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

Caryon	*Drabovaspis*	*Triopus*
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)	Chitinoid mollusc (Jahn 1893)
Aglaspidid-like arthropod (Van Roy 2006a)	Aglaspidid-like arthropod (Van Roy 2006a)	Aglaspidid merostome (Chlupáč 1963, 1965)
Illaenid trilobite (This study)	Xiphosuran (This study)	Cheloniellid arthropod (Dunlop & Selden 1998; Van Roy 2006b)

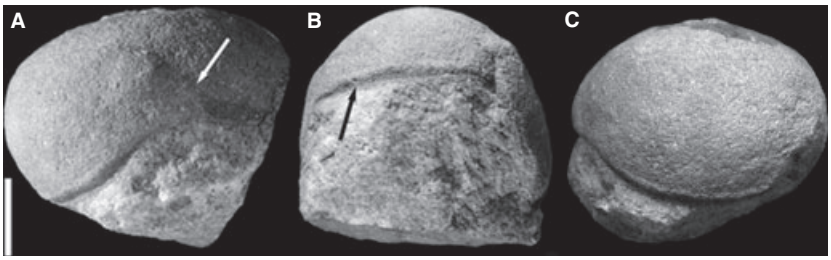

Fig. 1. Well-preserved internal mould of *Caryon bohemicum*, National Museum, Prague (L23576). A*, lateral view showing faint opisthoparian suture (arrow). B, ventral region with rostral suture (arrow) and wide space for rostral plate attachment. C, anterior view showing smooth surface and high convexity 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 preophthalmic 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

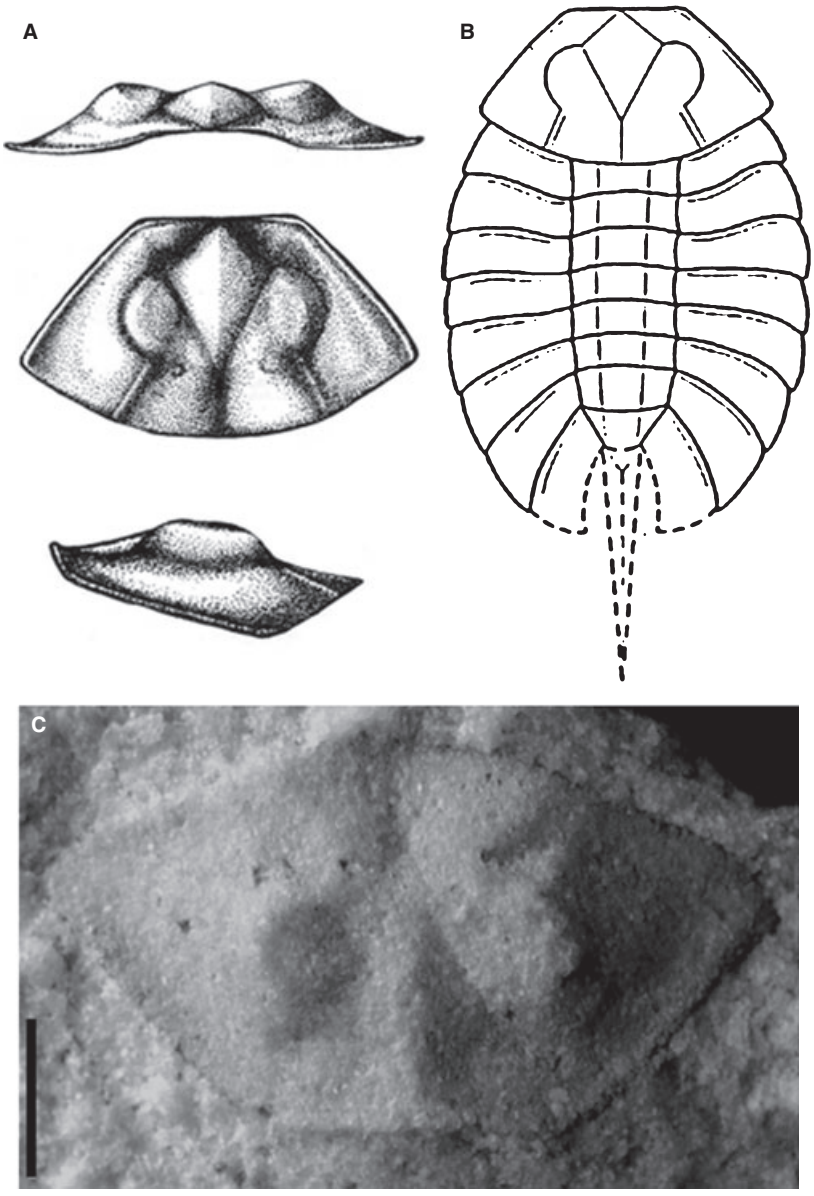

Fig. 3. Drabovaspis complexa. A, as figured by Chlupáč (1965). B, reconstruction of *Drabovaspis* + *Triopus* by Bergström (1968). C*, holotype (L23577), National Museum, Prague, illustrated in what is here interpreted as the correct orientation. Scale bar = 5 mm. *photograph has been flipped over its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

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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