

Eramosa Lagerstätte—Exceptionally preserved soft-bodied biotas with shallow-marine shelly and bioturbating organisms (Silurian, Ontario, Canada)

Peter H. von Bitter* Department of Natural History, Royal Ontario Museum and Department of Geology, University of Toronto, Toronto, Ontario M5S 2C6, Canada

Mark A. Purnell Department of Geology, University of Leicester, Leicester LE1 7RH, UK

Denis K. Tetreault Department of Earth and Environmental Sciences, University of Windsor, Windsor, Ontario N9B 3P4, Canada

Christopher A. Stott Department of Earth Sciences, University of Western Ontario, London, Ontario N6A 5B7, Canada

ABSTRACT

The middle Silurian Eramosa Lagerstätte of Ontario, Canada, preserves taxonomically and taphonomically diverse biotas including articulated conodont skeletons and heterostracan fish, annelids and arthropods with soft body parts, and a diverse marine flora. Soft tissues are preserved as calcium phosphate and carbon films, the latter possibly stabilized by early diagenetic sulfurization. It is significant that the biotas also include a decalcified, autochthonous shelly marine fauna, and trace fossils. This association of exceptionally preserved and more typical fossils distinguishes the Eramosa from other Silurian shallow-marine Lagerstätten, such as the Waukesha Lagerstätte, and suggests that the Eramosa is not the product of exceptional preservation in an atypical environment, a bias claimed for many post-Cambrian Lagerstätten. The Eramosa Lagerstätte may provide a more reliable, balanced measure of what has been lost from the Silurian fossil record.

Keywords: Eramosa Lagerstätte, soft-bodied preservation, conodont and heterostracan vertebrates, shelly marine fauna, trace fossils, middle Silurian, Ontario, Canada.

INTRODUCTION

Konservat Lagerstätten preserve fossil skeletons and soft tissue remains that normally disarticulate and decay. Consequently, they are of fundamental importance in (1) providing a record of the diversity of organisms of which we would otherwise be ignorant (e.g., >86% of genera in the Phyllopod Bed of the Burgess Shale; Conway Morris, 1986); (2) providing our only direct means of assessing the degree to which the fossil record of biodiversity is biased by the loss of nonbiomineralized organisms and tissues (Briggs, 2003); and (3) revealing the existence of organisms with unique character combinations, without which our understanding of the origins and evolution of major metazoan groups would remain significantly limited.

Exceptionally preserved biotas of Cambrian age have received particular attention, partly because of their significance in understanding the Cambrian explosion, but also because they are statistically overabundant (Allison and Briggs, 1993). Most Cambrian Lagerstätten preserve soft-bodied organisms as flattened carbon films (Burgess Shale-type preservation; Butterfield, 1995), with more labile tissues replicated by authigenic minerals (Orr et al., 1998; Gabbott et al., 2004), and their reduced post-Cambrian frequency has been attributed to an increase in the amount and depth of bio-

turbation, leading to changes in sediment properties and increased rates of decay (Plotnick, 1986; Orr et al., 2003).

Very few exceptionally preserved biotas of Silurian age were previously known (Allison and Briggs, 1993), but they are being increasingly reported (e.g., Briggs et al., 1996), especially from North America (Kluessendorf, 1994; Kluessendorf et al., 1999). The North American reports led Mikulic and Kluessendorf (2001) to characterize post-Cambrian Konservat Lagerstätten as forming in atypical marine environments, with Silurian deposits in North America containing few shelly taxa and lacking evidence of bioturbation.

The nature and atypical biotic composition of previously described shallow-marine Silurian Lagerstätten emphasize a major concern with using Konservat Lagerstätten to understand bias in the fossil record of biodiversity: if exceptional preservation requires exceptional conditions, to what degree do Konservat-Lagerstätten preserve contemporaneous biodiversity (Conway Morris, 1985)? Using them to understand the degree to which shelly faunas are unrepresentative could simply substitute one type of bias (taphonomic) for another (ecological).

We report a 425-m.y.-old Silurian Konservat-Lagerstätte from the Bruce Peninsula, Ontario, Canada (Fig. 1), that contains exceptionally preserved marine vertebrates, invertebrates, and plants associated with shelly biotas, and evidence of bioturbation.

ERAMOSALAGERSTÄTTE

The Eramosa Lagerstätte occurs in a 16 km outcrop belt of the upper Eramosa Formation (Brett et al., 1995), an ~15-m-thick middle Silurian (Wenlock) formation (Stott et al., 2001) interpreted by Armstrong (1993) as the lagoonal marine facies of the more massive, reefal Guelph Formation. Exceptional preservation is confined to an ~7–9-m-thick alternating dolostone, limestone, and bituminous shale sequence, the Interbedded Unit of Armstrong and Meadows (1988), recognized only on the Bruce Peninsula. The Lagerstätte, first identified and investigated by Tetreault (2001a), contains three biotas (Table 1) from different but laterally intergrading environments.

Biota 1

A complete articulated skeleton of a tolypelepid heterostracan preserves the first recorded traces of heterostracan soft-tissue remains as carbonaceous films associated with the calcium phosphate of the skeletal plates (Fig. 2A); previously, articulated Silurian heterostracans were known only from a single locality (Soehn and Wilson, 1990). Corvaspid heterostracan dermal elements are common; those of tolypelepid are rare. All fish remains fluoresce yellow-green under ultraviolet light. Scolecodonts and eurypterid molts occur as carbonaceous remains, leperditiid ostracodes as compressed valves of calcium carbonate, and beyrichiid ostracodes as three-dimensional internal calcite molds (Table 1).

Biota 1 occurs only at locality A (Fig. 1), in thin- to medium-bedded, shaly-weathering, gray microcrystalline limestone. Stenohaline organisms and evidence of bioturbation are absent. The organisms present are known to be tolerant of a broad range of salinities, occurring in nonmarine and transitional marine-terrestrial settings, and we interpret Biota 1 to have occupied the shallowest, most restricted of the Eramosa environments. The absence of indicators of hypersalinity suggests a stable, hyposaline body of standing water, such as a lake or a brackish nearshore marine environment.

Evidence of early authigenic mineralization of organic soft tissues is lacking. Energy dispersive X-ray analysis (EDX) of the exceptionally

*E-mails: peterv@rom.on.ca; mark.purnell@leicester.ac.uk; deniskt@uwindsor.ca; castott@uwo.ca.

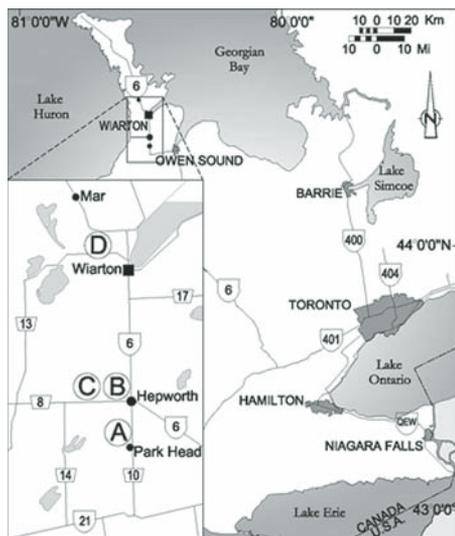


Figure 1. Location of biotas in the Eramosa Lagerstätte in town of South Bruce Peninsula (Bruce County, Ontario, Canada). **A:** Locality A (Park Head)—Biota 1. **B, C:** Localities B and C (Hepworth and 2.6 km west of Hepworth, respectively)—Biota 2. **D:** Locality D (Warton)—Biota 3.

preserved heterostracan organic traces and the eurypterid remains reveals that they are composed primarily of carbon and sulfur. Recent work suggests that such preservation was probably by in situ polymerization (e.g., Gupta et al., 2006), in this case possibly enhanced by diagenetic sulfurization. The latter taphonomic process, by which relatively labile organic molecules are preserved over geological time scales, may be more widespread than previously realized (e.g., McNamara et al., 2006).

Biota 2

Biota 2 (Table 1) is dominated by jawless vertebrates in the form of articulated conodont skeletons (von Bitter and Purnell, 2005) (Figs. 2B, 2C), many preserving remains of conodont eyes (Figs. 2C, 2D). The several hundred skeletons recovered, comprising at least seven taxa, are the most abundant and diverse assemblage of articulated conodont skeletons known, quadrupling the number known from the Silurian. Conodonts preserving remains of soft tissues were previously limited to three genera from three localities (Briggs et al., 1983; Mikulic et al., 1985a, 1985b; Aldridge et al., 1993; Aldridge and Theron, 1993; Gabbott et al., 1995). The Eramosa Lagerstätte adds two additional genera, with potential for more. Conodont soft tissue reported by Zhuravlev et al. (2006) cannot be verified, and the association of dispersed conodont elements and wrinkled “integument-like material” illustrated by Liu et al. (2006, p. 971; their Figs. 2D and 3) are most likely fecal remains.

Biota 2 occurs at localities B and C (Fig. 1) in laminated, brown, organic-rich calcareous shale,

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. confluens</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-spired gastropods, and tabulate corals. Algae: thallophytes, carbonaceous films rare; prasinophytes common. Trace fossils: <i>Chondrites</i> burrows.
3U	Annelids: articulated and disarticulated eunicid polychaete jaws common. Algae: thallophytes and dasyclads common.
3M	Arthropods: eurypterids and scorpions (Waddington and Jeram, 1997).
3L	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 apheroditid-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.

L, M, and U are Lower, Middle, and Upper Interbedded Unit.

and in the nodular, dolomitized, micritic limestone with which it alternates (von Bitter and Purnell, 2005). An ~1-cm-thick, heavily bioturbated bed of *Chondrites* burrows is present immediately above that containing the conodont skeletons at locality B. The composition of the fauna and the presence of articulated remains suggest that Biota 2 lived in a protected, quiet water, marine environment. The relative abundances of *Ozarkodina excavata* and *Ctenognathodus* cf. *murchisoni* at localities B and C, respectively, suggests more open marine conditions at locality B, with shallower, possibly slightly more restricted marine conditions at locality C (Fig. 1) (Aldridge and Jeppsson, 1999). The changes in biota indicate an environmental gradient between localities A–C.

As in Biota 1, evidence for early authigenic mineralization of soft tissue is lacking. Organic tissue of conodonts, graptolites, algae, and eurypterids is preserved as carbonaceous films. EDX analysis of conodont eye traces reveals the presence of carbon and sulfur (Figs. 2C, 2D), suggesting that preservation may have involved early diagenetic sulfurization, possibly of melamins, the complex biopolymer composition of which may have rendered them resistant to bacterial degradation.

Biota 3

Biota 3 (Table 1) contains a remarkable soft-bodied marine fauna on dolostone bedding planes at locality D (Tetreault, 2001a). It includes lobopodians preserving possible color banding (Figs. 2E, 2F), phosphatized polychaetes (Fig. 2G), possible annelids of *Myoscolex*-like form (Figs. 2H, 2I), branchiopod or remipede-

like arthropods (Fig. 2J), and a uniquely diverse marine flora (Tetreault and LoDuca, 2005).

Preservationally and taxonomically, this is the most diverse of the three biotas; it includes original phosphatic tissue (conodont skeletons, possible fish remains, *Sphenothallus*, conularids, and inarticulate brachiopods), early authigenic phosphate mineralization (soft tissues of phyllocarids, xiphosurans, enigmatic polychaetes [some with phosphatized muscle fibers, and yellow-green fluorescing setae], and lobopodians), and carbonaceous films (lightly sclerotized cuticle and apparently refractory soft tissues of eurypterids, scorpions, conodonts, scolecodonts, and algae). An autochthonous shelly marine fauna (Table 1), including articulated brachiopods, trilobites, ophiuroids, crinoids, and echinoids (whole and in life position; Tetreault, 2001b), occurs on many of the same bedding planes as the exceptionally preserved biota. The shelly fauna, originally mostly calcareous, has undergone decalcification; significant silicification, possibly following decalcification, particularly affected rhynchonellid brachiopods and crinoid remains. The siliceous spicules of articulated choiid demosponges are now desilicified. The sequence contains many bioturbated and burrowed horizons.

The mixture of preservational styles in Biota 3 indicates a complex taphonomic history. In the lower Interbedded Unit, phosphatized soft tissues retain a degree of three dimensionality, indicating that some decay-induced collapse, but not complete flattening of the organisms, had occurred at the time of mineralization. Other instances, such as the preservation of conodont eye traces, indicate that most of the body had decayed away

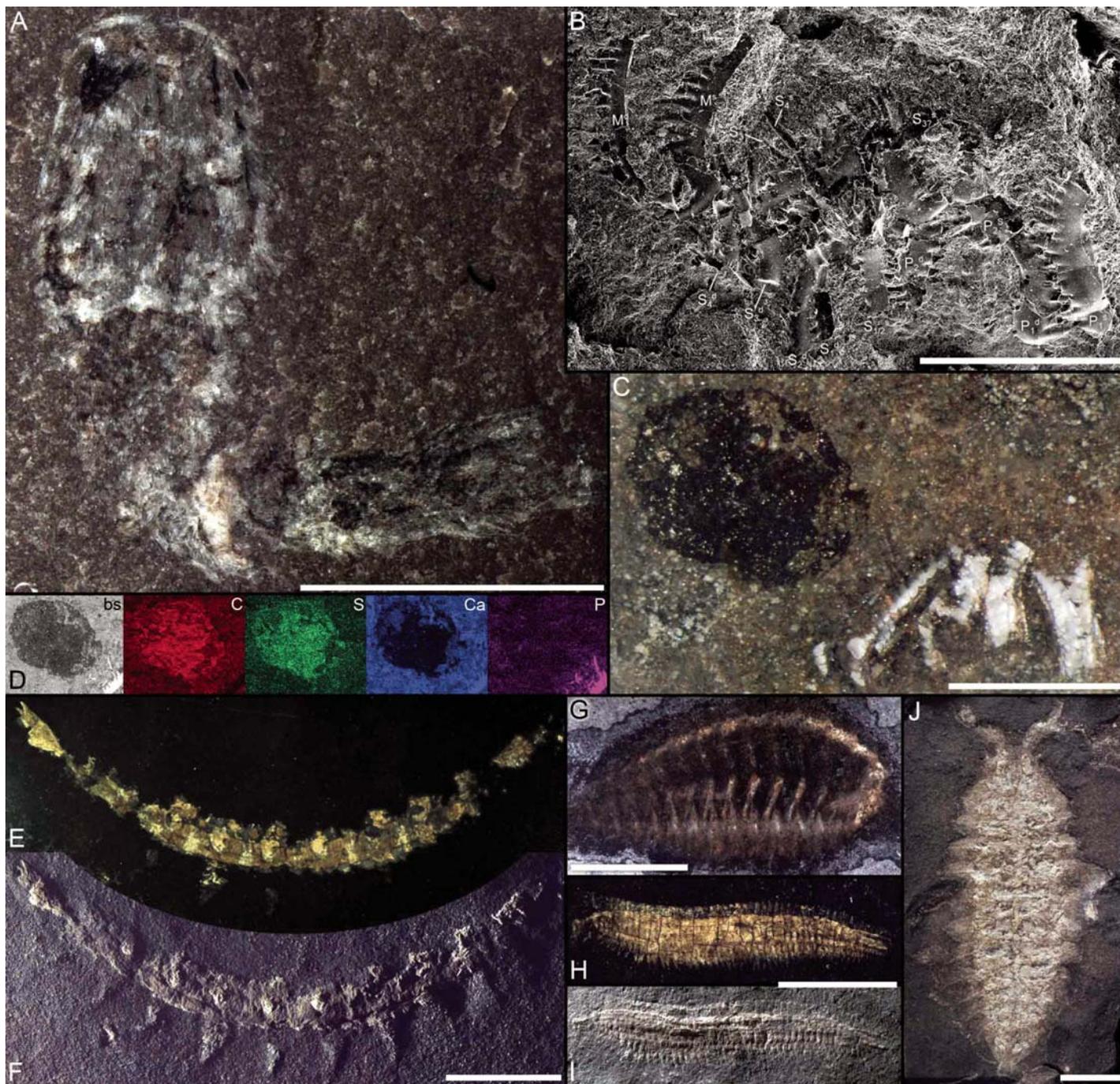


Figure 2. A: Tolyepepid heterostracan; articulated skeleton of original calcium phosphate. Soft-tissue traces are preserved as carbon and sulfur (evident as dark patches within outlines of skeleton). Biota 1, locality A, ROMV 56092. B, C: Articulated conodont skeletons of *Ozarkodina excavata* preserved as original calcium phosphate. Biota 2, locality B, ROMP 57892 and 57890. Conodont elements are labeled (in B); black circular conodont eye traces are shown (in C). D: Backscattered electron micrograph (bs) and energy dispersive X-ray analysis maps (carbon, sulfur, calcium, and phosphorus) of eye traces (shown in C), indicating the preservation of soft-tissue remains in carbon and sulfur. E, F: Lobopodian; phosphatized, with possible original color banding (ROMP 57893). G: Aphroditid-like polychaete with phosphatized muscle tissue (ROMP 57894). H, I: Possible annelid of *Myoscolex*-like form (ROMP 57980). J: Branchiopod or remipede-like arthropod with large, grasping, anterior appendages; phosphatized (ROMP 57891). E–J are Biota 3, locality D. Scale bars: B and C = 1 mm; A, D–J = 10 mm. A, C, E, G, and H are imaged with cross-polarized incident light: A is under water, others are under glycerol; B, scanning electron micrograph; F and I, low-angle incident light.

before stabilization of the remaining soft tissues, possibly through sulfurization. In the middle and upper Interbedded Unit, only originally sclerotized tissues, such as cuticle, scolecodonts, and algae, are preserved as carbonaceous remains, indicating much higher levels of decay.

SIGNIFICANCE OF THE ERAMOSALAGERSTÄTTE

The Eramosa Lagerstätte contains exceptionally and diversely preserved Silurian organisms in a unit that transects several intergrading environments: lacustrine to marginally marine

environments in the south (locality A), to fully marine conditions in the north (locality D). It is most similar to the slightly older (Llandovery) Waukesha Lagerstätte (Mikulic et al., 1985a, 1985b), with which it shares exceptionally preserved arthropods, including branchiopod

or remipede-like forms (Fig. 2J), xiphosurans (Moore et al., 2005), phyllocarid crustaceans, and lobopodians (Wilson et al., 2004). It differs, however, in possessing articulated heterostracans (Fig. 2A) and abundant and diverse conodont skeletons (Figs. 2B, 2C), with soft parts preserved as carbonaceous films, a variety of polychaete worms, eurypterids, marine scorpions, and a well-preserved marine flora (Tetreault and LoDuca, 2005). The Eramosa Lagerstätte also contains an autochthonous shelly marine fauna, as well as evidence of bioturbation. It is this mixture of diverse and exceptionally preserved organisms with a more typical marine fauna that distinguishes the Eramosa from other shallow-marine Silurian Lagerstätten, and suggests that the Eramosa Lagerstätte is not simply the product of an atypical environment. Biota 3, in particular, may provide a more reliable, less biased view of what has been lost from the post-Cambrian, and specifically from the Silurian, fossil record.

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