ORIGINAL ARTICLE

Do the Oaxacan Highlands represent a natural biotic unit? A cladistic biogeographical test based on vertebrate taxa

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ABSTRACT

Aim We analysed the distributional patterns of six terrestrial vertebrate taxa from the Oaxacan Highlands (Sierra Mazateca, Nudo de Zempoaltépetl and Sierra de Juárez) through a cladistic biogeographical approach, in order to test their naturalness as a biotic unit.

Location The Oaxacan Highlands, Mexico.

Methods The cladistic biogeographical analysis was based on the area cladograms of the *Pseudoeurycea bellii* species group (Amphibia: Plethodontidae), the genus *Chlorospingus* (Aves: Thraupidae), the genera *Microtus*, *Reithrodontomys* and *Habromys*, and the *Peromyscus aztecus* species group (Mammalia: Rodentia). We obtained paralogy-free subtrees, from which the components were coded in a data matrix for parsimony analysis. The data matrix was analysed with Nona through WinClada.

Results The parsimony analysis resulted in a single general area cladogram in which areas were fragmented following the sequence Sierra Madre Occidental, Trans-Mexican Volcanic Belt, Chiapas, Sierra Madre Oriental + Sierra Mazateca, Sierra Madre del Sur, Nudo de Zempoaltépetl and Sierra de Juárez.

Main conclusions The general area cladogram shows that the Oaxacan Highlands do not constitute a natural unit. The Sierra Mazateca is the sister area to the Sierra Madre Oriental, whereas the Nudo de Zempoaltépetl and the Sierra de Juárez are closely related to the Sierra Madre del Sur. The events that might have caused these patterns include cycles of expansion and contraction of mountain pinyon, juniper and oak woodlands during the Pleistocene.

Keywords
Amphibians, birds, cladistics, evolutionary biogeography, mammals, Mexico, Oaxaca.

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INTRODUCTION

The Middle American Highlands represent an ideal model system for studying evolutionary biogeography (Sullivan *et al.*, 2000). They include several distinct mountain ranges in central and southern Mexico and upper Middle America, and the region is characterized by having very high endemism (Fa & Morales, 1993; Flores-Villela & Gerez, 1994). These mountain ranges (Fig. 1a) include: the Sierra Madre Occidental (SMOcc) and the Sierra Madre Oriental (SMOr), which extend north–south in western and eastern Mexico, respectively; the Trans-Mexican Volcanic Belt (TVB), which runs east to west through

central Mexico; the Sierra Madre del Sur (SMS) along the south-western coast of Mexico; the complex highlands in central Oaxaca (OH); and the mountains of Chiapas and north-western Middle America (CHI). Forests occur at moderate to high elevations in each of these ranges. Although palaeoecological data for this region are too sparse to establish that these forests were formerly more extensive, their present disjunct distribution may be a result of Pleistocene fragmentation (Toledo, 1982; McDonald, 1993; Luna *et al.*, 1999).

Within these complex mountain systems, the Oaxacan Highlands may represent a key element to explain the biotic evolution of Mexico and Central America. A complete and
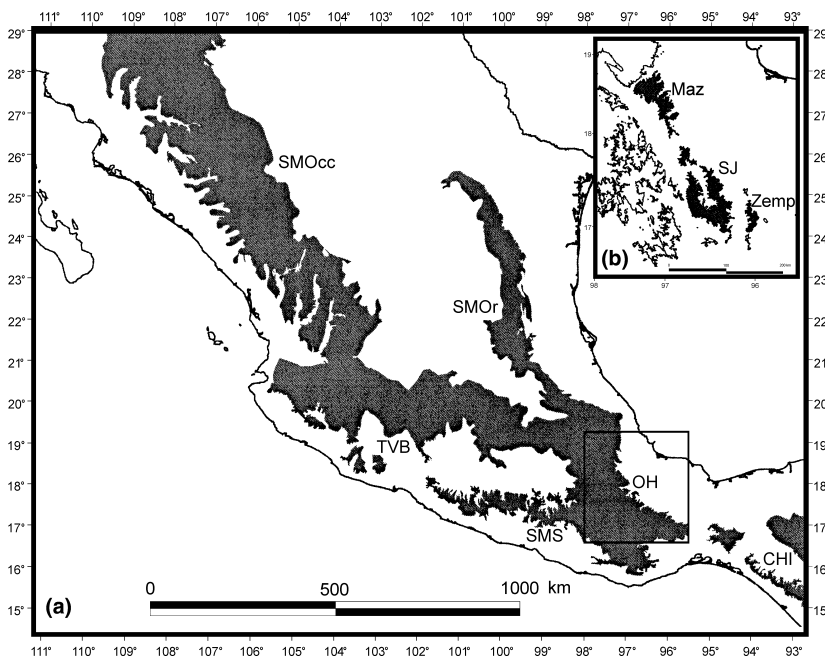
Figure 1 (a) Middle American Highlands. (b) Detail of the units within the Oaxacan Highlands: CHI, Chiapas Mountains; Maz, Sierra Mazateca; OH, Oaxacan Highlands; SJ, Sierra de Juárez; SMOcc, Sierra Madre Occidental; SMOr, Sierra Madre Oriental; SMS, Sierra Madre del Sur; TVB, Trans-Mexican Volcanic Belt; Zemp, Nudo de Zempoaltépetl.

detailed geological account for Oaxaca (Centeno-García, 2004) indicates that the oldest rocks are Precambrian and currently constitute a huge portion of northern and central Oaxaca. Evidence suggests that these rocks were originally South American, and that they were transferred to North America by a collision event in the Late Palaeozoic. Oaxaca's palaeography underwent significant changes during the Jurassic, when the eastern region and the Isthmus of Tehuantepec, formerly located at higher latitudes, were displaced to their current position. At the end of the Mesozoic and in the Early Cenozoic, a deformational event radically modified the inland Oaxacan landscape, and the seas withdrew permanently, being displaced by a landscape of mountains and valleys. Most of the present physiographic elements originated as a result of volcanic activity and the movement of major faults, active in the past 65 million years.

The Oaxacan Highlands are known as one of the most diverse areas in Mexico (Flores-Villela & Gerez, 1994; García et al., 2004), with species belonging to both Nearctic and Neotropical biotas. The sharpest differentiation in the biota of Oaxaca occurs at the Isthmus of Tehuantepec, which seems to be the north-western distributional limit of some Central American species and the south-eastern limit of some Mexican species (Goodwin, 1969; Escalante et al., 1993; Sullivan et al., 2000; Carleton et al., 2002) or, from a panbiogeographical viewpoint, a node (Morrone, 2006). Some authors (Ramírez-Pulido & Castro-Campillo, 1990; Arriaga-Cabrera et al., 1997) have recognized the Oaxaca biogeographical province, comprising parts of the Mexican states of Oaxaca, Veracruz and Puebla. Other authors have considered this area as the southernmost portion of the Sierra Madre Oriental (García-Moreno et al., 2004; Arellano et al., 2005), or part of the Trans-Mexican Volcanic Belt (Casas-Andreu & Reyna-Trujillo, 1990) or the Sierra Madre del Sur (Morrone, 2005). A cladistic

biogeographical analysis may allow a test of these alternative regionalizations and help derive a general area cladogram for understanding the biotic diversification of this area.

Cladistic biogeography searches for patterns of relationships among areas of endemism based on the phylogenetic relationships of the taxa inhabiting them (Morrone & Carpenter, 1994; Humphries & Parenti, 1999; Morrone, 2008). Interpretation of cladistic biogeographical results usually focuses on vicariance, because this process affects different taxa simultaneously (Nelson & Platnick, 1981). There are several cladistic biogeographical methods, and there is no agreement about which one is the most appropriate (Morrone, 2008). Among these methods, Brooks parsimony analysis (BPA) (Wiley, 1987; Kluge, 1988; Brooks, 1990) has been used extensively (Morrone & Carpenter, 1994; Marshall & Liebherr, 2000; Espinosa et al., 2006). Although BPA has been criticized by some authors because it uses dispersal and vicariance explanations to fit taxa and areas to the same tree (e.g. Siddall & Perkins, 2003), other authors (e.g. Brooks et al., 2001; Van Veller & Brooks, 2001) have defended it as a valid method. Nelson & Ladiges (1996) noted that when nodes and areas are associated in order to be included in a data matrix, geographical paralogy may result because of duplication or overlap in the distribution of taxa related by paralogous nodes. They implemented a program – Three Area Statements Analysis (TASS) – that identifies paralogy-free subtrees from each taxon–area cladogram analysed (Nelson & Ladiges, 1995). A parsimony analysis of these paralogy-free subtrees may thus be used to generate a more robust hypothesis, because geographical paralogy has been removed (Contreras-Medina et al., 2007).

Our goals are to evaluate whether the Oaxacan Highlands represent a natural biotic unit, applying a parsimony analysis of paralogy-free subtrees to some vertebrate taxa, and to compare our results with those of previous studies.

MATERIALS AND METHODS

Study areas

We analysed the mountain ranges of the Sierra Madre Occidental (SMOcc), Sierra Madre Oriental (SMOr), Trans-Mexican Volcanic Belt (TVB), Sierra Madre del Sur (SMS), mountains of Chiapas (CHI) and Oaxacan Highlands (Fig. 1a). In order to test the naturalness of the latter, we divided it into three different units: Sierra de Juárez (SJ), Nudo de Zempo-altépetl (Zemp) and Sierra Mazateca (Maz) (Fig. 1b).

Taxa

We analysed six vertebrate genera and species groups, selecting those with species that inhabit at least four of the areas of endemism described above, and for which there are published phylogenetic analyses: *Pseudoeurycea bellii* species group (Amphibia: Plethodontidae; Parra-Olea *et al.*, 2005), *Chlorospingus* (Aves: Thraupidae; García-Moreno *et al.*, 2004), *Habromys* (Mammalia: Rodentia; León Paniagua *et al.*, 2007), *Microtus* (Mammalia: Rodentia; Conroy *et al.*, 2001), *Peromyscus aztecus* species group (Mammalia: Rodentia; Sullivan *et al.*, 1997) and *Reithrodontomys* (Mammalia: Rodentia; Arellano *et al.*, 2005). These taxa are expected to have different life histories and dispersal strategies, so similar phylogenetic breaks may be taken as a basis for identifying vicariance events.

Cladistic biogeography

Taxonomic cladograms and distributional data of the species were used to generate taxon–area cladograms, by replacing their terminal taxa by the areas of endemism where they occur (Morrone, 2008). We used TASS (in TAX; Nelson & Ladiges, 1995) to obtain the paralogy-free subtrees (Fig. 2a–g), from which the components were coded in a data matrix (Table 1) for parsimony analysis. The data matrix (Table 1) was analysed with NONA (Goloboff, 1999) through WINCLADA (Nixon, 2002), applying multiple tree bisections and reconnections (TBR).

RESULTS

We identified seven paralogy-free subtrees: one from the *Pseudoeurycea bellii* species group (Fig. 2a), one from *Chlorospingus* (Fig. 2b), one from *Habromys* (Fig. 2c), one from

Table 1 Data matrix for the parsimony analysis of paralogy-free subtrees.

Root	000000000000000000000000000
CHI	??0011011011111000110111???
SMOcc	00????????00010000 1??????
SMS	110001?????????? 11111111???
SMOr	01011100011011101111???111
TVB	00????001010001001 11???001
Zemp	1111111110100011???????????
SJ	11????111011111111111???011
Maz	??1111000110111?????111111

Columns correspond to the components analysed (see Fig. 2). 0 = absence; 1 = presence.

CHI, Chiapas Mountains; Maz, Sierra Mazateca; SJ, Sierra de Juárez; SMOcc, Sierra Madre Occidental; SMOr, Sierra Madre Oriental; SMS, Sierra Madre del Sur; TVB, Trans-Mexican Volcanic Belt; Zemp, Nudo de Zempoaltépetl.
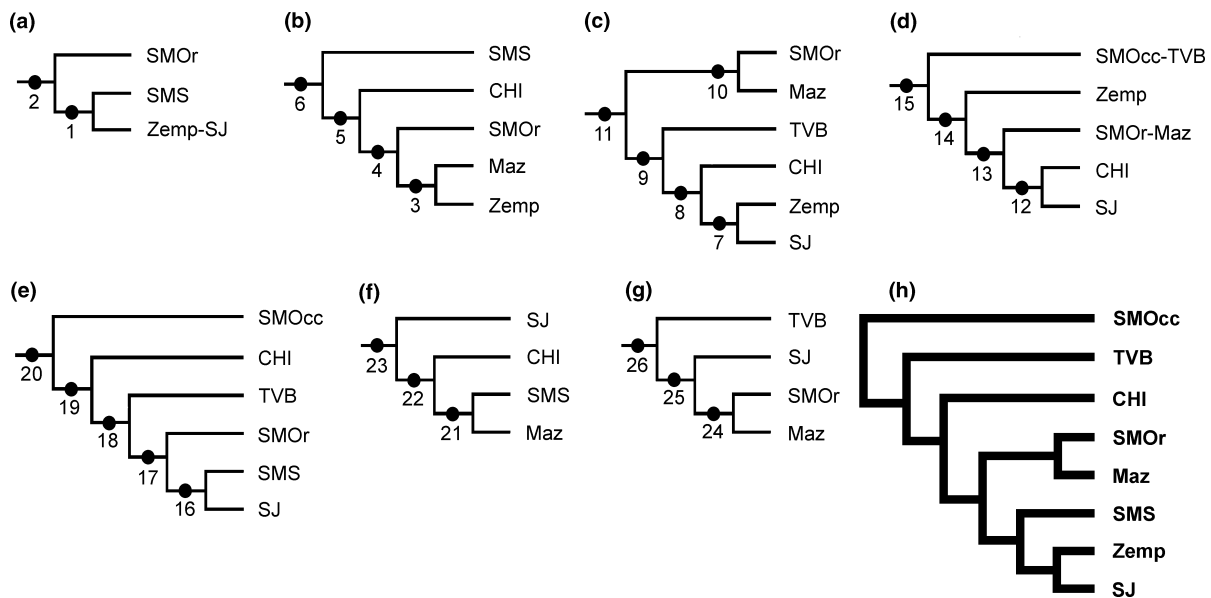

Figure 2 Paralogy-free subtrees and general area cladogram obtained: (a) *Pseudoeurycea bellii* species group; (b) *Chlorospingus*; (c) *Habromys*; (d) *Microtus*; (e) *Peromyscus aztecus* species group; (f), (g) *Reithrodontomys*; (h) general area cladogram. CHI, Chiapas Mountains; Maz, Sierra Mazateca; SJ, Sierra de Juárez; SMOcc, Sierra Madre Occidental; SMOr, Sierra Madre Oriental; SMS, Sierra Madre del Sur; TVB, Trans-Mexican Volcanic Belt; Zemp, Nudo de Zempoaltépetl.

Microtus (Fig. 2d), one from the *Peromyscus aztecus* species group (Fig. 2e) and two from *Reithrodontomys* (Fig. 2f, g). Their components were coded in a data matrix (Table 1). The parsimony analysis resulted in a single general area cladogram, with 34 steps, a consistency index of 0.76, and a retention index of 0.72 (Fig. 2h). In this general area cladogram, areas are fragmented following the sequence Sierra Madre Occidental, Trans-Mexican Volcanic Belt, Chiapas, Sierra Madre Oriental + Sierra Mazateca, Sierra Madre del Sur, Nudo de Zempoaltépetl and Sierra de Juárez.

The general area cladogram shows that the Oaxacan Highlands do not constitute a monophyletic unit. The Sierra Mazateca is the sister area to the Sierra Madre Oriental, whereas the Nudo de Zempoaltépetl and Sierra de Juárez are the sister areas to the Sierra Madre del Sur. The regionalization based on these results should recognize only two biogeographical provinces: Sierra Madre Oriental (including the Sierra Mazateca) and Sierra Madre del Sur (including the Nudo de Zempoaltépetl and Sierra de Juárez).

DISCUSSION

It is well known that within the state of Oaxaca, wide-ranging species of both Nearctic and Neotropical biotas broadly overlap. Some documented cases occur at the Isthmus of Tehuantepec (Goodwin, 1969, Escalante *et al.*, 2004; Morrone, 2006), but the sharpest differentiation in the vertebrate fauna of Oaxaca occurs in the confluence of the Sierra Madre Oriental, the Sierra Mazateca and the Sierra de Juárez. According to our general area cladogram, the Oaxacan Highlands do not represent a natural area but a mixture of at least two different biotic components, one in the Sierra Madre Oriental and the other in the Sierra Madre del Sur. Luna *et al.*'s (1999) parsimony analysis of endemicity of vascular plants from cloud forests showed similar relationships, with the Sierra de Huautla (= Sierra Mazateca) being a part of the Sierra Madre Oriental and La Chinantla (= Sierra de Juárez) being a part of the Serranías Meridionales. The events that might have caused these patterns include cycles of expansion and contraction of mountain pinyon, juniper and oak woodlands during the Pleistocene (Toledo, 1982; McDonald, 1993; Sullivan *et al.*, 1997).

The relationship between Nudo de Zempoaltépetl–Sierra de Juárez and the Sierra Madre del Sur is supported by the *Pseudoeurycea bellii* and *Peromyscus aztecus* species groups. It also agrees with Morrone (2005), who treated Arriaga-Cabrera *et al.*'s (1997) Oaxaca province as synonymous with the Sierra Madre del Sur. The relationship between the Sierra Mazateca and the Sierra Madre Oriental in our analysis is supported by the species of *Habromys* and *Reithrodontomys*. This close relationship was not supported by Luna *et al.* (1999), because they considered the Sierra de Huautla (= Sierra Mazateca) as the sister area to another area in Chiapas (El Triunfo). Nevertheless, they concluded that the relationship between the Serranías Transístmicas (basically the Sierra Madre del Sur and Chiapas) and the Sierra Madre Oriental is not clear. Additional

phylogenetic studies will allow investigation of the relationships of other interesting areas of Oaxaca in the future.

Escalante *et al.*'s (2007) cladistic biogeographical analysis of the Mexican biogeographical provinces showed an east–west split in the country, separating the lowland region of eastern Mexico along the Caribbean coastline from the remaining provinces, with the Sierra Madre Oriental constituting the eastern boundary of these provinces. This split is basically congruent with the results obtained herein. This is rather significant, because the Great American Biotic Interchange (Simpson, 1940, 1950; Stehli & Webb, 1985) does not predict it. Escalante *et al.* (2007) concluded that the biogeographical/geological divide implies that Early Tertiary geological events leading to the convergence of Neotropical and Nearctic elements in the Mexican Transition Zone may be younger (Miocene–Pleistocene) than those that led to the east–west pattern (Palaeocene). Molecular clock estimates for one of the taxa analysed herein (*Habromys*; León Paniagua *et al.*, 2007), however, indicate a Late Pliocene–Early Pleistocene age for vicariance in the area. Whether this represents a case of pseudo-congruence (different area cladograms showing the same area relationships, although the taxa diversified at different times, presumably under different underlying causes; see Donoghue & Moore, 2003) or not, may be evaluated in the future through a more detailed examination of the phylogeographical structure of the species analysed (Riddle & Hafner, 2006).

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