

Bilaterians of the Precambrian–Cambrian transition and the annelid–arthropod relationship

(Precambrian animals/phylogenies/hemocoel/coelom)

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ABSTRACT The Late Proterozoic fossil record contains the remains of animals that may represent a grade of organization not found among living metazoans. These forms were segmented and large enough to require a hemocoel, yet evidently were not capable of forming penetrating burrows, which are essentially absent from contemporaneous sediments containing locally common but chiefly horizontal trace fossils. As has been noted, there is no evidence that Late Proterozoic invertebrates possessed a coelom suited for peristaltic burrowing. Therefore, the annelidan body plan had probably not appeared. It is not implausible, however, that coelomic spaces in the form of ducts or organ sacs were present in Late Proterozoic segmented forms. Uniramians, some of which employ the hemocoel hydrostatically in lobopodal locomotion, may be allied to segmented hemocoelic forms not unlike sprigginids. Coelomic spaces may have been exploited in some protoarthropod lineages to enhance pedal-wave locomotion, but probably there are no eucoelomic forms in arthropod ancestry. Annelids may represent an early divergent branch of seriated worms, perhaps rather nemertine-like at first, that developed eucoelomic compartments only in Cambrian time. The extinct grade is most likely to have arisen from flatworm-like ancestors. Of all the proposed phylogenies examined, only that of Manton closely anticipates these interpretations of the early metazoan fossil record.

Important speculations as to the evolutionary relationships among living animal phyla began shortly after Darwin's seminal publications and have continued to the present time. Some workers have bemoaned the lack of an actual fossil record of early animal evolution, but descriptions now exist of an animal record that extends back more than a hundred million years earlier than that known in Darwin's time. It is true that this primitive fauna does not contain the sorts of ancestral forms implicit or envisaged in many phylogenetic schemes (1–5), but it can nevertheless contribute to questions of the evolution of animal phyla.

Fundamental to many animal phylogenies are questions of the origins and major patterns of the evolution of body cavities and their roles in the functional architecture of the various phyla. Two such spaces are of primary concern here. One body space, the hemocoel, consists of a system of sinuses and/or vessels through which blood is circulated to aerate the tissues. In some groups the hemocoel has important mechanical functions as well, for example, as a hydraulic skeleton in some mollusks and arthropods (6). The simplest living phylum to possess a definitive hemocoel is the Nemertina (7, 8), presumably descended from flatworms or a flatworm-like lineage that lacked a discrete circulatory system. The other body space, the coelom, lies within mesoderm and may also function as a hydrostatic skeleton. The coelom may be regionated, divided, or segmented by septa or

mesenteries (6, 8). Ducts or small spaces within the mesoderm that serve as a temporary reservoir or an avenue of transport for renal or reproductive products sometimes connect coelomic compartments to the exterior. In some groups (as in arthropodan phyla) such ducts or spaces are the only adult cavities that conform to the definition of a coelomic space (8). Which of the living coelomate phyla are considered to be the more primitive varies greatly among phylogenetic schemes.

Two major groups of hypotheses of the origin of the coelom have been proposed. One, the enterocoel theory (9), usually postulates that coelomic spaces arose as outpocketings of the gut or enteron of cnidarians or of common ancestors of cnidarians and coelomates. This notion removes the triploblastic acoelomates from any position as coelomate ancestors and entails other difficulties that have caused it to be criticized (6, 10) and even derided (11), though it continues to have supporters (3, 4, 12). Deuterostomes derive the coelom from enteric pockets, but this pattern could have arisen among triploblastic ancestors. The other hypotheses derive the coelom from a bilaterian acoelomate. The space that became the coelom is variously suggested to have originated *de novo* by schizocoely to accommodate metabolic wastes (13) or as a hydrostatic skeleton (14), or to have been derived from nephridia (15) or from gonadial sacs (16–18). The latter view, the gonocoel theory, has been the most widely supported, at least for the protostome coelom. Whatever the origin of coelomic space—and a polyphyletic origin has not by any means been ruled out and indeed seems probable—a strong case has been made that the primitive function of capacious segmented coeloms, such as the eucoelom of annelids, was as a hydrostatic skeleton for burrowing (6, 19).

Early Fossil Record of Body Plans

Both trace and body fossils of animals appear in Late Proterozoic rocks, with the greatest diversity of types found in the Pound Quartzite of South Australia (20, 21) and in roughly coeval rocks around the White Sea in the USSR (22, 23). If efficient hydrostatic skeletons, such as are provided by capacious segmented coeloms, had evolved at that time, burrows that penetrate the sediment should appear in appropriate facies. At one time this was thought to occur (24, 25) but rocks containing vertical burrows have proven to be Cambrian or very latest Vendian. Traces associated with Late Proterozoic faunas are horizontal or nearly so and did not penetrate the ancient sediments deeply, suggesting creeping surficial or semi-infaunal locomotion on the sea floor (21–23, 26, 27). The only documented penetrating vertical burrows known to be in place in Late Proterozoic rocks are microscopic and are unlikely to record the activities of coelomates (28), although Fedonkin (29) has noted that there is evidence of shallow burrowing in the shallowest water facies of Late Proterozoic sediments.

Body fossils of Late Proterozoic animals include a number of enigmatic forms that do not conform closely to the

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character of ancestral types implicit in most phylogenies. The three best-known groups that might be bilaterians are dickinsoniids, vendomiids, and sprigginids (21–23). They are found as body impressions and details of their anatomies are obscure. Dickinsoniids are flattened, range to a meter in length, and possess a series of close-set transverse annulations or divisions, separated at a median line across which they alternate (23). Dickinsoniids have been variously assigned to Cnidaria (20), Platyhelminthes (27, 30), Annelida (21, 31), and an extinct phylum, Proarticulata (23). Runnegar (31) has shown that they are too large to have been flatworms, which lack a circulatory system and rely upon diffusion of oxygen to internal tissues and cannot be much more than 1 mm in thickness. If triploblastic, dickinsoniids must have been vascularized at the least, but they may well have been diploblastic. Vendomiids are small (up to several millimeters) and are at least externally segmented, with few divisions (commonly five or six). They have an anterior shield-like structure and a median longitudinal ridge that separates the lateral segments, which may be either opposing or alternating (23). They have been assigned to the Arthropoda (21) and to Proarticulata (23). Their relationships are obscure.

Sprigginids are of more interest here; they are a few centimeters long and if triploblastic must have been vascularized. They appear to be segmented, with a longitudinally bilobed axial ridge and evidently opposing lateral segments that terminate in blunt appendage-like structures; the anterior segments, the first of which is crescentic, are enlarged (21, 22). Sprigginids have been assigned to Annelia (21), Arthropoda (23), and an intermediate phylum of their own, Annulipoda (32). The trace fossils indicate that a variety of narrow-bodied vermiform animals, presumably bilaterians but unknown as body fossils, were also associated with these groups (21, 22, 27, 47). Undoubted remains of coelomates (for example, brachiopods) are first known from the earliest Cambrian rocks.

Proposed Phylogeny

Proponents of the enterocoel theory usually derive annelids from cnidarians and then arthropods from annelids or protoannelids. If the enterocoel theory is disregarded, the great majority of suggested phylogenetic sequences proceed from flatworms to annelids and then to arthropods. Some large planarian flatworms have a seriated architecture with a sequence of gonads lodged between lateral gut diverticulae (6, 18). Locomotion in large flatworms is commonly by pedal waves, sometimes expressed most strongly at the lateral margins (6, 33). A popular hypothesis derives annelidan-style metamerism, with a compartmented eucoelom and segmented longitudinal muscles, from a seriated acoelomate (6, 18). Thus whatever source is hypothesized as the origin of coelomic space, it is widely accepted that arthropods have descended from some protoannelidan stock, the transition visualized as involving the elaboration of the cuticle into an exoskeleton, the loss of intersegmental septation and the replacement of those coelomic spaces that functioned as a hydrostatic skeleton by the hemocoel, which provides body turgor in adult arthropods and is associated with locomotion in some forms (6). There is evidence that arthropodization occurred independently perhaps three times to produce living phyla (Uniramia, Crustacea, and Chelicerata) (34–36), and perhaps occurred other times to produce trilobites (35) and/or other extinct groups. One of the important unanswered questions arising from this interpretation of arthropod phylogeny is why the coelom was replaced (6), a problem that is exacerbated if the replacement occurred several times.

If one takes account of the evidence from the fossil record, it is plausible that arthropodan stocks arose from seriated late Precambrian organisms that were acoelomate (23, 26) or,

more likely, possessed coeloms only as ducts or restricted sacs, but which had hemocoels that functioned as hydrostatic skeletons as required. In this view, arthropods did not replace a capacious eucoelom. Rather, they never had one. Arthropodization proceeded in parallel in a number of lineages as a trend toward generally increased efficiency in epibenthic locomotion. The various arthropod appendages may have arisen in association with increased sclerotization of a seriated form allied to *Spriggina*. If the lateral body extensions of sprigginids are interpreted as appendages, they are rather tightly packed (37), implying that they may not have operated with complete independence, but perhaps functioned somewhat like the pedal waves that occur along the lateral margins of some flatworms (33). The segmentation may have aided such pedal creeping and have involved longitudinal muscles of the body wall that became restricted to bundles of annular segments to localize the expression of *points d'appui* (points of support). This would enhance creeping efficiency in much the same way as the segmentation of annelid musculature promotes burrowing and swimming (6). A further possibility is that the lateral flexure of the body found in many sprigginid specimens indicates that lateral body undulations were involved in locomotion, much as observed today in many elongate organisms including phyllocid annelids (6, 38) and chilopod uniramians (35, 39). Turgor could have been supplied by the hemocoel. As M. LaBarbera (personal communication) has pointed out, intrinsic appendage muscles would not be required, for the transverse body-wall musculature could provide the "lift" required to raise the marginal appendages during their advancement by the flexing body. The animal thus visualized is at an advanced nemertine grade but with segmented musculature, internally seriated with "coelomic" ducts. The seriation was evidently not highly regularized as unequal numbers of appendages may sometimes be present. Manton (35) envisioned the ancestry of the arthropoda uniramians to lie in a hemocoelic, lobopodial segmented worm that could have arisen from flatworms. We may have segmented forms of just about such a grade, of which there are no living examples, among Late Proterozoic bilaterians.

Annelids may also have arisen from advanced nemertine-grade seriated animals, but perhaps from narrow-bodied forms responsible for some of the Late Proterozoic traces. As Manton's point (35) that annelid parapodia must have arisen independently from arthropod limbs seems valid, despite arguments to the contrary (40), and as annelid trunk segments and parapodia have coelomic hydrokeletal elements, the annelidan–arthropod split must lie deep within the postulated ancestral grade. Clues to the rise of the coelomic skeleton in annelids may lie in the mesodermal cavities of larval arthropods. The primitive function of these schizocoelic spaces is obscure and they serve a variety of functions as development proceeds (36). If they were present in the larvae of hemocoelic segmented flattened worms they would be available for exploitation for hydrostatic functions if needed. Small coelomic spaces may have become involved in peristaltic-like motions in flattened segmented worms that were semi-infaunal, guttering plowers, or burrowers. As rounder bodies and deeper burrowing habits evolved, these spaces may have expanded to surround the gut, with septa arising at their junctures. The eucoelom of round-bodied annelids was evidently not evolved until the very latest Proterozoic or perhaps the Cambrian, since the burrows of such animals do not appear earlier (23, 26, 29). In some well-studied sections, biological disturbance of sediments tends to be shallow within the lowest Cambrian Tommotian stage, and although there are penetrating burrows they are relatively small and rare; extensive deeper bioturbation, such as is associated with living coelomates, does not seem to appear until the overlying Atdabanian stage when large vertical burrows

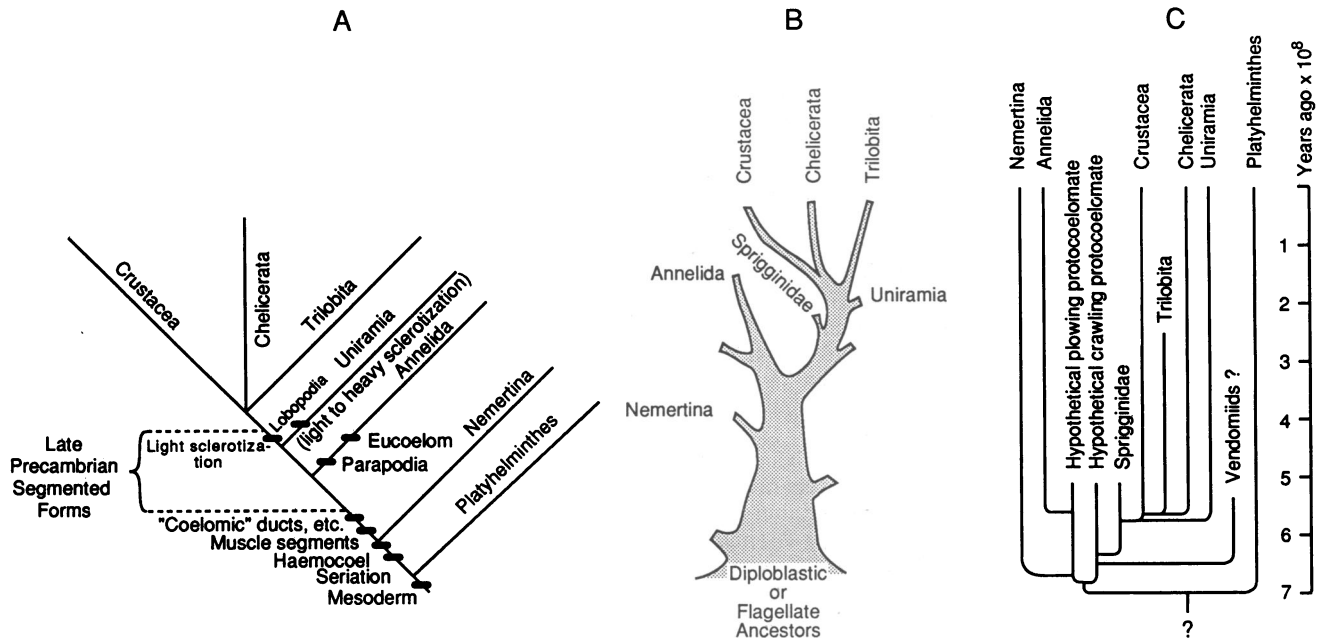


FIG. 1. Suggested phylogenetic relations among early seriated and segmented triploblastic animals. (A) Cladogram. (B) Phylogenetic tree. (C) Range chart. The range chart is scaled to a Precambrian–Cambrian boundary age of 570 million years, a common estimate although the date is in fact uncertain; changes in dating should not affect the topology of the cladograms, however.

become common and large durably skeletonized invertebrates, chiefly trilobites, also appear (41, 42). Whether the Tommotian or earlier burrowers were fully eucoelomate or included annelids is not certain; hemocoel-based (or other coelomate or pseudocoelomate) worms could have been responsible for the burrows. Certainly, there are full-fledged annelids by the Middle Cambrian (37). Three perspectives on the proposed phylogeny are given in Fig. 1.

Fedonkin (23, 26, 29) has emphasized that late Precambrian trace fossils indicate that the contemporaneous bilaterians lacked a eucoelom, and it is implicit in his systematics that the arthropods (to which he assigns sprigginiids) (23) did not arise from annelids. However, he derives segmented bilaterians directly from segmented cnidarian-grade precursors, partly on the basis of arguments from theories of symmetry (8), which does not account for flatworms and nemertines and leaves unanswered many problems concerning the origin of mesoderm, the hemocoel, and the coelom. The derivation of these features as adaptations to benthic creeping and to body-size increases in an initially minute flatworm-like ancestor entails fewer difficulties.

Evaluation of the relations between many animal phyla have been made by ribosomal RNA sequencing techniques (43). Considering the extent to which homoplasies and variations in the methodology of comparison can introduce distortions into molecular phylogenies, these findings are not conclusive but include the following features: cnidarians are not in the direct ancestry of bilaterians; flatworms lie or branch near the base of the phylogenetic tree; arthropods branch earlier than other coelomates; and, within the arthropods, uniramians form the deepest branch. These relations are not inconsistent with the phylogeny supported here; both dispose of the enterocoel theory of the origin of the coelom as usually conceived.

In sum, the main contention here is that the fossil record contains evidence of animals of a grade that is lacking today, consisting of segmented and seriated triploblastic forms possessing hemocoels, but either lacking a coelom or with coelomic spaces confined to ducts or sacs to serve or lodge specific organs. Although these organisms had cuticles that were perhaps lightly sclerotized in some lineages (44), they

did not possess jointed limbs or structures developed therefrom. Forms of this grade were neither arthropods nor annelids but may have given rise to each, although the split must have lain deep within this assemblage. Parallel arthropodization in several lineages becomes plausible from such ancestors, at least compared with a scheme involving a eucoelomate protoannelidan ancestry. Explosive radiations of different carapace and appendage types and combinations to exploit the possibilities of sclerotized segmented bodies and jointed limbs are documented in Cambrian arthropods (45, 46). As for annelid–arthropod relationships, it would seem closer to the truth to conclude, not that arthropods arose from some plexus of annelid precursors, but that annelids arose from among a plexus of arthropod ancestors.

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- Hyman, L. H. (1940) *The Invertebrates: Protozoa Through Ctenophora* (McGraw–Hill, New York).
- Hadzi, J. (1963) *The Evolution of the Metazoa* (Pergamon, Oxford).
- Marcus, E. (1958) *Q. Rev. Biol.* **33**, 24–58.
- Jagersten, G. (1972) *Evolution of the Metazoan Life Cycle* (Academic, London).
- Gutmann, W. F. (1981) *Am. Zool.* **21**, 63–81.
- Clark, R. B. (1964) *Dynamics in Metazoan Evolution* (Clarendon, Oxford, U.K.).
- Hyman, L. H. (1951) *The Invertebrates: Platyhelminthes and Rhynchocoela* (McGraw–Hill, New York).
- Beklemishev, W. N. (1969) *Principles of Comparative Anatomy of Invertebrates* (Chicago Univ. Press, Chicago).
- Sedgwick, A. (1884) *Q. J. Microsc. Sci.* **24**, 43–82.
- Hartman, W. D. (1963) in *The Lower Metazoa*, ed. Dougherty, E. C. (Univ. California Press, Berkeley, CA), pp. 55–77.
- Hyman, L. H. (1959) *The Invertebrates: Smaller Coelomate Groups* (McGraw–Hill, New York).

12. Remane, A. (1963) in *The Lower Metazoa*, ed. Dougherty, E. C. (Univ. California Press, Berkeley, CA), pp. 78–90.
13. Snodgrass, R. E. (1938) *Smithson. Misc. Collect.* **97** (6), 1–159.
14. Sarvaas, A. E. du M. (1933) *La Theorie du Coelome* Thesis (Univ. of Utrecht, The Netherlands).
15. Lankester, E. R. (1874) *Q. J. Microsc. Sci.* **14**, 365–391.
16. Berg, R. S. (1885) *Kosmos* **17**, 97–122.
17. Meyer, E. (1890) *Biologisches Zentralbl.* **10**, 296–308.
18. Lang, A. (1903) *Jena. Z. Naturwiss.* **38**, 1–373.
19. Trueman, E. R. (1975) *The Locomotion of Soft-Bodied Animals* (Edward Arnold, London).
20. Sprigg, R. C. (1947) *Trans. R. Soc. South Aust.* **71**, 212–224.
21. Glaessner, M. F. (1984) *The Dawn of Animal Life* (Cambridge Univ. Press, Cambridge, U.K.).
22. Fedonkin, M. A. (1981) *White Sea Biota of Vendian* (Nauka, Moscow).
23. Fedonkin, M. A. (1985) in *Vendian System*, eds. Sokolov, B. S. & Fedonkin, M. A. (Nauka, Moscow).
24. Valentine, J. W. (1975) *Am. Zool.* **15**, 391–404.
25. Valentine, J. W. (1977) in *Patterns of Evolution*, ed. Hallam, A. (Elsevier, Amsterdam), pp. 27–58.
26. Fedonkin, M. A. (1985) *Phil. Trans. R. Soc. London Ser. B* **311**, 27–45.
27. Palič, V. M., Posti, E. & Fedonkin, M. A. (1979) in *Upper Precambrian and Cambrian Paleontology of East-European Platform*, eds. Keller, B. M. & Rozanov, A. Yu. (Nauka, Moscow), pp. 49–82.
28. Awramik, S. M., McMenamin, D. S., Chongyu, Y., Zigiang, Z., Qixiu, D. & Shusen, Z. (1985) *Nature (London)* **315**, 655–658.
29. Fedonkin, M. A. (1987) in *Problematic Fossil Taxa*, eds. Hoffman, A. & Nitecki, M. H. (Oxford Univ. Press, Oxford, U. K.), pp. 59–67.
30. Conway Morris, S. (1981) *Parasitology* **82**, 489–509.
31. Runnegar, B. (1982) *Alcheringa* **6**, 223–239.
32. Birket-Smith, S. J. R. (1981) *Zool. Jahrb. Abt. Anat. Ontog. Tiere* **105**, 237–258.
33. Pantin, C. F. A. (1950) *Proc. Linn. Soc. London* **162**, 23–37.
34. Tiegs, O. W. & Manton, S. M. (1958) *Biol. Rev.* **33**, 255–337.
35. Manton, S. M. (1977) *The Arthropoda* (Clarendon, Oxford, U.K.).
36. Anderson, D. T. (1973) *Embryology and Phylogeny in Annelids and Arthropods* (Pergamon, Oxford, U.K.).
37. Conway Morris, S. (1979) *Phil. Trans. R. Soc. London Ser. B* **285**, 227–274.
38. Gray, J. (1968) *Animal Locomotion* (Weidenfeld & Nicolson, London).
39. Manton, S. M. (1965) *J. Linn. Soc. London Zool.* **45**, 251–484.
40. Grasshoff, M. (1981) *Palaeontol. Z.* **55**, 219–235.
41. Droser, M. L. & Bottjer, D. J. (1988) *Geology* **16**, 233–236.
42. Droser, M. L. & Bottjer, D. J. (1988) in *This Extended Land, Geological Journeys in the Southern Basin and Range*, eds. Weide, D. L. & Faber, M. L. (Geol. Soc. Am. Cordilleran Section, Las Vegas, NV), pp. 123–135.
43. Field, K. G., Olsen, G. J., Lane, D. J., Giovannoni, S. J., Ghiselin, M. T., Raff, E. C., Pace, N. R. & Raff, R. A. (1988) *Science* **239**, 748–753.
44. Seilacher, A. (1984) in *Patterns of Change in Earth Evolution*, eds. Holland, H. D. & Trendall, A. F. (Springer, Berlin), pp. 159–168.
45. Whittington, H. B. (1979) in *The Origin of Major Invertebrate Groups*, ed. House, M. R. (Academic, London), pp. 253–268.
46. Briggs, D. E. G. (1983) in *Crustacean Phylogeny*, ed. Schram, F. R. (Balkema, Rotterdam), pp. 1–22.
47. Cloud, P., Wright, J. & Glover, L. (1970) *Am. Sci.* **64**, 396–406.