History of reef-dwelling Decapod Crustaceans from the Palaeocene to the Miocene with comments about Mesozoic occurrences

A zátonylakó tízlábú rákok története a paleocéntől a miocénig — a mezozoos előfordulások rövid áttekintésével

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Összefoglalás

A bentosz egyik, ökológiai szempontból igen nagy jelentőségű és nagy diverzitású csoportjáról, a tízlábú rákokról az őslénytani ismeretanyag nagyon szegényes, s ez különösen érvényes a zátonyokon élő együttesekre. A zátonyokon élt tízlábú rákok története tehát nehezen követhető az adatok tér- és időbeli hiányossága miatt. A kainozoikumból viszonylag több adat van, mint a mezozoikumból, ezért a paleocéntől a miocén végéig részletesebben tárgyaljuk a faunában észlelt változásokat. Az adatok zöme Európából származik.

A fosszilizálódás és a gyűjtés torzító hatása elsősorban a nagy méretű fajok megmaradásának, illetve megtalálásának kedvez. Zátonykörnyezetben a fosszilizálódás viszonylag kevéssé szelektál, viszont a gyűjtési módszer, ha felülete (ami, különösen régebben, általános volt), nagyon erősen kedvezhet a nagyobb példányok és fajok megtalálásának. Ezért gazdag, kis fajokat is tartalmazó faunákat általában az egyetemi városok, kutatóközpontok közelében hamarabb várhatunk, mint azoktól távolabb.

A betemetődés és főleg a gyűjtési torzítások hatása ugyan számszerűen nehezen vehető figyelembe, mégis segít a kiértékelésben, hamis következtetések elkerülésében.

A fauna változása az időben nem követhető pontosan, de világos, hogy a primitívebb csoportok (Dromioidea) fajainak száma az időben csökken, míg a fejlettebbek, köztük a Xanthoidea főcsalád egyre nagyobb szerepet kap. A satnyafarkú rákokhoz (Anomura) tartozó Galatheidae és Porcellanidae családok tagjai alárendelten, de folyamatosan jelen vannak, az előbbiek a késő-jurától, az utóbbiak a paleocéntől kezdve.

A látszólagos diverzitás a taxonómiai összetételnél is erősebben torzul ismereteink hiányossága miatt. A paleocén alacsony fajszámot talán a kréta-paleocén határon történt kihalás okozza, de ezt bizonyítani nem lehet. A felső-eocén fajszám igen magas Európában, ami valódi nagy diverzitást jelez, s részben a trópusi klímát, részben a paleocén elejétől végbement jelentős fejlődést tükrözi, valamint azt a tényt, hogy az eocénben a Tethys ősföldrajzi kapcsolatok még nagyrészt nyitottak voltak.

A miocén viszonylag alacsony diverzitás, mely sok adaton alapul, valószínűleg a begyűjtött területek (Paratethys és Földközi-tenger) már ekkorra magasabb szélességi helyzetét és fokozódó elzártságát jelzi.

Egyes csoportokon belül jól megfigyelhető a hátpáncél (carapax) hosszúság/szélesség arányának változása: a páncélok a geológiai idővel szélesebbé válnak. Ez adaptációs folyamat eredménye lehet.

Abstract

The evolutionary history of decapod crustaceans living on reefs and other marine organic build-ups is followed from the Palaeocene to the Late Miocene, with comments about similar Mesozoic

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occurrences. Crabs live on modern reefs in a great diversity. Their fossil counterparts also show a diversity higher than that which lived on other habitats, although data are not very numerous and scattered in time, in geographic position and in palaeolatitude.

Changes in the taxonomic composition are explored. Due to the scarcity of data no clear picture emerges but the proportion of primitive crabs (Dromioidea, in terms of number of recorded species) seems to decrease, while more advanced forms, among others the Xanthoidea seem to gain in number.

The apparent diversity is highly dependent on the extent of our knowledge, but a relatively low diversity seems to occur in the Palaeocene, a much higher one in the Eocene. The known Miocene faunas mostly represent a quite high palaeolatitude (Hungary and surrounding countries), with moderate diversity, but one from southern Japan represent a more southern setting.

A more or less clear change in carapace form can be observed in the families Porcellanidae and Xanthidae: the carapace growth wider with the geological time.

Introduction

For a long time the striking fact remained unnoticed, that reefs are extremely favourable and exceptional places for fossilisation of decapod crustaceans. This means that in a high energy environment also small, extremely sensitive shells may be fossilised together with bigger, more resistant ones.

In most marine environments, decapod crustaceans, including crabs, are among the most conspicuous, most frequent macroinvertebrates. This is especially true for reefs. In striking contrast, decapods are only sporadically represented in the fossil record. This is mainly attributable to two different factors. On one hand a set of taphonomic factors limit their preservational potential (MÜLLER 1993: 4; FRAAIJE 2003). On the other, most collectors recognise only big specimens (MÜLLER 1984), while small ones are only found when special attention is paid on them. In any evaluation of the fossil record of decapods, these errors ("bias") must be kept in mind although for the moment these hardly can be quantified.

The goal of this paper is to summarise the scattered data about the evolutionary history of decapod crustaceans living on reefs and on other marine organic build-ups. In this environment generally only the brachyurans and some anomurans are preserved as fossils, thus our treatment is restricted to these two groups.

The decapods are ecologically very important components of marine benthic communities with a high degree of diversity. This group, however, is quite occasionally known from fossil environments, especially from reefs. This is due partly to taphonomic factors, but to a great extent also to collecting bias. The generally small sized decapod remnants often remained unattended by collectors in the field.

Consequently, one might expect many new palaeontological data from the study of this group. Indeed, the last 20–30 years yielded a lot of new knowledge, especially from Europe, Japan and the Unites States of America (e.g. KARASAWA 1993; DE ANGELI & GARASSINO 2003; MÜLLER 1984; MÜLLER & COLLINS 1991).

From all extant marine environments, diversity of crabs is by far the highest on reefal habitats. Relation of crabs and corals may be very diverse ranging from obligate commensalism to occasional coexistence. In the fossil material signs of obligate commensalism also could be recognised (e.g. MÜLLER 1984: 94).

Fossil reefs often are poorly dated, since planctonic forams, nannoflora and many other age indicators are missing or unavailable from them. Therefore decapod remnants may even be useful in dating of them.

Palaeontological collections (samples) from remnants of reefs or any other of any other environment, and the ensemble of taxonomic data based on it are seriously distorted in relation of the original population, for several reasons. This question will be examined here. There are two groups of factors which distort the taxonomic composition of a collection (sample), namely human (collecting, determining) ones and natural, mostly taphonomic ones.

Ecology and fossilisation of crabs in reefal environments

The environment

For the term "reef" is given highly different definitions by various authors. Here the term is used in a broad sense, to refer to: build-ups of sessile benthic organisms, which have been fossilised in situ. Thus patch-reefs, coral-carpets also are included. For the communities living on and around a reef the morphology and structure of the given build-up is decisive. Most of the studied communities lived on and around build-ups made dominantly by hermatypic corals. The Upper Jurassic localities are, on the other hand, often sponge-dominated (MÜLLER et al. 2000). The only studied Cretaceous locality, in Spain, is undefined in this respect, hermatypic corals are frequent, but the microfacies is not reef-like.

Remnants of reefs generally are carbonates, mostly limestones, with a dominating "bindstone" type microfacies. A higher amount of siliciclast is poorly tolerated by corals and other framebuilders, which predominantly have a calcium carbonate frame. Occasionally reef remnants may be found in marly matrix as well, e.g. in Visegrád (Middle Miocene, Hungary, see below). Possibly, the siliciclastic influx was periodical here.

Coral reefs, as environments, are extremely diverse, but they display some similarities, too. From patch-, barrier-, and fringe-reefs the studied crab material mostly comes from patch-reefs or coral-carpets.

From the studied material the Middle (or Early) Miocene fauna of Olérdola (Catalonia, Spain, MÜLLER 1993) might represent a fringe-, or, less probably, a barrier reef. The Cap Greco fauna in Cyprus (MÜLLER et al. in prep.; FOLLOWS 1992) probably came from a knoll reef or eventually a fringe reef. In the Austrian Palaeocene a locality, Kambühel (on older maps: Kammbühel) at Neunkirchen, Niederösterreich, of reefal origin is under study (MÜLLER et al. in prep.). This reef most probably was a fringe reef.

The cause of this limitations might be that Central European Eocene and Miocene environments of these parts of the late Tethys and Paratethys were usually more favourable for the formation of patch-reefs rather than of other types of reefs.

Reefs are among the most complex marine environments. The substratum is varied, providing various hiding places, refuges, their communities display an extremely high diversity at both specific and higher taxonomic level.

The main cause of this is an extreme variability of the surface, currents, the multitude of nutriment and many other factors which are characteristic for all types of coral reefs. In addition, biocenoses of reefs are the result of a long evolution.

As a result, the biodiversity is very high for many organisms, including crabs and other decapods (SERÈNE 1972). As an estimation, the number of species of brachyurans living on the reefs of the Indo-west-Pacific realm give more than one fourth of all brachyurans living there.

Reef-dwelling decapods are generally small sized. They attract little interest in contrast e.g. to some large decapods found in some Palaeogene marls, as *Zanthopsis, Harpactocarcinus, Lophoranina* or to some Neogene *Cancer* species (which can have a price of several thousand dollars in the trade). This condition evidently awakes the interest of collectors.

Adaptation to a reef-environment is widespread in many groups, including decapods (SERÈNE 1972). The history of this adaptation is generally poorly known, partly because, although brachyurans and some anomurans are fairly frequently fossilised in reefal environments, their study has been much neglected for a long time.

The probable beginning of the adaptation of decapods to reef environments has been relatively well known already in the nineteenth century, especially by the studies of von MEYER (1860) on Late Jurassic remnants of sponge build-ups (MÜLLER et al. 2000). In the Oxfordian and Kimmeridgian the environments where the crabs lived were predominantly sponge build-ups, but in the Kimmeridgian already coral reefs also occur built mostly by the genera *Thecosmilia, Isastraea* and *Dendrohelia* (MÜLLER et al. 2000). In the Tithonian corals generally dominate, often accompanied by bivalves of the genus *Diceras*. Decapods from algal patch reefs are described from the Portlandian of England (FRAAYE & COLLINS 1996).

We have only a few data about later Mesozoic reef environments containing decapods. VIA BOADA (1981, 1982) described from Monte Orobe (Navarra, Spain) a Decapod fauna from a Cenomanian locality containing corals. The exact facies is still unknown, however.

Sporadic data about Cretaceous reef decapods are from Transsylvania, Rumania (PATRULIUS 1969), Austria (WRIGHT 1997) and the Netherlands (FRAAIJE 2003).

From Denmark and Southern Sweden a rich Decapod fauna is known from a coral bearing Palaeocene limestone, Danian (SEGERBERG 1900; COLLINS & JAKOBSEN 1994). This does not come from a reef, however (FLORIS 1992).

From Italy and Hungary (e.g. BESCHIN et al. 2001; MÜLLER & COLLINS 1991; DE ANGELI & GARASSINO 2002; CHECCHIA-RISPOLI 1905) Eocene and Oligocene faunas have been documented.

From the Miocene of the Paratethys and the Mediterranean, as well as from Japan (KARASAWA 1993; MÜLLER 1984, 1984a, 1993, 1996; GÓRKA 2002) several reef decapod occurrences have been found.

These Tertiary reef remnants generally are patch-reefs, in some cases other types of reefs also occur (see below).

Taphonomical remarks

Decapod crustaceans belong to the rare macrofossils. The main reason for this is the remarkably low mass of decapod shells if compared to their surface. The weight of a typical brachyuran carapace of 10 cm width is about 4–6 grams. The weight of a marine bivalve shell of similar size is generally 30 to 50 grams. That of a gastropod shell of this size is usually even higher, often up to 100 grams.

Thus mollusc shells of similar size generally have a mass higher than decapod shells by an order of magnitude or more. Consequently, crab remnants (among them carapaces) may be transported on the sediment surface if the current speed at the bottom is about 0,1 m/sec or higher. Most of the sediment is generally carried on the bottom and do not cover the light shells.

This transport keeps decapod remnants over the sediment/water interface. Thus at a given place of embedding the origin of taphocenosis may be quite variable. In the case of a patch reef crab remnants theoretically may be transported from the lagoon surrounding it or even from the shoreline. In spite of this, most of the intensively documented Miocene reefs in Europe (MÜLLER 1984) and Japan (KARASAWA 1993) rarely contain elements which, using the closest living relative method, could be regarded as non-reefal. There are, however, some exceptions (e. g. Diósd, Hungary, MÜLLER 1984).

Embedding is possible where areas shadowed from current occur. On these low energy spots the light shells may settle and got embedded. Potential for in situ fossilisation of reefs is evidently quite high, at least on subsiding regions where they get easily covered. Fossil reefs are mostly built of "bindstone" type limestones.

Consequently, many fossil reefs are described in the literature from Tertiary and older levels. Reefs, especially coral reefs, have a very uneven surface and contain a lot of cavities, "pockets", and micro-lagoons, protected from currents and washout. These may be within or between colonies, partly as a result of bioerosion, partly due to the morphology of the corals (MÜLLER 1993: 4). These cavities and depressions are generally protected against subsequent erosion, bioturbation or sediment redeposition.

Decapod remnants in fossil reefs may thus be expected in sediments deposited in such "pockets" (GLAESSNER 1928: 211; MÜLLER 1993). Characteristically, the low level of energy in them and the high one around the reefs result in a poorly sorted sediment with a high amount of fine grains (micrite, or even silt and clay).

Remnants of decapods may equally be entire moulds or parts of them, or entire carcasses or fragments of them. Chelae, having a slightly higher mass relative to their surface than carapaces do, are generally sooner embedded than carapaces. Similarly, the remnants are selected by size as well, making the interpretation of taphocenosises difficult.

Taphonomical papers mostly deal with the embedding process on mobile substrates. However, ZUSCHIN et al. (2000) studied the fossilisation of Molluscs on recent reefs in the Red Sea. They explored the similarity of the living communities to the shells accumulated in depressions. They found that species feeding on coral colonies are washed the quickest into the depressions. They did not describe, however, the specific, taxonomic status of the accumulating shells. Sessile forms, in contrast to vagile ones, are embedded generally in situ.

Evidently, shells of the majority of decapods are subjects of a fast sweeping off. According to ZUSCHIN et al. (2000) these may accumulate in zones of deposition in the surrounding, especially in fissures and cavities, as also seen in fossilised reefs.

PLOTNICK et al. (1988) and SCHÄFER (1951) studied the fossilisation of brachyurans experimentally. SCHÄFER (1951) studied the chance of fossilisation on mobile substrates, but did not analyse the embedding from a sedimentological-mechanical point of view. PLOTNICK et al. (1988) made experiments in carbonate environments. They concluded that the chance of preservation of artificially embedded, covered specimens is high. They could find the buried specimens after a significant time, but they had not analysed the natural process of embedding.

The preservation of decapod remnants is influenced by two main factors, if compared to other macroinvertebrates. One is the relatively small mass of their shells, promoting an off-washing. The other one is the fact, that by moulting decapods often leave more than ten complete shells during their lifetime. During embedding these shells behave almost identically with carcasses except that these are lighter, not containing the soft parts. As fossils, the carcasses may hardly be distinguished from the moulds.

On reefs, however, in most cases the skeleton separates into parts, somites and articulae. Complete skeletons are found mostly in the case of big specimens, with carapaces of 4–5 cm width or bigger. But even in such cases an entire specimen is found only among dozens or hundreds of disarticulated ones (e.g. *Panopaeus wronai*, GROSSHÖFLEIN, MÜLLER 1984: pl. 82, figs 1, 2).

The habitats of Miocene or younger species may be deduced by the closest relative principle. In general, the family status of forms may provide some information. If in a given part of a fossil reef presumably non-reefal forms appear (e.g. Calappa in Diósd, MÜLLER 1984), it seems very probable that these are strangers having been washed in by currents, say, from a deeper part of a lagoon.

Reefs, during embedding and preserving fossils, seem to select shells only moderately by size. Smaller sized decapod remnants (carapace size below 1 cm) almost everywhere are dominant in most new collections made with the help of magnifying lenses (MÜLLER 1984, 1993, 1996; MÜLLER & COLLINS 1991). Such a dominance is also characteristic for extant communities.

Evidently there is a strong selection by the chemical composition and hardness of shells. Shrimps that contain less that 20% calcium carbonate in their shells, as well as members of the similarly soft shelled Hapalocarcinidae have never been reported from fossil reefs, although they are wide spread inhabitants of reefs. Hapalocarcinidae species, commensal with corals, live in gall-like formations. Such galls theoretically could be recognised, but so far these have not been reported from fossil corals.

Errors caused by the method of collection, the preparation and the interpretation

Collecting of crabs is time consuming if compared to most other macrofossils, not to speak about microfossils. MÜLLER & COLLINS (1991), using simple statistics, demonstrated that collecting with a head band magnifier increases the

recognition of small specimens (below 10 mm) by a factor of about 10. To a certain extent this applies to bigger specimens as well, between 10 to 20 mm. This means that a caution is necessary in comparing old and new faunal lists.

In the description and figures of extant decapods the carapace often is neglected, being that many other characters are available for zoologists. In the case of fossil crabs very often just the carapace is available. This is especially so with reefal species. Mostly because of this there is a significant difference between the zoological and palaeontological systematics and nomenclature. This can be reduced, but cannot be totally avoided.

The known record of fossil crabs well reflects human, artificial factors. The known range of the rich Jurassic Prosopidae and Galatheidae faunas (MÜLLER et al. 2000) coincides with the vicinity of university cities and research centres in Europe. A similar case is evident for the European, American and Japanese Miocene and Eocene decapods as well.

These considerations hardly may be used for improving numerical evaluations, because of the significant number of assumptions, but may help to avoid incorrect comparisons. However, a correction number has been proposed (MÜLLER 1984) based upon the size of the rock pieces broken during collection.

Obviously, collecting factors promote the recognition of large specimens as taphonomic factors do. The majority of extant anomurans and brachyurans are about one cm size or even smaller. Dominance of small species is especially characteristic for reef environments (SERÈNE 1972).

FELDMANN (1990) studied the impact of the size of palaeontological samples on the palaeogeographic reconstruction. He notes that the great majority of fossil crabs has been described from European and North American localities. His conclusion is that in a study based on small samples the lack of a taxon from a given territory or age does not permit to make any conclusion. The presence of a given taxon, of course, proofs its presence. His studies were based on decapods living on mobile substrata, mainly on members of the family Raninidae. His conclusions are valid to decapods living on reefs as well.

Our data about the presence of extant genera in geological times may or may not be valid as the use of generic names, respectively the assignment to a given taxon is not equally reliable. Some authors, especially of the early literature, tended to assign species into widespread, well known, "fashionable" genera. Some names, e.g. Cancer, Panopeus, Porcellana, Xantho or that of extinct genera as *Titanocarcinus* or *Xanthilites* are often used erroneously. Names of genera, now known to appear only in later geological times, have been repeatedly used for earlier forms. Such errors may only be avoided by consistent examinations.

Occurrence of fossil Decapods in rocks of reefal origin

Remarks about the Mesozoic material

Upper Jurassic reef dwelling decapods are known almost exclusively from Europe. To assume that this reflects their areal would be absurd. More likely this is caused by the collecting factor. Reefal Upper Jurassic layers occur outside Europe mostly at remote places or subterraneosly (MÜLLER et al. 2000: 70, WEHNER 1988).

These associations consist mainly of Prosopidae. While the first known member of this family has been found in Middle Jurassic layers, in sublittoral sediments, they are quite frequent and diverse in Late Jurassic sponge and coral reefs. Galatheidae are generally less frequent, but constant participants here. Some forms have been ranged, questionably, into the families Homolidae and Dynomenidae. These crabs are characteristically small (carapace length below 2 cm, often below 1 cm. Chelae, which are possibly hermit crab remnants (Paguroidea) are subordinate.

Cretaceous reef decapods are known only from few localities. WRIGHT (1997) established that a small fauna from Lower Austria (Niederösterreich), Klement, described by GLAESSNER (1931) as Tithonian, is in fact Cenomanian.

PATRULIUS (1969) mentions a rich Cretaceous reef associated decapod fauna from the Carpathians of Rumania, presumably of Barremian age. He enumerates some Galatheidae and Prosopidae species from *Requienia* containing limestones ("Urgonian") and mentions the presence of some undetermined brachyurans.

VIA BOADA (1981) published about a fauna from Monte Orobe, Navarra, Spain. This is Late Albian or Cenomanian, corresponds to the "Urgonian" facies. 20 coral species have been described from here (RUIZ DE GAONA 1943). The family Galatheidae is represented by 5 species, while the remaining 7 species are ranged into the families Prosopidae and Dynomenidae (s. l.). The brachyuran species are relatively large as compared to Jurassic ones, while the galatheids are similar in their size to their Tertiary and extant relatives. The reefal nature of the fauna, however, has not been clearly documented.

FRAAIJE (2003), summarising earlier papers gave an overview of the Maastrichtian type area, including data about the environment. Hardgrounds with coral colonies, small bioherms occur mainly in the Meersen Member.

From the Cretaceous there are some other sporadic finds which show some relationship with reefal forms but in the description there is no mention about reefal facies.

Palaeocene

The best known and well described material comes from Fakse, Denmark (COLLINS & JAKOBSEN 1994), and some other localities in Denmark and Sweden. These are, however, not reefs, but sublittoral surfaces with patches of ahermatypic corals (FLORIS 1992). Some authors even suggest that it was formed in the aphotic zone (BERNECKER & WEIDLICH 1990). No reef structure is visible in the outcrop. The superfamily Xanthoidea includes already a significant number of species.

In the Upper Austroalpine tectonic zone, near Neunkirchen (Lower Austria= Niederösterreich) on the Kambühel (on old maps: Kammbühel) remnants of a Palaeocene reef have been found (PLÖCHINGER 1967; HÖFLING et al. 1987). The locality has been studied in close details by TRAGELEHN (1996). Following his recommendation, I could collect a rich Decapod fauna (MÜLLER et al. in prep.) from the NE side of the hill, the Ragglitz Member, from the red "patch-reef" limestone, most probably of Selandian or Early Thanetian age.

The reef probably belonged to a barrier or fringe reef, that was preserved in situ. The red coloured matrix indicates a nearby land with lateritic soil. At least ten coral species occur here, of which the species *Actinacis cognata* OPPENHEIM could be determined.

Eocene

Apart from the Hungarian Eocene material (see below), some reefal forms were described from the Palermo region, Sicily, Italy (CHECCHIA-RISPOLI 1905, and DI SALVO 1933).

From the Upper Eocene rich material has been recently described from Northern Italy. From the Lower and Middle Eocene so far only sporadic occurrences are known. A more rich material is known from Sicily, Monreale at Palermo, (CHECCHIA-RISPOLI 1905; DI SALVO 1933) but the exact facies and age of this locality would need a re-examination. The character of the fauna is similar to the reef faunas of the Priabonian of Northern Italy (DE ANGELI & GARASSINO 2002, DE ANGELI pers. comm.) and Hungary (MÜLLER & COLLINS 1991) which suggest a similar facies (or even a similar age).

The North Italian reefal Priabonian has been just partly described so far, the Galatheoids are dealt with by DE ANGELI & GARASSINO (2002). Here the best localities are in the Berici Mountains (Monti Berici) near Vicenza. The fauna seem to be even more rich in species than the Hungarian one.

From Hungary a rich fauna is known (MÜLLER & COLLINS 1991). This originates mainly from Budapest, from quarries and surface exposures in the Buda Mts. This fauna has been described originally by LŐRENTHEY (LŐRENTHEY in LŐRENTHEY & BEURLEN 1929), this posthumous work has been only slightly modified by the co-author, Karl BEURLEN (see MÜLLER 1984: 7).

The large quarries of the nineteenth and early twentieth century became abandoned by the second half of the twentieth century. During the works extensive new surfaces were accessible for collectors (often the workers found the best specimens, as mentioned by LŐRENTHEY, in LŐRENTHEY & BEURLEN 1929). Some quarries have been worked briefly in the fifties and sixties of the last century.

Later only the abandoned quarries were available for collecting (MÜLLER & COLLINS 1991). Accordingly, the collector had to pay special attention to smaller specimens, using magnifying lenses, leading to a significant increase of the apparent diversity (MÜLLER & COLLINS 1991: 91).

The level containing the coral reefs is present in a part of the Buda Mts. (Budapest), on the Gugger Mt., in the valley called Szépvölgy, Kis-Svábhegy, and some other places, but absent elsewhere. The level called by MÜLLER & COLLINS (1991) as Facies 4, seems to be a series of braided patch-reefs or extended coral carpets, which reflects a unique constellation of environmental factors (depth, climate, nutrient level, etc.) favourable for corals. Barrier- or fringe reefs probably do not occur. The Budapest Eocene material (including new findings) consists of about 60 decapod species. It seems that all Budapest localities are coeval, although there are species in all localities absent from others, but the frequent ones are generally the same. This is not the case with the two localities outside

Budapest (Eger-Kiseged, LÖRENTHEY & BEURLEN 1929) and for the yet not described Nézsa, Northern Hungary. These may be uppermost Priabonian or even Early Oligocene (see below).

Oligocene

From the Lower Oligocene a rich fauna, 15 species of decapods are reported from a facies with hermatypic corals, the Castelgomberto Limestone (BESCHIN et al. 1996; BESCHIN et al. 2001; DE ANGELI & MESSINA 1997). In the locality Monte Grumi there is a well layered limestone with red algal and branching coral patches. Most probably the bulk of the decapods is associated with these small patch reefs.

At Nézsa, (N Hungary, county Nógrád) on the S slope of Palkó-hegy, a small faunula was collected from a grey micritic limestone containing corals and red algae. The limestone is indicated on geological maps as Priabonian. The only two specifically determined crabs (*Galathea (Palaeomunida) defecta* LOR., *Daragrapsus trispinosus* M.-C.) occur both in the Priabonian and Oligocene (at Monte Grumi). The most frequent Priabonian species are all lacking, however. Thus the Nézsa fauna may be Priabonian or Early Oligocene.

Neogene

Paratethys

REUSS (1871) mentions the first reefal form, *Daira speciosa* from the Paratethys region, Austria. Subsequently, BITTNER (1877) recognises *Carpilius* sp. from the same area. LÖRENTHEY (1911) was the first to recognise the reefal origin of a crab bearing layer from the Paratethys, namely at Rákos, Budapest. This locality has already been mentioned by BROCCHI (1883). LÖRENTHEY (1911) from Rákos (Budapest) recognised a reef-building organism (*Porites* sp., LÖRENTHEY determined it erroneously as *Millepora*).

GLAESSNER (1924, 1928) mentioned several decapods from an Austrian reef locality, Baden Rauchstallbrunngraben. Probably he was the first to recognise that crabs were preserved in deep fissures between coral colonies (GLAESSNER 1928: 211).

BACHMAYER (in BACHMAYER & TOLLMANN 1953) described a rich decapod fauna from the "Fenk" quarry at Grosshöflein (Nagyhöflány, Burgenland).

Our knowledge about Neogene reef decapods was based for a long time on European material, similarly to the case of the Late Jurassic.

MÜLLER (1984) described a set of Paratethyan Badenian localities (mainly from Hungary, but Austrian, Bulgarian and Slovenian localities also are dealt with). Later (MÜLLER 1984) recollected and described the Grobie locality (Góry Swietokrzyskie, "Holy Cross Mountains", South Poland), which was first mentioned by FÖRSTER (1979). An interesting point is that Grobie (with some other localities in the vicinity) represents the northernmost Neogene excursion of coral reefs on the Globe (see also GÓRKA 2002) pointing to exceptional climatic and oceanographic conditions at that time and in that area.

In Austria there are several reef limestone localities not yet described in detail. With Dr. Georg FRIEBE I collected a rich fauna from the quarry of the Retznei

cement fabric Styria, (FRIEBE 1990). FRIEBE (1987) described a fauna from Wurzing bei Wildon Styria.

Upper Badenian reefs were found near Budapest, in three localities: the railway cut between the stations Rákos and Kőbánya Felső (district 10, Budapest). Lőrenthey already described a reefal decapod from here, (*Chlorodiella mediterranea*). Here the reef is built almost exclusively of Porites and red algae, preserved mostly in situ (LELKES & MÜLLER 1984; KÓKAY et al. 1984; MÜLLER 1984). The crab fauna is moderately rich in species. At the N margin of the Tétény plateau (SW Budapest) at the road cut Kamaraerdei út (earlier: Katona út) there is a similar facies (MÜLLER 1984)

At Diósd (MÜLLER 1984), in an abandoned quarry, unfortunately filled in by now, three coral genera with four species, associated with red algae, built the reef. Voids between coral colonies often are filled with microbialit deposits (SAINT MARTIN et al. 2000). The crab fauna is more rich here than at Rákos. The depositional environment probably was more favourable for corals and decapods as well.

The material from the Paratethyan Badenian may be divided into two groups. The Lower Badenian is more rich in hermatypic corals (Törökmező – Visegrád, SCHOLZ 1970; MÜLLER 1984), at least 12 species occur in them. The Upper Badenian localities are poorer in coral species, they contain only one to four species.

The diversity of coral species of Early resp. Late Badenian reefs is different. 14–15 species was counted in the Lower Badenian localities, while one to four in the Upper Badenian ones. For decapods, the difference is less (27 resp. 22), but there are many as yet undescribed species, e.g. from Visegrád or Styria. Thus the difference is higher. The difference in diversity seems to reflect climatic factors: the climate of at least a part of the Early Badenian (early part of Middle Miocene) was probably an extremely hot period on the Northern Hemisphere (KARASAWA 1993; ITOIGAWA 1989; SCHWARZ 1997; HARZHAUSER et al. 2003), thus a cooling could partly account for the decrease of coral diversity (see above at the description of Grobie). Other factors, as a lower grade of stability in salinity, could also contribute to such changes (PISERA 1996).

In spite of differences in diversity, the Early and Late Badenian reef decapod faunas are fairly similar to each other. E.g. *Chlorodiella mediterranea* LŐRENTHEY, or a very similar form, *Ch. tetenyensis* MÜLLER are the dominating species in each. *Daira speciosa* (REUSS) is also frequent in both ages. One striking difference is the exclusive Lower Badenian presence of *Trapezia glaessneri* MÜLLER. Recent representatives of this family are obligate commensals with corals of the family Seriatoporidae. In the Lower Badenian this family is represented by the genus *Stylophora*, evidently this could be the host for *Trapezia*. The presence of the coral genus *Stylophora* is another proof for an almost tropical climate for the Early Badenian.

Mediterranean realm

From Algeria, near Oran, a small Messinian fauna has been described (SAINT-MARTIN & MÜLLER 1988). Another Messinian decapod fauna (MÜLLER 1984a) originated from Santa Pola, Spain, where a reef was built of large colonies of a few coral species (ESTEBAN 1977).

From the Mediterranean realm numerous Miocene coral reefs have been described (e.g. ESTEBAN 1977, 1980), but significant decapod faunas have not been found for a long time. From Spain a rich (26 species) Langhian (or Late Burdigalian) fauna was described from Olérdola (Catalunya — MÜLLER 1993).The reef was probably a barrier or a fringe reef. The red or pink colour of the matrix might point to a nearby lateritic land (similarly to the case of the Palaeocene of Kambühel).

Another small reef occurs in the vicinity, at Can Sala (MÜLLER 1993). The small decapod fauna (8 species) does not contain any form identical with the Olérdola ones. In the literature the two localities are dealt with as coeval (ALVAREZ et al. 1977). This difference in the decapod fauna, however, might reflect a significant difference in age.

On Cyprus, the Lower Miocene (Upper Burdigalian) Terra Formation (FOLLOWS 1992) yielded a small but well preserved decapod fauna at the localities Cap Greco and Prodromi (FRAAYE & MÜLLER in prep.). The most frequent species here is identical with "*Panopeus*" *viai* MÜLLER, frequent also at Olérdola, Spain, but not present in the rich fauna of the Paratethys.

Also from Cyprus, from the Tortonian Koronia member (FOLLOWS 1992) René FRAAYE (pers. comm.) collected a fauna (FRAAYE & MÜLLER in prep.).

Indo-West-Pacific region (Owerview)

From the Pacific Ocean only sporadic findings were described earlier. The Miocene material from Indonesia (BÖHM in MARTIN 1922) may have lived mostly on mobile substrata (Leucosiidae are dominant). Only the species *Chlorodiella junghuhni* (MARTIN) seems to be reefal.

From the Fiji Islands Middle Miocene and Late Miocene (this latter may be Early Pliocene as well, RATHBUN 1934, 1945) faunas were published. The first one consists of few, sporadic specimens. The second paper has been posthumously published from the author's preliminary notices. Even the material is not fully cleaned yet, some determinations seem to be doubtful. The material seems to be mixed, probably originates from a reef talus.

KARASAWA (1993) published a rich fauna from a coral reef in Southwest Japan, from the Megami Formation of early Middle Miocene age. So far 26 species has been described. The age is almost identical with that of Törökmező, Visegrád (Hungary) or Grobie (Poland). At family level the Japanese fauna is surprisingly similar to the mentioned European ones. The age of these deposits seems to represent one of the highest climatic peaks of the Northern Hemisphere Neogene (KARASAWA 1993; ITOIGAWA 1989; SCHWARTZ 1997).

History of Decapods in reef environments

As often in the case in palaeontology, the history of decapods of reef environments has to be studied from small samples, isolated from each other in space and time. Consequently, the nature of the changes (weather continuous or punctuated) may not be determined. Changes of the general character of the fauna and the higher taxonomic units can be followed only approximately.

As it has been mentioned in the chapter entitled: "Errors caused by the method..." the bias caused by collection is always high. Consequently, the faunal lists are of little use in making statements about the temporal change of diversity.

The Upper Jurassic material originates almost exclusively from a part of the Tethys region and from European inland seas connected with that Ocean. From Portugal and Sicily to Poland the fauna is very uniform, containing many widespread species (MÜLLER et al. 2000). This may reflect the good spreading potential of most decapods (MÜLLER 1984) and the palaeogeographic links as well. Consequently, the European material provides a good picture about the fauna of the great and relatively uniform province Tethys of that time.

The Cretaceous material comes only from a few localities, and must be very cautiously evaluated.

Study of the Palaeocene faunas is just at its beginning. The only true reef fauna comes from one locality, Kambühel in Austria, where the diversity seems to be quite low.

The Late Eocene fauna is quite rich but it originates from a rather restricted area. According to palaeogeographic reconstructions this area was open to the Ocean system and the climate was close to a tropical one. In accordance with this, the diversity is quite high.

The Oligocene material seems to represent an impoverished descendant of the Eocene one with a limited number of new elements. This may reflect an increasing isolation from the Ocean systems.

The European, especially the Paratethyan Miocene material is marginal in that it comes from the northern margin of the zone containing coral reefs. A comparison with the coeval fauna from Megami, S Japan revealed showed a series of similar traits. The family Xanthidae is dominating in both, the families Dynomenidae and Parthenopidae are represented with one similar taxon each (KARASAWA 1993).

Patterns of diversity

It is not easy to interpret changes in diversity of reef decapods as values strongly depend on collecting factors. It seems probable, that after the high number of Late Jurassic taxa the low value of Cretaceous ones reflect mostly such factors.

We do not know to which extent the first sample from the Palaeocene locality, Kambühel is representative. The quite low diversity might be characteristic for the given locality and age, in view of the significant number of collected specimens is quite high. This low diversity might be a result of the Cretaceous-Tertiary extinction event, but to test this statement many other localities need to be studied (for this, there is a good possibility in Europe).

The high number of Eocene species certainly reflect a genuinely high diversity

The study of Oligocene reef faunas has just has begun. It seems (BESCHIN et al. 2001) that a significant change occurred near to the Eocene–Oligocene boundary and several new forms did appear here, together with the disappearance of others.

The comparatively low number of European Miocene species mirrors the high latitude and (in the case of the Paratethys) the increasing degree of isolation of the region from the Ocean system (RÖGL 1998).

This trend is illustrated in *Fig. 1*. The role and species number of groups regarded as primitive (members of the superfamily Dromioidea), Prosopidae, Dynomenidae and Dromiidae decrease with time. In contrast, currently frequent and important groups, before all the Xanthidae family gain in importance.

In spite of distortions mentioned above it may be stated that the history of brachyurans (more precisely, the reefal ones) begins with the appearance of the family Prosopidae, a member of the superfamily Dromioidea. Carapaces of this family are similar to those of the family Homolodromiidae (MÜLLER et al. 2000) to an extent that GLAESSNER (1969) unified the two families under the name Prosopidae.

Presence of the family Prosopidae apparently strongly decreases at the Jurassic/Cretaceous boundary (MÜLLER et al. 2000). Probably this mirrors the fact that in Europe, the area of shallow water environments, consequently the presence of reefs, is strongly decreasing. Possibly, this is not a global, but a regional event. In the Cretaceous a set of prosopid forms occur, partly from reef facies (VIA BOADA 1982).

One species of the prosopids is reported even from the Danian [*Plagiophthalmus depressus* (SEGERBERG), COLLINS & JAKOBSEN 1994]. Probably the group survived the Cretaceous–Tertiary event.

Reef environments, however, radically changed by this event, among others by the disappearance of rudists (JABLONSKI 1995). We do not know, however, to which extent these events influenced the life and survival of reef-dwelling crabs, including members of the family Prosopidae.
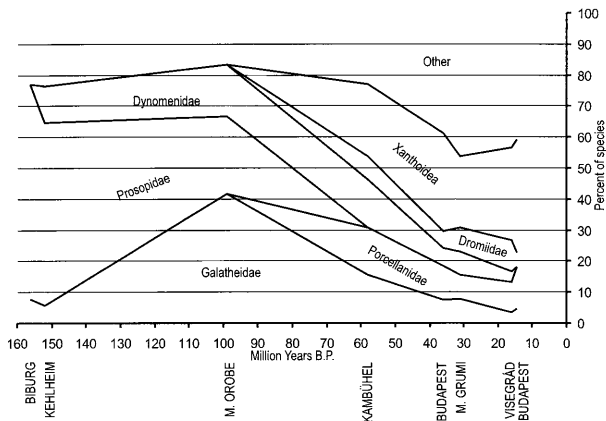

Fig. 1 Change in composition of decapod faunas of localities by time: the number of species in families or superfamilies

1. ábra. Geológiai korok (lelőhelyek) tízlábú rákfaunája összetételének változása: a fajok száma magasabb családonként vagy főcsaládonként

Reefal environments, and coral reefs are widespread, however, during the Palaeocene of Europe (e.g. BOSELLINI & RUSSO 1995; KÖHLER et al. 1993; LEIN 1982; TURNŠEK & DROBNE 1998), of which only one locality has been studied so far for decapods, namely the Kambühel Hill at Neunkirchen, Niederösterreich (Lower Austria, MÜLLER et al. in prep.). This locality yielded a rich decapod fauna of relatively low diversity. The superfamily Dromioidea is still significant here, but three Xanthoidea species dominate the fauna in terms of number of specimens.

Appearance of the family Dynomenidae also took place in the Late Jurassic (MÜLLER et al. 2000). However, it seems that the family as it is based on extant genera, hardly can encompass the Mesozoic and Palaeogene forms ranged here (Colin McLAY, personal communication). Unquestionable forms do appear in the Early Oligocene (BESCHIN et al. 2001) with the species *Dynomene lessinea* BESCHIN, DE ANGELI & CHECCHI. Middle Miocene forms appear in Japan (KARASAWA 1993) and in the Parathethys (MÜLLER 1984).

From the more advanced groups the presence of the superfamily Xanthoidea, consequently the family Xanthidae, on Cretaceous reefs has not yet been proven, except for the Maastrichtian (FRAAIJE 2003). In the Danian stage the both families Xanthidae and Panopeidae are present with forms of typical carapaces. The first surely known member of the family Trapeziidae is Late Eocene, but a species from the Palaeocene locality Kambühel, Austria, under study, may also belong here. Species of the family Carpiliidae are present quite frequently in Miocene reef formations.

Parthenopidae species live on mobile substrates. The closely related *Daira* (GUINOT 1967, either ranged into that family, or into a new one, Dairiidae), however, is a typical reef dweller. This seems to be the case of a specific adaptation to reef environments, interestingly resulting in a body shape similar to reef-dwelling xanthids.

The first member of the family Majidae appears in reef facies in the Upper Eocene. On reefs they always remain subordinate.

Swimming crabs, Portunidae are constant members of reef associations from the Eocene, but with a low number of species (e.g. *Neptocarcinus millenaris* LÓRENTHEY from the Priabonian). The majority of the group lives on open mobile environments, but reefs have their characteristic species: e.g. the living *Carupa tenuipes* DANA. At Visegrád, a very similar form occurs. Some *Thalamita* and *Charybdis* species appear consequently in reef facies.

The anomuran family Galatheidae appears in the Middle Jurassic. The first reefal form appears in the Kimmeridgian, often frequently, dominating in associations, but with a restricted number of species (MÜLLER et al. 2000: 65–66).

The first member of the family Porcellanidae ("*Porcellana*" *antiqua*, MILNE EDWARDS 1882) is known from a Cenomanian marl. Tertiary representatives of the family appear in almost all, better studied reef localities. At Kambühel, Austria, there are at least two species of porcellanids (*Fig. 1*).

The families Prosopidae, Dynomenidae and Dromiidae, parts of the superfamily Dromioidea loose their importance with time. During the Jurassic they contribute 60 to 70 percent of the species to the fauna, by the Danian this number falls below 40%, by the end of the Eocene as well as in the Miocene it is

Table 1 Temporal change of average values of length/width ratio of carapaces in different families
and superfamilies respectively

1. táblázat A hátpáncél hosszúság/szélesség arányának időbeli változása az egyes családoknál
(fajok értékének átlaga családonként, ill. főcsaládonként)

	Galatheidae	Porcellanidae	Dynomenidae	Prosopidae	Dromiidae	Xanthoidea
Miocene. Budapest	1.59	0.93	-	-	0.80	0.64
Miocene. Dunakanyar	1.59	1.08	0.78	-	0.84	0.66
Miocene. Olérdola	1.40	1.08	-	-	0.80	0.69
Miocene. Megami	1.71	1.00	0.83	-	-	0.69
Priabonian. Budapest	1.39	1.07	0.72	-	0.89	0.69
Selandian. Kambühel	1.75	1.40	0.93	-	1.00	0.77
Danian. Fakse	1.45	-	0.85	1.20	-	0.83
Albian. Orobe	1.42	-	0.73	1.05	-	-
Kimmeridgian. Kehlheim	1.54	-	0.99	1.26	-	-
Oxfordian. Biburg	1.48	-	-	1.33	-	-

about 10%. The role of Galatheidae is the highest in the Cretaceous. The superfamily Xanthoidea is dominating through the Cenozoic, but its relative importance depends highly by individual localities.

Changes of carapace form in some associations are summarised in *Table 1*.

Generally the elongate carapace is replaced in time by wider forms. This change is different in different families. Carapaces of the members of the family Galatheidae hardly change from the Jurassic to the Miocene (or today). Porcellanidae species gets wider from the Danian to the Priabonian. From the Late Eocene on an almost isometric form dominates.

Xanthidae forms show a slow and consequent broadening through geological times. Dromiidae species also widen slightly. The dominant group, in the Mesozoic the Prosopidae, further the Dynomenidae, and finally the Xanthidae, viewed together, reveal a continuous widening. This trend may reflect adaptational processes.

Acknowledgements

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