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Observations on the larval development of some Malagasy frogs, with notes on their ecology and biology (Anura: Dyscophinae, Scaphiophryninae and Cophylinae)

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ABSTRACT

In this paper, tadpoles belonging to three related groups of Malagasy frogs are described; both the Dyscophinae and the Cophylinae are subfamilies of the Microhylidae, while the Scaphiophryninae are alternatively assigned to this subfamily or to the Ranidae. The larvae were reared up to the juvenile stage in order to classify them.

The tadpole of *Dyscophus quinquelineatus* (Dyscophinae), the first to be described within the genus, is of the microphagous microhylid type; it has a median spiracle, neither denticles nor beak or papillae, the nostrils do not appear until shortly before the metamorphosis, and the forelimbs develop behind the branchial chambers.

The tadpole of *Pseudohemisus granulosus* (Scaphiophryninae), the first to be described within the genus with certainty, shows microhylid features, such as the absence of beak and denticles, the retarded appearance of the nostrils, and the development of the forelimbs behind the branchial chambers. However, the intermediate position of the spiracle, between median and sinistral, and the papillae around the mouth indicate affinities with other groups. The larval form of the Scaphiophryninae is just as difficult to classify as the adult. The systematic position of this subfamily is discussed and the assumption is made that it represents a relict of the ranoid stock from which the Microhylidae evolved.

The larval development in the arboreal species *Platyhyla grandis, Plethodontohyla notosticta* and *Anodonthyla boulengeri* (Cophylinae) is similar. The large eggs are deposited separately in arboreal holes filled with water, mainly in the dry season. The larva hatches just before the limb buds occur; it has neither spiracle, nor anus, beak, denticles or papillae, and it is free-swimming. It completes its development on the large amount of yolk within the nesting site.

It is demonstrated, that parental care occurs in this group. The male stayed with the developing spawn in all cases. Removal of the male caused a high mortality of the spawn, due to mould.

The food items, recovered from species of Cophylinae, consisted mainly of ants.

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Introduction

Parker (1934) subdivided the Microhylidae into seven subfamilies, of which three, the Dyscophinae, the Cophylinae and the Microhylinae occur in Madagascar. The first group is represented by the endemic genus *Dyscophus* Grandidier, 1872; the Cophylinae are confined to Madagascar, and the first malagasy species of the Microhylinae has been described recently (Guibé, 1973). The Scaphiophryninae, another endemic subfamily, is either placed in the Microhylidae or in the Ranidae, and is also included in this paper.

The life history of the malagasy microhylids is hardly known. Millot & Guibé (1951) examined tadpoles, collected in the presence of *Plethodontohyla notosticta* Günther, 1877, from the axil of a *Ravenala*, and of *Platypelis pollicaris* Boulenger, 1888, from a hollow bamboo. Guibé (1952) recorded tadpoles, collected in the presence of *Plethodontohyla tuberata* (Peters, 1883) from a burrow. All three species belong to the Cophylinae.

Angel (1931) assigned tadpoles, captured in the environment of *Pseudohemisus verrucosus* Angel, 1930, and *P. longimanus* Angel, 1930, to these species, which belong to the Scaphiophryninae. This allocation is questionable, however.

Parker (1934) emphasized the need for information regarding the life histories of the malagasy microhylids, in order to facilitate the determination of phylogenetic affinities, at present established solely by the comparison of adult morphological characteristics.

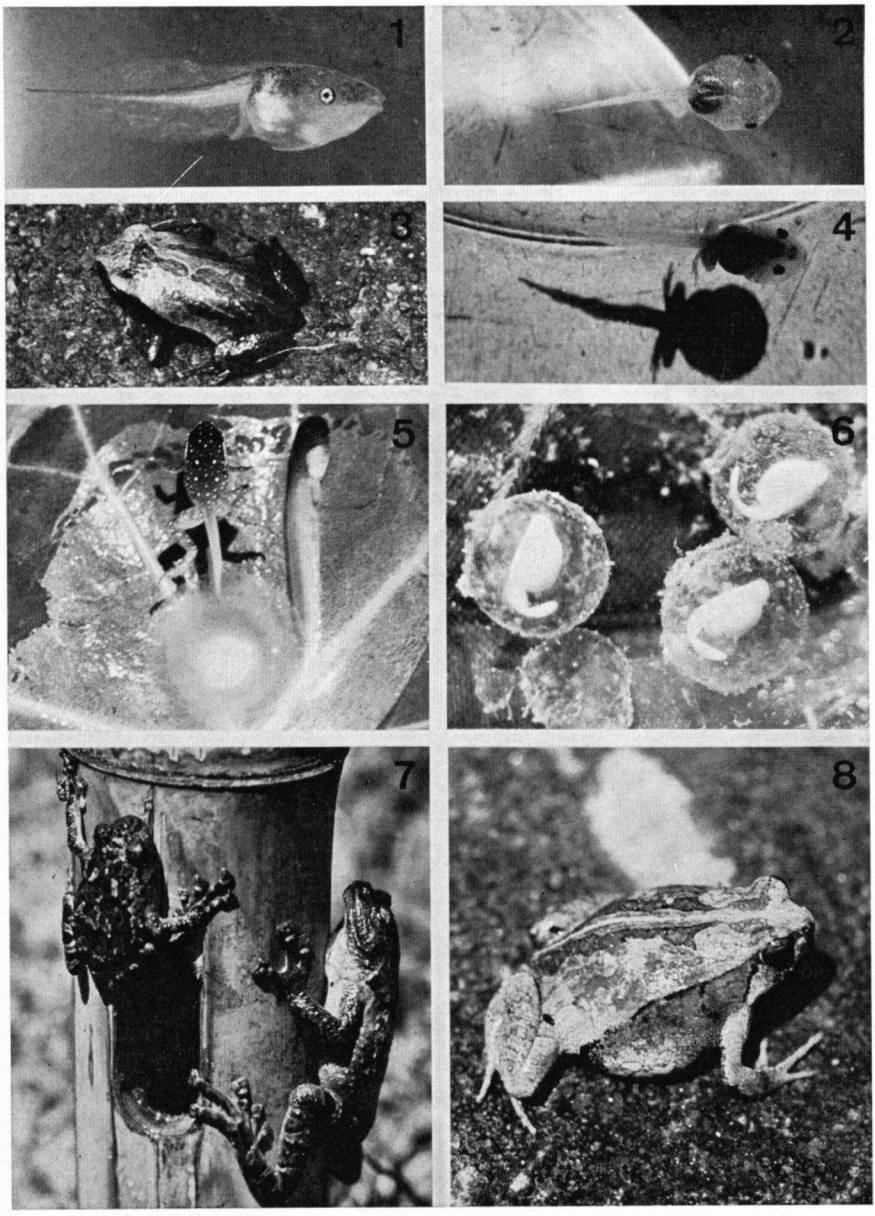
The present paper records the author's observations on the larvae of four microhylid species, representing two subfamilies, and of one species of the Scaphiophryninae. Field notes on eight other species are included. The results have been obtained during a stay in Madagascar from November 1970 till May 1973.

Dyscophinae

Dyscophus quinquelineatus (Boettger, 1913)

Material. — Three young specimens were collected on the forest floor under fallen leaves near Ampijoroa, Tsaramandroso, in the Ankarafantsika Forest, along Route Nationale 4 (Tananarive-Majunga) at 465 km (West Madagascar), during the day, on 23 April 1972 (ZMA No. 6705). In the same locality, numerous small tadpoles of the microhylid type were collected in small, shallow, well lighted, temporary pools, on 23 January 1973 (ZMA No. 6702-6704). The froglets reared from these tadpoles could be assigned to *D. quinquelineatus*.

Ecological notes. — The climate in the western Malagasy Region is hotter and drier than in the eastern Region and is characterized by the existence of two distinctly marked seasons. The rainfall, about 1000-1500 mm annually, is almost entirely restricted to the hot season (November-March), leaving seven to eight months without any precipitation of importance. In agreement



FIGS. 1—8. 1—3, *Dyscophus quinquelineatus*: 1, tadpole, lateral view; 2, tadpole, dorsal view; 3, froglet; 4, *Pseudohemisus granulosus*: tadpole, dorsal view; 5, *Plethodontohyla notosticta*: egg, tadpole and froglet; 6—7, *Platyhyla grandis*: 6, embryos; 7, female (left) and male on bamboo segment; 8, *Pseudohemisus granulosus*: adult female.

with this, the western type of forest exhibits a resting period in the dry season, during which most of the trees lose their leaves. Treefrogs are relatively scarce in this region, but the majority of fossorial malagasy Anura is found there (Guibé, 1948).

Larval development. — Figs. 1, 2, 9, 10. The tadpoles were reared in water very rich in algae, at a temperature of about 25° C. The water was collected from a pond fertilized by a colony of egrets, and changed twice a day. Some yeast suspension was provided every other day. The tadpole is completely microphagous; it floates horizontally in the water, motionless except for a slight undulation of the flimsy tail and a steady snapping of the mouth. This behaviour and the continuous production of green droppings show its permanent filtering activity.

The tadpoles were collected in stage 25 according to Gosner's (1960) tabular classification. The following description is based on the subsequent developmental series. Table I summarizes the growth in size and ratio of the

TABLE I. Length (mm) and tail-ratio in reared larvae of *Dyscophus quinquelineatus* from Ampijoroa.

Stage	n	Total length	Head plus body	Tail/total
25	17	7—14	2.5—5.5	0.59—0.64
26	8	13—18.5	5—7	0.59—0.62
27	3	18—23.5	7—8.5	0.61—0.63
28	2	22—24	9—10	0.58—0.59
30	2	21	9	0.61
31	1	23	9.5	0.58
33	1	25.5	10.5	0.59
34	2	25	10	0.60
38	1	33.5	13.5	0.59
39	2	31.5—32	13	0.58—0.59
40	1	34.5	13.5	0.60
41	1	32.5	12.5	0.61
46	7	—	13—15	—

tail to the total length. The body is round to slightly oval, flattened above, spheroidal ventrally. The eyes are lateral, visible from below. The ratio of the body width/length is 2/3 to 3/4 in alcohol, and in life almost 1. The nostrils are open from stage 41 onward; the distance between them is 1/6 of the interorbital distance; the nostrils are slightly nearer to the tip of the snout than to the eyes. The mouth is terminal, its width 1/3 of the width of the head at the level of the eyes. The upper lip is nearly straight; the lower lip has a median longitudinal notch (fig. 10). The spiracle is median, it is covered with a transparant sheath, the opening is situated at about the centre of the gut, 3/4 to 4/5 of the distance from the tip of the snout to the end of the body. The forelimbs develop behind the branchial chambers. The anus is median; the anal tube curves downwards and backwards, the opening is at the edge of the ventral fin (fig. 9). The caudal musculature is slender and

tapering distally, nearly reaching the tip of the fin. At midlength of the tail, the dorsal and ventral fins are of equal depth, about twice that of the caudal musculature. The dorsal fin is deepest at about midway the tail and extends to the body. The ventral fin is of uniform depth in the anterior half of the tail. Distally both fins narrow into a point.

In life and in alcohol, the coloration of the back is brownish, the skin is transparant. In stage 25 the back has an uniform speckled appearance. In older stages dark pigment is present in the middle of the back, from between the eyes to the end of the body, anteriorly diamond-shaped and terminating in a streak. Dark pigment is also present around the nostrils and in the upper part of the caudal musculature. The caudal fin and belly are transparant. The membrane surrounding the gut is black in stage 25 and silvery in later stages (fading in alcohol). A bladder-like structure filled with air is visible at both sides of the insertion of the tail on the back in stage 25, but gradually becomes masked by yellowish coloration in later stages (fading in alcohol).

From stage 25 onward, the metamorphosis was completed within two months. The reared frogs, rather large in size, resemble the adults of *D. quinquelineatus*: the colour pattern and the structural characters of the hands and the feet are identical; a well defined fold from the eye to the groin, with a short oblique branch above the tympanum to the insertion of the arm, as well as the vomerine and maxillary teeth are present. The colour in life is beige with chocolate brown (fig. 3).

SCAPHIOPHRYNINAE

Pseudohemisus granulosus Guibé, 1952 (fig. 8)

Material. — One male and four gravid females were collected on the forest-floor near Ampijoroa in the Ankarafantsika Forest (West Madagascar), the locality where *Dyscophus quinquelineatus* was found also, in the evening after a heavy thunderstorm on 29 November 1972 (ZMA No. 6706-6707). Numerous small tadpoles were collected at the same locality, in a shallow temporary pool in the shade of a big mango tree, on 23 January 1973 (ZMA No. 6708-6710). The froglets reared from these tadpoles could be assigned to *P. granulosus.*

Systematic remarks. — We compared our adult specimens with the type specimens of *Pseudohemisus granulosus* Guibé, 1952, and of *P. verrucosus* Angel, 1930. Our specimens agree with the first species, which was originally described from a single female of 20.5 mm body length. The body length of our male specimen is 26 mm, that of the four females 31 to 35 mm. Besides the smaller size, the male is distinguished from the females by a heavily pigmentated gular sac. Dissection of one female revealed 456 cream-white eggs with a brownish pole, 1 mm in diameter. In life, the coloration of the back is beige, with or without darker irregular patches and markings; the venter is cream-white; the chin and throat are densely mottled and dotted with brown, in the male more than in the female, the belly is scarcely mottled. *P. granulosus* is a fossorial species, provided with a shovel-shaped inner metatarsal and tarsal tubercle.

Larval development (figs. 4, 11, 12). — The tadpoles of *P. granulosus* were reared in the same way as those of *Dyscophus quinquelineatus*. Cooked lettuce was provided in addition to the diet of algae and yeast. These tadpoles fed also on their dead congeners. Most of the time, the tadpole filters the water, while floating in a horizontal position as does *D. quinquelineatus*, but it is a far more skillful swimmer than the latter species. It turns easily upside down to feed on particles on the water surface, or actively searches the bottom with the tail obliquely upwards at an angle of about 45°.

The tadpoles were collected in stages 25 and 26 according to Gosner's (1960) tabular classification. The following description is based on the subsequent developmental series. Table II summarizes the growth in size and the

TABLE II. Length (mm) and tail-ratio in reared larvae of *Pseudohemisus granulosus* from Ampijoroa.

Stage	n	Total length	Head plus body	Tail/total
25	3	7.5— 9.5	3 —4	0.59—0.61
26	5	8.5—11	3.5—4.5	0.58—0.61
27	6	9.5—11.5	3.5—4.5	0.60—0.65
28	2	10.5—15	4 —5.5	0.61—0.62
31	1	15	6	0.60
32	1	16	6.5	0.59
33	2	16.5—18	6.5—7	0.60—0.61
34	1	18	7.5	0.58
36	1	19.5	7	0.64
37	5	17.5—19.5	6.5—8	0.60—0.64
38	2	20.5	8	0.60
39	2	18 —19.5	7	0.61—0.64
40	3	18.5—20	7 —8	0.61—0.63
41	2	18.5—20	6.5—7	0.65
42	1	14	5.5	0.60
43	1	16	6	0.62
46	21	—	5.5—7.5	—

ratio of the tail to the total length. The head and body is flattened above, ovoid below. The eyes are dorsolateral. The ratio of the body width/length is 2/3 both in life and in alcohol. The nostrils are open from stage 41 onward; the distance between them is from 1/3 to 2/5 of the interorbital distance. The nostrils are slightly nearer to the tip of the snout than to the eyes. The mouth is terminal, its width is 1/3 of the width of the head at the level of the eyes. The mouth lacks a horny beak and teeth. The lower lip has an extended flap, which is even richer in papillae than the remaining contour of the lips (fig. 12). The spiracle is mediosinistral, it is covered with a transparant sheath, the opening is situated at about 2/3 of the distance from the tip of the snout to the end of the body and at 2/5 to 1/2 of the distance from the side of the body to the ventral median line.

The forelimbs develop behind the branchial chambers. The anus is median; the anal tube is straight, directed obliquely downwards, with its opening at the edge of the ventral fin. Half-way the tail, the dorsal and the ventral fins are of equal depth, about twice that of the caudal musculature. The dorsal

fin extends to the body; distally both fins narrow to a slightly rounded tip.

Dark pigment is present around the nostrils, on the upper part of the caudal musculature and on the middle of the back; between the eyes diamond-shaped. The caudal fin and belly are transparant.

From stage 25 onwards, the metamorphosis was completed in 2½ to 3½ weeks. The reared frogs resemble the adults in colour patterns; the principal colour was beige in 20 specimens; one was green. Three dorsal patterns can be distinguished, one evenly coloured, the other two as in figures 13 and 14. The structural characters of the hands and the feet of the juveniles are the same as in the adults of *P. granulosus*. The sharp granules on the back and the lateral folds are not yet as pronounced as in the adults specimens.

Discussion on the Dyscophinae and Scaphiophryninae

According to Parker (1934), the subfamily Dyscophinae, with *Dyscophus* Grandidier, 1872, in Madagascar, and with *Calluella* Stoliczka, 1872, and *Colpoglossus* Boulenger, 1904, (Inger (1966) synonymized the latter two) in the Indo-Malayan region, forms the remnant of the original stem from which the whole microhylid family is evolved. This author, too, considers the genus *Dyscophus* the most primitive of the Dyscophinae, since it approaches the Ranidae closely by the possession of a complete shoulder-girdle and an omosternum with ossified style. Savage (1973) excluded *Calluella* and *Colpoglossus* from the Dyscophinae and classified them among the Asterophryinae.

The tadpole of *Dyscophus*, for the first time described in the present paper, is of the microphagous microhylid type: with a median spiracle, neither denticles, nor a beak or papillae. As such it is similar to the tadpole of *Calluella guttulata* (Blyth, 1855) described by Parker (1934). In the Asterophryinae the development is direct, the metamorphosis is completed on the large amount of yolk within the egg (Tyler, 1963). Because the same kind of skeletal changes has occurred in different microhylid groups, making it extremely difficult to recognize and define natural groups of species, I tend to attach great weight to the larval development in the arrangement of the subfamilies in this family. I agree, therefore, with Parker's (1934) opinion and classify *Dyscophus* and *Calluella* in the subfamily Dyscophinae.

The malagasy genera *Pseudohemisus* and *Scaphiophryne* form a group showing affinities to both Microhylidae and Ranidae. They belong to the Dyscophinae in the classification of Noble (1931), because they have typically microhylid characters as dilated sacral diapophyses, the presence of palatal folds and a particular hyolaryngeal apparatus; they share with *Dyscophus* the possession of a complete shoulder-girdle, also found in the Ranidae.

Angel (1931) assigned ranid-like larvae to *Pseudohemisus verrucosus* Angel, 1930, and *P. longimanus* Angel, 1930, using circumstantial evidence. Parker (1934) excluded both genera from the Microhylidae, basing himself on Angel's paper, and stressing the fact that they have an undivided ethmoid, in contrast to the divided one in the Microhylidae. Laurent (1946) combined both genera

as Scaphiophryninae, a new subfamily in the Ranidae; Guibé (1956) proposed to refer the Scaphiophryninae to the Microhylidae. Savage's (1973) classification of this subfamily within the Hyperoliidae seems to be just an insufficiently founded extrapolation of Parker's (1934) opinion.

I agree with Guibé (1956) that Angel's (1931) identification of the *Pseudohemisus* tadpoles is open to serious doubt, because it was based mainly on the joint occurrence of unknown tadpoles with *Pseudohemisus* adults in the same locality. Therefore, it seems justified to consider the tadpole of *P. granulosus* as the first described in the subfamily Scaphiophryninae.

It is not possible to fit the tadpole of *P. granulosus* into the scheme of anuran larval types as established on account of the external morphology by Orton (1953, 1957), a scheme elaborated by Starrett (1973) with regard to muscular and skeletal characters. The external larval features might be listed as follows:

Type 1 larvae (Pipoidea Lynch, 1973): paired, ventrolateral spiracles; neither denticles nor beak; presence of long barbels; forelimbs develop behind the branchial chambers.

Type II larvae (Microhylidae): median spiracle; neither denticles nor beak or papillae; nostrils do not appear until shortly before metamorphosis; forelimbs develop behind the branchial chambers.

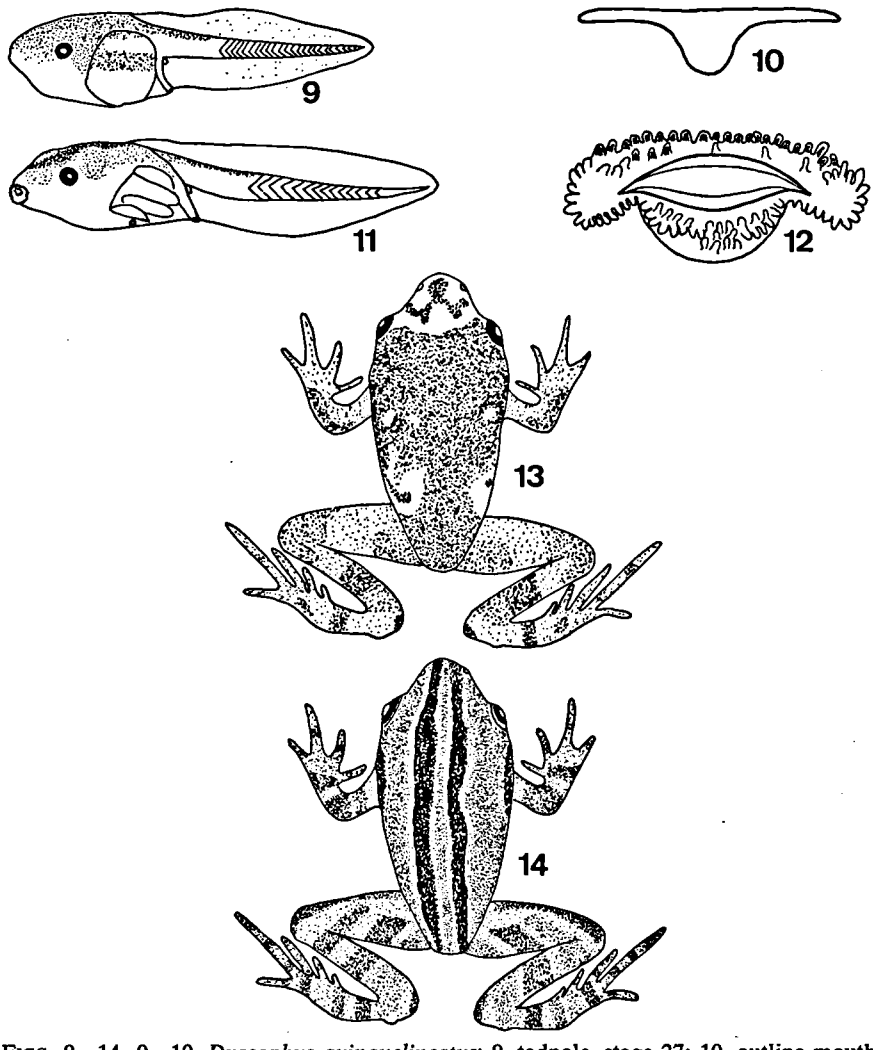
Type III larvae (Ascaphoidea Lynch, 1973): median spiracle; denticles, beak and papillae present; forelimbs develop close to branchial chambers; nostrils open in an early larval stage.

Type IV larvae (Pelobatoidea, Bufonoidea, Ranoidea (except Microhylidae), Lynch, 1973): sinistral spiracle; denticles, beak and papillae present; forelimbs develop within the branchial chambers; nostrils open in an early larval stage.

The tadpole of *Pseudohemisus granulosus* shows definite microhylid features, such as the absence of denticles and beak, the place where the forelimbs originate and the retarded appearance of the nostrils. However, the intermediate position, between median and sinistral of the spiracle and the presence of papillae around the mouth seem to indicate relationships with other groups. As such, the larva of *P. granulosus* is just as difficult to classify as the adult one. An internal anatomical study of this larva is in progress.

Two main theories exist concerning the phylogeny of the Microhylidae. In the oldest classification, nowadays supported by many authors (Griffiths, 1963, Tihen, 1965, Kluge & Farris, 1969, and Lynch, 1973), the Microhylidae are closely related to the Ranidae. In this classification they are placed in the same "advanced" suborder Diplasiocoela Nicholls, 1916, or superfamily Ranoidea Lynch, 1973. Other authors (Orton, 1953, Hecht, 1963, Inger, 1967, Starrett, 1973, and Savage, 1973) isolate the Microhylidae on the basis of their larval morphology as one of the most primitive groups of Anura, which branched off before the evolution of the "advanced" frogs, such as ranids and bufonids.

The tadpole of *P. granulosus* (a species which, on account of the adult morphology, at any rate belongs to the Ranoidea) shows affinities to the



FIGS. 9—14. 9—10, *Dyscophus quinquelineatus*: 9, tadpole, stage 27; 10, outline mouth, ventral view; 11—14, *Pseudohemisus granulosus*: 11, tadpole, stage 27; 12, mouth, ventral view; 13—14, juveniles.

Microhylidae in particular and in a lesser degree to the Ranidae. By its intermediate character, it demonstrates that transformation of tadpole type has occurred in both families. This discovery refutes the theory (on the basis of larval morphology only), that the Microhylidae stand isolated as one of the most primitive groups of frogs. It favours the opinion, that the Microhylidae and Ranidae form a unity.

Most probably, the stock from which the Ranoidea originated had a tadpole of Type IV, since all "advanced" families (except the Microhylidae) as well as the Pelobatoidea, which are considered transitional between the

"archaic" and "advanced" frogs by Noble (1922, 1931) and most subsequent authors, have larvae with a sinistral spiracle.

A median spiracle seems more primitive than an asymmetrical one in organisms that are essentially symmetrical. It is hard to evaluate the difference in function between a sinistral and dextral position of an asymmetrical spiracle. It seems reasonable, therefore, to interprete the universality of the sinistral spiracle as an indication that the asymmetrical spiracle originated only once during the evolution of the frogs. According to this point of view, the median spiracle in the Microhylidae must be derived from a sinistral one.

The functional significance of the lateral spiracle in tadpoles with horny beak and teeth is the free water outflow when they are lying on the bottom in order to feed; the sinistral spiracle is such an adaptation for feeding down the bottom. The median spiracle, however, is certainly a more valuable asset for maintaining balance while floating freely, as do the microphagous tadpoles of the Microhylidae while feeding.

It is very probable that the Scaphiophryninae, which approach the Dyscophinae (the most primitive group of the Microhylidae) closely in adult morphology, and have a tadpole which is mainly microphagous and shares characters of both Type II and IV larva, are a relict of the ranoid stock from which the Microhylidae were derived.

Cophylinae

Ecological notes. — Contrary to *Dyscophus* and *Pseudohemisus*, the species of the Cophylinae have been collected in the wetter eastern Malagasy region. The annual rainfall on the mid-east coast (Fénérive, Tamatave, Nosy-Varika) amounts to about 2500 mm, with monthly maxima of well over 300 mm in the summer (January-April) and minima of less than 150 mm in the winter (September-November). Ecologically dry months do not exist. On the eastern slopes of the plateaux (Anjozorobe, Perinet, Ranomafana) the annual rainfall is 1500-2000 mm. There is a more pronounced dry winter season here, the monthly precipitation being less than 100 mm from May to October.

Platyhyla grandis Boulenger, 1889

Material. — One calling male and two gravid females were found together in a water-hole in a tree-trunk near Anjozorobe (altitude 1300 m), 60 km North of Manjakandriana on 20 September 1971 (ZMA No. 6696). Two couples, each consisting of a calling male and gravid female, were captured, one in a water-hole in the trunk of a *Ficus*-tree and the other in water in an axil of a young *Ravenala madagascariensis* (Musaceae) near Perinet (altitude 900 m) on 23 September 1972 (ZMA No. 6695, 6693). One resting male was collected by Mr. A. Peyrieras under rotting wood in a forest near Ampasinambo (altitude 500 m), 55 km West of Nosy-Varika in February 1972 (ZMA No. 6692).

The male is larger than the female in each couple captured. Body length:

males 4.5-8.8 cm, females 4.3-6.1 cm. A large oval to semicircular inner metacarpal tubercle is present in both sexes.

Voice. — Calling males, always hidden in arboreal holes, were heard from 4 p.m. to 8 a.m. in the hot dry springtime, September and October. The call is a single, resonating blow, very much like the sound produced by the chopping of wood. The following description is based on tape recordings made of a male inside a bamboo-segment in the terrarium. Sonograms were made on a Vibralyzer (Kay Electric Co.). The single blast takes no more than half a second, and consists of frequencies from 8 to about 6000 Hz. The major frequencies are 500 and 1500 Hz (fig. 24). The single calls are separated by rather long intervals of silence; from a quarter of a minute to over 10 minutes.

Reproductive behaviour. — The two couples captured in Perinet were spotted on the sound of the males. Transferred to a terrarium the frogs moved around restlessly and the males stayed silent. This situation continued for several days, until some bamboo-segments with an opening drilled into the side were put in the terrarium. The opening was well above the bottom of the segment, which contained some water (fig. 7). One couple occupied a bamboo-hole immediately, and, once settled, the male resumed croaking. The other male tried to enter the same hole in vain, since the already settled male kept him out with grumbles and bites, or simply by inflating himself so as to fill the entrance. The dislodged male did not take a fancy to any of the other bamboos at first, and kept silent.

Inside the occupied bamboo the croaking went on for about two weeks; then it suddenly stopped almost entirely. The same day (10 October) freshly laid eggs were observed in the water inside the bamboo-hole. The female left the nesting site four days after oviposition and did not return. The male, however, stayed permanently inside, until the brood had developed into froglets. Afterwards, dissection revealed, that he had preyed upon the ants from a nest underneath the bamboo.

Although the second male later on occupied a bamboo also and started calling approximately one week after the first one had fallen silent, his attempt to attract the other female never met with success. Since the distance between croaking males in the forest is always considerable, the mating call of *P. grandis* may also play a territorial role.

Larval development. — Figs. 6, 15—19 (ZMA No. 6694).

The development of the brood in the vivarium was observed from day to day; the environmental temperature was never far from 25° C. About 90 eggs were laid in the bamboo, 25% were not fertilized. Dissection of a gravid female showed more than 100 eggs. Freshly laid eggs are creamy white, round, 4 mm in diameter (6 mm including the capsule); they float freely in the water without being mutually connected. There are only two envelopes; the vitelline and the outer envelope. The jelly is completely transparant.

The embryonic stage represented in fig. 16 is reached after 5 days. The developing embryo is ready to burst from the envelopes after 10 days (figs. 6, 17). It does not yet show any pigmentation. The vitelline envelope than

has a diameter of 8 mm. The tadpole as represented in fig. 18 develops in 17-21 days. Its total length is about 1.5 cm. It is free-swimming and non-feeding. The eyes, limbs and mouth opening begin to develop. The mouth opening is circular and somewhat glandular. The forelimbs develop in the operculum, just before the yolk mass, being 3/4 of the body length. The heart is visible between the forelimb buds. This tadpole still lacks nostrils and an anus. The dorsal surface has a uniformly speckled appearance of brown pigment.

The stage represented in fig. 19 is reached after about 4 weeks. Its total length is about 2 cm. The tail is muscular and twice as long as the body. The nostrils are almost at the tip of the snout. The internarial distance is equal to the interorbital distance: 1.5 times the diameter of the eye. The intestine possesses one coil, filled with yolk. The anus is median.

In five weeks metamorphosis is completed. The young frogs measure 7-8 mm from snout to vent. Their intestines are still filled with yolk. Their general appearance is greenish and smooth, contrary to the brownish and rough look of the adults.

The tadpoles of *P. grandis* do neither show adhesive organs nor spiracle or gills. Several times I tried to rear some tadpoles in clear water outside the bamboo in order to facilitate inspection of their development. They died, however, after a few days, having bladders on the body, probably caused by a mould infection. Since the mortality inside the bamboo was virtually zero, I suppose that the presence of the father is essential for a prosperous development of the larvae. If threatened, the male of *P. grandis* produces a white sticky secretion all over his body. Possibly, the nursing father also provides the larvae with a fungicidal protection.

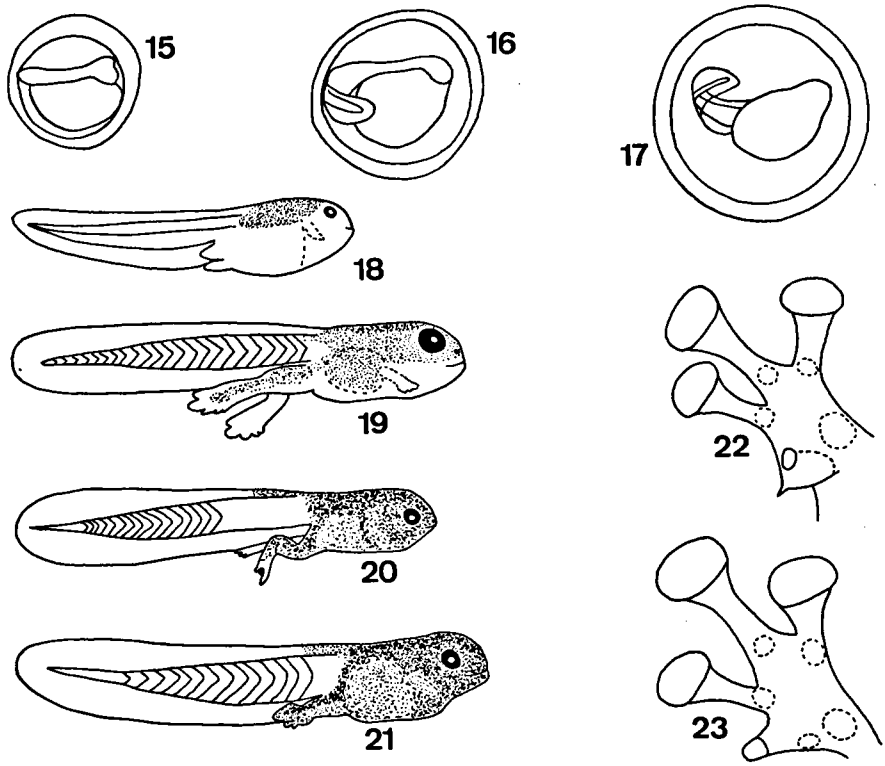
Plethodontohyla notosticta (Günther, 1877)

Material. — One gravid female bearing 120 eggs was found in the heart of a small tree-fern near Ranomafana (Fianarantsoa) at an altitude of 900 m on 2 July 1971 (ZMA No. 6682). One male, together with about 60 eggs and 60 tadpoles, was taken from the water in an axil of a young *Ravenala* near Fénérive-Est (East coast) on 16 October 1971 (ZMA No. 6684). One male and several juveniles were captured as they walked on the forest floor near Foulpointe (East coast) on 23 July 1972 (ZMA No. 6691).

The body length of the males is 27.5 and 32 mm, of the female 40 mm. The inner metacarpal tubercle is large semicircular in the male, small and oval in the female.

Larval development. — Figs. 5, 20. (ZMA No. 6681).

The development of this species is similar to that of *Platyhyla grandis*. The eggs and tadpoles collected along with a male in the same *Ravenala*-axil, were transferred to clear water in order to study their development. Because I did not realize the possible role of the father at that time, he was not placed with the brood. Of this brood a substantial part died of a mould infection.



FIGS. 15—23. 15—19, *Platyhyla grandis*: 15, embryo, two days old; 16, embryo, five days; 17, hatchling-stage, ten days; 18, tadpole, three weeks; 19, tadpole, four weeks; 20, *Plethodontohyla notosticta*: tadpole; 21—23, *Anodonthyla boulengeri*: 21, tadpole; 22, hand male; 23, hand female.

I estimate that the entire development, from egg up to froglet, takes four weeks. From the egg up to the stage of the caught tadpoles took two weeks, from this stage to metamorphosis another two. It could not be ascertained whether these two broods were laid by the same female in two portions with an interval of two weeks, or were of different origin. The presence of 120 eggs in the collected gravid female suggests, in my opinion, that the first possibility is the more probable one.

The eggs are creamy white, round, 3 mm in diameter, surrounded by two envelopes. There is no connection between them. The embryo bursts from the envelopes in the same stage as *P. grandis*. The tadpole is swimming freely and non-feeding. It becomes more pigmentated as the development continues. In fig. 20 the body length is 5 mm and the tail length 12 mm. Differences with the tadpole of *Platyhyla grandis* are: relatively smaller size and longer tail, and more pigmentation. The eye is smaller, the interorbital distance is 3 times the diameter of the eye and slightly broader than the internarial distance.

The newly metamorphosed frog is 6 mm from snout to vent. In life, the young froglet has a dark brown dorsal surface, covered with light spots, white in the sunlight, green in the shade; there are two silvery lateral lines, from the tip of the snout across the upper eyelid and above the tympanum, continuing almost to the groin. The adults also show these silvery lines, but their back is olivegreen with irregular brown patches and two light sacral spots; in some specimens a few more.

Notes. — The male with the brood in the *Ravenala* uttered a loud scream with the mouth open when captured. The gravid female became active at dusk, at least in captivity. The food items, recovered from the present species include many ants and one beetle.

Plethodontohyla laevis (Boettger, 1913)

One male measuring 41 mm was collected by Mr. A. Peyrieras from a burrow, spotted on the sound, near Tampoketsa d'Ankazobe (altitude 1600 m) on 5 September 1971 (ZMA No. 6688).

Plethodontohyla ocellata Noble & Parker, 1926

One gravid female of 62 mm body length, containing more than 100 eggs of 2 mm in diameter, was collected by Mr. A. Peyrieras under decaying wood in the forest near Ampasinambo (altitude 500 m), 55 km West of Nosy-Varika (East coast) in February 1972 (ZMA No. 6690). The stomach contained a large beetle.

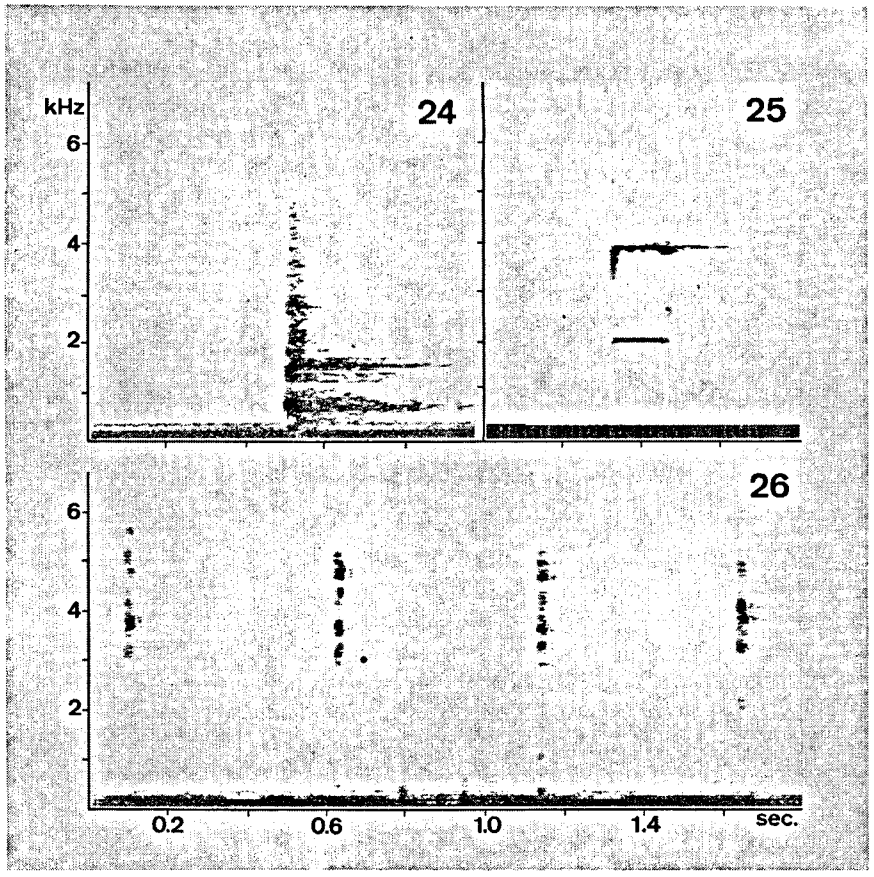
Plethodontohyla brevipes Boulenger, 1882

One female and one male of 32 mm body length, were collected by Mr. A. Peyrieras under decaying wood in a forest near Ampasinambo in February 1972 (ZMA No. 6689). The stomachs contained beetles.

Anodonthyla boulengeri Müller, 1892

Material. — One gravid female and one male from a *Ravenala*, near Fénérive-Est (East coast); 17 October 1971 (ZMA No. 6669); two gravid females from the same plant near Perinet (altitude 900 m); 21 October 1971 (ZMA No. 6674); one female in a scale-covered scar on the trunk of an tree-fern, left by a fallen leaf, on 2 July 1971 (ZMA No. 6672) and one gravid female in a tiny water-filled hole in a treetrunk on 1 January 1972 (ZMA No. 6673), both near Ranomafana (Fianarantsoa); one male and one female under fallen leaves and one male in a *Ravenala* near Foulpointe on 13 October 1971 (ZMA No. 6670); four males, two of which were accompanied by eggs and one by eggs as well as by tadpoles, and one gravid female, all in the water of different axils of *Typhonodorum lindleyanum*, 25 km North of Tamatave (East coast) on 22-29 July 1972 (ZMA No. 6671).

Nearly all specimens of this tiny species collected in the Traveller's Palm were located in the hollow leafstalks of rather young plants, which often



FIGS. 24—26. 24, *Platyhyla grandis*: sonogram, filter narrow; 25, *Paracophyla tuberculata*: sonogram, filter wide; 26, *Anodonthyla boulengeri*: sonogram, filter narrow.

harboured antnests as well. This also applies to another thirteen adult specimens, also collected on 17 October 1971 near Fénérive-Est, but subsequently lost.

Body length: males 17-18 mm, females 18-20 mm. The inner metacarpal tubercle is large, prominent and semicircular with a small spine in the males; small and oval in the females. The thumb is more reduced in males than in females (figs. 22, 23).

Voice. — The males call chiefly in the early morning and evening. Held in captivity from October till the end of December, they continued calling. The following description is based on tape recordings made of a male inside the terrarium. The call is a single short, high sounding trill, which is repeated after 0.5-0.6 seconds. The duration of the notes varies from 0.03-0.05 seconds. The range of frequencies is from 2700-2800 Hz to 5000-5500 Hz (fig. 26).

Larval development. — Fig. 21 (ZMA No. 6675).

The development is similar to that of the previous species of the Cophylinae. The number of eggs varied between 23-30; the eggs are creamy white, round, 2 mm in diameter (3 mm including the two envelopes) and there is no connection between them. The collected eggs were transferred to clear water, without the adult; many of them died from a mould infection.

The hatchling stage is reached in 8 days. The hatchling is white and measures 8.5 mm: body 3.0 and tail 5.5 mm; it swims freely and is non-feeding.

The tadpole as represented in fig. 21 is 11 mm long; the tail is slightly more than twice as long as the body; the pigmentation is similar to that of *Plethodontohyla notosticta*. The internarial distance is equal to the interorbital distance, which is twice the diameter of the eye. The metamorphosis is completed after 16-20 days. The froglets measure 3.5 mm; they have a brown appearance like the adults.

Note. — Ants were the only food items recovered from this species.

Platypelis tuberifera (Methuen, 1919)

Material. — One female and one male were captured in Perinet in June 1971 (ZMA No. 6700); one female and five juveniles near Fénérive-Est on 16 October 1971 (ZMA No. 6701); three juveniles near Foulpointe on 13 October 1971 (ZMA No. 6697) and one gravid female on 2 August 1972 (ZMA No. 6699). All specimens in water-holding axils of *Pandanus*.

Notes. — The eggs in the gravid female have a diameter of 2 mm each. Juveniles were found in water-filled axils of *Pandanus*; the smallest juvenile was 6 mm from snout to vent. So we can imagine that the breeding site and development of *P. tuberifera* are similar to those of the previously mentioned species of Cophylinae.

The food items recovered from this species include ants.

When disturbed the adults inflate themselves.

Platypelis pollicaris Boulenger, 1888

One male of 19.8 mm body length was found in the axil of a *Ravenala*, near Perinet on 20 October 1971 (ZMA No. 6686). One male of 19.2 mm body length was found in the axil of a *Pandanus* near Tampoketsa d'Ankazobe on 25 April 1973 (ZMA No. 6685). The stomachs contained ants.

Paracophyla tuberculata Millot & Guibé, 1951

Material. — Six males and four juveniles were collected near Perinet in the axils of *Pandanus* and *Crinum firmifolium* (Amaryllidaceae) on 21 October 1971, 23 September 1972, 12 November 1972, 18 April 1973 (ZMA No. 6677-6680).

Systematic remarks. — This species has originally been described after a single female, of 17 mm body length. The body length of our males is 18-24 mm. The coloration of the back is dark brown, with irregular patches or markings, which are orange or beige; a beige midline is sometimes present;

the hindlimbs are beige with dark brown cross-bandings. The sides of the dorsal part of the thighs, the underside of the thighs, shanks and fore-arms are red or moss-green. The chin is dark, sometimes with a faint whitish mid-line; the chest and the venter are mottled dark, less on the venter than on the chest.

Voice. — Held in captivity from October till the end of December, the males continued singing, mainly in the early morning from 6-8 a.m., and often in the afternoon and at dusk. In Perinet this species was heard on a dry, clear evening with full moon in September, while other frog species were silent, and at dusk in November. The call is a single melodius bell-like sound; the note repetition rate is 18-22 per minute. The following description is based on tape recordings made of a male inside the terrarium. The duration of the note is about 0.3 seconds; the fundamental frequency is about 1900 Hz, the major frequency 3850 Hz (fig. 25).

Mantipus alluaudi (Mocquard, 1901)

One female of 52 mm was found under a fallen tree-trunk near Mandraka (altitude 1200 m), 1 August 1971 (ZMA No. 6687).

Discussion on Cophylinae

Parker (1934) in his monograph of the Microhylidae noted the large size of the eggs in some female Cophylinae, and surmised that this subfamily would have an abbreviated or non-free larval stage. Millot & Guibé (1951) were the first to examine preserved larvae, collected together with an adult, of two members of this group; *Plethodontohyla notosticta* from the axil of a *Ravenala* and *Platypelis pollicaris* from a hollow bamboo. The observation that they had a large yolk sac and no spiracle, made these authors suggest that the Cophylinae would have a direct development similar to that of certain Asterophryinae and Sphenophryinae from the Papuan region, which have dispensed completely with the free larval stage and hatch as a froglet with a tail. Guibé (1952) observed also the fossorial breeding habit of *Plethodontohyla tuberata* (Peters, 1883). The tadpoles of this species have a large yolk sac and float in a mucous fluid, shielded by the female in small burrows.

My observations are restricted to some arboreal species of Cophylinae, viz. *Platyhyla grandis, Plethodontohyla notosticta* and *Anodontohyla boulengeri.* Like the previous records, their breeding behaviour and larval development show that there is little variation within this group.

Phytotelmes and other water filled holes in for example bamboo and tree-trunks ("biotope végétale", Millot & Guibé, 1951) provide both dwelling and breeding place. Gravid females and developing spawn were observed only in the dry season, except for one gravid female of *A. boulengeri.* Although the information is scarce, it is not inconceivable that there exists a positive correlation between the breeding period and the sites selected for the deposition of the eggs, because the chance to occupy a water-filled place of a more permanent character is much greater in the dry than in the wet season. As

the water in some phytotelmes, for instance in the Traveller's Palm, is generated by the plant itself, its existence during the dry season guarantees its permanence.

The large eggs are deposited in the water, in which the larvae are to develop. The tadpole hatches just before the limb-buds occur: it swims freely, is non-feeding, as far as we could observe, and does not possess a spiracle.

As far as I have observed developing spawn is always guarded by a male. Parental care is not a common phenomenon among frogs, and involves in many cases the transportation of developing spawn by an adult. However, within the Microhylidae, the protection of deposited spawn by an adult has been recorded in four subfamilies having non-feeding larvae.

Although data on breeding habits and larval development are available only for a minority of species of these four groups, they might be summarized as in Table III.

TABLE III. Comparison of available data on direct development and parental care in four microhylid subfamilies.

	Cophylinae	Asterophryinae & Sphenophryinae (Tyler, 1963)	Brevicipitinae (Wager, 1965)
caring parent	♂ (or ♀)	♀ or ♂	♀
egg size (mm)	2 — 4	1.5 — 6.5	3 — 4.5
no. of eggs per ♀	< 120	< 55	< 56
hatchling	limbless tadpole	froglet with tail	tailless froglet
dwelling and breeding site	arboreal and terrestrial	terrestrial and arboreal	terrestrial

The complete lack of observations of the contrary, indicates that both parental care and direct development represent basic characters of these subfamilies, and should be given much attention in the study of phylogenetic relationships within the Microhylidae. In my opinion, the different steps of postponement of hatching in the various subfamilies strongly suggests the way by which the narrow-mouthed toads may have found their independance from water.

Both Wager (1965) and Tyler (1963) tried to rear the spawn of ground-breeding microhylids, in absence of the adult. They succeeded poorly, because most eggs died with concurrent development of mould. I had the same experience with eggs of *Plethodontohyla notosticta* and *A. boulengeri*. The success of rearing *Platyhyla grandis*, with the adult present, strongly suggests that the parent not only guards the eggs from predators, but also from infective micro-organisms. Further rearings should be executed in the presence of the parents, notwithstanding the risk of some eggs being swallowed by the parent, as experienced by Tyler (1963).

Within the Microhylidae many more or less specialized ant-eaters occur. The predominance of these insects in the diet of Cophylinae is not exceptional.

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