

On WARSZEWICZ's trail: the identity of *Hyla molitor* O. SCHMIDT, 1857

KARL-HEINZ JUNGFER

Institute of Integrated Sciences, Department of Biology, University of Koblenz-Landau, Universitätsstr. 1, 56070 Koblenz, Germany

e-mail: khjungfer@aol.com

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Abstract. The Polish botanist JÓZEF WARSZEWICZ (1812–1866) travelled extensively in Central and South America between 1844 and 1853 and, apart from plants, also collected frogs subsequently used to describe new species. Several of his locality data proved to be erroneous and especially species purportedly from western Panama were later rediscovered in South America. I revisit parts of his itinerary, the history, type locality, and morphology of *Hyla molitor*, supposedly from western Panama, but never encountered again, and conclude that it is conspecific either with *Dendropsophus labialis* or *D. luddekei*, both Andean species from Colombia that are morphologically indistinguishable. Speculating that the types of *H. molitor* may have originated from the surroundings of Bogotá, where WARSZEWICZ had actually been, I consider it a senior synonym with priority over *D. labialis* and transfer the taxon to *Dendropsophus*.

Key words. Anura, Colombia, *Dendropsophus labialis*, *Dendropsophus molitor* nov. comb., Hylidae, Panama, synonymy, type localities, WARSZEWICZ.

Introduction

WARSZEWICZ and his travels in the Neotropics

JÓZEF WARSZEWICZ (also spelt JOSEF VON WARSZEWITSCH, WARSCHEWITSCH or WARSCEWICZ) Ritter von Rawicz (1812–1866) (Fig. 1) was a renowned botanist and one of the most dazzling orchid collectors of the 19th century, not an herpetologist. Nevertheless his amphibian collections in Central and South America are an important, even though sometimes puzzling, contribution to the herpetology of the Neotropics. Both his education and scientific interests and his collections connected him deeply with numerous European colleagues and institutions. Especially the German botanist HEINRICH GUSTAV REICHENBACH (1824–1889) profited much from his orchid material, because orchids, especially live ones, had usually been sold to British greenhouses before WARSZEWICZ sent his collections.

Polish by birth, he grew up in Vilnius, Lithuania, as the son of a family belonging to the lower nobility. While studying there, he became a gardener at the Vilnius University Botanical Gardens. He became involved in the November Uprising of 1830/31 against Russia and, like many other Poles of that time, had to emigrate (Anonymous in Wikipedia 2012). He was in charge of the public gardens at Insterburg (East Prussia, now Chernyakhovsk, Russia) (Anonymous 1854). After that he became an assistant gardener at the Berlin Botanical Gardens and between 1840 and 1844 made the acquaintance of numerous persons

in the fields of natural sciences, botany and gardening, among them ALEXANDER VON HUMBOLDT (1769–1859) (REGEL 1867, ZIELNICA 2004). In the December of 1844, he set off for Guatemala in order to collect and cultivate plants, financially supported by the Belgian horticulturist LOUIS BENOÎT VAN HOUTTE (1810–1876), but also helped by patrons like VON HUMBOLDT, who managed to obtain a small grant for him from the Prussian King. In Guatemala, he collected plants for Belgian gardens in 1845. The circumstances must have been arduous, for he survived a mast-breaking storm during his voyage and yellow fever killed all his travelling companions but him and a Belgian physician within four months after their arrival in Guatemala. One year later, he worked at his own expense and collected plants as well as seeds that he cultivated and shipped mainly to Germany and England (Anonymous 1854, REGEL 1867). Many of those were new to science, and numerous ones were subsequently described in honour of their collector, e.g., *Canna warszewiczzii*, *Catasetum warszewiczzianum*, *Philodendron warszewiczzii* or *Sobralia warszewiczzii* (BRZEZIŃSKI et al. 1927). OSSENBACH SAUTER (2010) lists 103 plant species and subspecies named after him in his honour. Although he was equipped with very limited financial means and weakened by yellow fever, he travelled to southern Mexico and as far as California, Oregon, and Texas. Later he proceeded on foot from "Chiapa" (Chiapas) (Anonymous 1849) or Guatemala (OSSENBACH 2009) to Panama, accompanied only by an indigenous companion,

always on the brink of starvation and with an extremely low budget, but driven by the quest to explore the marvellous flora. In Europe, he was admired for his findings, but also pitied for the ordeal he went through (HAMILTON 1993). His journey took him to San José, Costa Rica, in February of 1848. From there he crossed the border to New Grenada ("Neu-Granada"), the country that was later renamed Colombia. He collected in the western province of "Veragua", today the westernmost provinces Chiriquí, Bocas del Toro, and Veraguas of the Republic of Panama. He is known to have crossed the continental divide towards the Caribbean coast several times and climbed Chiriquí Volcano (Volcán Barú, 3,475 m a.s.l.), as communicated by a later traveller (WAGNER 1863). Later he travelled to Ecuador (Anonymous 1854). Evidence is provided by a sales list in which WARSZEWCZ (1850) offers an orchid from Guayaquil. During his journey he collected plants, especially orchids and gesneriads, but also seeds, bark samples, seashells, birds, amphibians, and reptiles.

In 1850, he went back to Europe for recovery, but returned to Latin America in early 1851, where he landed at Cartagena, Colombia, and from Chagres, Panama, went to western Panama again. Later that year he arrived in Guayaquil, Ecuador, where he was robbed of all his money and equipment. In 1852, he was in Lima, Peru, and followed the Río Marañón in northeastern Peru. He also visited La Paz, Bolivia, in the same year and is known to have collected in the northeastern part of the country, near the border

to Peru. He also reached Argentina and Chile when he obtained news of the death of his English sponsor, EDWARD SMITH STANLEY, Earl of Derby. He travelled back north to New Grenada where he visited several areas, among others, the surroundings of Buenaventura, Ocaña, Bogotá, and the cordilleras of Antioquia. On his journey down the Río Magdalena on a steamboat, he lost numerous boxes with plants in a shipwreck (Anonymous 1854). Probably due to a recurrence of yellow fever he returned to Europe in October 1853 and subsequently took a post as an inspector (chief gardener) of the Kraków Botanical Gardens that he held until his early death on 31 December 1866 (REGEL 1867, BRZEZIŃSKI et al. 1927, SAVAGE 1970, YEARSLEY 2004, ZIELNICA 2004, Anonymous in Wikipedia 2012, KÖHLER 2014).

Herpetological type material collected by WARSZEWCZ and described by SCHMIDT (1857)

Although famous for his botanical collections, WARSZEWCZ also gathered some herpetological material. Some was given to the Kraków Zoological Museum. A few of the specimens also found their way to other European museums, most of these to the Naturhistorisches Museum Wien (Vienna), but also to the British Museum of Natural History, London, and the Zoologisches Museum Berlin (SAVAGE 1970). His amphibian material at the Kraków Zoological Cabinet was diagnosed briefly in Latin by SCHMIDT (1857) and one year later described in more detail (SCHMIDT 1858). As WARSZEWCZ's foremost interest was plants, he collected amphibians only occasionally, and only those of small or medium size that would not cause him trouble (SCHMIDT 1858). This, or the difficult circumstances of the journey, may be the reason why some of the localities were later found to be recorded incorrectly and have caused considerable problems in assigning types to actual populations. Unfortunately, no itineraries of WARSZEWCZ are known and he did not publish any reports of his expeditions either, except for lists of plants. It is for this reason that some of his travelling routes remain fragmentary and contradictory (ZIELNICA 2004). In fact, even the descriptions of new orchid species (REICHENBACH 1854), to which in part he was supposed to have contributed at least the localities (YEARSLEY 2004), are often no more precise than "Neu-Granada" or "Peru" with respect to their type localities and do not allow for the reconstruction of an exact itinerary.

Sixteen amphibian taxa collected by WARSZEWCZ were described by SCHMIDT (1857) (Supplementary tables 1–3). Most of the specimens were reported to have originated from what is now western Panama (SCHMIDT 1857, 1858). However, despite intensive fieldwork on amphibians in the area from the 1920s on (e.g., DUNN 1924, 1931, SAVAGE 1968, SAVAGE & HEYER 1969, DUELLMAN 1970, MYERS & DUELLMAN 1982, JUNGFER 1988a, b, c, HERTZ et al. 2011), several species have never been found again, although a trans-Isthmian highway has been connecting the Pacific and Caribbean lowlands for the last 33 years and made access to the area much easier. Another species of frog purported-



Figure 1. Photograph of JÓZEF WARSZEWCZ. Courtesy of the Botanical Garden of the Jagiellonian University, Kraków.

ly from the same region, “*Dendrobates*” *maculatus* PETERS, 1873, known from a single specimen from “Chiriquí” (PETERS 1873a), also remains enigmatic. It had been collected by the German geographer and naturalist MORITZ WAGNER (1813–1887), who reported to have followed WARSZEWICZ’s trails with the very same guides the latter had employed from David, a town in the Pacific lowlands, to the Caribbean coast (1863). The frog has remained missing until today (MYERS 1982, LÖTTERS et al. 2007), although at least one of the two trails mentioned by WAGNER (1863), from Boquete to the village of Punta Róbalo on the Caribbean coast, still exists (pers. obs. in 2003). Also taking into account that numerous amphibian populations, if not species, have vanished in that area due to the amphibian fungus *Batrachochytrium dendrobatidis* since the 1990s (LIPS 1999), one might start believing that western Panama must be some kind of Bermuda Triangle for frogs. However, when the status of several of those frogs collected by WARSZEWICZ were assessed by SAVAGE (1968, 1969, 1970, 1972), SAVAGE & HEYER (1969), and DUELLMAN (1970), they found that specimens must have been mislabelled and actually come from localities different from those indicated by SCHMIDT (1857). Several authors since have rediscovered populations of incorrectly labelled species in other parts of the Neotropics (SAVAGE 1972, KLUGE 1979, DUELLMAN & DE LA RIVA 1999, DE LA RIVA 2004, COLOMA et al. 2007) (Supplementary table 3).

Results

The status and type locality of *Hyla molitor* SCHMIDT, 1857

SCHMIDT (1858) mentions three specimens of this taxon, apparently those now housed at the Naturhistorisches Museum Wien (NMW 16494, one specimen) and the Zoological Museum of the Jagiellonian University, Kraków (KM 1010/1341, two specimens). The former (Fig. 2) was designated lectotype of *Hyla molitor* by SAVAGE & HEYER (1969). The type locality “Am Chiriquiflusse unweit Bocca del toro” [along the Chiriquí River not far from Bocca del toro], appears somewhat confusing as there are several “Ríos Chiriquí” on the Pacific (Provincia Chiriquí) and the Caribbean versant (Provincia Bocas del Toro) found on present-day maps. Based on a contemporary map (WAGNER 1863: Table 2), SAVAGE (1970) was able to trace WARSZEWICZ’s route accurately and found out that the Río Chiriquí was what is today called Río Guarumo (also called Cabbage Creek). WAGNER’s map shows the river with the name “Río Chiriquí” and, at its mouth, “Cabbage Cr.” where a settlement of French traders (“Ranchos französisch. Händler”) was located in those days. It also indicates that one of the trails from the Pacific versant ended there. JAY M. SAVAGE (in litt., 12 February 2013) is convinced that WARSZEWICZ returned from there to David. The type locality of *Hyla molitor* therefore could be reworded into “along the Río Guarumo not far from Bocas del Toro”. With “Bocca del Toro” [= Bull’s Mouth], either the entrance to Bahía de(l

Almirante or, more likely, the provincial capital situated on Isla Colón is meant. This is unimportant for the localization of the purported type locality though.

Both SAVAGE & HEYER (1969) and DUELLMAN (1970, 2001) negated the Caribbean lowlands of western Panama as the provenance of *Hyla molitor* and stated that it was unlike any other known hylid frog occurring in lower Central America. In fact, in general appearance *Hyla molitor* rather resembles some stout-bodied frogs from the high Andes with narrow finger discs that are only moderately adapted to climbing, like those of *Pristimantis unistrigatus* or Andean species of the genus *Gastrotheca*. I have had the opportunity to examine the lectotype of *Hyla molitor* and compare it directly with the holotype and fresher material of an Andean hylid that was, until recently, known as *Dendropsophus labialis* (PETERS, 1863) (see Discussion). I conclude that both are conspecific.

Dendropsophus molitor (SCHMIDT, 1857) nov. comb.

- Hyla molitor* SCHMIDT, 1857
- Hyla labialis* PETERS, 1863
- Hyla molitor marmorata* SCHMIDT, 1857
- Hyla molitor* – NIEDEN 1923
- Hyla molitor* – SAVAGE & HEYER 1969
- Hyla molitor* – DUELLMAN 1970
- Hyla molitor molitor* – COCHRAN & GOIN 1970
- Hyla labialis* – DUELLMAN 1977
- Hyla molitor* – DUELLMAN 1977
- Hyla labialis* – RUIZ-CARRANZA, ARDILA-ROBAYO & LYNCH 1996
- Hyla molitor* – DUELLMAN 2001
- Dendropsophus labialis* – FAIVOVICH, HADDAD, GARCIA, FROST, CAMPBELL & WHEELER 2005
- Dendropsophus labialis* – GUARNIZO, ESCALLÓN, CANNATELLA & AMÉZQUITA 2012
- Dendropsophus ludeckeii* GUARNIZO, ESCALLÓN, CANNATELLA & AMÉZQUITA, 2012 [?]

Specimens examined are referred to by the following abbreviations: NMW – Naturhistorisches Museum, Wien; ZMB – Zoologisches Museum, Berlin. In the description, I followed the terminology of DUELLMAN (1970). Webbing formulae follow SAVAGE & HEYER (1967) as modified by MYERS & DUELLMAN (1982).

Justification of synonymy: The lectotype of *Hyla molitor* (NMW 16494) has been described in detail twice already (SAVAGE & HEYER 1969, DUELLMAN 1970, repeated in an expanded edition [DUELLMAN 2001]), so that it seems almost superfluous to do this once again and is done here merely for the sake of completeness. Specimen in good state, a little soft, colours faded, apparently a female (vocal sac absent) of 36.1 mm in snout–vent length (SVL). Snout rounded in dorsal and bluntly rounded in lateral aspect. Canthus rostralis rounded and indistinct. Loreal region barely concave. Nostrils opening anterodorsally. A moderately thick supratympanic fold from the midlevel of the eye, covering the upper part of the tympanic annulus, and arching towards the insertion of the arm. Tympanum vertically elliptical, its horizontal diameter slightly less than

half the diameter of the eye and separated from it by slightly less than one and a half times the tympanum width. Two thick short linear odontophores almost in contact with each other, bearing three and four teeth. Odontophores in between elliptical choanae. Tongue barely notched. A small appendage anterolaterally to the left (an asymmetric enlargement probably caused by regeneration after an injury). Belly, subanal area, and proximal portion of thighs ventrally coarsely granular. Throat and chest finely granular. Other surfaces smooth. A fold of skin on each side from the posterior part of the arm insertion almost meeting midventrally, thus forming an incomplete thoracic fold. An axillary membrane encompassing two thirds of the upper arm. Anal opening just below the upper level of the thighs. Relative finger lengths of adpressed fingers $3 > 4 > 2 > 1$. Finger discs only slightly wider than finger at midlevel of penultimate phalanx. Fingers about one fourth webbed; webbing formula I basal $\text{II}_{2+3}\text{III}_{3-2\frac{1}{2}}\text{IV}$. Subarticular tubercles single, except on Finger IV, where the

ultimate tubercle is bifid. An elliptical inner metacarpal tubercle. Relative toe lengths of adpressed toes $4 > 3 > 5 > 2 > 1$. Toe discs barely wider than toes at midlevel of penultimate phalanx. Toes are about one half webbed. Outer edge of Toe I fringed. Webbing formula $\text{I}_{1\frac{2}{3}-2}\text{II}_{1^+-2\frac{1}{4}}\text{III}_{1\frac{1}{2}-3}\text{IV}_{3-1\frac{1}{2}}\text{V}$. A large elliptical inner metatarsal tubercle, a low flat subplantar tubercle. A tarsal fold is present. Subarticular tubercles single. Dorsal surfaces light tan, ventrally creamy tan. No other markings are left. SCHMIDT (1858) describes (in translation) the frog as follows: Upper surface uniformly greyish blue, more intensive on the back, fading on the extremities and laterally. A finely dotted black streak along the canthus rostralis from the naris to the corner of the eye. Blackish marbling in the area of the corner of the arm, on the flanks and thighs in two of the three specimens.

The holotype of *Hyla labialis* PETERS, 1863 (ZMB 4913) was bought, according to the ZMB catalogue, from "LINDIG" (FRANK TILLACK, in litt.) [ALEXANDER LINDIG, a



Figure 2. *Hyla molitor* Schmidt, 1857, lectotype (NMW 16494) in (a) dorsal, (b) ventral, (c) lateral aspects; (d) details of throat and chest.

German bryologist and collector of various plants and animals, who lived in Bogotá for several years] in the “gebirigen Umgegend von [mountainous surroundings of] Bogotá” (PETERS 1863). It is a male of 32.1 mm in SVL. The specimen is very soft, and most of the coloration is faded. An axillary membrane is present, too (but see the definition of the *Hyla labialis* species group by DUELLMAN 1989). The description given for *Hyla molitor* agrees well, except in the following characters: The tongue is ovoid, but slightly wider anteriorly than posteriorly. The thoracic fold is less complete and has a wider midventral gap than in NMW 16494.

Four females (SVL 42.2–44.4 mm) and four males (SVL 31.7–34.8 mm) from Briceño, Cundinamarca, Colombia, in general agree well with the description of *Hyla molitor*. There is some variation, but NMW 16494 is always within the range except for SVL, which is very variable with altitude among different populations (the higher the altitude, the larger the frogs; LÜDDECKE 1997, 2002). In two females, the loreal region is flat rather than barely concave as in the others. Odontophores are thick and almost in contact or distinctly separated from each other. The supratympanic fold varies from moderately thick, covering the upper tympanic annulus, to indistinct. The skin folds from the arms towards the chest are present in all specimens, but their extent is variable and apparently dependent on the state of preservation. Webbing on the hand varies as follows: I basal $2\frac{1}{2}$ – $2\frac{1}{2}$ ⁺–(3–3) $\frac{1}{2}$ – $3\frac{1}{2}$ – $2\frac{1}{2}$ IV and on the toes I $(1\frac{1}{2}$ – $1\frac{1}{2}$)–(2–2) $\frac{1}{2}$ III $1\frac{1}{2}$ –(2–2) $\frac{1}{4}$ III $(1\frac{1}{4}$ –2)–3 IV $(2\frac{1}{3}$ –)($1\frac{1}{2}$) V. Patterns are variable, ranging from plain to marbled on all dorsal faces. Ventrally, most specimens are plain. There is some faint reticulation in the posterior part of the belly and on the thighs in one specimen.

Discussion

Until recently, *D. labialis* was known from the eastern Andes of Colombia, Departamentos Boyacá, Cundinamarca and Norte de Santander, at between 1,600 and 4,100 m a.s.l. (RUIZ-CARRANZA et al. 1996, GUARNIZO et al. 2009). Based



Figure 3. *Dendropsophus molitor* from near Bogotá International Airport El Dorado, 2,550 m, Colombia.

primarily on molecular data, GUARNIZO et al. (2012) concluded that actually two species were involved that could be distinguished genetically and bioacoustically, but not morphologically. They attributed the name *D. labialis* to the species with the southern distribution (in the Departamento Cundinamarca) and named a northern one, *D. luddeckei*, from northeast of a line between the towns of Chiquinquirá, Boyacá ($5^{\circ}10'16.21''$ N, $73^{\circ}40'05.52''$ W [sic; in error; GoogleEarth indicates $5^{\circ}36'57''$ N, $73^{\circ}48'56.23''$ W]) and Chocontá, Cundinamarca ($5^{\circ}10'16.21''$ N, $73^{\circ}40'05.52''$ W). Without morphological differences, the lectotype of *Hyla molitor* is not assignable to one of the two species, because the locality data have to be considered erroneous and thus unknown. WARSZEWCZ travelled extensively in search of plants and is known to have stayed in Bogotá towards the end of his second journey in 1853. Since he took a steamboat down the Río Magdalena (Anonymous 1854), he must have travelled overland from Bogotá northwest to the town of Honda, Cundinamarca, on the Magdalena, where he embarked. It may have been between Bogotá and Honda that he collected the specimens of *Hyla molitor*. According to GUARNIZO et al. (2012), this area is occupied by *D. "labialis"*, not *D. luddeckei*. His patron and advisor, ALEXANDER VON HUMBOLDT, had taken the same route reversely 50 years before (e.g., KRÄTZ 1997, HERRERA ÁNGEL 2010). There is no information on how WARSZEWCZ travelled to Bogotá.

Nonetheless, synonymizing *D. molitor* with *D. labialis* rather than with *D. luddeckei* remains speculative, assuming that it was more likely for WARSZEWCZ to have collected the specimen in the Bogotá-Honda area rather than in northern Cundinamarca, Boyacá, or Norte de Santander, where *D. luddeckei* occurs.

SCHMIDT (1857) described *Hyla molitor marmorata* (“Anova species?” [Latin: Whether a new species?]) from the same locality as *H. molitor*. I have not seen any of the three syntypes. But SAVAGE & HEYER (1969) have inspected and considered them conspecific with *H. molitor*. Given the same locality, SCHMIDT’s (1857) uncertainty and the variability of the species (LÜDDECKE 2002, GUARNIZO et al. 2012), this appears only too plausible.

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Appendix

Specimens examined

Dendropsophus molitor: NMW 16494 (lectotype of *Hyla molitor*): At the River Chiriquí not far from Bocca del toro, Panama (in error). ZMB 4913 (holotype of *Hyla labialis*): Mountainous surroundings of Bogotá, Departamento Cundinamarca, Colombia. Uncatalogued (8 specimens): Briceño, Departamento Cundinamarca, Colombia.

Supplementary material

Supplementary Table 1. Anuran species described by SCHMIDT (1857) and considered to be junior synonyms.

Supplementary Table 2. Anurans described by SCHMIDT (1857) and considered valid and apparently with correct locality data.

Supplementary Table 3. Anurans described by SCHMIDT (1857) and considered valid, but most likely with incorrect locality data.