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Objektyp: **Article**

Zeitschrift: **Eclogae Geologicae Helvetiae**

Band (Jahr): **97 (2004)**

Heft 3

PDF erstellt am: **21.07.2024**

Persistenter Link: <https://doi.org/10.5169/seals-169119>

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Decapod crustaceans from the Middle Jurassic Opalinus Clay of northern Switzerland, with comments on crustacean taphonomy

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Key words: Decapoda, Peracarida, Jurassic, Switzerland, ecology, crustacean taphonomy

ABSTRACT

Four species of decapod crustaceans from the Middle Jurassic Opalinus Clay (Aalenian) of Northern Switzerland are described. Of these, *Mecochirus* cf. *eckerti* is the most common one, while *Eryma* cf. *bedelta*, *Glyphea* sp. and *Aeger* sp. were present as individuals, or only a few specimens. The preservation of these crustaceans ranges from moderate to excellent, reflecting the favourable taphonomic conditions of the depositional environment. An interesting aspect of the taphocoenosis in the Opalinus Clay is that the decapod crustaceans are by far outnumbered by small peracarid crustaceans (isopods and tanaids). This is interpreted as reflecting the original differences in abundance. Yet this distribution is not frequently encountered in sedimentary sequences where decapods (although rare) are far more common than isopods and tanaids. In rare instances, this reflects the original predominance of decapods, more often it is a consequence of the differential taphonomic behaviour of these two groups. A new model relating the ecology to the taphonomic behaviour of decapod and peracarid crustaceans is proposed. According to this model, decapods dominate in settings that were deposited under extremely dysoxic (peracarids wiped out by seasonal anoxia) as well as under fully oxic conditions (peracarids destroyed by taphonomic processes). Only in muddy dysoxic depositional environments are peracarid crustaceans frequently preserved. In these settings with equal preservation potential of decapods and peracarids, the original composition of the crustacean fauna would show a predominance of peracarid crustaceans. Examples from some well known fossiliferous settings are provided to illustrate the use of the new model.

ZUSAMMENFASSUNG

Aus dem Opalinuston (Mittlerer Jura, Aalenian) der Nordschweiz werden vier Arten von decapoden Krebsen beschrieben. Von *Aeger* sp., *Eryma* cf. *bedelta* und *Glyphea* sp. wurden nur ganz wenige Exemplare gefunden, während *Mecochirus* cf. *eckerti* etwas häufiger ist. Die Erhaltungsbedingungen waren während der Ablagerung des Opalinustones günstig, was sich in einer geringen Disartikulations- und Fragmentationsrate der Krebse widerspiegelt. Ein interessanter Aspekt der Taphocoenose ist die deutliche Dominanz der Kleinkrebse (Peracarida: Isopoden und Tanaidaceen). Dies dürfte die Zahlenverhältnisse der ehemaligen Lebensgemeinschaft widerspiegeln. In den meisten Ablagerungen dominieren jedoch die decapoden Krebse, wogegen Peracarida äusserst selten sind. Nur in den wenigsten Fällen entspricht dies einem ursprünglichen Überwiegen der Decapoda, viel öfter ist es eine Folge des unterschiedlichen Fossilisationspotentials der beiden Gruppen. Hier wird ein neues Modell vorgeschlagen, welches Ökologie und taphonomisches Verhalten der decapoden und peracariden Krebse miteinander verknüpft. Nach diesem Modell dominieren die Decapoda in Ablagerungen, welche in stark dysoxischem (Peracarida werden durch anoxische Ereignisse ausgelöscht) oder in vollkommen oxischem Milieu (Peracarida werden durch taphonomische Prozesse zerstört) abgelagert wurden. Peracarida werden nur in feinkörnigen, unter dysoxischen Bedingungen abgelagerten Schichten erhalten, und in solchen Sedimenten blieb die ursprüngliche Dominanz der Kleinkrebse auch fossil erhalten. Die Brauchbarkeit des neuen Modells wird mit einigen Beispielen bekannter Fossilfundstellen illustriert.

1. Introduction

Compared with sandstones and carbonates, the fine-grained argillaceous sediments of the Swiss Jura mountains are still little investigated with respect to the fossil content. The main reason for this is a methodological one: in surface exposures, these pelites are deeply weathered and decay to small irregular fragments (e. g. Wetzel & Allia 2003). Intact fossil material can only be obtained in still active clay pits or through labourious field work. During systematic excavations at three localities in the Opalinus Clay of northern Switzerland, several thousand

macrofossils were collected (Etter 1990, 1995, 1996). While most of these fossils belonged to already known species, crustacean macrofossils with the exception of the tanaidaceans and isopods (Etter 1988, 2004) were previously not formally described.

The aim of the present paper is twofold: (1) to describe the decapod crustaceans found during these excavations in the Opalinus Clay, together with one obtained from a borehole, and (2) to seek an explanation for the rather unusual

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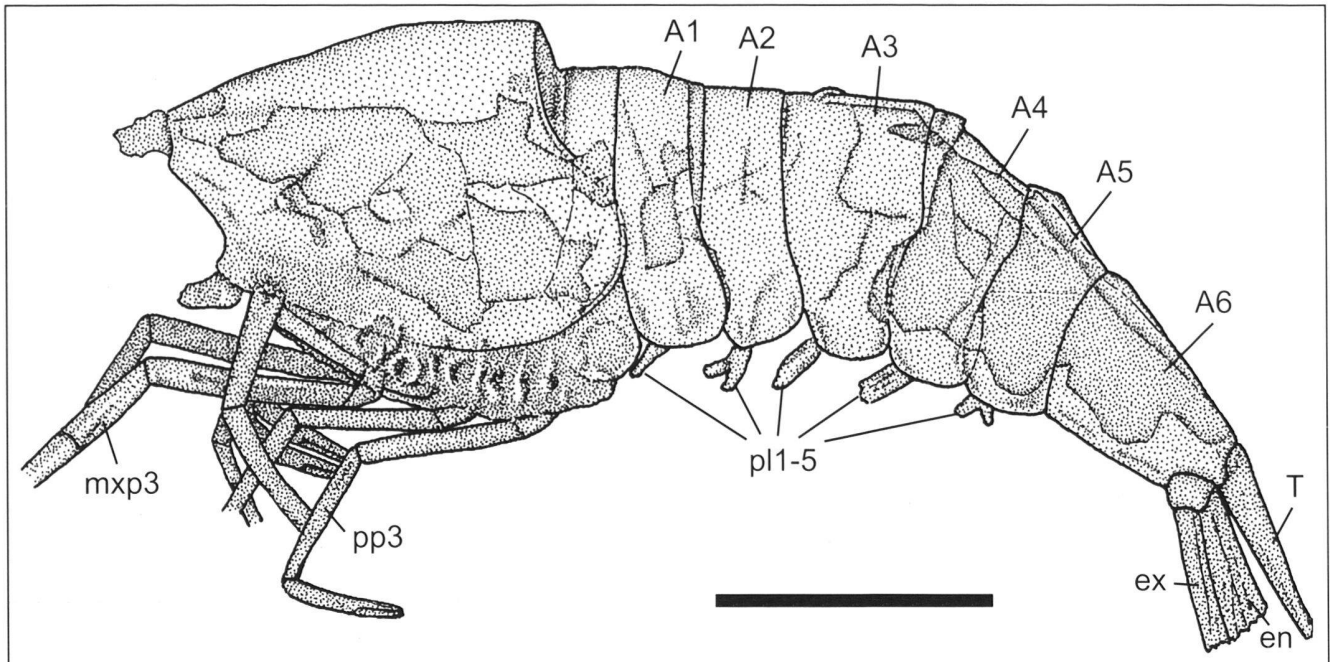


Fig. 1. *Aeger* sp., PIMUZ 5990, middle Opalinus Clay (Lower Aalenian), Riniken, canton Aargau, northern Switzerland. Abbreviations: A1–A6, abdominal somites 1–6; en, endopodite of uropod; ex, exopodite of uropod; pp3, pereopod 3; pl1–5, pleopods 1–5; mxp3, maxilliped 3; T, telson. Scale bar represents 1 cm.

fact that the small peracarid crustaceans (isopods and tanaidaceans) are far more common in the Opalinus Clay than the decapods.

2. Geological setting

The Opalinus Clay is the lowermost member of the Middle Jurassic of northern Switzerland. Biostratigraphically it belongs to the Opalinum subzone of the Lower Aalenian (Etter 1990; Wetzel & Allia 2003). In Switzerland, average thickness of this rather monotonous series of dark grey silty claystones is 80 to 120 meters (Etter 1995). The Opalinus Clay was deposited in a shallow epicontinental shelf sea surrounded by landmasses and topographic highs. Synsedimentary subsidence provided the accommodation space for the accumulating sediment. Deposition generally took place slightly below the storm wave base in a dysoxic bottom-water environment (Etter 1990, 1995; Wetzel & Allia 2003).

The fauna of the Opalinus Clay in Switzerland is dominated by ammonites and small epibenthic bivalves (*Bositra buchi*) and is of low diversity (Etter 1995). The benthic infauna is considerably less abundant than the epifauna. Crustaceans (with the exception of the ostracoda) are only a minor constituent of the fauna. Fossil preservation is good to excellent in terms of fragmentation and disarticulation ratios (Etter 1990, 1995). Aragonite shells were dissolved whereas calcite and even organic skeletal materials (periostracum, ligament, beaks of cephalopods) are preserved. Among the trace fossils even

those of the uppermost tier under a very thin mixed layer survived which is an excellent indication of dysoxic bottom-water conditions (Bottjer & Savrda 1990).

3. Material

The following descriptions of *Eryma* cf. *bedelta*, *Glyphea* sp. and *Mecochirus* cf. *eckerti* are based on material which was collected by the author between 1985 and 1988 in Opalinus Clay pits at Schinznach, Canton Aargau, and Hagendorf, Canton Solothurn (Etter 1990). Additional specimens of *Mecochirus* cf. *eckerti* were provided by R. Theiler. The single specimen of *Aeger* sp. was discovered in the core taken from a borehole near Riniken, Canton Aargau (Matter et al. 1987). All the specimens are deposited at the Palaeontological Institute and Museum of the University of Zurich under their respective PIMUZ numbers.

4. Systematic descriptions

Subphylum Crustacea PENNANT 1777
 Class Malacostraca LATREILLE 1802
 Subclass Eumalacostraca GROBBEN 1892
 Order Decapoda LATREILLE 1803
 Suborder Dendrobranchiata BATE 1888
 Superfamily Penaeoidea RAFINESQUE 1815
 Family Aegeridae MÜNSTER 1839
 Genus *Aeger* MÜNSTER 1839

Aeger sp.

(Fig. 1)

Material. – A single specimen from a borehole near the village of Riniken, Canton Aargau, northern Switzerland, PIMUZ 5990. The specimen comes from the middle part of the Opalinus Clay (the so-called “finely bedded slightly bioturbated dark Opalinus Clay” of Matter et al. 1987), about 58 m above the base of that member (at well depth 392.77 m; Matter et al. 1987).

Description. – The specimen is strongly laterally compressed, many diagnostic features are thus not observable. The overall length of the specimen is approximately 5 cm.

Carapace: The cervical and hepatic grooves are short and shallow. The hepatic spine in the angle between these two grooves is short. A branchiocardiac groove was not observed. The surface of the carapace is smooth except for a fine punctation (probably pores of fine setae). The anterior part of the carapace is fragmentary and the rostrum is missing. The foremost part of the carapace immediately behind the rostrum is not dentate and the rostrum was therefore probably also not dentate. The ocular incision is very shallow.

Abdomen: The abdominal somites 1 and 2 are the shortest, abdominal somite 6 the longest. The abdominal somites 5–6, perhaps also 4, were dorsally keeled. The pleural parts are rounded except for abdominal somite 5 where the pleural part is pointed posteriorly.

Ventral skeleton and appendages: The thoracic sternites and the legs are slightly displaced towards the ventral side. Most of the appendages have only poorly preserved distal parts. Only faint impressions of the proximal parts of the eyes, antennulae, antennae and maxilliped 2 are visible. Maxilliped 3 is the longest and most robust appendage. Slightly shorter and more slender are the pereopods 1–3 which all have chelae. No movable spines on the maxilliped 3 and on pereopods 1–2 are preserved and were, if once present, certainly not very prominent because no obvious spine attachments can be observed. The pereopods 4–5 are not preserved. The proximal parts of pleopods 1–5 are clearly visible. The exo- and endopodites of the uropods have a median groove, the terminal parts are not preserved. The telson is pointed and was perhaps dorsally keeled.

Comparisons and remarks. – The preservation of the specimen is not quite good enough for an unequivocal assignment. Judged from the form of the carapace and the abdomen, as well as the direction of the carapace grooves, it is doubtless a member of the Penaeoidea. Within that group a very robust maxilliped 3 is developed in the two genera *Aeger* and *Acanthochirana*. The best known species of these two genera are known from the Upper Jurassic lithographic limestones of southern Germany (Solnhofen limestone, Nusplingen limestone; Schweigert 2001a, b). Although there was some confu-

sion about certain species (Schweigert 2001b), the distinction of the two genera according to Förster (1967) still holds.

Species of *Acanthochirana* show a dentate rostrum, with the first teeth already situated on the carapace above the ocular incision. Species of *Aeger*, in contrast, have a non-dentate rostrum with granulate sides (Förster 1967). Although the rostrum is not preserved in the present specimen, the absence of dorsal teeth on the foremost part of the carapace are more typical of *Aeger* sp. A pregastric (= postorbital) tooth is present in *Aeger* but not in *Acanthochirana* (Förster 1967) but in the present specimen this region is insufficiently well preserved to decide whether such a tooth was present or not. In *Acanthochirana*, the abdominal somite 6 is considerably longer than abdominal somite 5, but only slightly so in *Aeger*. Yet this character is ontogenetically variable and hence of limited use (Förster 1967). More significant is the fine structure of the carapace which shows fine punctations in *Aeger*. In *Acanthochirana*, the carapace is smooth. According to this character, the present specimen can again be assigned to *Aeger* sp. Further differences between the two genera exist in the anatomy of the appendages. Compared to the situation in *Acanthochirana*, the carpi of the pereopods 2–3 are elongated in *Aeger* (Förster 1967). The pereopods 2–3 of the present specimen have indeed long and slender carpi and are therefore rather of the *Aeger*-type. Well preserved specimens of *Aeger* have movable spines on maxilliped 3 and pereopods 1–2 whereas *Acanthochirana* species bear such spines only on maxilliped 3 and pereopod 1 (Förster 1967). This latter condition could not be verified in the present specimen. Yet all the observable features clearly point to *Aeger* sp., albeit with some uncertainty.

The present specimen does not seem to be identical to the only *Aeger* species that was hitherto described from the Aalenian of central Europe, *A. franconicus* FÖRSTER (Förster 1980). The latter has much more pronounced cervical and hepatic grooves and possesses also distinct ventral and branchiocardiac furrows which appear to be absent in the specimen from the Opalinus Clay. Rather similar is the small *A. gracilis* FÖRSTER & CRANE from the uppermost Triassic of southern England (Förster & Crane 1984) although a comparison is difficult due to the different state of preservation (undeformed in *A. gracilis*, compressed in the Opalinus Clay specimen).

A. laevis (BLAKE) and *A. marderi* WOODWARD, both from the Lower Jurassic of southern England, have much more pronounced cervical, hepatic and branchiocardiac grooves (Woods 1922; Förster & Crane 1984). This is also the case in *A. brevis* VAN STRAELEN from the Callovian of La Voulte, France (Carriol & Riou 1991). From *A. brodiei* WOODWARD (lowermost Jurassic of southern England; Woods 1922), the Opalinus Clay specimen differs by having a much more elongate 6th abdominal somite.

Comparisons with the six *Aeger* species described from the Lower Jurassic of Osteno, northern Italy (Garassino & Teruzzi 1990) are hampered by the fact that these are all strongly compressed. Although many of the appendages of the Osteno spec-

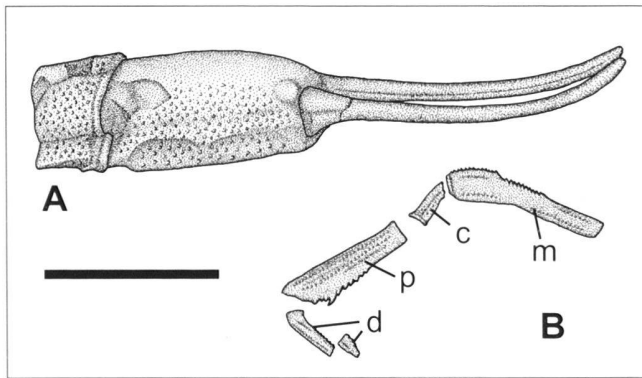


Fig. 2. A, *Eryma* sp. Quenstedt, 1857, PIMUZ 6102, lower Opalinus Clay (Lower Aalenian), Schinznach, canton Aargau, northern Switzerland. Chela with carpus. B, *Glyphea* sp., 1860, PIMUZ 6101, lower Opalinus Clay (Lower Aalenian), Schinznach, canton Aargau, northern Switzerland. Pereiopod 1. Abbreviations: m, merus; c, carpus; p, propodus; d, dactylus. Scale bar represents 1 cm.

imens are preserved in spectacular detail, most of the diagnostic features of the carapaces are not sufficiently well preserved.

Of the Upper Jurassic species, *A. tipularius* (SCHLOTHEIM) has recently been the subject to a revision (Schweigert 2001b). *A. tipularius* (syn. *A. bronni* OPPEL, *A. armatus* OPPEL) has a very long and robust maxilliped 3 which distinguishes this species clearly from the Opalinus Clay specimen. To a lesser degree, this is also the case for *A. spinipes* (DESMAREST) and *A. elegans* MÜNSTER. *A. spinipes* with its extremely long rostrum was regularly mistaken as *A. tipularius* in the past (Schweigert 2001b), and *A. elegans* was erroneously considered to be the smaller (male) sexual dimorph of the same species (Förster 1967). Yet Polz (2003) could demonstrate the presence of both sexes in all these three species from the Solnhofen Limestone.

Suborder Reptantia BOAS 1880
 Infraorder Astacidea LATREILLE 1803
 Family Erymidae VAN STRAELEN 1924
 Genus *Eryma* VON MEYER 1840

Eryma sp.

(Fig. 2A)

Material. – 2 chelae, from two different horizons of the lowermost 15 m of the Opalinus Clay of Schinznach and Hägendorf, PIMUZ 5984 and 6102.

Description. – Specimen 5984 is a 2.6 cm long chela. The proximal part of the propodus is almost as wide as long, very robust and shows a longitudinal hump on its ventral side. The pollex of the propodus and the dactylus comprise two thirds of the length of the chela. Both pollex and dactylus gradually taper towards the end and are gently curved upwards. The occlusal surfaces of pollex and dactylus are toothed.

Specimen 6102 consists of a 3 cm long chela and a 4.5 mm long carpus. The chela is much more slender than specimen 5984. The proximal part of the propodus is twice as long as wide. The pollex of the propodus and the dactylus are slender from the base to the tip, markedly curved and do not show teeth on the occlusal surfaces. Both chelae are slightly granulate, with the sculpture being more pronounced on the upper surface.

Comparisons and remarks. – More than 40 species of *Eryma* were described from the Jurassic and Early Cretaceous (Förster 1966; Feldmann & McPherson 1980; Garassino 1996). Among these, *E. amalthea* (QUENSTEDT) (Sinemurian – upper Pliensbachian), *E. bedelta* (QUENSTEDT) (Toarcian – Callovian), *E. guisei* (WRIGHT) (Bajocian – Bathonian), *E. ornata* (QUENSTEDT) (Callovian), *E. ventrosa* (H. V. MEYER) (Callovian – Kimmerdgian), and *E. radiata* OPPEL (Oxfordian) possess chelae that are comparable to the specimen 5984.

The chela 6102 poses somewhat of a problem. Chelae are variable, to some extent even within individuals (Förster 1966; see also Woods 1928). But with its untypically slender form and the absence of teeth on the occlusal surfaces, this specimen cannot be assigned to any of the above mentioned *Eryma* species. Both chelae are assigned here to *Eryma* sp. but the possibility cannot be ruled out that they belong to two different species.

Infraorder Astacidea LATREILLE 1803
 Family Glypheidae WINCKLER 1883
 Genus *Glyphea* VON MEYER 1835

Glyphea sp.

(Fig. 2B)

Material. – A single preiopod 1 from the lower Opalinus Clay (23 m above base) of Schinznach, PIMUZ 6101.

Description. – Total length of the first pereopod is 2 cm. Preserved in a slightly disarticulated fashion are merus, carpus, propodus and dactylus. The long merus is finely crenulate on its upper side and distally enlarged. The carpus is small and slender, the propodus distally enlarged and has a crenulate ventral margin. The main tooth of the propodus is well away from the articulation with the dactylus. The dactylus (broken in two pieces) is slightly hooked near its base and the ventral margin is finely crenulate. All the joints are sculptured with rows of fine tubercles.

Comparisons and remarks. – Since the description of a modern member of the Glypheidae, *Neoglyphea inopinata* FOREST & DE SAINT LAURENT, 1975, this family is now usually assigned to the Infraorder Astacidea (Forest & de Saint Laurent 1989; Martin & Davis 2001; Feldmann et al. 2002). Whether the Mecochiridae and Pemphicidae should also be transferred from the Palinura to the Astacidea is at present unresolved but

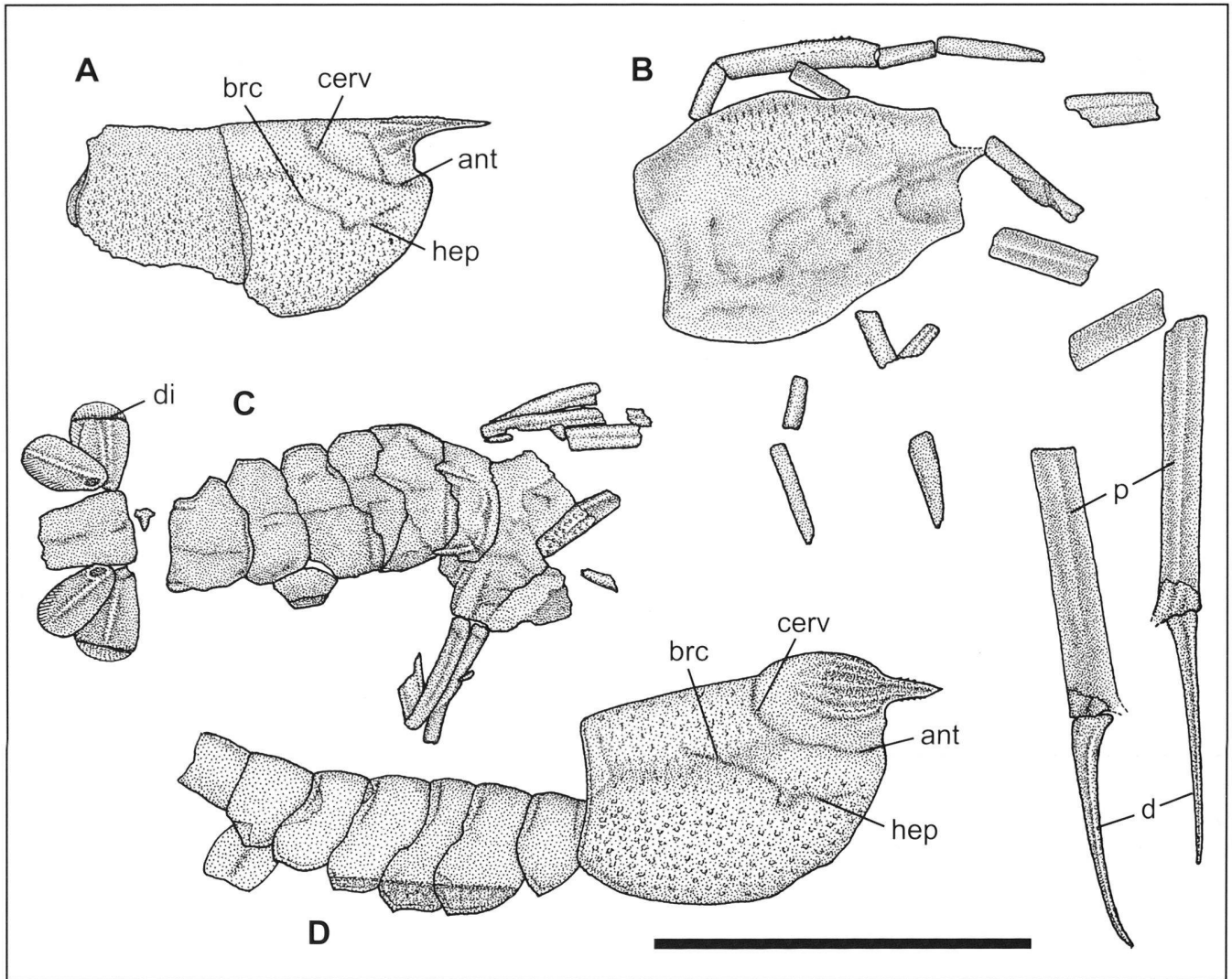


Fig. 3. *Mecochirus* cf. *eckerti* Frentzen, 1937, lower Opalinus Clay (Lower Aalenian), Schinznach, canton Aargau, northern Switzerland. A, PIMUZ 6100, carapace in lateral view. B, PIMUZ 6099, carapace in dorsal view, various pereiopod joints including the elongated propodus and dactylus of pereiopods 1. C, PIMUZ 6098, posterior part of the carapace, abdominal somites 1–6, telson and uropods in dorsal view. D, PIMUZ 5983, carapace in oblique view, abdominal somites 1–6 and incomplete telson. Abbreviations: ant, antennal groove; brc, branchiocardiac groove; cerv, cervical groove; hep, hepatic groove; di, diaeresis; d, dactylus of pereiopod 1; p, propodus of pereiopod 1. Scale bar represents 1 cm.

in accordance with Feldmann et al. (2002), the Mecochiridae are assigned here also to the Astacidea.

Species with strongly elongate first pereiopods without chelae occur in the families Glypheidae and Mecochiridae (Glaessner 1969; Förster 1971). The distinction of the genera currently recognized in these two families is based on the morphology of the carapace, mainly the prominence, direction and curvature of the grooves.

Yet a long first pereiopod with the tooth well away from the ventral angle of the propodus and several less prominent spines occurs only in the genera *Glyphe*a and *Pseudoglyphe*a. Of the different species of *Pseudoglyphe*a with sufficiently well

known first pereiopods all show a very strong main tooth and most show a series of well developed accessory spines on the propodus which are absent in the present specimen. In *Glyphe*a species with known appendages the first pereiopod is usually shorter and stouter than in the present specimen. An exception seems to be *G. solitaria* OPPEL (known from the Upper Toarcian – Aalenian of southern Germany; Opperl 1862; Beurlen 1928), but unfortunately Beurlen gives only a brief description of the first pereiopod of that species but no figure. A specimen that was figured and described by Förster (1980) as *Glyphe*a cf. *pustulosa* H. v. MEYER from the Upper Toarcian of Mistelgau, Franconia, shows the proximal part of the merus

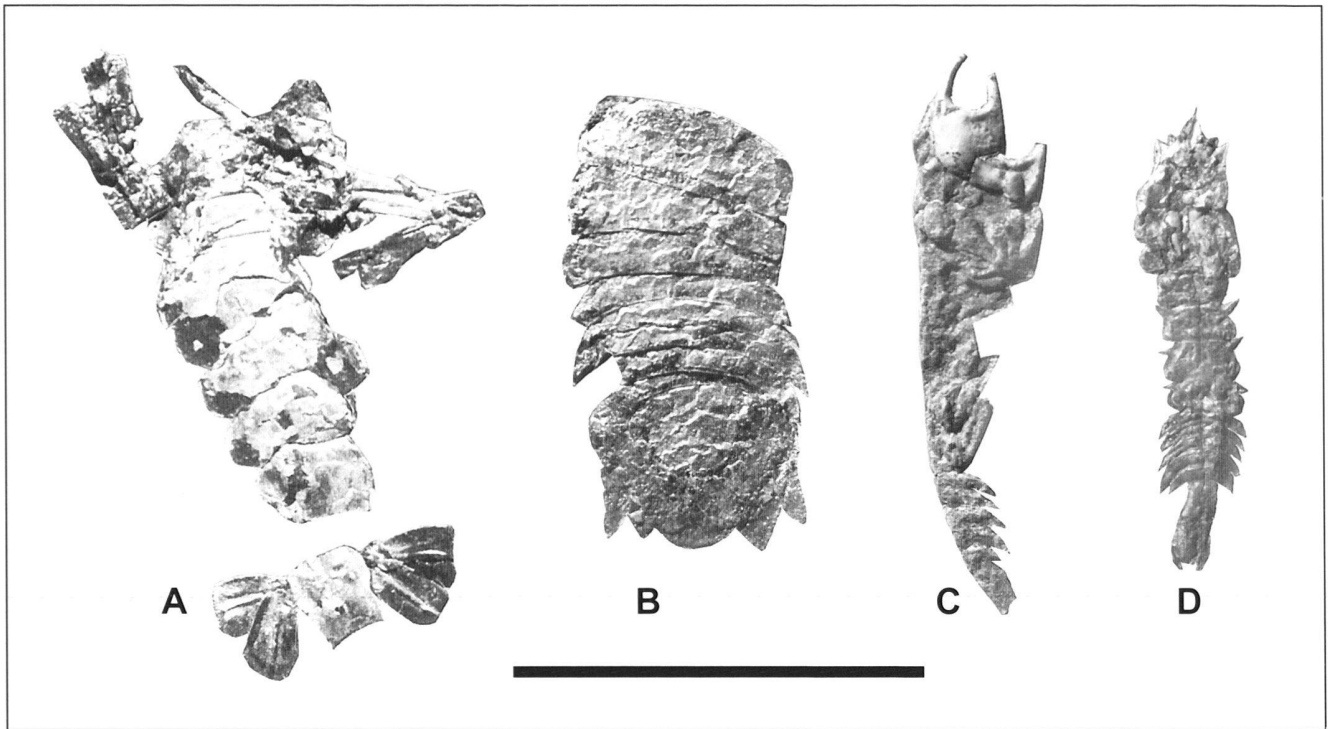


Fig. 4. Representatives of the Decapoda (A) and Peracarida (B–D) from the lower Opalinus Clay (Lower Aalenian) of northern Switzerland. Note the good preservation. A, *Mecochirus* cf. *eckerti* Frentzen, 1937, PIMUZ 6098, Schinznach, canton Aargau; posterior part of the carapace, abdominal somites 1–6, telson and uropods in dorsal view. B, *Palaega* cf. *jurassica* Stolley, 1910, PIMUZ 6104, Hägendorf, canton Solothurn; pereion somites 5–7, pleon somites 1–5, pleotelson and uropods in dorsal view. C, *Opsipeden gracilis* Heer, 1865, PIMUZ 6106, Hägendorf, canton Solothurn. D, *Opsipeden gracilis* Heer, 1865, PIMUZ 6107, Unterer Hauenstein, canton Solothurn. Scale bar represents 1 cm.

of the first pereiopod. This part is almost identical in its proportions and sculpture with the present specimen. According to the direction and curvature of the postcervical and branchiocardiac grooves, the broad posterior margin of the carapace and the evenly spaced crenulate cristae of the gastric region, the specimen of Förster should be placed in *G. solitaria*.

One additional character of the first pereiopod that might be important is the form of the dactylus. The dactylus is hooked near its base only in some species of *Glyphe*a but not in *Pseudoglyphe*a (see Woods 1924, 1925; Glaessner 1969). Based on its similarities with *G. solitaria* and the hooked dactylus, specimen 6101 is therefore assigned to *Glyphe*a sp., but it cannot be excluded that it could belong to *Pseudoglyphe*a sp.

Family Mecochiridae VAN STRAELEN 1925
Genus *Mecochirus* GERMAR 1827

***Mecochirus* cf. *eckerti* FRENTZEN 1937**

(Fig. 3A–D, 4A)

Material. – 11 specimens which all come from the lower 25 m of the Opalinus Clay of Schinznach and Hägendorf, PIMUZ 5974, 5976, 5977, 5978, 5979, 5981, 5982, 5983, 6098, 6099, 6100.

Description. – All the specimens are strongly flattened and slightly disarticulated (exuviae), but together the specimens give a rather complete picture of the morphology of this species.

Carapace: The cervical groove is well marked and obliquely oriented, passing into the anteriorly directed antennal groove. A gastroorbital groove is not present. The rostrum is well developed and finely dentate. The gastrical region has a finely dentate upper and lower gastric ridge, the antennal region shows one finely dentate ridge. The branchiocardiac groove is faint but clearly visible, the hepatic groove is shallow. A postcervical groove is not developed. The carapace is ornamented with small tubercles except for the dorsal part where it shows small pits.

Abdomen: The second abdominal somite is the largest and has expanded pleura. The size of the abdominal somites diminishes from the third to the fifth. The sixth abdominal somite is slightly elongated. Abdominal somites 1–5 have a dorsal groove in the posterior part and pointed pleura.

Ventral skeleton and appendages: Carpus, propodus and dactylus of pereiopod 1 are well preserved in PIMUZ 6099. The propodus is slightly shorter than the carapace. The dactylus is slender and slightly curved. The other pereiopods are only preserved in disarticulated remains. The pleopods are un-

known. Endo- and exopods of the uropods have a blunt median ridge and fine marginal striae. The exopod of the uropods shows a diaeresis.

Comparisons and remarks. – With the exception of the rostrum which is untypically large and finely dentate, all the characters clearly allow the assignment to the genus *Mecochirus* (see Förster 1971). From the Jurassic, more than two dozen species were described, but probably less than ten species are valid (Förster 1971). Comparisons of the material from the Opalinus Clay were only made with those Jurassic species which are reasonably well known.

M. olifex QUENSTEDT from the lower Sinemurian of southern Germany is a small species which differs from the Opalinus Clay specimens in that it possesses a distinct postcervical groove (Beurlen 1928). Furthermore it is also sculptured with tubercles on the dorsal part of the carapace, and the abdominal pleura are rounded instead of pointed.

M. eckerti FRENTZEN, although its carapace is insufficiently known, appears to be similar enough to the present specimens to allow a comparison. The first pereopod shows the same morphology and the same propodus to dactylus proportion, and the abdominal segments have the same shape. Yet there are also some differences to *M. eckerti* as described and figured by Frentzen (1937). The propodus of pereopod 1 is relatively longer in the specimen from the Posidonia Shale (longer than the carapace, although the estimate for the carapace given by Frentzen seems too short), whereas the propodus is slightly shorter in the specimens from the Opalinus Clay. However, the specimen from the Posidonia Shale is almost twice the size of the largest specimens from the Opalinus Clay, and it is a well known fact that the first pereopods grow longer with increasing size of the individual (Förster 1971). The specimens of the Opalinus Clay are assigned here with some uncertainty to *M. eckerti* but species identity could only be verified with the discovery of better preserved material from the Posidonia Shale.

The finely sculptured *M. clypeatus* (CARTER) from the Bathonian of southern England and the more coarsely sculptured *M. socialis* (VON MEYER) from the Callovian-Oxfordian of Germany, France and southern England differ from the Opalinus Clay specimens by the absence of an antennal crista and of the upper gastrical crista (Woods 1926; Förster 1971). In addition, the propodus: dactylus ratio of the first pereopod is around 1.7 in *M. clypeatus* and *M. socialis* whereas this ratio is 1.1–1.2 in *M. eckerti* (see Frentzen 1937) and in the Opalinus Clay specimens.

M. peytoni WOODWARD (syn. *M. minimus* (HEE); see Förster 1971) from the Kimmeridgian of northern France possesses only a very indistinct cervical groove (Woodward 1876; Hee 1924). The propodus: dactylus ratio of the first pereopod is 1.4. *M. leionoton* (KRAUSE) from the Kimmeridgian of northern Germany has a distinct postcervical groove (which is absent in Opalinus Clay specimens) in addition to the branchiocardiac groove (Krause 1891). Also the pleura of the ab-

dominal somites are much more triangular in outline (cf. Krause 1891). The appendages are not sufficiently known to make comparisons.

M. longimanatus (SCHLOTHEIM) from the Tithonian (Solnhofen Plattenkalk) of southern Germany (syn. *M. brevismanus* (MÜNSTER), *M. dubius* (MÜNSTER), *M. bajori* (GERMAR), *Mecochiria foresti* SECRETAN; see van Straelen 1925; Förster 1971), the type species of *Mecochirus* (see Woods 1927), is remarkable for its extremely long first pereopod which can attain five times the length of the carapace (Förster 1971). Yet as in all the species of this genus the relative length of the first pereopod increases considerably during ontogenesis, and in specimens of comparable size, the first pereopod shows the same proportions in *M. longimanatus* and *M. cf. eckerti*. Differences between the two species include the form of the abdominal pleura which are ventrally more pointed in *M. longimanatus*, and the form of the rostrum which is bent downward in *M. longimanatus* (van Straelen 1925).

M. marwicki GLAESSNER from the Kimmeridgian of New Zealand is distinguished from the present specimens by its much coarser sculpture (Glaessner 1960; Förster 1971). Another species from the Tithonian of New Zealand (*M. sp.*; Glaessner 1960) is not preserved in enough detail to allow comparisons to be made (Glaessner 1960; Förster 1971).

5. Discussion

Overall, the Crustacea from the Opalinus Clay show a good state of preservation (Fig. 4). While many of the remains are exuviae (molts), they nevertheless are mostly articulated. They do not show any signs of transportation, little fragmentation except for compactional patterns, and only moderate disarticulation. They can therefore be considered autochthonous which is also the case with the other fossil benthic organisms of the Opalinus Clay (Etter 1990, 1994, 1995).

The decapods of the Opalinus Clay represent several life styles. As most modern Penaeidae, *Aeger* sp. was probably demersal but with good swimming capabilities (see Dall et al. 1990). Food could have been detritus and/or small soft-bodied animals. For *Eryma* sp. with its stout lobster-like body, a mainly epibenthic mode of life is assumed with both the abilities for shallow burrowing and escape swimming (Förster 1966). Its food consisted probably of benthic molluscs, crustaceans, small fishes and carrion (Förster 1966).

With its rather strongly calcified carapace, *Glyphea* sp. was most probably epibenthic and occasionally produced shallow burrows (Förster 1971). For *Mecochirus* cf. *eckerti* with its weakly calcified carapace, a mainly endobenthic mode of life can be assumed but not in *Thalassinoides*-like burrows. For this species with its long first pereopods, it would have been impossible to turn around in such burrows (see Förster 1971). This is corroborated by patterns from the Schinznach and Hägendorf sections where *Mecochirus* and *Thalassinoides* never occur in the same and not even in adjacent horizons. Both *Glyphea* sp. and *Mecochirus* cf. *eckerti* were probing the sedi-

ment for food which consisted mainly of small invertebrates (Förster 1971).

The relative frequency of the various crustacean fossils is in need of an explanation. In the Opalinus Clay, representatives of the Peracarida (isopods and tanaidaceans; see Fig. 4B–D) are much more common than representatives of the Decapoda (Etter 2004). This is unusual for fossil crustacean communities where normally the decapods dominate. As will be shown in the following, there is good evidence that the observed crustacean frequencies in the Opalinus Clay largely reflect the original differences in abundances and are not the result of a taphonomic overprint.

Ecology and distribution of modern decapod and peracarid crustaceans

In terms of individual numbers, the invertebrate macrofauna on most marine soft-bottoms is dominated today by polychaete annelids. In a study of the southern California shelf covering a broad range of environments, polychaetes accounted on average for 60% of the individuals of the macrobenthos collected with 1.0 mm sieves (Ranasinghe et al. 2003). Arthropods (almost exclusively crustaceans), molluscs, echinoderms, and the remainder of the phyla each contributed to about 10% of the total abundances. Notable trends are an increase in the number of molluscs towards shallower depths and especially in protected bay areas, and an increase of echinoderms (mainly ophiuroids) in deeper shelf environments (Ranasinghe et al. 2003).

With respect to species numbers, polychaete annelids still dominate with little more than 50% of the taxa, followed by arthropods (20%) and molluscs. Echinoderms are with less than 4% of the species relatively unimportant (Ranasinghe et al. 2003). Again, in bay areas the importance of the molluscs increases considerably.

If biomass or standing crop is analyzed, polychaetes contribute to about 35% and echinoderms to nearly 30%. Molluscs and the “minor” phyla account for approximately 15% each although the molluscs tend to become dominant in bay areas with up to 60% of the biomass. The crustaceans are considerably less important with only 5% of the biomass (Ranasinghe et al. 2003).

Although surveys from other regions are usually not available with the same taxonomic acuity, they nevertheless display the same basic pattern as those from the temperate southern California shelf. This includes the soft-bottom benthos from the tropical Hawaiian Ridge (NOAA 2002; data courtesy of NOAA, Washington D. C.), the tropical Florida Bay and southern Florida Gulf (NOAA 1997, 2000; data courtesy of NOAA, Washington D. C.), and the boreal North Sea (Heip & Craeymeersch 1995; data courtesy of Flanders Marine Institute, Oostende, Belgium) although on tropical calcareous shelf bottoms there is usually an elevated number of epibenthic mollusks (Alongi 1990). On a local scale, major deviations can occur with e.g. a dominance of echiurans (Barnard & Hartman 1959; Jones 1969) or of the acraniate *Branchiostoma* (Alongi 1990) but such patterns are usually temporarily restricted.

Among the crustaceans, the small peracarids almost always exceed the individual numbers of the decapods by one to three orders of magnitude. This size-frequency distribution with larger population sizes of the small species probably simply reflects the ecological law that smaller organisms have lesser demands for space and food (e.g. Damuth 1998; Siemann et al. 1999). Interestingly, this distribution is also found at the species level where in almost any larger taxon there are more small and medium-sized species than larger ones although the underlying causes are still disputed (Siemann et al. 1999).

With respect to the peracarid and decapod crustaceans, it is the amphipods that dominate today (Coull & Bell 1983; Gutu & Sieg 1999). However this group was not yet present in the Mesozoic. But the tanaidaceans with their long evolutionary history (Schram et al. 1986; Etter 2004) are today the second most important peracarid group in terms of abundances and biomass (Gutu & Sieg 1999). Most if not all of the soft-bottom dwellers among them lead a cryptic mode of life in burrows and tubes (Gutu & Sieg 1999). Compared to the tanaidaceans, isopods have a much greater variety of life modes. They include epibenthic, endobenthic and parasitic groups (although the obligate parasitic and highly aberrant Epicaridea are excluded here from further consideration) and many of them are quite mobile (Roman & Dalens 1999).

Even without the amphipods, the remainder of the peracarids (mainly tanaidaceans and isopods) are much more common than the decapod crustaceans on most marine soft-bottoms (e.g. Heip & Craeymeersch 1995; data courtesy of Flanders Marine Institute, Oostende, Belgium; NOAA 1997, 2000, 2002; data courtesy of NOAA, Washington; Ranasinghe et al. 2003). There seem to be only two environments that do support a higher abundance of decapods than peracarids. One of them is littoral to shallow marine shifting sands where anomuran crustaceans (especially members of the Diogenidae, Paguridae, Hippidae, Callianassidae) can be the most common crustaceans (Monod & Laubier 1996). Here peracarid crustaceans seem to be excluded by the intense physical reworking of the sediment and perhaps also by the bioturbating activity (“bulldozing”; see Thayer 1983) of the larger infauna.

The other marine environment where peracarids but not decapods are absent is oxygen-deficient settings which experience episodic anoxic phases. Prolonged anoxia wipes out all the macrofaunal species but in contrast to the decapods, peracarid crustaceans lack a planktonic larval stage and show a very slow dispersal (Schram 1986; Gutu & Sieg 1999). Therefore they are not able to recolonize larger basins before the next anoxic event extinguishes all the benthic species (Boesch & Rabalais 1991).

Taphonomy and preservability of decapod and peracarid crustaceans

The taphonomic behavior of decapod crustaceans and mantis shrimps has been subject to numerous studies over the past

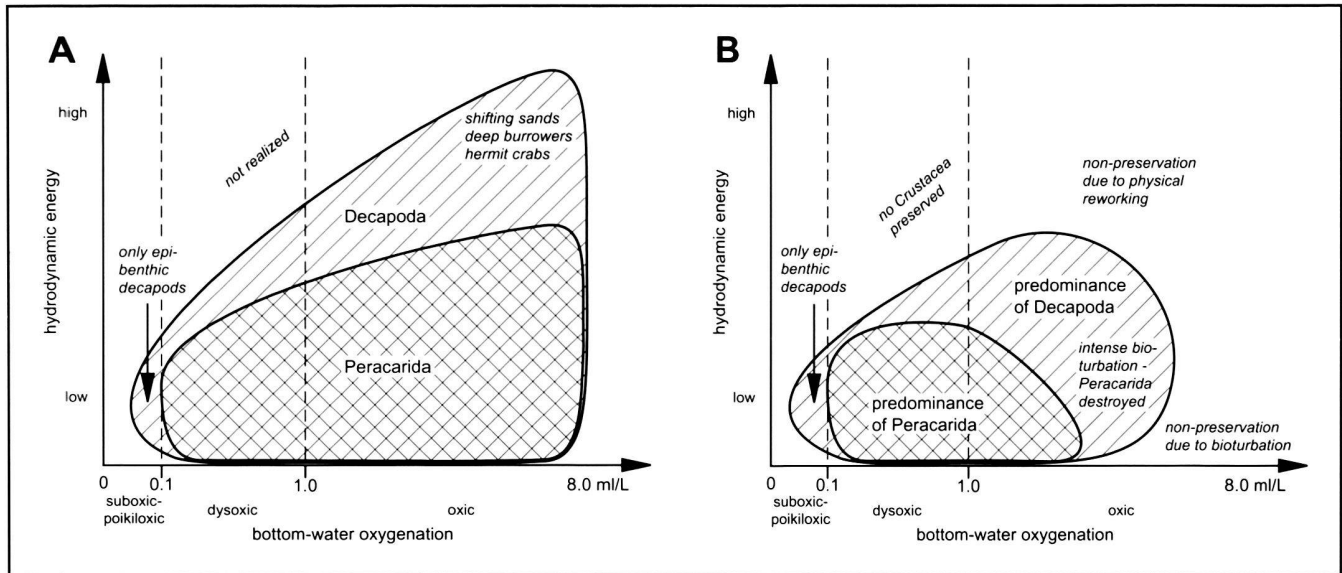


Fig. 5. A, Distribution of crustacean life-assemblages on marine soft-bottoms. In most environments, the peracarids are far more abundant than the decapods. Peracarids are only absent on and in shifting sands and in environments which experience episodic anoxia. B, Crustacean taphocoenoses; the destruction of remains through physical reworking and bioturbation leads to a reduced realm of peracaridean dominance. See text for further discussion.

decades (e. g. Schäfer 1972; Allison 1986; Bishop 1986; Plotnick 1986; Plotnick et al. 1988; Briggs & Kear 1994; Hof & Briggs 1997; Stankiewicz & Briggs 2001). By contrast, studies on the fossilisation potential of peracarid crustaceans are completely lacking. Yet the results from the decapod experiments alone give valuable insights into the processes affecting also the preservation of peracarid crustaceans.

On and in marine soft-grounds, the non-mineralized parts of the cuticle and the other soft-parts decay within a few days (Allison 1986; Plotnick 1986) and within a few weeks, the sclerotized parts of the cuticle become decalcified and hence softer (Plotnick 1986). Considerable transport without completely destroying the remains seems possible only within the first few days (Allison 1986). During this period, scavenging and the activity of burrowing infauna is primarily responsible for the destruction of the remains (Bishop 1986; Plotnick 1986; Plotnick et al. 1988). Oxygen-deficient bottom-water conditions are favourable for the preservation of fossil crustaceans by reducing the amount of bioturbation and scavenging (Bishop 1986; Plotnick 1986; Plotnick et al. 1988). Also early diagenetic mineralization of the remains is bound to reducing micro-environments (Allison 1988).

Peracarid crustaceans with their thinner and weaker cuticles are certainly more susceptible to the destructive biostratigraphic processes of bioturbation, scavenging and transportation. Especially in high-energy hydrodynamic regimes, this leads to a bias where decapod remains can survive but the peracarids are destroyed. In the transition from life assemblages to taphocoenoses, a shift can thus be expected with a shrinking range of peracaridean dominance (see Fig. 5).

A model relating environmental factors to decapod: peracarid – ratios

If judged from modern environments, a predominance of peracarid taxa over decapod crustaceans should be expected in the fossil record. Yet two important filters apply.

- (1) Ecologic filter: Peracarid crustaceans are largely excluded from shifting sand environments. Here decapod crustaceans dominate. Furthermore, peracarid populations cannot survive and re-establish themselves in environments that experience seasonal anoxia (poikilaerobic environment). In these environments only decapod crustaceans occur.
- (2) Taphonomic filter: Peracarid crustaceans are more easily destroyed by taphonomic processes including the physical reworking of the sediment and the bulldozing of the sediment by the larger infauna.

In most fossiliferous settings, the decapods are therefore the dominant group or are even the only fossilized part of the original macrofaunal crustacean community (Fig. 6). Examples of shallow-water deposits that experienced intense reworking and bioturbation include e. g. the Middle Triassic Muschelkalk of southern Germany (Aigner & Bachmann 1993) and the Middle Jurassic Hauptrogenstein of northwestern Switzerland (Wetzel et al. 1993). In both deposits many decapod crustaceans but no peracarids were found (Schmidt 1928, 1938; Hess 1972, 1975). At the other end of the spectrum, the Lower Jurassic Posidonia Shale of southern Germany with its world

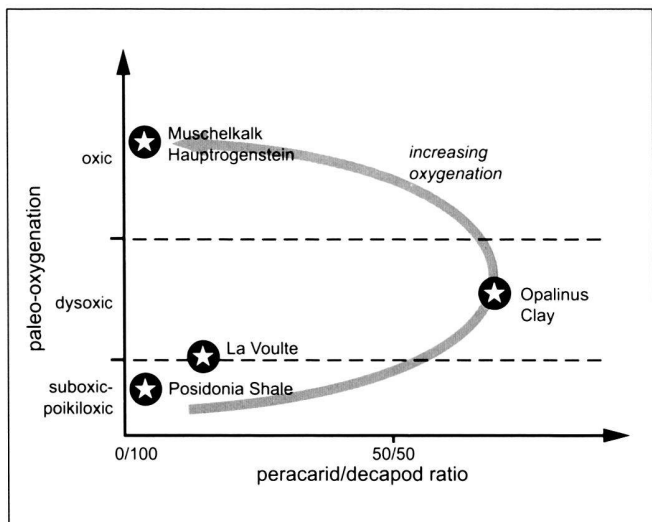


Fig. 6. Some well known fossiliferous settings arranged in a gradient of increasing bottom-water oxygenation. Only in dysoxic environments, the peracarid dominance was preserved (e. g. in the Opalinus Clay). Beds which experienced episodic anoxia during deposition (Posidonia Shale, La Voulte) and those deposited in high-energy shallow-water settings (Muschelkalk, Hauptrogenstein) contain only decapod crustaceans. See text for further discussion.

renowned and spectacularly preserved fauna was deposited under generally dysoxic bottom-water conditions with frequent anoxic phases (Seilacher 1990; Urlichs et al. 1994; Röhl et al. 2001). Although rare, decapods are present in different layers of the Posidonia Shale but peracarid crustaceans are completely lacking (Riegraf et al. 1984). The Middle Triassic Grenzbitumenzone of Monte San Giorgio and the Upper Jurassic Solnhofen limestone contain almost exclusively allochthonous crustaceans (Barthel et al. 1990; Etter 1994; Röper & et al. 2000) which includes in the latter also peracarid taxa (Barthel et al. 1990).

Fossiliferous settings that preserve the original predominance of peracarids required special depositional conditions: a low-energy dysoxic bottom-water environment with concomitant very low degrees of bioturbation and at the same time the absence of episodic anoxia. These conditions were met during the deposition of the Opalinus Clay but there are certainly many other settings which experienced a similar depositional history. For these, the present model predicts also a peracarid abundance which exceeds that of the decapod crustaceans. One such example is the Bathonian clays of Lower Saxony which yielded the many specimens of the tanaidacean *Jurapseudes friedericianus* described by Malzahn (1970).

From the lower Callovian of La Voulte-sur-Rhône a very rich decapod fauna is known (van Straelen 1925; Sayn & Roman 1928; Carriol & Riou 1991). Peracarids, however, are extremely rare and present only with one species of cumaceans (Bachmayer 1960). Bottom-water conditions are thought to have been generally dysoxic during deposition of the lower

Callovian sediments (Dietl & Mundlos 1972; Wilby et al. 1996; Wilby 2001) but according to the present model, the peracarids were excluded by repeated anoxic events.

The high lateral variability in the lower Callovian of that region (Elmi 1967) indicates a well developed bottom relief. Episodic anoxia most likely developed only in the depressions whereas peracarids could survive on topographic highs. These crustaceans could be transported to the oxygen-depleted depressions by storms. Indeed the cumaceans occur in thin mudflow layers which probably accumulated during such events.

Acknowledgements

The help of T. Badertscher, B. Balzerini, F. Fassnacht, H. Lanz and K. Tschanz was invaluable during field work. H. Furrer kindly loaned material from the collection of the Palaeontological Institute and Museum of the University of Zürich. R. Theiler donated some specimens of *Mecochirus cf. eckerli* from his private collection to the latter institute. With their constructive reviews, C. Klug and G. Schweigert helped considerably to improve the quality of the manuscript. K. Brown kindly improved the English.

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Manuscript received May 20, 2004
Revision accepted November 1, 2004