



# Trilobite and xiphosuran affinities for putative aglaspidid arthropods *Caryon* and *Drabovaspis*, Upper Ordovician, Czech Republic

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The problematic arthropods *Zonozoe draboviensis*, *Caryon bohemicum* and *Triopus draboviensis* were originally described by Barrande (1872). Chlupáč (1963, 1965) revised Barrande's material, and based a new genus and species, *Drabovaspis complexa*, on a single specimen formerly in *Zonozoe*. He regarded all these taxa as 'merostomes of the Order Aglaspidida...', which is the oldest order of limulid arthropods of the Subclass Xiphosura... (Chlupáč 1965, p. 7) based on an overall resemblance. Much debate revolves around the diagnostic features and exact affinities of the Aglaspidida. Almost all arthropods that have been allied to this Order share a similar morphology, including a semicircular and convex cephalon devoid of facial sutures and a faint glabellar region. Most have a pair of anterior oval eyes, although blind forms are recorded (Fortey & Rushton 2003). Most of these taxa have not been the subject of further study except for occasional comparison with morphologically similar arthropods (e.g. Bergström 1968; Fortey & Rushton 2003; Van Roy 2006a; Rak *et al.* 2009).

All of the fossils discussed here come from the Upper Ordovician Letná Formation in the Czech Republic. They co-occur with fragments of the trilobites *Dalmanitina proaeva socialis* and occasionally *Onnia goldfussi*; other fauna such as brachiopods, molluscs, conulariids and echinoderms are less frequent (Chlupáč 1965). The Letná Formation is notable for also preserving more exotic arthropods such as the cheloniellid *Duslia insignis* Jahn, 1893; the marrellomorph *Furca bohémica* Fritsch, 1908; and the bivalved ?arthropod *Nothozoe pollens* Barrande, 1872.

Preservation style in the Letná Formation has important implications for interpreting these fossils. Chlupáč (1965, 1999b) suggested a depositional environment corresponding to the shallow water neritic or littoral zone with strong currents, as evidenced by the alternating sandstone and siltstone layers. The fragmentary fossils are preserved in sandstone or siliceous concretions. However, most of the arthropods, including the trilobites and aglaspidid-like taxa, are preserved as internal moulds of isolated tagmata, making their interpretation challenging. Chlupáč (1988) also noted that the trilobites are usually coated with a thick layer of limonite. This replaces the calcium carbonate of unweathered specimens. Conversely, animals with only a thin shell or unmineralized cuticle (e.g. *Duslia*) are preserved with a very thin layer of limonite. The preservation in *Caryon* resembles that of the trilobites. *Drabovaspis* and *Triopus* are preserved in a similar way to unmineralized arthropods.

Here, we reinterpret the morphology and systematic position of *Caryon bohemicum* and *Drabovaspis complexa*, and review the affinities of *Triopus draboviensis*. All fossils referred to are housed at the National Museum, Prague.

## Reinterpretation of *Caryon*

Various affinities for *Caryon* have been suggested (Table 1). Chlupáč (1963, 1965) described the cephalon of *Caryon* as semi-elliptical, strongly rounded and convex. The convex and oval lateral eyes are positioned anterolaterally, with a narrow occipital band. The

ventral doublure has a slightly arched margin. Chlupáč (1963, 1965) proposed *Caryon bohemicum* as a possible representative of the Family Paleomeridae Størmer 1955 (=Strabopidae Gerhardt, 1932). Hou & Bergström (1997) interpreted *Caryon* as an aglaspidid and included it in their new Order Strabopida, along with *Strabops* Beecher, 1901, *Neostrabops* Caster & Macke, 1952, *Paleomerus* Størmer, 1955, *Lemoneites* Flower, 1969 and *Khankaspis* Repina & Okuneva, 1969.

Restudy of Barrande's collections allowed us to reinterpret some of the morphology of *Caryon*. Well-preserved specimens possess a pair of faint lines that extend from the eyes to the posterior margin of the cephalon (Fig. 1A). The position of these lines resembles internal impressions of opisthopteran eye sutures, a distinctive character of trilobites. The rounded extension of the anterior portion of the cephalon towards the ventral side terminates in an elevated ridge. This is interpreted as the impression of a rostral suture (Fig. 1B), and the wide empty ventral region bordered by this ridge may well represent the site of attachment for a broad rostral plate, indicating an illaenid trilobite affinity (Harrington *et al.* 1959).

Illaenid trilobites are widely represented in the Ordovician of the Czech Republic, most notably the genera *Ectillaenus* Salter, 1867, *Cekovia* Snajdr, 1956, *Zetillaenus* Barrande, 1852, *Stenopareia* Holm, 1886, *Zbirovia* Snajdr, 1956 and *Zdicella* Snajdr, 1956 (Bruthansová 2003; Doubrava & Vokáč 2004). *Caryon* is closest to the illaenid genera *Bumastoides* Whittington, 1954, *Zetillaenus* Barrande, 1852 and *Illaenoides* Weller, 1907; in terms of cephalon convexity, smooth axial region and eye position. No known specimen of *Caryon* displays the cephalic axial furrows characteristic of these trilobites; however, these structures can be very faint and only seen on well-preserved individuals (Harrington *et al.* 1959), so their absence may be a preservational artefact. Some species of *Ectillaenus* show high degrees of intraspecific variability due to ontogeny (Bruthansová 2003), as has been recorded in other illaenid species (Hammann 1992; Hughes & Chapman 1995). *Caryon* also displays such morphological variation, ranging from nearly flat individuals to highly convex specimens with a rounded and slightly elliptical profile (Fig. 2); however, this variation is most likely a combination of intraspecific variation and post-burial compaction.

With the removal of *Caryon* from the Aglaspidida, recognition of *Lemoneites* as a glyptocystitid echinoderm (Moore & Brady 2005), alignment of *Neostrabops* with cheloniellids (Dunlop & Selden 1998) and the uncertain affinities of *Khankaspis* (Repina & Okuneva 1969), the only valid taxa that remain in the Strabopida are *Strabops* and *Paleomerus*.

## Reinterpretation of *Drabovaspis*

The holotype and known only specimen of *Drabovaspis complexa* was originally included in the genus *Zonozoe* by Barrande (1872), but later assigned to a distinct taxon by Chlupáč (1963, 1965), who included it in the Order Aglaspidida Raasch, 1939; Family Aglaspididae Miller, 1877; based on the convexity of the prosoma and prominent compound eyes. Chlupáč (1963, 1965) further

Table 1. Differing phylogenetic interpretations of *Drabovaspis complexa*, *Caryon bohemicum* and *Triopus draboviensis*.

<i>Caryon</i>	<i>Drabovaspis</i>	<i>Triopus</i>
Ostracode (Barrande 1872)	Ostracode (Barrande 1872)	Trilobite (Barrande 1872)
Paleomerid (Chlupáč 1963, 1965)	Aglaspidid merostome (Chlupáč 1963, 1965)	Xiphosuran (Packard 1886; Neumayr 1887; Bergström 1968, 1971)
Strabopid (Hou & Bergström 1997)	Xiphosuran (Bergström 1968)	Chitinoïd mollusc (Jahn 1893)
Aglaspidid-like arthropod (Van Roy 2006a)	Aglaspidid-like arthropod (Van Roy 2006a)	Aglaspidid merostome (Chlupáč 1963, 1965)
Iliaenid trilobite (This study)	Xiphosuran (This study)	Cheloniellid arthropod (Dunlop & Selden 1998; Van Roy 2006b)

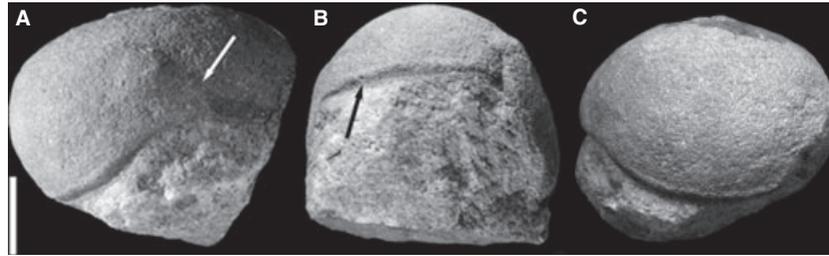


Fig. 1. Well-preserved internal mould of *Caryon bohemicum*, National Museum, Prague (L23576). A\*, lateral view showing faint opisthopari-an suture (arrow). B, ventral region with rostral suture (arrow) and wide space for rostral plate attachment. C, anterior view showing smooth surface and high convexity of cephalon. Scale bar = 10 mm. \*photograph has been flipped over its vertical axis to produce a mirror image of the specimen.



Fig. 2. Preservational variants of *Caryon bohemicum*. A, normal morphology. B, slightly depressed with antero-posterior elongation. C, completely flattened. Modified from Chlupáč (1965). Scale bar = 10 mm.

suggested a possible phylogenetic relationship with xiphosurids. The exoskeletal features of *Drabovaspis* according to Chlupáč (1965, 1999a), include a slightly convex prosoma of subtrapezoidal outline, narrow rim, pointed post-lateral angles without spines, large crescentic eye elevations, a bipartite glabellar region (with a long rhombic elevated flat anterior region and medially concave posterior parts) and posterolateral, trending ophthalmic ridges (Fig. 3A). As noted by Chlupáč (1965, p. 14), '*Drabovaspis complexa* differs markedly from all known aglaspidids and other merostomes'. Bergström (1968) compared *Drabovaspis* with the putative xiphosurid *Eolimulus* from the Lower Cambrian of Sweden, and later included them in his Suborder Belinurina, Superfamily Eolimulidae Bergström, 1968 (Bergström 1975), united by their large eyes, large anteromedian node, posterior ophthalmic ridges and elevated marginal rim. Bergström (1968) also proposed a relationship between *Drabovaspis* and *Eolimulus*, arguing that the weak development of the posterior interophthalmic region in *Drabovaspis* could be a secondary feature and the low convexity of the prosoma and large eyes were adaptations to a motile lifestyle. However, the validity of *Eolimulus* as a xiphosuran, and that of the Superfamily Eolimulidae as a whole, is doubtful, as it is based on fragmentary material. In the same study, Bergström reconstructed *Drabovaspis* as the cephalon of *Triopus draboviensis* (Fig. 3B), but this reconstruction was based on the assumption that both fossils represented the remains of xiphosurids and is considered here as invalid.

Previous studies have misidentified the orientation of the organism leading to misinterpretation of its morphology. We interpret

the 'rhombic component' of the 'bipartite glabellar region' as a cardiac lobe, and the 'medially concave posterior zone' as the pre-ophthalmic field. The ophthalmic ridges are thus considered to extend anteriorly, rather than posteriorly, and the anterior marginal rim is here interpreted as an occipital band (Fig. 3C). *Drabovaspis* and xiphosurans share the presence of a well defined triangular cardiac lobe, developed ophthalmic ridges, centrally placed eyes and presence of an occipital band. However, it differs from them in having an unusual trapezoidal outline, a low convexity of the cephalon and anteriorly positioned acute genal angles. Although aligned with aglaspidids (Chlupáč 1963, 1965), the morphology of *Drabovaspis*, with its trapezoidal outline, flat cephalon, developed cardiac lobe and elevated ophthalmic ridges, does not compare with generalized aglaspidid morphology (see introduction), not even as an aglaspidid-like arthropod, much less an aglaspidid *sensu stricto*. Reassessment of *Drabovaspis* supports the xiphosuran affinity suggested by Bergström (1968), although the re-orientation we propose provides a better interpretation of its morphology.

When Bergström (1968) proposed a xiphosuran identity for *Drabovaspis*, the known fossil record of Xiphosura did not support such affinities. Recently, the oldest unequivocal xiphosuran, *Lunataspis aurora*, was described from the Richmondian of Canada (Rudkin *et al.* 2008). The discovery of this species extended the stratigraphical range of xiphosurans back into the Upper Ordovician, drawing direct comparison to the age of the Letná Formation. *Drabovaspis* and *Lunataspis* also share a similar shallow marine palaeoenvironment (Chlupáč 1965; Rudkin *et al.* 2008). The

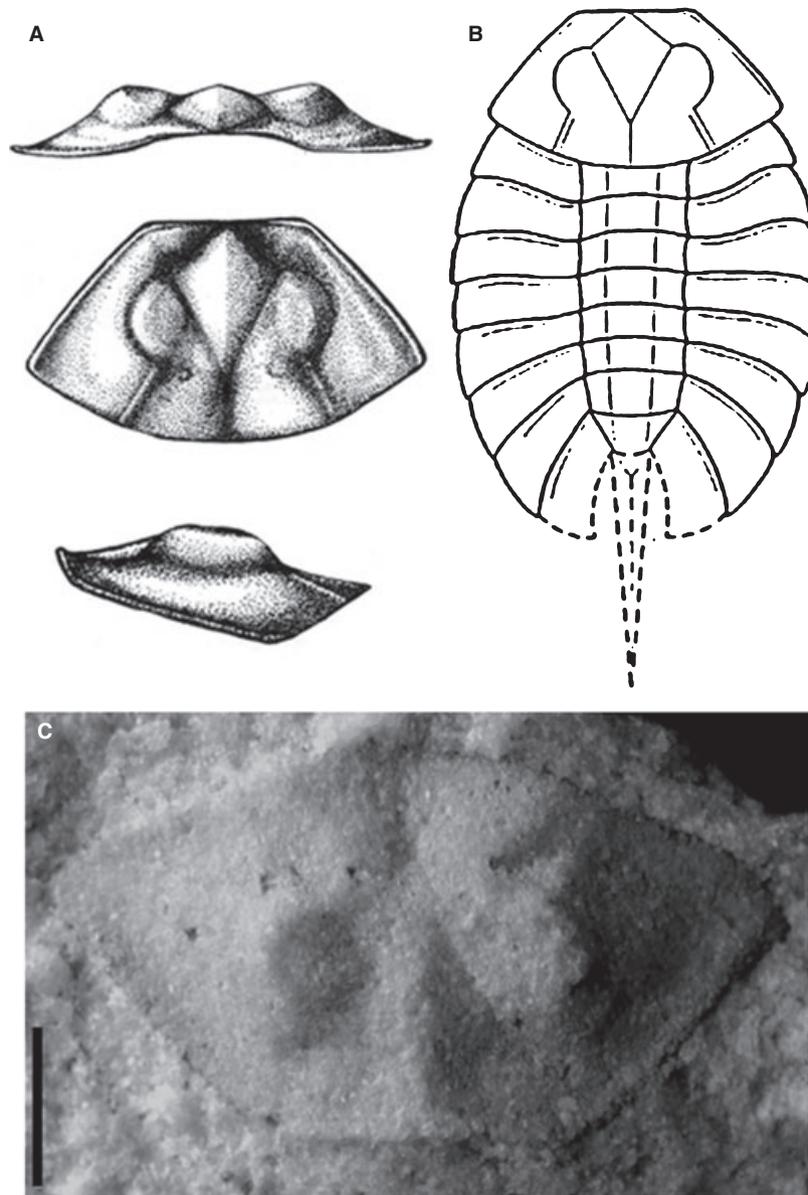


Fig. 3. *Drabovaspis complexa*. A, as figured by Chlupáč (1965). B, reconstruction of *Drabovaspis* + *Triopus* by Bergström (1968). C\*, holotype (L23577), National Museum, Prague, illustrated in what is here interpreted as the correct orientation. Scale bar = 5 mm. \*photograph has been flipped over its vertical axis to produce a mirror image of the specimen.

interpretation of *Drabovaspis* as a xiphosuran indicates a higher degree of morphological disparity during the early history of Xiphosura than previously thought. While *Lunataspis* possesses an array of derived and relatively primitive characters among xiphosurids (Rudkin *et al.* 2008), the unique morphology of *Drabovaspis* does not allow recognition of its precise position within the early evolutionary history of the Xiphosura, and may possibly be the only known representative of a yet undescribed group within this order.

### The status of *Triopus draboviensis*

Chlupáč (1965) described *Triopus* as the ‘incomplete opisthosoma of an aglaspid merostome’, hinting at the possibility that this fossil was the opisthosoma of either *Drabovaspis* or *Zonozoe*. At the time, the only specimen of *Triopus* (Fig. 4) was thought lost, and

Chlupáč’s (1965) interpretation was based on Barrande’s (1872) original and idealized illustration. Bergström (1968) disagreed with Chlupáč’s interpretation of the affinities of *Triopus*, assigning it instead to the Xiphosura. He reconstructed *Triopus* with the cephalon of *Drabovaspis*, arguing that ‘the present identification of both as xiphosurids makes this combination the only possible’ (Bergström 1968, p. 492) (Fig. 3B). Since then, the holotype of *Triopus* has been rediscovered and its affinities reassessed; Chlupáč (1988) compared it to the cheloniellid arthropods *Duslia insignis*, *Cheloniellon calmani* and *Pseudoarthron whittingtoni*, highlighting their marked longitudinal trilobation of the exoskeleton and radial arrangement of tergites. He noted differences in the convexity of their exoskeletons, the proportions of the axial lobe with the tergites and the spinose fringe of *Duslia*. Chlupáč (1988) also highlighted a completely different morphology between the anterior region of *Duslia* and the reconstruction of *Triopus* + *Drabovaspis* attempted by Chlupáč (1965) and Bergström (1968). Despite the similarities of *Triopus* with the aforementioned cheloniellids,

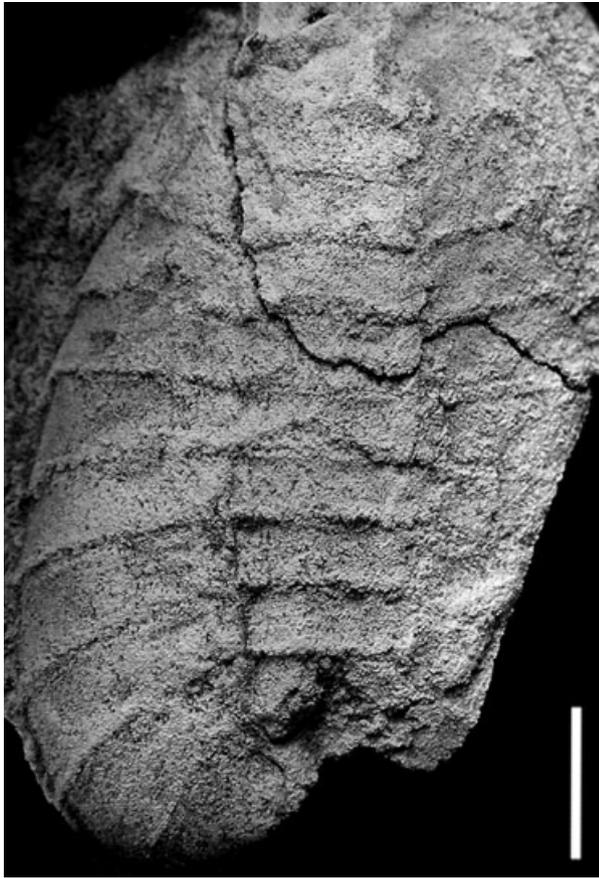


Fig. 4. *Triopus draboviensis*, holotype (L16736), National Museum, Prague. Scale bar = 10 mm.

Chlupáč (1988) did not propose any kind of phylogenetic relationships between these taxa.

The phylogenetic position of *Triopus draboviensis* has only been reviewed in a few studies. Delle Cave & Simonetta (1991) included *Triopus* in the Strabopida Gerhardt, 1932; based on Bergström's (1968) combined reconstruction (*Triopus* + *Drabovaspis*). They further emphasized the importance of these taxa as a link between the Middle Cambrian emeraldellids and the Ordovician – Silurian Xiphosura and Eurypterida. Similarly, Bousfield (1995) considered *Triopus* + *Drabovaspis* a merostome and common ancestor to xiphosurans, chasmataspids and eurypterids. Dunlop & Selden (1998) recognized the morphological similarity between *Triopus* and *Cheloniellon*, including both taxa in a cladistic analysis; *Triopus*, *Neostrabops*, *Duslia*, *Pseudoarthron* and *Cheloniellon* formed the clade Cheloniellida Broili, 1932; supported by the synapomorphy of a procurved posterior margin of the dorsal exoskeleton. Van Roy (2006b) reported the discovery of two new complete specimens of *Triopus* from the Upper Ordovician of Morocco, unequivocally confirming its status as a cheloniellid arthropod.

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