Bulletin of the Mizunami Fossil Museum, no. 32 (2005), p. 1–12, 2 pls., 5 figs., 3 tables.

The burrowing shrimp, *Protocallianassa faujasi* (Crustacea, Decapoda, Thalassinoidea), from the lower Campanian at Dülmen, Germany

Anja A. Mourik[1], René H.B. Fraaije[2], Gijsbert J. van der Zwaan[1], and Udo Scheer[3]

[1] Department of Paleontology and Stratigraphy, IVAU, Utrecht University, Budapestlaan 4, NL-3508 TA Utrecht, the Netherlands
<a.a.mourik@geo.uu.nl> <bzwaan@geo.uu.nl>
[2] Oertijdmuseum De Groene Poort, Bosscheweg 80, NL-5283 WB Boxtel, the Netherlands <info@oertijdmuseum.nl>
[3] Ruhrlandmuseum, Abt. Geologie, Goethestrasse 41, D-45128 Essen, Germany
<Udo.Scheer@ruhrlandmuseum.essen.de>

Abstract

Heavily calcified claws and other remains of the burrowing shrimp *Protocallianassa faujasi* are common in Campanian and Maastrichtian strata in the Netherlands, NE Belgium and Germany. In the present paper material of early Campanian age, collected at Dülmen (Germany), is compared to specimens from the Maastrichtian type area in the SE Netherlands and NE Belgium.

Biometric as well as morphological studies have been carried out to document sexual polymorphism in both populations. Three distinct morphotypes are distinguished: females, males and juvenile males. Biometric results point out that juveniles generally are smaller in size than mature males and females, although there is overlap. Females are characterised by a relatively longer propodus than the males, which has been related to their longer fingers.

During the early Campanian – late Maastrichtian no significant evolution in morphology appears to have taken place. This stasis may indicate that *P. faujasi* was a generalist, with an all-purpose hard-part morphology suited to life in a relatively unstable environment.

The observed underrepresentation of females in these collections can be explained by different factors. The possibility of *P. faujasi* having protandrous hermaphroditism has been suggested based on a similar pattern in sex ratio compared with modern decapod crustaceans. Although protandrous hermaphroditism is a common strategy in several species of extant decapod crustaceans, it is has not yet been reported for thalassinoid shrimps.

Key words: Crustacea, Decapoda, Thalassinoidea, polymorphism, Campanian, Germany

Introduction

Large numbers of the burrowing shrimp *Protocallianassa faujasi* (Desmarest, 1822) have been collected in Dülmen (Germany) from strata of early Campanian age. The same species is commonly found in the Maastrichtian type area of the Netherlands and Belgium (see Swen et al., 2001). Claws of *Protocallianassa* and other thalassinoidean shrimp abound in Cretaceous shelf sediments worldwide. Their mode of life and strongly calcified claws and fingers increased their preservation potential (Glaessner, 1969). After a pelagic larval stage most thalassinoidean shrimp spend their entire life in a self-constructed burrow which is used for shelter, reproduction and feeding (Griffis and Suchanek, 1991).

Although much work on fossil relatives of the extant genus *Callianassa* has been done previously, little is known about the palaeoecology of *P. faujasi*. The paper by Swen et al. (2001) is one of the few to have appeared subsequent to Mertin's (1941) work. Based on biometric data, Swen et al. (2001) recorded sexual polymorphism in *P. faujasi* documented on material from the Nekum and Meerssen members (Maastricht Formation; late Maastrichtian) at several quarries in the Maastrichtian stratotype area (southern Limburg, the Netherlands, and north-eastern Belgium). Three morphotypes were distinguished: males, females and juvenile males (Fig.1).

Over 1200 well-preserved specimens from Dülmen (Germany), allow us to record the morphology and evolution of *P. faujasi* in much more detail. Here we shall compare *P. faujasi* of late Maastrichtian age (see Swen et al., 2001) with material from the lower Campanian at Dülmen. Our main research questions were a) Does the population of *P. faujasi* found in Dülmen (Germany)

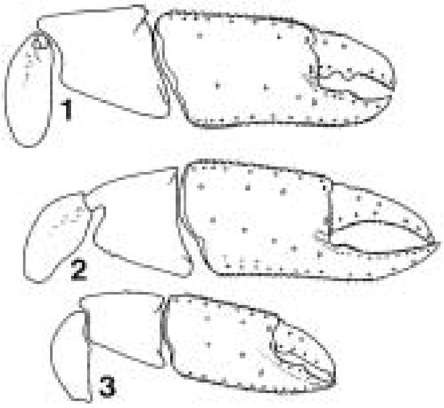


Fig. 1. Large claw pereiopod morphotypes of *Protocallianassa faujasi*, 1=adult male, 2=female, 3=immature male (after Swen et al., 2001).

have the same distinction between males, females and juveniles? And b) Has there been any evolution in the morphology of *P. faujasi* between the early Campanian and the late Maastrichtian?

Material

The fossils that have been used in this study are from the collections of the Ruhrlandmuseum Essen (Germany). They were collected in the last decades from several temporary outcrops near Dülmen (Germany) by Mr. K. H. Hilpert, an amateur palaeontologist, and handed over to the Ruhrlandmuseum in Essen (Germany). Some of the specimens are almost completely preserved in burrows (up to six in a row), which is normally quite a rare phenomenon.

The Dülmen Beds are of early Campanian age, and in terms of ammonite stratigraphy they comprise the *Placenticeras bidorsatum*, and the *Scaphites hippocrepis* III-Zone (Kennedy and Kaplan, 1995). *Gonioteuthis quadrata quadrata* and *Sphenoceramus lingua* occur in the Dülmen Beds and indicate the *lingua/quadrata*-Zone. According to micropalaeontological data the uppermost part of the Dülmen beds belongs to the *pilula*-Zone, but the decapods have been found well below this biozone.

In the outcrop where most of the specimens were collected, the sandpit Dülmen-Dernekamp, the fossil rich Dülmen Beds could be divided into seven sublayers based on lithology and fossil content. In general the layers, with a total thickness of 3.5 meters, consist of silty limestone with sandy limestone concretions. In the lower layers, bivalves have been found apart from *P. faujasi*. In sublayer 4, belemnites (*Gonioteuthis quadrata*) also have been found but they may actually belong to sublayer 5. In this latter layer, which is partly coloured red by Fe, a very diverse fauna has been found; sponges, bivalves, cephalopods (among which some very large ammonoids (Kennedy and Kaplan, 1995) of ca.1.50 m in diameter), gastropods (e.g. *Turritella sexlineata*), brachiopods (e.g. *Cretirynchia plicatelis*), echinoids (but rare), bryozoans, plant and fish remains. The upper layers are similar to the lower ones, with bivalves only.

Other decapods found in the Campanian of this region are a new species of *Xanthosia* (Van Bakel et al., in press), *Cretacoranina schloenbachi* (Jagt et al., 2003), both from the upper Campanian (Coesfeld Schichten) and the lobsters *Oncopareia* sp., *Paraclythia* sp. and *Enopoclythia* sp., all from the lower Campanian Kalkmergel Facies of the Holtwick Formation (the former Osterwicker Schichten).

From the 26 boxes of fossils, containing more than 1200 specimens in about 850 pieces, we selected 238 specimens with 245, mostly paired, first pereiopods that could be used for biometric analysis. The selection we made is a proportional reflection from the total collection; individuals from every layer and from every size were used.

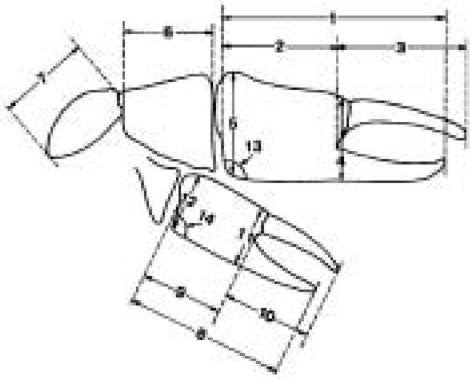
Method

Biometric methods are widely used in palaeontological and biological research. In palaeontology, for example, cores of marine sediments provide stratigraphic sequences in which variations in morphology of microfossils can be studied (e.g. Reyment, 1980). In this way, patterns of evolution can be traced. Reyment (1980) pointed to the fact that characters used for quantitative taxonomical studies are often chosen without concerning the relevance of each of the characters. Not every hard-part character has a functional morphological significance. Therefore, characters selected for measurement should be considered carefully.

Basically there are two classes of characters, continuous and discontinuous variables. The most commonly used characters are continuous variables, like length, height and width, which vary between a maximum and a minimum. Discontinuous characters are of the kind “presence or absence” of some ornamental features, such as spines and ridges. Swen et al. (2001) used several continuous characters to measure size (Fig. 2). Characteristics, on which the three morphotypes can be distinguished, were only described by them. We decided to use these characteristics as discontinuous variables so that size eventually could be related to sexual characters by Principal Component Analysis (PCA).

PCA is a data reduction technique and gives the eigenvectors of a data matrix. These eigenvectors represent different factors of influence on the data. In general the two first eigenvectors, or components, are responsible for the most variation in the data and their meaning can be derived from the variables that show a high relationship with these components. For a more detailed description of Data Reduction Techniques and Principal Component Analysis see Davis (2002).

For the continuous variables we took the same measurement-features as Swen et al. (2001) (Fig. 2). Unlike the fossils from the Maastrichtian type area, the shell of most chelae studied was lost during preparation. It was still possible to measure the absolute lengths, as the original shell material is always visible on the contact between sediment and fossil.



Large claw:
1. Propodus length
2. Manus length
3. Dactylus length
4. Front manus width
5. Distal manus width
6. Carpus length
7. Merus length

Small claw:
8. Propodus length
9. Manus length
10. Dactylus length
11. Front manus width
12. Distal manus width

Angle:
13. Between proximal and lower edge propodus of the large claw
14. Between proximal and lower edge propodus of the small claw

Fig. 2. Pereiopod measurements used by Swen et al. (2001) and in this study.

To see whether the Campanian specimens could be divided into the same three morphotypes presented by Swen et al. (2001), we derived a couple of morphotype specific characteristics from their study. We constructed a table in which we could compare our own observations with the characteristics by filling in '0' or '1', respectively 'no' or 'yes', and 'x' if preservation or preparation were too bad to pass sentence on it. Only the most pronounced characteristics were used for analysis (Table 1).

To determine morphotype, we first calculated percentages of correspondence with male, female and juvenile characteristics. No hierarchy was taken into account and all numbers '1' played an equal role in chelae type determination. Percentages of correspondence have been calculated by summing the present features (cells with '1') per morphotype and divide them by the total number of characteristics which had either '1' or '0'. In this way, by excluding cells with 'x', we prevented low percentages of correspondence due to bad preservation or preparation.

Although we were able to divide the data into three groups, some specimens were as much male as juvenile or as much juvenile as female. We therefore decided to double the weight of the most reliable features , which were judged to be "two large rounded teeth on the dactylus", a "triangular tooth at the base of the index", an "elongated dactylus", and a "convex lower margin of the manus" (Table 1), in order to get a better division in morphotypes.

The new division in morphotypes fitted better with our observations, but still we were sceptical about the very low number of females that appeared from both analyses. We designed a new

Table 1. Morphotype specific characteristics used for sexual dimorphism-analysis.

<table>
<tr><th>Type 1 (Adult Male)</th><th>Type 2 (Adult Female)</th><th>Type 3 (Juvenile Male)</th></tr>
<tr>
<td>• short fingers
• squat fingers
• curved fingers
• lower margin manus straight or sinuous
• triangular tooth in the middle of the index
• proximal half dactylus: only one tooth visible*
• proximal half dactylus: covered with two large, rounded teeth (x2)</td>
<td>• long fingers
• slender fingers
• stretched fingers
• lower margin manus straight or sinuous
• triangular tooth at the base of the index (x2)
• dactylus: sharp toothless** cutting edge
• sharply pointed dactylus
• elongated dactylus(x2)</td>
<td rowspan="2">• short fingers
• squat fingers
• curved fingers
• lower margin manus convex (x2)
• triangular tooth in the middle of the index
• broadly based index
• triangular shape of the index
• index relative flat in transverse section
• dactylus: sharp toothless cutting edge
• proximal half dactylus: only one tooth visible***
• dactylus: flat in transverse section
• dactylus: two incisions; one close to base, one close to tip</td>
</tr>
<tr><td colspan="2">* In most cases only one tooth is visible, but this also implies a male.
** No large rounded teeth.
*** Transitional forms between toothless dactylus and large rounded teeth were also found.
(x2) Doubled weight in the second analysis</td></tr>
</table>

method to distinguish the females from the males in different steps (Fig. 3). In the first step males and females have been separated based on the feature "triangular tooth", as this is the most reliable and straightforward characteristic for determining sex. After this step we identified 6 females, 185 males and 54 "unknown".

In a second step, we tried to extract some more morphotypes from the "unknown"-group. From the female features "long-, slender-, and stretched fingers" and "elongated dactylus" at least three had to be positive for being a female. Furthermore a female should have more female than juvenile characteristics, for which we selected "convex lower margin", "triangular index", "broadly based index" and "relative flat index". Second-step males became those who had three of the four following male characteristics: "short-, squat-, and curved fingers".

In a third step, juveniles were extracted from the male- and "unknown"-group. Juvenile condition had been assigned to specimens, which do *not* have two large rounded teeth, which have at least three of the selected juvenile characteristics, and more juvenile than second-step female characteristics. Eventually, in the adult male category remain all males except the well identifiable juveniles. From the 213 males and 20 "unknown", 94 were identified as juveniles and 124 as adult males (Fig. 3).

Next step was to combine the biometric data with the results of the morphological analysis, to see if the division in morphotypes was reflected in the biometry. Additionally we used a Principal Component Analysis to find the most important variables in our data. The problem of different measurement units is solved by a standardisation of the program itself, but without taking discreteness into account. To prevent an underestimation of the variance in the discontinuous data matrix, we changed all cells with '1' into '15', which was about the mean of the continuous variables measured in mm. Another adaptation to make our data suitable for multivariate analysis was to exclude some variables with too many gaps. After this selection, the matrix consisted of 18 variables. The variables used are given in Table 2.

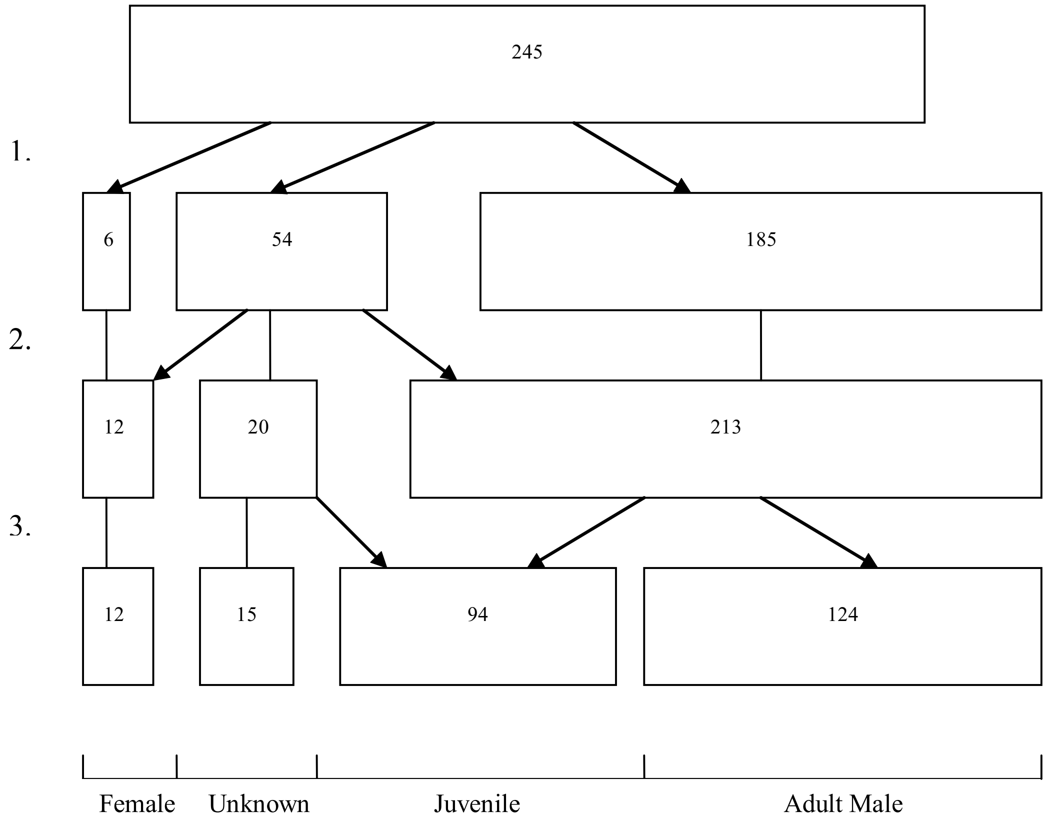


Fig. 3. Stepwise analysis of morphotypes. Step 1: "Female" is assigned to specimens with a triangular tooth at the base of the index, "male" to specimens with triangular tooth in the middle. Step 2. "Female" is assigned to specimens which have a) at least three of the following female characteristics: "long-, slender-, stretched fingers" and "elongated dactylus" and b) more female than juvenile characteristics: "convex lower margin", "triangular index", "broadly based index" and "relative flat index". Males are assigned to specimens with at least three of the following characteristics: "short-, squat-, curved fingers" and "(at least one) large rounded tooth on the dactylus". Step 3. Juveniles have been assigned to specimens which are unknown or male, which do *not* have two large rounded teeth, which have at least three of the selected juvenile characteristics, and more juvenile than female characteristics.

Table 2. Variables used for Principal Component Analysis.

Biometric	**Morphologic (Female)**	**Morphologic (Male)**
1. Propodus length	1. Long fingers	12. Short fingers
2. Manus length	2. Slender fingers	13. Squat fingers
3. Manus front width	3. Stretched fingers	14. Curved fingers
4. Propodus-Carpus angle	4. Lower margin sinuous	15. Lower margin convex
	5. Lower margin straight	16. Triangular tooth in the middle of the index
	6. Triangular tooth at the base of the index	17. Broadly based index
	7. Elongated dactylus	18. Triangular shape index

Results

By combining the biometric data with the results of the morphotype analysis, we were able to make a statistical plot comparable to that of Swen et al. (2001) (Fig. 4a, b). Both graphs show the size ranges of propodus length and manus length of the three different morphotypes. From both graphs it can be concluded that propodus length and manus length are well correlated and that a clear division into three biometrically distinct groups can be made (see also Plate 1).

Juveniles are generally smaller than males, although there is an overlap in both manus and propodus length. This can also be seen in the data from Swen et al. (2001) (Figs. 4a, b). Propodus length of early Campanian males ranges between 20 to 36 mm, with an optimum between 20 and 30 mm. In the late Maastrichtian, the range is between 15 and 35 mm, with an optimum between 20 and

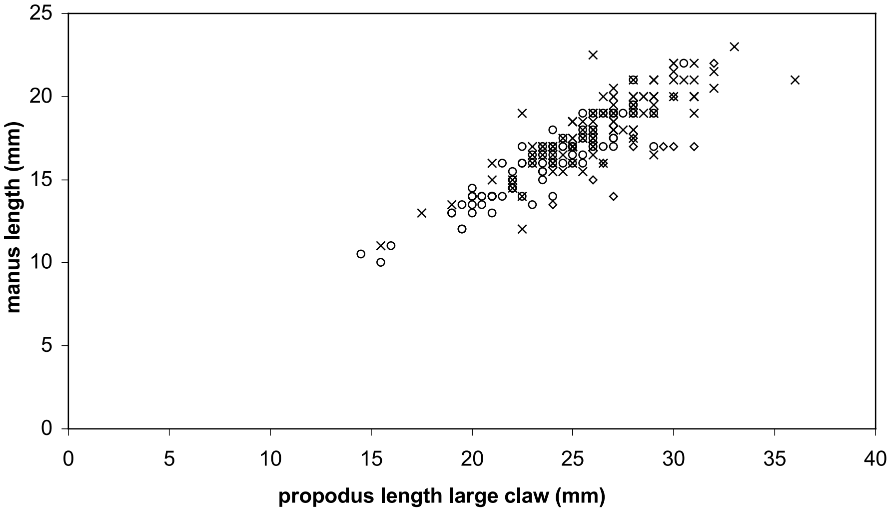


Fig. 4a. Propodus-manus ratios of *Protocallianassa faujasi* morphotypes (x=male, ◊=female, o=juvenile male) from the lower Campanian of Germany.

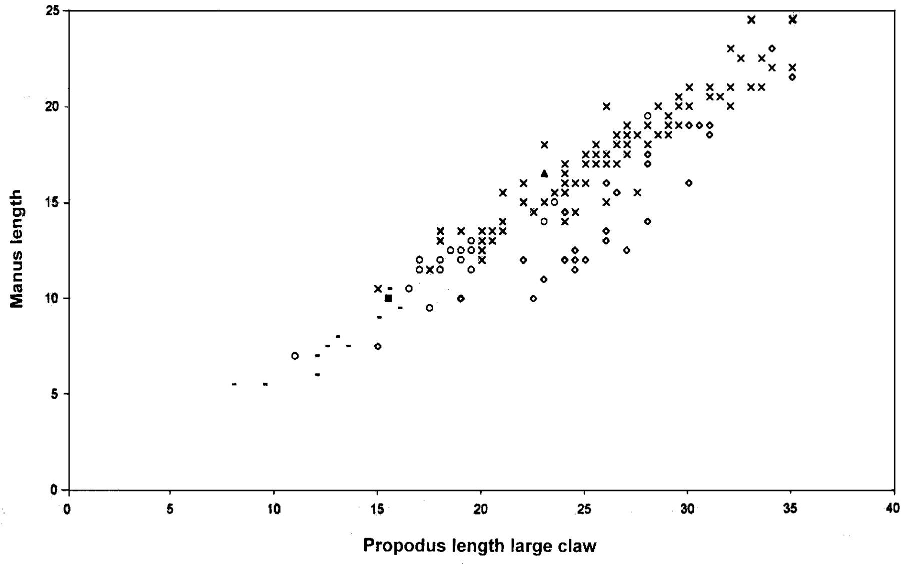


Fig. 4b. Propodus-manus ratios of *Protocallianassa faujasi* (x=male, ◊= female, o=juvenile male) morphotypes and *Corallianassa acucurvata* (-), *Protocallianassa mortoni* (_) specimens from the upper Maastrichtian of South Limburg (Swen et al., 2001) .

35 mm. The females have in general a relatively long propodus, which can be caused by their relatively long fingers. The female propodus length from the Campanian ranges from 23 and 32 mm (without a clear optimum) and in the Maastrichtian between 15 to 35 mm (optimum between 22 to 32 mm).

For the Principal Component Analysis we used a matrix with 4 biometrical and 14 morphological variables (see also Table 2). The two first components are visually presented as axes in Fig. 5. The variables scoring high on the X-axis (first component) are the female characteristics of the fingers: long, slender, stretched, and elongated. The major component of the data matrix used, explaining the largest variance, is thus based on the sexual difference in the fingers. On the Y-axis are high scores caused by the biometrical variables propodus- and manus length. Specimens that score high on the X-axis have a strong correspondence with the female morphologic features. If they also score high on the Y-axis they are also influenced by a biometric aspect, in this case length.

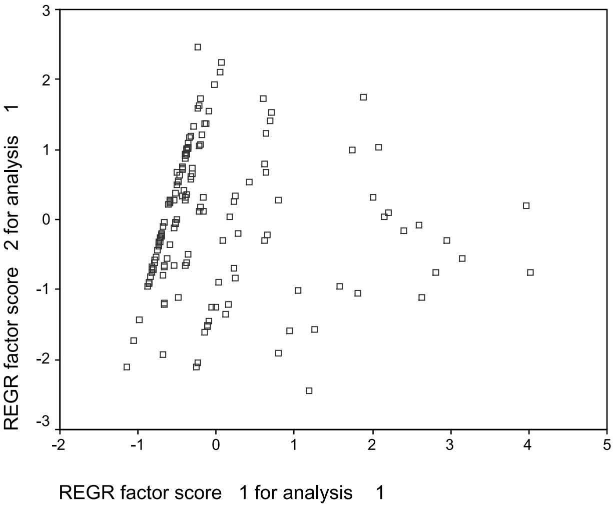


Fig. 5. Score plot of the Principal Component Analysis. First component (x-axis) shows variation in morphotype characters; second component (y-axis) shows variation in length.

Stasis during the early Campanian – late Maastrichtian interval

When comparing the biometrical and morphological data of *P. faujasi* from the early Campanian with the late Maastrichtian data of Swen et al. (2001), a remarkable correspondence can be noticed. While some 10 million years divide the two protocallianassid faunas, the morphology of *P. faujasi* did not change significantly. However, this is not as uncommon as it seems. There are many cases known from the fossil record that have shown a negligible morphological change over a geologically long period. This has been referred to as stasis (Sheldon, 1996). It is important to bear in mind that stasis is described as no significant net morphological change over a certain interval of time (Sheldon, 1996). Oscillations in between are not themselves stasis and therefore it is necessary to specify the time interval being considered.

That evolution was stepwise rather than gradual was first proposed in the paper of Eldredge and Gould (1972). In their punctuated equilibrium model they mentioned stasis as the normal state of a lineage between brief periods of rapid evolutionary change. This was quite different from the ‘phyletic gradualism’ viewpoint, which assumes that evolving lineages change at variable rates, but more or less continuously (anagenesis) (Benton and Pearson, 2001).

The pattern of rapid evolution and long periods of morphological stability has been affirmed by many research on shallow marine fauna (e.g. Sheldon, 1996). An analysis by Erwin and Anstey (1995) of the results of 58 studies on speciation patterns in the fossil record, demonstrates a widespread occurrence of stasis in the fossil record. Marine invertebrates and vertebrates seem to show punctuated patterns, with rapid speciation followed by long terms of stasis (Benton and Pearson, 2001). Several models have been developed to explain stasis.

Intuitively one might think that if the environment is stable, there is no need to change, and when the environment changes species have to evolve in order to survive in the new circumstances. Bretsky and Lorenz (1971) already demonstrated that this is not the case. They pointed out the fact that unstable onshore communities, compared with more stable offshore settings, tend to be less severely affected by sudden environmental change.

According to Sheldon’s (1996), “Plus Ça Change” model more widely fluctuating environments may have their own kind of stability (seen over geological rather than ecological timescales) *within wide reflecting boundaries.* In those environments, selection will favour “all-purpose” hard-part morphologies that are relatively inert to changes in the environment. These changes are physical variables that act on geological timescales, like changing sea level, substrate, salinity, and climate (e.g. mean temperature). The long-term “generalist” lineages that emerge then persist with no net change until thresholds are exceeded.

Another explanation has been given by Parsons’ (1994) model, which explains morphological stasis in terms of energetic costs to organisms living in varying degrees of stressful environments. Stable environments would cost less energy than unstable ones, leaving more energy for optimisation of the morphology. Costs become restrictive for evolutionary change in more unstable environments, thereby promoting stasis. Although costs may be too high for morphological change, physiological traits, such as metabolic rate, may be changing much more often (Parsons, 1994). Most physiological traits would not, however, be preserved in the fossil record.

The preservation problem might also be the explanation why stasis seems rather a rule than an exception. According to Sheldon (1996) punctuated equilibrium could be mistakenly perceived as the overwhelming pattern in the history of life because the environments in which gradualism predominated, on land, in the tropics, and in the deep sea, are rarely preserved in the fossil record. The vast majority of the macrofossil record comes from shallow marine sediments, where stasis would have predominated. So stasis in *P. faujasi* is thus no exception, it just is in accordance with the environment in which it has been living.

Biogeography of the genus *Protocallianassa*

Fossils of *Protocallianassa faujasi* are abundant in Upper Cretaceous strata around Western Europe. Other species assigned to the genus *Protocallianassa* have been found world-wide from Early Cretaceous to Eocene. However, the systematics of the genus *Protocallianassa* is confusing and inconsistent (Swen et al., 2001).

In 1930, Beurlen introduced the genus *Protocallianassa* and the subfamily Protocallianassinae. Dana had established the family Callianassidae in 1852, while the genus *Callianassa* already existed from 1814 (Leach, 1814). As a consequence, many species had to be renamed after Beurlen's publication in 1930. But until Mertin (1941) enumerated criteria to distinguish chelae of *Protocallianassa* from *Callianassa*, the two genera were often mixed up. In general, Cretaceous forms were named *Protocallianassa* and Tertiary forms *Callianassa*. With the study of Mertin, the problem had not yet been solved. In both groups many species have been distinguished due to heterochelous first chelae and sexual dimorphism (Aguirre Urreta, 1989) and even polymorphism (e.g. Swen et al., 2001), and many of them have to be synoymized. An overview of the occurrences that are known today are given in Table 3.

With numerous records of *Protocallianassa* in the northern hemisphere and the first occurrence of the genus in the southern hemisphere (Aguirre Urreta, 1983), the question arises if, and how, the species could disperse from the southern to the northern hemi-

Table 3. Occurrences of the genus *Protocallianassa* (+ = present). References: [1]Swen et al. (2001), [2]Mertin (1941), [3]Förster (1973), [4]Roemer (1841), [5]Milne-Edwards (1860), [6]Kris and Cech (1974), [7]Fritz (1867), [8]Fritz and Kafka (1887), [9]Aliev and Aliev (1989), [10] Roberts (1962), [11]Vega et al. (1995), [12]Beikirch and Feldmann (1980), [13]Bishop (1985), [14]Rathbun (1935) , [15]Feldmann (pers. comm.), [16]Feldmann et al. (1995), [17] Förster and Stinnesbeck (1987), [18]Aguirre-Urreta (1983), [19]Feldmann and Wilson (1988), [20]Taylor (1979), [21]Glaessner (1956)

		Europe	West Asia	North and Central America	South America	Antarctica	Australia
Tertiary	**Eocene**				+[15]	+[19]	
	Paleocene			+[10]	+[16]		+[21]
Late Cretaceous	**Maastrichtian**	+[1]		+[10,11]	+[17]		
	Campanian	+[2]		+[10-13]			
	Santonian	+[2,3]		+[14]			
	Coniacian	+[2]	+[9]	+[14]			
	Turonian	+[4-8]		+[11,14]			
	Cenomanian	+[5-8]		+[14]			
Early Cretaceous	**Albian**						
	Aptian					+[20]	
	Barremian				+[18]		
	Hauterivian						
	Valanginian						
	Berriasian						

sphere.

Connections in the high southern latitudes in the Early Cretaceous are known from benthic foraminifera and ostracod communities (Sigal et al., 1970) and from many parallels between the Cretaceous macrofossils of Australia, New Zealand, western Antarctica and South America (Stevens and Clayton, 1971). Feldmann et al. (1996) drew up an inventory of decapod faunas from Antarctica, Argentine, Chile, New Zealand and Australia. Works of various authors demonstrated that the decapod fauna of Mesozoic rocks in Antarctica (mainly Late Cretaceous) was diverse and that the taxa inhabiting that region were closely related to the taxa in lower latitudes. Results of their study also suggested that Antarctica might have played a central role in the distribution of decapods throughout the Southern Hemisphere.

A possible dispersal route from the Southern Hemisphere to the Northern Hemisphere could have been by movement along the shelves of the eastern Pacific. The Austral basin in South America, which developed south of latitude 45˚S, was in the Early Cretaceous connected to the Pacific. During the Cenomanian, when South America and Africa separated, a seaway to the South Atlantic established as well (Camacho, 1967). Although the ocean was still quite narrow, a South Atlantic Gyre was already developing (Gordon, 1973). On the west side of the South Atlantic, the occurrence of warm water, keeled globotruncanid foraminifera in the late Senonian of Argentina is taken by Bergquist (1971) as evidence for an ancestral Brazil Current. Absence of rudists on the Atlantic Coast of Africa indicates an equatorward flow that brought water from the high southern latitudes northward. Movement along the shelves of western Africa could have been a second way of dispersal to the northern hemisphere.

The first occurrence of *Protocallianassa* in the northern hemisphere seems to be both in the Cenomanian of the Atlantic Gulf (Rathbun, 1935) and Europe (Milne-Edwards, 1860; Kris and Cech, 1974; Fritz, 1867; Fritz and Kafka, 1887). This suggests that dispersal has taken place after opening of the South Atlantic Ocean. Records of *Protocallianassa* from the Early Cretaceous of the Central Americas and the North Atlantic region are questionable according to Schweitzer et al. (2002). A better look at *P. russelli* (Bishop, 1983) from the Albian of Texas, reveals indeed that this is not a *Protocallianassa*.

Schweitzer et al. (2002) studied the origin of the decapods in the tropical and subtropical regions of America based on first occurrences of taxa. Most genera appear to have originated within the area, some 20% originated in the North Atlantic region (Greenland, Iceland, the British Isles, Scandinavia, and northern continental Europe) and only from a few genera the origin is equivocal. Exchange between European and North- and Central American faunas could have taken place by larval dispersal along the continental shelves, as the two continents were still positioned relatively close to each other in the early Late Cretaceous (Schweitzer et al. 2002).

At the Cretaceous-Tertiary boundary, *Protocallianassa faujasi* disappeared from Europe. In North America *P. mortoni*, which is either closely related to *P. faujasi* (Toolson and Kues, 1996), or even is conspecific (Swen et al., 2001), is still found in Paleocene sediments (Roberts, 1962). In the Southern Hemisphere, *Protocallianassa* has still been found in Paleocene and Eocene sediments (Glaessner, 1956; Feldmann and Wilson, 1988; Feldmann et al.,1995; Feldmann, pers. comm.), but it is not clear whether the genus survived here, or reappeared. From the Albian to the Campanian we are not aware of any records of *Protocallianassa* on the southern hemisphere.

Preservation in burrows

Swen et al (2001) used the system of Griffis and Suchanek (1991) to classify the burrows of *P. faujasi* found in the Maastrichtian Emael and Nekum member in the Maastrichtian stratotype area. Based on the presence of long, straight shafts with horizontally extending side shafts, combined with often complex to dichotomous branched parts, subcircular turnarounds and short dead-ends or resting chambers (Picket et al., 1971) the burrows are assigned to type 4 (Swen et al., 2001), which suggests that *P. faujasi* has been a suspension feeder.

The presence of more than one individual in the burrows of *P. faujasi* suggests that this animal lived communally within a continuous burrow system. Also some recent *Callianassa* species show this living mode. Dworschak and Pervesler (1988) found in one burrow system 192-454 animals m^{-2} of *C. bouvieri*. Pryor (1975) was able to pump 100 shrimps out of 10 surface apertures, which he took to indicate that the animals lived together in one burrow system.

Some twenty collection pieces with two or more individuals have been found (Plate 2). In most cases these pieces are fossil burrows, which can be inferred from the fact that they have an elongated shape which fits the width of the animals. As preserved, we may be viewing the fossils from the underside. This can be concluded from the fact that they always lie on one side of the tube. Due to gravity, their skeletons sank down with the heaviest point, the large claw, at the bottom of the burrow. This claw now lies on top when viewing the pieces from below.

From many individuals the abdomen is preserved and is curled toward the cephalothorax. From post-mortem callianassids it is known that they are loosely enrolled (Grimm and Föllmi, 1994). Remarkable however, is that most fossils are rotated in the same direction. When examining the right or left handiness of the animals, it becomes clear that right-handed animals are rotated clockwise and left-handed animals anticlockwise. Although the division between right- and left handed *Protocallianassa faujasi* is almost 50:50 (this study), in several pieces containing more individuals the handiness was uniform, or nearly uniform.

Another remarkable fact is that their claws are aligned in almost the same direction. The curled tails point to a narrowing end of the tube. Pickett et al. (1971) examined also a burrow with complete animals and noticed the animals where probably situated in a dead-ending burrow with their claws pointing somewhat obliquely forwards to entrance. According to Pickett et al. (1971) these dead-endings are resting chambers that are occupied by the animal during non-burrowing periods.

The chelae found in the burrows were often thought to be moults (Mertin, 1941) because of their great abundance as well as the fact that often only chelae are found and not the whole animal. Mertin (1941) tried to answer the question about whether or not the fossil remnants in the burrows are bodies or just moults. He pointed to the way lobsters moult. Lobsters crack open between carapace and abdomen to crawl out, but the exoskeleton could flap back into its original state after the animal has moulted. This makes a distinction between exoskeleton and body in the fossil record impossible. A good argument for recognizing a moult could be that the body-parts lie in a strange position, with the carapace and abdomen still close together. But taphonomic processes could also have caused destruction of the bindings and loose or strange lying parts are therefore not for certain moults.

At least two reasons can explain why the fossils in the burrow are *not* moults. First of all, Lutze's (1938) description of a *Callianassa* moult forms a good argument. According to his observations the moulting process started in the burrow but the animal crawled outside to get rid of his exoskeleton. After moulting, which took only 10 minutes, it disappeared quickly into his burrow again. In this case moulting remnants would not be expected inside the burrows. Also according to Schäfer (1962), thalassinid moulting does not take place in the burrow. Secondly it is remarkable that all individuals that have been found in the burrows lie in the same position and that there is no example of a carapace and abdomen lying apart from each other. Therefore the remains are likely to be dead animals themselves.

If the fossils are indeed not moults, the question arises why the dead animals are often found in the dead-endings. A first explanation for finding dead animals in a burrow could be that sedimentation events closed off all entries. Although from recent callianassids it is known that they create a tube to re-establish an opening when their burrows become buried with sand (Bromley, 1990), rapid sedimentation events can also overwhelm the animals, causing in situ burial of decapods (Glaessner, 1969). However, it is not very likely that the animals found together in dead ending parts of the burrow system are killed *in situ*.

Another possibility is that these dead-endings are fossil mortuaries. Farrow (1971) noticed a curious aspect of callianassid burrows. Some tunnels were conspicuously packed with gravelly debris, while others are stuffed with eel-grass blades. Both size fractions packed into the tunnels represent material that would be most difficult for the organism to flush out. Dead individuals may have been carried away by the living ones in order to keep the burrow-system passable. The best way of transportation would then have been to grab the claws and place them with the curled abdomen into a dead-ending.

Female absence

Not all individuals from the Dülmen-collection are as equally preserved. Some could not be identified because the propodus was missing. It is remarkable that only 11 females out of 245 well preserved specimens have been identified. In the fossil burrows containing more than one individual no females were found at all, but with their very low abundance this might also just be a coincidence. Nevertheless, the fact that in both populations of the Maastrichtian and Campanian so few females have been found needs to be explained.

The fact that juveniles found by Swen et al. (2001) have a large triangular tooth in the middle of the dactylus, led them to the conclusion that all juveniles are probably males. The low number of females and juvenile females are, according to them, due to selective collection and preservation. Females are generally less calcified than adult males and might therefore be less interesting for collectors. But we do not expect a collection bias for the studied collection. The collection of the Ruhrlandmuseum consists of very well and very poorly preserved fossils from which we have chosen not only the best ones. Moreover, juveniles are also less calcified than adult males, but they have been found in large numbers. But, if it appears that juveniles do not show sexual dimorphism, the small number of female might have its origin here.

An ecological explanation of the under representation of the females may be that they lived separated from the males. Utilisation of different habitats by the two sexes, one sex being more active than the other, or an out-migration of one sex are all known to alter the sex-ratio of a sampled population (Wenner, 1972). It may be that the females lived just in the shallower parts of the burrows for optimal ventilation of the eggs. During storm-driven and gravity driven flows, when erosion of the sea bottom destroys the upper part of the burrows, it is likely that the animals present in this shallow part are taken away with the flow to be re-deposited elsewhere. Grimm and Föllmi (1990) who examined burrows of thalassinoides and gyrolithes in well laminated organic rich sediments of the San Gregorio Formation in Mexico, developed a model based on this phenomenon and called it the ‘Doomed Pioneer’ model. Events of high turbulence have a severe impact on benthic and endobenthic communities, but transported endobenthic fauna has a good change of survival due to its burrowing habits. Callianassids can survive exhumation, turbulent transport and re-deposition and may even be able to survive in an oxygen-depleted environment. However conditions for regeneration in such environments are very bad, and eventually the transported fauna disappears (Grimm and Föllmi, 1994). Although the occurrences of these turbulent sedimentation events may seem rare from human perspective, on a geological time scale they have been quite common. However, the problem of the absence of females has not been solved in this way. One might expect to find a complementary female biased population elsewhere in the re-deposited sediments, but until now we are not aware of such a record.

Another possibility causing the observed sex ratio in *Protocallianassa faujasi* is attributed by various researches to the reproductive activity of Decapoda. Heegaard (1967) studied the sex ratio of the penaeid shrimp *Solenocera membranacea.* He suggested a sex reversal based on the absence of any females “as small as, or smaller than, the average male size”. Also Ghiselin (1969) stated that a consistent lack of either males or females in the smaller size classes of a species generally leads to the unambiguous conclusion that sex reversal is a normal occurrence in that species. Sex reversal is also referred to as sequential hermaphroditism. If the sex reversal is from males to females it is called protandrous hermaphroditism. Females enter the population as juveniles have approached the sex reversal size. In the higher age classes relatively more females are found in the population.

The lack of juvenile females in our data clearly points to this conclusion. The average size of the few females we found is significant different from the average male and juvenile size, and small females have not been found. Although protandrous hermaphroditism is a common strategy in several species of decapod crustaceans (Yaldwyn, 1966; Gherardi and Calloni, 1993; Brook et al., 1994), it is yet not known for thallassinoid shrimps. Still, the under representation of females is no evidence of protandry. But as long as no small females are found in protocallianssids more research on protandrous hermaphroditism among fossil decapods must be done to test our suggestion.

Conclusions

When comparing *Protocallianassa faujasi* from the lower Campanian with those studied by Swen et al. (2001) from the upper Maastrichtian we can conclude that both populations show sexual polymorphism. Three biometrically distinct morphotypes can be divided. Juveniles (probably males) are smaller in size than mature males and females, although an overlap exists. Females are characterised by a relative long propodus, probably due to their longer fingers.

Based on stratigraphic analysis no evolution has taken place in the morphology of *Protocallianassa faujasi* during the early Campanian – late Maastrichtian interval. This stasis in the lineage of *P. faujasi* may indicate that the species was a generalist, with an all-purpose hard-part morphology for life in a relative unstable environment.

It seems that the origin of the genus *Protocallianassa* lies in the high southern latitudes, but more first occurrences of protocallianassids are needed to confirm this. Dispersal to the northern hemisphere could have taken place along the eastern Pacific shelves or along the west coast of Africa during the late Cenomanian when an equatorward flow developed in the South Atlantic Ocean. Migration between Europe and North-Central America will have been facilitated by the still narrow North Atlantic.

The observed under-representation of females in the collection can be explained by different factors. But to us the most likely is the possibility of protandrous hermaphroditism.. In the case of protandry, all young animals are males. As they approach sex reversal size some may become female. Although protandrous hermaphroditism is a common strategy in several species of recent decapod crustaceans, it has not been reported for thalassinoid shrimps. More research on this topic is needed as long as juvenile females remain absent.

Acknowledgements

We thank Karl-Heinz Hilpert who collected the specimens and supplied us with additional information. For extra information and help we thank M. B. Aguirre-Urreta, G. A. Bishop, D. Felder, R. M. Feldmann, N. L. Giesen, W. den Hartog, J. W. M. Jagt, U. Kaplan, H. Karasawa, A. Radwański, F. J. Vega and T. Visscher.

References

Aliev, O. B. and Aliev, R. A. (1989), Burrowing shrimp from the upper Cretaceous of the Malyi Kavkaz Mountains, USSR. *Paleont. Zhur.,* **5**, 141–143.

Aguirre-Urreta, M. B. (1983), Crustáceos Decapódos Barremianos de la región del Tucu-Tuco, provincia de Santa Cruz. *Ameghiniana*, **19**, 303–317.

Aguirre-Urreta, M. B. (1989), The Cretaceous Decapod Crustacea of Argentina and the Antarctic peninsula. *Palaeontology,* **32**, 499–552.

Beikirch, D. W. and Feldmann, R. M. (1980), Decapod crustaceans from the Pelugerville Member, Austin Formation (late Cretaceous: Campanian) of Texas. *J. Paleont.,* **54**, 309–324.

Benton, M. J. and Pearson, P. N. (2001), Speciation in the fossil record. *Trends in Ecology and Evolution,* **16**, 405–411.

Bergquist, H. R. (1971), Biogeographical review of Cretaceous Foraminifera of the Western Hemisphere. *North American Paleontological Convention Proceedings,* **L**, 1565–1609.

Beurlen, K. (1930), Vergleichende Stammesgeschichte Grundlagen, Methoden , Probleme unter besonderer Berücksichtigung der höheren Krebse. *Fortschr. Geol. Paleont.,* **8**, 317–586.

Bishop, G. A. (1983), Fossil decapod crustaceans from the Lower Cretaceous, Glen Rose Limestone of the Central Texas. *Trans. San Diego Soc. Nat. Hist.,* **20**, 27–55.

Bishop, G. A. (1985), Fossil decapod crustaceans from the Gammon Ferruginous Member, Pierre Shale (Early Campanian), Black Hills, South Dakota. *J. Paleont.,* **54**, 309–324.

Leach, W. E. (1814), Crustaceology. *In* Brewster, D. (ed.), *Edinburgh Encyclopedia,* **7**, 385–437.

Bretsky, P. W. and Lorenz, D. M. (1971), Adaptive response to environmental stability: a unifying concept in paleoecology. *North American Paleonological Convention Proceedings, 1969,* **1**, 522–550.

Bromley, R. G. (1990), Trace fossils. *Unwin Hyman. London.*

Brook, H. J., Rawlings, T. A. and Davies, R. W. (1994), Protogynous Sex Change in the Intertidal Isopod *Gnorimosphaeroma oregonense* (Crustacea: Isopoda). *Biol. Bull.,* **187**, 99–111.

Camacho, H. H. (1967), Las transgresiones del Cretáceo superior y

Terciario de la Argentina. *Rev. Asoc. Geol. Argentina,* **22**, 253–424.

Davis, J. C. (2002), Statistics and data analysis in geology. New York: Wiley, 2002.

Desmarest, A. G. (1822), Histoire naturelle des crustacés fossils, sous les rapports zoologiques et les crustacés proprement dites. Paris, 685 p.

Dworschak, P. C. and Pervesler, P. (1988), Burrows of *Callianassa bouvieri* Nobili, 1904 from Safaga (Egypt, Red Sea) with some remarks on the Biology of the Species. *Senckenbergiana marit.,* **20**, 1–17.

Eldredge, N. and Gould, S. J. (1972), Punctuated equilibria: an alternative to phyletic gradualism. *In* Schopf, T. J. M. (ed.), *Models in Paleobiology,* W. H. F reeman & Co., p. 82–115.

Erwin, D. H. and Anstey, R. L. (1995), Speciation in the fossil record. *In* Erwin, D, H. and Anstey, R. L. (eds.), *New Approaches to Speciation in the fossil record. Colombia Univ. Press. New York,* p. 11–38.

Farrow, G. E. (1971), Back-reef and lagoonal environments of Aldabra atoll distinguished by their Crustacean burrows. *Symp. Zool. Soc. London,* **28**, 455–500.

Feldmann, R. M. and Wilson, M. T. (1988), Eocene decapod crustaceans from Antarctica. *Geol. Soc. America, Mem.,* **169**, 465–488.

Feldmann, R. M., Aguirre Urreta, M., Chirino-Gálves, L. and Casadío, S. (1996), Paleobiogeography of Cretaceous and Tertiary Decapod Crustaceans from Southern South America: The Link with Antarctica. *The Antarctic Region. Geological Evolution and Process,* p. 1007–1016.

Feldmann, R. M., Casadío, S., Chirino-Gálvalez, L. and Aguirre Urreta, M. (1995), Fossil decapod crustaceans from the Jaguel and Roca formations (Maastrichtian-Danian) of the Neuquén Basin, Argentina. *Paleont. Soc. Mem.,* **43**, 1–22.

Förster, R. (1973), Die Krebse und ihre Bauten aus dem Santon der Gehrdener Berge. *Ber. Naturhist. Ges. Hannover,* **117**, 149–162.

Förster, R. and Stinnesbeck, W. (1987). Zwei neue Krebse, *Callianassa saetosa* n. sp. und *Homolopis chilensis* n. sp. (Crustacea, Decapoda) aus der Oberkreide Zentral Chiles. *Mitt. Bayer. Staatssl. Paläont. Hist. Geol.,* **27**, 51–65.

Fritsch, A. (1867), Uber die Callianassen der bohemischeb Kreideformation. *Abh, Kon. Bohm. Gesell. Wiss.* **15**, 1–12.

Fritsch, A. and Kafka, J. (1887), Die Crustaceen der Böhmischen Kreideformation. Selbstverlag Prag, 54 p.

Gherardi, F. and Calloni, C. (1993), Protandrous hermaphroditism in the tropical shrimp *Athanas indicus* (Decapoda: Caridea), a symbiont of sea urchins. *Jour. Crust. Biol.,* **13**, 675–698.

Ghiselin, M. T. (1969), The evolution of hermaphroditism among animals. *Quart. Rev. Biol.,* **44**, 189–208.

Gleassner, M. F. (1956), Crustacea from the Cretaceous and Eocene of Western Australia. *Jour. R. Soc. Western Australia,* **40**, 33–35.

Glaessner, M. F. (1969), Decapoda, p. R399-R533. *In* Moore R. C. (ed.), *Treatise on Invertebrate Paleontology, Part R, Arthropoda 4, volume 2.* Geol. Soc. America & University Kansas Press.

Gordon, W. A. (1973), Marine life and ocean surface currents in the Cretaceous. *Jour. Geol.,* **81**, 269–284.

Griffis, R. B. and Suchanek, T. H. (1991), A model of burrow architecture and trophic modes in thalassidinean shrimp (Decapoda: Thalassinidea). *Marine Ecology. Progress Series,* **79**, 171–183.

Grimm, K. A. and Föllmi, K. B. (1990), Doomed Pioneers: Event deposition and bioturbation in anaerobic marine environments. *Amer. Assoc. Petrol. Geol. Bull.,* **74**, 1–666.

Grimm, K. A. and Föllmi, K. B. (1994), Doomed Pioneers: Allochthonous Crustacean Tracemakers in Anarobic Basinal Strata, Oligo-Miocene San Gregorio Formation, Baja California Sur, Mexico. *Palaios,* **9**, 313–334.

Heegaard, P. (1967), On the behaviour, sex-ratio and growth of *Solenocera membranacea* (Risso) (Decapoda, Penaeidae). *Crustaceana,* **13**, 227–237.

Jagt, J. W. M., Fraaije, R. H. B., Van Bakel, B. W. M. and Coole, Y. (2003), New data on the raninid crab *Cretacoranina schloenbachi* (Schlüter, 1879) (Late Cretaceous, NW Germany). *Bull. Mizunami Fossil Mus.,* **30**, 51–55.

Kennedy, W. J. and Kaplan, U. (1995), *Parapuzosia* (*Parapuzosia*) *seppenradensis* (Landois) und die Ammonitenfauna der Dülmener Schichten, unteres Unter-Campan, Westfalen. *Geol. Paläontol. Westfalen,* **33**, 5–41.

Kriz, J. and Cech, S. (1974), *Protocallianassa* burrows from the Bohemian upper Cretaceous. *Casopis pro Mineralogii a Geologii,* **19**, 419–424.

Lutze, J. (1938), Über Systematik, Entwicklung und. Ökologie von *Callianassa. Helgol. Wissensch. Meeresuntersuchungen.* Band 1, Heft 2.

Mertin, H. (1941), Decapode Krebse aus dem Subhercynen und Braunschweiger Emscher und Untersenon, sowie Bemerkungen über einige verwandte Formen in der Oberkreide. *Nova Acta Leopoldina,* **10**, 149–264.

Milne-Edwards, A. (1860), Monographie des décapodes macrures fossiles de la famille des Thalassiniens. *Ann. Sci. Nat., Zool.,* (4), **14**, 294–357.

Parsons, P. A. (1994), Morphological stasis: an energetic and ecological perspective incorporating stress. *Jour. Theoretical Biol.,* **171**, 409–414.

Pickett, T. E., Kraft, J. C. and Smith, K. (1971), Crustacean burrows-Chesapeake and Delaware Canal, Delaware. *J. Paleont.,* **45**, 209–211.

Pryor, W. A. (1975), Biogenic sedimentation and alteration of argillaceous sediments in shallow marine environments. *Bull. Geol. Soc. America,* **86**, 1244–1254.

Rathbun, M. J. (1935), Fossil Crustacea of the Atlantic Gulf Coastal plain. *Spec. Pap. Geol. Soc. America,* **2**, 1–160.

Reyment, R. A. (1980), Morphometric Methods in Biostratigraphy. *London, Academic Press.*

Roemer F. A. (1841), Die Versteinerungen des norddeutsche Kreidegebirges. *Hannover.*

Roberts, H. B. (1962). The Upper Cretaceous decapod crustaceans of New Jersey and Delaware. *New Jersey Geol. Surv. Bull.,* **61**, 163–191.

Schäfer, W. (1962), Aktuo-paläontologie nach Studien in der Nordsee. W. Kramer (Frankfurt). 666 p.

Schweitzer, C. E., Feldmann, R. M., Gonzáles-Barba, G. and Vega, F. J. (2002), New crabs from the Eocene and Oligocene of Baja California Sur, Mexico and an assessment of the evolutionary and paleobiogeographic implications of Mexican fossil decapods. *Paleont. Soc. Mem.,* **59**, 1–43.

Sheldon, P. R. (1996), Plus ça change- a model for stasis and evolution in different environments. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **27**, 209–227.

Sigal, J., Grekoff, N., Cañón, A. and Ernst, M. (1970), Sur l’âge et les affinités “gondwaniennes” de microfaunes (Foraminifères et Ostracodes) malgaches, indiennes et chiliennes au sommet du

Jurassic et à la base du Crétacé. *C. R. Acad. Sci., Paris,* **271**, 24–27.

Stevens, G. R. and Clayton, R. N. (1971), Oxygen isotope studies on Jurassic and Cretaceous belemnites from New Zealand and their biogeographic significance. *N. Z. Jour. Geol. Geophys.,* **14**, 829–897.

Swen, K., Fraaije, R. H. B. and Van der Zwaan, G. J. (2001), Polymorphy and extinction of the Late Cretaceous burrowing shrimp *Protocallianassa faujasi* and the first record of the genera *Corallianassa and Calliax* (Crustacea, Decapoda, Thalassinoidea) from the Cretaceous. *Contr. Zool.,* **70**, 85–98.

Taylor, B. J. (1979), Macrurous Decapoda from the Lower Cretaceous of south-eastern Alexander Island. *Sci. Rep. Br. Antarctic Surv.,* **81**, 1–39.

Toolson, E. K. and Kues, B. S. (1996), Decapod crustaceans from the Semilla Sandstone Member, Mancos Shale (Upper-Cretaceous), North-Central New Mexico. *J. Paleont.,* **70**, 111–116.

Van Bakel, B. W. M., Fraaije, R. H. B. and Jagt, J. W. M. (2005), A new Early Campanian species of *Xanthosia* (Crustacea, Brachyura) from northwest Germany. *Crustaceana*, **78**(3), 287–297.

Vega, F. J., Feldmann, R. M. and Sour-Tovar, F. (1995), Fossil crabs (Crustacea: Decapoda) from the Late Cretaceous Cárdenas Formation, East Central Mexico. *J. Paleont.,* **69**, 340–350.

Wenner, A. M. (1972), Sex ratio as a function of size in marine Crustacea. The *American Naturalist,* **106**, 321–350.

Yaldwyn, J. C. (1966), Protandrous hermaphroditism in decapod prawn of the families Hippolytidae and Ampolonotidae. *Nature,* **209**, 1366–1378.

Manuscript accepted on August 3, 2005

Explanation of Plate 1

Three morphotypes of *Protocallianassa faujasi*.

All scales 3 cm. A. Female, B. Male, C. Juvenile, D. Two specimens in one burrow with abdomen preserved. All pieces are from the Dülmen Schichten, Germany.

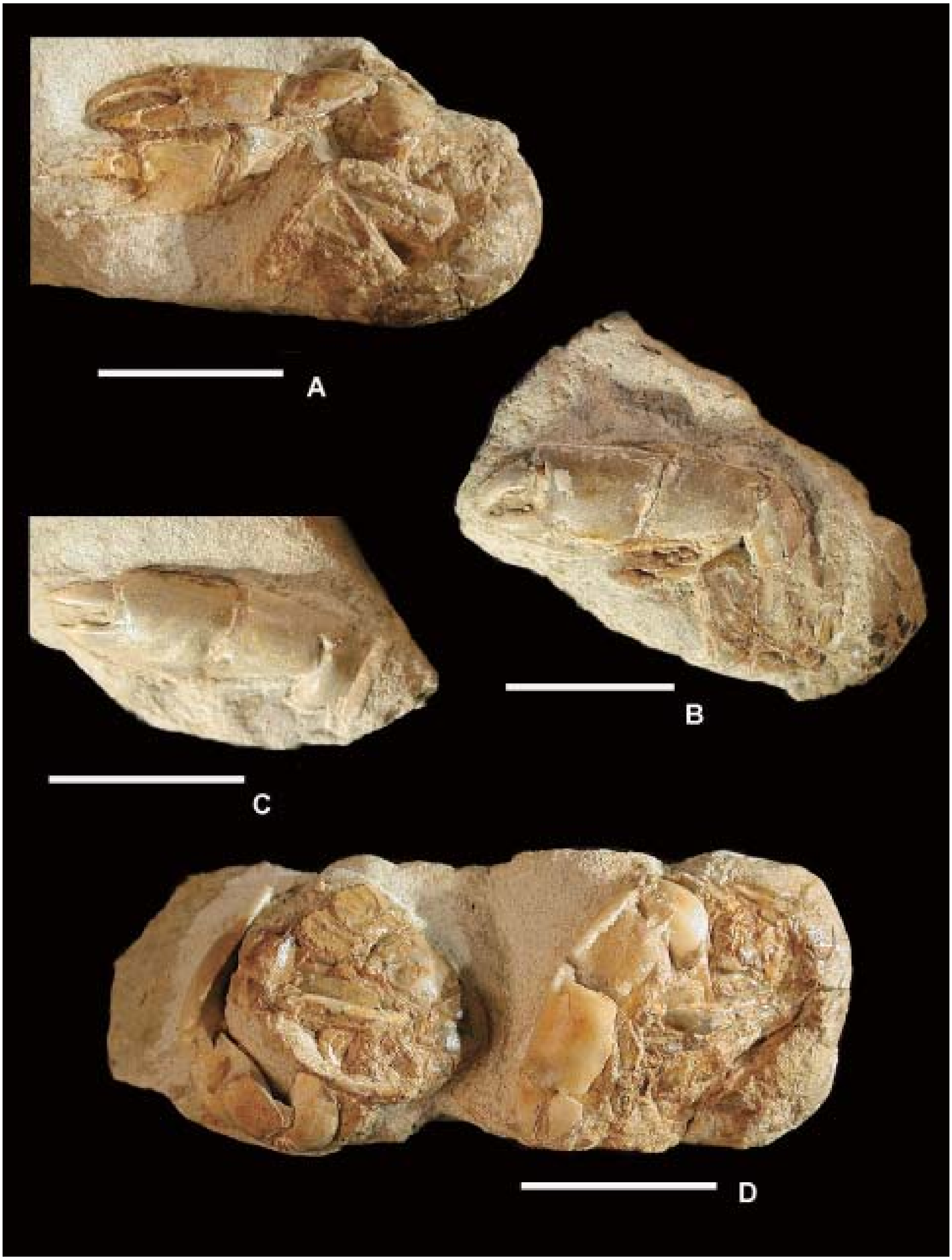
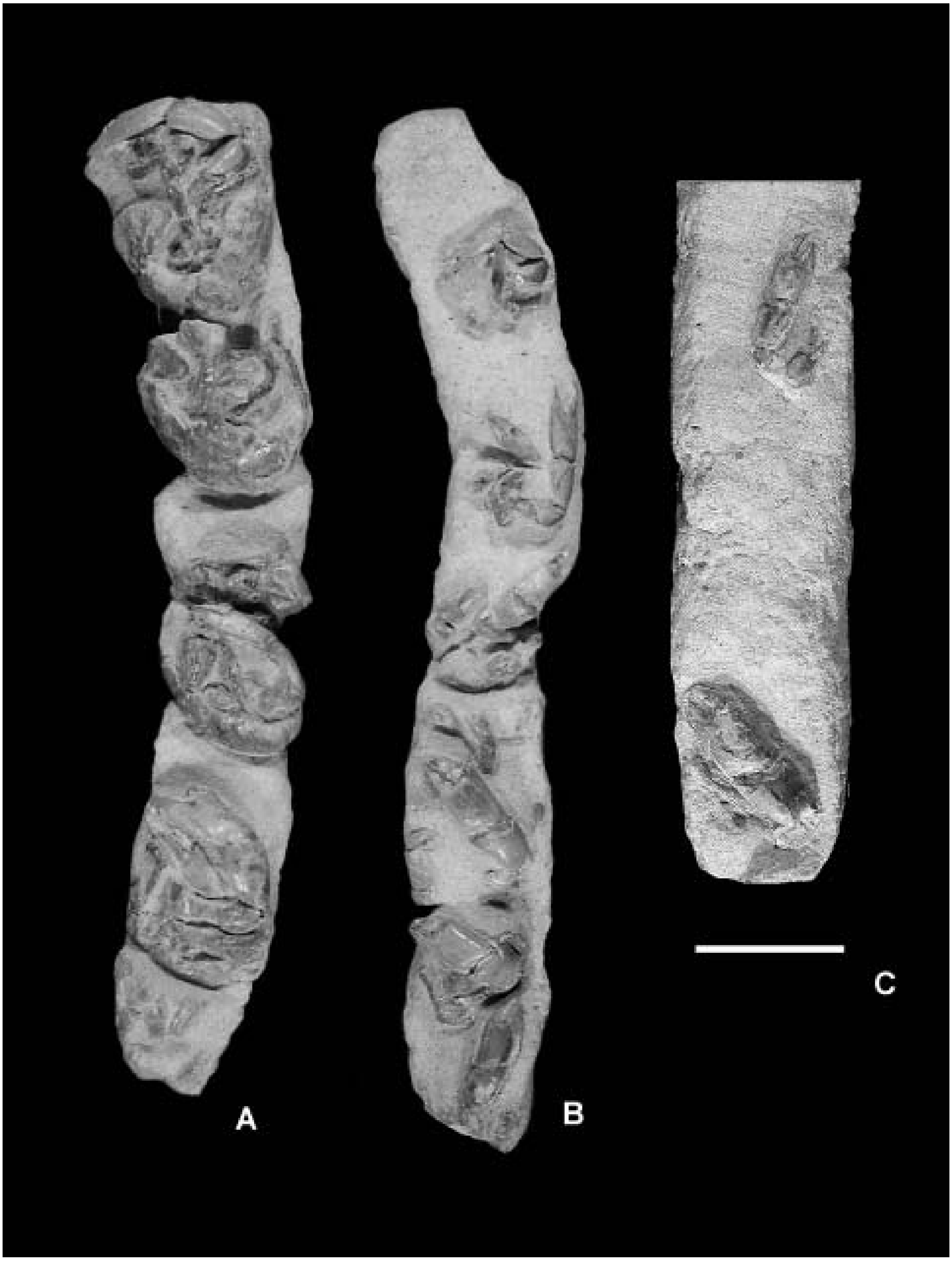

A
B
C
D

Plate 2

Preservation of several individuals in one burrow.

A. *Protocallianassa faujasi*, Dülmen Schichten, Schicht 3. Total length of the burrow: 270 mm. B. *Protocallianassa faujasi*, Dülmen Schichten, Schicht 3. Total length of the burrow: 340 mm. C. *Protocallianassa faujasi*, Male and Juvenile. Scale 4 cm. A and B are displayed in the Ruhrlandmuseum in Essen (Germany).


A
B
C