

A new regional biogeography of the Amazonian subregion, mainly based on animal taxa

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Resumen. La subregión Amazónica, que pertenece a la región Neotropical del reino Holotropical, se extiende a lo largo de la mayor parte del Brasil, las Guyanas, sudeste de Venezuela, sudeste de Colombia, este de Ecuador, este de Perú, Bolivia, norte de Paraguay y noroeste de la Argentina. Aquí se propone un nuevo esquema para la subregión, donde se reconocen las siguientes 13 provincias: Yungas (laderas orientales de los Andes, entre los 300 y 2500 m de altitud, desde el norte de Perú hasta el noroeste de la Argentina), Guyana (Escudo Guyanés, entre Venezuela, Colombia, Guyana, Surinam y norte de Brasil), Guyana Húmeda (sudeste de Venezuela, norte de Brasil, Surinam y Guyana), Napo (norte de Perú, sudeste de Colombia y este de Ecuador), Imerí (sudeste de Venezuela, sudeste de Colombia y norte de Brasil), Roraima (norte de Brasil, sudeste de Venezuela, Surinam y Guyana), Amapá (Surinam y noroeste de Brasil), Varzea (noroeste de Brasil y noroeste de Perú), Ucayali (este de Perú, norte de Bolivia y oeste de Brasil), Madeira (noreste de Brasil, limitada en el norte por el río Amazonas, en el oeste por los ríos Madeira y Beni, en el este por el río Xingu, y en el sur por la cordillera oriental de Bolivia), Tapajos-Xingu (noroeste de Brasil), Pará (noroeste de Brasil, limitada en el norte y oeste por los ríos Tocantins y Araguaia, en el sur por la Serra do Gurupi del norte del Maranhao y por el río Grajau, y en el este por el río Guaná), y Pantanal (sur centro de Brasil, noreste de Bolivia y norte de Paraguay).

Palabras clave: subregión Amazónica, América del Sur, biogeografía, regionalización.

Abstract. The Amazonian subregion, belonging to the Neotropical region of the Holotropical kingdom, ranges through most of Brazil, the Guyanas, southern

Venezuela, southern Colombia, eastern Ecuador, eastern Peru, Bolivia, northern Paraguay, and northwestern Argentina. A new biogeographic scheme for the subregion is proposed herein, where the following 13 provinces are recognized: Yungas (eastern slopes of the Andes, between 300 and 2500 m, from northern Peru to northwestern Argentina), Guianan (Guianan shield, between Venezuela, Colombia, Guyana, Suriname, and northern Brazil), Moist Guianan (southeastern Venezuela, northern Brazil, Suriname, and Guyana), Napo (northern Peru, southeastern Colombia, and eastern Ecuador), Imerí (southern Venezuela, southeastern Colombia, and northern Brazil), Roraima (northern Brazil, southeastern Venezuela, Suriname, and Guyana), Amapá (Suriname and northwestern Brazil), Varzea (northwestern Brazil and northwestern Peru), Ucayali (eastern Peru, northern Bolivia, and western Brazil), Madeira (northeastern Brazil, limited in the north by the Amazon river, in the west by the Madeira and Beni rivers, in the east by the Xingu river, and in the south by the Bolivian eastern cordillera), Tapajos-Xingu (northwestern Brazil), Pará (northwestern Brazil, limited in the north and west by the Tocantins and Araguaia rivers, in the south by the Serra do Gurupi of the northern part of Maranhao and by the Grajau river, and in the east by the Guaná river), and Pantanal (south central Brazil, northeastern Bolivia, and northern Paraguay).

Key words: Amazonian subregion, South America, biogeography, regionalization.

Introduction

The Amazonian basin is one of the most diverse areas in the Neotropics. During the last decades, distributional patterns of Amazonian plant and animal endemics have been usually explained through the refuge hypothesis, which postulates that the forest cover was reduced and fragmented by the ice age climate of the Pleistocene, resulting in an archipelago of forest patches or refuges (Haffer 1969, 1974; Prance 1982; Lourenço 1986). A pre-Quaternary age for Amazonian distributional patterns, however, has been postulated by Croizat (1958, 1976), Cracraft & Prum (1988), and Bush (1994). According to Croizat's (1958) insightful analysis, the basic Amazonian patterns were established in the late Cretaceous/early Tertiary, under a paleogeography consisting of fragmented geological forelands. In Croizat's words: "These main biogeographic divisions are function of the ancient tectonics of the South American (and Caribbean) continental mass, and it is these ancient tectonics that, whatever the degree, did primarily determine the centers of 'modern' form-making" (1958: 551). On the other hand, Colinvaux (1997, 1998) has recently argued that ice age climate was not sufficiently arid to fragment the Amazonian forest, and that vicariance was provided because climatic change created islands in the elevated areas; thus, the refuge hypothesis would have the facts reversed: ice-age climatic change raised an archipelago of islands while the forest sea remained intact (Colinvaux 1997). Another explanation of the Amazonian distributional

patterns is the 'Amazonian lake hypothesis' (Frailey *et al.* 1988). No matter the approach undertaken for studying Amazonian biogeographic patterns, I believe that a clear definition of the biogeographic units involved is still lacking.

My objective herein is to propose a new regional biogeography of the Amazonian subregion (briefly outlined in Morrone 1999), based on a track approach. I detail herein the provinces assigned to the subregion, their vegetation, and their endemic or characteristic taxa.

Material and methods

Distributional data for this study were obtained from the literature. Names and classification of the bird and mammal taxa follow Sibley & Monroe (1990) and Nowak (1991), respectively. Biogeographic schemes proposed by previous authors were compiled and the units recognized by them were compared. A track approach (Morrone & Crisci 1995; Craw *et al.* 1999) allowed to compare distributions of plant and animal taxa, in order to test whether these units represented natural units, and leading to lump some of them into a single unit when they could not be equated to a generalized track. The track approach basically consists of plotting distributions of different taxa on maps, connecting their separate localities together with lines called individual tracks. These tracks represent the geographical coordinates of species or higher taxa, and operationally are lines drawn on a map of their localities, which are connected according to their geographical proximity. When different individual tracks are superimposed, the resulting summary lines are considered generalised tracks. Generalised tracks were interpreted as indicating the preexistence of ancestral biotas, which subsequently become fragmented by tectonic and/or climatic change. If two or more generalized tracks intersect in a given area, they determine a node, which indicates that different ancestral biotic and geological fragments interrelate in space/time, as a consequence of terrain collision, docking or suturing, thus constituting a composite area. In the context of this analysis, a generalized track is equivalent to an area of endemism, and a natural biogeographic unit, whereas nodes are situated in the boundaries of different areas of endemism. For the subregion and each province, a list of taxa is provided and a representative individual track is illustrated. In addition, I included a list of 'synonyms', that represent identical or similar treatments of the biogeographic units recognized.

The resulting biogeographic classification in some respects represents a different arrangement of traditionally recognized units. On the other hand, the Amazonian subregion as a whole and the different provinces herein recognized should be taken as working hypotheses, where new evidence could corroborate or change their circumscription.

Results

Amazonian subregion

(Figs. 1, 2)

The Amazonian subregion (Morrone 1999) ranges through most of Brazil, the Guyanas, southern Venezuela, southern Colombia, eastern Ecuador, eastern Peru, Bolivia, northern Paraguay, and northwestern Argentina. It belongs to the Neotropical region of the Holotropical kingdom. The track of *Stygnus* (Fig. 2) is representative of the subregion. The similarity between this track and corridors C and D of Lourenço (1994) is striking.

Synonyms

Central zone: Shannon 1927: 3.

Amazonian district: Cabrera & Yepes 1940: 14.

Guianan Brazilian subregion: Rapoport 1968: 72.

Hylaea province: Fittkau 1969: 642.

Amazon basin: Sick 1969: 451.

Amazonian province: Cabrera & Willink 1973: 48; Ringuet 1975: 107; Fernandes & Bezerra 1990: 78.

Amazonian subregion: Paulson 1979: 171; Morrone 1999: 6.

Amazonian region: Takhtajan 1986: 251; Rivas-Martínez & Navarro 1994: map; Rangel *et al.* 1995: 82.

Amazon endemic region: Vari 1992a: 14.

Amazonian area: Coscarón & Coscarón-Arias 1995: 726; Morrone & Coscarón 1996: 2.

Amazonian bioregion: Dinerstein *et al.* 1995: map.

Vegetation. Basically forests, with a stratum of large trees, another of smaller trees and palms, and a lower one of herbs, shrubs and small palms, in addition to lianas, epiphytes and cryptogams (Cabrera & Willink 1973). Dominant plant species include *Aniba megaphylla*, *Bertholletia excelsa*, *Bonnetia martiana*, *Castilla ullei*, *Cedrela odorata*, *Chrysophyllum argenteum*, *Clathrotropis macrocarpa*, *Cordia goeldiana*, *Coumarouma odorata*, *Desmoncus* sp., *Dialium guianense*, *Dinizia excelsa*, *Erythrina ulei*, *Euxylophora paraensis*, *Geissospermum serium*, *Guatteria* sp., *Inga nobilis*, *Iryanthera ulei*, *Jessenia polycarpa*, *Lafoensia pacari*, *Lecythis* spp., *Leopoldinia piassaba*, *Magonia glabrescens*, *Manilkara huberi*, *Mauritia flexuosa*, *Micrandra* sp., *Perissocarpa* sp., *Protium* sp., *Rheedia* sp., *Scleronema praecox*, *Sterculia striata*, *Swietenia macrophylla*, *Virola* sp., and *Vouacapoua americana* (Fernandes & Bezerra 1990; Rangel *et al.* 1995).

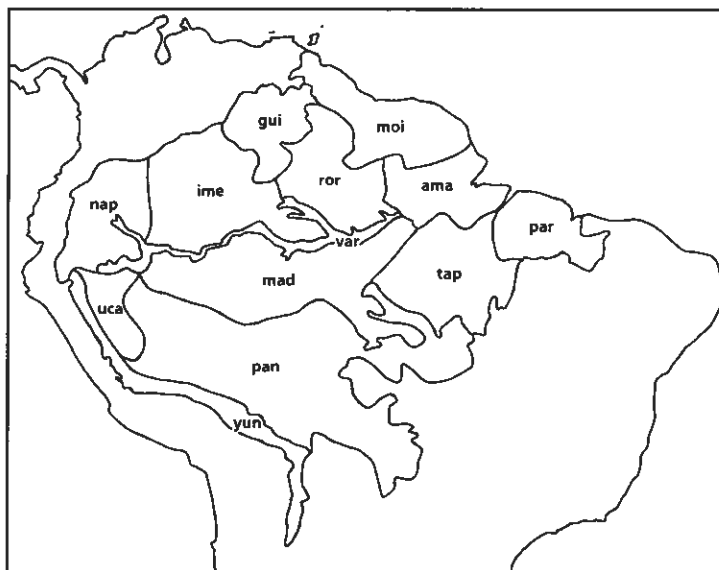
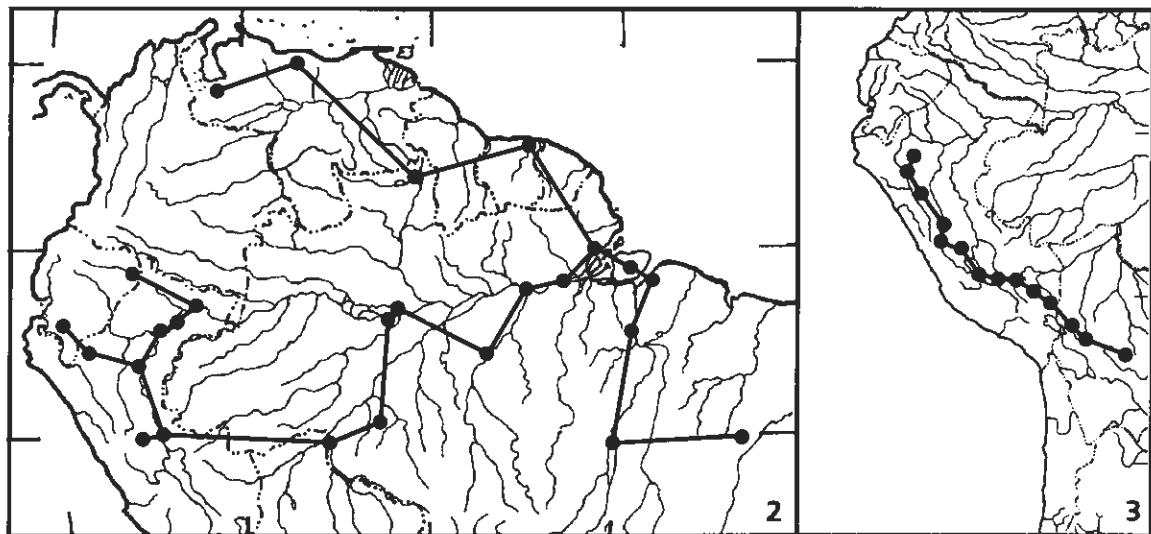


Fig. 1. Provinces of the Amazonian subregion. ama= Amapá, gui= Guianan, ime= Imeri, mad= Madeira, moi= Moist Guianan, nap= Napo, pan= Pantanal, par= Pará, ror= Roraima, tap= Tapajós-Xingu, uca= Ucayali, var= Varzea, yun= Yungas.



Figs. 2-3. Amazonian tracks. 2, Amazonian subregion (*Stygnus*); 3, Yungas province (*Fuchsia decussata*).

Taxa. MAGNOLIOPHYTA. Magnoliopsida. Rosales. Connaraceae: *Connarus punctatus* and *C. ruber* (Forero *et al.* 1983). Urticales. Cecropiaceae: *Cecropia ficifolia* (Franco & Berg 1997). **MOLLUSCA. Pelecypoda.** Eulamellibranchia. Hyriidae: *Calloaia*, *Castalia a. ambigua*, and *C. sulcata orbignyi* (Bonetto 1965). **ARTHROPODA. Arachnida.** Opiliones. Stygnidae: *Stygnus* (Pinto-da-Rocha 1997). Scorpiones. Buthidae: *Tityus silvestris* (Lourenço 1986, 1994). **Crustacea.** Decapoda. Trichodactylidae: *Sylviocarcinus devillei*, *S. maldonadoensis*, and *S. pictus* (Magalhães & Türkay 1996). **Hexapoda.** Coleoptera. Curculionidae: *Entimus granulatus*, *Eurhin aeneus*, *Hammatostylus consimilis*, *H. gronovii*, *Lancearius esau*, and *Sicoderus antilope* (Vaurie 1952, 1982; Vanin 1986); Elmidae: *Stenhelmoides strictifrons* (Spangler & Perkins 1989). Diptera. Simuliidae: *Simulium (Coscaroniellum)* (Coscarón 1987). Hemiptera. Pentatomidae: *Antiteuchus incurvia* species group and *Pseudevoplitis* (Rolston 1993; Grazia 1997); Polyctenidae: *Hesperoctenes* (Ronderos 1961); Reduviidae: *Eidmannia beniensis*, *E. guyanensis*, *E. matogrossensis*, *Melanolestes picinus*, *Rasahus albomaculatus*, *R. peruensis*, *Sirthenia peruviana orientalis*, and *Thymbreus ocellatus* (Morrone & Coscarón 1996). Hymenoptera. Apidae: *Geotrigona subgrisea* species group (Camargo & Moure 1996); Vespidae: *Protopolybia bituberculata* (Silveira & Carpenter 1995). Orthoptera. Acrididae: Copiocerinae, *Jagomphocerus*, and *Odontogryllus* (Mello 1992; Carbonell 1995; Cigliano & Lange 1998); Ommexechidae: *Ommexecha gracilis* (Ronderos 1977); Pyrgomorphidae: *Omura congrua* (Kevan 1977). **VERTEBRATA. Actinopterygii.** Characiformes. Curimatidae: *Curimata aspera*, *C. ocellata*, *C. vittata*, *Curimatella alburna*, *C. meyeri*, *Cyphocharax abramoides*, *C. festivus*, *C. notatus*, and *C. spiluroopsis* (Vari 1989, 1992a, b). Osteoglossiformes. Arapaimidae: *Arapaima gigas* (Lundberg 1993). **Amphibia.** Anura. Leptodactylidae: *Ceratophrys cornuta* (Lynch 1982); Pipidae: *Pipa pipa* (Báez 1977). **Crocodylia.** Crocodylidae: *Melanosuchus niger* (Donoso-Barros 1966). **Aves.** Anseriformes. Anatidae: *Neochen jubata* (Olrog 1984). Ciconiiformes. Charadriidae: *Vanellus cayanus* (Olrog 1984). Piciformes. Ramphastidae: *Pteroglossus bitorquatus* and *P. viridis* species groups (Cracraft & Prum 1988). Tinamiformes. Tinamidae: *Crypturellus undulatus* and *Tinamous tao* (Olrog 1984). **Mammalia.** Cetacea. Platanistidae: *Sotalia fluviatilis* (Emmons 1990). Carnivora. Canidae: *Atelocynus microtis* (Emmons 1990); Mustelidae: *Pteronura brasiliensis* (Emmons 1990). Didelphimorphia. Didelphidae: *Philander andersoni* (Emmons 1990). Primates. Callithrichidae: *Saguinus* spp. (Emmons 1990; Amorim & Pires 1996); Cebidae: *Aotus* spp. (Emmons 1990). Rodentia. Echimyidae: *Mesomys hispidus* and *Proechimys goeldii* species group (Patton 1987; Emmons, 1990). Xenarthra. Myrmecophagidae: *Cyclopes didactylus* (Emmons 1990).

Yungas province

(Figs. 1, 3)

Eastern slopes of the Andes, between 300 and 2500 m, from northern Peru to northwestern Argentina. The track of *Fuchsia decussata* (Fig. 3) is representative of this province.

Synonyms

Tucuman-Bolivian forests subregion: Hueck 1957: 40.

Yungas province: Cabrera 1971: 8; Cabrera & Willink 1973: 54; Cabrera 1976: 3; Rivas-Martínez & Navarro 1994: map; Ayarde 1995: 85; Morales *et al.* 1995: 163; Carpintero 1998: 148; Morrone 1999: 8.

Montane forests district: Cabrera 1971: 9, 1976: 8.

Montane woods district: Cabrera 1971: 10, 1976: 9.

Transition forests district: Cabrera 1971: 8, 1976: 7.

Marañón centre: Müller 1973: 97.

Yungas centre: Müller 1973: 89.

Northern Andean province: Ringuelet 1975: 107.

Yungas area: Coscarón & Coscarón-Arias 1995: 726; Acosta & Maury 1998a: 554, 1998b: 573.

Andean Yungas ecoregion: Dinerstein *et al.* 1995: 98.

Bolivian Yungas ecoregion: Dinerstein *et al.* 1995: 97.

Marañón dry forests ecoregion: Dinerstein *et al.* 1995: 101.

Peruvian Yungas ecoregion: Dinerstein *et al.* 1995: 97.

Vegetation. Cloud and dry forests, specially rich in Lauraceae and Myrtaceae, forests of *Alnus acuminata* and *Podocarpus* spp., and grasslands (Cabrera 1971; Cabrera & Willink 1973). Three vegetational types have been recognized by Morales *et al.* (1995): 1) premontane subtropical forest, 2) subtropical montane moist forest, and 3) temperate cloud forest.

Taxa. CONIFEROPHYTA. **Coniferopsida.** Coniferales. Podocarpaceae: *Podocarpus parlatoei* (Cabrera 1971; Covas 1995). MAGNOLIOPHYTA. **Magnoliopsida.** Asterales. Asteraceae: *Holocheilus fabrisii*, *Jungia pauciflora*, *J. polita*, *J. sordida*, *Perezia carduncelloides*, *Trixis grisebachii*, and *T. ragonesei* (Katinas 1995). Myrtales. Onagraceae: *Fuchsia boliviana*, *F. decussata* species group, *F. fontinalis*, and *F. pilosa* (Berry 1982). ARTHROPODA. **Arachnida.** Opiliones. Acropsopilionidae: *Prionostemma yungarum* (Ringuelet 1962). **Hexapoda.** Coleoptera. Curculionidae: *Hammatostylus inhumeralis* and *Sicoderus tringa* (Vanin 1986). Diptera. Simuliidae: *Gigantodax horcotiani* (Wygodzinsky & Coscarón 1989). Hymenoptera. Formicidae: *Probolomyrmex brujitae* (Agosti 1994). VERTEBRATA. **Actinopterygii.** Characiformes. Curimatidae: *Steindachnerina binotata* (Vari 1991). **Aves.** Craciformes. Cracidae: *Penelope dabbeni*

(Olrog 1984). Passeriformes. Frigillidae: *Atlappetes fulviceps*, *Hemispingus trifasciatus*, and *Saltator albicollis* (Müller 1973); Rhinocryptidae: *Melanopareia elegans maranonica* (Müller 1973). Tinamiformes. Tinamidae: *Nothocercus nigrocapillus* (Müller 1973). **Mammalia**. Artiodactyla. Cervidae: *Mazama chunyi* (Müller 1973). Didelphimorphia. Didelphidae: *Marmosa aceramarae* (Müller 1973). Rodentia. Echimyidae: *Proechimys boliviensis*, *P. hendeei*, and *P. simonsi* (Patton 1987).

Guianan province

(Figs. 1, 4)

Guianan shield, between Venezuela, Colombia, Guyana, Suriname, and northern Brazil, where there are sandstone plateaus, known as tepuis, of more than 2000 m altitude. The track of *Naupactus viloriai* (Fig. 4) is representative of this province.

Synonyms

Guianan highlands: Sick 1969: 452.

Guianan domain: Cabrera & Willink 1973: 67.

Guianan province: Cabrera & Willink 1973: 67; Morrone 1999: 6.

Pantepui centre: Müller 1973: 64.

Tepuis province: Rivas-Martínez & Navarro 1994: map.

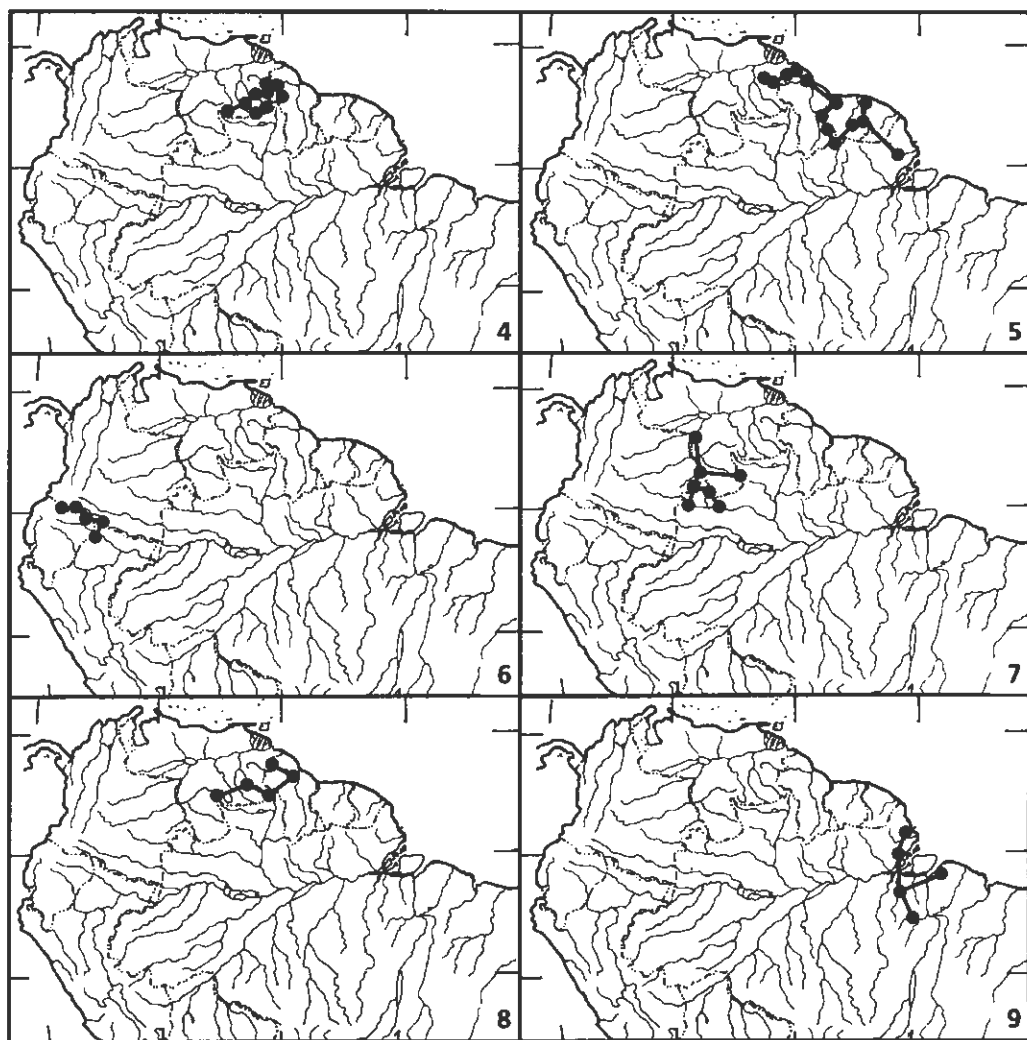
Guyana area: Coscarón & Coscarón-Arias 1995: 726.

Guianan highlands moist forests ecoregion: Dinerstein *et al.* 1995: 93.

Tepuis ecoregion: Dinerstein *et al.* 1995: 93.

Vegetation. Savannas alternating with moist forests (Cabrera & Willink 1973). More than half out of the 8,000 species of vascular plants of this province are endemic to it (Dinerstein *et al.* 1995).

Taxa. **MAGNOLIOPHYTA.** **Magnoliidae.** Asterales. Asteraceae: *Stenopadus* (Bremer 1993). **ARTHROPODA.** **Crustacea.** Anomopoda. Macrothricidae: *Streblocerus serricaudatus* (Paggi 1998). **Hexapoda.** Coleoptera. Curculionidae: *Naupactus bohumi* and *N. viloriai* (Bordón 1997); Elmidae: *Stenelmoides mimicus* and *S. variabilis* (Spangler & Perkins 1989). **VERTEBRATA.** **Squamata.** Crotalidae: *Bothrops lichenosus* (Müller 1973); Teiidae: *Arthrosaura versteegii* (Müller 1973). **Aves.** Passeriformes. Furnariidae: *Synallaxis macconelli* and *Xiphocolaptes p. promeropirhynchus* (Müller 1973); Muscicapidae: *Turdus olivater* (Müller 1973); Thamnophilidae: *Herpsilochmus roraimae* and *Myrmotherula behni* (Müller 1973); Tyrannidae: *Knipolegus poecilurus* (Müller 1973). Piciformes. Rhamphastidae: *Aulacorhynchus derbianus* (Müller 1973). Trochiliformes. Trochilidae: *Amazilia viridigatser* and *Polytmus milleri* (Müller 1973). **Mammalia.** Didelphimorphia. Didelphidae: *Monodelphis brevicaudata orinoci* (Müller 1973). Rodentia. Muridae: *Rhipidomys macconelli* (Müller 1973).



Figs. 4-9. Amazonian tracks. 4, Guianan province (*Naupactus viloriai*); 5, Moist Guianan province (*Cyphocharax helleri*); 6, Napo province (*Cyphocharax pantostictos*); 7, Imerí province (*Cyphocharax multilineatus*); 8, Roraima province (*Caprimulgus longirostris roraimae*); 9, Amapá province (*Cyphocharax gouldingi*).

Moist Guianan province

(Figs. 1, 5)

Southeastern Venezuela, northern Brazil, Suriname, and Guyana (Müller 1973). The track of *Cyphocharax helleri* (Fig. 5) is representative of this province.

Synonyms

- Guianan centre: Müller 1973: 69.
- Guianan province: Ringuelet 1975: 107.
- Guianan centre of endemism: Beven *et al.* 1984: 386.
- East Guiana refuge: Lourenço 1986: 580.
- Imataca refuge: Lourenço 1986: 580.
- West Guiana refuge: Lourenço 1986: 580.
- Northwestern Amazonia area: Cracraft 1988: 223.
- Guayanas province: Rivas-Martínez & Navarro 1994: map.
- Guyana area: Coscarón & Coscarón-Arias 1995: 726.
- Guianan moist forests ecoregion: Dinerstein *et al.* 1995: 94.
- Orinoco Delta swamp forests ecoregion: Dinerstein *et al.* 1995: 93.
- Orinoco wetlands ecoregion: Dinerstein *et al.* 1995: 106.
- Paramaribo swamp forests ecoregion: Dinerstein *et al.* 1995: 94.
- Moist Guianan province: Morrone 1999: 7.

Vegetation. Moist and swamp forests, flooded grasslands, and mangroves occur in habitat mosaic (Dinerstein *et al.* 1995).

Taxa. **FILICOPHYTA.** **Filicopsida.** Filicales. Dennstaedtiaceae: *Lindsaea sagittata* (Tryon 1972). **MAGNOLIOPHYTA.** **Magnoliopsida.** Urticales. Cecropiaceae: *Cecropia granvilleana* and *C. obtusa* (Franco & Berg 1997). **ARTHROPODA.** **Arachnida.** Araneae. Salticidae: *Chira guianensis* and *C. spinipes* (Galiano 1968). Opiliones. Stygnidae: *Actinostygnoides carus*, *Stenostygnoides cosmetitarsus*, *Stygnidius guerinii*, and *Stygnoplus longipalpus* (Pinto-da-Rocha 1997). Scorpiones. Buthidae: *Ananteris coineaui*, *A. pydanieli*, and *A. venezuelensis* (Lourenço 1986); Chactidae: *Brotheas gervaisi*, *B. granulatus*, *Broteochoactas fravalae*, *B. gaillardi*, and *B. scorzai* (Lourenço 1986). **Crustacea.** Decapoda. Trichodactylidae: *Dilocarcinus spinifer* (Rodríguez, 1992; Morrone & Lopretto 1996). **Hexapoda.** Coleoptera. Carabidae: *Amblygnathus lucidus* (Ball & Maddison 1987); Curculionidae: *Naupactus vilmae*, *Pileophorus procerus*, *Proscodermus gyllenhali*, *Sicoderus guyanensis*, and *S. nodieri* (Vanin & Reichardt 1977; Vanin 1986; Bordón 1997); Elmidae: *Stenelmoides beebei*, *S. grandis*, *S. grouvellei*, and *S. guyanensis* (Spangler & Perkins 1989); Scarabeidae: *Amblyoproctus boondocksius* (Ratcliffe 1988); Staphylinidae: *Cylindroxystus concavoperculus* (Herman 1991). Diptera. Ditomylidae: *Rhipidita primogenita* (Amorim & Pires 1996); Simuliidae: *Simulium pinto* (Coscarón & Coscarón-Arias 1995). Trichoptera. Polycentropidae:

Polycentropus surinamensis (Hamilton 1988). **VERTEBRATA. Actinopterygii.** Characiformes. Curimatidae: *Cyphocharax helleri*, *C. microcephalus*, *C. punctatus*, and *Steindachnerina runa* (Vari 1991, 1992a). **Aves.** Craciformes. Cracidae: *Penelope marail* (Müller 1973). Passeriformes. Tyrannidae: *Rupicola rupicola* (Müller 1973). Piciformes. Ramphastidae: *Selenidera culik* (Cracraft & Prum 1988). Psittaciformes. Psittacidae: *Pionopsitta caica* (Müller 1973; Cracraft & Prum, 1988). **Mammalia.** Rodentia. Echimyidae: *Proechimys cherriei* and *P. warreni* (Patton 1987).

Napo province

(Figs. 1, 6)

Northern Peru, southeastern Colombia, and eastern Ecuador. The track of *Cyphocharax pantosticos* (Fig. 6) is representative of this province.

Synonyms

Amazon centre: Müller 1973: 82.

Napo subcentre: Müller 1973: 83.

Northern Andean province: Ringuelet 1975: 107.

Napo centre of endemism: Beven *et al.* 1984: 386.

Northwestern Amazonia area: Cracraft 1988: 223.

Amazonian province: Hernández *et al.* 1992a: 138.

Loreto province: Rivas-Martínez & Navarro 1994: map.

Napo moist forests ecoregion: Dinerstein *et al.* 1995: 93.

Macarena montane forests ecoregion: Dinerstein *et al.* 1995: 94.

Western Amazonian swamp forests ecoregion: Dinerstein *et al.* 1995: 94.

Eastern Cordillera Real montane forests ecoregion: Dinerstein *et al.* 1995: 97.

Amazonian region: Rangel *et al.* 1995: 82.

Napo province: Morrone 1999: 7.

Vegetation. Moist forests, with a large meandering river system that creates habitat mosaics (Dinerstein *et al.* 1995).

Taxa. MAGNOLIOPHYTA. Liliopsida. Orchidales. Burmanniaceae: *Gymnosiphon capitatus* (Maas & Maas-van de Kamer 1988). **ARTHROPODA. Diplopoda.** Polydesmida. Chelodesmidae: *Tuberodesmus* (Shelley 1981). **VERTEBRATA. Actinopterygii.** Characiformes. Curimatidae: *Cyphocharax pantosticos* (Vari 1992a). **Aves.** Galbuliformes. Bucconidae: *Nonnula amaurocephala* (Müller 1973). Passeriformes. Tyrannidae: *Heterocercus flavivertex* (Müller 1973). Piciformes. Ramphastidae: *Selenidera reinwardtii* (Cracraft & Prum 1988). **Mammalia.** Primates. Callithrichidae: *Saguinus nigricollis* and *S. tripartitus* (Emmons 1990); Cebidae: *Pithecia aequatorialis* (Emmons 1990). Rodentia. Echimyidae: *Echimyus saturnus* and *Proechimys quadruplicatus* (Patton 1987; Emmons 1990).

Imerí province

(Figs. 1, 7)

Southern Venezuela, southeastern Colombia, and northern Brazil. The track of *Cyphocharax multilineatus* (Fig. 7) is representative of this province.

Synonyms

Amazon centre: Müller 1973: 82.

Imerí centre of endemism: Beven *et al.* 1984: 386.

Imerí refuge: Lourenço 1986: 580; Hernández *et al.* 1992b: 97.

Imerí area: Cracraft 1988: 223.

Guayana province: Hernández *et al.* 1992a: 131.

Orinoquía province: Hernández *et al.* 1992a: 129.

Rio Negro province: Rivas-Martínez & Navarro 1994: map.

Japura/ Negro moist forests ecoregion: Dinerstein *et al.* 1995: 94.

Amazonian savannas ecoregion: Dinerstein *et al.* 1995: 104.

Amazonian region: Rangel *et al.* 1995: 82.

Imerí province: Morrone 1999: 7.

Vegetation. This province has a great diversity of ecosystems: terra firme forests, igapo forests, varzea forests, swamp forests, and savannas. Some of the world's largest blackwater river systems occur here (Dinerstein *et al.*, 1995).

Taxa. **MAGNOLIOPHYTA.** **Liliopsida.** Orchidales. Burmanniaceae: *Burmannia grandiflora*, *B. dasyantha*, and *B. vaupesana* (Maas & Maas-van de Kamer 1988). **Magnoliopsida.** Rosales. Connaraceae: *Pseudoconnarus rhynchosioides*, *Rourea cuspidata*, and *R. neglecta* (Forero *et al.* 1983). Violales. Passifloraceae: *Passiflora coccinea* and *P. involucrata* (Escobar 1988). **ARTHROPODA.** **Arachnida.** Opiliones. Stygnidae: *Minax testraspinosus* and *Yapacana tibialis* (Pinto-da-Rocha 1997). Scorpiones. Buthidae: *Microtityus vanzolinii* (Lourenço 1986); Chactidae: *Chactopsis anduzei* and *C. sujirima* (Lourenço 1986). **VERTEBRATA.** **Actinopterygii.** Characiformes. Curimatidae: *Cyphocharax multilineatus* (Vari 1992a). **Aves.** Piciformes. Ramphastidae: *Pteroglossus flavirostris* and *Selenidera nattereri* (Cracraft & Prum 1988). Psittaciformes. Psittacidae: *Pionopsitta barrabandi* (Cracraft & Prum 1988). **Mammalia.** Primates. Callithrichidae: *Saguinus inustus* (Emmons 1990).

Roraima province

(Figs. 1, 8)

Northern Brazil, southeastern Venezuela, Suriname, and Guyana. The track of *Caprimulgus longirostris roraimae* (Fig. 8) is representative of this province.

Synonyms

- Roraima centre: Müller 1973: 62.
- Northwestern Amazonia area: Cracraft 1988: 223.
- Guianan savannas ecoregion: Dinerstein *et al.* 1995: 104.
- Uatama moist forests ecoregion: Dinerstein *et al.* 1995: 94.
- Roraima province: Morrone 1999: 6.

Vegetation. Basically savannas, there are also gallery forests bordering the rivers (Dinerstein *et al.*, 1995).

Taxa. **ARTHROPODA. Arachnida.** Scorpiones. Buthidae: *Ananteris dekeyseri* (Lourenço 1986). **Hexapoda.** Hemiptera. Miridae: *Notholopus roraimensis* (Carvalho & Carpintero 1986). **VERTEBRATA. Aves.** Passeriformes. Fringillidae: *Emberizoides duidae* and *Roraimia adusta* (Sibley & Monroe 1990); Furnariidae: *Automolus roraimae* (Sibley & Monroe 1990); Tyrannidae: *Myiophobus r. roraimae* (Sibley & Monroe 1990). Strigiformes. Caprimulgiformes: *Caprimulgus longirostris roraimae* (Müller 1973). **Mammalia.** Primates. Callithrichidae: *Saguinus bicolor* (Emmons 1990). Rodentia. Echimyidae: *Proechimys arabupu* and *P. vacillator* (Patton 1987); Muridae: *Podoxymys* (Müller 1973).

Amapá province

(Figs. 1, 9)

Suriname and northwestern Brazil. The track of *Cyphocharax gouldingi* (Fig. 9) is representative of this province.

Synonyms

- Amazon delta province: Rivas-Martínez & Navarro 1994: map.
- Roraima-Trombetas province: Rivas-Martínez & Navarro 1994: map.
- Amapá moist forests ecoregion: Dinerstein *et al.* 1995: 94.
- Eastern Amazonian flooded grasslands ecoregion: Dinerstein *et al.* 1995: 106.
- Amapá province: Morrone 1999: 7.

Vegetation. Moist forests and flooded grasslands (Dinerstein *et al.* 1995).

Taxa. **MAGNOLIOPHYTA. Magnoliopsida.** Urticales. Cecropiaceae: *Cecropia silvae* (Franco & Berg 1997). **ARTHROPODA. Arachnida.** Scorpiones. Chactidae: *Brotochactas sissomi* (Lourenço 1986). **Hexapoda.** Coleoptera. Curculionidae: *Sicoderus petilus* (Vanin 1986); Staphylinidae: *Cylindroxystus cavus*, *Neolindus hamatus*, *N. lodhii*, and *N. sinuatus* (Herman 1991). **VERTEBRATA. Actinopterygii.** Characiformes. Curimatidae: *Cyphocharax gouldingi* (Vari 1992a). **Mammalia.** Didelphimorphia. Didelphidae: *Monodelphis emiliae* (Emmons 1990).

Varzea province

(Figs. 1, 10)

Northwestern Brazil and northwestern Peru. The track of *Proscoderus mesosternalis* (Fig. 10) is representative of this province.

Synonyms

Amazon centre: Müller 1973: 82.

Loreto province: Rivas-Martínez & Navarro 1994: map.

Varzea forests ecoregion: Dinerstein *et al.* 1995: 95.

Varzea province: Morrone 1999: 7.

Vegetation. Flooded forests during the the rainy season (Cabrera & Willink 1973; Dinerstein *et al.* 1995). Dominant plant species include *Apulleia molaris*, *Bombax munguba*, *Calycophyllum spruceanum*, *Ceiba pentandra*, *Hevea brasiliensis*, *Triplaris surinamensis*, and *Virola surinamensis* (Fernandes & Bezerra 1990).

Taxa. **MOLLUSCA.** **Pelecypoda.** Eulamellibranchia. Mycetopodidae: *Anodontites trigonus trigonus* (Bonetto 1967; Castellanos & Landoni 1990). **ARTHROPODA.** **Arachnida.** Opiliones. Stygnidae: *Auranus hoefersocvitorum*, *A. parvus*, *Protimesius longipalpis*, and *Stygnus simoni* (Pinto-da-Rocha 1997). Scorpiones. Buthidae: *Tytius gasci* (Lourenço 1986). **Crustacea.** Decapoda. Trichodactylidae: *Trichodactylus erhardti* (Rodríguez 1992; Morrone & Lopretto 1996). **Hexapoda.** Coleoptera. Curculionidae: *Loncophorus longinasus*, *Pimelerodius reichardti*, *Proscoderus germari*, *P. mesosternalis*, *Sicoderus exilis*, *S. inermis*, and *S. matuete*, *Tyloderma tuberculatum* (Vanin 1986; Clark, 1988; Wibmer 1989). **VERTEBRATA.** **Actinopterygii.** Characiformes. Curimatidae: *Curimata knerii*, *Cyphocharax leucostictus*, *C. nigripinnis*, *C. vexillapinnus*, *Steindachnerina hypostoma*, and *S. quasimoduoi* (Vari 1989, 1991, 1992a). **Mammalia.** Rodentia. Echimyidae: *Proechimys boimensis*, *P. goeldii*, *P. hyleae*, *P. kermi*, and *P. riparium* (Patton, 1987). Sirenia. Trichechidae: *Trichechus inunguis* (Emmons 1990).

Ucayali province

(Figs. 1, 11)

Eastern Peru, northern Bolivia, and western Brazil. The track of *Proechymis brevicauda* (Fig. 11) is representative of this province.

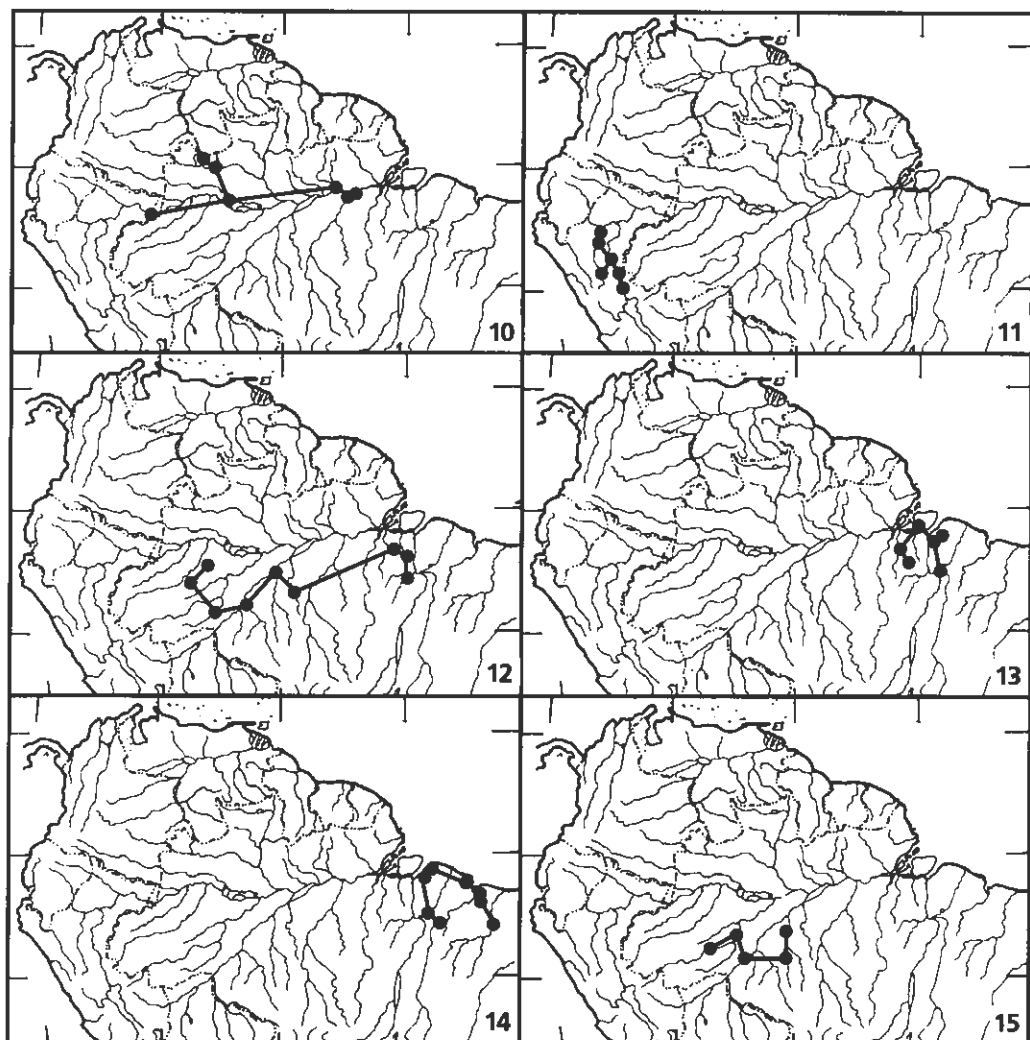
Synonyms

Amazon centre: Müller 1973: 82.

Ucayali subcentre: Müller 1973: 83.

Loreto province: Rivas-Martínez & Navarro 1994: map.

Ucayali moist forests ecoregion: Dinerstein *et al.* 1995: 94.



Figs. 10-15. Amazonian tracks. 10, Varzea province (*Proscoderus mesosternalis*); 11, Ucayali province (*Proechimys brevicauda*); 12, Madeira province (*Conopophaga melanogaster*); 13, Tapajos-Xingu province (*Simulium guianense*); 14, Pará province (*Geotrigona aequinoctialis*); 15, Pantanal province (*Steindachnerina fasciata*).

Western Amazonian flooded grasslands: Dinerstein *et al.* 1995: 106.
 Ucayali province: Morrone 1999: 7.

Vegetation. Moist forests and flooded grasslands (Dinerstein *et al.* 1995).

Taxa. ARTHROPODA. Arachnida. Opiliones. Stygnidae: *Innoxius magnus* and *Stygnus klugi* (Pinto-da-Rocha 1997). Scorpiones. Chactidae: *Chactopsis insignis* (Lourengo 1986). **Hexapoda.** Coleoptera. Curculionidae: *Proscoderus bohemani* (Vanin 1986). **VERTEBRATA. Aves.** Galbuliformes. Bucconidae: *Malacoptila semicincta* and *Nonnula slateri* (Müller 1973); Galbulidae: *Brachygalba albogularis*, *Galbalcyrhynchus leucotis*, *Galbula cyanescens*, and *G. pastazae* (Müller 1973). Passeriformes. Thamnophilidae: *Rhegmatorhina melanostica* (Müller 1973); Tyrannidae: *Heterocercus linteatus* and *Muscisaxicola fluviatilis* (Müller 1973). Psittaciformes. Psittacidae: *Aratinga weddelli* (Müller 1973). Tinamiformes. Tinamidae: *Crypturellus bartletti* and *C. strigulosus* (Müller 1973). Trochiliformes. Trochilidae: *Leucipus chlorocercus* (Müller 1973), *Phaetornis philippii* (Müller 1973). **Mammalia.** Rodentia. Echimyidae: *Proechimys brevicauda* and *P. hilda* (Patton 1987).

Madeira province (Figs. 1, 12)

Northeastern Brazil, limited in the north by the Amazon river, in the west by the Madeira and Beni rivers, in the east by the Xingu river, and in the south by the Bolivian eastern cordillera. The track of *Conopophaga melanogaster* (Fig. 12) is representative of this province.

Synonyms

Amazon centre: Müller 1973: 82.

Madeira centre: Müller 1973: 80.

Southwestern Amazonia area: Cracraft 1988: 223.

Madeira province: Rivas-Martínez & Navarro 1994: map; Morrone 1999: 8.

Juruá moist forests ecoregion: Dinerstein *et al.* 1995: 95.

Purus/ Madeira moist forests ecoregion: Dinerstein *et al.* 1995: 95.

Vegetation. Moist forests.

Taxa. ARTHROPODA. Hexapoda. Diptera. Simuliidae: *Araucnephia montana* (Coscarón & Coscarón-Arias 1995). Hymenoptera. Apidae: *Geotrigona subgrisea subfulva* (Camargo & Moure 1996). **VERTEBRATA. Aves.** Craciformes. Cracidae: *Penelope pileata* (Müller 1973). Passeriformes. Certhiidae: *Odontorchilus cinereus* (Müller 1973); Conopophagidae: *Conopophaga melanogaster* (Müller 1973); Furnariidae: *Dendrocolaptes certhia concolor* (Müller 1973); Thamnophilidae:

Myrmotherula sclateri and *Skutchia borbae* (Müller 1973); Tyrannidae: *Pipra nattereri* (Müller 1973). Piciformes. Ramphastidae: *Pteroglossus sturmi* (Cracraft & Prum 1988). Psittaciformes. Psittacidae: *Pionopsitta aurantigera* and *Pyrrhura rhodogaster* (Müller 1973; Cracraft & Prum 1988). **Mammalia**. Primates. Callithrichidae: *Callithrix humeralifer* and *Saguinus labiatus* (Emmons 1990); Cebidae: *Callicebus moloch hoffmanni* (Emmons 1990); Cebidae: *Chiropotes albinasus* (Emmons 1990).

Tapajos-Xingu province

(Figs. 1, 13)

Northwestern Brazil. The track of *Simulium guianense* (Fig. 13) is representative of this province.

Synonyms

Southeastern Amazonia area: Cracraft 1988: 223.

Tocantins province: Rivas-Martínez & Navarro 1994: map.

Xingu-Tapajos province: Rivas-Martínez & Navarro 1994: map.

Tapajos/ Xingu moist forests ecoregion: Dinerstein *et al.* 1995: 95.

Tapajos-Xingu province: Morrone 1999: 8.

Vegetation. Rainforests (Dinerstein *et al.* 1995).

Taxa. **ARTHROPODA.** **Arachnida.** Scorpiones. Chactidae: *Broteochactas goujei* (Loureço 1986). **Hexapoda.** Coleoptera. Curculionidae: *Achia bondari* (Burke & Kovarik 1986); Scarabeidae: *Hemiphileurus brasiliensis* and *H. insularis* (Ratcliffe 1988). Diptera. Simuliidae: *Simulium guianense* (Coscarón & Coscarón-Arias 1995). **VERTEBRATA.** **Aves.** Piciformes. Ramphastidae: *Pteroglossus reichenowi* (Cracraft & Prum 1988). Psittaciformes. Psittacidae: *Pionopsitta vulturina* (Cracraft & Prum 1988).

Pará province

(Figs. 1, 14)

Northwestern Brazil, limited in the north and west by the Tocantins and Araguaia rivers, in the south by the Serra do Gurupi of the northern part of Maranhao and by the Grajau river, and in the east by the Guaná river. The track of *Geotrigona aequinoctialis* (Fig. 14) is representative of this province.

Synonyms

Pará centre: Müller 1973: 75.

Belém centre of endemism: Beven *et al.* 1984: 386.

Southeastern Amazonia area: Cracraft 1988: 223.
 Amazonian Eastern sector: Fernandes & Bezerra 1990: 92.
 Amazonian delta province: Rivas-Martínez & Navarro 1994: map.
 Tocantins province: Rivas-Martínez & Navarro 1994: map.
 Tocantins moist forests ecoregion: Dinerstein *et al.* 1995: 96.
 São Luis flooded grasslands ecoregion: Dinerstein *et al.* 1995: 106.
 Pará province: Morrone 1999: 8.

Vegetation. Moist forests and flooded grasslands (Dinerstein *et al.* 1995).

Taxa. **ARTHROPODA.** **Arachnida.** Scorpiones. Chactidae: *Brotheas paraensis* (Lourengo 1986). **Hexapoda.** Coleoptera. Scarabeidae: *Palaeophileurus marcusoni* (Ratcliffe 1988); Staphylinidae: *Sterecephalus rufus* (Herman 1979). Hymenoptera. Apidae: *Geotrigona aequinoctialis* (Camargo & Moure 1996). **VERTEBRATA.** **Aves.** Craciformes. Cracidae: *Ortalis supercilialis* (Müller 1973). Passeriformes. Conopophagidae: *Conopophaga roberti* (Müller, 1973); Fringillidae: *Gymnostinops bifasciatus* (Müller 1973); Tyrannidae: *Pipra iris* and *Xipholena lamellipennis* (Müller 1973). Piciformes. Ramphastidae: *Pteroglossus bitorquatus* (Cracraft & Prum 1988). Psittaciformes. Psittacidae: *Aratinga guarouba* and *Pyrrhura perlata* (Müller 1973). **Mammalia.** Rodentia. Echimyidae: *Proechimys leioprimma*, *P. nesiotes*, and *P. oris* (Patton 1987).

Pantanal province

(Figs. 1, 15)

South central Brazil, northeastern Bolivia, and northern Paraguay. The track of *Steindachnerina fasciata* (Fig. 15) is representative of this province.

Synonyms

Alto Paraguay province: Ringuelet 1975: 107.
 Alto Parana province: Ringuelet 1975: 107.
 Rondonia centre of endemism: Beven *et al.* 1984: 386.
 Guapore refuge: Lourenço 1986: 580.
 Southeastern Amazonia area: Cracraft 1988: 223.
 Pantanal sector: Fernandes & Bezerra 1990: 148.
 Acre-Madre de Dios province: Rivas-Martínez & Navarro 1994: map.
 Beni province: Rivas-Martínez & Navarro 1994: map.
 Pantanal province: Rivas-Martínez & Navarro 1994: map.
 Beni savannas ecoregion: Dinerstein *et al.* 1995: 104.
 Beni swamp and gallery forests ecoregion: Dinerstein *et al.* 1995: 95.
 Bolivian lowland dry forests ecoregion: Dinerstein *et al.* 1995: 100.
 Pantanal ecoregion: Dinerstein *et al.* 1995: 107.

Rondonia/ Mato Grosso moist forests ecoregion: Dinerstein *et al.* 1995: 95.
 Southwestern Amazonian moist forests ecoregion: Dinerstein *et al.* 1995: 94.
 Rondonia province: Morrone 1999: 8.
 Pantanal province: Morrone 1999: 9.

Vegetation. The Pantanal province is constituted by a mosaic of flooded grasslands, savannas, gallery forests, and dry forests. During the rainy season, more than 80% of this area floods (Dinerstein *et al.* 1995).

Taxa. **ARTHROPODA. Arachnida.** Opiliones. Stygnidae: *Protimesius albilineatus*, *Stygnus marthae*, and *S. weyrauchi* (Pinto-da-Rocha 1997). Scorpiones. Buthidae: *Ananteris mariaterezae* (Lourenço, 1986). **Hexapoda.** Coleoptera. Curculionidae: *Proscoderus xingu* (Vanin 1986). Hymenoptera. Apidae: *Geotrigona fulvatra* and *G. fulvohirta* (Camargo & Moure 1996). **VERTEBRATA. Actinopterygii.** Characiformes. Curimatidae: *Steindachnerina fasciata* (Vari 1991). **Mammalia.** Rodentia. Echimyidae: *Proechimys rattinus* and *P. steerei* (Patton 1987); Sciuridae: *Sciurus ignitus* and *S. sanborni* (Emmons 1990).

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