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Description of *Phrynops williamsi*, A New Species of Chelid Turtle of the South American *P. geoffroanus* Complex

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ABSTRACT. *Phrynops williamsi*, sp. nov., is a distinctive member of the *P. geoffroanus* complex (Pleurodira: Chelidae). The species is characterized by heavy black facial bands with a separate, thick, horseshoe-shaped band on the ventral surface of the neck, fine well-delineated radiating carapace reticulations, and no plastral markings. The skull differs markedly from other species of the *P. geoffroanus* complex and from most *Phrynops* in general. A wide parietal roof, lack of exoccipital contact above the foramen magnum, and widely divergent trochlear processes appear to be primitive features. Robust anterior maxillary triturating surfaces with lingual ridges and a shovel-shaped mandible adapted for bottom feeding appear to be unique derived characters. The species has a limited distribution in southern Brazil (Rio Grande do Sul and Santa Catarina) and adjacent Uruguay.

INTRODUCTION

The South American side-necked turtles of the family Chelidae are among the most poorly known of all turtles. No comprehensive review has ever appeared, and much of the scattered literature has suffered from inaccuracies based on inadequate sample analysis. Elusive and often rare in the wild, museum collections usually include only haphazardly or incidentally collected specimens. Many descriptions of new taxa have been based on single specimens, often without comparative material at hand. No clear definition exists of the valid taxa and their distribution, variation, morphology and ecology. Only Gaffney (1977) has looked at the family in a relatively comprehensive manner, but his work dealt with supraspecific relationships based on cranial osteology and examined less than half the known species.

In an effort to clarify the taxonomy of the South American Chelidae, Ernest E. Williams and Paulo E. Vanzolini began an extensive review of the family during the late 1950's, but abandoned the project due to inadequate material. They turned their preliminary work over to us several years ago, and this data base has served as the foundation for our work. It is therefore particularly fitting that the first description of one of the new species of chelid turtles to arise from this material appear in a volume dedicated to Dr. Williams. In addition, it is with great pleasure that we name this new species in honor of Ernest E. Williams, both in appreciation of his wide-reaching contributions to herpetology and the study of turtles, as well as in gratitude for his un-

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failing support, his friendship, and his guidance in our studies of systematic biology over the years. This has been a most rewarding relationship, undiminished by our respective professional divergences into the fields of orthopaedic surgery and primate conservation, and we take this opportunity to offer him our thanks.

Both Wermuth and Mertens (1977) and Pritchard (1979) recognize 18 taxa of South American chelids, though they differ in their interpretation of subspecific rank in three cases. Of the four currently recognized genera *(Chelus, Hydromedusa, Phrynops, Platemys), Phrynops* is the most complex taxonomically, with eleven currently recognized taxa: *P. dahli, geoffroanus, gibbus, hilarii, hogei, nasutus, rufipes, tuberculatus, tuberosus, vanderhaegei,* and *wermuthi.* Three of these taxa *(P. geoffroanus, hilarii, tuberosus)* form a natural superspecies complex based on external and osteological similarities and will hereafter be referred to as the *P. geoffroanus* complex. Briefly, the forms within the complex share the general features of large, broad shells with moderately wide heads, parietal roof moderately broad, neurals usually numbering six or seven and contacting the nuchal bone broadly, carapace color either dark brown or reticulated with radial black markings, plastron color usually reddish, yellow or white and either immaculate or with scattered dark vermiculations or spots, head with characteristic lateral black stripe from snout through the eye and tympanic membrane and extending along the lateral surface of the neck, ventral surface of the neck with either broad black bands, scattered thinner vermiculations or spots.

During the course of our revision of the South American Chelidae, we have personally examined 353 specimens of members of the *P. geoffroanus* complex. Of this series, 54 represent the readily distinguishable *P. hilarii,* with its immaculate dark brown or gray carapace, black-spotted white plastron, and reduced head markings. Of the 299 other specimens of *P. geoffroanus* and *P. tuberosus,* several distinct geographic populations are identifiable. A complete analysis of the systematic status of these populations is beyond the scope of the present paper, but will be presented in a future publication. The most distinctive of the populations is represented by six specimens from Rio Grande do Sul and Santa Catarina in Brazil. Though allopatric in respect to other *P. geoffroanus* and *tuberosus,* the combination of external and osteological features present in this population warrant its recognition as a new species within the *P. geoffroanus* complex.

TAXONOMY AND MORPHOLOGY

Phrynops williamsi sp. nov.
Figures 1–6

Holotype. MCZ 64135, Rio Grande do Sul, Brazil, collected by H. von Ihering.

Paratypes. BMNH 84.2.5.1, 84.2.5.3, Rio Grande do Sul, Brazil, collected by H. von Ihering; MZUSP 2675, Pôrto Alegre, Rio Grande do Sul, Brazil; MNRJ 3146, Tubarão, Santa Catarina, Brazil; ZMB 6858, "Estancia Velha," Rio Grande do Sul, Brazil, collected by R. Hensel (probably collected at Pikada do Café, Rio Cadéa).

Type Locality. Since the holotype specimen has no specific locality, we hereby designate the type locality as Rio Cadéa, Rio Grande do Sul, Brazil, where the species was first collected by R. Hensel in 1865.

Synonymy

Platemys geoffreyana (partim) Hensel, 1868:350
Platemys geoffroyana (partim) Hensel, 1868:354; Boulenger, 1885:191, 1886:424; Strauch, 1890: 104; Lema, 1958:11
Hydraspis geoffroyana (partim) Boulenger, 1889: 223; Siebenrock, 1904:23; Goeldi, 1906:751; Siebenrock, 1909:576; Luederwaldt, 1926:433
Phrynops geoffroyana (partim) Vaz-Ferreira, 1955:xxv; Froes, 1957:19
Phrynops geoffroana geoffroana (partim) Mertens and Wermuth, 1955:404; Vaz-Ferreira and Sierra de Soriano, 1960:14
Phrynops geoffroanus geoffroanus (partim)

Wermuth and Mertens, 1961:333, 1977:130; Pritchard, 1967:234, 1979:787
Phrynops geoffroanus (partim) Freiberg, 1970:190, 1971:92, 1972:248, 1975:92; Lema and Fabian-Beurmann, 1977:65
Phrynops geoffroana (partim) Achaval, 1976:26
Phrynops geoffroanus sspp. (partim) Mittermeier, Medem, and Rhodin, 1980:15

Distribution. Low-lying areas (below 500 m elevation) of eastern coastal Santa Catarina and Rio Grande do Sul in Brazil as well as the northern half of Uruguay as far west as the Rio Uruguay, possibly including eastern portions of Entre Rios and southeastern Corrientes in Argentina as well as southwestern inland Rio Grande do Sul (Fig. 9). Apparently absent from southern coastal Uruguay and northwestern inland Rio Grande do Sul in the upper Rio Uruguay and Rio Pelotas drainages.

Diagnosis. A moderately-sized member of the *P. geoffroanus* complex characterized by three heavy black facial stripes including a separate thick horseshoe-shaped stripe on the ventral neck, well-delineated thin radiating carapacial reticulations and no plastral markings. Skull characterized by a wide parietal roof, lack of exoccipital contact above the foramen magnum, widely divergent trochlear processes, and robust anterior maxillary triturating surfaces with lingual ridges and shovel-shaped mandible.

External Morphology

Carapace. Carapace (Fig. 1) broadly oval, almost subcircular in juveniles, carapace length averaging 1.15 times width, becoming relatively narrower with increasing size, carapace length averaging 1.33 times width in subadults and smaller adults, 1.46 in larger adults (see Table 1 for all measurements and ratios of external features). Shell moderately deep, length averaging 3.39 times height in adults and subadults. No marginal flaring, recurving or broad expansion. Mid-lateral marginals slightly narrower than anterior and posterior ones. Entire marginal rim mildly serrate in juveniles, partially retained posteriorly in subadults and adults but less distinct. Small supracaudal notch. Nuchal approximately twice as long as broad, projecting slightly anterior to carapace margin. Vertebrals generally wider than long, including V4 which is notably wide. Intercostal lateral seam contacts at M2, 5, 7, 9, and 11. Vertebrals without furrow, trough, keel or knobs in subadults and adults. Very vague, low midline bulge posteriorly on V5, extending toward supracaudal notch, causing very mild keeling at posterior end of shell, more prominent in large adults than subadults. Juveniles with low inconspicuous vertebral bulges on V1-5 and costals.

Carapace color in preserved specimens medium to light brown with extensive thin black reticulations radiating in a well-delineated radial pattern on all vertebrals, costals and marginals. Center of radiating pattern located at site of original juvenile scute: posteriorly in midline on vertebrals, posteromedially on costals, and posterolaterally on marginals. Pattern as distinct in large adults as in juveniles. Black lines generally same thickness or thinner than interspersed brown base color. Color demarcation sharp and clear, with pattern extending fully to edge of marginal rim. Carapace color in live specimens brown with black reticulations and thin yellowish orange carapacial edge (Vaz-Ferreira and Sierra de Soriano, 1960).

Plastron. Plastron (Fig. 2) broad, length averaging 1.82 times width, carapace width averaging 1.60 times plastron width, anteriorly truncate, posteriorly slightly narrower. Anal notch moderately deep. Very small axillary and inguinal scutes present. Intergular short and broad. Plastral seam length formula Fem $>$ Ig $\geq$ An $>$ Abd $\geq$ Pect $\geq$ Hum.

Plastron color in preserved specimens yellowish brown, occasionally oxidized to darker brown. Immaculate on all ventral surfaces, though occasional large specimens with indistinct dorsal type color pattern on posterior ventral margin-

Figure 1. Dorsal view of carapace of ZMB 6858, a paratype of *P. williamsi*. Note the clearly delineated fine radiating reticulations.

als. Plastron color yellow in live specimens (Vaz-Ferreira and Sierra de Soriano, 1960).

Head and Neck. Head width moderately narrow, becoming relatively narrower as compared to carapace length with allometric growth (Fig. 8). Neck length fairly short.

Head and neck with distinctive color pattern (Fig. 3), primarily dark dorsally and light ventrally, characterized by three subparallel broad black bands. The uppermost band serves as the ventral border of the dark dorsal head and neck pattern, extending from the nostrils through the eye, through the upper one

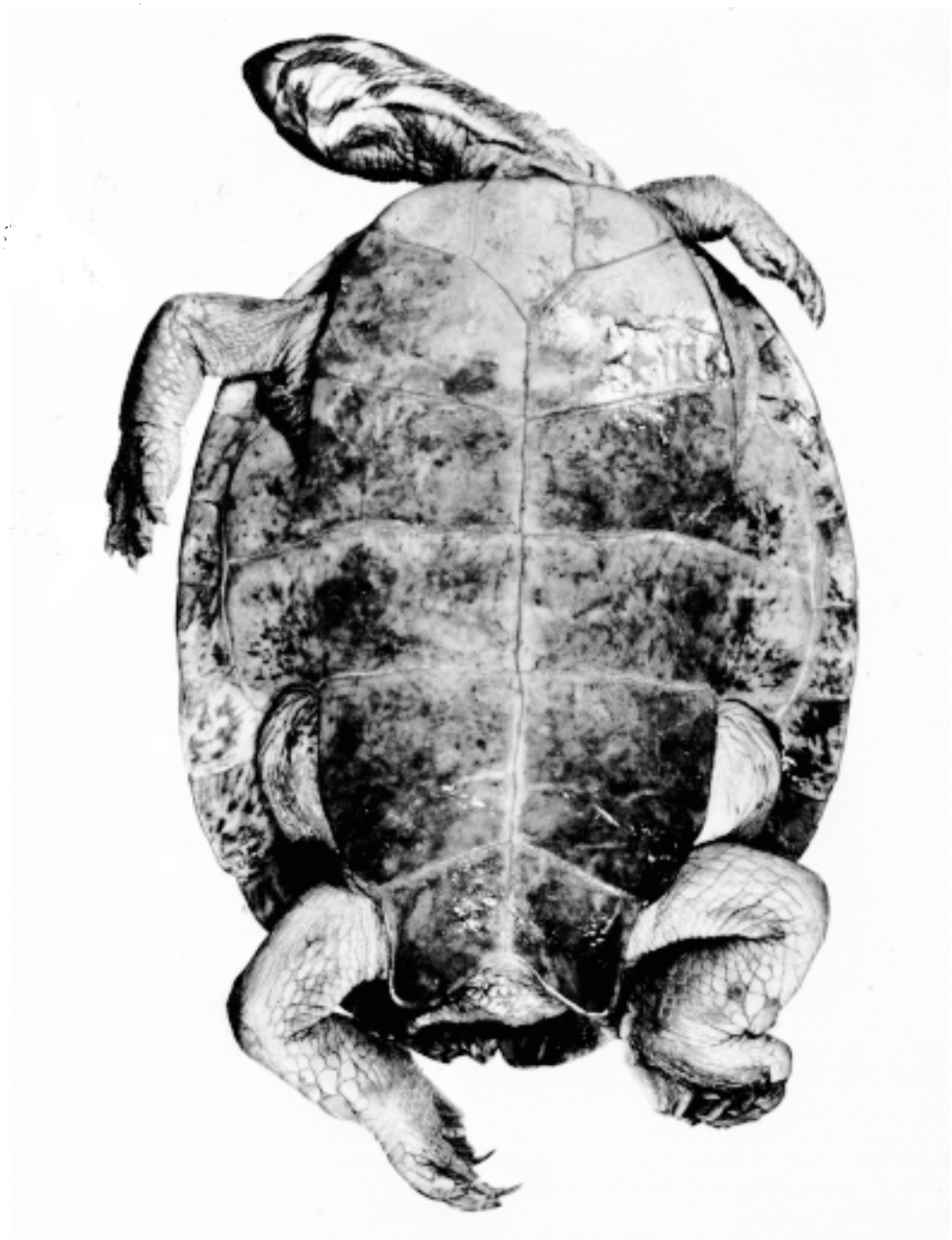

Figure 2. Ventral view of BMNH 84.2.5.3, a paratype of *P. williamsi.* Indistinct reticulations can be seen on marginals posterior to bridge.

Figure 3. Ventral and lateral views of head and neck of MCZ 64135, the holotype of *P. williamsi*. Ventral photograph slightly retouched to obscure small laceration present on specimen itself.

third to one half of the tympanum, and then along the mid-lateral surface of the neck, gradually fading caudally. The lowermost band forms a posteriorly directed horseshoe-shaped figure on the ventral chin, extending anteriorly to the base of the barbels, usually sharply discontinuous posteriorly, with an interruption at the level of the posterior border of the tympanum, before continuing for a short distance as short subparallel bands or elongate spots. The intermediate band extends caudally from the angle of the jaws, serving as a continuation of thin bands of dark pigment on the external tomial surfaces of the inferior portion of the maxillary and superior portion of the mandibular horny sheaths. The band then continues along the inferior border of the tympanic membrane and ventrolaterally along the neck, ending abruptly at approximately the same level as the last band or spot in the lowermost band. These three broad bands are usually totally separate from one another. Of seven specimens examined (including specimens figured in the literature), none had a connection between the upper and intermediate bands. Three out of seven specimens had very thin connections between the lower and intermediate bands posterior to the tympanum, two of them only unilateral and one with thin bilateral connections. One out of seven specimens had a discontinuous ventral horseshoe, narrowly lacking midline contact under the chin. The dorsal head pattern is relatively indistinct, composed of a dark background with narrow indistinct lighter lines subparallel to the uppermost dark band.

Live color of dorsal surface of head black with whitish lines, ventral surface of chin and neck reddish yellow or yellow with black bands (Vaz-Ferreira and Sierra de Soriano, 1960).

Two barbels present on the ventral surface of the chin, arising from the anterior portion of the horeshoe band. Barbels often unpigmented, though one sometimes the same color as the band.

Skin of top of snout, interorbital region and middle third of top of head adherent to bone, incompletely divided into apparent scales. Remaining dorsal surface of head (above temporal muscles) with more regular polygonal scales. Skin of dorsal aspect of neck plicate with only occasional more or less well defined papillae. Skin of ventral aspect of neck shallowly plicate, reticulate.

Limbs. Dorsal aspect of limbs with indistinct dark vermicular pattern. Ventral aspect light colored, juvenile with few scattered spots and vermiculations. Enlarged scales forming prominent swim flap on free ulnar skin edge of anterior limbs. Three pre-tibial scales enlarged, with the distal one prominent and cornified, resembling a blunt claw. No pretibial flap or ischial tuberosities. Claws numbering five on forelimbs, four on hindlimbs. Color of limbs in life blackish

TABLE 1. *PHRYNOPS WILLIAMSI* EXTERNAL MEASUREMENTS AND BASIC RATIOS.*

Specimen Number	*Sex*	*CL*	*CW*	*CD*	*PL*	*PW*	*HW*	*CL/CW*	*CL/CD*	*CL/HW*	*CW/PW*	*PL/PW*
MNRJ 3146	juv	77	67	28	65	40	16.0	1.15	2.75	4.81	1.68	1.63
MZUSP 2675	? ♀	140	108	40	119	70	24.0	1.30	3.50	5.83	1.54	1.70
MZVC-R 193†	♂	141	117					1.21				
MCZ 64135	? ♀	180	138	59	162	89	29.0	1.30	3.05	6.21	1.55	1.82
ZMB 6858	? ♂	201	154	54	171	92	31.5	1.31	3.72	6.38	1.67	1.86
BMNH 84.2.5.1	♀	243	179	70	206	112	38.0	1.36	3.47	6.39	1.60	1.84
BMNH 84.2.5.3	♀	252	183	79	212	112	37.5	1.38	3.19	6.72	1.64	1.89
MZVC-R 192†	♀	305	214					1.43				
Freiberg s/n†	♀	330	220					1.50				

*CL = carapace length, CW = carapace width, CD = carapace depth, PL = plastron length, PW = plastron width, HW = head width (tympanic). All measurements in mm.
†Recorded from the literature (Vaz-Ferreira and Sierra de Soriano, 1960; Freiberg, 1970).

TABLE 2. *PHRYNOPS WILLIAMSI* SKULL MEASUREMENTS AND BASIC RATIOS.*

Specimen Number	*CL*	*SL*	*SWT*	*SWM*	*SD*	*IOW*	*OW*	*PW*	*PtW*	*CL/SL*	*SL/SWT*	*SL/SWM*	*IOW/OW*	*IOW/PW*	*PW/PtW*	*SL/SD*	*PW/SWT*
ZMB 6858	201	35.8	30.0	20.2	11.8	6.0	7.5	11.8	12.8	5.61	1.19	1.77	0.80	0.51	0.92	3.03	0.39
BMNH 84.2.5.3	252	44.5	35.5	24.5	14.5	7.6	8.6	12.8	16.0	5.66	1.25	1.82	0.88	0.59	0.80	3.07	0.36

*CL = carapace length, SL = skull length (condylobasilar), SWT = skull width (tympanic), SWM = skull width (maxillary), SD = skull depth (midline, posteriorly), IOW = interorbital width, OW = orbital width, PW = parietal width (minimal), PtW = pterygoid width (minimal). All measurements in mm.

brown dorsally, reddish yellow or yellow ventrally, with red webbing on feet and red swim flap on forelimb (Vaz-Ferreira and Sierra de Soriano, 1960).

Sexual Dimorphism and Size. Sexual dimorphism not apparent from series examined. Large specimens with deep shells, short tails and flat plastrons represent females. No obvious males with shallow shells, long tails and concave plastrons present in series, but Vaz-Ferreira and Sierra de Soriano (1960) figure a 141 mm male with a long, thick tail. The largest specimen examined measured 252 mm carapace length, but Vaz-Ferreira and Sierra de Soriano (1960) recorded a specimen measuring 305 mm and Freiberg (1970) measured a 330 mm individual.

OSTEOLOGY

Skull. Rather than describe the skull of *P. williamsi* in detail, we prefer to discuss it in relation to other *Phrynops* and chelid skulls. We have examined two skulls of *P. williamsi* and have compared them to 47 skulls of other *Phrynops* (representing all known species), of which 22 represent other members of the *P. geoffroanus* complex. Most of this comparative material represents our unpublished data. However, Gaffney (1977) has discussed and figured skulls of *P. hilarii* (as *"P. geoffroanus"*) and *P. gibbus*, and we provide figures of *P. williamsi* (Figs. 4, 5) and *P. geoffroanus* (Figs. 5, 7) in this work. Other species mentioned (e.g., *P. rufipes, hogei, vanderhaegei*) will be fully discussed and figured in future publications. Table 2 lists all skull measurements and ratios for the two skulls of *P. williamsi* examined.

A number of features distinguish the skull of *P. williamsi* from the other members of the *geoffroanus* complex. In fact, it is among the most distinctive of all *Phrynops* skulls in many respects.

The lateral extent of the parietal roof is greater than in most other *Phrynops*, the sides being nearly parallel. There is considerably less posterior temporal emargination, with relative loss of overlap between the anterior and posterior temporal emarginations (slight overlap in the larger specimen). The temporal arch is shorter and thicker than in other *Phrynops*. There is very little lateral maxillary protrusion, but two other *Phrynops* (*hogei* and *rufipes*) show less protrusion, and other young *geoffroanus* complex species can have the same extent. This characteristic is ontogenetically variable and larger *williamsi* have a slightly more developed protrusion.

The two processi trochlearis pterygoidei show wide divergence from the longitudinal axis of the skull, making a ca. 70 to 90° angle with each other when viewed from above. No other *Phrynops* shows this condition, though *hogei* reaches 50 to 60° and *rufipes* 60 to 70°. All other *Phrynops* have an angle of 45° or less. The maxillary triturating surface has a moderately well-developed short lingual ridge anterior to the choanae, a condition not seen in any other *Phrynops*. Compared to other *geoffroanus* complex species, the anterior maxillary region of *williamsi* is much more pronounced and robust with a thicker, heavier maxilla, an angular rather than rounded snout, a wider maxillary triturating surface especially anteriorly and the presence of short lingual ridges. The only other *Phrynops* with prominent ventral snout development are *hogei* and *rufipes*, with *gibbus* and *vanderhaegei* showing an intermediate condition.

The mandible of *williamsi* is very distinctive, with the triturating surface being markedly widened and extremely flattened, coming very close to the horizontal. This is totally unlike other *geoffroanus* complex species or any other *Phrynops*, including *hogei* and *rufipes*. It most closely resembles the condition seen in the South American pelomedusine turtle *Podocnemis sextuberculata*. This shovel-like appearance of the mandible may represent a specialized adaptation to bottom feeding.

The exoccipitals of *williamsi* do not

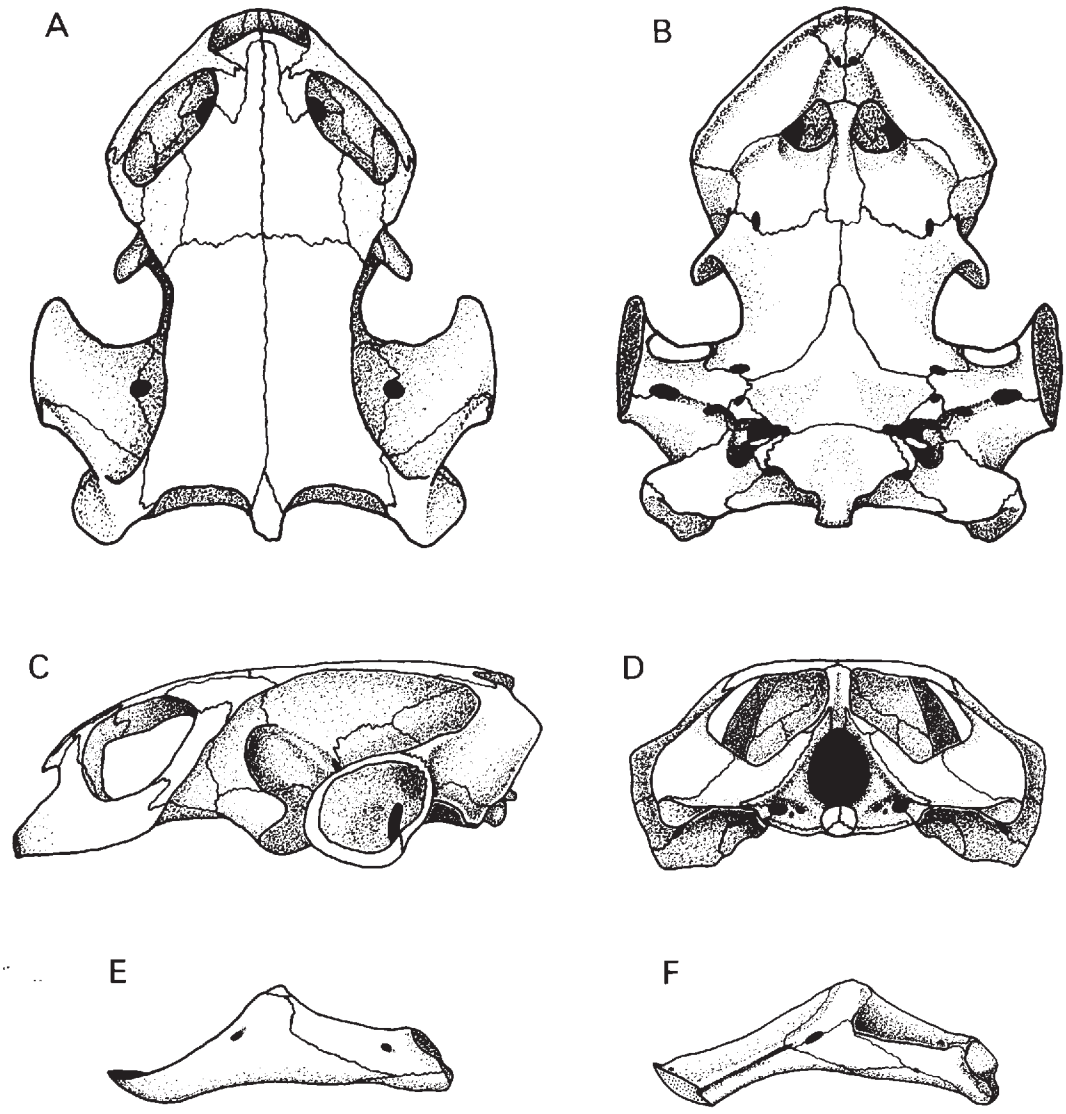

Figure 4. Osteology of skull and mandible of *P. williamsi* (ZMB 6858). A. dorsal view; B. ventral view; C. lateral view; D. posterior view; E. lateral view of mandible; F. medial and slightly dorsal view of right half of mandible. Refer to Gaffney (1979) and Rhodin and Mittermeier (1976) for skull nomenclature.

meet above the foramen magnum, being moderately separated by the supraoccipital. This feature is also shared by *hogei* and *rufipes*. The same feature, though less pronounced with only narrow separation, is variably present in *vanderhaegei*, *gibbus*, *hilarii* and *geoffroanus*. The normal condition in these species is either a narrow or moderate exoccipital contact. No other South American chelid has separated exoccipitals, the feature being shared only by the Australopapuan genera *Emydura*, *Elseya*, and *Pseudemydura* (Gaffney, 1977).

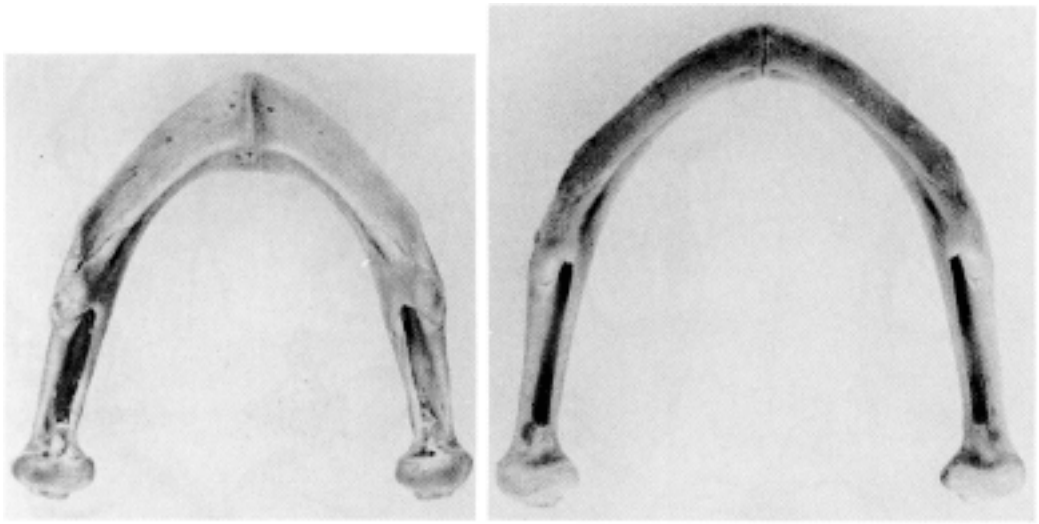

Figure 5. Dorsal views of mandibles of *P. williamsi* (*left*, BMNH 84.2.5.3) and *P. geoffroanus* (*right*, MZUSP 50; Rio Grande, Sao Paulo, Brazil; carapace length 250 mm, skull condylobasilar length 44 mm). Note markedly widened and flatter triturating surface in *P. williamsi*. Photographic enlargement slightly greater for *P. geoffroanus*.

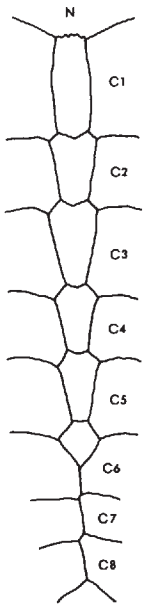

Figure 6. Neural bones of *P. williamsi* (BMNH 84.2.5.1).

The foramina nervi trigemini of *williamsi* face laterally, and are not visible from the dorsal aspect of the skull. In other *geoffroanus* complex species the foramina face dorsally and are easily visible from the dorsal aspect. The flattened horizontal portion of the pterygoid flare is relatively reduced in *williamsi* so that only a very small portion of the pterygoid is visible from the dorsal aspect of the skull. In other *geoffroanus* complex species the pterygoid flare is quite wide so that a broad expanse of pterygoid is visible from the dorsal aspect.

The postorbital wall of *williamsi* has a distinct sulcus jugalis and the medial portions of the jugal and postorbital face more posteriorly than all other *Phrynops*, where this wall faces more dorsolaterally and has a less well-developed sulcus jugalis.

The features of widely divergent trochleas, deep sulcus jugalis with overlying parietal roof, posteriorly facing postorbital wall, shovel-like appearance of

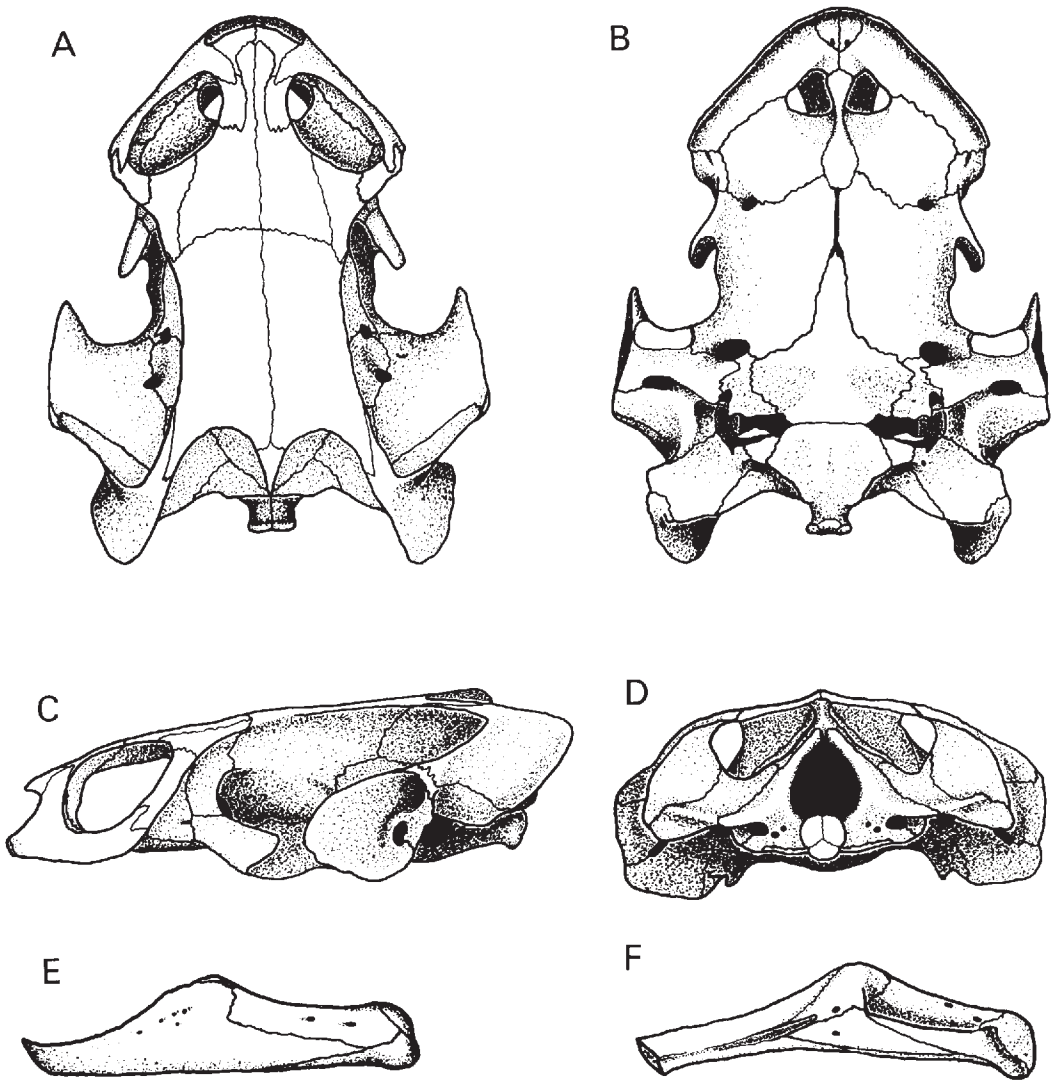

Figure 7. Osteology of skull and mandible of *P. geoffroanus* (MZUSP 2680; Ilha Solteira, Rio Parana, São Paulo, Brazil; carapace length 172 mm, skull condylobasilar length 33.7 mm). Views same as in Fig. 4.

the mandible and robust widened anterior maxillary triturating surface with lingual ridges appear to all represent feeding adaptations. The power of jaw closure is heightened through increased muscle mass in the anterior portions of the jaw adductors combined with divergent trochleas which improve leverage. This increased muscle mass is most prominent in the relatively enlarged area of the postorbital wall and sulcus jugalis. The modified triturating surfaces appear adapted for bottom feeding and crushing of large hard food such as snails or small bivalves. Other *Phrynops* do not possess this spectrum of characteristics

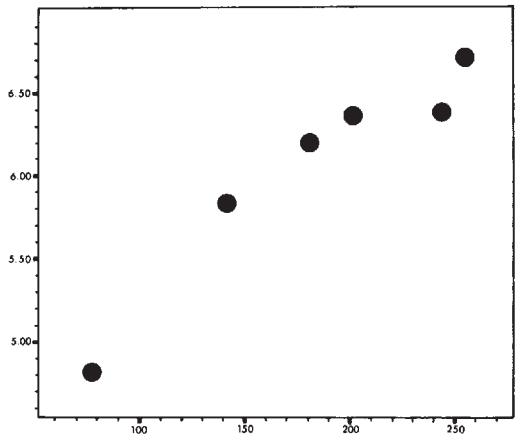

Figure 8. Head width in *P. williamsi*. Plot of carapace length in mm (abscissa) versus carapace length divided by head width (ordinate).

and many of them are known to be predatory feeders. Unfortunately, nothing is known of the feeding habits of *williamsi*.

The wide parietal roof, lack of exoccipital contact above the foramen magnum and widely divergent trochlear processes of *P. williamsi* appear to be primitive features within the genus *Phrynops*. These features show a similarity to the pelomedusine turtles of the genus *Podocnemis* as well as the Australopapuan chelids of the genera *Elseya, Emydura,* and *Pseudemydura* (see Gaffney, 1977 and McDowell, 1983). The robust anterior maxillary triturating surfaces with lingual ridges and shovel-shaped mandible may be primitive features, but more likely represent unique derived characters within the genus *Phrynops*, showing secondary convergence with *Podocnemis sextuberculata* due to similar feeding strategy.

Cervicals. One specimen examined has the typical central articulation pattern of all Chelidae as described by Williams (1950): (2(3(4(5)6)7(8).

Neurals. Six large contiguous neurals present (Fig. 6). N1 ca. twice as long as N2-5. N6 half as small as N2-5. N1 contacting nuchal widely, broadly rectangular. N2-5 roughly hexagonal, tapering posteriorly. N6 small and pentagonal, only partly separating C6. Pattern identical in the two specimens examined.

REPRODUCTION

No field data are available on eggs, nests or hatchlings of *P. williamsi*. One specimen, BMNH 84.2.5.3, a 252 mm female collected somewhere in Rio Grande do Sul, contained nine white, oval, brittle shelled oviductal eggs (four in the left oviduct, five in the right). The average egg size in this series was 33.3 × 27.0 mm with length ranging from 32.9–34.2 mm and width ranging from 26.7–27.6 mm. It is unclear when the specimen was collected, but egg deposition probably occurs in either November or December. *Phrynops hilarii* in northeastern Argentina nests in November (Gallardo, 1980) and in Rio Grande do Sul nests from late October to early January, with the peak activity occurring in November (Reischl *et al.*, 1979). *Pseudemys dorbignyi* (Emydidae) from the same area has the same nesting season but peaks primarily in December (Reischl *et al.*, 1979).

Clutch size in *P. hilarii* is apparently somewhat larger than in *P. williamsi*. In Rio Grande do Sul clutch size of *P. hilarii* averages 11, with the incubation period taking 105 to 140 days (Reischl *et al.*, 1979). Serrano (1977) notes that *P. hilarii* in Rio Grande do Sul lays clutches averaging 13.4 eggs (range 1–20) with spherical eggs measuring 33±4 mm in diameter. Saporiti (1960) indicates that *P. hilarii* in Buenos Aires lays 10 to 14 subspherical eggs averaging 32.9 × 30.8 mm in size. Cohen (personal communication) had a captive specimen lay 17 eggs averaging 36.1 × 33.8 mm in size.

Few comparative data are available for *P. geoffroanus* and *tuberosus*. Wied (1825) noted that populations of *P. geoffroanus* inhabiting the rivers of eastern coastal Brazil (e.g., Rios Pardo, Jequitinhonha, and Mucuri) laid from 12 to 18 spherical eggs from December through

February. Medem (1969) recorded three nests of *P. tuberosus* from Colombia as having from 10 to 18 subspherical eggs with average size measuring 33.9 × 32.5 mm. We have examined a specimen of *P. geoffroanus* from the Rio Tapajós, Pará, Brazil (MZUSP 2682) containing 13 subspherical shelled eggs, average size measuring 30.5 × 29.0 mm.

HABITAT

Vaz-Ferreira and Sierra de Soriano (1960) obtained two specimens at Picada del Negro Muerto, Uruguay, where the Rio Cuareim flows relatively rapidly over a rocky streambed. Hensel (1868) noted that the species occurred in the "rushing and stony brooks of the forest" and was not to be found in the slower lowland rivers with muddy bottoms.

DISCUSSION

The species here recognized as *Phrynops williamsi* was first collected and described as *Platemys geoffreyana* (Schweigger, 1812) by Hensel (1868). His description of an animal he collected in 1865 at Pikada do Café, Rio Cadéa, Rio Grande do Sul fits perfectly our description of *P. williamsi*. Another specimen of the same species may have been observed at Estancia Velha, but Hensel's description of that animal is not as clear and it may have been based on a specimen of *P. hilarii*. Hensel states that he was able to obtain only a single specimen of "*P. williamsi*" on his trip. This specimen was collected at Pikada do Café, Rio Cadéa and had a carapace length of 202 mm (Hensel's measurement). The *P. williamsi* paratype allegedly collected by Hensel at Estancia Velha (ZMB 6858) has a carapace length of 201 mm, and if indeed collected by Hensel, probably represents the original Rio Cadéa specimen, though now mislabeled as coming from Estancia Velha.

The species was next collected by von Ihering, whose specimens served as the basis for Boulenger's (1889) description of *Hydraspis geoffroyana* (Schweigger). One of these specimens is our *P. williamsi* holotype, two others are paratypes.

Clear descriptions of animals referable to *P. williamsi* did not re-appear in the literature until Vaz-Ferreira and Sierra de Soriano (1960) figured and described specimens of *P. geoffroana geoffroana* from Uruguay. Some of these and others as well were described and figured by Freiberg (1970) and served as his basis for the specific separation of *P. hilarii* from *P. geoffroanus* based on their Uruguayan sympatry.

The characteristics of *P. williamsi* discussed above readily distinguish it from any other *Phrynops*, as well as from any other member of the *P. geoffroanus* complex. The black bands on the head and neck coupled with the reticulate carapace pattern immediately differentiate it from *P. gibbus, rufipes, hogei, nasutus, dahli, wermuthi, vanderhaegei,* and *tuberculatus*. *Phrynops hilarii* is distinguished by its black spots on a white plastron, immaculate carapace and markedly reduced head and neck bands (see photos in Freiberg, 1970, 1975). *Phrynops geoffroanus* and *P. tuberosus* represent two recognized populations of a very wide-spread species complex with marked geographic variation, consisting of several previously unrecognized and undescribed forms. In general, *P. williamsi* is distinguished from all of these populations by the combination of features listed. The most marked distinction is in skull morphology, but this is a feature not always available for identification purposes. The carapacial reticulations of *P. williamsi* are thinner, finer and more clearly well developed than in *P. geoffroanus* or *tuberosus* where they tend to be either broad and thick, irregular, unclear, or reduced. Most populations of *P. geoffroanus* and *tuberosus* have plastrons with varying degrees of a dark vermiculate pattern. However, some also have immaculate plastrons, so this

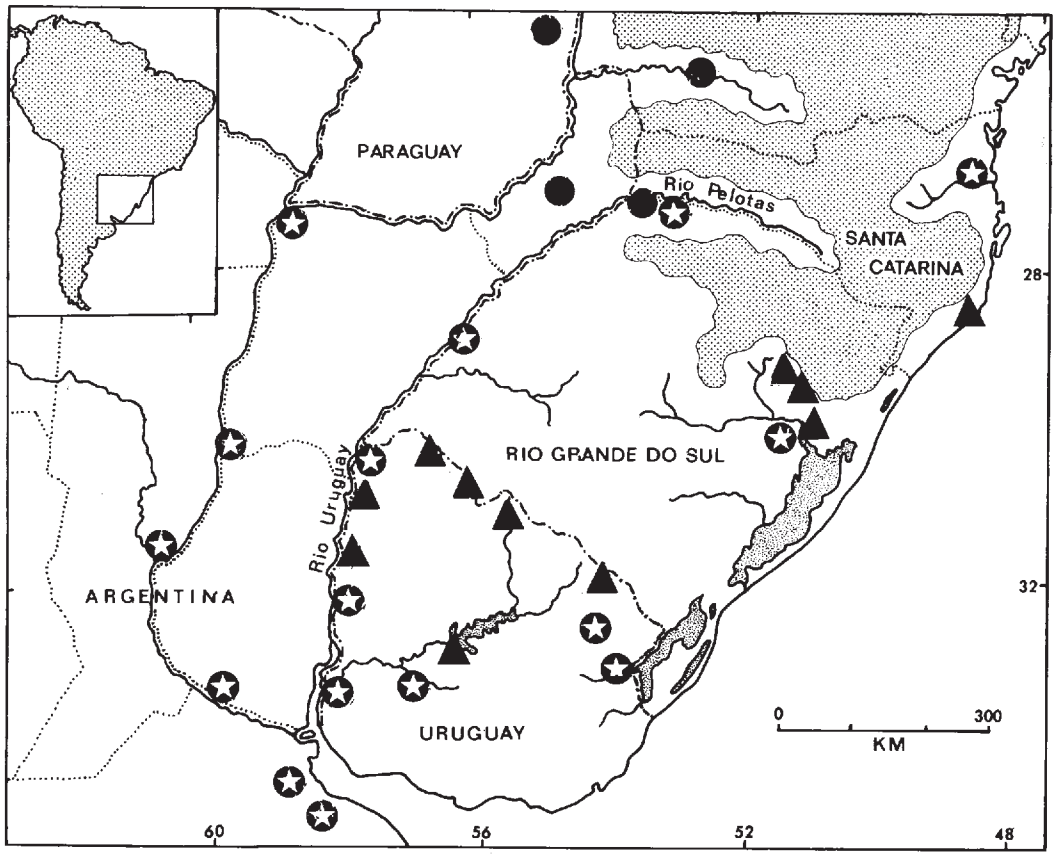

Figure 9. Map showing distribution of *P. williamsi* (▲), *P. geoffroanus* (●) and *P. hilarii* (✪). Geographic ranges of the latter two species only partially shown. Stippled areas correspond approximately to elevations greater than 500 m.

feature in itself is not diagnostic for *P. williamsi*. The black head and neck bands of *P. geoffroanus* and *tuberosus* are almost always relatively thin and usually confluent in several places. Some populations have very thin bands, others somewhat thicker ones, but none are as prominent as in *P. williamsi*. Though occasionally separated from each other, the facial bands of *P. geoffroanus* and *tuberosus* usually connect broadly either in front of the tympanum (intermediate and lower bands connecting), behind the tympanum (upper and intermediate bands connecting) or at several places along their course. Many populations have only two bands plus irregular vermiculations. A separate ventral horseshoe band is usually not present, though some specimens of one population of *P. geoffroanus* from eastern coastal Brazil occasionally exhibit this character as well.

Based on external morphology alone it would be difficult to determine whether *P. williamsi* is distinct from other *P. geoffroanus* and *P. tuberosus* at a specific or subspecific level. Though sympatric with *P. hilarii*, it is allopatric with respect to *P. geoffroanus*, the closest known

populations occurring approximately 300 km to the north in the Rio Pelotas drainage (Fig. 9). However, the intervening region has not been well collected, and a zone of sympatry may well exist. The distinct skull morphology of *P. williamsi* argues strongly for specific status. The unique combination of presumably primitive and derived features is not shared even by other *Phrynops*, let alone other members of the *P. geoffroanus* complex.

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APPENDIX: LOCALITY DATA

Italicized numbers represent specimens of *Phrynops williamsi* examined or confirmable literature records. BMNH = British Museum of Natural History; MCZ = Museum of Comparative Zoology, Harvard University; MHNM = Museo Nacional de Historia Natural, Montevideo; MNRJ = Museu Nacional, Rio de Janeiro; MZUSP = Museu de Zoologia da Universidade de São Paulo; MZVC-R = Museo de Departamento de Zoologia Vertebrados, Facultad de Ciencias, Universidad de la Republica, Montevideo; ZMB = Zoologisches Museum, Berlin.

BRAZIL: *Rio Grande do Sul:* MCZ *64135*, BMNH *84.2.5.1, 84.2.5.3*, Boulenger 1885, 1886, *1889*; Estancia Velha (29°39'S,51°11'W): ZMB *6858*, Hensel 1868; Pikada do Café, Rio Cadéa (29°37'S,51°15'W): Hensel *1868*; Pôrto Alegre (30°03'S,51°10'W): MZUSP *2675; Santa Catarina:* Tubarão (28°29'S,49°00'W): MNRJ *3146*. URUGUAY: *Artigas:* Freiberg 1970; Picada del Negro Muerto, Rio Cuareim (30°45'S,56°05'W): MZVC-R 192–3, Vaz-Ferreira and Sierra de Soriano *1960*; Salto de Agua del Penitente: MHNM 1582, Lema and Fabian-Beurmann 1977; *Paysandu:* Arroyo Chapicuy Grande (31°42'S,57°55'W): Freiberg *1970; Cerro Largo:* Arroyo Yaguarón (31°55'S, 53°55'W): MHNM s/n; *Rivera:* Arroyo Cunapirú (31°30'S,55°35'W): MZVC-R s/n; *Rio Negro:* Rincón del Bonete, Represa del Rio Negro (32°52'S, 56°27'W): Freiberg 1970; *Salto:* Rio Arapey (30°55'S,57°50'W): MHNM s/n.

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