Reassessment of the problematic Burgess Shale sponge *Takakkawia lineata* Walcott, 1920

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Abstract: The monotypic Burgess Shale sponge genus *Takakkawia* Walcott, 1920, has been previously assigned to the Protomonaxonida, despite showing several unique features. A reassessment of the genus, including restudy of previously described material and the addition of new material that includes partially disarticulated specimens, has allowed a greatly modified understanding of its structure. The sponge possessed four primary columns (each divided into two) of highly modified spicules, with an outer organic layer extended into a unique, complex flange that shows a fine microstructure. The flanges within one column overlap to give the impression of radial fins, and each column is surmounted by an enlarged marginal spicule of similar morphology. Multi-rayed spicules are present both within the primary column architecture and as marginalia lining the osculum. The architecture most closely resembles *Metaxyspongia* Wu et al., 2005, which is placed into the Takakkawiidae. This restudy supports an interpretation of the family as a very early-branching sponge lineage, diverging within the early stem group of Silicea or prior to the separation of Calcarea and Silicea.

Résumé : Le genre d'éponge monotypique du schiste de Burgess *Takakkawia* Walcott, 1920, a déjà été affecté aux Protomonaxonidés et ce, malgré le fait qu'il présente plusieurs caractères uniques. Une réévaluation du genre, incluant un ré-examen de matériel déjà décrit et l'ajout de nouveau matériel dont des spécimens partiellement désarticulés, a considérable-ment modifié la compréhension de sa structure. L'éponge possédait quatre colonnes primaires (chacune étant divisée en deux) de spicules fortement modifiés dotés d'une couche organique externe se prolongeant en une frange complexe et parti-culière présentant de fines microstructures. Les franges au sein d'une même colonne se superposent pour donner l'impres-sion d'ailettes radiales et chaque colonne est surmontée d'un spicule marginal plus grand que les autres, mais de morphologie semblable. Des spicules à plusieurs rayons sont présents dans l'architecture des colonnes et comme éléments marginaux bordant l'oscule. L'architecture s'apparente le plus à *Metaxyspongia* Wu et al., 2005, qui est affecté aux Takak-kawiidés. Le présent réexamen appuie une interprétation voulant que cette famille constitue une lignée d'éponges représen-tant un embranchement très précoce, divergeant à l'intérieur du groupe souche précoce des Silicea ou avant la séparation des Calcarea et des Silicea.

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Introduction

The monotypic family Takakkawiidae is currently based only on the species *Takakkawia lineata* Walcott, 1920, known only from the Burgess Shale of Canada. There have been records of *Takakkawia* from South China (Chen et al. 1997; Zhao et al. 1999; subsequently included in reviews by Dornbos et al. 2005 and Li et al. 2007), but these are either unrecognisable from the published illustrations or appear to be misidentifications of a wapkiid-like sponge (Rigby and Collins 2004). The genus is therefore currently known with certainty only from the Burgess Shale communities, but there it can be abundant at certain levels, particularly in the Wal-cott Quarry (Caron and Jackson 2008).

The described structure of this sponge is unlike any other known taxon, fossil or recent, even with recent advances in understanding the evolutionary framework of early sponges (Reitner and Mehl 1995; Botting and Butterfield 2005;

Botting et al. in press). A re-examination of its structure and relationships within an updated context is therefore necessary to establish its relationships to other taxa. According to the reconstruction of Rigby (1986), the tall, broadly conical body consists of a thin wall with transverse monaxial spi-cules, combined with eight twisted longitudinal ribbons of robust monaxons, each supporting a radially projecting fin that is also interpreted as being supported by monaxons running through it. The ribbons were seen as being cross-connected by a variable number (Walcott 1920; Rigby and Collins 2004) of transverse spicules that produce a rectangular reticulation. The strands were interpreted as diverging upwards into a fan-like splay in the oscular region, which culminated in the summits of the fins, converging slightly inwards. The species has been assigned to the Protomonaxonida (Finks and Rigby 2004), despite the radical differences in skeletal ar-chitecture between *Takakkawia* and other genera in this divi-sion of early supposed demosponges. This assignment is in

conflict with the observation of a hexactinellid-like reticulation by Rigby and Collins (2004) (although reticulosan-like architecture has also been noted in the Leptomitidae; Debrenne and Reitner 2001) and the presence of possible triactinal or hexactine-based spicules in the twisted strands (Rigby 1986; Finks and Rigby 2004).

Restudy of described material (that of Rigby and Collins 2004) and examination of important new material in recent and unstudied collections housed at the Royal Ontario Museum have led to a substantial revision of the structure of *Takakkawia lineata*. The flattened nature of all specimens, combined with dissolution of spicules, makes reconstructions of Burgess Shale sponges significantly interpretative. However, the uncertainties can be mitigated by combining information from multiple preservational styles, some of which have been largely overlooked in previous work. Among the most important material is a variety of disarticulating specimens that clearly show the form of the individual spicules and nature of the radial fins, which are seen to result from the overlap of extraordinary extensions of the outer, organic layer of individual spicules, rather than being continuous soft-tissue structures in which the spicules were embedded. These new elements to the description combine to produce a greatly revised understanding of the structure of the species.

Materials and methods

This study is based on examination of material from several Burgess Shale localities, housed in the Royal Ontario Museum (ROM), Toronto. Reference is also made to related taxa from South China, although these are not described in detail in this paper. Most specimens of *Takakkawia* have been recovered from the Walcott Quarry (see Rigby and Collins 2004 for discussion of sponge distributions within the assemblage). Specimens were examined using a Nikon SMZ1500 stereomicroscope and imaged with an attached LV-TV camera system (ROM). Imaging involved a combination of low-angle illumination with cross-polarized high-angle illumination to reveal specific details. Specimens preserved in different ways respond differently to different illuminations, with dominantly organic preservation being best illustrated through high-angle reflection. Photographs have been modified only through adjustments to brightness and contrast.

Systematic palaeontology

Phylum Porifera
Class, order undefined
Family Takakkawiidae De Laubenfels, 1955

EMENDED DIAGNOSIS: Thin-walled subconical sponges with hexactinellid-like spicules (sometimes largely reduced to monaxons) and structural tetraradial symmetry consisting of four (sometimes subdivided to eight) columns of modified, usually enlarged spicules running from base to osculum; oscular margin typically surrounded by enlarged marginalia with one vertical distal ray and at least two sub-vertical proximal rays.

INCLUDED GENERA: *Takakkawia* Walcott, 1920, and *Metaxyspongia* Wu et al., 2005. Isolated spicules described by

Bengtson (1986) are probably also referable to the family and may represent a distinct genus (see Discussion).

REMARKS: The revised familial diagnosis given here refers to several features that unite superficially disparate taxa. *Metaxyspongia* Wu et al., 2005, was described as a protospongiid, intermediate between *Protospongia* and *Diagoniella*, based on the columns of diagonally oriented spicules. Additional specimens of the genus, and undescribed but related taxa, have recently been collected from the Hetang Biota of South China (see Xiao et al. 2005); these are under description by J.P.B. and others but resemble *Metaxyspongia*. *Takakkawia* and *Metaxyspongia* share a tall vasiform body form with four columns (divided into eight at around one-quarter height in *Takakkawia*) of morphologically derived spicules. They also show similar enlarged, multi-rayed marginalia with one projecting distal ray and no discrete basalia.

The diagnosis stresses certain aspects that will not be visible except where exceptionally complete preservation occurs. The critical feature, recognisable even in partially articulated remains without soft tissue, is the presence of four (or eight) distinct vertical columns of hexactine-based spicules, which are typically of modified form. At present, any sponges with this type of architecture can be immediately assigned to the family, although it includes a wide range of variation in features such as the spicule arrays between the columns; in future, subdivision may be justified.

The Takakkawiidae possessed certain features reminiscent of hexactinellids but other aspects that indicate a more basal phylogenetic relationship. The hexactinellid-like features include hexactine and stauractine spicules, a thin-walled conical body, and local spicule reticulation in *Metaxyspongia*. However, the body also shows consistent structural tetraradial (sometimes divided into octaradial) symmetry. Although several groups of fossil hexactinellid-like sponges show prismatic symmetry of similar order (e.g., Hall and Clarke 1898), this is never expressed as structural divisions within the skeleton; the only similar structure is the less regular structural symmetry of the problematic *Petaloptyon danei* (see Rigby and Collins 2004), which has been assigned to the heteractinid Calcarea but the true affinities of which are problematic. The thick organic layer in the spicules of *Takakkawia* is a feature of extant Calcarea that is also seen in basal members of the sponge classes (Botting and Butterfield 2005; Harvey 2010; Botting et al. in press), but such an external spicule sheath is not present in modern Hexactinellida (except for rare exceptions such as the giant basalia of *Monorhaphis*; Müller et al. 2007). The expansion of this layer into vanes is not known from any other sponge. This combination of features precludes assignment to hexactinellids, and the structural symmetry could indicate a position basal to all other sponges.

Genus *Takakkawia* Walcott, 1920

TYPE SPECIES: *Takakkawia lineata* Walcott, 1920

EMENDED DIAGNOSIS: Takakkawiid with spicules in vertical columns reduced to somewhat curved monaxons, sometimes with transverse ray bridging gap between columns; successive spicules within a column overlap by roughly half their length, and organic sheath is extended into radiating, rounded flanges with fine concentric ridging; apical spicules of columns with elongate distal ray supporting similar but

Fig. 1. ROM53568, *Takakkawia lineata* Walcott, 1920, from the Burgess Shale (middle Cambrian, British Columbia). (A) Overall view (photo courtesy of J.-B. Caron, Royal Ontario Museum); (B) apical region showing terminal blades surrounding osculum; (C) basal region, showing convergence of spicule columns towards base but no discrete basalia; (D) structure of central region with prominent vertical spicule columns; (E) detail of central region, with columns of curved, vertically oriented spicules and transverse, often curved spicules bridging gap between columns. Scale bars: A, 10 mm; B–E, 1 mm.
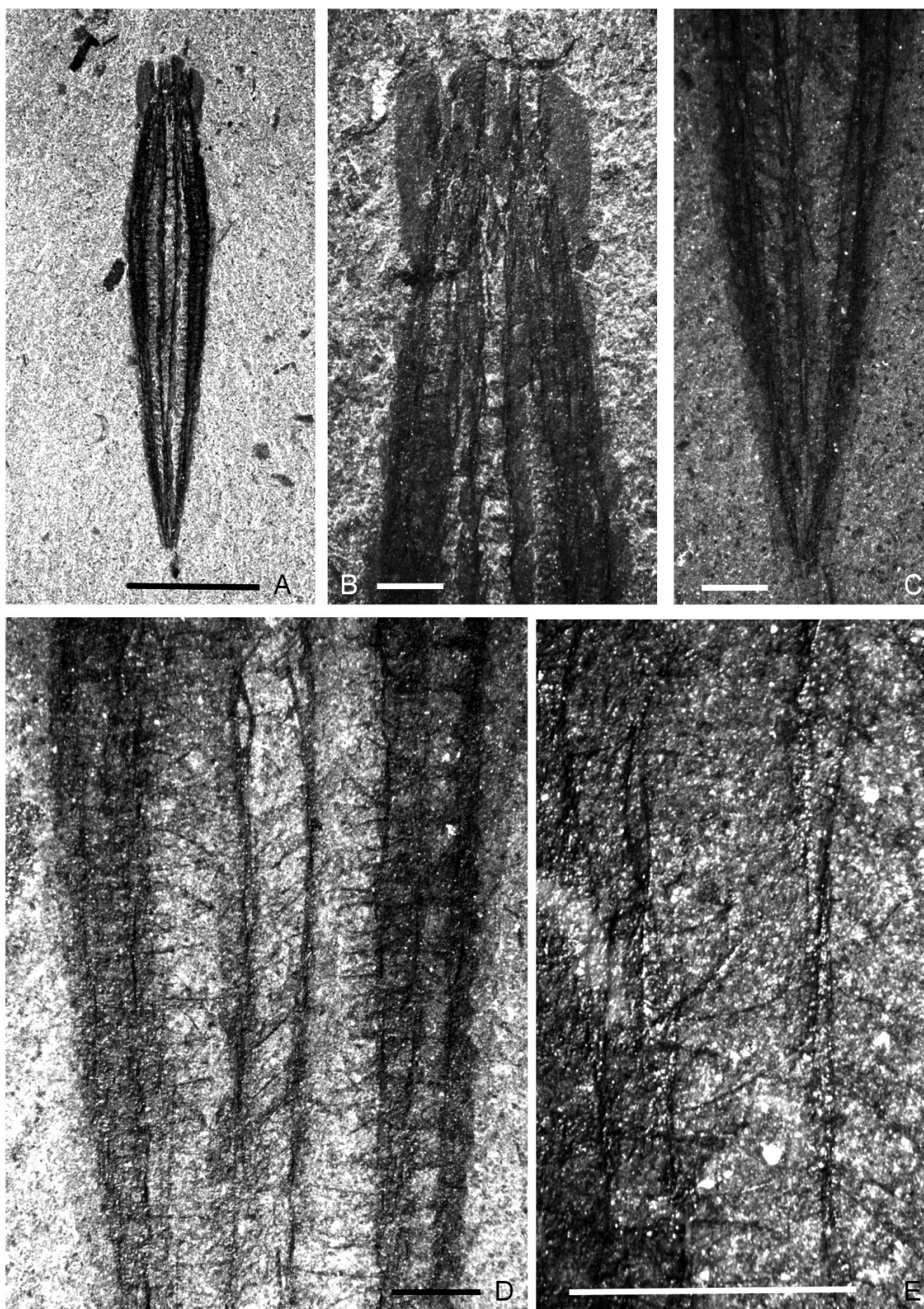
Fig. 2. *Takakkawia lineata* Walcott, 1920, from the Burgess Shale (middle Cambrian, British Columbia). (A–D) Specimens on slab ROM61822: (A) overall view of near-complete, partly disarticulating specimen with organic preservation; (B) basal regions of two near-complete specimens, partly disarticulating; (C) detail of Fig. 2A, showing morphology and structure of individual, overlapping flanged spicules within one column; (D) isolated flanged marginalia (compare with in-place examples in Fig. 2A). (E) Specimen on slab ROM61823, two overlying marginalia showing consistent development of flanges. Scale bars: 1 mm.
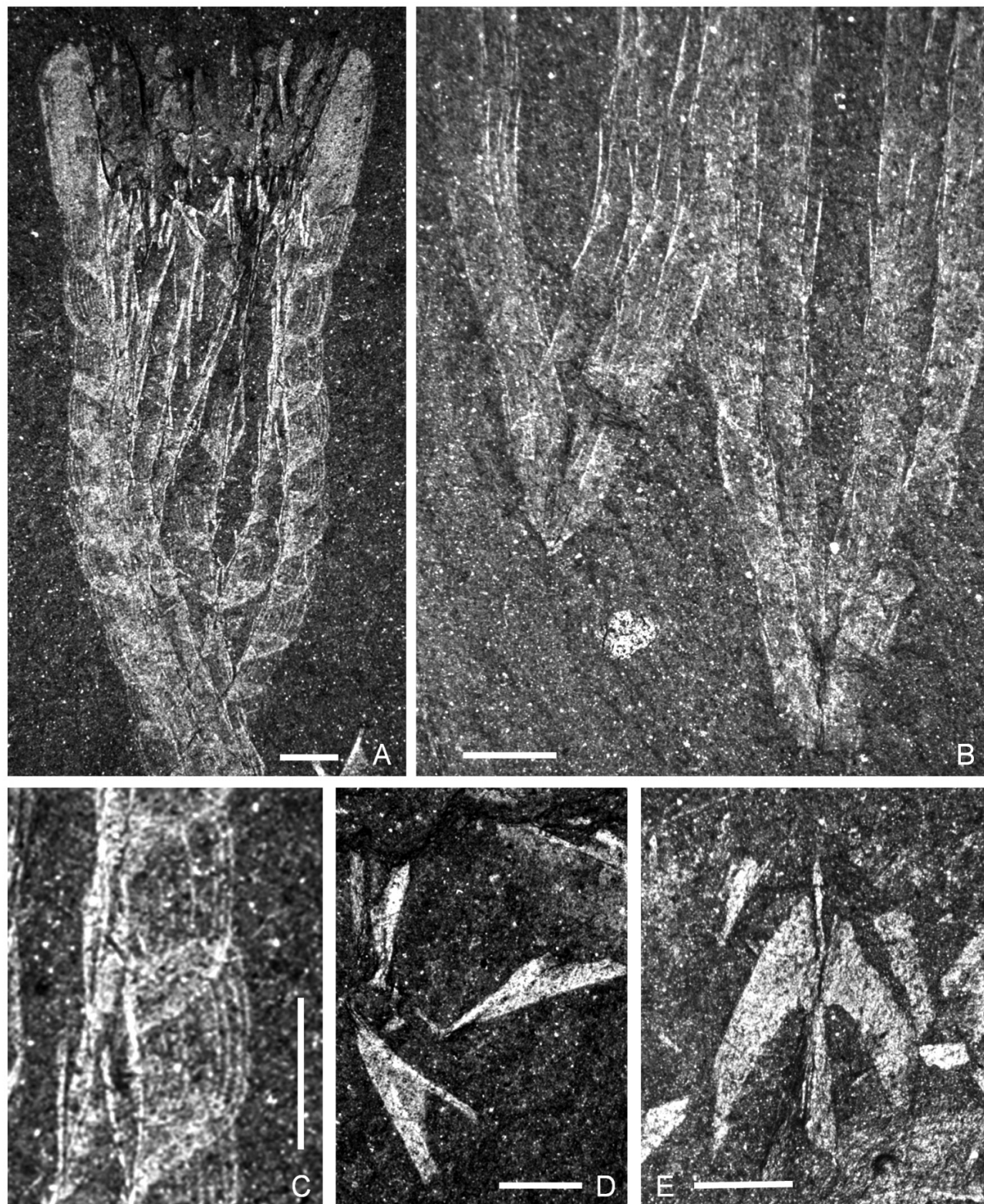
Fig. 3. *Takakkawia lineata* Walcott, 1920, from the Burgess Shale (middle Cambrian, British Columbia). (A–B) Specimen on slab ROM61822 showing isolated apical blade with preserved microstructure, including detail in Fig. 3B, showing apparent transverse structures between prominent concentric ridges. (C) Specimen on slab ROM61823, partially disarticulating specimen with pyritisation of flange overlap regions in addition to structural preservation of the flanges. (D–E) ROM53581, with taphonomic loss of organic flanges but strong pyritisation of the regions of overlap. (F–H) ROM53578, articulated specimen with weak organic preservation but impressions of mineral component of spicules generally retained: (F) overall view; (G) detail of central region with spicules including lateral rays as well as curved "monaxons" forming spicule columns; (H) detail of apical region, showing partial pyritisation of flange overlap and relatively strong organic preservation of apical blades. Scale bars: 1 mm.
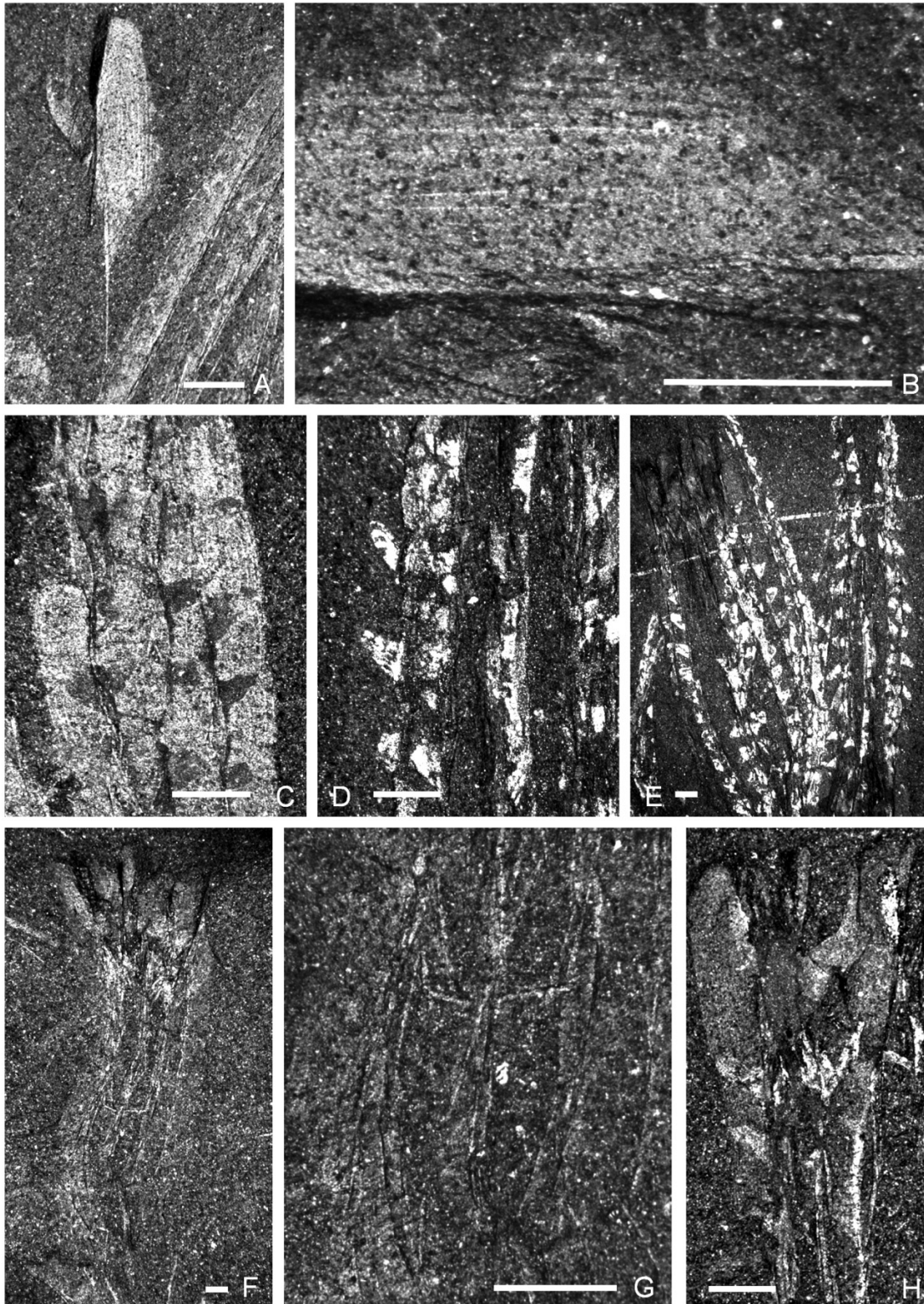
Fig. 4. Cut-away reconstruction of the skeleton of *Takakkawia line-ata* Walcott, 1920, from the middle Cambrian Burgess Shale of British Columbia, Canada, including details of (*a*) marginal fins, (*b*) inter-column marginalia, and (*c*) individual column spicules. The direction of overlap of successive spicules within a column is unknown but is drawn here as a consistent orientation. See text for discussion of the structures and their significance. Maximum height around 40 mm.
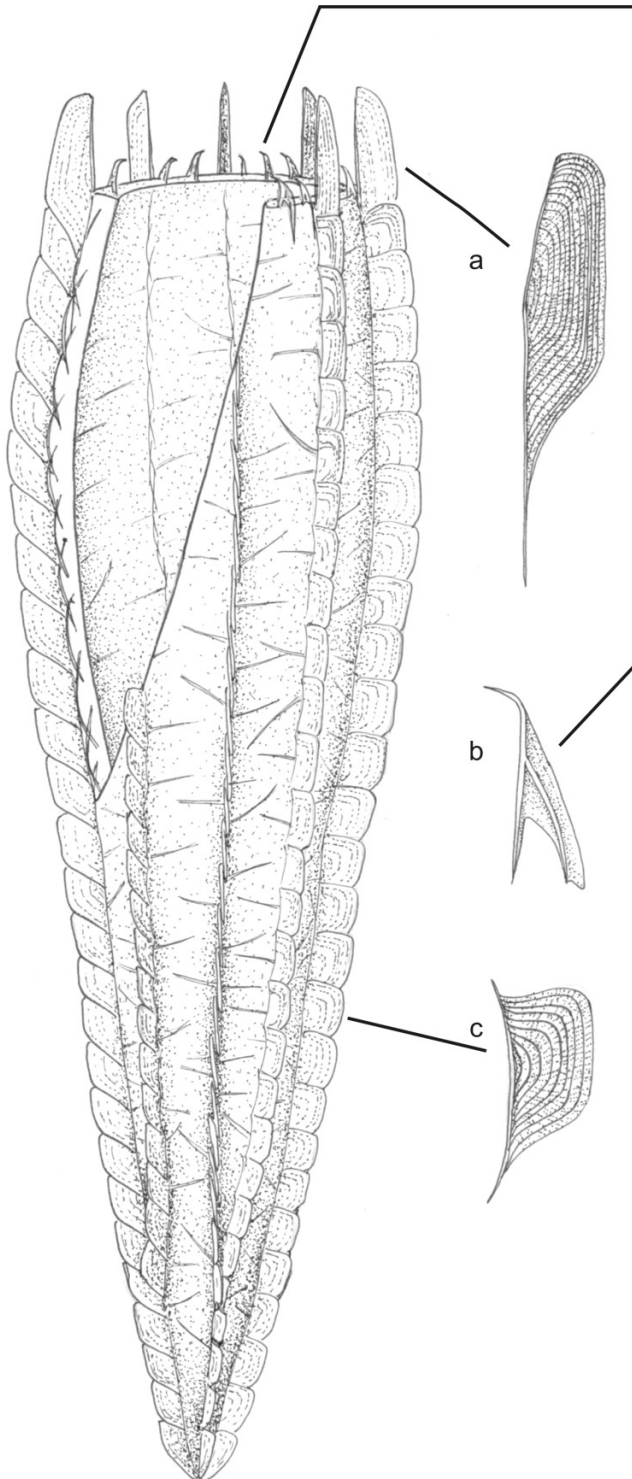
longer flanges; other marginalia also with flanges surrounding rays but not extended into pronounced radial fins.

Takakkawia lineata Walcott, 1920

Figures 1–4.

DIAGNOSIS: As for genus.

MATERIAL EXAMINED: Numerous specimens housed in the Royal Ontario Museum, Canada, but most particularly those studied by Rigby and Collins (2004): ROM53568, 53581, 53587, and 53598. The most important additional specimens are ROM61822 and ROM61823 (both slabs with numerous disarticulating specimens).

Description

This is a complete description of the reconstructed skeleton, based on all specimens studied and previously described in published literature. Specimens are preserved in a variety of taphonomic modes, with the extent of spicule mould preservation, organic material, and pyritisation varying greatly; each mode reveals different aspects of the morphology.

All specimens are tall, slender, slightly wider at three-quarters height than at the apex, and tapering downwards fairly evenly to a sharply pointed base (Fig. 1A). Maximum known height is 43 mm (Rigby 1986, although he also stated in the same work that maximum height was 34 mm and 30 mm), and the tallest specimens seen in this study are 37 mm in height. Specimens shorter than 15 mm are not currently described; the earliest growth stages are unknown. Maximum observed flattened width is 7 mm, in specimens around 35 mm tall, corresponding to a presumed original diameter of around 5 mm.

The primary skeleton consists of eight longitudinal columns of flanged spicules that are semi-fused to create the appearance of continuous fins (Fig. 2A). Basally there are four columns, but these divide at around one-quarter height (but with a wide range, both within and between individuals; Fig. 2B). Each column is composed of around 25 overlapping spicules in addition to the oscular apparatus, the apical spicules being structurally separated from the rest of the column. Between the columns are additional, usually transversely oriented rays and perhaps also discrete monaxon spicules (Figs. 1D, 1E). The original body wall thickness is difficult to ascertain, but the form of the marginalia (discussed later in the text) suggests a minimum thickness of approximately 1 mm, composed of unpreserved soft tissue.

Spicules forming vertical columns have mineral components that appear as simple, slightly curved monaxons (clearest in Fig. 3C), the convex side facing outwards. Spicules face outwards on both sides of each flattened specimen. In some cases there is a lateral ray (Fig. 1E), and in a few specimens (Fig. 3G) there is a possibility of two basal rays at a low angle to each other. The mineralogy of the spicules could not be identified, but in some cases they are preserved in relief, despite their small size (see Discussion). Spicules in general are equally sized through most of a column, although the basal few spicules are often slightly shorter. Individual spicules are up to 3–4 mm long and 0.05–0.10 mm in diameter.

All spicules within the columns possess an outer layer that is extended into an outward-directed flange (Figs. 2A–2C, 3C). This flange is preserved to different degrees in different

specimens but where visible is preserved as reflective, either carbonaceous or aluminosilicate films that are typical of soft tissues in Burgess Shale fossils. In some examples that show the mineral spicules in relief there is little or no trace of the flanges, which must have decayed. These features indicate an originally organic composition for the flanges, rather than a mineral phase. Although in some specimens there is a suggestion of a pair of flanges flattened onto each other, this could not be supported photographically, and it is assumed that each spicule supported only one such structure. In the largest specimens, these flanges are approximately 1.5 mm tall and extend outwards around 0.8 mm. The flanges are rounded and sub-trapezoidal (Fig. 2A), with the lower end joining the spicule in its basal third at around 60° and the upper end joining roughly orthogonally, close to the spicule apex (in some cases, the upper edge nearly parallels the lower edge; Fig. 2C). The lower, inclined edge of each flange curves smoothly into the vertical part of the outline, the upper corner of which is also rounded. Where preserved organically, the flanges show a series of concentric ridges or thickenings (Fig. 2C), which may represent growth increments. If interpreted as such, they imply that the earliest stages of flange growth were much less projecting than later stages, being initially smoothly rounded, and much longer than their radial extent.

Adjacent spicules within a column overlap by approximately half their length, such that the tips of each spicule are positioned roughly 0.2 mm internally to the centres of the ones immediately above and below (Fig. 2C). Some spicules may be linked at this point by minute cross-bracing monaxons, but compression and limited preservation prevent confirmation. This overlap implies a minimum soft-tissue wall thickness of 0.2–0.3 mm. The flanges overlap by a smaller proportion, as they do not occupy the full length of the spicule, but the overlap is sufficient that vertical parts of the outlines of successive flanges are almost continuous. In many specimens, the region of overlap of the flanges is pyritised (Figs. 3C–3E), implying an enclosed or partly enclosed microenvironment. Individual columns retain integrity even in disarticulating material (e.g., Figs. 2A, 2B, and isolated columns are present on the same slab), suggesting that the flanges are perhaps partly fused or otherwise bound. If there are paired flanges from each spicule, then this is inevitable, as adjacent spicules must intersect or pierce the flanges.

At the apex of each column is a prominent, isolated spicule projecting approximately 2 mm above the oscular margin in the largest specimens, and with a total length around 6 mm. This spicule is flanged similarly to those in the column, but the flange extends only down the apical 3 mm (Fig. 3A). The outer margin of the flange extends slightly further out than those of the column spicules, forming a prominent apical blade. The inner edge of the blade (the distal ray of the spicule) is straight but deflected slightly outwards relative to the vertical (Figs. 1B, 2A). These blades show the same fine ridges as in the column flanges (Fig. 3B), spaced approximately 0.05 mm apart and with a trace of extremely fine transverse structures between them (separated by 0.02–0.03 mm). These structures are slightly inclined to the major ridges, and this angle is constant around two sides of the blade, indicating that the feature is not a tectonic fabric. The organisation of these structures appears superficially similar

to that of lepidopteran scales (McNamara et al. 2011), although on a somewhat larger scale.

Between the apical blades are a series of distinct, isolated spicules with smaller flanges (Figs. 2D, 2E), disposed irregularly around the oscular margin (Fig. 2A). These spicules have one distal ray and two proximal rays, the proximal rays inclined at 30° to each other and approximately 1 mm apart at their tips (suggesting a minimum soft-tissue wall thickness, although the inclined ray could have projected from the surface). The distal ray is short and abruptly curves inwards to form a hook that projects horizontally over the edge of the osculum. Distinct flanges are developed on the outer of the two proximal rays, growing into the space between the rays and attaching to the basal half of the inner ray. A narrow flange also runs along the outer side of the outer ray. These spicules include a range of sizes within an individual, up to a maximum total length of around 2 mm.

Areas of the body wall between the vertical columns are often preserved almost devoid of skeletal structures except for occasional lateral rays from the column spicules (Fig. 2B). In other specimens these rays are abundant (e.g., Figs. 1D, 1E, 3F, 3G). In most individual cases, it is difficult to recognise whether they are lateral rays or separate monaxon spicules, but in at least some cases the rays are seen to connect with the apex of column spicules (Fig. 3G), and these are interpreted as lateral rays of reduced hexactine-like spicules. These rays can be straight but are more normally strongly curved, either upwards or downwards (Fig. 1D). In many cases they project entirely across the inter-column space (Fig. 3E), but some appear to be only half this long. None of these spicules show any flange development, but many are preserved with reflective films (Fig. 1E) suggestive of a robust organic sheath.

The base of the sponge (Fig. 2B) is composed of the tips of the lowest spicules and attached flanges in the four primary columns, which in these spicules extend to the tip but with variable outward extent. This extension of the flange in the basal spicules leads to the appearance of a short "stalk" in some specimens. No additional basalia-like spicules have been observed in this or previous studies, and they were presumably lacking.

Discussion

Although sparsely distributed at most locations, *Takakkawia* constitutes 2.61% of the fauna in the Walcott Quarry (Caron and Jackson 2008), with over a thousand specimens, and rarely exceeds 40 mm tall. Many specimens are preserved in a partially articulated state that allows the full reconstruction of the skeleton provided here (Fig. 4). Although there is substantial variation in some features, particularly in the number of transverse spicules bridging the gaps between columns, there appears to be a continuum of variation rather than a discrete difference that could reflect separate species. However, this aspect may be useful if future subdivision is found to be appropriate.

The combination of new observations requires a radically different structure from that previously understood, and varied preservation has been critical to the reinterpretation, including discussions of the original composition of the spicules. Preservation of the spicule axes in relief is typical

of an originally calcium carbonate composition in Burgess Shale fossils, but the original composition of other sponge taxa present in the biota is so poorly known that it is impossible to rule out a siliceous composition for *Takakkawia* spicules. Although some taxa such as *Hazelia* almost certainly represent crown-group Silicea, and probably Demospongiae (e.g., Rigby 1986; Finks and Rigby 2004), their minute spicules do not allow a clear taphonomic comparison. Taxa with larger spicules in the biota are more ambiguous in their relationships and therefore their spicular composition. The composition of *Takakkawia* spicule axes therefore remains uncertain, although the taphonomic observations provided above indicate an originally organic composition for the flanges.

This new reconstruction differs in many ways from those previously published (Walcott 1920; Rigby 1986; Rigby and Collins 2004), as a result of more detailed imaging techniques and a range of material in a variety of preservational styles. Specific differences include the recognition that the radial fins are not solid structures but assemblies of discrete skeletal elements; Walcott (1920) recognised a crenulated margin, but this was not evident in the specimens available to Rigby (1986). The flanges are also now seen to be outgrowths of the organic layer of the spicules, rather than soft-tissue structures supported by spicules. The spicules generating these flanges are slightly curved and overlap by half their length, giving the illusion of twisted strands (Rigby 1986); individual spicules were noticed by Rigby (1986, p. 48), where he recorded "bow-shaped" fragments, together with the lateral rays confirmed here. The marginalia described here explain the appearance of the previously described upwardly divergent fans of spicules at the oscular margin.

One aspect of potential interest is the presence of extremely fine structure on the radial flanges and blades of the spicules. The resemblance of these structures to lepidopteran scale architecture may be superficial, but it is also possible that they acted in a similar way to produce iridescence. Such structures can be preserved in the fossil record (McNamara et al. 2011), but it is unlikely that they have been preserved intact in the Burgess Shale, owing to its deep burial and metamorphic grade (Powell 2003), although it is possible that exceptionally preserved specimens will yield sufficient detail to assess the hypothesis.

The recognition of definitive multi-rayed spicules as marginalia, and also within the columns, shows that *Takakkawia* was not a protomonaxonid but was more closely allied to some group of hexactine-bearing sponges. Such sponges include not only the Hexactinellida but also stem-group Silicea and perhaps stem-group Porifera (Botting and Butterfield 2005). The protomonaxonids themselves include diverse early forms with hexactines (personal observation, 2012), such as *Hyalosinica* (Steiner et al. 1993), but these hexactines are distinctively short-rayed but otherwise regular spicules, and their monaxons are large and dominantly longitudinal. They also show no evidence of tetraradial or octaradial symmetry, and there is no structural resemblance to *Takakkawia*.

Both tetraradial symmetry and nearly identical modified marginalia are present in a group of hexactinellid-like sponges from South China, represented by *Metaxyspongia* Wu et al., 2005, and additional undescribed genera. This genus possessed four columns of highly distinctive spicules running the height of the sponge, a spiculate (often weakly, especially apically) intervening wall, with the columns terminating in a large modified spicule, and with smaller but similarly modified marginalia between. Although the spicules in *Takakkawia* have been reduced in terms of ray number, the architectural organisation is effectively identical. As this organisation includes otherwise unique features, *Metaxyspongia* is here reassigned to the Takakkawiidae. It is unclear whether *Metaxyspongia* spicules were adorned with the flanges seen in *Takakkawia*, as it has not yet been found with suitable soft-tissue preservation. Isolated spicules or sclerites reported from the late Cambrian of Australia (Bengtson 1986, fig. 10), referred to as "darts" and "blades," show very similar forms to those of *Takakkawia*, with the flanges preserved as silica. It is unclear whether these have been secondarily silicified to replace originally organic material or whether in that case they were partly silicified in life. The Australian specimens were extracted from limestone using acetic acid, so the group should be widely recognisable in microfossil assemblages.

Although the family certainly falls outside crown-group Hexactinellida, it is difficult to establish their precise relationships. The original mineralogy of the spicules is unknown, and it is possible that despite the hexactinellid-like spicule symmetry, these sponges belong to the stem group of Calcarea. The robust organic sheath to the spicules is a calcarean feature (Jones 1967; Sethmann and Wörheide 2008) that is almost unknown in modern Silicea but has also been recorded in Cambrian hexactinellid-like spicules (Harvey 2010) and in the heteractinid *Eiffelia* (Botting and Butterfield 2005) and the protomonaxonid *Lenica* (Botting et al. in press). The organic sheath therefore appears to be widely distributed among basal sponges and is probably related to the carbonate secretion phase in biminerallic spicules, hence being lost in Silicea. The organic sheath, with its remarkable modification in *T. lineata*, implies that the group cannot be assigned to crown-group Silicea (unless simplified siliceous spicules were derived independently in hexactinellids and demosponges) and probably not to the later part of their stem group. Furthermore, the structural tetraradial symmetry, not seen in any other group of sponges, suggests that the family is an early-branching taxon that probably evolved prior to the divergence of stem-group Silicea from stem-group Calcarea.

In conclusion, this paper clarifies the uniquely complex structure of a problematic Burgess Shale sponge and argues a close relationship to older hexactine-bearing taxa from South China. The family is interpreted as a previously unrecognised group of stem-group sponges, supporting the growing appreciation that deep branches in early sponge evolution are recognisable in the fossil record. The unique structures seen in *Takakkawia* indicate a much greater degree of morphological complexity than might be anticipated in the most basal metazoans and argue against the earliest sponges having been effectively amorphous colonies of choanoflagellates.

Acknowledgements

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