

Paläont. Z.	64	1/2	15-23	3 Abb.	Stuttgart, Juni 1990
-------------	----	-----	-------	--------	----------------------

A tubicolous animal from the Hunsrück Slate (Lower Devonian, Southern Germany)

KRISTIAN FAUCHALD and ELLIS L. YOCHELSON, Washington*

With 3 figures

Kurzfassung: Ein kleiner in einer Röhre wohnender Organismus wird als Sediment-Bewohner gedeutet. Diese Lebensweise wird abgeleitet aus dem Unterschied zwischen verkleideten Grabgängen und Röhren sowie zwischen weichen und steifen Röhren. Lamelläre Anhänge der Körperwand können der Wasserzufuhr für den wurmförmigen Teil des Körpers gedient haben. Die klaffende Apertur besitzt kein Operculum und kann fortlaufend geöffnet gewesen sein; der Rand der Öffnung wurde durch Spiculae verstärkt. Das Exemplar ist nicht segmentiert und kann deshalb nicht als annelider Wurm angesehen werden. Das Fehlen von Anneliden im Crinoiden-»Wald« des Hunsrück-Meeress ist merkwürdig, da dieser Biotop theoretisch für jene Organismen geeignet gewesen wäre.

Abstract: A small tube-dwelling organism is interpreted as living in the sediment. This life habit is inferred from the difference between lined burrows and tubes and between soft and rigid tubes. Lamellar extensions of the body-wall may have provided irrigation for the vermiform part of the body. The gaping aperture lacks an operculum and may have been open permanently; the apertural rim was strengthened by spicules. The specimen lacks segmentation and is thus not an annelid worm. Considering the theoretical suitability of the crinoid "forest" in the Hunsrück sea for such worms, the absence of Annelida is curious.

Introduction

We report here on an unusual specimen having preserved soft parts from the Hunsrück-schiefer, interpreted as a tube dwelling organism. Another poorly preserved fragment, not herein illustrated, may be a remnant of the tube without the contained organism. Apart from that vague possible association, the individual illustrated (WS 12853) is unique to the fauna and seemingly to the paleontologic record.

FAUCHALD acknowledges the support of the National Museum of Natural History, Smithsonian Institution, in helping to defray the cost of printing. YOCHELSON acknowledges the support of the National Science Foundation under grant No. INT-8521164 for German-American cooperation in science, which made possible study for a week in May, 1986 at Erlangen, FRG. Photographs were supplied by the late Professor Dr. W. STÜRMER. The STÜRMER radiograph archives are now at the Senckenberg Museum, Frankfurt, FRG. This paper is dedicated to WILHELM STÜRMER.

*Address of the authors: KRISTIAN FAUCHALD, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington D.C., 20560; ELLIS L. YOCHELSON, Research associate, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington D.C., 20560.

Description

The elongate specimen is relatively small: as preserved, it is 2 cm in length. On the exterior of a cleavage plane in the slate, it appears as an S-shaped lump (Fig. 1). The anterior end is oval, irregularly grooved, and separated from the rest of the animal by a depression. The posterior half is curved and the left side shows a series of low, distally truncated lamellar structures separated by a longitudinal groove. The right-hand side is partially obscured, but an indistinct groove suggests that additional lamellar structures could be present on that side.

An image-enhanced radiograph shows the same two main parts. The upper, ovate zone is limited by an outer, slightly thickened rim, marked off both internally and externally by a distinct pyritized "membrane", most distinctly seen in the upper left side of Fig. 2. Within this rim are bodies resembling rounded, clear vesicles. This whole area appears to be open to the exterior as a wide, shallow funnel, now oval in outline. The apertural rim is narrowed down posteriorly to a distinct shallow notch, which looks not unlike the lip of a pitcher (Fig. 1). The anterior end of this structure contains a series of spicules (Fig. 3). The upper zone is connected to the lower part of the organism by a poorly mineralized neck.

The lower part of the organism contains a central elongate dark area (beginning at a funnel-shaped "V" in the lightly pyritized area below the aperture; Fig. 2). The heavily pyritized dark mass shows no details; we interpret this area as the principal part of the digestive system. The dark region is outlined above and is flanked by lateral "spines". Although it is barely shown in the print illustrations, the negatives clearly indicate the presence of a lightly pyritized tube enclosing the lateral projections. The tube covers the lower part of the body from the level of the first spines and covers the posterior end of the animal completely. Seemingly, the "spines" do not extend to the posterior end of the animal. Although somewhat obscured, we can see that the body is sharply tapering posteriorly; additional pyritization below it may be the result of mineralization of soft parts extruded during compaction.

Close examination of the "spines" indicates that they are leaf-like structures. At least two rows can be seen on the radiograph and the relationship between the radiograph and the surface view indicates that more are present. The short distance between the base of this zone and the posterior end of the specimen suggests that this region could not have been extended out of the tube by use of a hydrostatic mechanism.

No segmentation can be observed in the body.

Systematic position

We cannot compare this fossil closely to any forms described from the recent or fossil record. The lamellar structures present on the posterior half of the animal may at first glance resemble annelid parapodia (cfr. *Phyllodoceidae* and *Nerididae*, FAUCHALD 1977). However, the radiographs do not show the presence of the supporting aciculae present in annelids with lamellar parapodia. No other features can be identified as even suggesting a segmental arrangement.

In spite of its unusual features, in our judgment, the single specimen described above does not warrant assignment of a generic and specific name. However, despite our decision not to bring it formally into the taxonomic literature, because of its peculiar morphology we think that the fossil has importance beyond this single record.



Fig. 1. To the right, the lower surface of WS 12853 photographed in natural light, a mosaic of several pictures. To the left, an image enhanced radiograph of the same surface. Both about $\times 7$. Insert – A radiograph of WS 12853 at natural size, taken from the upper surface; note reversal of image on the enlargements.



Fig. 2. A radiograph, image enhanced to show details of anterior end, including the anterior part of tube; the wide U-shaped "spout" is seen at the lowest part of the oval aperture. About $\times 17.5$.



Fig. 3. A radiograph, image enhanced to show details of spicules and part of the apertural rim; the orientation as in the insert of Fig. 1. About $\times 60$.

Tube or burrow-lining?

The Hunsrück specimen is partially enclosed in what might be interpreted either as a lined burrow or a tube. The difference between these kinds of structures is more than just definitional: Tubes are clearly delimited both towards the organism and towards the environment. They may be buried in sediment or above it as free-standing structures or attached. Lined burrows are delimited only towards the animal and are not clearly delimited against the environment; burrow linings fade into the matrix. An exception are the loosely constructed lined burrows produced by burrowing anemones, which by their very thickness take on tube-like properties.

In the Recent fauna both burrows and tubes are present in muddy and sandy environments, and at least below wave-base are equally well represented in all types of sediments. Sessile organisms in shallow, turbulent waters more characteristically live in tubes, as protection against the scouring effect of moving sand, silt and clay particles. Lined burrows in this kind of environment are rarer and are used primarily to ease the movement of an organism through the sediment. Protection against wave-action and the scouring effect of the sediment is also furnished by tubes being grouped into variously arranged dense clumps; these clumps change the water flow properties over the bottom and may function as sediment-baffles.

As defined here, tubes and burrows both may be open or may be closed at one end. The presence of a closed or open end does not per se indicate that the structure should be referred to as a lined burrow rather than a tube.

The chemical composition of soft tubes and burrow-linings is usually rather similar, consisting of a spectrum of muco-polysaccharides secreted by the animal. Hard tubes are impregnated with various materials – in Recent organisms, almost universally with calcium carbonate; calcium phosphate has never been recorded.

In the Recent annelid fauna both lined burrows and tubes present and tubes may be soft or mineralized. Even within a single genus, the structure of the tubes may vary a great deal. For example, in *Diopatra tridentata*, the tubes are cylindrical, hollow, segmented sacs, where each sac is clearly lined on both sides, but filled with the surrounding sediment, usually a fine silt. In contrast, even closely similar species form tubes that consist exclusively of material extruded by the organism (*D. splendidissima*) into which shell-fragments and pieces of algal material from the surrounding medium have stuck as the tubematerial hardened. Other species of *Diopatra*, as represented by *D. ornata* and *D. cuprea*, will decorate the upper projecting end of their tubes, but will keep the parts that are burrowed completely clean of foreign particles.

Both lined burrows and tubes in sediment increase in length in essentially the same fashion. When the organism settles, it proceeds to stabilize the sediment surface and forms a “dimple” in the surface. The water-sediment interface is often rather fluid: it is an increasing density gradient of particles downward, rather than a sharp boundary at least in soft muddy bottoms. Usually, little effort is required for the settling larva to accomplish this original “dimpling”. Even in sandy bottoms, the settling juveniles are often in the meiofaunal size-range and are capable of scrambling between sand particles at the time of settlement.

Both tubes and burrows, at least initially, increase in width as well as in length. the organism, depending on the particular kind, works its way deeper into the sediment, usually pushing the lower end of the tube into the sediment, and secreting new tube or burrow material at the free end. This process may be active, or it may be rather passive: The active movement of the encased organism may, in itself make it sink into the sediment; the production of added tube material may be related of the speed of sinking of the encased organism. Tubes and burrows of adult organisms may be uniformly tapering or more or less cylindrical. The difference is related to the kind of organism encased, but not to any difference between lined burrows and tubes.

Tube-dwelling organisms associated with hard substrates often have mineralized or organically reinforced tubes, probably as an anti-predator device. However, in Recent environments, such as the Halimeda-beds in tropical waters, tubicolous worms with thin, translucent tubes are often found attached to the thallus of the alga, and the stems of bryozoan and hydroid colonies are often densely infested with soft tubes of a variety of organisms. In the Hunsrück seas, the stalked crinoids would have taken the place of the calcareous alga, bryozoans, and hydroids, as a potential substrate for the attachment of soft tubes.

Organisms living in tubes must produce watercurrents along their bodies to avoid anoxic conditions; as a consequence, tubes and lined burrows alike are characteristically open at both ends. ALLER & YINGST (1978) have shown that these currents create an oxygenated halo around the organisms. That mechanism makes it possible for the organism to live at depths that would otherwise be impossible in anoxic sediments.

There are several different ways in which irrigation currents can be set up. Water-flow may be created by ciliary action along suitably arranged appendages, by the movement of lamellar structures, or by undulatory motions of the entire body. In tubes and burrows open at both ends, the water-flow will be unidirectional. However, beyond a certain minimal size water-flow is also required in organisms that have functionally closed tubes, such as the specimen described. The flow pattern through such tubes or burrows is U-shaped, going in on one side of the body and out on the other. All three mechanisms for creating flow are used among Recent organisms with closed tubes. The Hunsrück specimen described above has at least two series of lamellar flaps along part of the body that could easily have functioned in creating currents to irrigate the body. Indeed, we have considered a number of theoretical interpretations of these structures and find current production as the only tenable hypothesis.

The Hunsrück specimen certainly is contained in a tube, not a burrow lining, for the membrane defining the structure is well defined both internally and externally. The tube is closed at the posterior end and beyond this initial area expands at a slow, uniform rate. The animal could have lived in the sediment or it could have been on the surface of a substrate. On balance, we believe that this organism was a soft-sediment dweller because of the thin-walled soft nature of the tube. In addition we see no evidence of attachment either at the base or along the side of the tube.

Closure of tubes and burrows

Tubes and lined burrows are usually thin-walled distally compared to the rest of the length of the structure. Because of this delicate construction, the opening will close when the organism withdraws simply by collapsing. Tubes may be closed by at least two additional mechanisms: first, the exposed end of the tube may be bent over, facing the substrate, or second, an operculum may be present. An operculum may be a piece of foreign material which the organism pulls over the opening of its tube or burrow, or it may be a structure formed by the organism itself.

Opercula are more common in organisms living on hard substrates, where there is little problem, of sediment fouling. However, operculate serpulid polychaetes are present today in soft sediments, if not as commonly as on rocky surfaces. In Recent organisms, secreted opercula are commonly associated with reinforced, fairly rigid tubes, such as those of the vestimentiferans or serpulids.

For the Hunsrück specimen we see no evidence of any formed opercular structure, though the use of a piece of foreign matter can never be ruled out. The apertural spicules do not appear to have had any opercular function. They are not distributed uniformly around the aperture and they do not support any membrane which would close the aperture.

Feeding mechanism

The ovate anterior end of the Hunsrück specimen may have been a feeding structure supported by a flexible neck not enclosed in the tube. We interpret the structure as having a thickened outer rim supporting an open funnel which leads obliquely posteriorly to the mouth. We assume that this structure was held horizontally at or near the sediment-surface. Such a structure could be used to trap sediment particles moving over the bottom, or to trap small organisms by the use of mucus. Even if the upper surface of the funnel was completely ciliated, because of its small size the animal could not have been able to set up a sufficient current to be characterized as a filter-feeder. Recent organisms of similar size range may use regional turbulent flow, or current produced by larger organisms to bring suitable food particles into the reach of their feeding structures. The particles are removed from the flow more by entrapment with mucus, rather than by filtering currents.

Discussion

A variety of vermiform organisms occur in the Paleozoic fossil record. For some investigators, "vermiform" becomes translated subconsciously to "worm", and "worm" more often than not is interpreted as annelid.

The physical evidence is mainly various kinds of tubes and isolated opercula, none of which show soft-parts, and bioturbation of sediments, even further removed from the anatomy of the organism. The concept of "annelid worm" continues to be used by many paleontologists with more laxity than the evidence from the fossil record warrants.

Roughly half of all modern marine annelids do not form tubes of any sort. Some present-day sessile annelids construct a tube of calcium carbonate (e. g., *Spirorbis*) or cover an organic membrane with agglutinated grains (e. g., *Sabella* or *Diopatra*); other annelids form thin-walled tubes that perhaps might best be characterized as lined burrows. The sabellid and serpulid tubes are rigid structures, projecting well above the sediment surface or attached to hard substrates. The tube of *Sphenothallus* – demonstrated by its lack of segmentation in its enclosed soft parts not to be an annelid – although not quite so rigid was sufficiently strong to be a freestanding tube, projecting in the water some centimeters in length above a basal attachment disk (FAUCHALD, STÜRMER & YOCHELSON 1986). In addition, such non-annelid Recent organisms as the vestimentiferans (JONES 1985) have thick-walled, very rigid tubes.

Unless rigid tubes are closely similar to those of modern forms, they do not provide evidence for an annelid relationship for the tube builder. Considering how many other organisms build tubes and lined burrows of various sort, the presence of burrows or tubes are at best only supporting evidence for interpretation of any fossil as an annelid.

Far better evidence for the occurrence of at least some groups of annelids in the fossil records are the scolecodonts, representing jaws of various, mostly eunicean groups of annelids (BERGMAN 1987; Colbath 1986 and earlier authors). For annelids that lack both solid tube-structure and jaws, in fact for most annelids, we must rely on chance preservation, similar to those of the Hunsrück shales for evidence of presence.

One must keep in mind that many of the higher taxa in zoological systematics were based on living animals, not derived from the study of fossils. Traditionally, these taxa have been extended backwards into the fossil record. However, as a consequence of the efforts of this generation of paleontologists, who have discovered and described the Ediacara and Tommotian faunas and have redescribed the Burgess Shale fauna, there have been vivid demonstrations of many bizarre fossils which do not "fit in" to the currently accepted zoological constructs (YOCHELSON 1971).

The Hunsrück specimen described above does not fall within the accepted morphology of living Annelida. To date we have not seen any specimen from the formation which shows clear proof of segmentally arranged structures. The presence of segmentally arranged features, at the very least internally, is critical to an assignment of a modern form to that phylum.

Although negative evidence can be destroyed in an instant, we are prepared to place some importance on the lack of authentic annelids in the Hunsrück Sea. However, as demonstrated by ALLISON (1988: 145) modern annelids may not fossilize easily, even under anaerobic conditions, except under very unusual circumstances. Discovery of completely soft-bodied forms on radiographs is chance-based, in that these must occur on the same slab of slate as a pyritized mass or a fossil with distinct hard parts, for it is the irregularities reflected on the surface of a bedding plane which provide the rationale for preparing a radiograph.

Life among the colonies of stalked crinoids in the Hunsrück seas would seem to be an ideal habitat for Devonian annelids, as judged by modern animals. The pyritized crinoid material would provide the critical irregularity to lead to their discovery. So many radiographs of crinoids have been taken of the Hunsrück slates that one would expect an annelid to be found, were one present.

Further, a ctenophore, surely a kind of animal most unlikely to be preserved, has been discovered in the biota, and even a second specimen reported. A flatworm-like organism, unlike those living today, and a colonial "tunicate" also have been found in this deposit (FAUCHALD, STÜRMER & YOCHELSON 1988). Judging from the modern fauna, one would anticipate annelid worms to be well represented in fauna and as fossilizable under the circumstances.

References

- ALLER, R. C. & YINGST, J. Y. 1978. Biogeochemistry of tubedwelling: A study of the sedentary polychaete *Amphitrite ornata* (LEIDY). – J. Mar. Res. 36(2): 201–254, New Haven, Connecticut.
- ALLISON, P. A. 1988. The role of anoxia in the decay and mineralization of proteinaceous macro-fossils. – Paleobiology 14(2): 139–154, Lawrence, Kansas.
- BERGMAN, C. F. 1987. Silurian Paulinitid jawed polychaetes from Gotland. – Unpubl. Ph. D. Diss. Lunds University, NBGH-1010: 1–145, Lund.
- COLBATH, G. K. 1986. Jaw mineralogy in eunicean polychaetes (Annelida). – Micropaleontology 32(2): 186–189, Lawrence, Kansas.
- FAUCHALD, K. 1977. The polychaete worms. Keys and definitions to the orders, families and genera. – Nat. Hist. Mus. Los Angeles County, Sci. Ser. 28: 1–190, Los Angeles, California.
- FAUCHALD, K.; STÜRMER, W. & YOCHELSON, E. L. 1986. *Sphenothallus* "Vermes" in the Early Devonian Hunsrück Slate, West Germany. – Paläont. Z. 60: 57–64, Stuttgart.
- 1988. Two wormlike organisms from the Hunsrück Slate (Lower Devonian); southern Germany. – Paläont. Z. 62: 205–216, Stuttgart.
- JONES, M. L. 1985. On the Vestimentifera, new phylum: Six new species, and other taxa from hydrothermal vents and elsewhere. – Bull. Biol. Soc. Washington 6: 117–158, Washington D. C.
- YOCHELSON, E. L. 1971. Phylum and class nomenclature in systematics. – Systematic Zoology 20: 245–249, Lawrence, Kansas.

Eingang des Manuskriptes bei der Schriftleitung am 10. I. 1989.

Paläont. Z.	64	3/4	381	–	Stuttgart, Dezember 1990
-------------	----	-----	-----	---	--------------------------

Letter to the Editors

Correction: a major error in FAUCHALD, STÜRMER & YOCHELSON, 1988

KRISTIAN FAUCHALD and ELLIS L. YOCHELSON, Washington*

The paper by FAUCHALD, STÜRMER & YOCHELSON (1988), discussed a "flat" worm and an "elongate" worm from the Hunsrück Slate. Although the former remains plausible, the latter has been reinterpreted.

Following a suggestion by Prof. O. H. WALLISER, University of Göttingen, the radiographs showing the "elongate" worm were reexamined. In the original work, this was interpreted as a colonial tunicate on the basis of presumed sieve plates. We are now convinced that these features are actually the compound eyes of the common Devonian trilobite *Phacops*, a well-known form in the deposit. The parts considered sieve plates have the "holes" arranged in rows, characteristic of the trilobite, a feature which was overlooked. Further, under stereographic examination, it can be seen that the eye region does not curve downward, but is angulated, again a characteristic of this trilobite.

Several specimens are present, which lead to the notion that a colonial animal had been torn apart during burial. All in all, the tunicate interpretation was ingenious. Unfortunately, it was incorrect.

Reference

FAUCHALD, K.; STÜRMER, W. & YOCHELSON, E. L. 1988. Two worm-like organisms from the Hunsrück Slate (Lower Devonian), southern Germany. – *Paläontologische Zeitschrift* **62**: 205–215, Stuttgart.

Eingang des Manuskripts bei der Schriftleitung[†] am 12. 5. 1990.

*Addresses of the authors: Dr. KRISTIAN FAUCHALD, Department of Invertebrate Zoology, NMNH, Smithsonian Institution, Washington, D. C. 20560, USA; Dr. ELLIS L. YOCHELSON, Research Associate, Department of Paleobiology, NMNH, Smithsonian Institution, Washington, D. C. 20560, USA.

