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Phylogenetic relationships of the cyathaspidids (Heterostraci)

METTE LUNDGREN and HENNING BLOM

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Abstract: The present analysis investigates for the first time the phylogenetic relationships of the cyathaspidid heterostracans by the principle of global parsimony on the basis of 36 species and 1 outgroup taxon. In this study, which assumes cyathaspidid monophyly, states for 61 characters were compiled and analysed using maximum parsimony methods, resulting in nine shortest trees of 122 steps each. The strict consensus tree shows a high degree of homoplasy and challenges previous classification schemes. The consensus topology supports previous arguments that the tolypelepidids with their characteristic scale-like ornament occupy a basal position among the cyathaspidids.

Keywords: Palaeozoic; Heterostraci; Cyathaspididae; phylogeny.

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Introduction

The Heterostraci includes a group of extinct armoured jawless vertebrates characterized by a single external branchial opening on each side of the head (Janvier 1996a). Despite being historically associated with cephalopods (Kner 1847) and crustaceans (Roemer 1855), they are the most diverse group of the so-called “ostracoderms”, a heterogeneous group of Palaeozoic fossil fishes, which are particularly interesting since they form part of the stem group of the gnathostomes (jawed vertebrates) and thereby provide essential information about the gradual emergence of the jawed vertebrate body plan (Janvier 1981, 1996b; Forey 1984; Donoghue et al. 2000). The heterostracans have traditionally been placed together with the astraspidids and arandaspidids in a basal position on the gnathostome stem and thereby arguably demonstrate a plesiomorphic vertebrate architecture (Janvier 1996b; Donoghue et al. 2000). More recent studies have emphasized the inconclusiveness of morphological characters for phylogenetic resolution at the base of the vertebrate total group, with inherent consequences for our understanding of the origin of the gnathostome body plan (Donoghue & Smith 2001; Gess et al. 2006; Heimberg et al. 2010; Sansom et al. 2010; Blom 2012).

Many of the various “ostracoderm” groups are polymorphic and a majority of studies aiming to resolve the stem group as a whole have been hampered by the use of a model representatives, which did not necessarily represent the most plesiomorphic condition for the different higher taxa. The urgent need of a firm establishment of the plesiomorphic condition for the individual groups has advanced in recent years by analyses based on global parsimony on various “ostracoderm” groups, such as anaspidids (Blom & Märrs 2010; Blom 2012), thelodonts (Wilson & Märrs 2004, 2009) and osteostracans (Sansom 2008, 2009). Heterostracans, however, are still poorly known with respect to their morphological evolution.

In a phylogeny presented by Janvier (1996a), *Athenaegis chattertoni* Soehn & Wilson, 1990 is placed as the sister group to all other heterostracans, represented by the Pteraspidoformes, the cyathaspidid genera *Nahanniaspis*, *Torpedaspis* and *Anglaspis*; representatives of the Amphiaspidida; and *Ctenaspis* (Fig. 1A). *Nahanniaspis* has both subbranchial scales and free branchial plates. This places it as the sister group to *Torpedaspis* and *Anglaspis* (Fig. 1A), which includes species with free branchial plates only. The tolypelepidids are viewed by Janvier (1997) as derived from the Traquairaspidoformes and are placed in a basal position to both the two main subgroups of the Heterostraci, the Cyathaspidiformes and the Pteraspidoformes.

The Pteraspidoformes are perhaps the most studied group of heterostracans, but have suffered from disagreement with regard to classification (see Pernègre & Elliott 2008 for review). The Pteraspidoformes have been regarded as monophyletic on the basis of the characteristic ornamentation of concentric dentine ridges with serrated margins, supraorbital sensory-line canals meeting behind the pineal plate or pineal area and a dorsal spinal plate (Janvier 1996a), but a better account of the monophyly of the group has been given by Pernègre & Elliott (2008). Beside this latter work, only a few cladistic analyses have been carried out for the group (Illyes & Elliott 1994; Pernègre 2002; Pernègre & Goujet 2007).

The second major group, the Cyathaspidiformes, are characterized by an ornamentation of longitudinal dentine ridges with finely crenulated margins and have an earlier fossil record than the Pteraspidoformes (Janvier 1996a). Despite its importance for the early record of jawless vertebrates and the diversity in the Silurian, very little has been discussed regarding the phylogenetic context of the Cyathaspidiformes. Instead focus has been on taxonomy, classification and distribution (Denison 1964; Dineley & Loeffler 1976; Novitskaya 2004;

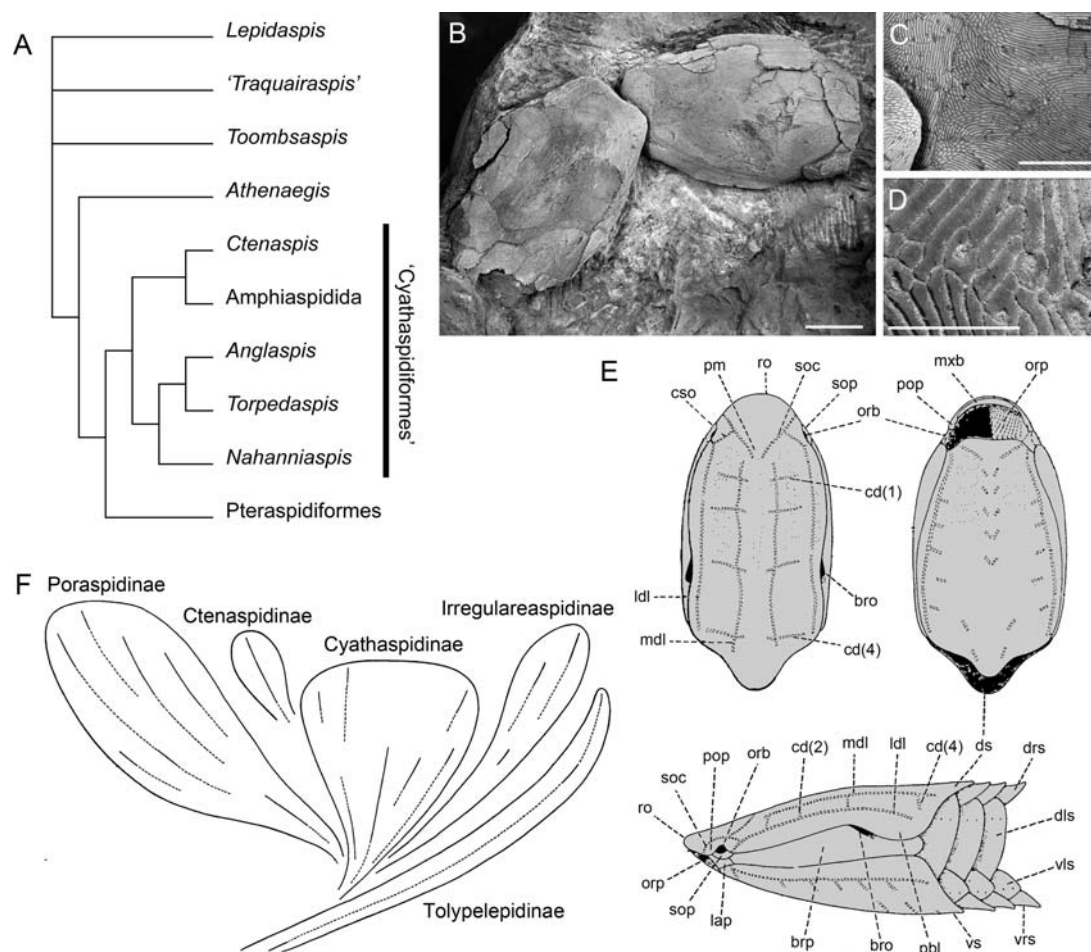


Fig. 1. The phylogenetic and morphological framework of the cyathaspidids. **A**. Summary of hypothesis of heterostracan interrelationships after Janvier (1996a). **B**. The shape, composition and arrangement of the dermal armour, exemplified by the associated head shields of the cyathaspid *A. lindstromi*. Scale bar = 10 mm. **C**. The ornamentation of the dermal armour plates, exemplified by the pineal triangle of *A. lindstromi*. Scale bar = 5 mm. **D**. The morphology of the presumed lateral line system, exemplified by an SEM of pores in *P. polaris*. Scale bar = 1 mm. **E**. Terminology of heterostracan head shields and anterior body scales on the basis of *Poraspis* (after Denison 1964): bro, branchial opening; brp, branchial plate; cd(1–4), first to fourth dorsal transverse sensory commissures; cso, transverse supraorbital sensory commissure; dls, dorsolateral scale; drs, median dorsal scale; ds, dorsal shield; lap, lateral plate; ldl, lateral dorsal sensory canal; mdl, medial dorsal sensory canal; orp, oral plate; pbl, postbranchial lobe; pm, pineal macula; pop, preorbital process; ro, rostrum; soc, supraorbital sensory canal; sop, suborbital plate; vls, ventrolateral scale; vrs, median ventral scale; vs, ventral shield. **F**. Simplified phylogenetical framework of the Cyathaspididae as presented by Denison (1964).

among others). Within the Cyathaspidiformes, the ranked classification has been reviewed several times and the family Cyathaspididae was revised by Denison (1964) and viewed as taxonomically corresponding to Kier's (1932) suborder Cyathaspidia. This classification, which forms the basis for this study, differs from the one presented by Janvier (1996a) by the inclusion of *Ctenaspis* in the Cyathaspididae (Fig. 1A). The phylogenetic relationships of the Cyathaspididae have been discussed by Tarlo (1962), Denison (1964) (Fig. 1F) and Novitskaya (1973), who all considered that the ornamentation pattern of the dorsal shield is of phylogenetic importance. These authors also concluded that the ornamentation pattern of scale-like units is regarded as a basal trait. Nevertheless, the phylogenetic relationships of the Cyathaspididae or the Cyathaspidiformes have never hitherto been subject to an analysis based on the principle of global parsimony.

In this study, we explore for the first time the phylogenetic framework for cyathaspidids based on a cladistic method. One

of the fundamental assumptions in this study is a monophyletic clade of cyathaspidids as defined by the classification of Denison (1964). This differs from Janvier's (1996a) cyathaspidiformes only by the exclusion of the amphiaspidids (Fig. 1A), which are extremely derived and virtually impossible to include in this analysis anyway. This character-based analysis and the construction of a character matrix (Table 1) builds on the established morphological features used in previous classifications, such as the morphology of the dermal exoskeleton and of the presumed lateral line system (Fig. 1B–E). The framework in use can be illustrated by the well-preserved head shields of *Archegonaspis lindstromi* (Lindström, 1895), which exemplifies head shield shape, the characteristic triangular ornamentation pattern around the pineal organ, and the lack of openings of the lateral line canal system which is otherwise often well developed and characteristic for various groups (Denison 1964) (Fig. 1D). Many of the cyathaspidid characters used in this study are indicated in the reconstruction

Table 1. Data matrix.

Taxon	10	20	30	40	50	60
<i>A. chattertoni</i>	1???	10110001000000001-001?	000-0?	1?0---	1111111100010100000000???	
<i>I. hoeli</i>	111110???	000000?00001000??	1?1001?	0---	000000010000010011110001	
<i>D. elizabethae</i>	1111?0???	0000000100001000?	111100110---	000000010000110010100000		
<i>N. mackenzie</i>	111110100000000010001-000?	111100110---	000000010000110010000???			
<i>H. borealis</i>	?????0???	000000?0001-000?	???????	0---	000000010000010000000???	
<i>H. nitida</i>	?????0???	1000000?00000000???	???????	0---	000000010000010001011???	
<i>A. americana</i>	?????0???	000?000?00000000???	???????	0---	000000010000???	01?000010
<i>P. polaris</i>	111010?0100000000000000?	0101000?	0---	000000010000000101011100		
<i>A. integra</i>	111??0???	000100?0001-001?	1???	0---	011?01111111000100000???	
<i>A. lindstromi</i>	?????0???	000000?0001-001?	???????	0---	000000110111000100000???	
<i>A. schmidt</i>	?????0???	000000?0001-001?	???????	0---	0000001101???	010110000???
<i>V. allenae</i>	?????0???	110000?00000001???	???????	0---	00000001000000???	00?0???
<i>V. tortuocosta</i>	?????0???	110100?00000001???	???????	0---	0000000100010001???	000???
<i>C. banksi</i>	?????0???	0?0100?00000001???	???????	0---	000000011000010000000???	
<i>P. acuticosta</i>	?????0???	1000000000000001?	0???	0---	000000010000???	0?11011???
<i>P. amplissima</i>	?????0???	10010000000100111???	???????	0---	000000010000010010000???	
<i>T. elongata</i>	111000???	1100000000001000?	010100000---	000000010000101000000100		
<i>D. yukonensis</i>	?????0???	100000?0000100???	0???	0---	000000010000010000100001	
<i>P. canadensis</i>	?????0???	00000000001-001?	???????	0---	011101111100000100000001	
<i>A. interstincta</i>	?????0???	1001000?00000001???	???????	0---	110?01000000000000000???	
<i>T. undulata</i>	111??0???	0000000?0001-001?	1???	0---	0100?0000?0100000001?010	
<i>T. lenzi</i>	?????0???	000000?0001-001?	???????	0---	1101100000010000?0000???	
<i>T. leopoldensis</i>	?????0???	000000?0001-001?	???????	0---	1101110000010000?0000???	
<i>L. canadensis</i>	1010111?00-	00100101--101??	10100???	0---	0000000100000100?0000???	
<i>A. heintzi</i>	11101010?00001000011-101??	10100000---	000000010000001000000100			
<i>L. philipovae</i>	?????0???	000010?001??	101???	0---	000000010000001001011100	
<i>A. platyrhina</i>	000001???	0-000?10100000?	000010???	0---	00000001000000010?000???	
<i>A. elliptica</i>	0000?0???	000000001001-000?	000010???	0---	000000010000001?0?000???	
<i>A. laticostata</i>	00001010000000001001-0001?	000010???	0---	000000010000001?0?000100		
<i>A. ornata</i>	?????0???	010010?0101-110???	001???	0---	0???	0?10000010000000???
<i>A. arctata</i>	?????0???	010010?0101-110???	001???	0---	000000010000010000000???	
<i>C. dentata</i>	0000?0???	000000101001-000?	000011111000000000000000----	000000		
<i>C. cancellata</i>	0000?0???	0000001010?1-000?	000001???	10100000000000000000----	000???	
<i>C. kiaeri</i>	0000?0???	000000101011-000?	000001???	10100000000000000000----	000???	
<i>A. obruchevi</i>	0000?0???	0000001010?1-000?	000001???	11010000000000000000----	000???	
<i>A. ornata</i>	0000?0???	0000001010?1-000?	000001???	11010000000000000000----	000???	
<i>Z. meemannae</i>	0000?0???	00000001001-000?	000001???	11010000000000000000----	000???	

of *Poraspis* (Fig. 1E), which in general shows an elongate, fusiform animal with a terminally placed mouth, a lateral branchial opening and a head carapace of large discrete plates. Only few taxa, such as *Anglaspis heintzi* (Kiær, 1932), *Dinaspis elizabethae* Blicek & Heintz, 1983, *Nahanniaspis mackenziei* Dineley & Loeffler, 1976, *Torpedaspis elongata* Broad & Dineley, 1973 and *Ctenaspis dentata* Kiær, 1930, are

known from specimens complete enough to show postcranial information, and the large dorsal and ventral shields are the main source of the morphological variation in most taxa. It is thus justified that most morphological characters are associated with the dorsal and the ventral head shields (Fig. 1E). We also refer to Denison (1964, p. 315, fig. 91) for more detailed and summarised descriptions of these terms.

Phylogenetic analysis

Taxon sampling

Taxa used in this study are primarily selected from Denison's (1964) revision of the Cyathaspididae, which included 63 species grouped in 19 genera, with the addition of subsequently established species assigned to the Ariaspidae, Ctenaspidae and Cyathaspidae. These three families now contain approximately 70 species, of which the following 36 have been included in the ingroup of this study: *Irregulareaspis hoeli* (Kiær, 1932); *D. elizabethae* Blieck & Heintz, 1983; *N. mackenziei* Dineley & Loeffler, 1976; *Homalaspidella borealis* Denison, 1963; *H. nitida* (Kiær, 1932); *Americaspis americana* Claypole, 1884; *Poraspis polaris* Kiær, 1930; *Archegonaspis integra* Kunth, 1872; *A. lindstromi* (Lindström, 1895); *A. schmidtii* Geinitz, 1884; *Vernonaspis allenae* Flower & Wayland-Smith, 1952; *V. tortuocosta* Dineley & Loeffler, 1976; *Cyathaspis banksi* Huxley & Salter, 1856; *Pionaspis acuticosta* Denison, 1964; *P. amplissima* Dineley & Loeffler, 1976; *T. elongata* Broad & Dineley, 1973; *Dikenaspis yukonensis* Denison, 1963; *Ptomaspis canadensis* Denison, 1963; *Asketaspis interstincta* (Dineley & Loeffler, 1976); *Tolypelepis undulata* Pander, 1856; *T. lenzi* (Dineley & Loeffler, 1976); *T. leopoldensis* Loeffler & Jones, 1976; *Listraspis canadensis* Denison, 1964; *A. heintzi* (Kiær, 1932); *Liliaspis philipovae* Novitskaya, 1973; *Alainaspis platyrhina* Elliott & Dineley, 1985; *Allocryptaspis elliptica* (Bryant, 1934); *A. laticostata* Denison, 1960; *Ariaspis ornata* Denison, 1963; *A. arctata* Elliott & Swift, 2010; *C. dentata* Kiær, 1930; *Ctenaspis cancellata* (Kiær, 1930); *C. Kieri* (Zych, 1931); *Arctictenaspis obruchevi* (Dineley, 1976); *A. ornata* (Dineley, 1976); *Zaphoctenaspis meemannae* Elliott & Blieck, 2010. Other known taxa have been excluded from this study since they are either considered *nomina nuda* or because their morphological diagnosis is based only on non-discrete characters, such as size, which are difficult to incorporate in a phylogenetic analysis. Other species, such as *Boothiaspis ovata* Broad, 1973, have been omitted due to lack of morphological information in essential regions (i.e. the branchial region in *B. ovata*). Whenever possible, the type species for each genus has been included in the study, but in a few cases other species have been used, because a type species has either not been designated or is less well preserved than other species of the same genus. For example, *I. hoeli* was originally listed by Kiær (1932) as *Dictyaspis hoeli*, but was later included in the genus *Irregulareaspis* by Denison (1964). *I. hoeli* is used in this study instead of the type species, *Irregulareaspis stensioei* Zych, 1931, of which the type material is missing. Also *A. heintzi* was included in this study instead of the type species *Anglaspis macculloughi* (Woodward, 1891), since the available data are considerably richer in *A. heintzi*. The material referred to as *Dinaspidella* sp. indet. by Dineley & Loeffler (1976) was named *D. elizabethae* in the subsequent revision by Blieck & Heintz (1983). *D. elizabethae* was included in this study instead of the type species *Dinaspidella robusta* (Kiær, 1932) due to the large number of specimens in the referred material of *D. elizabethae* and its informativeness regarding the trunk and tail. *P. acuticosta* was included instead of the type species *P. planicosta* Denison, 1964, since the type specimen lacks a large part of the rostral ornamentation. *Poraspis sericeus* (Lankester, 1873) is the type species of *Poraspis*, although *P. polaris* Kiær, 1930 is considerably better known and Kiær & Heintz (1935) based their

reconstruction of *Poraspis* on this species. There are many species of *Poraspis* established, but only *P. polaris* has been included in this study since most of the taxonomical diversity is distinguished by non-discrete properties. Several taxa are also represented by the type and only species. For some genera several species are used since the morphological diversity within these taxa is assumed to have phylogenetic significance.

The morphologically challenging *A. chattertoni* Soehn & Wilson, 1990 with its atypical branchial region including multiple scales and platelets, and its unknown position of the branchial opening, has been used as an outgroup. *A. chattertoni* temporally precedes the cyathaspidids in being Early Silurian (Wenlockian), and apart from the atypical branchial region, its dermal armour shows similarities to the dermal armour of the cyathaspidids in composition, shape and ornamentation (Soehn & Wilson 1990). *A. chattertoni* is the only reasonable outgroup available for the study, since all other possible outgroups have very limited morphological overlap with our cyathaspidid ingroup. In this way, we have model assuming monophyletic cyathaspidids, with a character set constructed for resolving the ingroup in a satisfactory way, and at the same time limiting the amount of inapplicable data for the outgroup.

Character list and description

Front carapace

1. Micromeric-like armour in the branchial region: one single smaller element or multiple smaller elements: (0) absent, (1) present.
Micromeric-like armour is coded as being present regardless of the shape and arrangement of the smaller dermal elements.
2. Free branchial plates: (0) absent, (1) present.
Multiple series of smaller platelets and scales are present between the dorsal and ventral shields of *A. chattertoni*, but the platelets are not defined as "branchial plates" as they are smaller and have a different shape compared to the branchial plates normally found in the cyathaspidids. Also, the branchial platelets of *A. chattertoni* are not known to be located in association with a branchial opening. It is unclear if the platelets of *A. chattertoni* are homologous to the branchial plates with a dorsal notch, which are present in some cyathaspidids such as *P. polaris* or *D. elizabethae*. Neither the location of a single branchial opening nor the location of theoretical multiple branchial openings has been identified in *A. chattertoni*. The branchial opening in *A. chattertoni* has instead been suggested to be posteriorly located (Soehn & Wilson 1990).
3. Distinguishable margins of branchial plates either along free branchial plates or as the borders of fused branchial plates: (0) absent, (1) present.
With *Allocryptaspis*, *Alainaspis*, *Ctenaspis* and *Arctictenaspis*, there are arguments (Elliott et al. 2004; Elliott & Blieck 2010) for the absence of branchial plates, not because of a complete fusion to the dorsal shield, but due to an initial different composition of the armour. In *L. canadensis* the branchial plate is evidently fused to the dorsal shield with the margins of the plate still being visible and the branchial opening preserved as a slit in the fused armour (Denison 1964).

4. Subbranchial scales: (0) absent, (1) present.
Subbranchial scales are present ventral to the branchial plate in *N. mackenziei* and *D. elizabethae*. The presence of subbranchial scales in *Irregulareaspis* has been suggested by Dineley & Loeffler (1976) due to the shape of the ventral shield.
5. Free suborbital plates or fused equivalents of suborbital plates: (0) absent, (1) present.
The suborbital plates in species such as *P. polaris* and *I. hoeli* are curved plates that follow the lower border of the orbit. A fused equivalent to a free suborbital plate is present in *L. canadensis* (Denison 1964).
6. Enclosed orbit: (0) absent, (1) present.
In *L. canadensis* the orbit is enclosed by the fused suborbital plate with a marked border, but in *A. platyrhina* there is no sign of the equivalent border of the suborbital plate (Elliott & Dineley 1985).
7. Lateral plates: (0) absent, (1) present.
The lateral plates are small plates located between the dorsal shield and the anterolateral corners of the ventral shield. A number of lateral plates have been identified in *A. laticostata*, but only one single lateral plate is believed to exist in *P. polaris* and a fused single plate is present in *L. canadensis* (Kiær, 1932; Denison, 1964).
8. Oral cover with a median postoral plate: (0) absent, (1) present.
An oral cover with a median postoral plate is present in *A. chattertoni*. This type of oral cover is typical of the pteraspids, but has otherwise not been reported in the cyathaspidids, ariaspids or ctenaspids.

The dorsal shield

9. Maxillary brim broad: (0) absent, (1) present.
The maxillary brim is formed from the downward folding of the rostral border of the dorsal shield. In *P. polaris* the brim is broad and covered with ridges parallel to the anterior edge (Kiær & Heintz 1935; Denison 1964). In *T. elongata* it is broad and its medial part forms the subrostral lamella of the preoral process (Broad & Dineley 1973).
10. Median rostral lobe or process: (0) absent, (1) present.
The rostral edge of the dorsal shield is most often evenly rounded, but may sometimes form a lobe or even a process. Denison (1964, p. 368) states in the diagnosis of *Vernonaspis* that “the median lobe of the rostral edge is strongly developed”. *T. elongata* has a conspicuous median rostral process (Broad & Dineley 1973), and a less conspicuous median rostral process is present in *D. yukonensis* (Denison, 1964).
11. Preorbital processes strongly developed: (0) absent, (1) present.
The orbits are delimited anteriorly by preorbital processes. The preorbital processes are strongly developed in the vernonaspids and ariaspids (Denison 1964), but are weakly developed in *T. undulata* (Märss, 1977). In the forms that show strongly developed preorbital processes, a marked downward flexure of the margin of the dorsal shield may be present in front of the eye (Denison 1964, p. 427).
12. Enlarged rostralateral brim: (0) absent, (1) present.

An enlarged brim, in appearance looking like “a too big shoe”, extends along the rostrum and along the lateral margins of *A. chattertoni* and *A. interstincta* (Dineley & Loeffler, 1976; Soehn & Wilson, 1990).

13. Flattened rostralateral brim: (0) absent, (1) present.
The inner part of the dorsal shield stands higher than the rostral brim in *V. tortuocosta* and *C. banksi*. This is in contrast to the “too big shoe” appearance of the rostralateral brims of *A. chattertoni* and *A. interstincta* (Denison, 1964; Dineley & Loeffler, 1976).
14. Lateral brim: (0) absent, (1) present.
Lateral brims extend from the anterior part of the shield to the posterior margin in *L. canadensis*, *A. heintzi*, *L. philipovae* and in the ariaspids (Denison 1964; Novitskaya 1973; Elliott & Swift 2010). The lateral brims are narrow or absent along the rostral margin in contrast to the rostralateral brims.
15. Serrated lateral brim: (0) absent, (1) present.
A serrated brim separating the dorsal shield from the ventrolateral lamella is characteristic of the ctenaspids and arctictenaspids. It is, however, not present in *Z. meemannae* (Elliott & Blieck, 2010).
16. Narrow ventral lateral brim extending from orbital to branchial region: (0) absent, (1) present.
Narrow ventral lateral brims are present in both *D. elizabethae* and *N. mackenziei* (Dineley & Loeffler, 1976). This type of brim might be present also in *Irregulareaspis*, which is very similar to *Dinaspidella* (Dineley & Loeffler, 1976).
17. Ventrolateral lamina: (0) absent, (1) present.
Morphologically, the ventrolateral lamina appears as an area that is continuous with the surface of the dorsal shield, but that extends underneath the ventral margin of the shield and thereby forms a shelf-like lamina. According to Denison (1964, p. 436), the ventrolateral lamina of *Allocryptaspis* has the same morphological relations as the branchial plates except that in *Allocryptaspis* they are situated anterior to the branchial openings. No correlations between the morphology of the ventrolateral lamina and the lack of branchial plates in *Allocryptaspis* and *Ctenaspis* are presumed to exist.
18. Downwardly directed lamina parallel to the lateral margins of the shield: (0) absent, (1) present.
The lamina of *A. ornata* consists of downwardly directed bands parallel to the lateral margin of the shield (Denison 1964). These bands are rather narrow along the margin of the dorsal shield in contrast to the ventrolateral lamina that forms larger areas on the ventral side of the shield, as described for character 17.
19. Posterior median crest on dorsal shield: (0) absent, (1) present.
A posterior median crest of the dorsal shield is present in *A. heintzi*, *C. banksi*, *L. canadensis* and *C. dentata*. *L. philipovae* is unique in having extra multiple crests in addition to the posterior median crest located along the presumed canal pattern of the lateral line system (Novitskaya 1973).
20. Postbranchial lobes weakly developed or lacking: (0) absent, (1) present.

The downward postbranchial flexure of the margin of the dorsal shield, “the postbranchial lobes”, is a frequently used concept in diagnoses and descriptions (Denison 1964; Dineley & Loeffler 1976). Denison (1964) distinguishes between long and short, shallow and deep, weakly and well-developed postbranchial lobes. Weakly developed lobes are here grouped together with lacking lobes as a morphological discrimination between the two different categories is difficult.

21. Margins of the postbranchial lobes abruptly truncated: (0) absent, (1) present.

The margins of the postbranchial lobes are abruptly truncated in *Dinaspidella*, *Dikenaspis* and *Irregulareaspis* (*Irregulareaspidines sensu* Denison, 1964) and in *P. amplissima* (Dineley & Loeffler, 1976).

22. Pointed posterolateral corners: (0) absent, (1) present.

In *Anglaspis*, the pointed posterolateral corners of the dorsal shield seem to vary between the different species of the genus (Denison 1964). The pointed posterolateral corners of the dorsal shields of *L. canadensis*, the ariaspids and *L. philipovae* are conspicuous.

23. Dorsal spine or projection: (0) absent, (1) present.

The type specimen of *A. ornata* has a dorsal shield with scale-like posterior spine (Denison 1964). The type specimen of *A. arctata* also has a dorsal shield, but the posterodorsal projection is less scale-like (Elliott & Swift 2010).

24. Epitegas: (0) absent, (1) present.

The dorsal shield of the head armour of the Cythaspididae has been divided into different subunits (Kiær 1932; Obruchev 1945; Stensiö 1958) termed “epitegas”. The epitegas are marked by differences in the superficial ridge pattern and possibly in some instances by sutures. The epitega concept and its ontogenetic aspects are discussed by Denison (1964, pp. 458–459) and epitegas are here coded as present in the same species as they are recognized by Denison (1964), Dineley & Loeffler (1976) and Soehn & Wilson (1990).

The ventral shield

25. Anterior border notched for the reception of oral or postoral plates: (0) absent, (1) present.

The anterior margin of *P. amplissima* has a median notch and two pairs of anterolateral notches (Dineley & Loeffler 1976, p. 66). The margin of *A. laticostata* is notched for the reception of postoral plates (Denison 1964, p. 318), and the anterior margin of *A. sandbergi* Elliott et al., 2004 shows a large median concavity which is flanked laterally by three depressions (Elliott et al. 2004). The notches in all three cases are interpreted to be for the reception of oral or postoral plates.

26. Ventral shield with indented lateral margins: (0) absent, (1) present.

The ventral shields of *Irregulareaspis*, *Nahanniaspis* and *Dinaspidella* have indented lateral margins (Dineley & Loeffler 1976).

Branchial region

27. Branchial plate with a posterior dorsal notch: (0) absent, (1) present.

The shape of the free branchial plate of *P. polaris*, which possesses a posterior dorsal notch, is outlined by Kiær & Heintz (1935).

28. Branchial plate with a posterior dorsal lobe: (0) absent, (1) present.

The branchial plate in genera such as *Dinaspidella* and *Nahanniaspis* shows a notch on the dorsal border of the plate and also a posterior lobe (Dineley & Loeffler 1976).

29. Branchial opening located between the branchial notch of the dorsal shield and the notch of a free or fused equivalent of a branchial plate: (0) absent, (1) present.

This arrangement of the branchial opening is present in Kiær’s (1932) reconstruction of *Anglaspis*.

30. Branchial opening preserved in the armour as an opening made up of notches symmetrically arranged on both sides of the border between the dorsal and ventral shields or is preserved as an opening in the dorsal shield extending from the border between the two shields: (0) absent, (1) present.

In *Alloccryptaspis* the branchial opening is shaped as a circular notch formed by symmetrically arranged semicircular notches in the dorsal and ventral shields on both sides of the axis between the dorsal and ventral shields. In *Alainaspis* the branchial opening is elongated and large, and abuts the border between the dorsal and ventral shields.

31. Branchial opening located at the posterolateral corners of the dorsal shield: (0) absent, (1) present.

It has been suggested that the ctenaspids and arctictenaspidids have the branchial opening in a posterolateral position at the corners of the dorsal shield (Elliott & Blieck 2010). This may also be the case in the ariaspids and in *A. chattertoni* (Soehn & Wilson, 1990).

Posterior part of body and caudal fin

32. Dorsolateral and ventrolateral scales of similar size and shape: (0) absent, (1) present.

Irregulareaspis, *Nahanniaspis* and *Dinaspidella* (Dineley & Loeffler, 1976) as well as *C. dentata* (Dineley, 1976) and *A. chattertoni* have ventrolateral and dorsolateral body scales of the same size. Dineley & Loeffler (1976) mention a poorly preserved specimen of *Homalaspis* cf. *H. borealis* with dorsolateral and ventrolateral scales of the same size.

33. Scale rings of posterior body more than eight in number: (0) absent, (1) present.

Anglaspis and *Torpedaspis* have fewer scale rings (six scale rings in *Anglaspis* and eight in *Torpedaspis*) than *Nahanniaspis* and *Dinaspidella* resulting in a less flexible body (Dineley & Loeffler 1976).

Ornamentation of the dorsal shield

34. Superficial layer: (0) absent, (1) present.

The absence of the superficial layer of the dermal armour distinguishes the ctenaspids, arctictenaspidids and *Z. meemanae* from the remaining species. The superficial layer of the dermal armour is also absent in *Skalviaspis* (Karatajute-Talimaa, 1989) and is possibly homoplastic within the heterostracans.

35. Tuberculate ornamentation mainly (of the reticular layer): (0) absent, (1) present.

The ornamentation of the dorsal shield in the ctenaspids is composed of tubercles or of a network of ridges. *C. dentata* has an ornament of fine pointed tubercles, but the ornament of *C. cancellata* is reticulate. *C. Kiæri* shows a graduation

- from a tuberculate ornament on the central part of the shield to a reticulate on the lateral part (Elliott & Blieck 2010).
36. Reticulate ornamentation (of the reticular layer) of the dorsal shield: (0) absent, (1) present.
See character 35.
37. Ornamentation (of the reticular layer) of the dorsal shield mainly consisting of coarser rounded tubercles: (0) absent, (1) present.
The arctitenaspids are distinguished from the ctenaspids by their ornament of coarser rounded tubercles in contrast to the pointed tubercles and reticulated ornament of the *Ctenaspis* species (Elliott & Blieck, 2010).
38. Postrostral band of tubercles: (0) absent, (1) present.
In some of the tolpelepidids, in *A. interstincta* and in *A. chattertoni* the different subareas of the shield are lined with an internal band of tubercles, referred by some authors to as the “interepitegal band of tubercles” (Dineley & Loeffler 1976; Soehn & Wilson 1990).
39. Scale-like units are part of the dorsal shield ornamentation: (0) absent, (1) present.
In some species, such as *A. chattertoni*, *A. interstincta*, the tolpelepidids and *P. canadensis*, the dorsal shield appears in to be composed partially or entirely of fused scales.
40. Ornamentation includes scale-like units, but scale-like units are absent from the anterior parts of the dorsal shield: (0) absent, (1) present.
In *A. chattertoni* scale-like units are absent from the postrostral region, where the ornamentation instead consists of short, coarse, irregularly arranged ridges (Soehn & Wilson 1990). *P. canadensis* lacks scale-like units in the postrostral regions of the shield (Denison 1964).
41. Differentiation of scale-like units along the anteroposterior axis of the dorsal shield: (0) absent, (1) present.
In *T. undulata*, the scale-like units look almost uniform regarding size and shape along the anteroposterior axis of the shield. In the other tolpelepidids, in *A. interstincta* and in *A. chattertoni*, the scale-like units tend to be more elongate in the central region of the shield and in some of the tolpelepidids they show an arrow-like morphology close to the posterior edge of the shield (Loeffler & Jones 1976).
42. Arrow-like, scale-like units in the posterior part of the dorsal shield: (0) absent, (1) present.
See character 41.
43. Low relief scale-like units: (0) absent, (1) present:
The scale-like units stand out less from the background in *A. chattertoni* and *A. interstincta*, and in the central part of the dorsal shield of *T. leopoldensis* as compared to, for instance, *T. undulata*.
44. Distinct ornamentation of the rostral and postrostral parts of the dorsal shield: (0) absent, (1) present.
The postrostral pattern of swirled ridges in *A. chattertoni* is very different from the postrostral ornamentation in *P. canadensis* and the archegonaspids. However, both kinds of ornamentation show a distinct pattern of ornamentation in the rostral and postrostral fields compared to the central and posterior parts of the shield.
45. Longitudinal, elongate ridges form part of the dorsal shield ornamentation: (0) absent, (1) present.
Ridges are elevated longitudinal ornamentation crests of the superficial layer. They may be regular or irregular and are found combined with other ornamentation in a variety of different ways.
46. Varying height of the ridges: (0) absent, (1) present.
P. canadensis and *A. integra* display the first character state (Denison 1964).
47. Postrostral field of triangular shape: (0) absent, (1) present.
The triangular postrostral ornamentation is typical of *Archegonaspis* species. A triangle consisting of small ornamental elements, “the pineal triangle”, lines the pineal macula in *A. integra* and *A. lindstromi*, but is less evident in *A. schmidtii*.
48. Pineal triangle: (0) absent, (1) present.
See character 47.
49. Fields of small, tessellate ornament on the posterior part of the shield: (0) absent, (1) present.
Small elements of ornamentation are found in triangle-shaped groups associated with the scale-like units on the posterior part of the dorsal shields of the tolpelepidids and on the posterior part of the dorsal shields of *A. integra* and *A. lindstromi* (Denison, 1964). In *V. tortuocosta*, tessellate ornament occurs in patches found over the entire dorsal shield (Dineley & Loeffler 1976).
50. Ornamentation of the postrostral area including several longitudinal ridges that together form concentric whorls in the rostral region: (0) absent, (1) present.
Whorled patterns of ridges is present in the postrostral area of species such as *D. elizabethae*, *N. mackenziei* and *T. elongata* (Broad & Dineley, 1973; Dineley & Loeffler, 1976).
51. Transverse rostral ridge pattern: (0) absent, (1) present.
When present, several transverse ridges line the outermost rostral tip or form an almost transverse part of a semicircular pattern close to the rostral tip.
52. Radiating rostral ridge pattern: (0) absent, (1) present.
The rostral ridge pattern radiates towards the margins of the dorsal shield.
53. Distinct V-shaped border in the ornamentation separates the posterior part of the dorsal shield from the anterior part and divides the shield in two parts: (0) absent, (1) present.
A distinct V-shaped border in the ornamentation is present in the archegonaspids and in *P. canadensis*, and also in *P. polaris*, *A. platyrhina* and the allocryptaspids (Kiær & Heintz 1935; Elliott & Dineley 1985; Elliott et al. 2004). The V-shaped border may be identical to a marked supraorbital commissure or (in the archegonaspids) be a distinct V-shaped border formed by the differences in ornamentation only, but that may possibly follow an indistinct or degenerate supraorbital commissure. A marked V-shaped border is present in *L. philipovae*, but the shield is divided in more than two parts by the other crests.
54. Indistinct pineal macula: (0) absent, (1) present.
In a number of species, the pineal macula is easily visible and in many cases ornamented with circular or elliptical ridges. In, for instance, *D. elizabethae* a distinct ornamentation of the pineal macula is lacking and the position of the pineal organ is considerably more difficult to trace.

55. Needle-shaped ridges: (0) absent, (1) present.
The lobes at the ends of the ridges, which are seen for instance in the elevated crests of *L. philipovae* (Novitskaya, 1973), give them a needle-like appearance.
56. Numerous, scattered pores: (0) absent, (1) present.
I. hoeli and *D. elizabethae* are examples of species that have numerous scattered pores all over the surface of the dorsal shield. In the case of *D. elizabethae*, the high number of pores is not as in *Irregulareaspis* linked to a branched lateral line system (Dineley & Loeffler 1976). *A. platyrhina* has numerous pores in the rostral area only, but is because of the restricted location of the pores coded as not having numerous pores present (Elliott & Dineley 1985).
57. Conspicuous pores: (0) absent, (1) present.
Conspicuous pores of the “lateral line system” are present on the surface of the dermal armour of for instance *P. polaris* and *H. nitida* Kiær, 1932. Pores are not visible (but are possibly present) on the surface of others cyathaspidids such as *A. lindstromi* despite, in general, apparently good preservation.
58. Needle-shaped pore-associated ridges confined to areas of the presumed underlying canal pattern: (0) absent, (1) present.
The needle-shaped, pore-associated ridges are present in *P. polaris* and *H. nitida* (Kiær & Heintz, 1935) and are also found along the thickened linear crests of *L. philipovae*.
59. Canal pattern of *P. polaris* type: (0) absent, (1) present.
The canal pattern of *P. polaris* is divided by Kiær & Heintz (1935) into two pairs of longitudinal lines, the lateral dorsal lines and the median dorsal lines, and into four transverse commissures. Denison (1964) adds to this terminology a supraorbital canal and a transverse supraorbital commissure. Denison’s reconstructions from 1964 of the canal pattern in the dorsal shield of *P. polaris* and in the dorsal shield of *A. macculloughi* are virtually similar to each other. In species such as *P. canadensis* and *C. dentata*, the fourth commissure is lacking; these two species are among those that are coded as lacking a canal pattern of *P. polaris* type.
60. Segmented canal pattern: (0) absent, (1) present.
In Denison’s (1964, pp. 326–327) presentation of the reconstructed canal pattern in the dorsal shield in different cyathaspidids, the canal pattern of *T. undulata*, *P. canadensis* and *A. americana* Claypole, 1884 is shown as consisting of shorter segments.
61. Branched canal pattern: (0) absent, (1) present.
The reconstruction of the canal patterns in the dorsal shields of *D. yukonensis* Denison, 1963 and *Irregulareaspis complicata* is shown by Denison (1964, pp. 326–327) as being highly branched. The branched pattern of *I. hoeli* is inferred.

Results

The data matrix was constructed from 61 characters and 37 taxa (Table 1) in MacClade 3.01 (Maddison & Maddison 1992) and processed using PAUP *4.0 (Swofford 2003). For the analysis, heuristic search methods and presence/absence coding were applied, resulting in nine most parsimonious trees, each with a length of 122 steps.

The strict consensus tree (Fig. 2) has a moderate degree of resolution with a consistency index of 0.48, retention index (RI) of 0.73 and rescaled consistency index of 0.36, showing a quite well-resolved topology within the assumed monophyletic Cyathaspididae, with the exception of *A. interstincta*, which is in a polytomy with the outgroup *A. chattertoni* and all the remaining cyathaspidids. The tolypelepidids come out paraphyletic and occupy the most basal positions in this clade. A clade slightly more derived than the tolypelepidids, including the various species of *Archegonaspis* and *P. canadensis*, shows low internal resolution (see Supplementary Information), but is well defined by the unique presence of a triangular postrostral field (Fig. 2).

The clade including the ctenaspidids, the allocryptaspidids and *A. platyrhina* is supported by homoplastic characters only, but comes out stronger than any other clades with a Bremer decay index showing that six additional steps are required to collapse this topology. A strong signal comes from a monophyletic assemblage of ctenaspidids in which the lack of the superficial layer is an apomorphic trait. The topology of the remainder of the tree is rather well resolved. The most prominent clade is the one including *Homalaspisidella*, *Anglaspis*, *Ariaspis* and *Torpedaspis*, among others, although internally it is only the clade including *Listraspis*, *Anglaspis*, *Liliaspis* and *Ariaspis* that is robust with two synapomorphies. Overall, the tree is characterized by quite a large degree of homoplasy with rather limited numbers of synapomorphies defining the various clades (Fig. 2 and Supplementary Information). This is partly illustrated by *Dinaspidella* and *Pionaspis*, which are represented by more than one species that turn out to be paraphyletic.

Discussion

The present results show that although there is quite a lot of homoplasy in the strict consensus tree (Fig. 2), morphological aspects such as the morphology of the branchial region, the ornamentation of the dermal armour and the canal pattern in the dorsal shield all contribute to the topology of the tree and its resolution. Of these three morphological features, the branchial region and the lateral canal pattern in the dorsal shield are sensitive with regard to character coding since they are to some extent based on available literature and relies on the assumption that these are accurate (Denison 1964). This emphasizes that this study must be regarded as preliminary and a first step towards a phylogeny of the cyathaspidids or Cyathaspidiformes *sensu* Janvier (1996a) as a whole. This exploration of character coding for the very monomorphic cyathaspidid group also stresses the need for further research on various aspects of heterostracan morphology, which would facilitate an expanded data set and ultimately explore the phylogenetic framework for an otherwise very polymorphic assembly of stem gnathostomes.

As this study relies heavily on the novel construction of character states in the branchial region, it should be stressed that the posterolateral position of the branchial openings is found to be homoplastic and occurs in both the ariaspids and the ctenaspidids. Neither *A. platyrhina*, nor any of the allocryptaspidids and ctenaspidids fall out as immediate sister groups to *L. canadensis*, in which the branchial plate evidently has become fused to the dorsal shield. Atypical solutions of the arrangements of the dermal armour in the branchial region might have existed



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Nahanniaspis, *Torpedaspis* and *Anglaspis*, as presented by the phylogeny of Janvier (1996a), is in agreement with the present phylogeny. On the other hand, there is a lot of disagreement with the classifications presented by Denison (1964) since very few of the established subfamilies are recognized as clades in the present analysis. This appears to be due to the homoplastic distribution of the characters that were particularly important for Denison's (1964) subfamily classification. This includes characters related to the presence or absence of apparent scale-like units in the shield, the pattern, length and uniformity of the superficial dentine ridges, and the branching of the lateral lines (Denison 1964). The latter is particularly interesting since the presumed lateral line system, illustrated by the pores of *P. polaris* (Fig. 1D), is open for discussion. The canal pattern in the cancellous layer of some cyathaspidids superficially resembles the cephalic canal pattern of the lateral line system of recent fishes (Kiær & Heintz 1935). No fossilized neuromasts are left to further indicate the function of this morphological pattern in the cyathaspidids, and indeed fossilized neuromasts are yet to be found in all the "lateral line systems" of basal vertebrate groups that are assumed on behalf of morphological similarities to have possessed a lateral line system reminiscent of that found in modern fishes. The function as a sense system is therefore here regarded as hypothetical rather than as a clear-cut homologue to the lateral line system of recent fishes. In any case, one should be careful to assume large-scale phylogenetic signals involving these characters, since patterns of lateral line canal systems are documented to show profound variation in recent fishes (Dijkgraaf 1962). The diversity of the lateral line system across species suggests that divergence in this sensory system plays a role in adaptation to different environments (Braun & Grande 2008). If a homology between the lateral line system of recent fishes and the morphologically similar counterpart in the cyathaspidids exists, then environmental changes might have affected the morphological divergence of the lateral line system in the cyathaspidids as well.

The cyathaspidids thrived in both marine and marginal marine habitats. These two habitats demand very different adaptations in the recent world – and likely did so as well in the Siluro-Devonian past. An exploration of the connections between biogeography, stratigraphy and phylogenetic patterns may, in the future, reveal many interesting secrets regarding the palaeobiology of this long-gone extinct group of early vertebrates.

Supplementary Information

Strict consensus tree showing characters and states with changes on the branches.

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