An Ordovician nectocaridid hints at an endocochleate origin of Cephalopoda

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Running Header: Internally shelled Ordovician nectocaridid

Abstract.—Nectocaridids are soft-bodied Cambrian organisms that have been controversially interpreted as primitive cephalopods, at odds with the long-held belief that these molluscs evolved from a shell-bearing ancestor. Here I document a new nectocaridid from the Whetstone Gulf formation, extending the group's range into the Late Ordovician. *Nectocotis rusmithi* n. gen., n. sp. possesses a robust internal element that resembles a non-mineralized phragmocone or gladius. Nectocaridids can be accommodated in the cephalopod total group if (1) cephalopods inherited a non-mineralized shell field from the ancestral mollusc; (2) the earliest cephalopods bore internal shells. This evolutionary scenario would overturn the traditional ectocochleate, *Nautilus*-like reconstruction of the ancestral cephalopod, and indicate a trend towards increased metabolic efficiency through the course of Cambrian–Ordovician evolution.

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Introduction

Cephalopod molluscs have been a prominent component of marine ecosystems for the past half billion years, and fossils of their mineralized shells provide an often detailed chronicle of their later evolutionary history.

Cephalopoda is divided into two major lineages. The fossil record of nautiloids begins in the latest Cambrian, proliferates through the Ordovician, and dwindles towards the present day. Palaeontologists are most familiar with stem group representatives of the neocoleoid lineage, namely the ammonoids and belemnoids that are abundant from the Devonian until their end-Cretaceous extinction (House, 1985; Teichert, 1986; Holland, 1987; Kröger et al., 2011); extant Neocoleoidea exhibit diminutive, non-mineralized or chemically fragile shells, and thus require unusual preservational conditions in order to enter the fossil record (Kear et al., 1995).

Whereas exceptional Mesozoic specimens greatly illuminate the diversification of neocoleoids (Doguzhaeva et al., 2007; Yancey et al., 2010), earlier taxa are often difficult to place phylogenetically (Sutton et al., 2016), a problem compounded by the increasing scarcity of exceptional preservation as one goes deeper into the Palaeozoic. With almost no non-biomineralized cephalopod tissue known prior to the Carboniferous period (Klug and Lehmann, 2015), there is little direct fossil evidence – ammonoids and belemnoids notwithstanding – from which to reconstruct the earliest emergence of the coleoids.

The oldest uncontroversial cephalopods are late Cambrian phragmocones – chambered shells in which adjacent chambers are connected by a siphuncular tube, which represents a cephalopod synapomorphy. The consensus view is that a shell was inherited from a molluscan common ancestor, with several chambered ‘monoplacophoran’ taxa (Yochelson et al., 1973; Brock and

Paterson, 2004) representing candidate intermediate forms. On this view, weakly-mineralized skeletal apparatuses such as the coleoid gladius, pen or pro-ostracum arose through the reduction of a robust mineralized shell, perhaps on multiple occasions, but no earlier than the Carboniferous (Kröger et al., 2011; Doguzhaeva and Mapes, 2015).

This model has no place for the problematic *Nectocaris pteryx*, a non-mineralizing early Cambrian organism from Burgess Shale-type deposits that strikingly resembles modern coleoids (Smith and Caron, 2010; Smith, 2013). To some extent, this similarity reflects characteristics that may have arisen convergently: camera-type eyes, lateral fins, denticulate mouthparts and anterior tentacles may each have arisen more than once among Metazoa (Mazurek and Zatoń, 2011). Insofar as unique combinations of individually non-unique characteristics can be instructive (Butterfield, 2005), it is noteworthy that cephalopods are the only organisms to display this particular combination. But a more definitive characteristic (Runnegar, 2011) is a wide axial cavity that contains a pair of gills and opens through a ventrally-directed anterior funnel. If this is correctly interpreted as a cephalopod mantle cavity (Smith and Caron, 2010; Smith, 2013), then it represents a cephalopod synapomorphy, and ascribes *Nectocaris* to the cephalopods as surely as a siphunculate phragmocone would.

The suggestion that this void might instead represent a gut (Kröger et al., 2011; Runnegar, 2011), which is presumably the basis for reconstructing a straight gut in *Nectocaris* (Kröger et al., 2011; Klug et al., 2015), has been firmly discounted (Smith, 2013); no gut has ever been observed in *Nectocaris* (Smith and Caron, 2011), though the anterior location of the funnel implies that the gut, along with the body axis, was folded into a U-shape during development (Runnegar, 2011).

Taken together, then, *Nectocaris* presents two characters known only in Cephalopoda – an axial mantle cavity and anterior funnel – along with a suite of characters that are only found together in cephalopods: internal gills, camera-type eyes, flexible muscular tentacles, muscular lateral fins with criss-crossing connective tissue, and denticulate chevron-shaped mouthparts.

Of course, no list of synapomorphies can conclusively establish affinity, and it remains possible that *Nectocaris* embodies extreme evolutionary convergence from an undetermined metazoan (or indeed non-metazoan) lineage (Kröger et al., 2011; Mazurek and Zatoń, 2011; Runnegar, 2011). Even so, it is difficult to pinpoint a lineage from which a nectocaridid-like morphology might plausibly be derived. There is no clear indication of an ecdysozoan, deuterostome or chaetognath affinity, and those trochophore phyla with complex free-living body plans have a reasonably well constrained evolutionary history: molluscs, annelids and brachiopods seem to have evolved from a grade of creeping organisms with dorsal imbricating scleritomes (Skovsted et al., 2015; Zhang et al., 2015; Sun et al., 2018) that bear no obvious similarity to *Nectocaris*.

To further inform the evolutionary position of *Nectocaris*, I here describe a new Katian (Late Ordovician) nectocaridid with an internal, non-mineralized skeletal element. *Nectocotis rusmithi* new genus, new species demonstrates that nectocaridids survived the terminal Cambrian extinction event that decimated phragmocone-bearing cephalopods (Kröger, 2013), and hints that coleoids, rather than nautiloids, are the most appropriate model for the ancestral cephalopod.

Materials and methods

This study concerns the part and partial counterpart of a single specimen from the Katian (Upper Ordovician, c. 450 Ma) Whetstone Gulf Formation, Lorraine Group, Lewis County, New York State. The specimen, which measures 11 mm from apex to anterior margin of funnel and 5 mm at point of maximum width (Fig. 1; Smith, 2019), occurs in a massive dark grey siltstone that contains rare sub-mm pyrite crystals. In contrast to the pyritization for which the Whetstone formation is known (Farrell et al., 2009), this specimen is preserved in Burgess Shale fashion (Butterfield et al., 2007). Blue colouration under bright-field illumination denotes the presence of aluminosilicate minerals that presumably templated an original carbon film. As with Burgess Shale fossils, these films appear dark under cross-polarized light (Fig. 1.1), but are brighter, becoming difficult to distinguish from the matrix, under non-polarized dark-field illumination (Fig. 1.2, 1.3).

Repository and institutional abbreviation.—Material is accessioned at the Royal Ontario Museum (ROM), Toronto, Canada.

Systematic paleontology

Family Nectocarididae Conway Morris 1976

Genus *Nectocotis* new genus

Type species.—Nectocotis rusmithi new species, by monotypy.

Diagnosis.—As for type species, by monotypy.

Etymology.—Reflecting the origin of the material from the Whetstone (Latin *cotis*) Formation.

Remarks.—The key difference between *Nectocotis* and *Nectocaris* is the presence of a robust internal skeletal component within the dorsal body region.

Nectocotis rusmithi new species

Figure 1

Holotype and only known specimen.—ROM IP 65341.

Diagnosis.—Nectocaridid whose body is spanned by a robust field in the shape of a convex Euclidian kite.

Description.—The overall construction of the specimen closely resembles *Nectocaris pteryx* (Smith and Caron, 2010; Smith, 2013). The body measures 4.4 mm at its widest point and 10.0 mm in length, discounting the head. Its widest point is 7 mm from the posterior. A gently flaring ventral structure extends 1.9 mm from the anteriormost part of the body, increasing in width from 1.2 mm to 2.0 mm at its distal end; this corresponds in position and shape to the *Nectocaris* funnel, whilst being proportionally larger in relation to the body (as fluid dynamic considerations would predict of an exhalent siphon at small body size; Smith, 2013). A pair of prominent eyes are preserved as dark structures with a diagenetic infill (Fig. 1.1, 1.5), presumably denoting a high concentration of preserved carbon, as in *Nectocaris*. A pair of smooth-margined tentacles (of which the basal 3.5 mm is preserved) emerge anterodorsally from the head. Dark axial elements in the body region (‘ac’ in Fig. 1) presumably represent gills within an axial cavity, but lack the preservational fidelity necessary for a confident interpretation.

The dorsal body region of *Nectocotis rusmithi* n. gen, n. sp. is predominantly occupied by a flat structure that I interpret as an internal skeletal element. Its central region is flatter than the uneven fracture surface of the surrounding matrix, whereas its margins exhibit prominent relief (Fig. 1.2, 1.3); taken together, these observations denote a structure that was originally robust and inflexible enough to resist deformation and compression. This resilience cannot represent early permineralization of muscular tissue: the muscular tentacles and funnel are preserved without relief, as in equivalent specimens in the Burgess Shale (Smith and Caron, 2010; Smith, 2013). The element occupies almost the full width of the organism, in contrast with the medial axial cavity observed in *N. pteryx*. It is difficult to see how rapid mineralization of, say, digestive tissue or gills could give rise to an entity with a well-defined quadrilateral margin. The only satisfactory account for the shape and relief of the structure is that it represents a robust (though seemingly not mineralized) skeletal element.

This skeletal element is laterally surrounded by a continuous region of soft tissue interpreted as a fin, based on its position and lateral deformation (cf. *Nectocaris*, Smith 2013). Anterior to the skeletal element, the fins bear a series of 100 μm-wide ridges (Fig. 1.3, 1.4) similar in proportion, orientation and three-dimensionality to the coarse stripes in the fins of *Nectocaris* (Smith, 2013). The fins overlap the skeletal element on the (ventrally preserved) fossil, whereas the tentacles, eyes and head lie in a plane deeper in the rock and thus dorsal to the skeletal element. Being sandwiched between these two layers of soft tissue and surrounded by the fins, the skeletal element is necessarily internal.

Etymology.—Patronym, for R. D. A. Smith, who generously donated the specimen from his private collections.

Remarks.—The presence of an internal skeletal element distinguishes *Nectocotis rusmithi* n. gen., n. sp. from *Nectocaris*. If such an element was present in *Nectocaris* during life, its absence in fossils would be hard to explain, given the routine association of rigid skeletal elements with relief in Burgess Shale-type deposits. The robust internal element in the posterior body of a single large specimen (Smith, 2013, fig. 11A) is the only possible candidate, but as this feature is diminutive, differs in shape, and occurs in but a single specimen, its homology with the newly described skeletal element must be considered uncertain.

Discussion

An internal skeletal element represents a further addition to the list of cephalopodan features present in nectocaridids. One of the most fundamental principles of phylogenetic systematics is Hennig's auxiliary principle (Hennig, 1953), which states that similarities should be assumed to reflect kinship rather than convergence (De Laet, 2005; Mooi and Gill, 2016). Only by interpreting nectocaridids as total group cephalopods (Fig. 2) can cephalopod similarities (funnel, internal gills, jet propulsion, tentacles, prominent eyes) be attributed to common ancestry. (By implication, features absent in nectocaridids – multiple arms; chitinous beak; shell chambers – arose later in the cephalopod lineage). If a mineralized shell was present in the ancestral cephalopod, then this position creates a 30 million year stratigraphic gap before the first undoubted cephalopod, the mineralized and siphunculate *Plectronoceras*. Such a gap might be filled by camerate shelly fossils such as *Knightoconus* and *Tannuella* (Yochelson et al., 1973; Brock and Paterson, 2004) (Fig. 2, blue), though there is no hard reason that these taxa must be cephalopods – septa have evolved independently many times, including in lophophorates (the hyolith *Cupitheca*, Skovsted et al., 2016), gastropods (Fretter and Graham, 1978), tentaculitoids (Weedon, 1990) and foramanifera. Alternatively, there may be a genuine gap in the fossil record – gaps of this magnitude are not unknown among either Cambrian shelly fossils (e.g. Runnegar and Pojeta, 1992) or Mesozoic coleoids (see Brayard et al., 2017).

Alternatively, this stratigraphic gap may indicate that the earliest cephalopod phragmocones, like the nectocaridid skeletal element, lacked biomineralization – in which case *Plectronoceras* represents the earliest cephalopod seen to mineralize its shell field (Fig. 2, orange). On this view, the shell field – a synapomorphy of Conchifera (Kniprath, 1981; Hohagen and Jackson, 2013) – is a primitively non-mineralized organ, consistent with its lack of biomineralization early in ontogeny (Bandel, 1989; Checa et al., 2015), and the non-mineralized nature of early mollusc relatives (Caron et al., 2006). (Parsimony analysis denotes that the mineralization of a non-mineralized shell field is not a unique event in cephalopod evolution, having occurred in Spirulida and conceivably Sepiida (Sutton et al., 2016).)

The morphology of the earliest cephalopod fossils has traditionally been modelled on living *Nautilus*, but nectocaridids suggest that the ancestral cephalopod more closely resembled a coleoid – most significantly in bearing an internal shell. There is no direct evidence (such as muscle scars) that the earliest cephalopod shells were external (Webers and Yochelson, 1989); the recognition that a range of nautiloid, orthocerid and ammonoid shells were internal (Turek and Manda, 2012; Doguzhaeva and Mutvei, 2015; Mutvei and Mapes, 2018) raises the possibility that shell externalization characterises only a small subset of cephalopod lineages, including certain orthocerids (Gabbott, 1999; Kröger et al., 2009), modern nautiloids and the ectocochleate ammonoids (Maeda and Seilacher, 1996).

Whatever its exact phylogenetic placement, nectocaridids indicate that the earliest cephalopod-like organisms had a high specific biomass: a correlate of power density and metabolic activity (O'Dor and Webber, 1991; Bambach, 1993; Brown et al., 2004). In contrast, the high shell volume in Cambro-Ordovician nautiloids denotes a lower metabolic rate and a higher physiological efficiency (O'Dor et al., 1993; Boutilier et al., 1996). This metabolic trend mirrors that observed in the brachiopod total group through the Cambrian (Sun et al., 2018), suggesting that early neocoleoid-like organisms such as *Nectocaris* and *Nectocotis* were largely supplanted by metabolically conservative, externally shelled, passively buoyant nautiloids in response to declining oxygen and energy availability in the late Cambrian / early Ordovician. Low-productivity Palaeozoic oceans (Bambach, 1993) saw a burgeoning of nautiloids, with nectocaridids scarcely diversifying (despite their persistence until at least the latest Ordovician). Jet-propelled organisms with neocoleoid body plans were evidently displaced from metabolically expensive niches for fast, highly active swimmers until the advent of the Carboniferous.

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Accessibility of supplemental data

High resolution light and electron micrographs are available from FigShare (Smith, 2019)

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Figures and Figure Captions

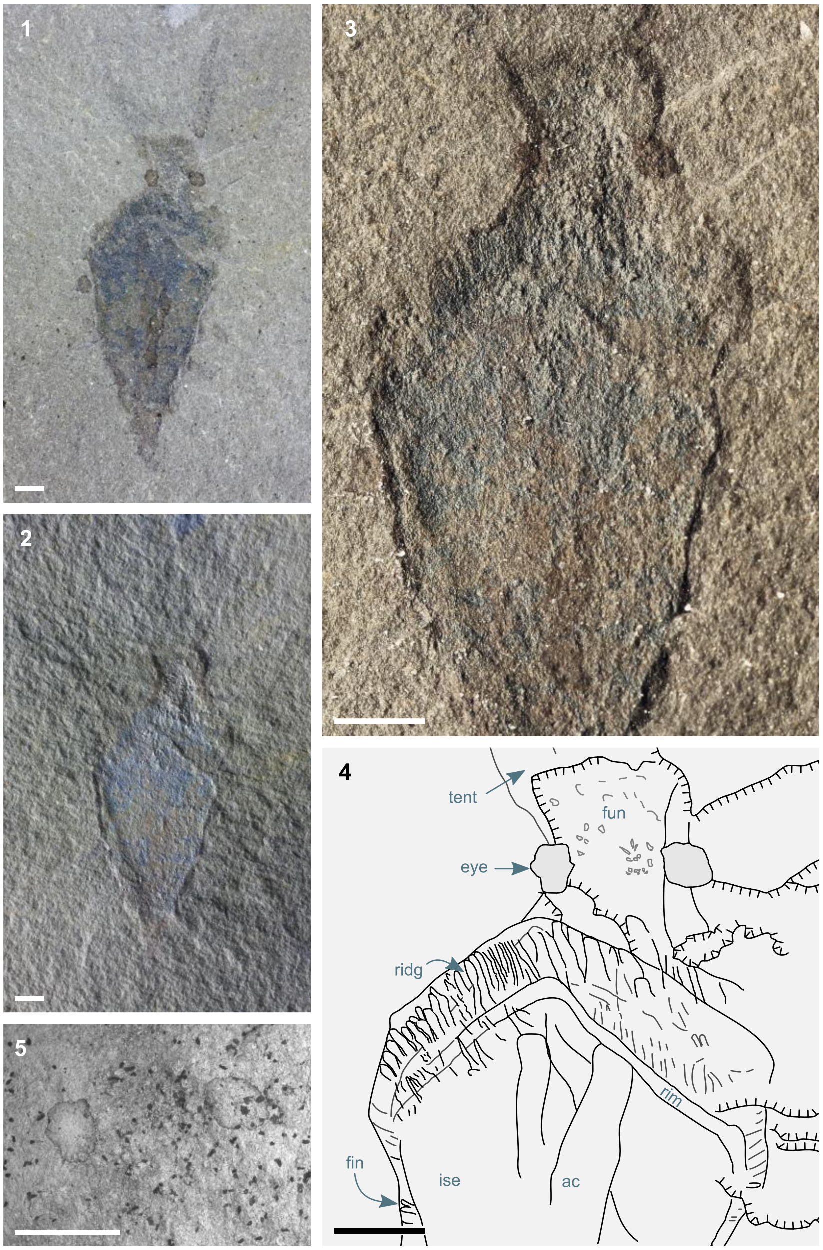

Figure 1. ***Nectocotis rusmithi*** **n. gen., n. sp. (ROM IP 65341).** (**1**) dorsal surface of complete specimen, bright field illumination, crossed polars. (**2**) dark field illumination, relief emphasized using the Grain Extract algorithm (GNU Image Manipulation Program 2.10, www.gimp.org) to superimpose images taken under two opposite illumination directions. Pixels assigned colour values from bright-field image. (**3**) dark field illumination. (**4**) sketch summarising features visible under different lighting conditions. (**5**) scanning electron micrograph of head region, showing relief and distinct composition of eyes. High resolution images are available at FigShare (Smith, 2019). Scale bars denote 1 mm.

Abbreviations: ac, decayed contents of axial cavity (gills?); fun, funnel; fin, fin; ise, internal skeletal element; ridg, ridges in anterior kite-shaped structure; rim, rim of kite-shaped structure; tent, tentacle.

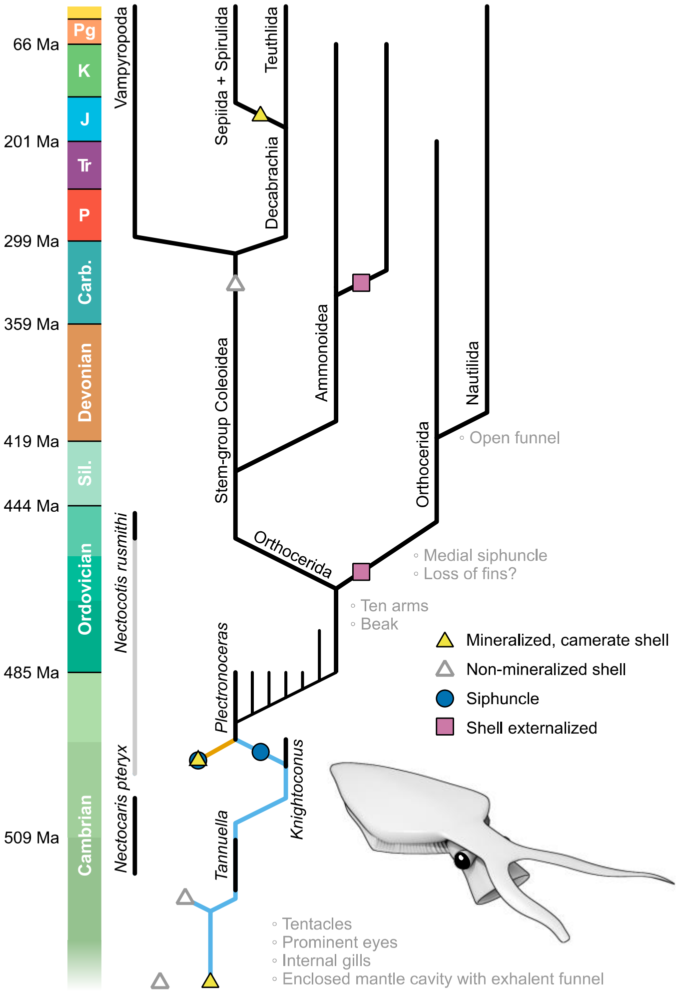

Figure 2. Simplified cephalopod phylogram. The absence of unambiguous shelly cephalopods in the early–mid Cambrian may be filled by the taxonomically ambiguous genera *Tannuella* (Brock and Paterson, 2004) and *Knightoconus* (Yochelson et al., 1973) (blue pathway), or may denote a primitively non-mineralized configuration (orange). Bold lines indicate mineralized lineages; faint lines denote ghost lineages. Inferred origins of key apomorphies indicated; time plotted to logarithmic scale. Inset: reconstruction of *Nectocotis rusmithi* n. gen., n. sp.