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Geographical distribution patterns of South American side-necked turtles (Chelidae), with emphasis on Brazilian species

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Abstract: The Chelidae (side-necked turtles) are the richest and most widespread turtle family in South America with endemic patterns at the species level related to water basins. Based on available literature records, the geographic distribution of the 22 recognized chelid species from South America was examined in relation to water basins and for the 19 Brazilian species also in light of climate and habitat characteristics. Species-distribution maps were used to identify species richness in a given area. Parsimony analysis of endemicity (PAE) was employed to verify the species-areas similarities and relationships among the species. For Brazilian species, annual rainfall in each water basin explained 81% of variation in turtle distribution and at a regional scale (country-wide) temperature also influenced their distribution. While rainfall had a significant positive relationship with species number in a given area, a negative but non-significant relationship was identified for temperature. Excepting an unresolved clade formed by some northern water basins, well-defined northern-northeastern and central-south groups (as identified for water basins) as well as biome differentiation give support to a hypothesis of a freshwater turtle fauna regionalization. Also, a more general biogeographical pattern is evidenced by those Brazilian species living in open or closed formations. The geographic distribution of Brazilian chelid species apparently reflects patterns of climate and vegetation physiognomies and can be associated with life-history traits such as low vagility. Since some Brazilian chelid species have a distribution encompassing diversity hotspots, the delimitation of endemism areas could be useful in defining conservation priority areas.

Key words: biogeography, Brazil, Chelidae, parsimony analysis of endemicity, South America, turtle.

Resumen: Patrones de distribución geográfica de las tortugas pleurodiras (Chelidae) sud-americanas, con énfasis en las especies brasileñas. – Las tortugas de la familia Chelidae (tortugas pleurodiras de cuello de serpiente) son las más abundantes y ampliamente distribuídas en América del Sur y presentan patrones de endemismo a nivel específico relacionados con las cuencas hidrográficas. Basándonos en la literatura disponible, examinamos la distribución geográfica de 22 especies de Chelidae reconocidas en América del Sur en relación con las cuencas hidrográficas. Para las 19 especies presentes en Brasil estudiamos además la relación con el clima y las características del hábitat. Los mapas de distribución de las especies fueron utilizados para calcular la riqueza de especies en un área determinada. También se empleó un análisis parsimonioso de endemicidad (PAE) para estudiar las semejanzas entre áreas y las relaciones entre especies. Para las especies brasileñas, la precipitación anual en cada cuenca hidrográfica explicó 81% de la variación en la distribución de las tortugas y a escala regional (de todo el país) la temperatura también afecta a su distribución. Mientras que la pluviosidad mostró una relación positiva y estadísticamente significativa con el número de especies en un área determinada, para la temperatura dicha relación fue negativa y no significativa. Con la única excepción de un clado no resuelto formado por algunas cuencas hidrográficas del norte, la existencia de grupos norte-nordeste y centro-sur bien definidos (y coincidentes con las cuencas hidrográficas) y la diferenciación de los biomas apoyan la hipótesis de regionalización de la fauna de tortugas de agua dulce. Además, las especies brasileñas que viven en formaciones abiertas o cerradas ponen de manifiesto

un patrón biogeográfico más general. La distribución geográfica de las especies de Chelidae brasileñas aparentemente refleja patrones climáticos y de fisionomía vegetal y podría estar asociada a algunos rasgos de su historia de vida como la escasa vagilidad. Dado que la distribución de algunas especies de Chelidae brasileñas incluye puntos calientes de diversidad, la delimitación de áreas de endemismo puede ser útil para definir áreas prioritarias para la conservación.
Palabras clave: América del Sur, análisis parsimonioso de endemicidad, biogeografía, Brasil, Chelidae, tortuga.

INTRODUCTION

Around 20% of all 278 extant species of turtles are found in South America, including representatives of Chelydridae, Emydidae, Geoemydidae, Kinosternidae, Podocnemididae, Chelidae, Testudinidae, Cheloniidae and Dermochelyidae (IVERSON, 1992b). The species diversity among these families is varied, the Chelidae (side-necked turtles), with 22 species, being the most speciose one. In contrast with other families that are restricted to a few water basins (e.g. the Podocnemididae, Geoemydidae, and Chelydridae), chelids are widespread in South America, ranging from northern Venezuela and the Guianas to Argentina. However, endemism patterns related to water basins can be detected at the species level (PRITCHARD & TREBBAU, 1984; IVERSON, 1992a, b; CABRERA 1998; IPPI & FLORES, 2001; MCCORD *et al.*, 2001). Although factors driving such local (water basin) and regional distribution patterns for these freshwater turtle species are poorly known, they could reflect processes influencing evolutionary history, including natural barriers, colonization, and local extinction. Recognizing species geographical distribution patterns can allow the recognition of the factors responsible for these patterns.

Extensive variation in ecosystems and topography occurs in South America in general and Brazil in particular (e.g. tropical and subtropical rainforests, Cerrado vegetation, mountainous and flat topographies) creates an interesting evolutionary background for research on Brazilian freshwater turtle biogeography. For instance, mountainous regions of southeastern Brazil are reported as geographical barriers for mammals (including bats) and reptiles (VANZOLINI, 1973; VANZOLINI & REBOUÇAS-SPIEKER, 1976; DIXON, 1979; SIMPSON, 1979; DITCHFIELD, 2000; LARA & PATTON, 2000; MORITZ *et al.*, 2000; SOUZA *et al.*, 2003), whereas Amazonian rivers may also play an important role in shaping the distribution patterns of a plethora of vertebrate species (see review in MORITZ *et al.*, 2000). On the other hand, complex vegetation habitats, including flooded areas, gallery and evergreen forests, and Cerrado physiognomies, can be found along the rivers and other water bodies inhabited by Brazilian freshwater turtles. With the only exception of marine turtles and representatives of the Podocnemididae (particularly *Podocnemis* spp.) which exhibit a high dispersal capability (VALENZUELA, 2001), all other aquatic turtle species from Brazil are quite sedentary, with home range size restricted to a small area and dispersal limited to a few meters/day (MAGNUSSON *et al.*, 1997; SOUZA & ABE, 1997, 2000). These life-history traits in conjunction with a landscape matrix that imposes still more dispersal restrictions (e.g. temperature, vegetation physiognomies, and geographical barriers) could constrain these organisms within local areas (SOUZA *et al.*, 2002a, b).

The family Chelidae consists of predominantly aquatic species, generally leaving the water only for basking or for nesting. According to IVERSON (1992b), on a global scale water basins that receive elevated annual rainfall also exhibit high turtle richness. While this assertion may apply globally, such a relationship could be not valid at a regional scale because local climate can be influenced by different environmental characteristics such as relief and the landscape matrix (including distinct vegetation physiognomies). In Brazil, tropical and subtropical climates are detected in a north-south gradient (NIMER, 1989), reflecting distinct patterns of temperature and annual rainfall. In turn, this climate gradient supports a diversity of habitats, from tall tree forests in lowland and mountainous regions to, xeromorphic vegetation in the Cerrado to grassland. Thus, rainfall, temperature, and habitat characteristics around water basins could be important factors affecting distribution patterns in Brazilian chelids.

In this paper, the distribution of the Brazilian freshwater side-necked turtles (Chelidae) was revisited in light of climate and habitat characteristics to determine which environmental or physical aspects could be relevant in shaping the biogeography of this taxon.

MATERIALS AND METHODS

The geographic distribution of South American Chelidae was compiled from available literature, including systematic reviews (MITTERMEIER *et al.*, 1978; VANZOLINI *et al.*, 1980; RHODIN *et al.*, 1982, 1984a, b; RHODIN & MITTERMEIER, 1983; PRITCHARD & TREBBAU, 1984; LEMA & FERREIRA, 1990; IVERSON, 1992a; VANZOLINI, 1994; CABRERA, 1998; MCCORD *et al.*, 2001) as well as recent faunistic surveys from poorly known regions (CABRERA, 1995; SOUZA *et al.*, 2000; ARGÔLO & FREITAS, 2002; BRANDÃO *et al.*, 2002; COLLI *et al.*, 2002; RIBAS & MONTEIRO-FILHO, 2002; KINAS *et al.*, in press). For systematic purposes, recent systematic reviews of the genus *Phrynops* by CABRERA (1998) and MCCORD *et al.* (2001) were followed. Thus, 22 Chelidae species could be assigned to South America and 19 to Brazil (Table 1).

The geographic distribution of Brazilian side-necked turtles was interpreted in relation to annual rainfall, latitude, longitude, altitude, mean annual air temperature, water basin area, mean annual precipitation in each water basin, and main biomes (see below). Brazilian water basin boundaries were outlined by ANA (2003) according to landscape complexity formed by country drainage and relief. Thus, we identified 12 major water basins in Brazil: Amazon, Atlantic-North eastern (Atl-Ne), Atlantic-North eastern Orient (Atl-Ne Orient), Atlantic-East (Atl-E), Atlantic-South eastern (Atl-Se), Atlantic-South (Atl-S), Parnaíba, Paraná, Tocantins, São Francisco, Paraguay, and Uruguay (Fig. 1), plus the Orinoco and Magdalena basins for South America. These water basins encompass distinct vegetation physiognomies (from Atlantic rainforest to Cerrado), distinct climatic regions (from an equatorial zone to a subtropical province), and different size areas (NIMER, 1989; IBGE, 1993; CUNHA, 2001). The mean annual rainfall in each water basin was compiled from CUNHA (2001) and NIMER (1989) that provided annual rainfall records from weather station throughout Brazil. The main Brazilian biomes were defined according to IBGE (1993). Roughly, these biomes can be represented by Amazon forest, Atlantic rainforest *sensu lato* (which includes physiognomies such as semideciduous forest in the southeastern inland, and *Araucaria angustifolia* forest in temperate regions), Cerrado (with its distinct physiognomies such as campo limpo, campo sujo and cerradão), Caatinga, Pantanal, and Southern grasslands.

For Brazil, turtle distribution maps were used to calculate species richness in a given area. The Brazilian territory was divided into a 2.5º × 2.5º latitude-longitude grid (ca. 90 000 km^2) on a 1:16 670 000 map, resulting in 136 quadrants. For each cell the number of turtle species was determined according to the literature. Latitude, longitude, mean annual rainfall, mean temperature, and mean altitude were calculate at the central point of each cell according to records from diverse topographical and climate data bases (NIMER, 1989; ANA, 2003; CNPM, 2003; IBGE, 2003). A forward multiple linear regression was performed to determine the influence of water basin area and mean annual rainfall in each water basin (calculated as above) on turtle species richness in the 12 major

TABLE 1. The data matrix (area × taxon) with distribution (1: presence; 0: absence) of the 22 South American Chelidae species according to 14 water basin and six major Brazilian biomes. Am: *Acanthochelys macrocephala*, Ap: *A. pallidipectoris*, Ar: *A. radiolata*, As: *A. spixii*, Bd: *Batrachemys dahli*, Bh: *B. heliostemma*, Bn: *B. nasuta*, Br: *B. raniceps*, Bt: *B. tuberculata*, Bz: *B. zuliae*, Bv: *Bufocephala vanderhaegei*, Cf: *Chelus fimbriatus*, Hm: *Hydromedusa maximiliani*, Ht: *H. tectifera*, Mg: *Mesoclemmys gibba*, Pp: *Platemys platycephala*, Pg: *Phrynops geoffroanus*, Ph: *P. hilarii*, Pt: *P. tuberosus*, Pw: *P. williamsi*, Rh: *Ranacephala hogei*, Rr: *Rhinemys rufipes*. Hyphens in biomes denote non-Brazilian species.

TABLA 1. Matriz de datos (área × taxón) de distribución (1: presencia; 0: ausencia) de las 22 especies de Chelidae sudamericanas en relación a 14 cuencas hidrográficas y a seis grandes biomas en Brasil. Am: *Acanthochelys macrocephala*, Ap: *A. pallidipectoris*, Ar: *A. radiolata*, As: *A. spixii*, Bd: *Batrachemys dahli*, Bh: *B. heliostemma*, Bn: *B. nasuta*, Br: *B. raniceps*, Bt: *B. tuberculata*, Bz: *B. zuliae*, Bv: *Bufocephala vanderhaegei*, Cf: *Chelus fimbriatus*, Hm: *Hydromedusa maximiliani*, Ht: *H. tectifera*, Mg: *Mesoclemmys gibba*, Pp: *Platemys platycephala*, Pg: *Phrynops geoffroanus*, Ph: *P. hilarii*, Pt: *P. tuberosus*, Pw: *P. williamsi*, Rh: *Ranacephala hogei*, Rr: *Rhinemys rufipes*. Los guiones en los biomas indican especies no brasileñas.

	Species																					
Basins	Am	Ap	Ar	As	Bd	Bh	Bn	Br	Bt	Bz	Bv	Cf	Hm	Ht	Mg	Pp	Pg	Ph	Pt	Pw	Rh	Rr
Orinoco	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	1	1	0	1	0	0	0
Magdalena	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amazon	0	0	0	0	0	1	1	1	0	0	1	1	0	0	1	1	1	0	1	0	0	1
Atlantic-Northeastern	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0
Parnaíba	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
Atlantic-Northeastern Orient	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
São Francisco	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Atlantic-Eastern	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Tocantins	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0
Paraguay	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Paraná	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0
Atlantic-Southeastern	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0
Uruguay	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1	0	0
Atlantic-Southern	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0
Biomes																						
Amazon forest	0	–	0	0	–	1	1	1	0	–	0	1	0	0	1	1	1	0	1	0	0	1
Caatinga	0	–	0	0	–	0	0	0	1	–	0	0	0	0	0	0	1	0	1	0	0	0
Pantanal	1	–	0	0	–	0	0	0	0	–	0	0	0	0	0	0	1	0	0	0	0	0
Cerrado	0	–	0	1	–	0	0	0	0	–	1	0	0	0	0	0	1	0	0	0	0	0
Atlantic rainforest	0	–	1	1	–	0	0	0	1	–	1	0	1	1	0	0	1	1	0	1	1	0
Southern grasslands	0	–	0	0	–	0	0	0	0	–	0	0	0	0	0	0	0	1	0	0	0	0

FIGURE 1. The 12 Brazilian river drainage considered in this study. 1: Amazon, 2: Atlantic-Northeastern, 3: Parnaíba, 4: Atlantic-Northeastern Orient, 5: São Francisco, 6: Atlantic-East, 7: Tocantins, 8: Paraguay, 9: Paraná, 10: Atlantic-Southeastern, 11: Uruguay, 12: Atlantic-South. Adapted from Brazilian Hydrological Information System (2003).

FIGURA 1. Las 12 cuencas hidrográficas brasileñas consideradas en el presente estudio. 1: Amazon, 2: Atlantic-Northeastern, 3: Parnaíba, 4: Atlantic-Northeastern Orient, 5: São Francisco, 6: Atlantic-East, 7: Tocantins, 8: Paraguay, 9: Paraná, 10: Atlantic-Southeastern, 11: Uruguay, 12: Atlantic-South. Adaptado de Brazilian Hydrological Information System (2003).

Brazilian basins, and to check the relationship between turtle richness and the five variables discerned above (latitude, longitude, mean annual rainfall, mean temperature, and mean altitude). Prior to these analyses, these variables were checked for normality, skewness, and kurtosis (ZAR, 1999). A correlation matrix was created for all five independent variables to check for redundancy. After this analysis, only one variable among a highly correlated pair ($r > 0.6$) was retained to be included in the regression model. Temperature and rainfall were chosen as climate variables since this prior analysis showed a highly negative relationship between latitude and temperature and a positive relationship between longitude and rainfall.

Methods using parsimony algorithms have been used as a biogeographic tool for detecting similarities among areas and establishing relationships among biogeographic units according to the organisms found in them (MORRONE & ESCALANTE, 2002). A parsimony analysis of endemicity (PAE) (MORRONE, 1994) was employed to verify such species-areas similarities and relationships among South American Chelidae species. PAE defines study units in biogeography by grouping areas based on shared species (MORRONE, 1994; DA SILVA & OREN, 1996; LUNA *et al.*, 1999; IPPI & FLORES, 2001; ROJAS-SOTO *et al.,* 2003). The method is particularly useful for those organisms with limited dispersal abilities (RON, 2000), such as the Chelidae (MAGNUSSON *et al.*, 1997; SOUZA & ABE, 1997, 2000). For the present purpose, the 14 identified water basins for South America and the six Brazilian biomes were defined as geographic provinces for turtle distribution (Table 1). In PAE, the data set is a matrix of presence (1; analogous to a derived character) or absence (0; primitive character) of species in a given geographic area, with a hypothetical area with no taxa (a rooting taxon or outgroup). PAE was performed using the algorithm implemented in NONA (GOLOBOFF, 1999) through Winclada (NIXON, 2002) by applying a heuristic search with 1000 replications on the data matrix. If multiple parsimonious trees resulted from the analyses, they were summarized by means of a strict consensus tree.

RESULTS

Magdalena basin has a unique chelid species. The Amazon basin is the richest among all 14 South American basins, with ten chelid species, followed by Orinoco (seven species), Atlantic-Southeastern and Uruguay (six species), Tocantins, Paraná, and Atlantic-South (five species), Paraguay (four species), and the remaining five basins with three species each. The Atlantic rainforest harbours 10 species, while nine species are found within the Amazon forest. Three species are recorded from both the Cerrado and Caatinga biomes, two species from the Pantanal, and just one species is found in the Southern grasslands (Table 1).

For Brazilian water basins, only mean annual rainfall in each basin was retained in the multiple linear model ($F_{2,9}$ = 18.99; P < 0.001), explaining 81% of the variation in Brazilian turtle distribution (R^2 = 0.808). In this model, mean annual rainfall in each basin had a positive significant relationship with the number of turtle species (β = 0.68; t = 3.57; P < 0.01). In a country wide analysis rainfall, temperature, and altitude explained only 27% of the variation in species richness ($F_{3,132}$ = 16.67; P < 0.0001; R^2 = 0.274). While rainfall had a significant positive relationship with richness (β = 0.452; t = 5.48; P < 0.001), a negative non-significant relationship was identified for both temperature (β = – 0.144; t = – 1.82; P = 0.07) and altitude (β = – 0.159; t = – 1.83; P = 0.07).

PAE showed distinct patterns of geographic distribution for the South American Chelidae species at a water basin level and for Brazilian species at a biome level. In relation to water basins, six most parsimonious trees of 32 steps were found. The strict consensus tree (consistency index: 68; retention index: 66) shows a two resolved clade formed by Amazon-Orinoco and Atlantic-North eastern basins (a northern-northeastern clade) and Atlantic-East and São Francisco basin in a not resolve (polytomy) branch that also includes Parnaíba, and Atlantic-North eastern Orient basins (Fig. 2A). Typical coastal areas from southeastern Brazil (Atlantic-Southeastern and Atlantic-South basins) plus Tocantins, Paraguay, Uruguay, and Paraná basins distinguish a central-southern clade. Magdalena basin, as expected, forms a unique clade, represented by its endemic species, *Batrachemys dahli*.

One single most parsimonious tree of 21 steps (consistency index: 90; retention index: 66) was found for the endemicity pattern related to Brazilian biomes (Fig. 2B). The Amazon forest shares species with the Caatinga while the Cerrado and Atlantic rainforest exhibit common species. The Pantanal shares species with all other biomes

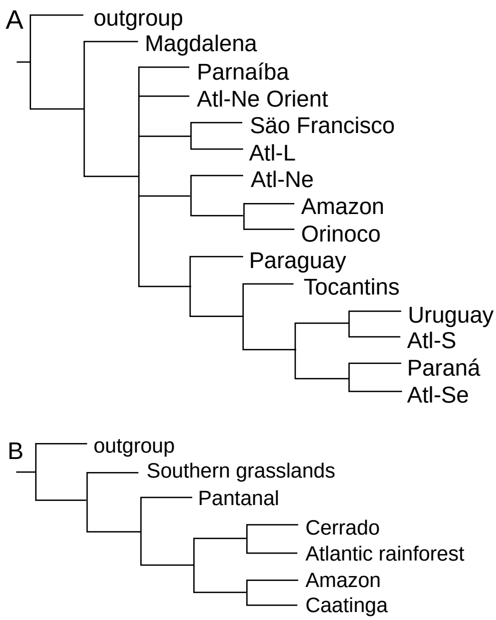

FIGURE 2. The strict consensus tree obtained by the parsimony analysis of endemicity with the raw distribution of the 22 South American chelid species in relation to water basins (A) and the single most parsimonious tree of the 19 Brazilian chelid species in relation to Brazilian biomes (B).

FIGURA 2. Árbol de consenso estricto obtenido mediante un análisis parsimonioso de endemicidad de los datos en bruto de distribución de las 22 especies de Chelidae sudamericanas en relación con las cuencas hidrográficas (A) y árbol más parsimonioso de las 19 especies de Chelidae brasileñas en relación con los biomas brasileños (B).

except the Southern grasslands that, in turn, shares its single species only with the Atlantic rainforest. Excepting the unresolved clade formed by some northern drainage basins, the well-defined northern-northeastern and central-south groups (as identified for drainage basins) as well as biome differentiation give support to the hypothesis of regionalization in the freshwater turtle fauna.

DISCUSSION

The geographic distribution of South American and Brazilian chelid species apparently reflects the patterns of climate and vegetation physiognomies found across the continent. Notwithstanding the possibility that distribution data set could be flawed or incomplete, and the fact that climate data was averaged for large quadrant areas, we believe that the results reported here provide a reasonable preliminary interpretation of Brazilian chelid biogeography.

Mean annual rainfall in each drainage basin was positively related to turtle species richness. Rainfall is considered an important climate variable in shaping freshwater turtle richness across the world (IVERSON, 1992a), and this is also true at a regional scale, represented by Brazilian drainage basins. At a more local scale, rainfall is again an important correlate, although temperature and altitude have some influence. Our findings illustrate that a single factor (abiotic or geographic) should not be assumed to drive turtle diversity. On the contrary, the data suggest that patterns of endemism together with both biome and drainage basin effects better define the biogeography of Brazilian side-necked turtles.

Freshwater aquatic organisms are useful in reconstructing historical biogeographic patterns since their vagility is restricted to defined linear habitats (VARI, 1988). As aquatic organisms, freshwater turtle species may have their geographic distributions constrained by this life-history trait. Even though terrestrial excursions are not uncommon in these organisms, especially during periods of drought or reproduction (PRITCHARD & TREBBAU, 1984; LEMA & FERREIRA, 1990; CABRERA, 1998), such dispersal behaviour is limited. Turtles generally move only to surrounding aquatic habitats such as riparian forests or to nearby seasonally flooded basins. Like fishes (MENEZES, 1988), different turtle species inhabiting the same river or the same drainage basin typically occur in the upper and lower reaches of these watercourses. Furthermore, geologic, ecologic or climatic barriers (or a combination of these) between suitable habitats may impose still more difficulties for species dispersal. This scenario may be true for South American and Brazilian chelids.

The distinct areas of endemism identified for the Brazilian chelids are similar to those found for other taxa, including birds (CRACRAFT, 1985), fish (MENEZES, 1988; VARI, 1988), and distinct lineages of South American turtles (IVERSON, 1992b; IPPI & FLORES, 2001). Roughly, two distinct patterns of geographical distribution are found in Brazilian chelids. Although unresolved, the combined Parnaíba and Atlantic-Northeastern Oriental plus the clades including Atlantic Eastern and São Francisco basins and Amazon, Orinoco, and Atlantic-Northeastern basins together with the Magadalena branch identifies a northern-northeastern species group distribution while the remaining six basins encompass a central-southern distribution. Although the multiple linear regression model failed to detect statistical significance for both temperature and altitude as environmental characteristics driving geographic distribution patterns for Brazilian chelids, some considerations must be noted. There are species typically found in areas exhibiting a mean annual air temperature around 26ºC, including all the Amazon forest, Caatinga, Pantanal and Cerrado species, within a geographic distribution encompassing the Amazon, Parnaíba, Atlantic-Northeastern, Atlantic-Northeastern Orient, Tocantins, São Francisco, and the northern part of Paraná basin. This broad area harbours 75% of the Brazilian chelid fauna. On the other hand, at least seven species (*Acanthochelys radiolata*, *A. spixii*, *Hydromedusa maximiliani*, *H. tectifera*, *Phrynops hilarii*, *P. williamsi*, and *Ranacephala hogei*) can be found in temperate areas of Brazil that experience harsh winters and a mean annual air temperature around 22ºC. An altitude distribution pattern is also detected for some freshwater turtle species where geographic range encompasses mountain areas ("upland species"). Similar to fish (VARI, 1988), amphibian (GIARETTA *et al.*, 1999), bird (MELO *et al.*, 2001), and mammal (BONVICINO *et al.*, 1997) communities, a species replacement mechanism can be observed across an altitude gradient in the two *Hydromedusa* spp. in some Atlantic rainforest areas of southeastern Brazil. In sympatry, *Hydromedusa maximiliani* inhabits areas above 600 m, whereas *H. tectifera* is found in lowland areas. In contrast, in areas where one of the species is absent, *H. maximiliani* can be detected in coastal rivers below 100 m (e.g. São Sebastião Island), whereas *H. tectifera* is reported up to 900 m in upland areas of Paraná State (RIBAS & MONTEIRO-FILHO, 2002). Thus, ecological interactions may also explain some distribution patterns observed at a local scale. In contrast to most Brazilian chelids, the distribution pattern exhibited by *Phrynops geoffroanus* is not congruent with either basins or biomes. The species has a "patternless distribution" (*sensu* VANZOLINI, 1988) and is absent only in high latitudes from southern Brazil that include part of the Uruguay and Atlantic-South drainage basins as well as Southern grassland biome. Given the climate gradient and the diversity of physiognomies encompassed by the drainage basins across Brazil, it is possible that *P. geoffroanus* is really a complex of sibling species (PRITCHARD & TREBBAU, 1984).

The Amazon forest and Caatinga share common species. The Amazon and Orinoco basin (equatorial forest) represents an area of endemism for seven species (*Batrachemys heliostemma*, *B. nasuta*, *B. raniceps*, *B. dahli*, *B. zuliae*, *Mesoclemmys gibba*, and *Rhinemys rufipes*) and share, with Atlantic-Northeastern, Atlantic-North eastern Orient, Tocantins, and Parnaíba basins three other species (*Phrynops tuberosus*, *Chelus fimbriatus*, and *Platemys platycephala*). In addition, endemism is found in the Paraguay (*Acanthochelys macrocephala*, *A. pallidipectoris*) and Atlantic-Southeastern (*Ranacephala hogei*) basins, which encompass Pantanal and Atlantic rainforest biomes, respectively. *Batrachemys tuberculata* has a geographic distribution ranging from an inland northeastern semi-arid region to the Atlantic-Northeastern basin, and *Phrynops tuberosus* inhabits coastal and inland areas in the Amazon and Northern-Northeastern basins (VANZOLINI *et al.*, 1980; IVERSON, 1992a; MCCORD *et al.*, 2001). Similarly, despite the generally dry Cerrado characteristics, this biome exhibits particular areas of wetland habitats such as flooded areas associated with gallery forests. These vegetation corridors along river edges are an important component of Cerrado structure influencing the population dynamic of several vertebrate species (REDFORD & FONSECA, 1986; DA SILVA & BATES, 2002). The Atlantic rainforest domains scattered throughout inland areas in humid valleys and along river systems. Thus, both Cerrado and Atlantic rainforest biomes are represented in Paraguay and Paraná basins, sharing such turtle species as *Bufocephala vanderhaegei* and *Hydromedusa tectifera*.

Life-history traits (mating system, dispersal ability), historical events (fragmentation, range expansion, colonization), and landscape matrix (mountain ridges, watersheds) are important components in shaping geographic distribution for organisms with low vagility such as freshwater turtles (SCRIBNER *et al*., 1986; WALKER & AVISE, 1998; SCRIBNER & CHESSER, 2001; SOUZA *et al*., 2003). The combination of these components can account for the endemism patterns detected for Brazilian chelids. A topographically complex region found throughout eastern Brazil (Atlantic-Eastern, Atlantic-Southeastern, and Atlantic-Southern basins) associated with an altitudinal gradient, medium to low temperature, and high rainfall clearly identifies areas of endemism in Brazilian Coastal range (e.g. *Phrynops hilarii*, *P. williamsi*, *Ranacephala hogei*, *Hydromedusa maximiliani*). In central Brazil, environmental stochasticity due to a pronounced wet-dry seasonality and specific habitat requirements apparently restrict the geographic distribution of *Acanthochelys macrocephala* to some areas of the Pantanal (RHODIN *et al*., 1984b; VINCKE & VINCKE, 2001; MAURO *et al*., 2004). Black water and clear water rivers as well as flooded and non-flooded areas from Amazonian rainforest are important environmental features shaping the geographical distribution of large Amazon river turtles (Podocnemididae) and some chelid species, including *Chelus fimbriatus* and *Rhinemys rufipes* (PRITCHARD & TREBBAU, 1984).

A more general biogeographic pattern evidenced by the Brazilian Chelidae is their ecological division into two major groups, represented by those species living in open- or closed-formations. This distribution pattern is similar to those described for species of frogs (HEYER, 1988) and lizards (VANZOLINI, 1988). The closed-formation group is represented by those species living in regions with closed forest canopy. In a broad sense, this formation is defined by an arc from Amazon rainforest to its linkage with Atlantic rainforest via northern Brazil and the Atlantic rainforest, with its distinct physiognomies from the northeastern coastal region inland to southeastern and southern Brazil. The open-formation group includes those species living in biomes such as the Cerrado, Pantanal, and Caatinga. Although tree cover along edges of water bodies (e.g. riparian forests) inhabited by the turtles from these regions is common, these areas typically have an open canopy. A diagonal strip from central to northern Brazil can define this open formation. Encompassing over one quarter of Brazil, the Cerrado, Pantanal, and Caatinga biomes harbour chelids typical of dry areas, such as *Acanthochelys macrocephala*, *Bufocephala vanderhaegei*, *Batrachemys tuberculata*, and *Phrynops tuberosus*. Contact zones between open- and closed-formation provide suitable areas for some species as *Acanthochelys spixii* and *Hydromedusa tectifera*.

The distribution patterns of organisms can shed light on historical factors that have shaped biodiversity across a given region. Besides, it highlights putative areas with common distribution characteristics (RON, 2000; ROJAS-SOTO *et al*., 2003). Delimiting areas of endemism is useful to prioritising areas for conservation (IPPI & FLORES, 2001). Although many of the Brazilian chelid species are found in continuous forests of the Amazon region, several species have a distribution restricted to the Atlantic rainforest and Cerrado, two of the most threatened ecosystems in the world and considered diversity hotspots (MYERS *et al.*, 2000). Since detailed knowledge of the distribution of many species is lacking and natural history data are also scant for several species, the results of this paper should be considered an initial effort to study the biogeography of freshwater turtles in South America and Brazil.

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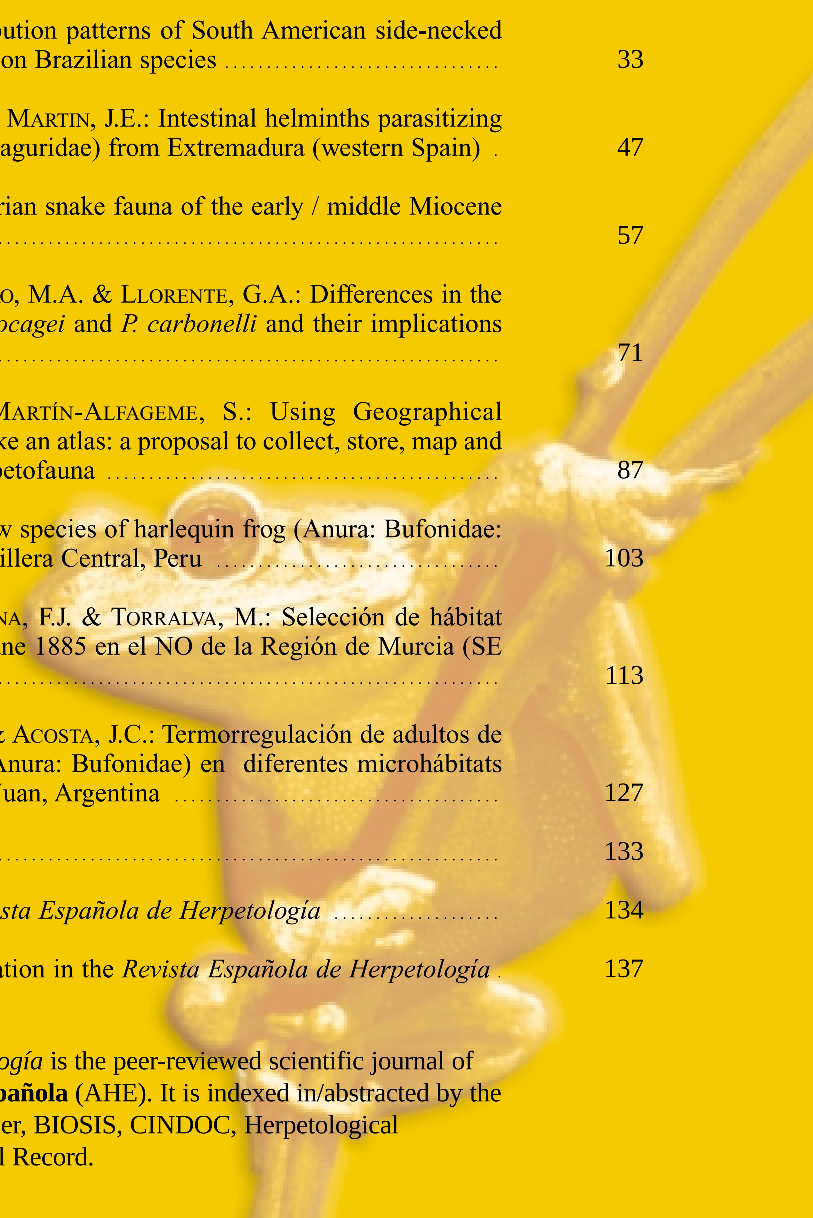

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