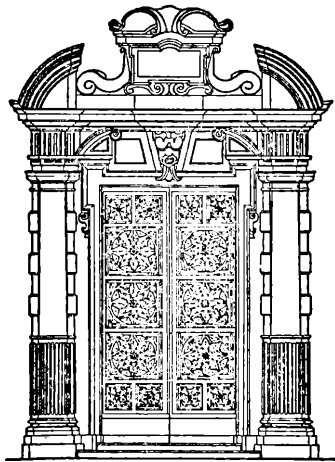


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On a Paraguayan sample of a long time  
confused species:  
*Physalaemus fuscomaculatus* (Steindachner, 1864)  
(Anura, Leptodactylidae)

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ESTRATTO

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ABSTRACT

The poorly known taxon *Physalaemus fuscomaculatus* (Steindachner, 1864) is now defined and illustrated on the basis of a still unidentified sample of Paraguayan specimens from the Zoological Museum of Turin, Italy, collected in 1893 by A. Borelli close to Rio Apa, a tributary of the Paraguay River. The comparison of such a sample with Steindachner's holotype was carried out and a suitable iconographic documentation is presented. The identity of Steindachner's holotype and Borelli's sample was unquestionably supported, and a new suitable description of the species, on the basis of the original description, is now available. This paper contributes to clarify more than a century of taxonomic confusion, having been long time neglected *Physalaemus biligonigerus* (Cope, 1860) owing to a misled diagnosis of *Physalaemus fuscomaculatus* (= *Paludicola fuscomaculata*) since Boulenger's time.

INTRODUCTION

*Pleurodema bibroni* was described by Tschudi (1838) from Montevideo, Uruguay. Cope (1860) described *Liuperus biligonigerus* from Buenos Aires, Argentina; then Steindachner (1863) described *Eupemphix nattereri* from Cuyabá, Brasil, and also (1864) the related species *Eupemphix fuscomaculatus* from Caissará, both collected by Natterer during his travels in tropical South America. The locality "Caissará" appears in the map drawn by the Wien Museum to illustrate Brazilian itineraries of J. E. Pohl and J. Natterer (1817-1831). It lies not far away from the Paraguay River, at about 17° South lat., in the State of Mato Grosso, Brasil, having been published as "Caiçará" by Steindachner, a spelling equally unreported in the recent Brazilian cartography.

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Jimenez de la Espada, in his work "Vertebrados del viaje al Pacifico. Batracios" (1865), described again *Pleurodema bibroni* and a new problematic *Pleurodema granulosum*, both from the environs of Montevideo. Furtherly with Boulenger (1882), who unified under the wide genus *Paludicola* a number of leptodactylid species, a long period of taxonomic disorder began. Both *Paludicola fuscomaculata* and *Paludicola biligonigera* were reported in his Catalogue, but under the first name the true *Eupemphix fuscomaculatus* Steindachner (to which *E. nattereri* was merely associated, although not included in the synonymic list), as well as evident specimens of *L. biligonigerus* Cope, were mixed. Samples reported at p. 233 of the Catalogue, e.g., such as Oran in Salta, Buenos Aires, Rio de Cordoba in Argentine Republic (sic), all belong to localities of the distribution area of *biligonigerus*, not of *fuscomaculatus*.

In the Parker's revision (1927), *Physalaemus fuscomaculatus* (Steindachner) and *Physalaemus biligonigerus* (Cope) were recognized, as well as *Pleurodema bibroni* Tschudi, named *Pleurodema darwini* Bell, 1843 during several decades, a taxon presently considered as a mere synonymous of *bibroni*. However, until the Milstead's critical note (1963), the bad use of the specific name *fuscomaculatus*, sensu Boulenger, was a very common one for the several populations of *biligonigerus* extending in southern South America, from Southern Brasil, Uruguay and Paraguayan Chaco to Central Argentina. Milstead pointed out the absence of vomerine teeth in the type of *Physalaemus biligonigerus* (Cope), suggesting to apply such a older name to the currently named *fuscomaculatus* populations from the above mentioned area, in spite of the generalized use of this latter taxon. However, also the Milstead's approach didn't succeed in a satisfactory solution of the still unclear systematic status of these southernmost *Physalaemus* populations. Two probable but undefined taxonomic entities were in fact postulated for the so wide "*biligonigerus*" complex: a small southern form to which the name *biligonigerus* would really apply, and a larger northern form to which would better apply the usual name "*fuscomaculatus*". It means in some way a return to the criticized Boulenger's ambiguous arrangement. Let us remember again that in the Steindachner's description of the type of *fuscomaculatus* the presence of maxillary and vomerine teeth was clearly pointed out. In accordance with the Milstead's settlement such a character state can primarily to set apart *fuscomaculatus* from *biligonigerus*.

In the same description of Jimenez de la Espada, remarkable affinities between *Pleurodema bibroni* and *Pleurodema granulosum* were supported and the possibility that this latter could be a variation of *bibroni* was suggested. The lack of maxillary and vomerine teeth and the tympanum concealed of *granulosum* contrast with the presence both of maxillary and vomerine teeth and a recognizable tympanum in *Eupemphix fuscomaculatus* Steindachner, 1864. Also the description of the pectoral girdle of *granulosum* by Jimenez de la Espada is referable to the pectoral girdle of *bibroni*. In spite of its very poor

state of conservation the type of *Pleurodema granulosum* in the Museo Nacional de Historia Natural de Madrid appears quite similar to a specimen of *Pleurodema bibroni*, and a small conical tubercle on the inner side of tarsus is indistinguishable.

It is then reasonable to disagree with a synonymic position of *Pleurodema granulosum* in the taxon *Paludicola fuscomaculata*, as in the Boulenger's Catalogue. This former erroneous identity was likely the origin of the inclusion of *Physalaemus fuscomaculatus* between the batrachians reported by Savage in the "Status of taxa proposed by Marcos Jimenez de la Espada", part of his Introduction to the "Vertebrados del Viaje al Pacifico. Batracios" (1978: new Edition). In accordance with the most careful and modern research (Gudynas: pers. comm.) *Physalaemus fuscomaculatus* d'nt exist in the Uruguayan territory.

As put in evidence through this summarized Introduction, *Physalaemus fuscomaculatus* is an ancient species still unfamiliar to the majority of the herpetological collections, being imprecise its morphological definition and more and more very poor its ecological knowledge. Also its distribution and biogeographical relationships with other related forms is uncertain, either in its Brazilian range or neighbouring countries (Cardoso: pers. comm.). That being so, the motive of the present paper was our finding of a remarkable sample of specimens at first sight referable to the Steindachner's form, between the still unidentified collections of the ancient Museo Zoologico, Università di Torino, Italy (MZUT). Such a sample, collected almost a century ago by A. Borelli, from the same Museum, will be here considered in the following Morphological observations and Discussion.

## MORPHOLOGICAL OBSERVATIONS

Dr. A. Borelli, naturalist of the Zoological Museum of the University of Turin, Italy, carried out field research and biological collections in 1893-94 through Paraguayan Chacoan territories, till Corumbá, Mato Grosso, Brasil, northwards. The Borelli's interest was primarily focussed on Planarians and Arthropods, such as *Dermattera* and scorpions, but important herpetological collections were also assembled, later mainly studied and classified by Peracca in Turin. During his field work in lagoons and swamps alongside Rio Apa, a tributary of the Paraguay river, a sample of seven specimens of a still undetermined leptodactylid frog was caught, labeled as An. 447 in the collection of the Zoological Museum of Turin (MZUT). By the reasons exposed in our previous Introduction, these specimens appeared worth observing and comparing, given their general features reminiscent of the fundamental characters of *Physalaemus fuscomaculatus* (Steindachner, 1864), paying attention to the lack

of topographical and ecological barriers between Rio Apa and the “Caissará” region, terra typica of the Steindachner’s species (cfr. map, Fig. 1). Measurements of these specimens, all in very good conditions, are given in the Table I. We estimate a suitable tool to reconsider here the original description of *Eupemphix fuscomaculatus*, comparing step by step its morphological characters with those of the Rio Apa specimens. Complementary or critical remarks shall be as well given. So, the morphological analysis of the Steindachner’s type follows.

***Eupemphix fuscomaculatus*, Tafel VIII, Fig. 3, 3a-3c**  
(cfr. our Fig. 2 and 3: Plate I and II)

....«Only a female specimen of this beautiful, slim species from Caiçará, Brasil, 26 mm snout/vent, collected by J. Natterer, belongs to the Imperial Museum. The head is triangular, short, with flattened upper and frontal regions. Mouth opening overhanged in front by a short but high snout, blunt nostrils opening near its tip. Canthus rostralis smooth, snout profile laterally blunt, without a defined corner. Eyeball equal to the snout length, clearly protruding outside and above. Tympanum hidden under tegument, somewhat behind and below the eye, smaller than eye diameter».

Pointed out in this begin of the Steindachner’s description, all these characters are present both in the holotype and specimens of the Rio Apa sample, with a remarkable similarity.

....«Mouth opening between jaw commissures slightly wider than long; tongue enlarged, narrow and thick, its volume only 1/3 mouth cavity. Maxillary teeth easily perceptible; small and scarce vomerine teeth recognizable as faint protuberances under 15 X magnification. Lumbar glands very flattened outside, equal to eye diameter. Limbs short: adpressed hindleg reaches beyond tip of snout with all fourth toe length, foreleg barely reaches the vent. Femur and tibia thick and equal. A small pointed tubercle behind the middle of tarsi, lacking in *Eupemphix nattereri*. Sharp fingers and toes, metatarsal tubercles very developed, half-moon shaped, with sharpened external layer, yellowish and waxen. Subarticular tubercles small in diameter, very slightly prominent. Dorsal and ventral skin thin, with scattered glandular ridges on the back. Ventrally smooth, only finely granular on lower surface of thighs, close to cloacal opening».

Also these morphological characters, from the above reported Steindachner’s description, are evident both in the holotype and the Rio Apa sample. A small pointed tubercle behind the middle of tarsus is no longer easily recognizable in most of the Rio Apa individuals. However, in contrast with the Steindachner’s statement, a small tarsal tubercle is likewise visible in totypic specimens of *Eupemphix nattereri* from Cuyabá, Mato Grosso. An oval post-commissural or ante-brachial gland, 2.5 mm long, unreported by Steindachner, is evident in all the adult Rio Apa specimens, being slightly distin-



guishable in young individuals (26-30 mm) and in the holotype. Vomerine teeth are present both in the holotype and the Rio Apa specimens, contrarily to their presumed absence - such as in *Physalaemus biligonigerus* and *P. nattereri* - still reported in recent accounts (Ceï, 1987). Dentigerous processes of the vomers are a rather unusual character within the *Physalaemus* species groups. According to Cannatella and Duellman (1984) such a condition, together other three unique character-states, may support a monophyletic position of the *pustolosus* group.

Table 1 - Morphometric characters of *Physalaemus fuscomaculatus* from rio Apa (in mm)

	MZUT An. 447 -1	447 -2	447 -3	447 -4	447 -5	447 -6	447 -7	NHM. Wien 4316 Holotype*
Snout/vent length	37.4	37.5	41.4	29.5	31.0	27.5	25.2	27.35
Head length	11.3	11.2	12.0	8.0	7.1	6.4	6.4	7.55
Head width	13.5	14.5	16.5	10.8	11.2	8.8	9.2	9.90
Foreleg length	20.0	19.1	22.1	14.8	15.1	14.2	13.6	17.03
Hindleg length	49.0	45.0	46.0	36.0	38.2	37.0	32.2	38.30
Interocular distance	4.0	3.6	4.0	3.0	3.1	2.9	2.9	1,77
Internarial distance	3.0	2.6	2.5	1.8	2.1	1.5	1.4	1.10
Distance between nostril and anterior corner of eye	4.2	3.5	4.1	2.4	2.4	2.3	2.2	2.20
When femurs are bent at right angle to body the tibio-tarsal articulation:	overlap	overlap	overlap	slightly overlap	slightly overlap	slightly overlap	slightly overlap	in touch with each other
The tarso metatarsal articulation reaches:	eye	eye	tympanum	eye	eye	eye	eye	about tympanum
Sex	male	male	female	young	young	young	young	young
Remarks: no sex dichromatism is present.								
* Measurements taken by Dr. H. Grillitsch.								

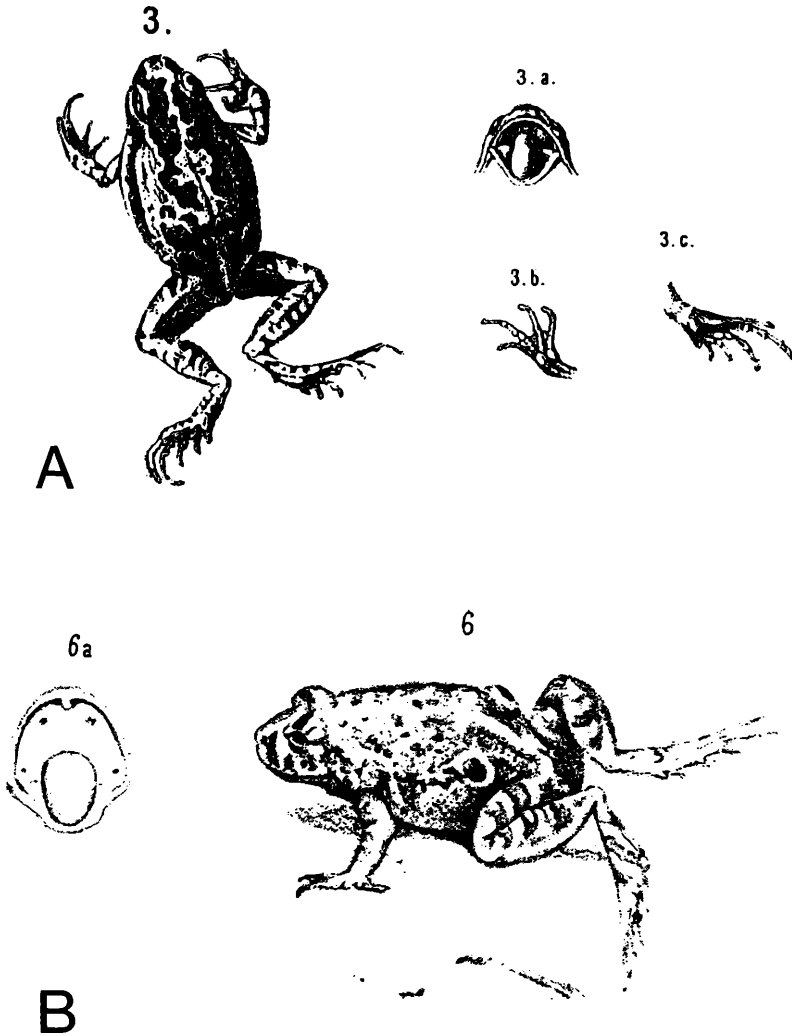


Fig. 2 - A - *Eupemphix fuscomaculatus*: Plate XIII, 3, 3a, 3b, 3c, from the original paper and description of Steindachner, 1864. B - *Pleurodema granulosum*: Plate 1, 6, 6a, from the Jimenez de la Espada's book "Viaje al Pacifico. Batracios anuros", 1865.



## PLATE I.

- 1 - *Physalaemus fuscomaculatus* (Steindachner, 1864). Male. Rio Apa, Paraguay: Col. A. Borelli, 1893. MZUT, An-447(1). (Dorsal view)
- 2 - The same specimen (ventral view).
- 3 - *Physalaemus biligonigerus* (Cope, 1860). Male. San Miguel, Tucumán Prov., Argentina: Col. J.M. Cei, XII, 1968. Chromatic polymorphism: "omega dorsal pattern".
- 4 - *Physalaemus biligonigerus*, male. Same locality, same data. Chromatic polymorphism: "striped dorsal pattern".
- 5 - *Physalaemus biligonigerus*, male. Same locality, same data. Chromatic polymorphism: "plain dorsal pattern".
- 6 - *Physalaemus biligonigerus*, female. Realicó, La Pampa Prov., Argentina. Col. J.M. Cei, 8, I, 1978. Southernmost locality of the species distribution. Chromatic polymorphism: "omega dorsal pattern".

PLATE I.



2



4



6

## PLATE II.

- 1 - *Physalaemus fuscomaculatus* (Steindachner, 1864). Males. Rio Apa, Paraguay: Col. A. Borelli, 1893. MZUT, An-447-1 (right), -2 (left).
- 2 - *Pleurodema bibroni* Tschudi, 1838. Male. Maldonado, Uruguay: Col. J.M. Cei, III, 1966.
- 3 - *Physalaemus nattereri* (Steindachner, 1863). Male. Cuyabá, Mato Grosso, Brasil: Col. W. Bokermann, 20, XII, 1956. (Topotypic specimen, dorsal view).
- 4 - Same specimen, locality and data (ventral view).
- 5 - *Physalaemus* Sp. Male. Cachoeira de Emas, Pirassanunga, São Paulo, Brasil: Col. W. Bokermann, 24, XII, 1961. (Probably a "Milstead's northern form" of the *biligonigerus* complex).
- 6 - *Physalaemus biligonigerus* (Cope, 1860). Male. Villa Marcos Paz, Tucumán Prov., Argentina: Col. J.M. Cei, 22, XII, 1966. (The "Milstead's southern form" of the *biligonigerus* complex).



PLATE II.



1



2



3



4



5



6

...«Dorsal surface is yellowish or whitish, with brownish shades. Two snake-like, reddish-brown, curved bands, often broken or transversally linked, are evident on the back, their run being approximately parallele along its whole extension: they are bordered with whitish and scattered with darker points. The remaining dorsal surface is confusely scattered with dark. Two small bow-shaped frontal spots are observed. Sides of the head yellowish or whitish, with irregular darker bands: some isolated zigzag transversal bands can be pointed out. Many transversal bands on upper surfacc of limbs, very distinct on femur and tibia, as well as on foreleg. Surface of lumbar gland brilliant dark brown, bordered by a distinct white band. On body sides, aboveall from the ocular region to the tarsal region, a reddish-brown band scattered with darker points is recognizable, specially along its upper border. Belly whitish, throat confusely spotted with brown».

Steindachner's description of color patterns of *Eupemphix fuscomaculatus* is in full agreement with the observable features of its old, somewhat faded holotype (Fig. 3), as well with the color patterns of the Rio Apa specimens (Plates I and II): a character-state always contrasting with the polymorphic chromatism of *Physalaemus biligonigerus* (cfr. Ceï, 1980). Thus, any morphological kind of evidence does not oppose the identity of the Rio Apa specimens and the *Physalaemus fuscomaculatus* holotype. Moreover, also metrical measurements of this latter fit too into the range of intraspecific variation of frogs of the Borelli's sample.

## DISCUSSION

The evident taxonomic status of these Paraguayan individuals as a southern population of *Physalaemus fuscomaculatus* (Steindachner, 1864) may contribute to a better knowledge and definition of such as yet discussed form. The several above examined significant characters lead to clear cut morphological differences between this species and the long time misled taxa of the *biligonigerus* group. We must remark that Peracca didn't want express his opinion on the Rio Apa specimens probably observed by him, as indicated by the dissected pectoral girdle shown by some individuals, to which our Fig. 4, A is referred.

Peracca's knowledge of the Chacoan fauna was good and several species of *Paludicola* (sensu Boulenger) have been reported in his papers on Borelli's collections in Paraguay, Mato Grosso and northern Argentina (1895, 1897, 1904). *Paludicola fuscomaculata* cited for Luque (Paraguay) and Resistencia (Chaco Argentino) was *Physalaemus biligonigerus*. Many specimens of *Paludicola signifera* (Girard, 1853) were cited for Villarica, Asución, and eastern Argentine Chaco, but affinities of some of them with *Paludicola biligonigera* were stressed. Perhaps the Boulenger's Catalogue (1882, 3:138) affected the Peracca's unwillingness to identify the unusual frogs An. 447 from Rio Apa, which disagree with the misled diagnosis of *Paludicola fuscomaculata* (sensu



Fig. 3 - Holotype of *Eupemphix fuscomaculatus* Steindachner, 1864, from the Naturhistorisches Museum of Wien (N° 4316): ventral, dorsal and lateral views. (Photo, F. Tiedemann)

Boulenger), as well as with the characters given for *P. biligonigera* by the same Author. A untied label with the notice "Pleurodema" was lying in the sample's container.

In the Frost's survey of World Amphibians (1985) no special comments on taxonomic problems associated with *Physalaemus fuscomaculatus* are concerned. A *biligonigerus* group is recognized, but *Physalaemus biligonigerus* itself is strangely assigned to a *cuvieri* group in the same work (Frost, 1985:251). In accordance with Frost's recent reports four natural groups are so distinguishable for the genus *Physalaemus*: a *pustulosus* group (*pustulosus*, *pustulatus*, *moreirae*, *petersi*, *coloradorum*); a *signifer* group (*signifer*, *olfersi*, *obtectus*, *nanus*); a *biligonigerus* group (*biligonigerus*, *santafecinus*, *nattereri*), 20 species being at last assembled into a broader *cuvieri* group. Besides some affinities to *nattereri*, the inclusion of *fuscomaculatus* into a *biligonigerus* group could be supported by a number of morphological features (pectoral girdle, somatic characters, coloration, etc). However, as postulated by Milstead (1963), the same real status of *biligonigerus* needs a careful research and revision. The Cope's nominate form and its sibling species *santafecinus* Barrio, 1965 belong to the Argentine herpetofauna (Cei, 1980, 1987), extending to the neighbouring countries (Paraguay, Uruguay, Southern Brasil). Formerly confused

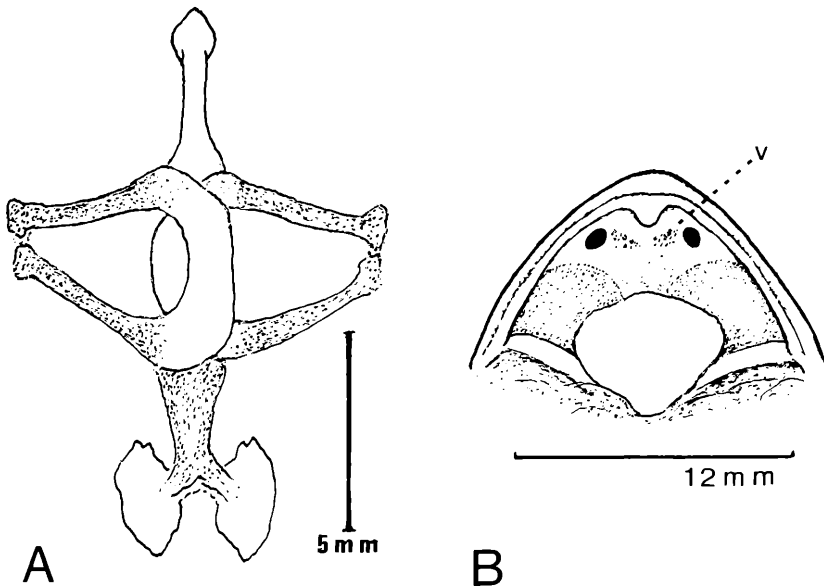


Fig. 4 - A - Pectoral girdle of *Physalaemus fuscomaculatus*: adult specimen of the Rio Apa sample (MZUT, An. 447-2); B - Mouth of the same specimen (palatine view): v, rudimentary patches of vomerine teeth between choanae.

under the misled taxonomic entity *fuscomaculatus* (crf. Cochran, 1955), the northernmost, all Brazilian, populations of *biligonigerus* probably represent different species with allo-sympatric distribution. Their next study and recognition should to be hoped.

## CONCLUSIONS

The sample MZUT, An. 447, collected by Borelli almost a century ago along Rio Apa, eastern Paraguay, enable us to reconsider the long time misled good species *Physalaemus fuscomaculatus* (Steindachner, 1864). Its careful study and comparison with the holotype N° 4316 of the Naturhistorisches Museum of Wien, allow to carry out a suitable redescription of the taxon on the same basis of the old but unquestionable Steindachner's description. A satisfactory iconographic illustration of this leptodactylid frog was now possible, its clear cut morphological differences with the recognized species of the *biligonigerus* group of the genus *Physalaemus* being put in evidence. Thus, after more than a century of taxonomic confusion, a revision of the above mentioned species group is made easier, establishing as a systematic milestone *Physalaemus biligonigerus* (Cope, 1860), whose southernmost distribution area is fairly well known, as well as its specific characters. Since the precursory, although unfortunately incomplete, Milstead's reassessment (1963), morphological uncertainties between *Physalaemus fuscomaculatus* and *P. biligonigerus* are now quite impossible. *Physalaemus biligonigerus* is a widespread frog with a remarkable individual variation. It is a very common opportunistic breeder in the wet northern and central Argentine territories, in the neighbouring Uruguayan and Southern Brazilian flats, and in the Central and Boreal districts of the Chacoan province of Paraguay and North-Western Argentina. *Physalaemus fuscomaculatus* is a relatively uncommon leptodactylid, likely sympatric with *biligonigerus* in several biotopes of its subtropical and tropical range. From Mato Grosso, its terra typica, extends to the lower basin of the Paraguay river, such as in the case of Rio Apa locality, probably reaching the marginal area of northern Argentine provinces southwards. Its biology is practically unknown, and no reports were given on breeding and reproduction, probably similar to those of *Physalaemus nattereri* (crf. Vizotto, 1967), formerly also assigned to the genus *Eupemphix*. By the thorough observations of Vizotto in north-eastern São Paulo state, Brasil, several differences may be observed between mating call, foam-nest, egg-laying and larval development of *P. nattereri* and those of *P. biligonigerus*. In accordance with Milstead's remarks, the northernmost Brazilian populations of *biligonigerus* stand out from the nominate form of Cope by size and other features. No research has been carried out yet on taxonomic status of these problematic frogs. Their to



be hoped recognition could contribute to a more suitable understanding of the *Physalaemus* species groups, apart from adding further information to the yet unsolved problem of the monophyly or paraphyly or the whole genus (Cannatella and Duellman, 1984).

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#### RIASSUNTO

Una antica raccolta di A. Borelli nella regione di Rio Apa, Paraguay, è stata studiata e confrontata con il tipo di *Physalaemus fuscomaculatus* (Steindachner, 1864), depositato nel Naturhistorisches Museum di Vienna. Confermata la sua identità con detta specie, rara e poco conosciuta, ne è stata possibile una nuova descrizione, redatta sulla base del lavoro originale di Steindachner e accompagnata da una soddisfacente documentazione iconografica. Si è dato così un contributo alla chiarificazione di una oscura situazione tassonomica, protratta per oltre un secolo e dovuta alla confusione di tale specie con *Physalaemus biligonigerus* (Cope, 1860), i cui reali limiti morfologici e biogeografici possono ora essere definiti e inquadrati in una generale discussione del genere *Physalaemus* e dei suoi gruppi naturali di specie affini.

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#### LITERATURE CITED

- BOULENGER G.A., 1882. Catalogue of the Batrachia Salientia sive Ecaudata and Batrachia Apoda in the collection of the British Museum. 2nd Ed., London, Brit. Mus.: 503 pp., XXX Pl.
- CANNATELLA D.C. and W.D. DUELLMAN, 1984. Leptodactylid frogs of the *Physalaemus pustulosus* group. *Copeia*, 4: 902-921.
- CEI J.M., 1980. Amphibians of Argentina. *Monit. zool. ital. (N.S.)*, Monogr. 2:609 pp.
- CEI J.M., 1987. Additional notes to "Amphibians of Argentina": an update, 1980-1986. *Monit. zool. ital. (N.S.)* 21: 209-272.

- COCIRAN D.M., 1955. Frogs of the Southeastern Brasil. Bull. US natn. Mus. 206: 1-422.
- COPE E.D., 1860. Description of new species of the Reptilian genera *Hyperolius*, *Liuperus* and *Tropidodipsas*. Proc. Acad. nat. Sci. 12: 517.
- FROST D.R. (Edit.), 1985. Amphibian species of the World. Publ. Allen Press Inc. & The Ass. Syst. Coll. Lawrence, Kansas. 732 pp.
- JIMENEZ de la ESPADA M., 1865. Vertebrados del Viaje al Pacifico. Batracios. Impr. M. Ginesta, Madrid: 208 pp., 6 Pl.
- MILSTEAD W.W., 1963. Notes on Brazilian frogs of the genera *Physalaemus* and *Pseudopaludicola*. Copeia, 3:565-566.
- PARKER H.W., 1927. A revision of the Frogs of the genera *Pseudopaludicola*, *Physalaemus* and *Pleurodema*. Ann. Mag. nat. Hist. S. 9, 20: 450-478.
- PERACCA G., 1895. Viaggio del dott. Alfredo Borelli nella Repubblica Argentina e nel Paraguay. Rettili e Anfibi. Boll. Mus. Zool. Anat. comp. R. Univ. Torino, 10 (195): 32 pp.
- PERACCA G., 1897. Viaggio del dott. Alfredo Borelli nel Chaco boliviano e nella Repubblica Argentina. Rettili e Anfibi. Boll. Mus. Zool. Anat. comp. R. Univ. Torino. 12 (274): 19 pp.
- PERACCA G., 1904. Viaggio del dott. Alfredo Borelli nel Mato Grosso brasiliano e nel Paraguay. Boll. Mus. Zool. Anat. comp. R. Univ. Torino. 19 (465): 41 pp.
- SAVAGE J.M., 1978. Introduction to: "Vertebrados del Viaje al Pacifico. Batracios" of M. Jiménez de la Espada (1865). Reprint. by SSAR: vi-xvi.
- STEINDACHNER F., 1863. Über einige neue Batrachier aus den Sammlungen des Wiener Museums. Sitzungsber. der kais. Akad. der Wissenschafte. Wien. 48: 186-192, Pl. 1.
- STEINDACHNER F., 1864. Batrachologische Mitteilungen. Verh. zool. bot. Ges. Wien. 14: 239-288, Pl. 9-16.
- TSCHUDI J.J., 1838. Classification der Batrachier, mit Berücksichtigung der fossilen Thiere dieser Abteilung der Reptilien. Mem. Soc. Sci. nat. Neuchatel: 99 pp, 1 Pl.
- VIZOTTO L.D., 1967. Desenvolvimento de Anuros da região norte-ocidental do Estado de São Paulo. Tese da Faculdade Filosofia, Ciências e Letras da Univ. São Paulo (Doutorado em Ciências), Dep. Zool: 167 pp.