

Track analysis of the Neotropical Entimini (Coleoptera: Curculionidae: Entiminae)

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ABSTRACT. Track analysis of the Neotropical Entimini (Coleoptera, Curculionidae, Entiminae). Distributional patterns of the species belonging to the tribe Entimini from the Neotropical region were analyzed. Based on a track analysis of 22 species of *Entimus*, *Rhigus*, and *Phaedropus*, for which distributional data were available, two generalized tracks were found. One is located in northern Brazil, corresponding to the Amazonian subregion, and is determined by *Phaedropus candidus* and *Rhigus speciosus*. The other is located in southern Brazil, corresponding to the Parana subregion, and is determined by *Entimus imperialis*, *E. excelsus*, *Phaedropus togatus*, *Rhigus dejeanii*, *R. faldermanni*, *R. horridus*, *R. lateritus*, *R. nigrosparsus*, and *R. tribuloides*. The development of the Chacoan subregion is hypothesized to have been the dynamic vicariant event that fragmented the former Amazonian-Parana forest.

KEYWORDS. Brazil; dynamic vicariance; evolutionary biogeography; Neotropical region; panbiogeography.

RESUMEN. Análisis de trazos de Entimini Neotropical (Coleoptera, Curculionidae, Entiminae). Se analizaron los patrones de distribución de la tribu Entimini en la región Neotropical. Con base en un análisis de los trazos de 22 especies de *Entimus*, *Rhigus* y *Phaedropus*, para los cuales se contaba con datos de distribución, se hallaron dos trazos generalizados. Uno se localiza en el norte de Brasil, en la subregión Amazónica, y está sustentado por *Phaedropus candidus* y *Rhigus speciosus*. El otro se localiza en el sur de Brasil, en la subregión Paranaense, y está sustentado por *Entimus imperialis*, *E. excelsus*, *Phaedropus togatus*, *Rhigus dejeanii*, *R. faldermanni*, *R. horridus*, *R. lateritus*, *R. nigrosparsus* y *R. tribuloides*. Se hipotetiza que el desarrollo de la subregión Chaqueña constituyó el evento de vicarianza dinámica que fragmentó el antiguo bosque Amazónico-Paranaense.

PALABRAS CLAVE. Brasil; biogeografía evolutiva; panbiogeografía; región Neotropical; vicarianza dinámica.

The tribe Entimini is comprised of 44 species belonging to eight genera: *Cydianerus*, *Cyriophthalmus*, *Entimus*, *Nasocomptus*, *Phaedropus*, *Polyteles*, *Rhigus*, and *Trachyus* (Alonso-Zarazaga & Lyal 1999; Morrone 1999; Vanin & Gaiger 2005). The Siberian genus *Cyriophthalmus* was assigned to the Entimini by Alonso-Zarazaga & Lyal (1999), although its distribution raises doubts regarding its placement in the tribe (Vanin & Gaiger 2005). The remaining genera inhabit the Neotropical region, from southern Mexico to central Argentina. The Neotropical region occupies the tropical areas of the Americas, in most of South America, all Central America, southern Mexico, the West Indies, and the southern part of the Florida peninsula, including the Caribbean, Amazonian, Chacoan, and Parana subregions (Morrone 2006).

Panbiogeography, originally proposed by Croizat (1958, 1964), basically plots distributions of organisms on maps and connects the disjunct distribution areas or collection localities together with lines called tracks. Individual tracks are then superimposed, and if they coincide, the resulting summary lines are considered generalized tracks, which indicate the pre-existence of ancestral biotas, which subsequently become fragmented by tectonic and/or climate change (Craw *et al.* 1999; Morrone 2009). The area where two or more generalized tracks intersect is a node, which indicates that different ancestral biotic and geological fragments interre-

late in space/time, as a consequence of terrane collision, docking, or suturing, thus constituting a composite area.

Our objective is to analyze the geographical distribution of the Neotropical Entimini, using a panbiogeographic approach. We intend to determine whether any vicariant event can be identified from the analysis of their distributional patterns.

MATERIAL AND METHODS

Distributional data for this study were obtained from the literature (Vaurie 1952; Viana 1958, 1968; Vanin 1983; Gaiger 2001; Morrone 2002). The species of *Cydianerus*, *Polyteles*, *Trachyus*, and *Nasocomptus* lack precise data or are present on a single locality, so they were not included in the analysis. The phylogenetic hypothesis for the genera of Entimini was taken from Vanin & Gaiger (2005), who did not include in their analysis the genera *Trachyus* and *Cyriophthalmus*.

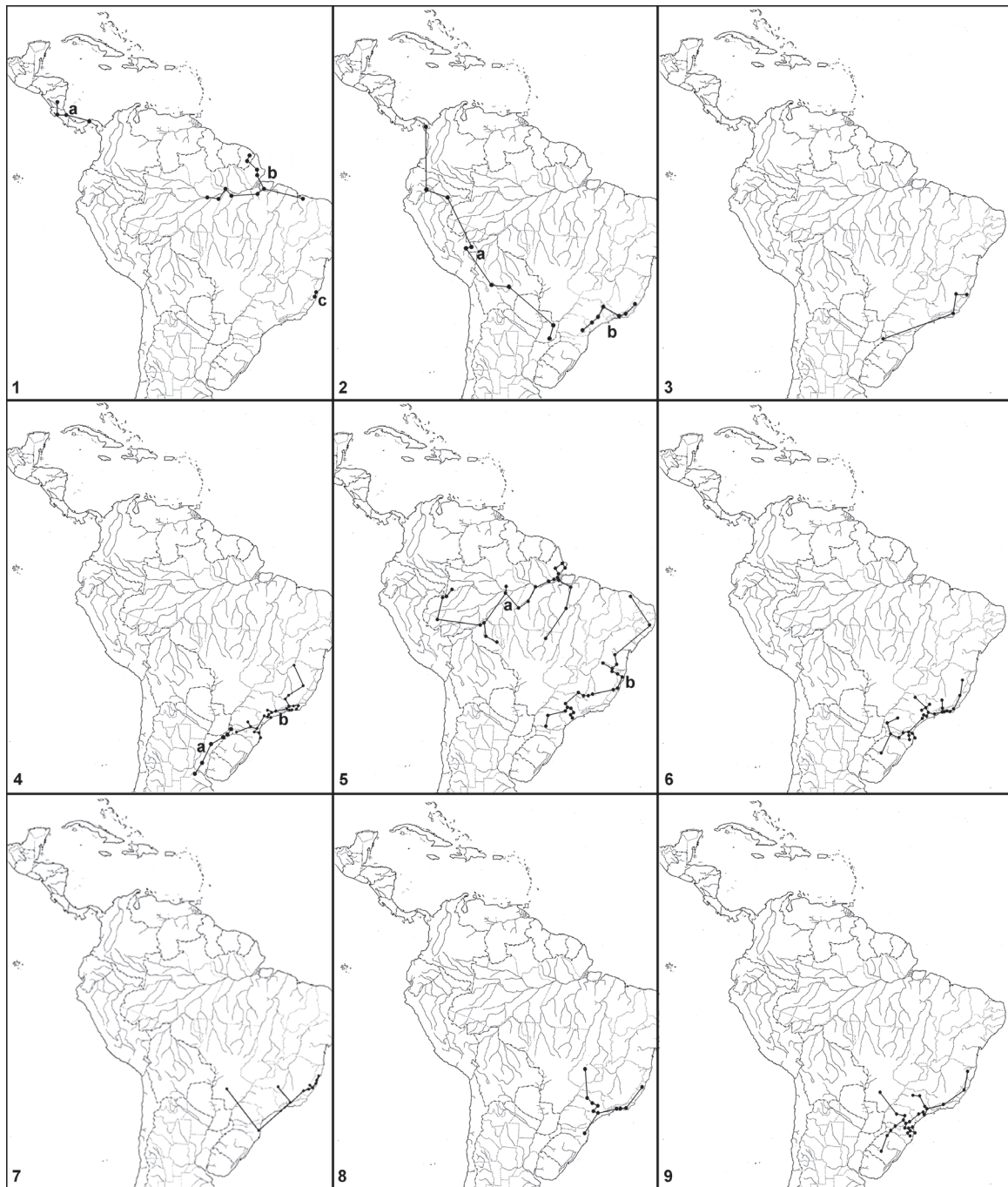
The panbiogeographic approach basically consists of plotting distribution of different taxa on maps, connecting their separate localities together with lines called individual tracks. These individual tracks represent the geographical coordinates of species or supraspecific taxa; operationally they are lines drawn on a map of their localities, connected according to their geographical proximity (unrooted minimum-spanning trees). When two or more individual tracks are

superimposed, the portions showing overlap are considered to represent generalized tracks, which are interpreted as indicating the pre-existence of ancestral biotas, fragmented by tectonic and/or climatic change. If two or more generalized tracks intersect in a given area, they determine a node, which indicates the different ancestral biotic and geological fragments that interrelated in space and time, constituting a composite area. For details on the panbiogeographic approach, see *Craw et al (1999)* and *Morrone (2009)*.

RESULTS

Individual tracks were obtained for five species of *Entimus* (Figs. 1-4), two species of *Phaedropus* (Figs. 1-2), and seven species of *Rhigus* (Figs. 4-9). The comparison of the individual tracks of the species reveals the existence of two areas of overlap, herein considered as generalized tracks (Fig. 10).

Generalized track 1: northern Brazil. It is determined by *Phaedropus candidus* and *Rhigus speciosus*. It corresponds



Figs. 1-9. Individual tracks. 1, a, *Entimus arrogans*; b, *Phaedropus candidus*; c, *E. excelsus*; 2, a, *E. granulatus*; b, *P. togatus*; 3, *E. imperialis*; 4, a, *E. sastrei*; b, *Rhigus tribuloides*; 5, a, *R. faldermanni*; b, *R. dejeanni*; 6, *R. faldermanni*; 7, *R. horridus*; 8, *R. lateritus*; 9, *R. nigrosparus*.

to the Amazonian subregion, where species of *Nasocomptus*, *Cydianerus*, and *Polyteles* (herein not analyzed) are also distributed.

Generalized track 2: southern Brazil. It is determined by *Entimus imperialis*, *E. excelsus*, *Phaedropus togatus*, *Rhigus dejeanii*, *R. faldermanni*, *R. horridus*, *R. lateritus*, *R. nigrosparus* and *R. tribuloides*. It corresponds to the Parana subregion, where species of *Cydianerus* (herein not analyzed) are also distributed.

As these generalized tracks do not intersect, no nodes were identified.



Fig. 10. Generalized tracks. a, Amazonian generalized track; b, Parana generalized track.

DISCUSSION

The biotic history of the Neotropical Entimini shows congruence with the history of the region as already shown by other taxa. Generalized track 1 (northern Brazil) corresponds to the Amazonian subregion of the Neotropical region, which extends in Brazil, the Guyanas, Venezuela, Colombia, Ecuador, Peru, Bolivia, Paraguay, and Argentina (Morrone 2000a, 2006), and has been recognized by authors working on several plant and animal taxa (e.g., Cabrera & Willink 1973; Takhtajan 1986; Fernandes & Bezerra 1990; Rivas-Martínez & Navarro 1994; Morrone & Coscarón 1996). Generalized track 2 (southern Brazil) corresponds to the Parana subregion of the Neotropical region, which is situated in northeastern Argentina, eastern Paraguay, southern Brazil (west of the Serra do Mar and toward central Rio Grande do Sul), and eastern Brazil, between 7–32° south latitude

(Cabrera and Willink 1973; Rivas-Martínez & Navarro 1994; Morrone 2001). In addition, some species of Entimini belonging to the genera *Entimus* and *Cydianerus* are distributed in the Caribbean subregion, although not constituting any generalized track. The presence of species of *Entimus* in the Caribbean subregion (Morrone 2002) might represent an ancient vicariant event, whereas the presence of species of *Cydianerus* in the same area might be due to a more recent dispersal. In order to distinguish both events, a phylogenetic hypothesis with a molecular clock might be useful.

Based on the basic pattern found, we postulate herein a possible vicariant event: the “savanna corridor” (Schmidt & Inger 1951) or “diagonal of open formations” (Vanzolini 1963), which corresponds to the Chacoan biogeographic subregion (Morrone 2000b, 2006). It has been hypothesized that during the Tertiary, the development of the xeric Chacoan subregion (including the Caatinga, Cerrado, Chaco, and Pampa provinces) split the former Amazonian-Parana forest into the current Amazonian and Parana subregions (Morrone & Coscarón 1998; Morrone 2000b). This represents an example of dynamic vicariance, where climatic changes act displacing gradually a biotic component (Zunino 2003). Vicariance between the Amazonian and Parana subregions has been already detected by recent analyses (Costa 2002; Morrone 2002; Nihei & Carvalho 2004, 2007; Sigrist & Carvalho 2009; Pires & Marinoni 2010), although patterns appear to be more complex. Costa (2002) found that the Amazonian and Parana forests were not exclusive in terms of their mammal species, overlapping broadly with Chacoan taxa. Nihei & Carvalho (2007) and Pires & Marinoni (2010) hypothesized that the Amazonian subregion might be a composite area.

The distribution of the taxa analyzed can be examined in terms of the phylogenetic hypothesis available (Vanin & Gaiger 2005). The two genera found in the Caribbean, Amazonian, and Parana subregions are not closely related, *Entimus* being the sister taxon to the remaining genera, and *Cydianerus* one of the most apomorphic genera. *Nasocomptus* and *Polyteles* are endemic to the Amazonian subregion, the former is the sister taxon to the remaining genera excepting *Entimus*, and the latter is the sister taxon to *Phaedropus*. *Polyteles* and *Rhigus* are distributed in the Amazonian and Parana subregions, the former is the sister taxon to *Phaedropus* and the latter is the sister taxon to *Cydianerus*. All the internal nodes in the area cladogram are paralogous, namely they show contradictory relationships due to sympatric speciation, lack of response to vicariance events or incorrect definition of areas (Nelson & Ladiges 2001), and so no informative relationships can be deduced for them. We hypothesize that the tribe Entimini might be relatively old, showing the basic vicariance pattern of the Neotropical region —(Caribbean (Chacoan, Amazonian, Parana))) (Morrone, 2006)—, although substantial extinction has obscured this biogeographic pattern. Additionally, we cannot rule out the possible existence of taxa not collected yet; the relatively recent description of *Nasocomptus* (Vanin & Gaiger 2005) supports this possibility.

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