Palaeobiogeography of the freshwater isopods Microcerberidae (Crustacea) from Caribbean and North America

Coineau N.[1] & Albuquerque, E.F.[2]

1 Université P. et M. Curie, Paris VI, Observatoire Océanologique de Banyuls, Laboratoire Arago, F-66650 Banyuls-sur-Mer, France. e-mail: n.coineau@obs-banyuls.fr
2 Universidade Santa Ursula, ICBA, R. Jorn. Orlando Dantas 59, 22231-010 Rio de Janeiro, RJ, Brasil. e-mail: ealbuquerque@alternex.com.br

Abstract

Freshwater species of the interstitial Microcerberidae (Crustacea Isopoda) occur in restricted, local areas of the world, compared to the world-wide distribution of the coastal marine representatives. In U.S.A., two inland species of *Microcerberus* form the sister group of the species from Rumania and Bulgaria. On Cuba, *Yvesia* lives in brackish water of wells. The two genera exhibit plesiomorphic characters. Both plate tectonics and Tethys regressions provide an understanding of their evolutionary history. The marine ancestors lived in the littoral of the Tethys since the opening of the Central Atlantic and could have settled in freshwater of Southeastern USA at the end of the Cenomanian regression. The Caribbean plate derived from the Pacific toward the East, between the North and South American plates and small islands emerged since the Aptian. On Cuba, the ancestor of *Yvesia striata* might have been left by one of the regressions from Aptian up to the Eocene.

Introduction

Microcerberids are small isopod crustaceans living in the interstitial groundwater of marine sandy beaches and freshwater aquifers. Most species are known from littoral brackish water and belong to the genus *Coxicerberus* (WÄGELE *et al.*, 1995), which exhibits a worldwide distribution. In contrast, freshwater species occur only in limited local areas of the globe, i. e. northeastern South Africa, Morocco, Bulgaria, Rumania, ex-Yugoslavia, southern USA and Cuba (COINEAU, 1986, WÄGELE *et al.*, 1995).

Freshwater species form a monophyletic group (in progress). According to WÄGELE (1983, 1990) and WÄGELE *et al.*, (1995), inland microcerberids have a freshwater origin. In contrast, for CHAPPUIS (1954), DELAMARE DEBOUTTEVILLE (1960), COINEAU (1986), WILSON (1997) and TABACARU & DANIELOPOL (1999), freshwater microcerberids evolved from marine ancestors.

The purpose of this work is to consider the origin of freshwater microcerberids from North America and the Caribbean, based on phylogeny and palaeogeographic data.

Zoogeographic pattern

Microcerberus carolinensis Wägele, Voelz & McArthur, 1995 is known from South Carolina, U.S.A.: Meyers Branch Creek, 33°10'54"N-81°34'53"W and 33°09'18"N-81°37'34"W (WÄGELE *et al.*, 1995), west of Charleston (Fig. 1).

Microcerberus sp., Strayer leg, occurs in NE of Anniston, Cleburne County, Alabama, U.S.A. (STRAYER *et al.*, 1995; ALBUQUERQUE & COINEAU, in prep.) (Fig. 1).

Yvesia striata Coineau & Botosaneanu, 1973 was collected by L. Botosaneanu from a well, western region of Santiago de Cuba, Cuba Island (Fig. 2).

Historical biogeography

Microcerberus carolinensis and the closely related species *Microcerberus* sp. from U.S.A. form the sister group of species from central Europe. As previously proposed, the genus *Microcerberus* is older than the opening of the Central Atlantic dated from the Kimmeridgian-Tithonian in the late Jurassic (146-144 Ma) (WÄGELE *et al.*, 1995). In the same way, the genus *Coxicerberus* existed before the opening of the Central and South Atlantic and the break up of the eastern Gondwana (COINEAU, 1986). Therefore, microcerberids constitute phylogenetically old lineages.

The "two step model of colonization and evolution" provides an understanding of both the establishment of marine surface ancestors in interstitial continental groundwater and of their evolution (BOUTIN & COINEAU, 1990; NOTENBOOM, 1991; COINEAU & BOUTIN, 1992; HOLSINGER, 1994). During the first stage, the surface marine ancestor actively colonized interstitial biotopes of shallow littoral bottom of the Tethys. The second step is the passive transition to subterranean freshwater during Tethys regressions (STOCK, 1980). Vicariance processes occur when the gene flow is no longer possible between the new limnostygobiont and the littoral remaining population. Further diversification may appear due to geologic events.

Hereafter, we examine if such a biogeographic model works when applied to the distribution pattern of *Microcerberus* from U.S.A. and Caribbean, based on palaeogeographic knowledge of these regions of the world.

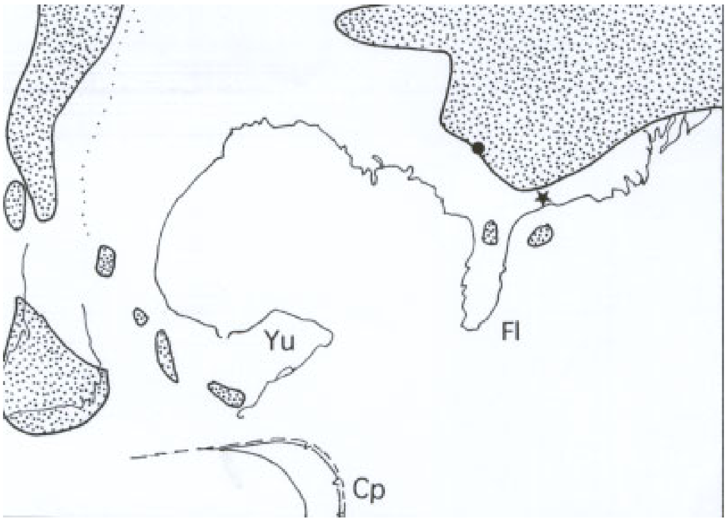

Figure 1 - Present location of Microcerberus carolinensis (*) and M. sp (.) in North America and shoreline of the Tethys during the Cenomanian, after Dercourt et al (Eds), 1993. Dotted areas: exposed lands. Below, the Caribbean plate (Cp) is drifting eastward. Yu: Yucatan, Fl: Florida.

a- Palaeobiogeography in southeastern U.S.A.

Before the Oxfordian-Kimmeridgian, North and South America formed a continuous emerged land. The Tethys opened to the West in the Kimmeridgian: it is the opening of the Central Atlantic. Marine ancestors of the species of *Microcerberus* were already interstitial in the littoral of the Tethys (first step of the model achieved). During this time, all exposed lands of the Laurasia and the Gondwana are closely distributed compared to the following periods. Both locations of *Microcerberus* sp. and *M. carolinensis* are on exposed lands (DERCOURT *et al.*, 1993, STEPHAN *et al.*, 1990; ITURRALDE-VINENT & MACPHEE, 1999). In the Tithonian (138-135 Ma/late Jurassic), *Microcerberus* sp. site is close to the Tethys shoreline, while *M. carolinensis* location is far from it. In the Aptian, *Microcerberus* sp. site is on exposed land, and that of *M. carolinensis* is near the Tethys coast. In the Cenomanian (94-92 Ma, late Cretaceous), the Tethyan transgression reached the lower southern part of the hercinian Appalachian Monts, and therefore *Microcerberus* sp. present location. During the regression, in the latter period, the littoral interstitial ancestral species of *Microcerberus* sp. settled in fresh groundwater. The region was never flooded by the Tethys after the Cenomanian. At the same time, *M. carolinensis* sites were covered by the sea and became littoral from the late Cretaceous up to the Rupelian (30-28 Ma), but were flooded again by the Tethys from the Eocene to the Tortonian (STEPHAN *et al.*, 1990). Since the species is very closely related to *Microcerberus* sp., the common ancestor of the two species left by the Cenomanian regression in the southern part of the Appalachian range might have reached the groundwater of the dowstream part of the rivers through passive drift. The entrance in freshwater of the ancestors in the Rupelian regression cannot be assumed because the region was widely covered by Tethyan embayments after this period. Furthermore, microcerberids are known for their old age and their low evolutionary rate (COINEAU *et al.*, 1999). Vicariance evolution might have occurred due to the uplift of the hercynian Appalachian range during the orogenesis of the western ranges and the subsequent erosion by new hydrographic systems.

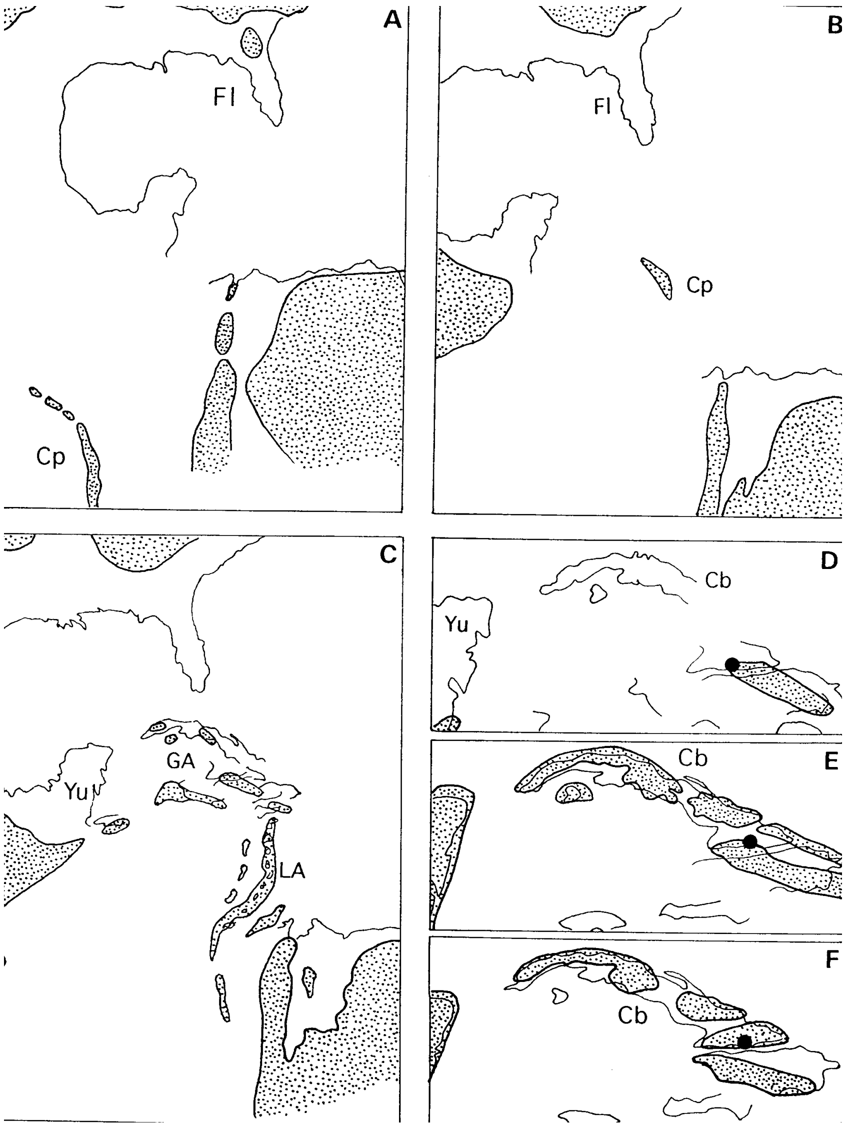

Figure 2 - Paleogeography in the Caribbean: A, in the lower Aptian; B, In the Santonian/Campanian; C, in the Maastrichtian. D, E, F, Greater Antillean in the late Paleocene (59 Ma), in the late Eocene (37 Ma) and in the early Miocene, after Stephan et al. 1990, and present location of Yvesia striata in Cuba. Dotted areas: exposed lands. Cp: Caribbean plate, Cb: Cuba, Yu: Yucatan, Fl: Florida, GA: Greater Antillean, LA: Lesser Antillean.

b. Palaeobiogeography in the Caribbean

The exposed lands (islands) of the Caribbean plate appeared in the Pacific just after the Central Atlantic opening in the Aptian and drifted to the East between North and South America (STEPHAN *et al.*, 1990; ITURRALDE-VINENT & MACPHEE, 1999). While drifting, one or several islands were quasi-permanently exposed and transgressions and regressions of the Tethys reached these lands from the Aptian up to the Middle Eocene (STEPHAN *et al.*, 1990). They will constitute the further Greater and Lesser Antillean (Fig. 2). The present location of *Yvesia striata* in southeastern Cuba corresponds to one of the Cuban blocks remaining emerged when drifting. Therefore, the marine ancestors which lived in the interstitial shallow waters of the Tethys might have been left on this block by one of the regressions from the late Cretaceous up to the Eocene periods.

Discussion

The three studied species of *Microcerberus* occur in areas formerly inundated by the Tethys. From the two alternative hypotheses, marine relicts versus freshwater origin of the inland groundwater microcerberids, the palaeogeographic data strongly indicate that they are relicts of marine embayments during the late Cretaceous, or Eocene in

Cuba. Such results are in close agreement with those of HOLSINGER (1986) for the weckelliid and bogidiellid amphipods from southern North America. Moreover, the geographic location of some species of these groups is similar to that of inland microcerberids both in North America and Europe. Numerous coastal species of microcerberids in brackish water favored also the marine origin, whereas the secondary occurrence in the littoral (WÄGELE, 1983) is questionable. The marine origin is largely consistent with our results under study in Morocco. Furthermore, in Cuba, *Yvesia striata* co-occur with thermosbaenaceans, hadziid amphipods and microparasellid isopods, which all derive from Tethyan ancestors. Sympatry with other stygobionts of marine origin is also observed in Europe and Morocco. From its emersion, Cuba has never been connected to exposed lands. As seen from STEPHAN *et al.* (1990) and ITURRALDE-VINENT & MACPHEE (1999) data, the Proto-Antillean archipelago (ROSEN, 1976) never existed, according also with STOCK (1986), and the vicariance origin of stygobionts through its fragmentation is no longer valid. Nevertheless, Cuba and Greater Antillean originated from a plate arising in the Pacific and drifting eastward.

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