

Material. — ZMA 6869 (1 ♀ and 1 ♂) 9.IV.72 at L 17, captured from the axil of *Pandanus*.

Colour in life. — Back lightbrown or green, with dark brown markings; inguinal region yellowish with dark brown spots; venter white.

Taxonomy. — Our material agrees with the original description of *R. peraccae*: the species has an oval inner and smaller round outer metatarsal tubercle (just like described by Boulenger); an outer metatarsal tubercle never occurs in *Rhacophorus* (= *Boophis* of author). Besides, the omosternum is widely forked posteriorly, which is likewise a character of *Mantidactylus*. Consequently I transfer this species to the genus *Mantidactylus*.

The *Mantidactylus pulcher* group

Definition. — Omosternum broadly forked posteriorly; greatest distance between lateral arms 4 or 5 times the width of one arm. Sternum slightly forked anteriorly. Bony style of sternum somewhat less, or equal, in length than that of style of omosternum (fig. 51). Femoral glands only in males, and not visible in all specimens, probably of seasonal occurrence; oval oblong thickened part in the middle of a larger granular area (fig. 55). Vocal sac not apparent externally. Lateral metatarsalia connected. Outer metatarsal tubercle present. Tibiotarsal articulation not reaching beyond tip of snout. Fingers with trace of web. Discs of fingers at least twice the diameter of the adjacent phalanx. Outside of testicle black, just as posterior part of gut. Small sized (25—38 mm) frogs, often conspicuously coloured. Contents: *M. pulcher* (Boulenger, 1882), *M. bicalcaratus* (Boettger, 1913), *M. flavobrunneus* sp.nov., *M. punctatus* sp.nov. and possibly also *M. liber* (Peracca, 1893).

Tadpoles: Found in phytotelmes. Mouth small. Margin of oral disc indented laterally. Papillary border with wide dorsal gap. Tooth formula $1/4 + 4/3$ or $1/5 + 5/3$. Horny beak well developed. Caudal musculature strong. Caudal fin reduced. Body strongly depressed.

Eggs: 2 mm in diameter, 30—60.

Chromosomes: Number $2n = 26$; N.F. = 52 in *M. pulcher*, *M. liber*, *M. bicalcaratus*, *M. flavobrunneus* (= *G. aff. bicalcaratus*, in Blommers-Schlösser, 1978), *M. punctatus* (= *G. aff. pulcher*, ibidem). Nuclear DNA amount 9.6—12.9 pg, in the first 4 species.

Habits and habitat: Inhabitants of leaf-axils near phytotelmes; the phytotelmes are used as a basin for the tadpoles (exception: *M. liber*). Treefrogs which often show a positive thigmotaxis. The eggs are deposited above the water in the axils in one mass.

Note: I place *M. liber* tentatively in this group, although it shares also some characters with the *M. depressiceps* group. *M. liber* has diffused femoral glands, and has a median gular sac. The tadpole of this species is also conform to that of the *M. depressiceps* group, and occurs in free water, not in phytotelmes.

Mantidactylus pulcher (Boulenger, 1882) comb. nov. fig. 58

Rhacophorus pulcher Boulenger, 1882: 467.

Gephyromantis pulcher; Guibé, 1975*: 1762, 4 figs. (equals *liber*); Guibé, 1978: 55, figs. 117—123 (equals *liber*, *methueni*, *albugularis*, *variabilis*, in part).

Material. — BMNH 1947.2.27.65 female lectotype of *Rhacophorus pulcher* by present designation. Type locality: Ankafana, Betsileo (= forest of Tsarafidy, Ambohimahasoa). Coll. Cowan. BMNH 1947.2.27.64 female paralectotype, same data as lectotype. Other paralectotypes not examined. ZMA 7213 (2) 23.IX.72; 7216 (one young) 20.X.71, at L 10, at 900 m alt. — ZMA 7214 (3) 25.VIII.71; 7217 (1 young) 29.VIII.72; 7215 (2) 29.VIII.72 at L 12. Tadpoles (ZMA 7156) 25.VIII.71 at L 12, were collected in the same *Pandanus* as the present species, but also together with *M. flavobrunneus* n.sp. Therefore, one cannot be sure about their identity, as attempts to rear them failed.

Habitat. — This species was only collected from *Pandanus* leaves.

Description of lectotype (BMNH 1947.2.27.65). (See Table II for metrical data). — Head slightly longer than wide, head length about 1/3 of body length. Snout acuminate with rounded tip in dorsal profile and round in lateral profile. Upper jaw strongly projecting over lower jaw. Snout longer than horizontal diameter of eye, equal to distance between anterior corners of eyes. Nostrils nearer to tip of snout than to eye. Distance from nostril to anterior corner of eye equals horizontal diameter of eye. Canthus distinct and angular. Loreal region vertical and hardly concave. Interorbital region flat. Interorbital distance equal to internarial distance. Ratio width upper eyelid to interorbital distance 3/5. Nostrils slightly protruding, opening laterally. Pupil horizontal, elliptical. Weak tympanic fold. Tympanum rather distinct, and round. Diameter of tympanum 1/3 of horizontal diameter of eye. Diameter of disc third finger equals diameter tympanum. Second finger longer than first. Subarticular tubercles small, oval and flat. Two oval, flat palmar tubercles, the inner large and the outer small, and one inner flat, oval metacarpal tubercle. Trace of web between fingers. Ventral surface of hand smooth. When limbs are laid along the side, knee and elbow meet. Adpressed heels overlap. When hindlimb is adpressed, heel reaches the centre of eye. Small, elliptical, protruding inner metatarsal tubercle, and smaller round outer metatarsal tubercle present. Discs of toes smaller than those of fingers. Subarticular tubercles small, round and flat. Fifth toe shorter than third, the difference being at least the vertical diameter of its disc. Formula of webbing of foot: 1 (1), 2i (1½), 2e (1), 3i (2½), 3e (1), 4i (2½), 4e (3), 5 (1). Ventral surface of foot smooth. Lateral metatarsalia connected. Anal opening directed posteriorly at upper level of thighs. Tongue distinctly bifid, and free behind. Vomerine teeth in 2 oblique groups medially behind choanae. Skin smooth, except posterior part of belly and posterior undersurface of thigh which is coarsely granular. Colour in alcohol: yellowish, punctate with vinaceous red, a streak of the same colour from tip of snout through the eye

Table II. *Mantidactylus pulcher*, *M. liber* and *M. bicalcaratus*: Dimensions in mm of adult specimens.
 A = snout to vent; B = length of lower arm; C = hand-length; D = length of hind limb; E = tibia length;
 F = length of foot and tarsus; G = foot length.

Reg.number	sex	A	B	B/A	C	C/A	D	D/A	E	E/A	F	F/A	G	G/A
<i>M. pulcher</i>														
BMNH 1947.2.27.65	♀	26	12	0.46	6.5	0.24	36	1.38	12	0.46	15	0.58	10	0.38
BMNH 1947.2.27.64	♀	28	12.5	0.45	7	0.25	40	1.43	13	0.46	16	0.57	11	0.39
ZMA 7213	♀	26	12	0.46	7	0.27	40	1.54	13	0.50	16	0.62	10	0.38
ZMA 7213	♀	24	11	0.46	6	0.25	35	1.45	12	0.50	15	0.63	9	0.38
ZMA 7214	♀	26	12	0.46	6.5	0.24	39	1.50	13	0.50	16	0.62	10.5	0.40
ZMA 7214	♂	25	11.5	0.46	6.5	0.26	38	1.52	13	0.52	16	0.64	10	0.40
ZMA 7214	♀	23	11	0.48	6	0.26	35	1.52	12	0.52	16	0.70	9.5	0.41
ZMA 7215	♀	22	10.5	0.48	5.5	0.25	34	1.55	11.5	0.52	15	0.68	9	0.41
<i>M. liber</i>														
BMNH 1947.2.8.63	♀	28	14	0.50	9	0.32	44	1.57	15	0.54	20	0.71	14	0.50
BMNH 1947.2.8.64	♀	28	14	0.50	9	0.32	43	1.53	14	0.50	19	0.68	13	0.46
MNHP 94.3	♀	28	13.5	0.48	9.5	0.34	45	1.61	15	0.54	21	0.75	14	0.50
MNHP 8147	♂	28	13.5	0.48	9	0.32	43	1.53	14	0.50	20	0.71	13	0.46
ZMA 6921	♀	28	14	0.50	9.5	0.34	45	1.61	15	0.54	21	0.75	13	0.46
ZMA 6921	♂	27	14	0.52	9	0.33	43	1.59	14	0.52	19	0.70	12.5	0.46
ZMA 6659	♂	26	13	0.50	8.5	0.32	42	1.61	14	0.54	18.5	0.71	12	0.46
ZMA 6659	♀	28	14	0.50	9	0.32	43	1.53	15	0.54	20	0.71	13	0.46
<i>M. bicalcaratus</i>														
SMF 6811	♀	28	12	0.43	7.5	0.27	42	1.50	14	0.50	18	0.64	12	0.43
MNHP 29—209	?	24	9.5	0.40	5.5	0.23	36	1.50	12	0.50	16	0.67	9.5	0.40
MNHP 29—212	?	24	9	0.38	5.5	0.23	34	1.42	12	0.50	15	0.63	9	0.38
ZMA 6956	♂	26	12	0.46	7	0.27	40	1.53	14	0.53	17	0.65	11	0.42
ZMA 6956	♀	29	12	0.42	7	0.24	42	1.45	14.5	0.50	18	0.62	12	0.42
ZMA 6956	♂	25	11	0.44	6	0.24	38	1.52	13.5	0.54	16	0.64	10.5	0.42
ZMA 6956	♂	26	12	0.46	7	0.27	40	1.53	13	0.50	17	0.65	11	0.42

over the tympanum to behind the insertion of the forelimb, and between and on the upperside of the eyes. Anterior upper rim of palpebral membrane pigmented with brown. Venter uniformly coloured. Boulenger mentions a bright green skeleton in the original description. I observed this also in living and freshly killed specimens. This phenomenon (chlorosis) is caused by the presence of biliverdin. It has been reported to occur in several families of frogs in South America and Africa (Hoogmoed, 1972). The specimens in our collection are conform to the lectotype. No differences were found between the sexes, except the vocal slits in the males, situated in the floor of the mouth near the commissure of jaws. In life, the colour is bright-green with dark violet patterns (fig. 58): a dark violet crossline from eye to eye is often present. The anterior or entire upper rim of the palpebral membrane is brown. Iris silvery grey with brown reticulation in the middle, surrounded by a dark brown ring.

Note. — The tadpoles are the same as those described for *M. punctatus* n.sp. in this paper, but when alive different in colour: blackish with small green spots. The posterior part of gut is also blackish as in the adults in this species group.

Mantidactylus liber (Peracca, 1893) comb. nov., bona species

Rhacophorus liber Peracca, 1893: 14; Guibé, 1975*: 1762 (in synonymy of *pulcher*); Guibé, 1978: 56 (in synonymy of *pulcher*).

Gephyromantis liber; Blommers-Schlösser, 1975: 15.

Gephyromantis albogularis Guibé, 1947: 151 (new synonymy); Guibé, 1978: 56 (in synonymy of *pulcher*).

Gephyromantis variabilis Millot & Guibé, 1951: 204, fig. 4 (new synonymy); Guibé 1978: 56 (in synonymy of *pulcher*).

Material. — BMNH 1947.2.8.63 female lectotype of *Rhacophorus liber* by present designation. Type locality: Andrangoloaka 19°02' S 47°55'E (near Manjakandriana). Coll. Peracca. BMNH 1947.2.8.64 female paralectotype of *Rhacophorus liber*, same data as lectotype. MNHP 94—3 female paralectotype of *Rhacophorus liber*, same data as lectotype. MNHP 8146 the male holotype, and MNHP 8147 the male paratype of *Gephyromantis albogularis*, Madagascar. Coll. Sikora, 1891. MNHP 1953—116 the holotype of *Gephyromantis variabilis*, Perinet. Coll. Millot. ZMA nos. 6634—6639, 6641—6668, cf. Blommers-Schlösser (1975).

Description of lectotype (BMNH 1947.2.8.63). (See Table II for metrical data). — Head as long as wide. Head length about 1/3 of body length. Snout round in dorsal and lateral profile. Upper jaw projecting over the lower jaw. Snout longer than horizontal diameter of eye, shorter than distance between anterior corners of eyes. Nostrils nearer to tip of snout than to eye. Distance from nostril to anterior corner of eye equals horizontal diameter of eye. Canthus rostralis distinct and round. Loreal region concave. Interorbital region flat. Interorbital distance equals internarial distance.

Interorbital distance is $1\frac{1}{2}$ times as wide as upper eyelid. Nostrils slightly protruding, opening laterally. Pupil horizontal, elliptical. Fold from behind eye over tympanum to insertion of forelimb. Tympanum distinct and round. Diameter of tympanum $\frac{2}{5}$ horizontal diameter of eye. Diameter of disc third finger equals diameter of tympanum. Second finger longer than first. Subarticular tubercles protruding, oval. Supernumerary tubercles present. Two oval, protruding palmar tubercles present, the outer small, the inner large; one protruding oval inner metacarpal tubercle. Rudiment of web between fingers. Ventral surface of hand tubercular. When limbs are laid along the body, knee and elbow overlap. Adpressed heels overlap. When hindlimb is adpressed, heel reaches centre of eye. Small, elliptical, protruding inner metatarsal tubercle, and smaller, protruding, round outer metatarsal tubercle present. Discs on toes smaller than those on fingers. Subarticular tubercles protruding and round. Fifth toe subequal to third. Webbing of foot: 1 (1), 2i (1), 2e (1), 3i (2), 3e (1), 4i (2), 4e (2), 5 (1). Ventral surface of foot finely tubercular. Lateral metatarsalia connected. Anal opening directed posteriorly at upper level of thighs. Tongue distinctly bifid, free behind. Vomerine teeth in 2 oblique groups medially behind choanae. Skin smooth, except belly and posterior part of lower surface of thigh, which is coarsely granular. Upper rim palpebral membrane with brown pigment. Back light brown. Limbs with indistinct cross-bands. Dark brown crossline from the edge of eyelid to the other and a dark brown streak from tip of snout to the eye. Tympanic fold dark brown. A white streak from beneath eye to commissure of mouth.

Our material agrees with the type material of *Rhacophorus liber*. The same holds true for the type material of *R. albogularis* and *G. variabilis*. The colour pattern in this species is very variable, as Peracca, 1893 reported already. Guibé, 1951 showed the various patterns in his description of *G. variabilis*. Notwithstanding this variety, a white streak from beneath the eye to the angle of the lower jaw, a few white spots in the inguinal region, a dark brown streak from the tip of the snout to the eye, and a dark brown tympanic fold and dark brown cross-bands over the limbs are always present. The iris is silvery grey with blackish areas, surrounded by a black ring. Anterior part and upper rim of the palpebral membrane with brown pigment. The skeleton is green (chlorosis).

The life history of *Mantidactylus liber* has been described previously (Blommers-Schlösser, 1975).

Differential diagnosis. — *M. liber* has larger hands and feet than *M. pulcher*. In the first species, the ratio hand length/body length is 0.32—0.34, in the second 0.23—0.28. The ratio foot length/body length is 0.46—0.50 in *M. liber*, and 0.38—0.43 in *M. pulcher*. The colour pattern, although variable in *M. liber*, and constant in *M. pulcher*, is different. *M. liber* has the feet more webbed than *M. pulcher*. The fifth toe is distinctly longer than the third in the latter species, while they are subequal in *M. liber*. They

Table III. *Mantidactylus bicalcaratus* (see also T. II), *M. punctatus* and *M. flavobrunneus*: Dimensions in mm of adult specimens.
 A = snout to vent; B = length of lower arm; C = hand-length; D = length of hind limb; E = tibia length;
 F = length of foot and tarsus; G = foot length.

Reg. number	sex	A	B	B/A	C	C/A	D	D/A	E	E/A	F	F/A	G	G/A
<i>M. bicalcaratus</i>														
ZMA 6952	♀	28	12	0.43	7	0.25	42	1.50	14	0.50	17	0.61	12	0.43
ZMA 6952	♂	25	11	0.44	6	0.24	38	1.52	12.5	0.50	16	0.64	10.5	0.42
ZMA 6955	♂	23	9	0.39	5.5	0.24	33	1.43	12	0.52	15	0.65	9	0.39
ZMA 6955	♀	28	11	0.39	6.5	0.23	42	1.50	14	0.50	18	0.64	11	0.39
<i>M. punctatus</i>														
ZMA 7171A	♂	24	10.5	0.43	6	0.25	36	1.50	12	0.50	16	0.66	9.5	0.40
ZMA 7171B	♂	24	11	0.46	6	0.25	35	1.46	12	0.50	15	0.62	9.5	0.40
ZMA 7170	♂	24	10.5	0.43	6	0.25	34	1.41	12	0.50	14	0.58	9	0.38
ZMA 7170	♂	23	11	0.48	6	0.26	35	1.52	11	0.48	14	0.60	9	0.39
ZMA 7170	♀	27	13	0.48	7.5	0.28	39	1.44	13	0.48	16	0.59	11	0.41
ZMA 7170	♂	24	11	0.46	6.5	0.27	36	1.50	12	0.50	15	0.63	9.5	0.40
ZMA 7170	♂	25	11	0.44	6.5	0.26	35	1.40	11	0.44	14.5	0.58	9.5	0.38
ZMA 7170	♂	24	12	0.50	6.5	0.27	37	1.54	12	0.50	15	0.63	10	0.42
ZMA 7170	♂	23	11	0.48	6.5	0.28	35	1.52	11	0.48	15	0.65	10	0.43
<i>M. flavobrunneus</i>														
ZMA 7172A	♂	33	17	0.52	8	0.24	50	1.52	16	0.48	21	0.63	14	0.43
ZMA 7172B	♀	38	19	0.50	10	0.26	57	1.50	19	0.50	24	0.63	16	0.42
ZMA 7173	♂	30	15	0.50	8	0.27	47	1.57	16	0.54	21	0.70	13	0.43

are sympatric species. The nuclear DNA amount in *M. pulcher* is 11.4 pg, whereas in *M. liber* it is 9.6 pg.

Mantidactylus bicalcaratus (Boettger, 1913) comb. nov. fig. 60.

Rhacophorus bicalcaratus Boettger, 1913: 320, pl. 23 fig. 5.

Gephyromantis bicalcaratus; Guibé, 1975a: 1762; Guibé, 1978: 55.

Gephyromantis methueni Angel, 1929: 361; (new synonymy); Angel, 1931: 536, pl. IX fig. 4; Guibé, 1945: 383; Razariheloisa, 1974a: 113 (tadpole). Guibé, 1978: 56 (equals *pulcher*).

Mantidactylus methueni; Ahl, 1931: 37.

Non *Gephyromantis methueni*; Millot & Guibé, 1951: 201, fig. 4. pl. VIII D. (redescription = *flavo-brunneus* sp. nov.).

Material. — SMF 6811, the female lectotype of *Rhacophorus bicalcaratus*, designed by Mertens (1967). Type locality: Sainte Marie Island (East Madagascar). Coll. Voeltzkow, 1904. MNHP 29—209, the lectotype of *Gephyromantis methueni* by present designation. Type locality: Ambila (lagune), province of Tamatave. Coll. Petit. MNHP 29—211 and 212, paralectotypes of *Gephyromantis methueni*, Lac Alaotra. Coll. Petit. ZMA 6955 (19) 22.VII.72; 6950 (2) 29.VII.72; 7220 (tadpoles) VII.72; 7221 (eggs and embryos) VII.72, at L 5. — ZMA 6951 (4) 9—23.VII.72; 6956 (7) 13—17.X.71, at L 6. — ZMA 6948 (1) 14.X.71 at L 8. — ZMA 6952 (5) 14—16.X.71 at L 9. — ZMA 6954 (8) 10—11.X.71 collected at L 4 (= type locality of *Gephyromantis methueni*). — ZMA 6953 (4) 31.XII.71 at L 2.

Habitat. — Eggs and tadpoles were always found in phytotelmes; in *Pandanus dauphinensis* in the dunes near the sea, and around lagoons, and in *Typhonodorum lindleyanum* in the coastal swamps; the frogs in the leaf-axils and on the leaves of the same plants.

Taxonomy. — Studying the type material of *R. bicalcaratus* and *G. methueni*, and our own collection, I was not able to trace morphological differences with *M. pulcher*. See also Table II and III for metrical data. The differences between *M. pulcher* and *M. bicalcaratus* mentioned by Boettger (1913) in the original description of the latter species do not hold for the type specimens I saw: in both species the tympanum is 1/3 of the horizontal diameter of the eye, and the diameter of the disc of the 3rd finger equals the diameter of the tympanum.

In the field, however, we could easily distinguish a bright green frog with dark violet markings (fig. 58) and a yellow-golden or light green frog with brown patterns (fig. 60). Since these two forms are different in nuclear DNA amount and karyotype, I consider them as separate species. The green with violet species could be easily determined as *M. pulcher* (see above). The other species shows a more variable pattern, which agrees with those originally described for both *M. bicalcaratus* and *M. methueni*. A dark brown streak from the anterior corner of the eye of the tip of the snout and a dark brown tympanic fold is constant. The middle of the back, the flanks and the upper surface of the limbs are golden yellow or light green with equally light brown

minute spots or lightbrown mottled; the brown pigment is sometimes condensed in larger dark-brown spots, mainly in young specimens, on the upper surface of the limbs dark-brown cross-bands are sometimes present. Most characteristic for *M. bicalcaratus* are two dorsolateral, irregular, narrow or broad unpatterned light streaks, bordered with a narrower irregular dark-brown punctate line; this is visible in nearly all specimens. Therefore, I consider *M. methueni* as a synonym of *M. bicalcaratus*, and I disagree with Guibé (1978) that it would be synonymous with *G. pulcher*. I have designated the specimen of Ambila as the lectotype of *G. methueni*, since the description of Angel, 1929 is based mainly on this specimen. Moreover, the figure of *G. methueni* of Angel (1931) agrees with specimens of our series of the same locality.

The eggs of *M. pulcher* are turquoise with black, in *M. bicalcaratus* beige with brown.

Notes. — The life history of *M. bicalcaratus* has already been described under the name of *G. methueni* by Razarihelisoa (1974^a). The tadpoles are the same as those of *M. punctatus* described in the present paper. The papillae around the mouth are identical, the gap in the ventral caudal fin is present at the same place and the anal tube is dextral. (These features are defined insufficiently by Razarihelisoa). The single egg mass was deposited above the water in the axil of a *Pandanus* leaf. The embryonic development is similar to those described for other *Mantidactylus* species in this paper.

Voice. — The males call, hidden in the axils of *Pandanus* and *Typhonodorum*, mainly in the evening, sometimes during the day by cloudy weather. The soft chirp was heard, during all our visits to the East Coast, where this species is very abundant. The call consists of one single note, uttered at rather long intervals. The sonagram (fig. 40), made of a male ZMA 6952 in October 1971 at 10 p.m. shows that there is an indistinct frequency intensity maximum at 4000 Hz, that the duration of one note is 0.4 sec. and consists of 4 pulses.

***Mantidactylus punctatus* sp. nov. fig. 29, fig. 66**

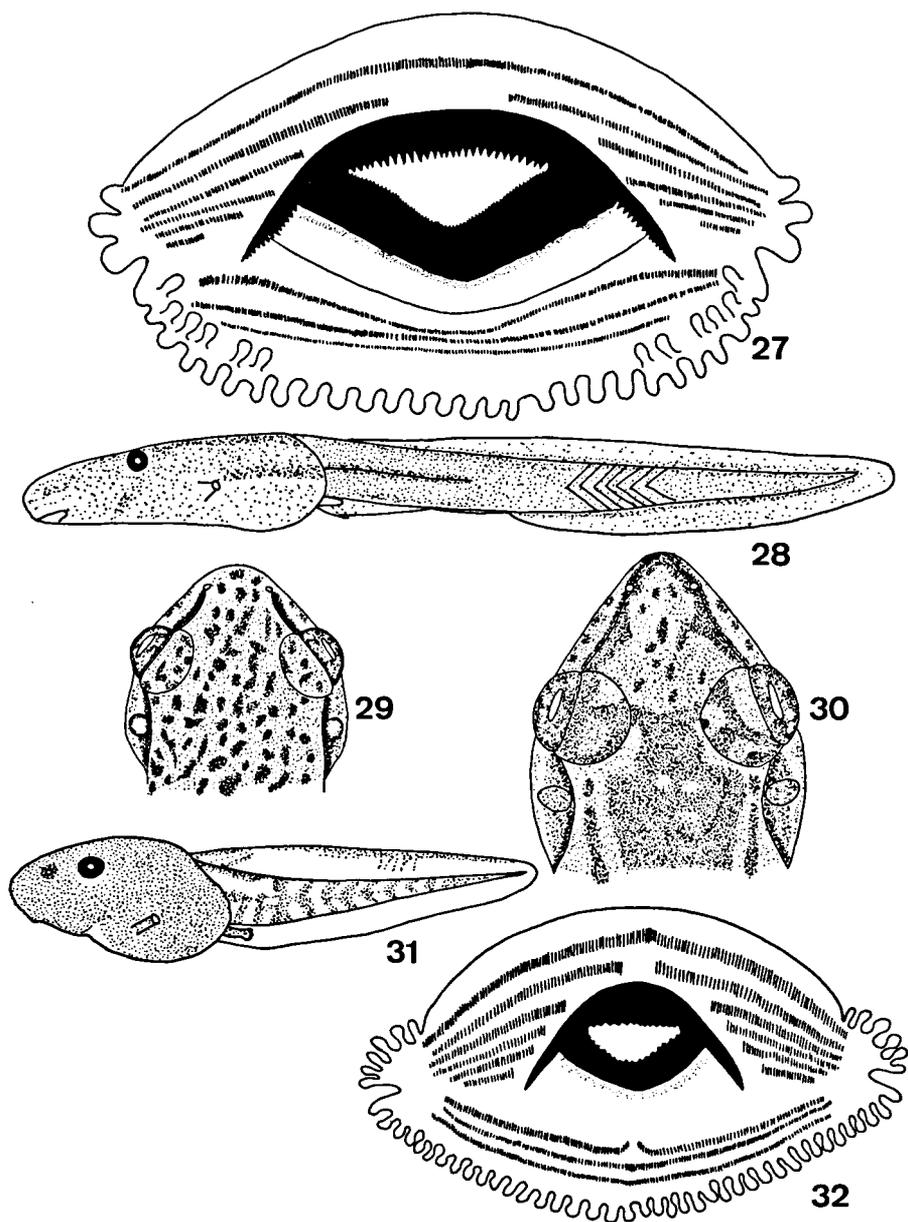
Material. — ZMA 7171 A male holotype 30.III.72; 7171 B male paratype 30.III.72; 7170 14 paratypes 12.IX.71; 7169 (tadpoles and young reared from them) 12.IX.71, all collected in axils of *Pandanus* at L 17, in the relict forest in the gulleys of the Tampoketsa.

Description of holotype. (See Table III for metrical data; fig. 29 dorsal view of the snout). — Head-length 7.5 mm; head-width 8.5 mm; horizontal diameter of tympanum 1.4 mm; horizontal diameter of eye 2.8 mm; width upper eyelid 2 mm. Head wider than long. Head about 1/3 bodylength. Snout broadly rounded in dorsal (fig. 29) and lateral profile. Upper jaw hardly projecting over lower jaw. Snout somewhat longer than horizontal diameter of eye, shorter than distance between anterior corners of eye. Canthus

distinct and round. Loreal region concave. Nostrils somewhat nearer to tip of snout than to eyes. Distance from nostril to anterior corner of eye shorter than horizontal diameter of eye. Interorbital region flat. Interorbital distance somewhat wider than internarial distance. Interorbital distance $1\frac{1}{2}$ times as wide as upper eyelid. Nostrils slightly protruding, opening dorsolaterally. Pupil horizontal, elliptical. Weak tympanic fold, covering dorsal margin of tympanum. Tympanum distinct and round. Diameter of tympanum half the horizontal diameter of eye. Diameter of disc third finger equals diameter of tympanum. Second finger longer than first. Subarticular tubercles small, oval and slightly protruding; proximal subarticular tubercles of third and fourth finger poorly developed. Two palmar tubercles, the inner large and oval, the outer small and round; one oval inner metacarpal tubercle. Small rudiment of web between second and third finger. Ventral surface of hand smooth, with a few weak supernumerary tubercles. When limbs are laid along the body, knee and elbow overlap slightly; adpressed heels overlap slightly, too. When hindlimb is adpressed, heel reaches the centre of the eye. Small, elliptical and protruding inner, and small, round outer metatarsal tubercle present. Discs on toes slightly smaller than those on fingers. Subarticular tubercles small, round and slightly protruding. Fifth toe somewhat shorter than third. Webbing rudimentary. Formula of webbing foot: 1 (1); 2i (2); 2e (1); 3i ($2\frac{1}{2}$); 3e (1); 4i (3); 4e (3), 5 (1). Ventral surface of foot smooth. Lateral metatarsalia connected. Anal opening directed posteriorly at upper level of thighs. Tongue distinctly bifid, free behind. Vomerine teeth in two oblique groups medially behind choanae. Vocal slits small, in the floor of mouth, somewhat behind commissure of jaws. Skin smooth, except the posterior part of belly which is finely granular, and the posterior part of ventral surface of the thigh which is moderately granular. Femoral gland oval and oblong, elevated and darkly pigmented (This gland is absent in female). Upperrim of palpebral membrane pigmented brown, iris silver-grey with brown reticulations, and surrounded by a brown ring. Dorsal surface light olive green with numerous brown spots; on the limbs these brown spots often condense into irregular cross-bands. Venter light green. A dark brown streak from tip of snout to anterior corner of eye. Tympanic fold dark brown, too.

Tadpoles. — Three tadpoles in stage 25 have body lengths of 6.5—8.5 mm and total lengths of 18.5—25 mm. The average ratio of tail to body length is 1.9 (range 1.8—1.9). Four tadpoles in stages 26—30 have body lengths of 9—14 mm and total lengths of 27—40 mm. The average ratio of tail length to body length is 2 (range 1.8—2.0). Four metamorphosing young have body lengths of 12—14 mm. The mouth and a lateral view of one tadpole in stage 30 (ZMA 7169) are illustrated in figs. 27, 28.

Body extremely depressed. Nostrils dorsal, situated at equal distances of eye and tip of snout. Eyes dorsal. Spiracle sinistral, aperture at $\frac{5}{8}$ from snout to end of body. Cloacal tube long and dextral to caudal fin. Caudal musculature strong, caudal fin reduced. Dorsal caudal fin not reaching the



Figs. 27—32. 27—29, *Mantidactylus punctatus*: 27, mouth of tadpole, ZMA 7169, x.25; 28, tadpole, ZMA 7169, x.3; 29, dorsal view of head, ZMA 7171A, x.3; 30, *M. flavobrunneus*: dorsal view of head, ZMA 7172, x.3; 31—32, *Aglyptodactylus madagascariensis*: 31, tadpole, ZMA 7179, x.3; 32, mouth of tadpole, ZMA 7179, x.25.

body. Ventral fin shows a gap, beginning at $1/5$ of tail length; here, the fin is replaced by a median groove formed by two parallel ridges (fig. 28). Height of caudal musculature represents $1/2$ of total tail height, at midlength of tail. Mouth small and directed downwards. Upper part of horny beak with heavy serrations. Margin of oral disc somewhat indented laterally. Papillary border with wide dorsal gap. One row of rather large papillae present, and lateroposteriorly a second inner row of small papillae. Tooth formula $1/5 + 5//3$ or $1/4 + 4//3$. Live colour brownish, anterior part of body reddish, as the blood shines through the delicate skin. The young resemble the adult; the dark streak from tip of snout to eye and the dark tympanic fold are already visible. The brown spots are less distinct; the body is light olive green, speckled with equally distributed dark pigment. The limbs are cross-banded.

The tadpoles wriggle about in the water at the leaf bases of *Pandanus*, and they are capable to leave the water by violent wiggling of the tail, and might move that way to the next lower axil. They probably feed by scraping the algal growth from the leaves, since the serrations of the horny beak are heavy. We could rear them on cooked lettuce, algae and the leaves of aquatic plants.

***Mantidactylus flavobrunneus* sp. nov., figs. 30 & 59**

Gephyromantis methueni; Millot & Guibé, 1951; 201, fig. 4, pl. VIII D; non Angel, 1929.

Material. — ZMA 7172 male holotype and female paratype collected 25.VIII.71 at L 12; 7173 male paratype VI.71 collected at L 10.

Habitat. — The frogs were all collected in the water containing axils of *Pandanus* in the rain forest on the eastern escarpment. Unlike the other species of this biotope, treated in the present paper, which are found on leaves and in leaf-axils near phytotelmes, this species is found in the phytotelmes. In the vivarium this species was also often in water, contrary to the other species collected from leaf-axils.

Description holotype. (See Table III for metrical data, fig. 30 for dorsal view of snout). — Head-length 11 mm; head-width 10 mm; horizontal diameter of tympanum 2 mm; horizontal diameter of eye 4 mm; width upper eyelid 2.8 mm.

Head slightly shorter than wide. Head-length one third of body-length. Snout acuminate, with rounded tip in dorsal profile (fig. 30), and round in lateral profile. Upper jaw projecting over lower jaw. Snout longer than horizontal diameter of eye, equal to distance between anterior corners of eyes. Canthus rostralis distinct and round. Loreal region concave. Nostrils nearer to tip of snout than to eyes. Distance from nostril to anterior corner of eye equal to horizontal diameter of eye. Interorbital region flat. Interorbital distance somewhat wider than internarial distance. Interorbital distance hardly wider than width of upper eyelid. Nostrils protruding, opening laterally. Pupil horizontal and elliptical. Weak tympanic fold present,

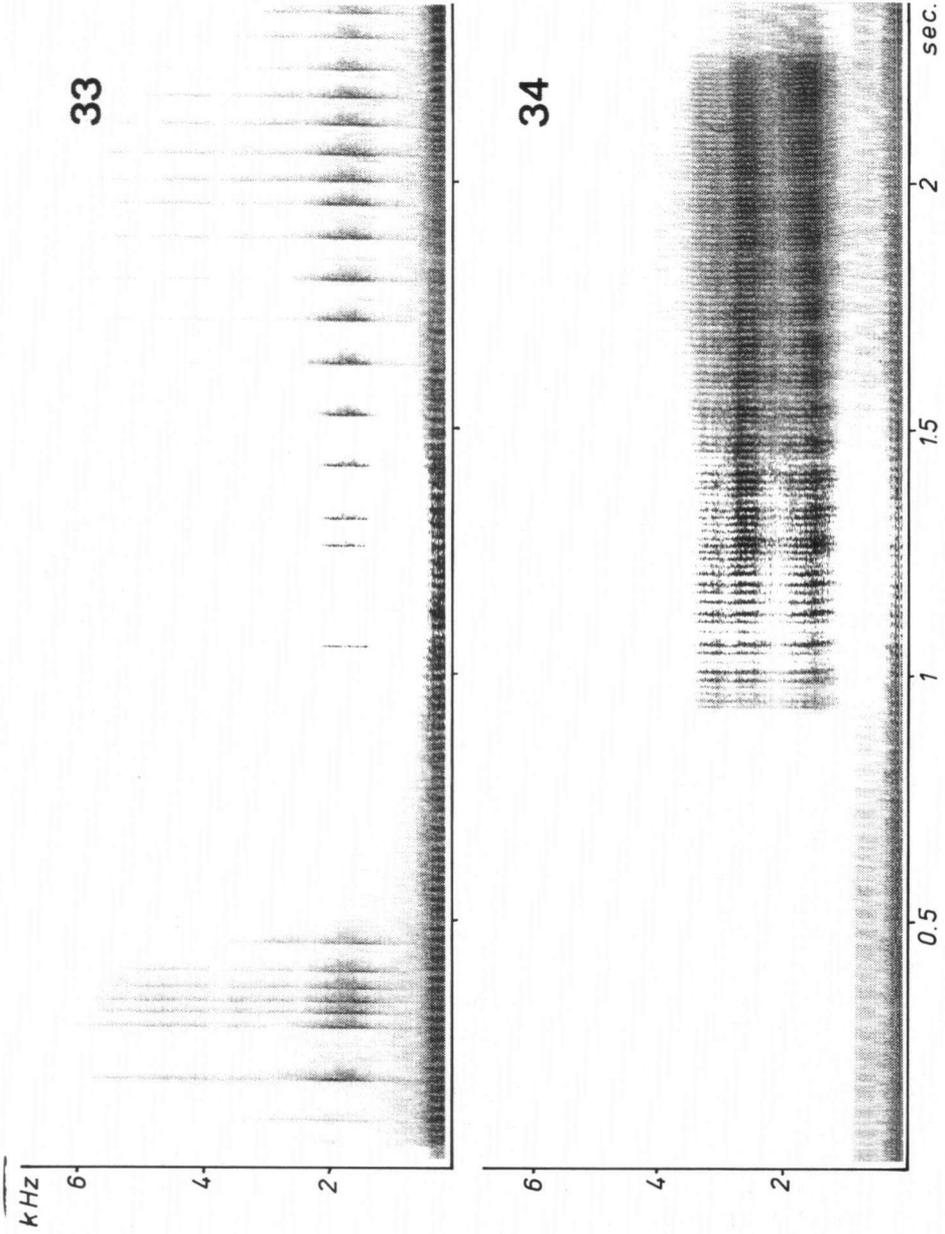
covering dorsal margin of tympanum. Tympanum distinct and round. Diameter of tympanum half the horizontal diameter of eye. Disc of third finger slightly smaller than tympanum. Second finger longer than first. Subarticular tubercles small, oval and slightly protruding. Proximal subarticular tubercles of third and fourth finger poorly developed. Two palmar tubercles, the inner large and oval, the outer small, round and flat. One oval inner metacarpal tubercle. Small trace of web between fingers. Ventral surface of hand smooth, with a few very weak supernumerary tubercles. When limbs are laid along the body, knee and elbow overlap slightly. Adpressed heels overlap strongly. When hindlimb is adpressed, the heel reaches the centre of eye. Small, elliptical and protruding inner metatarsal tubercle and small, round outer metatarsal tubercle present. Discs on toes smaller than those on fingers. Subarticular tubercles small, round and slightly protruding. Third toe slightly longer than fifth.

Formula of webbing foot: 1 (1), 2i (1½), 2e (1), 3i (2), 3e (1), 4i (2½), 4e (2½), 5 (1). Ventral surface of foot smooth, with weak granules. Lateral metatarsalia nearly entirely connected. Anal opening directed posteriorly at upper level of thighs. Tongue distinctly bifid, and free behind. Vomerine teeth in two oblique groups medially behind choanae. Vocal slits small, situated in floor of mouth behind the commissure of jaws. Skin smooth, except the posterior part of belly which is finely granular, and the posterior part of ventral surface of thigh which is moderately granular.

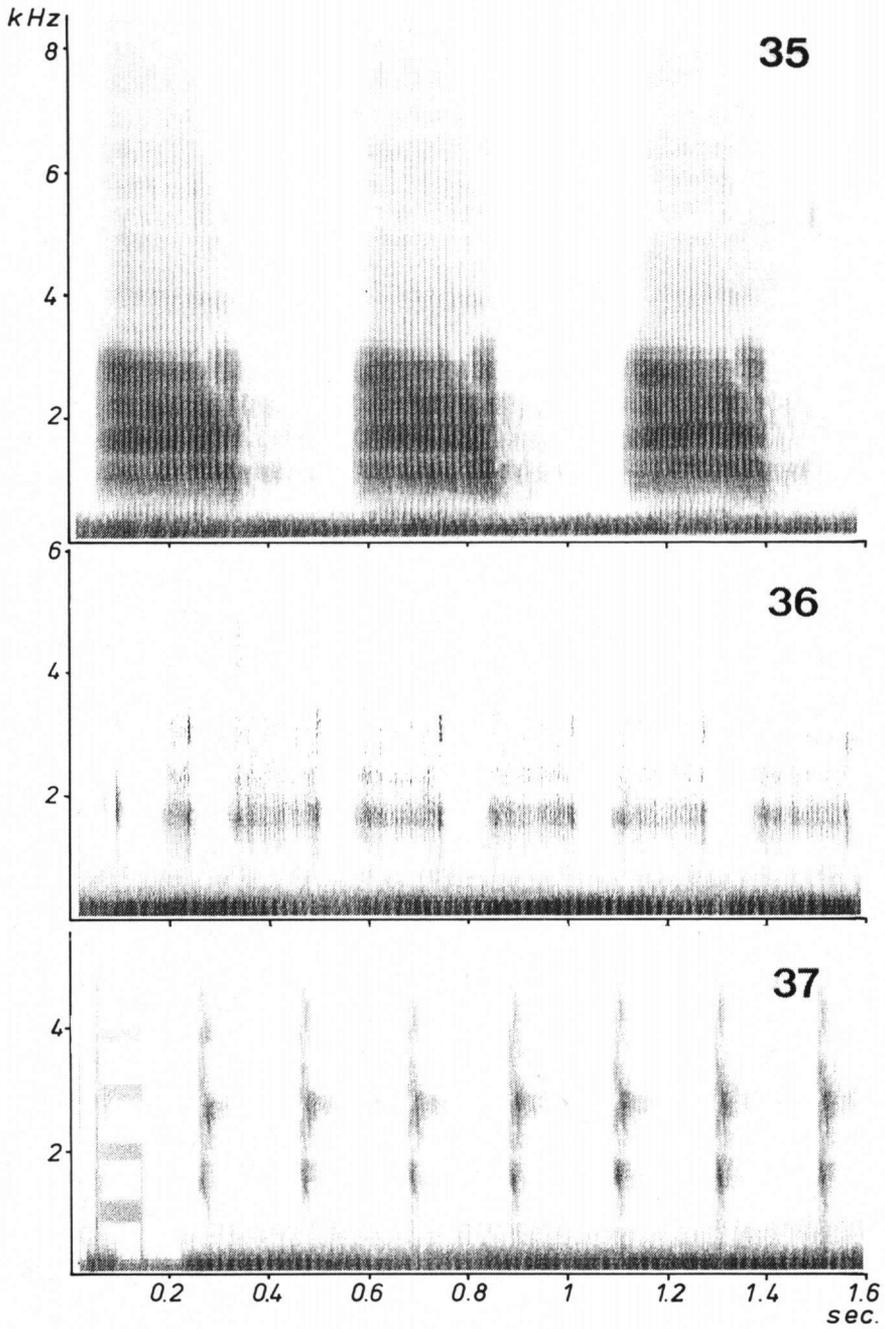
Femoral gland oval, oblong and thickened, pigmented white (more conspicuously in the male paratype than in the holotype). Palpebral membrane brown pigmented, the upper rim more than the rest. Iris brown with silver-grey reticulations, surrounded by a dark ring. Colour of back dark brown with lighter yellowish spots in a variable pattern, but mainly behind the eyes and dorsolateral. Ventral surface uniformly coloured. In life, the frog is dark brown with yellow.

The redescription and figures under the name of *G. methueni* by Millot & Guibé (1951) concern in fact the present species, and do not fit the type material of *G. methueni* (= *M. bicalcaratus*, see above).

Differential diagnosis of *M. pulcher*, *M. bicalcaratus*, *M. liber*, *M. flavobrunneus* and *M. punctatus*. — These species are recognized easily by their colour in life, as has been mentioned before. *M. liber* has relatively longer hands and feet. The ratio of hand length to body length is 0.32—0.34 in this species, and 0.23—0.28 in all others. The ratio of foot length to body length is 0.46—0.50 in *M. liber*, against 0.38—0.43 in the other species. *M. flavobrunneus* is larger than the other species. The tympanum is half the horizontal diameter of the eye, the third toe is hardly longer than the fifth, and the canthus rostralis is rounded in both *M. flavobrunneus* and *M. punctatus*. In *M. pulcher* and *M. bicalcaratus* the tympanum is 1/3 of the horizontal diameter of the eye, the third toe is at least the vertical diameter of the disc longer than the fifth, and the canthus is angular. Of all species, *M. punctatus* has the least developed web on the feet, and it differs from all



Figs. 33—34. Sonagrams, filter wide, 33, *Mantidactylus ulcerosus*; 34, *M. betsileanus*.



Figs. 35—37. Sonograms, filter wide. 35, *Mantidactylus alutus*; 36, *M. albofrenatus*; 37, *M. aerumnalis*.

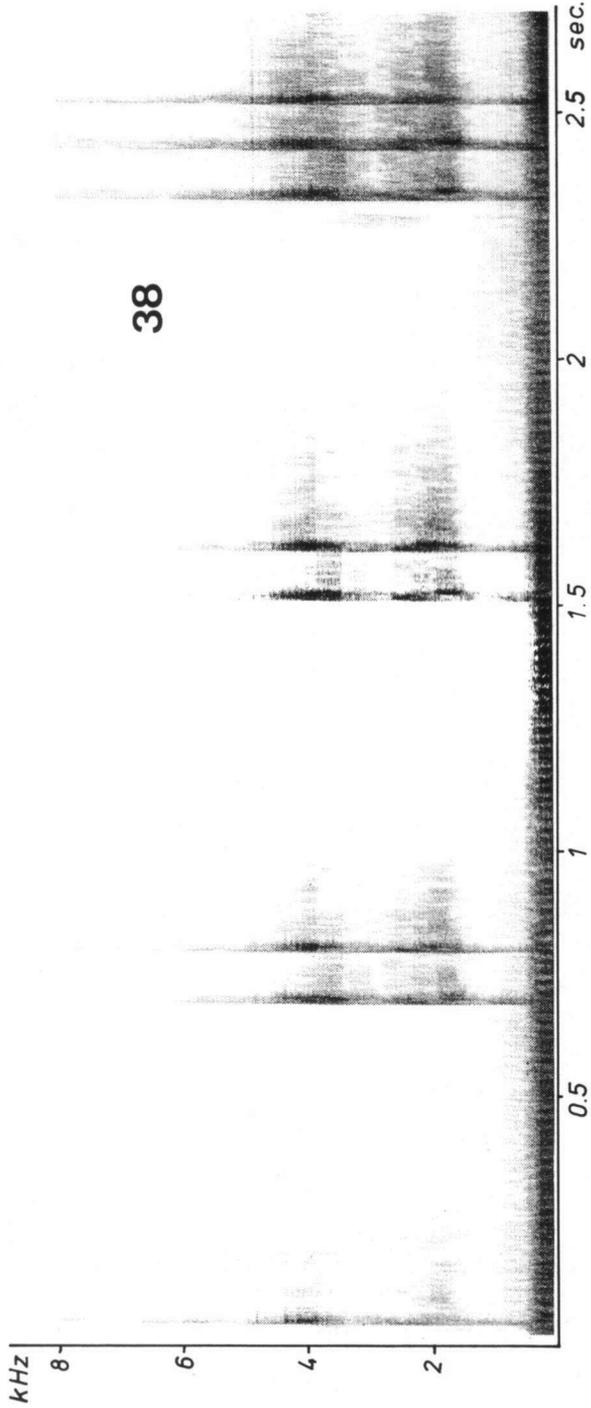
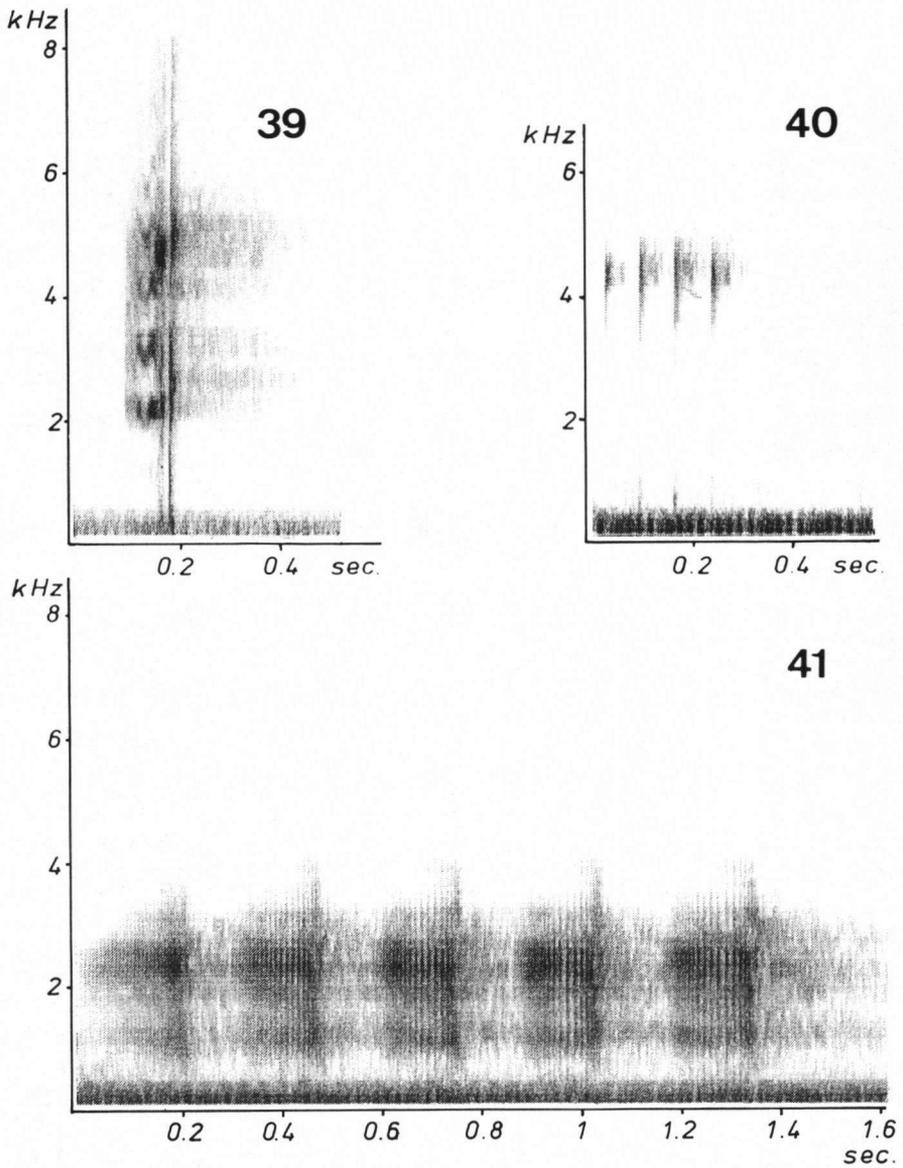


Fig. 38. Sonagram, filter wide, *Mantidactylus asper*.



Figs. 39—41. Sonagram, filter wide. 39, *Mantidactylus wittei*; 40, *M. bicalcaratus*; 41, *Aglyptodactylus madagascariensis*.

except *M. liber* by its short, broadly rounded snout. Morphological criteria to distinguish between *M. pulcher* and *M. bicalcaratus* were not discovered; they are different in colour. *M. pulcher* is bright green with violet. *M. bicalcaratus* is aureate or light green with brown.

Genus *Aglyptodactylus* Boulenger, 1919

Aglyptodactylus Boulenger, 1919: 257 (Type species: *A. madagascariensis* (Duméril, 1853)).

This monotypic genus differs from *Mantidactylus* in the following features: second tarsal not free, but connected with third and fourth tarsal. Terminal phalanges obtuse and ventromarginal groove of disc incomplete. Male without femoral glands, nuptial pad present on base of thumb in breeding season. Eggs deposited in water. Chromosomes: $2n = 26$; N.F. = 52. Nuclear DNA amount 6.1 pg.

I am inclined now to exclude *Aglyptodactylus* from the Mantellinae (see discussion p. 65. However, since previous authors consider *Aglyptodactylus madagascariensis* (Duméril) closely related to or belonging in *Mantidactylus*, it is treated here.

Aglyptodactylus madagascariensis (Duméril, 1853)

Limnodytes madagascariensis Duméril, 1853: 155.

Rana madagascariensis; Boulenger, 1882: 67.

Mantidactylus madagascariensis; Mocquard 1902: 17; Liem, 1970: 88.

Aglyptodactylus madagascariensis; Boulenger, 1919: 257 (equals *inguinalis*).

Mantidactylus (Aglyptodactylus) madagascariensis; Ahl, 1931: 35 (equals *inguinalis*); Laurent, 1943a: 2.

Aglyptodactylus madagascariensis; Guibé, 1978: 12, figs. 4—9 and 12 (equals *inguinalis* and *purpureus*).

Material. — ZMA 6821 (1) 17.II.72; 6826 (1) 10.II.73; 6827 (3) 13.XI.72; 6858 (1) 4.IV.72; 6800 (6) 6.II.72; 7179 (tadpoles and young reared from eggs) 22.X.72 at L 10. — ZMA 6857 (5 young) 1—3.VII.71; 6824 (29 juveniles) 1—3.VII.71; 6825 (3) 30.XII.71 at L 6. — ZMA 6822 (1) 28.V.72; 6823 (1) 13.X.72 at L 11.

Habits and habitat. — The present species is a ground-dwelling frog, which jumps very well. In danger, it flattens the body by pressing the belly to the ground. It becomes active at dusk. They are found in or near forest, often together with *Mantidactylus opiparis*. The eggs were found in a permanent pool, exposed to the sun, together with eggs of *Boophis granulosus* (Guibé, 1975).

Colour in life. — Back beige with dark brown markings, or beige in the middle with brown flanks. Venter yellow, undersurface of feet blackish, inguinal spots orange with black, posterior surface of thighs orange-red with black spots (orange colour absent in the young specimens).

Voice. — We only heard the calling males on the ground near the pools,

in the evening, in October and November. The call consists of a series of low pitched pulsed notes (4—5); the duration of the call group is about 2 sec. The sonagram (fig. 41), made of a male from Mandraka (ZMA 6823) in October at 9 p.m. shows that the duration of the notes varies from 0.28—0.32 sec. The number of pulses in one note is about 36. There is an indistinct dominant frequency at 2000 Hz.

Tadpoles. — Ten tadpoles in stage 25 have body lengths of 3.5—5 mm and total lengths of 9.5—14 mm. Five tadpoles in stages 26—30 have body lengths of 5—8 mm and total lengths of 14—21 mm. Twenty-two tadpoles in stages 31—39 have body lengths of 8—10.5 mm and total lengths of 21—30.5 mm. The average ratio of tail to body length is 1.7 (range 1.5—1.9) in stages 25—39. Fourteen metamorphosing young have body lengths of 10—15 mm (mean 12 mm). The mouth and lateral view of a tadpole in stage 35 are presented in figs. 31, 32. Body ovoid. Nostrils dorsolateral, aperture lateral, situated at equal distances from eye and tip of snout. Eyes situated laterally. Spiracular opening sinistral, situated at 2/3 from snout to end of body. Cloacal tube dextral to caudal fin. Caudal musculature slender. Caudal fin well developed. At midlength of tail, height of caudal musculature represents 3/10 of total tail height. Mouth small and directed anteroventrally. Margin of oral disc somewhat indented laterally. Papillary border with wide dorsal gap. One row of papillae present. Tooth formula $1/5 + 5//1/2 + 2$ or $1/6 + 6//1/2 + 2$.

The entire development took 4 to 6 weeks in the aquarium. The tadpoles were reared on boiled lettuce and pieces of earthworm.

Genus *Mantella* Boulenger, 1882

Mantella Boulenger, 1882: 141. Type species: *Mantella betsileo* (Grandidier, 1872) by designation of Liem, 1970: 100.

Mantella is very closely related to *Mantidactylus*, from which it differs in the following features: maxillary teeth absent, vomerine teeth always absent, toes free of web, and especially the brightly striking colouration. Contents: *M. aurantiaca* Mocquard, 1900; *M. betsileo* (Grandidier, 1872); *M. cowani* Boulenger, 1882; *M. pulchra* Parker, 1925.

Chromosomes: $2n = 26$; N.F. = 52 (*M. aurantiaca*, *M. betsileo*, *M. cowani*). Nuclear DNA amount 9.6—11 pg in the same three species.

Habits and habitat: Brightly coloured frogs of the forest bottom active during the day. The eggs are deposited outside the water and the tadpoles develop in temporary pools.

Mantella aurantiaca Mocquard, 1900

Mantella aurantiaca Mocquard, 1900: 110; Guibé, 1964: 260; Arnoult, 1966 (natural history) Oostveen, 1978: 51 (natural history).

Material. — ZMA 6764 (29) 21.X.71 collected near Perinet (Antaniditra) in swamp forest.

Colour in life. — Orange-red.

Life history. — The present species is active during the day; the frogs jumped in great numbers on the forest floor. This conspicuous frog is probably poisonous, since in contact with damaged skin it causes an itching and painful sensation. In the vivarium, it calls during the day in October and November, the call being a high pitched chirp. Arnoult (1966) and Oostveen (1978) observed the behaviour and larval development.

The male redoubles his mating call, when a female approaches. Then the male jumps towards the female and clasps her with his arms in either an inguinal or axillary embrace. The duration of the embrace is very short, a matter of minutes. Then the female follows the male and both disappear under the vegetable mould, so that it was not possible to follow the mating and oviposition. Arnoult observed once oviposition in the vivarium. The male embraced the female loosely and continued calling, the oviposition followed immediately. The egg mass is attached underneath a dead leaf or other object, outside the water. The eggs are 1.5—2 mm in diameter, 20—60, and cream-white. After 14 days the hatchling wriggled free from the liquified jelly mass and found its way to the water. The hatchling is identical to the hatchlings of certain *Mantidactylus* species described in the present paper: no external gills; a mouth opening, the rudiment of two oral suckers, eyes and anus present. The tadpole resembles those of the *Mantidactylus wittei* and *M. depressiceps* groups.

***Mantella betsileo* (Grandidier, 1872)**

Dendrobates betsileo Grandidier, 1872: 11.

Mantella betsileo; Boulenger, 1882: 141; Guibé, 1964: 263.

Material. — ZMA 6726 (1 female) 10.I.72 collected at Nossi-Bé, Mont Passot; between fallen leaves near temporary water in company of *Mantidactylus wittei*. The dissected female showed about 60 cream-white eggs, 2 mm in diameter.

Colour in life. — Middle of back orange-red; flanks black.

***Mantella cowani* Boulenger, 1882**

Mantella cowani Boulenger, 1882: 471; Guibé, 1964: 263.

Material. — ZMA 6719 (4) XI.71 collected by Dr. C. Blanc near Fort Dauphin. ZMA 6754 (4) 10.XI.70 collected by Dr. C. Blanc in the Andringitra mountains at an altitude of 1000 m.

Colour in life. — Venter black with light blue spots; undersurface of legs orange. Back grey in the middle, flanks black, arms turquoise, legs orange (Fort Dauphin). Back entirely green in the male, green with black in the female, the latter orange with black legs (Andringitra).

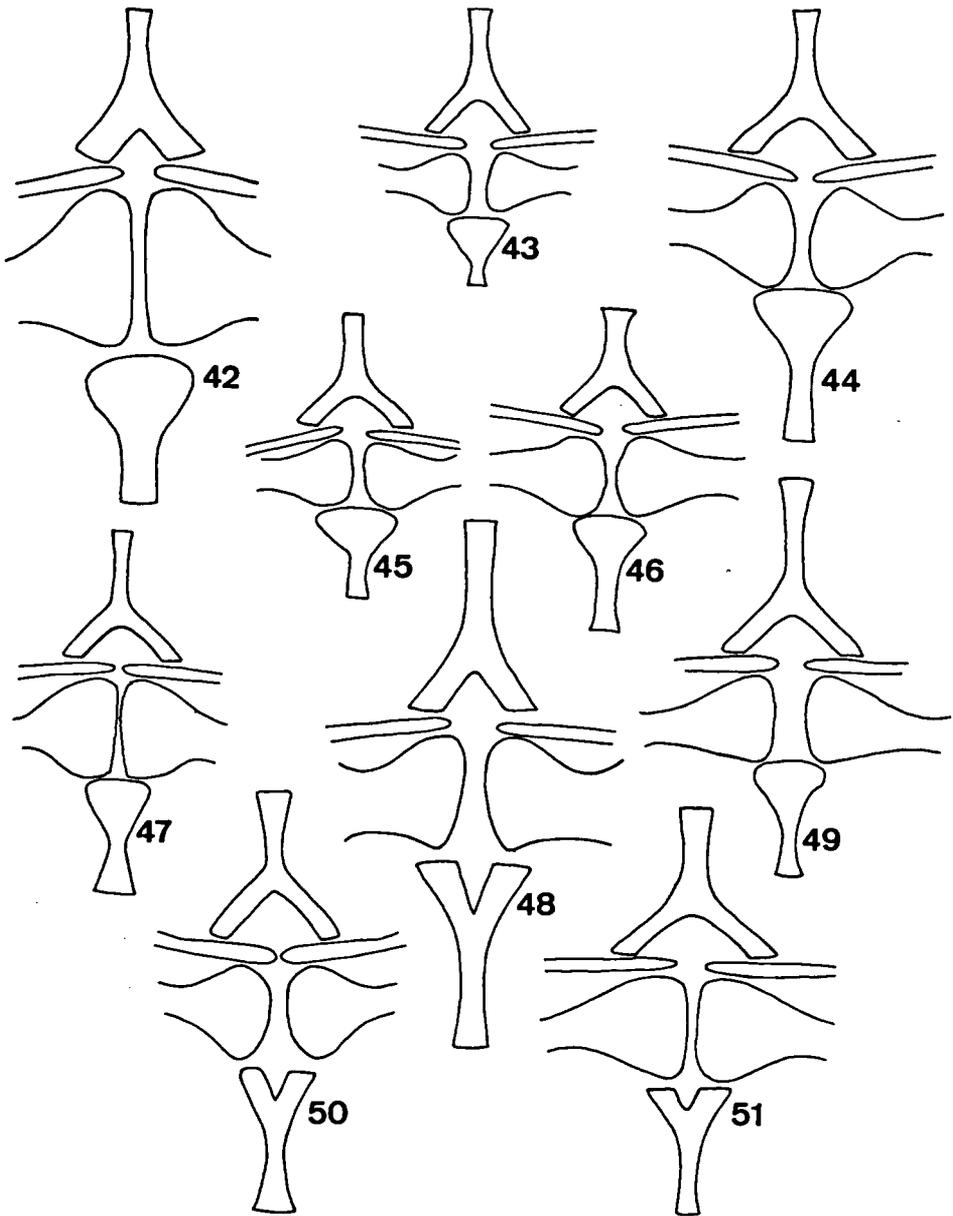
Notes. — The species was heard calling in the vivarium, in the morning and during the day in November and December. The call is a high-pitched chirping thrill, resembling the sound of *M. aurantiaca*. One egg mass (unfertilized) was deposited on a tree-trunk in the terrarium. It contained 65 eggs, 2.2 mm in diameter, white yellowish coloured.

GENERIC RELATIONSHIPS AND PHYLOGENETIC CONSIDERATIONS

The results of this study involve three main points: (1) The mutual affinities of the genera treated, and their relationship to the endemic genus *Boophis* Tschudi, 1839 (= Malagasy species of the genus *Rhacophorus* Kuhl, 1822, sensu Laurent, 1943) are elucidated. (2) The genus *Gephyromantis* Methuen, 1919, is synonymized with *Mantidactylus* Boulenger, 1895. (3) The genus *Mantidactylus* is divided into 10 species-groups.

The Malagasy genera studied in the present paper, together with the genus *Boophis* and several foreign genera are classified with the family Rhacophoridae by most authors (Ahl, 1931; Noble, 1931; Liem, 1970; Guibé, 1978). A division into subfamilies is not made. Moreover, these authors have suggested a clear mutual relationship between the genera treated in this paper and *Boophis*. This view was not accepted by Laurent (1946, 1951), who has suppressed the family Rhacophoridae, and divided the Ranidae into a greater number of subfamilies. In his opinion, the genus *Boophis* should be placed together with several non-Malagasy genera into the subfamily Rhacophorinae, whereas the Malagasy genera *Mantidactylus* (including *Aglyptodactylus* Boulenger, 1919, as a subgenus), *Gephyromantis* Methuen, 1919, *Trachymantis* Methuen, 1919, *Mantella* Boulenger, 1882, and the Asian genus *Pseudophilautus* Laurent, 1943, would form together the subfamily Mantellinae. In this system, the endemic genus *Boophis* is not so clearly related to the other aforementioned Malagasy genera. This agrees to a large extent with my findings.

Although the morphological differences between *Mantidactylus* and *Boophis* are scanty, I regard *Boophis* (cf. Blommers-Schlösser, in prep.) as a genus of quite different origin. The major argument, in my opinion, is the completely different way of mating, which is reflected in the main taxonomic character of *Mantidactylus* (including *Gephyromantis*): the possession of femoral glands. The mating act like we have seen it in *M. liber* (cf. Blommers-Schlösser, 1975), *M. depressiceps* and *M. blommersae* is almost furtive, and does not comprise an amplexus. During this short mating contact, the femoral glands of the male (accessory sexual character in *Mantidactylus*) touch the female, and oviposition starts immediately. This mode of mating is not quite appropriate for ground-dwelling species, because they have to deposit eggs on a more or less horizontal surface, and in this manner the sperm would not find its way to the eggs, and the male would not have enough grip. A short, loose axillary embrace is observed in *Mantella*



Figs. 42—51. Ventral views of bony elements of the shoulder girdle (cartilage not figured). From top to bottom. Bony style of omosternum, procoracoids, coracoids, bony style of sternum. 42, *Mantidactylus guttulatus*, ZMA 6817, x.3; 43, *M. ulcerosus*, ZMA 6819, x.6; 44, *M. albofrenatus*, ZMA 7001, x.12.5; 45, *M. lugubris*, ZMA 6747, x.6; 46, *M. aglavei*, ZMA 6871, x.6; 47, *M. asper*, ZMA 6868, x.10; 48, *M. boulengeri*, ZMA 6967, x.12.5; 49, *M. wittei*, ZMA 7059, x.12.5; 50, *M. depressiceps*, ZMA 6979, x.8; 51, *M. pulcher*, ZMA 7214, x.12.5.

aurantiaca (cf. Arnoult, 1966; Oostveen, 1978) as well as in *Mantidactylus curtus* (cf. Arnoult & Razarihelisoa, 1967), both ground-dwelling species.

I am led to conclude that the mating act of the terrestrial species is not fundamentally different from the mating act of the arboreal species. In both the mating is characterized by its brevity, and by the fact that the ventral surface of the thighs of the male touch the dorsal surface of the female. The amplexus of the ground-dwelling species is more an embrace, and not the strong clasp so common in the Anura. Therefore, I believe that the femoral glands are functional as a device for stimulation of oviposition, and perhaps for species recognition. This characteristic, short mating act occurs probably throughout the genera *Mantidactylus*, *Mantella* and *Trachymantis*, for the following reasons: We have never observed a real amplexus in any *Mantidactylus* or *Mantella* species. Also, the accessory sexual characters, which are normally present in males of species in which a strong amplexus forms an integral part of the mating contact, are absent in *Mantidactylus* and *Mantella*: the males of the Mantellinae lack nuptial excrescences and are hardly smaller than the females. Thirdly, a mating act, as observed in the Mantellinae, must necessarily take place on land. Our observations were consistent in this respect. The eggs of *Mantidactylus* and *Mantella* were always found outside the water, and the eggs are rather large-sized and small in number, as could be noted also in dissected females. We never came across the genus *Trachymantis*, in which femoral glands occur too, indicating a similar mating behaviour.

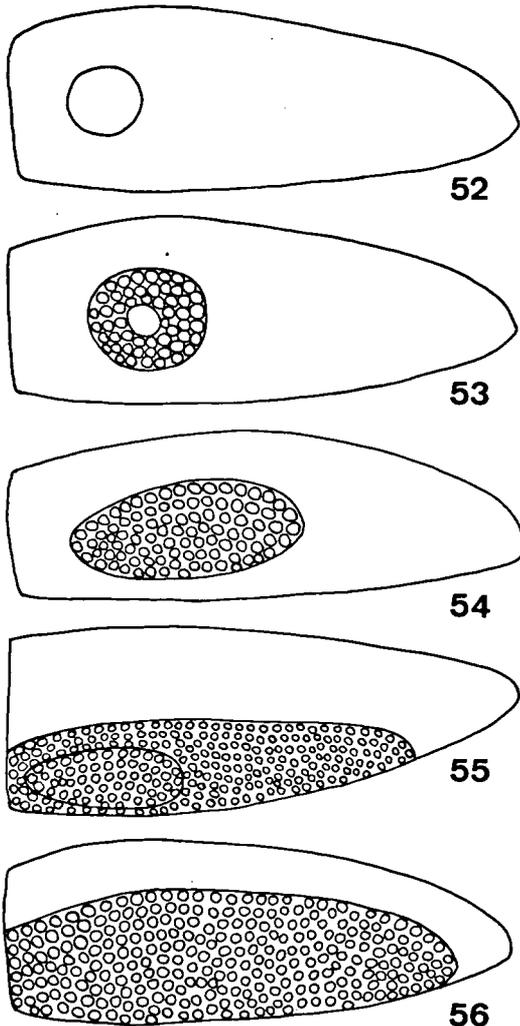
In contrast with the cursory mating act in the Mantellinae, we have observed frequently a long axillary amplexus in various species of *Boophis*, not different from that known in other Ranidae and Rhacophoridae. This difference in mating behaviour is, in my opinion, sufficient reason to consider the Mantellinae as a distinct group within the Ranid- Rhacophorid complex (including *Boophis*).

The genus *Mantella* is very closely related to the genus *Mantidactylus* (especially to the *wittei*, *depressiceps* and *pulcher* groups, see Table IV for comparison). The cytogenetic data agree with those of these three species groups (cf. Blommers-Schlösser, 1978). The tadpole resembles those of the *wittei* and *depressiceps* groups (cf. Arnoult, 1966). The lateral metatarsalia are entirely connected. The omosternum is widely forked posteriorly and the sternum is slightly forked anteriorly in *Mantella cowani* (cf. Guibé, 1978) and the femoral glands are diffuse.

The monotypic genus *Aglyptodactylus*, treated by Laurent (1946) as a subgenus of *Mantidactylus* should be excluded from the Mantellinae. Femoral glands are absent in this taxon, and the males, which are considerably smaller than the females, show nuptial pads in the breeding season. The eggs are deposited in the water, and are small. The cytogenetic data place this genus far from the Mantellinae. Probably, *Aglyptodactylus* is related to *Boophis*. The mode of reproduction is apparently the same. The second tarsal is not free, but connected with the third and fourth as in

Boophis, and the cytogenetic data bear resemblance to those of some *Boophis* species.

Guibé (1945, 1947) has defined the genus *Gephyromantis* only by a combination of two morphological characters. But the same author also noticed that the genus *Mantidactylus* shows such a great diversity in



Figs. 52—56. Schematic drawings of femoral glands (ventral surface of thigh) of males. 52, *Mantidactylus guttulatus* group; 53, *M. ulcerosus*; *M. lugubris*; *M. albofrenatus* groups; 54, *M. aglavei*, *M. asper* groups; 55, *M. boulengeri*; *M. wittei*; *M. pulcher* groups; 56, *M. depressiceps* group.

characters, that it is probably heterogeneous. Since the reproductive biology of both genera is the same, and the larvae and cytogenetic data do not fit in the existing generic division, I have studied and compared a number of morphological characters in the species collected by me, which represent about three-quarters of the species known in these genera. The external morphology of the various species was extensively studied, but of the internal characters only the form of the shoulder girdle was considered. More osteological (and muscular) characters of some *Mantidactylus* species were investigated by Laurent (1943a, 1943b, 1946, 1951) and Liem (1970) on the suprageneric relationships within the Ranidae and Rhacophoridae. Guibé (1975a, 1978) paid mostly attention to the characters of the vertebral column. The observations of these authors are often difficult to interpret. For example, Laurent (1943a) described a shoulder girdle of *Mantidactylus cowani* (= *M. lugubris*) which differs from what Guibé (1978) and I have observed in any *Mantidactylus* species, but agrees with the structure common in *Boophis*. Liem (1970) mentions nuptial pads in *Mantidactylus*, while he saw them most probably only in *Aglyptodactylus*. Finally, the observations, include various contradictions with regard to the type (procoelous or diplasiocoelous) of the vertebral column. The investigations of (Guibé, 1978) are the most reliable in this respect, since he treated the species taxonomically. In eleven of the thirteen species studied of the genera *Mantidactylus* and *Gephyromantis*, he found a diplasiocoelous vertebral column, in the other two: *Mantidactylus guttulatus* and *Gephyromantis pulcher* he found a procoelous vertebral column. Also this character is not correlated with the existing generic division: *Mantidactylus* and *Gephyromantis*.

To get more insight in this generic division, I have selected the homologous characters 1—6 (in Table IV), characters used commonly in frog taxonomy at genus level. I was not able to indicate the direction of the transformation of the different character states of these characters. Table IV shows clearly that none of the character states concurs consistently with any other. This holds true also for *Gephyromantis* character-states 2b and 5c, since the combination 2b and 5a is also found. In fact, the different character-states occur independently from each other in different combinations.

This typical patchwork of traits indicates that the group as a whole is homogeneous at genus level. Therefore, I have refrained from splitting this group into more genera, but instead, reinserted the *Gephyromantis*-species (species groups 7, 8, 10 partially) into *Mantidactylus*.

The occurrence of the various combinations of character-states (Table IV, row 1—6) have formed the basis for the division of the genus *Mantidactylus* into species-groups. These groups have been defined primarily on the morphological features of the adults (Table IV, also 7 and 8) and tadpoles. But, whereas the morphology of the frogs, whether adult or larvae, reflects both the phyletic relationships and the adaptations to different biotopes, the cytogenetic data reflect mainly the former. Hence, the grouping was done in

such a manner as to avoid contradiction with the cytogenetic data, which should be given priority in a contemplation on the evolutionary relationships between the species-groups.

The cytogenetic study (Blommers-Schlösser, 1978) revealed two different major changes in the evolution of the genomes within the genera *Gephyromantis*, *Mantidactylus* and *Mantella*. In the first group (the *Mantidactylus wittei*, *depressiceps* and *pulcher* groups in the present paper and *Mantella*) the morphology of the karyotype is stable, the diploid number is 26 and the N.F. is 52. However, the DNA amount of closely related species is different. This means that tandem gene duplications along the chromosomes have played a major role in the speciation of this group. In the second group (the *Mantidactylus guttulatus?*, *ulcerosus*, *lugubris*, *albofrenatus*, *aglavei*, *asper* and *boulengeri* groups) the DNA amount is stable. Two chromosome

Explanation of Table IV

Numbers 1 to 8 are morphological characters of the adult frogs, 9 is the habitat of the adult frog and 10 of the larvae, 11 and 12 are morphological characters of the tadpoles, 13 gives the cytogenetic data.

1. Omosternum. a = moderately forked; b = broadly forked.
2. Sternum. a = entire; b = slightly forked.
3. Femoral gland. a = oblong present in males; b = diffused in both sexes; c = round with a central notch in males, smaller without notch in females; c' = round without notch in males, smaller in females.
4. External vocal sac. a = not apparent; b = single median subgular; c = paired lateral subgular.
5. Lateral metatarsalia. a = separated; b = separated only by a groove; c = almost entirely to entirely connected.
6. Disc of fingers. a = larger than twice the diameter of the adjacent phalanx; b = equal to or smaller than twice the diameter of the adjacent phalanx.
7. Outer metatarsal tubercle: + = present; - = absent.
8. Exclusive characters. A. Body size of adults 90—120 mm (largest size in other groups 65 mm). B. Two dorsolateral glandular ridges, from behind eyes (not connected with tympanic fold) till end of back. C. Denticulated cutaneous fold borders anterior limb from elbow to outer finger and posterior limb from heel to outer toe. D. Triangular dermal appendage on heel. E. Testicle black on the outside. F. Posterior part of gut black.
9. Habitat of adult frog. a = arboreal; b = transitional between arboreal and terrestrial (this means that these frogs climb in the low vegetation, but jump also on the ground, in group 3 the discs are also used to attach to stones in running water); c = terrestrial.
10. Habitat of the larvae. a = stagnant water; a' = phytotelmes; b = running waters; b' = gently flowing to stagnant waters; c = outside the water: direct development.
11. Tail of tadpole. a = fins well developed, musculature moderate; b = caudal dorsal fin reduced anteriorly, musculature strong; c = fins reduced, musculature strong.
12. Mouth of tadpole. a = horny beak well developed, tooth formula $1/2 + 2/1 - 1/6 + 6/3$; oral disc indented laterally; b = horny beak well developed, tooth formula $2/1 + 1/2$; oral disc round; c = horny beak reduced, no teeth, enlarged flaps around the mouth; d = horny beak reduced, a few minute teeth.
13. Cytogenetic data. a: $2n = 26$, N.F. = 52, nuclear DNA amount variable; b: $2n = 26$, N.F. = 44—52, nuclear DNA amount stable; b': $2n = 24$, N.F. = 44—48, nuclear DNA amount stable.

Table IV. Characters and character states of the *Mantidactylus* species groups.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1. <i>M. guttulatus</i> group	a	a	c'	a	a	b	±	A	c	?	b	a	b?
2. <i>M. ulcerosus</i> group	b	a	c	a	a	b	±		c	b'	b	a	b'
3. <i>M. lugubris</i> group	b	a	c	a	a	a	±		b	b	b	b	b
4. <i>M. albofenatus</i> group	b	a	c	a	b	b	±	B	c	b	b	c	b
5. <i>M. aglavei</i> group	b	a	a	b	a	a	—	C	a	b	b	d	b'
6. <i>M. asper</i> group	b	a	a	c	a	a	±	D	b	c			b
7. <i>M. boulengeri</i> group	a	b	a	c	c	a	±		b	c?			b
8. <i>M. wittei</i> group	b	a+b	a	a	a+c	b	+	E	b	a	a	a	a
9. <i>M. depressiceps</i> group	b	a+b	b	b	a	a	+	E	a	a	a	a	a
10. <i>M. pulcher</i> group	b	b	a+b*	a+b*	c	a	+	E+F	a	a'+a*	c+a*	a	a

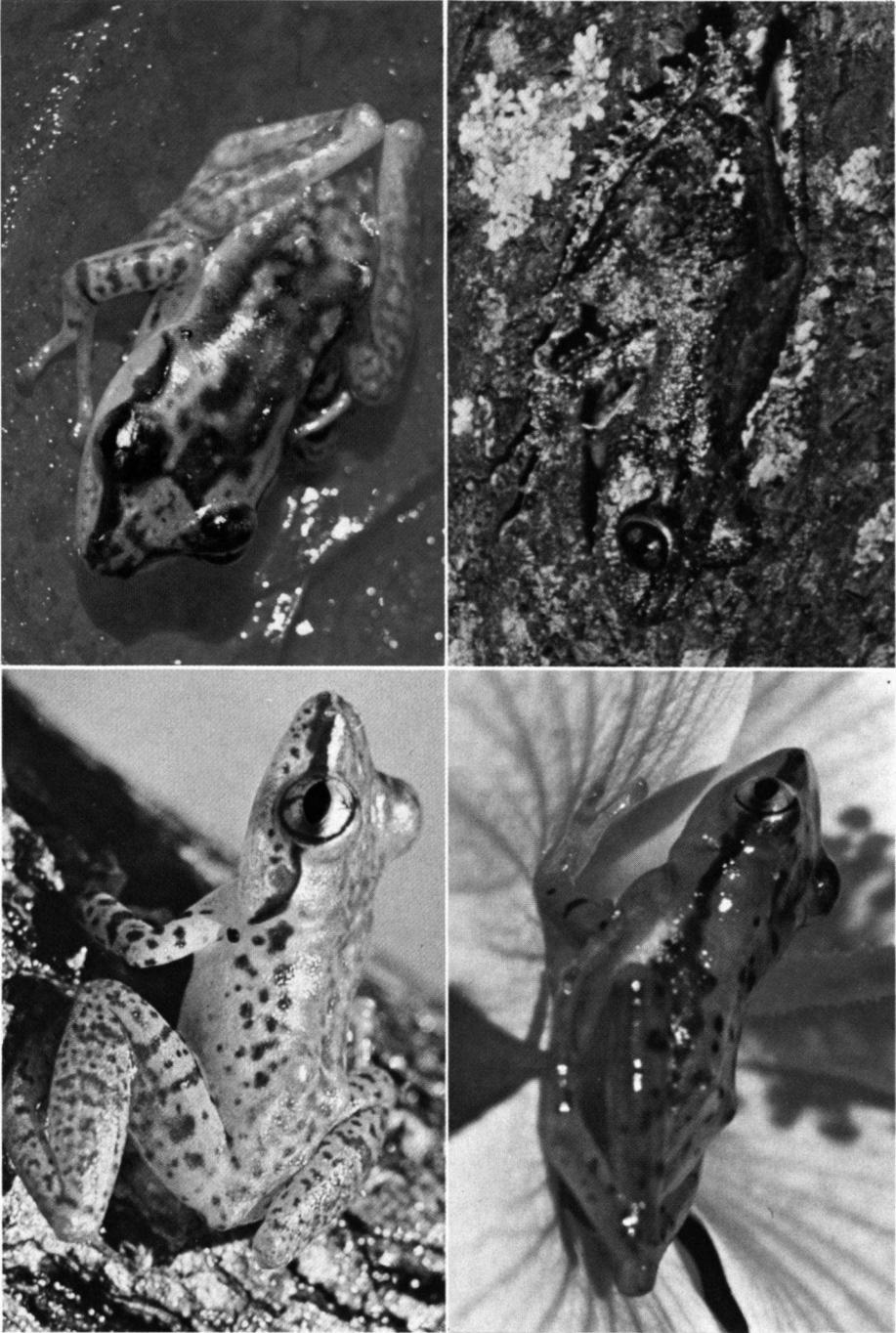
* = *M. liber*.

numbers occur 26 and 24, the latter is a derivative of the former. The N.F. is 44—52. The acrocentric chromosomes in this group illustrate that major changes in the karyotypes of this group are primarily the result of pericentric inversions.

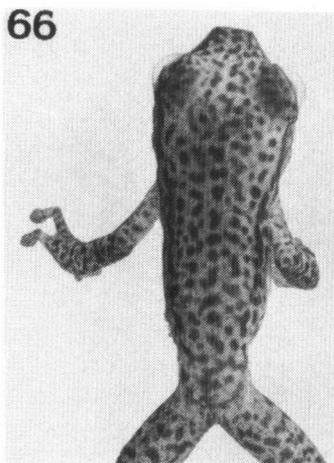
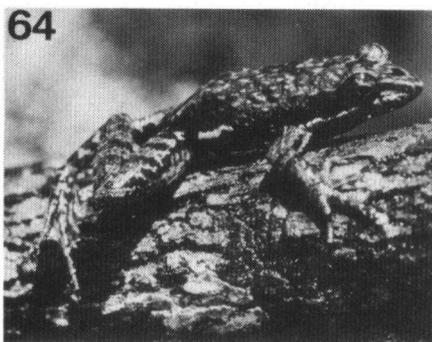
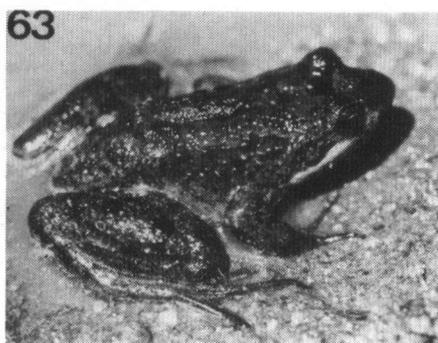
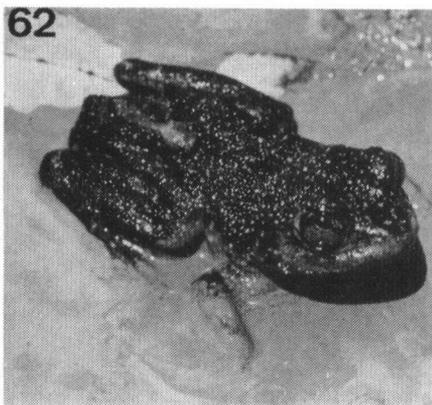
According to this view, groups 8—10 are more closely related (row 13a, Table IV). This lends more weight to the characters common to these three groups: they share the same shoulder girdle (1b and 2b), have black testicles (8E) and outer metatarsal tubercles (7+). It indicates also the affinity (11a+c, 12a) between the two types of larvae found in these groups. The larvae in groups 8 and 9, and those of *M. liber* (placed in group 10 for reasons of adult morphology; 5c and 8F) are similar, both in mouth-structure and in tail. The latter is moderately muscular and does not show a reduction of the fin. These tadpoles occur in stagnant water. In group 10, the entire larval development is completed in phytotelmes, and the larva is strongly flattened and shows a very pronounced reduction of the fins, as adaptations to this biotope. Since the adults in group 9 hide also in the axils of large plants, and because the position of *M. liber* is intermediate between groups 9 and 10, I regard the larva of group 10 as a specialized derivative of group 9.

The cytogenetic data indicate also a close relationship between groups 2—7 (13b, b'). Characters common to these groups as a whole do not exist, but in the arrangement of Table IV, each group shares character-states with the next. The tadpoles in each of the groups 2—5 have a characteristic mouth structure (12, a, b, c, d), but the tail is similar in all groups (11b). The tail musculature is heavy and the dorsal fin is anteriorly reduced. A heavy tail musculature can be explained as an adaptation to the life in streams, where the tadpoles of groups 3—5 are found. The mouth structures reflect probably the different ways of feeding in the groups, as shown in the tadpoles of group 2, which occur in (almost) stagnant water and have a mouth of the generalized pond type. The heavy tail in this group indicates its phyletic relationship to the groups 3—5. This relationship is also supported by the cytogenetic data. Direct development occurs in group 6 and probably also in group 7; the development in group 1 is not known.

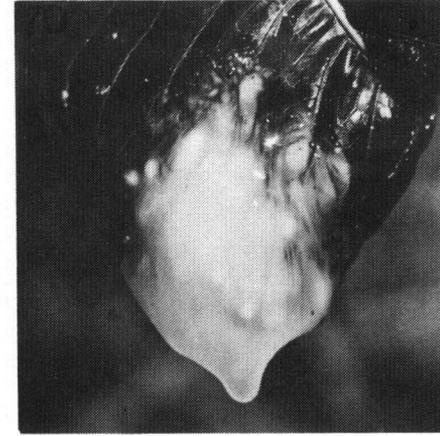
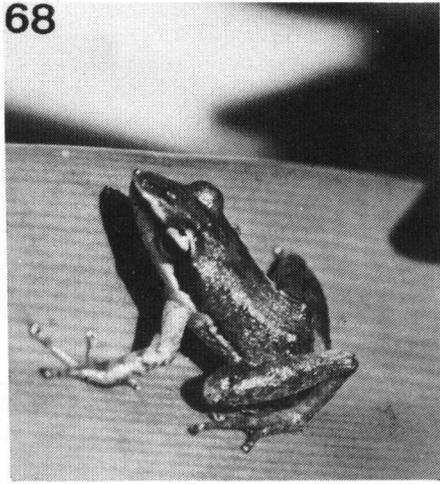
The division of *Mantidactylus* into species-groups demonstrates an adaptive radiation of this genus, which includes both adults and tadpoles. When considering the habitats of tadpoles and adults (9 and 10, Table IV), it is obvious that the combination of both habitats is almost typical for each group. The ancestor of all Mantellinae was probably a treefrog, because of the intercalary cartilage between the disc and the adjacent phalanx in all species.



Figs. 57—60. 57, (above right) *Mantidactylus aglavei*, male, ZMA 6871; 58 (below right), *M. pulcher*, female, ZMA 7214; 59 (above left), *M. flavobrunneus*, male, ZMA 7173; 60 (below left), *M. bicalcaratus*, female, ZMA 6952.



Figs. 61—66. 61, *Mantidactylus guttulatus*, ZMA 6817; 62, *M. grandidieri*, ZMA 7116; 63, *M. curtus*, ZMA 6863; 64, *M. femoralis*, male, ZMA 6789; 65, *M. aerumnalis*, female, ZMA, 6777; 66, *M. punctatus*, male, ZMA, 7170.



Figs. 67—70. 67, *Mantidactylus luteus*, male, ZMA 6725; 68, *M. wittei*, male, ZMA 7059; 69, *M. tornieri*, ZMA 7110; 70, *M. depressiceps*, egg mass, ZMA 6981.

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