

Variation in a species of «worm» from the Ordovician of Spitsbergen

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A sample from the Valhallfonna Formation (Arenigian-Llanvirnian Age) has produced a large number of enigmatic steinkerns in the 1-mm size range; rare cephalopods, ostracodes, and ?tentaculitids also occur. The steinkerns are smooth and may have filled tubes of calcium carbonate. The hundreds of tubes, presumably an unsorted population, show an incredible degree of variation, ranging from straight through curved and irregularly bent to coiled. Coiling may be irregular, helical, or bilaterally symmetrical. Both bilaterally and helically coiled forms cannot be distinguished from material that other authors have assigned to the Gastropoda, but the continuous variation from coiled to straight tubes demonstrates that these tubes cannot be gastropods.

An extremely difficult problem in paleontology is assignment of fossils to the phylum Mollusca. When one deals with an internal shell filling (steinkern) of small size, it is particularly difficult to find criteria that distinguish mollusks from some other organisms. It is too little appreciated that some groups within the “worms” can construct tubes that mimic the shells of small mollusks.

We thank authorities at the Paleontological Museum, Oslo, for making facilities available and for providing the samples studied. YOCHELSON acknowledges the permission granted him by the Director of the U.S. Geological Survey, for a temporary transfer of headquarters, which allowed him to participate in this research. We are both in debt to TOR MELLEME, Electron Microscopical Unit for Biological Sciences, University of Oslo; his assistance with photographs allowed us to document the great variation in the fossils examined. All photographs were taken with a JEOL JSM-S1, and specimens were uniformly coated with carbon followed by gold-palladium; the apparent shadowing seen on a few photographs is the result of background charging of electrons.

Sample locality, age, and preparation

The material discussed below was collected by DAVID BRUTON, Paleontologisk museum, Oslo, and RICHARD FORTEY, British Museum of Natural

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History, during the 1971 Paleontological Museum of Oslo Expedition to Northern Ny Friesland, Spitsbergen. A summary of the stratigraphy has been given by FORTEY and BRUTON (1973), the sample that concerns us having been obtained from melt stream "A" on their Figure 1, of the Olenidsletta, Hinlopenstredet. It was collected 17 m above the base of the Profilbekken Member, the upper member of the Valhallfonna Formation; this member is 110 m thick. The sample was fine-grained limestone, medium dark grey, with a tint of brownish grey (N4-5YR 4/1).¹

FORTEY and BRUTON consider the Valhallfonna Formation to be of late Canadian-Whiterockian Age (latest Early Ordovician to earliest Middle Ordovician) and close to the Arenigian-Llanvirnian boundary. 50 m below our sample, conodonts obtained from the middle part of the Olenidsletta Member have been tentatively identified as a form preceding *Prionodus evae* (LINDSTRÖM). *P. evae* is considered by BERGSTRÖM and COOPER (1973, p. 330) to span the *Didymograptus bifidus* zone, which they judge to extend across the upper Canadian and lower Whiterockian of the American stage sequence; thus the age of our sample probably corresponds to that of the *Didymograptus bifidus* zone.

Two slabs less than 2 cm thick and weighing 314 grams were treated with dilute acetic acid for about one week until all reaction was completed; the slabs were cubed before acid digestion. After the sample was digested in acid, it was washed in distilled water and sieved while wet; no additional chemical preparation was performed. The principal objective of preparation was to investigate ultramicrofossils, but all the insoluble residue was retained.

The insoluble residue amounts to 30.8 grams, indicating a limestone composed of about 90% calcium carbonate. Twenty-two grams of this residue consist of chunks, 2 to 4 cm long, composed of clays and silica particles cemented with silica; it need not be discussed further. The finer residue was fractionated with a saturated solution of zinc chloride. Isolated clay particles smaller than 45 μm were lost during washing.

Coarse fraction

Except for the chunks of matrix noted above, the largest pieces in this fraction are silicified shells of cephalopods as much as 1 cm in size. The silicified cephalopods are light gray, are curved or coiled, and have a rugose surface. The attached larval shell expands abruptly and also bears rugosities; a few of the juvenile forms have been found in the 1-2-mm size range and were identified by the rate of expansion and the rugosities. One example is illustrated in Fig. 6C. The few isolated larval shells are steinkerns and are not silicified.

Echinoderm columnals and fragments of plates are present and form about 25% of this fraction. The cavities in the skeletons are filled with white silica. Smaller fragments of echinoderms are easily identified by this color and by the spongy texture of the infillings. A few large dark-gray balls of silica and small irregular pieces of very light gray drusy silica compose the remainder of this fraction.

¹ Rock-Color Chart. Prepared by the Rock-Color Chart Committee. Distributed by the Geological Society of America. Boulder, Colorado 1970.

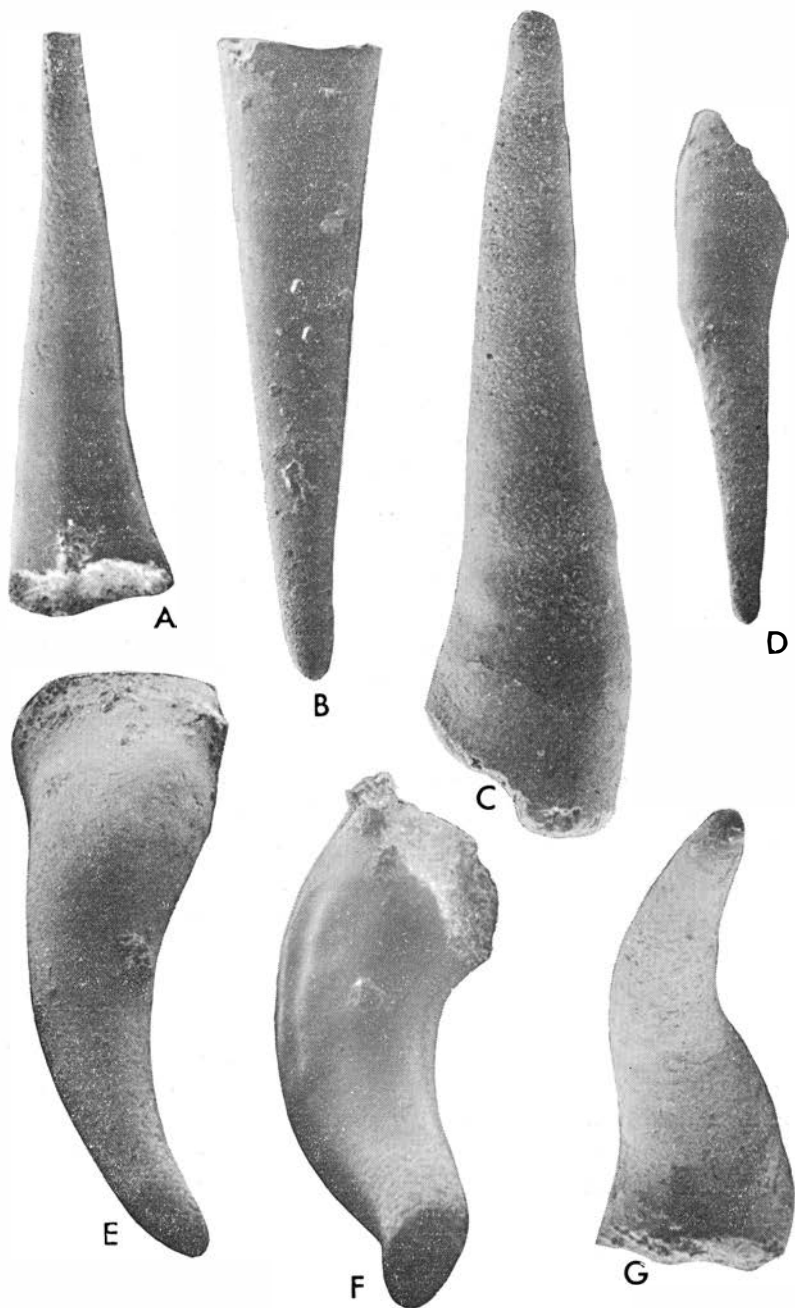


Fig. 1. Steinkerns of straight to curved "worm" tubes from 17 m above the base of the Profilbekken Member. A. PMO NF 3201/1, $\times 50$. B. PMO NF 3201/2, $\times 75$. C. PMO NF 3201/3, $\times 100$. D. PMO NF 3204/9, $\times 75$. E. PMO NF 3202/2, $\times 100$. F. PMO NF 3201/4, $\times 75$. G. PMO 3201/9, $\times 75$.

Fine fraction

Approximately 5.4 grams of fine-sized residue was obtained, most of it in the 1–2-mm size. More than 10% of this size range is organic. Dark-grey silicified ostracodes are present but rare. Trilobite fragments, also silicified, occur even more sporadically. Commonly, thorax fragments are gray, whereas glabella fragments are a rich dark brown. The preponderant forms in this fraction are steinkerns of tubes. Some of the nondescript material of small size could be partial filling of tubes, the smooth outer surface of the steinkern having been broken away.

Only four conodonts of the distacodid type were obtained, although samples from 15 m higher and above have produced a variety of conodonts in abundance. Conodonts have so far not been found in other samples from the lower part of the Profilbekken Member at this locality.

The texture of the steinkerns of the tubes varies from coarse to smooth; commonly both textures are found on the same specimen. The apical part is often coarser and more pitted than that near the aperture (Fig. 3C). Probably the finer texture is a result of easier infilling of matrix toward the aperture after death of the organism. Some of the steinkerns are so smooth that they appear polished (Fig. 1F). Still others, in addition to being smooth, have a bluish sheen on the surface, suggestive of a phosphate mineral.

In the size range below 1 mm, organic-walled fossils including acritarchs, chitinozoans, graptolites, and scolecodonts are absent, although these have been found in samples both above and below the 17 m level. Much of this finer material in our sample seems to consist of silicified echinoderm debris. The color and texture easily distinguish this debris from inorganic silica in sizes as small as 80 μm . Echinoderm debris of such fine size is quite rare in other samples from the Profilbekken Member, although larger pieces of silicified echinoderms do occur.

Steinkern A

We recognize two forms of tubelike steinkerns. The form arbitrarily designated A is characterized by annulations irregularly spaced. Two representative specimens are illustrated in Fig. 6B, E. Tubes are straight to slightly irregular, but are not curved or bent. The annulations are suggestive of those that occur in *Tentaculites* and *Cornulites*; some annulations have a slightly sinuous course around the tube. Commonly, the tip is not preserved in this form of Steinkern. We are unable to assign this material to any genus because it lacks all surface features, but we are reasonably confident of this generalized assignment. About 5% of the steinkerns recovered show annulations.

Steinkern B

We assign the bulk of the fossils obtained to another taxon. These consist of simple elongated tubes that seem to expand at a continuous low rate; no “flaring” of the apical area has been observed.

The extreme tip of the steinkern varies slightly from subpointed in a few specimens (Fig. 1D) to most commonly rounded (Fig. 1B, E). The maximum

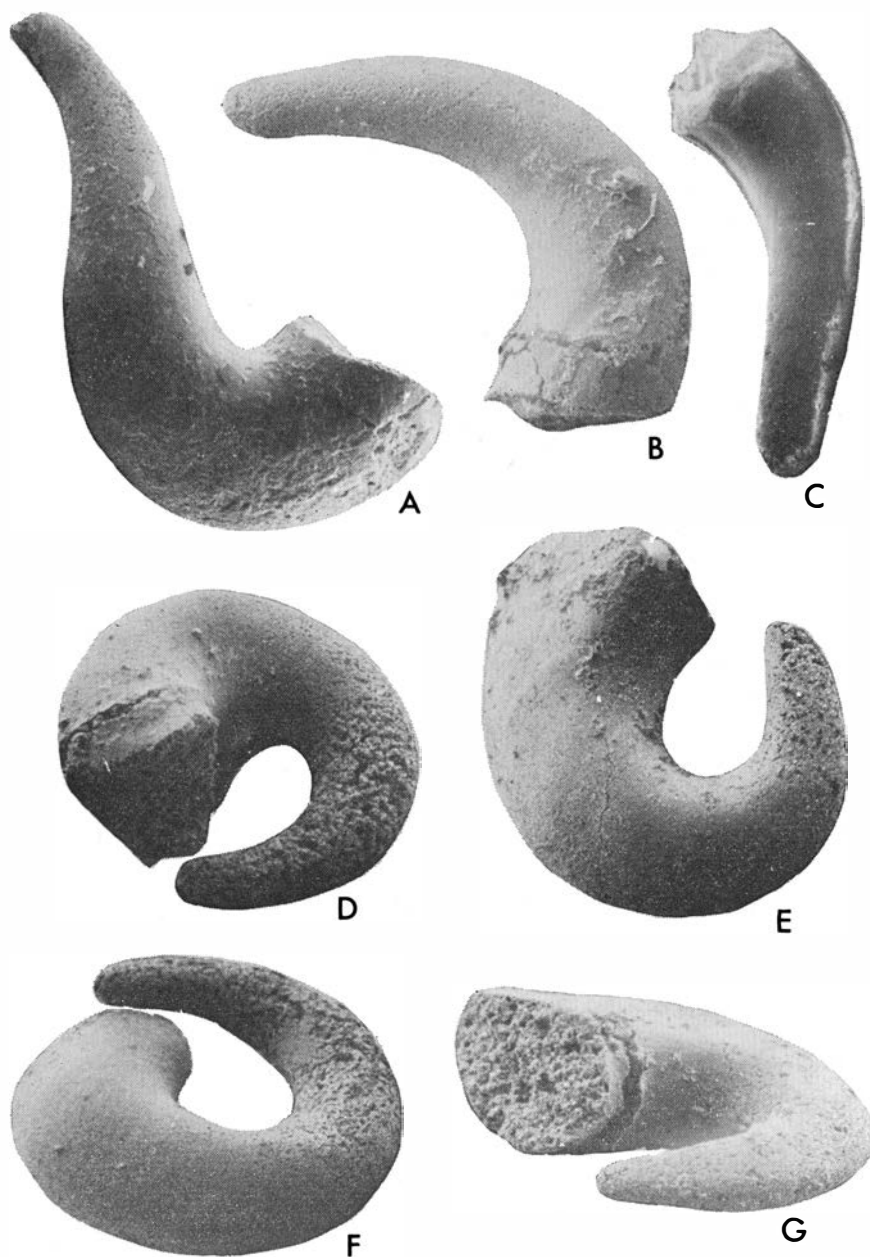


Fig. 2. Steinkerns of curved "worm" tubes from 17 m above the base of the Profilbekken Member.
A. PMO NF 3201/5, $\times 75$. B. PMO NF 3204/8, $\times 100$. C. PMO NF 3201/11, $\times 50$. D. PMO
NF 3202/2, $\times 100$. E. PMO NF 3202/3, $\times 75$. F. PMO NF 3203/5, $\times 100$.
G. PMO NF 3202/6, $\times 100$.

variation in this feature is trivial, and we do not consider it significant. The extreme apical area of a shell or tube is exceedingly thin. Some present-day animals strengthen this area by depositing calcium carbonate on the interior of the shell. Such a deposit may account for the minor variation observed. An equally plausible alternative is that the apex on the tube interior was relatively pointed, but the physics of infilling such a restricted area with tiny particulate matter commonly caused a rounded surface to form.

Beyond the apex, however, variation is remarkable in that a variety of bizarre shapes may be seen in the slightly curved shapes (Figs. 1C-E, 2B, C); some appear irregularly bent (Figs. 1F, 2A). In three-dimensional coiling, the coils may be irregular (Figs. 4E, 5I); one coil may be on top of another so that a cylinder shape is formed (Fig. 5C, D, F-H); or there may be helical coiling (Fig. 5A, E). Oriented with the apex upward, all the examples of helically coiled tubes have the aperture on the right.

Tubes also vary in shape from hooked-specimens (Fig. 2D, E) and those that are coiled in an extremely low helix, so that the “upper surface” is nearly in one plane (Fig. 2F, G), to those that are nearly bilaterally symmetrical, showing only a slight asymmetry of the whorl profile (Fig. 2A, B), and those that appear to be truly bilaterally symmetrical (Fig. 4D). This last form differs very slightly from the others in that a suggestion of a bulbous expansion appears at the tip (Fig. 4F). We have seen this in only a few examples and suspect that it is related to the tight bending required to complete the initial coil in a small restricted area.

Variation in the tubes is continuous from straight to coiled. There appears to be a few more straight to slightly irregular tubes than other “end member” forms illustrated. However, the vast majority of the tubes that deviate markedly from being straight, seem to have no preference for any particular shape. Specimens that appear to be perfectly bilaterally symmetrical are less common than specimens that deviate a small degree from these ideal shapes. Helically coiled specimens having an ideal logarithmic spiral in three dimensions are rare.

Paleoecological speculations

A prime consideration in any discussion of presumed life habits of former living animals is the question of whether material studied has been transported. In this sample, it is safe to assume that little movement has occurred. We base this interpretation on the occurrence of larger specimens along with small tubes. Supplemental support is provided by the delicate nature of larger pieces of silicified echinodermal debris. Perhaps the single most compelling evidence of significance of lack of bottom transport is the large numbers of steinkern B that have the tip preserved.

Because all specimens of steinkern B fall within a limited size range, a meaningful histogram of sizes cannot be made to see whether a survivorship curve can be constructed. We cannot determine whether we are dealing with a true sample of a living population or with an accumulation of organisms that lived and died through the interval of time necessary for the total thickness of the slabs to accumulate. We suggest that the latter situation is closest to the

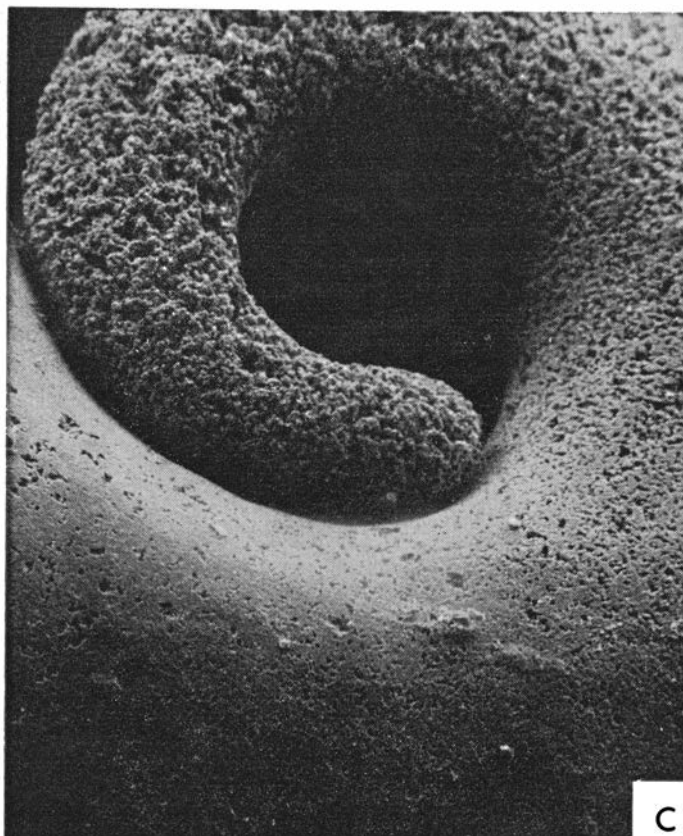
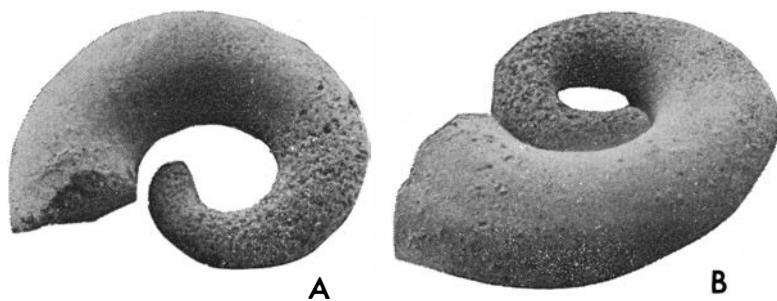


Fig. 3. Steinkerns of curved to coiled "worm" tubes from 17 m above the base of the Profilbekken Member.
A. PMO NF 3203/4, $\times 100$. B. PMO NF 3203/3, $\times 75$. C. Detail of shell of Fig. 3B, $\times 300$.

truth, for even when one deals with bedding-plane accumulations rather than a three-dimensional sample, there is no assurance that specimens dead prior to a sedimentological event have not been included. Nevertheless, even if we assume that the assemblage accumulated for a few years, an exceptionally large number of specimens is present, and it is appropriate to use the term “gregarious” for this accumulation.

None of the specimens show any evidence of attachment, which might be indicated by a flattening on one side; specimens that are essentially straight are nearly radially symmetrical. Likewise, the apex comes to a sharp tip in the better preserved specimens; had there been attachment in this area, the tip might have been flattened or bulbous.

The variety of shapes seen in the steinkerns suggests that there must have been some support during change in shape. Indeed, it is hard to see how some of the specimens that coil in three dimensions could have grown had they not been apex downward and coiling upward. We suggest that these specimens could have lived in or within an algal mat, their shape in part, perhaps, controlled by the reaction of a potentially deforming substrate to the increasing weight of the animals during growth.

There is no evidence from the limestone of algal mat deposition. Our speculation cannot be confirmed, but we find it difficult to arrive at a more satisfactory explanation for the great variety of shapes that occur together. This sample shows differences in faunal content from other Profilbekken Member samples, but we cannot arrive at any firm conclusions as to why these differences occur. Much of the Valhallfonna Formation is interpreted as a slope deposit; perhaps the thin layer containing abundant worm tubes represents a slightly shallower, nonpersistent shelf deposit.

Discussion

Steinkern A, presumably a tentaculitid, provides no important biologic data. It is also of limited stratigraphic utility, as tentaculitids significantly older in the Ordovician have been reported (FISHER and YOUNG 1955).

Steinkern B, by contrast, is remarkable for both its diversity and its abundance. Of the 70 samples from the Valhallfonna Formation studied to date, only this one has produced the wealth of tiny tubes. Although a few other residues have produced similar steinkerns, in all these samples the individuals are much less abundant. The steinkern is judged by us to be the filling of a calcareous tube, soluble in acetic acid. We find it interesting that in this sample, which contains the illustrated “worm” steinkerns in protusion, echinoderms and arthropods are silicified, as well as the larger cephalopods; the isolated larval cephalopod shells were not silicified. It is not uncommon for silicification to be differential among various groups in the same sample, but we think it significant that at least some of the undoubted mollusks have been silicified and these tubes have not. This is at least suggestive of some difference in the organic matrix, mineralogy, or structure which distinguishes the tube from a molluscan shell.

In another sample from this locality, 35.3 m above the base of the Profil-

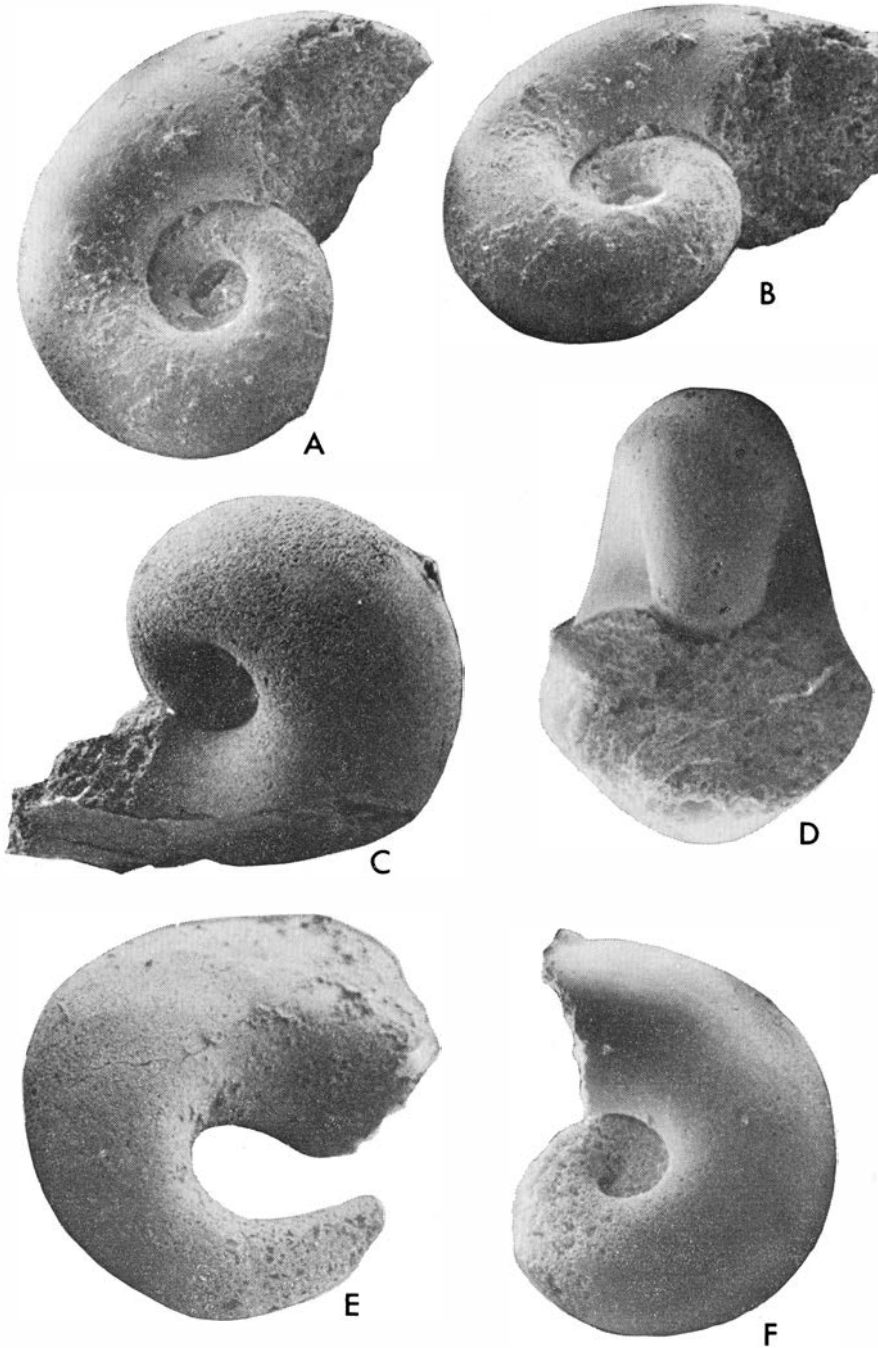


Fig. 4. Steinkerns of curved to bilaterally symmetrical coiled "worm" tubes from 17 m above the base of the Profilbekken Member. A. PMO NF 3203/6, $\times 75$. B. Specimen shown in 4A in an oblique view. C. PMO NF 3202/5, $\times 100$. D. PMO NF 3203/7, $\times 75$. E. Specimen shown in Fig. 2E from slightly different angle, $\times 100$. F. PMO NF 3202/4, $\times 75$.

bekken Member, one hollow specimen has been recovered. It is coiled much like a bellerophortid gastropod (Fig. 6D), though the whorls do not touch, suggesting that it may be a steinkern; the shell is thin and shows no obvious layering (Fig. 6F). It does not appear to be silicified but, rather, has close similarity in texture and color to calcium phosphate shells, rich in organic matter, of inarticulate brachiopods, which also occur in that sample. The specimen may have a true shell, may be silicified, or, less likely, may be composed of a thin phosphatic layer between a shell and more conventional steinkern material. The rarity precludes any chemical test to determine mineralogy. Some steinkerns of tubes are composed of glauconite. Unlike the lower sample, other faunal elements are both diverse and abundant. Ostracodes occur both as glauconitic steinkerns and silicified valves.

A third sample, 38.8 m above the base of the section, has produced a single straight tube (Fig. 6A), which is hollow, and a few steinkerns of tubes. Glauconite is not so common in this sample as in that immediately underlying, but the fauna of the insoluble residue is similar. Except for these two other samples, “worm” tubes are exceedingly rare in insoluble residues from the Valhallfonna Formation.

We are unable to provide any high-level classification of steinkern B. Although it might be a coleolid (FISHER 1966, p. W133), it might equally well fall within the fossil sedentary Annelida (HOWELL 1966, W155), or might belong in yet a third higher taxon. The Paleozoic worms are poorly known. We also choose not to assign any generic or specific name to the material, for an additional name not rigorously defined will simply add further confusion to the Paleozoic “worms”.

The steinkerns provide no information about the tubes exterior, although we suspect that the exterior may have been relatively smooth because of the absence of any elongated ridges impressed on the steinkerns. Several steinkerns do show the impression of a broad ridge on one side of the tube (Figs. 1F, 2C), but we are unable to separate them otherwise from the majority of the tubes. We prefer to regard this as an irregularity in outline of aperture of a few individuals rather than as a specific character on an indication of sexual dimorphism.

The incredible degree of variation in shape suggests that extreme caution be used when one is faced with a sample of a single or a few “worm” tubes, especially when the tube surface is smooth and principal characters are to be derived from the shape.

Perhaps, equally important is the homeomorphy of these tubes to tiny, helically coiled and bilaterally symmetrical gastropods. Were it not for the fact that all intermediate shapes leading to the straight tubes occur, we would have assigned those shapes to the gastropods without question. It is one of the advantages of mollusks that all growth stages are preserved during life. This study indicates that it is a more cautious procedure to observe the early growth stages of larger specimens, which are undoubted gastropods, than to simply examine isolated, tiny coiled specimens, for the assumption that all such coiled shells are larval gastropods is not correct.

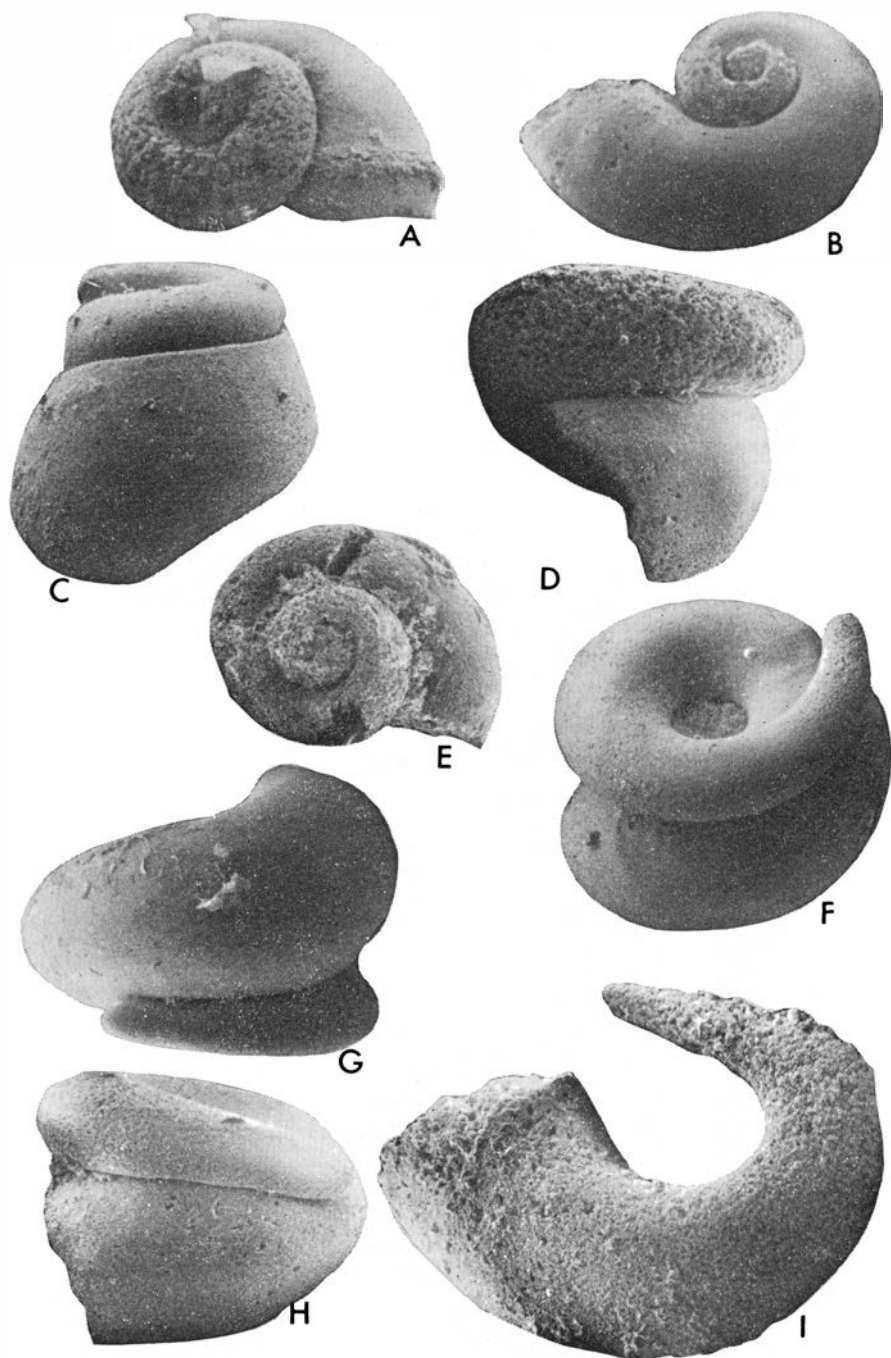


Fig. 5. Steinkerns of curved to helical coiled "worm" tubes from 17 m above the base of the Profilbekken Member. A. PMO NF 3204/1, $\times 100$. B. PMO NF 3204/2, $\times 100$. C. PMO NF 3204/3, $\times 100$. D. PMO NF 3203/1, $\times 100$. E. PMO NF 3201/8, $\times 100$. F. PMO NF 3204/5, $\times 75$. G. PMO NF 3204/4, $\times 75$. H. Specimen shown in 5D rotated about 90° , $\times 100$. I. PMO NF 3202/1, $\times 75$.

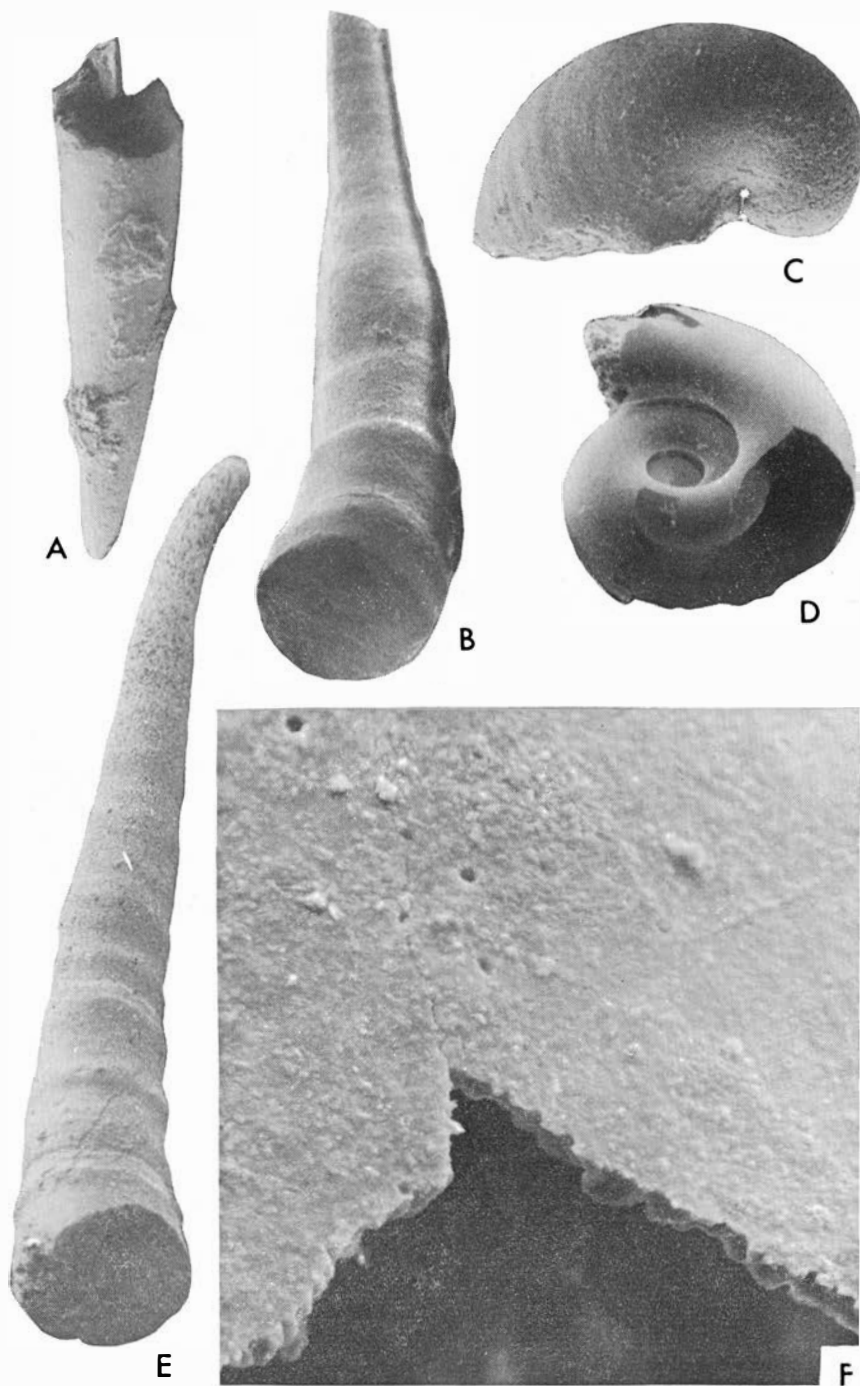


Fig. 6. A. Straight, hollow "worm" tube from 38.8 m above the base of the Profilbekken Member. PMO NF 3204/6, $\times 150$. B. E. Annulated steinkerns (B) from 17 m above the base of the Profilbekken Member. B. PMO NF 3201/6, $\times 75$. E. PMO NF 3204/7, $\times 75$. C. Cephalopod steinkern from 17 m above the base of the Profilbekken Member. PMO NF 3201/10, $\times 100$. D. F. Coiled hollow "worm" tube from 35.3 m above the base of the Profilbekken Member. D. PMO NF 3201/7, $\times 100$. F. Detail of shell of Fig. 6D, $\times 3000$.

The homeomorphy between worm tubes and small gastropods has to be kept in mind. It is especially important when dealing with steinkerns, where even more of the limited information available to the paleontologist for assignment of fossils is lost. To cite one example bearing on bilateral symmetrical forms, EISENACK (1966, Pl. 20, Fig. 4) illustrated one from a Silurian phosphatic residue as a gastropod. It is comparable with our Fig. 4D. We judge that this form illustrated by EISENACK is as plausible a “worm” tube as it is a gastropod.

To cite another example, involving helical forms, MISSARZHEVSKIJ (1969) described the genus *Aldanella* as a gastropod from the lowermost Cambrian (Tommotian) of Siberia. The type specimen of the type species is a phosphatic steinkern. RUNNEGAR and POJETA (1974, p. 313–314) accepted this assignment to the gastropods and used it as one of their points in reconstructing the early phylogenetic history of the mollusks. Yet in size and shape, *Aldanella* and similar enigmatic, small coiled forms that are known only from steinkerns should not be assigned to the mollusks, for there is no way to prove that they are mollusks, and our evidence from Fig. 5 shows that they could fit easily into the “worms”.

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