Morphological variation of Gomesophis brasiliensis and Ptychophis flavovirgatus (Serpentes, Dipsadidae, Xenodontinae)

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Abstract. Gomesophis and Ptychophis are both monotypic, poorly known genera. They are small, viviparous, opistoglyphous snakes with a semi-aquatic lifestyle. They belong to the tribe Tachymenini and occur in the highlands of southern and southeastern Brazil. Here we present a redescription of their holotypes and expand the species' diagnoses. We report on intraspecific variation, testing the differences amongst disjunctive subpopulations of Ptychophis flavovirgatus, and reporting on the sexual dimorphism of both species. We examined 155 Gomesophis brasiliensis and 52 Ptychophis flavovirgatus for meristic and morphometric character states. Ptychophis flavovirgatus is found in lotic-, clear- and cold-water environments in the Brazilian states of Minas Gerais, Paraná, Santa Catarina, and Rio Grande do Sul. Gomesophis brasiliensis is found in areas with slow-flowing waters, in the mud of wetlands, and along the margins of streams and ponds in the Federal District and Brazilian states of Minas Gerais, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul. Both species can be distinguished from all other Tachymenini genera by following combination of characters: 17/17/15 dorsal scale rows, round pupils, and three scales in contact with the eye. Externally, they can be distinguished from each other by colouration and the presence of keeled dorsal scales in P. flavovirgatus and smooth dorsal scales in G. brasiliensis. We found sexual dimorphism in both species mainly with respect to the number of ventral scales. Amongst the Tachymenini, both Ptychophis and Gomesophis are the only ones that present characters related to the usage of aquatic habitats, although further studies are necessary to assess their phylogenetic relationship and position within Tachymenini.

Key words. Squamata, Tachymenini, taxonomy, holotype redescription, hemipenis, sexual dimorphism, geographic distribution.

Introduction

The members of the tribe Tachymenini Bailey, 1966 are distributed throughout South America (Bailey 1966, Bailey 1981, Franco 2000, Franco et al. 2006) and included in the following genera: Calamodontophis Amaral, 1963; Gomesophis Hoge & Mertens, 1959; Pseudotomodon Koslowsky, 1896; Ptychophis Gomes, 1915; Tachymenis Wiegmann, 1834; Thamnodynastes Wagler, 1830; and Tomodon Duméril & Bibron, 1853 (Bailey 1966, Franco 2000, Franco et al. 2006). The Tachymenini genera are distinguished from other Xenodontinae by the following combination of characters: partially divided nasal (sometimes entire); opistoglyphous dentition with diastema and occasionally reduced numbers of maxillary teeth; low number of ventral scales, with absent or inverted sexual dimorphism (with a higher number of ventral scales in males);

viviparous mode of reproduction; pleuroperitoneal cavity pigmented with melanin; and reduced number of calyces on the hemipenial body and relatively distal division of the sulcus spermaticus (BAILEY 1966, 1981, FERRAREZZI 1994, FRANCO 2000, FRANCO et al. 2006, ZAHER et al. 2009).

Gomes (1915) described *Ptychophis flavovirgatus* as a new genus and species on the basis of a specimen from São Bento do Sul, state of Santa Catarina, Brazil. *Gomesophis* was proposed by Hoge & Mertens (1959) to include *Tachymenis brasiliensis* Gomes, 1918, from Pindamonhangaba, State of São Paulo, Brazil, based on the shape of pupils, number of maxillary teeth, and the articulation between pterygoid and ectopterygoid. Prudente (1993) emphasised that the geographic distribution, general morphology, number of ventrals, dorsal and subcaudals, as well as differences on the hemipenis structure were important to differentiate between the genera *Gomesophis* and *Tachymenis*.

LEMA (1967) described the monotypic genus *Paraptychophis* to accommodate *Paraptychophis meyeri* LEMA, 1967, based on the absence of a maxillary diastema. Hoge & Romano (1969) proposed *Paraptychophis meyeri* with *P. flavovirgatus* to be synonymous because of the variable condition (presence or absence) of the diastema in *P. flavovirgatus*. Porto & Caramaschi (1988) provided further data on the morphology, biology and geographic distribution to *P. flavovirgatus*, confirming Hoge & Romano's synonymy. Lema & Deiques (1992) extended the geographic distribution and provided additional data on the morphology and biology of *P. flavovirgatus*.

Ptychophis flavovirgatus and G. brasiliensis are endemic to the Brazilian Atlantic Rainforest and sympatric in many regions. They are restricted to upland areas with temperate to subtropical mountain climates in southeastern and southern Brazil, (PORTO & CARAMASCHI 1988, LEMA & DEIQUES1992, FRANCO 2000, THOMAS et al. 2006, BÉRNILS 2009).

Here we redescribe both *P. flavovirgatus* and *G. brasiliensis*, expand their diagnoses, and report on their morphological variation at population level. We also examine the sexual dimorphism of both species, and as *P. flavovirgatus* exhibits a disjunctive distribution, we also test the differences amongst its subpopulations.

Material and methods

We examined 52 Ptychophis flavovirgatus (19 females and 33 males), 155 Gomesophis brasiliensis (84 females and 71 males), and 116 specimens of other Tachymenini for comparative purposes. These specimens are housed in the following institutions: Argentina: Instituto Fundación Miguel Lillo (FML), San Miguel de Tucumán, Tucumán; Museu Argentino de Ciencias Naturales (MACN), Buenos Aires. Brazil: Herpetological Collection Alphonse Richard Hoge, Instituto Butantan (IBSP), São Paulo; Coleção Herpetológica da Universidade Federal de Santa Catarina (CHUFSC), Florianópolis, Santa Catarina; Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS), Porto Alegre, Rio Grande do Sul; Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN), Porto Alegre, Rio Grande do Sul; Museu de História Natural "Capão da Imbuia" (MHNCI), Curitiba, Paraná; Museu Nacional do Rio de Janeiro (MNRJ), Rio de Janeiro; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo; Universidade Federal de Viçosa (CHUV), Viçosa, Minas Gerais (Appendix 1).

We took snout-vent lengths (SVL) and tail lengths (TL) with a metal ruler and head measurements with Mitutoyo callipers to the nearest 1.0 and 0.1 millimetre, respectively. Our terminology for pholidosis follows that of Peters (1964), whereas ventral scales were counted using the Dowling (1951) method. Counts and measurements of paired structures are given as right/left. Where no such indication is given, the count was performed on the

right side unless stated otherwise. Our hemipenis terminology follows Dowling & Savage (1960), Myers & Cadle (1994) and Zaher (1999). Methods for preparing preserved hemipenes followed Pesantes (1994), with the subsequent modifications proposed by Zaher & Prudente (2003). Sexes were identified by the presence or absence of hemipenes through a ventral incision at the base of the tail. Hemipenis descriptions follow the system proposed by Zaher (1999).

All statistical analyses were performed with Statistics 7.0 (STATSOFT 2004). We use ANOVA for assessing the sexual dimorphism in the species, considering all variables assessed.

In order to test for differences amongst the geographical subpopulations of *P. flavovirgatus*, we divided the sample into three groups according to geographical proximity and the gaps between them: (MG) for the State of Minas Gerais; (PR+SC) for the States of Paraná and Santa Catarina, and (RS) for the State of Rio Grande do Sul. Then we considered the results of ANOVA (multivariate test of significance) in order to eliminate biases that could be caused by sex-related differences. Finally, we performed a Kruskal-Wallis test to assess if the subpopulations were significantly different for the following character states: number of supralabials, number of infralabials, number of ventrals, number of subcaudals, snout-vent length, and tail length.

Results

Ptychophis flavovirgatus Gomes, 1915 (Figs. 1–4)

1915: Ptychophis flavovirgatus Gomes, Ann. Paulista Med. Cirurg., 4: 128.

1967: Paraptychophis meyeri LeмA, Iheringia Zool., 35: 62.

Holotype: Adult male, IBSP 526, from São Bento do Sul (26°15' S, 49°22' W, 870 m a.s.l.), state of Santa Catarina, Brazil. It was received alive from Antonio Swarowsky Jr. in April 1914. The holotype of *P. flavovirgatus*, IBSP 526 (Figs 1+2), was recovered undamaged after the tragic fire in Instituto Butantan on 15 May 2010.

Diagnosis: *Ptychophis flavovirgatus* is distinguished from all other Tachymenini by the following combination of characters: semi-aquatic habits; 17/17/15 dorsal scale rows; scales roughly keeled, with two apical pits; two pre-ocular scales; three secondary temporal shields; loreal scales square; eight supralabials, third to fifth in contact with orbit; round pupil; ten infralabials, first to fourth in contact with first pair of chin shields and fifth infralabial in contact with second pair of chin shields; 50–68 subcaudals in males, 48–61 in females; 123–137 ventrals in males, 114–126 in females; hemipenis non-capitate and bifurcate only at the apex, poorly defined calyces covered by spinules; centrolineal *sulcus spermaticus*, hemipenial body homogeneously ornamented with small spines, larger at the base; post-ocular portion of the Harderian gland small and cov-

ered by the *adductor mandibulae externus superficialis*; maxillary teeth 16–20, palatine 12–15, pterygoid 17–22, and dentary 18–27.

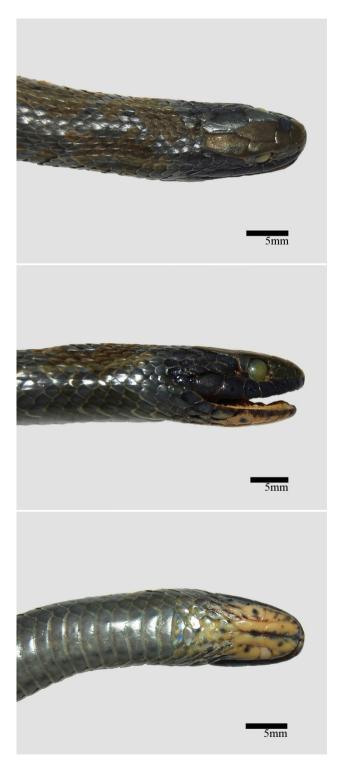


Figure 1. *Ptychophis flavovirgatus*. (Holotype: IBSP 526), adult male in dorsal (top), lateral (centre) and ventral (bottom) views of the head.

Redescription of the holotype (Figs 1–2): Adult male, IBSP 526, snout-vent length (SVL) 380 mm, head length 19.39 mm, and tail length (TL) 125 mm. Stout body, cervical constriction slightly evident. Thin tail, moderately long (24.8% of the total length); TL/SVL 0.33.

Head shields with irregular borders between internasals and prefrontals; rostral small, triangular, slightly visible from above; nasals rectangular (longer than wide) and partially divided on the inferior border; loreal small and square; preoculars paired on the right side (upper larger than lower) and fused on the left; two postoculars on both sides (upper longer than lower); temporals 2+3; internasals as wide as long; prefrontals wider than long; frontal with an irregular pentagonal shape, twice as long as wide; frontal length about twice the distance between frontal and snout; two supraoculars, longer than wide; two parietals longer than wide; snout-parietal distance about twice the parietal length; eight supralabials, third to fifth in contact with orbit, seventh taller than all other supralabials; ten infralabials, fist pair in contact behind symphysial; first five infralabials in contact with first pair of chin shields; fifth infralabial in contact with second pair of chin shields; mental groove conspicuous and relatively deep; primary chin shields similar in size to secondary ones; three gular rows between secondary chin shields and first preventral; five rows of gulars between first preventral and last infralabial; pupils round; eyes and nostrils directed anterodorsally; 17/17/15 dorsal scale rows; dorsals keeled, with two apical pits; 131 ventral scales; anal scute divided; 60 pairs of subcaudal scales; terminal spine acuminate; oral mucous membrane clear; maxillary teeth 17+2, fangs in the rear, with diastema and sulcate fangs.

Colour of the holotype in alcohol (Fig. 2): The general dorsal colour is homogeneously dark with greyish green lines. Top of head uniformly greyish green. A barely defined black postocular stripe, which extends from the postoculars to the last supralabial. A wide, dark brown vertebral stripe (seven to eight scales wide) extends from the nuchal region to the end of the tail. A pair of thin, light brown lines between the fourth and fifth dorsal scale rows, covering half of the upper and lower scales each, extending along the body. Continuous and conspicuous dorsolateral stripes begin in the posterior lateral region of the head, behind the temporal region and run down the entire body (on both sides) as far as the cloacal region, where they continue somewhat faded before fading away completely in the first third of the tail. These lines demarcate the dorsal and paraventral portions of the body, which are of the same colour and shade, as is the dorsal side of the tail. The ventral region of the head is cream in colour, with the mental shields being yellow and spotted with grey. The gulars are yellowish olive and the mental groove is dark grey. The ventrals are greyish with remnants of ventral lines indicated by fine speckling. The ventral colour of the tail is similar to the venter, but sports neither dots nor lines.

Colour in life (Fig. 3): Dorsal sides of head, body and tail dark brown from the snout to the tip of the tail. The dor-

sum is lined on either side with a bright yellow (or white) stripe. These stripes begin in the postocular region and extend to the cloacal region. The paraventral region has the same colour as the dorsum.

Meristic and morphometric variation: Largest male snoutvent length (SVL) 485 mm, tail length (TL) 165 mm (IBSP 27191); largest female SVL 425 mm, incomplete tail (IBSP 53995); largest female tail 145 mm (IBSP 8326); TL/SVL = 0.28-0.40 (n = 32, mean = 0.32, sd = 0.03) in males and 0.18-0.38 (n = 17, mean = 0.32, sd = 0.05) in females; nasals partially divided (n = 29), single (n = 17), or divided (n = 3); supralabials 8 (n = 88 sides), 9 (n = 6 sides), 7 (n =

5 sides), 10 (n = 1 side); third to fifth (n = 93 sides), fourth and fifth (n = 4 sides), or fourth to sixth (n = 3 sides) entering the orbit; infralabials 10 (n = 75 sides), 11 (n = 11 sides), or 9 (n = 14 head sides); first four (n = 82 sides), first five (n = 14 sides), or first six (n = 4 sides) infralabials in contact with primary mentals; infralabials in contact with secondary mentals five and six (n = 73 sides), six (n = 14 sides), five (n = 6 head sides), six and seven (n = 4 head sides), or only seven (n = 2 head sides); preoculars 2 (n = 54 sides) or 1 (n = 46 sides); postoculars 2 (n = 99 sides) or 1 (n = 1 side); temporals 2+2 (n = 23), 1+2 (n = 18), 2+2/1+2 (n = 6), 1+2/2+2 (n = 2), or 1+1/1+2 (n = 1); ventrals 123-137 (n = 33, mean = 130, sd = 3.6) in males and 114-126 (n = 18, mean =



Figure 2. General aspect of Ptychophis flavovirgatus (Holotype IBSP 526), adult male in dorsal (left) and ventral (right) views.



Figure 3. Ptychophis flavovirgatus: dorsal view of a live specimen. Photo: MARCOS DI BERNARDO.

121, sd = 3.1) in females, which suggest an inverted sexual dimorphism; subcaudals 50-68 (n = 33, mean = 58, sd = 4.4) in males and 48-61 (n = 16, mean = 56, sd = 3.4) in females, apical pits: 2 (n = 25), 0 (n = 13), or 1(n = 12); dorsal scale rows 17/17/15 (n = 49), 17/15/15 (n = 1), 17/17/16 (n = 1).

Hemipenis: straight, devoid of ornaments other than spinules and small-sized spines. Slightly bilobate only at the apex, non-capitate and non-calyculate. Bifurcation occurs after a distal constriction on the body, splitting it into two apical lobes with reduced calyces covered by spinules. *Sulcus spermaticus* centrolineal with branches divided in the distal region of the body, below the lobes in the region of constriction. The branches of the *sulcus spermaticus* run to the tip of the respective lobe. Hemipenis uniformly ornamented with rows of small vertical spines, which increase slightly in size from apex to base. The base of the hemipenis is bare (based on IBSP 9346 and ZAHER 1999).

Sexual dimorphism: The ANOVA multivariate test was significant ($F_{0.32} = 14.13$, p < 0.001, n = 50), demonstrating the presence of sexual dimorphism in *P. flavovirgatus*. Univariate tests showed significant levels of sexual

dimorphism only for the number of ventrals ($F_{845} = 73.7$, p < 0.001, n = 50), with higher counts in males than in females (males 123–137, mean = 129.7, sd = 3.5, n = 31; females: 114–135, mean = 121.6, sd = 4.6, n = 18). The other variables did not exhibit a significant sexual dimorphism: number of subcaudals ($F_{47.2} = 2.8$, p > 0.09, n = 50), snout–vent length ($F_{1011} = 0.171$, p > 0.60, n = 50), and tail length ($F_{48.2} = 0.06$, p > 0.80, n = 50).

Geographic distribution (Fig. 4): *Ptychophis flavovirgatus* is associated with lotic-, clear- and cold-water environments (Franco 2000, Lema 2002), where it finds shelter in cavities between stones in the water (Lema & Deiques 1992, Lema 2002). It can be found in the Brazilian states of Minas Gerais, Paraná, Santa Catarina and Rio Grande do Sul (Lema & Deiques 1992, Franco 2000) between latitudes 21°40' and 29°02' S and longitudes 44°18' and 53°54' W. It inhabits the highlands (316–1358 m a.s.l.), mean = 936 m a.s.l.). Most locations at which this species was found are situated above 800 m a.s.l., and the lower localities (316–687 m a.s.l.) are in the State of Rio Grande do Sul, where the climate is seasonal-subtropical under the influence of

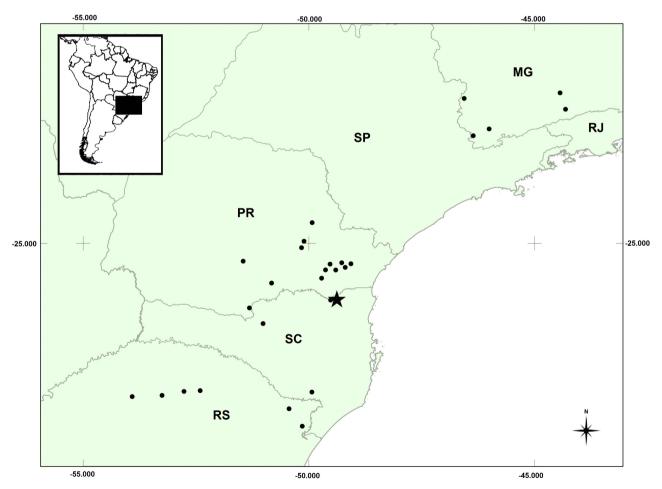


Figure 4. Geographic distribution as indicated by the preserved specimens of *Ptychophis flavovirgatus* used in this work. MG – Minas Gerais state, PR – Paraná state, RJ – Rio de Janeiro state, RS – Rio Grande do Sul state, SC – Santa Cararina state, SP – São Paulo state, star – type locality.

the higher latitudes. At these locations, vegetation can be open or made up of Araucaria forests (Porto & Caramaschi 1988). However, the species has not been recorded from the state of São Paulo, rendering the populations from the Serra Geral and the Serra da Mantiqueira discontinuous (Porto & Caramaschi 1988, Lema & Deiques 1992, Franco 2000). The distribution map of *P. flavovirgatus* shows two more discontinuities in the states of São Paulo and Santa Catarina, resulting in three separate subpopulations, in Minas Gerais (MG), Paraná, and northern Santa Catarina (PR+SC), and in Rio Grande do Sul state (RS).

Gomesophis brasiliensis (Gomes, 1918) (Figs. 5–8)

1918 *Tachymenis brasiliensis* GOMES, Mem. Inst. Butantan, 1(1): 78.

1959 Gomesophis brasiliensis, Hoge & Mertens, Senck. Biol., 40: 242.

Holotype: adult female, IBSP 1316, from Pindamonhangaba (22°55' S, 45°27' W; 552 m a.s.l.), state of São Paulo, Brazil. The specimen was received alive from Ribeiro and Irmãos Ltda in May of 1917 (Gomes 1918). The holotype (Figs 5+6) was probably lost in the fire gutting the herpetological collection of Instituto Butantan.

Paratypes: IBSP 847, adult female, collected by Alfredo Campos in February of 1915 in the municipality of São Paulo (23°32′55″ S, 46°38′20″ W), São Paulo state, Brazil; IBSP 1141, adult female, from Itararé (24°06′54″ S, 49°20′27″ W), São Paulo state, Brazil, collected by Javert Madureira in May of 1916; IBSP 1519, adult female, from São Paulo, found in the grounds of the Butantan Institute, collected by Augusto Esteves in March of 1918; IBSP 1363, adult male; IBSP 1370, adult female; IBSP 1371, adult female; IBSP 1372, adult female; collected by the Brigade Against Mosquitoes of the Sanitary Service in São Paulo in October of 1917 in the ground of Instituto Butantan, municipality of São Paulo, São Paulo state, Brazil.

Diagnosis: Gomesophis brasiliensis can be distinguished from the other Tachymenini by the following combination of characters: semi-aquatic habits; 17/17/15 dorsal scale rows, scales smooth, with one apical pit; one preocular; two secondary temporals; square-shaped loreal; eight supralabials, third to fifth in contact with orbit; round pupil; nine infralabials; first to fourth in contact with the primary chin shields and fifth infralabial in contact with the second pair of chin shields; 34-49 subcaudals in males, 28-42 in females; ventrals 127-151 in males, 117-144 in females. Hemipenis body with longitudinally directed, small spines, larger at the base; centrolineally forked *sulcus spermaticus*; apex calyculate, with spinules. Harderian gland large, in the postocular region, not covered by the adductor mandibulae externus superficialis; maxillary teeth 13-15, palatine 11-17, pterygoid 19-25, and dentary 18-23.

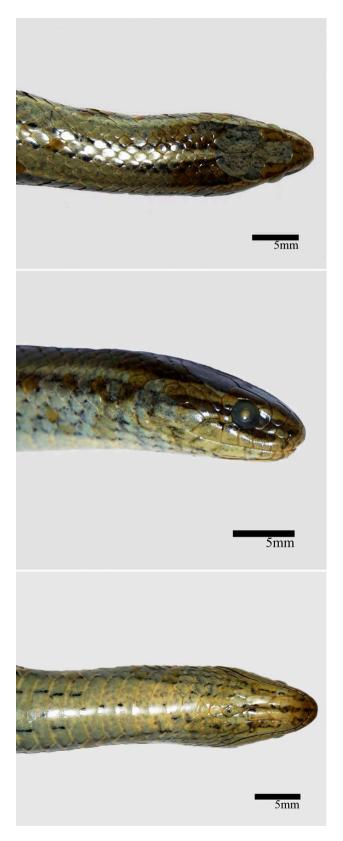


Figure 5. *Gomesophis brasiliensis* (Holotype IBSP 1316), adult female in dorsal (top), lateral (centre) and ventral (bottom) views of the head.

Redescription of the holotype (Figs 5–6): Adult female, SVL 466 mm; head length 14.4 mm; cervical constriction little evident; tail thin and short, TL 72 mm; (13.4% of the total length), body stout.

Head shields with irregular borders between the internasals and prefrontals; rostral small, triangular, little visible in dorsal view, almost as high as wide; nasal rectangular, partially divided on the inferior border; loreal small and square in shape; oculars 1+2 (upper larger than lower); temporals: 2+3/2+2; internasals paired, longer than wide, smaller than the prefrontals; prefrontals wider than long (1.5 ×); frontal with irregular pentagonal shape, twice as long as wide; distance from frontal to snout about twice the frontal length; two parietals, longer than wide; snout-

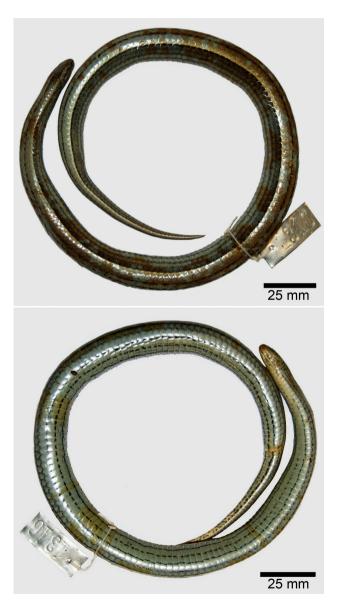


Figure 6. General aspect of *Gomesophis brasiliensis* (holotype IBSP 1316), adult female in dorsal (top) and ventral (bottom) views.

parietal distance 1.1 × parietal length; eight supralabials, third to fifth in contact with orbit, seventh taller than all others; nine infralabials, fist pair in contact behind the symphysial; first four infralabials in contact with first pair of chin shields; fifth infralabial with contact with second pair of infralabials; mental groove conspicuous and relatively deep; primary chin shields similar in size to secondary ones; three rows of gulars between secondary chin shields and first preventral; five rows of gulars between first preventral and last infralabial; pupils round; eyes and nostrils directed anterodorsally; 17/17/15 dorsal scale rows, dorsals smooth, one apical pit; 143 ventrals; 39 pairs of subcaudals, tip of the tail acuminate; oral mucous membrane clear; maxillary teeth 17+2, fangs in the rear, with diastema and sulcate fangs.

Colour of the holotype in alcohol 70% (Fig. 6): Background colour light and uniform greenish brown, with stripes. Top of head uniformly brown, with black spots. Dorsum divided by a vertebral line and four pairs of lateral lines (four on either side), which are arranged as follows: a brown vertebral line from the end of the parietals to the level of the cloacal region, lighter than the more lateral ones, faint and flanked by black dots, thinning and fading away in the form of black points towards the end. This line forms the division between a pair of similar paravertebral stripes that are brownish and extend from the dorsal side of the head as far as the tip of the tail. The second pair of stripes consists of thin, light lines, along the border of the fourth and fifth dorsal rows. They are less than half a scale wide, but in spite of their being narrow, they are much more clearly defined and conspicuous than the other stripes. They begin in the prefrontal region, are interrupted at eye level, and continue from the postocular region to the tail. The third pair of stripes consists of thicker and darker lines (greyish and reticulated with black), two scales wide (third and fourth dorsal rows, in the mediolateral region of the body). They are continuations of the postocular stripes (which begin in the temporal region) and extend as far as the end of the tail. The paraventral stripe (fourth pair) is greyish brown and the same shade as the first pair of longitudinal lines. It begins at the gular scales and is visible as far as the second third of the tail, where it fuses with the lines above it. It is two scales wide (the first and the second dorsal rows); in the middle of this stripe, between the first and second dorsal rows, there is a series of black dots, which extends along the body. A similar dotted line also occurs between the ventrals and the first dorsal row. The mental region is light yellow and the gular region light brown with a tinge of olive green. The venter is clear yellow and exhibits three continuous rows of points on the ventrals. The outer rows extend from the gular region as far as the end of the tail. The middle line, in contrast, begins in the first third of the body and continues as far as the cloaca. Only the lateral series continue on the tail.

Colour in life (Fig. 7): Background colour golden brown, with two thin, darker dorsal stripes, which start on the head (at the level of the parietals) and extend to the base of

the tail. The flanks are marked with a thin light brown line, which begins as a wide postocular stripe and will continue to the tip of the tail. The paravertebral region is darker than the dorsal stripes, i.e., dark brown.

Meristic and morphometric variation: Largest male SVL 520 mm and TL 95 mm (IBSP 1363); largest female SVL 524 mm and TL 83 mm (IBSP 1371); TL/SVL 0.17-0.29 (n = 59, mean = 0.21, sd = 0.02) in males, and 0.14-0.23 (n = 59, mean = 0.19, sd = 0.02) in females; nasals partially divided (n = 111), undivided (n = 17), or divided (n = 3); supralabials 8 (n = 220 sides), 7 (n = 43 sides), 6 (n = 1 side), or 9 (n = 1 side); supralabials three, four and five in contact with the eye (n = 219 sides), three and four (n = 26 sides), two, three and four (n = 12 sides), or four and five (n = 8 sides)sides); infralabials 9 (n = 179 sides), 8 (n = 55 sides), 10 (n =20 sides) or 7 (n = 5 sides); infralabials in contact with primary mentals one through four (n = 220 head sides), one through five (n = 22 head sides), or one through three (n =17 head sides); infralabials in contact with secondary mentals only five (n = 214 head sides), only four (n = 20 head)sides), four and five (n = 20 head sides), five and six (n = 13 head sides), three and four (n = 1 head side), or only six (n = 1 head side); loreal square (n = 127), tall (n = 3), or long (n = 2); preoculars 1 (n = 240 head sides), or 2 (n = 20 head)sides); postoculars 2 (n = 259 head sides), or 1 (n = 3 head sides); temporals 2+2 (n = 85), 2+3 (n = 7), 2+2/2+3 (n = 6), 2+3/2+2 (n = 5), 2+2/1+2 (n = 5), 1+2 (n = 5), 2+1/2+2 (n = 4), 2+2/2+1 (n = 3), 2+3/1+2 (n = 3), or 1+2/2+2 (n = 2). The other combinations, 1+1, 1+3, 2+1/2+1, 2+1/3+1, 2+2/1+1, 2+3/2+1, 3+2/2+2, had only one occurrence each; ventrals 127–151 (n = 64, mean = 136, sd = 4.95) in males and 117–144 (n = 71, mean = 132, sd = 5.6) in females; anal scute divided; subcaudals divided, 34–49 (n = 56, mean = 40, sd = 3.7) in males, and 28–42 (n = 61, means = 35, sd = 3.6) in females; dorsal scales keeled, apical pits 1 (n = 75), o (n = 49), or 2 (n = 9); abbreviated dorsal scale row formulae: 17/17/15 (n = 119), 17/15/15 (n = 15), the combinations 17/17/17, 17/15/13, 17/16/15, 16/17/15 had one occurrence each.

Hemipenis: Hemipenis straight, bilobate only in the apical region; centrolineally forked *sulcus spermaticus*, divided in the second apical third, with branches that run to the tip of the lobes, with reduced calyces covered with spinules; body ornamented with longitudinally directed small spines, larger at the base than at the apex. Sulcate and lateral faces ornamented with vestigial calyces, with large spines forming horizontal rows. Sulcate face with shorter calyces that are larger (wider) than the ones on the lateral and sulcate faces. The base of the hemipenis is bare (based on specimen IBSP 54456 and ZAHER 1999).

Sexual dimorphism: The ANOVA multivariate test of significance was highly significant for the presence of sexual dimorphism in *G. brasiliensis* ($F_{0.58} = 20.31$, p < 0.001, n = 115). Univariate tests were highly significant for the number of ventrals and for the number of subcaudals.

Males have significantly higher ventral and subcaudal scale counts than females (ventrals: $F_{878} = 30.4$, p < 0.001, n = 115; subcaudals: $F_{579.1} = 44.2$, p < 0.001, n = 115). Ventrals



Figure 7. Gomesophis brasiliensis, dorsal view of a live specimen. Photo: MARCOS DI BERNARDO.

vary in males from 127–151 (mean = 136.8, sd = 4.9, n = 56) and in females from 117–144 (mean = 131.3, sd = 5.7, n = 60). Subcaudals vary in males from 34–49 (mean = 39.8, sd = 3.7, n = 56) and in females from 28–42 (mean = 35.4, sd = 3.5, n = 60).

Males had significantly longer tails than females ($F_{1269} = 4.7$, p < 0.004, n = 115): males 20–95 mm (mean = 62.5, sd = 18.4, n = 56) and females 10–83 mm (mean = 55.9, sd = 14.2, n = 60). The snout–vent lengths showed no significant differences in length with this test ($F_{1298} = 0.18$, p > 0.05, n = 115).

Geographic distribution (Fig. 8): Gomesophis brasiliensis is commonly known as the "mud snake" because it occurs in areas with slow-flowing waters, often hiding in burrows dug into the mud of wetlands and margins of streams and ponds (Gomes 1918, Franco 2000, Lema 2002). It can be

found in the Brazilian states of Federal District, Minas Gerais, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul, between latitudes 21°11' and 30°31' S and longitudes 44°57' and 53°27' W (FRANCO 2000, BÉRNILS et al. 2001, GHIZONI JR. et al. 2009, FORTES et al. 2010).

It occurs sympatric, but not syntopic, with *P. flavovirgatus* in most parts of its geographical range. Like *P. flavovirgatus*, it is also restricted to elevated areas (from 427–1235 m a.s.l., mean = 808 m a.s.l.) with high rainfall levels and a cooler climate (Prudente 1993), although it can also be found at lower localities in Rio Grande do Sul because of the cooler subtropical climate.

There are records of two specimens collected in the Federal District, near Brasília, where PRUDENTE & BRANDÃO (1998) found a specimen (UNB 2970) at the Estação Ecológica das Águas Emendadas, Lagoa Bonita (15°35' S, 47°41' W), on 26 May 1992. The other specimen used to be

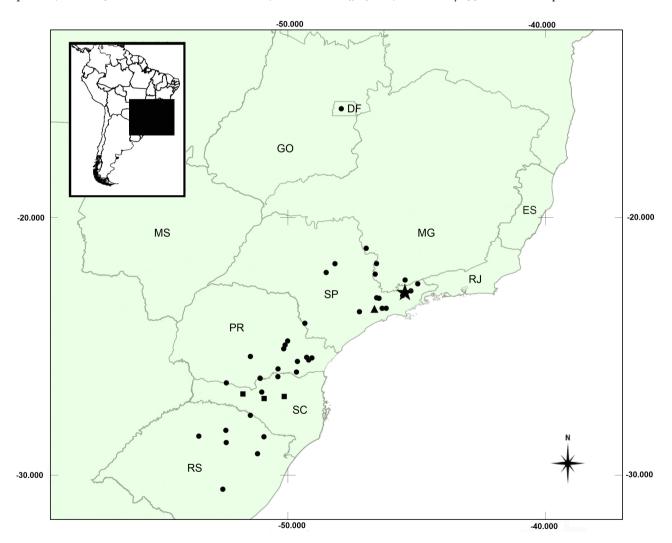


Figure 8. Geographic distribution as indicated by the preserved specimens of *Gomesophis brasiliensis* used in this work. ES – Espírito Santo state, DF – Federal District, GO – Goiás state, MS – Mato Grosso do Sul state, MG – Minas Gerais state, PR – Paraná state, RJ – Rio de Janeiro state, RS – Rio Grande do Sul state, SC – Santa Cararina state, SP – São Paulo state, star – type locality; triangle – locality where paratypes were collected; square – records in the literature not assessed in this work (Bérnils 2001, Ghizoni Jr. et al. 2009, Fortes et al. 2010).

in the collection of Instituto Butantan under the number IBSP 19185; it had been collected near Barragem do Paranoá (15°46' S, 47°55' W) on 17 July 1960.

Discussion

Both *Ptychophis flavovirgatus* and *Gomesophis brasiliensis* have stout and short bodies, round pupils and also share two postoculars, two primary temporals, 17/17/15 dorsal scale rows, and low number of ventrals (118–151 in *G. brasiliensis* and 107–138 in *P. flavovirgatus*). Their eyes and nostrils are directed forward and up, the preocular region is shortened, and they both have three supralabials in contact with the orbit.

Their hemipenes are almost identical: straight, bilobate only in the apical region, the apex has poorly defined calyces, ornamented with small spines, the *sulcus spermaticus* is centrolineal and divided at the apex, and the hemipenis body is homogeneously ornamented with vertical rows of small spines.

Ptychophis flavovirgatus is distinguished from Gomesophis brasiliensis (in parenthesis) by the following characters: moderately long tail (versus short); roughly keeled dorsals (versus smooth); with two apical pits (versus one); two preoculars (versus one); three secondary temporals (versus two); 10 infralabials (versus nine); subcaudals 48-68 (versus 28-49); postocular portion of the Harderian gland small and covered by the adductor mandibulae externus superficialis (versus Harderian gland with moderately large postocular portion not covered by the adductor mandibulae externus superficialis); maxillary teeth 16-20 (versus 13–15), and pterygoid teeth 17–22 (versus 19–25). Hemipenis devoid of ornaments other than spinules and smallsized spines, non-capitate and non-calyculate (versus ornamented with vestigial calyces, with large spines forming horizontal rows).

Ptychophis and Gomesophis are morphologically distinguished from Calamodontophis, Tomodon and Pseudotomodon by the number of maxillary teeth, number of dorsal rows, pupil shape and hemipenis morphology. These genera have a reduced number of maxillary teeth: 7-8 in Calamodontophis and Pseudotomodon, and o-5 in Tomodon (Franco 2000, Harvey & Muñoz 2004, Franco et al. 2006), and they also have undivided nasal plates (FRANco 2000). Ptychophis and Gomesophis, on the other hand, have a pre-diasternal dentition varying from 13 to 20 and a partially divided nasal. In Pseudotomodon, the pupil shape is elliptical and the number of ventrals is greater (141–155) (Franco 2000), and the genera Tomodon and Calamodontophis also have dark oral linings, which is absent in Gomesophis and Ptychophis (Franco 2000, Franco et al. 2006). In Calamodontophis, there is no reduction of the dorsal scale rows (15/15/15), the postocular stripe is blackish or absent, the hemipenes are more pronounced bilobate, and the *sulcus spermaticus* is divided just below the calyculate area, near the middle of the hemipenis body (FRANCO 2000, Franco et al. 2006).

Aditionally, *Tomodon dorsatus* has no loreal, and although such is present in *T. ocellatus* and *T. orestes*, these two species can be easily distinguished from *Ptychophis* and *Gomesophis* by differences in pholidosis (seven supralabials) and a dorsal colour pattern of ocellate spots (HARVEY & MUÑOZ 2004).

Tachymenis and Thamnodynastes are different from Ptychophis and Gomesophis in that both groups show vertical-elliptical pupils (round in Ptychophis and Gomesophis), the cervical constriction is evident (not so in Ptychophis and Gomesophis), and their colour patterns are distinctive, generally with chequered or reticulated patterns in the anterior portion and a lined pattern in the posterior part of the body (Franco 2000), i.e., very different from the colour patterns of Ptychophis and Gomesophis, both of which exhibit continuous lines or stripes.

In the phylogenetic hypothesis proposed by Franco (2000), *G. brasiliensis* and *P. flavovirgatus* were sister species closely related to *Tachymenis* and the other Tachymenini, excluding *Thamnodynastes*. More recent molecular phylogenies (Zaher et al. 2009 and Grazziotin et al. 2012) reject Franco's (2000) hypothesis, though, despite of the low support obtained in both hypotheses.

The close relationship between P. flavovirgatus and G. brasiliensis proposed by FRANCO (2000) was inferred on the basis of morphological characters that are apparently related to their semi-aquatic habits, such as eyes and nostrils directed anterodorsally and a shortened preocular region. These similarities along with the number of supralabials in contact with the eyes and other meristic characters are exclusively found in the group Ptychophis and Gomesophis, and not in the other Tachymenini genera (Franco 2000, this work). Although the low number of ventrals may show some overlap with other taxa in the tribe (FRANCO 2000), this might also be indicative of a common ancestry. Nevertheless, despite their morphological resemblance and considering the results of different molecular analyses for the genera Ptychophis and Gomesophis, we also suggest that further studies are necessary before any conclusive taxonomic decision can be taken.

Although *Gomesophis brasiliensis* is not a recently-described species, it has become known only from a few localities in Brazil, and its pattern of distribution has until now been poorly understood. While it can be found in some of the most densely populated areas of the country, it is not a common species. The gap in its distribution (from southern Minas Gerais to Brasilia, DF) is not yet fully understood, but we suggest it might be related either to a natural disjunction or the extinction of in-between populations.

The Kruskal-Wallis test showed no significant differences among the subpopulations of *P. flavovirgatus* in the assessed character states. This homogeneity throughout its distribution range, despite its discontinuous distribution, makes us conclude that the current distribution is fragmented. There are two major gaps in its distribution pattern and we believe that they are due to different causes:

the gap in a great portion of Santa Catarina state may be a result of undersampling, since only few specimens have been collected in the state (on the north border); on the other hand, no specimen of *P. flavovirgatus* has ever been collected in the state of São Paulo (the most populous region of the country and home of Instituto Butantan, which has been receiving thousands of snake specimens for more than a 100 years). Similar distributional patterns are also observed in at least ten other Brazilian snake taxa (Thomas et al. 2006). Thomas et al. (2006) and Bérnils (2009) suggest this gap being associated with the distribution of open formations of the Araucaria Forests on the Brazilian Southern Plateau and the slopes of the Serra da Mantiqueira.

Sexual dimorphism in snakes can be expressed in several ways, such as: differences in size and proportions of the body, size and position of organs and other structures, shapes and numbers of scales, and colour (SHINE 1993, 1994, PIZZATTO et al. 2007). Inverted sexual dimorphism is known only with regard to the number of ventrals, where males have a larger number of ventrals than females (FRANCO 2000). As far as the Tachymenini are concerned, both conventional and inverted sexual dimorphism may occur (Bailey 1981, Ferrarezzi 1944, Fran-CO 2000, FRANCO et al. 2006). In this study, P. flavovirgatus presented an inverted sexual dimorphism, with males having higher ventral counts than females. The other variables showed no significant differences. These results do not corroborate SCARTOZZONI & MARQUES (2004), who found no significant differences in body size, head dimensions or tail lengths between males and females, suggesting an absence of sexual dimorphism in the characters reviewed by them. Gomesophis brasiliensis, in turn, showed highly significant differences between males and females in the numbers of ventrals and subcaudals and significant differences in snout-vent length. Males had higher numbers of ventrals (inverted) and subcaudals (conventional). A significant difference also showed in the body of the female being slightly longer than in males (conventional). OLIVEIRA et al. (2003) found no sexual dimorphism in snout-vent length or head length in the specimens of G. brasiliensis they analysed. Our results contradict theirs with regard to SVL, while differences regarding head sizes have not been tested for here. However, our results corroborate those obtained by PRUDENTE (1993), who likewise found expressions of a sexual dimorphism in G. brasiliensis in ventral (inverted) and subcaudal counts (conventional).

Gomesophis and Ptychophis are snakes, of which little is known, for they are endemic, not much represented in collections, and rather rarely collected. Amongst the Tachymenini species, they are the only ones that present character states related to the usage of aquatic habitats. Even though they may resemble each other in various aspects of their pholidosis, we caution against any premature taxonomic steps and suggest further studies be taken first to assess their cladistic relationships with each other and within the tribe.

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Appendix Material examined

Ptychophis flavovirgatus: BRAZIL: Minas Gerais: unknown locality: IBSP 10548 F; Estiva (22°27'S, 46°01'W; 895 m above sea level = hereinafter "a.s.l."): IBSP 26572 M; Liberdade (22°01'S, 44°18'W; 1154 m a.s.l.): MNRJ 3726 F; MNRJ 3727 F; Munhoz (22°36'S, 46°21'W; 1235 m a.s.l.): IBSP 68662 M; Poços de Caldas (21°47'S, 46°33'W; 1238 m a.s.l.): IBSP 9003 M; IBSP 9082 M; IBSP 13204 F; São Vicente de Minas (21°40'S, 44°26'W; 983 m a.s.l.): IBSP 72770 F. Paraná: Araucária (25°35'S, 49°24'W; 867 m a.s.l.): IBSP 7821 F; Balsa Nova (25°35'S, 49°37'W; 903 m a.s.l.): IBSP 15971 M; Carambeí (24°56'S, 50°06'W; 1047 m a.s.l.): MHNCI 11763 M; Campo Largo (25°27'S, 49°31'W; 940 m a.s.l.): MHNCI 3364 F; Curitiba (25°25'S, 49°16'W; 922 m a.s.l.): IBSP 10501M; General Carneiro (26°25'S, 51°19'W; 1024 m a.s.l.): IBSP 25958 M; IBSP 25970 M; Guarapuava (25°23'S, 51°27'W; 1009 m a.s.l.): PUCRS 10979 M; Lapa (25°46'S, 49°43'W; 910 m a.s.l.): IBSP 5635 F; MHNCI 3490 M; Mallet (25°52'S, 50°49'W; 838 m a.s.l.): IBSP 21702 F; IBSP 29881 F; Pirai do Sul (24°32'S, 49°55'W; 1054 m a.s.l.): IBSP 12551 F; IBSP 32531M; Piraquara (25°26'S, 49°03'W; 909 m a.s.l.): MHNCI 7844 M; Ponta Grossa (25°05'S, 50°09'W; 848 m a.s.l.): IBSP 42612 M; IBSP 6786 M; São José dos Pinhais (25°32'S, 49°12'W; 899 m a.s.l.): IBSP 8377 M; MHNCI 7803 M; Santa Catarina: unknown locality: IBSP 3684 M; IBSP 3087F; Caçador (26°46'S, 51°00'W; 932 m a.s.l.): IBSP 10419 M; Rio Negrinho (26°15'S, 49°31'W; 859 m a.s.l.): IBSP 11343b F; IBSP 11343a M; IBSP 9346 M; São Bento do Sul (26°15'S, 49°22'W; 870 m a.s.l.): IBSP 526 (holotype) M; IBSP 3670 M; IBSP 6967 M; IBSP 7149 M; IBSP 7676 M; São Joaquim (26°37'S, 51°36'W; 1358 m a.s.l.): IBSP 53568 F; IBSP 53995 F; Rio Grande do Sul: Bom Jesus (28°39'S, 50°26'W; 1013 m a.s.l.): PUCRS 1526 M; Cambará do Sul (29°02'S, 50°09'W; 1024 m a.s.l.): PUCRS 2606 M; PUCRS 2607 M; PUCRS 2798 M; CHUFSC 00742 F; Carazinho (28°16'S, 52°45'W; 578 m a.s.l.): IBSP 8326 F; IBSP 11500 M; Ijuí (28°23'S, 53°54'W; 316 m a.s.l.): IBSP 27191 M; Passo Fundo (28°15'S, 52°24'W; 655 m a.s.l.): IBSP 7924 F; IBSP 8451 F; Santa Bárbara do Sul (28°21'S, 53°14'W; 527 m a.s.l.): IBSP 17101 M.

Gomesophis brasiliensis: BRAZIL: Distrito Federal: Brasília (15°46'S, 47°55'W; 1064 m a.s.l.) (Barragem do Paranoá): IBSP 19185 M; Minas Gerais: Albertina (22°11'S, 46°36'W; 1003 m a.s.l.): IBSP 54456 M; Itajubá (22°25'S, 45°27'W; 921 m a.s.l.): IBSP 8176 M; IBSP 8177 M; IBSP 8178 F; IBSP 8179 M; IBSP 8306 F; IBSP 8307 M; Monte Santo de Minas (21°11'S, 46°57'W; 836 m a.s.l.): IBSP 43207 M; IBSP 43209 F; IBSP 43211 M; IBSP 43213 M; Poços de Caldas (21°47'S, 46°33'W; 1235 m a.s.l.): IBSP 44043 M; IBSP 49514 F; IBSP 9736 F; IBSP 9746 F; IBSP 12191 M; MZSP 5933 F; São Paulo: unknown locality IBSP 75877 F; IBSP 9601 F; CHUV 1464 F; Aparecida (22°50'S, 45°13'W; 576 m a.s.l.): IBSP 23282 M; Araraquara (Bueno de Andrade) (21°40'S, 48°14'W; 685 m a.s.l.): IBSP 10290 M; Atibaia (23°07'S, 46°32'W; 791 m a.s.l.): IBSP 15561 M; IBSP 34493 F; IBSP 40494 M; Bocaina (22°08'S, 48°30'W; 568 m a.s.l.): IBSP 10982 F; Bom Jesus dos Perdões (23°08'S, 46°27'W; 711 m a.s.l.): IBSP 72604 M; Cruzeiro (22°34'S, 44°57'W; 526 m a.s.l.): IBSP 26638 F; IBSP 9644 M; Ibiúna (23°39'S, 47°13'W; 851 m a.s.l.): IBSP 42481 M; MZUSP 12474 F; IBSP 21042 M; Itararé (24°06'S, 49°20'W; 765 m a.s.l.): IBSP 1141 (paratype) F; IBSP 78890 M; Mogi das Cruzes (23°31'S, 46°11'W; 765 m a.s.l.): IBSP 9462 F; IBSP 9464 M; IBSP 18402 M; Pindamonhangaba (22°55'S, 45°27'W; 552 m a.s.l.): IBSP 1316 (holotype) F; IBSP 16909 M; IBSP 16910 M; IBSP 16953 F; IBSP 16954 M; IBSP 16971 M; IBSP 17102 F; IBSP 17103 F; IBSP 17104 F; IBSP 17105 F; IBSP 17106 F; IBSP 17107 M; IBSP 17108 F; IBSP 17109 F; IBSP 17110 F; IBSP 17111 M; Poá (23°31'S, 46°20'; 753 m a.s.l.): IBSP 9574 F; São Paulo (23°32'S, 46°38'W; 804 m a.s.l.): IBSP 847 (paratype) F; IBSP 1363 (paratype) M; IBSP 1370 (paratype) F; IBSP 1371 (paratype) F; IBSP 1372 (paratype) F; IBSP 1519 (paratype) F; IBSP 3671 M; IBSP 9648 F; IBSP 22105 F; IBSP 19694 F; (Butantan) IBSP 3083 M; IBSP 5200 M; IBSP 10420 M; Taubaté (23°01'S, 45°32'W; 580 m a.s.l.): IBSP 17737 F; IBSP 18342 F; Paraná: unknown localities: MHNCI 789 F; MHNCI 790 F; MHNCI 791 F; MHNCI 792 M; MHNCI 6602 M; MHNCI 6064 M; MHNCI 6601 F; MHNCI 8326 M; Balsa Nova (25°35'S, 49°37'W; 903 m a.s.l.): IBSP 22898 M; IBSP 22899 M; IBSP 5065 F; Campo do Tenente (25°58'S, 49°40'W; 809 m a.s.l.): IBSP 1829 F; Castro (24°47'S, 50°00'W; 985 m a.s.l.): IBSP 4323 F; Carambeí (24°56'S, 50°06'W; 1047 m a.s.l.): MHNCI 11209 M; Clevelândia (26°24'S, 52°21'W; 979 m a.s.l.): MHNCI 10126 M; Curitiba (25°25'S, 49°16'W; 922 m a.s.l.): IBSP 18815 F; IBSP 6943 F; MHNCI 745 M; Guarapuava (25°23'S, 51°27'W; 1009 m a.s.l.): MHNCI 3308 F; Piraquara (25°26'S, 49°03'W; 909 m a.s.l.): MHNCI 11793 M; MHNCI 7289 M; MHNCI 11910 M; Ponta Grossa (25°05'S, 50°09'W; 848 m a.s.l.): IBSP 45992 M; IBSP 45993 F; MHNCI 1835 F; MHNCI 1836 F; MHNCI 4566 F; São José dos Pinhais (25°32'S, 49°12'W; 899 m a.s.l.): MHNCI 595 M; MHN-CI 12240 M; São Mateus do Sul (25°52'S, 50°23'W; 781 m a.s.l.): MHNCI 1340 F; MHNCI 2452 M; União da Vitória (26°13'S, 51°05'W; 751 m a.s.l.): PUCRS 16399 M; MHNCI 4739 M. Santa Catarina: Caçador (26°46'S, 51°00'W; 932 m a.s.l.): PUCRS 12116 M; PUCRS 12117 F; PUCRS 16369 F; PUCRS 16396 M; PUCRS 16370 F; PUCRS 16371 F; PUCRS 16372 F; PUCRS 16373 F; PUCRS 16374 F; PUCRS 16375 F; PUCRS 16378 F; PUCRS 16380 F; PUCRS 16381 M; PUCRS 16383 F; PUCRS 16384 F; PUCRS 16385 M; PUCRS 16387 M; PUCRS 16397 M; PUCRS 16400 M; PUCRS 16402 F; MHNCI 10062 M; MHNCI 10066 M; MHNCI 10063 F; Canoinhas (Felipe Schmidt) (26°11'S, 50°40'W; 792 m a.s.l.); IBSP 32115 F; Porto União (26°14'S, 51°04'W; 756 m a.s.l.): IBSP 22945 F; IBSP 22946 M; PUCRS 16376 F; PUCRS 16377 F; PUCRS 16379 F; PUCRS 16382 M; Rio Grande do Sul: Barração (27°40'S, 51°27'W; 757 m a.s.l.): PUCRS 3230 M; Bom Jesus (28°39'S, 50°26°W; 1013 m a.s.l.): CHUFSC 1377 M; Caxias do Sul (29°10'S, 51°10'W; 744 m a.s.l.): IBSP 6484 F; IBSP 8498 F; PUCRS 12265 M; PUCRS 14500 M; PUCRS 7833 M; PUCRS 1165 F; PUCRS 3000 F; MCN 6422 F; MCN 6423 F; MCN 6424 F; MCN 6425 M; MCN 6426 F; MCN 6427 F; MCN 6428 M; MCN 6429 F; Encruzilhada do Sul (30°31'S, 52°31'W; 427 m a.s.l.): PUCRS 7873 F; Panambi (Belisário) (28°29'S, 53°27'W; 474 m a.s.l.): IBSP 18343 F; IBSP 18344 M; Passo Fundo (28°15'S, 52°24'W; 655 m a.s.l.): MNRJ 10080 F; Vacaria (28°30'S, 50°55'W; 942 m a.s.l.): PUCRS 2058 F.

Calamodontophis ronaldoi: BRAZIL: Paraná: General Carneiro (26°25'S, 51°19'W; 953 m a.s.l.): IBSP 55914.

Calamodontophis paucidens: BRAZIL: Rio Grande do Sul: Cachoeira do Sul (30°02'S, 52°53'W; 30 m a.s.l.): MCP 8607; MCP 9106.

Tachymenis chilensis: CHILE: Quebrada Paposo (23°38'S, 70°24'W; 10 m a.s.l.): MZUSP 9045; San Fabian (36°36'S, 72°6'W; 520 m a.s.l.): MZUSP 8842; Santiago (33°26'S, 70°39'W; 637 m a.s.l.): MZUSP 5407; MZUSP 4121; MZUSP 4122 M; MZUSP 4123; MZUSP 4140; MZUSP 4141; MZUSP 4141; MZUSP 4145; MZUSP 4146 M; MZUSP 4147 M; MZUSP 4148 M; MZUSP 4149; MZUSP 4150; MZUSP 8239; MZUSP 8242; MZUSP 8243; MZUSP 8838; MZUSP 8843.

Tachymenis peruviana: ARGENTINA: Tucuman (27°00' S, 65°30'W; 464 m a.s.l.): FML 012329; FML 1492; FML 1988; CHILE: Concepcion (36°50'S, 73°03'W; 34 m a.s.l.): MCN 4278; MCN 4279; PERU: Vale do Cusco (13°30'S, 71°58'W; 3795 m a.s.l.): IBSP 1924.

Thamnodynastes hypoconia: BRAZIL: São Paulo: Campinas (22°54'S, 47°03'W; 679 m a.s.l.) IBSP 15586, IBSP 28677, Caieiras (23°21'S, 46°44'W; 759 m a.s.l.): IBSP 12130; Cotia (23°36'S, 46°55'W; 835 m a.s.l.) IBSP 37439, IBSP 37442; Itu (23°15'S, 47°17'W; 604 m a.s.l.): IBSP 28572, IBSP 29007, IBSP 45648, IBSP 45669, IBSP 45801; Piedade (23°42'43"S, 47°25'40"W; 901 m a.s.l.) IBSP 58569; Planalto (21°02'S, 49°55'W; 789 m a.s.l.) IBSP 75131 F; São Carlos (22°01'S, 47°53'W; 828 m a.s.l.) IBSP 34394; IBSP 33366, IBSP 34394.

Thamnodynastes pallidus: FRENCH GUIANA: unknown locality: IBSP 13753 M.

Thamnodynastes rutilus: BRAZIL: Distrito Federal: Brasília (15°46'S, 47°55'W; 1064 m a.s.l.): IBSP 19183; IBSP 20584; IBSP 26761; São Paulo: Marília (22°12'S, 49°56'W; 634 m a.s.l.) IBSP 17815; Presidente Epitácio (21°45'S, 52°06'W; 281 m a.s.l.) IBSP 60258 F; UHE Ilha Solteira (20°25'S, 51°20'W; 356 m a.s.l.): IBSP 35230, IBSP 35934, IBSP 36221, IBSP 36311, IBSP 36481, IBSP 36736, IBSP 36820, IBSP 36900, IBSP 36901, IBSP 37213, IBSP 37214, IBSP 37723, IBSP 38314, IBSP 38315, IBSP 38316.

Thamnodynastes strigatus: BRAZIL: unknown locality: MZUSP 16850 M; MZUSP 16851; MZUSP 4374; M; MZUSP 16849; Goiás: Mambaí (14°29'S, 46°06'W; 704 m a.s.l.): MZUSP 17775 M; Minas Gerais: Poços de Caldas (21°47'S, 46°33'W; 1235 m a.s.l.): MZUSP 14068 M; Sapucaí-Mirim (22°44'S, 45°44'W; 888 m a.s.l.): MZUSP 11593; MZUSP 16489; São Paulo: Barueri (23°30'S, 46°52'W; 729 m a.s.l.): MZUSP 16559 M; Botucatu

(22°53'S, 48°26'W; 804 m a.s.l.): MZUSP 2362 F; Cotia (23°36'S, 46°55'W; 835 m a.s.l.): MZUSP 4206 M; Itu (23°15'S, 47°17'W; 604 m a.s.l.): MZUSP 4360 M; Mairinque (23°32'S, 47°10'W; 857 m a.s.l.): MZUSP 12445 M; MZUSP 12446 M; Nova Europa (21°46'S, 48°33'W; 486 m a.s.l.): MZUSP 3496 M; Pinhalzinho (22°46'S, 46°35'W; 916 m a.s.l.): MZUSP 16486; Santana de Parnaíba (23°26'S, 46°55'W; 715 m a.s.l.): MZUSP 14611 M; São Paulo (23°32'S, 46°38'W; 802 m a.s.l.): MZUSP 16504; Santa Catarina: UHE – Ita (27°17'S, 52°19'W; 516 m a.s.l.): MZUSP 17651; MZUSP 17650.

Tomodon dorsatus: BRAZIL: São Paulo: Barueri (23°30'S, 46°52'W; 729 m a.s.l.): MZUSP 16548 M; Boracéia (22°11'S, 48°46'W; 495 m a.s.l.): MZUSP 16524 M; MZUSP 3501; MZUSP 4518 F; MZUSP 4519 F; MZUSP 4520 M; MZUSP 4521 M; MZUSP 4578 F; Caieiras (23°21'S, 46°44'W; 759 m a.s.l.): MZUSP 16501 M; Cotia (23°36'S, 46°55'W; 835 m a.s.l.): MZUSP 16525; MZUSP 16530; MZUSP 14606 M; Itu (23°15'S, 47°17'W; 604 m a.s.l.): MZUSP 4084 F; Juquitiba (23°55'S, 47°04'W; 739 m a.s.l.): MZUSP 16520; MZUSP 16490 M; Mauá (23°40'S, 46°27'W; 800 m a.s.l.): MZUSP 16539; Santana de Parnaíba (23°26'S, 46°55'W; 715 m a.s.l.): MZUSP 16499; MZUSP 16558 F; Itapevi (23°32'S, 46°56'W, 757 m a.s.l.): MZUSP 14639 M, São Paulo (23°32'S, 46°38'W; 802 m a.s.l.): MZUSP 3505 M.

Tomodon ocellatus BRAZIL: Rio Grande do Sul: Uruguaiana (29°45'S, 57°05'W; 77 m a.s.l.): IBSP 5369; IBSP 5370; IBSP 5371; IBSP 5372; IBSP 5373; IBSP 5374; IBSP 5375; IBSP 5376; IBSP 5397.

Pseudotomodon trigonatus: ARGENTINA: Néuquen (38°58'S, 68°04'W; 272 m a.s.l.): MACN 2868; Mendoza (32°53'S, 68°50'W; 780 m a.s.l.): MACN 2978.