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2 // *Cochleatina*: an enigmatic Ediacaran–Cambrian survivor among small
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5 2 carbonaceous fossils (SCFs)
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23 10 **Abstract:** Conspicuously few body-fossil taxa are known to span the Ediacaran–Cambrian
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26 11 boundary, a pattern usually taken to signal either a terminal Proterozoic mass extinction, or
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28 12 taphonomic failure. We draw attention to the emerging record of small carbonaceous fossils
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30 13 (SCFs), which exhibit continuous preservation spanning this critical interval. Here we focus on
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32 14 the enigmatic SCF *Cochleatina*, a morphologically complex coil-shaped problematicum that
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34 15 ranges across the Ediacaran–Cambrian divide, and potentially among the oldest fossil
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36 16 occurrences of metazoans. We report new material of *Cochleatina canilovica* from the
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38 17 Ediacaran of Estonia and Ukraine, which offers new characters for assessing its palaeobiology.
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40 18 Significantly, new specimens include sets of three-alike triplets of *Cochleatina* adhering to
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42 19 organic sheets, suggesting a clustering habit, or grouping of elements within an individual
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44 20 during life; an important step in constraining the morphology and ecology of this Ediacaran–
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46 21 Cambrian problematicum. We present revised systematic descriptions for *Cochleatina* and *C.*
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48 22 *canilovica*, and critically evaluate previous biological interpretations, drawing comparisons with
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50 23 metazoan, algal and protistan analogues. We reject hypotheses supporting *Cochleatina* as a
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52 24 metazoan mouthpart, and suggest new grounds for viewing *Cochleatina* as a potential
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54 25 multicomponent predator that trapped protists among microbial mats. Most occurrences are
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56 26 from Baltica, but we synthesise sporadic reports of *Cochleatina* from other palaeocontinents,
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Ediacaran–Cambrian survivor *Cochleatina*

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2 27 pointing to its global distribution during the latest ~10 Myr of the Ediacaran and majority of the
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4 28 earliest Cambrian Fortunian Stage. As a rare example of an ‘Ediacaran survivor’, *Cochleatina*
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6 29 highlights the broader significance of SCFs as a novel means of tracking evolutionary patterns
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9 30 through the Proterozoic-Phanerozoic transition.

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12 31 **Key words:** Ediacaran–Cambrian survivor, oldest metazoan, Proterozoic mass extinction, small
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15 32 carbonaceous fossils, fossil problematica
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21 34 The Ediacaran–Cambrian boundary, approximately 541–539 Ma (Linnemann et al. 2019), is
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23 35 widely recognised as a juncture of exceptional ecological and evolutionary importance (Conway
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25 36 Morris 2000; Butterfield 2007; Budd and Jensen 2017). At around this time, the fossil record is
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27 37 permanently transformed by the appearance and radiation of diverse biomineralizing and
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29 38 agglutinating forms (Kouchinsky et al. 2012). This switching-on of the ‘shelly’ fossil record
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31 39 approximately corresponds with an increase in the degree and complexity of bioturbation
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33 40 (Jensen et al. 2006; Herringshaw et al. 2017), substantial shifts in the nature of biogenic
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35 41 sediments (fig. 1 of Davies et al. 2019), a disappearance of macroscopic Ediacara-style
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37 42 preservation (Butterfield 2003), and major changes in the composition of acritarch assemblages
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39 43 (Moczyłowska 1991; Butterfield 1997; Nowak et al. 2015). Identification of such
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41 44 ecological/evolutionary perturbations is heavily reliant on taphonomic continuity – in other
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43 45 words, the factors governing fossil preservation should not substantially change through the
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45 46 time interval of interest. If they do, then the traceability of lineages/taxa can be seriously
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47 47 compromised. The coincident opening and closure of several key taphonomic windows across
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49 48 the Ediacaran–Cambrian transition obscures the precise tracking of taxonomic ranges from this
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51 49 crucial interval. At present, only a handful of taxa known from body fossils are convincingly
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53 50 shown to span the boundary (e.g., Narbonne et al. 1997; Crimes and McIlroy 1999; Hagadorn et
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55 51 al. 2000; Narbonne 2005; Laflamme et al. 2013; Moczyłowska et al. 2014; Darroch et al. 2015;
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2 52 Budd and Jensen 2017; Simón 2018). The apparent disconnect in the body fossil record is
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4 53 contrasted by the relatively unbiased trace fossil record, which instead documents a signal of
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6 54 continuity between late Ediacaran and earliest Cambrian benthic bilaterian behaviour (e.g.,
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9 55 Jensen 2003; Mangano and Buatois 2017; Kesidis et al. 2019). Before a precise description of
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11 56 the magnitude, timing, and nature of this transition can reasonably be achieved, there is a
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13 57 pressing need for an improved accounting of non-biomineralizing taxa in order to discriminate
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15 58 genuine macroevolutionary patterns from localised signals or taphonomic shortfalls.
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19 59 Small carbonaceous fossils (SCFs) offer one means of tracking the Ediacaran–Cambrian
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21 60 transition without the associated biases of mineralization. Even under relatively indifferent
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23 61 taphonomic circumstances, cell walls, cuticle, and other recalcitrant components of non-
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25 62 biomineralizing organisms can be recognizably preserved (Butterfield and Harvey 2012). The
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27 63 widespread preservation of SCFs has recently been demonstrated from regions and time-
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29 64 intervals where other, more ‘exceptional’ evidence of non-biomineralizing taxa is lacking
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31 65 (Slater et al. 2017a, 2017b, 2018). In this study, we focus on an enigmatic SCF taxon,
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33 66 *Cochleatina*, a distinctive and widely distributed SCF taxon that appears to span the Ediacaran–
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35 67 Cambrian divide. *Cochleatina* is especially interesting given that it preserves in substantially
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37 68 different depositional environments than iconic boundary-spanning taxa such as *Cloudina*
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39 69 (Warren et al. 2014; Penny et al. 2014; Yang et al. 2016). Despite this, *Cochleatina* has so far
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41 70 been neglected from discussion of Ediacaran ‘survivors’, and so warrants renewed attention,
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43 71 particularly in the context of recent debate on rates of turnover, extinction and the nature of the
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45 72 Ediacaran–Cambrian transition (Budd and Jensen 2017; Darroch et al. 2018; Tarhan et al. 2018;
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47 73 Wood et al. 2019).
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54 74 *Cochleatina* is a coiled carbonaceous fossil formed as a spiral-shaped ribbon ornamented
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56 75 with fine serrations (Fig. 1). Examples of this fossil were first figured among acid-extracted
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58 76 material from the Ediacaran of the Ukraine by Aseeva (1974), but were initially interpreted as
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60 77 simple coiled filaments and ascribed to the filamentous form-taxon *Volyniella* (albeit as a new

Ediacaran–Cambrian survivor *Cochleatina*

1
2 78 species). Three further species were later added based on material from the Rovno (latest
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4 79 Ediacaran or earliest Cambrian) and Lontova (Cambrian) formations in Belarus, Lithuania and
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6 80 Latvia (Paškevičiene 1980), but remained assigned to *Volyniella* until Aseeva (1983a)
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8 81 established *Cochleatina* as a new genus to circumscribe these morphologically distinct fossils.
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10 82 Several succeeding studies mentioned or figured *Cochleatina* from sediments in Baltica and
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12 83 Siberia (e.g., Velikanov et al. 1983; Aseeva 1988; Rudavskaya and Vasilyeva 1989), but with no
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14 84 substantial revision until a major redescription and analysis by Burzin (1995), in which the four
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16 85 currently accepted species were amended: *C. canilovica*, *C. rara*, *C. rudaminica* and *C.*
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18 86 *ignalinica*. More recent reports of *Cochleatina*, recovered among acritarch preparations, have
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20 87 expanded its known geographic range beyond Baltica and Siberia to Avalonia and Gondwana
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22 88 (e.g., Sabouri et al. 2013; Palacios et al. 2018). Attempts to pin *Cochleatina* to the tree of life
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24 89 have been wide-ranging. Several authors have proposed a metazoan affinity (among annelids or
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26 90 molluscs; Butterfield and Harvey 2012), a premise which would clearly have significant
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28 91 implications if confirmed or refuted.
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35 92 Here we describe new material of *Cochleatina* from Ediacaran sediments of Estonia
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37 93 (Kotlin Formation) and Ukraine (Krushanovka Formation). We further discuss the broader
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39 94 significance of this SCF taxon in light of its status as a credible Ediacaran–Cambrian ‘survivor’,
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41 95 in the context of recently revised stratigraphy (Meidla 2017), and its emerging
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43 96 palaeobiogeographic distribution (Fig. 2). We further examine and test previous hypotheses for
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45 97 the biological affinity of *Cochleatina*, and propose new models for its possible mode of life.
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99 Geological Setting

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56 100 *Estonia*: The Kotlin Formation (Fig. 3) is widely developed across the Baltic States on the East
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58 101 European Platform, and equivalent strata occur from Poland in the west, to the margin of the
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60 102 Baltic craton in the east (Moczydłowska 1991; Pirrus 1992; Mens and Pirrus 1997). In Estonia,

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2 103 the Kotlin Formation is known exclusively from subsurface drillcore material, the nearest
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4 104 outcrop being on Kotlin Island (Russia) in the Gulf of Finland. The Kotlin Formation comprises
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6 105 a relatively homogeneous package of sediments composed predominantly of finely laminated
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8 106 grey, illite-smectite mixed-layer clays, with occasional interbeds of fine-grained sandstone and
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10 107 siltstone (Raidla et al. 2006; Mens and Pirrus 1997). Due to a relatively shallow burial depth and
11
12 108 quiescent regional tectonic history, Kotlin strata have experienced negligible thermal alteration
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14 109 over their more than half a billion year history (Raidla et al. 2006). In Estonia, the Kotlin
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16 110 Formation conformably overlies the coarser-grained sandy sediments of the Gdov Formation,
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18 111 and is in turn overlain by the correspondingly sandstone-rich Voronka Formation (Fig. 3; Mens
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20 112 and Pirrus 1997; Meidla 2017). Together, this package of Ediacaran sediments rests
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22 113 unconformably on a weathered crystalline basement (Puura et al. 1983; Nielsen and Schovsbo
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24 114 2011; Meidla 2017).

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30 115 Despite its relative homogeneity, the Kotlin Formation in Estonia is partitioned into
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32 116 three subdivisions (Mens and Pirrus 1997; Meidla 2017). The lowermost Jamma and uppermost
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34 117 Laagna members comprise relatively homogenous grey clays, whilst the middle Meriküla
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36 118 Member can be distinguished by its visible fine-scale intercalations of sand, silt, and clay
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38 119 ('varve-like' appearance; Pirrus 1992), abundance of sapropel films, and macroscopic
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40 120 'vendotaenid' fossils on bedding planes (Mens and Pirrus 1997).

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44 121 The Kotlin Formation was deposited in a shallow-marine pericratonic basin (Poprawa et
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46 122 al. 1999). Some authors have proposed brackish (Bityukova and Pirrus 1979) or even freshwater
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48 123 conditions within a basin with restricted circulation, based on suggestive boron concentrations in
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50 124 mudstones, localised absence of 'Ediacara-type' macrofossils, and a paucity of trace fossils.
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52 125 Certain regions where the Kotlin Formation developed, however, show clear evidence of marine
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54 126 deposition (see Burzin 1996), and the extent of freshwater/brackish influence remains
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56 127 controversial.

Ediacaran–Cambrian survivor *Cochleatina*

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2 128 The Kotlin Formation shares its name with the regional chronostratigraphic Kotlin stage,
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4 129 which in Estonia encompasses the Gdov, Kotlin and Voronka formations (Fig. 3). Although
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6 130 once placed relatively deep within the Ediacaran System (e.g., Sokolov 2011), the Kotlin
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9 131 Formation is now thought to have been deposited during the terminal ~10 Ma of Ediacaran time,
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11 132 based on correlation with strata from the Lubin Slope (Poland), Podillya (Ukraine), Urals, and
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13 133 White Sea region (Russia) where U–Pb zircon dates from volcanic tuff horizons have yielded
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16 134 lower boundary ages in the range of 551–548 Ma (Moczyłowska 1991; Grazhdankin et al.
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18 135 2011; Meidla 2017; Soldatenko et al. 2019).

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21 136 *Ukraine*: Ediacaran sediments of the Krushanovka Formation (Kanilovka Series) from Ukraine
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23 137 represent broadly coeval deposits, also belonging to the Kotlin regional stage (Fig. 3; Sokolov
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25 138 and Fedonkin 1985; Velikanov 1990; Iosifidi et al. 2005). Note that the Kanilovka Series of
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27 139 Podillya (alternatively Podolia) is not to be confused with the Kanilovka Formation of Volyn
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29 140 from which *Cochleatina* have been reported elsewhere in Ukraine (Burzin 1995). The
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31 141 Krushanovka Formation is widely known from drillcore in the Podillya region of Ukraine, and
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33 142 comprises a series of fine-grained, greenish-grey to white sandstones with substantial interbeds
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35 143 of reddish siltstones and claystones in its upper parts (Iosifidi et al. 2005). The formation rests
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37 144 conformably on the Zharnovka Formation (a sequence of coarse- to fine-grained sandstones)
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39 145 and is capped by the overlying Studentsa Formation (predominantly coarse- to fine-grained
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41 146 sandstones with occasional siltstones).

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47 147 There are two recognised subdivisions of the Krushanovka Formation, a lower (~45
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49 148 metre thick) Kryvchany Member, and an upper (~15 metre thick) Durnyakovka Member. The
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51 149 Kryvchany Member is generally coarser, with a larger proportion of sandstones, while the
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53 150 Durnyakovka Member is dominantly composed of distinctive red siltstones with occasional
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55 151 coarse sandstone beds (Sokolov and Fedonkin 1985; Iosifidi et al. 2005). Deposition occurred in
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57 152 a shallow-marine basin with storm influence (Iosifidi et al. 2005).
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2 153 *Sampling*: Sampling for microfossils targeted the most fine-grained lithologies (mudstones and
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4 154 siltstones) from both areas. In Estonia (Meriküla Member of the Kotlin Formation), we
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6 155 processed a total of 31 samples, 11 from the Maidla 75A drillcore, 2 from the Maidla F-238
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8 156 drillcore, 6 from the Toila 77 drillcore and 12 from the Meriküla F-169 drillcore. From the
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10 157 Podillya region of Ukraine, a total of 5 samples were processed from the Durnyakovka Member
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12 158 of the Krushanovka Formation, from the drillcore No. 700. Estonian cores are housed at the
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14 159 TUT Institute of Geology core-storage at Särgghaua (Estonia), and samples from the drillcore No.
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16 160 700 (Podillya, Ukraine) are hosted at the Institute of Precambrian Geology and Geochronology
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18 161 of the Russian Academy of Sciences in Saint Petersburg. SCF processing and examination
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20 162 followed a gentle, low-manipulation hydrofluoric acid maceration procedure aimed at the
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22 163 recovery of larger, delicate forms, otherwise destroyed by standard palynological processing
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24 164 (see techniques outlined in Butterfield and Harvey 2012).
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33 166 Results

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37 167 Our processing recovered a total of 103 individual *Cochleatina*, of which 70 are from the
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39 168 Estonian Kotlin Formation (Figs 4, 5), and 33 come from the Ukrainian Krushanovka Formation
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41 169 (Fig. 6). The majority of specimens were recovered from a small number of highly productive
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43 170 samples; Estonian specimens were recovered from a depth of 186–187 metres in the Maidla 75A
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45 171 drillcore, 180 metres depth in Maidla F-238 drillcore, 153 metres in the Toila 77 drillcore, and
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47 172 119.4 metres from the Meriküla F-169 drillcore, whilst those from the drillcore no. 700 in
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49 173 Podillya, Ukraine were sourced from a productive layer at 184 metres depth. Both the Estonian
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51 174 and Ukrainian samples of *Cochleatina* exhibit substantial taphomorphic variation. In the
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53 175 Estonian samples, all *Cochleatina*-bearing horizons produced masses of sapropel sheets,
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55 176 alongside occasional vendotaenids and filamentous microbes. Productive samples from Ukraine
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57 177 were also associated with sapropel sheets, but at substantially lower levels.
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5 179 *New material.* Specimens from the new Estonian Kotlin assemblage (Figs. 4, 5) are preserved as
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7 180 flattened spirals or incomplete sections of a spiral fused to sapropel films – sheets of relatively
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9 181 featureless organic matter, sometimes with identifiable filaments superimposed and variably
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11 182 fused together. These sapropel films are interpreted as compacted and variably fused
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13 183 sedimentary organic material and/or benthic mats (Figs 4, 5). Specimens consist of a coiled
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15 184 ribbon; coils reach 540 μm in maximum width (\bar{x} = 246, SD = 83, n = 70) and display a
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17 185 continuum of morphologies, ranging from tightly wound bobbin-like configurations (Fig. 4A,
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19 186 5G–J) to more open spiral forms (e.g., Fig. 5D, F, R, S, T). The ribbon narrows towards the
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21 187 centre of the spiral and is a complex of four distinct longitudinal zones running the entire ribbon
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23 188 length (Fig. 7). Thin, sharply pointed serrations project from the first inner zone, directed away
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25 189 from the centre of the coil, though these serrations are often obscured by the underlying organic
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27 190 sheet (e.g., Fig. 4L, 5E). Other zones are discernible by their thicknesses (Fig. 7; see Systematic
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29 191 Palaeontology below). Basal portions are either broken (e.g., Fig. 4I), or alternatively, where
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31 192 fused to a sheet, the ribbons have no obvious termination but instead fade into the sheet material
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33 193 (e.g., Fig. 5D–F, H, L).

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40 194 The new Ukrainian *Cochleatina* (Fig. 6) occur as individual isolates (with the possible
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42 195 exception of Fig. 6J, no clusters were recovered) and were never found in attachment to larger
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44 196 organic sheets (note the absence of organic material in the central opening of the bobbin; Fig. 6).
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46 197 The coils reach 320 μm in maximum width. Like the Estonian specimens, the ribbons are
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48 198 divided into four discernible zones which narrow towards the centre of the spiral (Fig. 7). The
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50 199 ribbons are optically darker than their counterparts from the Kotlin Formation, especially the
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52 200 first and third zones of the ribbon which are opaque in most specimens (Fig. 6). Serrations
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54 201 emanating from the inner first zone of the ribbon are also prominently visible in the majority of
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56 202 specimens (e.g., Fig. 6A–C, E, G, J). The ribbon tip has a brush-like termination of fibrous
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58 203 projections between 5–15 μm in length (e.g., Fig. 6C–G).

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5 205 *Comments.* The new specimens from Estonia and Ukraine are assigned to *C. canilovica* on the
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7 206 basis of their consistent spinose serration, ribbon oriented perpendicular to the bobbin axis, and
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9 207 four broad ribbon zones, features which are lacking in other taxa (see Systematic Palaeontology
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11 208 below). Both the Estonian and Ukrainian assemblages are consistent with the currently known
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13 209 range of *C. canilovica* which is reported from the Kotlin regional stage of the late Ediacaran,
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15 210 and the lowermost part of the Rovno regional Ediacaran/Cambrian stage. Although *Cochleatina*
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17 211 has been reported from elsewhere in the Baltic region (e.g., Paškevičiene 1980), these are the
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19 212 first reports from Estonian strata.

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24 213 The new assemblages of *Cochleatina* from Estonia and Ukraine differ in a number of
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26 214 aspects. For example, serrations appear more pronounced in the Ukrainian specimens. This,
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28 215 however, appears to be purely taphonomic – serrations are present in all well-preserved Kotlin
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30 216 *Cochleatina*, but are simply less prominent due to the obscuring presence of the
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32 217 underlying/fused organic sheet. *Cochleatina* from the Krushanovka Formation exhibit darker
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34 218 ribbons (particularly in zones one and three), however, this can be explained by variations in
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36 219 local post-depositional burial histories (e.g., different degrees of thermal alteration). When these
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38 220 taphonomic considerations are taken into account, it is clear that both assemblages of
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40 221 *Cochleatina* exhibit the same underlying morphology.

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48 223 *Clustered forms.* Among the more complete specimens of *Cochleatina* recovered from the
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50 224 Kotlin Formation are a notable subset that occur as clusters, consisting of three coils adhered to
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52 225 the same carbonaceous sheet (N = 6). The sheets are interpreted as the compacted remains of
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54 226 benthic organic material. No more than three coiled elements per cluster are seen, even on more
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56 227 extensive sheets. Within clusters, some coils are incomplete (Fig. 5H, K), and some partially
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58 228 overlap (Fig. 5D, F, H, L). Clusters can comprise tightly-wound bobbin-like and uncoiled forms,

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2 229 but within each cluster the coils are always of the same (potentially ontogenetic) stage/type. The
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4 230 asymmetry of the ribbon zones, in particular the overlap of the serrations, reveals that the coils
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6 231 occur as enantiomorphs (both right-handed and left-handed forms/chirality), which can co-occur
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9 232 in the same cluster (e.g., Fig. 5D, F). Occurrence as triplet clusters is an unexpected and novel
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11 233 insight into *Cochleatina* morphology. It is possible that the ‘individual’ *Cochleatina* reported in
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13 234 previous studies have been selectively disaggregated during more intensive, conventional
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15 235 palynological processing – indeed, low-manipulation processing appears essential to recovery of
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17 236 these delicate clusters. Since these *Cochleatina* are all at the same stage or type within a cluster,
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19 237 it is unlikely to represent fortuitous superposition via currents or fall-out from the water column.
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22 238 Either these clusters represent groups of three similar individuals from a population with a
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24 239 benthic ecology, or were clustered prior to sinking from suspension, or are the recalcitrant
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26 240 components of a single organism that has otherwise decayed away.
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242 Discussion

243 *Biological affinities*

244 Previous suggestions for the biological nature of *Cochleatina* have been broad ranging,
245 reflecting the dearth of suitable fossil or modern analogues (a problem shared with many
246 Ediacaran fossils). Proposed affinities have included the coiled ‘elaters’ of bryophyte-grade
247 plant spores (Fig. 8A; Ischenko 1983; Gnilovskaya 1988), defensive ejectosomes of
248 Cryptophyta (Fig. 8C; Burzin 1995), and subcomponents of a macroscopic alga (Burzin 1995).
249 Homology with the elaters of liverwort, hornwort, and *Equisetum* spores (Fig. 8A) can be ruled
250 out on both functional grounds (the ribbons of *Cochleatina* are solid with no internal cavity, and
251 therefore unsuitable for extension and retraction via hygroscopic turgor), and the fact that spores
252 assignable even to stem-embryophytes are not otherwise known until the Ordovician (Wellman
253 and Gray 2000; Edwards et al. 2014). The coiled ribbon-like ejectosomes of Cryptophyta bear a

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2 254 superficial resemblance to *Cochleatina* (Fig. 8C; cf., Hausmann 1985, fig. 132), but are
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4 255 intracellular organelles, orders of magnitude smaller than *Cochleatina*, making even an
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6 256 analogous function improbable. Similarly, the serrated filamentous ejectosomes of
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9 257 helicosporidial cysts are somewhat similar in form to *Cochleatina*, but are less than ten microns
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11 258 in size (Fig. 8B).

14 259 *Cochleatina* have been reported in rare instances adhering to the macroscopic fossil
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16 260 ‘alga’ *Kanilovia insolita* (Ischenko 1983) from the ‘Kotlin’ regional stage of Ukraine (e.g., Plate
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18 261 XVII.26 of Gnilovskaya 1988). This association with *Kanilovia insolita* (itself a problematicum)
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20 262 is intriguing, but whether the relationship is truly biological is difficult to ascertain: even if
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22 263 fortuitous superposition could be ruled out, there is the possibility that the *Cochleatina* were
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24 264 derived from epibionts or some other organism in association with *Kanilovia insolita*. Similarly,
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26 265 though the triplet associations of *Cochleatina* (Fig. 5, this study) are likely biological, the
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28 266 attachment of *Cochleatina* to organic sheets (e.g. Estonian material in this study) may or may
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30 267 not be biological. It is common among SCF-style preservation for multiple overlapping organic
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32 268 constituents to become fused into a single layer during diagenesis (Martí Mus 2014). The sheets
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34 269 themselves preserve little discernible morphology, and although they could represent fragments
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36 270 of thalli (some have regular margins), they could alternatively be regarded as sheets of degraded
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38 271 and depolymerised organic matter (sapropel), to which the more recalcitrant *Cochleatina* are
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40 272 fused. The consistent within-cluster similarity of *Cochleatina* in these instances would at least
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42 273 suggest the coils themselves represent structures from a single individual, or individuals from a
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44 274 single population (Fig. 5D, F, H, K).

51 275 Elsewhere among the fossil record, some of the more densely coiled *Cochleatina* bear a
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53 276 superficial resemblance to sheet-like fossils preserved in Terreneuvian (lower Cambrian)
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55 277 hydrothermal cherts from South China, which can exhibit a tightly enrolled coil-like habit, the
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57 278 coils even occurring in ‘clusters’ (Fig. 8G–H; see figs 5A, C–E, 6A, E, F and 7A of Yin et al.
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59 279 2017). These sheet-like fossils (interpreted as animal cuticles by the authors) also bear a fine

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2 280 surface covering of hair-like or dentate projections (fig. 4E, F of Yin et al. 2017). A more
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4 281 precise structural comparison to *Cochleatina*, however, is problematic; the surface spines on
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6 282 these silicified sheets are sparsely distributed hollow projections, quite unlike the regular rows
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9 283 of tooth-like serrations in *Cochleatina*. Moreover, *Cochleatina* is never found as distended,
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11 284 sinuous sheets or loops, but only occurs as regular coils. In instances where specimens are found
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13 285 on sheets (e.g., Figs. 4A, B, D, G, J, L, M, Q, S; 5D–K, P), there is no basal connection to a
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15 286 sheet-margin, indicating that *Cochleatina* cannot be the flattened enrolled margin of such a sheet
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18 287 or cuticle.
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24 289 *Cochleatina as a feeding structure*

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27 290 Although only a few of the previously proposed affinities for *Cochleatina* can be rejected
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29 291 outright, none offers a convincing basis for assigning it to any particular biological taxon.
30
31 292 Nevertheless, there are other extant and fossil examples that serve to elucidate at least some of
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33 293 the characteristics that set *Cochleatina* apart. Notably, *Cochleatina* can be usefully compared to
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35 294 a variety of feeding structures seen in extant and fossil heterotrophs, from protistan to
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38 295 eumetazoan grade.
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41 296 Comparisons have been made between *Cochleatina* and another serration-bearing
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43 297 carbonaceous fossil, *Redkinia* (Fig. 8F; Sokolov 1977; Burzin 1995), which also occurs in
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45 298 Ediacaran deposits, both as microfossils (Pl. 18, images 8–9 of Velikanov et al. 1983) and as
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47 299 bedding-plane visible mesofossils (fig. 2A of Golubkova et al. 2018). *Redkinia* was initially
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49 300 proposed to represent a disarticulated polychaete jaw (i.e., a scolecodont; Sokolov 1977), and
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51 301 later as the mandible-like jaws of a stem-arthropod (Conway Morris 1993); if the connection to
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53 302 *Redkinia* was established, it would potentially support a bilaterian affiliation for *Cochleatina*.
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55 303 Burzin (1995) highlighted the shared characteristics of *Redkinia* and *Cochleatina*, principally
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57 304 the first and second order serrations (inset in Fig. 8F), which are somewhat similar to those seen
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1
2 305 in *C. ignalinica*, and considered the possibility of the latter evolving from the former based on
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4 306 their stratigraphic relationships – but questioned the ability of *Cochleatina* to have functioned as
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6 307 a feeding apparatus. It is also questionable whether the two structures (*Cochleatina* and
7
8 308 *Redkinia*) are homologous; serrations are a deeply convergent morphological feature, and other
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10 309 than their carbonaceous habit, this is the only shared character which promotes any useful
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12 310 comparison.

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16 311 A further likeness to metazoan mouthparts was raised by Butterfield and Harvey (2012),
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18 312 who remarked on the broad similarity of *Cochleatina* to certain moluscan radulae. In particular,
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20 313 the simple pairs of coiled radulae borne by certain Solenogastres (Fig. 8H) are somewhat
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22 314 *Cochleatina*-like in overall appearance (see fig. 19F of Scheltema and Schander 2000, and figs.
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24 315 3 and 4 of Scheltema 2014). Cambrian radulae are known from SCFs (Butterfield 2008) and
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26 316 from the radula-like mouthparts of *Wiwaxia* and *Odontogriphus* (Smith 2012); *Cochleatina*
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28 317 substantially predates these occurrences. However, *Cochleatina* also lacks any belt-like
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30 318 arrangement of individual tooth-elements: the ribbon is a solid structure, with no joints or
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32 319 segments. Moreover, one of the species of *Cochleatina* – *C. rudaminica* – does not possess any
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34 320 serrations at all, making a radula-like function or homology unlikely.

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40 321 Among extant organisms, a particularly useful comparison is with the giant (>1 mm)
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42 322 single-celled ciliate *Stentor* (Tartar 1961; Slabodnick and Marshall 2014). Specifically, the
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44 323 coiled anterior region of oral cilia in *Stentor* is strikingly reminiscent of *Cochleatina* and reaches
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46 324 a similar size (Fig. 8J; figs. 1–6, 11–15 of Foissner and Wöflfl 1994; fig. 1 of Lanzoni et al.
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48 325 2019; fig. 2 and sup. fig. 4 of Zinskie et al. 2015). These cilia are fused into flat triangular plates
49
50 326 and borne on a coiled basal membranellar band. Environmental shocks can lead to the
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52 327 membranellar band being sloughed off and detached from the main body of the *Stentor* (Tartar
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54 328 1961; fig. 1 of Sood et al. 2017). When shed, the membranellar band does not disaggregate, but
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56 329 remains fused as an isolated ribbon which contracts in the transverse direction to form an even
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58 330 more tightly wound coil (Tartar 1961). The microanatomy of *Stentor* (particularly *S. coeruleus*)

Ediacaran–Cambrian survivor *Cochleatina*

1
2 331 has been studied in detail for its ability to regenerate, during which clusters of ciliary bands can
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4 332 form (e.g., figs 2, 4 of Tang and Marshall 2017). Similar clustering can occur naturally during
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6 333 reproduction or during the sessile rest state, where numerous individual *Stentor* can attach
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8 334 adjacently to a substrate via their posterior holdfast (Tartar 1961). The main obstacle to analogy
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10 335 with *Cochleatina* is taphonomic. Without any obvious robust macromolecular extracellular
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12 336 components to the ciliary band, it is difficult to envisage how such a structure could produce the
13
14 337 recalcitrant SCF *Cochleatina*. It is possible that relatively labile structures could fuse to more
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16 338 resistant organic materials during diagenesis, forming a composite structure (Martí Mus 2014),
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18 339 and it is worth noting that seemingly decay-prone tissues are occasionally captured in Burgess
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20 340 Shale-type *Lagerstätten* (e.g., ctenophores; Fu et al. 2019, fig. 2C). Regardless of taphonomic
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22 341 issues, these similarities with *Stentor* demonstrate that complex SCF structures like *Cochleatina*
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24 342 could in principle derive from protists.
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30 343 Another intriguing possibility, is that the coils of *Cochleatina* functioned as a spiral
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32 344 protozoan trap, analogous with the protistan traps of extant *Genlisea*, the corkscrew plant (Fig.
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34 345 8D–E; Barthlott et al. 1998). In *Genlisea*, specialised spiral rhizophylls with a narrow serrated
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36 346 slit serve to trap motile protists in the manner of an ‘eel trap’ (Rutishauser 2016). Progressively
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38 347 narrowed spirals or coils are prevalent among such traps in the broadest sense, including among
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40 348 ciliated predatory protists (e.g. *Stentor*), helical bryozoans (McKinney and McGhee 2003),
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42 349 coiled graptolites (e.g., *Cyrtograptus* and *Monograptus turriculatus*; Linnarsson 1881; Williams
43
44 350 and Zalasiewicz 2004), the spiral traps constructed by polychaetes (Minter et al. 2006), and even
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46 351 the bubble-traps of whales (Leighton et al. 2007). Viewed in this light, the multi-spiral and
47
48 352 bobbin shaped forms of *Cochleatina* may represent multiple traps under continuous
49
50 353 rejuvenation. Movement is key to predation; in a pre-muscular world (as also seen in plant and
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52 354 fungal predators), passive sit-and-wait trapping is expected to have been the standard feeding
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54 355 technique, with protozoans as the primary target. Whereas Ediacaran rangeomorphs may have
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56 356 extracted food via passive suspension, *Cochleatina* may represent a next-step in luring self-

1
 2 357 propelled prey (perhaps aided by attractive chemotaxis as in *Genlisea* [Barthlott et al. 1998] and
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 4 358 carnivorous fungi [Barron 1981]). Trapping of protistan prey may be seen as part of a broader
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 6 359 stepwise escalation of eukaryovory and predation running from the Tonian to the Cambrian
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 8 360 (Porter 2011; Cohen and Reidman 2018; Antcliff et al. 2019). Sponges (and angiosperms and
 9
 10 361 fungi) also display rare instances of trap-based carnivory (Vacelet and Boury-Esnault 1995), but
 11
 12 362 this style of hunting would have declined in importance in a world of increasingly motile
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 14 363 eumetazoan predators.
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 22 365 *An Ediacaran ‘survivor’*
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24 366 The oldest known *Cochleatina* are found in rocks of the Kotlin regional Baltic/Siberian stage
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 26 367 (this study; Burzin 1995, 1996; Golubkova and Raevskaya 2005). Under all schemes, the Kotlin
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 28 368 is regarded as Ediacaran in age (Grazhdankin et al. 2011; Meidla 2017). The youngest
 29
 30 369 *Cochleatina* are recovered from Fortunian strata of the regional Baltic Lontovan stage
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 32 370 (Paškevičiene 1980), which likely corresponds to the latter half of Fortunian time based on its
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 34 371 acritarch and trace fossil contents (in particular the appearance of the acritarchs
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 36 372 *Granomarginata prima* and *Asteridium tornatum* along with trace fossils such as *Treptichnus*
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 38 373 *pedum*, *Gyrolithes*, and *Monomorphichnus*; Moczyłowska 1991; Jensen and Mens 2001;
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 40 374 Palacios et al. 2017, 2018; Slater et al. 2018). The majority of reports, however, are sourced
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 42 375 from the intervening ‘Rovno’ regional Baltic/Siberian stage. In the older literature (e.g., Burzin
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 44 376 1995), the Rovno was generally regarded to form the uppermost division of the ‘Vendian’
 45
 46 377 System. It is currently unclear whether the Ediacaran–Cambrian boundary actually resides
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 48 378 within the Rovno stage (Mens et al. 1990; Moczyłowska 1991; Jensen and Mens 1999),
 49
 50 379 however, in places the upper part of the Rovno *Formation* is clearly Fortunian (*Treptichnus*
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 52 380 *pedum* and other typically basal Fortunian ichnofossils are found in the Rovno; Fedonkin 1983;
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 54 381 Paliy 1976). While some recent schemes regard the entire Rovno stage as of earliest Fortunian
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Ediacaran–Cambrian survivor *Cochleatina*

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2 382 origin (Meidla 2017), the scheme of Moczydłowska (1991) places the lower parts of the Rovno
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4 383 in the Ediacaran and the upper portion where trace fossils of Cambrian aspect appear in the
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6 384 Fortunian. Regardless of which scheme is used, *Cochleatina* ranges across the Ediacaran–
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8 385 Cambrian boundary (Fig. 9).

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12 386 The majority of *Cochleatina* have been found in Ediacaran–Cambrian sediments of the
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14 387 Baltic Basin and Ukraine (Fig. 2). Rare reports from beyond these sedimentary basins occur
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16 388 elsewhere on the palaeocontinent Baltica (Finnmark; Högström et al. 2013), as well as from the
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18 389 palaeocontinent Siberia (Rudavskaya and Vasilyeva 1989), and isolated reports from Avalonia
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20 390 (Palacios et al. 2018) and Iran (Sabouri et al. 2013; Etemad-Saeed et al. 2016). The current
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22 391 pattern is liable to change with increased exploration of undersampled regions, but taken at face
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24 392 value, the distribution of *Cochleatina* is centred on the margins of the Ægir Ocean (Torsvik and
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26 393 Rehnström 2001), as well as adjacent peri-Gondwanan terranes (Fig. 2).

31 394 *Cochleatina* demonstrates how SCFs can contribute to the emerging fossil record of
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33 395 Ediacaran–Cambrian ‘survivors’ (Fig. 9). Although all Cambrian taxa are necessarily derived
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35 396 from lineages that survived from the Ediacaran, the current picture of the Ediacaran–Cambrian
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37 397 boundary remains one of widespread fossil range truncation. Closer scrutiny, however, reveals a
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39 398 more complex pattern. ‘Terminal Ediacaran’ *Cloudina*, for example (Amthor et al. 2003), is now
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41 399 known to range into the Cambrian (e.g., Zhuravlev et al. 2012; Yang et al. 2016; Han et al.
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43 400 2017; Simón 2018), as do the ‘Ediacaran macrofossils’ *Swartpuntia* (see; Narbonne et al. 1997;
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45 401 Jensen et al. 1998; Hagadorn and Waggoner 2000; Hagadorn et al. 2000; Budd and Jensen 2017)
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47 402 and *Pteridinium* (see; Narbonne et al. 1997; Budd and Jensen 2017), while the Cambrian
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49 403 foraminiferan *Platysolenites* is documented in terminal Ediacaran strata (Kontorovich et al.
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51 404 2008). These are joined by a small but increasing number of Cambrian taxa which, on
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53 405 morphological grounds, appear to be examples of ‘Ediacara-biota’, but have thus far only been
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55 406 described from Cambrian rocks; e.g., *Thaumaptilon* (Conway Morris 1993) and *Stromatoveris*
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57 407 (Shu et al. 2006; Hoyal Cuthill et al. 2018). The current roster of ‘Ediacaran survivors’ is

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2 408 modest, but nonetheless significant. When combined with the continuity seen among the trace
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4 409 fossil record (e.g., McIlroy and Logan 1999; Jensen et al. 2000, 2006; Gehling et al. 2001;
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6 410 Jensen 2003; Jensen and Runnegar 2005; McIlroy and Brasier 2017), an increasing case can be
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8 411 made that differential preservation, rather than purely extinction, can account for at least some
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10 412 of the disconnect between Ediacaran and Cambrian biotas.
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17 414 *Conclusions*

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20 415 *Cochleatina* persisted for some ~15–20 Ma, from the latest Ediacaran to the latter part of the
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22 416 Cambrian Fortunian. The range of *Cochleatina* encompasses possibly the most dramatic biotic
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24 417 transition in Earth history, spanning the close of the Proterozoic until their apparent
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26 418 disappearance in concert with the classical Cambrian ‘explosion’ of shelly metazoans towards
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28 419 the end of the Fortunian. The Ediacaran was clearly a time of enormous experimentation in
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30 420 multicellularity, ecology and predation – an expansion of bilaterians in the Cambrian may have
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32 421 marginalised previously successful modes of predation, perhaps accounting for the
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34 422 disappearance of forms such as *Cochleatina*. Shelly and trace fossil records likely represent
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36 423 relatively reliable accountings of when various taxa and behaviours first appeared or
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38 424 disappeared during this part of the record: the same is not true for records from *Lagerstätten*,
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40 425 which are time-restricted and largely absent from this time-window (Butterfield 2003). The
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42 426 challenge at the Ediacaran–Cambrian boundary is to distinguish fossil taxa that are
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44 427 taphonomically recalcitrant enough to preserve outside *Lagerstätten* conditions, and so stand a
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46 428 chance of exhibiting a global range in the first place. SCFs appear to fulfil these criteria, at least
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48 429 through the latest Ediacaran and early Cambrian (Slater et al. 2018; Guilbaud et al. 2018; Slater
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50 430 and Willman 2019). Clearly the emerging distribution of *Cochleatina* reveals how SCFs can
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52 431 supplement a crucial geographical dimension to the problem of the Ediacaran–Cambrian biotic
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54 432 transition (Figs. 2, 9). *Cochleatina* is now known from four palaeocontinents and ten
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1
2 433 formations. Given this distribution, *Cochleatina* begins to enter the select realm of readily
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4 434 preserved, morphologically complex and widely distributed fossils from this time window,
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6 435 alongside iconic taxa such as *Cloudina*.
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12 437 Systematic Palaeontology

16 438 Incertae Sedis

19 439 Genus: COCHLEATINA Aseeva, 1983a emend. Burzin, 1995, emend.

22 440 *Type species.* *Cochleatina canilovica* Aseeva, 1974 emend. Aseeva, 1983a, emend.

25 441 *Emended diagnosis* (of genus). Coiled carbonaceous ribbon displaying a continuum of
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27 442 morphologies, ranging from tightly wound bobbin-like configurations to more open-coiled
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29 443 forms. The ribbons comprise a carbonaceous strap, widest at the ‘base’ (outermost terminus of
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31 444 the coil), narrowing toward the centre of the bobbin and terminating in a thin film of fibrous
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33 445 projections at the ‘tip’. Ribbon is divided into a complex of three to four lateral zones running
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35 446 the entire ribbon length, the zones varying in degree of thickening, possession of jagged or
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37 447 smooth margins, and presence or absence of serrations. If present, serrations run entire length of
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39 448 ribbon, project away from the centre of the bobbin and increase in size towards the base. Coils
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41 449 may occur as overlapping or adjacent clusters. No discernible basal attachment structure.
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46 450 *Discussion.* We apply principles of form taxonomy to the classification of *Cochleatina*,
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48 451 however, the distinctive and complex morphology of *Cochleatina* is sufficient to suggest true
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50 452 biological significance (i.e., *Cochleatina* likely forms a natural taxonomic group). Nevertheless,
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52 453 individual or clustered *Cochleatina* could in principle be subcomponents of an as yet unknown
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54 454 organism. Of the five described species, four are considered valid here based on their distinct
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56 455 ribbon morphologies (*C. canilovica*, *C. rara*, *C. rudaminica* and *C. ingnalinica*).
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2 456 The concept of distinct morphological zones across the ribbon (Fig. 7) was introduced by
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4 457 Paškevičiene (1980), and later modified by Burzin (1995; see fig. 3 of that study). Differences in
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6 458 the morphology of these zones forms much of the basis for the specific taxonomy of
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9 459 *Cochleatina*. For example, *C. rudaminica* and *C. ingnalinica* can be distinguished from other
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11 460 *Cochleatina* by their possession of sculpture on their outermost ribbon zone, and can be
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13 461 distinguished from each other by the presence (*C. ingnalinica*) or absence (*C. rudaminica*) of
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15 462 serrations. *C. canilovica* and *C. rara* both have pronounced serrations on the first ribbon zone.
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18 463 *C. rara*, however, exhibits a narrow, tightly coiled ribbon with no fourth zone, and a second
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20 464 zone which has a jagged sclerotized margin. *C. rara* differs from other *Cochleatina* in the
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22 465 orientation of the ribbon, which is coiled in a cylindrical fashion with respect to the bobbin axis.
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25 466 *C. concentrica* (Kolosov 1984) was a species initially assigned to *Volyniella* before assignment
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27 467 to *Cochleatina* by Jankauskas et al. (1989). This species, however, was rejected by Burzin
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29 468 (1995), since it appears to be a segmented filament (*Cochleatina* are not segmented), and unlike
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31 469 *Cochleatina* it can be found as a tangled mass, rather than a coil.
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38 471 *Cochleatina canilovica* Aseeva, 1974 emend. Aseeva, 1983a, emend.
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41 472 *Material*. 70 specimens from the Kotlin Formation (Estonia), 33 specimens from the
42
43 473 Krushanovka Formation (Ukraine).
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46 474 *Emended diagnosis*. A species of *Cochleatina* with a ribbon flattened perpendicular to the
47
48 475 bobbin axis and subdivided into four lateral zones running the entire length of the ribbon. The
49
50 476 innermost zone (with respect to the centre of the spiral) is optically dark and fringed with fine
51
52 477 (5–20 µm length) marginal serrations that point away from the centre of the spiral. This first
53
54 478 zone is usually the widest, and can reach up to approximately half of the total ribbon width
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56 479 (excluding serrations). The second zone, where preserved, is a thin, relatively translucent layer
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58 480 that is usually ~20% the total width of the ribbon. The third zone mirrors the darker, sclerotized
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Ediacaran–Cambrian survivor *Cochleatina*

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2 481 construction of the first zone but lacks serrations. It is of intermediate width between the first
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4 482 and second zones, but can be as wide as the first zone in open-coiled specimens. The outermost
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6 483 fourth zone is the narrowest (typically ~10% of the total ribbon width) and consists of a thin,
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9 484 filmy layer. It is often missing or has a ragged outer margin. At the tip, the ribbon structure is
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11 485 tightly bound with serrations abutting or overlapping the second and third zones of the ribbon.
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13 486 Towards the basal portion, the ribbon frequently tends to ‘unzip’, creating a parting (or
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15 487 ‘perforation zone’) between the serrated margin and remainder of the ribbon. The ribbon
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18 488 exhibits a continuum of tightly wound to open-coiled forms. Coils may occur in clusters.
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31
32
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34
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36
37
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Ediacaran–Cambrian survivor *Cochleatina*

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Ediacaran–Cambrian survivor *Cochleatina*

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2 848 Figure 1. Examples of *Cochleatina canilovica* from the Ediacaran of the Volyn region of
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4 849 Ukraine. Courtesy of M. Burzin. Scale bar = 100 μ m.
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10 851 Figure 2. Palaeogeographic distribution of fossil occurrences of *Cochleatina* sp. A, Localities in
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12 852 Baltica where *Cochleatina* sp. have been recovered; 1. Outcrop, Finnmark, Norway; 2. Toila 77
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14 853 and Meriküla F169 drillcores, Estonia (this study); 3. Ludza drillcore, Latvia; 4. Vishki
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16 854 drillcore, Latvia; 5. Butkunay drillcore, Lithuania; 6. Svedasay drillcore, Lithuania; 7.
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18 855 Drukshyay drillcore, Lithuania; 8. Tverečius drillcore, Lithuania; 9. Stradech-17 drillcore,
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20 856 Belarus; 10. Various cores from Volyn, Ukraine (e.g., drillcore No. 1562, Il'pan); 11. Various
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22 857 cores and outcrops from Podillya, Ukraine (drillcores – Bolotino, Vapnyarka No. 18, Malaya
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24 858 Sloboda No. 4, Bagovitsy No. 3, Pechora No. 2, Krushanovka No. 1, Zarechanka No. 11664;
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26 859 outcrops – Studenitsa village No. 202, Bakota village No. 238); 12. Drillcore No. 700, Podillya,
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28 860 Ukraine (this study); (see Fig. 9 for locality data; reconstruction of Baltica after Cocks and
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30 861 Torsvik 2005). B, Distribution of palaeocontinents during the Ediacaran–Cambrian transition
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32 862 showing reported occurrences of *Cochleatina* sp., mainly from Baltica, but also Siberia,
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34 863 Avalonia, and peri-Gondwanan terranes (continental distribution after various sources, e.g.
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36 864 McKerrow et al. 1992; see Fig. 9 for details on occurrence data).
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46 866 Figure 3. Ediacaran–Cambrian stratigraphy of Estonia and Ukraine (Podillya region). Red stars
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48 867 indicate position of samples analysed in this study.
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54 869 Figure 4. *Cochleatina* from the Kotlin Formation, northeast Estonia. Specimens A–F, H–J, L–O,
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56 870 Q–S from 153 metres depth in Toila 77 drillcore; G from 180 metres depth in Maidla F-238
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58 871 drillcore; K and P from 187 metres in Maidla 75A drillcore. Tallinn University of Technology
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2 872 acquisition numbers (GIT); A, 831; B, 842; C, 837; D, 838; E, 836; F, 843; G, 850; H, 841; I,
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4 873 828; J, 842; K, 851; L, 841; M, 829; N, 833; O, 838; P, 851; Q, 841; R, 839; S, 832. Scale bar =
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6 874 100 μm .

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12 876 Figure 5. *Cochleatina* from the Kotlin Formation, northeast Estonia. D–L, specimens adhered to
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14 877 large sapropel sheets; D, F, H, K, and L are clustered *Cochleatina*, note that within each cluster
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16 878 coils are at approximately the same size, shape, and thickness. Specimens A, B, D, F, K, Q–S
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18 879 from 189 metres depth in Maidla 75A drillcore; C, E, G, H, J, L–P, T from 153 metres depth in
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20 880 Toila 77 drillcore; I from 180 metres depth in Maidla F-238 drillcore. Tallinn University of
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22 881 Technology acquisition numbers (GIT); A, 845; B, 846; C, 840; D, 848; E, 832; F, 853; G, 838;
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24 882 H, 835; I, 850; J, 852; K, 849; L, 854; M, 829; N, 842; O, 834; P, 830; Q, 845; R, 847; S, 844;
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26 883 T, 852. Scale bars; A–F and M–T = 100 μm ; G–L = 200 μm .

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34 885 Figure 6. *Cochleatina* from the Krushanovka Formation, Podillya, Ukraine. Specimens sourced
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36 886 from a productive layer at 184 metres depth within drillcore no. 700. Tallinn University of
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38 887 Technology acquisition numbers (GIT); A–G, 855; H–J, 856. Scale bar = 100 μm .

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45 889 Figure 7. Schematic diagram of *Cochleatina canilovica*, including terminology of ribbon
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47 890 morphology used here. The ‘first zone’ comprises the dark innermost part of the coil, and is
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49 891 fringed with marginal serrations that point away from the centre of the spiral. The ‘second
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51 892 zone’, where preserved, is a thin, filmy part of the ribbon which is typically overlain by the
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53 893 spines emanating from the first zone. The ‘third zone’ is of similar construction to the first zone
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55 894 (dark, sclerotized), but lacks any serrations, and may be separated from the second zone by a
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Ediacaran–Cambrian survivor *Cochleatina*

895 ‘perforation zone’ toward the basal portion of the ribbon. The ‘fourth zone’ (frequently damaged
 896 or missing) is a thin, filmy region, similar to the second zone.

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898 Figure 8. Comparative extant and fossil analogues for *Cochleatina*. A. coiled elaters found in
 899 triplets on *Elaterites triferens* plant spores (Pennsylvanian) (see also figs. 1–8 of Good and
 900 Taylor 1974; figs. 1–18 of Baxter and Leisman 1967); B. SEM of dehisced helicosporidial cyst
 901 (parasitic green algae) showing uncoiled filamentous cell bearing barbed serrations; C.
 902 Reconstruction of the ribbon-like ejectosome of Cryptophyta algae (intracellular scale); D. SEM
 903 of the protozoan trapping structure of the corkscrew plant *Genlisea repens* (angiosperm); E.
 904 Close-up of D showing serrated coils where prey enters; F. *Redkinia spinosa* from the Ediacaran
 905 of northwest Russia, inset shows enlargement of serrations; G–H. Coiled organic sheets found in
 906 early Cambrian (Terreneuvian) cherts; I. Paired coiled radula of the extant mollusc *Plawenia*
 907 *sphaera*; J. Coiled anterior region of the ciliated protist *Stentor*. Images from; A (Taylor et al.
 908 2009), B (Boucias et al. 2001), C (based on diagram from Biocyclopedia; Cryptophyta), D–E
 909 (Rutishauser 2016), F (Golubkova et al. 2018), G–H (Yin et al. 2017), I (Scheltema and
 910 Schander 2000), J (Lanzoni et al. 2019). Scale bars; A = 225 μm , B = 7.5 μm , D = 1 mm, E =
 911 100 μm , F = 1 mm, G–H = 20 μm , I = 200 μm , J = 50 μm .

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913 Figure 9. Global stratigraphic range of body-fossils known to span the Ediacaran–Cambrian
 914 boundary compared to the range of *Cochleatina* sp. Temporal ranges for *Cochleatina* sp. from;
 915 1. Estonia (this study); 2. Podillya, Ukraine (this study; Aseeva 1974, 1976, 1983a, 1983b,
 916 1988; Velikanov et al. 1983); 3. Volyn, Ukraine (Keller and Rozanov 1979; Burzin 1995, 1996);
 917 4. Belarus (Paškevičiene 1980); 5. Lithuania (Paškevičiene 1980); 6. Latvia (Paškevičiene
 918 1980); 7. Finnmark, Norway (Högström et al. 2013); 8. Burin Peninsula, Newfoundland
 919 (Palacios et al. 2018); 9. Alborz Mountains, northern Iran (Sabouri et al. 2013; Etemad-Saeed et

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2 920 al. 2016); 10. Anabar Uplift, eastern Siberia (Rudavskaya and Vasilyeva 1989). Note that
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4 921 ‘Redkino’, ‘Kotlin’, and ‘Rovno’ are informal regional stages of Ediacaran–Cambrian
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6 922 chronostratigraphy used in Baltica and Siberia. Temporal ranges for other boundary-crossing
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8 923 body fossils compiled from various sources (McIlroy et al. 2001; Kontorovich et al. 2008;
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10 924 Palacios et al. 2018; Narbonne et al. 1997; Jensen et al. 1998; Hagadorn and Waggoner 2000;
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12 925 Hagadorn et al. 2000; Winchester-Seeto and McIlroy 2006; Moczydłowska et al. 2014; Budd
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14 926 and Jensen 2017; Zhuravlev et al. 2012; Yang et al. 2016; Han et al. 2017; Simón 2018; Wood
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16 927 et al. 2019).

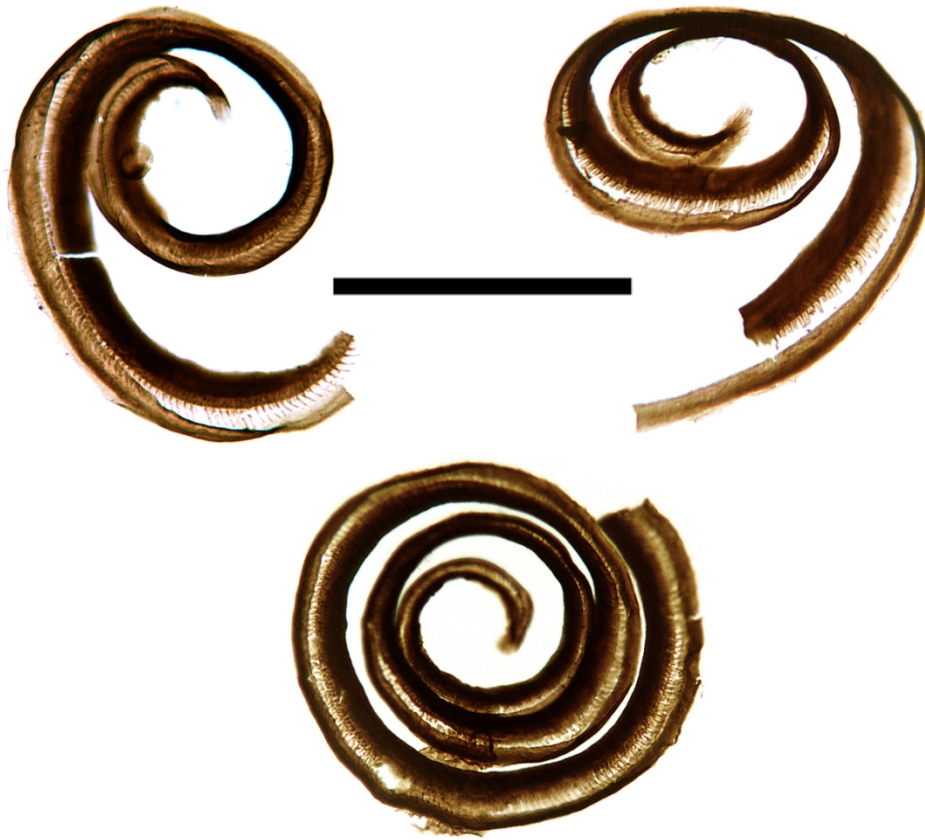


Figure 1. Examples of *Cochleatina canilovica* from the Ediacaran of the Volyn region of Ukraine. Courtesy of M. Burzin. Scale bar = 100 μm .

109x101mm (300 x 300 DPI)

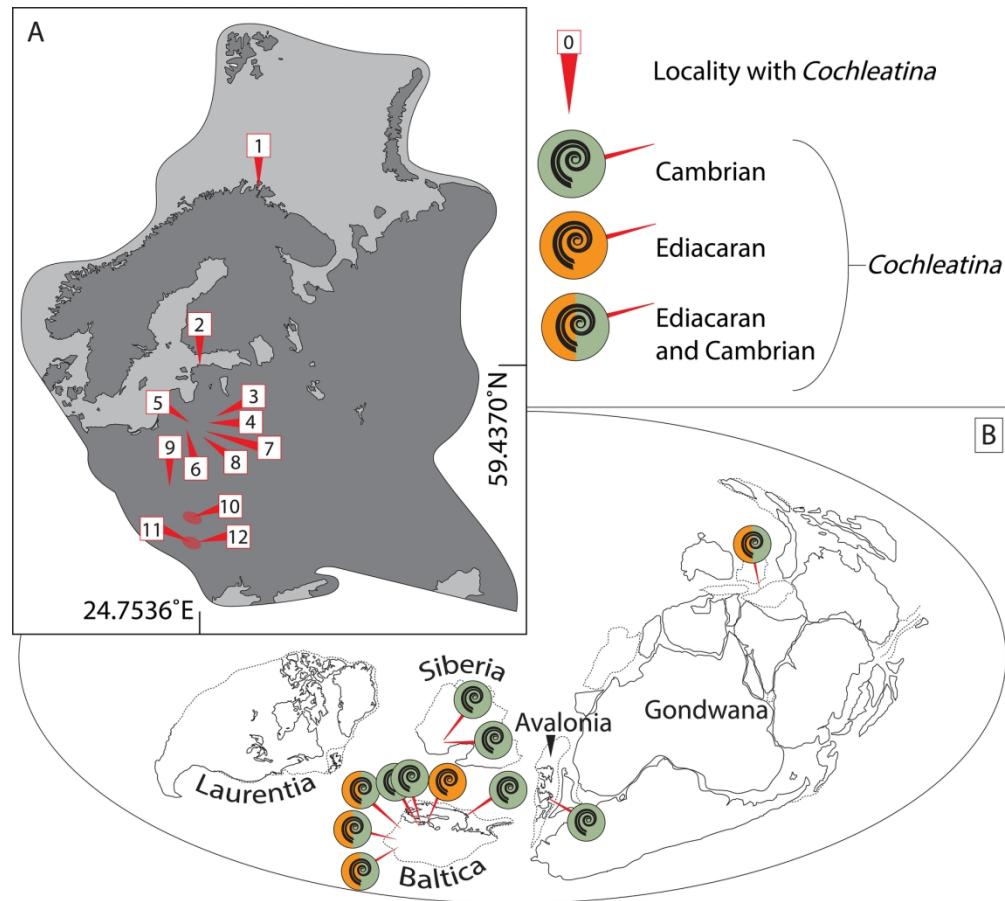


Figure 2. Palaeogeographic distribution of fossil occurrences of *Cochleatina* sp. A, Localities in Baltica where *Cochleatina* sp. have been recovered; 1. Outcrop, Finnmark, Norway; 2. Toila 77 and Meriküla F169 drillcores, Estonia (this study); 3. Ludza drillcore, Latvia; 4. Vishki drillcore, Latvia; 5. Butkunay drillcore, Lithuania; 6. Svedasay drillcore, Lithuania; 7. Drukshyay drillcore, Lithuania; 8. Tverečius drillcore, Lithuania; 9. Stradech-17 drillcore, Belarus; 10. Various cores from Volyn, Ukraine (e.g., drillcore No. 1562, Il'pan); 11. Various cores and outcrops from Podillya, Ukraine (drillcores – Bolotino, Vapnyarka No. 18, Malaya Sloboda No. 4, Bagovitsy No. 3, Pechora No. 2, Krushanovka No. 1, Zarechanka No. 11664; outcrops – Studenitsa village No. 202, Bakota village No. 238); 12. Drillcore No. 700, Podillya, Ukraine (this study); (see Fig. 9 for locality data; reconstruction of Baltica after Cocks and Torsvik 2005). B, Distribution of palaeocontinents during the Ediacaran–Cambrian transition showing reported occurrences of *Cochleatina* sp., mainly from Baltica, but also Siberia, Avalonia, and peri-Gondwanan terranes (continental distribution after various sources, e.g. McKerrow et al. 1992; see Fig. 9 for details on occurrence data).

165x149mm (300 x 300 DPI)

Estonia				Ukraine (Podillya/Podolia)				
Series	Regional stage	Formation	Member	Series	Regional stage	Formation	Member	
Ediacaran	Valdai	'Kotlin'	Voronka Formation	Kannuka Member	Kanilovka	'Kotlin'	Studenitsa Formation	Komarovo Member
				Sirgala Member				Polivanov Member
		Kotlin Formation	Laagna Member			Krushanovka Fm.	★ Durnyakovka Member	
			★ Meriküla Member				Kryvchany Member	
			Jaama Member			Zarnovka Formation	Staraya Ushitsa Member	
		Gdov Formation	Uusküla Member				Kuleshovka Member	
			Moldova Member			Danilovka Formation	Shebutintsy Member	
			Oru Member				Pilipy Member	
		'Redkino'						
Cambrian	Baltic	'Rovno'		Baltic	'Rovno'			
		'Lontova'			'Lontova'			

Figure 3. Ediacaran–Cambrian stratigraphy of Estonia and Ukraine (Podillya region). Red stars indicate position of samples analysed in this study.

165x130mm (300 x 300 DPI)

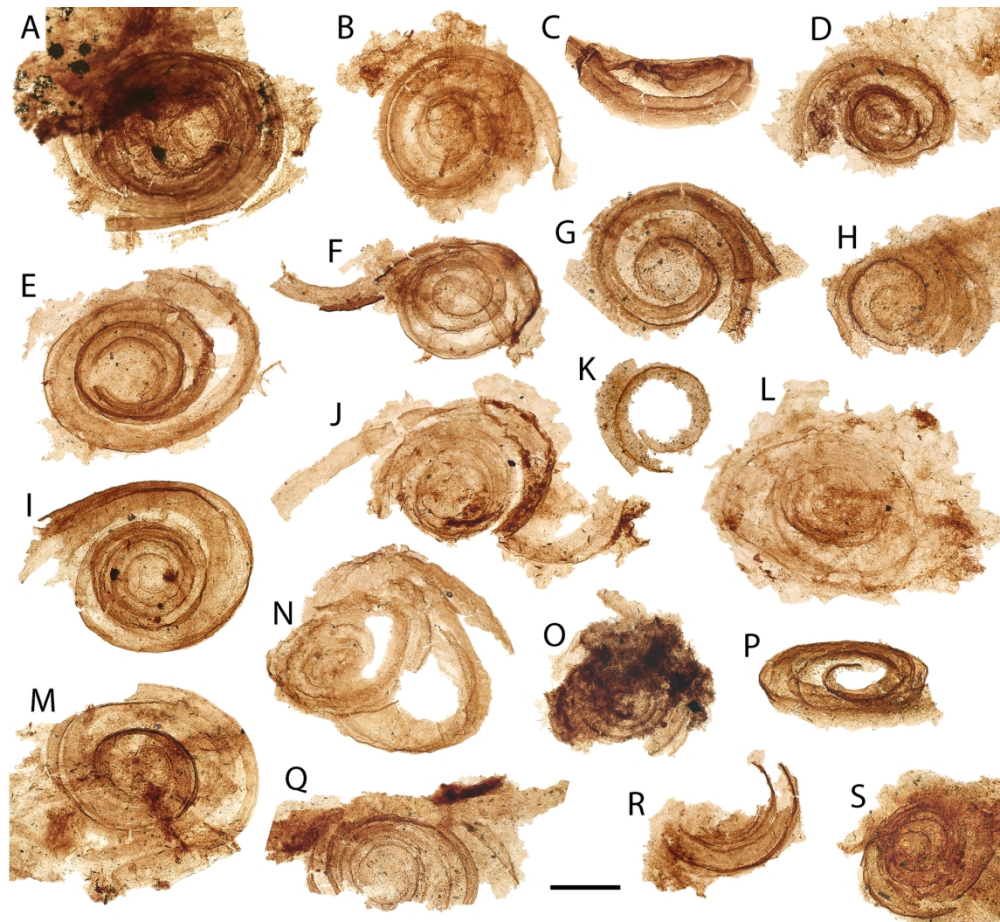


Figure 4. *Cochleatina* from the Kotlin Formation, northeast Estonia. Specimens A–F, H–J, L–O, Q–S from 153 metres depth in Toila 77 drillcore; G from 180 metres depth in Maidla F-238 drillcore; K and P from 187 metres in Maidla 75A drillcore. Tallinn University of Technology acquisition numbers (GIT); A, 831; B, 842; C, 837; D, 838; E, 836; F, 843; G, 850; H, 841; I, 828; J, 842; K, 851; L, 841; M, 829; N, 833; O, 838; P, 851; Q, 841; R, 839; S, 832. Scale bar = 100 μ m.

165x151mm (300 x 300 DPI)

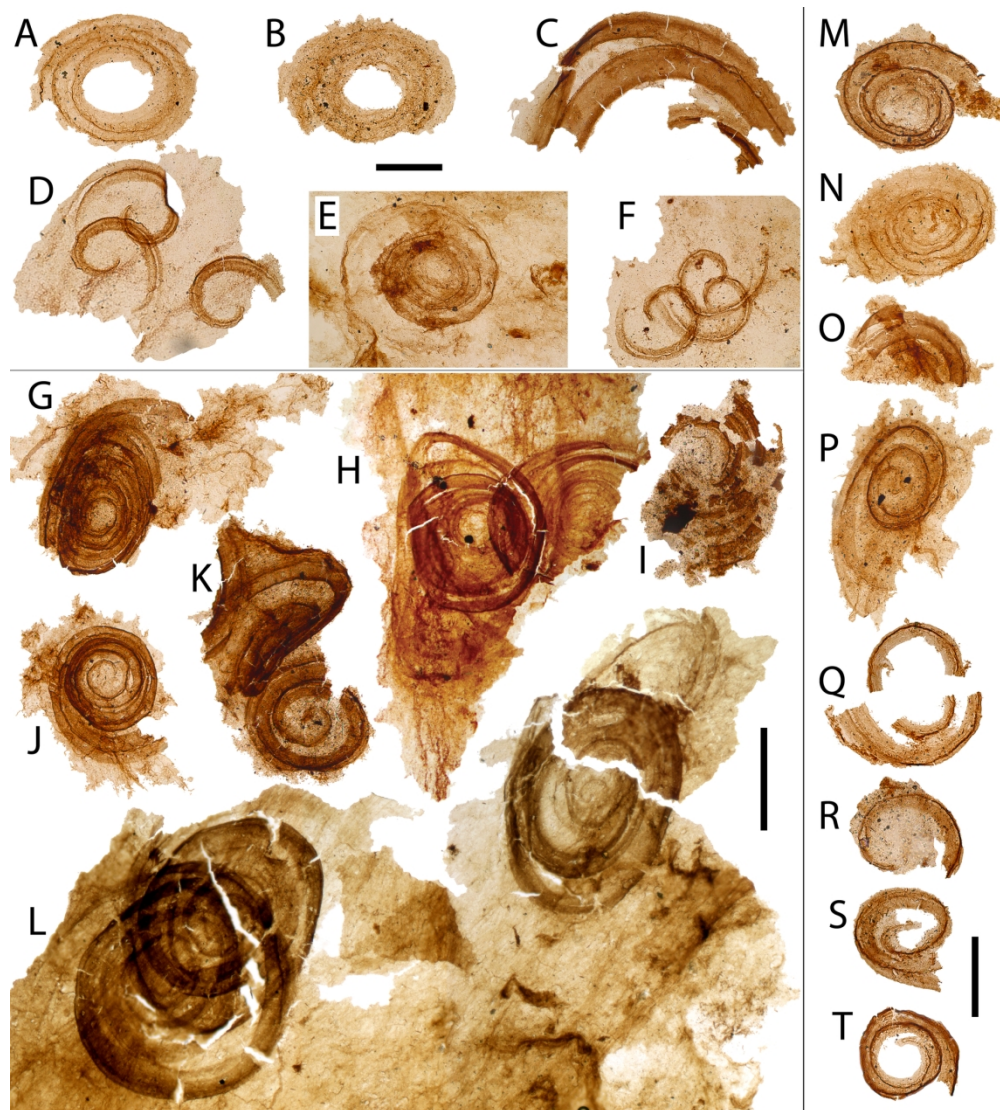


Figure 5. *Cochleatina* from the Kotlin Formation, northeast Estonia. D–L, specimens adhered to large sapropel sheets; D, F, H, K, and L are clustered *Cochleatina*, note that within each cluster coils are at approximately the same size, shape, and thickness. Specimens A, B, D, F, K, Q–S from 189 metres depth in Maidla 75A drillcore; C, E, G, H, J, L–P, T from 153 metres depth in Toila 77 drillcore; I from 180 metres depth in Maidla F-238 drillcore. Tallinn University of Technology acquisition numbers (GIT); A, 845; B, 846; C, 840; D, 848; E, 832; F, 853; G, 838; H, 835; I, 850; J, 852; K, 849; L, 854; M, 829; N, 842; O, 834; P, 830; Q, 845; R, 847; S, 844; T, 852. Scale bars; A–F and M–T = 100 µm; G–L = 200 µm.

165x183mm (300 x 300 DPI)

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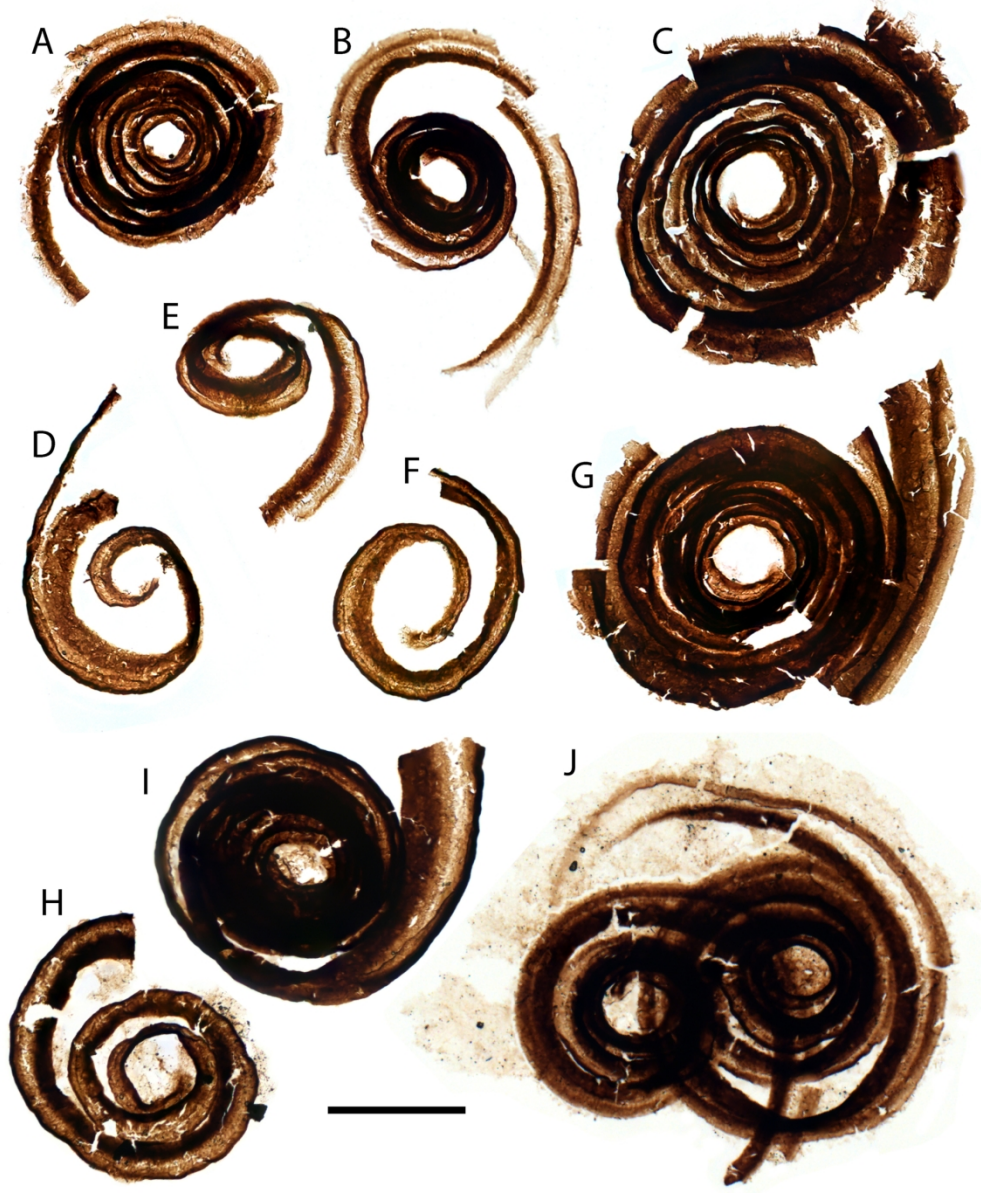


Figure 6. *Cochleatina* from the Krushanovka Formation, Podillya, Ukraine. Specimens sourced from a productive layer at 184 metres depth within drillcore no. 700. Tallinn University of Technology acquisition numbers (GIT); A–G, 855; H–J, 856. Scale bar = 100 μ m.

165x202mm (300 x 300 DPI)

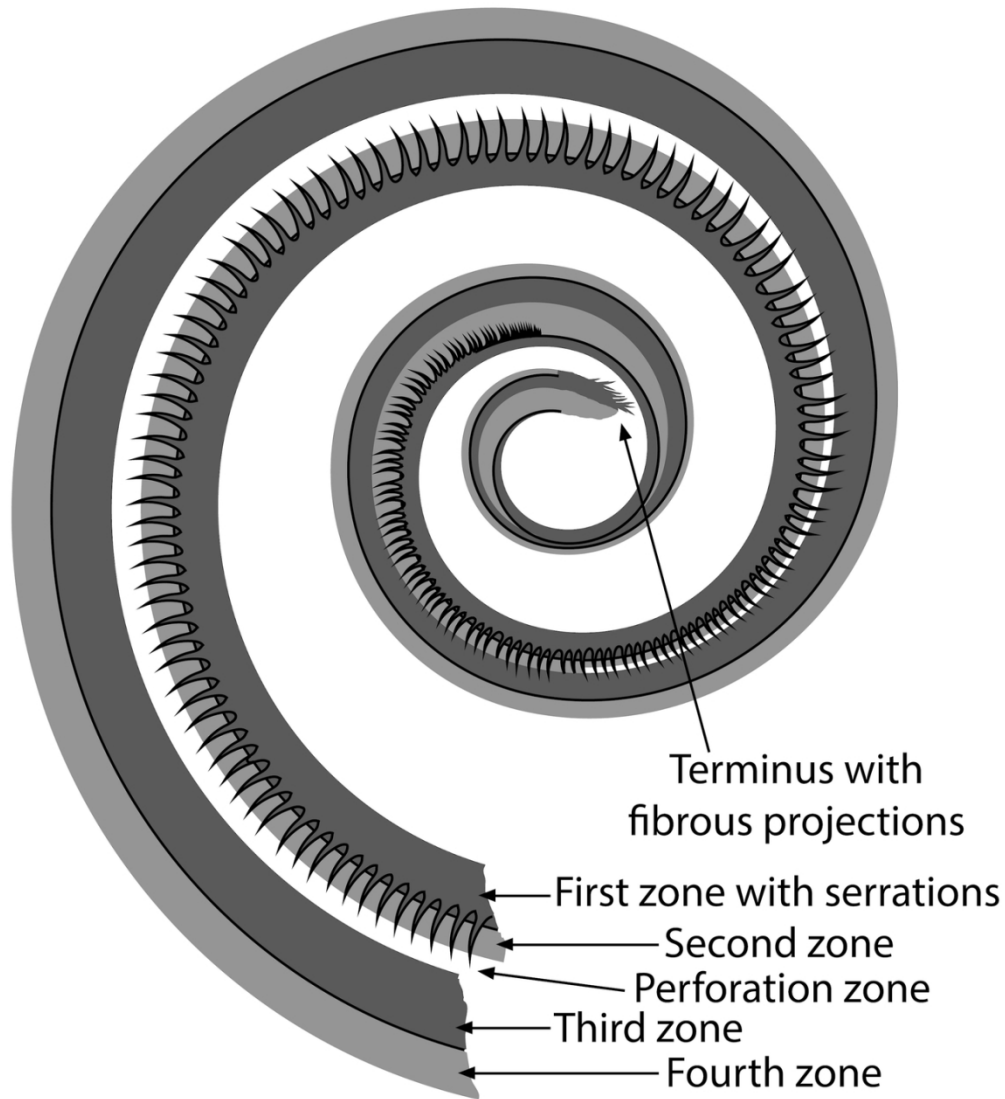


Figure 7. Schematic diagram of *Cochleatina canilovica*, including terminology of ribbon morphology used here. The 'first zone' comprises the dark innermost part of the coil, and is fringed with marginal serrations that point away from the centre of the spiral. The 'second zone', where preserved, is a thin, filmy part of the ribbon which is typically overlain by the spines emanating from the first zone. The 'third zone' is of similar construction to the first zone (dark, sclerotized), but lacks any serrations, and may be separated from the second zone by a 'perforation zone' toward the basal portion of the ribbon. The 'fourth zone' (frequently damaged or missing) is a thin, filmy region, similar to the second zone.

109x120mm (300 x 300 DPI)

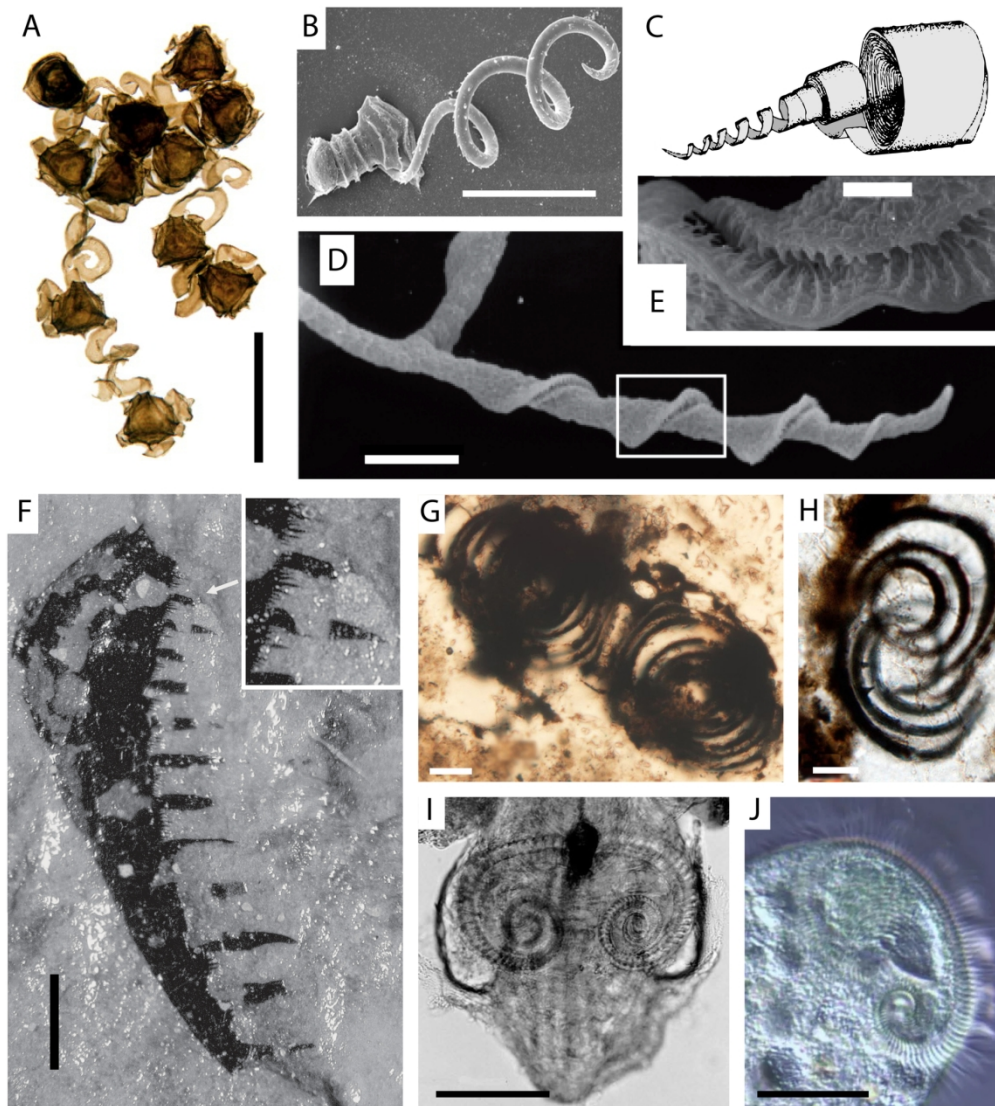


Figure 8. Comparative extant and fossil analogues for *Cochleatina*. A. coiled elaters found in triplets on *Elaterites triferens* spores (Pennsylvanian) (see also figs. 1–8 of Good and Taylor 1974; figs. 1–18 of Baxter and Leisman 1967); B. SEM of dehisced helicosporidial cyst showing uncoiled filamentous cell bearing barbed serrations; C. Reconstruction of the ribbon-like ejectosome of Cryptophyta (intracellular scale); D. SEM of the protozoan trapping structure of the corkscrew plant *Genlisea repens*; E. Close-up of D showing serrated coils where prey enters; F. *Redkinia spinosa* from the Ediacaran of northwest 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 and Schander 2000), J (Lanzoni et al. 2019). Scale bars; A = 225 μm , B = 7.5 μm , D = 1 mm, E = 100 μm , F = 1 mm, G–H = 20 μm , I = 200 μm , J = 50 μm .

166x183mm (300 x 300 DPI)

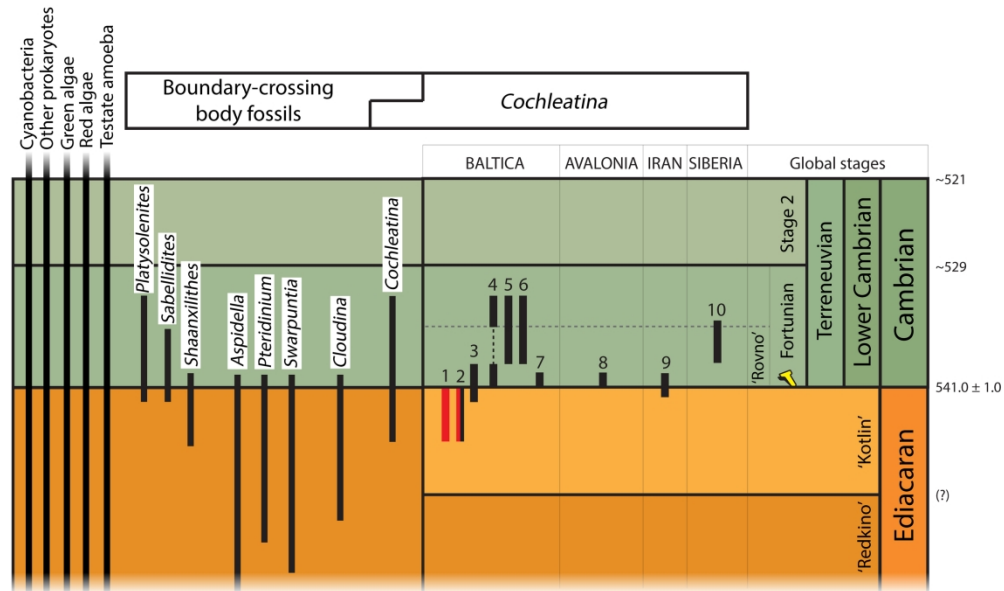


Figure 9. Global stratigraphic range of body-fossils known to span the Ediacaran–Cambrian boundary compared to the range of *Cochleatina* sp. Temporal ranges for *Cochleatina* sp. from; 1. Estonia (this study); 2. Podillya, Ukraine (this study; Aseeva 1974, 1976, 1983a, 1983b, 1988; Velikanov et al. 1983); 3. Volyn, Ukraine (Keller and Rozanov 1979; Burzin 1995, 1996); 4. Belarus (Paškevičiene 1980); 5. Lithuania (Paškevičiene 1980); 6. Latvia (Paškevičiene 1980); 7. Finnmark, Norway (Högström et al. 2013); 8. Burin Peninsula, Newfoundland (Palacios et al. 2018); 9. Alborz Mountains, northern Iran (Sabouri et al. 2013; Etemad-Saeed et al. 2016); 10. Anabar Uplift, eastern Siberia (Rudavskaya and Vasilyeva 1989). Note that 'Redkino', 'Kotlin', and 'Rovno' are informal regional stages of Ediacaran–Cambrian chronostratigraphy used in Baltica and Siberia. Temporal ranges for other boundary-crossing body fossils compiled from various sources (McIlroy et al. 2001; Kontorovich et al. 2008; Palacios et al. 2018; Narbonne et al. 1997; Jensen et al. 1998; Hagadorn and Waggoner 2000; Hagadorn et al. 2000; Winchester-Seeto and McIlroy 2006; Moczyłowska et al. 2014; Budd and Jensen 2017; Zhuravlev et al. 2012; Yang et al. 2016; Han et al. 2017; Simón 2018; Wood et al. 2019).

225x140mm (300 x 300 DPI)