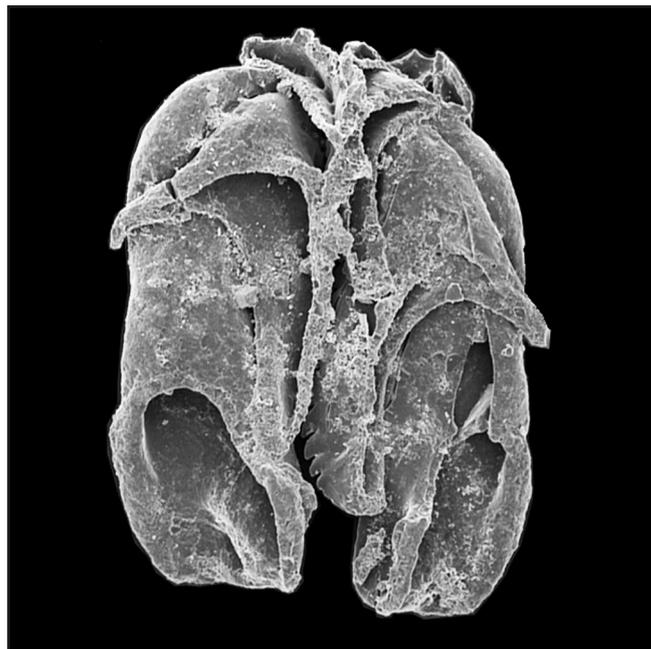


The fossil wonders of the Silurian Eramosa Lagerstätte of Canada: the jawed polychaete faunas

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Bachelor's thesis
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Cover Picture: Full jaw apparatus of a polychaete.

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Abstract: The Silurian Eramosa Lagerstätte in Ontario, Canada, is represented by three distinguished biotas (1 to 3) with exceptionally well preserved fossils. In this study, the jawed polychaete fauna is described and discussed for the first time, on the basis of scolecodonts and jaw apparatuses, recovered from Biota 1 and 3. One new paulinitid species, *Kettnerites* sp. a, is described from a wealthy collection of specimens recovered through acid digestion of rocks from the locality Park Head (comprising Biota 1), the strata of which were probably formed in very shallow, possibly lagoonal environments. The abundant and monospecific material allowed confident reconstruction of the full dorsal maxillary apparatus and the new taxon is compared to previously known, approximately coeval ones from other regions. Attempts at finding evidence of jaw moulting for *Kettnerites* sp. a were inconclusive; similar to a previous study from the Silurian of Gotland, Sweden, no unambiguous evidence for distinct size frequency classes was revealed. In addition to the Park Head collection, bedding plane material from the locality Wiarton (comprising Biota 3) revealed two other taxa; *Kettnerites* sp. b and *Oeononites* cf. *curvidens*. The strata at Wiarton have been interpreted as representing environments with good water circulation and open marine conditions. Based on their relative abundance, jaw bearing polychaetes apparently played a significant role in the Silurian marine biotas that are currently preserved in the Eramosa Lagerstätte and this study provides a fuller picture of this lagerstätte. Moreover, the results reinforce the fact that different polychaete species had variable environmental preferences during the Silurian and that *Oeononites* and *Kettnerites* formed two of the most common and widely distributed genera.

Keywords: Eramosa Lagerstätte, Silurian, polychaete faunas, scolecodonts, palaeoecology, palaeobiogeography.

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Fossila underverk från den siluriska Eramosa Lagerstätte i Kanada: de käkbärande polychaeterna

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Sammanfattning: Eramosa Lagerstätte i Ontario, Kanada, representeras av tre olika identifierade biota (1-3) med exceptionellt välbevarade fossil. I denna rapport så beskrivs och diskuteras för första gången polychaetfaunan, baserat på scolecodonter och käkapparater, från biota 1 och 3. En ny paulinitidart, *Kettnerites* sp. a, har beskrivits utifrån stora mängder material som utvunnits genom syraupplösning av kalkstenar som insamlats på lokalen Park Head (som representeras av biota 1). Lagren i Park Head bildades förmodligen i en väldigt grundmarin, möjligen lagunartad, miljö. Den stora mängden exemplar och den ensidiga artsammansättningen från Park Head gjorde det möjligt att övertygande rekonstruera hela käkapparaten och få god insikt i inomartsvariationen. Arten har även jämförts med likåldriga arter från andra områden. Vidare undersöktes om *Kettnerites* sp. a successivt bytte käkar under sin livstid. Resultaten gav inga entydiga bevis för storleksklasser och regelbunden käkömsning, vilket stämmer väl överens med en liknande studie som gjorts på siluriska paulinitider från Gotland. Förutom *Kettnerites* sp. a från Park Head så har även två andra arter hittats, *Kettnerites* sp. b och *Oeononites* cf. *curvidens*, bevarade på skiktytor från lokalen Wiarton (som representeras av biota 3). Miljön i Wiarton har beskrivits som öppen marin miljö med god vattencirkulation. Den relativt stora mängden fossil av käkbärande polychaeter antyder att dessa djur spelade en viktig roll i de siluriska marina ekosystem som nu är bevarade i form av Eramosa Lagerstätte. Den här studien ger också en djupare inblick i denna Lagerstätte. Resultaten stärker uppfattningen att olika polychaetarter hade varierande miljöpreferenser under silurtiden och att *Oeononites* och *Kettnerites* var två av de vanligaste och mest utbredda släktena under samma period.

Nyckelord: Eramosa Lagerstätte, silur, polychaeter, scolecodonter, paleoekologi, paleobiogeografi.

Ämnesinriktning: Berggrundsgeologi

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1 Introduction

Scolecodonts are microfossils which come from polychaete annelid worms. The first scolecodont was described almost 150 years ago by Eichwald (1854) as the remains of some Silurian fish (Eriksson et al., 2004 and references therein). Because of the largely soft-bodied anatomy of polychaete worms, they have poor preservation potential. The jaws, or scolecodonts, however fossilized well and provide a good fossil record of the polychaetes (Kielan-Jaworowska, 1966; Hints & Eriksson, 2007). Polychaete worms exist in modern oceans and are among the most abundant and diverse marine invertebrates (Glasby et al., 2000; Hints & Nölvak, 2006).

Scolecodonts are known from the latest Cambrian however their oldest record is poor and it was not until the Middle Ordovician, that the scolecodont-bearing polychaetes significantly diversified and many new species evolved (Hints & Eriksson, 2007; Suttner & Hints, 2010). The mass extinction event at the end of the Ordovician Period, during which large amounts of invertebrate taxa disappeared, does not seem to have had a major influence on the polychaetes, although detailed studies are still pending (Eriksson et al., 2004; Hints & Eriksson, 2007). However, it has been shown that a number of events during the Silurian Period, that significantly changed the marine environment and had a great impact on the benthic and pelagic invertebrate faunas, affected the polychaetes (Jeppsson 1998; Eriksson et al., 2004). Even if there is much information on Ordovician and Silurian scolecodonts, data from other time periods are relatively restricted (Eriksson et al., in press). Our general knowledge about scolecodonts is still meager compared to that of most other fossil groups and most of the scolecodont information comes from Laurentia and Baltica which obviously gives a skewed view on their global fossil record (Hints & Eriksson, 2007). One of the reasons why paleontologists have been largely neglecting scolecodonts even if they generally are found in great numbers and diversity is their problematic taxonomy. Recent studies have, however, shown that this obstacle can be overcome and that most scolecodonts can be identified to species level with some experience (Bergman 1989; Eriksson & Bergman 1998; Eriksson et al., in press).

The jaw apparatus of Paleozoic eunicidan polychaetes consists of one pair of supporting, massive ventral mandibles, and a dorsal complex maxillary apparatus (Kielan-Jaworowska, 1966; Eriksson et al., 2004; Suttner & Hints, 2010). The maxillary apparatus of paulinitid polychaetes, one species of which is described herein, consists of four paired maxillae, one unpaired element and paired carriers in the posteriormost part (Fig. 1) (Bergman, 1989). The maxillae are abbreviated M and numbered in roman numerals from the posterior to the anterior. Thus, the MI is the first, or posteriormost, maxilla and MV is the anteriormost one. The main objectives of this thesis

are to describe and discuss the previously unknown jawed polychaete fauna of the Eramosa Lagerstätte, based on scolecodonts and jaw apparatuses, and also to provide a brief general overview of this lagerstätte and the distribution and ecology Silurian polychaetes.

2. Methods

All specimens analyzed herein were collected by Peter von Bitter (Toronto) from the Eramosa Lagerstätte in Canada and kindly sent to M. E. Eriksson (Lund) for further studies. The material, which includes specimens preserved on bedding plane surfaces and isolated ones recovered through acid digestion of the rocks, was recovered from two localities with slightly different biotas; the bedding plane specimens are from locality D, Biota 3 (Fig. 2), whereas the isolated specimens comes from locality A, Biota 1 (Fig. 2) (described by von Bitter et al. 2007; see also below). In order to digest the samples from locality A, acetic acid was used (method described by Bergman 1989 p. 27-28) and subsequently the sample residues were dried, hand-picked and sorted into microfossil slides.

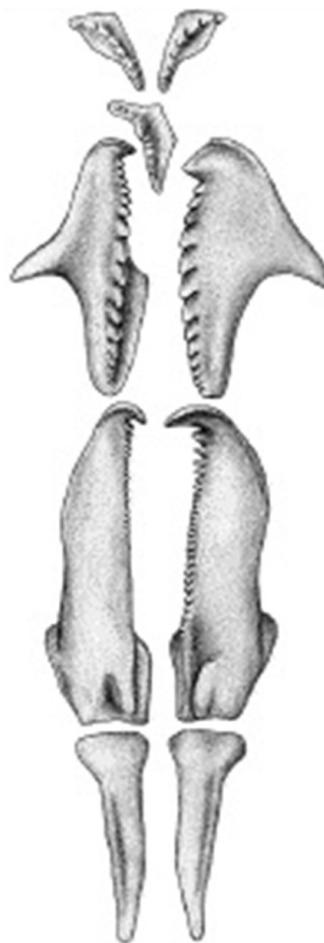


Fig. 1. The complete dorsal maxillary jaw apparatus of a paulinitid polychaete (here exemplified by *Kettnerites (Aeolus) sisyphi klasaardensis*). Adopted from Eriksson et al. (2004)

The specimens were studied in a binocular light microscope and identified as far as possible based on the published literature on Silurian scolecodonts. Some scanning electron microscopy (SEM) photomicrographs and the digital images of the bedding plane specimens were provided to me by M. Eriksson. Additional specimens were studied and photographed in SEM. All images were subsequently adjusted, in terms of brightness and contrast, cropped and compiled into photographic plates using the Adobe photoshop software. Measurements for the descriptive paleontology and the size-frequency distribution analysis were made using a light microscope fitted with a measuring ocular.

3. Geological setting

The Eramosa Lagerstätte is a part of a 16 km long outcrop belt which occurs in the Wenlock (middle Silurian), upper Eramosa Formation, which is ~15 m thick (von Bitter et al., 2007; Collette & Rudkin, 2010). Williams coined the “Eramosa beds” in 1915 for a distinctive eurypterid-bearing lithofacies located in a bituminous dolostone near the top of a local Silurian succession at Guelph, Ontario, Canada (Collette & Rudkin, 2010). Similar and coeval rocks from the Western Ontario Peninsula, also known as Bruce Peninsula, were also included in the Eramosa bed (Collette & Rudkin, 2010). Even if Williams was the first to name the Eramosa bed, the Lagerstätte was not identified and investigated until 2001 in a doctoral thesis by Tetreault (Tetreault, 2001; von Bitter et al., 2007).

There are only a few Lagerstätten known from the Silurian (Kluessendorf, 1994; Collette & Rudkin, 2010) although new ones are being reported at an increasing rate. Among these, the Eramosa Lagerstätte of Ontario is not typical because of the mixture of non-biomineralized and shelly organism with trace fossils (von Bitter et al., 2007; Collette & Rudkin, 2010).

According to Collette & Rudkin (2010) the faunal elements of the biota found in the Eramosa Lagerstätte have been known for many years but intense study on these elements has only been initiated recently. Still many aspects with regards to sedimentology and paleoenvironments of the Eramosa Lagerstätte have not yet been investigated. The exceptional preservation is restricted to a 7-9 m thick unit consisting of an alternating sequence of dolostone, limestone and bituminous shale (von Bitter et al., 2007). The Eramosa Lagerstätte contains organisms from several different, yet laterally intergrading environments, ranging from lacustrine to fully marine environments (von Bitter et al., 2007; von Bitter & Purnell, 2009). Of the four localities examined by von Bitter et al. (2007) there was a significant difference in the environment from the northern to the southern locality. Von Bitter & Purnell (2009) suggested, on the basis of the fossil

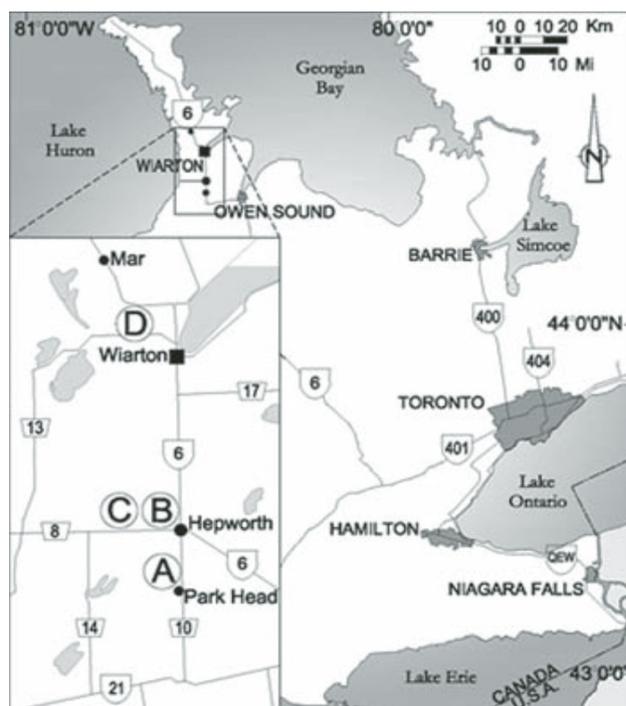


Fig. 2. Map showing the study area and the scolecodont-yielding localities. The new species (*Kettnerites* sp. a) was found at locality A (Park Head) whereas the remaining material (bedding-plane specimens) come from locality D (Warton). Figure adopted from von Bitter et al. (2007).

record, an open marine environment or a lagoonal environment with open marine circulation in the northern part of the Lagerstätte. This gradually changed to a restricted marine environment where the circulation has decreased and almost ceased in the central part and in the south a non-marine or possibly a near shore environment dominated.

The Eramosa Lagerstätte has some preserved faunal elements in common with the slightly older, (Llandovery, Early Silurian) Waukesha Lagerstätte of Wisconsin (Mikulic et al., 1985), however, to say that they contain the same fauna would not be justified because there are many taxa that differ between the two (von Bitter et al., 2007).

The Eramosa contains an exceptionally preserved fauna including conodonts with associated eye capsules, fully articulated scorpions, algae, polychaetes, corals and fish remains along with *Chondrites*, *Planolites* and phyllocarid burrows as common trace fossils (von Bitter et al., 2007; Collette & Rudkin, 2010). Evidence of bioturbation is very unusual for Silurian Lagerstätten (von Bitter et al., 2007).

In 2007 von Bitter and others identified three biotas which were characterized by different fossil assemblages (see Table 1; Fig. 2). They found eunicidan polychaete jaws (scolecodonts) in two of the three distinguished biotas (Biota 1 and 3). These two biotas are found in the northern and the southern part of the Lagerstätte and come from different environments, and therefore the preservation of the fossils included differ.

Table. 1. The composition of the 3 biotas distinguished in the Eramosa Lagerstätte (Adopted from von Bitter et al. 2007). Biota 3 is split into three smaller biotas (Biota 3 U, 3 M, 3 L) depending on where they were found. U stand for upper part, M stands for middle part and L stands for lower part.

Biota	Composition
1	Vertebrates: tolypelepid heterostracans, disarticulated dermal elements and complete articulated skeleton rare; corvaspids, disarticulated dermal elements and element concentrations common. Arthropods: erettopterid eurypterids, molts common; leperditiid and beyrichiid ostracodes. Annelids: articulated and disarticulated eunicid polychaete jaws.
2	Vertebrates: conodonts, complete skeletons, often with eye traces, common; isolated elements; at locality B, <i>Ozarkodina excavata</i> common, <i>O. confl uens</i> , a new genus and species (<i>Ozarkodina?</i> sp. nov. of Aldridge, 1985), <i>Ctenognathodus</i> cf. <i>murchisoni</i> , <i>Pseudooneotodus borensis</i> , and <i>Panderodus</i> sp. rare; at locality C, <i>Ct.</i> cf. <i>murchisoni</i> , <i>Ozarkodina?</i> sp. nov. and <i>Panderodus</i> sp.; Arthropods: hughmilleriid eurypterids rare; leperditiid ostracodes, articulated, compressed calcareous valves common. Graptolites: monograptids rare. Sparse, shelly recrystallized fauna of meristellid brachiopods, orthocone cephalopods, low-spined gastropods, and tabulate corals. Algae: thal- lophytes, carbonaceous films rare; prasinophytes common. Trace fossils: <i>Chondrites</i> burrows.
3 U	Annelids: articulated and disarticulated eunicid polychaete jaws common. Algae: thallophytes and dasyclads common.
3 M	Arthropods: eurypterids and scorpions (Waddington and Jeram, 1997).
3 L	Vertebrates: Conodonts: exceptionally preserved, articulated skeletons of <i>Ozarkodina excavata</i> , often with eye traces, rare; ?Fish, concentration of blue-weathering, ?vertebrate phosphate (ROMV 56598 a&b) rare. Arthropods: phyllocarid and ostracode crustaceans, xiphosuran chelicerates, lobopodians, arthropods of uncertain affinities (cf. branchiopods or remipedes of Mikulic et al., 1985a, 1985b). Annelids: <i>Myoscolex</i> -like forms, polychaetes (including possible aphroditid-like forms with phosphatized muscle tissue), spirorbiform tubes and annulated worms of uncertain affinity. Associated shelly fauna of decalcified, silicified, articulated rhynchonellid brachiopods, lepidocentrid echinoids (in life position; Tetreault, 2001b), ophiuroids with intact arms and rare complete crinoids; desilicified choiid demosponges; trilobites, conularid cnidarians, <i>Sphenothallus</i> , articulate and inarticulate brachiopods, bivalves, gastropods, and cephalopods. Trace fossils: <i>Planolites</i> -type and phyllocarid burrows common. Algal mats.

Carbon and sulfur seem to be the primary elements of preservation of Biota 1. Such preservation can indicate an *in situ* polymerization which could have been enhanced by diagenetic sulfurization (von Bitter et al., 2007).

The polychaetes in Biota 3 were found in the upper Interbedded Unit of von bitter et al., (2007) which is characterized by a broad range of preservation styles, indicating a complex taphonomic history (Table 1). The polychaetes were preserved either by an early authigenic mineralization or as carbonaceous films, also the carbonaceous remains of the scolecodonts indicate a high degree of decay (von Bitter et al., 2007).

4. Systematic Paleontology

Scolecodont descriptive terminology follows that of Kielan-Jaworowska (1966) and Bergman (1989). All figured specimens are currently housed at the Department of Geology at Lund University. Since they are not formally described and named no type numbers are provided in this thesis.

Phylum: Annelida Lamarck 1809
Class: Polychaeta Grube 1850
Order: Eunicida Dales 1963
Superfamily: Eunicea Grube 1852
Family: Paulinitidae Lange 1947
Genus: *Kettnerites* Žebera 1935

Kettnerites sp. a
(Figs 3 and 4)

Diagnosis – Right MI: Thin ligament rim. Pronounced basal plate, clearly standing out from the basal furrow.

Left MI: Jaw ends in a fang or hook, bent to the dorsal side.

Right MII: A cusp followed by a single intermediate denticle. Myocoele opening extends for 3/5–4/5 of the length.

Left MII: The tip if the ramus is bent at the posterior. Ligament rim is narrow and goes out to the ramus. Single cusp with no pre-cuspidal denticles

Left MIII: Second denticle half the length of surrounding denticles. Bent ramus. Cusp at the anterior.

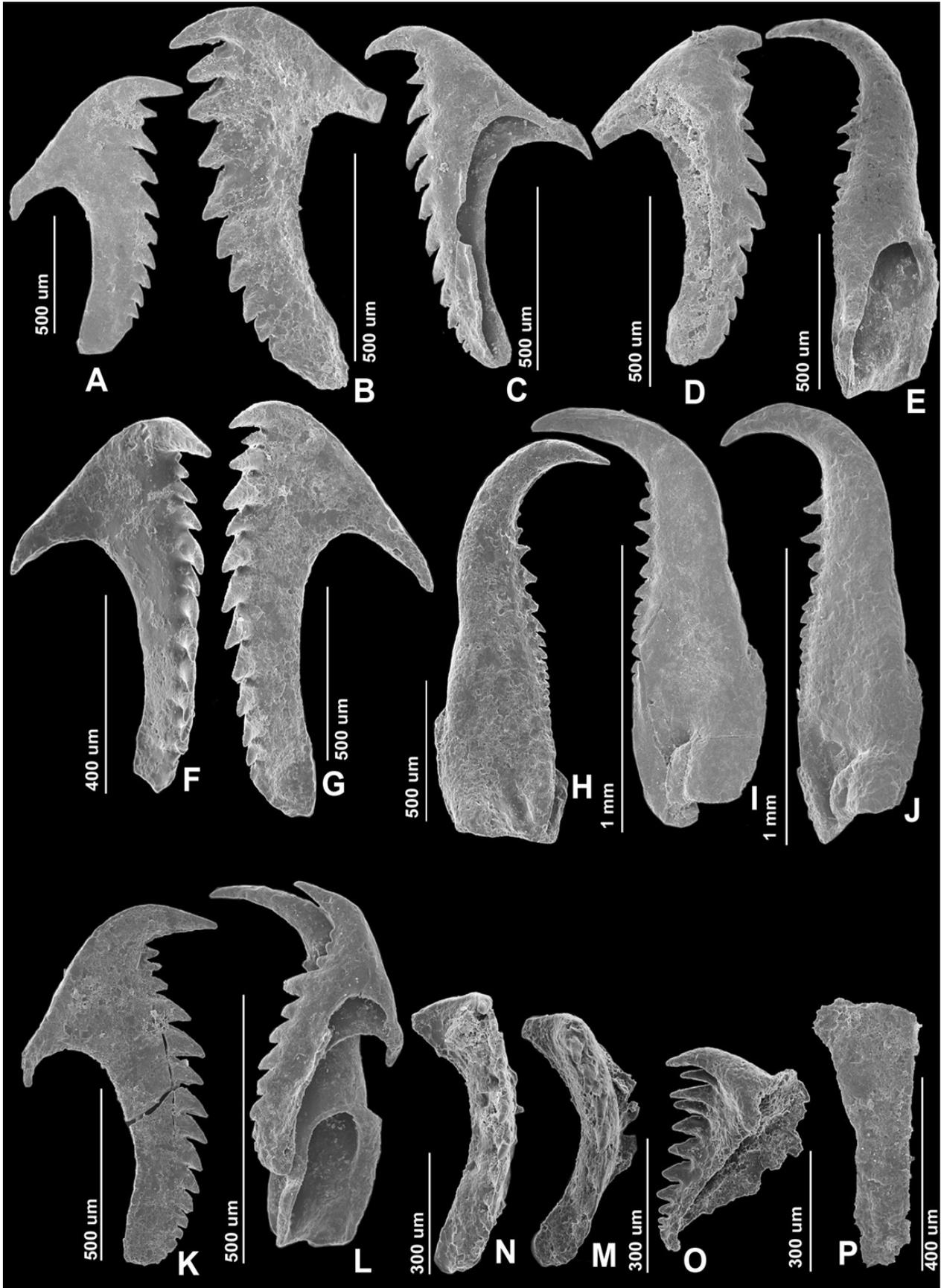


Fig. 3. SEM-micrographs of *Kettnerites* sp.a in dorsal view (A, B, F-K, M-P) and ventral view (C-E, L). All specimens are from locality A (Park Head) of the Eramosa Lagerstätte, Ontario, Canada. A: Left MII. B: Right MII. C: Left MII. D: Right MII E: Left MI. F: Left MII. G: Right MII. H: Left MI. I: Right MI. J: Right MI. K: Left MII. L: Left MI and MII. M: MIII. N: MIII. O: Right MIV. P: Carrier.

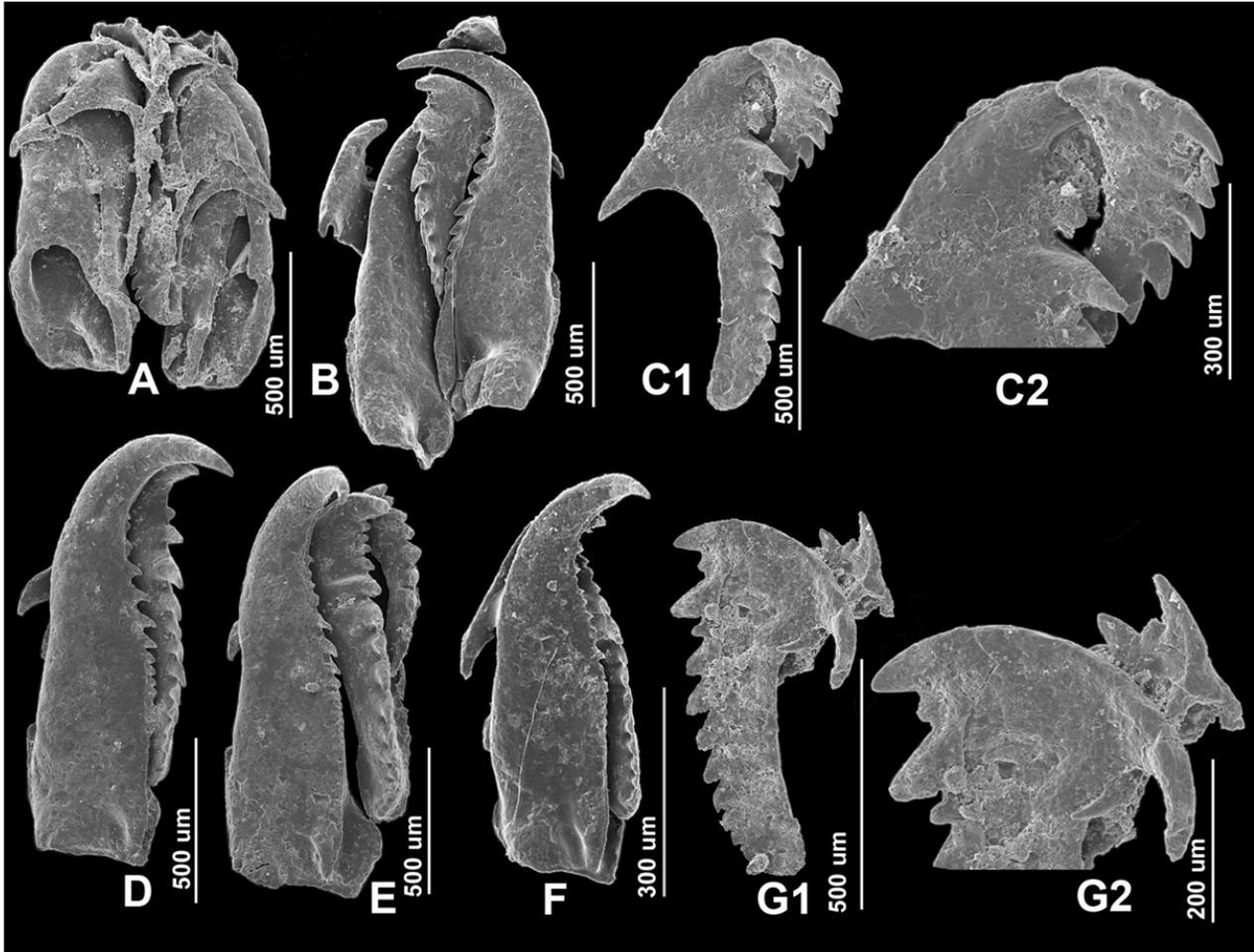


Fig. 4. SEM-micrographs of *Kettnerites* sp.a. All specimens in dorsal view except A. All specimens are from locality A (Park Head) of the Eramosa Lagerstätte, Ontario, Canada. A: Left and right MI, MII, MIV and MIII. B: Left and right MI, MII and MIII. C1: Left MII and MIII. C2: Same specimen as C1 with an enlargement on MIII. D: Left MI and MII. E: Left MI, MII and MIII. F: Left MI and MII. G1: Right MII and MIV. G2: Same specimen as G1 with an enlargement on MIV.

Right MIV: Slanting denticles, decreasing posteriorly.

Left MIV: Almost mirror image of right MIV.

Carriers: Straight inner margin. Outer part of the head is straight while the shaft tapers to the end of the carriers. Some specimens shaft tapers all the way from the head to the end of the shaft.

Description – Right MI, dorsal side: Length 0,52–1,82 mm, width about $\frac{1}{3}$ of the length of the jaw. It is thickest in the posterior part and tapers to the anterior which ends with a distinguished fang or hook. Dental growth starts at the end of the basal portion with 5–7 small slanting denticles and followed by 3–4 denticles that are larger in the top anterior part. The dentary extend along the inner margin for 0,5–0,6 of the jaw length and starts with prominent undenticulated ridge. The undenticulated ridge ends in a sharply-ended shank. The falcal arch is undenticulated or has 1–2 small knobs. The inner margin is straight and leaning inwards against the outer margin, or it is convex with a thicker part in the middle of the jaw, which gives the jaw the tapering shape. The outer margin is straight from the basal portion to the falcal arch or slightly convex with a thick part at the end of the basal portion. The basal furrow is deep and long but restricted by the

basal plate at the outer margin.

Ventral side: The myocoele opening tapers anteriorly and extends for $\frac{2}{5}$ – $\frac{1}{2}$ of the jaw length. The ligament rim is very narrow at the anterior part and thickens on the outer margin, at the inner margin it is almost absent and goes out to the inner wing. The inner wing is triangular starting from the shank and up to the ligament rim in the anterior.

Left MI, dorsal side: Length 0,54–1,69 mm, width about $\frac{1}{3}$ of the length of the jaw. The jaw ends at the anterior part with a fang or well developed hook. The hook can be bent outwards against the dorsal plane. The inner margin start with an undenticulated ridge the first quarter of the margin, then there are 6–9 slanting denticles of which the last 2–3 are slightly larger and some which slant to the anterior. The falcal arch is undenticulated or has a few small denticles or possibly knobs. The dentary occupies approximately 0,4 of the length of the jaw. The inner margin is slightly convex. The inner margin ends in a triangular shank. The outer margin is also slightly convex. The basal furrow is deep and long, it stops at the very end of the posterior part. The inner wing is triangular and slightly downfolded at the outer part.

Ventral side: The myocoele opening extends for approximately half of the length of the jaw and has

a thick ligament rim in the inner and outer margin and is thinner in the anterior.

Right MII, dorsal side: Length 0,39–1,3 mm, width about half the length or slightly more. There are 10–13 slanting denticles along the denticulated ridge. The jaw has a cusp in the anterior part followed by a smaller intermediate denticle which is half the length of the cusp. The intermediate denticle is followed by a denticle of approximately the same size as the cusp and another denticle in the same size as the intermediate denticle. In some specimens the intermediate denticles are absent or not fully developed. After the four first denticles there are 6–9 denticles which decrease gently in size posteriorly. The shank is a little thicker at the anterior part and tapers to the posterior, occupying slightly more than half the length. The inner margin is convex while the outer margin is concave which gives the shank its tapering shape. The ramus is bent against the posterior part, it tapers to the end. From the cusp to the tip of the ramus is a straight line on some, while some are convex where it thickens on the middle.

Ventral side: The myocoele opening seams to extend to $\frac{3}{5}$ – $\frac{4}{5}$ of the jaw length, the ligament rim is narrow along the anterior and inner margin.

Left MII, dorsal side: Length 0,55–1,26 mm, width about $\frac{1}{2}$ – $\frac{3}{5}$ of the length of the jaw. The anterior part ends with a distinguished cusp. The post-cuspidal dentary consists of 1–4 intermediate denticles of the same size and are followed by 6–9 larger slanting denticles. In some specimen the intermediate dentary is not fully developed, making all the denticles except for the cusp approximately the same size. The denticulated ridge stretches the whole length of the jaw. The shape of the shank is very similar to that of the right MII except for the length which is $\frac{2}{3}$ on the left MII with a convex inner margin and a concave outer margin which tapers posteriorly. The bight angle varies from 60–90°. The ramus is slender and tapers towards the outer margin, it ends in a sharply pointed tip which is often bent to the posterior. The ramus is approximately half of the jaw width or slightly less.

Ventral side: The myocoele opening extends for $\frac{2}{3}$ of the length of the jaw and has a narrow ligament rim along the inner margin to the anterior and out along the ramus.

Left MIII, (unpaired element), dorsal side: Length 0.53–0.68 mm, width about $\frac{1}{4}$ of the length of the jaw. The jaw is arcuate and has a concave inner margin and a convex outer margin. The ramus is slightly bent inwards against the inner margin. Denticles are decreasing in size posteriorly with the exception of the second denticle which is half the length of the two surrounding denticles.

Right MIV, dorsal side: Length 0,32–0,75 mm, width $\frac{1}{3}$ of the length of the jaw. 6–8 slanting denticles decrease in size posteriorly with the largest denticle at the most anteriorly part. The denticulated ridge is straight or slightly convex.

Left MIV. Nearly mirror reflection of the right MIV.

Carrier: The head tapers posteriorly as does the

shaft. After half the length of the shaft the outer part becomes straight while the inner margin is straight all the way. Both margin of the shaft therefore runs parallel to the posterior blunt end of the shaft. In some specimens the shaft ends in a pointy extremity making the outer part taper all the way.

Material – A couple of hundreds of specimens, including all elements of the dorsal maxillary apparatus.

Occurrence – The Wenlock Eramosa Lagerstätte; at the present the species is only known from the locality Park Head (Fig. 2).

Discussion – This species was the only one found in the acid resistant residues from the locality Park Head of the Eramosa Lagerstätte. It was, however, recovered in great abundance. It is a species with a diagnostic morphology and because there are no identical taxa previously described, it is believed to represent a new species. Still, it is kept in open nomenclature for the purpose of this thesis. The specimens of *Kettnerites* sp.a are well preserved and the wealth of material allowed detailed studies of the individual elements, including intraspecific and ontogenetic variability. Moreover, the recovery of all these specimens, including some partial apparatuses, allowed the entire dorsal maxillary apparatus to be confidently reconstructed.

The MI of *Kettnerites* sp.a is similar to those of the majority of the known *Kettnerites* species with the large slanting denticles at the anterior part which decrease in size posteriorly. There are some known Silurian paulinitid species similar to the Eramosa species, e.g. *Kettnerites* (*A.*) *sisyphi klasaardensis* and *Kettnerites* (*K.*) *martinssonii* (see Bergman (1989)) which also have large denticles on the MI that taper posteriorly.

Similar to many other paulinitids the left MII of the Eramosa species has a large and distinguished cusp followed by smaller intermediate denticles. However, *Kettnerites* (*K.*) *bankvaetensis*, *Kettnerites* (*K.*) *polonensis* described by Bergman (1989) and *Ildralites exactus* described by Eller (1940) differ on this point with a double cusp. Following the key for the right MII by Bergman (1989, p. 37), the only species similar to the Eramosa species, with regards to that element, is *Kettnerites* (*K.*) *versabilis* since it lacks pre-cuspidal denticles and only have a single cusp.

The number and size of denticles on the right MI depends on the size of the jaw. Smaller jaws normally have fewer denticles and the smallest of these are only developed to small knobs. Among the MI some specimens have a convex outer margin whereas others have a concave outer margin. The intermediate denticles on the left and right MII seem to be missing in some of the specimens at hand. If this is normal or if the intermediate denticles simply are undeveloped in these specimens is difficult to say. However, no connection to size was found.

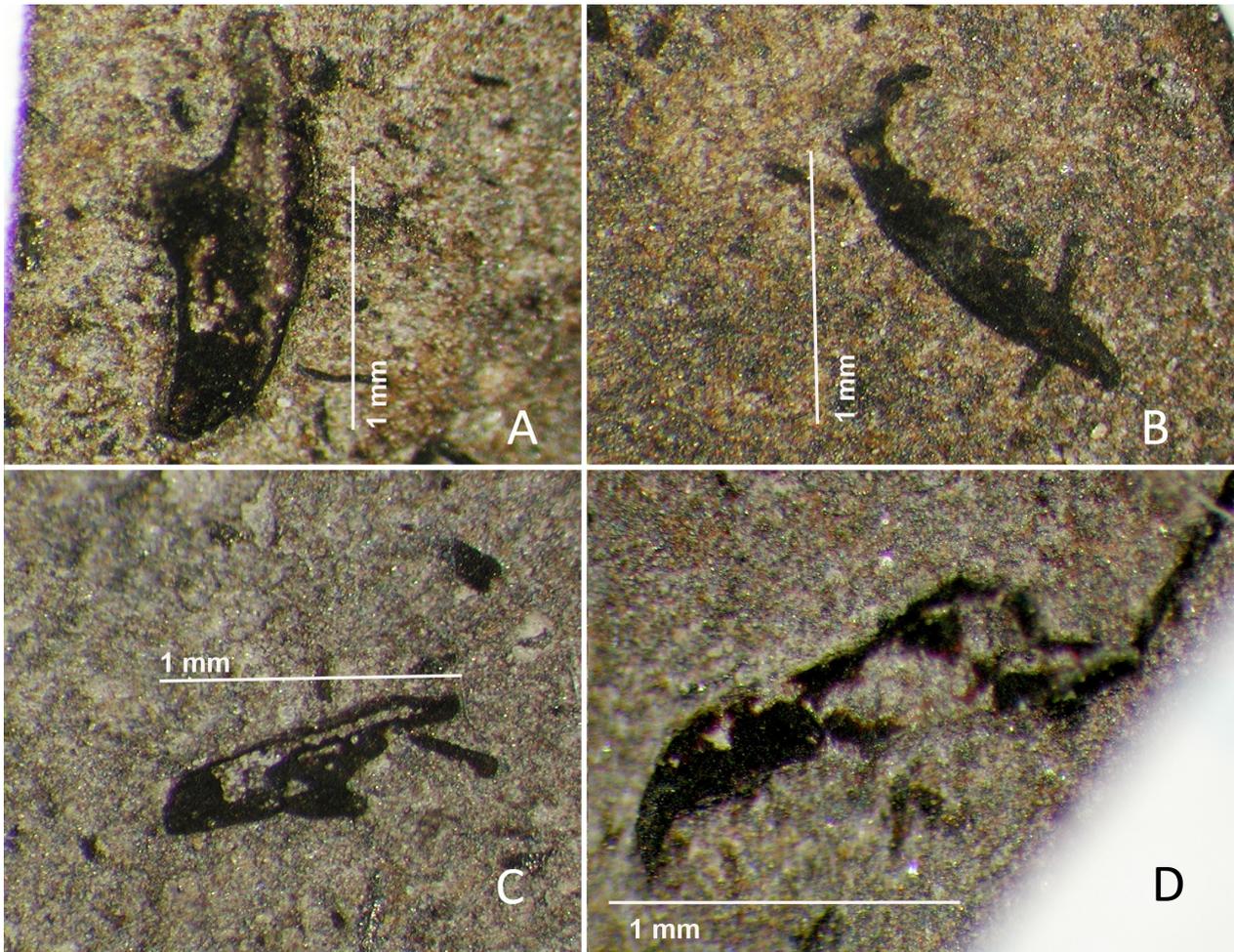


Fig. 5. Light microscope photographs of bedding-plane scolecodonts. All specimens are from locality D (Wiarion) of the Eramosa Lagerstätte, Ontario, Canada. A— C: *Oeononites* cf. *curvidens* D: *Kettnerites* sp. b.

Kettnerites sp. b
Fig. 5D

Remarks – One paulinitid MI with a straight inner margin and a prominent shank was recorded on a bedding plane surface from Wiarion. Although the specimen is relatively poorly preserved and parts of the dorsal surface is missing it can be concluded, based on the external morphology, that it belongs to *Kettnerites* albeit a different species than *Kettnerites* sp. a described above. The preservation does, however, not allow an unambiguous species determination why it is left in open nomenclature.

Material – One specimen (MI) preserved on a bedding plane surface.

Occurrence – The Wenlock Eramosa Lagerstätte, locality Wiarion (Fig. 2).

Family: Polychaetaspidae Kozłowski, 1956

Genus: *Oeononites* Hinde 1879

Oeononites cf. *curvidens*
Fig. 5A-C

Remarks – Three right MI were recorded that belong to the common Ordovician and Silurian polychaetaspid genus *Oeononites*. All specimens are considered to belonging to the same species and their morphology, with a distinct club-shaped ramus at mid-length, make them closely similar to *O. curvidens* Hinde, the type species of the genus (see also Eriksson, 1997). This species or groups of closely related ones are common in Silurian strata from Baltoscandia (e.g. Eriksson 1997; Hints 1998). Because of the preservation of the Eramosa specimens and because they are partly concealed by matrix, they are tentatively assigned to *O. curvidens*.

Material – Three specimens (right MI) preserved on bedding plane surfaces.

Occurrence – The Wenlock Eramosa Lagerstätte, Wiarion (Fig. 2).

5. Palaeoecology

It has been suggested that fossil jawed polychaetes were facies controlled, i.e., their distribution were restricted by bathymetry and/or substrate (e.g. Eriksson et al., 2004; Whittle et al., 2008). They were pro-

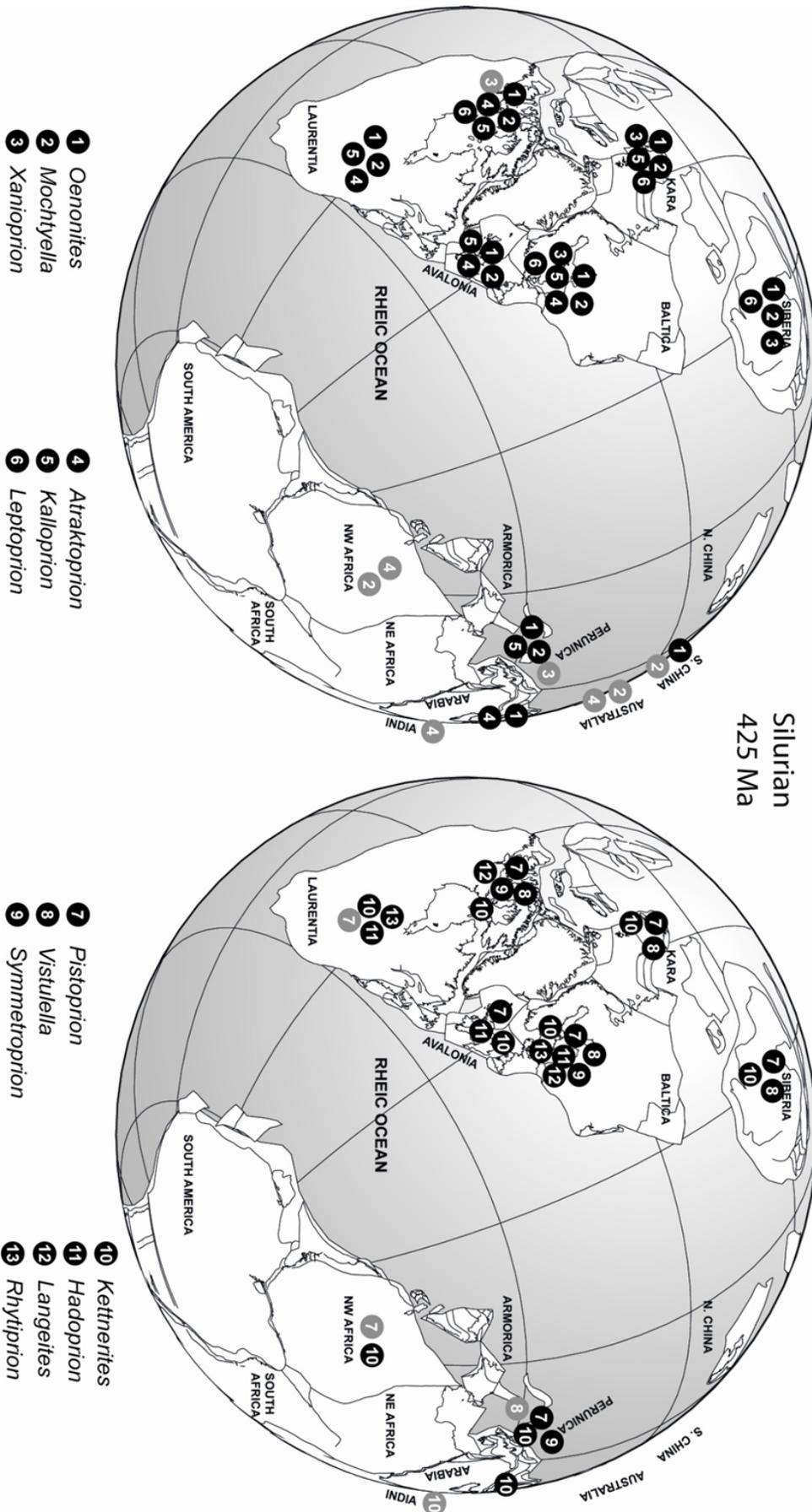


Fig. 6. Palaeogeographic map showing the distribution of the most common genera during the Silurian (reproduced from Eriksson et al. in press).

bably restricted also by other factors, such as temperature, oxygen, salinity, turbidity and access of nutrients, all of which can more or less be related to depth (Bergman 1989; Eriksson et al., 2004).

It appears that some taxa were restricted to one specific type of sediment (stenotopic), whereas others seem to have been able to adapt and can be abundant in many different type of facies (eurytopic) (Bergman, 1989; Eriksson et al., 2004). There also seems to be a connection between the abundance and diversity of scolecodonts with proximity to the paleo-shoreline (Bergman, 1989; Eriksson et al., 2004; Whittle et al., 2008). The faunas in the deep water is often of lower diversity and can only support smaller faunas while the environments in the shallower parts are better suited for supporting richer faunas and greater abundance (Hints, 2000; Eriksson et al., 2004). On Gotland the faunas with the highest diversity and abundance inhabited the bottoms at lagoons and restricted environments where the water energy was low which offered the optimal conditions for paulinitid polychaetes (Bergman, 1989).

The ecology at Eramosa is differing depending on which of the localities that are examined (von Bitter & Purnell 2009). In the northern part (Wiarton) there are many fossils, especially the remains of rare fishes and the conodont *Wurmiella excavata*, that indicate a good water circulation in an open marine environment (von Bitter & Purnell, 2009). The diverse and abundant Biota 3 of von Bitter et al. (2007) was found in this environment. All bedding-plane scolecodonts described herein were recovered from Biota 3 at Wiarton.

The new species described in this report (*Kettnerites* sp. a) comes from Biota 1 and is found at the southern locality Park Head (Fig. 2). This biota is characterized by many different fossils, including scolecodonts. The fossil record suggests a non-marine to brackish water with a broad range of salinities (von Bitter & Purnell, 2009), where the brackish water could be an explanation to the relatively lower diversity compared to that of Biota 3.

The middle location (Hepworth) is also interpreted as an open marine environment, and again dominated by *Wurmiella excavata*, however, the other conodonts found at this locality gives some other indications about the environments (von Bitter & Purnell, 2009). At this locality it is still open marine environment but the circulation seems to slow down and the marine water seems to diminish (von Bitter & Purnell, 2009). So far, no scolecodonts have been recorded from Biota 2 of this part of the Eramosa Lagerstätte.

6. Palaeobiogeography

The data on Silurian scolecodonts have a relatively good geographical coverage and those fossils have been found on every present-day continent except for Antarctica (Eriksson et al. 2004). Even if scolecodonts are found on almost every continent, their state of pre-

servation, diversity and the abundance differ considerably. Relatively large collections of Silurian scolecodonts are known from several regions e.g., Estonia, Sweden, North America, the British Isles and Arctic Russia (Severnaya Zemlya) but in Gondwana and peripheral areas the data available are very limited (Eriksson et al., 2004; Hints & Eriksson, 2009). The latest Llandovery through Ludlow succession of Gotland, Sweden, is so far the area where most detailed studies of Silurian scolecodonts have been made, starting with the work by Hinde (1882) (Eriksson et al., 2004; in press). The number of species on Gotland alone is estimated to exceed 100 and they belong to no less than 28 genera (Eriksson et al., 2004).

The Silurian polychaete faunas are largely dominated by the same genera as those that dominated the late Ordovician faunas (e.g., *Kettnerites*, *Oenonites*, *Mochytella*), although some taxa have only been found in the Silurian (Hints & Eriksson, 2007; Eriksson et al., in press).

The finding of the polychaete fauna in the Eramosa Lagerstätte confirms the present view and understanding of the palaeobiogeography. The polychaete genera found in this Lagerstätte, *Kettnerites* and *Oenonites*, are previously known from other places in North America and several other locations worldwide (Fig. 6). Their presence in the Eramosa Lagerstätte is a further testament to their status as some of the most common faunal elements in Silurian polychaete assemblages.

7. Jaw moulting

Eunicidan polychaetes have two different parts of the jaw apparatus. The two ventral elements are called mandibles and the dorsal apparatus is composed of maxillae (Kielen-Jeworowksa, 1966; Bergman, 1989; Paxton & Safarik, 2008). Nowadays most scientists believe that the mandibles grow continuously throughout the lifetime of the animal, whereas the maxillae, instead were moulted or replaced (Paxton & Safarik, 2008).

Studies on jaw moulting are far from complete and detailed analyses have only been done for a few taxa. It is still not yet determined if all polychaetes, and particularly the fossil ones, replaced or moulted their maxillae since the evidence is difficult to verify (Bergman, 1989). Moreover the number and timing of moulting is still being studied, since it is not yet clear if they only changed their jaws one time during their lifetime or if it coincides with seasons or growth of the body (Bergman, 1989; Paxton & Safarik, 2008). In the report by Paxton & Safarik (2008) they found six moult stages, named larva, juvenile and four type of adult (A, B, C and D), in the extant species *Diopatra aciculata*. Paxton & Safarik (2008) also noted that the late adult stages might not even shed their jaws at all. Before the report by Paxton (2006) there had only been one report of ongoing moulting or replacement by Ehlers (1868), who observed a specimen of *Eunice*

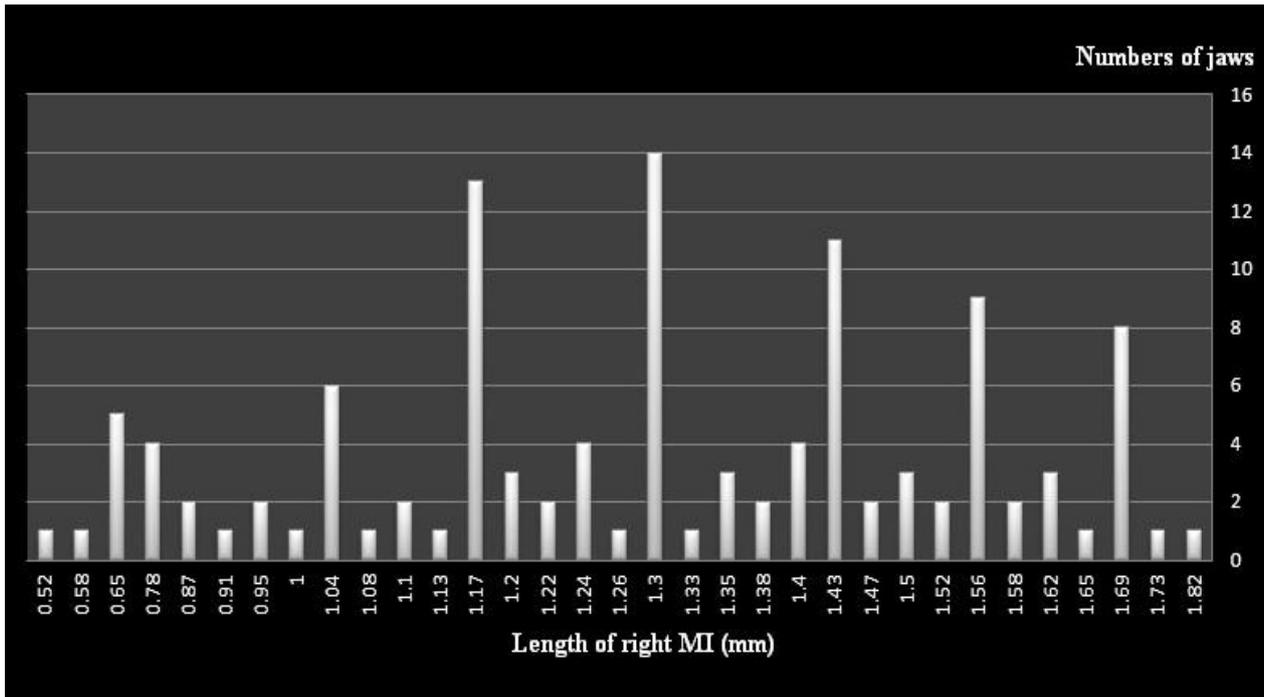


Fig. 7. Histogram showing the size-frequency distribution of 117 right MI of *Kettnerites* sp.a from the Eramosa Lagerstätte (all specimens from Park Head).

harassii with fully formed jaws which were white and soft. Ehlers (1868) concluded that the animal was in the process of moulting its jaw to adult maxillae, where the old jaws were lost and the new ones were not yet sclerotized (Paxton, 2006). Paxton (2006) was able to study the ongoing moulting process of *Dioptatra aciculata*. Mierzejewski (1978) discussed the different lines of indirect evidence for jaw moulting, and gave one possible explanation that the new jaws were developed inside the myocoele opening. These jaw-in-jaw structures, where the old jaws detach and indicate moulting, have been found in fossil records (Mierzejewski, 1978; Bergman, 1989; Paxton, 2006).

In this study 117 right MI were measured in order to examine the possibility of jaw moulting. The results are shown in Fig. 7, and show no obvious trends or evidence of jaw moulting.

While I did not find any connection that could be described as evidence of jaw moulting, it is still too early to rule out that possibility. The results are moreover somewhat ambiguous as the measuring scale may have been too crude for such an analysis. I only had a scale for each .13 millimeters which makes the readings in between less reliable (and extrapolated) which also probably resulted in the artificial peaks in Fig. 7. Another problem with these kinds of measurements is to get precisely the same measuring angle for each specimen.

It is however noteworthy that Bergman (1989) performed a similar analysis on specimens of *Kettnerites* (*K.*) *bankvaetensis* from the Silurian of Gotland and he did not either find evidence for size frequency classes.

My results do not coincide with the result of Paxton & Safarik (2008). In their study they found a

relationship between the length of the MI and six different moulting stages (Larva, Juvenile, Adult A, Adult B, Adult C, Adult D). Looking at Fig. 7 there are six large peaks, however, there is no connection between the peaks and different stages. Based on the morphology of the herein measured elements of *Kettnerites* sp. a, they are all adult/subadult (Paxton & Eriksson, submitted) which also makes comparisons to the results of Paxton & Safarik (2008) somewhat difficult.

8. Discussion and conclusions

The polychaetes' ecological differentiation on Gotland has been studied by Bergman (1989) and Eriksson et al. (2004), and they concluded that shallower environments housed the most diverse and abundant polychaete faunas. As noted above the northern part (Wiarthon) of the Eramosa Lagerstätte was described by von Bitter & Purnell (2009) as a deeper water segment. From this part of the lagerstätte the most diverse polychaete fauna was found, whereas the shallower, almost lagoonal environments in the southern part (von Bitter et al., 2007) contained a monospecific but abundant fauna. Biota 2 from locality B and C (Hepworth) (Fig. 2) surprisingly contains no scolecodonts, even if this part of the lagerstätte is described as representing a shallow marine environment by Purnell & von Bitter (2009). Thus, one would expect these localities to yield at least some scolecodonts. Why they are absent is not entirely clear. It would however be interesting to examine why they are missing in a zone where they should be as most diverse. One explanation could be that these localities are not yet sampled and examined in enough detail.

The fossil record is continuously being updated with newly recorded taxa. The fossil record would not be as diverse and well understood if it would not have been for the Konservat-Lagerstätten found all over the world and from different geological ages (e.g. Kluessendorf, 1994; von Bitter et al., 2007; Young et al., 2007; Briggs & Bartels, 2010). Organisms with hard parts are favored in the fossil record, whereas soft-bodied organisms are often rapidly decayed and impossible to trace in normal successions (Kluessendorf, 1994; von Bitter et al., 2007). Therefore the special type of preservation in Lagerstätten makes them so valuable for our understanding of the fossil record; in Lagerstätten soft-bodied organisms can be found and identified (Kluessendorf, 1994; von Bitter et al., 2007; Young et al., 2007). Lagerstätten can also be useful to better understand the ecology and biodiversity at a particular time, as well as the understanding of the origin and evolution of many species which would otherwise remain limited (Kluessendorf, 1994; von Bitter et al., 2007; Briggs & Bartels, 2010). Scolecodonts and other remains of polychaete worms are common faunal elements in the Eramosa Lagerstätte, just as they have proven to be in many other Silurian Lagerstätten around the world (Kluessendorf, 1994). This study increases our understanding of the Eramosa Lagerstätte and its fauna, with particular focus on the polychaete fauna. The search for more Lagerstätten continues, all in order to better understand fossil organisms and life in ancient times.

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