

BIOGEOGRAPHY OF CARIBBEAN OLIGOCENE AND MIOCENE DECAPODS (THALASSINIDEA: BRACHYURA)

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Abstract

Oligocene and Miocene decapods occur in the Caribbean area. Most of the taxa belong to tropical or subtropical extant genera which inhabit both carbonate and silicic, soft clastic, shallow marine substrates, supported by the occurrence of most of the fossils in clastic units. The Oligo-Miocene genera reported herein exhibited either a Tethyan or North Pacific distribution, typical of Oligo-Miocene decapods of the region (Schweitzer, 2001). The open Caribbean Seaway facilitated dispersal of fauna throughout the region between the Atlantic and Pacific oceans.

Keywords: Decapoda, Thalassinidea, Brachyura, Paleogeography, Paleobiogeography, Oligocene, Miocene, Caribbean

Introduction

Fossil decapod crustaceans have been reported from the Caribbean region for over 100 years. Caribbean, east coastal Mexican, and Central American occurrences from the Cretaceous through Miocene were recently summarized (Schweitzer et al., 2002, in press), and numerous Pliocene and Pleistocene decapods have been reported from the Caribbean (Collins and Morris, 1976; Collins et al., 1996; Collins and Donovan, 1995, 1997; Collins and Portell, 1998). Here we refer to their paleoecology and paleobiogeography.

List of Caribbean fossil decapods

The following table from Schweitzer et al. (in press) is a compiled list of Caribbean fossil species referable to the Portunidae.

Taxon	Original Genus	Age	Location
<i>Portunus yaucoensis</i> Schweitzer et al., in press	<i>Portunus</i>	lower Oligocene	Yauco, Puerto Rico
<i>Portunus ateuicitlis</i> Vega et al., 1999	<i>Portunus</i>	Miocene	Eastern Mexico
<i>Portunus gabbi</i> Rathbun, 1919	<i>Portunus</i>	Miocene	Haiti
<i>Portunus haitensis</i> Rathbun, 1923	<i>Portunus</i>	Miocene	Haiti
<i>Portunus oblongus</i> Rathbun, 1920	<i>Portunus</i>	Miocene	Dominican Republic; Puerto Rico?
<i>Portunus</i> spp.	<i>Portunus</i>	lower-middle Miocene	Dominican Republic; Cuba
<i>Necronectes nodosa</i> Schweitzer et al., 2002	<i>Necronectes</i>	Oligocene	Baja California Sur, Mexico

<i>Necronectes summus</i> Collins and Donovan, 1995	<i>Necronectes</i>	Oligocene	Antigua
<i>Necronectes proavitus</i> (Rathbun, 1918)	<i>Gatunia</i>	Miocene	Panama; Puerto Rico
<i>Necronectes collinsi</i> Schweitzer et al., in press	<i>Necronectes</i>	lower Oligocene-lower Miocene	Puerto Rico
<i>Necronectes tajinensis</i> Vega et al., 1999	<i>Necronectes</i>	Miocene	Eastern Mexico
<i>Scylla costata</i> Rathbun, 1919	<i>Scylla</i>	lower Oligocene; Miocene	Puerto Rico; Haiti
<i>Euphylax callinectias</i> Rathbun, 1918	<i>Euphylax</i>	Miocene	Panama
<i>Euphylax domingensis</i> (Rathbun, 1919)	<i>Podophthalmus</i>	Miocene	Haiti
<i>Euphylax fortis</i> Rathbun, 1918	<i>Euphylax</i>	Miocene	Panama
<i>Euphylax fortispinosus</i> Collins et al., 2001	<i>Euphylax</i>	Pleistocene	Jamaica
<i>Podophthalmus yaquinensis</i> (Rathbun, 1919)	<i>Sandomingia</i>	Miocene	Caribbean
<i>Psygmophthalmus lares</i> Schweitzer et al., in press	<i>Psygmophthalmus</i>	Miocene	Puerto Rico

General Distribution of the Caribbean Portunidae

Neocallichiru has already been reported from the fossil record in the Caribbean (Collins et al., 1996), and other fossil occurrences span the Tethyan realm of the Eocene through Pleistocene (Schweitzer et al., 2004).

Calappa was a speciose genus in the Caribbean during the late Tertiary; this should not be surprising because it is quite speciose in the region today (Rathbun, 1937; Williams, 1984) as well as in the Indo-Pacific (Galil, 1997; Davie, 2002). The genus has apparently been quite successful since it first appeared during the Eocene; these earliest occurrences are recorded from Antarctica (Feldmann and Wilson, 1988) and Oregon (Rathbun, 1926). As previously summarized (Schweitzer and Feldmann, 2000a), it is interesting that these earliest occurrences show an amphitropical distribution, because the later Oligocene, Miocene, and Recent occurrences of the genus are nearly all subtropical to tropical.

Necronectes is known from the Oligocene and Miocene of the Tethyan realm. Oligocene occurrences include *Necronectes nodosus*, *N. summus*, and *N. vicksburgensis*, from Pacific coastal Mexico, the Caribbean, and the North American Gulf Coastal Plain respectively (Schweitzer et al., 2002; Collins and Donovan, 1995; Rathbun, 1935). *Necronectes nodosus* was mistakenly reported as Eocene (Schweitzer et al., 2002); that occurrence is in fact Oligocene in age. The remainder of the occurrences of the genus are Miocene in age, from Central America, the Caribbean, east coastal North America, and Tethyan Europe. The genus appears to have dispersed via a Tethyan distribution route, apparently from west to east, based upon its first occurrences in North America.

Scylla is represented by four extant species known only from the Indo-Pacific (Ng, 1998). Confirmed fossil species are known from the early to middle Miocene of Japan (Karasawa, 1993); lower Oligocene and lower Miocene rocks of the Caribbean (Rathbun, 1919; Schweitzer et al., in press); Miocene rocks of India (Das-Gupta, 1925); and Pliocene,

Pleistocene, and subfossil occurrences of the Indo-Pacific and South Africa (Etheridge and McCulloch, 1916; Van Straelen, 1928; Cooper and Kensley, 1991). Withers (1924) reported *Scylla costata* from the late Oligocene of Anguilla, but that occurrence is based only upon broken chelae; the other unconfirmed reports based solely on chelae are from Europe and the Indo-Pacific (A. Milne-Edwards, 1860; Ebert, 1887; Böhm, 1922) and range in age from Eocene through Miocene. Thus, based upon confirmed occurrences, the genus appeared during the late Oligocene or early Miocene and exhibited a Tethyan distribution early in its history, as evidenced in its occurrences in circum-tropical and equatorial regions during the Miocene. Even if the older chelae were to be confirmed as members of the genus, the distribution pattern would still clearly be a Tethyan one; this genus seems to prefer warm climates. The current range in the Indo-Pacific is a relict of this once broader distribution.

The Subfamily Podophthalminae (*Euphylax*, *Psygmophthalmus*) are not common in the fossil record, occurrences being limited to the Oligocene and Neogene. *Euphylax* is known from fragmental Oligocene occurrences and robust Miocene and later occurrences, whereas *Podophthalmus* is known only from Pliocene and Pleistocene of the Indo-Pacific (Schweitzer, Scott-Smith, and Ng, 2002). *Psygmophthalmus* (Schweitzer et al., in press) is reported from early Miocene rocks of Puerto Rico. The limited and relatively recent occurrences in the fossil record may be due to the apparently very specialized orbits and eyestalks of the subfamily, which appear to have evolved rather late within the Portunidae. Many of the other portunid subfamilies appeared in the Eocene or earlier, including the Portuninae, Polybiinae Ortmann, 1893, and Psammocarcininae Beurlen, 1930 (Glaessner, 1969; Feldmann et al., 1995).

Euphylax appears to have evolved in the western Pacific and dispersed eastward to the Americas. If the western Pacific occurrences were to be excluded, the genus would have a solely American distribution throughout its geologic range.

Species of *Megokkos* are only known from Eocene and Oligocene rocks of the North Pacific Ocean. *Megokkos macrospinus* is the oldest known member of the genus, from the middle to late Eocene of Washington (Schweitzer et al., 2000). Late Eocene species include *M. feldmanni* and *M. hexagonalis* from Washington, USA, and Japan, respectively (Nyborg et al., 2003; Nagao, 1932). *Megokkos alaskensis* is known from Oligocene rocks of Alaska, Washington, and Oregon, USA, and British Columbia, Canada (Rathbun, 1926; Tucker and Feldmann, 1990; Schweitzer and Feldmann, 2000b; Schweitzer et al., 2003). The genus exhibited a North Pacific distribution (Schweitzer, 2001).

Paleogeography

The Caribbean realm was very active tectonically during the Late Cenozoic (Mann et al., 1990; Iturralde-Vinent and MacPhee, 1999), and this is reflected in the paleogeographic evolution of the area, as illustrated by Fig. 1. At about the Eocene-Oligocene transition, there was a general uplift in the Caribbean realm and surrounding continental margins, but beginning in the second half of the lower Oligocene, a general inundation took place, and many previously exposed areas were transgressed by shallow marine waters (Iturralde-Vinent and MacPhee, 1999). As a consequence, the amount of land drastically reduced, and the marine environments were widely interconnected by both deep and shallow water channels (Fig. 1).

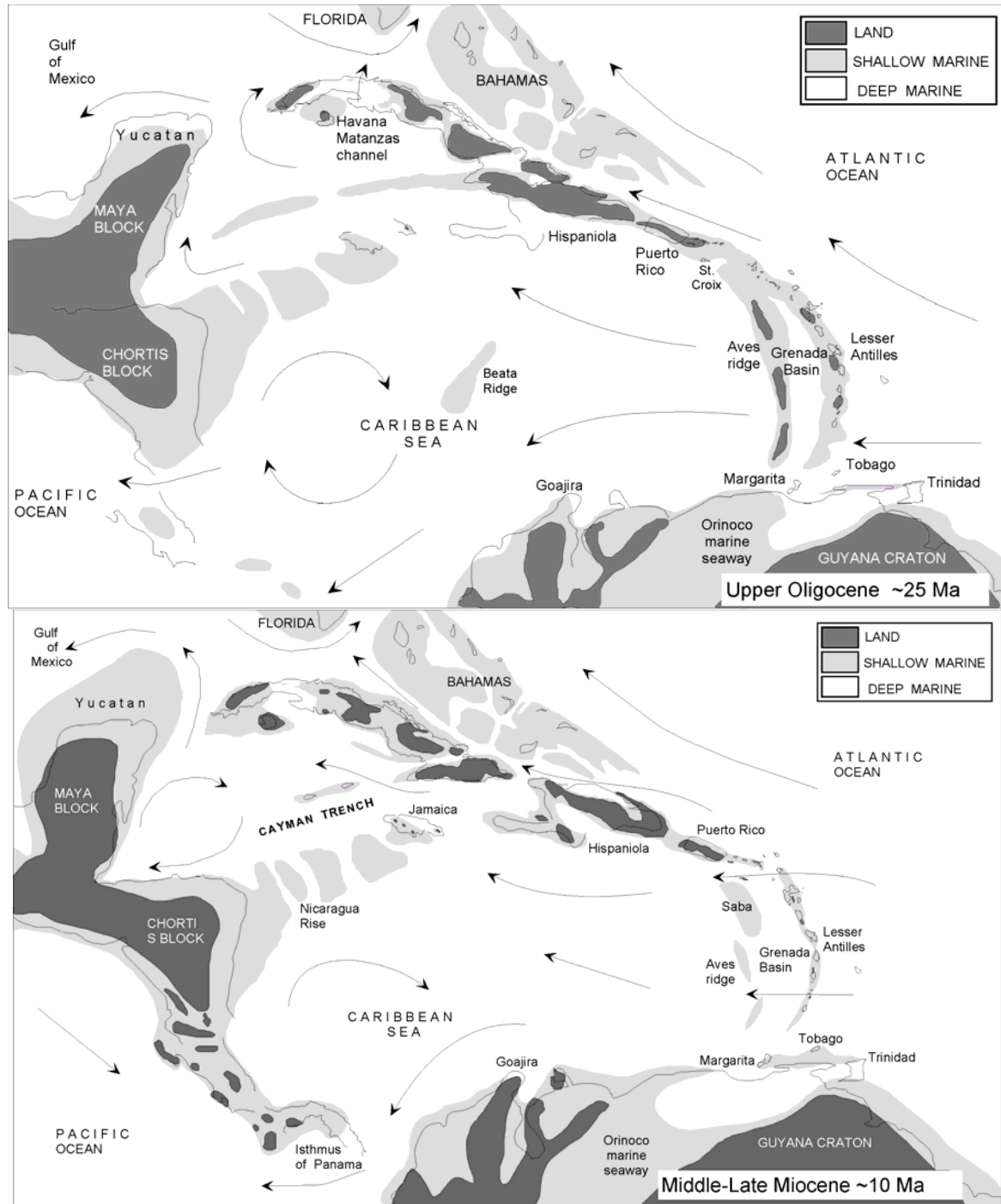


Figure 1. Late Oligocene and Middle-Upper Miocene paleogeographic maps of the Caribbean. Arrows are hypothetical direction of surface marine currents. Adapted and updated from Iturralde-Vinent and MacPhee (1999).

Within the continental margin areas surrounding the Caribbean, as well as within the shallow banks and island shelf areas, sea grass muddy plains, calcareous detrital and coralline environments, and siliciclastic ramps and deltas developed, which mutually intermingled in time and space (Iturralde-Vinent and MacPhee, 1999). Some of these environments are exemplified by appendix 1 of Iturralde-Vinent and MacPhee (1999).

During the late lower to upper Miocene, with a spike in the middle Miocene, extensive carbonate platforms are recognized; thus, Caribbean coralgal communities were widespread and increasing in areal development, probably due to a general warming process and the input of nutrients from the Central Atlantic. Likewise, surrounding emerged land areas and shallow sea grass plains developed, and extensive marginal lagoon environments are recorded in the columnar section in appendix 1 of Iturralde-Vinent and MacPhee (1999). After the middle Miocene, tectonic uplift dominated in almost every topographic high within the Caribbean area, a process that produced an increase of land areas and ultimately the present-day Caribbean islands (Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent, 2001).

During the Oligocene and Miocene, Atlantic, Caribbean and Pacific waters were united, and the Circum-Tropical Marine Current generally drifted westward (Berggren and Hollister, 1974; Droxford et al., 1998; Iturralde-Vinent, 2003). This scenario lasted until the Pliocene, when the Isthmus of Panama progressively uplifted (Coates and Obando, 1996), and eventually emerged as a barrier since the Lower Pleistocene (Beu, 2001). As a result, since the Pliocene, and perhaps as early as the Miocene (Bice et al., 2000), the Atlantic-Caribbean and Pacific marine biotas were poorly connected only during sea level highs, but since the lower Pleistocene have been completely separated (Beu, 2001).

Paleobiogeography

This late Cenozoic paleogeographic evolution provides the scenario for the dispersal and evolution of the Caribbean portunids and other decapods. Nearly all of the decapods reported from the Caribbean displayed a Tethyan distribution pattern during their history. In addition, nearly all required an open Central American Seaway for dispersal between the Atlantic and Pacific oceans. *Neocallichirus* and *Necronectes* have already been described as having a Tethyan distribution (Schweitzer and Feldmann, 2002; Schweitzer et al., 2002; Schweitzer et al., 2004), originating and dispersing throughout the Tethyan region, and the Caribbean occurrences described herein only confirm that pattern. Based upon the occurrences of *Portunus* spp. beginning in the Eocene, the genus appears to have originated in the Tethyan realm and displayed a Tethyan distribution throughout the Cenozoic (Schweitzer et al., 2002), and is today cosmopolitan in warm and temperate oceans (Glaessner, 1969). *Scylla* originally displayed a Tethyan distribution early in its history (Miocene), with some species reaching southern Africa by the Holocene (Cooper and Kensley, 1991), and it now exhibits a relict Tethyan, Indo-Pacific distribution.

Because the Podophthalminae is a small subfamily (only three included genera), we have chosen to examine its paleobiogeography at the subfamily level as well as that of one of the included genera, *Euphylax*. *Euphylax* apparently originated in the North Pacific (Japan), not uncommon in the Paleogene (Schweitzer, 2001), and subsequently dispersed to the eastern Pacific and other Indo-Pacific localities. The subfamily as a whole displays a similar pattern; it appears to have originated in the North Pacific and subsequently dispersed to other Indo-Pacific locations and the Caribbean, probably following North Pacific currents or continental shelves. The group would have reached the Caribbean via the open Central American Seaway (Bice et al., 2000).

Calappa spp. displayed a broad geographic distribution in the fossil record. *Calappa* appears to have originated in the high southern latitudes during the Eocene (Feldmann and Wilson, 1988), with subsequent dispersal to the Central Americas and Northern Hemisphere (Schweitzer and Feldmann, 2000a). It displays a cosmopolitan distribution in tropical modern oceans (Schweitzer and Feldmann, 2000a).

Portunid diversity

The vast number of portunid taxa known from the Oligocene and Miocene of the Caribbean is notable (Table 1). Not only were the portunids diverse, they also appear to have been one of the most abundant taxa in the fossil record of the region; for example, portunid samples account for the vast majority of brachyuran samples in this study. Based upon Oligocene through Pleistocene fossil species described from dorsal carapace material or well-preserved, complete cheliped material, there are a total of five named and three unnamed species of *Portunus*; five species of *Necronectes*; four species of *Euphyllax*; and one species each of *Scylla*, *Podophthalmus*, and *Psygmophthalmus*. This abundance and diversity is probably due to at least two major factors. First, portunid crabs in modern oceans are abundant and diverse in warm, tropical seas, inhabiting a broad variety of niches and habitats (Rathbun, 1930; Williams, 1984; Apel and Spiridinov, 1998; Ng, 1998). The Oligocene, Miocene, and Pliocene Caribbean clearly exhibited these climatic characteristics, and the family continues to be abundant and speciose in the region today (Rathbun, 1930; Williams, 1984). The Portunidae are currently most diverse in the Indo-Pacific (Davie, 2002), and the open connection between the Pacific and Caribbean during the Oligocene and Miocene would have facilitated the dispersal of these crabs, perhaps leading to the high portunid diversity seen in the Caribbean during that time. Second, portunid crabs often inhabit soft, clastic bottoms but can also inhabit rocky or coral substrates or mangrove habitats. Based upon our paleogeographic reconstruction, it is likely that all of these habitats were abundant during the late Paleogene and Neogene, resulting in abundant suitable niches and therefore high diversity among the Portunidae.

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