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Cyrtograptids from the Telychian (upper Llandovery) of Kinnekulle Mountain, southern Sweden

Emma H. M. Arvestål¹ & Michael Streng¹

The late Llandovery graptolite fauna of the Retiolites Shales on Kinnekulle Mountain in the province of Västergötland has long been known but never illustrated or studied in detail. New collections of graptolites from an interval at the very top of the exposed succession confirm previous reports of cyrtograptids, which make the shales on Kinnekulle the youngest preserved Palaeozoic rocks in the area. The co-occurrence of *Oktavites spiralis* and *Cyrtograptus lapworthi* constrain the strata to the lower *lapworthi* Biozone of the upper Telychian. The associated graptolite fauna comprises numerous monograptids and *Retiolites geinitzianus* as well as a new species of *Cyrtograptus*. The new species, *C. kinnekullensis* n. sp., is characterised by its open coiling and the presence of a second order cladium on the second thecal cladium. This early occurrence of a cyrtograptid species with a second order cladium on Baltica matches evolutionary patterns observed in Laurentia, suggesting that the ability to grow cladia of both first and higher order evolved approximately synchronously and at the very beginning of cyrtograptid evolution. Analysis on the positions of cladia in *C. lapworthi* indicates that the most proximal cladium was not necessarily the first to be formed. It appears that the first cladium originated distally and more proximal cladia formed afterwards as a counterbalance to the growing rhabdosome, allowing the organism to remain stable in the water column.

Keywords: *Cyrtograptus*, Graptoloidea, Llandovery, Telychian, Kinnekulle, Västergötland, Sweden.

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Introduction

The graptoloid genus *Cyrtograptus* Carruthers first appeared during the late Llandovery (late Telychian, *Cyrtograptus lapworthi* Biozone and equivalents) (Lenz & Melchin 1989) and became rapidly diverse and ubiquitous in the early Wenlock (e.g., Jackson & Etherington 1969, Lenz 1978, Williams & Zalasiewicz 2004). It reached its highest diversity in the mid Wenlock *lundgreni* Biozone, before it went extinct at the end of this zone (Urbanek & Teller 1997, Williams & Zalasiewicz 2004). Since *Cyrtograptus* is cosmopolitan, generally common and distinctive, it is widely used in biostratigraphy and international correlation (e.g., Huo & Shu 1986, Bjerreskov 1992, Williams & Zalasiewicz 2004, Loydell 2012). Certain species of *Cyrtograptus* are of particular importance since they define biozones of late Telychian to early Homeric age, i.e., *C. lapworthi*, *C. insectus*, *C. centrifugus*, *C. murchisoni*, and *C. lundgreni*. The oldest cyrtograptid biozone is the *lapworthi* Biozone of the upper Telychian, which is recognised in Avalonia, Baltica, peri-Gondwana and South China and can be correlated with the time-equivalent *sakmaricus* Biozone of Laurentia (e.g., Loydell 2012). On Baltica, the *lapworthi* Biozone is known from Scania (southernmost Sweden) (Tullberg 1883) and the island of Bornholm (Denmark) (Laursen 1940, Bjerreskov 1975). It has also been recognised on Kinnekulle mountain in Västergötland (southern Sweden, Fig. 1) (Waern 1948), but no more detailed description of the Kinnekulle graptolite fauna has been conducted.

Over the last few years, a rich fauna of graptolites has been recovered from a locality near Högkullen on Kinnekulle (Fig. 1), including specimens of *C. lapworthi* and two *C. lapworthi*-like specimens. The latter specimens resemble *C. lapworthi* in many ways, but also show some significant new characters not been previously recorded in this species. The two specimens are considered to represent a new species, which is described herein as *Cyrtograptus kinnekullensis* n. sp. and compared with other cyrtograptids from Baltica, in

particular *C. lapworthi*, but also other cyrtograptids of similar age and appearance. The significance of the cyrtograptids and associated fauna for constraining the age of the strata at Högkullen is discussed.

Methods

The two thecae repeat distance (2TRD) (Howe 1983) employed herein is the commonly used method for measuring thecae spacing in graptoloid taxa. 2TRD data may be shown in diagrams or plotted against values of dorso-ventral width (Howe 1983), but in general, measured values are instead given in tables for a selected number of thecae (e.g., Williams & Zalasiewicz 2004; Tab. 1). In addition to such a table, we have also chosen to plot measured 2TRD values against the corresponding thecae numbers. This allows us to visually compare specimens and their growth patterns, despite the fact that many may be incomplete proximally as no sicula could be distinguished. It is also possible to use the plot for an estimation of the completeness of the rhabdosome. In order to differentiate between potential incomplete rhabdosomes (i.e., without preserved sicula) and complete ones with sicula, two different thecae numbering systems are employed. Thecae in rhabdosomes showing a sicula are referred to by standard abbreviation thX; thus th1 corresponds to the first formed theca. In incomplete rhabdosomes, thecae are instead referred to as vthX, where vth1 is the first *visible* theca.

The graptolite specimens have been studied by light microscopy and photographed using a Nikon DS-5M digital camera attached to a Leica MZ7.5 stereomicroscope. To enhance contrast the specimens were coated with a sublimate of ammonium chloride prior to photography. Specimens of *Cyrtograptus kinnekullensis* n. sp. as well as other illustrated graptolites from Högkullen are deposited in the collections at the Museum of Evolution, Palaeontology (acronym PMU), Uppsala University, Sweden. The type and topotype material

of *C. lapworthi* used for comparison is housed in the collections of the Swedish Geological Survey (acronym SGU).

Geological setting and material

During the Pleistocene, glacial action removed most of the sedimentary rocks in Sweden, exposing the gneisses and granites of the Precambrian basement. Sedimentary rocks are still present locally, mainly in tectonic structures that protected them from erosion (e.g., impact structures, downfaulting). In the province of Västergötland, however, undisturbed sedimentary rocks are preserved as several isolated table-mountain-like hills, elevated above the Precambrian peneplain. Each of the hills is built up of a more or less flat-lying sequence of lower Palaeozoic sedimentary rocks, which is capped by early Permian doleritic sills (e.g., Priem et al. 1968, Martinsson 1974). The sills, locally reaching thicknesses of 30 to 45 m (Westergård 1928), intruded at different levels into the lower Palaeozoic rocks and were thereby able to protect the stratigraphically underlying beds from glacial erosion. At Kinnekulle Mountain, the youngest lower Palaeozoic strata of the area are preserved, i.e., the doleritic sill intruded at the highest preserved stratigraphic level. These rocks are early Silurian shales (greyish to greenish siltstones), which are informally called the Retiolites Beds or Retiolites Shales (e.g., Waern 1948). The shales are exposed around Högkullen, near the mountaintop, and have a thickness of about 25 m (e.g., Westergård et al. 1943, Waern 1948). The Retiolites Beds contain a rich fauna of mainly graptolites, but also brachiopods and molluscs (gastropods, orthoconic cephalopods and their aptychi) are occasionally observed (Arvestål & Streng, unpublished data). According to Waern (1948), the lower part of the Retiolites Beds bears various species of *Monoclimacis* and *Monograptus*, as well as *Oktavites spiralis* (*Spirograptus spiralis* of Waern 1948) and *Diversograptus* sp. In the upper part *Retiolites geinitzianus* and *Cyrtograptus* aff. *lapworthi* were reported to occur. This

association is typical for the upper Telychian (compare, e.g., Bjerreskov 1975, Lenz 1978) and the occurrence of *Oktavites spiralis* throughout the Retiolites Beds and the appearance of *Cyrtograptus* in the upper part indicate that both the *spiralis* and *lapworthi* Biozones are present on Kinnekulle (for graptolite biozonation, see, e.g., Loydell 2012). However, none of the specimens determined by Waern (1948) has ever been illustrated or described in detail.

For this study new material was collected from where Waern (1948) found *Cyrtograptus* aff. *lapworthi*. The locality is near the top of a talus slope, about 100 m north of the Kinnekullegården restaurant, at approximately 58° 35.897' N and 13° 24.902' E (Fig. 1). All specimens were collected from an interval of about 1.5 m. The top of this interval is marked by a break in slope (Fig. 2). Here, the talus of the Retiolites Beds can easily be removed to expose the bedrock. The top of the sampled level is about 3 m below the contact with the dolerite sill and represents the highest level from which determinable graptolites may be obtained. Waern (1948) noted the presence of graptolites in the uppermost interval, but the strata are thermally altered leaving the graptolites undeterminable. Graptolites within the sampled interval are preserved as three-dimensional, somewhat compressed hollow cavities, representing external moulds. Despite the three-dimensional preservation, details of the rhabdosome and particularly the thecae are unclear. The cavities are filled with yellowish-brownish fine particles (possibly hydrated iron oxides), which further disguise morphological details. The same is true for the more delicate specimens of *Retiolites*, which, however, are also occasionally preserved as compressed imprints. Molluscs and brachiopods are represented by decalcified moulds.

Systematic Palaeontology

Order Graptoloidea Lapworth, 1875

Family Cyrtograptidae Bouček, 1933

Genus *Cyrtograptus* Carruthers, 1867

Diagnosis.—Main stipe more or less spirally coiled, can be helicoidally at proximal end, bearing one or more thecal cladia (primary cladia), which may have cladia themselves (2nd and higher orders); thecae biform, hooked, or proximally triangulate with retroflexed apertures, becoming simpler distally (after Bulman 1955, 1970).

Type species.—*Cyrtograptus murchisoni* Carruthers, 1867 (by original designation) from the Buihth Mudstones Formation, Pencerrig Stream, Powys, central Wales (lower Wenlock, *murchisoni* Biozone)

Other species included.—Since the description of the type species by Carruthers (1867) more than 60 species of *Cyrtograptus* have been described. However, many species initially referred to *Cyrtograptus* have subsequently been assigned to other genera (e.g., *Barrandeograptus* Bouček) or have been synonymised. Furthermore, the description of a number of species is based on incomplete specimens casting doubt on the generic affiliation (e.g., Rickards et al. 1995, *partim* Ruedemann 1947). Based on the present concept of the genus (see *Diagnosis*), an estimate of about 40 valid species of *Cyrtograptus* might be realistic. Detailed review of these species is beyond the scope of this study.

Occurrence.—The stratigraphic range of *Cyrtograptus* is typically given as upper Telychian (*lapworthi* Biozone) to lower Homerian (end of *lundgreni* Biozone) (e.g., Lenz & Melchin 1989, see also Lenz & Kozłowska 2006). Nevertheless, there are indications that *Cyrtograptus* might already be present in the *spiralis* Biozone (e.g., *Cyrtograptus* n. sp. of Bjerreskov 1981 and *Cyrtograptus?* sp. of Melchin 1989). These reports need confirmation though. Putative specimens of *Cyrtograptus* younger than the *lundgreni* Biozone come from the early Gorstian (*nilssoni* Biozone) of Australia and are described as *Cyrtograptus?*

elegantulus (Rickards et al. 1995). However, the lack of cladia in this species questions the generic assignment, and therefore *C.? elegantulus* is herein not considered as a species of *Cyrtograptus*.

The spatial distribution of *Cyrtograptus* appears to reflect a preference for palaeocontinents situated in tropical to subtropical latitudes, but also reports from temperate areas are known. Thus, the genus has been reported from Avalonia (e.g., Williams & Zalasiewicz 2004); Laurentia (e.g., Berry & Murphy 1975, Lenz & Melchin 1991); Baltica (e.g., Bjerreskov 1975, Urbanek & Teller 1997); North China (e.g., Fu 1985); South China (e.g., Huo & Shu 1986); peri-Gondwana, e.g., the Czech Republic, Poland, Germany, Romania, Spain (e.g., Bouček 1933, Tomczyk 1956, Schauer 1968, Rickards & Jordan 1975, Loydell et al. 2009); and Australasia (e.g., Pickett 1982 *vide* Sherwin 1979); as well as part of Uzbekistan and the Russian Far East (e.g., Golikov 1974, Obut et al. 1967).

Discussion.—*Cyrtograptids* have been subdivided based on the coiling of the main stipe, development of cladia (primary or higher orders) and the shape of the thecae (e.g., Jackson & Etherington 1969). Since the morphological differences within the genus are quite distinct, particularly of the thecae, the genus is likely polyphyletic (e.g., Lenz & Melchin 1989, Bjerreskov 1992). Various groups or lineages have been proposed (e.g., Bouček 1933, Rickards et al. 1977, Fu 1985, Urbanek & Teller 1997) based mainly on thecal and rhabdosome morphologies and number and type of cladia. Thus, e.g., Urbanek & Teller (1997) proposed five separate evolutionary lineages, labelled A to E. Of these five lineages groups B and D compare best with the *cyrtograptids* from Västergötland. In group B, *cyrtograptids* are described as having “an incomplete or closed planispiral coiling of the proximal part, a fairly simple thecal morphology, and thecal cladia budding at varying distances [sic] from one another [...]. The presence of the cladia of the second [...], or third [...] order is another important character of this group” (Urbanek & Teller 1997, p. 27). *C.*

murchisoni and *C. laqueus* among others are placed therein. Group D, in which *C. lapworthi* and *C. insectus* are found, “comprises those forms whose proximal part is coiled planispirally, whose thecal morphology resembles that of the first group [i.e., group A] and whose cladia are considerably reduced. No more than two or three cladia are present as a rule” (Urbanek & Teller 1997, p. 27). However, this classification appears oversimplified. E.g., *C. insectus* is accommodated in group D, the group with reduced cladia, despite the fact that second and third order cladia are known from topotype material (Bouček 1933). *C. lapworthi* is placed in the same group, but up to five thecal cladia have been described for this species (Bjerreskov 1975). Following Urbanek and Teller (1997), the new species *C. kinnekullensis* described below should be placed in group B, as it bears a second order cladium. However, its overall morphology and in particular the thecal shapes suggest a close relationship to species such as *C. lapworthi* and *C. insectus* (see below), i.e., group D. For these reasons, the group system of Urbanek & Teller (1997) is not applied herein (see also Williams & Zalasiewicz 2004 for a similar discussion).

The oldest cyrtograptids are considered to bear cladia of the first order only. In Britain, *C. lapworthi* is the first occurring cyrtograptid (Zalasiewicz et al. 2009), while in Canada it occurs in association with *C. sakmaricus* and the somewhat younger *C. laqueus* in the *C. sakmaricus*-*C. laqueus* Biozone (Lenz 1979, Bjerreskov 1986). Probably the first cyrtograptid known to develop second order cladia is *C. laqueus*, while the slightly younger *C. insectus* can have cladia of both second and higher orders (e.g., Bouček 1933, Bjerreskov 1975). *C. laqueus* is currently known only from Laurentia (e.g., Jackson & Etherington 1968, Lenz 1978, 1979) and potentially North China (Deng 1986) where it co-occurs with *C. sakmaricus* and *O. spiralis* (Lenz 1979). This contrasts with occurrences on Baltica and Avalonia, where the first species with second order cladia, i.e., *C. insectus*, does not appear below the *insectus* Biozone (e.g., Bjerreskov 1975, Loydell & Cave 1996). However, with the

occurrence of the new species *Cyrtograptus kinnekullensis* in the *lapworthi* Biozone (see below), a taxon bearing second order cladia, the Baltic cyrtograptid evolution matches that documented in Laurentia. It is likely therefore that the ability of cyrtograptids to grow primary as well as higher order cladia evolved at approximately the same time worldwide.

Cyrtograptus lapworthi Tullberg, 1883

Figures 3, 5B-E

Synonymy.—v*1883 *Cyrtograptus Lapworthi* n. sp., Tullberg, pl. 3, figs. 8-11; p1933 *Cyrtograptus lapworthi* Tullb. 1883, Bouček, text-fig. 2, pl. 3, figs. 6-7, pl. 4 fig. 3, non figs. 1, 2; 1940 *Cyrtograptus Lapworthi* Tull., Laursen, pl. 4, fig. 2; ?1974 *Averianowograptus malgusaricus* sp. nov., Golikov, pl. 8, figs. 1-3, pl. 9, figs. 1-2; 1975 *Cyrtograptus lapworthi* Tullberg, Bjerreskov, pl. 13, fig. C; 1975 *Cyrtograptus lapworthi* Tullberg, Berry & Murphy, text-fig. 22b, pl. 13, fig. 1; ?1975 *Cyrtograptus* aff. *C. lapworthi* Tullberg, Berry & Murphy, text-fig. 22c, pl. 10, fig. 1; ?1978 *Cyrtograptus* aff. *lapworthi* Tullberg, Lenz, text-fig. 2.7, pl. 1, fig. 2, pl. 2, figs. 3, 5, 6; ?1985 *Cyrtograptus lapworthi* Tullberg, Fu, pl. 2, figs. 3, 4; ?1986 *Cyrtograptus lapworthi* Tullberg, Fu & Song, pl. 18, figs. 1-9; ?1986 *Cyrtograptus lapworthi* (Tullberg), Deng, fig. 2.3; 1988 *Cyrtograptus lapworthi* Tullberg, Lenz, fig. 5H, I, L; ?1989 *Cyrtograptus lapworthi* n. ssp., Melchin, fig. 14G; ?1996 *Cyrtograptus lapworthi* Tullberg, Loydell & Cave, fig. 11j, n, s; 1992 *Cyrtograptus lapworthi* Tullberg, Bjerreskov, fig. 7E, F; ?1992 *Cyrtograptus lapworthi* n. ssp. Melchin, Bjerreskov, fig. 7A-D; ?2000 *Cyrtograptus lapworthi* Tullberg, Lüning et al., pl. 1, figs. F, G. (Further potential synonymy is stated in Bouček 1933, Berry & Murphy 1975, and Bjerreskov 1975)

Material.—Twelve specimens: seven newly collected specimens from Högekullen; two of the three type specimens originally illustrated by Tullberg from Röstånga, Scania, southern

Sweden [SGU type 5681a, b (Tullberg 1883, pl. 3, figs. 8, 9; designated as lectotype by Bjerreskov 1975, p. 85); SGU type 5683 (Tullberg 1883, pl. 3, fig. 11); the third specimen depicted by Tullberg (1883, pl. 3, fig. 10) appears to be lost]; additional three specimens have been discovered in the collections of Swedish Geological Survey among topotypic material collected by Tullberg in 1879 [SGU9663-1, SGU9663-2, SGU9664].

New diagnosis.—Rhabdosome with openly coiled proximal part, straightening out distally. Typically with one to three cladia, rarely up to five; cladia of the first order only. A ventral-dorsal torsion of the main stipe typically takes place distally of the last cladium. Thecae subtriangular, hooked and with apertural spines, becoming simpler distally. Sricula small, its apex reaching the top of theca 1.

Description of type material.—The rhabdosome is openly coiled, with the proximal part of the main stipe moderately curved and the distal part (after the last cladium) much less so; coiling does not reach a whole volution (Fig. 3A, 3B). Measured degrees of coiling range from 19° and 23° per 2.5 mm in the most proximal part to 2.7° and 4° per 2.5 mm in the distal part of the rhabdosome. The main stipe exhibits torsion of about 90 degrees, which occurs close to or just beyond the last cladium, not far from where the coiling has straightened out (Fig. 3D). Preserved lengths of main stipes are 9 cm and 10 cm, respectively. Neither of the specimens has a detectable sricula, and it is therefore possible that the most proximal thecae are missing. However, thecal spacing and rhabdosome width and shape, all indicate that the most proximal visible part of the main stipe might represent the actual proximal part of the rhabdosome. Cladia are of the first order only and can be straight to slightly curved, and, like the main stipe, experience some torsion. One of Tullberg's type specimens bears two cladia, both broken after 2.1 cm and 1.5 cm, respectively (Tullberg 1883, pl. 3 fig. 11; SGU type 5683; Fig. 3B). The other specimen (Fig. 3A) bears three cladia of which the first and third are rather short and broken after 1.2 cm and 1.3 cm, while the second one is longer but still

incomplete, reaching 4 cm (Tullberg 1883, pl. 3, figs. 8-9, SGU type 5681; note: Tullberg's illustrations are partly incomplete and/or idealized). The first theca of each cladium has an elongated appearance but their poor preservation does not allow any measurement. The position of the cladia varies between specimens. In the specimen with two cladia, the cladia arise after visible theca 12 (vth12) and 31 (vth31), in contrast to the form with three cladia, in which they arise after vth5, 12 and 27, respectively. The thecae are subtriangularly shaped, with the proximal ones being hooked and occasionally preserved with short apertural spines. For 2TRD and other measurements see Fig. 4 and Tab. 1.

Description of topotype material.—The overall morphology of the three topotypic specimens matches the description of the types. Two of the specimens (SGU9663-1 and SGU9663-2) left only a faint impression in the rock, showing one and two cladia respectively, of which only the most proximal parts are preserved. The main stipes measure 6.3 and 4.7 cm in length and show torsion distally. Thecal counts and detailed measurements were not possible due to the poor preservation. The third specimen (SGU9664; Fig. 3C, F) is in better condition, showing details not observed in the type material. Although only the untwisted proximal part of the main stipe is preserved, i.e., about 3.5 cm, this part shows three cladia and detailed thecal morphology. The cladia originate from th6, th14, and th33, respectively, all of which experienced torsion of about 90 degrees. The first two cladia are broken after 5.4 and 8.3 mm, respectively, whereas the third one reaches a length of almost 5 cm before it ends at the margin of the rock slab. The thecae of the main stipe are hooked with short apertural spines (Fig. 3F). Thecal morphology on cladia not visible due to torsion. The sicula is small, measuring 1.1 mm in length and 0.26 mm in apertural width. Its wall is slightly convex, resulting in a maximum width of 0.29 mm not at the concave aperture but at about 0.85 mm from the apex. A short, somewhat bent virgella is present. For 2TRD and DVW measurements see Tab. 1.

Description of Högkullen material.—The specimens assigned to *C. lapworthi* from Högkullen are strikingly similar to the type and topotype material in their general appearance, although preserved in less detail. Of the seven collected specimens, the 2TRD could only be analysed in the proximal part of two specimens (Fig. 5B, 5D; Tab. 1). None of the specimens is complete and distal parts of the main stipe and also of the cladia are often missing due to breakage of either the specimen or the rock. The largest and best preserved specimen (PMU 26982, Fig. 5D-E) has a main stipe reaching 14.5 cm in length, still with its most distal part missing. It has two cladia of which the first one is broken with only about 1.1 cm of its length preserved, whereas the second cladium measures 8.2 cm and appears to be complete. The remaining six specimens are less complete, with preserved lengths of the main stipe varying between 3.6 and 8.1 cm and either one (five specimens) or two cladia (one specimen). In their proximal part, individual thecae are poorly distinguished, while the more distal parts of the main stipes are either equally poorly preserved, have experienced torsion or are completely lacking. The torsion of the main stipe begins a few thecae after the most distal cladium, but seems to not exceed 90 degrees even in the most distal part of the larger specimens. The number of cladia varies between one and two, and if preserved completely, their curvature resembles the one of the main stipe. It is worth noting that when only one cladium is present, it extends from somewhere between vth21 and 24. When two cladia are present, the proximal one emerges already at vth16, while the distal cladium extends not earlier than vth25. No sicula has been observed in any of the Högkullen specimens, but as for the type material, characters of the proximal part of the main stipe, such as degree of curvature, 2TRD, and dorso-ventral width, suggest a complete or almost complete preservation of the proximal end in most specimens.

Discussion.—As previously pointed out by Bjerreskov (1992), *C. lapworthi* is highly variable and rather ill defined and would benefit from a redefinition. Variations can typically

be seen in the number of cladia developed, the degrees of curvature and torsion of the main stipe, and to a lesser extent in the dorso-ventral widths of the main stipe and cladia. Reasons for the observed variation within *C. lapworthi* might partly be regional and/or ecological, or a taxonomic bias, i.e., unrecognized species currently accommodated within *C. lapworthi* (see, e.g., *Synonymy*).

Most illustrated and described specimens of *C. lapworthi* possess only one cladium (e.g., Bouček 1933, Berry & Murphy 1975, Lenz 1988) but up to five have been observed (Bjerreskov 1975). Noteworthy is that specimens with more than three cladia have been reported only from Baltica, i.e., the island of Bornholm (Bjerreskov 1975). The theca(e) from which the cladia originate varies between different specimens and appears to be linked to the number of cladia developed (see also *Description* above and *Remark* below). The most proximal cladium originates from between theca 6 and 24 or even higher (e.g., Fig. 3F, Bjerreskov 1975 vs. Bouček 1933, Loydell et al. 2009, fig. 6h). The second cladium, if present, develops between 6 and 19 thecae distal to the most proximal one (e.g., Lenz 1988, see *Description* above). Any cladium distally of the second one appears at intervals between 15 to 30 mm (Bjerreskov 1975). The number of developed cladia might reflect a regional pattern, with specimens having three or more cladia coming from Baltica (Tullberg 1833, Bjerreskov 1975) or peri-Gondwana (Bouček 1933). However, a preservational bias cannot be excluded.

The rhabdosome of *C. lapworthi* is generally described as openly coiled, but the degree of curvature of the main stipe appears highly variable. Thus, Bjerreskov (1975) described the curving of the proximal part of the main stipe to vary from approximately 180° to a maximum of one volution. Distally the degree of coiling typically decreases (e.g., Tullberg 1833, Berry & Murphy 1975), sometimes completely straightening out (Lenz 1988). A relationship between coiling variability and regional distribution (as well as ecology) is

unlikely as Bjerreskov (1975) describes tightly coiled to openly coiled specimens from two nearby localities from the island of Bornholm.

Torsion of the post-cladial portion of the main stipe is a diagnostic character of the species. The degree of torsion, however, appears to be variable. Whereas the studied Baltic specimens (including the type material) show a torsion of only about 90 degrees, a torsion of 180 degrees has been described for specimens from Bohemia and Canada (Bouček 1933, Lenz 1988). Although Tullberg (1883) illustrates one of his specimens as having such a torsion, showing the most distal thecae on the concave side of the main stipe (Tullberg 1883, pl. 3, fig. 9), the torsion of this specimen (SGU 5681) does not exceed 95 degrees (Fig. 3A).

Despite the incomplete preservation of the specimens from Högkullen, they can all confidently be assigned to *C. lapworthi*. Measured 2TRD values, the characteristic curving of the proximal part of the main stipe, the number of cladia, the width and torsion of the main stipe, as well as the shape of the thecae all agree with the characters of the type material. Unusual is solely the length of the second cladium in one specimen (Fig. 5D).

Remark.—As mentioned above (*Description*), the *C. lapworthi* specimens from Högkullen bear either one or two cladia, both of which appear to have a certain preference for their point of origination from the main stipe. Hence, if only one cladium is developed, it arises from between vth21 and 24, whereas when two cladia are developed, they extend from around vth16 and 27, respectively. It could therefore be argued that, since there are no specimens with a single cladium at theca 16, the most proximal cladium in *C. lapworthi* might in fact not be the first to develop. This questions not only the sequential cladia formation, with the most proximal cladium being the oldest and most distal one the youngest, as has been proposed for cyrtograptids (Fortey & Bell 1987), but it also challenges the principles of cladial development postulated for cyrtograptids (Thorsteinsson 1955). A non-sequential

formation of cladia in *C. lapworthi* is further supported by the analysed specimens from the type locality. Here, the two specimens with three cladia show a very proximal first cladium originating from vth5 and th6, respectively. This contrasts the specimens with one or two cladia, in which the first cladium arises about 10 thecae later. In fact, the two cladia of specimen SGU5683 arise rather where cladium two and three of specimen SGU5681 and SGU9664 would be located.

It appears likely that the formation of cladia is merely a response to an “unbalance” of the entire rhabdosome, an unbalance initially caused by the increasing length of the main stipe and the concurrent shift of the centre of mass from a proximal towards a more distal part of the rhabdosome. By adding a cladium in an appropriate position (this position is likely to be dependent on the size and curvature of the main stipe), the cladium acts as a counterbalance and keeps the centre of mass of the rhabdosome in a proximal position. The same would apply for additional cladia forming after the initial one. Each new cladium would grow in a position where it could act as a counterbalance to the already existing cladia and main stipe, successively keeping the growing rhabdosome as a whole in balance. However, more data of complete specimens from different environments is needed to confirm this theory as current thecae counts might be imprecise.

Cyrtograptus kinnekullensis n. sp.

Figures 6-8

Material.—Two specimens; one specimen consisting of part and counterpart (holotype), whereas for the second specimen (paratype) only an incomplete part is available.

Holotype.—Specimen PMU26985 (Fig. 6A-H). Type locality and horizon: Högkullen on Kinnekulle, Sweden (approximately 58° 35' 54'' N, 13° 24' 55'' E, see Fig. 1), Retiolites Shales, late Llandovery, uppermost Telychian, *Cyrtograptus lapworthi* Biozone.

Diagnosis.—Species of *Cyrtograptus* with main stipe openly coiled in proximal part, straightening out distally. Several first order cladia developed of which the second one bears at least one second order cladium. Proximal thecae hooked, distal thecae more simple. Sicula small with its apex reaching top of theca 1.

Description (based on holotype if not otherwise stated).—The main stipe is openly coiled in its proximal part (Fig. 6C, 8A), curving about three quarters of a revolution before beginning to straighten out slightly before the third cladium. Most proximal tip of main stipe somewhat tighter coiled than rest of proximal part (Fig. 10A). No torsion has been observed on the main stipe, whose preserved length is about 8 cm when it reaches the margin of the rock. The dorso-ventral width of the main stipe measures about 0.5 to 0.8 mm in the first thecae and reaches 1.2 mm distally. Five cladia of the first order are recognised, originating from th16, 26, 38, 55, and possibly 79 (Tab. 2). Since the main stipe is broken just distally to the fifth cladium, the development of more cladia is possible. From the second thecal cladium a second order cladium is developed, originating from theca 16 on the holotype and from theca 21 on the paratype. The second cladium is the best preserved one, being approximately 8 cm long (about 10 cm in paratype), while only the initial 1-2 cm of the other cladia are preserved. The fourth cladium, however, reappears after a 2.7 cm long gap, having a total length of about 4.5 cm. All but the second cladium appear to be straight, but it is likely that they are gently dorsally curved and only straight in their most proximal, preserved parts. The fourth cladium indicates that this might be the case, since its most distal part has a slightly different direction compared to the proximal part (Figs. 6A, 8A). This is further supported by the slight curvature of the presumed third cladium of the paratype (Fig. 7A). Several of the

cladia, unlike the main stipe, exhibit torsion. In its distal part, the second cladium experiences minor gradual torsion to the right. The second order cladium also shows this dextral torsion, as does the distal part of the fourth cladium. The same is true for the paratype, in which all preserved cladia exhibit torsion of about 90 degrees.

The general poor preservation excludes any statements on detailed thecal morphology, except for the variation in curvature of the ventral thecal wall, which allows identification of two distinct thecal types. The first type is represented by the proximal thecae, which are triangular in outline and hooked (primary type of Thorsteinsson 1955) (Fig. 8B, 8D). After the third cladium, at th38, the inclination between the ventral wall of the thecae and the main stipe decreases, although the hook is still present. This decrease in inclination might be a result of the reduced dorsal curvature of the rhabdosome, causing the thecae to appear to be closer to the rhabdosome even though no actual change might have occurred. A definitive change to the second thecal type can be observed after the appearance of the fourth cladium. Here the inclination between ventral thecal wall and main stipe decreases even further and the hooks become clearly less pronounced (secondary type of Thorsteinsson 1955) (Fig. 8C). Still, some curvature is present even in its most distal parts, as can be seen in th76 and th78.

The 2TRD reveals an increase in thecal spacing from the proximal to the distal end, which is more rapid initially, and quite moderate after about 23 mm, or 25 thecae (Fig. 9, Tab. 1). The highest observed 2TRD is 2.76 mm (between th71 and th73).

The first theca of each cladium is elongated compared to ordinary thecae, measuring between 1.9 and 2.9 mm in length. As in the main stipe, the dorso-ventral width of the cladial thecae increases distally, ranging between 0.5 and 0.88 mm in the first thecae of each cladium (if measurable), and reaches a maximum of 1.2 mm at the end of the second cladium.

A small, faintly delineated sicula can be distinguished on the holotype (counterpart only). It is 0.8 mm long with its apex reaching the top of th1 (Fig. 8D). The state of preservation, however, does not allow a confident assessment of its completeness.

Derivation of name.—After the locality where it was found, the Kinnekulle table mountain in Västergötland, Sweden.

Discussion.—*C. kinnekullensis* n. sp. and *C. lapworthi* have several similarities. They are both openly coiled, but *C. kinnekullensis* n. sp. is even more open in the proximal part (Fig. 10). The straight distal part of *C. kinnekullensis* has also been observed in *C. lapworthi*. The torsion of the main stipe present in *C. lapworthi* as well as in many other cyrtograptids is, however, not seen in the preserved part of *C. kinnekullensis*. Rhabdosome torsion could still occur in this species, distally to the breakage of the main stipe. This is supported by the fact that cyrtograptids typified by cladia occurring at irregular intervals usually have their torsion beyond their last cladium (Urbanek & Teller 1997) and the last (preserved) cladium in *C. kinnekullensis* originates from the last preserved theca. Still, there would be a difference between the two species since the torsion of *C. lapworthi* has already advanced quite far after 3.5 cm, while there is no sign of it in the 8 cm long main stipe of *C. kinnekullensis*.

C. lapworthi usually possesses one cladium, but up to five first order cladia have been observed in specimens found on Bornholm (Bjerreskov 1975), and five is also the number of cladia found in *C. kinnekullensis*. The cladia of *C. lapworthi* are commonly slightly dorsally bent but can be straight as well, which is also the case for four of the cladia of *C. kinnekullensis*. The second cladium of *C. kinnekullensis*, however, possesses a second order cladium, an attribute not known from *C. lapworthi*, neither from Bornholm nor elsewhere.

The described distributions of cladia are highly variable in *C. lapworthi*. The first cladium can appear at about th6 to th23 (even at th35 according to Bouček 1933) and the second cladium after yet another 6 to 19 thecae (e.g., Berry & Murphy 1975, Bjerreskov

1975, Lenz 1988; *Description of C. lapworthi* above). Any further cladium can appear at an interval of about 15-30 mm (Bjerreskov 1975), which agrees with our measurements on the specimens with three cladia. In these specimens the third cladium originates after 15 and 19 thecae, respectively (Tab. 2), corresponding to 14.2 and 17.4 mm. This large variation makes it rather easy for *C. kinnekullensis* to fall within these observed intervals, and highlights the need of a redefinition of *C. lapworthi*.

The thecal shape of *C. lapworthi* is subtriangular, being hooked in the proximal part and has rather straight ventral thecal walls distally. This also seems to be the case in *C. kinnekullensis*, and even though the preservation makes it difficult to determine the exact theca where the change to the secondary thecal type occurs, it appears to be significantly later than in *C. lapworthi*.

The 2TRD values of the main stipe of *C. kinnekullensis* and *C. lapworthi* show proximally a fairly similar increase in distance per two thecae. The distal values are, however, larger in *C. kinnekullensis* than in the *C. lapworthi* syntypes (Tab. 1; Fig. 9). The dorso-ventral width is about the same for both species, although the torsion prevents it being measured in the distal parts of *C. lapworthi*. Subtle differences between specimens of *C. lapworthi* from Högkullen and from Scania might be related to environmental factors or simply reflect a natural variability.

Of the cyrtograptids with higher order cladia, *C. insectus* is the species that resembles *C. kinnekullensis* the most. However, *C. insectus* differs in having greater distances between its cladia, a characteristic tightly coiled proximal part (see Bouček 1933, pl. 6, fig. 1), a more strongly curved rhabdosome distally, more strongly curved cladia and more cladial thecae prior to the development of second order cladia. The narrow dorso-ventral width of *C. kinnekullensis* n. sp. in combination with low 2TRD of its distal part are further distinguishing features. The greater distances between the cladia of *C. insectus* might be a less significant

argument, considering the high degree of variation within *C. lapworthi*. So far *C. kinnekullensis* is only known from the lower *lapworthi* Biozone, whereas *C. insectus* first appears somewhat later, defining the base of the subsequent Biozone. *C. kinnekullensis* could be ancestral to *C. insectus*.

Characters of *C. kinnekullensis* fit quite well with the definition of the genus *Averianowograptus* Obut, a genus very similar to *Cyrtograptus*. Differences between *Cyrtograptus* and *Averianowograptus* are currently limited solely to the position of second order cladia, which in the latter genus originate from the second thecal cladium only (e.g., Bulman 1970), as in *C. kinnekullensis*. However, in *Averianowograptus* second order cladia are multiple, whereas so far only one second order cladium is known from *C. kinnekullensis*. This feature of *C. kinnekullensis* shows that *Averianowograptus* is in need of re-examination, as its current diagnostic features might not be sufficient and too arbitrary to separate it on a generic level from *Cyrtograptus*. *Averianowograptus* may be a junior synonym of *Cyrtograptus*.

Summary

Fauna.—The Retiolites Beds at Högkullen are dominated by straight monograptid taxa (chiefly *Monograptus* spp. and *Monoclimacis* spp.) together with *Retiolites geinitzianus* Barrande (Fig. 5G), *Oktavites spiralis* (Geinitz) (Fig. 5A), *Oktavites?* sp. aff. *Spirograptus* sp. (Fig. 5F), *Cyrtograptus lapworthi* Tullberg (Fig. 5B-E), and *Cyrtograptus kinnekullensis* n. sp. (Figs. 6, 7). The associated fauna consists of few poorly preserved articulate brachiopods and orthoconic cephalopods as well as an isolated bivalved aptychosid operculum (cf. *Aptychopsis primus* Barrande). The cyrtograptids described from Högkullen represent the first cyrtograptids illustrated from Västergötland.

Cyrtograptus kinnekullensis n. sp.—The new species from Högkullen is distinguished from other species of *Cyrtograptus* by its openly coiled proximal part, by a high number of thecal cladia, the increasing distance between cladia, and the presence of a second order cladium on the second thecal cladium. It might represent an intermediate form between *C. lapworthi* and *C. insectus*.

Age of Högkullen strata.—*Oktavites spiralis* and *Cyrtograptus lapworthi* are the eponymous fossils of two adjacent biozones in the upper Telychian (e.g., Loydell 2012) with *O. spiralis* extending into the lower part of the *lapworthi* Biozone (e.g., Loydell 1998). The co-occurrence of both taxa (e.g., Fig. 5C) at Högkullen and the observed presence of *O. spiralis* in the highest sampled level (ca. 3 m below the contact with dolerite), indicate the lower *lapworthi* Biozone. This makes the Retiolites Shales at Högkullen the youngest preserved Palaeozoic succession in Västergötland, confirming the results of Waern (1948). Other Silurian strata in the area typically comprise only the Rastrites Shales, which are stratigraphically below the Retiolites Shales. However, Westergård (1928) reported the presence of the Retiolites Shales at a single locality on Billingen, a table mountain ca. 20 km southeast of Kinnekulle. Here, only the lowermost 2 m of the Retiolites Shales are present, containing *Oktavites spiralis* and *Retiolites geinitzianus* (Westergård 1928), suggesting the *spiralis* Biozone.

Evolution of cyrtograptids.—*Cyrtograptus kinnekullensis* is the oldest cyrtograptid in Baltica bearing second order cladia. Its more or less synchronous appearance with the oldest cyrtograptid *C. lapworthi* matches the pattern observed in Laurentia, where the first cyrtograptids with second order cladia co-occur with the first cyrtograptid having only thecal cladia (see *Remarks to Genus Cyrtograptus* above). This indicates that the ability to grow cladia, of first and higher order, evolved (potentially worldwide) roughly at the same time, i.e., at the very beginning of cyrtograptid evolution.

Growth of cyrtograptids.—Observations on the position of cladia in *C. lapworthi* indicate that the most proximal cladium is not necessarily the first one to be formed. It may be that the first cladium originates distally and more proximal cladia form afterwards. It is suggested that cladia develop when and where a counterbalance is needed to compensate for the increasing length of the main stipe (and already present cladia).

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Figure captions

Fig. 1. Locality map. **A.** Map of southern Sweden with study area indicated (B). **B.** Geography of Kinnekulle area in Västergötland with locality marked (C). **C.** Detailed map of locality near Högekullen on Kinnekulle.

Fig. 2. Outcrop situation at Högekullen. **A.** Sample location on talus slope with sampled interval (1) (arrows point to small pits dug to expose bedrock for in situ sampling; see B), flattened part towards contact with dolerite (2), and contact to dolerite covered by burnt alum shale mine waste (3). **B.** One of the sampling pits with flat lying Retiolites Shales exposed (hammer for scale).

Fig. 3. *Camera lucida* drawings of the syntypes and a topotype of *Cyrtograptus lapworthi* Tullberg from Röstånga, Scania. **A.** Specimen SGU5681; note long second cladium, which originally was illustrated to be much shorter (Tullberg 1883, pl. 3, figs. 8, 9), also a sicula as indicated by Tullberg (1883, pl. 3, fig. 8) cannot be seen. **B.** Specimen SGU5683 (Tullberg 1883, pl. 3 fig. 11). **C.** Specimen SGU9664 with long third cladium. **D.** Close-up of the proximal end of the counterpart of A showing hooked thecae. **E.** Close-up of D illustrating shape of thecae and their preservation. **F.** Proximal part of C with sicula and hooked thecae. Scale bar equals 1 cm (A-C); 0.5 cm (D), and 0.2 cm (E-F).

Fig. 4. Two thecae repeat distance (2TRD) of the main stipe of the two syntypes of *Cyrtograptus lapworthi* Tullberg. Specimen SGU5681 (A) shows proximally higher and more rapidly increasing 2TRD values than SGU5683 (B), but distal measurement are similar. Differences might be due to incomplete preservation of the proximal part of SGU5681. (x-axis denotes number of visual theca, y-axis the measured 2TRD in mm).

Fig. 5. Graptolites from Högekullen, Västergötland, co-occurring with *Cyrtograptus kinnekullensis* n. sp. **A.** *Oktavites spiralis* (Geinitz) (PMU26978). **B-E.** *Cyrtograptus lapworthi* Tullberg. **B.** Specimen

with incomplete main stipe and single cladium (PMU26979). **C.** Specimen with long main stipe and single cladium (PMU26980) in association with cf. *Oktavites spiralis* (Geinitz) (PMU26981). **D.** Specimen with long main stipe, short (broken) proximal cladium and long second cladium (PMU26982). **E.** Close-up of D showing proximal part with hooked thecae. **F.** Sheared? rhabdosome of *Oktavites?* sp. aff. *Spirograptus* sp. (PMU26983). **G.** *Retiolites geinitzianus* Barrande (PMU26984). Scale bar equals 1 cm (D), 0.8 cm (C, F), 0.4 cm (A, B, E), and 0.2 cm (G).

Fig. 6. Cyrtograptus kinnekullensis n. sp. from Höggkullen, Västergötland, Sweden (PMU26985, holotype). **A.** Part showing main stipe with five first order cladia and a single second order cladium on the second thecal cladium. **B.** Counterpart with proximal parts of main stipe and second cladium missing. **C.** Close-up of counterpart showing hooked thecae of proximal part. **D-G.** Close-ups of origination points of first order cladia. **D.** First cladium. **E.** Second cladium. **F.** Third cladium. **G.** Fourth cladium. **H.** Close-up on origination point of second order cladium. Scale bar equals 1 cm (A, B), 0.5 cm (C), and 0.1 cm (D-H).

Fig. 7. Cyrtograptus kinnekullensis n. sp. from Höggkullen, Västergötland, Sweden (PMU26986, paratype). **A.** Part showing only minor section of main stipe and two cladia of which one shows a second order cladium. Arrow marks the point of origin of second order cladium. Cladia are interpreted to represent the second and third thecal cladium of the rhabdosome. **B.** Same as A but with specimen traced and labelled for clarification (abbreviations: ms, main stipe; 2t, second thecal cladium; 3t, third thecal cladium; x, second order cladium). Scale bar equals 1 cm for A.

Fig. 8. Camera lucida drawings of holotype of *Cyrtograptus kinnekullensis* n. sp. **A.** Entire specimen (part); margins of rock slab indicated. **B.** Detail of main stipe between second and third cladium (part). **C.** Thecae in the distal section of main stipe (part). **D.** Detail of proximal part of rhabdosome with sícula (counterpart). Scale bar equals 1 cm (A) and 0.2 cm (B-D).

Fig. 9. Comparison of 2TRD for *Cyrtograptus kinnekullensis* n. sp. (circles; PMU26985) and *C. lapworthi* (crosses; SGU5683, same as Fig. 4B). *C. kinnekullensis* shows a distinct increase of thecal size proximally and a less pronounced, but steady increase distally. Thecal sizes of *C. lapworthi* appear to be generally smaller (x-axis denotes number of theca, i.e., thX for *C. kinnekullensis* and vthX for *C. lapworthi*, y-axis the measured 2TRD in mm).

Fig. 10. Schematic to-scale comparison of rhabdosome size and cladia origination of *Cyrtograptus kinnekullensis* and *Cyrtograptus lapworthi*. **A.** *C. kinnekullensis* n. sp. (holotype); **B.** *C. kinnekullensis* n. sp. (paratype). **C.** *C. lapworthi* (SGU9664). **D.** *C. lapworthi* (PMU26982). **E.** *C. lapworthi* (SGU5683, syntype). Scale bar equals 1 cm.

Table 1. Two thecae repeat distance (2TRD) and dorso-ventral width (DVW) of *C. lapworthi* Tullberg and *C. kinnekullensis* n. sp. (all measurements in mm). All specimens of *C. lapworthi* except SGU9664 show no preserved sicula. Accordingly, listed measurements refer to the first and second visible thecae (vth) and the visual proximal end of the rhabdosome, respectively. In *C. kinnekullensis* and specimen SGU9664 of *C. lapworthi* the first visual theca equals the first formed theca (th). See *Methods* for details.

		(v)th1	(v)th2	5 mm	15 mm	35 mm	distal
<i>C. lapworthi</i> (SGU5681, syntype)	2TRD	-	1.67	1.74	1.96	2.05	1.95
	DVW	0.55	0.64	0.87	1.28	-	-
<i>C. lapworthi</i> (SGU5683, syntype)	2TRD	-	1.26	1.58	1.74	1.83	2.00
	DVW	0.59	0.71	0.83	0.90	-	-
<i>C. lapworthi</i> (SGU9664)	2TRD	-	1.53	1.67	1.88	-	-
	DVW	0.58	0.61	0.76	1.00	-	-
<i>C. lapworthi</i> (PMU26982)	2TRD	-	1.40	1.84	1.84	2.16	-
	DVW	0.40	0.60	0.68	0.88	-	-
<i>C. lapworthi</i> (PMU26979)	2TRD	-	1.80	2.0	2.2	-	-
<i>C. kinnekullensis</i> n. sp. (PMU26985, holotype)	2TRD	-	1.65	1.85	2.06	2.10	2.44
	DVW	0.56	0.61	0.72	0.87	0.98	1.18

Table 2. Observed number of thecae between individual cladia in *C. kinnekullensis* n. sp. and *C. lapworthi* Tullberg from Sweden.

	between cladia	1 & 2	2 & 3	3 & 4	4 & 5
<i>C. kinnekullensis</i> (holotype)		9	11	16	23
<i>C. kinnekullensis</i> (paratype)		?	ca. 19	?	?
<i>C. lapworthi</i> (SGU9664)		7	18	--	--
<i>C. lapworthi</i> (SGU5681)		6	14	--	--
<i>C. lapworthi</i> (SGU5683)		18	--	--	--
<i>C. lapworthi</i> (PMU26982)		11	--	--	--

Figure 1

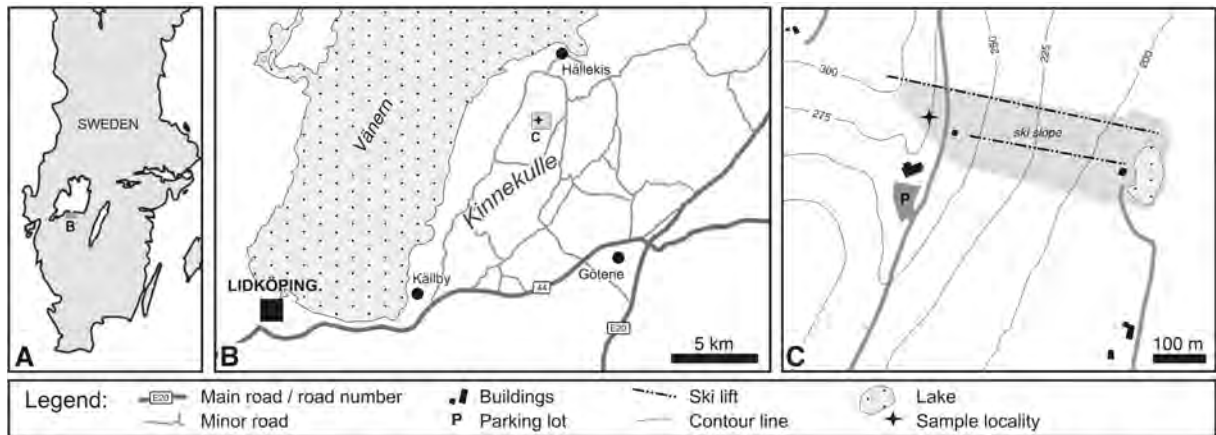


Figure 2



Figure 3

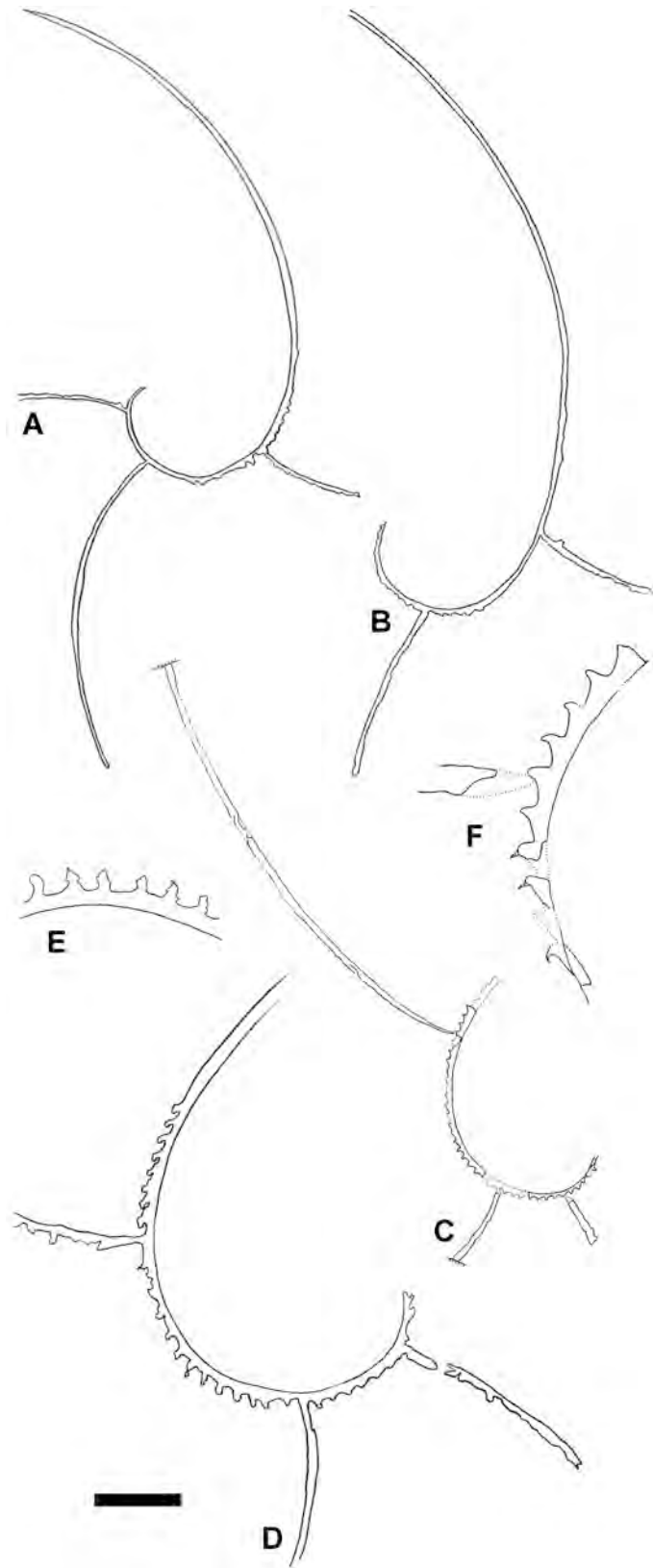


Figure 4

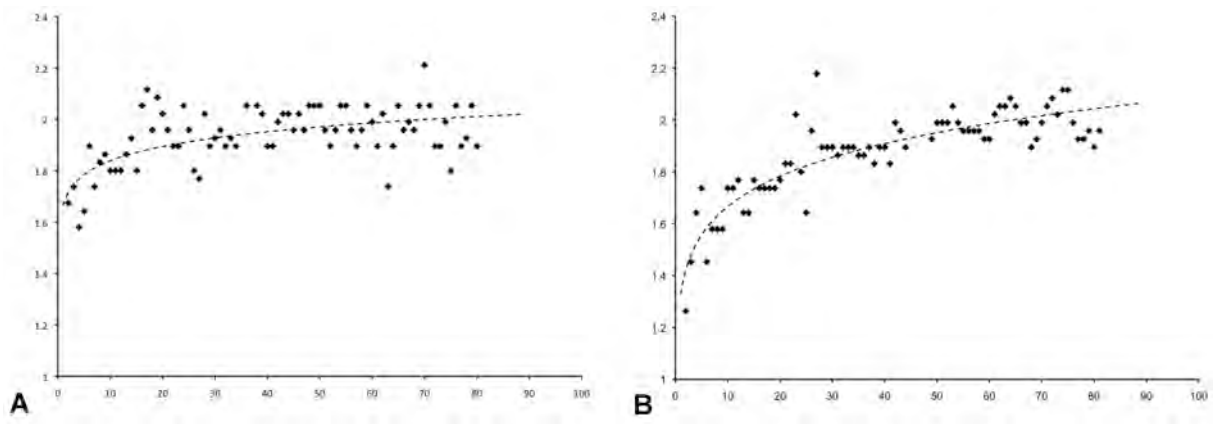


Figure 5

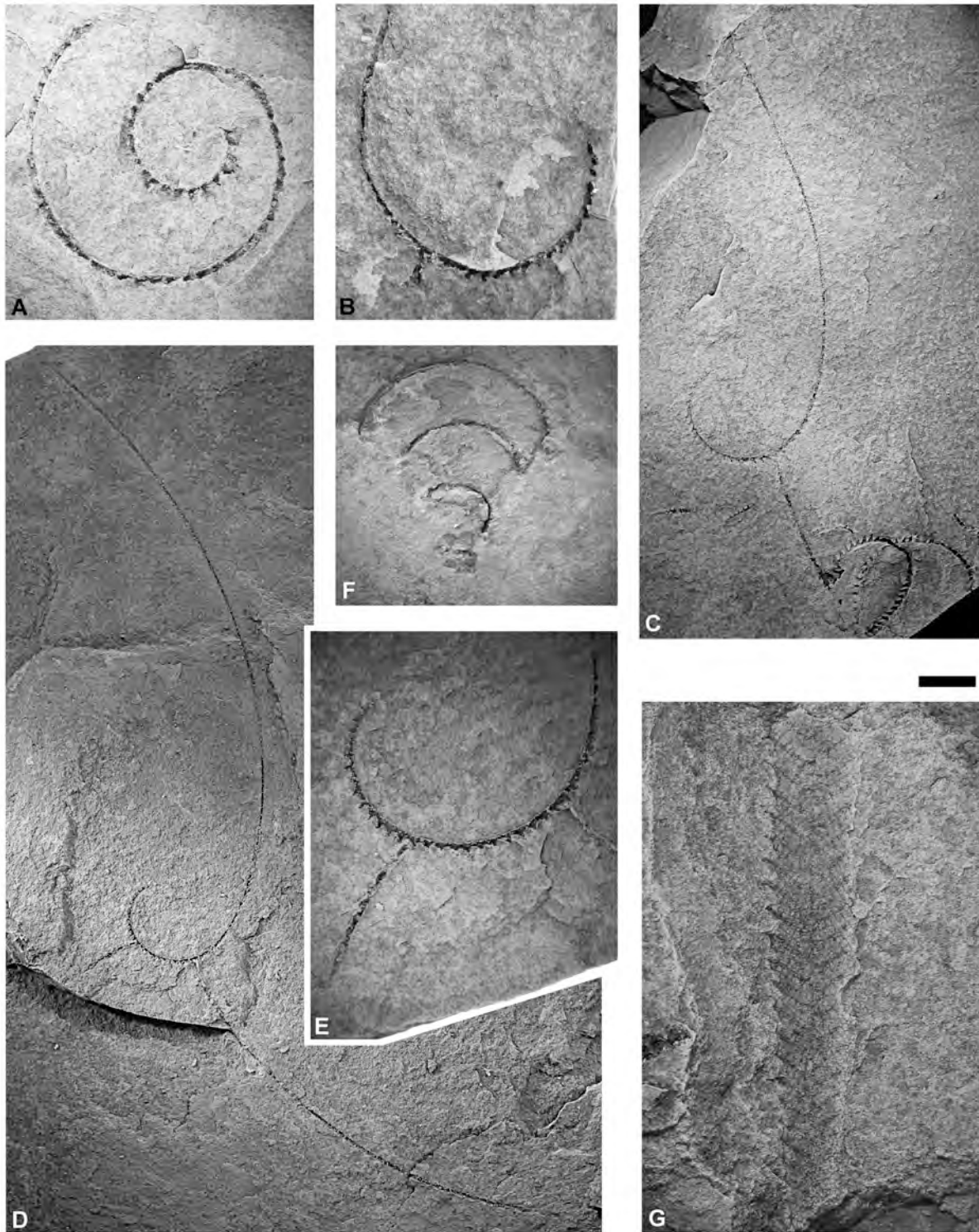


Figure 6

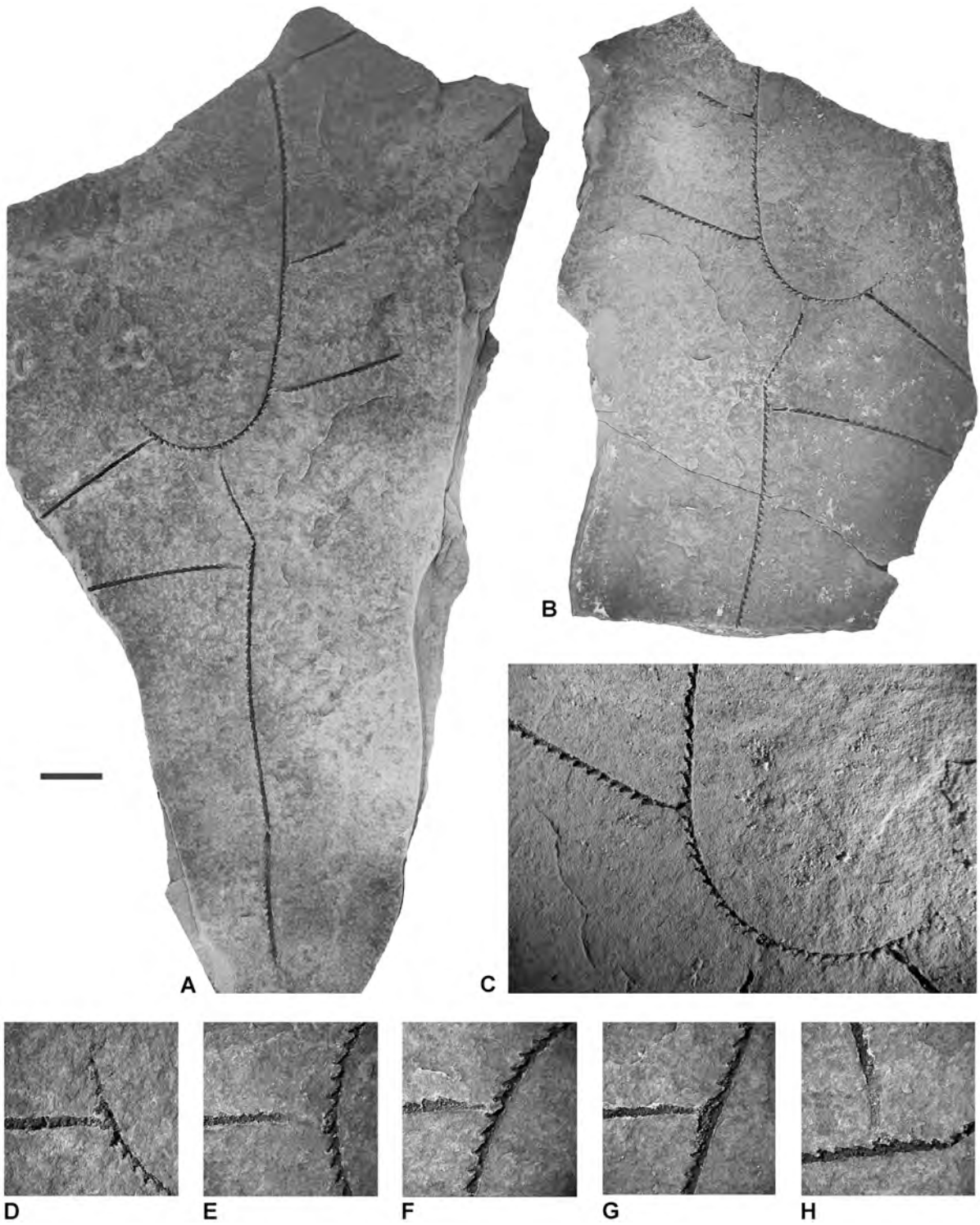


Figure 7

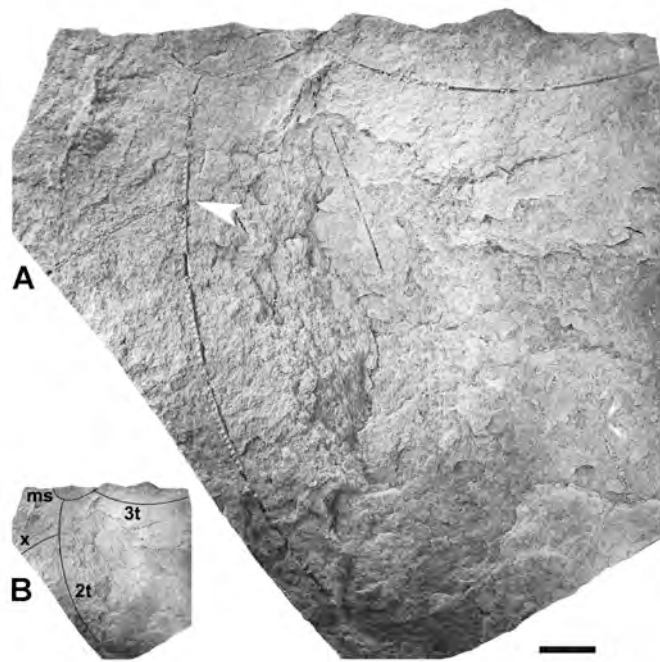


Figure 8

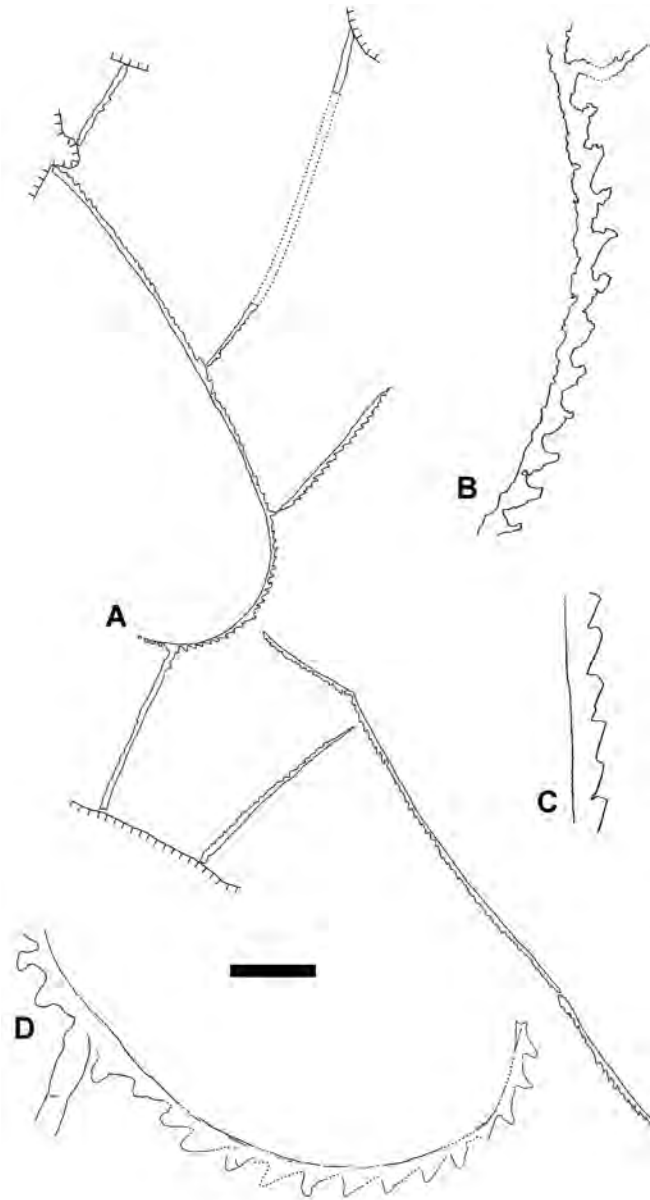


Figure 9

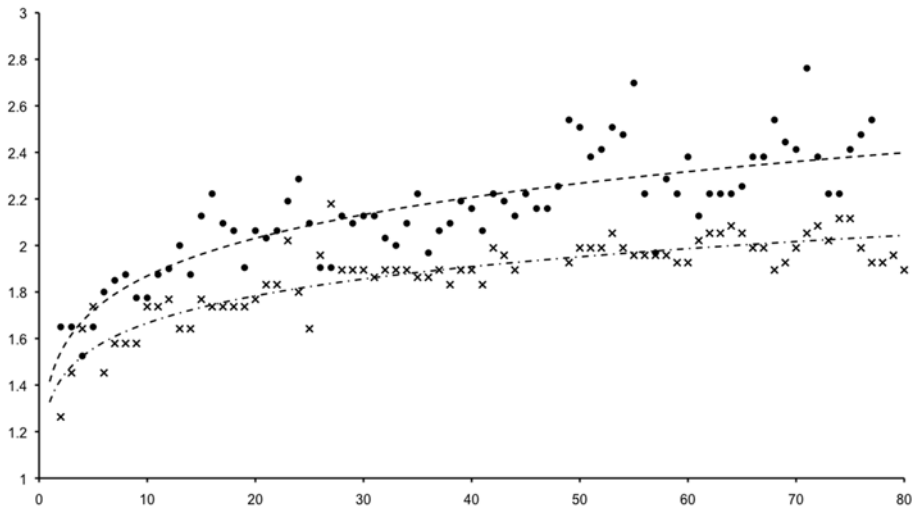


Figure 10

