the host, as in most caligids; this is a modification necessary in the evolutionary transition from slow-moving invertebrate hosts to fast-moving fish (8).

Cladocyclus gardneri, the host fish, is a member of the Ichthyodectidae, an extinct group of primitive teleostean fish ranging from the Upper Jurassic to the uppermost Cretaceous. It is unlikely that the ichthyodectids are phylogenetically related to any of the extant teleostean cohorts (9), so that it is not surprising that Cladocyclus was host to copepods morphologically close to forms (Dichelesthium) now restricted to sturgeons. The fish-bearing horizons of the Santana Formation have been thought to be marine (10), brackish (3), or in part hypersaline (11), but ostracods associated with the two fish under discussion indicate that they, at least, died in fresh waters (5). The superfamily Dichelesthioidea, to which the parasites are related, is exclusively marine. This suggests that Cladocyclus gardneri was euryhaline, acquiring marine parasites at sea and migrating into fresh waters. A recent analog would be salmon, where fishermen recognize fresh-run fish by the presence of sea lice on the gills. As far as we know, this is the first evidence of euryhalinity in any extinct species of fish.

The apparent rarity of fossil free-living copepods is probably mainly due to the fragility of these animals. Most parasitic copepods are much more heavily sclerotized than their free-living relatives, and might fossilize more readily. The association of our specimens with ostracods showing unique preservation of the appendages and soft parts (5) suggests that the occurrence is due to unusual circumstances, but we wish to alert those making acid preparations of fossil fish to the possibility of finding parasitic copepods.

Since it is universally accepted that all parasites evolved from free-living ancestors, the discovery of parasitic copepods in the Lower Cretaceous indicates that free-living copepods were in existence before that time, and greatly lengthens the fossil record of the class Copepoda.

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Silurian Echiuroids: Possible Feeding Traces in the Thorold Sandstone

Abstract. Problematic trace fossils collected from the Middle Silurian Thorold Sandstone bear a striking resemblance to feeding traces made by the proboscises of modern echiuroid worms. Paleoecological approximations of depth and salinity may be possible depending on population densities. Echiuroids may have been a significant element of the Paleozoic benthos.

The Thorold Sandstone is the lowest unit of the Clinton Group (Middle Silurian) found in southwestern Ontario. It is a "massive white to light grey, fine-grained, dense compact quartzose sandstone" (1) ranging in thickness from roughly 1.5 to 4 m. Body fossils are rare in the Thorold; however, the formation does contain a fascinating variety of trace fossils: tracks, burrows, trails, mounds, fecal aggregations, and problematic markings. Several of these markings are described here as having been made by echiuroid worms (phylum Echiuroidea). If correct, this interpretation represents the first description of fossil echiuroid feeding traces, and the oldest occurrence of echiuroids in the fossil record.

Trace fossils reported here were collected at the Jolley Cut, Highway 403 and Sydenham Road sections, in or near Hamilton, Ontario. The best specimens came from scree blocks, and thus assignment of stratigraphic position is impossible.

As exposed on bedding planes, the traces are fan-shaped or bugle-shaped, occurring in imbricated series radiating from a focal area, in which there is often a depression possibly representing a burrow (Fig. 1). The "fan" may be relatively narrow, or may extend almost full circle; in some cases there is symmetrical development on either side of the focus. The half-dozen specimens examined average 5 cm long by 3 cm wide, and range in length from 3 to 7 cm.

In section, there is no three-dimensional nature to the fan-shaped traces, such as would be expected in Arthrophycus or Daedalus (2). X-ray radiographs of several specimens show definite "burrow" structures continuing downward from the focus of the fan. In some well-preserved specimens, these burrows continue down to the bottom of the block on which the feeding traces occur, a maximum distance of 5 to 6 cm. The configuration and maximum depth of the burrows cannot be determined.

The most logical explanation of the Thorold traces is that they are feeding traces left by some protrusible element of a burrowing invertebrate. This protrusible element must have been a single unbranched organ such as a palp or proboscis, rather than a tentacle ring. Very few modern animals meet these specifications. According to Seilacher's (3) classification of trace fossils, traces left by the protrusible element would be pascichnia, or grazing traces, while the central burrows themselves would be domichnia, or more or less permanent shelters.

Live specimens of the echiuroid Listriolobus pelodes Fisher collected from Santa Barbara Channel, off Southern California, by K. Fauchald, were maintained in the original mud at the Santa Catalina Marine Biological Laboratory of the University of Southern California. The bodies of the worms were 4 to 5 cm long by 1 to 2 cm wide; the proboscis length was highly variable. The worms lived about 5 to 6 cm below the surface of the sediment, in "galleries" consisting of large horizontal cavities lined with mucus and having up to four sloping openings to the surface. On the surface of the sediment, the presence of the worms during an inactive phase was indicated by burrow
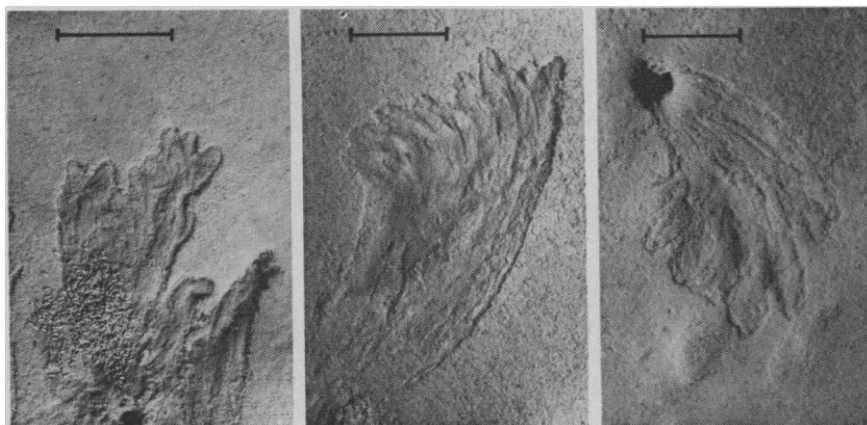
Fig. 1. Possible echiuroid feeding traces preserved in the Thorold Sandstone (Middle Silurian). Probable burrows are located at the apex of each fan-shaped trace. Scale bars, 1 cm.

openings 3 to 4 mm wide and prodigious number of fecal pellets (approximately 2 mm long and 0.5 mm wide). If the animals were left undisturbed for long periods of time, the fecal pellets built up large cones around each opening. When feeding, the proboscis extended over the layers of fecal pellets. In the natural habitat, it is unlikely that such a buildup of fecal pellets would occur. The pellets periodically are expelled forcefully, to heights of at least 3 cm in *Listriolobus* and 4 cm in the related *Echiurus* (4); large fecal cones could build up only in absence of currents.

When I introduced a slurry of mud collected from nearby bottom sediments, feeding activity immediately increased. The proboscis extended from one of the openings a distance of up to 10 cm, or approximately twice the length of the body. Generally the proboscis slid along or very slightly below the sediment-water interface, but sometimes it reared up and waved to and fro in an investigative fashion. After the initial retraction of the proboscis, each successive pass was made

so that it just overlapped a previous mark (Fig. 2). The resulting traces were fanlike, imbricated, of varying width, and sometimes bilaterally symmetrical about the burrow. These traces bear a striking resemblance to those in the Thorold.

Gislén (4) described the proboscis of *Echiurus* as "assuming the form of an unfolding fan" or "a cornet-shaped fan." He mentioned the "food track" produced on the surface of the sediment and attributed this to browsing on the available film of detritus. This food track also resembles the Thorold traces, but not as closely as do the *Listriolobus* ones.

The greatest difficulty with the interpretation of the Thorold traces as feeding tracks made by echiuroid proboscides lies in the lack of large quantities of associated fecal pellets. Some pellets may be present in the fossil traces, but the amount is negligible compared with the capacity of *Listriolobus* or *Echiurus*. It is possible that currents or wave action were sufficiently strong to disperse or break up the pellets; oscillation ripple marks occur at many horizons

in the Thorold. It is also possible that pellets were never produced. Fisher (5) noted that "in the same species from different localities the intestinal pellets vary with the character of the bottom," a phenomenon previously reported by Stephen (6). In the case of animals living on coarse bottoms, it is probable that distinct pellets will not be formed. Fisher (5) mentioned that "a specimen from Los Frailes, Baja California, has the intestine distended with sand not in pellets." The bottom in that area is very coarse sand.

Although there is a marked resemblance between the *Listriolobus pelodes* traces and the Thorold examples, it is improbable that this species made the fossil markings. The Thorold fans are evidently the result of feeding by an echiuroid with a stouter and shorter proboscis, perhaps intermediate between those of *Listriolobus* and *Echiurus*. *Echiurus* feeding traces are much shorter and blunter, and seem to lack the imbricated fan structure.

Similar traces reported from the sand flats of Aldabra atoll in the Indian Ocean (7) were formed by a species of *Arenicola* (the lugworm). These markings were presumably made by the protrusible pharynx, although this is not stated. However, in *Arenicola* the pharynx is relatively short compared to the body length; presumably, such a large, muscular body would leave some visible trace in the sands below. *Arenicola* also produces copious quantities of coiled fecal strings, which are absent from the vicinity of the Thorold traces. Such piles would be washed away only with difficulty.

There is so far no evidence of galleries of the *Listriolobus* type in sections of the Thorold traces; there are several reasons why these may not have been preserved. Echiuroids are not the strongest of burrowers; one of the live specimens of *Listriolobus* was unable to burrow back into the sediment from which it had been removed. *Echiurus* is a better burrower than *Listriolobus*, although it has trouble keeping the burrow from collapsing if the sediment is clean sand. If the burrow continues to collapse, the animal may simply leave (4) and the burrow is not preserved. Even under ideal conditions, the burrow or gallery is larger in diameter than the exit holes, although sometimes angles in the burrows of *Echiurus* become partly blocked by fecal pellets. Feeding in the specimens I observed is always more active immediately after
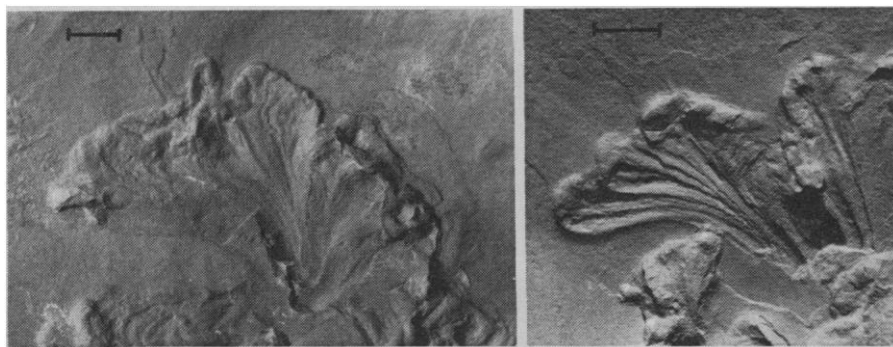

Fig. 2. Feeding traces of *Listriolobus pelodes* Fisher. The burrow and fecal pellets are visible in the photograph at the left. Scale bars, 1 cm.

a fresh fall of sand or mud; this would increase the probability of the proboscis making a recognizable trace on the sediment. If successive sediment falls thick enough to preserve the feeding trace, the animal might be buried and unable to dig itself out. Some echiuroids do not burrow well in soft, newly deposited sediment; influx of a thick layer could either kill them by suffocation or cause them to leave. In either case, because of their restricted openings the burrows would not be filled in by the new sediment, but instead would collapse. The only remnant in the subsurface would be a thin carbonaceous film, evidence of the mucous lining. Several carbonaceous films are present in the Thorold sections, but there are many possible origins aside from collapsed echiuroid burrows. There are also several linear depressions near the feeding traces that may be the result of collapsing burrows.

Echiuroids are exclusively marine, and are found from the intertidal zone (4–6) to more than 10,000 m down in the Philippine Trench (8). Most are burrowing filter feeders (Urechis) or deposit feeders (Listriolobus, Echiurus) with a wide range of body types, while some burrow into shells of other benthic invertebrates. Joysey (9) described possible echiuroid borings in a Cretaceous echinoid test. Most burrowing echiuroids (Listriolobus is an exception) construct U-shaped tubes of varying depths: about 14 inches (35 cm) for Urechis (10) and 50 cm for Echiurus (11).

High population densities of echiuroids are probably characteristic of shelf depths. In the deep sea, the transition from a bathyal to a hadal or ultra-abyssal fauna is characterized by an increase in the number of echiuroid species (12).

If these traces have been made by echiuroids, their major paleoecological contribution may lie in the fact that echiuroids are stenohaline (4); there are few known occurrences of echiuroids in shallow water subject to periodic feshwater influxes. Boron analyses of shale interbeds in the Thorold have already indicated a normal marine environment (13).

I have recently collected traces from the Guelph and Lockport dolomites in the vicinity of Dundas, Ontario, which closely resemble the Thorold traces. It is possible that echiuroids were significant members of the bottom fauna of the shallow Paleozoic seas, and that their presence has not been recognized.

Even if feeding traces are absent, the presence of echiuroids could be established by carefully searching for their characteristically sickle-shaped ventral or anal setae.

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Genetic Abnormality of the Visual Pathways in a "White" Tiger

Abstract. "White" tigers show an inherited reduction of pigment, produced by an autosomal recessive gene. The brain of one of these tigers shows an abnormality of the visual pathways similar to abnormalities that are associated with albinism in many other mammals. There is a close relationship between the reduced pigment formation, the pathway abnormality, and strabismus.

From time to time, tigers with a reduced amount of pigmentation are seen in the wild. In 1951 one of these "white" tigers was captured in India, and from it a line of white tigers was bred by the Maharaja of Rewa (1–3). In many respects the gene controlling coat color in these tigers resembles chinchilla, an allele of the albino series (4). The white tigers have the gray-brown stripes characteristic of a normal tiger, but in place of the normal yellow, they have an off-white stripe. The white tends to be darkened by low environmental temperatures (3). The tigers have reduced pigment in the iris, which looks blue, and the gene controlling these features appears to be an autosomal recessive (2).

One of these tigers was brought to the Smithsonian Institution's National Zoological Park, Washington, D.C., and several tigers have been bred from her. One of these, Rewati (see cover), is currently there, and we become interested in the white tigers when it was pointed out to us that Rewati has a strabismus (3, 5). Siamese cats, which are homozygous for an allele of the albino series (4), also commonly have a strabismus, and we have shown that this abnormality is related to an abnormality of the central visual pathways (6, 7). In Sia-

mese cats, some of the nerve fibers that come from the temporal part of the retina go to the opposite side of the brain, instead of staying on their own side as is normal. We have found this abnormality in all Siamese cats, even those that are not obviously cross-eyed. It is probable that the size of the abnormality is related to the strabismus (7).

The abnormality is not confined to Siamese cats. Among carnivores, similar abnormalities have been found in albino ferrets (8) and mink (9), and albinos of every other mammalian species that has been studied also show the abnormality (9, 10). In addition, some mink that have a wild-type gene at the albino locus, but lack pigment due to the action of other genes, also have the abnormal pathway (11).

In carnivores, which have a clearly laminated lateral geniculate nucleus, the geniculate layers that normally receive their input from the ipsilateral eye are broken up in the abnormal individuals. These layers, instead of forming a continuous cell mass as is normal, form distinct islands, and the islands that receive an abnormal contralateral input tend to fuse with adjacent layers that normally receive a contralateral input. Thus, it is possible to look at the laminar