



THE GENUS *PHILODRYAS* (WAGLER, 1830) (SERPENTES: DIPSADIDAE) IN PARAGUAY: DISTRIBUTION AND ECOLOGICAL AFFINITIES

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Abstract.- The snake genus *Philodryas* is distributed in South America and is characterized by having dorsal scale rows with reduction before the vent, rounded pupils, enlarged diastema in maxilla and opisthognath dentition. Nine species are recorded from Paraguay: *Philodryas aestiva*, *P. agassizii*, *P. baroni*, *P. livida*, *P. mattogrossensis*, *P. nattereri*, *P. olfersii*, *P. patagoniensis*, and *P. psammophidea*. Here we analyze 176 records from scientific collections and literature, and compare them with the ecoregions of Paraguay. Four species are present in the Atlantic Forest, Humid Chaco and Dry Chaco, two in the Pantanal and Central Paraguay and three in the Cerrado and the Mesopotamic Grasslands. *Philodryas aestiva* and *P. patagoniensis* are the species with higher number of records, being the latter more widely distributed in Paraguay. *Philodryas baroni* and *P. psammophidea* show a high degree of sympatry reaching a true homopatry in Paraguay. Since *P. livida*, *P. nattereri* are known from a single Cerrado locality is hard to establish their biogeographic characteristics compared to other species. The record of *Philodryas aestiva* from Presidente Hayes Department is the first record of the species in the Humid Chaco ecoregion and represents the westernmost record of the species.

Key words: Ecoregions, Neotropics, *Philodryas*, sympatry.

Resumen.- El género de serpientes *Philodryas* se distribuye en Sudamérica y se caracteriza por tener reducción de escamas dorsales antes de la cloaca, pupilas redondeadas, un gran diastema en el maxilar y dentición opisthognata. En Paraguay nueve especies están registradas: *Philodryas aestiva*, *P. agassizii*, *P. baroni*, *P. livida*, *P. mattogrossensis*, *P. nattereri*, *P. olfersii*, *P. patagoniensis*, and *P. psammophidea*. Analizamos 176 registros de colecciones científicas y literatura, y comparamos estos con las Ecorregiones de Paraguay. En total cuatro especies están presentes en el Bosque Atlántico, Chaco Húmedo y Chaco Seco, dos en el Pantanal y Paraguay Central y tres en el Cerrado y los Pastizales de la Mesopotamia. *Philodryas aestiva* y *P. patagoniensis* son las especies con mayor cantidad de registros, siendo esta última la de mayor distribución en Paraguay. *Philodryas baroni* y *P. psammophidea* muestran un alto grado de simpatria alcanzando una verdadera homopatria en Paraguay. *P. livida* y *P. nattereri* son conocidas de una única localidad en el Cerrado, lo que dificulta su comparación a escala biogeográfica con las demás especies. El registro de *Philodryas aestiva* del Departamento de Presidente Hayes es el primero en la ecoregion Chaco Húmedo y representa el registro más al oeste de la especie.

Palabras clave: Ecorregiones, Neotrópico, *Philodryas*, simpatria.

Philodryas is a South American snake belonging to the subfamily Xenodontinae (Grazziotin *et al.*, 2012). The genus is characterized by having dorsal scale rows with reduction before the vent, rounded pupils, an enlarged diastema in maxilla, opisthognath dentition, aggressive behavior and some species are harmful for humans (Thomas, 1976; Ceï, 1993; Carreira *et al.*, 2005). Recent studies placed the genus, along with *Ditaxodon*, in the Tribe Philodryadini (Zaher *et al.*, 2009; Grazziotin *et al.*, 2012). Nine species are currently known from Paraguay: *Philodryas aestiva*, *P. agassizii*, *P. baroni*, *P. livida*, *P. mattogrossensis*, *P. nattereri*, *P. olfersii*, *P.*

patagoniensis, and *P. psammophidea* (Cacciali, 2009; Smith *et al.*, 2013; Smith *et al.*, 2014).

Thomas's (1976) unpublished dissertation extensively revised the genus, providing data mainly on distribution, taxonomy and morphological variation. The author also provided an identification key for species and subspecies. Other studies on distribution and ecological affinities of *Philodryas* are Vitt (1980), Ceï (1993), Giraudo (2002), Giraudo & Scrocchi (2002), Carreira *et al.* (2005) and Hartmann & Marques (2005). Norman (1994), Leynaud & Bucher (1999) and Cacciali (2009) provided data on distribution and ecology of Paraguayan *Philo-*

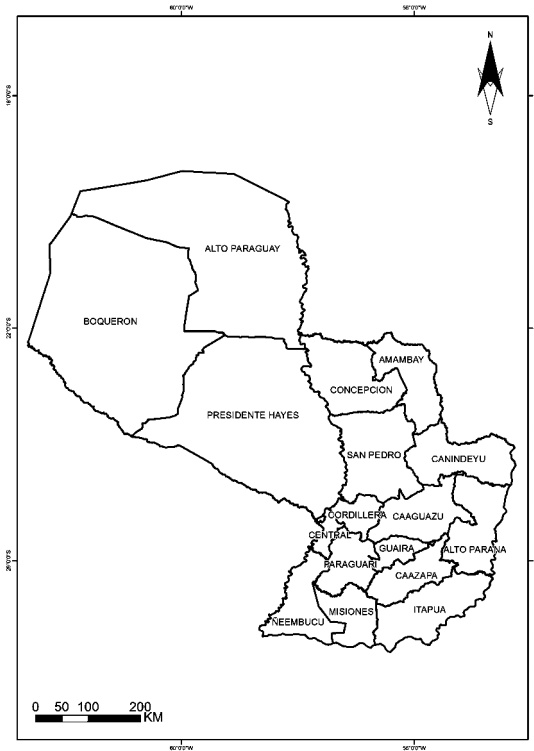


Figure 1. Map showing of the political division of Paraguay.

dryas aestiva, *P. baroni*, *P. mattogrossensis*, *P. olfersii*, *P. patagoniensis*, and *P. psammophidea*.

This paper updates the knowledge about the distribution and ecological affinities of the genus *Philodryas* in Paraguay.

MATERIALS AND METHODS

Paraguay has an area of 406,752 km² divided into two regions, the “Chaco Paraguayo” or “Western Region” at the west of Paraguay River and the “Eastern Region” at the east (Figure 1). We follow Dinerstein *et al.* (1995) for ecoregional references, with modifications made by Del Castillo & Clay (2005) and Cacciali (2010) (Figure 2).

Specimens examined are listed in Appendix I. They came from the following collections:

CBMI-R: Colección Biológica del Museo de Itaipú-Reptiles (Hermandarias, Paraguay).

CZ-FaCEN: Colección Zoológica de la Facultad de Ciencias Exactas y Naturales (San Lorenzo, Paraguay).

CZPLT: Colección Zoológica Para la Tierra (Santa Rosa del Aguaray, Paraguay).

MNHNP: Museo Nacional de Historia Natural del Paraguay (San Lorenzo, Paraguay).

AMNH: American Museum of Natural History (New York, U.S.A.).

UNNEC: Colección Herpetológica de la Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste (Corrientes, Argentina).

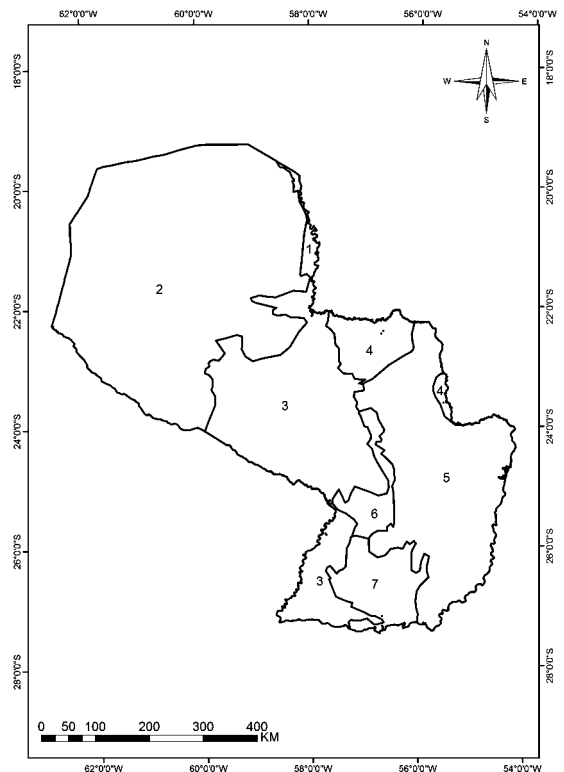


Figure 2. Ecoregions of Paraguay extracted from Cacciali (2010). (1) Pantanal. (2) Dry Chaco. (3) Humid Chaco. (4) Cerrado. (5) Atlantic Forest. (6) Central Paraguay. (7) Mesopotamian Grassland.

Criteria for biological distributions follow Papavero *et al.* (1994) where homopatry is the perfect congruence of two or more distributions, endopatry is when a taxon's distribution is completely included within another distribution, allelopatry is when the distribution of two or more taxa partially overlap, and allopatry when there is no overlap between distributions. Records were digitized and plotted using ArcGis 10.

Taxonomy follows Grazziotin *et al.* (2012). Given that subspecies validity of *P. aestiva* and *P. olfersi* is still under discussion (D'Agostini, 1998; Achaval, 2001; Giraud, 2002; Giraud & Scrocchi, 2002; Carreira *et al.*, 2005; Ávila *et al.*, 2009), here we consider them as separate species.

RESULTS

We analyzed 176 records of the following species: *Philodryas aestiva* (52), *P. agassizii* (1), *P. baroni*, (5), *P. mottogrossensis* (21), *P. nattereri* (3), *P. olfersii* (31), *P. patagoniensis* (54), and

P. psammophidea (9). Records of *P. livida* are based on Smith *et al.* (2014). In Table 1 we present relations among taxa and ecoregions.

Philodryas aestiva (Duméril, Bibron and Duméril, 1854)

(Figs 3-4)

Type locality: South America.

Distribution: Northern and central Argentina, southeastern Brazil, Bolivia, Paraguay, and Uruguay (Thomas, 1976; D'Agostini, 1998; Giraud & Scrocchi, 2002; Cacciali, 2009; Celsi *et al.*, 2008). In Paraguay it is represented by specimens from Canindeyú, Caaguazú, Itapúa, San Pedro, and Presidente Hayes departments (Figure 4). Most of the specimens came from the sampling effort on Isla Yacyreta (Itapúa) following the completion of the Yacyreta hydroelectric dam on the Paraná River (See Specimens examined in Appendix I).

Ecological affinities: In Alto Paraná Atlantic Forest, Humid Chaco, Mesopotamian Grasslands ecoregions and the transitional



Figure 3. *Philodryas aestiva*. Specimen MNHNP 4938 (Photograph: Nicolás Martínez).

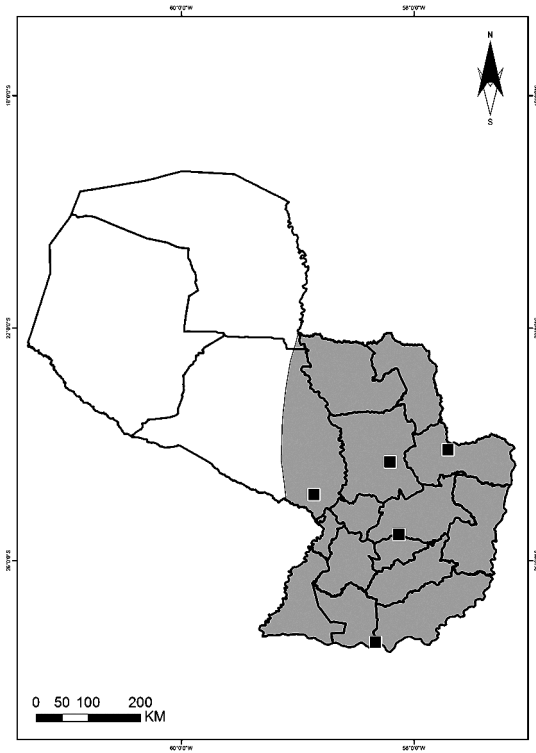


Figure 4. Distribution of *Philodryas aestiva* in Paraguay.

zones between them. It is associated to moist environments.

***Philodryas agassizii* (Jan, 1863)**

(Fig. 5)

Type locality: Uruguay.

Distribution: Northeastern of Argentina, central, south and southeastern Brazil and Uruguay (Peters & Orejas-Miranda, 1970; Giraudo & Scrocchi, 2002; Carreira *et al.*, 2005; Marques *et al.*, 2006; Pérez *et al.*, 2012). This is a very rare snake in Paraguay, only known from one specimen without specific locality data.

Ecological affinities: Unknown in Paraguay.

***Philodryas baroni* Berg, 1895**

(Figs 6-7)

Type locality: Tucumán and Riacho de Oro, Chaco, Argentina.

Distribution: Central and northern Argentina, Bolivia, and Paraguay (Thomas, 1976; Leynaud & Bucher, 1999; Giraudo & Scrocchi, 2002; Cacciali, 2009). In Paraguay, this species is recorded just from Boquerón Department (Figure 7).

Ecological affinities: In the Dry Chaco ecoregion, an environment with xerophytic



Figure 5. *Philodryas agassizii*. Laguna Capitán, Presidente Hayes, Paraguay (Photograph: Paul Smith).



Figure 6. *Philodryas baroni*. Campo Iris, Boquerón, Paraguay (Photograph: Chris Englehardt).

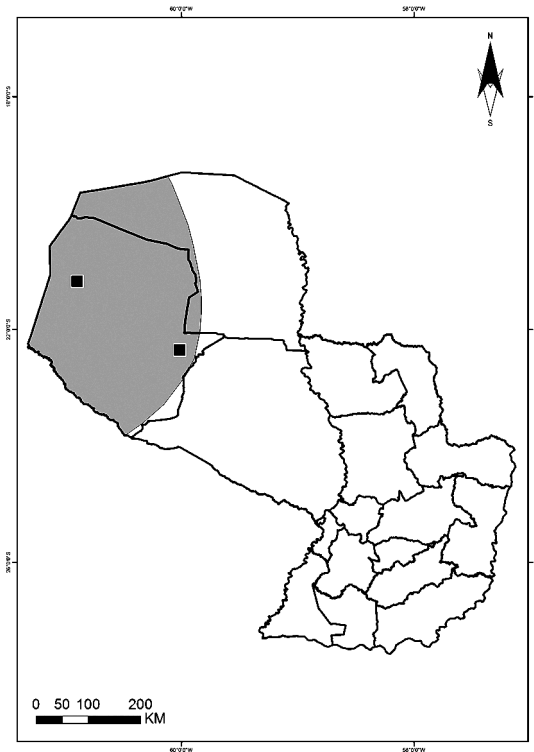


Figure 7. Distribution of *Philodryas baroni* in Paraguay.

vegetation, clayish or sandy soils, and scattered dunes with short and spiny vegetation.

***Philodryas livida* (Amaral, 1923)**

(Figs 8 and 12)

Type locality: Guaicurús, Mato Grosso do Sul, Brasil.

Distribution: Central and southeast Brazil (Peters & Orejas-Miranda, 1970; Thomas & Fernandes, 1996), and recently recorded from Reserva Natural Laguna Blanca (San Pedro Department) in the north of the Eastern Region of Paraguay (Figure 12) (Smith *et al.*, 2014).

Ecological affinities: Its habitat in Paraguay is Cerrado (Smith *et al.*, 2014).

***Philodryas mattogrossensis* Koslowsky, 1898**

(Figs 9-10)

Type locality: Miranda, Mato Grosso, Brazil.

Distribution: Northern Argentina, southern Bolivia, southwestern Brazil and northwestern



Figure 8. *Philodryas livida*. Laguna Blanca, San Pedro, Paraguay. (Photograph: Paul Smith).



Figure 9. *Philodryas mattogrossensis*. Specimen MNHNP 6525 (Photograph: Nicolás Martínez).

Paraguay (Peters & Orejas-Miranda, 1970; Thomas, 1976; Leynaud & Bucher, 1999; Giraudo & Scrocchi, 2002; Cacciali, 2009). In Paraguay

there are two populations with marked allopatry: one in the departments of Alto Paraguay, Boquerón, and Presidente Hayes, and the other

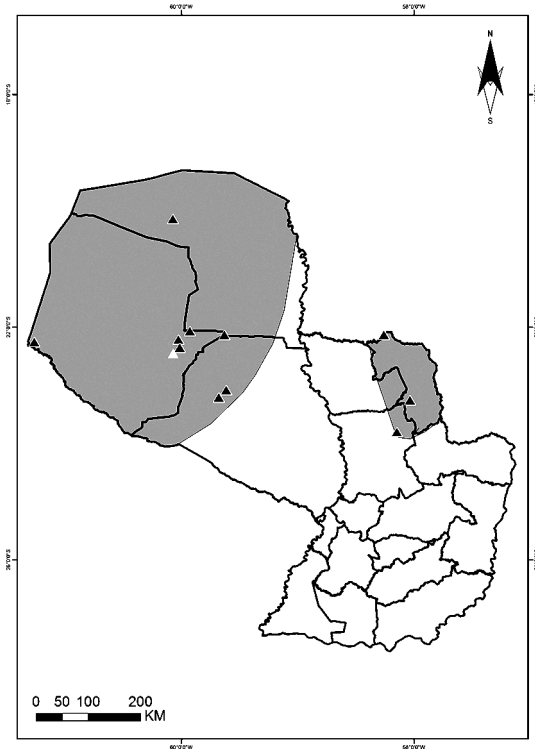


Figure 10. Distribution of *Philodryas mattogrossensis* in Paraguay. White triangle corresponds to the record by Ziegler *et al.* (2002).

in Amambay and San Pedro departments, east of Paraguay River (Figure 10).

Ecological affinities: In the Dry Chaco and Cerrado, being absent in wet intermediate areas between these two environments (Thomas, 1976; Amaral, 1977; Norman, 1994; Cacciali, 2009).

***Philodryas nattereri* (Steindachner, 1870)**
(Figs 11-12)

Type locality: Mato Grosso, Brazil.

Distribution: Northeastern and southwestern Brazil and Colombia (Thomas, 1976; Amaral, 1977; Mattos *et al.*, 2011). Peters & Orejas-Miranda (1970) record this species from Paraguay without specific localities. However, it was recently found in Laguna Blanca Natural Reserve in San Pedro Department (Figure 12) (Smith *et al.*, 2013).

Ecological affinities: The only Paraguayan record is related to Cerrado. This snake seems to be associated with relatively dry and semi-arid zones (Thomas, 1976; Amaral, 1977; Vitt, 1980).



Figure 11. *Philodryas nattereri*. Laguna Blanca, San Pedro, Paraguay. (Photograph: Karina Atkinson).

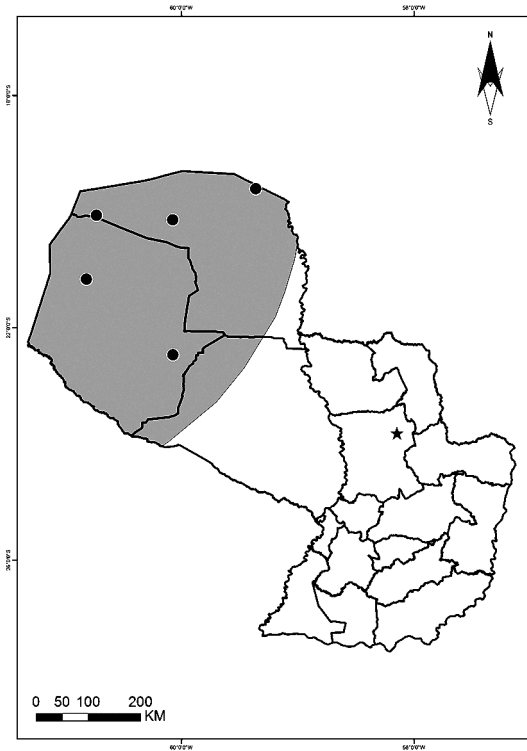


Figure 12. Distribution of *Philodryas nattereri*, *P. livida* (star) and *P. psammophidea* (circles).

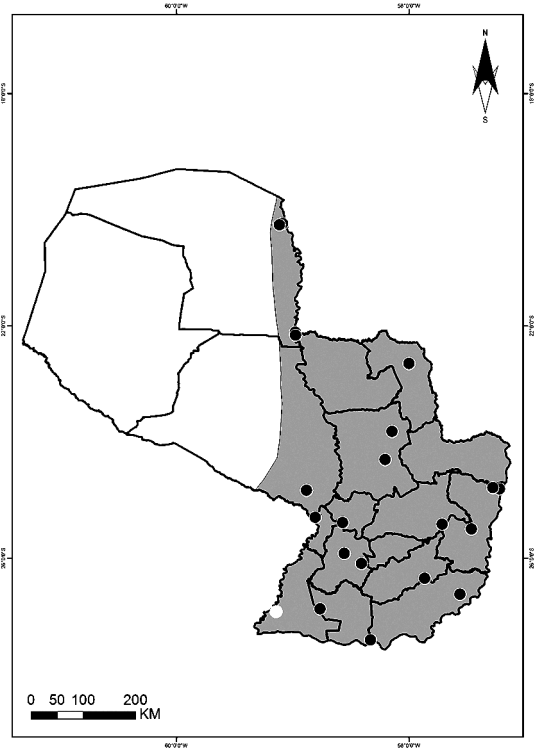


Figure 14. Distribution of *Philodryas olfersii* in Paraguay. White circle: record by Giraudo & Contreras (1994).



Figure 13. *Philodryas olfersii*. Without locality data. (Photograph: Pier Caccioli).

***Philodryas olfersii* (Lichtenstein, 1823)**

(Figs 13-14)

Type locality: Brazil

Distribution: From Colombia, Venezuela, and Guayanas, southwards through Brazil and Bolivia, to central Argentina and Uruguay (Peters & Orejas-Miranda, 1970; Thomas, 1976; Giraudo & Scrocchi, 2002; Cacciali, 2009). In Paraguay, the species is present in almost all the departments of the Eastern Region, and in Alto Paraguay and Presidente Hayes departments in the Western Region (Figure 14).

Ecological affinities: In Atlantic Forest, Cerrado, Humid Chaco, Central Paraguay, Mesopotamian Grasslands and Pantanal ecoregions, associated with dense forest and open areas (Thomas, 1976; Giraudo, 2002).

***Philodryas patagoniensis* (Girard, 1857)**

(Figs 15-16)

Type locality: Mouth of the Rio Negro, Patagonia, Argentina.

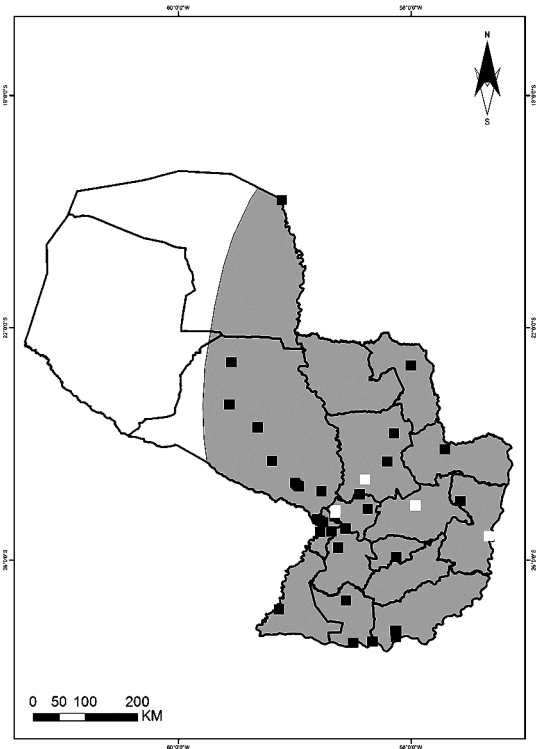


Figure 16. Distribution of *Philodryas patagoniensis* in Paraguay. White squares: records of Thomas *et al.* (1977).



Figure 15. *Philodryas patagoniensis*. Without locality data. (Photograph: Pier Cacciali).

Distribution: Central and northern Argentina, central and east Bolivia, southeast Brazil, Paraguay, and Uruguay (Peters & Orejas-Miranda, 1970; Leynaud & Bucher, 1999; Giraudo & Scrocchi, 2002; Carreira *et al.*, 2005; Cacciali, 2009). In Paraguay, it can be found in the entire Eastern Region, and in Alto Paraguay and Presidente Hayes departments (Norman, 1994; Aquino *et al.*, 1996; Cacciali, 2009) (Figure 16).

Ecological affinities: The species seems to be widely distributed in the entire country, associated with all ecoregions. It inhabits open areas, such as grasslands, and Chaco forest (Thomas, 1976; Giraudo, 2002).

***Philodryas psammophidea* Günther, 1872**

(Figs 12 and 17)

Type locality: Tucumán, Argentina.

Distribution: Central and northern Argentina, Bolivia, central Brazil and western Paraguay (Thomas, 1976; Leynaud & Bucher, 1999; Giraudo & Scrocchi, 2002). In Paraguay it is distributed in Alto Paraguay and Boquerón

departments (Aquino *et al.*, 1996; Cacciali, 2009) (Figure 12).

Ecological affinities: Found exclusively in Dry Chaco, in the most xeric areas of the country.

DISCUSSION

In Paraguay there are nine species of *Philodryas* (Cacciali, 2009; Smith *et al.*, 2013; Smith *et al.*, 2014) being *P. aestiva* and *P. patagoniensis* the *taxa* with higher number of records. On the other hand, *P. livida* and *P. nattereri* are only known from a single locality and *P. agassizii* has a single record without specific locality data. *Philodryas patagoniensis* is the most widely distributed species of the genus in Paraguay and shows the greatest ecological versatility, being absent only from the Cerrado (Thomas, 1976; Norman, 1994; López & Giraudo, 2008; Cacciali, 2009).

Philodryas baroni and *P. psammophidea* show a high degree of sympatric overlaps in xerophytic environments, reaching a true ho-



Figure 17. *Philodryas psammophidea* Parque Nacional Teniente. Agripino Enciso, Boquerón (Photograph: Paul Smith).

mopatry in Paraguay. The western and eastern population of *P. mattogrossensis* also inhabits this xeric vegetation in the Dry Chaco, but it is also present in the Atlantic Forest, Cerrado, and Humid Chaco.

Philodryas baroni and *P. psammophidea* show an endopatric distribution with respect to *P. mattogrossensis*. There is also a high level of chorological overlap between *P. olfersii* and *P. patagoniensis*, and, to a lesser degree, among those two species and *P. aestiva*, whose distribution is more restricted to the eastern Region with only a few records west of the Paraguay River. Given that *P. livida* and *P. nattereri* are known from a single locality in the Cerrado ecoregion, it is difficult to establish their biogeographic characteristics in the country respect to their congeners, although this species could have a homopatric distribution with the Eastern populations of *P. mattogrossensis* due to the ecological traits of the habitats in which both species are present. The three species in Eastern Region are associated to Cerrado and zones between Cerrado and sub-humid deciduous forest (Smith *et al.*, 2013).

Basically, these results are consistent with previous studies. Thomas (1976) mentions that *P. aestiva* can be common in gallery forests, where they can be arboreal, also this species can be found in open formations, forested areas, and in urban areas. The record from Presidente Hayes Department is the first record of the species in the Humid Chaco ecoregion and represents the westernmost record of the species (Giraud, 2002; Cabrera, 2004; Carreira *et al.*, 2005; Celsi *et al.*, 2008; Ávila *et al.*, 2009).

With respect to *Philodryas agassizii*, Marques *et al.* (2006) stated that the species is a habitat specialist in southwest Brazil, inhabiting exclusively areas of shrubby grasslands, a typical Cerrado habitat. This snake has not been recorded in disturbed areas, and seems to be very susceptible to habitat changes (Marques *et al.*, 2006). Giraud (2002) recorded the species from Argentina from Santa Ana, Misiones Province,

and this record is about 3.25 km from the Paraguayan border. In Paraguay, it may be associated to the Cerrado, Humid Chaco and Mesopotamian Grasslands ecoregions: more studies are needed to confirm its presence in these habitats. *Philodryas baroni* is also a species with few records, although its ecological affinities are well known in Paraguay, restricted to the Dry Chaco being endemic to Chaco ecoregion (Leynad & Bucher, 1999; Cabrera, 2004; Cacciali, 2009).

Philodryas olfersii is found in areas with dense vegetation (Thomas, 1976). Vitt (1980), based on ecological observations, stated that *P. olfersii* inhabit terrestrial areas with dense vegetation in agreement with Thomas (1976). In Argentina this species is associated to forest, gallery forest and grasslands (Giraud, 2002). Ávila & Ferreira (2007) mentioned that in the Pantanal the species is related to rocky areas; in Paraguay, the species shows a preference for forests, gallery forests, grasslands, and shrublands.

Finally, Giraud (2002) recorded an individual of *P. psammophidea* in the northeast area of Corrientes Province, Argentina, far from its known distribution, but the collection data may be incorrect. In Paraguay all the records show an exclusive Chacoan distribution, fitting with the known distribution of the species in Argentina and Bolivia, in which it occurs associated with savannas and shrublands (Thomas, 1976; Cabrera, 2004). In Brazil are associated to chaparral and savannas in Matto Grosso state (Thomas, 1976).

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APPENDIX 1

Specimens Examined (all from Paraguay):

Philodryas aestiva: (52). PARAGUAY (MNHNP 2665, 9495). CAAGUAZÚ: Colonia Insfran (MNHNP 3543). CANINDEYÚ: Reserva Natural del Bosque Mbaracayu (MNHNP 9437). GUAIRA: Aldea Tuna (MNHNP 2579). ITAPUÁ: Isla Yacyreta (MNHNP 4627-30, 4730, 4819-26, 4840-5, 4898-902, 4936-8, 4966, 6706, 6711, 8330, 8334, 8337, 8341-3, 8361-3, 8402, UNNEC 475). PRESIDENTE HAYES: Ruta IX, Km 60 (MNHNP 9142). SAN PEDRO: Colonia Primavera (UNNEC 4376).

Philodryas agassizi: (1). PARAGUAY (MNHNP 9534).

Philodryas baroni: (5). BOQUERÓN: Filadelfia (MNHNP 2570, 2572); Parque Nacional Teniente Encizo (MNHNP 2571, 3500, 5119).

Philodryas mattogrossensis: (21). PARAGUAY (MNHNP 9244, 9248, 9515, 9567). ALTO PARAGUAY: Parque Nacional Defensores del Chaco (MNHNP 2573-5, 7228). AMAMBAY: 2 km Oeste de Bella Vista (MNHNP 3501); Estancia Paicuará (MNHNP 5225, 6525). BOQUERÓN: 5 km oeste de Filadelfia (MNHNP 10030); Campo Loro (MNHNP 10658); Filadelfia (CZ-FaCEN 419, MNHNP 2576); Pozo Hondo (MNHNP 2654, 6528). PRESIDENTE HAYES: Estancia Palo Santo (MNHNP 1045, 4196); Ruta IX, km 335 (MNHNP 3502). SAN PEDRO: Reserva Natural Laguna Blanca (CZPLT 101-2).

Philodryas nattereri: (3). SAN PEDRO: Reserva Natural Laguna Blanca (CZPLT 017, 295, 310).

Philodryas olfersii: (31). PARAGUAY (MNHNP 3513, 9247, 9299, 9517, 9551, 9586). ALTO PARAGUAY: Bahía Negra (MNHNP 10223); Colonia Potrerito (MNHNP 5177). ALTO PARANÁ: Itaipu Reserves (CBMI-R 72, 109, 117-8); Reserva Limoy (CZ-FaCEN 378). AMAMBAY: Parque Nacional Cerro Corá (MNHNP 2580). CAAGUAZÚ: Colonia José Domingo Campos (MNHNP 2581). CAAZAPÁ: Parque Nacional San Rafael (MNHNP 8851). CENTRAL: (CZ-FaCEN 205). CONCEPCIÓN: Vallemí (MNHNP 11128); 1 km este de San Lázaro (MNHNP 5179). CORDILLERA: Caacupé (MNHNP 3499). ITAPUÁ: Isla Guazu'i (MNHNP 4823); Isla Yacyreta (MNHNP 6708, 8493). MISIONES: 80 km Este Pilar en la Ruta IV (MNHNP 11187). PARAGUARÍ: Acahay (MNHNP 228); Parque Nacional Ybycuí (MNHNP 5180-1, 6547). PRESIDENTE HAYES: Ruta IX, Km 70 (MNHNP 10989). SAN PEDRO: Lima (MNHNP 3404); Reserva Natural Laguna Blanca (CZPLT 060).

Philodryas patagoniensis: (54). PARAGUAY (MNHNP 9268, 9460, 9498, 9528). ALTO PARAGUAY: Estancia Cerrito (MNHNP 3932). ALTO PARANÁ: Itakyry (CBMI-R 104). AMAMBAY: (MNHNP 3076). CANINDEYÚ: Reserva Natural del Bosque Mbaracayú (MNHNP 10863). CENTRAL: Alrededores de Asunción (AMNH 75314-5); Nueva Italia (MNHNP 8523); Villeta (MNHNP 3078). CORDILLERA: Piribebuy, Compañía Cañada, Camino a Cerro Verá (CZ-FaCEN 504); Ruta III entre Arroyos y Esteros y 25 de Diciembre (MNHNP 11072-4). GUAIRA: Beato Roque González de Santa Cruz (MNHNP 3075). ITAPUÁ: Isla Modesto (MNHNP 4836); Isla Paloma (MNHNP 8195, 8349); Isla Talavera (MNHNP 4662); Isla Yacyreta (MNHNP 4661, 4887-95, 4928, 4957-8, 4962, 8367, 8414-5, 10630). MISIONES: 32 km Sur de Villa Florida (MNHNP 10028); 4 km oeste de Corateí (MNHNP 3962). PARAGUARÍ: Ruta I, km 83 (MNHNP 3080). PRESIDENTE HAYES: 30 km Noroeste de Villa Hayes (MNHNP 6716); Estancia Golondrina (MNHNP 329, 3081, 3961); Ruta IX, km 84 (MNHNP 3077); Ruta IX, km 93 (MNHNP 10651); Ruta IX, km 100 (MNHNP 10622); Ruta IX, km 233 (MNHNP 3082); Ruta IX, km 306 (MNHNP 8496). SAN PEDRO: Colonia Primavera (AMNH 103202); Reserva Natural Laguna Blanca (CZPLT 381); Lima (MNHNP 3079).

Philodryas psammophidea: (9). ALTO PARAGUAY: Estancia Punto Alto (MNHNP 10205); Parque Nacional Defensores del Chaco (MNHNP 5251, 6530); Fortín Pikyrenda (MNHNP 9189). BOQUERÓN: Fortín Toledo (MNHNP 10015); Parque Nacional Teniente Encizo (CZ-FaCEN 739, MNHNP 5123, 5250, 6572, 10015).