

A RECONSTRUCTION OF AN EVOLUTIONARY SCENARIO FOR THE
BRACHYURA (DECAPODA) IN THE CONTEXT OF THE
CRETACEOUS-TERTIARY BOUNDARY

BY

ANDREAS BRÖSING^{1,2)}

¹⁾ Humboldt-Universität zu Berlin, Institut für Biologie/Vergleichende Zoologie, Philippstr. 13,
D-10115 Berlin, Germany

ABSTRACT

In this article, I map the currently known brachyuran fossil record on a recent cladogram of Brachyura, the true crabs. The hypothesis of brachyuran phylogenetic relationships is based on a cladistic analysis of brachyuran foregut characters. With this approach, the following scenario of the evolution of Brachyura is proposed. The representatives of Brachyura that occur earliest in the fossil record (Dromioidea) take the most basal position in the cladogram, followed by Homolidae. These taxa reach their highest species diversity during the Cretaceous, together with Raninidae and Cyonomidae sensu lato. The analysis reveals that the majority of the “higher” crabs (Xanthoidea, Portunidae, Cancridae, and Oxystomata sensu lato) as well as their common ancestor existed already by the end of the Cretaceous. In particular, a constant increase of brachyuran species diversity has been registered from the Eocene to the Miocene. Most taxa of the Brachyura (with the exception of the Carcineretidae) remained unaffected by the events at the Cretaceous-Tertiary-boundary. Hence, the data suggest the events at the K/T-boundary have had a weaker influence on the species diversity of the Brachyura and of the Decapoda in general, than originally presumed: i.e., there was no mass-extinction of crabs.

ZUSAMMENFASSUNG

Die vorgestellte Hypothese, resultierend aus der kladistischen Analyse von Merkmalen der Vorderdarm-Morphologie, wurde mit dem gegenwärtig bekannten Fossilbericht verglichen. Basierend auf diesem Ansatz wird folgendes evolutives Szenario für die Stammesgeschichte der Brachyura vorgeschlagen. Die Vertreter der Brachyura mit den frühesten bekannten fossilen Vorkommen (Dromioidea) nehmen auch in der kladistischen Analyse die basale Position ein, gefolgt von den Homolidae. Diese Taxa zeigen zusammen mit den Raninidae und den Cyonomidae ihre größte Artenvielfalt während der Kreidezeit. Es ist ebenfalls anzunehmen, daß die Mehrheit der “höheren Krabben” (Vertreter der Xanthoidea, Portunidae, der Cancridae und der Oxystomata) ebenso ihr gemeinsamer Vorfahre schon am Ende der Kreidezeit existierten. Besonders vom Eozän zum Miozän

²⁾ Present address: Technische Universität Ilmenau, Institut für Physik, Weimarer Str. 32, D-98684 Ilmenau, Germany; e-mail: andreas.broesing@tu-ilmenau.de

ist ein Anstieg der Artenvielfalt zu verzeichnen. Innerhalb der neu vorgeschlagenen Neobrachyura sind neben den traditionellen Thoracotremata zusätzliche Taxa mit kontrovers diskutierten phylogenetischen Verwandtschaftsbeziehungen zusammengefaßt. Für die ursprünglich beschriebenen Thoracotremata (Ocypodidae, Mictyridae, Gecarcinidae und Grapsidae) kann basierend auf Merkmalen der Gonoporen in beiden Geschlechtern von einem monophyletischen Ursprung ausgegangen werden. Nach Vorlage der verfügbaren Daten wird ein Event an der Kreide-Tertiärgrenze angenommen, welches einen kleineren Einfluß auf die Artenvielfalt der Brachyura, bzw. der Decapoda hatte, als ursprünglich angenommen. Vergleiche von rezenten und fossilen Taxa zeigen, daß die meisten Taxa der Brachyura (mit Ausnahme der Carcineretidae) auf Familien- und Gattungsniveau vom Kreide-Tertiär-Event unbeeinflusst blieben.

INTRODUCTION AND METHODS

Brachyuran crabs are the most speciose taxon among the decapod crustaceans (Martin & Davis, 2001). Their relations to other decapod taxa, their origin, and the phylogeny of fossil and recent taxa are, however, still under discussion (Glaessner, 1960; Felgenhauer & Abele, 1983; Martin & Abele, 1986; Scholtz & Richter, 1995; Crandall et al., 2000; Schram, 2001; Dixon et al., 2003; Ahyong et al., 2007).

Within the last couple of decades, morphological and molecular studies on recent taxa have been used to address phylogenetic questions concerning major groups within the extant Brachyura (cf. Gordon, 1963; Števíć, 1971a, b; Guinot, 1977, 1978, 1979; Števíć & Gore, 1981; Rice, 1983; Martin & Abele, 1986; De Saint Laurent, 1989; Spears et al., 1992; Jamieson, 1994; Jamieson et al., 1995; Marques & Pohle, 1995, 1998; Bellwood, 1996; Guinot et al., 1998; Harrison & Crespi, 1999; Sternberg et al., 1999; Schubart et al., 2000a, b; Guinot & Tavares, 2001, 2003; Rosenberg, 2001; Sternberg & Cumberlidge, 2001; Brösing et al., 2002, 2007; Tavares, 2003; Ahyong et al., 2007).

The inclusion of data from the fossil record into phylogenetic discussions and cladistic analysis of decapod crustaceans has become increasingly important (e.g., Tucker, 1998; Schweitzer & Feldmann, 2000a, b, c, 2005; Karasawa & Kato, 2001, 2003; Schram & Dixon, 2003, 2004; Amati et al., 2004; Karasawa & Schweitzer, 2004). Fossils can help to test the results of any cladistic analysis, and, in particular, the phylogenetic and evolutionary conclusions drawn from it in several ways (e.g., Ax, 1984; Sudhaus & Rehfeld, 1992; Sudhaus, 2007). Fossils can be either directly included in the cladistic analysis, alone, or together with Recent taxa. Or the fossil record is mapped on existing phylogenetic hypotheses. All these approaches have advantages and disadvantages. Here I discuss the fossil record of brachyuran crabs in the framework of cladistic analyses gained from Recent specimens.

I use the results of the cladistic analysis of Brösing et al. (2007) (figs. 1, 2) as a framework for the discussion of the brachyuran fossil record. The result of the cladistic analysis was combined with the currently known minimum age of

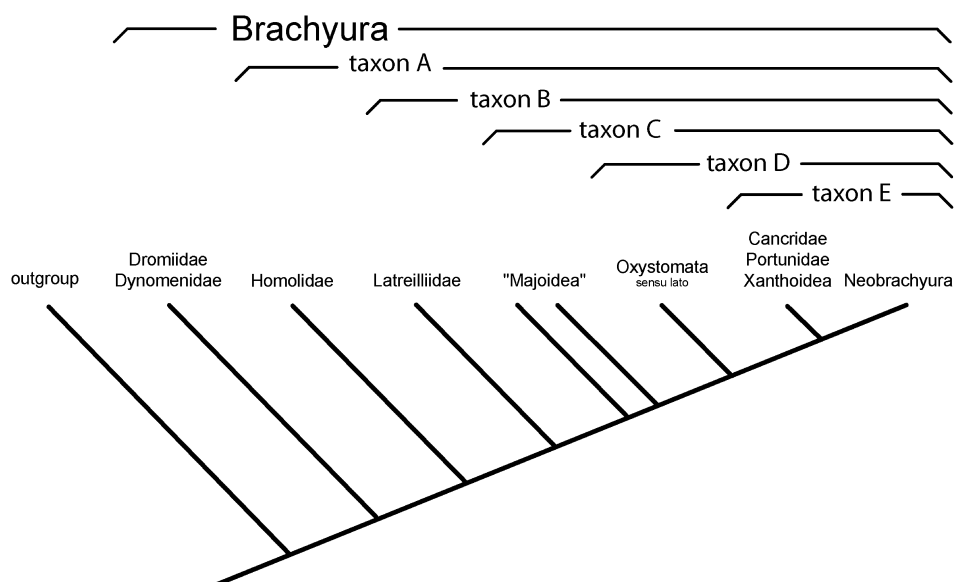


Fig. 1. Cladogram summary hypothesis on the phylogeny of the Brachyura (after Brösing et al., 2007).

these taxa to yield an outline of a time scale related to their phylogeny. Based on the suggested sister group relationships, the minimum age of some taxa was reconstructed in respect to their proposed common ancestor. This way I created some quite long ghost ranges for several taxa (fig. 3).

RESULTS AND DISCUSSION

Cladistic analysis and the fossil record

The observed foregut morphology of 66 species of Brachyura confirms that the evolution of the foregut structures is closely related to the phylogeny of the respective taxa (“families” and related ranks) (Felgenhauer & Abele, 1989). This means that the monophyly of the classical brachyuran “families” and related ranks (with the notable exception of the “Majidae”) is basically supported by this analysis (see Brösing et al., 2007). In contrast to previous accounts of the analysis of the brachyuran fossil record (e.g., Schweitzer & Feldman, 2005) I follow a strict phylogenetic reasoning, i.e., I accept only monophyletic groups — and this is also the case for the discussion of extinction events. It is obvious that discussions about extinction rates of “families” or “genera” are meaningless if these do not represent monophyletic taxa in the sense of phylogenetic systematics or cladistics. In most cases, the monophyly of the traditional “families” is confirmed by the phylogenetic

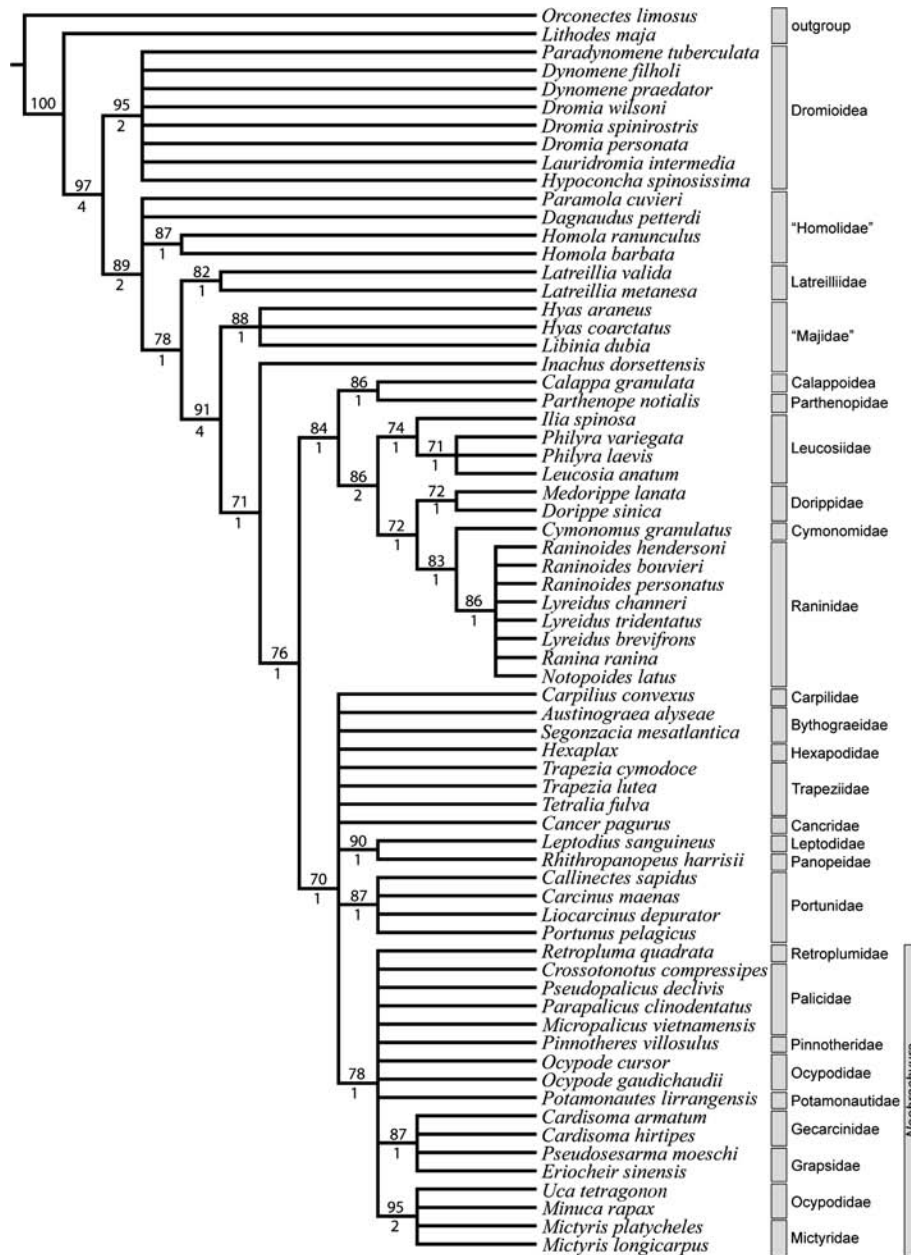


Fig. 2. Phylogenetic analysis of the Brachyura (66 taxa) and 2 out-group taxa based on 43 foregut characters. Strict consensus tree of 207 calculated trees with 121 steps. Upper number, bootstrap values; lower number, Bremer support; CI, 0.43; RI, 0.89; program used: NONA (Goloboff, 1993). [Changed after Brösing et al., 2007.]

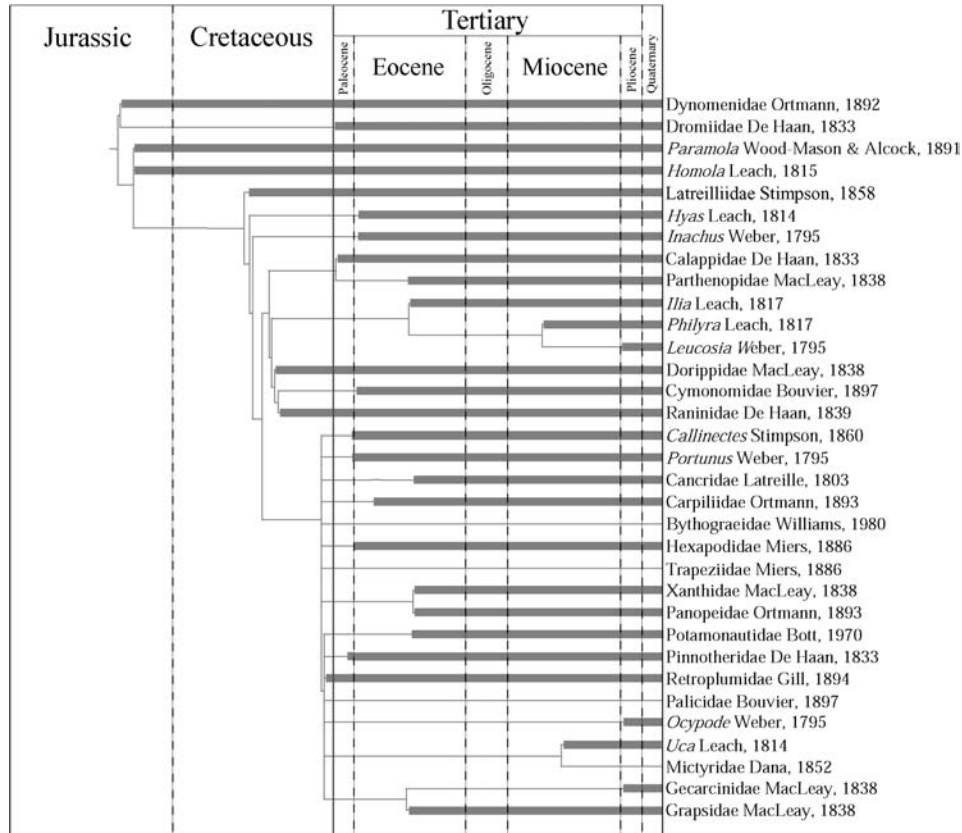


Fig. 3. Correlation of the cladistic analysis with the brachyuran fossil record. Bold line, currently known minimum age (fossil record); broken line, reconstructed minimum age; thin line, cladogram.

analysis of Brösing et al. (2007). For the sake of simplicity in the following discussion, it is assumed that this is also true for fossil “family” groupings although this is not always clear.

Dromioidea

In the analysis of Brösing et al. (2007), neither the monophyly of the Dromiidae nor of the Dynomeidae is supported, but together they form a well defined clade (see also Ahyong et al., 2007). The first fossil representatives assigned to the classical “Dromiidae” are known from several species in the Palaeocene, in particular from the Danian of Denmark, and from North America (Glaessner, 1969). “Dynomenidae” are represented by at least 10 fossil genera from the Upper Jurassic. Nine of these genera are considered as having become extinct, and only two recent genera, *Dynomene* Desmarest, 1822 and *Acanthodromia* A. Milne-Edwards, 1880 possess fossil representatives (McLay, 1999). There is no doubt

that these groups derived from ancestors that occurred in the Tethys Sea of the Upper Jurassic (McLay, 1999). Based on the monophyly of the Dromioidea, we propose a common ancestor for this taxon that must have occurred in the Upper- or Middle Jurassic.

“Homolidae”

Brösing et al. (2007) gained only ambiguous results concerning the monophyly of homolids (see also Ahyong et al., 2007). The genus *Homola* Leach, 1815 of the homolids is well known, with its first fossil occurrence in the Cretaceous of North America (Schweitzer, 2001a, b). Schweitzer assumed an early distribution of this genus within the North Polar region during the Cretaceous, followed by world-wide colonization.

Latreilliidae

There exist only a few data for the Latreilliidae, which certainly form a clade. The first fossils of the Latreilliidae are registered from the middle of the Cretaceous (Glaessner, 1960).

“Majidae”

In our cladistic analysis Majidae do not form a monophyletic group (Brösing et al., 2007) (fig. 1). Accordingly, a discussion about the fossil record of Majidae as a group is not possible. Hence, we treat species which were assigned to former Majidae independently. †*Micromaja* Bittner, 1875 is known from the Eocene of Egypt, Italy, and Hungary, as well as from the Oligocene of northern Germany (Glaessner, 1969). Moreover, findings of the genus *Hyas* Leach, 1814 from the Miocene (Germany), the genera *Inachus* Weber, 1795 and *Macropodia* Leach, 1814 from the Oligocene (Wladikawka), and the genus *Libinia* Leach, 1815 from the Miocene of North America are well known (Glaessner, 1969).

Calappoidea

Within the monophyletic Calappoidea, two major clades are established (Bellwood, 1996). In 1968, Förster assigned a further taxon, Necrocarcininae to the Calappidae, consisting of exclusively fossil genera. The fossil time interval of this taxon extends from the Aptian (lower Cretaceous) up to the Eocene. The occurrence of Necrocarcininae in Aptian formations before the first appearance of the other representatives of Calappidae, suggests that Necrocarcininae represent the stem line of Dorippoidea (cf. Schweitzer & Feldmann, 2000c).

Parthenopidae

First fossils are reported for Parthenopidae sensu lato, from the middle Eocene of Europe, Central America, and India (Glaessner, 1969). Because of its assumed sister group relationship with Calappoidea, an extension of the fossil record of the parthenopids into the middle Cretaceous can be hypothesized.

Leucosiidae

The very diverse taxon Leucosiidae, with more than 300 described extant species, has its origin in the Late Eocene. The genus *Philyra* Leach, 1817 is represented with its first fossil record in the Pliocene of the Indo-Pacific. While the genus *Leucosia* Weber, 1795 extends into the Miocene only (Indo-Pacific), the genus *Ilia* Leach, 1817 was present in the Eocene of Italy (Glaessner, 1969).

Dorippoidea

Dorippoidea are known from the Cretaceous to the Recent. The first occurrences of the genus *Orithopsis* Carter, 1872 from Orithopsidae, are in the Late Cretaceous (Schweitzer et al., 2003). On the other hand, representatives of the genera *Goniochelle* Bell, 1858 and *Dorippe* Weber, 1795 of Dorippidae have been recorded for the Oligocene and Eocene, respectively.

Cyclodorippoidea

According to the classification by Martin & Davis (2001), the taxon Cyclodorippoidea comprises three families with unclear monophyly: Cyclodorippidae, Cymonomidae, and Phyllotymolinidae. Only a few data exist of their fossil record. Glaessner (1969) mentioned two extinct genera (*Doratiopus* Woods, 1953 and *Torynomma* Woods, 1953), which were assigned to Tymolinae, within the Dorippidae. In 1980, Glaessner proposed that the Cretaceous genera *Torynomma*, *Doratiopus* Woods, 1953, *Binkhorstia* Noetling, 1881, and provisionally *Eodorippe* Glaessner, 1980 form a new family Torynommidae, within the Cyclodorippoidea.

Raninidae

In a study on the fossil and recent genera of Raninidae, 188 species in 31 genera are described (Tucker, 1998). Ten of these genera are also present today, three of them possess fossil representatives. The other 21 genera are described exclusively from fossil forms. The earliest record of Raninidae is from the Albian (Lower Cretaceous) (Tucker, 1995). According to our data, we assume a common ancestor for Raninidae and Cymonomidae occurred in the middle of the Cretaceous.

Carpiliidae

The oldest fossils of the Carpiliidae are *Harpactoxanthopsis* Via, 1959, from the middle Upper Eocene of Europe, and *Paleocarpilius* A. Milne-Edwards, 1861-1865, from the Middle and Upper Eocene of Europe, India, and Egypt.

Bythograeidae

For the taxon Bythograeidae, so far no fossil data are known. After available results, this taxon exhibits a closer relationship to representatives of the Xanthoidea, the Portunidae, the Hexapodidae, the Trapeziidae, and the Cancridae. Based on this allocation a minimum age of the Bythograeidae, comparable with that of the Xanthidae, respectively, the Panopeidae, is accepted, which reaches up to the middle Eocene. The same assumption is proposed for the taxon Trapeziidae, since also here only a few data on their biology and fossil record are present.

Hexapodidae

The first representatives of Hexapodidae in the fossil report are *Goniocypoda rajasthanica* Glaessner & Rao, 1960, from the Palaeocene of India, and *Paleopinixa rocaensis* Feldmann, Casydino, Chirino-Gálvez & Aguirre Urreta, 1995, from the Palaeocene of Argentina (cf. Feldmann et al., 1995; Schweitzer & Feldmann, 2001).

Cancridae

There is an extensive fossil record for Cancridae. This extensive data set was the basis for a re-examination of the entire family, including both fossil and recent representatives (Schweitzer & Feldmann, 2000b). The earliest accepted representatives of the Cancridae are *Lobocarcinus* Reuss, 1867 (Lobocarcininae), from the middle Eocene of Egypt, and *Notocarcinus* Schweitzer & Feldmann, 2000b (Cancrinae), from the middle Eocene of South America. It cannot be decided, where and when the first representatives of the Cancridae arose, but I assume that their common ancestor evolved before the middle Eocene.

Panopeidae

A further taxon of Xanthoidea, the Panopeidae, emerged for the first time in the Eocene of Europe. *Laevicarcinus* Lőrenthey & Beurlen, 1929, from the Eocene up to the Pliocene of Europe, and *Lophopanopeus* Rathbun, 1898, from the Eocene of Italy, are the earliest representatives of this family (Schweitzer, 2000). The first fossils of Xanthidae also occur in the Eocene.

Portunidae

Proterocarcinus lophos Feldmann, Casydino, Chirino-Gálvez & Aguirre Urreta, 1995 from the Danian of Argentina represents the earliest fossil of Portunidae (cf. Feldmann et al., 1995). Representatives of the extinct taxon Carcineretidae are suggested as possible stem group of the Portunidae (cf. Schweitzer & Feldmann, 2000a). All occurrences of Carcineretidae originate from the late Cretaceous, and this is possibly one of the few cases of an extinction in Brachyura at the end

of the Cretaceous (Fraaye, 1996; Schweitzer & Feldmann, 2000a, 2005). Due to the limited stratigraphic range of the genus *Carcinereetes* Withers, 1922, restricted to the end of the Maastrichtian, and its geographic proximity to the site of the Chicxulub impact crater, this genus is regarded as an index fossil for the early Maastrichtian (Vega et al., 2001a).

Basal Neobrachyura

Due to a lack of resolution (Brösing et al., 2007) (fig. 2) it is difficult to estimate the range of the basal groups of Neobrachyura comprising Retroplumidae, Pinnotheridae, Potamonautidae, Palicidae, and Ocypodidae. Accordingly, only the time range of the origin of Neobrachyura can be resolved.

Retroplumidae

The Indopacific distribution of the nine recent genera of Retroplumidae Gill, 1894 represents a relic of a far larger extension of this family, with representatives in the Upper Cretaceous of West-Africa and India (De Saint Laurent, 1989). A worldwide regression of the oceans in the late Cretaceous had a negative influence on benthic species-diversity of the shelf faunas, which led to extinctions within the retroplumids of America and the decrease of the African and Indian populations. This subsequently led to a shift of these forms into the deep sea (Vega & Feldmann, 1992).

Palicidae

We have few data concerning fossil Palicidae Bouvier (1898). This is true also for the biology of these animals (Castro, 2001). Only two fossil genera are known, but their taxonomic affiliation appears unclear (Glaessner, 1969).

Pinnotheridae

Pinnotheridae De Haan (1833) occur for the first time with the genus *Viapinnixa* Schweitzer & Feldmann, 2001 in the Danian (Paleocene) of Greenland and in the middle part of the San Juan Formation, Chiapas, Mexico (middle Eocene) (Collins & Rasmussen, 1992; Schweitzer & Feldmann, 2001; Vega et al., 2001b).

Ocypodidae

Ocypode, like also all other taxa of the Ocypodidae Rafinesque, 1815, the Mictyridae Dana, 1852, the Gecarcinidae MacLeay, 1838, and the Grapsidae MacLeay, 1838 are very often insufficiently represented in the fossil record. Their habitats (mangroves and estuarine areas) do not offer optimal conditions for good fossil preservation. For the genus *Ocypode*, only a few records from the Pleistocene of the U.S.A. are described (Glaessner, 1969).

Potamonautidae

For the taxon Potamonautidae (freshwater crabs) only a few fossil data exist at present, recorded from the Miocene of sub-Saharan Africa, the Nile in Egypt, and Madagascar (Martin & Trautwein, 2003).

Gecarcinidae

The grapsid sister taxon Gecarcinidae, documented by this study, possesses its first fossil records from the Pliocene of the Fiji-Islands. Based on the suggested minimum age of the Grapsidae, also for the taxon Gecarcinidae an age reaching up to the middle Eocene is accepted.

Grapsidae

A further semi-terrestrial brachyuran taxon, the Grapsidae, is documented for the middle Eocene. Within the Grapsidae, three fossil genera are described: *Metopograpsus* H. Milne Edwards, 1853 of the lower Miocene of Hungary, *Pachygrapsus* Randall, 1840 of the middle Miocene of Hungary and Poland, and *Planes* Bowdich, 1825 of the lower Miocene of the Caucasus. The closely related subfamily Sesarminae Dana, 1851 is registered with three fossil species from the lower Miocene of Brazil and from the Pleistocene of Australia. Karasawa & Kato (2001) described four fossil genera of the Varuninae H. Milne Edwards, 1853 from the beginning of the middle Eocene.

Ocypodidae

The genus *Uca* Leach, 1814, also known as fiddler crabs, possesses first fossil representatives from the Pliocene of North America, Panama, and East India.

Mictyridae

Similarly to the Potamonautidae Bott, 1970, also for the Mictyridae only insufficient fossil data exist. Their minimum age is expanded due to a sistergroup-relationship with the genus *Uca* into the Pliocene.

CONCLUSIONS

The combined analysis of the results of a cladistic analysis with the known brachyuran fossil record allows some statements with regard to a possible evolutionary scenario of this taxon (fig. 3). Those representatives of the Brachyura with the earliest known fossil occurrences (Dromioidea) also take the most basal position in the result of the cladistic analysis, followed by the Homolidae. These taxa reach their largest species diversity, together with the Raninidae and Cymonomidae, during the Cretaceous.

Despite some problems in resolution, it is evident that already by the end of the Cretaceous the majority of the “higher” crabs (representatives of the monophyla Xanthoidea, Portunidae, Cancridae, Oxystomata sensu lato, and Neobrachyura) existed. Their common ancestor even dates back to the Middle Cretaceous. In particular from the Eocene to the Miocene, a constant increase in species diversity is observed. These taxa become one of the dominant factors in the marine fauna of that time.

According to Brösing et al. (2007), within the Neobrachyura, the thoracotrematan crabs (Guinot, 1978) and some additional taxa with controversially discussed phylogenetic relationships are included. The fossil records of the Retroplumidae and Pinnotheridae, reaching up to the Upper Cretaceous and Palaeocene, the clearly described sternal position of the male-gonopores in the Palicidae (cf. Castro, 2001), a suggested sister group relationship of the Palicidae to the Thoracotremata (cf. Schubart et al., 2000a, b), morphological similarities of the foreguts, as well as characters of the carapace and the peraeopods, would lead to assume that they could be a basal taxon of the Thoracotremata. For the Thoracotremata as originally proposed by Guinot (1977) (Ocypodidae, Mictyridae, Gecarcinidae, and Grapsidae) one may assume a monophyletic origin, supported by characters of the gonopores in both sexes (Guinot, 1977, 1978, 1979; Jamieson et al., 1995; see also Brösing et al., 2007).

In view of the data available, it is suggested that the event at the K/T-boundary has had less influence on the species diversity of the Brachyura, and on that of the Decapoda in general, than originally presumed (see Schweitzer & Feldmann, 2005). Comparisons of fossil and recent taxa show, that most taxa of the Brachyura (with the exception of the Carcineretidae, Retrorsichelidae, and Dakoticancriidae, at both family and generic level, remained unaffected by the event at the K/T-boundary (Zinsmeister et al., 1989; Feldmann et al., 1995; Schweitzer & Feldmann, 2005). Collins & Jakobsen (1994) documented that approx. 66% of the genera of the Brachyura of the Danian of Denmark and Sweden survived the K/T-boundary event.

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