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## HERPETOFAUNA OF PALAEOQUATERNARY SAND DUNES OF THE MIDDLE SÃO FRANCISCO RIVER: BAHIA: BRAZIL. VI. TWO NEW SPECIES OF *PHIMOPHIS* (SERPENTES: COLUBRIDAE) WITH NOTES ON THE ORIGIN OF PSAMMOPHILIC ADAPTATIONS

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### ABSTRACT

*Two new species of psammophilous pseudoboine snakes are described from the Palaeoquaternary dune fields of the middle São Francisco river. They are attributed to the genus *Phimophis* although the strongly projecting rostral characteristic of the genus is absent in both. *Phimophis scriptorcibatus* sp. n., from Ibiraba on the left bank of the river and *Phimophis chui* sp. n., from the opposite margin are apparently closely related. This is the fourth example of a reptile species pair that is separated by the São Francisco river. The relevance of the allopatric distributions of species in these pairs to an understanding of the recent history of the river and speciation is discussed. A model for the origin and maintenance of psammophilic adaptations in this arenicolous fauna is proposed.*

### INTRODUCTION

The Palaeoquaternary dune fields of the middle São Francisco river are a specially favourable site for systematic, ecological and evolutionary studies. They are in the morphoclimatic domain of Caatingas in the state of Bahia (latitudes 9 and 11, longitudes 41 and 43). The rich reptile fauna is characterized by striking psamophilic adaptations. There are at least 35 species of lizards and amphisbaenians which is more species than occur in some Amazonian assemblages; fourteen of these species are endemic (Rodrigues, 1991, a, b, c, d; Vanzolini, 1991, a, b). However, it is unlikely that the species inventory of these sand dunes is complete.

Three groups of ecologically and taxonomically closely related species are known in the area: the tropidurids *Tropidurus amathites* and *Tropidurus divaricatus*, the fossorial gymnophthalmids *Calyptommatus sinebrachiatus/nicterus* and *Calyptommatus leiolepis* and the amphisbaenids *Amphisbaena ignatiana* and *Amphisbaena hastata*. Each group has a species, or two in the case of *Calyptommatus*, on the right bank of the river whereas the other species in the group inhabits the left bank only. The recurrence of this pattern in different families of lizards and amphisbaenians with distinct ecology suggests widespread allopatric speciation provoked by the

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São Francisco river, which acts as a dispersal barrier. Furthermore, the exceptional richness of this assemblage relative to other reptile faunas of caatingas (Vanzolini, Ramos-Costa & Vitt, 1980; Rodrigues, 1987) indicates a high speciation rate in the study area. Rodrigues (1986; 1991a) proposed that gene flow among psamophilous populations was extensive when the São Francisco river drained endorheically (approximately 12,000 years ago). At the end of the Würm-Wisconsin glacial period, the river began to drain to the sea and isolated populations on opposite banks of palaeoquaternary sands. Subsequently, these populations evolved differentially in isolation.

The two new species of *Phimophis* described here provide additional support for the hypothesis that as a dispersal barrier, the São Francisco river has stimulated increased rates of speciation among reptiles of the area.

***Phimophis scriptorcibatus*, sp. n.**

(Figures 1 and 2)

Holotype: MZUSP 10.062, male, Brazil: Bahia: Ibiraba. 26.viii.88, MRodrigues col., field number 88.6299.

Paratypes: MZUSP 10.061, 10.063, other data as for holotype; MZUSP 10.064 - 10.067, Ibiraba, Ba, 9-10.ii.89; MZUSP 9591 - 9592, Ibiraba, Ba, 3.x.87; MZUSP 10.292, 10.293, Queimadas, Ba, 12-13.x.90.

**DIAGNOSIS**

Dorsal ground colour dark gray with an inconspicuous collar on the neck of the adult. Young brick red with a dark gray collar on the neck; venter cream-colored, immaculate. Ventrals 131-150; 36 to 52 pairs of subcaudals.

**DESCRIPTION**

Rostral normal, not prominent, wider than high, practically not visible from above. Internasal small, slightly wider than long, smaller than the prefrontals and about the size of the eye. Prefrontals wider than long, and, as the internasals, in full contact on the middle. Frontal subtriangular, longer than broad, almost as long as its distance from the tip of the snout. Supraoculars longer than wide, anterolateral to the frontal. Parietals a little longer than frontal. Nasal divided, the nostril on the median suture. Loreal fused to the posterior larger, the prefrontal. One pre- and two postoculars, latter slightly larger. One anterior and two posterior temporals. Eight supralabials, 4th and 5th under the eye. Eye round, pupil vertically elliptic.

Symphysial small, subtriangular. Eight or nine infralabials, the first pair in contact behind the symphysial. Two pairs of chin shields, imbricate, the anterior larger and in contact with the first four infralabials; only the fifth infralabial touches the second pair of chin shields.

Dorsals smooth, with one apical pit, in 19/19/17 rows. Ventrals 131-150. Subcaudals 36-52, paired. Anal entire.

Dorsal ground color dark grayish, except in the two lower rows of paraventrals, chin are light cream colored, as is the belly. An inconspicuous but distinct neck collar.

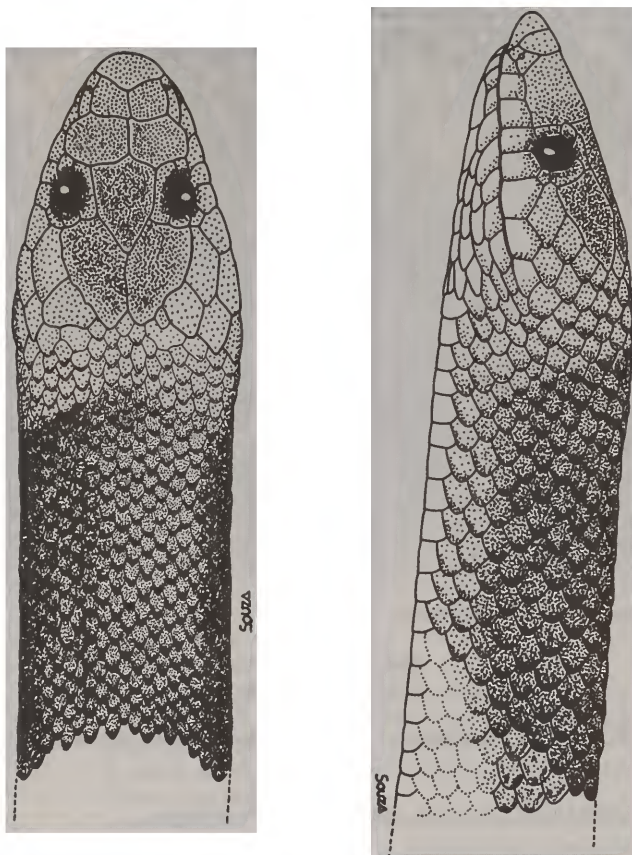


Figure 1, *Phimophis scriptorcibatus*: Ibiraba, Ba.

Hemipenis globular, bilobate, distinctively capitate at each lobe. Lateral face with large and lightly scattered spines. In the sulcate face smaller and more scattered spines to the level of bilobation; above them calyces with terminal spines. Sulcus spermaticus forked from the base of the organ, centrifugal. Asulcate face with spines much smaller than the corresponding side. Measurements of the holotype: body size 246 mm; tail 70 mm.

**Etymology:** the name is “the one that eats writers” and refers to the fact that the microteiids of the genus *Calyptommatus* are part of the diet of *Phimophis scriptorcibatus*. In the sandy areas near of the São Francisco river these lizards are popularly called as “escrivões” (writers) because of the tracks leave in the sand.



Figure 2, *Phimophis scriptorcibatus*: Ibiraba, Ba.

***Phimophis chui*, sp. n.**

(Figure 3)

**Holotype:** MZUSP 10.291, male, Brazil: Bahia: Santo Inácio; 6.x.90, field number MRodrigues 90.7212.

**Paratype:** MZUSP 10.025, 23.viii.88, other data as for the holotype.

**DIAGNOSIS**

Dorsal ground colour brick red both in the adult and juvenile with a characteristic dark brown neck collar; venter immaculate. Rostral normal, not prominent. Ventrals 164-169; 47 pairs of subcaudals.

**DESCRIPTION**

Rostral not prominent, visible from above, wider than long. Internasals longer than broad, maintaining strict median contact, their suture a little longer than that of the prefrontals. Frontal broader than long, approximately the same size as the parietals, that are a little longer than the frontal. Supraocular longer than broad. Nasal divided; nostril occupying the middle of suture between posterior and anterior nasals; the last largest. One preocular and two postoculars loreal absent, fused to prefrontal. An anterior temporal and two posterior temporals. Eight supralabials, 4th and 5th under the eye. Eye practically equalling in size the internasal; pupil vertical.



Figure 3, *Phimophis chui*, Santo Inácio, Ba.

Symphysial subtriangular. Eight or nine infralabials, the first pair in contact behind the symphysial. Two pairs of imbricate chin shields, the anterior largest and contacting infralabials 1-4; the second pair of chin shields only touching the fifth infralabial.

Dorsals smooth, with an apical pit and disposed in 19/19/17 rows. Ventrals 164 to 169. Subcaudals paired, in 47 rows. Anal plate entire.

Ground dorsal colour uniform brick red, except in the two lower rows of paraverntals which are cream, uniform and immaculate as the ventral colour. A black or dark brown dorsal collar on the neck. There is no ontogenetic variation in the colour pattern.

Hemipenis globous, bilobate, bicapitate. Lateral face with large and scattered spines. Sulcate side smooth, lacking spines to the level of bifurcation, above there are calyces with terminal spines. Asulcate side with very small spinules. Sulcus spermaticus centrifugal, divided from the base of the organ. Measurements of holotype: Body 300 mm, tail 70 mm.

**Etymology:** The name honors Dr. Tien Hsi Chu a research associate of Dr. Yatiyo Yonenaga-Yassuda of the Cytogenetics Laboratory of the Instituto de Biociências, University of São Paulo. For several years, Chu has patiently obtained fibroblast cultures for the chromosomal preparations of our animals. I dedicate this species to him with great pleasure. Incidentally the species name refers to one of the diagnostic features: "chu" in chinese is red.

#### SYSTEMATICS

The neotropical colubrid snakes of the genera *Clelia*, *Pseudoboa*, *Oxyrhopus*, *Drepanoides*, *Rachidelus*, *Siphlophis*, *Phimophis* and *Tripanurgos* were recognized as a natural group, the

pseudoboines, by Bailey (1967). Biochemical (Cadle, 1984, 1985), cytogenetic (Beçak, 1965; Beçak & Beçak, 1969, 1971; Beçak et al 1975; Gorman, 1974) and morphological studies (Jenner & Dowling, 1985) confirm the monophyly of this group. Jenner & Dowling (1985) tentatively suggested the inclusion of *Tropidodryas* and *Saphenophis* in the tribe Pseudoboini. However, with few exceptions, no morphological characters other than hemipenian structure strongly support the present generic arrangement of the pseudoboines, a problem typical of many snake genera (Myers, 1974). For example, Boulenger (1896) included species of *Clelia*, *Pseudoboa* and *Phimophis* (*Rhinostoma*) within *Oxyrhopus* whereas *Rachidelus* was considered distinct (Boulenger, 1908). Certainly the highly modified and prominent rostral that characterizes *Phimophis* is a derived character. Among the four species of *Phimophis* (*guerini*, *iglesiassi*, *guianensis* and *vittatus*), the rostral is least prominent in *iglesiassi*, which in addition, has undergone fusion of the loreal with the prefrontals. As no other pseudoboine lacks a loreal, its absence in *Phimophis* is probably derived. The somewhat unique shield morphology of *iglesiassi* probably reflects its fossorial ecology. Similarly, the two new species of *Phimophis* described here lack loreals and have a less prominent rostral associated with fossorial habits. Morphologically, ecologically and geographically *Phimophis chui* and *Phimophis scriptorcibatus* are closest to *Phimophis iglesiassi*.

Besides the materials referred in the description of *chui* and *scriptorcibatus* I used the following: a young male (not a female as reported by Hoge et al. , 1979) of *iglesiassi* of the Instituto Butantã collection (IB 42 486) from Parnaguá, state of Piauí. A second specimen of *iglesiassi* from Nova Rodelas, Ba, was generously lent to me by Dr. A.S. Abe. To complete the sample of *iglesiassi* I used the data published by Gomes (1915) in the original description of *Rhinostoma iglesiassi* and those furnished by Lutz & Mello (1923) in their description of *Rhinostoma bimaculatus*, a synonym of *Phimophis iglesiassi*. I have also a juvenile of *Phimophis* without loreal that I obtained at Alagoado in the state of Bahia (9° 29' S; 41° 21' W). The specimen is a male with 170 ventrals and 46 subcaudals. Although in bad shape, the condition of the rostral indicates that this specimen is *iglesiassi*. The specimen is noted here but not further utilized in the comparisons.

The head shields are very similar in the three species. The rostral of *iglesiassi* is short but distinctively prominent and well visible from above; it is clearly rounded and not prominent in *chui* and *scriptorcibatus*. The position, number and proportions of the other head shields are practically identical in the three species.

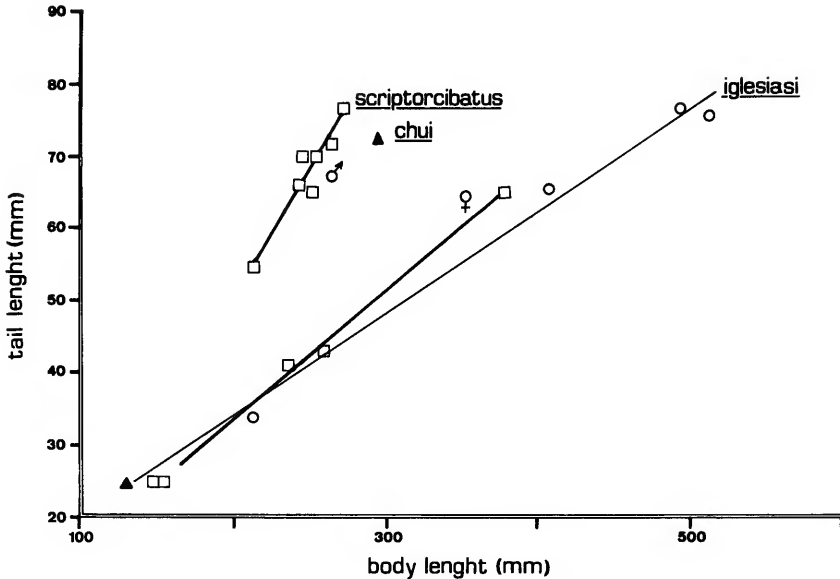
The only relevant variations refer to the number of temporals and postoculars. One of the *iglesiassi* specimens (IB 42.486) has just one anterior temporal; the specimen of Nova Rodelas, two. In the original description of *Rhinostoma bimaculatus* Lutz & Mello point out that the specimen has two anterior temporals and utilize the character as diagnostic to separate it from *iglesiassi*. As there is good agreement between the *iglesiassi* specimens with one and two anterior temporals it is clear that this difference should be attributed to individual variation. Similarly one of the *scriptorcibatus* specimens show two anterior temporals whereas the other specimens has just one scale.

Only one specimen of *scriptorcibatus* has a single postocular, whereas the remainder have two scales. *Phimophis scriptorcibatus* has lower ventral counts (131-150) followed by *iglesiassi* and *chui* with similar values (respectively 160-170 and 164-169). The subcaudal number is not completely diagnostic. *Phimophis iglesiassi* has 38 to 45 pairs; *scriptorcibatus* 36 to 52 and *chui* 47.

The sample of *scriptorcibatus* is the largest and indicates strong intersexual variation in these characters. The ventral counts vary from 131 to 134 in males and 141 to 150 in females and a similar variation exist in the subcaudals: 47 to 52 in males; 36 to 40 in females.

Graph 1 shows the regression of tail length on body length. *Phimophis scriptorcibatus* and *Phimophis chui* are the smaller species, *iglesiassi* the largest. The sample of *scriptorcibatus* shows also a strong sexual dimorphism in tail length.

The numbers of *chui* and *iglesiassi* specimens are insufficient to comment upon them.



Graph 1, regression of tail length on body length of *Phimophis chui*, *P. iglesiasi* and *P. scriptorcibatus*.

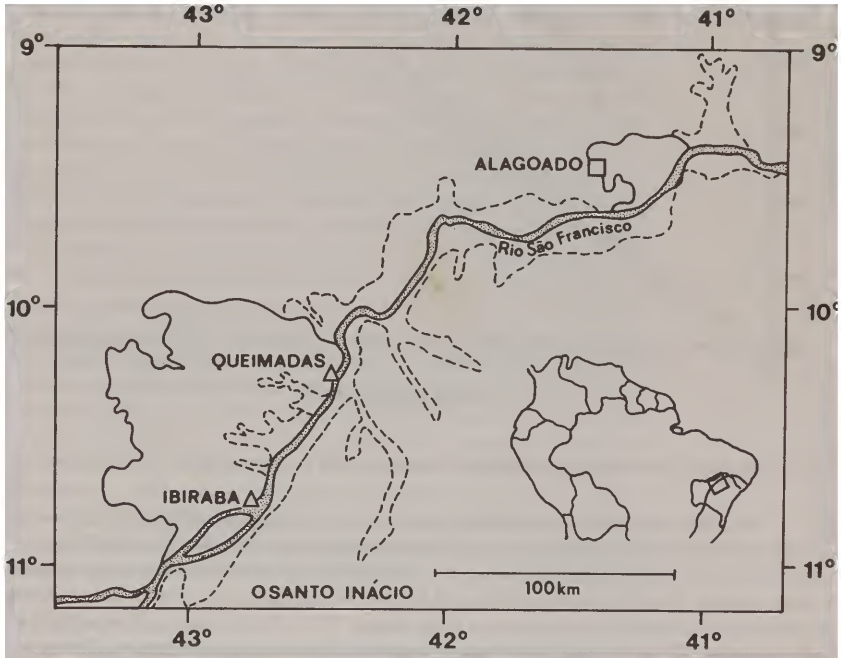
The adult color pattern is perfectly diagnostic for the three species. *Phimophis iglesiasi* is dorsally reddish with a dark mark on the nape. The dorsals have distinctive black borders. *Phimophis scriptorcibatus* is dorsally dirty gray with a dark mark on nape but with the black borders restricted to some dorsals. Finally, *chui* is reddish and has the black nape collar with a pronounced concentration of melanophores on the apice of the dorsals. The venter is cream and immaculate in the three species. The ontogeny of color pattern constitutes another diagnostic feature. *Phimophis scriptorcibatus* and *iglesiasi* show ontogenetic variation. Their juveniles are reddish, as are the young of *Clelia*, *Pseudoboa*, *Drepanoides* and *Rachidelus* (Bailey, 1967) and the juvenile coloration differs considerably from the adult colour. Juveniles and adults of *chui* have the same colour pattern. The fact that the three species have the lowest ventral scale counts of the genus is another argument for their close relationship.

#### ECOLOGY AND DISTRIBUTION

The predominantly subterranean ecology of *Phimophis* explains their scarcity in collections. The large sample of *Phimophis scriptorcibatus* was obtained in conjunction with efforts to collect fossorial microteiidids of the genera *Calyptommatius* and *Nothobachia* in the same area. All the specimens of *scriptorcibatus* were found in sand 5 to 20 centimeters above surface. The snakes were initially localized just a few centimeters above the leaf litter deposited around clumps of vegetation. Their agility and quickness in the sands hindered immediate capture. One of the stomachs of *scriptorcibatus* contained a specimen of *Calyptommatius leiolepis* and one of *Vanzosaura rubricauda* (formally *Gymnophthalmus multiscutatus*, see Rodrigues, 1991c).

In more than 300 hours of intense diurnal fieldwork and approximately 200 hours of

nocturnal work no specimen was seen in activity and no tracks observed that could be attributed to the genus. The conditions of capture and the stomach contents suggest that *Phimophis scriptorcibatus* catch their prey in the sand. *Phimophis scriptorcibatus* was obtained at Ibiraba and Queimadas, both localities in the dune fields of the left margin of the São Francisco river. (Map 1). The two localities are 80 kilometers apart and both are physiognomically very similar.



Map 1, records of *Phimophis chui*, *scriptorcibatus* and *iglesiassi* in the dune field study area.

Figure 4 shows the habitat where the species was found; more information can be obtained in Rodrigues (1991a).

The two specimens of *Phimophis chui* were obtained in similar conditions in the sands of Santo Inácio on the opposite margin of the river.

Map 2 shows the approximate distribution of *iglesiassi*, *chui* and *scriptorcibatus*. It is apparent that *iglesiassi* is more widely distributed and sympatric with the two new species. The two new species are allopatric and apparently limited to sandy areas along the river.

#### DISCUSSION

In a previous work belonging to this series, I proposed that speciation among members of this psammophilic fauna resulted from division and isolation of populations by the São Francisco river (Rodrigues, 1991a). At the time just two closely related pairs of species with one member on each side of the river were known to lend support to the model. Recently Vanzolini (1991 a,b) described three new species of *Amphisbaena* from the area. Two of them, *Amphisbaena ignatiana* from Santo Inácio and *Amphisbaena hastata* from Ibiraba conform to the same ecological and





Figure 4, Habitat of *Phimophis scriptorcibatus* at Queimadas, Ba.

geographic relationship of *Tropidurus* and *Calyptommatus*: both are psammophilic with *ignatiana* restricted to the right side of the river and *hastata* to the opposite bank.

The amphisbaenians cited are the two most slender and long tailed species of genus. Although generally quite similar there are distinct differences in preanal pores and head shape. Based on these differences Vanzolini did not consider the two species as closely related and attributed their resemblances to convergent evolution in a psammophilic habit. However, I propose that these two small *Amphisbaena* share a recent ancestor that was divided into two isolated populations by the São Francisco river. The following evidence supports this hypothesis: the high level of morphological divergence between *Amphisbaena hastata* and *Amphisbaena ignatiana* is not abnormal for two closely related species. For example, *Tropidurus amathites* and *Tropidurus divaricatus*, the pair of iguanids of the study area, show strong morphological divergence. Yet, cytogenetic and biochemical studies (Kasahara, Yonenaga-Yassuda & Rodrigues, 1987; Martins, 1991) support a close relation between *amathites-divaricatus*. Phylogenetic relationships among amphisbaenids require much clarification yet but the distributional and ecological parallels with the sympatric *Tropidurus* species are striking. Additionally, there are no examples of convergent evolution leading to body slendering and enlargement of tail related to psammophilic habit in *Amphisbaena*.

*Phimophis scriptorcibatus* and *Phimophis chui* are the fourth apparently closely related pair of species that are highly adapted for life in sand and are separated by the São Francisco river. Furthermore, this geographical division of two taxonomically and ecologically similar species occurs in four groups of reptiles: Tropiduridae, Gymnophthalmidae, Amphisbaenidae and Colubridae.

The dimensions of the dune fields on the left bank of the São Francisco indicate that the river had an endorheic phase (Tricart, 1974). Such a period permitted large sand accumulation. One can hypothesize that in an anterior phase previous to the origin of psammophilic adaptations, the



Map 2, Approximate distributions of *Phimophis iglesiasi* (open circles); *Phimophis scriptorcibatus* (solid circles) and *Phimophis chui* (triangle). 1. Regeneração; 2. Pamaguá; 3. Ibiraba; 4. Queimadas; 5. Santo Inácio; 6. Alagoado; 7. Nova Rodelas; 8. Pirapora.

local fauna lived in typical caatinga dipressions with inselbergs and disarticulate hills. During a subsequent endorrheic phase these habitats were flooded and sand accumulated from lacustrine deposition. Some of the fauna may have become isolated on disjunct hills that remained above the flooded lowlands. Later, with the onset of a semiarid climate, the water level dropped and exposed sand deposits to sun and wind. The hills were, in essence, faunal refugia in a sandy desert (see Vanzolini & Williams, 1981). Species with preadaptations for life in sand expanded into the embryonic dune field whereas others became extinct.

This paleolacustrine hypothesis explain only the origin and differentiation of the ancestral stocks of the psammophilic fauna of the area. The final speciation phase occurred when the São Francisco attained full exorheism dividing the formerly continuous sands and isolating them on opposite banks. This period probably corresponded to the end of the Würm-Wisconsin glacial, roughly 12,000 years before present (Tricart, 1974).

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