Mesozoic–Cenozoic crustaceans preserved within echinoid tests and bivalve shells

Rok Gašparič, René H.B. Fraaije, Barry W.M. van Bakel, John W.M. Jagt &
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Associations of crustaceans with echinoids (Echinodermata) and bivalves (Mollusca) are not uncommon in modern oceans. Here we record the occurrence of anomurans, brachyurans and isopods within echinoid tests and bivalve shells from the Middle Jurassic of France, the Upper Jurassic of the Czech Republic, the Eocene of Croatia and the Miocene of Austria. Additionally a new genus and species of fossil cirolanid isopod from the Middle Jurassic of France is described. The present examples are interpreted as crustacean sheltering, probably for safe and undisturbed moulting (ecdysis), within a vacant host test or shell. However, accidental association (washed in) or even food remains cannot be ruled out entirely. • Key words: Crustacea, Decapoda, Isopoda, commensalism, sheltering, taphonomy.

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The association of decapod crustaceans with invertebrate hosts has been documented in detail from present-day marine environments (*e.g.*, Morton 1989). Examples include the following. Inside the articulated shell of the pinnid bivalve *Pinna rudis* Linnaeus, 1758 at least one, usually two, specimens of the shrimp *Pontonia pinnophylax* (Otto, 1821) have been noted in the majority of individuals near Príncipe and Săo Tomé islands (Wirtz & d'Udekem d'Acoz 2008). The number of individuals occurring inside the host appeared to be in direct correlation with the latter's size, in that smaller-sized hosts sheltered only single individuals, while larger ones were more likely to contain a pair or even a small group, consisting of a pair of adults and several juveniles.

Zullo & Chivers (1969) recorded the pea crab *Pinnixa faba* (Dana, 1851) from within articulated valves of the marine bivalve *Tresus capax* (Gould, 1850) occurring in upper Pleistocene terrace deposits in Oregon, USA. Amongst 124 articulated shells, 27 contained either complete or fragmentary crabs. As far as we have been able to ascertain, this is the first and sole example of brachyurans preserved within bivalves that has been documented from the fossil record.

Jaramillo *et al*. (1981) described an association of the bivalve *Mytilus chilensis* Hupé, 1854 and the isopod *Edotea magellanica* Cunningham, 1871 from intertidal settings in southern Chile. The greatest number of isopods was noted in mussels that measured between 30 and 45 mm in overall length.

In the Sea of Japan the extant pinnotherid crab, *Pinnotheres laquei* Sakai, 1961, has been recorded from within the mantle cavity of the brachiopod *Laqueus rubellus* (Sowerby, 1846). Feldmann *et al*. (1996) were the first to provide quantitative data regarding this association. Pinnotherids are common associates of molluscs and echinoderms and tend to be host specific. The crabs appeared to be more common in larger-sized brachiopods, implying a size correlation between crab and brachiopod. No physical evidence, such as malformation of the shell or lophophore, was observed in the host brachiopods. For that reason, this association was judged to be either commensal or mutualistic, the crabs being able to enter and exit the

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mantle cavity at will. This pinnotherid/brachiopod association constitutes the only known occurrence of infestation of brachiopods by crabs in extant seas.

Recently, a small crab, *Ferricorda kimberlyae* (Bishop, 1987), has been discovered within part of a phragmocone of a baculitid cephalopod from the Gammon Ferruginous Member (lower Campanian) of the Pierre Shale in Butte County, South Dakota (Landman *et al.* 2014). The crab retains its carapace and all pereiopods, parallel to, and in between, two septa within the cephalopod shell. This enigmatic occurrence is interpreted as the first example of crab inquilinism within a heteromorph ammonite. For other examples of sheltering extinct decapod crustaceans within cephalopod shells, reference is made to Fraaye & Jäger (1995), Fraaije & Pennings (2006), Schulz (2002) and Klompmaker & Fraaije (2012).

Carapaces of the raninoidean crab *Necrocarcinus labeschii* (Deslongchamps, 1835) have been documented within the ultimate whorls of ammonites and gastropods from the lower Cenomanian of Orne, France. Breton (2008) interpreted these as exuvia of crabs that found shelter inside the molluscan shells during ecdysis.

Several species of small-sized crabs in the sediment fill of large gastropods from the Pliocene of Belgium were illustrated and discussed by Van Bakel *et al.* (2004), while a complete moulted specimen of a new sand crab, *Albunea turritellacola*, within a large-sized turritellid gastropod from the Miocene of France was described by Fraaije *et al.* (2008). It would appear that empty gastropod shells are perfect places for undisturbed ecdysis for all kinds of comparatively small decapod crustaceans.

Bishop & Portell (1989) described specimens of a new porcellanid crab, *Petrolisthes myakkensis*, associated with abundant asteroids, *Heliaster microbrachius* Xantus, 1860, from the upper Pliocene of Charlotte County, Florida, USA. The crab/asteroid association is preserved in calcareous quartzitic sandstone. The fauna is dominated by the asteroids and crabs, but barnacles are also present. Preservation as entire, fully articulated, fragile, hollow specimens preserved with articulated sea stars attests to a lack of transport. This close association, taken together with the commensal habits of other porcellanid crabs, and the commensal relationships of crabs with echinoderms lead to the conclusion that *Petrolisthes myakkensis* and *Heliaster microbrachius* were commensals.

Garth (1957) noted pinnotherids from the internal cavity of echinoids in Chilean waters, while Ng & Manning (2003) recorded such crabs from inside the rectum of echinoids and holothuroids.

Only few records of extinct echinoids that preserve other organisms inside are known. Ernst (1967) described a broken test of the irregular echinoid *Echinocorys* with numerous bivalve and gastropod shells preserved inside, from the mid-Campanian of northwest Germany. Coeval finds, from the Hannover area (Germany), are also known and pertain to heteromorph ammonites inside micrasterid echinoids (Frerichs 2004), arcid bivalves and small-sized patelliform gastropods inside irregular echinoids (Krüger 1995a, b). Micrasterid echinoids from Turonian marls of Erwitte quarries, Münsterland, Germany, occasionally are filled with faecal pellets, possibly produced by crustaceans (pers. obs., RHBF).

Institutional abbreviations. – To indicate the repositories of specimens described here, the following abbreviations are used: MAB, Oertijdmuseum De Groene Poort, Boxtel, the Netherlands; RGM, Naturalis Biodiversity Center, Leiden, the Netherlands (formerly Rijksmuseum van Geologie en Mineralogie); RGA/SMNH, Slovenian Museum of Natural History, Ljubljana, Slovenia (R. Gašparič Collection).

Isopod/bivalve association – Middle Jurassic of France

To date, there are 62 extant genera considered valid within the family Cirolanidae (Schotte *et al.* 2010), and six extinct ones (*e.g.*, Hyžný *et al.* 2013, Etter 2014). (Near-) complete extinct cirolanids are very rare; most frequently only the posterior part of the pereonites, together with the pleonites and pleotelson, are preserved (*e.g.*, Quayle 1982, Feldmann *et al.* 1990, Karasawa *et al.* 1992, Fraaye & Summesberger 1999, Feldmann & Goolaerts 2005, Feldmann & Rust 2006, Pasini & Garassino 2012a–c, Hyžný *et al.* 2013, Jarzembowski *et al.* 2014). This incomplete preservation, without the cephalon and the first four pereonites, is explained by biphasic moulting (Feldmann & Goolaerts 2005, Feldmann & Rust 2006, Hyžný *et al.* 2013), in which the posterior part remains intact, while the anterior part is disarticulated and fragmentary. For this reason, most fossil isopods are represented solely by the posterior exoskeleton. In the absence of antennae, mouthparts or pereopods, it is impossible to assign extinct forms to a clearly defined extant genus (N.L. Bruce, pers. comm., June 2014). More complete fossil isopods, however, do show enough variation in their exoskeleton to be differentiated at the generic level. Hyžný *et al.* (2013) published a useful key for fossil cirolanid genera exclusively on the basis of posterior exoskeleton parts.

According to this key, the 31 mm long present specimen, preserved within a pholadomyid bivalve, is confirmed to be a cirolanid. The general shape of the exoskeleton closely resembles the extant male paratype of *Cirolana diminuta* Menzies, 1962 (see Brusca *et al.* 1995, p. 19, fig. 11B). The lateral margins of pleonites 4 and 5 are particularly prominent in dorsal view. In that character there is some resemblance to genera such as *Baharilana*

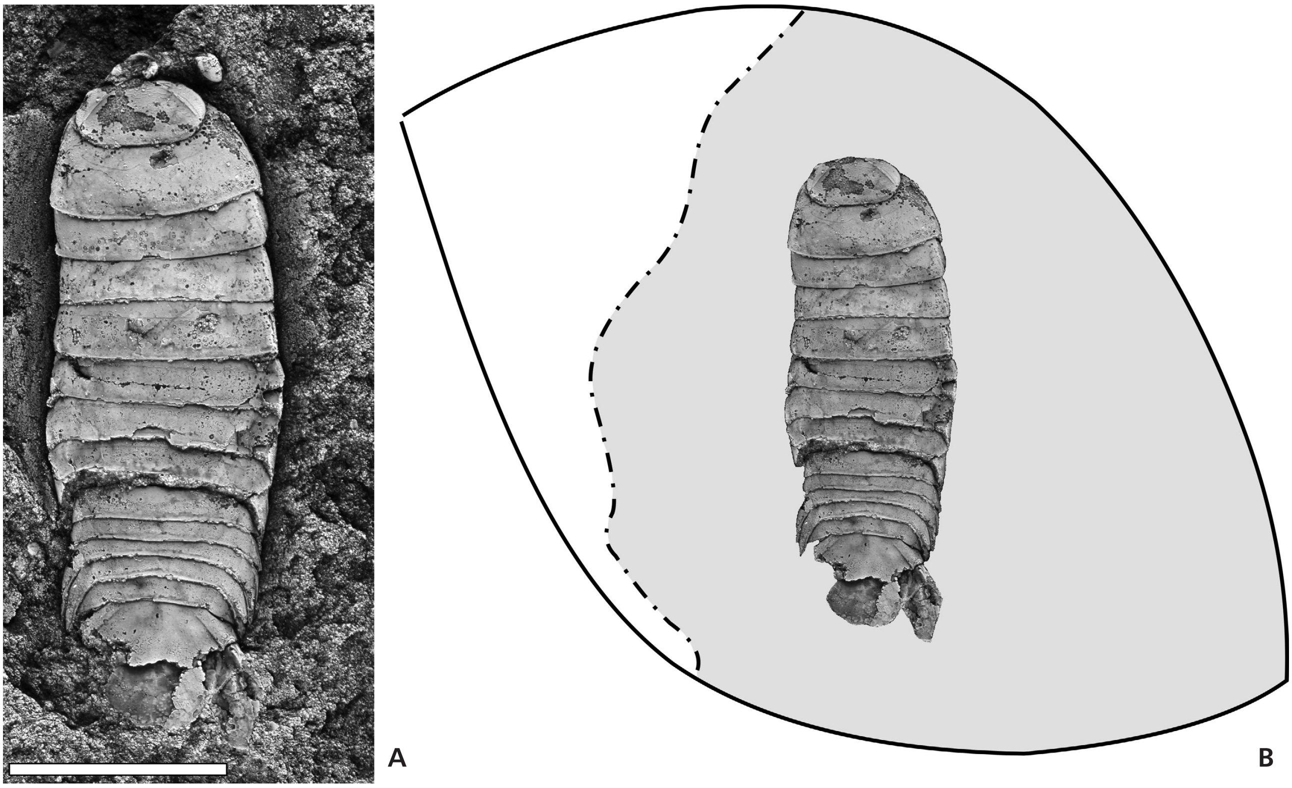

Figure 1. *Pleovideolana gijsberti* gen. et sp. nov., Middle Jurassic "Marnes à *Pholadomya*", Metz-le-Comte (Département Nièvre, central France). • A – holotype (RGM244996). Specimen whitened with ammonium chloride prior to photography. Scale bar is 10.0 mm. • B – supposed position of *Pleovideolana gijsberti* gen. et sp. nov. within a pholadomyid bivalve.

Bruce & Svavarsson, 2003, *Plakolana* Bruce, 1993 and *Aatolana* Bruce, 1993. However, all fossil and extant species of *Cirolana*, and closely related genera, have pleonite 1 largely concealed by pereonite 7. In the present specimen, pleonite 1 is clearly visible. In addition, a straight to slightly convex posterior border of the cephalon is uncommon. Most cirolanid genera have a concave or angular posterior cephalic border. Thus, these differences warrant the introduction of a new genus of cirolanid.

Systematic palaeontology

Order Isopoda Latreille, 1817
Suborder Cymothoida Wägele, 1989
Family Cirolanidae Dana, 1852

Pleovideolana gen. nov.

Etymology. – In allusion to the clearly visible pleonite 1 and the ending -*lana* used for many genera within the family Cirolanidae.

Type species. – *Pleovideolana gijsberti* sp. nov.

Diagnosis. – Cephalon subelliptical, with blunt rostrum; large elongated eyes bordered by slightly concave interocular carina, posteriorly almost parallel to lateral border of pereonite 1 and ending anteriorly aside rostrum; body about three times as long as wide, widest at pereonite 5–6; form of pereonites 2–4 similar to that of pereonites 5–7; pleonite 1 not concealed by pereonite 7 in dorsal view; lateral margins of pleonites 4 and 5 prominent in dorsal view; pleotelson subtriangular with anterolateral grooves and anterocentral depression, without a central keel; uropods biramous.

Discussion. – Pleovideolana gen. nov. differs from all other fossil and extant related genera, in having a combination of a non-concealed pereonite 1 by pereonite 7 and in having a straight to slightly convex posterior border of the cephalon.

Pleovideolana gijsberti sp. nov.

Figure 1A, B

Etymology. – In honour of Professor Dr Gijsbert (Bert) J. Boekschoten, who collected the holotype during a student field trip in 1977.

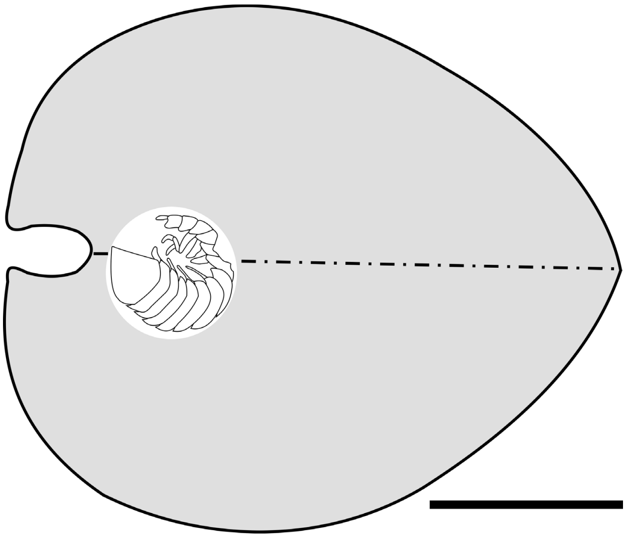

Figure 2. Stomach contents (*i.e.*, a possibly unnamed cirolanid isopod) of an extant carnivorous poromyid bivalve, *Dilemma spectralis* (modified after Leal 2008). Scale bar is 5.0 mm.

Diagnosis. – The same as for the genus.

Description. – Body elongate, lateral margins subparallel, 31 mm long and 11 mm wide (l/w ratio = 2,82), widest at pereonite 5–6. Dorsal surface smooth, except for faint transverse marginal lines on all pereonites and faint transverse posterior marginal ridges on all pleonites. Cephalon subelliptical, length/width ratio 1:2, about two-thirds of maximum width of pereionite 1, and ornamented with transverse crenulations. Compound eyes, anterolaterally directed, well developed and elongated, with several dozens of ommatidia, and bordered by slightly concave interocular carina, posteriorly running almost parallel to lateral border of pereonite 1 and ending anteriorly aside short, blunt rostrum. Pereonites 2-4 similar in form, with greater height/width ratio than pereonites 5–7. Pleonite 1 not concealed by pereonite 7 in dorsal view. Pleonites 3 and 4 with pointed posterolateral margins, directed posteriorly, extending beyond posterior margin of pleonite 5. Posterolateral margin of pleonite 4 clearly overlapping posterolateral margin of pleonite 5. Partially preserved pleotelson subtriangular with anterolateral grooves and anterocentral depression, lacking central keel; uropodbiramous.

Material and stratigraphy. – The holotype (RGM244996), and sole specimen known to date, was collected at a disused gravel pit a few hundred metres west of the small village of Metz-le-Comte (Département Nièvre, central France), close to the local First World War monument and opposite the Rousset Père-Fils vineyard, where the Middle Jurassic "Marnes à *Pholadomya*" crop out.

Remarks. – Cirolanids occur worldwide, inhabiting cool-temperate waters to tropical coral reefs. Most species have been recorded from the intertidal to depths of 1,000 metres (Bruce 2004). The majority are free-living predators or carnivorous scavengers, well capable of swimming and spending much time burrowed in sand, under rocks or in crevices. They can also be found in any suitable hiding place such as mussel beds, masses of intertidal worm tubes, kelp holdfasts or burrows of other animals (Brusca *et al.* 1995). Gonzalez & Jaramillo (1991) studied associations of the clam *Mulinia edulis* Linnaeus, 1758 and the isopod *Edotea magellanica* Cunningham, 1871 on subtidal sand bars in southern Chile. The percentage of isopod occupation of bivalves in nearby estuaries varied between 1.5–4.2%, while on the sand bars the ranges were 21.1–80.7%. The highest percentage of isopod occupation in the clams collected from the sand bars occurred in bivalves with shell lengths ranging between 50 and 60 mm, and isopod females outnumbered males at all localities.

Leal (2008) described a new carnivorous poromyid bivalve, *Dilemma spectralis*. An examination of the stomach contents of the holotype revealed a relatively intact specimen of a possibly unnamed cirolanid (Fig. 2). The stomach was greatly distended and there was no evidence of eyes, ommatidia, or pigment, which led that author to conclude that the prey item was an eyeless isopod. However, it cannot be completely ruled out the isopod was an inhabitant of the mantle cavity of the bivalve.

In the present case of *Pleovideolana gijsberti* gen. et sp. nov. within a pholadomyid bivalve, it is most likely that the isopod sought shelter, but it might also constitute a commensal occurrence or even stomach contents.

Galatheoid/echinoid association – Late Jurassic–Early Cretaceous of the Czech Republic

Within a nucleolitid echinoid test, of a maximum length of 38 mm, a near-complete carapace of the galatheoid *Galatheites zitteli* (Moericke, 1889) (maximum length 6 mm) is preserved. The specimen was collected in June 2014 by one of the authors (PS) from level 5 at Kotouč quarry, Štramberk (Moravia, Czech Republic). Based on new ammonite data, the age of this specimen is the latter part of the early Tithonian (PS, pers. obs.). Traditionally, the limestones at this locality have been assumed to be of Tithonian age (Houša 1975), which may be correct for the main interval of reef development. Age estimates from calpionellid and ammonite stratigraphy, however, indicate a much longer time span, *i.e.*, from the uppermost Kimmeridgian to the lower Berriasian for the deposition of the Štramberk Limestone (Fraaije *et al.* 2013). Calpionellid stratigraphy provides evidence for a latest early Tithonian to earliest Berriasian age, reaching up to the *Remaniella ferasini* Subzone.

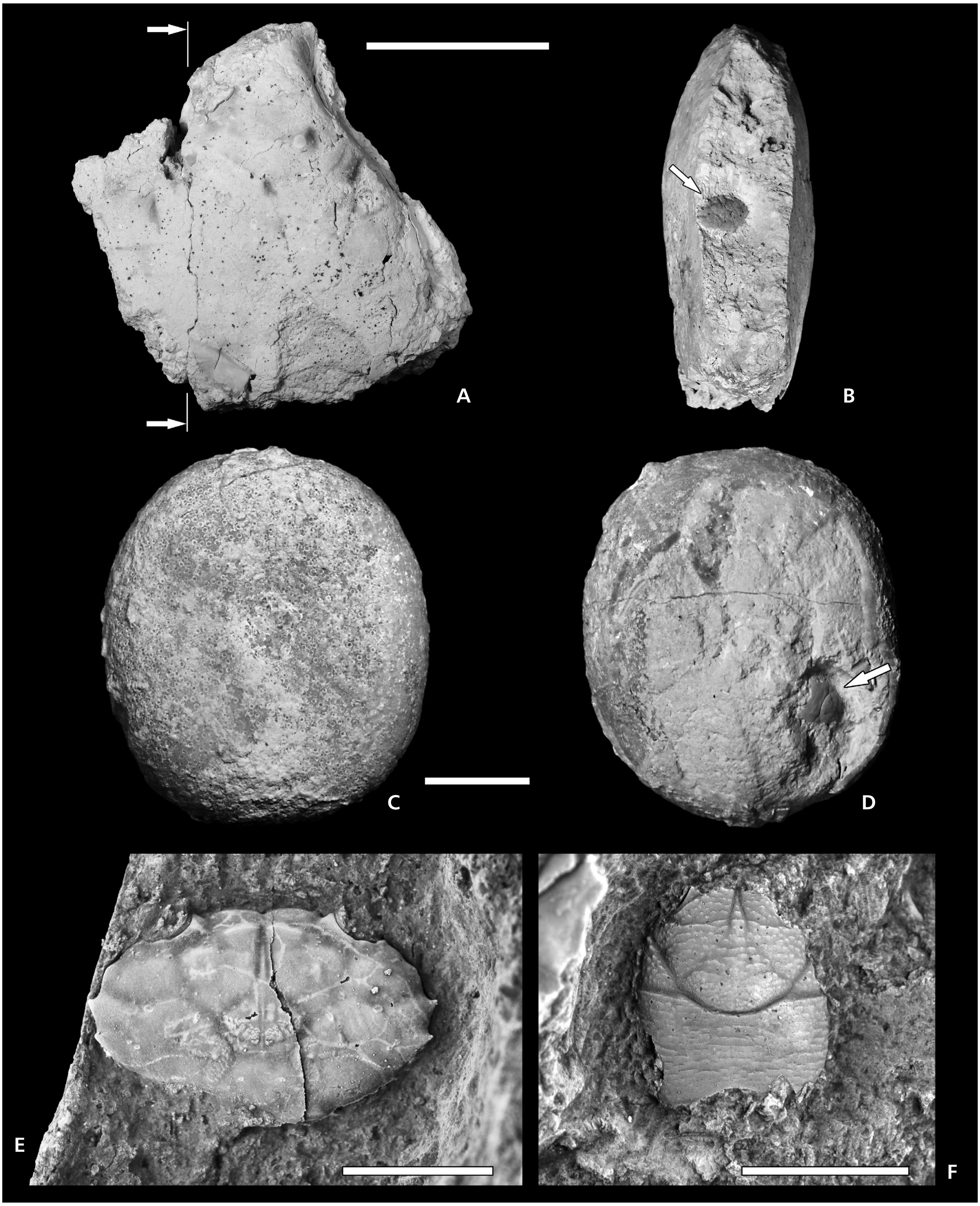

Figure 3. A, B – position of *Chlorodiella tetenyensis* Müller, 1984, within an articulated specimen of the bivalve *Isognomon maxillatum* (Lamarck, 1819), late Langhian (middle Miocene), Müllendorf quarry, eastern Austria, MAB k.3554A–B. Scale bar is 50.0 mm. • C, D – *Galatheites zitteli* (Moericke, 1889) within a nucleolitid echinoid test, early Tithonian, level 5 at Kotouč quarry, Štramberk (Moravia, Czech Republic), MAB k.3555A–B. Scale bar is 10.0 mm. • E – *Chlorodiella tetenyensis* Müller, 1984. Specimen whitened with ammonium chloride prior to photography. Scale bar is 5.0 mm. • F – *Galatheites zitteli* (Moericke, 1889). Specimen whitened with ammonium chloride prior to photography. Scale bar is 5.0 mm.

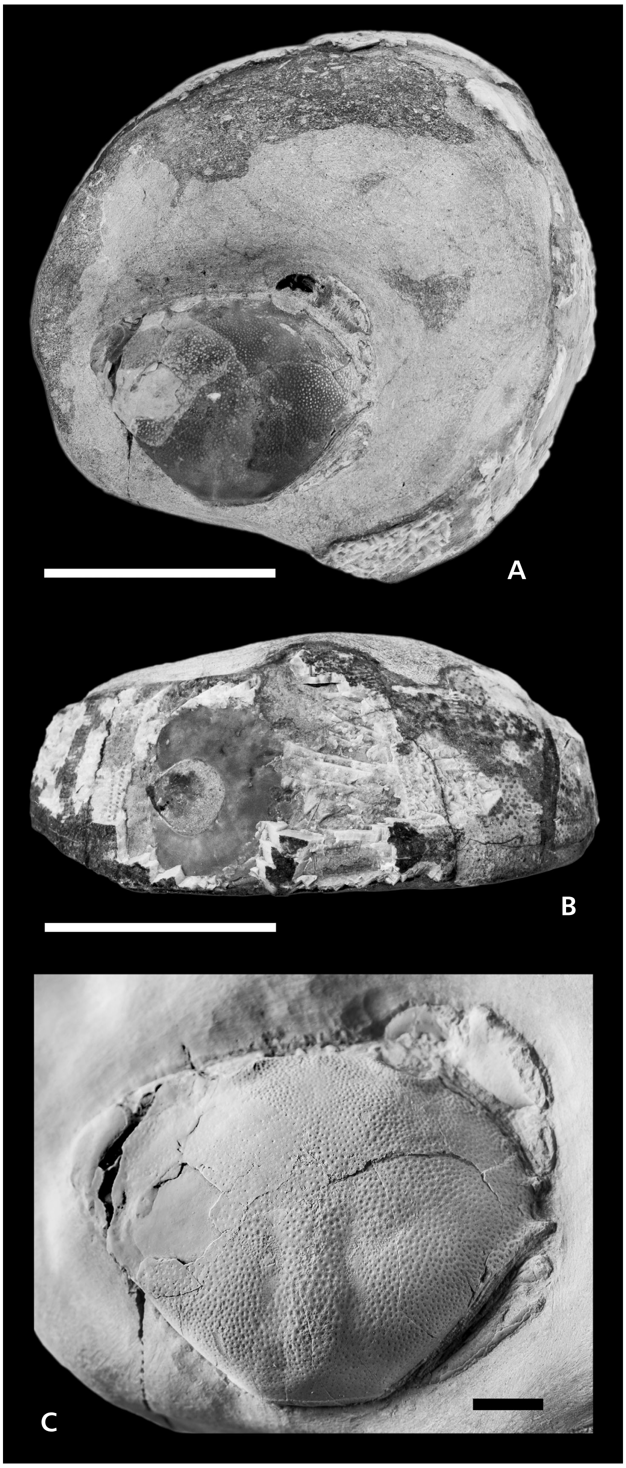

Figure 4. A – *Harpactoxanthopsis quadrilobatus* (Desmarest, 1822) within a test of *Conoclypus conoideus* (Leske, 1778), middle Eocene at Roč, Istria, Croatia, RGA/SMNH 1626. Scale bar is 50.0 mm. • B – side view of the broken *Conoclypus conoideus* test, showing small epibiont oyster attachment scar. Scale bar is 50.0 mm. • C – articulated carapace of *Harpactoxanthopsis quadrilobatus* (Desmarest, 1822). Specimen whitened with ammonium chloride prior to photography. Scale bar is 10.0 mm.

The echinoid is well preserved, with only the apical part missing (Fig. 3C, D). The relatively small galatheoid carapace lies subparallel to ambulacrum IV (see *e.g.*, Moyne *et al.* 2005) with its rostrum pointing orally and its posterior margin pointing apically (Fig. 3F). The anomuran entered the test either via the damaged portion, or via the periproctal opening. In view of the small size of the test openings and the relative completeness of the carapace, this mode of preservation is interpreted as an example of sheltering, although an accidental association (*i.e.*, washed in) cannot be ruled out completely.

Echinoid/crab association – Eocene of Croatia

Within a large test (maximum length 125 mm) of *Conoclypus conoideus* (Leske, 1778), collected by amateur collector Mr. Tomaž Hitij from the middle Eocene at Roč, Istria, is contained a well-preserved individual of *Harpactoxanthopsis quadrilobatus* (Desmarest, 1822), retaining all pereiopods and both chelae. Remains of decapod crustaceans are common in Middle Eocene rocks (*e.g.*, "marls with crabs", of Pavlovec & Pavšič 1985) of Slovenia and Istria (Croatia), but diversity is low (Bachmayer & Nosan 1959). All extinct decapod crustaceans on record to date from Istria are brachyurans, and the majority comprise species of the genera *Harpactocarcinus* A. Milne-Edwards, 1862 and *Harpactoxanthopsis* Via, 1959 (see Schweitzer *et al.* 2005). In addition, finds of the raninoidean *Lophoranina* are common as well (Mikuž 2003). Decapod-rich layers constitute a transitional unit, sandwiched between *Nummulites* limestones of the carbonate platform and the basinal flysch deposits. These beds are of middle Eocene (early Lutetian) age (Mikuž 2010), and consist of sandy to brecciated limestones, sandstones and marls. Most decapod crustacean specimens have been collected from laminated sandstones and marls, which represent a sequence of lesser water energy in the palaeoenvironment. On the other hand, tests of *Conoclypus conoideus* are found exclusively in brecciated and olistostrome limestones below sandstones and marls, from which only few decapod crustaceans have been recorded to date (Mikuž 2003). The present specimen originates from hard calcareous sandstone directly above the olistostrome limestone, for which a much greater energy level can be postulated. The foraminiferal and nannoplankton assemblage indicates warm water of lower salinity, which would suggest proximity of the shoreline (Pavlovec & Pavšič 1985), and glauconitic grains in sandstones confirm the subsidence of the carbonate platform and its transition into basinal flysch sedimentation, which overlies the transitional marl beds with decapod crustaceans.

Conoclypus is characterised by a massive, oval test that commonly reaches diameters of over 100 mm, the oral surface being flat, and the aboral side tall and conical with a sharp edge. Its reduced lantern served for feeding on algae and seaweed (Smith & Kroh 2014). The relationship between *Conoclypus* and other organisms also indicates a shallow-water setting. Mitrovič-Petrovič (2002) reported several individuals of *C. conoideus* with epibiont ostreid bivalves. Oysters are shallow-water inhabitants, mostly occurring down to depths of 40 m and dependent of energetic waters with abundant food particles and oxygen. Many tests of *C. conoideus* exhibit fractures and mechanical damage of the aboral surface similar to the specimen illustrated here.

The abundance of broken tests of these massively tested echinoids in high-energy environment would serve as a logical natural selection of refuge for decapod crustaceans. The crab is within the echinoid (Fig. 4A), the aboral surface of which was broken. The top part of the test was broken prior to deposition and fossilisation (Fig. 4B), as demonstrated by the absence of this test portion and by the fact that the sediment within the test is level. The specimen also exhibits a small epibiont oyster attachment scar on the inside of the lateral wall of echinoid test (Fig. 4B). This supports the assumption that the test was lying broken and exposed on seabed for some time before being filled with sediment and thus presented a sturdy shelter for the crab. The 60 mm wide crab carapace is positioned off centre, close to the test wall; most likely, it is a corpse, rather than a moult, because it retains articulated pereiopods with chelae, the echinoid test having protected it from any *post-mortem* disarticulation. The carapace is wider than long, ovate and high arched, with dorsal regions poorly defined (only branchiocardiac groove is clearly seen), and its cuticular surface punctate (Fig. 4C). The front has four spines, including the inner orbital spines, while the anterolateral margin is convex, bearing five spines. The posterolateral margin is straight, the posterior margin narrow and straight as well. Chelae are strong, massive and heterochelous.

A difference in sediment fill can be observed (Fig. 4A), between calcareous sandstone inside the echinoid test. The sediment on top of the crab is softer and of a light grey colour, and that further down darker and more indurated. This could be a difference of mineralisation, or actually representation of two generations of sediment infill, with softer sandy sediment rapidly burying the crab corpse inside its refuge.

Bivalve/crab association – Middle Miocene of Austria

A carapace (maximum width 12 mm) of the crab *Chlorodiella tetenyensis* Müller, 1984 (Fig. 3E) within an articulated specimen of the bivalve *Isognomon maxillatum* (Lamarck, 1819) (Fig. 3A, B) was collected in 2006 by one of the authors (RHBF) from the lowermost accessible part of the Müllendorf quarry, eastern Austria. This part of the section exposed was characterised by a succession of *Hyotissa*, *Isognomon* and bioclastic coralline algal-molluscan facies types. The sequence at Müllendorf quarry is assigned to the Upper Lagenid and *Spiroplectammina* zones (see Wiedl *et al*. 2013, fig. 4), indicating a middle "Badenian" (= late Langhian) age for the specimen studied.

The present specimen was collected from the *Isognomon* facies (see Wiedl *et al*. 2013, fig. 2, section A), which is characterised by the common occurrence of articulated shells of *Isognomon maxillatum* (*ca* 100 mm in length), often in life position, which form distinct coquinas within coralline algal rudstones with a packstone matrix. The shells usually are preserved as internal moulds (steinkerns), but occasionally remains of the calcitic shell are preserved. Coral debris (*Porites* spp.) occurs as well. Coralline algal macroids (diameter 5–10 mm) are common, as are some other bivalve taxa, echinoids, small gastropods and celleporiform bryozoans. Textulariid and rotaliid foraminifera are rare. In this facies, the amount of siliciclastics is low (Wiedl *et al*. 2013).

Being a warm-water, re-entering immigrant from the Mediterranean, *Isognomon* is a typical shallow-water, intertidal thermophilic, suspension-feeding epibiont. Its presence is interpreted to be indicative of a shallow subtidal setting, at a depth of 1–5 m (Harzhauser *et al*. 2003, Wiedl *et al*. 2013). The high percentage of articulated shells, often in life position and forming small biostromes, demonstrates that these concentrations are autochthonous. About twenty articulated specimens of *Isognomon* were broken up mechanically, yet only one contained a crab carapace. The carapace is preserved in the centre, close and perpendicular to one of the valves. Both valves have internal epibionts such as bryozoans and serpulids. This inquiline preservation could well have been the result of sediment trapping or washing in, but the completeness of the delicate carapace does not rule out that this is in fact a moult of an individual that hid in the bivalve.

The genus *Chlorodiella* comprises about a dozen of extant species (Ng *et al*. 2008). All of them predominantly inhabit low intertidal to shallow subtidal coral reefs in the tropical Indo-West Pacific (Morton 1989, Davie 2002, Lasley *et al*. 2013). In samples of dead coral in reefs along several islands in Vietnamese seas, *Chlorodiella* specimens comprised more than half of all brachyurans collected, *i.e.*, 72 species, in 32 genera and four families. The two most common species, *C. corallicola* Miyake & Takeda, 1968 and *C. laevissima* (Dana, 1852), accounted for only 3% of all species, but they did represent 54% of the total number of individuals (Tan & Thi 2007). A very similar palaeoecological and numerical occurrence for

Chlorodiella can be postulated along the middle Miocene "Leitha Island" reefs in the Paratethys (Müller 1984).

Müller (1984, pp. 88, 89) described a subspecies, *Chlorodiella mediterranea tetenyensis*, but already stated that, "Though the two forms were found together, they are clearly separated. The much stronger regional definition and the very long and deep grooves along the mesogastric process, which are absent in *C. mediterranea*, warrant the new status of *C. tetenyensis.* " This interpretation is followed here, and the present form is afforded full specific status.

Discussion

At least some of the above-mentioned examples appear to represent cases in which crustaceans selected empty and dead shell of host organisms, most likely seeking shelter. Similar behaviour can be observed in the extant cancrid crab, *Cancer magister* (Dana, 1852). Juveniles of the species seek a sheltered mode of living among clams, *Mya arenaria* Linnaeus, 1758, and oysters *Crassostrea gigas* (Thunberg, 1793) in the first months of their benthic life (Fernandez *et al.* 1993). Crabs actively select a habitat which provides the lowest risk of mortality by predation during vulnerable times, and move out to subtidal mudflats after reaching size of > 35 mm when they are able to avoid most predators on account of their greater size. Although this example is given for the larval to juvenile stages of crab life, which tends to have highest mortality rate (Wilson *et al.* 1990), the same *modus operandi* can be stipulated for moulting, which is a time when adult crustaceans are most vulnerable. It would be reasonable to assume that individuals at time of moulting would seek shelter in empty shells of bivalves and echinoids like they did in ammonite and nautiloid shells (*e.g.*, Fraaije & Jäger 1995, Fraaije & Pennings 2006, Klompmaker & Fraaije 2012, Landman *et al.* 2014). Another possible explanation for habitat selection within empty shells would be to lie in hiding for hunting and preying upon passing prey.

The octopus *Amphioctopus marginatus* (Taki, 1964) preys on crabs from a lair, which usually is in between the valves of a bivalve (Finn *et al.* 2009). If small octopids used empty bivalves for a lair already in the Miocene, the carapace within *Isognomon* from Müllendorf quarry, Austria could also present the remains of such an octopod dinner.

Conclusions

The presented associations represent evidence of sheltering behavior of crustaceans in Mesozoic–Cenozoic environments. The importance of such refuge, especially during moulting, is highlighted in isopod/bivalve association from middle Jurassic of France, where a delicate, nearly complete extinct cirolanid *Pleovideolana gijsberti* gen. et sp. nov. is described for the first time.

We present three further associations from high-energy environments, which would necessitate additional protection of crustaceans during vulnerable time of moulting. This is supported by the corresponding palaeoecological data, which points to high-energy reefal, intertidal and shallow-marine environments. Such turbulent waters would be unfavorable to freshly moulted individuals, which would find refuge inside sturdy structures of robust intertidal invertebrates. Although such examples from the fossil record are rare, we postulate that this mode of preservation probably is a commoner phenomenon in comparison to extant biotic associations in the sea.

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