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PANBIOGEOGRAPHY OF THE YUCATAN PENINSULA BASED ON CHARAXINAE (LEPIDOPTERA: NYMPHALIDAE)

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Supplementary material (Checklist of American Charaxinae) online at http://www.fcla.edu/FlaEnt/fe943.htm#InfoLink2

Abstract

We have studied the origin of the Charaxinae lepidopteran fauna of the Yucatan Peninsula in a panbiogeographical analysis. The expectation was that this biota had a single origin (one generalized track) from Central America. A database was generated with worldwide distributional records of Charaxinae. The panbiogeographical analysis used the program *Trazos2004*, an extension for *ArcView.* A total of 22,124 records and 304 species were obtained, and 226 individual tracks were generated. Seventeen generalized tracks were obtained for the Americas; 2 of these penetrate into the Yucatan Peninsula. We conclude that the origin of the Yucatec Charaxinae fauna is tropical, following in America the Neotropical pattern, the so-called Mexican biogeographic "Y". This fauna originates from 2 putative Mesoamerican invasions: an older one (perhaps Miocene), that penetrated across the "Sierrita de Ticul" (a low mountain range); the other one more recent (Pliocene), which invaded along the Caribbean coast.

Key Words: Charaxinae, lepidopterofauna, Neotropical, Panbiogeography, historical biogeography, Yucatan

Resumen

Se identifica el origen de la lepidopterofauna de Charaxinae de la península de Yucatán mediante un análisis panbiogeográfico, bajo la hipótesis de que esta biota tuvo un solo origen (un solo trazo generalizado) desde Centroamérica. Se generó una base de datos con los registros de Charaxinae a nivel mundial. Para el análisis panbiogeográfico se utilizó el programa *Trazos2004*, una extensión para *ArcView.* Se obtuvieron 22,124 registros y 305 especies y se generaron 226 trazos individuales. Se obtuvieron 17 trazos generalizados para el continente americano; dos de ellos penetran en la península de Yucatán. Se concluye que el origen de la fauna yucateca de Charaxinae es tropical, siguiendo el patrón típico neotropical llamado la "Y" biogeográfica mexicana. Esta fauna se originó de dos posibles invasiones mesoamericanas: una más antigua (tal vez mioceno), que penetró por la Sierrita de Ticul; la otra, más reciente (plioceno), invadió a lo largo de la costa del Caribe. Los dos trazos obtenidos se añaden a los cinco patrones neotropicales previamente establecidos para el México neotropical.

The biota of the Yucatan Peninsula (YP) is influenced by 2 Neotropical components (Morrone & Márquez 2003; Morrone 2006): Central and South American (Mesoamerican; Espejel 1987), and Antillean, in addition to endemic elements (Estrada-Loera 1991). Some authors have considered the Mesoamerican component to be dominant, comprising approximately 60% of all species (Estrada-Loera 1991), while others report that the Antillean affinity could be the most important (Miller & Miller 2001). Some workers consider that there were several invasions, at different times, and with more than 1 origin (e.g., Schmitter-Soto 2002; Schmitter-Soto & Salazar-Vallejo 2003). Liebherr (1988) thought that the relationship between the Antillean and the Mesoamerican insect faunas depended on migration events; however, other authors think that the Antillean component is secondary, albeit interesting (Estrada-Loera 1991; Carnevali et al. 2003).

The oldest rocks in YP are Paleozoic; nevertheless, throughout its history, YP has been at times completely covered by a shallow sea, for instance during the Cretaceous, whereas in the Paleocene-Eocene YP was partially emergent. During the mid-Eocene the peninsula totally sank again, and at the end of this period it rose again, leaving underwater just parts of the northeast and the Caribbean littoral, which remained as a shallow sea until the early Miocene. The sea advanced during the rest of the Miocene and the early Pliocene, pushing the eastern coast inland as far as Lake Chichancanab, which today is close to the geographic center of YP. The main marine regression occurred during the transition Pliocene-Pleistocene (Beutelspacher 1984; Espejel 1987; Suárez-Morales 2003).

The Papilionoidea co-evolved with the dicotyledonous plants, about 110 million years ago (mya), during the Cretaceous (Miller & Miller 2001); however, the Nymphalidae evolved 70-65 mya (transition Cretaceous-Tertiary), so the distribution of these butterflies was still under the influence of the "Gondwana effect", because at that time the last connections of this ancient continent still remained (Ehrlich 1958; Grimaldi & Engel 2005). The distribution of the Rhopalocera in the Americas became established during the Pliocene, when the mountain ranges known as Sierra Madre Occidental and Sierra Madre Oriental arose, resulting in the peculiar Y-shaped pattern (the "Mexican biogeographic Y") of Neotropical species (Morrone & Márquez 2003; Vargas et al. 2006).

The aim of this work is to examine the possible origin of the diurnal lepidopteran fauna in YP, in particular the subfamily Charaxinae as a focal group, because these butterflies display high abundance and richness in the region, compared to other Lepidoptera groups; moreover, the Charaxinae have been used previously as diagnostic species to classify biogeographic regions (Vargas et al. 2006), as well as bioindicators of conservation (Pozo et al. 2009).

We propose to determine whether more than 1 biotic component (more than 1 putative origin) can be recognized within the Charaxinae fauna of YP. Panbiogeography was the analytical tool of choice, because this technique generates explicit spatial hypotheses on the distributional patterns of taxa rather than simple faunal similarity. This analysis helps to establish *spatial homologies*, that is, the historical biogeographic coherence of faunal components (Croizat-Chaley 1982; Craw 1988; Morrone & Crisci 1995; Grehan 2003). Our original hypothesis was that there might be only 1 component in YP, a generalized track coming in from Central America, as suggested by Estrada-Loera (1991) for plants.

Materials and Methods

Focal Group

The Charaxinae are regionally abundant, compared to other Lepidoptera (e.g., Papilioninae and Libytheinae: Pozo et al. 2003; Maya et al. 2005) and their taxonomy is well known (Vargas et al. 2006; Wahlberg & Brower 2008). Many of the species are tropical and most of their distributional limits are in Mexico and the Amazon. Most Charaxinae do not migrate, and they are rather well-associated with particular types of vegetation (Ehrlich 1958; Ackery 1984; DeVries 1987; Mielke et al. 2004; Vargas et al. 2006; Wahlberg & Brower 2008). The detailed phylogeny is unknown, but the subfamily is considered monophyletic (Wahlberg & Brower 2008).

Study Area

The YP is a biogeographical province, with low relief and conspicuous humidity gradient (dry in the north, wet in the south), which correlates with vegetation (Estrada-Loera 1991) that is mainly subperennial rainforest, subdeciduous rainforest, evergreen rainforest, low deciduous forest, low floodable forest, and other plant assemblages including mangrove (Smith 1941; Escalante et al. 2003; Arita & Vázquez-Domínguez 2003; Carnevali et al. 2003; Orellana et al. 2003).

Sampling

American Charaxinae data came from documented records (Godman & Salvin 1879-1901; Godman et al. 1887-1901; Comstock 1961; d'Abrera 1988; de la Maza & Gutiérrez-Carbonell 1992; Llorente & Luis, 1992; Caldas 1994; Llorente & Luis 1994; Bizuet-Flores et al. 2001; Pozo et al. 2003; Maya et al. 2005; Maya et al. 2009, among others), scientific collections (American Museum of Natural History, Cleveland Museum of Natural History, Colección Nacional de Insectos [CNIN], Museo de Zoología de ECOSUR, Museo de Zoología de la Facultad de Ciencias de la UNAM "Alfonso L. Herrera", San Diego Natural History Museum, The McGuire Center for Lepidoptera and Biodiversity) and electronic databases (CONABIO; Opler et al. 2006; Willmott & Hall 2006; among others). Most records included latitude and longitude; when the records did not include latitude and longitude, we consulted atlases to estimate a geographical position for the locality.

Track Analysis

For every American taxon of Charaxinae we generated an individual track using ArcView (ESRI, Redlands), with an extension named Trazos2004 (Rojas 2007). We ignored species known from only 1 locality. Extension Trazos2004 applied the method of the closest neighbor to generate the track (Rojas 2007). The generalized tracks are the intersection of several individual tracks, and are interpreted as biotas that share a biogeographic history. Finally, maps showing generalized tracks that penetrate into YP were drawn.

RESULTS

The database included 22,124 records belonging to 304 American Charaxinae species and yielded 226 individual tracks. Seventy eight records were not taken into account to build the generalized tracks (Appendix 1 in supplementary material online), either because they had no intersection with any other individual track, or because they represented species with limited distribution. The individual tracks resulted in 17 Neotropical generalized tracks (Table 1), 2 of which penetrate into YP (Figs. 1 and 2), a fact that called into question our hypothesis that there might be a single origin for the Charaxinae fauna of the Yucatan.

Generalized Track I consists of 6 genera (*Prepona, Memphis, Fountainea, Hypna, Zaretis*, and *Siderone*) and 33 species (Table 1; Fig. 1); it extends into South America (Bolivia, Peru, Ecuador, and Colombia), with 1 branch towards Venezuela and the other into Central America, across Nicaragua, El Salvador, and Guatemala. In Guatemala the track bifurcates, with a line towards central Mexico (the base of the "Mexican Y" documented by Morrone 2006) and another line that invades the YP, where it goes around the center of the peninsula, along the Caribbean coast and the north of Yucatan. Most of this track is located in Pliocene-age terrain and indicates a Central American-Caribbean coast origin for the Yucatec Charaxinae.

Generalized Track II penetrates into the YP across the "Sierrita de Ticul" (low mountain-range), with 2 genera (*Memphis* and *Fountainea*) and 4 species (Fig. 2). The track originates in Ecuador-Colombia-Venezuela (north of the Amazon); at the base of the "Mexican Y" it bifurcates, with a Yucatec branch over Eocenic terrains, indicating a Central American-inland origin for the fauna under study, and another branch along the Gulf of Mexico and across the Balsas depression to the Pacific coast. The species *Fountainea halice maya*, endemic to the YP (Vargas et al. 2006), is part of this track.

DISCUSSION

The Mexican fauna of Charaxinae originated in South and Central America, as already observed by other authors (Miller & Miller 2001). Five subpatterns of distribution have been proposed for the "Mexican Y": Neotropical, Pacific, North Pacific, South Pacific, Gulf of Mexico and Chiapas (Luis-Martínez et al. 2006; Morrone 2006), but none of these includes the YP, so a major contribution of the present investigation is to establish 2 additional subpatterns (Tracks I and II). Because more than 1 of these generalized tracks penetrates into YP, our initial expectation of a homogeneous invasion of YP is not supported. Our interpretation of these analyses is that 1 invasion followed the Caribbean coast (Generalized Track I), and the other went across the "Sierrita de Ticul". This fauna is purely Mesoamerican and not Antillean. The fact that the biota in YP has multiple origins and is not the result of a homogeneous invasion has been proposed for other taxa (Schmitter-Soto 2002; Yáñez-Ordóñez et al. 2008).

Generalized Track I represents a more recent invasion into the YP, because its terrains are younger (Pliocene). Schmitter-Soto (2002) detected a similar pattern for species (or lineages) of the fish genus *Astyanax*. Two invasions by *Astyanax* species were proposed (1 of them Pleistoce-

TABLE 1. GENERALIZED TRACKS OF CHARAXINAE.

Track	Location	Number of species
I	Central-South America-Mexico (Gulf and Pacific slopes)	33
II	Central-South America-Mexico (Gulf slope)	4
III	Central-South America	85
IV	Central-South America	27
V	South America	15
VI	South America-Antilles	10
VII	Central-South America	6
VIII	South America (North of Amazon)	5
IX	South America	3
X	Cuba-Antilles	4
XI	South America (Center of the Amazon)	11
XII	South America	4
XIII	South America (South of Amazon)	2
XIV	North America (Central USA)	3
XV	South America (East of Amazon)	3
XVI	Central-South America	2
XVII	Mexico Gulf (Sierra Madre del Sur)	9

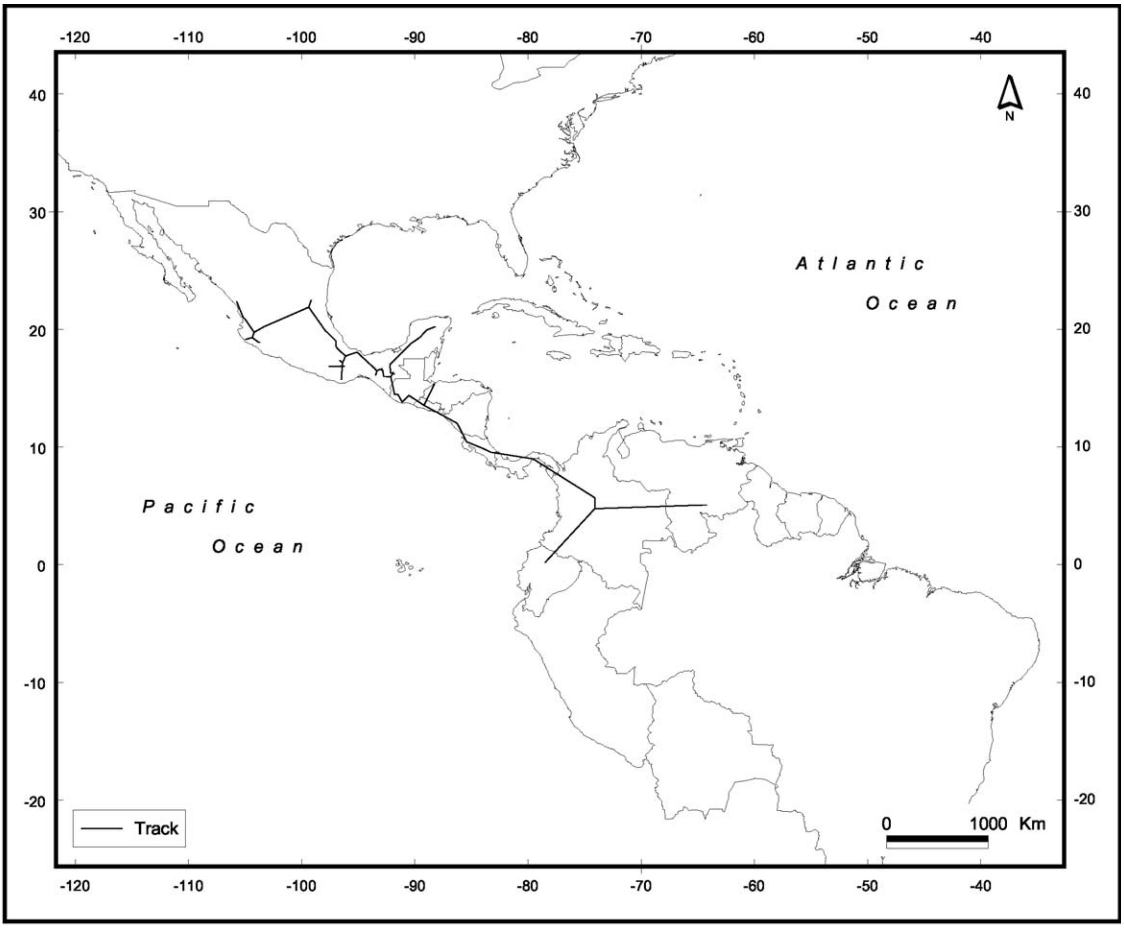

Fig. 1. Generalized Track I of Charaxinae Fauna.

nic), both of them Central American in origin. Similar generalized tracks have been suggested before (Álvarez & Morrone 2004, birds; Yáñez-Ordóñez et al. 2008, bees).

Moreover, the extreme portion of this generalized track follows a largely east-to-west pattern, which coincides with the trajectories of hurricanes that enter Yucatan peninsula, and might indicate an influence of these meteorological phenomena on butterfly dispersion.

Generalized Track II includes taxa that cross over to the Pacific across the "Eje Neovolcánico" and the Balsas depression. This generalized track lies over the oldest terrain in YP. This biotic exchange between the Gulf and the Pacific accounts in part for the diversity in both versants, but especially in the river Balsas basin (Hoffman 1940, fauna; Pérez et al. 2001, vegetation). According to Marshall (1998) and Morrone (2006), the evolution of the Neotropical biota, like that of mammals, is marked by the vicariant events associated with the emersion of the isthmi of Tehuantepec and Panama, an event known as the Great American (Biotic) Interchange. The corridor formed by the Isthmus of Tehuantepec dates from the Miocene (López 2003).

The multiple origins of the fauna of Charaxinae of the YP are mirrored by the biogeography of the coastal vegetation of the YP (Espejel 1987), possibly due to 6 genera that provide potential habitat for these butterflies (*Caesaria* (Flacourtiaceae), *Croton* (Euphorbiaceae), *Inga* (Fabaceae), *Piper* (Piperaceae), *Swartzia* and *Pithecellobium* (Leguminosae)). Estrada-Loera (1991) found a similar distribution pattern for the plants that provide food for larvae of Charaxinae (*Caesaria nitida, Piper yucatanense* and *Swartzia cubensis*); this author also argues that the coastal strip along the north and northwest of YP is richer in endemics, restricted to this strip because of lack of suitable conditions elsewhere in the YP. It is interesting to see that Generalized Track I neatly follows this coastal strip, from the Caribbean to northern Yucatan.

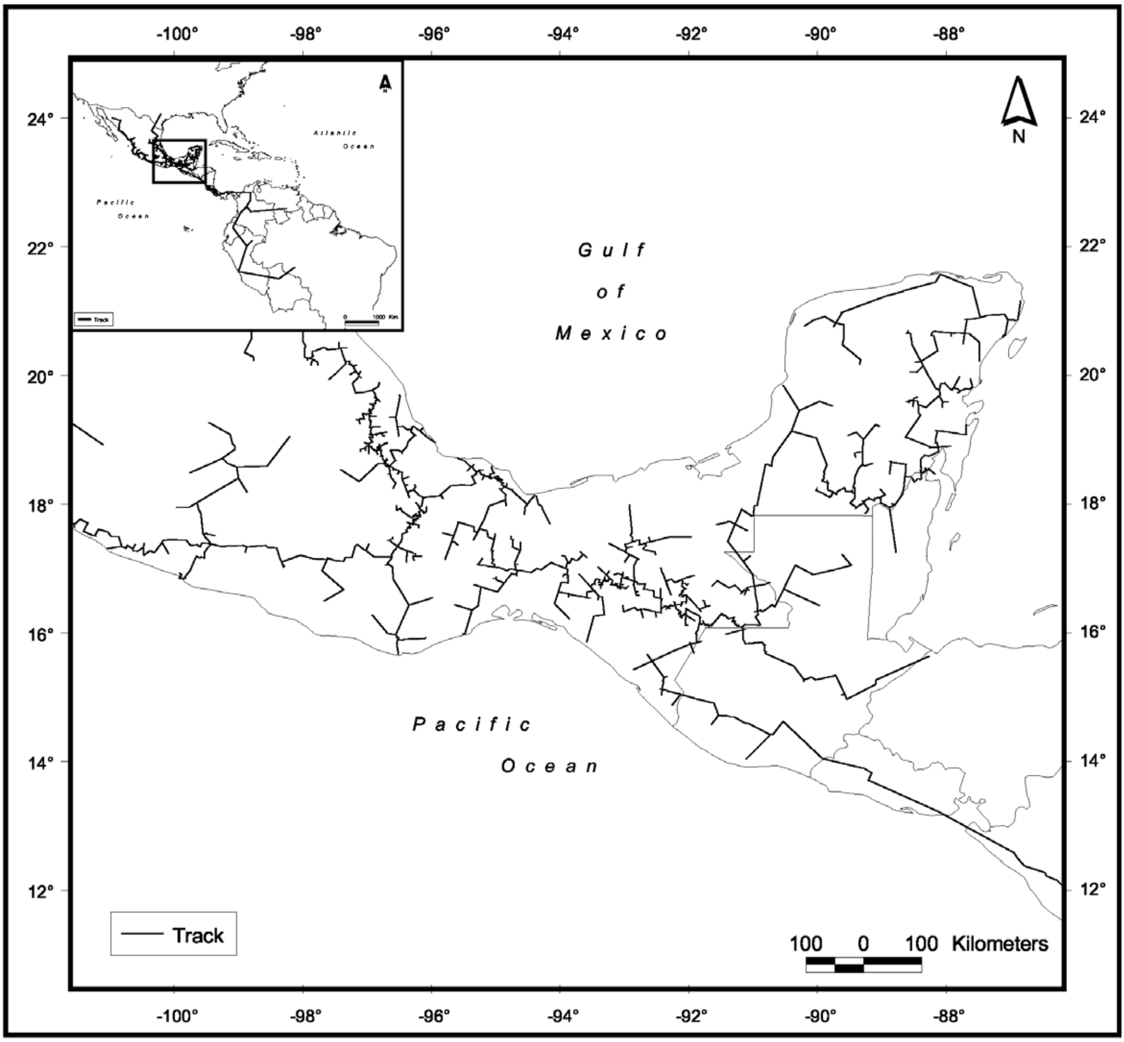

Fig. 2. Generalized Track II of Charaxinae Fauna.

There is evidence for a relatively recent origin of the group, based on molecular and morphological cladograms that suggest that the Charaxinae are among the most derived nymphalid subfamilies (Wahlberg et al. 2008). In that scenario, the first Charaxinae must have dispersed between South America and Africa (Wahlberg 2006), or alternatively the family Nymphalidae must be older than currently thought.

Conclusion

The origin of the Charaxinae fauna in the Yucatan Peninsula (YP) is a mixture of at least 2 biotic components that followed 2 courses into the peninsula, probably in different geological times: 1 track along the Caribbean coast, the other across the "Sierrita de Ticul". These generalized tracks may be seen as 2 subpatterns of the general Neotropical pattern in Mexico (the "Mexican Y").

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REFERENCES CITED

Ackery, P. R. 1984. Systematic and faunistic studies on butterflies, pp. 9-21 *In* R. I. Vane-Wright and P. R. Ackery [eds.], The Biology of Butterflies. Academic Press, London.

ÁLVAREZ, M., E., AND MORRONE, J. J. 2004. Propuesta de áreas para la conservación de aves de México, empleando herramientas panbiogeográficas e índices de complementariedad. Interciencia 29: 112-120.

ARITA, H. T., AND VÁZQUEZ-DOMÍNGUEZ, E. 2003. La fauna y la conformación de la provincia biótica yucateca: biogeografía y macroecología, pp. 69-81 *In* P. Colunga-GarciaMarín and A. Larqué-Saavedra [eds.], Naturaleza y Sociedad en el Área Maya. Pasado, presente y futuro. CICY, Mérida, Mexico.

BEUTELSPACHER, C. R. 1984. Mariposas de México. La Prensa Medica Mexicana, Mexico City.

BIZUET-FLORES, Y., LUIS-MARTÍNEZ, A., AND LLORENTE-BOUSQUETS, J. 2001. Mariposas del Parque Nacional El Chico, Hidalgo y sus relaciones biogeográficas con cinco zonas aledañas al Valle de México, México (Lepidoptera: Papilionoidea). SHILAP Rev. Lepid. 29: 145-159.

CALDAS, A. 1994. Biology of *Anaea ryphea* (Nymphalidae) in Campinas, Brazilian J. Lepid. Soc. 48: 248-257.

CARNEVALI, G., RAMÍREZ, I. M., AND GONZÁLEZ-ITURBE, J. A. 2003. Flora and vegetation of the Yucatan Peninsula, pp. 53-68 *In* P. Colunga-GarciaMarín and A. Larqué-Saavedra [eds.], Naturaleza y Sociedad en el Área Maya. Pasado, Presente y Futuro. CICY, Mérida, Mexico.

COMSTOCK, W. P. 1961. Butterflies of the American Tropics. The genus *Anaea* Lepidoptera Nymphalidae. A Study of the Species heretofore included in the Genera *Anaea, Coenophlebia, Hypna, Polygrapha, Protogonius, Siderone* and *Zaretis*. The American Museum of Natural History, New York.

CRAW, R. C. 1988. Panbiogeography, pp. 405-435 *In* A. Myers and P. Giller [eds.], Analytical Biogeography: An Integrated Approach to the Study of Animal and Plant Distributions. Chapman and Hall, London.

CROIZAT-CHALEY, L. 1982. Vicariance/Vicariism, Panbiogeoegraphy, "Vicariance Biogeography," etc.: a clarification. Syst. Zool. 31: 291-304.

D'ABRERA, B. 1988. Butterflies of the Neotropical Region. Part V. Nymphalidae and Satyridae (Conc.). Hill House, Victoria.

DE LA MAZA, R. G., AND GUTIÉRREZ-CARBONELL, D. 1992. Rhopaloceros de Quintana Roo, su distribución, origen y evolución. Rev. Soc. Mexicana Lepid. 15: 3-14.

DEVRIES, P. J. 1987. The Butterflies of Costa Rica and their Natural History. Papilionidae, Pieridae, Nymphalidae. Princeton University Press, Princeton NJ.

EHRLICH, P. R. 1958. The comparative morphology, phylogeny and higher classification of the butterflies (Lepidoptera: Papilionoidea). J. Kansas Entomol. Soc. 39: 305-375.

ESCALANTE, T., ESPINOSA, D., AND MORRONE, J. J. 2003. Using parsimony analysis of endemicity to analyze the distribution of Mexican land mammals. Southwest Natatruralist 48: 563-578.

ESPEJEL, I. 1987. A phytogeographical analysis of coastal vegetation in the Yucatan Peninsula. J. Biogeogr. 14: 499-519.

ESTRADA-LOERA, E. 1991. Phytogeographic relationships of the Yucatan Peninsula. J. Biogeogr. 18: 687-697.

GODMAN, F. D., AND SALVIN, O. 1879-1901. Insecta. Lepidoptera-Rhopalocera. Vol. I. R.H. Porter, London.

GODMAN, F. D., SALVIN, O., AND HUBBARD SCUDDER, S. 1887-1901. Insecta. Lepidoptera-Rhopalocera. Vol. II. R.H. Porter Editor, London.

GREHAN, J. 2003. Panbiogeografía y la biogeografía de la vida, pp. 181-196 *In* J. Llorente- Bousquets and J. J. Morrone [eds.], Introducción a la Biogeografía en Latinoamérica: Teorías, Conceptos, Métodos y Aplicaciones. UNAM, Mexico City.

GRIMALDI, D., AND ENGEL, M. S. 2005. Evolution of the Insects. Cambridge University Press, Cambridge.

HOFFMAN, C. C. 1940. Catálogo sistemático y zoogeográfico de los lepidópteros mexicanos. Primera parte. Papilionoidea. An. Inst. Biol. Univ. Nac. Autón. México, Ser. Bot. 12: 237-294.

LIEBHERR, J. K. 1988. The Caribbean: fertile ground for zoogeography, pp. 1-14 *In* J. K. Liebherr (ed.), Zoogeography of Caribbean insects. Comstock, Ithaca.

LLORENTE, J. B., AND LUIS, A. M. 1992. Distribución de *Consul electra* (Westwood) y una nueva subespecie de México (Nymphalidae: Charaxinae; Anaeini). Anales Inst Biol Univ Nac Autón México, Ser Zool 63: 237-247.

LLORENTE, J., AND LUIS, A. 1994. Mariposas de Chiapas. Trop. Lepidoptera 5: 108

LÓPEZ R. E. 2003. Evolución tectónica de América Central, del Sur y el Caribe, desde el Jurásico hasta el reciente, pp. 15-22 *In* J. Llorente-Bousquets and J. J. Morrone [eds.], Introducción a la Biogeografía en Latinoamérica: Teorías, Conceptos, Métodos y Aplicaciones. UNAM, Mexico City.

LUIS-MARTÍNEZ, A., TRUJANO, M., LLORENTE-BOUSQUETS, J., AND VARGAS-FERNÁNDEZ, I. 2006. Patrones de distribución de las subfamilias Danainae, Apaturinae, Biblidinae y Heliconiinae (Lepidoptera: Nymphalidae), pp. 771-866 *In* J. J. Morrone and J. Llorente-Bousquets [eds.], Componentes Bióticos Principales de la Entomofauna Mexicana. Volumen II. UNAM, Mexico City.

MARSHALL, L. G. 1988. Land mammals and the Great American Interchange. American Sci. 76: 380-388.

MAYA M., A., POZO, C., AND MAY U. E. 2005. Las mariposas (Rhopalocera: Papilionidae, Pieridae y Nymphalidae) de la selva alta subperennifolia de la región de Calakmul, México, con nuevos registros. Folia Entomol. Mexicana 44: 123-143.

MAYA-MARTÍNEZ, A., POZO, C., AND SCHMITTER-SOTO, J. J. 2009. Distribution patterns of Charaxinae (Lepidoptera: Nymphalidae) in Yucatan Peninsula, Mexico. Acta Zool. Mexicana (n. s.) 25: 283-301.

MIELKE, C. G. C., MIELKE, O. H. H., AND CASAGRANDE, M. M. 2004. Estudio comparado da morfología externa de *Zaretis itys itys* (Weswood) e *Agrias claudina claudina* (Gray) (Lepidoptera, Nymphalidae, Charaxinae) I. Cabeça, apêndices e região cervical. Rev. Brasileira Zool. 21: 357-369.

MILLER, J. Y., AND MILLER, L. D. 2001. The biogeography of the West Indian butterflies (Lepidoptera): an application of a vicariance/dispersalist model, pp. 127-156 *In* C. A. Woods and F. E. Sergile [eds.], Biogeography of the West Indies: Patterns and Perspectives. 2nd ed. CRC Press, Boca Raton.

MORRONE, J. J. 2006. Biogeografía de América Latina y el Caribe. CYTED, ORCYT-UNESCO, SEA, Zaragoza.

MORRONE, J. J., AND CRISCI, J. V. 1995. Historical biogeography: Introduction to methods. Annu. Rev. Ecol. Syst. 26: 373-401.

MORRONE, J. J., AND MÁRQUEZ, J. 2003. Aproximación a un atlas biogeográfico mexicano: componentes bióticos principales y provincias biogeográficas, pp. 217-220 *In* J. J. Morrone and J. Llorente-Bousquets [eds.], Una perspectiva latinoamericana de la biogeografía. CONABIO, UNAM, Mexico City.

OPLER, P. A., PAVULAAN, H., STANFORD, R. E., AND POGUE, M. (coordinators) 2006. Butterflies and Moths of North America. Bozeman, MT: NBII Mountain Prairie Information Node. http://www.butterfliesandmoths.org/. Accessed 7 May 2006.

ORELLANA, R., ISLEBE, G., AND ESPADAS, C. 2003. Presente, pasado y futuro de los climas de la península de Yucatán, pp. 37-52 *In* P. Colunga-GarciaMarín and A. Larqué-Saavedra [eds.], Naturaleza y Sociedad en el Área Maya. Pasado, Presente y Futuro. CICY, Mérida, Mexico.

PÉREZ G., E. A., MEAVE, J., AND GALLARDO, C. 2001. Vegetación y flora de la región de Nizanda, Istmo de Tehuantepec, Oaxaca, México. Acta Bot. Mexicana 56: 19-88.

POZO, C., LUIS-MARTÍNEZ, A., UC-TESCUM, S., SALAS-SUÁREZ, N., AND MAYA-MARTÍNEZ, A. 2003. Butterflies (Papilionoidea and Hesperioidea) of Calakmul, Campeche, Mexico. Southw. Nat. 48: 505-525.

POZO, C., SALAS-SUÁREZ, N., PRADO-CUÉLLAR, B. Y AND MAY-UC E. 2009. Riqueza de mariposas diurnas (Lepidoptera: Rhopalocera) en el Santuario del Manatí y una propuesta para su uso en el monitoreo de ambientes terrestres del area, pp. 139-147 *In* J. Espinoza-Ávalos, G. A. Islebe, and H. A. Hernández-Arana [eds.], El Sistema Ecológico de la Bahía de Chetumal / Corozal: Costa Occidental del Mar Caribe. ECOSUR, Chetumal, Quintana Roo, México.

ROJAS P., C. A. 2007. Una herramienta automatizada para realizar análisis panbiogeográficos. Bull. Syst. Evol. Biogeogr. Assoc. 1: 31-33.

SCHMITTER-SOTO, J. J. 2002. Ictiogeografía de Yucatán, pp. 103-116 *In* M.L. Lozano-Vilano [ed.], Libro Jubilar en Honor al Doctor Salvador Contreras Balderas. Universidad Autónoma de Nuevo León, Monterrey.

SCHMITTER-SOTO, J. J., AND SALAZAR-VALLEJO, S. I. 2003. Ecosistemas acuáticos y biogeografía de la península de Yucatán, pp. 81-93 *In* P. Colunga-GarciaMarín and A. Larqué-Saavedra [eds.], Naturaleza y Sociedad en el Área Maya. Pasado, Presente y Futuro. CICY, Mérida, Mexico.

SMITH, H. M. 1941. Las provincias bióticas de México, según la distribución geográfica de las lagartijas del género *Sceloporus*. An. Esc. Nac. Cienc. Biol 2: 103-110.

SUÁREZ-MORALES, E. 2003. Historical biogeography and distribution of the freshwater calanoid copepods (Crustacea: Copepoda) of the Yucatan Peninsula, Mexico. J. Biogeogr. 30: 1851–1859.

VARGAS-FERNÁNDEZ, I., TRUJADO, M., LLORENTE-BOUSQUETS, J., AND LUIS-MARTÍNEZ, A. 2006. Patrones de distribución de las subfamilias Ithomiinae, Morphinae y Charaxinae (Lepidoptera: Nymphalidae), pp. 867-944 *In* J. J. Morrone, and J. Llorente-Bousquets [eds.], Componentes Bióticos Principales de la Entomofauna Mexicana, Vol. II. UNAM, Mexico City.

WAHLBERG, N. 2006. That awkward age for butterflies: insights from the age of the butterfly subfamily Nymphalinae (Lepidoptera: Nymphalidae). Syst. Biol. 55: 703-714.

WAHLBERG, N., AND BROWER, A. V. Z. 2008. Charaxinae Doherty 1886. http://tolweb.org/Charaxinae/12192/2008.04.03 *In* The Tree of Life Web Project, http://tolweb.org/. Accessed 03 April, 2008.

WILLMOTT, K. R., AND HALL, J. P. W. 2006. Butterflies of Ecuador. www.butterfliesofecuador.com/. Accessed 7 May 2006.

YÁÑEZ-ORDÓÑEZ, O., TRUJANO-ORTEGA, M., AND LLORENTE-BOUSQUETS, J. 2008. Patrones de distribución de las especies de la tribu Meliponini (Hymenoptera: Apoidea: Apidae) en Mexico. Interciencia 33: 41-45.