New Early Jurassic thylacocephalan assemblage from the Western Carpathians in Slovakia

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Gerbe, A., Hyžný, M., and Schlögl, J. 2025. New Early Jurassic thylacocephalan assemblage from the Western Carpathians in Slovakia. *Acta Palaeontologica Polonica* 70 (3): 557–571.

Thylacocephalans (Euarthropoda: Pancrustacea) are extinct marine pancrustaceans characterised by a folded shield, with fossils known from the Upper Ordovician to the Upper Cretaceous, reaching a diversity peak in the Triassic. We described two new thylacocephalan taxa, *Dollocaris toarcica* sp. nov. and *Zazrivacaris jodorowskyi* gen. et sp. nov., from the lower Toarcian, Lower Jurassic black shales of the "Hrýzeň beds" of the Šariš Unit (Grajcarek Succession) exposed in Zázrivá, Slovakia. Thylacocephalans are an accessory element of an euarthropod association, dominated by dendrobranchiate shrimps. This occurrence represents not only the first record of thylacocephalans from Slovakia but also their first formal description from the Toarcian. *Dollocaris toarcica* sp. nov. is the third described species of its genus, previously known from the Middle Jurassic (Callovian) of France and Upper Jurassic (Tithonian) of Germany, expanding the stratigraphic span of the genus to the Lower Jurassic. The newly described genus *Zazrivacaris* shows morphological similarities with *Mayrocaris*, yet another genus known from the Upper Jurassic (Tithonian) of Germany. Considering current knowledge, we present a review of all known micro- and macro-structural patterns present on thylacocephalan shields. These structures appear to be unique to each genus and/or species and are therefore important for taxonomic evaluation.

Key words: Arthropoda, Thylacocephala, *Dollocaris*, *Zazrivacaris*, Lower Toarcian, Jurassic, Slovakia, Carpathians.

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Received 18 June 2024, accepted 1 July 2025, published online 10 September 2025.

Introduction

Thylacocephalans are among the most intriguing group of extinct marine pancrustaceans. They are characterised by a folded shield enclosing a major part of the body. Three pairs of sub-chelate raptorial appendages and large compound eyes suggest that at least some of these animals were likely predators (Schram et al. 1999; Vannier et al. 2006, 2016; Charbonnier et al. 2010, 2017; Broda and Zatoń 2017; Jobbins et al. 2020). Fossils of thylacocephalans have been known since the 19th century. Firstly, they were interpreted as representatives of Phyllocarida Packard, 1879 (Meek and Worthen 1868), Stomatopoda Latreille, 1816 (Hilgendorf 1885) or Mysida Haworth, 1825 (Van Straelen 1923). Discoveries made at the end of the 20th century, especially from Italy (Arduini et al. 1980; Pinna et al. 1982, 1985), Australia (Briggs and Rolfe 1983), France (Secretan and Riou 1983; Secretan 1985), and Germany (Polz 1994) helped to understand the unique systematic position of thylacocephalans among known arthropod groups and recognise them as probable representatives of the clade Pancrustacea Zrzavý & Štys, 1997 (Schram 2014; Schram and Koenemann 2022). A few decades later, our knowledge of these animals has significantly improved thanks to descriptions of soft part morphology and anatomy of their bodies (Charbonnier et al. 2010; Haug et al. 2014; Vannier et al. 2016; Jobbins et al. 2020; Laville et al. 2021a, 2023a), allowing for evaluation of taxonomic relationships of Thylacocephala within

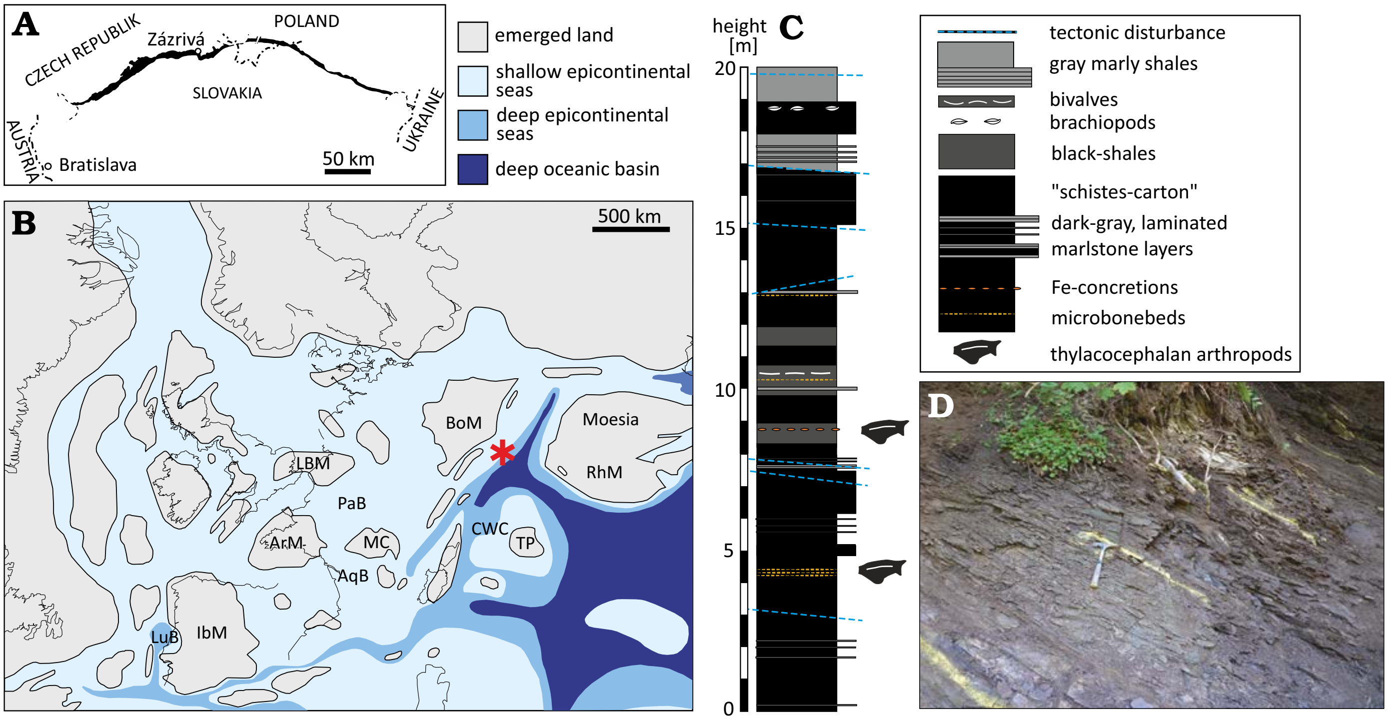


Fig. 1. **A**. Geographical location of the Zázrivá village. Dark area represents remains of the Pieniny Klippen Basin. **B**. Palaeogeographical position of the Hrýzeň section (asterisk) during Toarcian. AqB, Aquitaine Basin; ArM, Armorican Massif; BoM, Bohemian Massif; CWC, Central Western Carpathians; IbM, Iberian Massif; LBM, London-Brabant Massif; LuB, Lusitanian Basin; MC, Massif Central; PaB, Paris Basin; RhM, Rhodope Massif; TP, Tisza Plate. Map modified after Thierry (2000) and Dera et al. (2010). **C**. Middle part of the Hrýzeň section with the distribution of thylacocephalan fossils. **D**. The field photo showing typical black shale lithofacies bearing the crustacean remains. Level 9 marked by hammer, the succession is in overturned position, so the numbering descents towards the top of the outcrop.

euarthropods (e.g., Haug et al. 2014; Broda and Zatoń 2017; Laville et al. 2021b). In this respect, every new occurrence helps to add much needed data for understanding the evolution and diversity of these animals.

The known fossil record of Thylacocephala includes 70 species (Table 1) and spans from the Upper Ordovician (Van Roy et al. 2021) to the Upper Cretaceous (Hilgendorf 1885; Roger 1946; Schram et al. 1999; Lange et al. 2001; Charbonnier et al. 2017), reaching a diversity peak in the Triassic (Charbonnier and Brayard 2019). Thylacocephalan fossils have been found throughout the world, including Europe (e.g., Van Straelen 1923; Glaessner 1931; Arduini et al. 1980; Charbonnier et al. 2010; Broda and Zatoń 2017; Rak et al. 2018; Braig et al. 2019), Asia (Dames 1886; Roger 1946; Ehiro et al. 2015, 2019; Charbonnier et al. 2017; Ji et al. 2017, 2021; Ehiro and Kano 2024), Africa (Arduini 1990; Jobbins et al. 2020; Laville et al. 2021c), North America (e.g., Schram 1990; Hegna et al. 2014; Charbonnier and Brayard 2019; Laville et al. 2021a), and Australia (Briggs and Rolfe 1983; Haig et al. 2015).

The occurrence of Thylacocephala from the Lower Jurassic (Toarcian) of Slovakia reported herein not only represents the first report of these animals from the respective country but also the first formal description of Thylacocephala from the Toarcian. Previous report on thylacocephalans from the Toarcian by Williams et al. (2015) is limited to a mere statement without taxonomic evaluation or figures. Our contribution also refines the classification and morphological characterization of the shield structures of thylacocephalans, serving as a foundation for future studies on shield structures.

Institutional abbreviations.—SNM Z, Natural History Museum of Slovak National Museum in Bratislava, Slovakia.

Other abbreviations.—Aad, anterodorsal angle; Aav, anteroventral angle; Apd, posterodorsal angle; Apv, posteroventral angle; Ha, anterior shield height; Hmax, maximum shield height; Hp, posterior shield height; L, length; Ls, maximum shield length.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in Zoobank: urn:lsid:zoobank.org:pub:1110D1FC-DDC7-42D6-84C8-5AE1446E4ED3.

Geological setting

The material forming the basis of this study was collected from a natural outcrop on the root of the Hrýzeň Hill (GPS N49.283299°, E19.175561°; Zázrivá district, Slovakia; Fig. 1). The Hrýzeň Hill is a narrow ridge on the left side of the Kozinský potok Brook Valley (Kozinská settlement), ca. 800 m east-northeast of the Zázrivá Centre and 300 m east of the crossroad Končitá-Havrania-Kozinská.

The ridge is predominantly formed by grey spotted marly limestones (Fleckenmergel-Fleckenkalk facies) that most probably belong to the Lower–Middle Jurassic Krempachy Marl Formation (equivalent of the Allgäu Formation). In the middle part of the ridge, there are signs of old mining attempts in the Toarcian black, brown weathered, Mn-bearing shales. In addition, clasts of micaceous quarzitic sandstones and black crinoidal limestones occur in the debris, possibly representing allodapic limestones from the upper part of the Middle Jurassic Szlachtowa Formation. The whole succession has been tentatively affiliated with the Šariš Unit (Grajcarek Succession) by Plašienka et al. (2021).

The black shale sequence at the washed-out bank of the Kozinský potok Brook was studied by Schlögl et al. (2012) and later in more detail by Suan et al. (2018). The studied section is 36 meters thick and is in a stratigraphically reversed position, with a dip of strata oriented to the SW. The lower and middle parts of the section are essentially composed of dark grey to black, finely laminated shales (black shales or "schistes-carton"), locally interrupted by dark grey laminated siltstone-mudstone beds. Black shales are locally rich in macrofauna, including ammonites, soft bodied cephalopods (Schlögl et al. 2012), bivalves, arthropods, echinoids, and fish remains. Marls in the upper part of the succession are grey in colour. Based on ammonites and calcareous nannofossils, the early Toarcian age was proposed for this sequence and was related to the Toarcian Oceanic Anoxic Event (T-OAE). Informally, this sequence is designated as the "Hrýzeň beds" (Plašienka et al. 2021: fig. 2.6). The locality records organic-rich sedimentation at the margin of NW-European shelf (Suan et al. 2018).

Ammonites and calcareous nannofossils provide the basis for the biostratigraphy of the black shales (Suan et al. 2018). The co-occurrence of scarce *Eleganticeras elegans* Sowerby, 1815, and *Eleganticeras exaratum* Young & Bird, 1828, together with common *Hildaites* ex. gr. *murleyi–levisoni* in the middle part of the section, indicates the lower Toarcian Exaratum Subzone of the Serpentinum Zone. Overlying grey marls are poor in ammonites; however, *Hildaites* cf. *subserpentinus* and *Harpoceras* ex. gr. *falciferum* indicate the Falciferum Subzone of the late Serpentinum Zone. The first occurrence (FO) of calcareous nannofossil *Carinolithus superbus* Deflandre, 1954, marks the base of the NJ6 zone and the FO of *Discorhabdus striatus* Rood et al., 1971 characterises the base of the NJ7 zone (Bown and Cooper 1998; Mattioli and Erba 1999). Thylacocephalan pancrustaceans occur in two stratigraphic intervals, an older one between 4.1 m and 4.33 m and a slightly younger one between 8.4 m and 10.4 m (Fig. 1C). *Zazrivacaris jodorowskyi* gen. et sp. nov. comes only from the younger interval, whereas *Dollocaris toarcica* sp. nov. comes from both intervals. While only two specimens of *D. toarcica* sp. nov. were recovered from the 4.1–4.33 m interval, the vast majority of the thylacocephalan material, including both newly identified species, originates from the 8.4–10.4 m interval. The deposition of the intervals with thylacocephalans took place under sulphidic and anoxic conditions (euxinia) interrupted by brief events of improved oxygenation (Suan et al. 2018).

Material and methods

Fossils were collected during several field campaigns organized by the Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University in Bratislava. The material consists of 18 specimens representing laterally flattened near complete shields, or fragments preserved in black shales. The specimens were further prepared under a stereomicroscope using a vibrating needle and later also preparatory needles.

Samples have been observed and documented in detail with a Leica DVM6 digital microscope with two different objectives: a PLANAPO FOV 12.55 and a PLANAPO FOV 43.75 with a polarized light. Additional documentation was done by Leica M205 C with a PLANAPO 0.63. An attempt to document fossils using the UV light was unsuccessful; the specimens from the studied locality do not exhibit UV fluorescence.

The morphological terms adopted in descriptions follow Laville et al. (2021b) and are provided in Fig. 2A. We refrained from using "anterior spine"; instead, we used the term "rostrum" which is widely used in descriptions of thylacocephalan shield (e.g., Charbonnier et al. 2017; Rak et al. 2018; Laville et al. 2021c). Measurements were made digitally with ImageJ and follow Laville et al. (2021b). Because the nature of the shield structures of *D. toarcica* sp. nov. is

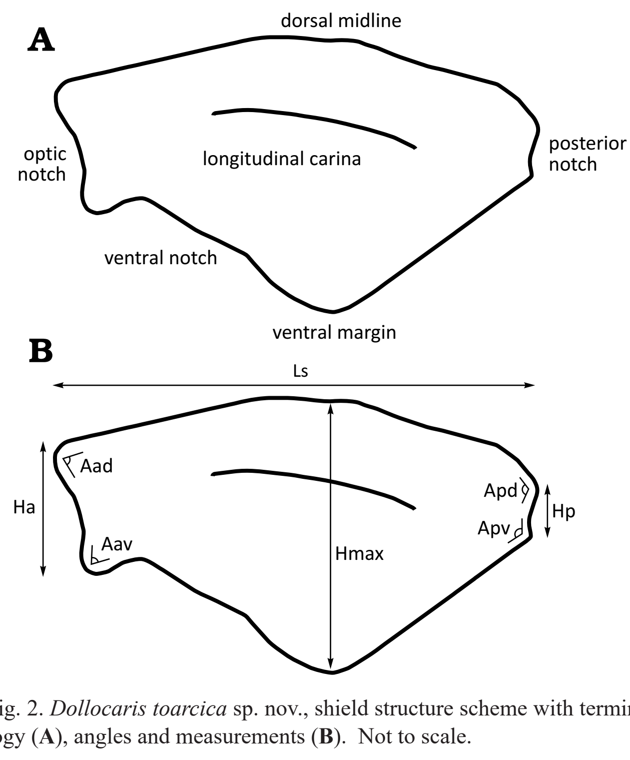


Fig. 2. *Dollocaris toarcica* sp. nov., shield structure scheme with terminology (**A**), angles and measurements (**B**). Not to scale.

Table 1. Species of Thylacocephala described to date with notion on the presence/absence of micro-/macro-structures. – indicates a true absence; × indicates that shield structures have not been investigated.

Species	Micro-structures	Macro-structures	Age	Country	References
Bohemiacaris libori Van Roy et al., 2021	×	–	Late Ordovician	Czech Republic	Van Roy et al. 2021
Pseudoprotozoea irenae Van Roy et al., 2021	×	–	Late Ordovician	Czech Republic	Van Roy et al. 2021
Ainiktozoon loganense Scourfield, 1937	×	–	Llandovery	Scotland	Van der Brugghen et al. 1997
Thylacares brandonensis Haug et al., 2014	×	×	Llandovery	USA	Haug et al. 2014
Concavicaris desiderata (Barrande, 1872)	×	–	Early Devonian	Czech Republic	Chlupáč 1963
Concavicaris sinuata (Meek & Worthen, 1868)	scale	–	Pennsylvanian	USA	Meek and Worthen 1868; Zangerl and Richardson 1963; Briggs and Rolfe 1983; Schram 1990; Rak et al. 2018; Broda et al. 2020
Concavicaris campi Briggs & Rolfe, 1983	tube-like	carina(e)	Late Devonian	Australia	Briggs and Rolfe 1983; Broda et al. 2020
Concavicaris elytroides (Meek, 1812)	–	ridges/carina(e)	Late Devonian–Mississippian	USA	Meek 1871, 1875; Cooper 1932
Concavicaris glenisteri Briggs & Rolfe, 1983	tube-like	carina(e)/pits	Late Devonian	Australia	Briggs and Rolfe 1983; Broda et al. 2020
Concavicaris incola Chlupáč, 1963	scale	–	Late Devonian	Czech Republic	Chlupáč 1963; Rak et al. 2018; Broda et al. 2020
Concavicaris martinae Broda et al., 2020	polygonal/ setal lumina/ grooves	carina(e)	Late Devonian	Czech Republic	Broda et al. 2020
Concavicaris milesi Briggs & Rolfe, 1983	scale/ setal lumina	ridges/carina(e)	Late Devonian	Australia	Briggs and Rolfe 1983; Broda et al. 2020
Concavicaris pikae Zatoń et al., 2014	polygonal/ setal lumina/ tube-like	carina(e)	Late Devonian	Poland	Broda et al. 2015; Broda and Zatoń 2017; Broda et al. 2020
Concavicaris playfordi Briggs & Rolfe, 1983	polygonal	carina(e)/pits	Late Devonian	Australia	Briggs and Rolfe 1983; Broda et al. 2020
Concavicaris submarinus Jobbins et al., 2020	polygonal	depression(s)	Late Devonian	Morocco	Jobbins et al. 2020
Concavicaris woodfordi (Cooper, 1932)	×	depression(s)	Late Devonian	USA	Cooper 1932; Briggs and Rolfe 1983; Laville et al. 2023b
Concavicaris woodruffensis Broda et al., 2020	polygonal/ setal lumina	carina(e)	Late Devonian	USA	Broda et al. 2020
Harrycaris whittingtoni Briggs and Rolfe, 1983	scale/ setal lumina	ridges/ carina(e)	Late Devonian	Australia	Briggs and Rolfe 1983; Broda et al. 2020
Suttropocaris bottkei Koch et al., 2003	×	carina(e)	Late Devonian	Germany	Koch et al. 2003
Concavicaris bradleyi (Meek, 1871)	polygonal	carina(e)	Mississippian	USA	Meek 1871, 1875; Briggs and Rolfe 1983; Rak et al. 2018
Paraconcavicaris viktoryni Rak et al., 2018	linear	ridges/carina(e)	Mississippian	Czech Republic	Rak et al. 2018; Broda et al. 2020
Concavicaris georgeorum Schram, 1990	×	carina(e)	Pennsylvanian	USA	Schram 1990; Laville et al. 2021a
Convexicaris mazonensis Schram, 1990	×	carina(e)	Pennsylvanian	USA	Schram 1990; Laville et al. 2021a
Eodollocaris keithflinti Laville et al., 2021a	×	tubercules	Pennsylvanian	USA	Laville et al. 2021a
Ankitokazocaris acutirostris Arduini, 1990	linear	pore(s)/tubercules/ Groove(s)	Early Triassic	Madagas-car	Arduini 1990; Laville et al. 2021c
Ankitokazocaris bandoi Ehiro et al., 2015	×	carina(e)	Early Triassic	Japan	Ehiro et al. 2015
Ankitokazocaris chaohuensis Ji et al., 2017	×	carina(e)	Early Triassic	China, Japan	Ji et al. 2017; Ehiro et al. 2019; Laville et al. 2021c
Ankitokazocaris parva (Ehiro et al., 2019)	×	pits	Early Triassic	Japan	Ehiro et al. 2019
Ankitokazocaris triassica (Charbonnier & Brayard, 2019)	×	ridges/carina(e)/ groove(s)	Early Triassic	USA	Charbonnier and Brayard 2019; Laville et al. 2021c
Diplacanthocaris chaohuensis Ji et al., 2021	×	–	Early Triassic	China	Ji et al. 2021
Ankitokazocaris utatsuensis Ehiro et al., 2015	×	ridges	Early Triassic	Japan	Laville et al. 2021c
Ligulacaris parisiana Charbonnier & Brayard, 2019	×	carina(e)	Early Triassic	USA	Charbonnier and Brayard 2019; Laville et al. 2021c
Microcaris rectilineatus Ji et al., 2021	×	ridges/carina(e)	Early Triassic	China	Ji et al. 2021
Paraostenia ambatolokobensis (Arduini, 1990)	×	ridges/carina(e)/ furrow(s)	Early Triassic	Mada-gascar	Arduini 1990; Laville et al. 2021c, 2024b
Parisicaris naoyai Ehiro & Kano, 2024	×	ridges	Early Triassic	Japan	Ehiro and Kano 2024
Yangzicaris xiangxiensis Shen, 1983	×	carina(e)/tubercules	Middle Triassic	China	Shen 1983

Species	Micro-structures	Macro-structures	Age	Country	References
Ferrecaris magransi Calzada & Mañé, 1993	×	ridges	Middle Triassic	Spain	Calzada and Mañé 1993
Atropicaris lintveri Laville et al., 2024a	×	ridges/carina(e)/ tubercules	Middle Triassic	Slovenia	Laville et al. 2024a
Kamnikaris cemazevkaensis Laville et al., 2024a	×	ridges	Middle Triassic	Slovenia	Laville et al. 2024a
Ankitokazocaris lariensis Ji & Tintori, 2024	×	carina(e)	Middle Triassic	Italy	Ji and Tintori 2024
Stoppanicaris grignaensis Ji & Tintori, 2024	×	–	Middle Triassic	Italy	Ji and Tintori 2024
Microcaris minuta Pinna, 1974	×	ridges/carina(e)	Late Triassic	Italy	Pinna 1974, 1976; Arduini 1988; Dalla Vecchia 1993; Dalla Vecchia and Muscio 1990
Microcaris ajdovskae Laville et al., 2024b	×	ridges	Late Triassic	Slovenia	Laville et al. 2024b
Paraostenia striata (Glaessner, 1931)	×	ridges/tubercules/ furrow(s)/ groove(s)	Late Triassic	Austria	Glaessner 1931; Laville et al. 2024b
Austriocaris carinata Glaessner, 1931	×	carina(e)/ punctuations/ tubercules/groove(s)	Late Triassic	Austria	Glaessner 1931; Forchielli and Pervesler 2013; Laville et al. 2024b
Clausocaris pinnai Arduini, 1992	×	–	Late Triassic	Italy	Arduini 1992; Dalla Vecchia 2012
Atropicaris rostrata Arduini & Brasca, 1984	×	ridges/carina(e)	Late Triassic	Italy	Arduini and Brasca 1984; Arduini 1988
***Dollocaris toarcica* sp. nov.**	–	ridges/carina(e)	Early Jurassic	Slovakia	this study
***Zazrivacaris jodorowskyi* gen. et sp. nov.**	–	–	Early Jurassic	Slovakia	this study
Ostenocaris cypriformis Arduini et al., 1980	×	carina(e)	Early Jurassic	Italy	Arduini et al. 1980; Pinna et al. 1985; Alessandrello 1991
Austriocaris secretanae Laville et al., 2023a	×	ridges/carina(e)/ pore(s)	Middle Jurassic	France	Laville et al. 2023a
Dollocaris ingens Van Straelen, 1923	lattice organs?	ridges/carina(e)	Middle Jurassic	France	Van Straelen 1923; Secretan and Riou 1983; Secretan 1985; Charbonnier et al. 2010; Vannier et al. 2016
Kilianicaris lerichei Van Straelen, 1923	×	carina(e)/pore(s)/ groove(s)/ depression(s)	Middle Jurassic	France	Van Straelen 1923; Secretan and Riou 1983; Secretan 1985; Charbonnier et al. 2020; Laville et al. 2023a
Ostenocaris ribeti (Secretan, 1985)	×	carina(e)/tubercules	Middle Jurassic	France	Secretan 1985; Laville et al. 2023a
Paraclausocaris harpa Laville et al., 2023a	×	ridges/carina(e) pore(s)/serrations/ depression(s)/ groove(s)/hump	Middle Jurassic	France	Laville et al. 2023a
Paraostenia voultensis Secretan, 1985	×	carina(e)/pore(s)/ punctuations/ furrow(s)/hump	Middle Jurassic	France	Secretan 1985; Laville et al. 2023a
Clausocaris lithographica Oppenheim, 1888	×	–	Late Jurassic	Germany	Polz 1989, 1990, 1992; Haug et al. 2014; Laville et al. 2021b
Dollocaris michelorum Polz, 2001	×	ridges/carina(e)	Late Jurassic	Germany	Polz 2001
Falcatacaris bastelbergeri Braig et al., 2019	×	carina(e)	Late Jurassic	Germany	Braig et al. 2019
Mayrocaris bucculata Polz, 1994	–	ridges/carina(e)/ pore(s)	Late Jurassic	Germany	Polz 1994, 1997; Haug et al. 2014; Laville et al. 2021b
Polzia eldoctorensis Hegna et al., 2014	×	–	mid-Cretaceous	USA	Hegna et al. 2014
Victoriacaris muhiensis Hegna et al., 2014	×	–	mid-Cretaceous	USA	Hegna et al. 2014
Globulocaris garassinoi Charbonnier et al., 2017	×	–	mid-Cretaceous	Lebanon	Charbonnier et al. 2017
Paradollocaris vannieri Charbonnier in Charbonnier et al., 2017	×	carina(e)/ punctuations	mid-Cretaceous	Lebanon	Charbonnier et al. 2017
Thylacocaris schrami Audo & Charbonnier in Charbonnier et al., 2017	×	punctuations	mid-Cretaceous	Lebanon	Charbonnier et al. 2017
Hamaticaris damesi (Roger, 1946)	lattice organs/ tube-like	carina(e)/ punctuations/ groove(s)/pits	Late Cretaceous	Lebanon	Schram et al. 1999; Lange and Schram 2002; Charbonnier et al. 2017; Broda et al. 2020
Keelicaris deborae Teruzzi & Charbonnier in Charbonnier et al., 2017	×	ridges/carina(e)/ punctuations	Late Cretaceous	Lebanon	Charbonnier et al. 2017
Protozoea hilgendorfi Dames, 1886	lattice organs/ tube-like	pore(s)	Late Cretaceous	Lebanon	Schram et al. 1999; Lange and Schram 2002; Charbonnier et al. 2017; Broda et al. 2020
Pseuderichthus cretaceus Dames, 1886	×	pore(s)	Late Cretaceous	Lebanon	Schram et al. 1999; Lange and Schram 2002; Charbonnier et al. 2017
Thylacocephalus cymolopos Lange et al., 2001	×	pore(s)	Late Cretaceous	Lebanon	Lange et al. 2001; Lange and Schram 2002

uncertain (ornamentation vs. integumental hemolymphatic circulatory network), we are using the term "shield structure" rather than "shield ornamentation".

The material presented herein is deposited in the Natural History Museum of Slovak National Museum in Bratislava, Slovakia.

Systematic palaeontology

Euarthropoda Lankester, 1904

Thylacocephala Pinna et al., 1982

Genus *Dollocaris* Van Straelen, 1923

Type species: Dollocaris ingens Van Straelen, 1923, by monotypy; Callovian, Middle Jurassic, France (la Voulte-sur-Rhône).

Original diagnosis (Secretan and Riou 1983).—The shield covers almost the entire body, except for a caudal mass that slightly protrudes posteriorly. It is approximately twice as long as it is wide, with a height roughly equal to its width. The lower lateral margins fold strongly over the sternal side. The shield is bordered by a marginal groove along its entire outline.

A longitudinal dorsal median groove extends along its full length. A short, pointed rostrum, slightly curved downward, extends from a medio-longitudinal ridge, which becomes more elevated towards the posterior before thinning abruptly and ending in a sudden step at the posterior third of the shield length. On either side of the rostrum, a very large notch in the anterior margin, terminating below in a strong spine, accommodates an extremely large, apparently sessile compound eye, which arises from a broad peduncle located beneath the shield. A transverse longitudinal ridge marks the shield laterally. A strong oblong protuberance elevates its lower region.

On either side of a short posterior median dorsal spine, a notch, less pronounced than that of the anterior margin, allows the caudal mass of the body to extend beyond the shield. The body consists of several differentiated tagmata. The anteroventral margin of the shield is the point of emergence for two categories of appendages. The first category consists of short appendages, presumed to be cephalic. The second category, presumed to be thoracic, consists of long appendages that increase in size posteriorly, bend forward, and are laterally superimposed. The last three are believed to end in spiniform pincers. A branchial chamber extends above these appendages under the shield, containing large, lamellar gills, with at least eight pairs.

The posteroventral margin is the point of origin for filamentous appendages emerging from strong, aligned plates that continue onto the caudal mass protruding beyond the shield. The posterior end of the body is known only by the presence of a short, apparently unpaired spine and indistinct foliaceous scales. No traces of a furca have been observed. [Translated from French from Secretan and Riou 1983: 78–79.]

Emended diagnosis.—Shield outline pentagonal to hexagonal in lateral view, approximately twice as long as hight, with median carina; optic notch higher than posterior notch; rostrum, if present, sharp and slightly curved downward; anterior midline convex; posterior notch round and concave; posterodorsal and posteroventral corners sharp; posteroventral margin descending about halfway up the shield; anteroventral margin ascending anteriorly; ventral margin with more- or less-pronounced ventral notch.

Remarks.—Ventral notch observed in the material from Zázrivá are unique to two genera: *Dollocaris* Van Straelen, 1923, and *Mayrocaris* Polz, 1994. *Dollocaris* differs from *Mayrocaris* in several aspects: its shield is almost twice as long as it is high, with a concave posterior notch and with a ventral margin, which is less curved anteriorly than in *Mayrocaris*. The new species presented further below exhibits a set of characters suggesting its attribution to *Dollocaris*.

Dollocaris can be distinguished from other thylacocephalan genera by several distinct shield features. *Dollocaris* possesses a ventral notch, which is missing in *Ankitokazocaris* Arduini, 1990, *Clausocaris* Oppenheim, 1888, *Concavicaris* Rolfe, 1961, *Kilianicaris* Van Straelen, 1923, *Ligulacaris* Charbonnier & Brayard, 2019, *Ostenocaris* Arduini et al., 1980, *Paraostenia* Secretan, 1985, and *Yangzicaris* Shen, 1983. Moreover, *Dollocaris* exhibits a less pronounced rostrum than that in *Falcatacaris* Braig et al., 2019, *Microcaris* Pinna, 1974, and *Ferrecaris* Calzada &Mañé, 1993.

Stratigraphic and geographic range.—Toarcian to Tithonian, Lower Jurassic to Upper Jurassic; France, Germany, Slovakia.

Dollocaris toarcica sp. nov.

Figs. 3, 4.

Zoobank LSID: urn:lsid:zoobank.org:act:31AF80D8-9941-4396-A1A7-71AD192F12CF.

Etymology: In reference to the stratigraphic occurrence (Toarcian stage of the Lower Jurassic) of the species.

Type material: Holotype SNM Z 41680, complete shield. Paratypes SNM Z 41034–41041, 41683, nine shields in various states of completeness, from the type locality and horizon.

Type locality: The Hrýzeň Hill, Zázrivá district, Slovakia.

Type horizon: Serpentinum Zone (Exaratum Subzone), lower Toarcian, Lower Jurassic.

Material.—Type material and SNM Z 41042–41046, 41682, six shields of fragmentary nature, all from the type locality and horizon.

Diagnosis.—Shield outline hexagonal in lateral view; anteroventral margin with ventral notch extending from anteroventral corner to posteroventral margin; optic notch concave without rostrum; anteroventral corner rounded; posterior notch small and concave.

Description.—Shield outline hexagonal in lateral view, longer than height (Ls/Hmax mean ratio: 1.99; min: 1.76; max: 2.23). Optic notch large and not well pronounced (Ha: mean

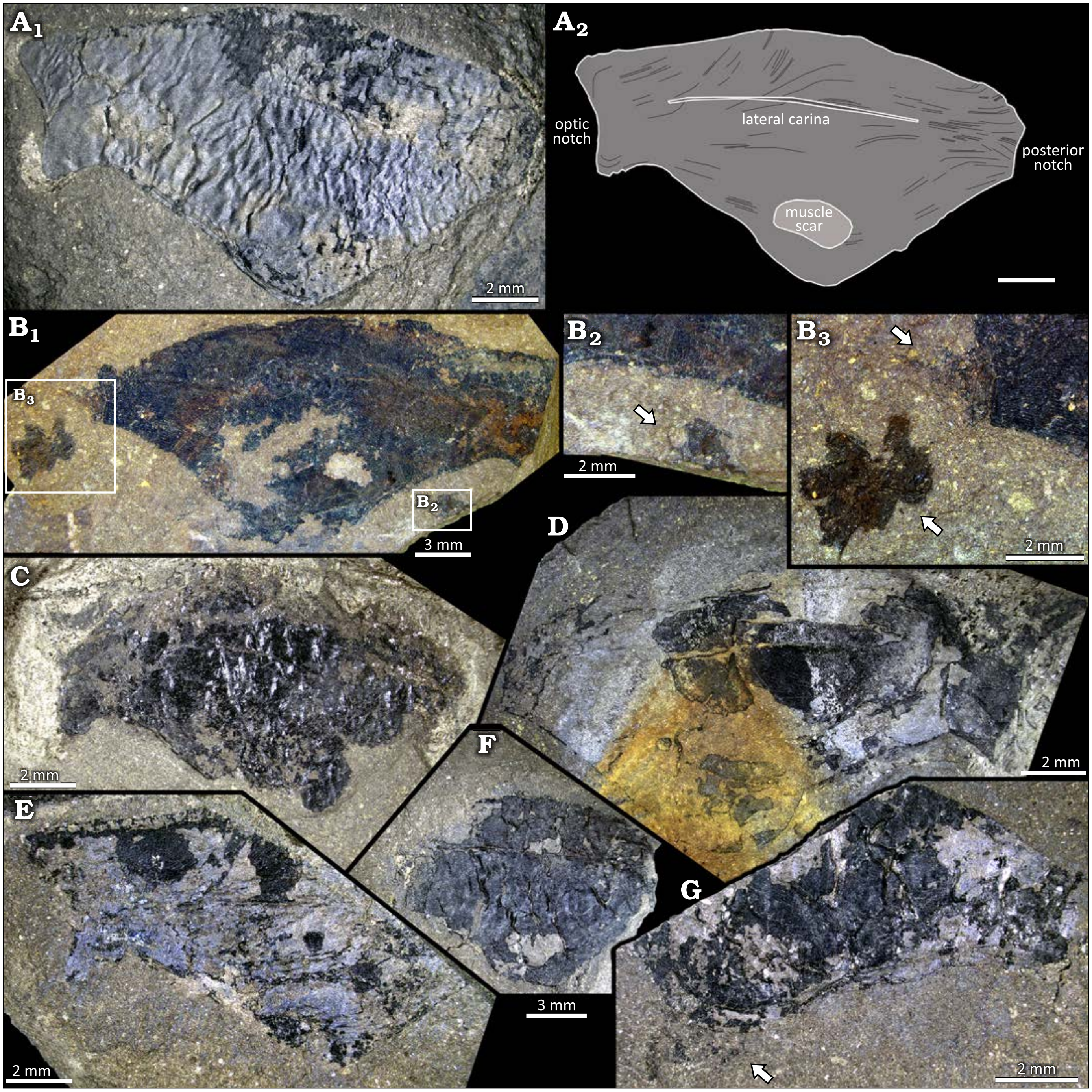


Fig. 3. Thylacocephalan arthropod *Dollocaris toarcica* sp. nov. from the lower Toarcian, Lower Jurassic of the Hrýzeň section, Zázrivá, Slovakia. **A**. Holotype SNM Z 41680, photograph (A_1), line drawing (A_2). **B**. Paratype SNM Z 41035; general view (B_1), close-up pictures of potential anterior trunk appendages (B_2), close-up pictures of potential posterior trunk appendages (B_3). **C**. Paratype SNM Z 41038. **D**. Paratype SNM Z 41043. **E**. Paratype SNM Z 41036. **F**. Paratype SNM Z 41046. **G**. Paratype SNM Z 41683. Arrows indicate anterior (B_2, G) and postarior (B_3) possible trunk appendages.

4.57 mm; min 3.70 mm; max 5.76 mm). Anteroventral corner rounded with mean angle 57° (min 41.88°; max 70.33°). Anteroventral margin with well-developed square-shaped ventral notch. Posteroventral margin slightly concave and ascending posteriorly. Posteroventral corner sharp (Apv: mean 105.95°; min 93.28°; max 114.311°). Small posterior notch (Hp: mean 1.83 mm; min 1.16 mm; max 2.30 mm) rounded and concave. Posterodorsal corner sharp (mean 111.31°; min 83.81°; max 133.80°). Dorsal midline convex. Anterodorsal corner with mean angle 56° (min 41.89°; max 71.55°). Rounded muscle scar located at mid-length close to ventral margin. Shield with longitudinal carina taking approximately two thirds of shield length. Presence of curved ridges arranged largely sub-horizontally that could be interpreted as an integumental hemolymphatic circulatory network (see Discussion). Anteriorly, ridges converging at

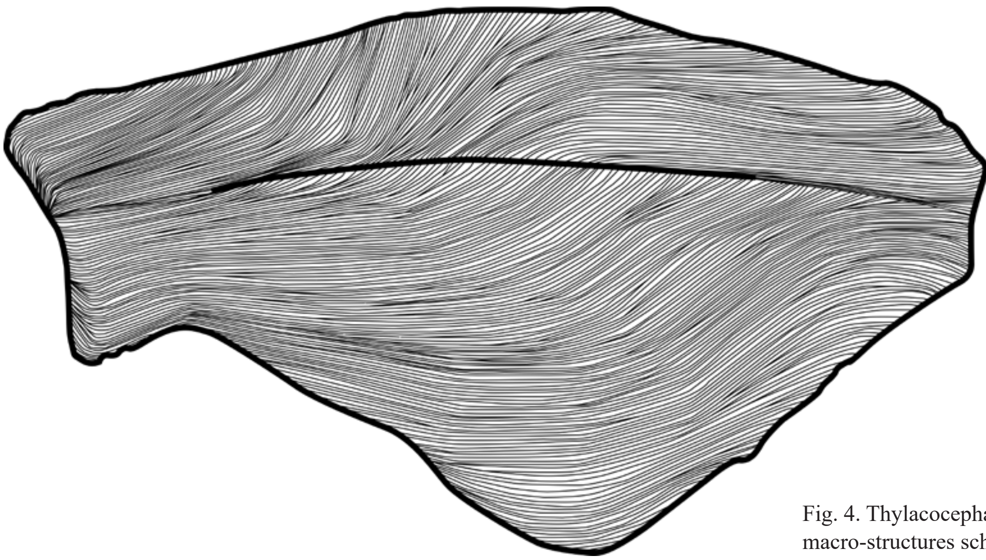


Fig. 4. Thylacocephalan arthropod *Dollocaris toarcica* sp. nov., macro-structures scheme of subparallel lines. Not to scale.

centre of shield; posteriorly, ridges converging to ventral margin; ventrally, ridges parallel with ventral margin. On dorsal part, near to carina, ridges end on other ridges. On ventral part, some ridges start in middle part of shield, near to carina.

Remarks.—*Dollocaris toarcica* sp. nov. differs from its congeners, *Dollocaris ingens* Van Straelen, 1923, and *Dollocaris michelorum* Polz, 2001, in several aspects. The shield of both previously described congeners are pentagonal and possess a well-developed rostrum, which is hexagonal, and the rostrum is absent in the species described herein. The anterior and posterior notches are less pronounced in *D. toarcica* sp. nov. than in *D. michelorum* and *D. ingens.* The latter shows an abrupt drop (i.e., dorsal carina) in the posterior third of the shield's length that is absent in the new species. The ventral notch in *D. michelorum* is very slightly pronounced.

Clearly recognizable appendages and eyes are not preserved in the studied material of *Dollocaris toarcica* sp. nov., thus, these features cannot be readily compared with those in *D. ingens*. Nevertheless, some specimens of *D. toarcica* sp. nov. exhibit poorly preserved structures close to the anterior and posterior notches (SNM Z 41035, Fig. 3B) which could represent remains of anterior raptorial and posterior trunk appendages.

Present material is the first known occurrence of *Dollocaris* from Slovakia, while all previously reported occurrences are known from France (Van Straelen 1923; Secretan and Riou 1983; Secretan 1985; Charbonnier et al. 2010; Vannier et al. 2016) and Germany (Polz 2001; Laville et al. 2021b). *Dollocaris ingens* and *D. michelorum* are known from the Middle Jurassic (Callovian) and Upper Jurassic (Tithonian), respectively; thus, *D. toarcica* sp. nov. from the Lower Jurassic (Toarcian) of Slovakia is the oldest occurrence of the genus and represents a significant extension of its known geographic range and stratigraphic span.

Stratigraphic and geographic range.—Type horizon and locality only.

Genus *Zazrivacaris* nov.

Zoobank LSID: urn:lsid:zoobank.org:act:4411883A-DE40-4C8D-BF92-683A23E30FE1.

Type species: *Zazrivacaris jodorowskyi* sp. nov., by monotypy; Toarcian, Lower Jurassic, Zázrivá, Slovakia.

Etymology: In reference to the settlement of Zázrivá, from where the type material originates. Gender of the genus: feminine.

Diagnosis.—As for the type species (by monotypy).

Remarks.—*Zazrivacaris* gen. nov. can be distinguished from *Ankitokazocaris*, *Falcatacaris*, *Kilianicari*s, *Microcaris*, *Ferrecaris*, and *Concavicaris* by the absence of a rostrum. The newly erected genus differs from *Clausocaris* by the overall morphology of the shield, which is cone-shaped in *Clausocaris*, while it is subtrapezoid in *Zazrivacaris* gen. nov. *Paraostenia* and *Ostenocaris* differ from *Zazrivacaris* gen. nov. by the rounded anteroventral and posteroventral corner and by the concave anterior margin, respectively. *Austriocaris* Glaessner, 1931, and *Paraclausocaris* Laville et al., 2023a, differ from the new genus by an outline of the optic notch, which is concave and asymmetric. In *Austriocaris*, the optic notch is restricted to the ventral portion of the anterior margin, whereas in *Zazrivacaris* gen. nov. it extends along both the ventral and dorsal margins. Additionally, the dorsal midline in *Austriocaris* is straight, while in *Zazrivacaris* gen. nov. the posterior third exhibits a slight downward slope. *Paraclausocaris* is further distinguished by the presence of small sinuous ridges on the carapace shield, a feature absents in the new genus. *Zazrivacaris* gen. nov. differs from *Dollocaris* by the morphology of the ventral and dorsal margins, as well as the absence of a ventral notch. The overall morphology of the shield of *Zazrivacaris* gen. nov. is similar to *Mayrocaris*, indicating a possible close relationship between the two genera. However, the absence of a ventral notch, rounded and concave posterior notch and the anteroventral angle with rounded outline support the erection of a new genus.

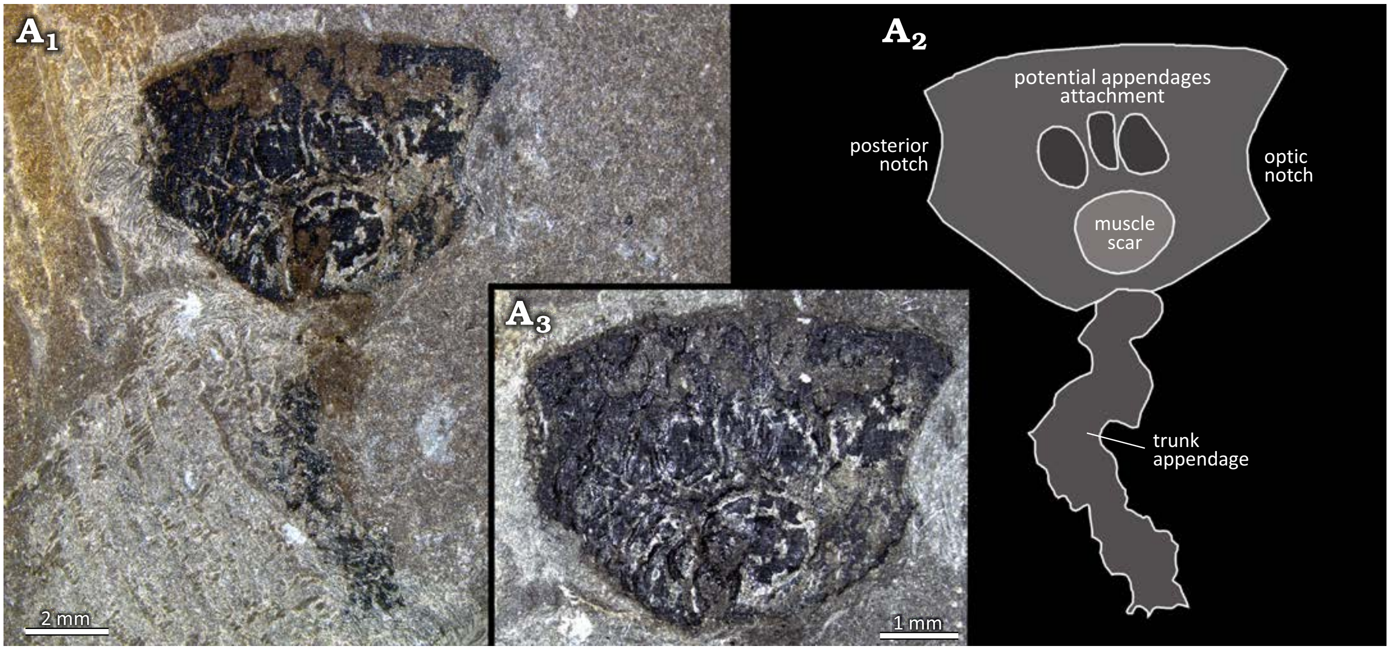


Fig. 5. Thylacocephalan arthropod *Zazrivacaris jodorowskyi* gen. et sp. nov. holotype (SNM Z 41047) from the lower Toarcian, Lower Jurassic of the Hrýzeň section, Zázrivá, Slovakia. Photograph (A_1), line drawing (A_2), close-up picture of the shied (A_3).

Stratigraphic and geographic range.—Type locality and horizon only.

Zazrivacaris jodorowskyi sp. nov.

Fig. 5.

Zoobank LSID: urn:lsid:zoobank.org:act:96376AC1-D08A-4E72-9A16-52CAA3A3BDA8.

Etymology: In honour of Alejandro Jodorowsky (born 17.02.1929), a Chilean and French avant-garde filmmaker and comic book writer, whose surreal imagery is reminiscent of uncommon morphology of thylacocephalan pancrustaceans.

Type material: Holotype SNM Z 41047, near-complete shield. Paratype SNM Z 41681, one fragmented shield, from the type locality and horizon.

Type locality: The Hrýzeň Hill, Zázrivá district, Slovakia.

Type horizon: Serpentinum Zone (Exaratum Subzone), lower Toarcian, Lower Jurassic.

Diagnosis.—Shield subtrapezoid in lateral view, optic notch concave, asymmetric and not clearly delineated; two thirds of dorsal midline straight, last third descending slightly posteriorly; posterior notch symmetrical and concave; rostrum absent; posteroventral margin straight and descending at 39° to central part of shield, from here anteroventral margin straight rising at 37° anteriorly. Large raptorial appendage as long as shield length.

Description.—Shield small, with subtrapezoid outline in lateral view (Ls 8.8 mm; Hmax 6.2 mm; Ls/Hmax ratio 1.4); asymmetrical optic notch (Ha 3.97 mm) taking up almost two thirds of maximum shield height, absence of rostrum. Anterodorsal angle sharp (Aad 89.26°). First two thirds of dorsal midline straight, last third descending slightly posteriorly. Posterodorsal angle sharp (Apd 81.64°). Posterior notch symmetrical and concave (Hp 2.60 mm). Posteroventral angle sharp (Apv 108.19°), posteroventral margin straight and descending at 39° anteriorly. Anteroventral margin rising to 37° anteriorly. Muscle scar very large. Potential location where appendages were attached visible above muscle scar. Antero ventral angle sharp (Aav 103.79°). Raptorial appendage poorly preserved (L 8.78 mm), indistinct delimitation between each appendage element.

Remarks.—The asymmetric and concave optic notch, symmetric and concave posterior notch, two thirds of dorsal midline straight, last third descending slightly posteriorly, the ventral margin subdivided into an anterior sub-horizontal part, and a posterior part slightly descending anteroventrally, absence of rostrum and the large appendages represent a unique combination of characters warranting a designation of a new genus. The general morphology of the shield is somewhat similar to *Ankitokazocaris chaohuensis* Ji et al., 2017, from the Triassic of China. However, our specimen presents Ls/Hmax ratio of 1.4, while it is 2.0 in *A. chaohuensis* (Ji et al. 2017). The anteroventral and the posteroventral margins of our specimen are of approximately the same size (anteroventral margin: 4.5 mm, posteroventral margin: 4.7 mm), while *A. chaohuensis* exhibits a shorter posteroventral margin (Ji et al. 2017). In our material, anterior and medial ventral margins form an angle of 107°, while in *A. chaohuensis* the angle is 125–145° (Ji et al. 2017). Moreover, *Zazrivacaris jodorowskyi* gen. et sp. nov. has a concave posterior notch, while *A. chaohuensis* has a straight posterior margin.

Another morphologically similar species is *Mayrocaris bucculata* Polz, 1994, which, however, differs in the presence of ventral notch and sub-quadratic posterior notch. The mean value of the Apd in *M. bucculata* (Apd 81.68°; Laville et al. 2021b) is similar to the mean value in *Zazrivacaris* *jodorowskyi* gen. et sp. nov (Apd 81.64°). The Hp is 2.6 mm in both species (Laville et al. 2021b; this study). The Ls/Hmax ratio is also quite similar, the mean ratio is 1.6 mm in *M. bucculata* (Laville et al. 2021b) and 1.4 in *Z. jodorowskyi* sp. nov. However, Ha (3.97°), Apv (89°) and Aav (103°) of the new species differ significantly from *M. bucculata* (Ha 5.9°; Apv 66.15°; Aav 114.3°) (Laville et al. 2021b).

Zazrivacaris jodorowskyi gen. et sp. nov. differs from co-occurring *Dollocaris toarcica* sp. nov. by several features, including the shield outline, outline of the optic notch, absence of a ventral notch and a faint posterior notch. Additionally, the Ls/Hmax ratio is 1.4 for *Z. jodorowskyi* sp. nov., while it is 2.0 in *D. toarcica* sp. nov. The posterior notch is wider, and the optic notch is smaller in *Z. jodorowskyi* sp. nov. than in *D. toarcica* sp. nov..

Stratigraphic and geographic range.—Type locality and horizon only.

Discussion

Anatomy of *Zazrivacaris jodowskyi* gen. et sp. nov.—The holotype of *Zazrivacaris jodorowskyi* sp. nov. displays three structures situated above the muscle scar. Although their precise function remains uncertain, their number and general morphology suggest that they represent attachment sites for thoracic appendages, reminiscent of those observed in some shrimps. Interestingly, similar structures have been observed in shrimp specimens from the same assemblage as the thylacocephalans described herein (AG, unpublished data). Moreover, the appendages of *Mayrocaris bucculata* (i.e., a taxon potentially closely related to *Zazrivacaris jodorowskyi* gen. et sp. nov.) appear to extend at least halfway up the optic notch (see Laville et al. 2021b: figs. 4b, c, f, g; 6b, d; 8d, e; 11c; 12c; 16). The position and morphology of the structures observed in *Zazrivacaris jodorowskyi* gen. et sp. nov. may also suggest a possible interpretation as gills. In thylacocephalans, gills were typically laminar and located in the anterior to mid-body region, just above the raptorial trunk appendages (e.g., Secretan and Riou 1983; Laville et al. 2023b). However, only three putative gills are visible in the specimen, whereas up to eight pairs are usually reported (Secretan and Riou 1983). Given the preservation state of the material, the identity and function of these structures remain uncertain.

Morphological variations.—Because majority of studied specimens of *Dollocaris toarcica* sp. nov. represents incomplete shields, not all measurements are available for every specimen (for measurements, see SOM 1, Supplementary Online Material available at http://app.pan.pl/SOM/app70-Gerbe_etal_SOM.pdf). Due to this limited dataset, statistical analyses could not be performed. The measured values of Hp, Aad, and Apd exhibit a large variability, Hp 1.15–2.29 mm; Aad 41.88–71.55° and Apd 83.81–133.808°. The values of Hmax, Ha, Aav, and Apv also vary, but to a lesser extent. Most of the maximum values were recorded for SNM Z 41680, while most of the minimum values were measured on SNM Z 41043. Dimorphism among thylacocephalans is still largely unknown. Laville et al. (2021b) observed a bimodal distribution for Aad, which might be linked to dimorphism for *Mayrocaris bucculata*, although the connection remains somewhat unclear. Charbonnier et al. (2017) hypothesised that morphological variation in size could also be linked to sexual dimorphism but have not been able to demonstrate this due to our limited knowledge of thylacocephalan biology. Briggs and Rolfe (1983) suggested a potential sexual dimorphism for *Concavicaris milesi* Briggs & Rolfe, 1983, and *Concavicaris playfordi* Briggs & Rolfe, 1893. The small sample size and lack of statistical analyses prevent us from reaching a definitive conclusion about the presence of dimorphism in the newly described material from Zázrivá.

Shield features of *Zazrivacaris jodorowskyi* gen. et sp. nov. are characterized by a short shield and a large optic notch occupying almost the entire height of the shield. These features are associated with juveniles (Briggs and Rolfe 1983; Lange et al. 2001). Charbonnier et al. (2010) presented juveniles of *Dollocaris ingens* based on the morphological size variation. In addition, Laville et al. (2023a) suggested, based on a morphometric analysis, that juveniles of *Paraostenia voultensis* Secretan, 1985, may be represented by smaller absolute size, square-shaped shield, posterior margin tilted and no field of punctuactions; instead of adult representatives that showed larger absolute size, trapezoidal-shaped shield, vertical posterior margin and a field of punctuations. However, since *Z. jodorowskyi* gen. et sp. nov. is known from only two specimens, investigating possible ontogenetic changes is not possible.

Shield structures.—In Thylacocephala, shield surface structures are important features for taxonomic evaluation which have been used as diagnostic characters on lower (e.g., Rak et al. 2018) and also higher taxonomic levels (e.g., Charbonnier et al. 2017). Two main types of surface structures have been recognized: micro-structures and macro-structures (Figs. 6, 7; see also Rak et al. 2018; Broda et al. 2020). The micro-structure consists of the morphology of the cells (often called micro-ornamentation) that have been divided into three types: linear, polygonal or scale-like (Broda et al. 2020). Several other features are considered as surface micro-structures such as lattice organs, setal lumina, grooves and tube-like structures (Fig. 6; Lange and Schram 2002; Broda et al. 2020). The surface macro-structures have not been investigated or exhaustively synthetised as micro-structures. However, different patterns in macro-structures are observable: ridges (often called terraces, lirae, lines or ribs) (e.g., Calzada and Mañé 1993; Ehiro et al. 2015; Rak et al. 2018; this study), pore(s) (e.g., Charbonnier et al. 2017; Schram and Koenemann 2022; Laville et al. 2023a), carinae (e.g., Briggs and Rolfe 1983; Ji et al. 2017; Charbonnier and Brayard 2019), punctuations (e.g., Charbonnier et al. 2017; Laville et al. 2023a, 2024b), furrow(s) (e.g., Laville et al. 2021c, 2024b), tubercles (e.g., Laville et al. 2024a, b), grooves, depressions (e.g., Laville et al. 2021c,

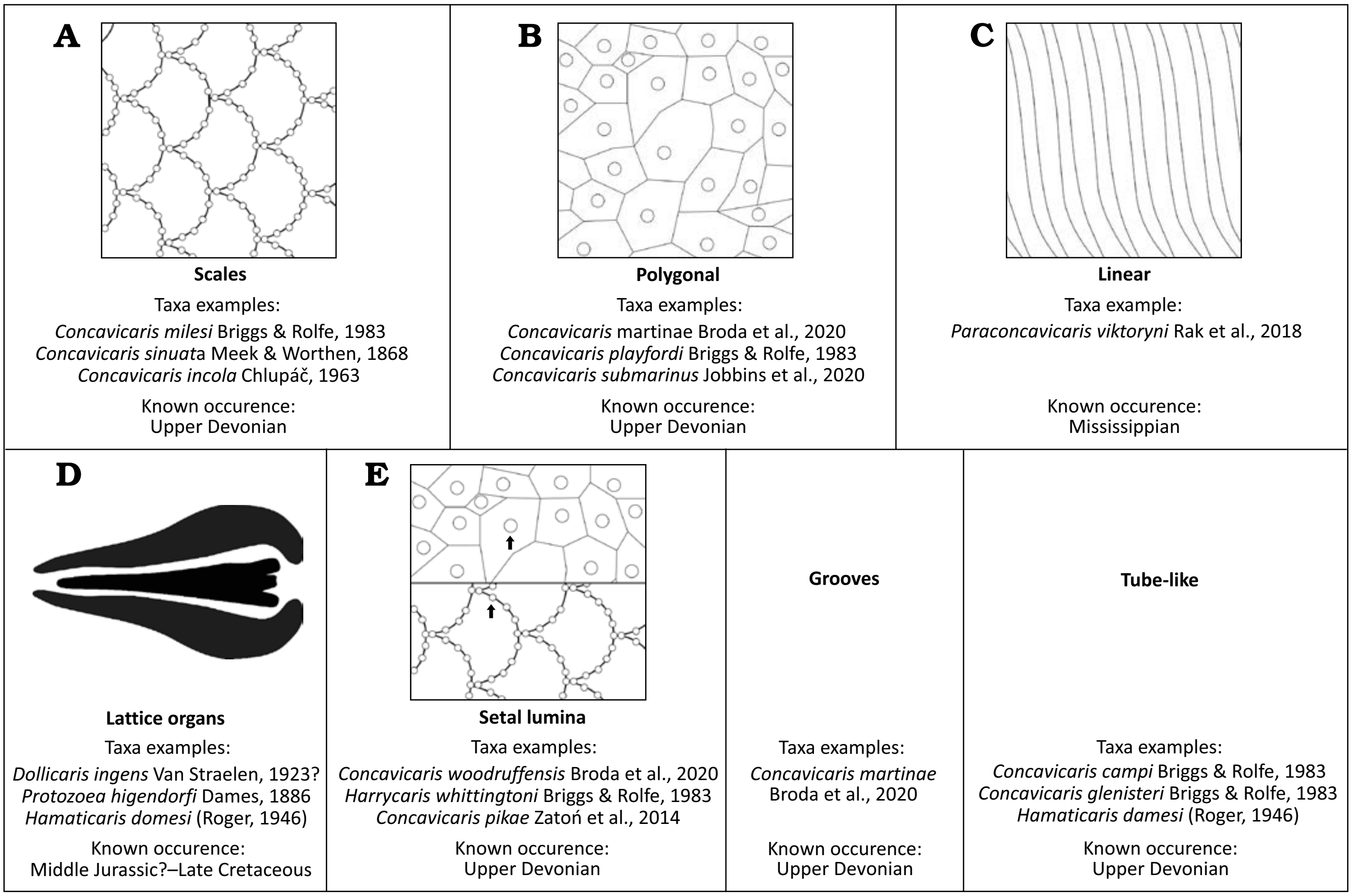
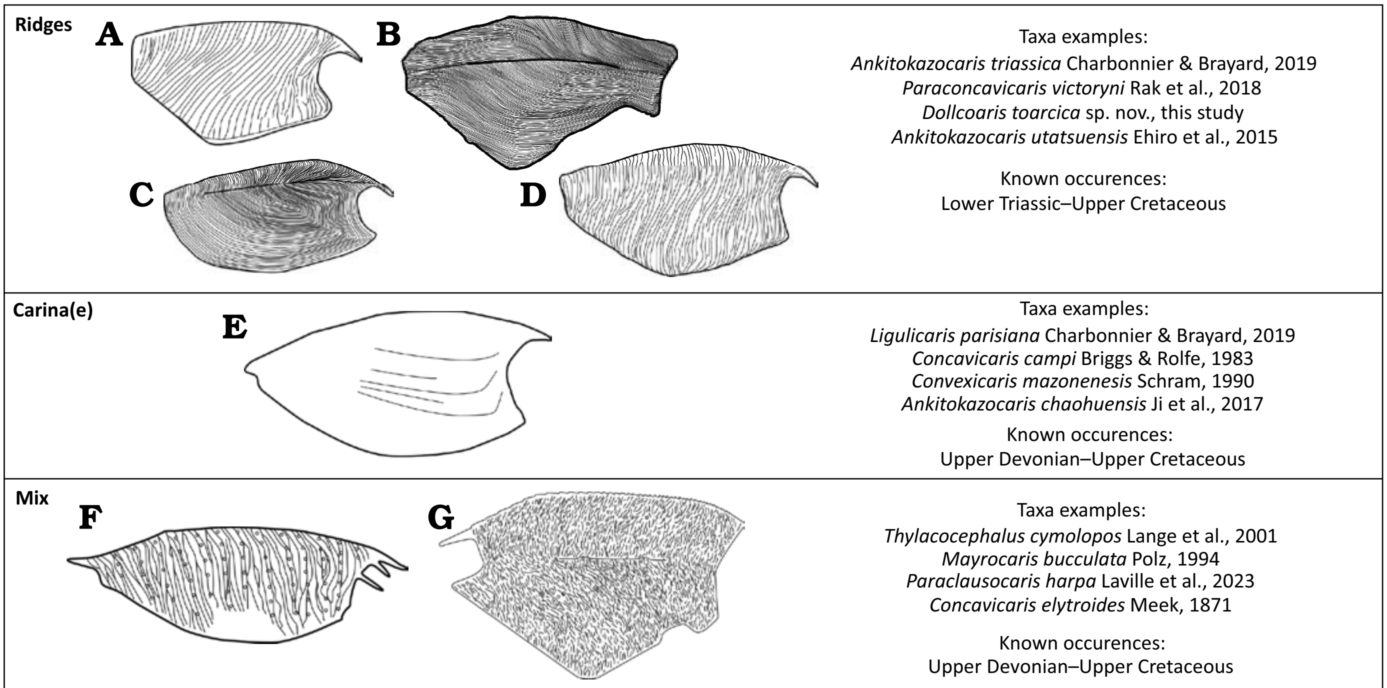


Fig. 6. Line drawings of all surface shield micro-structures known to date. A–C, E, based on Broda et al. (2020); D, based on Lange and Schram (2002).

2024b), pits (e.g., Briggs and Rolfe 1963; Charbonnier et al. 2017), serrations (Laville et al. 2023a), humps (Laville et al. 2023a) or a combination of multiple types, for instance ridges plus pores (e.g., Charbonnier et al. 2017; Laville et al. 2021b; Fig. 7). The macro-structures are defined by the type of structures (punctuations, carinae, ridges and/or other macro-structures), the quantity/density of structures, and their overall pattern/orientation in respect to main shield axes. As far as we know, ridges can be oriented vertically (e.g., Ehiro et al. 2015), obliquely (Charbonnier and Brayard 2019) or following a more complex pattern (e.g., Rak et al. 2018; this study). Each thylacocephalan species discovered so far exhibits a unique macro-structures (if present) pattern which can therefore be used for an assignment on the species level. It is of note that terminology describing surface micro- and macro-structure features is not uniform across published contributions; the same morphological features are described using various terms. For instance, ridges have been called lirae (Rak et al. 2018; Broda et al. 2020), vertical ridges (Laville et al. 2021c), rugations (Charbonnier et al. 2017), terraces (Briggs and Rolfe 1963) or ribs (Ehiro et al. 2015). Several terms have been introduced without precise definitions, resulting in different terms being used for similar or maybe identical surface structures, such as punctuations, pores, and pits (e.g., Briggs and Rolfe 1983; Charbonnier et al. 2017; Ehiro et al. 2019; Laville et al. 2023a), or grooves, depressions, and furrows (e.g., Charbonnier and Brayard 2019; Jobbins et al. 2020; Laville et al. 2023a). It should be noted that we focused our synthesis exclusively on the surface structures. Therefore, structures found along the shield margins are not included such as pores (e.g., Laville et al. 2021a), serrations (e.g., Arduini and Brasca 1984; Arduini 1992), spines (e.g., Ji and Tintori 2024; Laville et al. 2024a), or square-shaped tooth-like structures (e.g., Braig et al. 2019).

In respect to current literature data, stratigraphically oldest thylacocephalans from the Ordovician and Silurian have smooth shields (Van Roy et al. 2021; Haug et al. 2014, respectively), while the first occurrence of thylacocephalans bearing shield structures is dated to Devonian (Chlupáč 1963; Briggs and Rolfe 1983; Broda et al. 2020). Ridges seem more often present in Triassic thylacocephalans (e.g., Arduini 1990; Ehiro and Kano 2024; Laville et al. 2024a), whereas pores appear more common from Middle Jurassic to Late Cretaceous species (Dames 1886; Roger 1946; Lange et al. 2001; Charbonnier et al. 2017; Laville et al. 2023a) (Table 1). The smooth shield of the Ordovician specimens may be due to misidentification, as the material reported by Van Roy et al. (2021) may not belong to thylacocephalans. Indeed, the characteristic appendages are not visible. As for the only known Silurian specimen, it represents an



Pore(s)	**Punctations**	**Furrow(s)**	**Tuberculates**
Taxa examples: *Pseuderichthus cretaceus* Dames, 1886; *Protozoea hilgendorfi* Dames, 1886; *Ankitokazocaris acutirostris* Arduini, 1990	Taxa examples: *Austriocaris carinata* (Glaessner, 1931); *Paraostenia voultensis* Secretan, 1985; *Keelicaris deborae* Teruzzi & Charbonnier in Charbonnier et al., 2017	Taxa examples: *Paraostenia ambatolokobensis* (Arduini, 1990); *Paraostenia striata* (Glaessner, 1931); *Paraostenia voultensis* Secretan, 1985	Taxa examples: *Eodollocaris keithflinti* Laville et al., 2021; *Atropicaris lintveri* Laville et al., 2024; *Ostenocaris ribeti* (Secretan, 1985)
Known occurences: Lower Triassic–Upper Cretaceous	Known occurences: Upper Triassic–Upper Cretaceous	Known occurences: Lower Triassic–Middle Jurassic	Known occurences: Pennsylvanian–Middle Jurassic

Grooves	**Depressions**	**Pits**	**Serrations**	**Hump**
Taxa examples: *Ankitokazocaris triassica* (Charbonnier & Brayard, 2019); *Kilianicaris lerichei* Van Straelen, 1923	Taxa examples: *Concavicaris submarinus* Jobbins et al., 2020; *Paraclausocaris harpa* Laville et al., 2023	Taxa examples: *Hamaticaris damesi* (Roger, 1946); *Ankitokazocaris parva* (Ehiro et al., 2019)	Taxa example: *Paraclausocaris harpa* Laville et al., 2023	Taxa example: *Paraostenia voultensis* Secretan, 1985
Known occurences: Lower Triassic–Upper Cretaceous	Known occurences: Upper Devonian–Middle Jurassic	Known occurences: Upper Devonian–Upper Cretaceous	Known occurence: Middle Jurassic	Known occurence: Middle Jurassic

Fig. 7. Line drawings of all surface shield macro-structures known to date. **A**. *Ankitokazocaris triassica*. **B**. *Dollocaris toarcica* sp. nov. **C**. *Paraconcavicaris viktoryni*. **D**. *Ankitokazocaris utatsuensis*. **E**. *Ligulacaris parisiana*. **F**. *Thylacocephalus cymolopos*. **G**. *Mayrocaris bucculata.*

insufficiently preserved shield, preventing any assessment of potential surface structures. Interestingly, only the species of *Paraostenia* Secretan, 1985, present furrows on their shield and might be a specific structure to *Paraostenia*. The "furrow and ridge" structure described in *Ankitokazocaris bandoi* may correspond to a lateral carina that is poorly preserved. Nevertheless, the fossil record of thylacocephalans is still patchy and major conclusions cannot be drawn yet.

Not all thylacocephalan taxa exhibit some type of shield structures. Nevertheless, the absence of micro-structure can be caused by exfoliation of the external, ornamented cuticle layers (Broda et al. 2015, 2020) and can therefore represent a taphonomic artefact. Moreover, several taxa were examined in earlier studies (e.g., Glassner 1931; Arduini and Brasca 1984; Secretan and Riou 1983; Polz 2001; Laville et al. 2021a; Ehiro and Kano 2024), in which authors did not specifically address micro-structures. The presence of structures on the shield are important features for taxonomic evaluation and could be linked with the mode of life of the thylacocephalans.

Similar ridges found in *Dollocaris toarcica* sp. nov. have been described on the inner layer of the shield in other thylacocephalans such as *D. ingens* (Secretan & Riou, 1983; Vannier et al. 2016), *Paraostenia ambatolokobensis* (Arduini, 1990) (Laville et al. 2021c), *Concavicaris rostellata* Rolfe, 1969 (species not formally described); *Concavicaris elytroides* Meek, 1872 (Briggs and Rolfe 1983) and the possible thylacocephalan *Decoracaris hildebrandi* Briggs et al., 2015. Vannier et al. (2016) interpreted these macro-structures as an integumentary hemolymphatic circulatory network, given their resemblance to those observed in certain myodocopans.

Thylacocephalan association.—The presence of *Dollocaris* and *Zazrivacaris* gen. nov. (possibly related to *Mayrocaris*) appears to be close to other Jurassic assemblages. From the Callovian La Voulte-sur-Rhône and Tithonian Solnhofen Lagerstätten, associations of *Dollocaris* and *Mayrocaris* have been reported (Polz 1994, 1997, 2001; Laville et al. 2023a). This observation is not surprising, because all these localities were once parts of the same marine basin, the Tethys Ocean.

Mode of life.—Thylacocephalans with and without structures have been found in diverse sedimentary settings, including carbonates (e.g., Lange et al. 2001; Ehiro et al. 2015; Charbonnier et al. 2017; Rak et al. 2018; Charbonnier and Brayard 2019), siliciclastic rocks (e.g., Glaessner 1931; Van Roy et al. 2021; this study), or concretions of various kind (e.g., Schram 1990; Briggs and Rolfe 1983; Jobbins et al. 2020; Laville et al. 2021a). The shales with *Dollocaris toarcica* sp. nov. originated under sulphidic and anoxic conditions interrupted by short events of improved oxygenation (Suan et al. 2018). The black shales at Zázrivá contain a decapod pancrustacean assemblage similar to that of the La Voulte-sur-Rhône Lagerstätte (Charbonnier et al. 2010). The presence of polychelidan lobsters (AG unpublished data) suggests a deep-sea environment. It is likely that the newly described thylacocephalans from this setting were benthic or nectobenthic and were probably killed during dysoxic or anoxic events. Unfortunately, only isolated shields of *D. toarcica* sp. nov. have been found; no preserved appendages were associated with shields. The black shales at Zázrivá delivered decapod pancrustaceans with preserved appendages. This may suggest that empty thylacocephalan shields were transported to their place of burial, although given the type of sedimentation the transport likely was not long.

Conclusions

The occurrence of Thylacocephala from the Toarcian, Lower Jurassic of Slovakia reported herein is the first report of this group of euarthropods from the respective country. The assemblage from the Zázrivá locality consists of two taxa, *Dollocaris toarcica* sp. nov. and *Zazrivacaris jodorowskyi* gen. et sp. nov., and represents the only formally described Thylacocephala from the Toarcian stage. The newly described species *D. toarcica* sp. nov. is the third described species of the genus *Dollocaris*, previously known from the Middle Jurassic (Callovian) of France and Upper Jurassic (Tithonian) of Germany, expanding the stratigraphic span of the genus to the Lower Jurassic. *Zazrivacaris* is a newly described genus, presenting unique combination of characters. Additionally, we examined the micro- and macrostructures of the thylacocephalan shield to better understand their macroevolution. However, due to preservation constraints and historical biases, no definitive conclusions can be drawn. Future studies utilizing advanced imaging technologies and/or newly discovered material will undoubtedly offer valuable insights into the evolutionary patterns of these structures.

Acknowledgements

Barbara Zahradníková (SNM) and Jozef Klembara (Comenius University, Bratislava, Slovakia) are thanked for access to the documentation facilities with the Leica DVM6 and Leica M205 C digital microscopes, respectively. We thank Thomas Laville (Ludwig-Maximilians-Universität, Munich, Germany) and Sylvain Charbonnier (Muséum national d'Histoire naturelle, Paris, France) for their helpful reviews. The research was supported by the Slovak Agency for Research and Development (APVV-22-0523) and the Slovak Scientific Grant Agency (VEGA 2/0106/23).

Editor: Andrzej Kaim

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