

A REVIEW OF THE TAXONOMY OF THE *HYPEROLIUS VIRIDIFLAVUS* COMPLEX

ANIA M. WIECZOREK¹, ALAN CHANNING¹ AND ROBERT C. DREWES²

¹*Department of Biochemistry, University of the Western Cape, Private Bag X17, Bellville 7535, South Africa*

²*Department of Herpetology, California Academy of Sciences, San Francisco, California 94118, USA*

This paper reviews the problematic taxonomy of the superspecies *Hyperolius viridiflavus* (the senior synonym of *H. marmoratus*) (Anura: Hyperoliidae). The classifications proposed by various authors for the complex are summarized and compared. Significant differences in classification have resulted in the complex being divided into as few as three species (with numerous subspecies) or as many as 18 species (with a number of subspecies). The review shows that the taxonomy of this complex has not been resolved, as a consequence of dependence on the use of dorsal colour patterns as diagnostic characters. Colour pattern is polymorphic within taxa, and shows both geographical as well as non-geographical variation. Recent work has shown molecular techniques to be a valuable means of distinguishing taxa previously considered to be subspecies. It is proposed that the use of molecular techniques and phylogenetic analysis of these data is the most suitable means of resolving the taxonomy of the members of this complex.

INTRODUCTION

The Old World tree frogs of the family Hyperoliidae are a diverse and colourful group, found throughout much of Africa and the islands of Madagascar and the Seychelles. Although many hundreds of species have been named, currently about 200 are recognized. Adults vary in size and most are arboreal. Although the greatest diversity occurs in the tropics, they are found throughout sub-Saharan Africa.

One of the widespread taxa in this family is known as *Hyperolius viridiflavus*. In the southern part of its range the name *Hyperolius marmoratus* is applied. There is little morphological variation discernible, and dorsal colour patterns have been used as a basis for subspecific taxonomy. Various populations appear to have dominant colour patterns, although pattern polymorphism is the rule. The group has been the subject of extensive debate (Broadley, 1965). The taxonomic confusion arises out of the apparently stable pattern polymorphisms within each population, and the difficulty of reconciling different taxonomies based upon populations from west, east, central and southern Africa.

The present review was prompted because this complex of taxa is of evolutionary interest, comprises a considerable proportion of the African amphibian fauna, and has conservation value. We review the major literature, highlight existing confusion, and show that molecular techniques have started to solve some long-standing problems.

THE OLD WORLD TREE FROGS

The first major taxonomic revision of the African tree frogs placed them into a single family with 527 species in 12 genera (Ahl, 1931). Laurent (1951) examined the osteology of the African and Asiatic tree frogs, and pro-

posed a split into two families, the Hyperoliidae and the Ranidae. Liem (1970) recognized two families: the Hyperoliidae and the Rhacophoridae, believing them to be diphyletically derived from primitive ranoids. His proposal was based on an analysis of internal and external morphological characters. Drewes (1984) extended the study by incorporating material from more taxa, and including more characters. Current taxonomy (Frost, 1985) retains the Hyperoliidae and Rhacophoridae. The systematics of this group, however, are uncertain, particularly in genera like *Hyperolius*, and the question of whether subfamilies such as Hyperoliinae are monophyletic remains unanswered.

THE FAMILY HYPEROLIIDAE

Liem (1970) proposed that the Hyperoliidae evolved from ranoid stock in Africa. Detailed investigations by Drewes (1984), based on a cladistic analysis of skeletal, myological and cartilaginous characters, placed *Leptopelis* as the most primitive genus in the family. *Hyperolius* and *Afrixalus* constituted a monophyletic clade, with the Malagasy *Heterixalus* as sister group. A re-analysis of the available data by Channing (1989) supported the monophyly of the Hyperoliidae, but suggested minor rearrangements, such as placing *Hyperolius* as the sister group to *Cryptophylax* and *Chrysobatrachus*. Richards & Moore (1996) were able to use molecular methods to contribute to this debate.

The status of genera within the family is not stable. Perret (1988) erected the genera *Nesionixalus* for *Hyperolius thomensis*, *Alexeroon* for *H. ostetricans*, *Arlequinus* for *H. krebsi* and *Chlorolius* for *H. kohleri*.

The family also has a number of taxonomic problems at species level, for example, within the genus *Hyperolius* (Poynton & Broadley, 1987). This interest-

ing genus has been considered to be 'one basic morphological type' with many dorsal colour patterns (Poynton, 1964).

THE *HYPEROLIUS VIRIDIFLAVUS* COMPLEX

The taxa included in this species have been placed in *Hyperolius marmoratus*, *H. parallelus*, *H. tuberculatus* or *H. viridiflavus* by various authors. The taxa included may indeed belong to only one or to a number of different species. No generic-level phylogeny is available to adequately resolve all these issues. For the purposes of this review, we will regard all the taxa within this group (sometimes referred to as a superspecies) to be nominally part of *Hyperolius viridiflavus*.

Schiøtz (pers comm.) is no longer convinced of the need to maintain specific status for *H. parallelus*. The recognition of this species was based on five reported cases of supposed sympatry between two forms in the complex. Poynton & Laurent (in press) doubt four of these cases, leaving only the sympatry at Sango Bay, Uganda. The Sango Bay case can be explained by a recent immigration to the west of Lake Victoria from the south and north.

BIOGEOGRAPHY

Hyperolius viridiflavus occurs throughout sub-Saharan Africa. It is absent from arid areas, and the highlands of Ethiopia and southern Africa. Various fac-

TABLE 1. Comparison of various taxonomies for the *Hyperolius viridiflavus* complex.

Laurent (1951)	Poynton (1964)	Schiøtz (1971)	Laurent (1976)	Poynton & Broadley (1987)
<i>Hyperolius marmoratus angolensis</i>	<i>Hyperolius angolensis</i>	<i>Hyperolius parallelus angolensis</i>	<i>Hyperolius marginatus angolensis</i>	<i>Hyperolius marmoratus angolensis</i>
<i>Hyperolius marmoratus aposematicus</i>	<i>Hyperolius aposematicus</i>	<i>Hyperolius parallelus aposematicus</i>	<i>Hyperolius marginatus aposematicus</i>	<i>Hyperolius marmoratus aposematicus</i>
<i>Hyperolius marmoratus argentovittis</i>		<i>Hyperolius parallelus argentovittis</i>	<i>Hyperolius marginatus argentovittis</i>	<i>Hyperolius marmoratus argentovittis</i>
	<i>Hyperolius marmoratus broadleyi</i>	<i>Hyperolius parallelus broadleyi</i>	<i>Hyperolius marginatus broadleyi</i>	<i>Hyperolius marmoratus broadleyi</i>
	<i>Hyperolius marmoratus marginatus</i>		<i>Hyperolius marginatus marginatus</i>	<i>Hyperolius marmoratus marginatus</i>
<i>Hyperolius marmoratus nyassae</i>		<i>Hyperolius viridiflavus nyassae</i>	<i>Hyperolius marginatus nyassae</i>	<i>Hyperolius marmoratus nyassae</i>
<i>Hyperolius marmoratus rhodoscelis</i>		<i>Hyperolius viridiflavus rhodoscelis</i>	<i>Hyperolius marginatus rhodoscelis</i>	<i>Hyperolius marmoratus rhodoscelis</i>
<i>Hyperolius marmoratus rhodesianus</i>	<i>Hyperolius rhodesianus</i>	<i>Hyperolius parallelus rhodesianus</i>	<i>Hyperolius marginatus rhodesianus</i>	<i>Hyperolius marmoratus rhodesianus</i>
<i>Hyperolius marmoratus swynnertoni</i>		<i>Hyperolius parallelus swynnertoni</i>	<i>Hyperolius marginatus swynnertoni</i>	<i>Hyperolius marmoratus swynnertoni</i>
<i>Hyperolius marmoratus taeniatus</i>	<i>Hyperolius marmoratus taeniatus</i>	<i>Hyperolius viridiflavus taeniatus</i>		<i>Hyperolius marmoratus taeniatus</i>

TABLE 2. Subspecies of *Hyperolius* listed by Schiøtz (1975) (excluding *Hyperolius sheldricki* from southern and eastern Kenya for which no subspecies were recognized, and *Hyperolius marginatus*, which is of doubtful status).

<i>Hyperolius tuberculatus</i> from forest in central and west Africa	<i>Hyperolius viridiflavus</i> from savanna in west, east and southern Africa	<i>Hyperolius parallelus</i> from savanna in western central Africa
<i>H. t. tuberculatus</i>	<i>H. v. spatzi</i>	<i>H. p. parallelus</i>
<i>H. t. hutsebauti</i>	<i>H. v. nitidulus</i>	<i>H. p. angolensis</i>
<i>H. t. nimbae</i>	<i>H. v. pallidus</i>	<i>H. p. argentovittis</i>
	<i>H. v. pachydermis</i>	<i>H. p. melanoleucus</i>
	<i>H. v. viridiflavus</i>	<i>H. p. epheboides</i>
	<i>H. v. variabilis</i>	<i>H. p. pyrrhodictyon</i>
	<i>H. v. coerulescens</i>	<i>H. p. aposematicus</i>
	<i>H. v. karissimbiensis</i>	<i>H. p. rhodesianus</i>
	<i>H. v. xanthogrammus</i>	<i>H. p. broadleyi</i>
	<i>H. v. ferniquei</i>	<i>H. p. albofasciatus</i>
	<i>H. v. grandicolor</i>	<i>H. p. swynnertoni</i>
	<i>H. v. ommatostictus</i>	
	<i>H. v. goetzei</i>	
	<i>H. v. rhodoscelis</i>	
	<i>H. v. mariae</i>	
	<i>H. v. nyassae</i>	
	<i>H. v. taeniatus</i>	
	<i>H. v. marmoratus</i>	
	<i>H. v. verrucosus</i>	

tors have been suggested to account for frog distribution in southern Africa (Van Dijk, 1971; Poynton & Bass, 1970). Detailed distributional data for *H. viridiflavus* is poor for some areas, notably central Angola and southern Zaire.

SPECIAL CHARACTERISTICS

A number of unique characteristics serve to define and delimit the complex. The members of the complex are distributed (1) in tropical savannas in Africa at low and medium altitude; (2) populations are usually large and a conspicuous component of frog breeding aggregations; (3) members of the group share a number of morphological and behavioural characters, although they are extremely variable in dorsal colour pattern, both within and between populations (Schiøtz, 1971).

Various colour phases are recognized: a juvenile (J) phase, which is typically cryptic, and an adult female (F) phase, which may be cryptic or aposematic (Schiøtz, 1971). Mature females are always phase F, but mature males may be either phase J or F. In *H. parallelus* (*sensu* Schiøtz, 1971), the F phase is polymorphic, with three morphs showing independent geographic variation. The variation in the F phase has been suggested to be the result of recent hybridization (Schiøtz, 1971). Zimmerman (1979) showed that more

than 45 hybrid colour patterns could be obtained within a few generations from four breeding adult *Hyperolius*. The role of hybridization as the source of the pattern polymorphism has not been experimentally demonstrated.

Typical external features of *H. viridiflavus* are the short, almost truncated snout, giving a 'pug-face' appearance, and extensive webbing reaching the distal subarticular tubercle of the fourth toe on both sides (Poynton, 1964). The vocal sac and gular gland are large relative to the snout-vent length, and females have a transverse gular fold (Schiøtz, 1971). Taxonomy based on morphological characters is difficult in this group, owing to the fact that there are many similarities shared by the members of the complex. Some characters, such as the dorsal colour pattern, are convenient to describe but are highly variable, which makes them of questionable use in taxonomy.

TAXONOMY

Broadley (1965), in a review of *H. viridiflavus* in central and southern Africa, described the group as a 'taxonomic nightmare'. In Table 1 we compare the nomenclature applied to certain taxa by different authors. Schiøtz (1971) suggested that the complex may be in the process of rapid evolution with many morphologi-

cally similar species exhibiting great variation with a propensity for geographical splitting. He lists five species (Schjötz, 1975) with many subspecies (Table 2). A molecular-level genetic study is required to determine if the group consists of old or recent species.

Laurent's (1951) concept of the group regarded *H. tuberculatus* as being an isolated, possibly primitive, species occurring in clearings within the forest belt. *Hyperolius marmoratus* was considered to be a polytypic species occurring in savanna south of a line through Kivu, Burundi, northern Tanzania and the Tana river valley of Kenya. The form occurring north of the line was named *H. viridiflavus*. Table 1 illustrates how various authors have subsequently regarded these taxa, with many being shifted between the species *marmoratus*, *parallelus* and *marginatus*, or being regarded as full species in their own right.

Schjötz (1971) questioned the validity of the northern and southern species, as the only character used to separate them was a supposed difference in J phase. The value of the J phase as a taxonomic character is doubtful (Schjötz, 1971; Richards, 1981). Although *H. marmoratus* was considered a junior synonym of *H. viridiflavus* (Schjötz, 1971), he states that more than one species is involved in the material he examined.

Not all the taxa are allopatric, as classical subspecies concepts suggest. *H. v. argentovittis* occurs together with various other 'subspecies': for example in Uganda with *H. v. bayoni*, and in Rwanda with *H. v. schubotzi* (Schjötz, 1971). Further complicating the issue, Schjötz (1971) emphasizes a great similarity in pattern between a number of forms covering a huge area in the Republic of Congo, Angola, Zambia, Zimbabwe and Malawi. Although the geographical pattern polymorphism in *H. viridiflavus* is great, a character such as the brown dorsum is found in all taxa from west and north central Africa (Schjötz, 1971). Schjötz (1971) demonstrated that individual characters (1) have a wider distribution than the conventional subspecies; (2) change gradually over the area; (3) change independently of one another; and (4) do not show steep clinal steps. He recommends the use of the subspecies category only as a convenient short-hand way of describing distinct forms.

The pattern of polymorphism may be maintained as a predator avoidance strategy, or may merely be the result of ongoing hybridization in relatively recent savanna, for example between the Congo forest and Lake Victoria. Laurent (1983) defended his earlier view of a north-south split, based on morphometric analyses of a number of body proportions. This kind of numerical approach has not gained general acceptance.

Poynton (1985) investigated the subspecies *H. m. taeniatus* and *H. m. broadleyi*, and attempted to determine whether they were deserving of subspecific status. He stated that there is general agreement that there are one or more species of marmorate reedfrog in the southern half of Africa, and that their dorsal pattern shows a vicariate distribution. He then goes on to indi-

cate that although there is agreement on which taxa may be erected on the basis of presently collected material, there is widespread disagreement in the literature as to which species these should be assigned to. The problem appears to be largely related to the use of the subspecies as a taxonomic unit (Poynton, 1985). The subspecies concept is largely based on allopatric but relatively similar taxa, and whether they intergrade or not when their distributions overlap. The *H. marmoratus* complex confounds this definition, as various forms may be collected from one locality with distinct differences, while at other localities, complete series from one form to another may be collected. Poynton's (1985) study of subspecies arose from confusion surrounding these taxa. As a result of there being intergrades with each other in the south of their distribution, a series including forms that may be *H. parallelus* or *H. marmoratus* is observed, even showing intergrades with "non-marmorate" *H. marginatus* in central and western Zimbabwe. This contrasts with Schjötz (1971), however, who separated *taeniatus* and *broadleyi*.

This decision evidently results from confusion of material examined, and Poynton (1985) suggests that the divisions of Schjötz (1975) and Laurent (1976), placing intergrades under various species are incorrect, and that the name *marmoratus* should be applied.

In a more recent paper, Poynton & Broadley (1987) confirm that, although the members of the complex share morphology that separates them from the rest of the genus *Hyperolius*, the delimitation of all currently recognized subspecies in the complex is open to question. They suggest that the featureless plateau areas inhabited by these frogs in the west, and the degree of variation and merging of forms, may frustrate the nomenclatural process in that part of Africa, as clear-cut ranges can not be defined.

The use of colour patterns to determine relationships and taxonomy in this group may lead to confusion if the Mendelian basis for pattern inheritance is not understood. Richards (1981) showed that three colour variants of *H. viridiflavus*, 'striped', 'hourglass', and 'female', were allelic. She hypothesized that 'striped' was dominant over 'hourglass', and that 'hourglass' and 'female' patterns were recessive, producing both patterns in a 1:1 ratio in crossing experiments. Similar findings have been reported for other anurans (Pyburn, 1961). Adult colour patterns are switched on hormonally at maturity. Richards (1982) was able to force colour pattern changes at metamorphosis by appropriate hormone treatment. A particular individual frog may show either a juvenile or adult pattern depending on its state of sexual maturity.

MOLECULAR TECHNIQUES

Molecular techniques have made important contributions in resolving similar issues in other species of anurans (e.g. Hillis & Davis, 1986) and they may be of

use in providing much-needed data on some of the systematic problems in the *Hyperolius viridiflavus* complex.

Hess *et al.* (1995) used RFLPs (Restriction Fragment Length Polymorphisms) to compare *H. v. broadleyi* from eastern Zimbabwe and *H. v. verrucosus* from South Africa. They used 37 restriction sites on nuclear genes, and concluded that the differences between these two taxa warranted recognition at the species level. They did not attempt to determine the geographical ranges of these two subspecies. Wiczorek & Channing (in press) present DNA sequence data from a mitochondrial gene that confirms the differences found by Hess *et al.* (1995), and also indicates that some presently recognized 'subspecies' are genetically identical. Molecular work on other species within the Hyperoliidae (Richards & Moore, 1996) has demonstrated that DNA sequence data is a valuable approach to producing hypotheses of phylogeny.

Molecular techniques thus seem able to produce sufficient data that can be objectively evaluated to lead to a phylogeny of the group. The resolution of the problems of taxonomy will follow.

CONCLUSIONS

The Hyperoliidae is a monophyletic family, derived from ranoid stock. The Hyperoliinae consists of arboreal species inhabiting trees or other vegetation. The genus *Hyperolius* contains a number of colourful and diverse species. It appears that the complex of forms presently included in the *Hyperolius viridiflavus* complex may be of relatively recent origin. This hypothesis is supported by the presence of unstable hybrid populations (Schlötter, 1971) and the large number of subspecies recognized. This complex is distributed throughout the tropical African savanna, with a closely related form, *H. tuberculatus*, patchily distributed in forests.

Taxonomy in the *Hyperolius viridiflavus* complex is largely based on dorsal colour pattern. However, there is a large amount of variation both between and within populations which confuses the taxonomy. Many pattern intergrades exist, which adds to the taxonomic uncertainty that plagues this taxon.

A phylogeny that adequately resolves the taxa included in the *Hyperolius viridiflavus* complex is not available. Recent attempts to use molecular techniques have demonstrated that these will be able to provide sufficient data to produce a phylogeny.

Although DNA sequences show the promise of resolving this long-standing problem, two issues remain: Most, if not all, museum specimens are not suitable for these techniques, so that the material that is the basis for the present debate will not be part of the solution, unless the same localities are revisited and recollected. Secondly, many parts of Africa where *Hyperolius viridiflavus* is likely to occur have never had adequate collections made. The taxonomic confusion in the *Hyperolius viridiflavus* complex is likely to remain un-

til detailed fieldwork and extensive laboratory analyses can be completed.

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