New cheloniellid arthropod with large raptorial appendages from the Silurian of Wisconsin, USA

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Abstract

Cheloniellids comprise a small, distinctive group of Paleozoic arthropods of whose phylogenetic relationships within the Arthropoda remain unresolved. A new form, *Xusus*, n. gen, n. sp. is reported from the Waukesha Lagerstätte in the Brandon Bridge Formation (Silurian: Telychian), near Waukesha, Wisconsin, USA. Exceptionally preserved specimens show previously poorly known features including biramous appendages; this is the first cheloniellid to show large, anterior raptorial appendages. We emend the diagnosis of Cheloniellida; cephalic appendages are uniramous and may include raptorial appendages; trunk appendages are biramous.

Introduction

Non-biomineralized or lightly skeletonized arthropods are common in Paleozoic Konservat-lagerstätten (e.g., [1–4]). However, owing to preservational biases and a high degree of morphological diversity, their affinities are commonly difficult to interpret. Non-biomineralized arthropods with raptorial or grasping appendages are often referred to as ‘great appendage arthropods’ or ‘megacheirans’ until their affinities have been resolved (e.g., [5–6]). The ‘great appendage arthropods’ comprise a morphologically diverse assortment of species. The term probably refers to a taxonomic wastebasket, and relationships to each other and within the Arthropoda are ambiguous (e.g., [5–18]).

Here we report a new arthropod with large raptorial appendages that suggests inclusion as a ‘great appendage arthropod’ in the broad sense, but which is also referable to the order Cheloniellida (Figs. 1, 2). A large number of specimens from the Waukesha Lagerstätte in the Brandon Bridge Formation (Silurian) of southeastern Wisconsin offer the opportunity to describe previously unknown or little-known features in the group. Cheloniellids are a group of non-biomineralized or lightly skeletonized Paleozoic arthropods characterized by a wide, ovoidal carapace, forward curved or angled posterior cephalic margin and pleural tips that are anterolaterally directed at the front and become increasingly posterolaterally directed toward the rear (e.g., [19–20]). This new form is among the best preserved fossil cheloniellids and allows for a rediagnosis of the group.

Material and Methods

This study is based principally on five of the better preserved specimens collected from the Waukesha Lagerstätte at the Waukesha Lime and Stone Company quarry near Waukesha, Wisconsin. Specimens are deposited in the University of Wisconsin Geology Museum, Madison, Wisconsin, USA (UWGM).

Specimens were photographed with a Canon EOS Rebel T3i Digital SLR with a Canon MP-E 65 mm macro lens and full spectrum lighting. Specimens, where noted, were whitened with ammonium chloride to enhance contrast. Images were z-stacked using Adobe Photoshop CC and measurements were made using ImageJ.

Geological Setting

Exceptionally preserved fossils occur in a 12 cm layer of finely laminated dolomitized plattenkalk at the base of the Brandon Bridge Formation [21–23]. The Brandon Bridge Formation (Silurian) in southeastern Wisconsin contains graptolites of the *Oktavites spiralis* Zone, which suggests correlation with the Llandovery Series, Telychian Stage [21–22, 24–25]. Fossils occur either in thinly laminated, fissile, organic-rich, argillaceous dolomudstone (termed flinz; see [26]) or thinly laminated, non-fissile, dolomudstone (termed fäule; see [26]). All but one specimen reported here is preserved in flinz. Specimens from flinz layers are preserved by a coating of authigenic phosphate overlying a thin dark organic film and are generally more detailed [24–25]. UWGM 2345 is in a fäule layer and is preserved by a thin coating of organic film.

Sedimentary and microbial structures in the Brandon Bridge Formation indicate that organisms are parautochthonous, having been washed in from nearby areas and accumulated in

small sedimentary traps along a tidally influenced shoreline [24–25]. Organisms were neither consumed nor readily decayed, thus increasing their chances of preservation. High salinity or other environmental factors were evidently limiting to most macroscopic organisms. Limited bioturbation indicates that this environment was devoid of most burrowers and grazers that allowed a diverse microbial biota, including microbial mats, to develop and flourish. Microbial-mediated processes, such as authigenic mineralization, facilitated the preservation of much of the Waukesha Biota [24–25] including non-biomineralized and lightly skeletonized organisms (compare [27–32]).

Systematic paleontology

Phylum Arthropoda von Siebold, 1848 [33]

Class Uncertain

Order Cheloniellida Broili, 1932 [34]

Emended diagnosis. Small to medium-size, biramous, arthropods having wide, ovoidal, flattened, non-biomineralized or lightly skeletonized dorsal exoskeleton. Cephalon short, with suture separating procephalon from gnathocephalon; eyes present; trunk wider than cephalon, with 8 to 13 tergites; trunk normally with narrow, convex medial area and nearly flat plural areas; distal ends of first few tergites directed anterolaterally, becoming increasingly posterolaterally directed rearward. Terminal tergite cylindrical or round, bears anus, and encompassed by previous tergite. Caudal assembly consists of an elongate, forked, posteriormost segment bearing anus; elongate medial spine may articulate with it. Cephalic appendages

uniramous, consisting of long paired antennae and five pairs of endopods, all except the first endopod bear ganthobases. One appendage pair may be modified to raptorial appendages. Trunk appendages biramous, with one pair per segment, consisting of an endopod and shorter, brush-like exopod, not present on terminal tergite.

Discussion. Cheloniellids, as reviewed by Dunlop [20], range from the Early Ordovician (Tremadoc) to the Early Devonian (Emsian). Prior to this paper, six monospecific genera were described and referred to the group: *Triopus drabowiensis* [35] (Ordovician of the Czech Republic), *Duslia insignis* [36] (Ordovician of the Czech Republic and Morocco), *Cheloniellon calmani* [34] (Devonian of Germany), *Neostrabops martini* [37] (Ordovician of the USA), *Pseudarthron whittingtoni* [38] (Silurian of Scotland), and *Paraduslia talimaae* [20] (Devonian of Russia). In addition, an undescribed cheloniellid, has been illustrated from the Ordovician of Morocco ([1], fig 2b; [39], figs 2a, b). Two arthropods left in open nomenclature, both from the Silurian, are here referred to the Chelonieliida. One species is from Ontario ([40], fig 2j), and the other, which is described from articulated material below, is from Wisconsin (previously illustrated [22], figs 16, 21). A head shield described as *Drabovaspis complexa* [35] (see [41–42]) from the Ordovician of the Czech Republic may also be a cheloniellid.

Affinities of the Cheloniellida within the Arthropoda are uncertain. In one early interpretation, Jahn [36] referred them to phylum Mollusca. All other authors have referred the group to the Arthropoda. By various authors they have been interpreted as Crustacea [35, 43], Trilobita [44], Arachnomorpha [45–46], Aglaspida [47], Xiphosura (Bergström [48] and as a sister group to Chelicerata [49].

Cheloniellids are characterized by a wide, ovoidal carapace; a procurved or forward angled

posterior cephalic margin; and a thickened or lobed medial region, except in *Neostrabops*. The anterior cephalic margin is often thickened (e.g., [50], fig 4; [39], figs 2a, b). With the exception of *Cheloniellon*, cheloniellids were reported to lack eyes. However, eyes are evident in published figures (e.g., [38], fig 4b; [51], plate 56, fig 5, on either side of the axial lobe; [52], figs, 6.2, 6.4, 6.10, 6.11, 6.12). Cephalic sutures were reported in some cheloniellids (e.g., [51], text-fig 1). *Cheloniellon* has a reduced head segment, which we regard as a procephalon, with a larger segment (gnathocephalon) bearing gnathobases.

Cheloniellids have a wide, ovoid trunk with between 8 (*Pseudarthron*) and 12 (*Xus* n. gen.) tergites. Tergites are narrow medially and wider laterally. The anterior 2-3 pleural tips are directed forward, and the rest become increasingly posterolaterally directed toward the rear. *Cheloniellon* has an expanded second to last tergite ([50], fig 11a). Some forms have a marginal spiny fringe around the entire organism (*Duslia*, Moroccan form and *Xus* n. gen.).

The terminal tergite is either cylindrical or round and partly surrounded by the previous tergite. Both Stürmer & Bergström [50] and Cotton & Braddy [49] reported a segment behind the terminal tergite that they referred to as a telson in cheloniellids. Cotton & Braddy [49] described a ‘faint tergite boundary’ on the terminal tergite indicating the presence of a small telson in *Duslia* ([51], plate 57, fig. 4). We consider this to likely be taphonomic in origin, though it could be construed as evidence of a median spine. Similarly, *Cheloniellon* was reconstructed with a large telsonic segment, behind the insertion of the furcae ([50], figs 1, 2). However, figured specimens do not appear to reflect this reconstructed morphology (compare [50], figs 10, 11). Unlike Stürmer & Bergström [50] and Cotton & Braddy [49], we find no evidence of a telson behind the terminal tergite in cheloniellids.

Cheloniellids display a wide range of morphological variation in the postabdomen.

Cheloniellid species with preserved posterior regions have caudal furcae attached to the terminal tergite. *Cheloniellon* possesses long, flexible furcae, whereas *Paraduslia*, *Duslia*, the Moroccan form and *Xus* n. gen. possess short furcae. Species with short furcae are further differentiated by the structure and shape of the furcae, seemingly being either flexible tassels (*Paraduslia*) or inflexible spines (*Duslia*, Moroccan form and *Xus* n. gen). *Xus* is further differentiated by the presence of a separate, longer medial spine.

Appendages are poorly known in cheloniellids. Prior to this description, *Cheloniellon* was the only described species with preserved appendages. *Cheloniellon* has six uniramous paired cephalic appendages, including long, narrow antennae and five endopods; the posterior four endopods bear gnathobases ([50], fig 7). An unusual brush-like structure was also noted by Stürmer & Bergström [50] on the second cephalic appendage but it was not included in the reconstruction or diagnosis. The undescribed Moroccan cheloniellid preserves long antennae; no other appendages are apparent ([1], fig 2b; [39], figs 2a, b). Trunk appendages are biramous, based on several frilled, ovoid elements on one specimen of *Cheloniellon* that are interpreted to be gilled exopods ([50], fig 8).

Genus *XUS* n. gen.

Etymology. From Latin, *X*, hunter, and *US*, extraordinary (masculine), in reference to the raptorial appendages.

Diagnosis. As for the species.

Type species. *Xus yus* n. sp.

Diagnosis. Exoskeleton small, wide, ovoidal, nearly flat except for convex eyes and axis with spiny marginal fringe. Cephalic shield short and wide; anterior margin rounded, thickened, upturned; posterior margin angled forward. Lateral eyes large, located midway from anterior margin; paired suture extending from anteromedial area to eyes; trunk with 11-12 tergites each with a thickened rim; first two tergites directed anterolaterally, third tergite directed laterally, remaining tergites become increasingly posterolaterally directed; terminal tergite round with centrally located anus; caudal apparatus articulates to terminal tergite and is composed of paired lateral spines and separate longer medial spine; cephalic appendages consisting of small paired setal appendages and large paired, laterally oriented raptorial appendages; trunk appendages biramous?, hooked endopod and possible brush-like exopod; appendages present on all but last tergite.

Discussion. *Xus yus* is most similar to two other cheloniellids, *Duslia* [51] and an undescribed cheloniellid from the Ordovician of Morocco ([1], fig 2b; [390, figs 2a, b). All three forms have spiny marginal fringes and forked spines (furcae). Neither *Duslia* nor the Moroccan form preserve evidence of raptorial appendages.

An unnamed arthropod, ROM 57980 ([40], fig 2J), may be congeneric based on the presence of putative raptorial appendages, a thickened medial region and a poorly preserved laterally expansive pleural region.

Xus yus n. sp.

Figure 1A–1L

1985a ?branchiopod crustacean Mikulic et al. [21], p. 716, fig. 2d.

1985b branchiopod or remipede crustacean Mikulic et al. [22], p. 80, fig. 16.

Etymology. From Latin, *yus*, a three-pronged spear, in reference to the caudal assembly.

Holotype. UWGM 2439 (Figs 1A, 1B, 1C).

Paratypes. UWGM 2345 (Fig 1D), UWGM 2436 (Figs 1E, 1F, 1H, 1J, 1K); UWGM 2575 (Figs 1G, 1I); UWGM 2437 (Fig 1L).

Additional material. 14 specimens.

Occurrence. Silurian (Llandovery, Telychian), occurring in a 12 cm layer in the lower Brandon Bridge Formation, Waukesha Lime and Stone Company quarry, north of State Highway 164, Waukesha, Wisconsin, USA.

Diagnosis. As for genus.

Description. Exoskeleton nearly flat except for eyes and axis and likely weakly mineralized. Length ranging to at least 45 mm. Body width approximately 70% of the body length excluding furcae. Cephalic shield has short, wide, rounded anterior margin with upturned edge; posterior margin angled forward. Lateral eyes large, ovoid located midway between anterior and posterior margins, directed anteromedially. Cephalic shield raised medially between eyes extending

posteriorly through trunk.

Abdomen ovoid, wider than cephalon with 11-12 tergites present. Trunk widest at tergites 5 and 6. Medial region moderately wide with thickened cuticle. Pleural region cuticle thin, commonly poorly preserved. Tergites appear wider laterally and thinner medially. Anterior two pleural tips directed forward, third tergite is directed laterally and the rest become increasingly posterolaterally directed toward the rear. Terminal tergite is circular and bears anus medially.

Caudal apparatus composed of two parts, a forked sclerite with stout, bowed posteriorly directed spines and a moderately long, stout median spine. Forked sclerite abuts and wraps around edges of the terminal segment. Lateral spines situated ventrally, whereas the median spine is dorsally situated.

Two pairs of appendages observed on the cephalic shield. Small paired setae bearing appendages and raptorial appendages extending anterolaterally, consisting of approximately five elongate podomeres. Base of the raptorial appendage attaches adjacent to inferred position of the mouth. Distal podomere articulates at 90° to preceding podomere; terminates in a sharp, stout, tip. Trunk limbs extend just beyond the medial region and consist of sharply hooked endopod. Brush-like structures may represent exopods.

Discussion. *Xus yus* is one of the more common organisms reported by Mikulic et al. [21–22] from the Waukesha Lagerstätte. It is known from more than 20 specimens. UWGM 2439 (Figs 1A, 1B) and UWGM 2345 (Fig. 1D) are preserved in dorsal view, and all others are in ventral view. Some specimens are partly split through the exoskeleton (Figs 1A, 1B, 1E, 1I, 1L). Studied specimens are predominately incomplete and show varied preservational conditions including the loss of cephalic appendages (Fig 1L), differential preservation of medial and pleural regions of

the abdomen (Fig 1E, 1I), and secondary authigenic, early mineralization (Fig 1E). Often specimens do not preserve the pleural regions well, giving the appearance of a more slender organism (compare Fig 1E to 1D). This condition entered into the original interpretation of this unusual arthropod ([22], fig 21). The positions of the pleural margins in some specimens can be approximated by the more easily identifiable microbial decay halo (see [53]), which lies just beyond the ends of the tergites (Figs 1F, 1L). The cuticle of the pleural regions may have been quite thin in life, which leads to some difficulty in interpretation. Sufficiently well-preserved material is necessary for correct interpretation of morphology and affinities. Without the thin lateral areas of the carapace, this animal resembles a branchiopod crustacean (as noted by Mikulic et al. [21–22]).

Non-biomineralized arthropod cuticle, primarily composed of chitin, is relatively rare in the fossil record [54]. In most environments, it is readily digested by microorganisms and macroorganisms [53]. Specific environments have been shown to limit biodegraders and the biodegradation of chitin, allowing the chitin to survive long enough to fossilize. Mikulic et al. [21–22], Wendruff [24] and Wendruff et al. [25] discussed paleoenvironmental and depositional conditions leading to exceptional preservation in the Waukesha Lagerstätte. The Waukesha Biota was deposited in a microbially-rich environment that facilitated exceptional preservation [24–25]. Macroorganisms including *Xus yus* were transported into a nearshore environment where breakdown of chitin was inhibited. Non-biomineralized and lightly skeletonized arthropods in the Waukesha Lagerstätte tend to be compressed and have secondary phosphatic overgrowths [24–25, 55]. Overgrowths are commonly crinkled and tend to distort or obscure morphologic features [24–25, 55].

All observed specimens of *Xus yus* are articulated. Taphonomic experiments demonstrate

that arthropods can remain at the sediment surface for weeks before complete disarticulation [56–57]. Limbs and gills are among the first structures to be lost in arthropods. They begin to separate from the exoskeleton in about one week [56–58]. Endopods are commonly present, whereas the gilled exopods are commonly lost. Babcock & Chang [56] and Babcock et al. [57] found that the first structures to disarticulate in extant arthropods are gills, followed by limbs. Most specimens retain some walking legs. All but one specimen of *X. yus* has lost the brush-like structures. If these structures are gills, then the gills were the first body parts lost in *X. yus*, which would suggest burial within about two weeks of death.

Ambiguity in the limb structure of cheloniellids should be noted. Within the cephalon of *Cheloniellon*, unusual brush-like structures were noted on ‘uniramous’ appendages by Stürmer & Bergström ([50], fig 5). Similar structures are preserved on a ventrally preserved specimen of *Xus yus* (Figs 1G, 1I) across the head and trunk. These brush-like elements may represent gilled exopods or possibly structures that supported the marginal frill. We infer that these structures were lost quite readily, whether they functioned as gills or not, and we do not suggest homology or function.

The general morphology of *Xus yus* indicates affinity with cheloniellids supported by the posterior margin of the head, widely ovoid body, posterolaterally trending tergites and caudal furcae among other features. However, it possesses some unusual morphology that is unique within the cheloniellids including raptorial appendages (Fig 1J) and a medial spine (Fig 1K). Originally, *X. yus* was interpreted by Mikulic et al. [21–22] as bearing affinities to either branchiopod or remipedian crustaceans on the basis of large, specialized cephalic appendages. Without a large number of differentially preserved specimens, the inferred affinities of *X. yus* would be different.

In general, chelionellids could easily be confused with a number of other Paleozoic arthropods that have grossly similar body forms including the trilobite *Burlingia* [59] (see also [60–62]) and non-biomineralized arthropods, such as *Arthroaspis* [63] and aglaspid-like arthropods [64]. Even some extant arthropods share similar morphology including serolid isopods (compare [65]) and larval water penny beetles (compare [66]). Cheloniellids such as *Xus yus* also could be confused with great appendage arthropods. Without a preserved pleural region, the raptorial appendages appear as more prominent structures.

Raptorial appendages within arthropods greatly vary in function and form. Anomlocaridid-type grasping appendages (e.g., [13, 67]) and mantis-shrimp-like raptorial appendages (e.g., [5, 68]) are common in Paleozoic arthropods and functioned dorso-ventrally. The raptorial appendages of *Xus yus* appear to have functioned laterally with the appendage tips meeting at the midline, possibly to pierce and immobilize prey. Dorso-ventral oriented appendages were more likely used for crushing, slicing or capturing prey. In this respect, the appendages of *Xus yus* are apparently unique among known raptorial appendage-bearing Paleozoic arthropods.

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Fig 1. *Xus yus*, n. gen. n. sp. from the Waukesha Lagerstätte in Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin preserved in dolomudstone.

UWGM 2439, holotype, counterpart (A) photographed dry and part (B) photographed wet; (C) closeup of the small anterior appendage and spiny marginal fringe of the holotype, UWGM 2439; (D) UWGM 2345 preserving dorsal anatomy; (E) UWGM 2436 preserving ventral anatomy and limbs; (F) UWGM 2436 whitened with ammonium chloride and photographed under low-angle lighting, arrows indicate pleural segments; (G) closeup of brush-like (gills?) exopods of UWGM 2575; (H) closeup of hooked exopods of UWGM 2436; (I) UWGM 2575 preserving ventral anatomy and brush-like structures; (J) closeup and whitened raptorial appendages of UWGM 2436; (K) closeup of caudal apparatus of UWGM 2436; (L) UWGM 2437 preserving ventral anatomy with limbs and partially preserved pleural region, arrows indicates decay halo. Scale bar equals 5 mm for A, B, D–F, I, L; 2 mm for C, G, H, J, K.

Abbreviations: 1-11, numbered tergites; an, anus; e, eyes; en, endopod; ex, exopod; fs, facial suture; ls, lateral spines; mr, median region; ms, median spines; ra, raptorial appendage; rs, round sclerite; saa, small anterior appendage; smf, spiny marginal fringe; tcr, thickened cephalic rim; ttr, thickened tergite rim.

Fig 2. Reconstruction of *Xus yus*, n. gen. n. sp.