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Banffia constricta, a putative vetulicolid from the Middle Cambrian Burgess Shale

Jean-Bernard Caron

ABSTRACT: Although *Banffia constricta* was first described in 1911, the affinities of this soft-bodied fossil animal have remained unclear. *Banffia* is redescribed here, on the basis of over 300 specimens. *Banffia* has a bipartite body measuring up to 10 cm in length. The entire body is axially twisted along a spiral, clockwise as seen from the front. The anterior section consists of two fused carapace-like units with a prominent crown-like structure at the anterior end surrounding the mouth. This crown-like structure is composed of three concentric circlets. A single antenniform outgrowth lies posterior to the mouth. The posterior section of *Banffia* is composed of 40 to 50 lightly sclerotised segments. The anus is terminal, and situated in a caudal notch. The gut is straight. Simple serially repeated structures along the gut may represent metameric mid-gut diverticulae. *Banffia* is considered to have been an epibenthic gregarious animal and possibly a deposit-feeder.

Banffia is putatively classified as an end-member of the phylum Vetulicolia, in a new class, the Banffozoa. If the vetulicolids represent a stem-group deuterostome, the absence of gills and a possible endostyle in *Banffia* is problematic. The presence of mid-gut diverticulae in *Banffia* may represent a link with the protostomes.

KEY WORDS: Body plan, Cambrian explosion, crown-group, Deuterostome, mid-gut diverticulae, origins of bilaterians, Problematica, Protostome, stem-group.

The origin of modern animal phyla and their relationships have become subjects of increasing interest and debate in recent years, due primarily to the development of molecular techniques (e.g. Davidson *et al*. 1995; Nielsen 1995; Aguinaldo *et al*. 1997; Balavoine & Adoutte 1998; Knoll & Carroll 1999), and new discoveries in the fossil record in the Lower and Middle Cambrian (e.g., Conway Morris 1998; Budd 1999; Hou *et al*. 2004). Molecular studies have revealed different branching topologies for the origins of animal phyla, but to date are unable to provide details on the morphology of the last common ancestors of the various phyla. In this search for relationships at high taxonomic levels, problematic taxa, or Problematica from the early Palaeozoic, may represent an important source of new information. Problematica cannot currently be assigned to living phyla (Bengtson 1986; Briggs & Conway Morris 1986); however, given their unique sets of characters, Problematica could be crucial indicators of the earliest ancestry of body plans (Ramsköld & Hou 1991; Ramsköld 1992; Budd 1996, 1999; Budd & Jensen 2000).

Banffia constricta is one of the rarest and least known problematic fossils from the Burgess Shale. The goal of this study is to provide a thorough description of *Banffia* that is long overdue, and to investigate its ecology and putative affinities. This paper is based on 15 specimens from the original Walcott collection and more than 300 specimens collected by Royal Ontario Museum field parties from 1984 to 1999.

1. History of research

1.1. Early works

Walcott originally described *Banffia* on the basis of only half a dozen specimens (1911) (Fig. 1a). This rarity has triggered much controversy on its affinity. Walcott (1911) considered *Banffia* to be linked to the class Gephyrea (together with *Pikaia* and *Oesia*), as based on its elongated body and segment-like annulations. This class is now regarded as polyphyletic and invalid (Echiura, Sipuncula, and Priapula: Hyman 1959; Brusca & Brusca 1990). According to Meyer (1933), Lang (1953), and Golvan (1958), *Banffia* and *Ottoia* are not sipunculans but belong, within the gephyreans, to the Aschelminthes, sharing affinities with the phyla Acanthocephala and Priapula. Hyman (1959) removed *Ottoia* and *Banffia* from the phylum Sipuncula based upon the segmentation and placed these taxa closer to the phylum Annelida.

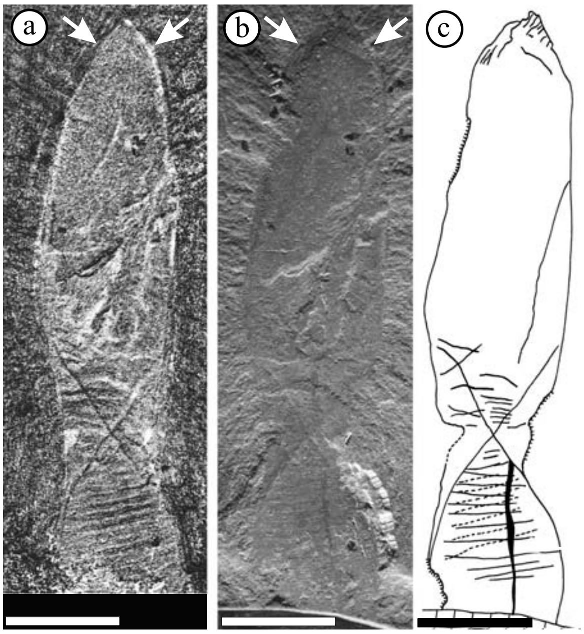

Figure 1 Lectotype of *Banffia constricta* Walcott, 1911, USNM 57638, scale bars = 10 mm: (a) Walcott's original, retouched photo (plate 21, fig. 6 *in* Walcott 1911); white arrows indicate where the original outline has been retouched (compare with (b)); (b) new photograph; white arrows indicate the original outline of the specimen; (c) camera lucida drawing of (b).

Gekker & Ushakov (1962) proposed that *Banffia* may represent a member of the class 'Priapuloidea' within the phylum Nemathelminthes (the phylum Priapula within the superphylum Aschelminthes) whereas Termier & Termier (1968) considered *Banffia* as a Priapulida *sensu stricto*. All these previous studies were based on Walcott's original publication but not on examination of the fossils themselves.

1.2. The problematic status of *Banffia*

Conway Morris (1976a) undertook a critical reappraisal of *Banffia constricta* based on the original specimens collected by Walcott. Unfortunately, this study was not published beyond the PhD thesis, because the few specimens did not allow thorough interpretation (S. Conway Morris, pers. comm. 2001), and *Banffia* was included later with 20 other Burgess Shale taxa within the Problematica (Briggs & Conway Morris 1986). Investigation of the original specimens and the many new specimens collected by the Royal Ontario Museum was begun in 1999 by the present author (Caron 1999). Despite new study, no obvious affinities of *Banffia* with known phyla were recognised and its status within the Problematica was confirmed (Caron 1999; Caron & Collins 1999). However, a possible connection between *Banffia* and problematic fossils from the Lower Cambrian Chengjiang biota of China was recognised early on (Caron 2001). These Chinese fossils included *Banffia confusa* (Chen *et al.* 1996; Chen & Zhou 1997; Hou *et al.* 2004), *Vetulicola* (Hou 1987; Chen *et al.* 1996; Chen & Zhou 1997; Hou *et al.* 2004) and *Xidazoon* (Shu *et al.* 1999). *Vetulicola* and *Banffia confusa* were originally interpreted to be arthropods (Hou 1987; Chen *et al.* 1996). In a preliminary study, the present author suggested all these animals form a stem-group of limbless arthropods based on the possession of a 'bivalved carapace' at the front and a sclerotised segmented trunk (Caron 2001). Soon after, a similar grouping of taxa from the Chengjiang biota was independently described and interpreted by Shu *et al.* (2001). A connection with the arthropods was disputed and ultimately rejected, and Shu *et al.* (2001) interpreted the group as stem-group deuterostomes (the Vetulicolia), with *Banffia* as the most primitive member. However, poorly known taxa are especially likely to be misinterpreted as Problematica (see Yochelson 1991), and a detailed description of *Banffia*, and a justification of its affinities remain to be published.

2. Depositional environment and associated biota

The new findings of *Banffia* specimens above the Phyllopod Bed by the Royal Ontario Museum expeditions occur within the section studied by Walcott (1911). This section corresponds to the Raymond Quarry Shale Member and the Emerald Lake Oncolite Member of the Burgess Shale Formation described by Fletcher & Collins (1998). Most of the specimens (236) were collected from a 2-metre thick stratigraphic sequence from the upper part of the Emerald Lake Oncolite Member (Fig. 2). Only 3 specimens were collected in the Raymond Quarry Shale Member (Fig. 2). About 100 more specimens came from talus above the Walcott Quarry, which limits the potential source of these specimens to the Raymond Quarry Shale Member or above. Preliminary fossil lists from the Emerald Lake Oncolite Member and the Raymond Quarry Shale Member are available in Fletcher & Collins (1998). In the Emerald Lake Oncolite Member the following taxa have been observed on the same bedding surface and associated with *Banffia*: the brachiopods *Diraphora* and *Lingulella* (Walcott 1924), the arthropod *Sidneyia* (Bruton 1981), the anomalocaridid *Hurdia* (Walcott 1912a), and the problematica *Nectocaris* (Conway Morris 1976b) and *Haplophrentis* (Marek & Yochelson 1976).

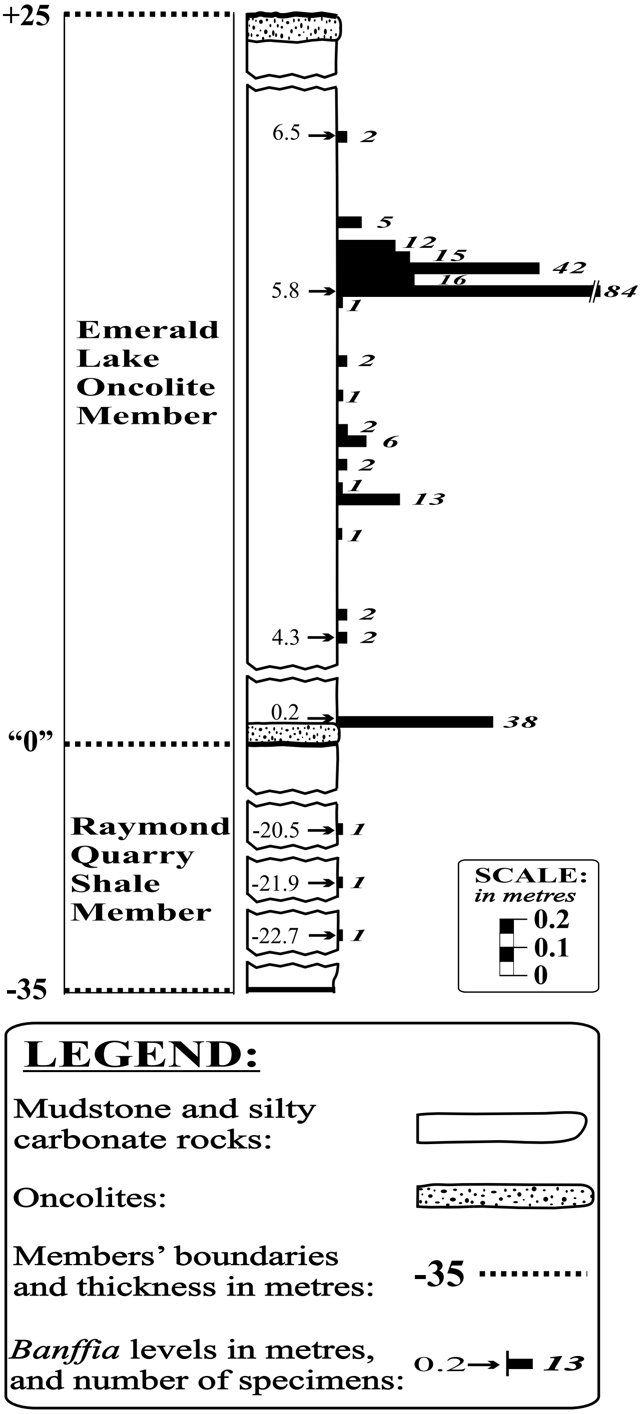

Figure 2 Occurrences of *Banffia* through the Wash Section in the western slope of Fossil Ridge, near the town of Field (B.C.). The reference level '0' is at the base of the first oncolite layer separating the Raymond Quarry Shale Member from the Emerald Lake Oncolite Member (see Fletcher & Collins, 1998).

Banffia specimens typically occur together in large number and are associated with brachiopods, burrows and microichnofossils on single laminae. A 350-cm^2 slab contains more than 60 specimens, with specimens overlapping one another with no or little sediment separating them, and no preferential orientation (Fig. 3a). The brachiopods are represented by semi-attached valves oriented convex-up, and the surface of the valves does not seem to be abraded or eroded (Fig. 3a, b). The burrows are Y-shaped or rectilinear (around 1 cm in diameter), and are filled mostly with sand-size shelly fragments (Figs 3a–c, 4a, f). These observations suggest little or no transport of the biota and a nearly *in-situ* environment. Some

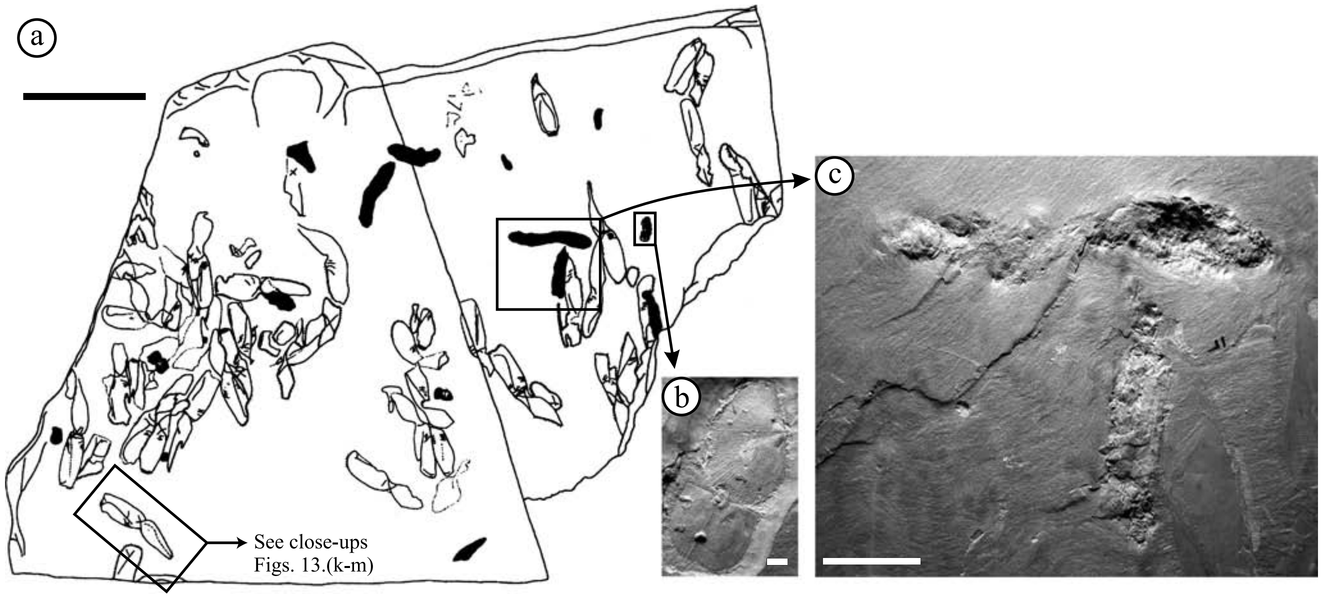

Figure 3 *Banffia constricta* Walcott, 1911. (a–c) '*Banffia slab*' ROM 53647: (a) composite explanatory drawing based on both part and counterpart of the complete slab, scale bar = 10 cm; (b) close-up view of brachiopod valves, scale bar = 2 mm; (c) close-up view of horizontal burrows, scale bar = 10 mm.

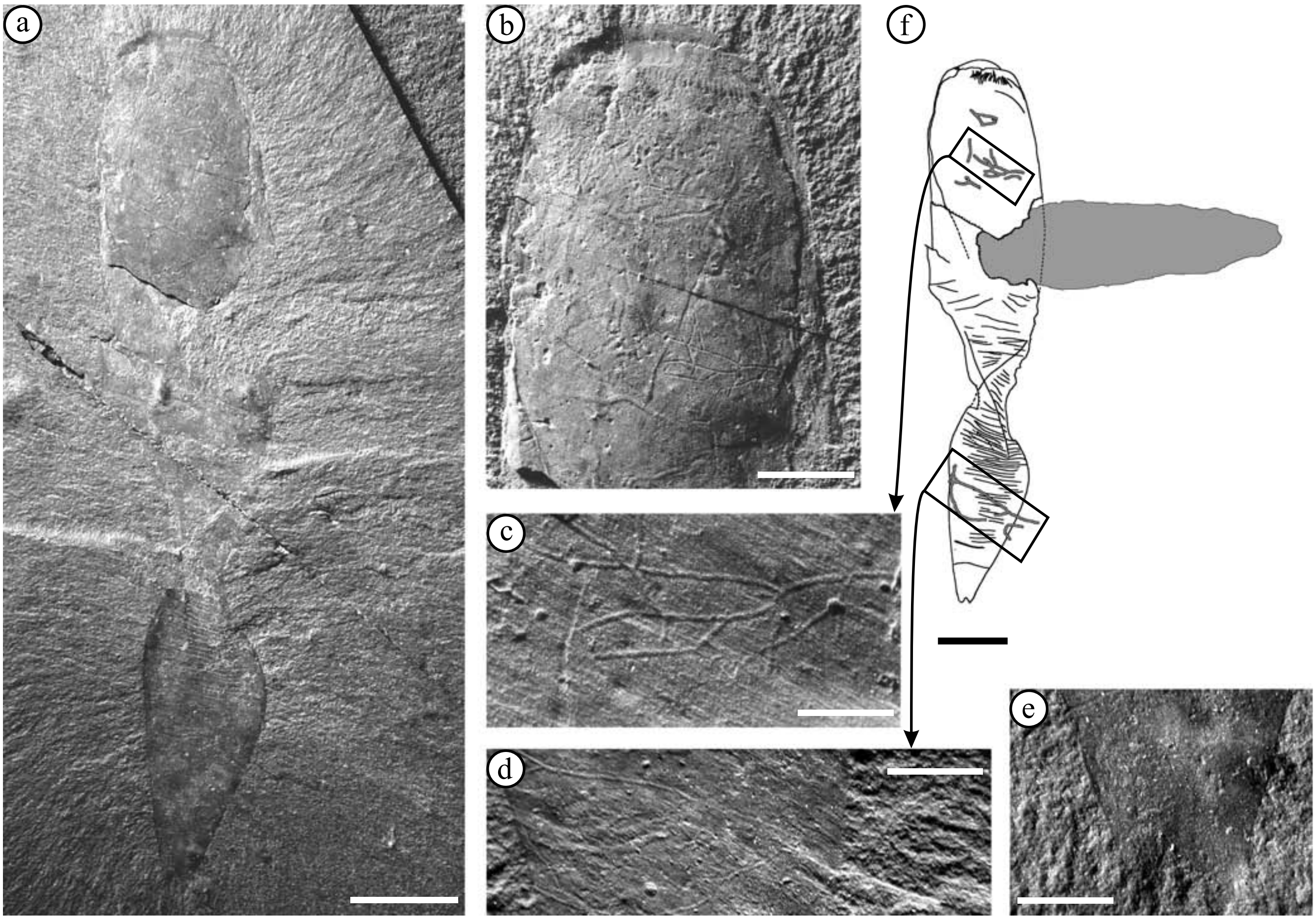

Figure 4 *Banffia constricta* Walcott, 1911. (a–f) presumed dorsal side, part, ROM 49893: (a) the complete specimen with a horizontal burrow, scale bar = 10 mm; (b) detail of the fused anterior section, scale bar = 5 mm; (c) close-up view of micro-ichnofossils on the surface of the fused anterior section, scale bar = 2 mm; (d) close-up view of micro-ichnofossils on the surface of the posterior section extending into the matrix, scale bar = 3 mm; (e) detail of the posterior end of the posterior section, scale bar = 4 mm; (f) composite camera lucida drawing of both part and counterpart of the complete specimen associated with a horizontal burrow (shaded area), scale bar = 10 mm.

specimens of *Banffia* themselves bear rectilinear or dichotomous micro-ichnofossils (Fig. 4a–d, f), that are unlikely to be diagenetic in nature (R. Bromley, pers. comm. 2003). Their diameters do not exceed 0·1 mm. Some extend to the matrix, which demonstrates post-mortem emplacement (Fig. 4d). Similar micro-ichnofossils have been found associated with other

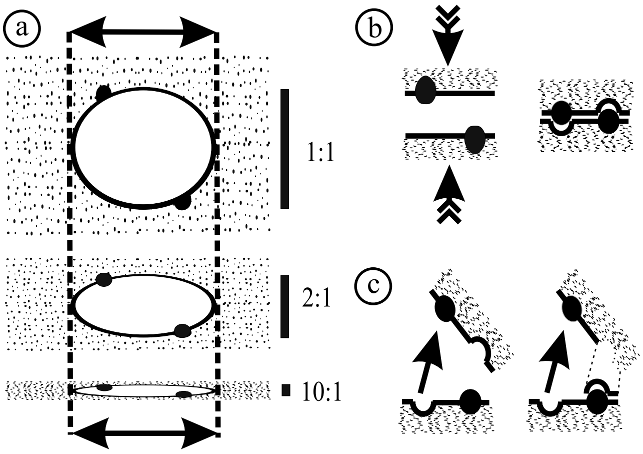

Figure 5 Schematic transverse sections of *Banffia* with the longitudinal axis parallel to the bedding plane. Thicker elements of the fossil are represented by black dots: (a) successive compressions of the fossil (in the ratios indicated) do not affect the original lateral dimensions; (b) after compression the thicker structures imprint into the opposite fossil layer; (c) separation of fossil layers can occur in different ways depending on how the fossil splits along fragile zones.

Burgess-Shale type organisms from both the Chengjiang (M. Y. Zhou, pers. comm. 2003), and Sirius Passet (Conway Morris & Peel 1995, Fig 16a). Due to their small size, they may have been made by necrophagous organisms such as algae, fungi, and possibly small metazoans which may have been able to live in low oxygen levels, especially if they correspond to rhizomes of fungi (N. Butterfield, pers. comm. 2003). A detailed study of traces associated with *Banffia* is beyond the scope of the present paper.

3. Material and methodology

As emphasised by Banta & Rice (1970), Burgess Shale fossils are difficult to photograph because of their extremely low relief and poor contrast with the matrix. To emphasise details, which are usually not seen under a single angle of light, Walcott's photographs were retouched by a professional artist (Walcott 1911). Unlike digital graphic tools that can enhance features that are difficult to photograph (Bengtson 2000) and which is sometimes used here, retouching is subjective and may compromise the value of manually redrawn details (e.g., compare Fig. 1a, b). In the present study, camera lucida drawings have been placed opposite the photographs to facilitate identification of low relief or barely visible features (e.g., Fig. 1c).

Like most other soft-bodied or weakly mineralised animals of the Burgess Shale fauna, *Banffia* appears darker than the surrounding rock (Whittington 1971; Briggs 1977; Bruton 1981). However, most specimens are weathered and have a yellowish or brownish colour. In the few fossils that were collected on freshly split slabs, the colour is dark and the matrix is light grey or blue grey. *Banffia* specimens were compressed by forces perpendicular to the bedding plane due to post-burial compaction of sediments. Therefore, most of the original three-dimensional aspects of the animal have been lost vertically, but without lateral deformation as it is typically the case for other Burgess Shale animals (e.g., Whittington 1975; and see Briggs & Williams 1981). Because of compression, features of both sides of a fossil are juxtaposed on parallel planes (Fig. 5a, b). Depending on the angle of burial, the bodies may become oriented at different angles. Some animals are compressed parallel to the bedding plane, while others are obliquely compressed. These differences of orientation are common among Burgess Shale animals (Whittington 1971; Briggs 1976; Conway Morris 1977) and almost certainly imply a rapid burial (Whittington 1985). When the fossils are split apart, portions of the fossil usually adhere to both sides, thus forming a part and a counterpart (Fig. 5c). The part is designated as the piece of the fossil preserved in relief, which often shows more details than the counterpart. During compaction, one plane of the fossil can be imprinted on different layers (Fig. 5b). In contrast to other Burgess Shale fossils, the separation plane in *Banffia* cuts across at least two different layers at the anterior section (as in some arthropods from this shale, e.g., Bruton 1981), and usually one layer at the posterior section (as in some worms, e.g., Conway Morris 1977). For some specimens, the sediment-coated parts were cleared by preparatory techniques: an engraving tool, along with a reamer made of tungsten carbide was used to remove the matrix. The posterior end of the specimens generally could not be cleared of matrix because the fossils were too thin to allow a proper separation of the rock coat. Some specimens were cleaned with a low concentration of hydrochloric acid solution (3 to 5 per cent) to remove superficial calcite crystals. Polished perpendicular sections of specimens were examined with a binocular microscope for possible ultra-structures. Some specimens were moulded using silicone-based rubber to replace missing counterparts and to reveal surface relief details. Some specimens were immersed in water to eliminate reflections; this increased the contrast between the fossil and the matrix, thus revealing internal organs that are difficult to see when dry. This contrast was greater when applying polarising filters to both a camera and the light-source (see also Bengtson 2000). A 1 mm slide gauge was used for measurements of body length and width, and a 0·1 mm slide gauge for measurements of width of segments. Other measurements on the order of 0·1 mm were made with a binocular lens for sections perpendicular to the planes of the fossils. Scanning electron microscope (SEM) photographs of surfaces and perpendicular fractures of the anterior body section were taken with a Hitachi® S-2500 microscope at the University of Toronto (Botany Department).

4. Systematic palaeontology

Phylum Vetulicolia Shu *et al.*, 2001
Class Banffozoa, Class nov.

Diagnosis. Putative vetulicolian (?). Entire body asymmetrical, twisted dextrally as seen from the front. Gut with simple and non-ramified metameric mid-gut diverticulae. Anterior body section with no lateral groove. Absence of gills.

Family Banffiidae, fam. nov.

Diagnosis. With the characters of the class Banffozoa.
Type genus. *Banffia* (Walcott 1911), designated herein.

Banffia constricta (Walcott, 1911)
(Figs 3.b–c, 4, 8, 9, 10, 13, 14, 16, 18, 20)

1911 *Banffia constricta* gen. and sp. nov.; Walcott, p. 110–111, 128, 130–131, pl. 21, figs 5, 6.
1912a *Banffia grandis* Walcott, p. 153.
1912b *Banffia constricta* (Walcott); Walcott, p. 188, 190.
1925 *Banffia* sp. Nicholas, p. 29.
1933 *?Banffia* Meyer, p. 524.
1953 *Banffia* (Walcott); Lang, p. 338.
1958 *Banffia* (Walcott); Golvan, p. 580.

1959 *Banffia* (Walcott); Hyman, p. 666–667.
1962 *Banffia constricta* (Walcott); Howell, p. 168–170, fig. 107.3.
1962 *Banffia* (Walcott); Gekker & Ushakov, p. 828.
1968 *?Banffia* Termier & Termier, p. 185.
1969 *Banffia* (Walcott); Clark, p. 4.
1976a *Banffia constricta* (Walcott); Conway Morris, p. xiii, xiv, 132–141, 230, text-fig. 36; plate 31, figs 1, 2, 4–6; plate 32, fig. 1, 2; plate 33, fig. 1.
1986 *Banffia constricta* (Walcott); Briggs & Conway Morris, p. 170, 172, fig. 5.
1989 *Banffia constricta* (Walcott); Conway Morris, p. 345, fig. 4b.
1989 *Banffia* (Walcott); Gould, p. 212.
1989 *Banffia* (Walcott); Collins, p. 314.
1991 *Banffia* (Walcott); Bergström, p. 32.
1991 *Banffia* (Walcott); Conway Morris, p. 21.
1993 *Banffia constricta* (Walcott); Willis & Sepkoski, p. 550.
1998 *Banffia* (Walcott); Fletcher & Collins, p. 429.
1999 *Banffia constricta* (Walcott); Caron & Collins, p. 34–35.
2001 *Banffia constricta* (Walcott); Caron 2001, p. 39.
2001 *Banffia*; Shu *et al.* 2001, p. 424.

Types. Walcott (1911) did not designate a type specimen for this species but figured two specimens USNM 57637 and USNM 57638 (pl. 21, figs 5, 6).

Material examined. a,b; part and counterpart; USNM: 57637, 57638 (Fig. 1a–c); ROM-UE (Upper *Ehmaniella* Zone): 49890a,b (specimen a, Figs. 8a–f, 15b); 49892a,b (Fig. 16d–f); 49893a,b (Fig. 4a–f); 49897a,b (Fig. 16a–c); 49898a,b (Fig. 13a–d); 49900a,b (Fig. 10b); 49910a,b (Fig. 9h–k); 49914a,b (specimen a, Figs. 15c, 20a–e); 49915a,b (specimen a, Figs. 15a, 18j–n); 49917a,b (specimens c and f, Fig. 15e, f); 49922a,b (Fig. 9d–g); 49924a,b (Fig. 9a–c); 49930a,b (Fig. 13e–j); 53640a,b (Fig. 8g–l); 53644a,b (Fig. 20j–m); 53647a,b (Figs. 3a, 13k–m); 53769 (Fig. 18g–i); 53770 (Fig. 15g); 53772a,b (Fig. 10a); 54341 (Fig 15h); 54342a,b (Fig 15d); 57575a,b (Fig. 10c, d); ROM-Talus; 53757 (Fig. 20f–i).

Other material examined. USNM, 13 specimens; ROM, some 192 additional specimens.

Diagnosis. Flexible posterior section composed of 40 to 50 lightly sclerotised, and superficial segments. Crown-like structure around the antero-ventral mouth composed of three circlets. Frontal antenniform (?) outgrowth present, caudal to mouth. Simple and narrow alimentary canal. Anus terminal, surrounded by caudal notch.

Remarks. The anterior section of *Banffia confusa* from the Lower Cambrian Chengjiang fauna of China (Chen & Zhou 1997), is perforated with 'gill slits' along lateral grooves. Therefore, *Banffia confusa* is related to the class Vetulicolida, and belongs to another genus than *Banffia* (possibly *Heteromorphus* Luo *et al.*, 1999).

5. Description

5.1. General dimensions

The general morphological terms used for the measurements are summarised in Figure 6. Owing to generally incomplete preservation, only 31 specimens, intact (from mouth to anus) and parallel to the bedding plane, were measured (Fig. 7). The results show an approximately normal distribution of sagittal length (Fig. 7a), a low correlation between the lengths of the anterior section and posterior sections (Fig. 7b) and an even lower correlation between the width and length of the anterior section (Fig. 7c).

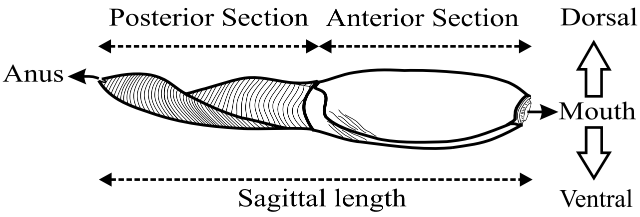

Figure 6 *Banffia constricta* diagram showing the main axes of symmetry and descriptive terminology.

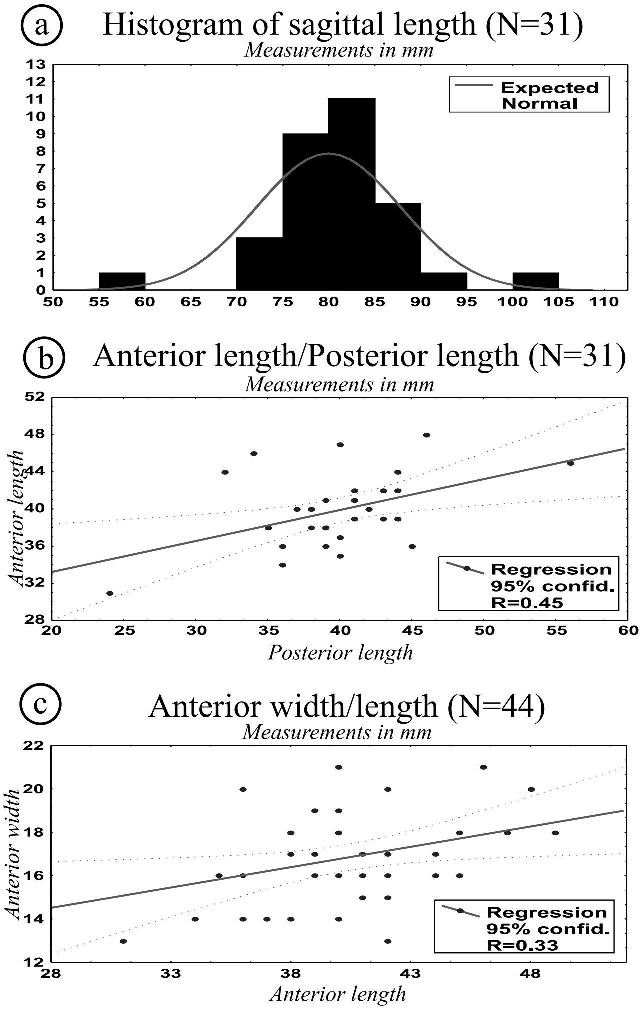

Figure 7 *Banffia* main dimensions: (a) histogram of sagittal length; (b) ratios anterior length/posterior length; (c) ratios anterior width/length.

5.2. Morphology

Anterior section. To facilitate interpretation within the following description, in all the figures the specimens are oriented with body vertical and the anterior facing the top. The surface of the anterior section is smooth, except for wrinkles that are interpreted as artefacts of post-mortem compression (e.g., Figs. 8a, f; 9d, g). The space within the anterior section is filled with sediment, which seems to be identical to the surrounding matrix, and indicates that the body cavity in the anterior section was large (Fig. 10a). Two narrow, oblique grooves with thickened borders (e.g., Fig. 8i) wind along the anterior section and delimit the margins of two main exoskeletal elements, which are here named carapaces or carapace-like structures (e.g., Figs. 8g, h, l; 13a, d): the right groove or margin runs from the left to the right-hand side (e.g., Fig. 8a, f), the left margin runs from the right to the left-hand side (e.g., Fig. 8g, h, l). The grooves are neither open nor

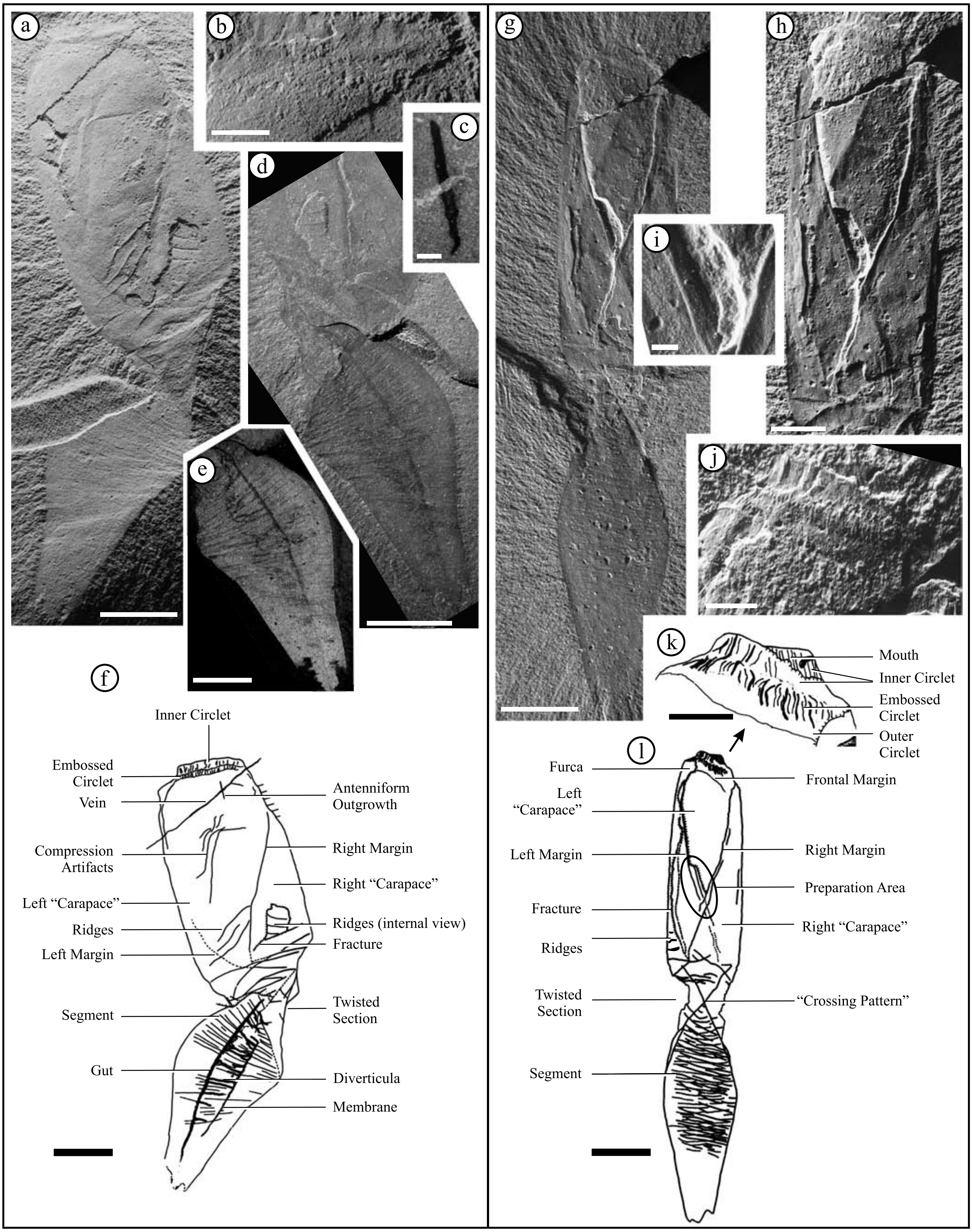

Figure 8 *Banffia constricta* Walcott, 1911: (a–f) presumed dorsal side, ROM 49890. (a–c) part: (a) the complete specimen, scale bar = 10 mm; (b) detail of the crown-like structure in dorsal view, scale bar = 3 mm; (c) detail of the frontal antenniform outgrowth, scale bar = 0·5 mm. (d–e) counterpart: (d) posterior of the anterior section and the posterior section, scale bar = 10 mm; (e) detail of the posterior section showing internal organs (immersed in water with crossed nicols and using the blending mode 'multiply' in Adobe Photoshop 6®), scale bar = 10 mm. (f) composite explanatory drawing based on both the part and counterpart of the complete specimen, scale bar = 10 mm. (g–l) presumed lateral side, part, ROM 53640: (g) the complete specimen, scale bar = 10 mm; (h) detail of the fused anterior section, scale bar = 5 mm; (i) detail of the fused margins on the anterior section, scale bar = 1 mm; (j) detail of the crown-like structure and the mouth in lateral view, scale bar = 2 mm; (k) explanatory drawing based on (j), scale bar = 3 mm; (l) composite explanatory drawing based on both the part and counterpart of the complete specimen, scale bar = 10 mm.

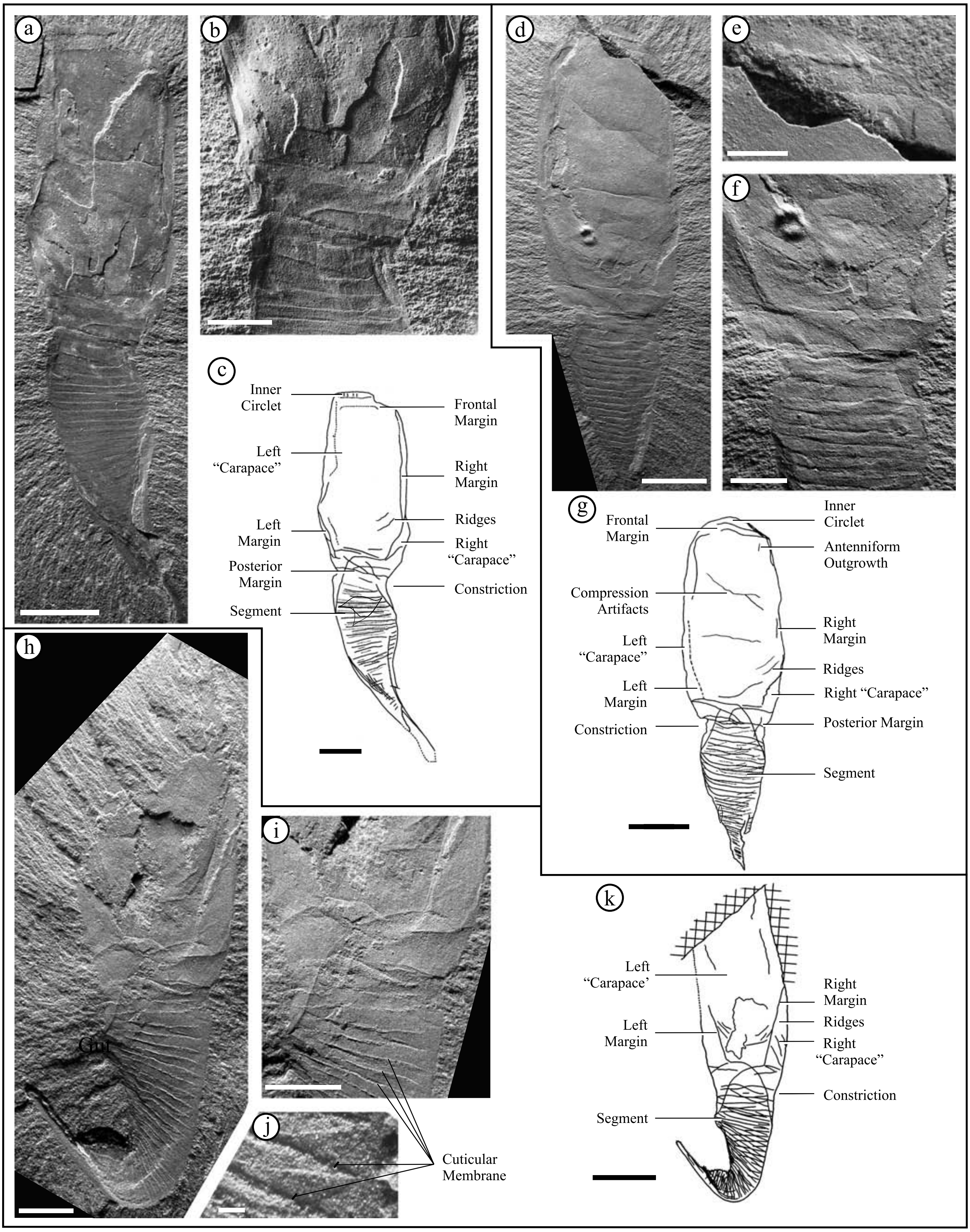

Figure 9 *Banffia constricta* Walcott, 1911: (a–c) presumed dorsal side, part, ROM 49924; (a) the complete specimen, scale bar = 10 mm; (b) detail of the constricted midbody, scale bar = 5 mm; (c) composite explanatory drawing based on both the part and counterpart of the complete specimen, scale bar = 10 mm. (d–g) presumed dorsal side, part, ROM 49922: (d) the complete specimen, scale bar = 10 mm; (e) detail of the of the crown-like structure, scale bar = 3 mm; (f) detail of the constricted midbody, scale bar = 5 mm; (g) composite explanatory drawing based on both the part and counterpart of the complete specimen, scale bar = 10 mm. (h–k) presumed dorsal side, part, ROM 49910: (h) the complete specimen, scale bar = 5 mm; (i) detail of the constricted midbody, scale bar = 5 mm; (j) detail of the segments, scale bar = 0·5 mm; (k) composite explanatory drawing based on both the part and counterpart of the complete specimen, scale bar = 10 mm.

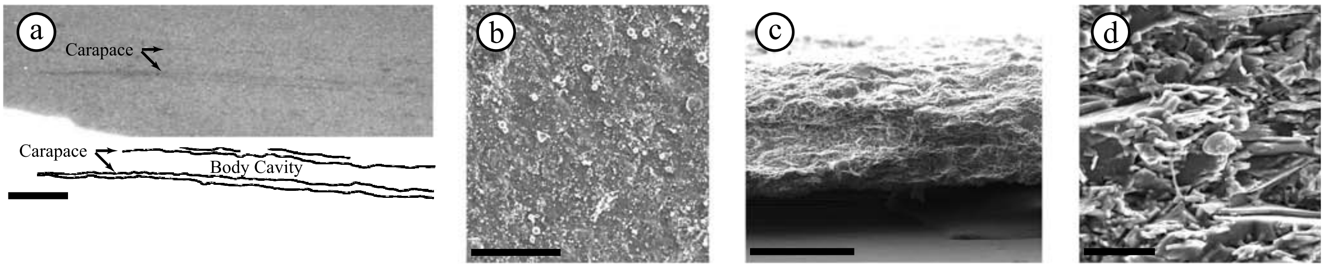

Figure 10 *Banffia constricta* details of the carapace: (a) cross section (perpendicular to the sagittal plan) of specimen ROM 53772 showing the carapace thickness, and body cavity. One carapace is about 0·15 mm thick, scale bar=1 mm. (b–d), SEM carapace photographs: (b) surface of specimen ROM 49900, scale bar=50 µm; (c) unpolished perpendicular section of specimen ROM 57575, scale bar=100 µm; (d) close-up of the same specimen showing replacement of the original cuticle by randomly arranged clay minerals, scale bar=10 µm.

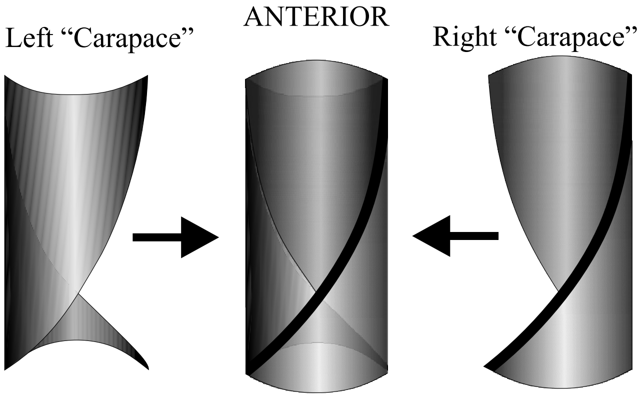

Figure 11 The anterior section of *Banffia constricta*, schematic diagram. The right and left carapaces are helically-fused along margins. The margin of the right section is emphasised to show that the right carapace does overlap on the left carapace on the dorsal surface; a symmetric pattern with the left carapace overlapping the right carapace occurs on the left margin, i.e. on the ventral surface.

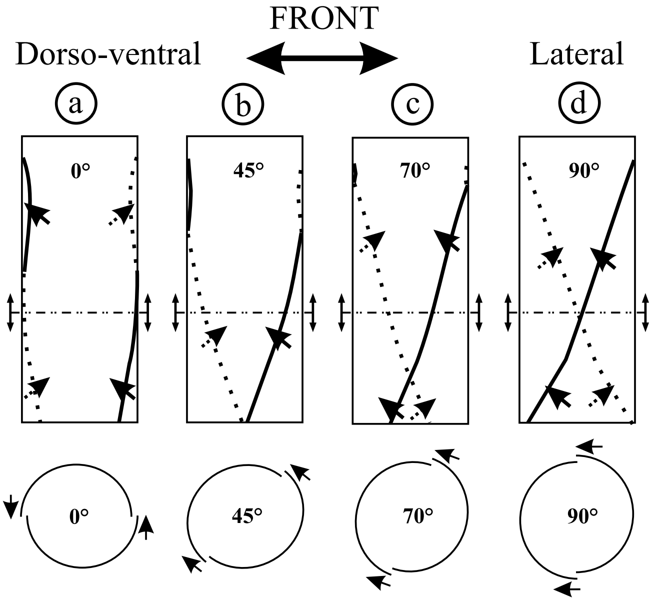

Figure 12 *Banffia constricta*, diagrams of the anterior section showing the positions of the margins in different specimens (a–d); the anterior section is parallel to the bedding plane and oriented parallel to the side of the page. The margins are oblique; the plain lines represent them on the 'visible' surface of the fossil, the dotted lines represent them underneath the fused anterior section. The arrows indicate the direction of overlap. Cross-sections are drawn underneath each specimen. The planes of these cross sections are indicated by the thin, two headed arrows above.

displaced, suggesting that the carapaces had closely fused margins. Thus the anterior section of the body represents a helicoid arrangement of the two fused carapaces rotating around a central axis of symmetry, turning clockwise as seen from the front (see models Figs. 11; 12). The anterior section tapers off towards a straight posterior margin (Fig. 9a–d, f, g).

SEM photographs of surfaces and perpendicular fractures of the anterior section failed to recognise any microstructures (Fig. 10b, c). The original carapace thickness seems to be entirely replaced by randomly oriented clay minerals (Fig. 10d).

'Crown-like structure'. A 'crown-like structure' composed of three circlets surrounds the mouth (e.g., Figs. 8g, h, j–l; 13a, b, d–f, k–m, n–p; 14). The mouth, in its original situation, was slightly displaced from a terminal position presumably toward the ventral side (e.g., Figs. 8g, h, j–l; 13e–h). In lateral view the inner circlet is spatulate, wrinkled, and has the shape of an inverted funnel (e.g., Figs. 8j, k; 13g, h). In dorsal view, it has a straight anterior margin (e.g., Figs. 8b, f; 9a, c; 13n–p). The next posterior unit, referred here as the embossed circlet, retains a slight three-dimensional preservation, and bears closely spaced ridges (e.g., Figs. 8a, b, f–h, j, k; 13g, h, o, p). The number of ridges varies between specimens of similar size and for specimens oriented in a similar way to the bedding plane, which suggest that these ridges are simply compression artefacts of an originally three-dimensional structure. In one specimen, the ridges seem to be paired, which may indicate the original external design of the embossed circlet (Fig. 13i, j). The most posterior circlet is recessed (e.g., Figs. 8j, k; 13g, h), and limited posteriorly by a margin (e.g., Figs. 8j–l; 9a, c, e, g; 13g, h, o, p). This margin encompasses the crown-like structure and converges to the margins of the anterior section (Fig. 13e, f, k, m).

'Antenniform outgrowth'. A thin dark structure, referred herein as 'antenniform outgrowth' due to its shape and position, is present in a few specimens posterior to the crown-like structure and is consistent enough that it is unlikely to be an artefact (e.g., Figs. 8b, c, f; 9e, g; 20a, d, e). This structure is parallel to the long axis of the body, and its length varies from 2 to 2·8 mm in the complete specimens (Fig. 15).

'Posterior ridges'. Helically arranged ridges radiate from the posterior dorsolateral and ventrolateral surfaces of the anterior section in all specimens studied (e.g., Figs. 8; 16: 'Ridges'). The ridges are usually parallel to the carapace margins, and occur in two groups of three to seven on either side of the margins (e.g., Figs. 8a, d, f; 16a–f, and see model Fig. 17). Ridges could represent twisting artefacts or impressions of internal structures or a combination of both. In the first hypothesis, the height, and the number of the ridges, seems to be a function of rotation of the posterior section (see paragraph on the posterior section for further explanation). In specimens with a twisted posterior section, ridges are numerous and prominent (e.g., Fig. 16), but in specimens which are

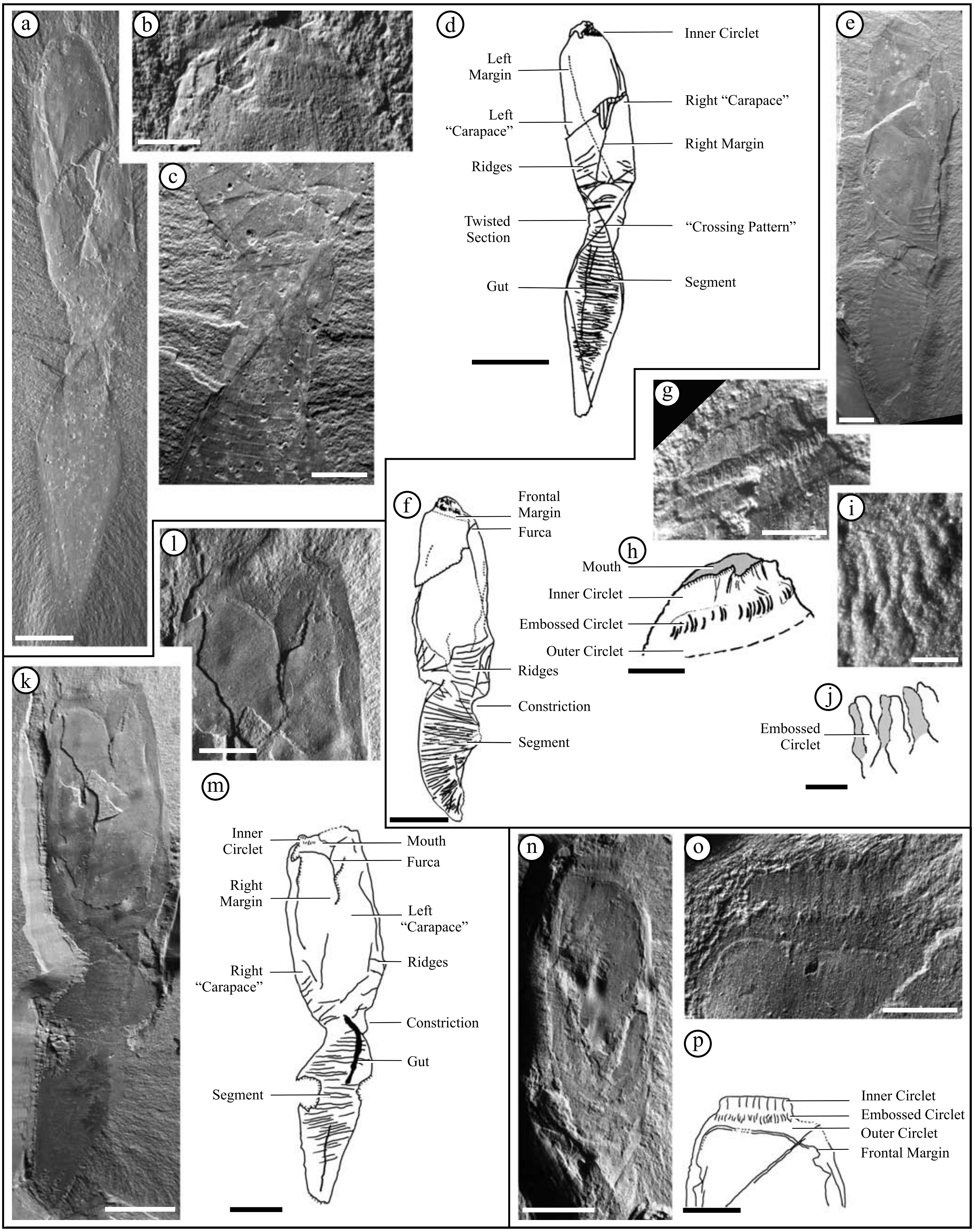

Figure 13 *Banffia constricta* Walcott, 1911: (a–d) presumed lateral specimen, part, ROM 49898: (a) complete specimen, scale bar = 10 mm; (b) detail of the crown-like structure, scale bar = 3 mm; (c) detail of the twisted midbody with the typical 'crossing pattern', scale bar = 5 mm; (d) composite explanatory drawing based on both the part and counterpart of the complete specimen, scale bar = 20 mm. (e–j) presumed lateral specimen, ROM 49930: (e) part, complete specimen, scale bar = 5 mm; (f) composite explanatory drawing based on both the part and counterpart of the complete specimen, scale bar = 10 mm. (g–j) counterpart of same specimen: (g–h) detail of the crown-like structure in lateral view; (g) detail of the embossed circlet, scale bar = 2 mm; (h) explanatory drawing based on (g); (i) close-up of (g), scale bar = 0·5 mm; (j) explanatory drawing based on (i), scale bar = 0·5 mm. (k–m) presumed ventral specimen, part, ROM 53647 (specimen dβ, see also Figure 3a); (k) complete specimen, scale bar = 10 mm; (l) detail of the mouth and furca zone, scale bar = 5 mm; (m) composite explanatory drawing based on both the part and counterpart of the complete specimen, scale bar = 10 mm. (n–p) presumed dorsal specimen, ROM 53647 (specimen k): (n) complete specimen, scale bar = 10 mm; (o) detail of the crown-like structure and the frontal margin, scale bar = 3 mm; (p) explanatory drawing based on (o), scale bar = 5 mm.

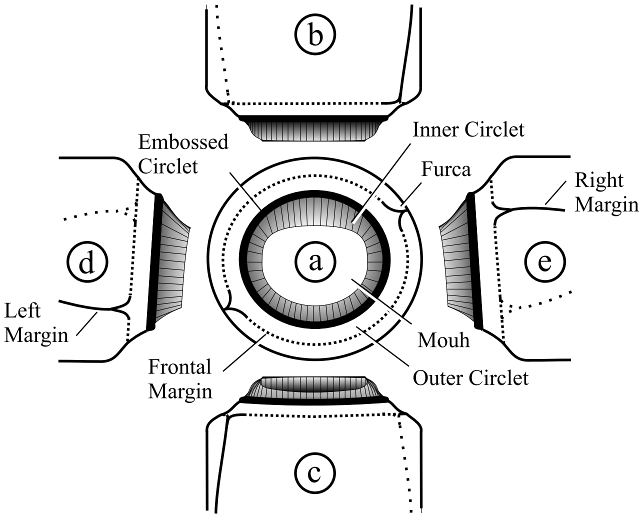

Figure 14 *Banffia constricta*, mouth model as viewed in five different ways: (a) frontal view; (b) dorsal view; (c) ventral view; (d) left lateral view; (e) right lateral view.

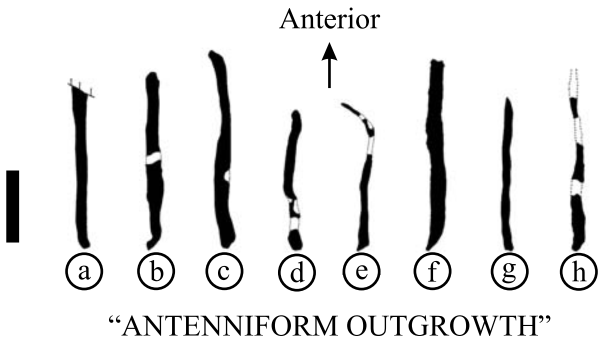

Figure 15 *Banffia constricta* frontal antenniform outgrowth, scale bar = 1 mm: (a) ROM 49915; (b) ROM 49890; (c) ROM 49914; (d) ROM 54342; (e) ROM 49917 (specimen c); (f) ROM 49917 (specimen f); (g) ROM 53770; (h) ROM 54341.

not twisted these ridges are faint (e.g., Fig. 9a–d, f, g). Ridges may also represent the imprints of internal structures that are sometimes compressed on the inner side of the anterior section. One specimen has three ridges on the external surface of the left carapace (Fig. 8a, d, f). In this example, part of the right carapace has been detached along fractures, and three grooves on the internal surface of the right carapace can be seen (Fig. 8a, d, f). The nature of the internal structures imprinting the inner side of the anterior section is unknown but this imprint indicates that the anterior section is weakly sclerotised and relatively flexible (e.g., Fig. 16). However, because the ridges are especially prominent in specimens with a twisted posterior section (e.g., Fig. 16), it is possible that they are the imprints of helically arranged muscles. In this scenario, muscles are connected to the posterior section and may leave imprints on the inner side of the anterior section when the posterior section is twisted. This hypothesis is reinforced by the clockwise rotation of the ridges that indicates that the hypothetical muscles are turning in the same direction as the body.

Posterior section. Overall, the posterior section is fusiform; tapering towards both ends (e.g., Fig. 9a, c). At the anterior–posterior section boundary, as seen from a dorso-ventral view lies a constriction (e.g., Fig. 9a–d, f–i, k). In addition, the posterior section is usually twisted creating a 'crossing-pattern' (e.g., Figs. 8g, l; 13a–c; 16a, c, d, e; 18a–f). This 'crossing-pattern' varies in location in different specimens from the front of the posterior section to as far back as nearly half the length of the posterior section (e.g., Fig. 18j, m) and suggests a twisting artefact. However, like the anterior section, the posterior section is always dextrally twisted in all specimens (Fig. 19). Therefore, the twisted nature of the posterior section is interpreted as a primary morphological feature.

'Superficial segments'. The posterior section is composed of about 40 to 50 weakly sclerotised segments (presumably superficial), which are oblique to the edge of the posterior section (e.g., Fig. 9h, j, k). The segments articulate by a cuticular membrane that may have permitted sliding movements and increased the flexibility of the posterior section (e.g., Fig. 9j). The distance between adjacent segments varies from 0·1 to 2 mm; the anterior ones being the widest (e.g., Fig. 9d, g). The last segment is short and terminates as a caudal notch (Figs. 4a, e, f; 18g, i). The segments on opposite sides have somewhat different orientations, so they form a low-angle crossing pattern with one another, as seen in both laterally and dorso-ventrally flattened specimens and have a typical crossing pattern (e.g., Figs. 9a–g; 18l, n). The crossing pattern of the segments suggests that they were helically arranged and independently confirms that the posterior section was dextrally twisted and was flexible.

Internal organs. Traces of internal organs are preserved in more than 50 specimens. A simple narrow dark strand is interpreted as the gut (e.g., Fig. 8e, f). The gut (considered herein as an intestine) extends from the base of the anterior section to the terminal anus (Fig. 20a, b, c, e, j–m). The gut seems to be located somewhat ventrally in the posterior section (Figs. 8a, f; 20a, d). However, the position and polarity of the gut is difficult to assess due to the rotation of the posterior section. In a few specimens, the probable anus is seen in the caudal notch (e.g., Fig. 18g–i). The nature of the foregut from the mouth to the posterior section is currently unknown. The gut is sometimes preserved in three-dimensions (e.g., Figs. 13k, m; 20f, h, i). However, the three-dimensional aspect of the gut is considerably altered by flattening (e.g., Fig. 20h), and compression has impressed segment boundaries along the gut (e.g., Fig. 20h). The three-dimensional aspect of the gut is probably due to mud-filling instead of permineralisation prior to replacement by clay minerals (see also Butterfield 2002).

'Mid-gut diverticulae'. In a few specimens, the gut is connected by a series of paired short perpendicular strands possibly ventrally oriented. These perpendicular strands are present from the anterior of the gut to about two-thirds of its distance to the anus (Figs. 8d–f; 20a–c, e, g, i–m). In some specimens, a poorly defined strand seems to represent the edge of a structure that runs axially around the gut and the short strands, and may represent a membrane (e.g., Figs. 8d–f; 20a–c, e, g, i–m). The perpendicular strands associated with the gut may be interpreted as mid-gut diverticulae. Firstly, in specimens without mud filling of the gut, the type of preservation of the diverticulae and the gut is similar (Figs. 8d–f; 20a–d, j–m), which may indicate that they were originally of the same tissue composition, and secondly, the diverticulae seem to be arranged on either side of the gut, and may have blind distal terminations (Fig. 20j–m, see model Fig. 21a).

Alternatively this system may be interpreted as a semi-closed circulatory system with a dorsal vessel (if the intestine is ventral) supplying the gut by lateral 'hearts' (see model Fig. 21b). This interpretation is uncertain however because the irregular dark strand that parallels the gut is not clearly preserved (i.e., it is not continuous as a dorsal vessel would be), and might rather be interpreted as lateral compaction of the distal parts of gut diverticulae (Vannier & Chen 2002).

In a few specimens, a faint line runs parallel and just under the outer body surface (Fig. 20a–c, e) and could be interpreted as remnant of the body wall.

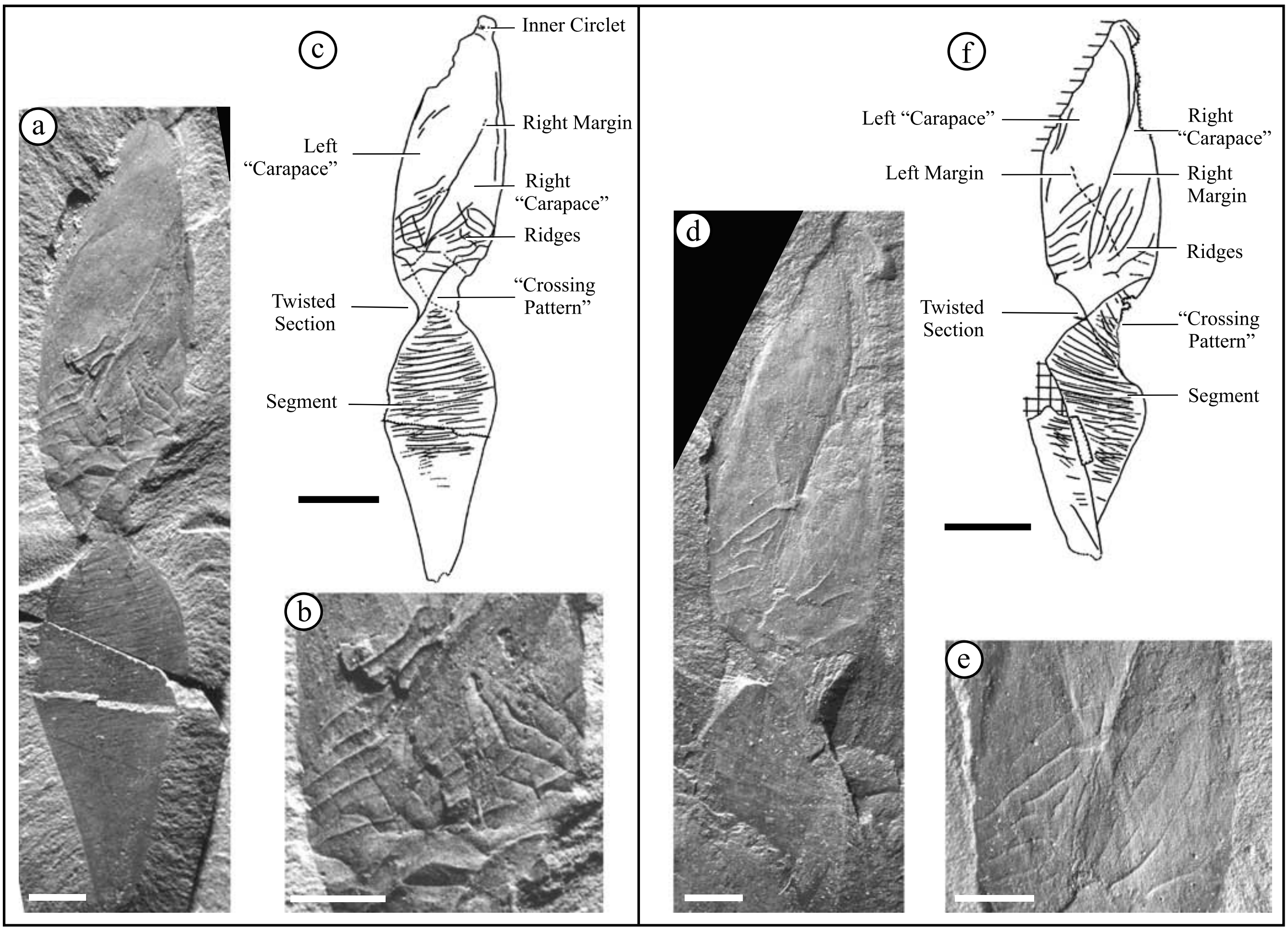

Figure 16 *Banffia constricta* Walcott, 1911: (a–c) presumed lateral specimen, part, ROM 49897; (a) complete specimen, scale bar = 5 mm; (b) detail of the ridges, scale bar = 4 mm; (c) composite explanatory drawing based on both the part and counterpart of the complete specimen, scale bar = 10 mm. (d–f) presumed lateral specimen, part, ROM 49892; (d–e) silicone mould from the counterpart; (d) complete specimen, scale bar = 10 mm; (e) detail of the ridges; (f) explanatory drawing based on the complete specimen, scale bar = 4 mm.

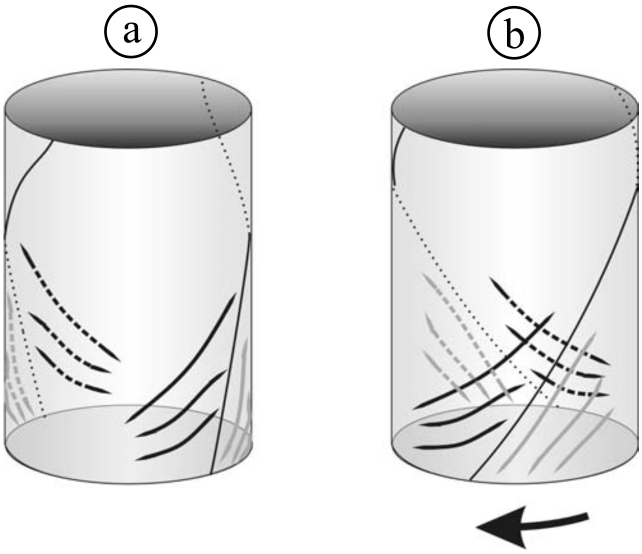

Figure 17 *Banffia constricta*: model of the ridge structure. The structures at the back are represented by dotted lines; (a) dorso-ventral view; (b) lateral view.

6. Discussion

6.1. Taphonomy

The discovery of specimens of *Banffia* perforated by burrows and micro-ichnofossils demonstrates that these were buried with some local oxygen present in the environment and that soft-body preservation was possible despite the presence of oxygen. Such burrows are known from other Burgess Shale localities at similar stratigraphic levels, or slightly below the Emerald lake Oncolite Member in the Raymond Quarry (Allison & Brett 1995). In Allison & Brett's study (1995), the burrows are associated with a semi-autochthonous shelly biota in low-diversity layers. These low-diversity layers are intercalated with high-diversity layers that contain soft-bodied animals and a limited shelly fauna but no burrows (Allison & Brett 1995). This succession of low and high-diversity layers is thought to be controlled by variations of the oxycline (Allison & Brett 1995). That is, low-diversity layers were interpreted as *r*-selected colonisation events during periods of benthic oxygenation. On the other hand, high-diversity layers were interpreted as assemblages dominated by soft-bodied animals, which were preserved when the sediment and bottom water became anoxic after the burial event (therefore explaining the absence of burrows). *Banffia* belongs to low-diversity layers and could therefore represent a pioneer species.

In one specimen of *Banffia*, the superficial cuticle is highly degraded, but internal organs are well preserved (Fig. 20a–d). Such a mode of preservation has been documented in other animals from the Burgess Shale, for example, in the archaeopriapulids (Conway Morris 1977, p. 31). The enhanced preservation of the gut and diverticulae of *Banffia* may be controlled by differences in chemical reactivity within the gut, which

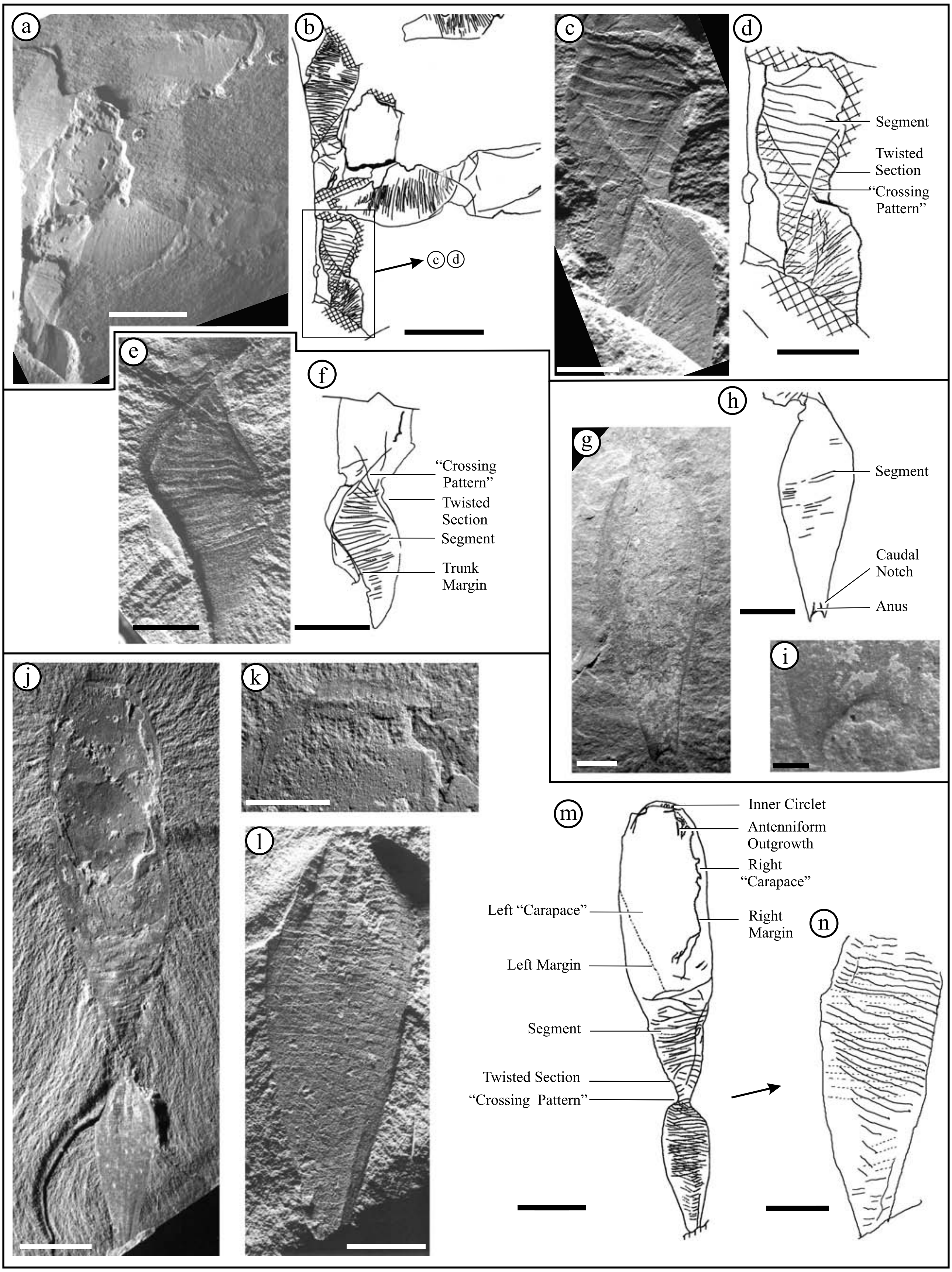

Figure 18 *Banffia constricta* Walcott, 1911: (a–d) USNM 188632: (a) overall slab, scale bar = 20 mm; (b) camera lucida drawing of (a), scale bar = 20 mm; (c) close-up of the posterior section of specimen 'd', scale bar = 5 mm; (d) camera lucida drawing of specimen 'd', scale bar = 10 mm. (e–f) USNM 200550; (e) detail of the posterior section, scale bar = 5 mm; (f) composite explanatory drawing based on both the part and counterpart of the complete specimen, scale bar = 10 mm. (g–i) ROM 53769: (g) detail of the posterior section, scale bar = 5 mm; (h) composite explanatory drawing based on both the part and counterpart of the complete specimen, scale bar = 10 mm; (i) detail of the posterior part of the posterior section, scale bar = 1 mm. (j–n) dorso-ventral specimen, part, ROM 49915: (j) complete specimen, scale bar = 10 mm; (k) detail of the crown-like structure, scale bar = 4 mm; (l) detail of the posterior section, scale bar = 5 mm; (m) composite explanatory drawing based on both the part and counterpart of the complete specimen, scale bar = 10 mm; (n) composite explanatory drawing based on both the part and counterpart of the posterior section, scale bar = 5 mm.

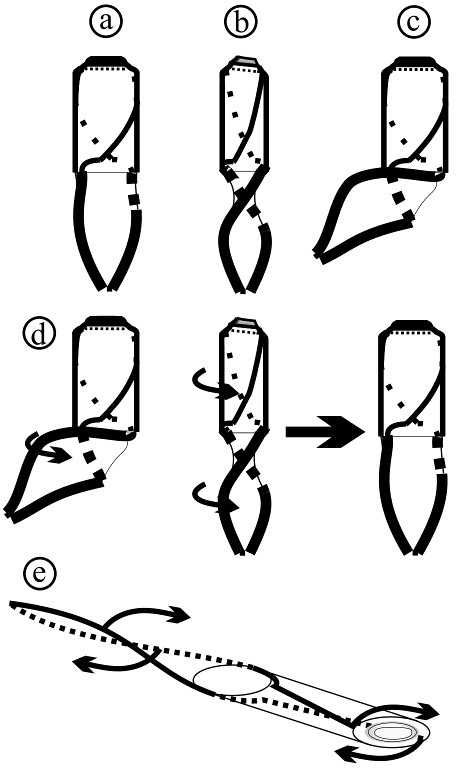

Figure 19 *Banffia constricta* twisted section models, structures at the back are represented with dotted lines: (a) dorso-ventral view; (b) lateral view; (c) dorso-ventral view with the posterior section tilted towards the left; (d) either a retrodeformation of the last specimen (c) or a 90° rotation of a specimen in lateral view (b) would show similar features as the specimens in dorso-ventral views (a); (e) 3-d fronto-lateral model showing the clockwise rotation of the anterior section and posterior section margins.

typically, but not ultimately, leads to early mineralisation of the structure (Butterfield 2002). In *Banffia* the gut wall, like the rest of the body is not mineralised, but seems to be preserved as organic carbon (Butterfield 1990, 1995).

6.2. Ecology

The mode of feeding of *Banffia* can be inferred from both the morphology of its mouth apparatus and the anatomy of the gut and its constituents. The absence of claws or chewing parts, unlike in the taxa discussed by Butterfield (2002) and Vannier & Chen (2002), makes it unlikely that *Banffia* was a predator or a scavenger. The intestine of *Banffia* is long, straight and narrow, which is correlated with a muddy diet (Butterfield 2002). Thus, there is some evidence that *Banffia* was indeed a deposit and/or filter feeder. The lack of mud in the gut diverticulae in specimens with intestines filled with sediment is more difficult to explain (Fig. 18f–h). If this mud was emplaced when the animal was alive, it is possible that the mid-gut diverticulae were sites for enzyme production (not digestion), and that the enzymes were released into the gut lumen during the digestion process. The hypothesised habit of *Banffia* as a deposit and/or suspension feeder may be comparable to that of *Xidazoon*, which was originally conceived as a deposit feeder (Shu *et al.* 1999, 2001; but see Shu *et al.* 2003). Giving this interpretation of its feeding habits, *Banffia* was benthic, living in the uncompacted layer of mud on the sea floor. It is dorsoventrally flattened, a morphology often associated with benthic animals. Its posterior section could have propelled it along the sea floor (Fig. 22). The high concentration of *Banffia* in some slabs is evidence that *Banffia* was a gregarious animal.

6.3. Affinities

All vetulicolids share the same general body plan: two body sections of similar length connected by a constriction, an anterior section composed of fused 'carapace-like' structures, a prominent crown-like mouth, and a segmented posterior section (Shu *et al.* 2001). *Banffia* possesses all these characters strongly indicating it is a vetulicolian (Caron 2001). However, certain features justify the placement of *Banffia* in a separate class of the phylum Vetulicolia: the body of *Banffia* is asymmetrical, twisted dextrally from the front. It is not streamlined, but rather unspecialised, with no ventral nor dorsal keel; the anterior section is not segmented as it is in other vetulicolids (assuming that the so-called anterior segments in the other vetulicolids are not preservational folds, see Ramsköld *et al.* 1996); it does not have lateral grooves, and is not perforated by 'gill pouches'; the terminal segment of the posterior section is much shorter and is not round, but furca-like and triangular; the mid-gut of *Banffia* has possible diverticulae; and the infill of sediment in the intestine of *Banffia* is not spirally arranged like in many vetulicolids.

What is the phylogenetic affinity of vetulicolids? They were originally considered to be limbless arthropods (see below: Hou 1987), but Shu *et al.* (2001) regarded the lack of appendages as crucial evidence against an arthropod relationship. The presence, therefore, of an arthropod-like anterior section and an articulated tail (posterior section) in the Vetulicolia was attributed to evolutionary convergence (see Shu *et al.* 2001), and the group was interpreted as primitive deuterostomes based on the possession of gill slits, endostyle, and an internal skeleton (see Shu *et al.* 2001). The latter is thought to be represented by a surface membrane along all the margins of the animal, including the lateral mid-lines. Alternatively, a position close to a stem-group tunicate has been recently proposed based on the general resemblance of the anterior section to the external tunic of sessile tunicates (Lacalli 2002). However, of the three 'key' deuterostome characters defined by Shu *et al.* (2001), neither the interpretation of gills or the endostyle, or the internal skeleton, is unequivocal.

Gills. The three-dimensional preservation of the purported gill slits in such vetulicolians as *Xidazoon* and *Didazoon* has led some authors to suggest that these 'gills' may instead represent arthropodian mid-gut glands (Butterfield 2003). More significantly, successive gill pouches in these vetulicolians were described as connected by a tube running from the back of one pouch to the front of the next, but such connections never occur between the gill pouches of fishes or other deuterostomes (Lagler *et al.* 1977). Thirdly, Shu *et al.* (2001) admitted that the vetulicolians gills might indeed represent an example of evolutionary convergence (Shu *et al.* 2001, p. 423). If the gill character is not a homology, it should not be used to define affinities with the deuterostomes.

Endostyle. The interpretation of an endostyle at the inner surface of the carapace-like cuticle of *Xidazoon* and *Didazoon* is equivocal, even supposing such a non-cuticular soft structure can be preserved. The so-called endostyle is described as a dark strand (Shu *et al.* 2001), but similar dark strands run close to the dorsal and posterior margins of the anterior sections in *Vetulicola*, and are accompanied by a greater number of wrinkles. It is possible that the dark strands together with the wrinkles result from compression of cuticular structures, thus representing artefacts.

'Internal skeleton'. The third character interpreted by Shu *et al.* (2001) as an 'internal skeleton' (Shu *et al.* 2001), is only obvious in *Vetulicola*, and is mostly defined by a difference of colour. However, in certain specimens this layer is characterised by a faint reticulate pattern. The outer edge, which covers

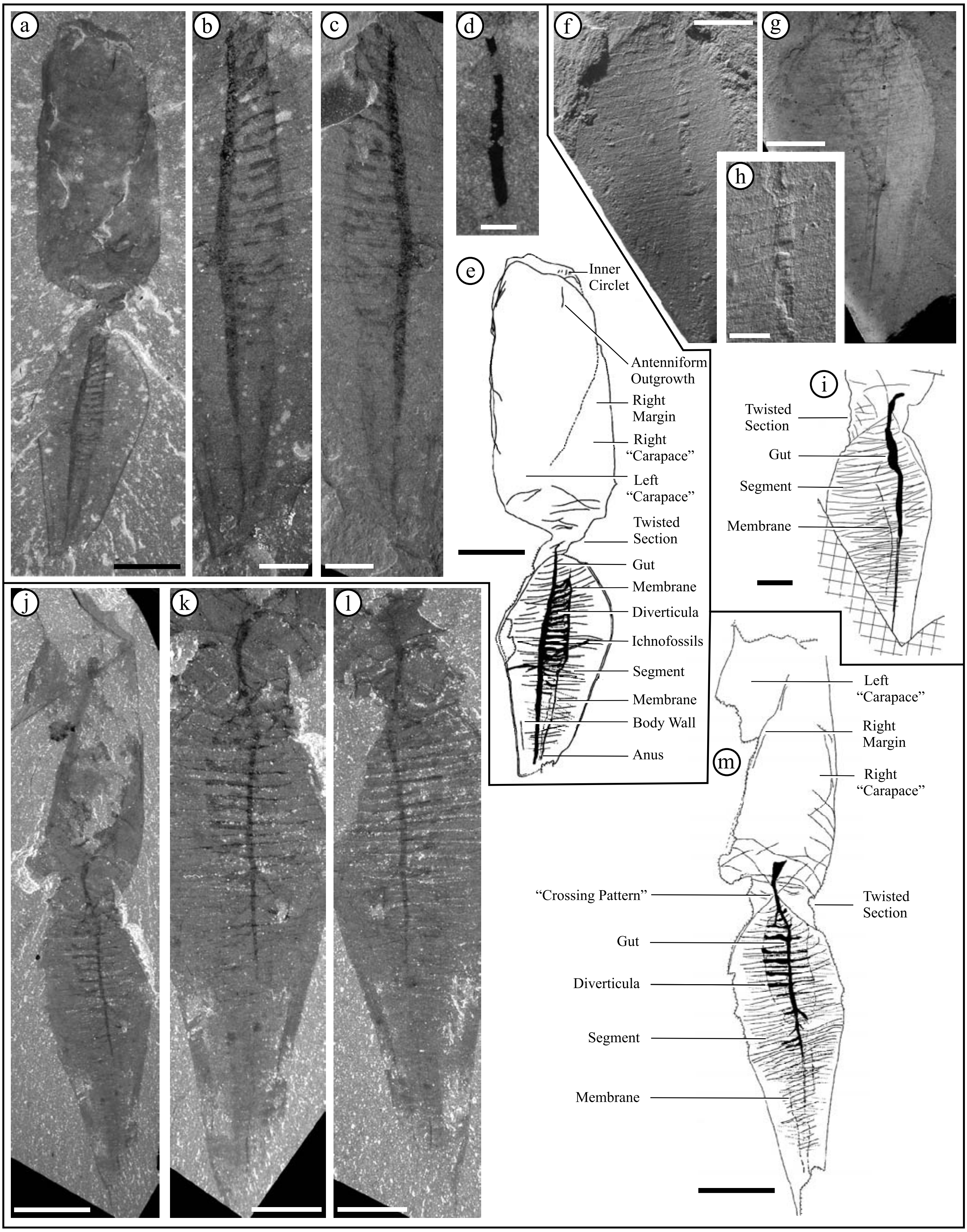

Figure 20 *Banffia constricta* Walcott, 1911: (a–e) dorso-ventral specimen, ROM 49914: (a) part, complete specimen, scale bar=10 mm; (b) part, detail of the posterior section showing internal organs (immersed in water with crossed nicols and using the blending mode 'multiply' in Adobe Photoshop 6®), scale bar=3 mm; (c) counterpart, same as (b), scale bar=3 mm; (d) detail of the frontal antenniform outgrowth, scale bar=0·5 mm; (e) composite explanatory drawing based on both the part and counterpart of the complete specimen, scale bar=10 mm. (f–i) ROM 53757: (f) posterior section, scale bar=5 mm; (g) posterior section showing internal organs (immersed in water with crossed nicols and using the blending mode 'multiply' in Adobe Photoshop 6®), scale bar=5 mm; (h) detail of the gut region, with mud-infill, scale bar=2 mm; (i) explanatory drawing based on the posterior section, scale bar=5 mm. (j–m) ROM 53644: (j) part, complete specimen, scale bar=10 mm; (k) part, detail of the posterior section showing internal organs (immersed in water with crossed nicols and using the blending mode 'multiply' in Adobe Photoshop 6®), scale bar=5 mm; (l) counterpart, same as (k), scale bar=5 mm; (m) composite explanatory drawing based on both the part and counterpart of the complete specimen, scale bar=10 mm.

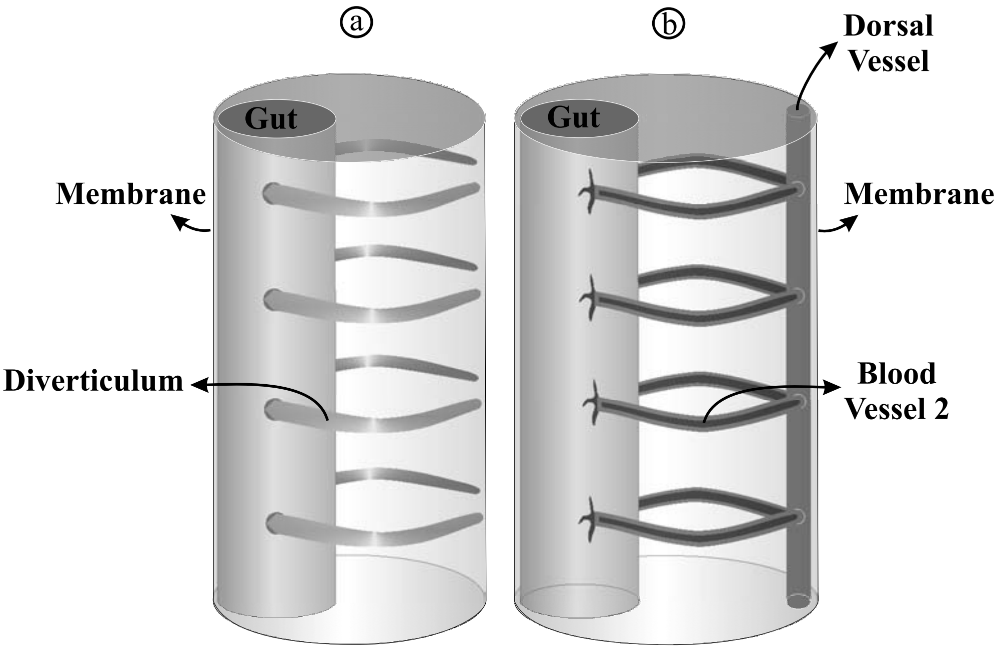

Figure 21 Possible interpretations of the organs associated with the gut: (a) a series of simple mid-gut diverticulae; (b) a circulatory system, the dorsal vessel is connected to the gut by metameric diverticula (in black). In both models, a membrane surrounds the gut and associated organs.

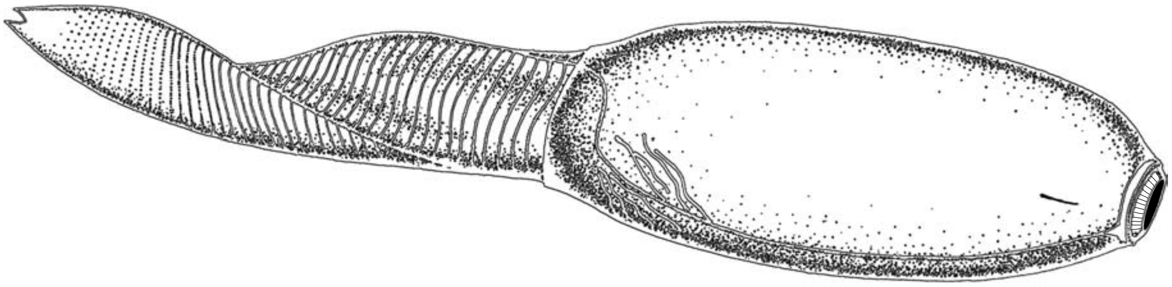

Figure 22 *Banffia constricta* Walcott, 1911: reconstruction (original hand-drawing courtesy of Di-Ying Huang).

the 'internal skeleton', is usually of clearer colour, much thinner, and less wrinkled than the 'internal skeleton' itself. Together, this multilayered structure is suggestive of an arthropod-like cuticle. The presence of the 'outer-edge' may represent a newly moulted cuticle that is not sclerotised. The reticulated 'internal skeleton' is superficially reminiscent of reticulated patterns in bivalved arthropods such as *Tuzoia* (Resser 1929). A detailed study of the cuticle microstructure, if preserved, is beyond the scope of the present study.

Arthropod-like features in the vetulicolids have long been presumed (Hou 1987; Chen *et al.* 1996; Chen & Zhou 1997; but see Shu *et al.* 1995), and include a bivalved carapace at the front and a paddle-like posterior section composed of telescoping segments joined by an intersegmental membrane. Possible mid-gut diverticulae (see Butterfield 2003), a multilayered carapace with a reticulate pattern, and the existence of at least one pre-oral segment (crown-like structure) could represent additional evidence. The pre-oral segment has been described as an important feature of the euarthropod body-plan (Dewel *et al.* 1999). *Banffia*, with its long posterior section bearing numerous faint segments, its bivalved anterior section, and primitive cephalisation, resembles *Odaraia* and *Branchiocaris*, two arthropod taxa that have retained a peytoia-mouth part (assuming an homology with the crown-like structure), and lost posterior limbs (G. Budd, pers. comm. 2003). In contrast to the previously mentioned taxa, however, the vetulicolids have no limbs at all. However, the antenniform outgrowth in *Banffia* might be interpreted as a single pre-oral appendage (see Budd 2002). If the homology of this character is confirmed, then the vetulicolids may be closer to a basal crown-group euarthropod. Of all the characters described above, the possession of mid-gut diverticulae favours a protostome relationship. Mid-gut diverticulae are widely expressed in phyla belonging to the protostomes (see Brusca & Brusca 1990), but are absent from deuterostomes.

If, however, the characters described by Shu *et al.* (2001) are correctly interpreted, then the presence of putative mid-gut diverticulae and the lack of gill elements in *Banffia* remain problematic. One hypothesis is that the gills may have been lost or that the Banffozoa branched off before gills evolved. *Banffia* may represent either the most primitive vetulicolid (Shu *et al.* 2001), or a highly specialised vetulicolid that lost gills. If *Banffia* is the most primitive vetulicolid, and if vetulicolians are considered stem deuterostomes, then the presence of putative mid-gut diverticulae could suggest a possible protostome origin for the deuterostomes.

7. Conclusions

This study provides the first detailed morphological description of *Banffia constricta*. *Banffia* may represent an end-member of the vetulicolids, a group having putative affinities with the deuterostomes. However, with its unique preservation of possible mid-gut diverticulae and antenniform outgrowth, *Banffia* may challenge the existing interpretation of the vetulicolids as deuterostomes. Detailed comparisons of Lower and

Middle Cambrian specimens would certainly help to refine and possibly re-evaluate the status of *Banffia constricta* in the vetulicolids, and the position of the Vetulicolia within the bilaterians.

8. Acknowledgements

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