

First evidence of Late Cretaceous decapod crustaceans from Åsen, southern Sweden

Aron Praszker

Dissertations in Geology at Lund University,
Bachelor's thesis, no. 368
(15 hp/ECTS credits)



Department of Geology
Lund University
2013

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Praszkie, A., 2013: First evidence of Late Cretaceous decapod crustaceans from Åsen, southern Sweden. *Dissertations in Geology at Lund University*, No. 368, 13 pp., 15 hp (15 ECTS credits).

Abstract: Decapod crustacean remains were uncovered in 2011 at Åsen, the first from this site. Åsens Late Cretaceous strata are part of the Kristianstad Basin, in southernmost Sweden. Seven cheliped moulds and a number of other remains such as pereopod imprints were found in carbonate-cemented nodules within the sediments of the Campanian *B. balsvikensis* zone. Several different morphologies are present, and three of the samples are interpreted as belonging to the family Callanassidae of infraorder Axiidea, with a probable association of *Protocallianassa*. The burrowing mode of life points to the conclusion that the nodules may be fossilized burrows, also explaining why they are constrained to a singular layer in the sequence.

Keywords: Decapoda, Crustacean, Axiidea, Cretaceous, Campanian, Åsen, Kristianstad basin, Scania, Sweden.

Supervisors: Elisabeth Einarsson, Vivi Vajda

*Aron Praszkie, Department of Geology, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden.
E-mail: alias1591@gmail.com*

De första fynden av senkretaceiska decapoda kräftdjur från Åsen i Skåne

ARON PRASZKIER

Praszkie, A., 2013: De första fynden av senkretaceiska decapoda kräftdjur från Åsen i Skåne. *Examensarbeten i geologi vid Lunds universitet*, Nr. 368, 13 sid., 15 hp.

Sammanfattning: Under 2011 hittades fossil från decapoda kräftdjur på Åsen, de första från denna lokal. Åsens lager från sen Krita är en del av Kristianstadbassängen i sydligaste Sverige. Sju chelipedavgrutningar och ett antal andra fossila lämningar som pereopodavtryck hittades i karbonatcementerade noduler i sedimenten i den Campaniska *B. balsvikensis*-zonen. Ett flertal olika morfologier finns representerade och tre av proverna tolkas som tillhörande familjen Callanassidae av infraordningen Axiidea och troligen tillhörande Protocallianassa. Den grävande infaunalivsstilen pekar mot att nodulerna kan vara fossiliserade grävgångar, vilket också skulle förklara varför dessa är begränsade till ett enda lager i sekvensen

Nyckelord: Decapoda, Kräftdjur, Axiidea, Krita, Campan, Åsen, Kristianstadbassängen, Skåne, Sverige.

Handledare: Elisabeth Einarsson, Vivi Vajda

Ämnesinriktning: Berggrundsgeologi

*Aron Praszkie, Geologiska institutionen, Lunds universitet, Sölvegatan 12, 223 62 Lund
E-mail: alias1591@gmail.com*

1 Introduction

Between 2010 and 2012, annual excavations under the heading of Elisabeth Einarsson, of the geological institution at Lund University, has been undertaken at the Åsen locality. The excavations at Åsen are aimed to mapping out the variations of fossil content of the Late Cretaceous strata found there. During sorting of collected materials, remains from what was unmistakably a decapod crustacean cheliped was discovered in a carbonate-cemented nodule, the first of this kind from the site. The scope of this project has been to further examine the collected materials and try and collect more crustacean specimens, examine and possibly identify the remains.

1.1 Systematics

The arthropod order Decapoda, or “ten footed”, is estimated to contain close to 15 000 species in 2700 genera, including around 3300 fossil species (De Grave, et al. 2009). The systematics of the order has undergone several revisions, and aspects of the taxonomical classifications are still somewhat fluid. Older classifications divided the order by mode of transportation, into Natantia and Reptantia, or swimming and walking lineages, respectively (Bracken et al. 2009). More recent works divide Decapoda into the suborders Dendrobranchiata and Pleocyemata, the latter which contains all but Penaeoid and Sergestoid shrimps (Toon et al. 2009). The suborders were defined through characteristics, such as gill structure and the brooding of eggs on the female pleopods (Porter et al. 2005). This division has been reported by de Grave et al. (2009) to have achieved a broad consensus, although groupings using the mode of locomotion as a defining characteristic still seem to be used (Schram 2001; Porter et al. 2005, Bracken et al. 2009). The number of infraorders is an ongoing issue to be resolved. The more well-known (due to their economic importance), and supposedly less controversial ones include: Caridea and Stenopodidea (shrimps), Astacidea and Achelata (crayfish and lobsters), Brachyura (crabs) and lastly Anomura (hermit and king crabs). Approximately half of all decapod species belong to the infraorder Brachyura, although this infraorder is still subject to debate and revisions. (Porter et al. 2005; De Grave, et al. 2009). A recent change in the systematics is the division of infraorder Thallasinoidea into two separate infraorders, Gebiidea and Axiidea, after phylogenetic studies suggested that the infraorder was paraphyletic. The former Thalassinideans are commonly known as mud lobsters, mud shrimp or ghost shrimp, due to their fossorial mode of life (Dworschak et al. 2012; Robles et al. 2009; De Grave et al. 2009).

1.2 Fossil Record

The first known decapod fossil dates back to the Late Devonian (Schram 2009). Following the Permian-Triassic extinction event the order Decapoda rapidly diversified, partially attributed to the extinction of

competing arthropods, such as trilobites (Zonneveld et al. 2002). However, phylogenetic studies suggest that all the major lineages had already been established in the Devonian (Porter et al. 2005). Cretaceous decapod crustacean fossils span all infraorders, and occur on all continents. Brachyuran crabs are particularly common, although that may be due to the immenseness of the infraorder itself. There is evidence for a Cretaceous decapod radiation, with a number of families appearing, and with faunal dispersion and exchanges between regions. The Cretaceous-Paleogene extinction event had little impact on decapod crustaceans, with only three families (the Mecochiridae, Dakoticaneridae and Carcineretidae) shown to have gone extinct during the Late Cretaceous (Feldmann 2003; Schweitzer 2001).

Axiid representation in the geological record largely consist of chelae and trace fossils, due in part to the weak calcification of the body and strong calcification of the first chelae to facilitate burrowing (Dworschak et al. 2012; Swen et al. 2001). Chelae from the genus *Callianassa* are particularly common in the fossil record (Hyžný 2010). Fossils of the species *Protocallianassa faujasi*, in the form of multiple morphologies of primary chelae, is common to Campanian and Maastrichtian deposits in the Netherlands, Belgium and Germany. Phylogenetic studies have estimated that the order diverged from other reptant (walking) decapods within the Permian (Bracken et al. 2010).

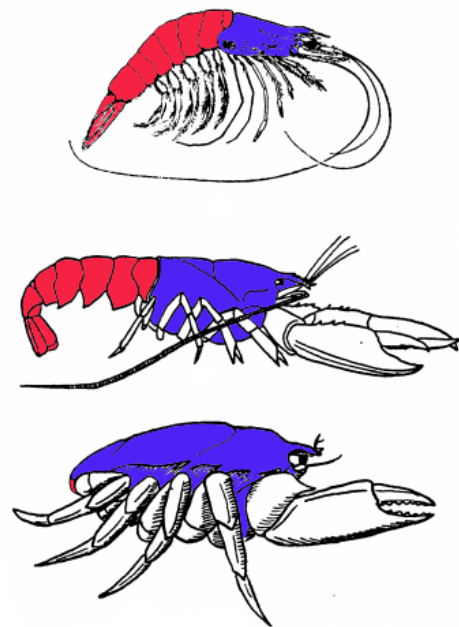


Fig. 1: Decapod Morphology. Cephalothorax in blue, and abdomen in red. Modified from Glaessner (1960)

1.3 Morphology

The basic body plan of decapods consist of five segments of head fused with eight underlying thoracic segments, forming a cephalothorax which is covered by a carapace. The first three pairs of the eight pairs of thoracic legs have evolved into maxillipeds (mouth parts). The remaining legs called pereiopods, or chelipeds if they have evolved pincers gives the order its

name. Following the thorax we have the pleon or abdomen, consisting of six segments with a number of pleopods or swimmerets (Glaessner 1960, Schram 2009).

The orderly body plan belies the great morphological diversity and breadth of adaptations within decapods. Using recent examples, the sizes can vary from the 7 millimeter long carapace of a species of hermit crab to the several meter wide leg span of Japanese spider crabs (Martin & Davies 2001). As previously mentioned, there is a distinction between swimming and walking decapods, with several morphological adaptations in abdomen, pleo- and pereopods. While the abdomen and pleopods are beneficial for a benthic mode of life, they get in the way for reptant species, such as many crabs, and are often reduced in size, and folded under the cephalothorax. (Glaessner 1960).

Chelipeds, or claws, are in themselves a testament to the morphological variability within the decapods, subject to adaptations, sexual dimorphism and heterochely within individuals. Heterochely is generally expressed as a larger crushing claw, and a smaller cutting claw (Collins 1999). The adaptation of a crushing claw, with 'molariform' denticles or a curved denticle near the base of the dactyl is interpreted as a means of predation, crushing prey or breaking the shells of, for instance, bivalves. The cutting claw is then used to render the tissues into pieces to be eaten (Schweitzer & Feldmann 2010).

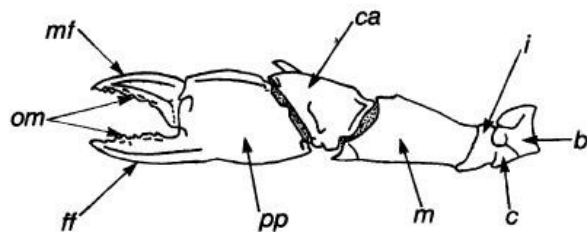


Fig. 2: Schematic view of crab cheliped (Collins 1999). b: basis c: coxa ca: carpus ff: fixed finger i: iscium m: merus mf: dactylus or moveable finger om: opposing margins pp: manus (manus + fixed finger = propodus)

2 Geological Setting

The Kristianstad Basin is situated in Scania, the southernmost province of Sweden. The basin, situated in the tectonical deformation zone known as the Tornqvist zone, is formed by two half grabens bordered by horsts to the southwest and ending in irregular outcrops in the north (Einarsson et al. 2010; Surlyk & Sørensen 2010). During the Cretaceous, sea levels were up to a hundred meters higher than today, and the area was submerged, forming a shallow marine environment with horsts and hills as islands in an archipelago (Kominz et al. 2008; Surlyk & Sørensen 2010). The area contains several well-known paleontological localities exposing Cretaceous sediments, such as Ignaberga and Ullstorp. Additionally, Ivö Klack and Åsen are situated only a few kilometers from each other.

The fossil content of the sediments is rich in both invertebrate and vertebrate fragmentary remains. The area had a diverse invertebrate fauna with evidence of corals, echinoderms, cephalopods and bivalves. Invertebrate remains are dominated by oyster shells and belemnite rostra. Vertebrate remains are also common, including multiple species of sharks, bony fish, turtles, crocodiles, mosasaurs and plesiosaurs (Einarsson et al. 2010; Lindgren & Siverson 2002; Sørensen et al. 2013).

2.1 Åsen

Åsen is located a few kilometers north of the small town of Bromölla in the Kristianstad Basin. The site itself is currently a municipal landfill and recycling center. The Cretaceous strata at Åsen consist of unconsolidated glauconitic and calcareous quartz sands, interspersed with clay and gravel, overlying flood plain sediments. The sands are of latest early, to earliest late Campanian age, biostratigraphically dated by the presence of *Belemnelloccamax mammilatus* and *Belemnelloccamax balsvikensis* belemnite rostra (Christensen 1976). The thickness of both biozones totals approximately 4 meters. The *B. mammilatus* zone is the older of the two and rests atop a layer of Cretaceous flood plain clays. The strata are further subdivided into layers characterized by color and fossil content. For the *B. mammilatus* zone this consists of a coquina, a thin storm deposit, followed by a layer of greensand. On top of this rests an oyster bank, whose fossil content is dominated by oysters and is notably less affected by glauconite coloring than the layers surrounding it. Above the oyster bank is the *B. balsvikensis* zone, whose layers consist of a greenish layer followed by a yellowish (Einarsson et al. in press). Grain sizes and minerogenic content is similar in the different zones, with the exception of the balsvikensis yellow layer, which contains large carbonate-cemented nodules. Nodules can also be found in smaller sizes and numbers in the balsvikensis green layer, but are significantly less common (Einarsson et al. in press). The nodules are up to 20 cm in diameter, largely made up of grains of sand and silt, and rather porous. The cohesion is varied, with some specimens easily broken apart, whereas others withstand breakage.

The fossils found at Åsen are generally disarticulated. The invertebrate fossils found mainly consist of shell fragments from bivalves, notably oysters, and also belemnite rostra. Common invertebrate finds also include corals and echinoderm spines. Åsen has been mentioned as the most productive site for vertebrate remains in Sweden, and the site is rich in shark teeth, vertebra from bony fish and reptilian bones, including mosasaur and plesiosaur teeth and bones (Lindgren & Siverson 2002, Einarsson et al 2010).

3 Methods

Prior to any fieldwork, the site was cleared of Quaternary deposits overlying the Cretaceous strata.



Fig. 3: Carbonate-cemented nodule from Åsen

As the dig site is accessible top-down the fieldwork consisted of digging with shovels until the Cretaceous strata were reached. The different zones were determined by the belemnite rostra content of the excavated sediments. Buckets of extracted sand was carried to a small pool and then sieved with a 2 mm mesh in order to remove sand, silt and clay.

The material collected in the mesh was then preliminarily sorted, with larger shell fragments, shark teeth and assorted bone fragments put aside. This still left a large volume of gravel and fossil content to be examined. All collected material was packaged and marked by date and zone association for later examination and sorting in the lab.

The material collected in the field was sieved again as needed, in order to further remove clay and sand. A more thorough sorting of the materials was then carried out. For the scope of this project, most of the examination consisted of rinsing and visually examining the carbonate-cemented nodules, and carefully scraping away granules obscuring any fossil content.

Carbonate-cemented nodules containing suspected or identified decapods crustacean remains were put aside, marked with field collection dates and zone association. The selected specimens were then photographed, given a unique identifier and entered into a spreadsheet with a description of the fossil content, the zone association and other field data. From these the specimens to be presented were then selected for further study.

4 Results

From the extracted materials 63 carbonate cemented nodule samples with possible decapod crustacean remains were selected for further study. Twelve of these were selected for further study, and are presented in Figs. 4 and 5. Most of these were imprints and fragments of indeterminate origin, and marked as possible decapod crustacean remains. Out of the samples seven cheliped moulds were positively identified, with a further number of pereopod segments and a number of

negative cheliped and manus imprints, one of which is presented in plate 2. No cephalothorassic or abdominal fossils were identified. All but sample B from plate 2, which is of the balsvikensis green layer comes from the balsvikensis yellow layer.

4.1 Samples from Fig. 4

4.1.1 A

A three-dimensional mould of a cheliped with carpus, manus and the dactyl. The fossil is approximately 5.2 cm from tip of the dactyl to end of the carpus. A small segment of what could be the merus is barely visible at a right angle to the end of the carpus. Both manus and carpus are longer than wide. The carpus widens distally while the manus thins slightly. The carpus is rounded whereas the manus is subrounded with noticeable rounding only taking place along the margins. The fossil is smooth with no discernible warts or spines. The dactyl lack any dentation.

4.1.2 B

A well preserved manus with fixed finger. The fossil is approximately 3 cm long from the tip of the fixed finger to the base of the manus. The shape of the manus is flat with slight rounding in the center of the inside surface. There is only minor distal horizontal thinning, with the margin of the manus terminating in a straight edge. Along the margin a row of what is likely to be setal pits can be discerned along the entire length from the base of the manus to the tip of the finger. The finger displays a single denticle at approximately half the length of the finger.

4.1.3 C

This specimen consists of a manus with fixed finger and a carpus. The specimen is 5.5 cm from the tip of the fixed finger to the end of the carpus, and it is approximately 2 cm wide at its widest point. Both the manus and carpus are slightly longer than wide. The carpus widens distally whereas the manus thins. The manus is flat with a slight vaulting along the middle. The carpus is noticeably vaulted, and flattens to end in straight edges along the length of the margins. No visible surface structures are visible on either segment, and no dentation on the fixed finger is discernible.

4.1.4 D

A Propodial with carpus and unidentified disarticulated pieces nearby on the same nodule, possibly consisting of the merus, and other proximal pereopod segments. The fossil is a well preserved mould of a propodial with joint manus. From the tip of the fixed finger to the end of the manus it measures approximately 3.6cm. The propodial is longer than wide, whereas the carpus is approximately as wide as it is long. The propodial seems to slightly thin, distally, and the carpus widens slightly. The propodial is smooth and somewhat rounded on the outside, with rounding beginning from the middle rather than near the margins.

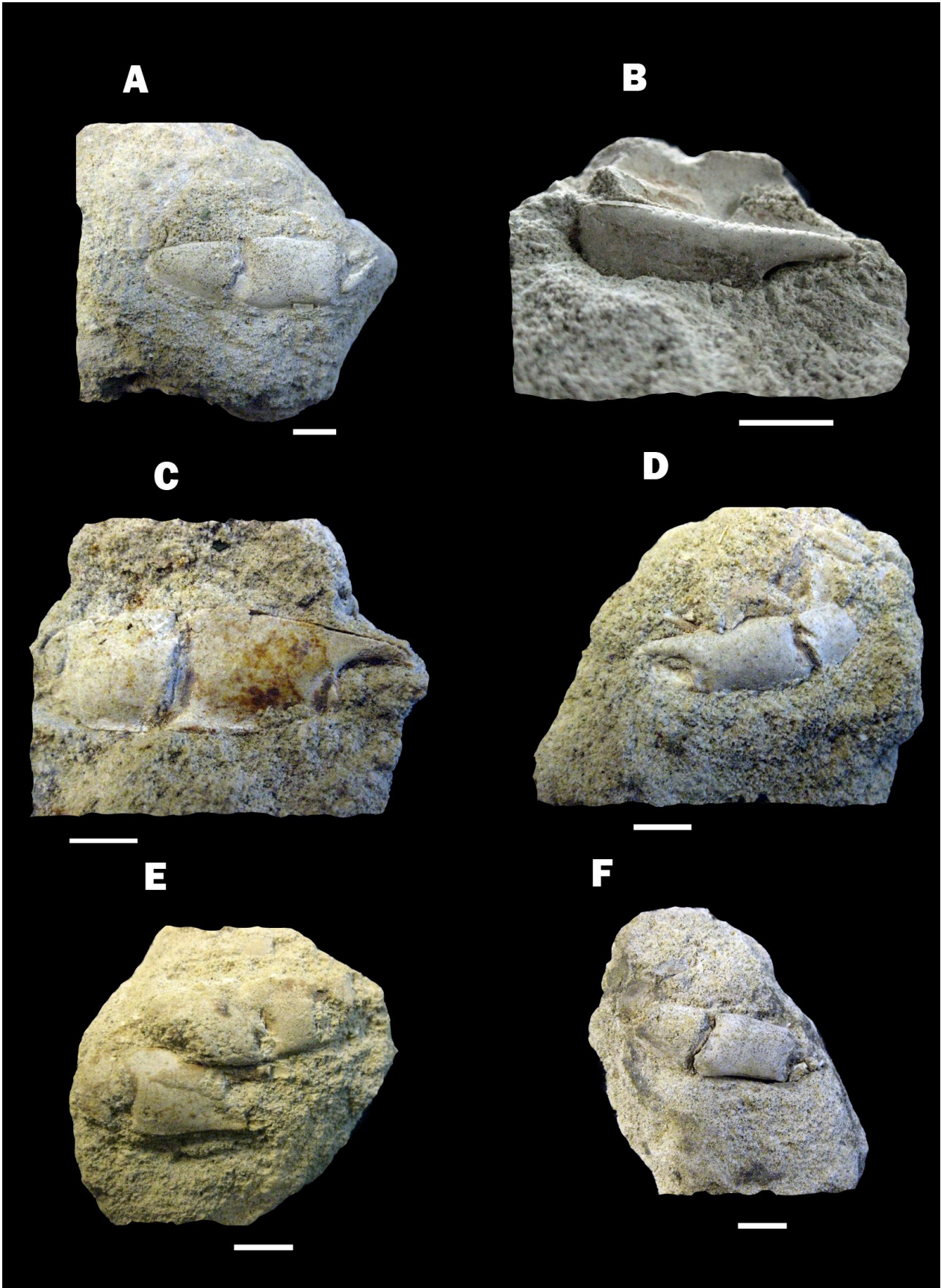


Fig. 4: Cheliped moulds found at Åsen. A: Carpus and manus with dactyl B: Manus with fixed finger and possible setal pits. C: Carpus and manus with fixed finger. D: Carpus and propodial. E: Two cheliped propodials with remains of manuses. F: Carpus and manus with fragmented dactyl. Scale bar measures one centimeter.

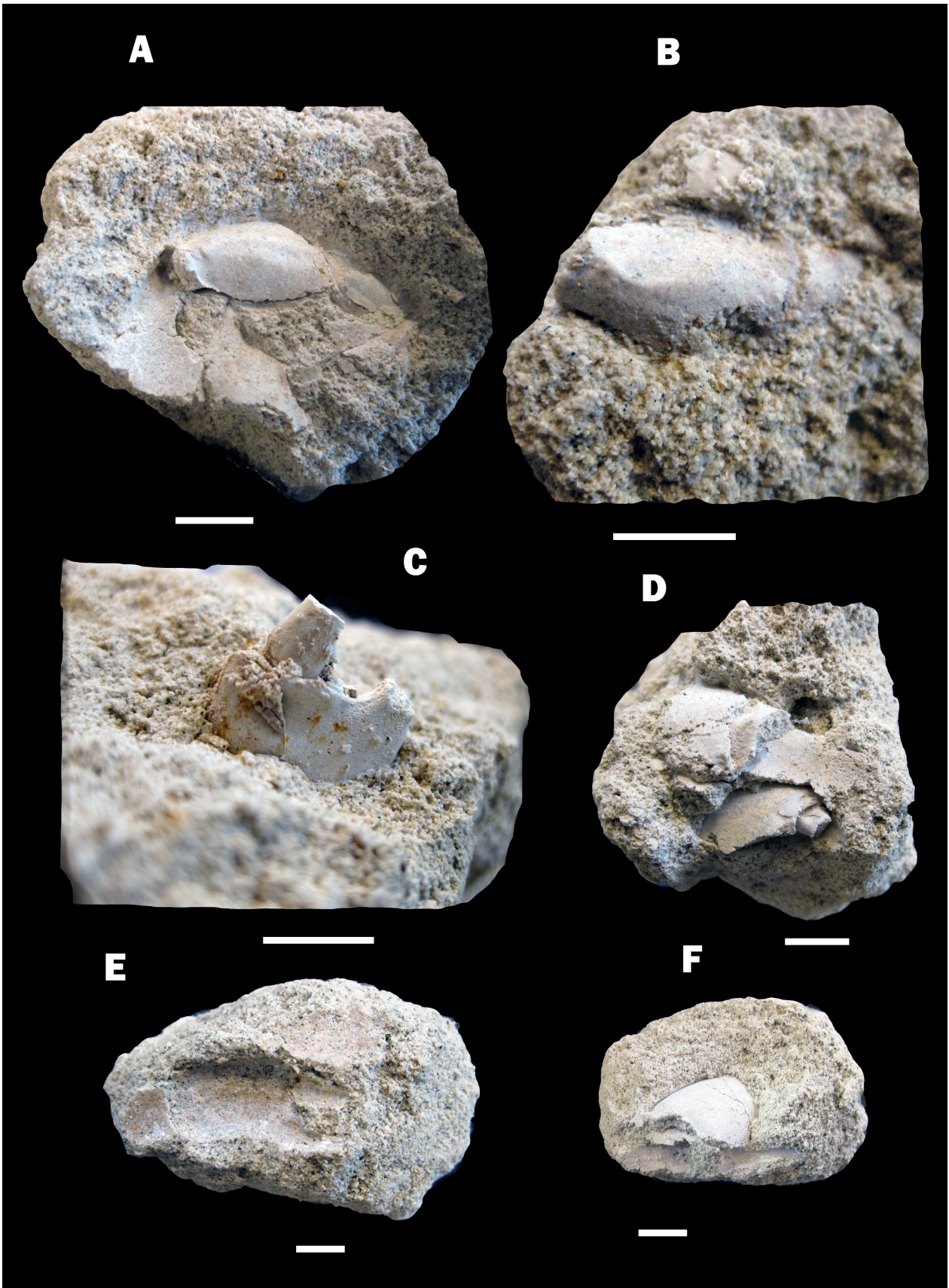


Fig. 5: Additional samples of decapod crustaceans from Åsen. A: Propodial with well-preserved manus. B: Pereiopod segment. C: Propodial with broken fingers. A denticle is visible near the base of the dactyl. D: Possible manus and dactyl, with unidentified shell fragments superimposed. E: Imprint of a propodial and carpus. Note the slight bend in the carpus. F: Unidentified shell fragments, possibly a carpus, with imprints of pereiopod segments below. Scale bar measures one centimeter.

The carpus is only slightly rounded. The dactyl is barely showing, whereas the fixed finger is visible and has a visible denticle approximately in the middle of its length.

4.1.5 E

The sample consists of moulds of two propodials with carpii, one overlaying the other. The topmost cheliped is approximately 4 cm long and the bottom one measures 3.4 cm in length. The topmost cheliped is badly weathered and most details are indiscernible.

In both chelipeds the proximal edge of the carpus is not preserved. The propodials are heteroform, with the topmost one being wider than its long, and the bottom propodial being longer than wide. What remains of the topmost carpus is approximately twice as long as its corresponding propodial, not including fingers. Both propodials thin distally. Any further details is indiscernible from the topmost cheliped, but the bottom propodial is slightly vaulted and ends in straight edges. No surface structures or finger dentation is discernible on either cheliped.

4.1.6 F

The sample consists of the mould of a manus with a dactyl, as well as the carpus and impressions of proximal cheliped segments. The fossil measures 4.4 cm from the proximal edge of the carpus to the distal edge of the manus. Both carpus and manus are longer than they are wide. The carpus widens distally whereas the manus thins slightly. The carpus has come loose and the dactyl has fractured into three pieces. This, however, allows observation of the manus from both sides. The outside is flat with a minor rounding near the margins. The inside is slightly vaulted along the length of the dactyl side, with the fixed finger side thinning and terminating in a straight edge. The manus is approximately 0.7cm thick, compared to the width which is 1.7 cm.

4.2 Samples from Fig. 5

4.2.1 A

The fossil consists of moulds and impressions of a pereiopod. The best preserved part of the fossil is the large three dimensional mould of what is probably a manus. The segment measures approximately 1.6 cm in length and is longer than it is wide. The sample is oval in shape, and vaulted, with a ridge running along the length, creating “facets”. The proximal joint is prominent, and round in cross-section. The fossil is fragile and has therefore been left in the condition it was found in for fear of any further work shattering it.

4.2.2 B

The sample consists of an unidentified pereiopod segment, approximately 1.8 cm long. The sample is vaulted and slightly angular in cross-section. A prominent wart is discernible near what is assumed to be the proximal joint of the fossil. Similar in three dimensional structure to sample A of Fig. 5.

4.2.3C

The sample consists of a propodial with broken fingers. The sample is approximately 1.4 cm wide and flat on both sides in what is visible of the cross section. A denticle is visible near the base of the dactyl. This sample seems to have actual exoskeletal remains, rather than an internal mould of the dactyl.

4.2.4 D

The fossil consists of a three dimensional mould of what is likely a manus with the base of the dactyl still remaining. Unidentified disarticulated remains approximately 4 cm long and 2 cm wide overlay the specimen.

4.2.5 E

A negative impression of a propodial measuring approximately 2.8 cm in length. The impression curves in and downward at the base of the fingers, a feature reminiscent of brachyuran crabs, where the cheliped is held against the cephalothorax in “resting position”.

4.2.6 F

A mould of a probable manus segment overlying a negative impression of pereiopod segments. The width of the mould is approximately 2 cm wide.

5 Discussion

While several decapod fossil samples were excavated from Åsen, no cephalothoracic or abdominal remains were identified. It has been suggested that decapods are underrepresented in the fossil record, due in part to weak calcification of their exoskeleton, the deep water mode of life of many taxa, and the rapid decomposition of soft tissues, leaving the brittle and easily disarticulated outer surface of the carapace (Feldmann 2003).

Most samples only consist of internal moulds of the chelipeds. This may have removed surface structures such as denticles and tubercles, and even changed the cross-section of the segments. Some samples were also found fully exposed on the surface of the carbonate cemented nodules, and were thus subject to weathering.

In the fossil assemblage found at Åsen, several of the chelipeds display similar morphological characteristics, which is to be expected.

- Sample C and E from Fig. 4 are similar in manus shape and are likely related.
- Sample A and F from Fig. 4 are very similar to one another in morphology, and unfortunately in preservation, with any dentation or tubercles likely to have weathered away.
- Sample B and D from Fig. 4 are different in carpal morphology from all other cheliped fossils found at Åsen. Sample B has less proximal thinning than the C-E grouping, and is flatter than A-F. Sample D, on the other

hand, is more rounded than both A-F and C-E, and with less distal thinning than the latter.

A comparison with available literature has led to the conclusion that the morphology of samples A, D and F from Fig. 4, are reminiscent of species belonging to the family Callianassidae of the infraorder Axiidea. Sample A and F are decidedly not crab-like, with long manus and no adaptations for folding the carpus to rest against the cephalothorax. There are definite morphological similarities to *Protocallianassa faujasi*, a species, as previously mentioned, common to Campanian strata in the Netherlands, Belgium and Germany. In this species, three distinct chelae morphotypes have been identified: males, females and juvenile males (Swen et al. 2001; Mourik et al. 2005). This is relevant in this case, since we have several different groups of chelae, with the plates provide resembling some of the finds from Åsen. Sample D from Fig. 4 was included in the grouping after comparison to the plates as it resembles the juvenile male morphotype of *P. faujasi*.

This leaves sample B, C and E. As previously mentioned sample C and E are similar in shape. They are however somewhat dissimilar to the A-F grouping in the general shape of the manus, with C-E having a pronounced distal thinning, whereas A-F are almost rectangular in shape. The multiple cheliped specimens on sample E, interpreted as the same individual, and the long carpus on sample C still points to an association of a species not crab-like in shape. The two chelipeds on sample E, are different in proportions. This may be due to heterochely, or that they are of different pairs of chelipeds. If the latter is the case, then the likely association would be a species of similar morphology to Axiidea or Gebiidea, both formerly of the infraorder Thalassinoidea.

Sample B consists of a singular manus, dissimilar to the other finds from Åsen. While well preserved, with dentation and what seems to be setal pits present, it still presents a problematic specimen to identify. With less distal thinning of the carpus than C-E, and flatter than A, D and F, it is not apparently associated with either group. The sample could conceivably be of Brachyuran origin or alternatively be an example of strong heterochely, but without more samples this remains pure conjecture.

The samples from Fig. 5, mainly consisting of pereopod segments and disarticulated chelae are less easy to draw any conclusions from. Sample A and B consist of pereopod moulds and due to their comparatively good preservation and solidity, may represent remains from other species than Axiids. Sample C, extending from the nodule is one of the few samples where actual exoskeletal remains have been preserved. The sample has not been further prepared as it is unfortunately rather brittle as it is, and would likely shatter. What can be seen of the sample is morphologically similar to samples A-F from Fig. 4, with a slight rounding to the edges of the carpus. Sample E, an im-

print of a propodial, has a slight inward bending towards the fixed finger, distally. This is likely an adaptation for folding the cheliped against the cephalothorax and is reminiscent of carcinoid species. Unfortunately, no moulds or exoskeletal remains with this morphology have been found.

The fossorial mode of life of Callianassids is significant to our findings from Åsen. With heavily calcified chelae to facilitate the burrowing and weakly calcified body, it explains the prevalence of chelae and little else in the specimens (Swen et al 2001). The mode of life may also have further consequences. All specimens were found preserved in carbonate cemented nodules. While the nodules may have facilitated preservation of fossils, they may themselves be the burrows of the very same organisms. Virtually all of the nodules come from the *B. balsvikensis* yellow stratum, with a few small outliers in the layer below. This is a plausible explanation for the sudden appearance of these, rather large structures, in an otherwise largely homogenous stratigraphic sequence. A side effect of this would be that the nodules and fossils may have a more recent origin than the deposition of these sediments. Protocallianassa extends beyond the Campanian (Hyžný 2011). Oyster shells and belemnite rostra have been found in the nodules, but these may have been deposited earlier and coincidentally ended up on the side of a burrow. This scenario cannot be substantiated as the Cretaceous sediments from Åsen ends at the Campanian.

6 Conclusions

Some of the chelae found at Åsen are likely representing several morphotypes of the same species, likely to be of the family Callianassidae and the genus Protocallianassa. The species is undetermined, but could possibly be *Protocallianassa faujasi*. Samples A, D and F from Fig. 4 are interpreted as belonging to this group, with sample C and E interpreted as belonging to a different species of crayfish-like decapod, and sample B being less certain in origin. Samples from Fig. 5 may represent remains from different species and infraorders, such as brachyuran crabs. Due to the fragmental nature of these remains no definite association has been established. The processes behind the formation of the carbonate cemented nodules are not determined, but a likely explanation together with the fossils is that they could be fossilized burrows.

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