



LUND UNIVERSITY

Darriwilian (Middle Ordovician) worms of southern Sweden

Eriksson, Mats E.; Lindskog, Anders; Servais, Thomas; Hints, Olle; Tonarová, Petra

Published in:
GFF

DOI:
[10.1080/11035897.2016.1181102](https://doi.org/10.1080/11035897.2016.1181102)

2016

Document Version:
Peer reviewed version (aka post-print)

[Link to publication](#)

Citation for published version (APA):
Eriksson, M. E., Lindskog, A., Servais, T., Hints, O., & Tonarová, P. (2016). Darriwilian (Middle Ordovician) worms of southern Sweden. *GFF*, 138(4), 502-509. <https://doi.org/10.1080/11035897.2016.1181102>

Total number of authors:
5

General rights

Unless other specific re-use rights are stated the following general rights apply:
Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Read more about Creative commons licenses: <https://creativecommons.org/licenses/>

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

LUND UNIVERSITY

PO Box 117
221 00 Lund
+46 46-222 00 00

"This is the peer reviewed version of the following article: Eriksson, M.E., Lindskog, A., Servais, T., Hints, O. & Tonarová, P., 2016. Darriwilian (Middle Ordovician) worms of southern Sweden. *GFF* 138, 502-509., which has been published in final form at <https://www.tandfonline.com/doi/full/10.1080/11035897.2016.1181102>

Darriwilian (Middle Ordovician) worms of southern Sweden

MATS E. ERIKSSON^{1,2}, ANDERS LINDSKOG¹, THOMAS SERVAIS², OLLE HINTS³ and PETRA TONAROVÁ⁴

Eriksson, M.E., Lindskog, A., Servais, T., Hints, O. & Tonarová, P. 2015. Darriwilian (Middle Ordovician) worms of southern Sweden. *GFF*.

Abstract: The record of scolecodonts (polychaete jaws) from the Ordovician of Sweden is very poor. In this paper we document a Darriwilian (Middle Ordovician) assemblage recovered from palynological samples from the ‘orthoceratite limestone’ (Lanna and Holen limestones) of Mount Kinnekulle, Västergötland, southern Sweden. The collection of diminutive specimens forms an assemblage taxonomically composed mainly of simple placognath (mochtyellids, xanioprionids) and ctenognath (tetraprionids) taxa whereas labidognaths (polychaetaspids) and taxa with other evolutionary grade-type apparatuses are very rare or absent. In addition, putative priapulid (penis worm) teeth were identified, possibly representing the first fossil representatives recorded in Sweden. The highest scolecodont abundance coincides with the lower to middle part of the ‘Täljsten’ interval (lower Kunda Baltoscandian Stage). These strata are interpreted as having been formed during a marked regressional phase, suggesting that the palaeobathymetry and/or bottom substrate was optimal for polychaete colonization at that time. This new assemblage from Kinnekulle adds to the global scolecodont record in which data on Middle Ordovician and older specimens are still rudimentary but of importance for understanding early polychaete phylogeny.

Keywords: Scolecodonts, polychaetes, priapulids, ‘orthoceratite limestone’, Darriwilian, Middle Ordovician, Sweden.

¹*Department of Geology, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden; mats.eriksson@geol.lu.se, anders.lindskog@geol.lu.se*

²*CNRS-UMR 8198 Evo-Eco-Paléo, Université Lille 1, Bâtiment SN5, Avenue Paul Langevin, 59655 Villeneuve d'Ascq Cedex, France; thomas.servais@univ-lille1.fr*

³*Institute of Geology at Tallinn University of Technology, Ehitajate 5, 19086 Tallinn, Estonia; olle.hints@ttu.ee*

⁴*Czech Geological Survey, Geologická 6, 152 00 Prague 5, Czech Republic; petra.tonarova@geology.cz*

Introduction

Most geologic depositional environments are unfavourable for the preservation of organisms composed primarily of soft tissue. One such animal group, which has a very rich and diverse occurrence in oceans today, is the polychaete annelid worms. Body fossils of these organisms are therefore a rare commodity although spectacularly preserved examples are known from Lagerstätten around the world (e.g., Bracci & Alessandrello 2005; Briggs & Bartels 2010; Parry et al. 2014, 2015; and references therein). However, even outside Lagerstätte strata the presence of polychaete worms in the past marine environments can be evident by a range of fossil remains, including, e.g., dwelling tubes, ichnofossils, and, for some taxa, scolecodonts (Hints & Eriksson 2007; Parry et al. 2014). The latter can be extracted as acid resistant microfossils – being resistant to hydrofluoric acid they can also be categorized as palynomorphs – in great numbers. They are a testimony not only to the presence of

errant, jaw-bearing polychaetes at certain times in the Earth History, but may very well show that these animals were once a diverse and abundant component of the biota even if other polychaete remains are lacking. Thus, similar to the research history of conodonts, the very bulk of the fossil evidence of jawed polychaetes is derived from their oral elements (Eriksson & von Bitter 2015) whereas full body fossils, regardless of their information-prone biological significance, form exclusive exceptions to the rule.

The fossil record of scolecodonts extends from the latest Cambrian and onwards but it was not until the Middle Ordovician that the abundance and diversity increased dramatically (Hints & Eriksson 2007). The Palaeozoic forms are almost exclusively represented by eunicidan polychaetes which, like today, were equipped with a complex, multi-element jaw apparatus, as opposed to the phyllodocidans that appeared in the late Palaeozoic and have a considerably more sparse fossil record also from then on (Szaniawski 1996; Eriksson et al. 2013; Parry et al. 2014).

Although our knowledge of the global distribution of polychaete worms in the Ordovician has been continuously growing over the last few decades (Hints & Eriksson 2007; Hints et al. 2010, 2015; Eriksson et al. 2013), that of Sweden is still very poor (Eriksson & Frisk 2011). In this study we report on a small faunal assemblage of polychaete worms from the Darriwilian of Kinnekulle, southern Sweden, based on scolecodonts recorded in palynological samples. These specimens form the first and only evidence of the presence of this animal group in these strata, except for some trace fossils that might have been produced by annelids, and are important also because the global record of Early (in particular) through Middle Ordovician scolecodonts is meagre, but important for understanding the early polychaete evolution.

Geological setting and stratigraphy

Throughout the Ordovician, an epeiric sea covered large parts of Sweden and its surroundings in Baltoscandia. The regional Ordovician succession shows a gradual shift from cold- to warm-water sedimentation (e.g., Lindström 1971; Dronov & Rozhnov 2007), as the palaeocontinent Baltica drifted from southern subpolar into subtropical latitudes during this time (Cocks & Torsvik 2006). In the Middle Ordovician, Baltica was situated in the temperate realm and widespread (cool-water) carbonate deposition occurred in the vast epicontinental basin. The ‘orthoceratite limestone’ forms the main rock type in the Swedish Middle Ordovician (e.g., Jaanusson 1982).

The table mountain Kinnekulle in Västergötland, south-central Sweden, preserves a near-complete succession of Cambrian through lower Silurian rocks (Fig. 1; Holm 1901; Westergård 1943). On the northwestern slope, the abandoned Hälleki quarry (WGS 84 coordinates N58°36’33”, E13°23’42”) hosts a c. 40-m-thick Middle Ordovician succession. Most of the exposed quarry succession, which is c. 27 m thick, belongs to the Lanna and Holen limestones, which form the ‘orthoceratite limestone’ across the table mountain. The Holen Limestone is disconformably overlain by the c. 8-m-thick Gullhögen Formation which, in turn, is overlain by the basal beds of the Ryd Limestone (e.g., Lindskog et al. 2015). The succession spans the lowermost Volkhov to uppermost Uhaku Baltoscandian stages, corresponding to the lowermost Dapingian through uppermost Darriwilian global stages (Dp1–Dw3; see Bergström et al. 2009). A hiatus, spanning the entire Aseri Baltoscandian Stage (upper Dw2) and most of the succeeding Lasnamägi Stage (lower Dw3), separates the Holen Limestone and the Gullhögen Formation.

The active Thorsberg (Österplana) quarry (N58°34’45”, E13°25’46”) is situated on the southeastern slope of Kinnekulle (Fig. 1). The locality hosts a c. 6-m-thick succession of rocks, corresponding to the lower through middle parts of the Holen Limestone (Kunda Stage). The quarry provides raw materials for stone masonry, and the flat and vertically cut rock surfaces enable study of fine details *in situ* (e.g., Lindskog et al. 2015). The Thorsberg quarry has become widely known as a spectacular source of fossil meteorites, the presence of which record events in the asteroid belt (Schmitz 2013, and references therein).

The herein studied succession at Kinnekulle spans most of the Lanna Limestone and the entire Holen Limestone (*sensu* Lindskog et al. 2014), in total c. 22 m corresponding to the middle Volkhov through middle Kunda Baltoscandian stages (Fig. 2). This interval is characterized by rusty-red, macroscopically homogeneous ‘orthoceratite limestone’. A temporary change into grey limestone takes place in the Kundan, across the boundary between the *Asaphus expansus* and *Asaphus raniceps* trilobite zones. This conspicuous, c. 1.5-m-thick, grey interval is by quarry workers known as the ‘Täljsten’ (‘carving stone’). The ‘Täljsten’ is associated with a coarsening of limestone textures and a shift in the overall fauna, and relatively high biodiversity. Some beds in the ‘Täljsten’ host exceptionally large numbers of *Sphaeronites* cystoids (see Eriksson et al. 2012; Lindskog et al. 2015). The individual beds of the ‘Täljsten’ are informally named as quarry units (see Schmitz 2013) which are referred to herein and in Fig. 2.

Materials and methods

A series of 20 limestone samples from the Volkhov-Kunda interval in the Hällekis section were processed for palynomorphs, i.e., organic-walled microfossils (Figs. 1, 2). One sample was collected for comparison also from the Thorsberg quarry (Fig. 1), from the ‘Likhall’ bed. In order to avoid recent contaminants each rock sample was trimmed with a rock saw so that only internal and intact cores with freshly cut surfaces were used for palynological processing. As an added safety precaution all sawn surfaces were subsequently roughly polished on a diamond grinding disc and washed in distilled water. The rock samples were then shipped off to Global Geolab Limited in Alberta, Canada, for standard palynological processing (c. 75 g per sample) using HCL and HF to digest the rocks. The residues were filtered with a 10 µm mesh and placed onto glass slides for microscopy studies.

As expected, the samples collected from the reddish (oxidized) strata stratigraphically below and above the grey ‘Täljsten’ only rarely contained palynomorphs but were nonetheless taken for reference. By sharp contrast, the material from the ‘Täljsten’ yielded very rich, diverse and well preserved palynomorph assemblages. In addition to the scolecodonts (and other possible worm remains) the samples contain, e.g., rare chitinozoans and graptolite fragments, amorphous organic matter, and a rich acritarch palynoflora. These fossil groups will be the subject of forthcoming studies and are not treated further herein. All scolecodont-yielding samples are shown in Fig. 2.

The scolecodonts in the palynological slides were studied and photographed at the Evo-Eco-Paleo Department of University Lille 1, France, using a Zeiss 190 AxioCam ERc5s mounted on a Zeiss Axio Imager A2 transmitted light-microscope, with a 63× Plan-Apochromat objective. The slides with the material figured herein are all stored at the Department of Geology, Lund University, Sweden. Slides housing figured specimens are marked LO for Lund Original, and stored in the type collection.

Remarks on the worm assemblage

A total of 122 scolecodonts (including fragmentary specimens) and two putative priapulid (penis worm) teeth are included in this study (Figs. 2, 3). In addition, approximately two dozen minor scolecodont fragments were observed in the slides. Even though this is a relatively small number of individual specimens, the recovery of scolecodonts was somewhat unexpected in the palynological residues. The reason for this is that these Darriwilian strata have been intensively studied during several field campaigns over the last few years. This has included samples collected for the recovery of conodonts and other acid resistant microfossils (e.g., Mellgren & Eriksson 2010; Eriksson et al. 2012; Lindskog et al. 2015). After digestion in acetic acid the insoluble residues of those samples, with a sample weight typically of one to two kilograms each, have been picked for microfossils and no scolecodonts were recorded in the process. Thus, the palynomorph samples studied herein show that scolecodonts indeed are present in these strata and that they in some intervals are relatively common, even based on the limited sample materials. It is possible that the specimens from Kinnekulle are too

small and have simply been overlooked in the larger acetic acid residues, which were sieved using 63 µm as finest mesh size. Regardless of which, the palynomorph samples provide the first and only evidence for the presence of polychaete worms in the Darriwilian sea of the area (except for some trace fossils that might have been produced by worms) and also that such animals formed a non-negligible part of the invertebrate biotas. Selected representative specimens are shown in Fig. 3.

The specimens at hand are very small; complete ones range in size from c. 20 µm in length (minor anterior maxillae and accessory elements such as intercalary or lateral teeth) to c. 210 µm (first maxillae). Either the polychaetes living in this environment were overall small, or had small jaws, or the fossil assemblage is skewed for some (taphonomic/hydrodynamic) reason and represents mostly earlier ontogenetic stages, although no unambiguously larval jaws were recorded (cf. Paxton & Eriksson 2012). The specimens are moderately well to well preserved with the thin cuticles sometimes showing even fine reticulate to polygonal patterns on the ventral side (Fig. 3M, V, AD). In rare occasions two or more jaw elements were found still joint into partial jaw apparatuses (Fig. 3AE, AF).

Based on total specimen counts, including fragments, the abundance exceeds 400 specimens/kg of rock (or 0.4 specimens/g) in the most productive samples (Fig. 2). This should be regarded as an ‘at least’ abundance value as it is calculated from the weight of the unprocessed rock samples and the entire (HF) acid resistant residue is not always used for the resulting palynological slides (note also that for literature comparisons this value is sometimes calculated on the first maxillae only). The richest samples with regards to scolecodonts are from the lower and middle parts of the ‘Täljsten’ (Fig. 2); the ‘Botten’, ‘Gråkartan’, ‘Blymåkka’ and ‘Likhall’ quarry units. According to Mellgren & Eriksson (2010) a regressive event started in the pre-‘Täljsten’ interval and reached its maximum in the Blymåkka quarry unit. The increase in scolecodont abundance and diversity may thus reflect shallower water settings and/or muddier bottom substrates more suitable for infaunal polychaete colonization, or slower rate of deposition. The many well-developed hardgrounds seen within the ‘Täljsten’ suggest that sedimentation rates were extremely slow throughout this interval, although several sedimentological features indicate that individual beds were both rapidly formed and indurated (e.g., Eriksson et al. 2012; Lindskog 2014). In addition to more favourable living conditions for worms, the depositional environment associated with the ‘Täljsten’ may thus have contributed to an unusually favourable situation for the preservation of scolecodonts.

The assemblage is strongly biased towards simple, ‘saw-plate-type’ elements, characteristic of taxa with placognath and ctenognath type apparatuses (see Kielan-Jaworowska 1966). The most common specimens represent placognath elements that probably belong to mochttyellids and xanioprionids (Fig. 3A–I). Mochttyellids are common in Ordovician and Silurian strata (Kielan-Jaworowska 1966; Eriksson et al. 2013) but the first maxillae can be difficult to assign to certain species if the accessory ridges are preservationally absent, which is the case with the collection at hand. A few posterior maxillae might represent ctenognath tetraprionids (Fig. 3K–M; see also below). Quite a significant proportion of the fragmented maxillae recorded also have placognath and/or ctenognath affinity, based on their simple, saw-plate morphology (Fig. 3S–AF).

Polychaetes with labidognath type jaw apparatuses typically appear later in the fossil record than placognaths and do not become recurring faunal elements until the Middle Ordovician and onwards (Hints & Eriksson 2007). Labidognaths are very rare in the Kinnekulle collection and only one right MI was recorded from sample HÅ07-7 (‘Gråkartan’; Fig. 3AG). The specimen belongs to the polychaetaspid genus *Oenonites* Hinde, 1879, a very common and globally distributed genus in the Ordovician and Silurian (Hints & Eriksson 2007; Tonarová et al. 2012; Eriksson et al. 2004, 2013). In addition, there are a number of anterior maxillae (MII, MIV?) of suspected polychaetaspid affinity (Fig. 3AH–AL).

Another common component in the collection at hand is small specimens with a characteristic and simple, cone-shaped morphology comprising a wide base and a denticulated apex (Fig. 3AO–AT). Similar elements have been assigned to the single-element-based, ‘wastebasket’ genera *Anisocerasites* Eller, 1955 or *Belegenys* Jansonius & Craig, 1971 (see Jansonius & Craig 1971). It is not clear yet to what higher taxon or taxa these belong, but it is reasonable to assume that

they represent anterior teeth of placognath/ctenognath worms (cf. Jansonius & Craig 1971, p. 265) whose major (posterior) jaws are also present in the collection. Similar elements are known to be present in several mochtlyellid apparatuses (Kielan-Jaworowska 1966) and thus the generic names *Anisocerasites* and *Belegenys* need revision. Interestingly, Tonarová et al., (2016, fig. 4G) recently described a putative *Tetraprion* specimen from the Devonian of Germany in which the anterior jaws are reminiscent of the specimens shown herein (Fig. 3AO–AT). The variability in fine morphological details of the Kinnekulle specimens at hand suggest that either they represent several different taxa, or that there was a relatively high degree of morphological plasticity within one and the same species, depending on the position of the element in the jaw apparatus.

Finally, the Kinnekulle collection contains several simple, smooth and cone-shaped jaw elements that represent small intercalary teeth and/or lateral teeth (Fig. 3AU–AW; note that the specimen figured in 3AW might represent part of a molluscan radula). Such elements are, as is the case in many anterior maxillae, homeomorphic between different taxa even at relatively high taxonomic level, and cannot be assigned to certain taxa if they are not preserved associated with the remainder of a jaw apparatus.

As summarized by Eriksson & Frisk (2011, p. 283) the record of Ordovician scolecodonts from Sweden is meagre, including only a handful of publications spanning the Middle through Upper Ordovician. More recently, the oldest known scolecodonts have been recorded from the Province of Scania, southernmost Sweden, being represented by a few fragments extracted from a limestone bed in the earliest Ordovician (Terfelt et al. 2014). Compared to other Swedish scolecodont collections, one described by Eisenack (1976; see also Eriksson & Frisk 2011) is of particular interest. It is derived from the Hälludden section on the island of Öland, southeastern Sweden, and is coeval with the collection described herein. Moreover, Eisenack's (1976) collection was also extracted through palynological processing and the faunal composition, including representatives of *Xanioprion*, '*Anisocerasites*', *Mochtlyella*-like specimens and possibly *Oeononites*, is similar to the Kinnekulle material. It should be noted that some of the specimens of Eisenack (1976, pl. 1, figs. 5–8) might also represent priapulid teeth rather than scolecodonts (see discussion below). This remains to be tested pending the recovery of new sample material from Öland.

The occurrence of early Middle Ordovician scolecodonts has previously been reported from northern Estonia (Hints 2000), from rocks representing shallower water settings in the eastern part of the Baltoscandian basin. Recently, additional scolecodonts (still unpublished) from the Volkhov and Kunda regional stages have been obtained from conodont samples from the Uuga Cliff, NW Estonia (Hints et al. 2012). Examination of that material shows that the Volkhov Stage (*Paroistodus originalis* Conodont Zone) is characterised by low abundance and diversity of scolecodonts, most of which belong to 'primitive' placognath/ctenognath taxa, like those in the Kinnekulle assemblage. Strata corresponding to the 'Täljsten' interval are missing due to a stratigraphic gap in NW Estonia and thus direct comparison is not possible. However, the younger Kundan fauna (*Eoplacognathus pseudoplanus* Conodont Zone) in NW Estonia is rather different. It has a much higher proportion of 'advanced' labidognath forms and placognaths with compound maxillae, and higher diversity and abundance compared to those of underlying strata. In both Estonian assemblages the average size of scolecodonts is larger than that in the Kinnekulle material described herein. This may be due to methodological differences (small specimens may have been overlooked in the Estonian samples). Collectively the Swedish and Estonian data suggest that a major change in Baltoscandian polychaete faunas occurred during the early Kundan, close to the 'Täljsten' interval. This coincides with pronounced environmental changes within the basin, including major fluctuations in sea level (the 'Täljsten' interval coincides with a distinct lowstand followed by drowning) and cooling sea water temperatures, and is associated with steeply increased biodiversity (Rasmussen et al. 2016). Recent data (ibid.) suggest that the global climate entered into an icehouse state around this time.

As for the global record of jawed polychaetes, those of the Early through Middle Ordovician are rather poorly understood (Underhay & Williams 1995; Hints & Nölvak 2006; Hints & Eriksson 2007; Eriksson et al. 2013). For that reason the material at hand is important, despite

difficulties in lower level taxonomic determination of the specimens. Based on what is currently known the Kinnekulle material fits well compositionally with approximately coeval assemblages from other regions. They typically are comprised of placognath and ctenognath taxa with few specimens of labidognaths (such as the polychaetaspid genus *Oeononites*). This study also shows that scolecodonts can be successfully recovered from palynomorph samples and in very small size fractions and thereby provide additional important data that might otherwise be overlooked.

A few specimens recorded probably do not represent scolecodonts but instead they may be teeth of priapulid worms (or penis worms). The specimen shown in Fig. 3AM possesses characteristic denticles with minute ‘secondary denticles’ superimposed resulting in a saw-toothed, or jagged, appearance. The main denticles are attached to a basal part and result in overall sub-triangular jaw elements. To our knowledge only the Middle Ordovician–Silurian (Wenlock) polychaete genus *Rakvereprion* Mierzejewski, 1978, has similar secondarily denticulated denticles, but on the basal and laeobasal plates that are shaped like flat ‘saw blades’. Recently, however, also a specimen of the enigmatic genus *Lunoprionella* Eisenack, 1975, from Llandovery (Silurian) strata of the Hilliste quarry (Estonia) has been recorded with such denticles (PT, personal observations, 2015).

The specimen shown in Fig. 3AN also looks like a priapulid tooth, although the denticles in this specimen are smooth (see similar specimens in Butterfield & Harvey 2012; Smith et al. 2015). However, it is not possible to unambiguously evaluate whether the specimens in Fig. 3AM, AN are bilaterally symmetrical from the angle they are trapped in the palynological slide.

If these specimens comprise priapulids they are, to our knowledge, the first such specimens recorded from the Ordovician of Sweden. Priapulids have an extensive fossil record, with stem groups dating back to the early Cambrian and with the Burgess Shale genus *Ottoia* Walcott, 1911, as the most well-known fossil example (Conway Morris 1977; Vannier et al. 2010; Smith et al. 2015). During the last few years more priapulid specimens have been unearthed also as components of the so-called ‘small carbonaceous fossils’ (SCFs) (Butterfield & Harvey 2012; Smith et al. 2015). Similar to the more well-known ‘small shelly fossils’ (Matthews & Missarzhevsky 1975), SCFs have proven useful for extending the stratigraphic range and palaeogeographic distribution of certain taxa that are rarely preserved as full body fossils. The presence of putative priapulids and other suspected SCFs in the samples from Kinnekulle and the aforementioned Hälludden section on Öland, suggest that it would be worthwhile searching for additional such fossils by applying a gentler palynological processing technique to those rocks than that used herein (see Butterfield & Harvey, 2012).

Acknowledgements.- Thanks to University of Lille 1 for a guest professorship in October 2015 for MEE. MEE thanks the Swedish Research Council (grant no. 2015-05084), AL thanks the Royal Physiographic Society in Lund, PT thanks the Czech Science Foundation (project GJ15-13525Y), and OH thanks Estonian Research Council grant PUT611, for funding their research. Thanks also to T. Harvey for discussions on priapulids and SCFs. Finally, we thank two anonymous reviewers for improving the manuscript.

References

- Bergström, S.M., Chen, X., Gutiérrez-Marco, J.C. & Dronov, A., 2009: The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to $\delta^{13}\text{C}$ chemostratigraphy. *Lethaia* 42, 97–107.
- Bracchi, G. & Alessandrello, A., 2005: Paleodiversity of the free-living polychaetes (Annelida, Polychaeta) and description of new *taxa* from the Upper Cretaceous *Lagerstätten* of Haqel, Hadjula and Al-Namoura (Lebanon). *Memorie Della Societa' Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 32, 64 p.

Briggs, D.E.G. & Bartels, C., 2010: Annelids from the Lower Devonian Hunsrück Slate (Lower Emsian, Rhenish Massif, Germany). *Palaeontology* 53, 215–232.

Butterfield, N.J. & Harvey, T.H.P., 2012: Small carbonaceous fossils (SCFs): A new measure of early Paleozoic paleobiology. *Geology* 40, 71–74.

Cocks, L.R.M. & Torsvik, T.H., 2006: European geography in a global context from the Vendian to the end of the Palaeozoic. In D.G. Gee & R.A. Stephenson (eds.): *European Lithosphere Dynamics*, 83–95. Geological Society, London.

Conway Morris, S., 1977: Fossil priapulid worms. *Special Papers in Palaeontology* 20, 1–95.

Dronov, A. & Rozhnov, S., 2007: Climatic changes in the Baltoscandian basin during the Ordovician: Sedimentological and palaeontological aspects. *Acta Palaeontologica Sinica* 46, S108–S113.

Eisenack, A., 1975: Beiträge zur Anneliden-Forschung, I. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 150, 227–252.

Eisenack, A., 1976: Mikrofossilien aus dem Vaginatenkalk von Hälludden, Öland. *Palaeontographica Abteilung A* 154, 181–203.

Eller, E. R., 1955: Additional scolecodonts from the Potter Farm Formation of the Devonian of Michigan. *Annals of the Carnegie Museum* 33, 347–386.

Eriksson, M.E. & Frisk, Å.M., 2011: Polychaete palaeoecology in an early Late Ordovician marine astrobleme of Sweden. *Geological Magazine* 148, 269–287.

Eriksson, M.E. & von Bitter, P.H., 2015: Jaw-bearing polychaetes of the Silurian Eramosa Lagerstätte, Ontario, Canada. *Journal of Paleontology* 89, 222–235.

Eriksson, M.E., Bergman, C.F. & Jeppsson, L., 2004: Silurian scolecodonts. *Review of Palaeobotany and Palynology* 131, 269–300.

Eriksson, M.E., Hints, O., Paxton, H. & Tonarová, P., 2013: Ordovician and Silurian polychaete diversity and biogeography. In D.A.T. Harper & T. Servais, (eds.): *Early Palaeozoic Biogeography and Palaeogeography*, 265–272. Geological Society, London, Memoirs, 38.

Eriksson, M.E., Lindskog, A., Calner, M., Mellgren, J.I.S., Bergström, S.M., Terfelt, F. & Schmitz, B., 2012: Biotic dynamics and carbonate microfacies of the conspicuous Darriwilian (Middle Ordovician) ‘Täljsten’ interval, south-central Sweden. *Palaeogeography, Palaeoclimatology, Palaeoecology* 367–368, 89–103.

Hinde, G.J., 1879: On annelid jaws from the Cambro-Silurian, Silurian and Devonian formations in Canada and from the Lower Carboniferous in Scotland. *Quarterly Journal of the Geological Society of London* 35, 370–389.

Hints, O., 2000: Ordovician eunicid polychaetes of Estonia and surrounding areas: review of their distribution and diversification. *Review of Palaeobotany and Palynology* 113, 41–55.

- Hints, O. & Eriksson, M.E., 2007: Diversification and biogeography of scolecodont bearing polychaetes in the Ordovician. *Palaeogeography, Palaeoclimatology, Palaeoecology* 245, 95–114.
- Hints, O. & Nölvak, J., 2006: Early Ordovician scolecodonts and chitinozoans from Tallinn, North Estonia. *Review of Palaeobotany and Palynology* 139, 189–209.
- Hints, O., Delabroye, A., Nölvak, J., Servais, T., Uutela, A. & Wallin, Å., 2010: Biodiversity patterns of Ordovician marine microphytoplankton from Baltica: Comparison with other fossil groups and sea-level changes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 294, 161–173.
- Hints, O., Viira, V. & Nölvak, J., 2012: Darriwilian (Middle Ordovician) conodont biostratigraphy in NW Estonia. *Estonian Journal of Earth Sciences* 61, 210–226.
- Hints, O., Paris, F. & Al-Hajri, S., 2015: Late Ordovician scolecodonts from the Qusaiba-1 core hole, central Saudi Arabia, and their paleogeographical affinities. *Review of Palaeobotany and Palynology* 212, 85–96.
- Holm, G., 1901: I. Kinnekulles berggrund. In G. Holm & H. Munthe (eds.): *Kinnekulle: Dess geologi och den tekniska användningen af dess bergarter*. Sveriges Geologiska Undersökning C172, 1–76.
- Jaanusson, V., 1982: Introduction to the Ordovician of Sweden. In D.L. Bruton, & S.H. Williams (eds.): *Field Excursion Guide. 4th International Symposium on the Ordovician System*. Paleontological Contributions from the University of Oslo 279, 1–10.
- Jansonius, J. & Craig, J.H., 1971: Scolecodonts: I – Descriptive terminology and revision of systematic nomenclature; II – Lectotypes, new names for homonyms, index of species. *Bulletin of Canadian Petroleum Geology* 19, 251–302.
- Kielan-Jaworowska, Z., 1966: Polychaete jaw apparatuses from the Ordovician and the Silurian of Poland and a comparison with modern forms. *Palaeontologia Polonica* 16, 1–152.
- Lindskog, A., 2014: Palaeoenvironmental significance of cool-water microbialites in the Darriwilian (Middle Ordovician) of Sweden. *Lethaia* 47, 187–204.
- Lindskog, A., Eriksson, M.E. & Pettersson, A.M.L., 2014: The Volkhov-Kunda transition and the base of the Holen Limestone at Kinnekulle, Västergötland, Sweden. *GFF* 136, 167–171.
- Lindskog, A., Eriksson, M.E., Tell, C., Terfelt, F., Martin, E., Ahlberg, P., Schmitz, B. & Marone, F., 2015: Mollusk maxima and marine events in the Middle Ordovician of Baltoscandia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 440, 53–65.
- Lindström, M., 1971: Vom Anfang, Hochstand und Ende eines Epikontinentalmeeres. *Geologische Rundschau* 60, 419–438.
- Matthews, S.C. & Missarzhevsky, V.V., 1975: Small shelly fossils of late Precambrian and early Cambrian age: a review of recent work. *Journal of the Geological Society* 131, 289–304.
- Mellgren, J.I.S. & Eriksson, M.E., 2010: Untangling a Darriwilian (Middle Ordovician) palaeoecological event in Baltoscandia: conodont faunal changes across the ‘Täljsten’ interval. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 100, 353–370.

- Mierzejewski, P., 1978: New placognath Eunicida (Polychaeta) from the Ordovician and Silurian of Poland. *Acta Geologica Polonica* 28, 273–281.
- Parry, L.A., Tanner, A. & Vinther, J., 2014: The origin of annelids. *Palaeontology* 57, 1091–1103.
- Parry, L.A., Wilson, P., Sykes, D., Edgecombe, G.D. & Vinther, J., 2015: A new fireworm (Amphinomidae) from the Cretaceous of Lebanon identified from three-dimensionally preserved myoanatomy. *BMC Evolutionary Biology* (2015) 15:256. DOI 10.1186/s12862-015-0541-8
- Paxton, H. & Eriksson, M.E., 2012: Ghosts from the past – ancestral features reflected in the jaw ontogeny of the polychaetous annelids *Marphysa fauchaldi* (Eunicidae) and *Diopatra aciculata* (Onuphidae). *GFF* 134, 309–316.
- Rasmussen, C.M.Ø, Ullmann, C.V., Jakobsen, K.G., Lindskog, A., Hansen, J., Hansen, T., Eriksson, M.E., Dronov, A., Frei, R., Korte, C., Nielsen, A.T. & Harper, D.A.T., 2016: Onset of main Phanerozoic marine radiation sparked by emerging Mid Ordovician icehouse. *Scientific Reports* 6, 18884; doi: 10.1038/srep18884.
- Schmitz, B., 2013: Extraterrestrial spinels and the astronomical perspective on Earth's geological record and evolution of life. *Chemie der Erde* 73, 117–145.
- Smith, M.R., Harvey, T.H.P. & Butterfield, N.J., 2015: The macro- and microfossil record of the Cambrian priapulid *Ottoia*. *Palaeontology* 58, 705–721.
- Szaniawski, H., 1996: Scolecodonts. In *Palynology: principles and applications* (eds J. Jansonius & D.C. McGregor), pp. 337–354. American Association of Stratigraphic Palynologists Foundation, Volume 1.
- Terfelt, F., Eriksson, M.E. & Schmitz, B., 2014: The Cambrian–Ordovician transition in dysoxic facies in Baltica — diverse faunas and carbon isotope anomalies. *Palaeogeography, Palaeoclimatology, Palaeoecology* 394, 59–73.
- Tonarová, P., Eriksson, M.E. & Hints, O., 2012: A jawed polychaete fauna from the late Ludlow Kozłowski event interval in the Prague Basin (Czech Republic). *Bulletin of Geosciences* 87, 713–732
- Tonarová, P., Hints, O., Königshof, P., Suttner, T.J., Kido, E., Da Silva, A.-C. & Damien, P., 2016: Middle Devonian jawed polychaete fauna from the type Eifel area, western Germany, and its biogeographical and evolutionary affinities. *Papers in Palaeontology*. Accepted.
- Underhay, N.K. & Williams, S.H., 1995. Lower Ordovician scolecodonts from the Cow Head Group, western Newfoundland. *Canadian Journal of Earth Sciences* 32, 895–901.
- Vannier, J., Calandra, I., Gaillard, C. & Žylińska, A., 2010: Priapulid worms: Pioneer horizontal burrowers at the Precambrian-Cambrian boundary. *Geology* 38, 711–714.
- Walcott, C.D., 1911: Middle Cambrian annelids. *Smithsonian Miscellaneous Collections* 57, 109–144.
- Westergård, A.H., 1943: Den kambro-siluriska lagerserien. In S. Johansson, N. Sundius & A.H. Westergård (eds.): *Beskrivning till kartbladet Lidköping*. Sveriges Geologiska Undersökning Aa182, 22–89.

Figures

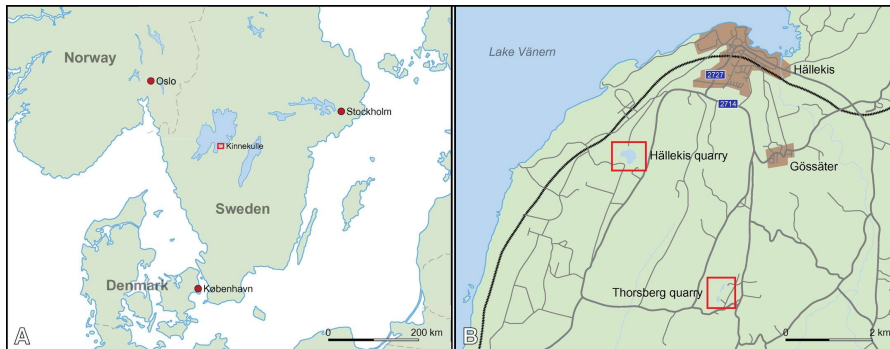


Fig. 1. A. Map of southern Sweden and its geographic surroundings showing the location of Mount Kinnekulle. B. Detail map of northern Kinnekulle with the location of the Hälleklis and Thorsberg quarries (modified from Lindskog 2014).

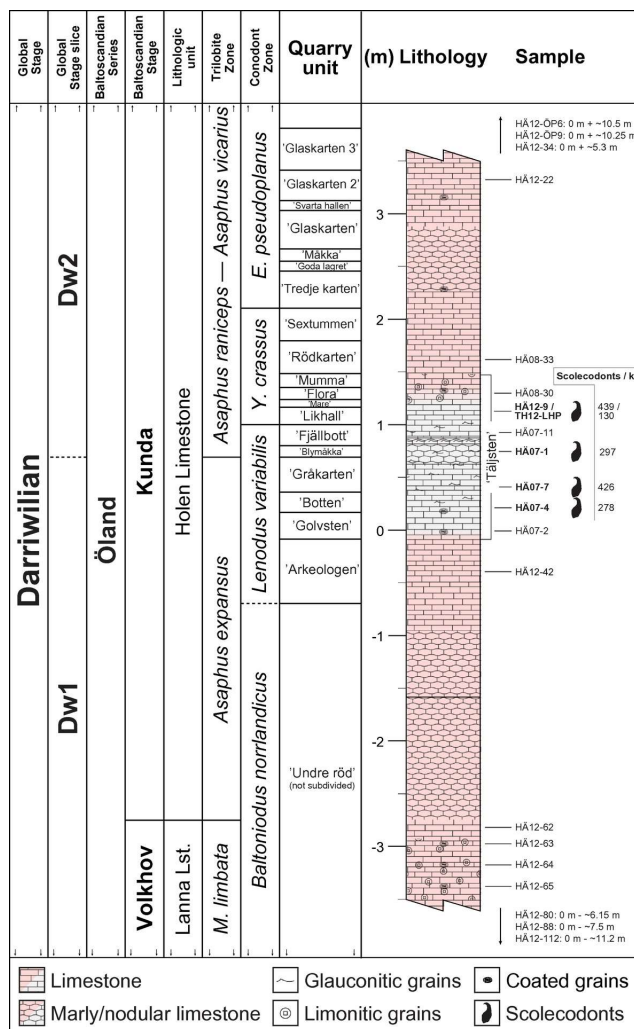


Fig. 2. Sedimentary profile of the sampled section at Hälleklis (modified from Lindskog et al. 2015, with quarry units added from Schmitz 2013). All palynomorph samples are included and those yielding scolecodonts are marked with a symbol (note that sample HÄ12-64 and HÄ12-80 yielded one possible scolecodont fragment each). The abundance (number of specimens per kg of rock) is included.



Fig. 3. Photomicrographs of selected representative scolecodonts recorded from Kinnekulle, Västergötland, southern Sweden. Scalebar 20 μ m. A–I. Placognath jaws tentatively assigned to mochtyellids, specimens probably represent first maxillae. **A.** LO 12339t-a, HÄ12-9. **B.** LO 12340t-a (possible xanioprionid), TH12-LHP. **C.** LO 12339t-b, HÄ12-9. **D.** LO 12341t-a, HÄ12-9. **E.** LO 12341t-b, HÄ12-9. **F.** LO 12342t-a, HÄ07-7. **G.** LO 12343t-a, HÄ07-7. **H.** LO 12344t-a, HÄ07-4. **I.** LO 12341t-c, HÄ12-9. **J.** First maxilla(?), ctenognath?, LO 12342t-b, HÄ07-7. K–M. Possible ctenognath (tetraprionid) right maxillae; **K.** LO 12345t-a, HÄ07-1. **L.** LO 12343t-b, HÄ07-7. **M.** LO 12346t-a, HÄ07-1. N–S. First maxillae (some might represent basal/laeobasal ridges). Mochtyellid, tetraprionid and/or *Lunoprionella*-like jaws. **N.** LO 12341t-d, HÄ12-9. **O.** LO 12341t-e, HÄ12-9. **P.** LO 12346t-b, HÄ07-1. **Q.** LO 12345t-b, HÄ07-1. **R.** LO 12343t-c, HÄ07-7. **S.** LO 12344t-b, HÄ07-4. T–AD. Unidentified scolecodonts of probable placognath/ctenognath affinity. **T.** LO 12344t-c, HÄ07-4. **U.** LO 12344t-d, HÄ07-4. **V.** LO 12340t-b, TH12-LHP. **W.** LO 12347t-a, TH12-LHP. **X.** LO 12341t-f, HÄ12-9. **Y.** LO 12341t-g, HÄ12-9. **Z.** LO 12345t-c, HÄ07-1. **AA.** LO 12339t-c, HÄ12-9.

AB. LO 12342t-c, HÄ07-7. **AC.** LO 12344t-e, HÄ07-4. **AD.** LO 12347t-b, TH12-LHP. **AE–AF.** Partial jaw apparatuses of placognath affinity. **AE.** LO 12346t-c, HÄ07-1. **AF.** LO 12348t-a, HÄ07-4. **AG.** Right MI of *Oeononites* sp., LO 12342t-d, HÄ07-7. **AH–AI.** left and right MII probably belonging to *Oeononites*. **AH.** LO 12342t-e, HÄ07-7. **AI.** LO 12342t-f, HÄ07-7. **AJ–AL.** anterior maxillae (MIV?) probably belonging to *Oeononites*. **AJ.** LO 12343t-d, HÄ07-7. **AK.** LO 12344t-f, HÄ07-4. **AL.** LO 12343t-e, HÄ07-7. **AM–AN.** Putative priapulid teeth. **AM.** LO 12343t-f, HÄ07-7. **AN.** LO 12344t-g, HÄ07-4. **AO–AT.** Anterior maxillae (sometimes assigned to ‘*Anisocearasites*’ or ‘*Belegenys*’). **AO.** LO 12345t-d, HÄ07-1. **AP.** LO 12341t-h, HÄ12-9. **AQ.** LO 12343t-g, HÄ07-7. **AR.** LO 12348t-b, HÄ07-4. **AS.** LO 12344t-h, HÄ07-4. **AT.** LO 12342t-g, HÄ07-7. **AU–AW.** Accessory teeth of polychaete jaw apparatuses, such as intercalary or lateral teeth. **AU.** LO 12346t-d, HÄ07-1. **AV.** LO 12347t-c, TH12-LHP. **AW.** LO 12347t-d (part of molluscan radula?), TH12-LHP.