

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo



Middle and Late Jurassic roots of brachyuran crabs: Palaeoenvironmental distribution during their early evolution

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ARTICLE INFO

Article history: Received 11 November 2006 Received in revised form 11 April 2007 Accepted 10 January 2008

Keywords:
Decapoda
Brachyuran crabs
Jurassic
Palaeoecology
Palaeobiogeography

ABSTRACT

Knowledge of early, Mesozoic crabs is still rudimentary, mainly due to the poor preservational potential of crustacean decapods. Fossil evidence suggests that the family Prosopidae is ancestral to all other brachyurans, including Podotremata, with a very close phylogenetic relationship to Homolodromiidae, Dromiidae, Homolidae, Latreillidae, Dynomenidae, Xanthidae, Cyclodorippoidea and Calappoidea. Prosopidae is an extinct family, consisting mostly of Mesozoic species, almost exclusively known by their carapaces. This family appeared in the late Early Jurassic (Late Pliensbachian) and disappeared at the end of the Danian. The Early Jurassic (Pliensbachian) oldest crab species, Eocarcinus praecursor Withers, is transitional in many of its observable traits between the macruran Glypheoidea (Middle Triassic Pseudopemphix) and the early brachyuran prosopids, especially the earliest known species, Eoprosopon klugi Förster (Late Pliensbachian). Middle Jurassic prosopids lived in shallow-sea, soft bottom environments. The oldest known prosopid species lived on a silty sea floor, as did the first known crab (late Early Pliensbachian), and their presumed ancestors (Pemphicidae) were probably also shallow water organisms. Middle Jurassic prosopids lived both in shallow warm waters within organic buildups/shelly accumulations, and on silty sea-floors during the Bajocian/ Bathonian, as illustrated by a new example from central Poland. Prosopids had an evolutionary climax during the Late Jurassic and were widely distributed in sponge-microbial (Oxfordian) buildups and coral reef (Kimmeridgian-Tithonian) environments of Europe (Pithonoton, Coelopus, Longodromites, Prosopon, Nodoprosopon, Lecythocaris, Glaessneropsis). When biohermal and reef facies retreated at the end of the Jurassic, favourable conditions for prosopid crabs diminished and Cretaceous prosopids are rare and spatially dispersed. Their closely related descendants, the homolodromiids, preferentially inhabited soft muddy bottoms in deeper, colder waters, as is well documented by Cenozoic and Recent occurrences.

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1. Introduction

The most primitive crabs (Brachyura) of the extinct family Prosopidae are represented mostly by Jurassic and Cretaceous species. The origin of these crabs is more or less enigmatic and mainly based on morphological changes in the surface of their carapaces. Prosopids appeared in the late Early Jurassic (Pliensbachian) and most probably include the ancestors of all brachyurans (Fig. 1). Only one genus survived into the Early Palaeogene (Danian) (Müller et al., 2000). Prosopid species are almost exclusively known by their carapaces. Both Withers (1932) and Förster (1979), who described the oldest crab species, *Eocarcinus praecursor* Withers, agreed that this species is in many respects transitional between the macruran Glypheoidea and the early brachyurans. This idea is widely accepted, suggesting that this Early Pliensbachian *Eocarcinus* is a transitional form between the Triassic glypheoids (*Pseudopemphix*) and the earliest, Late Pliensba-

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chian prosopid (*Eoprosopon klugi* Förster) (Förster, 1979, 1986) (Fig. 1). Additionally, general phylogenetic relationships suggests that the family Prosopidae is very close to other, younger families, including Homolodromiidae, Dromiidae, Homolidae, Latreillidae, Dynomenidae, Xanthidae, Cyclodorippidae, Necrocarcinidae and Calappidae (Müller et al., 2000; Karasawa et al., 2006) [newest results of a systematic classification for some Jurassic Brachyura (Homolodromioidea), which transferred several taxa to new systematic positions, have been published during editorial work of this paper (Schweitzer and Feldmann, 2007; Schweitzer et al., 2007)].

Wright and Collins (1972) and Wehner (1988) gave monographic accounts of prosopids from the Cretaceous and Jurassic respectively. Meyer (1842, 1860) was the first to report prosopid crabs and recognise their dromiid affinities. He arranged the 25 known species into the new family Prosopidae. Beurlen (1928, 1933) described the "explosiven Formenbildung", arguing for an early branching of Brachyura. He suggested that the ancestors of most extant crabs may be identified among early members of the family Prosopidae. However, the very close relationship of prosopids and the Homolodromiidae is universally accepted (e.g., Wehner, 1988; Schweitzer

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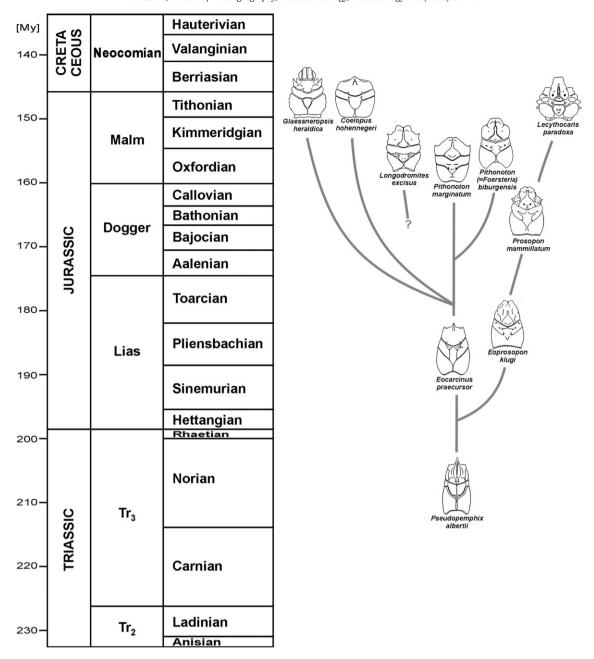


Fig. 1. Stratigraphical distribution of representatives of Late Triassic macrurans and Jurassic primitive crabs (phylogenetic relationships based on Wehner, 1988).

et al., 2004), and seems to be well established from the similarity in carapace traits, patterns of furrows, ventral parts, and in part the chelae. More detailed phylogenetic relationships between several brachyuran families have been described by Wright and Collins (1972), Wehner (1988) and Collins (1997), and summarized by Müller et al. (2000, and references therein).

The evolution of prosopid crabs apparently began in Early Jurassic, shallow, soft bottom marine environments. The worldwide Callovian transgression made the formation of bioherms and reefs in the Late Jurassic possible, simultaneously creating ecological niches for the rapidly diversifying prosopids. These crabs quickly migrated all over Europe in the Oxfordian and began to flourish, occupying sponge megafacies from Portugal to Poland in great numbers. During the Kimmeridgian, the area of known prosopid occupancy shrank, probably connected to a decrease in reef facies. A Tithonian regression in the peri-Tethyan area resulted in a change of habitat and colonisation of coral reefs by prosopids.

2. Ecology and biogeography

Most prosopid species have been found in Upper Jurassic limestones, while the Early and Middle Jurassic fossil record of crabs is very poor (e.g., Förster, 1985a,b; Wehner, 1988; Müller et al., 2000; Schweigert, 2006). Therefore, each new discovery of fossils of Early or Middle Jurassic age is important to an understanding of the palaeobiogeographical roots and early stages of prosopid evolution. The large number of crab species present after the Oxfordian growth of organogenic, mainly sponge-bearing, buildups points to a close ecological relationship (e.g., Müller et al., 2000). These Late Jurassic cyanobacterial-sponge limestones were deposited in deep sublittoral to littoral settings, and contain abundant sponges and occasional hermatypic corals (Matyszkiewicz, 1999; Matyszkiewicz et al., 2006a,b, and references therein). Although it is difficult to reconstruct the ecology of individual prosopid species, their high diversity and abundance may well be connected to these reef-like environments. The great success

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