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ARTICLE

Historical biogeography and distribution of the freshwater cyclopine copepods (Copepoda, Cyclopoida, Cyclopinae) of the Yucatan Peninsula, Mexico

Eduardo Suárez-Morales^{1,2*}, Janet W. Reid³, Frank Fiers⁴ and Thomas M. Iliffe⁵

¹El Colegio de la Frontera Sur (ECOSUR), Chetumal, Quintana Roo, Mexico, ²National Museum of Natural History, Smithsonian Institution, Washington, DC, USA, ³Virginia Museum of Natural History, Martinsville, VA, USA, ⁴Royal Belgian Institute of Natural Sciences, Invertebrate Section, Brussels, Belgium and ⁵Department of Marine Biology, Texas A&M University at Galveston, Galveston, TX, USA

ABSTRACT

Aim To determine and analyse the distribution of the freshwater cyclopine copepod fauna of the Yucatan Peninsula (YP) and its relationship with the geological and climatic history of this Neotropical karstic zone.

Location The Yucatan Peninsula, Mexico.

Methods Plotting of georeferenced sites, analysis of local and regional geological and climatic history, analysis and comparison of regional and local faunistic records.

Results Distinct dispersal and/or vicariant processes seem to be linked to the current distributions of the seven genera known in the YP. In general, the endemic hypogean or benthic crevicular forms (i.e. *Diacyclops chakan*, *D. puuc* and *Mesocyclops chaci*), derived from epigeal, tropical, widely distributed forms (some of them South American) may have been among the earliest colonizers of the subterranean habitats in the YP. The distribution of these and other endemic forms seem to be related to the Holocene dry periods that desiccated the largest bodies of water and isolated local populations of different species. These vicariant processes resulted in forms with restricted distributional areas; some of these formed sister species that speciated in geographically close localities but related to a common identifiable ancestor. Overall, the processes of cyclopine colonization of the YP show the influence of the South American fauna, as the closest relatives of some species endemic to the YP are South American forms; the Nearctic influence is low. The cyclopine fauna of the YP is formed by a mixture of Nearctic-derived (species of *Acanthocyclops*), Neotropical (i.e. *M. edax*, *M. longisetus*, *A. panamensis*, *Thermocyclops inversus* and *T. tenuis*), and epigeal and hypogean endemic forms. The highly dynamic geomorphology of the YP and the recent climatic changes in the Holocene define the YP as a peculiar subregion that harbours a diverse fauna of cyclopine copepods with a high endemism.

Main conclusion The current distribution of cyclopine copepods reflects relatively recent, post-Pliocene biogeographical patterns; probably older patterns are involved as well. The eastern coast of the Yucatan is the most recently colonized by cyclopine copepods. Most of the genera are linked with South American forms, and the Nearctic influence is weakly represented. This group has no marine relatives, but there is evidence of vicariant events involving cave-dwelling forms.

Keywords

Limnology, distributional patterns, freshwater biogeography, karstic environments, zooplankton.

*Correspondence: Eduardo Suárez-Morales, El Colegio de la Frontera Sur (ECOSUR), Km. 5.5. Av. Centenario, Chetumal, Quintana Roo 77000, Mexico. E-mail: esuarez@ecosur-qroo.mx

INTRODUCTION

The Yucatan Peninsula (YP), a neotropical karstic plain in south-east Mexico has been the source of many relevant faunistic discoveries, most of them related to the anchialine caves (Iliffe, 1992; Suárez-Morales & Rivera-Arriaga, 2000). Evidence provided by previous faunistic surveys in the YP (Wilkens, 1982; Holsinger, 1986; Schmitter-Soto, 1998) suggests that different vicariant and dispersal processes occurred during the palaeogeographical history of the Yucatan plain and adjacent zones. Basically, stranded marine forms remained isolated after the marine transgression/regressions episodes and became adapted to anchialine or epigeic conditions thus forming an interesting faunal assemblage (see Danielopol *et al.*, 2000). However, not all the karstic or the hypogean invertebrate fauna in the YP can be related to a marine ancestor (Suárez-Morales, 2003). The processes by which the strictly freshwater forms spread in the YP remain practically unstudied (Schmitter-Soto, 1998).

With more than 700 species known, cyclopoids are one of the most conspicuous and diverse group of freshwater copepods (Boxshall & Jaume, 2000). Cyclopoids tend to have wide distributional patterns and include many species regarded as cosmopolitan; it is recognized now, however, that cosmopolitanism among the freshwater cyclopoids is not as common as was thought a few decades ago (Reid, 1998b).

Continental cyclopoid copepods are represented by the family Cyclopidae, divided into two subfamilies, Cyclopinae and Eucyclopinae. Only the first family, of which seven genera and more than 20 species are present in the YP, are examined herein. The YP cyclopine copepods have been surveyed by several authors (see Fiers *et al.*, 1996, 2000; Suárez-Morales *et al.*, 1996; Suárez-Morales & Rivera-Arriaga, 2000; Elías-Gutiérrez *et al.*, 2001); the earliest taxonomic accounts were published in the first decades of the 1900s (Wilson, 1936; Pearse & Wilson, 1938). An updated, revised list of the YP freshwater copepods, including the Cyclopinae was recently assembled by Suárez-Morales & Reid (2003). This subfamily contains relatively diverse genera with world-wide distributions and distinct biogeographical affinities (i.e. *Acanthocyclops*, *Diacyclops*, *Mesocyclops* and *Thermocyclops*) and with taxonomic problems that are being solved by world-wide or regional revisions: Einsle (1996) for *Acanthocyclops*, Stoch (2001) for *Diacyclops*, Mirabdullayev *et al.* (2003) for *Thermocyclops*, and Holynska (2000), Suárez-Morales & Gutiérrez-Aguirre (2001) and Holynska *et al.* (2003) for the Australasian region, the Mexico-Central America subregion, and the world species of *Mesocyclops*, respectively.

Overall, the YP harbours a high number of endemic species of freshwater cyclopoid copepods (Suárez-Morales & Reid, 2003), only comparable with the endemic fauna of the entire insular Caribbean, presumably with more adequate conditions for isolation and speciation processes. In this work we analyse the currently known distributions of the 23 species of cyclopine cyclopoid copepods recorded in the YP and its possible relationships to the different events involved in the geological history of the peninsula.

STUDY AREA

The Yucatan Peninsula is a karstic plain with a complex geological history linked in many ways with that of the Caribbean and Central America (Iturralde-Vinent & MacPhee, 1999). The oldest rocks known in the YP date from the Palaeozoic. The YP has been influenced by episodes of marine regressions and transgressions of variable extent. The entire YP was submerged during the Lower and Upper Cretaceous (Weyl, 1966, 1980). A regression uncovered part of the YP (the central core) in the Palaeocene–Eocene, but another complete transgression occurred in the middle Eocene, followed by an incomplete regression in the Upper Eocene that left the northern and part of the western sections submerged. The same general pattern continued in the Upper Oligocene–Lower Miocene: the northern (mainly) and western coastline fringes of the YP were covered by the sea, and the eastern coast remained emerged. The sea advanced in the Middle and Upper Miocene and the early Pliocene, covering the eastern coast and turning the Laguna of Chichankanab into an arm of the sea (Weyl, 1966, 1980; López-Ramos, 1975). The current littoral perimeter of the YP was reached during the Late Pliocene–Pleistocene (López-Ramos, 1975) with interglacial fluctuations; the main regression started in the Early Pliocene. The Holocene period was marked in the YP and adjacent areas by successive climate changes with at least two extremely dry periods, one c. 8000–7000 yr BP during which most major surface basins, including Chichankanab, dried; and the other between 6000–5000 yr BP (Metcalf *et al.*, 2000; Curtis *et al.*, 2001). The current knowledge about the physical and chemical characteristics of the sinkholes is still very limited (Cervantes-Martínez *et al.*, 2002); hence, these factors were not evaluated herein.

METHODS

Zooplankton samples were collected at 45 different localities that included all three Mexican states (Campeche, Yucatán and Quintana Roo) in which the YP is divided. Details on the geographical location, physiographical characteristics and specimens examined in most of these localities can be found in Suárez-Morales *et al.* (1996) and Fiers *et al.* (1996, 2000). Samples were collected using different methods including surface trawls of a standard plankton net (mesh size: 0.150 mm) in the limnetic zone, traps and a hand-net in near-shore samplings. Additional records and localities were obtained from the early surveys of the Yucatan aquatic fauna by Wilson (1936) and Pearse & Wilson (1938). Other, previously unpublished records were obtained from the collection in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; from the data base of the Colección de Zooplankton held in El Colegio de la Frontera Sur (ECOSUR) in Chetumal, Mexico; and from unpublished personal observations. Most localities were georeferenced and distribution maps were prepared using these data (Fig. 1). Therefore

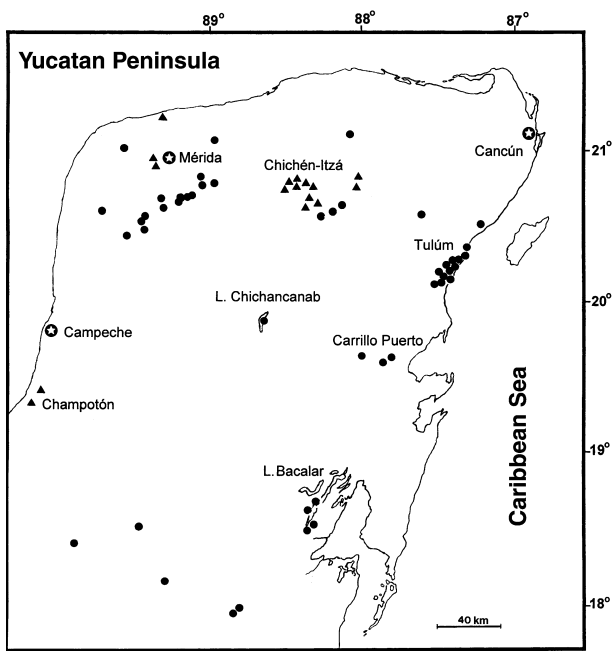


Figure 1 Map of the Yucatan Peninsula showing the localities from which cyclopine copepods have been collected. Dots indicate samples or data from recent sources (Fiers *et al.*, 1996, 2000; Suárez-Morales *et al.*, 1996), whereas triangles represent localities samples by the earliest expeditions to the Yucatan (Wilson, 1936; Pearse & Wilson, 1938).

each individual site was marked to show the distributional patterns depicted herein.

RESULTS AND DISCUSSION

Up to 23 species of cyclopine copepods have been recorded in the YP: *Acanthocyclops rebecca* Fiers, 2001; *A. robustus* (G.O. Sars, 1863); *A. smithae* Reid & Suárez-Morales, 1999; *Apocyclops panamensis* (Marsh, 1919); *Diacyclops bernardi* (Petkovski, 1986); *D. chakan* Fiers & Reid, 1996; *D. ecabensis* Fiers & Ghenne, 2000; *D. pilosus* Ghenne & Fiers, 2000; *D. puuc* Fiers, 1996; *Mesocyclops chaci* Fiers, 1996; *M. edax* (S.A. Forbes, 1891); *M. longisetus* s.str. (Thiébaud, 1912); *M. longisetus curvatus* Dussart, 1987; *M. pescei* Petkovski, 1986; *M. reidae* Petkovski, 1986; *M. yutsil* Reid, 1996; *Microcyclops ceibaensis* (Marsh, 1919); *M. dubitabilis* Kiefer, 1934; *M. pilosus* Fiers & Ghenne, 2000; *M. rubellus* (Lilljeborg, 1901); *Neutrocyclops brevifurca* (Lowndes, 1934); *Thermocyclops inversus* Kiefer, 1936; and *T. tenuis* (Marsh, 1909) (Suárez-Morales & Reid, 2003). The general distribution of these species in the YP is presented in Figs 2–6.

Some of the species show a wide distribution, occurring in different areas of the YP (i.e. *M. reidae*, *M. longisetus curvatus* and *T. inversus*), whereas others have more restricted ranges and some are considered to be endemics (i.e. *A. rebecca*, *M. yutsil*, *M. chaci*, *D. puuc*, *D. pilosus*, *D. ecabensis* and *Microcyclops pilosus*) (see Fiers *et al.*, 1996, 2000). Most of the species recorded are epigeal or planktonic forms, whereas

some others have been collected only in hypogean or benthic crevicular environments (*M. yutsil*, *M. chaci*, *D. chakan*, *D. puuc*).

Analysis of the genera

Acanthocyclops

This is a widely distributed genus; species of *Acanthocyclops* occur in temperate and subarctic Eurasia and North America (NA) and also in southern South America (SA) (Einsle, 1996). Three species of this genus have been recorded in the YP. One of them, *A. robustus*, is a widely distributed form in the region; it has been found in different zones of Mexico (Reid, 1990; Suárez-Morales & Reid, 1998) but only in one site of the Yucatan. The other two species seem to have a more restricted distributional range; *A. rebecca* has been found at only one site, in the Calakmul area, at the base of the YP (see Fig. 2a) (Fiers *et al.*, 2000), whereas *A. smithae*, found in an area adjacent to the inner coastline of Chetumal Bay (Fig. 2c), is known also from Honduras and is possibly present in Cuba (Reid & Suárez-Morales, 1999). Both *A. rebecca* and *A. smithae* are members of the taxonomically complex *A. vernalis-robustus* clade (Suárez-Morales & Reid, 1998; Fiers *et al.*, 2000). This genus may have invaded Mexico from the Nearctic region; *A. robustus* or a closely related ancestral member of the *vernalis-robustus* clade could have colonized southern Mexico and the emerged lands of the Yucatan by dispersing from temperate areas of NA. The wide distribution of *A. robustus* in Mexico (Suárez-Morales & Reid, 1998) and the absence of both this species and the genus from lower Central America (CA) and northern SA, suggests that this ancestral form could have been present in southern Mexico and the YP area as early as the Palaeocene, when northern and central Mexico were connected and CA was isolated. Therefore, this species, and probably the genus as a whole, had intermittent local dispersal events between marine transgressions when the YP land emerged, but it did not disperse farther southwards into CA.

Acanthocyclops rebecca occurs in the oldest area of the YP, one that was connected for a longer time with Central Mexico and the rest of NA. This species has a clear morphological similarity to *A. robustus* (Fiers *et al.*, 2000); populations of an epigeal, widespread form related to the *A. robustus-vernalis* clade might have reached the YP base even as early as the Palaeocene and underwent local extinctions with the succeeding transgressions. It is likely, however, that this epigeal form (*A. rebecca*) is a result of a more recent process of isolation by the extremely dry holocenic climatic periods during which the largest bodies of water desiccated (Leyden *et al.*, 1993; Hodell *et al.*, 1995), thus isolating the aquatic populations (Schmitter-Soto, 1998) and favouring sympatric local vicariant processes.

The presence of *A. smithae* on the western coast of Chetumal Bay, a coastal system that was formed recently, during the Middle Holocene (Seele, 1993) and acquired its final form c. 5000 yr BP (Olivera-Gómez, 2002), seems to indicate that its

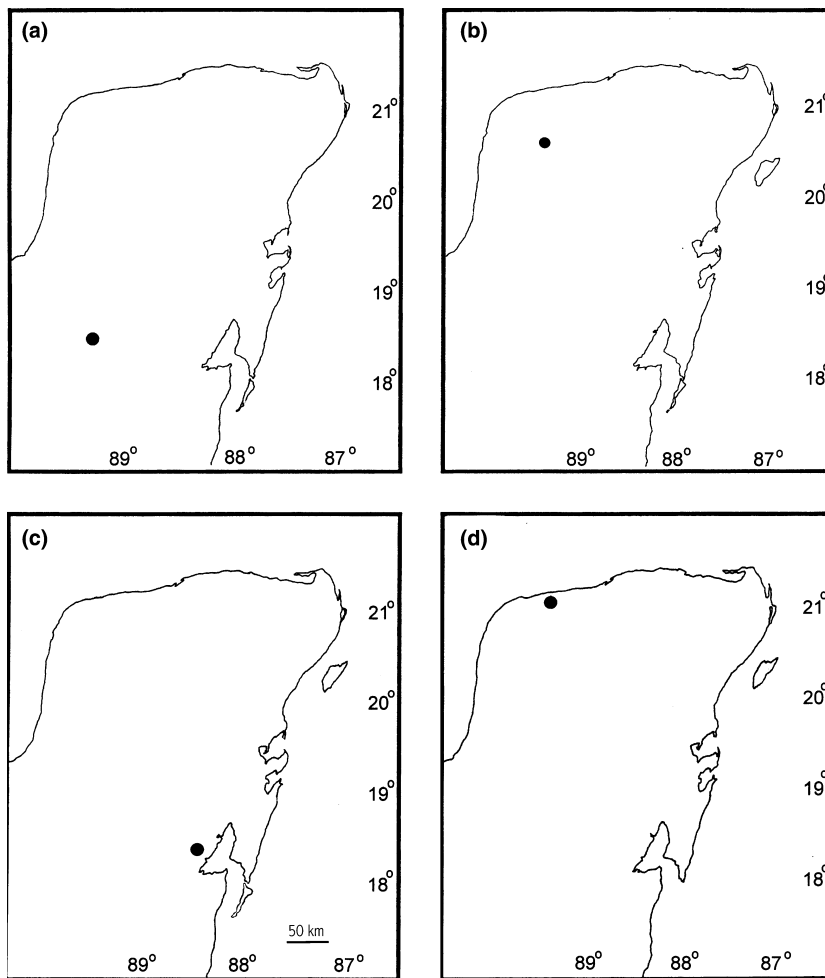


Figure 2 Distribution of the freshwater cyclopine copepods collected in the Yucatan Peninsula. (a) *Acanthocyclops rebecca*; (b) *A. robustus*; (c) *A. smithae*; (d) *Apocyclops panamensis*. Distribution is represented by individual positive localities.

arrival in the Yucatan is relatively recent. This species is also related to the *vernalis-robustus* clade, and it probably represents the result of an isolation vicariant process similar to that described for *A. rebecca* (Fig. 7).

Dispersing forms of temperate nearctic *Acanthocyclops* may have invaded the Yucatan at least twice, once during the earliest stages of the development of the YP, as part of the Central Mexico passage to nuclear Central America (starting in the Palaeocene and ending in the middle Eocene with the complete marine transgression in the YP). Stock populations were widely distributed in central and southern Mexico, which remained connected with NA and uncovered by the sea since the late Palaeozoic, a long time before the re-emergence of the Yucatan plain. The Upper Eocene–Oligocene regression allowed a second, relatively recent invasive event of the *Acanthocyclops* clade with a retreat from the eastern coast during the Middle and Upper Miocene transgression. A new dispersion might have occurred in the Upper Pliocene after the emergence of areas that were submerged in the early Pliocene. The fact that the only two true neotropical forms of the genus are present in the YP seems to support the hypothesis that the dynamic geological and climatic history of the Yucatan promoted a tropical diversification of Nearctic forms.

Apocyclops

The only species of this small genus that has been recorded in the YP (*A. panamensis*) is a widespread form, present in the entire Neotropical region (Reid, 1990; Reid *et al.*, 2002). Its wide distribution and its presence along the coast of northern SA suggests that this species originated as a tropical form probably related to the Protoantilles–Central America complex and its general distribution agrees with a South American–Caribbean track (Rosen, 1976). This would explain its occurrence in Cuba and the Antilles. Stock (1986) sustained that the Lesser Antilles have a different origin than that of the Protoantilles-related Greater Antilles; *A. panamensis* is also present in the Lesser Antilles (Bonaire, Barbuda). The low sea level in the region *c.* 17,000 yr BP (Domeier, 1986) could have provided a passage for the dispersal of this eurytopic species into the Lesser Antilles, either through the islands or through the north-east SA. It is probable that this species was more widely distributed in the YP than it is now, the marine transgressions of the Eocene and Pliocene and the drastic climatic variations of the Holocene probably prevented this species from being more frequent in the YP. This is noteworthy because this species succeeds in waters of varying salinity in which strict

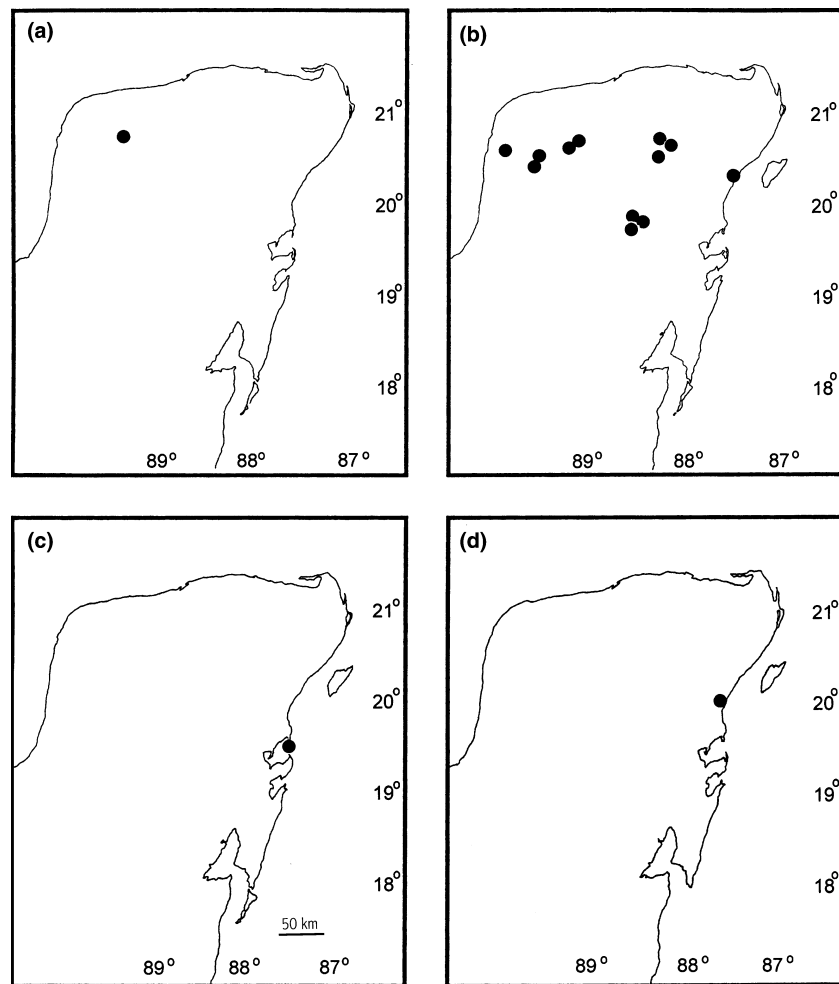


Figure 3 Distribution of the freshwater cyclopine copepods collected in the Yucatan Peninsula. (a) *Diacyclops bernardi*; (b) *D. chakan*; (c) *D. ecabensis*; (d) *D. pilosus*. Distribution is represented by individual positive localities.

freshwater and true marine cyclopoids do not do well; these kind of habitats, mostly along the northern and eastern coasts of the YP have been sampled and this species is absent. This would suggest that these young areas have not been colonized by this otherwise ubiquitous species.

Diacyclops

This is a widely distributed temperate group that contains more than 100 species, it is the largest genus in the Cyclopidae. Efforts are being made to solve different taxonomic problems within this taxon (Stoch, 2001). In spite of the overall diversity of the genus, records from the tropics are relatively sparse: only two species of *Diacyclops* were known from the upper Neotropical region only a decade ago (Petkovski, 1986; Reid, 1990). In the YP, Reid (1993) recorded *D. bernardi* (Petkovski, 1986) and Suárez-Morales *et al.* (1996) recorded *Diacyclops chakan* (as *Diacyclops* sp. A); recent surveys (Fiers *et al.*, 1996, 2000) have added three more species: *D. ecabensis*, *D. pilosus* and *D. puuc*. The former two were collected in the same area of the YP, and both are epigeic forms (Fiers *et al.*, 2000) (see Fig. 3c,d). *Diacyclops puuc* has been collected only in a few localities on the north-central part of the YP, basically in

hypogean systems (wells and cone-shaped cenote) (Fiers *et al.*, 1996, 2000) (Fig. 3a).

The most widely distributed species in the Yucatan is *D. chakan*, a benthic-crevicular species found in different environments (even caves) in the area of Mérida and in several other sites of the northern and central parts of the peninsula (Fig. 3b). The localities for this species are aligned along the Pliocene coast of the Yucatan (see Fig. 3b; López-Ramos, 1975, 1976; Weyl, 1980). An epigeic, planktonic relative of this species may have invaded the crevicular and hypogean environments between marine transgressions; this form eventually diverged and formed a distinct species. Based on the morphologic analysis by Fiers *et al.* (1996), *D. chakan* and *D. puuc*, sister species, could have originated from an ancestral planktonic form similar to *D. bernardi* or to *D. hispidus*. *Diacyclops hispidus* is absent from the YP, but *D. bernardi* has been found (Reid, 1993) in the area where *D. chakan* is widely distributed, in cenotes near Mérida (Fiers *et al.*, 1996). It is likely that this parental species had a wider distribution in the YP. This process might have started during the early post-Pliocene period as part of a new dispersal of the original *D. bernardi*-like forms in the recently emerged land; this would explain the coincidence of the distributional pattern with the

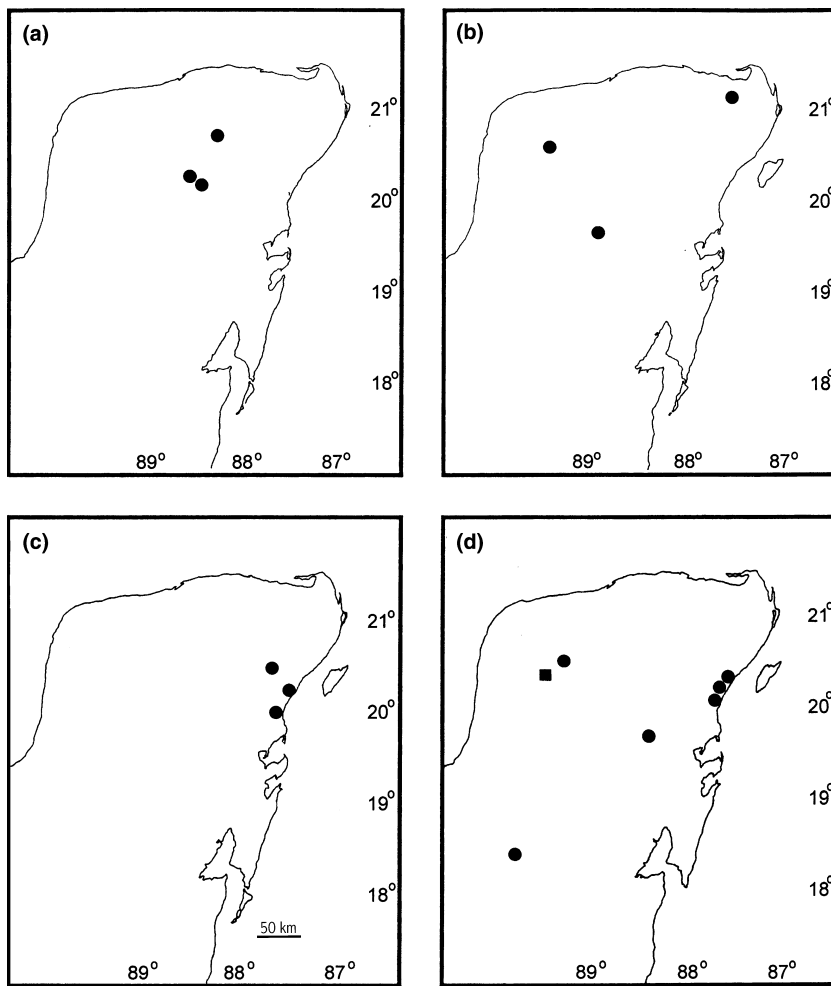


Figure 4 Distribution of the freshwater cyclopine copepods collected in the Yucatan Peninsula. (a) *Diacyclops puuc*; (b) *Mesocyclops chaci*; (c) *M. edax*; (d) *M. longisetus s.str.* (■) and *M. longisetus curvatus* (●). Distribution is represented by individual positive localities.

Pliocene coastline. Later on, during the Holocene climate changes (Leyden *et al.*, 1993; Hodell *et al.*, 1995) individual populations became isolated forming the two sibling species: *D. chakan* and *D. puuc*. The dry Holocene conditions might have been a factor driving adaptation to the use of benthic, crevicular environments. This would explain the observed restricted current distribution of *D. bernardi* and the locally widespread populations of *D. chakan* in the same geographical area.

The other two endemic species of the genus, *D. pilosus* and *D. ecabensis*, represent probably a different trend as suggested by their distribution, morphological links, and habitat (fully epigeal, possibly epibenthic or planktonic). According to the analysis by Fiers *et al.* (2000), they are closely related to the South American *D. uruguayensis* Kiefer, 1935 and *D. hispidus* Reid, 1988 (Kiefer, 1935; Reid, 1988, 1998b); moreover, these neotropical forms (*D. ecabensis*, *D. pilosus*, *D. hispidus*, *D. uruguayensis*) seem to represent a well-defined group that differ from most Eurasian forms in having a dimorphic male leg 3. A form related to either of these SA forms may have dispersed northwards and colonized the YP after the Pliocene bridge was consolidated, and then adapted and speciated in the YP independently from either *D. chakan* or *D. puuc*. The current

distribution of both *D. pilosus* and *D. ecabensis* in the edge of the eastern coast of the Yucatan, which are the youngest emerged lands of the YP seems to indicate a quite recent presence there, between 8000 and 5000 years ago. The main embayments and coastal systems of the eastern coastline, including the Bahía de la Ascensión and Punta Allen, where the type localities of these sister species are located, were formed during this time period (Seele, 1993). The coastal fringe was submerged during the Upper Miocene and the Lower Pliocene (Schmitter-Soto, 1998). It is possible then that the dryness of the Holocene (8000 and 3000 yr BP) was related to the isolation of many small and medium-sized water bodies thus favouring a recent vicariant speciation of these two forms, *D. ecabensis* and *D. pilosus*, even in geographically close localities. Schmitter-Soto (1998) described the Holocene aridity as a factor both of extinction and of isolation of local populations of freshwater fishes in the YP. The formation of resistance eggs and stages in Cyclopoida (Dahms, 1985) may have been an important factor that allowed these isolated populations to survive and eventually reproduce in dry conditions. The distribution of these species near the coastline is a feature shared with both SA forms (*D. uruguayensis* and *D. hispidus*), which are found mainly near the coastlines in SA; they are able to survive in fully freshwater habitats (wells and

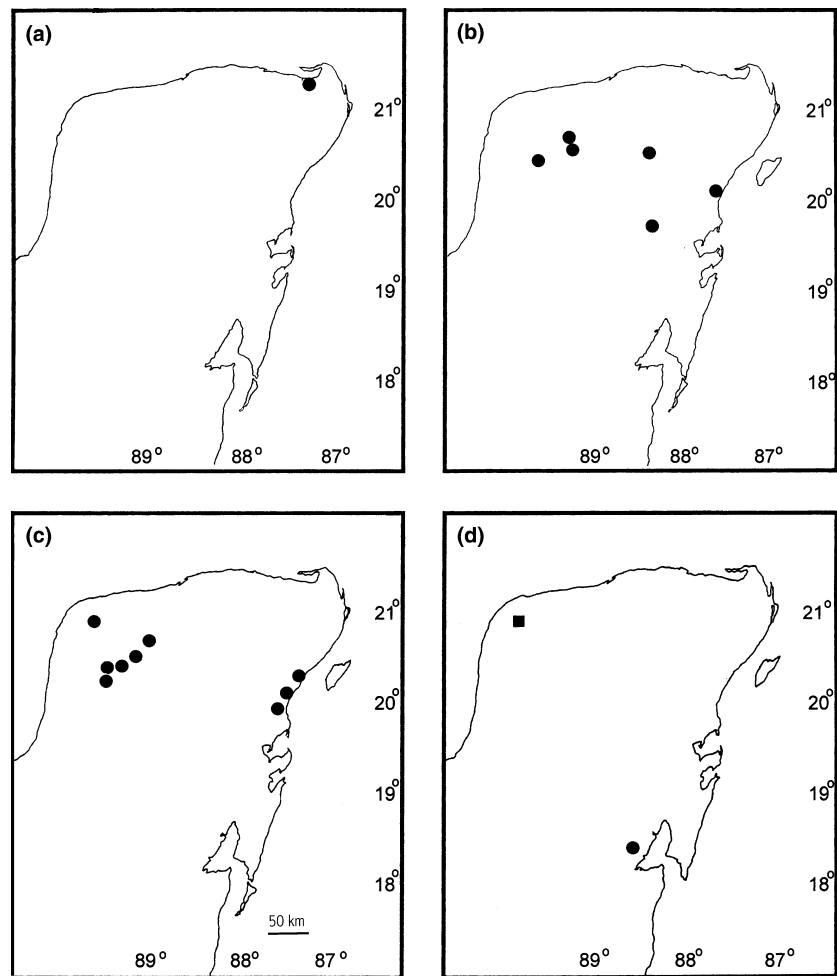


Figure 5 Distribution of the freshwater cyclopine copepods collected in the Yucatan Peninsula. (a) *Mesocyclops pescei*; (b) *M. reidae*; (c) *M. yutsil*; (d) *Microcyclops ceibaensis* (●) and *M. dubitabilis* (■). Distribution is represented by individual positive localities.

temporary ponds) (Fiers *et al.*, 1996, 2000; Reid, 1998a) and in shallow brackish waters (Reid, 1988). Therefore, recent dispersal of these resistant forms could have been easier along the coastlines and they could survive and adapt to the changes of the highly dynamic coast of CA and the Yucatan during the last 3–5000 years (Fig. 8).

Mesocyclops

This is a primarily tropical to warm-temperate genus distributed world-wide in many different freshwater environments; nearly 60% of the known species occur in tropical Asia and Africa (Holynska *et al.*, 2003). More than 15 species have been reported in the upper Neotropical region (Gutiérrez-Aguirre & Suárez-Morales, 2001); in the YP the genus is represented by six species and one subspecies (Fiers *et al.*, 1996, 2000; Suárez-Morales *et al.*, 1996). The most widely distributed species in the Yucatan is *M. yutsil*, present in several hypogean habitats (freshwater and anchialine caves) along the eastern coastal fringe, and in the north-western area of the peninsula (Fig. 5c). Together with *M. chaci*, these are the only two hypogean, crevicular forms of the genus found in the YP. The other species are basically epigeal (Fiers *et al.*, 1996, 2000).

The epigeal forms (*M. edax*, *M. reidae*, *M. longisetus s. s.* *M. longisetus curvatus* and *M. pescei*) are present in different areas of the peninsula (Figs 4c, 5b, 4d and 5a, respectively). The widespread distribution of *M. edax* and *M. reidae* in the Nearctic region suggests that these species dispersed northwards and became adapted to the nearctic conditions while maintaining their epigeal habits. The morphological closeness of *M. pescei* with the nearctic *M. americanus* Dussart, 1985 (Fiers *et al.*, 2000) suggests that *M. pescei*, known from Florida, Cuba and the Yucatan, or a *pescei*-like neotropical ancestor could have originated *M. americanus*, from dispersal events into the nearctic region. The other forms (*M. longisetus s. s.* *M. longisetus curvatus*), both widely distributed in northern SA and CA, could have evolved also from a Neotropical ancestor and also spread northwards reaching the southern USA (Holynska *et al.*, 2003).

The morphological analysis of the hypogean forms by Fiers *et al.* (1996) indicates that *M. yutsil* and *M. chaci*, together with *M. reidae*, form a well-defined clade. The latter species is an epigeal form with a tendency to dwell in benthic habitats, whereas *M. chaci* is a benthic crevicular form and *M. yutsil* tends to live in more open spaces, near the surface. Fiers *et al.* (1996) considered that *M. yutsil* and *M. chaci* shared a

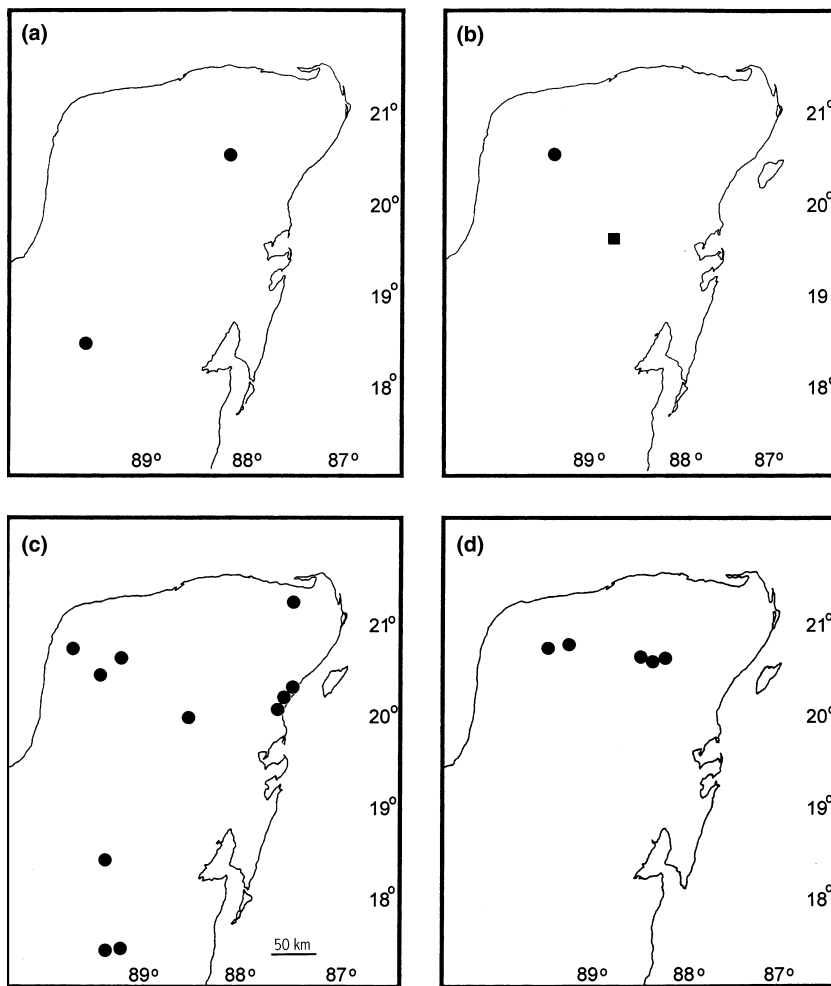


Figure 6 Distribution of the freshwater cyclopine copepods collected in the Yucatan Peninsula. (a) *Microcyclops rubellus*; (b) *Microcyclops echinatus* (■) and *Neutrocyclops brevifurca* (●); (c) *Thermocyclops inversus*; (d) *T. tenuis*. Distribution is represented by individual positive localities.

crevicular-living ancestor that evolved in the former to a planktonic existence. *Mesocyclops reidae* is known from the Antilles, Central America and southern Mexico (Reid, 1990; Suárez-Morales & Reid, 1998). It is possible that this regionally predominant form represents an ancestral stock that spread in the YP and diversified. Its occurrence in sites along the Pliocene coast and in the epicontinental area of the eastern coast suggests that it had a post-Pliocene invasion and a more recent, Holocene, one (as described for *D. chakan*), when the coast was formed, 3000–5000 yr BP. The local diversification of the genus that resulted in these two forms (*M. chaci* and *M. yutsil*) could be related to: (1) the Holocene desiccation-isolation processes that favoured vicariance in relatively small areas (as also hypothesized for some species of *Diacyclops*); this process is suggested also by the morphological similarity and geographical closeness of *M. chaci* and *M. yutsil* in different areas (Fiers *et al.*, 1996). This hypothesized vicariance process is related to recent (Pleisto-Holocene) colonization events. (2) The adaptation of these species to the hypogean environments; it is possible that these ancestral epigeic forms (*M. reidae*-like) had enough time to adapt fully to the hypogean conditions and speciate. This adaptation process would be related to geologically older areas of the peninsula, as suggested by the current distribution of

M. chaci (Fig. 9). In addition, it is likely that this and other unknown specialist forms could not survive when the roofs of the caves collapsed opening the system to the epigeic influence and to the colonization of widespread epigeic forms such as *M. edax* or *M. longisetus* (see Fiers *et al.*, 1996). Both the wider distribution of *yutsil* and that it is found in the same general sectors as *M. reidae*, may be related to the recent dispersal of both these species as planktonic, epigeic forms; as such they could have been passively transported to adjacent bodies of water over the land surface during floods and hurricanes, or dispersed by phoretic transportation.

Microcyclops

This genus has a high diversity but only a few species are known to be distributed in the Neotropical region (Reid, 1990). The description of *M. echinatus* was based on specimens obtained in a plankton sample from Laguna Esmeralda in the centre of the peninsula (Fiers *et al.*, 2000). *Microcyclops echinatus* is most closely related to *M. elongatus* (Lowndes, 1934) and *M. furcatus* (Daday, 1905) (Fiers *et al.*, 2000); both species are known only from SA, in Uruguay. It is suggested that *M. echinatus* represents a result of a post-Pliocene

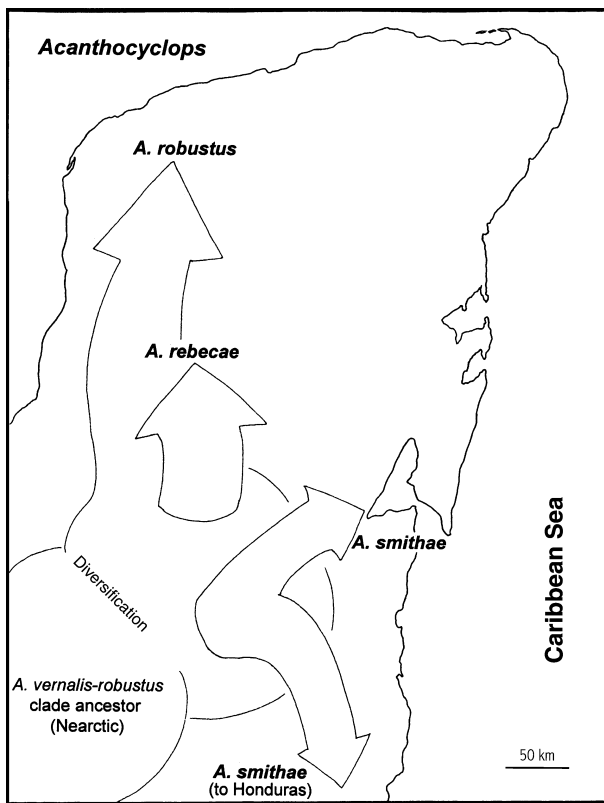


Figure 7 Hypothesized origin and dispersal route of the genus *Acanthocyclops* in the Yucatan Peninsula.

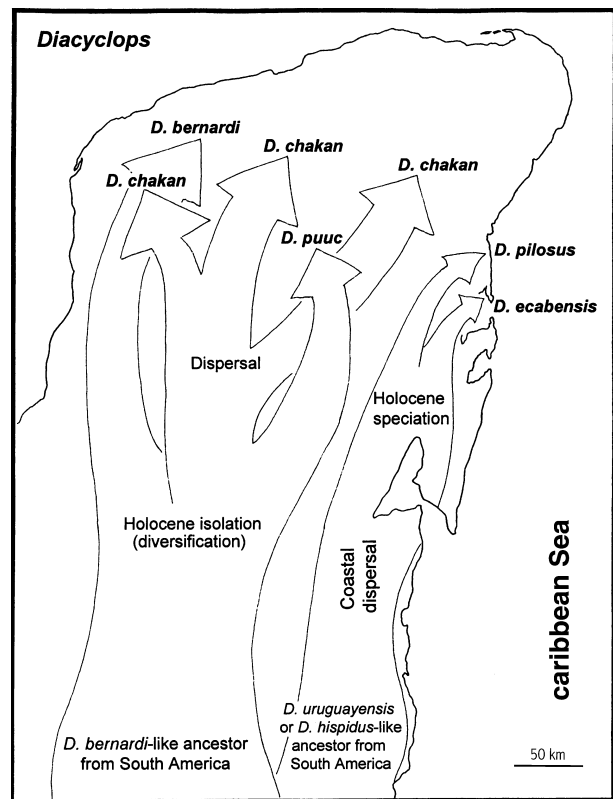


Figure 8 Hypothesized origin and dispersal route of the genus *Diacyclops* in the Yucatan Peninsula.

invasion of South American forms related to *M. elongatus* or *M. furcatus* that reached the YP area and then speciated by isolation during the Holocene dry periods (Fig. 10).

Microcyclops dubitabilis Kiefer, 1934 was for long considered to be a synonym of *M. ceibaensis* (Reid, 1990). It was recorded by Fiers *et al.* (2000) at one site in the northern part of the Yucatan (Fig. 5d); its presence in the YP is also post-Pliocenic as it is present in SA, from where it may have dispersed northwards along with other congeners.

Neutrocyclops

This monotypic genus has a wide distribution in the Neotropical region, including Central America, the Lesser Antilles, Mexico and SA (Reid, 1990; Suárez-Morales & Reid, 1998). It has been collected only once in the YP. It is probable that this species spread from northern SA into CA and the YP, and even to the Lesser Antilles during the post-Pliocene period.

Thermocyclops

This is a cosmopolitan genus, with its highest diversity in the tropical-subtropical continental belt (Mirabdullayev *et al.*, 2003). There are up to 51 recognized species and subspecies; nearly 80% of the known species are distributed in the tropical Afro-Asian region and only six are considered to be

confined to a continent, three of them in the Americas. Reid (1990) recognized six species in Mexico, Central America, and the Caribbean area. Recent refinements have been made for some species and *M. antillensis* was added with species rank to the Caribbean fauna (Mirabdullayev *et al.*, 2003).

Only two species widespread in the neotropics (*T. inversus* and *T. tenuis*) have been recorded in the Yucatan (Suárez-Morales *et al.*, 1996; Suárez-Morales & Reid, 2003; Fig. 6c,d). In the Americas, ancestral forms of this tropical genus might have radiated in the Neotropical region and some forms were able to reach NA; it is clear, however, that *T. inversus* and *T. tenuis* and the pantropical *T. decipiens* were very successful in dispersing in the tropical zone but did not reach the Nearctic region. The widespread distribution of *T. inversus* in the YP is probably the result of different dispersal events. The earliest of these episodes may be related to the Pliocene connection if the genus is considered to have radiated from northern SA, and successive invasions would have taken place during the re-emergence periods of the Yucatan land. The evident adaptability of these species may be a factor in their survival during the Holocene climatic fluctuations.

General remarks

Based on the general assumption that high diversity is related to a longer period of diversification, cyclopid copepods were

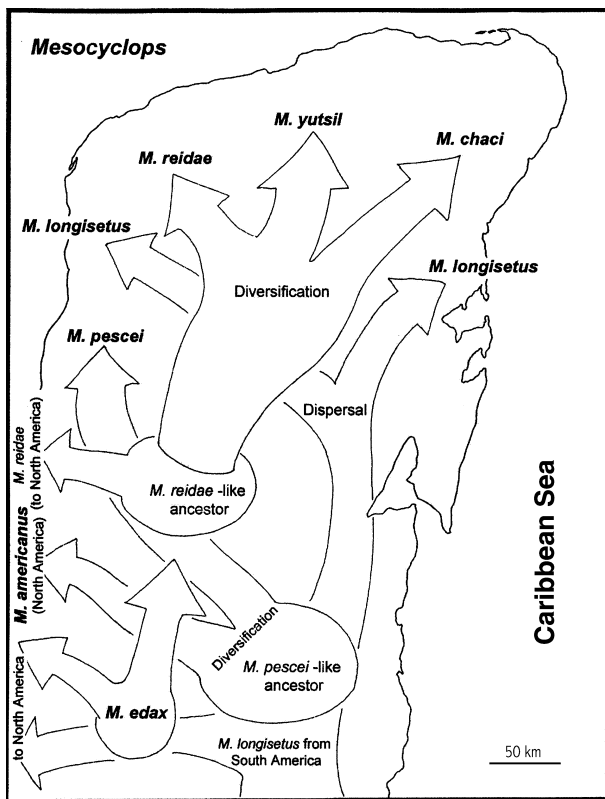


Figure 9 Hypothesized origin and dispersal route of the genus *Mesocyclops* in the Yucatan Peninsula.

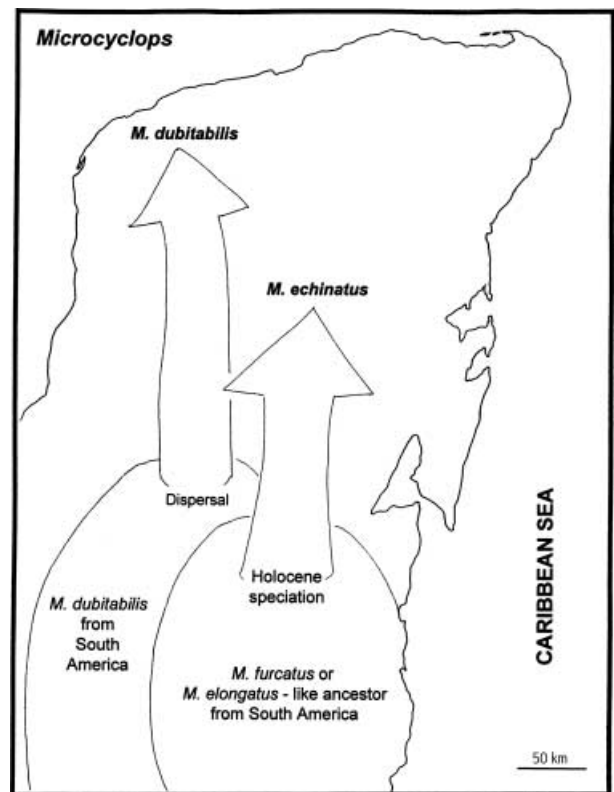


Figure 10 Hypothesized origin and dispersal route of the genus *Microcyclops* in the Yucatan Peninsula.

considered by Boxshall & Jaume (2000) to be the oldest freshwater colonizers, present in continental aquatic habitats probably prior to the break-up of Pangaea. In addition, the fact that several cyclopid species considered as cosmopolitan are present in Eurasia and NA and SA (Reid, 1998b) seems to support this early colonization hypothesis. Therefore, being a primarily freshwater taxon, it was not expected that marine ancestors or marine-related relict forms of Cyclopinae would be present in the continental waters of the YP, as found in other crustacean groups such as decapods, bogdiellid amphipods, and cirrolanid isopods (Iliffe, 1992). The colonization of ancient coastal caves by crustaceans in the YP is related to the post-Jurassic separation of Pangaea 180–200 Myr BP (Cals & Monod, 1988).

However, the freshwater calanoid copepods (Diptomidae) apparently underwent colonization and dispersal processes different from those in the YP Cyclopinae. This hypothesis is supported by the different regional faunistic affinities of both groups (Suárez-Morales & Reid, 2003). While an invasion of Nearctic species of Diptomidae seems to explain part of the distributional patterns in the Neotropical region (Boxshall & Jaume, 2000; Suárez-Morales, 2003), this is not so clear for the Cyclopidae, with widely distributed forms from different presumed origins (see Suárez-Morales & Reid, 1998), some forms even related to South American species. Also, as opposed to the YP cyclopid copepods, cave-dwelling/adapted diptomids are not present in the YP (Suárez-Morales, 2003).

There are several hypogean species of cyclopid copepods found in the Yucatan; none of these forms has a close marine relative. Therefore, they probably evolved as colonizers of the hypogean habitats from epigean-crevicular or epibenthic forms.

The geological connection between NS and SA was consolidated by the end of the Pliocene. The nearctic or Central American diptomid fauna did not reach SA, because the contact between NA and SA is relatively recent, and this explains the absence of Nearctic representatives in the SA diptomid fauna or SA forms in the upper Neotropical or Nearctic subregions. Contrariwise, our results show that the YP cyclopid fauna shares several species with SA, all of them forms that are widely distributed throughout the entire neotropical region (i.e. *A. panamensis*, *M. edax*, *M. longisetus curvatus*, *M. ceibaensis*, *N. brevifurca*, *T. inversus* and *T. tenuis*) (see Reid, 1990; Holynska *et al.*, 2003). Other SA cyclopid species are present in central or southern Mexico (i.e. *M. brasilianus*) (Suárez-Morales & Gutiérrez-Aguirre, 2001). In addition, the fact that some species distributed in the YP have their closest relatives in SA indicates that the SA cyclopid fauna had an even stronger influence than that suggested by the records alone; most of these early colonizations are post-Pliocene events.

The high number of species of Cyclopinae in the YP contrasts with the depauperate lower Central America cyclopid fauna, for which no endemics are known (Suárez-

Morales & Reid, 2003). This is true also for the freshwater ichthyofauna (Bănărescu, 1995) and the distribution of high-altitude freshwater Harpacticoida (Löffler, 1972). This part of CA remained relatively isolated from both subcontinents and nearctic or SA invasions did not reach much farther than marked by the transgression lines of the Pliocene. Therefore, it is considered that any faunistic influence of SA in CA and Mexico including the YP is a post-Pliocene event.

In general, the patterns presented by the cyclopine copepods surveyed herein follow two different track patterns as described by Rosen (1976): the South American-Caribbean track, that links those species found in the YP which have their closest relatives in SA (i.e. *Diacyclops pilosus*, *D. ecabensis* and *M. echinatus*). Even widely distributed species such as *Apocyclops panamensis*, *Thermocyclops tenuis* and *T. inversus* could fit in the reaches of this basically Neotropical track. The North American-Caribbean track is represented in our study by Nearctic-affinity taxa that dispersed southwards; some speciated in the tropical areas, including the YP (i.e. *Acanthocyclops*).

Freshwater copepods have efficient dispersal strategies and tend to colonize small, relatively unstable ponds (Rundle *et al.*, 2002). In the historical frame depicted herein for the YP, this would explain, at least partially: (1) the wide distribution of the purported ancestors and (2) the local dispersal into small ponds (karstic systems, sinkholes and fragmented aquatic systems) that favoured the vicariance of many species and the resulting endemisms.

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BIOSKETCHES

Eduardo Suárez-Morales was born in Mexico City (1960) and has a Doctorate in Sciences (1992) (Biology) from the Facultad de Ciencias, National University of Mexico (UNAM). He is Senior Researcher at El Colegio de la Frontera Sur (ECOSUR), in charge of the project 'Marine and freshwater zooplankton of Mexico', and Head of the Department of Aquatic Ecology and Systematics of ECOSUR (1996–2002). He has to his credit more than 180 peer-reviewed publications on taxonomy and ecology of marine and freshwater zooplankton. He is also a General Secretary of the World Association of Copepodologists (1996–2005), Member of the Inland Water Crustacean Specialist Group, and Head of the Group of Copepoda, The World Conservation Union (IUCN).

Janet W. Reid is a private consultant specializing in the free-living copepod crustaceans of the Americas. Her research focuses on the morphologically based alpha-taxonomy and faunal composition of copepods in semi-terrestrial, ephemeral and subterranean habitats. She was formerly associated with the National Museum of Natural History (Smithsonian Institution). Since 2002 she has been a Research Associate of the Virginia Museum of Natural History, where she is developing a regional collection of copepods.

Frank Fiers works as a researcher at the Royal Belgian Institute of Natural Sciences in Brussels. For the past 20 years he has been developing research projects in the field of systematics and biogeography of marine harpacticoid copepods. Lately, he returned to his primary interest, namely the systematics and phylogeography of subterranean and cryptic living copepods.

Dr Tom Iliffe is an Associate Professor of Marine Biology who has been at Texas A & M University at Galveston since 1989. He has a PhD from the University of Texas Medical Branch in Galveston. For the past 25 years he has conducted studies on the animals inhabiting saltwater caves. He has led research expeditions to study the biology of marine and freshwater caves to different countries throughout the world. He is co-chairman of the International Biodiversity Observation Year project 'Exploration and Conservation of Anchialine Faunas'. He has been a scuba diving instructor since 1975 and a cave diving instructor since 1981. At TAMUG, he teaches courses in biospeleology, scientific diving and tropical marine ecology.
