

What's in a name?: Mesoamerica

¿Qué hay en un nombre?: Mesoamérica

Luis A. Sánchez-González¹✉, Adolfo G. Navarro-Sigüenza¹, Juan Francisco Ornelas² and Juan J. Morrone¹

¹Museo de Zoología "Alfonso L. Herrera", Facultad de Ciencias, Universidad Nacional Autónoma de México. Apartado postal 70-399, 04510 Mexico, D. F., México.

²Departamento de Biología Evolutiva, Instituto de Ecología A. C., Carretera antigua a Coatepec Núm. 351, El Haya, 91070 Xalapa, Veracruz, México.

✉ lasg@ciencias.unam.mx

Definition of biogeographic regions, the primary objective of biogeographic regionalization (Escalante, 2009), has been under considerable debate, as the limits between some of them are often poorly defined as a consequence of geological and/or biotic complexities (Cox, 2001; Morrone, 2002; Riddle and Hafner, 2010). These limits may coincide with transitional complex regions—like the Mexican Transition Zone (Halftter, 1976; Savage, 1960, 1966; Morrone, 2010)—which show mixed biotic elements from 2 different biogeographic regions (the Nearctic and Neotropical regions). The admixture of biotic elements in such transition zones implies that delimitation of biogeographic regions is not an easy task, as the history of biogeography has shown (e.g., Townsend, 1895; Halftter, 1976; Ortega and Arita, 1998).

In an attempt to describe a system that would “reflect the origination and development of distinctive avian biotas”, P. L. Sclater proposed a scheme dividing the Earth into biogeographic regions (Brown and Lomolino, 2000). Sclater acknowledged that different biogeographic schemes had been proposed before him; however, these were based mainly on non-natural properties, such as latitude or longitude (Sclater, 1858). Sclater's scheme was greatly improved by Wallace (1876), who analyzed the geographical distribution of different vertebrate taxa, focusing on organismic attributes such as their dispersal abilities. Although Wallace's biogeographic scheme included sharp divisions between regions and subregions, he was the first author to propose natural boundaries for regions by using a bathymetric scale for description of isolation in archipelagos, as in Southeast Asia (Brown and Lomolino, 2000). Clearly, attempts by Sclater (1858), Wallace (1876), and other authors to delimit biogeographic regions were directed at understanding biotic evolutionary patterns on ecological and environmental bases, not at defining arbitrary boundaries, as was recognized

by Udvardy (1975). In this sense, the recognition of biogeographic regions on the basis of politically defined boundaries is not useful, as they are not ecologically or evolutionary meaningful.

Recently, Winker (2011) commented on the usage of a name for a particular region in order to use a single and appropriate English term that reflects accurately a biogeographic pattern. This gives us an opportunity to discuss the usage of Middle America *versus* Mesoamerica for a biotically complex region. The Mesoamerican region, especially as applied in ornithology, has experienced an evolving definition in which different geographic areas have been excluded and included back and forth. The first biogeographic definition cited by Winker (2011) is that of Baird (1864), who used the term Middle America to cover the region delimited between a line drawn from the mouth of the Río Bravo in the Gulf of Mexico and that of the Yaqui river, near Guaymas, Sonora (excluding most of the Baja California Peninsula) south to the Darién region (Panama) and all of the Caribbean islands, excepting Trinidad and, perhaps, Tobago. A later definition by the same author (Baird, 1872) maintained the same basic scheme, except that the northern boundary was relocated at the U.S.-Mexico border, excluding the arid lands of the Mexican plateau. Different bird taxonomic treatises have used this definition together with that of North America for including all species in the region (e.g., AOU, 1998), although the southern limit has changed to that of the Panama-Colombia border.

These definitions—and the term Middle America—relying on geopolitical boundaries (“...the lands between the United States of America and South America”; Winker, 2011:5) persisted in the scientific literature in English for convenience or, perhaps, to retain control over regional bird listings (e.g., AOU, 1983, 1998), but were not based on detailed distributional data of biotas, geology, and/or biogeographic and phylogeographic studies testing distributional patterns, as recognized by Winker (2011). Winker (2011:5) argues that: “...the geological uniting of

North and South America is conveniently delimited by the Panama–Colombia border”; however, this border does not represent the real boundary for North and South America. If such a region may be located, it would correspond roughly to the Panama Canal Basin area (Whitmore and Stuart, 1965; Coates and Obando, 1996), which may have been the southern part of the North American subcontinent prior to the closure of the Isthmus of Panama, as different known fossil faunas have suggested (Kirby and MacFadden, 2005). On the other hand, biogeographic and phylogenetic evidence using DNA sequences are continuously supporting a relationship that extends Central America to the Chocoan subregion (eastern Panama to northwestern Ecuador) for a number of vertebrates (e.g., Ron, 2000; Dingle et al., 2006).

The northern boundary is also conflicting. Winker (2011) follows the AOU (1983) proposal in declaring the U.S.-Mexico border as the limit for “Middle America”. Again, this is not based on any natural criterion, but only on geopolitical grounds; however, it has been retained because it has been regarded as reasonably close to the northern limits of the tropics. Although this is roughly true, more realistic natural limits correspond to those of the lowland rainforest along the Gulf of Mexico slope, located near the Soto La Marina river in Tamaulipas (see Gehlbach et al., 1976 for avian examples), and to the northern limits of the tropical dry forests in western Mexico, at the Yaqui river in southern Sonora (Morrone, 2001). These limits effectively exclude the Baja California Peninsula and the arid lands of the Mexican plateau, which biotically correspond to the Nearctic region. Considerable confusion around the northern limits may be a product of the complex nature of the region, as it contains biotic elements from both the Nearctic and Neotropical regions, thus constituting the Mexican Transition Zone (Halffter, 1976, 1987; Morrone, 2006, 2010). Winker (2011) argues that maintaining the U.S.-Mexico border as the northern limit for “Middle America” is “arguably as good as any that might be proposed for this transition zone”. We believe that, although no sharp limits may be located for all of the taxa in the area, endemism in both the lowland rainforest and the tropical dry forests may be better indicators of the limits for this region, as those elements may have closer evolutionary relationships with other Mesoamerican taxa than to North American species, both from a biogeographic (García-Trejo and Navarro-Sigüenza, 2004; Ríos-Muñoz and Navarro-Sigüenza, 2012) and a phylogenetic perspective (e.g., DaCosta and Klicka, 2008; DaCosta et al., 2009).

The use of Middle America as the appropriate English term for Mesoamerica in the literature of non-human biology advocated by Winker (2011), beyond the

popularity argument of coining another etymological gem, has seen both loose and variable definitions. For example, its English popular usage in the United States includes the use for the middle class in the US and for native Americans, and for towns and counties of the culturally defined Midwest (Wuthnow, 2010). Such English usage of Middle America would certainly not spill over into biogeography. The recognition of “Middle America” for management and protection policies may be an adequate, politically correct term, as laws and regulations may apply in different ways according to the interests within each country. It is only in this sense, not from a biogeographic point of view, that the term is relevant, as Winker (2011) points out. However, the continuous distribution of many floristic and faunistic elements in the region, from southern Sonora, Baja California, and Tamaulipas all the way south to Costa Rica, Panama or the Chocó-Darién region, motivated the emergence of many government, non-government, and academic organizational initiatives to study, manage, and conserve the second most threatened biodiversity hotspot characterized by a complex topography, geology, species diversity, and endemism (Myers et al., 2000). The conservation challenge is deeply grounded in the cultural and therefore political basis of identity and collaboration by people who have used and ultimately preserved the biological resources in their surroundings, but today face poverty and one of the highest deforestation rates (Flores-Villela and Gerez, 1994; Bray, 2009).

Although the name Mesoamerica was coined by Kirchoff (1943) in order to unify the wording among anthropologists, the term was later also applied in biogeography (Vivó, 1943). As Winker (2011) points out, the geographic coverage of Mesoamerica excludes the eastern portions of Honduras, Nicaragua, and Costa Rica, thus forming only a subset of “Middle America”. However, the definition of Middle America defended by Winker (2011) *also* excludes important biogeographic portions of the biogeographic area (e.g., the Chocó in the southern limit) and includes portions of others that extend into the Nearctic region (e.g., the Californian, Sonoran, Mexican Plateau, and Tamaulipas biogeographic provinces), thus rendering “Middle America” as a subset. Then, the problem is not solved; it is only ignored on behalf of convenient perceptions.

We agree with Winker (2011) that the indistinct application of the terms Mesoamerica and/or Middle America may be wrong and that a unifying term for biogeographic purposes is badly needed. We also agree that using a term defining a subset of the region is not the best choice; however, neither Mesoamerica nor Middle America would be correct, as they *both* define subsets of the area to be considered (see above). An alternative

name would be Caribbean subregion (Morrone, 2001, 2006). This subregion is bounded in the north by the Yaqui River in the Pacific and the Soto La Marina River in the Gulf of Mexico, and its southern limits would include the Venezuelan Llanos and the dry regions in western Ecuador and northwestern Peru (Morrone, 2001, 2006). Different cladistic biogeographic analyses have shown that the subregion is closely related to the rest of the Neotropical subregions (Amorim and Pires, 1996; Ron, 2000; Morrone, 2006), suggesting that from a biogeographic perspective, the subregion is natural, thus valid. Within this subregion, however, if a smaller area needs to be recognized, it would be the Mesoamerican dominion (Morrone, 2006), which we believe is a more accurate term defining the Mexican-Central American portion. Reasons cited by Winker (2011) for the rejection of the term Mesoamerica in biotic studies, also apply for not adopting the term Middle America for a “correct” biogeography.

The defense of the term Middle America (not Mesoamerica), on behalf of English and biogeography, made by Winker (2011) is a narrative without adequate scrutiny from a biogeographic perspective. It ignores some of the most compelling evidence demonstrating that Mesoamerica is not only a term adopted by anthropologists to refer to a cultural entity (Kirchoff, 1943; Vivó, 1943), but a valid term also for the biota (West, 1964; Myers et al., 2000), which contains distinctive species assemblages equivalent in rank to the Nearctic and Neotropical regions (e.g., Savage, 1966; Humphries, 1982; see Rzedowski, 1991 for examples in plants). Hopefully, future biogeographic and comparative phylogeographic studies will shed light on the origin and diversification of the Mesoamerican biota, in which some of the biogeographical patterns will be discovered and named after testing dispersal and vicariant scenarios, and evaluating the influence from the North American, South American, and Caribbean biotas in shaping the extant biota in the region and/or vice versa.

We thank Kevin Winker, Oliver Komar, Michael Heads, Octavio Rojas-Soto, Mario Favila Castillo and four anonymous reviewers for comments on previous drafts of the manuscript, which greatly improved its content.

Literature cited

- Amorim, D. S. and M. R. S. Pires. 1996. Neotropical biogeography and a method for maximum biodiversity estimation. *In* Biodiversity in Brazil: a first approach, C. E. M. Bicudo and N. A. Menezes (eds.). CNPq, São Paulo. p. 183-219.
- Baird, S. F. 1864-1872. Review of American birds in the museum of the Smithsonian Institution. Part I. North and Middle America. Smithsonian Institution, Washington, D. C. 478 p.
- Bray, D. B. 2009. Forest cover dynamics and forest transitions in Mexico and Central America: towards a “Great Restoration”? *In* Reforesting landscapes, H. Nagendra, and J. Southworth (eds.). Landscape Series 10. Springer, New York. p. 85-120.
- Brown, J. H. and M. V. Lomolino. 2000. Biogeography. 2nd Ed. Sinauer Associates Inc., Sunderland, Massachusetts. 691 p.
- Coates, A. G. and J. A. Obando. 1996. The geologic evolution of the Central American Isthmus. *In* Evolution and environment in Tropical America, J. B. C. Jackson, A. F. Budd and A. G. Coates (eds.). University of Chicago Press, Chicago. p. 21-56.
- Cox, C. B. 2001. The biogeographic regions reconsidered. *Journal of Biogeography* 28:511-523.
- DaCosta, J. M. and J. Klicka. 2008. The great American interchange in birds: a phylogenetic perspective with the genus *Trogon*. *Molecular Ecology* 17:1328-1343. doi: 10.1111/j.1365-294X.2007.03647.x
- DaCosta, J. M., G. M. Spellman, P. Escalante and J. Klicka. 2009. A molecular systematic revision of two historically problematic songbird clades: *Aimophila* and *Pipilo*. *Journal of Avian Biology* 40:206-216. doi: 10.1111/j.1600-048X.2009.04514.x
- Dingle, C., I. J. Lovette, C. Canaday and T. B. Smith. 2006. Elevational zonation and the phylogenetic relationships of the *Henicorhina* wood-wrens. *The Auk* 123:119-134.
- Escalante, T. 2009. Un ensayo sobre regionalización biogeográfica. *Revista Mexicana de Biodiversidad* 80:551-560.
- Flores-Villela, O. A. and P. Gerez. 1994. Biodiversidad y conservación en México: Vertebrados, vegetación y uso del suelo, segunda edición, Universidad Nacional Autónoma de México / Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. Mexico, D. F. 439 p.
- García-Trejo, E. A. and A. G. Navarro-Sigüenza. 2004. Patrones biogeográficos de la riqueza de especies y el endemismo de la avifauna en el oeste de México. *Acta Zoológica Mexicana* 20:167-185.
- Gehlbach, F. R., D. O. Dillon, H. L. Harrell, S. E. Kennedy and K. R. Wilson. 1976. Avifauna of the Rio Corona, Tamaulipas. Mexico: Northeastern limit of the tropics. *The Auk* 93:53-65.
- Halfpiter, G. 1976. Distribución de los insectos en la zona de transición mexicana: relaciones con la entomofauna de Norteamérica. *Folia Entomológica Mexicana* 35:1-64.
- Halfpiter, G. 1987. Biogeography of the montane entomofauna of Mexico and Central America. *Annual Review of Entomology* 32:95-114
- Humphries, C. J. 1982. Vicariance biogeography in Mesoamerica. *Annals of the Missouri Botanical Garden* 69:444-463.
- Kirby, M. X. and B. MacFadden. 2005. Was southern Central America an archipelago or a peninsula in the Middle Miocene? A test using land-mammal body size. *Palaeogeography, Palaeoclimatology, Palaeoecology* 228:193-202.
- Kirchoff, P. 1943. Mesoamerica. *Acta Americana* 1:92-107.
- Morrone, J. J. 2001. Biogeografía de América Latina y el Caribe. M&T-Manuales & Tesis SEA, vol 3. Zaragoza. 148 p.

- Morrone, J. J. 2002. Biogeographic regions under track and cladistic scrutiny. *Journal of Biogeography* 29:149-152.
- Morrone, J. J. 2006. Biogeographic areas and transition zones of Latin America and the Caribbean Islands based on panbiogeographic and cladistic analyses of the entomofauna. *Annual Review of Entomology* 51:467-494.
- Morrone, J. J. 2010. Fundamental biogeographic patterns across the Mexican Transition Zone: An evolutionary approach. *Ecography* 33:355-361.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.
- Ortega, J. and H. T. Arita. 1998. Neotropical-Nearctic limits in Middle America as determined by distributions of bats. *Journal of Mammalogy* 79:772-781.
- Riddle, B. R. and D. J. Hafner. 2010. Integrating pattern with process at biogeographic boundaries: the legacy of Wallace. *Ecography* 33:321-325.
- Ríos-Muñoz, C. A. and A. G. Navarro-Sigüenza. 2012. Patterns of species richness and biogeographic regionalization of the avifaunas of the seasonally dry tropical forest in Mesoamerica. *Studies on Neotropical Fauna and Environment* 47:171-182.
- Rzedowski, J. 1991. Diversidad y orígenes de la flora fanerogámica de México. *Acta Botanica Mexicana* 14:3-21.
- Savage, J. M. 1960. Evolution of a peninsular herpetofauna. *Systematic Zoology* 9:184-212.
- Savage, J. M. 1966. The origins and history of the Central American herpetofauna. *Copeia* 1966:719-766.
- Ron, S. R. 2000. Biogeographic area relationships of lowland Neotropical rainforest based on raw distributions of vertebrate groups. *Biological Journal of the Linnean Society* 71:379-402.
- Sclater, P. L. 1858. On the general geographical distribution of members of the class Aves. *Journal of the Linnean Society of Zoology* 2:130-145.
- Townsend, C. H. T. 1895. On the bio-geography of Mexico, Texas and New Mexico, and Arizona with special reference to the limits of the life areas, and a provisional synopsis of the bio-geographic divisions of America. *Transactions of the Texas Academy of Science* 1:71-96.
- Udvardy, M. D. F. 1975. A classification of the biogeographical provinces of the world. *IUCN Occasional Paper Núm. 18, Morges*. 48 p.
- Vivó, J. A. 1943. Los límites biogeográficos en América y la zona cultural mesoamericana. *Revista de Geografía* 3:109-131.
- Wallace, A. R. 1876. *The geographical distribution of animals*. McMillan, London. 632 p.
- West, R. C. (ed.). 1964. *Handbook of Middle American Indians*. Vol. I: Natural environment & early cultures. University of Texas Press, Austin. 550 p.
- Whitmore, A. C. and R. H. Stewart. 1965. Miocene mammals and Central American seaways. *Science* 148:1801-85.
- Winker, K. 2011. Middle America, not Mesoamerica, is the accurate term for biogeography. *Condor* 113:5-6.
- Wuthnow, R. 2010. *Remaking the heartland: Middle America since the 1950s*. Princeton University Press, Princeton. 376 p.