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Slika na naslovni strani: Novo opisani zgornjejurski fosilni rak samotar *Mesoparapylocheles janetjacksonae* iz Štramberka (Češka). Fosil je poimenovan po pevki Janet Jackson, saj spada v isto družino rakov samotarjev kot *Mesoparapylocheles michaeljacksoni*, ki je bil odkrit leta 2012.

Cover page: Newly described Upper Jurassic fossil hermit crab *Mesoparapylocheles janetjacksonae* from Štramberk (Czech Republic). The fossil is named after the singer Janet Jackson as it belongs to the same family of hermit crabs as *Mesoparapylocheles michaeljacksoni*, a fossil discovered in 2012.

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Editorial

This issue of Geologija focuses on new discoveries in the field of extinct decapod crustaceans, a group that evolutionarily ranks amongst the most successful multicellular organisms. They form a diverse assemblage of arthropods that are found in different habitats: shallow areas of continental shelves to deep ocean floors, but also occurring in rivers, lakes and cave systems; several species are even adapted to life on land. Due to their great economic importance, modern decapods have received more attention than other crustaceans within the biological sciences, while global palaeontological research into this group has never attained the high level of stratigraphical importance of other biota, such as molluscs. Fossil decapods were studied in detail during the first decades of the twentieth century, but after that the interest waned. Only from the 1970s, has there been a steady growth of scientific research in this field and there has been a remarkable increase in the activity of palaeontologists from the 1990s and continuing to the present day.

Currently, about 40 to 50 researchers from around the world, study fossil decapods. A small team of palaeontologists is responsible for the rapid advancement of our knowledge of the evolution of decapods. In spite of the good online connections amongst these researchers, the regular organisation of Symposia on Mesozoic and Cenozoic Decapod Crustaceans, every three years, is also crucial for sharing experiences and comparing research outcomes. The first meeting of the Working Group on Fossil Decapods was thus held at Montecchio Maggiore (Vicenza, Italy) in 2000 (First Workshop on Mesozoic and Tertiary Decapod Crustaceans, October 6-8, 2000). Subsequent symposia were then staged at Boxtel, the Netherlands (2003), Milan, Italy (2007), Eichstätt, Germany (2010), Kraków, Poland (2013) and Villers sur Mer, France (2016).

From the 17th to 21st of June 2019 we organised the 7th Symposium on Mesozoic and Cenozoic Decapod Crustaceans in Ljubljana, with the assistance of the Geological Survey of Slovenia, the Museum of Natural History of Slovenia and the Department of Geology at the Faculty of

Uvodnik

Tokratna številka Geologije je posvečena novim dognanjem v raziskavah izumrlih fosilnih rakov deseteronožcev, ki so evolucijsko ena od najbolj uspešnih skupin večceličnih organizmov. Tvorijo zelo raznoliko skupino členonožcev, ki naseljujejo različna bivalna okolja: plitva območja kontinentalnih polic in globoka morska dna oceanov, najti jih je moč v rekah, jezerih in jamskih sistemih, več vrst pa je prilagojenih tudi življenju na kopnem. Zaradi njihove velike ekonomske pomembnosti so sodobni deseteronožci znotraj bioloških znanosti deležni več pozornosti kot ostali raki. Kljub temu paleontološke raziskave deseteronožcev v svetovnem merilu nikoli niso dosegle pozornosti stratigrafsko pomembnih skupin kot so mehkužci. Fosilni deseteronožci so bili sicer deležni večje pozornosti raziskovalcev v prvih desetletjih dvajsetega stoletja, kasneje pa le redko. Od sedemdesetih let dalje lahko opazimo povečanje zanimanja znanosti na tem področju, izjemen porast aktivnosti paleontologov pri preučevanju fosilov deseteronožcev pa se je zgodil šele v devetdesetih letih prejšnjega stoletja in traja še danes.

Trenutno se s preučevanjem fosilnih deseteronožcev ukvarja okoli 40 do 50 raziskovalcev z vsega sveta. Majhna skupina paleontologov in dobra komunikacija je zaslužna za hiter napredek znanja o evoluciji deseteronožcev. Kljub dobri povezanosti teh raziskovalcev preko spleta, pa je za izmenjavo izkušenj in primerjavo zadnjih izsledkov ključna tudi redna organizacija tematskih simpozijev o fosilnih deseteronožcih (Symposium on Mesozoic and Cenozoic Decapod Crustaceans / simpozij o mezozojskih in kenozojskih rakih deseteronožcih), ki jih organiziramo vsaka tri leta. Prvo srečanje delovne skupine o fosilnih deseteronožcih je tako potekalo leta 2000 v Montecchio Maggiore – Vicenza v Italiji (Prva delavnica o mezozojskih in terciarnih rakih deseteronožcih, 6. - 8. oktober 2000). Ostali simpoziji so bili nato organizirani še v Boxtelu na Nizozemskem (2003), Milanu v Italiji (2007), Eichstättu v Nemčiji (2010), Krakowu na Poljskem (2013) ter v Villers sur Mer v Franciji (2016).

Med 17. in 21. junijem 2019 smo v Ljubljani organizirali že sedmi simpozij o mezozojskih in ke-

Natural Sciences and Engineering, University of Ljubljana. At the symposium, 44 researchers from as many as 17 countries presented scientific discoveries in the form of lectures and posters, and the meeting was held in a relaxed informal atmosphere. The participants left Slovenia armed with new ideas and new ties and greatly impressed, after having done fieldwork, with the geological diversity available in such a small area as Slovenia. After the presentation of preliminary data on the palaeobiological diversity of Slovenia's fossil decapods, it would appear almost unlikely that in Slovenia one can study fossil decapods from Late Triassic lagoons, across Jurassic coral reefs and into coastal environments of the Miocene Paratethys, and all of this within a distance of merely 100 km. Sometimes even Slovenian palaeontologists do not grasp the whole fossil diversity that lies within the country's sedimentary rocks.

In the present issue of Geologija, we are excited to present some of the research discussed at the symposium. Fraaije et al. record remains of hermit crabs of Tithonian to early Berriasian age from Štramberk, Czech Republic, which is one of the more diverse fossil paguroid faunas. New representatives of five families and five genera of hermit crabs are represented, including a species named after the singer/songwriter Janet Jackson and featured on the cover of this issue.

Late Jurassic decapods are also described in contributions by Schweigert et al. and Gašparič et al. The first focuses on two new types of erymid lobster from lagoonal limestone in Bavaria, Germany, and the second paper discusses a new type of squat lobster from reef olistolith in Slovenia. Mesozoic contributions are completed by González-León et al., who, based on the cuticle structure of the Early Cretaceous lobster *Atherfieldastacus magnus* from Mexico, have recognised differences between fossil corpses and moults of these.

In the following, Jakobsen et al. describe two new types of hermit crabs from Lower Paleocene levels at Faxe, Denmark. The only known example of a raninid crab from the renowned Eocene site 'Pesciara di Bolca' (Verona, Italy) is presented by Busulini et al., and De Angeli and Garassino describe a new species of *Neoliomera* from the Lower Eocene of northeastern Italy. Ossó and Domínguez, based on a new specimen of the species *Pyreneplax basaensis* from the Upper Eocene of Spain, revise its description and confirm placement in the family Vultocinidae. Decapods of Oligocene age are described by Marangon and

nozojskih rakih deseteronožcih (7th Symposium on Mesozoic and Cenozoic Decapod Crustaceans). Srečanje je potekalo s pomočjo Geološkega zavoda Slovenije, Prirodoslovnega muzeja Slovenije in Oddelka za Geologijo, Naravoslovnotehniške fakultete Univerze v Ljubljani. Na simpoziju je znanstvene izsledke v obliki predavanj in plakatov predstavilo 44 raziskovalcev iz kar 17 držav, srečanje pa je potekalo v sproščenem neformalnem vzdušju. Udeleženci so Slovenijo zapustili oboroženi z novimi idejami in stkanimi novimi vezmi ter navdušeni nad geološko pestrostjo, ki se skriva na tako majhni površini. Po predstavljenih predhodnih izsledkih o biološki pestrosti in raznolikosti fosilnih deseteronožcev Slovenije, se marsikomu zdi skoraj neverjetno, da lahko v Sloveniji na razdalji le nekaj 100 km raziskujemo fosilne deseteronožce od zgornjetriasnih lagun, preko jurskih koralnih grebenov pa vse do priobalnih okolij miocenskega morja Paratetide. Marsikje še ne poznamo fosilne pestrosti, ki se skriva v sedimentnih kamninah Slovenije.

V tokratni številki Geologije vam navdušeno predstavljamo nekatere izsledke raziskav, ki so bile predstavljene na simpoziju. Fraaije s sod. predstavlja ostanke rakov samotarjev tithonijske do spodnjeberriasijske starosti iz Štramberka na Češkem, ki se uvršča med najbolj raznolike fosilne paguroidne faune. Predstavljeni so novi predstavniki petih družin in petih rodov rakov samotarjev. Med njimi je tudi vrsta, ki so jo avtorji poimenovali po pevki Janet Jackson in krasi tudi naslovnico tokratne številke.

Zgornjejurske deseteronožce v svojih prispevkih predstavljata tudi Schweigert s sod. in Gašparič s sod. Prvi opisujejo dve novi vrsti erymidnih jastogov iz lagunskih ploščastih apnencev z Bavarske v Nemčiji, drugi prispevek pa obravnava novo vrsto raka skakača iz grebenskega olistolita v Sloveniji. Mezozojske prispevke zaključuje González-León s sod., ki so na podlagi strukture kutikule spodnjekrednega jastoga *Atherfieldastacus magnus* iz Mehike, prepoznali razlike med trupli in levi fosilnih deseteronožcev.

V nadaljevanju Jakobsen s sod. opiše dve novi vrsti rakov samotarjev iz spodnjepaleocenskih plasti v Faksu na Danskem. Edini do sedaj znani primerek raninidne rakovice iz znanega eocenskega nahajališča ‚Pesciara di Bolca' (Verona, Italija) predstavlja Busulini s sod., De Angeli in Garassino pa v prispevku opišeta novo vrsto *Neoliomere* iz spodnjega eocena severovzhodne Italije. Ossó in Domínguez na podlagi novega primerka vrste *Pyreneplax basaensis* iz zgornjega eocena Španije dopolnjujeta opis vrste in

De Angeli, who introduce a new genus and a new species of homolid crustacean from Lower Oligocene strata in the Ligurian-Piedmont Basin in northern Italy, while Hyžný et al. revise the crab *Plagiolophus sulcatus* and record a new specimen of this taxon from the Upper Oligocene of Trbovlje in Slovenia.

The paper by Wallaard et al. presents the first find of a Miocene age hermit crab shield from the Upper Miocene reefal limestones in Cyprus, on the basis of which they erect a new species that they name after Joe Collins, a prolific decapod crustacean workers from London, who passed away in 2019. Ossó et al. present new specimens of the Middle Miocene leucosioid crab *Iphiculus eliasi* from Catalonia, while the paper by Pasini et al. records new decapods from Lower Pleistocene levels at Poggi Gialli in Tuscany: two new species and a new genus are described, and an updated list of all fossil decapods from the site is added as well.

This issue on fossil and recent decapod crustaceans is completed by Spiridonov with a neontological contribution to an update of the phylogenetic reconstruction, classification and morphological characters of extant crabs of the superfamily Portunoidea. The paper combines the classification of extant and extinct material and introduces new subfamilies within the Carcinidae and Portunidae.

With the present issue of Geologija, the guest editors hope to bring as many readers as possible closer to the wonderful world of decapod crustaceans. There are still many challenges out there and ample room for passionate research by an increasing number of researchers around the world. A final word of thanks to all colleagues who assisted with the peer reviews of the various submissions.

Rok Gašparič, John W. M. Jagt,
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(guest editors)

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uvrstitev v družino Vultocinidae. Med fosilnimi deseteronožci oligocenske starosti Marangon in De Angeli predstavita nov rod in novo vrsto homolidnih rakov iz spodnjeoligocenskih plasti v Ligursko-piemontskem bazenu na severnu Italije, Hyžný s sod. pa revizijo rakovice *Plagiolophus sulcatus* in novi primerek iz zgornjega oligocena iz Trbovelj.

Wallaard s sod. v prispevku predstavlja prvo najdbo ščita raka samotarja miocenske starosti iz zgornjemiocenskih grebenskih apnencev na Cipru, na podlagi katere je opisana nova vrsta, poimenovana po leta 2019 preminulem raziskovalcu fosilnih rakov Joe Collinsu. Ossó s sod. predstavlja nove primerke leukosioidnih rakov *Iphiculus eliasi* srednjemiocenske starosti iz Katalonije. V prispevku Pasini s sod. pa beremo o novih deseteronožcih iz spodnjepleistocenskih plasti nahajališča Poggi Gialli v Toskani. Med najdbami sta opisani dve novi vrsti in nov rod, prispevku pa je dodan tudi posodobljen seznam vseh fosilnih deseteronožcev iz nahajališča.

Prvo letošnjo številko, posvečeno fosilnim in recentnim rakom deseteronožcem, zaključuje Spiridonov z neontološkim prispevkom o posodobitvi filogenetske rekonstrukcije, klasifikacije in morfoloških znakov recentnih rakovic iz družine Portunoidea. Prispevek združuje klasifikacijo neontološkega in paleontološkega materiala in predstavi novo poddružino Parathranitiinae znotraj družine Carcinidae in novo poddružino Achelouinae znotraj Portunidae.

Gostujoči uredniki upamo, da bomo s predstavljenimi prispevki v tej številki Geologije čim večjemu številu bralcev približali čudovit svet rakov deseteronožcev. Pri raziskavah le-teh nas še vedno čakajo številni izzivi in dovolj priložnosti za raziskovalno strast vedno večjega števila raziskovalcev po svetu. Na koncu bi se želeli zahvaliti vsem kolegom, ki so pomagali pri recenzijskih postopkih posameznih člankov.

Rok Gašparič, John W. M. Jagt,
Andreja Žibrat Gašparič & Luka Gale
(gostujoči uredniki)

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Paguroid anomurans from the upper Tithonian–lower Berriasian of Štramberk, Moravia (Czech Republic)

Zgornjethitonijski–spodnjeberiasijski raki samotarji iz Štramberka, Moravska (Češka)

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Ključne besede: Paguroidea, zgornjethitonijski–spodnjeberiasijski, Štramberk, Moravska, Češka republika

Abstract

Subsequent to a preliminary report on a handful of paguroid remains from the Tithonian (uppermost Jurassic) to lower Berriasian (Lower Cretaceous) Štramberk Limestone in Moravia (eastern Czech Republic), published in 2013, several field campaigns were organised by our research team during the summers of 2012–2015 and 2018. These resulted in the recovery of additional paguroid shields (or, anterior carapaces) that form the basis of the present study. The currently available material documents a diverse paguroid fauna. In fact, it ranks amongst the most diverse fossil paguroid assemblages known, following faunas from the upper Kimmeridgian of Nusplingen (southern Germany) and the Tithonian of Ernstbrunn (northeast Austria). New representatives of five families and five genera are described, named and illustrated, as follows: *Annuntidiogenes sagittula* sp. nov. (Diogenidae), *Protopagurus cerebellum* sp. nov. and *Protopagurus duopupae* sp. nov. (Paguridae), *Mesoparapylocheles janetjacksonae* sp. nov. (Parapylochelidae), *Masticacheles septemgradu* sp. nov. (Pilgrimchelidae) and *Ammopylocheles romankijoki* sp. nov. (Pylochelidae).

Izvleček

Po prvih poročilih o ostankih rakov samotarjev (Paguroidea) titonijske (zgornje jurske) do spodnje beriasijske (spodnje kredne) starosti iz apnencev v kamnolomu Štramberk na Moravskem (vzhodna Češka), ki so bila objavljena leta 2013, smo med leti 2012-2015 in poleti 2018 opravili več dodatnih terenskih raziskav. Pri raziskavah smo odkrili številne nove ščite (sprednje dele oklepa) rakov samotarjev, ki so predstavljeni v pričujočem članku. Opisan fosilni material predstavlja raznovrstno favno rakov samotarjev, ki se uvršča med najbolj raznolike znane fosilne paguroidne združbe, primerljive z zgornjo kimeridžijsko združbo regije Nusplingen (južna Nemčija) in titonijsko paguroidno združbo nahajališča Ernstbrunn (severovzhodna Avstrija). Opisani in predstavljeni so novi predstavniki petih družin in petih rodov rakov samotarjev: *Annuntidiogenes sagittula* sp. nov. (Diogenidae), *Protopagurus cerebellum* sp. nov. in *Protopagurus duopupae* sp. nov. (Paguridae), *Mesoparapylocheles janetjacksonae* sp. nov. (Parapylochelidae), *Masticacheles septemgradu* sp. nov. (Pilgrimchelidae) in *Ammopylocheles romankijoki* sp. nov. (Pylochelidae).

Introduction

The Štramberk Limestone, exposed along several exploitation levels at Kotouč quarry in the immediate vicinity of the town of Štramberk (Moravia, Czech Republic), comprises variably sized carbonate megablocks, breccias and conglomerates that represent deposition on a carbonate platform along the northern Tethyan margin in the area of the present-day Outer Western Carpathians during the latest Jurassic and earliest Cretaceous (Vašíček et al., 2018; Vaňková et al., 2019). In recent years, numerous macrofossils have been collected from this quarry thanks to an agreement between the VSB-Technical University of Ostrava and the management of Kotouč quarry. From about 1910 onwards, the quarry at Kotouč Hill has been the main source of macro- and microfossils that have been described in numerous palaeontological studies (see Vašíček & Skupien, 2004, 2005, 2019 for references). The reefal limestone facies at the quarry varies widely, ranging from very coarse-grained to gravelly layers or lenses, formed by e.g. molluscan shells and corals, to very fine-grained micritic limestones and (most commonly) fine-grained biodetrital limestones (e.g., Houša & Vašíček, 2005).

Fieldwork carried out by our research team in the Upper Jurassic–Lower Cretaceous reefal limestones at Kotouč quarry during the summers of 2012–2015 and 2018, has provided a highly diverse decapod crustacean fauna comprising remains of isopods, macrurans, anomurans, and brachyurans. Paguroid material collected during the first campaign was recorded in a preliminary paper; this included a handful of shields (or, portions of anterior carapaces) and a single sixth abdominal tergite (Fraaije et al., 2013). In 2015, Gašparič et al. described the galatheoid *Galatheites zitteli* (Moericke, 1889) from the infill of a test of a nucleolitid echinoid, collected in June 2014.

With at least 18 species, in eight families, the Tithonian (Late Jurassic) paguroid fauna from Ernstbrunn (Austria) is by far the most diverse fossil assemblage recorded to date. In second place, with 13 species in six families, follows that from Nusplingen (upper Kimmeridgian, southern Germany), just ahead of the assemblage described below, which comprises 11 species in seven families. Herein, we follow Vašíček & Skupien (2019) and Vaňková et al. (2019) for the stratigraphical placement of the material studied. Seven species are here recorded from the upper Tithonian, and four from the lower Berriasian part of the section exposed at Kotouč.

Material and methods

Specimens, usually only partially exposed, were mechanically prepared under a LOMO MBS-10 stereomicroscope, using needles and pneumatic airscribes of the types Hardy Winkler HW-1 and HW-70/3. Accidentally chipped pieces were glued back by Starbond super fast thin CA glue.

For photography, specimens were first dyed with black water colour, and when dry, coated with ammonium chloride, in order to gain maximum contrast of fine details. Specimens were photographed using a Canon digital SLR in aperture priority, Zeiss Luminar 100 mm and 63 mm macrolenses on a Nikon PB-4 bellows unit. A copy stand was used, and a Euromex coldlight source for illumination. Post-processing was done in GIMP 10.0; levels and curves were adjusted for white balance and contrast, the sharpness slightly enhanced with an ‘unsharp mask’.

Systematic palaeontology

We here adopt the carapace-based classification and descriptive terminology of extinct paguroids proposed by Fraaije (2014) and Fraaije et al. (2019). All material is contained in the collections of the Oertijdmuseum, Boxtel (the Netherlands; abbreviation: MAB).

Order Decapoda Latreille, 1802
Infraorder Anomura H. Milne Edwards, 1832
Superfamily Paguroidea Latreille, 1802
Family Annuntidiogenidae Fraaije, 2014
Genus *Annuntidiogenes* Fraaije, Van Bakel,
Jagt & Artal, 2008

Type species: *Annuntidiogenes ruizdegaonai* Fraaije, Van Bakel, Jagt & Artal, 2008, by original designation.

Included species: *Annuntidiogenes sagittula* sp. nov., *An. elongatus* Fraaije, Robins, Van Bakel, Jagt & Bachmayer, 2019, *An. hoelderi* Fraaije, Robins, Van Bakel, Jagt & Bachmayer, 2019, *An. jurassicus* Fraaije, 2014, *An. massetispinosus* Fraaije, Van Bakel & Jagt, 2017, *An. sunuciorum* Fraaije, Van Bakel, Jagt & Artal, 2008, *An. ruizdegaonai* and *An. worfi* Fraaije, Van Bakel, Jagt, Klompmaker & Artal, 2009.

Annuntidiogenes sagittula sp. nov.
(Pl. 1.1)

Diagnosis: Shield longer than wide, divided into distinct regions by grooves; long triangular rostrum extending beyond postocular and postantennal spines; convex postrostral ridge; scabrous ornament on anterior gastric region; long and wide central gastric groove forming arrow-shaped figure in conjunction with rostrum; elongated, bipartite massetic region; pronounced triangular anterior branchial area; posterior intragastric grooves parallel to cervical groove.

Derivation of name: Latin *sagittula*, meaning small arrow, in reference to the typical arrowhead shape of the central anterior groove in conjunction with the triangular rostrum.

Type material: The holotype, and sole specimen known to date (MAB k.3631), is a near-complete shield; as preserved, maximum carapace length measures 4.0 mm, maximum shield width is 3.0 mm.

Type locality and type level: Kotouč quarry (Štramberk, Moravia, Czech Republic), level 5; lower Berriasian (see Vašíček & Skupien, 2019, p. 39, fig. 3, locality 10; Vaňková et al., 2019, section B, layer B22).

Description: Shield longer than wide (L/W ratio 1.14), divided into distinct regions by grooves; long, spinose and ridged triangular rostrum extending beyond postocular and postantennal spines; very shallow convex orbital and antennal cavities; convex postrostral ridge; long and wide central gastric groove, forming arrowhead-shaped configuration in conjunction with triangular rostrum; scabrous ornament on anterior gastric region, central gastric groove not extending posteriorly; elongated, bipartite massetic region; small, elongated keraial region; pronounced triangular anterior branchial area; posterior intragastric grooves parallel to cervical groove.

Remarks: Intragastric grooves (also known as Y-linea in extant paguroids) are parallel to the cervical groove; this is a unique feature shared by representatives of the family Annuntidiogenidae. *Annuntidiogenes sagittula* sp. nov. can be distinguished from all congeners known to date by the unique combination of a very wide central anterior gastric groove, a bipartite massetic region and a triangular, ridged rostrum; in conjunction with the gastric groove, this forms a typical arrowhead shape.

Family Diogenidae Ortmann, 1892

Genus *Bachmayerus* Fraaije, Van Bakel, Jagt & Skupien, 2013

Type species: *Bachmayerus cavus* Fraaije, Van Bakel, Jagt & Skupien, 2008, by original designation.

Bachmayerus cavus Fraaije, Van Bakel, Jagt & Skupien, 2013

(Pl. 1.2)

Type locality and type level: Kotouč quarry (Štramberk, Moravia, Czech Republic), level 7; upper Tithonian (see Vašíček & Skupien, 2019, p. 39, fig. 3).

Type material: The holotype, and sole specimen known to date (MAB k.3631), is a near-complete shield; as preserved, maximum carapace length measures 4.0 mm, maximum shield width is 3.0 mm.

Remarks: For a detailed description, reference is made to Fraaije et al. (2013).

Genus *Eopaguropsis* Van Bakel, Fraaije, Jagt & Artal, 2008

Type species: *Eopaguropsis loercheri* Van Bakel, Fraaije, Jagt & Artal, 2008, by original designation.

Eopaguropsis cf. ***nidiaquilae*** Fraaije, Krzemiński, Van Bakel, Krzemińska and Jagt, 2012

(Pl. 1.3)

Locality and level: Kotouč quarry (Štramberk, Moravia, Czech Republic), level 6; upper Tithonian (see Vašíček & Skupien, 2019, p. 39, fig. 3, locality 3).

Material: The specimen (MAB k.3759), is an incomplete shield; as preserved, maximum carapace length measures 7.0 mm, maximum shield width is 5.0 mm.

Remarks: For a detailed description, reference is made to Fraaije et al. (2012c).

Family Gastrodoridae Van Bakel, Fraaije, Jagt & Artal, 2008

Genus *Gastrodorus* von Meyer, 1864

Type species: *Gastrodorus neuhausensis* von Meyer, 1864, by monotypy.

Included species: *Gastrodorus bzowiensis* Krzemińska, Krzemiński, Fraaije, Van Bakel & Jagt, 2015, *G. cretahispanicus* Klompmaker, Artal, Fraaije & Jagt, 2011, *G. kotoucensis* Fraaije, Van Bakel, Jagt & Skupien, 2013 and *G. neuhausensis* von Meyer, 1864.

Gastrodorus kotoucensis Fraaije, Van Bakel, Jagt & Skupien, 2013
(Pl. 1.4)

Type locality and type level: Kotouč quarry (Štramberk, Moravia, Czech Republic), level 7; upper Tithonian (see Vašíček & Skupien, 2019, p. 39, fig. 3).

Remarks: For a detailed description, reference is made to Fraaije et al. (2013).

Family Paguridae Latreille, 1802
Genus *Protopagurus* Fraaije, Robins, Van Bakel, Jagt & Bachmayer, 2019

Type species: *Protopagurus janoscheki* Fraaije, Robins, Van Bakel, Jagt & Bachmayer, 2019, by original designation.

Included species: *Protopagurus janoscheki*, *Protopagurus cerebellum* sp. nov. and *Protopagurus duopupae* sp. nov.

Remarks: To date, we are unaware of any representative of the family Paguridae from Oxfordian and Kimmeridgian strata, in spite of intensive fieldwork in southern Germany and southern Poland over several years. The oldest known pagurid has recently been described from the middle to lower upper Tithonian of Ernstbrunn (Austria; see Fraaije et al., 2019). The new taxa from the lower Berriasian of Moravia appear to substantiate the notion that this group rose to dominance during the latest Jurassic (and up to the present day) and ousted the more ancient groups of symmetrical hermit crabs.

Protopagurus duopupae sp. nov.
(Pl. 1.5)

Diagnosis: Well-areolated shield, slightly longer than wide; large, elongated massetic region, anteriorly covered with scale-like ornamentation; shallow central gastric groove centrally indenting convex postfrontal ridge; anterior part of gastric region covered with scale-like ornamentation; thin, elongated anterior branchial area; well-delineated, reniform keraial region; shield irregularly covered with (setal) pores.

Derivation of name: Latin *duo* and *pupa* (-*e*), a noun in apposition, or two puppets, in allusion to the morphology of the gastric region.

Type material: The holotype, and sole specimen known to date (MAB k.3626), is an incomplete shield of a maximum carapace length, as preserved, of 12.0 mm; the maximum shield width is 13.0 mm.

Type locality and type level: Kotouč quarry (Štramberk, Moravia, Czech Republic), level 5; lower Berriasian (see Vašíček & Skupien, 2019, p. 39, fig. 3, locality 10; Vaňková et al., 2019, section B, layer B22).

Description: Well-areolated shield, slightly longer than wide; large, elongated massetic region, anteriorly covered with scale-like ornamentation, posteriorly covered with broad, shallow, pitted furrow slightly curving from anteriormost keraial region to mid-massetic edge; shallow central gastric groove centrally indenting convex postfrontal ridge; anterior part of gastric region covered with scale-like ornamentation; posteriorly a row of large pits is forming subtransverse furrow; thin, elongated anterior branchial area; well-delineated, reniform keraial region; shield irregularly covered with (setal) pores. Frontal area and posteriormost part of shield not preserved.

Protopagurus cerebellum sp. nov.
(Pl. 2.1)

Diagnosis: Well-areolated shield, slightly longer than wide; convex orbital cavity, ending in triangular postocular projection; large, elongated massetic region, with large pores; central gastric groove centrally indenting convex postfrontal ridge; anterior part of gastric region covered with brain-like ornamentation; thin, elongated anterior branchial area; small, reniform keraial region; shield irregularly covered with (setal) pores.

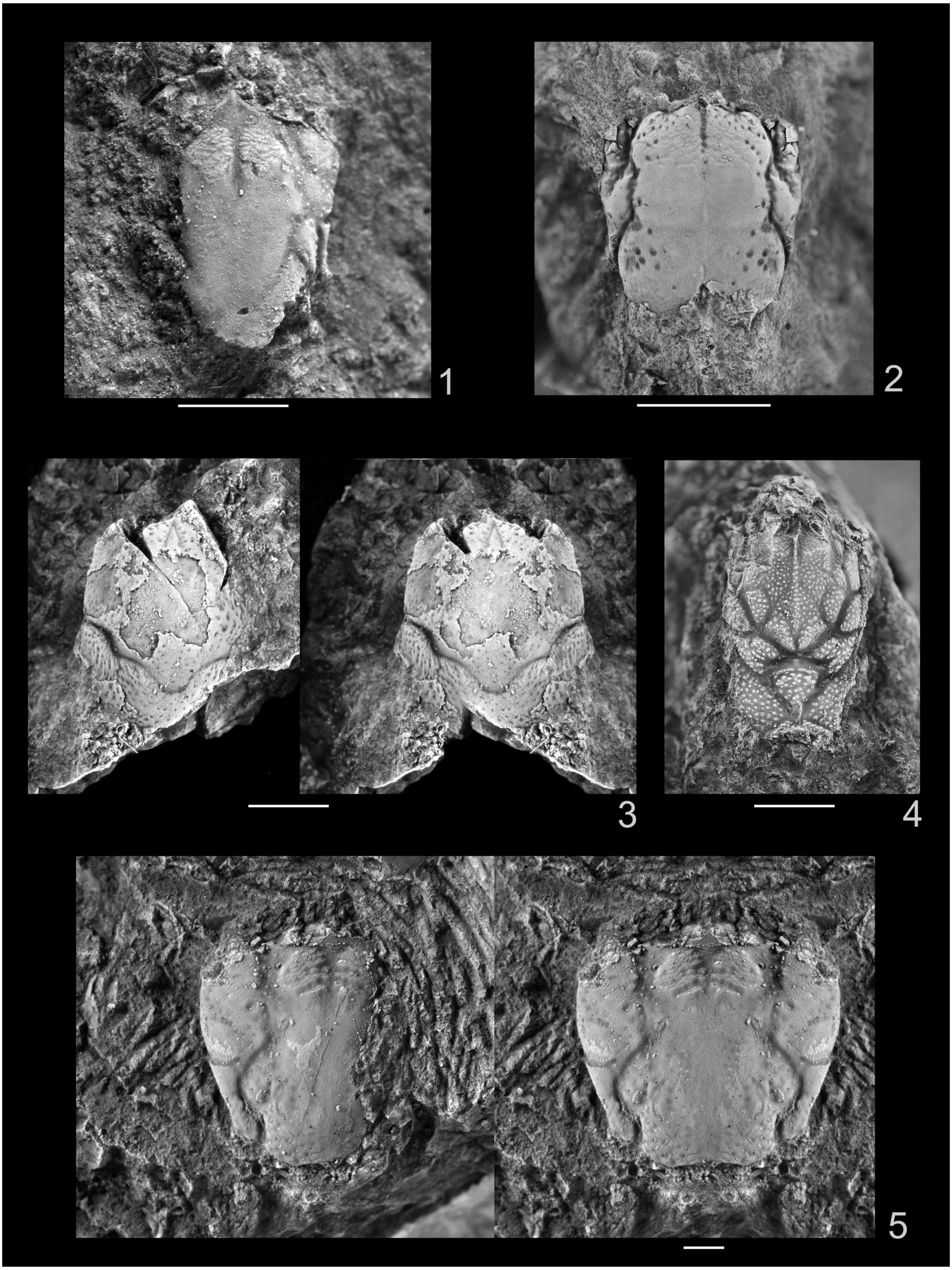
Derivation of name: Latin *cerebellum*, or brains (noun used in apposition), referring to the brain-like ornament of the anterior gastric region.

Type material: The holotype, and sole specimen known to date (MAB k.3628), is a near-complete shield of a maximum carapace length, as preserved, of 3.0 mm; the maximum shield width is 3.0 mm.

Type locality and type level: Kotouč quarry (Štramberk, Moravia, Czech Republic), level 5; lower Berriasian (see Vašíček & Skupien, 2019, p. 39, fig. 3, locality 10; Vaňková et al., 2019, section B, layer B22).

Description: Well-areolated shield, longer than wide; rostrum not preserved; convex orbital cavity with smooth rim, ending in triangular postocular projection; large, elongated massetic region, irregularly covered with large pores, also on anterior lateral edge; central gastric groove centrally indenting convex postfrontal ridge; an-

PLATE 1



1 – ***Annuntidiogenes sagittula*** sp. nov.;
2 – ***Bachmayerus cavus*** Fraaije, Van Bakel, Jagt & Skupien, 2013;
3 – ***Eopaguropsis cf. nidiaquilae*** Fraaije, Krzemiński, Van Bakel, Krzemińska and Jagt, 2012, original (left), composite (right);
4 – ***Gastrodorus kotoucensis*** Fraaije, Van Bakel, Jagt & Skupien, 2013;
5 – ***Protopagurus duopupae*** sp. nov., original (left), composite (right); all scale bars 2 mm.

terior part of gastric region covered with brain-like ornamentation, posteriorly ending convexly; thin, elongated anterior branchial area; small, reniform keraial region; shield irregularly covered with (setal) pores.

Family Parapylochelidae Fraaije, Klompmaker & Artal, 2012a

Genus *Housacheles* Fraaije, Van Bakel, Jagt & Skupien, 2013

Type species: *Housacheles timidus* Fraaije, Van Bakel, Jagt & Skupien, 2013, by original designation.

Housacheles timidus Fraaije, Van Bakel, Jagt & Skupien, 2013

(Pl. 2.2)

Type locality and type level: Kotouč quarry (Štramberk, Moravia, Czech Republic), level 5 (see Vašíček & Skupien, 2019, p. 39, fig. 3).

Remarks: For a detailed description, reference is made to Fraaije et al. (2013).

Genus *Mesoparapylocheles* Fraaije, Klompmaker & Artal, 2012a

Type species: *Mesoparapylocheles michaeljacksoni* Fraaije, Klompmaker & Artal, 2012a, by original diagnosis.

Included species: *Mesoparapylocheles jaegeri* Fraaije, 2014, *M. michaeljacksoni*, *M. schweigerti* Fraaije, 2014, *M. strouhali* Fraaije, Robins, Van Bakel, Jagt & Bachmayer, 2019 and *M. zapfei* Fraaije, Robins, Van Bakel, Jagt & Bachmayer, 2019.

Mesoparapylocheles janetjacksonae sp. nov.

(Pl. 2.3)

Diagnosis: Shield well calcified, longer than wide, well areolated; globose massetic region; prominent triangular rostrum; triangular postocular spines. Gastric region of arrowhead shape, pointing posteriorly. Distinct and complete U-shaped branchiocardiac groove, parallel to V-shaped cervical groove.

Derivation of name: Named after Janet (Damita Jo) Jackson, well-known American singer, songwriter, actress, dancer and sister of the late Michael Jackson after whom the first member of this genus was named.

Type material: The holotype, and sole specimen known to date (MAB k.3623a, b), is a near-complete carapace of a maximum carapace length, as preserved, of 5.0 mm; the maximum shield width is 3.5 mm.

Type locality and type level: Kotouč quarry (Štramberk, Moravia, Czech Republic), level 7; upper Tithonian (see Vašíček & Skupien, 2019, p. 39, fig. 3).

Description: Well-calcified, smooth, areolated shield, subcylindrical transversely, slightly convex longitudinally; pronounced, slightly downarched triangular rostrum, base wider than long, slender spinose tip; ocular-frontal area exceeding half of total maximum width; orbital cavity subcircular, bounded by distinct triangular postocular spines; thin, central gastric groove centrally indenting convex postfrontal ridge; gastric region of arrowhead shape, pointing posteriorly with a pair of gastric pits close to keraial region; elongated keraial region with straight lateral margin; prominent, reniform, globose massetic region; cardiac region anteriorly not delineated; elongated mesobranchial region with deep incision centrally running parallel to cervical groove; distinct U-shaped branchiocardiac groove, parallel to deep, V-shaped cervical groove.

Remarks: *Mesoparapylocheles janetjacksonae* sp. nov. differs from all other Jurassic paguroids in the combination of an elongated keraial region with a straight, rather than convex, lateral margin; a narrower reniform, rather than broader, trapezoidal, massetic region, as well as a very convex postfrontal ridge. The new species differs from the mid-Cretaceous *M. michaeljacksoni* in having elongated keraial and massetic regions (rather than globose ones) and a cardiac region that is not posteriorly delineated as in *M. michaeljacksoni*.

Family Pilgrimchelidae Fraaije, 2014

Genus *Masticacheles* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2014

Type species: *Masticacheles longirostris* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2014, by original diagnosis.

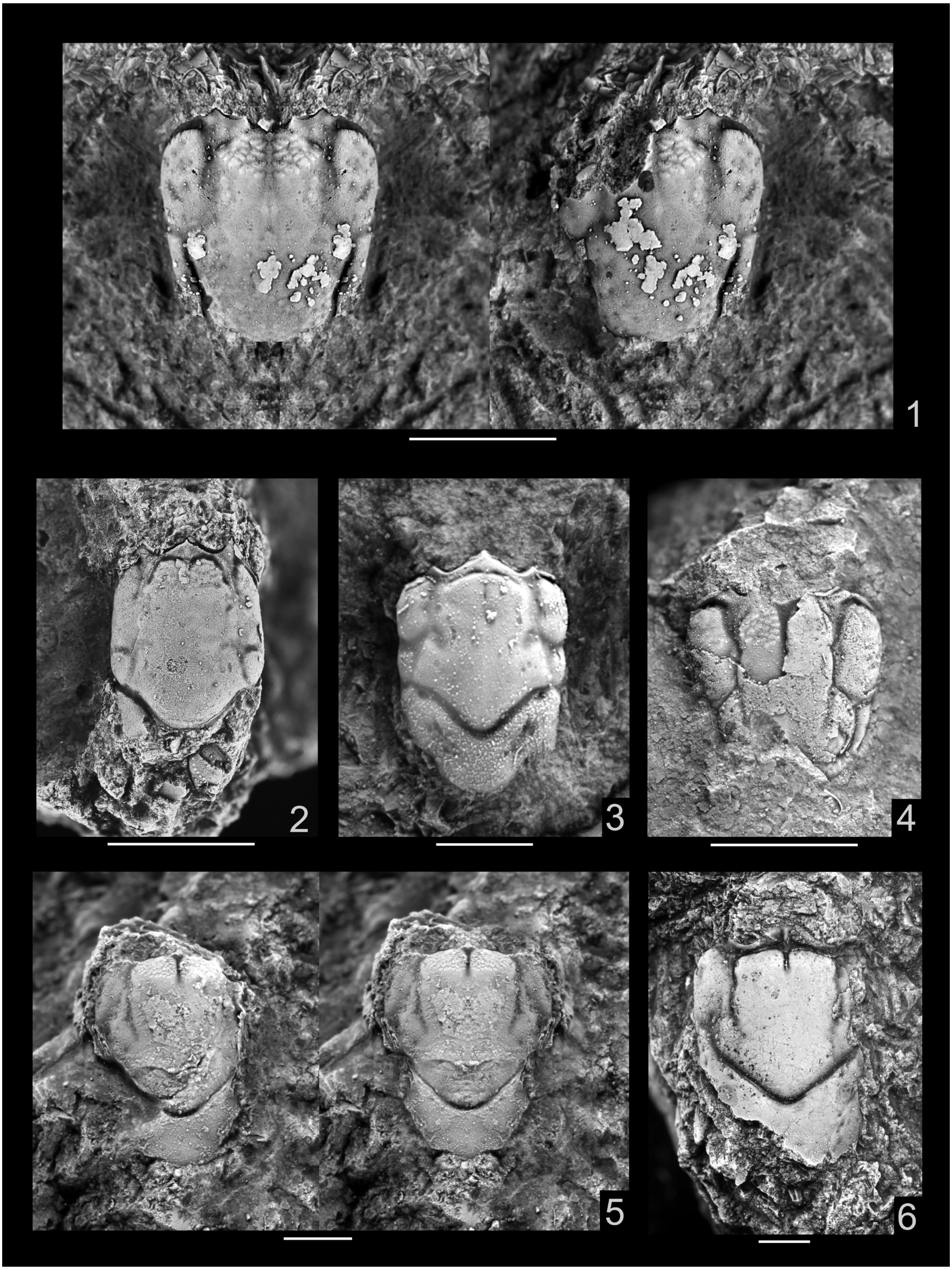
Included species: *Masticacheles longirostris* and *Masticacheles minimus* Fraaije, 2014 and *Masticacheles septemgradu* sp. nov.

Masticacheles septemgradu sp. nov.

(Pl. 2.4)

Diagnosis: Shield well calcified, well areolated, with distinct regions; convex orbital cav-

PLATE 2



1 – ***Protopagurus cerebellum*** sp. nov., original (right), composite (left);
2 – ***Housacheles timidus*** Fraaije, Van Bakel, Jagt & Skupien, 2013;
3 – ***Mesoparapylocheles janetjacksonae*** sp. nov.;
4 – ***Masticacheles septemgradu*** sp. nov.;
5 – ***Ammopylocheles mclaughlinae*** Van Bakel, Fraaije, Jagt & Artal, 2008, original (left), composite (right);
6 – ***Ammopylocheles romankijoki*** n. sp.; all scale bars 2 mm.

ity with sharp postocular projection, convex post-rostral ridge centrally indented by long central groove; anterior part of gastric region crenulated; large, elongated massetic region; crescent keraial region; narrow anterior branchial area.

Derivation of name: Named after 'Level 7' at Kotouč quarry (see e.g., Vašíček & Skupien, 2019, fig. 3); Latin *septem* and *gradu*, noun used in apposition.

Type material: The holotype, and sole specimen known to date (MAB k.3757), is an incomplete shield of a maximum carapace length, as preserved, of 2.5 mm; the maximum shield width is 2.5 mm.

Type locality and type level: Kotouč quarry (Štramberk, Moravia, Czech Republic), level 7; upper Tithonian (see Vašíček & Skupien, 2019, p. 39, fig. 3).

Description: Well-calcified and clearly areolated shield, convex transversely, slightly convex longitudinally; convex orbital cavity bordered with sharp postocular projection; ocular-frontal area equalling about 60 per cent of total maximum width; convex post-rostral ridge centrally indented by long central groove; anterior part of gastric region crenulated; prominent, globose and elongated massetic region; crescent keraial region laterally convex with its anterior tip centrally/forwardly directed; relatively narrow anterior branchial area; rostrum and posterior part of carapace not preserved.

Remarks: Until now, the family Pilgrimchelidae appeared to be confined to the Jurassic, to be replaced subsequently by, for instance, annuntidiogenids. *Masticacheles septemgradu* sp. nov. can be differentiated from congeners by the typical crescentic morphology of the keraial region, with its anterior tip directed centrally/forwardly rather than laterally/forwardly, as well as a narrower anterior branchial area.

Family Pylochelidae Bate, 1888
Subfamily Trizochelinae Forest, 1987
Genus *Ammopylocheles* Van Bakel, Fraaije, Jagt & Artal, 2008

Type species: *Ammopylocheles mclaughlinae* Van Bakel, Fraaije, Jagt & Artal, 2008, by original designation.

Included species: *Ammopylocheles mclaughlinae*, *Am. petersi* Fraaije, 2014, *Am. robertboreki* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2012b and *Am. romankijoki* sp. nov.

Ammopylocheles mclaughlinae Van Bakel, Fraaije, Jagt & Artal, 2008
(Pl. 2.5)

Locality and level: Kotouč quarry (Štramberk, Moravia, Czech Republic), level 8; upper Tithonian (see Vašíček & Skupien, 2019, p. 39, fig. 3).

Material: The specimen (MAB k.3760) is an incomplete shield with part of the posterior carapace; as preserved, maximum carapace length measures 7.0 mm, maximum shield width is 5.5 mm.

Remarks: For a detailed description, reference is made to Van Bakel et al. (2008). Members of the genus *Ammopylocheles* range from the middle Oxfordian (Fraaije et al., 2012b) to the lower Berriasian (the present study). *Ammopylocheles mclaughlinae* is by far the commonest element in Kimmeridgian deposits at Nusplingen (Fraaije, 2014) and at Geisingen (Van Bakel *et al.*, 2008) in southern Germany, but it is rather uncommon to rare at Ernstbrunn (Austria). The same appears to hold true for Štramberk.

Ammopylocheles romankijoki n. sp.
(Pl. 2.6)

Diagnosis: Typical smooth carapace of pylochelid; carapace longer than broad, shield of equal width and length; broad rostrum and convex, rimmed orbital cavity; pronounced postfrontal ridge, centrally indented by deep, short central gastric groove; elongated massetic region; reniform keraial region, distinct V-shaped cervical groove.

Derivation of name: Named after Roman Kijok (Poland), who collected the specimen and kindly donated it to the Oertijdmuseum, Boxtel.

Type material: The holotype, and sole specimen known to date (MAB k.3758), is a near-complete shield with part of the posterior carapace, measuring 10.0 mm in maximum total length and 7.0 mm in width.

Type locality and type level: Kotouč quarry (Štramberk, Moravia, Czech Republic), level 5; lower Berriasian (see Vašíček & Skupien, 2019, p. 39, fig. 3, locality 10; Vaňková et al., 2019, section B, layer B22).

Description: Carapace longer than broad, shield as wide as long, strongly convex in transverse section, slightly convex in longitudinal section; broad rostrum posteriorly extending into pronounced central ridge, effacing towards central gastric groove; broad and convex, rimmed orbital cavity; postantennal projections obtuse;

transverse, convex, post-rostral ridge, with few large pores, medially subdivided by a short, deep, central gastric groove; elongated, more or less oval massetic region; subrounded keraial region not well delineated, about one third size of massetic region; deep V-shaped cervical groove, posterior part of carapace less well calcified (partially preserved), smooth with irregularly distributed large (setal) pores.

Remarks: This new species, of early Berriasian age, is the youngest member of the genus. It differs from its middle Oxfordian congener *A. robertboreki* in having a larger, wider rostrum, a shorter central gastric groove and a more clearly V-shaped cervical groove. *Ammopylocheles romankijoki* sp. nov. differs from *A. mclaughlinae* in having a much larger massetic region, a wider and more pronounced rostrum and a more angular V-shaped cervical groove. The new species differs from *Am. petersi* in having a much smaller and more subrounded keraial region, in lacking ornament on the anterior and posterior gastric regions and in having a more angular V-shaped cervical groove.

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New erymid lobsters from the Nusplingen and Usseltal formations (Upper Jurassic) of southwest Germany

Novi jastogi iz družine Erymidae iz formacij Nusplingen in Usseltal (zgornja jura) iz jugozahodne Nemčije

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Ključne besede: dekapodni raki, Erymidae, kimmeridgij, tithonij, litografski apnenec, tafonomija

Abstract

Two new species of Late Jurassic erymid lobsters, *Stenodactylina devillezi* sp. nov. and *Stenodactylina geigerae* sp. nov., are described on the basis of isolated, but well-preserved chelipeds from the upper Kimmeridgian of Swabia and the lower Tithonian of Bavaria, respectively. The incomplete nature of the material indicates that these lobsters were not autochthonous elements of the Plattenkalk lagoons, but resulted from predation in nearby shallow-water settings.

Izvleček

V prispevku predstavljamo dve novi vrsti zgornjejurskih jastogov iz družine Erymidae, to sta *Stenodactylina devillezi* sp. nov. in *Stenodactylina geigerae* sp. nov. Novi vrsti sta opisani na podlagi izoliranih, vendar dobro ohranjenih škarnikov iz zgornjega kimmeridgija Švabske in spodnjega tithonija Bavarske. Slabša ohranjenost primerkov kaže, da tovrstni jastogi niso bili avtohtoni prebivalci zgornjejurskih lagun, ampak so verjetno poseljevali bližnja plitvovodna okolja.

Introduction

The Upper Jurassic Solnhofen-type lithographic limestones (“plattenkalks”) of southwest Germany are renowned for their exceptionally preserved fossils, making them one of the classic examples of conservation Fossillagerstätten (Seilacher et al., 1985). In addition to iconic vertebrate fossils such as the ancient bird *Archaeo-pteryx* von Meyer, 1861, hundreds of taxa have been recorded over the centuries (e.g., Leich, 1968; Barthel et al., 1990; Frickhinger, 1994, 1999; Arratia et al., 2015). However, it should be noted that fossils labelled “Solnhofen” come from various deposits of different lithology and age (Schweigert, 2007, 2015a). Decapod crustaceans from these lithographic limestones, and erymid lobsters in particular, have been described from the early 19th century onwards (e.g., Desmarest, 1817, 1822; von Schlotheim, 1822; zu Münster, 1839; Oppel, 1861, 1862). More recently, Beurlen (1928) and Förster (1966) studied Jurassic erymids. However, some of their systematic assignments remained questionable. Taxa based on material from shallow-water deposits consist either of carapace remains or of isolated chelae. More complete specimens, with the carapace and corresponding chelae preserved, are only found when conditions were favourable or within concretions (e.g., Hyžný et al., 2015). At generic level, erymid lobsters are distinguished mainly by their characteristic carapace groove pattern (Devillez & Charbonnier, 2017, 2019, 2020; Devillez et al., 2018), while chela shape is less characteristic, at least in *Eryma* s. str. In the latter, there is one clade that has chelae with relatively short fingers; this group is distinguished from another with strikingly longer, straight fingers, although the groove pattern of the carapace is the same. As a result, some species of *Eryma* of the second clade, previously included in a distinct genus, *Erymastacus* Beurlen, 1928 (see Hyžný et al., 2015), have later been considered to belong to *Eryma* s. str. (Devillez & Charbonnier, 2017, 2019, 2020). However, there are further taxa that have long and curved fingers, but a different groove pattern on their carapace. These are now included in the genus *Stenodactylina* Beurlen, 1928. Remains of *Stenodactylina* are easily recognised on the basis of their chelae even if such occur isolated (Devillez & Charbonnier, 2019a, 2019b). Most Late Jurassic remains of *Stenodactylina* represent chelae or chelipeds from coral-bearing limestones or other shallow-water lithologies (e.g., Étallon, 1859, 1861; Krause, 1891; Bachmayer, 1959). Here we describe the first examples of *Stenodactylina* from Upper Jurassic lithographic limestones.

Geological settings

Two of the specimens of *Stenodactylina* described here come from the upper Kimmeridgian Nusplingen Plattenkalk, also known as Nusplingen Lithographic Limestone. The site of provenance is located in the western part of the Swabian Alb (Fig. 1). The Nusplingen Plattenkalk was deposited in a *c.* 80-100 metres deep lagoon surrounded by shallower areas and small islands (Stevens et al., 2014). Known since the mid-19th century, it has meanwhile provided more than 400 fossil taxa, among them pterosaurs, marine crocodiles, sharks and numerous other fishes, but also squid-like teuthoids and decapod crustaceans (Dietl & Schweigert, 2011). Ammonites have allowed to date it as late *Beckeri* Zone, *Ulmense* Subzone, *hoelderi* Biohorizon (Schweigert, 2007, 2015a). Especially common are large-sized penaeid prawns (Schweigert, 2001b, 2017; Odin et al., 2019), but polychelid, glypheid and erymid lobsters have been recorded as well (Fraas, 1855; Oppel, 1861, 1862; Schweigert & Dietl, 1999; Schweigert et al., 2000; Schweigert, 2001a; Charbonnier et al., 2013; Audo et al., 2014). Erymid material from Nusplingen is often incomplete due to predation or decay; however, several valid taxa have been described on the basis of such incomplete specimens (Oppel, 1861, 1862; Schweigert et al., 2000). Recently, this material has been restudied within the context of a comprehensive review of all Late Jurassic erymid lobsters (Devillez & Charbonnier, 2020).

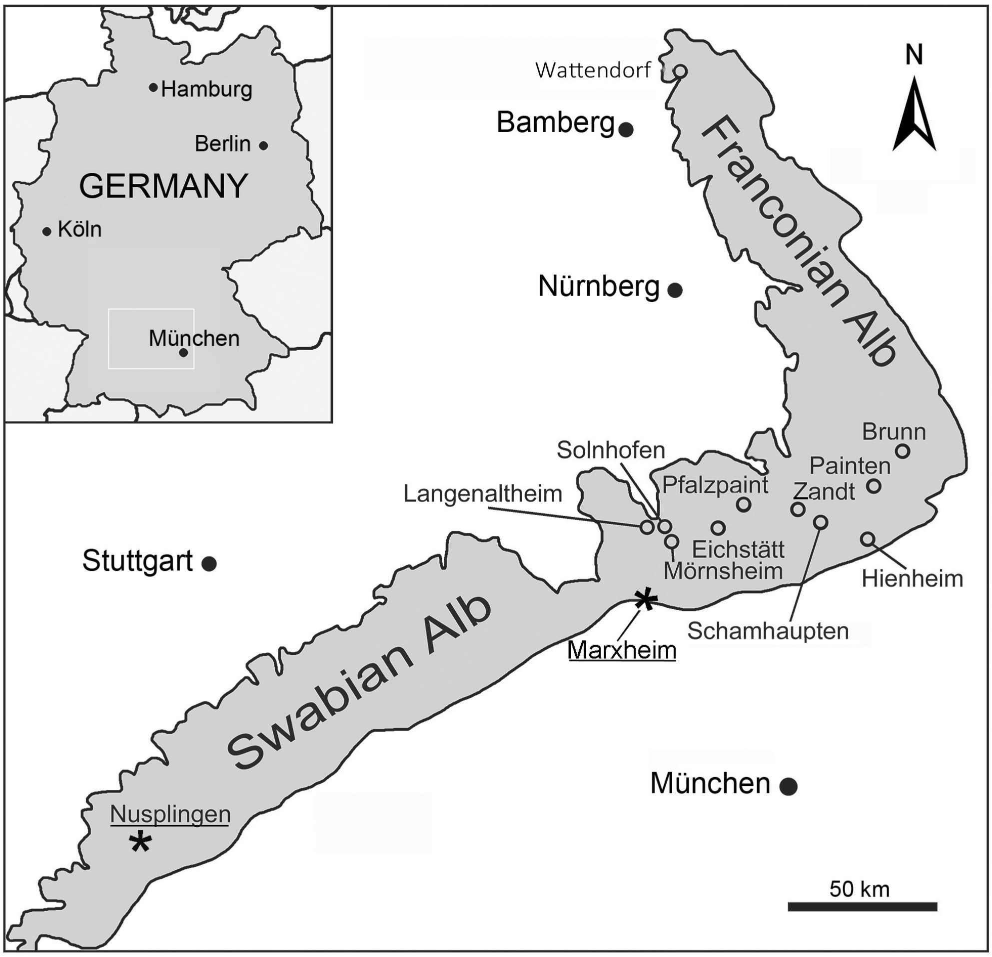

Fig. 1. Localities that yielded the material of *Stenodactylina* (asterisks) and additional Upper Jurassic Plattenkalk localities in southwest Germany (modified from Fürsich et al., 2007).

A third specimen of *Stenodactylina* comes from Upper Jurassic plattenkalks exposed at the northern hillside of the River Danube, southwest of the village of Marxheim (Fig. 1). These plattenkalks had not been studied previously for their fossil content. Fesefeldt (1962) mapped the area around Marxheim and described several sections and outcrops. From his descriptions the plattenkalks in question match the so-called "Spindeltal-Schiefer", an informal lithological unit which is included in the lower Tithonian Usseltal Formation (Zeiss, 1977; Niebuhr & Pürner, 2014). For a determination of the age of these plattenkalks, several ammonite remains were sampled from the scree; these include *Subplanitoides spindelense* Zeiss, 1968 (Fig. 2), *Subplanitoides* sp., "*Torquatisphinctes*" *regularis* Zeiss, 1968 and *Usseliceras* sp. This association clearly indicates the *franconicum* Biohorizon of the lower Tithonian *Mucronatum* Zone (see Schweigert, 2015a). The Submediterranean *Mucronatum* Zone corresponds approximately to the Tethyan *Darwini* Zone (Scherzinger & Schweigert, 2003). Assuming the duration of a biohorizon to have been around 165 ka (Schweigert, 2006), the Tithonian type horizon of the specimen from Marxheim is around 1.15 myr younger than the Kimmeridgian Nusplingen site.

Methods

The specimens studied were carefully prepared mechanically with needles and scalpels using a binocular with 50 × magnification. Photographs were taken with digital cameras under normal or ultraviolet illumination. Ultraviolet illumination is often used to enhance the contrast between phosphatic fossils and the surrounding rock matrix (e.g., Haug et al., 2009; Tischlinger, 2015). The photographs were finally mounted as illustrations using Adobe Photoshop version CS5.1.

Systematic palaeontology

Class Malacostraca Latreille, 1802
Order Decapoda Latreille, 1802
Superfamily Erymoidea Van Straelen, 1925
Family Erymidae Van Straelen, 1925
Genus *Stenodactylina* Beurlen, 1928

Included species: *Stenodactylina armata* (Secretan, 1964), *S. australis* (Secretan, 1964), *S. burgundiaca* (Crônier & Courville, 2004), *S. delphinensis* (Moret, 1946), *S. devillezi* sp. nov. (herein), *S. falsani* (Dumortier, 1867), *S. geigerae* sp. nov. (herein), *S. guisei* (Wright, 1881), *S. insignis* (Oppel, 1862), *S. lagardettei* (Hyžný, Schlögl, Charbonnier, Schweigert, Rulleau & Gouttenoire, 2015), *S. liasina* Beurlen, 1928 (type species), *S. rogerfurzei* Schweigert, 2013, *S. spinosa* (Étallon, 1861), *S. strambergensis* (Bachmayer, 1959), *S. triglypta* (Stenzel, 1945) and *S. walkerae* (Feldmann & Haggart, 2007).

Stenodactylina devillezi sp. nov.

2003 *Erymastacus* sp. nov. – Schweigert & Garassino, fig. 2B.
2020 [fragmentary] *Stenodactylina*. – Devillez & Charbonnier, in press.

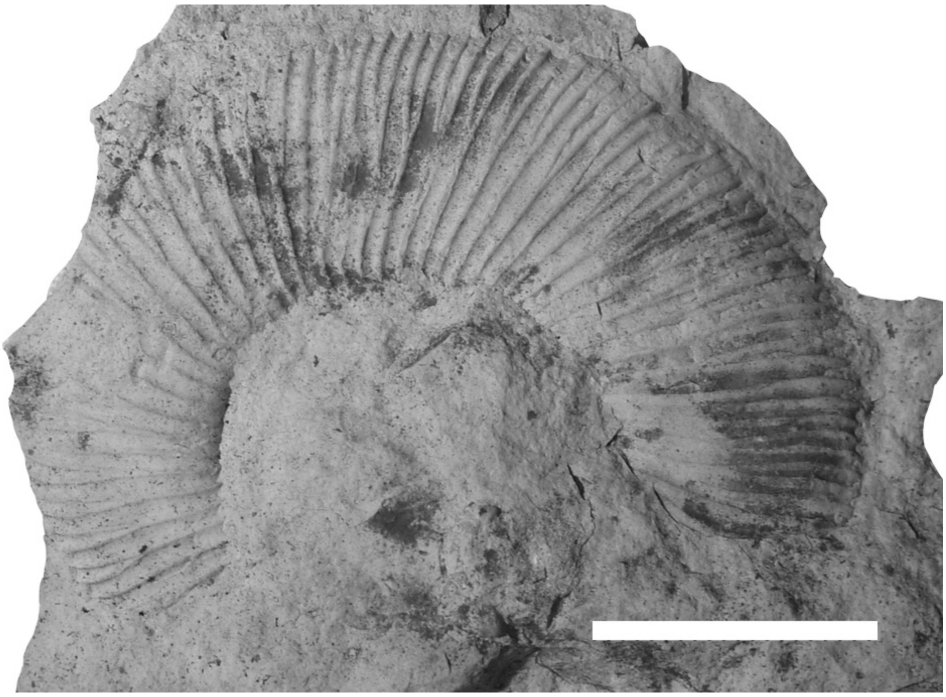

Fig. 2. The ammonite *Subplanitoides spindelense* Zeiss, 1968 from the lower Tithonian, *Mucronatum* Zone (= *Darwini* Zone), 'Spindeltalschiefer' of Usseltal Formation, Marxheim (leg. K. Geiger). Photograph: K. Geiger. Scale bar equals 20 mm.

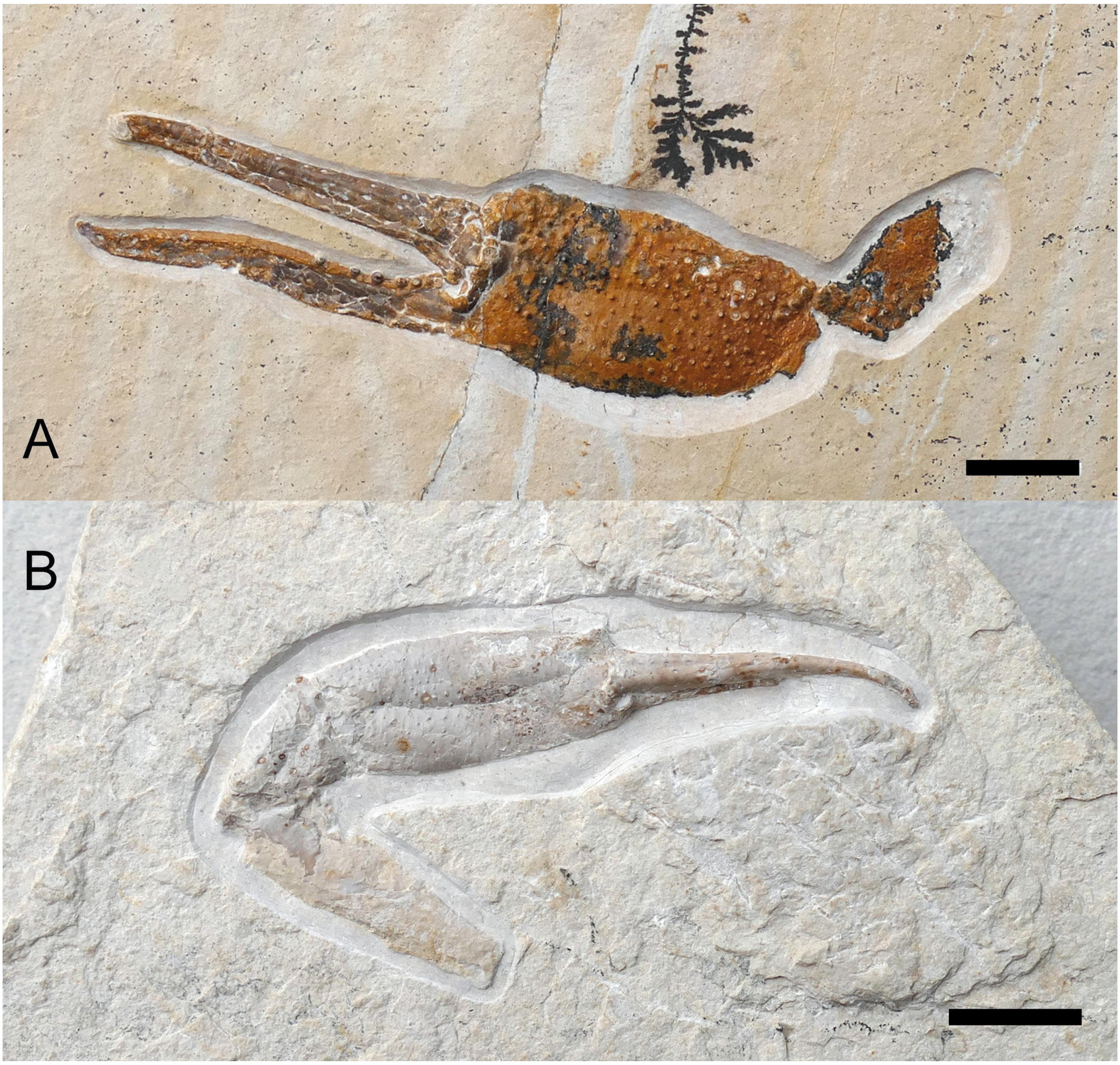

Fig. 3. *Stenodactylina devillezi* sp. nov., A, holotype, SMNS 64872; B, paratype, SMNS 70506. Upper Kimmeridgian, *Beckeri* Zone, *Ulmense* Subzone, Nusplingen Formation, Nusplingen Quarry, Westerberg hill west of Nusplingen, southwest Germany. Photographs: G. Schweigert. Scale bars equal 10 mm.

Holotype: SMNS 64872, from the Nusplingen Formation (upper Kimmeridgian, *Beckeri* Zone) of Nusplingen, Baden-Württemberg, southwest Germany (Fig. 1).

Paratype: SMNS 70506, from same locality and biohorizon as the holotype.

Etymology: Named after Julien Devillez (Paris), who revised all previously described erymid taxa from the Jurassic and Cretaceous.

Type locality and horizon: Nusplingen Quarry, west of Nusplingen, southwest Swabian Alb (Fig. 1); Nusplingen Formation (upper Kimmeridgian, *Beckeri* Zone, *Ulmense* Subzone; see Schweigert, 2007).

Diagnosis: Species of *Stenodactylina* with a P1 chela that is characterised by a slender subrectangular manus, a completely toothless dactylus and an index with seven teeth in the proximal half and a sinuosity in the distal part.

Description: The holotype is a relatively large left cheliped consisting of a well-preserved chela with manus and remains of the carpus. Manus subrectangular, length 33 mm, width 17 mm. Manus and carpus covered with fine, randomly scattered pustules; fingers lacking pustules, only with a few setal pits. Dactylus length 34 mm; index and dactylus terminally curved inwards. Occlusal surface of dactylus toothless; index bearing seven teeth in its proximal part, the strongest one is the third as counted from the distal side, with a longer distance between the first and the second. Distal half of index with a sinuosity.

The paratype is a right cheliped consisting of a manus with chela, the carpus and merus. Manus

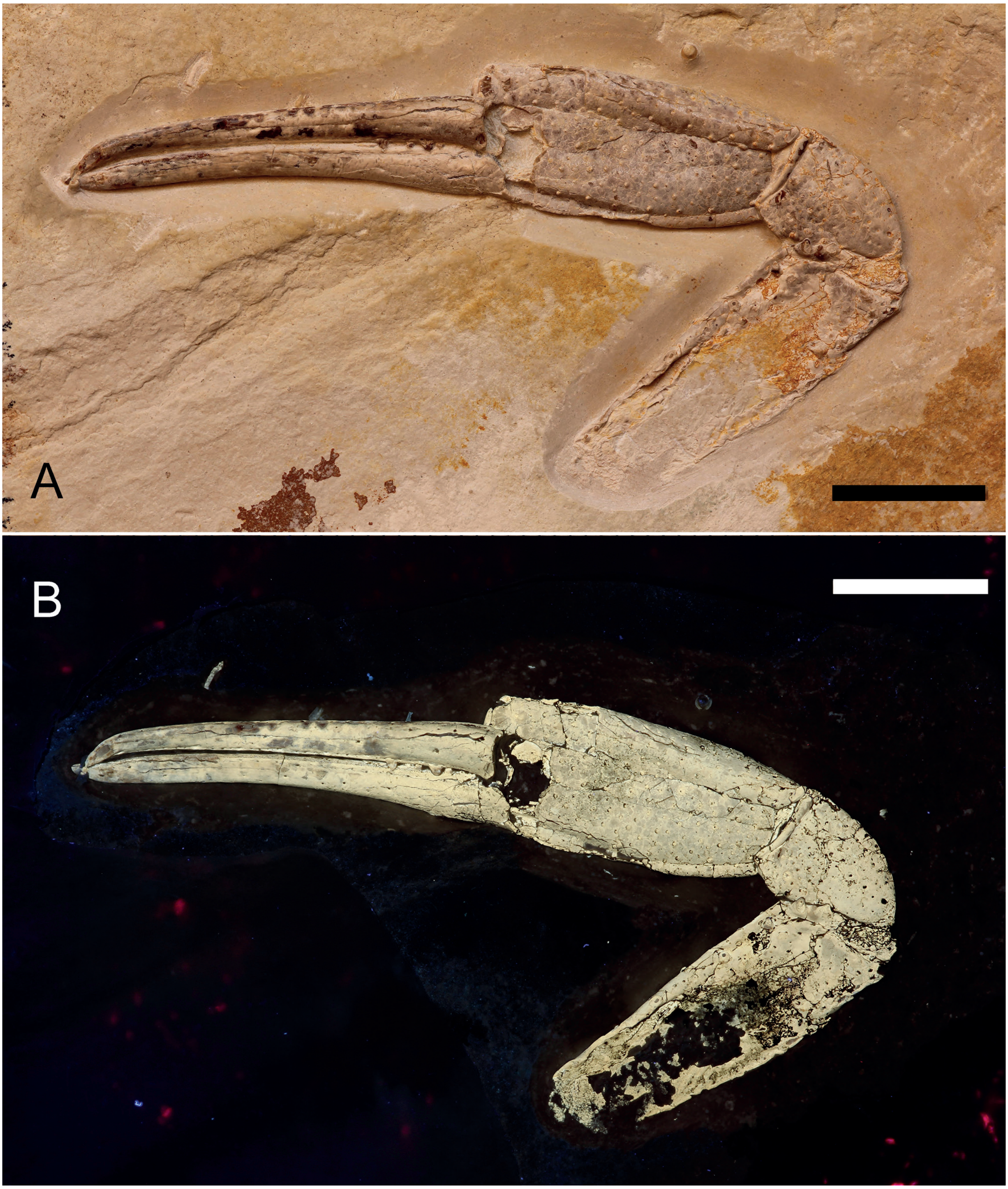

Fig. 4. *Stenodactylina geigerae* sp. nov., holotype, SMNS 70507. A: photographed under normal illumination; B, photographed under ultraviolet illumination. Lower Tithonian, *Mucronatum* Zone (= *Darwini* Zone), 'Spindeltalschiefer' of Usseltal Formation, Marxheim, southwest Germany. Photographs: J. Härer. Scale bars equal 10 mm.

subrectangular, length 22 mm, width 10.5 mm. Carpus 10.5 mm long; merus poorly preserved, 26 mm long. Ornamentation of manus and carpus identical to that in the holotype. Dactylus length 26 mm, with some setal pits, otherwise smooth, distally curved, slightly dislocated during burial. Index mostly covered by dactylus, distal half broken off.

Remarks: The slight differences in the fingers/manus length ratio between the left and right cheliped (although observed in different individuals) point to heterochely in *S. devillezi* sp. nov., which is well known in other species of *Stenodactylina* (see Hyžný et al., 2015). A very fragmentary chela from Nusplingen that shows long and slender fingers with strong and widely spaced teeth, originally recorded in open nomenclature (Schweigert et al., 2000: pl. 5, fig. 4, as "Erymidae gen. et. sp. indet."), possibly belongs to *Enoploclytia* M'Coy, 1849, another erymid genus recently recorded from the Upper Jurassic (Devillez et al., 2018). The rather atypical, slender appearance of the propodus is caused by incomplete preservation. No further specimen has been found so far.

Stenodactylina geigerae sp. nov.

Holotype: SMNS 70507, from the Usseltal Formation (lower Tithonian, *Mucronatum* Zone) of Marxheim, Bavaria, southwest Germany (Fig. 1).

Etymology: Named after Katharina Geiger (Munich), who found and kindly donated the specimen.

Type locality and horizon: Northern hillside of the River Danube, southwest of Marxheim, Bavaria, Germany (Fig. 1), Usseltal Formation, lower Tithonian, *Mucronatum* Zone (= Submediterranean equivalent of Tethyan *Darwini* Zone).

Diagnosis: Species of *Stenodactylina* with a P1 chela that is characterised by only two teeth in the proximal third of the dactylus and index.

Description: The holotype is a left cheliped with the manus, carpus and merus preserved. Several fine cracks are detectable resulting from compaction of the hollow fossil. Manus subrectangular, 19 mm long, 9.5 mm wide. Merus, carpus and manus covered with randomly scattered small pustules; coarser tubercles occur only along the inner margins of the merus and carpus. Merus length 23 mm, with a few spiny tubercles along the articulation towards the carpus. Carpus length 12 mm, distally bordered by a smooth seam. Fingers *c.* 28 mm long, lacking any pustules, only bearing a few tiny setal pits. Occlusal surfaces of dactylus and index each with two prominent teeth in the most proximal parts, otherwise smooth. Strongest tooth is the first one, counted from the proximal side of each finger.

Discussion

The preservation of isolated chelipeds of *Stenodactylina* in lithographic limestones probably results from predation activity in nearby shallower environments. The lobsters themselves usually did not inhabit the hostile sea floor of the lagoons. The most common way for erymid lobsters and most other decapod crustaceans to become fossilised complete in Solnhofen-type plattenkalks is via exuviae (Schweigert & Garassino, 2003). The bulk of exuviae, however, represent juvenile specimens, whereas larval stages are rare as well due to their poor sclerotization (Haug et al., 2011). Juvenile stages of erymid lobsters are not easy to differentiate and much more material is needed to reconstruct their ontogenies.

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Mesogalathea ardua sp. nov., a new species of squat lobster (Decapoda, Galatheidae) from the Upper Jurassic olistolith at Velika Strmica (Dolenjska, Slovenia)

Nova vrsta raka *Mesogalathea ardua* sp. nov. (Decapoda, Galatheidae) iz zgornjejurskega olistolita pri Veliki Strmici (Dolenjska, Slovenija)

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Ključne besede: Anomura, Galatheoidea, kimmeridgij-tithonij, Slovenija, nova vrsta

Abstract

A new species of squat lobster, *Mesogalathea ardua* sp. nov., is described on the basis of newly collected dorsal carapaces from an Upper Jurassic reefal limestone olistolith at Velika Strmica. The fossiliferous olistolith is situated within Upper Cretaceous flysch-type deposits, but originally formed within the central parastromatoporoid zone of a Jurassic reef complex. *Mesogalathea ardua* sp. nov. represents the first formal description of a Jurassic squat lobster from Slovenia and extends the known palaeobiogeographical distribution of galatheoid anomurans.

Izvleček

Predstavljena je nova zgornjejurska vrsta raka skakača *Mesogalathea ardua* sp. nov., opisana na podlagi na novo zbranih primerkov iz grebenskega olistolita pri Veliki Strmici. S fosili bogat olistolit se nahaja znotraj zgornjekrednih flišnih plasti, njegov izvor pa je v parastromatoporoidni coni centralnega dela jurskega koralnega grebena. Novo opisana vrsta *Mesogalathea ardua* sp. nov. je prvi opis jurskega raka skakača iz Slovenije in širi do sedaj znano paleobiogeografsko razširjenost galatheoidnih rakov.

Introduction

The Upper Jurassic of Europe was a hotspot in galatheoid speciation (Bracken-Grissom et al., 2013; Klompmaker et al., 2013; Fraaije, 2014; Robins et al., 2012, 2013, 2015, 2016; Robins & Klompmaker, 2019). These so-called squat lobsters inhabited primarily shallow areas of the tropical Tethys Ocean. Many of the fossil galatheoids are found within limestone blocks interpreted as parts of former coralgal reefs. The largest number of Late Jurassic galatheoid species (and greatest number of specimens) come from a series of olistoliths in the vicinity of Ernstbrunn (Austria), as well as from numerous other olistoliths labelled "Štramberk Limestones" across the border of the modern-day Czech Republic and Poland (for further details, see Robins et al., 2013, 2016). Several galatheoid-producing localities within modern-day Romania are in place (Feldmann et al., 2006; Schweitzer et al., 2017); however, several others within the Carpathians represent olistoliths as well (Schweitzer et al., 2018). All of these originate from reefal environments. This redeposition of Jurassic material within Cretaceous deposits adds additional levels of complexity as far as their depositional and palaeoenvironmental history is concerned. The better-known Jurassic Solnhofen-type limestones, in contrast, are not reefal in nature. Galatheoids are incredibly rare there, with only a single species recorded to date from the area (Feldmann et al., 2016). In non-Solnhofen carbonate rocks in southern Germany, only a single munidopsid species, *Gastrosacus wetzleri* von Meyer, 1851, is present. This species is known mainly from sponge-microbial reefs and associated limestones (Robins et al., 2015).

The present study discusses a new record of Late Jurassic squat lobsters from Slovenia, describing a new species of *Mesogalathea* Houša, 1963, on the basis of newly collected material. These specimens extend the palaeobiogeographical distribution of Late Jurassic galatheoids.

Geological setting

The locality of Velika Strmica, some 10 km northwest of Novo mesto, belongs structurally to the Dinarides, i.e. the folded and thrusted former northeastern margin of the Adria tectonic microplate (Placer, 1999, 2008; Vrabec & Fodor, 2006). According to Kastelic et al. (2008), the main phase

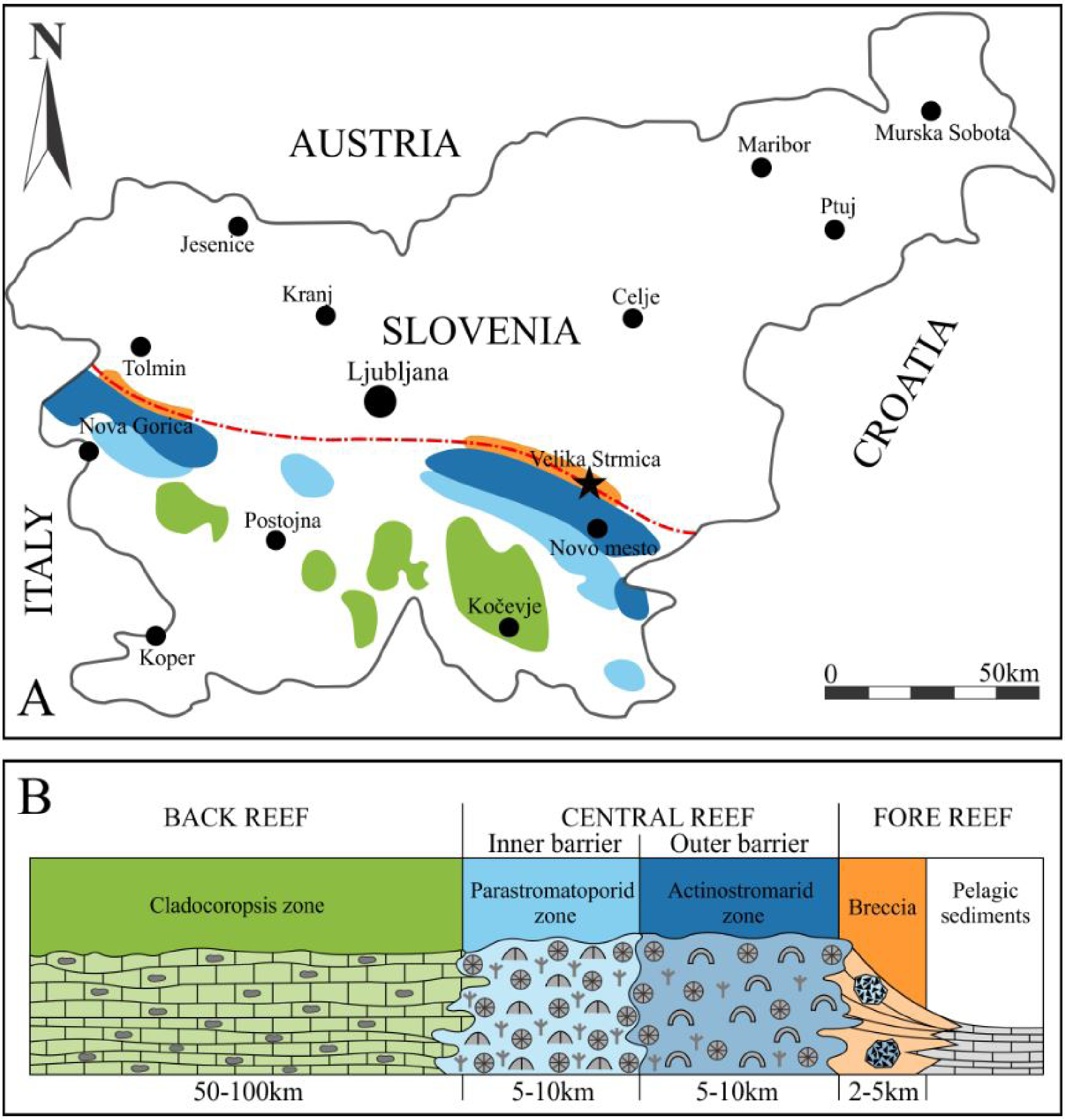

Fig. 1. Position of the locality. A - Simplified geographical map showing the locality of Velika Strmica (star) and present-day position of the Upper Jurassic barrier reef complex in Slovenia. B - Palaeoenvironmental differentiation of the Jurassic barrier reef complex (adapted after Turnšek, 1997).

of the NE- to SW-directed folding and thrusting took place during the Eocene. The northeastern part of the Dinarides was further dissected after the Miocene by the SE-NE trending, post-Miocene strike-slip faults of the Mid-Hungarian tectonic zone. These faults, together with the W-E striking Periadiatic tectonic zone to the north and the NW-SE trending strike-slip faults of the Idrija tectonic zone to the east, form the so-called Sava compressive wedge (Placer, 1999).

The stratigraphical succession at Velika Strmica is incomplete due to the strongly faulted structure of the area. The lower part of the succession comprises Triassic, Jurassic and Lower Cretaceous carbonates (Pleničar & Premru, 1977; Trotošek, 2002; Buser, 2009), deposited on or at the margin of the Adriatic carbonate platform, which covered large parts of the continental crust of the Adria microplate during the Mesozoic (Buser, 1989; Vlahović et al., 2005). Platform carbonates are discordantly overlain by upper Santonian to mid-Campanian grey and red marly limestone with chert and subordinate intercalations of calcarenite and calcrudite (Trotošek, 2002), or by Campanian-Maastrichtian flysch-type deposits, comprising basal carbonate breccia or calcarenite and marlstone (Pleničar & Premru, 1977; Trotošek, 2002). West of the village of Velika Strmica, the marlstone from the flysch series comprises also a series of Upper Jurassic (Kimmeridgian/Tithonian) carbonate blocks of reefal limestone (Fig. 1). The fossils studied originate from one of these olistoliths, from which a diverse decapod crustacean fauna has been recovered (Gašparič & Gale, 2018). The Late Jurassic age of the olistolith has previously been determined on the basis of occurrences of the corals *Dermoseris* sp. and *Dermosmilia etalloni* Koby, 1884 (Trotošek, 2002).

Material and methods

The present study is based on 15 specimens of galatheoid preserved in a coral limestone matrix. They were mostly found by mechanically breaking down a rock sample, except in rare cases where specimens were visible on weathered surfaces. Because specimens are heavily recrystallised, there is only poor separation between the rock and the thin cuticle. Cuticle is partially preserved in some specimens, although occasionally damaged in weathered or prepared specimens. However, presence or absence of cuticle seemingly has no significant impact on carapace ornamentation in galatheoids (Robins et al., 2016). Material described and illustrated are part of the collections of the Natural History Museum Ljubljana (Slovenia).

Decapod specimens were prepared and studied under a stereomicroscope Leica EZ 4D. Photographs were taken with a digital camera Nikon D750. Some specimens were whitened with ammonium chloride sublimate prior to photography in order to enhance details of cuticle ornamentation.

Microfacies analysis was performed on nine thin sections, prepared from four samples. Thin sections are now held in the repository of one of us (L.G.; thin sections with number 1231). Microfacies types are characterised according to the classifications of Dunham (1962) and Embry & Klovan (1971). Quantity grain analysis for grainstone was done on three images at magnifications of ×12.5 and ×25 with JMicroVision v2.7 computer software (Nicolas Roduit, 2002-2008). Over 200 points per image were counted. Completely micritized grains were counted as peloids, in contrast to intraclasts, which still preserve original texture. Rounded (abraded) fragments of bounding organisms were also treated as intraclasts. Whenever the origin of a peloid could be recognised, e.g., due to incomplete micritization, such a grain was added to non-micritized grains of the same type.

Description of olistolith

The isolated limestone block, measuring approximately 2 m in diameter, consists of grainstone in its lower part, followed by sponge floatstone. Macroscopically, the latter facies contains a rich fauna with sponges, decapod crustaceans, corals and brachiopods. Within the grainstone, clasts represent 70 % of the bulk rock. They range in size from 0.08 to 1.32 mm, with most grains around 0.25 mm in diameter. The sediment is moderately well sorted. Grains are subangular to subrounded, mostly with point contacts. Intraclasts account for 28 % of the area. Most are strongly micritized. Unclear particles can be detected, and some represent abraded fragments of encrusting algae. Boring and predating abrasion is seen in some of the latter. Sparitic fragments, abraded and micritized to various degrees, are the next common grain type (21.5 %). Peloids account for 14.5 %, and echinoderms for 5 %. Other components (foraminifera, bryozoans, brachiopods) are very rare. Bryozoan colonies were fragmented and later abraded. Zooecia are filled with micrite. Most of the benthic foraminifera are fragmentary, whereas planktonic forms are much better preserved, with numerous short spines apparent at the surface. Among the former, *Protopeneroplis striata* Weynschenk, 1950 and *Ammobaculites* sp. were identified. Other forms present belong to lagenids, miliolids and planktonic taxa. Intergranular space is filled with drusy-mosaic calcite cement.

In the sponge floatstone, clasts larger than 2 mm represent 20-40 % of the area. Sorting is very poor. Most of these are tabular sponges; corals and brachiopods are subordinate. Sponges and corals are commonly encrusted by *Lithocodium/Pseudolithocodium*-like crusts (see comments in Schlagintweit et al., 2010), sessile foraminifera, serpulids, red algae and sponges. Serpulids are also found within internal canals of sponges. Microborings are also very common on the outer surface of sponges and corals. Brachiopod shells are preserved with closed valves. The matrix consists of bioclastic wackestone and packstone. Clasts are strongly fragmented and sparitic fragments predominate. Complete bivalve and gastropod shells are rarely preserved. Original shells seem to have been dissolved during diagenesis and moulds were first lined with bladed rim cement, followed by clear drusy-mosaic calcite cement. Other grains include foraminifera, echinoderm ossicles (including echinoid spines), fragmented bryozoans and ostracods. Among foraminifera, *Protopeneroplis striata*, *Earlandia tintinniformis* (Mišik, 1971), indeterminate miliolids and nodosariids of the meandrospiroid form, and *Astacolus* sp. were identified.

Abbreviations

Abbreviations of dorsal carapace characters of Galatheoidea used in the illustrations are as follows: L – length, excluding rostrum; R – rostrum length; LR – total length, including rostrum; GH – gastric region length, from base of rostrum to cervical groove; MW – maximum width of specimen; RW – maximum rostrum width; TW – width at anterior margin; ro – rostrum; os – orbital sinus; as – anterolateral spine; cg – cervical groove; gr – undifferentiated gastric region; br – undifferentiated branchial region.

RGA/SMNH - Slovenian Museum of Natural History, Ljubljana, Slovenia (R. Gašparič Collection).

Systematic palaeontology

Order Decapoda Latreille, 1802
Infraorder Anomura MacLeay, 1838
Superfamily Galatheoidea Samouelle, 1819
Family Paragalatheidae Robins, Feldmann, Schweitzer & Bonde, 2016
Genus *Mesogalathea* Houša, 1963

Type species: *Galathea striata* Remeš, 1895, by original designation.

Diagnosis: Carapace subrectangular to suboval; strongly convex, maximum width roughly equal to length; ornamented exclusively with transverse ridges. Rostrum very broad, without keel, ending in broadly tridentate tip. Cervical groove weakly to moderately defined; regions usually undefined (after Robins et al., 2016).

Remarks: This genus is known exclusively from the Upper Jurassic, with records from Austria, the Czech Republic, Poland, Romania and Slovenia, of the following species: *Mesogalathea striata* Remeš, 1895, *M. macra* Robins, Feldmann, Schweitzer & Bonde, 2016, *M. pyxis* Robins, Feldmann, Schweitzer & Bonde, 2016 and *M. retusa* Robins, Feldmann, Schweitzer & Bonde, 2016.

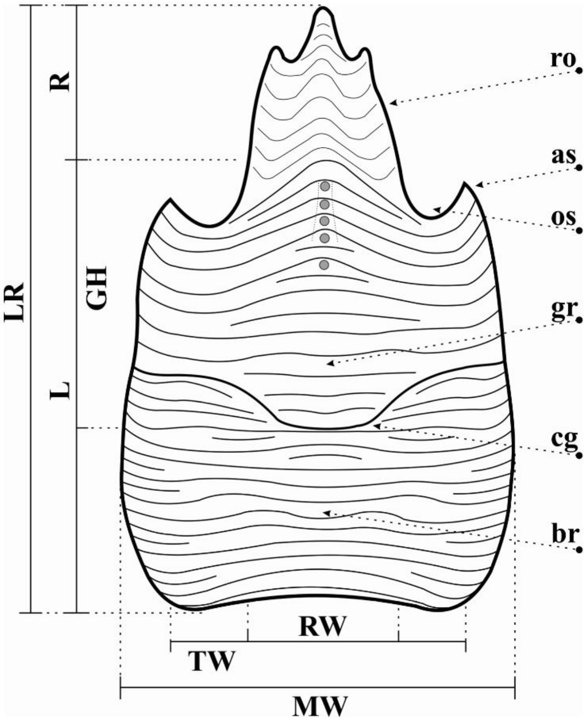

Fig. 2. Schematic reconstruction of the dorsal carapace of *Mesogalathea ardua* sp. nov., with descriptive terminology and carapace measurements used in the text (for terminology see "Abbreviations").

Mesogalathea ardua sp. nov.

(Figs. 3-5)

Etymology: from the Latin "*ardus*" meaning steep, in reference to the locality name Velika Strmica, which translates as "steep hill".

Diagnosis: Carapace L/MW 1.3; L/TW 1.4 (average). Lateral margins straight; arching inwards anteriorly and posteriorly; maximum width posterior of cervical groove. Rostrum large, spatulate; covering approximately half total width of anterior of dorsal carapace and representing more than one-third of carapace length (L). Lateral edges of rostrum converging anteriorly; distinctly tridentate, with three pointed tips; central tip extending furthest. Carapace and rostrum ornamented with continuous transverse ridges that extend to lateral margins. Defined cervical groove extending across carapace, broadly concave and straightening at centre; turning sharply anteriorly at lateral margins.

Holotype: RGA/SMNH 1783 (Figs. 3A-B, 4A).

Paratypes: RGA/SMNH 2173 (Fig. 4D), RGA/SMNH 1786 (Fig. 4C), RGA/SMNH 2215 (Fig. 5A), RGA/SMNH 2115 (Fig. 4B), RGA/SMNH 2117 (Fig. 5B) and RGA/SMNH 2094.

Type locality: Velika Strmica, Slovenia.

Type age: Late Jurassic, Kimmeridgian/Tithonian.

Distribution: Only known from the type locality.

Measurements: details in Table 1.

Description: Carapace subrectangular to suboval in shape; narrows slightly at extreme anterior and posterior, maximum width (MW) in posterior third. Carapace strongly convex transversely; moderately convex longitudinally; longer than wide, L/MW relatively constantly at 1.3, L/TW ranging between 1.3 and 1.5. Rostrum very large, spatulate; covering approximately half anterior width of frontal margin of dorsal carapace; representing more than one-third of carapace length (L); rostrum comprising larger portion of total carapace length in smaller than in larger specimens. Rostrum with lateral edges higher at midpoint; smooth lateral margins; moderately deflected; bearing no keel. Lateral edges of rostrum subparallel, converging in anteriormost third; rostrum ending in distinct tridentate tip; all three tips pointed, central tip of trident extending more than double the length of lateral

Table 1. Dimensions (in millimetres) of *Mesogalathea ardua* sp. nov.

Spec. No.	L	LR	R	MW	RW	TW	GH	L/MW	L/TW	RW/TW
RGA 1783	8.4	10.9	2.5	6.4	2.8	5.5	4.5	1.3	1.5	0.5
RGA 2173	5.0	6.6	1.6	4.0	2.0	3.9	3.0	1.3	1.3	0.5
RGA 1786	4.1	5.6	1.5	3.1	1.4	2.7	2.2	1.3	1.5	0.5
RGA 2215	—	—	—	8.8	3.6	6.8	5.8	—	—	0.5
RGA 2115	—	—	2.6	—	3.0	5.6	—	—	—	0.5
RGA 2117	—	—	2.9	—	3.5	5.4	—	—	—	0.6
RGA 2094	9.3	—	—	7.2	4.1	7.1	5.4	1.3	1.3	0.6

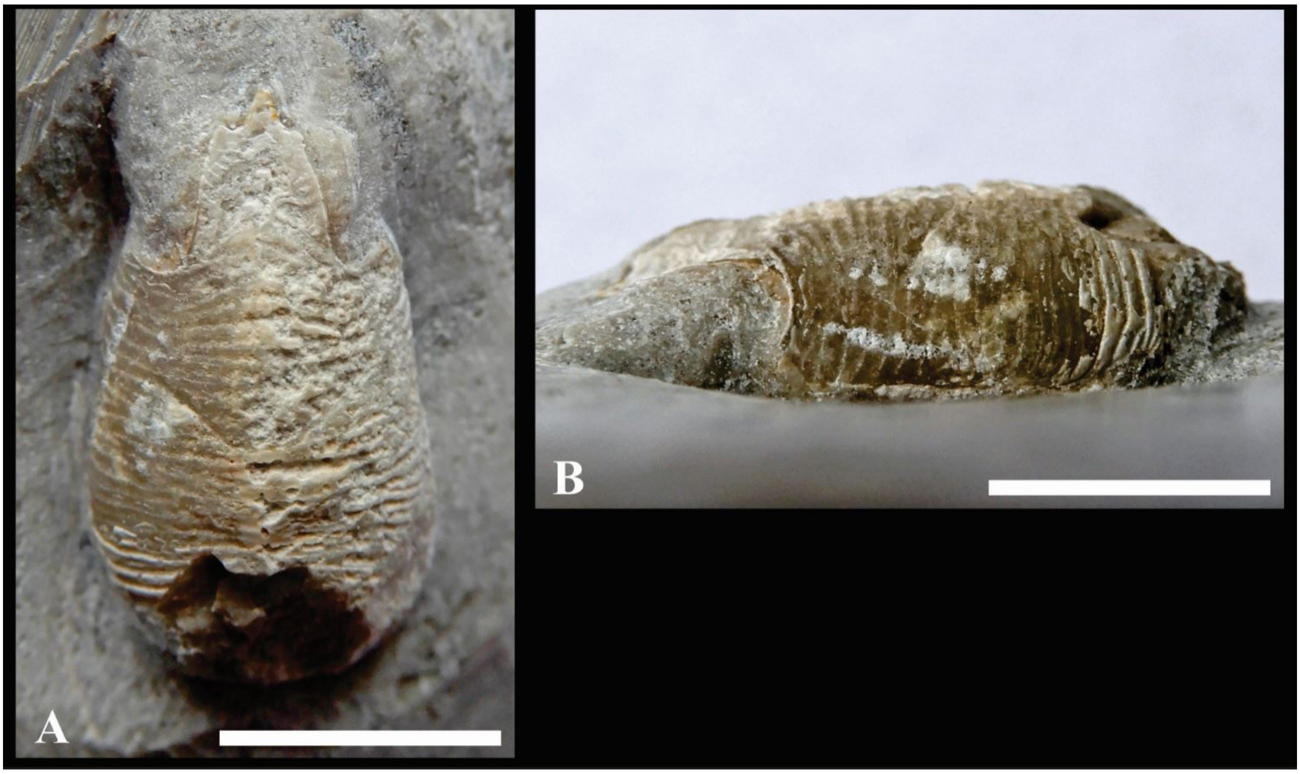

Fig. 3. *Mesogalathea ardua* sp. nov. A - RGA/SMNH 1783 (holotype), dorsal carapace; B - RGA/SMNH 1783 (holotype), lateral view of carapace. Scale bars equal 5 mm.

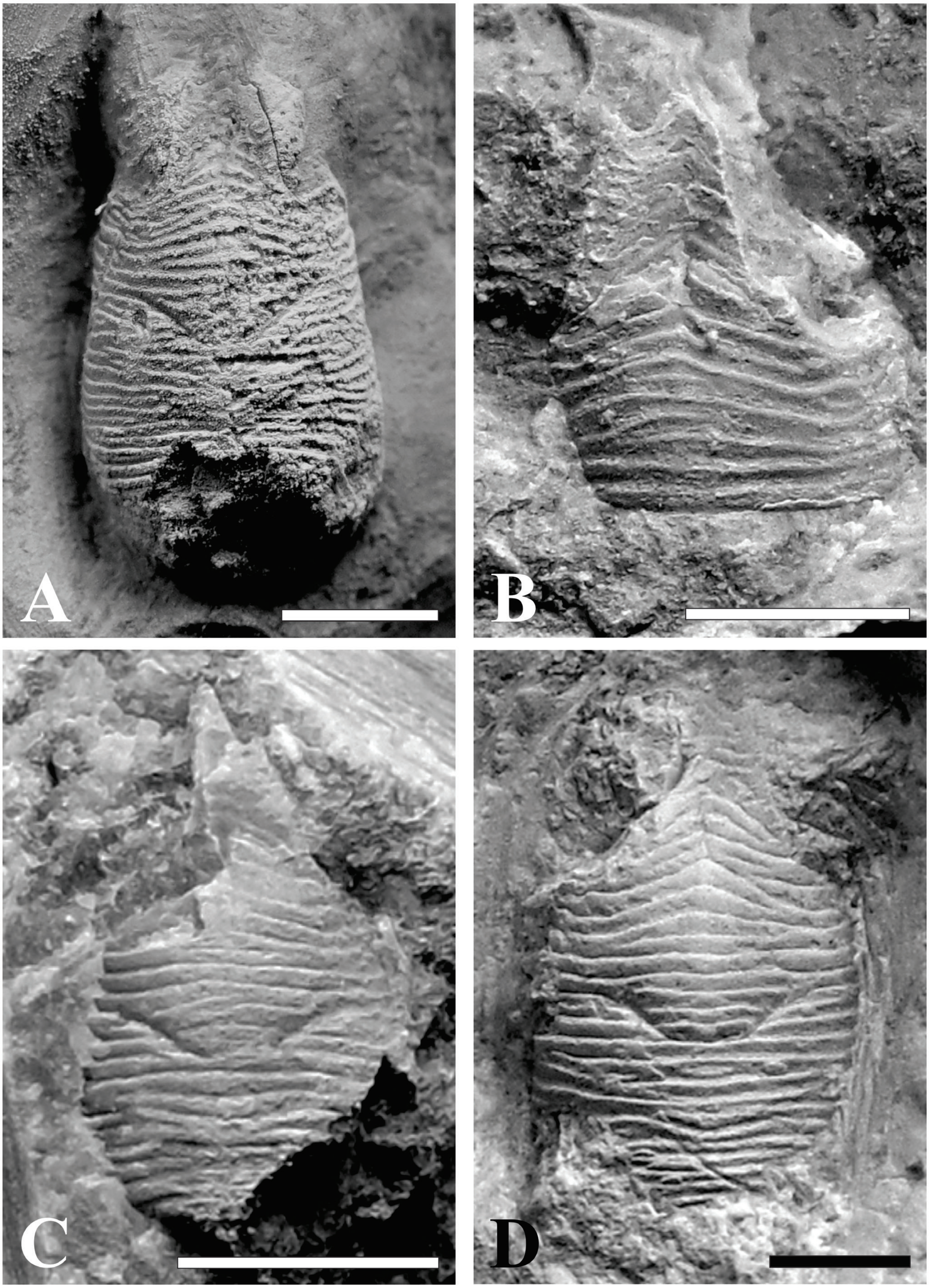

Fig. 4. *Mesogalathea ardua* sp. nov. A - RGA/SMNH 1783 (holotype), dorsal carapace; B - RGA/SMNH 2115 (paratype), partial dorsal carapace; C - RGA/SMNH 1786 (paratype), dorsal carapace; D - RGA/SMNH 2173 (paratype), dorsal carapace. Scale bars equal 3 mm (A, B) and 2 mm (C, D).

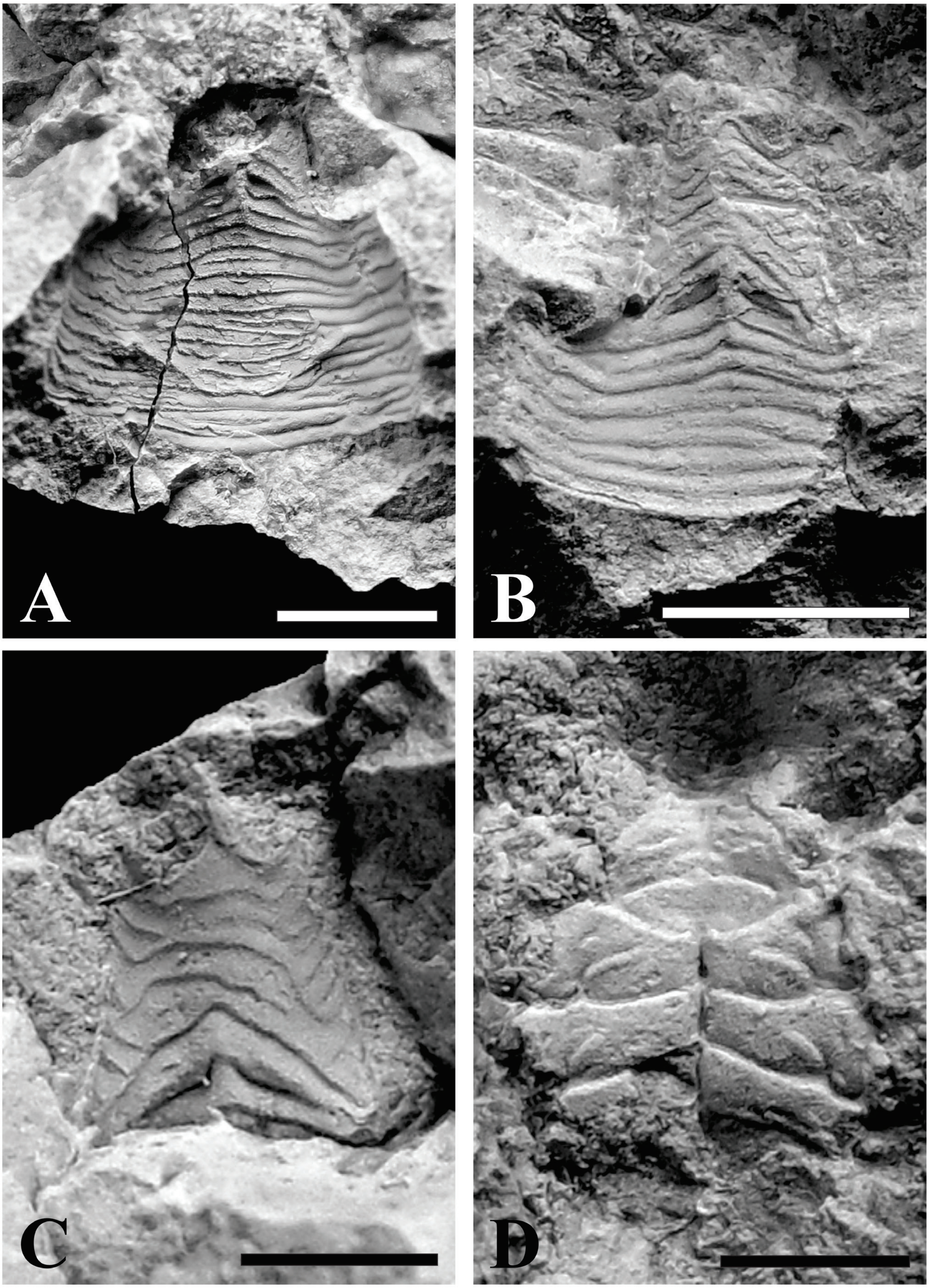

Fig. 5. *Mesogalathea ardua* sp. nov. A - RGA/SMNH 2215 (paratype), partial dorsal carapace; B - RGA/SMNH 2217 (paratype), partial dorsal carapace; C - RGA/SMNH 2101, rostrum; D - RGA/SMNH 1784a, sternal plastron. Scale bars equal 3 mm (A, B) and 2 mm (C, D).

tips. Rostrum adorned throughout by strong meandering, transverse ornamentation; ornamentation of rostrum mirroring trident rostrum shape. Orbits shallow and directed forwards, apparently continuing under rostrum. Supraorbital margin concave, unornamented, with one forwardly directed spine at anterolateral angle.

Lateral margin straight; smoothly arching inwards both anteriorly and posteriorly. Defined cervical groove extending across carapace, broadly concave and straightening at centre; running progressively anteriorly across carapace and turning sharply anteriorly immediately prior to lateral margins. Branchio-cardiac groove not present. Regions not defined; depressed subparallel converging tip of mesogastric region located posteriorly to rostrum, intersected by ornamentation, longitudinally depressed and adorned with circular depressions interspaced between transverse ridges. Carapace ornamented with long prominent, uninterrupted, transverse ridges; occasionally interspersed with smaller ridges. In anterior part of gastric region, ornamentation continuing smoothly onto rostrum, ridges centrally convex; posterior gastric ridges straightening and becoming concave, reflecting cervical groove. Anterior branchial regions ornamented with slight concave transverse ridges; straightening where approaching posterior part of branchial region. All ornamentation extending to lateral edges and turning sharply anteriorly at lateral margins.

Ventral surface (sternal plastron) (Fig. 5D) and preserved appendages disarticulated; hence it is not possible to assign them to *Mesogalathea ardua* sp. nov. with any confidence, but this is likely in view of size, abundance and relative proximity.

Discussion: Based on overall carapace shape, a long, broad and tridentate rostrum without a keel, ornamentation of exclusively transverse ridges; a defined cervical groove, but a lack of other defined grooves or regions, the new species can be confidently assigned to the genus *Mesogalathea*. *Mesogalathea ardua* sp. nov. resembles *Mesogalathea striata* in overall carapace shape and prominent transverse ornamentation, whereas the ridges in the new species are straighter and more regularly continuous across the carapace. Additionally, *Mesogalathea ardua* sp. nov. possesses a wider, more concave and more deeply incised cervical groove and a pointed tridentate ornamented rostrum, with a longer median tip and a well-developed tip of the mesogastric region. The new species has a more prominent transverse ornamentation, a rostrum with a distinctly longer tridentate tip, anterolateral spines and a deeper cervical groove than in *Mesogalathea macra* and *Mesogalathea retusa*. *Mesogalathea pyxis* has a more convex carapace, a more irregular transverse ornamentation and ornamented orbits that lack anterolateral spines, as in *Mesogalathea ardua* sp. nov.

Palaeoecology and palaeoenvironment

The fossil assemblage recovered from the olistolith studied hints at its provenance from the Upper Jurassic reef complex which stratigraphically underlies the Lower Cretaceous flysch-type deposits. The Late Jurassic reef complex of the External Dinarides is considered the largest preserved fossil reef in Slovenia. It was a barrier reef that extended along the northern margin of the Dinaric Carbonate Platform, which passes northwards into the deep-marine Slovenian Basin (Fig. 1A; Turnšek et al., 1981; Turnšek, 1997). Turnšek et al. (1981) subdivided the Upper Jurassic reef complex of the External Dinarides into fore-reef, central reef and back-reef, the last-named containing local patch reefs. Based on reefal communities, the central reef area was further subdivided into an outer “actinostromarid zone” and an inner “parastromatoporoid zone” (Fig. 1B). The relative abundance of *Protopeneroplis striata* in the olistolith studied, as well as the presence of planktonic foraminifera, is suggestive of original deposition on the upper slope. This view is supported by the occurrence of *Lithocodium*/*Pseudolithocodium*, also known from shallow- to deeper-water settings (see Schlagintweit et al., 2010). We conclude that the Upper Jurassic olistolith that has yielded the decapod crustaceans described here developed in the central parastromatoporoid zone of a Jurassic coral reef complex.

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Well-preserved cuticle of *Atherfieldastacus magnus* (Decapoda, Glypheida) from the Aptian of Mexico

Dobro ohranjena kutikula raka *Atherfieldastacus magnus* (Decapoda, Glypheida) iz aptijskih plasti v Mehiki

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Ključne besede: Pleocyemata, Mecochiridae, kutikula, spodnja kreda, Chihuahua, Mehika

Abstract

The cuticle structure of fossil decapod crustaceans is an important tool, not only for palaeocological and taphonomic interpretations, but also as a potential way to characterise systematically genera and even species the cuticle of which has not been severely altered by diagenetic processes. Localities with abundant decapod crustacean remains can be interpreted either as reflecting mass mortality events or just simple accumulations of exuviae, on the basis of completeness and comparison of cuticle structures between specimens of the same species from different localities. Association with anoxic events by microfacies analyses can offer clues to explain the unusual abundance of decapod crustacean remains. This is the case for the Early Cretaceous lobster *Atherfieldastacus magnus* (M'Coy, 1849), which is found in large numbers in different Lower Cretaceous (mainly Aptian) lithostratigraphic units across the globe. In this case, we document the well-preserved cuticle structure of specimens from the upper Aptian of Chihuahua (Mexico), preserved three-dimensionally, mainly in concretions, which were studied in different transverse sections showing the cuticle in diverse portions of the lobster body. Thin cuticle layers show the typical crustacean cuticular structure that suggest these are corpses preserved in an anoxic environment.

Izvleček

Analiza strukture kutikule fosilnih deseteronožcev je pomembno orodje ne le za paleoekološke in tafonomske interpretacije, ampak tudi kot možen način za sistematsko opredelitev rodov in celo vrst, v kolikor kutikula ni diagenetsko spremenjena. Na podlagi ohranjenosti in primerjave strukture kutikule med primerki iste vrste z različnih nahajališč razlikujemo nahajališča s pogostimi ostanki rakov. Ta lahko kažejo na množičen pogin ali zgolj na akumulacije levov deseteronožcev. V povezavi s prepoznanimi anoksičnimi dogodki v mikrofacialnih analizah nam lahko metoda služi za razlago množičnih nakopičenj fosilnih deseteronožcev na nekaterih lokacijah. Tak primer je zgodnjekredni jastog *Atherfieldastacus magnus* (M'Coy, 1849), katerega številne ostanke najdemo v različnih litostratigrafskih enotah spodnje krede (predvsem v aptiju) po vsem svetu. V prispevku predstavljamo dobro ohranjeno strukturo kutikule osebkov iz zgornjega aptija iz nahajališča Chihuahua (Mehika). Vzorce tridimenzionalno ohranjene kutikule primerkov iz konkrecij smo pregledali na različnih prečnih presekih z različnih delov telesa jastoga. Tanke plasti kutikule z značilno strukturo kažejo, da gre v našem primeru za trupla, ki so se ohranila v anoksičnem okolju.

Introduction

An interesting factor of the study of decapod crustaceans is the review and examination of their cuticule structure. At most localities, cuticle structure is obscured by mineral replacement of the original carbonate, but modified by diagenetic processes as well (Vega et al., 2005). In previous studies (e.g., Dennell, 1960; Hegdahl et al., 1977a, b; Roer & Dillaman, 1984), cuticle structure of Recent taxa has been studied, while other authors have demonstrated the presence of cuticle in the fossil record (e.g., Neville & Berg, 1971; Feldmann & Tshudy, 1987; Vega et al., 1994, 2005; Feldmann & Gaździcki, 1998; Guinot & Breton; 2006; González-León et al., 2016, 2018, among others). Studies of the functional morphology and taphonomic implications have been addressed by various authors (Schäfer, 1951; Guinot, 1979; Plotnick et al., 1988; Savazzi, 1988; Haj & Feldmann, 2002; Waugh et al., 2004). The use of this structure for taxonomic purposes is complicated because there are only few well-established characters. With this in mind, Waugh et al. (2009) analysed the morphological characters of some decapod crustaceans for possible future phylogenetic analysis.

Decapod crustaceans rank amongst the most common animals inhabiting a number of different environments, both at the present day (Abele, 1974) and in the past (Klompmaker et al., 2013; Schweitzer & Feldmann, 2014). The calcified cuticle of decapod crustaceans comprises the hard exoskeleton of the animal and is composed of three layers (Haj & Feldmann, 2002); these layers have been documented in some fossil decapod crustaceans as well (Neville & Berg, 1971; Taylor, 1973; Dalingwater, 1977; Vega et al., 1994, 1998; Feldmann & Gaździcki, 1998; Haj & Feldmann, 2002; Waugh & Feldmann, 2003; Vega et al., 2005; Waugh et al., 2006; Amato et al., 2008; Waugh et al., 2009; González-León et al., 2016, 2018). The decapod cuticle has a very distinctive structure when observed in cross section. In spite of the fact that decapod crustacean cuticle is frequently preserved in material from Mesozoic and Cenozoic shelf deposits (Vega et al., 2005), very few efforts have been made as to how to distinguish corpses from exuviae. For this reason, it is important to recognise and characterise the microstructure as a potential tool in preliminary identification of, at least, major decapod crustacean groups and taphonomic interpretations (Feldmann & Tshudy, 1987; Vega et al., 1994; Klompmaker et al., 2015). The present paper analyses and complements information on cuticule structure of numerous specimens of *Atherfieldastacus magnus* that are preserved in concretions from the upper Aptian La Peña Formation in Chihuahua State (northern Mexico).

Locality and stratigraphy

The main locality is in the Cerro Chino region (Chihuahua State), close to the towns of Coyame del Sotol and Cuchillo Parado (Fig. 1). Specimens were collected from upper Aptian strata assigned to the La Peña Formation (Fig. 2); for details on these localities and local stratigraphy, reference is made to Ovando-Figueroa et al. (2017) and González-León et al. (2018).

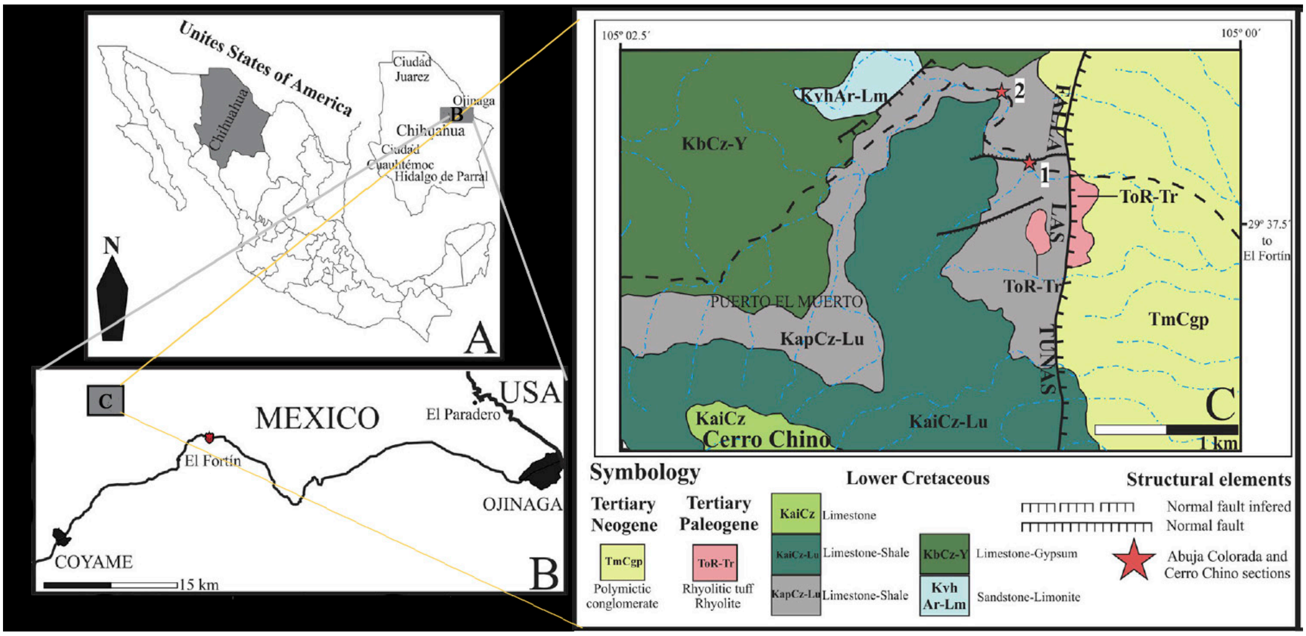

Fig. 1. Locality map showing the fossil site in northern Mexico (Chihuahua State) (modified from González-León et al., 2018).

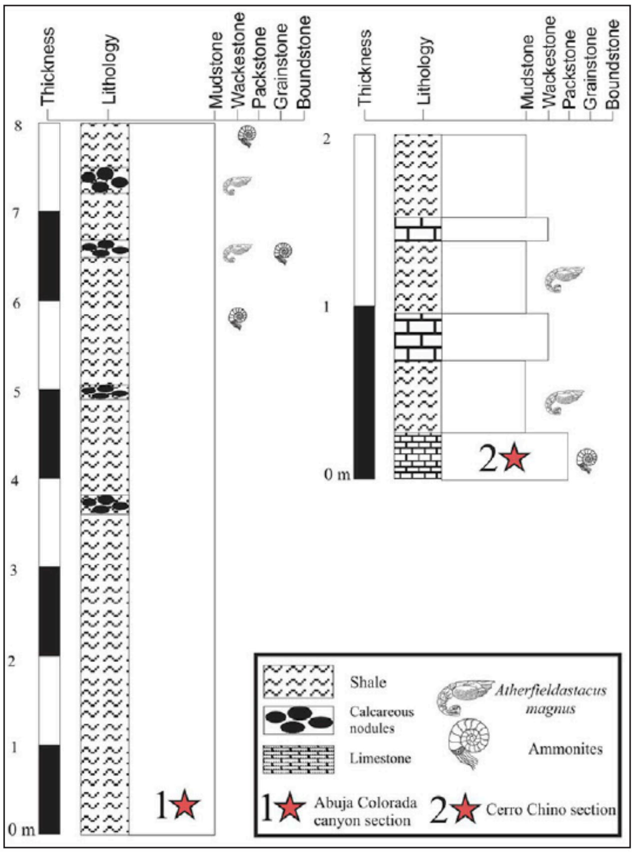

Fig. 2. Stratigraphical sections of outcrops of upper Aptian strata in Chihuahua State, showing fossiliferous beds (modified from González-León et al., 2018).

Material and methods

About 20 calcareous concretions were collected near Abuja Colorada, in a fossiliferous section dominated by shale. Specimens recorded herein were recovered from concretions of varying size, between 3 and 12 cm in length (Fig. 3) and were prepared with a Paleotools ME-9100 pneumatic percutor and subsequently sectioned transversely with a diamond saw blade and glued to microscopic slides with resin, which were then polished by hand, using Kemet polishing abrasive. A Zeiss polarising microscope, with an adapted Canon EOS Mark I camera, was used to take numerous images of cuticule structure. Thin sections and complete specimens are deposited in the Colección Nacional de Paleontología "María del Carmen Perrilliat", Instituto de Geología, Universidad Nacional Autónoma México (abbreviation: IGM).

Systematic palaeontology

Order Decapoda Latreille, 1802
Suborder Pleocyemata Burkenroad, 1963
Infraorder Glypheida Zittel, 1885
Superfamily Glypheoidea von Zittel, 1885
Family Mecochiridae Van Straelen, 1925
Genus *Atherfieldastacus* Simpson *in* Robin, Charbonnier, Merle, Simpson, Petit & Fernandez, 2016

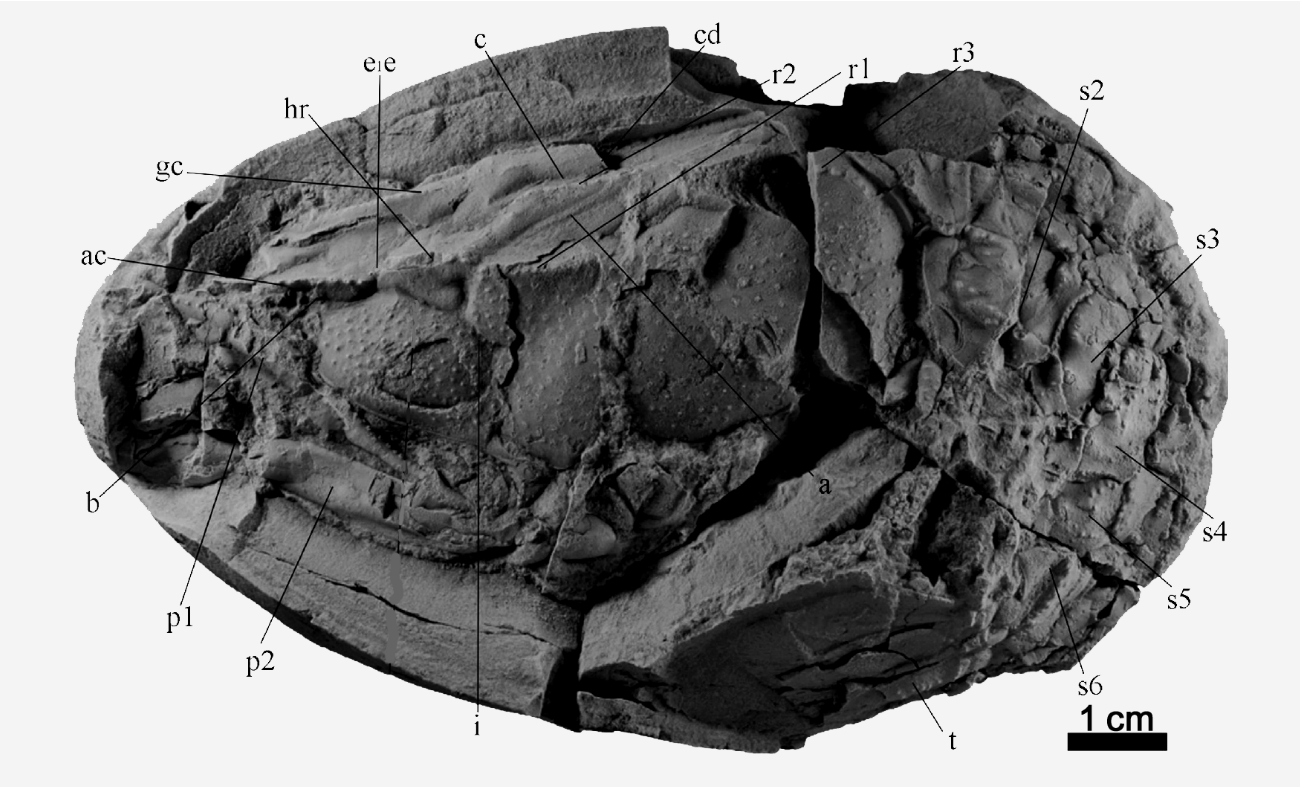

Fig. 3. *Atherfieldastacus magnus* (M'Coy, 1849), Abuja Colorada Canyon section (locality 1), Chihuahua State, northern Mexico; a near-complete specimen (IGM 9478) preserved in a calcareous nodule. Anatomical abbreviations are as follows: a = branchiocardiac groove; ac =antennal carina; b = antennal groove; c = post-cervical groove; cd = cardiac groove; e1e = cervical groove; gc = gastro-orbital carina; hr = hepatic ridge; i = inferior groove; p1-2 = pereiopods; r1-r3 = branchial ridges; s2-6 = pleonal somites; t = telson. Scale bar in cm. Photograph: Josep A. Moreno-Bedmar (modified from González-León et al., 2018).

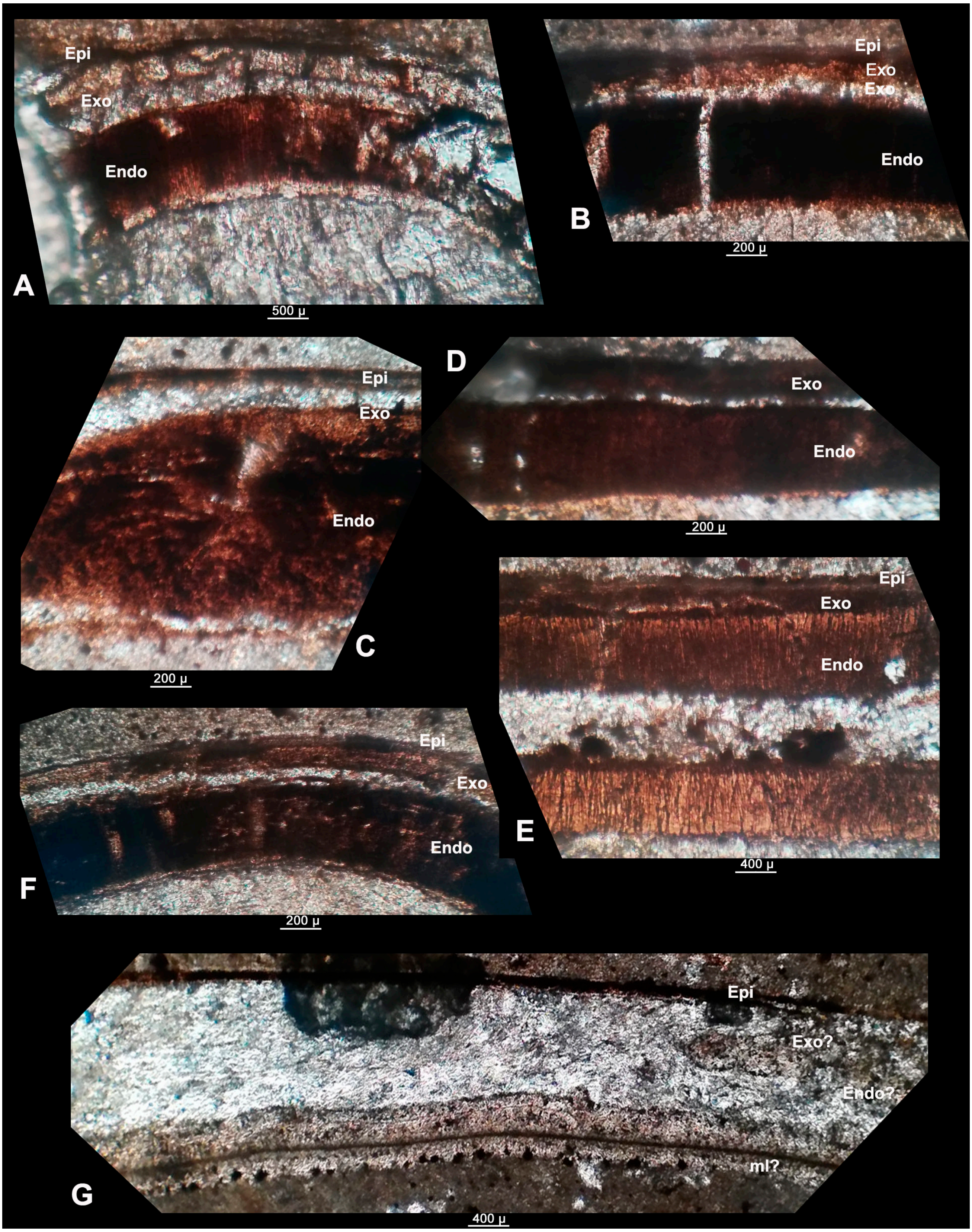

Fig. 4. A-G, Several views of thin sections of *Atherfieldastacus magnus* (M'Coy, 1849) from the upper Aptian of Chihuahua State, northern Mexico. Abbreviations: Endo = endocuticle; Epi = epicuticle; Exo = exocuticle.

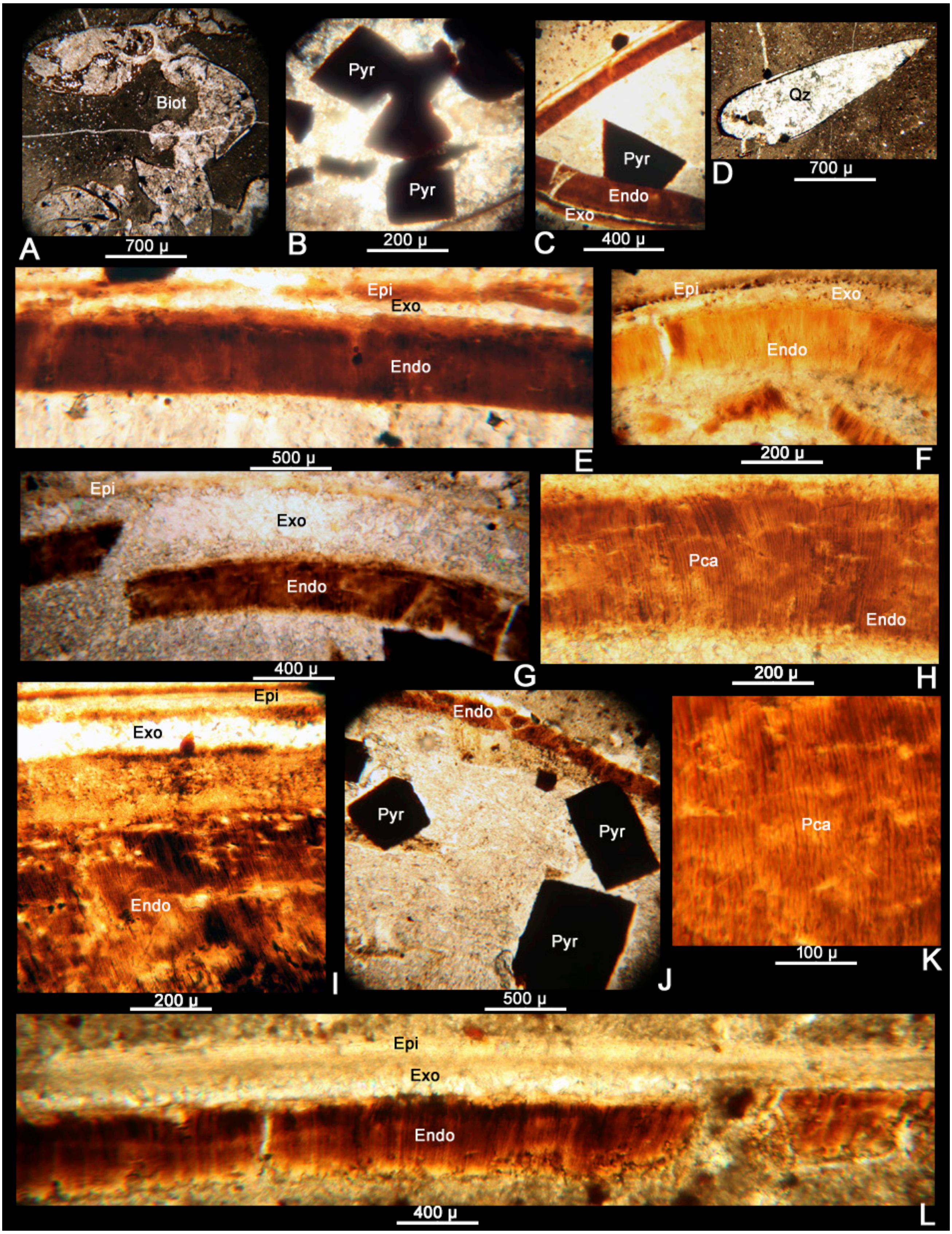

Fig. 5. Several views of thin sections of *Atherfieldastacus magnus* (M'Coy, 1849) from the upper Aptian of Chihuahua State, northern Mexico. Abbreviations: Biot = bioturbation; Endo = endocuticle; Epi = epicuticle; Exo = exocuticle; Pca = pore channels; Pyr = pyrite; Qz = quartz. Scale bars in μm.

Type species: *Meyeria magna* M'Coy, 1849, by original designation.

Other included species: *Atherfieldastacus rapax* (Harbort, 1905) and *A. schwartzi* (Kitchin, 1908).

Atherfieldastacus magnus (M'Coy, 1849)
(Fig. 3)

Diagnosis: See González-León et al. (2018).

Material examined: Specimens in 22 calcareous concretions, of which eight were sectioned for analysis of cuticular structure; in total, 30 thin sections of different portions of the lobster body were obtained.

Cuticle structure

Analysis and discussion: In our analysis of cuticule structure, it was possible to recognise clearly the three cuticle layers. In some cases, only a single layer was discernible. Elements of cuticule microstructure, such as pore canals, were also observed (Figs. 4, 5). Previously, such features had been recorded by Feldmann & Tshudy (1987), Vega et al. (1994) and González-León et al. (2016, 2018), both for other species and for *Atherfieldastacus magnus*, but recrystallised cuticles do not show clear layers (González-León et al., 2016).

The newly collected specimens clearly present three discrete layers of cuticle. The first layer observed is the epicuticle (epi), which normally has a thin bilaminar structure; this could not be observed. Below the epicuticle is the second layer or exocuticle (exo), composed of chitin protein fibres, stacked in layers with variable orientations (Green & Neff, 1972; Haj & Feldmann, 2002). This layer is altered, but still discernible in almost all specimens studied (Fig. 4). The microstructure is replaced by sparry calcite, as seen in Figures 4A-C and G, although some fibres can still be noted (Fig. 4E). The most strongly calcified layer is the third one; this is the endocuticle (endo) which presents broad lamellae in the outer portion and thin laminations on the inner part (Feldmann & Tshudy, 1987). Vertical laminations within the endocuticle were noted in specimens from Chihuahua and interpreted as pore channels (Figs. 4A, E; 5H, K). A pigmented layer at the top of the endocuticle could also be observed (Fig. 4D-F). This might be associated with the original pigment (quinona), as previously recognised by Taylor (1973) and Vega et al. (1994). An example of how the microstructure and boundaries between layers can be altered by diagenetic processes was observed as well (Fig. 4G). The epicuticle can be clearly recognised (Figs. 4B, E; 5F, G, I, L), but only as a single layer, not as a double layer, which is typical. The membranous layer was not preserved, similar to what has been recorded for other extinct species (Roer & Dillaman, 1984; Vega et al., 1994, 2005; Haj & Feldmann, 2002).

Conclusions

The completeness of cuticule structure (especially the basis of the endocuticle) and the 3-D preservation and articulation of carapaces with appendages suggest that the Chihuahua specimens represent corpses that were accumulated during anoxic events. The presence of small pyrite crystals in the matrix and larger ones in appendages (Fig. 5B, C, J) supports such an interpretation, along with bioturbations observed in some thin sections; these were possibly caused by scavengers that were feeding on cuticle remains and other organic matter (Fig. 5A). Abundant pyrite has also been observed in specimens of *Atherfieldastacus magnus* from the Aptian of Colombia (González-León et al., 2016). This suggests that localities around the world, where *A. magnus* is abundant, may represent anoxic events that either killed the lobster populations and/or preserved the remains of this globally distributed species during the Early Cretaceous.

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New early Paleocene (Danian) paguroids from deep-water coral/bryozoan mounds at Faxe, eastern Denmark

Novi zgodnjepaleocenski (danijski) raki samotarji iz globokovodnih koralno-briozojskih kop nahajališča Faxe na vzhodnem Danskem

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Ključne besede: Anomura, Paguroidea, paleogen, morfologija škarnikov, Danska

Abstract

During recent decades, decapod crustacean faunas from middle Danian (lower Paleocene) strata at Faxe (Sjælland, Denmark) have been studied in detail. However, paguroid anomurans have not yet been described formally. Two new species of hermit crab have lately been recognised in the collections of the Geomuseum Faxe. Percentages of total paguroid assemblages and feeding behaviour derived from the morphology of its chelae indicate that one of these, *Dardanus faxensis* sp. nov., as a generalist, was better adapted to inhabit the deep-water reefal environment of the Faxe carbonates than the more specialised, suspension-feeding *Paguristes frigoscopulus* sp. nov.

Izvleček

V zadnjih desetletjih so bile podrobno proučene združbe rakov deseteronožcev iz srednjedanijskih (spodnjepaleocenskih) plasti v Faxu (Sjælland, Danska), vendar raki samotarji do sedaj še niso bili opisani. Pri pregledu zbirk muzeja Geomuseum Faxe sta bili prepoznani dve novi vrsti rakov samotarjev, ki ju predstavljamo v tem prispevku. Zastopanost ostankov v celotni združbi in način prehranjevanja, ki ga kaže funkcionalna morfologija škarij, pričajo, da je bil eden od teh, to je vrsta *Dardanus faxensis* sp. nov., kot generalist bolje prilagojen za bivanje v globokomorskem grebenskem okolju od bolj specializiranega suspenziofaga *Paguristes frigoscopulus* sp. nov.

Introduction

In general, records of paguroid remains from Danian-aged rocks are scarce and hermit crab assemblages of this age remain largely understudied. Vega et al. (2007) recorded a right and an incomplete left chela of a diogenid from the Rancho Nuevo Formation at Coahuila (Mexico), while Armstrong et al. (2009) described a right paguroid palm, without systematic placement, from the Midway Group of Texas, USA. In addition, Cope et al. (2005) noted *Paguristes johnsoni* Rathbun, 1935, on the basis of a single, well-preserved propodus and an additional fragment of a carpus that were closely comparable to the type material illustrated and described by Rathbun (1935) from the Sucarnoochee Formation of Alabama (USA).

Robin et al. (2017) mentioned an indeterminate species of *Paguristes* Dana, 1851 from a privately held collection of Danian decapod crustaceans from Vigny, France. It would appear that this locality was very rich in paguroids of earliest Paleocene age (Wallaard et al., 2020), but unfortunately this material is not currently accessible for scientific assessment and publication.

A brief visit to the collections of the Geomuseum Faxe (September 2019) has now resulted in the recognition of fourteen hermit crab specimens along with the material from the collections at the Natural History Museum (Copenhagen), all partially complete chelae. The two new paguroid taxa erected to accommodate these forms from the middle Danian of Faxe present a valuable addition to the hermit crab faunas from this time interval.

Geological setting

A large, cool-water, subphotic coral/bryozoan mound complex at Faxe developed in the Danish Basin during the early Danian, shortly after the Cretaceous/Paleogene boundary event (e.g., Bjerager et al., 2018; Schrøder & Surlyk, 2019). During the middle Danian, a low-diversity scleractinian coral fauna initiated the formation of extensive cold-water coral mound complexes that intercalated with bryozoan mounds (e.g., Lauridsen et al., 2012). The coral mounds started to grow below the photic zone over the easternmost part of the Ringkøbing-Fyn High, only 2 million years after the mass extinction at the K/Pg boundary (Lauridsen et al., 2012).

The middle Danian limestones exposed at Faxe quarry (Fig. 1) document the extraordinary preservation of a 63-myr-old, cold-water coral mound ecosystem. Bryozoan mounds dominate the stratigraphically lower parts and are overlain by interfingering coral and bryozoan mounds. The Faxe quarry exposes a large mound complex that includes individual coral mound bodies. The mound complex is dominated by the frame-building scleractinian coral species, *Dendrophyllia candelabrum* (Hennig, 1899), which is associated with common *Faksephyllia faxoensis* (Lyell, 1837) and minor numbers of *Oculina becki* (Brünnich Nielsen, 1922). A highly diverse fauna is found in middle Danian strata at Faxe quarry, including serpulid annelids, arthropods, brachiopods, bryozoans, coelenterates, echinoderms, sponges and molluscs (Lauridsen et al., 2012, table 1).

The quarry at Faxe comprises the best-studied Danian decapod crustacean fauna worldwide (Jakobsen & Collins, 1997). Studies dealing with such taxa, in chronological order, are the follow-

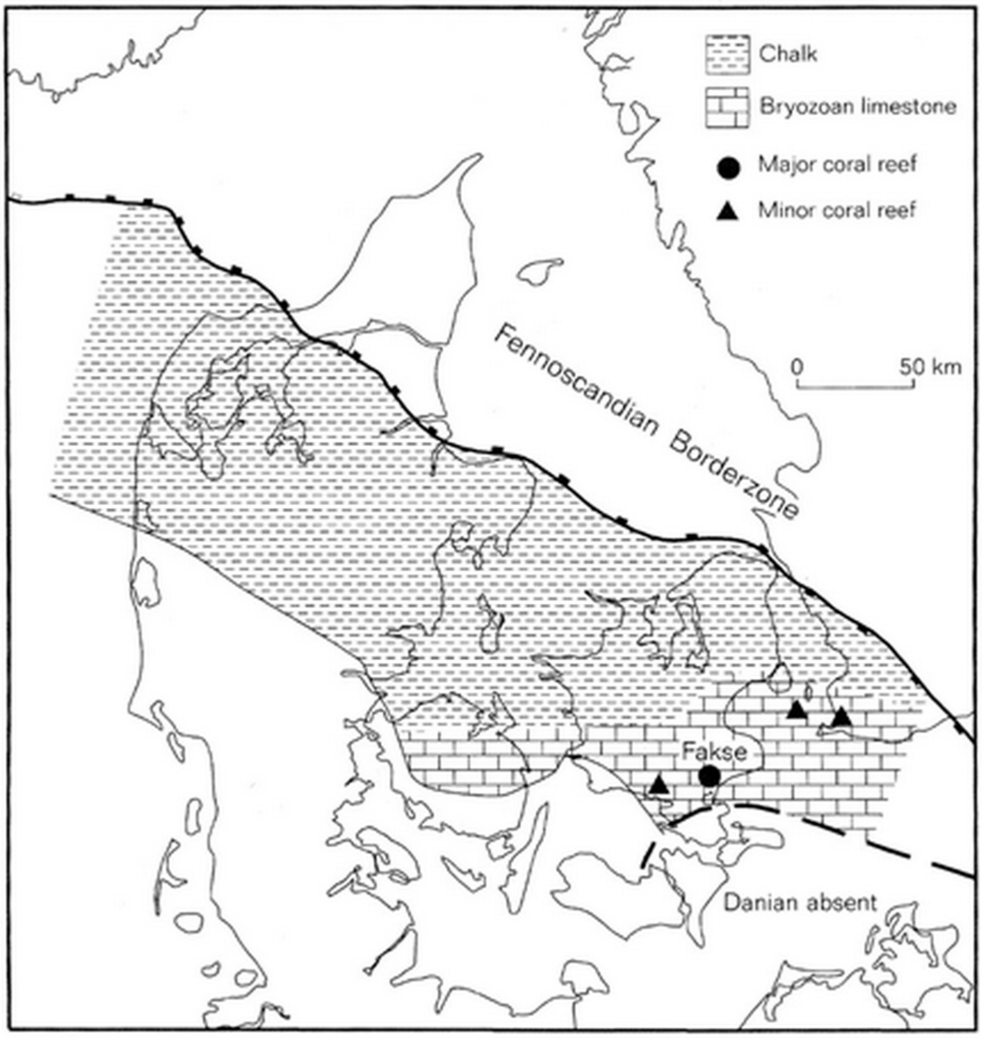

Fig. 1. Position of Faxe quarry and the main structure of the Danish area during the middle Danian (compilation by Dr Erik Thomsen, Geological Institute, Aarhus University, Denmark).

ing: von Schlotheim (1820), Reuss (1859), von Fischer-Benzon (1866), Segerberg (1900), Woodward (1901), Rasmussen (1973), Förster (1975), Jagt et al. (1993), Collins & Jakobsen (1994), Jakobsen & Collins (1997), Fraaije (2003), Jakobsen (2003), Jakobsen & Feldmann (2004), Collins (2010), Robin et al. (2015) and Klompmaker et al. (2015, 2016). However, in none of these are any paguroid remains recorded, so that our present note is the first formal description of middle Danian hermit crab taxa from Faxe.

Material and methods

The taxonomic descriptions are based on material stored at the Geological Museum (now Natural History Museum of Denmark) and and Geomuseum Faxe. Our material comprises fourteen specimens belonging to two genera, represented by two new species. The material included in the present study was collected mainly by Curator Søren Bo Andersen and the late amateur palaeontologist, Alice Rasmussen, of Faxe. In 2012, the latter was awarded the prestigious Mary Anning Prize of the Palaeontological Association (London) in recognition of her outstanding work on fossils from the type locality of the Danian Stage at Faxe. The present material was collected in various parts of the quarry over many years.

The chelae are preserved mainly in the form of internal and external moulds in the coral limestone and therefore our descriptions are in part based on casts. However, that of the holotype of *Paguristes frigoscopulus* relied on the internal mould (‘steinkern’). Preparation and photography of the material followed the procedures outlined in Jakobsen & Feldmann (2004).

Institutional abbreviations. MGUH, Natural History Museum of Denmark (Geological Museum), Copenhagen, Denmark; OESM, Geomuseum Faxe, Faxe, Denmark.

Systematic palaeontology

Order Decapoda Latreille, 1802
Infraorder Anomura H. Milne Edwards, 1832
Superfamily Paguroidea Latreille, 1802
Family Annuntidiogenidae Fraaije, 2014
Genus *Dardanus* Paul’son, 1875

Dardanus faxensis sp. nov.
(Figs. 2-5)

2005 Eremitkrebs 20 mm**; Damholt & Rasmussen, p. 22, unnumbered figures.
2005 Klo fra eremitkrebs 20 mm**; Damholt & Rasmussen, p. 38, unnumbered figure.
2010 Eremitkrebs 20 mm**; Damholt et al., p. 23, unnumbered figures.
2010 Klo fra eremitkrebs 20 mm***; Damholt et al., p. 42, unnumbered figure.

Diagnosis: Palm transversely oval; inner and outer sides longitudinally and transversely convex; outer side of palm covered with forwardly directed, largely spinose tubercles; proximal part of outer side of palm and distal part of inner side irregularly covered with capsulated setae arranged in a curved row; fixed finger elongated, with a horseshoe-shaped, spoon-like tip.

Etymology: In reference to the type locality.

Type material: The holotype, OESM 6811, is a near-complete right palm with fixed finger, measuring 10 mm in length and 6 mm in greatest width; both external and internal moulds are present (Fig. 2A-G). Paratypes are MGUH 33401, MGUH 33402, OESM 581, OESM 10178 OESM 10179 and OESM 10180, all representing incomplete right palms; MGUH 33403, MGUH 33404, MGUH 33405, MGUH 33406 and MGUH 33408 are incomplete left palms.

Locality and stratigraphy: The coral limestone assigned to the Faxe Formation has been known for centuries due to the extensive quarrying. The middle Danian levels exposed at Faxe quarry represents an extraordinary preservation of a 63-myr-old, cold-water coral mound complex. This coral limestone complex was formally described as a new formation by Lauridsen et al. (2012). The type locality of the Faxe Formation is a Danish GeoSite and is accessible to all members of the public. The formation was dated as middle Danian (calcareous nannoplankton zones D5-6 of Perch-Nielsen, 1979 and NNTp3-NNTp4a of Varol, 1998).

Description: Cross section of palm transversely oval; inner and outer sides longitudinally and transversely convex, curving slightly inwards; dorsal edge straight, ventral edge concave at central part; outer side of palm covered with forwardly directed, largely spinose tubercles, largest tubercles irregularly arranged along dorsal edge and outer distal half and proximal half of fixed finger, proximal part of outer side of palm irregularly covered with multiple capsulated setae arranged in circles or rows; inner side of palm smooth with on distalmost part few curved rows of multiple setae (Fig. 3B); fixed finger elongated, curved inwardly, with horseshoe-shaped, spoon-like tip, which is covered on outer side with a row of very large pits; the cutting edge is covered with about three variably sized, molar-like calcareous teeth.

Fig. 2. *Dardanus faxensis* sp. nov., holotype (OESM 6811). The top three - silicone rubber casts of external mould; the bottom four internal mould. Scale bar in millimetres.

Remarks: Normally, setal pits are situated around the bases of tubercles and/or on the adjacent integument, but usually not on the tubercles themselves. Multiple capsulated pits have previously been recorded for both fossil and extant species of paguroids (see Fraaije et al., 2011, 2015a; Hyžný et al., 2016). During the Paleogene, the genus *Dardanus* appears to have been highly successful and widely distributed (Fraaije & Polkowsky, 2016). In the case of *Dardanus faxensis* sp. nov. all tubercles on the outer side of the palm have large setal pits (Fig. 2A); this morphological trait differentiates it immediately from all congeners. For a list of all known fossil species referred to the genus, reference is made to Fraaije et al. (2011) and to Fraaije & Polkowsky (2016). The shape of the chelae is indicative of a deposit feeder that was also capable of browsing, scavenging and suspension feeding. This type of paguroid fed by scraping material from corals or other solid surfaces using the tips of the spoon-like chelae (compare Schembri, 1982). One specimen, MGUH 33406, is totally covered with epibionts, mainly subcircular colonies of bryozoans (Fig. 4).

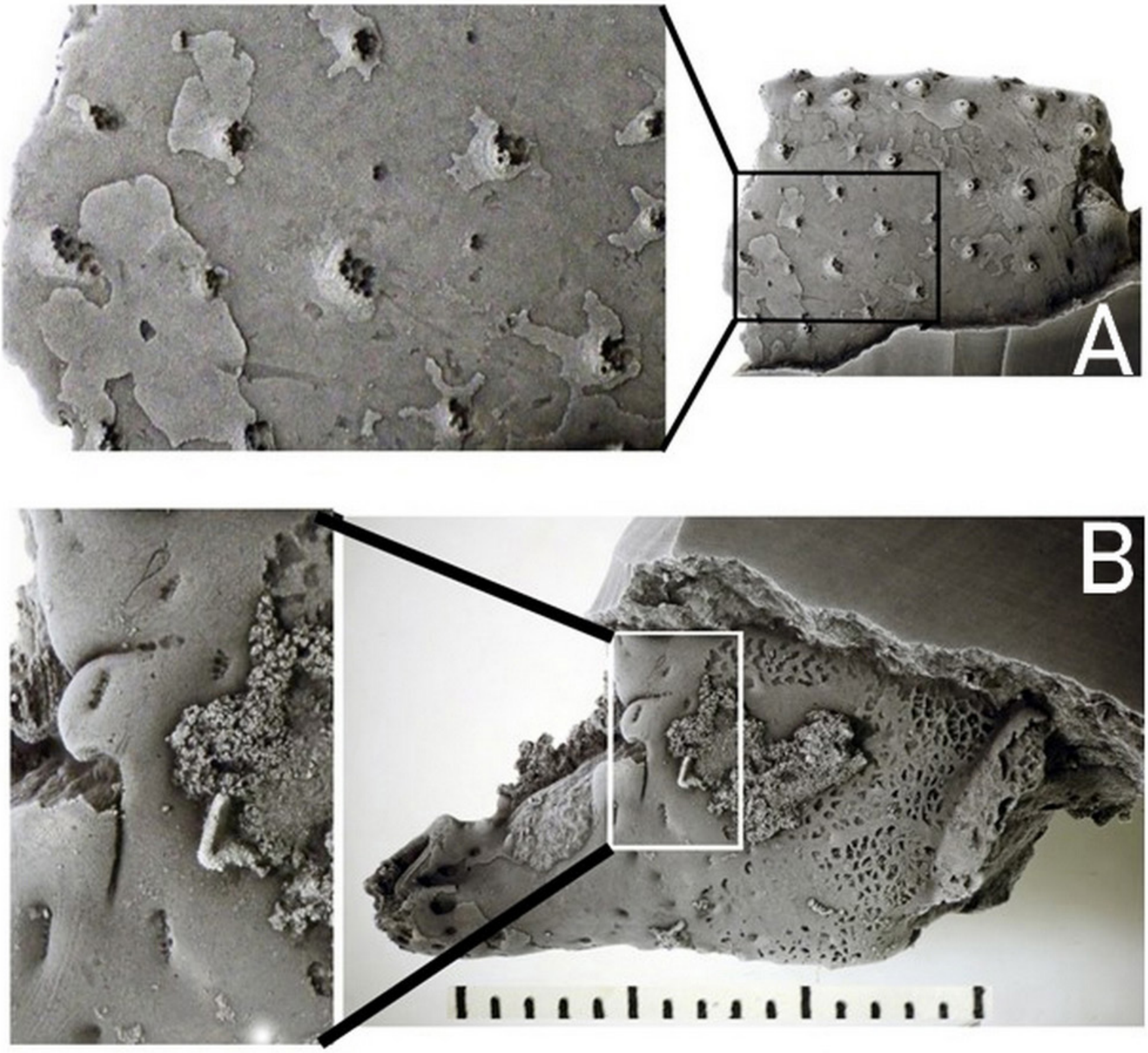

Fig. 3A. *Dardanus faxensis* sp. nov., silicone rubber cast of external mould of incomplete right palm, outer side (OESM 10178), showing setal pits and tubercles; B. Silicone rubber cast of external mould of incomplete right palm (MGUH 33401, GMF 2004-1802), showing rows of multiple setal pits. Scale bar in millimetres.

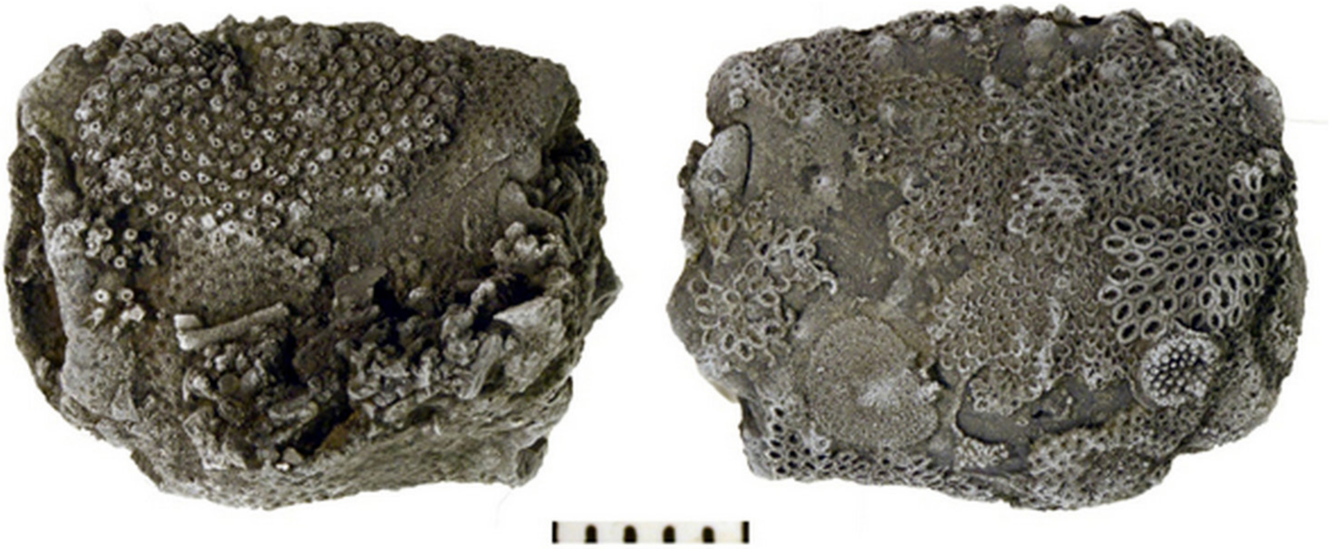

Fig. 4. *Dardanus faxensis* sp. nov., MGUH 33405, incomplete left palm covered with epibionts. Scale bar in millimetres.

Fig. 5. *Dardanus faxensis* sp. nov., specimens OESM 6811, OESM 10180 and OESM 10179, respectively, with remains of serpulid/spirorbid annelids (arrows) on the outer palm surface near the base of the fixed finger. Scale in millimetres.

Three specimens of *D. faxensis* sp. nov. bear remains of serpulid/spirorbid annelids on the outer palm surface at the base of the fixed finger (Fig. 5). This appears to have been a symbiotic relationship, rather than *post-mortem* serpulid attachment to moulted anomurans, as described by Jakobsen & Feldmann (2004).

Family Diogenidae Ortmann, 1892
Genus *Paguristes* Dana, 1851
Paguristes frigoscopulus sp. nov.
(Fig. 6A-E)

Diagnosis: Right cheliped transversely oval; outer, dorsal and ventral sides convex, inner side almost straight; outer side covered with regular, dense cover of fine, forwardly directed tubercles, fixed finger short, stout and triangular.

Etymology: From Latin, *frigus*, meaning cold, and *scopulus*, meaning reef.

Type material: The holotype, OESM 6705, is a near-complete right palm with fixed finger, measuring 8.5 mm in length and 5.5 mm in greatest width. The paratype, MGUH 33407, is an incomplete right palm, still embedded in coral-limestone.

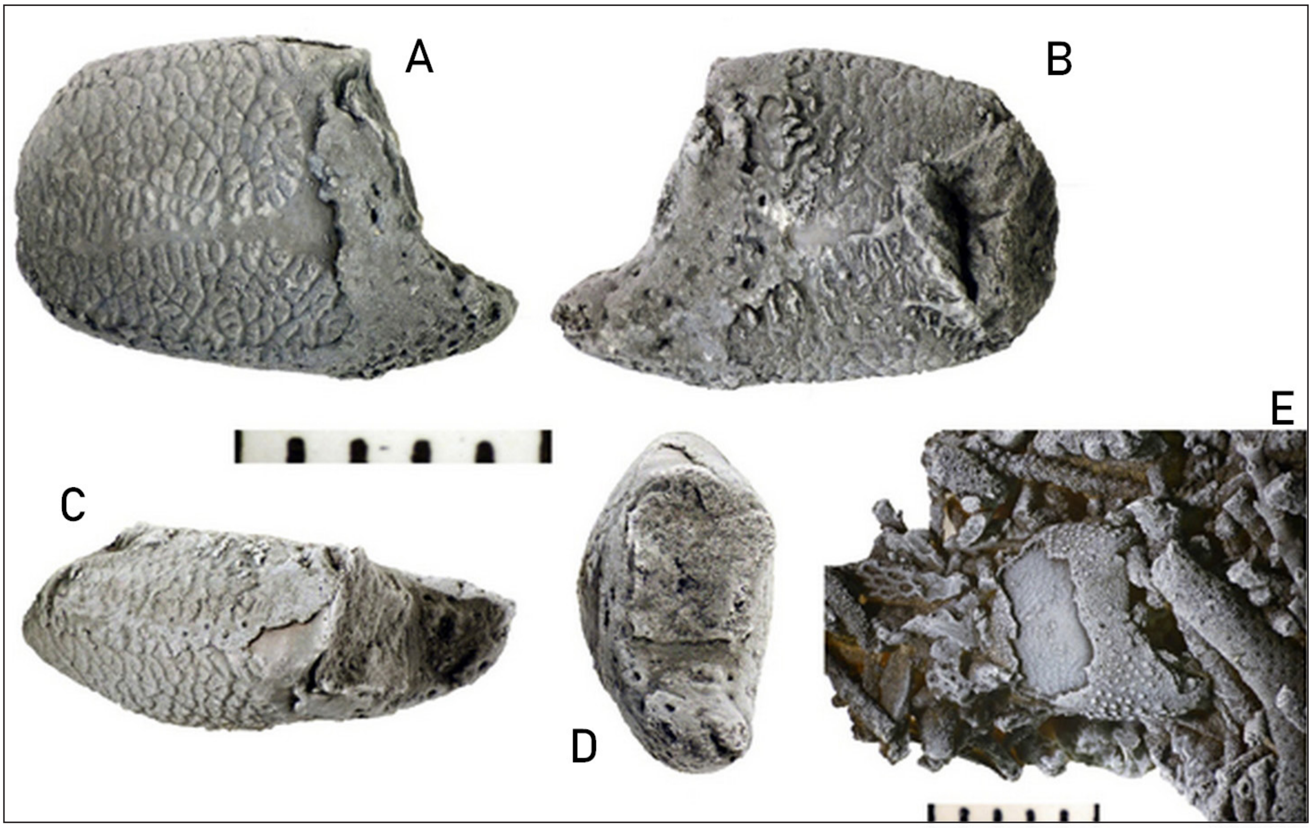

Fig. 6A-E. *Paguristes frigoscopulus* sp. nov., A-D. Holotype (OESM 6705), a near-complete right palm in internal mould preservation; E. Paratype (MGUH 33407), an incomplete right palm, still embedded in coral limestone. Scale bar in millimetres.

Locality and stratigraphy: The same as for *Dardanus faxensis* sp. nov. (see above).

Description: Cross section of right palm transversely oval; outer, dorsal and ventral sides convex, inner side almost straight; outer side with regular, dense cover of fine, forwardly directed tubercles; fixed finger short, stout and triangular; occlusal margin straight without teeth, surrounded by few large pores; interdigital margin oblique; length of fixed finger about one quarter of total length.

Remarks: Fraaije et al. (2015b) listed all extinct species of *Paguristes* known at that time. With a convex dorsal and ventral edge and a short, convex triangular fixed finger, *P. frigoscopulus* sp. nov. is morphologically closest to the late Albian *P. liwinskii* Fraaije, van Bakel, Jagt & Machalski, 2015 from east-central Poland and *P. santamartaensis* Feldmann, Tshudy & Thomson, 1993, from the Campanian of Antarctica. It differs in having a less dense, more forwardly directed, tuberculose ornamentation.

Conclusions

In total, fourteen specimens were available for the present study. Of these, about 86 % (12 specimens) are attributed to *D. faxensis* sp. nov. and only *c.* 14 % (2 specimens) to *P. frigoscopulus* sp. nov. Unfortunately, there are no detailed studies yet that relate cheliped morphology to feeding strategy. Schembri (1982) is one of the few studies that documented a close relationship between cheliped morphology and types of feeding. If we extrapolate his data to *Dardanus faxensis* sp. nov., that species may be considered to have been a generalist and better adapted to the Danian deep-water reefal environment of Faxe than *P. frigoscopulus* sp. nov., which probably was mainly a filter feeder.

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Lophoranina maxima Beschin, Busulini, De Angeli & Tessier, 2004 (Decapoda Brachyura, Raninidae) from Lower Eocene laminites of the "Pesciara di Bolca" (Verona, northeast Italy)

Lophoranina maxima Beschin, Busulini, De Angeli & Tessier, 2004 (Decapoda Brachyura, Raninidae) iz spodnjeeocenskih laminiranih apnencev "Pesciara di Bolca" (Verona, severovzhodna Italija)

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Ključne besede: raki, deseteronožci, tafonomija, paleogen, Sredozemlje

Abstract

The sole specimen of a raninid crab found to date in the Lower Eocene Fossil-Lagerstätte of the "Pesciara di Bolca" (Verona, northeast Italy) and referred to *Lophoranina maxima*, is described. Results of a CT analysis of this specimen and of a study of its cuticle are discussed.

Izvleček

Opisan je edini primerek raninidne rakovice, ki je bila do sedaj najdena v spodnjeeocenskih apnencih znanega nahajališča "Pesciara di Bolca" (Verona, severovzhodna Italija) in pripada vrsti *Lophoranina maxima*. Predstavljeni so rezultati CT analize primerka in analiza kutikule oklepa.

Introduction

Among representatives of the so-called "minor fauna" from the Lower Eocene Fossil-Lagerstätte called "La Pesciara" (Bolca, Vestenanova, Verona, northeast Italy; Fig. 1) abundant specimens of malacostracan crustaceans have been found; these are referred to the Isopoda, Decapoda and Stomatopoda. Most of these are housed in the collections of the Natural History Museum in Verona, the Fossil Museum at Bolca, the University of Padua and the Natural History Museum in Milan. After incomplete analyses published during the 19th century, they were studied in detail by Secretan (1975). Amongst brachyurans she described species of the families Macropipidae Stephenson & Campbell, 1960, Portunidae Rafinesque, 1815, Panopeidae Ortmann, 1893, Eriphiidae MacLeay, 1838 and, probably, of the Ocypodidae Rafinesque, 1815. Since then some of these remains have been revised and additional specimens recovered. Vonk et al. (2015) studied the Isopoda, while additional papers dealt with stomatopods (see Giusberti et al., 2014). Finally, Pasini et al. (2019a, b) thoroughly revised the crustacean fauna from this area.

The sole specimen of the genus *Lophoranina* Fabiani, 1910a from the "Pesciara" laminites (Fig. 2) is on display in the permanent exhibition of the Natural History Museum in Verona. Despite easy access to this fossil it has never been analysed in full. The reason why it was not included in her study by Secretan (1975) is unknown: at that time, it certainly was already housed in the palaeontological collections of the Veronese museum. It was recorded for the first time by Beschin et al. (2011) as *Lophoranina marestiana*

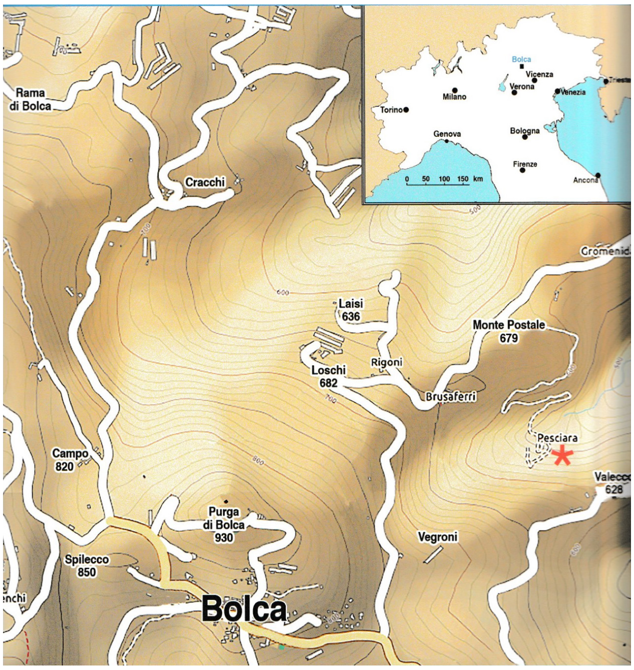

Fig. 1. Location of the "Pesciara di Bolca" site (modified after Beschin et al., 2016b).

(König, 1825), but not described. Later, Zorzin et al. (2019) referred it to *Lophoranina maxima* and this attribution has subsequently been confirmed by Pasini et al. (2019b). This note presents a detailed description and analysis of this particular individual.

Geological setting of the "Pesciara di Bolca"

The Bolca area, with its famous Fossil-Lagerstätten of the "Pesciara" and Monte Postale, is located in the eastern part of the Lessini Mountains at an altitude of about 800 metres above sea level near the watershed between the high Alpone Valley (Vestenanova, Verona) and the Chiampo Valley (Altissimo, Vicenza). This territory is part of the Southern Alpine tectonic unit; in a general geological framework it is constituted mainly by volcanic rocks and secondarily by small outcrops of carbonate rocks of Cretaceous–Paleogene age that rest on the so-called Trento Platform palaeogeographical unit. During the Middle Jurassic it formed a structural high between the Lombard and Belluno lateral basins; later it completely subsided and up to the Paleocene it assumed the character of a pelagic plateau with marine sedimentation. During Alpine Orogeny this area responsed rigidly to tectonic stresses and was broken up into blocks. Some of these rose up to shallow sea conditions; on these small carbonate platforms came into existence. Afterwards they built a unique structure called the Lessini Shelf (Bosellini, 1989).

Important faults produced during the Paleocene and Early and Middle Eocene activated volcanic cycles with emissions of great amounts of basic lavas, mostly submarine, associated with extensional tectonics (Piccoli, 1965, 1966). Late Eocene volcano-tectonic activity resulted in the opening of the Alpone-Agno graben or semigraben, a wide and lengthy depression delimited to the west by the Castelvero Fault and to the east by the Schio-Vicenza fault system. During quiescent phases of volcanism in the Early and Middle Eocene, carbonate sediments and marls were cyclically laid down in this graben (Barbieri et al., 1991; Zampieri, 1995). Despite intense magmatic activity, a rich fauna, represented by crustaceans,

Fig. 2. Panoramic view of the "Pesciara" site.

bivalves, gastropods, echinoids and other macrobiota inhabited the sea floor. Fossils are perfectly preserved and particularly abundant within the Eocene tuffites cropping out in the Chiampo Valley and in the Roncà area (central and southern Alpone Valley): they have been studied with great interest since the 18th century.

Tectonic stresses produced fragile responses on the calcareous rocks with the isolation of a series of blocks bounded by faults; some of these collapsed as olistolithes in the basin (Barbieri & Zampieri, 1992; Zampieri, 1995). This is the case for the "Pesciara" outcrop which is made up of a series of Lower Eocene calcareous strata, about 19 metres thick, and completely surrounded by volcanoclastic rocks (Papazzoni & Trevisani, 2006).

Fossils recovered from the "Pesciara", mostly fish and plants, are preserved in five successive horizons made of extremely fine-grained, thinly laminated limestones that are interbedded with detrital calcareous levels that yield invertebrate remains, mostly larger foraminifera, bivalves and gastropods. This succession of fine- and coarse-grained limestones testifies to cyclic phases of different environmental conditions.

The environment of the "Pesciara" is characterised by deposition of calcareous muds within an intra-platform basin, in which anoxic bottom conditions and a microbial film that developed on corpses enabled perfect preservation of its rich and diverse fossil fauna (Marramà et al., 2016; Friedman & Carnevale, 2018). The presence of coral reefs that are similar to the ones observed along the coasts of the present-day St. Croix Island (Caribbean Sea) cannot be excluded, at least along the outer margin of the "Pesciara" lagoon (Beschin et al., 2017).

The "Pesciara" is the most famous and important Eocene Fossil-Lagerstätte in Italy. Excavations since the 16th century, and particularly those in the 2000s on the instigation of the Museum of Natural History in Verona, have allowed to recover not only a great number of fish (Bosellini et al., 2014), but also remains of reptiles and birds and a rich "minor fauna". The latter comprises crustaceans (malacostracans and ostracods), scorpions, bivalves, cephalopods, gastropods, brachiopods, bryozoans, worms, corals, jellyfish and foraminifera.

Material and methods

The specimen studied here exposes the carapace in dorsal view as well as both chelipeds and is preserved as two slabs (width about 245 mm; length about 195 mm); it is housed in the collections of the Natural History Museum in Verona (Museo Civico di Storia Naturale di Verona), under registration numbers CR 55 and CR 56.

CR 55 is the negative (Figs. 3a, b), CR 56 the positive (Figs. 4a, b). CR 56 was computed tomography (CT) scanned and its cuticle was studied with the use of a stereoscopic microscope (Leica M165C).

Systematic palaeontology

Order Decapoda Latreille, 1802
Infraorder Brachyura Linnaeus, 1758
Section Podotremata Guinot, 1977
Subsection Gymnopleura Bourne, 1922
Superfamily Raninoidea De Haan, 1839
Family Raninidae De Haan, 1839
Genus *Lophoranina* Fabiani, 1910a

Type species: *Ranina marestiana* König, 1825, by original designation.

Lophoranina maxima Beschin, Busulini,
De Angeli & Tessier, 2004

1983 *Lophoranina reussi*; Busulini et al., p. 61, pl. 2, fig. 1 (*non* Woodward, 1866).

1988 *Lophoranina* cf. *reussi*; Beschin et al., p. 185, fig. 8, pl. 5, fig. 1; pl. 8, figs 1-4; pl. 9, fig. 1.

2004 *Lophoranina maxima* Beschin, Busulini, De Angeli & Tessier, p. 110, text-figs. 1, 2; pl. 1, figs. 1-3; pl. 2, figs. 1, 2.

2006 *Lophoranina maxima*; De Angeli & Garassino, p. 35.

2010 *Lophoranina maxima*; Schweitzer et al., p. 73.

2011 *Lophoranina marestiana*; Beschin et al., p. 38 (*pars*).

2011 *Lophoranina maxima*; Beschin et al., p. 46, text-fig. 9, pl. 4, fig. 1.

2019 *Lophoranina maxima*; Zorzin et al., p. 97, figs. 1, 2.

2019b *Lophoranina maxima*; Pasini et al., p. 261, fig. 17A, B.

Measurements (in mm): Carapace: maximum width ~ 95; posterior width ~ 50; length > 85. Right carpus: height ~ 20. Right propodus: maximum length ~ 50; maximum height ~ 35. Right dactylus: length ~ 30; height ~ 10.

Description (based on both positive and negative): Subovate carapace, dorsoventrally compressed and strongly damaged in both anterior and posterior parts; only right part of wide fronto-orbital margin preserved with a strong and

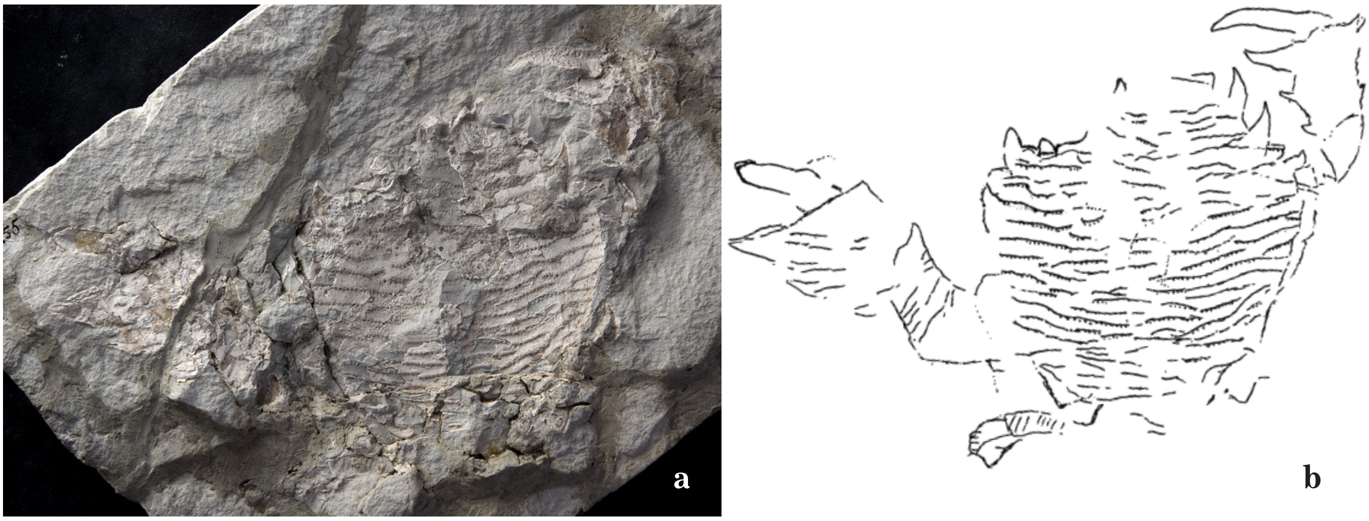

Fig. 3. CR 55, negative (maximum width 95 mm), in photograph (a) and line drawing (b).

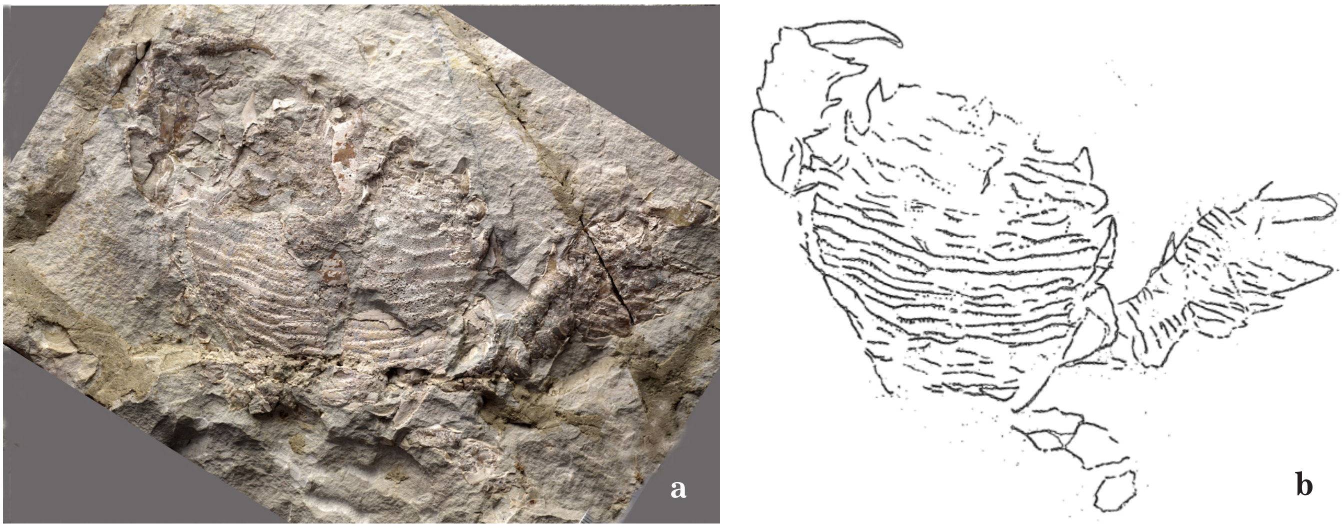

Fig. 4. CR 56, positive part (maximum width 95 mm), in photograph (a) and line drawing (b).

pointed lateral tooth and a supraorbital tooth defined by two fissures (Fig. 5a). Lateral margins convergent; almost completely preserved and appearing double because of separation of upper and lower part of carapace during fossilisation (Fig. 5b). In anterior part of right margin, traces of two large teeth visible; two spiny large teeth can be observed on left margin (Fig. 5c) linked to a fragment of carapace that was thrown forwards probably during fossilisation and so dislocated from original position. Rear part of right lateral margin showing granulated rim (Fig. 5d). Posterior margin, that should have been narrower than fronto-orbital margin, is lacking. Dorsal ornament with at least 21 subparallel transverse terraces, well preserved mainly in intermediate part of carapace, where terraces are nearly continuous from one side to the other, while rear ones appear interrupted. As far as can be seen, the frontal area was short. On terraces, bases of small spines that constituted them are visible as regularly spaced, tiny pits.

In median anterior part, there is a structure recognised as the sternal plate using CT scanning (Fig. 6b); it shows some weak transverse terraces that probably are traces of ornament of carapace impressed on it.

Both chelipeds are preserved: left one is settled near carapace, almost in anatomical position and covered with matrix; right one outstretched and shows propodus and carpus; both large, stout, covered with subparallel transverse ridges. Carpus appears almost squarish with a spine on upper distal angle; propodus shows a spine on upper margin and three spines on lower margin (including fixed finger); dactylus is long and sickle-shaped. Distal part of right fifth pereiopod with paddle-like dactylus.

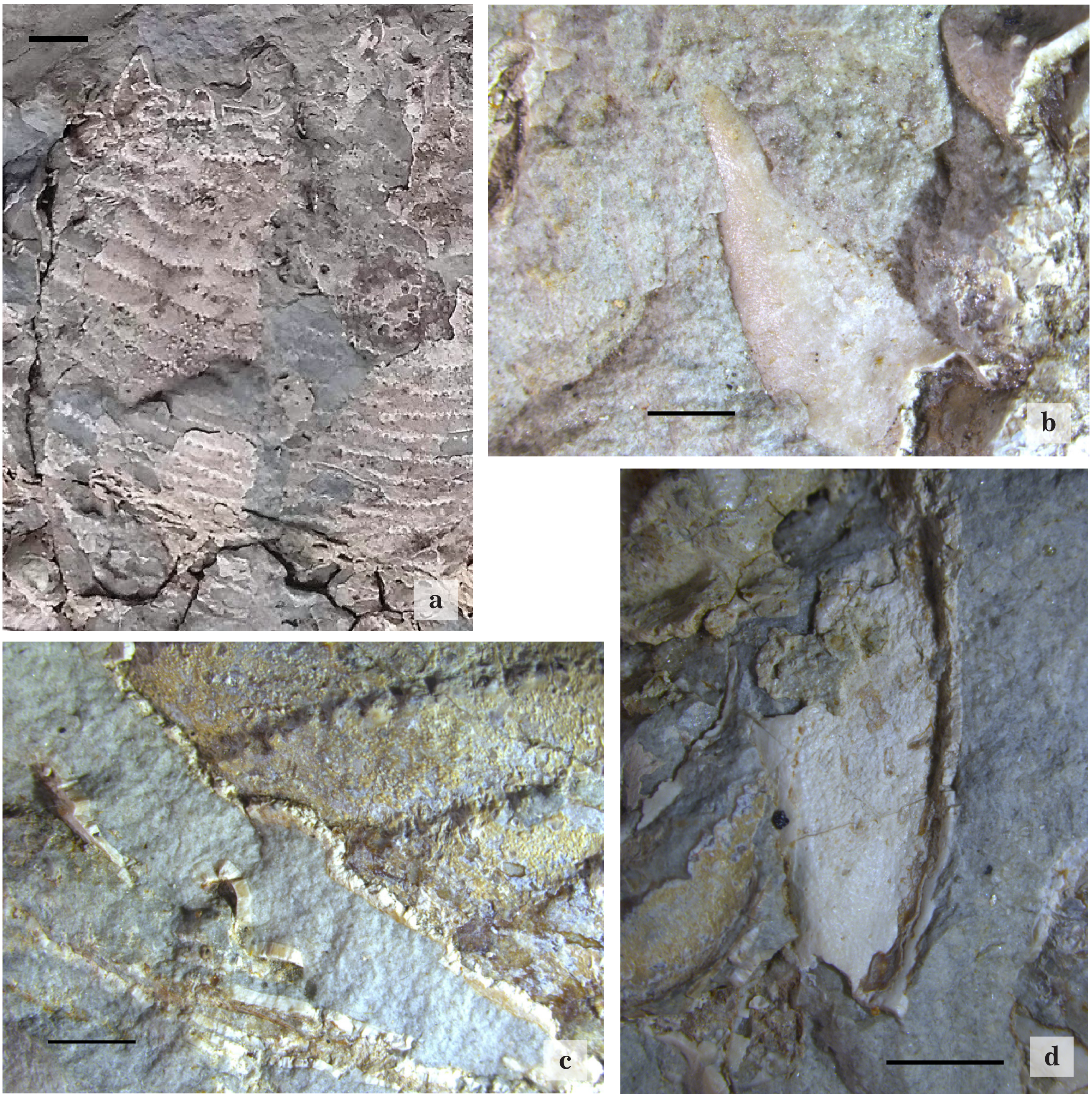

Fig. 5. Details of carapace: A. CR 55 (negative), right orbital and lateral margins (scale bar equals 10.0 mm); B. CR 56, double left posterolateral margin (scale bar equals 2.8 mm); C. CR 56, left anterolateral tooth (scale bar equals 2.5 mm); D. CR 56, right posterolateral margin (scale bar equals 4.0 mm).

Distribution: *Lophoranina maxima* has previously been recorded only from Lutetian (Middle Eocene) rocks at Main Quarry (Arzignano-Vicenza) and Case Pozza di San Giovanni Ilarione (Verona). It is now recognised in Ypresian (Lower Eocene) levels in the "Pesciara di Bolca" (Verona) and, according to Pasini et al. (2019b), also at Monte Postale.

Discussion

Fabiani (1910a; see also Fabiani, 1910b) erected the genus *Lophoranina* to accommodate species that had previously been included in *Ranina* Lamarck, 1801, but showed transverse terraces composed of tiny, forwardly inclined spines on the dorsal carapace surface. This extinct genus has a worldwide distribution and a stratigraphical range from the Eocene to the Miocene. In Veneto (northeast Italy), representatives of *Lophoranina* are highly characteristic of Eocene levels of volcanoclastic origin and include numerous species such as *L. avesana* (Bittner, 1883), *L. bittneri* (Lőrenthey, 1902), *L. laevifrons* (Bittner, 1875), *L. marestiana* (König, 1825), *L. maxima*, *L. reussi* (Woodward, 1866), *L. straeleni* Vía Boada, 1959 and, probably, *L. aldrovandii* (Ranzani, 1818) (see Beschin et al., 1988, 2011, 2016a). The structure of the dorsal terraces and the large

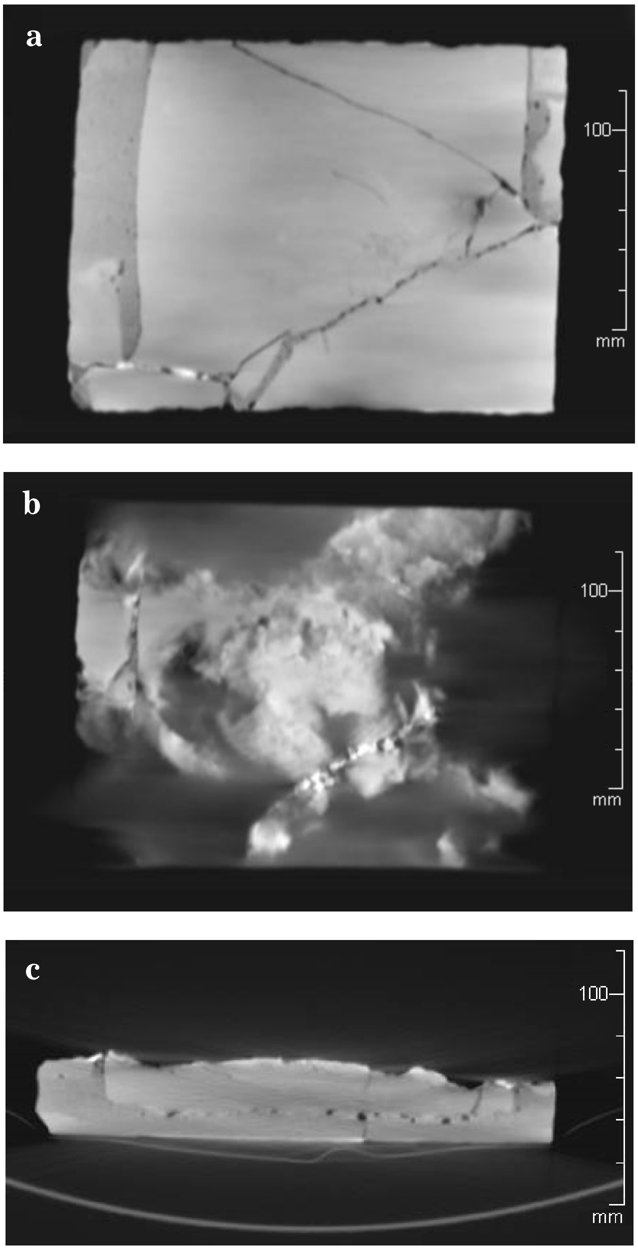

Fig. 6. CR 56. A. CT coronal reconstruction of the slab under the specimen (depth 20.1 mm); B. CT coronal reconstruction showing the specimen (depth 8.6 mm); C. CT axial scan (81 mm from the anterior margin of the slab).

carapace size, the short fronto-orbital region, the position and number (two) of anterolateral spines, the relatively short propodus of chelipeds with only three spines on the lower margin, all suggest that specimen CR 55/56 belongs to *Lophoranina maxima*. As far as comparisons with other large-sized species of *Lophoranina* are concerned, *L. avesana* has fewer ridges on the dorsal surface but these are more continuous and form a general anterior concavity; moreover, the anterolateral spines are spatulate rather than spiny, and the propodus of the cheliped is longer with a dentate lower margin. *Lophoranina marestiana* has a longer fronto-orbital area, more regular ridges, less acute anterolateral spines that are situated more anteriorly, the propodus of the cheliped with six spines (including the fixed finger) on the lower margin. The differences with the other species are greater.

Our CT analysis of specimen CR 56 (positive) has revealed that the matrix piece in which the specimen is preserved was broken into four main pieces along three straight fractures (Fig. 6a). One fracture cuts the specimen in the rear part of the carapace and a second one runs through the propodus of the right cheliped (Fig. 4a).

During restoration, fragments were fixed with a thick cement on a calcareous slab (in its turn divided into two parts) as a reinforcement (total thickness about 37 mm) (Fig. 6c). This preparation method was applied to fossils found in the "Pesciara" during the 1930s (Massimo Cipriano Cerato, pers. comm., 2019; the Cerato family of Bolca are the owners of the "Pesciara" site, where excavations have been ongoing for about two centuries, and during the last fifty years under supervision of the Museum of Natural History in Verona). Hence, specimens CR 55/66 of *Lophoranina maxima* was presumably collected during those years. The CT axial scan shows that the frog crab is almost completely dorsoventrally flattened and produced only a weak relief of the surface of the slab. The CT coronal reconstruction shows the outline of the carapace with a thick fracture in its rear part and the collapsed cardiac part; a small shield-shaped structure in the anterior part is reminiscent of the sternal plate (Fig. 6b); it was probably dislocated during fossilisation.

The general preservation of this specimen confirms observations made by Secretan (1975), who noted that the crustaceans found in the "Pesciara" were almost flattened and lost any reliefs, their outlines being "confused" and part of the cuticle removed and dislocated.

Cuticle is preserved mainly in specimen CR 55 (negative): it shows almost the entire carapace cuticle in its inner, deeper part (Fig. 5a). In specimen CR 56 (positive) only a few shreds of the cuticle can be seen. An analysis using a stereoscopic microscope detected thick cuticle in a natural cross section along the lateral margins of the carapace and at the tip of the dactylus, and revealed details of the deep structure of the finger. As can be seen in Figure 7a, the preserved cuticle in its upper margin is composed of a thick endocuticle that shows undulate laminations in its deep portion; each undulation corresponds to a small globular swelling in the amorphous filling of the dactylus surmounted

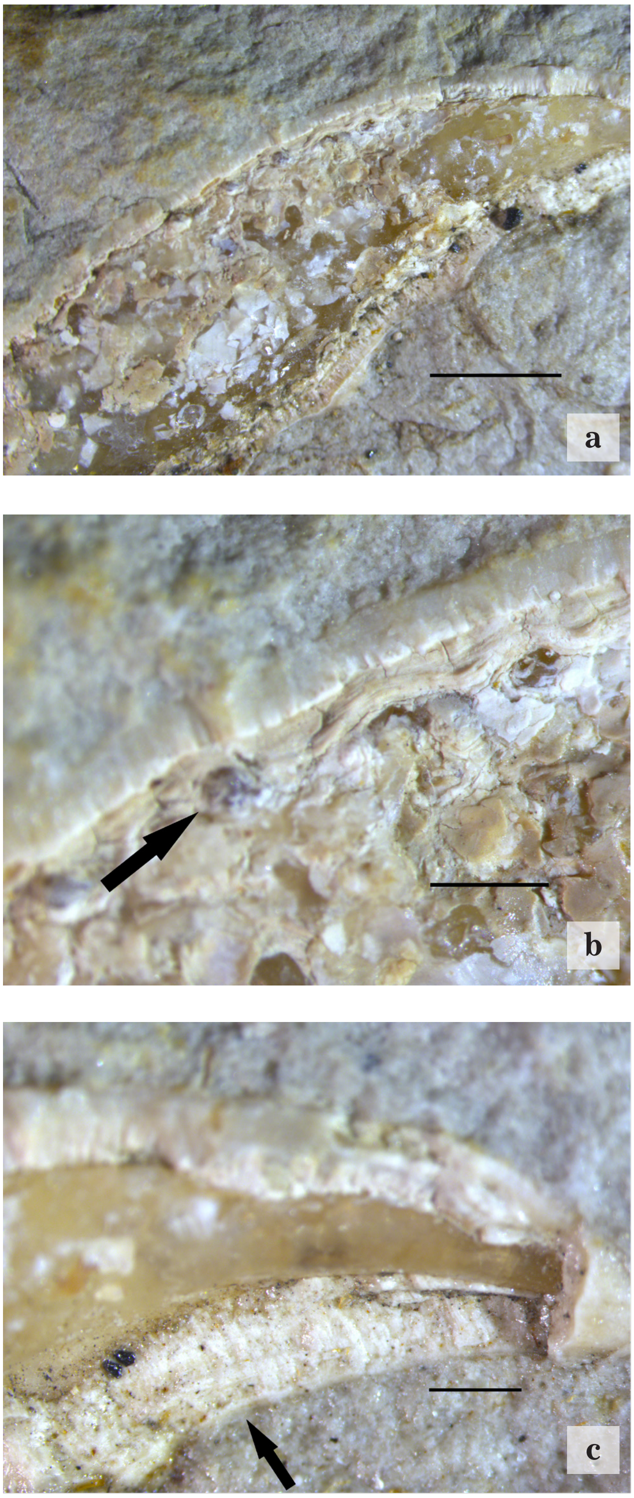

Fig. 7. CR 56. A. distal part of left dactylus (scale bar equals 4.0 mm); B. cuticle of dactylus: the arrow indicates a globular swelling associated with a tegumental canal (scale bar equals 1.0 mm); C. tip of left dactylus: the arrow indicates the exocuticle (scale bar equals 1.0 mm).

by a possibly tegumental canal (i.e., a vestige of a mechanoreceptive sensillum or a tegumental gland) (Fig. 7b) (Waugh et al., 2009a, b; Davie et al., 2015). On the lower margin of the dactylus, a fragmentary exocuticle can be observed as well (Fig. 7c).

The presence of a crab with burrowing habits may appear improbable in a palaeoenvironment that has generally been considered as anoxic, but many fish and also crustaceans found in the “Pesciara” were benthic species. Our analysis also aimed at determining whether or not this particular specimen was a moult or a corpse. Most of the individuals of *Lophoranina* in volcanoclastic rocks in Veneto are moults (in open moult position, or Salter’s position). The particular preservation of the specimen found in the “Pesciara” laminites does not allow this to be determined; however, the position of the chelipeds and the collapsed cardiac region suggest that it could be a corpse (Bishop, 1986). The good condition of the lower cuticle layer is in agreement with this hypothesis, although Waugh et al. (2009a) pointed out that this feature does not allow to determine with certainty the nature of a specimen in fossil material.

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A new xanthid crab, *Neoliomera zovoensis* sp. nov. (Decapoda, Brachyura), from the Lower Eocene beds of Zovo (Vestenanova, Verona, northeast Italy)

Neoliomera zovoensis sp. nov. (Decapoda, Brachyura), nova vrsta rakovice iz spodnjeeocenskih plasti nahajališča Zovo (Vestenanova, Verona, severovzhodna Italija)

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Ključne besede: Crustacea, Xanthidae, taksonomija, paleogen, Italija

Abstract

A new species of *Neoliomera* Odhner, 1925, *Neoliomera zovoensis* sp. nov. from the Lower Eocene (Ypresian) of Zovo (Vestenanova, Verona), which co-occurs with other decapod crustacean species in a richly fossiliferous coral-algal-reef in the Monti Lessini (Verona area, northeast Italy) is herein described.

Izvleček

V prispevku opisujemo novo vrsto rodu *Neoliomera Odhner*, 1925, *Neoliomera zovoensis* sp. nov. iz spodnjega eocena (Ipresij) iz nahajališča v Zovu (Vestenanova, Verona). Nova vrsta se pojavlja v združbi z drugimi deseteronožci v fosilno bogatem grebenskem apnencu s koralami in algami v regiji Monti Lessini (območje Verone, severovzhodna Italija).

Introduction

The rich arthropod fauna from the Paleogene levels in the Veneto region, which includes mysidaceans, isopods, stomatopods, and decapod crustaceans, has been recorded over the last two centuries. The decapod crustacean assemblage is rich in genera and species (see Fabiani, 1910; De Angeli & Beschin, 2001). Recent fieldwork has yielded numerous new decapod species in association with a bioherm or a smallsized coral reef (for a checklist of species and complete references see De Angeli & Garassino, 2006; De Angeli et al., 2019).

Geological and stratigraphical setting

The Bolca area (Verona, northeast Italy; Fig. 1) with fossil-rich deposits of "Pesciara" and Monte Postale, is renowned for the exceptional preservation of plants, invertebrates, and vertebrates, chiefly fishes. For a detailed description of the local geology and stratigraphy, see Fabiani (1914, 1915), Barbieri & Medizza (1969), Medizza (1980a, b), and Pasini et al. (2019).

Above the Scaglia Rossa (Late Cretaceous, Campanian) follows the so-called "Calcari di Spilecco" (late Paleocene-early Eocene), which is in turn overlain by *Lithothamnium* and *Nummulites* limestones, the fish-bearing strata of Pescara and Monte Postale, and the *Alveolina* limestones, plus marine, brackish, and terrestrial limestones of Monte Postale. Higher upsection, *Alveolina* and *Nummulites* limestones are exposed (hamlet of Brusaferri), a thick volcanic mass, containing terrestrial plants and freshwater molluscs (Monte Vegroni), shales with *Cypris* ostracod shells, and a coal bed with crocodilian and turtle remains (Monte Purga). The uppermost unit, at the

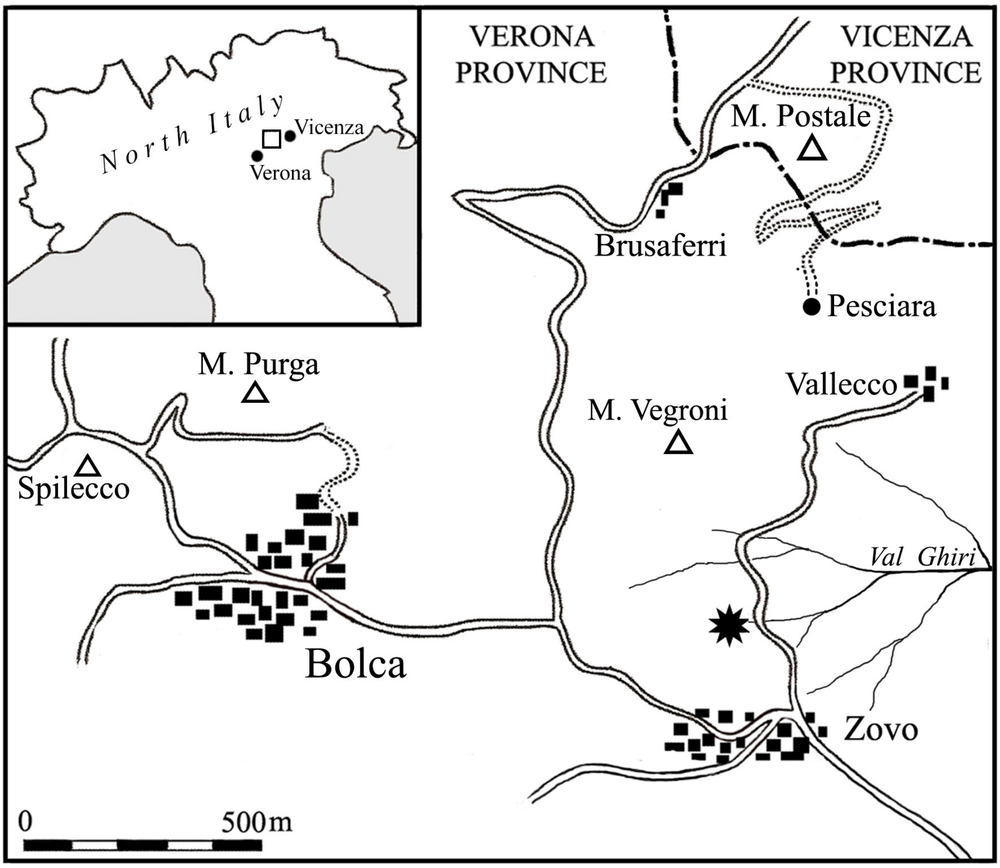

Fig. 1. Map of the Bolca area; the asterisk denotes the locality where the type specimen of *Neoliomera zovoensis* sp. nov. was collected (modified after De Angeli & Garassino, 2014).

top of Monte Purga, comprises columnar basalts. The uppermost stratified limestones along the northern side of Purga di Bolca are dated as late Ypresian (Barbieri & Medizza, 1969). The age of the reptile-bearing coal beds is still uncertain, but could possibly be Lutetian (middle Eocene).

The studied specimen was collected from white crystalline limestones with alveolinid and nummulitid foraminifera (Brusaferri Limestones), which also contain volcanic material, to the southeast of Bolca, along the road connecting Zovo and the hamlet of Vallecco (Fig. 1). The fossiliferous level at Zovo, containing coralligenous algae, corals, microforaminifera, scarce molluscan internal moulds, and exuviae of small-sized decapod crustaceans, was associated with a bioherm or a small-sized coral reef, which originated within the AlponeAgno graben. Formations such as this have been recorded from the Valle del Chiampo between Mussolino and Zovo di Castelvecchio (De Zanche, 1965) and along the eastern margin of Monti Lessini (Beschin et al., 2007; De Angeli & Garassino, 2002; De Angeli & Ceccon, 2012). Currently, the decapod crustacean assemblage from Zovo includes 24 species (for complete references see Beschin et al. 2016; De Angeli et al., 2019).

Material

One carapace preserving its entire cuticle within a small piece of coralligenous rock. It is housed in the palaeontological collection of the Museo Civico “D. Dal Lago” of Valdagno, Vicenza (MCV).

Abbreviations – lcxp: carapace length, wcxp: carapace width, wf: front width, wof: orbito-frontal width;

Systematic palaeontology

For the higher-level classification, we follow the arrangement proposed by Schweitzer et al. (2010).

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Section Eubrachyura de Saint Laurent, 1980
Subsection Heterotremata Guinot, 1977
Superfamily Xanthoidea MacLeay, 1838
Family Xanthidae MacLeay, 1838
Subfamily Liomerinae Sakai, 1976

Genus *Neoliomera* Odhner, 1925

Type species: *Zozymus pubescens* H.Milne Edwards, 1834, by original designation.

Included fossil species: *Neoliomera interme-*

dia Odhner, 1925 (fossil and extant), *N. kuohwai* Hu, 1981 (fossil), *N. minuta* Beschin, Busulini & Tessier, 2015 (fossil), *N. paleogenica* Beschin, Busulini, De Angeli & Tessier, 2007 (fossil), *N. pubescens* (H. Milne Edwards, 1834) (fossil and extant), *N. richteroides* Sakai, 1969 (fossil and extant); *N. zovoensis* sp. nov. (herein).

Neoliomera zovoensis sp. nov.
(Figs. 2.1a, 1b)

Diagnosis: Subhexagonal carapace, convex longitudinally, broader than long; bilobed front; small suboval orbits; raised, granulate supraorbital margin; elongate, convex anterolateral

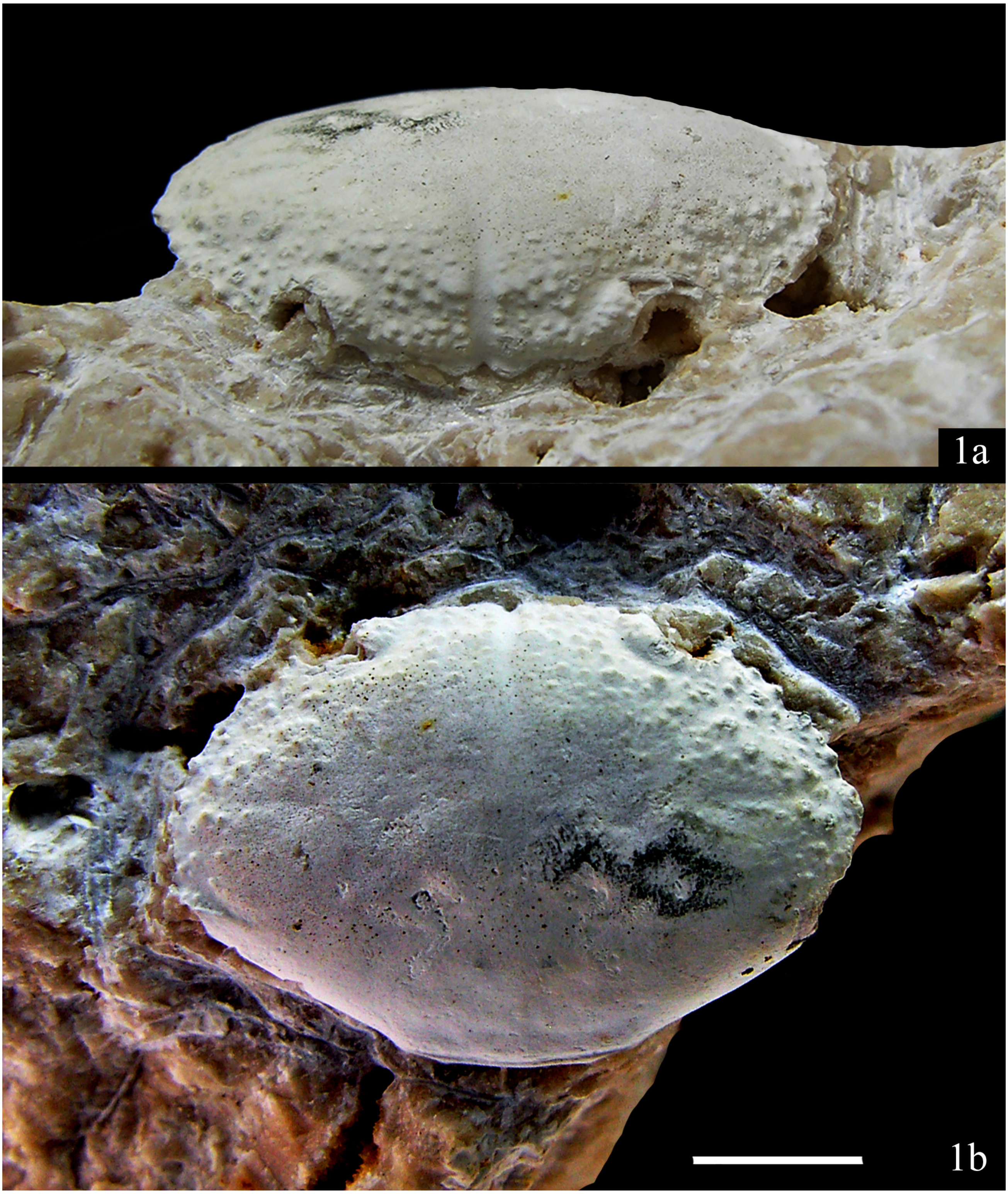

Fig. 2. *Neoliomera zovoensis* sp. nov., Holotype, MCV 19/09. 1a - carapace in frontal view; 1b - carapace in dorsal view. Scale bar equals 5 mm.

margins, with four short spiny lobes; fourth anterolateral lobe with granulate ridge extending on branchial region; short, convergent posterolateral margins; undifferentiated dorsal regions; one longitudinal median groove in frontal region; cervical groove dividing hepatic region from branchial ones; smooth dorsal carapace surface, except for some tubercles uniformly arranged in frontal region and in the outer parts of hepatic and epibranchial regions.

Etymology: after Zovo where the studied specimen was discovered.

Holotype: MCV 19/09.

Type locality: Zovo (Vestenanova, Verona, northeast Italy).

Measurements: MCV 19/09 – lcxp: 13.3 mm; wcxp: 29.5 mm; wof: 11.5 mm; wf: 8 mm.

Description: Subhexagonal carapace, convex longitudinally, broader than long (lcxp/wcxp = 0.45); orbito-frontal margin moderately wide (wof/wcxp = 0.38); bilobed front grooved medially and downturned; frontal margin with small tubercles arranged uniformly; small subround orbits with raised, granulate supraorbital margin; convex inner orbital angle well distinct from the front by an indentation; elongate, convex anterolateral margins, with two or three small spines, close each other, forming four short convex spiny lobes, divided by weak fissures: first with two small spines (excluding the extra-orbital tooth), second and third with three spines, and fourth, at level of anterolateral angle, with one spine and one granulate ridge (branchial ridge) extending on the branchial region; shorter posterolateral margins, strongly converging to the posterior margin; posterior margin as wide as the front, weakly convex and rimmed; undifferentiated dorsal regions; one deep longitudinal median groove in the frontal region; cervical groove dividing hepatic region from the branchial ones; weak transverse depression in the cardiac region; weak branchiocardiac grooves, more evident along the cardiac region margins; smooth dorsal carapace surface, except some tubercles uniformly arranged in the frontal region and in the outer parts of hepatic and epibranchial regions; small pits arranged uniformly on dorsal surface, richer in frontal and hepatic regions.

Discussion: Based upon Sakai (1976) and Serène (1984), the studied specimen shows the main morphological characters of the extant *Neoliomera* in having a carapace broader than long; anterolateral margins crested and entire, although marked with three to four demarcated, rounded lobes; and poorly defined regions. *Neoliomera* is currently widely distributed in the Indo-West Pacific area with 17 species inhabiting rocky beach, under stones or in coral reef, and shallow waters (Ho & Ng, 2014).

Neoliomera is known in the fossil record of northern Italy with two species, *N. paleogenica* Beschin, Busulini, De Angeli & Tessier, 2007, from the early Eocene of contrada Gecchelina (Monte di Malo, Vicenza) and *N. minuta* Beschin, Busulini & Tessier, 2015 from the early Eocene of Cava Braggi (Vestenanova, Verona). The former differs from *N. zovoensis* sp. nov. in having meso-, metagastric, and cardiac regions that are well differentiated by grooves and thick tuberculate ornamentation uniformly arranged on the whole dorsal surface (Beschin et al., 2007). The latter differs from the new species in having a more oval carapace outline, dorsal surface of carapace with randomly arranged small tubercles, an anterior mesogastric process that does not reach the front, a carapace that is not marked by a cervical groove, an anterolateral margin with four smooth lobes, and an anterolateral angle without branchial ridge (Beschin et al., 2015).

Neoliomera zovoensis sp. nov. has a shallow cervical groove and a weak granulate ridge on the branchial regions, as in the extant *N. themisto* (De Man, 1889), widespread in the Persian Gulf (see Guinot, 1964). This extant species differs, however, from the fossil one in having more distinct hepatic and branchial regions with larger and more numerous tubercles.

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A new homolid crab, *Cherpihomola italica* gen. nov., sp. nov. (Decapoda, Brachyura), from the Rupelian of the Ligure-Piemontese Basin (Alessandria, northern Italy)

Nov homolidni rak *Cherpihomola italica* gen. nov., sp. nov. (Decapoda, Brachyura) iz spodnjeoligocenskih (rupelijskih) plasti Ligursko-piemontskega bazena (Alessandria, severna Italija)

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Ključne besede: Homolidae, spodnji oligocen, južna Evropa, nova vrsta

Abstract

A new genus and species of homolid from lower Oligocene (Rupelian) strata in the Ligure-Piemontese Basin (northern Italy) is introduced. *Cherpihomola italica* gen. nov., sp. nov. represents the first record of homolids from Oligocene deposits across Europe and extends the palaeogeographical distribution of extinct homolids.

Izvleček

V prispevku predstavljamo nov rod in novo vrsto homolidnih rakov iz spodnjeoligocenskih (rupelijskih) plasti v Ligursko-piemontskem bazenu (severna Italija). *Cherpihomola italica* gen. nov., sp. nov. je prva najdba homolidnih deseteronožcev iz oligocenskih nahajališč v Evropi, kar nam omogoča boljše poznavanje paleogeografske razširjenosti te skupine fosilne rakov.

Introduction

Studies of decapod crustaceans of the Ligure Piemontese Basin started with Sismonda (1846, 1861), who recorded brachyurans of Miocene age from the Turin hills. Later, Michelotti (1861) and Crema (1895) added material from Miocene and Pliocene deposits in the same area, while Ristori (1889) described new species from the Rupelian of Sassello, Santa Giustina, Fornaci and Dego. Recently, Allasinaz (1987), Marangon & De Angeli (1997, 2007), De Angeli & Marangon (2001, 2003a, b), Larghi (2003), Busulini et al. (2014), Pasini & Garassino (2017a, b) and Pasini et al. (2019) described a number of new species from this area.

The carcinological fauna includes the following species: *Hoploparia* sp., *Callianassa canavarii* Ristori, 1889, *Callianassa* sp., *Pagurus* sp., *Zygopa galantensis* (De Angeli & Marangon, 2001), *Alcespina ovadaensis* Pasini & Garassino, 2017 [= *Ranina* (*Ranina*) *speciosa*, *sensu* Allasinaz, 1987], *Lophoranina* sp. (= *Lophoranina ?aldrovandi*, *sensu* Sismonda, 1861), *Calappa demarcoi* Pasini & Garassino, 2017, *Stenodromia mainii* (Allasinaz, 1987) (as *Calappilia*), *Calappilia verrucosa* A. Milne-Edwards *in* Bouillé, 1873, *Calappilia vicentina* Fabiani, 1910, *Mursiopsis postulosus* Ristori, 1889, *Cherpiocarcinus rostratus* Marangon & De Angeli, 1997, *Retroplurna* sp., *Portunus ristorii* Karasawa, Schweitzer

& Feldmann, 2008 (= *P. convexus* Ristori, 1888), *Coeloma vigil* A. Milne-Edwards, 1865, *Palaeocarpilius aquitanicus* A. Milne-Edwards, 1862 (= *P. macrocheilus*, *sensu* Allasinaz, 1987), *Eriphia* sp. and *Grapsus* sp. To this list, we here add *Cherpihomola italica* n. gen., sp. nov.

Geological and stratigraphical setting

Lithologically, Rupelian strata in the Ligure Piemontese Basin are characterised by an alternation of greyish marls with nodular elements and silt-rich marls, occasionally sandy, resting on the "Formazione di Pianfolco", which is of Rupelian age. Macrofossils are preserved mainly within pebbles or nodules that were eroded from the highest levels exposed of this sedimentary complex, which is referred to as "Formazione di Molare". These levels overlie terrestrial units of the "Brecce di Costa Cravara and Pianfolco", studied by Charrier et al. (1964) and dated as early Rupelian (see also Gelati & Gnaccolini, 1978; Gnaccolini, 1978). The crab-bearing levels were attributed to the transition between the "Formazione di Molare" and the overlying "Marne di Rigoroso" by Allasinaz (1987) and to the biozone of the benthic foraminifer *Operculina complanata* (Bianco, 1985; Balossino & Bianco, 1986). Other studies on Oligocene deposits in this area were carried out by Franceschetti (1967), Gelati & Gnaccolini (1980) and Fantoni et al. (1983). The palaeoenvironment of the Case Cherpione area documents three Rupelian phases, from a fully terrestrial setting with forests and rivers that transported abundant plant remains (early Rupelian), to a marine, warm-water lagoon with moderate currents and coasts nearby (middle Rupelian) and finally, during the late Rupelian, different platform conditions, a bathymetric change and a different benthos/plankton ratio which led to the disappearance of the macrofauna (Gelati & Gnaccolini, 1980; Fantoni et al., 1983).

The material studied here originates from the top levels of the "Molare Formation" (middle Rupelian) at Case Cherpione (Alessandria, northern Italy); it is preserved in nodules of diagenetic origin (Fig. 1).

Material and methods

Two specimens from the middle Rupelian of Case Cherpione (Ovada, Alessandria) are housed in the palaeontological collections of the Museo Civico "G. Zannato", Montecchio Maggiore, Vicenza (abbreviation: MCZ). They are three-dimensionally preserved; preparation was easy because of the unconsolidated matrix. Dimensions are in millimetres. For higher-level classification, we follow the recent arrangement proposed by Guinot et al. (2013).

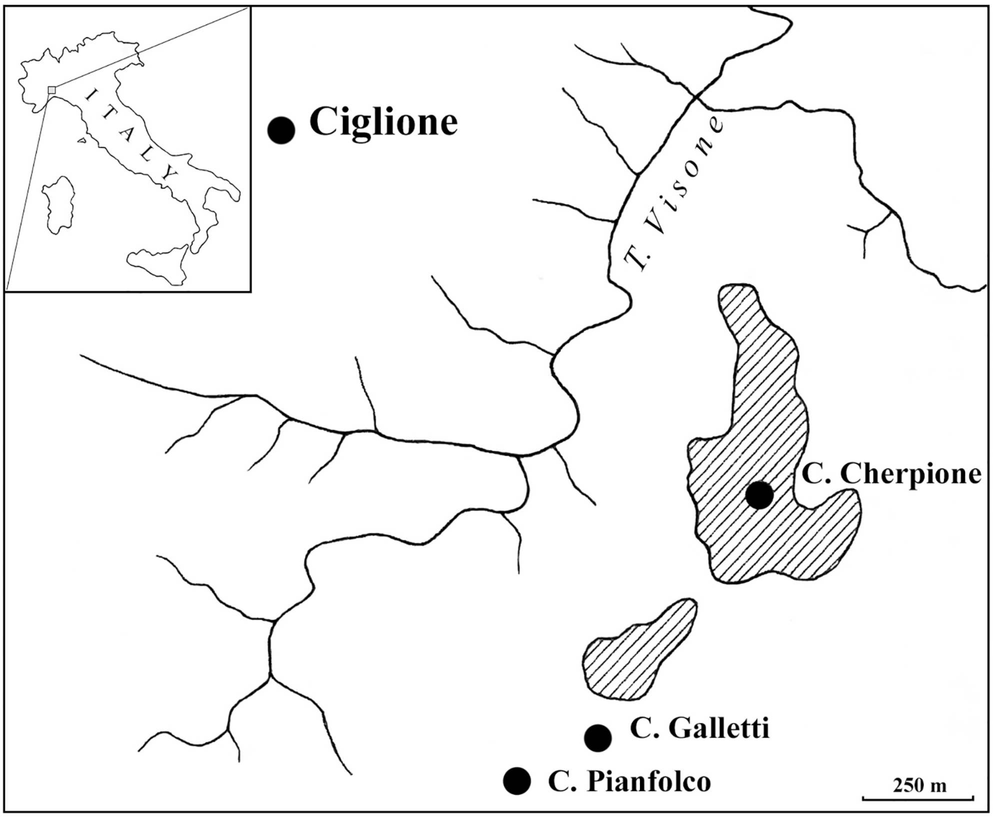


Fig. 1. Outcrops of Rupelian strata in Case Cherpione (Alessandria, northeast Italy).

Systematic palaeontology

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Subsection Homoliformia Karasawa, Schweitzer & Feldmann, 2011
Superfamily Homoloidea H. Milne Edwards, 1837
Family Homolidae H. Milne Edwards, 1837

Discussion: The superfamily includes the families Homolidae, Poupiniidae Guinot, 1991 and Latreillidae Stimpson, 1858 (Guinot & Richer de Forges, 1995). The typical features of Recent homolids have been outlined in detail by Guinot & Richer de Forges (1995) and Davie et al. (2015), while extinct forms have been discussed by Collins (1997), Schweitzer et al. (2010), Nyborg & Garassino (2017) and Garassino et al. (2015, 2019).

According to several authors (notably Schweitzer et al., 2010; De Angeli & Alberti, 2012; Garassino et al., 2015; Nyborg & Garassino, 2017 and Garassino et al., 2019), eighteen fossil genera (four also with Recent representatives) should be assigned to the Homolidae, as follows: *Cretalamoha* Nyborg & Garassino, 2017, *Dagnaudus* Guinot & Richer de Forges, 1995 (both fossil and Recent), *Doerflesia* Feldmann & Schweitzer, 2009, *Homola* Leach, 1815 (both fossil and Recent), *Homoliformis* Collins, Schulz & Jakobsen, 2005, *Homolopsis* Bell, 1863, *Hoplitocarcinus* Beurlen, 1928, *Latheticocarcinus* Bishop, 1988, *Lignihomola* Collins, 1997, *Lindahomola* Garassino, Weaver, Portell & Vega, 2019, *Londinimola* Collins & Saward, 2006, *Nogarhomola* De Angeli & Alberti, 2012, *Palehomola* Rathbun, 1926, *Paromola* Wood-Mason, *in* Wood-Mason & Alcock, 1891 (both fossil and Recent), *Paromolopsis* Wood-Mason, *in* Wood-Mason & Alcock, 1891 (both fossil and Recent), *Peedeehomola* Garassino, Clements & Vega, 2015, *Prohomola* Karasawa, 1992 and *Zygastrocarcinus* Bishop, 1983.

Genus ***Cherpihomola*** gen. nov.

Type species: *Cherpihomola italica* sp. nov.

Etymology: The generic name refers to Case Cherpione, the locality which yielded the type specimens.

Diagnosis: Carapace longitudinally square in outline, as long as wide; well-developed *linea homolica*, sinuous in outline, acute rostrum, one pseudorostral spine, one infra-orbital spine, one hepatic spine, one anterolateral spine, two posterolateral spines, regions nearly smooth and slightly raised.

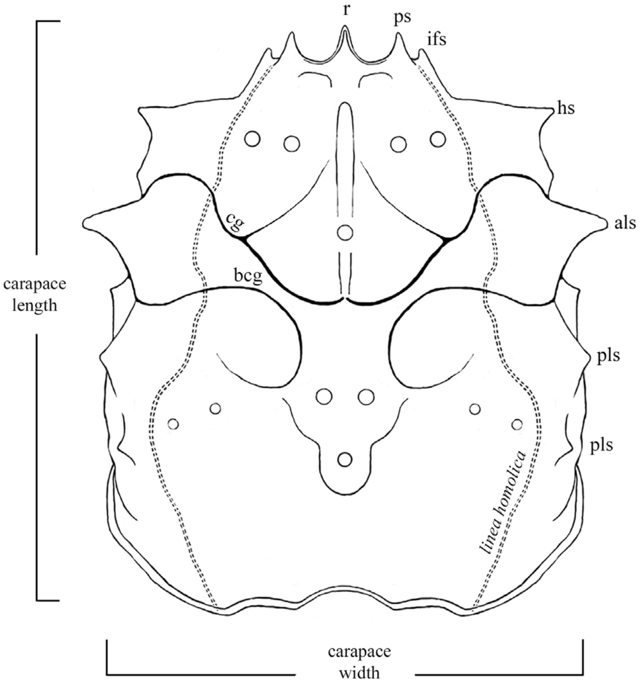


Fig. 2. *Cherpihomola italica* n. gen., n. sp., reconstruction of dorsal carapace (r: rostrum; ps: pseudorostral spine; ifs: infra-orbital spine; hs: subhepatic spine; als: anterolateral spine; pls: posterolateral spine; cg: cervical groove; bcg: branchiocardiac groove).

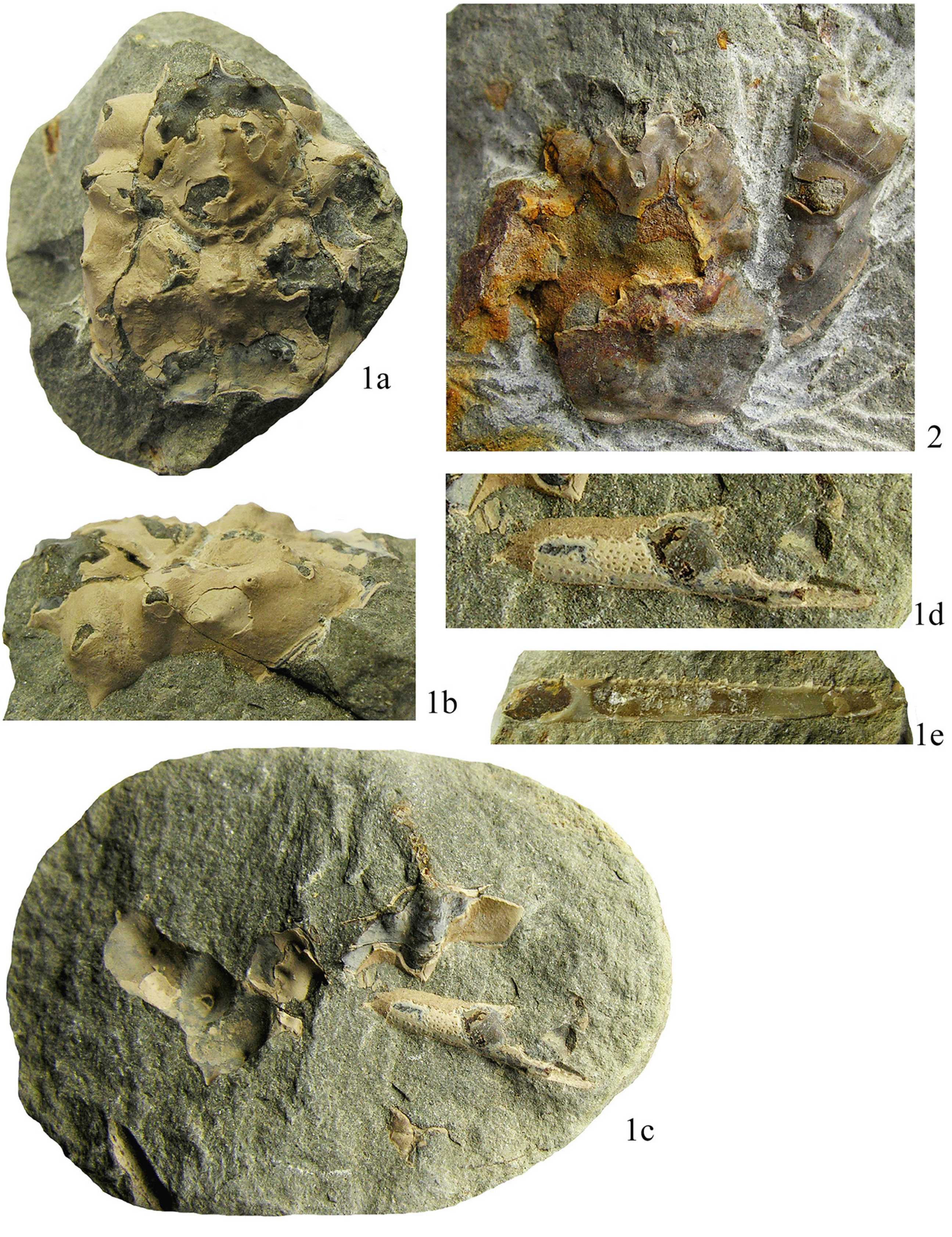
Cherpihomola italica sp. nov.

Fig. 2; Pl. 1

Material and measurements: Two carapaces; the holotype is MCZ 5759 (carapace length 17.5 mm; carapace width 16.4 mm); the paratype is MCZ 5760 (carapace length 20.6 mm).

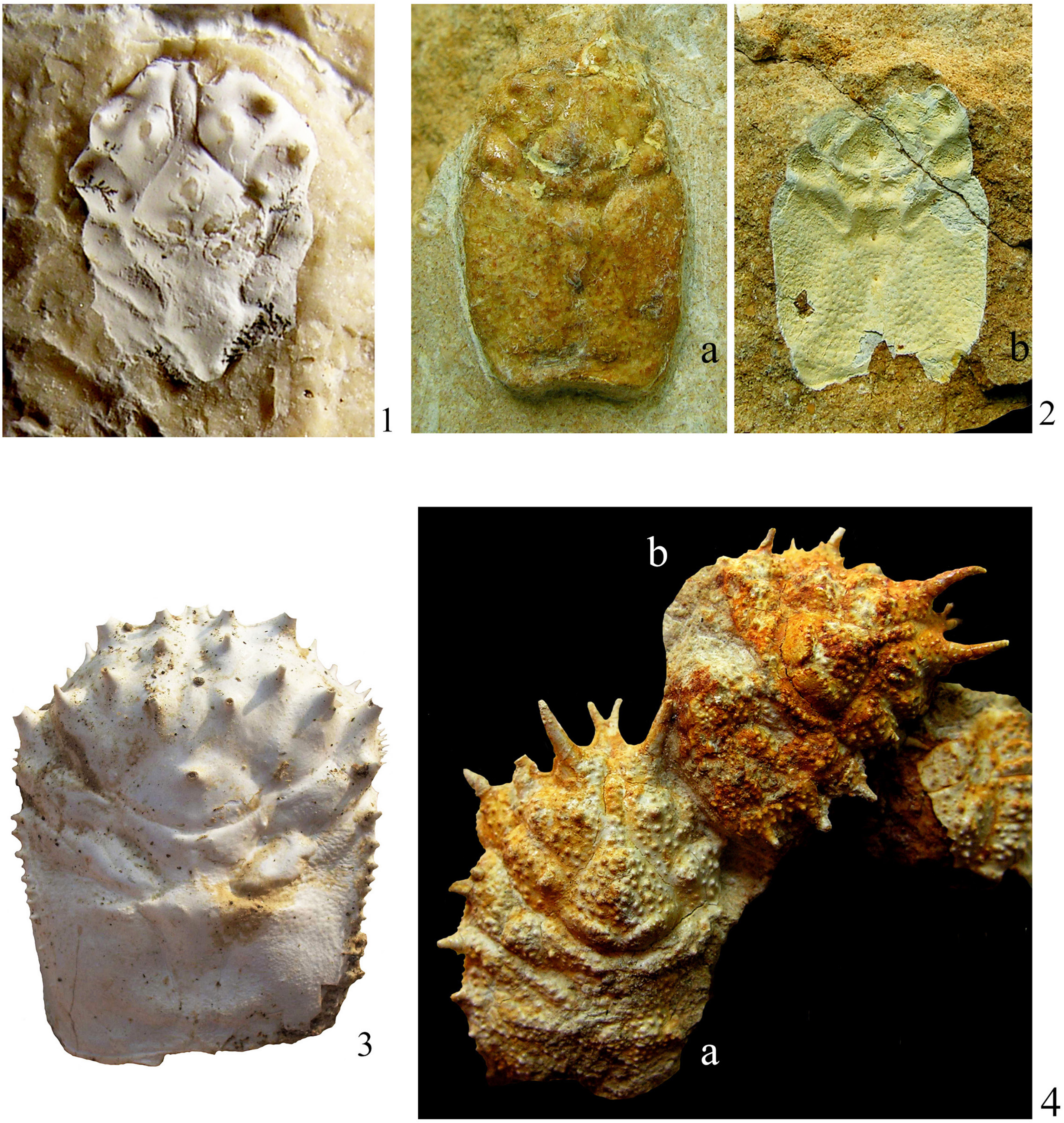
Description: Carapace longitudinally square, as long as wide, well-developed *linea homolica*, sinuous; moderately vaulted transversely, less so longitudinally, lateral sides slanted, nearly subvertical; regions smooth well marked by grooves; triangular rostrum not sulcate axially; one pseudorostral spine, as long as the rostrum; a short infraorbital spine; anterolateral margin with one prominent subhepatic spine directed outwards; a second short spine is present ventrally, not visible in dorsal view; one prominent anterolateral spine directed outwards present between cervical and branchiocardiac grooves; posterolateral margin with two short spines; posterior margin wide, concave and rimmed; deep cervical groove, convex laterally to epibranchial lobe, strongly inclined between inferior margin of mesogastric region; branchiocardiac groove almost straight proximally, downturned posteriorly to gastric lobe, curved and continuous on branchial region; epigastric lobe defined by pair of tubercles positioned just posterior to pseudorostral spines;

PLATE 1



Cherpihomola italica n. gen., sp. nov.; 1a-e: MCZ 5759, holotype; a - dorsal view of carapace; b - lateral view of carapace; c - nodules of diagenetic origin associated with cheliped; d - right propodus; e - ambulatory legs; 2 - MCZ 5760, paratype, dorsal view of carapace.

PLATE 2



1. *Latheticocarcinus italicus* De Angeli & Ceccon, 2013, holotype; 2. *Homola vanzoi* Beschin, De Angeli & Zorzin, 2009, holotype, part (a) and counterpart (b); 3. *Homola barbata* (Fabricius, 1793); 4. *Nogarhomola aurorae* De Angeli & Alberti, 2012, holotype (a) and paratype (b).

mesogastric lobe marked by smooth grooves laterally and well-defined cervical groove posteriorly; protogastric lobe with two tubercles; narrow mesogastric lobe; triangular cardiac lobe, with three tubercles; long, narrow and smooth intestinal lobe, slightly depressed; metabranchial lobe with two small tubercles aligned along *linea homolica*; smooth dorsal surface. Chelae with elongate palm with upper and lower margins almost parallel; outer surface of palm densely covered by punctuation, fixed finger about two-thirds of palm, long and straight. Long ambulatory legs, with denticulated upper margin.

Discussion: The carapace of this new homolid is characterised by a well-marked *linea homolica*, acute rostrum, one pseudorostral spine, one infra-orbital spine, one sub-hepatic spine, one anterolateral spine and two posterolateral spines, a deep cervical groove, nearly smooth and slightly raised dorsal regions and a narrow cardiac region, with three tubercles. Although *Cherpihomola* gen. nov. shares features of the rostrum and pseudorostral spines with *Paromola*, the latter has convex lateral margins with numerous spines and tuberculated dorsal regions, delimited by shallow grooves. *Paromola* is known from six modern and two extinct species, namely *Paromola vetula* Crawford, 2008 from the Paleogene of Río Negro Province (Argentina) and *Paromola roseburgensis* Nyborg & Garassino, 2017 from the Roseburg Formation (lower Oligocene) of Oregon (USA).

The new genus has affinities with *Latreillopsis* in showing near-parallel lateral margins, a similar arrangement of the frontal and lateral spines, a near-smooth dorsal surface and a narrow cardiac region with three tubercles. However, *Latreillopsis* has longer pseudorostral spines and one or more accessory spines in the rostrum, an epibranchial margin without a spine, while the posterolateral margin has a single robust spine.

Of other Cenozoic genera, *Prohomola* has densely tuberculated dorsal regions and deep cervical and branchiocardiac grooves (see Karasawa, 1992; Blow & Manning, 1996). *Dagnaudus* has a triangular, acute rostrum, long pseudorostral spines with two accessory spines, lateral margins with spines and tuberculated regions bounded by shallow grooves (see Jenkins, 1977). *Nogarhomola* has convex lateral margins with spines, a bifid rostrum and dorsal regions with tubercles (De Angeli & Alberti, 2012), while *Palehomola* has an oval carapace (larger posteriorly), a long, pointed rostrum that is strongly downturned, pseudorostral spines that are slightly longer than the rostrum and with two small basal spinules, as well as a large, inflated subhepatic region, with one large triangular spine and well-developed cervical and branchiocardiac grooves (Nyborg & Garassino, 2017).

Fossil homolids from Italy

To date, only three genera are known from the fossil record. *Homola* Leach, 1815 with *H. vanzoi* Beschin, De Angeli & Zorzin, 2009 pl. 2, figs. 2a-b from the lower Eocene (Ypresian) of San Giovanni Ilarione (Verona) and *H. barbata* (Fabricius, 1793) pl. 2, fig. 3, inhabiting the modern Atlantic Ocean (Portugal) and the Mediterranean Sea and occurring as a fossil in the upper Pleistocene (Tyrrhenian) of Trumbacà (Reggio Calabria). *Latheticocarcinus italicus* De Angeli & Ceccon, 2013 pl. 2, fig. 1 is known from the lower Eocene (Ypresian) of Monte Magrè (Schio, Vicenza), while *Nogarhomola aurorae* De Angeli & Alberti, 2012 pl. 2, figs. 4a-b has been described from the middle Eocene (Lutetian) of Nogarole Vicentino (Vicenza) (Beschin et al., 2009; Garassino et al., 2010; De Angeli & Alberti, 2012; De Angeli & Ceccon, 2013). The new genus and species erected herein represents the first record of homolid crabs from Oligocene strata in Europe, thus enlarging their palaeogeographical distribution.

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Revision of species *Plagiolophus sulcatus* Beurlen, 1939 (Decapoda, Brachyura) from the Oligocene of Hungary and Slovenia

Revizija vrste *Plagiolophus sulcatus* Beurlen, 1939 (Decapoda, Brachyura) iz oligocena Madžarske in Slovenije

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Ključne besede: raki deseteronožci, rakovica, *Glyphithyreus*, oligocen, rupelij, chattij

Abstract

The crab species *Plagiolophus sulcatus* Beurlen, 1939 from the Oligocene (Rupelian) Kiscell Clay of Hungary is revised and its holotype is reillustrated for the first time since its original publication. Material from the upper Oligocene (Chattian) of Trbovlje (Slovenia) is here considered conspecific with *P. sulcatus*. Attribution of this species to the genus *Glyphithyreus*, as proposed by Hiroaki Karasawa and Carrie Schweitzer in 2004, is confirmed. *Glypthithyreus sulcatus* differs from congeners in possessing protogastric regions that are subtriangular in outline and in having fewer and coarser tubercles on elevated carapace regions.

Izvleček

Revidirana je vrsta rakovice *Plagiolophus sulcatus* Beurlen, 1939, iz oligocenskih (rupelijskih) kiscellijskih glinenih plasti. Prvič po prvotni objavi je predstavljen holotip in novi primerek iz zgornjega oligocena (chattija) Trbovelj (Slovenija), ki prav tako pripada vrsti *P. sulcatus*. Potrjena je pripadnost te vrste rodu *Glyphithyreus*, kar sta predlagala Hiroaki Karasawa in Carrie Schweitzer leta 2004. *Glypthithyreus sulcatus* se od drugih pripadnikov tega rodu razlikuje po tem, da ima trikotno obliko protogastrične regije in manjše število, a izrazitejše oblikovane bradavice na višjih delih oklepa.

Introduction

Beurlen (1939) described a decapod crustacean faunule from the Oligocene Kiscell Clay of Hungary. The ghost shrimps of this assemblage have since received proper re-evaluation (Hyžný & Dulai, 2014), the three species of brachyuran crabs, including *Plagiolophus sulcatus*, remained unrevised in respect with modern classification until now. This species was tentatively retained in the genus *Plagiolophus* Bell, 1858 (*non* Pomel, 1857) by Karasawa & Schweitzer (2004) in their revision of *Glyphithyreus* Reuss, 1859. Those authors noted that, "the placement of *G. sulcatus* is somewhat tentative and is based upon our translation of Beurlen's (1939) original description in German and the very poorly reproduced illustration in our copy of the work (Karasawa & Schweitzer, 2004, p. 148)". Thus, since the erection of the species by Beurlen (1939), the type material of *P. sulcatus* has not yet been re-examined.

Bittner (1884) presented an extensive overview of Cenozoic sedimentary rocks and their fossil contents in the vicinity of Sagor (nowadays Zagorje ob Savi) and Trifail (nowadays Trbovlje). Among other faunal elements, Bittner (1884: 29) also mentioned the presence of a crab that was morphologically close to *Plagiolophus*. Several crab specimens from Trbovlje have recently been traced by one of us (MH) during a detailed screen of the main fossil collections in Austria (Hyžný & Gross, 2016; Hyžný & Zorn, in press). One of these indeed represents *Plagiolophus* (= *Glyphithyreus*) and has been considered to be conspecific with *P. sulcatus* by Hyžný & Gross (2016). However, this decision was not based on a first-hand examination of the type material.

The aim of the present note is to provide a revised description of *Glyphithyreus sulcatus* on the basis of the type specimen of *Plagiolophus sulcatus* from Hungary and of additional material from Slovenia.

Geological settings

The material that forms the basis for the present study comes from two localities, as follows:

Budapest area (Hungary): the holotype of *Plagiolophus sulcatus* originated from the Kiscell Clay of Óbuda (currently a part of the city of Budapest; Fig. 1). The Kiscell Clay Formation consists of grey, well-bioturbated, calcareous clay and clayey marl (Báldi, 1983), the type area being Óbuda, where brickyards were in operation during the second half of the 19th century. The most famous of these was the Újlak brickyard (formerly Holzspach brickyard); this was the type locality of *Plagiolophus sulcatus*.

The calcareous nannoflora of the Kiscell Clay is indicative of the lower part of zone NP 24 (upper Kiscellian) (compare Nagymarosy & Báldi-Beke, 1988). This assemblage probably equates with the topmost part of zone P 20 and the lower part of zone P 21 in the planktonic foraminiferal zonation (Horváth, 1998). In the upper part of the Kiscell Clay, the assemblage also belongs to the upper Kiscellian (NP 24 nannoplankton zone and P 21 planktonic foraminiferal zone) (see Horváth, 1998, 2002). K-Ar dating of glauconite from the Kiscell Clay at Pilisborosjenő, north of Budapest, has yielded a date of 33+/-3 Ma (Báldi et al., 1975). The Kiscellian is a regional stage in the Central Paratethys that is used for part of the Lower Oligocene (Rupelian). It was first proposed by Báldi (1979) and later defined in a type section by Báldi (1986). The Kiscellian is now considered to correspond with the Rupelian (Báldi et al., 1999; Piller et al., 2007).

Generally speaking, the Kiscell Clay is not very rich in macrofossils. Strata assigned to this unit, however, were mined at several brickyards along the margins of the Buda Mountains for nearly a century, which explains why their fauna is relatively well known, including foraminifera (Hantken, 1875; Majzon, 1966; Sztrákos, 1974;

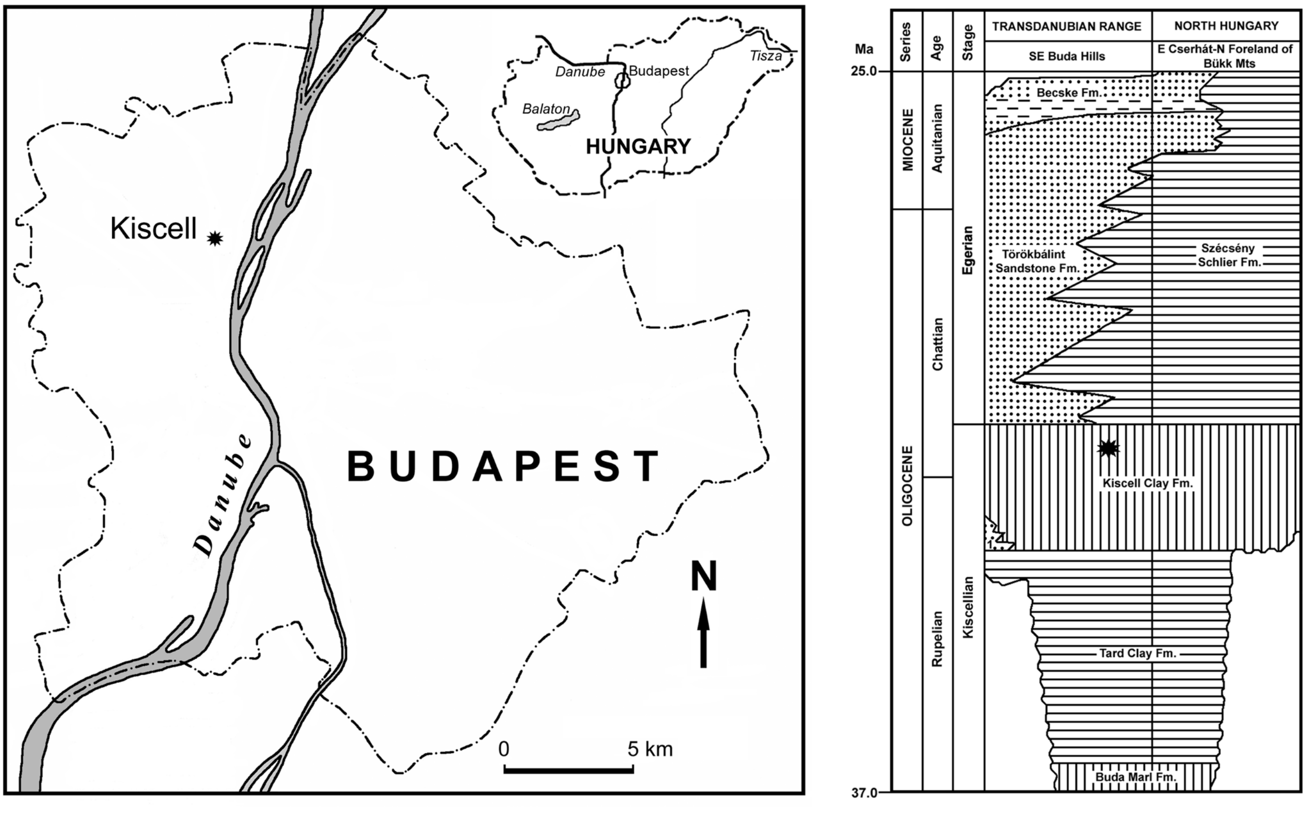

Fig. 1. Left – Simplified map of Hungary and the Budapest area with the position of the former Újlak brickyard (asterisk). Right – Simplified lithostratigraphical scheme of the Hungarian Oligocene at the Buda Hills area (modified after Császár, 1997); the asterisk indicate approximate position of the Kiscell Clay decapod assemblage. 1 = Hárshegy Sandstone Formation

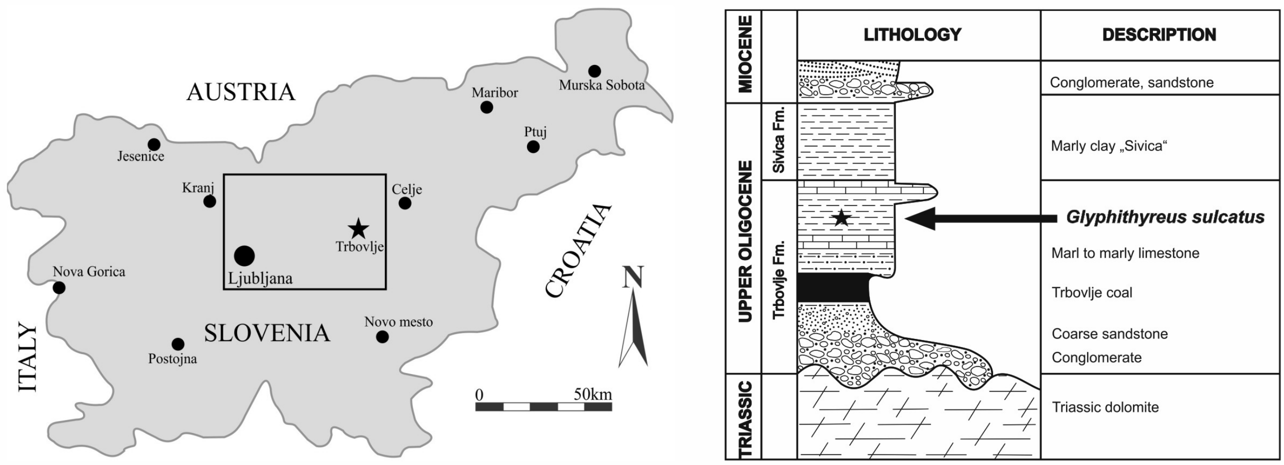

Fig. 2. Left – Simplified map of Slovenia and locality of provenance (star) of specimen of *Glyphithyreus sulcatus* (Beurlen, 1939) studied herein. Right – Simplified lithostratigraphical section of the Trbovlje locality (modified after Bechtel et al., 2004); strata that have yielded crab specimens are marked.

Gellai-Nagy, 1988; Horváth, 2002, 2003), gastropods and bivalves (Noszky, 1939, 1940; Báldi, 1986), cephalopods (Szörényi, 1933; Wagner, 1938); brachiopods (Meznerics, 1944), ostracods (Monostori, 1982, 2004), cirripedes (Szörényi, 1934), decapod crustaceans (Beurlen, 1939; Hyžný & Dulai, 2014), and fishes (Weiler, 1933, 1938; Nolf & Brzobohatý, 1994; Szabó & Kocsis, 2016).

Trbovlje (Slovenia): The locality of Trbovlje is situated in the Laško Syncline and belongs to geotectonic unit of the Sava folds (Placer, 1999; Jelen & Rifelj, 2002). Oligocene and Miocene sedimentary rocks were laid down disconformably on Triassic and Cretaceous fine-grained, clastic rocks (Hafner, 2000). Successive regressive and transgressive sequences suggest alternating cycles of deepening and shallowing in the depositional environment. The stratigraphical sequence also shows a variably strong influence of marine and terrestrial conditions.

The locality studied is a disused coal pit (GPS co-ordinates: 46°08’56” N, 15°04’03” E), situated some 3 km east of the city of Trbovlje, along the road to Hrastnik (Fig. 2). The area was intensively mined for lignite (brown coal) during the last two centuries. On account of the rich brown coal deposits, the area has been thoroughly studied in the past (Bittner, 1884; Petrascheck, 1952; Kuščer, 1967; Jelen et al., 1992; Placer, 1999; Hafner, 2000).

The Cenozoic sequence here starts with the upper Oligocene Trbovlje Formation, which disconformably overlies Triassic rocks. The coal-bearing Trbovlje Formation is also known as the Socka beds (“Sotzkaschichten”) or Pseudo-Socka beds in the older literature (Bechtel et al., 2004). This unit starts with basal conglomerates, sandstones layers and greyish coloured marls to marly limestones. The marly beds contained an economically important coal seam. Pollen and coal analysis have demonstrated the taxodiacean–cupressacean origin of the main coal seam (Bruch, 1998; Križnar, 2000) and most likely a transition to a reed marsh in the upper part. The overlying marls and marly limestones are the most fossil-rich beds (Fig. 2), with diverse molluscan and fish assemblages (Križnar, 2015; Buckeridge, in press) and abundant floral remains (Lorencon, 2019). The sequence continues with a horizon of grey marine clay of the Sivica Formation. In the top part of the clay succession occur individual layers and lenses of fine-grained clastic rocks, particularly sandstones and conglomerates. The transition to the clastic beds of the lower Miocene Govce Formation is continuous (Hafner, 2000).

The crab-bearing strata of the Trbovlje Formation are Late Oligocene in age (Odin et al., 1994; Bechtel et al., 2004).

Material and methods

The crabs studied herein are part of historical collections and have not been prepared further. Specimens were photographed with and without ammonium chloride coating.

Abbreviations

GBA: Geological Survey of Austria, Vienna (Austria).

HNHM: Department of Palaeontology and Geology, Hungarian Natural History Museum, Budapest (Hungary).

UMJGP: Department for Geology & Palaeontology, Universalmuseum Joanneum, Graz (Austria).

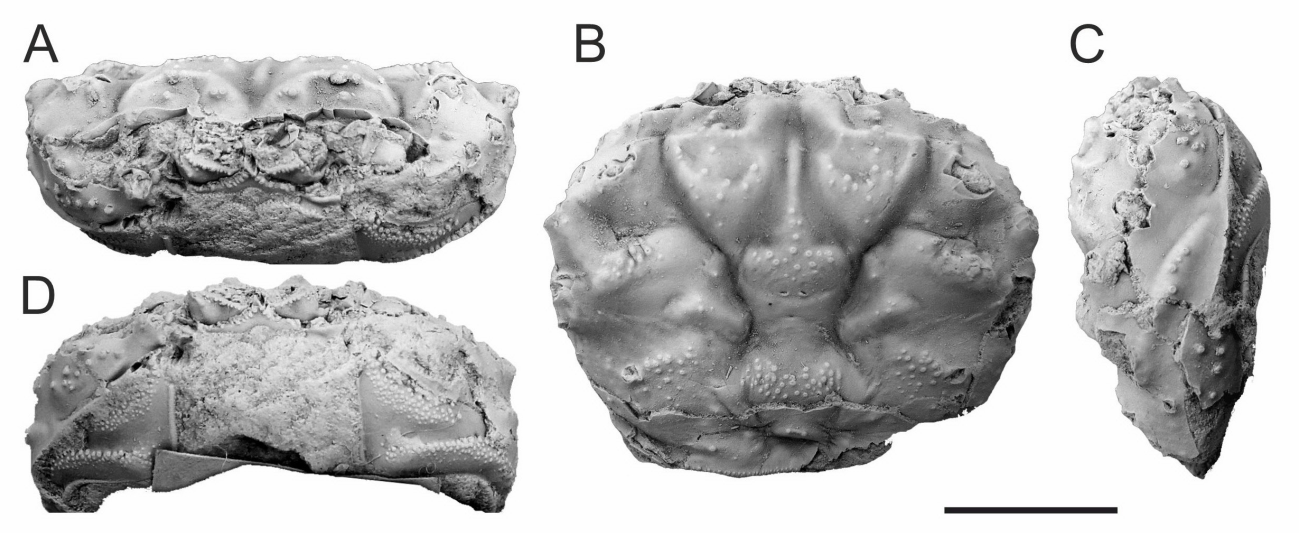

Fig. 3. *Glyphithyreus sulcatus* (Beurlen, 1939), the holotype of *Plagiolophus sulcatus* (HNHM M.59.4692) from the Kiscellian (Rupelian) of the Budapest area, Hungary. A – Frontal view. B – Dorsal view. C – Left lateral view. D – Ventral view. The specimen was coated with ammonium chloride prior to photography. Scale bar equals 10 mm.

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Subsection Heterotremata Guinot, 1977
Superfamily Xanthoidea MacLeay, 1838
Family Panopeidae Ortmann, 1893
Subfamily Eucratopsinae Stimpson, 1871
Genus *Glyphithyreus* Reuss, 1859
(= *Plagiolophus* Bell, 1858, *non* Pomel, 1857)

Type species: *Glyphithyreus formosus* Reuss, 1859, by original designation.

Diagnosis: See Karasawa & Schweitzer (2004: 147).

Glyphithyreus sulcatus (Beurlen, 1939) emend.
Figures 3–5

*1939 *Plagiolophus sulcatus* Beurlen, p. 155, pl. 7, fig. 11.

2004 *Glyphithyreus sulcatus* (Beurlen) – Karasawa & Schweitzer, p. 148.

2010 *Glyphithyreus sulcatus* (Beurlen) – Schweitzer et al., p. 121.

2016 *Glyphithyreus sulcatus* (Beurlen) – Hyžný & Gross, p. 110, fig. 15.1.

Emended diagnosis: Carapace subhexagonal in outline, widest in anterior one-third of length; fronto-orbital margin about 65 per cent of maximum carapace width; carapace grooves and regions well defined, with granular transverse ridges; regions covered with coarse granules at elevations; protogastric regions subtriangular in outline.

Material studied: HNHM M.59.4692, a near-complete carapace, the holotype of *Plagiolophus sulcatus*; Óbuda, Hungary (Fig. 3); UMJGP 56664, a near-complete individual, retaining pereiopods, inclusive of chelipeds, from Trbovlje, Slovenia; GBA 2007/024/0005 (Fig. 4A), counterpart of UMJGP 56664 from Trbovlje, Slovenia (Figs. 4B–C). Interestingly, part and counterpart of the specimen from Trbovlje ultimately landed up in two collections (see also Hyžný & Gross, 2016, fig. 15.1; Hyžný & Zorn, in press, pl. 25, fig. 2).

Description: Carapace subhexagonal in outline; L/W (length/width) ratio 0.8, widest in anterior one-third of carapace. Fronto-orbital margin about 65 per cent of maximum carapace width; front broken; orbits poorly preserved. Anterolateral margin strongly convex with four blunt teeth, including outer orbital tooth; posterolateral margin sinuous, converging posteriorly. Carapace grooves and regions well defined; epigastric regions well developed, rectangular in outline; protogastric regions subtriangular in outline, with steep ridges anteriorly; mesogastric region well developed, with elongate, narrow anterior process; metagastric region with granular transverse ridge and two distinct gastric pits posteriorly, separated from smooth urogastric region by narrow groove; cardiac region as wide as metagastric region, with broad, granular transverse ridge; hepatic regions well defined, delimited by deep cervical groove posteriorly; branchial region divided into two portions by distinct branchio-cardiac groove, each bearing granular transverse ridge. Regions covered with coarse granules at elevations, with cardiac region

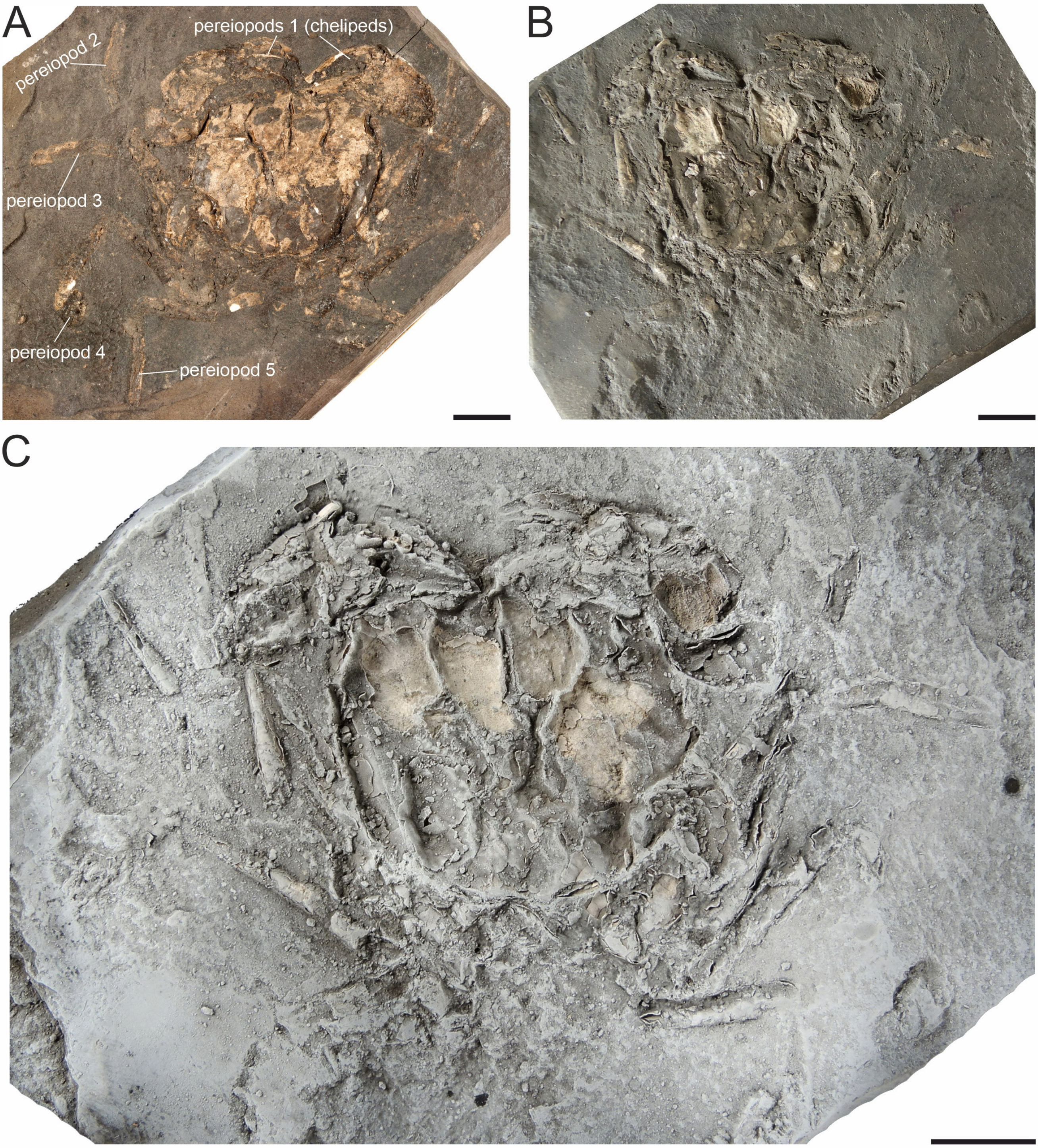

Fig. 4. *Glyphithyreus sulcatus* (Beurlen, 1939) from the upper Oligocene (Chattian) of Trbovlje, Slovenia. A – GBA 2007/024/0005 (unwhitened). B – UMJGP 56664 (unwhitened). C – UMJGP 56664 (whitened with ammonium chloride). Scale bars equal 10 mm.

being densely granulated, whereas protogastric, meso- and metagastric and branchial regions having only limited number of relatively large tubercles. Chelipeds (pereiopods 1) with robust chelae, insufficiently preserved; carpus subquadrate in outline; manus approximately two times longer than tall, converging proximally; fingers shorter than manus. Pereiopods 2–5 slender, distal elements not preserved sufficiently.

Remarks: Karasawa & Schweitzer (2004, p. 148) noted that, “the description of *G. sulcatus* clearly indicates two transverse ridges on the branchial regions, separated by a very deep cavity, which is certainly characteristic of *Glyphithyreus*.” We can confirm this and thus corroborate the transfer of this species to this genus.

As far as carapace outline is concerned, *Glyphithyreus sulcatus* appears to be close to *G.*

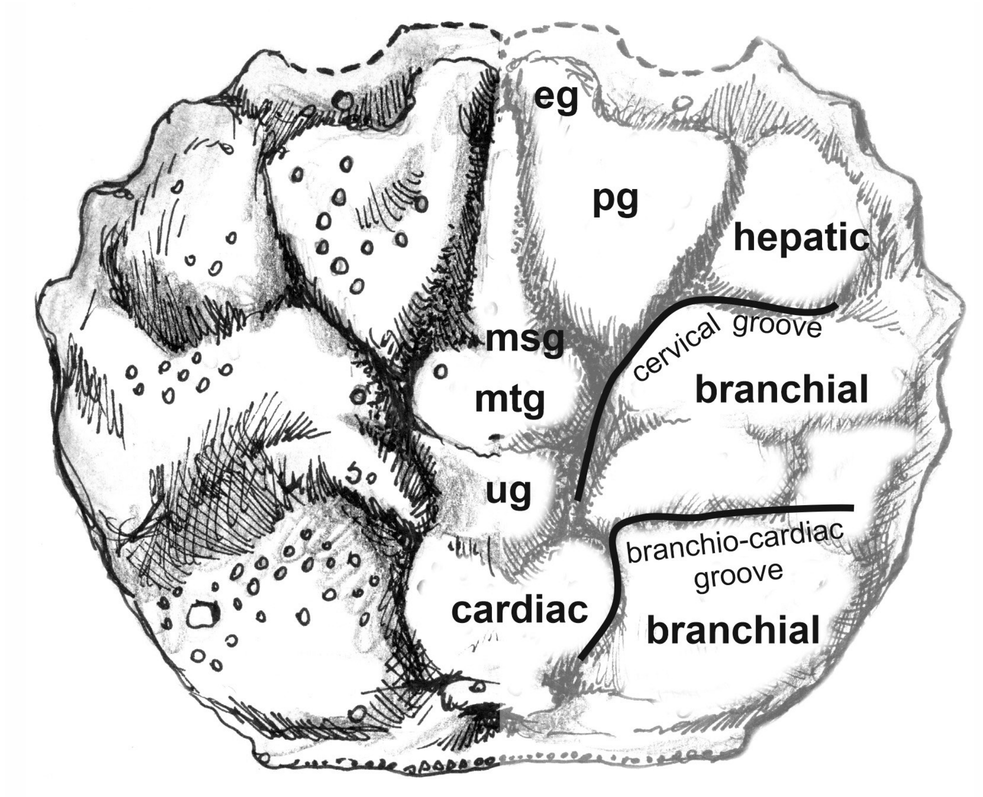

Fig. 5. *Glyphithyreus sulcatus* (Beurlen, 1939), reconstruction scheme of dorsal carapace. Abbreviations: eg = epigastric region, msg = mesogastric regions, mtg = metagastric region, pg = protogastric region, ug = urogastric region.

ellipticus Bittner, 1875 from the Eocene of Italy (Bittner, 1875), as far as the published figure allows to judge this. However, the latter differs in having more rounded protogastric regions; these are subtriangular in outline in *G. sulcatus*. Additionally, *G. sulcatus* has fewer granules on the elevated parts of carapace regions (Figs. 3, 5). In this respect, this species differs from all congeners known to date, including *G. formosus* Reuss, 1859 and *G. wetherellii* (Bell, 1858), in which carapace regions have a much finer granulation distributed over a larger area. Moreover, *G. formosus* has a wider fronto-orbital margin (Reuss, 1859, pl. 2, fig. 1) than *G. sulcatus*.

Conclusions

A revised description of *Plagiolophus sulcatus*, based both on its type specimen from the lower Oligocene (Rupelian) of Hungary and additional material from the upper Oligocene (Chattian) of Trbovlje (Slovenia), is presented. Interestingly, part and counterpart of the specimen from Trbovlje were transferred to the Universal Museum Joanneum at Graz and the Geological Survey at Vienna. The holotype of the species is refigured for the first time here since its original publication. Attribution of *P. sulcatus* to *Glyphithyreus*, first suggested by Karasawa & Schweitzer (2004), is confirmed. Comparison with congeners suggests that *G. sulcatus* is differentiated by having subtriangular protogastric regions and fewer and coarser tubercles on elevated carapace regions.

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The first record of a paguroid shield (Decapoda, Anomura, Annuntidiogenidae) from the Miocene of Cyprus

Prva najdba ščitov rakov samotarjev (Decapoda. Anomura, Annuntidiogenidae) iz miocenskih plasti Cipra

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Ključne besede: Paguroidea, sredozemlje, kenozoik, miocen, Ciper, nova vrsta

Abstract

For the first time, a paguroid shield is recorded from upper Miocene reefal strata (Koronia Member, Pakhna Formation) that crop out along the northern margin of the Troodos Massif, north of the village of Mitsero, Cyprus. Described here as *Paguristes joecollinsi* sp. nov., it constitutes the first paguroid shield known from Miocene deposits. The paucity of Cenozoic paguroid shields can probably be linked to a collecting bias in view of their relatively small size; in addition, suitable gastropod shells and internal moulds of such should be screened for 'hidden' hermit crabs.

Izvleček

Predstavljamo prvo najdbo ščita raka samotarja iz zgornjemiocenskih grebenskih apnencev (člen Koronija, formacija Pakhna), ki izdanjajo vzdolž severnega roba masiva Troodos, severno od vasi Mitsero na Cipru. V prispevku predstavljamo novo vrsto *Paguristes joecollinsi* sp. nov., ki je hkrati tudi prva najdba paguroidnega ščita miocenske starosti. Odsotnost kenozojskih paguroidnih ščitov je verjetno povezana z njihovo majhnostjo, saj jih hitro spregledamo. Pri iskanju ostankov rakov samotarjev je treba natančno preveriti tudi lupine in kamena jedra polžev.

Introduction

Up to now, abundant paguroid shield material has been recorded only from Jurassic reefal deposits (e.g., Van Bakel et al., 2008; Fraaije, 2014a; Fraaije et al., 2019) and mid- and Upper Cretaceous strata of comparable lithologies (e.g., Fraaije et al., 2008, 2009, 2012). In stark contrast is the current record of just a single hermit crab shield from Eocene coral-algal limestones in northern Italy as recorded by Beschin et al. (2016, 2017) and of an individual of *Dardanus colosseus*, preserved *in situ* in an internal mould of a gastropod from the Eocene of Austria (Fraaije & Polkowsky, 2016). Recently, six partially preserved shields have been briefly described and illustrated on the internet by a private collector, who had recovered them from reefal strata of Danian age at a quarry near Vigny (Paris Basin, France) (Buridan.over-blog.com 2018). All of the above constitute the current meagre record of paguroid shields of Paleogene and Neogene age that we are aware of.

Although relatively common in the fossil record, hermit crabs rarely become fossilised within the empty gastropod shells they usually inhab-

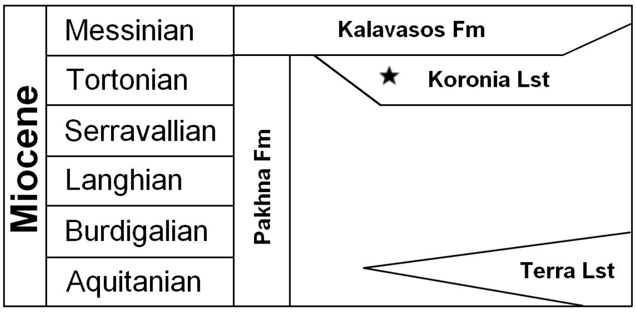

Fig. 1. Stratigraphical position (asterisk) of the holotype and sole specimen of *Paguristes joecollinsi* sp. nov. known to date.

it, probably because the animals abandon these when under stress (Dunbar & Nyborg, 2003). Alternative hypotheses are that the hard parts fall out of the gastropod shell upon decay of the hermit crab and not all Mesozoic hermit crabs inhabited gastropods (e.g., Fraaije, 2003). A recent study by Klompmaker et al. (2017) has revealed that the decay of complete paguroid animals is a rapid process, in comparison to other decapod crustaceans such as lobsters and crabs. They also demonstrated that, in addition to paguroid claws, anterior carapaces (shields) also have a relatively high preservational potential compared to the less calcified posterior shield. This result suggests that the paucity of extinct paguroid carapaces/shields might be a matter having been overlooked by collectors in the field on account of their small to diminutive size in comparison to other associated decapod crustaceans. Additionally, extensive checking of the content of gastropod shells or their internal moulds is likely to yield more paguroid specimens.

The new specimen described here was collected in May 2017 by one of us (RHBF) while doing fieldwork together with the fourth author (AAK) in upper Miocene reefal deposits at Mitsero, Cyprus (Figs. 1, 2). Following the record of a new, shallow-water munidopsid anomuran by Fraaije (2014b), this is only the second study on decapod crustaceans from the Miocene of Cyprus. More material from various localities in Cyprus is now contained in the collections of the Oertijdmuseum at Boxtel (the Netherlands). Below we adopt the morphological terminology of paguroid carapaces as described by Fraaije et al. (2019).

Institutional abbreviation: MAB, Oertijdmuseum, Boxtel, the Netherlands.

Systematic palaeontology

Order Decapoda Latreille, 1802
Infraorder Anomura MacLeay, 1838
Superfamily Paguroidea Latreille, 1802
Family Annuntidiogenidae Fraaije, 2014a
Genus *Paguristes* Dana, 1851

Type species: *Paguristes hirtus* Dana, 1851, by the subsequent designation of Stimpson (1858).

Included species: For fossil taxa, reference is made to Gagnaison (2012), Fraaije et al. (2015, table 1), Karasawa & Fudouji (2018, p. 23) and Beschin et al. (2018). For extant species, see Lemaitre & McLaughlin (2019).

Fig. 2. Location of a number of basins with Miocene strata, with the type locality of *Paguristes joecollinsi* sp. nov. marked by a large asterisk; the provenance of the only other anomuran recorded to date from the Miocene of Cyprus, *Palmunidopsis muelleri* Fraaije, 2014b, is marked by a small asterisk. Image modified from Fraaije (2014b, fig. 1)

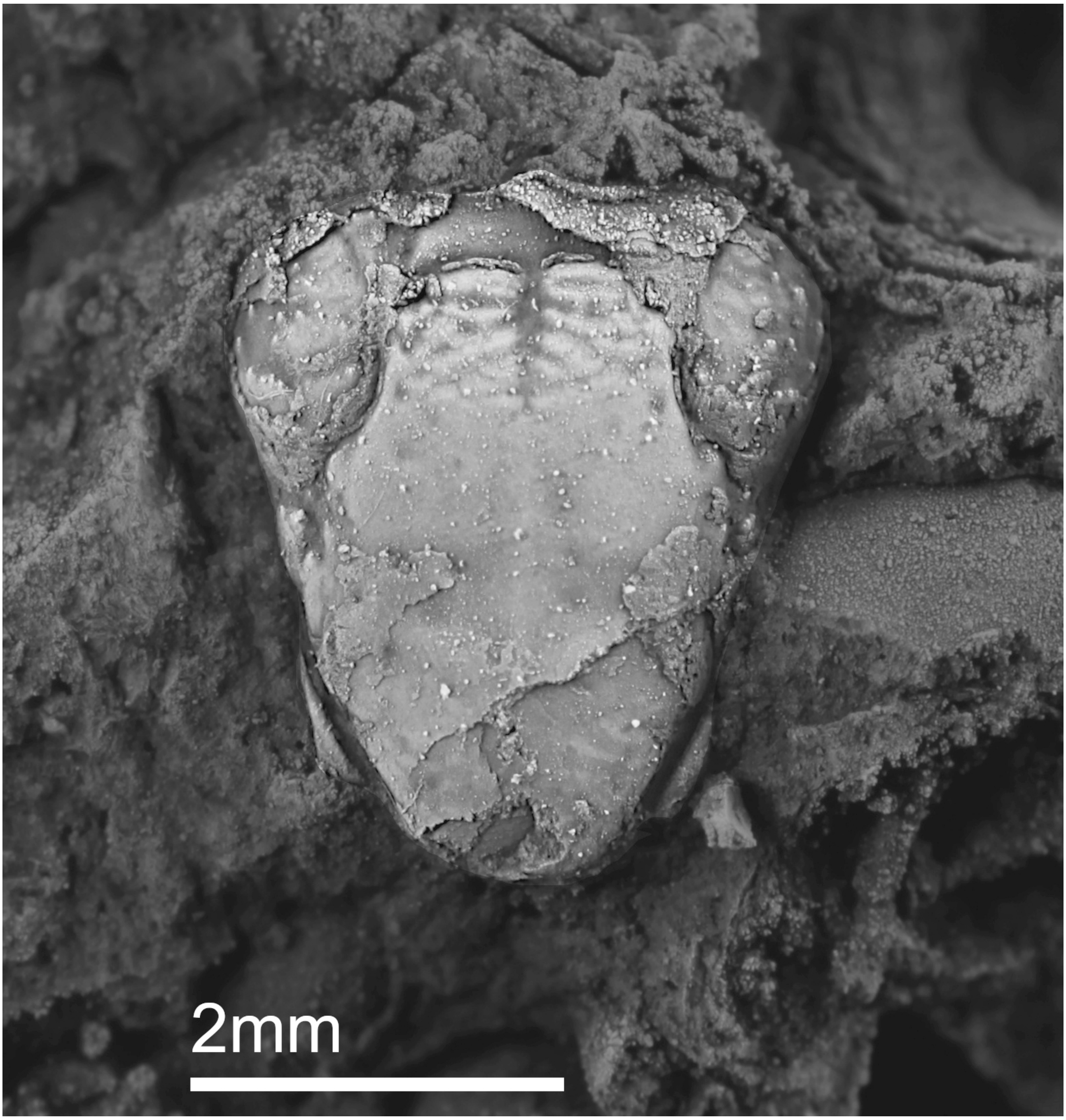

Fig. 3. Dorsal view of the shield of the holotype of *Paguristes joecollinsi* sp. nov. (MAB 10456a) as described here. No image of the lateral side is provided because the specimen sits in a depression, making further preparation too risky.

Paguristes joecollinsi sp. nov.

Diagnosis: Shield elongated (length/width ratio *c.* 1.15); broad, rimmed and shallow orbital cavity; convex postrostral ridges indented medially by central gastric furrow; pronounced, globose and spinose massetic region; reniform keraial region; narrow and spinose lateral branchial area. Anterior gastric region with transversely crenulated muscle scar; V-shaped cervical groove.

Material: The holotype and sole known specimen to date (MAB 10456a,b: part and counterpart) is an anterior part of the carapace with a maximum length of 3.8 mm and a maximum width of 3.3 mm.

Etymology: The species is named after our recently departed friend and colleague, Joseph ('Joe') S.H. Collins of London (England), who did so much to stimulate decapod crustacean studies by three of us (RHBF, BWMvB and JWMJ). We owe him a great deal.

Locality and stratigraphy: To the west of Kreatos Hill, about one kilometre to the north-north-west of the village of Mitsero, in coral-reef talus of the upper Miocene (Tortonian, 11.6-7.2 Ma) Koronia Member (Pakhna Formation; see Fig. 1). The shield was recovered from a block of bioclastic rock measuring about one square metre. The sedimentology and stratigraphy of this region have been described in detail by Robertson et al. (1991) and Follows (1992).

Description: Shield elongated (L/W ratio *c.* 1.15), convex transversely, almost straight longitudinally, divided into distinct regions by grooves (as shown in Fig. 3); broad, rimmed and shallow orbital cavity, broad, slightly convex postrostral ridges centrally indented by central gastric furrow, extending posteriorly in faint central line; pronounced, very globose and spinose massetic region, posteriorly covered with finely spinose ridges; tiny reniform but clear keraial region; narrow and spinose lateral branchial area; anterior gastric region alongside central furrow with transversely crenulated ornament; V-shaped cervical groove; shield irregularly covered with large (setal) pores.

Remarks: The new species is assigned to *Paguristes* because the shape of the anterior shield, the grooves such as a central gastric groove, and the regional definition conform well with those of many modern species (e.g., Forest et al., 2000). Numerous representatives of *Paguristes* have been described from the fossil record, from the Albian (late Early Cretaceous) onwards (see Fraaije et al., 2015, table 1), but nearly all of these are based exclusively on chelae, with the exception of two, namely a partial shield from the upper Pleistocene of southern Italy, referred to *Paguristes* cf. *syrtensis* de Saint Laurent, 1971, by Garassino et al. (2014) and a specifically indeterminate form, *Paguristes* sp., from the lower Eocene of northern Italy (Beschin et al., 2016). A comparison with this specimen is not made here, because this species will be placed in a different genus (Fraaije et al., 2020). *Paguristes joecollinsi* sp. nov. differs from *P.* cf. *syrtensis* in having less convex orbital cavities, a much more globose massetic region, less convex upper orbital margins and substantially fewer (setal) pores across the shield, although the cuticle is less well preserved. We have also compared the species to extant representatives from the same geographical region, the Mediterranean, which was a nearly enclosed basin during the Tortonian (e.g., Rögl, 1999). After all, decapods crustaceans with stratigraphical ranges of 10 million years or more have been reported occasionally (Klompmaker et al., 2012, p. 792-793; Hyžný, 2016, table 1). This region may also harbour one or more descendants of the species in the present study. However, the shields of extant Mediterranean species of *Paguristes* are not morphologically identical or very close to the new species. *Paguristes joecollinsi* sp. nov. differs from *P. eremita* (Linnaeus, 1767) [= *P. oculatus* (Fabricius, 1775) and *P. maculatus* (Risso, 1827)] (see Pipitone, 1998; Koçak et al. 2005, for drawings and images), *P. streaensis* Pastore, 1984 and *P. syrtensis* in that the general shape is more triangular and the massetic region is more pronounced in the new species. The shield appears to show impressions of the anterior gastric muscles (sensu Klompmaker et al., 2019, fig. 14F) in the anterior portion.

The assemblage from Mitsero also contains paguroid appendage fragments, but more research is needed to check whether one or more specimens might be ascribed to *P. joecollinsi* sp. nov. Ascribing disarticulated paguroid elements to one species is difficult, but it is essential to evaluate the true diversity of paguroids within assemblages. For example, Fraaije et al. (2013) have attempted to link sixth abdominal tergites to shield-based species based on the relative abundance of these isolated elements. None of the propodi within the Mitsero assemblage known to date is comparable to another Miocene *Paguristes, P. cserhatensis* Müller, 1984, from the middle Miocene of Hungary, or with *Paguristes gagnaisoni* from the middle Miocene of France (Gagnaison, 2012).

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On the occurrence of *Iphiculus eliasi* Hyžný & Gross, 2016 (Decapoda, Brachyura, Leucosioidea) from the Miocene of Catalonia (northeastern Iberian Peninsula)

Novi podatki o razširjenosti vrste *Iphiculus eliasi* Hyžný & Gross, 2016 (Decapoda, Brachyura, Leucosioidea) iz miocena Katalonije (severovzhod Iberijskega polotoka)

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Ključne besede: Leucosioidea, Iphiculidae, miocen, langhij, Katalonija

Abstract

Recovery of two specimens of leucosioid crabs in Langhian (middle Miocene) strata at Vilafranca del Penedès (Alt Penedès, Catalonia) and a re-examination of another leucosioid from the palaeontological collections of the Vinseum (Vilafranca del Penedès, Catalonia) have led us to consider all of these as conspecific with *Iphiculus eliasi* Hyžný & Gross, 2016, described first from the middle Miocene of Austria. The sternal and pleonal remains preserved in one of the Catalonian specimens allows to emend the original description of the species. Likewise, a specimen from the middle Miocene of Portugal, previously described as a paguroid, is herein transferred to this species. The occurrence of *I. eliasi*, either in outcrops along the northeastern and southwestern coasts of the Iberian Peninsula, corroborates the close relationship between decapod assemblages which inhabited similar palaeoenvironments in the Central Paratethys, the western Mediterranean and even the nearest Atlantic waters, during the middle Miocene.

Izvleček

Dva nova primerka leukosioidnih rakov langhijske (srednjemiocenske) starosti iz kraja Vilafranca del Penedès (Alt Penedès, Katalonija) in dodaten primerek iz muzeja Vinseum (Vilafranca del Penedès, Katalonija) smo določili kot *Iphiculus eliasi* Hyžný & Gross, 2016, ki je bil prvič opisan iz srednjemiocenskih plasti Avstrije. Na podlagi dobro ohranjenih morfoloških podrobnosti sternuma in pleona lahko dopolnimo originalni opis vrste. Primerek iz srednjega miocena Portugalske je določen kot *I. eliasi*, ki je bil opisan kot ostanek raka samotarja. Razširjenost vrste *I. eliasi* na iberijskem polotoku dodatno potrjuje podobnosti med fosilnimi združbami deseteronožcev, ki so v srednjem miocenu poseljevale centralno Paratetido, zahodno Sredozemlje in plitvovodna območja v Atlantskem oceanu.

Introduction

Miocene decapod crustacean assemblages of the Vallès-Penedès and Camp de Tarragona basins (northeastern Iberian Peninsula) have been studied by a number of scholars and are well known (Almera, 1896; Via, 1932; Solé & Via, 1989; Müller, 1993; Artal, 2008; Garassino et al., 2009; Ossó, 2010). Moreover, due to collecting efforts by enthusiastic fossil hunters new occurrences are constantly being reported, thus expanding our knowledge of fossil decapod crustacean assemblages of these areas. One such occurrence is recorded in the present contribution.

Müller (1993) summarised Neogene decapod crustaceans known at that time from Catalonia and described a number of new taxa, mainly from the reef limestones of Olèrdola, as well as from Vilafranca del Penedès and Santa Margarida i Els Monjos (Alt Penedès). More than a decade ago, a large number of fossil decapods, mainly *Palaeopinnixa mytilicola* Vía, 1966 were recovered in the so-called Vilafranca marls (Langhian), extracted during construction works for the high-speed railway line on the outskirts of Vilafranca del Penedès. Among these, remains of a carapace and a counterpart of a male venter of a leucosioid crab were recovered. The taxonomic assessment of this leucosioid is the goal of the present report.

Geological setting

The material studied comes from the localities of Vilafranca del Penedès and Santa Margarida i els Monjos, both within the Vallès-Penedès Basin and exposing Miocene strata. This basin represents a NE-SW-oriented depression limited to the northwest and to the southeast by the Prelitoral and Litoral ranges, respectively, which are made of Palaeozoic and Mesozoic rocks. The Vallès-Penedès Basin corresponds to the emerged part of the NE-SW and NNW-SSE horst and half-graben system formed during the Oligocene-Miocene opening of the western Mediterranean (Bartrina et al., 1992; Cabrera & Calvet, 1996; Roca et al., 1999; Cabrera et al., 2004) (Fig. 1). Rifting and thermal subsidence related with this opening led to the accumulation of marine and continental sediments in the Vallès-Penedès Basin,

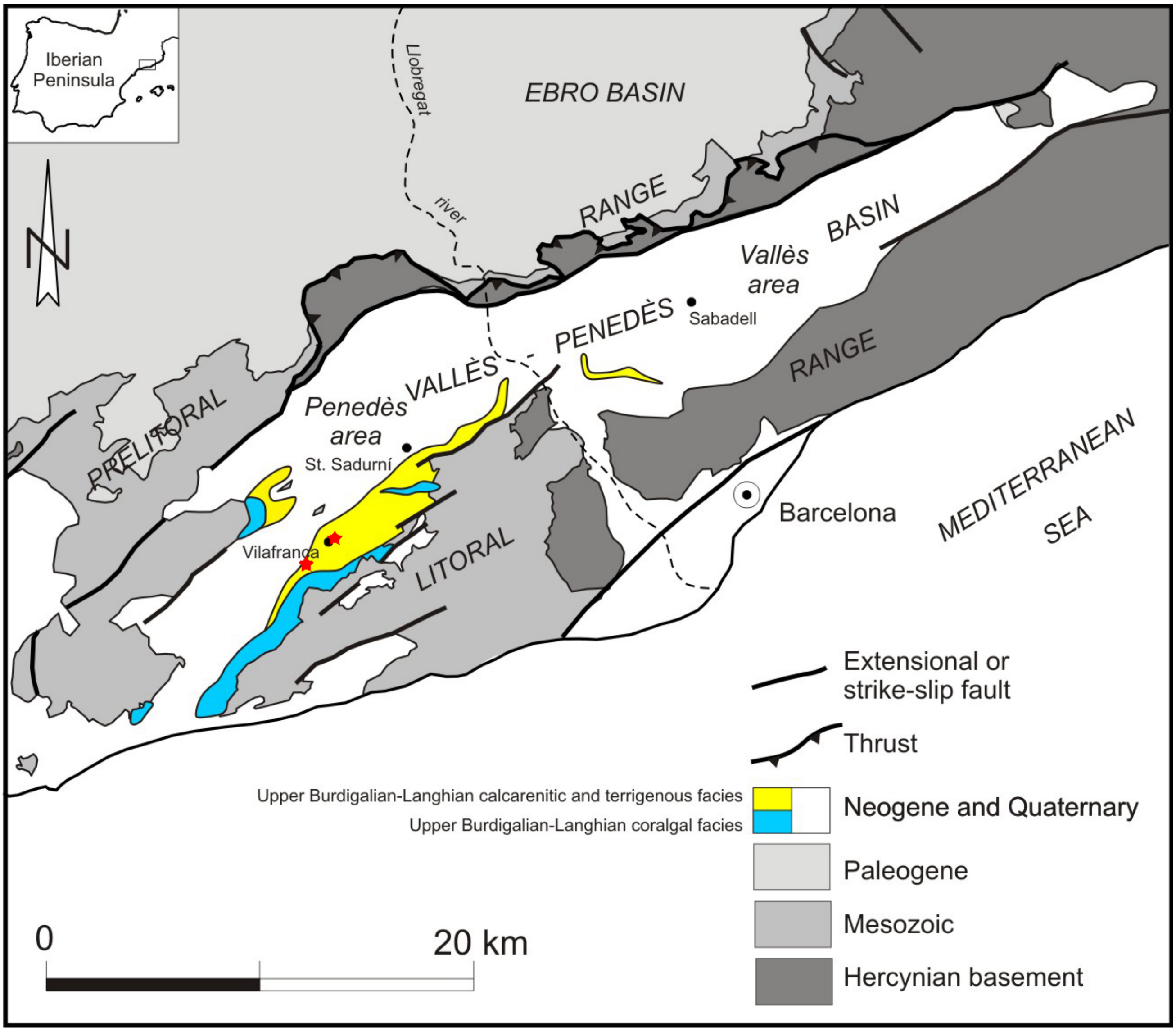

Fig. 1. Simplified geological map of the Vallès-Penedès Basin (modified from Roca et al., 2004). The main upper Burdigalian-Langhian coralgal and calcarenitic-terrigenous facies are indicated. The red stars indicate the location of the outcrops.

from the early to late Miocene (early Burdigalian to Tortonian), as discussed in detail by Cabrera et al. (2004) and Casanovas-Vilar et al. (2016). Although most of the Vallès-Penedès sedimentary infill is of terrestrial origin, three transgressions occurred during the late Burdigalian, Langhian and early Serravallian, leading to the deposition of various marine facies (Cabrera et al., 1991; Cabrera & Calvet, 1996; Roca et al., 1999). During the most significant Langhian transgression, a shallow sea developed in the Penedès area, where fringing reefs, carbonate platform and ramp sediments, open marine marls and transitional shales and sands were laid down.

At the Vilafranca site, grey marls with interbedded levels of fine sands, located predominantly at the top of the unit, are exposed. Based on borehole data, the unit attains a thickness of approximately 300 m (Permanyer, 1982; Cabrera et al., 1991) and it extends across the Penedès Basin and also south of the Llobregat River, including the southernmost part of the Vallès Basin. The presence of the unit is more significant in the southwest of the Penedès depression, where it occupies a central part below younger terrestrial and marine deposits. Towards the northeast, the grey marls are thinner and located along the southeastern margin of the basin. The unit is well exposed in a number of outcrops near the towns of Vilafranca del Penedès, Sant Sadurní d'Anoia, Can Rosell (Subirats), Cerdanyola or Rubí; some of them have yielded decapod crustacean remains (Müller, 1993; Artal, 2008; Garassino et al., 2009). The Vilafranca marls contain also bivalves, gastropods, echinoids, benthic and planktonic foraminifera, as well as remains of flora (Permanyer, 1982). The age of the unit is based on planktonic foraminifera: late Burdigalian to Langhian (Macpherson, 1994). The marls are interpreted to have formed in an offshore environment (Permanyer, 1982; Cabrera et al., 1991), although towards the top of the unit they must have originated in a progressively shallower environment. The crab-bearing levels are located in the middle of the sections studied and are attributed to the Langhian.

At the Santa Margarida site, about two kilometres southwest of Vilafranca del Penedès, fossiliferous and intensely bioturbated yellowish calcarenites, alternating with calcisiltites or marls, crop out. Calcisiltites and marls are more frequent towards the middle of the basin (to the northwest), whereas calcisiltites prevail towards the basinal margin (to the southeast). These sediments are several tens of metres thick and are well exposed along a SW-NE strip attached to the Prelitoral range, south of the town of Vilafranca, near the villages of Moja, Santa Margarida i els Monjos and Castellet, among others. The calcarenites are rich in fragments of red algae, planktonic and benthic foraminifera, corals, molluscs, echinoids, fish teeth and decapod crustaceans. Their age ranges from late Burdigalian to Langhian (Macpherson, 1994). The unit is located in a transition zone between the carbonate ramp to the southeast and the open marine basin marls to the northwest. It is interpreted to represent distal deposits as a result of erosion and transport of sediments originating in the adjacent coralgal complex. Decapod crustacean assemblage at the Santa Margarida site is dominated by portunids such as *Portunus monspeliensis* (A. Milne-Edwards, 1860) and *Necronectes batalleri* (Via, 1941). The crab-bearing calcarenites and marls of this unit are similar to Serravallian strata in the Camp Basin, which also yield remains of the same crab species (Via, 1932; Ossó, 2010).

Repositories: MGB, Museu de Geologia de Barcelona-Museu de Ciències Naturals de Barcelona (Catalonia); MV, Museu de Vilafranca "Vinseum" (Vilafranca del Penedès, Catalonia).

Systematic palaeontology

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Section Eubrachyura de Saint Laurent, 1980
Subsection Heterotremata Guinot, 1977
Superfamily Leucosioidea Samouelle, 1819
Family Iphiculidae Alcock, 1896

Iphiculus Adams & White, 1849
Type species - *Iphiculus spongiosus* Adams & White, 1849, by monotypy.

Iphiculus eliasi Hyžný & Gross, 2016
Figures 2A-E, 3A-E

1941 Illinae, Ebaliinae? - Vía, p. 68, pl. 10, fig. 75.

partim 1965 *Petrochirus* cfr. *priscus* Brocchi - Veiga Ferreira, p. 142, pl. 2, fig. 8 [*non* figs. 7, 9, 11, 12 = *Petrochirus priscus*]

1993 *Randallia*? sp. - Müller, p. 12, figs. M-N.

2016 *Iphiculus eliasi* Hyžný & Gross, p. 266, figs. 2A, 3A-E, 4A-C.

Material and measurements (in mm): MGB 89842 (internal mould of near-complete dorsal carapace): length=14.5; width=17.0; fronto-orbital width=6.0. MV15169 (internal mould of complete dorsal carapace preserving remains of cuticle): length=14.5; width=17.5; fronto-orbital width=6.0. MGB 89843 (counterpart of a male venter): length=8.0; width=10.5.

Emended description: Carapace small, transversely subovate in outline, widest at midlength (at level of posteriormost anterolateral spine), dorsal surface moderately convex in both directions. Front not projected, bilobed, slightly raised, very narrow, about 0.13 of total width, medially notched, strongly divergent. Orbits small, concave, anteriorly directed; outer orbital spine acute; inner orbital spine fused with frontal lobe; supraorbital margin with subtriangular spine, bounded by two open fissures. Fronto-orbital margin about 0.35 of total width. Lateral margins with 6 conical teeth; anterolateral margin with 4 teeth, fourth being most prominent; posterolateral margin with 2 teeth; corners between posterolateral and posterior margins pointed; posterior margin straight, narrow, medially notched. Dorsal surface of carapace evenly covered with numerous densely packed granules, nearly identical in size (when cuticular surface preserved) or with round concave pustules (when cuticular surface

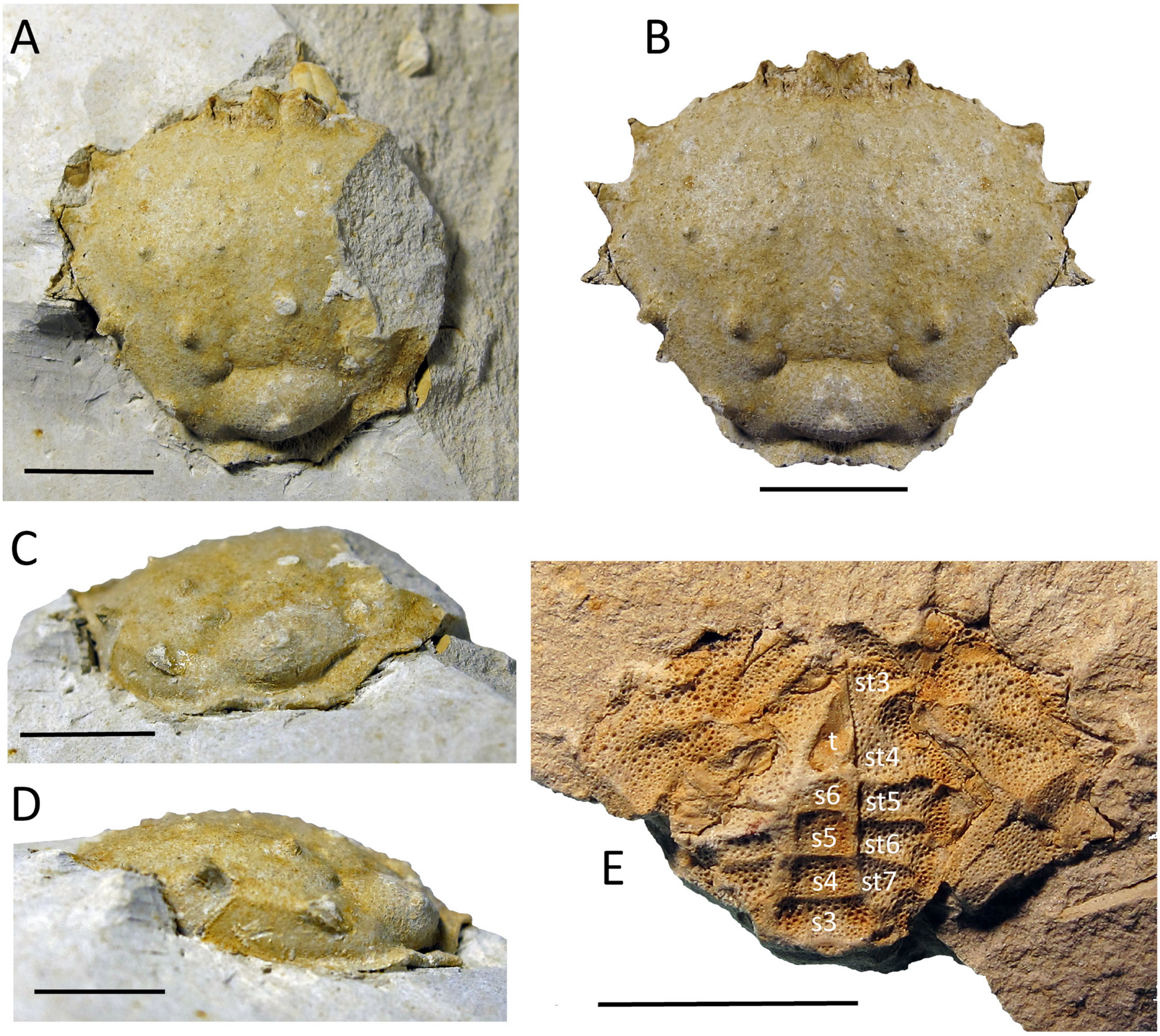

Fig. 2. *Iphiculus eliasi* Hyžný & Gross, 2016. A-D, MGB 89842 from the Langhian of Vilafranca del Penedès (Catalonia); A: dorsal view; B: dorsal view (digital reconstruction); C: posterior view, closeup of posterior part of carapace; D: left lateral view. E, MGB 89843 (male) from the Langhian of Vilafranca del Penedès (Catalonia): ventral view. Abbreviations: st = thoracic sternites; s = pleonal somites; t = telson. Scale bars equal 5 mm.

missing). Carapace surface covered evenly with large rounded tubercles; hepatic region with 1 tubercle; protogastric region with one pair of transversely aligned tubercles in each lobe, and 2 tubercles aligned at the basis of mesogastric region, branchial region with 3 tubercles. Carapace grooves absent in anterior carapace portion, well developed in posterior carapace portion. Gastric region large, indistinctly demarcated with grooves. Cardiac region ovate in outline, strongly arched. Branchial regions broad. Intestinal region narrow. Thoracic sternum relatively wide, maximum width at level of fifth thoracic sternite, sterno-pleonal cavity reaching end of sternite 3; sternite 3 subtriangular, inverted; sternite 4 subtrapezoidal, wider than sternite 3; sternite

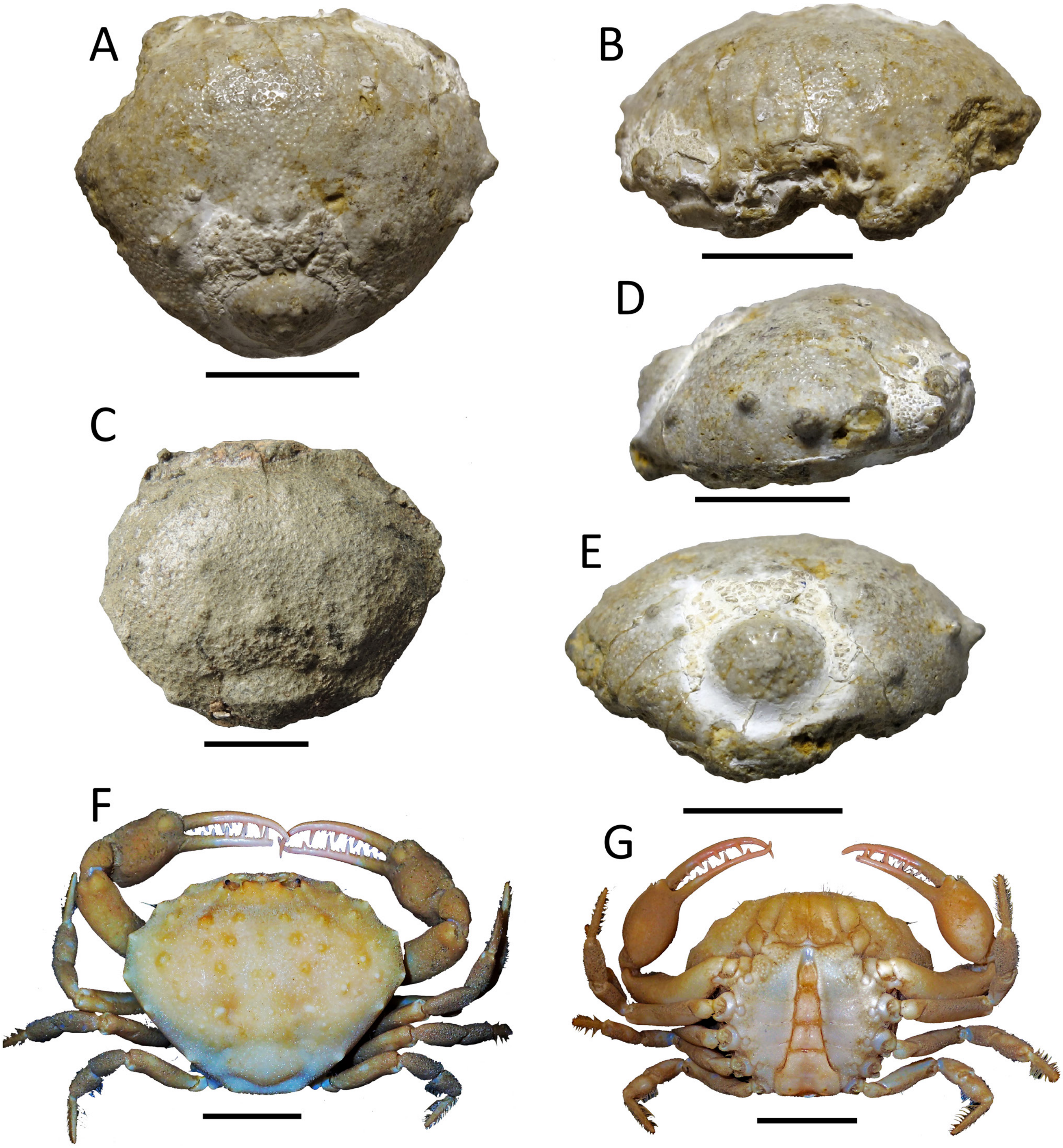

Fig. 3. *Iphiculus eliasi* Hyzny & Gross, 2016 in *I. convexus Ihle*, 1918 . A, B, D, E: *Iphiculus eliasi* Hyzny & Gross.: MV15169, from the Langhian of Santa Margarida i Els Monjos (Catalonia); A: dorsal view; B: frontal view; D: right lateral view; E: posterior view. C: holotype UMJGP 75.612, from the lower Badenian of Wetzelsdorf, Austria; C: dorsal view. F, G, *Iphiculus convexus* Ihle, 1918, ZRC 2009.0462 (male specimen from Vanuatu); F: dorsal view; G: ventral view. Scale bars equal 5 mm, except for F and G in which it is 10 mm. Photographs of F-G by P.K.L. Ng.

5 subrectangular transversely elongate; sternite 6 subtrapezoidal transversely elongate; sternite 7 subtrapezoidal, directed posteriorly, shorter than sternite 6. Episternite 4 laterally directed; episternites 5-6-7 progressively posteriorly directed. Suture 3/4 laterally visible, opened; sutures 4/5, 5/6 and 6/7 apparently complete. Male pleon extremely narrow, inverted T-shaped, all pleonal somites free; somite 3 being widest, subrectangular transversely elongate; somites 4, 5, and 6 subrectangular, narrowing progressively to the telson; telson subtriangular longitudinally elongate, sharp pointed, twice as long as somite 6. Pterygostome subtrapezoidal. All ventral surface, sternum, pleon, pterygostome and branchiostegite densely granulate. Exognath of third maxilliped elongate, inner side smooth.

Remarks: Hyžný & Gross (2016) described a new species, *Iphiculus eliasi* (Fig. 3C), from the Middle Miocene of Austria (Steiermark). In their paper, Hyžný & Gross (2016, p. 268) pointed out that a leucosioid found in outcrops at Santa Margarida i Els Monjos (Alt Penedès, Catalonia), described and figured first as "Iliinae, Ebaliinae?" by Via (1941, p. 68-69, pl. 10, fig. 75) and subsequently as "*Randallia*? sp." by Müller (1993, p. 12, figs. 5M-N), could be an iphiculid related to *I. eliasi*. Access to this sample of "*Randallia* sp.?" (Fig. 3A, B, D, E), housed in the Museum of Vilafranca (now Vinseum), has now allowed to conclude that, despite the different types of preservation as a result of different lithologies at outcrops, it is conspecific with the Vilafranca specimens and likewise, both specimens are also conspecific with the Austrian one described by Hyžný & Gross (2016) as *Iphiculus eliasi* (see Hyžný & Gross, 2016, p. 268). Additionally, a small counterpart of a well-preserved male venter, recovered in the Vilafranca outcrop, is available (Fig. 2E). This exhibits the main diagnostic characters of the Iphiculidae, such as a very narrow male pleon with all somites free (Figs. 2E, 3G; Ng et al., 2008, p. 87); this allows us to attribute it to a single iphiculid known from the area, *I. eliasi*.

A carapace preserved in dorsal aspect from the Middle Miocene of Quinta da Farinheira, Lisboa (Portugal), described and figured by Veiga Ferreira (1965, p. 142-143, pl. 2, 8) as *Petrochirus* cf. *priscus* Brocchi, 1883, does not represent part of a hermit crab, but rather the carapace of a leucosioid crab. Actually, the material is considered conspecific with *Iphiculus eliasi*, thus widening the distribution of the species further to the west.

Discussion

Müller (1993, p. 5, table 1) already pointed out the affinities between the Langhian and Serravallian decapod crustacean assemblages of the westernmost Proto-Mediterranean and roughly coeval Badenian assemblages of the Central Paratethys. Although he concluded that only 9 of 22 identified Miocene species of Catalonia were reported also in the Central Paratethys, recent reports present further taxa that are present in both areas (Díaz-Medina et al., 2018; herein). Nevertheless, some Iberian occurrences are slightly younger, being of Late Miocene age (Díaz-Medina et al., 2017).

The presence of *Iphiculus eliasi* in the northeast and southwest of Iberian Peninsula represents the westernmost (fossil) record for the genus and for the family. Extant representatives of the family Iphiculidae are found mainly in the Indo-West Pacific, in a depth range of 11 to 177 m (Chen, 1989; Chen & Sun, 2002), preferring muddy and sandy bottoms (Galil & Ng, 2007), similar environments to that inhabited by *Iphiculus eliasi*.

Conclusions

The ventral counterpart, preserving diagnostic sternal and pleonal characters, allows to emend the original description of *Iphiculus eliasi* and further corroborate its original systematic assignment. Its presence in the Middle Miocene of the northeastern coast of the Iberian Peninsula, as well as along the southwestern Iberian coast (Portugal), supports the circum-Mediterranean distribution of decapod crustacean assemblages during that time interval (Gašparič & Ossó, 2016; Hyžný & Gross, 2016; Díaz-Medina et al., 2018 and references therein).

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Additional records of decapod crustaceans from the lower Pleistocene beds of Poggi Gialli (Tuscany, central Italy)

Nove najdbe rakov deseteronožcev iz spodnjepleistocenskih plasti v kamnolomu Poggi Gialli (Toskana, Italija)

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Ključne besede: Decapoda, Astacidea, Anomura, Brachyura, kenozoik, Sredozemlje

Abstract

Additional species of decapod crustaceans are recorded from the lower Pleistocene beds exposed at the Poggi Gialli quarries (Sinalunga, Tuscany, central Italy). They include *Galathea tuscia* sp. nov., *Ilia* sp., *Liocarcinus* cf. *L. maculatus* (Risso, 1827), and *Aliaplax tyrsenorum* gen. nov., sp. nov. Novel morphological details for *Distolambrus rasnus* De Angeli, Garassino & Pasini *in* Baldanza, Bizzarri, De Angeli, Famiani, Garassino, Pasini & Pizzolato, 2017, based on a single newly collected specimen, are added, as is the rare record of an indeterminate nephropid. These additions augment our knowledge of the composition of carcinological faunas in this peculiar environment from the early Pleistocene of central Italy. An updated list of decapod crustacean species from Poggi Gialli is also provided herein.

Izvleček

V prispevku predstavljamo nove najdbe in nove vrste rakov deseteronožcev iz spodnjepleistocenskih plasti v kamnolomu Poggi Gialli (Sinalunga, Toskana, osrednja Italija). Najdbe vključujejo vrste *Galathea tuscia* sp. nov., *Ilia* sp., *Liocarcinus* cf. *L. maculatus* (Risso, 1827) in *Aliaplax tyrsenorum* gen. nov., sp. nov. Dodatno opisujemo tudi nove morfološke podrobnosti vrste *Distolambrus rasnus* De Angeli, Garassino & Pasini na Baldanzi, Bizzarri, De Angeli, Famiani, Garassino, Pasini & Pizzolato, 2017, ki temeljijo na novo odkritem primerku. Opisujemo tudi redko najdbo nedoločenega nefropidnega raka. Opisan material dopolnjuje naše znanje o sestavi združb deseteronožcev v tem nenavadnem okolju zgodnjepleistocenske starosti. Prispevku je dodan tudi posodobljen seznam vseh fosilnih deseteronožcev iz kamnoloma Poggi Gialli.

Introduction

Both fully marine and transitional sedimentary rocks that crop out in a relatively restricted quarried area at Poggi Gialli (Sinalunga, Siena, Tuscany) have yielded diverse macrofossil assemblage from the early Pleistocene, including molluscs, echinoids, bryozoans, corals, decapod crustaceans, isopods, and plant remains (for a full list, see Baldanza et al., 2017). The rich and peculiar decapod crustacean assemblage, which is incomparable to other communities previously recorded from the Pleistocene of Tuscany and from the Mediterranean basin, has recently been discussed in detail by Baldanza et al. (2017) who also provided a sedimentological, stratigraphic and palaeoenvironmental interpretations of the Poggi Gialli quarries.

Subject of the present note is a description of a number of recently collected specimens of decapod crustaceans that are referred to species, unknown from this locality until now.

Material and methods

In the Poggi Gialli area there are two disused quarries that are traversed by the Siena-Bettole highway and formally named as Poggi Gialli North (PGN) and Poggi Gialli South (PGS) respectively (see Baldanza et al., 2017, p. 43, fig. 4).

The studied specimens are mostly preserved three-dimensional, partially mineralised, inner moulds embedded in small chunks of loose yellow-grey, sandy clay. They were collected from the PGS quarry section and are housed in the palaeontological collections of the Museo di Storia Naturale dell'Accademia dei Fisiocritici (Siena) (MUSNAF).

The Anomura includes *Galathea tuscia* sp. nov. (Galatheidae Samouelle, 1819) (1 specimen); the Brachyura includes *Ilia* sp. (3 specimens) (Leucosiidae Samoulle, 1819); *Distolambrus rasnus* (Parthenopidae MacLeay, 1838) (1 specimen); *Liocarcinus* sp. cf. *L. maculatus* (Risso, 1827) (Portunidae Rafinesque, 1815) (1 specimen); and *Aliaplax tyrsenorum* gen. nov., sp. nov. (Goneplacidae MacLeay, 1838) (2 specimens). Finally, one specimen was assigned to a nephropid (Astacidea Latreille, 1802), genera and species indeterminate.

Abbreviations – lcxp: carapace length (including rostrum); lpa: palm length (excluding index); P1-P5: pereiopods 1 to 5; pll: pleon length; plw: pleon width; s1-s6: pleonal somites 1 to 6; St: thoracic sternites; wcxp: carapace width; wpa: palm width.

Systematic palaeontology

The classification used in this paper follows Ng et al. (2008) and Schweitzer et al. (2010), while for the description of leucosiids and parthenopids we follow, in part, the terminology proposed by Ihle (1918) and Tan & Ng (2007), respectively.

Order Decapoda Latreille, 1802
Infraorder Astacidea Latreille, 1802
Superfamily Nephropoidea Dana, 1852
Family Nephropidae Dana, 1852

Nephropidae genus and species indeterminate
(Plate 1 A)

Material: A single, three-dimensionally preserved P1 palm, with an incomplete index and dactylus (MUSNAF/GEO/7175 – lpa: *c*. 17 mm; wpa: 6 mm).

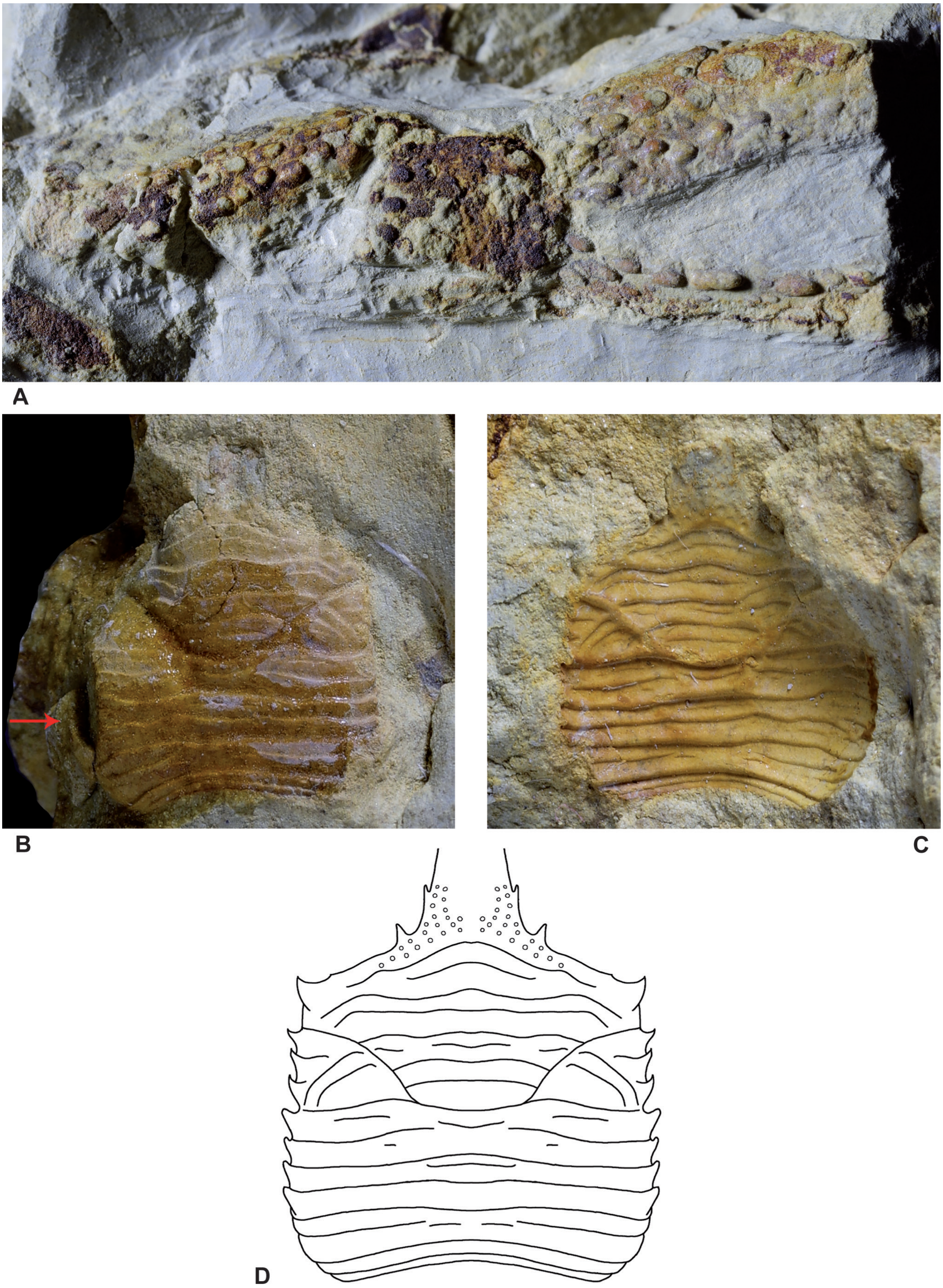
Description: Elongate slender and subrectangular P1 chela; subparallel upper and lower margins, with rounded tubercles; palm surface slightly convex, partially crushed, covered by sparse, irregular tubercles of different sizes; elongate straight index, with upper margin bearing a rim of strong pointed tubercles directed upwards; occlusal margin of index not observable; sparse tubercles, similar to those at the upper margin, extending over entire index length; dactylus stouter than index; index with line of stronger elongate tubercles directed upwards along the occlusal margin; distal extremity of index and dactylus not preserved.

Discussion: The shape and some characters of this P1 chela allow it to be compared with chelae of a number of extant and fossil representatives of the Nephropidae. We consider the coarse ornamentation of the palm and dactylus, consisting of more or less pointed to rounded coarse tubercles of different sizes to be partial internal casts of possibly pointed spines protruding on the original exocuticle, as in extant representatives of Nephropidae. According to Garassino & De Angeli (2004, p. 35), among Nephropoidea "only the representatives of the family Nephropidae exhibit a slender and very elongate propodus of the chelae". For example, the elongate and slender spiny chelae with rows of pointed spines is a feature of the extant and fossil *Nephrops norvegicus* (Linnaeus, 1758). This species differs, however, from the studied specimen in the general ornament of the palm, lacking the strong spiny rims along both fingers. Unfortunately, the poor preservation and incompleteness of the studied specimen make impossible a more detailed systematic assignment.

Baldanza et al. (2017, p. 49, fig. 9A) recorded another indeterminate nephropid from the PGN quarry. This specimen differs, however, from the studied one in having a wider flattened palm covered by sparse, irregular pointed tubercles directed upwards; an elongate straight index gently decreasing towards the tip; an occlusal margin of the index with unequal molariform, rounded teeth proximally, followed by subtriangular equal-sized teeth; a median longitudinal rim with pointed tubercles, rimmed by two lateral longitudinal grooves; an elongate straight dactylus with a molariform tooth in the median part; and two longitudinal grooves that extend along the middle longitudinal part of the flat dactylus.

In the Mediterranean area, nephropids from the late Cenozoic (Plio-Pleistocene) are quite

PLATE 1



A – Nephropidae genus and species indeteterminate, MUSNAF/GEO/7175 (× 6).

B, C – *Galathea tuscia* sp. nov., Holotype, MUSNAF/GEO/7176a, b with a rounded inflated bulge on the left branchial chamber margin as a result of isopod (bopyrid) infestation (red arrow) (× 8).

D – *Galathea tuscia* sp. nov., carapace, line drawing.

rare and mostly poorly preserved. Indeed only two genera have previously been recorded from Italy, namely *Nephropsis* sp. from the Pleistocene of the Enza River (Emilia-Romagna; Garassino & De Angeli, 2004) and *Nephrops* cf. *N. norvegicus* (Linnaeus, 1758) from the early Pleistocene of Poggio i Sodi (Tuscany; Baldanza et al., 2013).

Infraorder Anomura MacLeay, 1838
Superfamily Galatheoidea Samouelle, 1819
Family Galatheidae Samouelle, 1819
Genus *Galathea* Fabricius, 1793

Type species: *Cancer strigosus* Linnaeus, 1761, by original designation.

Fossil species: *Galathea affinis* Ristori, 1886; *G. berica* De Angeli & Garassino, 2002; *G. caporiondoi* De Angeli & Ceccon, 2017; *G. hexacristata* Beschin, Busulini & Tessier *in* Beschin, Busulini, Fornaciari, Papazzoni & Tessier, 2018; *G. keijii* Karasawa, 1993; *G. lovarica* Beschin, De Angeli, Checchi & Zarantonello, 2016; *G. lupiae* Robineau-Desvoidy, 1849; *G. mainensis* Ceccon & De Angeli, 2012; *G. sahariana* Garassino, De Angeli & Pasini, 2008; *G. spitzbergica* Gripp, 1927; *G. strigifera* Fischer-Benzon, 1866; *G. tuscia* sp. nov. (this study); *G. valmaranensis* De Angeli & Garassino, 2002; *G. weinfurteri* Bachmayer, 1950.

Galathea tuscia sp. nov.

(Plate 1 B-D)

Diagnosis: Subsquare carapace (excluding rostrum), slightly convex in transverse section; rostrum wide, triangular, with slight median depression, large dorsal tubercles and two lateral spines; cervical groove laterally bifurcated; carapace with nine main uninterrupted sinuous transverse ridges, intercalated with five interrupted transverse ridges; anterior branchial region with two main diagonal uninterrupted ridges.

Etymology: from the Latin *tuscus*, *tusci* = Tuscia or Etruria, the southern part of Tuscany inhabited by Tusci or Etruschi people between 900 to 27 BC.

Holotype: MUSNAF/GEO/7176a, b (part-counterpart).

Measurements: MUSNAF/GEO/7176 – lcxp: 9.5 mm; wcxp: 7 mm.

Description: Carapace subsquare in dorsal view, as long as wide, transversely convex and enlarged chiefly in posterior third; wide triangular rostrum, enlarged towards base, well developed anteriorly, with at least one median spine along lateral margins; first rostral spine (supraorbital spine) shorter than the other one; dorsal surface of rostrum with a weak median depression and covered with many large uniformly arranged tubercles; wide orbits; extraorbital spine apparently shorter than the supraorbital one; one strong anterolateral spine directed forwards; anterior branchial margins slightly convex, with three spines, equal in size and directed forwards; posterior branchial margins convergent posteriorly, with four spines, equal in size and directed forwards; posterior margin wide, slightly concave and marked by one thin marginal ridge; deep cervical groove laterally bifurcated; epigastric region with one main uninterrupted sinuous transverse ridge and one weak laterally interrupted ridge; proto-, meso-, and metagastric regions not well separated, with five main uninterrupted sinuous transverse ridges, intercalated with two medially interrupted transverse ridges; subtriangular anterior branchial regions, with two main short uninterrupted strongly diagonal ridges; posterior branchial regions with three main uninterrupted sinuous transverse ridges, intercalated with one weak medially interrupted transverse ridge and one laterally interrupted transverse ridge.

Discussion: According to Robins et al. (2013, p. 174) and MacPherson & Robainas-Barcia (2015, p. 13), the broad, subtriangular rostrum, with lateral teeth and the poorly defined cardiac region allow to assign the studied specimen to the Galatheidae.

Fossil representatives of the Galatheoidea are very rare in Tuscany, being limited to only two genera, *Galathea* Fabricius, 1793 and *Munida* Leach, 1820. Baldanza et al. (2013, p. 343) noted that of *Galathea* there was only a single record, *Galathea* sp. from the early Pleistocene of Poggi i Sodi (Siena, Tuscany); this differs from the *G. tuscia* sp. nov. in having the dorsal carapace regions with only uninterrupted ridges. Later, Garassino & Pasini (2015, p. 40) described *Munida grossetana* Garassino & Pasini, 2015 from the Pliocene of Monterotondo Marittimo (Grosseto, Tuscany), its needle-like rostrum ruling out any congeneric assignment of the new species.

The sole species that is close, stratigraphically speaking, is *Galathea affinis* Ristori, 1886 from the late Pliocene of Bianchi (Sicily) and from the Miocene of Capo San Marco (Sardinia) (Lőrenthey, 1909). A detailed comparison, however, with the new species is impossible because the holotype and additional sample are lost. Additionally, the poor description and the poor quality of the line drawing provided by Ristori (1886, p.

126, 127, pl. 2, fig. 18) preclude to note diagnostic characters of *G. affinis*. Based on these observations, we herein consider *G. affinis* to be a *nomen dubium*.

We justify the erection of the new species, *G. tuscia*, based on these characters: dorsal carapace regions without hepatic, epigastric, parahepatic, anterior branchial, and postcervical spines; such are always present in extant species of the Mediterranean Sea (Zariquey Alvarez, 1968; Falciai & Minervini, 1992) and occassionally in some Eocene and Oligocene species (Beschin et al. 2016, 2018; Ceccon & De Angeli, 2012; De Angeli & Ceccon, 2017; De Angeli & Garassino, 2002) and two uninterrupted strongly diagonal ridges on the anterior branchial regions – this is a peculiar character not seen in any other fossil species of *Galathea* from the Italian fossil record.

Note: The studied specimen shows a typical rounded inflated bulge on the left branchial chamber margin, most probably denoting isopod (bopyrid) infestation. Isopod parasitism in decapod crustaceans, including squat lobsters, has been recorded by several authors for Mesozoic and Cenozoic taxa (for full references see Klompmaker & Boxshall, 2015).

The only examples of isopod parasitism in fossil material from Italy are those recorded by Ceccon & De Angeli (2013) for the Eocene of Vicenza, which we can here supplement with a record from the early Pleistocene.

Infraorder Brachyura Latreille, 1802
Section Eubrachyura de Saint Laurent, 1980
Subsection Heterotremata Guinot, 1977
Superfamily Leucosioidea Samouelle, 1819
Family Leucosiidae Samouelle, 1819
Subfamily Ebaliinae Stimpson, 1871
Genus *Ilia* Leach, 1817

Type species: *Cancer nucleus* Linnaeus, 1758, by monotypy.

Included fossil species: see Schweitzer et al. (2010).

Ilia sp.
(Plate 2 A–B)

Material: Two pleons in ventral view (MUSNAF/GEO/7177 – pll: 10 mm; plw: 10 mm; MUSNAF/GEO/7178 – pll: 8 mm; plw: 8 mm); and a single, incomplete P1 [MUSNAF/GEO/7179 – lpa: 15 mm (including index); wpa: 3 mm].

Description: Pleon – Sternum ovoid, with granulate surface; thoracic sternites exposed, subpetaloid in shape, decreasing in size and length posteriorly; St 1-4 fused; triangular elongate sternum pleonal cavity deeply excavated, narrowing to the anterior part of sternum.

P1 – elongate globular palm, preserved as an inner mould, ovoid in transverse section; straight upper and inferior margins, narrowing distally; thin very elongate pointed index directed downwards, curved distally with small conical alternating occlusal teeth.

Discussion: Based on the proxy characters, these rounded granulate pleons and typically elongate chela are compared with those of some representatives of the family Leucosiidae and, tentatively, with *Ilia* Leach, 1817.

The studied pleon has affinities in shape and ornamentation with that of the fossil representatives of *Ilia nucleus* (Linnaeus, 1758), as recorded and illustrated by Garassino et al. (2012, p. 28, fig. 14C) from the early Pliocene of La Serra quarry (San Miniato, Tuscany), whereas the globular elongate palm and index are comparable in shape with those of the extant representatives of the same species (Garassino et al., 2012, p. 28, fig. 14H). The studied specimens seem to have, however, a larger, coarse granules on the pleon, whereas the palm, preserved as an inner mould, does not allow any comparison of the external ornamentation of the chela. We prefer to leave the studied specimens in open nomenclature, awaiting the discovery of more complete material.

Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Subfamily Polibinae Ortmann, 1893
Genus *Liocarcinus* Stimpson, 1871

Type species: *Portunus holsatus* Fabricius, 1798, by original designation.

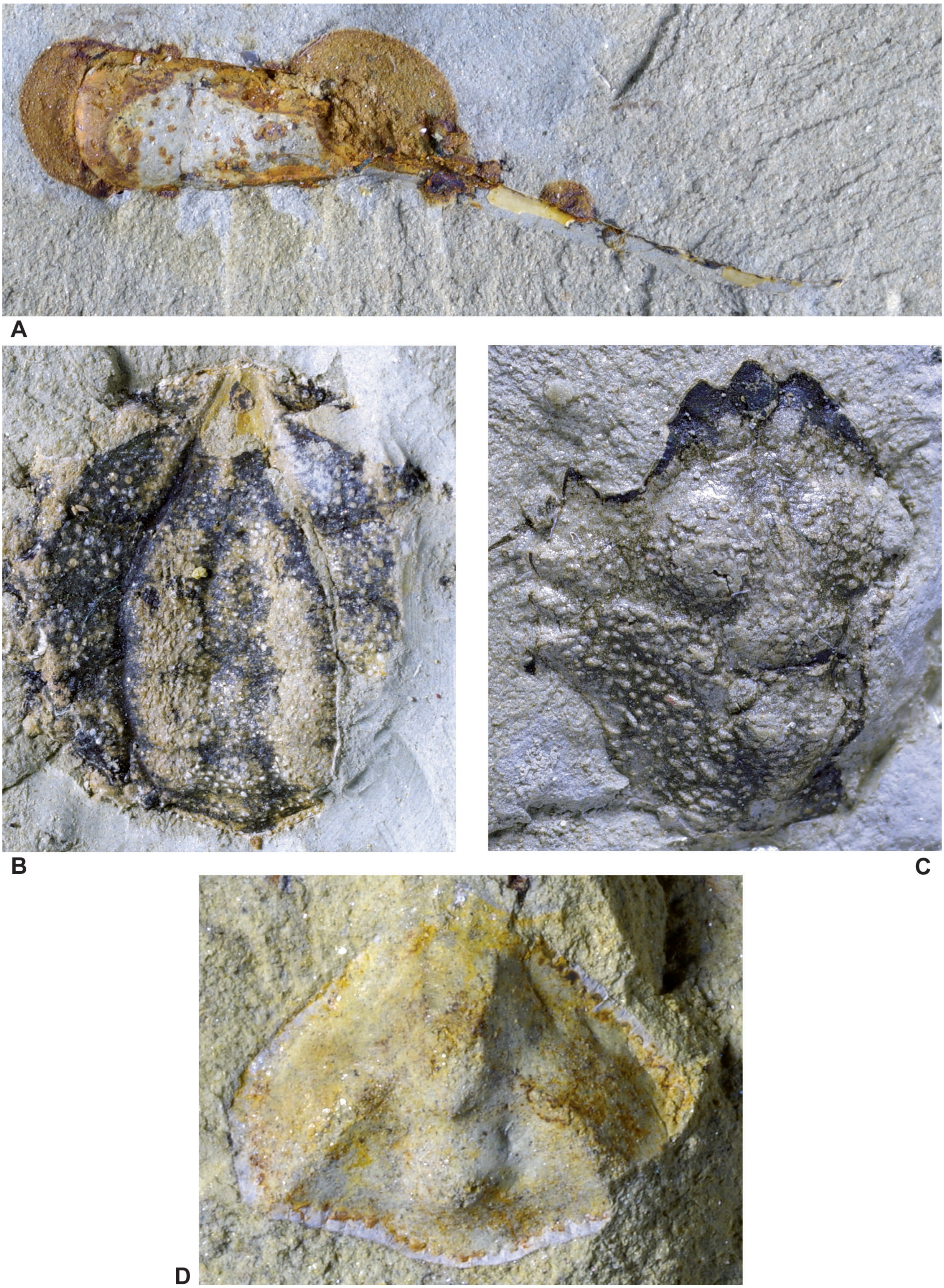
Fossil species: see Schweitzer et al. (2010).

Liocarcinus cf. ***L. maculatus*** (Risso, 1827)
(Plate 2 C)

Material and measurements: A single, near-complete carapace in dorsal view (MUSNAF/GEO/7180 – lcxp: 8 mm; wcxp: 7 mm).

Description: Small-sized, subhexagonal carapace weakly convex transversely; front with three spines projecting beyond the orbits, median slightly longer and sharper than lateral ones; anterolateral margins, with four triangular spines, directed anterolaterally (excluding extraorbital spine), fourth spine smaller than the others; convergent posterolateral margins concave and longer than

PLATE 2



A, B – *Ilia* sp., MUSNAF/GEO/7179, P1 in lateral view (× 8) and MUSNAF/GEO/7177, thoracic sternum and pleon (× 8.5).

C – *Liocarcinus* cf. *L. maculatus* (Risso, 1827), MUSNAF/GEO/7180, carapace in dorsal view (× 13.5). D – *Distolambrus rasnus* De Angeli, Garassino & Pasini *in* Baldanza, Bizzarri, De Angeli, Famiani, Garassino, Pasini & Pizzolato, 2017, MUSNAF/GEO/7181a, carapace in dorsal view (× 15).

the anterolateral ones; rounded and well-raised protogastric regions; subtriangular mesogastric region strongly tuberculate; undifferentiated branchial regions; cardiac region with three bulges; tuberculate dorsal surface.

Discussion: The morphological characters of the anterolateral margins with spines, as well as the configuration of the front match those of the *Liocarcinus* "*pusillus*" group (i.e. "small sized *Liocarcinus* having front projecting beyond the orbits") as recognised by Froglia & Manning (1982, p. 257), and especially into those of the extant *Liocarcinus maculatus* (Risso, 1827) in particular, as based on the diagnosis provided by Froglia & Manning (1982, p. 262). However, we prefer prudence in our comparison of the studied specimen with *L. maculatus* due to the lack of carpus and antennal flagellum; those provide essential specific diagnostic characters (Froglia & Manning, 1982, p. 264). Although the studied specimen is only likened to the extant taxon, it would constitute the first mention of *L. maculatus* from the fossil record. The extant species inhabits the Mediterranean Sea at sublittoral (5-73 meters) depths (Froglia & Manning, 1982, p. 262).

Note: Baldanza et al. (2017, p. 69, fig. 15D), recorded *Liocarcinus depurator* (Linnaeus, 1758), from the PGS quarry based on a single, small and incomplete carapace, lacking the frontal margin. A revision of this specimen might also document *L. maculatus* rather than *L. depurator*.

Superfamily Parthenopoidea MacLeay, 1838
Family Parthenopidae MacLeay, 1838
Subfamily Parthenopinae MacLeay, 1838
Genus *Distolambrus* Tan & Ng, 2007

Type species: *Heterocrypta maltzani* Miers, 1881, by original designation.

Fossil species: *Distolambrus rasnus* De Angeli, Garassino & Pasini *in* Baldanza, Bizzarri, De Angeli, Famiani Garassino, Pasini & Pizzolato, 2017.

Distolambrus rasnus De Angeli, Garassino & Pasini, 2017 *in* Baldanza, Bizzarri, De Angeli, Famiani Garassino, Pasini & Pizzolato, 2017
(Plate 2 D)

2017 *Distolambrus rasnus* De Angeli, Garassino & Pasini *in* Baldanza, Bizzarri, De Angeli, Famiani Garassino, Pasini & Pizzolato; p. 57, Fig. 14A, B.

Material and measurements: A single complete carapace in dorsal view (MUSNAF/GEO/7181a, b – lcxp: 5 mm; wcxp: 6 mm).

Description: Very small-sized carapace for the genus, trapezoidal transversaly; dorsal surface with raised granulate ridges on gastric, epibranchial, and cardiac regions; protruding triangular rostrum; serrate straight anterolateral margins, tapering frontally; serrate posterolateral margins gently convex medially ending in a point at level of the posterior margin; V-shaped granulate gastric ridge; diagonal branchial granulate ridge not continuous with the gastric ridge; strong raised, round tubercle on the median cardiac region, bearing some small sparse tubercles dorsally; intestinal region flat expanded posteriorly; convex epibranchial margin; posterior margin convex medially.

Discussion: This specimen shows the main diagnostic characters of *Distolambrus rasnus* described from PGS quarry by De Angeli, Garassino & Pasini *in* Baldanza, Bizzarri, De Angeli, Famiani Garassino, Pasini & Pizzolato (2017, p. 57, fig. 14A, B), as follows: subpentagonal and smooth carapace; triangular and pointed rostrum domed depressed medially, with serrate margins; serrate antero- and posterolateral margins; raised, granulate ridges on gastric, epibranchial and cardiac regions; V-shaped ridge on the gastric region; oblique branchial ridge not continuous with the gastric one; strong median cardiac tubercle; and intestinal region flat. Here we wish to remark that the antero- and posterolateral margins in the studied specimen are not distinctly separated by a small hepatobranchial notch as the one seen in the type specimen, which is possibly due to its smaller size or this could reflect intraspecific variation.

This is only the second specimen of this uncommon fossil species, reported from the Poggi Gialli quarries only.

Superfamily Goneplacoidea MacLeay, 1838
Family Goneplacidae MacLeay, 1838
Subfamily Goneplacinae MacLeay, 1838

Genus *Aliaplax* gen. nov.

Diagnosis: Carapace trapezoidal, strongly elongate transversely, twice wider than long, broadest at exorbital angle; orbital angle outwardly projected in a pointed spine; distinctly T-shaped narrow front directed downwards; very elongate orbit grooves occupying the entire frontal margin, deeper proximally; supraorbital margin smooth slightly sinuous; suborbital margin smooth, notably sinuous, projected frontally, exceeding supraorbital margin; diagonal posterolateral margins slightly convex gently tapering posteriorly to the wide posterior margin, wider than the half of the total frontal margin; dorsal carapace convex fronto-posteriorly and smooth, with one weak horizontal uninterrupted ridge on the posterior third, without clear indications of regions; protogastric region with a drop-shaped bulge, extending from the frontal base to the mesogastric region; intestinal region with one transverse arched groove, concave dorsally behind the metabranchial regions slightly constricted forming two lateral rounded depressions.

Etymology: From the name of the mythical marine nereid Alia, described by Homer as the nymph with "large eyes", and the suffix *–plax*. Gender: feminine.

Type species: *Aliaplax tyrsenorum* sp. nov., by monotypy.

Fossil species: *Aliaplax tyrsenorum* sp. nov. (this study).

Discussion: According to Castro (2007, p. 616) the studied specimens have been assigned to the Goneplacidae in having transversely rectangular carapace, narrow front, wide and long orbits, and dorsal surface with horizontal ridges, without clear indication of regions.

According to De Angeli et al. (2019), goneplacids are represented in the fossil record of Italy by five genera: *Albaidaplax* Garassino, Pasini & Castro, 2013 from the early Pliocene-early Pleistocene of Tuscany and Umbria; *Astiplax* Garassino & Pasini, 2013 from the late Pliocene of San Pietro (Asti, Piedmont), *Goneplax* Leach, 1814 from the Miocene to early Pleistocene of Piedmont, Emilia-Romagna, Tuscany, Lazio, and Sicily; *Magyacarcinus* Schweitzer & Karasawa, 2004 from the middle Eocene-late Eocene of Veneto; and *Ommatocarcinus* White, 1851 from the early Pleistocene of Tuscany.

The subrectangular carapace, slightly wider than long, the front as wide as the orbits, and the short posterior margin rule out assignment of the studied specimens to *Albaidaplax*, while the strongly tuberculate carapace, the very narrow front, and the presence of gastric pits and branchiocardiac groove exclude *Astiplax*. The studied specimens cannot be placed in *Goneplax* because the carapace has a strong outer orbital tooth, the notch between the front, and one anterolateral tooth, while the subsquare carapace, the wide straight front, the deep branchiocardiac groove, and the swollen subhepatic regions set them apart from *Magyacarcinus*. *Ommatocarcinus*, recently recorded from Poggi Gialli by De Angeli, Garassino & Pasini *in* Baldanza, Bizzarri, De Angeli, Famiani Garassino, Pasini & Pizzolato (2017, p. 62), shares some characters with the studied specimens, as follows: carapace transversely rectangular, much wider than long; orbits wide, greatly expanded laterally; supraorbital margin sinuous; dorsal surface of carapace smooth, with one weak horizontal ridge, without clear indication of regions; the outer orbital angle with one tooth; and anterolateral tooth absent. The studied specimens, however, differ from *Ommatocarcinus* in having shorter, T-shaped front; very elongate orbit grooves occupying the entire frontal margin; smooth suborbital margin notably projected frontally, exceeding supraorbital margin; median drop-shaped bulge on gastric region; intestinal transverse groove concave dorsally behind the metabranchial regions that are slightly constricted forming two lateral rounded depressions; and wide posterior margin.

Castro (pers. comm, 2019) identified strictly morphological affinities, such as the shape of the frontal region, outer orbital angle with conspicuous acute tooth, and the long straight posterior margin when comparing the studied specimens with two extant Indo-Pacific genera of the Goneplacinae, *Singhaplax* Serène & Soh, 1976 and *Microgoneplax* Castro, 2007. However, the studied specimens differ from these extant genera in having protogastric regions with a drop-shaped bulge, intestinal region with one transverse arched groove, and one weak horizontal uninterrupted ridge on the posterior third of the dorsal carapace surface.

Based upon these observations, we believe the description of a new genus is warrented to accommodate these specimens.

Aliaplax tyrsenorum sp. nov.
(Plate 3 A–D)

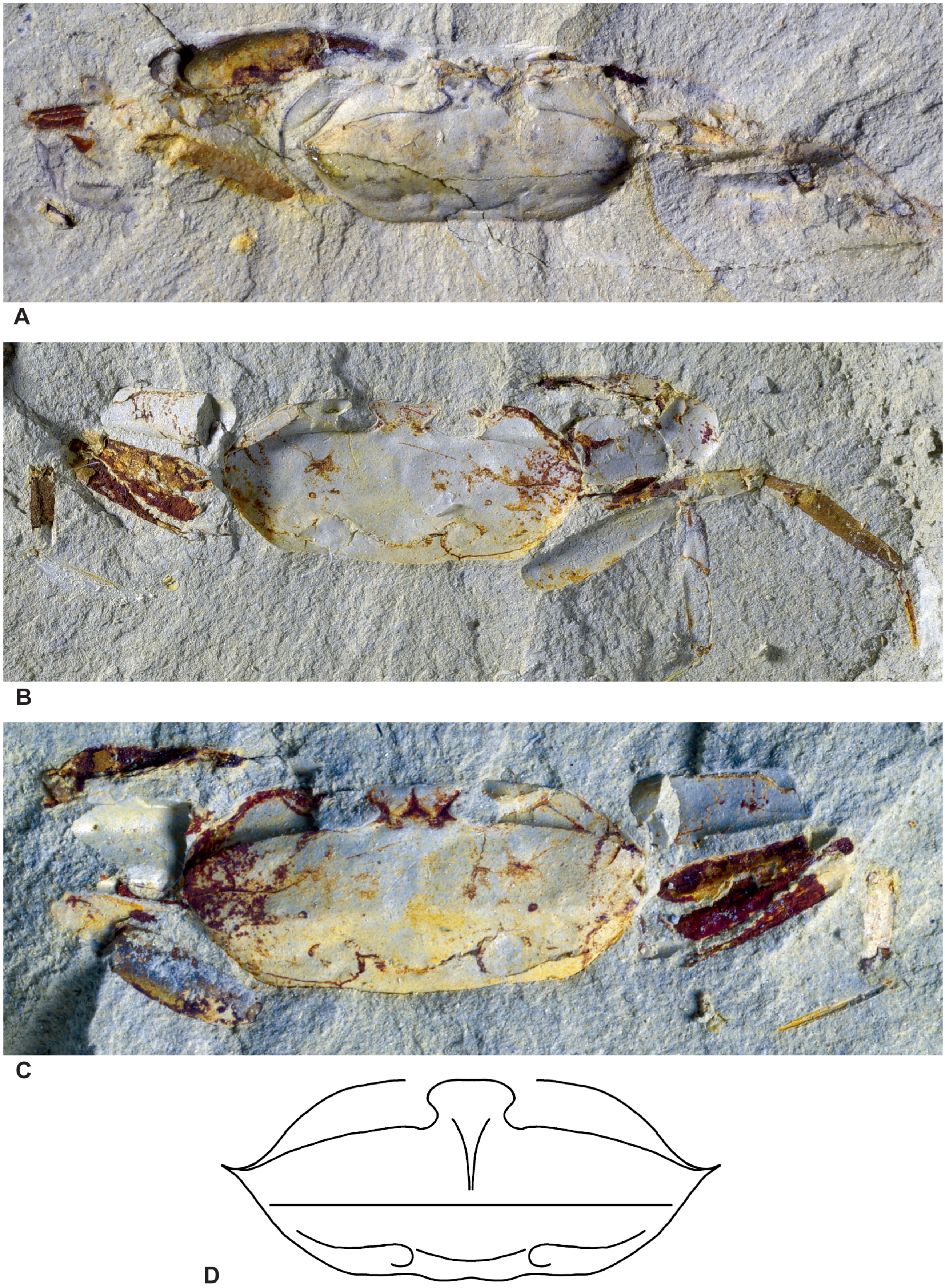
Etymology: The trivial name originates from the Tyrseni, the ancient Greek name for the inhabitants of the Etruscan regions.

Holotype: MUSNAF/GEO/7183.

Paratype: MUSNAF/GEO/7182 a, b.

Material and measurements: One complete specimen in dorsal view (part-counterpart) (MUSNAF/GEO/7182a, b – lcxp: 6 mm; wcxp: 13 mm, excluding lateral spine), and another in counterpart only (MUSNAF/GEO/7183 – lcxp: 4.5 mm; wcxp: 10 mm, excluding lateral spine).

PLATE 3



Aliaplax tyrsenorum gen. nov., sp. nov.

A – Holotype, MUSNAF/GEO/7183 (× 5).

B, C – Paratype, MUSNAF/GEO/7182a, b (× 6.5).

D – Carapace, line drawing.

Description: Carapace trapezoidal, strongly elongate transversely, twice wider than long, broadest at exorbital angle; orbital angle outwardly projected in a pointed spine; distinctly T-shaped narrow front directed downwards; very elongate orbit grooves occupying the entire frontal margin, deeper proximally; supraorbital margin smooth slightly sinuous; suborbital margin smooth, notably sinuous, projected frontally, exceeding supraorbital margin; diagonal anterolateral margins slightly convex gently tapering posteriorly to the wide posterior margin, wider than the half of the total frontal margin; dorsal carapace convex fronto-posteriorly and smooth, with one transverse uninterrupted ridge on the posterior third; protogastric region with a drop-shaped bulge, extending from the frontal base to the mesogastric region; intestinal region with one transverse arched groove, concave dorsally behind the metabranchial regions that appears slightly constricted forming two lateral rounded depressions. P1 elongate, heterochelous with stout rectangular right palm and shorter left palm; dactylus gently curved; P4-P5 elongate, with pointed dactyli.

Conclusions

The present study updates the rich and peculiar Poggi Gialli decapod crustacean assemblage by adding a few new, recently collected and not previously recorded taxa. Among these is a new squat lobster *Galathea tuscia* sp. nov.; in addition, the presence of *Aliaplax tyrsenorum* gen. nov., sp. nov., is remarkable. The presence of a few goneplacids that have closer affinities to some Indo-Pacific genera than to those from the Mediterranean calls for a discussion of their presence, diffusion, and extinction in the paleo-Mediterranean Sea. Moreover, the presence of swimming macrurans is herein corroborated by a new record of an indeterminate nephropid.

The new data corroborate the previous characterisation of the paleoenvironment suggested by Baldanza et al. (2017, p. 67), with “a sub-tidal marine shallow to moderate deep environment with some terrestrial fresh water influence (possibly from a few to less than 100 m deep), in temperate waters at low levels of water energy…”.

Updated list of decapod crustacean species from the early Pleistocene of Poggi Gialli (Siena, central Italy) is herein provided. Taxa with an asterisk (*) appear to be confined to Poggi Gialli (after De Angeli, Garassino & Pasini *in* Baldanza, Bizzarri, De Angeli, Famiani, Garassino, Pasini & Pizzolato, 2017; this study).

Superfamily Thalassinoidea Latreille, 1831
Family Laomediidae Borradaile, 1903
Genus ***Jaxea*** Nardo, 1847
Jaxea nocturna Nardo, 1847

Superfamily Galatheoidea Samouelle, 1819
Family Galatheidae Samouelle, 1819
Genus ***Galathea*** Fabricius, 1793
Galathea tuscia sp. nov.*
Superfamily Paguroidea Latreille, 1802
Family Paguridae Latreille, 1802
Genus ***Anapagurus*** Henderson, 1886
Anapagurus cf. *A. breviaculeatus* Fenizia, 1937

Superfamily Raninoidea De Haan, 1839
Family Lyreididae Guinot, 1993
Subfamily Lyridinae Guinot, 1993
Genus ***Lyreidus*** De Haan, 1841
Lyreidus paronae (Crema, 1895)

Superfamily Dorippoidea MacLeay, 1838
Family Ethusidae Guinot,1977
Genus ***Ethusa*** Roux, 1830
Ethusa cf. *E. mascarone* Herbst, 1785

Superfamily Leucosioidea Samoulle, 1819
Family Leucosiidae Samoulle, 1819
Subfamilu Ebaliinae Stimpson, 1871
Genus ***Leucosiraja*** De Angeli, Garassino & Pasini *in* Baldanza, Bizzarri, De Angeli, Famiani, Garassino, Pasini & Pizzolato, 2017
Leucosiraja manta De Angeli, Garassino & Pasini *in* Baldanza, Bizzarri, De Angeli, Famiani, Garassino, Pasini & Pizzolato, 2017*
Genus ***Merocryptus*** A. Milne-Edwards, 1873
Merocryptus viperinus De Angeli, Garassino & Pasini *in* Baldanza, Bizzarri, De Angeli, Famiani, Garassino, Pasini & Pizzolato, 2017*

Superfamily Majoidea Samouelle, 1819
Family Majidae Samouelle, 1819
Subfamily Majinae Samouelle, 1819
Genus ***Eurynome*** Leach, 1814
Eurynome italica De Angeli, Garassino & Pasini *in* Baldanza, Bizzarri, De Angeli, Famiani, Garassino, Pasini & Pizzolato, 2017*

Superfamily Parthenopoidea MacLeay, 1838
Family Parthenopidae MacLeay, 1838
Subfamily Parthenopinae MacLeay, 1838
Genus ***Distolambrus*** Tan & Ng, 2007
Distolambrus rasnus De Angeli, Garassino & Pasini *in* Baldanza, Bizzarri, De Angeli, Famiani, Garassino, Pasini & Pizzolato, 2017*

Superfamily Retroplumoidea Gill, 1894
Family Retroplumidae Gill, 1894
Genus ***Retropluma*** Gill, 1894
Retropluma craverii (Crema, 1895)

Superfamily Cancroidea Latreille, 1802
Family Cancridae Latreille, 1802
Subfamily Lobocarcininae Beurlen, 1930
Genus ***Lobocarcinus*** Reuss, 1857
Lobocarcinus sismondai (von Meyer, 1843)

Superfamily Xanthoidea MacLeay, 1838
Family Xanthidae MacLeay, 1838
Subfamily Euxanthinae Alcock, 1898
Genus ***Monodaeus*** Guinot, 1967
Monodaeus bortolottii Delle Cave, 1988

?Superfamily Xanthoidea MacLeay, 1838
Genus *Ancipitecancer* Pasini, Luque & Garassino, 2020
Ancipitecancer collinsi Pasini, Luque & Garassino, 2020*

Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Subfamily Polybinae Ortmann, 1893
Genus ***Liocarcinus*** Stimpson, 1871
Liocarcinus depurator (Linnaeus, 1758)
Liocarcinus cf. *L. maculatus* (Risso, 1827)

Superfamily Goneplacoidea MacLeay, 1838
Family Goneplacidae MacLeay, 1838
Subfamily Goneplacinae MacLeay, 1838
Genus ***Aliaplax*** gen. nov.
Aliaplax tyrsenorum gen. nov., sp. nov.*
Genus ***Goneplax*** Leach, 1814
Goneplax rhomboides (Linnaeus, 1758)
Genus ***Ommatocarcinus*** White, 1851
Ommatocarcinus occidentalis De Angeli, Garassino & Pasini *in* Baldanza, Bizzarri, De Angeli, Famiani, Garassino, Pasini & Pizzolato, 2017*

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On the systematic placement of *Pyreneplax* Ossó, Domínguez & Artal, 2014 (Decapoda, Brachyura, Vultocinidae)

Taksonomska uvrstitev rodu *Pyreneplax* Ossó, Domínguez & Artal, 2014 (Decapoda, Brachyura, Vultocinidae)

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Ključne besede: Goneplacoidea, Martinocarcinidae, sistematika, eocen, priabonij, Evropa

Abstract

Examination of the thoracic sternum and pleonal elements of a new male specimen of *Pyreneplax basaensis* Ossó, Domínguez & Artal, 2014 from the upper Eocene of northern Spain confirms its assignment to the family Vultocinidae Ng & Manuel-Santos, 2007 and reveals the presence of an old lineage (*Pyreneplax* and possible allies) that appeared during the Eocene, persisting to the present day.

Izvleček

V prispevku opisujemo nove fosilne ostanke primerka samca vrste *Pyreneplax basaensis* Ossó, Domínguez & Artal, 2014 iz zgornjega eocena na severu Španije. Ohranjene podrobnosti delov oprsja in repa potrjujejo njegovo uvrstitev v družino Vultocinidae Ng & Manuel-Santos, 2007 in razkrivajo prisotnost stare linije (*Pyreneplax* in sorodni taksoni), ki se je pojavila v eocenu in je prisotna še danes.

Introduction

A new specimen of *Pyreneplax basaensis* with complete sternal and pleonal features and remains of ambulatory legs reveals additional features that were not seen in the type series. It has allowed observation of additional similarities to the extant species *Vultocinus anfractus* Ng & Manuel-Santos, 2007 and a more detailed comparison between both taxa (see Domínguez & Ossó, 2019).

The genus *Pyreneplax* Ossó, Domínguez & Artal, 2014 was erected to accommodate *P. basaensis* from the Priabonian of the south Pyrenean basins of Spain. Subsequently, other, closely similar species have been recorded from the Eocene of the Atlantic Coast of North America and from northern Italy. On the basis of dorsal carapace morphology, fossil crab species such as *Lobonotus saundersi* (Blow & Manning, 1997) from South Carolina (USA) and *L. granosus* (Beschin, Busulini, De Angeli & Tessier, 2002) and *L. sommarugai* Beschin, Busulini & Tessier, 2009 from northern Italy, have lately been transferred to the genus *Pyreneplax* (see Ossó, Domínguez & Artal, 2014; De Angeli, 2014).

Dorsal and ventral (thoracic sternum, pleon) features of *Pyreneplax basaensis* confirm its family relationship with *Vultocinus anfractus*, in spite of the time span that separates both species, placing the origins of the family Vultocinidae in the late Eocene. Furthermore, new DNA molecular studies of *Vultocinus anfractus* have revealed that, "it comes out as a long branch inside the Heterotremata, far away from the rest of the Goneplacoidea" (Ng & Tsang, pers. comm., June/2019).

The studied material is housed at Museo de Ciencias Naturales de la Universidad de Zaragoza (Spain), under acronym MPZ.

Systematic palaeontology

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Section Eubrachyura de Saint-Laurent, 1980
Subsection Heterotremata Guinot, 1977
Superfamily Goneplacoidea MacLeay, 1838
Family Vultocinidae Ng & Manuel-Santos, 2007
Genus *Pyreneplax* Ossó, Domínguez & Artal, 2014 , emend.

Type species: *Pyreneplax basaensis* Ossó, Domínguez & Artal, 2014.

Other species included: *Pyreneplax granosa* (Beschin, Busulini, De Angeli & Tessier, 2002), *Pyreneplax saundersi* (Blow & Manning, 1997) and *Pyreneplax sommarugai* (Beschin, Busulini & Tessier, 2009).

Diagnosis (emended): Small- to medium-sized carapace, suboctagonal, from wider than long to slightly wider than long, slightly convex in anterior third, widest at level of third anterolateral tooth. Dorsal regions well defined, elevated, ornamented with granules; delimited by large and smooth grooves. Frontal margin bilobed, slightly advanced, edge granulated. Orbits oval, oblique, separated from frontal margin by deep fold; supraorbital margin with three teeth separated by two notches, inner orbital tooth subtriangular, prominent. Anterolateral margins with four rounded and granulated teeth (outer orbital spine excluded); first one smallest, at lower level. Posterolateral margins slightly convex, ornamented with granules. Posterior margin slightly convex, medially depressed, rimmed. Cervical and hepato-gastric grooves well marked, broad, smooth. Gastric process well marked; epigastric lobes swollen; protogastric lobes, swollen, oval, U-shaped, anterior portion medially depressed; mesogastric lobe broad posteriorly; anterior portion slender, low, long, reaching basal portion of epigastric lobes; metagastric lobe indistinct; urogastric region swollen, well delimited from meso-metagastric lobe by narrow groove with gastric pits. Cardiac region swollen, broadly T-shaped. Intestinal region transversely elongate, inflated, narrow, subparallel along posterior margin, medially divided by small smooth depression. Hepatic region inflated. Branchial regions well defined by swollen lobes, separated by broad, shallow, smooth grooves; epibranchial lobe subdivided into two: supra-epibranchial lobe transversely elongate, from horizontal to oblique, directed to fourth anterolateral tooth; sub-epibranchial lobe from rounded to triangular; both delimited by shallow smooth groove; mesobranchial lobe inflated. Male thoracic sternum flattened, covered by coarse granules; sternopleonal cavity narrow, deep; sternite 3 with a shallow longitudinal median groove connecting with sternopleonal cavity, reaching end of sternite 4; sternites 1 and 2 fused, subtriangular; sternite 3 subtriangular; sternite 4 subtrapezoidal, with prominent lateral edges, with marked grooves paralleling edges; sternites 5, 6 and 7 subtrapezoidal, elongate; sternite 7 shorter than sternite 6; suture 1/2 absent; suture 2/3 complete; suture 3/4 distinct, defined by groove, suture visible only laterally; sutures 4/5, 5/6 medially interrupted; episternites not laterally extended, episternite 7 strongly produced, spur shaped, reaching coxa of P5. Male pleon narrow, with free somites, axially vaulted; somites 1, 2 not folded ventrally, visible dorsally; somites 1 to 5 subrectangular, transversely narrow, somite 6 almost as long as broad; somite 3 largest, reaching coxa of P5; somites 4, 5, 6, with slightly concave upper and lateral margins covered by uniformly distributed granules; telson subtriangular, rounded tip. Ischium of third maxilliped subrectangular with median sulcus, inner margin convex, outer margin concave, covered by scarce granules; exognath slender; merus subquadrate. Ambulatory legs keeled, spiny.

Remarks: At the time, the dorso-ventral similarities highlighted by Ossó et al. (2014, pp. 36-38) were considered sufficient to place the Late Eocene *Pyreneplax* within the extant family Vultocinidae (Fig. 1); the additional sternal and pleonal features observed in the new specimen (Fig. 2) confirm this course of action (Domínguez & Ossó, 2019, pp. 70-72). Indeed, in the new specimen, a male, the sternopleonal cavity is deep and relatively narrow, almost reaching the end of sternite 4, as in *Vultocinus* (Ng & Manuel-Santos, 2007, p. 43, figs. 12A, 9A). The position of the press-button in *Vultocinus,* considered important by Ng & Manuel-Santos (2007, p. 42), cannot be observed in the new specimen due to preservation; however, in view of the position of the pleon,

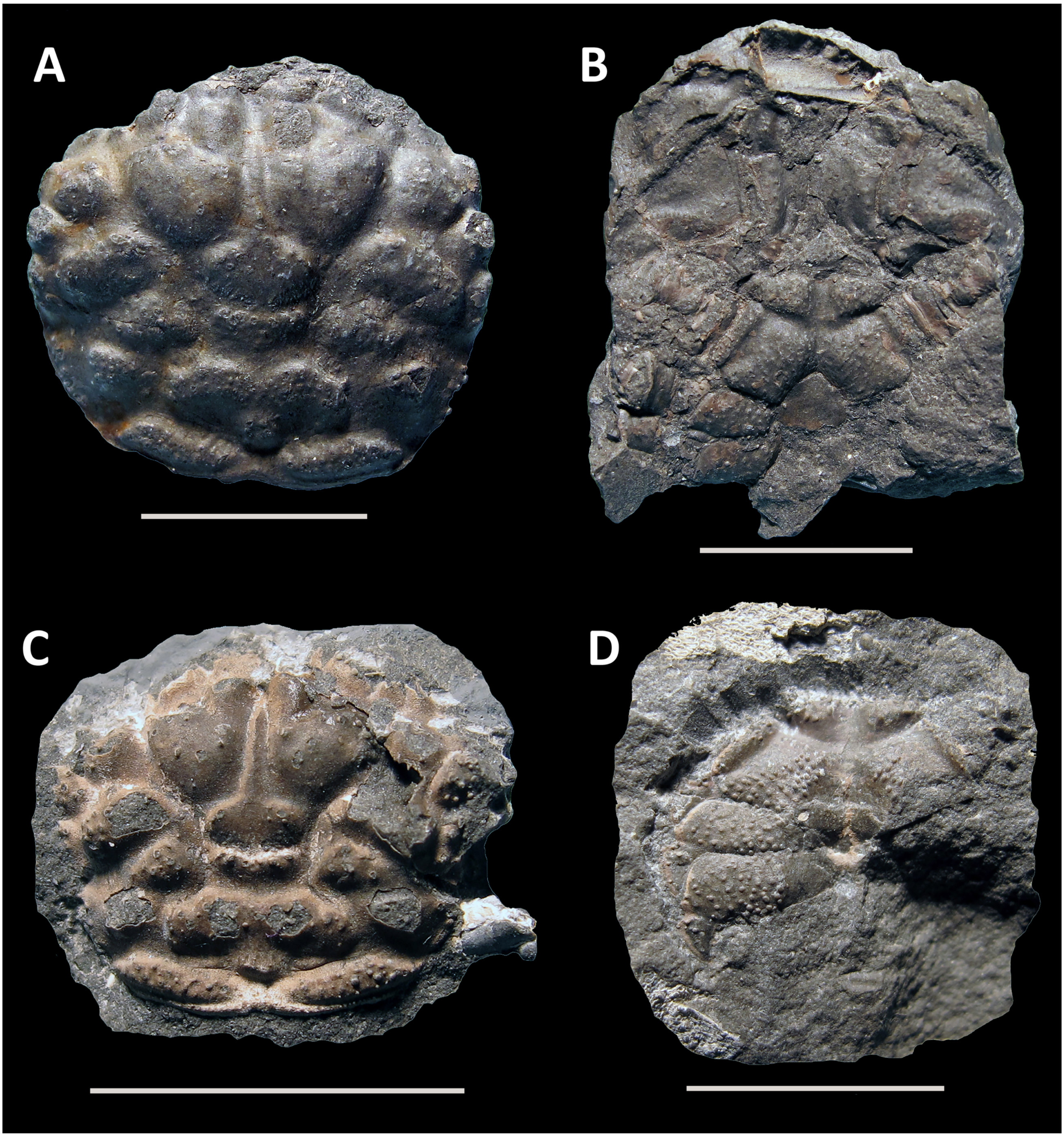
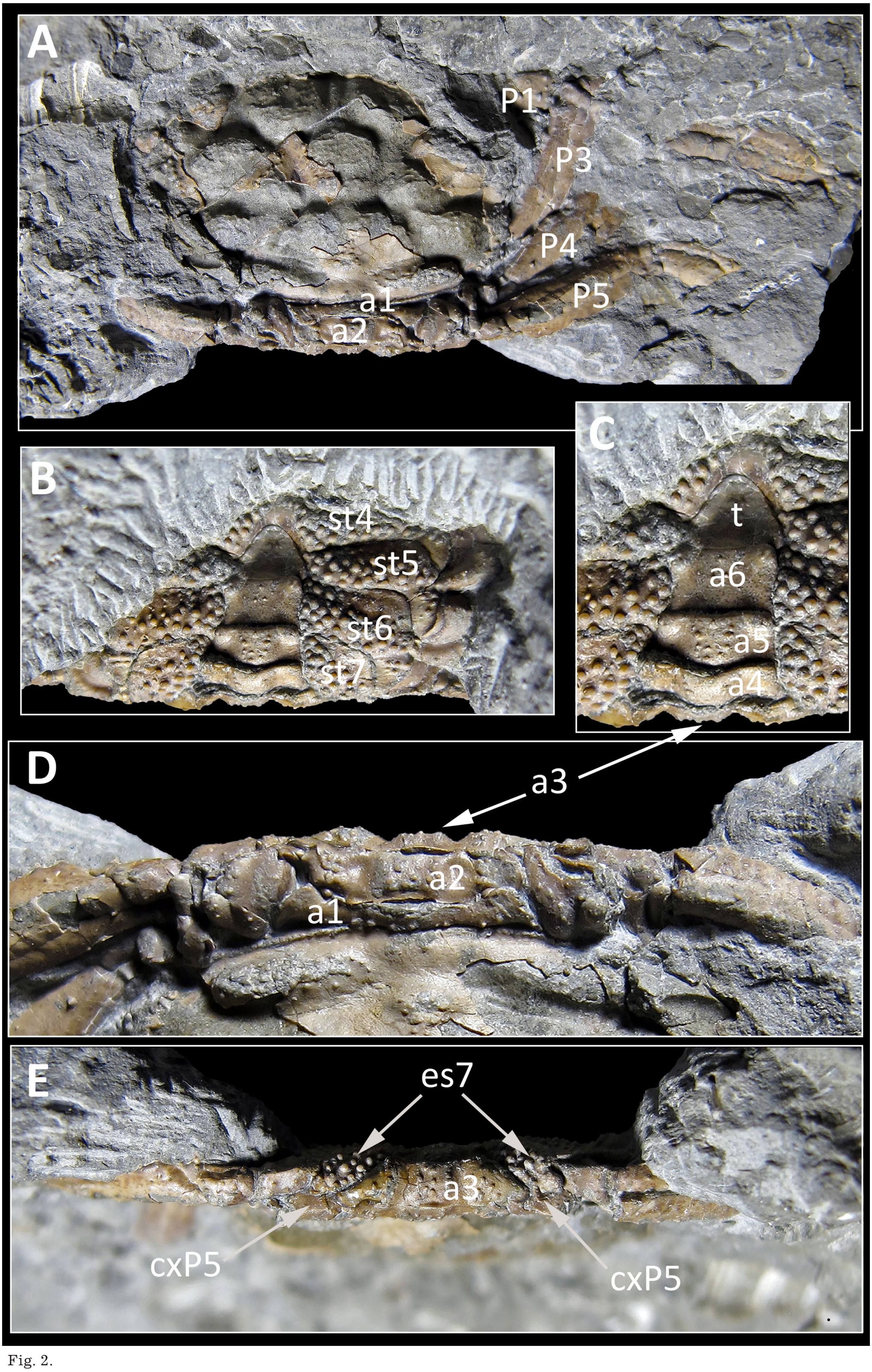


Fig. 1. *Pyreneplax basaensis* Ossó, Domínguez & Artal, 2014 from the Priabonian (Upper Eocene) of the central Pyrenees of Huesca (Aragón, Spain). A: holotype MPZ 2013/80, dorsal view; B: ventral view of holotype. C: paratype MPZ 2013/82, dorsal view. D: paratype MPZ 2013/83, ventral view. Scale bars equal 10 mm.

slightly shifted down, it is believed that it is on the posterior part of sternite 5, close to sternite 6, as in *Vultocinus* (Figs. 2B, C).

It should be noted that the male pleonal somites 1 and 2 of the new specimen do not appear to be folded ventrally and are therefore located in dorsal position, as in *Vultocinus anfractus* (Figs. 2A, D; compare Ng & Manuel-Santos, 2007, figs. 1B-C, 2). Likewise, it presents a pleonal pattern similar to that of *Vultocinus anfractus*, namely free pleonal somites, axially vaulted, pleonal somites 4 to 6 showing slightly concave upper and lateral margins and pleonal somite 6 almost as long as broad (Figs. 2C, D; Ng & Manuel-Santos, 2007, figs. 5B, 9A, 10A, 11A; Ng & Richer de Forges, 2009, fig. 1B).


A
P1
P3
P4
P5
a1
a2
B
st4
st5
st6
st7
C
t
a6
a5
a4
D
a3
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a1
E
es7
a3
cxP5
cxP5

Fig. 2.

In addition, the posterior edge of episternite 7 in *Pyreneplax basaensis* is, similar to *Vultocinus anfractus*, "strongly produced posteriorly to form a spur which reaches coxa of P5" (Ng & Manuel-Santos, 2007, p. 44). This character, considered "unusual" by Ng & Manuel-Santos (2007), which together the lateral expansion of pleonal somite 3 covers the penis completely, differentiates the Vultocinidae from other goneplacoid families (Ng & Manuel-Santos, 2007, pp. 44, 49, figs. 13A-B; Castro et al., 2010). It is also seen in *Pyreneplax* (Fig. 2E).

Discussion: Penis protection is present, in a range of expressions, among the Heterotremata (Guinot et al., 2013, pp. 84-90). In most goneplacoid families, to which the vultocinids were initially compared, it is usually present as an extension of sternite 7. For example, Davie et al. (2015) noted this condition in the families Acidopsidae Števčić, 2005, Chasmocarcinidae Serène, 1964, Conleyidae Števčić, 2005, Euryplacidae Stimpson, 1871, Goneplacidae MacLeay, 1838, Litocheiridae Števčić, 2005, Progeryonidae Števčić, 2005 (just touching coxa P5) and Scalopidiidae Števčić, 2005. This sternal protection is not present in the Mathildellidae Karasawa & Kato, 2003, Progeryonidae Števčić, 2005 and Sotoplacidae Castro, Guinot & Ng, 2010. However, none of the families that have penis protection possess the spur-shaped prolongation that is seen in *Vultocinus anfractus* and *Pyreneplax basaensis*. This unique character, shared by both genera, in addition to the set of the above-mentioned characters, shows their clear family relationship.

In this respect, the Eocene *Martinocarcinus ickeae* Böhm, 1922 (family Martinocarcinidae Schweitzer, Feldmann & Bonadio, 2009 within the Goneplacoidea) also deserves attention. Indeed, Schweitzer et al. (2009, p. 4) already pointed out the striking similarities in sternal and pleonal features of *Martinocarcinus* and *Vultocinus* (Schweitzer et al., 2009, pl. 1, fig. 4; pl. 2, figs. 1-5), but in view of the substantial differences in dorsal carapace and chelae, they did not conclude that there was a close relationship between them. Ossó et al. (2014, p. 38) also noted the sternal and pleonal similarities between *Martinocarcinus* and *Pyreneplax* but argued against a family relationship, based on differences of dorsal carapace morphology. However, in view of the new pieces of evidence provided by the new specimen of *Pyreneplax*, regarding penis protection, a re-examination of the holotype of *Martinocarcinus ickeae* would appear to be interesting, in particular to see whether or not it has the same pattern of penis protection as in *Vultocinus anfractus* and *P. basaensis*; this cannot be seen in the illustrations of Schweitzer et al. (2009). This character may well connect these three taxa phylogenetically.

Another Eocene taxon, *Agostella terrersensis* Ossó-Morales, 2011 (Goneplacoidea, *incertae sedis*), reveals an extension of sternite 7, as a plate that reaches the coxa of P5, with the lateral margin of pleonal somite 3 completely covering the penis (Ossó, 2011, fig. 4.3). This pattern of penis protection is similar to that seen in some goneplacoid families (Ng & Manuel-Santos, 2007, fig. 10), which supports its original placement within this superfamily and consequently rejects inclusion in the Tumidocarcinidae Schweitzer, 2005 (see Schweitzer et al., 2018, pp. 10-12, fig. 8/1a, b).

The nomenclature of *Pyreneplax saundersi* (Blow & Manning, 1997) (formerly *Eohalimede saundersi*) must be retained as it was originally spelled by Blow & Manning (1997), instead of the correct *sandersi* (see Blow & Manning, 1998). This change of spelling is not allowed under the current Code (ICZN, 1999), in accordance with articles 32.5.1 and 32.5.1.1 (Ng, pers. comm., November/2019).

Conclusions

Molecular studies carried out recently, using several mitochondrial and nuclear genes, have demonstrated that *Vultocinus* sits in its own deep lineage within the Heterotremata and is not related to any of the known goneplacoids, including those without living relatives (Ng & Tsang, pers. comm., October/2019). These results are consistent with what had already been stated in the original paper by Ng & Manuel-Santos (2007, p. 40) that, "*Vultocinus*, new genus, possesses a suite of unusual characters that make its precise affinities difficult to ascertain".

The fossil evidence suggests that we are dealing with a case of an extinct family with an ex-

Fig. 2. *Pyreneplax basaensis* Ossó, Domínguez & Artal, 2014, MPZ 2019/265, from the Priabonian of the central Pyrenees of Huesca (Aragón, Spain). A: dorsal view; B: ventral view; C: closeup view of pleon; D: closeup view of posterior margin of carapace; E: closeup view of the spur-shaped prolongation of sternite 7 (episternite). Abbreviations: a - pleonal somites; cxP5 - coxa of fifth pereiopod; es - episternite; P - pereiopods; st - thoracic sternites; t - telson. Scale bar equals 10 mm.

tant representative rather than an extant family with fossil representatives. The dorsal morphology of *Pyreneplax* is relatively common in numerous Eocene genera, but only preserved sternal and pleonal features can establish the relationship among these (Ossó et al., 2014, p. 41; Jagt et al., 2015, p. 883). The persistence of this dorsal carapace pattern is interpreted either as evolutionary success or an example of convergence. In the case of the Vultocinidae and in view of the preserved ventral features now observed in *Pyreneplax basaensis*, this indicates that the unusual penis protection structures are a successful adaptation and hence persisted over time. Future works and new discoveries will be expected to shed light on the suprafamily relationships of this family and their possible allies.

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An update of phylogenetic reconstructions, classification and morphological characters of extant Portunoidea Rafinesque, 1815 (Decapoda, Brachyura, Heterotremata), with a discussion of their relevance to fossil material

Posodobitev filogenetske rekonstrukcije, klasifikacije in morfoloških znakov recentnih rakovic Portunoidea Rafinesque, 1815 (Decapoda, Brachyura, Heterotremata) z razpravo o njihovi pomembnosti za fosilni material

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Abstract

The classification of extant Portunoidea has recently been significantly rearranged on the basis of morphological revision and molecular phylogenetic reconstructions. There is an urgent need to reach compatibility of fossil portunoid taxa with this new classification. Furthermore, several genera with a variety of both Recent and fossil representatives, e.g., the genus *Portunus* (*sensu lato*), have been split into other genera, but referring fossil species to these is still problematic. In order to facilitate the development of an integrated system that includes both extant and extinct portunoid taxa, a review of recent results regarding the phylogeny of portunoid crabs, an update of their extant taxa classification and a reappraisal of important morphological characters that can be used for assessment of both fossil and contemporary species are presented. A new subfamily, Parathranitiinae, is established within the Carcinidae and within the Portunidae, another new subfamily, Achelouinae, is introduced. Integration of palaeontological data and the evolutionary classification of extant Portunoidea is a challenging task that requires further development of comparative morphological, ecological and molecular genetic studies of modern species.

Izvleček

Razvrstitev recentnih portunoidnih rakovic je bila v zadnjem času bistveno preurejena na podlagi revizije morfologije in molekularnih filogenetskih rekonstrukcij. Potrebno je zagotoviti združljivost fosilnih portunoidnih taksonov z novo klasifikacijo. Več rodov z živečimi in fosilnimi predstavniki, na primer rod *Portunus* (*sensu lato*), je bilo razdeljenih na druge rodove, zato je uvrščanje fosilnih vrst vanje problematično. Da bi zagotovili razvoj integriranega sistema, ki vključuje obstoječe in izumrle portunoidne taksone, je potreben pregled novih spoznanj o filogeniji portunoidnih rakov, posodobitev njihove obstoječe klasifikacije in ponovna ocena pomembnih morfoloških znakov, ki jih je mogoče uporabiti za določanje fosilnih in recentnih vrst. V okviru družine Carcinidae je ustanovljena nova poddružina Parathranitiinae, znotraj Portunidae pa nova poddružina, Achelouinae. Vključevanje paleontološkega materiala in evolucijske klasifikacije recentnih portunoidnih rakovic je zahtevna naloga, ki zahteva nadaljnji razvoj primerjalno morfoloških, ekoloških in molekularno genetskih raziskav obstoječih vrst.

Introduction

Portunoid crabs (superfamily Portunoidea) comprise over 420 extant and more than 200 extinct species (De Grave et al., 2009), making it one of the most diverse and species-rich groups of Brachyura. Their characteristic features include a specific construction of pereopods 5, preadapted for burrowing and constituting part of the swimming apparatus (Garstang, 1897a, b; Schäfer, 1954; Hartnoll, 1971; Steudel, 1998; Spiridonov et al., 2014). Another important feature of portunoids is the peculiar morphology of the chelae, which is essential in maintaining the habit of active generalist predators and scavengers (Schäfer, 1954; Spiridonov et al., 2014). Portunoid crabs have a worldwide distribution (with the exception of subarctic waters of the North Pacific, Arctic and Antarctic), live in a variety of biotopes, although predominately on soft bottoms, from the intertidal and upper subtidal (Fig. 1) to deep waters of the continental slope and underwater rises (e.g., Geryonidae; see Manning & Holthuis, 1989; but also some representatives of generally shallow-water groups; see Spiridonov & Türkay, 2001). Particular groups have symbiotic relationships with a variety of animal and plant taxa (Evans, 2018). Being abundant predators, portunoid crabs play a significant role of ecosystems, hold a leading position among human-mediated invaders (Brockerhoff & McLay, 2011) and include several highly important commercial species (Figs. 1G, H). Classification of Recent portunoids had been stable for about half a century, owing to the dominating taxonomic concept of Stephenson (1972). This state was largely reflected in the 'Systema Brachyurorum' by Ng et al. (2008), although it accommodated several revisions of particular species and genera and descriptions of new taxa introduced during the 1990s and early 2000s. Right after this ground-laying publication the taxonomy and classification of the Portunoidea entered a major revision. The impetus for this was given by palaeontologists (Karasawa et al., 2008), who suggested the first phylogenetic reconstruction of the Portunoidea based on morphological cladistics and attempted to construct a new classification for both extant and extinct portunoid taxa. Subsequent molecular phylogenetic reconstructions (Schubart & Reuschel, 2009; Spiridonov et al., 2014; Evans, 2018; Mantelatto et al., 2018) have significantly changed the very concept of what are portunoids, challenged both the traditional (Stephenson, 1972; Ng et al., 2008) and Karasawa et al. (2008) views on major groups and evolutionary lineages, stimulated new comparative morphological analysis of extant groups and revised the classification of the Portunoidea (see a scheme that reflects recent changes in Evans, 2018, fig. 5).

In the present paper, I shall review recent developments in phylogenetic reconstruction, taxonomy, variability and classification of morphological structures and characters in order to facilitate the integration of palaeontological and neontological data in a coherent system of the Portunoidea. It is not really my intention here to classify extinct taxa but rather to comment on some of them to stimulate further taxonomic revision by palaeontologists or jointly by palaeontologists and neontologists. Therefore, palaeontological data are here presented only as examples without any ambitions to provide their comprehensive coverage.

The purpose of the present contribution is to review recent studies on extant Portunoidea and facilitate their integration with palaeontological data, in order to: 1) synthesise relevant molecular phylogenetic reconstructions and fossil records of extant genera; 2) update the classification of modern portunoid crabs; 3) make a comparative description of the taxonomic value of morphological characters that can be applied to both extant and fossil material.

Fig. 1. Examples of portunoid crabs showing characteristic habit and commercial importance. A: *Carcinus maenas* (Linnaeus, 1761), medium size (to about 80 mm carapace width, CW), common inhabitant of intertidal-low subtidal habitats, northeast Atlantic; a global invader; rocky intertidal, North Sea, German Bight, Wilhelmshaven. B. *Carcinus aestuarii* Nardo, 1869, medium-sized species, a common inhabitant of Mediterranean Sea, low subtidal, in semi-burrowed condition, Black Sea. C. *Liocarcinus vernalis* (Risso, 1816), medium-sized species, a common inhabitant of low subtidal sandy habitats in the Mediterranean Sea, swimming over sand bottom, Black Sea. D. same specimen as C, burrowed in sand. E. *Thalamita crenata* Rüppell, 1830, medium-sized species, a common inhabitant of intertidal habitats in Indo-Pacific; after burrowing in sediments, mangrove, Dam Bay, Tre Island, Vietnam, South China Sea. F. *Xiphonectes* sp., small (to about 50 mm CW) species, in coral rubble; Mot Island, Vietnam, South China Sea. G. *Portunus trituberculatus* Miers, 1879, a large (about 300 mm CW) commercially important species in East Asia; fish market in Busan, Korea. H. *Scylla paramomosain* Estampador, 1949, a large, commercially important and cultured species in southeast Asia, fish market in NhaTrang, Vietnam. Photograph credits: V. Spiridonov (A, E, G, H); S. Anosov (B, C, D) and T. Antokhina (F).

Fig. 1.

Material and methods

The present study is based on my 20+ years' work with collections of portunoid crabs at the Natural History Museum London, UK (NHMUK), the Naturhistorisches Museum Wien, Vienna, Austria (NHMW), the Senckenberg Museum, Frankfurt am Main, Germany (SMF), the Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia (ZIN-RAS), the Zoological Museum of Moscow University, Moscow, Russia (ZMMU), the Zoologisches Museum, Museum für Naturkunde, Berlin, Germany (ZMB), where specimens illustrated are deposited, as well as other European, American and Australian collections.

Morphological terms generally follow usage in Stephenson & Hudson (1957), Apel & Spiridonov (1998), Ng et al. (2008) and Evans (2018). In the carapace description the epithets "quasi-hexagonal", "quasi-trapezoidal" etc. are preferred over "subhexagonal", "subtrapezoidal" etc.

The simplified scheme of the phylogenetic relationships of extant portunoid genera (Fig. 2) is based on results obtained by recent molecular phylogenetic reconstructions (Schubart & Reuschel, 2009; Spiridonov et al., 2014; Evans, 2018; Mantelatto et al., 2018). The branching of the tree follows particular patterns agreed between different reconstructions; where there is no agreement between particular studies, the relationships are shown as an unresolved polytomy.

The updated classification of Recent Portunoidea is based on the principles of evolutionary systematics (Simpson, 1961), which requires compatibility with phylogenetic reconstructions but implies a thorough morphological analysis for definition of the boundaries of taxa.

In linking particular extant portunoid genera to their palaeontological records I generally follow Müller (1984) and Karasawa et al. (2008) with additions of recent fossil records, for instance, of *Geryon* Krøyer, 1838 (Feldmann et al., 2010), *Bathynectes* Stimpson, 1871 (Ossó & Stalennuy, 2011) and *Liocarcinus* Stimpson, 1871 (De Angeli et al., 2019). Since most pre-Pleistocene records of *Callinectes* Stimpson, 1860 are based on incompete and poorly preserved material, the known range of *Callinectes* was corrected according to well-preserved specimens reported by Collins et al. (2014). As fossil crabs identified as *Portunus* (*sensu lato*) may indeed refer to several genera, I have specifically checked the original figure of one of the oldest representatives, namely *Portunus kochi* Bittner, 1893 (see Bittner, 1893, pl. 1, fig. 1). For further explanations, reference is made to the caption of Figure 2.

A review of the phylogeny of the Portunoidea based on published molecular genetic reconstructions and palaeontological history of extant taxa

The genera *Geryon* (living in the northeast Atlantic), *Chaceon* Manning & Holthuis, 1989 (inhabiting continental slopes and underwater rises worldwide), *Raymanninus* Ng, 2000 (occurring in the deep water of the Caribbean) form a distinct clade in all molecular phylogenetic reconstructions, which shows sister relationships to the deep-water Indo-Pacific *Benthochascon* Alcock & Anderson, 1899 or the *Benthochascon* + *Ovalipes* clade. Species of *Ovalipes* occur mostly in the Southern Hemisphere but are also known from the northeast Pacific and northwest Atlantic. This clade is interpreted as the basal portunoid lineage that possesses a number of plesiomorphic character states and shows a close affinity to one of the most ancient potential portunoid taxa, the genus *Eogeryon* Ossó, 2016 from the upper Cenomanian (Ossó, 2016). The clade comprises the family Geryonidae (*sensu* Evans, 2018) and shows sister relationships to other studied portunoids (Fig. 2).

The latter in turn are well separated into two major clades which are resolved in all reconstructions (Schubart & Reuschel, 2009; Spiridonov et al., 2014; Evans, 2018), although with varying internal topologies. Following the most comprehensive study by Evans (2018), one of this major lineages includes the Indo-Pacific taxa *Parathranites* Miers, 1886 and *Coelocarcinus* Edmondson, 1930 as basal groups. All published phylogenetic trees define the related clades *Carcinus* Leach, 1814 + *Portumnus* Leach, 1814 and *Pirimela* Leach, 1816 or *Pirimela* + *Sirpus* Gordon, 1953. All these taxa are originally confined to the North Atlantic. Their possible sister clade includes morphologically diverse genera such as *Thia* Leach, 1816, *Bathynectes*, *Macropipus* Prestandrea, 1833, *Necora* Holthuis, 1987 and *Liocarcinus*, also living mostly in the Atlantic. The topology of relationships between these groups differ in the reviewed studies, so in Figure 2 no resolved branching is shown. *Polybius* Leach, 1820 is nested within *Liocarcinus* in all reconstructions (see also Plagge et al., 2016) and is not shown in the present scheme (Fig. 2). All the genera mentioned were combined in the newly defined family Carcinidae (*sensu* Evans, 2018). Most fossil records of thus defined carcinids are no older than Miocene, and only records of *Liocarcinus* spp. date back to the Eocene (De Angeli et al., 2019; Á. Ossó, pers. comm., January 2020).

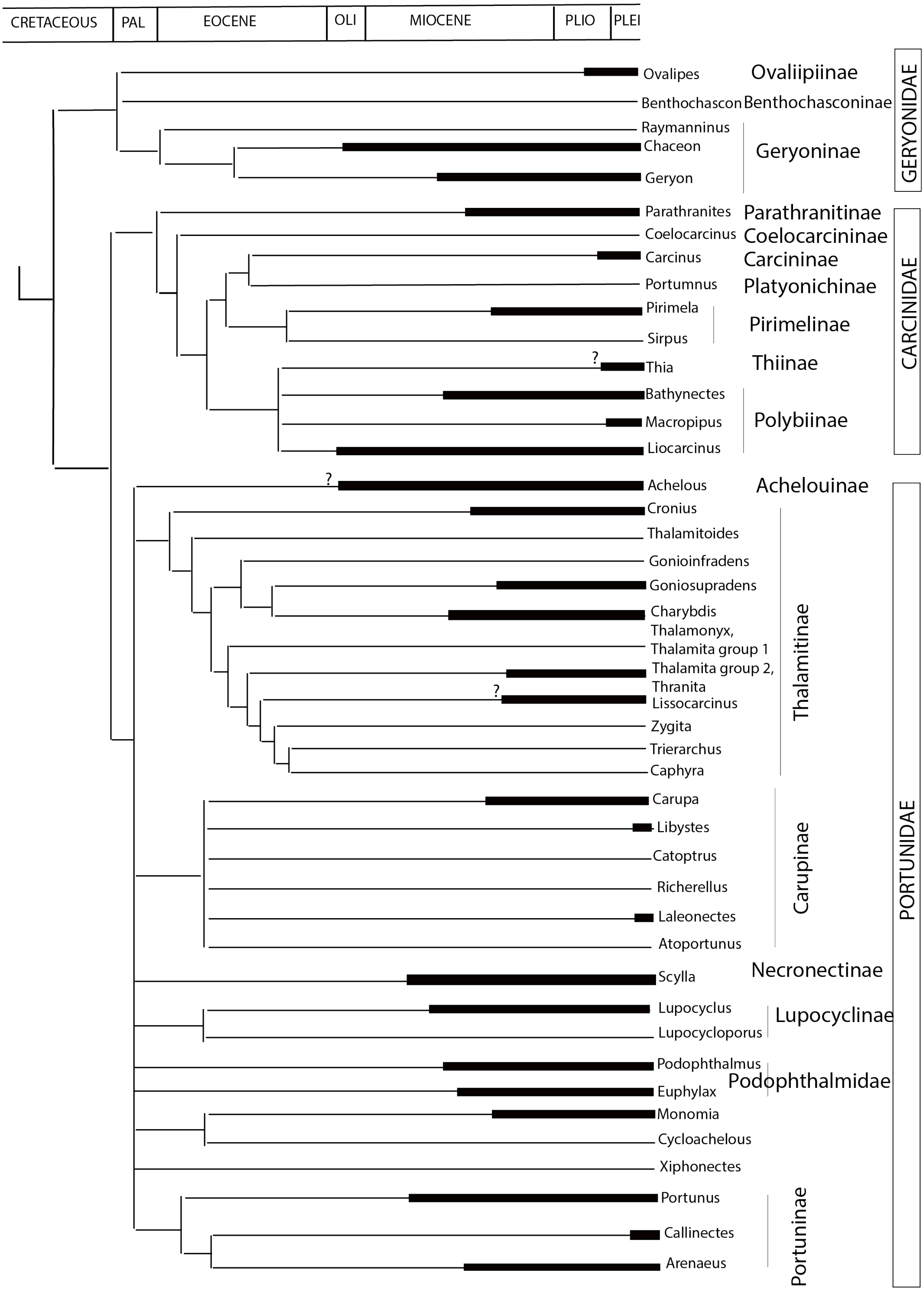

Fig. 2. Schematic phylogenetic tree of extant portunoid genera based on molecular phylogenetic reconstructions by Schubart & Reuschel (2010), Spiridonov et al. (2014), Evans (2018) and Mantelatto et al. (2018). Black bands indicate the temporal extension of particular genera from the first palaeontological record onwards. The tree does not have an unbiased temporal scale; the positions of nodes only indicate that the divergence between families occurred not later than the Cretaceous, the divergence between major genera not later than the Eocene, Oligocene or Miocene. Abbreviations of geological epochs: PAL – Paleocene; PLEI – Pleistocene; PLIO – Pliocene; OLI – Oligocene.

Another large group which shows sister relationships to the Carcinidae are the Portunidae (*sensu* Schubart & Reuschel, 2009; Spiridonov et al., 2014). The topology of clades within the Portunidae is not stable through reviewed reconstructions, although the clade of taxa referred to the Thalamitinae (sensu Apel & Spiridonov, 1998), plus symbiotic taxa formerly referred to the Caphyrinae Paulson, 1875 is always revealed (Fig. 2). The Atlantic-eastern Pacific genus *Cronius* Stimpson, 1860 was shown to be basal to this clade, the other species of which have a mostly Indo-Pacific distribution (Evans, 2018). All molecular phylogenetic studies indicate that the American and eastern Atlantic species earlier considered to belong to the subgenus *Achelous* De Haan, 1833 of the genus *Portunus* Weber, 1795 (Ng et al., 2008) constitute a distinct clade, which in some reconstructions show sister relationships to the Thalamitinae (Spiridonov et al., 2014; Evans, 2018; Mantelatto et al., 2018).

Species of *Portunus* (*sensu stricto*) (occurring in the Indo-Pacific and Atlantic) are revealed as having close phylogenetic relationships with the Atlantic genera *Arenaeus* Dana, 1851 and *Callinectes*. Several Indo-Pacific genera, most of them earlier included in the Carupinae (*sensu* Apel & Spiridonov, 1998), such as *Atoportunus* Ng & Takeda, 2003, *Carupa* Dana, 1851, *Catoptrus* A. Milne-Edwards, 1870, *Laleonectes* Manning & Chace, 1990, *Libystes* A. Milne-Edwards, 1867 and *Richerellus* Crosnier, 2003) are also phylogenetically related, although their tree cannot be perfectly resolved to date (Fig. 2). Other genera do not show a stable pattern of relationships in particular reconstructions (except for *Monomia* Gistel, 1848 and *Cycloachelous* Ward, 1942), and therefore the general phylogeny of the Portunidae may now be schematically presented as a polytomy ("bush" rather than a tree).

One of the oldest known portunids, "*Portunus*" *kochi* (Bittner, 1883) from the Upper Eocene, can be referred to *Achelous* according to the morphology of the frontorbital and anterolateral margins and carapace ornamentation (see Bittner, 1893: pl. 1, fig. 1). This suggests a significant geological age of the Achelouinae. Such genera as *Scylla* De Haan, 1833 are known to have occurred since at least the Miocene, while *Necronectes* A. Milne-Edwards, 1881, which is morphologically very similar to *Scylla*, is at least of Oligocene age (Karasawa et al., 2008; Ossó & Gagnaison, 2019). Therefore, the divergence of major portunid lineages most probably took place no later than Middle Eocene or even in pre-Eocene times (Fig. 2)

Updated classification of recent Portunoidea

Family Geryonidae Colosi, 1923

Diagnosis: Spiridonov et al. (2014).

Type genus: *Geryon* Krøyer, 1837.

Subfamily Benthochasconinae Spiridonov, Neretina & Schepetov, 2014

Diagnosis: Spiridonov et al. (2014).

Genus: *Benthochascon* Alcock & Anderson, 1899

Subfamily Geryoninae Colosi, 1923

Diagnosis: Spiridonov et al. (2014).

Genera: *Chaceon* Manning & Holthuis, 1989; *Geryon* Krøyer, 1837(type genus); *Raymanninus* Ng, 2001 and *Zariquieyon* Manning & Holthuis, 1989.

Subfamily Ovalipiinae Spiridonov, Neretina & Schepetov, 2014

Diagnosis: Spiridonov et al. (2014).

Genera: *Ovalipes* Rathbun, 1898 (type genus).

Remarks: Originally, this taxon was established at the family level, although possible sister relationships to the Geryonidae were assumed (Spiridonov et al., 2014). On the basis of his molecular phylogenetic reconstruction, Evans (2018) argued for even closer relationships of *Ovalipes* with geryonids and suggested to consider this group as a subfamily of the Geryonidae. I accept his concept here. Although *Ovalipe*s spp. are characterised by a number of apomorphies in relation to other geryonids, they share with them apparently plesiomorphic conditions of non-fused pleomeres of the male pleon and long gonopods 2, and an apparently apomorphic tendency for reduction of one of the orbital fissures (see below).

The grammatically correct form for the family/subfamily name is Ovalipiinae, not Ovalipinae as suggested by Spiridonov et al. (2014). It is corrected here.

Genera *incertae sedis*: *Echinolatus* Davie & Crosnier, 2006 and *Nectocarcinus*A. Milne-Edwards, 1861.

Remarks: These genera share with the Geryonidae such plesiomorphic conditions as non-fused pleomeres of the male pleon and long gonopods 2, a tendency for reduction of one orbital fissure, as well as an even number of frontal lobes and four anterolateral teeth, characters not commonly found in the Carcinidae. On the other hand, species assigned to these genera have some characters that are unique to portunoid crabs, such as a double inner carpal spine and additional anterolateral teeth in *Echinolatus* spp. These genera have not yet been included in molecular phylogenetic reconstuctions. I tentatively assign them to the Geryonidae, although they may deserve separate status.

Family Carcinidae MacLeay, 1838

Diagnosis: Evans (2018).

Type genus: *Carcinus* Leach, 1814.

Subfamily Carcininae MacLeay, 1838

Diagnosis: Spiridonov et al. (2014).

Genera: *Carcinus* Leach, 1814 (type genus).

Subfamily Coelocarcininae Števčić, 1991

Diagnosis: Evans (2018).

Genera: *Coelocarcinus* Edmondson, 1930 (type genus).

Subfamily Parathranitiinae Spiridonov subfam. nov.

Zoobank: urn:lsid:zoobank.org:act:74EF-9937-1342-4BF6-8847-5F220ED11882

Diagnosis (new): Carapace distinctly quasi-hexagonal, regions well defined, with well-defined ridged and granular ornamentation. Frontal margin subdivided into 4 teeth. Infra-orbital margin consisting of several lobes. Posteriormost of five anterolateral teeth distinctly longer than others. Posterolateral corners of carapace angular or spiniform. Cheliped with spines on anterior and posterior faces of merus, carpus with outer spines, propodus with upper spines, dactyli of last pereopods lanceolate.

Genera: *Parathranites* Miers, 1886 (type genus).

Remarks: *Parathranites* spp. (see Crosnier, 2002) differ from all Carcinidae in having well-defined regions of the carapace, spiniform posterolateral corners of the carapace, and from most of the carcinids by upper spines on the chela palm (propodus) and four frontal teeth/ lobes. Molecular phylogenetic reconstruction (e.g., Evans, 2018; see Fig. 2 here) indicates the basal position of the genus in relation to other groups of the family. To emphasise this peculiar position, I find it reasonable to define a new subfamily, Parathranitiinae, within the Carcinidae.

Subfamily Platyonichinae Dana, 1851 (= Portumninae Ortmann, 1899; see Davie et., 2015 for a discussion of the synonymy).

Diagnosis: Spiridonov et al. (2014; as Portumninae).

Genera: *Portumnus* Leach, 1815 (type genus) and *Xaiva* MacLeay, 1838.

Subfamily Pirimelinae Alcock, 1899

Diagnosis: Spiridonov et al. (2014; as family Pirimelidae).

Genera: *Pirimela* Leach, 1816 (type genus) and *Sirpus* Gordon, 1953.

Subfamily Polybiinae Ortmann, 1893

Diagnosis: Spiridonov et al. (2014: 422, as family Polybiidae).

Genera: *Bathynectes* Stimpson, 1871; *Coenophthalmus* A. Milne-Edwards, 1873; *Liocarcinus* Stimpson, 1871; *Macropipus* Prestandrea, 1833; *Necora* Holthuis, 1987 and *Polybius* Leach, 1820 (type genus).

Subfamily Nautilocorystinae Ortmann, 1893

Diagnosis: Spiridonov et al. (2014).

Genera: *Nautilocorystes* H. Milne Edwards, 1837 (type genus).

Subfamily Thiinae Dana, 1852

Diagnosis: Spiridonov et al. (2014; as Thiidae)

Genera: *Thia* Leach, 1816 (type genus).

Remarks: *Nautilocorystes* was referred to the Thiidae by Ng et al. (2008) on the basis of important morphological similarities. In spite of an appearance that is highly unusual for portunoid crabs, *Nautilocorystes* has several characters, such as a cheliped morphology typical of portunids (Spiridonov et al., 2014). *Thia* has repeatedly been shown to nest within the polybiine clade (Schubart & Reuschel, 2009; Spiridonov et al., 2014; Evans, 2018), although its significant morphological peculiarity calls for a separate status. Therefore, a subfamily rank for the Thiinae was accepted by Evans (2018) and it is here too. The relationships of *Nautilocorystes* to the Carcinidae in the current concept remain unclear, as no molecular phylogenetic study of this taxon has been conducted to date. Here, I tentatively place Nautilocorystinae as a separate subfamily of the carcinids.

Family Portunidae Rafinesque, 1815

Diagnosis: Spiridonov et al. (2014).
Type species: *Portunus* Weber, 1795.

Subfamily Achelouinae subfam. nov.

Zoobank: urn:lsid:zoobank.org:act:B094745A-E-EB2-408A-B91F-E30DE868449A

Diagnosis (new): Carapace more than 1.5 times wider than long, quasi-hexagonal; regions well expressed; with distinct granular ridges and groups of granules both in anterior and posterior parts. Nine sharp anterolateral teeth: teeth 1 to 8 subequal, last tooth distinctly longer than others. Front narrower than posterior border, consisting of 4 or 6 lobes; outer lateral lobes may be fused with inner supraorbital lobes. Chelipeds with several teeth on anterior margin and a single posterior tooth; carpus with a single outer spine; inner spine well expressed and may be very long, reaching to chela fingers; propodus strongly costate, with a single spine; heterochely moderate; larger chela with flattened molariform tooth. Dactyli of pereopods 2–4 strong, knife-shaped. Merus of pereopod 5 much broader than meri of pereopods 2–4, posterior spine may be present although obsolete; propodus without spinules on posterior margin, dactylus paddle-like. Male pleon triangular, unclear sutures may be present at fused pleomere 3–5. Gonopod 1 of generalised shape, curved, thinning apically, with microspopic spinules. Female genital opening large, occupying about one third of sternite.

Remarks: Numerous Atlantic and eastern Pacific species referred to *Achelous*, *Lupella* Rathbun, 1897 or *Portunus* (except for *Portunus sayi* (Gibbes, 1850) form a distinct monophyletic clade which does not show clear relationships to other groups (Spiridonov et al., 2014; Mantelatto et al., 2018) and are characterised by distinct morphological characters. It justifies placing them in a separate subfamily, Achelouinae.

Genera: *Achelous* De Haan, 1833 (type genus) and *Lupella* Rathbun, 1897.

Subfamily Carupinae Paulson, 1875

Diagnosis (extended from Apel & Spiridonov, 1998): Carapace much wider than long, up to about twice, transversely oval, elliptical or indistinctly quasi-hexagonal, relatively convex; regions poorly expressed; usually with only epibranchial ridge or smooth; sometimes with diffuse granules. Supraorbital fissures may be reduced, infraorbital margin variously modified. Front much narrower than posterior border, four-, or two-lobed, or nearly entire; anterolateral border convex, toothed or entire. Posterolateral reentrant poorly developed, or not at all. Secondary sulci of sternum may be absent. Basal antennal segment narrow, long, lying obliquely, not lobulate, antennal peduncle entering orbital hiatus. Chelipeds of various construction, spines on cheliped segments usually reduced in number or absent. Some representatives are secondarily homoiochelic and homoiodontic, with long and thin chelae. Pereopods 2–4 usually long and thin, non-costate. Merus of pereopod 5 long and thin, not broader or not much broader than meri of pereopods 2–4, without posterior spinule; dactylus styliform, lanceolate, or knife-shaped. Male pleon triangular. Gonopod 1 usually with relatively robust subterminal spines. Female genital openings large, without cuticular emargination and caps.

Genera: *Atoportunus* Ng & Takeda, 2003; *Carupa* Dana, 1851 (type genus); *Catoptrus* A. Milne-Edwards, 1870; *Kume* Naruse & Ng, 2012; *Laleonectes* Manning & Chace, 1990; *Libystes* A. Milne-Edwards, 1867; *Pele* Ng, 2011 and *Richerellus* Crosnier, 2003.

Remarks: The name of the author of the subfamily is often spelled "Paul'son" following the English translation of the original monograph in the Russian language (Paulson, 1875). I prefer, however, "Paulson" because Otto Paulson used this spelling in his German-language publications (i.e. Paulson, 1862).

Subfamily Lupocyclinae Paulson, 1875

Diagnosis (new): Cephalothorax quasi-hexagonal or quasi-circular in outline, dorsally convex. Carapace with granular ridges and/or patches. Front narrower than posterior border, consisting of 4 lobes or teeth, markedly produced beyond inner supraorbital lobes. Orbit circular. Anterolateral margin with 5–9 teeth. Posterolateral margin with rounded corners. Expansion of basal antennal segment not produced into orbit being directed nearly anteriorly; flagellum standing in orbital hiatus. Chelipeds long, homoiochelic or slightly heterochelic; merus with 4–7 spines on anterior margin and 2 spines on posterior margin; carpus with a single spine on outer face; manus with two subdistal spines on dorsal face. Chelae very long and thin, distinctly thinner than cheliped meri. Heterodonty not expressed or poorly expressed. Distal parts of chelae fingers curved in sagittal plane. Pereopods 2–4 long, thin, dactyli narrow, ensiform, Merus of P 5 broader and shorter than meri of pereopods 2–4, with a small posterodistal spine; dactlylus lanceolate or paddle-like. Male pleon triangular. Gonopod 1 of generalised shape, relatively straight or curved, with sharpened distal part, without large subterminal spines. Female genital openings large, occupying half or more of length of mesial part of sternite, without cuticular emargination and caps.

Genera: *Lupocycloporus* Alcock, 1899 and *Lupocyclus* Adams & White, 1848 (type genus).

Subfamily Necronectinae Glaessner, 1928

Diagnosis (modified after Karasawa et al., 2008): Carapace of intermediate outline between quasi-hexagonal and oval, dorsally convex, smooth with recognisable gastric and epibranchial finely granular ridges. Front narrower than posterior border, usually consisting of 4 lobes or teeth, not produced beyond inner supraorbital lobes. Orbit semi-oval. Anterolateral margin with 9 (or 8 in some fossil taxa) teeth. Posterolateral margin with rounded corners. Basal antennal segment with latero-distal spine; flagellum standing in orbital hiatus. Cheliped merus with 3 spines on anterior margin and 2 distal spinules on posterior margin; carpus with 1-3 spinules (often reduced) on outer face; manus nearly smooth, with 1 or 2 subdistal spinules on dorsal face. Heterochely and heterodonty well expressed; chela inflated; molariform teeth present on both chelae. Distal parts of chelae fingers not curved in sagittal plane. Dactyli of pereopods 2–4 relatively broad and strong, ensiform. Merus of pereopod 5 much shorter than meri of pereopods 2–4, without a posterior spine; propodus without posterior spinules; dactylus paddle-like. Male pleon triangular. Gonopod 1 sinuous or slightly curved, without large subterminal spines. Female genital openings without cuticular emargination and caps.

Genera: *Scylla* De Haan, 1833 and *Sanquerus* Manning, 1989.

Type genus: *Necronectes* A. Milne-Edwards, 1881 (extinct).

Subfamily Podophthalminae Stimpson, 1860

Diagnosis: Apel & Spiridonov (1998: 169).

Genera: *Euphylax* Stimpson, 1860 and *Podophthalmus* Lamarck, 1801 (type genus).

Subfamily Portuninae Rafinesque, 1815

Diagnosis (new): Cephalothorax quasi-hexagonal in outline, dorsally flattened. Carapace granular, usually with granular ridges and/ or patches. Frontal margin of carapace divided into even number of lobes or teeth (usually 4), usually not distinctly produced beyond inner supraorbital lobes. Orbit elliptoidal. Anterolateral margin divided into 9 teeth, usually without indication of reduction of particular teeth. Posterolateral reentrant well developed; posterolateral margin usually with rounded corners. Expansion of basal antennal segment produced into orbit but not filling orbital hiatus completely, flagellum standing in orbital hiatus. Cheliped merus with 3–4 spines on anterior margin and 1–2 spines on posterior margin; on dorsal face along posterior margin there may be a suture and a granular line terminated at one of posterior spines. Carpus with a single spine or without spines but carina on outer face. Manus with one or two subdistal spines on dorsal face. Heterochely usually expressed. Heterodonty usually expressed by a molariform tooth developed to various degrees at base of larger chela dactylus; in some cases symmetrical chelae present. Distal parts of chelae fingers not curved in sagittal plane. Dactyli of pereopods 2–4 robust, ensiform or narrowly lanceolate. Merus of P 5 much shorter and broader than meri of pereopods 2–4, without a posterior spine, propodus without spinules on posterior margin, dactylus paddle-like. G 1 of simple shape or modified (very thin), without large subterminal spines. Female genital openings relatively compact, occupying less than half of length of mesial part of sternite, often with emarginations and caps.

Genera: *Arenaeus* Dana, 1851; *Callinectes* Stimpson, 1860 and *Portunus* Weber, 1795 (type genus).

Genera tentatively included here: *Cavoportunus* Nguyen & Ng, 2010; *Cycloachelous* Ward, 1942 and *Monomia* Gistel, 1848.

Remarks: Portuninae had been the largest subfamily of Portunidae when the lumping concept of Stephenson (1972) became dominant. With the subsequent revalidation and redefinition of the Lupocyclinae, Thalamitinae and Necronectinae, this subfamily has been considered in an increasingly restricted sense (e.g., Apel & Spiridonov, 1998; Karasawa et al., 2008; Ng et al., 2008). To date, even this restricted concept is no longer supported by molecular phylogenetic reconstructions and comparative morphology (Schubart & Reuschel, 2009; Spiridonov et al., 2014; Evans, 2018; Mantelatto et al., 2018). In particular, the genus *Portunus* (*sensu lato*) of Stephenson's (1972) classification is now considered to consist of several not closely related and morphologically different genera. The American-eastern Atlantic genus *Achelous* is here taken to represent a separate subfamily. *Xiphonectes* A. Milne-Edwards, 1873, which has been considered as a subgenus of *Portunus* (Ng et al., 2008), appears to be polyphyletic as well and is, for the time being, listed as a genus *incertae sedis* within the Portunidae. I tentatively include here in the Portuninae three additional genera previously combined in *Portunus*. This makes possible to formulate a consistent morphological diagnosis, until more detailed ongoing molecular genetics and comparative morphological studies provide sufficient data for a more appropriate classification of *Cavoportunus*, *Cycloachelous* and *Monomia*.

Subfamily Thalamitinae Paulson, 1875

Diagnosis: Evans (2018: 40).

Genera: *Caphyra* Guérin, 1832; *Charybdis* De Haan, 1833; *Cronius* Stimpson, 1860; *Goniosinfradens* Leene, 1938; *Goniosupradens* Leene, 1938; *Lissocarcinus* Adams & White, 1848; *Thalamita* Latreille, 1829 (type genus); *Thalamitoides* A. Milne-Edwards, 1869; *Thalamonyx* A. Milne-Edwards, 1873; *Thranita* Evans, 2018; *Trierarchus* Evans, 2018 and *Zygita* Evans, 2018.

Remarks: Thalamitinae was recognised as a morphologically distinct subfamily of Portunidae by Paulson (1875), but the taxon was subsequently largely ignored until revalidation and redefinition by Apel & Spiridonov (1998). Spiridonov et al. (2014) provided molecular phylogenetic support for the monophyly of the most speciose thalamitine genera, *Charybdis* and *Thalamita*. Recently, Evans (2018) has presented evidence of the basal position of *Cronius* (formerly assigned to the Portuninae) in the thalamitine phylogenetic tree and has demonstrated the phylogenentic relationships of Thalamitinae (*sensu stricto*) and *Caphyra* and *Lissocarcinus* (formerly considered to belong to the subfamily Caphyrinae Paulson, 1875, by Ng et al., 2008). The latter two genera, along with some groups formerly referred to *Thalamita* (*Trierarchus, Zygita*), form a symbiotic clade within the Thalamitinae in the new concept (Evans, 2018).

Genus *incertae sedis*: *Carupella* Lenz & Strunk, 1914

Remarks: Two syntypes of *Carupella natalensis* Lenz & Schtrunk, 1914 that I have examined (ZMB 19917) are juvenile, just settled crabs, most likely belonging to the Portuninae (although assignment to the Lupocyclinae in its present concept cannot be completely ruled out). They may in fact belong to yet another known species for which precise identification is currently difficult due to a lack of knowledge on age-related variation in portunids. Thus, the genus *Carupella* may be synonymous with another, established genus. The holotype of *Carupella banlaensis* Tien, 1969 (ZIN-RAS 1/58265) is certainly a juvenile specimen of *Portunus* sp. The type of the third species of the genus, *Carupella epibranchialis* Zarenkov, 1970, has not been traced in the ZMMU collections where it would presumably have been deposited. It is thus appropriate to consider *Carupella* as a genus *incertae sedis* within the Portunidae until new comparative research will clarify its status.

Genus *incertae sedis*: *Xiphonectes* A. Milne-Edwards, 1873

Remarks: See above under the subfamily Portuninae.

Family Brusiniidae Števčić, 1991

Genus: *Brusinia* Števčić, 1991.

Remarks: *Brusinia* spp. are very peculiar morphologically (Spiridonov et al., 2014) and are not nested within the Portunoidea in updated phylogenetic trees based on the 16S RNA gene (Evans, 2018). The family is tentatively considered as a portunoid group until more comprehensive data become available.

Morphological characters of Portunoidea applicable to fossil material

Carapace morphology

Most portunoid crabs have a quasi-hexagonal carapace shape, with the maximum width usually exceeding the maximum length (Fig. 3). This general carapace outline portunoids share with a number of other heterotremate crabs such as the superfamilies Cancroidea, Goneplacoidea and Pilumnoidea (Guinot, 1979; Ng et al., 2008; Davie et al., 2015).

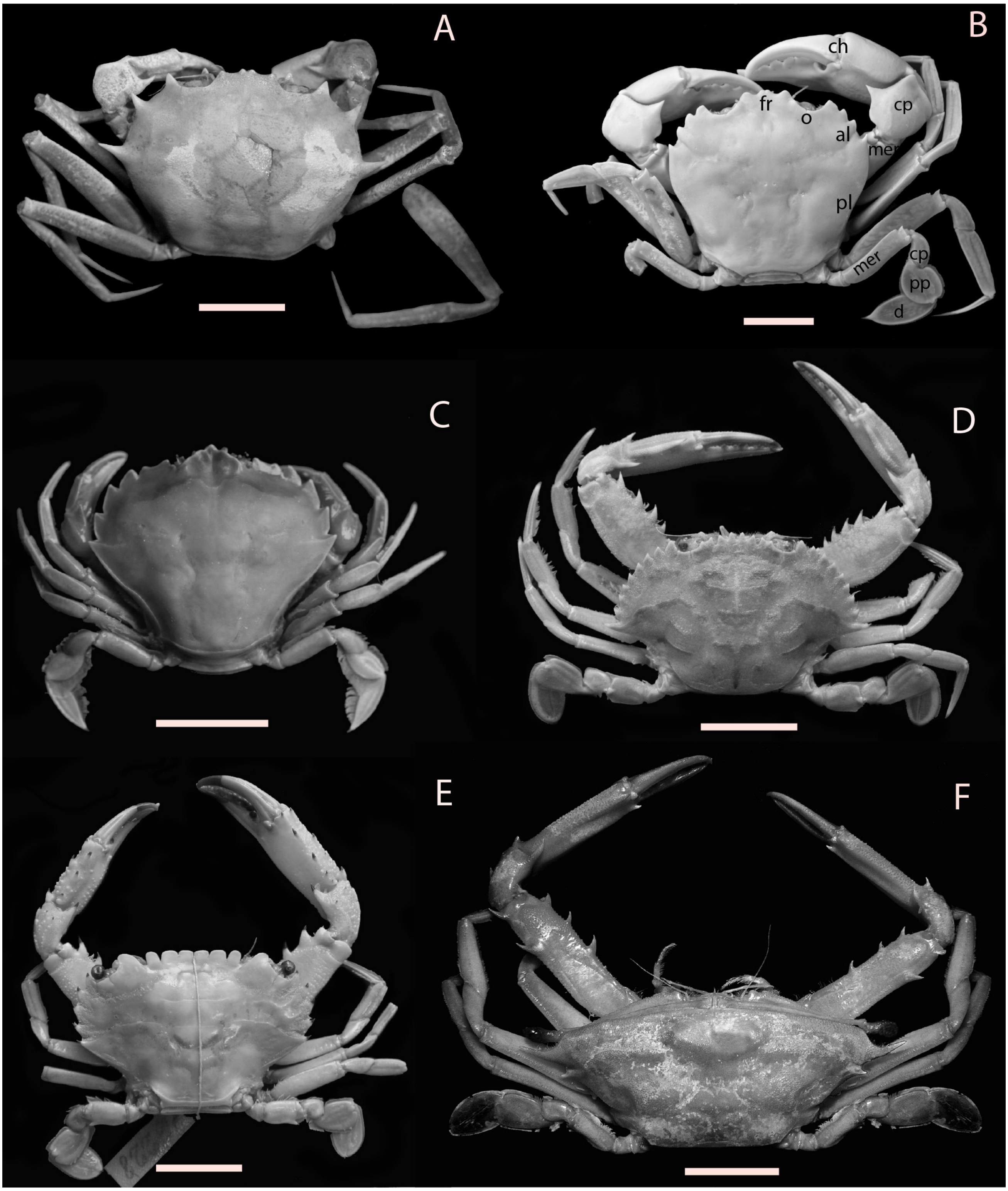

Fig. 3. Examples of portunoid crabs with a typical quasi-hexagonal (A–E) and a derived quasi-trapezoidal carapace (F). A. *Geryon trispinosus* Krøyer, 1838, North Sea, ZMMU Ma 2921; B. *Benthochascon hemmingi* Alcock & Anderson, 1899, South China Sea, ZIN-RAS 88509; C. *Xaiva biguttata* (Risso, 1816), North Sea, SMF 3969; D. *Achelous spinimanus* Latreille, 1819, Jamaica, SMF 31987; E. *Thalamita spinimana* Dana, 1852, Indo-Pacific, SMF 3881; F. *Podophthalmus vigil* Fabricius, 1798, Vietnam, collections of the Department of Hydrobiology of Moscow University. Abbreviations: f – frontal margin; o – orbit; al – anterolateral margin; pl – posterolateral margin; mer – merus; cp – carpus; pp – propodus; d – dactylus; ch – chela. Scale bar equals 5 mm.

In some portunoid taxa the cephalothorax is comparatively lengthened, so that the length becomes equal to or greater than the maximum width. The carapace morphology in such taxa shows a transition to a pear-shaped (*Portumnus*, *Brusinia*) or a nail-shaped (*Thia*, *Nautilocorystes*) outline (Fig. 4). The carapaces of *Brusinia* and *Nautilocorystes* are also distinctly longer than broad, which is an exception in the Portunoidea. The former genus may not even belong to the portunoid crabs phylogenetically (Evans, 2018), while the phylogenetic relationships of the latter are not yet reconstructed using molecular markers. However, all these taxa with a carapace shape that is unusual for portunoids have typical characters of burrower ecomorphs (Schäfer, 1954), while some of them (e.g., *Portumnus* and *Thia*; Figs. 4B, E) are definitely known to spend most of time burrowed in sandy sediments (Spiridonov et al., 2014).

In various subfamilies and genera of Recent portunoids one can also see transitions from quasi-hexagonal to other carapace shapes. Species of *Ovalipes* are flattened and approach an ovoid shape owing to arching of lateral carapace margins (Fig. 4A). Several actively swimming Podophthalminae, e.g., *Euphylax dovii* Stimpson, 1860, are also flat and ovoid. Arching of lateral carapace margin is more expressed in the Lupocyclinae which have a quasi-circular carapace and the Carupinae with broad quasi-oval carapaces (Fig. 5H). In the latter subfamily (genera *Atoportunus*, *Carup*a and *Catoptrus*) this type of carapace morphology is associated with living in reef cracks and caves (Spiridonov et al., 2014). In the non-reef-dwelling and likely non-swimming genus *Libyste*s (Carupinae), e.g., *L. edwardsi* Alcock, 1900, the carapace is quasi-hexagonal with a convex anterolateral margin bearing notable teeth, while these teeth are strongly reduced and the general outline approaches the oval one in *Libystes* aff. *nitidus* (Apel & Spiridonov, 1998: figs 5a, 6a), reaching a perfect oval condition in *Libystes nitidus* A. Milne-Edwards, 1867 (Fig. 5H). Another group with ovoid or quasi-circular carapaces includes symbiotic *Caphyra* and *Trierarchus rotundifrons* (A. Milne-Edwards, 1869), associated with green algae (Crosnier, 1975; Evans, 2018). A very unusual quasi-circular carapace shape with protruding frontal and posterior regions is known for the Coelocarcininae which inhabit coarse coral sand and rubble (Ng, 2002).

A trapezoidal carapace is characteristic of several portunids with extended frontorbital margin, which approaches the maximum breadth between posterior anterolateral teeth or becomes the widest part of the carapace. This is seen in *Podophthalmus vigil* (Fabricius, 1798) and some Thalamitinae. In the first case the extension is achieved owing to enlargement of the orbits, being associated with long eyestalks, and is commonly recorded among various and not closely related brachyuran taxa (e.g., Ocypodidae, Macrophthalmidae, some Goneplacidae). The second case is associated with the extension of the basal antennal segment and the frontal margin and seems to be practically unique among crabs.

The posterior part of carapace may be markedly longer than the anterior one (Geryonidae and most Carcinidae), or be nearly equal to it (a quasi-symmetrical shape in relation to the maximum width axis carapace), and even shorter, which is characteristic of active swimmers in the Portunidae (see Schäfer, 1954: fig. 41). It is worth noting that the Parathranitiinae, a taxon apparently separate from most other extant carcinids, also has such quasi-symmetrical carapaces (see Crosnier, 2002). It is furthermore characteristic of *Echinolatus* (see Davie & Crosnier, 2006), a genus *incertae sedis*, which I here tentatively place in the Geryonidae.

Fossil portunoids, or taxa resembling portunoids, are mostly characterised by quasi-hexagonal or ovoid carapaces which are mostly asymmetrical in relation to the maximum width axis (e.g., Karasawa et al., 2008; Ossó, 2016). In some cases, for instance in the Lithophylacidae Van Straelen, 1936 from the Cenomanian (lower Upper Cretaceous) quasi-trapezoidal carapaces have been reported (Guinot & Breton, 2006). In the Cretaceous family Carcineretidae Beurlen, 1930 an intermediate condition between the quasi-quadrate and quasi-trapezoidal outline of the carapace is characteristic of the type genus *Carcineretes* Withers, 1922 (Withers, 1922, pl. 16; Vega et al., 2001, fig. 1; Schweitzer et al., 2007). Another Cretaceous taxon with a near-quadrate carapace is *Binkhorstia ubaghsii* (Van Binckhorst, 1857) currently included in the family Longusorbiidae Karasawa, Schweitzer & Feldmann, 2008 (see Schweitzer et al., 2007, figs. 2 A-C). The Late Cretaceous *Ophthalmoplax* Rathbun, 1935, earlier considered within the Carcineretidae and currently within the Macropipidae (*sensu* Karasawa, Schweitzer & Feldmann, 2008) also has a subquadrate carapace (Schweitzer et al., 2007; Vega et al., 2013). In general, the carapace outline and symmetry/asymmetry patterns are characters of considerable taxonomic value at the genus or family level.

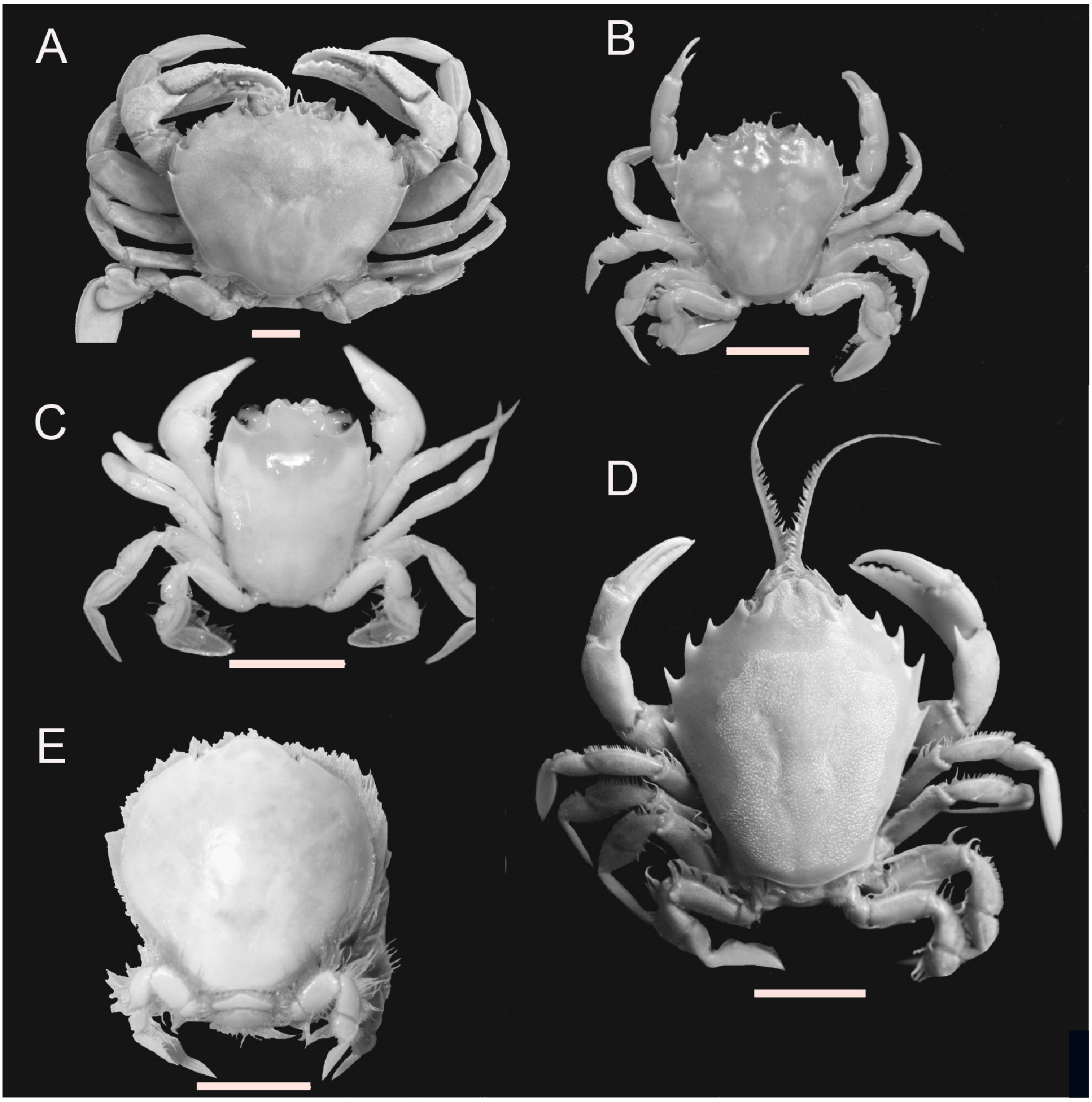

Fig. 4. Examples of portunoid crabs with modified carapace. A. *Ovalipes punctatus* De Haan, 1833, Japan, SMF, no catalogue number; B. *Portumnus latipes* Leach, 1814, Black Sea, ZIN-RAS 25087: C. *Brusinia brucei* Števćić, 1991, southern Australia, Museum of Victoria MV J 61074; D. *Nautilocorystes ocellatus* H. Milne Edwards, 1837, NHMW, from the collection of the frigate "Novara" Expedition, # 83; E. *Thia scutellata* Fabricius, 1793, North Sea, SMF 38490. Scale bar equals 5 mm.

Carapace regions

The carapace of Decapoda is subdivided into regions which correspond to location of particular internal organs of the cephalothorax (Glaessner, 1960). These regions may be separated by furrows expressed with various degrees of distinctness, or practically smoothed (Figs. 1, 3, 4, 5E, H). Amongst the Portunoidea, relatively distinct carapace regions are usually found in many groups with quasi-hexagonal carapace outlines (Figs. 3B, D, 5E). The species with another carapace outline, particularly ovoid or rounded, usually have smooth carapace regions (Fig. 4). The smooth carapace regions are typical of burrowing (*Portumnus* spp.; Fig. 4 B) or actively swimming species (e.g., *Charybdis smithii* MacLeay, 1838); in the latter case, this is in contrast to related species (see Türkay & Spiridonov, 2006, pl. 1).

Most fossil portunoids appear to have few differences from Recent representatives of the superfamily in the expression of carapace regions. Representatives of Cretaceous families referred to the Portunoidea are illustrated as having more strongly separated carapace regions compared to those in extant families: Carcineretidae (see Vega et al., 2001, fig. 1), Lithophylacidae Van Straelen, 1936 (see Guinot & Breton, 2006), Longusorbiidae (see Schweitzer et al., 2007, figs 2A-C). Most records of *Ophthalmoplax brasiliana* (Maury, 1930) also show quite distinct carapace regions, more expressively separated than in the majority of extant portunoid taxa (Vega et al., 2013, fig. 5). The distinctness of carapace regions may be considered as a character of varying taxonomic value although it tends characterise taxa at the genus level or higher.

Carapace ridges and cuticular structures

The dorsal carapace surface in portunoid crabs may be practically smooth as in *Brusinia*, *Benthochascon*, *Portumnus*, *Nautilocorystes* and *Thia*, evenly covered with granules (as in some *Ovalipes* and *Chaceon*) or carry complex sculpture, such as granular ridges, groups of granules, terraces and tubercles. Smooth carapaces are characteristic, first of all, of those species which spend a significant length of time burrowed in sandy sediments (see Garstang, 1897a, b; Schäfer, 1954), and also of those spending much time swimming in the water column, such as *Polybius henslowi* Leach, 1820 or *Charybdis smithii* (see Türkay & Spiridonov, 2006). The absence of sculpture on the carapace decreases friction and is most likely a derived condition. Most portunoid crabs possess epibranchial granular ridges that continue from last anterolateral tooth to the middle longitudinal axis of the body. In geryonids and carcinids these ridges consist of relatively sparse granules and are often interrupted and indistinct (Figs. 3A, B), similarly to many other heterotrenate crabs which have only epibranchial ridges. This is most probably a plesiomorphic condition for the Portunoidea. Among the Carcinidae, some species of *Liocarcinus* (e.g., *Liocarcinus corrugatus*; see Plagge et al., 2016) and *Necora* (see Holthuis, 1987) have additional granular ridges and even terraces. *Parathranites* (Fig. 5E) is characterised by a heavily sculptured carapace (see Crosnier, 2002), while in the Portunidae, particularly in the Thalamitinae and such genera as *Monomia* and *Xiphonectes* that sculpture is most diverse and spectacular (see e.g., Fig. 1F). The location of granular ridges and patches create specific patterns useful for distinguishing species and their groups in speciose genera such as *Achelous, Charybdis*, *Cycloachelous*, *Monomia*, *Thalamita* and related taxa, and *Xiphonectes*.

Fossil taxa also show a variety of dorsal carapace structures. Several Cretaceous genera have strong transverse ridges, even described as keels: across most of carapace regions as in *Ophthalmoplax* (see Vega et al., 2013, figs. 4-1) and Icriocarcinidae Števčić, 2005 (Phillips et al., 2014), or across the protogastric region as in *Carcineretes* (Schweitzer et al., 2007). Icriocarcinidae and Longusorbiidae are characterised by a row of massive tubercles along the posterolateral margin, particularly well developed in *Binkhorstia* Noetling, 1881 (see Schweitzer & Feldmann, 2011, fig. 8.1). Significant differences in carapace ornamentation of fossil taxa, judging from the variation observed in extant portunoids, support their distinctness and a relatively high taxonomic rank (i.e. family).

Frontorbital margin

The front *per se* is usually subdivided into several lobes or teeth, the number of which is either even (2–6), or odd (1–3). The functionality of the frontal lobes and space between them may be related to the sensory functions of antennules, their protection and cleaning, although this is largely unstudied. In the Geryonidae, the subfamily Geryoninae is characterised by a pair of separated median teeth and the lateral teeth are completely fused with inner orbital lobes (Fig. 3A). This fusion can be inferred from the presence of inner orbital lobes in with distinct two parts in some species of *Chaceon* and *Zariquieyon* (Manning & Holthuis, 1989, figs. 12, 14, 18). In the Benthochasconinae the median lobes are fused and the lateral frontal lobes can be recognised as distinct from the much smaller outer lateral lobes (Fig. 3B). In most species of *Ovalipes*, the frontal margin has two teeth (Fig. 6A). In *O. molleri* (Ward, 1933) these teeth are fused at the base so that they can be considered as a single, bifid tooth. Low projections of the frontal margin, possible rudiments or vestiges of lateral frontal lobes, are located laterally (Fig. 6B). In *O. iridescens* Miers, 1886, the species most closely similar to *O. molleri*, only a single median tooth is present and lateral concavities can be recognised in the largest specimens (Fig. 6C). In *O. ocellatus* (Herbst, 1799) nothing besides a sharp median frontal tooth can be seen (Fig. 6D). *Nectocarcinus* (Fig. 5B) and *Echinolatus* (see Davie & Crosnier, 2006) have a 4-lobed front that provides additional support to their placement in the Geryonidae.

With few exceptions, Brusiniidae and Carcinidae mostly have a 3-lobed front. The 4-lobed frontal region of *Bathynectes* (Fig. 5D) and *Par-*

athranites (Fig. 5E) largely resembles the condition in the Benthochasconinae. *Nautilocorystes*, a taxon with a burrowing habit, is characterised by a narrow bilobed front with lateral frontal lobes fused with the inner supraorbital ones (Fig. 4D). However, the relationships of the above-mentioned three genera to the Carcinidae remain to be clarified. A unique, for Recent carcinids, case of a broad bilobed front is represented by *Coenophthalmus* whose position within the Carcinidae also remains unclear. There are several cases of transformation of a 3-lobed to an entire front, even within a single genus, e.g., in *Liocarcinis navigator* (Herbst, 1794). with indication of fusion of the original three lobes. Other examples of a practically entire front include *Coelocarcinus* (see Ng, 2002) and *Thia* (Fig. 4E).

The Portunidae show a variety of frontal shapes, although most have an even number of teeth/lobes. In some genera the number of lobes varies: 4 to 6 in *Achelous*, and 2 to 6 in *Thalamita* (*sensu lato*). In these, not closely related, taxa, some species with transitional states are also reported, for instance *Thalamita bevisi* (Stebbing, 1921) (= *T. dakini* Montgomery, 1931; see Apel & Spiridonov, 1998, fig. 53a, c, d). An entire frontal margin in some species of *Libystes* has been apparently evolutionarily derived from an indistinctly bilobed front, characteristic of other species of the genus, less deviating from the general portunoid appearance, like in *Libystes edwardsi* (see Apel & Spiridonov, 1998, fig. 5a). There are relatively few portunid taxa with 3-lobed fronts; most of these belong to the genus *Xiphonectes*, which is most probably heterogenous (Spiridonov et al., 2014). In several *Xiphonecte*s with a 4-lobed front the lateral lobes are broad and produced forwards, while the median ones are small and often partly fused. This may be a condition from which a 3-lobed front, characteristic of some species of the genus, such as *X. tenuipe*s (De Haan, 1833), could evolve. Another example refers to some symbiotic species of *Lissocarcinus* in which the frontal margin is transitional between triangular entire and indistinctly 3-lobed ones, while other species of the genus have an indistinctly bilobed front (see Evans, 2018, fig. 3C, D). In the Podophthalminae the T-shaped frontal region is strongly reduced due to the enormous development of the orbits. Thus, the frontal margin shows a possibility for transformation, where both fusion and separation of the lobes seem possible in phylogeny, although the core groups of the main portunoid taxa are characterised by relatively constant patterns of frontal lobes.

Most fossil portunoid taxa were reported to have an even number of frontal teeth or lobes, or a flattened frontal margin with protuberances, usually even in number (Müller, 1984; Schweitzer & Feldmann, 2000; Karasawa et al., 2008). A 3-lobed front was particularly reported for species assigned to *Liocarcinus* and for such taxa as "*Xaiva*" *bachmayeri* Müller, 1984, *Mioxaiva psammophila* Müller, 1984 and "*Lissocarcinus*" *szoeraenyiae* (Müller, 1974) from the Miocene (Müller, 1984). An example of a possible portunoid, although not referable to any Recent family, is a species with an odd number of frontal teeth, *Psammocarcinus hericarti* Desmarest, 1822 from the Eocene, in which the prolonged front "has three spiniform teeth: the middle one is the largest; the lateral ones merge with the inner orbital angle" (A. Milne-Edwards, 1860, 279; translation by Karasawa et al., 2008). A unique frontal margin in the form of a deflected rostrum is characteristic of the Carcineretidae (Schweitzer et al., 2007). *Ophthalmoplax* spp. also possess a peculiar front: relatively narrow, deflected and bifid (Vega et al., 2013; Internet 1). Another frontal region that is unusual for portunoids is interpreted for *Longusorbis* Richards, 1975 (Upper Cretaceous–Eocene) as located "between interior-most orbital notches, axially produced into long, blunt-tipped rostrum, rostrum axially sulcate, strongly down-turned distally so that distal part is nearly perpendicular to dorsal carapace" (Karasawa et al., 2008, 95). The morphology of the frontal margin, its subdivision into teeth or lobes and inferred patterns of their transformation thus provide a set of characters highly applicable at the generic and suprageneric levels of taxonomic hierarchy.

Orbit

The orbit is a complex morphological structure, consisting of several lobes, separated by notches or fissures. The margins of the lobes may be rounded or polygonal. The number of lobes is a relatively stable character, although there are some exceptions. The supraorbital margin of one of the basal portunoid genera, *Chaceon*, consists of inner, median and outer supraorbital lobes separated by narrow fissures (Fig. 5A). The infraorbital part includes a tooth-like inner lobe, following which the inner orbital margin continues, smoothly forming an outer lobe (= 1st anterolateral tooth) (Fig. 5C). Such construction is similar to the one observed in most other portunoids although they usually have one more fissure or notch laterally of the outer lobe; moreover, in some taxa an outer infraorbital lobe,

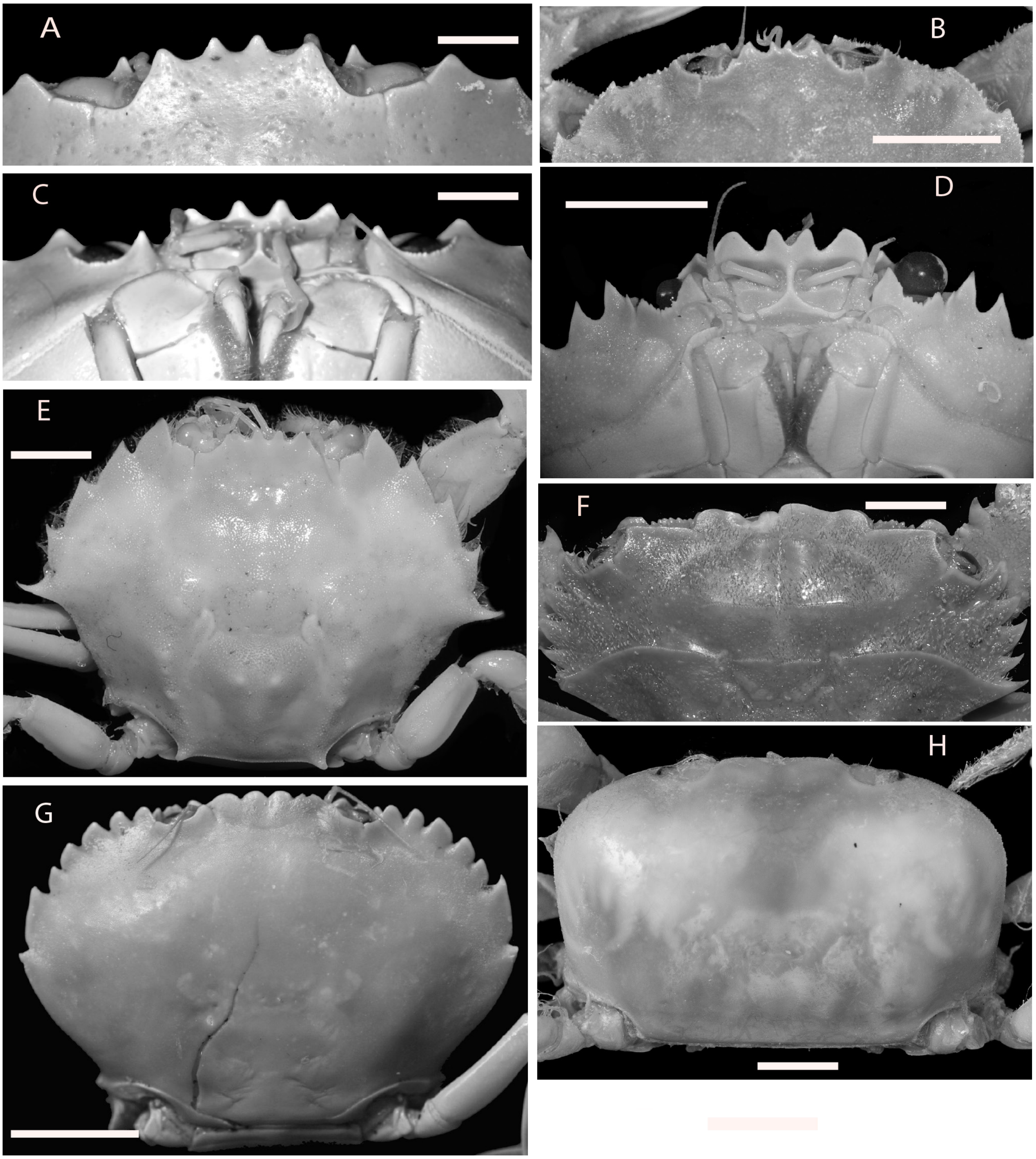

Fig. 5. Examples of frontorbital margins and carapaces. A. *Chaceon macphersoni* Manning & Holthuis, 1988, southwestern Indian Ocean, ZMMU Ma 4044, dorsal view; B. *Nectocarcinus bennetti* Takeda & Miyake, 1969, Maquarie Islands, ZMMU Ma 2301; C. *Chaceon macphersoni* Manning & Holthuis, 1988, ZMMU Ma 4044, ventral view; D. *Bathynectes longispina* Stimpson, 1871, Amper Seamount, Atlantic Ocean, ZMMU Ma 2392; E. *Parathranites orientalis* Miers, 1886, ZMB, without catalogue number; F. *Thalamita savignyi* A. Milne-Edwards, 1861, Gulf of Aden, ZMB 15592; G. *Carupa tenuipes* Dana, 1851, Japan, SMF, without catalogue number; H. *Libystes nitidus* A. Milne-Edwards, 1867, Maldive Islands, NHM 1991-156-1. Scale bars equal 10 mm (A, B, C, G), 5 mm (D, E, F) and 2 mm (H).

separated from the 1st anterolateral tooth, is also present. In some portunoids belonging to taxa that otherwise have numerous plesiomorphies (Spiridonov et al., 2014), one (in *Nectocarcinus*; Fig. 5B here; in *Zariquieyon* Manning & Holthuis, 1989, figs. 18, 19) or both supraorbital fissures (in *Geryon*; Fig. 3A) are strongly reduced. In the *Ovalipes iridescens* group only a single fissure is present: this is morphogenetically correlated with a transformation of the front with paired median teeth to a single tooth condition (Fig. 6). Finally, *Brusinia* (Fig. 4C), *Catoptrus* and *Libystes* (Fig. 5H) lack supra- and infraorbital fissures, while in *Portumnus* only a single strongly reduced supraorbital fissure is present (Fig. 4D). These groups are morphologically different and apparently belong to different phylogenetic lineages (except for the relatively closely related *Catoptrus* and *Libystes*). Forms with reduced fissures or an entire supraorbital margin in many cases belong to deep-water (Geryonidae) or burrowing (*Ovalipes*) species or are inhabitants of reef cavities and underwater caves (*Catoptrus*). They are characterised by a reduction of orbits, which may be achieved by fusion of orbital lobes. An opposite case also leading to the disappearance of the orbital fissure is a long but open and shallow orbit of the Podophthalminae where their long eyestalks are held. Thus, it is very likely that portunoid crabs originally had a 3-lobed supraorbital margin but in particular lineages transformation of morphogenetic pattern took place, thus leading to formation of a bilobed or an entire margin.

Derived conditions from the 3-lobed supraorbital margin involve modifications of lobes. The outer and inner lobes have various relative sizes and shapes, and may be modified to teeth, such as in *Pirimela* which has a long and sharp median supraorbital tooth (Fig. 3C). An unusually looking infraorbital margin in *Bathynectes* is subdivided into three denticulated teeth (Fig. 5E), although this condition may be a derivation of the typical 3-lobed one.

Where the details of orbit morphology can be recognised, fossil taxa often show a condition that is characteristic for extant portunoids. two or one supraorbital fissures. In one of the earliest, Cretaceous portunoids, *Eogeryon elegius* Ossó, 2016, the supraorbital margin closely resembles that of *Benthochascon* (Fig. 3B), while the infraorbital margin appears to be 3-lobed (Ossó, 2016, figs 5A, B). Orbits of some Cretaceous portunoid families (Carcineretidae, Longusorbiidae) are markedly broad at the expense of a narrow front and are similar in that respect to the orbits of the Podophthalminae. *Carcineretes* is diagnosed as having a sinuous orbit, “with two or three intra-orbital spines and notches (Schweitzer et al., 2007, 19). The original reconstruction of *Carcineretes woolacotti* Withers, 1922 shows four lobes of different width and shape and three notches (Withers, 1922; pl. 16). Protuberances and spines without fissures are characteristic of the orbits of *Longusorbis* (Schweitzer et al., 2007). The other Cretaceous genus with a narrow front, wide orbits and long eyestalks, *Ophthalmoplax*, also has three supraorbital lobes and two intra-orbital spines (Schweitzer et al., 2007; Vega et al., 2013, figs. 3, 13). The median orbital tooth similar to the one in Recent Pirimelidae is seen in the Miocene *Pirimela lorentheyi* Müller, 1984 (Müller, 1984, pl. 60, fig. 3). Some extinct portunoid taxa are also reported to have an entire supraorbital margin, e.g., *Psammocarcinu*s A. Milne-Edwards, 1860 (see Desmarest, 1822, pl. V, fig. 5; A. Milne-Edwards, 1860). The most unusual orbit with a completely denticulated supraorbital margin is found in *Pheophthlamus mochaensis* Feldmann, Schweitzer & Encinas, 2010 (assigned to the Podophthalminae) from the Neogene of South America (Feldmann et al., 2010, fig. 11), although most of the taxa included in this subfamily have a relatively simple supraorbital margin. Thus, the orbits of portunoids provide an important set of characters that may be used at various levels of taxonomic hierarchy.

Anterolateral carapace margin

The anterolateral margin of the carapace is subdivided into several teeth, the first corresponding to the outer orbital lobe. The functional significance of the anterolateral teeth was first interpreted by Garstang (1897a), who considered them as part of the apparatus preventing entering sediment particles to the branchial cavity in burrowing crabs. Brusiniidae, Geryonidae and Carcinidae do not have more than five teeth. In geryonids their number varies from three (*Geryon*, *Raymanninus*) to five (Ovalipiinae). In *Chaceon*, which typically has five anterolateral teeth, some teeth become obsolete with age. *Benthochascon*, *Nectocarcinus* and *Echinolatus*, which are tentatively referred to this family (but are considered by me as genera *incertae sedis*) are characterised by four large teeth. Some species of the last-named genus possess a unique character of additional denticles on the anterior margin of the anterolateral teeth or bifid teeth (Davie & Crosnier, 2006, fig. 3). Most of the Carcinidae have five anterolateral teeth. Important examples of reduction of anterolateral teeth in the Carcinidae are *Coenophthalmus* with three teeth and *Thia* with a nearly entire anterolateral margin, although one can see four notches on this margin which mark the position of five reduced teeth. A very dense belt of setae bordering the lateral margin in this burrowing species probably plays the role of branchial cavity protection in the absence of anterolateral teeth (Fig. 4E).

The number of anterolateral teeth in the Portunidae varies from two to nine and is largely a taxonomic character used at the generic level.

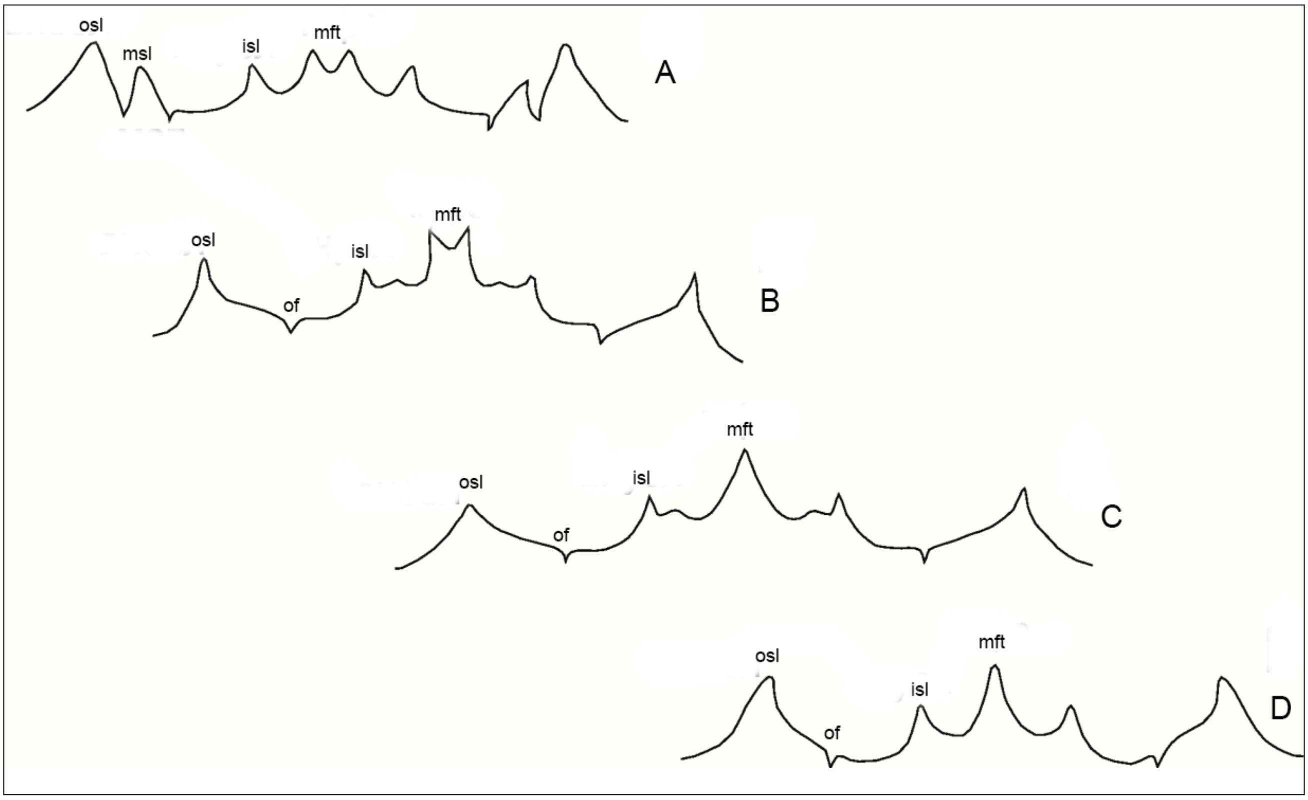

Fig. 6. Frontorbital margin of carapaces in *Ovalipes* spp. A. *O. trimaculatus* (De Haan, 1833), Patagonia, ZMMU, without catalogue number. B. *O. molleri* (Ward, 1933) (drawn on basis of photograph in Davie & Short, 1989, fig. 14B). C. *O. iridescens* Miers, 1886, southwestern Indian Ocean, ZMMU Ma 2300. D. *O. ocellatus*, northwest Atlantic, coast of Georgia, USA, SMF 7325. Abbreviations: isl: inner supraorbital lobe; mft: median frontal teeth (tooth); msl: medial supraorbital lobe; of: orbital fissure; osl: outer supraorbital lobe.

Spiridonov et al. (2014) argued that the nine teeth corresponded to a plesiomorphic condition for this family and the number of teeth showed various patterns of reduction in particular genera. Evans (2018) provided additional evidence for this in the Thalamitinae (which generally have a reduced number of teeth, from six to three) and suggested a nomenclature of teeth based on their general pattern and presumed homologies. Some oval forms, such as *Libystes*, have anterolateral teeth that are strongly reduced to nearly completely absent (see Apel & Spiridonov, 1998, figs. 5, 6a). Podophthalmines also show a reduction of teeth (up to two), which is apparently connected to their habits and a characteristic shortening of the anterolateral margin. Noteworthy, the single extinct portunoid taxon that is characterised by nine anterolateral teeth, but not referred to the Portunidae is *Archaeoportunus* Artal, Ossó & Domínguez, 2010, for which a separate family was introduced (Artal et al., 2010). Otherwise, fossil taxa do not show such morphological peculiarities of the anterolateral margin that remarkably exceed variation observed in extant portunoids (see e.g., Internet 2). Although the number of lateral teeth is subject to change in particular groups of portunoids, the major taxa have a distinct pattern of variation of this character.

Posterolateral and posterior carapace margin

A supra-dorsal position of the 5th pair of pereopods is morphologically correlated with the development of the posterolateral reentrant which extends motion possibilities for the last pair of legs, used for burrowing and swimming. Although this reentrant is feebly developed in the non-swimming Geryonidae (Figs. 3A–B), or carcinids like *Carcinus* (not swimming, and not commonly burrowing) and *Portumnus*, *Thia*, *Nautilocorystes* and *Brusinia*, presumably using all legs for burrowing (Figs. 4B–D).

The posterior carapace margin is bordered by a cuticular “wall” touching the 1st pleonal tergite. This margin is usually straight or gently convex (e.g., Figs. 3, 4). Much rarely, for instance in *Benthochascon*, this margin is concave (Fig. 3B). The majority of portunoids have rounded transitions between the posterolateral and posterior carapace margins. In some groups these corners are angled (e.g., subgenera *Goniohellenus* and *Gonioneptunus* of the genus *Charybdis*; see Türkay & Spiridonov, 2006) or even spined, as in *Xiphonectes* (see Spiridonov, 2016) in the Portunidae. The only Recent carcinoid genus having angled, or spiny posterolateral corners is *Parathranites* (Fig. 5E; see also Crosnier, 2002). Most fossil portunoids studied that have variously expressed posterolateral reentrants are characterised by rounded posterolateral corners (Karasawa et al., 2008; see also examples via Internet 3). There are few exceptions, e.g., *Psammocarcinus* which shows an angled posterolateral corner (see Desmarest, 1822, pl. 5, fig. 3). A unique morphology of the posterolateral margin with a series of teeth is seen in *Styracocarcinus meridionalis* (Secretan, 1961), a Campanian crab considered within the Portunoidea but not assigned to any family (see Ossó, 2016, fig. 6A, B). The characters associated with the posterior part of the carapace are thus important for the diagnosis of genus-level taxa within portunoid families.

Pterygostomial and subhepatic regions

Surfaces of the carapace regions located ventral to the anterolateral margin determine both an absolute and a relative height of the carapace, which is a taxonomically important character at higher levels. In most groups these surfaces are smooth, granular or markedly setose. Particular taxa such as not closely related *Ovalipes* and *Laleonectes* are characterised by the presence of granular lines and other cuticular armature constituting parts of the stridulating apparatus which counterparts constitute processes of chelipeds. The construction of this apparatus is a set of characters at the species level, for instance in *Ovalipes* (see Stephenson & Rees, 1968). In the deep-water species of this genus a reduction of the stridulatory apparatus occurs, which is correlated with the development of an optical communication system on the basis of iridescent surfaces reflecting polarised light under conditions of practical darkness (Parker et al., 1998).

Sternal part of cephalothorax

Sternites and episternites are sclerites of the sternal part of the cephalothorax. The latter join the former in their posterolateral part by distinct or partly interrupted sutures. The hollow space between the lateral margin of the sternite and the respective episternite houses the condyle of the pereopod coxa, and the entire structure forms a sterno-coxal articulation. The major part of episternites 4 to 6 is usually sickle shaped; it is extended posteriorly, touching the lateral margin of the next sternite over more than half of its extension. The shape of episternites 7 and 8 usually strongly deviates from the sickle-shaped one and may characterise taxa at family and subfamily levels (Fig. 7). In most portunoid crabs the width of episternites is several times less than the width of sternites but in *Thia* sternites are less than twice wider than episternites (Fig. 7B).

Sternites and episternites of thoracomeres 1–4 is consolidated as a thoracic sternum, the parts of which may be separated by furrows of various distinctness. This has taxomomic significance for diagnosing particular families, subfamilies and genera. The longitudinal median groove is characteristic of most Portunoidea, although may be present in other taxa as well.

Sutures between sternites 4–8 may be interrupted in various ways that usually characterise particular genera and subfamilies. The Portunidae have secondary sulci between sternites 6 and 7, which are considered as their unique synapomorphy, although *Libystes* lacks this character (Karasawa et al., 2008). Sternal characteristics are relatively well preserved and have been widely used in the taxonomy of fossil portunoids (Schweitzer et al., 2007; Karasawa et al., 2008).

Antennules and antennae

Antennules of most portunoids are relatively short, transversely folded and generally similar even in such distant groups as geryonids and portunids. In completely folded conditions, the antennules are concealed under the frontal margin and not seen dorsally. Only in podophthalmines, with their very narrow front, folded antennules cannot be completely hidden in dorsal view.

Antennae differ first of all by a so-called basal antennal segment which is interpreted as a fusion of the original segments 2 and 3 of the antennae (Ng et al., 2008). In a number of portunoid crabs this segment tends to form a distolateral process entering the orbital hiatus. Size and form of this process are important taxonomic characters. The tendency for enlargement reaches a maximum in the Thalamitinae: the process contacts the orbital margins and isolates the antennal flagellum from the orbital hiatus. The enlarged basal antennal segment itself often bears armature, e.g., granules, ridges and spines, the pattern of which is an important taxonomic character at the species level in thalamitines (Stephenson & Hudson, 1957; Apel & Spiridonov,

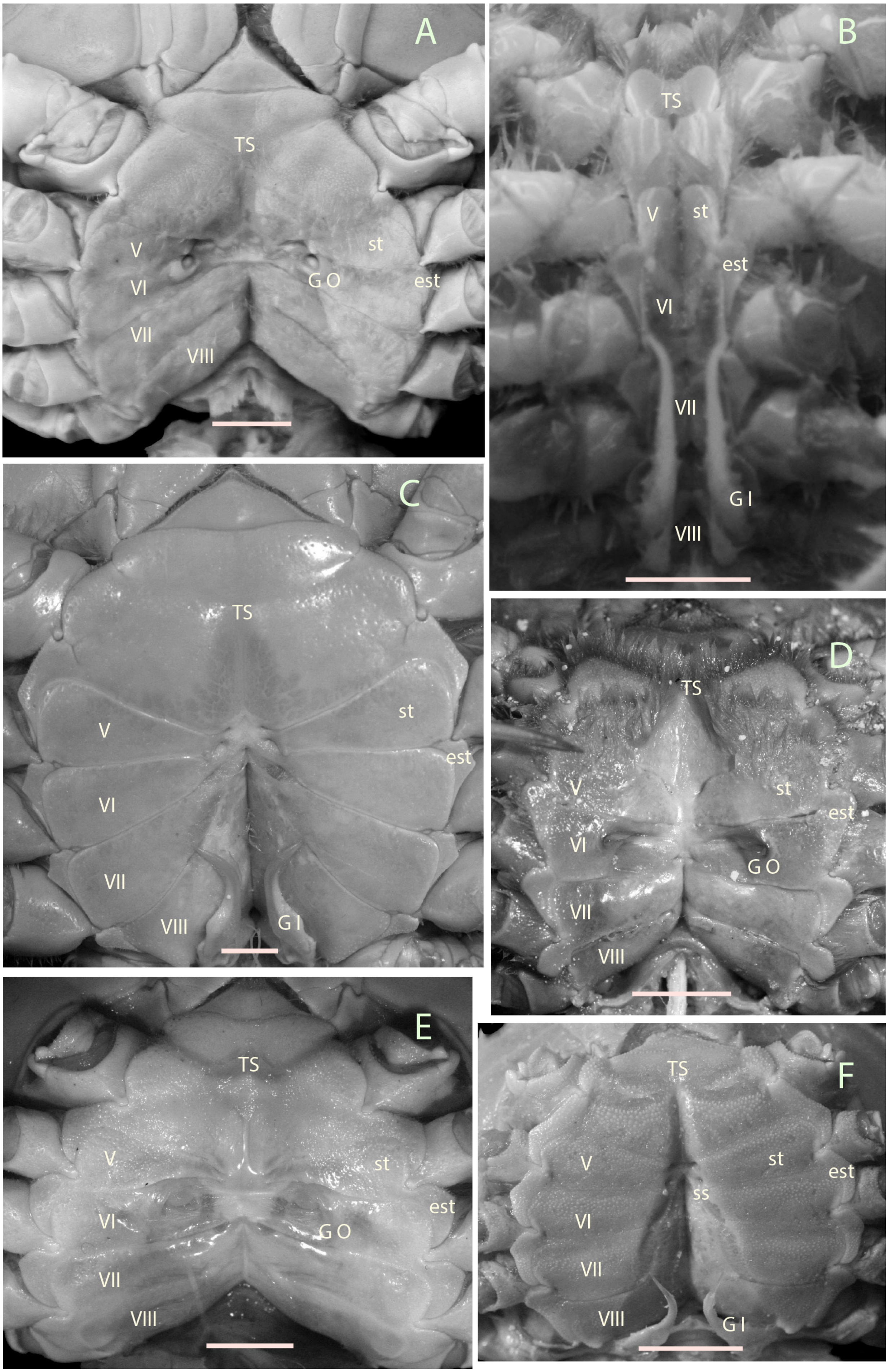
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Fig. 7.

1998). A highly unusual antennular morphology for portunoids is seen in *Nautilocorystes*, which has long setose antennae (Fig. 4D), similar to the ones of *Corystes* Bosc, 1802 that are in turn associated with the burrowing habit of this crab (Schäfer, 1954: fig. 28). The details of antennae and antennules are rarely enough preserved to be considered for fossil taxa.

Maxillipeds

Although mouthparts including mandibles, maxillae and maxillipeds 1 and 2 are usually not preserved, maxilliped 1 should be mentioned here as having particular significance in portunoid taxonomy. The upper part of its endopod has a quasi-triangular or quasi-trapezoidal shape. Antero-mesially the so-called "portunid lobe" is attached; this usually is dentiform, stick-shaped or finger-shaped. This lobe is present in all Portunidae but also in some carcinids, for example in *Bathynectes*, *Liocarcinus* and *Macropipus*, although absent in the Carcininae, Geryoninae and Ovalipinae along with *Nectocarcinus* (Spiridonov et al., 2014). In *Benthochascon*, the lobe is morphologically different from the one observed in other portunoids (Spiridonov et al., 2014). Currently, it is difficult to judge if the observed pattern is a result of parallel origin of lobes or reduction of this structure takes place independently in particular families. Functional properties of the maxilliped 1 lobe have not been studied.

Maxillipeds 3 are of similar construction in all Portunoidea. The shape of the meropodite, which covers the mouth cavity anteriorly is about as long as wide, quasi-quadrilateral, with a convex setose mesial margin and is not much different in geryonids and carcinids, except for some burrowing species in which it is more elongated. In the Thalamitinae and Portuninae, meropodites of maxilliped 3 are most diverse and may have a different shape, with rounded or angular anterior margins and varying setal coverage and granulation. These usually are characters that are taxonomically important at lower taxonomic level (species, species groups and small genera).

Chelipeds

The relative length of the chelipeds is a character that marks taxa at the family level. While relatively short, not exceeding in length pereopods 2 and 3, chelipeds are most probably a plesiomorphy, characteristic of Carcinidae and most Geryonidae (Figs. 3A–C), except for some species of *Ovalipes*, for instance the *Ovalipes iridescens* group. Chelipeds of the Portunidae are the longest pair of pereopods, on acount of their long meri and chelae (Figs. 3D–F).

Meri of chelipeds may be smooth or possess spines. Geryonines possess a solitary spine on the posterior surface of merus. Nearly all Portunidae and few non-portunid portunoids (*Bathynectes*, *Parathranites* and species of the *Ovalipes iridescens* group) have spines on the anterior face of the merus (Figs. 3D–F). Long and spiny chelipeds are advantageous for defence (in particular, in typical defensive reaction), prey capture, courtship and mating behaviour (Schäfer, 1954; Spiridonov et al., 2014).

Carpi of chelipeds may have various shapes, although the respective taxonomic characters are associated mostly with carpal spines. All portunoid crabs, along with several other heterotreme taxa, have an inner spine on the after carpus its length is varying between taxa but is particularly significant in some species of *Achelous*. On the other hand, this is obsolete, in *Callinectes* spp. The taxa referred to the Geryonidae with reservation, such as *Echinolatus* (see Davie & Crosnier, 2006) and some *Nectocarcinus*, e.g., *Nectocarcinus benneti* Takeda & Miyake, 1969 are characterised by double carpal spines, similar to the ones seen in the Mathildellidae (Goneplacoidea).

Spines on the outer face of carpus are characteristic, first of all, of the Portunidae, but are also present in *Parathranites* (see Crosnier, 2002). They may undergo reduction; in particular, one of the differences between related species of *Xiphonectes*, *X. tenuipes* (De Haan, 1835) and *X. pseudotenuipes* (Spiridonov, 1999) is the reduced spines in the latter (Spiridonov, 1990, figs 2E, 3B). An important character in *Thalamita* and related genera is an additional spinule on the upper face of the cheliped carpus. It appears to have a parallel origin in several groups of species and genera (Spiridonov & Neumann, 2008; Evans, 2018).

Fig. 7. Sternal regions. A. *Benthochascon hemingi* Alcock & Anderson, 1899, South China Sea, ZIN-RAS 88509; B. *Thia scutellata* Fabricius, 1793, North Sea, SMF 38490. C. *Ovalipes iridescens* Miers, 1886, southwestern Indian Ocean, ZMMU Ma 2300. D. *Carcinus aestuarii* Nardo, 1848, Black Sea, Ma 5181. E. *Bathynectes longispina* Stimpson, 1871, Atlantic, Amper Seamount, ZMMU Ma 2392; F. *Achelous spinimanus* (Latreille, 1819), Gulf of Mexico, ZMMU Ma 4848. Abbreviations: G I – gonopod 1; G O – genital opening; TS – thoracic sternum; st – sternite; est – episternite; V – VIII – number of sternites. Scale bar equals 5 mm.

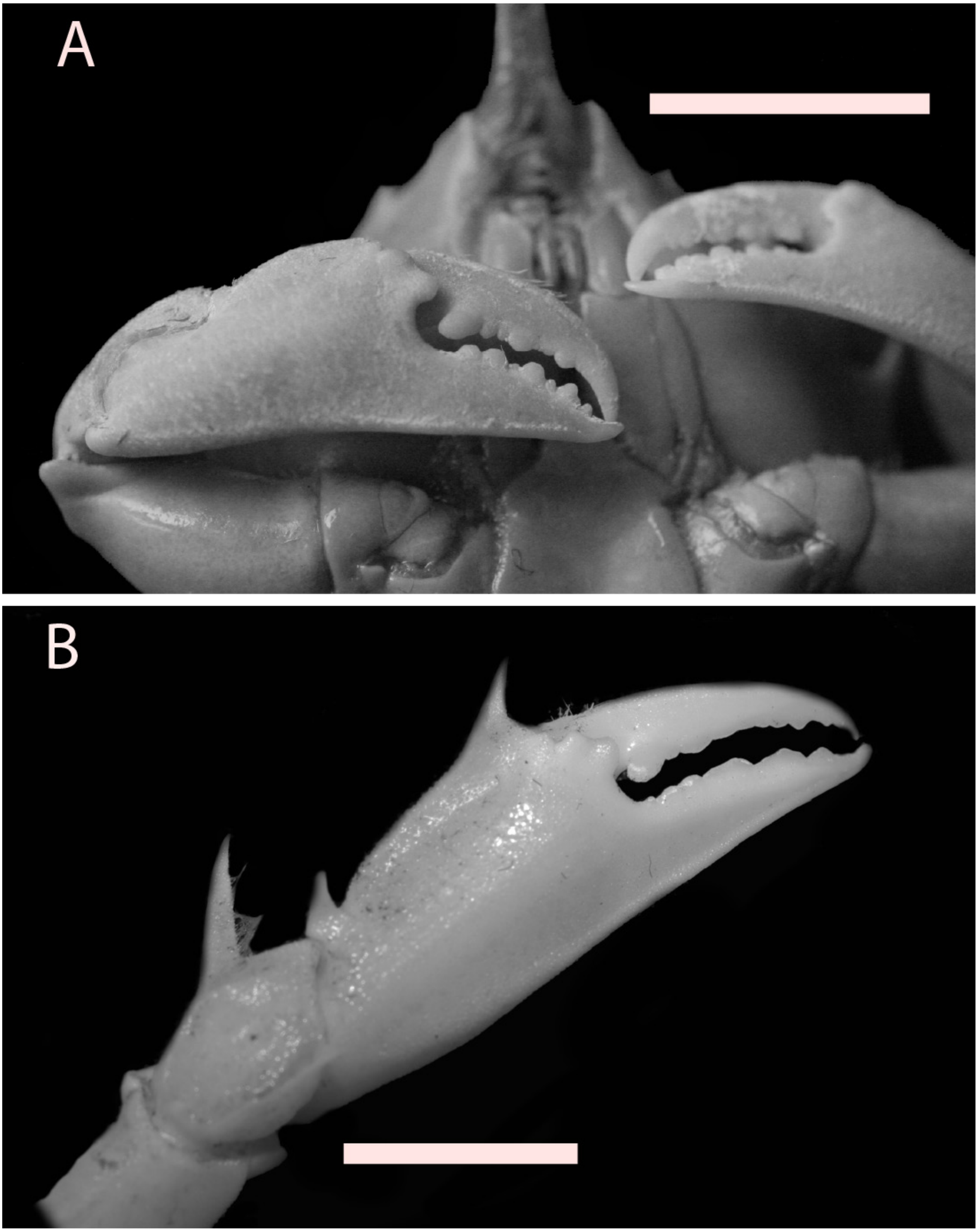

Fig. 8. Chelae. A. *Nauticorystes ocellatus*, NHMW, from the collection of the frigate "Novara" Expedition, # 83. B. *Patrathranites orientalis* Miers, 1886, ZMB, without catalogue number. Scale bar equals 5 mm.

Chela morphology and patterns of heterochely

Chela morphology is essential for morphological characterisation of the Portunoidea (Schäfer, 1954; Manning & Holthuis, 1981; Spiridonov et al., 2014), the presence of a large proximal molariform tooth on the dactylus of one of the chelae (heterodonty) along with serial bi- and trilobed conical teeth on the dactylus and the polex of both chelae. Serial teeth separated into lobes increase the cutting edge and work as scissors.

The presence of a massive molariform tooth allows the portunoid chelae to maintain significant crushing capacity and perform various crushing techniques when feeding on molluscs. Various modifications from this basic plan and symmetrisation of chelae construction have been described by Spiridonov et al. (2014, figs. 2, 3) and interpreted in terms of belonging to particular ecomorphs: burrowers, walkers and swimmers. Reference is made to that paper for a detailed description. Typical portunoid heterodont chelae are found in *Nautilocorystes* (Fig. 8), which otherwise has a very peculiar “non-portunoid” general appearance which possibly is associated with a burrowing habit (Fig. 4D). Surprisingly, this chela is very similar to the that of the Polybiinae with a very different habit (see Spiridonov et al., 2014, fig. 2). Chelae are usually well preserved in fossil taxa which can often be recognised as portunoids by the characteristic morphological features of their palms (Müller, 1984; Schweitzer & Feldmann, 2000, 2011; Schweitzer et al., 2007; Karasawa et al., 2008; Phillips et al., 2013).

Pereopods 2–4 (ambulatory legs)

In portunoid crabs, pereopods 2–4 are usually similar but differ in size from front to rear, P2 or P3 being the longest. The orientation of the sterno-coxal articulation allow for the parallel position of pereopods which become in that case somewhat inclined in relation to the transverse axis of the body. Meri, carpi and propodi are compressed so that the morphologically dorsal face is exposed anteriorly. In most geryonids an anterodistal process or lobe is present in meri; in *Ovalipes* only low lobes can be traced there. Other processes and spines are rare on pereopods 2-4 and, usually, are characters used at intermediate hierarchical levels (e.g., goups of species and genera), such a series of spines on the anterior face of the merus is seen in *Coenophthalmus* (Steudel, 1998, figs. 37c-d).

In most portunoids, dactyli (fingers) of pereopods 2–4 are relatively similar, piercer shaped, or narrow knife-shaped, costate, often setose on the flexor margin. Active natatory species, such as *Callinectes* spp., *Portunus pelagicus* (Linnaeus, 1758) and related species, *Polybius henslowii* Leach, 1820, *Euphylax dovii* Stimpson, 1860 and *Charybdis smithii*, have leaf-shaped leg fingers, which are used in swimming. However, the morphology of dactyli in the the overwhelming majority of cases does not differ between pereopods. Heterodactyly (differing between pereopods 2–4 shape of fingers) is characteristic of a few taxa known or presumed for their burrowing habits (*Brusinia*, *Thia*, *Nautilocorystes*, *Ovalipes*, *Portumnus*) (Fig. 4). However, the pattern of heterodactyly in these groups differs, which makes it a taxonomic character of a relatively high level (subfamily or family).

In fossil portunoid taxa, the morphology of ambulatory legs varies significantly, although this mostly refers to the more proximal segments of legs, while dactyli are less frequently preserved. In particular, in the Carcineretidae, pereopod 4 has a flattened carpus and merus (Schweitzer et al., 2007).

Pereopod 5

The dorsal position of the last pair of pereopods that is typical of portunoid crabs is achieved by a higher position of their coxae in relation to other legs (the so-called dorsal coxal shift). The fewer differences in the plane where the coxae of the 5th and other pereopods are located are known for *Brusinia* and *Portumnus*. The highest dorsal coxal shift is characteristic of such taxa as *Coenophthlamus* (non-swimming ecomorph), *Liocarcinus*, *Portunus*, *Thalamita* (all swimming or at least lifting over substrate) and *Caphyra* (non-swimming symbionts of cnidarians). A peculiar morphology of a modified pereopod 5 is an important portunoid character, used for swimming, burrowing and attaching to a host. The modification affects a shortening and broadening of the merus, flattening of the propodus, and ensiform, ovate, lanceolate, or hook shape of the dactylus. This construction, however, is not shared by all portunoid taxa, in particular *Chaceon* and *Geryon* have the last pair of pereopods not particularly different from others (Fig. 3A). This is probably also the case for such fossil family as the Icriocarcinidae (Phillips et al., 2013) of Cretaceous age.

The shape of segments of pereopod 5 provides a number of taxonomic characters which are used at various hierarchical levels. It is of interest to note that within a single (although probably non-monophyletic) genus *Liocarcinus* both broad (for instance in *L. vernalis*; see Fig. 1C) and relatively narrow dactyli of the last pair of legs are known (e.g., in *L. navigator*). Even greater variation is known for symbiotic *Lissocarcinus* spp. (an apparently monophyletic group; see Evans, 2018), where the dactyli are variously modified, possibly depending on the relationships of a particular species with its host.

Wherever preservation conditions enable an examination of the last pair of ambulatory legs in

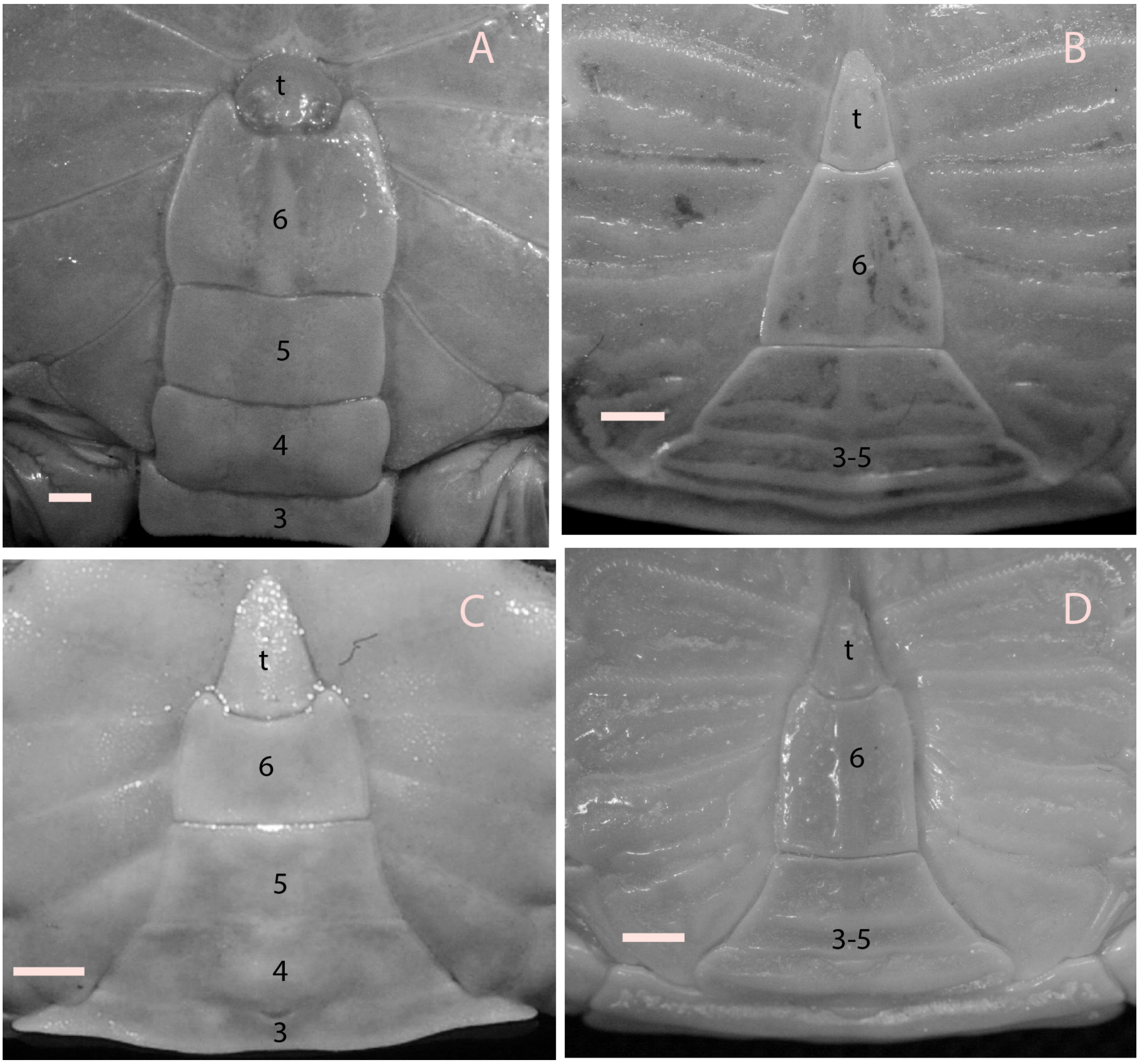

Fig. 9. Male pleons. A. *Ovalipes iridescens* Miers, 1886, southwestern Indian Ocean, ZMMU Ma 2300. B. *Achelous hastatus* (Linnaeus, 1767), Mediterranean, ZMMU Ma 1910; C. *Parathranites orientalus* Miers, 1886, Indo-Pacific, ZMB, without catalogue number; D. *Monomia petrea* Alcock, 1899, western Indian Ocean, ZMMU 2294. Abbreviations: 1–6 – pleomeres; t – telson. Scale bar equals 1 mm.

fossil crabs assigned to the Portunoidea, we see modified propodi and dactyli. While the Recent Geryoninae have the segments of pereopod 5 not much different from the anterior legs, *Chaceon peruvianus* (d'Orbigny, 1842) from the Miocene of South America clearly possessed broadened propodi and narrow-lanceolate dactyli of pereopod 5 (Schweitzer & Feldmann, 2000, fig. 10-1). This indicates that a characteristic construction of pereopod 5 can undergo evolutionary reversal and/or evolve as a parallelism (Simpson, 1961) in various groups of portunoids.

Pleon

A nearly universal characteristic of the portunoid pleon is the presence of a transverse keel on the tergite of the 3rd pleomere (Figs. 9B–D) (absent in *Brusinia*, *Ovalipes* [Fig. 9A] and *Carupa*). Male pleons are characterised by a tendency for fusion of pleomere terga 3 to 5, which is, however, not a universal characteristic of the group. Six separate pleomeres and the telson are apparently a plesiomorphic condition typical of most Heterotremata (Guinot, 1979; Davie et al., 2015).

In *Geryon*, *Chaceon*, *Benthochascon*, *Ovalipes* (Fig. 9A), *Echinolatus*, *Nectocarcinus*, and *Brusinia* pleomeres 3–5 are separated, although an ability of individual motion may be lost. In most carcinids and portunids they are fused, while some sutures or their traces may remain (Figs. 9B–D).

It is of interest to note that similar, possibly convergent or parallel fusion of the pleomeres is known for the American freshwater brachyuran family Trichodactylidae (Rodriguez, 1992). The functional significance of the pleomere fusion is unknown. It is possible that it is correlated with particular mechanisms of copulation (Karasawa et al., 2008). All portunoids with fused pleomeres also have short gonopods 2 (see below). Geryonids that have separated pleomeres possess also long gonopods 2 (Spiridonov et al., 2014).

A unique condition is observed in the males of *Thia*, where separated pleomeres (a unique character of carcinids) are associated with short gonopods 2. Since *Thia* is a quite specialised and not a basal taxon to the Carcinidae, it is unclear how this condition could originate and whether a reversal to non-fused pleonal segments is possible.

Males of most portunoids have a triangular or (in the Portunidae) T-shaped pleon (Figs. 9B– D), although a different condition is observed in *Ovalipes* with its quasi-rectangular pleon (Fig. 9 A). In most fossil portunoids male pleons are also triangular, while in *Proterocarcinus* it is quasirectangular (Feldmann et al., 2005, fig. 5 E), in some respect similar to that of *Ovalipes*.

Not all fossil taxa can be characterised by pleon morphology owing to preservation conditions. However, separated pleomeres 3–5, although probably immovable, are known for ancient geryonines (e.g., Schweitzer & Feldmann, 2000, fig. 9), Longusorbiidae (Karasawa et al., 2008), Icriocarcinidae (Philips et al., 2013), Lithophylacidae (Guinot & Breton, 2006) and the genus *Ophthalmoplax* (Schweitzer et al., 2007; Vega et al., 2013; Ossó-Morales et al., 2010). Surprisingly, separation of pleomeres is also characteristic of such genus as *Archaeoportunus*, which in several other respects is similar to the Portunidae (Artal et al., 2013, fig. 4b), although such Cretaceous taxa as *Carcineretes* had fused pleomeres (Schweitzer et al., 2007). The shape of the male pleon and the pattern of pleomere fusion can thus be regarded as important taxonomic characters for higher-level portunoid taxa, in most cases of family/subfamily rank.

Discussion

Recent morphological and molecular phylogenetic studies have indicated that several high-level extant taxa of portunoid crabs (families and subfamilies) are much more diverse morphologically than had been intuitively expected, although possible morphogenetic transitions between different character states may be inferred in many cases, as in the case of the frontal margin of *Ovalipes* (Fig. 6). Furthermore, each internally diverse taxon of portunoid crabs is characterised by a core suit of characters, which may be even called an “archetype” (I use this term only instrumentally, without a reference to essentialism; see Lyubarskiy, 1995) and peripheral conditions. This is a result of mosaic evolution and leads to polythetic diagnoses of taxa in many eukaryotic groups (see Mayr & Bock, 2002; Takhtajan, 2009) and varying resolution of particular taxonomic characters (Zarenkov, 1974). A proper description and understanding of this “archetype” may help to classify extinct taxa using a comparative approach to extant ones.

Firstly, several families established earlier by palaeontologists and redefined by Karasawa et al. (2008), such as the Carcineretidae, Lithophylacidae, Longusorbiidae and Psammocarcinidae, appear to have a distinct suit of characters that do not fit even peripheral conditions of extant portunoid families.

Similarities of these families to extant portunoid taxa may be the result of parallelism rather than of common origin. Although testing this is currently hardly possible, and the Portunoidea that contain the above-mentioned families should be considered as an evolutionary taxon in Simpson’s (1961) sense. The composition of the Portunoidea, including the extant families along with the Carcineretidae, Lithophylacidae, Longusorbiidae and Psammocarcinidae, appears to be appropriate and can be only rejected if a completely convergent origin of the core portunoid character suit in extant and extinct families is demonstrated.

Ossó (2016) established the family Eogeryonidae based on *Eogeryon elegius*. This family apparently has an affinity to portunoids, in particular to the Geryonidae, although shows some important differences. However, taking the significant variability of taxa combined in the Geryonidae (e.g., Geryoninae, Benthochasconinae and Ovalipiinae, possibly *Echinolatus* and *Nectocarcinus*), it would not be surprising to find additional support for considering *Eogeryon* as a taxon close to the ancestral geryonid. The subrectangular male pleon of *Eogeryon* is indeed similar to the one of *Ovalipes*, while the general carapace outline of this fossil portunoid resembles that of *Benthochascon*.

Karasawa et al. (2008) performed a morphological cladistic analysis of Recent and extinct genera of portunoids and some other taxa, showing affinity to this group. To make classification compatible with reconstructed phylogenies they redefined the family Macropipidae Stephenson & Campbell, 1960 and included in this several fossils (Cretaceous to Neogene) genera (e.g., *Ophthalmoplax*), along with Recent taxa. This resulted in a quite broad diagnosis of the taxon. The extant Macropipidae (*sensu* Karasawa et al., 2008) turned out to be incompatible with molecular phylogenetic reconstructions (Schubart & Reuschel, 2009; Spiridonov et al., 2014; Evans, 2018). This indicated the necessity of splitting them between various groups of the newly defined Carcinidae (*Bathynectes*, *Macropipus*, *Parathranites*) and Geryonidae (*Raymanninus*, and possibly *Echinolatus* and *Nectocarcinus*). In this case, extinct genera return to an uncertain status, which is not a desirable situation. Briefly commenting on this, I can suggest to examine the relationships of the genera that have numerous plesiomorphies, such as *Proterocarcinus* to the Geryonidae in the broad new concept, and others such as *Portunites* to the Parathranitinae. *Ophthalmoplax* apparently does not have affinities to the Geryonidae, but it is also different from the Carcinidae. The general quasi-guadrate outline of the carapace, well-developed carapace regions and transverse ridges, narrow bilobed frontal margin, orbits and the construction of chela (Vega et al., 2013) are not typical of any extant subfamily. Few taxa within the Recent Carcinidae have spines on the upper face of cheliped dactylus, e.g., *Parathranites* and *Bathynectes*. The former genus is also characterised by an odd number of frontal lobes, similar to *Ophthalmoplax*. However, in other respects they do not have anything in common to assume close relationships. *Ophthalmoplax* apparently shows a unique combination of plesiomorphic and apomorphic character states that makes close relationships with an unknown ancestor of the Recent Carcinidae unlikely, so it would be better considered within a separate family.

Several other well-preserved and relatively speciose genera, such as *Coeloma* A. Milne-Edwards, 1865, mostly of Eocene – Oligocene age, have been variously treated since their discovery (Karasawa et al., 2008; De Grave et al., 2009; Jagt et al., 2010). I would agree with Ossó (2016) on their very likely affinity to the Geryonidae, particularly considering the new concept of this family. Another particular, but important, task is to revise the good fossil record of the carcinid genus *Liocarcinus* (Hyžný et al., 2015) in the light of its recently documented paraphyly (Plagge et al., 2016), its significant persistence in the geological time (Fig. 2) and the new concept of the Carcinidae.

Within the Portunidae there generally are fewer problems in interpreting and positioning fossil taxa, although the classification of extant taxa at the subfamily level is still far from perfect. Classification of extinct taxa could thus significantly benefit from the progress of taxonomic studies of contemporary faunas. A particularly important issue is the relatively numerous fossil examples of *Portunus* (*sensu lato*) which may, in fact, belong to other genera such as *Portunus* (*sensu stricto*), *Achelous*, *Monomia* and others. Distinguishing between them is not an easy task because many important characters are not available for study. For example, as stated above, the oldest species of the group, "*Portunus*" *kochi* resembles *Achelous* in several morphological characters. "*Portunus*" *atecuicitlis* Vega, Feldmann, Villalobos-Hiriart & Gio-Argaez, 1999, a common species from the Lower and Middle Miocene of Mexico, also likely belongs to *Achelous* on account of the construction of the front and chelae (Vega et al., 2009). Another common Miocene species in the Tethys and Paratethys, "*Portunus*" *monspeliensis* A. Milne-Edwards, 1860, could be referred either to *Achelous* and *Monomia* on account of the single visible spine on the cheliped manus and well-developed sculpture of the carapace (see Marangon & De Angeli, 2009, fig. 3; Gašparič & Ossó, 2016, pl. I, E, G), although the shape of the front and orbits and the relative size of the 1st anterolateral tooth support assignment of this species to *Achelous*. "*Portunus*" *miocaenicus* Müller, 1984 was referred to *Monomia* (as a subgenus) by the author himself. Examination of the published photograph (Müller, 1984, pl. 62, fig. 5) does not disapprove nor approve this because several important characters, i.e. the sternum, pleon and merus of cheliped remain unavailable for study. A few other species may be relatively confidently referred to *Portunus* (*sensu stricto*), such as *Portunus neogenicus* Müller, 1979, which shows a similarity to the extant Indo-Pacific species *Portunus sanguinolentus* (Herbst, 1783) (Müller, 1984, pl. 62, figs. 3, 4). A complete revision of fossil "*Portunus*" spp. is a challenge but it is worth to undertake this task because these numerous records may tell much more about the history of Cenozoic faunas when properly assigned to genera.

Conclusions

It is trivial to say that our understanding of evolution of any taxonomic group, including portunoid crabs, would strongly benefit from integration of knowledge of extant and fossil taxa. However, we should carefully and clearly define a background for successful integration. Combining extant and fossil groups of portunoid crabs into a coherent classification that is compatible with phylogenetic reconstructions implies an acceptance of the concept of vertical taxa (Simpson, 1961). That is what palaeontologists explicitly or implicitly do when referring fossils to particular genera or families established on extant material, even though they necessarily work with incomplete sets of characters. Some standard characters for extant taxa, such as genital structures, maxillipeds, even dactyli of pereopods 2–4 and others are rarely available for comparative study of fossil taxa. This calls for extension of comparative morphological studies of Recent groups in order to find new characters that can help to classify fossil forms.

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GEOLOGIJA *63/1*, 167-169, Ljubljana 2020

Report/Poročilo

7th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, 17th–21st June 2019, Ljubljana (Slovenia)

Rok GAŠPARIČ

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The 7th triennial Symposium on Mesozoic and Cenozoic Decapod Crustaceans was held in Ljubljana (Slovenia) this time, a European capital with a long history. The aim of the symposium is to meet with other decapod researchers every three years to discuss their research and to promote international collaborative work on fossil decapod crustaceans. The 44 attending palaeontologists and marine biologists from 17 countries exchanged new concepts and ideas in the fields of palaeobiology, with contributions on taxonomy, systematics, taphonomy, palaeobiogeography and macroevolution of decapods. Decapod crustaceans are evolutionarily one of the most successful groups of multicellular organisms. They form a diverse group of arthropods that inhabit various environments, ranging from shallow continental shelves to deep ocean floors, found in rivers, lakes and cave systems, with species even adapted to life on land. To advance and transform decapod palaeontology by sharing new findings and approaches, close scientific exchange between scientists, students and enthusiasts is necessary.

Comprising 26 oral presentations and 20 posters presented in two days of scientific sessions and followed by four fieldtrips, the symposium was staged by a Slovenian organising committee, consisting of Rok Gašparič (Oertijdmuseum, Boxtel), Luka Gale (Geological Survey of Slovenia, Faculty of Natural Sciences and Engineering, Ljubljana), Matija Križnar (Slovenian Museum of Natural History, Ljubljana), Boštjan Rožič (Faculty of Natural Sciences and Engineering, Ljubljana), Bogomir Celarc (Geological Survey of Slovenia, Ljubljana) and Matic Rifl (Charles University, Faculty of Science, Prague).

The reception and ice breaker took place on the first day (17th June 2019) at the Slovenian Museum of Natural History, where attendees were greeted by museum director Breda Činč Juhant and had a chance to visit the temporary exhibition on Slovenian fossil decapod crustaceans. The scientific part of the symposium was hosted by the Geological Survey of Slovenia. The scientific session was opened by words of the organising committee chairman, Rok Gašparič, and Geological Survey director, Miloš Bavec. Two days of scientific sessions (18th and 19th June 2019) were concluded in a spirit of good co-operation with relaxed informal discussions and plenty of opportunity for individual meetings in between the session breaks. We opened the first day with a keynote lecture by Adiël Klompmaker on "Evolutionary and ecological trends in decapods" and concluded with a poster session, whereas the second day was kick-started by keynote speaker Matúš Hyžný on the state-of-the-art and future directions in research on Paratethyan decapods. We concluded the scientific part of the symposium with a final address, in which Zaragoza (Spain) was chosen as the next venue of the 8th Symposium on Mesozoic and Cenozoic Decapod Crustaceans in 2022, followed by a dinner in one of Ljubljana's authentic Slovenian restaurants.

Weather throughout the symposium was wonderful, so there were no issues with conducting the final two days of the symposium (20th and 21st June), which were reserved for field trips to the four fossil decapod-bearing localities in Slovenia. On Thursday (20th June) we started our field trip at the Geological Survey in Ljubljana and travelled south to explore the decapod-rich, upper Eocene (Lutetian) deposits along the road Gračišče–Kubed, and visited a nearby 12th century church of the Holy Trinity at Hrastovlje to admire the famous 15th century frescoes of Dance of Death or *Dance Macabre*. In the afternoon, the virgin forests of Trnovo Plateu protected us from the heat and gave us the opportunity to observe the Upper Jurassic (Oxfordian) coral barrier reef preserved *in situ*. The reef complex is composed of sponges, corals and stromatoporids, but also diverse molluscs, echinoderms and frequent decapods are found between stromatoporid and corals framework, which enabled preferential preservation of delicate carapaces.

For the last day (Friday, 21st June) the delegates were transported through the Miocene Paratethys sea all the way back to the Middle Triassic Tethyan Ocean. The final excursion started with a visit to the active quarry of Lipovica in middle Miocene (Langhian) limestone, where we followed the safety regulations and explored the abundant outcrops for the remains of Miocene decapods and lucky finds of the charismatic Paratethyan crab *Tasadia carniolica*. The final destination was a visit to one of the most picturesque European glacial alpine valleys, Logarska Valley, where we visited an exhibition on Middle Triassic fossil fauna at Solčava and hiked to a nearby outcrop of Middle Triassic (Anisian) bituminous, thin-bedded limestones with vertebrate remains and shrimp fossils. The field trip was concluded with an enjoyable dinner accompanied by many good-natured discussions and forgings of future collaborations.

We cordially thank all participants for attending the 7thSymposium on Mesozoic and Cenozoic Decapod Crustaceans in Ljubljana and for presenting their latest research in the exciting field of palaeocarcinology. The organisation of the symposium would not have been possible

Fig. 1. Opening address by Rok Gašparič to participants of the 7th Symposium on Mesozoic and Cenozoic Decapod Crustaceans at the ice breaker evening in the Slovenian Museum of Natural History in Ljubljana (photo: Matija Križnar).

Fig. 2. Scientific session at the Geological Survey of Slovenia in Ljubljana. Oral presentation by René H.B. Fraaije on new advances in paguroid evolution (photo: Rok Gašparič).

Fig. 3. Poster session at the Geological Survey of Slovenia. Explanation of poster by Antonio De Angeli on homolid crabs of Italy (photo: Matija Križnar).

Fig. 4. Closing dinner on Wednesday 21st June at Sokol restaurant in Ljubljana. A toast to speedy recovery to Rodney Feldmann, who was not able to attend the symposium (photo: Barry van Bakel).

without a lot of hard and selfless work from all the colleagues in the organising committee. In addition, we would like to express our thanks to the following organisations for their support: the Geological Survey of Slovenia, the Slovenian Museum of Natural History and the Faculty of Natural Sciences and Engineering at the University of Ljubljana. Our sincere thanks to all volunteers and people who helped in the preparation of the symposium: Stanka Žibert, Valerija Majer and Matevž Novak (Geological Survey of Slovenia) for their organisational support, Andreja Žibrat Gašparič (University of Ljubljana, Faculty of Arts, Department of Archaeology) for thorough proofreading and editorial work on the abstract book, Tomaž Hitij (Dental School, Faculty of Medicine, University of Ljubljana) and Jure Žalohar (T-TECTO d.o.o.) for help on Triassic localities, Manca Hočevar (Slovenian Museum of Natural History) for support in preparation of the reception at the museum, Željko Pogačnik (Georudeko d.o.o.) for access to the Lipovica quarry, Alex Žagar for work on the symposium webpage design, as well as Anja Kocijančič, Kristina Peulič and Miha Marinšek for their logistic support during the symposium.


Fig. 5. Participants on the first-day field trip to Eocene exposures of Gračišče, led by Matija Križnar (photo: Rok Gašparič).


Fig. 6. Luka Gale explaining the geology of Jurassic reefal limestones in Trnovo Plateau (photo: Rok Gašparič).


Fig. 7. Željko Pogačnik explaining the geology and safety measures of collecting fossils from Miocene rocks at the Lipovica quarry (photo: Matija Križnar).


Fig. 8. Field trip participants collecting decapods from Triassic laminated limestones in the Logarska Valley (photo: Rok Gašparič).

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