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Redescription of *Physalaemus spiniger* (Anura: Leptodactylidae) and Description of Two New Reproductive Modes

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ABSTRACT.—**We redescribe *Physalaemus spiniger* and describe its tadpole and its reproductive modes. This species has the following three alternative reproductive modes: (1) foam nest on pond and feeding tadpoles in pond (the typical mode for the genus *Physalaemus*); (2) foam nest on humid places on the forest floor near a pond, and feeding tadpoles in pond; (3) foam nest on water accumulated on the axils of terrestrial bromeliads and feeding tadpoles in pond. These last two modes were not included in the reviews of reproductive modes in anurans. The vocalizations of *P. spiniger* are described and compared with the vocalizations of *P. nanus*, a sibling species.**

Miranda-Ribeiro (1926) described *Engystomops spinigera* from Iguape, São Paulo State, southeastern Brazil, attributing the specific name to Boulenger because the specimens were so identified in the collection of the Museu Paulista (currently Museu de Zoologia da Universidade de São Paulo). However, Boulenger never described *Engystomops* (=*Physalaemus*) *spinigera* and accordingly the short account by Miranda-Ribeiro (1926) serves as the original description. The specific name *Engystomops spinigera* was apparently forgotten and ignored by subsequent authors (e.g., Cochran, 1955; Bokermann, 1966a; Lynch, 1970; Frost, 1985; Heyer and Wolf, 1989; Duellman, 1993). Lynch (1970) recognized four species groups in the genus *Physalaemus*: *P. biligonigerus* group, *P. cuvieri* group, *P. pustulosus* group, and *P. signifer* group; *P. deimaticus* and *P. rupestris* are not presently allocated to any species group (Sazima and Caramaschi, 1986; Caramaschi et al., 1991). Ten species are presently allocated to the *Physalaemus signifer* group (Pombal and Madureira, 1997): *P. bokermanni* Cardoso and Haddad, *P. caete* Pombal and Madureira, *P. crombiei* Heyer and Wolf, *P. maculiventris* (A. Lutz), *P. moreirae* (Miranda-Ribeiro), *P. nanus* (Boulenger), *P. obtectus* Bokermann, *P. olfersii* (Lichtenstein and Martens), *P. signifer* (Girard), and *P. spiniger* (Miranda-Ribeiro). In recent years we collected and observed specimens of *P. spiniger* at several localities in southern and southeastern Brazil. Herein, we redescribe this species and its tadpole. The vocalizations are described and compared with the vocalizations of *P. nanus*, a sibling species. Also, we provide information on reproduction, including two new reproductive modes for anurans.

MATERIALS AND METHODS

Specimens used in the description or examined for comparisons are deposited in AL-MN (Adolpho Lutz collection, deposited in Museu Nacional, Rio de Janeiro, RJ, Brasil), CFBH (Célio F. B. Haddad collection, deposited in Departamento de Zoologia, Universidade Estadual Paulista, Rio Claro, SP, Brasil), MNRJ (Museu Nacional, Rio de Janeiro, RJ, Brasil), MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo, SP, Brasil), WCAB (Werner C.A. Bok-

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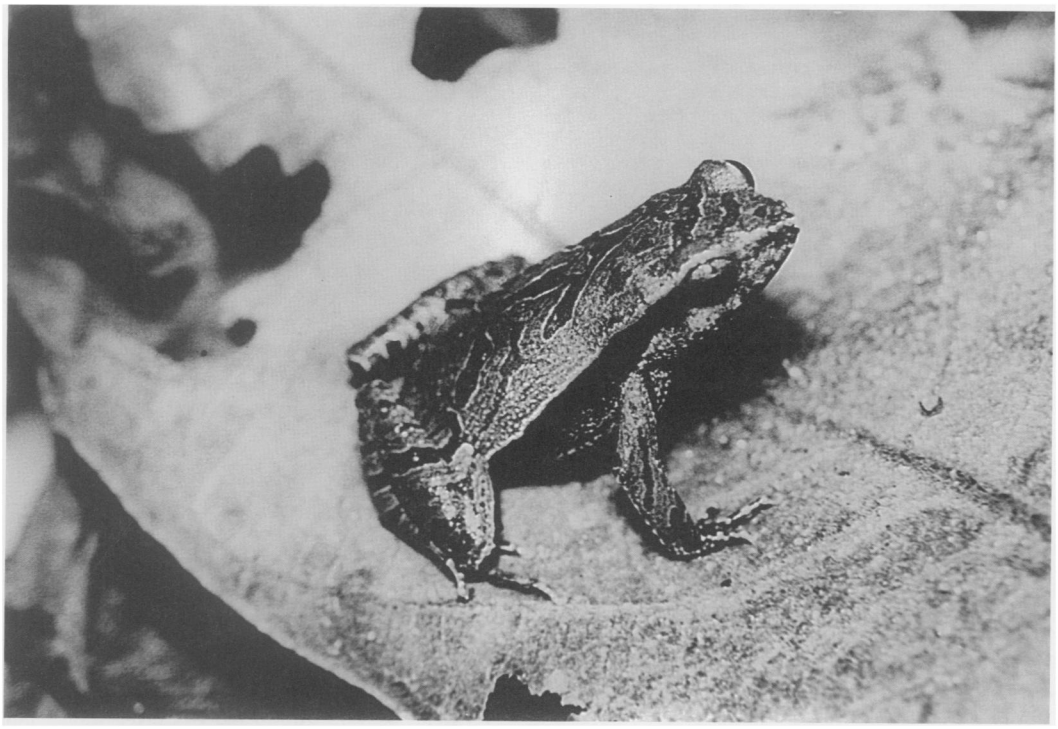

FIG. 1. *Physalaemus spiniger*, an adult male in life from Ilha do Cardoso, Cananéia, SP, Brazil.

ermann collection, deposited in Museu de Zoologia da Universidade de São Paulo, São Paulo, SP, Brazil), ZUEC (Museu de História Natural, Universidade Estadual de Campinas, Campinas, SP, Brasil). Additional specimens examined are listed in Appendix 1.

Abbreviations used in the measurements of the adults are SVL (snout–vent length), HL (head length), HW (head width), ED (eye diameter), THL (thigh length), TBL (tibia length), and FL (foot length). All measurements are expressed in millimeters. The measurements of the adults follow Duellman (1970) and Cei (1980). Measured adult specimens were fixed in 10% formalin and maintained in 70% ethyl alcohol. Eggs and tadpoles were fixed and maintained in 5% formalin. For measurements we used an ocular micrometer in a Zeiss stereomicroscope, except that SVL was measured with calipers. Drawings of the adult and tadpole were made using a Zeiss stereomicroscope with a drawing tube. Vocalizations were recorded using a Nagra E tape recorder with a Sennheiser ME 80 microphone at a tape speed of 19 cm/s. The sonagrams were produced by a Macintosh computer coupled to the MacRecorded Sound System 2.0.5, using 8 bit resolution, 22 kHz sampling frequency, and FFT with 256 points.

RESULTS

Diagnosis and Comparison with other Species.— A species belonging to the *Physalaemus signifer* group (sensu Lynch, 1970), characterized by (1) small size (males 17.1–21.3 mm SVL, females 20.6–22.0 mm SVL); (2) canthus rostralis distinct; (3) dorsal skin texture smooth to rugose; (4) belly orange in life; (5) structure of the advertisement call.

Physalaemus spiniger is distinguished from *P. caete*, *P. moreirae*, *P. obtectus*, and *P. olfersii* by its smaller size (combined SVL of males ranging 22.5–34.5 mm; Bokermann, 1966b; Heyer, 1985; Heyer and Wolf, 1989; Heyer et al., 1990; Pombal and Madureira, 1997). By its larger size and distinct advertisement call, *P. spiniger* differs from *P. bokermanni* (*P. bokermanni* males with 15.3–17.0 mm SVL; see Cardoso and Haddad, 1985). *Physalaemus spiniger* differs from *P. signifer* by smoother dorsal skin (more rugose in *P. signifer*), larger black spot on the inguinal glands, and smaller mean length (*P. signifer* males with SVL = 20.1–22.4, $\bar{x}$ = 21.7, SD = 0.7, N = 20). *Physalaemus spiniger* differs from *P. crombiei* by the orange belly (pinkish in *P. crombiei*; Heyer and Wolf, 1989) and distinct advertisement call (see below and Heyer and Wolf, 1989). *Physalaemus spiniger* differs from *P. maculiventris* by wider

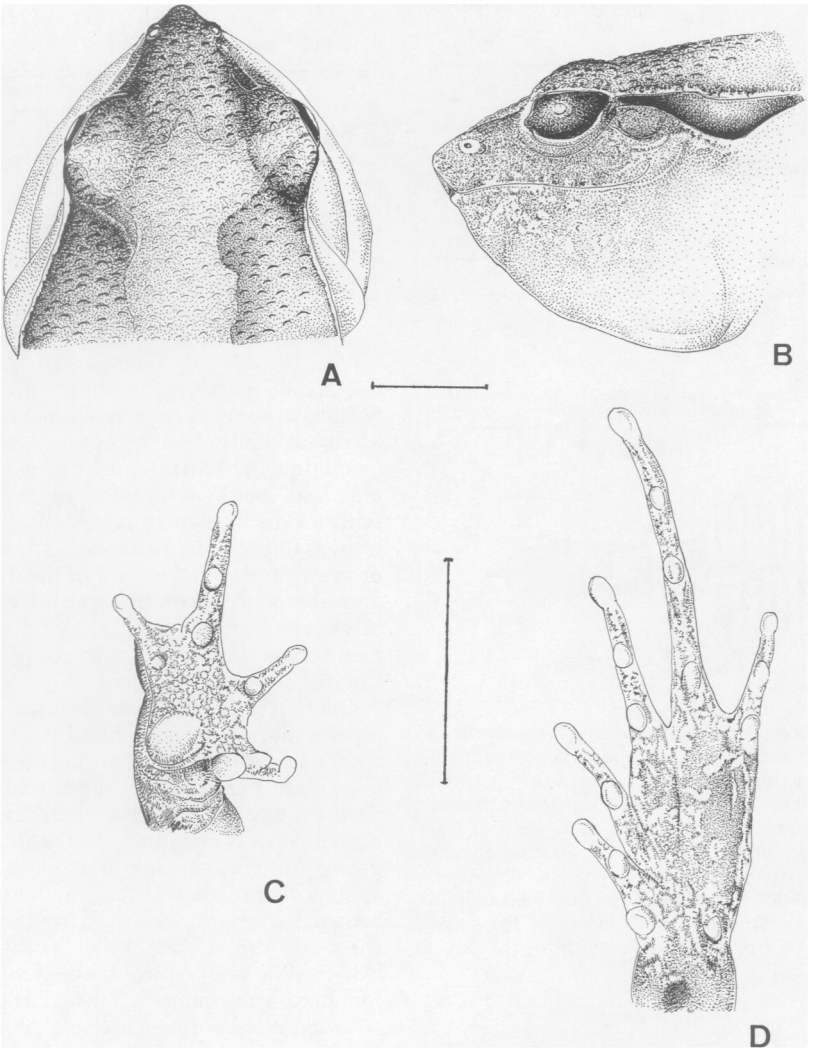

FIG. 2. *Physalaemus spiniger*, CFBH 0307. (A) Dorsal and (B) lateral views of head; ventral views of (C) hand and (D) foot (scales = 3.0 mm).

head and snout, and by posterior belly light colored (boldly dark and light mottled in *P. maculiventris*). Preserved specimens of *P. nanus* and *P. spiniger* are indistinguishable; however, they have different advertisement calls (see below).

Description of Adults.—Body slender (Fig. 1); head wider than long; snout rounded and protruding in dorsal and lateral views (Fig. 2A, B); nostril slightly protuberant, directed laterally; canthus rostralis distinct; loreal region concave; eye slightly protuberant; tympanum indistinct to weakly distinct; distinct supratympanic fold from tympanum to shoulder; narrow dorsolateral fold extending from posterior corner of eye to inguinal region; males with subgular vocal sac, expanded externally, extending to border of chest; vocal slits present in males; choanae small, nearly round; tongue narrow, long; vomerine teeth absent; maxillary teeth not visible, but discernible by probe. Arms slender, forearms moderately robust in males (in females slender); fingers short; brown nuptial pad on thumb in males; subarticular tubercles single, protruding and rounded; outer metacarpal tubercle large to small, rounded (81% of specimens) or ovoid (19% of specimens); inner metacarpal tubercle large to medium, nearly elliptical, sometimes rounded; supernumerary tubercles small; finger tips not expanded; finger lengths I = IV (or rarely IV < I) < II < III (Fig. 2C). Legs moderately robust; tibia longer than thigh; foot with an inner metatarsal tubercle

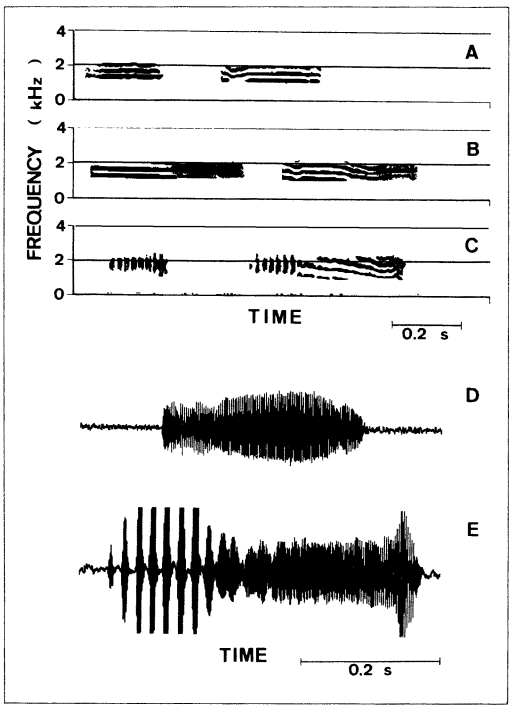

FIG. 3. Sonograms of the calls of *Physalaemus spiniger*: (A) advertisement calls and (B) encounter calls of two interacting males; air temperature = 15.5 C, water temperature = 21 C; Ilha do Cardoso, Cananéia, São Paulo, Brazil. (C) Sonagrams of the calls of *Physalaemus nanus*: advertisement call and vocalization composed by two parts, respectively; air = 23.5, water = 22 C; São João do Rio Vermelho, Florianópolis, Santa Catarina, Brazil. (D) Waveform of the second vocalization in Fig. 3A. (E) Waveform of the second vocalization in Fig. 3C.

slight protruding, elliptical to nearly rounded; outer metatarsal tubercle small, slightly protruding, rounded; well-developed subarticular tubercles, single, protruding, round; supernumerary tubercles small; toe tips slightly expanded; toe lengths I < II < V < III < IV (Fig. 2D). Inguinal glands small to large (21% of specimens with large glands); dorsal skin texture smooth to rugose (25% of specimens with rugose skin texture), undersurface textures smooth. Measurements of males and females are in Table 1.

Color in Preservative.—Dorsum brown or gray with a dark, nearly continuous and symmetrical pattern consisting of an interorbital bar, an arrow pointing to the head just behind the shoulder followed by three branches starting from the posterior part of the arrow; the two lateral branches terminating over the black spots on the inguinal gland, and the middle branch terminating before the cloaca; the interorbital bar and the arrow marks sometimes with a fine light border, in some specimens dorsal marks not evident; a white line on the dorsolateral fold (sometimes absent); flanks below the dorsolateral fold, black; forearm light brown or gray, with a dark brown transverse bar; elbow dark brown; thigh, tibia, and foot light brown, brown or gray, similar to the color of the dorsum; thigh and tibia with a dark brown transverse bar; two black bars on the upperparts of thigh and tibia; anal region dark; belly cream or gray; chest and throat gray or dark brown.

TABLE 1. Measurements (in mm) of males and females of *Physalaemus spiniger*.

	Males (N = 28)			Females (N = 4)		
	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range
SVL	18.8	1.0	17.1–21.3	21.1	0.6	20.6–22.0
HL	5.2	0.4	4.0–5.8	5.9	0.3	5.7–6.5
HW	5.9	0.3	5.2–6.5	6.3	0.1	6.2–6.5
ED	2.1	0.2	1.8–2.6	2.3	0.3	2.0–2.7
THL	8.6	0.3	8.1–9.3	9.5	0.4	9.1–10.0
TBL	9.3	0.4	8.5–10.5	10.2	0.3	9.9–10.7
FL	9.1	0.4	8.2–10.0	10.2	0.2	9.9–10.4

Color in Life.—Dorsum yellowish brown to brown; dorsal marks (interorbital bar and arrow) dark brown; in some specimens the dorsal marks are not evident; snout brown to cream; dark brown lateral stripe from snout, through nostril, eye, tympanum, and arm insertion to groin; groin orange; inguinal gland with a black spot; forearm, thigh, tibia, and foot yellowish brown to brown with a dark transverse bar; chest and throat dark brown with white spots; belly, axilla, and ventral surfaces of thigh, tibia, foot, and arm orange; anal region black.

Vocalizations.—When an isolated male of *Physalaemus spiniger* is calling it emits pulsed advertisement calls that are observed in the sonagram as three sidebands between approximately 1.2 and 2.1 kHz (Fig. 3A). However, the waveform shows a pulsed structure in the advertisement calls (Fig. 3D). The mean duration of the advertisement calls is 0.25 sec (SD = 0.03, range = 0.17–0.31, N = 54 vocalizations of two males). When two males are interacting, the first calling male emits an advertisement call with nearly constant frequencies (as in the vocalizations described here) and the second calling male emits an advertisement call with strong initial descending and ascending frequencies (Fig. 3A). The frequencies of the encounter calls of *P. spiniger* are similar to those of the advertisement calls; the mean duration of the encounter calls is 0.48 sec (SD = 0.13, range = 0.32–0.70, N = 14 vocalizations of two males). In the first part of the encounter calls there are the same sidebands observed for the advertisement calls; in

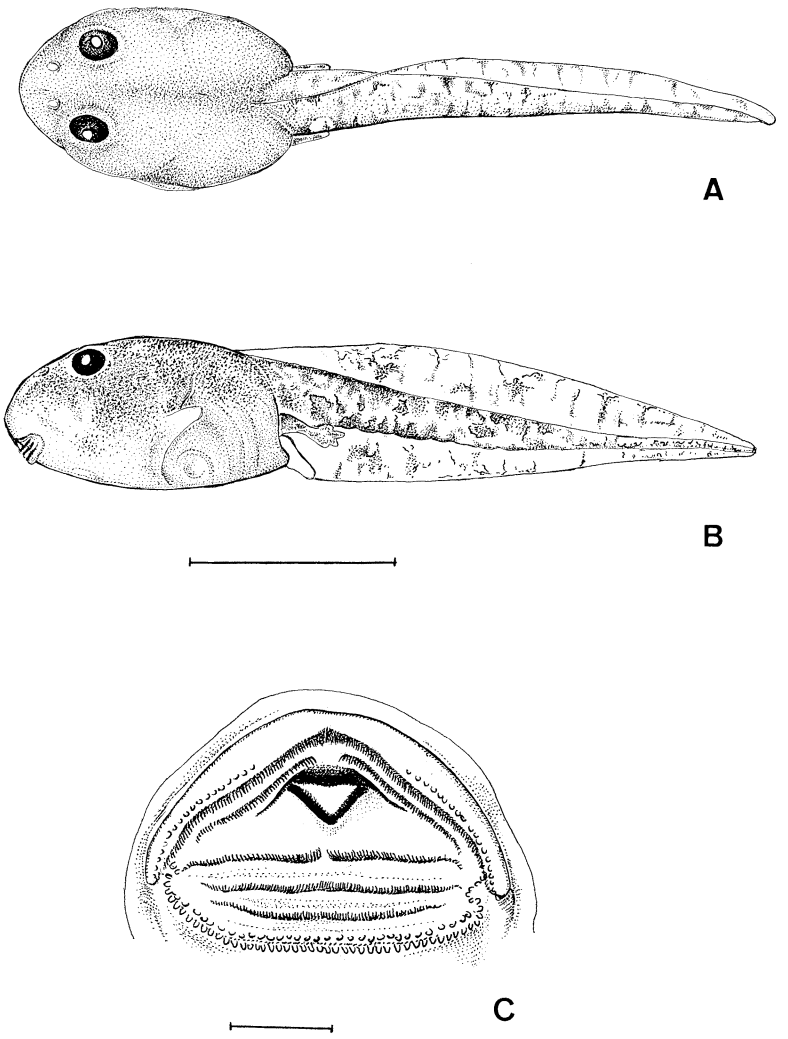

FIG. 4. Tadpole of *Physalaemus spiniger*, Stage 36; (A) Dorsal and (B) lateral views; (C) oral disc (upper scale = 5.0 mm; bottom scale 0.5 mm).

the last part of these vocalizations the sidebands are replaced by a creaking sound as a result of a decrease in pulse rate. The encounter calls emitted by the first calling male do not show the strong initial descending and ascending frequencies that are observed in the encounter calls of the second calling male (Fig. 3B).

In *Physalaemus nanus* the mean duration of the advertisement calls is 0.18 sec (SD = 0.01, range = 0.16–0.20, N = 10 vocalizations of one male). This vocalization has 7–9 notes ($\bar{x}$ = 7.9, SD = 0.57, N = 10 vocalizations of one male) with a frequency between 1.0 and 2.3 kHz (Fig. 3C). A second type of vocalization, emitted after the emission of a variable number of advertisement calls, shows frequencies between 1.0 and 2.3 kHz and mean duration of 0.46 sec (SD = 0.05, range = 0.39–0.52, N = 8 vocalizations of one male). This vocalization is composed of two different parts. In the first part there are six to 10 introductory notes ($\bar{x}$ = 8.13, SD = 1.36, N = 8 vocalizations of one male) similar to those observed in the advertisement calls; the second part has a pulsed structure observed in the sonagram as three to five sidebands very similar to the advertisement and encounter calls of *P. spiniger* (Fig. 3A–E).

Tadpoles.—Larvae were obtained at the municipality of Sete Barras, State of São Paulo. The following description is based on a tadpole in developmental Stage 36 (Gosner, 1960). Body ovoid in dorsal (Fig. 4A) and ventral views, depressed/globular in lateral view (Fig. 4B); body wider than high; snout rounded; eyes small,

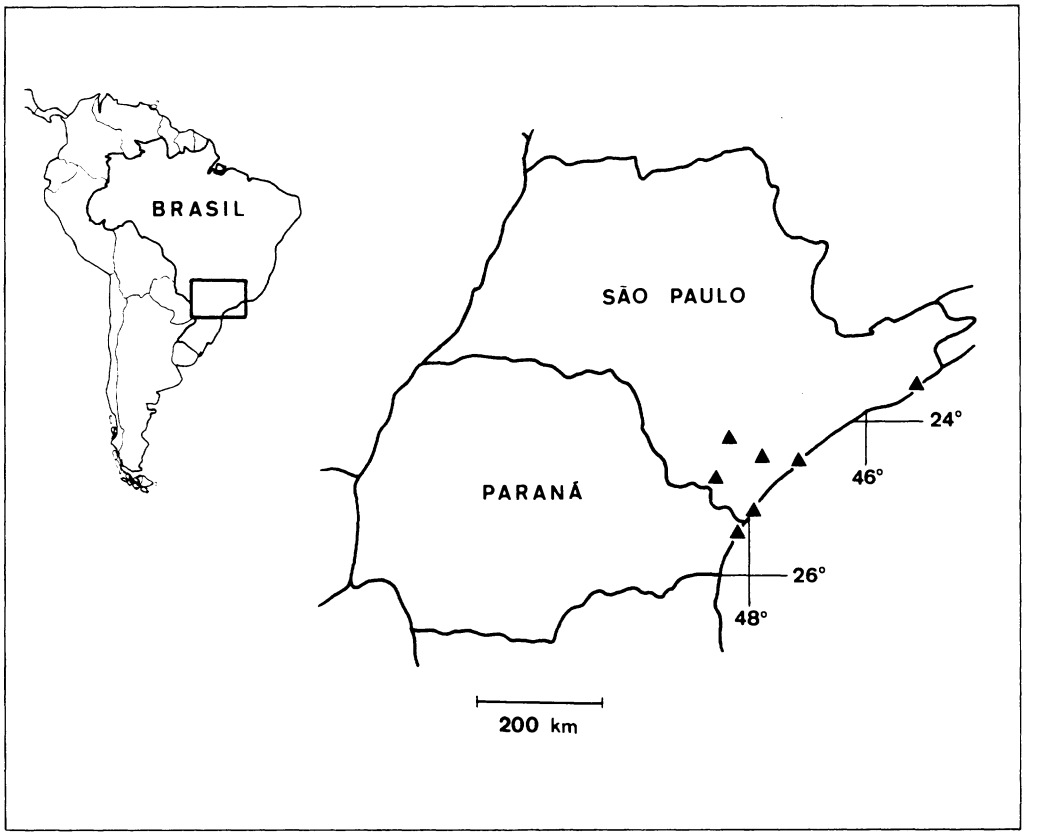

FIG. 5. Geographic distribution of *Physalaemus spiniger* in southern and southeastern Brazil.

dorsolateral; nostrils dorsal, small and rounded; nostrils about midway between the eyes and the tip of snout; spiracle sinistral, its opening posterior to the middle of body; cloacal tube medium sized, median; caudal musculature slender; dorsal fin originating on body; dorsal fin wider than ventral. Oral disc (Fig. 4C) directed ventrally and bordered by papillae, interrupted along a large area on the anterior labium; tooth row formula 2 (2)/3 (1); jaw sheath strongly developed and serrate; posterior jaw sheath v-shaped. In preservative, body gray; caudal musculature with scattered pigmentation; fins translucent with scattered pigmentation.

Measurements of five tadpoles in developmental Stage 36: range ($\bar{x}$, SD), total length 17.3–21.2 (19.56, 1.98); body length 5.8–7.5 (6.74, 0.74); body height 3.5–4.1 (3.72, 0.27); body width 4.3–5.7 (5.0, 0.62); internarial distance 0.7–1.0 (0.82, 0.13); interorbital distance 0.9–1.2 (1.12, 0.13); eye-nostril distance 0.5–0.6 (0.56, 0.05); eye diameter 0.8–1.0 (0.86, 0.09).

Distribution.—Physalaemus spiniger is known from the states of Paraná (Guaraqueçaba) and São Paulo (Ilha do Cardoso, Cananéia; Estação Ecológica da Juréia, Iguape; Caverna do Diabo, Iporanga; Saibadela, Sete Barras; Jacupiranga; Caraguatatuba) (Fig. 5). Although the *P. signifer* group occurs from the State of Alagoas, in northeastern Brazil, through southeastern to the State of Santa Catarina, in southern Brazil (Frost, 1985; Pombal and Madureira, 1997), most species of this group have restricted distributions (Heyer and Wolf, 1989), but *P. spiniger* has a moderately broad distribution.

Reproductive Modes.—Physalaemus spiniger reproduces during the rainy season (October–February) near areas subject to flooding on the forest floor. Males call from the edges of forest ponds, and the eggs are laid in a foam nest that is deposited on the water, anchored on the margins of ponds or on the humid leaf litter near the ponds; embryos were observed developing inside the foam mass, and feeding tadpoles were observed developing in ponds. At Ilha do Cardoso, during the last part of the dry season (September), a pond where *P. spiniger* reproduced dried up; after a light rain, a large chorus formed near the empty depression. Males were observed calling during both day and night, from terrestrial bromeliads that accumulate water near the depression. We counted 25 foam

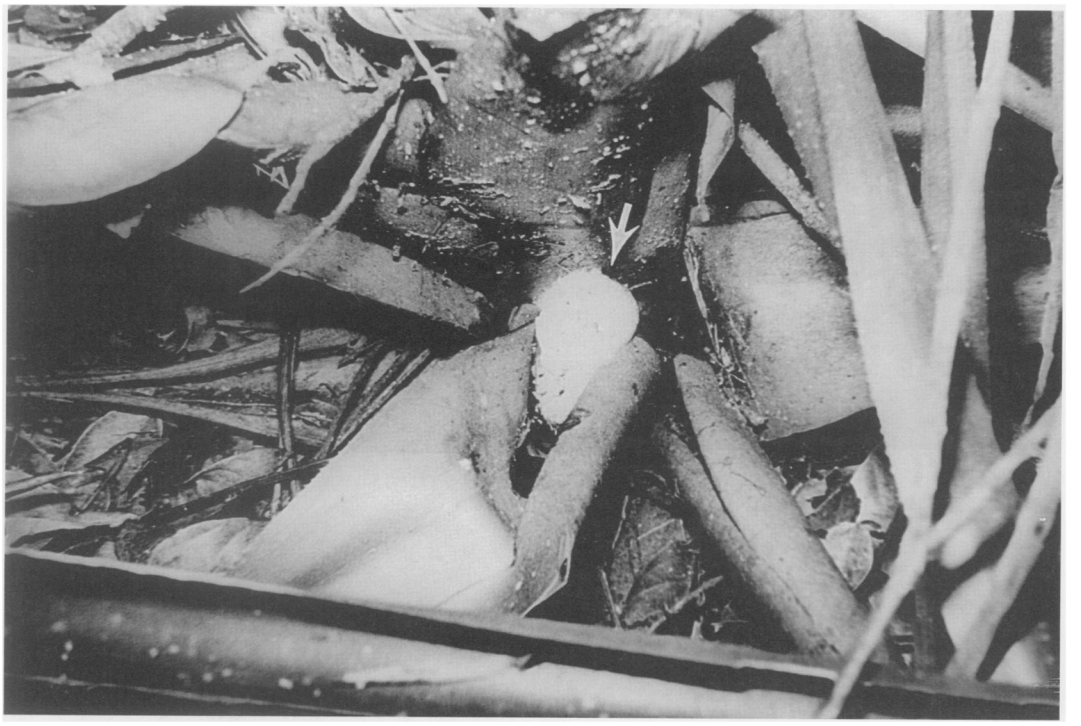

FIG. 6. Foam nest (arrow) of *Physalaemus spiniger* on water accumulated in the axils of a terrestrial bromeliad.

nests: 21 on the water accumulated in the axils of bromeliads (Fig. 6) and four on the leaf litter. The foam nests observed in bromeliads were on the leaves near the ground, between 2.6–22.0 cm from the ground ($\bar{x}$ = 10.31, SD = 5.933, N = 16). The mean number of eggs per nest, collected from the bromeliads, was 29.7 (SD = 7.6, range = 23–38, N = 3). We did not find tadpoles developing in the bromeliads, but embryos were developing inside the foam mass. During the rainy season at Ilha do Cardoso we observed foam nests on the water of temporary ponds and on the leaf litter. Eggs are unpigmented, with an average diameter of 1.62 mm (SD = 0.09, range = 1.4–1.8 mm, N = 15 eggs from three clutches).

DISCUSSION

The *Physalaemus signifer* group contains species difficult to characterize on the basis of morphological attributes of preserved specimens. Preserved specimens of *P. nanus* and *P. spiniger* are morphologically indistinguishable. However, the differences between the advertisement calls of *P. nanus* and *P. spiniger* are sufficient to separate both species. Advertisement calls have been used to characterize sibling species of frogs because they are typically stereotyped, allowing an unequivocal selection by the females, therefore acting as an isolating mechanism among different species (see Heyer et al., 1996 and references therein). *Physalaemus nanus* and *P. spiniger* clearly have strong evolutionary affinities observable by the indistinguishable morphology and by the resemblance of the pulsed structures present in the vocalizations of both species. The study of vocalizations is a promising way to uncover other sibling species in the genus *Physalaemus*.

We observed the following three alternative reproductive modes for *Physalaemus spiniger*: (1) foam nest on pond and feeding tadpoles in pond (Lynch, 1970; Mode 8 of Duellman and Trueb, 1986); (2) foam nest on humid places on the forest floor near a pond, and feeding tadpoles in pond; (3) foam nest on water accumulated on the axils of terrestrial bromeliads and feeding tadpoles in pond. These last two modes were not listed in the reviews of reproductive modes of anurans (Duellman, 1985, 1989; Duellman and Trueb, 1986).

Foam nests in humid places of the forest floor, as observed for *P. spiniger*, were observed for three other species in the *Physalaemus signifer* group: *P. bokermanni*, *P. crombiei*, and *P. signifer* (Haddad and Pombal, unpubl. data). However, for *P. caete* (Pombal and Madureira, 1997) and *P. olfersii* (Haddad and Pombal, unpubl. data) only the generalized mode for the genus (foam nesting on pond and feeding tadpoles in pond) has

been observed. Cruz and Peixoto (1985) observed foam nests of an unidentified species, probably of *Physalaemus*, on terrestrial bromeliads growing in a floor depression inside a forest at Santa Tereza, State of Espírito Santo, Brazil. These authors concluded that the tadpoles would not meet suitable conditions to develop in the bromeliads. The bromeliads could probably provide the necessary humidity for keeping eggs and embryos alive until the rain water flooded the depression, allowing the embryos to pass to the pond, enabling an early colonization of the pond by the embryos and tadpoles. These conclusions are valid for the eggs of *P. spiniger* deposited on the bromeliads. Probably, when foam nests of *Physalaemus* are deposited on the forest floor or in the axils of terrestrial bromeliads, the transportation of the embryos is made by the rain water that washes and carries the foam nests and embryos until a nearby temporary pond.

The alternative options of reproductive modes described here for *P. spiniger* are apparently related to rainfall unpredictability and to the presence of a foam nest involving the eggs. While eggs or larvae are within a foam nest, most are protected from desiccation (Heyer, 1969). When the rains fill the pond, the larvae are released from the foam nest and enter the pond with a temporal advantage over other anuran species reproducing at the pond. Differen → stages of a continuum from an aquatic to a terrestrial reproductive mode are known for species in the family Leptodactylidae (Heyer, 1969). *Physalaemus spiniger* is a singular leptoactylid frog because in one population it is possible to observe different reproductive modes as steps toward a more terrestrial life.

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APPENDIX 1

Additional Specimens Examined

Physalaemus caete: MNRJ 9712–17 (Murici, AL); MNRJ 9803 (holotype), 9801–02, 9804–05, 9848–50 (paratopotypes), 18280 (lot of tadpoles, Passo de Camaragibe, AL). *Physalaemus bokermanni*: MZUSP 59551 (holotype), MZUSP 59552, WCAB 48146, ZUEC 4520–21 (paratypes, Santo André, SP). *Physalaemus crombiei*: MNRJ 17694–745 (Aracruz, ES). *Physalaemus maculiventris* AL-MN 684 (syntype, "Alto da Serra de Cubatão"); MNRJ 4228–30 (Paranapiacaba, SP); MNRJ 1797, 9975–10020 (Serra de Araraquara, PR). *Physalaemus moreirae*: MNRJ 464 (holotype, Paranapiacaba, Santos, SP). *Physalaemus nanus* CFBH 081 (São José, SC); CFBH 2771, MNRJ 12827–32 (Florianópolis, SC). *Physalaemus obtectus*: MNRJ 4025, 14206–07 (paratypes, Linhares, ES). *Physalaemus olfersii*: MNRJ 2428 (Parati, RJ); MNRJ 0482, 5525–26, 12826 (Teresópolis, RJ). *Physalaemus signifer*: MNRJ 1123, 6616–35 (Duque de Caxias, RJ); MNRJ 2753, 12461–62 (Barro Branco, Duque de Caxias, RJ); MNRJ 2766, 12477–80 (Pendotiba, Niteroi, RJ); MNRJ 12837–42 (topotypes, Jacarepaguá, Rio de Janeiro, RJ). *Physalaemus spiniger*: CFBH 312–17, 319–21, MNRJ 18474, ZUEC 6878, 6881–82 (Cananéia, SP); ZUEC 9333–43 (Caraguatatuba, SP); CFBH 2479 (Eldorado, SP); MNRJ 18475–76 (Guaraqueçaba, PR); CFBH 307–10, 410, 835, MNRJ 18470–72, 18473, ZUEC 6876–77 (topotypes, Iguape, SP); ZUEC 3250 (Jacupiranga, SP).