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SOUTH AMERICAN BUFONIDS (AMPHIBIA: ANURA: BUFONIDAE), AN ENIGMA FOR TAXONOMISTS

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PALABRAS CLAVE: <u>Bufo typhonius</u>, <u>Andinophrynes</u>, <u>Osornophryne</u>, America del Sur, Fecundación interna.

ABSTRACT

Current problems in South American bufonids are reported, especially the situation in the so-called "Bufo typhonius group", which turns out to be composed of several sympatric species, as many as seven species occurring in one locality. The name Bufo typhonius is not applicable to the species it is associated with at the moment and could better be suppressed. Some instances of names to be revalidated are mentioned. Additional notes are given on the genera Andinophryne and Osornophryne and a possible instance of internal fertilization in South American anurans is mentioned.

The study of South American bufonids started when LINNAEUS (1758) described two species of toads, most likely originating from Suriname (HOOGMOED, 1973). One of these was Bufo marinus L., the giant toad that originally occurred from the southwestern USA to southern Brazil, but which was recently spread by man throughout the Caribean and large parts of the Pacific area, including Australia and New Guinea (EASTEAL, 1981). Since the early twentieth century it became apparent that what till then had been considered as one species, in reality consisted of several species, especially at the southern edge of the distribution area, where Bufo ictericus Spix and Bufo paracnemis Lutz replace B.marinus, whereas along the eastern foot of the Andes B.poeppigi Tschudi occurs (CEI, 1968, 1972). This at least is what our present knowledge of the group indicates. However, from personal fieldexperience I have retained the impression that much more study of variation in this group is necessary, as in several places, among others in Suriname, giant specimens of up to 25 cm snout-vent length occur in untouched inland areas, whereas "antropogenic" coastal environments, heavily influenced reproducing adults of the "same" species only reach half the size of the inland specimens. For convenience's sake all of these have been considered conspecific, but it will be evident that size differences of this magnitude either signalize the presence of several different taxa (perhaps polyploids) or of some unusual wide variation not known in any other species of frog. As I did not yet investigate further into this matter, I will not pursue it here, and confine myself to just mentioning it.

The other South American species described by Linnaeus was Bufo typhonius, about which most confusion arose, partly because of its rather large variability, partly because of the presence of many superficially similar species. The confusion already started with its description. Linnaeus' description was based either on material by his pupil Rolander or else was based on a short diagnosis provied by Rolander. Which exactly of the two possibilities is not clear (ANDERSSON, 1900). The description states that the species lived in America (which in this context means Suriname [HOOGMOED, 1973]) and at night called horribly loud like a crow. The back is described as having four longitudinal ridges and black spots. The hands have four free fingers, the feet five narrow toes, without rounded nails (= no discs at the tip?), connected by web. The diagnosis reads: R(ana) auricularibus lobis ovatis, meaning a frog having egg-shaped earlobes. In the past this diagnosis has been interpreted as referring to the well developed bony crests over the ear, as present in some South American toads. However, the so-called earlobes in my, and ANDERSSON's (1900) opinion are nothing but inflated external vocal sacs, a feature not occurring in any Bufo. External vocal sacs are known in members of the neotropical genus Leptodactylus, but they do not have fully webbed feet. The combination of external vocal sacs and fully webbed toes strongly points to a species of Rana having been described by Linnaeus.

ANDERSSON (1900) studying Linnaeus' type material, under the name Rana typhonia indeed did find a specimen of Rana tigerina Daudin with extended vocal sacs. Also the description of the skin and the pattern fit this specimen and make it unlikely that a mix-up of specimens occurred after Linnaeus' description. This conclusion is strengthened by the fact that GMELIN (1789) in the 13th edition of the Systema Naturae considered Rana typhonia different from Rana margaritifera based on three figures in SEBA (1734). BONNATERRE (1789) considered Rana typhonia L. different from Rana margaritifera Laurenti and by a remark of SCHNEIDER (1799) that, according to the catalogue of the Museum Houttuinianum, the toad depicted by SEBA (1734) was unknown to Linnaeus and that under Rana typhonia he had (1768) described Rana been describing something else. LAURENTI margaritifera Laurenti, a species which he named Rana Gemmata. This, in my opinion is correct and the name of the "species" sofar known as Bufo typhonius better should be suppressed. If it would not be suppressed it would take precedence over Rana tigerina Daudin, 1802 and cause an undesirable reshuffling of names that might give rise to a lot of misunderstanding, especially as R.tigerina is involved in the trade in froglegs and figures in Appendix II of CITES. Therefore involvement of the International Commission on Zoological Nomenclature would be necessary. Because of the many complications I will not pursue this matter here, but will deal with it more extensively in another paper on this group of toads. Suffice it to say that the correct name for the taxon with large cephalic crests, occurring in the Guianas would be Bufo margaritifera Laurenti, 1768. As this name already has been used for this taxon in the past, it should not pose that much of a problem. In the light of what will follow, it is even preferrable that we get rid of the name "typhonius", as it is heavily compromised, and its suppression would give us a chance to start "anew". However, for the time being I will adhere to the current usage of the name Bufo typhonius for convenience's sake.

According to HOOGMOED (1985a), based (and this should be stressed) only on published literature, <u>B.typhonius</u> as it is presently understood, occurs from Panama in the north, through the Amazonian part of South America to southern Brazil and Bolivia, with disjunct populations in Pacific Ecuador and Chocoan Colombia, and in the Atlantic coastal forest area in Brazil. Generally (HOOGMOED, 1986) it is considered to be a species having a well ossified skull, more or less distint cranial ridges (sometimes culminating in enormous supratympanic flanges), bony knobs on the angles of the jaws, a pointed snout, a row of several large vertebral knobs, scattered warts on back and limbs, pointed tubercles between the warts, parotoids, an oblique row of tubercles from the parotoids to the groinf, well developed webbing between the toes and with the skin of the flanks attaching to the thighs closer to the knee than to the body. The length is stated to be up to 84 mm. Colour and pattern are very variable, often showing a light vertebral stripe and symmetrically arranged black

spots ("dead leaf pattern"), but also uniformly coloured specimens occur. The above description is rather loose and accommodates quite a lot of specimens. The supposedly high variability of the "species" is shown by the impressive synonymies provided by NIEDEN (1923) and COCHRAN (1970). GÜNTHER (1858), PETERS (1873) and BOULENGER (1882) synonymised a number of nominal taxa described from Amazonian South America with Bufo typhonius (which was called B.margaritifer by DUMERIL 7 BIBRON [1841]) and in this were followed by nearly all later authors. The effect of the aforementioned authors' action has been to confuse the systematics of South American tropical lowland (and lower montane) bufonids seriously. Generally all specimens more or less conforming to the above diagnosis considered B.typhonius and variation was explained away by sex-differences, local variation and differences in age. Though all these factors actually do play a role in the taxonomy of this group, they apparently have been interpreted too widely, causing the inclusion of a number of different taxa. Only few species were recognised as separate from, but nevertheless related to, B.typhonius (e.g. B.ceratophrys Boulenger, B.dapsilis Myers Carvalho and B.nasicus Werner). LEAVIT (1933) considered chanchanensis Fowler , and alatus Thominot both described as species within Bufo, subespecies of B.typhonius. Recent study of the typeseries of B.chanchanensis, augmented with recently collected material, showed that this name is a synonym of B.caeruleostitus Günther. THOMINOT (1884) described Bufo alatus from Obispo, Panama. Examination of the holotype showed this to be a specimen without large cephalic crests, just having low ridges and no knob on the corner of the mouth. This conforms exactly to recent specimens of so-called B. "typhonius" from Panama, which probably should be known as B.alatus Thominot. The real status of this taxon is not yet clear, but it is also possible that it is identical to B.acutirostris Spix, now known to occur in W. Brazil, S. Venezuela and Colombia (HOOGMOED, 1986) This should be confirmed by further studies which are now under way.

MELIN (1914) described <u>B.Tvphonius roqueanus</u> from a locatity in N. Peru. This taxon has large, smooth-edged supratympanic flanges, extremely angular corners of the jaws, which end in a bony knob, relatively large protruding vertebral spines on the back and a relatively smooth skin. I consider this a well defined taxon meriting specific rank.

Other taxa described were sunk into synonymy nearly as soon as they were described. Some of these were excellently described by the Spanish herpetologist JIMENEZ DE LA ESPADA (1875), a member of the "Comisión Científica del Pacífico", which was established to explore South America and actually was in the field between 1862 and 1866. During this period the members of the "Comisión" traversed a large part of South America (and California), visiting Brazil, Uruguay, Argentina, Chile, Peru, Ecuador, Colombia and Panama. At the end of the expedition Jimenez de la Espada and three of his colleagues descended the Amazon along the greater part of its



length, starting in Ecuador and terminating the voyage in Belém (MILLER, 1983). During this expedition numerous specimens were collected and sent to Spain. Many of these are still extant in good condition in the Museo de Ciencias Naturales in Madrid, where I could study the toads described by Jimenez de la Espada and thus confirm their identity. In his book JIMENEZ DE LA ESPADA (1875) extensively described three species of toads which he referred to the genus Oxyrhynchus, a name coined by SPIX (182/ nominal taxa with pointed nose and rough instead of granular skin nasutus. semilineatus. granulosus, acutirostris proboscideus). Under O.typhonius, JIMENEZ DE LA ESPADA (1875) synonymised Spix's Bufo naricus and acutirostris. His material turned out to contain several species, but I will not pursue this matter further here. Under O.proboscideus, JIMENEZ DE LA ESPADA (1875) described 12 specimens from Archidona de Ouijos in Ecuador and thought these were identical with the species described under that name by SPIX (1824). However, Spix's type, a male in breeding condition only has a snout-vent length of 47 mm. and lacks bony crests on the head (HOOGMOED GRUBER, 1983), whereas Jimenez's material reached about 90 mm and had well developed bony crests encircling the anterior and dorsal part of the eye-socket and continuing as a distinct but relatively low supratympanic crest till the parotoids. More material of this evidently unnamed species, so aptly described by Jimenez de la Espada, was found in museum collections and provided insight in variation and distribution. So far it is only known from a limited area in eastern Ecuador and adjacent Peru (material reportedly from NW Ecuador apparently has been mislabelled).

The third species referred to Oxyrhynchus by JIMENEZ DE LA ESPADA (1875) according to him was new and he named it after its collector, the botanist Isern, who was a fellow member of the "Comisión", O.iserni. The single female was collected in the Chanchamayo area, Peru. The name was soon relagated to synonymy by BOULENGER (1882), and was reinstated as a species name only by SAVAGE (1978), without comment. Study of additional material from Chanchamayo, Perene and Cahuapanas in central Peru along the Amazonian slopes of the Andes, showed that Jimenez and Savage were right: B.iserni is a very distinctive species, females reaching 74 mm, males 67 mm, with a blunt snout, skin with flat tubercles, angles of the mouth rounded, an oblique lateral row of tubercles, no protruding vertebrae, no tympanum nor inner ear, very distinct triangular parotoids, skin of head co-ossified with skull; parietal area in females forming a shallow cup, delimited by the parotoid, the parietal ridge and the supratympanic ridge; in males the supratympanic ridge is thickened, as wide as the parotoid; males lack vocal slits and have very strongly developed arms with nuptial asperities on fingers 1-3. Characters are such that the species can not be confused with any other. Fieldwork in Peru in 1983 with the object to collect this species was unsuccesful. Though the habitat of the species is mot known, we may assume it inhabits forest. Forests in the

Chanchamayo-Perene area are disappearing fast and only can be found nowadays on very steep slopes as small remnants. None of the forestremains searched yielded specimens of this species and neither did cultivated land. Taking into account the apparently localised occurrence of this taxon, we have all reasons to be concerned about its future.

The most interesting area from the point of view of studying <u>Bu(c)</u> "typhonius" is eastern Ecuador and adjacent Peru, where at least seven species occur sympatrically (HOOGMOED, 1986), and probably ever microsympatrically.

Studying these toads in the museum and in the field it became evident that several species that are morphologically very similar, in the field can be distinguished rather easily on the basis of characters like mating call, colour of iris, habitat and behaviour, especially in connection with reproduction, but in the museum they can hardly be distinguished, except sometimes on the basis of size of adult specimens. In order to obtain more tangible evidence for species recognition, blood- and muscle samples were taken in the field from fresh material and send to Dr. Linda Maxson (Urbana) for further analysis and for determining immunological distances between several populations, thus obtaining a measure for the relationship between them. The work is still in aninitial stage and samples are fewer than we would wish, but the data obtained sofar are highly congruent with the outcome of the morphological study and indicate that several taxa are widely separated immunologically, even to such a degree that the whole so-called Bufo "typhonius" assemblage appears to be a highly artificial one, not only containing related species, but rather an amalgam of superficially similar species on the one hand and closely related species on the other. Sofar chromosomes have not been studied, but it might show that polyploidy also plays a role in this complex group.

Dealing with species of the <u>Bufo</u> "<u>typhonius</u>" group, I kept finding all sorts of different taxa hiding under this name in museum collections. Mostly they were other species of <u>Bufo</u>, but also representatives of other bufonid genera. Therefore it seems useful to give a short overview of the other South American bufonid genera, the more so while recently the entire family at last has been receiving some long overdue attention. This partly is caused by intensified studies of museum collections (CANNATELLA, 1986a, 1986b) and partly by increased activity in the field of herpetologists, especially in Ecuador and in the Cerro Neblina area on the border of Brazil and Venezuela (unpublished data McDiarmid, Washington). In order to provide a background for my further remarks I may venture to provide a short listing of the other South American (derived) bufonid genera. Most of these occur on the Amazonian side of the Andes, The exceptions being <u>Andinophrvne</u> and part of <u>Atelopus</u>.

<u>Dendrophryniscus</u>: in the Atlantic forest of Brazil, in Amazonian Ecuador, Peru, Brazil and the Guyanas.

Frostius was recently erected (CANNATELLA, 1986a) to accommodate a



species formerly considered to belong to <u>Atelopus</u> and occurring isolat from other <u>Atelopus</u> in Pernambuco, Brazil.

Melanophryniscus: in northern Argentina, Uruguay, Paraguay a southern Brazil.

<u>Rhamphophryne</u>: along the east foot of the Andes in Panama, Colombi Ecuador and Peru (recently found there by McDiarmid), and one isolat species in Bahia, Brazil.

The following three genera do not occur in the lowlands, but a associated with mountainranges:

Oreophrynella is restricted to sandstone mountains in southeaste Venezuela and Guyana.

Osornophryne occurs in rather high elevations on the Amazonian slop of the Andes in southern Colombia and in central to northern Ecuador.

Andinophryne is known only from the Pacific slopes of the Andes southern Colombia and Ecuador, from moderate elevations.

Atelopus is known from both sides of the Andes, from the cent: Andean valleys and paramos and from the Amazonian lowlands.

To conclude I would like to make some remarks on a few of the genmentioned. Andinophryne was recently described (HOOGMOED, 1985b) on basis of one described and two undescribed species. Since its descript more material, that was only recently collected, has become available. species of Andinophryne are united by the presence of an omosternum, anteriorly firmisternal and posteriorly arciferal pectoral girdle, a w developed ear, partly webbed hands, the absence of the musculus adduc longus, and the presence of elongate parotoids. The species of this ge only are known from moderate elevations on the Pacific slopes of Andes, from southern Colombia to southern Ecuador.

The genus Osornophryne at the moment is only known from h elevations (2700-3700) in the Andes of northern Ecuador and south Colombia (CANNATELLA, 1986b). The localities are on the Amazonian side divide. So far only three species of this genus are knc O.bufoniformis Peracca, O.percrassa Ruiz-Carranza Hernandez-Camacho, O.talipes Cannatella which was only described in August 1986. Osornoph: is among others characterized by its completely firmisternal pects girdle, its urostyl with wide lateral flanges which is fused to sacrum, its widely expanded sacral diapophyses, significant fusions in vertebral column, and extensively webbed fleshy hands and feet with I or less extensive phalangeal reductions. During recent studies Ecuadorian material I found two additional species of this genus 1 further south in Ecuador and partly at least from slightly le elevations (2100 m.). The first of these two species is represented by females (35 mm) from the Sierra de Guacamayos, an eastern spur of Andes, and it can easly be recognised from other species by the shape its fact and hands with the two external toes, respectively fingers

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Melanophryniscus: in northern Argentina, Uruguay, Paraguay and southern Brazil.

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To conclude I would like to make some remarks on a few of the genera mentioned. Andinophryne was recently described (HOOGMOED, 1985b) on the basis of one described and two undescribed species. Since its description more material, that was only recently collected, has become available. All species of Andinophryne are united by the presence of an omosternum, an anteriorly firmisternal and posteriorly arciferal pectoral girdle, a well developed ear, partly webbed hands, the absence of the musculus adductor longus, and the presence of elongate parotoids. The species of this genus only are known from moderate elevations on the Pacific slopes of the Andes, from southern Colombia to southern Ecuador.

The genus Osornophryne at the moment is only known from high elevations (2700-3700) in the Andes of northern Ecuador and southern Colombia (CANNATELLA, 1986b). The localities are on the Amazonian side of divide. So far only three species of this genus are known: O.bufoniformis Peracca, O.percrassa Ruiz-Carranza Hernandez-Camacho, and O.talipes Cannatella which was only described in August 1986. Osornophryne is among others characterized by its completely firmisternal pectoral girdle, its urostyl with wide lateral flanges which is fused to the sacrum, its widely expanded sacral diapophyses, significant fusions in the vertebral column, and extensively webbed fleshy hands and feet with more or less extensive phalangeal reductions. During recent studies Ecuadorian material I found two additional species of this genus from further south in Ecuador and partly at least from slightly lower elevations (2100 m.). The first of these two species is represented by two females (35 mm) from the Sierra de Guacamayos, an eastern spur of the Andes, and it can easly be recognised from other species by the shape of its feet and hands with the two external toes, respectively fingers, of

about the same length and much longer than the others.

The second species only is represented by an adult male (19 mm) collected on the southeastern slopes of Volcan Antisana. Its fingers and toes are extremely reduced, essentially only leaving a distinct third finger and fourth toe, with other fingers and toes visible as small buts, barely jutting out from the platelike palm, respectively sole. The single male apparently is adult and has well developed nuptial asperities on the prepollex, pollex, second finger and on the tip of the third finger. Its most interesting character, however, is the shape of its cloacal opening. In related species the cloaca opens at the upper level of the thighs, in the present species it is situated at the end of a tube which runs down the back of the thighs, ventrally even slightly curving anteriorly, and opening ventrally. This suggests some peculiarity in its way of reproduction. Related species are known to have a lumbar amplexus (EUIZ-CARRANZA HERNANDEZ-CAMACHO, 1976), in which the relatively small male is positioned rather posteriorly and vertically on the posterior part of the female. It could be supposed that we are here dealing with the first evidence of internal fertilization in an anuran in South America. The fact that eggs in Osornophryne are few, large and unpigmented HERNANDEZ-CAMACHO, 1976) seems to point to direct development, either in a terrestrial environment or even inside the female. This supposition seems to be strengthened by the fact that O.percrassa can not swim and eventually will drown in water (RUIZ-CARRANZA EMENANDEZ-CAMACHO, 1976). RUIZ-CARRANZA HERNANDEZ-CAMACHO (1976) already reached the conclusion that Osornophryne could not deposit its eggs in streams or ponds because of its inability to swim, and neither could it deposit them in epiphytic bromeliads as it can not climb either. Thus, the only places left to deposit the eggs in their opinion would be depressions which would later fill with water and thus provide a habitat for larvae, or protected wet sites that would not be subject to flooding and thus permit direct development of the eggs. In my opinion RUIS-CARRANZA EXPLANDEZ CAMACHO (1976) with the latter suggestion were hinting in the right direction and further studies might show that Osornophryne in comparable to the African bufonid genus reproductive habits is Nectophrynoides, which inhabits mountainous areas and isolated mountains in East and West Africa respectively, and which shows all stages from ewiposition with aquatic or terrestrial tadpoles, via direct development of the eggs and ovoviviparity to true viviparity. As far as known all species of Nectophrynoides practise internal fertilization by cloacal DUELLMAN TRUEB, 1985). Although apposition (GRANDISON, 1978; MIIZ-CARRANZA HERNANDEZ-CAMACHO (1976) describe and depict the amplexus in both species of Osornophrvne known to them, they did not mention anything about fertilization of eggs or of sperm transfer. However, considering the attitudes adopted during amplexus, it seems possible that sperm is transferred directly by cloacal apposition in O.bufoniformis and

Opercrassa. The structure of the cloacal tube in the new species of Opercophryne from Antisana in that case could be interpreted as an improvement in the process of sperm transfer, by realising a better fitting of the two cloacas. The direct evidence of internal fertilization still has to be provided, either by direct observation in the field or in the laboratory, or by the dissection of pregnant females having either sperm in the oviducts or eggs showing a certain degree of development. I do not doubt this evidence will come forth, the shape of cloacal tube (and information obtained from McDiarmid regarding a related species from Cerro Neblina) is too suggestive. The occurrence of interna fertilization opens the possibility that ovoviviparity or even true viviparity may occur in Osornophryne, and either of these reproductive modes would be a novelty for South American anurans. Therefore Osornophryne merits special attention.

Unfortunately, the single available male of the new species of Osornophryne only allows us to make a few speculations, and much more material, collected throughout the year would be necessary, in order to make firmer statements and start meaningful comparisons of the reproductive modes of South American and African derived bufonids, and to establish whether these reproductive modes evolved independently or whether they reflect common ancestry.

For advanced frogs, and the bufonids are considered to be advanced, a lumbar amplexus is rather unusual, and Osornophryne (and Nectophrynoides) are the only bufonids exhibiting this type of amplexus. RUIZ-CARRANZA HERNANDEZ-CAMACHO (1976) consider this to be a primitive feature of Osornophrvne. However, it may also be considered as an apomorphic character dictated by the difference in size between males and females, and as an adaptation to internal fertilization. In that case, the position of the genus in the group of derived South American bufonids might need to be reconsidered. The recent analysis be CANNATELLA (1986a) of the phylogenetic relationships of neotropical bufonid genera was primarily based only on morphological characters and did not take into account biological data on larvae, development and amplexus, though some of them were mentioned subsequently. Now that more data on these biological characters and on serology are becoming available (e.g. also for Oreophrynella, McDiarmid Gorzula, pers. com.) it would be interesting to see what influence they would have on the phylogeny established on morphological data only.

I hope these notes have served to indicate the possibilities for further study in South American bufonids that are still open and, in order to obtain a better insight in their relationships and evolution, should be explored further.

RESUMEN

Bufonidos Sudamericanos (Amphibia: Anura: Bufonidae), un enigma para los taxónomos.

Se discuten problemas actuales en los Bufonidae de América del Sur, principalmente la situación del llamado "grupo <u>Bufo typhonius</u>", compuesto de algunas especies simpátridas, con al menos siete especies citadas en una misma localidad. El nombre de <u>Bufo typhonius</u> no es aplicable a la especie con la que actualmente se encuentra asociado y seria conveniente suprimir este taxón. Se mencionan algunos casos de taxones que deberían ser revalidados. Se presentan notas adicionales sobre los géneros <u>Andinophryne</u> y <u>Osornophryne</u>; y se menciona un posible caso de fecundación interna en anuros de América del Sur.

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Addenda et corrigenda.

Unfortunately the author did not see proofs before the article was published and a number of rather annoying mistakes is present. Corrected words or parts missing are in bold face. p. 168 line 17 from below: based either on material collected by his...

p. 168 line 16 from below: provied = provided

p. 169 line 13 from above, add:.... margaritifera based on three figures in SEBA (1743). BONNATERRE (1789) considered Rana typhonia L. different from Rana margaritifera Laurenti, a species.....

p. 169 line 4 from below: groinf = groin

p. 170 line 20 from above: subespecies = subspecies

" : B.caeruleostitus = B.caeruleostictus 22

15 below: ara = are

" : B.Typhonius roqueanus = B. typhonius 14

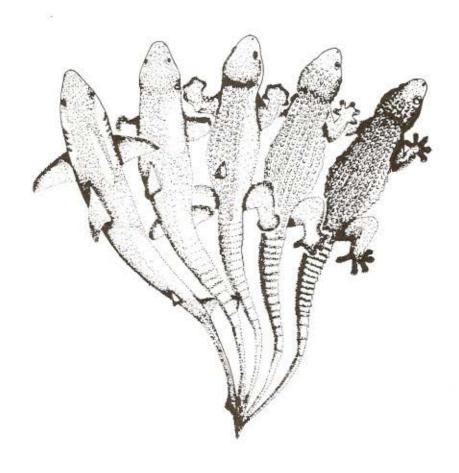
roqueanus

- p. 171. The figure is of a: Female B. margaritifera with well developed bony crests, from the neighbourhood of Moengo Tapoe in eastern Suriname. Specimen in the collection of the Rijksmuseum van Natuurlijke Historie (RMNH) in Leiden.
- p. 173 line 20 from above: aninitial = an initial
- p. 174. The figure is of a: Male B. margaritifera from Zanderij in central coastal Suriname. Specimen in the collection of the RMNH.
- p. 176 line 15 from below: RUIS-CARRANZA = RUIZ-CARRANZA
- p. 177 line 8 " above: the shape of the cloacal tube p. 179 line 22 " below: Bufo "thyphonius" = Bufo "typhonius"

On pages 170, 172,173, 176 and 177 duo's of authors are mentioned that should have been separated by a &.

NOVEMBRE 1989

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TREBALLS D'ICTIOLOGIA I HERPETOLOGIA

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