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ORIGINAL ARTICLE

Does the Trans-mexican Volcanic Belt represent a natural biogeographical unit? An analysis of the distributional patterns of Coleoptera

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ABSTRACT

Aim We analysed the geographical distribution of beetle species of the families Buprestidae, Cerambycidae, Dryophthoridae, Melolonthidae, Passalidae and Staphylinidae from the Trans-mexican Volcanic Belt (TVB) through a track analysis and a parsimony analysis of endemicity (PAE), in order to test its naturalness and determine its affinities.

Location The area analysed corresponds to the TVB, which is a biogeographical province of the Mexican Transition Zone.

Methods The panbiogeographical analysis was based on the comparison of the individual tracks of 299 species of Buprestidae, Cerambycidae, Dryophthoridae, Melolonthidae, Passalidae and Staphylinidae (Coleoptera). The TVB was divided into $1^o \times 1^o$ grid cells and we also included in the analysis the remaining Mexican biogeographical provinces. Parsimony analysis of endemicity with progressive character elimination (PAE-PCE) was applied to classify areas by their shared taxa according to the most parsimonious cladograms. The nested sets of areas were represented as generalized tracks.

Results Three generalized tracks were obtained: (1) grid cells 9C, 9D, 10D, 10E, Sierra Madre Oriental, Chiapas, Mexican Gulf and the Sierra Madre del Sur; (2) grid cells 3B, 3C, 4B, 4C, 5C, 6C, 7C, Sierra Madre Occidental, Sierra Madre del Sur, Balsas Basin and the Mexican Pacific Coast, and (3) grid cells 8D, 9C, 9D, 10D, 10E, Yucatán Peninsula, Chiapas, Sierra Madre Oriental and the Mexican Gulf.

Main conclusions We conclude that the TVB does not represent a natural biogeographical unit because it shows different relationships with other biogeographical provinces, being clearly transitional between the Nearctic and Neotropical provinces. Some parts of the TVB are related to Neotropical provinces (Chiapas, Mexican Gulf and Mexican Pacific Coast) and others to the remaining provinces of the Mexican Transition Zone (Sierra Madre Oriental, Sierra Madre del Sur, Sierra Madre Occidental and Balsas Basin).

Keywords
Biogeography, Buprestidae, Cerambycidae, Dryophthoridae, Melolonthidae, Mexico, Nearctic, Neotropics, Passalidae, Staphylinidae.

INTRODUCTION

The Trans-mexican Volcanic Belt (TVB) corresponds to Central Mexico, in the states of Guanajuato, Mexico, Distrito Federal, Jalisco, Michoacán, Morelos, Puebla, Oaxaca, Tlaxcala and Veracruz (Morrone, 2001, 2005; Morrone *et al.*, 2002). It constitutes a biogeographical province, which has been assigned to the Mexican Transition Zone (Morrone, 2004, 2006). It is relatively young geologically, dating from the Tertiary (Ferrusquía-Villafranca, 1993; Ferrusquía-Villafranca & González-Guzmán, 2005). It represents the largest mountainous system that extends transversely across Mexico, between the states of Jalisco and Veracruz. The belt is separated from the Sierra Madre del Sur by the Balsas Basin, except in its

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easternmost limit where both mountain ranges are closely associated (Marshall & Liebherr, 2000). According to Ortega & Arita (1998), the major barriers in North America are the TVB, the Sierra Madre Occidental and the Sierra Madre Oriental, situated at the limits between the Neotropical and Nearctic regions. Marshall & Liebherr (2000) highlighted the relevance of the TVB as the boundary between the Nearctic and Neotropical regions, whereas others placed such a boundary at the Isthmus of Tehuantepec (Leopold, 1983; Halffter, 1987; Cole *et al.*, 1994; Morrone & Márquez, 2001; Carleton *et al.*, 2002; Corona & Morrone, 2005).

Beetles (Coleoptera) represent a megadiverse insect order, with approximately 358,000 species, representing 40% of all insects and 30% of the animal kingdom. In the Neotropical region 6703 genera and 72,476 species have been described, which belong to 127 families (Costa, 2000). In Mexico, 35,500 species in 114 families are estimated (Morón & Valenzuela-González, 1993; Navarrete-Heredia & Fierros-López, 2001). If we compare these numbers with Brazil, where 104 families and 26,755 species have been described, we can see that Mexico has a higher apparent diversity, in spite of being a smaller country. Knowledge of Mexican beetles is scarce (Michán & Morrone, 2002) because there are few specialists and surveys have been undertaken sporadically and only in certain localities, mainly in central and southern Mexico. In spite of this impediment, several biogeographical analyses have been published in recent years (e.g. Ball, 1992; Liebherr, 1994; Halffter *et al.*, 1995; Lobo & Halffter, 2000; Marshall & Liebherr, 2000; Morrone & Márquez, 2001, 2003; Morrone *et al.*, 2002; Márquez & Morrone, 2003, 2004; Reyes-Castillo, 2004; Corona *et al.*, 2005; Corona & Morrone, 2005; Corona & Toledo, 2006; Cuevas, 2006; Márquez & Asiain, 2006; Morón, 2006; Reyes-Castillo *et al.*, 2006; Toledo & Corona, 2006).

Our objective is to contribute to the biogeographical characterization of the TVB through a track analysis and a parsimony analysis of endemicity (PAE) of the species of six families of Coleoptera, which are among the most diverse and studied families in Mexico: Buprestidae (863 described species), Cerambycidae (1605), Dryophthoridae (125), Melolonthidae (1147), Passalidae (105) and Staphylinidae (1456) (Corona & Toledo, 2006; Cuevas, 2006; Márquez & Asiain, 2006; Morón, 2006; Reyes-Castillo *et al.*, 2006; Toledo & Corona, 2006). We also test the naturalness of this biogeographical province and determine its affinities.

MATERIAL AND METHODS

Data set

We obtained records from 100 species of 22 genera of Buprestidae, 76 species of 34 genera of Cerambycidae, 33 species of 10 genera of Dryophthoridae, 35 species of 26 genera of Melolonthidae, 24 species of 11 genera of Passalidae and 31 species of 20 genera of Staphylinidae from published taxonomic revisions, scientific notes, descriptions of new species and biogeographical studies (Bates, 1879; Dugès, 1891; Linsley, 1962; Nelson, 1962, 1971, 1975, 1980, 1991, 1994, 2000; Chemsak, 1963a,b, 1964, 1969, 1972, 1977, 1999; Chemsak & Linsley, 1965, 1975, 1976, 1982, 1983, 1986, 1988; Martins & Chemsak, 1966; Hespenheide, 1974; Nelson & Westcott, 1976; Westcott *et al.*, 1979, 1989; Nelson *et al.*, 1981; Westcott, 1983, 1998; Barr, 1992; Noguera, 1993, 2002; Westcott & Noguera, 1993; Bellamy & Westcott, 1995, 1996, 2000; Nelson & Bellamy, 1996, 2004; Bellamy, 1997; Chemsak & Noguera, 1997, 1998, 2001, 2003; Giesbert & Chemsak, 1997; Noguera & Chemsak, 1997; Toledo, 1997, 2005a,b; McCarty, 2001; Bellamy & Hespenheide, 2002; Chemsak & Hovore, 2002; Noguera *et al.*, 2002; Davidson, 2003; Corona, 2005; Corona & Toledo, 2006; Cuevas, 2006; Márquez & Asiain, 2006; Morón, 2006; Reyes-Castillo *et al.*, 2006; Toledo & Corona, 2006) (see Appendix S1 in Supplementary Material).

Study area

The TVB was divided into 50, $1^o \times 1^o$ grid cells (Fig. 1) to apply the PAE. In addition, we analysed the remaining Mexican biogeographical provinces, defined according to Morrone *et al.* (2002) and Morrone (2005, 2006): the Mexican Plateau (MP), California (CAL), Baja California (BCAL), the Mexican Gulf (GULF), the Mexican Pacific Coast (MPC), the Chiapas (CHIS), the Balsas Basin (BAL), the Sierra Madre Occidental (SMOC), the Sierra Madre Oriental (SMO), the Sierra Madre del Sur (SMS), Sonora (SON), Tamaulipas (TAMPS) and the Yucatán Peninsula (YUC).

Track analysis

The track analysis consists of plotting localities of different taxa on maps, and connecting them together with lines called individual tracks. When different individual tracks overlap, the resulting summary lines are considered generalized tracks, which indicate the pre-existence of ancestral biotic components subsequently fragmented by tectonic and/or climatic changes. If two or more generalized tracks converge in a given area, they determine a node, which represents a complex area where different ancestral geological and biotic components interrelate in time and space (Morrone & Crisci, 1995; Craw *et al.*, 1999; Morrone, 2004). Individual and generalized tracks were drawn using the software ArcView 3.2 (ESRI, 1998).

Parsimony analysis of endemicity with progressive character elimination

PAE classifies areas by their shared taxa according to the most parsimonious cladogram, in order to detect areas of endemism or generalized tracks (Rosen, 1988; Morrone, 1994, 1998, 2004). Parsimony analysis of endemicity with progressive character elimination (PAE-PCE) (Luna-Vega *et al.*, 2000; García-Barros *et al.*, 2002; García-Barros, 2003) consists of the application of successive parsimony analyses, eliminating in each run the synapomorphic species that define the area clades. This procedure results in alternative groups of areas to the

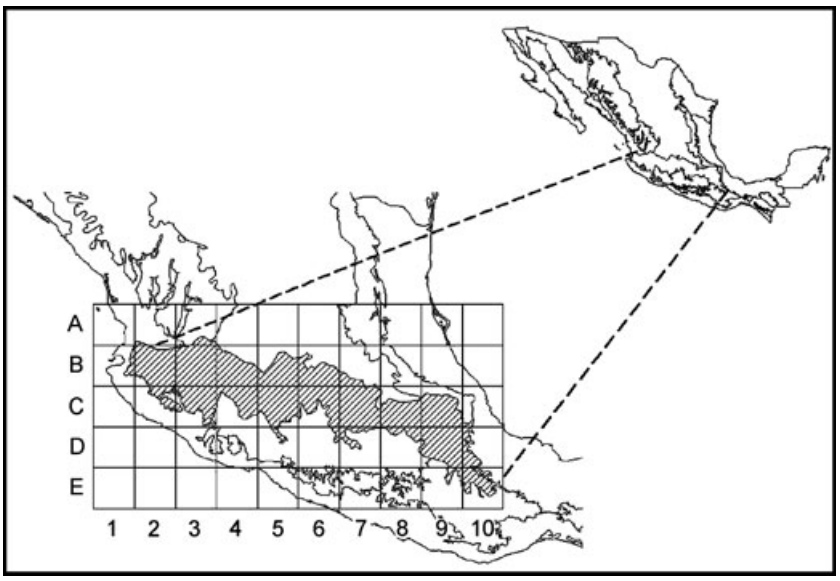

Figure 1 The Trans-mexican Volcanic Belt biogeographical province and $1^o \times 1^o$ grid cells used in the analysis.

most parsimonious arrangement. From the consensus cladograms obtained in each run, area clades supported by at least two taxa were mapped as generalized tracks. Two hundred and ninety-nine species of Buprestidae, Cerambycidae, Dryophthoridae, Melolonthidae, Passalidae and Staphylinidae were coded in a data matrix for their presence (1), or absence (0) in 63 areas (grids cells and provinces) (Appendix S1). Taxa present in a single locality were excluded from the analysis. Twenty-four grid cells and two biogeographical provinces were excluded from the analysis because we did not find any records for them. The matrix (see Appendix S1) was analysed using NONA version 2.0 (Goloboff, 1993) and WINCLADA 1.00.08 (Nixon, 2002), with a heuristic algorithm (tree bisection and reconnection, 100 replications).

RESULTS AND DISCUSSION

On the basis of the analysis of 299 species, we found that five species of Buprestidae (*Agrilus fossulatus*, *Agrilus megerlei*, *Agrilus perlucidus*, *Buprestis ventralis* and *Chalcangium longipenne*), two of Cerambycidae (*Aneflomorpha crinita* and *Euderces biplagiatus*) and one of Passalidae (*Pseudocanthus mexicanus*) are endemic to the TVB. Parsimony analysis of endemicity produced the four most parsimonious cladograms, with 1512 steps, a consistency index of 0.19 and a retention index of 0.49. The strict consensus cladogram had 1531 steps, a consistency index of 0.19 and a retention index of 0.48. One clade supported by 14 species was used to define generalized track 1 (Fig. 2). The second run of PAE-PCE produced five cladograms, with 1472 steps, a consistency index of 0.19 and a retention index of 0.49. Two clades, supported by four and two species, respectively, were used to define generalized tracks 2 and 3 (Figs. 2 & 3). A third run led to 24 cladograms with 1455 steps, a consistency index of 0.19 and a retention index of 0.48. No clades were supported by more than one species.

Generalized track 1 corresponds to grid cells 9C, 9D, 10D, 10E, the Sierra Madre Oriental, the Chiapas, the Mexican Gulf and the Sierra Madre del Sur. It is defined by 14 species:

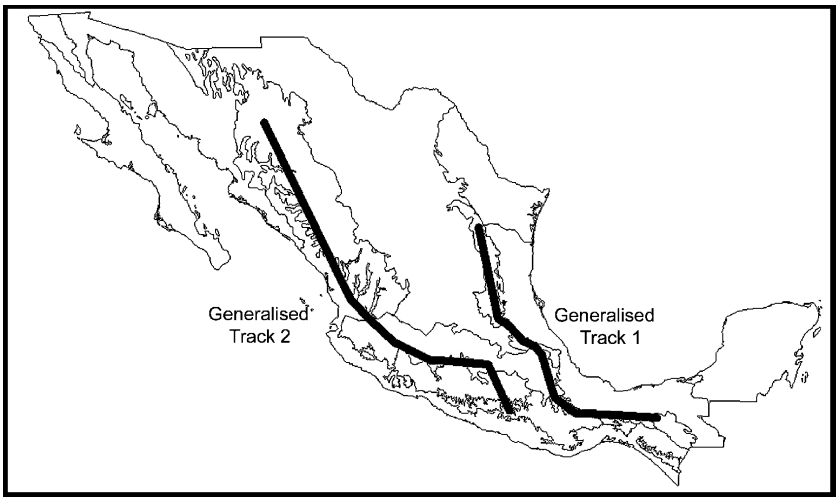

Figure 2 Two of the three generalized tracks found in the analysis. Generalized track 1 (grid cells 9C, 9D, 10D, 10E, the Sierra Madre Oriental, the Chiapas, the Mexican Gulf and the Sierra Madre del Sur) is defined by 14 species and generalized track 2 (grid cells 3B, 3C, 4B, 4C, 5C, 6C, 7C, the Sierra Madre Occidental, the Sierra Madre del Sur, the Balsas Basin and the Mexican Pacific Coast) is defined by four species.

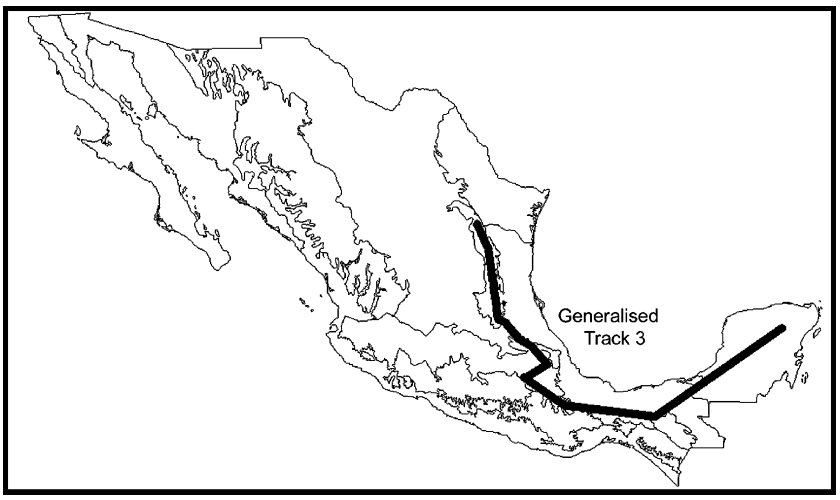

Figure 3 The third generalized track found in the analysis (grid cells 8D, 9C, 9D, 10D, 10E, Yucatán Peninsula, Chiapas, Sierra Madre Oriental and Mexican Gulf) is defined by two species.

Belonochus dichrous, *Lispinus costarisensis*, *Oileus rimator*, *Pachyschelus signatus*, *Passalus* (*Pertinax*) *inops*, *Passalus* (*Pertinax*) *cognatus*, *Petrejoides recticornis*, *Phaea saperda*, *Proculeius brevis*, *Spurius bicornis*, *Thracophorus sallaei*, *Verres corticicola*, *Verres cavicollis* and *Vindex agnoscendus*, which have mainly Mesoamerican Mountain distributions according to Halffter (1987). This indicates that the north-eastern part of the TVB (central Puebla) is more closely related to the Sierra Madre Oriental biogeographical province and that the south-eastern part (south-eastern Puebla and northern Oaxaca) is more closely related to the south-eastern part of the Sierra Madre del Sur (Mexican Transition Zone) and the Mexican Gulf and Chiapas (Neotropical region).

Generalized track 2 includes grid cells 3B, 3C, 4B, 4C, 5C, 6C, 7C, the Sierra Madre Occidental, the Sierra Madre del Sur, the Balsas Basin and the Mexican Pacific Coast, and is defined by four species: *Lampetis* (*Spinthoptera*) *mexicana*, *Omochyseus terminalis*, *Phyllophaga* (*Listrochelus*) *cavata* and *Strategus cessus*. It indicates that the south-central part of the TVB is closely related to the Balsas Basin and the Sierra Madre del Sur biogeographical provinces and the north-western part is more closely related to the Sierra Madre Occidental and the Mexican Pacific Coast biogeographical provinces.

Generalized track 3 includes grid cells 8D, 9C, 9D, 10D, 10E, the Yucatán Peninsula, the Chiapas, the Sierra Madre Oriental and Mexican Gulf. It is defined by two species: *Actenodes bifasciata* and *Passalus* (*Passalus*) *puctiger*. It is similar to generalized track 1.

The western part of the TVB associated with the Sierra Madre Occidental could represent an older geological formation, which could have originated in the Cretaceous, and developed during the Oligocene and early Miocene (Marshall & Liebherr, 2000; Becerra, 2005). The TVB was formed progressively in different parts, from west to east, and started in the west 23 million years ago (Ma) and ended in the east approximately 2.5 Ma (Becerra, 2005). At that time, the eastern part of the TVB could have been connected with the Sierra Madre Oriental and the Sierra Madre del Sur. These geological associations are evident in the first two generalized tracks.

Márquez & Morrone (2004) analysed the biogeographical relationships and geographical boundaries of the Sierra Madre Oriental, based on the distribution of 88 different beetle species and by applying PAE. They found that the TVB is more closely related to the Sierra Madre del Sur, Oaxaca, the Chiapas, the Mexican Gulf and the Sierra Madre Oriental. Corona *et al.* (2005) studied the biogeographical relationships of the provinces of the Mexican Transition Zone, analysing distribution data of 222 species of Coleoptera and applying PAE. They found a close relationship between the TVB, the Balsas Basin, the Sierra Madre del Sur, the Chiapas and the Sierra Madre Oriental. We can see the relationships of both analyses in our generalized track 1.

We obtained cladograms with few synapomorphies and many homoplasies, which do not support the TVB as a geographical unit. An important factor potentially influencing this analysis, however, is the lack of systematic surveys of the taxa studied in the TVB. The majority of our data indicate that these groups have been collected in few localities and mainly in the tropical areas of Mexico. It is to be hoped that future analyses will be undertaken, including more species belonging to other taxa, to test our model.

We suggest that the TVB cannot be considered as a natural unit, because of its varied relationships with other areas. Like areas of the Mexican Transition Zone, this area is the result of events of biotic hybridization, caused by historical and ecological changes that allowed interaction among different biotic elements (Morrone, 2004, 2005; Corona *et al.*, 2005).

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1. Data matrix of taxa (Columns) × areas (files) analysed by parsimony analysis of endemicity (PAE).

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365–2699.2006.01666.x (This link will take you to the article abstract).

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BIOSKETCHES

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