Reports

A Silurian Soft-Bodied Biota

Abstract. *A new Silurian (Llandoverian) biota from Wisconsin with a significant soft-bodied and lightly sclerotized component is dominated by arthropods and worms. The fauna includes the earliest well-preserved xiphosure, a possible marine uniramian, three new arthropods of uncertain affinity, and possibly the first Paleozoic leech. This may be only the second locality to yield a conodont animal. Lack of a normal shelly fauna suggests an unusual environment. The discovery adds significantly to the few such exceptionally preserved faunas known from Lower Paleozoic rocks.*

Occurrences of soft-bodied organisms are of great importance in a fossil record overwhelmingly dominated by mineralized skeletal remains. Such *Konservat Lagerstätten* (*1*) are the only evidence suggesting the true biotic diversity of ancient environments, the history of taxa with low fossilization potentials, and the nature of soft and lightly sclerotized tissue of shelly forms. Few *Lagerstätten* are known from the 100-million-year interval between the famous Middle Cambrian Burgess shale of British Columbia (*2*) and the Lower Devonian *Hunsrückschiefer* of West Germany (*3*). A new biota from the lower Silurian of Waukesha County, near Milwaukee, helps to fill this interval.

The Waukesha biota comes from a unique depositional environment represented by basal Brandon Bridge strata (*4*) in finely laminated argillaceous dolomite found at only one locality. These rocks are dated as latest Llandoverian on the basis of the graptolite *Monograptus spiralis*; late Llandoverian to early Wenlockian conodonts occur in the uppermost Brandon Bridge (*5*). The occurrence of the trilobite *Stenopareia* indicates that the Brandon Bridge is no younger than early Wenlockian.

Strata containing soft-bodied fossils are found only where the Brandon Bridge wedges out against an 8-m-high scarp of cherty dolomite (Fig. 1). North of this scarp Brandon Bridge is absent; to the south the cherty dolomite is absent. Thus distribution of the Waukesha biota appears to be strictly controlled by depositional and preservational processes related to the environment of the scarp.

The fauna is dominated by arthropods. The most numerous and diverse are trilobites, which lack soft parts; a dalmanitid dominates the 13 genera. All three other major arthropod groups—crustaceans, chelicerates, and uniramians—are represented by lightly sclerotized forms. New arthropods, which can be assigned to these groups only tentatively, if at all, are also present. There are at least four worm taxa. Ostracodes, graptolites, and conulariids are common in places. Algae, ?hydroids, monaxonid sponges, nautiloids, and brachiopods are rare. Microfauna includes conodont elements (including coniform fused clusters) (*6*) and foraminiferans.

The shelly fossils are decalcified and slightly compacted. The soft-bodied and lightly sclerotized taxa are flattened except where infilled by diagenetic fluorapatite. Cuticle sculpture is unusually well preserved in most specimens of worms and phyllocarids; hexagonal lenses of compound eyes are occasionally evident. Predominantly articulated trilobites and the absence of any fossil alignment or variation in orientation in bedding suggest gentle transport.

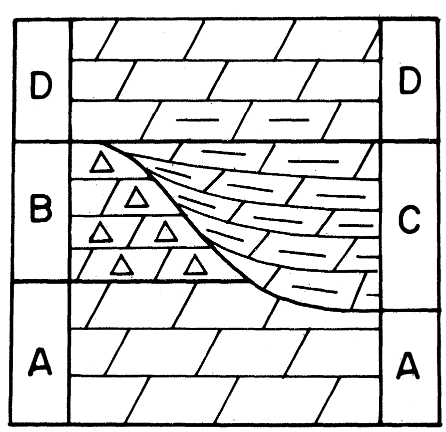

Fig. 1. Diagram showing stratigraphic relation between the lower Silurian Brandon Bridge and adjacent Silurian units. (A) Kankakee Formation; (B) unnamed cherty dolomite; (C) Brandon Bridge strata; and (D) Waukesha Dolomite. Soft-bodied biota occurs only where Brandon Bridge (C) wedges out against cherty dolomite (B). Vertical scale approximately, 15 m; horizontal scale, 100 m.

Crustaceans include phyllocarids and a leperditicopid ostracode. The earliest example of the Order Concavicarida, an enigmatic group that may comprise crustaceans, is also present. The separate status of these arthropods was recognized only recently; the previously oldest known example is from the early Devonian (Emsian) of Czechoslovakia (*7*). Our material shows at least three of the raptorial appendages, which are otherwise known only from genera in the Jurassic of Italy and France (*8*). This Silurian occurrence extends the temporal range of the group by about 40 million years.

The fauna includes what may be the earliest completely preserved xiphosuran chelicerate (Fig. 2A), which is only the second known Paleozoic example showing evidence of limb morphology (*9*). The semicircular prosoma has pronounced radiating ridges in the interophthalmic area. One specimen shows traces of six pairs of prosomal limbs; the tip of the sixth appears to bear a chela, the first known documentation of this feature in the group. This arthropod bears some similarity to the poorly known *Bunaia woodwardi* from the Silurian Bertie Waterlime of New York, but appears to be a new Synziphosurine (*10*).

With the possible exception of *Aysheaia* from the Middle Cambrian (*11*), the oldest uniramians are latest Silurian myriapods of the Scottish Old Red Sandstone (*12*). Although myriapods are terrestrial, it is widely assumed that they originated in water. Thus a myriapod-like animal (Fig. 2B) in our material is particularly interesting. The animal has a distinct head bearing ?eyes and at least three limbs, a trunk of about 11 limb-bearing divisions, and a terminal telson with a posteriorly projecting ventral process. Each trunk division appears to consist of two sections, the longer appendage-bearing, the shorter not; they resemble diplosegments although each bears only one pair of limbs. The limbs are jointed, have an expanded base, and taper distally; there is no evidence that they are biramous. This animal may represent a new class of marine uniramians.

The affinities of the other new arthropods in the fauna are more problematic. The most common lightly sclerotized taxon (Fig. 2C) is elongate and wormlike, with an anterior head shield and 30 to 40 trunk tergites. A large compound eye and at least one antenna-like appendage project anteriorly beyond the head shield. The head also bears two pairs of long segmented limbs. The poorly known trunk limbs are short lobe-like structures. This arthropod bears some resemblance to the Kazacharthra, an extinct order of branchiopod crustaceans known only from the Jurassic (*13*).

The best preserved arthropod (Fig. 2D) has large compound eyes overlying a massive head appendage, which may have been adapted to seize prey. Other head appendages may have existed but are not clearly preserved. The trunk has about 11 somites in most specimens, increasing to 30 in rare individuals more than 80 mm long. Each somite bears a pair of apparently biramous appendages with a slender segmented inner branch and a long flap-like outer branch. The trunk ends in a short apodal unit of fused somites ending in spines. This animal shows some similarity to two groups of crustaceans, the anostracan branchiopods and the new class Remipedia. No substantiated pre-Tertiary anostracans are known, but the earliest well-documented branchiopod is the tiny *Lepidocaris* (Order Lipostraca) from the Lower Devonian Rhynie Chert of Scotland (*13*). Carboniferous insect nymphs have been mistaken for anostracans, but any similarity to a nymph is superficial in this case (*14*). The Remipedia have no proven fossil record; the possibility of a relation with the problematic Pennsylvanian arthropod *Tesnusocaris* is equivocal (*15*). The affinities of this Waukesha arthropod are uncertain.

The most problematic member of the fauna is poorly preserved (Fig. 2E). Large, laterally extending, slightly convex structures may represent a bivalved carapace. Small specimens (10 to 20 mm long) show an axial line, possibly a hinge, and a pronounced posterior indentation beyond which extends a trunk-like structure of seven to eight divisions. The presumed head region, bearing two large lateral circular structures that may be eyes, tapers anteriorly beyond the "carapace." The carapace displays a characteristic sculpture of striations crisscrossing the "valves"; this pattern may have been exaggerated during diagenetic infilling with fluorapatite. Very large structures similar in pattern and outline to the carapace reach lengths up to 85 mm (parallel to the hinge) and widths of 220 mm but show no trace of the trunk. These may be remnants of exuviae of the same animal. Its affinities are uncertain, but it may be a bizarre phyllocarid-like arthropod.

The most common worm belongs to an assemblage of papillate forms referred to *Protoscolex* and *Palaeoscolex*. These annulate worms, ranging from Lower Cambrian to upper Silurian, form a distinct group that may be a separate class of annelids (*16*).

A larger, rare annulate worm (Fig. 2F) appears to lack papillae, although the cuticle is not preserved. The best specimen terminates in a circular structure at the only end preserved. Setae or other lateral projections are not evident. The circle resembles the suckers of leeches but in the absence of more diagnostic characters any assignment is tentative. Fossil Hirudinea are otherwise known only from the Upper Jurassic of West Germany (*17*). The large size of this worm relative to the rest of the fauna suggests that, if it were a leech, it was more likely predatory than parasitic. Scolecodonts indicate that polychaete worms were present, although their soft tissue has yet to be discovered.

The Waukesha locality yields abundant conodont elements, including a small proportion of fused clusters. One bedding plane assemblage has been discovered, an apparatus of coniform elements referable to *Panderodus*; it is associated with soft parts (Fig. 2G). This may be only the second locality to yield a conodont animal (*18*). At least 11 elements are present, overlapping and partially obscured by sediment; some are obviously paired in position and point in opposite directions, giving the assemblage the appearance of interdigitated fingers of a pair of hands. This may be the first bedding plane apparatus of coniform euconodont elements to be discovered, and the first of any kind from the Silurian. The fluorapatite in which some of the soft parts are preserved does not extend as far as the elements, but the following evidence indicates that both belonged to the same animal: (i) a light-colored reduced area on the reddened shale surface continues from the soft parts to the apparatus, (ii) the soft parts and apparatus share the same axis of symmetry, and (iii) the soft parts are in the expected position posterior to the apparatus and a raised area connects the two. Although no detail is preserved, the animal was elongate and segmented. The specimen is incomplete but traces of about 19 segments are evident.

The debate on conodont affinities centers on whether they are more closely related to chordates or chaetognaths (*18*). The main argument for chaetognath affinity is the structural similarity between their grasping spines and the elements of protoconodonts (Precambrian to Ordovician). It is not certain, however, whether protoconodonts gave rise,

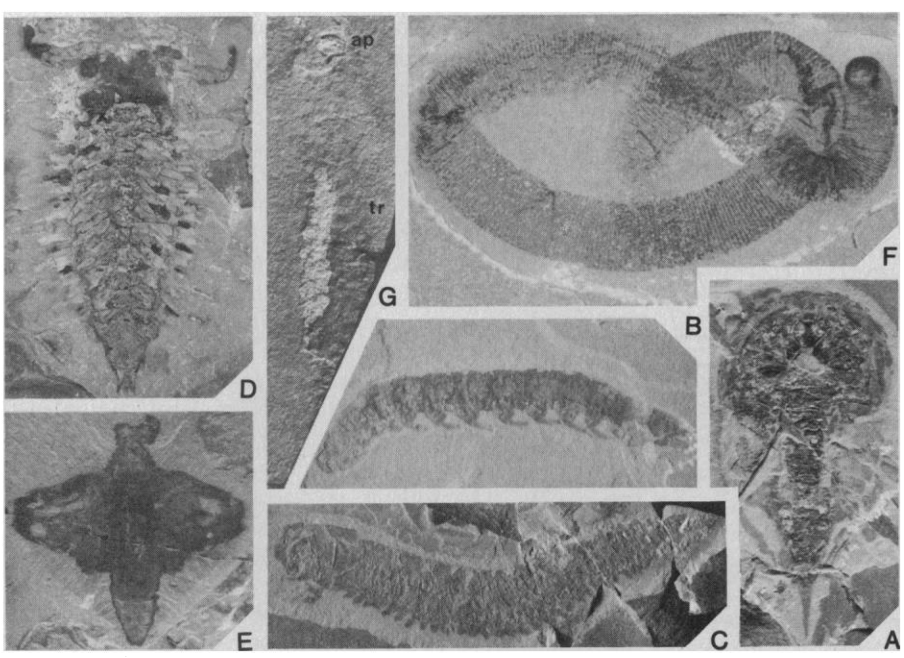

Fig. 2. Representative soft-bodied and lightly sclerotized animals from the lower Silurian Waukesha biota. (A) Xiphosure, dorsal views [University of Wisconsin (UW) specimen 4001/1a] (×0.9). (B) Myriapod-like animal, left lateral view (UW 4001/2a) (×2.1). (C) Wormlike arthropod, left lateral view (UW 4001/3) (×0.9). (D) ?Branchiopod crustacean, ventral view (UW 4001/4) (×2.1). (E) Bizarre phyllocarid-like arthropod, dorsal view (UW 4001/5) (×1.3). (F) ?Leech (UW 4001/6) (×1.2). (G) Conodont animal, dorsal view, showing apparatus (ap) anteriorly and faint transverse segmentation of trunk (tr) (UW 4001/7a) (×4). (All material held by the Geology Museum, University of Wisconsin, Madison.)

through paraconodonts, to euconodonts or "true" conodonts (*19*) such as the Waukesha animal. In addition, there is no structure in chaetognaths equivalent to the segmentation in the fossil. The euconodonts, at least, may be more closely related to the chordates.

In addition to the exceptional preservation of soft-bodied taxa, an important aspect of this biota is the absence or rarity of most shelly groups normally found in Silurian assemblages. Echinoderms, mollusks, brachiopods, bryozoans, and corals are all very rare. Only trilobites are abundant and diverse. These factors suggest that the Waukesha biota represents unusual environmental conditions as well as taphonomic processes. The only comparable *Lagerstätten* from the Silurian occur in the inliers of southern Scotland (*20*), but these are dominated by fish and eurypterids.

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21. We thank E. Reeseman, D. Dewey, R. Hodgins, D. Green, and W. Knuese of Waukesha Lime & Stone Company for permission and aid in collecting and for donating material, much of which was collected by G. Gunderson and R. Meyer, who also discovered some of the taxa; K. Westphal and the Department of Geology at the University of Wisconsin for loan of specimens; C. Klug, S. LoDuca, and S. Mikulic for field assistance; and D. B. Blake and the Field Museum of Natural History for facilities. P. Graham carried out x-ray diffraction analysis. D. B. Blake, S. Conway Morris, and R. L. Langenheim, Jr., reviewed the report. R. J. Aldridge and M. P. Smith discussed the conodont animal. D.E.G.B. was supported by Goldsmiths' College Research Fund, the Royal Society, and the Field Museum Visiting Scientist Program. J.K. was supported in part by a grant-in-aid from Sigma Xi, the Scientific Research Society, and the Department of Geology and Graduate College, University of Illinois.

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Study by Synchrotron Radiation of the Structure of a Working Catalyst at High Temperatures and Pressures

Abstract. *A relation among activity, composition, and structure was determined for a working catalyst by means of a stainless-steel reactor cell of novel design that permitted operation at temperatures and pressures similar to those in industrial reactors. Molybdenum K-edge x-ray absorption spectra were used to probe the structural environment of molybdenum in CoMoS/γ-alumina catalysts while hydrodesulfurization of benzothiophene was proceeding at high temperature and pressure. For catalyst samples with different contents of cobalt, radial structure functions obtained from extended x-ray absorption fine structure data presented the same features as those obtained from the spectra of MoS_2/γ-alumina reference samples. Moreover, Mo–S and Mo–Mo coordination numbers were maximum for the sample with an atomic ratio of Co to (Co + Mo) of 0.33; this sample was also the most active catalyst tested.*

Heterogeneous catalysts are used in the majority of industrial chemical processes, most of which take place at pressures and temperatures far removed from ambient conditions. Catalytic materials are examined by various physical techniques (*1, 2*), including most recently x-ray absorption spectroscopy (*3–5*). In particular, extended x-ray absorption fine structure (EXAFS) has become a useful technique for determining structural parameters (such as interatomic distances and coordination numbers) of supported metal catalysts where the metal is in the form of clusters less than 1 nm in size (*6*). However, most previous studies have been done with the catalyst sample in a nonreactive atmosphere under ambient conditions of pressure and temperature, before and after the chemical reaction took place. The assumption that the catalyst does not change during cooling and depressurization was implicit in the analysis of those results.

The study of a catalyst under realistic reaction conditions in situ has been a long-sought goal in heterogeneous catalysis (*7*). Earlier we observed that the structure of a hydrodesulfurization (HDS) catalyst did not change during reaction (*8*). We now describe catalysts of different composition and measure their rates of reaction.

In view of increasing concerns about the environmental impact of sulfur, perhaps one of the most important catalytic processes in refining oil and synthetic fuels is the HDS of hydrocarbons. The removal of sulfur from oil fractions or coal slurries is accomplished by the reaction of sulfur-containing species with hydrogen gas on molybdenum- or tungsten-based catalysts promoted by cobalt or nickel atoms (*9*). In HDS, the sulfur is removed as H_2S gas. Hydrotreating crude oil is a major process in refining. Removal of sulfur from crude oil is necessary not only because of SO_2 emission restrictions but also because of catalyst poisoning by sulfur compounds in other refinery processes. Because of the continuing depletion of petroleum resources, larger quantities of lower grade, high-sulfur crude oils are reaching the refineries, and the trend is likely to continue. Efforts have been directed toward describing the structure of HDS catalysts so that the relation between structure and HDS activity can be understood.

We have designed a reactor cell in which the absorption of x-rays by HDS catalysts can be measured while the reaction is carried out under pressures and temperatures similar to those in industry (*10*). The x-rays enter the cell through a thin beryllium window and pass through the catalyst before leaving the cell through a second beryllium window. The intensity of the x-ray beam is measured