

In situ fossil hermit crabs (Paguroidea) from northwest Europe and Russia. Preliminary data on new records

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ABSTRACT

*For reasons still unknown, the record of fossil paguroids preserved in situ is scanty. Here we present four examples from the Mesozoic and Cenozoic of northwest Europe and Russia, either collected recently or contained in old museum collections and recognised previously, but not yet published. The first concerns a right propodus, and the imprint of the left chela, preserved within the conch of an amaltheid ammonite from the upper Pliensbachian (lower *spinatum* Zone, *apyrenum* Subzone; Lower Jurassic) of Banz (southern Germany). The second example involves the remains of both chelipeds, pereopods, shield and ?cephalic appendages preserved in an internal mould of a ?volutid gastropod from the upper Maastrichtian (Upper Cretaceous) of Kunrade (southern Limburg, the Netherlands). The third specimen also preserves fragments of both chelipeds and pereopods, and possibly also of shield and appendages(?), and is found in the internal mould of a volutid gastropod from the Middle Eocene of Yantarnyi (Kaliningrad district, Samland Peninsula, Russia; formerly Palmnicken, East Prussia), while the fourth specimen is preserved within an internal mould of an indeterminate (?volutid) gastropod from the Miocene of Liessel (Noord-Brabant, the Netherlands) and comprises the major cheliped and some pereopods. The taxonomic assignment of fossil paguroids has always been problematic, and in systematic descriptions the use of 'lump genera' such as *Palaeopagurus* or *Pagurus* (sensu lato) has often been favoured. For the time being, we here adopt this policy, but hope that further preparation may reveal additional features of taxonomic value, enabling a more reliable generic assignment of the present material.*

Keywords. Crustacea, in situ, Mesozoic, Cenozoic, Europe, Russia.

RESUMEN

*Por razones aún desconocidas, el registro fósil de paguroideos preservados in situ es escaso. Presentamos aquí cuatro ejemplos del Mesozoico y Cenozoico del noroeste de Europa y Rusia, de ejemplares colectados recientemente y otros depositados en antiguas colecciones de museos, reconocidos previamente pero no publicados. El primer ejemplo corresponde a un propodo derecho y la marca de una quela izquierda, preservados en el interior de la concha de un amonite amaltheid del Pliensbachiano superior (Zona inferior *spinatum*, Subzona *apyrenum*; Jurásico Inferior) de Banz (sur de Alemania). El segundo ejemplo involucra los restos de ambos quelípedos, pereópodos, escudo y ?apéndices cefálicos,*

preservados en el molde interno de un gasterópodo ?volútido del Maastrichtiano superior (Cretácico Superior) de Kunrade (sur de Limburgo, Holanda). El tercer espécimen también preserva fragmentos de ambos quelípedos y pereiópodos, y posiblemente también del escudo y apéndices(?), y se encuentra en el molde interno de un gasterópodo volútido del Eoceno Medio de Yantarnyi (Distrito de Kaliningrado, Península de Samland, Rusia; anteriormente Palmnicken, este de Prusia), mientras que el cuarto espécimen está preservado dentro de un molde interno de un gasterópodo ?volútido indeterminado del Mioceno de Liessel (Noord-Brabant, Holanda) e incluye al quelípedo mayor y algunos pereiópodos. La ubicación taxonómica de los paguroideos fósiles ha sido siempre problemática, y en descripciones sistemáticas, el uso de 'géneros comodines' como *Palaeopagurus* o *Pagurus* (sensu lato) ha sido frecuente. Por el momento, aquí adoptamos esa costumbre, en espera que una mejor preparación de los ejemplares revele caracteres adicionales de valor taxonómico y permita una ubicación genérica más confiable del material descrito.

Palabras clave. Crustacea, in situ, Mesozoico, Cenozoico, Europa, Rusia.

INTRODUCTION

Being obligatory occupants of empty gastropod and other mollusc shells, hermit crabs (Paguroidea) are often found as dissociated remains in shell-rich deposits (coquinas, lumachelles), but for reasons still unknown (although hinted at and speculated upon; see Dunbar and Nyborg, 2003), only a handful of *in situ* fossil paguroids have made it into the literature. All these records concern preservation within various species of gastropod (Mertin, 1941; Hyden and Forest, 1980; Feldmann and Keyes, 1992; Hu and Tao, 1996; McLaughlin and Forest, 1997; Jagt *et al.*, 2000; Karasawa, 2002; Collins and Jakobsen, 2004; Todd and Collins, 2006), except for a specimen from the Speeton Clay (Hauterivian, Lower Cretaceous) of Speeton (England) preserved within a simbirskitine ammonite (Fraaije, 2003).

In view of their rarity, each and every specimen of fossil paguroid preserved *in situ* warrants description, despite the fact that it is seldom possible to refer fossil material to extant genera with confidence, as was aptly discussed by Schweitzer and Feldmann (2001) and Schweitzer *et al.* (2002). Van Bakel *et al.* (2003) provided a list of records of fossil paguroids, found both *in situ* and as dissociated remains, mostly chelipeds; this needs not be repeated here. However, during preparation of that paper, or subsequent to its publication, additional material has been described by Górka (2002), Schweitzer and Feldmann (2002), Dunbar and Nyborg (2003), Crônier and Courville (2004), Feldmann and Schweitzer (2004), van Bakel *et al.* (2004), Garassino and De Angeli (2004), Garassino *et al.* (2004), Schweitzer *et al.* (2004), Beschin *et al.* (2006), Cope *et al.* (2006) and Radwański *et al.* (2006). In cases where (portions of) the shield and/or associated chelipeds are preserved, there is a better chance of a more reliable generic assignment by comparisons with extant material, as some of the present examples suggest.

The material for which preliminary data are here given comprises four specimens, all preserved in museum collections, and three of them previously recognised to be paguroid by earlier workers who, for some reason, refrained

from publishing these records. This becomes even more surprising in the light of the preservation of (portions of) the shield and cephalic appendages in two of these specimens. In part, the present material is in need of further preparation after which we shall undertake a detailed comparison of this material with extant genera (features of both chelipeds, of shield and cephalic appendages), with the aim to 'narrow down' the generic assignment. This is bound to be a time-consuming exercise, which is why formal descriptions of the present specimens will be published elsewhere.

In stratigraphic age, the new material covers the Lower Jurassic (Lias, upper Pliensbachian), the uppermost Cretaceous (upper Maastrichtian), the Middle Eocene (Lutetian) and the Miocene of localities in Russia, Germany and the Netherlands. To denote the repositories of material described below, the following abbreviations are used: IRScNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MAB: Oertijdmuseum De Groene Poort, Boxtel, the Netherlands; MB: Museum für Naturkunde der Humboldt Universität, Berlin, Germany; NHMM: Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands.

PRELIMINARY DESCRIPTIONS

Early Jurassic material

A fragmentary body chamber of the amaltheid ammonite *Pleuroceras solare* (Phillips, 1829) (det. Prof. H. Keupp, Freie Universität Berlin) from the lower *spinatum* Zone (*apyrenum* Subzone, Lias δ_{2a} = upper Pliensbachian) at Banz (near Coburg, Franken; southern Germany), preserved in the collections of the Museum für Naturkunde (Humboldt Universität, Berlin; MB.A 1113), contains a right cheliped, lacking the dactylus, and shows an imprint of the other cheliped (Figures 1, 2); the former has recently been prepared free from the matrix (Figures 3-5). In overall proportions and ornament, this cheliped recalls material of Middle Jurassic – Early Cretaceous age referred to paguroids (*e.g.*,

de Tribolet, 1875; van Straelen, 1925; Fraaije, 2003; Crônier and Courville, 2004; Ilyin, 2004), but details of ornament, handedness (right *versus* left), length/width ratio and the fact that fingers appear to have been stout and short rather than long and slender, suggest it may be an undescribed form, here referred to as '*Palaeopagurus*' n. sp., at least for the time being. On account of the characteristic shape and morphology of this propodus, we are confident it represents a paguroid, rather than the remains of an astacidean lobster. Astacidean lobsters have been reported to inhabit body chambers of ammonites by Fraaye and Jäger (1995).

One of the associated label reads, '*Glyphea liasina* H. v. Meyer, Banz (coll. zu Münster)'. This is but the second record of a fossil paguroid preserved within an ammonite, the only other documented instance being that of *Palaeopagurus vandenengeli* Fraaije, 2003 (Figure 6) from the Hauterivian (Lower Cretaceous) of Speeton (England). The present find becomes even more interesting when the recent observation by Williams and McDermott (2004, p. 87) is considered, that, '... a few citations of hermit crabs from the early Jurassic (Glaessner, 1969) are based on chelae of questionable affinity (McLaughlin, personal communication).' However, those authors also noted that there is evidence suggesting that paguroids occupied a new niche in marine ecosystems since the Middle Jurassic (see also Walker, 1992; Taylor and Wilson, 2003). The present specimen, of Early Jurassic age, thus represents the oldest definite record of an *in situ* paguroid yet. The size of the chelae relative to that of the aperture of the ammonite body chamber is smaller than what is seen in later paguroid occurrences, where chelae (almost) fully occupy this space. This may indicate an early stage in the evolution of paguroid occupation of ammonite conchs.

Late Cretaceous material

From the type area of the Maastrichtian Stage (south-east Netherlands, northeast Belgium), at least three or four species of paguroid are known, in the form of isolated chelipeds and propodi (IRScNB, MAB and NHMM collections), only one of which has been formally named to

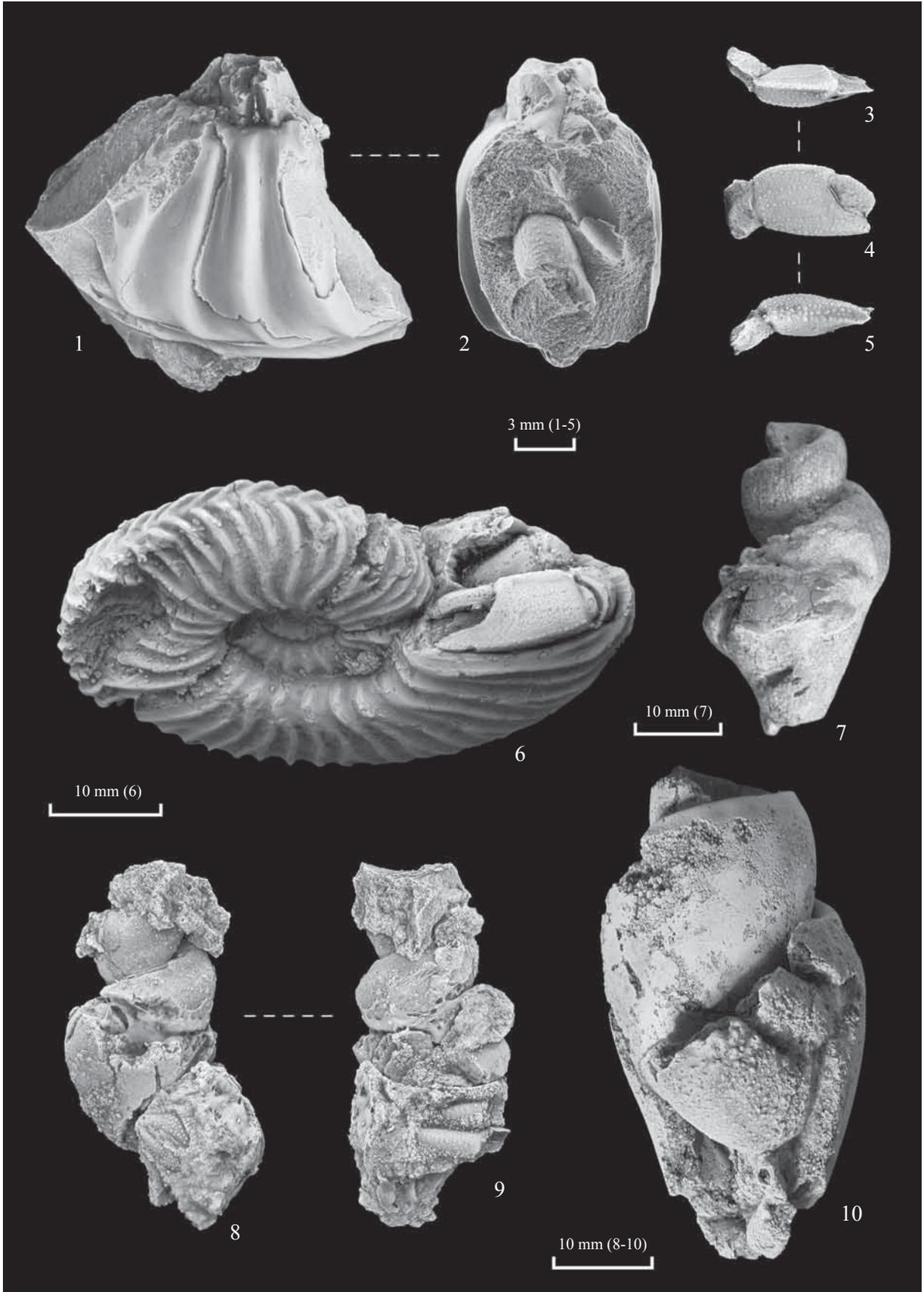
date, *Paguristes florum* Collins, Fraaye and Jagt, 1995. This species is known from the Emael, Nekum and Meerssen members of late Maastrichtian age. The apparent lack of paguroids preserved *in situ* is puzzling in the light of highly diverse gastropod faunas in these units (see Kaunhowen, 1898), with species of all shapes and sizes, and the neritid *Otostoma retzii* (= *Nerita rugosa*; see Squires and Saul, 1993) in particular. Many hundreds of specimens of this species have so far been collected; the calcitic outer shell is well preserved, even though the thick inner aragonitic one has dissolved and left an infilled plug 'swimming' within. So far, no paguroid remains have been demonstrated in any of these. Of note is the fact that in one specimen a single cheliped of a necrocarcinid crab, *Paranecrocarcinus quadrisissus* (see Collins et al., 1995; Fraaije, 2002), has been found (NHMM JJ 12873). This specimen will be described in detail elsewhere.

In the collections of the Institut Royal des Sciences Naturelles de Belgique (Brussels) is the internal mould of a ?volutid gastropod containing a paguroid (Figure 7) from the Kunrade Limestone facies of the Maastricht Formation, of late Maastrichtian age. The associated labels read, 'Loc: Kunraed, Coll. Ubaghs. 1898. I.G. 6521.' and 'Crustacé inconnu Kunraed' and a small interpretative drawing, possibly by the late Victor van Straelen, is included as well. Although preservation is far from ideal, this specimen comprises (portions of) both chelipeds, as well as pereopods and the largest part of the shield, plus ?cephalic appendages. The ornament of the shield is well visible and should enable this to be compared in detail with extant genera. Additional preparation is needed, in particular of the partially decalcified chelipeds. From what is visible of these (shape, ornament), it appears this specimen is not conspecific with *Paguristes florum*.

Middle Eocene material

From the so-called 'Bernsteinformation, Zone A1', Noetling (1885, p. 434 [161], pl. 6, figs. 9, 9a-c) recorded some associated paguroid pereopods in an internal mould of a gastropod, under the new name of *Pagurus damesii*. The type, if still extant, should be in the collections of

Figures 1-10. *In situ* hermit crabs (Paguroidea) from the Lower Jurassic, Upper Cretaceous, Eocene and Miocene of northwest Europe and Russia. All specimens were whitened with ammonium chloride prior to photography. Figures 1-5: '*Palaeopagurus*' sp. (MB.A 1113), in fragmentary body chamber of *Pleuroceras solare* from the lower *spinatum* Zone (*apyrenum* Subzone; Lias δ_{2a} , upper Pliensbachian) of Banz (Franken, southern Germany); 1, 2. specimen prior to preparation; note imprint of left cheliped in upper right-hand corner; 3-5: right cheliped in various views (compare with Figure 6). Figure 6: *Palaeopagurus vandenengeli* Fraaije, 2003, holotype (MAB k.0012), from the middle Hauterivian, Speeton Clay Bed C4, at Speeton (Yorkshire, England); oblique view of simbirskitine ammonite conch to illustrate the large left cheliped (compare with Figures 2-5). Figure 7: Indeterminate paguroid (IRScNB, Ubaghs Colln, IG 6521) within last whorl of a ?volutid gastropod (internal mould), from the Kunrade Limestone facies (Maastricht Formation, upper Maastrichtian) of Kunrade (southern Limburg, the Netherlands), revealing shield and some appendages; the chelipeds are just visible to the left of the shield. Figures 8, 9: *Pagurus* sp. (aff. *bernhardus* Linné, 1758) (MAB k.2400), in an indeterminate (?volutid) gastropod (internal mould), consisting of right cheliped and fragmentary pereopods, from the Miocene of Liessel (Noord-Brabant, the Netherlands). Figure 10: Indeterminate paguroid (= *Pagurus damesii* Noetling, 1885, *nomen dubium*) (MB.A 1114), from the Middle Eocene (Bernsteinformation, Zone A1) of the Kaliningrad area (Samland Peninsula, Russia; formerly Palmnicken, East Prussia). Note the stout and heavily tuberculate chelipeds, with associated remains of pereopods.



the Bundesanstalt für Geowissenschaften und Rohstoffe (Berlin), since it is there that the Noetling Collection is registered (BGR Berlin X 09439; see von Daniels *et al.*, 1999). Strictly speaking, the type specimen is indeterminate at the generic and specific levels, and thus is a *nomen dubium*.

In the collections of the Museum für Naturkunde (Humboldt Universität, Berlin) there has now been recognised a second specimen (MB.A 1114; Figure 10), better preserved than the type, inside an internal mould of a volutid gastropod. The accompanying label reads, 'Pagurus Damesii Noetl. Sehr selten! Bernsteinformation Zone A, Palmnicken d.d. et det. Nötling 1884'. This shows that Noetling himself collected this specimen, which makes it even more astounding to see why he did not select this specimen to base the new species upon, and illustrate it.

Although preparation has not yet been completed, this specimen preserves portions of both comparatively stout and tuberculate chelipeds (Figure 10), some pereopods and most probably also (portions of) the shield. The matrix is a dark, indurated glauconitic and 'pelletoid' sandstone, which tends to obliterate details and makes preparation difficult. It is our hope to develop this specimen further and reveal taxonomically reliable features, allowing a proper description of all elements preserved and a comparison with extant paguroids.

The stratigraphic age assignment of the 'Bernsteinformation' at Yantarnyi, Samland Peninsula (Kaliningrad district, Russia; formerly Palmnicken, East Prussia) goes back to Noetling (1885) and is based mainly on a rich marine fauna, principally composed of molluscs, echinoderms, crustaceans and bryozoans. Comparisons with coeval faunas in the Cenozoic of northern Germany at first suggested correlation of this unit with the lower Oligocene, based mainly on molluscan evidence. This stratigraphic placement has long been widely accepted, but recent studies (*e.g.*, radiometric dating of glauconites; see Ritzkowski, 1997) have demonstrated that the deposition of the 'blaue Erde' (= blue earth) occurred during the Middle Eocene (Lutetian). This is the age accepted here for paguroids from the Kaliningrad district.

Miocene material

At a gravel- and sandpit in Liessel (Noord-Brabant, the Netherlands), until recently fossiliferous glauconitic/sideritic concretions of (Middle/Late) Miocene age were dumped. A lot of this material is contained in the collections of Oertijdmuseum de Groene Poort, amongst them specimen MAB k.2400 (Figures 8, 9). This shows remains of the right cheliped of a paguroid, plus a number of appendages, preserved in the internal mould of a ?volutid gastropod. Size, shape and ornament of the major cheliped suggest this to be closely related, yet not conspecific, with the extant *Pagurus bernhardus*. Additional preparation is needed, but the shield does not appear to be preserved.

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