COCHLEATINA: AN ENIGMATIC EDIACARAN–CAMBRIAN SURVIVOR AMONG SMALL CARBONACEOUS FOSSILS (SCFs)

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Abstract: Conspicuously few body-fossil taxa are known to span the Ediacaran–Cambrian boundary, a pattern usually taken to signal either a terminal Proterozoic mass extinction, or taphonomic failure. We draw attention to the emerging record of small carbonaceous fossils (SCFs), which exhibit continuous preservation spanning this critical interval. Here we focus on the enigmatic SCF Cochleatina, a morphologically complex coil-shaped problematicum that ranges across the Ediacaran–Cambrian divide, and is potentially among the oldest fossil occurrences of metazoans. We report new material of Cochleatina canilovica from the Ediacaran of Estonia and Ukraine, which offers new characters for assessing its palaeobiology. Significantly, new specimens include sets of three-alike triplets of Cochleatina adhering to organic sheets, suggesting a clustering habit, or grouping of elements within an individual during life; an important step in constraining the morphology and ecology of this Ediacaran–Cambrian problematicum. We present revised systematic descriptions for Cochleatina and C. canilovica, and critically evaluate previous biological interpretations, drawing comparisons with metazoan, algal and protistan analogues. We reject hypotheses supporting Cochleatina as a metazoan mouthpart, and suggest new grounds for viewing Cochleatina as a potential multicomponent predator that trapped protists among microbial mats. Most occurrences are from Baltica, but we synthesize sporadic reports of Cochleatina from other palaeocontinents, pointing to its global distribution during the latest ~10 myr of the Ediacaran and majority of the earliest Cambrian Fortunian Stage. As a rare example of an ‘Ediacaran survivor’, Cochleatina highlights the broader significance of SCFs as a novel means of tracking evolutionary patterns through the Proterozoic–Phanerozoic transition.

Key words: Ediacaran–Cambrian survivor, oldest metazoan, Proterozoic mass extinction, small carbonaceous fossils, fossil problematica.

The Ediacaran–Cambrian boundary, approximately 541–539 Ma (Linnemann et al. 2019), is widely recognized as a juncture of exceptional ecological and evolutionary importance (Conway Morris 2000; Butterfield 2007; Budd & Jensen 2017). At around this point, the fossil record is permanently transformed by the appearance and radiation of diverse biomineralizing and agglutinating forms (Kouchinsky et al. 2012). This switching-on of the ‘shelly’ fossil record approximately corresponds with an increase in the degree and complexity of bioturbation (Jensen et al. 2006; Herringshaw et al. 2017), substantial shifts in the nature of biogenic sediments (Davies et al. 2019, fig. 1), a disappearance of macroscopic Ediacara-style preservation (Butterfield 2003), and major changes in the composition of acritarch assemblages (Moczydlowska 1991; Butterfield 1997; Nowak et al. 2015). Identification of such ecological or evolutionary perturbations is heavily reliant on taphonomic continuity; in other words, the factors governing fossil preservation should not substantially change through the time interval of interest. If they do, then the traceability of lineages/taxa can be seriously compromised. The coincident opening and closure of several key taphonomic windows across the Ediacaran–Cambrian transition obscures the precise tracking of taxonomic ranges from this crucial interval. At present, only a handful of taxa known from body fossils are convincingly shown to span the boundary (e.g. Narbonne et al. 1997; Crimes & McIlroy 1999; Hagadorn et al. 2000; Narbonne 2005; Laflamme et al. 2013; Moczydlowska et al. 2014; Darroch et al. 2015; Budd & Jensen 2017).
The apparent disconnect in the body fossil record is contrasted by the relatively unbiased trace fossil record, which instead documents a signal of continuity between late Ediacaran and earliest Cambrian benthic bilaterian behaviour (e.g. Jensen 2003; Mángano & Buatois 2017; Kesidis et al. 2019). Before a precise description of the magnitude, timing and nature of this transition can reasonably be achieved, there is a pressing need for an improved accounting of non-biomineralizing taxa in order to discriminate genuine macroevolutionary patterns from localized signals or taphonomic shortfalls.

Small carbonateous fossils (SCFs) offer one means of tracking the Ediacaran–Cambrian transition without the associated biases of mineralization. Even under relatively indifferent taphonomic circumstances, cell walls, cuticle, and other recalcitrant components of non-biomineralizing organisms can be recognizable preserved (Butterfield & Harvey 2012). The widespread preservation of SCFs has recently been demonstrated from regions and time-intervals where other, more ‘exceptional’ evidence of non-biomineralizing taxa is lacking (Slater et al. 2017a–b, 2018). In this study, we focus on an enigmatic SCF taxon, Cochleatina, a distinctive and widely distributed taxon that appears to span the Ediacaran–Cambrian divide. Cochleatina is especially interesting in that it is preserved in substantially different depositional environments to iconic boundary-spanning taxa such as Cloudina (Penny et al. 2014; Warren et al. 2014; Yang et al. 2016). Despite this, Cochleatina has so far been neglected from discussion of Ediacaran ‘survivors’, and so warrants renewed attention, particularly in the context of recent debate on rates of turnover, extinction and the nature of the Ediacaran–Cambrian transition (Budd & Jensen 2017; Darragh et al. 2018; Tarhan et al. 2018; Wood et al. 2019).

Cochleatina is a coiled carbonateous fossil formed as a spiral-shaped ornamented with fine serrations (Fig. 1). Examples of this fossil were first figured among acid-extracted material from the Ediacaran of the Ukraine by Aseeva (1974), but were initially interpreted as simple coiled filaments and ascribed to the filamentous form-taxon Volyniella (albeit as a new species). Three further species were later added based on material from the Rovno (latest Ediacaran or earliest Cambrian) and Lon-tova (Cambrian) formations in Belarus, Lithuania and Latvia (Paskevičienė 1980), but remained assigned to Volyniella until Aseeva (1983a) established Cochleatina as a new genus to circumscribe these morphologically distinct fossils. Several succeeding studies mentioned or figured Cochleatina from sediments in Baltica and Siberia (e.g. Velikanov et al. 1983; Aseeva 1988; Rudavskaya & Vasilyeva 1989), but with no substantial revision until a major redescription and analysis by Burzin (1995), in which the four currently accepted species were amended: C. cantalovica, C. rara, C. rudaminica and C. ignalinica.

More recent reports of Cochleatina, recovered among acritarch preparations, have expanded its known geographic range beyond Baltica and Siberia to Avalonia and Gondwana (e.g. Sabouri et al. 2013; Palacios et al. 2018). Attempts to pin Cochleatina to the tree of life have been wide-ranging. Several authors have proposed a metazoan affinity (among annelids or molluscs; Butterfield & Harvey 2012), a premise which would clearly have significant implications if confirmed or refuted.

Here we describe new material of Cochleatina from Ediacaran sediments of Estonia (Kotlin Formation) and Ukraine (Krushanovka Formation). We further discuss the broader significance of this SCF taxon in light of its status as a credible Ediacaran–Cambrian ‘survivor’, in the context of recently revised stratigraphy (Meidla 2017), and its emerging palaeobiogeographical distribution (Fig. 2). We further examine and test previous hypotheses for the biological affinity of Cochleatina, and propose new models for its possible mode of life.

GEological SETTING

Estonia

The Kotlin Formation (Fig. 3) is widely developed across the Baltic States on the East European Platform, and equivalent strata occur from Poland in the west, to the margin of the Baltic craton in the east (Moczydłowska 1991; Pirrus 1993; Mens & Pirrus 1997). In Estonia, the Kotlin Formation is known exclusively from subsurface drillcore material, the nearest outcrop being on Kotlin Island (Russia) in the Gulf of Finland. The Kotlin Formation comprises a relatively homogeneous package of sediments composed predominantly of finely laminated grey, illite–smectite mixed-layer clays, with occasional interbeds of fine-grained sandstone and siltstone (Mens & Pirrus 1997; Raidla et al. 2006). Due to a relatively shallow burial depth and quiescent regional tectonic history, Kotlin strata have experienced negligible thermal alteration over their more than half a billion year history (Raidla et al. 2006). In Estonia, the Kotlin Formation conformably overlies the coarser-grained sandy sediments of the Gdov Formation, and is in turn overlain by the correspondingly sandstone-rich Voronka Formation (Fig. 3; Mens & Pirrus 1997; Meidla 2017). Together, this package of Ediacaran sediments rests unconformably on a weathered crystalline basement (Puura et al. 1983; Nielsen & Schovsbo 2011; Meidla 2017).

Despite its relative homogeneity, the Kotlin Formation in Estonia is partitioned into three subdivisions (Mens & Pirrus 1997; Meidla 2017). The lowermost Jaama and uppermost Laagna members comprise relatively homogenous grey clays, whilst the middle Meriküla Member can
be distinguished by its visible fine-scale intercalations of sand, silt, and clay (‘varve-like’ appearance; Pirrus 1992), abundance of sapropel films, and macroscopic ‘vendotaenid’ fossils on bedding planes (Mens & Pirrus 1997).

The Kotlin Formation was deposited in a shallow-marine pericratonic basin (Poprawa et al. 1999). Some authors have proposed brackish (Bityukova & Pirrus 1979) or even freshwater conditions within a basin with restricted circulation, based on suggestive boron concentrations in mudstones, localized absence of ‘Ediacara-type’ macrofossils, and a paucity of trace fossils. Certain regions where the Kotlin Formation developed, however, show clear evidence of marine deposition (see Burzin 1996), and the extent of freshwater/brackish influence remains controversial.

The Kotlin Formation shares its name with the regional chronostratigraphic Kotlin stage, which in Estonia encompasses the Gdov, Kotlin and Voronka formations (Fig. 3). Although once placed relatively deep within the Ediacaran System (e.g. Sokolov 2011), the Kotlin Formation is now thought to have been deposited during the terminal ~10 myr of Ediacaran time, based on correlation with strata from the Lublin Slope (Poland), Podillya (Ukraine), Urals and White Sea region (Russia) where U–Pb zircon dates from volcanic tuff horizons have yielded lower boundary ages in the range of 551–548 Ma (Moczydlowska 1991; Grazhdankin et al. 2011; Meidla 2017; Soldatenko et al. 2019).

Ediacaran sediments of the Krushanovka Formation (Kanilovka Series) from Ukraine represent broadly coeval deposits, also belonging to the Kotlin regional stage (Fig. 3; Sokolov & Fedonkin 1985; Velikanov 1990; Iosifidi et al. 2005). Note that the Kanilovka Series of Podillya (alternatively Podolia) is not to be confused with the Kanilovka Formation of Volyn from which specimens of Cochleatina have been reported elsewhere in Ukraine (Burzin 1995). The Krushanovka Formation is widely known from drillcore in the Podillya region of Ukraine, and comprises a series of fine-grained, greenish-grey to white sandstones with substantial interbeds of reddish siltstones and claystones in its upper parts (Iosifidi et al. 2005). The formation rests conformably on the Zharnovka Formation (a sequence of coarse to fine-grained sandstones) and is capped by the overlying Studenitsa Formation (predominantly coarse to fine-grained sandstones with occasional siltstones).

There are two recognized subdivisions of the Krushanovka Formation: a lower (~45 m thick) Kryvchany Member, and an upper (~15 m thick) Durnyakovka Member. The Kryvchany Member is generally coarser, with a larger proportion of sandstones, while the Durnyakovka Member is dominantly composed of distinctive red siltstones with occasional coarse sandstone beds (Sokolov & Fedonkin 1985; Iosifidi et al. 2005). Deposition
occurred in a shallow-marine basin with storm influence (Iosifidi et al. 2005).

**Sampling**

Sampling for microfossils targeted the most fine-grained lithologies (mudstones and siltstones) from both areas. In Estonia (Meriküla Member of the Kotlin Formation), we processed a total of 31 samples: 11 from the Maidla 75A drillcore; 2 from the Maidla F-238 drillcore; 6 from the Toila 77 drillcore; and 12 from the Meriküla F-169 drillcore. From the Podillya region of Ukraine, a total of 5 samples were processed from the Durnyakovka Member of the Krushanovka Formation, drillcore No. 700. Estonian cores are housed at the Tallinn University of Technology Institute of Geology.
(GIT) core-storage at Särghaa (Estonia), and samples from drillcore No. 700 (Podillya, Ukraine) are hosted at the Institute of Precambrian Geology and Geochronology of the Russian Academy of Sciences in Saint Petersburg. SCF processing and examination followed a gentle, low-manipulation hydrofluoric acid maceration procedure aimed at the recovery of larger, delicate forms, otherwise destroyed by standard palynological processing (see techniques outlined in Butterfield & Harvey 2012).

RESULTS

Our processing recovered a total of 103 individual Cochleatina specimens, of which 70 are from the Estonian Kotlin Formation (Figs 4, 5), and 33 come from the Ukrainian Krushanovka Formation (Fig. 6). The majority of specimens were recovered from a small number of highly productive samples; Estonian specimens were recovered from a depth of 186–187 m in the Maidla 75A drillcore, 180 m depth in Maidla F-238 drillcore, 153 m in the Toila 77 drillcore, and 119.4 m from the Meriküla F-169 drillcore, whilst those from the drillcore No. 700 in Podillya, Ukraine were sourced from a productive layer at 184 m depth. Both the Estonian and Ukrainian samples of Cochleatina exhibit substantial taphomorphic variation. In the Estonian samples, all Cochleatina-bearing horizons produced masses of sapropel sheets, alongside occasional vendotaenids and filamentous microbes. Productive samples from Ukraine were also associated with sapropel sheets, but at substantially lower levels.

New material

Specimens from the new Estonian Kotlin assemblage (Figs 4, 5) are preserved as flattened spirals or incomplete sections of a spiral fused to sapropel films (sheets of relatively featureless organic matter, sometimes with identifiable filaments superimposed and variably fused together).
These sapropel films are interpreted as compacted and variably fused sedimentary organic material and/or benthic mats (Figs 4, 5). Specimens consist of a coiled ribbon; coils reach 540 μm in maximum width (x = 246, SD = 83, n = 70) and display a continuum of morphologies, ranging from tightly wound bobbin-like configurations (Figs 4A, 5G–J) to more open spiral forms (e.g. Fig. 5D, F, R, S, T). The ribbon narrows towards the centre of the spiral and is a complex of four distinct longitudinal zones running the entire ribbon length (Fig. 7). Thin, sharply pointed serrations project from the first inner zone, directed away from the centre of the coil, though these serrations are often obscured by the underlying organic sheet (e.g. Figs 4L, 5E). Other zones are discernible by their thicknesses (Fig. 7; see Systematic Palaeontology, below). Basal portions are either broken (e.g. Fig. 4I), or alternatively, where fused to a sheet, the ribbons have no obvious termination but instead fade into the sheet material (e.g. Fig. 5D–F, H, L).

The new Ukrainian *Cochleatina* (Fig. 6) occur as individual isolates (with the possible exception of Figure 6J, no clusters were recovered) and were never found in attachment to larger organic sheets (note the absence of organic material in the central opening of the bobbin;
Fig. 6. The coils reach 320 μm in maximum width. Like the Estonian specimens, the ribbons are divided into four discernible zones which narrow towards the centre of the spiral (Fig. 7). The ribbons are optically darker than their counterparts from the Kotlin Formation, especially the first and third zones of the ribbon which are opaque in
FIG. 6. Cochleatina from the Krushanovka Formation, Podillya, Ukraine. Specimens sourced from a productive layer at 184 m depth within drillcore No. 700. Tallinn University of Technology acquisition numbers (GIT): A–G, 855; H–J, 856. Scale bar represents 100 μm.
most specimens (Fig. 6). Serrations emanating from the inner first zone of the ribbon are also prominently visible in the majority of specimens (e.g. Fig. 6A–G, E, G, J). The ribbon tip has a brush-like termination of fibrous projections between 5 and 15 μm in length (e.g. Fig. 6C–G).

Comments

The new specimens from Estonia and Ukraine are assigned to *C. canilovica* on the basis of their consistent spinose serration, ribbon oriented perpendicular to the bobbin axis, and four broad ribbon zones, features which are lacking in other taxa (see Systematic Palaeontology, below). Both the Estonian and Ukrainian assemblages are consistent with the currently known range of *C. canilovica* which is reported from the Kotlin regional stage of the late Ediacaran, and the lowermost part of the Rovno regional Ediacaran/Cambrian stage. Although *Cochleatina* has been reported from elsewhere in the Baltic region (e.g. Paškevičiene 1980), these are the first reports from Estonian strata.

The new assemblages of *Cochleatina* from Estonia and Ukraine differ in a number of aspects. For example, serrations appear more pronounced in the Ukrainian specimens. This, however, appears to be purely taphonomic; serrations are present in all well-preserved Kotlin *Cochleatina*, but are simply less prominent due to the obscuring presence of the underlying/fused organic sheet. *Cochleatina* from the Krushanovka Formation exhibit darker ribbons (particularly in zones one and three), however, this can be explained by variations in local post-depositional burial histories (e.g. different degrees of thermal alteration). When these taphonomic considerations are taken into account, it is clear that both assemblages of *Cochleatina* exhibit the same underlying morphology.

Clustered forms

Among the more complete specimens of *Cochleatina* recovered from the Kotlin Formation are a notable subset that occur as clusters, consisting of three coils adhered to the same carbonaceous sheet (N = 6). The
sheets are interpreted as the compacted remains of benthic organic material. No more than three coiled elements per cluster are seen, even on more extensive sheets. Within clusters, some coils are incomplete (Fig. 5H, K), and some partially overlap (Fig. 5D, F, H, L). Clusters can comprise tightly-wound bobbin-like and uncoiled forms, but within each cluster the coils are always of the same (potentially ontogenetic) stage/type. The asymmetry of the ribbon zones, in particular the overlap of the serrations, reveals that the coils occur as enantiomorphs (both right-handed and left-handed forms/chirality), which can co-occur in the same cluster (e.g. Fig. 5D, F). Occurrence as triplet clusters is an unexpected and novel insight into Cochleatina morphology. It is possible that the ‘individual’ Cochleatina reported in previous studies have been selectively disaggregated during more intensive, conventional palynological processing; indeed, low-manipulation processing appears to be essential for recovery of these delicate clusters. Since these Cochleatina are all at the same stage or type within a cluster, they are unlikely to represent fortuitous superposition via currents or fall-out from the water column. Either these clusters represent groups of three similar individuals from a population with a benthic ecology, or were clustered prior to sinking from suspension, or are the recalcitrant components of a single organism that has otherwise decayed away.

**DISCUSSION**

**Biological affinities**

Previous suggestions for the biological nature of Cochleatina have been broad ranging, reflecting the dearth of suitable fossil or modern analogues (a problem shared with many Ediacaran fossils). Proposed affinities have included the coiled ‘elaters’ of bryophyte-grade plant spores (Fig. 8A; Ischenko 1983; Gnilovskaya 1988), defensive ejectosomes of Cryptophyta (Fig. 8C; Burzin 1995) and subcomponents of a macroscopic alga (Burzin 1995). Homology with the elaters of liverwort, hornwort and Equisetum spores (Fig. 8A) can be ruled out on both functional grounds (the ribbons of Cochleatina are solid with no internal cavity, and therefore unsuitable for extension and retraction via hygroscopic turgor), and the fact that spores assignable even to stem-embryophytes are not otherwise known until the Ordovician (Wellman & Gray 2000; Edwards et al. 2014). The coiled ribbon-like ejectosomes of Cryptophyta bear a superficial resemblance to Cochleatina (Fig. 8C; cf. Hausmann 1985, fig. 132) but are intracellular organelles, orders of magnitude smaller than Cochleatina, making even an analogous function improbable. Similarly, the serrated filamentous ejectosomes of helicosporidial cysts are somewhat similar in form to Cochleatina, but are less than ten microns in size (Fig. 8B).

Cochleatina specimens have been reported in rare instances adhering to the macroscopic fossil ‘alga’ Kanilovia insolita (Ischenko 1983) from the ‘Kotlin’ regional stage of Ukraine (e.g. Gnilovskaya 1988, pl. 17.26). This association with Kanilovia insolita (itself a problematicum) is intriguing, but whether the relationship is truly biological is difficult to ascertain; even if fortuitous superposition could be ruled out, there is the possibility that the Cochleatina were derived from epibionts or some other organism in association with Kanilovia insolita. Similarly, though the triplet associations of Cochleatina (Fig. 5) are probably biological, the attachment of Cochleatina to organic sheets (e.g. Eosinian material in this study) may or may not be biological. It is common among SCF-style preservation for multiple overlapping organic constituents to become fused into a single layer during diagenesis (Martí Mus 2014). The sheets themselves preserve little discernible morphology, and although they could represent fragments of thalli (some have regular margins), they could alternatively be regarded as sheets of degraded and depolymerized organic matter (sapropel), to which the more recalcitrant Cochleatina are fused. The consistent within-cluster similarity of Cochleatina in these instances would at least suggest the coils themselves represent structures from a single individual, or individuals from a single population (Fig. 5D, F, H, K).

Elsewhere among the fossil record, some of the more densely coiled Cochleatina bear a superficial resemblance to sheet-like fossils preserved in Terreneuvian (lower Cambrian) hydrothermal cherts from South China, which can exhibit a tightly enrolled coil-like habit, the coils even occurring in ‘clusters’ (Fig. 8G–H; see Yin et al. 2017, figs 5A, C–E, 6A, E–F, 7A). These sheet-like fossils (interpreted as animal cuticles by the authors) also bear a fine surface covering of hair-like or dentate projections (Yin et al. 2017, fig. 4E, F). A more precise structural comparison to Cochleatina, however, is problematic; the surface spines on these silicified sheets are sparsely distributed hollow projections, quite unlike the regular rows of tooth-like serrations in Cochleatina. Moreover, Cochleatina is never found as distended, sinuous sheets or loops, but only occurs as regular coils. In instances where specimens are found on sheets (e.g. Figs 4A, B, D, G, J, L, M, Q, S; 5D–K, P) there is no basal connection to a sheet-margin, indicating that Cochleatina cannot be the flattened enrolled margin of such a sheet or cuticle.

**Cochleatina as a feeding structure**

Although only a few of the previously proposed affinities for Cochleatina can be rejected outright, none offers a
FIG. 8. Comparative extant and fossil analogues for Cochleatina. A, coiled elaters found in triplets on Elaterites triferos plant spores (Pennsylvanian) (see also: Good & Taylor 1974, figs 1–8; Baxter & Leisman 1967, figs 1–18). B, SEM of dehisced helicosporidial cyst (parasitic green algae) showing uncoiled filamentous cell bearing barbed serrations. C, reconstruction of the ribbon-like ejectosome of Cryptophyta algae (intracellular scale). D–E, SEM of the protozoan trapping structure of the corkscrew plant Genlisea repens (angiosperm); E, close-up of D showing serrated coils through which prey enters. F, Redkinia spinosa from the Ediacaran of north-west Russia, inset shows enlargement of serrations. G–H, coiled organic sheets found in early Cambrian (Terreneuvian) cherts. I, paired coiled radula of the extant mollusc Plawenia sphaera. J, coiled anterior region of the ciliated protist Stentor. Images from: A, Taylor et al. (2009); B, Boucias et al. (2001); C, based on diagram from Biocyclopedia (Cryptophyta); D–E, Rutishauser (2016); F, Golubkova et al. (2018); G–H, Yin et al. (2017); I, Scheltema & Schander (2000); J, Lanzoni et al. (2019). Scale bars represent: 225 μm (A); 7.5 μm (B); 1 mm (D, F); 100 μm (E); 20 μm (G–H), 200 μm (I); 50 μm (J).
convincing basis for assigning it to any particular biological taxon. Nevertheless, there are other extant and fossil examples that serve to elucidate at least some of the characteristics that set *Cochleatina* apart. Notably, *Cochleatina* can be usefully compared to a variety of feeding structures seen in extant and fossil heterotrophs, from protistan to eumetazoan grade.

Comparisons have been made between *Cochleatina* and another serration-bearing carbonateous fossil, *Redkinia* (Fig. 8F; Sokolov 1977; Burzin 1995), which also occurs in Ediacaran deposits, both as microfossils (Velikanov et al. 1983, pl. 18, images 8–9) and as bedding-plane visible mesofossils (Golubkova et al. 2018, fig. 2A). It was initially proposed that *Redkinia* represented a disarticulated polychaete jaw (i.e., a scolecodont; Sokolov 1977) and later, the mandible-like jaws of a stem-arthropod (Conway Morris 1993a); if the connection to *Redkinia* was established, it would potentially support a bilaterian affiliation for *Cochleatina*. Burzin (1995) highlighted the shared characteristics of *Redkinia* and *Cochleatina*, principally the first and second order serrations (inset in Fig. 8F), which are somewhat similar to those seen in *C. ignalinica*, and considered the possibility of the latter evolving from the former based on their stratigraphic relationships (but questioned the ability of *Cochleatina* to have functioned as a feeding apparatus). It is also questionable whether the two structures (*Cochleatina* and *Redkinia*) are homologous; serrations are a deeply convergent morphological feature, and other than their carbonateous habit, this is the only shared character which promotes any useful comparison.

A further likeness to metazoan mouthparts was raised by Butterfield & Harvey (2012), who remarked on the broad similarity of *Cochleatina* to certain molluscan radulae. In particular, the simple pairs of coiled radulae borne by certain Solenogastres (Fig. 8I) are somewhat *Cochleatina*-like in overall appearance (see: Scheltema & Schander 2000, fig. 19F; Scheltema 2014, figs 3, 4). Cambrian radulae are known from SCFs (Butterfield 2008) and from the radula-like mouthparts of *Wiwaxia* and *Odontogriphus* (Smith 2012); *Cochleatina* substantially predates these occurrences. However, *Cochleatina* also lacks any belt-like arrangement of individual tooth-elements; the ribbon is a solid structure, with no joints or segments. Moreover, one of the species of *Cochleatina* (*C. rudaminica*) does not possess any serrations at all, making a radula-like function or homology unlikely.

Among extant organisms, a particularly useful comparison is with the giant (>1 mm) single-celled ciliate *Stentor* (Tartar 1961; Slabodnick & Marshall 2014). Specifically, the coiled anterior region of oral cilia in *Stentor* is strikingly reminiscent of *Cochleatina* and reaches a similar size (Fig. 8J; Foissner & Wöllf 1994, figs 1–6, 11–15; Zinskie et al. 2015, figs 2, 54; Lanzoni et al. 2019, fig. 1). These cilia are fused into flat, triangular plates and borne on a coiled basal membranellar band. Environmental shocks can lead to the membranellar band being sloughed off and detached from the main body of the *Stentor* (Tartar 1961; Sood et al. 2017, fig. 1). When shed, the membranellar band does not disaggregate, but remains fused as an isolated ribbon which contracts in the transverse direction to form an even more tightly wound coil (Tartar 1961). The microanatomy of *Stentor* (particularly *S. coeruleus*) has been studied in detail for its ability to regenerate, during which clusters of ciliary bands can form (e.g. Tang & Marshall 2017, figs 2, 4). Similar clustering can occur naturally during reproduction or during the sessile rest state, when numerous individual *Stentor* can attach adjacent to a substrate via their posterior holdfast (Tartar 1961). The main obstacle to analogy with *Cochleatina* is taphonomic. Without any obvious robust macromolecular extracellular components to the ciliary band, it is difficult to envisage how such a structure could produce the recalcitrant SCF *Cochleatina*. It is possible that relatively labile structures could fuse to more resistant organic materials during diagenesis, forming a composite structure (Martí Mus 2014), and it is worth noting that seemingly decay-prone tissues are occasionally captured in Burgess Shale-type Lagerstätten (e.g. cenophores; Fu et al. 2019, fig. 2C). Regardless of taphonomic issues, these similarities with *Stentor* demonstrate that complex SCF structures like *Cochleatina* could, in principle, derive from protists.

Another intriguing possibility is that the coils of *Cochleatina* functioned as a spiral protozoan trap, analogous with the protistan traps of extant *Genlisea*, the corkscrew plant (Fig. 8D–E; Barthlott et al. 1998). In *Genlisea*, specialized spiral rhizophylls with a narrow serrated slit serve to trap motile protists in the manner of an ‘eel trap’ (Rutishauser 2016). Progressively narrowed spirals or coils are prevalent among such traps in the broadest sense, including those of ciliated predatory protists (e.g. *Stentor*), helical bryozoans (McKinney & McGhee 2003), coiled graptolites (e.g. *Cyrtograptus* and *Monograptus curriculatus*; Linarsson 1881; Williams & Zaslavieicz 2004), the spiral traps constructed by polychaetes (Minter et al. 2006) and even the bubble-traps of whales (Leighton et al. 2007). Viewed in this light, the multi-spiral and bobbin shaped forms of *Cochleatina* may represent multiple traps under continuous rejuvenation. Movement is key to predation; in a pre-muscular world (as also seen in plant and fungal predators), passive sit-and-wait trapping is expected to have been the standard feeding technique, with protozoans as the primary target. Whereas Ediacaran rangeomorphs may have extracted food via passive suspension, *Cochleatina* may represent a next-step in luring self-propelled prey (perhaps aided by attractive chemotaxis as in *Genlisea* (Barthlott et al. 1998) and
carnivorous fungi (Barron 1981)). Trapping of protistan prey may be seen as part of a broader stepwise escalation of eukaryovory and predation running from the Tonian to the Cambrian (Porter 2011; Cohen & Riedman 2018; Antcliffe et al. 2019). Sponges (and angiosperms and fungi) also display rare instances of trap-based carnivory (Vacelet & Boury-Esnault 1995), but this style of hunting would have declined in importance in a world of increasingly motile eumetazoan predators.

An Ediacaran ‘survivor’

The oldest known Cochleatina are found in rocks of the Kotlin regional Baltic/Siberian stage (this study; Burzin 1995, 1996; Golubkova & Raevskaya 2005). Under all schemes, the Kotlin is regarded as Ediacaran in age (Grazhdankin et al. 2011; Meidla 2017). The youngest Cochleatina are recovered from Fortunian strata of the regional Baltic Lontovan Stage (Paskeviciene 1980), which probably corresponds to the latter half of Fortunian time based on its acritarch and trace fossil contents (in particular the appearance of the acritarchs Granomarginata prima and Asteridium tornatum along with trace fossils such as Treptichnus pedum, Gyrolithes and Monomorphichinus; Moczydłowska 1991; Jensen & Mens 2001; Palacios et al. 2017, 2018; Slater et al. 2018). The majority of reports, however, are sourced from the intervening ‘Rovno’ regional Baltic/Siberian stage. In the older literature (e.g. Burzin 1995), the Rovno was generally regarded as forming the uppermost division of the ‘Vendian’ System. It is currently unclear whether the Ediacaran–Cambrian boundary actually resides within the Rovno stage (Mens et al. 1990; Moczydłowska 1991; Jensen & Mens 1999), however, in places the upper part of the Rovno Formation is clearly Fortunian (Treptichnus pedum and

![Image](image_url)
other typically basal Fortunian ichnofossils are found in the Rovno; Palij 1976; Fedonkin 1983). While some recent schemes regard the entire Rovno stage as of earliest Fortunian origin (Meidla 2017), the scheme of Moczydłowska (1991) places the lower parts of the Rovno in the Ediacaran and the upper portion, in which trace fossils of Cambrian aspect appear, in the Fortunian. Regardless of which scheme is used, Cochleatina ranges across the Ediacaran–Cambrian boundary (Fig. 9).

The majority of Cochleatina specimens have been found in Ediacaran–Cambrian sediments of the Baltic Basin and Ukraine (Fig. 2). Rare reports from beyond these sedimentary basins occur elsewhere on the palaeocontinent Baltic (Finnmark; Högström et al. 2013), as well as from the palaeocontinent Siberia (Rudavskaya & Vasilyeva 1989), with isolated reports from Avalonia (Palacios et al. 2018) and Iran (Sabouri et al. 2013; Etemad-Saeed et al. 2016). The current pattern is liable to change with increased exploration of undersampled regions, but taken at face value, the distribution of Cochleatina is centred on the margins of the Ægir Ocean (Torsvik & Rehnström 2001), as well as adjacent peri-Gondwanan terranes (Fig. 2).

Cochleatina demonstrates how SCFs can contribute to the emerging fossil record of Ediacaran–Cambrian ‘survivors’ (Fig. 9). Although all Cambrian taxa are necessarily derived from lineages that survived from the Ediacaran, the current picture of the Ediacaran–Cambrian boundary remains one of widespread fossil range truncation. Closer scrutiny, however, reveals a more complex pattern. ‘Terminal Ediacaran’ Cloudina, for example (Amthor et al. 2003), is now known to range into the Cambrian (e.g. Zhuravlev et al. 2012; Yang et al. 2016; Han et al. 2017; Simón 2018), as do the ‘Ediacaran macrofossils’ Swarptunia (see; Narbonne et al. 1997; Jensen et al. 1998; Hagadorn & Waggoner 2000; Hagadorn et al. 2000; Budd & Jensen 2017) and Pteridinium (see; Narbonne et al. 1997; Budd & Jensen 2017), while the Cambrian foraminiferan Platysolenites is documented in terminal Ediacaran strata (Kontorovich et al. 2008). These are joined by a small but increasing number of Cambrian taxa which, on morphological grounds, appear to be examples of ‘Ediacara-biota’, but have thus far only been described from Cambrian rocks; e.g. Thaumaptilon (Conway Morris 1993b) and Stromatoveris (Shu et al. 2006; Hoyal Cuthill & Han 2018). The current roster of ’Ediacaran survivors’ is modest, but nonetheless significant. When combined with the continuity seen among the trace fossil record (e.g. McIlroy & Logan 1999; Jensen et al. 2000, 2006; Gehling et al. 2001; Jensen 2003; Jensen & Runnegar 2005; McIlroy & Brasier 2017), an increasing case can be made for differential preservation, rather than purely extinction, accounting for at least some of the disconnect between Ediacaran and Cambrian biotas.

CONCLUSIONS

Cochleatina persisted for some ~15–20 myr, from the latest Ediacaran to the latter part of the Cambrian Fortunian Stage. The range of Cochleatina encompasses possibly the most dramatic biotic transition in Earth history, spanning the close of the Proterozoic until their apparent disappearance in concert with the classical Cambrian ‘explosion’ of shelly metazoa towards the end of the Fortunian. The Ediacaran was clearly a time of enormous experimentation in multicellularity, ecology and predation; an expansion of bilaterians in the Cambrian may have marginalized previously successful modes of predation, perhaps accounting for the disappearance of forms such as Cochleatina. Shelly and trace fossil records probably represent a relatively reliable account of when various taxa and behaviours first appeared or disappeared during this part of the record; the same is not true for records from Lagerstätten, which are time-restricted and largely absent from this time-window (Butterfield 2003). The challenge at the Ediacaran–Cambrian boundary is to distinguish fossil taxa that are taphonomically recalcitrant enough to preserve outside Lagerstätten conditions, and so stand a chance of exhibiting a global range in the first place. SCFs appear to fulfil these criteria, at least during the latest Ediacaran and early Cambrian (Guilbaud et al. 2018; Slater et al. 2018; Slater & Willman 2019). Clearly the emerging distribution of Cochleatina reveals how SCFs can supplement a crucial geographical dimension to the problem of the Ediacaran–Cambrian biotic transition (Figs 2, 9). Cochleatina is now known from four palaeocontinents and ten formations. Given this distribution, Cochleatina begins to enter the select realm of readily preserved, morphologically complex and widely distributed fossils from this time window, alongside iconic taxa such as Cloudina.

SYSTEMATIC PALAEOONTOLOGY

INCERTAE SEDIS

Genus COCHLEATINA Aseeva, 1983a emend. Burzin, 1995, emend

Type species. Cochleatina canilovica Aseeva, 1974 emend. Aseeva, 1983a, emend.

Emended diagnosis. Coiled carbonaceous ribbon displaying a continuum of morphologies, ranging from tightly
wound bobbin-like configurations to more open-coiled forms. The ribbons comprise a carbonaceous strap, widest at the 'base' (outermost terminus of the coil), narrowing toward the centre of the bobbin and terminating in a thin film of fibrous projections at the 'tip'. Ribbon is divided into a complex of three to four lateral zones running the entire ribbon length, the zones varying in degree of thickening, possession of jagged or smooth margins, and presence or absence of serrations. If present, serrations run entire length of ribbon, project away from the centre of the bobbin and increase in size towards the base. Coils may occur as overlapping or adjacent clusters. No discernible basal attachment structure.

**Remarks.** We apply principles of form taxonomy to the classification of **Cochleatina**, however, the distinctive and complex morphology of **Cochleatina** is sufficient to suggest true biological significance (i.e. **Cochleatina** probably forms a natural taxonomic group). Nevertheless, individual or clustered **Cochleatina** could in principle be subcomponents of an as yet unknown organism. Of the five described species, four are considered valid here based on their distinct ribbon morphologies (**C. canilovica**, **C. rara**, **C. rudaminica** and **C. ingnalinica**).

The concept of distinct morphological zones across the ribbon (Fig. 7) was introduced by Paškevičiene (1980), and later modified by Burzin (1995, see fig. 3). Differences in the morphology of these zones forms much of the basis for the specific taxonomy of **Cochleatina**. For example, **C. rudaminica** and **C. ingnalinica** can be distinguished from other **Cochleatina** by their possession of sculpture on their outermost ribbon zone, and can be distinguished from each other by the presence (**C. ingnalinica**) or absence (**C. rudaminica**) of serrations. **Cochleatina canilovica** and **C. rara** both have pronounced serrations on the first ribbon zone. **Cochleatina rara**, however, exhibits a narrow, tightly coiled ribbon with no fourth zone, and a second zone which has a jagged sclerotized margin. **Cochleatina rara** differs from other **Cochleatina** in the orientation of the ribbon, which is coiled in a cylindrical fashion with respect to the bobbin axis. **Cochleatina concentrica** (Kolosov 1984) was a species initially assigned to **Volymiella** before assignment to **Cochleatina** by Jankauskas et al. (1989). This species, however, was rejected by Burzin (1995), since it appears to be a segmented filament (**Cochleatina** are not segmented), and unlike **Cochleatina** it can be found as a tangled mass, rather than a coil.

**Emended diagnosis.** A species of **Cochleatina** with a ribbon flattened perpendicular to the bobbin axis and subdivided into four lateral zones running the entire length of the ribbon. The innermost zone (with respect to the centre of the spiral) is optically dark and fringed with fine (5-20 µm length) marginal serrations that point away from the centre of the spiral. This first zone is usually the widest, and can reach up to approximately half of the total ribbon width (excluding serrations). The second zone, where preserved, is a thin, relatively translucent layer that is usually ~20% of the total width of the ribbon. The third zone mirrors the darker, sclerotized construction of the first zone but lacks serrations. It is of intermediate width between the first and second zones, but can be as wide as the first zone in open-coiled specimens. The outermost fourth zone is the narrowest (typically ~10% of the total ribbon width) and consists of a thin, filmy layer. It is often missing or has a ragged outer margin. At the tip, the ribbon structure is tightly bound with serrations abutting or overlapping the second and third zones of the ribbon. Towards the basal portion, the ribbon frequently tends to 'unzip', creating a parting (or 'perforation zone') between the serrated margin and remainder of the ribbon. The ribbon exhibits a continuum of tightly wound to open-coiled forms. Coils may occur in clusters.

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