Reports

The Early Radiation and Relationships of the Major Arthropod Groups

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Cambrian arthropods are now well known, but there has been little agreement on how they contribute to an understanding of arthropod phylogeny. Fossils have either been lumped together as "trilobitomorphs" or, more recently, have been the subject of speculation invoking a multiple polyphyletic origin of arthropods. Cladistic analysis of characters of Cambrian and living representatives (excluding Uniramia) shows that trilobites and chelicerates are relatively advanced compared with "crustaceans," and there are doubts whether the latter constitute a national group. An undue emphasis on singular autapomorphies of problematic fossils has obscured these relationships in the past. "Trilobitomorphs" were simply an artificial taxon based on shared primitive characters. The arthropods that evolved during the Cambrian radiation show no more apparent morphological diversity than do the living groups. The evidence of well-preserved problematica is critical to understanding the nature of this radiation and the affinities of the groups that remain today.

WHETHER ARTHROPODS ARE monophyletic or polyphyletic is a contentious question (*1–3*). The wide range of well-preserved Cambrian arthropods provides data to test whether fossils can contribute to an understanding of phylogenetics. Of the three major groups of living arthropods, Crustacea, Chelicerata, and Uniramia, only the last, which is essentially terrestrial, has no unequivocal Cambrian representatives, and is not discussed further here. A fourth group, the trilobites, has an excellent fossil record, becoming extinct at the end of the Paleozoic; the relationships of this group within the arthropods is also a matter of widely divergent opinion (*4, 5*). All four groups have been regarded as separate phyla on the one hand, or as classes within the Arthropoda on the other. The polyphyletic view is favored by those who emphasize undoubted differences in functional morphology and embryology between the major groups, the monophyletic view by those who point out the improbability of a polyphyletic origin of the characters shared by these groups. This paper assesses the Cambrian evidence of arthropod relationships, and reveals how different approaches to phylogenetics influence our perception of the significance of problematic taxa in the Precambrian-Cambrian radiation of the Metazoa.

One of the most important results of recent work on exceptionally preserved early fossil biotas (*Konservat-Lagerstätten*) has been the discovery of significant numbers of metazoans that cannot readily be assigned to living higher taxa (*6*). Such so-called problematica are most common in the Cambrian (most are known from the Burgess Shale), and decline rapidly through the Paleozoic. They also occur among the arthropods (*7*), where they can be analyzed in comparison with living taxa because of the relatively high number of preservable characters. The problematic Cambrian arthropods can be interpreted as taxa of equivalent rank and independent origin from the major arthropod groups. Alternatively, they can be considered as showing features that bridge the major groups, in which case a polyphyletic origin of the arthropods is improbable. Hence the taxonomic treatment of these arthropods goes beyond the question of how to classify them—it affects our understanding of the nature of the Cambrian radiation.

Past paleontological practice lumped the problematica together with the trilobites in a taxon Trilobitomorpha (*8, 9*), linked by the possession of a broadly defined biramous trilobite-like limb. Under this scheme there was essentially one major extinct group and three living ones. In the seventies, the results of studies of the functional morphology and embryology of the major living groups were used to argue separate origins for the Crustacea, Chelicerata, and Uniramia (*2, 10*). Reevaluation of exceptionally preserved arthropods of the Middle Cambrian Burgess Shale showed that the importance of trilobites, with their calcified exoskeleton, was exaggerated and that only a small percentage of the other arthropods present could be readily assigned to the major living groups (*7*). These developments resulted in interpretations of multiple origins for the arthropods, a model of extreme polyphyly, which was initially illustrated, and subsequently caricatured, as a phylogenetic "lawn" (*11*). This picture of many parallel lineages crossing the Precambrian-Cambrian boundary obscures possible relationships between these arthropods, and denies that the data they represent can reveal anything about the nature of early Metazoan radiation. This deficiency can be addressed by a cladistic approach.

Although only a small fraction of the number of Cambrian arthropods is preserved, the sample may be reasonably representative of higher taxonomic levels. Furthermore, the Cambrian biotas clearly provide a more representative sample from the the first radiation of the arthropods than does the living fauna. The major groups of living arthropods are defined by character complexes in an advanced state, but these must have been derived in stages. Cambrian representatives may well show earlier steps in the development of these character complexes because the synapomorphies are incompletely expressed. The Cambrian arthropods include an evolutionary mosaic of intermediate forms that have become extinct; their particular combination of characters is not represented in the living fauna. Viewed in this way it is not after all surprising that we cannot assign many Cambrian arthropods to the major living groups, nor to the trilobites.

We selected 23 Cambrian taxa that are preserved in sufficient detail to allow a large number of character states (a high proportion of the 46 enumerated) to be coded. These arthropods come from a very small number of *Konservat-Lagerstätten*: nineteen from the Middle Cambrian Burgess Shale (*7*), one from an adjacent locality (*12*), three from the Upper Cambrian Orsten of southern Sweden (*13*), and one from the Upper Cambrian of Wisconsin (*14*). We added living sister taxa—the chelicerate *Limulus*, and the crustaceans *Hutchinsoniella* and *Speleonectes*—selected because they have been regarded as living plesiomorphic representatives of the aquatic clades (*15*). *Triarthrus*, the well-preserved Ordovician trilobite (*16*), and *Baltoeurypterus*, representing the eurypterids (*17*), a major extinct clade of aquatic chelicerates, were also included.

The arthropods were analyzed cladistically by the use of the PAUP (phylogenetic

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analysis using parsimony) program (2.4.1). The data matrix (*18*) was constructed using the morphology of *Marrella* as the primitive outgroup. The selection of *Marrella* reflects the result of previous studies (*7, 19*), and the position that it consistently occupied when the lobopod animal *Aysheaia* was used to establish polarity for the analysis. In order to avoid incorporating a priori assumptions about the significance of different attributes in determining affinity, the characters were given equal weighting.

A matrix of 28 taxa and 46 characters can give an almost infinite number of possible trees. The cladogram presented here (Fig. 1), however, is unique, the single most parsimonious solution for this set of data. We do not present this cladogram as a definitive solution to the relationships of the Cambrian arthropods, because its consistency index is rather low (0.384). Some positions on the cladogram are questionable, and adding further taxa or other attributes alters the result in detail, but in several other variants the general pattern remains the same.

Crustaceans and crustacean-like arthropods occupy a primitive position on the cladogram. The advanced status indicated for the trilobites has not been argued before. They have normally been regarded as indicative of the generalized primitive morphology that gave rise to the other arthropod groups (*1, 4, 20*). Other authors have also grouped the trilobites and chelicerates as sister groups (the concept of the Arachnomorpha), but with the implication that the crustaceans were more derived (*8, 21*).

The steps involved in moving from one taxon to the next identified by the cladistic analysis do not require implausible novelties. The fossils support the hypothesis of monophyly by "filling in" some of the intermediate steps. Relationships between the arthropods are revealed by a reasonable series of synapomorphies and require no recourse to polyphyly. The classification of the problematica can be resolved by this more rigorous taxonomic method.

The small number of clades, and the large proportion of genera isolated as plesions, is regarded as characteristic of the early stages of an adaptive radiation. It reflects the predominance of primitive character complexes among the Cambrian arthropods. The extinction of intermediates leaves a clear morphological separation between the living crustaceans and chelicerates. It should therefore not be surprising that the most important morphological attribute used in distinguishing them, the segmentation of the head (and its corollary, the arrangement of the head appendages) is of limited use in the Cambrian (only 7 of the 46 characters gave a lower consistency index). Even in *Canadaspis* and *Sanctacaris*, taxa identified on a number of grounds as a crustacean (*22*) and chelicerate (*12*), respectively, the characteristic head segmentation has not fully evolved.

The view of the Cambrian arthropods originating as a multiplicity of separate lineages reflected the differences between them. It was influenced, at least in part, by some of the more bizarre attributes of the Burgess Shale genera: the two massive spinose projections from the head shield of *Marrella* (*23*), for example. It led to a perception of the Cambrian radiation as resulting in a much greater morphological as well as taxonomic diversity of arthropods than is displayed by the living representatives (*24*).

The cladistic approach, on the other hand, focuses on shared characters. Unique attributes, autapomorphies, are of no use in assessing relationship and are consequently accorded little significance. Few if any of the autapomorphies displayed by the Cambrian arthropods, with the possible exception of the postventral plate of aglaspids (*14*) (a similar structure occurs in *Emeraldella*) (*25*)

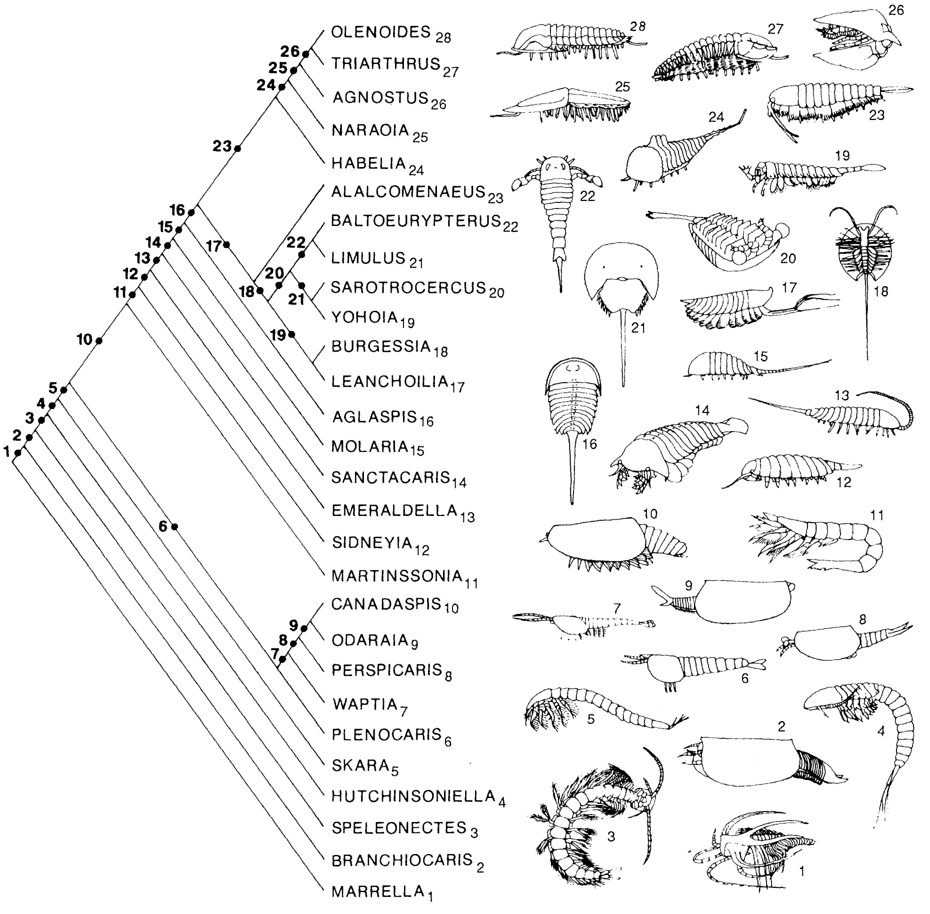

Fig. 1. Cladogram of Cambrian and other arthropods. Synapomorphies for each node as identified by PAUP (*18*); (characters that are not considered very robust—some reversals and losses—are indicated by an asterisk): 1: flexure of body lateral and dorsoventral*; 2: cephalic shield and tergites, five cephalic appendages, cephalic gnathobases, movable appendages on telson; 3: two trunk tagmata, gnathobases on all trunk appendages, trunk somites reduced to 16 to 24, loss of appendages on posteriormost tagma (excluding telson), limbs not diminishing in size posteriorly; 4: trunk somites reduced to 12 to 14; 5: outer ramus not segmented; 6: cephalic shield and tergites reduced to cephalic shield alone, shield bivalved; 7: loss of doublure, first antenna reduced, second head appendage antenniform, 15 trunk somites*; 8: mandible, outer ramus lacking narrow filaments; 9: pretelson appendages present,* no movable appendages on telson*; 10: anus ventral, loss of telson appendages; 11: pleural overlap, styliform telson (autapomorphic in *Sidneyia*); 12: posteriormost tagma with appendages*; 13: trilobation, presence of unfurrowed pleurae, marginal rim present; 14: four cephalic limbs,* just one trunk tagma*; 15: pretelson appendages present*; 16: dorsoventral flexure of body only; 17: pleura absent,* first cephalic appendage not antenniform (that is, specialized in some way); 18: loss of trunk gnathobases*; 19: loss of doublure,* loss of labrum,* marginal rim absent,* loss of cephalic gnathobases*; 20: uniramous trunk appendages, reduced or absent inner ramus; 21: unfurrowed pleura,* loss of cephalic gnathobases,* lateral and dorsoventral flexure of the body,* loss of pretelson appendages*; 22: eyes on carapace, median eye, six cephalic appendages, marginal sutures; 23: increase in trunk somites from 11 to 12–14*; 24: pygidium, gut diverticula, distal lobe on outer ramus, posterior extremity of trunk rounded*; 25: $CaCO_3$ skeleton, eyes on carapace, marginal suture, genal spines, two trunk tagmata; 26: dorsal ecdysial sutures, eye ridges, half-ring. Autapomorphies of individual taxa are not shown.

and the three-"fluked" tail of *Odaraia* (*26*), are strictly unique. And a number involve the structure of the limbs, or the tail, features which may be functionally diverse even among closely related arthropods.

The PAUP analysis provides an additional measure of morphological separation, by the calibration of distances on the cladogram in terms of changes in coded character states. This shows that *Olenoides* and *Limulus*, bona fide trilobite and chelicerate, respectively, are the taxa furthest from the origin of the cladogram. This is hardly surprising as they are members of the most derived groups in the analysis, but it does emphasize that the problematic Cambrian taxa do not show any remarkable morphological separation. This leads to the expectation that the addition of further taxa (either later Paleozoic examples, or new Cambrian discoveries) would narrow rather than widen the morphological gaps between them.

The arrangement of taxa on the cladogram raises the possibility that the living crustaceans are a paraphyletic group. Analyses of the Recent crustaceans have emphasized that "aside from the features of the head, it is impossible to characterize crustaceans except by noting tendencies toward certain conditions or states" (*19, 21,* p. 3). The cladistic analysis of the Cambrian arthropods shows that the features of the head are poorly developed and that other criteria are more useful in identifying groupings. Thus the characters used to diagnose living crustaceans may be primitive or convergently acquired.

The significance of Cambrian problematica in formulating hypotheses of relationship has been largely ignored [the echinoderms are a notable exception (*27*)], or they have been simply set aside as groups of independent origin, thus obscuring their importance in phylogenetic analysis. The somewhat counterintuitive results of this analysis illustrate how critical the evidence of well-preserved fossils can be to understanding the affinities of living groups (*28*).

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28. See J. Gauthier, A. G. Kluge, T. Rowe, *Cladistics* **4**, 105 (1988) for a tetrapod example.

29. We thank P. L. Forey for running the PAUP program and for discussion of the method and results. P. Baldaro drew the figure.

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Detection of Cell-Affecting Agents with a Silicon Biosensor

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Cellular metabolism is affected by many factors in a cell's environment. Given a sufficiently sensitive method for measuring cellular metabolic rates, it should be possible to detect a wide variety of chemical and physical stimuli. A biosensor has been constructed in which living cells are confined to a flow chamber in which a potentiometric sensor continually measures the rate of production of acidic metabolites. Exploratory studies demonstrate several applications of the device in basic science and technology.

CHANGES IN THE BIOLOGICAL, chemical, and physical environment of a cell must be reflected in the concentrations and fluxes of molecules within the cell. The extensive interconnections among different biochemical processes assure that changes ripple outward from primary sites of action, and a sufficiently sensitive analytical method might detect a response in cellular characteristics not normally associated with the primary stimulus. The integrative role of catabolism makes it an excellent candidate for the indirect detection of responses.

We have constructed an instrument, which we have named a silicon microphysiometer, to investigate these phenomena. We report that ligand-receptor interactions can produce prompt changes in cellular catabolic rates. In addition, we find that cytotoxic and cytopathic effects can be detected. The physiological basis of the device is the acidity of the principal catabolic products in mammalian cells, lactate and CO_2. The acidity of the culture medium bathing a small sample of cells can be determined with a light-addressable potentiometric sensor (LAPS) (*1*), and the rate of acidification is used as a measure of catabolic rate.

The LAPS device configured as a biosensor is shown in Fig. 1. In the flow chamber the silicon forms the bottom wall of a fluid channel that is rectangular in cross section. The top wall of the fluid channel is formed by a glass cover slip that is coated on the channel side with a transparent conductive layer of indium–tin oxide. Typical channel

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