

Rare primitive deuterostomes from the Cambrian (Series 3) of Utah

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Abstract.—The fossil record of early deuterostome history largely depends on soft-bodied material that is generally rare and often of controversial status. Banffiids and vetulicystids exemplify these problems. From the Cambrian (Series 3) of Utah, we describe specimens of *Banffia episoma* n. sp. (from the Spence Shale) and *Thylacocercus ignota* n. gen. n. sp. (from the Wheeler Formation). The new species of *Banffia* Walcott, 1911 shows significant differences to the type species (*B. constricta* Walcott, 1911) from the Cambrian (Series 3, Stage 5) Burgess Shale, notably in possessing a prominent posterior unit but diminished anterior section. Not only does this point to a greater diversity of form among the banffiids, but also *B. episoma* indicates that the diagnostic median constriction and crossover of either side of the body are unlikely to be the result of taphonomic twisting but are original features. Comparisons extend also to the Cambrian (Series 2) *Heteromorphus* Luo and Hu in Luo et al., 1999 and, collectively, these observations support an assignment of the banffiids to the vetulicolians. The new taxon *T. ignota* represents the first discovery of a vetulicystid from beyond China and also significantly extends its stratigraphic range from Series 2 Cambrian into Series 3 Cambrian. Despite overall similarities in bodyplan, *T. ignota* differs from other vetulicystids in a number of respects, notably the possession of an anterior zone with broad tentacle-like structures. This new discovery is consistent with the vetulicystids representing stem-group ambulacrarians.

Introduction

The evolutionary history of the deuterostomes is important for several reasons. First, along with many other groups such as tunicates and echinoderms they encompass the vertebrates, and hence the group to which we belong. Second, although perhaps not unique in this respect, modification of the primitive bodyplan into forms as disparate as bats, enteropneusts, and brittlestars is impressive. Third, in recent years their earlier history has become clearer as the result of a series of significant discoveries in the Cambrian. These include new information on the origin of pterobranchs (Caron et al., 2013), the bilateral nature of the earliest echinoderms (Zamora et al., 2012) and the subsequent initiation of pentaradiality (Smith and Zamora, 2013), and early fish (Conway Morris and Caron, 2014). In their various ways they confirm that the principal stages in the initial divergence of the deuterostomes had been achieved no later than Series 3 Cambrian and, as such, add compelling evidence to the reality of the Cambrian “explosion.” Nevertheless, numerous questions remain as to the history of this diversification, not least among yet more primitive forms. In this respect, the lower and middle Cambrian were populated by a variety of candidate groups, notably vetulicolians, yunnanozoans (e.g., Shu et al., 2010), and vetulicystids (Shu et al., 2002). In each case, however, their status is controversial and accordingly new material may be of particular value.

Here, we describe two new taxa that augment our understanding of this critical stage in the evolution of early

deuterostomes. One is a new species of *Banffia* Walcott, 1911 (*B. episoma* n. sp.; Figs. 1–4), a taxon that most likely belongs within the vetulicolians (Caron, 2006). While sharing the bipartite body with its anterior unit and segmented tail, *Banffia* is distinctive among vetulicolians in its possession of a median constriction. This often displays an associated and distinctive “crossing over” between the anterior and posterior units that may be either original or alternatively the result of postmortem torsion. In addition, and in marked contrast to all other vetulicolians (e.g., Ou et al., 2012), there is no clear indication of the five lateral openings on either side of the anterior that appear to represent gill slits. Our new material throws some additional light on the nature of the “crossing over” and a possible reason for the putative absence of anterior openings.

Vetulicolians are recorded from South China (e.g., Shu et al., 2010; Ou et al., 2012), Australia (García-Bellido et al., 2014) and Laurentia (Butterfield, 2005; Caron, 2006; Vinther et al., 2011). In addition to these Laurentian occurrences, a possible vetulicolian (*Skeemella clavula* Briggs et al., 2005) occurs in the Wheeler Shale of Utah (Briggs et al., 2005). While the status of this animal has been debated (e.g., Shu, 2005; Aldridge et al., 2007; Shu et al., 2010), it is worth noting that as a putative deuterostome the only known specimen was recovered 48–54 m stratigraphically above the *Thylacocercus ignota* n. gen. n. sp. of this paper. In contrast to these vetulicolians, vetulicystids to date are known only from the celebrated Series 2 Cambrian Chengjiang Lagerstätte (Shu et al., 2002). Here we report a single specimen of a new genus and species of

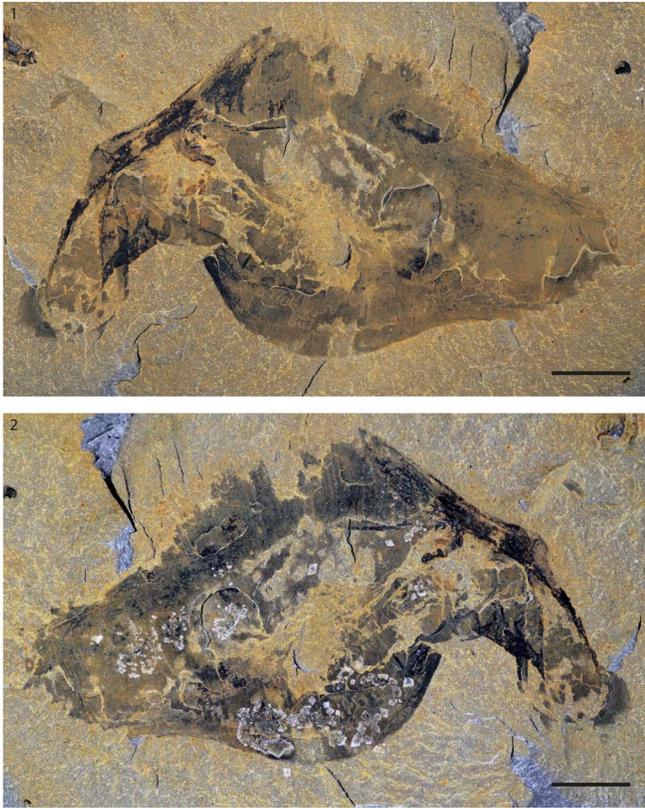


Figure 1. *Banffia episoma* n. sp. ROM 59645, holotype. (1) counterpart; (2) part. Scale bars = 10 mm. Pictures courtesy of ROM.

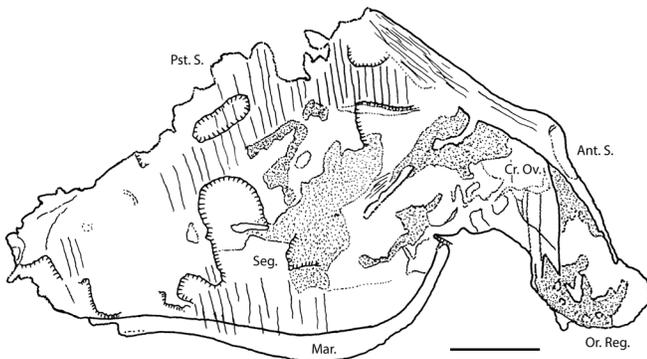


Figure 2. *Banffia episoma* n. sp. ROM 59645, holotype. Explanatory drawing of Figure 1.2. Ant. S. = anterior section, Cr. Ov. = crossover, Mar. = margin, Or. Reg. = oral region, Pst. S. = posterior section, Seg. = segments. Scale bar = 10 mm.

vetulicystid (*T. ignota*; Fig. 5) that both extends the confirmed geographical range of this group to Laurentia but also shows significant differences from the Chinese type material.

Material and methods

Banffia specimens come from the Spence Shale Member, Langston Formation, (Cambrian Series 3, Stage 5) of Wellsville Mountains, Miners Hollow, Utah. ROM 59645 (holotype) and 59646–59648 are from the 150 foot level (above base of section), ROM 59649 from the 110 foot level (“trilobite layer”), KUMIP 314017 and 314018 are from ~ 160 foot level, KUMIP

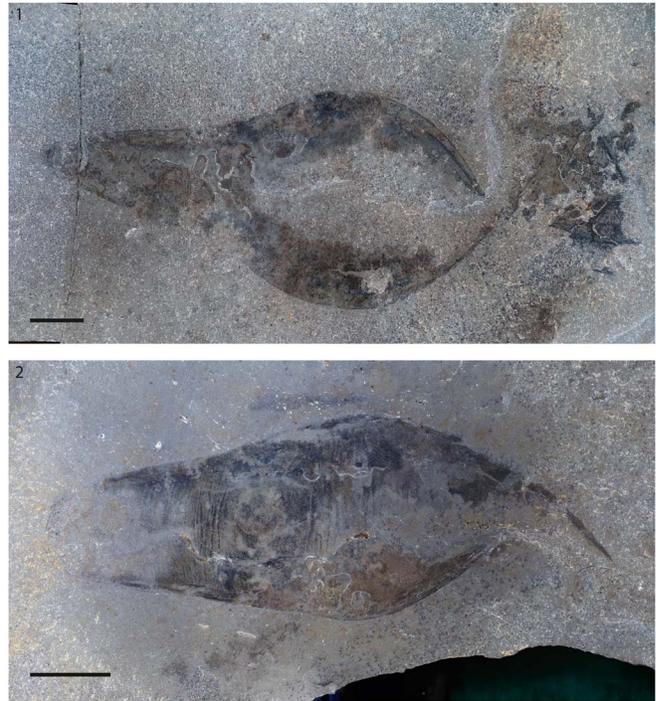


Figure 3. *Banffia episoma* n. sp. Posterior to left in both specimens. (1) KUMIP 31401, carbonaceous areas to right remains of anterior section; (2) KUMIP 314021, note anterior extension of cuticular margin as part of the cross-over between anterior and posterior. Scale bars = 10 mm.

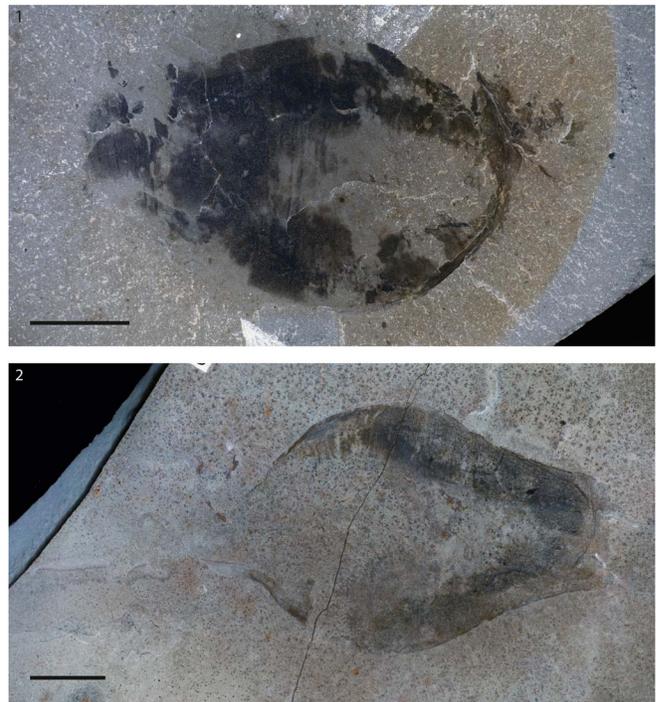


Figure 4. *Banffia episoma* n. sp. (1) KUMIP 314018, posterior to left; (2) KUMIP 314019, posterior to right. Scale bars = 10 mm.

314021 from about the top third of unit, KUMIP 314019 from float.

The unique specimen of *Thylacocercus* comes from the Wheeler Formation (Cambrian Series 3, Stage 5/Drumian) of the

Drum Mountains, Millard County, Utah. The collecting locality is in SE 1/4 NE 1/4 sec. 20, T15S, R10 W, Drum Mountains Well, 7.5' quadrangle: 39° 30' 12.8" N, 112° 59' 24.0" W. This specimen is within the gamma-ray "hot zone" in which numerous soft-bodied specimens have been found (Briggs et al., 2008; Halgedahl et al., 2009). This clay-rich mudstone is ~235 m above the Wheeler contact with the underlying Swasey Limestone and ~37 m below the base of a limestone identified as the boundary between the Wheeler and overlying Pierson Cove Formation (Halgedahl et al., 2009).

Photographs were taken using a Canon EOS 5D MkIII camera either with a Canon 50 mm macro lens or on a Leica MZ16 stereomicroscope. Specimens were photographed either dry (Fig. 5.2) or under 70% alcohol (all others), and in cross-polarized light to enhance contrast. For each specimen, several photographs were taken at different levels of focus and then stacked using Adobe Photoshop CS6 to ensure all parts of each specimen were in focus. Interpretative drawings were made using a camera-lucida extension to a Wild binocular microscope.

Systematic paleontology

For *Banffia* terms used, we follow Caron (2006); and as far as they are comparable, our description of the new vetulicystid follows Shu et al. (2002). *Banffia* material resides in the Royal Ontario Museum, Toronto (ROM) and the University of Kansas Natural History Museum, Lawrence (KUMIP). The only known specimen (part and counterpart) of *Thylacocercus* resides in the collection of the Department of Geology and Geophysics, University of Utah, Salt Lake City (UU).

?Stem-group deuterostome Vetulicolia Shu et al., 2001

Class Banffozoa Caron, 2006

Family Banffiidae Caron, 2006

Genus *Banffia* Walcott, 1911

Type species.—*Banffia constricta* Walcott, 1911.

Banffia episoma Conway Morris and Selden, new species
Figures 1.1, 1.2, 3.1, 3.2, 4.1, 4.2

Holotype.—ROM 59645 (part and counterpart).

Diagnosis.—Bipartite body. Anterior substantially shorter, narrower than posterior, termination apparently circular and presumed oral region. Anterior section separated from posterior section by prominent constriction with complex cross-over whereby opposite (dorsal and ventral) sides of posterior and anterior are transposed. Posterior variable in shape, globose to relatively elongate, distinct margins and prominent transverse segmentation.

Occurrence.—Spence Shale Member, Langston Formation, Cambrian Series 3, Stage 5, polymerid *Glossopleura* Assemblage Zone (Robison, 1976).

Description.—Apart from differences in length:width of posterior unit, available specimens are all similar in appearance

with length of posterior section ranging from ~5–9 cm (and width from ~2.5–4 cm). Apart from holotype (ROM 59645) where anterior section is well preserved, in every other case only fragments of this region remain. Anterior section about half length of posterior. Unit subdivided into wider proximal region, narrower anterior component. Anteriormost area somewhat expanded, more or less circular. Shape of posterior varies from globose (Figs. 1, 3.1, 4) to relatively elongate (Fig. 3.2), well-defined margins, presumably composed of more resistant cuticle. Posterior tapers in either direction, bears prominent segmentation (~8 per cm), often somewhat sinuous giving the segments irregular appearance. Terminus of posterior apparently rounded and simple; one specimen (Fig. 4.2) has an arcuate structure near posterior and this may represent margin of body cavity. In opposite direction, posterior section narrows significantly with a prominent constriction formed by transposition of either side resulting in a cross-over. Accordingly, cuticular margins meet and cross on anterior unit, defining a triangular area (Figs. 1–4).

Etymology.—Reference to the broader proportions of the posterior section in comparison to *B. constricta*; episomos, Greek for fat or bulky.

Materials.—ROM 59646–59648 (all part and counterpart); KUMIP 314017 (part and counterpart) and 314018 (donated by the Gunther family), 314019 (part and counterpart), 314021 (part and counterpart; donated by R. and N. Meyers).

Remarks.—*Banffia episoma* differs from the type species (*B. constricta*) in four principal ways. With a length of ~80 mm this taxon is similar to the median length of *B. constricta* (Caron, 2006, fig. 7a), but in contrast *B. episoma* is substantially less slender, especially with regard to the posterior unit. In addition, while in *B. constricta* the anterior and posterior tend to equivalent lengths (Caron, 2006, fig. 7b), if the holotype of this new taxon is a reliable guide then the relative proportions tend to one extreme of *B. constricta*. In contrast to the type species, where the cuticular margin of the posterior is generally narrow (e.g., Caron, 2006, fig. 20a), that of *B. episoma* is markedly wider. Finally, the segments of *B. constricta* are more widely separated and while taphonomic disruption cannot be ruled out, if original then they were somewhat less well defined.

Although originally referred to *Banffia* (Chen and Zhou, 1997, figs. 138–140; also Hou et al., 1999, figs. 192, 193), the related *Heteromorphus* Luo and Hu in Luo et al., 1999 (we note that we regard *H. longicaudatus* Luo and Hu in Luo et al., 1999 as a junior synonym of *H. confusa* (Chen and Zhou, 1997)) (e.g., Chen et al., 2002, pl. 12, figs. 5, 6) is similar in as much as in at least some specimens the segments of the posterior section are somewhat irregular (e.g., Chen et al., 1996, fig. 255). By contrast, while the anterior of this Chinese taxon is not frequently preserved (e.g., Chen, 2004, figs. 507, 508; Hou et al., 2004, fig. 18.4) it is somewhat more similar to *B. constricta*. In the wider context of vetulicolian evolution, however, *H. confusa* offers some complementary insights. First, like other banffiids there is a crossover at the anterior-posterior junction (e.g., Chen, 2004, fig. 507). This crossover also has the interesting implication that it is the dorsal and ventral sides that

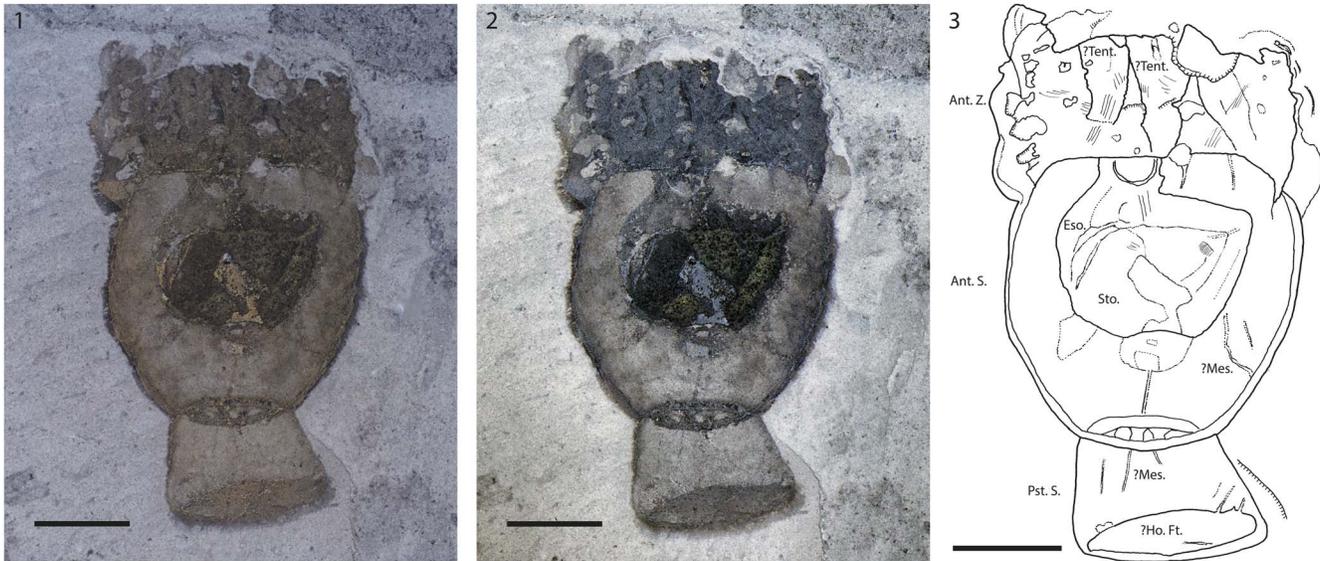


Figure 5. *Thylacocercus ignota* n. gen. n. sp. UU 14011.01, holotype. (1) part, under alcohol; (2) part, dry; (3) explanatory drawing for (1) and (2). Ant. S. = anterior section, Ant. Z. = anterior zone, Eso. = esophagus, ?Ho. Ft. = possible hold-fast, ?Mes. = possible mesentery, Pst. S. = posterior section, Sto. = stomach, ?Tent. = possible tentacles. Scale bars = 5 mm.

are effectively reversed between the anterior and posterior sections. The presence of this crossover in *H. confusa* would also support the notion of it being an original feature rather than being taphonomic. In conclusion, although *Banffia* appears to be a secure generic concept, the variations between the three known species suggest varying ecologies. In addition, and notwithstanding the apparent absence of anterior gills, the banffids appear to belong within the vetulicolians (cf. Caron, 2006).

?Total group Ambulacraria Metschnikoff, 1881

Stem group Vetulocystids Shu et al., 2002

?Family Vetulocystidae Shu et al., 2002

Genus *Thylacocercus* Halgedahl, Jarrard and Conway Morris,
new genus

Type and only known species.—*Thylacocercus ignota* n. sp.

Etymology.—From *thylacos* (Greek) and *kerkus* (Greek), in reference to the bag-like anterior and tail-like posterior, respectively.

Thylacocercus ignota Halgedahl, Jarrard, and Conway Morris,
new species
Figure 5.1, 5.2

Holotype.—UU 14011.01 a, b.

Diagnosis.—Bipartite body. Anterior cup-shaped, smooth margins except at anterior, distinct zone with broad ?tentacles. Posterior section smaller, flares in posterior direction, possibly attachment area at terminus. Gut with assumed stomach and esophagus in mid-section of anterior.

Occurrence.—Wheeler Formation, Cambrian Series 2, Stage 5/Drumian, *Ptychagnostus atavus* Zone.

Description.—Known only from single specimen (part and counterpart), has bipartite body (Fig. 5). In outline anterior section cup-shaped, arcuate contact with posterior section and gently expanding margins that connect to an anterior zone. Total length 19 mm (of which anterior zone ~9 mm), maximum width 13 mm. Margins of anterior smooth, but with fairly well-defined rim. Centrally located darker area tentatively interpreted as alimentary canal with presumed esophagus and prominent stomach. Faint strands may represent mesenteries. Anterior zone difficult to resolve, but appears to have broad tentacle-like structures, possibly bifurcating. Posterior section smaller (length and maximum width 6 mm and 9 mm), flares toward posterior. Terminal area elongate oval; may represent holdfast.

Etymology.—From *ignota* (Greek), in acknowledgment of its unusual appearance and problematic phylogenetic position.

Remarks.—With its bipartite body, overall outline and anterior: posterior ratio *T. ignota* is somewhat larger but otherwise strikingly similar to other vetulicystids, especially *Vetulocystis catenata* Shu et al., 2002. *Thylacocercus ignota* differs, however, in that the anterior section is cup-like, whereas *V. catenata* has a more or less circular outline. In the latter taxon the posterior section has a segmental division, but no counterpart appears to exist in *T. ignota*. A more significant difference is that the anterior zone fringe of *T. ignota* finds no counterpart in either *V. catenata* or any of the other Chengjiang vetulicystids (Shu et al., 2002). Although details are difficult to discern there is some evidence that the zone may have incorporated broad tentacle-like structures, apparently expanding in width distally and showing possible bifurcation. The other obvious contrast is that the anterior section of *T. ignota* is more or less smooth and shows no indication of the diagnostic anterior cone (?mouth), posterior cone (?anus), and respiratory organ (?gill slits) that are features of the Chengjiang vetulicystids.

The absence of these structures in *T. ignota* may simply be on account of angle of burial. If, however, the anterior zone is correctly interpreted then this suggests that the mouth was not anterolateral (as appears to be the case in the Chengjiang vetulicystids) but was centrally located (the position of the assumed esophagus would support this interpretation). The apparent completeness of the anterior zone may also indicate that the gut was not U-shaped and that the anus had a lateral location in a manner reminiscent of the Chengjiang vetulicystids, albeit without the associated cone.

The wider evolutionary significance of *T. ignota* and the vetulicystids in general remains somewhat problematic. Shu et al. (2002) suggested this group were ancestral echinoderms. Supported in part by relative stratigraphic position, it is possible that *T. ignota* is more derived than the Chengjiang taxa and in particular the tentacles were coelomic structures that were the distant precursors of feeding ambulacra. In this context, attention should also be drawn to *Yanjiahella* Guo et al., 2012 from the Series 2 Cambrian (Guo et al., 2012). Although nominally three species, it is possible that these represent taphonomic variants. In any event, the circular anterior bearing arm-like structures, a possible opening (regarded as a “madreporite” by Guo et al., 2012), and elongate “tail”, are reminiscent of the vetulicystids but are also comparable to primitive echinoderms.

Whatever role early vetulicystids may have had in the evolution of echinoderms, it is worth noting that this, the youngest known vetulicystid, lived in an environment in which unequivocal echinoderms thrived locally. These included the eocrinoid *Gogia spiralis* Robison, 1965, as well as ctenocystids (*Ctenocystis colodon* Ubaghs and Robison, 1988). In the nearby House Range, equivalent stratigraphy has yielded abundant specimens of *G. spiralis*, the stylophoran *Archaeoarthrus bifida* (Ubaghs and Robison, 1988), and the homoiostelean *Castericystis vali* Ubaghs and Robison, 1985.

Discussion

Banffia episoma.—Robison (1991) discussed the overall paleoecological environment of the Spence Shale in which *B. episoma* was deposited. Like other banffiids, *B. episoma* is assumed to have been benthic. Variation in the shape of the posterior is suggested to have been original, and as such the relative inflation and narrowing could serve in the standard burrowing cycle of terminal and penetration anchors. In other vetulicolians, the posterior unit was evidently propulsive and the segmental muscles in the posterior of *B. episoma* would have served a similar purpose. While the division into posterior and anterior is diagnostic of all vetulicolians, the degree of constriction in the banffiids is more pronounced than in other members of this group. If a burrower, then this constriction may have been instrumental in allowing the posterior to achieve hydrostatic independence of the anterior unit. This inferred mode of life may also explain an obvious difference between the banffiids and other vetulicolians, that is the apparent absence of any gill openings. Chen (2004, fig. 508) depicted four gill openings in his reconstruction of the related *Heteromorphus*, but these are not obvious in the fossil material (e.g., Hou et al., 2004). Nor have corresponding structures been identified in any

other banffiid (Caron, 2006). If they were originally present, the vetulicolian bodyplan indicates that such openings should in principle be located in the shallow grooves on the anterior section that are an extension of the median crossover. In that case, given the narrowness of these grooves, any gill openings would have been very small. This putative absence (or reduction) could be linked to the mode of life of the banffiids, inasmuch as with the exception of the pelagic *Vetulicola* Hou, 1987 (e.g., Ou et al., 2012), the remaining taxa seem to have been epifaunal (e.g., Shu et al., 2001). It is possible, therefore, that if banffiids were not only benthic but led an infaunal existence then this would have militated against such openings and that respiratory exchange, possibly augmented by peristaltic pumping in the burrow, was principally across the thin cuticle of the anterior section.

Preservation of *B. episoma* is typical of Burgess Shale-type faunas. The fossil films presumably are carbonaceous, but dotted by small nodules (?pyrite), especially near margins. With the exception of the holotype, this contrast between the completeness of the posterior versus the anterior suggests the latter possessed a more delicate body wall and/or had a thinner cuticle, rendering it more vulnerable to decay. Some support for this suggestion comes from the related *Heteromorphus*. In this Cambrian Series 2 species from the Chengjiang Lagerstätten complete specimens are known, but Chen and Zhou (1997, p. 85) noted that “Most specimens are incomplete, preserving only the abdomen [= posterior unit]”. In his description of the type species, Caron (2006) was equivocal as to whether the constriction and associated crossover were original or the result of post-mortem twisting. The consistency of the crossover in *B. episoma*, along with lack of evidence of any torsion in the adjacent posterior region, suggests that this feature is primary rather than the result of taphonomy. One specimen is associated with faint simple burrows. This is comparable to other examples of Burgess Shale-type faunas (e.g., Wang et al., 2009; Mángano et al., 2012) and most likely represents exploitation of decay products from the banffiid carcass by infaunal worms.

Thylacocercus ignota.—Shu et al. (2002) suggested that vetulicystids may have been capable of limited locomotion, but were predominantly sessile. The possible holdfast of *T. ignota* indicates that this taxon was most likely a member of the sessile epifauna. The apparently tentacular anterior points towards *T. ignota* being a suspension feeder. Of the diverse assemblage of other infaunal and epifaunal fossils found at the same locality and meter interval as *T. ignota* (Halgedahl et al., 2009), none has been identified as a suspension feeder. However, a single 2 m interval about 4 m below the *T. ignota* horizon contains numerous sponges.

Conclusions

Banffiids and vetulicystids are problematic fossils from the Cambrian, but this new material helps to extend our knowledge of these putative deuterostomes. *Banffia episoma* n. sp. suggests the diagnostic constriction and associated cross-over are original features, but in other respects banffiids are similar to known vetulicolians. The absence (or small size) of the gill openings may possibly be a reflection of an infaunal mode of life. *Thylacocercus ignota* n. gen. n. sp. is the first report of a

vetulicystid from beyond China and it is also substantially younger (ca. 10 Ma). Absence in *T. ignota* of features such as oral and anal cones may be artifacts of preservation. The presence, however, of anterior tentacles suggests some significant differences with the Chengjiang vetulicystids, but they are not inconsistent with this group falling within the stem-group ambulacrarians. In this respect, they may be informative as to the appearance of pre-echinoderms.

Acknowledgments

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