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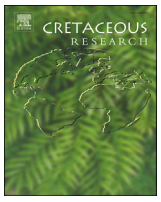

A new mid-Cretaceous hermit crab (Crustacea, Anomura) from Central Russia sheds new light on paguroid evolution☆

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ABSTRACT

Paguroid anomurans constitute a large portion of modern-day decapod crustacean assemblages in all oceans and seas across the globe. However, their palaeontological record is still rather patchy, which partly explains why their phylogeny remains poorly understood. A newly collected specimen of an extinct paguroid is here shown to have a major impact on the evolutionary history of this group of anomurans. A new genus and species, *Mutotylaspis tripudium*, are here erected to accommodate a well-preserved, extraordinarily crab-like hermit crab from the lower Albian (mid-Cretaceous) of Vladimir Oblast (Central Russia) that appears closely related to the extant enigmatic deep-sea taxon *Tylaspis anomala* Henderson, 1885, as well as to other members of the extant family Probeebeidae Boone, 1926. Ongoing palaeontological research during the last two decades has provided ample evidence that paguroid evolution was much more intricate and complex than gleaned solely from extant hermit crabs. The newly collected specimen named herein is the first fossil member of the family Probeebeidae and constitutes an additional key species for unravelling paguroid evolution and extending the stratigraphical range of the family downwards into the mid-Cretaceous.

1. Introduction

In Central Russia (Moscow and surrounding areas), Triassic, Jurassic and Cretaceous deposits are widely distributed (Mitta et al., 2012). Triassic strata, mostly terrestrial, are confined mainly to northern areas (Yaroslavl Oblast) (Kirikov, 2015), while Jurassic and Cretaceous rocks generally are marine in origin over the entire territory of Central Russia, yielding decapod crustacean remains (Fig. 1). These include mostly members of the malacostracan superfamilies Erymoidea and Glypheoidea (Table 1) (Meyer, 1840; Trautschold, 1866; Lahusen, 1894; Gerasimov, 1955; Gerasimov et al., 1995; Shmakov, 2016; Mironenko, 2020); in general, these are preserved as fragmentary remains of carapaces, or more often, portions of chelipeds and/or appendages. Finds of more or less complete carapaces, associated with appendages, are very rare. The majority of specimens recovered require detailed identification; the names used here (Table 1) are in need of a modern revision.

In addition to these taxa (Table 1), there are literature references (Shmakov, 2016) to finds of claws from Callovian strata provisionally identified as ?*Hoploparia* sp. and of a member of the family Solenoceridae, *Archeosolenocera straeleni* Carriol & Riou, 1991, from Callovian–Oxfordian levels. Decapod crustaceans of Jurassic age have also been recorded from regions to the south-east of Central Russia, i.e., from the Volga area, such as finds of *Mecochirus* sp. in Oxfordian strata of the Saratov area (Tesakova, 2008), as well as numerous remains of *Glypheopsis* sp. from Volgian deposits in the Samara area (Paperny, 2017).

To date, only few carapaces of Jurassic and Cretaceous brachyuran crabs have been recorded from the Moscow Oblast (Van Bakel et al., 2021). One of these is *Homolopsis glabra* Wright and Collins, 1972, from Albian strata (Kolchugino Group, Gavrilkovo

☆ https://zoobank.org/NomenclaturalActs/E090D97A-B7CB-4F2D-B741-D03C135E7C31.

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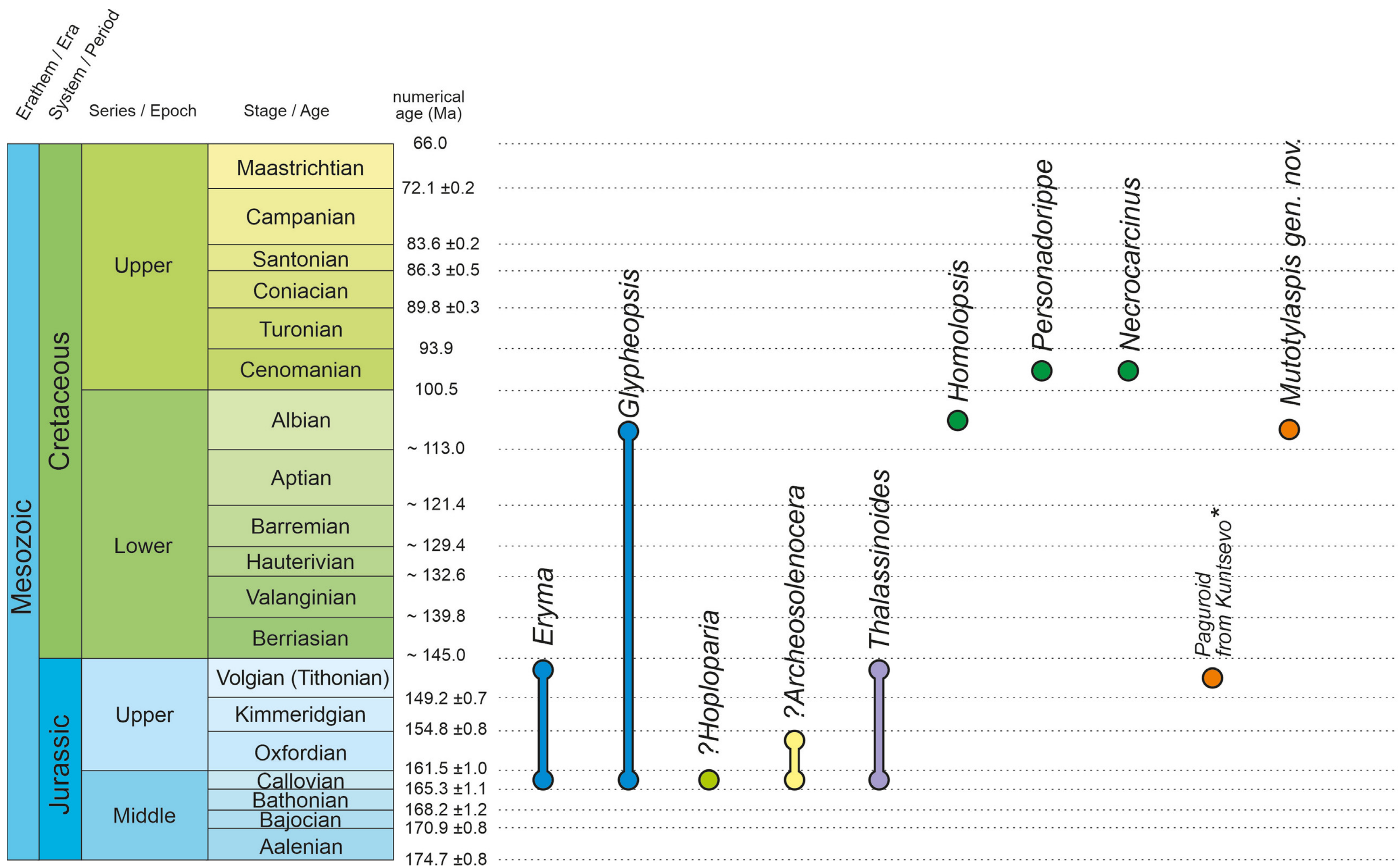

Fig. 1. Stratigraphical distribution of decapod crustacean genera in Jurassic and Cretaceous marine strata in Central Russia. A paguroid, preserved inside an ammonite shell from Kuntsevo has recently been recorded (Mironenko, 2020).

Table 1
Malacostracan taxa recorded from Jurassic and Cretaceous strata in Central Russia, with indication of stratigraphical ranges and pertinent references.

Eryma quadriverrucata Trautschold, 1866 (Trautschold, 1866; Gerasimov, 1955; Shmakov, 2016): Callovian–Volgian (Tithonian)
Eryma mosquensis Lahusen, 1894 (Lahusen, 1894; Gerasimov, 1955; Gerasimov et al., 1995; Shmakov, 2016): Volgian (Tithonian)
Eryma gracilimana Lahusen, 1894 (Lahusen, 1894; Gerasimov, 1955; Shmakov, 2016): Oxfordian–Volgian (Tithonian)
Eryma mandelslohi (von Meyer, 1840) (Meyer, 1840; Shmakov, 2016): Oxfordian
Glypheopsis vosinskyi (Lahusen, 1894) (Lahusen, 1894; Gerasimov, 1955; Gerasimov et al., 1995; Shmakov, 2016): Callovian–Volgian (Tithonian)
Eryma sp. (Shmakov, 2016): Callovian
?*Hoploparia* sp. (Shmakov, 2016): Callovian
Archeosolenocera straeleni Carriol and Riou, 1991 (Shmakov, 2016): Callovian–Oxfordian
Thalassinoides ichnofossils (Rogov, 2017): ?Callovian–Volgian (Tithonian)
Paguroidea gen. et sp. indet (Mironenko, 2020): Volgian (Tithonian)
Homolopsis glabra Wright and Collins, 1972 (Ilyin, 2005): Albian
Personadorippe kalashnikovi Van Bakel, Mychko, Spiridonov, Jagt and Fraaije, 2021: Cenomanian
Necrocarcinus gorbenkoi Mychko, Schweitzer, Feldmann, & Shmakov, 2023: Cenomanian

Formation (Olferev, 1986)) near the village of Gavrilkovo (Dmitrovsky district, River Volgusha) (Ilyin, 2005). Another species is *Personadorippe kalashnikovi* van Bakel et al., 2021, which is stratigraphically younger, having been recovered from the Lyamino Formation of Cenomanian age (Van Bakel et al., 2021). Finally, a carapace of *Necrocarcinus gorbenkoi* Mychko et al., 2023, from the same unit near the village of Varavino in the Moscow Oblast is known (Mychko et al., 2023).

In comparison to remains of lobsters, shrimps and crabs, those of anomurans, such as hermit crabs, are extremely rare in Mesozoic strata of Central Russia. A paguroid preserved within the body-chamber of an ammonite shell from Volgian (=Tithonian) deposits in the Moscow Oblast has recently described (Mironenko, 2020), with interesting palaeoecological conclusions. Here we describe and name a well-preserved hermit crab from Albian strata in the Vladimir Oblast.

2. Stratigraphy

Strata of Cretaceous age are widely distributed in the Vladimir area, with the exception of the north, in the pre-Quaternary valleys, and exposed in river valleys, ravines and gullies, overlying Jurassic deposits unconformably. The bottom of the Cretaceous sequence plunges from an absolute height of 103 m in the south-east to 20 m in the north-west. Recognised within the Cretaceous are a Lower (Valanginian, Hauterivian–Barremian, Aptian and Albian) and an Upper Series (Cenomanian, Turonian–Coniacian and Santonian) (Shipilov and Bastrakova, 1970).

All three substages of the Albian are represented in the area, comprising mainly sands and silts, with interlayers of clays, phosphorites, concretions and pebbles (Baraboshkin, 1992), richly fossiliferous, yielding mostly ammonites. The locality from where the new hermit crab originates is around 5 km away from a composite section of multiple outcrops along the River Eza, a right tributary of the River Koloksha (Fig. 2). Some workers consider this to be a reference section for the lower Albian on the Russian Platform; it has been studied in great detail (Baraboshkin, 1992; Baraboshkin et al., 2020).

Three assemblages of ammonites have been identified within this section, corresponding to ammonite zones of the Boreal standard (Baraboshkin and Guzhikov, 2018), as follows: *Arcthoplites jachromensis* Zone, *Anadesmoceras strangnlatum* Zone and *Anadesmoceras vladimirovi* Zone (Baraboshkin et al., 2020).

3. Locality

The locality of Pavlovskoe-1 is situated in a shallow, forested ravine (Fig. 3C), on the right bank of the River Kuftiga near the village of Pavlovskoe (Yuryev-Polsky district, Vladimir Oblast, Central Russia). Its absolute elevation is about 165 m above sea level. At the bottom of the ravine is a bed of a temporary stream, after rain or snow melt in spring. The site is located on the northern slope of the ravine at a height of 3–5 m above the riverbed. Primary deposits are hidden by talus deposits, soil and vegetation. In the ravine, phosphorite concretions, washed out from the bedrock, are abundant. Near this locality there are other coeval outcrops, such as Chekovo-1, Kishleevo-1, Kishleevo-2, Bukholovo-1, Kutukovo-1, Yeza and others.

In September 2021, one of us (LSB), joined by other amateur palaeontologists, manually excavated bedrock layers of Albian age at the site of Pavlovskoe-1 over a period of two months, thereby discovering a phosphorite horizon with numerous remains of ammonites and other fauna, including the hermit crab described herein.

The sequence of levels exposed is as follows (Fig. 3A, B):

1) A unit of light quartz sands, 2 m in thickness; light grey layers alternate with yellowish (ochrous), cross-bedded ones. In the upper part of this unit, some 30 cm below the top, sandy concretions of 5–10 cm in size, oval or spherical in shape, are occasionally found. In these, the same fossil fauna was found as at the base of the overlying level in the phosphorite horizon. Bioturbation of the *Skolithos* ichnofacies is developed.
2) Clay-sandy layer with numerous phosphorite concretions (Fig. 3D–F), enclosed in a sandy "shell"; this is the so-called phosphorite horizon, varying in thickness between 10 and 30 cm. Nodule size varies between 5 and 25 cm; nodule shape varies from small and shapeless to large and loaf-shaped. The nodules contain the following fossils: ammonite shells (*Arcthoplites bogoslowski*, *A. gerassimovi*, *A.* sp. and others), bivalves (*Cyprina*, *Modiolus*, Pectinoida and others); small gastropods, rare echinoid tests (*Nucleolites* sp.) and stalk fragments of crinoids, as well as serpulids and decapod crustacean carapaces. The last-named are occasionally complete, but more often fragmentary. Wood is sometimes found in various states of preservation (Fig. 3G), as well as conglomeratic lenses with concretions. The conglomerate comprises numerous yellow and black quartz pebbles ranging in size from 0.5 to 2 cm.
3) A unit of green-grey glauconitic quartz, bioturbated cross-bedded sands around 40 cm in thickness.
4) A thin (15–25 cm) dark brown clayey sand layer.
5) A layer of dark green-grey quartz-glauconite sand with small (on average 2–5 cm) phosphorite concretions, spherical to elongated in shape. In one of the concretions, measuring about 15 cm in size, a single, indeterminate ammonite was found. The thickness of the layer is 3–5 cm.
6) A member of green-grey glauconite-quartz, cross-bedded bioturbated sands with clayey interbeds, the upper part of which is hidden by talus deposits.

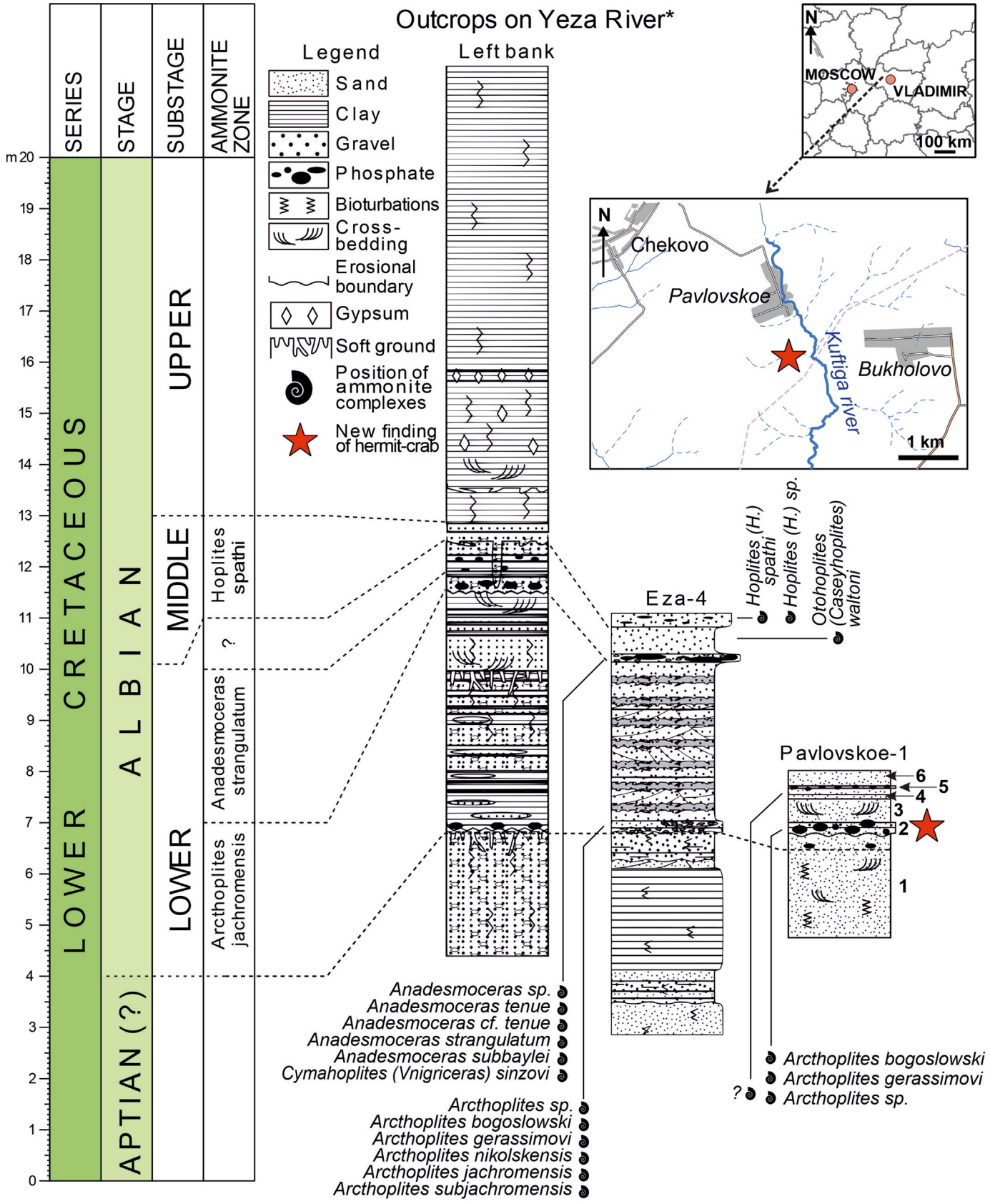

Fig. 2. Map of the locality Pavlovskoe-1 and stratigraphical position in correlation with the main sections along the River Yeza (modified from Baraboshkin et al., 2020).

Fig. 3. The locality of Pavlovskoe-1: **A, B**. main excavation; levels indicated by numbers; **C**. general view of the locality; **D**. searching for nodules (concretions); **E, F**. nodules (concretions); **G**. driftwood. The red star indicates the level of provenance of the type specimen of *Mutotylaspis tripudium* gen. et spec. nov.

4. Fossil assemblage and palaeoecological conditions

Fossils from Albian strata at Pavlovskoe-1 and other, coeval localities located nearby are quite diverse, representing various groups of marine biota (Fig. 4). Finds of polychaete worm tubes such as representatives of the genus *Parsimonia* (Fig. 4P) are common, as are other traces of worm-like, burrowing organisms. Molluscs include numerous bivalves (Fig. 4H–O) (*Cyprina*, *Modiolus*, *Oxytoma*, Pectinoida and others), indeterminate internal moulds and shells of gastropods and ammonites (Fig. 4A–G). The last-named are commonest and constitute a fairly large complex of numerous species and forms, such as *Arcthoplites gerassimovi*, *A. bogoslowskyi*, *A. jachromensis*, *A. subjachromensis*, *A.* sp., *Hoplites spathi*, *H. dentatus*, *H.* sp., *Otohoplites* (*Caseyhoplites*) *waltoni*, *Dimorphoplites* sp., *Anadesmoceras tenue*, *An.* cf. *tenue*, *An. strangulatum*, *An. subbaylei*, *An. costatum*, *An.* sp., *Cymahoplites* (*Vnigriceras*) *sinzovi*, *Lautihoplites* sp. and others.

Decapod crustacean remains are found at various outcrops and are confined mainly to the ammonite zone of *Arcthoplites jachromensis*. Basically, these are fragments of carapaces and claws. We

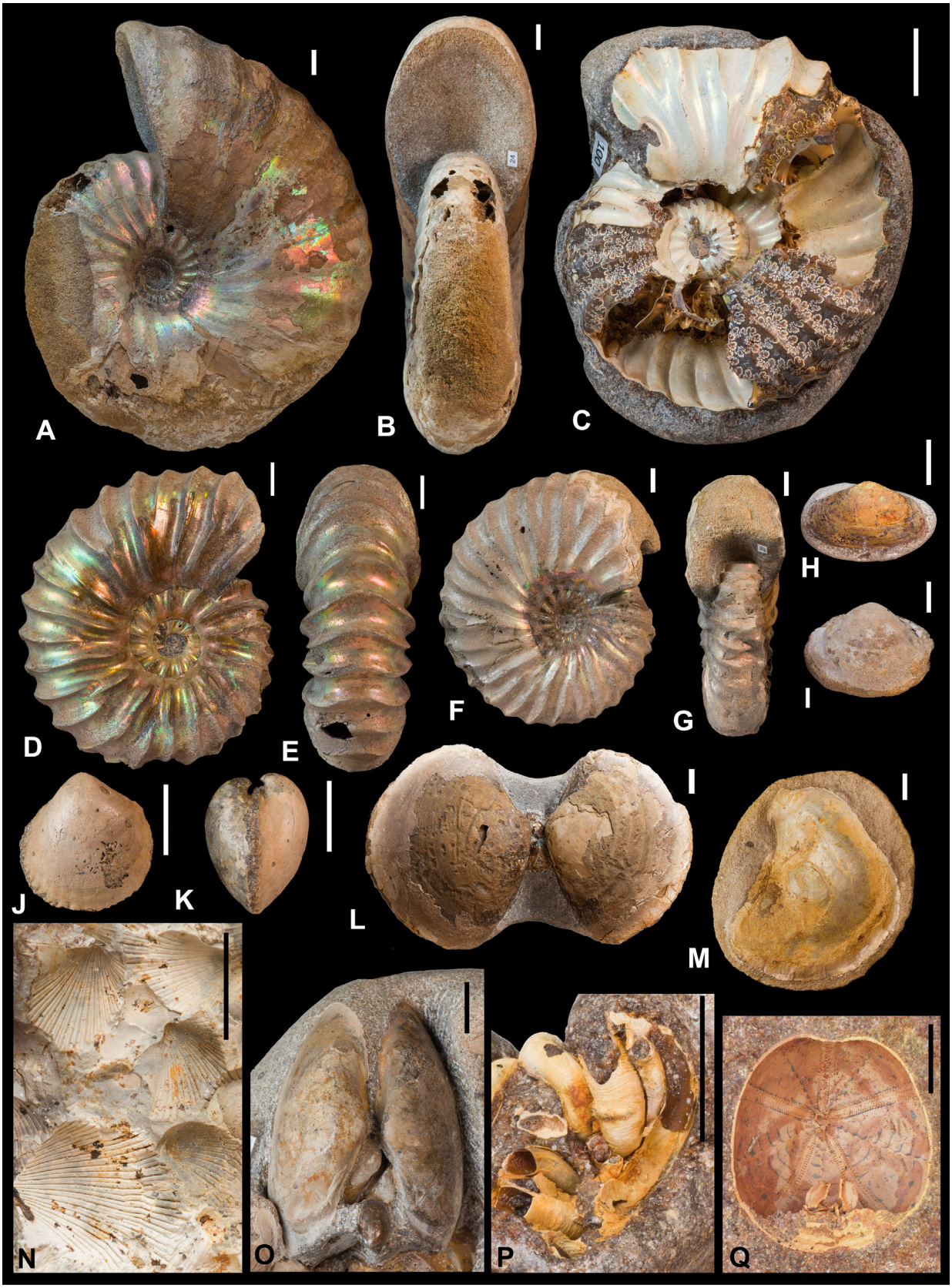

Fig. 4. Macrofossil taxa from the lower Albian at Pavlovskoe-1: **A-G**. ammonites; **A, B, F, G.** *Arcthoplites bogoslowskyi*; **C-E**. *A. gerassimovi*; **H-O**. bivalves (indeterminate); **P.** serpulid, *Parsimonia* sp; **Q**. echinoid, *Nucleolites solovjevi*. Specimens **A-P** stored in the personal collection of L.S.B.; **Q** – in the Regional Museum of Geography of Saratov State University (Saratov, Russia), №. SGU KEA 201.1/1-1; 201.1/1-2. Scale bar equals 10 mm.

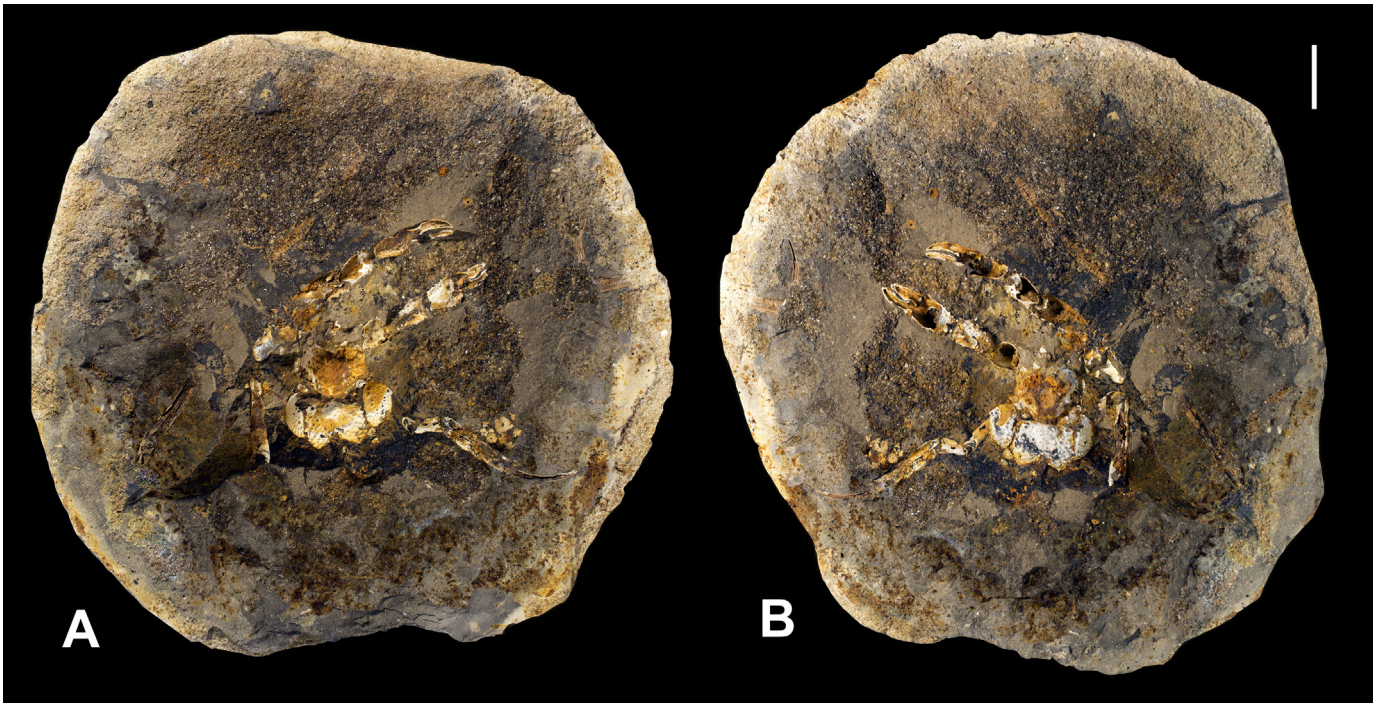

Fig. 5. Two halves (**A** – left and **B** – right) of a concretion (nodule) containing the type specimen (SVSR, ГМ-436) of *Mutotylaspis tripudium* gen. et spec. nov. Vladimir Oblast, Yuryev-Polsky district, right bank of the River Kuftiga, near the village of Pavlovskoe, locality Pavlovskoe-1, lower Albian (*Arcthoplites jachromensis* ammonite Zone). Scale bar equals 10 mm.

are also aware of an external mould of a carapace of *Glypheopsis* sp., in addition to the hermit crab carapace described herein. Sea urchins are represented by complete tests as well as fragments and casts of *Nucleolites solovjevi* (Fig. 4Q), described recently from this locality (Kalyakin and Barsukov, 2023). Concretions often contain both scattered segments and stems of various crinoids identified as isocrinids and comatulids, as well as fragments of starfish of the family Goniasteridae. Finally, there are remains of bony fish (scattered vertebrae, bones and scales), as well as rare remains of cartilaginous fish (teeth of ?*Paraorthacodus* and chimaeroid mandibular plate, in particular) and remains of marine reptiles such as a possible plesiosaur vertebra.

The rich ammonite assemblages and lithology of this section has made it possible to assess the water depth during deposition. During the early Albian, palaeodepth varied between 0 and 50 m, and conditions changed from calm coastal shallow water to mobile shallow water beyond bars and sand bars. During the middle Albian, depth increased to 50–100 m, and in the late Albian to 100–150 m (Baraboshkin and Nikulshin, 2006).

Numerous pieces of drift wood, inclusive of large fragments of trunks (up to 2 m in length; at Chekovo-1), indicate deposition of the levels studied relatively close to the coast. The shallow-water conditions are confirmed by examples of burrows of the *Skolithos* type, which suggest a high-energy setting close to shore.

5. Systematic palaeontology

Order Decapoda Latreille, 1802
Infraorder Anomura H. Milne Edwards, 1832
Superfamily Paguroidea Latreille, 1802
Family Probeebeidae Boone, 1926

Mutotylaspis gen. nov.

Type species. Mutotylaspis tripudium sp. nov., the sole species known to date.

Etymology. A combination of 'Muto', a giant parasitic monster (daikaiju) from the Godzilla universe that walks on four legs, and the generic name *Tylaspis*, for the extant paguroid that appears most closely related.

Diagnosis. Shield strongly convex, well calcified, length-to-width ratio of *approximately 1:1.5*, with distinct bulges (i.e., keraial and massetic regions) laterally, strong spinose ornament. Cervical and branchial grooves encompassing small branchial regions. Posterior carapace well calcified, broadly inflated, with dense spinose ornament. Well-developed cardiac grooves encompassing cardiac region. Chelipeds of similar size, dactylus and manus of third pereiopod of similar length.

Remarks. Amongst extant paguroids only the genera *Labidochirus* Benedict, 1892, *Probeebei* Boone, 1926, *Tisea* Morgan & Forest, 1991, and *Tylaspis* Henderson, 1885, have completely ornamented carapaces, similar the one of *Mutotylaspis* gen. nov. In none of the other hermit crab families recognised currently has a uniform ornamentation with tuberculate lateral margins been observed. Some other common characteristics of members of the family Probeebeidae include a very well-calcified posterior carapace and a dactylus and manus of the third pereiopod that are of similar length. Extant members of this family are amongst the most primitive of modern-day hermit crabs (Fraaije et al., 2022).

Mutotylaspis tripudium sp. nov.
Figs. 5A, B, 6A-C, 7

Material. Concretion, in two halves, with carapace and appendages; this is the **holotype**, housed in the State Vladimir Suzdal Reserve (Vladimir, Russia) under registration number SVSR, ГМ-436 (= GM-436). The specimen was recovered from the Vladimir Oblast (Yuryev-Polsky district), along the right bank of the River Kuftiga near the village of Pavlovskoe, locality Pavlovskoe-1; lower Albian (*Arcthoplites jachromensis* ammonite Zone). A cast of the holotype is deposited in the collections of the Oertijdmuseum (Boxtel, the Netherlands) under number MAB13846.

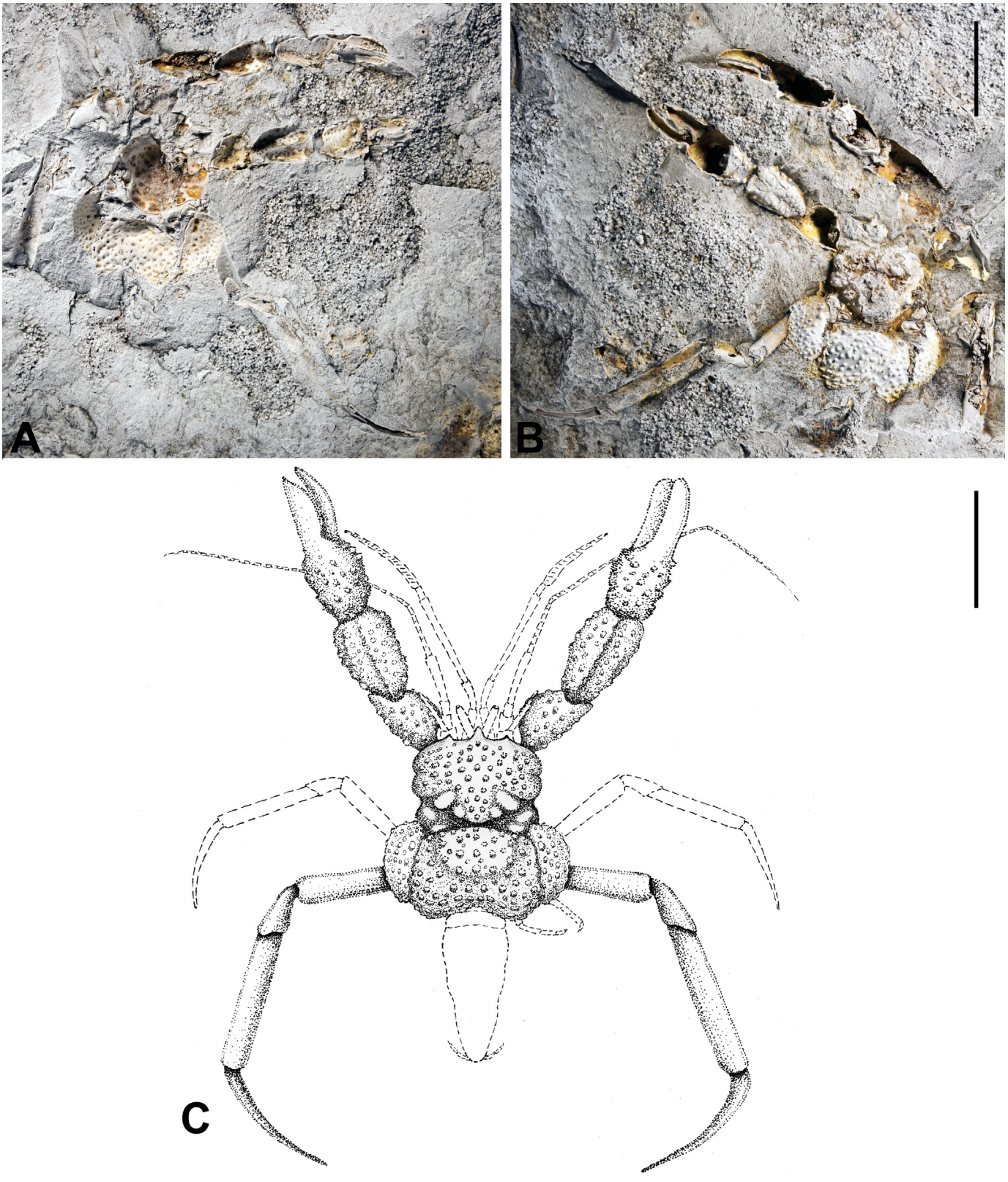

Fig. 6. *Mutotylaspis tripudium* gen. et sp. nov. **A, B**. Enlarged image of the type specimen, coated with ammonium chloride prior to photography. **C**. Reconstruction of the dorsal appearance of the new taxon by artist Yulia V. Kosheleva. Scale bar equals 10 mm.

Fig. 7. Artist's impression (by Sergey V. Krasovsky) of *Mutotylaspis tripudium* gen. et spec. nov., with an anemone on its abdomen at the bottom of the sea that flooded present-day Central Russia during the Albian.

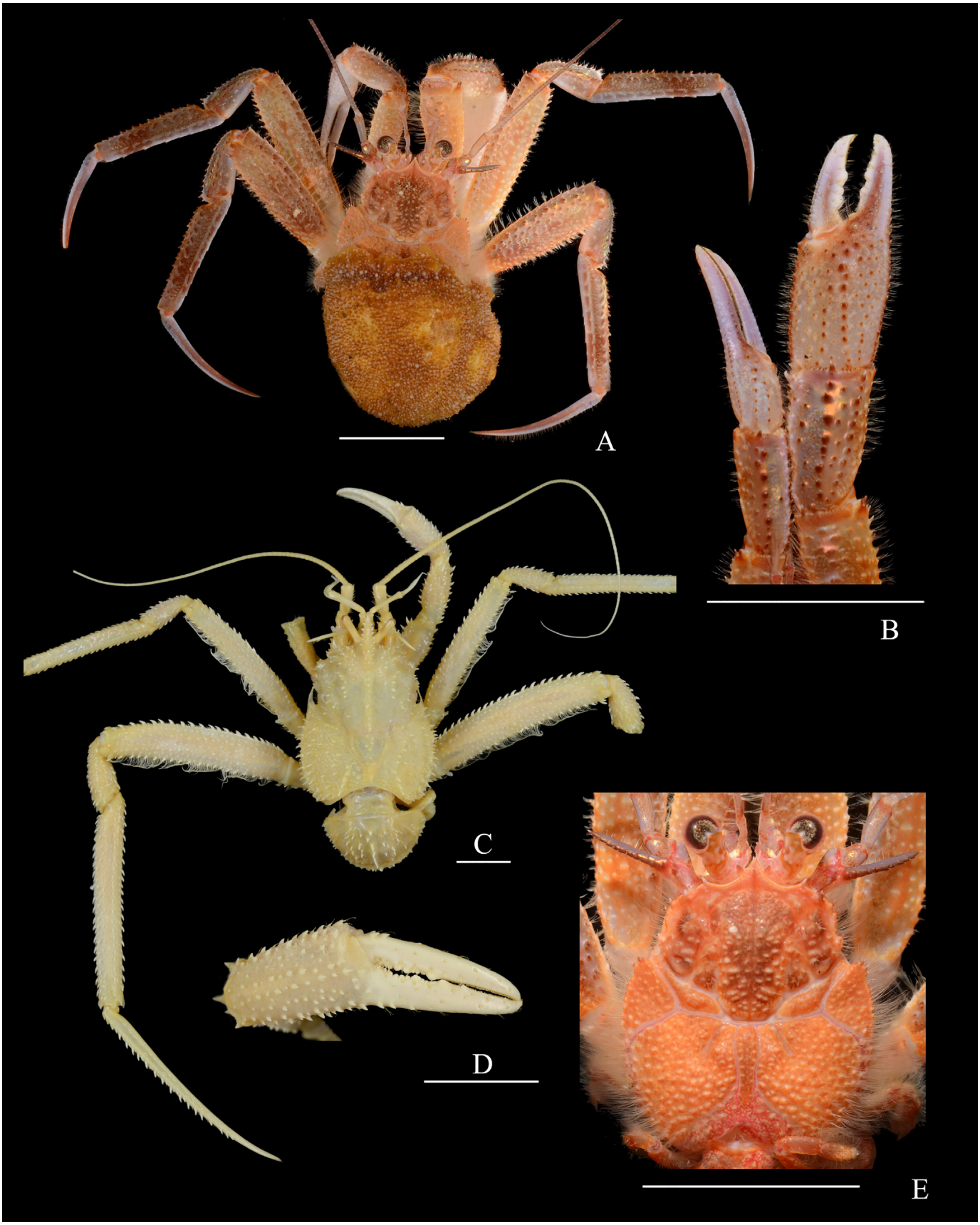

Fig. 8. A. *Labidochirus splendescens* (Owen, 1839) vicinity of San Juan Island, from the Florida Museum of Natural History collections (http://creativecommons.org/licenses/by-nc/3.0/), B. both chelipeds, E. carapace, C. *Probeebei mirabilis* from the Singapore collection (ZRC 1998.0006) provided by Peter K. Ng and Jose Christopher Escano Mendoza (both National University of Singapore), D. right cheliped. Scale bar equals 10 mm.

Etymology. From Latin '*tripudium*', meaning 'dancing', in reference to the way the paguroid sits within the concretion.

Diagnosis. As for genus.

Description. Shield strongly convex, about 1.5 times wider than long, well calcified, with distinct lateral bulges (i.e., keraial and massetic regions), strong spinose ornament. Rostrum with broad base; triangular post-orbital projections. Globose massetic region divided into two equal-sized parts by short groove. Keraial region also twofold, posterior part about one third the size of anterior part. Deep cervical and branchial grooves, encompassing small branchial regions. Posterior carapace well calcified, length about 0.5 times width, broadly inflated, with dense spinose ornament. Well-developed cardiac grooves encompassing broad, spherical and elevated cardiac region.

Chelipeds isochelous. Globose manus, carpus and merus, uniformly covered with coarse spines, arranged in irregular rows. Manus longer than broad, lateral and mesial sides rounded. Carpus about twice as long as wide. Merus longer than wide. Slender fingers smooth, subequal to length of manus, terminating in inwardly curved tips, cutting edges with irregularly sized teeth.

Ambulatory legs very long and slender, covered with rows of small spines; second walking leg (third pereopod) distinctly longer than others, dactylus as long as manus, carpus half the size of merus.

Remarks. In general morphology, the carapace of *Mutotylaspis tripudium* gen. et sp. nov. most closely resembles that of *Tylaspis anomala*, from which it differs in having a coarser carapace ornament, in particular on the shield, as well as in the possession of isochelous, rather than heterochelous, chelipeds. The new species differs from *Probeebei mirabilis* in having a rounded cardiac region (*vs* triangular), in lacking a central tuberculate ridge on the shield and cardiac region, and in having a straighter frontal area (*vs* triangular). Species of *Labidochirus* differ in having a more elongated, less globose posterior carapace with very elongated cardiac region. *Tisea grandis* may be differentiated on possessing a much larger elongated posterior carapace with a minute triangular cardiac region.

Labidochirus (Fig. 8A, B, E) is known from the Pacific Ocean at depths between 20 and 100 m (McLaughlin, 1974), while *Probeebei* (Fig. 8C, D) has been recorded from the same ocean at depths between 1145 and 4775 m and *Tylaspis* from between 2075 and 4344 m (Lemaitre, 1998; Arnés-Urgellés et al., 2020). In the Indian Ocean, *Tisea* has been documented from depths in excess of 250 m (Morgan and Forest, 1991). The presence of *Mutotylaspis tripudium* gen. et sp. nov., the ancestor of the closely related extant probeebeids, in the faunal assemblage described above indicates a shallow-marine setting, with water depths of between 0 and 50 m, i.e., a much shallower depth than all of its modern-day relatives.

6. Discussion

On the basis of a list of 'remnant' basal carapace characteristics, the family Probeebeidae has recently been resurrected and a Jurassic origin for these enigmatic paguroids has been suggested (Fraaije et al., 2022). Basal morphological characters of carapaces as observed in the fossil record are the presence of 1. a branchial groove; 2. a long rostrum; 3. a well-ornamented carapace; 4. a mid-dorsal ridge on the shield; 5. a mesogastric process; 6. a well-calcified posterior carapace; 7. a calcified, delineated cardiac region and 8. tuberculose lateral margins. Also considered basal in paguroids are isochelous chelipeds (Fraaije et al., 2022).

Unfortunately, the preservational state of the type specimen of *Mutotylaspis tripudium* gen. et sp. nov. offers no clues as to the structure of the rostrum and the mesogastric process or the mid-dorsal ridge, but all of the remaining five carapace characters are present. In addition, the new taxon has isochelous chelipeds. Biologists have previously assumed this group to represent advanced forms that evolved from shell-dwelling ancestors and considered carapace calcification to have evolved secondarily as a specialisation for a free-living lifestyle (Wolff, 1961; Richter and Scholtz, 1994). However, in 1998, Lemaitre (Lemaitre, 1998) had already hinted at another explanation for the asymmetry in abdominal tergites and pleopod condition in females of *P. mirabilis*. He suggested that it could represent a reproductive modification to egg-carrying, rather than a morphological trait retained from a shell-carrying ancestor. With the discovery of this mid-Cretaceous probeebeid paguroid the stratigraphical gap between the postulated (Late) Jurassic origin by Fraaije et al. (2022) and extant forms has been considerably shortened.

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