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TAXONOMIC REVIEW OF THE SPECIES COMPLEX OF *CROSSODACTYLUS DISPAR* A. LUTZ, 1925 (ANURA, HYLODIDAE)

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Taxonomic Review of the species complex of *Crossodactylus dispar* A. Lutz, 1925 (Anura, Hylodidae)

Bruno V.S. Pimentá Carlos Alberto Gonçalves Cruz & Ulisses Caramaschi

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TAXONOMIC REVIEW OF THE SPECIES COMPLEX OF *CROSSODACTYLUS DISPAR* A. LUTZ, 1925 (ANURA, HYLODIDAE)

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ABSTRACT

The analysis of numerous specimens referred to as Crossodactylus dispar A. Lutz, 1925 in the literature revealed the occurrence of many distinct forms under this name. We discovered that the syntypes belong to two different species, so we designate a lectotype for C. dispar and associate the paralectotypes with Calamobates boulengeri De Witte, 1930, currently a junior synonym of C. dispar and herein revalidated under the new combination Crossodactylus boulengeri. The full species status of Crossodactylus grandis B. Lutz, 1951, originally described as a subspecies of C. dispar, is confirmed and the species is redescribed and illustrated. Crossodactylus timbuhy sp. nov. and Crossodactylus wernerii sp. nov., previously associated with C. dispar, are described and illustrated based on specimens from the states of Espírito Santo, Minas Gerais, Rio de Janeiro, and São Paulo, Brazil. Populations from the states of Paraná and Santa Catarina are assigned to Crossodactylus caramaschii Bastos & Pombal, 1995. We discuss patterns of distribution, the organization of species in groups, and conservation status based on museum data.

KEY-WORDS: Hylopididae; *Crossodactylus dispar* species complex; Taxonomy; Geographic distribution; Conservation.

INTRODUCTION

A species complex is a taxonomic artifact that results from grouping distinct species under a single name, mostly due to the lack of data on individual variation and geographic ranges. The existence of unrecognized cryptic species masks the real richness of a group and poses a serious challenge to taxonomists and conservation planners. One of the most immediate consequences of splitting one taxon into two or

more species is the change in geographic distribution patterns, which may have a great impact on the assessment of their conservation status. The Neotropical region presents many recent examples on the resolution of species complexes, based on morphological, morphometric, acoustic, molecular, and other characters (e.g., Baldissera *et al.*, 2004; Heyer, 2005; Caramaschi, 2006).

Crossodactylus Duméril & Bibron, 1841 currently comprises 11 diurnal species that inhabit

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montane streams in the Atlantic Forest or Campos Rupestres montane savanna, from the State of Alagoas in northeastern Brazil to the Province of Misiones in northeastern Argentina (Nascimento *et al.*, 2005). Izecksohn & Carvalho-e-Silva (2001) emphasized the need for a taxonomic review of *Crossodactylus* due to the difficulty in associating some names with natural populations and Haddad *et al.* (2003) recognized this genus as the least taxonomically resolved within Hyloidae Günther, 1858 (therein referred to as Hyloidae). Both the literature and museum collections are replete with unidentified and incorrectly identified specimens due to the scarcity of data on variation and geographic distribution of species of *Crossodactylus* (Pimenta *et al.*, 2008).

Crossodactylus dispar A. Lutz, 1925 was described on the basis of three syntypes from Fazenda do Bonito, Serra da Bocaina, State of São Paulo, Brazil (Cochran, 1955; Bokermann, 1966). The original description of *C. dispar* is remarkably brief, presenting few diagnostic characters and no illustrations (A. Lutz, 1925). Subsequently, A. Lutz (1930), Cochran (1955), Cei & Roig (1961), and Braun & Braun (1976) referred a great number of taxa and/or populations to this species, giving the greatest distribution in the genus to *C. dispar* that extended from southeastern and southern Brazil, and Misiones, Argentina. It also made *C. dispar* the species of the genus with the most confused taxonomy. Bokermann (1963), Heyer *in* Weygoldt (1986), and Heyer *et al.* (1990) were the first to emphasize taxonomic problems on this species.

Analysis of types and topotypes of *Crossodactylus dispar* and *Calamobates boulengeri* De Witte, 1930 (currently a junior synonym of *C. dispar*) and specimens of many of the populations referred to *C. dispar* in the literature revealed the existence of distinct species under this name. These species can be distinguished by external morphological characters and body dimensions. The purpose of this paper is to resolve the taxonomy of the species complex of *C. dispar*.

MATERIAL AND METHODS

Specimens examined are listed in Pimenta *et al.* (2008) and additional specimens are listed in the Appendix. Museum acronyms follow Sabaj Pérez (2013), except for R (formerly ZMUC; Zoological Museum, University of Copenhagen, Denmark).

External morphological characters were analyzed based on their occurrence, shape, and degree of development and extension following Lynch (1971).

However, some characters and character states were redefined. The terminology proposed by Cei (1980), Heyer *et al.* (1990), Lynch & Duellman (1997), and Grant *et al.* (2006) was used to characterize glands, skin texture, snout, *canthus rostralis*, loreal region, tympanic annulus, folds, tubercles, fingers, finger and toe fringes, and vocal sac. Herein, we describe only the characters used to discriminate distinct species. For definitions and abbreviations of measurements and proportions, see Pimenta *et al.* (2008).

Species accounts are organized as follows: we first redescribe *Crossodactylus dispar* in order to precisely define this species and allow other species in this complex to be diagnosed. We then revalidate and/or redescribe valid species currently in the synonymy of *C. dispar*. Finally, we describe new species for populations mistakenly identified as *C. dispar*. Synonymies include both the taxonomic acts involving each taxon and the names used to refer to these taxa in the literature. We included all non-taxonomic publications referring to species of *Crossodactylus* that we know of, but this compilation was not intended to be exhaustive.

Historical Resume

The description of *Crossodactylus dispar* by A. Lutz (1925) was first published in French and was subsequently translated into Portuguese and English (A. Lutz, 1926). The description is an extremely brief account of external morphology and coloration and lacks illustrations. The type locality in the French and Portuguese versions is referred to as “mountains of the State of Rio de Janeiro” (in a literal translation to the English), whereas the English translation presents it only as “mountains near Rio”.

In 1930, A. Lutz erected the subfamily Eloisiinae, which included the genera of the current family Hyloidae and also the genus *Basanitia* Miranda-Ribeiro, 1923 (now a junior synonym of *Ischnocnema* Reinhardt & Lütken, 1862), and provided a taxonomic review of this group in which he concluded that *C. dispar* was a junior synonym of *C. fuscigula* (Fitzinger, 1861 “1860”). *Crossodactylus bresslaui* Müller, 1924 and the recently described *Calamobates boulengeri* De Witte, 1930 were also included in the synonymy of *C. fuscigula*. A fair re-description and a plate of a male specimen of *C. dispar* from Serra da Bocaina (here reproduced as Fig. 1) were presented. Under the name *C. fuscigula*, A. Lutz emphasized the large difference in arm thickness between males and females as a conspicuous dimorphic character of the species, mentioning that the sexual dimorphism in

arm thickness and ventral coloration were the reasons he had chosen the name “dispar”.

B. Lutz (1951) described *Crossodactylus dispar grandis* from the Serra do Itatiaia, observing that it was very similar to the nominal subspecies but was much larger. She also removed *C. dispar* and *C. bresslaui* (currently a junior synonym of *C. trachystomus* [Reinhardt & Lütken, 1862 “1861”] *vide* Cochran, 1955 “1954”) from the synonymy of *C. fuscigula*, which she noted was a *nomen nudum*. The collection date and number of paratypes were listed in an English translation of the description (B. Lutz, 1952), but museum numbers were not provided.

Cochran (1955 “1954”) made no reference to *Crossodactylus dispar grandis* in her monograph on the frogs of southeastern Brazil. She corrected the type locality of *C. dispar* to “Bonito, Serra da Bocaina” (a regional name for the portion of the Serra do Mar situated between the states of Rio de Janeiro and São Paulo, southeastern Brazil; this is the same locality where the specimen described and illustrated by A. Lutz in 1930 was collected). She followed A. Lutz (1925) in considering *Calamobates boulengeri* to be a junior synonym of *C. dispar*. Cochran’s (1955 “1954”) redescription of *C. dispar* was based on the syntype USNM 96739, which she identified as male. Like A. Lutz (1930), she noted the sexual dimorphism in forearm thickness, as well as the “blunt snout and swollen head” of males. She also mentioned that the two other syntypes presented “small, irregular teeth”, absent in USNM 96739, along most of the length of the vomerine ridge, and that syntype USNM 96740, “apparently a male”, presented a “circllet of black-tipped tubercles around the upper lip”. The geographic distribution of *C. dispar* was greatly extended by records from the States of Minas Gerais, Rio de Janeiro, São Paulo, and Santa Catarina, Brazil.

Cei & Roig (1961) cited the occurrence of *Crossodactylus dispar* for San Pedro, Province Misiones, Argentina, based on the collection of a single male specimen, and also described its tadpole. Soon thereafter, Bokermann (1963) described the tadpole of *C. dispar* from Paranapiacaba (a railway village in the Municipality of Santo André, *ca.* 820 m elevation; Pombal & Haddad, 1999), State of São Paulo, with no reference to the study of Cei & Roig (1961). Although he employed the usage proposed by Cochran (1955 “1954”), he pointed out that it was difficult to apply that name to this population.

Bokermann (1966) more precisely defined the type locality of *Crossodactylus dispar* as Fazenda do Bonito, Serra da Bocaina, Municipality of São José do Barreiro, State of São Paulo, Brazil (a locality near the

border with the State of Rio de Janeiro; approx. 22°46’S, 44°32’W, *ca.* 1,500 m a.s.l.). He also corrected the type locality of *Calamobates boulengeri* to Paranapiacaba, State of São Paulo, Brazil. Both localities are situated in the Serra do Mar, a mountainous complex extending from the State of Espírito Santo, southeastern Brazil, to the State of Santa Catarina, southern Brazil.

Lynch (1971) was the first author to recognize *Crossodactylus grandis* as a full species, with no justification. Since then, this species has appeared in all species lists for the genus (*e.g.*, Caramaschi & Sazima, 1985; Nascimento *et al.*, 2005; Frost, 2013). Braun & Braun (1976, 1980) reported *C. dispar* in the meridional Brazilian State of Rio Grande do Sul and considered it to be the southernmost species in the genus. Cei (1980) provided accounts for the Argentinean species of *Crossodactylus* but added no new information beyond Cei & Roig (1961). Caramaschi & Sazima (1985) proposed three species groups to accommodate all the *Crossodactylus* recognized until then. *Crossodactylus dispar* and *C. grandis* were assigned to the species group of *C. trachystomus*, characterized by short, rounded snout and poorly marked *canthus rostralis*.

Weygoldt (1986) reported the occurrence of *Crossodactylus cf. dispar* in the Municipality of Santa Teresa, State of Espírito Santo, Brazil, mentioning that Dr. W.R. Heyer (USNM) had informed him that his specimens could not be correctly identified in that moment because the genus needed to be reviewed. Heyer *et al.* (1988, 1990) tentatively referred the specimens of *Crossodactylus* most commonly found at the Estação Biológica de Boracéia (23°39’S, 45°53’W), Municipality of Salesópolis, State of São Paulo, Brazil, to *C. dispar*, noting that the systematics of the genus was confused and that it was not clear which name should be applied to this species.

Faivovich (1998) analyzed the tadpoles described by Cei & Roig (1961) and Cei (1980) as *Crossodactylus dispar* and concluded that they do not belong to *Crossodactylus*. Guix *et al.* (2000) referred populations from Serra de Paranapiacaba (a continental portion of the Serra do Mar complex from the northern region of the State of São Paulo to the mid-western region of the State of Paraná) in southwestern São Paulo, to *Crossodactylus aff. dispar*.

RESULTS

External morphology

The external morphology of specimens of the several populations currently referred to *Crossodactylus*

dispar presented great variation. In order to organize the presentation of the main diagnostic characters/states found, we used a numbered sequence as adopted, among others, by Cisneros-Heredia & McDiarmid (2007), which we found to be very useful for readers. Characters are organized into an anatomical and morphometric sequence as follows: body and head (1-6), limbs (7-10), skin and glands (11-14), and coloration (15-17).

- (1) **Body build:** Specimens presented distinct body builds, which we defined as slender and robust (Fig. 2).
- (2) **Head width/head length:** The head can be nearly as wide as long, wider than long, or longer than wide.
- (3) **Snout shape:** The snout can be rounded or nearly pentagon-shaped (described by Heyer *et al.*, 1990 as “slightly truncate and nearly rounded”) in dorsal view and rounded or protruding in lateral view. Pimenta *et al.* (2008) indicated that *C. aeneus* and *C. gaudichaudii* only have nearly pentagon-shaped snouts, but we observed some specimens with rounded snouts.
- (4) **Shape of *canthus rostralis*:** The *canthus rostralis* can be poorly defined (rounded) or well defined (sharp).
- (5) **Tympanum:** Tympanum can be distinct or weakly distinct.
- (6) **Vocal sac:** We suspect that the “unexpanded” state used to diagnose *C. dantei* and *C. lutzorum* (Carcerelli & Caramaschi, 1992) appears to be related to preservation conditions, since recently preserved males of other species usually have expanded vocal sacs, albeit subtly.



FIGURE 1: Original watercolor plate of *Crossodactylus dispar* by P. Sandig. A black and white version of this same drawing was reproduced in the review of Elosiinae by A. Lutz (1930).

The unavailability of recently collected males of *C. dantei* and *C. lutzorum* prevented us from ascertaining if vocal sac condition differs from their descriptions; hence, the state “unexpanded” is maintained for these species. We confirmed that most species of *Crossodactylus* here analyzed seem to have bilobate, subgular vocal sac (*sensu* Cei, 1980; e.g., *C. caramaschii*; Bastos & Pombal, 1995) shown by the presence of dermal folds under the mouth corners not observed in species with median, subgular vocal sacs. We



FIGURE 2: Different states of body build in *Crossodactylus*. From left to right: slender build (MZUSP 109698, SVL 23.7 mm) and robust builds (USNM 318200, SVL 27.8 mm; MNRJ 3285, SVL 39.0 mm).

make no reference to the degree of development of vocal sac, as noted by Pimenta *et al.* (2008) for *C. bokermanni* (described as “weakly expanded”); at present, we are interested only in vocal sacs character states that diagnose species, which are unexpanded, median-subgular, and bilobate-subgular.

- (7) **Thumb spines:** In Grant *et al.* (2006), when cornified spines occur on finger I (characters 24 and 25), they are necessarily large. Such spines occur in all *Crossodactylus*, but differ in relation to their size: they can be small, developed (when the region around their bases is also cornified) or strongly developed (when all area between the spines is cornified, connecting its bases through a thin layer of keratin, or when the spines are so large that their bases touch each other). Thumb spines may be absent, mainly in juveniles and females of some species, or vary from one to six. The size of each spine apparently depends on the total number of spines on finger I: the higher the number, the smaller the size. In species with developed or strongly developed spines the occurrence of more than three spines is rare due to their large sizes.
- (8) **Fringes on toes and tarsi:** Males may present weak, moderate, or extensive fringes on toes and tarsi. As discussed in Pimenta *et al.* (2008), fringes are normally well developed in males and weak in females. This sexual dimorphism was observed in all species of *Crossodactylus* they analyzed, and we extend their finding to the additional species examined herein, with the additional observation that fringe development also varies in males of *C. grandis*.
- (9) **Finger tips:** Finger tips are always rounded and may be dilated or not.
- (10) **Toe tips:** Toe tips can be rounded or truncate, dilated or not.
- (11) **Postriatal tubercle:** All species of *Crossodactylus* here examined present an elongated swelling between the tympanum and the shoulder (called “tubercle below the tympanum” in Bastos & Pombal, 1995, and “gland posterior to the buccal commissure” in Nascimento *et al.*, 2005). This may be a large diffuse swelling or a line of small discrete granules (Fig. 3).
- (12) **Glandular crest on arm:** A thin, apparently glandular crest may extend along the entire or distal half of the anterior surface of the upper arm (not equivalent to the gland presented in character 27 of Grant *et al.*, 2006). It may also be absent.

(13) **Dorsal skin texture:** Dorsal skin texture is always posteriorly granular (state 1 of character 0 of Grant *et al.*, 2006). Scattered granules may occur in other body regions, such as head, flanks, limbs, cloacal region, and venter.

(14) **Dorsal/dorsolateral glandular ridges:** Skin may present dorsal and/or dorsolateral glandular ridges of variable length and development.

(15) **Color in the region between snout and shoulder:** We found two very distinctive color patterns for this area among specimens examined. It may present a poorly delimited area of some light color, marbled/punctuated of different tones of brown, or a uniform white or cream stripe (referred to as “light stripe from the snout to the arm insertion” in Nascimento *et al.*, 2005) (Fig. 4).

(16) **Oblique lateral stripe:** The species of *Crossodactylus* analyzed may present a partial oblique lateral stripe (state 0 of character 56 of Grant *et al.*, 2006; called “lateral stripe on the posterior half of the flank” by Nascimento *et al.*, 2005 and “stripe on the flank” in Pimenta *et al.*, 2008). It may also be absent.

(17) **Belly coloration:** The belly can be immaculate or reticulated (as in character 63, states 0 and 1, respectively, of Grant *et al.*, 2006). Variation in coloration was not related to sex in the specimens analyzed.

In addition to the characters presented and/or described above, we also refer to the structure Lynch (1971) called “dermal, scute-like glandular pads” and Grant *et al.* (2006; character 1) called “paired dorsal digital scutes”, “paired dermal scutes”, or “digital scutes” simply as “scutes”, following Bastos & Pombal (1995) and Nascimento *et al.* (2005). Scutes are a synapomorphy of Nobleobatia (Grant *et al.*, 2006) and were observed in all *Crossodactylus* we examined, so they are not considered a diagnostic character.

The presence, degree of development, and color of the upper lip spines (called “tubercles on the edge of the upper lip” in Heyer *et al.*, 1990 and “minuscule keratinized spines” or “labial spines” in Nascimento *et al.*, 1995) varied greatly within species, as observed in *C. bokermanni* (Pimenta *et al.*, 2008), and it was not possible to find diagnostics states in each of these characters. Upper lip spines may be small or strongly developed, black, brown, or white; when present, the row of spines may be restricted to the anterior portion or extend along the entire upper lip.

We also determined that the morphometric characters proposed by Caramaschi & Sazima (1985) as diagnostic for groups of species of *Crossodactylus*

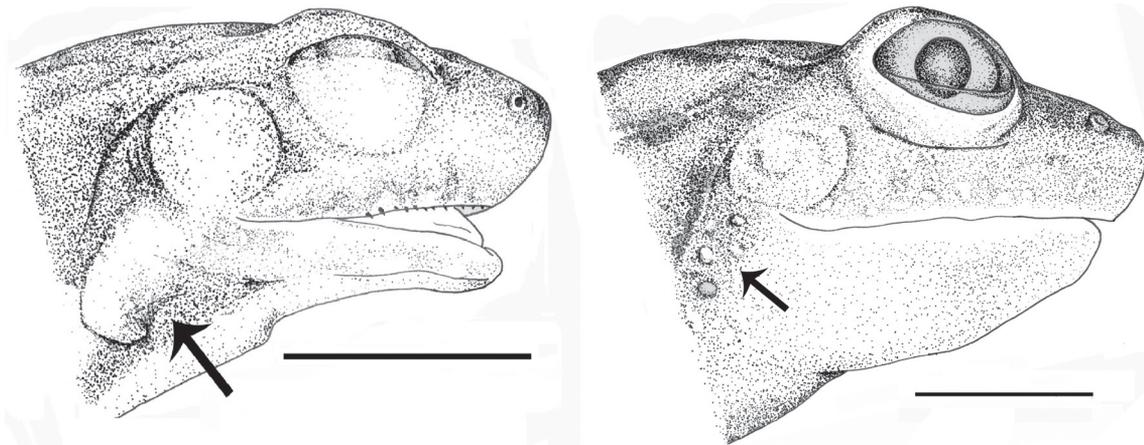


FIGURE 3: Left, elongated continuous postrictal tubercle (arrow; MZUSP 111047, SVL 23.0 mm; bar = 5 mm); right, tubercle fragmented into small granules (arrow; MZUSP 109494, SVL 32.6 mm; bar = 5 mm).

cannot be applied for that purpose. Ranges of the characters analyzed overlap extensively in all species, except in *C. grandis*. Therefore, we suggest that morphometric characters should not be considered to define phenetic groups in *Crossodactylus*.

Species Accounts

Crossodactylus dispar A. Lutz, 1925

Figures 5-6

Crossodactylus dispar A. Lutz, 1925 (part), 1926 (part), 1930 (part); Cochran, 1955 “1954” (part); Heyer *et al.*, 1988; Heyer *et al.*, 1990; Garcia *et al.*, 2009 (part).

Phyllobates fuscigula (non Fitzinger, 1861 “1860”) – A. Lutz, 1930.

Crossodactylus fuscigula – A. Lutz, 1930.

Crossodactylus dispar dispar – B. Lutz, 1951, 1952.

Lectotype: USNM 96739, adult female (Fig. 5), collected at Fazenda do Bonito (approx. 22°46'S, 44°32'W, ca. 1,500 m a.s.l.), Serra da Bocaina, Municipality of São José do Barreiro, State of São Paulo, Brazil, by A. Lutz, 20 January 1925.

Paralectotypes: USNM 96738, adult female, and USNM 96740, adult male, collected with the lectotype. Both belong to a distinct species (see below).

Diagnosis: (1) body robust; (2) head nearly as wide as long; (3) snout short, rounded in dorsal and lateral views; (4) *canthus rostralis* rounded, ending before the nostrils; (5) tympanum distinct; (6) vocal sac median,

subgular; (7) thumb spines developed or strongly developed; (8) males with moderate fringes on toes and tarsi, females with weak fringes; (9) finger tips undilated; (10) toe tips rounded, undilated; (11) postrictal tubercle fragmented into a line of discrete granules; (12) presence of a glandular crest on the anterior surface of the arm; (13) dorsal skin posteriorly granular; (14) presence of dorsal and dorsolateral glandular ridges; (15) a poorly delimited area marbled of brown between snout and shoulder; (16) no oblique lateral stripe; (17) belly immaculate.

Comparison with other species: Character states for the other species are shown in parenthesis. *Crossodactylus dispar* is readily separated from all congeneric species, except for *C. grandis*, due to its head nearly as long as wide (longer than wide), moderate fringes on toes and tarsi of males (extensive), undilated fingers (dilated), and postrictal tubercle fragmented into a line of discrete tubercles (a large diffuse swelling). It also differs from all congeneric species, except for *C. grandis* and *C. schmidtii*, due to its rounded *canthus rostralis* (sharp). *Crossodactylus dispar* further differs from *C. caramaschii*, *C. dantei*, and *C. lutzorum* due to its rounded snout in dorsal view (nearly pentagon-shaped) and median, subgular vocal sac (bilobate, subgular in *C. caramaschii*; unexpanded in *C. dantei* and *C. lutzorum*). *Crossodactylus dispar* is distinguished from *C. aeneus*, *C. caramaschii*, *C. cyclopinus*, and *C. gaudichaudii* by the developed or strongly developed thumb spines (small) and from *C. aeneus*, *C. bokermanni*, *C. caramaschii*, *C. cyclopinus*, *C. gaudichaudii*, and *C. trachystomus* by the rounded toe tips (truncate). It is separated from *C. aeneus*, *C. caramaschii*, *C. cyclopinus*, *C. dantei*,



FIGURE 5: *Crossodactylus dispar* A. Lutz, 1925, lectotype (USNM 96739, SVL 25.4 mm).

C. gaudichaudii, *C. lutzorum*, and *C. schmidti* due to the presence of a glandular crest on the anterior surface of the arm (absent), and from *C. lutzorum* and *C. schmidti* due to the presence of dorsal and dorsolateral glandular ridges (absent). It differs from *C. bokermanni*, *C. caramaschii*, *C. cyclospinus*, *C. schmidti*, and

C. trachystomus due to the presence of a poorly delimited area marbled of brown between snout and shoulder (uniform white or cream stripe between snout and shoulder), and from *C. aeneus*, *C. bokermanni*, *C. cyclospinus*, *C. gaudichaudii*, and *C. trachystomus* by the absence of an oblique lateral stripe (present; presence is variable in *C. caramaschii* and *C. schmidti*). *Crossodactylus dispar* is distinguished from *C. bokermanni*, *C. caramaschii*, *C. cyclospinus*, and *C. trachystomus* by its immaculate belly (reticulated in *C. bokermanni*, *C. caramaschii*, and *C. trachystomus*; with brown scattered blotches and short stripes in *C. cyclospinus*).

As previously mentioned, *Crossodactylus dispar* is most similar to *C. grandis*, differing from this species by the smaller size (males SVL 23.6-33.7 mm, females 20.9-33.8 mm in *C. dispar*; males SVL 31.5-42.0 mm, females 29.6-39.2 mm in *C. grandis*), more protruding snout, and distinct tympanum (weakly distinct in *C. grandis*).

Description of the lectotype (Fig. 6): Body robust; a marked constriction between head and body. Head nearly as long as wide. Snout approx. 37% of HL, rounded in dorsal and lateral views; nostrils located laterally, directed superolaterally, closer to tip of snout than to eye. *Canthus rostralis* rounded; loreal region oblique, slightly concave. Eyes approx. 36% of HL, prominent. Tympanum distinct, approx. 68% of ED, rounded; supratympanic fold well developed, extending as a concave arch from the posterior corner of the eye to the shoulder (Fig. 6). Upper lip spines small, white, appearing on the whole extension of lip. Tongue medium, ovoid, narrow, approximately half of mouth floor, not notched behind. Choanae small, ovoid, distant from each other. No vomerine teeth.



FIGURE 4: Color pattern in the region between snout and shoulder, showing at left the poorly delimited area of light color, marbled/punctuated of brown or light brown (MNRJ 40551, SVL 27.9 mm), and at right the uniform white or cream stripe (MNRJ 38473, SVL 22.9 mm).

Arms and hands robust; forearms thicker than upper arms; fingers slender, tips undilated; finger lengths II-IV<I<III; three strongly developed spines on each thumb, arranged triangularly; the spine on the inner margin of thumb is smaller than the others. Scutes weakly developed on upper surfaces of finger tips; small dermal folds with rounded margins on the joints of distal phalanges; fringes on fingers poorly developed. Carpal tubercle rounded, large; thenar tubercle rounded, slightly smaller than carpal tubercle; subarticular tubercles rounded, protruding, most developed on finger I (Fig. 6); no supernumerary tubercles.

Legs robust; the sum of tibia, thigh, and foot lengths 1.6 times the SVL; toes slender, long, weakly fringed, with rounded, undilated tips; toe lengths

I<II<V<III<IV. Scutes on upper surfaces of toes more developed than on fingers; small dermal folds with truncate margins on the joints of distal phalanges. Inner metatarsal tubercle elongated, protruding; outer metatarsal tubercle small, rounded, protruding; subarticular tubercles rounded, protruding, more developed than on fingers; no supernumerary tubercles. Fringes joined at base; weak tarsal fringe, continuous distally with outer fringe of toe I, almost reaching the joint with the tibia; outer fringe of toe V ending right after the posterior margin of basal tubercle of toe (Fig. 6).

Dorsum skin posteriorly granular, presenting a vertebral glandular ridge from the interorbital area to sacral region, interrupted at the end of the second third of body, and a pair of dorsolateral glandular ridges

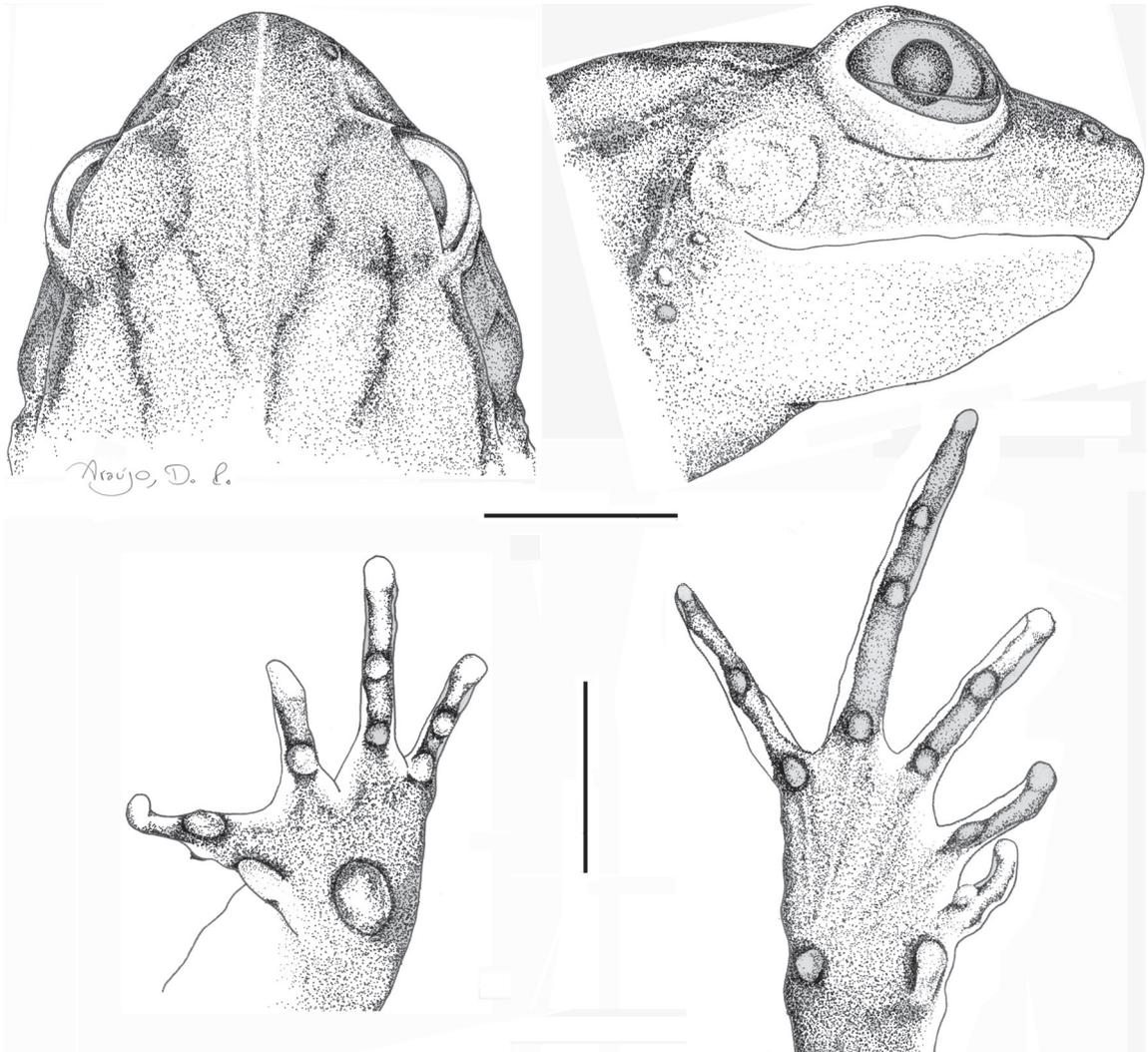


FIGURE 6: *Crossodactylus dispar* A. Lutz, 1925, topotype (MZUSP 109494, male, SVL 32.6 mm). Dorsal and lateral views of head and ventral views of hand and foot (scale bars = 5 mm).

from the posterior corner of eyes to inguinal region. Upper eyelids finely rugose; a pair of short, oblique glandular ridges from the upper eyelids, meeting the vertebral ridge at the end of the head, and another pair from the upper eyelids, meeting the vertebral ridge at the level of arms insertion; flanks with many small granules; cloacal region covered with scattered, small granules. Postrictal tubercle indistinct, probably due to time and/or conditions of preservation. Ventral surfaces smooth.

Color in preservative (70% ETOH) is based on topotype MZUSP 109494 (the lectotype is completely faded). General pattern light brown; dorsal and dorsolateral glandular ridges and sacral granules brown; a brown stripe from nostrils to the anterior corner of the eyes; area from the snout to the shoulder marbled of brown over a cream background; tympanum and postrictal tubercle cream. Arms light brown and hands cream, both densely dotted of brown. Legs and feet light brown with three poorly defined brown transverse bars. Ventral surfaces cream; region between throat and chest with a few discrete brown blotches; belly immaculate. Palms of hand, plants of feet, and posteroventral region of thighs densely dotted of brown.

Measurements of the lectotype: SVL 25.4; HL 9.1; HW 8.9; TBL 11.7; THL 10.5; FL 18.7; TD 2.2; ED 3.2; END 2.2; NSD 1.2; IND 2.8; IOD 2.8.

Variation: Both males and females have thick forearms, but males' forearms are even thicker than in females. Upper lip spines may be developed and black, light brown and scarce, or even absent; they also may not occur all over the length of upper lip. Two to five spines, arranged as a square when in four or as row of spines at the outer margin of the thumb and one or two smaller spines at the inner margin when in four or five, may occur on thumbs and the whole space among them may be also keratinized, connecting their bases. Males show moderate fringes on feet, weak on females. A few granules occur on outer surfaces of forearms and one or two small granules occur on ventral surfaces of tarsi. Vertebral glandular ridge on dorsum may be continuous from the interorbital area to sacral region. Flanks may present some granules. Two of the small granules forming the postrictal tubercle may be anastomosed, forming an irregular narrow short line. Morphometric variation is shown in Table 1.

Distribution, natural history, and conservation status: *Crossodactylus dispar* occurs on the northern range of the Serra do Mar in the States of São Paulo and Rio de

TABLE 1: Mean, standard deviation (SD), and range of some measurements (in mm) of *Crossodactylus dispar*.

	Males (n = 37)			Females (n = 41)		
	Mean	SD	Range	Mean	SD	Range
SVL	28.5	2.73	23.6-33.7	26.9	2.55	20.9-33.8
HL	10.2	0.83	8.9-12.0	9.7	0.77	8.3-11.6
HW	10.2	1.09	8.2-12.5	9.5	0.94	7.5-12.1
TBL	13.1	0.88	11.6-15.0	12.4	0.81	10.6-14.6
THL	13.2	1.15	11.0-15.3	12.2	1.11	10.2-15.4
FL	20.7	2.20	12.8-24.0	19.7	1.64	16.2-23.6
TD	1.9	0.29	1.3-2.6	1.8	0.27	1.2-2.2
ED	3.3	0.30	2.7-4.2	3.2	0.31	2.6-3.9
END	1.9	0.24	1.4-2.5	1.9	0.21	1.5-2.5
NSD	1.0	0.19	0.6-1.3	1.0	0.19	0.7-1.5
IND	3.1	0.27	2.3-3.5	3.0	0.27	2.0-3.7
IOD	2.9	0.31	2.1-3.6	2.8	0.29	2.1-3.4

Janeiro, southeastern Brazil, between the Municipality of Bananal and the Estação Biológica de Boracéia (Fig. 7). The scarce data on natural history available for this species was summarized by Heyer *et al.* (1990) for the population from Boracéia.

In light of our redescription of *C. dispar*, we confirmed that there are no records in collections after January 1977, when specimens USNM 318225, 318227, and 318230 were caught at Boracéia. Heyer *et al.* (1988) reported on the disappearance of this population, probably associated with a severe frost that occurred in 1979. The most recent update on the species status from this area (Bertoluci & Heyer, 1995) showed no recovery. Garcia *et al.* (2009) considered *C. dispar* as "Endangered" (EN) in the State of São Paulo, stating that it is not found in two of the three localities it occurred. The population from Paranapiacaba, the third locality mentioned by Garcia *et al.* (2009), corresponds to a distinct species which is currently a junior synonym of *C. dispar* but is re-validated below.

Remarks: The type series of *Crossodactylus dispar* consists of specimens presenting very distinct states in some characters. Syntype USNM 96739 (now the lectotype, which we identified as female due to the forearm thickness), used in Cochran's (1955 "1954") redescription, has a robust body, rounded snout in dorsal and lateral views, and rounded *canthus rostralis*. Syntypes USNM 96738 (female) and USNM 96740 (male) have slender bodies, snouts nearly pentagon-shaped in dorsal view and protruding in lateral view, and sharp *canthus rostralis*.

A. Lutz (1925, 1926, 1930) and, subsequently, Cochran (1955 "1954") always considered the robust specimens found at Serra da Bocaina to be males and

the slender specimens to be females of a single species, *C. dispar*. We analyzed topotypes and specimens from other localities, which agree with both forms represented in the type series, including some dissected specimens. We confirmed that each of these forms includes male and female specimens. This observation, together with the aforementioned morphological differences found among the syntypes, led us to conclude that the type series includes two species. The remaining question was which syntype should bear the name *C. dispar*.

All descriptions of *Crossodactylus dispar* (A. Lutz, 1925, 1926, 1930; Cochran, 1955 “1954”) were based mainly on the robust syntype or robust topotypes;

when slender specimens were not treated as females they were considered variant males (see Cochran, 1955 “1954”). On the single occasion where the species was figured, in the review of the Elosiinae (A. Lutz, 1930: LXV 14-16; here reproduced as Fig. 1), the illustration agrees perfectly with the robust specimens, including the dorsal color pattern. Moreover, B. Lutz (1951) described *C. grandis* as a subspecies of *C. dispar* because they are similar in their robust bodies. Therefore, we chose to designate the robust syntype as the lectotype of *C. dispar*.

The name *Crossodactylus dispar* was applied to numerous populations of *Crossodactylus* from southeastern Brazil and northeastern Argentina. Our

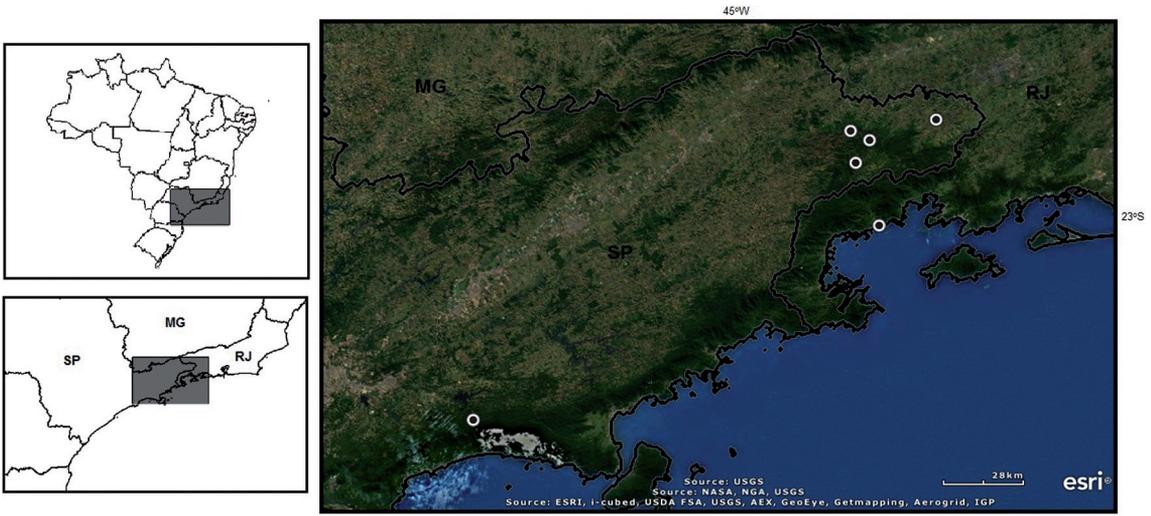


FIGURE 7: Geographic distribution of *Crossodactylus dispar* (black dots). MG = State of Minas Gerais; RJ = State of Rio de Janeiro; SP = State of São Paulo.

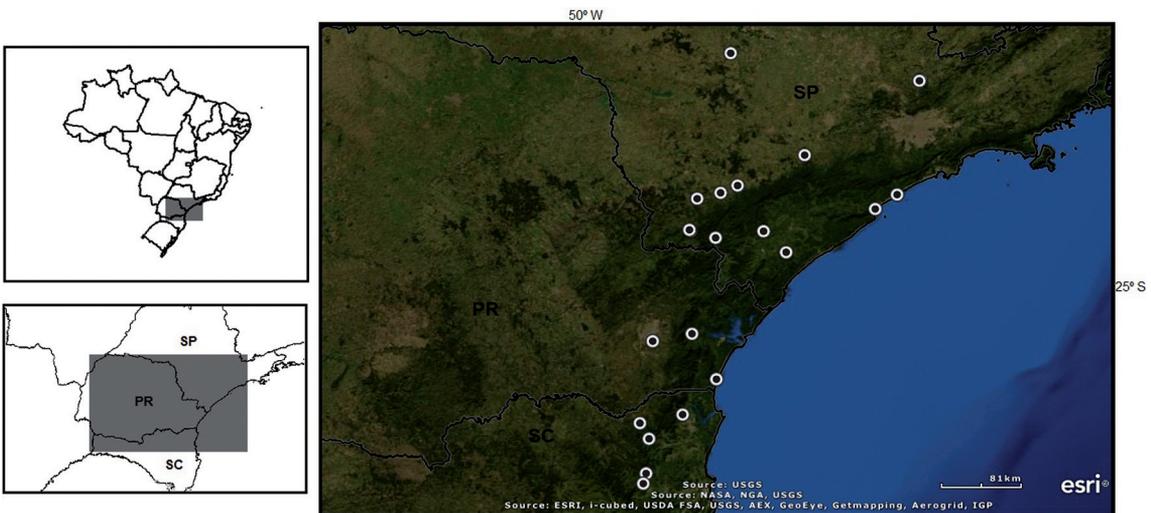


FIGURE 8: Geographic distribution of *Crossodactylus caramaschii* (black dots). PR = State of Paraná; SC = State of Santa Catarina; SP = State of São Paulo.

analysis of specimens from these populations revealed the existence of distinct species within the taxon "*C. dispar*". Most of these species have slender bodies and sharp *canthus rostralis* and all species are smaller than *C. dispar* and *C. grandis*.

We examined the specimens Cochran (1955 "1954") determined as *Crossodactylus dispar* from Hansa (USNM 129369-129379; specimen USNM 129376 is also mentioned as *C. dispar* in Heyer, 1975) and additional specimens from Guaratuba, Humboldt, Pirabeiraba, Rio dos Cedros, São Bento do Sul, and Timbó (see Appendix), all localities in the State of Santa Catarina, Brazil, and concluded that they are conspecific with *C. caramaschii* Bastos & Pombal, 1995. Hansa and Humboldt currently correspond to the Municipality of Corupá (26°26'S, 49°14'W; Gutsche *et al.*, 2007). Pimenta *et al.* (2008) already reported on a specimen of *C. caramaschii* from São João da Graciosa, Municipality of Morretes, State of Paraná, southern Brazil. We also determined previously unidentified specimens from the Municipality of São José dos Pinhais, Paraná, as *C. caramaschii* (see Appendix). The recognition of these populations extending the distribution of this species from the currently known range, in the southern region of the State of São Paulo (Frost, 2013), south to the States of Paraná and Santa Catarina, Brazil (Fig. 8). The specimens from Atibaia, State of São Paulo, referred to as "*Crossodactylus* sp. nov." by Giaretta *et al.* (1999), are also *C. caramaschii*. The specimens from Serra de Paranapiacaba, southwestern São Paulo, referred to as *C. aff. dispar* by Guix *et al.* (2000) probably are also *C. caramaschii*, since it was the only species of *Crossodactylus* found by Bertoluci & Rodrigues (2002), Araujo *et al.* (2010), and Forlani *et al.* (2010) in the same locality.

Paulo C.A. Garcia (*pers. comm.*) redetermined the Braun & Braun's (1976) specimens of *C. dispar* from the State of Rio Grande do Sul, Brazil (MCN 9554-9557, Municipality of São Borja) as *Leptodactylus podicipinus* (Cope, 1862), and we concur with his assessment.

The male specimen from San Pedro, Misiones, Argentina, identified as *Crossodactylus dispar* by Cei & Roig (1961) is lost (J. Faivovich and S. Rosset, *pers. comms.* to BVSP) and could not be examined. However, the descriptions and illustrations in Cei & Roig (1961) and Cei (1980) show a specimen with a protruding snout, sharp *canthus rostralis*, five small spines on the thumb, extensively fringed toes and tarsi, and an oblique lateral stripe (*C. dispar* has a rounded snout, poorly marked *canthus rostralis*, developed or strongly developed spines on the thumb, reduced or moderate fringes on toes and tarsi, and no

oblique lateral stripe). It is clear that this Argentinean specimen is not *C. dispar* and is probably *C. schmidti* Gallardo, 1961, whose distribution range includes the locality of San Pedro [according to Frost (2013), this species occurs in Misiones, Argentina; western Paraná, extreme northern Rio Grande do Sul, and western Santa Catarina, Brazil; and in southeastern Paraguay]. Moreover, we have analyzed several specimens of *C. schmidti* and could not find snouts as short as shown in the original description of the species; the type was either illustrated incorrectly or represents an anomalous morph. Consequently, it could agree with the specimen from San Pedro, which has a protruding snout.

***Crossodactylus boulengeri* (De Witte, 1930) –
comb. nov.**

Figures 9-10

Calamobates boulengeri De Witte, 1930.

Crossodactylus dispar (non A. Lutz, 1925) – A. Lutz, 1930; Cochran, 1955 "1954"; Garcia *et al.*, 2009 (part); Verdade *et al.* (2009).

Crossodactylus gaudichaudii (non Duméril & Bibron, 1841) – Carnaval *et al.*, 2006 (part).

Holotype: IRSNB 1022, adult male (according to the original description) (Fig. 9), collected at Paranapiacaba (approx. 23°45'S, 46°22'W; coordinates taken from Pombal & Haddad, 1999), Municipality of Santo André, State of São Paulo, Brazil, in September 1922.

Diagnosis: (1) body slender; (2) head longer than wide; (3) snout nearly pentagon-shaped in dorsal view, protruding in lateral view; (4) *canthus rostralis* sharp; (5) tympanum distinct; (6) vocal sac bilobate, subgular; (7) thumb spines developed or strongly developed; (8) males with developed fringes and females with reduced fringes on toes and tarsi; (9) finger tips dilated; (10) toe tips truncate, dilated; (11) postcranial tubercle continuous; (12) presence of a glandular crest on the anterior surface of the arm; (13) dorsal skin posteriorly granular; (14) presence of dorsolateral glandular ridges; (15) a poorly delimited area marbled of dark brown between snout and shoulder; (16) presence of oblique lateral stripe variable; (17) belly reticulated.

Comparison with other species: Character states for the other species are shown in parenthesis. *Crossodactylus boulengeri* is readily distinguished from *C. dispar*



FIGURE 9: *Crossodactylus boulengeri* (De Witte, 1930) comb. nov., holotype (IRSNB 1022, SVL 26.4 mm). Photo by G. Lenglet.

and *C. grandis* by its slender body (robust), head longer than wide (nearly as wide as long), snout nearly pentagon-shaped in dorsal view and protruding in lateral view (rounded in dorsal and lateral views), sharp *canthus rostralis* (rounded), bilobate, subgular vocal sac (median, subgular), males with extensively fringed feet (moderate), dilated finger tips (undilated), truncate and dilated toe tips (rounded, undilated), postriatal tubercle continuous (fragmented into small granules), absence of dorsolateral glandular ridges (present), and reticulated belly (immaculate). It further differs from *C. grandis* due to its distinct tympanum (weakly distinct in *C. grandis*) and smaller size (males 20.2–27.1 and females 20.4–27.8 mm SVL in *C. boulengeri*; males 31.5–42.0 and females 29.6–39.2 mm in *C. grandis*).

Crossodactylus boulengeri differs from *C. aeneus*, *C. dantei*, and *C. gaudichaudii* by its slender body (robust), and from *C. bokermanni*, *C. cyclopinus*, *C. schmidti*, and *C. trachystomus* by its nearly pentagon-shaped snout in dorsal view (rounded; variable in *C. aeneus* and *C. gaudichaudii*). It is distinguished from *C. schmidti* by the sharp *canthus rostralis* (rounded) and from *C. aeneus*, *C. bokermanni*, *C. cyclopinus*,

C. dantei, *C. gaudichaudii*, *C. lutzorum*, *C. schmidti*, and *C. trachystomus* due to the bilobate, subgular vocal sac (unexpanded in *C. dantei* and *C. lutzorum*; median, subgular in the other species). *Crossodactylus boulengeri* is separated from *C. aeneus*, *C. caramaschii*, *C. cyclopinus*, and *C. gaudichaudii* by the developed or strongly developed thumb spines (small; variable in *C. bokermanni* and *C. schmidti*), and from *C. dantei*, *C. lutzorum*, and *C. schmidti* due to its truncate toe tips (rounded). It is distinguished from *C. caramaschii* and *C. lutzorum* due to the developed postriatal tubercle (a slight ridge), and from *C. aeneus*, *C. caramaschii*, *C. cyclopinus*, *C. dantei*, *C. gaudichaudii*, *C. lutzorum*, and *C. schmidti* due to the presence of a glandular crest in the anterior surface of the arm (absent). The presence of dorsolateral glandular ridges separates *C. boulengeri* from *C. cyclopinus*, *C. dantei*, *C. lutzorum*, and *C. schmidti* (ridges absent). It differs from *C. bokermanni*, *C. caramaschii*, *C. cyclopinus*, *C. schmidti*, and *C. trachystomus* by having an undefined, light, marbled/dotted area from snout to shoulder (a white or cream stripe from the snout to the shoulder). *Crossodactylus boulengeri* is distinguished from *C. aeneus*, *C. dantei*, *C. gaudichaudii*, *C. lutzorum*, and *C. schmidti* by its reticulated belly (immaculate), and from *C. gaudichaudii* due to its smaller males (SVL 20.2–23.0 mm in *C. boulengeri*; 23.5–30.4 mm in *C. gaudichaudii*).

Description: Description based on topotype MZUSP 111047 (Fig. 10); holotype could not be loaned due to curatorial policy. Body slender. Head longer than wide; nostrils located laterally, directed antero-laterally, closer to the tip of snout than to the eye. Snout approx. 29% of HL, nearly pentagon-shaped in dorsal view, protruding in lateral view. *Canthus rostralis* well marked, sharp; loreal region oblique, slightly concave. Eyes approx. 34% of HL, prominent. Tympanum distinct, approx. 45% of ED, rounded; supratympanic fold well developed, extending from the posterior corner of the eye to the shoulder. Vocal sac bilobate, subgular, perceptible through skin folds below mouth corners (Fig. 10). Upper lip spines developed, black, appearing on the whole extension of lip. Tongue narrow, ovoid, half of the mouth floor, slightly notched behind. Choanae small, ovoid, distant from each other. No vomerine teeth.

Arms slender; forearms slightly thicker than upper arms; fingers tips slightly dilated; finger lengths II<I–IV<III; three strongly developed spines on each thumb, arranged triangularly; the spine on the inner margin of thumb smaller than the others; the whole space among spines also keratinized, connecting their

bases. Scutes poorly developed on upper surfaces of finger tips; small dermal folds with rounded margins on the joints of distal phalanges; fringes on fingers poorly developed. Carpal tubercle rounded; thenar tubercle elongated, as long as the diameter of carpal tubercle; subarticular tubercles rounded, protruding, more developed on finger I; supernumerary tubercles scarce, small (Fig. 10).

Legs slender; the sum of tibia, thigh, and foot lengths 1.7 times the SVL; toes slender, extensively fringed, with truncate, dilated tips; toe lengths $I < II < V < III < IV$. Scutes on upper surfaces of toes more developed than on fingers; small dermal folds with truncate margins on the joints of distal phalanges. Inner metatarsal tubercle large, elongated, protruding; outer metatarsal tubercle small, rounded, protruding;

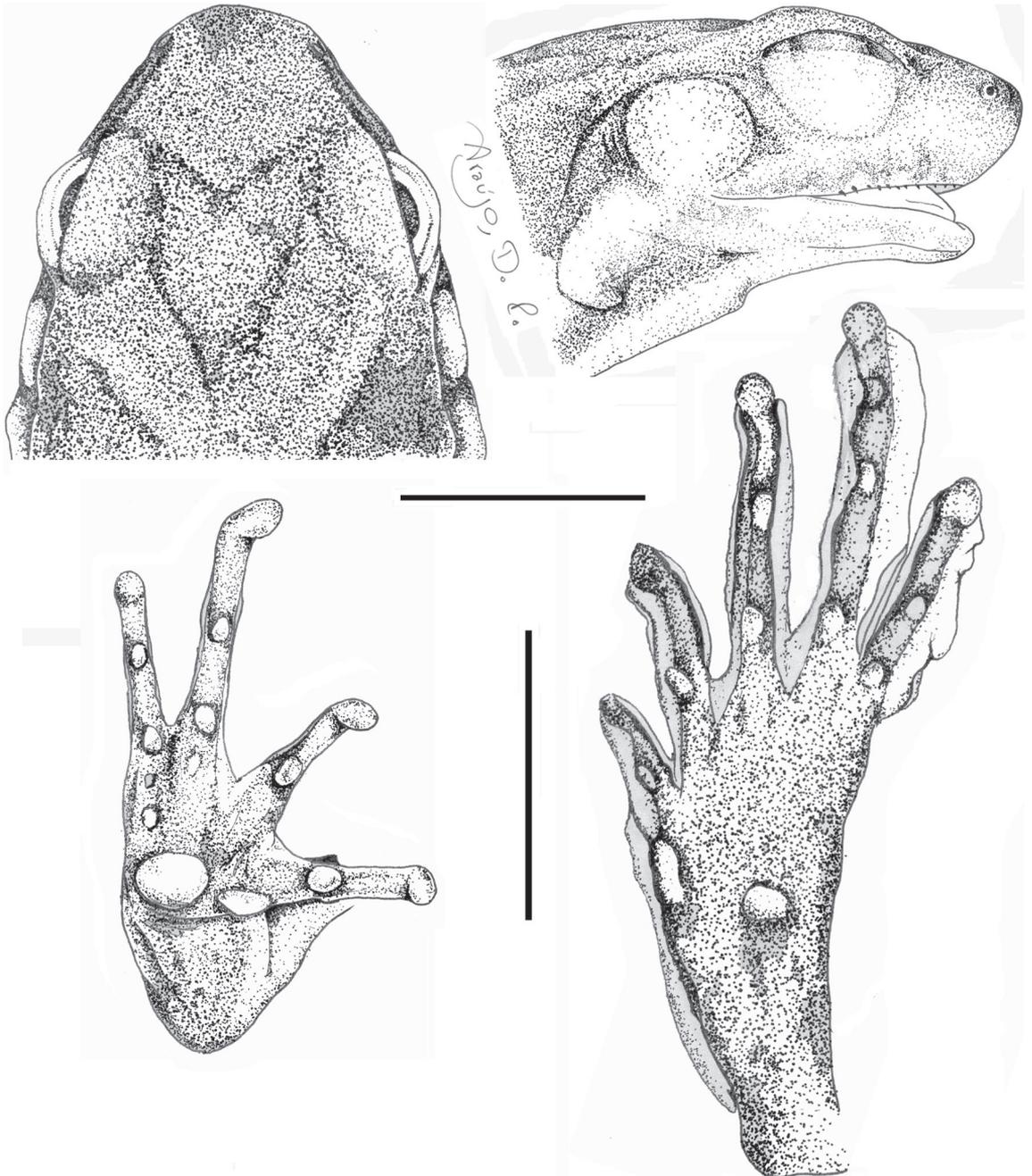


FIGURE 10: *Crossodactylus boulengeri* (De Witte, 1930) comb. nov., topotype (MZUSP 111047, male, SVL 23.0 mm). Dorsal and lateral views of head and ventral views of hand and foot (scale bars = 5 mm).

TABLE 2: Mean, standard deviation (SD), and range of some measurements (in mm) of *Crossodactylus boulengeri*.

	Males (n = 46)			Females (n = 36)		
	Mean	SD	Range	Mean	SD	Range
SVL	24.0	1.32	20.2-27.1	24.6	1.63	20.4-27.8
HL	8.8	0.42	8.0-9.6	8.9	0.48	7.6-10.1
HW	7.7	0.36	7.0-8.7	7.8	0.44	6.7-9.0
TBL	12.1	0.81	10.4-13.8	12.5	0.94	10.0-13.9
THL	11.4	0.67	10.0-13.1	11.7	0.75	10.2-13.2
FL	17.8	1.30	14.5-20.0	18.6	1.32	15.1-20.7
TD	1.7	0.28	1.1-2.2	1.5	0.21	1.1-2.1
ED	2.9	0.34	2.3-3.8	2.7	0.34	2.1-3.7
END	1.7	0.26	1.4-2.4	1.6	0.17	1.3-2.2
NSD	0.9	0.24	0.3-1.6	0.9	0.16	0.6-1.3
IND	3.0	0.37	2.4-3.7	3.0	0.29	2.4-3.6
IOD	2.7	0.40	1.9-3.6	2.7	0.28	2.0-3.5

subarticular tubercles rounded, protruding; no supernumerary tubercles. Fringes joined at base; tarsal fringe very developed, continuous distally with outer fringe of toe I, almost reaching the joint with the tibia; outer fringe of toe V ends after the posterior margin of basal tubercle of toe in a distance approximately equal its diameter (Fig. 10).

Dorsal skin posteriorly granular; a pair of developed dorsolateral glandular ridges from the posterior corner of eyes to inguinal region and another immediately above this one, from the scapular region to inguinal region; cloacal region with scattered granules; dorsal surfaces of thighs and shanks granulated; posterior surface of thighs finely aureolate; flanks and the region between the dorsolateral glandular ridges with many granules; ventral surfaces smooth. Postrictal tubercle very developed, continuous with a thin glandular crest on the upper arm.

In preservative (70% ETOH), general pattern brown; a pair of short oblique dark brown stripes starting at the anterior corner of the inner margins of upper eyelids, meeting at the interorbital region; another pair of longer oblique dark brown stripes starting at the end of the second third of the inner margins of upper eyelids, meeting at the scapular region; a third pair starting at the scapular region and extending to midbody, without meeting each other. Light brown dorsolateral glandular ridge from the posterior corner of eyes to inguinal region; another one immediately above, dark brown. Region from snout to shoulder and tympanum marbled/dotted of dark brown over light brown background; postrictal tubercle and glandular ridge on the arm cream. Region of the vocal sacs below the mouth corners dark brown with cream blotches; a dark-brown stripe from the vocal sacs to the anterior surface of upper arm. Arms light brown with

two brown transverse bars surrounding the elbow and two brown transverse bars on forearm. Legs brown; five dark brown narrow transverse bars on thighs and four on shanks and tarsus-foot. Sacral granules dark brown. Ventral surfaces light brown; gular region and chest marbled of brown; belly reticulated. Hands and feet heavily dotted of dark brown with light brown tubercles; fringes cream, but translucent, with a few dark brown minute dots.

Measurements of the topotype: SVL 23.0; HL 8.3; HW 7.2; TBL 10.8; THL 10.8; FL 16.5; TD 1.3; ED 2.9; END 1.6; NSD 0.9; IND 2.4; IOD 2.3.

Variation: In males, forearms are slightly thicker than upper arms and finger bases are enlarged, making females' fingers look longer; only the base of finger I is enlarged in females. Males MZUSP 109687 and MZUSP 109703 present four spines on the right hand; the two larger spines seem "merged", whereas the other two are smaller than normal. In some females thumb spines and the postrictal tubercle is not observed, as well as the glandular crest on the anterior surface of the arm. Finger tips are more dilated than in males. Toe and tarsus fringes are reduced in females. Transverse bars on thighs vary from three to five. Degree of marbling on gular region, chest, and belly is also highly variable, ranging from nearly absent to extensively stained. Some specimens present partial oblique lateral stripe. Morphometric variation is shown in Table 2.

Distribution, natural history, and conservation status: *Crossodactylus boulengeri* is currently known from a narrow portion of Serra do Mar between the states of Rio de Janeiro and São Paulo, from the Municipality of São José do Barreiro to the Municipality of Santo André, State of São Paulo, Brazil (Fig. 11). We verified it is the same species recorded as *C. dispar* in Angra dos Reis, State of Rio de Janeiro, by Cochran (1955 "1954"). It is probably syntopic with *C. dispar* in São José do Barreiro, since it was very common to find mixed lots of specimens deposited in museums during this study. There are no records in literature or jar labels concerning the habitats used by both species at Serra da Bocaina. The information on natural history provided by Verdade *et al.* (2009) for this species (as *C. dispar*) was based on information from Heyer *et al.* (1990) on *C. dispar* from Boracéia.

Crossodactylus boulengeri is not collected since March 1970, when specimen EI 9941 was caught at Paraty, State of Rio de Janeiro. It was apparently very abundant at Serra da Bocaina; many of the specimens

examined belong to large lots collected within periods of a few days. It disappeared from the type locality well before, where it last specimens were collected in 1958. Verdade *et al.* (2009) reported on serious environmental damages at Paranapiacaba due to the heavy pollution from Cubatão, an industrial town at the lowlands of the State of São Paulo, during the late 1970's and early 1980's. These damages included water acidification, which would pose a serious threat to stream-dweller species, like *Crossodactylus*. According to these authors, many species that declined or disappeared in Boracéia also declined or became locally extinct at Paranapiacaba. However, there is a significative time gap from the disappearance of *C. boulengeri* in Paranapiacaba to the emission of pollution in Cubatão. Hence, two hypotheses emerge: first, researchers were not able to detect specimens of *C. boulengeri* after 1958 and the species disappeared later due to environmental changes; second, pollution was not responsible for the decline of *C. boulengeri* in Paranapiacaba.

Tadpole: Bokermann (1963) and Weber & Caramaschi (2006) described the external morphology and the oral internal morphology, respectively, of a tadpole referred to as *C. dispar* from Paranapiacaba. Although Bokermann (1963) stated that there was no doubt in associating the tadpole described to the form occurring at Paranapiacaba, because it was the only *Crossodactylus* known to occur there, we found another different species from this locality deposited in Brazilian collections and not yet described. Hence, it is not possible for the moment to know to which species the described tadpoles belong. The new species from Paranapiacaba has never been explicitly associated with *C. dispar*, so its description is beyond the scope of the present study.

Remarks: We were not able to borrow the holotype of *Crossodactylus boulengeri* due to curatorial policy (G. Lenglet, *pers. comm.*). However, the analysis of the available topotypes and of high quality photographs of the holotype provided by Dr. Georges Lenglet (IRSNB) allowed us to recognize *C. boulengeri* as a slender species, thus distinct from *C. dispar*. As previously mentioned, we refer the paralectotypes of *C. dispar* USNM 96738 and USNM 96740 to *C. boulengeri*.

It is also clear from the photographs of the type that it presents an undefined, light, marbled/dotted area from snout to shoulder. Moreover, its snout is not rounded, as stated in the original description, but is deformed due to preservation; all topotypes show

nearly pentagon-shaped snouts. De Witte (1930) stated that the SVL of the type of *Crossodactylus boulengeri* was 29 mm. Dr. Georges Lenglet (IRSNB) kindly re-measured the type and found its SVL to be 26.4 mm.

A. Lutz (1925) mentions the occurrence of black spots on the throat and chest of *C. dispar*, a character we have not observed on any of the analyzed specimens. It is in fact a character state found on specimens of *C. boulengeri*.

We have not found the specimens referred to as *Crossodactylus* sp. aff. *dispar* by Haddad & Sazima (1992) from Serra do Japi, Municipality of Jundiá, State of São Paulo, in the collections visited. However, we examined the specimen figured in that publication, collected at the Cidade Universitária "Armando Salles de Oliveira", Municipality of São Paulo (ZUEC 2268). It is a small slender specimen, similar to *C. boulengeri*, but the lack of other specimens from the same locality for comparison with topotypes hindered the safe association with this name. If it is confirmed to be *C. boulengeri*, this would be the most recent record for this species, since it was collected in December 1972.

***Crossodactylus grandis* B. Lutz, 1951** **Figures 12-13**

Crossodactylus dispar grandis B. Lutz, 1951 – B. Lutz, 1952.

Crossodactylus dispar – Cochran, 1955 "1954" (part).
Crossodactylus grandis – Lynch, 1971; Caramaschi & Sazima, 1985.

Holotype: MNRJ 3285, male (Fig. 12), collected at Brejo da Lapa (22°21'S, 44°44'W; 2,200 m a.s.l.; coordinates taken from Caramaschi & Pombal, 2006), Parque Nacional do Itatiaia, Municipality of Itamonte, State of Minas Gerais, Brazil, on 29 March 1951.

Paratypes: According to B. Lutz (1952), "eleven specimens with the same collection data", now MNRJ 14238-14247 (three males, five females, and two unsexed specimens) and MNRJ 38969 (male).

Diagnosis: (1) body robust; (2) head wider than long; (3) snout rounded in dorsal and lateral views; (4) *canthus rostralis* rounded; (5) tympanum poorly distinct, upper part of *annulus tympanicus* partially hidden by supratympanic fold; (6) vocal sac median, subgular; (7) thumb spines developed or strongly developed; (8) males with reduced or moderate fringes on toes and tarsi, females with reduced fringes; (9) finger

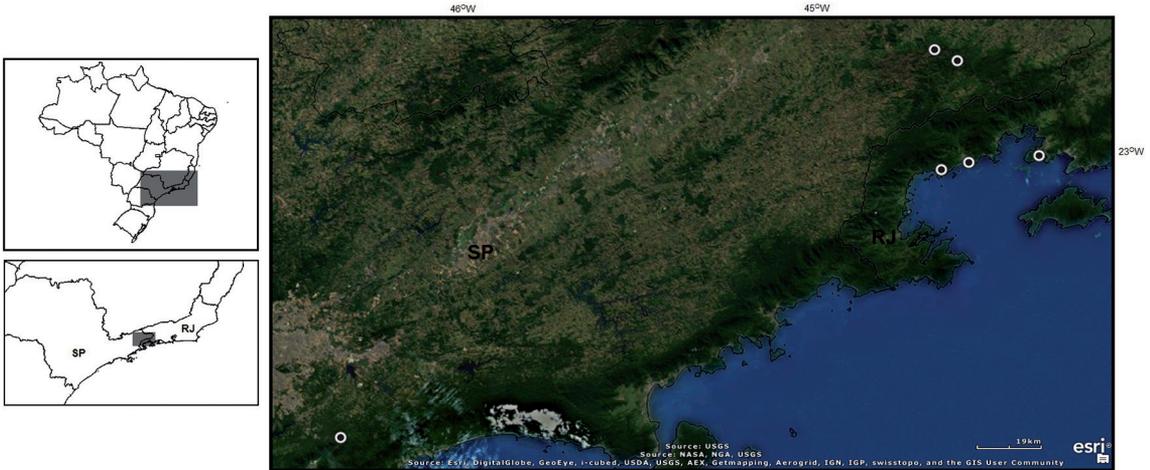


FIGURE 11: Geographic distribution of *Crossodactylus boulengeri* (black dots). RJ = State of Rio de Janeiro; SP = State of São Paulo.



FIGURE 12: *Crossodactylus grandis* B. Lutz, 1951, holotype (MNRJ 3285, SVL 39.0 mm).

tips rounded, undilated; (10) toe tips rounded, undilated; (11) postriental tubercle fragmented into a line of small granules; (12) presence of a glandular crest on the anterior surface of the arm; (13) dorsal skin posteriorly granular; (14) presence of dorsal and dorsolateral glandular ridges; (15) a poorly delimited

area marbled of brown between snout and shoulder; (16) no oblique lateral stripe; (17) belly immaculate.

Comparison with other species: Refer to the account of *C. dispar* for the differences between this species and *C. grandis*. Character states for the other species of *Crossodactylus* are shown in parenthesis. *Crossodactylus grandis* is readily separated from the other species of *Crossodactylus* due to the wider than long head (longer than wide), poorly distinct tympanum (distinct), reduced or moderate fringes on toes and tarsi of males (extensive), undilated fingers (dilated), postriental tubercle fragmented (continuous), and larger males (male SVL 31.5-42.0 mm in *C. grandis*; combined SVL of males of the other species 18.7-30.4 mm).

Crossodactylus grandis further differs from *C. boulengeri*, *C. caramaschii*, *C. dantei*, and *C. lutzorum* due to its rounded snout in dorsal view (nearly pentagon-shaped; variable in *C. aeneus* and *C. gaudichaudii*) and from these species and *C. aeneus*, *C. bokermanni*, *C. cyclopinus*, *C. gaudichaudii*, and *C. trachystomus* due to its rounded *canthus rostralis* (sharp). It is distinguished from *C. caramaschii*, *C. dantei*, and *C. lutzorum* due to its median, subgular vocal sac (bilobate, subgular in *C. caramaschii*; unexpanded in *C. dantei* and *C. lutzorum*) and from *C. aeneus*, *C. caramaschii*, *C. cyclopinus*, and *C. gaudichaudii* by the developed or strongly developed thumb spines (small). *Crossodactylus grandis* is separated from *C. aeneus*, *C. bokermanni*, *C. caramaschii*, *C. cyclopinus*, *C. gaudichaudii*, and *C. trachystomus* by the rounded toe tips (truncate), from *C. aeneus*, *C. caramaschii*, *C. cyclopinus*, *C. dantei*, *C. gaudichaudii*, *C. lutzorum*, and *C. schmidti* due to the presence of a glandular crest on the anterior surface of the arm (absent), and from *C. lutzorum* and *C. schmidti* due to the presence of

dorsal and dorsolateral glandular ridges (absent). It differs from *C. bokermanni*, *C. caramaschii*, *C. cyclopinus*, *C. schmidtii*, and *C. trachystomus* due to the presence of a poorly delimited area marbled of brown between snout and shoulder (uniform white or cream stripe between snout and shoulder) and from *C. aeneus*, *C. bokermanni*, *C. cyclopinus*, *C. gaudichaudii*, and *C. trachystomus* by the absence of an oblique lateral stripe (present; variable in *C. boulengeri*, *C. caramaschii*, and *C. schmidtii*). *Crossodactylus grandis* is distinguished from *C. bokermanni*, *C. boulengeri*, *C. caramaschii*, *C. cyclopinus*, and *C. trachystomus* by its immaculate belly (reticulated in *C. bokermanni*, *C. boulengeri*, *C. caramaschii*, and *C. trachystomus*;

with brown scattered blotches and short stripes in *C. cyclopinus*) and from *C. bokermanni*, *C. boulengeri*, *C. caramaschii*, *C. lutzorum*, and *C. trachystomus* by its larger females (SVL 29.6-39.2 mm in female *C. grandis*; combined SVL 20.4-27.5 mm in females of these species).

Description of the holotype (Fig. 13): Body robust. Head wider than long; nostrils located dorsolaterally, directed anterolaterally, closer to the tip of snout than to the eye. Snout approx. 30% of HL, rounded in dorsal and lateral views (although slightly protruding in lateral view). *Canthus rostralis* rounded, straight; loreal region oblique, slightly concave. Eyes approx.

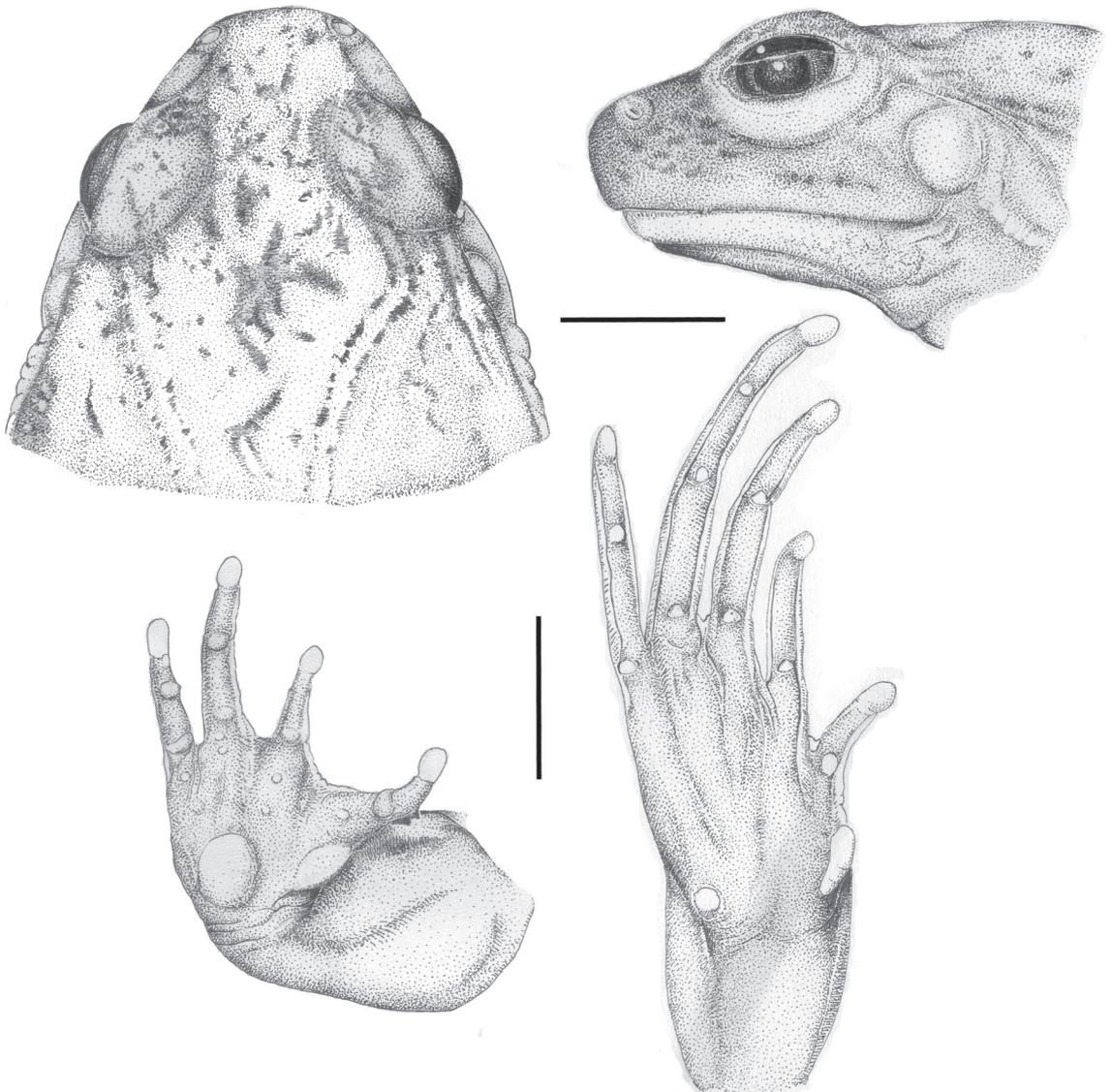


FIGURE 13: *Crossodactylus grandis* B. Lutz, 1951, holotype (MNRJ 3285, SVL 39.0 mm). Dorsal and lateral views of head and ventral views of hand and foot (scale bars = 5 mm).

38% of HL, prominent. Tympanum poorly marked, approx. 36% of ED, rounded; supratympanic fold well developed, partially hiding the upper part of *annulus tympanicus*, extending from the posterior corner of the eye to the shoulder (Fig. 13). Vocal sac median, subgular. Upper lip spines developed, black, appearing on the whole extension of lip. Tongue large, ovoid, covering almost the whole mouth floor, not notched behind. Choanae small, ovoid, distant from each other. No vomerine teeth.

Arms and hands robust; forearms thicker than upper arms; fingers slender, undilated; finger lengths II<I-IV<III; three strongly developed spines on each thumb, arranged triangularly; the whole space among spines also keratinized, connecting their bases; the spine on the inner margin of thumb is smaller than the others. Scutes poorly developed on upper surfaces of finger tips; small dermal folds with rounded margins on the joints of distal phalanges; fringes on fingers poorly developed. Carpals tubercle rounded, close to the ovoid thenar tubercle, their sizes nearly equal; subarticular tubercles rounded, protruding, more developed on finger I (Fig. 13); no supernumerary tubercles.

Legs robust; the sum of tibia, thigh, and foot lengths 1.6 times the SVL; toes slender, long, with reduced fringes and rounded, undilated tips; toe lengths I<II<V<III<IV. Scutes on upper surfaces of toes more developed than on fingers; small dermal folds with truncate margins on the joints of distal phalanges. Inner metatarsal tubercle elongated, protruding; outer metatarsal tubercle small, rounded, protruding; subarticular tubercles rounded, protruding, more developed than on fingers; no supernumerary tubercles. Fringes joined at base; tarsal fringe reduced, continuous distally with outer fringe of toe I, almost reaching the joint with the tibia; outer fringe of toe V ends right after the posterior margin of basal tubercle of toe (Fig. 13).

Dorsal skin posteriorly granular, presenting a pair of dorsolateral glandular ridges from the posterior corner of the eye to the inguinal region. A pair of short oblique glandular ridges from the upper eyelids to the median region of the body, meeting at the end of the head; a second pair of oblique glandular ridges from the upper eyelids towards the median region of the body, diverging at the plan of arms insertion becoming parallel and fragmented, following to the cloacal region. Other ridges and granules scattered on dorsum, sometimes forming short lines. Flanks with scattered granules; cloacal region nearly smooth. Postrectal tubercle fragmented into four small granules disposed in line, very close to each other. Ventral surfaces smooth. It is possible to observe a large

TABLE 3: Mean, standard deviation (SD), and range of some measurements (in mm) of *Crossodactylus grandis*.

	Males (n = 41)			Females (n = 28)		
	Mean	SD	Range	Mean	SD	Range
SVL	36.7	2.39	31.5-42.0	34.5	2.63	29.6-39.2
HL	13.0	0.90	11.2-14.7	12.1	0.78	10.7-13.6
HW	13.9	0.99	12.1-16.0	12.7	1.07	10.6-14.4
TBL	16.3	0.96	14.4-17.8	15.8	0.95	14.1-17.4
THL	17.0	1.30	13.6-19.7	16.2	1.46	13.8-18.8
FL	26.3	2.07	22.2-29.7	25.1	1.74	22.6-28.6
TD	2.0	0.31	1.6-3.2	2.0	0.40	1.0-2.6
ED	3.9	0.47	3.0-4.8	3.8	0.50	2.8-4.7
END	2.2	0.31	1.6-3.0	2.2	0.31	1.7-2.7
NSD	1.2	0.30	0.7-2.3	1.3	0.31	0.9-2.1
IND	3.6	0.47	2.6-4.7	3.6	0.45	2.9-4.7
IOD	3.4	0.52	2.6-4.6	3.5	0.59	2.7-4.6

concentration of small glands under the skin on the anterior part of the thighs.

In preservative (70% ETOH), general pattern light brown with brown glandular ridges and granules. Region from snout to shoulder and tympanum marbled/dotted of dark brown over brown background. Arms with dark brown blotches; legs with four poorly distinct brown transverse bars. Venter cream; glandular region of thighs yellowish.

Measurements of the holotype: SVL 39.0; HL 12.4; HW 13.5; TBL 18.0; THL 17.8; FL 26.0; TD 1.7; ED 4.7; END 2.5; NSD 1.3; IND 4.0; IOD 4.0.

Variation: Determination of sex in *Crossodactylus grandis* is difficult, because both sexes have very thick forearms and moderate fringes on toes and tarsi are observed only in very large males, as well as the black keratinized spines on the upper lip (used as a diagnostic character in B. Lutz, 1951). However, thumb spines in females are less developed than in males. No variation on number of thumb spines was observed. Some specimens show a glandular ridge, normally fragmented, between the dorsolateral ridge and the second pair of oblique ridges, from the region of arms insertion to inguinal region. General color pattern varies from brown to dark brown. Some specimens present a fragmented vertebral line from the interorbital region to the vent. Throat, chest, and anterior portion of the belly light brown and posterior portion of belly cream in darker specimens. Morphometric variation is shown in Table 3.

Vocalization: Unknown. B. Lutz (1951, 1952) mentioned that the advertisement call resembles a "Paludicola-like croak", similar to that emitted as a prelude

to the trilled advertisement call of other species of *Crossodactylus*.

Distribution, natural history, and conservation status: *Crossodactylus grandis* was known only from the type locality at Parque Nacional do Itatiaia, in the borders of the states of Minas Gerais and Rio de Janeiro. Its range is expanded *ca.* 110 km SW, occupying a narrow portion of the Serra da Mantiqueira mountain complex from the type locality to the Municipality of Santo Antônio do Pinhal, State of São Paulo, Brazil (Fig. 14). B. Lutz (1952) reported its occurrence from 1,300 to 2,500 m a.s.l. in the type locality. No data on natural history is available. The last specimen of *C. grandis* which entered collection was caught in October 1969 at Parque Nacional do Itatiaia (ZUEC 10).

Remarks: *Crossodactylus grandis* was originally described as a subspecies of *C. dispar* (B. Lutz, 1951, 1952) due to the similar morphological characters between these. Cochran (1955 “1954”) did not mention this species in her monograph, but we verified that some of the specimens from Serra do Itatiaia she associated with *C. dispar* (AMNH 17050-17052) are in fact specimens of *C. grandis*.

***Crossodactylus timbuby* sp. nov.**

Figures 15-16

Crossodactylus cf. *dispar* – Weygoldt, 1986, 1989.

Holotype: MZUSP 69129, adult male (Fig. 15), collected at Reserva Biológica (REBIO) Augusto Ruschi (formerly REBIO Nova Lombardia; between coordinates 19°45' and 20°00'S, 40°27' and 40°38'W according to IBAMA, no date of publication), Municipality of Santa Teresa, State of Espírito Santo, Brazil, on 01 January 1978, by W.R. Heyer.

Paratypes: MBML 09-13, three males and two females, collected at Estação Biológica de São Lourenço, Municipality of Santa Teresa, State of Espírito Santo, Brazil, in 04/10/1970, by J.P. Agravaya; MBML 14, adult male, collected 6 km NE from “Mata da Reserva”, Municipality of Santa Teresa, State of Espírito Santo, Brazil, in 03/04/1971, by J.P. Agravaya; MBML 3723, adult female, collected at Sítio do Furlani, Lombardia, Municipality of Santa Teresa, State of Espírito Santo, Brazil, in 18/06/2005, by D. Ribeiro and A. Carolina; MNRJ 30440, adult female, collected at the type locality in 08/10/2002 by J.E. Simon; MNRJ 31927, adult female, collected

at the Municipality of Santa Teresa, State of Espírito Santo, Brazil, in 15-16/01/1983, by S.P. Carvalho-Silva, A.L. Izecksohn, and E. Izecksohn; MZUSP 69117-69118 and MZUSP 69120-69121, four adult females, collected at the type locality in 31/12/1977, by W.R. Heyer; MZUSP 69127, adult male, collected with the holotype; USNM 239928-239931, four adult males, collected at the Municipality of Santa Teresa, State of Espírito Santo, Brazil, in 28/07/1980, by P. Weygoldt; USNM 318101, 318103, 318106, 318109-318114, and 318118-318120, two males and ten females, collected near the edge of the type locality (19°50'S, 40°35'W) in December 1977, by R. Crombie, M. Duchene, W.R. Heyer, and F. Val.

Diagnosis: (1) body slender (2) head longer than wide; (3) snout nearly pentagon-shaped in dorsal view, protruding in lateral view; (4) *canthus rostralis* well marked, sharp; (5) tympanum distinct; (6) vocal sac median, subgular; (7) thumb spines small; (8) males with extensively fringed toes and tarsi, females with reduced fringes; (9) finger tips dilated; (10) toe tips truncate, dilated; (11) postrectal tubercle continuous; (12) presence of a glandular crest on the anterior surface of the arm; (13) dorsal skin posteriorly granular; (14) presence of glandular dorsolateral ridges; (15) a poorly delimited area marbled of brown over light brown background between snout and shoulder; (16) no oblique lateral stripe; (17) belly reticulated.

Comparison with other species: Character states for the other species are shown in parenthesis. *Crossodactylus timbuby* promptly differs from *C. dispar* and *C. grandis* by its slender body (robust), head longer than wide (nearly as long as wide in *C. dispar*; wider than long in *C. grandis*), snout nearly pentagon-shaped in dorsal view and protruding in lateral view (rounded in dorsal and lateral views), sharp *canthus rostralis* (rounded), small spines on thumbs (developed or strongly developed), males with extensively fringed feet (moderate in *C. dispar*; reduced or moderate in *C. grandis*), dilated finger tips (undilated), truncate and dilated toe tips (rounded, undilated), continuous postrectal gland (fragmented into small granules), and reticulated belly (immaculate). *Crossodactylus timbuby* is further distinguished from *C. grandis* by its distinct tympanum (poorly distinct) and smaller size (males 20.4-26.9 mm SVL, females 21.9-28.3 in *C. timbuby*; males 31.5-42.0 mm, females 29.6-39.2 mm in *C. grandis*).

Crossodactylus timbuby is separated from *C. aeneus*, *C. dantei*, and *C. gaudichaudii* due to its slender body (robust) and from *C. bokermanni*, *C. cyclospinus*,

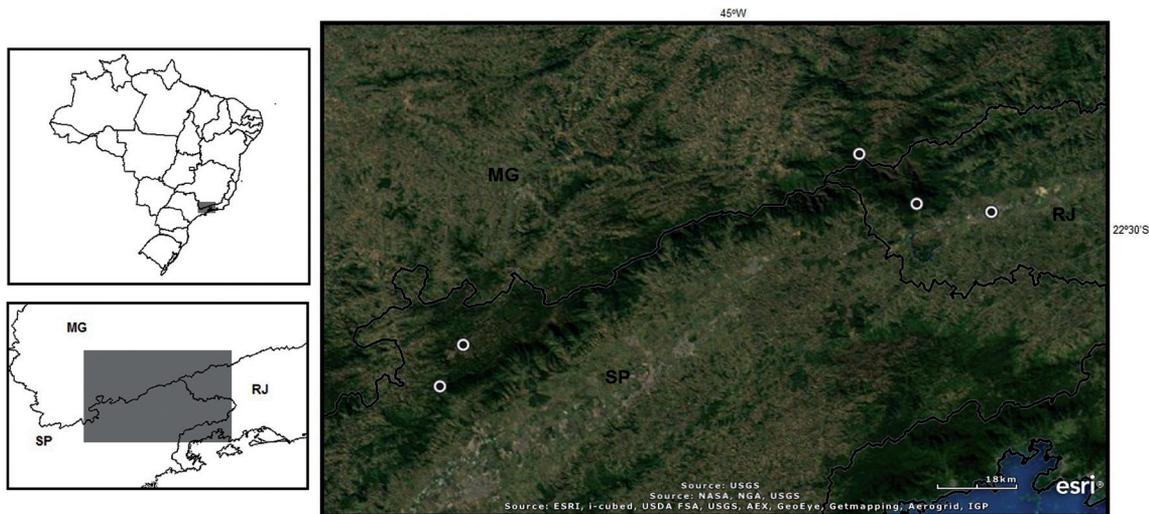


FIGURE 14: Geographic distribution of *Crossodactylus grandis* (black dots). MG = State of Minas Gerais; RJ = State of Rio de Janeiro; SP = State of São Paulo.



FIGURE 15: *Crossodactylus timbuhy* sp. nov., holotype (MZUSP 69129, SVL 22.7 mm). Photo by I. Nunes.

C. schmidtii, and *C. trachystomus* by the nearly pentagon-shaped snout in dorsal view (rounded; variable in *C. aeneus* and *C. gaudichaudii*). *Crossodactylus timbuhy* is distinguished from *C. schmidtii* by its

sharp *canthus rostralis* (rounded) and from *C. boulengeri*, *C. caramaschii*, *C. dantei*, and *C. lutzorum* due to its median, subgular vocal sac (bilobate, subgular in *C. boulengeri* and *C. caramaschii*; unexpanded in *C. dantei* and *C. lutzorum*). It differs from *C. boulengeri* because of its small thumb spines (developed or strongly developed) and from *C. dantei*, *C. lutzorum*, and *C. schmidtii* due to its truncate toe tips (rounded). *Crossodactylus timbuhy* is distinguished from *C. caramaschii* and *C. lutzorum* due to its developed postriatal tubercle (a slight ridge), and from *C. aeneus*, *C. caramaschii*, *C. cyclospinus*, *C. dantei*, *C. gaudichaudii*, *C. lutzorum*, and *C. schmidtii* due to the presence of a glandular crest in the anterior surface of the arm (absent). The presence of dorsolateral glandular ridges separates *C. timbuhy* from *C. cyclospinus*, *C. dantei*, *C. lutzorum*, and *C. schmidtii* (ridges absent in these species). It is separated from *C. bokermanni*, *C. caramaschii*, *C. cyclospinus*, *C. schmidtii*, and *C. trachystomus* by having an undefined, light, marbled/dotted area from snout to shoulder (a white or cream stripe from the snout to the shoulder) and from *C. aeneus*, *C. bokermanni*, *C. cyclospinus*, *C. gaudichaudii*, *C. schmidtii*, and *C. trachystomus* due to the absence of an oblique lateral stripe (present; variable in *C. boulengeri*, *C. caramaschii*, and *C. schmidtii*). *Crossodactylus timbuhy* is distinguished from *C. aeneus*, *C. dantei*, *C. gaudichaudii*, *C. lutzorum*, and *C. schmidtii* due to its reticulated belly (immaculate).

Description of the holotype (Fig. 16): Body slender. Head longer than wide; nostrils situated and directed laterally, closer to the tip of snout than to the eye. Snout approx. 30% of HL, nearly pentagon-shaped in

dorsal view, protruding in lateral view. *Canthus rostralis* well marked, sharp; loreal region oblique, slightly concave. Eyes approx. 32% of HL. Tympanum distinct, approx. 58% of ED, rounded; supratympanic fold weakly marked, extending from the posterior corner of the eye to the shoulder (Fig. 16). Vocal sac median, subgular. Upper lip spines small, white, appearing on the whole extension of lip. Tongue large,

ovoid, covering almost the whole mouth floor, not notched behind. Choanae small, ovoid, distant from each other. No vomerine teeth.

Arms slender; forearms thicker than upper arms; finger tips dilated; finger lengths II-IV < I < III; three small spines on each thumb, arranged triangularly; the spine on the inner margin of thumb is smaller than the others. Scutes poorly developed on upper

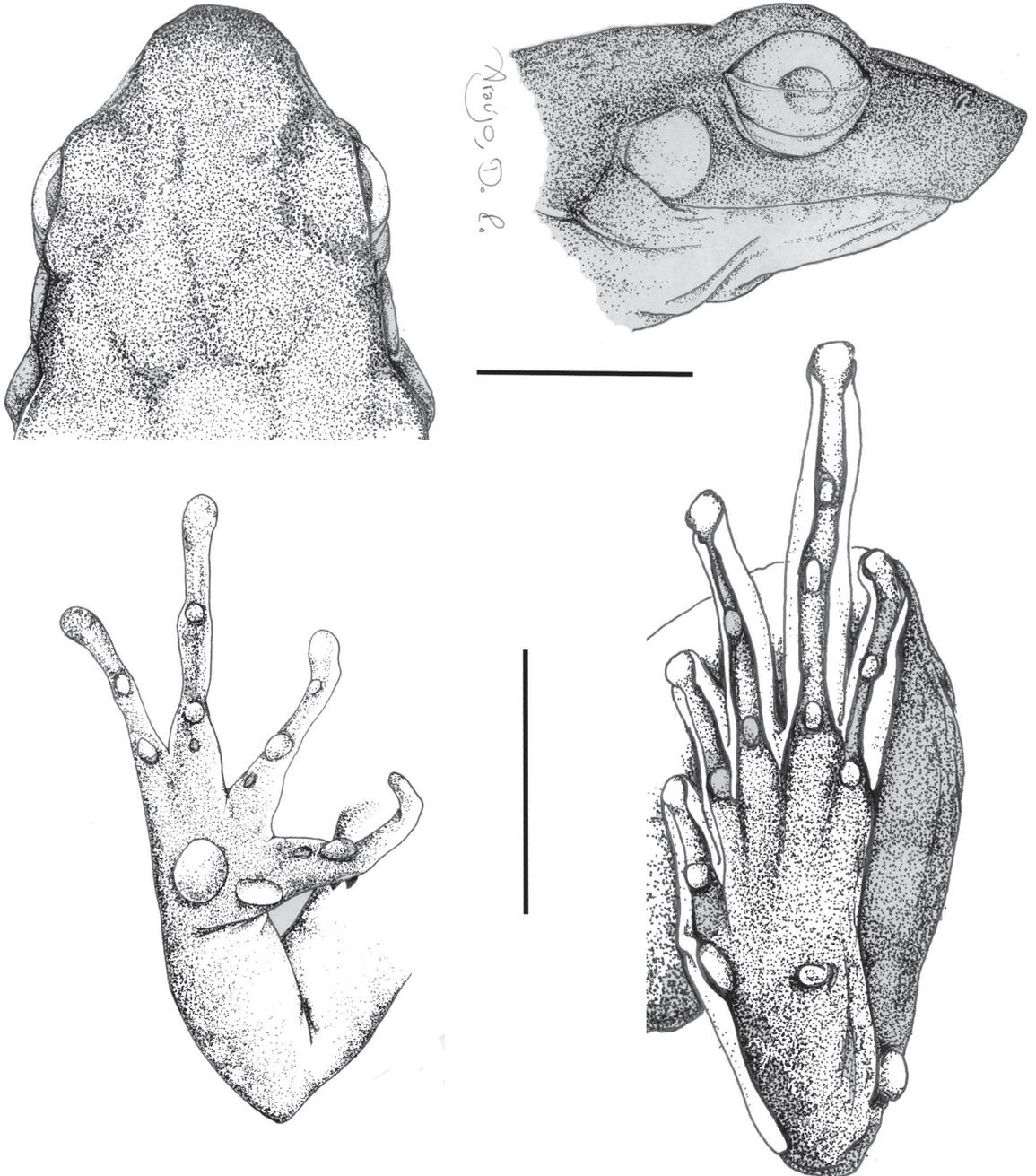


FIGURE 16: *Crossodactylus timbuby* sp. nov., holotype (MZUSP 69129, SVL 22.7 mm). Dorsal and lateral views of head and ventral views of hand and foot (scale bars = 5 mm).

TABLE 4: Mean, standard deviation (SD), and range of some measurements (in mm) of males of *Crossodactylus timbuhy*.

	Males (n = 14)			Females (n = 20)		
	Mean	SD	Range	Mean	SD	Range
SVL	23.2	1.00	20.8-24.9	25.8	1.62	21.9-28.3
HL	8.6	0.34	7.9-9.0	9.2	0.43	8.3-9.7
HW	7.4	0.31	6.8-8.0	7.9	0.41	7.2-8.7
TBL	11.9	0.78	10.7-13.4	12.8	0.59	11.5-13.8
THL	11.0	0.68	9.8-12.1	12.0	0.81	10.8-13.2
FL	17.0	0.83	15.3-18.8	18.2	1.17	15.4-20.0
TD	1.8	0.23	1.5-2.2	1.7	0.16	1.4-2.1
ED	3.1	0.28	2.6-3.5	3.2	0.26	2.9-3.7
END	1.7	0.16	1.5-1.9	2.0	0.18	1.6-2.2
NSD	0.8	0.13	0.6-1.0	0.8	0.14	0.4-1.0
IND	2.9	0.33	2.1-3.4	3.1	0.26	2.6-3.5
IOD	2.6	0.32	2.1-3.2	2.8	0.31	2.4-3.4

surfaces of finger tips; small dermal folds with rounded margins on the joints of distal phalanges; fringes on fingers poorly developed. Carpal tubercle rounded; thenar tubercle elongated, as long as the diameter of the carpal tubercle; subarticular tubercles rounded, protruding, more developed on finger I; supernumerary tubercles scarce, small (Fig. 16).

Legs slender, the sum of tibia, thigh, and foot lengths 1.8 times the SVL; toes slender, extensively fringed, with truncate, dilated tips; toe lengths I<II<V<III<IV. Scutes on upper surfaces of toes more developed than on fingers; small dermal folds with truncate margins on the joints of distal phalanges. Inner metatarsal tubercle large, elongated, protruding; outer metatarsal tubercle small, rounded, protruding; subarticular tubercles rounded, protruding; no supernumerary tubercles. Fringes joined at base; tarsal fringe very developed, continuous distally with outer fringe of toe I, almost reaching the joint with the tibia; outer fringe of toe V ends after the posterior margin of basal tubercle in a distance approximately equal the half of its diameter (Fig. 16).

Dorsal skin posteriorly granular; a pair of weakly marked dorsolateral glandular ridges from the posterior corner of the eyes to the inguinal region; flanks with scattered small granules; cloacal region nearly smooth, with dispersed small granules; legs with scattered granules. Postrectal tubercle continuous; glandular ridge on the anterior surface of the arm extending from half of the arm to the elbow. Ventral surfaces smooth, except for the aureolate posterior surface of thighs.

In preservative (70% ETOH), general pattern brown; glandular ridges dark brown; tympanum and postrectal tubercle cream with scattered brown dots. Flanks brown, progressively lighter from the limit with the dorsum to the limit with the venter. Region from

snout to shoulder and tympanum marbled/dotted of brown over cream background. Two transversal dark brown bars on forearms; dark brown blotch on the anterior surface of upper arm. Five dark brown transversal bars on thighs, four on tibia, and four on tarsus-foot. Ventral surfaces cream with a narrow longitudinal dark brown line on the throat; chest and belly reticulated with brown. Palms of hands and plants of feet cream, blotched with brown; carpal and thenar tubercles brown; fringes cream, but translucent, with small brown dots. Cream tubercles on the lateral of the head, flanks, and sacral region caused by mite infestation.

Measurements of the holotype: SVL 22.7; HL 8.6; HW 7.4; TBL 11.5; THL 11.3; FL 17.3; TD 1.6; ED 2.7; END 1.6; NSD 1.0; IND 2.7; IOD 2.1.

Variation: Upper lip spines are very rare or absent in females. No variation on number of thumb spines was observed. Males present developed fringes on toes and tarsi, which are reduced in females. The glandular crest on the anterior surface of the upper arm extends from the half of the arm to the elbow only in well preserved specimens; dehydrated specimens show this crest from the shoulder to the elbow. Supernumerary tubercles on hands may be abundant, arranged in line on finger bases. Some specimens present a light fragmented vertebral line from midbody to the groin or to the vent. The number of transversal bars on legs varies from three to five, and they may also be poorly marked. Throat, chest, and belly may appear immaculate, but a thorough observation under magnification reveals the presence of faded blotches. The infestation by mites can also occur on throat and belly. Morphometric variation is shown in Table 4.

Vocalization: The advertisement call was briefly described by Weygoldt (1986), where the species is referred to as *Crossodactylus cf. dispar*. According to him, it is a trilled call composed of five or six series of pulses produced on a rate of 9 pulses/second. Frequency ranges from 2.2 to 4.0 kHz.

Etymology: The specific epithet “*timbuhy*” is used as a noun in apposition and refers to the locality which later became the town of Santa Teresa: the nucleus of Timbuhy, Colony of Santa Leopoldina, established by Italian immigrants in 1874 (www.ape.es.gov.br/immigrantes/html/historico.html).

Distribution, natural history, and conservation status: *Crossodactylus timbuhy* is known from the municipalities of Santa Teresa and Cachoeiro de Itapemirim,



FIGURE 17: Geographic distribution of *Crossodactylus timbuhy* sp. nov. (black dots). ES = State of Espírito Santo.



FIGURE 18: *Crossodactylus weneri* sp. nov., holotype (MZUSP 113897, SVL 24.1 mm). Photo by I. Nunes.

State of Espírito Santo, Brazil (Fig. 17). Weygoldt (1986) reported that the species was not very abundant at the type locality, for he was able to found five or six specimens at most on each visit to the creeks of the region. Later on, he reported on the decline of this population (Weygoldt, 1989). However, *Crossodactylus timbuhy* can still be found at Santa Teresa as shown by recent records in different localities of this municipality, including legally protected areas.

Remarks: The museum numbers presented in Weygoldt (1986) for the recording vouchers of *Crossodactylus timbuhy* (USNM 239935-239936) are not correct. An analysis of this collection revealed that the only specimens captured by Weygoldt in Santa Teresa, State of Espírito Santo, Brazil, and identified as *C. dispar* deposited in USNM are 239928-239931.

***Crossodactylus weneri* sp. nov.**
Figures 18-19

Crossodactylus (sic) *vomerinus* – Miranda-Ribeiro, 1926.

Crossodactylus dispar (non A. Lutz, 1925) – Cochran, 1955 “1954” (part); Bastos & Pombal, 1995 (part); Carnaval *et al.*, 2006.

Crossodactylus gaudichaudii (non Duméril & Bibron, 1841) – Carnaval *et al.*, 2006 (part).

Holotype: MZUSP 113897, adult male (Fig. 18), collected at Parque Nacional do Itatiaia (22°26'S, 44°36'W, 1,067 m a.s.l. – coordinates from park facilities taken from Google Earth for reference purposes only), States of Minas Gerais and Rio de Janeiro, Brazil. No data on date, municipality or collector available.

Paratypes: DZSJRP 6047-6049, two males and one female, collected at Parque Nacional do Itatiaia, Municipality of Itatiaia, State of Rio de Janeiro, Brazil, on 18 April 1977, no data on collector available; MZUSP 113869, MZUSP 113873, MZUSP 113875, MZUSP 113882-113883, MZUSP 113886, MZUSP 113889, and MZUSP 113895, eight females, collected at the type locality between 23 and 27 September 1964 by C.A.C Seabra, F.M. Oliveira, and W.C.A. Bokermann.

Diagnosis: (1) body robust; (2) head longer than wide; (3) snout rounded in dorsal view, protruding in lateral view; (4) *canthus rostralis* poorly marked, rounded; (5) tympanum distinct; (6) vocal sac median, subgular; (7) thumb spines developed or

strongly developed; (8) males with developed fringes and females with reduced fringes on toes and tarsi; (9) finger tips dilated; (10) toe tips truncate, dilated; (11) postrictal tubercle continuous; (12) presence of a glandular crest on the anterior surface of the arm; (13) dorsal skin posteriorly granular; (14) presence of glandular dorsal and dorsolateral ridges; (15) a white or cream stripe or a poorly delimited area marbled of brown over light brown background between snout and shoulder; (16) presence of oblique lateral stripe variable; (17) belly immaculate or reticulated.

Comparison with other species: Character states for the other species are shown in parenthesis. *Crossodactylus weneri* is readily separated from *C. dispar* and *C. grandis* due to the head longer than wide (nearly as long as wide in *C. dispar*; wider than long in *C. grandis*), males with extensively fringed feet (moderate in *C. dispar*; reduced or moderate in *C. grandis*), dilated finger tips (undilated), truncate and dilated toe tips (rounded, undilated), and continuous postrictal tubercle (fragmented into small granules). It further differs from *C. grandis* by its distinct tympanum (poorly distinct in *C. grandis*), and smaller size (males 18.6–24.1 mm and females 20.1–28.7 mm SVL in *C. weneri*; males 31.5–42.0 mm and females 29.6–39.2 mm SVL in *C. grandis*).

Crossodactylus weneri is distinguished from *C. bokermanni*, *C. boulengeri*, *C. caramaschii*, *C. cyclopinus*, *C. lutzorum*, *C. schmidti*, *C. timbuhy*, and *C. trachystomus* by its robust body (slender) and from *C. boulengeri*, *C. caramaschii*, *C. dantei*, *C. lutzorum*, and *C. timbuhy* due to its rounded snout (nearly pentagon-shaped; variable in *C. aeneus* and *C. gaudichaudii*). It differs from all species of *Crossodactylus*, except for *C. dispar*, *C. grandis*, and *C. schmidti*, by its rounded *canthus rostralis* (sharp) and from *C. boulengeri*, *C. caramaschii*, *C. dantei*, and *C. lutzorum* due to its median, subgular vocal sac (bilobate, subgular in *C. boulengeri* and *C. caramaschii*; unexpanded in *C. dantei* and *C. lutzorum*). *Crossodactylus weneri* is separated from *C. aeneus*, *C. caramaschii*, *C. cyclopinus*, *C. gaudichaudii*, and *C. timbuhy* by its developed or strongly developed thumb spines (small) and from *C. dantei*, *C. lutzorum*, and *C. schmidti* due to its truncate toe tips (rounded in these species). It is distinguished from *C. caramaschii* and *C. lutzorum* due to its developed postrictal tubercle (a slight ridge), and from *C. aeneus*, *C. caramaschii*, *C. cyclopinus*, *C. dantei*, *C. gaudichaudii*, *C. lutzorum*, and *C. schmidti* due to the presence of a glandular crest in the anterior surface of the arm (absent). The presence of dorsal and dorsolateral glandular ridges separates *C. weneri* from

C. cyclopinus, *C. dantei*, *C. lutzorum*, and *C. schmidti* (ridges absent).

Description of the holotype (Fig. 19): Body robust. Head longer than wide; nostrils located laterally, directed anterolaterally, closer to the tip of snout than to the eye. Snout 28% of HL, rounded in dorsal view, protruding in lateral view. *Canthus rostralis* poorly marked, ending at the line of the nostrils; loreal region oblique, slightly concave. Eyes 33% of HL, prominent. Tympanum distinct, 43% of ED, rounded; supratympanic fold well developed, extending as a concave arch from the posterior corner of the eye to the shoulder (Fig. 19). Vocal sac median, subgular. Upper lip spines small, brown, appearing on the whole extension of lip. Tongue medium, ovoid, narrow, approximately half of mouth floor, not notched behind. Choanae small, ovoid, distant from each other. No vomerine teeth.

Arms and hands robust; forearms thicker than upper arms; finger tips dilated; finger lengths II–IV < I < III; three strongly developed spines on each thumb, arranged triangularly; a thin horny layer between spines, connecting their bases; the spine on the inner margin of thumb smaller than the others. Scutes poorly developed on upper surfaces of finger tips; small dermal folds with rounded margins on the joints of distal phalanges; fringes on fingers poorly developed. Carpal tubercle rounded; thenar tubercle rounded, slightly smaller than carpal tubercle; subarticular tubercles rounded, protruding, more developed on finger I (Fig. 19); no supernumerary tubercles.

Legs robust; the sum of tibia, thigh, and foot lengths 1.7 times the SVL; toes slender, long, extensively fringed, with truncate, dilated tips. Toe lengths I < II < V < III < IV. Scutes on upper surfaces of toes more developed than on fingers; small dermal folds with truncate margins on the joints of distal phalanges. Inner metatarsal tubercle large, elongated, protruding; outer metatarsal tubercle small, rounded, protruding; subarticular tubercles rounded, protruding, as developed as on fingers; no supernumerary tubercles. Fringes joined at base; extensively developed tarsal fringe, continuous distally with outer fringe of toe I, almost reaching the joint with the tibia; outer fringe of toe V ends right after the posterior margin of basal tubercle of toe (Fig. 19).

Dorsal skin posteriorly granular; vertebral glandular ridge low, extending from the interorbital area to sacral region, and a pair of poorly developed dorsolateral glandular ridges from the posterior corner of the eyes to the groin; upper eyelids smooth; a pair of oblique glandular ridges from the upper eyelids,

meeting the vertebral ridge near the sacral region. Flanks smooth; cloacal region covered with scattered, small granules. Postrictal tubercle indistinct; glandular crest on the anterior surface of the arm, from its insertion to the elbow. Ventral surfaces smooth.

In preservative (70% ETOH), general pattern light brown; tympanum, stripe from the snout to the shoulder, and oblique lateral stripe cream. Arms and legs with brown dots and no transversal bars. Ventral surfaces cream; throat, chest, and belly immaculate.

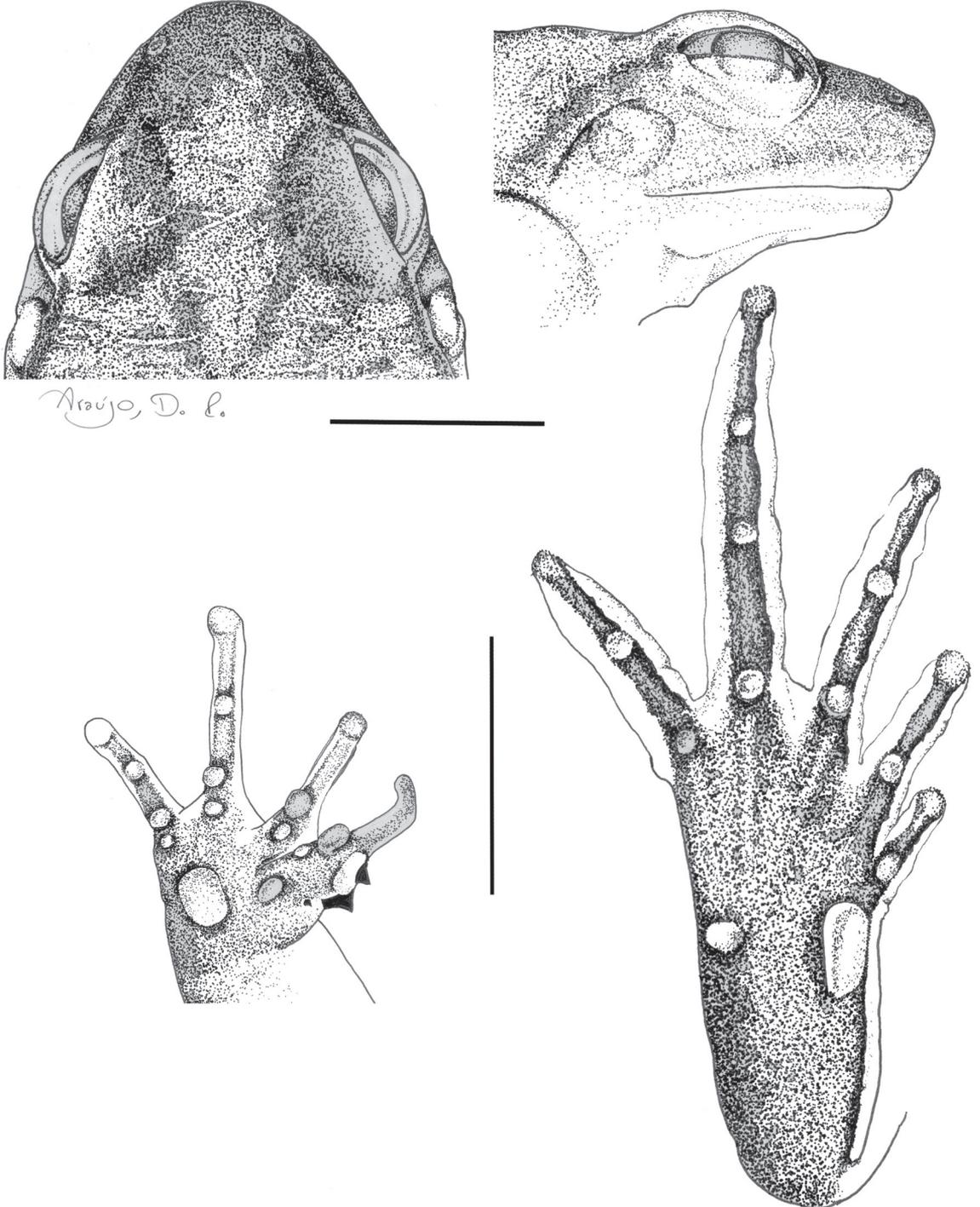


FIGURE 19: *Crossodactylus werneri* sp. nov., holotype (MZUSP 113897, SVL 24.1 mm). Dorsal and lateral views of head and ventral views of hand and foot (scale bars = 5 mm).

TABLE 5: Mean, standard deviation (SD), and range of some measurements (in mm) of *Crossodactylus wernerii*.

	Males (n = 36)			Females (n = 66)		
	Mean	SD	Range	Mean	SD	Range
SVL	22.1	1.20	18.6-24.1	24.1	1.90	20.1-28.7
HL	8.2	0.37	7.1-9.2	8.5	0.53	7.2-10.0
HW	7.4	0.38	6.7-8.5	7.8	0.59	6.7-10.5
TBL	10.2	0.54	8.6-11.3	10.7	0.63	9.0-13.8
THL	10.3	0.80	9.0-12.3	10.6	0.80	8.8-14.4
FL	16.6	0.98	14.7-18.5	17.8	1.22	15.4-23.1
TD	1.4	0.21	1.0-1.9	1.6	0.24	1.1-2.2
ED	2.7	0.18	2.3-3.0	2.8	0.25	2.1-3.8
END	1.5	0.10	1.3-1.7	1.6	0.23	1.3-2.5
NSD	0.8	0.12	0.7-1.2	0.8	0.14	0.6-1.2
IND	2.4	0.24	2.0-3.0	2.6	0.23	2.0-3.1
IOD	2.1	0.28	1.7-2.9	2.3	0.28	1.7-2.9

Palms of hands and plants of feet densely dotted with brown; fringes cream, but translucent.

Measurements of the holotype: SVL 24.1; HL 9.2; HW 8.5; TBL 11.1; THL 11.7; FL 18.4; TD 1.3; ED 3.0; END 1.7; NSD 0.9; IND 2.6; IOD 1.9.

Variation: Fringes on feet are developed in males and reduced in females; forearm is slightly thicker than upper arm in males than in females. Upper lip spines may be absent or white. Up to four spines may be found on thumbs. Most specimens examined present the postrictal tubercle developed, white or cream. Dorsal and dorsolateral glandular ridges may be weak or strongly developed; another glandular ridge may occur immediately under the dorsolateral ridge, from the upper margin of the tympanum to the groin, partially merging with the oblique lateral stripe (when it is present). General color pattern varies from light to dark brown. The region from the snout to the shoulder may show a uniform white or cream stripe or a poorly delimited cream or brown area marbled/dotted with brown or dark brown. Two dark brown transversal bars may be present on arms and four on legs, always poorly marked, but most specimens show irregular dark brown blotches over brown background. Throat, chest, and belly can be immaculate or reticulated. Morphometric variation is shown in Table 5.

Distribution, natural history, and conservation status: *Crossodactylus wernerii* is known from a narrow portion of the Serra da Mantiqueira, from the Parque Nacional do Itatiaia, between the States of Minas Gerais and Rio de Janeiro, to the Municipality of Santo Antônio dos Pinhais, State of São Paulo, and also from

Teresópolis, state of Rio de Janeiro, Brazil (Fig. 20). It is probably syntopic with *C. grandis*, for it was common to find jars with mixed lots of these species in collections. Information on habitat is available only from original jar labels. At the type locality, the species occurred between 1,500 and 2,300 m, whereas in Teresópolis it was found in marshy areas at 1,000 m. However, only one lot with ten specimens collected in April 1945 is available from Teresópolis and we do not discard the possibility of a locality error.

The most recent collected specimens of *C. wernerii* were caught in January 1978 at Parque Nacional do Itatiaia (ZUEC 10126-10127); we found no other records after that despite researchers continued sampling on its range, mainly at this locality.

Etymology: The species name honors the late Professor Werner C.A. Bokermann for his enormous contribution to the knowledge of Brazilian anurans. He collected most of the specimens from Serra da Bocaina and Serra do Itatiaia used in this study, which were crucial to the resolution of the taxonomic issues in *Crossodactylus dispar*.

Remarks: We examined the syntypes USNM 15481-15482 of *Elosia vomerina* Girard, 1853 and also the specimens Miranda-Ribeiro (1926) associated to this taxon under the combination *Grossodactylus* (sic) *vomerinus*. The specimens of Miranda-Ribeiro are smaller, have rounded snout in dorsal view and rounded *canthus rostralis*. We have examined several topotypes which show these same characters. Although the syntypes of *E. vomerina* are poorly preserved, it is possible to observe their nearly pentagon-shaped snouts in dorsal view and sharp *canthus rostralis*. After a direct comparison, we confirmed that *E. vomerina* agrees with *C. gaudichaudii*, as previously established by Cochran (1955 "1954"). Hence, the taxon described by Miranda-Ribeiro (1926) cannot be considered a junior synonym of *E. vomerina*, since he did not apply this name to the same species as Girard (1853). It also cannot be considered a secondary homonym, because the *E. vomerina* of Girard has never been published in combination with the genus *Crossodactylus* (see Article 53, item 53.3 of the ICZN, 1999). However, the Article 49 of the ICZN (1999) states that "A previously established specific (...) name wrongly applied to denote a species-group taxon because of misidentification cannot be used as an available name for that taxon...". Therefore, the name *Crossodactylus vomerinus* Miranda-Ribeiro, 1926 is not available and that is why we described a new species for this taxon.



FIGURE 20: Geographic distribution of *Crossodactylus werneri* sp. nov. (black dots). MG = State of Minas Gerais; RJ = State of Rio de Janeiro; SP = State of São Paulo.

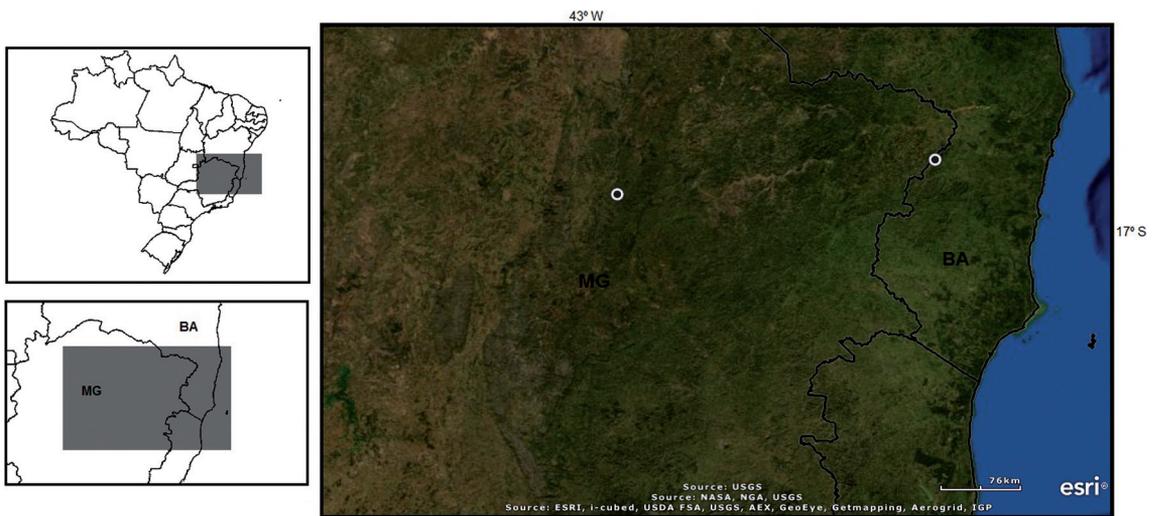


FIGURE 21: Geographic distribution of *Crossodactylus cyclospinus* (black dots). BA = State of Bahia; MG = State of Minas Gerais.

DISCUSSION

With the resurrection of *Crossodactylus boulengeri* and the description of *C. timbuby* and *C. werneri*, *Crossodactylus* is now composed of 14 species. Although taxonomic studies are increasingly relying on DNA sequences to resolve species complexes, morphological characters are still a useful tool in the taxonomy of *Crossodactylus*, allowing the recognition of three species that had been conflated with *C. dispar*. Other species complexes have been addressed recently using morphological characters (e.g., Baldissera *et al.*, 2004; Heyer, 2005; Caramaschi, 2006) and this kind of revision may result in a taxonomic “boom” within

the group studied, because several elements for species diagnosis are provided making identification much easier (for examples, see the case of the Atlantic Rainforest species of *Chiasmocleis* after Cruz *et al.*, 1997 and of the *Hypsiboas polytaeniis* clade after Cruz & Caramaschi, 1998). Hence, we expect other new species of *Crossodactylus* to be found in collections and in the field, increasing the taxonomic knowledge and richness within this group.

During specimen comparisons, we encountered a number of problems with the characters used by Caramaschi & Sazima (1985) to delimit species and groups in *Crossodactylus*. First, *C. trachystomus* possessed a sharp *canthus rostralis* and must be removed

from the *C. dispar* group, currently diagnosed by short, rounded snout and poorly marked *canthus rostralis*, and placed in the group of *C. gaudichaudii*, diagnosed by the acuminate snout and sharp *canthus rostralis*. This state of character is also found in *C. boulengeri* and *C. timbuhy*, so they should be placed in the group of *C. gaudichaudii* as well.

Second, according to the snout shape standards of Heyer *et al.* (1990), no species of the *C. gaudichaudii* group present acuminate snouts. We found rounded or protruding snouts in lateral view. Thus, the only putative morphologic apomorphy supporting this group is the sharp *canthus rostralis*.

Third, the *C. schmidti* group is currently diagnosed by very short snout, rounded *canthus rostralis*, and large interorbital distance (IOD). As mentioned above, the short snout of the holotype of *C. schmidti* was misfigured or it is an anomalous specimen, since other specimens do not show this state of character. Regarding IOD, relative measurements of all species overlap. Hence, these characters should not be used to diagnose this group. Moreover, the rounded *canthus rostralis* is a character state shared with the *C. dispar* group. As such, we found no apomorphies supporting the group of *C. schmidti*.

Crossodactylus weneri cannot be placed in any of these groups. It could only be placed in the *C. dispar* group if we alter its diagnosis to include character states also found in other species groups. For example, the rounded *canthus rostralis* is shared with *C. schmidti* and the robust body is shared with species of the *C. gaudichaudii* and *C. dispar* groups.

The only phenetic group that might reflect a natural group is that formed by *C. dispar* and *C. grandis*, due to the number of putative morphologic synapomorphies found. This group could be diagnosed by robust body, undilated finger tips, fringes on feet reduced or moderate in males, and postrictal tubercle fragmented into small granules. However, given the fragility of the states and characters which previously based the formation of species groups in *Crossodactylus* and the lack of a phylogenetic analysis for the genus, we do not recommend the use of phenetic groups and refrain from proposing new arrangements or new groups.

We have also ascertained that the circular arrangement of spines on thumbs of *C. cyclospinus*, originally used as a diagnostic character (Nascimento *et al.*, 2005), is only one of the manners which thumb spines can be distributed in this species. The most common arrangement is composed of a row of spines at the outer margin of the thumb and one or two smaller spines at the inner margin (found in eight

thumbs of nine specimens), exactly as observed in specimens of *C. gaudichaudii* with the same number of thumb spines. The circular arrangement in *C. cyclospinus* was found in five thumbs of nine specimens, as well as the arrangement as a 'V', where the vertex is the spine closer to the base of the thumb.

Geographic distribution: Geographic ranges of some species of *Crossodactylus* are apparently related to mountainous complexes in Southeastern Brazil. *Crossodactylus dispar* occurs in the northern portion of Serra do Mar in the States of São Paulo and Rio de Janeiro, from Bananal, at Serra da Bocaina, to Estação Biológica de Boracéia; *C. boulengeri* also occurs at Serra da Bocaina, from São José do Barreiro, State of São Paulo, to Angra dos Reis and Paraty, State of Rio de Janeiro, south to Paranapiacaba, Santo André, State of São Paulo. *Crossodactylus grandis* occurs at Serra da Mantiqueira, between the States of Minas Gerais and São Paulo, very close to the range of *C. dispar* and *C. boulengeri*, but separated from them by the valley of the Paraíba do Sul river. Most of the range of *C. weneri* is within Serra da Mantiqueira in the State of São Paulo, with a disjunct population from Teresópolis, at Serra dos Órgãos (part of the Serra do Mar complex) in the State of Rio de Janeiro. *Crossodactylus timbuhy* is known from two localities at the montane region of the State of Espírito Santo.

Crossodactylus cyclospinus is known from two localities on the banks of the Jequitinhonha river (Pimenta *et al.*, 2008; Fig. 21) and its distribution could be associated with its basin instead of a mountain range as the other species. The coordinates of the type locality of this species presented by Nascimento *et al.* (2005) are incorrect; they refer to a locality at the Municipality of Bandeiras, State of Minas Gerais, ca. 74 km NW from Fazenda Duas Barras. The type locality of *C. cyclospinus* is situated at the coordinates 16°25'S, 40°03'W (CAGC, *pers. obs.*), ca. 300 km W from the record from Cristália presented in Pimenta *et al.* (2008).

Species declines: We are aware that museum data are often inadequate to permit precise inferences of amphibian declines and that dates presented herein as the time species were last collected are only rough estimates of when they probably vanished from nature. Nevertheless, we were surprised by the length of time since most of the species of the former *Crossodactylus dispar* complex were last collected. Only *C. timbuhy* can still be found at known localities. Based on the specimens examined, *C. boulengeri* has not been seen for more than forty years; the other three species of the

C. dispar complex seemed to disappear between the late 1960's and the early 1980's. *Batrachochytrium dendrobatidis*, the chytrid fungus, has been associated to the decline of many anuran populations around the world. Carnaval *et al.* (2006) screened many specimens from Itatiaia and Itamonte, in the Parque Nacional do Itatiaia, and found one infected adult of *Bokermannohyla gouveai* collected in 2005 at Brejo da Lapa. Itatiaia and Itamonte are within the range of *C. grandis* and *C. weneri* [the record of *C. gaudichaudii* for "Itamonte (Parque Nacional de Itatiaia, Brejo da Lapa), MG" in Carnaval *et al.* (2006) is a mistake (A.C.O.Q. Carnaval, *pers. com.*). Specimen MNRJ 3868 of their study is actually MNRJ 31868, from Floresta da Tijuca, Rio de Janeiro]. Some specimens of *C. weneri* from this locality (referred to as *C. dispar* in Carnaval *et al.*, 2006) were screened for the presence of the fungus, with negative results. Specimens of *Crossodactylus* from Eugênio Lefrève, Santo Antônio do Pinhal (within the range of *C. grandis* and *C. weneri*) and Santa Teresa (within the range of *C. timbuihy*) were not infected too. Moreover, the oldest known case of amphibian infection in Brazil dates from 1981 (Carnaval *et al.*, 2006), much later than most of the declines presented herein. These facts alone do not indicate that *B. dendrobatidis* was not the cause or one of the causes of *Crossodactylus* crashes in these localities, but that more research is needed on museum material in order to verify the spatial and temporal distribution of infections throughout Brazil. Heyer *et al.* (1988) related the decline of some species in Boracéia to an unusual severe frost occurred in 1979. It is quite coincident to the disappearance of *C. dispar* from collections (last specimens caught in 1977). The frost in Boracéia could explain the local extinction of *C. dispar*, but other factors may have affected the populations from São José do Barreiro, São Paulo (last recorded in 1976), and Mambucaba, Rio de Janeiro (collected only once, in 1951). To date, no specimens of *C. dispar* have been tested for *B. dendrobatidis*.

Another enigmatic aspect of *Crossodactylus* declines is the temporal gap between disappearances of syntopic species. We verified that populations of *C. grandis* disappeared nine years before *C. weneri* at Parque Nacional do Itatiaia. This also occurred with *C. dispar* and *C. boulengeri*, with the latter disappearing eight years before the former at São José do Barreiro. This observation supports the hypothesis that multiple factors cause declines or local extinctions of species of *Crossodactylus*. At present, we are not aware of any localities where multiple species of this genus occur syntopically.

RESUMO

A análise de exemplares referidos na literatura como *Crossodactylus dispar* A. Lutz, 1925 revelou a ocorrência de várias formas distintas sob esse nome. Verificamos que os síntipos pertencem a duas espécies diferentes e, portanto, designamos um lectótipo para *C. dispar* e associamos os paralectótipos a *Calamobates boulengeri* De Witte, 1930, atualmente considerado sinônimo júnior de *C. dispar* e aqui revalidado sob a nova combinação *Crossodactylus boulengeri*. O status de espécie plena de *Crossodactylus grandis* B. Lutz, 1951, originalmente descrito como subespécie de *C. dispar*, é confirmado e a espécie é redescreta e ilustrada. *Crossodactylus timbuihy* sp. nov. e *Crossodactylus weneri* sp. nov., anteriormente referidas como *C. dispar*, são descritas e ilustradas baseando-se em exemplares oriundos dos estados do Espírito Santo, Minas Gerais, Rio de Janeiro e São Paulo, Brasil. Populações dos estados do Paraná e de Santa Catarina são associadas a *Crossodactylus caramaschii* Bastos e Pombal, 1995. Discutimos padrões de distribuição, organização das espécies em grupos e estado de conservação baseado em dados de museus.

PALAVRAS-CHAVE: Hyloidae; complexo de espécies de *Crossodactylus dispar*; Taxonomia; Distribuição geográfica; Conservação.

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APPENDIX

Additional Specimens Examined

Crossodactylus aeneus (BRAZIL): *Rio de Janeiro*: Cremerie, Petrópolis: EI 722; Guapimirim: EI 2469, 10192-10193, 35987-35988; Cachoeiras de Macacu: MNRJ 38961; Estação Biológica Paraíso, Guapimirim: MNRJ 42293-42327, 42329-42330; Fazenda Guinle, Teresópolis: MNRJ 2702; Garraão, Guapimirim: MNRJ 35985-35986; Parque Estadual dos Três Picos, Cachoeiras de Macacu: MNRJ 47763-47768; Parque Nacional Serra dos Órgãos, Guapimirim/Teresópolis: MNRJ 47930; Sítio Dona Ana, Barreira, Guapimirim: MNRJ 44585-44589.

Crossodactylus bokermanni (BRAZIL): *Minas Gerais*: Água Limpa, km 417 of the BR 135 road, Nova Lima: ZUEC 10806-10809, 10811-10813; Casa de Pedra, Congonhas do Campo: ZUEC 3438; Colégio do Caraça, Santa Bárbara: ZUEC 5025; road from Vespasiano to Conceição do Mato Dentro, Serra do Cipó, Santana do Riacho: CFBH 6249, ZUEC 2200, 2457-2458, 2470, 3344, 3349, all paratypes, CFBH 300, ZUEC 1553, 1566, 1622-1624, 1673, 1677, 1886-1891, 2089, 2201, 2235-2236, 2531-2532, 2540-2541, 2560-2561, 2774, 2867, 3022, 3030; Gorduras, Serra do Curral, Nova Lima: ZSM 31/1947/1-6, paratypes of *C. bresslaui*.

Crossodactylus boulengeri (BRAZIL): *Rio de Janeiro*: Angra dos Reis: USNM 70544, 70546-70548; Mambucaba, Angra dos Reis: MNRJ 48313-48320; Tarituba, Paraty: EI 9941. *São Paulo*: Bonito de Cima, Serra da Bocaina, São José do Barreiro: MNRJ 32000; Campo de Fruticultura da Bocaina, São José do Barreiro: MZUSP 109084, 109090-109091, 109106, 109110, 109113, 109120, 109125-109126, 109129, 109137, 109166, 109171, 109178, 109187, 109198, 109502-109503, 109505, 109510, 109552, 109555, 109558, 109561, 109593, 109596, 109598, 109600-109603, 109607, 109609, 109612-109613, 109615, 109618, 109675, 109677, 109681, 109687, 109689-109690, 109692, 109694, 109698, 109700, 109703-109704; Fazenda do Bonito, Serra da Bocaina, São José do Barreiro: MNRJ 31775, 38968, 48311-48312, 48323; Serra da Bocaina: AL-MNRJ 2073, 2075, 2077, USNM 96626; Paranapiacaba, Santo André: MNRJ 95, 5059, MZUSP 8856-8857, 13867-13868, 111020, 111047-111054.

Crossodactylus caramaschii (BRAZIL): *Paraná*: São José dos Pinhais: DZSJRP 4460, DZSJRP 4466-4477, DZSJRP 4469, DZSJRP 6094-6095, DZSJRP 6294-6295. *Santa Catarina*: Alto Palmeiras, Rio dos Cedros: MNRJ 48505-48506; Corupá: MNRJ 0545, 5634, 5637, 5639-5640, 5644-5645, 5648, 5651, 5664-5671, USNM 66574, 129369-129379; Pirabeiraba: USNM 318235, 318249, 318251; Rio Vermelho, São Bento do Sul: CFBH 4436; Serra de Araraquara, Guaratuba: MNRJ 48510; Timbó: EI 9825-9827. *São Paulo*: Atibaia: CFBH 5200-5201; Botucatu: ZUEC 11422-11425; Caverna do Diabo, Eldorado: ZUEC 1695, 8255-8258, 9191, all paratypes, ZUEC 8255-8258, ZUEC 9090, holotype; Engenheiro Ferraz, São Vicente: ZUEC 2219; Fazenda João XXIII, Pilar do Sul: CFBH 6119-6124, 6128, 6130, 6132, 6136, 6144-6146, 6150, 6152; Guapiara: CFBH 14700, 14714; Parque Estadual da Serra do Mar – PESM, Núcleo Pedro de Toledo, Trilha Rio do Ouro, Peruíbe: CFBH 12248, 12271; Parque Estadual Turístico do Alto Ribeira – PETAR, Iporanga: CFBH 12097; Parque Florestal do Itapetinga, Atibaia: ZUEC 10112-10119, 11413-11414, 11437-11438; PESM, Núcleo Curucutu, Itanhaém: CFBH 15971-15972, 15974; PETAR, Núcleo Santana, Iporanga: CFBH 6298-6300; Pilar do Sul: CFBH 4249, 7554; Ribeirão Grande: ZUEC 13783-13784; S.E.A.R.A., Pariqueira-Açu: ZUEC 12238, paratype.

Crossodactylus dispar (BRAZIL): *Rio de Janeiro*: Mambucaba, Serra da Bocaina: MNRJ 48333-48335. *São Paulo*: Bonito de Cima, Serra da Bocaina: MNRJ 48324-48332; Campo de Fruticultura da Bocaina, São José do Barreiro: MZUSP 75609, 76988, 109476-109487, 109492, 109494-109496, 109674, 109684; Estação Biológica da Boracéia, Salesópolis: MZUSP 4066, 4068-4069, 4141, 6474, 23577-23578, 23584-23589, 23591-23596, 37570-37571, USNM 318197-318201, 318204-318207, 318211-318212, 318214, 318222-318223, 318225, 318227, 318230; Fazenda do Bonito, Serra da Bocaina, São José do Barreiro: MNRJ 48364-48369; Fazenda do Veado, São José do Barreiro: USNM 318185; Posto de Biologia e Criação de Trutas, Bananal, Serra da Bocaina: EI 1176; Serra da Bocaina: AL-MNRJ 2060, 2062-2068, 2070-2072, 2074, MZUSP 23466, USNM 96617, 96619, 96623-96624.

Crossodactylus gaudichaudii (BRAZIL): *Rio de Janeiro*: Floresta da Tijuca, Rio de Janeiro: EI 732-735, 736-739, 7055-7060, MNRJ 1857, 13689, 13692, 26930-26934, 31864-31865, 31917-31919, 40551-40560, 40586, 47983; Parque Estadual da Pedra Branca, Rio de Janeiro: MNRJ 27569-27572, 27610-27611, 27615, 27706-27708, 27725; Parque Lage, Rio de Janeiro: MNRJ 40750-40751; Parque Natural Municipal da Serra do Mendanha, Rio de Janeiro: MNRJ 39067; Rio de Janeiro: EI 740-742, MNRJ 2674, 47982; Rio Trapicheiro, Rio de Janeiro: EI 304-307, MNRJ 1503, 47980-47981.

Crossodactylus grandis (BRAZIL): *Minas Gerais*: Brejo da Lapa, Parque Nacional do Itatiaia, Itamonte: MNRJ 14243, 14247, 48336-48345, 48354-48358. *Minas Gerais/Rio de Janeiro*: Parque Nacional do Itatiaia: MNRJ 14235, 38969, 48412-48413, MZUSP 7913-7914, 7916, 7941, 8058. *Rio de Janeiro*: Macieiras, Serra do Itatiaia, Itatiaia: AMNH 17050-17051, MNRJ 48346-48353, 48359-48363; Maromba, Resende: MNRJ 38962-38966. *São Paulo*: Campos do Jordão: EI 301-303, MNRJ 992, 1979, 10467-10470, MZUSP 110110, 110114, 110116-110117, 110141, 110143, 110145, USNM 164108-164109; Eugênio Lefèvre, Santo Antônio do Pinhal: MZUSP 10949-10951, 11349-11350, 11352-11353, 11356, 11360; Fazenda Lagoinha, Campos do Jordão: MZUSP 110119-110126, 110152-110156; Pico do Itapeva, Campos do Jordão: MZUSP 110166, 110169-110171, 110173-110174, 110176.

Crossodactylus schmidti (ARGENTINA): *Departamento Guarany*: San Vicente, Misiones: CFBH 9495-9497, MZUSP 129278-129279.

Crossodactylus timbuihy (BRAZIL): *Espírito Santo*: Santa Teresa: USNM 200449-200451.

Crossodactylus trachystomus (BRAZIL): *Minas Gerais*: Morro Velho, Nova Lima: MNRJ 2549; Parque das Mangabeiras, Belo Horizonte: MNRJ 37046-37048, 41819, 41822.

Crossodactylus werneri (BRAZIL): *Minas Gerais*: Caxambu: EI 8602-8603; Marmelópolis: EI 2475-2477, 2479, 2481-2486, 2488-2489, ZUEC 3501; Parque Nacional do Itatiaia, Itamonte: MNRJ 38791, 41808-41818, MZUSP 69097, 69099-69100, USNM 146606, 318140, 318144-318146, 318148-318149, 318153, 318155. *Minas Gerais/Rio de Janeiro*: Parque Nacional do Itatiaia: EI 915, 7066, MNRJ 38455-38463, MZUSP 113868-113871, 113873-113875, 113881-113886, 113888-113889, 113891, 113893, 113895-113897. *Rio de Janeiro*: Connection from road BR 354 to Rebouças shelter, km 8.0 to 9.6, next to Parque Nacional do Itatiaia, Itatiaia: ZUEC 7981, 8310-8313, 10127; Lagoa Esgotada, Itatiaia: MNRJ 92, MNRJ 5058; Teresópolis: MNRJ 50911-50920. *São Paulo*: Campos do Jordão: MZUSP 110109; Engenheiro Passos road, km 13, Queluz: EI 7073-7075; Eugênio Lefèvre, Santo Antônio do Pinhal: MZUSP 10952-10954, 11345, 11348, 11364, 11366-11370, 11369, 11371, 11376, 11379-11381, 11385-11387, 11390-11394, 11396, 11400, 11403-11405, 11409, 11412, 11415, 11418-11419, 11421, 13405-13406, 13408-13410, 13413, 13415, 13417-13418, USNM 318192; Pico do Itapeva, Campos do Jordão: MZUSP 110165, 110181, 110184-110188, 110191; Rancho Alegre, Campos do Jordão: MZUSP 110146-110147.

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