

Rapid Communication

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A possible vicissicaudatan arthropod from the Late Carboniferous Mazon Creek Lagerstätte

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Abstract

The Vicissicaudata, a group of arthropods, originated and reached their highest diversity during the Cambrian period. However, relatively few vicissicaudatan species are known from the Paleozoic. Here we report a new species of vicissicaudatan arthropod, sister to the cheloniellids, from the Late Carboniferous Mazon Creek Lagerstätte. The two specimens preserve a small eyeless head, a trunk comprising seven tergites with wide pleural lobes, a narrower postabdomen bearing two long, posteriorly directed caudal appendages, and a short, shield-shaped telson. This new species not only extends the stratigraphic range of the Vicissicaudata into the Late Paleozoic but also represents an intermediate morphology between the cheloniellids and other vicissicaudatans.

1. Introduction

The arthropods were a major component during the evolution of the Cambrian marine fauna (Hesselbo, 1992; Hou & Bergström, 1997; Ortega-Hernández *et al.* 2013; Lerosey-Aubril *et al.* 2017; Du *et al.* 2023). Within the arthropods, the Vicissicaudata exhibited their highest diversity during the Cambrian and remained fairly widespread and diverse throughout the Ordovician (Lerosey-Aubril *et al.* 2017). Post-Ordovician, the Vicissicaudata are represented by only a few taxa. Most are cheloniellids, a rare but important group of arthropods that originated in the Late Ordovician (Braddy & Dunlop, 2021; Van Roy *et al.* 2022). The post-Ordovician cheloniellids include *Pseudarthron whittingtoni* from the late Silurian Ludlow Series in Scotland (Selden & White, 1983), *Cheloniellon calmani* from the Lower Devonian Hunsrück Shale in Germany (Stürmer & Bergström, 1978), and *Paraduslia talimaae* from the Lower Devonian Severnaya Zemlya Formation from Russia (Dunlop, 2002). In addition to cheloniellids, the post-Ordovician vicissicaudatans include *Carimersa neptuni* from the Silurian Herefordshire Lagerstätte in the UK (Briggs *et al.* 2023). Here, we describe a new vicissicaudatan arthropod which resolves as the sister taxon to the cheloniellids, *Tardisia broedeae* gen. et sp. nov., from the Late Carboniferous Mazon Creek fossil site. This new record extends the stratigraphic range of the vicissicaudatan arthropods to the late Paleozoic in the paleotropics and provides new morphological data to reconcile the evolutionary history of crown vicissicaudatans.

2. Materials and methods**2.a. Specimens**

Two specimens from the Invertebrate Paleontology collections of the Field Museum of Natural History in Chicago, Illinois, USA were included in this study: FMNH PE928 and FMNH PE88856. FMNH PE928 was collected and then donated to the Field Museum by George Langford and is one-half of a siderite concretion without its counterpart. The counterpart of this specimen was at one point in the possession of George Langford; his notes, including a photograph of the part and counterpart of this specimen and his line-drawing reconstruction, were reproduced and published by the Earth Science Club of Illinois (Langford, 2018). Langford donated his specimens to either the Field Museum or the Illinois State Museum (Langford, 2018); however, we could not find the counterpart to this specimen in either collection. FMNH PE88856 is similarly one-half of a siderite concretion without its counterpart. It was originally collected by Thomas V. Testa and was donated to the Field Museum by Jack Wittry.

2.b. Geologic background

The Late Carboniferous (~308.6–308.4 Ma (Montañez *et al.* 2016)) Mazon Creek fossil site is famous for its exceptionally diverse and abundant assemblage of fossils preserved inside siderite

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(FeCO₃) concretions (Clements *et al.* 2019; Burke *et al.* 2024). The concretions are found in a three- to eight-metre-thick layer located near the base of the Francis Creek Shale, a grey shale that is up to 25 metres thick (Baird, 1979, 1997; Baird *et al.*, Shabica & Hay, 1997; Clements *et al.* 2019; Burke *et al.* 2024). The Mazon Creek fossils are traditionally divided into two assemblages (Baird *et al.* 1985a; Baird *et al.*, 1986; Burke *et al.* 2024): the Braidwood assemblage, which includes terrestrial fauna and flora washed in from a nearshore coal swamp as well as a low-diversity brackish-freshwater fauna; and the Essex assemblage, which encompasses marine-to-brackish animals living in the nearshore delta where the concretions formed. However, some authors argue that the Braidwood/Essex biota split is not accurate, because it represents the endpoints of a continuum rather than two discrete biotas (Clements, Purnell & Gabbott 2019).

Of the two fossils included in this study, FMNH PE928 does not have very specific locality information. The general region given for where it was collected, between Wilmington, Braidwood, and Coal City, mostly encompasses localities known for the Braidwood assemblage, although also some Essex assemblage localities (Baird *et al.* 1985a). FMNH PE88856 was found in Pit 11, one of the classic Essex assemblage localities (Johnson & Richardson, 1966; Burke *et al.* 2024). The specific environment in which *T. broedae* lived is therefore not clearly constrained.

2.c. Photography

Specimens were photographed with a Canon EOS R5 with a 60mm Macro lens, aperture of f/11, exposure of 1/5 second, ISO of 12800, and no flash under polarized light. Measurements were taken from specimen photographs using ImageJ (Schneider *et al.* 2012).

2.d. Computed tomography

Both specimens were scanned together separated by a thin piece of wrapping foam using a GE dual tube μ CT scanner at the PaleoCT lab in the Department of Organismal Biology and Anatomy at the University of Chicago. The scan used a 240 kV micro-focus tube at 120kV and 130 μ A at 250 ms exposure timing, using filter of 0.3 mm Cu. Resolution of voxel $x = y = z = 15.1080 \mu\text{m}$ with 2000 projection images was achieved. The μ CT volumes were visualized using Avizo Software 3D 2023.1 (Thermo Fisher Scientific, Waltham, MA, United States). For features that were only visible in the CT scans, measurements were taken from CT scan images using imageJ (Schneider *et al.* 2012). The computed tomography data have been deposited at <https://www.morphosource.org/concern/media/000624704?locale=en>

2.e. Phylogenetic analysis

The new arthropod was coded into the dataset of Briggs *et al.* (2023) in order to ascertain its phylogenetic affinities. The character matrix was unmodified except for the addition of the new species, resulting in a dataset consisting of 104 characters coded for 79 taxa (Tables S1, Table S2). This matrix was analyzed under maximum parsimony optimality criteria using TNT v. 1.5 (Goloboff & Catalano, 2016). The parsimony search strategy employed 10,000 random addition sequences with all characters unordered and of equal weight (Congreve & Lamsdell, 2016), each followed by tree bisection-reconnection (TBR) branch swapping. Jackknife (Farris *et al.* 1996), Bootstrap (Felsenstein, 1985) and Bremer (Bremer, 1994) support values were also calculated in TNT. Bootstrapping was performed with 50% resampling for 1,000

repetitions, while jackknifing was performed using simple addition sequence and tree bisection-reconnection branch swapping for 1,000 repetitions with 33% character deletion.

3. Systematic palaeontology

Arthropoda Siebold (1848)

Artiopoda Hou and Bergström (1997)

Vicissicaudata Ortega-Hernández *et al.* (2013)

Remarks. The newly described species is assigned to the Vicissicaudata because it shows several characteristic vicissicaudatan features (Lerosey-Aubril *et al.* 2017; Briggs *et al.* 2023). The Vicissicaudata have a trunk of 6–19 segments, all except for 1–4 of the posterior-most ones with wide pleura. The new species has seven thoracic tergites in the trunk with wide pleurae, and a one-segment postabdomen, which lacks wide pleurae. In addition, the postabdomen of the new species bears a pair of posteriorly directed caudal appendages, a feature commonly seen in Vicissicaudata. Finally, posterior to the postabdomen is a telson. This assignment is further supported by the results of our phylogenetic analysis.

Tardisia gen. nov.

Etymology. The genus name *Tardisia* (feminine) is inspired by the TARDIS time machine in the TV show Dr. Who, and refers to the large stratigraphic gap between this species and the next youngest members of the Vicissicaudata.

Type species. *Tardisia broedae* gen. nov. sp. nov. by monotypy.

Localities and horizon. As for the type species, by monotypy.

Diagnosis. As for the type species, by monotypy.

T. broedae sp. nov.

Etymology. The species name *broedae* honours Irene Broede, a Mazon Creek collector who volunteers for the Field Museum and is an active member of the Earth Science Club of Northern Illinois (ESCONI).

Holotype. FMNH PE928 (Fig. 1a–c). Almost-complete specimen in dorsal view, preserving part of the head, thorax, postabdomen with caudal appendages and telson. Preserved in a siderite concretion, part only.

Additional material. Paratype FMNH PE88856 (Fig. 1d–f). Almost-complete specimen in dorsal view, preserving the head, thorax and postabdomen with caudal appendages, but missing the telson. Preserved in a siderite concretion, part only.

Localities and horizon. Francis Creek Shale Member of the Carbondale Formation. The holotype, FMNH PE928, was collected between Wilmington, Braidwood, and Coal City, in Will County, Amazon Creek Region, of Illinois, USA. FMNH PE88856, was collected from Pit 11, Peabody Coal Company Northern Mine Locality T31N R9E Sec 6 SE1/4, SE1/4, 41.189128, –88.226618, Mazon Creek Region, Kankakee County, Illinois, USA.

Diagnosis. Head shield smaller than the first thoracic tergite, no eyes. Seven thoracic tergites with wide pleural lobes ending in posteriorly directed points. Eighth trunk segment differentiated into a postabdomen without wide pleural lobes, bearing a pair of long, posteriorly directed, caudal appendages. Short, wide, shield-shaped telson overlaps the bulbous base of the caudal appendages where they insert into the postabdomen.

Description. The holotype, specimen FMNH PE928 (Fig. 1a–c) comprises one-half of a siderite concretion with the fossil preserved in negative relief (Fig. 1a). The overall shape of the body approximates an elongated oval, with its widest point at the third thoracic tergite (Fig. 1a–c). This specimen is missing the anterior-most portion of the head shield, but the preserved portion of the

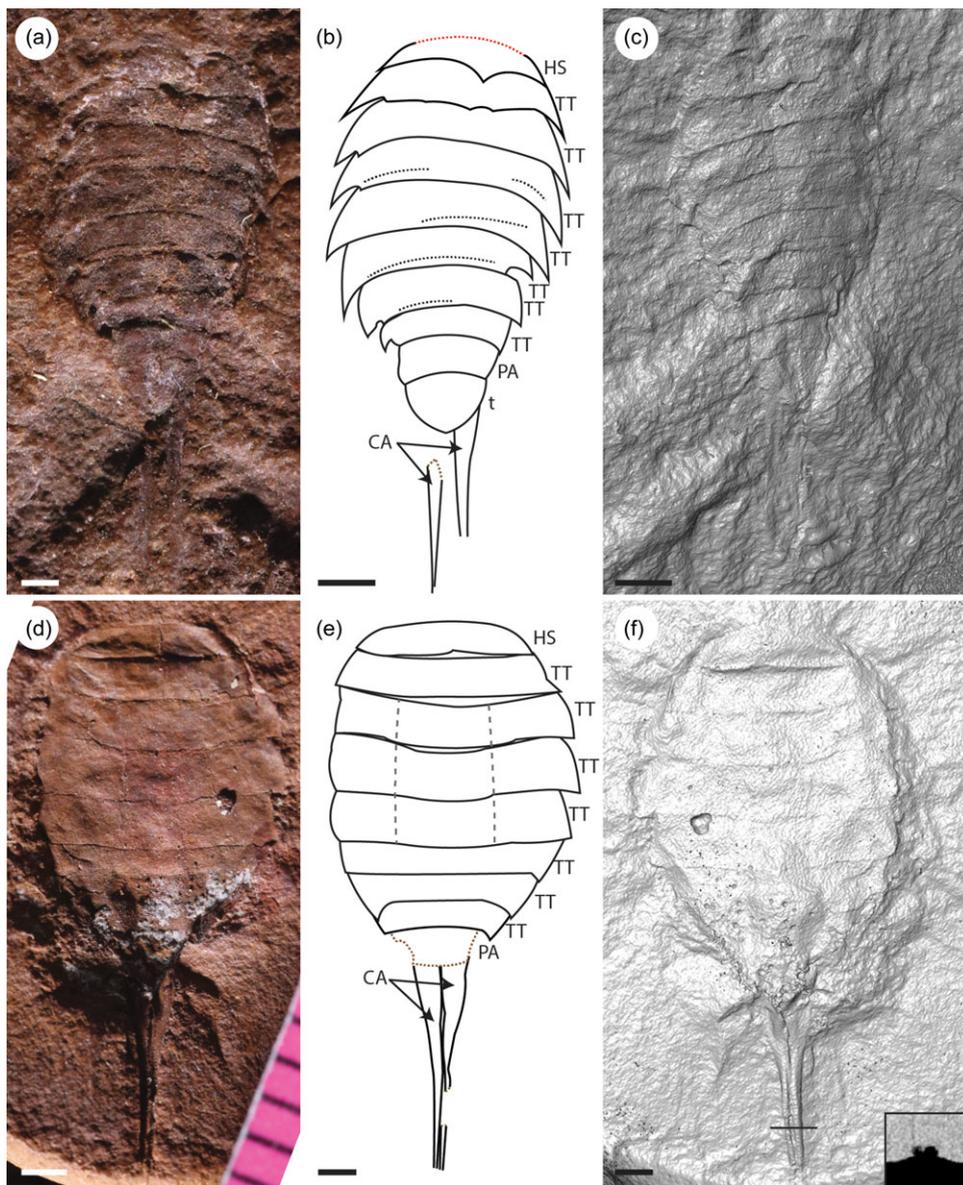


Figure 1. *Tardisia broedeae* gen. et sp. nov. specimens, line drawings, and CT scans. (a–c) Holotype, FMNH PE928. (a) Fossil specimen, photographed under cross-polarized light. (b) Line drawing of FMNH PE928, black dotted lines indicate overlap between the tergites, brown dotted lines show where the specimen is overlain by concretionary material, and the red dotted line at the anterior of the head indicates the anterior margin of the head as reconstructed by Langford. HS is for head shield, TT is for thoracic tergite, PA is for postabdomen, t is for telson, and CA is for the caudal appendages. (c) CT scan of FMNH PE928, reconstructed as if looking through the concretion, and showing the surface of the fossil currently obscured by the concretion. The arrows indicate the bulbous bases of the appendages. (d–f) Paratype FMNH PE 88856. (d) Fossil specimen, photographed under cross-polarized light. (e) Line drawing of FMNH PE 88856, grey dotted lines indicate where the tergite curvature changes, which likely delineates the axis. Brown dotted lines indicate the preserved edges of the postabdomen, which likely do not reflect the complete original shape. HS is for head shield, TT is for thoracic tergite, PA is for postabdomen, t is for telson, and CA is for the caudal appendages. (f) CT scan of FMNH PE88856, reconstructed as if looking through the concretion, and showing the surface of the fossil currently obscured by the concretion. Note the rounded anterior margin of the head. Inset is a digital slice of the CT scan, at the point in the fossil indicated by the black line, showing the appendages in cross section. All scale bars = 1 mm.

body is 10.6 mm long from the anterior-most preserved part of the head to the posterior-most tip of the telson, and 6.2 mm wide at its widest point in the third trunk tergite. According to Langford’s photograph and line drawing (Langford, 2018), the head shield was fully preserved in the half of the concretion that is now lost and was rounded and sub-semicircular (~106° arc), smaller than the first thoracic tergite and lacking eyes (Fig. 1b).

The trunk comprises seven tergites, a postabdomen and a telson (Fig. 1a–c). Seven tergites comprise the thorax and terminate in posteriorly directed points. In four of these, the posterior margin of the tergite overlaps the anterior margin of the next tergite, suggesting that each tergite overlaps the posterior one (Fig. 1a, b). The eighth trunk segment is differentiated into a narrower postabdomen, lacking wide pleura, which bears a pair of caudal appendages. The seven trunk tergites and the postabdomen are all approximately 1 mm long. From the first to the seventh trunk tergite, their respective widths are 5.7 mm, 5.9 mm, 6.2 mm, 5.7 mm, 4.9 mm, 3.9 mm and 3.0 mm; the postabdomen is 2.5 mm wide. The telson is shield-shaped (Fig. 1a–c), 1.6 mm long and

2.1 mm wide at its widest point (its anterior end). The axis is not clearly differentiated in this specimen.

The caudal appendages preserved in this specimen, either on the concretion half we have, or on the half that is now lost (Langford, 2018); no appendages preserved inside the concretion were observed in the CT scan. The caudal appendages on the postabdomen are not fully preserved, both lack their posterior-most end, and the region where the left appendage intersects the telson is obscured by some concretionary material (Fig. 1a–c). The right appendage is 0.5 mm wide where it intersects the telson, and the left appendage (which has a longer preserved length) extends 4.5 mm beyond the telson. In the fossil (Fig. 1a, b), both appendages narrow continuously from anterior to posterior. In the CT scan (Fig. 1c), it is apparent that these appendages have bulbous anterior ends where they meet the postabdomen, which is covered by the telson. Based on the CT scans (Fig. 1c), the appendages are about 1 mm wide where they meet the postabdomen, and the maximum preserved appendage length is 6.1 mm. These appendages are straight, and there is no

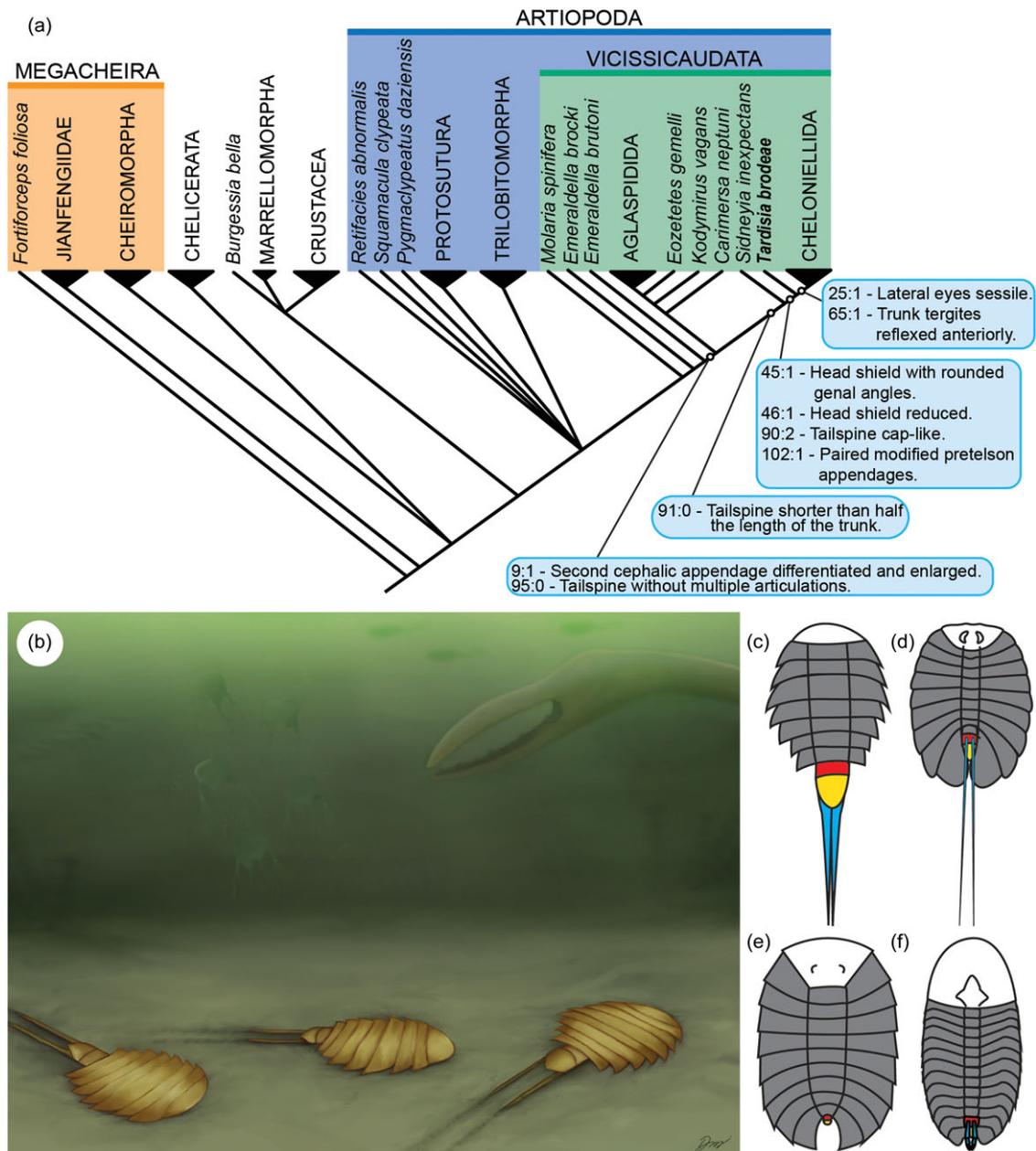


Figure 2. Phylogenetic analysis, artist's reconstruction of *Tardisia broedeae* gen. et sp. nov., and line-drawing comparisons to some cheloniellids. (a) Phylogenetic tree showing the placement of *T. broedeae* as the sister taxon to the cheloniellids. (b) Artist's reconstruction of *T. broedeae* in the Mazon Creek ecosystem; appendages other than the caudal appendages are not reconstructed; art by Sofia Herrera. (c–f) Line drawings of *T. broedeae* and other cheloniellids (not to scale with each other) showing key morphological comparisons. Appendages other than the caudal appendages are omitted from the line drawings. The head shield is white, the thoracic tergites are grey, the postabdomen is red, the telson is yellow, and the caudal appendages, if present, are blue. (c) *T. broedeae*. (d) *Cheloniellon calmani*, redrawn and simplified from Stürmer and Bergström (1978). (e) *Triopus draboviensis*, redrawn and simplified from Van Roy et al. (2022). (f) *Paraduslia talimaee*, redrawn and simplified from Dunlop (2002).

evidence as to whether they were flexible or movable. Their preservation in these specimens when the trunk biramous appendages were not preserved suggests the caudal appendages were heavily sclerotized, with similarly robust cuticles as the dorsal exoskeleton.

The paratype specimen FMNH PE88856 (Fig. 1d–f) also comprises one-half of a siderite concretion with the fossil preserved in negative relief (Fig. 1d). The overall shape of the body is oval, with its widest point at the third trunk tergite (Fig. 1d–f). This specimen is missing the telson, and the postabdomen is poorly preserved

(Fig. 1d–f), but the preserved portion of the body measures 8.6 mm long from the head to the posterior-most preserved part of the postabdomen, and 5.6 mm wide at its widest point in the third thoracic tergite. The head shield of this specimen is completely preserved. It is smaller than the first trunk tergite and bears no eyes. In the fossil, the head shield appears to have a straight anterior margin (Fig. 1d). However, in the CT scan, it is clear that the head is rounded and sub-semicircular (~94° arc) (Fig. 1f).

The trunk comprises seven tergites, a poorly preserved postabdomen, and the telson is not preserved (Fig. 1d–f).

The first seven tergites, which form the thorax, terminate in posteriorly directed points, although these are less pronounced than in FMNH PE928 (Fig. 1). The curvature of some of the trunk tergites changes abruptly, which likely delineates the axis of the body (Fig. 1d–f). The axis is ~2 mm wide in all the segments where it can be measured. The first three tergites have tergopleurae that curve slightly towards the anterior of the body (Fig. 1d–f); this might just be due to flattening the three-dimensional body at an angle (Van Roy *et al.* 2022). The eighth trunk segment is too poorly preserved to confirm its differentiation into the postabdomen (Fig. 1d–f); however, it does bear a pair of caudal appendages. The first four trunk tergites are ~1 mm long, the fifth through seventh trunk tergites are each ~0.6 mm long and the postabdomen is too poorly preserved to measure. From the first to the seventh trunk tergites, their respective widths are 5.0 mm, 5.4 mm, 5.6 mm, 5.4 mm, 4.6 mm, 3.8 mm and 2.9 mm. The telson is not preserved.

As with FMNH PE928, the caudal appendages on the postabdomen are the only appendages preserved in this specimen and no appendages preserved inside the concretion were observed in the CT scan. In this specimen as well as in FMNH PE928, there is no evidence as to whether the caudal appendages were flexible or movable. The appendages are not fully preserved, and both lack their posterior-most end (Fig. 1d–f). The bulbous base of the appendages, where they meet the postabdomen, is clearly visible for both appendages; this was obscured by the telson in FMNH PE928 (Fig. 1a–c) and indicates that the telson is not preserved in FMNH PE88856. The appendages are ~0.6 mm wide where they meet the postabdomen and extend 4.7 mm posterior to the postabdomen. These appendages have a striated appearance (Fig. 1d). These appendages are preserved with high relief and are semicircular in cross section (Fig. 1f inset); however, the appendages may have been compressed during fossilization, in which case they could have originally had more relief, potentially to the point of being circular in cross section. The cross section (Fig. 1f inset) also shows that the two appendages are separate. Based on the features revealed in the CT scan – two separate structures that are semicircular to circular in cross section – we can discard a tailspine interpretation for these appendages.

4. Discussion

The lack of preserved trunk biramous appendages in *T. broedae* gen. et sp. nov. makes it difficult to directly evaluate it for the diagnostic arthropod features, which all refer to the appendages (Stein & Selden, 2012). However, the results of our phylogenetic analysis are congruent with those of Briggs *et al.* (2023) and place *T. broedae* within the arthropods and specifically within the Vicissicaudata as the sister group to the Cheloniellida (Fig. 2a; Fig. S1). The cheloniellids, including the position of *Tardisia* as sister taxon, are one of the more well-supported groups in the phylogeny with high internal node support values. *T. broedae* does exhibit the morphological characters which unite the Vicissicaudata (Lerosey-Aubril *et al.* 2017; Briggs *et al.* 2023): trunk of 6–19 segments, all except for 1–4 of the posteriormost ones with wide pleura, the last trunk segment bearing a pair of caudal appendages. It is unusual in that it lacks eyes, contrary to most vicissicaudatans (Lerosey-Aubril *et al.* 2017), although many cheloniellids, such as *Neostrabops martini*, *Duslia insignis*, an

unnamed *Duslia*-like cheloniellid from Morocco, and *Paradusila talimaae* are reported to lack eyes (Dunlop, 2002; Braddy & Dunlop, 2021).

Cheloniellids are united by a number of features, some of which can be evaluated in *T. broedae*. Like cheloniellids, *T. broedae* has a wide, oval body, with a head shield narrower than the first tergite (Dunlop, 2002; Braddy & Dunlop, 2021). Many vicissicaudatans have a narrow, elongate tail spine (Lerosey-Aubril *et al.* 2017; Briggs *et al.* 2023); in contrast, cheloniellids have a short pointed telson described as conical or cap-shaped (Stürmer & Bergström, 1978; Braddy & Dunlop, 2021; Van Roy *et al.* 2022), which, if dorsoventrally flattened, would likely appear very similar to the shield-shaped telson of *T. broedae*. However, the cheloniellid telson, along with its postabdomen, are reduced in size, and are relatively much smaller than the postabdomen and telson of *T. broedae*. The tergites of cheloniellids, with the exception of *Neostrabops martini* (Braddy & Dunlop, 2021), typically exhibit a pronounced, narrow axis (Dunlop, 2002). The axis of *T. broedae* is not particularly distinct, and the axis and tergopleurae each make up about one-third the width of the thoracic tergites. Moreover, the tergopleurae in cheloniellids exhibit a distinct radial arrangement (Braddy & Dunlop, 2021; Van Roy *et al.* 2022) which is not seen in *T. broedae*. Van Roy *et al.* (2022) identified a unique articulating device in *Triopus draboviensis* and suggested it may represent a cheloniellid apomorphy; *T. broedae* does not appear to preserve a similar articulating device. Finally, the elongate pair of posteriorly directed caudal appendages on the postabdomen of *T. broedae* seem generally very similar to the furca on the postabdomen of cheloniellids, and particularly to the elongate filament-like furca with expanded anterior ends in *C. calmani* (Stürmer & Bergström, 1978), although it is not clear from these specimens if these appendages of *T. broedae* insert dorsally as do the furca in cheloniellids (Dunlop, 2002; Lerosey-Aubril *et al.* 2017; Braddy & Dunlop, 2021; Van Roy *et al.* 2022).

T. broedae, from the Late Carboniferous Mazon Creek deposit, is the youngest vicissicaudatan yet described and extends the stratigraphic range of the group into the late Paleozoic. The next youngest, from the Devonian, are *C. calmani* (Stürmer & Bergström, 1978) and *P. talimaae* (Dunlop, 2002). However, post-Ordovician vicissicaudatans are rare and typically represented by only a small number of near-complete, well-preserved specimens (Stürmer & Bergström, 1978; Dunlop, 2002; Briggs *et al.* 2023). Further investigations of Late Paleozoic Lagerstätten may yield additional examples. In particular, other Mazon Creek-type fossil assemblages, which have similar environments, similar faunas, and similar preservation (Baird *et al.* 1985b; Briggs & Gall, 1990) could be a fruitful place to explore.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/S001675682400044X>

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Competing interests. The authors declare none.

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