First evidence of the Cretaceous decapod crustacean
Protocallianassa from Sweden

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Abstract: An assemblage of the burrowing ghost shrimp, Protocallianassa faujasi, is described, providing the first evidence of this decapod species from Sweden. The fossils occur in successions of the informal earliest late Campanian Belemnellosumax balsvikensis zone at Åsen and the latest early Campanian B. mammillatus zone at Ivö Klack, both in the Kristianstad Basin of NE Skåne. Numerous, heavily calcified chelipeds were found within a restricted bed at Åsen that was rich in carbonate-cemented nodules. Based on the burrowing lifestyle of modern mud shrimps, we interpret these nodules as infilled burrow chambers. The low abundance of molluscs within the Protocallianassa beds is also consistent with analogous extant communities, indicating that a similar ecologically exclusive relationship ruled within the Late Cretaceous shallow-marine ecosystems.

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The Kristianstad Basin in the southernmost Swedish province of Skåne hosts a richly fossiliferous succession of Upper Cretaceous marine deposits. The Kristianstad Basin incorporates two half-graben that are bordered by horsts to the SW; the entire faulted system occurs within a zone of tectonic deformation known as the Tornqvist Zone (Ernstström & Gabrielson 1992). During the mid-Late Cretaceous, repeated transgressive episodes occurred in what today represents southern Scandinavia (Vajda & Solakius 1999; Larsson et al. 2000). These created islands in the Kristianstad Basin that were surrounded by shallow seas forming paralic environments (Kominz et al. 2008; Sørensen & Sørensen 2010) adjacent to the deeper Tethyan shelf to the SW. Today, these palaeoenvironments are represented by several well-known fossil deposits, such as those exposed at Ignaberga, Ullstorp, Ivö Klack and Åsen (Fig. 1) (Bergström & Sundquist 1978; Erstström & Gabrielson 1992). The successions at Åsen and Ivö Klack are especially rich in vertebrate remains, including sharks, rays, actinopterygian fishes, mosasaurs, plesiosaurs, marine and freshwater turtles, aquatic birds, and rare non-avian dinosaur bones (Einarsson et al. 2010; Sørensen et al. 2013). The material for this study was recovered from the earliest late Campanian succession at Åsen and the latest early Campanian succession at the Ivö Klack localities, and represents the first evidence of Protocallianassa, a burrowing shrimp, from Sweden. The morphology, stratigraphical provenance and environmental context of the studied specimens are discussed.

Geological setting

Åsen is situated a few kilometres north of the small town of Bromölla in the Kristianstad Basin (56° 08′ 56.1″ N, 14° 29′ 56.0″ E: Fig. 1). The site is currently a municipal landfill and recycling centre (Einarsson et al. 2010; Sørensen et al. 2013). The strata at Åsen have been correlated with the mid-Campanian informally termed Belemnellosumax mammillatus and Belemnellosumax balsvikensis biozones (Fig. 2) (Lindgren & Siverson 2002). These equate to approximately 4 m of laterally thinning marine sediment (Fig. 2) resting upon upper Santonian and/or lower Campanian fluvio-lacustrine argillaceous clays (Skarby 1968). The decapod fossils occur in carbonate-cemented porous sand represented by sea-urchin spines (Erstström & Gabrielson 1992; Sørensen & Sørensen 2011; Sørensen et al. 2013). The material for this study was recovered from the earliest late Campanian succession at Åsen and the latest early Campanian succession at the Ivö Klack localities, and represents the first evidence of Protocallianassa, a burrowing shrimp, from Sweden. The morphology, stratigraphical provenance and environmental context of the studied specimens are discussed.
nODULES SET IN UNCONSOLIDATED QUARTZ SAND WITH ABUNDANT GLAUCONITE.

Ivö Klack, historically called ‘Blaksudden’ (Christensen 1969), is a world-renowned fossil site located at the northern point of Ivö Island (56°08′21.6″N, 14°24′05.8″E: Fig. 1). It is an abandoned limestone and kaoline quarry that closed in the 1950s. Stratigraphically basal kaolin clay that formed during the early Mesozoic from weathering granites (Lidmar-Bergström et al. 2013) is overlain by quartz sands and a thin bed of dark clay, which was deposited under freshwater conditions (Christensen 1969). The overlying marine succession comprises upper Campanian siliciclastic calcarenites (Surlyk & Christensen 1974).

**Methods**

Eighteen calcified chelipeds of *Protocallianassa faujasi* were measured based on their characters, illustrated in Figure 3, following the methods of Swen et al. (2001). The material is hosted at the Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden. Institutional abbreviations: NRM-PZ Ar 63926–NRM-PZ Ar 63944 (Table 1).

**Systematic palaeontology**

Order **Decapoda** Latreille, 1802
Infraorder **Axidea** de Saint Laurent, 1979
Family **Callianassidae** Dana, 1852
Subfamily **Protocallianassinum** Beurlen, 1930
Genus **Protocallianassa** Beurlen, 1930

*Protocallianassa faujasi* Desmarest, 1822
(Figs 4a–h & 5a–k)

**Description.** The decapod remains, all chelipeds of moderate quality preservation, occur within carbonate-cemented nodules that were collected from the earliest late Campanian, informal *B. balstvikensis* zone at Åsen between 2010 and 2012 (NRM-PZ Ar 63926–NRM-PZ Ar 63933). Isolated fossils were also found in slightly older strata (*B. mammillatus* zone) at Ivö Klack (NRM-PZ Ar 63934–NRM-PZ Ar 63944) by Richard Hägg in 1903. This assemblage also shows moderate preservation. The recovered propodi all have intact fixed fingers, but the accompanying movable finger is preserved in only a few specimens. The propodi size is typical for *Protocallianassa faujasi* (Swen et al. 2001; Mourik et al. 2005). Other notable features include a rectangular (longer than wide) manus, setal pits on the manus and fingers, in some...
Fig. 2. Stratigraphic section for the Åsen locality. Crustacean-bearing level within the *B. balsvikensis* zone is indicated. Note that sections further south along the quarry wall include a bed (up to 0.5 m thick) of *B. mammillatus* zone-age below the 'Coquina bed' (Siverson pers. comm.).

| Age Zone | Metres | Lithology |
|----------|--------|-----------|
| ?Santonian - early Campanian | 0 | Coquina bed |
| | | Continental floodplain deposits |
| earliest late Campanian | 1.0 | Coquina bed |
| | | Glaconitic greensand |
| latest early Campanian | 2.0 | Balsvikensis green |
| | | Balsvikensis yellow |
| | 3.0 | Oyster bank |
| | 4.0 | Sandstone |
| | | Concretions with decapod claws |
| | | Siliciclastic mudstone |
| | | Plant roots and fossil wood |

CRETACEOUS DECAPOD FROM SWEDEN
specimens (probably abraded in others), and a carpus–propodus angle exceeding 100°.

**Measurements.** Pereiopod measurements (mm) were made according to Swen *et al.* (2001): maximum, (mean) and minimum dimensions are listed in Tables 1 and 2:

- propodus length: 37, (28.5) and 23 based on 12 specimens;
- manus length: 28, (21) and 16 based on 16 specimens;
- manus width: 17, (14.6) and 10 based on 16 specimens;
- fixed finger length: 11, (7) and 4 based on 12 specimens;
- carpus length: 21, (16.7) and 12 based on nine specimens;
- angle manus/carpus: 100°, (107°) and 115° based on 15 specimens.

**Remarks.** Important taxonomic characteristics, such as the propodus/manus ratio and the angle of the carpus–propodus joint, in the Kristianstad Basin

### Table 1. Cheliped measurements based on the specimens from the Åsen and Ivö Klack localities included in this study

| Specimen number | Length of carpus (mm) | Length of propodus (mm) | Length of manus (mm) | Width of manus (mm) | Length of fixed finger (mm) | Angle (°) |
|-----------------|-----------------------|-------------------------|----------------------|---------------------|-----------------------------|-----------|
| Åsen locality   |                       |                         |                      |                     |                             |           |
| NRM-PZ Ar 63926 | 18.5                  | –                       | 24                   | 16                  | –                           | 108       |
| NRM-PZ Ar 63927 | –                     | 30                      | –                    | –                   | 10                          | –         |
| NRM-PZ Ar 63928 | 17                    | 31                      | 21                   | 17                  | 11                          | 100       |
| NRM-PZ Ar 63929 | 12                    | 24.5                    | 16                   | 10                  | 8                           | 113       |
| NRM-PZ Ar 63930 | –                     | –                       | –                    | –                   | –                           |           |
| NRM-PZ Ar 63931 | –                     | 24                      | 16                   | 15                  | 8                           | –         |
| NRM-PZ Ar 63932 | 21                    | –                       | 20                   | 14                  | –                           | 102       |
| NRM-PZ Ar 63933 | –                     | –                       | –                    | –                   | –                           |           |
| Ivö Klack       |                       |                         |                      |                     |                             |           |
| NRM-PZ Ar 63934 | 15                    | 23                      | 18                   | 14                  | 5                           | 105       |
| NRM-PZ Ar 63935 | 17                    | –                       | 21                   | 15                  | –                           | 100       |
| NRM-PZ Ar 63936 | 16                    | –                       | 20                   | –                   | –                           | 110       |
| NRM-PZ Ar 63937 | 16                    | –                       | 21                   | 15                  | –                           | 106       |
| NRM-PZ Ar 63938 | –                     | 33                      | 24                   | 14                  | 6                           | 112       |
| NRM-PZ Ar 63939 | 18                    | 27                      | 21                   | 15                  | 6                           | 115       |
| NRM-PZ Ar 63940 | –                     | 30                      | 22                   | 14                  | 8                           | 100       |
| NRM-PZ Ar 63941 | –                     | 33                      | 24                   | 17                  | 8                           | 110       |
| NRM-PZ Ar 63942 | –                     | 27                      | 21                   | 14                  | 6                           | 100       |
| NRM-PZ Ar 63943 | –                     | 23                      | 19                   | 12                  | 4                           | 115       |
| NRM-PZ Ar 63944 | –                     | 37                      | 28                   | 17                  | 9                           | 112       |
| Mean values     | 16.7                  | 28.5                    | 21.0                 | 14.6                | 7.0                         | 107       |
Protocallianassa faujasi specimens (Fig. 6; Table 2) closely approximate other examples of this species (Vega et al. 1995; Swen et al. 2001; Mourik et al. 2005).

Occurrence. Protocallianassa ranges from the Early Cretaceous (Barremian) to the Eocene (Mourik et al. 2005), of which the European record only spans the Cenomanian–Maastrichtian (mid- to end-Cretaceous). Protocallianassa is common in younger deposits at a few locations including the USA (Roberts 1962), Argentina (Feldmann et al. 1995), Chile (Förster & Stinnesbeck 1987) and Antarctica (Feldmann & Wilson 1988). Campanian Protocallianassa have been described previously from Germany (Mertin 1941; Mourik et al. 2005), the USA (Roberts 1962; Bishop 1985) and from Mexico (Vega et al. 1995). Other Cretaceous occurrences include the Maastrichtian of The Netherlands and Belgium (Swen et al. 2001), the USA (Roberts 1962), Mexico (Vega et al. 1995) and Chile (Förster & Stinnesbeck 1987). Early Cretaceous (Aptian–Barremian) occurrences are represented only in the southern hemisphere: Argentina (Aguirre-Urreta 1983) and Antarctica (Taylor 1979).

Discussion

The present study adds to the distribution of Late Cretaceous Protocallianassa, extending its northern range into Scandinavia. At the close of the Cretaceous, Protocallianassa was replaced by representatives of other subfamilies such as Corallianassa. This might be linked to the Cretaceous–Palaeogene extinction event, the consequence of an asteroid impact in Yucatan, Mexico around 66 Ma (Schulte et al. 2010). Several families of decapod crustaceans went extinct at that time, including the Mecochiridae, Dakoticancridae and Carcineretidae (Schweitzer 2001; Feldmann 2003). The turnover amongst Protocallianassinae appears to have been more severe in Europe, where the youngest record
Fig. 5. Cheliped of *Protocallianassa faujasi* from the Ivö Klack (Blaksudden) locality, Kristianstad Basin, southern Sweden: (a) propodus with dactylus and carpus; merus and iscium from both chelipeds, NRM-PZ Ar 63934; (b) manus with fragmentary fixed finger, carpus, merus and part of coxa iscium, NRM-PZ Ar 63935; (c) propodus, NRM-PZ Ar 63936; (d) manus with fragmentary fixed finger and carpus, setal pits visible along propodus NRM-PZ Ar 63937; (e) propodus with dactylus, NRM-PZ Ar 63938; (f) propodus and carpus, NRM-PZ Ar 63939; (g) propodus with dactylus, setal pits visible NRM-PZ Ar 63940; (h)–(k) propodi, NRM-PZ Ar 63941–NRM-PZ Ar 63944. Scale bars 1 cm.
is from the Maastrichtian in The Netherlands and Belgium (Swen et al. 2001). The replacement by Corallianassa and other taxa appears to have been delayed in high-latitude southern hemisphere settings (Feldmann & Wilson 1988; Aguirre-Urreta 1989). This is consistent with the extinction patterns seen in the post-impact vegetation, with more severe extinctions seen in northern hemisphere floras (Vajda & Bercovici 2014).

Feldmann (2003) suggested that decapods are under-represented in the fossil record because their exoskeleton is weakly calcified, leaving a brittle and disarticulated exterior carapace after rapid decomposition of the soft tissues. However, thick calcification of chelipeds increases their preservational potential (Glaessner 1960), and the latter is enhanced by the specific lifestyle of thalassinoidean shrimps, which inhabit burrows that infill with sediments after the animal’s death (Griffis & Suchanek 1991). In recent studies from the Upper Miocene deposits of Slovakia, Hungary and Austria, Hyžný (2011) and Hyžný et al. (2015) showed that Callianassidae also produced burrows in brackish lake environments, causing significant bioturbation. The extant mud shrimp Neotrypaea californiensis excavates burrows up to 24 cm deep, and can incorporate as many as seven chambers (Volkenborn et al. 2012). This is consistent with the Protocallianassa fossils from Åsen and Ivö Klack, which comprise isolated chelipeds (often represented by internal casts) but no recognizable cephalothoracic or abdominal components. Moreover, they occur preserved within carbonate-cemented nodules that resemble chambered hollows of thalassinoidean burrows, presumably infilled and cemented by CaCO$_2$ after decomposition of the remainder of the carapace and soft tissues. A comparable process has been observed in the Maastrichtian of Sweden and Denmark, where the Thalassinoides burrows in chalk are filled with precipitated silica-forming chert (Surlyk et al. 2006).

In modern ecosystems, Thalassinoides species inhabit the littoral zone down to a shelf depth of 100 m (Müller 1984). This is especially consistent with the shallow-marine depositional setting for Åsen. The abundance of decapod remains within the informal $B$. balsvikensis zone (particularly Balsvikensis yellow) might explain the concomitant dearth of bivalves and other molluscs. It might further explain the slightly yellowish colour for this part of the succession compared to the underlying Balsvikensis green, as the bioturbated interval might have been more prone to weathering. This is based on comparisons with the extant ghost shrimp Neotrypaea californiensis, which displays a similar inverse relationship driven by the consumption

Table 2. Propodus/manus ratios for the Protocallianassa faujasi specimens of this study

| Specimen       | Propodus length (mm) | Manus length (mm) |
|----------------|----------------------|-------------------|
| NRM-PZ Ar 63928| 31                   | 21                |
| NRM-PZ Ar 63929| 24.5                 | 16                |
| NRM-PZ Ar 63931| 24                   | 16                |
| NRM-PZ Ar 63934| 23                   | 18                |
| NRM-PZ Ar 63938| 33                   | 24                |
| NRM-PZ Ar 63939| 27                   | 21                |
| NRM-PZ Ar 63940| 30                   | 22                |
| NRM-PZ Ar 63941| 33                   | 24                |
| NRM-PZ Ar 63942| 27                   | 21                |
| NRM-PZ Ar 63943| 23                   | 19                |
| NRM-PZ Ar 63944| 37                   | 28                |

Fig. 6. Propodus/manus ratios for the Protocallianassa faujasi specimens of this study.
of mollusc larvae during sediment disturbance by the shrimps during burrowing (Peterson 1977; Posey et al. 1991). Such intense bioturbation has also been shown to impact on decomposition processes via aeration of subsurface sediment layers (Tudhope & Scoffin 1984). Similar interactions probably occurred with Protocallianassa in the Campanian of Sweden, where the 'shrimp bed' strata contain a larger fraction of coarser-grained material than the clay–silt-dominated underlying beds.

Conclusions

- This study constitutes the first record of decapod crustaceans from the Mesozoic of Sweden and adds to the global record of Protocallianassa. The 18 measured specimens were recovered from the Kristianstad Basin, southern Sweden and are represented by chelipeds, chiefly propodi, identified as Protocallianassa faujasi (burrowing shrimps).
- The beds hosting the fossil assemblage have been assigned to the informal Belennellocamax balsvikensis zone and dated to the earliest late Campanian by belemnites. The decapods where encountered in calcified concretions, most probably representing burrow chambers.
- The bed hosting the fossil decapods is poor in other fossils (e.g. molluscs) that are otherwise abundant in the succession. This is best explained by the ecological competition between these groups, which has been noted in comparable modern shallow-marine ecosystems.

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