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ON THE ORIGIN OF THE MALAGASY *MANTELLA*

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ABSTRACT.- The species of the genus *Mantella* have brillant colors and patterns, especially *Mantella aurantiaca,* and are active during the day. Due to these characteristics, more than 100 years ago herpetologists classified them together with the South American « dart-poison frogs » into the family Dendrobatidae. Recently, toxicologists discovered that the skin of *Mantella* contains similar toxins to those found in dendrobatid frogs. Nowadays, the Malagasy poison frogs and the neotropical dart-poison frogs belong to two separate taxa , the Mantellinae and the Dendrobatidae, geographically separated by more than 12 000 km by reason of the continental drift. FORD (1989) has studied the same phenomenon in Dendrobatidae and Arthroleptidae of Africa. Since behavioral characters are postulated to be important for reconstructing phylogeny, I will examine this hypothesis by comparing 52 characters of the Malagasy *Mantella* with the neotropical Dendrobatidae and the behavior of an outgroup of *Hyla* with regard to homology criteria. A testable phylogeny is established predominantly based on shared behavioral characters. It implies that both the frog groups *Mantella* and Dendrobatidae and probably also *Arthroleptis,* originate from a direct common ancestor which must have likely lived in Gondwanaland (Africa) before Madagascar and South America become isolated.

KEY-WORDS - Phylogeny, Ethology, Biogeography, Dendrobatid frogs, *Mantella*

RESUME.- Les espèces du genre *Mantella* sont exceptionelles parmi les grenouilles de Madagascar. Ce sont des animaux diurnes à couleur brillantes et attractives, en particulier *M. aurantiaca.* Ainsi, les herpétologues les ont classé ensemble, il y a plus d' un siècle, avec les « grenouilles à poison de flêche » d'Amérique de Sud dans la famille des Dendrobatidae. En plus, les toxicologues ont récemment découvert que la peau des *Mantella* contient des toxines similaires à celles trouvées dans les grenouilles dendrobates. Cependant les « grenouilles à poison de Madagascar » et les « grenouilles à poison de flêches » néotropicales sont actuellement classées dans deux taxa différents, le Mantellinae et le Dendrobatidae, qui sont géographiquement séparés par plus de 12 000 suite à la dérive des continents. En 1989, FORD avait étudié le même phénomène sur la Dendrobatidae et l'Arthroleptidae d' Afrique. Si on considère que les caractères comportementaux sont des facteurs importants pour reconstruire une phylogénie, une hypothèse est tentée en comparant 52 caractères des *Mantella* de Madagascar avec ceux des Dendrobatidae néotropicaux et ceux d'un groupe extérieur, le *Hyla.* L'ensemble étant basé sur des critères d' homologie. En effet, une phylogénie basée sur des caractères comportementaux communs a été établie. Ce qui suggère que, les deux groupes de grenouilles (*Mantella* et Dendrobatidae) et aussi probablement l'*Arthroleptis,* proviennent directement d'un ancêtre commun qui aurait vécu sur l'ancien continent gondwanien.

MOTS-CLES.- Phylogénie, Ethologie, Biogéographie, Grenouilles Dendrobatidae, *Mantella*

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INTRODUCTION

The 14 species of *Mantella* inhabit the rain forest and wetland areas of Madagascar and are active only during the day. Most of them have brillant colours, terrestrial oviposition behavior and a terrestrial way of life. Therefore, initially *Mantella* were placed in the genus *Dendrobates* (GRANDIDIER, 1872); later in their own genus in the family Dendrobatidae (BOULENGER, 1882), later by NOBLE (1931) in the Polypedatidae (=Rhacophoridae), then in the subfamily Mantellinae of the family Ranidae (LAURENT, 1943, 1946, 1951), then as Mantellinae in the family Rhacophoridae (LIEM, 1970), once more in the family Ranidae (GUIBE, 1978; BLOMMERS-SCHLÖSSER, 1979, 1980; BUSSE, 1981) and together with *Laurentomantis* and *Mantidactylus* in the family Mantellidae (BLOMMERS-SCHLÖSSER & BLANC, 1991). A new classification of BLOMMERS-SCHLÖSSER (1993) retains only two genera, the diurnal *Mantella* and the nocturnal, very heterogeneous and numerous genus *Mantidactylus* in the subfamily Mantellinae.

The members of the poison frog family Dendrobatidae number about 160 living species. They are both terrestrial and diurnal, found in the rain forests of Central and South America and are also provided with brilliant colours like mantellas. It is hardly possible to distinguish many morphs and species externally from some *Mantella* species. Following the last taxonomy of FORD (1989) and FORD and CANNATELLA (1993) they are members of the superfamily Ranoidea. The families Dendrobatidae and Arthroleptidae form together a sister group (DUELLMAN, 1993a; FORD, 1989, 1993) in this superfamily.

It is well known since the discovery of the first dendrobatid frogs that they produce a very strong skin toxin with different compounds. Surprisingly the same toxin with many of the same compounds are found also in species of *Mantella*. Having investigated the social and reproductive behavior, it is fascinating to establish the same behavior parameters of courtship. Therefore this study will examine a phylogenetical relationship between these taxa.

MATERIAL AND METHODS

Both systematic biologists and ethologists agree that for classification not only morphological and biochemical criteria, but also behavioral characteristics should be considered (HENNIG, 1982; LORENZ, 1978; MAXON & MYERS, 1985; MAYR, 1975). Many behavioral characters are to be closely correlated with certain morphological characters (HALLIDAY & ARANO, 1991).

This study follows an investigation of ZIMMERMANN and ZIMMERMANN (1988) about behavioral, systematics and zoogeography of the formation of species groups in dart-poison frogs Dendrobatidae.

Behavioral investigations have been carried out in the laboratory and in the field during the last 22 years on 32 species of dendrobatid frogs (see above) and during the last 8 years on 6 species of *Mantella* (*Mantella aurantiaca, M. betsileo, M. crocea, M. madagascariensis, M. pulchra, M. viridis*). Field observations of *Mantella aurantiaca, M. crocea, M. madagascariensis, M. pulchra* have been carried out in the Madagascar rain forest and wetland around 25 km from Andasibe (=Périnet), East Madagascar, during the months October to April from 1989-1994, field observations of *Mantella* *betsileo* within and on the border of the rain forest on the island of Nosy Bohara (=Sainte Marie) in December 1989.

Observations and analysis of behavior which I document here have been carried out by protocolling, by photography, drawings from nature, and with a video camera Canon Precision-Engineered AF Zoom lens 10x Piezo. It has not been possible to make studies on *M. betsileo, M. madagascariensis, M. pulchra,* and *M. viridis* as complete as on *M. aurantiaca* and *M. crocea.*

We utilized characters that were homologous among taxa (HASZPRUNAR, 1994; REMANE, 1952; RIEDL, 1975; RIEGER & TYLER, 1975, 1985; TYLER, 1988; *In:* W. WIESER ed. 1994). For more clearness in comparison the 8 dendrobatid species groups (=32 species) in ZIMMERMANN and ZIMMERMANN (1988) are compressed to 4 similar groups and compared with the *Mantella* group. As an outgroup with well-described social and courtship behavior, two neotropical frog species *Hyla rosenbergi* and *Hyla faber* (KLUGE, 1981; MARTINS & HADDAD, 1988) are compared with the other frog groups (the sound analysis will be dealt within another study).

The parameters are listed as the occurrence of characters of the species groups from bottom to top . This method of « shared characteristics » or « graduated similarity » gives a first survey of the total 52 patterns from 32 species of Dendrobatidae (ZIMMERMANN & ZIMMERMANN, 1988), 8 species of *Mantella* (this work) and 2 species of *Hyla* (KLUGE, 1981; MARTINS & HADDAD, 1988).

A schematic representation of a complex stimulus-reaction chain during courtship behavior are drawn according to photos from two species groups, the *Phyllobates terribilis* group, and the *Mantella aurantiaca* group, and a photo documentation of the non-amplexus mating of *Mantella aurantiaca.*

Because toxicologists have found the same alkaloids in dendrobatids and mantellas I will refer to these similar frog toxins, *e.g.* pumiliotoxin B, which is found in the skin of both, *Dendrobates pumilio* and *Mantella aurantiaca.*

Figure 1 shows the configuration of Africa, Madagascar and South America in the earliest Cretaceous (100 -140 MYA). At that time, South America and Madagascar were isolated from Gondwana and had drifted in the East-West direction. Figure 1 also shows the modern configuration of the continents and the island of Madagascar with registration of the distribution of dendrobatids and mantellas and their enormous radiation.

RESULTS

It is quite natural that single or several « similar » characters of behavior or other patterns are shown by many frog species. In contrast the appearance of the same feature in dendrobatids and *Mantella* frogs is extraordinary in many ways as illustrated below:

1. Both dendrobatids and mantellas have the ability of producing the same skin poison, alkaloids. This nerve toxin induces an alteration in the channels of the « end-plate ». One of these toxin compounds, Batrachotoxin, is the most potent non-protein toxin in nature, stronger than curare. The frogs of the *Dendrobates histrionicus* group and the *Mantella* group produce less strong alkaloids. Pumiliotoxin from the skin of

Mantella aurantiaca and *Dendrobates pumilio* are never found in non-dendrobatid frog species. (DALY *et al.*, 1984; MYERS & DALY, 1983).

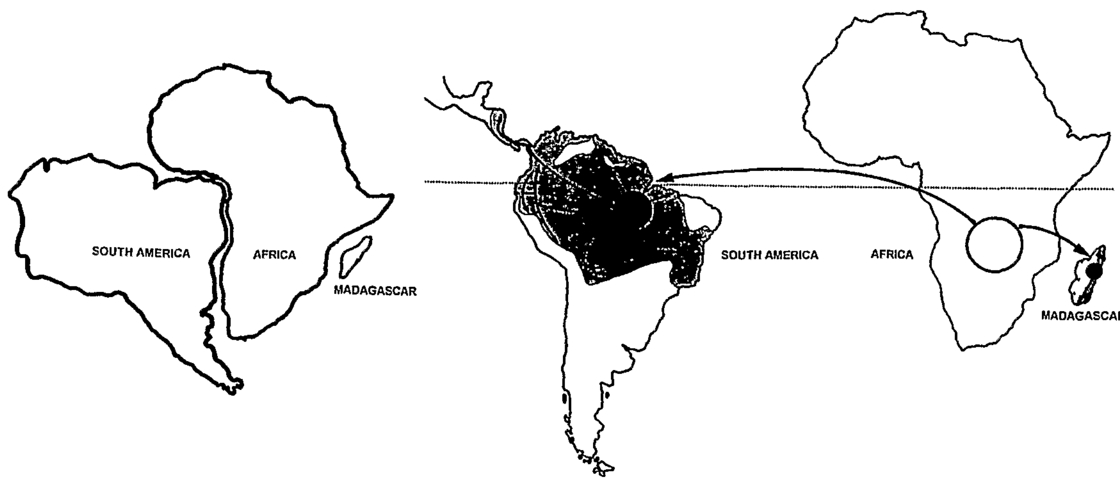


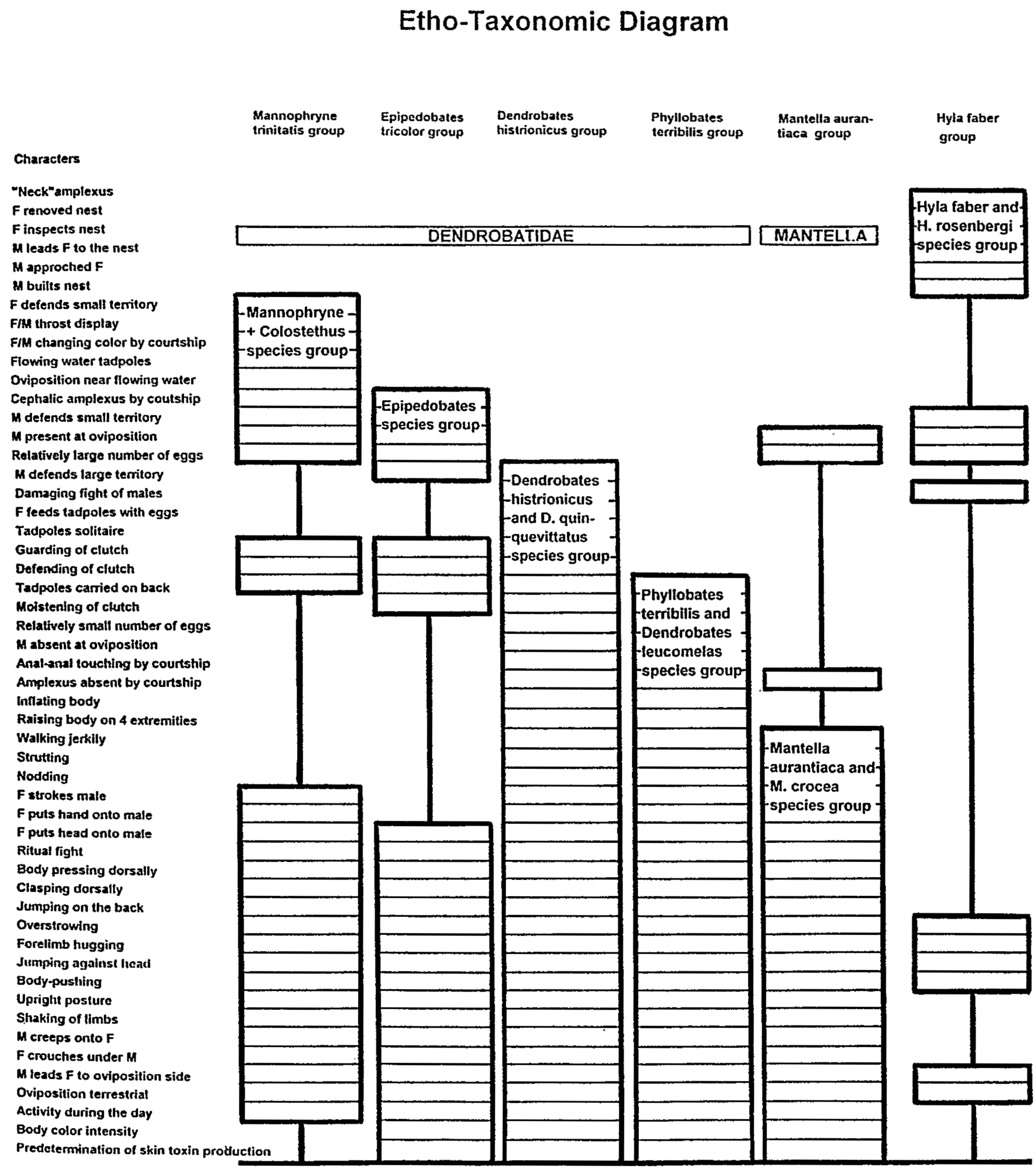
Fig. 1. The configuration of Africa, Madagascar, and South America in the earliest Cretaceous (left) by PINDELL *et al.*, and the modern configuration with registration of the dispersal of *Dendrobatidae* (left) and *Mantella* (right).

2. The similarity of body colors or body patterns are widespread among frogs. But the similarity in colors and patterns of the morphs of the poison-dart frogs *Dendrobates* and the Malagasy poison frogs *Mantellas* is surprising, *e.g.*, the Malagasy golden frog, *Mantella aurantiaca*, looks similar to the red morph of *Dendrobates histrionicus* (Ecuador), or *Dendrobates pumilio* (Costa Rica); the same red-black body patterns are found in morphs of both *Mantella cowani* and *Dendrobates histrionicus* of Colombia.

3. A single similar character such as terrestrial oviposition or the diurnal activity is not unusual. The remarkable thing is the great number of the similar courtship behavior features displayed in both frog taxa. The same movements in action and reaction between males and females during mating can found in the stimulus reaction chain during courtship, *e.g.*, in the mating behavior of the *Phyllobates-Dendrobates* groups and the *Mantella* group (Fig. 2).

4. Different amplexus patterns are usual in frog behavior. In all investigated dendrobatid species and *Mantella* species, amplexus appears during the struggle behavior of male-male or female-female interactions . But I have never observed an amplexus during courtship in any species of the *Dendrobates histrionicus* group, the *Phyllobates terribilis* group, or the *Mantella aurantiaca* group (see latest phase of mating in *Mantella aurantiaca* , photo of one female with two males, Fig. 3).

Table I. Etho-Taxonomic Diagram: Different degrees of similarities in specific behavior characters are used to indicate relationships among species groups.



5. The Etho-Taxonomic Diagram (Table I) contains altogether 52 employable parameters of 6 species groups. It presents a comparison of the similar 26 characters of *Dendrobatidae* and *Mantella,* 24 alone in the *Mantella aurantiaca* species group, in the *Dendrobates histrionicus* group and in the *Phyllobates terribilis* group. It gives us a basic idea of the phylogenetical relationship among members of the *Mantella* group and

the 4 dendrobatid groups by the degree of similar behaivioral traits. Remarkable is that 24 character states form a circle of the courtship behavior alone but not of the circle « territoriality » nor of « brood care behavior ».

6. Comparative investigations in frog behavior are rather rare or incomplete in non-dendrobatid frogs.

Therefore I shall select as an outgroup an exceptionelly well-studied frog group of neotropical *Hyla,* the *Hyla faber* group (KLUGE, 1981; MARTINS & HADDAD, 1988) for comparison. Although these frogs show terrestrial oviposition, the comparison demonstrates only 6 of the common 24 characters of the *Mantella* and dendrobatid groups (Table I).

Hence, the diagram demonstrates the high level of common behavioral characters of the dendrobatids and the *Mantella* groups in contrast to the *Hyla faber* group.

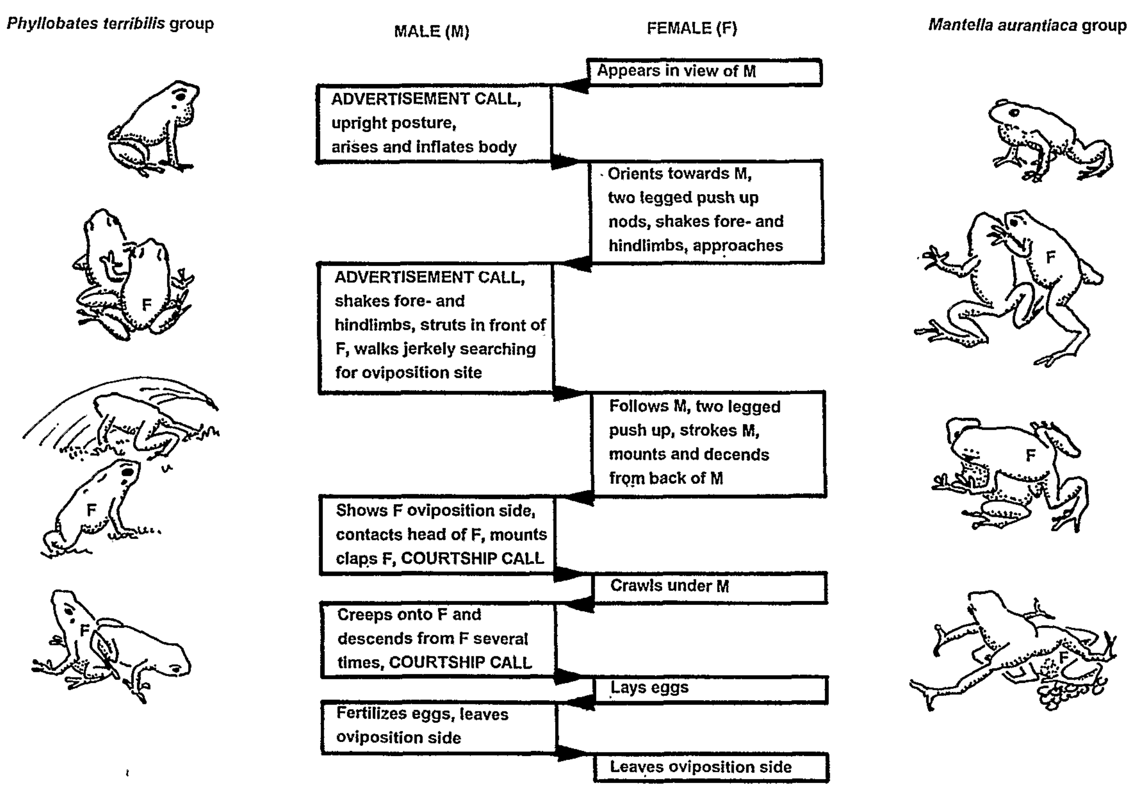


Fig. 2. Stimulus reaction chain during courtship of *Phyllobates terribilis* (left) and *Mantella aurantiaca* (right).

DISCUSSION

DUELLMAN and TRUEB (1986) have confirmed that the « higher taxonomy of anurans is not well established and the placement of some genera and subfamilies has shifted from one family to another » (see introduction). Also the question of classification and phylogenetical relationship between *Mantella* and dendrobatids is very old. BUSSE (1981) supposed that the similarities in dendrobatids and mantellas are to be considered as a convergence phenomenon, because of external morphological features such as colors and patterns in both taxa, but he does not explain this phenomenon explicitly. Due to the similarity of many features, appearance, habits and coloration of mantellas and dendrobatids, GLAW and VENCES (1993) state the genus *Mantella* exhibits a « high level of convergence ».

A comparison of osteological characters between these groups would be helpful. Also, no fossils are known from either taxa (DUELLMAN & TRUEB, 1986; DUELLMAN, 1993a). Tadpole morphology has not been studied in any of these species , and it may be that comparative data on these frog species for a phylogenetic approach are less useful given the enormous variability in the environment (STARRLETT, 1973) *e.g.* *Mantella laevigata* larvae are found in tree holes (GLAW & VENCES, 1994), *Mantella aurantiaca* in wetlands and swamps (ARNOULT, 1965; ZIMMERMANN *et al.*, 1994), *Mantella madagascariensis* near rivulets (ZIMMERMANN *et al.*, 1990), *Dendrobates histrionicus, Dendrobates quinquevittatus* in bromeliads (ZIMMERMANN, 1989) and *Epipedobates boulengeri* near flowing water (ZIMMERMANN & ZIMMERMANN, 1988).

Similar difficulties appear when using bioacoustic patterns alone for relating species separated by great distances or different habitats like dendrobatids and mantellas. Only when considering a limited number of taxa and using biochemical and morphological data (COCROFT & RYAN, 1995) and ethological patterns do answers on phylogenetic questions become evident.

Frogs of both the dendrobatid and *Mantella* taxa are provided oddly enough with the same skin toxin (DALY *et al.*, 1984). Research in toxicology suggests that the common occurrence of alkoloids provides an evolutionary perspective on the genera *Dendrobates* and *Phyllobates* (MYERS, 1983). Nevertheless, the occurence of the same toxins in dendrobatids and mantellas are treated as convergent (DALY *et al.*, 1984).

Ethological research has been carried out with many species of *Dendrobatidae* (ZIMMERMANN & ZIMMERMANN, 1988, *in lit.*) and *Mantella* (ARNOULT, 1965; ZIMMERMANN, 1992; ZIMMERMANN & ZIMMERMANN, 1992, 1994). Such studies in living animals are very complex and time-consuming (HENNIG, 1982). Some hardships include animal dying during the experiments, the difficulty of making field observations in natural habitats such as swamps or rainforest canopies or even in laboratories with inadequate conditions. But these studies can give us insight in the foundation of systematics, and the nature of many characters themselves (TRUEB, 1973).

Often ethological studies lack in the differentation the weighing parameters of behavior for phylogenetical use. The homology criteria demands that the applied characters should have only little adaptive value, *e.g.* behavior parameters of the circle « territoriality » or « brood care » show many adaptive characters and are not very valuable for phylogenetic use. On the other hand the characters of courtship behavior are more independent of environment influence, *e.g.* the clasping position of the male in mating behavior (NUSSBAUM, 1984) and their characters have great value for systematics and phylogenetics (MAYR, 1975), especially by using consequential series of mating patterns in many species (HENNIG, 1982).

Fig. 3. Males of *Mantella aurantiaca* show no amplexus during mating (here 2 males and 1 female)

New studies of classification of Dendrobatidae (FORD, 1993; FORD & CANNATELLA, 1993; based on GRIFFITHS,1959,1963 and DUELLMAN & TRUEB, 1986) are both a demonstration of the ranid hypothesis for dendrobatids and a reference to the affinities to another frog taxon from another continent: to the *Arthroleptidae* from Africa. Many common morphological characters show that *Arthroleptidae* and *Dendrobatidae* are sister groups. Unfortunately, there is less information in recent literature about behavioral parameters of *Arthroleptis* (PASSMORE & LARRUTERS, 1979; STEWART, 1976; WAGER, 1965) comparing *Arthroleptis* with *Mantella* and *Dendrobates* behavior. But these are indications of great interest in the relationship between anuran taxa of Africa and South America.

Since the acceptance of the continental drift theory, the relationship of many taxa has been explainable and confirmed, for example, the Malagasy reptiles *Oplurus, Chalarodon* with the iguanids of the New World or the *Acranthophis* and *Sanzinia* of Madagascar and the neotropic boids (BRIGGS, 1987). Only studies of phylogenetic relationships are missing. DUELLMAN and TRUEB (1986) explain that ranids consisted of ranines and the stock that gave rise to the mantellines were present in Gondwanaland at the time of the separation of Madagascar about 140 million years ago.

Additionally, see BLOMMERS-SCHLÖSSER and BLANC (1993) « L'ouverture du canal de Mozambique et d'Océan Indien nord-occidental a dû isoler une partie du stock originel des Mantellidae. Leurs descendants se sont éteints en Afrique; ils ont donné à Madagascar, une de plus riches radiations adaptive de toute la faune des Amphibiens. »

CONCLUSION

Research of today spreads rapidly. Since the appearence of Amphibian Species of the World in 1985, 519 new amphibian species (DUELLMAN, 1993b) have been identified as of 1993. By the latest indications, dendrobatids, arthroleptide and mantellas are closely related; they could be considered as sister groups with a common ancestor of the *Ranoidea* stock that arose in Gondwanaland. Additional investigations, especially DNA-analysis, are needed to confirm this hypothesis.

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