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▶ **To cite this version:**

Sylvain Charbonnier, Arnaud Brayard, Kevin G. Bylund, Gilles Escarguel, Emmanuel Fara, et al.. New thylacocephalans from the Early Triassic Paris Biota (Bear Lake County, Idaho, USA).. Geobios, 2019, 54, pp.37-43. 10.1016/j.geobios.2019.04.005 . hal-02168426

HAL Id: hal-02168426
https://hal.science/hal-02168426

Submitted on 21 Nov 2019

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New thylacocephalans from the Early Triassic Paris Biota (Idaho, U.S.A.)

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Abstract

Two new genera and species of thylacocephalans (Arthropoda, Thylacocephala), *Parisicaris triassica* and *Ligulacaris parisiana*, are described from the early Spathian Paris Biota. These new occurrences are the first reports of thylacocephalans from Triassic rocks in North America. They considerably enlarge the spatiotemporal distribution of these enigmatic arthropods and highlight their relatively high generic richness during the Early Triassic. It also confirms that the Triassic was the taxonomically richest period for Thylacocephala.

Keywords: Euarthropoda, Thylacocephala, new genera, Triassic, Spathian, Paris Biota

1. Introduction

Thylacocephalans are among the most intriguing euarthropods of the Palaeozoic and Mesozoic. They have a stratigraphic range extension from the Silurian (Haug et al., 2014) and possibly earlier (Vannier et al., 2006: Cambrian) to the Late Cretaceous (Dames, 1886; Schram et al., 1999; Charbonnier et al., 2017), when they probably became extinct. They also show a high palaeobiogeographic distribution and are known from all continents except Antarctica and South America (Hegna et al., 2014). They are notably known from Scotland, Spain, France, Germany, Italy, Austria, Slovenia, Lebanon, Madagascar, China, Australia, United States, Mexico, and more recently from Japan (Ehiro et al., 2015).

Their anatomy, mode of life and phylogenetical affinities have remained largely unresolved (Rolfe, 1985; Schram et al., 1999; Lange et al., 2001; Vannier et al., 2006, 2016; Schram, 2014). Thylacocephalans are characterized by a metamerized body protected by a sclerotized "bivalved" carapace (in the wide sense), a pair of compound eyes, sometimes very large, and three pairs of prominent prehensile appendages with spiny tips converging towards the mouth. In the case of some Jurassic taxa such as *Dollocaris* Van Straelen, 1923, these appendages distantly recall the raptorial appendages of extant mantis shrimps (stomatopod crustaceans) and suggest predatory and hunting habits (Charbonnier, 2009, Charbonnier et al., 2010; Vannier et al., 2016).

Historically, thylacocephalans have been tentatively assigned to a great variety of crustacean groups such as stomatopods (Fraas, 1878; Hilgendorf, 1885; Roger, 1946), decapods (Secrétan, 1985) or cirripeds (Arduini et al., 1980). More recently, Haug et al. (2014) proposed a sister-group relationship with Remipedia based on morphological similarities

between *Thylacares* Haug et al., 2014 from the Silurian Waukesha fauna (Wisconsin, U.S.A.) and extant remipeds. These resemblances are the multisegmented and undifferentiated nature of the trunk, and the number and detailed morphology of the sub-chelate raptorial appendages. According to Vannier et al. (2016), this tentative placement of Thylacocephala close to remipeds is questionable given major differences between the two groups in terms of body organisation and exoskeletal structure. At the time of writing, the exact affinities of Thylacocephala remain an open question.

This paper reports new occurrences of thylacocephalans in the early Spathian (Early Triassic) Paris Konservat-Lagerstätte, i.e., the Paris Biota. It increases the taxonomic richness of the Triassic representatives of the group. As stated by Ehiro et al. (2015) and Ji et al. (2017), the Triassic was probably the time period when the generic diversity of Thylacocephala was highest through time. Thus, the present discovery confirms that the Triassic is actually the taxonomically richest period for thylacocephalans and provides new insights on their early Mesozoic radiation.

2. Materials and methods

The examined thylacocephalans come from the Paris Biota (early Spathian, Early Triassic, southeastern Idaho, U.S.A.) in Paris Canyon (five specimens) and a strictly coeval exposure in the neighbouring locality of Georgetown (one specimen) (Fig. 1). They were collected during three scientific missions in 2014, 2015 and 2017.They are housed in the palaeontological collections of the Université de Bourgogne, Dijon, France (acronym: UBGD). Thylacocephalans from the Paris Biota correspond to isolated carapaces preserved flattened on thin-bedded silty limestones (see geological settings in Brayard et al., 2017, this volume).

The cuticles are partially well preserved but are generally removed due to the splitting of the slabs. Thylacocephalans (and also crustaceans) from the Paris Biota are distinctly autofluorescent under UV light (appear yellow; Brayard et al. 2017). The specimens were therefore documented under macro-fluorescence setting to enhance the contrast between fossil and surrounding matrix. UV fluorescence is obtained by illuminating the fossil by a "dark-light" (blue to UV light). Under this kind of light, numerous fossil euarthropods, especially from limestone display a strong yellow autofluorescence (for instance see: Haug et al., 2009; Charbonnier et al., 2017). Pictures are digitally white-balanced to ease the visualisation of fluorescence. Imaging of specimens were realized in natural light or UV fluorescence. Some of the best-preserved specimens were partially prepared manually with a fine needle to allow a more detailed description. All the specimens were observed under binocular microscope with polarized light both dry and covered in 95 per cent ethanol to see cuticular remains with a low angle light to reveal relief and potential soft parts. Line drawings were produced using camera lucida.

3. Systematic palaeontology

In the early 1980s, three higher taxonomic levels were applied to thylacocephalans: the class Thylacocephala Pinna, Arduini, Pesarini and Teruzzi, 1982, class Conchyliocarida Secrétan, 1983, and order Concavicarida Briggs and Rolfe, 1983. Rolfe (1985) adopted the class Thylacocephala for the entire group, comprising two orders: Conchyliocarida and Concavicarida. This systematic classification was followed by Schram (1990), Schram *et al*. (1999), and Lange *et al*. (2001), although the genera included within each order are different in each paper. No family level designations have been made, except for the Austriocarididae

Glaessner, 1931. Recently, Schram (2014) attempted, for the first time, to classify the thylacocephalans to the family level. However, Ehiro *et al*. (2015) considered that no clear definition was given to these families and it seems that further examination is necessary for family-level classification. Even if it is probably perfectible, and according to Charbonnier et al. (2017), we follow the classification ("working hypothesis") proposed by Schram (2014).

Class THYLACOCEPHALA Pinna, Arduini, Pesarini and Teruzzi, 1982

Order CONCAVICARIDA Briggs and Rolfe, 1983

Family Microcarididae Schram, 2014

Included genera: *Atropicaris* Arduini and Brasca, 1984; *Ferrecaris* Calzada and Mañé, 1993; *Microcaris* Pinna, 1974; *Kitakamicaris* Ehiro and Kato in Ehiro, Sasaki, Kano, Nemoto and Kato, 2015; *Parisicaris* nov. gen.

Genus ***Parisicaris*** nov. gen.

Derivation of the name: Derived from the name of the type locality, the Paris Canyon, west of the Paris city, Bear Lake County, Idaho. The gender of the genus is feminine.

Type species: *Parisicaris triassica* nov. sp.

Occurrence: Paris Canyon and Georgetown, Bear Lake County, Idaho.

Diagnosis: Carapace with relatively large optic notch, clearly defined, and limited by short rostrum and subrounded antero-ventral process; concave optic notch with straighter margin above the antero-ventral process ; thick, sharp, downward-curved rostrum, broadly fused with the carapace; antero-ventral process upwardly directed; regular, convex dorsal margin; ventral margin with anterior part showing distinctive ventral notch, and straight, oblique posterior part; short, vertical straightened to slightly concave posterior margin; short, dotted longitudinal lateral carina ; elaborate carapace ornamentation composed of transverse rib-shape incisions.

Remarks: *Parisicaris* nov. gen. is assigned to Concavicarida based upon the following morphological characters: relatively large optic notch, clearly defined and limited by rostral and antero-ventral processes, thick rostrum broadly fused with the carapace, well-developed antero-ventral process. All these morphological characters are more like concavicaridans and more precisely like Microcarididae. Indeed, the carapace ornamentation with subvertical ribs is also very similar to what occurs in several other genera of Microcarididae (*Atropicaris Microcaris*, *Kitakamicaris*). Especially, the general morphology of *Parisicaris* resembles *Kitakamicaris* from the Triassic of Japan, but some important differences can be reported: the ventral notch is absent in *Kitakamicaris* and the subvertical ribs are very dense. The dotted longitudinal lateral carina in dorsal region of *Parisicaris* is also probably present in *Kitakamicaris* (see Ehiro et al., 2015: fig. 8.5). Among Microcarididae, *Parisicaris* differs from *Atropicaris*, *Ferrecaris*, *Kitakamicaris* and *Microcaris* by its peculiar ventral notch (absent in all other four genera), and by its large optic notch delimited by well-developed antero-ventral process. More generally, *Parisicaris* is clearly distinguished from all other Triassic genera by its really noticeable ventral notch.

One can note that *Parisicaris* presents also some affinities with Conchyliocarida. For instance, the ventral notch is relatively similar to what occurs only in *Mayrocaris* Polz, 1994 (Dollocarididae Schram, 2014) from the Jurassic of Germany. A relatively similar dotted longitudinal lateral carina is also known in *Mayrocaris* but more in the central region of carapace (Polz 1994, 1997). The straightened to slightly convex posterior margin is also present in *Ostenocaris* Arduini, Pinna and Teruzzi, 1984 (Ostenocarididae Schram, 2014).
In conclusion, the placement of *Parisicaris* in Microcarididae is likely, but future investigations in thylacocephalan phylogeny might move things along.

Parisicaris triassica nov. sp.
Figs. 2, 3

Derivation of the name: The specific epithet alludes to the Triassic age of the Paris Biota.

Type material: Holotype UBGD 30561 (Fig. 2A-D); three paratypes UBGD 30613 (Fig. 2E-G), UBGD 30614 (Fig. 3A-C), UBGD 30615 (Fig. 3D).

Type locality and horizon: Paris Canyon, west of the Paris city, Idaho, United-States of America; paratype UBGD 30615 comes from the neighbouring locality of Georgetown (see Fig. 1); Early Triassic, early Spathian (after Brayard et al., 2017).

Description: Bivalved carapace, laterally compressed, longitudinally elongated (holotype: length: ca. 41 mm; height: ca. 24 mm), with relatively large optic notch and subvertical posterior margin of similar size; convex dorsal margin separating carapace in two identical valves, regular (i.e. without crest), prolonged frontally by the rostrum; concave optic notch

broadly excavated, limited by short rostrum and subrounded antero-ventral process; concave optic notch with straighter, downwardly inclined margin above the antero-ventral process; thick, sharp, downward-curved rostrum, broadly fused with the carapace, bearing short, convex lateral carina; antero-ventral area developed as plate-like lobe, upwardly directed and subrounded distally; ventral margin with anterior part showing distinctive ventral notch (at level of muscle scar area, known in many thylacocephalans, but not herein visible) and posterior part (where trunk limbs or pleopod-like appendages usually protrude in thylacocephalans, but not herein visible) straight and inclined at about 140° angle to the longitudinal axis of carapace, joined to posterior margin by small, rounded postero-ventral process; vertical, straightened to slightly concave posterior margin, as high up as optic notch; short, slightly convex, dotted longitudinal lateral carina, in dorsal area; carapace with elaborate ornamentation composed of transverse, slight falciform rib-shape incisions; about 20 primary ribs running parallel to each other from the dorsal margin to the ventral margin; secondary ribs inserted sporadically in both dorsal (ca. 12 ribs) and ventral (ca. 12 ribs) areas, most of them interrupted before reaching the middle of the caparace; organisation of rib-shape incisions more complex in antero-ventral and cephalic areas (junction of some branches); soft parts and appendages not preserved.

Remarks: In the holotype of *Parisicaris triassica*, the left valve is only visible along the dorsal margin and suggests the specimen is laterally compressed. The ventral notch is found in only two thylacocephalan genera (*Parisicaris*, *Mayrocaris*) and we do not known if this unusual structure is really a distinctive antero-ventral embayment or a well-developed mid ventral flap. Such ventral flap, but with an extreme development in that case, is observed in the very peculiar keel-shaped carapace of *Keelicaris* Teruzzi and Charbonnier in Charbonnier et al., 2017 from the Cretaceous of Lebanon (see Charbonnier et al., 2017).

The paratype UBGD 30613 (Fig. 2E-G) is poorly preserved but shows the two disconnected valves of the carapace. The splitting of the carapace with the displacement of the two valves evoke a molted specimen and a probable exuvia. This kind of molting position is frequently found in fossil decapod crustaceans (for instance see Glaessner, 1969; Charbonnier et al., 2012).

The paratype UBGD 30614 (Fig. 3A-C) is relatively complete but its carapace is slightly broken and displaced at level of the ventral notch. This suggests that the ventral margin was less carinated at level of ventral notch as observed in the holotype where the marginal belt is clearly interrupted. The paratype UBGD 30615 (Fig. 3D) is very incomplete and the superposition of the valves of the carapace also evoke a probable exuvia. It was probably a large specimen but posterior and anterior parts are missing (e.g., dorsal and posterior margins, and ventral and optic notches not visible).

Family Concavicarididae Schram, 2014

Included genera: *Concavicaris* Rolfe, 1961; *Ankitokazocaris* Arduini, 1990; *Harrycaris* Briggs and Rolfe, 1983; *Ligulacaris* nov. gen.

Genus ***Ligulacaris*** nov. gen.

Derivation of the name: Derived from the Latin *ligula* (“strap”, “spoon”), alluding to the small tongue-shaped carapace. The gender of the genus is feminine.

Type species: *Ligulacaris parisiana* nov. sp.

Occurrence: Paris Canyon, west of the Paris city, Bear Lake County, Idaho.

Diagnosis: Carapace with deep optic notch, limited by short rostrum and subrounded antero-ventral process; hypertrophied eye; regular, convex dorsal and ventral margins; narrow posterior margin with small ventral posterior notch; subcircular muscle scar; carapace with several longitudinal lateral carinae or stripes (wrinkled texture), well-developed from median to anterior regions.

Remarks: *Ligulacaris* nov. gen. is assigned to Concavicarida based upon the following morphological characters: large optic notch, clearly defined and limited by rostral and antero-ventral processes, rostrum fused with the carapace, hypertrophied eye; posterior notch present. All these morphological characters are more like concavicaridans and more precisely like Concavicarididae. Among Concavicarididae, *Ligulacaris* differs from *Concavicaris*, *Ankitokazocaris*, and *Harrycaris* by its numerous longitudinal lateral stripes forming a very unique wrinkled texture (two to three carinae in *Concavicaris*; only one dorsal lateral carina in *Ankitokazocaris*; no lateral carina in *Harrycaris*), and by its large optic notch (relatively narrow in *Concavicaris*; surrounded by the meeting of down-turned rostrum and upwardly directed antero-ventral process in *Harrycaris*). The carapace morphology of *Ligulacaris* seems similar to that of *Concavicaris*. For instance, its carapace outline is relatively closed to those of *C. campi* Briggs and Rolfe, 1983, and *C. playfordi* Briggs and Rolfe, 1983 (Devonian, Australia) and also *C. desiderata* (Barrande, 1872) and *C. incola* Chlupáč, 1963 (Devonian, Czech Republic). The numerous longitudinal lateral stripes characterizing the new genus are also present, but in lower number, in *C. campi* (three lateral carinae) and *C. playfordi* (two lateral carinae). Moreover, the lateral stripes in *Ligulacaris* are at the origin

of a wrinkled texture whereas the carapace surface is strongly carinated (e.g., with acute angles in *Concavicaris*).

Ligulacaris parisiana nov. sp.

Fig. 4

Derivation of the name: The specific epithet alludes to the Paris Biota.

Type material: Holotype UBGD 30562, paratype UBGD 30616.

Type locality and horizon: Paris Canyon, west of the Paris city, Idaho, United-States of America; Early Triassic, early Spathian (after Brayard et al., 2017).

Description: Bivalved carapace, laterally compressed, longitudinally elongated (holotype: length: ca. 16 mm; height: ca. 7.5 mm), with deep optic notch and very narrow posterior margin; concave optic notch broadly excavated, limited by short rostrum and subrounded antero-ventral process; optic notch limited by thick orbital margin; hypertrophied eye; convex dorsal margin separating carapace in two identical valves, regular (i.e. without crest), prolonged frontally by the rostrum; regular, convex ventral margin converging posteriorly with dorsal margin; narrow posterior margin with small ventral posterior notch; subcircular muscle scar; carapace with longitudinal lateral carinae or stripes (wrinkled texture), slightly concave, well-developed from median to anterior regions; among longitudinal lateral stripes, three (dorsal, median and ventral stripes) are curved upward before joining orbital margin, and two others (median stripes) are short and limited to central region of carapace; appendages not preserved.

Remarks: The carapace of paratype UBGD 30616 is incomplete (posterior part absent) and poorly preserved (weathered surface), but shows anteriorly the imprint of a hypertrophied eye only well-visible under UV light or when the specimen is covered in 95 per cent ethanol.

4. Conclusions

Until now, Early Triassic thylacocephalans have been reported only from the Dienerian-Smithian of Madagascar (Arduini, 1990), but they have also recently been described from the late Spathian of Japan (Ehiro et al., 2015) and South China (Ji et al., 2017), and briefly mentioned from the Smithian of Western Australia (Haig et al., 2015). The Paris Biota comprises two new genera represented by isolated carapaces. They are the first reports of thylacocephalans from Triassic rocks in North America, and therefore considerably expand their known palaeobiogeographic distribution in the Early Triassic. The two new genera reveal that the thylacocephalan paleobiodiversity is still substantially underestimated. Early Triassic thylacocephalans thus exhibit a generic diversity comparable to the Middle (three genera) and Late Triassic (five genera): five genera are now documented for the Early Triassic (among which two are from the western USA basin) from a total of eleven genera reported for the entire Triassic (Table 1).

According to Ji et al. (2017), with emerging discoveries of new species, the Triassic will soon be recognized as the taxonomically richest period for Thylacocephala.

Acknowledgments

We thank Masayuki Ehiro (Tohoku University Museum, Japan) and an anonymous reviewer for their valuable reviews of this work and for their useful advices. Philippe Loubry and Lilian Cazes (UMR 7207 CR2P), Gaëlle Doitteau and Jocelyn Falconnet (MNHN, E-Recolnat, ANR-11-INBS-0004), and Jérôme Thomas (UMR 6282 Biogéosciences; E-Recolnat, ANR-11-INBS-0004) provided excellent photographs of specimens. This work is a contribution to the ANR project AFTER (ANR-13-JS06-0001-01) and was also supported by the French "Investissements d'Avenir" program, project ISITE-BFC (ANR-15-IDEX-03). We acknowledge the Bear Lake County road department and D. M. Clow (Ogden) for allowing access to the studied exposures.

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Table and figure captions

Table 1. List of the thylacocephalans from the Triassic with their distribution.

Fig. 1. Map of southeastern Idaho showing the location of the thylacocephalan specimens found in the Paris Biota at Paris Canyon (red circle) and Georgetown (yellow circle).

Fig. 2. *Parisicaris triassica* nov. gen, nov. sp. from the early Spathian Paris Biota (Idaho, U.S.A.). **A-D.** holotype UBGD 30561, complete carapace in right lateral view: natural light (A), UV light (B), interpretative line drawing (C), detail of the dotted longitudinal lateral carina in dorsal region (D). **E-G.** paratype UBGD 30613, incomplete and splitted carapace (probable exuvia) in left lateral view: natural light (E), UV light (F), interpretative line drawing (G). Abbreviations: avp= antero-ventral process, dm= dorsal margin, lc= lateral carina, lv= left valve, on= optic notch, pm= posterior margin, pvp= postero-ventral process, r= rostrum, ri= rib-shape incisions, rv= right valve, vm= ventral margin, vn= ventral notch. Scale bars: 10 mm except (D)= 5 mm. Line drawings: S. Charbonnier. Photographs: G. Doitteau (A, D) and P. Loubry (B, E, F).

Fig. 3. *Parisicaris triassica* nov. gen, nov. sp. from the early Spathian Paris Biota (Idaho, U.S.A.). **A-C.** paratype UBGD 30614, subcomplete specimen (counterpart) in right lateral view: natural light (A), UV light (B), interpretative line drawing (C). **D.** paratype UBGD 30615, incomplete and deformed specimen (probable exuvia). Abbreviations: avp= antero-ventral process, dm= dorsal margin, lc= lateral carina, on= optic notch, pm= posterior margin, pvp= postero-ventral process, r= rostrum, ri= rib-shape incisions, rv= right valve, vm= ventral margin, vn= ventral notch. Scale bars: 5 mm. Line drawing: S. Charbonnier. Photographs: J. Falconnet (A), P. Loubry (B), and J. Thomas (D).

Fig. 4. *Ligulacaris parisiana* nov. gen, nov. sp. from the Spathian Paris Lagerstätte (Idaho, U.S.A.). **A-C.** holotype UBGD 30562, specimen in right lateral view: natural light (A), UV

light (B), interpretative line drawing (C). **D-F**. paratype UBGD 30616, incomplete specimen (posterior part absent) and poorly preserved (weathered surface), right lateral view: natural light (under 95% ethanol) (A), UV light (B), interpretative line drawing (C); note the hypertrophied eye appearing as a black diffuse spot. Abbreviations: avp= antero-ventral process, dm= dorsal margin, eye= hypertrophied eye, lc= lateral carina, ms= muscle scar, om= orbital margin, on= optic notch, pvn= postero-ventral notch, r= rostrum, rv= right valve, vm= ventral margin. Scale bars: 5 mm. Line drawings: S. Charbonnier. Photographs: G. Doitteau (A), L. Cazes (B), J. Falconnet (D), and P. Loubry (E).