A scratch circle origin for the medusoid fossil *Kullingia*

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**LETHAIA**

*Kullingia* is considered a key taxon in demonstrating the presence of terminal Proterozoic–early Cambrian chondrophorine hydrozoans. However, *Kullingia concentrica* from the Lower Cambrian of northern Sweden possesses several features that show that it is not a body fossil but that it was formed by current or wave-induced rotation of an anchored tubular organism, possibly a sabelliditid. A scratch circle interpretation applies also to several other reports of Lower Cambrian *Kullingia*, including *Kullingia delicata* from the Chapel Island Formation of Newfoundland. Given the considerable number of problematic fossils that have been interpreted as chondrophorines, it is difficult to put an age on the oldest fossil chondrophorines, but it may be as late as the Devonian. Overall, scratch circles appear to be rarely preserved. The occurrence of these scratch circles in Lower Paleozoic storm deposits is probably related to low levels of bioturbation that enhanced both the likelihood of formation and preservation of these structures.

Despite the seemingly ephemeral nature of cnidarian medusae, there is a substantial literature discussing processes by which these may enter the fossil record, generally involving preservation as casts and moulds along a sediment interface and often invoking strand- ing in shallow waters (e.g. Schäfer 1941; Bruton 1991). However, fossils that preserve diagnostic morphological detail are rare (e.g. Maas 1902) and the vast majority of reports of fossil marine jellyfish subsequently have been re-interpreted. For example, most purported jelly fish from the terminal Proterozoic Ediacara biota are now widely thought to have been benthic organisms (e.g. Seilacher 1984; Gehling 1991).

An interesting group of free-swimming medusoid hydrozoans are the Chondrophorina, characterized by a chitinous float (the pneumatophore) consisting of a series of concentrically enveloping air chambers (e.g. Stanley 1986). Represented today by two pleustonic genera, including the by-the-wind-sailor *Velella*, 11 fossil genera ranging from the terminal Proterozoic to the Mesozoic were tabulated in a summary of fossil chondrophorines (Stanley 1986), and new taxa have been added after that (see Bell et al. 2001). Stanley (1986) noted the simple, conservative, nature of the group, and attributed the relatively rich fossil record to the resistant float. Fossils attributed to the Chondrophorina are generally preserved as casts and moulds, showing variously developed concentric ornamentation, and rarely with purported imprints of a sail. A number of these are re-interpretations of forms originally reported as univalved molluscs (e.g. Yochelson & Stanley 1981; Yochelson & Gil Cid 1984). Considering the relative simplicity of the fossils it is not surprising that questions have been raised regarding the interpretation of many of these forms (e.g. Conway Morris 1993; Conway Morris et al. 1991). Among purported terminal Proterozoic chondrophorines, *Eoporpita, Chondroplon*, and *Ovatoscutum*, only *Ovatoscutum* remains a possible candidate, though the simplicity of its morphology makes any assignment problematic. Moreover, none of the Cambrian forms attributed to the Chondrophorina in Stanley’s (1986) list remain credible. *Velumbrella* has been interpreted as a benthic form related to eldoniids (e.g. Dzik et al. 1997), and the original interpretation of *Scenella morenensis* as a mollusc appears more likely (Geyer 1994). Mindful of the uncertain nature of these forms, Narbonne et al.
(1991) proposed that the discoid fossil *Kullingia*, including finds from the Lower Cambrian of Newfoundland, provide important evidence for the presence of terminal Proterozoic and Cambrian chondrophorines.

In this article we present evidence showing that the Cambrian material of *Kullingia* does not represent impressions of a chambered float but rather were formed by current or wave-induced rotation of an anchored tubular organism that imparted concentric scratches on the sediment. This was first suggested in a German thesis (Stodt 1987), but has remained poorly known. A scratch circle interpretation for *Kullingia* has important implications for the fossil record of the Chondrophorina and highlights questions concerning the timing of the appearance and evolution of the various groups within the Cnidaria (cf. Collins & Waggoner 2001). In addition, this interpretation sheds light on Cambrian substrate properties (e.g. Droser et al. 2002).

If the proposed pseudofossil interpretation of *Kullingia* gains acceptance, the name *Kullingia* should in the future be used as a non-italicized descriptor in analogy with such sedimentary structure pseudofossils as Eophyton or Rhysonetron (cf. Hofmann 1971: p. 5).

**Kullingia** from Northern Sweden

The type material of *Kullingia concentrica* originates from the Torneträs Formation of northern Sweden. The Torneträs Formation consists of about 100 m of dominantly siliciclastic rocks representing fluvial and shallow marine tidal and storm influenced deposits (e.g. Kulling 1964, 1972; Thelander 1982). Close to the top of the formation, late Early Cambrian trilobites occur (e.g. Ahlberg 1985). *Kullingia* is found in a narrow interval (1–2 m) of interbedded sandstone and siltstone in the lower portion of the formation, where it occurs with the tubular fossil *Sabellidites* isp., vendotaenid filaments, and trace fossils of Cambrian (or younger) aspect including *Treptichnus* (Jensen & Grant 1998). This demonstrates that the *Kullingia* bearing interval is earliest Cambrian (Jensen & Grant 1998) rather than terminal Proterozoic, as previously thought.

There are about 40 specimens of *Kullingia* in museum collections. Of these, at least 13 specimens are complete or nearly complete discs consisting of nested sets of concentric ridges (on the base of beds) or furrows (on the top of beds) in several specimens with part and counterpart. The most characteristic preservation is on the base of sandstone beds, which is the mode of preservation referred to in the following description (Fig. 1). Spacing between ridges typically is about 2 mm, but closer spacing occurs (Fig. 1A, B, H). The discs generally are of low relief; in many specimens the sediment between the ridges is a direct continuation of the bedding plane. The central portion of the disc may be slightly conical and may have a distinct central protuberance (Fig. 1A, C), more rarely a low central disc may be present (see Jensen & Grant 1998, their fig. 3B). In typical specimens, the ridges are regularly spaced, but specimens with a more irregular development also occur (Fig. 1E, G). Outer dimensions range from a few centimetres to more than 15 cm.

Glaessner (in Føyn & Glaessner 1979) erected the new genus and species *Kullingia concentrica* based on the unique set of characters of concentric fine ribs, but absence of both deep concentric furrows and radial sculpture. Føyn & Glaessner (1979) compared the ribbing in *Kullingia* to that of certain Ediacaran fossils that had been allied to chondrophorines but left open the position of *Kullingia* in the Cnidaria, though suggestions were made of a benthic life style. In the interpretation of Narbonne et al. (1991) the concentric ridges in *Kullingia* are filled impressions of the concentrically chambered pneumatophore.

Several lines of evidence show that *Kullingia* from northern Sweden is not a body fossil but was formed by the rotation of a tubular anchored organism, as first suggested by Stodt (1987).

First, there are specimens that preserve impressions within the disc of a tubular organism, conterminous with the disc (Fig. 1A, C). Such a tube is not present on the specimen that Glaessner designated type (Fig. 1B). Identical tubes are also found preserved isolated on the same bedding plane as the *Kullingia* discs (Fig. 1D, I), which makes it unlikely that they are an internal structure of an organism. Duplication of ridges suggests that there sometimes was displacement along the tube’s axis as it was being rotated (Fig. 1E). One specimen preserves within the disc what appear to be imprints made by a tube immediately after it was uprooted (Fig. 1H).

Second, the centre of the disc generally possesses a distinct central tubercle (Fig. 1A, C; see also Jensen & Grant 1998, their fig. 3C). This bears no resemblance to any structure in a chondrophorine interpretation such as a central feeding polymp, which would be highly unlikely to leave such regular distinct impressions. The central structure, however, is easily explicable as filling of part of the cavity where an organism was inserted in the sediment.

Third, there are specimens with grooves present at more than one vertical level (Fig. 1C). However, this is not analogous to undertrack fall-out in for example arthropod trace fossil, as there is no change in the nature of the grooves.
The scratch circle pseudofossil *Kullingia concentrica* from the Lower Cambrian Torneträsk Formation, northern Sweden. A–E, G–I are from the upper part of the Lower siltstone member; F is from the upper part of the Red and green siltstone member (see Thelander 1982; Jensen & Grant 1998). All specimens are in sole view. 

**A.** Two specimens with distinct and regular concentric ridges. The specimen to the upper left preserves an annulated tube in direct continuation with the concentric ridges and conterminous with the disc, ×0.6. **B.** The ‘holotype’ of *Kullingia concentrica*, SGU Type 22, ×0.6. **C.** A specimen that preserves ridges on several closely spaced vertical planes. Note that the ridges on the lower level (to the left) do not differ as would be expected if they were under-track fallout. A faint ridge running from the centre of the disc probably is the impression of a tube, ×0.85. **D.** An isolated tube identical to those found within the discs of *Kullingia*, ×1. **E.** A partially preserved specimen in which the ridges show evidence of horizontal displacement, ×0.85. **F.** A small scratch circle (at right arrow) on the sole of a sandstone bed that also preserves delicate trace fossils. An enigmatic structure that could be the cast of a tube, or possibly a trace fossil, is at the left arrow, ×1.4. **G.** A specimen with a pronounced central region and a distorted outline, ×0.6. **H.** A large specimen with relatively faintly preserved ridges. To one side are several parallel ridges (indicated by arrows) that have the same spacing as the concentric ridges and probably represent the passage of an uprooted tube, ×0.9. **I.** An isolated tube identical to those found within the discs of *Kullingia*, ×1.
The nature of the sweeping tool has to be inferred from imprints of what presumably is the external surface. In several, but not all, specimens, the ridges are not symmetrical, but have one sharper side and one more gently slanting side (Fig. 1A, E). Invariably the latter side faces towards the centre. This suggests that the tube had the appearance of a cone-in-cone structure. This type of organization is found in a number of terminal Proterozoic–Early Cambrian tubular fossils. The only Baltic fossil that matches in terms of shape, overall size and size are sabelliditids, long organic tubes of uncertain affinity. The genus Saarina Sokolov, 1965, is constructed from funnel-shaped increments, and includes specimens that reach 4–7 mm in diameter. An organism such as Saarina juliae Gniovskaya, 1996 (albeit that this species is from the terminal Proterozoic) with a pronounced frill at the funnel opening makes a likely model producer of the Kullingia scratch circles. Being organic and perhaps chitinous, sabelliditids would have been tough and flexible enough to form these scratches.

During fieldwork in the Torneträsk Formation, we (SJ, SWFG) found a small specimen of Kullingia, about 7 mm wide, consisting of three incomplete concentric ridges, about 25 m up-section from the main Kullingia bearing level (Fig. 1F). Next to this specimen is found a possible tubular fossil (Fig. 1F). This specimen bears great similarity to some forms that have been reported as Laevicyclus, including material from the Lower Cambrian of Pakistan (Seilacher 1955). The nature of the various forms that have been identified as Laevicyclus has been the subject of much discussion, including suggestions of the sweeping motion of feeding tentacles and formation during water or gas escape (see Frey 1970 for a discussion). Laevicyclus; probably comprises a heterogeneous group of objects, but an origin due to the sweeping motion of a tethered object needs be considered (e.g. D’Alessandro 1980).

**Kullingia from Newfoundland**

Narbonne et al. (1991) reported specimens of Kullingia delicata from the lower part of the Chapel Island Formation (member 2), about 10 m above the Precambrian–Cambrian boundary. During fieldwork, we (MLD, JGJ, SJ) found additional specimens of Kullingia at several levels higher in member 2 of the Chapel Island Formation. Similar to Kullingia from northern Sweden, the Newfoundland material is preserved on the base of sandstone and siltstone beds. One of these specimens in particular shows that a scratch circle origin applies also to the Newfoundland material (Fig. 2). It is a moderately deep form, with a relief of about 10 mm, possessing fine apparently concentric ridges (Fig. 2A). A narrow curved tube with variously preserved transverse ribbing extends from the central region to the limit of the slab. The tube shows a gradual outward increase in diameter from about 1 mm close to the centre to 2 mm distally. The transverse ornamentation of the tube is indifferently preserved but in places shows closely spaced ridges separated by 0.3–0.4 mm. The disc is not of the same height on either side of the tube but shows about 2 mm difference in relief. This relief exceeds the preserved diameter of the tube, which
suggests that the tube is preserved as an internal mould.

The only body fossils known from this interval of the Chapel Island Formation are *Sabellidites* sp. and vendotaenids (Landing et al. 1989). The sessile, transversely ornamented, elongate calcareous tube ‘Ladatheca’ *cyclindrica* first appears about 60 m higher in the Fortune Section (Landing et al. 1988). The *Kullingia* tube appears to have a more strongly developed segmentation, but otherwise is comparable in size and in degree of tube tapering. It is open to question, however, if the calcareous tube would have had the flexibility that probably would have been required for it to act as a tool.

A second specimen from the Chapel Island Formation (Fig. 2 B) has poorly developed concentric ridges that are well preserved only on one quadrant. Fortuitous cracking shows a sediment filled tube extending from the centre of the disc and up at an angle into the rock. Thus, in this instance the tubular organism was not pressed flat against the sediment surface onto which it had produced concentric scratches, but became entombed in sediment.

Both of the above described scratch circles are found on bedding planes that yielded casts of tubular organisms that presently have not been identifiable. It can hardly be doubted that these *Kullingia* specimens are genetically related to the material described by Narbonne et al. (1991), especially given the considerable variability shown among *Kullingia* specimens from northern Sweden. The argument for a pelagic origin of the Chapel Island Formation *Kullingia* was based on a difference in the number of tool marks preserved under the disc and adjacent bedding surfaces, as well as the presence of a prod-free shadow on the down-current side (Narbonne et al. 1991). These arguments are not compelling and a scratch circle interpretation can easily explain these features.

Other scratch circles described as body fossils

There are several other reports of *Kullingia*, some of which may also be interpreted as scratch circles. *Kullingia concentrca* from the Lower Cambrian of the Ukraine (Gureev 1985, 1987) fall within the morphological range of specimens from northern Sweden. Apparently no tubular fossils have been found in direct association with the Ukrainian material.

*Kullingia* from the Uratanna Formation in South Australia were probably not formed by tubular organisms acting as the sweeping tool. These occur on the same sets of beds that yield Ediacara-type fronds (Jensen et al. 1998) of a size that is consistent with the fronds acting as the tool. Ediacaran fossils previously had been implicated in the production of tool marks. Fedonkin (1976) erected *Suzmites volutatus* for sets of curved ridges and suggested that these were formed by the costate portion of a *Pteridinium*, specimens of which were found in close proximity and which have a segment spacing comparable to that in *Suzmites* (Fedonkin 1976). The specimens of *Suzmites* are fragmentary, which makes it difficult to assess if these had a true centre of rotation.

Other forms that consist of concentric ridges preserved as casts or moulds in siliciclastic sediments also need to be considered in terms of a scratch circle origin. However, careful evaluation of each case will be needed. For example, Gureev (1985) synonymized
Cyclomedusa delicata Fedonkin, 1981, from the terminal Proterozoic of the White Sea area, with Kullingia concentrata, but it is not clear that these are identical. Similarly, a scratch circle interpretation cannot be automatically applied to several reports of terminal Proterozoic Kullingia (e.g. Narbonne & Aitken 1991; Bekker 1996).

Kullingia was not the first scratch circle that had been identified as a chondrophorine hydrozoan. Caster (1942) described Palaeoscia foweri based on two specimens from the Ordovician Corryville Member of Ohio as a porpitid chondrophorine. This material possesses outer concentric ornaments and central radiating lines emanating from a central pore. Finds of additional material from the type area convinced Osgood (1970) that these are not body fossils but either sweep marks of an agglutinated tube or feeding traces. From the same unit Osgood (1970) also described several specimens that he considered to be undoubted sweep marks.

One additional form that we believe should be interpreted as of scratch circle origin is Nimbia occlusa from the Upper Cambrian of Eire (Crimes et al. 1995). It occurs as small disc-shaped objects possessing concentric rings on the sole of turbidite beds (Fig. 3B). Most specimens consist of semicircular arches with a central tubercle, and uniformly oriented in a down-current direction. Crimes et al. (1995) interpreted these forms as transported rigid-bodied fossils analogous to Ediacaran fossils. We find the hydrodynamics of the proposed mode of preservation problematic. A simpler explanation is for the central tubercle to be the site of attachment of an organism with the form of the disc controlled by the dominant current direction (Fig. 3A).

Discussion

Kullingia should be removed from discussions about the early fossil record of the Chondrophorina. Hence, the terminal Proterozoic and early Paleozoic record of chondrophorines is problematic. Renewed attention is required to properly interpret the numerous terminal Proterozoic and Cambrian reports, notably Ovatoscutum and also to specimens from the Burgess Shale (Conway Morris 1993). At present, it is difficult to precisely identify the oldest undoubted chondrophorine. The Devonian Plectodicus are rather compelling, though also for these there are remaining issues at least with some reports (Otto 2000).

Previously we used the presence of Kullingia in earliest Cambrian sediments as a biostratigraphical indicator (Jensen et al. 1998). In light of the above re-interpretation and the likelihood that more than one type of organism acted as a tool in the formation of Kullingia the apparently restricted biostratigraphical range of most Kullingia is unexpected. This may, however, provide information on Cambrian sediment properties, as discussed below.

Modern scratch circles are most easily observed in eolian settings, where grass may create highly regular circular or semi-circular imprints (e.g. Koerfer & Schwartbach 1971; Müller 1983), but the same process occurs also subaequously. Rarely, there may be radial marks in the central area. In addition to plants, pennatulaceans and hexactinellid sponges have been observed acting as tools (Heezen & Hollister 1964; Gaillard 1991). The fossil record of scratch circles appears to be rather poor. In a comprehensive textbook on sedimentary structures, Allen (1982) refers to a single known fossil example from the Weald Clay of southern England (Prentice 1962). This overlooks at least one earlier report, as already at the end of the 19th century, Nathorst (1886) described scratch circles on the base of a Lower Cambrian sandstone from Sweden. Other examples of scratch circles had been interpreted as body fossils. This includes Dystacophycus mammalimum Miller & Dyer, 1878, from the Ordovician of Ohio that in the classical literature was considered a “fucoid” or a bryozoan, but which was convincingly shown by Osgood (1970) to be casts of the rotational sweepings of crinoid stems.

The above examples show that the number of scratch circles has been underestimated. A literature-based compilation of scratch circles is presented in Tables 1 and 2. This probably represents a highly incomplete compilation of scratch circles in the existing literature. A substantial proportion of this record of scratch circles were originally interpreted as body fossils (Table 2). Most of the Cambrian occurrences were found in heterolithic bedding in portions of sections interpreted as subtidal with episodic influence of storms resulting in deposition of silts and sands. Taken at face value, this list shows a clear trend in that Carboniferous and younger examples were recovered from intertidal and continental settings, whereas older examples are largely from subtidal storm-influenced deposits, including the Ordovician Palaeoscia from the Corryville Member in Ohio (e.g. Goldman 1998). The Carboniferous and younger scratch circles from intertidal and continental settings probably relate to the presence of resistant vascular plants acting as tools. The great scarcity of preserved scratch circles in post-Ordovician shallow subtidal settings (a report of Laevicyclus from the Carboniferous Price West Formation of West Virginia (Bjersted 1987) may be an exception) is intriguing.
Table 1. Reports of scratch circles.

<table>
<thead>
<tr>
<th>Period</th>
<th>Location</th>
<th>Characteristics</th>
<th>Tool</th>
<th>Depositional setting</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jurassic</td>
<td>Towaco Fm., New Jersey, USA</td>
<td>A few widely spaced ridges</td>
<td></td>
<td>Floodplain</td>
<td>Metz 1991</td>
</tr>
<tr>
<td>Triassic</td>
<td>Pont de Suert Fm., north-east, Spain</td>
<td>A few widely spaced ridges?</td>
<td>Seaweeds?</td>
<td>Intertidal</td>
<td>Dixon 1987</td>
</tr>
<tr>
<td>Carboniferous</td>
<td>Horton Bluff Fm., Nova Scotia, Canada</td>
<td>Several prominent ridges and a central tuberade</td>
<td>Rooted vegetation</td>
<td>Beach-to-shoreface sand on prograding, wave-dominated delta</td>
<td>Calder et al. 1998</td>
</tr>
<tr>
<td>Carboniferous</td>
<td>Pride Mountain Fm., Alabama, USA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ordovician</td>
<td>Economy beds, Kentucky, USA</td>
<td>Sharp ridges subscribing one quadrant</td>
<td></td>
<td></td>
<td>Rindsberg 1994</td>
</tr>
<tr>
<td>Cambrian</td>
<td>Corryville Member, Ohio, USA</td>
<td>Conical forms first described as <em>Dystacop攸cus</em></td>
<td>Crinoid stem</td>
<td>Subtidal, storm influenced</td>
<td>Osgood 1970</td>
</tr>
<tr>
<td>Terminal</td>
<td>Us Pinega Fm., Arkhangelsk area, n. Russia</td>
<td>1–4 ridges, less than 180 deg., down-current of central knob</td>
<td></td>
<td>Shallow marine</td>
<td>Nathorst 1886</td>
</tr>
<tr>
<td>Proterozoic</td>
<td></td>
<td></td>
<td></td>
<td>Sandy shoal</td>
<td>Grazhdankin 2000</td>
</tr>
</tbody>
</table>

Table 2. Body fossils and trace fossils reinterpreted as scratch circles.

<table>
<thead>
<tr>
<th>Period</th>
<th>Location</th>
<th>Original interpretation</th>
<th>Tool</th>
<th>Deposit, setting</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cretaceous</td>
<td>Apeleg Fm., Chile</td>
<td><em>Aysenspriggia aplegenensis</em>, chondrophorine hydrozoan</td>
<td></td>
<td>Shelf, below wave base</td>
<td>Bell et al. 2001</td>
</tr>
<tr>
<td>Carboniferous</td>
<td>Price Fm., West Virginia, USA</td>
<td><em>Laevicylea</em>, vertical dwelling burrow of suspension feeder</td>
<td></td>
<td>Outer shelf</td>
<td>Bjersted 1987</td>
</tr>
<tr>
<td>Ordovician</td>
<td>Grant Lake Fm., Ohio, USA</td>
<td><em>Palaeosco floweri</em>, chondrophorine hydrozoan</td>
<td></td>
<td>Off-shelf, with episodic storms</td>
<td>Caster 1942; Osgood 1970</td>
</tr>
<tr>
<td>Cambrian</td>
<td>Booley Bay Fm., Eire</td>
<td><em>Nimbia occulsa</em>, rigid-bodied Ediacaran-type organism</td>
<td></td>
<td>Submarine fan</td>
<td>Crimes et al. 1995</td>
</tr>
<tr>
<td>Cambrian</td>
<td>Magnesian sandstone, Pakistan</td>
<td><em>Laevicylea</em>, feeding trace</td>
<td></td>
<td></td>
<td>Seilacher 1955</td>
</tr>
<tr>
<td>Cambrian</td>
<td>Chapel Island Fm., Newfoundland, Canada</td>
<td><em>Kollinga delicata</em>, chondrophorine hydrozoan</td>
<td></td>
<td>Shallow marine</td>
<td>Narbonne et al. 1991</td>
</tr>
<tr>
<td>Cambrian</td>
<td>Khmelnitsk Fm., the Ukraine</td>
<td><em>Kollinga concentrica</em>, benthic cnidarian</td>
<td></td>
<td>Shallow marine</td>
<td>Gureev 1985, 1987</td>
</tr>
<tr>
<td>Cambrian</td>
<td>Uratanna Fm., South Australia</td>
<td><em>Kollinga concentrica</em>, benthic fossil</td>
<td>? Ediacara-type frond</td>
<td>Shallow marine, subtidal</td>
<td>Jensen et al. 1998</td>
</tr>
<tr>
<td>Cambrian</td>
<td>Tornetrask Fm., Sweden</td>
<td><em>Kollinga concentrica</em>, cnidarian medusoid</td>
<td>? Sabelliditid</td>
<td>Shallow marine, subtidal</td>
<td>Kulling 1972; Stoldt 1987; Foy &amp; Glaessner 1979</td>
</tr>
</tbody>
</table>
This could be related to the increased extent and depth of bioturbation after the earliest Cambrian which reduced the preservation of thin storm deposits (cf. Sepkoski 1982; Sepkoski et al. 1991), and therefore would have been detrimental to the preservation of these structures. Furthermore, the low levels of bioturbation probably meant that Cambrian substrates had a sharper sediment–water interface (e.g. Bottjer et al. 2000) and led to an early dewatering of the sediment that resulted in cohesive muddy sediments conducive to the preservation of shallow trace fossil tiers (Droser et al. 2002). Cambrian siliciclastic sediments may therefore have been particularly suited to record and preserve scratch circles.

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References


Goldman, L.I. 1998: The Corryville Member of the Grant Lake Formation (Upper Ordovician, southwestern Ohio). In Davis, R.A. & Cuffey, R.J. (eds): Sampling the Layer Cake That Isn’t the Stratigraphy and Paleontology of the Type – Cincinnatian, 64–78. Guidebook – State of Ohio, Department of Natural Resources, Division of Geological Survey, Columbus, Ohio.


Kulling, O. 1972: The Swedish Caledonides. In Strand, T. &
LETHAIA 35 (2002)


Natherst, A.G. 1886: Om de sandslipade stenarnes förekomst i den kambriska lagren vid Lugnäs. Översikt af Kongliga Vetenskapliga-Förhandlingar 1886(6), 185–192.


