

The record of the early "Scaphopoda" (?Mollusca) reevaluated

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(With 4 text-figures)

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Abstract

Of the four known reports of Scaphopoda in the Ordovician, two were discounted by earlier investigations. New data is presented for the "scaphopod" *Plagioglypta iowaensis* (JAMES) and it returned to *Coleolus*?, a "worm tube". The published information concerning *Rhytidentalium kentuckyensis* POJETA & RUNNEGAR is subject to reinterpretation, and no feature except logarithmic curvature supports assignment to the Scaphopoda. That taxon is transferred to Phylum Incertae Sedis. Authentic Scaphopoda occur in the Early Carboniferous. Living scaphopods prey on foraminifers in the upper layers of the substrate. It is speculated that the Scaphopoda developed their specialized mode of semi-infaunal life and hunting after the time that calcareous foraminifers became abundant; lack of great morphologic diversity may be related to stability of this restricted habitat and food source.

Zusammenfassung

Von vier bekannten Berichten über ordovizische Scaphopoden sind zwei in früheren Publikationen nur mit Vorbehalt berücksichtigt worden. Neue Ergebnisse über den „Scaphopoden“ *Plagioglypta iowaensis* (JAMES) werden vorgelegt, der wieder als *Coleolus*?, eine „Wurmhöhle“ klassifiziert wird. Die publizierten Daten über *Rhytidentalium kentuckyensis* POJETA & RUNNEGAR werden neu interpretiert. Abgesehen von der logarithmischen Krümmung stützt kein Merkmal seine Zugehörigkeit zu den Scaphopoden. Dieses Taxon wurde in das Phylum Incertae Sedis überstellt. Echte Scaphopoden erscheinen im Frühen Karbon. Rezente Scaphopoden ernähren sich mit Foraminiferen aus den obersten Lagen des Substrats. Es wird diskutiert, ob Scaphopoden ihre spezielle halb-infaunale Lebens- und Ernährungsweise erst seit dem massenhaften Auftreten kalkschaliger Foraminiferen entwickelt haben. Ihre geringe morphologische Diversität könnte mit der Stabilität dieses Lebensraumes und der Nahrungsgrundlage in Beziehung stehen.

Introduction

It is appropriate that a paper honoring Heinz KOLLMANN should be concerned with Mollusca, his favorite group of fossils. Equally, it is appropriate that the work and word of earlier investigators should not be accepted uncritically, for the inquiring mind of Heinz KOLLMANN does not operate in such a fashion. In contrast to these noble sentiments, the subject of Paleozoic Scaphopoda hardly befits a significant milestone in a life, for by almost any criterion, these constitute an inconsequential group of fossils. The phylum Mollusca is second only to the Arthropoda in diversity, yet this Class shows almost no change through time. Still, the older scaphopods may yield a few crumbs of scientific interest.

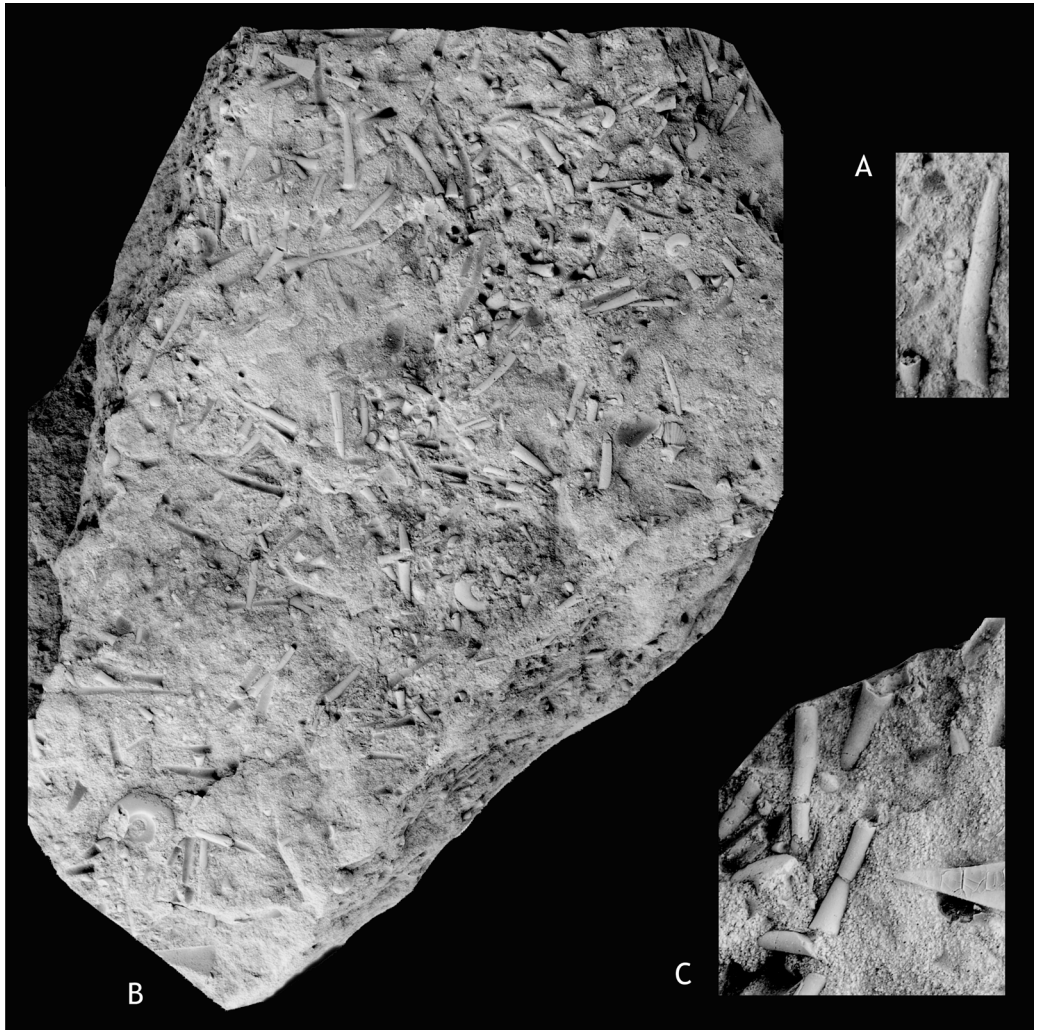
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Some elements of the Recent Mollusca have been examined for millennia. In a general sense, as one moves back in time, Cenozoic mollusks are better known than those of the Mesozoic, though admittedly selected fossil groups have been studied in considerable detail. The Paleozoic Mollusca differ even more from the Recent fauna and are less well-known, in part because of the longer time interval and in part because of a smaller number of investigators. The further back in the Paleozoic that one ventures, the greater the differences from the Recent at all taxonomic levels. There now seems to be general agreement among paleontologists and neontologists that at least one extinct class of Mollusca, the Rostroconchia, existed in the Paleozoic (POJETA et al. 1972, POJETA & RUNNEGAR 1976). It is possible that there may have been a multiple number of extinct molluscan classes in the Paleozoic (YOCHELSON 1978, 1979, 2000). The literature contains a variety of suggestions on the interrelationships of the extant and extinct classes of Mollusca and there is no consensus.

One small point of agreement is that among the extant molluscan classes, the Scaphopoda appeared in the geologic record later than any of the other extant classes; accordingly they were not mentioned in a review of early molluscan phylogeny (YOCHELSON 1979). This generalization of later appearance of the Scaphopoda is irrespective of the arguments concerning the first occurrence of the shell-bearing members of the other extant classes, for there is again no agreement concerning the assignment of Early Cambrian mollusks or mollusk-like fossils. Despite the accepted view that the Scaphopoda are "later," there remains the question as to how much later in the fossil record did the Scaphopoda appear. Within the Linnaean taxonomic hierarchy, all taxa at the same level are of equal importance, for differences among comparable taxa ought to be based on basic morphologic distinctiveness, rather than on the amount of diversity shown by included lower taxonomic levels. Thus, despite the limited diversity of the Scaphopoda, what is the oldest authentic fossil scaphopod should be as valid an issue to pursue as, for example, what is the oldest authentic gastropod or of oldest authentic cephalopod, and it could be of interest for more general issues of interpreting phylogeny.

Some persons argue that the fossil record is so imperfect that the first occurrence of a fossil form provides only a limited amount of data, for earlier examples must have existed and eventually may be found. Such an argument is founded on negatives that are impossible to refute and such philosophical speculations can hardly be of utility when actually considering specimens. It is my general assumption that after more than two centuries of activity by paleontologists, the overall aspect of distribution of fossils through time is fairly accurate, provided the fossils are correctly assigned.

Mollusks are curious-looking animals and perhaps the Scaphopoda hold the distinction of being the strangest. Recent forms are divided into two major groups, now commonly called Dentaliida and Gadilida, but it is only those more or less similar to *Dentalium* that are of concern here. An informal term is "elephant-tusk" shell from the curvature, but the slowly expanding conical shell is bilaterally symmetrical, not trochiform. Equally important, the "tusk" lacks an apex, for both aperture and apical area are open. A marvelous summary of these animals, which discusses both the outside calcareous shell and the inside soft parts, has been published (REYNOLDS 2002).

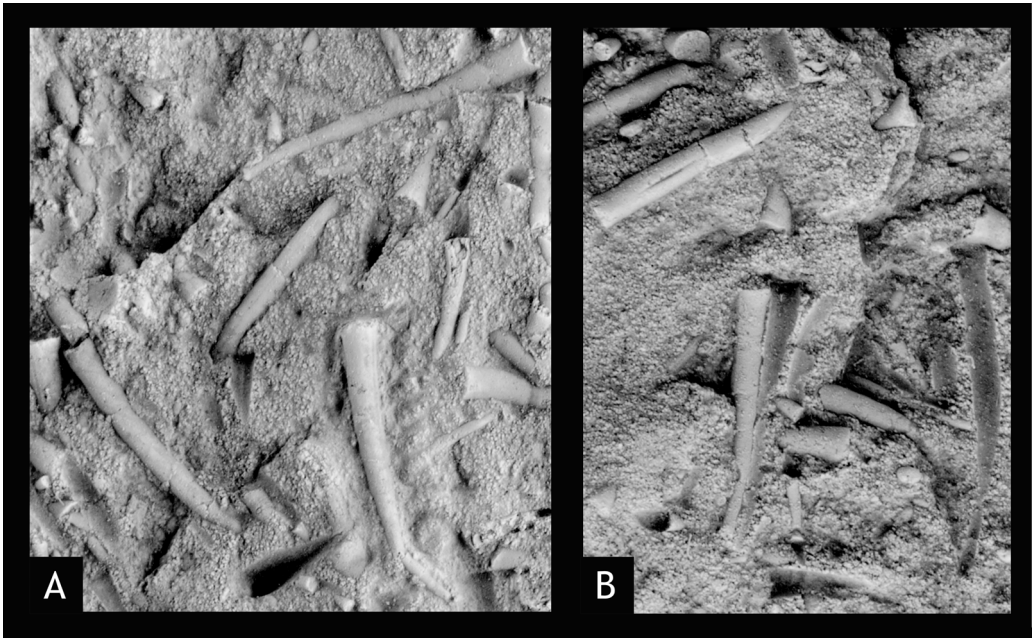


Text-fig. 1: Type specimens of *Coleolus ? iowaensis* JAMES

A: A paralectotype, on a small subrectangular slab (about 5cm x 4cm) which bears only a few individuals, the one figured oriented with the apex upward. Despite partial concealment by matrix, the apical area expands at a lesser rate than most of the tube length of the tube; overall, the tube is nearly straight. An oblique crack is present on the tube. – X 3.9, USNM 516592.

B: The slab which bears the lectotype, seen at the upper left, below and the right of the paper triangle. Several small gastropods occur along with a profusion of tubes; the tubes show no evidence of alignment or sedimentary sorting. – X 1.45, USNM 34628 and 516591.

C: Several broken paralectotypes, which may be current oriented, on a small triangular slab (about 5 cm on a side) exhibiting only a few individuals. – X 1.45, USNM 516593.



Text-fig. 2A, B: Type and topotype specimens of *Coleolus ? iowaensis* JAMES

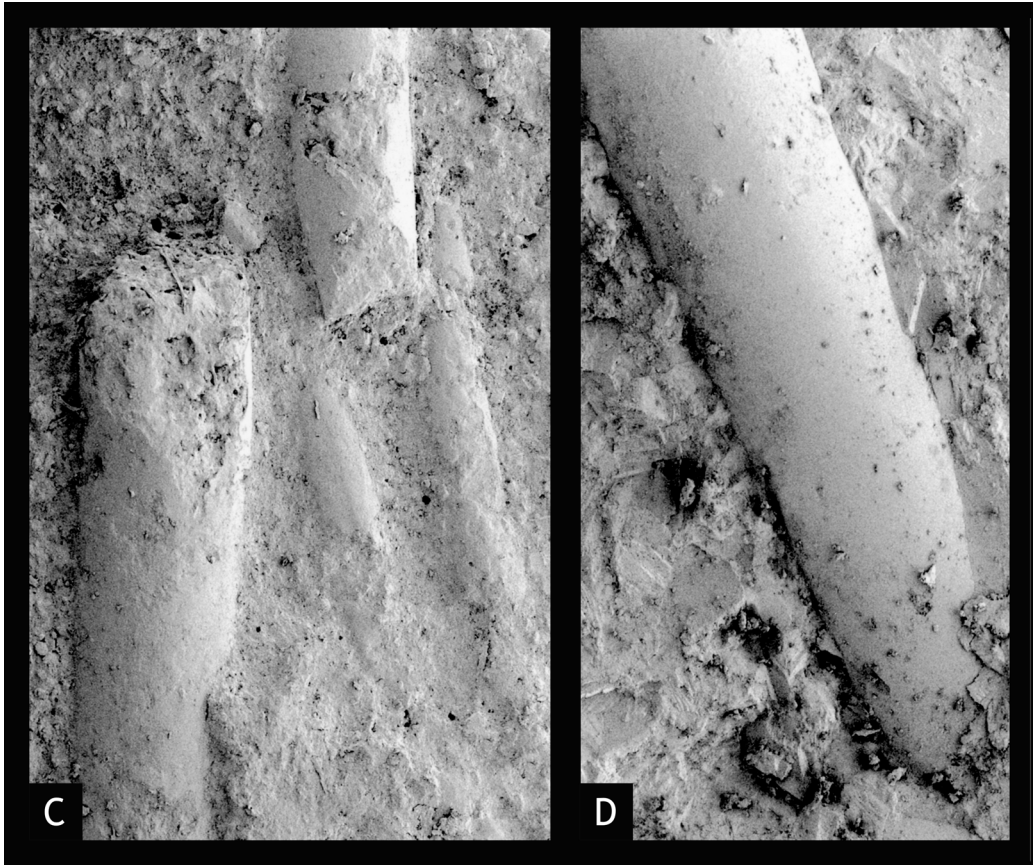
A: The lectotype, the nearly straight specimen to the lower right; it is broken at the apex and a fragment lying in that area gives the appearance of an abrupt bend. – X 1.8, USNM 34628.

B: Other paralectotypes from near the left side center of text-figure 1B. To the far right, an external impression is distinctly curved, with a tiny mold below, and to its left and in the upper left are two essentially straight specimens. – X 4.8, USNM 516591.

Reports of Ordovician scaphopods

So far as the literature is known to me, there have been four reports of Scaphopoda in the Ordovician. Two of these earlier interpretations have been refuted. For the first, CLARK (1925) named *Polylophia* for a fossil from the middle Middle Ordovician Murfreesboro Formation of Tennessee, USA. FISHER (1958) assigned it to the Scaphopoda, though later he (FISHER 1962: W137) transferred it to "Phylum, Class, and Order uncertain." On the basis of new material, YOCHELSON (1968) determined that the type species had a closed apex and therefore was conclusively not a scaphopod; he judged it to be an orthothecid hyolith mollusk.

In regard to the second report, a Russian cephalopod specialist (KISELEV 2002) has re-examined reports from the St. Petersburg region of Middle Ordovician scaphopods by EICHWALD (1860) and KOKEN (1925). Some of the original material has been lost and what remains are steinkerns. His preliminary conclusion is that these reports are probably based on broken steinkerns which infilled part of the body chamber of orthoconic nautiloid cephalopods from the "Cephalopod limestone." Even though this is a prelimi-



Text-fig. 2C, D: Type and topotype specimens of *Coleolus ? iowaensis* JAMES

C: An SEM photograph of a tiny specimen between larger ones, the specimen seemingly tapering toward the apex. – X 26.5, USNM 516598.

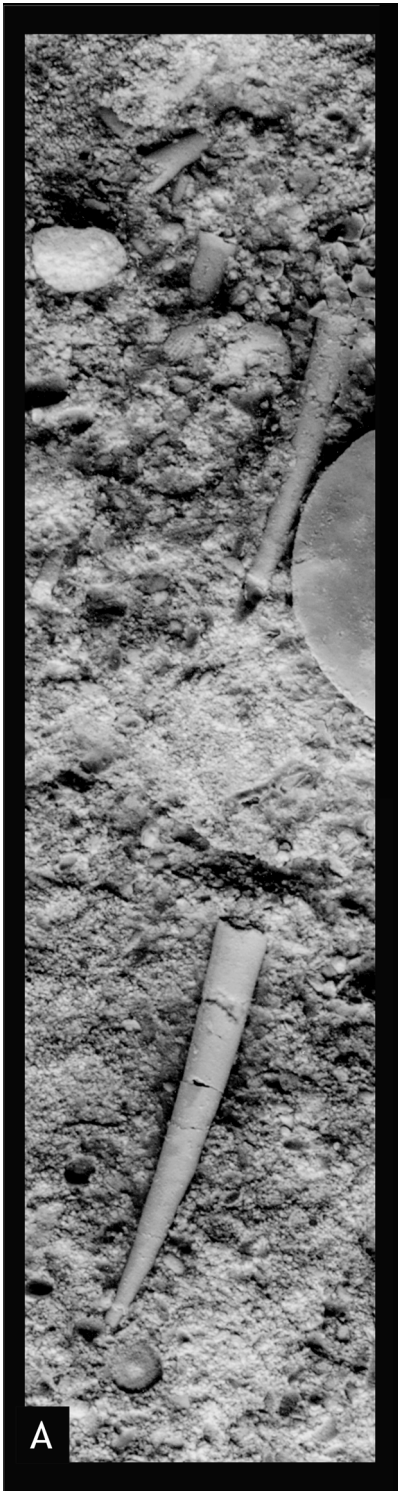
D: An SEM of one of the smallest specimens observed; near the apical end, the specimen seems to taper more abruptly. – X 108, USNM 516599.

nary conclusion, the published illustrations show no features which demonstrate or even suggest that these fossils are correctly assigned to the Scaphopoda.

There remain two reports of Ordovician Scaphopoda from the United States to be considered.

The issue of *Plagioglypta iowaensis* (JAMES)

JAMES (1890: 354-355) discussed and described *Coleolus?* sp. from the late Late Ordovician Maquoketa Shale of Iowa, USA, but did not illustrate it. He ended a paragraph with "Should this prove to be a new species, I propose the name of *Iowaensis* for it." At that time, such a provisional designation of a new species was acceptable in zoological



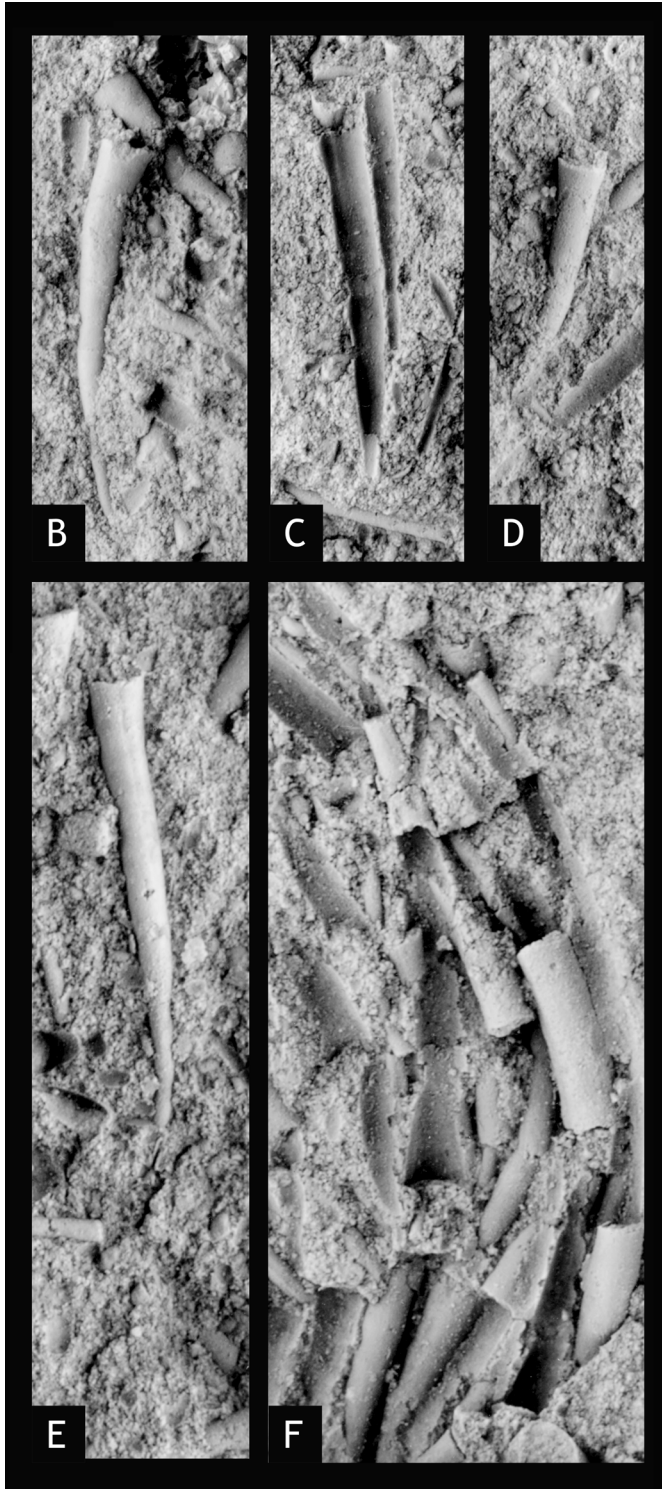
nomenclature. In accord with the intent of the author, this trivial name should go with *Coleolus?* and not *Coleolus*. Following the original description, *Coleolus? iowaensis* JAMES (1890: 355) did not figure prominently in the literature. BASSLER (1915: 256) listed only the original description, with a notation that the species occurs in Illinois and Iowa. LADD (1929: 384) included the name in a faunal list.

The species had a moment of fame when BRETSKY & BERMINGHAM (1970) transferred what they termed *Coleolus iowaensis* to *Plagioglypta* as a member of the Scaphopoda and designated a lectotype (text-fig. 2A) (BRETSKY & BERMINGHAM 1970: Pl. 131, fig. 2). The species has never been compared to other species of *Coleolus*, though BRETSKY & BERMINGHAM (1970) did compare it to several species of *Plagioglypta* and presumably that comparison validated the provisional name. As discussed below, on the basis of restudy, I cannot support the transfer to *Plagioglypta* and the species is herewith returned to *Coleolus?* To the best of my knowledge the species has not been restudied since 1970.

The type lot, in the collection of the National Museum of Natural History, consists of six pieces of somewhat weathered, yellowish-brown, relatively soft matrix, each piece bearing one or more specimens. The original lot number, USNM 34628, is retained for the lectotype. The remaining specimens on the lectotype slab and those on the other five pieces, USNM 516591-516596, both figured and unfigured are assigned the status of paralectotypes. The lectotype slab (text-fig. 1B) and a few paralectotypes (text-figs. 1A, 1C, 2B, 3) are illustrated. They are from a railway cut near Graf, Iowa (BRETSKY & BERMINGHAM 1970: 911), in the basal portion of the formation. A summary of the Graf section and an interpretation of lower part of the section was published by WITZKE et al. (1997).

Text-fig. 3A: Type specimens of *Coleolus ? iowaensis* JAMES

A. Two paralectotypes, on a trapezoidal slab (about 7 cm by 5 cm); the lower one is curved slightly and the upper, to the left of the label, is essentially straight. – X 5.9, USNM 516594



Text-fig. 3B-F: Type specimens of *Coleolus ? iowaensis* JAMES

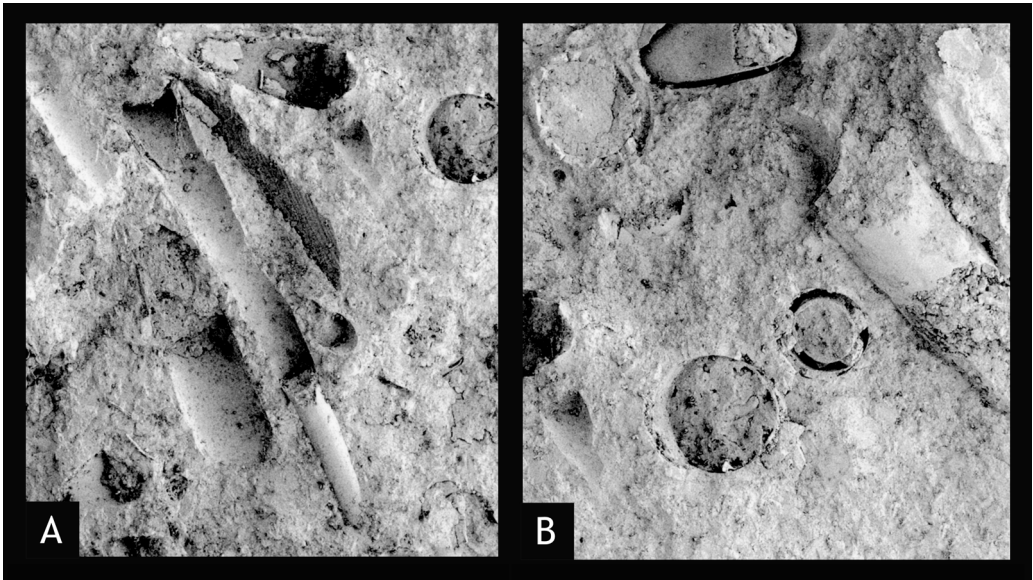
B: A distinctly curved paralectotype on a trapezoidal slab (approximately 7 cm by 6cm); the right side of the broken aperture appears to expand, or flare, at a greater rate than the main portion of the tube below it. – X 5.1, USNM 516595.

C: Two paralectotypes preserved as external impressions, neither of which shows any indication of growth lines. – X 5.1, part of same slab as above, USNM 516595.

D: An incomplete paralectotype preserved as an external impression and an incomplete paralectotype, a steinkern, to its left. The apertural area of the steinkern is expanded at a greater rate than the lower portion of the tube immediately below; the external impression suggests a similar flaring, but this may be a function of irregular height of matrix along the walls of the impression. – X 5.3, part of same slab as above, USNM 516595.

E: A paralectotype to the upper left, which despite partial covering by matrix, seems to show a lesser rate of expansion in the apical area, and is nearly straight. To the lower right, another paralectotype, mainly preserved as an external impression, is distinctly curved. – X 6.8, part of same slab as above, USNM 516595.

F: Closely spaced, broken paralectotypes on part of a small rectangular slab (about 5 cm by 2 cm); the curved pattern of the fossils and the topography of the slab suggests that a current swept them into a slight depression. – X 7, USNM 516596.



Text-fig. 4A, B: Topotype specimens of *Coleolus ? iowaensis* JAMES

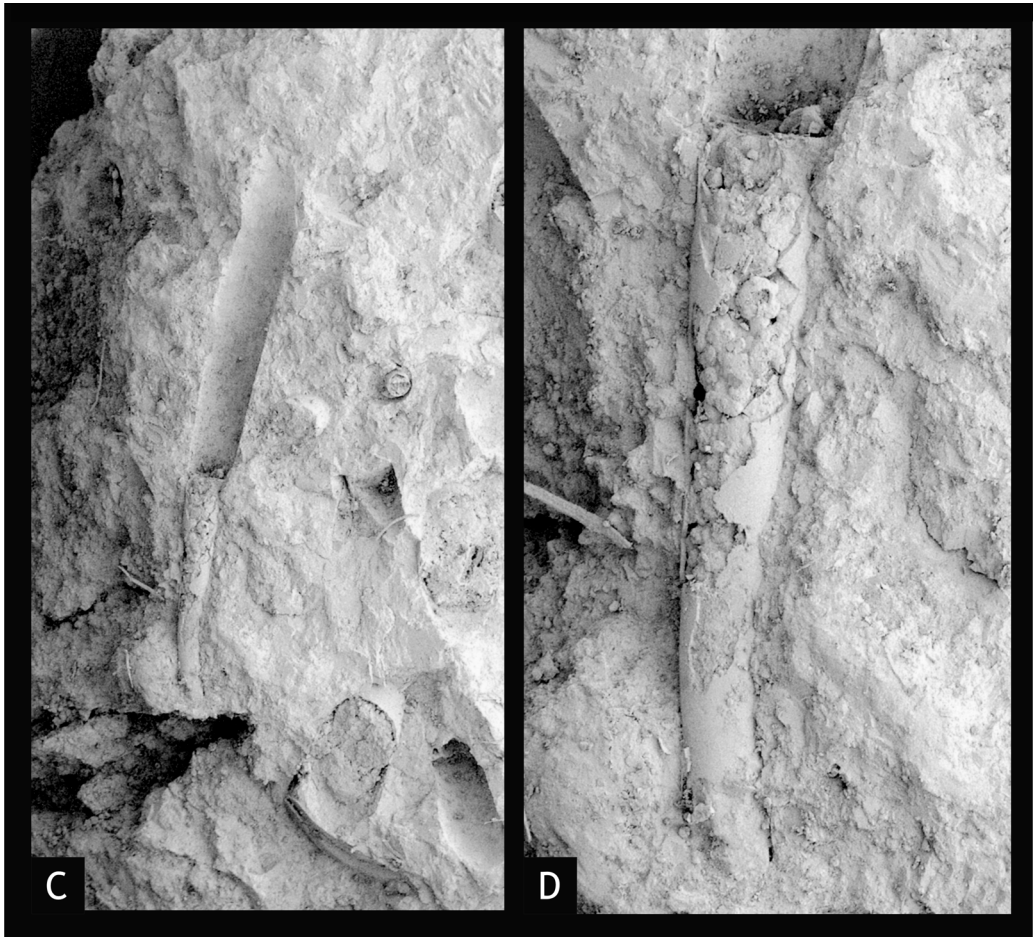
A: An SEM photograph of a small steinkern from the apical area and the longer associated external impression; no growth lines are seen on the impression. – X 14, USNM 516597.

B: An SEM photograph of several cross sections: the specimen to the upper right of 4A is to the lower left. The shell of the smaller cross-section is thinner than that of the larger, suggesting that the large specimen was broken across near the growing aperture; both cross-sections suggest the presence of several shell layers. – X 19, USNM 516597.

In addition to the types, I have examined topotype specimens from Graf, Iowa. These are in unweathered limestone, light gray in color. Combined with the type lot, this material indicates that the specimens occur through at least 4 cm of strata, but are most abundant on a bedding plane surface. Some slabs show that the specimens have been transported (text-figs. 1C, 3F), a well-known feature of the Maquoketa fauna, but others show no alignment of specimens. SEM photographs of the topotypes (text-fig. 4) add new details; the size of the pieces in the type lot precluded use of SEM with them.

As mentioned above, one feature of scaphopod morphology is two shell opening, one at the aperture and a second modified by bioerosion of the apical area. If there is any apical opening on these shells, it can be demonstrated to be exceedingly tiny at most (text-figs. 1A, 2B, 3A, 3B, 3E), and, on at least two specimens, almost certainly the apex is closed (text-figs. 2D, 4D). If so, this is conclusive evidence that the form cannot be assigned to the Scaphopoda. Commonly, among most Paleozoic occurrences of larger tubular fossils, the apical, or narrower portion, is broken and therefore the presence or absence of an apical opening cannot be studied. It is rare to find an unbroken tip, even among fossils the size of these Iowa examples; styliolines, novakiids, and other tubular fossils of a smaller size range more commonly show a closed apex.

Several ancillary points also argue against assignment to Scaphopoda. First, as noted by JAMES, specimens show considerable variation in shape, from distinctly curved (text-



Text-fig. 4C, D: Topotype specimens of *Coleolus ? iowaensis* JAMES

C: An SEM photograph of one of the larger specimens, mainly as an external impression; no growth lines are seen on the impression. – X 17, USNM 516597.

D: An SEM photograph of the steinkern shown in 4C; the curvature of the lower portion of the tube is greater than that of the part above, resulting in a slight bend, rather than a smooth curve. – X 58, USNM 516597.

figs. 3B, 3E), though gently curved (text-figs. 3A, 3C, 4C) to essentially straight (text-figs. 3A, 3E); most Recent scaphopods do not show such a degree of variation in curvature. There is some slight evidence that the apical portion of the shell expands at lower rate than the main body of the tube (text-figs. 1A, 2D) though this may be a result of varying levels of matrix partially enclosing the tube. There is also a suggestion, somewhat more reliable that the apertural area flares out slightly from the uniform expansion of the main portion of the tube (text-figs. 3B, 3D). Second, the shell seems relatively thin compared to living scaphopods of the same size (text-figs. 4A, 4B). A molluscan shell is "knife edge" thin at the apertural margin and gradually thickens internally as the

growing edge moves forward. An internal filling or steinkern, which lacks the shell show s this in terms of a flare, or wider area adjacent to the apertural margin. On some gastropod steinkerns, this flaring may be observed. Scaphopod shells increase in thickness so gradually that no such flaring is seen. Indeed, because the scaphopod shell has two openings, infilling to form a steinkern is unlikely; I have never observed a steinkern of a scaphopod.

Third, on the lectotype slab (text-fig. 1B) intermixed with the *Coleolus?* specimens are a few low-spired gastropods (text-fig. 1B); rare high-spired gastropods are on a topotype slab. The tubes on the lectotype slab show no indication of current alignment and because the gastropod shape has different hydrodynamic properties than the smaller tubes one might be permitted to speculate that there has been little or no significant movement of these specimens. Allowing for some breakage, the *Coleolus?* are all within a limited size range. Since mollusks typically grow continuously, if these tubular fossils were mollusks one might anticipate that some larger specimens could be present, comparable in size to the high-spired gastropods.

Fourth, the population density is remarkably high (text-fig. 1B); as with the previous point, this is admittedly a weak criterion for differentiating "worms" from mollusks. In defense of it, I quote from Phillip PALMER (written communication, 2003) who has specialized for many years on the study of Scaphopoda. "Some years ago, during a very low spring tide combined with a high pressure system, I was able to walk for a while in Portland Harbour, Dorset, literally on the bottom of the sea. There were scattered dead shells, including *Antalis vulgaris*. I noticed shallow depressions in the silty mud, at the bottom of which were the apices of *Antalis*. We pulled some out for dissection. The living ones were distributed at intervals varying from one to three feet, as also were the dead shells! Unlike the huge densities of *Ditrupa*, scaphopods do not live 'cheek-by-jowl'! So even if it is the 'weakest argument,' it is the first which 'clicks in' with me, and won't go away until something conclusive arrives, like bioeroded apices."

Coleolus is generally accepted as a "worm tube." It was named from the Middle Devonian and among its other features, the tube is calcareous. Accordingly, the question mark also points to the biologic issue of whether the Maquoketa species is correctly assigned to that genus. Some individuals suggest that the shell structure consists of several thin layers, a feature not typical of mollusks (text-figs. 4A, 4B). *Polylophia* was judged to have multiple shell layers (FISHER 1958), a feature I interpreted as due to imbrication of specimens by current transport. Regardless of whether some *Coleolus?* were transported, that explanation cannot be applied to these tubes. External impressions (text-figs. 3C, 3D, 4A, 4C) show no indication of growth lines.

Many years ago, a sensitive chemical test for P₂O₅ demonstrated that phosphorus is abundant in the shell of several topotype specimens and more recently, electron probe of another specimen again indicated the presence of large amounts of phosphorus. Specimens which are phosphatic and those which have been secondarily phosphatized are difficult to distinguish. If the Maquoketa species is phosphatic, clearly it is fundamentally different from *Coleolus*, but if it is phosphatized, the species might belong to that taxon. Many steinkerns in this unit, though not all, show a phosphatic "sheen." Whether that is a result of weathering or differential phosphatization is an issue beyond the bounds of this work. A few specimens of several classes of undoubted mollusks occur in the same horizon,

and none of the steinkerns or broken shells I have observed show any indication of phosphatization. Other paleontologists, more interested in chemistry and shell structure may pursue the issue of comparing the composition of these scaphopod-shaped tubes with the accompanying mollusks. In my view, the morphologic differences from authentic Scaphopoda alone are sufficient to return the JAMES species to *Coleolus*?

The issue of *Rhytidentalium kentuckyensis* POJETA & RUNNEGAR

In contrast to the previous species, I cannot contribute new data concerning this species and genus (POJETA & RUNNEGAR 1979); neither the figured types, nor unfigured specimens are available in the collections of the National Museum of Natural History. A few years prior to the publication of this taxon, YOCHELSON and POJETA were engaged in collecting from the Middle Ordovician of Kentucky, USA. Limestone blocks were dissolved in hydrochloric acid to obtain the silicified fossils contained therein. The emphasis in collecting these blocks was on molluscan-bearing localities, and although no figures were kept, some tons of limestone were dissolved in acid.

At the time we removed these fossils from the acid bath, I was impressed with the large number of specimens which form the basis for the genus and species and made a comment on the gregarious accumulation. Whereas genera of gastropods and pelecypods were widely distributed among the Kentucky outcrops, half of the 46 reported specimens of this taxon are from one locality in the late Middle Ordovician and the remainder are from three other localities. In and of itself, this difference in distribution pattern may mean little. I also offered an opinion that the cross-section did not appear to be circular. Both these issues were considered by POJETA & RUNNEGAR (1979) and dismissed; two apertural views are illustrated by POJETA & RUNNEGAR (Pl. 1, figs. 12 and 13) and one is distinctly oval.

One feature of *Rhytidentalium* is that "the only known sculpture is concentric and consists of growth lines, which indicate prolonged periods of minimum growth on some specimens; otherwise, the shell is smooth;" (POJETA & RUNNEGAR 1979: 531). On page 536 they mention "pronounced irregular growth lines" and later "Such prominent irregular growth lines are very common on various living scaphopods."

Comparison in the illustrations is to specimens of the Recent *Spadentalina*, and the features are there referred to as growth stoppages. The irregularities noted at some of these stoppages indicate that the apertures were broken and subsequently repaired. Whether this feature is the result of predation or breakage by movement through the substrate is unknown, but the growth stoppages and the growth lines, where the shell is being normally secreted and not repaired, are not the same in *Spadentalia*. There is no reason to assume that the growth stoppages of *R. kentuckyensis* bear any similarity to growth lines. Indeed, the two growth stoppages shown on the illustrations of the holotype and one of the paratypes (POJETA & RUNNEGAR 1979: Pl. 1, figs. 14 and 16) have slightly different orientations. Some specimens show growth stoppages and others do not, which suggests that the stoppages were not a fundamental feature.

It is to be emphasized that all known specimens are silicified. Occasionally, the process of silicification may replace one shell layer, but not a second. Although this is an un-

likely event, the taphonomic fact cannot be ignored and was not considered in discussion of the assignment of this genus. Because of the replacement, it is impossible to make any comments on the original composition or structure of the shell, which eliminates one potential source of data on whether the specimens belong in the Mollusca. Essentially all one can conclude is that the shell may have been thin, hardly a dramatic feature of small specimens.

Eight of the nine specimens illustrated show curvature which may follow a logarithmic curve; presumably all specimens showed curvature. Comparison among the illustrated specimens suggests that the curvature is uniform, except that plate 1, figures 11 and 14 of the authors hint at a subtle difference.

With one exception, the apical end of the holotype and illustrated paratypes are not illustrated. This exception is shown in plate 2, figure 7, and one may assume that this is the only specimen on which the apical area was not broken away. As illustrated, the shell tapers apically toward a hole, the degree of tapering changing near the hole. One may readily compare this hole with the apical region of a *Dentalium* shown on their plate 3, figure 12, that has been modified by bioerosion; they are not similar. The illustrated specimen is either heavily coated with extraneous silica or was a shell lying on the bottom that was later encrusted by a bryozoan colony. If it were a dead shell, there are many mechanisms by which the hole could have formed.

The authors compared their genus and species to a variety of other fossils, including several kinds of Recent tube-secreting worms. The assignment of *Rhytiotalium* to the Scaphopoda was done "... on the basis of its shape, its logarithmic growth form, the fact that the shell is not composed of agglutinated particles and because some specimens of *R. kentuckyensis* have irregular very prominent growth lines, which are also very common in living scaphopods" (POJETA & RUNNEGAR 1979: 536). In my summary, there is no information on the composition of the tube. There are no growth lines on the specimens to reflect the shape of the aperture. There is no apical opening which can be demonstrated to be the result of bioerosion during the life of the animal; POJETA & RUNNEGAR (1979: 531) note "slit and pipe absent."

Logarithmic curvature of the tube is the only feature which is scaphopod-like. The Late Carboniferous *Clavulites* GIRTY (see YOCHELSON 1971) was originally described as a scaphopod, but was reassigned to the "worms" because of the cross-sectional shape and a difference course of its growth lines; nevertheless, the curvature and size is comparable to that of *Rhytiotalium*. The Late Carboniferous *Dentalium meekianum* Geinitz is even closer in terms of size and curvature to this taxon, but, again, other features of morphology demonstrate that it is not a scaphopod (NÜTZEL & YOCHELSON, unpublished). The Late Devonian *Coleolus curvatus* KINDLE (see YOCHELSON & HLAVIN 1985) is a wider, shorter cone found standing upright life position with its closed apex in the sediment. Some nonsense included in the paper regarding specimens curving to the right or the left is a error by YOCHELSON who did not recognize parts and counterparts as being the same specimen; a correction was distributed but not published.

In the legal system of the United States, a jury delivers a verdict of "guilty" or "innocent." In Scotland, a jury has the additional option of "not proven." This third option is the best verdict that I would bestow on *Rhytiotalium*. If this option was not available, I would vote that the genus is innocent of being a scaphopod.

Discussion

It is my experience that removing a taxon from the literature or transferring it to a different higher taxon is many times more difficult and time consuming than publishing a new taxon. Fortunately, the International Rules of Zoological Nomenclature make it clear that up to the family level of classification, the latest publication is authoritative. Thus, any such reinterpretation may stand unchallenged for what might be a long interval of time, for changes indicated in regard to an earlier published taxonomic investigation remain in force until a subsequent publication produces yet another change. Accordingly, on the basis of my investigation, *Plagioglypta iowaensis* (JAMES) reverts to *Coleolus? iowaensis* JAMES. If the reasons presented for this change are accepted, no one will reinvestigate this taxon. Until such time as that taxonomic statement is refuted by any subsequent publication, a third Ordovician "scaphopod" is herewith removed from Class Scaphopoda.

Above the family level of classification there are no formal rules, only customs and a certain degree of common sense, combined with the weight of generally accepted practice. For example, to suggest today that the bivalved *Pecten* be transferred to the Brachiopoda goes against practice and common sense. A century and a half ago, Brachiopoda and Pelecypoda were united as part of the Molluscoidea, but that was a long time ago. For less studied groups, a transfer may be made without creating any uproar, such as the above example would surely provoke. Still, the transfer of a taxon away from one taxonomic group, especially without precise indication of which higher taxonomic group it should be affiliated, is far more difficult to accept than the moving of a species from one genus to another.

In classifying a fossil, the questions of what that fossil is and what it is not do not constitute mirror image questions. If as a result of various consideration, I do not find the evidence convincing that *Rhytiodontalium* is a scaphopod, stating that opinion does not require that I also present data to support placement in a different higher level group. My unofficial judgment is that the genus may be based on a "worm tube," but there are several major kinds of Recent tube-forming worms, and who knows how many extinct forms were formerly present. So long as I can present a reasonable case that *Rhytiodontalium* may not be a scaphopod, it seems more prudent at this time to let the issue of where it might be assigned with greater biologic credibility remain open.

In some sense, the assignment of *Rhytiodontalium* to any phylum or class is a "yes it is/no it is not" argument, but the point cannot be dismissed that simply. It is nature of systematics that the positive position of a definite assignment is almost always the one first taken. Only additional data, or reevaluation can change the original assignment, and unfortunately without new data, reevaluation may descend to the "no it is not" type of shouting argument. The worse case situation is that of using authority as the sole basis for making a statement on reevaluation.

Having made that comment, my position is that I do not regard *Rhytiodontalium* as having been demonstrated by its morphology to be a member of the Scaphopoda. In my view, it does not follow that a curved tube is automatically evidence of a relationship to the Scaphopoda; more morphologic information is needed to demonstrate such assignment. To rephrase this issue, does one assign all curved fossil tubes into the Scaphopo-

da or does one place undoubted fossils in the Scaphopoda and set aside questionable forms? The first course makes for easier identification, but it may lead to an unwieldy and artificial grouping which could mask developments through time. The second course, which I prefer, results in one group of fossils more clearly defined morphologically and a separate group requiring further investigation. To follow this second course, I am formally removing *Rhytidentalium* from Phylum Mollusca, Class Scaphopoda and transferring it to Phylum Incertae Sedis.

Whereas formal taxonomic effort is required to change the placement of the JAMES taxon, a simple published disagreement that my arguments are based on "a house of cards" or "smoke and mirrors" might be sufficient to return *Rhytidentalium* back to the Scaphopoda. On the other hand, if the new interpretation of *R. kentuckyensis* POJETA & RUNNEGAR is accepted, there currently are no valid reports of Scaphopoda in the Ordovician.

Speculations

Seemingly, there have been no reports of Silurian Scaphopoda in the literature (LUDBROOK 1960). Reports of Devonian Scaphopoda have been either refuted by transfer to other groups (YOCHELSON & GOODISON 1999, YOCHELSON 2002) or strongly questioned for the material assigned to the Scaphopoda does not show morphologic features which are indicative of the class (YOCHELSON & HOLLAND 2004).

As I understand that issue, unless there is clear evidence of modification of the shell at the apical end of the shell by bioerosion, one cannot be certain that a tubular fossil is a member of the Scaphopoda. On the other hand, if the apex is closed, scaphopod affinities are conclusively ruled out. Beyond that, it is difficult, if not impossible, to list criteria from the hard parts alone which characterize a fossil as a mollusk, let alone assign it to a class. A combination of thick shell, closely spaced, gently oval growth lines, and a slight degree of logarithmic curvature are suggestive of scaphopod affinities, but under no circumstances can they be considered diagnostic.

BRETSKY & BERMINGHAM (1970: 910) cited early several papers that mentioned the occurrence of Scaphopoda in the Devonian, but curiously enough they neglected the publication of GOLDFUSS (1841). I have not investigated all these Devonian references, but have seen enough of the early literature and early collections to appeal to authority and state that further interpretations probably will show that this earlier literature contains either readily refuted inaccurate assignments or is based on material inadequate to demonstrate that the fossils in question are authentic members of the Scaphopoda. Of course, one cannot really predict the future, and it could be that tomorrow an undoubted Devonian or Ordovician member of the Scaphopoda will be found. Still, as some American card playing gamblers would state, I would "bet the farm" that there are no Scaphopoda of lower and middle Paleozoic age.

There are undoubted Lower Carboniferous Scaphopoda. At least one was illustrated by de KONINCK (1883; GODFROID & YOCHELSON, unpublished) and several specimens are known from Scotland (YOCHELSON, unpublished). By undoubted, I mean that not only do these fossils convincingly show that the inclined surface of apical area has been modified by bioerosion, but the apical opening also includes a notch or a short vertical slit. The slit is more or less at right angles to growth lines.

In no way should this refutation of pre-Carboniferous Scaphopoda be considered a disparagement of the efforts of others, but rather it could be judged as an attempt to advance ideas based on increasing knowledge of the class. Some descriptions of presumed scaphopods were published at a time when the class was not yet even differentiated from the Gastropoda. Other descriptions were based on the assumption that longitudinal lirae were a feature of Scaphopoda, with little understanding that a few Paleozoic orthoconic Cephalopoda were similarly lirate; that rare nautiloids are curved "orthocones" further confounded correct assignment (HOLLAND & YOCHELSON 2000). Indeed, it provides an unexpected complication to the concept of convergence or homeomorphy (YOCHELSON & HOLLAND 2004). Still other confusion stems from the lack of interest in detailed study of tubular fossils which might be attributed to worms. A number of both living and fossil presumed scaphopod species have turned out to be serpulid worm tubes (PILSBRY & SHARP 1897), but other kinds of tube-forming worms are known.

From time to time, a few Mesozoic and Cenozoic species are still being removed from the class and placed in the "worms" (for example, PALMER 2001). Even though undescribed taxa of Scaphopoda are known from the Late Paleozoic and a detailed study of a fossil group almost invariably results in older species being "split," it is unlikely that this class will show much more diversity on the generic and higher-level than is currently known.

Current theoretical studies place much emphasis on evolution - change through time - but little on stasis. The Scaphopoda show essentially no change in basic morphology throughout their geologic range, and by one definition they might be thought of as living fossils, in the same sense that *Lingula* is a living fossil. Regardless of the terminology, the Scaphopoda would seem to be an excellent example of non-evolution.

Recent scaphopods are predators, trapping foraminifers in the upper layers of bottom sediments with an ingenious system of tentacles (SHIMEK 1988, 1990; REYNOLDS 2002). There is no reason to assume that earlier fossils had a different life habit. If a habitat does not change, why should a well-adapted organism be subject to change? Concurrence of two events does not prove cause and effect and often is only coincidence. Still, some Lower Carboniferous limestones contain the oldest occurrences of abundant calcareous foraminifers. Likewise, the Early Carboniferous is the oldest occurrence of authentic Scaphopoda in the fossil record.

If one looks at the Dentaliida, the principal group of Scaphopoda, it appears that essentially the only prime morphologic change is the mid-Mesozoic development of prominent coarse liration in a few genera. The development of such coarsely lirate forms occurs at approximately the last time limestones are abundant in the geologic record. Perhaps the underlying reason for this change in ornament is related to a change in the habitat of some foraminifers.

It has been speculated that this morphologic feature enabled the coarsely lirate forms to burrow into slightly coarser sediments (YOCHELSON et al. 1983). Detailed study of sediment size and composition for a variety of living scaphopods is needed to confirm or refute this notion, and seemingly the data does not exist. The minor change in substrate habitat, postulated above, placed *Dentalium* and its close allies in the habitat of predatory gastropods, such as *Polinices*, which bore shells. Despite high levels of predation, apparently these scaphopods have developed no evolutionary mechanism to counter that threat, another example where the ugly facts yielded by these beasts confounds elegant theory.

To some extent, every investigator is a prisoner of his own preconceptions and no one is an entirely independent observer. In the model of molluscan evolution proposed by RUNENGAR & POJETA (1974), the major extant classes were to be developed early in the geologic record, and thereby the presence of scaphopods in the Ordovician fit into theory. POJETA & RUNNEGAR (1976) suggested that ribeirioid rostroconchs gave rise to the Scaphopoda. In the ENGESER & RIEDEL (1996) model, a later group, the conocardoid rostroconchs were suggested as ancestral forms; this approach, in part, may have based on the view that the oldest scaphopods occurred in the Devonian, for there are more references to Devonian scaphopods in the German literature than in that of any other country. In my model of evolution (YOCHELSON 1978), I also uncritically accepted a Devonian age for the start of the class. Because I could not find a reasonable ancestor for the Scaphopoda, I speculated that a shell-less mollusk existed until that time, a hypothesis for which I have been properly criticized by several different authors. As a replacement for that failed idea, I suggest that a great deal of evolution may occur rapidly – that is in the geologic sense - in the free floating larval stage. The "hopeful monster" of GOLDSCHMIDT receives little respect, but the idea may be more fundamental than generally accepted. After all major "missing links" between classes and phyla, still remain missing.

Once one begins on the path of evolutionary speculation, the slope is slippery and it is difficult to stop. A number of ideas of the interrelations of Scaphopoda to the other extant molluscan classes have appeared in the literature (STEINER 1992). The oldest view is that the scaphopods are allied in some way to the pelecypods; that opinion seemed to predominate in the literature for decades. POJETA & RUNNEGAR (1976) proposed the term Diastoma to include the Rostroconchia, Pelecypoda (=Bivalvia) and Scaphopoda, with their Cyrtostoma used for the combination of Monoplacophora, Gastropoda and Cephalopoda.

As a modification of the pelecypod- scaphopod relationship, building on earlier views they had discussed, POJETA & RUNNEGAR (1979) postulated that the ribeirioid rostroconch *Pinnocaris* could have been the ancestral form which gave rise to the scaphopods in the Ordovician. After extended discussion, this concept was accepted by STEINER (1992), Discovery of the protoconch in fossil scaphopods (ENGESER et al. 1993) refocused attention on the protoconch of Recent forms and led to the view that scaphopods appeared in the Devonian and were derived from conocardoid rostroconchs.

More recently assignment of Scaphopoda within the Cyrtostoma has been proposed. An old idea of relationship to the Gastropoda has been replaced by the suggestion that scaphopods are related to cephalopods (STEINER & DREYER 2003). The Scaphopoda possess a radula, and seeming the only way to resolve that problem among the Diastoma is to infer that the fossil rostroconchs had a radula. By suggesting that the Scaphopoda have a head which is much reduced and have lost organs of sight, among other simplifications, the radula question is resolved. On the other hand, there is tremendous amount of morphologic difference and habitat change between cephalopods and scaphopods. Recent cephalopods differ from other living mollusks in having direct development within egg capsules. Such a stable environment may be appropriate for gradual change, but probably it would not subject a trochophore larva to dramatic environmental pressures and strong selection. Rather than worrying about presence or absence of a radula, based on no evidence, the issue would then become one of when did the cephalopods lose their larval stage. This is again a concern for which there is no evidence, but, if nothing else, it would be ranked as a more major problem.

Probably the only way to end an endless stream of speculations about Scaphopoda is to note an American truism. No matter how difficult and complex the problem, when it is approached in a scientific manner, it will become worse!

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References

- BASSLER, R. S. (1915): Bibliographic index of American Ordovician and Silurian fossils. – United States National Mus. Bull., **92** [two volumes].
- BRETSKY, P. B. & BERMINGHAM, J. J. (1970): Ecology of the Paleozoic scaphopod genus *Plagioglypta* with special reference to the Ordovician of eastern Iowa. – Jour. Paleont., **44**: 908-524.
- CLARK, T. H. (1925): On the nature of *Salterella*. – Trans. Royal Soc. Canada, **19**: 12 p.
- EICHWALD, E. d' (1860): Lethaea rossica ou paléontologie de la Russie, décrite et figurée. – Vol. 1, Seconde Section de l'ancienne Période.
- ENGESER, T. & RIEDEL, F. (1996): The evolution of the Scaphopoda and its implications for the systematics of the Rostroconchia (Mollusca) . – Mitt. Geol. Paläont. Inst. Univ. Hamburg, **79**: 117-138.
- , — & BANDEL, K. (1993): Early ontogenetic shells of Recent and fossil Scaphopoda. – Scripta Geol., special issue **2**: 83-100.
- FISHER, D. W. (1958): *Polylophia* Clark, an Ordovician scaphopod [Tenn.] . – Jour. Paleont., **32**: 144-146.
- (1962): Small conoidal fossils of uncertain affinities: 98-145. – In: MOORE, R. C. (ed.): Treatise on Invertebrate Paleontology, Part W, Miscellanea. – University of Kansas Press and Geological Society of America.
- GOLDFUSS, G. A. (1841-1844): Petrefacta Germania tam ea, quae in Museo Universitatis Regiae Borussicae Fridericiae Wilhelmae Rhenanae servantur quam alia quaecunque in Museis Hoeninghusiano, Muensteriano aliisque extant, iconibus et descriptionibus illustrata. – **III** (8). [This work was published in parts and is commonly cited as 1844; the relevant portion appeared in 1841].
- HOLLAND, C. H. & YOCHELSON, E. L. (2000): *Dentalium inornatum* M'Coy, 1844, is not a scaphopod. – Irish Jour. Earth Sci., **18**: 123-125.
- JAMES, J. F. (1890): On the Maquoketa shales, and their correlation with the Cincinnati group of southwestern Ohio. – The Amer. Geologist, **5**: 335-356.
- KISELEV, G. N. (2001): [On the nature and systematic position of *Dentalium acus* Eichwald, 1860 found in the Ladoga Lake region (the Russian platform) dating back to the Early-Middle Ordovician.] – Vestnik St. Petersburg State Univ., (7) 2001/4: 89-91 [In Russian].

- KOKEN, E. (1925): Die Gastropoden des baltischen Untersilurs. – Mém. de l'Acad. Sci. Russie, 8^e sér., Class Physico-Mathématique, **37/ 1**. (Edited by J. Perner and commonly cited as Koken & Perner).
- KONINCK, L. G. de (1883): Fauna du calcaire carbonifère de la Belgique, 4^e partie, Gastéropodes (suite et fin) . – Ann. Musée royal d'Histoire naturelle de Belgique, sér. paléontologique, **8**.
- LADD, H. S. (1929): The stratigraphy and paleontology of the Maquoketa Shale of Iowa: Part I. – Iowa Geological Survey, **34**: 304-448.
- LUDBROOK, N. (1960): Scaphopods: 137-147. – In: MOORE, R. C. (ed.): Treatise on Invertebrate Paleontology, Part I, Mollusca **1**. – University of Kansas Press and Geological Society of America.
- PALMER, P. (2001): *Dentalium giganteum* Phillips: a serpulid worm tube. – Proc. Yorkshire Geological Soc., **53/3**: 253-255.
- PILSBRY, H. S. & SHARP, B. (1897-1898): Manual of Conchology- Structural and Systematic. – **17**. – Philadelphia (Academy of Natural Sciences). [The Manual was issued in parts, with parts 65 and 66, containing the information cited, published in 1897 and parts 67, 68 and 65a, published in 1898].
- POJETA, J., JR. & RUNNEGAR, B. (1976): The paleontology of the rostroconch mollusks, and the early history of the Phylum Mollusca. – U. S. Geol. Survey, Professional Paper **968**.
- & — (1979): *Rhytidentalium kentuckyensis*, a new genus and new species of Ordovician scaphopod, and the early history of the scaphopod mollusks. – Jour. Paleont., **53**: 530-541.
- POJETA, J., JR., RUNNEGAR, B., MORRIS, N. J. & NEWELL, N. D. (1972): Rostroconchia: a new class of bivalved mollusks. – Science, **177**: 264-267.
- REYNOLDS, P. D. (2002): The Scaphopoda. – Advances in Marine Biology, **42**: 139-236.
- RUNNEGAR, B. & POJETA, J., JR. (1974): Molluscan phylogeny: the paleontological viewpoint. – Science, **186**: 311-317.
- SHIMEK, R. L. (1988): The functional morphology of scaphopod captacula. – The Veliger, **30**: 213-221.
- (1990): Diet and habitat utilization in a northeastern Pacific Ocean scaphopod assemblage. – Amer. Malacological Bull., **7**: 147-169.
- STEINER, G. (1992): Phylogeny and classification of Scaphopoda. – Jour. Molluscan Studies, **58**: 385-400.
- & DREYER, H. (2003): Molecular phylogeny of Scaphopoda (Mollusca) inferred from 18SrDNA sequences: support for a Scaphopoda-Cephalopoda clade. – Zoologica Scripta, **32**: 343-356.
- WITZKE, B. J., BETTIS, E. A., ANDERSON, R. R., & HEATHCOTE, R. J. (1997): Geology in the Dubuque area. – Geol. Soc. of Iowa, Guidebook **67**.
- YOCHELSON, E. L. (1968): On the nature of *Polylophia*. – U. S. Geol. Survey, Prof. Paper **593-F**: 1-7.
- (1971): The little-known Pennsylvanian *Clavulites* reinterpreted as a worm. – Jour. Paleont., **45**: 126-129.
- (1978): An alternative approach to the interpretation of the phylogeny of early mollusks. – Malacologia, **17/2**: 185-191.

- (1979): Early radiation of Mollusca and Mollusc-like Groups: 323-358. – In: HOUSE, M. R. (ed.): The origin of Major Invertebrate Groups. – Systematics Association, Special Volume **12**.
- (2000): Concerning the concept of extinct classes of Mollusca: or what may/may not be a class of mollusks. – Amer. Malacological Bull., **15/2**: 195-202.
- (2002): Restudy and reassignment of *Dentalium antiquum* Goldfuss, 1841 (Middle Devonian). – Paläont. Zeitschrift, **76**: 297-304.
- , DOCKERY, D. & WOLF, H. (1983): Predation on sub-Holocene scaphopod mollusks from southern Louisiana. – U. S. Geol. Survey, Prof. Paper **1282**.
- & GOODISON, R. H. (1999): *Dentalium martini* Whitfield, 1882, is not a mollusk, but a worm. – Jour. Paleont., **73**: 634-640.
- & HLAVIN, W. L. (1985): *Coleolus curvatus* Kindle ("Vermes") from the Cleveland Member of the Ohio Shale, Late Devonian (Famennian) of Ohio. – Jour. Paleont., **59**: 1298-1304.
- & HOLLAND, C. H. (2004): *Dentalium saturni* Goldfuss (Eifelian) reconsidered: Is it really a scaphopod? – Paläont. Zeitschrift **78**: 97-102.