When molecules claim for taxonomic changes:  
New proposals on the classification of Old World treefrogs  

(Amphibia, Anura, Ranoida)  

Miguel Vences & Frank Glaw

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Recent phylogenetic data, mainly based on mitochondrial DNA analyses,  
indicates that current classification of neotropical anurans is in need of revision. In the  
present paper, we review the literature pertaining the molecular and morpholog-  
ical phylogeny of Old World treefrogs. The molecular phylogenies indicate that,  
among non-hylid Old World treefrogs, one clade is formed by the endemic  
genera from Madagascar, and a second one by the Asian and African genera. Both  
these lineages are nested within the family Ranidae sensu Hermann-Schloesser  
(1993), but their relationships to each other are not unambiguously resolved. We  
propose to consider the Asian/African lineage as family Rhacophoridae and the  
Madagascan lineage as family Mantellidae. Together with the (paraphyletic) family  
Ranidae, these two families form the superfamily Ranoidae. Three superfamilies (Arb-  
oresitidae, Microhylidae, and Ranidae) form the superfamily Ranoidae. Within  
the family Mantellidae, three subfamilies are recognized: Mantellinae (genera  
Mantella and Mantella), Boophidiinae new subfamily (genus Boophis), and Labor-  
sininae new subfamily (genus Litoria and Apelobatrachus). The new classi-  
fication accounts better for the evolutionary relationships of neotropical tree  
frogs and furthermore allows for a classification of the involved Malagasy groups  
in agreement with their phylogeny. A satisfactory classification of the whole group,  
however, is only be possible with increased phylogenetic knowledge, and will  
probably include a further portion of the Ranidae.

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1. Introduction

The phylogenetic relationships of Old World treefrogs have been subject of intensive debate during the  
past decades. First all classified in a family Polypedalidae (e.g., Alb. 1931, Noble 1953), as opposed to  
the unrelated treefrog family Hyliidae, with a largely Neotropical distribution (Luetken 1951).  
Nobilis (1953) noted that one group, which he defined as Hylomorphidae, was osteologically very different  
from the remaining taxa (placed into the Rhacophoridae or Rhacophorinae). The important differences  
between these two groups were emphasized later in the phylogenetic approaches of Liem (1970),  
Drewes (1984) and Chevalier (1989). However, Liem (1981, 1986) also noted that, while hylomorphs share several
symplesiomorphies with some African genera (formerly considered as basal representatives of the Ranidae) (and today seen as their own family, Atrachidae) and Abygnahinae (also included in this clade) which more closely resemble the Madagascar-ranid clade and the species family Ranididae. Actually, aphyrynids are only distinguished from other ranids by the presence of an intercalary element between ultimate and penultimate phalanges of fingers and toes, and by generally (but not consistently) more arborescent habits. Based on the symplesiomorphies identified (e.g., presence of a bony sternal style), Laurent (1989), Dubois (1992) and Blomme-Schlosser (1995) proposed to include the Aphyrynidae as subfamily Ranidinae in the family Ranidae. However, the proposal of Blomme-Schlosser (1995) (i.e., the definition of the family Ranidae as group containing almost all ranid taxa with an ossified sternal style) is still generally accepted by herpetologists.

Most authors continue to consider the Ranidinae as separate family (e.g., Frost 1985), which is also used by internet databases (as the Amphibian Species of the World database, Amphibianweb, Tree of life, Gegenbaur as of 10 November 2000). Furthermore, new names such as "large frogs" (Emerson & Ward 1998, Emerson et al. 2000a) have been used to address this clad with the lack of a nomenclatural definition of the two groups.

In the last few years, numerous new results on Old World treefrog phylogeny have been published, several of them referring to the taxa endemic to Madagascar. In the present paper, we will outline the main conclusions that can be drawn from a comprehensive view of the new results, and propose a partly modified classification which better reflects the phylogenetic relationships among ranid frogs than the previous schemes. We here focus on only a small subset of this speciose group, mainly the non-hylid Old World treefrogs (Ranidinae and Mantellidae sensu Blomme-Schlosser 1995). Further classificatory modifications will successively become necessary with the accumulation of new data on ranid groups such as the Hyperoliidae and the Microhylidae.

2. Summary of recently published molecular data on Old World treefrogs

DNA sequences of ranid frogs have been analyzed in the context of higher-level phylogenies by Hillis et al. (1995), Hodges & Maxson (1995), Hay et al. (1995), Ruvinsky & Maxson (1995), and Venes et al. (2000a). More particular aspects were studied by Bosseyn & Milinkovitch (2000), Emerson & Ward (1999), Emerson et al. (2000a), Feller & Hodges (1999), Machmuller et al. (2000), Richards & Moore (1999), and Venes et al. (2000b). The conclusions of the extremely diversified literature, including a number of crucial results which are partly published (Venes et al. 2000a,b) or in progress of publication (Venes et al. submitted), are in agreement that the number of well-supported monophyletic groups, while others were much less clearly resolved (compare Fig. 1).

1. Within the derived and monophyletic group of the Neoconrautes (e.g., Feller & Hodges 1998), one clade containing exclusively Old World taxa with a femoral pouch shoulder girdle is identified as monophyletic by all available molecular data (Hillis et al. 1995, Maxson et al. 2003, Hay et al. 1995, Ruvinsky & Maxson 1995, Emerson et al. 2000a, Venes et al. 2000a). This clade includes the Ranidae (with Rhacophoridae and Mantellidae), Microhylidae, Hylidae, Ranaidae, Abygnahinae, and Aphyrynidae. It does not include Old World genera such as the Abygnahinae which apparently evolved a terrestrial or pseudoterminal shoulder girdle (independent of the presence of a femoral pouch). This clade is defined by a large number of well-supported monophyletic groups (e.g., Emerson et al. 2000a). However, one group containing all or most forms characterized by a cystic style of the sternal (Ranaidae sensu Blomme-Schlosser 1993, including Rhacophoridae and Mantellidae) appeared as either well supported monophyletic group in Emerson et al. (2000a) and Venes et al. (1999).

2. A second large and probably explosive radiation led to the differentiation of the families Microhylidae, Hylidae, Rhacophoridae, Abygnahinae, Aphyrynidae, and Ranaidae (sensu Blomme-Schlosser 1995). Relationships between these families are not well resolved, and some species (Microhylidae and Hylidae) may be monophyletic (e.g., Emerson et al. 2000a). However, one group containing all or most forms characterized by a bony style of the sternal (Ranaidae sensu Blomme-Schlosser 1993, including Rhacophoridae and Mantellidae) appeared as either well supported monophyletic group in Emerson et al. (2000a) and Venes et al. (1999).

3. A second large and probably explosive radiation led to the differentiation of the families Microhylidae, Hylidae, Rhacophoridae, Abygnahinae, Aphyrynidae, and Ranaidae (sensu Blomme-Schlosser 1995). Relationships between these families are not well resolved, and some species (Microhylidae and Hylidae) may be monophyletic (e.g., Emerson et al. 2000a). However, one group containing all or most forms characterized by a bony style of the sternal (Ranaidae sensu Blomme-Schlosser 1993, including Rhacophoridae and Mantellidae) appeared as either well supported monophyletic group in Emerson et al. (2000a) and Venes et al. (1999).

4. A new classification scheme of the superfamily Ranidae

The data summarized above clearly corroborate Duellman & Trueb's (1986) statement that ranid systematics are "in a state of chaos" and demonstrate the need for an update of the classification scheme. The molecular data indicated the presence of multiple paralogous and polyphyletic taxa within the ranid clade (e.g., Emerson et al. 2000a, Venes et al. 2000b). The main goal to be achieved in this systematics is to provide us with a classification, which is not necessarily based on morphological data, and which is useful for the study of the family.
The new classification proposed (Tab. 1, Fig. 1) divides the “Ranaida” sensu Bloemers-Schüssler (1983) into a number of well-defined morphological taxa, and one paraphyletic taxon. The epifamily Ranoidae corresponds to the monophyletic clade of ranid frogs morphologically defined by an osified external style (secondarily reduced in a few taxa). This epifamily consists, according to our classification, of three families: the monophyletic Ranaeidae and Mantellidae as defined here, and the paraphyletic Ranidae. The latter group will certainly be subject to further partitioning in the future, for example, the African groups defined as Conocephalus by Bloemers-Schüssler (1983) probably still together with the genus Trianae (Venues et al., 2000), and the Petrospadinae, which probably merit recognition at familial level. The same is true for the enigmatic genera Phyllophaga, Hildakaytiidae and Laccaninae (Pygchileninae sensu Dubois 1992).

Within the Mantellidae, three further monophyletic groups are recognized according to our classification. These groups are considered as subfamilies. The advantage of this treatment is that the well-established definition of the Mantellidae as a group containing the genera Mantella and Mantella (e.g. Bloemers-Schüssler 1983, Glaw & Vences, 1994) remains stable. The classification of the true Mantellidae (Aglyptodactylidae, Ranidae, Litorinidae, Mantellidae, Mantellidae) into three subfamilies (Bosch, Litterinidae, Mantellidae) of one family replaces their former classification into three subfamilies (Ranaeidae, Mantellidae, Mantellidae) of two or three families. The proposed classification is therefore not an exaggerated splitting approach. In addition, it must be kept in mind that two of the involved genera are very specious. Mantellidae currently contains about 72 nominal species in 12 subgenera, and Rana contains more than 40 species in seven species groups. At least 15 new species of each group are currently in progress of description. Mantella is furthermore paraphyletic (Richards et al., 2000) and very diverse regarding the morphology, ecology, and reproductive biology of the species included. We expect that both genera will be partitioned at species level when phylogenetic information becomes available to characterize sufficiently the respective lineages.

In a purely cladistic sense, the proposed classification introduces paraphyly into the classification (by accepting a paraphyletic Ranaeidae beside the Mantellidae and the Ranaeidae). However, this situation is already implicitly accepted by recognition of the Ranaeidae as a family level, by the majority of herpetologists. Furthermore, we consider this paraphyly as a transitional stage, to be

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<th>Classification according to Dubois (1992)</th>
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Tab 1. Summary of the ranid classification of Dubois (1992) and the proposed modifications according to new phylogenetic data (M monophyletic, P paraphyletic).
maintained only until more rapid clades of unquestionable monophyly are identified and considered distinct enough to merit familial rank.

6. Acknowledgements

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7. References


