

## DISTRIBUTION PATTERNS OF THE AMERICAN SPECIES OF THE FRESHWATER GENUS *EUCYCLOPS* (COPEPODA: CYCLOPOIDA)

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### ABSTRACT

Based on the superposition of 19 individual tracks of American species of the freshwater copepod genus *Eucyclops*, two generalized tracks were found. The Western Amazonian track (southern Peru, eastern Brazil, and central Colombia) corresponding to the Amazonian subregion and the South American Transition Zone, and the Mesoamerican-Northwestern South American track (central Colombia, Central America, and northeastern Mexico) corresponding to the Neotropical region, the Mexican Transition Zone, and the Nearctic region. One node was found in Colombia, an area where both generalized tracks intersect. The distributional patterns of *Eucyclops* apparently involve two cenocrons: one Holarctic, and another Paleotropical. The Western Amazonian generalized track can be correlated with the existence of rivers that function either as barriers or dispersal passageways, the uplift of the Andes, and the presence of the Miocene "Pebas lake/wetland system." The Mesoamerican-Northwestern South American generalized track can be associated with climate changes resulting from the uplift of North American mountain ranges, the presence of marine barriers (Isthmus of Tehuantepec and Panama) and the uplift of mountains in southern Mexico and Central America. The closing of the marine barrier represented by the Isthmus of Panama seems to have been a key event in the northward and southward dispersal of *Eucyclops* in the Americas.

**KEY WORDS:** copepods, Cyclopinae, *Eucyclops*, generalized tracks, individual tracks, panbiogeography

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### INTRODUCTION

The freshwater copepod genus *Eucyclops* Claus, 1893 comprises 106 nominal species and subspecies (Dussart and Defaye, 2006). It is one of the most taxonomically challenging genera in Cyclopidae, containing several problematic taxa and some species groups with a high intraspecific variability. This, together with incomplete descriptions, has generated a taxonomic history that includes many species with an uncertain status (Collado et al., 1984; Reid, 1985; Ishida, 1997) and a complex taxonomy that relies on only a few relatively stable characters. The species of *Eucyclops* are divided into three subgenera: *Eucyclops* sensu stricto, which contains most of the known species; *Stygocyclops* Pleša, 1971, with a single species (*E. [S.] teras* [Graeter, 1907]) from Switzerland, and *Isocyclops* Kiefer, 1957, which includes two species endemic to Lake Tanganyika (Dussart and Defaye, 2001, 2006; Suárez-Morales, 2004). In the Americas, there are more than 800 records of the genus, corresponding to 28 nominal species, most of which are distributed in eastern United States, Mexico, Argentina, and Brazil.

Few works have analyzed the biogeographic affinities of the freshwater copepods of the New World. Menu-Marque et al. (2000) studied the species of *Boeckella* Guerne and Richard, 1889 using a track analysis. They found that their biogeographical patterns reflect the existence of an ancient Austral biota, the biotic evolution of which was influenced

greatly by the break-up of the Gondwana supercontinent, this genus is also distributed in Australia and New Zealand. Suárez-Morales et al. (2004) analyzed the distributional patterns of the cyclopoid species of the Yucatan Peninsula and suggested that it reflects post-Pliocene events, with a major Neotropical biotic influence. In a phylogenetic analysis of all known species of *Mesocyclops* Sars, 1914, Holyńska (2006) highlighted the high level of endemism of this genus in South America because of its isolation during the Cretaceous, which allowed the preservation of ancient lineages. De los Ríos et al. (2010) analyzed the distributional patterns of the Chilean cyclopoids, finding some species endemic to the Atacama and Magellanic Moorland biogeographic provinces, and others reported in several areas in South America.

Evolutionary biogeography integrates distributional, phylogenetic, molecular, and paleontological data in order to discover biogeographic patterns and assess the historical changes that shaped them (Morrone, 2009). It follows a series of steps that include: 1) identification of biotic components, which are sets of spatio-temporally integrated taxa that coexist in given areas, graphically represented as generalized tracks and areas of endemism; 2) testing relationships between biotic components, with help of cladistic biogeography, which uses information on the cladistic relationships between taxa and their geographic distribution to postulate

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hypotheses on relationships between areas; 3) regionalization, which implies the recognition of successively nested areas that allow a biogeographic classification; 4) identification of cenocrons, which are sets of taxa that share the same biogeographic history, constituting identifiable subsets within a biotic component by their common biotic origin and evolutionary history; and 5) construction of a biotic scenario, by accounting biological and non-biological data, which are used to integrate a plausible scenario to help explain the episodes of vicariance or biotic divergence and dispersal or biotic convergence (Morrone, 2009).

The recognition of biotic components, the first step of an evolutionary biogeographic analysis, can be done using the panbiogeographic approach, which emphasizes the spatial or geographic dimension of biodiversity to allow a better understanding of evolutionary processes. Morrone (2006), after a series of panbiogeographic analyses, recognized 70 biotic components in Latin America and the Caribbean region that were deemed as biogeographic provinces. These, in turn, were grouped into major biotic components considered as regions, subregions, and dominions; also, two transition zones were distinguished. These biogeographic provinces have been recognized by different authors analyzing several groups including mammals, tropical snakes, fish parasites, freshwater decapods and copepods, and terrestrial arthropods (Lopretto and Morrone, 1998; Menu-Marque et al., 2000; Márquez and Morrone, 2003; Abrahamovich et al., 2004; Escalante et al., 2004; Morrone and Márquez, 2008; Yáñez-Ordoñez et al., 2008; Rosas-Valdéz and Pérez-Ponce de León, 2008; Arzamendia and Giraud, 2009; Asian et al., 2010; Maya-Martínez et al. 2011).

Herein we analyze the geographical distribution of the species of *Eucyclops* in the Americas using a track analysis, which has been previously applied to other crustacean taxa (Morrone and Lopretto, 1994; Lopretto and Morrone, 1998; Menu-Marque et al., 2000). We identify individual and generalized tracks, in order to contribute to the knowledge of the spatial evolution of this copepod taxon.

## MATERIALS AND METHODS

### Data

Distributional data were obtained from the literature (Marsh, 1893; Juday, 1915; Kiefer, 1926, 1929, 1931, 1934, 1936, 1956; Pearse and Wilson, 1938; Osorio-Tafall, 1943; Comita, 1950; Lindberg, 1955; Robertson and Gannon, 1981; Collado et al., 1984; Dussart, 1984; Reid, 1985; Suárez-Morales et al., 1985; Dussart and Frutos, 1986; Defaye and Dussart, 1988; Zamudio-Valdez, 1991; Reid and Marten, 1995; Zannata-Juárez, 1995; Dodson and Silva-Briano, 1996; Santos, 1997; Grimaldo-Ortega et al., 1998; Suárez-Morales and Reid, 1998; Gutiérrez-Aguirre, 1999; Álvarez-Silva and Gómez-Aguirre, 2000; Elias-Gutiérrez, 2000; Fiers et al., 2000; Reeves, 2000; Barbiero et al., 2001; Ishida, 2001; Rodríguez-Almaráz, 2002; Carling et al., 2004; Suárez-Morales, 2004; Bruno et al., 2005; Frisch et al., 2005; Alekseev et al., 2006; Gaviria and Aranguren, 2007; Elías-Gutiérrez et al., 2008; Jiménez-Trejo and Vásquez-Vargas, 2008; Mercado-Salas, 2009; Suárez-Morales and Walsh, 2009; De los Ríos et al., 2010). Additional records were obtained from the collection databases

of the Smithsonian Institution-National Museum of Natural History and the zooplankton collection of El Colegio de la Frontera Sur-Unidad Chetumal, ECO-CH-Z.

For some records lacking geographical data, localities were geo-referenced with the aid of Google-Earth. Other species, including *Eucyclops macrurus* (Sars, 1863), *E. neotropicus* Kiefer, 1936, *E. ariguanabaensis* Brehm, 1948, *E. chilensis* Löffler, 1961 (Menu-Marque and Locascio, 2011), *E. siolii* Herbst, 1962, *E. breviramatus* Löffler, 1963, *E. neomacruroides* Dussart and Fernando, 1990, *E. borealis* Ishida, 2001, and *E. cuatrocieneegas* Suárez-Morales and Walsh, 2009 have been cited for a single locality each. These records do not provide relevant information for the track analysis and were thus excluded. The records of *E. pectinifer* (Cragin, 1883), *E. serrulatus* (Fischer, 1851), and *E. agilis* (Koch, 1838) were a priori treated as referring to a single species, following Alekseev et al. (2006). *Eucyclops agilis* has been considered as a valid species by several authors in the Americas, but its original description is not accurate enough to consider it as a valid species; it is currently recognized as a synonym of *E. serrulatus* (Alekseev et al., 2006). *Eucyclops serrulatus* is distributed in North Africa, the Mediterranean region, Europe, Russia, and probably also in Central Asia. Records of the species in the Americas should be carefully reexamined before assigning them to the American form *E. pectinifer*, because some of them could belong in fact to *E. serrulatus*. According to Alekseev (personal communication to NFM-S, 2011) the latter may have been introduced in the Americas by human agency, other records could be *E. pectinifer* or even undescribed species. Records of *E. speratus* (Lilljeborg, 1901), *E. elegans* (Herrick, 1884), and *E. solitarius* (Herbst, 1959) were merged into a single species, following Reid and Marten (1995). After this process we obtained a database of 446 records for *E. pectinifer*, *E. delachauxi* (Kiefer, 1925), *E. silvestri* (Brian, 1927), *E. neumani neumani* (Pesta, 1927), *E. prionophorus* Kiefer, 1931, *E. bondi* Kiefer, 1934, *E. ensifer* Kiefer, 1936, *E. festivus* Lindberg, 1955, *E. leptacanthus* Kiefer, 1956, *E. alticola* Kiefer, 1957, *E. neumani titicacae* Kiefer, 1957, *E. demacedoi* Lindberg, 1957, *E. serrulatus montanus* Harris, 1978, *E. subciliatus* Dussart, 1984, *E. pseudoensifer* Dussart, 1984, *E. conrowae* Reid, 1992, *E. torresphilipi* Suárez-Morales, 2004, *E. chihuahuensis* Suárez-Morales and Walsh, 2009, and *E. elegans*.

### Methods

Panbiogeography is an approach originally proposed by Croizat (1958, 1964), that aims to analyze the spatial and temporal distribution patterns of organisms based on a correlation between the history of the biota and the history of the Earth. The panbiogeographic approach is based on three basic concepts: 1) the individual track, which represents the spatial coordinates of the taxon in space (the geographical area in which its evolution has taken place), operationally corresponding to a line that connects localities where a species or supraspecific taxon is distributed; after these tracks are constructed, their orientation or direction can be determined using a baseline (geological feature such as an ocean or sea basin, or other major tectonic structure, crossed by the track), main massing (a concentration of

numerical, genetical or morphological diversity within a taxon in a given area), or phylogenetic evidence available (directing the track from the most primitive to the most derived taxa); 2) the generalized track, which is the distribution pattern obtained from the overlapping of at least two individual tracks, indicates the existence of a shared biogeographic history of the biota and the areas involved; and 3) the node, which is a complex area where two or more generalized tracks superimpose and are usually interpreted as a tectonic/biotic convergence area (Morrone, 2009). For details of the panbiogeographic methodology see Morrone and Crisci (1995) and Morrone (2009).

To perform the panbiogeographic analysis, individual databases were made for each species. Individual tracks were obtained by using ArcView GIS 3.2 software and the extension Trazos 2004 (Rojas, 2004); generalized tracks were obtained superimposing the individual tracks. The biogeographical system used in this work follows Morrone (2006).

## RESULTS

We obtained 19 individual tracks (Figs. 1 and 2). Ten species are restricted to South America, one is exclusive to Cuba, and seven species are restricted to North America. Mexico is the country with most species recorded (12), followed by Colombia (7), Brazil, the United States, Venezuela, and Ecuador (6), Argentina and Peru (4), Chile, Canada, Nicaragua, and Paraguay (3), Uruguay, Bolivia, and Cuba (2), and Haiti, Jamaica, Costa Rica, Honduras, and French Guiana (1). Considering the biogeographic regions and transitional areas recognized for the Americas (Morrone, 2006), the Neotropical region shows the highest number of species recorded (18), with *E. demacedoi*, *E. neotropicus*, *E. siloi*, *E. neumani neumani*, and *E. silvestri* being endemic to it. The Nearctic region is the second in species richness with 14 species, with *E. macrurus*, *E. cuatrociene-gas*, *E. borealis*, and *E. agilis monticola* being Nearctic endemics. The third richest area is the Mexican Transition Zone, with 10 species, none of them endemic. The South American Transition Zone has seven species, *E. brevira-matus* being the only endemic. Finally, the Andean region includes only two species (*E. pectinifer* and *E. ensifer*), widespread in other regions as well. *Eucyclops pectinifer* is the most widely distributed species, found in all the regions and transition zones.

Based on the superposition of the individual tracks, two generalized tracks were found (Fig. 2):

1) Western Amazonian track: southern Peru, eastern Brazil, and central Colombia. It corresponds to the Amazonian subregion (Pantanal, Madeira, Napo, Imeri, and Venezuelan Llanos biogeographic provinces) and the South American Transition Zone (Puna province). Species and subspecies supporting this track are *E. alticola*, *E. demacedoi*, and *E. neumani titicacae*.

2) Mesoamerican-Northwestern South American track: central Colombia, Central America, and northeastern Mexico. It corresponds to the Neotropical region, the Mexican Transition Zone, and the Nearctic region, in the Venezuelan Llanos, North Andean Paramo, Magdalena, Cauca, Choco, Eastern Central America, Western Panamanian,

Mexican Pacific Coast, Chiapas, Sierra Madre del Sur, Balsas Basin, Transmexican Volcanic Belt, Sierra Madre Occidental, and Mexican Plateau biogeographic provinces. The species supporting this track are *E. bondi*, *E. chihuahuensis*, *E. delachauxi*, *E. festivus*, *E. leptacanthus*, *E. pseudoensifer*, and *E. torresphilipi*.

One node was found in Colombia (Neotropical region), in the area where both generalized tracks intersect.

## DISCUSSION

The knowledge of the diversity of the American species of *Eucyclops* is still growing; several species have been described recently from different environments. In South America, many species with a restricted distribution were described from explorations performed between 1920 and 1990 (Kiefer, 1926, 1929, 1931, 1934, 1936, 1956; Lindberg, 1955; Dussart, 1984; Reid, 1985; Dussart and Frutos, 1986; Defaye and Dussart, 1988). In North America, the distribution of several species that were previously considered cosmopolitan, e.g., *E. serrulatus* and *E. pseudoensifer*, was reevaluated, revealing some new species, probably with restricted distribution; this suggests that the diversity of the genus may be underestimated (Reid, 1992; Suárez-Morales, 2004; Alekseev et al., 2006; Suárez-Morales and Walsh, 2009). In Central America, the knowledge about this genus is still quite limited because surveys in the area are relatively scarce (Suárez-Morales, 2004; Alekseev et al., 2006; Suárez-Morales and Walsh, 2009).

The distributional patterns of *Eucyclops* involve two cenocrons (sensu Morrone, 2009): one Holarctic and the other Paleotropical. The species of the Holarctic cenocron have dispersed to the Americas by the Thulean bridge (connecting North America and Europe) and the Beringian bridge (connecting North America and eastern Asia) that existed in the early Eocene when weather conditions were warmer and wetter (San Martín et al., 2001; Wyngaard et al., 2009). The individual track of *E. pectinifer* (Fig. 1) supports this hypothesis, as the species complex to which it belongs occurs in Eurasia. According to Alekseev et al. (2006), *E. serrulatus* is distributed in North Africa, the Mediterranean region, Europe, Russia, and probably extends to Central Asia. The ancestor of *E. pectinifer* may have dispersed to North America and then spread southwards. There is a disjunction between North and South America, as there are no records of this species in Central America, linking the individual track from southern Mexico (near the borderline with Guatemala and Belize) with the Galapagos Islands. A similar connection through the Galapagos has been described for other organisms such as the staphylinid beetle genus *Rothium* (Grehan, 2001). Croizat (1958) considered the Galapagos Islands as a node that includes the intersection of three tracks. He predicted that the line of the west coast of America to the Galapagos previously included and extended to Chile and Hawaii. Pacific tracks identified by Croizat constitute evidence of geological connections with East Asia, which resulted in a composed origin of North and South America, though the union of lands in the Pacific, Gondwana, and Laurasia. Grehan (2001), based on panbiogeographic and geological evidence, considered that at least some elements of the Galapagos biota have derived

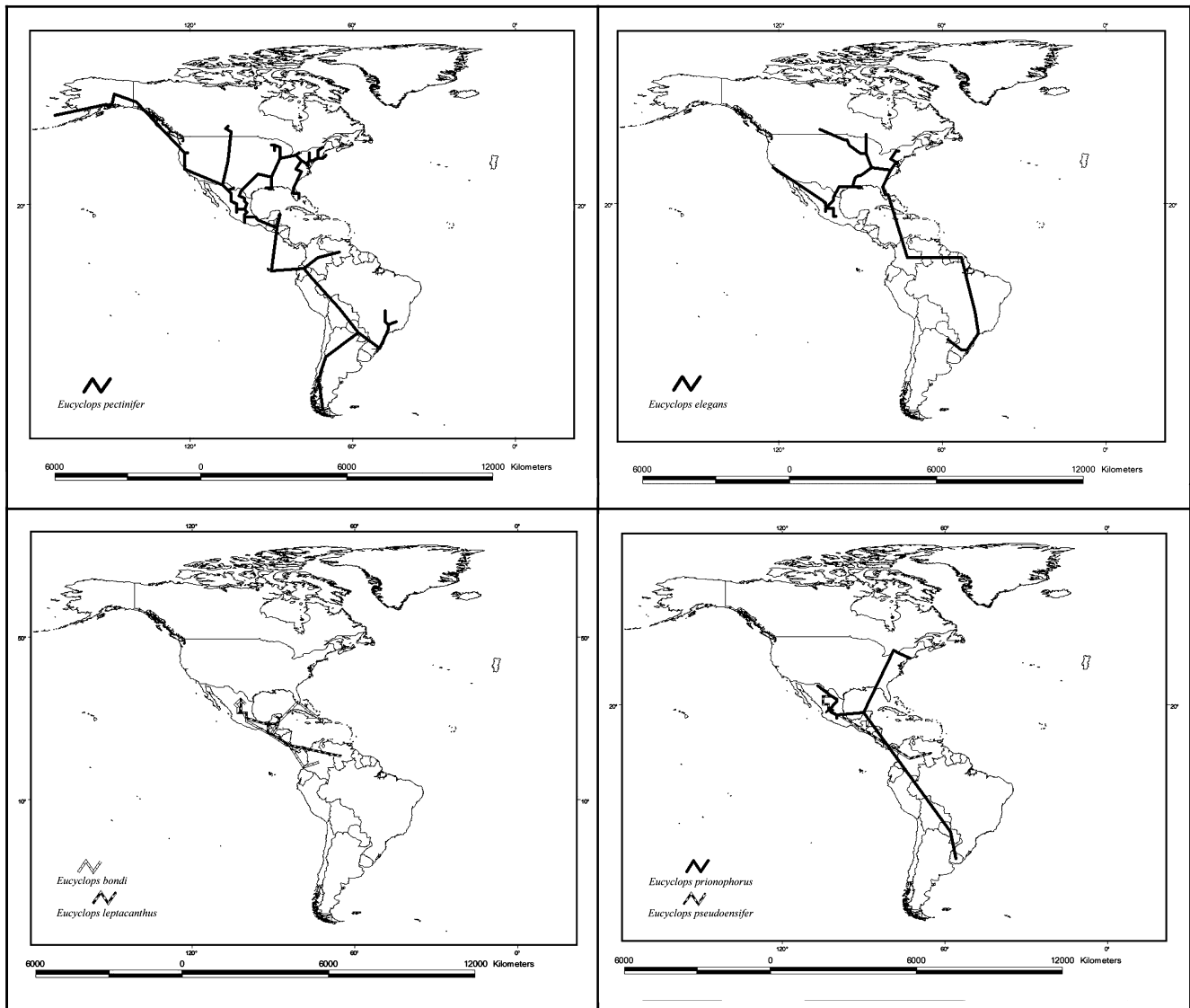


Fig. 1. Individual panbiogeographic tracks of American species of *Eucyclops*. *Eucyclops pectinifer*, *E. elegans*, *E. bondi*, *E. leptacanthus*, *E. prionophorus*, *E. pseudoensifer*.

from the Pacific Islands biota that were in contact with the Galapagos Islands, and then moved eastward to finally crash with North or South America.

Ancestors of the South American *Eucyclops* evolved in the Afro-Brazilian tropical fragment of Gondwana and diverged following its breakup in the Cretaceous. This has been proposed by Banareescu (1992), Suárez-Morales et al. (2005), Hotońska (2006), and Wyngaard et al. (2009) for other copepods, such as calanoids (Boeckellidae and Diaptomidae, considered to represent ancient freshwater lineages) and the cyclopoid genus *Mesocyclops*. Most of the species of *Eucyclops* are distributed in Africa, Central and Southern Asia, Australia, South America, and Mexico, supporting the hypothesis that the origin of the genus is in the Afro-Brazilian tropical fragment of Gondwana. This hypothesis is also supported if we consider the main massing concept (center of great diversity), because the distribution of most species of *Eucyclops* in the Americas extends from northern-

central Mexico through Colombia, representing 42% of the species (see individual tracks of *E. bondi*, *E. leptacanthus*, *E. pseudoensifer*, *E. torresphilipi*, *E. prionophorus*, *E. ensifer*, *E. conrowae*, and *E. serrulatus montanus*), and five species have north-south tracks within South America (*E. alticola*, *E. neumani titicacae*, *E. demacedoi*, *E. silvestri*, and *E. neumani neumani*).

The proximity of the individual tracks of *E. neumani neumani*, *E. subciliatus*, *E. elegans*, *E. pectinifer*, and *E. silvestri* in the vicinity of northeastern Argentina and southern Brazil (Chaco, Pampa, and Parana Forest biogeographic provinces) can be related to the separation of the Paraguay and Paraná rivers from the Amazonas basin. Castellanos (1965) postulated that the Paraguay River was a former tributary of the Amazon River, and then splitted when the Andean orogeny created an area of fracture where the Paraguay and Parana rivers currently flow, thus changing its drainage to the La Plata Basin, and acting as a vicariant event separating the

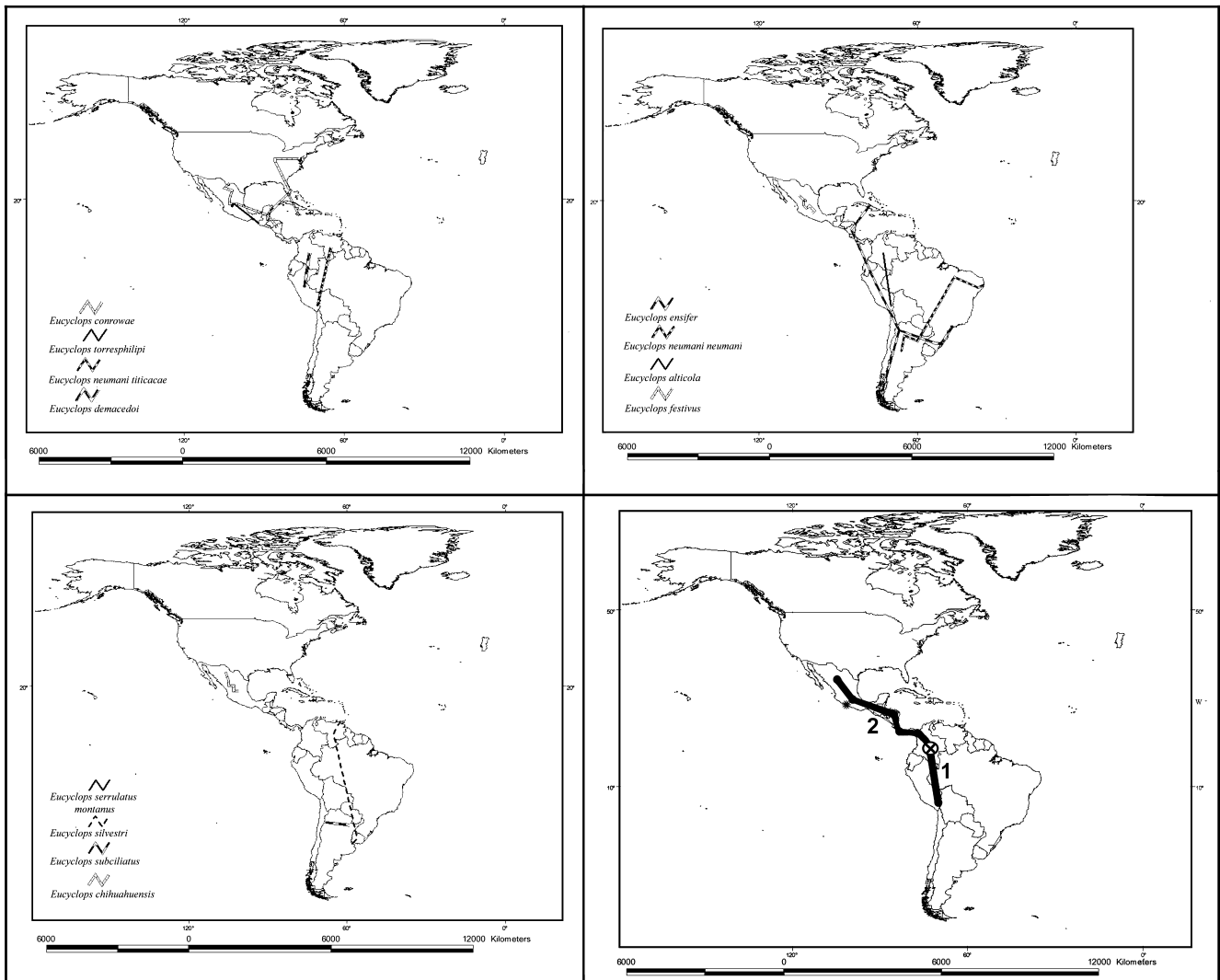


Fig. 2. A-C, Individual panbiogeographic tracks of American species of *Eucyclops*. *Eucyclops conrowae*, *E. torresphilipi*, *E. neumani titicacae*, *E. demacedoi*, *E. ensifer*, *E. neumani neumani*, *E. alticola*, *E. festivus*, *E. serrulatus montanus*, *E. silvestri*, *E. subciliatus*, *E. chihuahuensis*. Generalized tracks: 1) Western Amazonian; 2) Mesoamerican-Northwestern South American. The circle with the "x" represents the node.

Amazon and La Plata biotas. The Chaco and Pampa biogeographic provinces belong to the Chacoan subregion, which includes the Caatinga Province, where the oldest copepod fossil was found (*Kabatarina pattersoni*, a parasite of a teleost fish from the late Cretaceous about 69 m.y.a.) (Huys and Boxshall, 1991; Lange and Schram, 1999).

The Western Amazonian track is defined by the exclusive presence of three species, *E. alticola*, *E. demacedoi*, and *E. neumani titicacae*. It is localized mainly in the Amazonian subregion, the largest of the Neotropical subregions. The history of the Amazonian biota has been reconstructed differently by different authors. One of the first explanations was provided by Wallace (1852), who considered that the rivers of the Amazonian basin acted as barriers. Contrariwise, Arzamendia and Giraud (2009) recently considered the rivers as dispersal corridors for snake species. Antonelli et al. (2009) suggested that the uplift of the tropical Andes in the Neogene strongly affected the history of South America, changing the course of the Amazon River from a

northwestwards flow to the modern pattern flowing to the Atlantic. This event changed the climate of the region by forming the only barrier to atmospheric circulation in the Southern hemisphere. Wesseling (2006) proposed another explanation, who based his theory on the Miocene "Pebas lake/wetland system," viz., a shallow system of lakes and wetlands that straddled the Equator in western Amazonia between 9 and 23 m.y.a. This system resulted from the uplift of the eastern Cordillera in the Central Andes that caused the western Amazonia to become flooded. The inland sea thus formed acted as a barrier between the Andes and lowland Amazonia. Aquatic conditions seem to have persisted in western-central Amazonia until 7 m.y.a., when the modern Amazon system came into existence; this event could represent the vicariant event associated with the Western Amazonian track.

If divided into two sectors, the Mesoamerican-Northwestern South American generalized track can be compared to that found for other taxa. The northern part in-

cludes mainly the Mexican Plateau and part of the Sierra Madre Occidental biogeographical provinces, and agrees with the Mexican Mountain general track proposed by Abrahamovich et al. (2004) for hymenopteran insects and the western part of the northern Mexican generalized track proposed by Rosas-Valdéz and Pérez-Ponce de León (2008) for helminth parasites of ictalurid fishes. It covers almost all arid areas of north-central Mexico, formed between the Late Oligocene and Middle Miocene, and was part of a general trend toward greater aridity resulting from climate change associated to intense volcanic activity and tectonics of the Cenozoic, when the Rocky Mountains, the Mexican and Central-American Plateaus, and the Sierras Madre were formed. The formation of the Sierra Madre Occidental and Sierra Madre Oriental during the Eocene and up until the middle Miocene provided a new barrier to the atmospheric flow, blocking the masses of warm, moist air from the Pacific Ocean and the Gulf of Mexico, and causing a severe drought and aridity in the Mexican Plateau. The Miocene climate change segregated the species along latitudinal and longitudinal gradients, thus favoring radiation processes in some lineages (Devitt, 2006). It has been suggested that some areas (such as Cuatro Ciénegas in Coahuila) functioned as refugia during the Pleistocene glaciations (Banarescu, 1992). The southern part of this portion includes the intersection between the Balsas Basin, Transmexican Volcanic Belt, and Sierra Madre del Sur biogeographic provinces, where nodes were identified for arthropods (Morrone and Márquez, 2008; Yáñez-Ordóñez et al., 2008) and mammals (Escalante et al., 2004). This pattern agrees with the Mesoamerican generalized track found by Asiain et al. (2010) for beetles of the genera *Agrodes* and *Plochionocerus*. It also coincides with the Meridional distribution pattern of Maya-Martínez et al. (2011), based on Charaxinae, the Southern Mesoamerican track found by Abrahamovich et al. (2004) for species of *Bombus*, the Septentrional Mesoamerican and Meridional Mesoamerican generalized tracks described by Márquez and Morrone (2003) for the staphylinids *Heterolinus* and *Homalolinus*, and also with the Southern generalized track of Morrone and Márquez (2001), based on beetles. These authors postulated different vicariant events, which occurred in different periods of time, including the development of the marine barrier of the Isthmus of Tehuantepec, the emergence of the mountains in Chiapas, Guatemala, Honduras, and Nicaragua, the development of the Nicaraguan lowlands, and the highlands of Costa Rica and Panama, and finally the development and closure of the marine barrier represented by the Isthmus of Panama. The intrusion of copepod species into Mexico from the south has been associated with the Usumacinta basin, mainly by the development of rivers and terraces in the Pleistocene (Gutiérrez-Aguirre and Suárez-Morales, 2001).

The node found in this study appears to be the result from the mixture of Nearctic and Neotropical biotas after the closure of the Panama Isthmus, when the connection of the two subcontinents was consolidated. As already stated (Menu-Marque et al., 2000), it is important to emphasize that biogeographic patterns are the consequence not only of vicariant events, but dispersal and/or extinction processes.

We attempted herein to clarify the distribution of American freshwater copepods using a panbiogeographic approach and covering a wide geographical area. We recognized some of the biogeographic provinces proposed by Morrone (2006), but there are still many unexplored regions. Of course, more detailed local and regional records would allow a better understanding of the history and evolution of the group. A morphological study of the species of *Eucyclops* in Mexico is now being conducted in order to correctly define the species boundaries and clarify their distributional patterns. This study will serve as a platform to define the taxonomic status of the species of *Eucyclops* in the Americas and their distributions, which will be analyzed in subsequent papers.

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