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First record of brachyuran decapods (Crustacea, Decapoda) from Fur Formation (early Eocene) of Mors and Fur Island, Denmark

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Abstract

Two new genera and species of crabs are described and figured from the early Eocene of Denmark; *Homoliformis vagus* gen. et sp. nov., found attached to driftwood in the Fur Formation of Mors Island is the first known European member of the family to be recorded from a deep-water deposit, and *Portufuria enigmatica* gen. et sp. nov. from the Stolleklint Clay of Fur Island, preserves characters attributable to two subfamilies, Polybiinae and Carcininae.

Key words: Crabs, new species, early Eocene Fur Formation, Stolleklint Clay Mors and Fur Islands, Denmark.

Introduction

The fossil record of the Fur Formation (early Eocene) comprises a rich fauna of especially well-preserved vertebrates and insects that has attracted the attention of numerous palaeontologists through the last hundred years resulting in a relatively rich literature.Like most marine invertebrates (molluscs and echinoderms) the decapod crustacean fauna of the Fur Formation and the underlying Stolleklint Clay is exceedingly rare and has received very little attention.

The first record was an unidentified shrimp briefly mentioned and figured by Bonde (1987) and Jakobsen (1991). That specimen, together with additional material, was recently described as *Morscrangon acutus* (Garassino & Jakobsen, 2005). Subsequently Bonde (2003), in his unpublished paper, briefly outlined the presence of crustaceans in the Danish Eocene deposits and notice was drawn to undescribed species of brachiopods and cirripeds (presumably related to *Catophragmus*) attached to driftwood from Fur Formation. According to the Danish “Danekrae-legislation” – the law of protection of earth found objects of natural history that are of unique scientific or display value – a number of shrimps have been declared Danekrae and have recently been described as two new species of *Penaeus* (Garassino & Harper, 2004).

The purpose of this work is to describe the first occurrence of a homolid crab associated with driftwood and a portunoid crab from the above mentioned Formation and the underlying Stolleklint Clay respectively. *Homoliformis vagus* sp. nov. is the youngest known member of the family to be recorded from a deep-water deposit. The only other record for a deep-water species of homolid is for *Homola vancouverensis* Schweitzer, 2001 from the Upper Eocene, Hoko River Formation of Washington, USA, where it is accompanied by 20 other crab species – although Feldmann (1991) made the reservation that some of the species may have been swept into the deposit from shallower water environments. Such could be an explanation for the present species in the Fur Formation.

Apart from an individual occurrence of the Recent homolid *Paramola cuvieri* (Risso, 1816) found in a rockpool (Gordon, 1956) there is a preference for a deep water environment among Recent homolids and with species taken from depths down to and beyond 2000 m (Guinot & de Forges, 1995, p. 490). That the only known homolid from the Fur Formation is associated with driftwood, raises the question whether or not it was endemic or transported among the epifauna (bivalves) attached to the presumed log. The *linea homolicae* appear to be intact, indicating the specimen is a corpse, rather than a moult; its mode of preservation – adhering to the substrate to expose the dorsal surface – would suggest death ensued when the log became waterlogged and sank, for it would seem logical that if the crab sought refuge and expired under the log on the sea-floor, preservation revealing its ventral surface could be expected. On the other hand, powerful and rapid swimming activity among aquarium-kept specimens of *Homola barbata* (Fabricius, 1793) has been recorded by Hartnoll (1970). Acceptance, therefore, of the former suggestion above, presupposes the ability of the individual herein named *Homoliformis vagus* sp. nov. to swim away before conditions (e.g. pressure) became intolerable. The new portunoid – here described as *Portufuria enigmatica*, not only considerably extends the known stratigraphic range of the Portunidae, but has characters in common with two subfamilies Polybiinae Ortmann, 1893 and Carcininae MacLeay, 1838. Regrettably, the principal deciding factor – the structure of the 4th walking leg (5th pereiopod) – is not preserved. Nevertheless, the possession of characters closely resembling Recent portunoid species indicates advanced development of the family from presumed Cretaceous stock, possibly from within the Portunoidea, rather than the Xanthidae as envisaged by some authors.

Localities and stratigraphy

Sediments belonging to the Fur Formation are exposed in several localities in north-western part of Denmark, in particular of the Islands of Fur and Mors from where the studied specimens were found (Fig. 1).

The Fur Formation (Early Eocene) is composed of approximately 60 m thick unit of highly porous diatomite (earlier named mo-clay and locally termed “Molér”) interbedded with 179 distinct layers of volcanic ash which have facilitated the establishment of a detailed local stratigraphy. The layers −39 to −34 occur in the underlying Stolleklint Clay. The ash-layers have historically been numbered according to their relative age, from −39 (the oldest layer) to +140 (the youngest layer). The distinct sequence of volcanic ash layers are identified beyond Denmark in a number of locations in North-Western Europe, which enables absolute correlation of the different deposits (Heilmann-Clausen, 1985). The ash layer correlation has recently been reported in the Austrian Alps (Egger et al., 2000).

Frustules of marine diatoms constitute c. 65 % (by weight) of the diatomite and clay minerals, make up the remainder. The clay minerals were transported by rivers from the continents surrounding the Paleocene “North Sea” called the Selandia Sea. The clay minerals are very fine grained and form a matrix between the diatom frustules. The dominant clay mineral is smectite, which also predominates in coeval deposits from central Jutland, Lillebælt and north-western Zealand (Røsnæs).

Diatoms bloom once a year or more irregularly. During the bloom their number increases dramatically and the large production of opaline frustules results in the deposition of a thin lamina of diatom frustules on the sea floor. The organic tissue decays rapidly but the frustules of biogenic opal are preserved and constitute the main component of the diatomite deposits. A total of 110 species of diatoms are identified and these are referred to 41 genera (Homann 1991). Slight variations in the relative supply of diatom frustules and clay minerals are undisturbed in laminated diatomite and obliterated by total bioturbation is structureless; these three facies alternate throughout the sequence (Pedersen, 1981).

The diatomite of the Fur Formation was deposited as a result of an upwelling of nutritious bottom water coming from the Norwegian Trench, maybe as the North Atlantic rift zone gradually opened access to the Barents Shelf (Bonde, 1972). Where the water by the shelf was pushed to the surface the sunlight enabled regular blooms of diatoms. The occurrence of pseudomorphs after the mineral Ikaite in the Fur Formation indicates that the upwelling water before rising was probably around 6–8 deg. C. The ikaite growth is probably also a product of degassing and sea level changes causing adiabatic cooling locally in the sediment. The entire build of the upwelling and growth of ikaite in the bottom sediment of a semi tropic sea, however, is still subject to investigation.

The Fur Formation is divided into two members. The lower member is called the Knudeklint Member and is some 30 m thick, consisting of two 30 cm thick silicified shale horizons that are very poor in fossil material. The rest of the member is made up by diatomite holding few ash layers and large calcareous concretions – so called cementstone.

The upper member is called the Silstrup Member some 25 m thick, comprises the positive ash layer from +1 to +140. The member includes several horizons of calcareous concretions and abundance of large pseudomorphs after ikaite. Recently two chemically

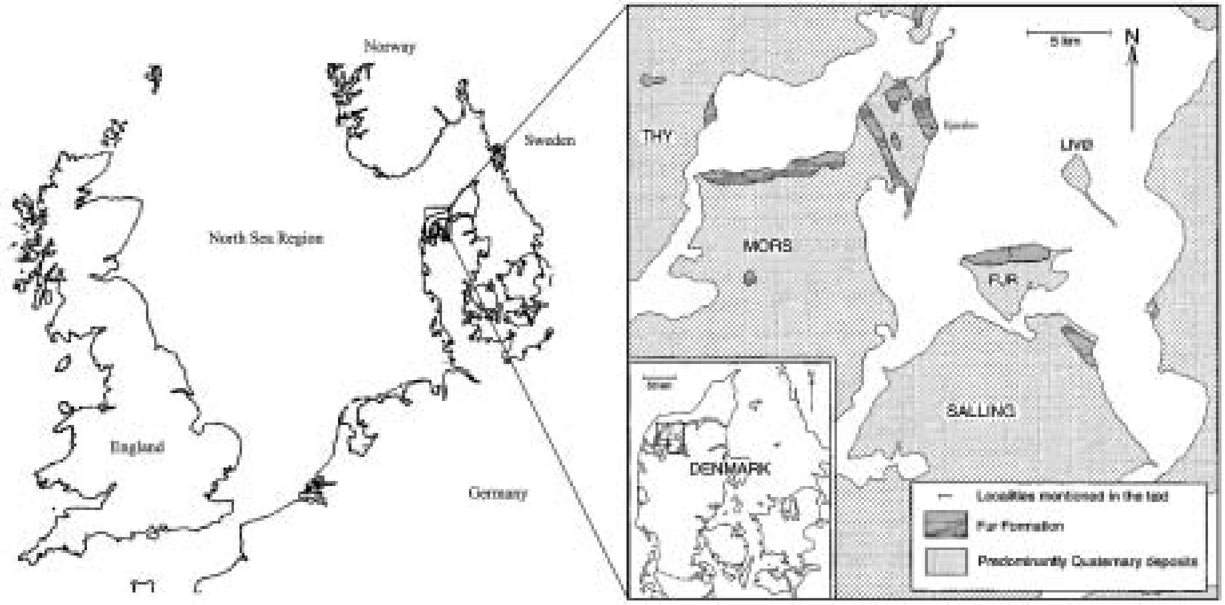

Fig. 1. Key map of localities discussed in the text.

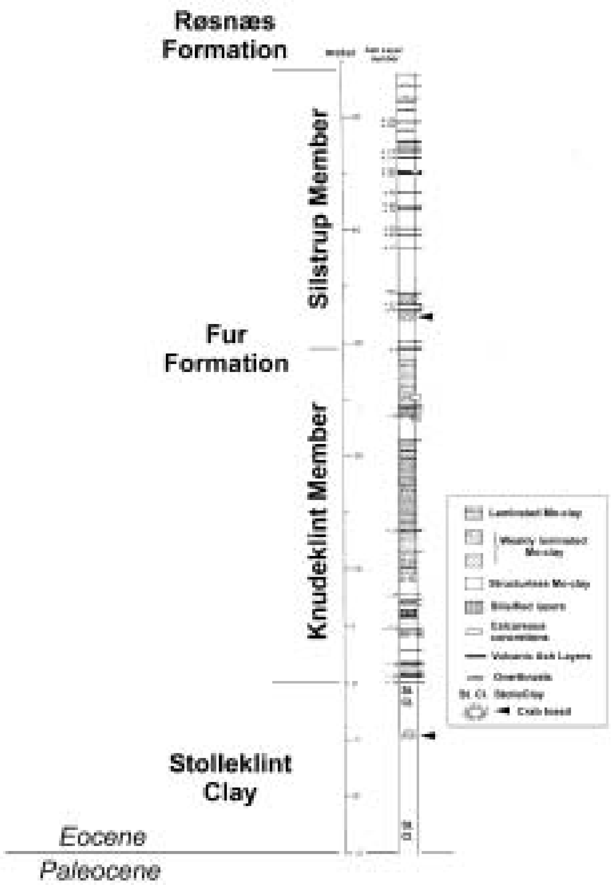

Fig. 2. Composite section of Stolle Klint and Fur Formation with indication of the stratigraphic level of the crabs.

distinct ashlayers have been dated with good radiometrically precision: 54,52 +/- 0,05 Ma (ash-layer -17) and 54,04 +/- 0,14 Ma (ash layer +19) (Chambers et al., 2003). This giving an estimated sedimentation ratio in this part of the formation of 40 mm/ky.

Under the Fur Formation is a roughly 14 m thick deposit of olive black, laminated silty clay named the Stolleklint Clay. The boundary between the Fur Formation and the Stolleklint Clay is set around ash layer −33. The Stolleklint Clay correlates to part of the Ølst Formation in other Danish locations The Stolleklint Clay includes in the upper part a fossil bearing silicified mudstone comprising some lamination. Otherwise it holds only sporadic wood fragments and fish remains. The stratigraphic position of the Fur Formation has long been a subject of controversy.

Through the last century, various geologists have alternatively referred the Formation to the Upper Paleocene and the Lower Eocene. The International Subcommission on Paleogene Stratigraphy, however, has defined the Paleocene/Eocene boundary to be at the base of the CIE (Carbon Isotope Excursia) (ref: ISPS Newsletter No. 9 Nov. 2000). This definition of the P/E boundary implies a boundary position in Denmark probably at the base of the Stolleklint Clay (Sehmitz et al., 2004).

There are several indications that the mean temperature declined from the Initial Eocene Thermal Maximum (IETM) defined by CIE in Denmark placed at the base of the Stolleklint Clay. Among these indications is the paleocontinental fauna of North America (pers. comm. Heilmann-Clausen, 2004). In the basin covering Northern Jutland deposition changes during the deposition from the dark Stolleklint clay to of the deposition of a diatomite. The fish fauna and abundance of small wood fragments in the lower part of the moclay around ash-layers −24 to −28 indicate that the evolution of the initial Eocene Sea has been one of a sea cut of from contact to deep waters and with land or an environment producing wood fragments, like mangrove swamps, not too far away from to a sea in contact with open water introducing a pelagic fish fauna (Bonde, 1987).

The rivers carried not only soil into the sea. The numerous finds of fossil wood indicate that large parts of the Scandinavian Shield were covered by woods. The flora and fauna suggest that climate was warmer than the present (Pedersen, Pedersen & Noe, 1994).

The distribution of calcareous concretions and silicified layers are confined to specific horizons. Their distribution appears to be somewhat randomly. This uneven distribution of modes of preservation makes difficult to judge the true extent of traces of epifaunal animals as they cannot be seen on wood preserved only as iron oxid coloured imprints in the diatomite. The distribution of fossilized wood carrying mytilid bivalves and cirripeds appears to be more random of nature that belonging to certain conditions. Around the ash layers −11 to −13 the depositional conditions where oxic long time enough to introduce a bottom fauna of ophiuroids (*Ophiura furiae*) and asteroids (*Coulonia colei, Echinaster jacobseni*) and few species of gastropods and bivalves. Microfossils such as foraminifera have long been considered absent, but have recently been discovered (pers. comm. H. Madsen, Molermuseet, 2004).

Systematic descriptions

Section Podotremata Guinot, 1977
Subsection Homolidea de Haan, 1839
Superfamiliy Homoloidea de Haan, 1839
Family Homolidae de Haan, 1839 (ICZN Opinion, 1987)
Genus *Homoliformis* gen. nov.

Type species: By monotypy *Homoliformis vagus* gen. et sp. nov. herein.

Diagnosis: Carapace subquadrate; margins within *linea homolicae* weakly convex; lobes well defined weakly tumid; incipient nodes on protogastric and hepatic lobes; cervical furrow crosses midline in shallow curve, sinuous to margin; branchiocardiac furrow laterally weak, posterobranch almost obsolete.

Homoliformis vagus gen. et sp. nov.

(Pl. 1, figs. 1. 2)

Derivation of name: Like *Homola*.

Diagnosis: As for genus.

Material: Holotype and sole specimen (MHM-D220) deposited in Molermuseet, Mors The specimen is attached to partialy preserved wood with associated bivalves (mytilids) contained in a large boulder (480 mm length) of calcareous diatomite (cement-stone) from Fur Formation at Ejerslev Molergrav, Island of Mors, Denmark.

Derivation of name: From the Latin – wandering.

Description: Carapace outline between the *linea homolicae* gently convex anteriorly, rather more so posterior to the cervical notch; almost flat in transverse section. The entire front is missing; estimated length almost equals the width, widest about midlength. The anterolateral margins are weakly convex, posterolateral margins more strongly convex to acute posterior angles leading to weakly sinuous posterior margin about three fifths carapace width and bounded by a fine ridge and groove. From a pair of gastric pits the cervical furrow crosses the midline rather more than half the distance from the front, curving gently to the lateral angle of the mesogatric lobe, it is sinous to the lateral margin, forming a "notch" at the *linea homolicae*. About as wide as the cervical, a barely discernable furrow defines an ovate hepatic region. Running parallel to the cervical furrow, weak branchiocardiac furrows divide, the forward branch delimits the anterior part of the cardiac region and urogastric where it recurves and reaches the margin, the fainter hinder branch separates the cardiac from the metabranchial lobes and a small, rectangular intestinal region. Subovate mesobranchial lobes are sharply attenuated to the margin and weakly "ridged"; epigastric lobes are subtriangular. The anteromesogastric process extending midway between short, rectangular epigastric lobes, is weakly constricted before broadening into the subpentagonal mesogastric lobe. There are three tumid areas on each protogastric lobe, set more or less triangularly, with largest basally and two interior nodes. A groove as strong as the cervical furrow, separates a crescentic urogastric lobe from the subquadrate, smooth cardiac region. Sparse, minute granules covering the gastric region become larger and denser on the branchial regions. There is a discrete anterior node on each hepatic region, and three, in an inverted triangle on the cardiac region. Sidewall margins are largely damaged; there is a ventral granule behind the branchiocardiac furrow and, leading from it, three others increase in size posteriorly.

Discussion: The rostrum, presence or absence of frontal spines and length/width proportions cannot be ascertained. However, although the new genus shares some characters with the diagnoses of *Homola* Leach, 1815, *Homolopsis* Bell, 1863 and *Latheticocarcinus* Bishop, 1988 as defined by Schweitzer et al. (2004), the combination of characters is not consistent with any one of them. The relatively smooth carapace of *Homoliformis* compares with that of *Homola etheridgei* Guinot & de Forges, 1995 which also has a vaguely defined hepatic region, it differs in having a longer urogastric lobe and a restricted branchiocardiac furrow (Schweitzer et al., 2004) and differs further in having defined hepatic regions and a completely recurved branchiocardiac furrow.

Homolopsis has a partially defined hepatic region, is tuberculate and has a restricted branchiocardiac furrow, it agrees with *Homoliformis* in having a relatively narrow, crescentic urogastric lobe and, like *Homola*, a line of discrete granules bordering the lateral extension of the branchiocardiac furrow.

Section Heterotremata Guinot, 1977
Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Genus *Portufuria* gen. nov.

Type species: By monotypy, *Portufuria enigmatica* sp. nov., by designation herein.

Diagnosis: Carapace subhexagonal, four pairs of anterolateral spines, rostrum sharp, triangular. Chelipeds heterochelate, long, robust, inner margin of (left) propodus carinate; pereiopods 2–4 slender, as long as, or longer than chelipeds.

Range: Early Eocene – Stolleklint Clay.

Derivation of name: A combination of the prefix of *Portunus* and the type locality, Fur Island, Denmark.

***Portufuria enigmatica* sp. nov.**

(Pl. 1, figs. 3a, b)

Diagnosis: As for genus.

Derivation of name: Latin – a puzzle.

Material: Holotype MGUH 27742 and the sole specimen. A dorso-ventrally compressed individual revealing little more than basic carapace outline through fragmented shell-layers, and limbs.

Type locality: Stolle Klint (Fur Island, Denmark), Stolle Klint Clay (early Eocene).

Description: Carapace subhexagonal, length about six sevenths of the width, widest in anterior third. The orbitofrontal margin occupies rather less than half the carapace width, of this the front takes up the median third. The sides of short, sharp triangular rostrum curve broadly to a notch before an obscure inner orbital spine. The upper orbital margins are directed slightly obliquely forward to a contrastingly larger outer spine which is longer than the first of four triangular anterolateral spines. Female sternites are typically portunid-chordate.

Well preserved chelipeds are heterochelate, the left being slightly the larger, otherwise similar in outline as far as preserved. The carpus is sub-pentagonal with the base of a ?stout spine at the inner distal angle. The proximal height of the propodus is about two thirds that of the basal length, the straight upper margin terminates in a short spine. The stout fixed finger is weakly depressed and about two thirds the length of the manus. The proportionally stout dactylus may have a few granules on the upper margin. The upper inner surface of the manus is flattened, the lower margin ridged; a shorter, median ridge extends from between the fingers about two thirds of the manus length, while a third ridge along the fixed finger extends almost to the carpal margin. The total length of the chelipeds exceeds the carapace width. 2nd–4th pereiopods (walking legs 1–3) are much of the same size; accounting for missing dacyli, all three pairs are longer than the chelipeds. The meral width of the 4th pereipod is about one fourth of its length.

Despite the compressed nature of the carapace the pleural suture remains intact suggesting the specimen to be that of a corpse, rather than a moult.

Discussion: The stratigraphical position of the new species places it as the earliest known European member of both Polybiinae and the Carcininae, and it shares characters of both subfamilies, thus justifying its inclusion in a distinct genus, the subfamilial position of which could be determined in the event of the details of the 5th pair of limbs coming to light.

Difficulty arises in placing this species in a suitable subfamily. According to Stephenson (1972, p. 3) the relative proportions of the pereiopods to cheliped length are key factors determining subfamilies of Portunidae; *eg* (key) "3 (2) Chelipeds and legs both long, chelipeds longer than the legs, carapace typically broad", as applies to Portuninae, is immediately negated by the proportions of the limbs as described above. And (key) "4 (3); Chelipeds and legs both long, one pair of legs as long as cheliped (modified by Ingle, 1980, p. 100, to at least one pair). Last legs typically more leg-like than paddle-like, if swimming paddles distal portion acute, ...", as applied to the Carcininae is acceptable in the absence of the 5th pereiopods. However, the nature of the limbs is decidedly closer to species within Polybiinae, about which latter subfamily Stephenson's key reference concerns only the 5th pereiopods. Nevertheless, Ingle (1980) stated, " at least one pair of pereiopods usually as long as chelipeds." Indeed, those in *Liocarcinus* provide almost identical comparison. The chelipeds of, for instance *Liocarcinus depurator* (Linnaeus, 1758) are shorter than pereiopods 1-3; the left propodus has a flattened upper surface, almost identical ridges on the inner surface of the manus and a depressed fixed finger; the front is similarly separated by notch from the inner orbital spine, but more advanced than that of *Portufuria* and the orbits are transverse.

Quoting Schweitzer & Feldmann (2000), "Rice (1980) suggested that the Polybiinae Ortmann, 1893 was most likely the ancestral subfamily within the Portunidae." Those authors then remarked upon the polybiinid, *Proterocarcinus lophus* Feldmann et al., 1995, from the Danian of Argentina, as being the oldest authentic portunid. The carapace outline of *P. lophus* with a broad orbitofrontal margin and narrow front, is contrastingly different from *Portufuria enigmatica* which nearly approaches that of *Liocarcinus*. Such advanced distinctions between the two species within the comparatively short geological interlude, and distance involved, suggest extreme divergence from common ancestral stock, or polyphyletic origins from stocks as yet unknown.

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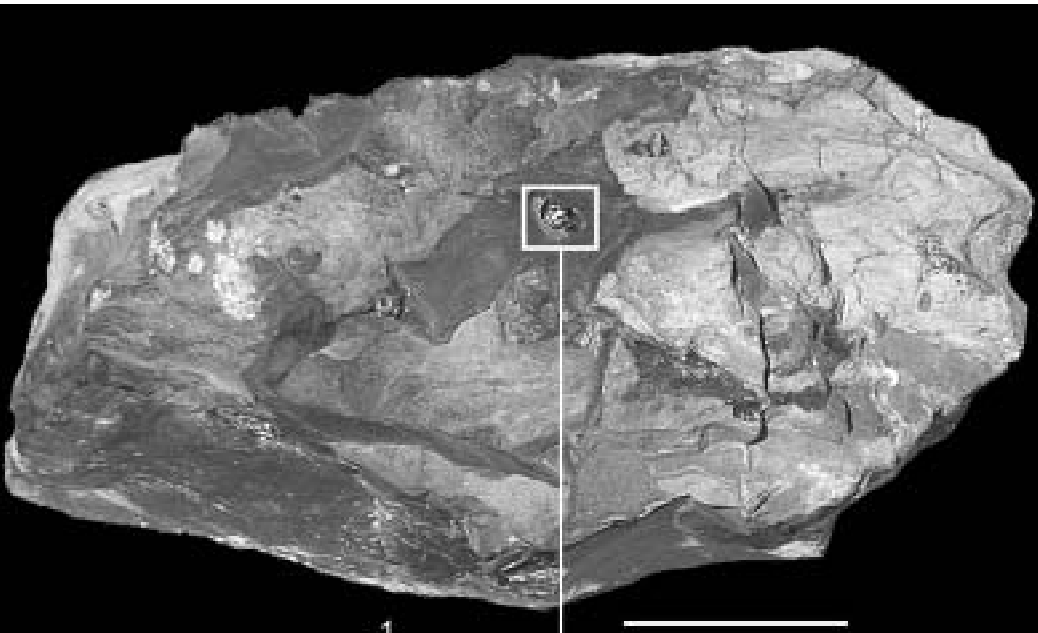
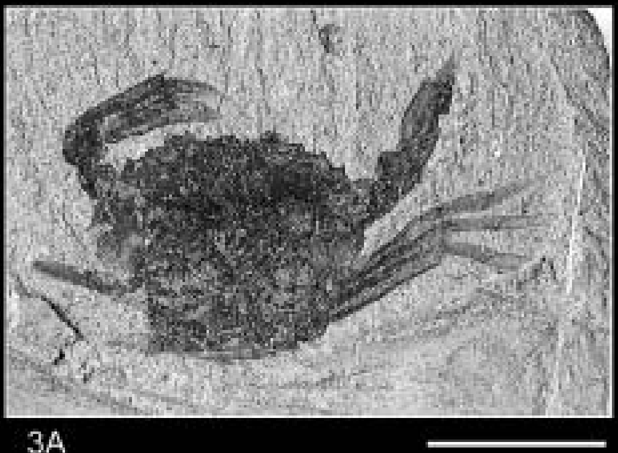
Explanation of Plate 1

1. Fossilized wood preserved in calcareous cementstone with attached mytilid bivalves. Scale bar 100 mm.
2. The crab species *Homoloformis vagus* sp. nov. Scale bar: 10 mm.
3. Part and counterpart of the crab species *Portufuria enigmatica* sp. nov., 3a dorsal view and 3b ventral view. Scale bar 10 mm.



1

2



3A

3B