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Freshwater crabs from the highlands of the Venezuelan Guayana

Cangrejos dulceacuícolas de las tierras altas de la Guayana venezolana

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ABSTRACT

Neotropical freshwater crabs have a wide distribution range from southern Mexico to Peru, including the entire Amazon basin and the Guianas. Among them, highland species of the genus *Microthelphusa* Pretzmann, 1968, have a very peculiar biogeography. Their distribution is insular and discontinuous, presenting considerable separation between them. Twelve species are found south of the Orinoco River, of which six are found in the Venezuelan Guayana, and of these, five are endemic to the highlands of the tepuis. In this paper I attempt to explain the distribution of the species of *Microthelphusa* and their occurrence in the upper elevations of the tepuis.

Keywords: biogeography, freshwater crabs, insular distribution, *Microthelphusa*, Neotropics, taxon cycle, tepuis.

RESUMEN

Los cangrejos de agua dulce neotropicales tienen un amplio rango de distribución desde el sur de México hasta Perú, incluida toda la cuenca del Amazonas y las Guayanas. Entre ellos, las especies de grandes altitudes del género *Microthelphusa* Pretzmann, 1968, tienen una biogeografía muy peculiar. Su distribución es insular y discontinua, presentando una separación considerable entre ellos. Doce especies se encuentran al sur del río Orinoco, de las cuales seis se encuentran en la Guayana venezolana, y de estas, cinco son endémicas del altiplano de los tepuyes. En este artículo intento explicar la distribución de las especies de *Microthelphusa* y su presencia en las elevaciones superiores de los tepuyes.

Palabras clave: biogeografía, cangrejos dulceacuícolas, ciclo de taxones, distribución insular, *Microthelphusa*, Neotrópico, tepuyes.

INTRODUCTION

The Amazon basin supports the greatest terrestrial biodiversity (Wilson 1992, Webb 1995). But why this singularity? Largely it is due to the complexity of the geological changes that the South American continent has undergone since its separation from Pangea during the Lower Cretaceous and its gradual shift to its present position (Shell de Venezuela & Creole Petroleum Corporation 1964, Gayet *et al.* 1992, Ruban *et al.* 2009). One of those geological features that characterize South America are the Andes, the world's longest mountain range, which is the product of the slow subduction of the Nazca Plate beneath the South American plate from the Late Cretaceous to the present. This has led to a gradual and differentiated uplift of the mountain ranges that concluded at the end of the Miocene with the emergence of the Serranía de Perijá and the Venezuelan Andes. This process differs markedly from the uprising of other mountain systems such as the Alps, the Himalayas and the Rockies, which are the product of large clashes of continental masses (Weeks 1956, Harrington 1962, Ricardi 1987, Kroonenberg *et al.* 1990, Andriessen *et al.* 1993, Rossetti *et al.* 2005, Jaimes & de Freitas 2006, Ramos & Moreno 2006, Cardona Molina *et al.* 2006, Ramon & Rosero 2006, Cortés *et al.* 2006, Silva Tamayo *et al.* 2008, Leier *et al.* 2013).

Another important feature is that the separation of South America from Africa was a slow process that initially allowed the migration of species between the two continents for a long period and the slow formation of the South Atlantic (Iturralde-Vinent 2003, Allibon *et al.* 2008, Dentzien-Dias *et al.* 2008, Brookfield *et al.* 2009, Woodburne 2010, Teixeira *et al.* 2019). At the end of this separation, the South American continent is positioned in a stable climatological zone, although the creation of the Atlantic produced great changes in the global climate and in the patterns of marine currents. From this moment on, the continent was subject to regressions and marine transgressions that at different times were modulated by the presence of the great continental cratons and the Andes. During the periods of marine transgressions the emerged lands acted as islands and "laboratories" for the diversification of species, which were dispersed and mixed during the marine regressions. The presence of the epicontinental seas had an overwhelming impact on the diversity of the continent's aquatic fauna, represented by a large number of species of fish, mammals, mollusks and crustaceans of direct marine origin, currently found in the Amazon and the eastern slopes of South America. This phenomenon is very interesting because as the Andes were lifted by pulses, they were framing the epicontinental sea, at first allowing connections between it and the Pacific, the Proto-Caribbean and the South Atlantic, and then gradually closing these portals, which created an immense estuary in which the marine forms were slowly evolving to their current freshwater forms. The last growth pulse of the Andes at the end of the Miocene produced a dramatic change in this immense estuary, as it changed the direction of the flow of the Proto-Amazonas-Orinoco and gradually guided them to their current mouths. This drained the estuarine lake and created the current Amazon and Orinoco River basins (Haq *et al.* 1987, Habib & Miller 1989, Lundberg 1992, Hoorn 1993, 1994, Rasanen 1995, Monsch 1998, Rull 1999, Hamilton *et al.* 2001, Schram 2001, Feldmann 2003, Bush *et al.* 2004, Albert *et al.* 2006, Anderson *et al.* 2006, Cunha-Ribeiro 2006, Cozzuol 2006, Feijó-Ramos 2006, Hoorn & Vonhof 2006, Hulka *et al.* 2006, Kaandorp *et al.* 2006, Kay & Cozzuol 2006, Lovejoy *et al.* 2006, Muñoz-Torres *et al.* 2006, Rebata *et al.* 2006, Wesselingh & Macsotay 2006, Westaway 2006, Almeida-Filho & Miranda 2007, Latrubesse *et al.* 2007, Flynn *et al.* 2008, Jasper *et al.* 2008, Mantelatto *et al.* 2008, Bond-Buckup *et al.* 2010, Leonhardt & Lorscheitter 2010, Shephard *et al.* 2010, Anger 2013, Lasso *et al.* 2013, Wade 2013, 2017, Cumberlidge *et al.* 2014, Perkins 2014, Lovejoy 2017, Posada-Swafford 2017, Davis *et al.* 2018).

The importance of these geological phenomena that I have tried to summarize here can be easily modeled through the brachyuran decapod crustaceans, of which there is a more or less well documented fossil record since the end of the Jurassic (Ortmann 1902, Stevcic 1971, Cisne 1974, Rodríguez & Díaz 1977, Cracraft 1988, Vega & Felman 1991, Malabarba *et al.* 1998, Von Sternberg *et al.* 1999, Feldmann & Schweitzer 2006, Limarino & Spalletti 2006, Fabbrin Pires & Guerra Sommer 2009, Candeiro & Rich 2010, Hoorn & Wesselingh 2010, Haug *et al.* 2015, Klaus *et al.* 2017).

FRESHWATER CRABS OF SOUTH AMERICA AND THEIR PECULIAR DISTRIBUTION IN THE HIGHLANDS

Among the decapod crustaceans, the Brachyura is the most successful lineage, possessing more than seven thousand species with a great variety of morphotypes. They have managed to conquer almost every habitat in the world, from underwater volcanic vents on the oceanic ridges to the top of mountains at 2,000m above sea level. The vast majority of species are marine, but about 1,300 are freshwater species and some of these are semiterrestrial (Haug *et al.* 2015). In the Neotropics we find two families of freshwater crabs, the Trichodactylidae, restricted almost exclusively to the aquatic environment (Díaz & Rodríguez 1977), although there is evidence that they can carry out terrestrial migrations under heavy rains. These have an altitudinal distribution that goes from approximately 0 m a.s.l. to 550 m a.s.l. They are distributed in the coastal plains of the Guianas and Brazil, in the great fluvial plains of the Amazon, the Orinoco, Paraguay and Paraná and in the separate basins of Magdalena and Lake Maracaibo. Two genera are also found in southern Mexico (Rodríguez 1992).

The other family, Pseudothelphusidae, represents an evolutionary leap for the conquest of terrestrial environment, developing pseudolungs to take the atmospheric air, transforming their gills to recover sodium and potassium. They have a dense cover of hairs in their legs and in the gill region to allow the absorption of water from the surrounding air passing it to the respiratory chamber. In addition, they have direct development inside the egg, and exhibit parental care.

Although these are great evolutionary achievements, it is still far from possible to consider these organisms as terrestrial, since their cephalothorax is still too permeable and they dry out easily if they are not in contact with very humid surfaces. Their altitudinal distribution ranges from 400 m a.s.l., up to 2,000 m a.s.l., and extends from the State of Sonora in Mexico to the outskirts of Lima in Peru, including the Great Antilles (except Jamaica) and the Guianas. The family is composed of two subfamilies, Epilobocerinae and Pseudothelphusinae.

Epilobocerinae is the most primitive and has only one genus *Epilobocera* Stimpson, 1860, found in the Greater Antilles. The second, Pseudothelphusinae, with five tribes: Strengerianini, with four genera: *Strengeriana* Pretzmann, 1971*, Chaceus* Pretzmann, 1965*, Martiana* Rodríguez, 1980 and *Phallangothelphusa* Pretzmann, 1965, distributed in northern Colombia. Hypolobocerini, with eleven genera: *Hypolobocera* Ortmann, 1897*, Moritschus* Pretzmann, 1965*, Neostrengeria* Pretzmann, 1965*, Ptychophallus* Smalley, 1964*, Phrygiopillus* Smalley 1970*, Spirothelphusa* Pretzmann, 1965*, Camptophallus* Smalley, 1965*, Elsalvadoria* Bott, 1967*, Lobithelphusa* Rodríguez, 1982*, Raddaus* Pretzmann, 1965 and *Achlidon* Smalley, 1964, distributed through the Andes to Peru. Potamocarcinini, with four genera: *Potamocarcinus* H. Milne-Edwards, 1853, *Typhlopseudothelphusa* Rioja, 1952*, Odontothelphusa* Rodríguez, 1982 and *Allacanthos* Smalley, 1964, that are distributed across the Atlantic coast from Central America to Mexico (Rodríguez 1982). Pseudothelphusini, with three genera*: Ehecatusa* Ng & Low, 2010 (= *Epithelphusa* Rodríguez & Smalley, 1970)*, Tehuana* Rodríguez & Smalley, 1969 and *Pseudothelphusa* Saussure, 1857, distributed from the Atlantic coast of Mexico, crossing to the Pacific and extending to the Sierra Madre in Sonora; and Kingsleyini, with 10 genera: *Eudaniela* Pretzmann, 1971*, Rodriguezus* Campos & Magalhães, 2005*, Microthelphusa* Pretzmann, 1968*, Neopseudothelphusa* Pretzmann, 1965*, Kingsleya* Ortmann, 1897*, Orthothelphusa* Rodríguez, 1980*, Oedothelphusa* Rodríguez, 1980*, Prionothelphusa* Rodriguez, 1980*, Fredius* Pretzmann, 1967 and *Guinotia* Pretzmann, 1965, distributed from the Venezuelan Andes, passing through the Cordillera de la Costa to Trinidad and Tobago then turning to the Guiana Shield to the left margin of the Amazon (Rodríguez 1982, Campos *et al.* 2002, Campos & Magalhães 2004, Suárez 2006, 2013, Magalhães & Pereira 2007, Cumberlidge *et al*. 2009, Magalhães, 2009, Pereira *et al.* 2009).

The presence of both families on the continent is older than it had previously been considered. If we observe the new models for the Caribbean geologic formation (Meschede & Frisch 1998; Iturralde-Vinent 2003; Klaus *et al.* 2017) that show how the Greater Antilles were part of Pangea 160 Ma, and considering that the oldest species are in the external limit of the distribution of the family (Rapoport 1975), we can assume that the Epilobocerinae were already distributed in the north of South America in the middle of the Jurassic and could be considered living fossils. We now know that brachyuran megalope fossils similar to the present ones, already inhabited the oceans 150 Ma (Haug *et al.* 2014). This might explain the disjunct distribution of the subfamily in the Greater Antilles.

The oldest known fossil record of a Trichodactylidae to date is *Sylviocarcinus piriformis* (Pretzmann, 1968), a species which has currently a disjunct distribution between the Lake Maracaibo Basin, the Cesar River Valley and the Magdalena River Valley sector between Puerto Boyacá and the Gualanday River (Rodríguez 1997, Souza-Carvalho *et al.* 2017, Klaus *et al.* 2017). This living fossil is possible evidence of the existence of an opening that allowed the Proto-Amazonas-Orinoco to flow towards the Pacific, which was closed at the end of the Miocene with the rise of the Sierra de Perijá and the Venezuelan Andes. This geological event also promoted the uplift of the Coastal Range of Venezuela and the subsequent colonization of Pseudothelphusidae species along this mountains system (Stephan *et al.* 1990, Coates *et al.* 1992, Collins *et al.* 1996, Murdock *et al.* 1997, Haug & Tiedemann 1998, Haug *et al.* 2001, Restrepo & López 2008, Martínez *et al.* 2010, Woodburne 2010).

INSULAR DISTRIBUTION OF PSEUDOTHELPHUSID CRABS OF THE PANTEPUI

One of the genera from south of the Orinoco that colonized these new spaces since the late Miocene, beginning in the Andean foothills, is *Microthelphusa* Pretzmann, 1968. It has a wide distribution range, from the Cordillera de Mérida (Venezuela) through the Cordillera de la Costa to Trinidad, here its distribution suffers a disjunction and reappears in the southern margin of the Orinoco River, from the Venezuelan Guayana, the Venezuelan Amazon, Guyana and Surinam to the Amazonas State of Brazil (Fig. 1). Altitudinal distribution of the genus ranges from 500 m a.s.l. to 2,000 m a.s.l. in the north, and from 400 m a.s.l. to 1,600 m a.s.l. in the southern margin of the Orinoco, which confers an insular distribution to the species. In addition, *Microthelphusa* species are associated in the base of their altitudinal distribution with other genus of greater size that in the case of the species of the north range is *Rodriguezus* Campos & Magalhães, 2004 and in those that are in the southern margin of the Orinoco is *Fredius* Pretzmann, 1967. These genera are of large size (between 5 and 12 cm of cephalothorax width in the case of *Rodriguezus* and between 4 and 9 cm of cephalothorax

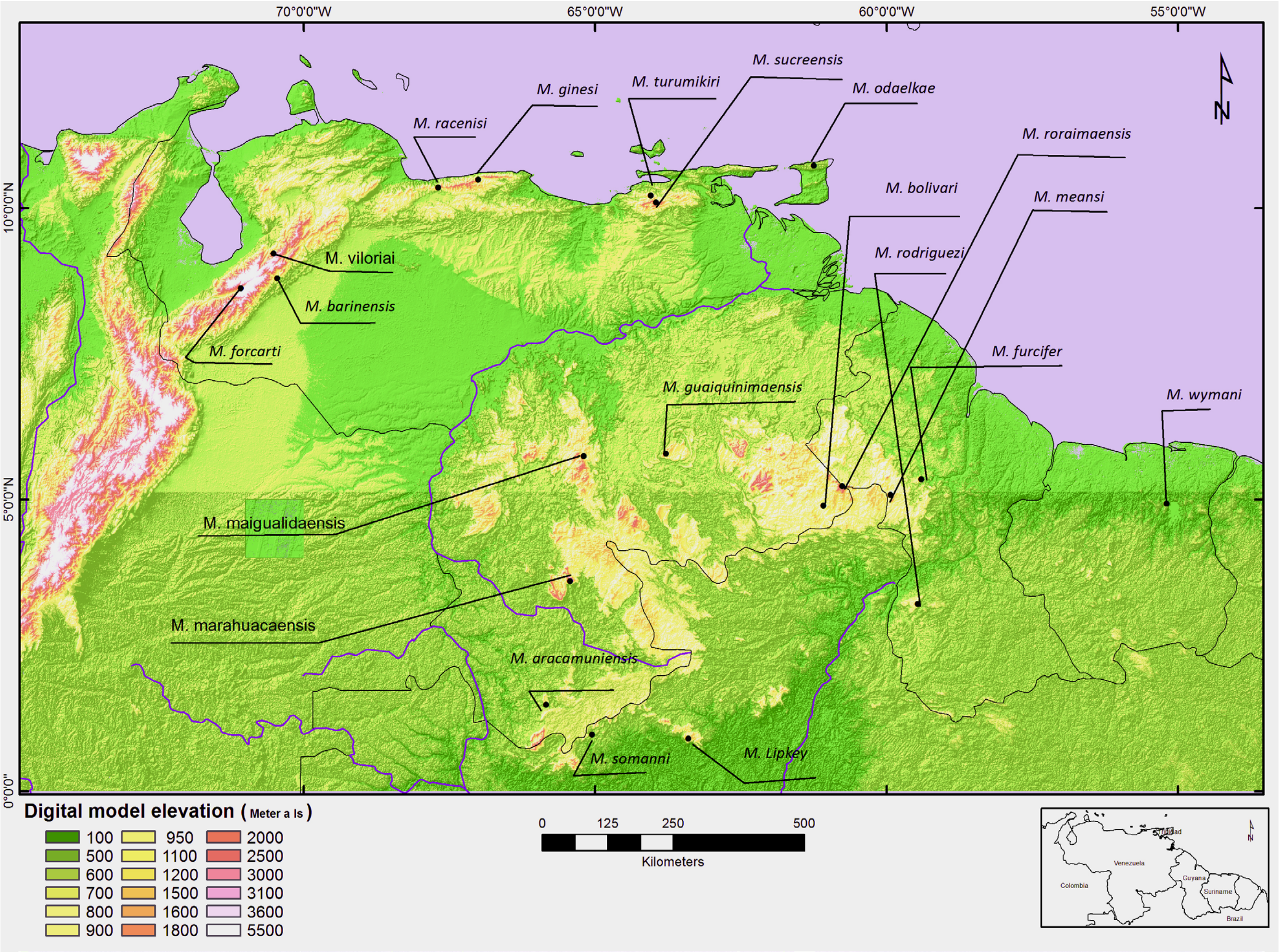

Figure 1. Map of the distribution area of the genus *Microthelphusa* Pretzmann, 1968.

width in the case of *Fredius*), compared with *Microthelphusa* (whose width of cephalothorax oscillates between 1.5 and 3 cm) (Fig. 2).

Figure 1 shows the distribution range of species of *Microthelphusa* in the northern border of Venezuela, between the Andes to Trinidad and the Orinoco to the Amazon River, from the high savannas of Surinam and Guyana, to the Tepuis of Venezuela (in Amazonas and Bolívar states) and Serra do Aracá in the state of Amazonas of Brazil. The lowest altitude species in this group is *Microthelphusa furcifer* Pedraza & Tavares, 2014 (440 m a.s.l.), followed by *M. roraimensis* Suárez, 2015 (900 m a.s.l.) (Fig. 2A), *M. wymani* (Rathbun, 1905) (506 m a.s.l.), *M. aracamuniensis* Suárez, 2015 (1,000-1,500 m a.s.l.) (Fig. 2C), *M. rodriguezi* Pretzmann, 1968 (800 to 950 m a.s.l.), *M. bolivari* Rodríguez 1980 (1,000 m a.s.l.), *M. meansi* Cumberlidge, 2007 (1,135 m a.s.l.) and *M. lipkey* Magalhães, 2010 (1,000-1,200 m a.s.l.), *M. guaquinimaensis* Suárez, 2015 (1,380-1,400 m a.s.l.) (Fig. 2B), *M. marahuacaensis* Suárez, 2015 (1,500 m a.s.l.) (Fig. 2D) and *M. maigualidaensis* Suárez, 2015 (1,500 m a.s.l.) (Fig. 2E) (Table 1). All these species are found within what was named Pantepui, by Mayr & Phelps, Jr (1955).

"The sandstone plateaus located in the Bolivar and Amazonas states of Venezuela and in the border regions of Guyana, Suriname, Brazil and Colombia". This definition has an explicit geographic criterion related to the extension in surface and height, as well as an implicit biological criterion, referring to the conditions of life in the area in question (Costa *et al.* 2014a). Subsequently, several researchers offered different interpretations of the term Pantepui (Müller 1973, Hoogmoed 1979, Steyermark 1979, Brown 1987, Neild 1996, 2008), which departed from the original concept. To clearly define it from the geographical and biological point of view Huber (1987), describes it as: "The Pantepui biogeographic province, which is part of the Guiana Region, includes the set of orographic ecosystems developed in the tabular mountains (Tepuis), of the

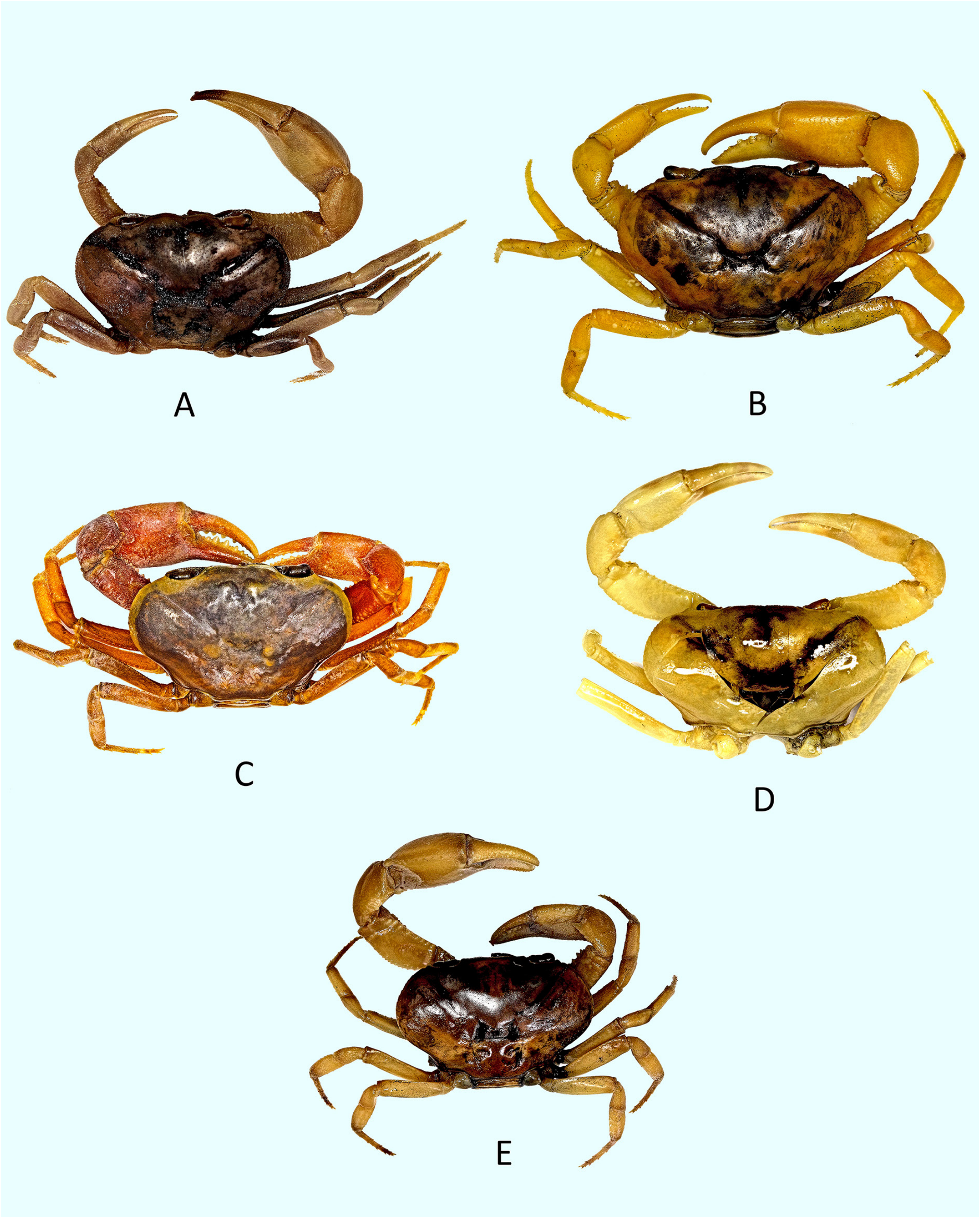

Figure 2. Dorsal view of the cephalothorax and habitus of several species of *Microthelphusa* Pretzmann, 1968, from the highlands of the Venezuelan tepuis, present in the Crustacean Collection of IVIC: **A.** *M. roraimensis*; **B.** *M. guaiquinimaensis*; **C.** *M. aracamuniensis*; **D.** *M. marahuacaensis*; **E.** *M. maigualidaensis.*

Table 1. Altitudinal distribution of the species of freshwater crabs of the genus *Microthelphusa* Pretzmann, 1968.

Species	Locality	Altitude (m. a.s.l.)
Species present between the Venezuelan Andes and Trinidad		
M. forcarti	Tabay, Merida State, Venezuela	1,603-1,800
M. barinensis	Between La Soledad and Barinitas, Barinas State, Venezuela	530-570
M. viloriai	Santa Ana, Trujillo State, Venezuela	1,500
M. racenisi	Rancho Grande, Aragua State, Venezuela	1,400-2,000
M. ginesi	El Guacatal, Hacienda El Limón, Distrito Federal, Venezuela	1,224
M. turumikiri	Mount Turumikire, Sucre State, Venezuela	1,500
M. sucreensis	Negro River, near the village of Las Cabeceras. Sucre State, Venezuela	1,730-1,980
M. odaelkae	Aripo Peak, Trinidad	600-800
Species present between the Orinoco and the Amazon rivers		
M. aracamuniensis	Aracamuni Peak, Amazonas State, Venezuela	1,000-1,500
M. maigualidaensis	Maigualida Sierra, Amazonas State, Venezuela	1,500
M. marahuacaensis	Marahuaca Peak, Amazonas State, Venezuela	1,500
M. guaiquinimaensis	Guaiquinima Peak, Amazonas State, Venezuela	1,380-1,400
M. meansi	Potaro Siparuni, Wokomung Massif, Guyana	1,135
M. lipkey	Aracá Mountain, Amazonas State, Brazil	1,133
M. bolivari	El Dorado-Santa Elena Road, Bolivar State, Venezuela	1,000
M. roraimaensis	Mount Roraima, Bolivar State, Venezuela	950
M. rodriguezi	Rupununi River, Melville, Guyana	827
M. wymani	Brownsberg Nature Preserve Park, Witti Creek, Surinam	506
M. furcifer	Potaro-Siparuni Region, Kuribrong River, Guyana	440
M. somanni	Marauia River, affluent of the Negro River. Near the Venezuela Border. Brazil.	113

Roraima Formation of the Guiana Shield, extending from 1,200-1,500 to 3,045 m a.s.l. It is a tropical orobiome in the sense of Walter (1976), the "orobioma tepuyano", in which are included all the ecosystems of the upper slopes and summits of the Tepuis, located in the meso- and subthermal altitudinal tropical floors". Costa *et al.* (2014a), report the existence of more than fifty tepuis, and present a map of their distribution and of the mountain massifs that reach at least 1,500 m a.s.l., in the Guiana shield.

These tabular mountains have fascinated researchers and the imagination of the general public for centuries since Sir Walter Raleigh described them in his notes "The discovery of the great, rich and beautiful Empire of Guayana". For Sir Arthur Conan Doyle (1912), in his fictional novel "The lost World", these mountains of vertical walls were the reservoir of extinct fauna and flora of the Jurassic (Schubert 1993). However, radio carbon studies carried out on the peatlands of the Venezuelan tepuis show that they are between 8,000 and 9,000 years old before the present (Schubert & Fritz 1985, Schubert 1986, 1986a, Schubert *et al.* 1994). Therefore, it is inferred that the present fauna and flora of the tepuis have only developed since the Quaternary (Steyermark 1979).

The majority of the species that cohabit in these mountains are endemic of the tops where they occur and show an insular distribution, in addition they are organisms adapted to sudden changes of temperature, low nutrients availability, and acid waters, among other factors. Why a crab rises to these high peaks in which calcium availability in the water is not enough to regenerate their cephalothorax? Their body size decreases to facilitate oxygen uptake, and they develop special strategies for food acquisition, such as living inside the tubular leaf tanks of *Brocchinia* species (Magnoliophyta: Bromeliaceae) (Hokche *et al.* 2008, Wehrtmann *et al.* 2016), in addition to increasing the size of their eggs to have a more efficient direct development, which makes the number of eggs also smaller, thus affecting their reproductive efficiency.

What makes an animal like that to live in such extreme conditions as those of the tepuis? A catastrophic event that separates species and creates extreme conditions may force species to take this course. But there are more finely tuned factors, such as interspecific competition between organisms occupying similar niches in ecosystems, Wilson (1959, 1961) coined the term "taxon cycle" to refer to variations in the distribution of species on islands. When new species arrive, they tend to expand and the range of distribution of resident species decreases, to a point where they are relegated to the margin of their original distribution. If there are elevations in these spaces, it is observed that the old species are forced to ascend in altitude and gradually reduce their size. This allows to create a transitory balance between the new and the old species, marked by the altitudinal floors. This has been observed by Ricklefs (1970) and Ricklefs & Eldredge (2002) in birds of the Antilles.

The genus *Microthelphusa* (Fig. 2), presents a distribution that agrees with the statements of this theory, but also fits the model of distribution of species enunciated by Rapoport (1975), according to which the oldest species should be at the outer limit of the distribution of the genus. In this analysis *Microthelphusa forcarti* (Pretzmann 1967) is the one that presents the most primitive characters of its genus and is located in the Venezuelan Andes (Fig. 2, Table 1), we also know that the genus did not go past this point, so its expansion towards the north must have coincided with the raising of the barrier of the Venezuelan Andes and with the gradual migration of the Orinoco towards its current drainage. Among the species of the Andean foothills and the Coastal Cordillera, it is worth highlighting the case of *M. ginesi* Rodríguez & Esteves, 1972, found above 1,000 m a.s.l. in the upper part of the Federal District (Venezuela) mountains and *Rodriguezus ranchograndensis* (Rodríguez 1966), with a wider altitudinal range in the same mountains (from 100 to 1,000 m a.s.l.) overlapping the distribution area of *Microthelphusa ginesi*.

Today *Rodriguezus ranchograndensis* is found above 1,200 m a.s.l., and *M. ginesi* has not been recaptured for more than 40 years. Therefore, it appears that the latter was displaced by *R. ranchograndensis* and might currently be extinct. The vertical migration of *R. ranchograndensis* is directly associated to the urban development at the foothills of these mountains, deforestations and pollution streams and rivers which forced *R. ranchograndensis* to go up and enter in direct competition with *M. ginesi* (and generally the biggest eats the small one). A similar case is observed in the Mount Aripo of Trinidad, where *M. odaelkae* (Bott 1970) has been substituted by *Rodríguezus garmani* (Rathbun, 1898), possibly by the same reasons as *M. ginesi* in Venezuela. This corroborates what was expressed by Wilson (1959, 1961) in his "taxon cycle" theory.

The *Microthelphusa* species located between the Orinoco River and the northern margin of the Amazon River (Fig. 3), present more modern characters in their distribution than in areas where there is no record of another bigger crab genera. They are found in low altitudinal levels. In areas where big *Fredius* species occur, they are found at higher altitudes up to the top of the tepuis. Rapoport (1975), proposed that the most recent species are found near the distribution center of the genus, which coincides with what we see here. But this is not an exclusive biogeographical pattern of the genus *Microthelphusa*, the same can also be seen within the genus *Fredius*. *Fredius cuaoensis* Suárez, 2015, from the Upper Cuao River, at 1,000 m a.s.l., is the smallest species in the genus. *Fredius chaffanjoni* (Rathbun, 1905) occurs in the mouth of this river and in its middle course. Being the latter a species of large size, a parallel case to that of *Microthelphusa* appears to occur: both species of *Fredius* segregate at different altitudinal levels.

CONCLUSIONS

We currently accept that the extant species of freshwater crabs found on top of the tepuis are of Quaternary age and that the evolution of at least the new species of decapod crustaceans, responds to the principles of the "taxon cycle" theory. We can also state that these mountains, far from being a lost world, are a new world where one can appreciate with all intensity the force of life and the different strategies of evolution that guide it. It should be noted that several of these once pristine mountains are now under assault by indiscriminate tourism that destroys the fragile ecology of these spaces. The knowledge of these environments is still very poor, so it is not possible to determine, at least in the case of the crustaceans, the size of the populations and their extension. All specimens known have been found in casuistic events, which is why it is observed that in the collections there are only two specimens of each species.

The relatively few scientific expeditions that have been conducted to the tepuis were mainly focused on geology (Stern 1954, Schubert 1985, 1986, 1986a Barreat *et al.* 1986, Colmenares & Terán 1993, Fundación TERRAMAR 1993, Schneider Santos *et al.* 2003), botany (Gilliard 1942, Paba Silva & van der Hammen 1960, Molano Campuzano 1971, Diazgranados 1979, Huber 1988, Rull 1991, Fundación TERRAMAR 1993, Estrada & Fuertes 1993, Galvis Vergara 1994, Riina 1996, Cortes & Franco 1997, Harbele 1997, Banco de Occidente 1999, Harbele & Maslin 1999, Maslin & Burns 2000, Etter 2001, Rull *et al.* 2005, 2009, Rull & Villa-Rubia 2006, Fouquet *et al.* 2012), reptiles, birds (Fundación TERRAMAR 1993) and butterflies (Costa *et al.* 2014a, 2014b, 2016, 2017, 2018, 2019a, 2019b, 2019c, 2020, [2021]a, 2021b). Working in the mountains of the green hell, as some have called the Amazon rainforest, is not easy. It is very expensive and risky, but there is still much to discover.

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REFERENCES

Albert, J. S., N. R. Lovejoy & W. G. R. Crampton. 2006. Miocene tectonism and the separation of cis- and trans- Andean river basins: evidence from Neotropical fishes. *Journal of South American Earth Sciences* 21: 14–27.

Allibon, J., P. Monjoie, H. Lapierre, E. Jaillard, F. Bussy, D. Bosch & F. Senebier. 2008. The contribution of the young Cretaceous Caribbean Oceanic Plateau to the genesis of late Cretaceous arc magmatism in the Cordillera Occidental of Ecuador. *Journal of South American Earth Sciences* 26: 3555–3568.

Almeida-Filho, R. & F. P. Miranda. 2007. Mega capture of the Rio Negro and formation of the Anavilhanas Archipelago, Central Amazonia, Brazil. Evidences in an SRTM digital elevation model. *Remote Sensing of Evironment* 110: 387–392.

Anderson, L. C., J. H. Hartman & F. Wesselingh. 2006. Close evolutionary affinities between freshwater corbulid bivalves from the Neogene of western Amazonia and Paleogene of the northern Great Plains, USA. *Journal of South American Earth Sciences* 21: 28–48.

Andriessen, P. A. M., K. F. Helmens, H. Hooghiemstra, P. A. Riezebos & T. van der Hammen. 1993. Absolute chronology of the Pliocene-Quaternary sediment sequence of Bogota Area, Colombia. *Quaternary Science Reviews* 12: 483–501.

Anger, K. 2013. Neotropical *Macrobrachium* (Caridea: Palaemonidae): on the biology, origin, and radiation of freshwater-invading shrimp. *Journal of Crustacean Biology* 33(2): 151–183.

Barreat, F., A. Barreto, S. Gorzula, O. Huber, G. Medina-Cuervo & C. Schubert. 1986. Reconocimiento preliminar del Macizo del Chimantá, Estado Bolívar (Venezuela). *Acta Científica Venezolana* 37: 25–42.

Bond-Buckup, G., C. G. Jara, L. Buckup, M. Pérez-Lozada, A. A. P. Bueno, K. A. Crandall & S. Santos. 2010. New species and new records of endemic freshwater crabs from the Atlantic forest in Southern Brazil (Anomura: Aeglidae). *Journal of Crustacean Biology* 30(3): 495–502.

Bott, R. 1970. Betrachtungenüber die Entwicklungs geschichte und Verbreitung der Süsswasserkrabbennach der Sammlung des Naturhistorischen Museums in Genf/Schweiz. *Revue Suisse de Zoologie* 77 (2): 327–344.

Brown, K. S., Jr. 1987. Biogeography and evolution of Neotropical butterflies. pp. 66–104. *In*: Whitmore, T. C. & G. T. Prance (eds.). *Biogeography and Quaternary history of Tropical America*. Oxford: Clarendon Press.

Bookfield, M. E., D. P. Hemmings & P. Van Straaten. 2009. Paleoenvironments and origin of the sedimentary phosphorites of the Napo Formation (Late Cretaceous, Orient Basin, Ecuador). *Journal of South American Earth Sciences* 28: 180–192.

Bush, M. B., P. E. de Oliveira, P. A. Colinvaux, M. C. Miller & J. E. Moreno. 2004. Amazonian paleoecological histories: one hill, three watersheds. *Paleogeography, Paleoclimatology, Paleoecology* 214: 359–393.

Campos, M. R., C. Magalhães & G. Rodríguez. 2002. The freshwater crabs of southern Colombia and their biogeographical affinities (Brachyura: Pseudothelphusidae). *Nauplius* 10(1): 15–25.

Campos, M. R. & C. Magalhães. 2004. *Achagua* Campos, 2001, a new synonym of *Eudaniela* Pretzmann, 1971, and the decription of *Rodriguezus* gen. nov. (Decapoda: Brachyura: Pseudothelphusidae). *Nauplius* 12(2): 95–97.

Candeiro, C. R. A. & T. Rich. 2010. Overview of the Late Cretaceous Biota of the western Sao Paulo State, Brazil. *Journal of South American Earth Sciences* 29(2): 346–353.

Cardona Molina, A., U. G. Cordani & W. D. MacDonald. 2006. Tectonic correlations of pre-Mesozoic crust from the northern termination of the Colombian Andes, Caribbean region. *Journal of South American Earth Sciences* 21: 337–354.

Cisne, J. L. 1974. Evolution of the world fauna of aquatic free-living arthropods. *Evolution* 22(3): 337–366.

Coates, A. G., J. B. C. Jackson, L. S. Collins, Th. M. Cronin, H. J. Dowsett, L. M. Bybell, P. Jung & J. A. Obando. 1992. Closure of the Isthmus of Panama: the near-shore marine record of Costa Rica and western Panama. *Geological Society of America Bulletin* 104: 814–828.

Collins, L. S., A. G. Coates, W. A. Berggren, M. P. Aubry & J. Zhang. 1996. The Late Miocene Panama isthmian strait. *Geology* 24(8): 687–690.

Colmenares, O. A. & L. V. Terán. 1993. A biostratigraphy study of Paleogene sequences in southwestern Venezuela. *Palynology* 17: 67–89.

Compañía Shell de Venezuela & Creole Petroleum Corporation. 1964. Paleozoic rocks of Merida Andes, Venezuela. *The Bulletin of the American Association of Petroleum Geologists* 48(1): 70–84.

Cortes, B. R. & R. P. Franco. 1997. Análisis panbiogeográfico de la flora de Chiribiquete, Colombia. *Caldasia* 19(3): 465–478.

Cortés, M., B. Colleta & J. Angelier. 2006. Structure and tectonics of the central segment of the Eastern Cordillera of Colombia. *Journal of South American Earth Sciences* 21: 437–465.

Costa, M., Á. L. Viloria, S. Attal, M. Benmesbah, S. Fratello & Zs. Bálint. 2019b. Lepidoptera from the Pantepui. Part VII. A distinctive *Lamprospilus* species from the Guiana Highlands (Lepidoptera: Lycaenidae, Theclinae). *Opuscula Zoologica* (Budapest) 50(2): 111–128.

Costa, M., Á. L. Viloria, S. Attal, M. Benmesbah, A. F. E. Neild & Zs. Bálint. 2018. Lepidoptera from the Pantepui. Part V. New Lycaenidae (Theclinae: Eumaeini). *Opuscula Zoologica* (Budapest) 49(2): 163–179.

Costa, M., Á. L. Viloria, S. Attal, P. Blandin, A. F. E. Neild & M. Benmesbah. 2020. Lepidoptera del Pantepui. Parte IX. Nuevos Nymphalidae (Satyrinae) y Riodinidae (Riodininae). *Antenor* 7(1): 19–41.

Costa, M., Á. L. Viloria, S. Attal, A. F. E. Neild, S. Fratello & M. Benmesbah. 2019c. Lepidoptera del Pantepui. Parte VIII. Nuevos Nymphalidae (Charaxinae y Satyrinae) y Riodinidae (Riodininae). *Anartia* 29: 20–48.

Costa, M., Á. L. Viloria, S. Attal, A. F. E. Neild, S. A. Fratello, C. Callaghan & J. Y. Gallard. 2017. Lepidoptera del Pantepui. Parte IV. Nuevos Riodinidae Riodininae y Pieridae Pierinae. *Bulletin de la Société Entomologique de France* 122(3): 269–286.

Costa, M., Á. L. Viloria, S. Attal, A. F. E. Neild, S. Fratello & S. Nakahara. 2016. Lepidoptera del Pantepui. Parte III. Nuevos Nymphalidae, Cyrestinae y Satyrinae. *Bulletin de la Societé Entomologique de France* 121(2): 179–206.

Costa, M., Á. L. Viloria, S. Attal & A. Orellana. 2014b. Lepidoptera del Pantepui. Parte II. Descripción de nuevos Nymphalidae (Papilionoidea). *Bulletin de la Societé Entomologique de France* 119(1): 39–52.

Costa, M., Á. L. Viloria, S. Attal, A. Orellana & M. Benmesbah. 2019a. Lepidoptera del Pantepui. Parte VI. Nuevos Hesperiidae (Hesperiinae) y Nymphalidae (Limenitidinae y Satyrinae). *Bulletin de la Société Entomologique de France* 123(1): 77–102.

Costa, M., Á. L. Viloria, S. Attal, A. Orellana, A. F. E. Neild; M. Benmesbah & N. V. Grishin. [2021]. Lepidoptera del Pantepui. Parte X. Nuevos Pieridae (Dismorphiinae) y Hesperiidae (Pyrrhopyginae). *Antenor* 7(2): 82–105.

Costa, M., Á. L. Viloria, C. Callaghan, M. Trujano-Ortega, A. F. E. Neild, M. Benmesbah, S. Attal & N. V. Grishin. 2021. Lepidoptera del Pantepui. Parte XI. Nuevos Riodinidae (Riodininae), Pieridae (Dismorphiinae) y Nymphalidae (Satyrinae). *Antenor* (8(1): 2–28.

Costa, M., Á. L. Viloria, O. Huber; S. Attal & A. Orellana. 2014a. Lepidoptera del Pantepui. Parte I: Endemismo y caracterización biogeográfica. *Entomotrópica* 28(3): 193–216.

Cozzuol, M. A. 2006. The Acre vertebrate fauna: age, diversity, and geography. *Journal of South American Earth Sciences* 21: 185–203.

Cracraft, J. 1988. Deep-history biogeography: retrieving the historical pattern of evolving continental biotas. *Systematic Zoology* 37(3): 221–236.

Cumberlidge, N. 2007. A new species of freshwater crab of the genus *Microthelphusa* (Brachyura: Pseudothelphusidae) from a remote isolated cloud forest on a tabletop mountain in western Guyana, South America. *Zootaxa* 1447: 57–62.

Cumberlidge, N., P. K. L. Ng, D. C. J. Yeo, C. Magalhães, M. R. Campos, F. Alvarez, T. Naruse, S. R. Daniels, L. J. Esser, F. Y. K. Attipoe, F. L. Clotilde-Ba, W. Darwall, A. McIvor, J. E. M. Baillie, B. Collen & M. Ram. 2009. Freshwater crabs and the biodiversity crisis: importance, threats, status and conservation challenges. *Biological Conservation* 142: 1665–1673.

Cumberlidge, N., F. Alvarez & J. L. Villalobos. 2014. Results of the global conservation assessment of the freshwater crabs (Brachyura, Pseudothelphusidae and Trichodactylidae): the Neotropical Region, with and update on diversity. *Zookeys* 457: 133–157.

Cunha Ribeiro, A. 2006. Tectonic history and biogeography of the freshwater fishes from the coastal drainages of eastern Brazil: an example of faunal evolution associated with a divergent continental margin. *Neotropical Ichthyology* 4(2): 225–246.

Dentzien-Dias, P. C., C. L. Schultz & C. Bertoni-Machado. 2008. Taphonomy and palaecology inferences of vertebrate ichnofossils from Guará Formation (Upper Jurassic), southern Brazil. *Journal of South American Earth Sciences* 25: 196–202.

Diaz, H. & G. Rodríguez. 1977. The branchial chamber in terrestrial crabs: a comparative study. *Biological Bulletin* 153: 485–504.

Diazgranados, D. 1979. Geografía. pp. 7–77. *In*: *La Amazonia colombiana y sus recursos*. *Proyecto Radargramétrico del Amazonas. Colombia*. Bogotá, D. C.: Italgraf, S. A.

Estrada, J. & J. Fuertes. 1993. Estudios botánicos de la Guayana Colombiana, IV. Notas sobre la vegetación y flora de la Sierra de Chiribiquete. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 18(71): 488–498.

Etter, A. (ed.). 2001. *Puinawai y Nukak. Caracterización ecológica de dos reservas Nacionales, Naturales de la Amazonia colombiana*. Ambiente y desarrollo. Serie Investigación 2. Bogotá: Instituto de Estudios Ambientales para el Desarrollo, Universidad Javeriana, 271 pp.

Fabbrin Pires, E. & M. Guerra Sommer. 2009. Plant-arthropod interaction in the Early Cretaceous (Berriasian) of the Araripe Basin, Brazil. *Journal of South American Earth Sciences* 27: 50–59

Feijó Ramos, M. I. 2006. Ostracods from the Neogene Solimoes Formation (Amazonas, Brazil). *Journal of South American Earth Sciences* 21: 87–95.

Feldmann, R. M. 2003. The Decapoda: new initiatives and novel approaches. *Journal of Paleontology* 77(6): 1021–1039.

Feldmann, R. M. & C. E. Schweitzer. 2006. Paleobiogeography of Southern Hemisphere decapod Crustacea. *Journal of Paleontology* 80(1): 83–103.

Fouquet, A., B. P. Noonan, M. T. Rodrigues, N. Pech, A. Gilles & N. J. Gemmell. 2012. Multiple Quaternary refugia in Eastern Guiana Shield revealed by comparative phylogeography of 12 frog species. *Systematic Biology* 61(3): 461–489.

Fundación TERRAMAR (ed.). 1993. Informe técnico sobre los Tepuyes. Formación Roraima, Venezuela. *Acta Terramaris* 6: 1–74.

Flynn, J. J., R. Charrier González, D. A. Croft, P. B. Gans, T. M. Herriott, J. A. Wertheim & A. R. Wyss. 2008. Chronologic implications of new Miocene mammals from Cura-Mallin and Trapa Trapa Formations, Laguna de Laja area, south central Chile. *Journal of South American Earth Sciences* 26: 412–423.

Galvis Vergara, J. 1994. Estudio geológico de la Sierra de Chiribiquete y zonas aledañas (Parque Nacional Natural Chiribiquete). *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 19(73): 275–286.

Gayet, M., J. C. Rage, Th. Sempere & P. Y. Gagnier. 1992. Modalités des échanges de vertébrés continentaux entre l'Amérique du Nord et l'Amérique du Sud au Crétacee Superieur et au Paléocène. *Bulletin de la Societe Géologique de France* 163(6): 781–791.

Gilliard, E. T. 1942. The Cordillera Macarena, Colombia. *The Geographical Review* 32(3): 463–470.

Habib, D. & J. A. Miller. 1989. Dinoflagellate species and organic facies evidence of marine transgression and regression in the Atlantic Coastal Plain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 74: 23–47.

Hamilton, H., S. Caballero, A. G. Collins & L. R. Brownell, Jr. 2001. Evolution of river dolphins. *Proceedings of the Royal Society B* 268: 549–556.

Haq, B. U., J. Hardenbo & P. R. Vail. 1987. Chronology of fluctuating sea levels since Triassic. *Science* 235: 1156–1167.

Harberle, S. 1997. Upper Quaternary vegetation and climate history of the Amazon Basin: correlating marine and terrestrial pollen records. *Proceedings of the Ocean Drilling Program, Scientific Results* 155: 381–396.

Harberle, S. G. & M. A. Maslin. 1999. Late Quaternary vegetation and climate change in the Amazon Basin based on a 50.000 year pollen record from the Amazon Fan, ODP Site 932. *Quaternary Research* 51: 27–38.

Harrington, H. J. 1962. Paleogeographic development of South America. *Bulletin of the American Association of Petroleum Geologists* 46(10): 1773–1814.

Haug, G. H. & R. Tiedemann. 1998. Effect of formation of the Isthmus of Panama on Atlantic Ocean thermohaline circulation. *Nature* 393: 673–676.

Haug, G. H., R. Tiedemann, R. Zahn & A. Ch. Ravelo. 2001. Role of Panama uplift on oceanic freshwater balance. *Geology* 29(3): 207–210.

Haug, J. T., J. W. Martin & C. Haug. 2015. A 150 million year old crab larva and its implications for the early rise of brachyuran crabs. *Nature Communications* doi: 10.1038/ncomms7417.

Hokche, O., P. E. Berry & O. Huber. 2008. *Nuevo catálogo de la flora vascular de Venezuela*. Caracas: Fundación Instituto Botánico de Venezuela Dr. Tobías Lasser, 859 pp.

Hoogmoed, M. S. 1979. The herpetofauna of the Guianan region. pp. 241-279. *In*: Duellman, W. E. (ed.). *The South American herpetofauna: its origin, evolution and dispersal*. Monograph 7. Lawrence: University of Kansas, Museum of Natural History.

Hoorn, C. 1993. Marine incursions and influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: results of a palynostratigraphic study. *Palaeogeography, Palaeoclimatology, Palaeoecology* 105: 267–309.

Hoorn, C. 1994. An environmental reconstruction of the palaeo-Amazon River system (Middle-Late Miocene, NW Amazonia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 112: 187–238.

Hoorn, C., J. Guerrero, A. G. Sarmiento & M. A. Lorente. 1995. Andean tectonics as a cause for changing drainage patterns in Miocene northern South America. *Geology* 23(3): 237–240.

Hoorn, C. & H. Vonhof. 2006. Neogene Amazonia: Introduction to the special issue. *Journal of South American Earth Sciences* 21(1-2): 1–4.

Hoorn, C. & F. P. Wesselingh (eds.). 2010. *Amazonia: landscape and species evolution. A look into the past*. Chichester, UK and Hoboken, NJ, USA: Wiley-Blackwell, xiii + 447 pp.

Huber, O. 1987. Consideraciones sobre el concepto de Pantepui. *Pantepui* (Caracas) 1(2): 2–10.

Huber, O. 1988. Vegetación y flora del Pantepui, Región Guayana. *Acta Botánica Brasileira* 1(2): 41–52.

Hulka, C., K. U. Gräfe, B. Sames, C. E. Uba & C. Heubeck. 2006. Depositional setting of the Middle Miocene Yecua Formation the Chaco Foreland Basin, southern Bolivia. *Journal of South American Earth Sciences* 21: 135–150.

Iturralde-Vinent, M. A. 2003. The conflicting paleontologic versus stratigraphic record of the formation of the Caribbean Seaway. pp. 75-88. *In*: Bartolini, C., R. T. Buffler & J. Blickwede (eds.). *The Circum-Gulf of Mexico and the Caribbean: Hydrocarbon habitats, basin formation, and plate tectonics: AAPG Memoir* 79.

Jaimes, E. & M. de Freitas. 2006. An Albian-Cenomanian unconformity in the northern Andes: evidence and tectonic significance. *Journal of South American Earth Sciences* 21: 466–492.

Jasper, A., D. Uhl & V. Guerra-Sommer & M. Mosbrugger. 2008. Palaeobotanical evidence of wildfires in the Late Paleozoic of South America – early Permian, Rio Bonito Formation, Paraná Basin, Rio Grande do Sul, Brazil. *Journal of South American Earth Sciences* 26: 435–444.

Kaandorp, R. J. G., F. P. Wesselingh, & H. B. Vonhof. 2006. Ecological implications from geochemical records of Miocene Western Amazonian bivalves. *Journal of South American Earth Sciences* 21: 54–74.

Kay, R. F. & M. A. Cozzuol. 2006. New platyrrhine monkeys from the Solimoes Formation (Late Miocene, Acre State, Brazil). *Journal of Human Evolution* 50: 673–686.

Klaus, S., C. Magalhaes, R. Salas-Gismondi, M. Gross & P. O. Atoine 2017. Palaeogene and Neogene brachyurans of the Amazon Basin: a revisited first appearance date for primary freshwater crabs (Brachyura, Trichodactylidae). *Crustaceana* 90(7-10): 953–967.

Kroonenberg, S. B., J. G. M. Bakker & A. M. van der Wiel. 1990. Late Cenozoic uplift and paleogeography of the Colombian Andes: constraints on the development of high-Andean biota. *Geologie en Mijnbouw* 69: 279–290.

Lasso, C. A., J. Hernández-Acevedo, E. Alexander, J. C. Señaris, L. Mesa, H. Samudio, J. Mora-Day, C. Magalhaes, A. Shushu, E. Mauruwanaru & R. Shoni. 2013. Aquatic biota: fishes, decapod crustaceans and mollusks of the Upper Essequibo Basin (Konashen COCA), southern Guyana. pp. 43–54. *In*: McCullough, J., P. Hoke, P. Naskrecki & Y. Osei-Owusu (eds.). *A rapid Biological assessment of the Konashen Community Owned Conservation Area*. Arlington, VA & Georgetown, Guyana: Conservation International.

Latrubesse, E. M., S. A. F. da Silva, M. Cozzuol & M. L. Absy. 2007. Late Miocene continental sedimentation in southwestern Amazonia and its regional significance: biotic and geological evidence. *Journal of South American Earth Sciences* 23: 61–80.

Leier, A., N. McQuarrie, C. Garcione & J. Eiler. 2013. Stable isotope evidence for multiple pulses of rapid surface uplift in the Central Andes, Bolivia. *Earth and Planetary Science Letters* 371/372: 49–58.

Leonhardt, A. & M. L. Lorscheitter. 2010. The last 25,000 years in the eastern Plateau of Southern Brazil according to Alpes de Sao Francisco record. *Journal of South American Earth Sciences* 29: 454–463.

Limarino, C. O. & L. A. Spalletti. 2006. Paleogeography of the upper Paleozoic basins of southern South America: an overview. *Journal of South American Earth Sciences* 22: 134–155.

Lovejoy, N. R., J. S. Albert & W. G. R. Crampton. 2006. Miocene marine incursions and marine/freshwater transitions: evidence from Neotropical fishes. *Journal of South American Earth Sciences* 21: 5–13.

Lovejoy, Th. E. 2017. The Amazon region. *Science Advances.* 3(11): eaar3677.

Lundberg, J. G. 1992. A Miocene fossil of the Amazonian fish Arapaima (Teleostei, Arapaimidae) from the Magdalena River region of Colombia – biogeography and evolutionary implications. *Biotropica* 24(1-2):14.

Magalhães, C. & G. Pereira. 2007. Assessment of the Crustacea Decapoda diversity in the Guayana Shield region aiming conservation decisions. *Biota Neotropica* 7(2): 111–124.

Magalhaes, C. 2010. A new species of freshwater crabs of the genus *Microthelphusa* from a Tepui in the Serra do Araca, state of Amazonas, Brazil. pp. 453–460. *In:* Franzen, C., S. de Grave & P. Ng (eds.). *Studies on Malacostraca*. Lipke Bijdeley Holthuis Memorial Volume. Monographs 14.

Maguire, B. 1979. Guyana, region of the Roraima Sandstone Formation. pp. 223–238. *In*: K. Larsen & L. B. Holm-Nielsen (eds.). *Tropical Botany*. London, New York, San Francisco: Academic Press.

Malabarba, L. R., R. E. Reis, R. P. Vari, Z. M. S. Lucena & C. A. S. Lucena 1998. *Phylogeny and classification of Neotropical fishes*. Porto Alegre, Brasil: EDIPUCRS, 603 pp.

Mantelatto, F. L., L. Pileggi, H. Suárez & C. Magalhães. 2008. First record and extension of the known distribution of the inland prawn, *Macrobrachium aracamuni* Rodríguez, 1982 (Decapoda, Palaemonidae) in Brazil. *Crustaceana* 81(2): 241–246.

Martínez, J. I., Y. Yokoyama, A. Gómez, A. Delgado, H. Matsuzaki & E. Rendón. 2010. Late Holocene marine terraces of the Cartagena region, Southern Caribbean: the product of neotectonism or former high stand in sea level? *Journal of South American Earth Sciences* 29: 214-224.

Maslin, M. A. & S. J. Burns. 2000. Reconstruction of the Amazon Basin effective moisture availability over the past 14,000 years. *Science* 290: 2285–2287.

Meschede, M. & W. Frisch. 1998. A plate tectonic model for the Mesozoic and Early Cenozoic history of the Caribbean Plate. *Tectonophysics* 296: 269–291.

Molano Campuzano, J. 1971. Un tesoro del Mundo: la Sierra de la Macarena. *Boletín de la Sociedad Geográfica Colombiana* 27(103): 1–31.

Monsch, K. A. 1998. Miocene fish faunas from the northwestern Amazonian basin (Colombia, Peru, Brazil). With evidence of marine incursions. *Palaeogegraphy, Palaeoclimatology, Palaeoecology* 143: 31–50.

Müller, P. 1973. *The dispersal centers of terrestrial vertebrates in the Neotropical realm: a study in the evolution of the Neotropical biota and its native landscape*. The Hague: Junk, 244 pp.

Muñoz-Torres, F. A., R. C. Whatley & D. van Harten. 2006. Miocene ostracod (Crustacea) biostratigraphy of the upper Amazon Basin and evolution of the genus *Cyprideis*. *Journal of South American Earth Sciences* 21: 75–86.

Murdock, T. Q., A. J. Weaver & A. F. Fanning. 1997. Palaeoclimatic response of the closing of the Isthmus of Panama in a coupled ocean-atmosphere model. *Geophysical Research Letters* 24(3): 253–256.

Neild, A. F. E. 1996. *The butterflies of Venezuela. Part I. Nymphalidae I (Limenitidinae, Apaturinae, Charaxinae). A comprehensive guide to the identification of adult Nymphalidae, Papilionidae, and Pieridae*. Greenwich, London: Meridian Publications, 144 pp.

Neild, A. F. E. 2008. *The butterflies of Venezuela. Part 2. Nymphalidae II (Acraeinae, Libytheinae, Nymphalinae, Ithomiinae, Morphinae). A comprehensive guide to the identification of adult Nymphalidae, Papilionidae, and Pieridae*. Greenwich, London: Meridian Publications, 275 pp.

Ortmann, A. E. 1902. The geographical distribution of freshwater decapods and its bearing upon ancient geography. *Proceedings of the American Philosophical Society* 41(171): 267–400.

Paba Silva, F. & T. van der Hammen. 1960. *Sobre la Geología de la Parte Sur de la Macarena*. Bogotá: Servicio Geológico Nacional, 30 pp.

Pedraza M. & M. Tavares. 2014. A new species of freshwater crabs of the genus *Microthelphusa* Prezmann, 1968 (Crustacea: Brachyura: Pseudothelphusidae) from the Amazon region of Guyana. *Zootaxa* 3847(2): 267–274.

Pereira, G., C. A. Lasso, J. Mora-Day, C. Magalhaes, M. A. Morales-Betancourt & M. Campos. 2009. Lista de los crustáceos decápodos de la cuenca del Río Orinoco (Colombia-Venezuela). *Biota Colombiana* 10(1-2): 75–87.

Perkins, S. 2014. Why the Amazon flows backward. *Science News.* https://www.science.org/content/article/why-amazon-flows-backward

Posada-Swafford, A. 2017. Advances. Amazon Atlantis. *Scientific American* 317(1):12-14.

Pretzmann, G. 1967. Über einige südamerikanische Süsswasserkrabben (Pseudothelphusidae). Vorläufige Mitteilung. *Entomologische Nachrichtenblatt* 14: 23–26.

Pretzmann, G. 1968. Weitere neue südamerikanische Süsswasserkrabben. *Entomologische Nachrichtenblatt* 15(2): 1–6.

Ramon, J. C. & A. Rosero. 2006. Multiphase structural evolution of the western margin of the Girardot subbasin, Upper

Magdalena Valley, Colombia. *Journal of South American Earth Sciences* 21: 493–509.

Ramos, V. A. & M. Moreno. 2006. Tectonic evolution of the Colombian Andes. *Journal of South American Earth Science* 21: 319–321.

Rapoport, E. H. 1975. *Areografia. Estrategias geográficas de las especies*. México: Fondo de Cultura Económica, 214 pp.

Räsänen, M. E, A.M. Linna, J. C. R. Santos & F. R. Negri. 1995. Late Miocene tidal deposition in the Amazonian foreland basin. *Science* 269: 386–390.

Rathbun, M. 1898. A contribution to a knowledge of the freshwater crabs of America. The Pseudothelphusinae. *Proceedings of the U.S. National Museum* 21 (1158): 507–537.

Rathbun, M. 1905. Les crabs d 'eau douce (Potamonidae). *Nouvelles Archives du Museum National d' Histoire Naturelle* 4(8): 33–122.

Rebata, H. L. A., M. E. Räsänen, M. K. Gingras, V. Vieira, Jr., M. Barberi & G. Irion. 2006. Sedimentology and ichnology of tide-influenced Late Miocene successions in western Amazonia: the gradational transition between the Pebas and Nauta formations. *Journal of South American Earth Sciences* 21: 96–119.

Restrepo, J. D. & A. López. 2008. Morphodynamics of the Pacific and Caribbean deltas of Colombia, -South America. *Journal of South American Earth Science* 25: 1–21.

Riccardi, A. C. 1987. Cretaceous paleogeography of southern South America. *Paleogeography, Palaeoclimatology, Palaeoecology* 59: 169–195.

Riina, R. 1996. *El elemento fitogeográfico andino en la Provincia Pantepui, región Guayana, Venezuela*. Caracas: Universidad Central de Venezuela. Facultad de Ciencias. Escuela de Biología, 107 pp. [biology thesis]

Ricklefs, R. E. 1970. Stage of taxon cycle and distribution of birds on Jamaica, Greater Antilles. *Evolution* 24: 475–477.

Ricklefs, R. E. & B. Eldredge. 2002. The concept of the Taxon Cycle in biogeography. *Global Ecology and Biogeography* 11: 353–361.

Rodríguez, G. 1966. The freshwater crabs of the genus *Pseudothelphusa* from northern Venezuela and Trinidad. *Zoologische Mededelingen* 41:111–135, 7 pls.

Rodríguez, G. & H. Díaz. 1977. Note sur queques restes de Crabes d`eau douce (Pseudothelphusidae) provenant d`un Kjoekken-Moedding du Venezuela. *Crustaceana* 33(1): 107–109.

Rodríguez, G. 1980. Description préliminaire de quelques espèces et genres nouveaux de Crabes d'eau douce de l'Amerique tropicale. *Bulletin du Museum National d'Histoire Naturelle* 4(2): 889–894.

Rodríguez, G. 1982. *Les crabes d'eau douce d'Amérique. Famille des Pseudothelphusidae*. FauneTropicalle XXII. Paris: ORSTOM Editions, 223 pp.

Rodríguez, G. 1992. *The freshwater crabs of America. Family Trichodactylidae and supplement to the family Pseudothelphusidae*. Faune Tropicale XXXI. Paris: Orstom Editions. 189 pp.

Rodríguez G. 1997. Trichodactylid crabs. pp. 80–83. *In*: Kay, R. F., R. H. Madden, R. L. Cifelli & J. J. Flynn (eds.). *Vertebrate paleontology in the Neotropics. The Miocene fauna of La Venta, Colombia*. Washington, D. C.: Smithsonian Institution.

Rodríguez, G. & M. R. Campos. 2000. *Microthelphusa sucreensis*, a new species of Pseudothelphusidae (Decapoda), with notes on abnormalities in the sexual appendages of freshwater crabs. *Journal of Crustacean Biology* 20 (special number 2): 332–336.

Rodríguez, G. & A. E. Esteves. 1972. Una nueva especie de cangrejo de agua dulce (Decapoda: Pseudothelphusidae) del centro de Venezuela. *Memoria de la Sociedad de Ciencias Naturales La Salle* 92: 133–137.

Rossetti, D. F., P. Mann de Toledo & A. M. Góes. 2005. New geological framework for Western Amazonia (Brazil) and implications for biogeography and evolution. *Quaternary Research* 23: 78–89.

Ruban, D. A., H. Zerfass & V. I. Pugatchev. 2009. Triassic synthesis of southern South America (Sothwestern Gondwana) and the western Caucasus (the northern Neothethys), and global tracing of their boundaries. *Journal of South American Earth Sciences* 28: 155–167.

Rull, V. 1991. Contribución a la paleoecología de Pantepui y la Gran Sabana (Guayana Venezolana): clima, biogeografía y ecología. *Scientia Guaianae* 2: 133 pp.

Rull, V. 1999. Paleoclimatology and sea-level history in Venezuela. *Interciencia* 24(2): 92–101.

Rull, V., T. Vegas-Villarrúbia & S. Nogué. 2005. Cambio climático y diversidad de la flora vascular en las montañas tabulares de Guayana. *Orsis* 20: 61–71.

Rull, V. & T. Vegas-Villarrúbia. 2006. Unexpected biodiversity loss under global warming in the Neotropical Guayana highland: a preliminary appraisal. *Global Change Biology* 12: 1–9.

Rull, V. & T. Vegas-Villarrúbia, S. Nogué & O. Huber. 2009. Conservation of the unique Neotropical vascular flora of the Guayana highlands in the face of global warming. *Conservation Biology* 23(3): 1323–1327.

Shell de Venezuela & Creole Petroleum Corporation. 1964. Paleozoic rocks of Mérida Andes, Venezuela. *The Bulletin of the American Petroleum Association of Petroleum Geologists* 48(1): 70–84.

Schneider Santos, J. O., P. E. Potter, N. J. Reis, L. A. Hartmann, I. R. Fletcher & N. J. McNaughton. 2003. Age, source and regional stratigraphy of the Roraima Super group and Roraima-like outliers in northern South America base on U-Pb geochronology. *Geological Society of America Bulletin* 115(3): 331–348.

Schram, F. R. 2001. Phylogeny of decapods: moving towards a consensus. *Hydrobiologia* 449: 1–20.

Schubert, C. 1985. Orígenes de la Gran Sabana (Escudo de Guayana), Venezuela. *Nachrichten der Deustsch-Venezolanischen Gesellschaft*. Jg. III. 3/4: 164–168.

Schubert, C. & P. Fritz. 1985. Radiocarbon ages of peat, Guayana Highlands (Venezuela). *Naturwissenschaften* 72: 427–429.

Schubert, C. 1986. Paleoenvironmental studies in the Guayana Region Southeast Venezuela. *Current Research in the Pleistocene* 3: 88–90.

Schubert, C. 1986a. Terrazas aluviales en el escudo de Guayana: Informe preliminar. *Acta Científica Venezolana* 37: 226–238.

Shubert, C. 1993. El mundo perdido no está en el Macizo de Guayana. *Revista Geográfica Venezolana* 34: 129–134.

Schubert, C., P. Fritz & R. Aravena. 1994. Late Quaternary paleoenvironmental studies in the Gran Sabana (Venezuelan Guayana Shield). *Quaternary International* 21: 81–90.

Shephard, G. E, R. D. Muller, L. Liu & M. Gurnis. 2010. Miocene drainage reversal of the Amazon River driven by plate-mantle interaction. *Nature Geoscience Letters* 3: 870–875.

Silva Tamayo, J. C., G. M. Sierra & L. G. Correa. 2008. Tectonic and climatic driven fluctuations in the stratigraphic base level of a Cenozoic continental coal basin, northwestern Andes. *Journal of South American Earth Sciences* 26: 369–382.

Souza-Carvalho, E. A., C. Magalhaes & F. L. Mantelatto. 2017. Molecular phylogeny of the *Trichodactylus fluviatilis* Latreille, 1828 (Brachyura: Trichodactylidae) species complex. *Journal of Crustacean Biology* 37(2): 187–194.

Stephan, J. F., B. Mercier de Lepinay, E. Calais, M. Tardy, C. Beck, J. C. Carfatan, J. L. Olivet, J. M. Vila, P. Bouysse, A. Mauffret, J. Bourgois, J. M. Thery, J. Tournon, R. Blanchet & J. Dercourt. 1990. Paleogeodynamic maps of the Caribbean: 14 steps from Lias to Present. *Bulletin de la Société Géologique de France* 8(6): 915–919.

Stern, C. M. 1954. La génesis del Casiquiare. *Acta Científica Venezolana* 5(2): 52–53.

Stevcic, Z. 1971. The main features of brachyuran evolution. *Systematic Zoology* 20: 331–340.

Steyermark, J. A. 1979. Plant refuge and dispersal centres in Venezuela: their relict and endemic elements. pp. 185–221. *In*: Larsen, K. & L. B. Holm-Nielsen (eds.). *Tropical Botany*. London, New York, San Francisco: Academic Press.

Suárez, H. 2006. New species of freshwater crab from Venezuela and redescription of *Microthelphusa rodriguezi* Pretzmann, 1968 (Brachyura: Pseudothelphusoidea: Pseudothelphusidae). *Journal of Crustacean Biology* 26(2): 242–247.

Suárez, H. 2015. Six new species of freshwater crabs from Pantepui, Venezuela (Crustacea: Decapoda: Pseudothelphusidae). *Anartia* 25: 64–94.

Teixeira, W., M. A. Hamilton, V. A. V. Girardi, F. M. Faleiros & R.E. Ernst. 2019. U-Pb baddeleyite ages of key dyke swarms in the Amazonian Craton (Carajás/Río María and Río Apa areas): tectonic implications for events at 1880, 1110 Ma, 535 Ma and 200 Ma. *Precambrian Research* 329: 138–155.

Vega, F. J. & R. Feldmann. 1991. Fossil crabs (Crustacea, Decapoda) from the Maastrichtian Difunta Group, Northeastern Mexico. *Annals of the Carnegie Museum* 60(2): 163–177.

Von Sternberg, R., N. Cumberlidge & G. Rodríguez. 1997. On the marine sister groups of the freshwater crabs (Crustacea: Decapoda: Brachyura). *Journal of Zoological Systematics and Evolutionary Research* 37: 19–38.

Wade, L. 2013. The Amazon in 4D. *Science* 341: 234–235.

Wade, L. 2017. Was the Amazon once an ocean? *Science*. doi: 10.1126/science.aal1142.

Walter, H. 1976. *Die oekologischen Systeme der Kontinente (Biogeosphaere). I.* Stuttgart: G. Fischer Stuttgart, 131 pp.

Webb, S. D. 1995. Biological implications of the Middle Miocene Amazon Seaway. *Science Perspectives* 269: 361–362.

Weeks, L. G. 1956. *Paleogeografía de América de Sur*. Lima: Universidad Mayor de San Marcos, Facultad de Letras, Instituto de Geografía, 76 pp.

Magalhaes, C. & O. C. Bello-González. 2016. First confirmed report of a primary freshwater crab (Brachyura: Pseudothelphusidae) associated with bromeliads in the Neotropics. *Journal of Crustacean Biology* 36(3): 303–309.

Wesselingh, F. P. & O. Macsotay. 2006. Pachydonhettneri (Anderson, 1928) as indicator for Caribbean-Amazonian lowland connections during the Early- Middle Miocene. *Journal of South American Earth Sciences* 21: 49–53.

Westaway, R. 2006. Late Cenozoic sedimentary sequences in Acre state, southwestern Amazonia: fluvial or tidal? Deductions from the IGCP 449 fieldtrip. *Journal of South American Earth Sciences* 21: 120–134.

Wilson, E. O. 1959. Adaptive shift and dispersal in a tropical ant fauna. *Evolution* 13: 122–144.

Wilson, E. O. 1961.The nature of the taxon cycle in the Melanesian ant fauna. *American Naturalist* 95: 169–193.

Wilson, E. O. 1992.*The Diversity of Life.* Cambridge: Belknap, 464 pp.

Woodburne, M. O. 2010. The Great American Biotic Interchange: dispersals, tectonics, climate, sea level and holding pens. *Journal of Mammal Evolution* 17(4): 245–264.