SMALL CARBONACEOUS FOSSILS (SCFs) FROM THE TERRENEUVIAN (LOWER CAMBRIAN) OF BALTICA

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Abstract: We describe a new assemblage of small carbonaceous fossils (SCFs) from diagenetically minimally altered clays and siltstones of Terreneuvian age from the Lontova and Voosi formations of Estonia, Lithuania and Russia. This is the first detailed account of an SCF assemblage from the Terreneuvian and includes a number of previously undocumented Cambrian organisms. Recognizably bilaterian-derived SCFs include abundant protoconodonts (total-group Chaetognatha), and distinctive cuticular spines of scalidophoran worms. Alongside these metazoan remains are a range of protistan-grade fossils, including *Retiranus balticus* gen. et sp. nov., a distinctive funnel-shaped or sheet-like problematicum characterized by terminal or marginal vesicles, and *Lontohystrichosphaera grandis* gen. et sp. nov., a large (100–550 μm) ornamented vesicular microfossil.

Together these data offer a fundamentally enriched view of Terreneuvian life in the epicratonic seas of Baltica, from an episode where records of non-biomineralized life are currently sparse. Even so, the recovered assemblages contain a lower diversity of metazoans than SCF biotas from younger (Stage 4) Baltic successions that represent broadly equivalent environments, echoing the diversification signal recorded in the coeval shelly and trace-fossil records. Close comparison to the biostratigraphical signal from Fortunian small shelly fossils supports a late Fortunian age for most of the Lontova/Voosi succession, rather than a younger (wholly Stage 2) range.

Key words: Cambrian explosion, small carbonaceous fossils, Terreneuvian, Lontova, acritarchs, Baltica.

THE earliest Cambrian Terreneuvian Series represents one of the most transformative intervals in Earth history. Bracketed by the Ediacaran System below, and Cambrian Series 2 above, it witnessed the Cambrian 'explosion' of animals, biomineralization, bioturbation and protists, as well as the establishment of an essentially modern marine biosphere. Curiously, the most obviously 'explosive' part of the radiations occurs several million years after the *c.* 541 Ma base of the Cambrian, more or less in the middle of the Terreneuvian (Budd & Jensen 2000; Maloof *et al.* 2010). The Terreneuvian itself consists of two parts: a lower Fortunian Stage (*c.* 541–529 Ma), and an upper 'Stage 2' (*c.* 529–521 Ma), broadly equivalent to the Tommotian of Siberia (Kouchinsky *et al.* 2012).

Several lines of palaeontological inquiry confirm that much of the initial radiation of bilaterian animals does indeed lie in the Terreneuvian (Budd 2003, 2013). A pronounced increase in the origination rate of small shelly fossil (SSF) taxa occurs at or near the beginning of Stage 2 (Bengtson *et al.* 1990; Maloof *et al.* 2010; Kouchinsky *et al.* 2012). Current records of SSFs, ichnofossils and acritarchs from the Fortunian point to relatively low-diversity ecosystems compared to Stage 2, or younger counterparts. Phosphatic SSF assemblages from this earliest Cambrian interval are dominated by enigmatic tubular forms (e.g. *Anabarites*, *Hyolithellus*, *Hexaconularia*) and protoconodonts (*Protohertzina*), typically referred to the *Anabarites trisulcatus–Protohertzina anabarica* Zone (Hamdi *et al.* 1989; Steiner *et al.* 2004*a*; Kouchinsky *et al.* 2012). Fortunian trace fossils record comparatively low degrees of sediment mixing, and are typified by assemblages of simple, shallow tiering treptichnid-type habits (e.g. *Treptichnus*, *Didymaulichnus*), which are joined by *Rusophycus*-type arthropod traces at *c.* 536 Ma (Jensen 2003; Mangano & Buatois 2016). The signal from Fortunian plankton is also relatively subdued, characterized by long-ranging acritarch taxa belonging to the *Asteridium tornatum–Comasphaeridium velvetum* Zone (Moczydłowska 1991, 1998) and the *Asteridium–Heliosphaeridium–Comasphaeridium* assemblage (Yao *et al.* 2005). No Burgess Shale-type (BST) Lagerstätten are known from the Terreneuvian, and apart from a handful

of sites bearing phosphatized algae and metazoan larvae in South China (Steiner *et al.* 2004*b*; Liu *et al.* 2017), there is remarkably little accounting of the non-biomineralizing clades that dominate the diversity of most ecosystems.

One alternative source of palaeontological data comes from small carbonaceous fossils (SCFs), which have fundamentally expanded the view of non-biomineralized organisms in younger Cambrian strata (Butterfield & Harvey 2012; Harvey *et al.* 2012; Smith *et al.* 2015; Slater *et al.* 2017*a*). An extension of this SCF record into the Terreneuvian offers a novel means of tracking diversification through the 'Cambrian Explosion' interval, and a complementary record to the signal from SSFs. Indeed, at least some SCFs appear to be diagenetically de-mineralized versions of SSF elements, fossilized by virtue of their periostracum or intercrystalline organic matrix (e.g. Butterfield & Harvey 2012; Martí Mus 2014; Slater *et al.* 2017*a, b*); equally, some SSFs could be diagenetically mineralized remains of originally carbonaceous or lightly mineralized forms; e.g. phosphatized wiwaxiid sclerites (Porter 2000) and hallucigeniid spines (Skovsted & Peel 2001). SCFs can therefore extend the ranges of SSF-type taxa into previously unsampled depositional (or diagenetic) environments. Importantly, however, a majority of SCFs record body parts or taxa that are otherwise unrepresented in the fossil record.

A rich diversity of SCFs has recently been documented in early, but not earliest, Cambrian siliciclastic sediments of the western Baltic Basin (Slater *et al.* 2017*a*). Across this part of the basin Cambrian sediments are draped unconformably over a peneplained Proterozoic gneissic basement, and over most of the region the earliest preserved Cambrian record begins in Stage 4 (i.e. younger than 514 Ma; Nielsen & Schovsbo 2007, 2011; Slater *et al.* 2017*a*). In the eastern Baltic region, however, these epicratonic successions continue down into the Terreneuvian, spanning the full range of the early Cambrian (Nielsen & Schovsbo 2011; Meidla 2017). These poorly lithified clays and silts form the local Baltic 'Lontovan' stage. The Lontovan has been widely regarded as equivalent to the lowermost part of the 'Tommotian' stage of the Siberian craton (see Bergström 1981; Moczydłowska & Vidal 1988), which forms the upper part (*c.* 525–521 Ma) of Cambrian Global Stage 2 (*c.* 529–521 Ma) (see Kouchinsky *et al.* 2012). This age assignment was based primarily on early acritarch studies (e.g. Ogurtsova 1975, 1977). In contrast, however, more recent analysis of acritarchs, trace and body fossils suggests that the bulk of the Lontovan is instead Fortunian in age (cf. Volkova *et al.* 1990; Jensen & Mens 1999; Suuroja & Suuroja 2010; Nielsen & Schovsbo 2011; Palacios *et al.* 2017). Whether these sediments represent a pre-explosion (~Fortunian) interval or were deposited during the Cambrian explosion (~Stage 2) itself is crucial for understanding early Cambrian evolution on Baltica. Here we report a unique SCF accounting of the Lontova and laterally contiguous Voosi Formations of Estonia, Lithuania and western Russia.

GEOLOGICAL SETTING

The Lontova Formation (Figs 1, 2) underlies large areas of the eastern Baltic States, extending into Russia and the Gulf of Finland. It is exposed locally in clay quarries along the north Estonian coastline and widely encountered in drillcore (Mens 2003; Nielsen & Schovsbo 2011). In the western Estonian mainland and islands of Hiiumaa and Saaremaa, contemporaneous sedimentary units are referred to as the Voosi Formation (Figs 1, 2).

Sediments of the Lontova Formation comprise a relatively homogeneous and laterally extensive sequence of poorly lithified illite-smectite rich claystones/siltstones known locally as 'Cambrian Blue Clay' (Mens 2003; Raidla *et al.* 2010; Budd *et al.* 2011). A combination of shallow burial depth and a tectonically stable setting has resulted in remarkably little lithification or thermal alteration over the past half a billion years (Kirsimäe *et al.* 1999; Kirsimäe & Jørgensen 2000; Winchester-Seeto & McIlroy 2006). Properties of the clay mineralogy and acritarch colour-alteration in these sediments signify maximum burial temperatures not exceeding 50°C, ideal for the preservation of SCFs (Talyzina 1998; Ivanovskaya & Geptner 2004). Across its >500 km extent, the Lontova Formation rests transgressively above sediments of the 'Rovno' (latest Ediacaran to Fortunian) or 'Kotlin' (latest Ediacaran) regional Baltic stages, or directly on Proterozoic crystalline gneissic basement (Mens *et al.* 1990; Jensen & Mens 1999). Despite its homogeneity, it is possible to recognize four subdivisions of the Lontova Formation, based primarily on differences in the relative ratios of sediment types. The lowermost Sämi Member consists of a heterolithic succession of sandstones and silty claystones (Mens & Isakar 1999), and hosts a low-diversity ichnofossil assemblage including *Treptichnus pedum* (Palij *et al.* 1983). The Sämi Member is overlain by the green-grey to red-brown silt-rich claystones of the Mahu Member. The succeeding Kestla Member is predominantly claystone, but has numerous thin fine sand and silt beds, and hosts a low-diversity SSF assemblage including the helcionelloid molluscs *Aldanella kunda* and *Anabarella plana* (Isakar & Peel 2007). The uppermost Tammaneeme Member is restricted to the western region of the Estonian Lontova Formation, and consists of coarser dark grey siltstones (Mens & Pirrus 1977; Kirsimäe *et al.* 1999; Figs 1, 2).

Sediments of the more westerly Voosi Formation are relatively sandier, though there is still a significant proportion of argillaceous material. Three members of the
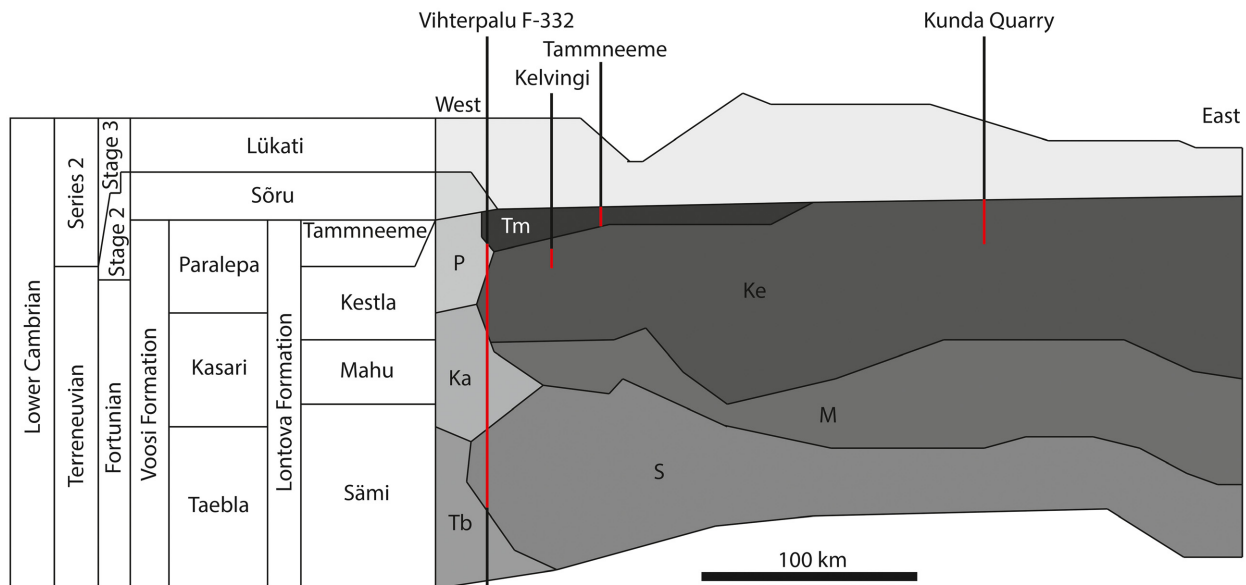
FIG. 1. Map showing distribution of sampled drillcores and sites of exposure. A, region depicted in map C. B, possible relationship of Lontova and Voosi Formation to local Baltic, Siberian and global Cambrian chronostratigraphic stages, dashed lines indicate approximate age of the 'Lontovan' suggested in this paper. C, map of eastern Baltic region with overlay showing modern extent of Lontova and Voosi Formations, and extrapolated palaeogeographical reconstruction based on Nielsen & Schovsbo (2011). *Locality abbreviations*: Estonia: Ku, Kunda quarry; Ke, Kelvingi; Ta, Tammneeme; Vp, F332-Vihterpalu drillcore; Lithuania: Tv, Tverečius-336 drillcore; Russia: Ko, Kostovo-13 drillcore. Sampled core intervals; *c.* 105 m of F332-Vihterpalu (90–195 m), 15.4 m of Tverečius-336 (453.1–437.7 m), and *c.* 110 m of Kostovo-13 (126–238 m). Lontova Formation (surface sections, Tverečius-336 core, Kostovo-13 core and F332-Vihterpalu core); Voosi Formation (parts of F332-Vihterpalu core).

FIG. 2. Stratigraphy of Lontova and Voosi Formations along the North Estonian coastline. *Abbreviations*: Ka, Kasari Member; Ke, Kestla Member; M, Mahu Member; P, Paralepa Member; S, Sämi Member; Tb, Taebla Member; Tm, Tammneeme Member. Red lines indicate sampled portions of sections intersected by drillcore or surface exposure. Position of Kunda quarry (59°30.9′ N, 26°31.8′ E). (Based on Kirsimäe *et al.* 1999, fig. 2.)

Voosi Formation have been established. The basal Taebla Member consists of fine-grained glauconitic sandstones and preserves abundant *Sabellidites cambriensis* alongside a low-diversity ichnofauna including *Didymaulichnus tirasensis*, *Gyrolithes* and *Planolites* (Jensen & Mens 2001). The middle Kasari Member is a more richly glauconitic sandstone with agglutinating tubular fossils *Platysolenites antiquissimus* and *Yanichevskyites petropolitanus* (Posti 1978; Mens & Posti 1984). The uppermost Paralepa Member is a heterolithic unit consisting of clays and glauconitic sandstones, and preserves a moderate diversity of small shelly fossils (SSFs) including *Aldanella kunda*, *Platysolenites spiralis*, *P. lontova* and *P. antiquissimus* (Mens & Isakar 1999).

The Lontova/Voosi succession was deposited in a shallow epicratonic sea with the clay-rich sediments of the Lontova accumulating in the 'outer shelf' region (Fig. 1) and the Voosi representing the corresponding 'inner shelf' (Fig. 1; see Nielsen & Schovsbo 2011). Lontova and Voosi mudstones are pervasively laminated, with a characteristic pattern of small (mm-scale) lightly pyritized meandroid trace fossils, suggesting a persistently dysoxic water column (Mens & Pirrus 1977; Palij *et al.* 1983; Jensen & Mens 1999, 2001).

Together, the Lontova and Voosi formations encompass the bulk of the 'Lontovan' local Baltic stage of the Lower Cambrian (Nielsen & Schovsbo 2011). Sediments of the Lontova and Voosi formations lack trilobites, so biostratigraphical schemes have relied on SSFs, acritarchs and trace fossils. The SSF *Aldanella kunda* occurs in the uppermost parts of the Lontova Formation in Estonia and is widely considered to be a junior synonym of *A. attleborensis* (Landing 1988; Isakar & Peel 2007; Parkhaev & Karlova 2011). *A. attleborensis* has previously been suggested as a potential Stage 2 index fossil (e.g. Landing *et al.* 2013); however, it first appears below the Fortunian/Stage 2 boundary and within Fortunian to Stage 2 transitional beds in many Siberian sections (see Kouchinsky *et al.* 2017). Taken together, the Lontovan SSF assemblage is characteristic of the *Platysolenites antiquissimus* Zone (Mens & Pirrus 1997), which spans the whole of the Terreneuvian, precluding any finer scale intra-Terreneuvian stratigraphic resolution (Kouchinsky *et al.* 2012). Of the four acritarch biozones proposed for the early Cambrian of Baltica, the Lontova falls within the most basal, the *Asteridium tornatum–Comasphaeridium velvetum* Zone (Volkova *et al.* 1979; Moczydłowska 1991; Szczepanik & Żylińska 2016). Again, this broad-ranging zone is thought to be essentially equivalent to the Nemakit-Daldynian local stage of Siberia (Moczydłowska 1991), thus spanning the whole of the Fortunian and much of Stage 2 (Kouchinsky *et al.* 2012; Fig. 1).

The Lontova and Voosi formations are overlain by the younger early Cambrian Sõru and/or Lükati formations, though the Sõru is missing from eastern regions (Fig. 2). The Lükati contains trilobites belonging to the Stage 3 *Schmidtiellus mickwitzi* Zone (Bergström 1973; Mens & Pirrus 1977; Ahlberg *et al.* 1986). The subjacent Sõru

Formation has conventionally been assigned to the *Ruso-phycus parallelum* ichnofossil Zone (Mens *et al.* 1990), which could span Stage 2 and/or 3. Since the boundary between the Sõru/Lükati and Voosi/Lontova is discon-formable (Nielsen & Schovsbo 2011; Meidla 2017), there is potentially a large time gap between the deposition of these units in any case. Assigning an older, Fortunian, or at least partly Fortunian age to the Lontova would help to explain the apparent discordance between the Lontova Formation and the Lontovan regional stage in certain areas. In eastern Latvia, for example, the Lontova Forma-tion is considered to span both the earliest Cambrian Rovno and Lontovan regional stages (Birkis *et al.* 1972; Jensen & Mens 1999). On the basis of the SSFs, trace fos-sils (treptichnid assemblage in the Lontova and Voosi for-mations; Jensen & Mens 2001), abundant *Sabellidites cambriensis* (Jensen & Mens 1999; Suuroja & Suuroja 2010; Nielsen & Schovsbo 2011) and SCF data (this study), there is a strong case for identifying the Lontova and Voosi formations as predominantly Fortunian in age.

MATERIAL AND METHOD

Samples of Lontova blue clay were collected from three exposures along the North Estonian coastline, at Tamm-neeme (59°31.9′ N, 24°53.4′ E), Kelvingi (59°33.4′ N, 24°49.6′ E) and the Kunda quarry (59°30.9′ N, 26°31.8′ E) (Figs. 1, 2). For surface sections (e.g. the *c.* 9 m of Lontova Formation exposed in the Kunda quarry) samples were selected at 1 m intervals, with denser sampling in finer-grained lithologies. Subsurface material was also sampled from three regionally separated drillcores (Figs 1, 2): (1) F332-Vihterpalu, western Estonia (59°15′42.732″ N, 23°51′13.104″E), housed at the Arbavere Geological Survey Core Store, Estonia; (2) Tverečius-336, south-eastern Lithuania (55°18′50.148″ N, 26°35′40.992″ E), housed at the Vievis core facility, Lithuania; and (3) Kostovo-13, Leningrad Oblast, Russia (59°32′06.8″ N, 31°13′33.4″ E), housed at the TUT Institute of Geology core-storage at Särghaua, Estonia. Samples were collected at roughly one metre intervals in each core, focusing on finer grained siltstones and mud-stones. Approximately 50 g of each sample were processed for SCFs using a low-manipulation hydrofluoric acid macer-ation procedure, with fossils recovered individually by pip-ette and mounted for light microscopy (see Butterfield & Harvey 2012).

SMALL CARBONACEOUS FOSSILS

A wide range of SCFs and acritarchs were recovered from early Cambrian sediments of the Lontova and Voosi for-mations (Figs 1, 2). Of 71 processed samples, a total of 1488 microfossils from 21 productive samples were per-manently mounted onto 73 glass slides. Slides are housed at the Swedish Museum of Natural History, Stockholm (NRM). The recovered fossils include >10 distinct forms, two of which are clearly derived from bilaterian meta-zoans; the remainder are phylogenetically problematic, with most forms representing a protistan grade of organi-zation.

Protoconodont spines. SCFs recovered from the Lontova and Voosi formations frequently include flattened car-bonaceous spines with a more or less curved, horn-like shape and basal opening (Figs 3, 4A–G). The spines reach >2.1 mm in maximum length ($\bar{x}$ = 934 μm, SD = 416 μm, n = 81), and a maximum basal width of >1 mm ($\bar{x}$ = 323 μm, SD = 198 μm, n = 81) and an average length to base ratio of 3.4:1. Occasional exam-ples of these spines were recovered from the Kestla Member of Tverečius-336 and Kostovo-13, but they were particularly abundant in the Kunda quarry, where a *c.* 50 g sample of Kestla Member claystone yielded in excess of 200 spines, for example. The spines show a continuum of morphologies (no bimodality), varying from curved, scimitar-shaped forms, through to straight forms with sharply pointed tips. Microstructurally, the spines have an outer smooth wall (e.g. Fig. 3A–AB) and exhibit an internal fabric of longitudinal and occasion-ally interwoven fibres (e.g. Fig. 3AE, AL, AM, AO, AQ, BL–BS). One, or both of the margins are frequently thicker than the rest of the spine (e.g. Fig. 3AL, AR–AT). The tips terminate in an acute point, but are often broken; commonly just the outer portion is missing, exposing a thinner internal tip composed of fibrous material (e.g. Fig. 3AL). The basal opening is often incomplete, but occasionally preserves as a sharp trunca-tion of the main spine attached to an extended portion of fibrous material (Fig. 3AZ–BF). Based on their shared construction and the continuum of the populations both within and between assemblages, we infer a single monospecific origin for these spines.

Similar spines have previously been reported in Lon-tovan and equivalent strata. A single curved spine was described as a bedding-plane compression from the Kunda quarry (Mens & Pirrus 1977, pl. 16.6). Compara-ble spines are also reported from the upper part of the Lontova Formation in eastern Latvia (Birkis *et al.* 1972), and from the early Cambrian of Ukraine (Kiryanov 1968 *in* Krandievski *et al.* 1968). Often, spines of this type have been referred to the acritarch/organic-walled form-taxon *Ceratophyton vernicosum* (Paškevičiene 1980; Volkova *et al.* and Kiryanov *in* Urbanek & Rozanov 1983; Palacios *et al.* 2017). Apart from their approxi-mately triangular outline, however, the Lontovan spines share few morphological features with other

FIG. 3. *Protohertzina compressa* sp. nov.; protoconodont spines from the Kestla Member of the Lontova Formation. Holotype specimen; BA. Slide numbers (all numbers have the prefix NRM-PZ X): A, AM, AQ, CA, CB = 7027; B, G, AN, AS, AT, AY = 7031; C, E, BK = 7019; D, V, AK, BM, BN = 7029; F, J, L, M, O, Y, AZ, BP = 7033; H, AC, AD, AG, AU, BH = 7036; I, K, N, S, T, U, AI, AO, BQ = 7034; P, BR, BX, BY = 7015; Q, R, AP, BZ = 7030; W, AE, AV, AX, CC = 7022; X, AA, AB, BC, BD, BE = 7035; Z, BB = 7023; AF, BJ = 7013; AH, AJ, BO = 7028; AL, BW = 7020; AR = 7016; AW = 7025; BA = 7032; BF = 7017; BG, BI, BL = 7037; BS = 7026; BT, BV = 7018; BU = 7014. Scale bar represents 400 μm.

'*Ceratophyton*' (see Hagenfeldt 1989; Smith *et al.* 2015; Slater *et al.* 2017a).

The closest morphological comparison of these spinose SCFs lies among various phosphatized protoconodonts common in Terreneuvian-age SSF assemblages globally (e.g. Missarzhevsky 1973, 1982; Chen 1982; Yang & He 1984; Bengtson *et al.* 1990; Azmi 1996). In particular, many of the Lontova spines bear close similarities to slender *Protohertzina* forms with a fibrous microstructure, such as *Protohertzina anabarica* Missarzhevsky, 1983

(Nowlan *et al.* 1985, fig. 8A–F; Brasier 1989, fig. 7.1), *P. unguliformis* Missarzhevsky ,1973, *P. siciformis* Missarzhevsky, 1973 (Pyle *et al.* 2006; Topper *et al.* 2009), several morphologies from the early Cambrian Machari Formation of Korea (Lee *et al.* 2009, figs 6–7) and a semi-articulated *Protohertzina* cluster from the early Cambrian of Newfoundland (McIlroy & Szaniawski 2000, fig. 2). Phosphatized *Protohertzina* have variously developed lateral ridges which form a 'keel' running the length of the spine, features that form the basis of their species-
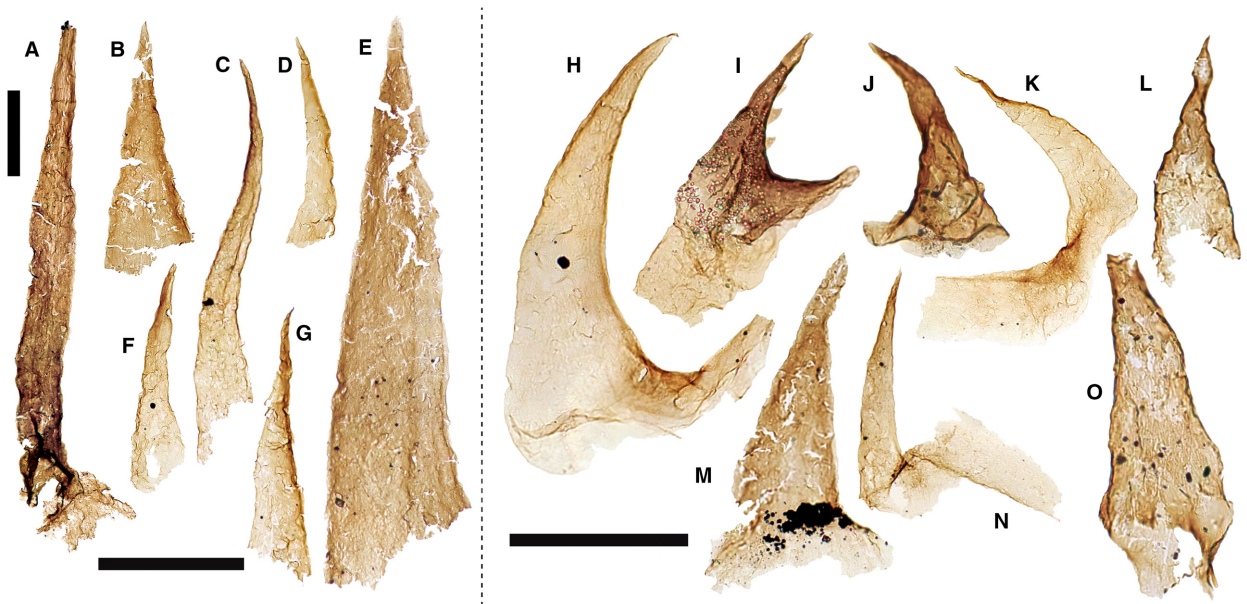
FIG. 4. Metazoan-derived SCFs from the Kasari Member of the Voosi Formation. A–G, large protoconodonts of the same morphology to those found in the contemporaneous Kestla Member of the Lontova Formation (*P. compressa* sp. nov.). H–O, smaller scalidophoran-derived elements; based on their hook-shaped curvature and prominent basal spur, specimens H–K and N are scalids. Slide numbers (all numbers have the prefix NRM-PZ X): A = 7053; B = 7056; C, N = 7051; D = 7047; E = 7055; F = 7040; G, K, = 7038; H = 7045; I = 7048; J = 7049; L = 7050; M = 7054; O = 7057. Scale bars represent: 200 μm (A); 200 μm (B–G); 100 μm (H–O).

level taxonomy (see Brasier 1989, fig. 7.3). The flattened nature of the carbonaceous Lontova spines precludes any accurate reconstruction of their cross-sectional morphology; however, the presence of optically darker, presumably thickened portions running the length of many specimens (e.g. Fig. 3AR–AT) potentially records the original position of an analogous flattened keel. These characteristic features point to these Lontovan spines being protoconodonts. An originally non-biomineralized condition is supported by the wholly organic expression (which contrasts with the preservation of co-occurring phosphatic SSFs), combined with the lack of brittle fractures (cf. Butterfield & Nicholas 1996), and justifies the erection of a species name that suggests a biologically distinct entity, rather than a taphomorph. Despite their two-dimensional preservation, we assign them to the form-genus *Protohertzina*, and establish a new species *P. compressa* sp. nov. to accommodate the lack of mineralization (see Systematic Palaeontology below).

Szaniawski (1982, 2002) has argued convincingly that protoconodonts represent the grasping spines of chaetognath worms, based on their fibrous microstructure, overall form, and evidence suggestive of secondary (diagenetic) phosphatization. The conspicuously two-dimensional *Protohertzina compressa* sp. nov. in the Lontova assemblage strongly support an originally non-biomineralizing habit, consistent with their interpretation as total-group Chaetognatha (see Vannier *et al.* 2007).

Although extant chaetognaths typically bear 1–2 rows of small rasping 'teeth' in addition to their grasping spines, we have not detected analogous structures among the Lontovan SCFs, and they have not been reported from corresponding SSF assemblages. It is notable, however, that the feeding apparatuses of fully articulated fossil chaetognaths, middle Cambrian *Capinator praetermissus* (Briggs & Caron 2017) and early Cambrian *Ankalodus sericus* (Shu *et al.* 2017) also lack such differentiated 'teeth'. The curved grasping spines of *Capinator praetermissus* are most similar to the Lontovan *Protohertzina* but exhibit a uniformly narrower base. Together, the considerable diversity of phosphatized/phosphatic (and now carbonaceous) Cambrian protoconodonts, coupled with the surprisingly varied grasping spine configurations in articulated Cambrian examples (e.g. *Ankalodus sericus*, *Capinator praetermissus*) point to a broader diversity of feeding apparatus among stem chaetognaths.

Scalidophorans. Other spine-shaped SCFs recovered from the Voosi Formation (F332-Vihterpalu) exhibit a fundamentally different architecture (Fig. 4H–O). These curved, hook-shaped spines lack the characteristic fibrous construction of *Protohertzina*, and often include a basal 'spur' oriented at a right angle to the primary spine (Fig. 4H–K, N). Some specimens also bear multiple secondary denticles in two parallel rows along the interior curve of the hook (Fig. 4I).

Together, these features characterize the cuticular sclerites of many scalidophoran worms (cycloneuralian ecdysozoans). 'Sclerites' of the same general architecture adorn the integument of modern priapulids in various body positions (introvert scalids, pharyngeal teeth, and tail hooks; e.g. van der Land 1970; Wennberg *et al.* 2009) and also Cambrian stem-priapulids known from BST-macrofossils (Smith *et al.* 2015). Actualistic taphonomic experiments on modern *Priapulus* have shown these scalidophoran cuticular components to be particularly robust to decay (Sansom 2016), and they are regularly preserved in Cambrian SCF assemblages (Butterfield & Harvey 2012; Harvey *et al.* 2012; Smith *et al.* 2015; Slater *et al.* 2017a). It is worth noting that broadly comparable hooks are also found in some sipunculans, including forms with elaborations such as a bidentate outline or a secondary spine or comb along their inner margin (e.g. Schulze *et al.* 2005, fig. 2; Gómez *et al.* 2013, fig. 6). However, as far as we are aware, sipunculan hooks do not express double rows of more clearly separated denticles, as seen in the denticulate Lontova specimens (Fig. 4I), whereas these are a widespread feature among both modern and Cambrian priapulids (e.g. Smith *et al.* 2015).

In both modern and fossil scalidophorans, the sclerites of the introvert or trunk are referred to as scalids, whilst those of the pharynx are termed teeth (van der Land 1970; Smith *et al.* 2015). A subset of the Lontovan specimens (Fig. 4H–K, N) are classifiable as candidate scalids based on their elongate hook-like shape, spur, and where present, spines borne in rows close to the midline (Fig. 4I; cf. Smith *et al.* 2015, fig. 4). This is in contrast to the broader, spade-shaped outlines and marginally distributed denticles typically expressed in pharyngeal teeth, which we have not yet distinguished in the Lontova samples, although not all Cambrian scalidophorans exhibit a clear morphological distinction between scalids and teeth (e.g. *Eopriapulites*, Liu *et al.* 2014; *Markuelia*, Dong *et al.* 2010). One of the individual scalids (Fig. 4H) closely resembles the SSF form-taxon *Mongolodus*, sharing an extended basal spur with a posterior imargination (cf. Steiner *et al.* 2004a, fig. 8 image 7), pointing to a possible shared phylogenetic affinity. Other specimens (e.g. Fig. 4L, M, O) lack sufficient detail to resolve their particular habit, and may represent the distal portions of scalids, and/or fragments of coronal spines or tail hooks. The small numbers of these scalids (*n* = *c*. 10) precludes their reliable assignment to any known Cambrian priapulid-like worm or previously described SCF-based taxon (cf. Slater *et al.* 2017a). Nonetheless, these examples add to a sparse but increasing diversity of scalidophoran-like SCFs from Terreneuvian strata, including examples from northern Siberia (Nagovitsin 2011), a single specimen from Poland (Moczydłowska *et al.* 2015; *c*. 190 m above a tuff layer in a laterally correlated borehole dated at

551 ± 4 Ma; Compston *et al.* 1995) and several elements from the Cambrian Stage 2 of Newfoundland (Palacios *et al.* 2017, fig. 7b–d). Together with the Lontovan material, such SCFs point to the widespread presence of scalidophoran/cycloneuralian grade worms prior to any known BST macrofossil evidence.

Problematica

Tubes. Tubular fossils bearing transverse annulations or flanges were recovered from throughout the Voosi Formation (F332-Vihterpalu) and from the Kestla Member of the Lontova Formation (Kunda and Tverečius-336) (Fig. 5). The tubes are predominantly parallel-sided, but undulate slightly in places and typically taper towards one end. Transverse flanges are distributed at approximately regular intervals (spaced at *c*. 25% of the tube diameter) along the length of the primary tube-wall, though these flanges frequently divide and merge with neighbouring examples producing a wrinkled appearance (Fig. 5A, B, E, H). The flanges are often restricted to the expanded (presumably distal) parts of the tube and are absent from the tapered (presumably basal) portion of the tube which is smooth-walled and optically darker (Fig. 5G, P). In most cases, the flanges appear to have ragged margins (e.g. Fig. 5H, R). The maximum tube length is *c*. 2 mm.

These annulated tubes are broadly comparable to a number of organic-walled tubular taxa known from bedding-plane macrofossils, though they are substantially smaller. Ediacaran *Saarina*, for example, exhibits broadly comparable annuli (Gnilovskaya 1996), but these are more funnel-shaped, and obviously taper into the adjacent underlying cylinder. Other tubular fossils in the Lontova Formation include *Platysolenites antiquissimus*, *P. lontova*, *Yanichevskyites petropolitanus*, *Sabellidites cambriensis* and *Hyolithellus* sp. (Mens & Pirrus 1977, pl. 16). The transversely annulated tubular fossil *Hyolithellus* sp. co-occurs as rare bedding-plane compressions in the Kunda quarry (Mens & Pirrus 1977, pl. 16 figs 8–9), and is found throughout the Mahu and Kestla members of the Lontova Formation (Mens & Pirrus 1977); however, the conspicuously uniform annulations and absence of smooth portions in specimens of *Hyolithellus* distinguish them from the SCFs. The spacing of transverse flanges in the SCF specimens are similar to those seen in some specimens of *P. lontova* (e.g. Mens & Pirrus 1977, pl. 16.2), though the agglutinating construction of the latter (McIlroy *et al.* 2001) undermines any close comparison. An apparently identical mode of construction, however, is found among flanged tubes described as *Sokoloviina costata* (Kiryanov 1968 *in* Krandievski *et al.* 1968, pl. 3.4–8) from equivalent strata in the early Cambrian of north-

FIG. 5. *Sokoloviina costata*; problematic tubular SCFs with transverse flanges, from the Lontova Formation. G, specimen where upper expanded portion exhibits transverse flanges and lower portion is predominantly smooth walled. H, prominently flanged specimen, where flanges exhibit ragged margins, the base of this specimen tapers to a narrow opening and is folded across the upper portion of the tube. J, pair of tubes with twisted and closed termini, possibly an ontogenetic or taphonomic feature. P, smooth walled length of tube tapering to a narrow base. R, tube with pronounced ragged transverse flanges. Slide numbers (all numbers have the prefix NRM-PZ X): A, C, D, F, I, R = 7061; B, J, K–O = 7062; E = 7059; G, P = 7060; H = 7063; Q = 7064. Scale bar represents 200 μm.

west Ukraine, which likewise occur in a carbonaceous mode of preservation (both extractable and *in situ*) and express equivalently flanged or smooth-walled tube regions. We therefore identify the tubular Lontovan SCFs as *Sokoloviina costata* Kiryanov (1968), expanding the known geographical range of this taxon and adding to the conspicuously broad range of tubular microfossils already documented from the Baltic Lontovan, and from Terreneuvian assemblages more generally (e.g. Kouchinsky *et al.* 2012; Budd & Jackson 2016; Pang *et al.* 2017).

Vesicle-fringed sheets (Retiranus balticus gen. et. sp. nov.). All processed samples of the Kasari Member (Voosi Formation, F332-Vihterpalu core) and a single sample from the Tverečius-336 core (443 m) yielded populations of distinctive sheet-like SCFs consisting of a thalloid portion fringed with anatomically connected vesicles (Fig. 6). The sheets reach >2 mm in maximum dimensions ($\bar{x} = c.$ 1700 μm, SD = 538 μm; $n = 26$) with marginal spheroidal to ovoid vesicles reaching maximum diameters of $c.$ 300 μm ($\bar{x} = c.$ 163 μm, SD = 54 μm; $n = 36$). The population as a whole is conspicuously variable, with some forms consisting of narrow stalk-like thalli terminating in one or more vesicles (Fig. 6A–H), and others represented by large crenelated sheets ringed with multiple marginal vesicles (Fig. 6L, N–P). In many examples, only the widest, flabelliform (expanding fan-shaped) portion of the sheet bears marginal vesicles, while the opposing part tapers towards a narrow 'base' (e.g. Fig. 6I). A possible basal holdfast structure is occasionally preserved, consisting of a flattened ovoid extension (Fig 6F, U). Biological margins can readily be distinguished from broken or torn ones, since the former align with an expanding sequence of regularly spaced concentric banding that broadens toward the vesicle-bearing margin in the largest specimens (e.g. Fig. 6P). All sheets with intact margins possess marginal vesicles. The vesicles occasionally exhibit a single spherical dark spot at the
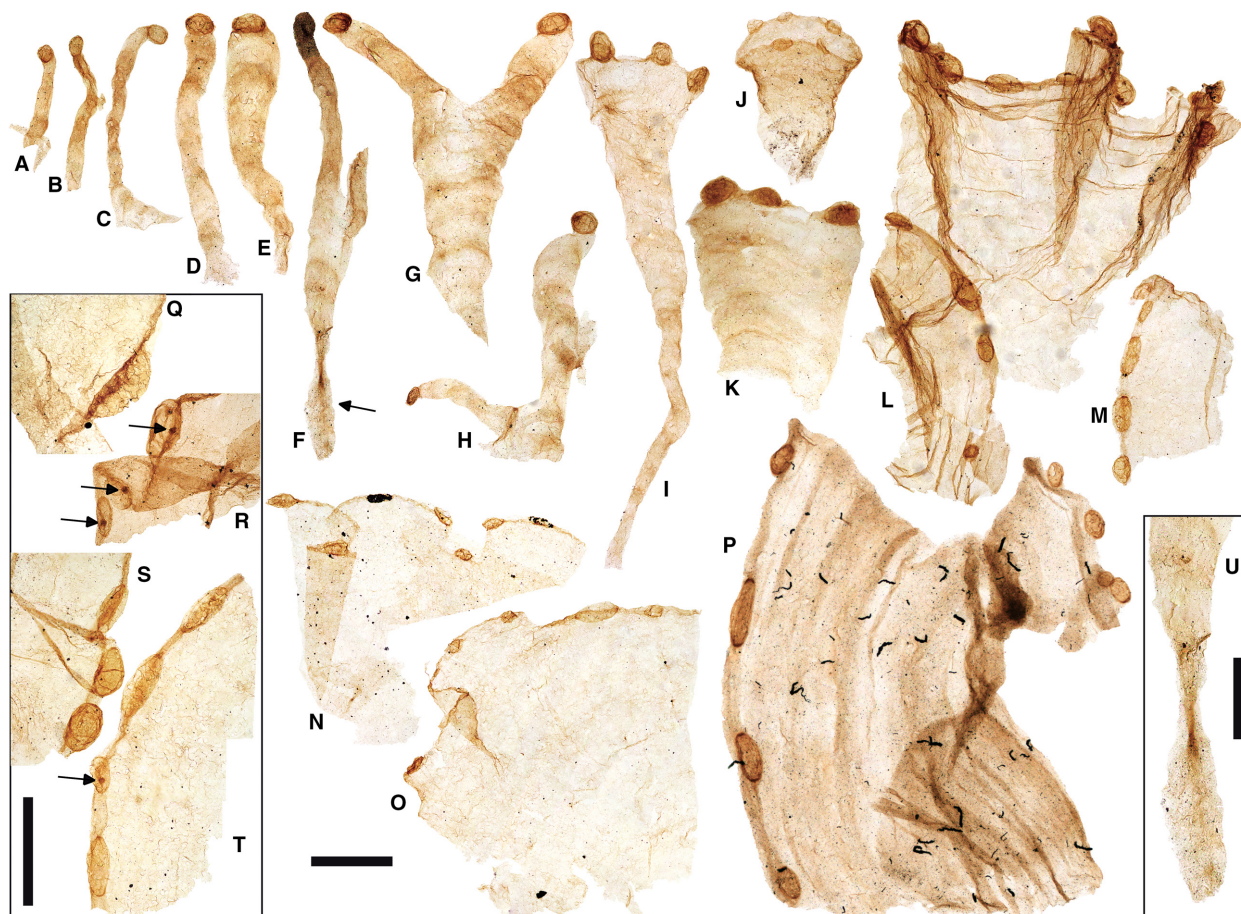
FIG. 6. Problematic vesicle-fringed sheet-like fossils from the Voosi Formation, *Retiranus balticus* gen. et sp. nov. A–E, specimens terminating in a single vesicle. F, specimen with basal holdfast structure (arrow). G–H, divergent specimens forming two 'stalks' each ending in a single vesicle. I–K, specimens expanding to flabelliform termini fringed by multiple vesicles. L–P, large specimens consisting of portions of the expanded termini fringed with multiple typically ovoid vesicles, specimens N and O exhibit crenelated margins (note that darkened vesicles in specimen N are filled with pyrite). P, holotype specimen. Q–T, details of marginal vesicles, arrows indicate position of distinctive dark spots which occur in some vesicles. U, close-up of basal holdfast structure in specimen E. Slide numbers (all numbers have the prefix NRM-PZ X): A, E, H, K = 7059; B, D = 7058; C, F, G, I, U = 7060; J = 7047; L = 7041; M, T = 7038; N = 7046; O, Q = 7044; P = 7062; R = 7051; S = 7043. Scale bars represent: 400 μm (A–P, Q–T); 200 μm (U).

centre, typically *c.* 10% the total diameter of the vesicle (Fig. 6R, T). The smallest thalli, with relatively fewer vesicles, possess more or less spheroid vesicles. As the sheets attain a larger size, the margins tend to become more crenelated, and the vesicles acquire a more ovoid shape. Other characteristics of the vesicles (e.g. possession of dark spot structures; Fig. 6R) are typically consistent within a single sheet, suggesting that neighbouring vesicles are at the same ontogenetic stage. In addition, the vesicles become more evenly spaced around the sheet margins as thalli size increases.

The phylogenetic affinity and basic biology of these fossils is problematic. Some of the larger specimens (e.g. Fig. 6N–P) have an outline similar to some extant brown algae, for example *Padina* (e.g. Ni-Ni-Win Hanyuda *et al.*

2011, figs 3–5), though superficial comparisons can also be made with xenophyophoran foraminifera (e.g. *Stannophyllum*; Kamenskaya *et al.* 2015). Neither of these taxa, however, are known to differentiate marginal vesicles. In terms of grade of organization, a more comparable architecture is found among various clades of lichenized fungi which produce broad foliose thalli with marginally distributed ovoid apothecia (e.g. *Peltigera*). The stalked morphotypes with terminal vesicles (Fig. 6A–H) also resemble the overall morphology of various matchstick lichen (e.g. *Pilophorus*, *Cladonia*; Jahns 1981). Broadly comparable grades of architecture can also be found among several photosynthetic epiphytes, for example, the kidney fern (*Hymenophyllum nephrophyllum*; Brownsey & Perrie 2016, figs 78–83) and the green alga *Phycopeltis epiphyton* (Zhu

et al. 2015). Even so, the lack of any clear cellular arrangement in the sheets, along with the non-aquatic nature of the analogous modern plants and lichens, precludes a more detailed comparison. Among early fossils, a useful comparison can be drawn with the Ediacaran macroalgae *Flabellophyton*, which occurs abundantly as carbonaceous compressions from the Lantian biota of South China (Yuan *et al.* 2013). Although substantially larger, *Flabellophyton* exhibits a similar overall thallus shape and holdfast structure, but lacks the distinguishing marginal vesicles (Wan *et al.* 2013, figs 3–4). The vesicles could conceivably represent parasites or exosymbionts attached at the margins of the thalli, but this seems unlikely given the consistent relationship between the shape and arrangement of the vesicles and thallus size. Even distinguishing whether these fossils are multicellular is problematic (see Zhu *et al.* 2016), though they probably represent eukaryotes of a protistan grade. Despite their

phylogenetic ambiguity, these fossils are sufficiently distinctive to be recognized as a true biological taxon, adding to the records of early Cambrian diversity. We establish a new genus and species, *Retiranus balticus* gen. et. sp. nov. to circumscribe these problematic Cambrian organisms (see Systematic Palaeontology below).

Large acanthomorphic acritarchs. The Kestla Member of the Lontova Formation in the Kunda quarry preserves significant populations of large (100–550 μm diameter; *c.* 390 ± 35 μm, $n = 41$) process-bearing spheroidal vesicles of unknown affiliation; i.e. acanthomorph acritarchs (Figs 7, 8). The 1–24 processes per vesicle are heteromorphic, hollow, and open basally into the vesicle (Fig. 8). Although some of the processes are preserved with a distally pointed tip (Fig. 8F, I), most are open distally, indicating breakage and taphonomic shortening; this is best illustrated in specimens with relatively complete processes
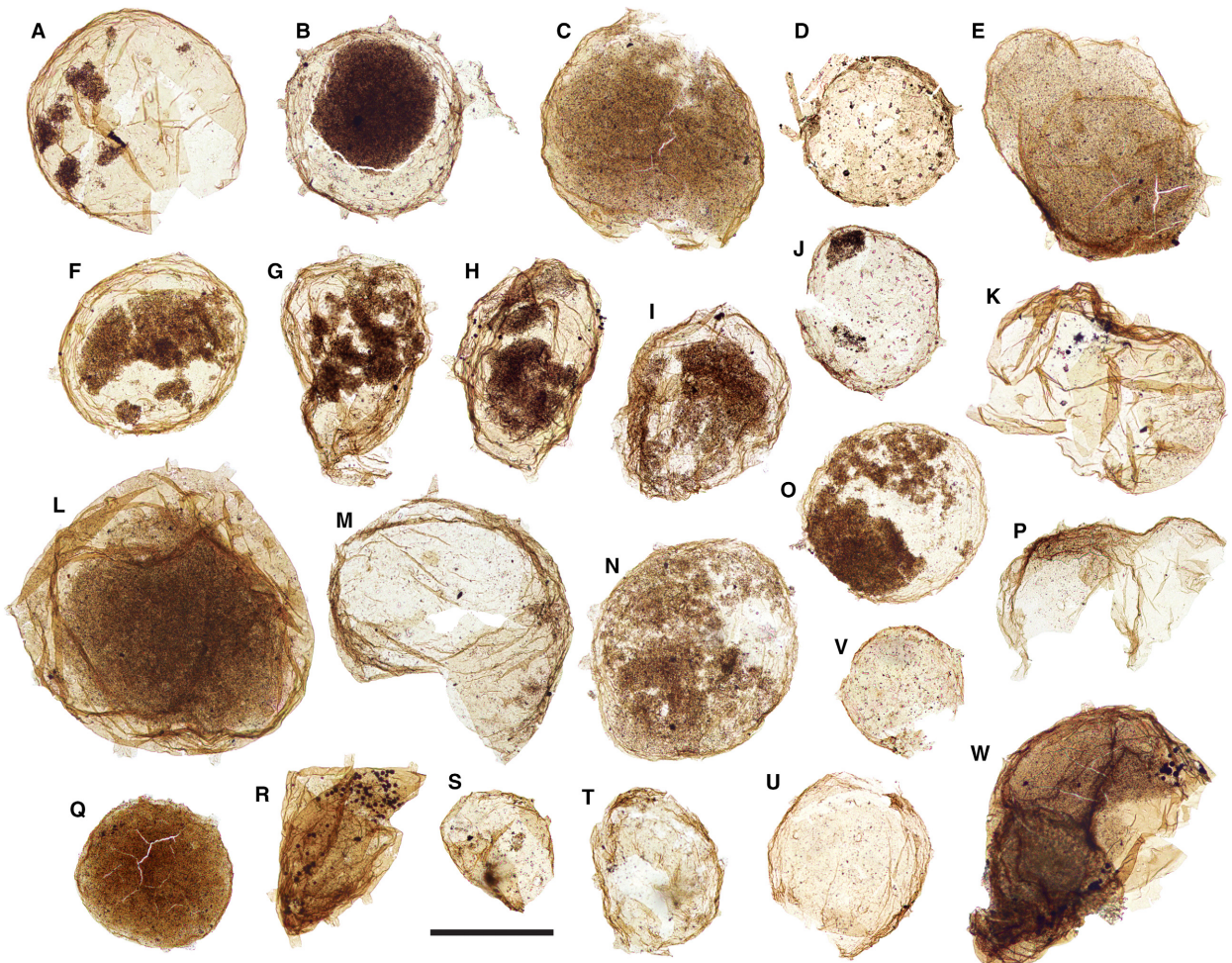

FIG. 7. Large ornamented acritarchs from the Kestla Member of the Lontova Formation (*Lontohystrichosphaera grandis* gen. et sp. nov.). L, holotype specimen. Slide numbers (all numbers have the prefix NRM-PZ X): A, F, I–L, O = 7023; B = 7016; C, E, Q, W = 7021; D = 7024; G, S = 7013; H, U, V = 7014; M, T = 7018; N = 7022; P = 7019; R = 7025. Scale bar represents 200 μm.
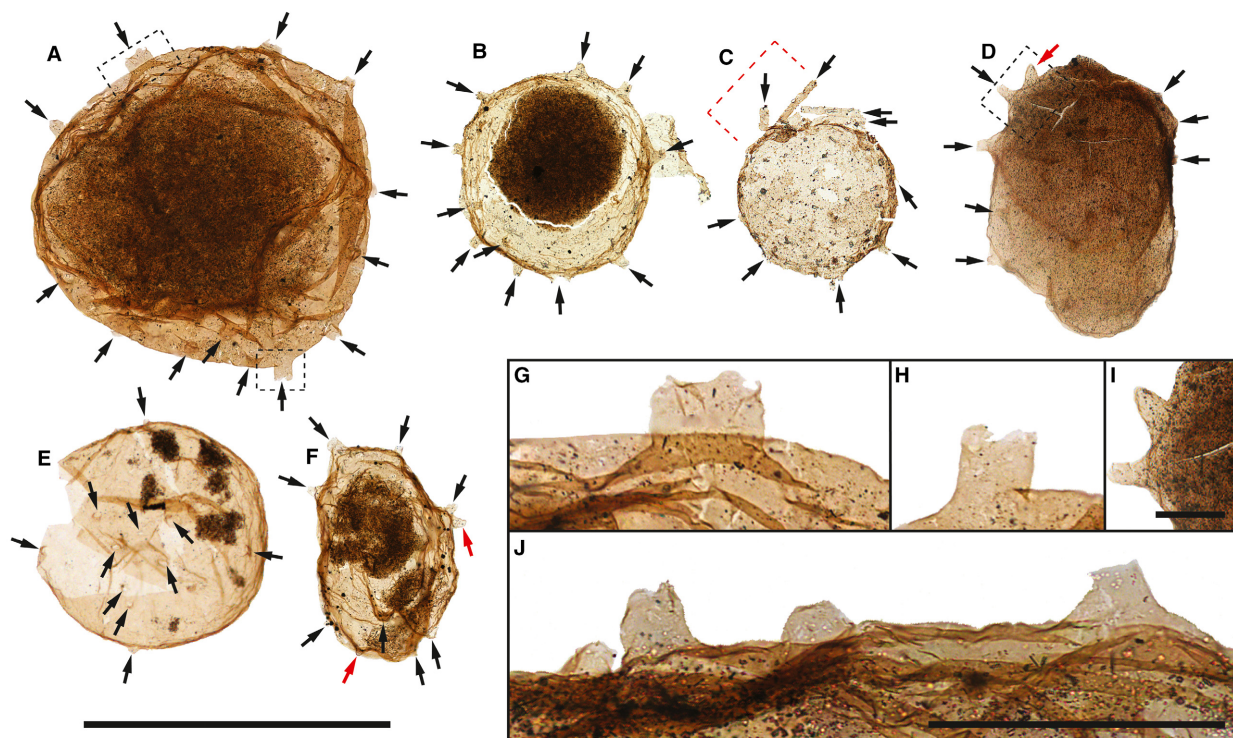
FIG. 8. Distribution and details of surface ornamentation on *Lontohystrichosphaera grandis* gen. et sp. nov. from the Kestla Member of the Lontova Formation. Black arrows in specimens A–F indicate position of broken surface processes, red arrows indicate unbroken, incipient processes. C, dashed red line indicates length of the longest preserved surface process. G–H, close-ups of ornamentation shown in dashed boxes on specimen A (holotype). I, close-up of ornamentation shown in dashed box on specimen D. J, range of ornamentation in close proximity on a single specimen. Slide numbers (all numbers have the prefix NRM-PZ X): A, E, G, H = 7023; B = 7016; C = 7024; D, I = 7021; F = 7014; J = 7026. Scale bars represent: 500 μm (A–F); 50 μm (G, H, J); 50 μm (I).

(Fig. 8C). The distribution of processes on host vesicles is apparently random, but with a tendency towards more even distribution with increasing process number. The presence of small bump-like protrusions on some vesicles may represent incipient processes suggesting continuous ontogenetic acquisition (Fig. 8F). Apparently paired processes (e.g. Fig. 8I) are more likely to be a product of taphonomic flattening/superposition than an original biological feature. There is often a darkened mass within the vesicle, presumably degraded cytoplasm or inner layers (Fig. 7B, F–I, L, O; cf. Grey 2005; Pang *et al.* 2013). Several specimens appear to have developed outgrowths from the vesicle, which occasionally form smaller, contiguously attached vesicles (e.g. Fig. 8D); others exhibit a more irregular hemispherically bulging habit (Figs 7G–H, 8F).

These early Cambrian microfossils are fundamentally larger and more irregular than typical Cambrian acanthomorphic acritarchs. They are, however, broadly comparable to various Proterozoic acanthomorphs that display a continuum of vegetative growth forms (see Discussion below); e.g. Palaeo-/Mesoproterozoic *Tappania*, the *Germinosphaera* phase of the Wynniat Formation 'Tappania' (Butterfield 2005; Adam *et al.* 2017; Javaux & Knoll 2017)

and late Meso-/Neoproterozoic *Trachyhystrichosphaera* and *Blastanosphaira* (Butterfield *et al.* 1994; Butterfield 2005; Beghin *et al.* 2017). Secondary vesicles (Fig. 8D) resemble those seen in *Trachyhystrichosphaera* (cf. Butterfield 2005, fig. 9; Tang *et al.* 2013, fig. 11e–g; Baludikay *et al.* 2016, fig. 6). Two somewhat irregular specimens (Figs 7G, 8F) share features with specimens described as *Eotylotopalla? grandis* from the Neoproterozoic Liulaobei Formation, North China (Tang *et al.* 2013, fig. 12E–F).

Though there are some broad similarities, the Lontovan specimens display significant differences to these Proterozoic forms; in *Trachyhystrichosphaera*, for example, the processes may be polarized on the vesicle, a pattern not observed in any of the Lontovan specimens. Further, no traces of any outer mucilaginous membrane or discrete intracellular body occurs in any Lontovan example despite the large number of well-preserved specimens. The absence of such features is therefore likely to be original. The suite of features seen in these large Cambrian forms are sufficient to warrant classification as a new acritarch form-taxon. We establish a new taxon, *Lontohystrichosphaera grandis* gen. et. sp. nov. (see Systematic Palaeontology below).

Other carbonaceous forms. Lontova/Voosi samples yielding metazoan SCFs invariably yielded a background of other organic-walled microfossils. Nearly all fossiliferous horizons, for example, also preserve relatively large (>200 μm diameter) spheroids (*Leiosphaeridia* sp.; Fig. 9K–Q). These more conventional acritarchs, filaments and other forms are conspicuously more common in samples producing *Protohertzina*, suggesting that their preservation is subject to similar ecological or taphonomic controls. Filamentous forms are the most common, typically consisting of single filaments but also including compound *Polythrichoides*-like specimens in the Kestla Member (Kunda quarry) (Fig. 9B, C), which most likely represent cyanobacteria based on their lack of branching and bundled habit (cf. Samuelsson & Butterfield 2001, fig. 9; Tang *et al.* 2013, figs 13–14). Other, pseudo-segmented filaments in the Kestla Member are assignable to the form-taxon *Rugosoopsis* (Fig. 9D; see Butterfield *et al.* 1994). A single large oval fossil, a millimetre long, 0.46 mm wide, with a distinctive 'cross-hatch' microstructure was recovered from the Kasari Member of the Voosi Formation (Fig. 9A). Comparably sized ovoid cross-hatched forms

from the early Cambrian of the East European Platform were described as *Leiovalia* Eisenack 1965 (Volkova *et al.* 1979, fig. 8.15–17). These specimens (as well as the new Voosi Formation example), however, fall well outside the morphology of the form-taxon *Leiovalia*, which (aside from being substantially smaller) is a smooth-walled acritarch that lacks any comparable surface texture (e.g. Żylińska & Szczepanik 2009, pl. 7.31–33). Masses of frass-like organic material with compacted margins are also abundant in *Protohertzina*-bearing samples, and consist of either cylindrical forms, or lengths of adjoined spheres, ranging from *c.* 300–800 μm in length $\bar{x} = c.$ 550 μm, SD = 159 μm) (Fig. 9F–J). Given their broadly cylindrical to lobate form, they are most likely to represent microcoprolites (see Harvey & Butterfield 2011; Slater *et al.* 2017*b*).

DISCUSSION

These Lontovan data are the first systematic accounting of SCFs from the Terreneuvian Series, substantially
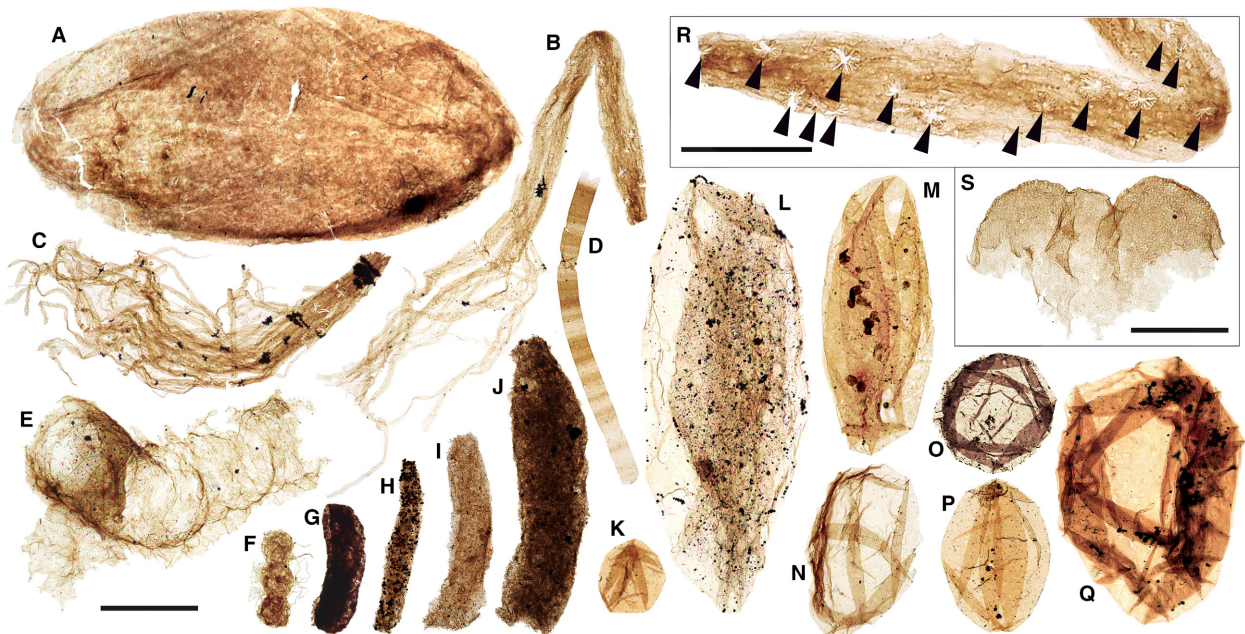

FIG. 9. Collection of problematic fossils from the Estonian Lontova and Voosi Formations. A, large ovoid 'acritarch' with distinctive cross-hatch surface texture from the Kasari Member of the Estonian Voosi Formation. B–C, bundled filamentous *Polythrichoides*-like fossils from the Kestla Member of the Estonian Lontova Formation. D, *Rugosoopsis*-like segmented filament, Kestla Member, Estonian Lontova Formation. E, series of tightly-packed overlapping organic rings, may represent the remains of a collapsed organic-walled tube. F–J, agglomerations of compacted frass-like material, possible microcoprolites. K–Q, large leiosphaerid acritarchs, common in all processed samples from this study, morphologies vary between ovoid (L–M) and spheroidal (N–Q) forms. R, close-up of surface detail of bundled filamentous fossil in B; arrows point to regular star-shaped perforations which are distributed over the entire surface of specimens B and C. S, portion of unknown cuticle with punctate surface ornamentation from the Kestla Member of the Estonian Lontova Formation, possibly metazoan. Slide numbers (all numbers have the prefix NRM-PZ X): A, G = 7062; B–D, R = 7051; E = 7052; F = 7038; H–K = 7023; L = 7055; M = 7056; N = 7035; O = 7022; P = 7013; Q = 7019; S = 7039. Scale bars represent: 200 μm (A–Q); 100 μm (R, S).

complementing and expanding upon the more conventional records of shelly fossils, acritarchs and trace fossils. In many aspects, the biological signal is comparable to that of Fortunian SSFs; for example, the prevalence of protoconodonts/*Protohertzina*, tubular forms and simple scalidophoran-derived spines (Kouchinsky *et al.* 2012; Guo *et al.* 2014; Yang *et al.* 2014a; Nagovitsin *et al.* 2015; Budd & Jackson 2016). But there are also forms that have no counterparts among the SSF record, representing previously undetected aspects of Terreneuvian ecology, in particular thalloid *Retiranus balticus* gen. et sp. nov. and vesicular *Lontohystrichosphaera grandis* gen. et sp. nov.

SCF vs SSF signals

Congruence between Lontovan SCFs and typical Fortunian SSF assemblages is revealing; taken together with examples of wiwaxiids, hyoliths, hallucigeniids and palaeoscolecids from younger Cambrian SCF/SSF assemblages, these records point to a substantial overlap between the two taphonomic modes. In the case of originally mineralized structures found as SCFs, preservation is usually best explained by the fusion of internal and external organic constituents into a single carbonaceous layer following the dissolution of mineral components (cf. Martí Mus 2014). The converse scenario, in which wholly non-biomineralized structures are replicated in phosphate, is a more complex and perhaps less well understood process. While the majority of phosphatic fossils are the products of secondarily replaced carbonate skeletons, or components originally constructed from phosphate, others were originally organic (Brasier 1990). Examples of the latter include cyanobacterial remains (*Spirellus*, *Cambricodium*; Brasier 1990), tubes (e.g. crumpled *Hyolithellus*; Pyle *et al.* 2006, fig. 8.6–7), cnidarians (e.g. *Olivooides*; Dong *et al.* 2016), metazoan cuticle (e.g. Pyle *et al.* 2006, fig. 8.11–19), articulated larval panarthropods (e.g. Orsten-style preservation; Maas & Waloszek 2001; Eriksson *et al.* 2012) and a rich variety of coprolites (e.g. Peel 2015).

Protoconodonts are among the most common SSFs from Fortunian strata (Kouchinsky *et al.* 2012). Structural and chemical analysis of protoconodont spines has demonstrated that they were originally constructed of three primarily organic layers, and only secondarily phosphatized (Szaniawski 2002), though their marked abundance as SSFs would suggest that they were histologically prone to phosphatization, possessed a lightly biomineralized component, or that some forms were originally biophosphatic (Brasier 1990; Kouchinsky *et al.* 2017). Detection of abundant carbonaceous *Protohertzina compressa* sp. nov. in Lontovan sediments supports a primarily organic habit for at least some protoconodont

grasping spines, a premise further reinforced by the preservation of carbonaceous grasping spines among Burgess Shale-type deposits (Conway Morris 2009, fig. 1C; Briggs & Caron 2017; Shu *et al.* 2017). Scalidophoran spines, common in SCFs assemblages, also have a record of phosphatized counterparts. Outside palaeoscolecids, phosphatized examples of Cambrian scalidophorans or stem-scalidophorans include the embryonic *Markuelia* (Dong *et al.* 2005; Donoghue *et al.* 2006; Haug *et al.* 2009; Zhang *et al.* 2017), kinorhynch-like *Eokinorhynchus* (Zhang *et al.* 2015) and priapulid-like *Eopriapulites* (Liu *et al.* 2014; Shao *et al.* 2016). Comparisons of the integumentary spines of these phosphatized juveniles with isolated SSFs (e.g. *Kaiyangites*) has led to an emerging recognition of probable disarticulated counterparts among SSF assemblages (Dong *et al.* 2009; Zhang *et al.* 2015; Kouchinsky *et al.* 2017). Other scalid-like elements among SSFs could include *Fomitchella* (e.g. Matthews & Missarzhevsky 1975, pl. 3 fig. 8; Kouchinsky *et al.* 2017, figs 59–67; Zhu *et al.* 2017, fig. 2P), some specimens assigned to *Seletellus seletinicus* (Yang *et al.* 2014b, fig. 2a–d), *Mongolodus* sp. (Steiner *et al.* 2004a, fig. 8.7; Betts *et al.* 2016, fig. 21W; but see Skovsted *et al.* 2006) and *Hennaniodus* sp. (Zhi-Wen 1992, fig. 6.4–6; Yun *et al.* 2016, fig. 5O). Though scalids among SSFs may have been overlooked, their dominance among SCFs points to a deeper bias, possibly reflecting their size; SSFs that may represent disarticulated scalids are typically >500 μm from base to tip (e.g. Kouchinsky *et al.* 2017, figs 59–67), whereas SCF scalids are usually <200 μm in maximum length (e.g. Fig. 4, I–O; Slater *et al.* 2017a, fig. 7). It is possible that a cryptic record of smaller scalids is being selectively removed from SSF assemblages during processing.

The profusion of secondary phosphatization in early Cambrian fossils probably relates to broad scale palaeoceanographic controls on the abundance of phosphate in Ediacaran and early Cambrian marine environments (Porter 2004). Why originally organic scalids, and protoconodont elements in particular, are so readily replicated in phosphate though, is unclear. One factor may simply be their shape: protoconodonts and scalidophoran cuticular spines both share a broadly cone-like habit. It is well-known that the size, shape and orientation of shells affects their replication in phosphate (Brasier 1990). Indeed, there is evidence to suggest that narrow, conical and tubular morphologies may be preferentially phosphatized (e.g. the prevalence of molluscan steinkerns), since they act as traps in which P-saturated pore waters can become concentrated (Brasier 1990; Creveling *et al.* 2014). Analogous microenvironments could feasibly form in the interiors of a range of hollow bioclasts, whether or not they possessed originally mineralized walls.

Preservation of protoconodonts, tubes and scalids among both SCF and SSF records offers further grounds for recognizing yet more SSF taxa as the diagenetically phosphatized remains of non-biomineralizing organisms (as opposed to the phosphatized remains of aragonitic or calcitic forms, or phosphatic steinkerns). In addition to capturing entirely new aspects of early Cambrian palaeobiology, SCFs also offer a degree of continuity with SSF, and potentially even Doushantuo and Orsten-type phosphatic preservation. This overlap is particularly important in the Cambrian, since detection of comparable fossils across multiple taphonomic modes is crucial for distinguishing any underlying evolutionary signal from that of an ecological/taphonomic megabias.

Such taphonomic correspondence between SSFs and SCFs also has taxonomic implications; both SSFs and SCFs are commonly the isolated parts of originally multi-element scleritomes (Bengtson 1985; Smith *et al.* 2015). Since mineralized and non-mineralized components can potentially be preserved under either of these taphonomic pathways, this raises the possibility of different taphonomic expressions of the same component (see Sciotaxon; Bengtson 1985); or even similar expression of different components. The problems presented by dissociated remains and contrasting preservation states is not unlike the situation faced by palaeobotanists dealing with 'organ-taxa' found in states of permineralization versus flattened compression fossils (e.g. Bateman & Hilton 2009). In all cases where it can be confidently verified, the goal should ultimately be to integrate form classifications into biological taxa, either by establishing that co-occurring sclerites derive from the same scleritome (see Smith *et al.* 2015), through recognition of the parent organism(s) (see Caron *et al.* 2013), or ideally via the identification of articulated scleritomes (cf. Conway Morris & Peel 1990). As potential connections arise, an increased awareness of the taphonomic overlaps in SCF/SSF preservation will aid interpretation of latent synonymies as these respective records continue to grow. In this study we justify the establishment of a new species of *Protohertzina*, *P. compressa* sp. nov., on the basis of its distinct carbonaceous, two-dimensional habit, which is consistent between and within large populations. Although it may eventually prove to be a junior synonym of a phosphatized 3-D *Protohertzina* species, the name usefully delineates the fossil morphology.

New insights into early Cambrian protistan diversity

The Lontovan SCFs shed new light on the diversity of early Cambrian protists, and perhaps signal the existence of 'firmground' seafloor conditions more usually associated with pre-Cambrian environments; Fortunian SSFs (and now SCFs) demonstrate that these poorly mixed and firm early Cambrian seafloor environments (Jensen *et al.* 2005), like their Ediacaran precursors, were host to numerous sedentary organisms, many in the form of enigmatic mineralized, unmineralized and agglutinating 'tubes' (Budd & Jackson 2016; Yang *et al.* 2016) and thalloid forms (LoDuca *et al.* 2017). Other components of the benthos recovered as SCFs appear to be metabolically active, protistan-grade organisms of a kind not previously documented in the Cambrian and perhaps more suitably compared to Proterozoic forms (Javaux *et al.* 2001; Adam *et al.* 2017; Javaux & Knoll 2017). *Lontohystrichosphaera grandis* gen. et sp. nov., for example, is substantially larger and more irregular than typical Cambrian acanthomorphic acritarchs, regularly exceeding 200 μm, and occasionally more than 500 μm in diameter (see Cohen *et al.* 2009, fig. 1). Previously described Lontovan acanthomorphic acritarchs have been uniformly small (5–50 μm) and symmetrical (e.g. *Asteridium tornatum*; Vidal & Moczydłowska 1992), probably reflecting the differing processing techniques: whereas conventional palynological processing recovers smaller cyst-like forms, our low manipulation technique preferentially recovers relatively larger, more delicate fossils.

Unlike more conventional Cambrian acanthomorphic acritarchs *Lontohystrichosphaera grandis* gen. et sp. nov. also shows no evidence of excystment structures, while its conspicuously variable distribution and expression of processes and secondary vesicles points to a continuously growing, metabolically active organism (cf. Butterfield 1997, 2005, 2007; Knoll *et al.* 2006; Javaux & Knoll 2017). Moreover, such large irregular morphologies are functionally incompatible with a planktic habit. As such, *L. grandis* can be reliably interpreted as a metabolically active member of the Lontova shallow-water benthos. Although most likely a photosynthetic alga (a constituent of the 'microphytobenthos'; MacIntyre *et al.* 1996), it is difficult to rule out alternative habits, such as the heterotrophy/osmotrophy of fungi and oomycetes.

Retiranus balticus gen. et sp. nov. similarly represents a benthic (large size and basal holdfast), probably photosynthetic, protist (thalloid habit and shallow-water setting), in this instance almost certainly capturing a larger part of its life cycle as it differentiates what appear to be marginal propagules. The potential recovery of such vesicular propagules among spheroidal acritarchs once again raises potential taxonomic issues, whereby alternate generations of the same organism, when found in isolation, may lead to the establishment of multiple taxa. In any event, it is clear that SCF processing also offers entirely new insights into both metazoan and protistan-grade components of early Cambrian ecosystems, complementing other records of 'soft-bodied' Cambrian 'algae' (cf. LoDuca et al. 2017).

Age of the Lontova/Voosi succession

Like many Terreneuvian strata worldwide, the precise stratigraphic position of the Lontova and Voosi formations has been difficult to constrain. It has been particularly problematic to resolve sequence stratigraphic boundaries in the Lontova Formation, since nearshore sections are almost ubiquitously eroded. Acritarchs and SSFs have been more promising, identifying the Lontovan as Terreneuvian; however, the long ranging biostratigraphic schemes do not conclusively resolve the intra-Terreneuvian stratigraphy of these sediments (i.e. whether Fortunian or Stage 2 in age). The predominance of protoconodonts and tubular fossils among the new SCFs data adds further weight to the signal from compression fossils (*Sabellidites cambriensis*, which were probably restricted to the Fortunian (Kouchinsky *et al.* 2012)), and trace fossils (treptichnid assemblage (Jensen & Mens 2001)) that the Lontovan is primarily Fortunian in age (Volkova *et al.* 1990; Palacios *et al.* 2017).

The principal phase of 'explosive' diversification in the SSF record is broadly coincident with the Fortunian/Stage 2 boundary. Though all fossil biotas are to a greater or lesser degree facies-specific, the correspondence of Lontovan SCFs and trace fossils to 'pre-explosion' SSF biotas and bioturbation indices is revealing. SCF biotas from comparable environments in younger (Stage 4) Baltic and Laurentian strata typically produce a richer diversity of metazoans; together with the Lontovan SCFs, this appears to echo the traditionally recognized 'explosion' signal established from carbonate hosted SSFs, giving credence to a broad-reaching diversification pulse during this interval, as opposed to a peculiarity of the biomineralization record. In concert with acritarchs and trace fossils, these SCFs contribute novel data to a longstanding stratigraphic conundrum in a difficult-to-date sequence relatively devoid of age-diagnostic shelly fossils. Further, the broad geographic and stratigraphic coverage of this study establishes a foundation for comparison with interregional Terreneuvian SCF assemblages. Future sampling of other Cambrian cratons will reveal the degree to which this assemblage is endemic to Baltica or, alternatively, part of a globally characteristic Terreneuvian SCF biota.

SYSTEMATIC PALAEONTOLOGY

Total group of Phylum CHAETOGNATHA Leuckart, 1854
Incertae familiae

Genus PROTOHERTZINA Missarzhevsky, 1973

Type species. *Protohertzina anabarica* Missarzhevsky, 1973. *Anabarites trisulcatus* Zone, Cambrian Fortunian Stage, Kotuikan River, Siberia, Russia (type specimen lost).

Protohertzina compressa sp. nov.
Figures 3, 4A–G

LSID. urn:lsid:zoobank.org:act:6FB392AE-CD73-4AB6-81CB-1379E4B3DC3F

Derivation of name. With reference to preservation as carbonaceous compressions.

Holotype. NRM-PZ X 7032 (Fig. 3BA; Slater *et al.* 2018).

Diagnosis. Simple, spine-shaped carbonaceous elements, up to 2.2 mm long. Spines expand continuously from the tip towards the flared basal part with an average length to base ratio of 3.4:1. Individual spines range from gently curved up to *c.* 90° curvature from base to tip in longer specimens. A smooth outer wall is often missing, exposing layers of longitudinally oriented, occasionally crossing fibres. Convex and concave margins of spines typically thickened and optically darker. Basal opening frequently flattened or broken, occasional specimens reveal an originally oval cross section.

Distribution. Known from the early Cambrian (Terreneuvian) Kestla Member of the Lontova Formation, north-west Estonia (Kunda Quarry), Kasari Member of the Voosi Formation, north-west Estonia (F332-Vihterpalu drillcore).

Remarks. Comparison of the cross-sectional morphology of carbonaceous *Protohertzina compressa* sp. nov. with apatitic *Protohertzina* is precluded by the flattened nature of the former. Nonetheless, other aspects of the morphology lend themselves to comparison, particularly with the type species *P. anabarica*; the longitudinal fibrous structure of *P. compressa* is similar to that of *P. anabarica* (compare Fig. 3AL with Kouchinsky *et al.* 2017, fig. 57, f1). *Protohertzina compressa* sp. nov. is on average smaller than *P. anabarica* (which reaches up to 3 mm in length), and the latter is straighter from base to tip. The (lost) holotype of *Protohertzina anabarica* (Missarzhevsky 1973, pl. 9.1–2) is probably missing the basal portion, but comparison with other *P. anabarica* and topotype material (Kouchinsky *et al.* 2017) reveals that the base is typically broader in *P. compressa* sp. nov., particularly in larger specimens. *Protohertzina compressa* sp. nov. is consistently stouter than *P. anabarica* and other broad forms such as *P. robusta* (Qian 1977).

Incertae sedis

Genus RETIRANUS nov.

LSID. urn:lsid:zoobank.org:act:DB7A1685-4DEB-4192-8614-8373610D24B9

Derivation of name. Named for its resemblance to a weighted-casting-net, after the gladiator class retiarius, who were armed with a weighted net fringed with stones, and the Norse sea deity Ràn, who used a net to capture sailors.

Type species. Retiranus balticus sp. nov. by monotypy.

Diagnosis. As for type species.

Retiranus balticus sp. nov.
Figure 6

LSID. urn:lsid:zoobank.org:act:E6D1CBA3-6FCC-4309-AB5E-EFD03B8A0F7F

Derivation of name. With reference to the Baltic Basin.

Holotype. NRM-PZ X 7062 (Fig. 6P; Slater *et al.* 2018).

Diagnosis. Sheet-like or funnel-shaped organisms consisting of a main 'thallus' bearing apically/marginally distributed spheroidal to ovoid vesicles with a unilayered apparently acellular wall. Apical portion may terminate in a single vesicle, branch to multiple vesicles, or expand to a wide flabelliform sheet fringed with many vesicles. Vesicles may exhibit a darkened spot *c.* 10% the size of the parent vesicle. Complete specimens up to 2.5 mm in maximum dimension, with regularly spaced concentric banding emanating from the narrow base and widening toward the flabelliform terminus. Narrow base emanates from an ovoid basal holdfast. Marginal vesicles are typically darker than the main sheet. Larger thalli may exhibit a crenelated margin, where the majority of vesicles are borne on the outermost lobes and the depressions house comparatively fewer vesicles. Vesicle size does not scale to the overall size of the sheet; however, in the largest specimens with crenelated margins the vesicles are dominantly ovoid.

Distribution. Known from the early Cambrian (Terreneuvian) Kasari Member of the Voosi Formation, north-west Estonia (F332-Vihterpalu drillcore) and Lontova Formation, south-eastern Lithuania (Tverečius-336 drillcore).

Remarks. The biological affinity of these fossils is unresolved.

Incertae sedis

Genus LONTOHYSTRICHOSPHAERA nov.

LSID. urn:lsid:zoobank.org:act:C3265483-EA86-44F0-A38B-91039D1CDB67

Derivation of name. Named for its occurrence in sediments of the Lontova Formation, and for its spine-covered spherical appearance.

Type species. Lontohystrichosphaera grandis sp. nov. by monotypy.

Diagnosis. As for type species.

Lontohystrichosphaera grandis sp. nov.
Figures 7, 8

LSID. urn:lsid:zoobank.org:act:A07DA56F-E84E-4EEF-936B-5D350AF570B2

Derivation of name. With reference to the relatively large size of these microfossils compared to other vesicular forms.

Holotype. NRM-PZ X 7023 (Fig. 7L; Slater *et al.* 2018).

Diagnosis. Large spheroidal or oval vesicles, with one to many irregularly distributed heteromorphic hollow processes. Vesicle wall is smooth. Processes open basally directly into the main vesicle. Processes may be tubular, conical or consist only of small protrusions of the vesicle wall. When complete, longer processes terminate in a pointed or rounded tip. Contiguous secondary vesicles occasionally occur, smaller than the primary vesicle. An optically darker internal mass often occurs within the vesicle(s), typically around two-thirds the size of the main vesicle.

Distribution. Early Cambrian (Terreneuvian) Kestla Member of the Lontova Formation, north-west Estonia (known from the Kunda Quarry).

Remarks. Specimens of *Lontohystrichosphaera grandis* appear to be particularly delicate, and do not survive conventional palynological processing. The biological affinity of these microfossils is unclear; however, the variability of outline and process distribution and length, and presence of contiguous sub-vesicles suggest that *Lontohystrichosphaera grandis* represents the remains of an ontogenetically and metabolically active eukaryotic organism, and not a dormant protistan cyst.

DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: http://zoobank.org/References/C5EB3F45-98C9-470A-8775-FA57F54736AB

Additional high resolution images of the holotypes described in this paper are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.8hn63

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