PHYSALAEMUS CROMBIEI
(AMPHIBIA: LEPTODACTYLIDAE), A NEW FROG SPECIES FROM ESPÍRITO SANTO, BRAZIL WITH COMMENTS ON THE P. SIGNIFER GROUP

W. Ronald Heyer and Alan J. Wolf

Abstract.—Physalaemus crombiei, a new species of the P. signifer group, is described from the State of Espírito Santo, Brazil. Members of this group are most easily distinguished from each other by advertisement call, although morphological differences also exist. The relationships and distributions of members of this species group are not well understood at present.

One species group of frogs of the genus Physalaemus breeds in forest puddles and/or swamps within the Atlantic Forest system of Brazil. Members of this group are more easily distinguished from each other by advertisement calls than by their morphologies. Perhaps because of this, several species have been described since field recording equipment has become more available. We describe another new species of this group, to be known as:

Physalaemus crombiei, new species

Fig. 1

Holotype.—MZUSP 66252, adult male from Brazil: Espírito Santo; adjacent to Reserva Biológica Nova Lombardia, near Santa Teresa, approximately 19°55'S, 40°36'W. Collected on 31 Dec 1977 by one of collectors of paratopotypes.


Diagnosis.—Physalaemus crombiei is a member of the P. signifer group. The signifer group differs from other Physalaemus species groups (Lynch 1970) by the following characteristics: absence of an inner tarsal tubercle, first finger shorter than second, lack of parotoid glands, small to large inguinal glands, slender build and a size range of 15–35 mm SVL.

Physalaemus crombiei differs from P. deimaticus Sazima and Caramaschi 1986 (which apparently does not belong to any of Lynch’s (1970) species groups) by the following characteristics: relatively smooth skin (granular in deimaticus), slender build (stocky), and inverse V-shaped marks on back (absent).

Physalaemus crombiei can be distinguished from other members of the P. signifer group [P. signifer (Girard, 1853), P. olfersi (Lichtenstein & Martens, 1856), P. nanus (Boulenger, 1888), P. maculiventris (A. Lutz, 1925) (Frost 1985:253, is in error in placing maculiventris in the cuvieri group), P. obtectus Bokermann, 1966, P. bokermannii Cardoso & Haddad, 1985, and P. franciscae Heyer, 1985] as follows. Physalaemus crombiei differs from bokermannii, obtectus, olfersi, and signifer by size (P. crombiei 19–22 mm SVL, bokermannii 15–17 mm, obtectus 22–27 mm, olfersi 30–35 mm, signifer 24–31 mm). Physalaemus crombiei also differs from olfersi by the absence of a light outline on the ventral border of the lateral stripe from the eye to the arm (present in olfersi). It is distinguished from bokermannii, maculiventris and nanus by the presence of tubercles on the sole of the foot.
Physalaemus crombiei differs from obtectus by the lack of numerous small round markings closely associated with the inverse V-shaped marks on the back, by its sharp canthus rostralis, and pointed snout (numerous small round marks associated with the dorsal pattern, rounded canthus rostralis, less pointed snout in obtectus). Physalaemus crombiei has a relatively light colored posterior belly differing from the boldly dark and light mottled posterior belly of franciscae and maculiventris.

Description of holotype.—Snout subelliptically pointed from above, rounded in profile; canthus rostralis rather sharp in cross section; tympanum barely discernible externally, large, about two-thirds eye diameter; maxillary teeth not visible, but discernible by probe; vomerine teeth absent; vocal slits present, elongate; vocal sac single, noticeably but not greatly expanded externally, extending to level in front of arms; finger tips slightly expanded, not disked; fingers lacking fringe and web; subarticular tubercles large, globose, pungent; pair of tan nuptial pads on inner surface of each thumb, rounded-oblong medial pad associated with inner metacarpal tubercle, narrowly separated from elongate distal pad; no prepollex; no ulnar ridge; forearm slightly hypertrophied; extremely weak supratympanic fold; no dorsolateral fold; large ovate lumbar gland in groin; dorsal skin texture smooth in appearance but with scattered small fleshy tubercles, especially on upper eyelid; posterior part of vocal sac wrinkled, rest of throat and belly smooth, under surfaces of thighs areolate; toe tips slightly expanded, toes III and IV most expanded; toes without webs, sides of toes with or without weak ridges; subarticular tubercles globose, rounded, pungent; well-developed rounded metatarsal tubercle about half the size of well-developed oblong inner metatarsal tubercle; short, weakly developed inner tarsal fold on distal one-fourth of tarsus, narrowly separated from inner metatarsal tubercle, remainder of tarsus smooth; heel smooth; foot with four series of small but distinct fleshy tubercles.

Color in preservative: Dorsum creamy tan with indistinct brown markings including an inverted V-shaped mark in shoulder area, an indistinct interorbital mark, a pair of acute marks in sacral area, and a pair of very distinct black, white-outlined spots, one on each upper portion of lumbar glands; sides of head mottled brown, distinctly separated along canthus rostralis from lighter dorsal color and leaving a light stripe on very tip of snout; tympanum brown, distinguished from surrounding areas by color pattern; distinct dark (almost black) supratympanic stripe extending along flank towards belly, terminating below mid-lumbar gland level, distinct dorsal dark stripe with white outline, brief white outline from posterior tympanum midway to shoulder ventrally, rest of stripe blending into ventral pattern and not distinct ventrally; upper limb surfaces indistinctly cross-banded, forearms with darker brown blotch medially, each outer shank with series of three blackish spots; throat dark brown with small, light irregular spots; anterior half of belly mottled brown and cream, posterior belly cream; ventral forearm region dark brown laterally, irregularly but distinctly separated from lighter dorsal color pattern; ventral surface of thighs mottled brown and cream, lighter medially, posterior portions with small white dots; outer tarsus brown medially with irregular dark brown elongate markings centrally with lighter dorsal color laterally; sole of foot brown, subarticular and metatarsal tubercles cream; light dorsal pattern dipping irregularly but with distinct border onto posterior surface of each thigh, lowest on medial half of thigh, remainder of lower portions of thigh almost uniform brown, with a few ventral white dots.

Snout–vent length 20.3 mm, greatest tympanum diameter 1.7 mm, head length 7.0 mm, head width 7.7 mm, thigh length 9.3 mm, shank length 9.3 mm, foot length 9.7 mm.
Fig. 1. Holotype of Physalaemus crombiei (MZUSP 66252, SVL = 20.3 mm, male), dorsal and ventral views.

Variation.—The dorsal patterns range from almost uniform brown to distinct dark interorbital bands and two dark, white-outlined confluent arrows, one on the mid-scapular area, the other on the mid-sacral area. In a few specimens the interorbital and arrow markings join. In some individuals a distinct small mid-scapular light spot is present. In a few specimens the interorbital and arrow markings join. In some individuals a distinct small mid-scapular light spot is present. One individual (USNM 285048) has a faint but distinct light mid-dorsal pin stripe from the tip of the snout to just past the sacrum. Most individuals lack a light border posterior to the tympanum defining a portion of the ventral border of the dark lateral stripe. The stripe is distinct (black) in most individuals, and fainter but distinct in a few. The dark spots on the lumbar glands are distinct in all individuals. The ventral pattern described for the holotype is characteristic of nearly all individuals, although a couple have lighter bellies than does the holotype. In some individuals the dorsal and posterior thigh patterns are distinct only medially, near the vent; most have the same pattern as described for the holotype.

The following measurements are based on 7 adult male (listed first) and 14 adult female (listed second) paratopotypes: SVL 18.9–20.0 mm, 19.2–21.8 mm; head length 33–38% SVL (mean 35%), 32–36% SVL (mean 34%); head width 35–39% SVL (mean 37%), 33–36% SVL (mean 35%); thigh length 43–48% SVL (mean 46%), 42–46% SVL (mean 44%); shank length 45–48% SVL (mean 47%), 43–48% SVL (mean 45%); foot length 44–49% SVL (mean 47%), 40–46% SVL (mean 44%).

Color in life.—Brief color notes are available for two individuals. In both, the iris was bronze. In USNM 285051 a slight red wash occurred in the groin and front and back of the thighs. In USNM 285052 the groin and belly had a pinkish cast and the dorsum was red-brown and brown.

Advertisement call.—Data from a series of calls presumably given by a single un-captured individual; another captured individual (USNM 285070) was heard to give a similar call. Call rate approximately one/sec; average call duration 0.376–0.418 sec
Fig. 2. Advertisement call of *Physalaemus crombiei*. Wave form of second call shown on audiospectrogram, total signal length 0.428 sec. Recorded (no voucher) by W. R. Heyer, 30 December 1977, air temperature 21.5°C (USNM Tape 7, Cut 5).

(mean 0.399 sec); interval between calls 0.521-0.651 sec (mean 0.574 sec); 8-10 notes per call (mean 8.6); note length (other than final note) 0.029-0.043 sec (mean 0.039 sec), final note length 0.043-0.088 sec (mean 0.061); notes weakly to markedly pulsatile, for pulsed notes, 6-16 pulses/note (mean 13.7), pulse rate 344-454 pulses/sec (mean 394), first notes often not pulsatile, final note pulsatile initially and unpulsed at end; frequency range of call about 690-1840 Hz, dominant frequency about 1060 Hz with a second strong frequency band at about 1450 Hz; harmonic structure not apparent (Fig. 2).

*Etymology.*—Named for Ronald I. Crombie, who not only helped collect the type series of this new species, but has added to our knowledge of the Brazilian herpeto-fauna in general through his determined collecting efforts.

*Distribution.*—Known only from the type locality.

**Discussion**

Our knowledge of members of the *Physalaemus signifer* group is characterized overwhelmingly by what we do not know rather than any real understanding of the relationships among members of this group (and other species within the genus) or their distributions. Of critical importance is the number of species contained in the *signifer* group. At first glance, the group seems to represent a modest radiation. However, three of the currently recognized species were described prior to 1900, one was described in 1925, another in 1966, and including *P. crombiei*, three have been described since 1985. No doubt several more species in this group are unnamed. Accordingly, we think it premature to attempt to resolve the relationships not only within the *signifer* group, but also within the genus and concur with Cannatella & Duellman (1984) on this point.

Certain points resulting from our studies deserve comment.

Definition of the *Physalaemus signifer* group definition was unsatisfactory to Lynch (1970:493-494) who reluctantly placed *olfersi* in the *signifer* group. All *signifer* group species described since Lynch’s 1970 definition are more similar externally to other *signifer* group members than they are to *olfersi*. One character, presence (*olfersi*) or absence (remaining species) of teeth, used by Lynch no longer separates *olfersi* from the other species. Teeth are visible (under a dissecting microscope) in *P. olfersi*. In all other species of the *signifer* group, teeth are not
Table 1.—Comparison of call characteristics for members of the *Physalaemus signifer* group. Call unavailable for *P. nanus*.

<table>
<thead>
<tr>
<th>Call duration</th>
<th>Calls with notes</th>
<th>Calls with pulses</th>
<th>Rate of smallest discrete sound structure</th>
<th>Broadcast frequency range</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>bokermannii</td>
<td>0.2 s</td>
<td>+</td>
<td>7 notes/s</td>
<td>2500–5200 Hz</td>
<td>Cardoso &amp; Haddad 1985</td>
</tr>
<tr>
<td>crombiei</td>
<td>0.4 s</td>
<td>+</td>
<td>390 pulses/s</td>
<td>690–1840 Hz</td>
<td>This study</td>
</tr>
<tr>
<td>franciscae</td>
<td>0.5–0.7 s</td>
<td>+</td>
<td>250 pulses/s</td>
<td>600–1600 Hz</td>
<td>Heyer et al. 1989</td>
</tr>
<tr>
<td>maculiventris-</td>
<td>Boracéia</td>
<td>0.2–0.8 s</td>
<td>– + 130–170 pulses/s</td>
<td>700–3700 Hz</td>
<td>Heyer et al. 1989</td>
</tr>
<tr>
<td>maculiventris-</td>
<td>Teresópolis</td>
<td>0.2 s</td>
<td>– + 120 pulses/s</td>
<td>860–2340 Hz</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td>olfersi</td>
<td>3.4–4.0 s</td>
<td>– + 200–225 pulses/s</td>
<td>1000–2700 Hz</td>
<td>Heyer et al. 1989</td>
</tr>
<tr>
<td></td>
<td>signifer</td>
<td>0.3 s</td>
<td>– + 300–350 pulses/s</td>
<td>700–2500 Hz</td>
<td>Bokermann 1966</td>
</tr>
</tbody>
</table>

visible and are either very small or absent. Teeth can be felt by probe in all individuals of *bokermannii, franciscae*, and *oblectus*. No teeth can be felt by probe in *maculiventris* and *nanus* individuals. The condition is variable within *crombiei* and conflicting literature reports and our observations suggest the same might be true for *signifer*. As teeth may be present and still not felt by probe, final resolution of the toothed condition will require extensive clearing and staining preparations. It is clear with the evidence at hand that the difference in tooth condition between *olfersi* and the other group members is qualitative, not discrete, however.

Each of the character states used by Lynch (1970) to define the *signifer* group could be primitive, as pointed out by Cannatella & Duellman (1984); thus there is no assurance that the *signifer* group is monophyletic. With the exception of *olfersi*, it is our intuitive impression that the remaining species comprise a monophyletic group. The extreme morphological similarity and available habitat and reproductive data indicating intimate association with Atlantic Forests and small forest breeding pools support this view. Without additional evidence, it is inappropriate to remove *olfersi* from the *signifer* group, however.

As considerable confusion exists concerning the identity of *Physalaemus signifer*, an explanation of our use and understanding of this species is in order. *Rhinoderma signifera* Girard was described from Rio de Janeiro (Girard 1853). We have no reason to contradict Bokermann’s (1962) interpretation that the locality represented the city of Rio de Janeiro rather than being a general locality for the region where collections were made while the expeditionary ship was in the port of Rio de Janeiro. With Bokermann’s (1962) removal of *maculiventris* from the synonymy of *signifer* and the description of *franciscae* (Heyer, 1985), our understanding is that *signifer* is the relatively large species of the group presently known only from around the city of Rio de Janeiro and the Organ Mountains. B. Lutz (e.g. 1954) clearly thought that a single species inhabited both the city of Rio de Janeiro and the Organ Mountains, although she used the name *bresslau*, described by Müller (1924) from Teresópolis, Organ Mountains for the taxon involved. We follow Bokermann (1962) in considering *bresslau* a synonym of *signifer*. The anuran fauna from Rio de Janeiro and the nearby coastal lowland differs from the Organ Mountain anuran fauna (examples in Heyer 1983, 1984). The only published call information for *signifer* is from Itaguai, a coastal locality near Rio de Janeiro (Bokermann 1966). If
Fig. 3. Advertisement calls of Physalaemus maculiventris. Upper set of figures recorded from Boracéia, São Paulo, Brazil; wave form of call on left in audiospectrogram, total signal length 0.428 sec; recorded from USNM 209278 by W. R. Heyer, 13 December 1976, air temperature 17.6°C (USNM Tape 2, Cut 7). Lower set of figures recorded from Teresópolis, Rio de Janeiro, Brazil; wave form of call on left in audiospectrogram, total signal length 0.428 sec; recorded from series of specimens, USNM 285076–78 and field numbers 6609-16 to be catalogued in MZUSP collections, by W. R. Heyer, 20 December 1977, air temperature 18-20°C! (USNM Tape 7, Cut 3).

the Organ Mountains population proves to be distinct at the species level, the name bresslaui is available.

The distributions of signifer group members are poorly known. Physalaemus olfersi stands out in having a rather broad distribution within the Atlantic Forest region from the State of Santa Catarina to at least the State of Espírito Santo (based on examination of museum specimens by WRH). In contrast, P. bokermanni, franciscae, obiectus, and crombiei currently are known only from their type localities or nearby areas. Physalaemus maculiventris and nanus apparently have moderate distributions, but the situation with maculiventris requires comment.

In the introduction, we stated that the known advertisement calls of members of the signifer group were distinctive (see Table 1). We have two samples of calls of maculiventris-like animals, one from Boracéia, São Paulo, and one from Teresópolis, Rio de Janeiro. The available recordings show differences between calls from the two sites (Table 1, Fig. 3), but not of the magnitude found among other species in the group (Table 1). We also found difficult to verbalize subtle differences in the adult color patterns of the two populations, involving the relative clarity of a light ventral outline of the dark lateral stripe in the eye-shoulder region and the appearance of the dark lateral stripe itself. We have no geographically intermediate samples at hand. Two specimens of maculiventris were collected with the type
series of crombiei; with only two specimens, we are unable to determine any populational differences between these and the specimens from the Teresópolis or Boracéia populations. Our present conclusion is that the variation observed in calls and morphology is best considered intraspecific. Thus, it would appear that some signifer group species have broad distributions without notable differentiation, others have moderate distributions with some geographic differentiation, but most apparently have very localized distributions. Clearly, in order to understand the systematics and distributions of species that have been included in this group, much more field work, especially with voice recordings, is necessary.

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