

Biosystematics of South American Bufonidae, with special reference to the *Bufo* "typhonius" group

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Abstract. South American Bufonidae presently are grouped into nine genera, with several new genera still to be described. One of the most confused groups was formed by the toads grouped under the catch-all *Bufo* "typhonius". Thirteen of the 17 species names associated with it are removed or synonymized. The complexity of the taxa generally assigned to *Bufo* "typhonius" is discussed and a hypothesis is presented for the function of the hypertrophied cephalic crests in females of some of the species. Differences in ecology are mentioned and a short overview of the distribution of several taxa is given. Relationships are still unclear, though only few species seem to be closely related. Microcomplement fixation tests will be needed.

Key words. Amphibia, Anura, Bufonidae, *Bufo typhonius*, South America.

Introduction

Systematics of Bufonidae, and especially those of South America, have been in turmoil since McDiarmid (1971) redefined the family and included *Atelopus*, *Dendrophryniscus*, *Melanophryniscus* and *Oreophrynella*, till then considered a separate family Atelopodidae. He convincingly argued for their inclusion in the Bufonidae and in this was followed by all later authors (Ruíz-Carranza & Hernández-Camacho 1976, Frost 1985). Since McDiarmid's review several new genera have been described, partly based on species of *Atelopus* and *Bufo*, partly on new material. Skeletal and myological morphology was used, in addition to external characters, to define these genera.

Trueb (1971) described *Rhamphophryne* from moderate elevations on the eastern versant of the Andes in Ecuador, Colombia and extreme eastern Panama, characterized by seven or eight presacral vertebrae, the arciferal pectoral girdle, extended ossifications at the anterior part of the sphenethmoid and nasal cartilages, by the rather well-webbed hands, the large unpigmented eggs and other characters. Izecksohn (1976) added a species from "Bahia", Brazil, that had remained, until then, in *Atelopus*. Ruiz-Carranza & Hernández-Camacho (1976) described *Osornophryne* from high elevations on the eastern versant of the Andes in Colombia and Ecuador, characterized by six presacral vertebrae, the firmisternal pectoral girdle, the fused sacrum and coccyx, bony flanges along the coccyx,

the reduced number of phalanges in fingers and toes, the strongly webbed hands and feet, the absence of parotoids, the large unpigmented eggs and other characters. Cannatella (1986b) and Hoogmoed (1987) described three additional species. *Bufo cophotis* Boulenger from Peru has large, flat warts on the back and on the tibia, no tympanum, top of head concave and flattened toes and could well turn out to be a species of *Osornophryne*. Hoogmoed (1985b) described *Andinophryne* from the western versant of the Andes in southern Colombia and adjacent northern Ecuador, on the basis of *B. atelopoides* Lynch & Ruiz-Carranza and two new species, characterized by eight presacral vertebrae, the arciferal/firmisternal pectoral girdle, the presence of a small omosternum, the elongate parotoid glands, the normal number of phalanges, the extensively webbed fingers and toes and the numerous small, unpigmented eggs. Cannatella (1986a) described *Frostius* based on a species of *Atelopus* only known from Pernambuco, Brazil, and characterized by eight presacral vertebrae, the firmisternal pectoral girdle, the fused sacrum and coccyx, the normal number of phalanges, the completely ossified sphenethmoid complex and the few yellow eggs. In describing these genera, life history data and anatomy were increasingly taken into account.

Recently I obtained some bufonids from eastern Peru, which show several characters of *Andinophryne* and several of *Osornophryne*, thus suggesting this taxon might belong to a distinct genus.

Several South American toads, now considered species of *Bufo*, may well turn out to actually represent distinct genera. E. g. the *Bufo guttatus* group, containing *B. anderssoni* Melin, *B. blombergi* Myers & Funkhouser, *B. caeruleostictus* Günther, *B. glaberrimus* Günther, *B. guttatus* Schneider and *B. haematiticus* Cope (of these *anderssoni* and part of the material called *glaberrimus* might well turn out to be synonymous with *guttatus*) is characterized by the presence of a small omosternum, a broad skull lacking cranial ridges, long legs, elongate parotoids which exude yellow poison, hypertrophied testis, and mostly smooth skin. More research has to be done into this subject to be certain, but it is very likely that the generic status of this group will soon be evident.

Recent studies showed that *Bufo hypomelas* Boulenger, formerly considered to belong to the *B. guttatus* group by Cochran & Goin (1970) and Hoogmoed (1985a), could not be assigned to any group because of lack of information on skeletal characters (Hoogmoed 1989).

Another questionable taxon, as to generic position, is *B. nesiotes* Duellman & Toft, which has an arciferal pectoral girdle, a very large tympanum, indistinct parotoids, extensively webbed fleshy feet, a distinctly constricted neck, and in general does not look like a *Bufo*.

Relationships of the Neotropical non-*Bufo* bufonids were analysed by Cannatella (1986a), who reached the conclusion that *Crepidophryne* (Central America), *Peltophryne* (Greater Antilles) and *Rhamphophryne* were most closely related to *Bufo* because of their completely arciferal pectoral girdle, and the presence of parotoids and cranial ridges, and more distantly with the other South American non-*Bufo* bufonids, viz. *Frostius* and the "atelopodids" *Atelopus*, *Melanophryniscus*, *Dendrophryniscus*, *Oreophrynella* and *Osornophryne*, to which can be added *Andinophryne*, all having a partly or completely firmisternal pectoral girdle.

Sufficient data of the taxa mentioned with indeterminate status are still lacking to make a complete analysis.

Notwithstanding the transfer of several species, the genera *Bufo* and *Atelopus* remain speciose, the first having its main distribution at lower altitudes, the second being more concentrated in the Andes of Ecuador and Colombia, with species extending north and south and even into the Amazonian lowlands. I will not further discuss *Atelopus* here, but confine myself to *Bufo*.

South American *Bufo*

One of the largest groups within this genus, at least nominally, is the rather mythological *Bufo* "*typhonius*" group. The species *B. "typhonius"* is said to occur from Panama through the Amazon area south to Bolivia and southern Brazil, with disjunct populations in Pacific Ecuador and Chocóan Colombia, and in the Atlantic coastal forest belt in SE Brazil (Hoogmoed 1986, 1989b), whereas a great number of species, said to belong to the *B. "typhonius"* group (Cei 1968, 1972, Hoogmoed 1985a), are spread along the periphery of this area. As has been mentioned elsewhere (Hoogmoed 1986, 1989a) the species *B. "typhonius"*, which has long been 'known', is composed of several taxa, that differ in adult size, development of cephalic crests, wartiness of skin, colour of iris, mating call, ecological preference and in a number of cases show large immunological distances. During the past few years I have been studying these toads in order to sort out what the real situation is.

Taxonomy in the *Bufo* "*typhonius*" group

The first fact that could be established was that quite a number of the 17 species relegated to this group (Cei 1968, 1972, Hoogmoed 1985a) do not have anything to do with it. The following names can be eliminated from the *Bufo* "*typhonius*" group of recent authors, as compiled by Hoogmoed (1985a):

B. atelopoides Lynch & Ruiz-Carranza was shown by Hoogmoed (1985b) to belong to the genus *Andinophryne*.

B. caeruleostictus Günther according to Hoogmoed (1989a) is most likely a member of the *B. guttatus* group.

B. chanchanensis Fowler according to Hoogmoed (1989a) is a synonym of *B. caeruleostictus*.

B. fissipes Boulenger: Examination of the type specimen (BM 1947.2.20.64) showed that this form has no cephalic crests or ridges, the tympanum is hidden and covered by spinulose skin, whereas the parotoids are elongate and show a row of enlarged tubercles down the middle. It is quite evident that this species has no relationship with *B. "typhonius"* whatsoever, though it is not clear where its real relationships may lie.

B. inca Stejneger was described on the basis of one specimen, and two more were later assigned to it. Barbour & Noble (1920) already suggested that the differences between this taxon and *B. ockendeni* Boulenger (= *B. veraguensis* Schmidt) were so small that these two taxa might represent only races of the same species. Mertens (1942) considered *B. inca* a subspecies of *B. ockendeni* and

Vellard (1959) synonymized the two forms under the name *B. ockendeni*. Cei (1968, 1972), Gorham (1974) and Hoogmoed (1985a) again treated it as a full species. After examination of the type specimen (USNM 49557), a female, I have come to the same conclusion as Vellard (1959) and consider it a synonym of *B. veraguensis*. It goes without saying that there is no relationship to *B. "typhonius"*. Also see remarks under *B. leptoscelis*.

B. intermedius Günther according to Hoogmoed (1989a) is a species wrongly reported from South America. In reality it is of Middle American origin and belongs to the *B. valliceps* group.

B. iserni Jimenez de la Espada was considered a synonym of *B. "typhonius"* for a long time. It lacks an internal ear, high cranial ridges and protruding vertebrae, and after examination of the holotype (MCNM 3057) and more recently collected material, I have come to the conclusion (Hoogmoed 1986) that it is a perfectly valid species not related to *B. "typhonius"*.

B. leptoscelis Boulenger is only known from the holotype (BMNH 1947.2.21.95). Examination showed it to be a female, and comparison with the type series (all males) of *B. ockendeni* (BM 1947.2.21.21-27) including the lectotype (= neotype of *B. veraguensis*), convinced me that *B. leptoscelis* is nothing but the female of *B. ockendeni* (= *B. veraguensis*), an opinion strengthened by Gallardo's (1961) table comparing several forms. Vellard (1959) already noticed that the single specimen known of *B. leptoscelis* came from a locality from which the only other known species of *Bufo* was *B. ockendeni*. He suggested that when more material became available, it might be possible to establish whether we were dealing with a good species, or with sexual or individual variation. An additional female specimen has since become available in the form of the holotype of *B. inca*, and it agrees well with that of *B. leptoscelis*. They differ from male *B. veraguensis* (the valid name for *B. ockendeni*) in having a very distinct tympanum, in being more spinose on the back, and in having less webbing between the toes. Thus, there is a distinct sexual dimorphism in *B. veraguensis*. Cei (1980) recognized the *B. ockendeni* group, renamed the *B. veraguensis* group by Hoogmoed (1985a) on nomenclatorial grounds, as Savage (1969) convincingly showed that *B. veraguensis* and *B. ockendeni* were identical and had to be synonymized, *B. veraguensis* having priority over *B. ockendeni*. Examination of the type material of *B. inca*, *B. leptoscelis* and *B. ockendeni* (all synonyms of *B. veraguensis*), clearly shows that there is no relation to *B. "typhonius"*.

B. manicorensis Gallardo was said to differ "from all neotropical toads in the shape of the head and cephalic crests which recall certain Asiatic forms. In the Neotropical area the nearest species is *Bufo intermedius* Günther". However, direct comparison of the types of *B. intermedius* with that of *B. manicorensis* (BM 98.3.10.1) showed that the two are not even closely related (see above, and Hoogmoed 1989a). Though in the original description no mention is made of any relationship to *B. "typhonius"*, Cei (1968, 1972) placed it with his *B. "typhonius"* group, though stating that its position was not very clear. Examination of the holotype convinced me that this specimen is *B. granulosus* Spix.

B. ocellatus Günther, despite its unique habitus was synonymized with *B. "typhonius"* by Boulenger (1882), who synonymized a lot of South American

toads with this species and very often incorrectly so. Leão & Cochran (1952) studied new material and revalidated *B. ocellatus*, stating that it "is apparently not closely related to any other Brazilian form, although superficially it somewhat resembles *Bufo granulosus* and *Bufo d'orbignyi* in stoutness of body and in limb proportions. Its characteristic pattern distinguishes it at once from all other Brazilian toads. In shape of parotoids it suggests *Bufo marmoreus* of Mexico." Despite this clear article, Cei (1968, 1972) mentioned *B. ocellatus* again in relation to the *B. "typhonius"* group, admittedly with the proviso that its relationship was unclear. Examination of the holotype (BM 1947.2.21.86) showed that the remark made by Leão & Cochran (1952) is correct and that there is no relation to *B. "typhonius"*.

B. quechua Gallardo in the original description was compared to *B. ockendeni*, *B. inca*, *B. leptoscelis* and *B. fissipes*, most of which are now placed in the *B. veraguensis* group (see above), but no reference at all was made to *B. "typhonius"*. From this comparison it might be concluded that its relationships are with the *B. veraguensis* group. For reasons unclear to me Cei (1968, 1972) associated it with the *B. "typhonius"* group, and for administrative reasons, this was copied by Hoogmoed (1985a). Though I did not have an opportunity to study the holotype of this taxon, from the description and the accompanying picture I distinctly get the impression that there is no relation between this taxon and the *Bufo "typhonius"* group, and consequently I adhere to Gallardo's (1961) original opinion that it belongs to the *B. veraguensis* group.

B. vellardi Leviton & Duellman was proposed as a replacement name for *B. spinulosus orientalis* Vellard. Leviton & Duellman (1978) and Cei (1968, 1972) agreed that this taxon, either as a full species or as a subspecies of *B. limensis* Werner belonged to the *B. spinulosus* group. Hoogmoed's (1985a) statement that it belonged to the *B. "typhonius"* group clearly was incorrect.

Among the *B. "typhonius"* group names listed by Hoogmoed (1985a) one still remains a problem: *B. sternosignatus* Günther generally was considered a valid species, though Shreve (1947) treated it as a subspecies of *B. typhonius*. Most authors (Rivero 1961, Cochran & Goin 1970) agree that this species resembles *B. typhonius*, though Cei (1968, 1972) indicated it might alternatively be related to *B. granulosus*, whereas Porter (1964) synonymized it with *B. valliceps* Wiegmann, without argumentation. Generally, statements about relationship seem to have been made on the basis of general appearance (colour and pattern) and not on any hard morphological data. Examination of the Venezuelan syntypes (BM 1947.2.21.68-70) showed that these certainly are not *B. valliceps* and that they are not related to *B. granulosus* either. At the moment I am not quite certain yet about the true nature of this taxon, but I do not want to rule out the possibility that it is identical with *B. "typhonius"* from Panama and adjacent northern South America. Direct comparison of type-material should shed light on the matter. If they turn out to be identical it will be necessary to establish the correct name for this taxon from among several available names.

As a consequence of this work only the following names, considered to represent good species, remain in the so-called *B. "typhonius"* group, and even about them I do not feel quite happy: *B. ceratophrys* Boulenger, *B. dapsilis* Myers &

Carvalho, *B. nasicus* Werner and *B. margaritifera* Laurenti (= *B. typhonius* L. auct. [Hoogmoed 1989b]), all characterized by having a more or less pointed snout, (well) developed cranial ridges, distinct tympanum, parotoids, a lateral row of tubercles, more or less protruding dorsal spines of vertebrae 3-8, skin of flanks mostly attaching to the thighs closer to the knee than to the body, males with smooth, females with granular skin (exception *B. dapsilis*, of which only one female with smooth skin is known), and all having the so-called dead-leaf pattern. At the moment my impression is that even these four do not form a natural group. Especially here it will be important to have data from microcomplement fixation at hand, but unfortunately no samples are available yet from *B. ceratophrys*, *B. dapsilis* and *B. nasicus*.

As mentioned before, within the so-called species *B. "typhonius"* several good species can be distinguished. For some of these old names will be re-established, like *B. proboscideus*, *B. acutirostris* and *B. margaritifera* (Hoogmoed 1989b), others will have to be named, and the subspecies *B. typhonius roqueanus* Melin should be elevated to specific rank. Some of these taxa are sympatric, showing distinct morphological, behavioural and ecological differences, others are allopatric. Some seem to have rather extensive ranges within Amazonia, and sympatric with several others, which seem to be more localized. From here on I think the name *B. typhonius* (group) should be dismissed completely, not only because of nomenclatorial reasons (Hoogmoed 1989b), but also because of the confusion that has surrounded this name. Until now the so-called *B. "typhonius"* has been a catch-all for South American toads which only agreed in having a dead-leaf pattern on the back (and sometimes not even that), and according to the literature should have cranial crests and ridges. However, practice showed that under that name specimens of very different sizes, with and without crests were thrown together, which only agreed more or less in dorsal pattern. It now has become clear that we are dealing here with a mixture of differently sized specimens belonging to several taxa, and superimposed on that with sexual dimorphism, which may express itself in the development of cephalic crests, length of dorsal spines of vertebrae, granularity or smoothness of skin, and in size. Things were complicated from the beginning by Boulenger's (1882) rather liberal view of the species, sinking many described forms into synonymy, his example being followed by many later authors. Cochran (1955) introduced the misconception that "The usual well-marked black thumb of the male, a valid secondary sexual character in most species of *Bufo*, is of no value in determining sex in this species, since black spots on the joints of the thumb occur as part of the color pattern of nearly all specimens." Actually, males in the species here considered, during the mating season do have the normal dark patches of nuptial asperities on the inner fingers, and the character can perfectly well be used to identify sex. Apparently Cochran never examined the "black thumbs" of males under magnification, because in that case she would have noticed the different morphology of the area. Cochran & Goin (1970) further added to the confusion by stating that protruding vertebrae and large head crests occur in their "most extreme form in old males". As an example they cite USNM 108987, which already had been depicted by Cochran (1955). However, upon dissection of this specimen, it turned out to be



Fig. 1: *Bufo margaritifera* Laurenti, male from Zanderij, Suriname (field no. MSH 1975-325, in Nationaal Natuurhistorisch Museum [RMNH]).



Fig. 2: Unnamed small species of *Bufo* from Shiona, Ecuador (RMNH 21794).

an adult, egg-bearing female. My present studies have confirmed these observations: hypertrophied cranial crests and dorsal spines of vertebrae only occur in females. Males of the same taxon only have low cranial crests and the dorsal processes of the vertebrae are only indicated. Other characters subject to sexual variation are the texture of the skin: in females it is granular with many spinulous warts, in males the skin is nearly smooth with only few warts left, and size: females are larger than males.

In my opinion these characters may have an evolutionary advantage. Possibly they help to prolong amplexus once it has been established and diminish interference from other males. Because of its smaller size, the clasping male in an amplexic pair of a taxon with hypertrophied cranial crests in females, will partly be protected on the sides by these elevated crests and thus be less vulnerable to 'attacks' of other males wishing to court the female. In addition the smooth skin of the male will present a difficult grip for would-be suitors, whereas the grip of the male already amplexing the female is made more effective by her rougher, more granular skin. Thus, the hypertrophied crests more or less force a male in the right amplexic position, at the same time ensuring that the male that is in that position has an advantage over males that also would like to mount the female. In explosive breeders (like most of these toads seem to be), where many individuals aggregate in a small space at the same time, such structures ensuring a firm amplexus once it has been established, seem to be advantageous as they prevent or reduce unnecessary loss of energy in fights over females.

Ecology

In French Guiana, apart from a large, crested form (*B. "typhonius"* L. auct.), which should be called *B. margaritifera* (Hoogmoed 1989b), two small, unnamed species occur, differing from *B. margaritifera* and from each other by behavioural and ecological differences. The large species breeds at night in large congregations, with males calling from flooded parts of the rainforest and even entering secondary vegetation. Males of one of the small species only call in daytime from positions elevated above the ground in the rainforest, whereas the other one calls from a special type of swampy habitat ('pri-pri') at the edge of rainforest. Apart from the morphological and ecological differences there are differences in the advertising call (duration, pulse repetition rate, frequency range), which are significant. The medium-sized *B. proboscideus* from central and western Amazonia, incorrectly referred to as *B. dapsilis* by Zimmerman & Bogart (1988), according to recent personal field-observations breeds in small bodies of water that had accumulated in empty pods of Brazil nut (*Bertholletia excelsa*) on the ground, in deep grooves in the trunk of certain fallen trees (*Minquartia guianensis*) and in small holes in the ground in areas (terra firme) where other (standing) water was rare. In one case calling males were found in small pools at the swampy edge of a creek, the only place where Zimmerman & Bogart (1988) found the species and which they indicated as "baixon". Males of this species call after heavy rains, both at night and in daytime.

In western Amazonia a small species breeds in swampy areas bordering rainforest creeks, with males calling in daytime. Males of another small species near Tefé, Brazil were found calling in daytime from the edge of small, but deep pools in terra firme forest. It has not yet been established what the exact relationship between these two forms is, but sonagrams of the calls, and their morphology suggest them to be different species. Of most other taxa in this group no mating or advertisement calls are available, due to the fact that all these species seem to be explosive breeders that only assemble and start calling during strictly limited periods, probably mostly directly after heavy rains at the beginning of and during the wet season (Wells 1979, Zimmerman & Bogart 1988), and consequently are unpredictable in their behaviour and thus difficult to collect.

Distribution

From the foregoing it will have become evident that the simple statement about *Bufo* "typhonius" occurring from Panama to southern Brazil needs rigorous revision. It now seems that there is a large number of species involved, most with relatively small distribution areas, partly overlapping, partly allopatric, and that only a few indeed do have extensive distributions. E. g. *B. margaritifera* may occur throughout the Amazon basin, though I still say this with reservation, as differences between local populations from areas separated by large distances sometimes are rather big and may indicate that we are dealing not with local variation but with different taxa. Here again microcomplement fixation could provide much needed additional information. In a number of cases blood samples to provide the information are now available, but tests still have to be run.

Several other species are known to occur in more restricted areas, like the still unnamed species from the lower Amazon and French Guiana in which both males and females are relatively smooth and have no cranial ridges. Another small species with a rather pointed snout, granular skin and no cranial ridges occurs in Guiana, roughly north of the divide between the Amazon and rivers flowing north. *Bufo proboscideus*, with a well developed pointed snout, seems to occur in the middle and western reaches of the Amazon river. *B. roqueanus* occurs along the eastern foot of the Andes in lowland localities in southern Ecuador and adjacent northern Peru. A very large and flat species, with well developed cranial crests and protruding vertebrae occurs in a small part of the range of *B. roqueanus* and may even be microsympatrically with it.

At least one small species occurs west of the Andes in Ecuador and Colombia, and this may be identical to similar toads in Panama. Another species occurs in the Atlantic coastal forests of Brazil, one in Bolivia and at least another one over large parts of Amazonian Ecuador, Peru and Colombia.

Specimens known from isolated localities are still studied and might belong to different taxa. The data available so far, do not yet allow zoogeographic conclusions, except that in the Amazonian lowlands of eastern Peru and Ecuador and adjacent western Brazil there seems to be a concentration of species. Further

study of relationships is necessary before a meaningful opinion on this matter can be given.

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