



New hermit crab species (*Anomura*, *Paguroidea*) from the upper Miocene St. Marys Formation of Maryland (USA), preserved in their host shells

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Abstract

Two new species of hermit crab are recorded from the upper Miocene (Tortonian) St. Marys Formation of Maryland, named *Pagurus hazenorum* n. sp. and *Paguristes timoni* n. sp. and assigned to the families Paguridae Latreille, 1802, and Annuntidiogenidae Fraaije, 2014, respectively. Both new species are morphologically close to present-day congeners, but can be differentiated on details of ornament (tubercles, granules and teeth).

Key words: Paguridae, Annuntidiogenidae, *Paguristes*, *Pagurus*, new species, eastern North America

Introduction

In general, *in-situ* preservation of hermit crabs in their host shells is rare in the fossil record (Dunbar & Nyborg 2003; Jagt *et al.* 2006), in spite of several recent records (see e.g., Fraaije *et al.* 2008; Garassino *et al.* 2009a; Fraaije & Polkowsky 2016; Pasini *et al.* 2020). The most ancient examples known to date are of those preserved in ammonite shells, with records from the upper Pliensbachian (Lower Jurassic) of southern Germany (Jagt *et al.* 2006), the Upper Jurassic of central Russia (Mironenko 2020) and the Hauterivian (Lower Cretaceous) of Yorkshire, United Kingdom (Fraaije 2003). During the Early Cretaceous, paguroids appear to have made the switch from ammonite conchs to empty gastropod shells (Van Bakel *et al.* 2008), as has been documented by fairly numerous finds from central Europe in recent years. Comparable Late Cretaceous material is known from Germany (Mertin 1941), the Netherlands (Jagt *et al.* 2000, 2006; Fraaije *et al.* 2008) and France (Breton & Collins 2007). In addition, there are younger (Paleogene and Neogene) records from Kaliningrad, Russia (Eocene; Jagt *et al.* 2006), Denmark (Eocene; Collins & Jakobsen 2004), northern Italy (Eocene; Garassino *et al.* 2009a, Pliocene; Pasini & Garassino 2010), Spain (Eocene; Ferratges *et al.* 2021, 2022), Austria (Eocene; Fraaije & Polkowsky 2016), Japan (Oligocene; Karasawa 2002), Washington State (USA) (Oligocene; Pasini *et al.* 2020), the Netherlands (Miocene; Jagt *et al.* 2006), Taiwan (Miocene; Hu & Tao 1996), New Zealand (Miocene; Hyden & Forest 1980; Feldmann & Keyes 1992), Panama (Miocene; Todd & Collins 2006), California (USA) (Pliocene; Dunbar & Nyborg 2003) and Taiwan (Holocene; Hu & Tao 1996). A notable recent example is that of a completely preserved hermit crab outside its host gastropod shell from the Eocene of Spain (Ferratges *et al.* 2020).

Several hypotheses have been put forward to explain the paucity of *in-situ* hermit crabs in the fossil record, but all of them have remained speculative (Dunbar & Nyborg 2003). Following death, the paguroid body rapidly

becomes dislodged from its host shell and starts decaying (Klomp maker *et al.* 2017), which probably contributes greatly to the low preservation potential of *in-situ* hermit crabs (Dunbar & Nyborg 2003).

As with specimens preserved *in situ*, paguroid carapaces are rare as well, but this can, at least in part, be ascribed to collection bias in view of their generally small size (e.g., Garassino *et al.* 2009b; Fraaije *et al.* 2019; Wallaard *et al.* 2020). More common are isolated major chelipeds, but these are often fragmentary (lacking moveable fingers) and may prove difficult to identify at the generic and/or specific level (e.g., Hyžný *et al.* 2016; Feldmann *et al.* 2018; Jakobsen *et al.* 2020; Fraaije *et al.* 2020; Hyžný & Dulai 2021, and references therein), despite being also described and illustrated in papers on extant paguroid genera and species (e.g., McLaughlin 2003).

During the shift from ammonite conchs to gastropod shells, cheliped morphology became adapted and changed from elongated, occasionally nearly straight-fingered ones, well suited to block off ammonite apertures, toward more rounded for those of gastropods (Fraaije 2003).

On the basis of two specimens preserved in their shells from the upper Miocene St. Marys Formation of Maryland, we here describe the pagurid, *Pagurus hazenorum* **n. sp.**, and the annuntidiogenid, *Paguris timoni* **n. sp.**

Geological context

The Calvert Cliffs along the western shore of the Chesapeake Bay in Calvert County (Maryland) represent one of the best Miocene exposures along the Atlantic coastline. The cliffs are comprised of three formations, in ascending order, Calvert, Choptank, and St. Marys, that make up the Neogene Chesapeake Group. Each of these three units contains many sequences of transgressions and regressions; however, the overall trend is a shallowing of the sea over the 9 million years represented at Calvert Cliffs (Kidwell *et al.* 2015). Thus, the St. Marys Formation represents the shallowest, coastal and lagoonal, facies along the Calvert Cliffs. A shallow, tide-influenced depositional environment is evidenced by rapid facies changes along the outcrop (Kidwell *et al.* 2015). The St. Marys Formation is characterized by shell-rich, sandy beds interspersed with layers of clay and silt (Kidwell *et al.* 2015). An abundant fauna of invertebrate fossils has been discovered and described from Calvert Cliffs with a great diversity in the St. Marys Formation (Clark *et al.* 1904; Ward 1992; Vokes *et al.* 2000; Ward & Andrews 2008). The paguroid specimens described in the present study came from the St. Marys Formation in the cliff south of Little Cove Point, Calvert County, Maryland.

Systematic paleontology

We here follow the classification of extinct paguroids by Fraaije *et al.* (2017, 2022). *Institutional abbreviation*: CMM—Calvert Marine Museum.

Order Decapoda Latreille, 1802

Infraorder Anomura MacLeay, 1838

Superfamily Paguroidea Latreille, 1802

Family Paguridae Latreille, 1802

Genus *Pagurus* Fabricius, 1775

Type species. *Cancer bernhardus* Linnaeus, 1758, by monotypy.

Species included. For data on extinct forms, reference is made to lists provided by Schweitzer *et al.* (2010) and to subsequent records by Beschin *et al.* (2012), De Angeli & Caporiondo (2017) and Polkowsky & Fraaije (2019). Extant species have recently been discussed by Lemaitre & McLaughlin (2021a).

***Pagurus hazenorum* n. sp.**

(Fig. 1)

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Diagnosis. Major carpus (right) covered with small, randomly scattered tubercles, increasing in size toward outer margin, there becoming setose. On minor carpus (left), tubercles arranged in rows and slightly increasing in size toward distal end. Both claws densely covered with large granules, decreasing in size toward outer margin. Outer margins of propodus and dactylus covered with blunt teeth, smaller on dactylus. Outer lateral surface of dactylus with longitudinal, medially elevated surface. Walking legs covered with row of teeth, decreasing in size toward distal end. Dactylus of walking leg only covered by blunt teeth and surface with some longitudinal grooves.

Type material. The holotype, and sole specimen known to date, is CMM-I-4785. It is preserved inside its gastropod host shell (*Buccinofusus parilis* Conrad, 1832), which is severely damaged and allows the hermit crab inside to be observed in more detail. The right and left chelipeds are preserved within the gastropod aperture. A relatively complete walking leg, consisting of carpus, propodus and dactylus, is seen posterior of that aperture. A second walking leg, of which only the carpus is preserved, is found anterior of the aperture, while several fragments of other legs are present just behind the chelipeds. The carapace should have been situated here, but this part of the individual has suffered considerable damage and there is no trace of a carapace.

Etymology. In honor of Dr Robert M. Hazen, senior staff scientist at the Carnegie Institution for Science, and his wife, Margaret Hazen, writer and historian.

Locality and stratigraphy. Driftwood Beach, Calvert County, Maryland, from the upper Miocene (Tortonian) Little Cove Point Member of the St. Marys Formation in a silty lens within Bed E (Ward & Andrews 2008). Kidwell *et al.* (2015) identified this level as belonging to “SM-C,” assigned to Shattuck zones 22–23 and part of dinocyst zone 8.

Description. Chelipeds stout, broad, with propodus of major (right) claw measuring 21 mm by 14 mm; that of minor (left) claw measuring 16 mm by 12 mm. Entire surface of carpus of major claw covered with small, randomly scattered tubercles, increasing in size and setation toward outer margin. Carpus of minor claw with tubercles arranged in rows and slightly increasing in size toward distal end. Both left and right propodi densely covered with large granules, decreasing in size toward outer margin. Outer margin of propodus arcuate; that of dactylus almost straight. Outer margin of both propodus and dactylus covered with blunt teeth, smaller on latter. Outer lateral surface of dactylus covered with longitudinal, medially elevated ridge.

Walking legs covered with row of teeth, decreasing in size toward distal end. Dactylus of walking leg with blunt teeth; surface with some longitudinal grooves.

Remarks. The new species compares fairly well with the extant *Pagurus impressus* (Benedict, 1892), from the west coast of Florida (Provenzano 1959), as well as with *Diacanthurus rubricatus* Henderson, 1888, from the coast of New Zealand and *P. bernhardus* (Linnaeus, 1758) from the eastern North Atlantic.

Discussion. The assignment of the Maryland material to the genus *Pagurus* is based on several morphological features which *P. hazenorum* n. sp. has in common with extant congeners, as described below.

Although *P. hazenorum* n. sp. is preserved *in situ* within its gastropod shell, the carapace appears to be missing, most likely as a result of the damage to the host shell. Overall, the shape of the dactylus is more elongated and bears a closer cover of granules in *P. impressus*, whereas that of *P. hazenorum* n. sp. is stout, with blunt teeth along the outer edge and a cover of large granules. Chelipeds of the present-day *D. rubricatus* bear small spines, in equal density as in *P. hazenorum* n. sp. *Pagurus bernhardus* is comparable as well; this has a coarse ornament which, however, is less dense than that of *P. hazenorum* n. sp. (see Hyžný & Dulai 2021: fig. 35.8).

Our comparison of *P. hazenorum* n. sp. with both extant and extinct species has yielded numerous forms with closely comparable anatomical features. Molecular and genetic research carried out recently on extant representatives of the genus *Pagurus* has shown that this is in fact a wastebasket taxon, comprising forms with closely comparable morphologies, but widely divergent genetic structures (e.g., Olguin & Mantelatto 2013; Sultana *et al.* 2018). Naturally, genetic research cannot be carried out on extinct forms, which makes any workable subdivisions of the genus *Pagurus* even more difficult. This morphological similarity amongst genetically diverse species is most likely a reflection of functional morphology. Particularly in paguroids, the shell has a marked impact on cheliped shape, and most hermit crabs inhabit comparable mollusks, which explains the closely comparable morphology of the chelipeds.

In the fossil record, isolated paguroid chelipeds (mostly propodi) are quite common, whereas carapaces are extremely rare. In view of this, it is highly unlikely that the difficulties surrounding the ‘lump’ taxon *Pagurus* can be resolved on the basis of extinct forms.

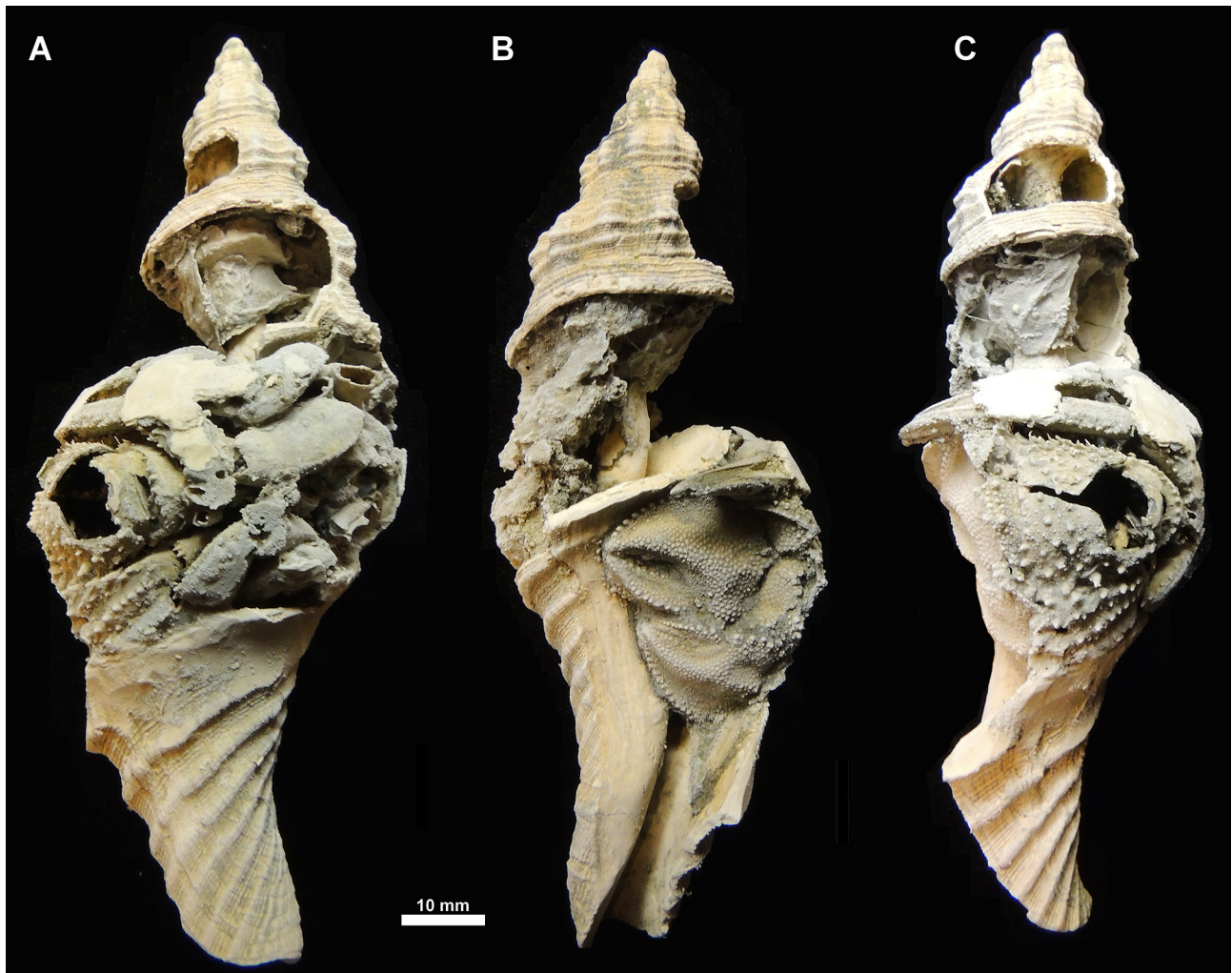


FIGURE 1. *Pagurus hazenorum* n. sp., holotype, CMM-I-4785, from the upper Miocene St. Marys Formation in the cliff south of Little Cove Point, Calvert County, Maryland, USA, preserved in its host shell, and in dorsal (A), ventral (B), and dorso-ventral (C) aspects.

Family Annuntidiogenidae Fraaije, 2014

Genus *Paguristes* Dana, 1851

Type species. *Pagurus weddellii* H. Milne Edwards, 1848.

Included species. For a listing of fossil taxa, reference is made to Schweitzer *et al.* (2010), Gagnaison (2012), Beschin *et al.* (2016, 2018), De Angeli & Caporiondo (2017), Karasawa & Fudouji (2018), Jakobsen *et al.* (2020), Marangon & De Angeli (2020) and Wallaard *et al.* (2020). For extant forms, reference is made to Lemaitre & McLaughlin (2021b).

Paguristes timoni n. sp.

(Fig. 2)

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Diagnosis. Keeled merus with row of small teeth on distal margin; moveable finger corneous; fixed finger covered with rows of alveolate tubercles, decreasing in size on distal end. Upper margin with tubercles; cutting edge with several teeth proximally. Walking legs with keeled edge and row of tubercles.

Type material. The holotype, and sole specimen known to date, is CMM-I-4600.

Etymology. Named after the legendary misanthrope and hermit, Timon of Athens, who was popularized in the play ‘Timon of Athens’ by William Shakespeare (1564–1616).

Locality and stratigraphy. Driftwood Beach, Calvert County, Maryland, from the upper Miocene (Tortonian) Little Cove Point Member of the St. Marys Formation in a silty lens within Bed E (Ward & Andrews 2008). Kidwell *et al.* (2015) identified this level as belonging to “SM-C,” assigned to Shattuck zones 22–23 and part of dinocyst zone 8.

Description. CMM-I-4600, preserved inside gastropod shell (*Busycon* sp.), length 25 mm, greatest width 17 mm. Manus missing from major (left) cheliped, carpus and merus preserved. Keeled merus with row of small teeth on distal margin. Minor (right) cheliped comprising complete propodus, lodged in gastropod aperture, measuring 7 mm length, 2 mm maximum width. Moveable finger corneous, fixed finger covered with rows of alveolate tubercles decreasing in size on distal end; most tubercles with alveoli, indicative of setal insertions; upper margin covered with tubercles; cutting edge with several teeth proximally; distal side not visible.

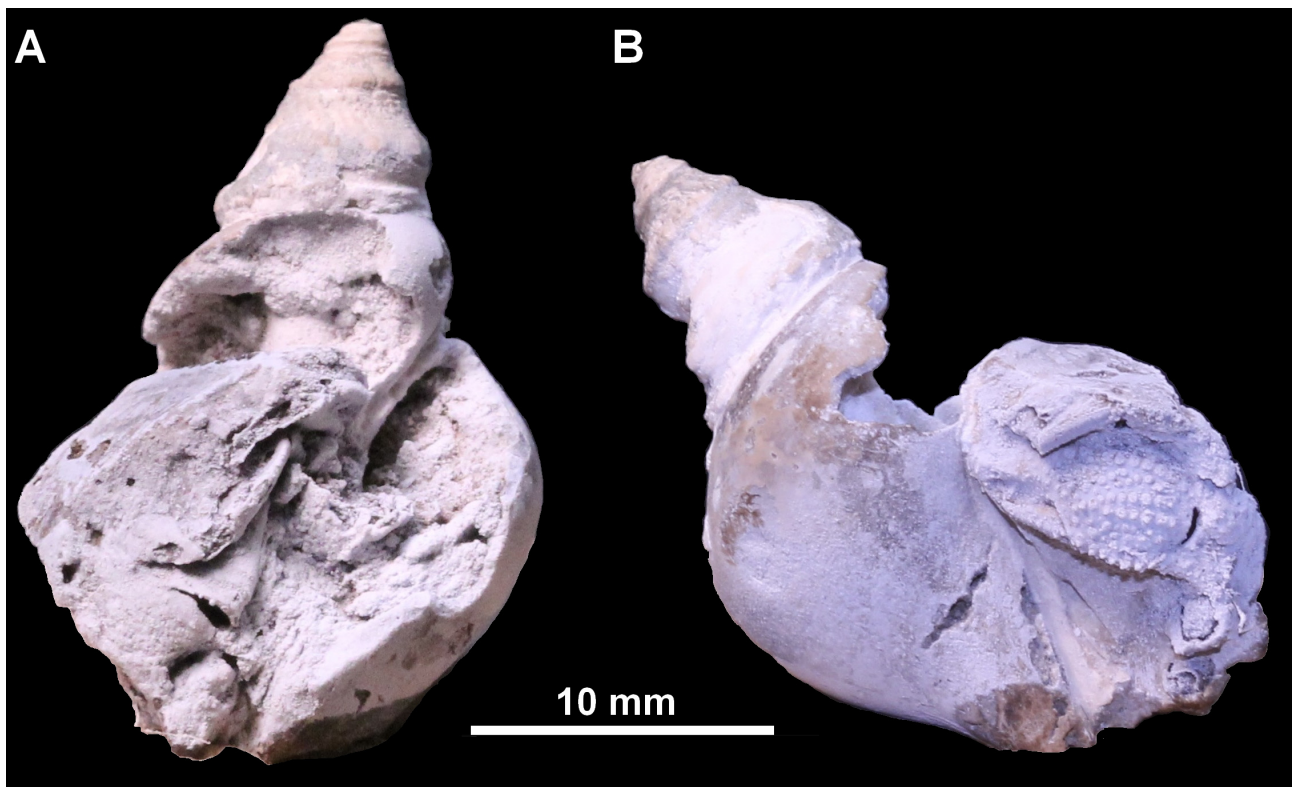


FIGURE 2. *Paguristes timoni* n. sp., holotype, CMM-I-4600, from the upper Miocene St. Marys Formation in the cliff south of Little Cove Point, Calvert County (Maryland), in its host shell, and in ventral (A) and dorsal (B) aspects.

Carapace fragment preserved but covered; small portion visible lacking any specific details;

Single fragment of walking leg preserved showing keeled edge with row of tubercles. Several other fragments preserved, but unidentifiable due to weathering of specimen.

Remarks. In this novel form, the left cheliped is larger than the right one, which is diagnostic feature of diogenid and annuntidiogenid hermit crabs (McLaughlin 2003; Fraaije 2014). The Maryland specimen is remarkably similar to the extant *Paguristes candela*e De Matos-Pita & Ramil, 2015, from Mauritania (see below).

Discussion. Cheliped shape and ornament in *P. timoni* **n. sp.** compare closely with those of *P. candelae*, in that both have rows of tubercles and setae and tubercles decrease in size toward the distal end. The dorsomesial margin in *P. candelae* has three large tubercles; these are absent from *P. timoni* **n. sp.** The dorsal cheliped surface in the latter appears to be less convex in comparison with that of *P. candelae*, while the teeth along the cutting edge appear to be larger in the extinct form. The walking legs in both taxa show a keeled ridge with a row of spines, although the one in *P. timoni* **n. sp.** seems more acute.

Conclusions

The two new paguroid species recorded here from the upper Miocene (Tortonian) St. Marys Formation of Maryland are morphologically close to extant forms. *Pagurus hazenorum* **n. sp.** matches *Pagurus impressus* (west coast of Florida, USA), *Diacanthurus rubricatus* (New Zealand) and *Pagurus bernhardus* (eastern North Atlantic), while *Paguristes timoni* **n. sp.** is remarkably similar to the extant *Paguristes candelae* from Mauritania. Differences in ornament (tubercles, granules, and teeth) allow the extinct forms to be distinguished from their living congeners.

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