A CRYPTIC RECORD OF BURGESS SHALE-TYPE DIVERSITY FROM THE EARLY CAMBRIAN OF BALTICA

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Abstract: Exceptionally preserved 'Burgess Shale-type' fossil assemblages from the Cambrian of Laurentia, South China and Australia record a diverse array of non-biomineralizing organisms. During this time, the palaeocontinent Baltica was geographically isolated from these regions, and is conspicuously lacking in terms of comparable accessible early Cambrian Lagerstätten. Here we report a diverse assemblage of small carbonaceous fossils (SCFs) from the early Cambrian (Stage 4) File Haidar Formation of southeast Sweden and surrounding areas of the Baltoscandian Basin, including exceptionally preserved remains of Burgess Shale-type metazoans and other organisms. Recovered SCFs include taxonomically resolvable ecdysozoan elements (priapulid and palaeoscolecid worms), lophotrochozoan elements (annelid chaetae and wiwaxiid sclerites), as well as 'protoconodonts', denticulate feeding structures, and a background of filamentous and spheroidal microbes. The annelids, wiwaxiids and priapulids are the first recorded from the Cambrian of Baltica. The File Haidar SCF assemblage is broadly comparable to those recovered from Cambrian basins in Laurentia and South China, though differences at lower taxonomic levels point to possible environmental or palaeogeographical controls on taxon ranges. These data reveal a fundamentally expanded picture of early Cambrian diversity on Baltica, and provide key insights into high-latitude Cambrian faunas and patterns of SCF preservation. We establish three new taxa based on large populations of distinctive SCFs: *Baltiscalida njorda* gen. et sp. nov. (a priapulid), *Baltichaeta jormunganda* gen. et sp. nov. (an annelid) and *Baltinema rana* gen. et sp. nov. (a filamentous problematicum).

Key words: Cambrian explosion, small carbonaceous fossils, Burgess Shale-type preservation, priapulids, *Wiwaxia*, annelids.

LOWER Cambrian sediments of Sweden have long been known to contain a variety of shelly macrofossils (Åhman & Martinsson 1965; Bergström 1968; Topper & Skovsted 2014), small shelly fossils (SSFs) (Bengtson 1968), ichnofossils (Linnarsson 1871; Jensen 1990, 1997; Jensen & Bergström 2000) and acritarchs (Vidal 1981; Hagenfeldt 1989, 1994; Eklund 1990; Hagenfeldt & Bjerkéus 1991). Body fossils of non-biomineralizing organisms, however, are limited to a handful of isolated euarthropods and lobopodians (Størmer 1956; Bergström 1971; Krumbiegel *et al.* 1980; Dzik & Krumbiegel 1989), with no evidence of the diverse Burgess Shale-type (BST) macrofossil assemblages that have revolutionized our understanding of early Cambrian palaeobiology in Laurentia, South China and Australia (Butterfield 2003). The only documented occurrence of Cambrian macroscopic BST preservation currently recorded from Baltica is three specimens

from a deep drillcore of the Zawiszyn Formation, Poland (Lendzion 1975; Dzik & Lendzion 1988; Daley & Legg 2015).

There is, however, an alternative means of capturing a measure of BST diversity, even in the absence of exceptional macrofossil preservation. The (mostly) disarticulated, taphonomically recalcitrant elements of these organisms are widely recovered as 'small carbonaceous fossils' or SCFs (Butterfield & Harvey 2012). Like their 'small shelly' counterparts, SCFs are deeply polyphyletic, united by little more than their size and a particular search image, in this case organic-walled fossils that are too small to be seen on bedding surfaces, but too large or delicate to be reliably recovered via conventional palynological processing. Despite their fragmentary nature, however, many SCFs can nonetheless be resolved to a taxonomically informative level. Importantly, what SCFs

lose from disarticulation they gain in abundance and distribution, offering a fundamentally enhanced account of palaeobiogeographical and stratigraphical patterns. The key to recovering these large-scale patterns, of course, is global sampling, though most Cambrian SCF studies to date have been centred on relatively few localities in western Canada and South China (Butterfield 1994; Butterfield & Harvey 2012; Harvey *et al.* 2012*a, b*; but see Smith *et al.* 2015*a*). Here we expand this record to the palaeogeographically isolated palaeocontinent of Baltica.

Global palaeogeographical reconstructions of the early Cambrian vary considerably (e.g. McKerrow *et al.* 1992; Li *et al.* 2008; Meert & Lieberman 2008), but there is general agreement that the sedimentary depocentres of Scandinavia/Baltoscandia and the East European Platform belonged to a coherent craton, Baltica, separated from other contemporary landmasses by substantial expanses of ocean (Torsvik & Cocks 2005; Cawood & Pisarevsky 2006; Meert 2014). During the early Cambrian, present-day Scandinavia lay in an inverted position, facing the South Pole (Hartz & Torsvik 2002; Cocks & Torsvik 2005; Álvaro *et al.* 2016). Although once thought to oppose Laurentia across the Iapetus Ocean (see Hartz & Torsvik 2002, fig. 1), the Scandinavian margin is now considered to have faced Siberia on the margins of the Ægir Ocean (Nielsen & Schovsbo 2011). Moreover, almost all palaeomagnetic data place Baltica in the mid to high temperate palaeolatitudes (35–60° S) during the early Cambrian (Torsvik & Rehnström 2001; Meert & Lieberman 2004; Cocks & Torsvik 2005; Landing *et al.* 2013). By contrast, all of the well-known Cambrian BST-Lagerstätten fall within the palaeotropics.

GEOLOGICAL SETTING

The File Haidar Formation (early Cambrian, Stage 4) is locally exposed at the surface in and around southern Sweden, and subcrops extensively beneath the Baltic Sea (Figs 1, 2; Hagenfeldt 1989, 1994; Nielsen & Schovsbo 2007). Deposition took place in a shallow epicontinental sea, broadly mirroring the architecture of the modern Baltic and Bothnian seas, and separated from the Russian margin by a substantial hinterland (Flodén 1980; Lidmar-Bergström 1988; Nielsen & Schovsbo 2011, figs 82–86).

The File Haidar Formation consists of fine-medium sandstones interspersed with recurrent mudstones and siltstones, overlying a weathered gneissic basement (Holm 1901). Across much of its extent, the File Haidar Formation is terminated by a regional unconformity corresponding to the 'Hawke Bay event' (Fig. 2; see Nielsen & Schovsbo 2015) and is overlain by the predominantly middle Cambrian (Stage 5) Borgholm Formation (Nielsen & Schovsbo 2007). In places, however, this latter contact

is gradational, and parts of the Borgholm Formation (e.g. the Grötlingbo Member) are recognized as latest early Cambrian in age, with the diachronous boundary younging westwards (Nielsen & Schovsbo 2011). The subsurface portions of the File Haidar Formation are well known from drillcore, and have been extensively studied both sedimentologically (e.g. Nielsen & Schovsbo 2007, 2011) and for acritarch biostratigraphy (Hagenfeldt 1989, 1994; Eklund 1990).

The early Cambrian age (Stage 4; *c.* 514–509 Ma) of the File Haidar Formation, used here following the scheme of Nielsen & Schovsbo (2011), is based on a combination of acritarch biostratigraphy (*Heliosphaeridium dissimilare* – *Skiagia cilosa*, *Volkovia dentifera* – *Liepaina plana* assemblage zones (Hagenfeldt 1989, 1994; Moczydłowska & Vidal 1986; Moczydłowska 1991, 1998)) and detailed sequence-stratigraphical correlation (Nielsen & Schovsbo 2007, 2011) to the *Holmia kjerulfi* and 'Ornamentaspis' *linnarssoni* trilobite zones (Bergström & Ahlberg 1981; Ahlberg & Bergström 1993). Shelly fossils are rare in the File Haidar Formation, confined to occasional fragmentary trilobite remains (Ahlberg 1984; Ahlberg *et al.* 1986) and rare brachiopods, though some surface exposures yield abundant SSFs including *Mobergella* (Åhman & Martinsson 1965); trace fossils typical of early Cambrian assemblages are also locally abundant (Jensen 1997). The underlying crystalline basement is substantially older, with bounding age constraints of 1700 and 900 Ma (Welin *et al.* 1982).

Sediments of the File Haidar Formation record marine deposition in a storm-influenced nearshore sand belt. Proximal environments are sand-dominated, with distal regions of the inner-shelf grading into siltstones and shales (Nielsen & Schovsbo 2007). The formation is subdivided into five members based on lithology and thin conglomeratic marker beds (Figs 2, 3; Nielsen & Schovsbo 2007, 2011). Sediments of the lowermost Viklau Member consist of interbedded green-grey quartz sandstones, bioturbated siltstones and green shales. The overlying När Shale Member is dominated by quartz sandstone in proximal settings (e.g. in the File Haidar-1 core; Fig. 3), grading distally into successions of heavily bioturbated green-grey siltstones and shales with subordinate sandstones (e.g. in the Grötlingbo-1 core; Fig. 3). The När Sandstone Member is dominated by fine-medium grained quartz sandstones with occasional subordinate siltstone beds. The proximal equivalents of these three members are the Mickwitzia Sandstone and overlying Lingulid Sandstone members; both of these are extensively bioturbated, though the Mickwitzia is more thinly bedded, contains numerous clay horizons, and preserves a substantially greater diversity of ichnotaxa, including both hunting and priapulid-like trace fossils (Bergström 1973; Jensen 1990, 1997; Jensen & Bergström 1995; Rydell *et al.* 2001).

FIG. 1. Map showing distribution of sampled drill-cores intersecting the File Haidar Formation. *Abbreviations*: Gr-1, Grötlingbo-1; FH-1, File Haidar-1; Ha-1, Hamnudden-1; BH, Böda Hamn; Bå-2, Bårstad-2; Be-2, Bernstorp-2; Fi, Finngrundet. Preserved extent of File Haidar Formation shown in dark grey.
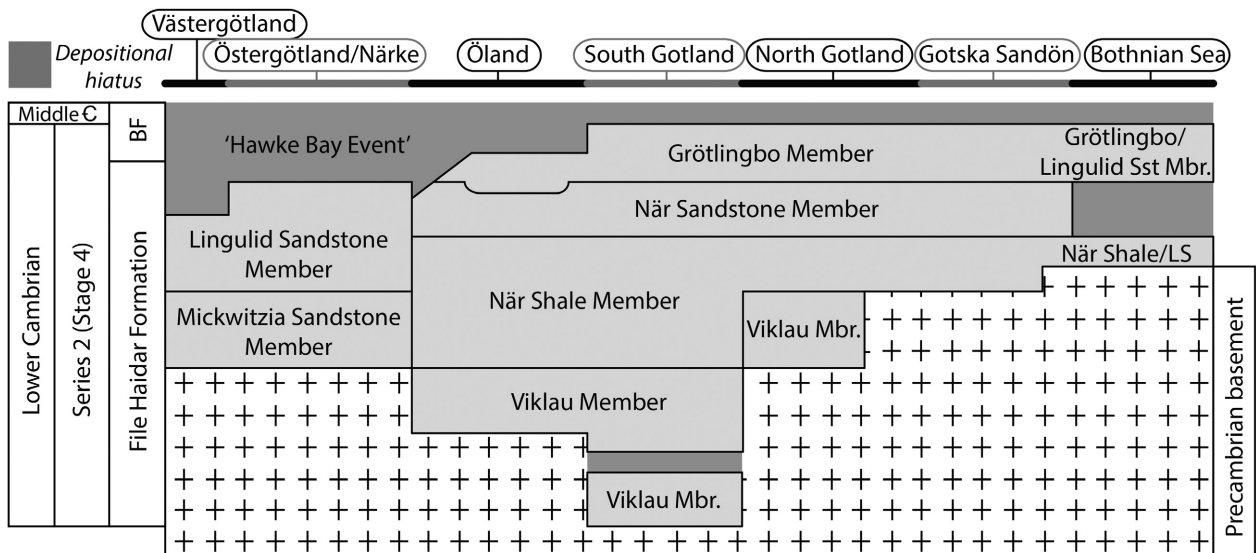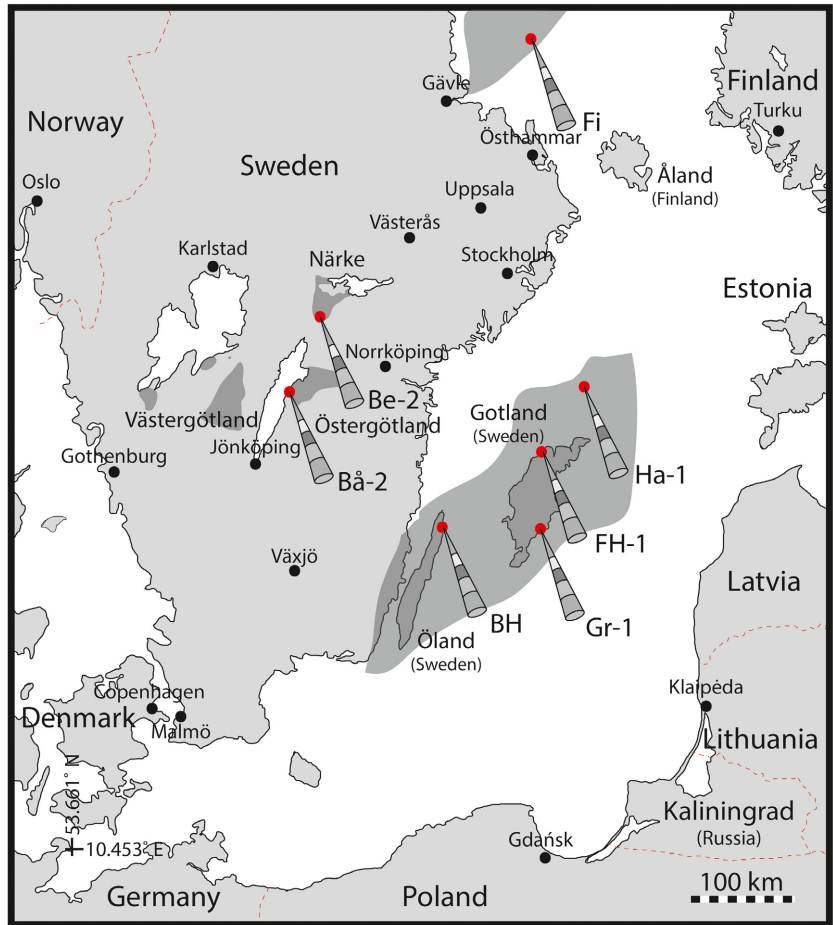
FIG. 2. Subdivisions (members) and occurrence of the File Haidar Formation across southern Sweden and the Bothnian Sea (after Nielsen & Schovsbo 2011, fig. 7). *Abbreviations*: BF, Borgholm Formation; LS, Lingulid Sandstone Member.

The Viklau, När Shale and När Sandstone members are all substantially developed in subsurface drillcores around Öland and Gotland (Thorslund & Westergård 1938; Hessland 1955); the Viklau Member is absent in the southern Bothnian Sea, however, where the Cambrian succession begins with the Når Shale (Fig. 2). Significant

surface exposures of these members include the distinctively red-striated and well-cemented Kalmarsund sandstone, which crops out on the southwest coast of mainland Sweden and is now interpreted as diagenetically altered Viklau, När Shale and När Sandstone strata (Nielsen & Schovsbo 2007). Further inland, the Mickwitzia Sandstone and Lingulid Sandstone members are locally exposed at the surface around Västergötland, Östergötland and Närke, where they are also known from drillcore material (Figs 1, 2).

MATERIAL AND METHOD

The File Haidar Formation was sampled from seven widely separated drillcores in and around southern Sweden (Figs 1, 3); Grötlingbo-1 (Gr-1), File Haidar-1 (FH-1), Hammnudden-1 (Ha-1), Böda Hamn (BH), Bårstad-2 (Bå-2), Bernstorp-2 (Be-2) and Finngrundet (Fi). All cores are housed in the drillcore repository of the Geological Survey of Sweden at Eggebyholm, near Knivsta, Uppland, Sweden. Our sampling protocol included all unoxidized mudstones, siltstones and sandstones, apart from pure quartz arenites. At least one sample was collected per metre of suitable lithology, yielding a total of 217 samples representing all five of the constituent members (Fig. 3). Approximately 50 g of each sample was digested and processed for SCFs using a low-manipulation hydrofluoric acid maceration procedure, and resultant organic residues were hand-picked for SCFs (see Butterfield & Harvey 2012).

SMALL CARBONACEOUS FOSSILS

A total of 3613 SCFs were mounted onto 261 slides from 66 productive samples. Although all seven boreholes yielded fossils, samples from Gr-1, FH-1, BH-1 and Bå-2 were by far the most abundant and diverse, with fissile siltstones and fine-grained glauconitic sandstones producing the bulk of specimens (Fig. 3). Most of the recovered SCFs are recognizably metazoan/bilaterian and can be classified as having either ecdysozoan or lophotrochozoan affiliations; phylogenetically less resolved forms are assigned to 'unresolved metazoans' or 'non-metazoan problematica'.

Ecdysozoa

The protostome superphylum Ecdysozoa includes both the Panarthropoda (euarthropods, onychophorans and tardigrades) and Cycloneuralia (scalidophorans and nematoids), all of which are characterized by a variably tanned/sclerotized cuticle periodically shed through ecdysis. The inherent recalcitrance of this extracellular material, combined with a propensity for body parts to disarticulate along lines of cuticular jointing or thinning, means that ecdysozoans are particularly conducive to the production of SCFs. Arthropods are by far the most abundant and diverse ecdysozoans today, and dominate a number of Cambrian SCF assemblages (e.g. Harvey *et al.* 2012*b*). Scalidophoran worms (represented by modern priapulids, kinorhynchs and loriciferans) were also a significant component of Cambrian ecosystems, represented by trace fossils, Burgess Shale-type macrofossils and, increasingly, SCF assemblages (Harvey *et al.* 2012*a*; Butterfield & Harvey 2012; Smith *et al.* 2015*b*); we expand upon this record here.

Priapulid-like scalids, teeth and hooks. Sub-triangular, thick-walled elements bearing denticles, projections and/or polygonal surface micro-ornament are locally abundant in parts of the Viklau and När Shale Members of the Gr-1 and FH-1 cores (Figs 3, 4, 5A–Q). Considerable variation is evident among the recovered specimens, but all conform to the same basic architecture, consisting of a prominent conical 'prong' at the distal tip of a thickened chevron-shaped 'arch' which caps an ovoid 'basal pad' (Fig. 4A; Smith *et al.* 2015*b*) though the thinner-walled basal pad has been secondarily lost from all but a few specimens (e.g. Fig. 5B). In most specimens the arch is fringed by an array of smaller conical 'denticles' which flare at the base and taper to an acute point (Fig. 5A–Q). Beyond this basic architecture, the specimens exhibit a considerable range of outlines and marginal ornamentations, forming a broad continuum encompassing three apparent end-members or 'types'. Type 1 specimens exhibit an elongate triangular outline with small, closely-spaced marginal denticles distributed along most of the length of the arch/prong complex (e.g. Fig. 5F, H). Type 2 specimens bear fewer, more robust denticles that increase in size towards the central prong, and have a broader, more equidimensional outline (e.g. Fig. 5A). Type 3 specimens are more elongate with an acute-angled arch that tapers to a pronounced prong, and exhibit a significant gap between the most distal denticles and the tip of the central prong (e.g. Fig. 5B–E, G). The denticles in type 3 specimens are sometimes branched at their tips (e.g. Fig. 5O, Q) and are frequently arranged in an asymmetrical pattern on either margin of the arch; in contrast to type 2 specimens, there is no clear size trend among the denticles (e.g. Fig. 5B).

Taken together, these denticulate File Haidar SCFs are reliably interpreted as the dispersed cuticular remains of priapulid-like scalidophoran worms. 'Sclerites' of the same fundamental construction to those found in the Gr-1 and FH-1 cores are found in a variety of modern
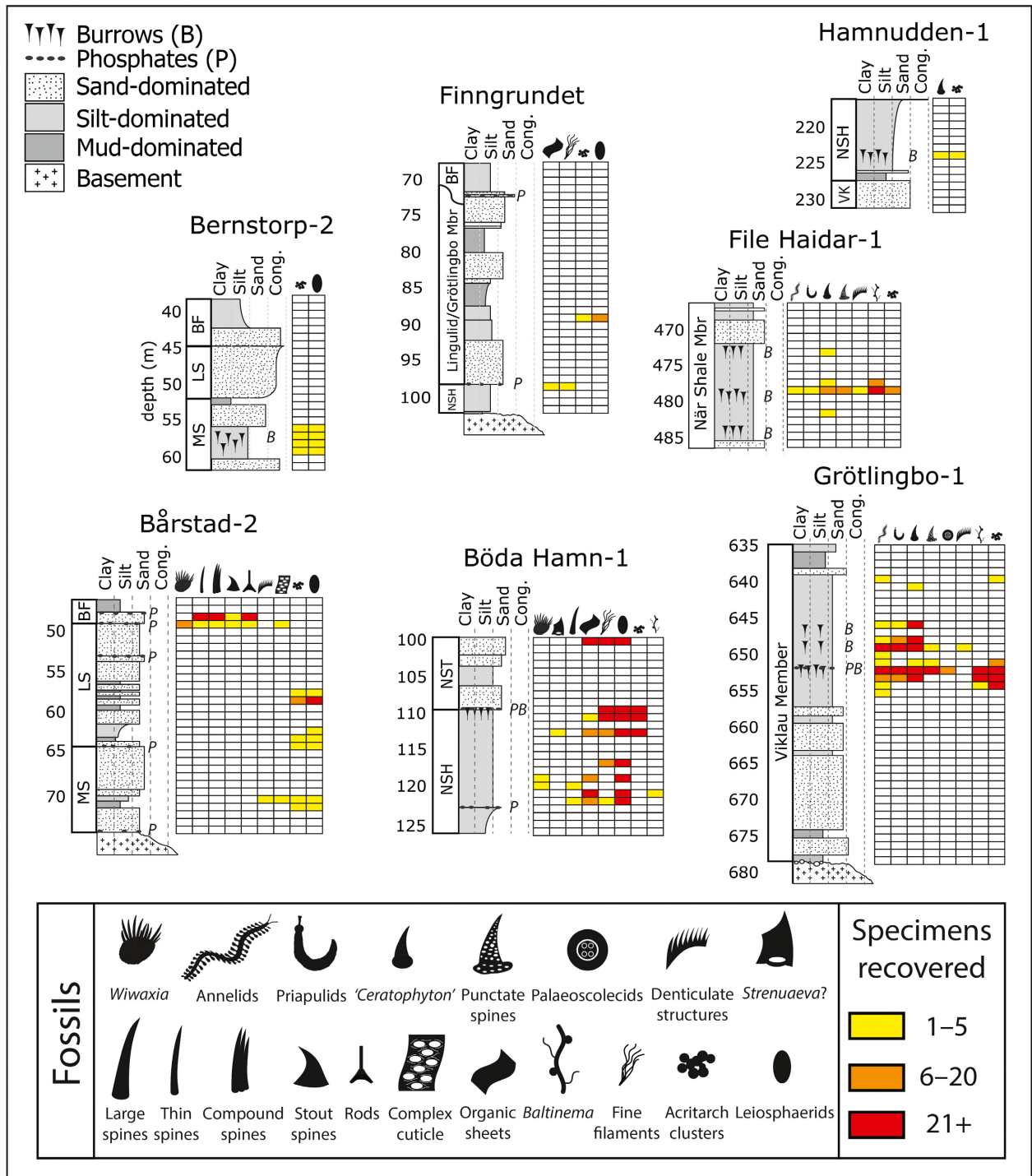
FIG. 3. Stratigraphical distribution of SCFs recovered from core material intersecting the File Haidar Formation. Sedimentary logs after Nielsen & Schovsbo 2011 and personal observations. *Abbreviations*: BF, Borgholm Formation; LS, Lingulid Sandstone Member; MS, Mickwitzia Sandstone Member; NST, När Sandstone Member; NSH, När Shale Member; VK, Viklau Member. Number of samples: Ha-1, 11; Be-2, 9; Fi, 39; FH-1, 8; Bå-2, 33; BH-1, 56; Gr-1, 51. For location of cores see Fig. 1.

priapulids (e.g. van der Land 1970; Wennberg *et al.* 2009), as well as Cambrian stem-priapulids such as *Ottoia* and the tubicolous genus *Selkirkia* (Smith *et al.* 2015*b*);

they are also abundant in many previously-described SCF assemblages (Butterfield & Harvey 2012; Harvey *et al.* 2012*a*, *b*). In particular, it is the approximately bilaterally
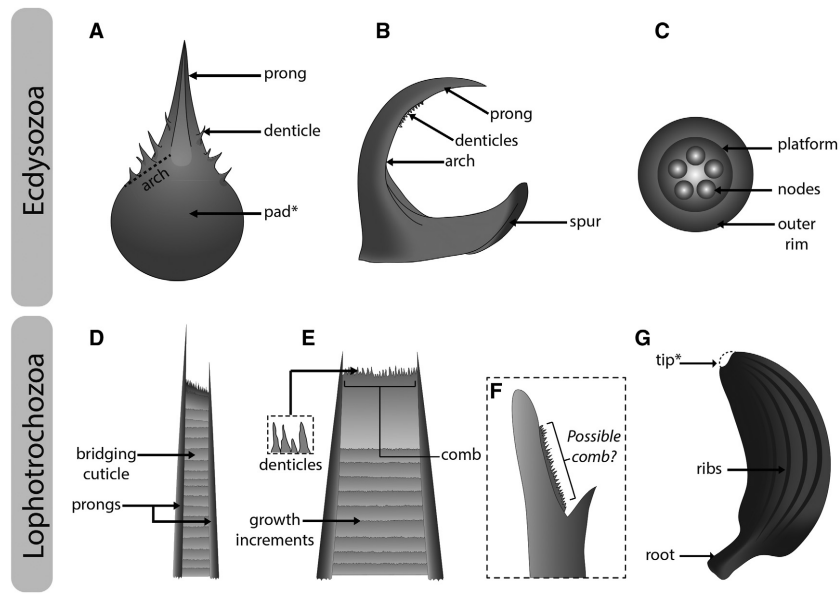
FIG. 4. Schematic guide to File Haidar SCF terminology. A–B, priapulid teeth and scalids. C, palaeoscolecid plates. D–F, annelid chaetae: D, E, *Baltichaeta jormunganda* showing morphological end members; F, distal tip of *Burgessochaeta setigera* chaeta for comparison. G, wiwaxiid sclerite (ventrolateral sclerite). * indicates usually damaged or missing in recovered specimens.

symmetrical outline combined with a flattened-oval or triangular basal attachment shape that distinguishes these priapulid-type sclerites from simpler, less phylogenetically informative conical structures and from annelid scolecodonts (see discussions in Smith *et al.* 2015*b*, p. 713; Eriksson *et al.* 2016); the absence of an inner groove, strongly developed ridges (rugae), or fine parallel growth lines rules out comparisons with superficially similar machaeridian annelid plates (e.g. Adrain *et al.* 1991, figs 1, 2). In modern priapulids, spinose cuticular projections of the anterior body regions are termed 'scalids' when they occur on the introvert or trunk, whereas 'teeth' are positioned on the pharynx and point forward when everted (van der Land 1970), a distinction that is usefully applied to various fossil scalidophorans (Harvey *et al.* 2012*a*; Smith *et al.* 2015*b*). The specimens in Fig. 5A–Q are likely to be 'teeth' based on their outline shapes and prominent fringing spines, whereas scalids tend to be more elongate and are often unadorned, or have spines in rows closer to the midline, rather than marginally (Smith *et al.* 2015*b*).

The type 2 teeth described here are broadly comparable to the type B teeth in *Ottoia prolifica* (cf. Smith *et al.* 2015*b*, fig. 3) unlike the more elongate outlines of the type 1 and type 3 specimens. Even so, the prong is substantially less clearly differentiated from the supporting arch than in *Ottoia*, and none of the particular morphologies in the File Haidar has been previously documented, either from BST macrofossils or among priapulid-like SCFs. Type 1 and type 3 specimens are also distinct from other known priapulid teeth, but given the consistent co-occurrence of all three tooth types in our samples, as well as the tooth zonation patterns known from pharyngeal apparatuses of extant and articulated macrofossil priapulids (cf. Schmidt-Rhaesa 2013, fig. 4.1.8 A; Smith *et al.* 2015*b*), the File Haidar teeth are likely to be of a conspecific origin. At the same time, we consider the File Haidar tooth morphologies sufficiently distinct from those of any previously described priapulid to warrant the establishment of a new taxon, *Baltiscalida njorda* gen. et. sp. nov. (see Systematic Palaeontology below).

The File Haidar samples that preserve priapulid teeth also yield recurved hooks with a pronounced 'spur' (Figs 4B, 6). Broadly comparable forms have been reported from a number of SCF assemblages from Canada and South China (Butterfield 2008; Butterfield & Harvey 2012; Harvey *et al.* 2012*a*; Smith *et al.* 2015*b*), though these latter occurrences are typically distinguished by serially arranged denticles or fine projections along the inner curve of the hook (see Butterfield 2008, fig. 6); such elaboration is absent from all but one of the File Haidar examples (Fig. 6X). Because these hook-like SCFs consistently co-occur in samples with types 1, 2 and 3 priapulid teeth, and exhibit a morphological range consistent with the variation seen within individual fossil worms (cf. Smith *et al.* 2015*b*), we interpret them as scalid elements conspecific with *Baltiscalida njorda* gen. et. sp. nov. (see Systematic Palaeontology below).

Palaeoscolecids. Small (~40–100 μm diameter) discoidal elements occur locally in the Viklau Member of the GB-1 core (Fig. 5R–V). These plate-like SCFs have a thin outer rim, and a darker, thicker central region that bears between three and five protuberances or 'nodes'. Mineralized (phosphatic) plates of this size and form are
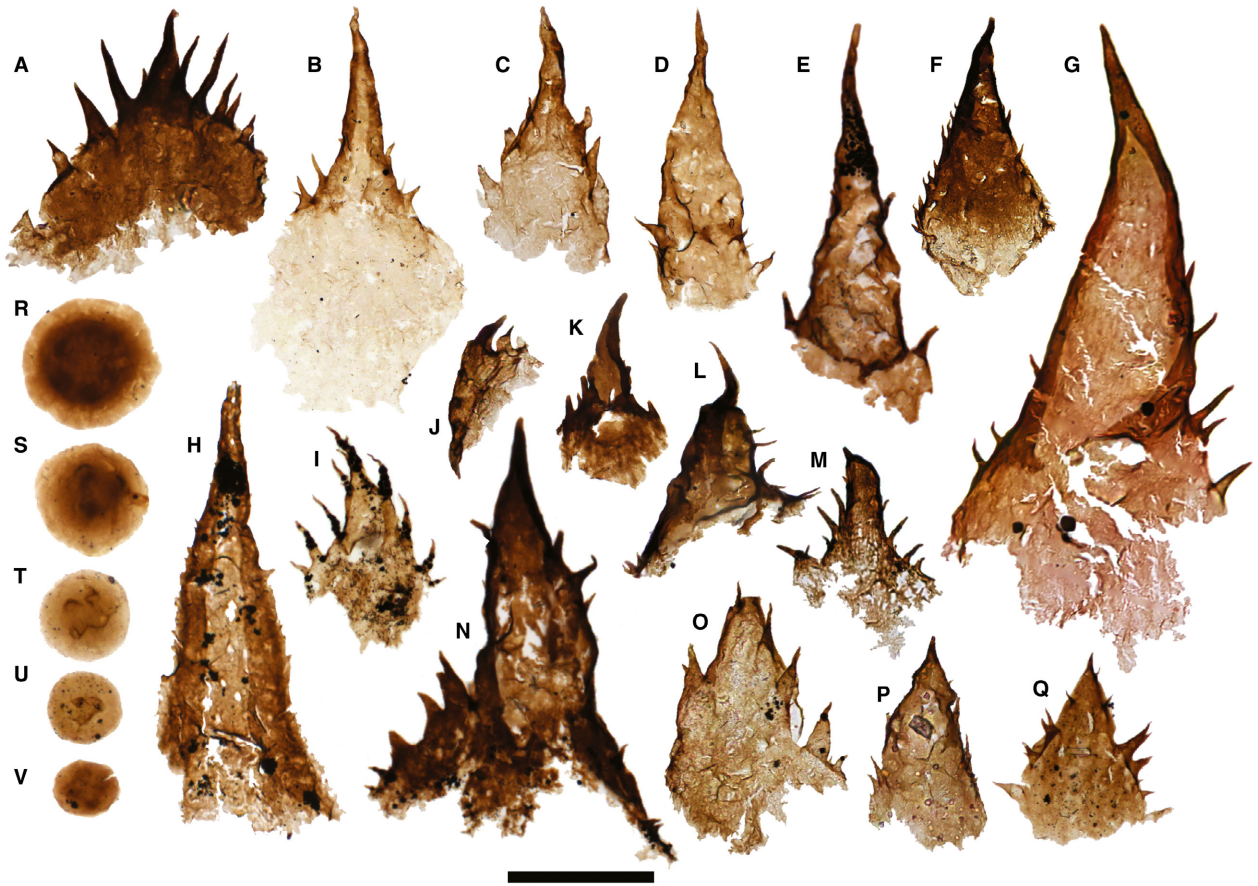
FIG. 5. Priapulid teeth (A–Q) and palaeoscolecid plates (R–V) recovered from the Viklau and När Shale Members of the File Haidar Formation. A, type 2 tooth. B, type 3 tooth, holotype of *Baltiscalida njorda* gen. et sp. nov (England-finder co-ordinates; N.50-3). C–E, type 3 teeth. F, type 1 tooth. G, large type 3 tooth. H, type 1 tooth. I, type 2 tooth. J–Q, type 3 teeth, smaller forms displaying an intermediate morphology between types 2 and 3. R–V, *Hadimopanella*. All slide numbers have the prefix NRM PZ X: A, C, P, 6150; B, F, 6152; D, K, 6156; E, 6184; G, 6176; H, 6166; I, N, 6190; J, 6148; L, 6175; M, 6185; O, 6160; Q, 6188; R, 6219; S, 6214; T–V, 6216. Sample depths from Gr-1 core: A, C, J, P, 648.94 m; B, D, F, K, 648.99 m; H, O, 651.07 m; E, I, M, N, Q, 651.00 m; G, L, 651.64 m; R, 563.60 m; S, 647.75 m; T–V, 565.80 m. Scale bar represents 100 μm.

conventionally assigned to the form-genus *Hadimopanella* which occurs widely in Cambrian assemblages of SSFs. Though originally described from isolated sclerites, *Hadimopanella*-type plates are now known to have adorned the surface of palaeoscolecids, an extinct group of early Palaeozoic worms with an annulated armoured trunk, a retractile introvert and tail hooks (Hinz *et al.* 1990), now recognized as stem-priapulids (Harvey *et al.* 2010; Wills *et al.* 2012). Because the morphology and distribution of *Hadimopanella*-type plates varies substantially within individuals (e.g. Ivantsov & Wrona 2004; Topper *et al.* 2010; Streng *et al.* 2016), isolated plates cannot usually be used to identify a particular taxon (see discussions in García-Bellido *et al.* 2013; Smith 2015).

Along with a preliminary report from the Furongian of western Canada (Butterfield & Harvey 2012), the identification of *Hadimopanella*-type sclerites from siliciclastic sediments of the File Haidar Formation substantially expands the known biogeographical and taphonomical ranges of a prominent group of early Palaeozoic worms. Both occurrences are most parsimoniously interpreted as the taphonomically demineralized remains of an originally phosphatic form, though it is possible that they represent a distinct non-biomineralizing habit (see Butterfield & Nicholas 1996; Harvey 2010).

Cuticular 'spines'. Alongside the distinctively scalidophoran-type teeth, hooks and cuticular plates, the File Haidar assemblage preserves a diversity of more simple coniform and spinose SCFs. The most common of these are stout, conical spines with a flared, elliptical to circular base (Figs 3, 7A–H, N–R). Other forms include thicker-walled spines (presumably reflecting a more heavily sclerotized composition in life) (Fig. 7S–U), and broader,
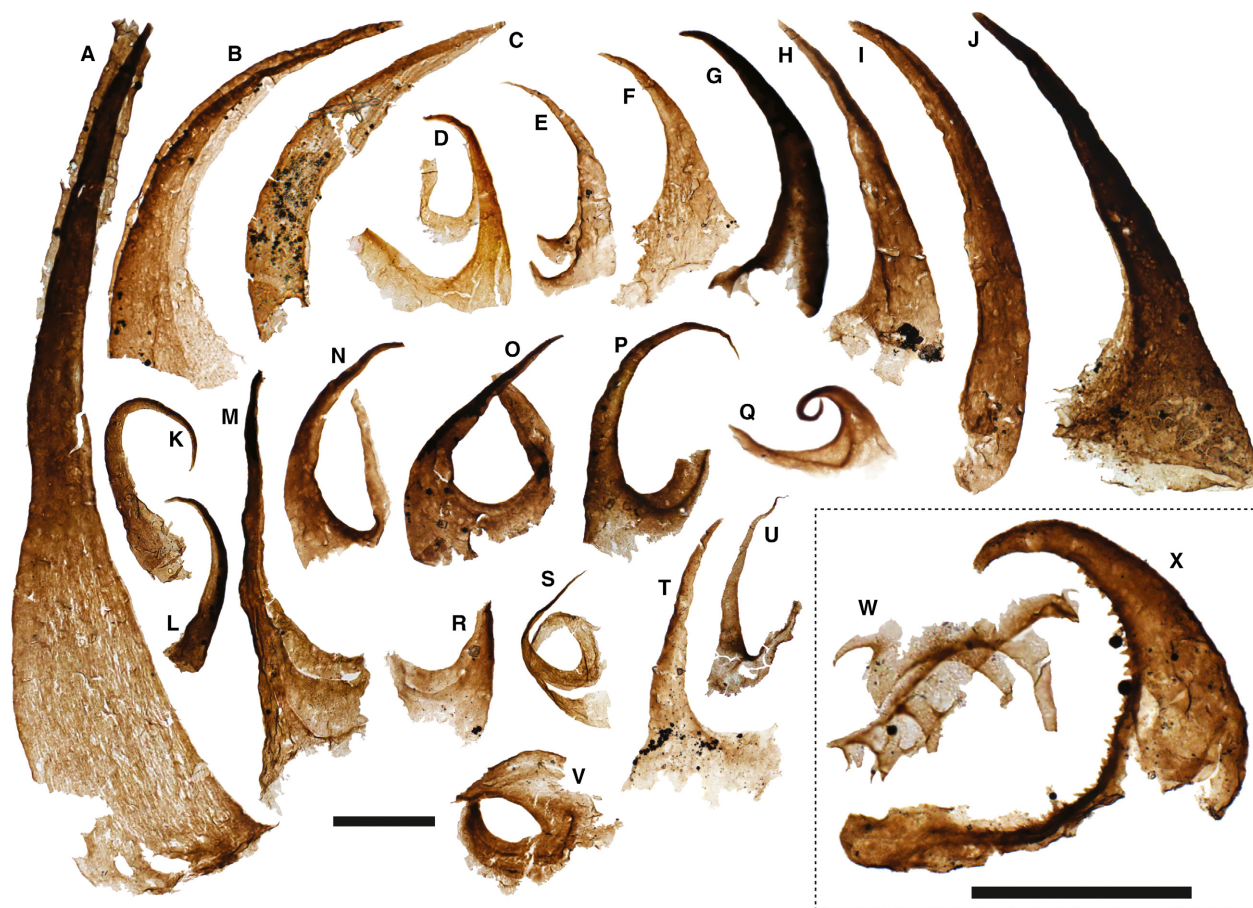
FIG. 6. Scalids representing a mixture of tail and introvert hooks derived from stem priapulids. A–V, variety of scalids lacking any evident denticles; distal curling of some specimens (e.g. Q) is probably a taphonomic feature. W, cluster of scalids with extended portion of cuticle. X, probable introvert hook bearing short denticles along the arch. All slide numbers have the prefix NRM PZ X: A, 6197; B, 6169; C, 6234; D, 6238; E, F, 6154; G, 6188; H, R, 6155; I, N, 6156; J, L, S, 6192; K, 6152; M, 6193; O, T, 6153; P, 6177; Q, V, 6221; U, 6200; W, 6149; X, 6157. Sample depths from FH-1 core: D, 479.00 m; C, 479.05 m. Sample depths from Gr-1 core: A, J, L, M, S, 651.10 m; B, 651.59 m; E, F, H, I, K, N, O, R, T, X, 648.99 m; G, 651.00 m; P, 652.23 m; Q, V, 646.25 m; U, 653.00 m; W, 648.94 m. Both scale bars represent 100 μm.

often much larger (up to 600 μm) coniform specimens with a densely perforated construction (Fig. 7I–M). Both of these latter forms are represented by occasional specimens with reticulate or polygonal basal extensions (Fig. 7K–L, S, U), presumably the remains of a contiguous external cuticle.

A significant subset of the shorter, thinner-walled File Haidar spines (Fig. 7A–H, N–R) are indistinguishable from microfossils that have been assigned to the 'acritarch' form-taxon *Ceratophyton* (Kiryanov 1979 in Volkova *et al.* 1979; Hagenfeldt 1989, 1994; Wright *et al.* 1993; Konzalová 1995; Jachowicz & Moryc 1995; Zang *et al.* 2007; Palacios *et al.* 2011). Despite this implied protistan-grade affiliation, however, there is a strong case for recognizing such SCFs as metazoan (Steiner & Fatka 1996; Moczydłowska 2008; Agić *et al.* 2016), and, more

specifically, scalidophoran in origin (Butterfield & Harvey 2012; Smith *et al.* 2015b). Specimens with ovoid bases and the long axis of the cone oblique to the basal attachment, for example, or a polygonal micro-ornamentation of the basal cuticle, share these features with more complex and definitively priapulid-like scalids and teeth (cf. Smith *et al.* 2015b). Moreover, several of the File Haidar '*Ceratophyton*' exhibit basal extensions suggesting they were once attached to a larger cuticular sheet (e.g. Fig. 7C, N), and a few specimens are preserved in articulation with other spines (Fig. 7D). Indeed, many of the spinose SCFs in the File Haidar could represent simple conical priapulid-like scalids of the sort borne on the embryonic/juvenile Cambrian scalidophorans *Markuelia* and *Eopriapulites* (see Dong *et al.* 2005, fig. 2; Liu *et al.* 2014; Shao *et al.* 2016).

FIG. 7. Cuticular spines, probably derived from scalidophoran 'worms'. A–H, N–R, simple stout spines with a flared, roughly circular base ('*Ceratophyton*'-type spines); B–F, N–P, display attachment to extended sheets; D, two spines with extended basal sheets in attachment, the distal tip of the lower spine has been flattened. S–U, heavily sclerotized spines with reticulate basal architecture. I–M, perforated spines; K, L, display basal extension with reticulate structure reminiscent of scalidophoran cuticle. All slide numbers have the prefix NRM PZ X: A, C, 6194; B, D, H, U, 6184; E, 6175; F, 6186; G, 6190; I, K, S, T, 6221; J, 6193; L, 6148; M, 6153; N, 6164; O, 6204; P, 6166; Q, 6189; R, 6197. Sample depths from Gr-1 core: A, C, J, R, 651.10 m; B, D, F–H, Q, U, 651.00 m; E, 651.64 m; I, K, S, T, 646.25 m; L, 648.94 m; N, P, 651.07 m; M, 648.99 m; O, 653.00 m. Scale bar represents 100 μm.

Lophotrochozoa

The other major protostome clade, the Lophotrochozoa, includes a wide range of palaeontologically important groups, including molluscs, annelids, brachiopods and bryozoans. Various lophotrochozoans possess a non-mineralizing but potentially preservable integument, although inherently recalcitrant components are typically limited to mouthparts and preferentially tanned chaetae (Butterfield 1990*a*). Chaetae (or chaetal homologues) are found among a disparate range of lophotrochozoan clades including annelids, brachiopods, and certain bryozoans and molluscs, collectively pointing to a deep lophotrochozoan symplesiomorphy (Butterfield 2006, 2008; Dunn *et al.* 2008; Giribet *et al.* 2009; Struck *et al.* 2011; Topper *et al.* 2015; Tilic *et al.* 2015*a*, *b*). All lophotrochozoan 'chaetae' are microvilli-secreted via basal addition,

imparting a distinctive microstructure of longitudinally arranged parallel internal channels (Schroeder 1984; Butterfield 1990*b*; Purschke 2002; Hausen 2005). In combination with external morphology, this characteristic microstructure allows a significant subset of SCFs to be assigned to this super-phylum.

Annelid chaetae. Strap-shaped SCFs with distinctively bifid tips (Fig. 8) are particularly common in parts of the Viklau and Här Shale Members (GB-1 and FH-1 cores; Fig. 3). Most occur as isolated shafts but one semi-articulated specimen is represented by five constituent elements (Fig. 8B, Z). Individual specimens are ~35–210 μm wide with a maximum (incomplete) length in excess of a millimetre. Preserved tips consist of a pair of lateral prongs (thickened longitudinal margins) with thinner material in between forming a comb-like series of serrations
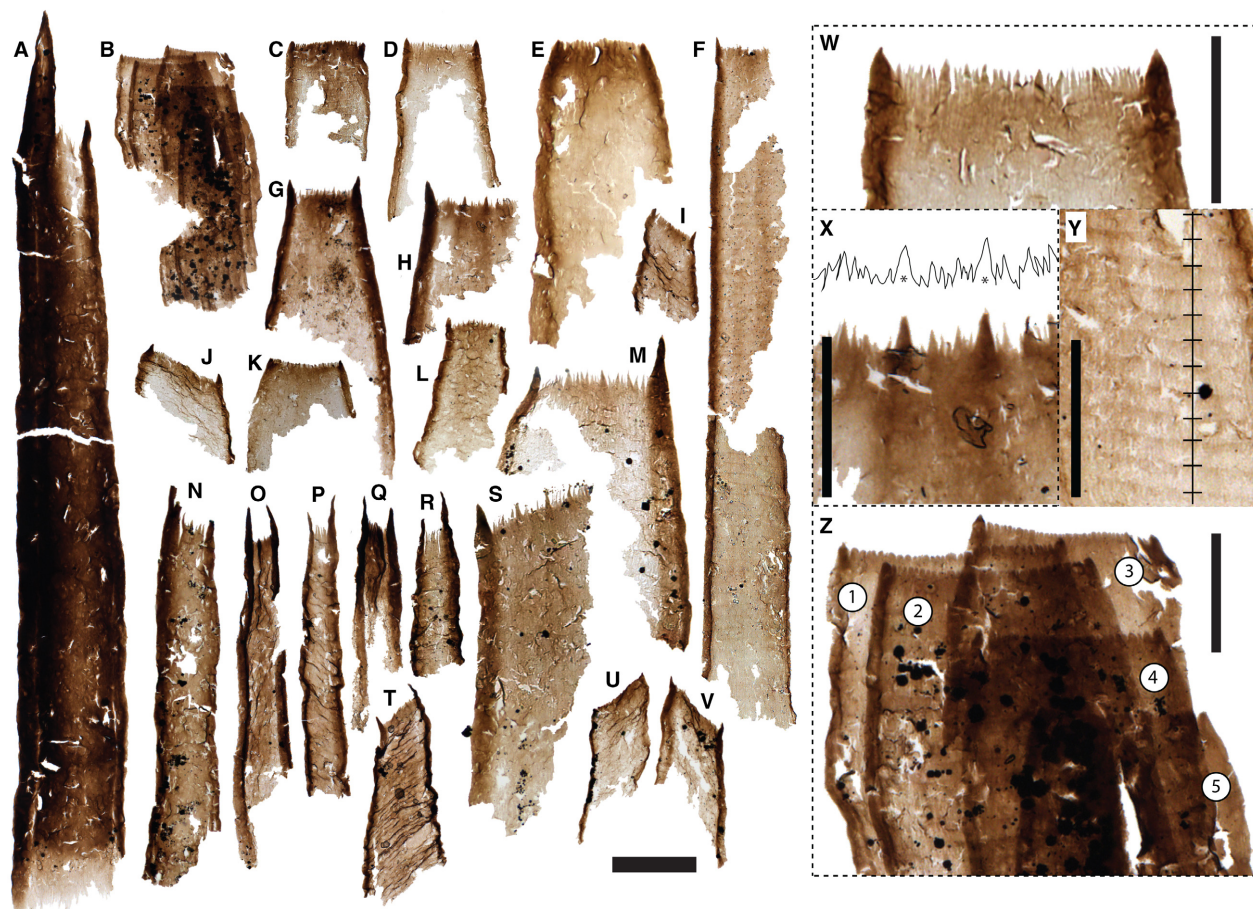
FIG. 8. Chaetae of *Baltichaeta jormunganda* gen. et sp. nov. A, holotype specimen (England-finder co-ordinates; L.49-4). B, cluster of five chaetae of the squatter morphology. W, close-up of D, showing brush-tip. X, close-up of H, showing serrations of brush-tip, including two prominent serrations marked * in corresponding line-drawing. Y, equally spaced increments developed inside chaetae. Z, close-up of clustered specimen B, derived from a partially preserved chaetiger, individual chaetae marked 1–5. All slide numbers have the prefix NRM PZ X: A, O, Y, 6154; B, P, Z, 6156; C, 6152; D, W, 6197; E, 6191; F, 6153; G, L, U, V, 6190; H, I, T, X, 6155; J, R, 6193; K, 6192; M, 6176; N, S, 6198; Q, 6157. Sample depths from Gr-1 core: A–C, F, H, I, O–Q, T, X, Y, Z, 648.99 m; D, E, J, K, R, W, 651.10 m; G, L, U, V, 651.00 m; N, S, 651.50 m; M, 651.64 m. Scale bars represent: 100 μm (A–V); 50 μm (W–Z).

(Figs 4D–E, 8W). The prongs always extend beyond the intervening serrations, though they vary considerably in size both within and between individual specimens. Individual serrations of the comb either taper to a point (e.g. Fig. 8X) or are somewhat rounded (e.g. Fig. 8Z), the latter type typical of specimens with more symmetrical termini and shorter serrations of consistent dimensions. As a population, the distal morphology varies along a continuum between two co-occurring end-members, one in which asymmetrical prongs project well beyond the comb tip (e.g. Fig. 8A), and the other with proportionately broader, shorter prongs of approximately equal length (e.g. Fig. 8B–E); the latter form has substantially wider combs and often exhibits two hyper-developed serrations that divide the comb approximately into thirds (Fig. 8X). Other features of these strap-shaped fossils include a

pattern of regularly spaced transverse ridges with a ~5–12 μm interval (Fig. 8Y), and, in well-preserved specimens, an internal microstructure of densely packed, <1 μm non-overlapping striations (Fig. 8W–Y) directly comparable to that of microvilli-secreted chaetal structures.

The combination of microvilli-like microstructure, complex tip morphology and bundled occurrence seen in these SCFs is directly comparable to that of annelid chaetae (cf. Hausen 2005; Merz & Woodin 2006; Tilic *et al.* 2015*a*). In particular, close morphological comparisons can be made with the 'brush-chaetae' of certain 'polychaete' annelids (Mettam 1971, 1984; Roy 1974; Knight-Jones 1981; Rouse & Pleijel 2001). The characteristically complex-tipped chaetae of annelids, particularly marine polychaetes, contrast with the simple spines or rods

secreted by other groups, for example brachiopod setae or bryozoan teeth (cf. Gordon 1975; Zhang *et al.* 2007; Zhang & Holmer 2013; Topper *et al.* 2015). Additional support for an annelidan affinity comes from the cluster of five superimposed elements, which we interpret as a fragmentary portion of a single polychaete chaetiger – a fan of chaetae borne on the lateral margins of a body segment (Fig. 8B, Z).

The chaetae of modern annelids exhibit an enormous diversity of form, which at the broadest scale fall into two categories: simple or compound, with the latter characterized by an internally jointed articulation and/or dentate terminal hooks. Like all other known Cambrian annelid chaetae (see Parry *et al.* 2014, 2016), the File Haidar specimens are simple; the transverse ridges (Fig. 8Y) in the File Haidar specimens are likely to be growth ridges acquired as the plastic chaetal material hardened incrementally within the chaetoblast (cf. O'Clair & Cloney 1974), rather than differentiated articulations. Among modern annelid groups, chaetal morphologies that are at least broadly similar to those of the File Haidar SCFs are found among the Eunicidae (Rouse & Pleijel 2001), but also some enigmatic terrestrial non-oligochaete annelids (cf. Pižl & Chalupský 1984; Rota & Lupetti 1996; Dózsa-Farkas & Schlaghamerský 2013).

The closest comparison, however, is found in the Burgess Shale 'polychaete' *Burgessochaeta setigera* (Conway Morris 1979*a*, *b*), whose simple strap-shaped chaetae are similarly distinguished by a bifid tip with asymmetric prongs (Fig. 4F; see Eibye-Jacobsen 2004). Even so, the asymmetry of *Burgessochaeta* chaetae is conspicuously more pronounced than in the File Haidar forms, with the lateral prongs diverging only distally to yield a distinctively splayed 'Y'-shape tip (the 'lyrate-chaetae' condition; Rouse & Pleijel 2001); by contrast, the lateral/marginal prongs of the File Haidar specimens are uniformly parallel, leaving space for the expanded brush-like comb (the 'brush-chaetae' condition; Rouse & Pleijel 2001). Bedding-plane macrofossils do not permit microstructural analysis on a par with SCFs, but if any analogous fine brush is present in *Burgessochaeta*, it would necessarily be confined to the larger inclined prong as in some modern lyrate-chaetae (Fig. 4F). Nonetheless, the brush-tipped Baltic SCFs are sufficiently distinct to be recognized as a new genus of *Burgessochaeta*-like annelid, *Baltichaeta jormungandr* gen. et. sp. nov. (see Systematic Palaeontology below).

Wiwaxiid sclerites. Isolated sclerites of *Wiwaxia* were recovered from the När Sandstone Member of the Böda Hamn core (Figs 3, 9AC) and from the early–middle Cambrian boundary interval at the base of the Borgholm Formation in the Bårstad-2 core (Figs 3, 9Z–AB). The majority of these specimens are asymmetrical, originating from the 'ventrolateral' region of the compound dorsal scleritome. One of the Boda Hamn (File Haidar) specimens (Fig. 9AC) is close to a millimetre long (0.8 mm), the largest *Wiwaxia* sclerite yet recovered as an SCF, roughly corresponding to a whole-organism body length of ~3 cm (see Smith 2014). This same sclerite is further characterized by its blunt termination and associated collar-like thickening, suggesting a biologically mediated loss of the tip.

Most of the recovered *Wiwaxia* sclerites have prominently developed ribs and in this respect are indistinguishable from the Burgess Shale type species *Wiwaxia corrugata*. The single specimen with a thickened distal collar appears to be qualitatively different from all other occurrences, but will require a larger sample size to legitimize separate species recognition. Other named species of *Wiwaxia* have been established on the basis of distinctive rib thickness, sclerite outline, root morphology and/or surface ornament (Smith *et al.* 2015*a*). Given their conspicuously chaeta-like habit and microvillar microstructure, all wiwaxiid sclerites can be confidently placed in total-group Lophotrochozoa, despite on-going debate regarding their phylum-level status (Butterfield 1990*b*, 2006; Smith 2014; Zhang *et al.* 2015*b*; Smith *et al.* 2015*a*).

Unresolved metazoans

Beyond the recognizable ecdysozoan and lophotrochozoan elements, the File Haidar SCF assemblage includes a further range of forms that are clearly bilaterian, but are otherwise lacking taxonomically diagnostic features. The most distinctive of these are sporadically distributed multidenticulate structures represented by series of progressively larger conical-elements, usually connected via a basal membrane (Fig. 10). Such architecture is comparable to the denticulate mouthparts of various bilaterians, including, but not limited to, the jaws of eunicid and phyllodocid polychaete annelids (fossilized as 'scolecodonts'; see Eriksson et al. 2016, fig. 3), molluscan radulae (Butterfield 2008), the feeding apparatus of fossil *Wiwaxia/Odontogriphus* (Caron *et al.* 2006) and fossil conodonts. Although some of the File Haidar specimens (e.g. Fig. 10A) are comparable to 'possible wiwaxiid mouthparts' identified in a Cambrian SCF assemblage from Columbia (see Smith *et al.* 2015*a*, fig. 3), it is notable that these do not occur in the same samples yielding *Wiwaxia* sclerites here.

The File Haidar SCF assemblage also includes a range of spines and rods (Figs 3, 9A–T), which in some beds are extremely abundant (e.g. > 200 in a 50 g sample). Recurrent morphologies include elongate spinose elements (20–160 μm wide, 150–800 μm long), sometimes

FIG. 9. Wiwaxiid sclerites and taxonomically uncertain metazoan-derived spines and cuticle. A–T, spinose, rod-shaped and unguiliform metazoan elements. U, fragment of unknown metazoan ornament. V, broadly resembles trilobite cuticle, possibly from the anterior part of librigenae (see outline of librigenae in the pouch-brooding trilobite *Strenuaeva inflata* from the Cambrian Series 2 of Sweden; Cederström *et al.* 2011, fig. 9). W–Y, fragmentary portions of perforated and 'pock marked' metazoan cuticle, resembles similar cuticular fragments from the early Cambrian Mahto Formation of Alberta, Canada (see Butterfield 2008, fig. 9); thick cuticle Y, possesses broad (~70 μm diameter) circular to hexagonal indentations. Z–AC, wiwaxiid sclerites. All slide numbers have the prefix NRM PZ X: A–C, F, G, S, T, 6240; D–R, 6239; U, 6166; V, 6226; W, Y, 6252; X, 6253; Z–AB, 6250; AC, 6228. Sample depths from BH-1 core: V, 112.4 m; AC, 118.20 m. Sample depths from Bå-2 core: A–T, 49.98 m; W, Y, 70.90 m; X, 70.25 m; Z, AA, AB, 50.50 m. Sample depths from Gr-1 core: U, 651.07 m. Scale bar represents 100 μm.

preserved as semi-articulated clusters (Fig. 9B, I–K, S); other associated forms have a stouter construction (Fig. 9H) or exhibit rod-like, unguiliform or 'X-shaped' morphologies (Fig. 9L–O, T). A number of these SCFs are reminiscent of various SSF taxa (cf. Pyle *et al.* 2006, fig. 6), in particular the clustered spines which resemble demineralized versions of the 'protoconodont' element *Protohertzina* (Missarzhevsky 1973).

Non-metazoan problematica

There is nothing specifically metazoan about SCFs of course, the only qualifying criteria being acid resistance and sufficiently large dimensions to be seen and hand-picked (> 40–50 μm). It is certainly notable that a majority of the File Haidar SCFs are metazoan, but there is a conspicuous subset that are demonstrably not. We include these non-metazoan SCFs here because they represent a further range of forms that have been systematically overlooked/destroyed by conventional techniques, and for what they contribute to the larger scale palaeo-environmental and taphonomic patterns. Apart from animals, carbonaceous fossils of early Cambrian age might conceivably include fungi, protistan-grade eukaryotes and prokaryotes, though these can often be difficult to distinguish solely on the basis of fossil morphology.

Despite their problematic affinities, some of the non-metazoan SCFs in the File Haidar assemblage are sufficiently distinctive to be recognized as biologically

FIG. 10. Multi-denticulate metazoan SCFs. A–D, from File Haidar Formation. E, similar multi-denticulate SCF from the early Cambrian (Stage 3) Lükati Formation, Estonia, for comparison. All slide numbers have the prefix NRM PZ X: A, 6238; B, 6247; C, 6248; D, 6249. Sample depth from FH-1 core: A, 479.00 m. Sample depth from Bå-2 core: B–D, 70.23 m. Scale bar represents 100 μm.
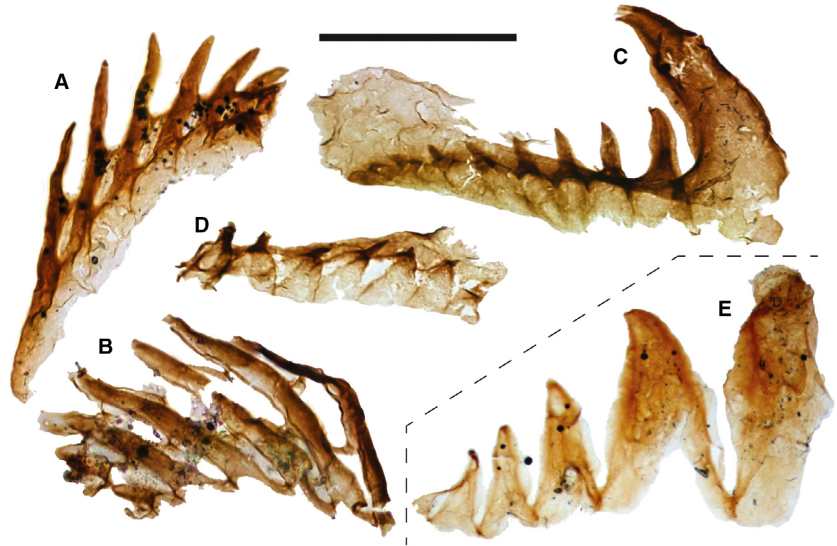
meaningful form-taxa. Among the most common are filamentous fossils recovered from the När Shale and Viklau members (Figs 3, 11A–M). Individual specimens typically comprise a thick (~70–130 μm wide) sinuous main 'filament,' from which a variety of smaller filaments emerge and may themselves branch further (e.g. Fig. 11D). Where preserved, the tips of the main filament and sub-branches taper to a blunt terminus (Fig. 11C). The fossils are further distinguished by the presence of multiple spheroidal to flask-shaped vesicles, anatomically connected to the main filament (Fig. 11E–K, M). Carbonaceous fossils of this morphology have not previously been described from the Cambrian, but a loose comparison can be drawn with certain Ediacaran-age 'vendotaenids' (Gnilovskaya *et al.* 1988). We establish a new taxon for these enigmatic organisms: *Baltinema rana* gen. et. sp. nov. (see Systematic Palaeontology below).

Notably, our processing did not recover any of the spiny/acanthomorphic acritarchs expected in early Cambrian mudstones, and previously reported from the File Haidar Formation (Hagenfeldt 1989, 1994), presumably because they fall below the size range detectable using our hand-picking technique. The only vesicular acritarchs recovered in our samples were clusters of smooth-walled forms (Fig. 11N–S) which are locally abundant throughout the File Haidar Formation, but become concentrated around horizons yielding metazoan SCFs (Fig. 3). Individual clusters often exceed 100 μm (rarely > 500 μm) in maximum dimension. The absence of consistent cell counts or observable inter-cell connections argues against a green-algal-type coenobial habit (cf. Butterfield 2009) and limits taxonomic resolution; comparable clusters from Proterozoic and Palaeozoic assemblages are usually referred to as *Synsphaeridium* (e.g. Riedman *et al.* 2014, fig. 2) but remain of unknown biological affinity.

DISCUSSION

The array of SCFs described here presents a fundamentally new picture of early Cambrian palaeobiology in the File Haidar Formation and, by extension, Baltica. Although a non-biomineralizing fauna has long been apparent in the File Haidar from its trace fossils (e.g. Jensen 1997), there is a conspicuously limited record of associated body fossils, with the rare though notable records of the arthropod *Paleomerus* and lobopodian *Xenusion* (Størmer 1956; Bergström 1971; Krumbiegel *et al.* 1980; Dzik & Krumbiegel 1989). Our data provide the first direct record of priapulids, annelids and wiwaxiids in Baltica, along with a range of other metazoans and non-metazoan forms. At the same time, the broad lithostratigraphic and geographic coverage of our dataset provides a novel view of the local to regional controls on fossil distribution (Figs 1, 3).

Stratigraphical and geographical occurrence

All stratigraphical members of the File Haidar Formation yielded SCFs, but with significant internal partitioning. Wiwaxiid and protoconodont remains were only found in samples from proximal environments (the Lingulid Sandstone and När Shale of the Bå-2 and BH-1 cores; Fig. 3), while samples bearing annelid and priapulid remains were confined to outboard settings and tended to co-occur with concentrations of *Baltinema rana* gen. et sp. nov.
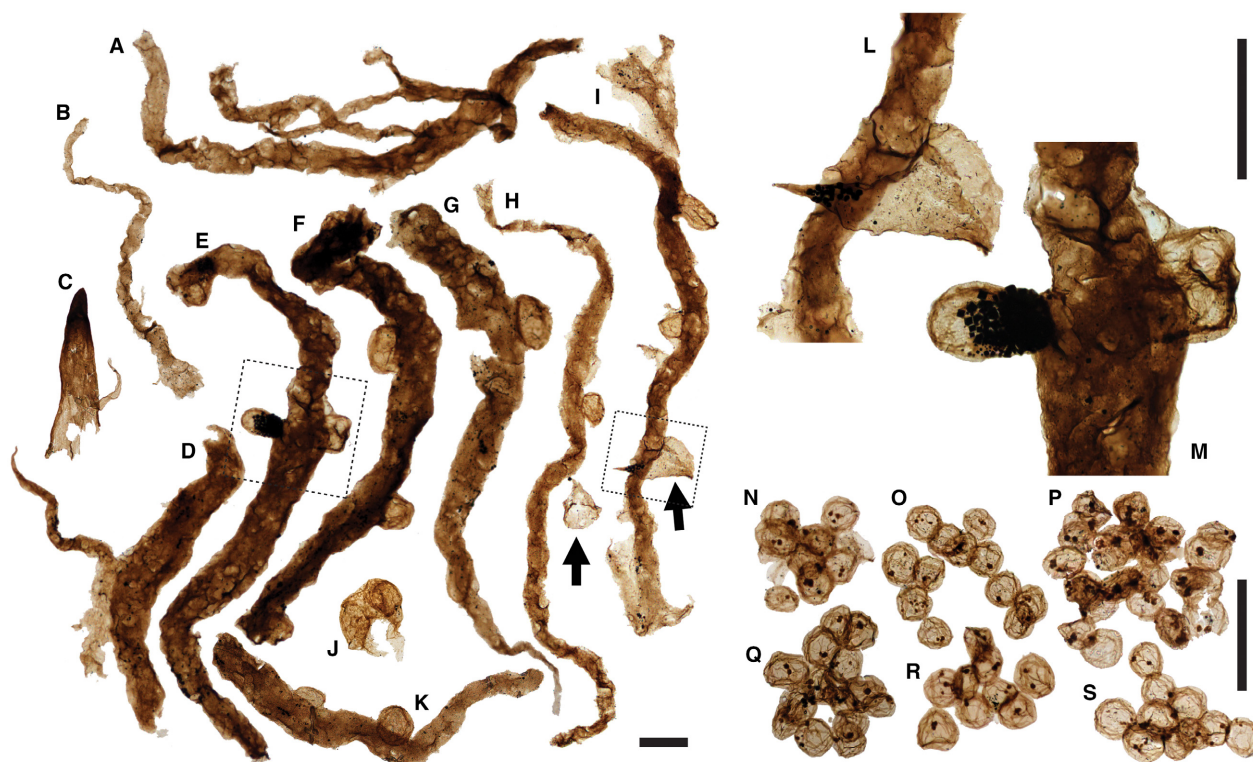
FIG. 11. Problematica. A–M, *Baltinema rana* gen. et sp. nov; E, holotype specimen (England-finder co-ordinates; H.36-4); arrows indicate '*Ceratophyton*'-type scalidophoran spines fortuitously superimposed on filaments; L, close-up of spine from dashed box in specimen I; M, close-up of vesicular outgrowths from dashed box in holotype specimen E. N–S, clusters of smooth-walled vesicular acritarchs. All slide numbers have the prefix NRM PZ X: A–B, D–G, J, M, 6204; C, 6200; H–I, L, P, 6203; K, 6201; N, R, 6194; O, 6193; Q, 6192; S, 6197. Sample depths from Gr-1 core: A–M, P, 653.00 m; N, O, Q, R, S, 651.10 m. All scale bars represent 100 μm.

and acritarch clusters (the Viklau and Närr Shale of the FH-1 and Gr-1 cores; Fig. 3). Potentially, these patterns reflect regional palaeobathymetric controls on distribution (see Nielsen & Schovsbo 2011). No SCFs were recovered from coarser sandstone units, but even within silt- and mud-dominated facies, productive samples were limited to stratigraphically discrete horizons separated by extended intervals noticeably devoid of fossils (Fig. 3). One of the most recurrent features shared by fossil-bearing samples is the localized abundance of cross-cutting and vertical burrows, often accompanied by the presence of sand-sized glauconite (typically in mudstone-hosted lenses), phosphorite clasts, and syneresis or dewatering cracks filled with coarser sand (Figs 3, 12; see Nielsen & Schovsbo 2011). Termed *Kråksten* or 'crow-rock' in the regional literature (e.g. Hadding 1924), these conspicuously bioturbated and glauconitic sediments have been interpreted as sub-sequence drowning surfaces (cf. Posamentier & Allen 1999), where local sediment supply is outstripped by sea level rise (Nielsen & Schovsbo 2011; Álvaro *et al.* 2016). Time-averaging during such episodes

of sediment-starvation could conceivably account for the increased bioturbation as successive communities of burrowers colonized the same sediment tier (Bromley 1996; McIlroy 2004).

The occurrence of organic-walled fossils in bioturbated sediments is unexpected, particularly in light of the strong negative correlation between Burgess Shale-type preservation and bioturbation (Orr *et al.* 2003). Recognizable ichnogenera associated with SCF-bearing horizons in the File Haidar Formation cores include *Teichichnus*, *Treptichnus* and *Gyrolithes*. Insofar as at least some treptichnid ichnofossils may be the traces of priapulid-like worms (Orłowski & Żylińska 1996; Dzik 2005, 2007), and Cambrian priapulids are known to be generalist predators/scavengers (Huang *et al.* 2004; Vannier 2012), it is notable that all of the priapulid sclerites and annelid chaetae in this study were recovered from burrowed sediments (see Fig. 3). Unlike their macrofossil counterparts, SCFs are relatively immune to physical disturbance, moderate levels of time averaging and even gut-passage (e.g. Vannier 2012). As such, the enhanced

FIG. 12. Microfacies typical of fossiliferous/SCF-productive horizons. A–C, core material from Gr-1 core: A, 645.65–645.70 m, containing syneresis cracks and *Teichichnus* burrows; B–C, close-ups of A, showing syneresis cracks in finely laminated mudstone (green-grey) filled with coarser sandstone (pale yellow), these have subsequently been deformed through compaction. D, plan view of bioturbated core from 479.03 m of the FH-1 core. Scale bars represent: 1 cm (A, D); 4 mm (B, C).
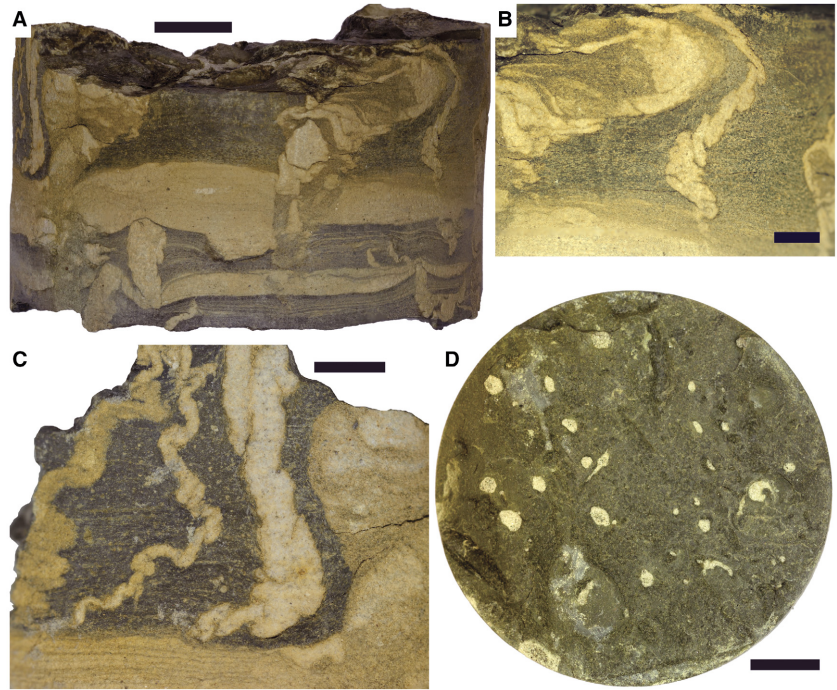
recovery of SCFs in bioturbated horizons may well derive from their localized concentration by scavenging metazoans, with or without the compounding effects of low sediment input and associated time averaging. To this extent, the distribution of SCFs is often more comparable to that of biostratinomically recalcitrant shelly fossils than to delicate articulated carcasses or moults, a factor with important implications for future studies.

Global significance

With a Cambrian palaeolatitude of 30–60° and clear separation from any other contemporaneous cratons, Baltica offers an important new view of early palaeobiogeographical partitioning. Our recovery of diverse SCFs from the File Haidar represents the first significant occurrence of non-biomineralizing 'Burgess Shale-type' metazoans from this palaeocontinent. New sclerites from Baltica confirm the presence of *Wiwaxia* on every major Cambrian craton (Fig. 13). With the addition of *Baltiscalida njorda* gen. et sp. nov., the record of Cambrian priapulids also acquires a fully global coverage (Fig. 13). In contrast to the cosmopolitan wiwaxiids and priapulids (Figs 13, 14), the chaetae of annelids have not featured in dispersed SCFs assemblages before now, despite their localized extraction from Burgess Shale macrofossils (Butterfield 1990*b*) and their demonstrable recalcitrance in actualistic taphonomic studies (Briggs & Kear 1993). Indeed, *Baltichaeta jormunganda* gen. et sp. nov. represents one of only eight

known Cambrian polychaete taxa, and the only one known from beyond palaeotropical, macroscopic BST-Lagerstätten (Figs 13, 14).

Surprisingly, the File Haidar assemblage is broadly comparable to lower palaeolatitude BST 'worm'–biotas from Laurentia and South China, which also exhibit a predominance of priapulid, palaeoscolecid, protoconodont, wiwaxiid and polychaete 'worms' (cf. Conway Morris 1989*a*, *b*; Han *et al.* 2008). At least at these coarse taxonomic levels, there appears to be little indication of palaeobiogeographical or palaeolatidudinal partitioning; in marked contrast to the pronounced endemism displayed by many contemporaneous shelly taxa (cf. Samson *et al.* 1990; Meert & Lieberman 2008). The File Haidar SCFs do, however, exhibit significant differences at lower taxonomic levels. Although priapulids and polychaetes are present, none of these is directly comparable to previously described species or genera. Both *Baltiscalida* and *Baltichaeta* could well be endemic to Baltica and/or high palaeolatidudes (cf. Smith *et al.* 2015*b*), though limited sampling leaves this open to further validation. Certainly the macrofossil record of polychaetous annelids in the Cambrian, currently known from just four biotas worldwide, is too sparse to derive a reliable biogeographic signal (Figs 13, 14). Even so, there are strong grounds for expecting inter-regional distinctions in species distributions (Meert & Lieberman 2008; Alroy 2010), and the fine level of detail provided by SCFs has the potential to illuminate such patterns (cf. Smith *et al.* 2015*b*).
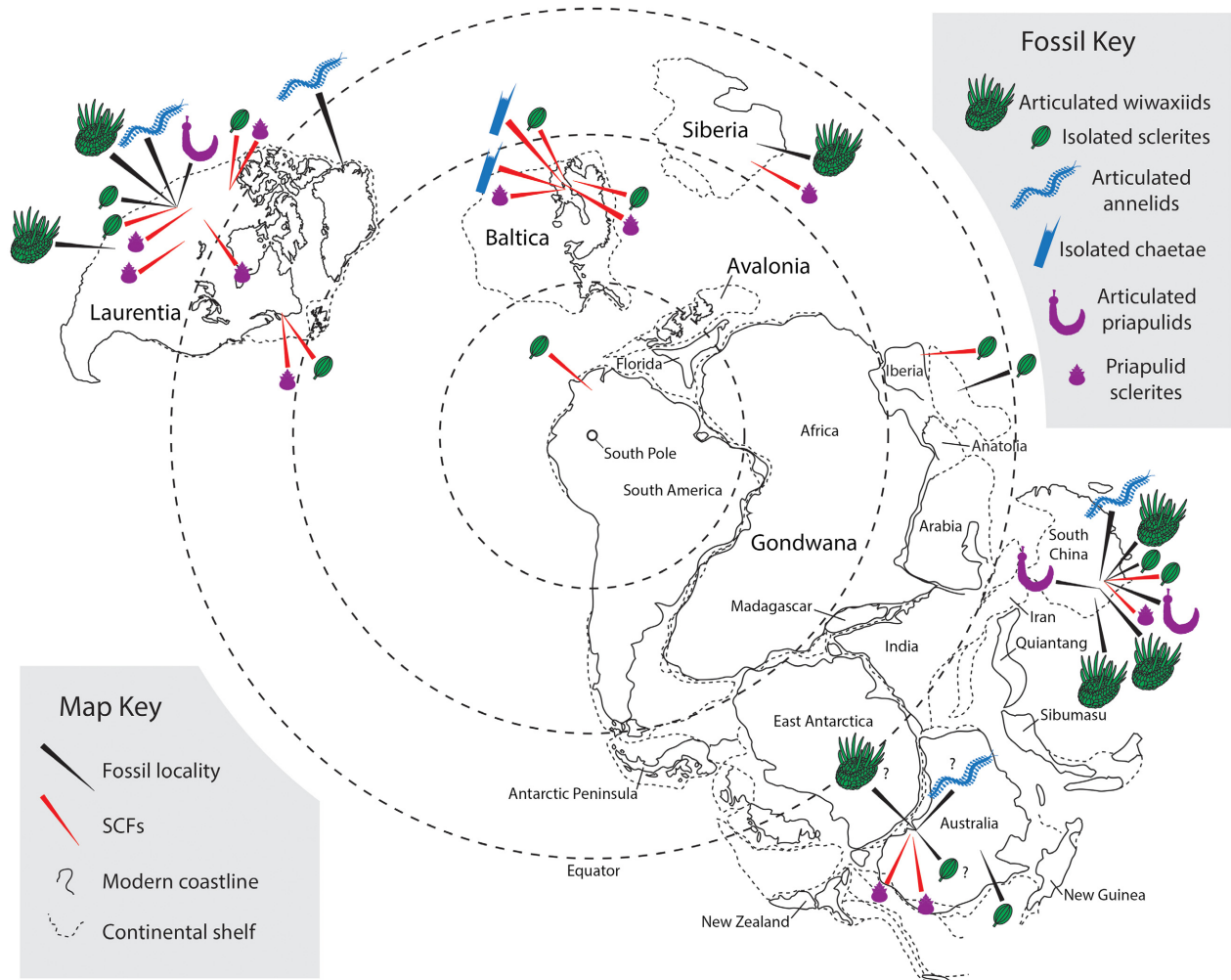
FIG. 13. Global distribution of palaeocontinents in the early Cambrian showing reported occurrences of *Wiwaxia* macrofossils and disarticulated sclerites, priapulid macrofossils and SCFs, and 'polychaete' annelid macrofossils and isolated chaetae. Palaeogeographic reconstruction after McKerrow *et al.* (1992), Kirschvink *et al.* (1997) and Torsvik & Cocks (2013). See Fig. 14 for details of occurrence data.

Despite the predominance of priapulids (including palaeoscolecids) in almost all Burgess Shale-type 'worm' biotas (Conway Morris 1979*a*, *b*; Zhang *et al.* 2006; Harvey *et al.* 2012*a*; Smith *et al.* 2015*b*) it is notable that both priapulids and polychaete annelids have been recovered together from the File Haidar sediments; indeed, *B. jormunganda* gen. et sp. nov. chaetae are locally far more abundant, and often better preserved, than the associated priapulid and wiwaxiid sclerites. Such expression rules out differential histology as a significant factor in the global expression of Cambrian polychaetes, pointing instead to their general marginalization in priapulid-dominated Cambrian oceans (Conway Morris 1979*a*, 1989*b*). At another level, however, it is clear there are fundamental differences between the 'typical' Burgess Shale-type biotas found in deeper water, low-oxygen (dysaerobic) environments, and those from

shallower more fully oxygenated facies (Butterfield & Harvey 2012). The epicratonic Mount Cap and Deadwood biotas of western Canada, for example, include a surprisingly modern diversity of crustacean and molluscan SCFs, none of which appear in contemporaneous deeper water biotas (Harvey & Butterfield 2008; Harvey *et al.* 2012*b*). Intriguingly, both the Mount Cap and Deadwood successions contain bioturbated and syneresis-cracked glauconitic sandstone horizons, directly comparable to the fossiliferous '*Kråksten*' facies in the Baltic Basin. Once again, it is too soon to draw broad conclusions, but the discovery of a new polychaete taxon in well oxygenated/bioturbated horizons of the File Haidar Formation suggests that the current record is steeply biased in favour of dysaerobic, priapulid-dominated environments conducive to the preservation of Burgess Shale-type macrofossils.
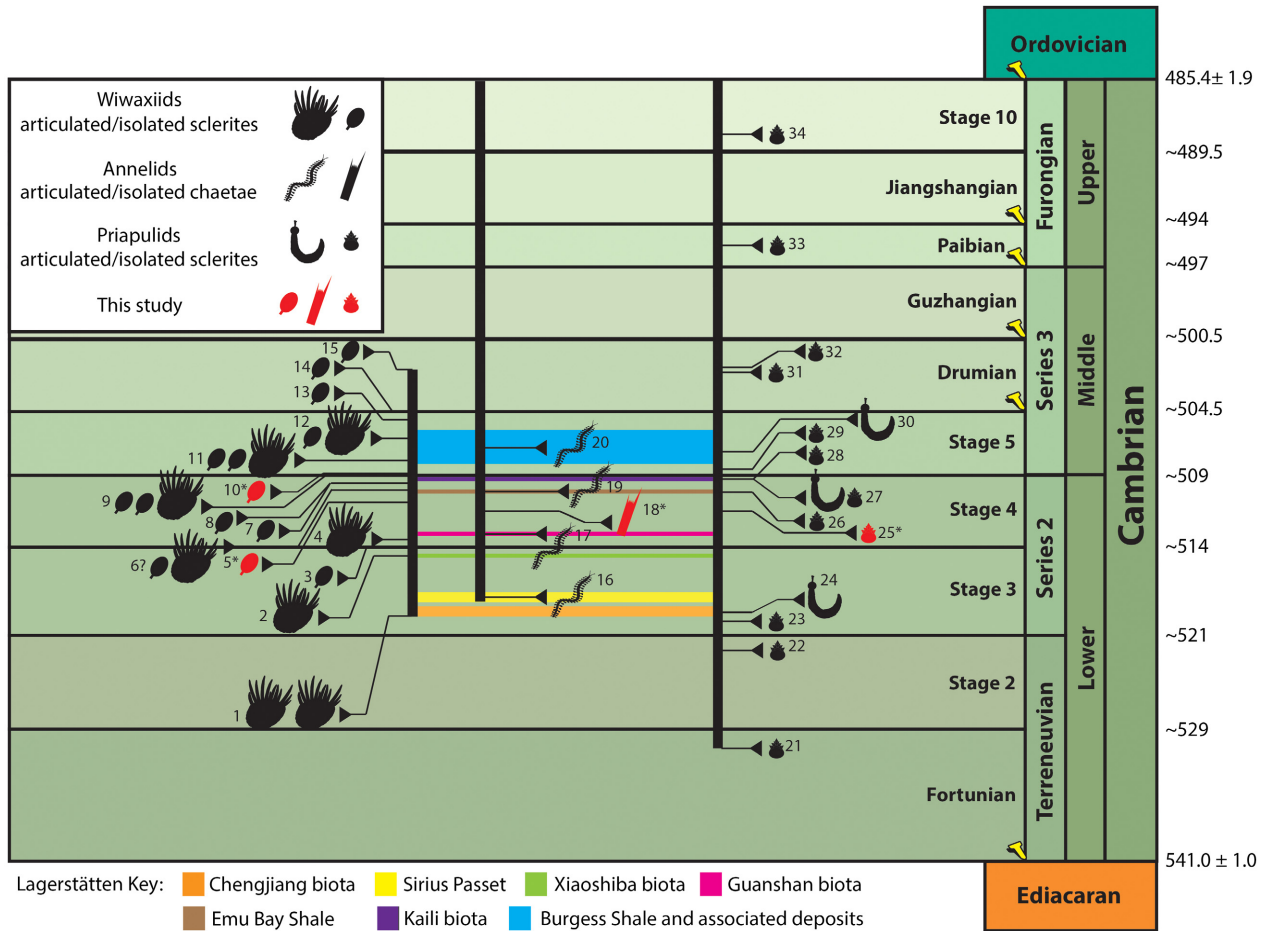
FIG. 14. Stratigraphical occurrence of wiwaxiids, 'polychaete' annelids and priapulids in the Cambrian, showing temporal distribution of those identified from the File Haidar Formation in relation to other known SCFs and bedding-plane macrofossils. Occurrence key: 1, *Wiwaxia papilio* and *Wiwaxia* sp., Chengjiang, Kunming, China (Zhao *et al.* 2015; Zhang *et al.* 2015*a, b*); 2, *Wiwaxia foliosa*, Xiaoshiba, Kunming, China (Yang *et al.* 2014); 3, Lancara Formation, northern Spain (Palacios *et al.* 2014); 4, Sinsk Shale, Siberia, Russia (Ivantsov *et al.* 2005*a, b*); 5*, File Haidar Formation, Öland, Sweden (this study); 6?, Emu Bay Shale, South Australia (C. Nedin pers. comm. *in* Porter 2004); 7, Mount Cap Formation, NWT, Canada (Harvey & Butterfield 2011); 8, Forteau Formation, Newfoundland, Canada (Butterfield & Harvey 2012); 9, *Wiwaxia taijiangensis*, Kaili, Guizhou, China (Zhao *et al.* 1994); 10*, File Haidar – Borgholm Formation boundary, Östergotland, Sweden (this study); 11, *Wiwaxia corrugata*, Burgess Shale, British Columbia, Canada (Walcott 1911); 12, *Wiwaxia herka*, Utah, USA (Conway Morris *et al.* 2015); 13, Buchava Formation, Czech Republic (Fatka *et al.* 2011); 14, Georgina Basin, Australia (Southgate & Shergold 1991; Porter 2004); 15, Llanos Basin, Colombia (Smith *et al.* 2015*a*); 16, Sirius Passet, Greenland, two species (Parry *et al.* 2015); 17, *Guanshanchaeta felicia*, Guanshan biota, China (Liu *et al.* 2015); 18*, *Baltichaeta jormunganda*, File Haidar Formation, Sweden (this study); 19, Emu Bay Shale, South Australia (Greg Edgecombe, pers. comm. 2013 *in* Parry *et al.* 2014; figured but undescribed by Paterson *et al.* 2016); 20, Burgess Shale and associated units, British Columbia, Canada, five species plus an additional undescribed form from Marble Canyon (see Parry *et al.* 2015); 21, Kessyusa Formation, Siberia, Russia, priapulid teeth SCFs (Nagovitsin 2011); 22–24, 26–34, see Smith *et al.* 2015*b*; 25, *Baltiscalida njorda*, File Haidar Formation, Sweden (this study). Golden spike symbols indicate formally defined stage boundaries.

SYSTEMATIC PALAEONTOLOGY

We establish three new monospecific genera based on SCF material recovered from the File Haidar Formation. All specimens are permanently mounted on glass slides and are housed in the Swedish Museum of Natural History, Stockholm (NRM). Although these taxa are

established on the basis of disarticulated elements, they are sufficiently distinctive to be used, in practice, as natural biological taxa. Like *Halkieria* (Conway Morris & Peel 1990) and the conodont animal (Briggs *et al.* 1983), we expect the whole-organism morphology associated with these SCFs to be discovered in due course. Our approach reflects prevailing practices in the taxonomy of SSFs

derived from multi-element scleritomes (e.g. Skovsted & Peel 2007; Topper *et al.* 2009).

Superphylum ECDYSOZOA Aguinaldo *et al.*, 1997
CYCLONEURALIA
SCALIDOPHORA
Total group of Phylum PRIAPULIDA Delage & Hérouard, 1897
Incertae familiae

Genus BALTISCALIDA nov.

LSID. urn:lsid:zoobank.org:act:DE398F3F-38A7-4D54-B7AA-70666CDB590E

Derivation of name. With reference to the Baltic Basin.

Type species. Baltiscalida njorda sp. nov. by monotypy.

Diagnosis. As for type species.

Baltiscalida njorda sp. nov.
Figure 5B–E, G

LSID. urn:lsid:zoobank.org:act:D586CA6B-DD5A-413F-8D33-E9B8157EB280

Derivation of name. After the sea deity, Njord, in Norse mythology.

Holotype. NRM PZ X 6152, Fig. 5B; slide 6152, England-finder coordinates N.50-3. 4 designated paratypes: Fig. 5C–E, G (NRM PZ X 6150, 6156, 6176, 6184).

Diagnosis. A priapulid or priapulid-like scalidophoran with pharyngeal teeth that have an acute arch tapering to a central prong which is aligned with the angle of the arch; at least three tooth morphotypes present. In all teeth the arch is denticulate, with hollow distally-projecting stout marginal denticles which taper to a point and occasionally branch. Type 1 teeth with a narrow elongate outline and numerous short, closely-spaced denticles extending almost to the tip. Type 2 teeth with an equant outline and medium to long denticles arranged along a size gradient with the longest denticles nearest the prong. Type 3 teeth with an elongate outline and sparse denticles of moderate length with no size gradient in their distribution, and typically asymmetrically arranged with a gap between the distalmost denticles and the arch apex/prong.

Distribution. Viklau and När Shale Members of the early Cambrian (Stage 4) File Haidar Formation, Gotland, Sweden (known from Grötlingbo-1 and File Haidar-1 cores).

Remarks. The three morphotypes of isolated pharyngeal teeth of *B. njorda* gen. et sp. nov. commonly co-occur in samples and occupy a range of morphologies that is typically observed within a single species of priapulid. In addition, the three principle tooth morphotypes commonly co-occur with other tooth- and scalid-like morphologies (Figs 6, 7) which potentially belong to the same species; these other sclerites, however, lack distinctive features and are not formally included in the description. Occasionally smaller sclerites (e.g. Fig. 5M) display an intermediate morphology between types 2 and 3 teeth, probably reflecting ontogeny or variation along the introvert. The basal pad in *B. njorda* teeth is usually poorly preserved, suggesting it was comparatively labile in contrast to the heavily sclerotized spinose portions. A possible 'spur' may be developed in some specimens and is usually visible in co-occurring scalids; this is commonly adpressed to the remainder of the sclerite, however, obscuring its original morphology and orientation.

Superphylum LOPHOTROCHOZOA Halanych *et al.*, 1995
Total group of Phylum ANNELIDA Lamarck, 1809
Incertae familiae

Genus BALTICHAETA nov.

LSID. urn:lsid:zoobank.org:act:C082DEC4-7DAB-4C75-8649-23FEE6E1135B

Derivation of name. With reference to the Baltic Basin.

Type species. Baltichaeta jormunganda sp. nov. by monotypy.

Diagnosis. As for type species.

Baltichaeta jormunganda sp. nov.
Figures 8A–V

LSID. urn:lsid:zoobank.org:act:5B489254-058E-47EE-9B4A-79987E7D7596

Derivation of name. After Jormungandr, a sea serpent in Norse mythology.

Holotype. NRM PZ X 6154, Fig. 8A; slide 6154, England-finder coordinates L.49-4. 21 designated paratypes: Fig. 8B–V (see caption for slide numbers).

Diagnosis. An annelid with simple comb chaetae. Blade-like shafts terminate distally in extended lateral prongs, separated by an interval of fine serrations. Prongs always project beyond the brush tip and may be either symmetrically or asymmetrically developed to different degrees.

Serrations of the comb have acute tips in larger specimens or sub-rounded tips in smaller forms. Comb may be laterally divided into thirds by two prominent serrations approximately twice the size of the average for the comb. Densely-packed linear striations run the internal length of the chaetae, perpendicular to this is a series of equally spaced horizontal ridges, spaces between ridges increasing with respect to the size of the chaetae.

Distribution. Viklau and När Shale Members of the early Cambrian (Stage 4) File Haidar Formation, Gotland, Sweden (known from Grötlingbo-1 and File Haidar-1 cores).

<div align="center">

Incertae sedis

Genus BALTINEMA nov.

</div>

LSID. urn:lsid:zoobank.org:act:B253AEE3-AD94-4B51-8C75-34E53FF543C1

Derivation of name. With reference to the Baltic Basin.

Type species. *Baltinema rana* sp. nov. by monotypy.

Diagnosis. As for type species.

<div align="center">

Baltinema rana sp. nov.
Figure 11A–M

</div>

LSID. urn:lsid:zoobank.org:act:7B79C52A-EDAF-40EC-A3C7-CC6B03F86409

Derivation of name. After the sea deity, Ràn, in Norse mythology.

Holotype. NRM PZ X 6204, Fig. 11E; slide 6204, England-finder coordinates H.36-4. 8 designated paratypes: Fig. 11A–D, F–K (see caption for slide numbers).

Diagnosis. Filamentous organisms consisting of a sinuous primary axis bearing medially distributed secondary sinuous branches and globose lateral outgrowths. Length highly variable but always considerably exceeds the width. Main axis has an irregular 'pock-marked' appearance and is typically darker than the secondary structures. Apical terminations of primary axis taper to a rounded tip. Globose outgrowths roughly the width of the parent axis occur either in isolation or in pairs on opposing sides of the main axis. Branches resemble smaller versions of the primary axis and occasionally sub-branch but do not bear globose extensions.

Distribution. Viklau and När Shale Members of the early Cambrian (Stage 4) File Haidar Formation, Gotland and Öland, Sweden (known from Grötlingbo-1, File Haidar-1 and Böda Hamn-1 cores).

Remarks. The biological affinity of these forms is unresolved. The thick, wrinkled, central axis of *B. rana* does not appear to be composed of a compound cluster of filaments, but instead has conspicuous surficial and internal pock-marked cavities throughout. In overall architecture *B. rana* bears similarities to certain Ediacaran 'vendotaenids' such as *Eoholynia* (see Urbanek & Rozanov 1983, fig. XLV-1; Gnilovskaya et al. 1988) and other Neoproterozoic microfossils such as *Pseudodendron* (see Butterfield *et al.* 1994, fig. 28); however, it is significantly smaller than the dichotomously branching *Eoholynia*, and *Pseudodendron* lacks globose outgrowths.

DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: http://zoobank.org/References/AB48F49C-9D32-44C4-BDE8-349794BBE51A

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