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1 **An Ordovician nectocaridid hints at an endocochleate origin of**
2 **Cephalopoda**

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8
9 **Running Header:** Internally shelled Ordovician nectocaridid

10

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

21

22 UUID: <http://zoobank.org/ED594200-37B9-4642-BD8F-4FB72DC544EB>

23

24 **Introduction**

25

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

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

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

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

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

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

63 The suggestion that this void might instead represent a gut (Kröger et al., 2011; Runnegar,
64 2011), which is presumably the basis for reconstructing a straight gut in *Nectocaris* (Kröger et al.,
65 2011; Klug et al., 2015), has been firmly discounted (Smith, 2013); no gut has ever been observed
66 in *Nectocaris* (Smith and Caron, 2011), though the anterior location of the funnel implies that the
67 gut, along with the body axis, was folded into a U-shape during development (Runnegar, 2011).

68 Taken together, then, *Nectocaris* presents two characters known only in Cephalopoda – an
69 axial mantle cavity and anterior funnel – along with a suite of characters that are only found

70 together in cephalopods: internal gills, camera-type eyes, flexible muscular tentacles, muscular
71 lateral fins with criss-crossing connective tissue, and denticulate chevron-shaped mouthparts.

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

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

87

88 **Materials and methods**

89

90 This study concerns the part and partial counterpart of a single specimen from the Katian (Upper
91 Ordovician, c. 450 Ma) Whetstone Gulf Formation, Lorraine Group, Lewis County, New York
92 State. The specimen, which measures 11 mm from apex to anterior margin of funnel and 5 mm at

93 point of maximum width (Fig. 1; Smith, 2019), occurs in a massive dark grey siltstone that
94 contains rare sub-mm pyrite crystals. In contrast to the pyritization for which the Whetstone
95 formation is known (Farrell et al., 2009), this specimen is preserved in Burgess Shale fashion
96 (Butterfield et al., 2007). Blue colouration under bright-field illumination denotes the presence of
97 aluminosilicate minerals that presumably templated an original carbon film. As with Burgess
98 Shale fossils, these films appear dark under cross-polarized light (Fig. 1.1), but are brighter,
99 becoming difficult to distinguish from the matrix, under non-polarized dark-field illumination (Fig.
100 1.2, 1.3).

101

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

104

105 **Systematic paleontology**

106

107 Family Nectocarididae Conway Morris 1976

108

109 Genus *Nectocotis* new genus

110

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

112

113 *Diagnosis.*—As for type species, by monotypy.

114

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

116

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

119

120

Nectocotis rusmithi new species

121

Figure 1

122

123 *Holotype and only known specimen.*—ROM IP 65341.

124

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

127

128 *Description.*—The overall construction of the specimen closely resembles *Nectocaris pteryx*
129 (Smith and Caron, 2010; Smith, 2013). The body measures 4.4 mm at its widest point and
130 10.0 mm in length, discounting the head. Its widest point is 7 mm from the posterior. A gently
131 flaring ventral structure extends 1.9 mm from the anteriormost part of the body, increasing in
132 width from 1.2 mm to 2.0 mm at its distal end; this corresponds in position and shape to the
133 *Nectocaris* funnel, whilst being proportionally larger in relation to the body (as fluid dynamic
134 considerations would predict of an exhalent siphon at small body size; Smith, 2013). A pair of
135 prominent eyes are preserved as dark structures with a diagenetic infill (Fig. 1.1, 1.5), presumably
136 denoting a high concentration of preserved carbon, as in *Nectocaris*. A pair of smooth-margined
137 tentacles (of which the basal 3.5 mm is preserved) emerge anterodorsally from the head. Dark

138 axial elements in the body region ('ac' in Fig. 1) presumably represent gills within an axial cavity,
139 but lack the preservational fidelity necessary for a confident interpretation.

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

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

160

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

163

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

171

172 **Discussion**

173

174 An internal skeletal element represents a further addition to the list of cephalopodan features
175 present in nectocaridids. One of the most fundamental principles of phylogenetic systematics is
176 Hennig's auxiliary principle (Hennig, 1953), which states that similarities should be assumed to
177 reflect kinship rather than convergence (De Laet, 2005; Mooi and Gill, 2016). Only by interpreting
178 nectocaridids as total group cephalopods (Fig. 2) can cephalopod similarities (funnel, internal gills,
179 jet propulsion, tentacles, prominent eyes) be attributed to common ancestry. (By implication,
180 features absent in nectocaridids – multiple arms; chitinous beak; shell chambers – arose later in the
181 cephalopod lineage). If a mineralized shell was present in the ancestral cephalopod, then this
182 position creates a 30 million year stratigraphic gap before the first undoubted cephalopod, the
183 mineralized and siphunculate *Plectronoceras*. Such a gap might be filled by camerate shelly fossils

184 such as *Knighthoconus* and *Tannuella* (Yochelson et al., 1973; Brock and Paterson, 2004) (Fig. 2,
185 blue), though there is no hard reason that these taxa must be cephalopods – septa have evolved
186 independently many times, including in lophophorates (the hyolith *Cupitheca*, Skovsted et al.,
187 2016), gastropods (Fretter and Graham, 1978), tentaculitoids (Weedon, 1990) and foramanifera.
188 Alternatively, there may be a genuine gap in the fossil record – gaps of this magnitude are not
189 unknown among either Cambrian shelly fossils (e.g. Runnegar and Pojeta, 1992) or Mesozoic
190 coleoids (see Brayard et al., 2017).

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

200 The morphology of the earliest cephalopod fossils has traditionally been modelled on living
201 *Nautilus*, but nectocaridids suggest that the ancestral cephalopod more closely resembled a coleoid
202 – most significantly in bearing an internal shell. There is no direct evidence (such as muscle scars)
203 that the earliest cephalopod shells were external (Webers and Yochelson, 1989); the recognition
204 that a range of nautiloid, orthocerid and ammonoid shells were internal (Turek and Manda, 2012;
205 Doguzhaeva and Mutvei, 2015; Mutvei and Mapes, 2018) raises the possibility that shell
206 externalization characterises only a small subset of cephalopod lineages, including certain

207 orthocerids (Gabbott, 1999; Kröger et al., 2009), modern nautiloids and the ectocochleate
208 ammonoids (Maeda and Seilacher, 1996).

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

222

223 **Acknowledgments**

224

225 I thank R. D. A. Smith for obtaining and generously donating the fossil material.

226

227 **Accessibility of supplemental data**

228

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

230

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357

358 **Figures and Figure Captions**

359

360 **Figure 1. *Nectocotis rusmithi* n. gen.,**

361 **n. sp. (ROM IP 65341). (1) dorsal**

362 **surface of complete specimen, bright**

363 **field illumination, crossed polars. (2)**

364 **dark field illumination, relief**

365 **emphasized using the Grain Extract**

366 **algorithm (GNU Image Manipulation**

367 **Program 2.10, www.gimp.org) to**

368 **superimpose images taken under two**

369 **opposite illumination directions.**

370 **Pixels assigned colour values from**

371 **bright-field image. (3) dark field**

372 **illumination. (4) sketch summarising**

373 **features visible under different**

374 **lighting conditions. (5) scanning**

375 **electron micrograph of head region,**

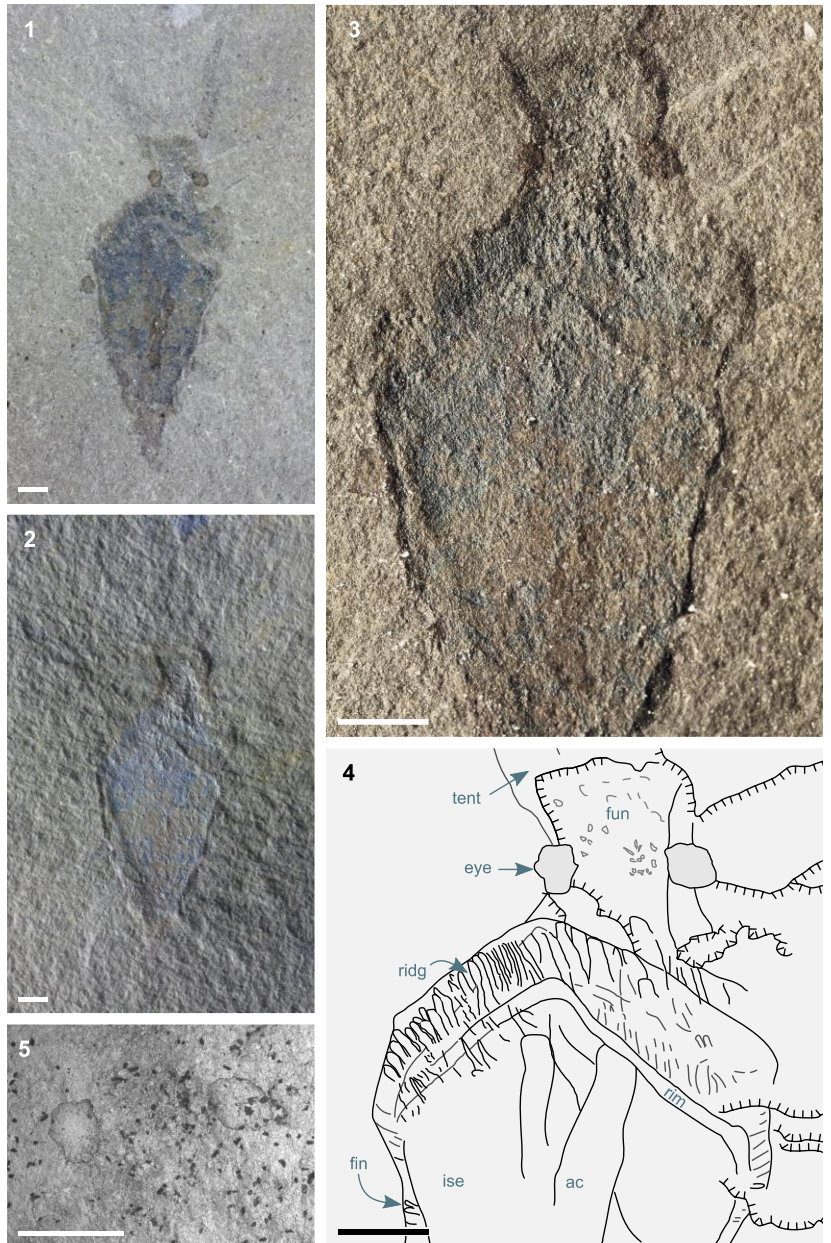
376 **showing relief and distinct composition of eyes. High resolution images are available at FigShare**

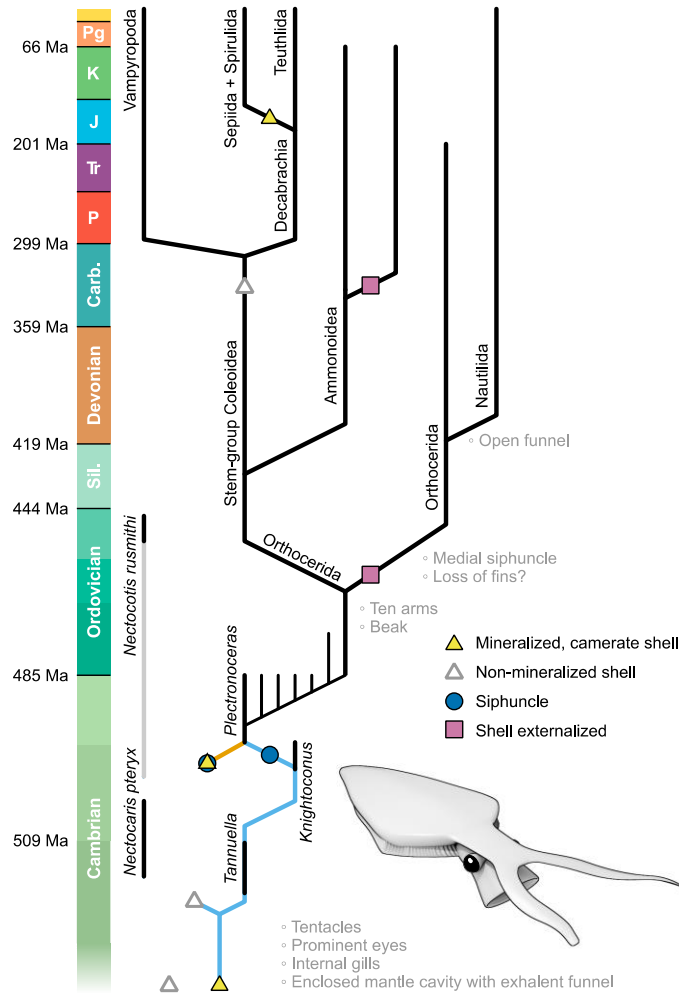
377 **(Smith, 2019). Scale bars denote 1 mm.**

378 **Abbreviations: ac, decayed contents of axial cavity (gills?); fun, funnel; fin, fin; ise, internal**

379 **skeletal element; ridg, ridges in anterior kite-shaped structure; rim, rim of kite-shaped structure;**

380 **tent, tentacle.**





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