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New species of Thylacocephala, *Eodollocaris keithflinti* n. gen., n. sp., from the Mazon Creek Lagerstätte, Illinois, United States (c. 307 Ma) and redescription of other Mazon Creek thylacocephalans

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ABSTRACT

Thylacocephala is an enigmatic ingroup of Euarthropoda. Thylacocephalans, only known from Palaeozoic and Mesozoic fossils, are characterized by a particular anatomy: a prominent folded shield enveloping most of the body, large compound eyes, three pairs of large, presumably raptorial appendages and a trunk with 8-22 stout segments bearing swimming appendages. However, lifestyle(s) and phylogenetic relationships of Thylacocephala are still largely unknown. This study is focused on thylacocephalans from the Mazon Creek Lagerstätte (c. 307 Ma, Middle Pennsylvanian, Carboniferous). A new species is described from a siderite concretion of Mazon Creek: *Eodollocaris keithflinti* n. gen., n. sp. The new species displays a particular mixture of characters typical for Palaeozoic species on the one hand and Mesozoic species on the other hand. Additionally, new details of the appendages and of the trunk are provided for already known species from the same locality, namely *Concavicularis georgeorum* Schram, 1990 and *Convexicaris mazonensis* Schram, 1990. These new informations are helpful to better understand the possible lifestyle of these representatives of Thylacocephala.

KEY WORDS

Thylacocephala,
Mazon Creek,
Lagerstätte,
Carboniferous,
lifestyle,
morphological diversity,
new genus,
new species.

RÉSUMÉ

Une nouvelle espèce de thylacocéphale (Eodollocaris keithflinti n. gen., n. sp.) du Lagerstätte de Mazon Creek, Illinois, États-Unis (c. 307 Ma) et re-description des autres thylacocéphales de Mazon Creek.

Les thylacocéphales forment un groupe interne énigmatique d'Euarthropoda. Les thylacocéphales, seulement connus au Paléozoïque et au Mésozoïque, se caractérisent par une anatomie particulière: une carapace bivalve enveloppant la majorité du corps, de larges yeux composés, trois larges paires d'appendices préhensiles présumés et un tronc avec 8 à 22 segments corpulents portant des appendices nageurs. Cependant, le(s) mode(s) de vie et les relations phylogénétiques des thylacocéphales restent encore majoritairement inconnus. Cette étude se concentre sur les thylacocéphales du Lagerstätte de Mazon Creek (c. 307 Ma, Pennsylvanien moyen, Carbonifère). Une nouvelle espèce est décrite à partir d'une concrétion sidéritique de Mazon Creek: *Eodollocaris keithflinti* n. gen., n. sp. La nouvelle espèce présente un mélange particulier de caractères typiques des espèces paléozoïques d'un côté et d'espèces mésozoïques de l'autre. De plus, de nouveaux détails sur les appendices et sur le tronc sont donnés pour des espèces déjà connues de la même localité, à savoir *Concavicularis georgeorum* Schram, 1990 et *Convexicularis mazonensis* Schram, 1990. Ces nouvelles informations sont utiles pour mieux comprendre le mode de vie possible de ces thylacocéphales.

MOTS CLÉS

Thylacocephala,
Mazon Creek,
Lagerstätte,
Carbonifère,
mode de vie,
diversité morphologique,
genre nouveau,
espèce nouvelle.

INTRODUCTION

Thylacocephala Pinna, Arduini, Pesarini & Teruzzi, 1982, is a group of enigmatic fossil animals, generally accepted as an ingroup of Euarthropoda and furthermore often considered as an ingroup of Eucruseacea (Haug *et al.* 2014). Thylacocephalans are known in the fossil record from at least the Silurian (435 Ma, *Thylacares brandonensis* C. Haug, Briggs, Mikulic, Kluessendorf & J.T. Haug, 2014 (United States) up to the Upper Cretaceous (Santonian, 84 Ma, several species, Lebanon; Hilgendorf 1885; Dames 1886; Schram *et al.* 1999; Lange *et al.* 2001; Charbonnier *et al.* 2017) when they probably became extinct. Whether Early Cambrian fossils such as *Zhenghecaris shankouensis* Vannier, Chen, Huang, Charbonnier & Wang, 2006 or specimens of *Isoxys* or *Tuzoia* (Vannier *et al.* 2006) are representatives of Thylacocephala is still unclear.

Even though important discoveries on the anatomy of thylacocephalans were made in the last decade (Haug *et al.* 2014; Vannier *et al.* 2016; Broda & Zatoń 2017), their lifestyles and their systematic relationships are still largely unknown. Yet, most fossils of the group Thylacocephala are easily identified as such, as they are characterised by a rather unique body organisation: a prominent sclerotized shield envelopes almost the entire body, large compound eyes protrude from under the shield, as are three pairs of large sub-chelate appendages, often eight sets of gills and eight to at least twenty-two posterior trunk segments bearing paddle-like appendages are distinguishable. In several species (Arduini *et al.* 1980; Secretan 1985; Charbonnier *et al.* 2010; Haug *et al.* 2014) the raptorial appendages bear prominent spines, in this aspect resembling the raptorial appendages of extant spearer-type mantis shrimps (Stomatopoda). The combination of such appendages with large forward directed eyes has usually been interpreted as an

indication of a predatory mode of life for thylacocephalans (Haug *et al.* 2014; Vannier *et al.* 2016). Moreover, fossilised food contents found inside Jurassic thylacocephalans support this interpretation (Pinna *et al.* 1985; Vannier *et al.* 2016).

Since the 19th century, fossils now considered to be representatives of Thylacocephala or the entire group have been interpreted as representatives of various groups of Eucruseacea, including Stomatopoda (usually as larval forms; Hilgendorf 1885; Dames 1886; Roger 1946), Phyllocarida (Meek & Worthen 1868; Rolfe 1961), Cirripedia (Arduini *et al.* 1980), Decapoda (Secretan 1985) and more recently as a possible sister group to Remipedia (Haug *et al.* 2014); the representatives of the latter group are likewise raptorial and enigmatic, but, unlike thylacocephalans, blind.

Thylacocephalan fossils have a global geographic distribution, known from all continents except Antarctica and South America (Hegna *et al.* 2014). They are known from China (Ji *et al.* 2017), Japan (Ehiro *et al.* 2015), Australia (Briggs & Rolfe 1983), Lebanon (Schram *et al.* 1999; Lange *et al.* 2001; Charbonnier *et al.* 2017), Madagascar (Arduini 1990), Morocco (Jobbins *et al.* 2020), Austria (Glaessner 1931), France (Secretan 1985), Germany (Polz 1990, 1994, 2001), Italy (Arduini *et al.* 1980; Pinna *et al.* 1985), Scotland (Van Der Bruggen *et al.* 1997), Slovenia (Križnar & Hitij 2010), Spain (Calzada & Mañé 1993), Mexico (Hegna *et al.* 2014) and the United States of America (Schram 1990). Thylacocephalans mostly occur in the fossil record as isolated shields in Konservat-Lagerstätten, making the study of these supposed predators quite challenging. Resolving relationships of thylacocephalans within Euarthropoda and among each other will require a better understanding of the tagmatism and of little known soft structures such as the raptorial and trunk appendages.

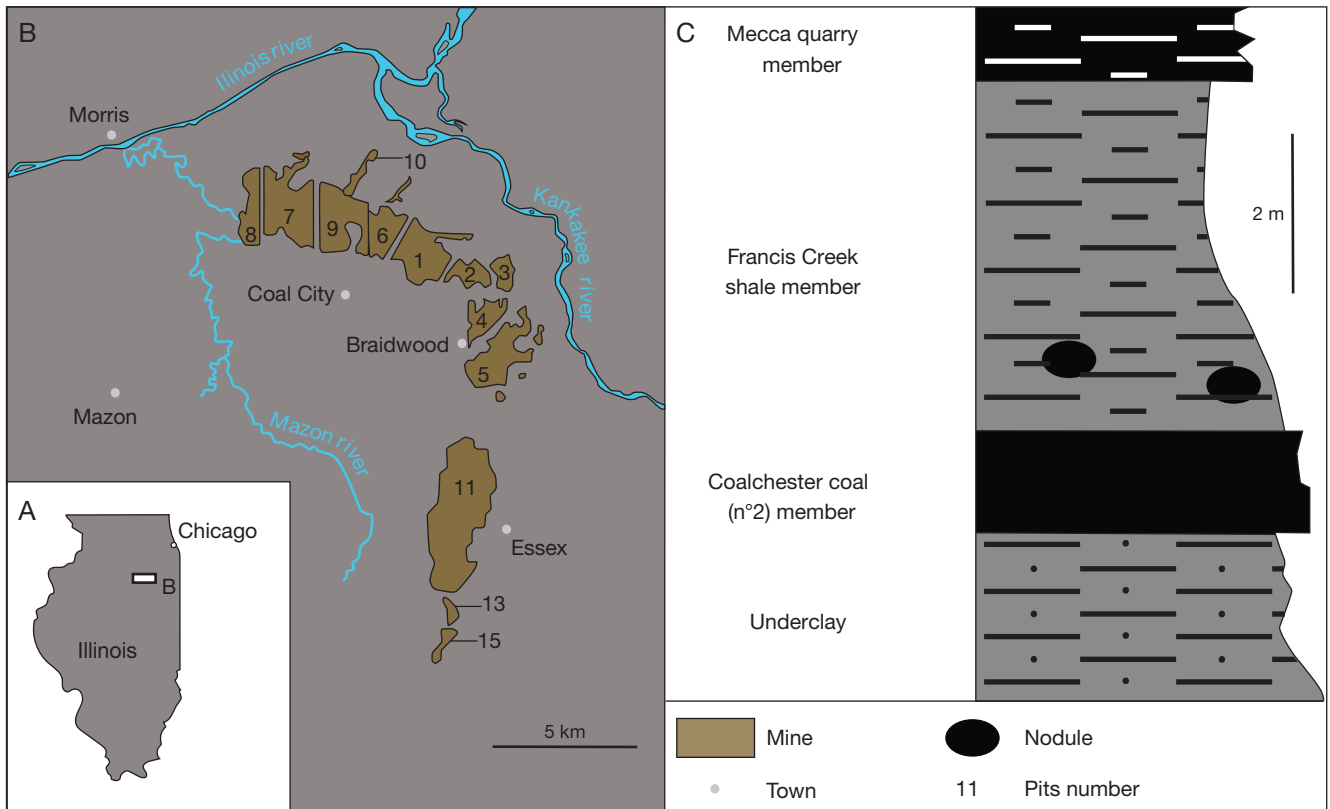


FIG. 1. — Mazon Creek Lagerstätte: **A**, location of the Mazon Creek area; **B**, map of the Mazon Creek area (adapted from Baird *et al.* 1986); **C**, stratigraphy of Mazon Creek area (adapted from Cotroneo *et al.* 2016).

Here we report new occurrences of thylacocephalans from the Mazon Creek Lagerstätte (c. 307 Ma, Middle Pennsylvanian, Carboniferous), including a new species. The new species described herein shows particular body structures so far not known in Palaeozoic species and new details of the appendages. We also provide new details of the previously known species from the same formation.

GEOLOGICAL SETTINGS OF MAZON CREEK

Schram (1990) described three thylacocephalan species from the Mazon Creek area: *Concavicaris georgeorum* Schram, 1990, *Concavicaris remipes* Schram, 1990 and *Convexicaris mazonensis* Schram, 1990. The Pennsylvanian Mazon Creek Lagerstätte is located in Illinois, United States of America (Fig. 1A, B). It displays an exceptional diversity of fossils with soft-tissue preservation of both plants and animals, fossilised in small concretions. These organisms come from quite a range of environments including terrestrial, freshwater, brackish water or shallow marine environment (Baird *et al.* 1986; Feldman *et al.* 1993). More than 350 species of plants (Locatelli *et al.* 2016) and 465 species of animals have been described, including representatives of Cnidaria (Schram & Nitecki 1975), Annelida (Johnson & Richardson 1966), Arachnida (Tetlie & Dunlop 2008), Insecta (Carpenter 1944, 1964), Eucrustacea (Schram *et al.* 1999) and also the supposed vertebrate *Tullimonstrum gregarium* (Clements *et al.* 2016; but see Sallan *et al.* 2017 for possible other affinities).

Also traces of ecological interactions, such as plant-insect interactions have been found in the concretions (Labandeira 1997). The Mazon Creek biota has been usually described as two assemblages: a terrestrial and freshwater assemblage in the northeast (Braidwood assemblage) and a brackish one in the southwest (Essex assemblage). However, recent discoveries made it unclear if the Braidwood assemblages is really representing a freshwater environment (Schultze 2009; Clements *et al.* 2019).

The actual Lagerstätte corresponds to the Francis Creek Shale Member of the Carbondale formation (Westphalian D; Fig. 1C; Baird 1997). It was deposited on the northeastern edge of Illinois basin, an epeiric sea located 4-10° south of the palaeoequator (Wanless 1975; Cecil *et al.* 2003). During the Middle Pennsylvanian, the Mazon Creek area was an environment of a prograding delta under a tropical climate (Chaloner & Creber 1973; Shabica 1979). The Francis Creek Shale Member is a constructional, silty mudrock recording the infilling of a series of coastal bays deposited during different stages of an important marine transgressive episode (Kuecher *et al.* 1990). Its thickness is ranging from 5 to 26 m (Smith 1970). Fossils are preserved in siderite concretions (FeCo₃) including variable amounts of phyllosilicates, iron oxides or pyrites (Cotroneo *et al.* 2016). These concretions formed in clay-rich horizons of the lower 3-4 m of the Francis Creek Shale Member, where the member is at least 15 m thick (Baird & Shabica 1980).

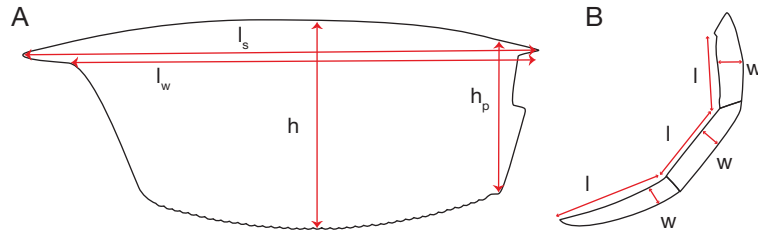


FIG. 2. — Scheme of measurements: **A**, shield measurements; **B**, appendage measurements. Abbreviations: **h**, maximum height; **h_p**, posterior height; **l**, appendage element length; **l_s**, shield length; **l_w**, shield length without rostrum; **w**, appendage element width.

MATERIAL AND METHODS

MATERIAL

Five specimens were in the centre of the study. They are deposited in the Invertebrates Paleontology collection of the Royal Ontario Museum, Toronto, Canada, under repository numbers ROMIP 47987, 61586, 61587, 61588, 61591. They originally mostly come from pit 11 of the Mazon Creek area (Fig. 1B). All specimens are preserved as part and counter-part in siderite concretions. Specimens for comparison come from the lithographic limestones of Southern Germany. They are housed in the Staatliches Museum für Naturkunde Stuttgart, Germany, under repository numbers SMNS 67901 and 70193/4.

DOCUMENTATION METHODS

Specimens were photographed under cross-polarized light with a Canon Rebel T3i camera and a MPE-65 mm macrolens. High-resolution composite images were produced for each specimen (Haug *et al.* 2008; Haug *et al.* 2011). Line drawings were made using Adobe Illustrator CS6.

ABBREVIATIONS

Measurements

Measurements were taken with ImageJ (public domain, Schneider *et al.* 2012), including the following dimensions, for the shield (Fig. 2A):

h	maximum shield height;
h _p	posterior shield height;
l _s	shield length;
l _w	shield length without rostrum;

for the appendages (Fig. 2B):

l	appendage element length;
w	appendage element width.

Institutions

MCP	Northeastern Illinois State University, Mazon Creek Study Center, Chicago;
PE	Field Museum of Natural History, invertebrate paleontology collections, Chicago;
ROM	Royal Ontario Museum, Toronto;
SDSNH	San Diego Society of Natural History Paleontology collection;
SMNS	Staatliches Museum für Naturkunde Stuttgart.

SYSTEMATIC PALAEOLOGY

PRELIMINARY REMARKS

Schram (2014) made an attempt of a classification for Thylacocephala. However, as mentioned by the author, ‘the scheme of classification proposed here [in Schram 2014] for Thylacocephala is not perfect’. Thus we decided not to follow this classification.

EUCRUSTACEA *sensu* Waloszek (1999)

THYLACOCEPHALA

Pinna, Arduini, Pesarini & Teruzzi, 1982

Genus *Concavicaris* Rolfe, 1961

Colpocaris Meek, 1872: 33 (junior homonym of *Colpocaris* von Meyer, 1862).

TYPE SPECIES. — *Ceratiocaris (Colpocaris) bradleyi* Meek, 1872, from the Waverly formation (Mississippian) of Kentucky, United States.

DIAGNOSIS (repeated from Rolfe 1961). — Carapace with a fused hinge line, a rostrum extended anteriorly, a pronounced optic notch, and up to three lateral longitudinal ridges.

Concavicaris georgeorum Schram, 1990

(Fig 3; 4)

TYPE MATERIAL. — Holotype: SDSNH 36777. — Paratypes: SDSNH 36759, 36762, 36793, 36764, 36768, 36769, 36774; PE 10853, 10916, 11020, 14105 15346, 15356, 23144, 23145, 23146, 24566, 24589, 24590, 24591, 29466, 29469, 30556, 30575, 31049, 31752, 32957, 40107, 45969, 51937; MCP 591, 595, 596.

TYPE HORIZON. — Carbondale Formation, Francis Creek Shale Member, *c.* 307 Ma, Westphalian D, Middle Pennsylvanian, Carboniferous

TYPE LOCALITY. — Mazon Creek area, Pit 11, Illinois, United States.

DIAGNOSIS (repeated from Schram 1990). — Carapace suboval in outline with a short rostrum, an optic notch prominently occupying half of the anterior aspect, a ventral margin marked by a notch anterior of its midpoint, a pointed postero-dorsal aspect and a single, dorsally situated longitudinal ridge.

EXAMINED MATERIAL. — ROMIP61586, 61587, 61591 (lateral view).

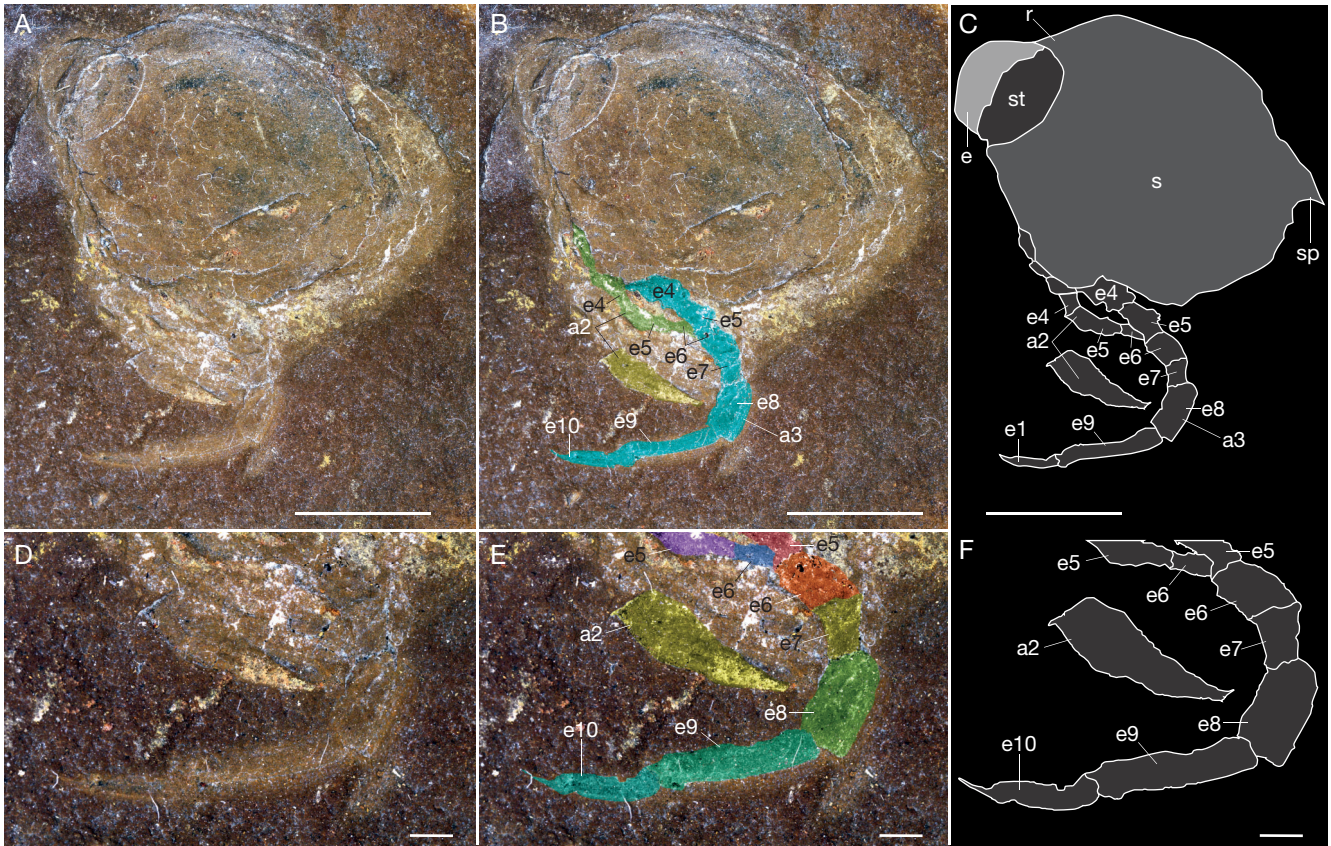


FIG. 3. — *Concavicularis georgeorum* Schram, 1990, ROMIP61587: **A**, general view; **B**, general view (color-marked); **C**, line drawing of general view; **D**, close-up of the third raptorial appendage; **E**, close-up of the third raptorial appendage (color-marked); **F**, line drawing of the third raptorial appendage. Abbreviations: **a2**, **a3**, second, third raptorial appendages; **e**, eyes; **e4-e10**, element 4-10; **r**, rostrum; **s**, shield; **sp**, posterior spine; **st**, stalk. Photographs: C. Haug and J. T. Haug. Line drawings: T. Laville. Scale bars: A-C, 5 mm; D-F: 1 mm.

DESCRIPTION

Prominent appendage 2 (possible appendage of post-ocular segment 5, maxilla?) emerged from an anterior concavity of the shield (Fig. 3A-C). Proximal region not accessible, only the more distal parts recognisable. Six elements apparent. Proximal three not fully accessible, as they are partly concealed by the shield and only recognisable as compressed-through structures. Element 4 short, rectangular in lateral view, longer than wide, about $1.6\times$ ($l = 0.94$ mm; $w = 0.58$ mm); oriented postero-ventrally. Element 5 elongated, longer than wide, about $2\times$ ($l = 1.50$ mm; $w = 0.75$ mm); oriented posteriorly. Element 6, distal element, not clearly visible, appears quite thin.

Prominent appendage 3 (possible appendage of post-ocular segment 6, maxilliped?) with ten elements (Figs 3D-F; 4A-H). Curved, with the proximal part directed antero-ventrally and the distal part directed anteriorly. Most proximal element, element 1, rectangular in lateral view, longer than wide, $1.6-1.8\times$ ($l = 1.10-1.22$ mm; $w = 0.65-0.76$ mm), with a spine in the latero-distal angle. Element 2 appears square-shaped, almost as wide as long ($l = 0.91$ mm; $w = 0.81$ mm). Element 3 is wider than long, $1.2\times$ ($l = 0.8$ mm; $w = 0.98$ mm). The fourth element is trapezoidal, wider proximally than distally ($l = 1.43-1.90$ mm; $w_{\max} = 2.56$ mm; $w_{\min} = 1.34$ mm). It is directed ventrally. The fifth element is longer than wide, $1.2\times$ ($l = 1.29$ mm; $w = 1.06$ mm). The sixth element is rectangular,

longer than wide, $1.5\times$ ($l = 1.32$ mm; $w = 1.05$ mm). The seventh element is also rectangular and is the shortest; it is longer than wide, $1.5\times$ ($l = 1.19$ mm; $w = 0.78$ mm). The eighth element is massive and rectangular. It is longer than wide, $1.76\times$ ($l = 2.13$ mm; $w = 1.21$ mm) and is angled at 44.3° anteriorly from the seventh one. The ninth element is elongate, longer than wide, $5\times$ ($l = 2.88-3.84$ mm; $w = 0.64-0.77$ mm). It is angled at 50° anteriorly from the eighth element. The tenth element is thinner, longer than wide, $5.9\times$ ($l = 2.89$ mm; $w = 0.49$ mm). It becomes thinner distally, forming a tip.

The trunk consists of seven visible segments. The first of the posterior trunk appendages seems to end with a spiny tip. The trunk terminates in a specialised terminal structure (furca?; Fig. 4). The terminal structure becomes thinner distally and ends with three spines. The ventral one is longer than the other spines, $1.3\times$.

REMARKS

Schram (1990) interpreted a rectangular structure in the ventral part of the shield as the midgut. A similar structure is present in one of the new fossils (Fig. 4C, D). Yet it is probably not the midgut. Instead it seems more likely to be the proximal part of the third prominent appendage. This interpretation would explain the apparent subdivision into discrete units already recognised by Schram (1990). Most likely, these units correspond to the proximal three elements, the most proximal

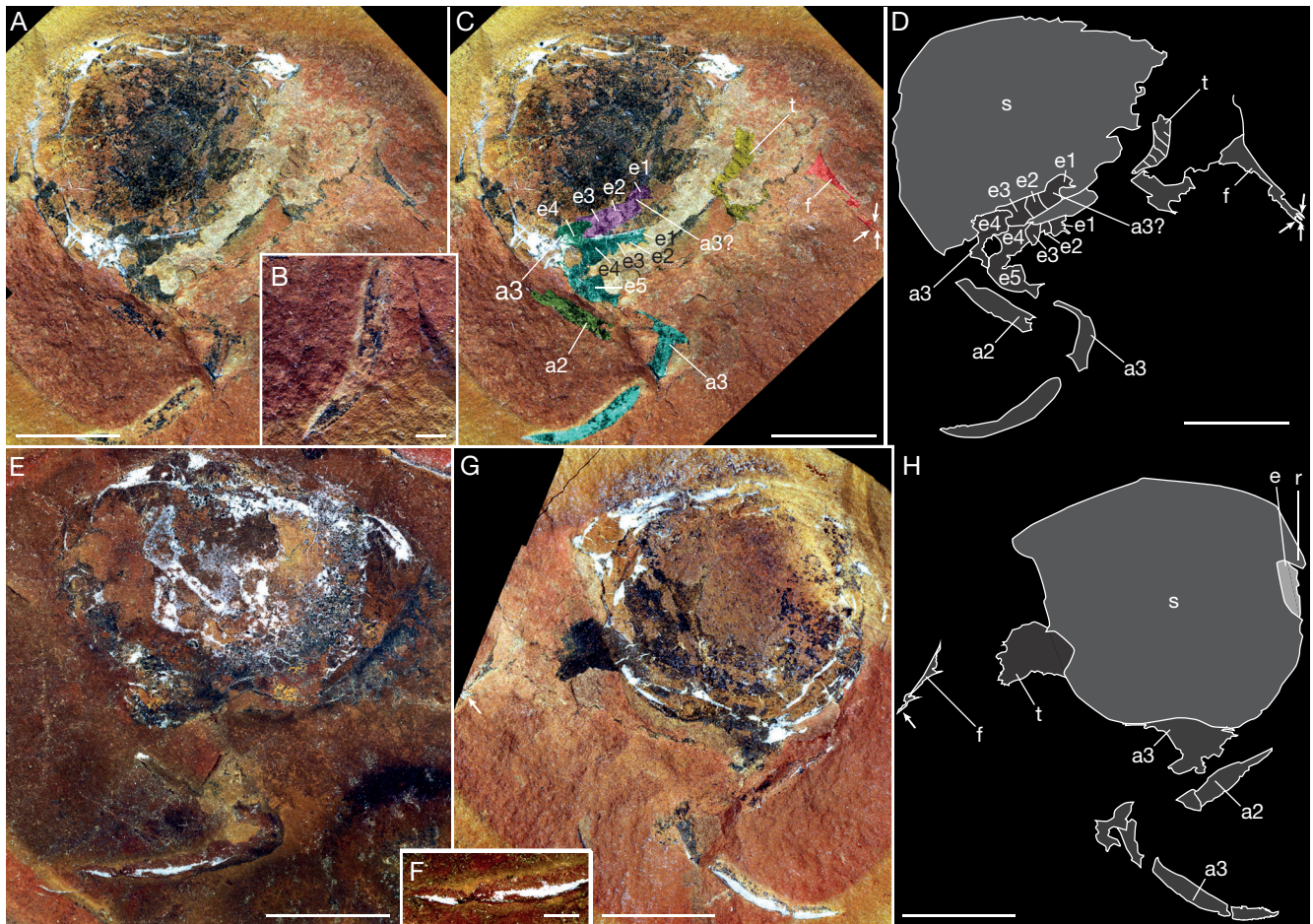


FIG. 4. — *Concavicularis georgeorum* Schram, 1990: **A-D**, ROMIP61591, part; **A**, general view; **B**, close-up of the third raptorial appendage; **C**, general view (color-marked); **D**, line drawing; **E, F**, ROMIP61588; **E**, general view; **F**, close-up of the third raptorial appendage; **G, H**, ROMIP61591, counter-part; **G**, general view; **H**, line drawing. Abbreviations: **a2, a3**, second, third raptorial appendages; **e**, eyes; **e1-e5**, element 1-5; **f**, furca?; **r**, rostrum; **s**, shield; **t**, trunk. Arrows indicate the spines of the possible furca. Photographs: C. Haug and J. T. Haug. Line drawings: T. Laville. Scale bars: A, C-E, G-H, 5 mm; B, F, 1 mm.

one most likely representing the basipod. If this interpretation is correct, the insertion of the appendage is further posterior than so far assumed.

The new specimens of *C. georgeorum* possess a specialised terminal structure that could represent a furca. So far, a comparable terminal structure was only known in *Concavicularis mazonensis*. The terminal structure in *C. georgeorum* differs from that of *Co. mazonensis* by bearing three spines distally, while the structure in *Co. mazonensis* is long paddle-shaped. Also it seems that the terminal structure in *C. georgeorum* might not be paired; if this is the case, an identity as furca is unlikely.

Genus *Concavicularis* Schram, 1990

TYPE SPECIES. — *Concavicularis mazonensis* Schram, 1990 from Carbondale Formation, Francis Creek Shale Member, Mazon Creek area, Illinois, United States.

DIAGNOSIS (repeated from Schram 1990). — Sinuously shaped carapace displaying a rounded antero-dorsal part, a convex antero-lateral margin, and a blunt postero-ventral aspect. Elongate subchelate raptorial limbs composed of narrow articles. Body ending by long caudal rami.

Concavicularis mazonensis Schram, 1990 (Fig. 5)

TYPE MATERIAL. — Holotype: PE 32958. — Paratypes: PE 11255, 23525, 38169, 39350, 40076, 45692, 45695; SDSNH 36781; MCP 594.

TYPE HORIZON. — Carbondale Formation, Francis Creek Shale Member, c. 307 Ma, Westphalian D, Middle Pennsylvanian, Carboniferous

TYPE LOCALITY. — Mazon Creek area, Pit 11, Illinois, United States.

EXAMINED MATERIAL. — ROMIP47987 (lateral view).

DIAGNOSIS. — Same as for genus.

DESCRIPTION

The new specimen provides important details about the trunk, especially about the appendages (Fig. 5A-D). The shield is longer than high, 2.1× ($l_s = 16.7$ mm; $h = 7.85$ mm). The posterior trunk is obviously organised into eight discrete segments, especially indicated by eight rectangular appendages emerging from under the shield. The distal end of the appendages appears bifid. The appendages are 1.69 mm to 1.89 mm long.

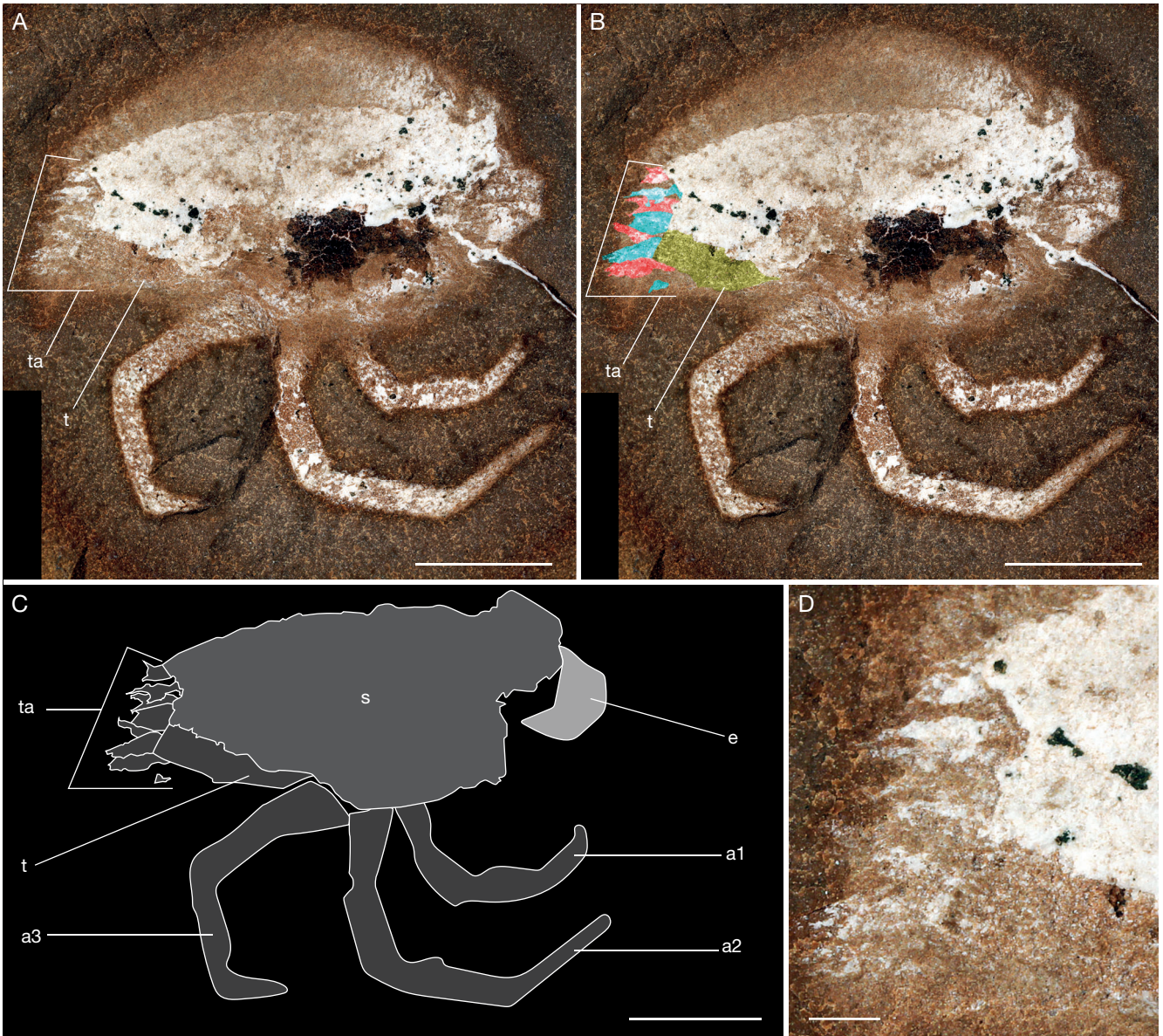


FIG. 5. — *Convexicaris mazonensis* Schram, 1990, ROMIP47987: **A**, general view; **B**, general view (color-marked); **C**, line drawing; **D**, close-up on trunk appendages. Abbreviations: **a1-a3**, first, second, third raptorial appendages; **e**, eyes; **s**, shield; **t**, trunk; **ta**, trunk appendages. Photographs: C. Haug and J. T. Haug. Line drawings: T. Laville. Scale bars: A-C, 5 mm; D, 1 mm.

REMARKS

Trunk appendages have been known for several species of Thylacocephala (Arduini *et al.* 1980; Secretan 1985; Arduini 1992; Polz 1990, 1994, 2001; Lange *et al.* 2001; Haug *et al.* 2014; Ji *et al.* 2017; Braig *et al.* 2019; Jobbins *et al.* 2020). In most cases they appear to be either paddle-like or multi-annulated. The morphology observed here, paddle-like, but with a bifid distal end, appears new. Yet, in fact our knowledge of the posterior trunk appendages is rather incomplete. Therefore, this may in fact be a more common feature.

Although Schram (1990) suggested that *Co. mazonensis* should possess eight posterior trunk segments with swimming appendages, this was not really apparent in his specimens. The new specimen now clearly shows eight distinct

such appendages and hence supports the assumption by Schram (1990).

Genus *Eodollocaris*

Laville, J.T. Haug & C. Haug, n. gen.

[urn:lsid:zoobank.org:act:52E16EC8-EAB2-457C-94D2-C187234EC1A3](https://zoobank.org/act:52E16EC8-EAB2-457C-94D2-C187234EC1A3)

ETYMOLOGY. — Referring with ‘-dollocaris’ to the similarities to *Paradollocaris vannieri* Charbonnier, 2017 and the Mesozoic form more generally, and ‘Eo-’ to refer to an early form of it

TYPE SPECIES. — *Eodollocaris keithflinti* n. gen., n. sp.

DIAGNOSIS. — As for the species.

Eodollocaris keithflinti

Laville, J.T. Haug & C. Haug n. gen., n. sp.
(Figs 6; 7)

urn:lsid:zoobank.org:act:1D59F66C-0B63-460B-94AB-F177841EC908

ETYMOLOGY. — In honor of the late Keith Flint from the band ‘The Prodigy’. As the specimen exhibits a certain “aggressiveness” and the fossil is preserved in bright red colour reminding of fire, we herewith tribute to the song ‘Firestarter’ of the band.

TYPE MATERIAL. — Holotype: ROMIP61586.

TYPE HORIZON. — Carbondale Formation, Francis Creek Shale Member, c. 307 Ma, Westphalian D, Middle Pennsylvanian, Carboniferous.

TYPE LOCALITY. — Mazon Creek area, Pit 11, Illinois, United States.

DIAGNOSIS. — Trapezoidal shield displaying a rounded rostrum, a tube-shaped dorsal midline, a finely tuberculated ventral margin, a dorsal midline ending posteriorly with a spine and a posterior margin with a notch in its dorsal part. Third prominent appendage bearing seven spines on its most distal element.

DESCRIPTION

Body

Largely enveloped by prominent folded shield (Figs 6A-D; 7A, B). Few structures protruding from it. Exact origin of shield unclear, most likely relatively far anterior, possibly from segments of head. Shield trapezoidal in lateral view; longer than high, about 2.8× ($h = 6.13$ mm, $h_p = 4.97$ mm; $l_s = 16.93$ mm; $l_w = 15.23$ mm). Antero-dorsal corner drawn out anteriorly into a rostrum with a rounded tip ($l = 1.70$ mm). The anterior margin is straight, oriented postero-ventrally (c. 30°). No clear optical notch distinguishable. Dorsal midline is slightly convex. Postero-dorsal corner drawn out posteriorly into small spine. Ventral margin is convex. Rim in this region is bearing numerous fine tubercles and appears slightly bent in its central part (Fig. 6F). Posterior margin further dorsally concave forming distinct notch, ventral part straight and oriented antero-ventrally (c. 30°). Dorsal midline connecting the two valves tube-shaped, with numerous pores along the entire dorsal line, terminated by the rostrum (Fig. 6E).

Large eyes

Anteriorly protruding from under the shield, prominent ($l = 0.94$ mm; Fig. 6A-D). Appear to arise from massive proximal stalks. Posterior to eyes, a massive oval structure emerging ventrally from the shield. Exact origin unclear.

Two prominent appendages

Protruding from under the shield (Figs 6G, H; 7C, D), interpreted as raptorial appendages 2 and 3 (possibly appendages of post-ocular segments 5 and 6 = maxillae? and maxillipeds?). Proximal parts concealed by a tube-shaped structure, probably a part of the body.

Raptorial appendage 2

Differentiated into four elements. Element 1 rectangular in lateral view, longer than wide, 1.2× ($l = 1.53$ mm; $w =$

1.33 mm). Element 2 rectangular, longer than wide, about 2.1× ($l = 1.85$ mm; $w = 0.87$ mm), angled in the specimen at 51° downward from the first article. Element 3 not well-preserved. Width appears similar to that of preceding element. Element 4 longest (Fig. 6G), thin, longer than wide, 5.6× ($l = 3.92$ mm; $w = 0.70$ mm), angled at 50° inward from element 3. Distally bearing two spines on its median margin. First spine smaller ($l = 0.79$ mm). Second spine very distal. Spine longer than the first one and directed anteriorly.

Raptorial appendage 3

Better preserved, longer than raptorial appendage 2. Differentiated into four elements (Fig. 7C, D). Element 1 rectangular, almost square-shaped ($l = 2.13$ mm; $w = 2.03$ mm); bearing a stout spine in the central part of the lateral margin ($l = 0.38$ mm). Element 2 hexagonal in outline, slightly rounded, wider in its central part than at its extremities ($w_{max} = 2.19$ mm; $w_{min} = 1.05$ mm; $l = 1.79$ mm). Bearing a spine on central part of lateral and median margin. Lateral spine longer ($l = 0.28$ mm) than median one ($l = 0.16$ mm). Element 3 rectangular, longer than wide, about 3.6× ($l = 4.27$ mm; $w = 1.18$ mm), angled at 24.3° from element 2. One spine on median margin ($l = 0.37$ mm). Element 4, distal one, also the longest one ($l = 6.32$ mm); rectangular, thin and elongated, longer than wide, about 7.2× ($w = 0.88$ mm), angled at 56.6° anteriorly from element 3. Bears seven spines on median margin (Fig. 7C, D). First one is thin ($l = 0.65$ mm); second one also thin ($l = 0.58$ mm), third also thin, longest of the series ($l = 0.68$ mm); fourth spine shorter ($l = 0.44$ mm); fifth similar to fourth ($l = 0.45$ mm); sixth spine shortest ($l = 0.20$ mm), close to seventh spine. Seventh spine corresponds to distal end of appendage; slightly curved, longer than the previous spine, about 3.2× ($l = 0.64$ mm).

Posterior part of trunk

Only the posterior part of trunk is visible. Carrying three appendages. First posterior trunk appendage paddle-like. Second one not well preserved but bearing a spine distally. Third, also paddle-like, arising from end of trunk.

REMARKS

The new specimen possesses a so far unique combination of characters. The rostrum with a rounded tip seems to be a common feature in Palaeozoic species of Thylacocephala, especially in species of *Concavicularis* Rolfe, 1961. The presence of such a rostrum has also been suggested to be a diagnostic feature of representatives of the group *Ankitokazocaris* Arduini, 1990 of the Triassic.

However, it differs from known representatives of both groups, *Concavicularis* and *Ankitokazocaris*, by the absence of a well-developed optic notch. Also, the new specimen possesses a posterior spine and a posterior notch, both structures are absent in species of *Concavicularis* and *Ankitokazocaris*. Yet, they are well known in specimens from younger deposits, such as representatives of *Atropicaris* Arduini & Brasca, 1984, *Dollocaris* Van Straelen, 1923 or *Mayrocaris* Polz, 1994. In these species, the posterior notch occupies the entire posterior

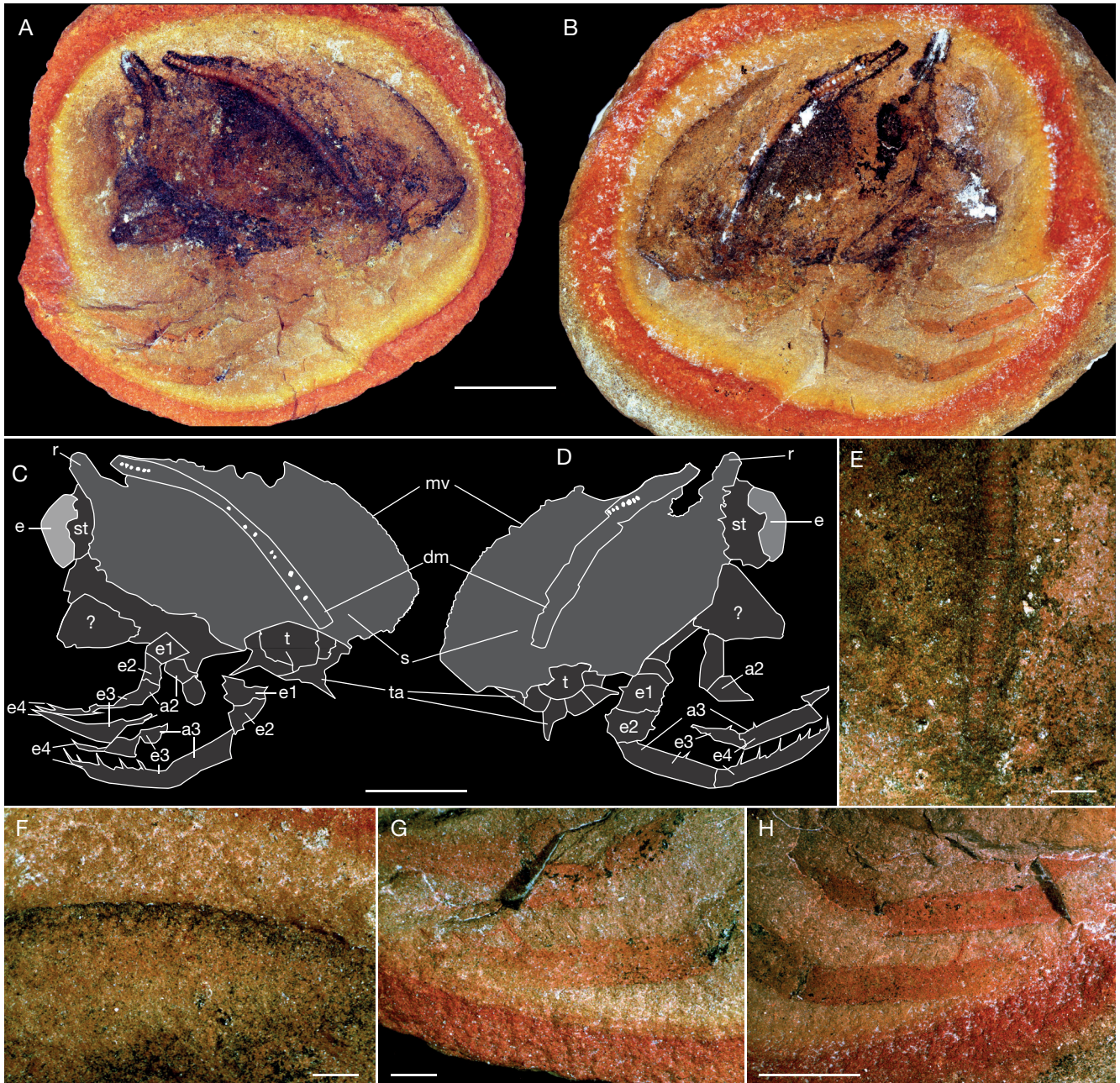


FIG. 6. — *Eodollocaris keithflinti* Laville, J.T. Haug & C. Haug, n. gen., n. sp., ROMIP61586: **A, B**, general view of part and counter-part; **C**, line drawing of **A**; **D**, line drawing of **B**; **E**, close-up of the dorsal midline of **A**; **F**, close-up of ventral margin of **A**; **G**, close-up of prominent appendages of **A**; **H**, close-up of prominent appendages of **B**. Abbreviations: **a2, a3**, second, third raptorial appendages; **e**, eyes; **e1-e4**, element 1-4; **dm**, dorsal midline; **mv**, ventral margin; **r**, rostrum; **s**, shield; **st**, stalk; **t**, trunk; **ta**, trunk appendage; **?**, indeterminate oval plate. Photographs: C. Haug and J. T. Haug. Line drawings: Thomas Laville. Scale bars: A-D, 5 mm; E-H, 1 mm.

margin whereas in the new specimen it is restricted to the dorsal part of the margin.

Among the species from younger deposits, especially *Paradollocaris vannieri* Charbonnier, 2017 shows many similarities concerning shield shape with the new specimen. The shield is trapezoidal with a convex dorsal midline. Anteriorly it is drawn out into a rostrum, which is rounded distally. The posterior end is also drawn out into a spine. The posterior margin also has a pronounced notch. Similar to other species from the Mesozoic, the notch occupies the entire posterior margin.

The ventral margin of the new specimen seems unique with the anterior part being tuberculated.

Concerning the raptorial appendages, the new specimen exhibits particular differences in form and armature compared to other thylacocephalans from Mazon Creek. *Convexicaris mazonensis* and *Concavicaris georgeorum* have less robust appendages, and they do not display any spines. Due to the significant differences of the new specimen we interpret it as a representative of a new, so far unrecognised species: *Eodollocaris keithflinti* n. gen., n. sp.

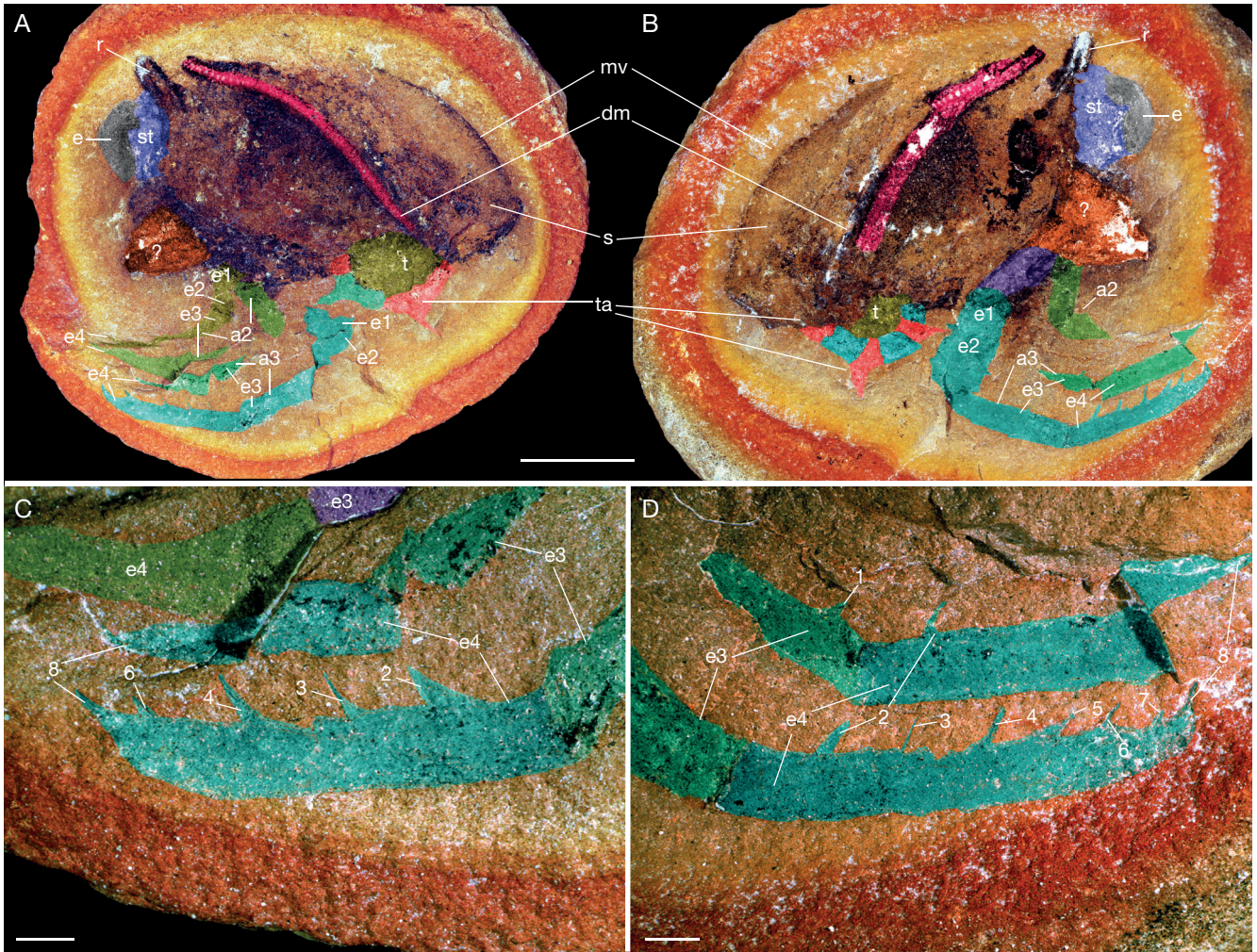


Fig. 7. — *Eodollocaris keithflinti* Laville, J.T. Haug & C. Haug, n. gen., n. sp., ROMIP61586: **A, B**, general view of part and counter-part (color-marked); **C**, close-up of appendages of A (color-marked); **D**, close-up of appendages of B (color-marked). Abbreviations: a2, a3, second, third raptorial appendages; e, eyes; e1-e4, element 1-4; dm, dorsal midline; mv, ventral margin; r, rostrum; st, stalk; t, trunk; ta, trunk appendage; ?, indeterminate oval plate; 1-8, spines 1-8. Photographs: C. Haug and J. T. Haug.. Scale bars: A, B, 5 mm; C, D, 1 mm.

DISCUSSION

STRUCTURAL INTERPRETATIONS OF *EODOLLOCARIS KEITHFLINTI* N. GEN., N. SP. *The “oval plate”*

Between the eyes and the prominent appendages, the new fossil possesses a prominent structure, an oval plate. An at least roughly comparable structure was reported by Polz (1990) for *Clausocaris lithographica* (Oppenheim 1888). Polz (1990) considered this structure covering the eyes as an exterior layer of the surface of the eyes. In *Clausocaris lithographica* the structure appears to bear numerous small spiny structures (Fig. 8A-G). This would be rather unusual for the surface of the eye.

A possible structure of comparable shape is the exopod of the antennae. The exopod is paddle-shaped in some ingroups of Eucrustacea, especially in Eumalacostraca (Boxshall & Jaume 2013), but also in Remipedia (Yager & Humphreys 1996), the possible sistergroup of Thylacocephala (Haug *et al.*

2014). It is therefore possible that the “oval plate” indeed represents the exopod of the antenna.

The dorsal midline

The new fossil displays a particular dorsal midline morphology, with numerous rounded pores. An at least comparable arrangement has been described from a specimen found in the Cretaceous of Lebanon (Lange & Schram 2002). In this specimen, 23 pairs of pores are arranged in rows around the dorsal midline. Lange & Schram (2002) compared these pores to the lattice organs of thecostracans, such as barnacles. In lattice organs the pores are in fact partly invaginated setae, having a chemosensory function. Yet, the arrangement is very different, the lattice organ is clearly divided into an anterior set of six pores and a posterior one of four.

In malacostracan larvae, a similar arrangement of pores is known. Also here we find a distinct arrangement into an anterior group of four pores and a posterior group of six (Lerosey-Aubril & Meyer 2013).

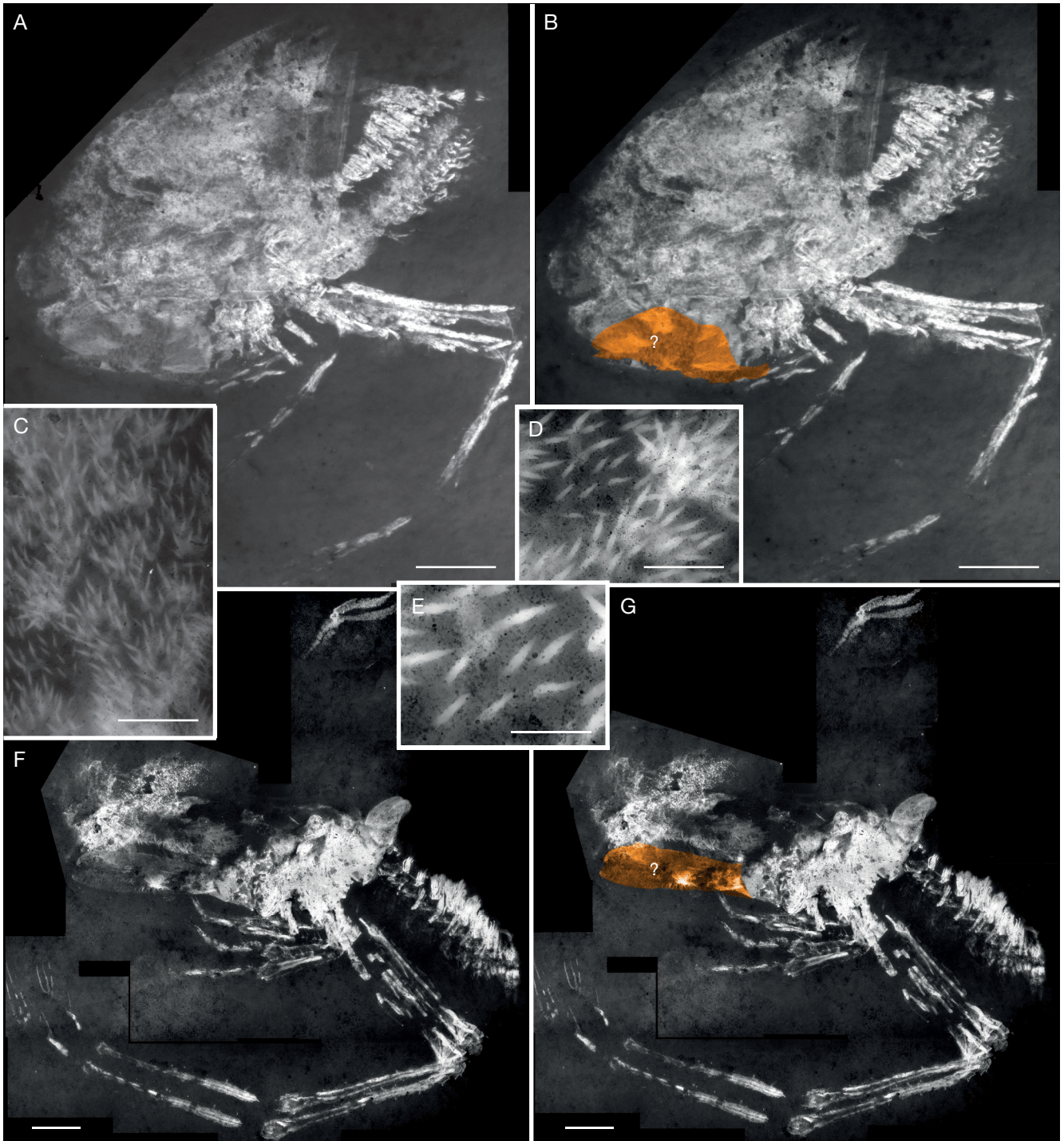


FIG. 8. — *Clausocaris lithographica* (Oppenheim, 1888): **A–E**, SMNS 70193/4; **A**, general view; **B**, general view (color-marked); **C**, close-up of the eye region; **D**, close-up of the eye region; **E**, close-up of the eye region; **F, G**, SMNS 67901; **F**, general view; **G**, general view (color-marked). Abbreviation: ?, indeterminate oval plate. Photographs: C. Haug and J. T. Haug. Scale bars: A, B, 5 mm; C, 1 mm; D, 0.5 mm; E, 0.25 mm; F, G, 2 mm.

The arrangement in thylacocephalans is very different in the new specimen, but also for the specimens from Lebanon. Also in other thylacocephalans we find comparable structures on the shield, for example, in *Paraostenia voutensis* Secretan, 1985 from the Callovian of France or in *Concavicaris* sp. aff. *bradleyi* from the Late Devonian of Poland (Broda *et al.* 2015). Secretan (1985) interpreted dorsal cavity enclosing

capsules in *P. voutensis* as possible chemoreceptors. Rolfe (1985) gave an alternative hypothesis: such structures might be photophores which would have been useful for predation. Broda & Zatoń (2017) distinguished two kinds of perforations: small scattered perforations associated with cuticular polygon and ventral and dorsal circular perforations aligned perpendicularly to the cuticle and associated

with canal-like structures. The first type of perforations were interpreted as setal-fixing pores. The second might have had a sensorial function as they are quite similar to sensory dorsal organs in crustaceans. Sensory dorsal organs have sensory and secretory functions (Lerosey-Aubril & Meyer 2013). It remains difficult to find clear support for this interpretation in Thylacocephala.

Ventral margin

The ventral margin of the shield of the new fossil (Fig. 9A) appears unique within Thylacocephala. The presence of tuberculation on the ventral margin has not yet been observed in any other species of Thylacocephala. Yet, ornamentation of ventral margin is not an unusual feature. *Protozoa hilgendorfi* Dames, 1886 from the Santonian of Lebanon displays teeth on the posterior part of the ventral margin. The ventral margin of *Hamaticaris damesi* (Roger, 1946) carries a small tubercle.

POSSIBLE LIFESTYLES OF THYLACOCEPHALANS

The presence of a specialised posterior process seems to be a common feature in the Carboniferous thylacocephalan species as *C. georgeorum* (Fig. 9C) and *Co. mazonensis* (Fig. 9B). It remains largely unclear what this structure corresponds to and whether it is always the same structure in all Carboniferous forms.

Many representatives of Eucrustacea possess a paired structure arising from the telson, the furca or, referring to the two separate entities, furcal rami. The structure has caused quite some discussion, starting already with its name. Some authors address the structure as “caudal rami” or “caudal furca”, which is unfortunate as crustaceans have an anterior-posterior axis, but lack a cranium and therefore have no cranial-caudal axis known from representatives of Vertebrata. Furthermore, there has been ample discussion what characterises a furca (Bowman 1971; Schminke 1976). Whether thylacocephalans have a true furca or not is still unclear. Still, we can try to infer functional interpretation of these structures.

In extant eucrustaceans, the furca can have different functions, for example as a grooming device, but the most common function is probably locomotion, either by producing thrust or by providing stability (e.g. Hessler 1985). Vannier *et al.* (1997) recognised the importance of the furca for swimming in *Nebalia bipes* (Fabricius, 1780), a representative of Phyllocarida. They also suggested that the furca in *N. bipes* is important for escaping from predators.

Some similarities are apparent, especially in the case of *Co. mazonensis*. The long terminal structures may act similar to the furca in forms of Phyllocarida. This could indicate an original swimming behaviour. Additionally, the bifid, or v-shaped, trunk appendages of *Co. mazonensis* might have been important for swimming. However, one important feature on the appendages and on the terminal structure is missing, setae. Setae provide supplementary surface area, allowing to produce more force during the power stroke (Boudrias 2013). In thylacocephalans from Mazon Creek, there is no indication of setae on trunk appendages and on the terminal structure. Yet, this might be linked to the

preservation of the fossils and is not necessarily indicative of primary absence. It is therefore not possible to conclude with any certainty that the species from Mazon Creek were active swimmers.

Concavicularis remipes also possesses a terminal structure. As pointed out by Schram (1990), the paddle-like posterior structure of *Concavicularis remipes* (Fig. 9D) resembles the furca of representatives of Myodocopida such as that of *Vargula hilgendorfi* (Mueller, 1890). Additionally, the shape of the shield is quite similar to the one of extant representatives of Myodocopida. To think this aspect further: if we compare the shield shape to other forms of Thylacocephala, *C. remipes* proves quite special. It is possible that these specimens might not at all be representatives of Thylacocephala, but of Myodocopida.

Yet, other modes of life were proposed for Thylacocephala. Pinna *et al.* (1985) suggested a burrowing and benthic mode of life for *Ostenocaris cypriformis*. However, this mode of life seems difficult to reconcile with some forms from the Cretaceous of Lebanon that suggest good swimming abilities. Taking into account the previous remarks on Mazon Creek thylacocephalans, various lifestyles could have been adopted by thylacocephalans over times. More information especially on the thoracic appendages, on the body shape and on the anatomy are needed to better understand the mode of life of the different species of Thylacocephala.

MORPHOLOGICAL DIVERSITY OF CARBONIFEROUS THYLACOCEPHALANS

The thylacocephalans from Mazon Creek exhibit an important morphological diversity, especially concerning the shield shape and the morphology of the appendages. The new species increases not only the specific diversity of thylacocephalans during the Carboniferous but also morphological diversity.

Indeed, the morphology of the new species can be considered rather derived in some aspects. Several features remind of the morphology of different Mesozoic forms of Thylacocephala. As pointed out before, a posterior notch is a feature only shared by Mesozoic species such as representatives of *Atropicaris*, *Dollocaris*, *Mayrocaris*, *Paradollocaris* or *Thylacocaris*.

The raptorial appendages of the new species are also different from those of other thylacocephalans from Mazon Creek. They are more robust and stronger and have pronounced armature. In this aspect they are more similar to corresponding structures in Mesozoic species, such as *Dollocaris ingens* Van Straelen, 1923 or *Ostenocaris cypriformis* Arduini, Pinna & Teruzzi, 1984 which also have spine-bearing, rather robust appendages. In the Paleozoic, spiny appendages are only described in *Thylacares brandonensis* (Haug *et al.* 2014). Also the presence of pores on the rectangular dorsal midline is quite similar to the condition in the Cretaceous species *P. hilgendorfi*. The oval-shaped plate is also only so far known in the Jurassic species *Cl. lithographica*. In summary, many characters resemble those among the Mesozoic forms. The new species *Eodollocaris keithflinti* n. gen., n. sp. possesses a ‘mosaic’ of characters known from other Palaeozoic species

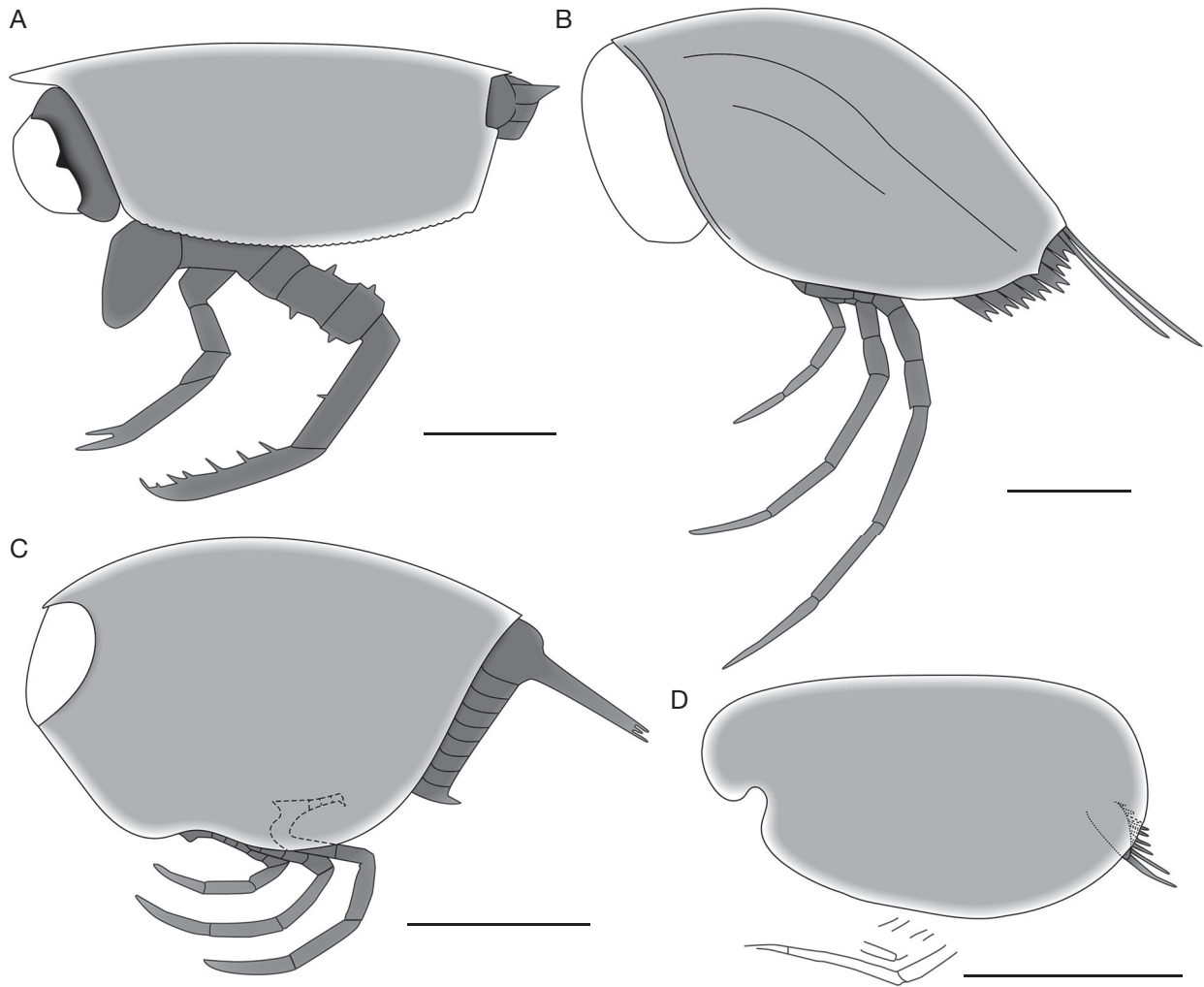


FIG. 9. — Mazon Creek thylacocephalans and possible representative of Myodocopida: **A**, reconstruction of *Eodollocaris keithflinti* n. gen., n. sp.; **B**, reconstruction of *Convexicaris mazonensis* Schram, 1990; **C**, reconstruction of *Concavicaris georgeorum* Schram, 1990; **D**, reconstruction of *Concavicaris remipes* Schram, 1990. **B-D**, adapted from Schram (1990). Scale bars: A-D, 5 mm.

as well as Mesozoic species. Such a character mixture occurs due to mosaic evolution, in which some characters remain in their old (plesiomorphic) state while other characters evolve to new (apomorphic) states. This “mixed morphologies” provide important insights into evolutionary steps between the already known forms and with this lead to a finer graded evolutionary reconstruction. Hence the new species has a rather derived morphology, but co-occurs with other species with a more “typical” Palaeozoic morphology.

CONCLUSIONS AND OUTLOOK

The new species *Eodollocaris keithflinti* n. gen., n. sp. increases the species diversity of Carboniferous thylacocephalans, but also the morphological diversity. With its rather derived morphology, it provides a new insight into the late Palaeozoic diversification of Thylacocephala. Additionally, we provided new details of other species, deepening our knowledge about possible lifestyles of thylacocephalans. Quantitative

approaches to such patterns have the potential to resolve the diversification events in the thylacocephalan lineage.

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