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Trilobites and the Origin of Arthropods

X-ray studies of trilobites indicate that the arthropod exoskeleton evolved independently in two ancestral groups.

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Arthropods, more than 800,000 living species of them, may have had more than one evolutionary origin. The traditional view of their evolutionary history has been that the three major modern groups (*1*)—Crustacea (for example, shrimp), Chelicerata (spiders and horseshoe crabs), and Uniramia (centipedes and insects) (*2*)—shared a common arthropod ancestor prior to the beginning of the Cambrian (*3–5*). Arthropodization, the development of the jointed exoskeleton that is characteristic of the arthropods, is thus explained as having occurred only once, in a common ancestor. However, through the work of Tiegs and Manton (*6–8*), it has come to be realized that many of the external anatomical features thought to link together the modern groups as the phylum Arthropoda may have evolved independently within each group. The evolutionarily conservative features that characterize each group are expressed primarily in "soft" internal anatomy, embryonic development, and functional morphology (*6–9*). Differences among modern representatives of the major groups are so great and discontinuous as to suggest that each one may have evolved independently from ancestors that were not themselves arthropods (*6–9*). In this case, the Arthropoda would not constitute a phylum in the sense that it has a common ancestry but rather a heterogeneous group of phyla. It has already been proposed that the Uniramia and perhaps both the Crustacea and Chelicerata be recognized as distinct phyla (*2, 8, 9*). Thus arthropodization may have occurred three times at least—that is, separate groups of metamerically segmented, nonarthropodized animals may have independently solved the same adaptive problems by developing a jointed exoskeleton.

The problem of arthropod origins can only be solved through combining knowledge of living forms with knowledge of the arthropod fossil record (*10*). The idea that arthropods had three evolutionary origins is based on studies of the characteristics of modern animals, particularly of the characteristics that can be studied only in live animals. The information so obtained, because it lacks the dimension of time on an evolutionary scale, can be used to infer evolutionary history only on the basis of certain a priori assumptions about how evolution has proceeded. The fossil record, fragmentary though it usually is, is the only historical record of what has actually happened in evolution.

While all information on their modern representatives indicates that the major arthropod groups are well circumscribed and quite distinct from one another, the fossil record reveals that this has not always been the case. The fossil record shows that the major modern groups were present in the Cambrian together with a number of extinct forms which, if classified strictly according to the scheme used for modern forms, would fall into yet other major groups (*1*). Arthropods were formerly more diverse in basic modes of body organization, and this diversity has decreased through geologic time. The variety of primitive Paleozoic arthropods, such as the "trilobitoids" from the Cambrian Burgess Shale, suggests a broad spectrum in modes of body organization, a spectrum including both crustaceans and chelicerates (*6, 11*), groups which are mutually isolated in later time. In the past, the major modern groups may not have been so distinct from one another in the sense that they formed only parts of a much more continuous range of arthropod types that arose in the initial evolutionary radiation of arthropods some 600 million years ago. With changes occurring in the major groups comprising it, the ways in which the Arthropoda would be characterized as a taxonomic group have changed correspondingly through geologic time.

The relationships of trilobites, perhaps the most familiar of extinct arthropods, is a critical question because trilobites are among the most primitive arthropods known. Their relationships to other groups may help delineate the major branches into which arthropods first diverged. But, ironically, the crucial evidence that would enable one to determine their relationships—their internal anatomy, embryonic development, and functional morphology—is either not intrinsically preservable or never, or almost never, preserved in the fossil record. On the basis of less reliable evidence, the Trilobita have been generally recognized as a class allied to the Chelicerata (*12*), though they are placed in a collateral group Trilobitomorpha, a sort of "taxonomic wastebasket" (*13*), together with the "trilobitoids." However, recent work on trilobites that has provided new answers to questions of their relationships also points to new answers to the question of arthropod origins and to the problem of how a fossilizable exoskeleton may have evolved among arthropods.

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A New Look at Old Fossils

Recent x-ray studies on pyritized trilobite specimens in which limbs and parts of the internal anatomy are preserved (*14–16*) have provided much of the information bearing on the question of trilobite relationships. For *Triarthrus eatoni* (Hall), an Ordovician olenid that is the most completely known trilobite, the anatomy of the exoskeletal, skeletomuscular, and digestive systems is known in some detail (*16–18*). It is now possible to integrate the anatomy of trilobites into the study of the comparative anatomy of modern arthropods in attempting to discern evolutionary relationships.

New findings significant to the problem of trilobite relationships include:

1) The trilobite head characteristically includes four, not five, limb-bearing segments (*19*). Three postoral segments (C_1 to C_3) bearing limbs little differentiated from trunk limbs are present behind the preoral antennal segment (A, in Fig. 1). Because head structure is the basis of arthropod classification at the superclass level (*1, 3*), this structure distinguishes Trilobita from all modern superclasses.

2) Limb structure is variable among trilobites and is of no great value in ascertaining their relationships (*13*). *Triarthrus* does not have a "trilobitan limb" in the sense of Størmer (*12*). Its postoral limbs are unlike those of any modern superclass, though they do combine certain features found in crustaceans and chelicerates. The exite ("gill branch") is attached near the middle of the coxa (basal limb segment) on its outer edge, not near the coxa-body joint. A definitive precoxa is absent. The trunk coxa is blade-like and bears a large basendite with about eight large setae along its inner edge (Fig. 1). It is becoming apparent that the "trilobitan limb," the supposed unifying characteristic of the Trilobitomorpha (*12*), is a faulty construct (*13–16, 20*). The Trilobitomorpha is probably a heterogeneous and unnatural group of marine arthropods united by possession of no more than a generally primitive body organization.

As has long been apparent, a multiramous postoral limb links trilobites with crustaceans and chelicerates but distinguishes them from uniramians. While finer details of limb structure remain as features to be accounted for in constructing phylogenies, they do not in themselves provide clear indications of relationships between class-level groups (*6*).

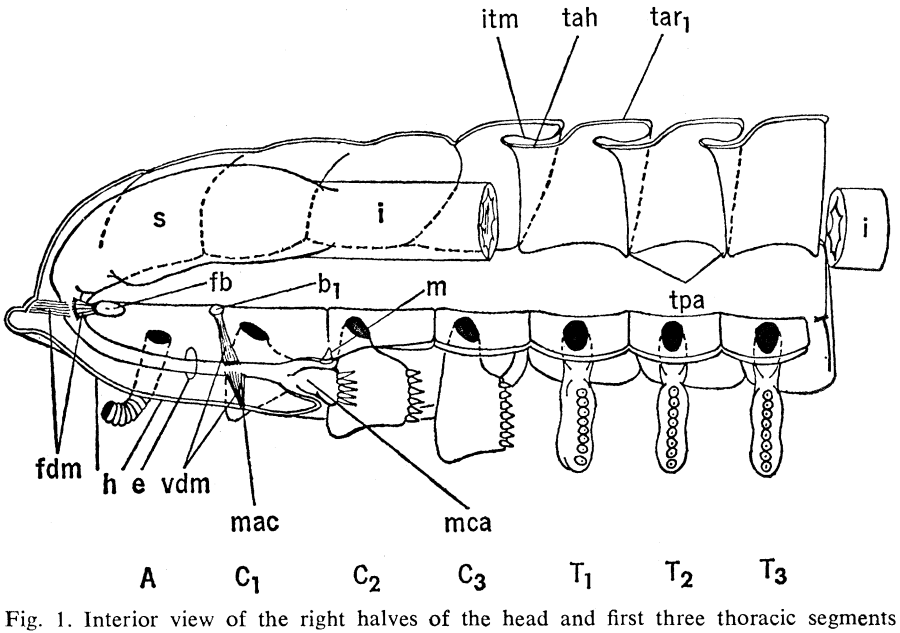

Fig. 1. Interior view of the right halves of the head and first three thoracic segments of the Ordovician trilobite *Triarthrus eatoni* (Hall) showing the digestive tract. This part of the animal is, at most, 1 cm long. Abbreviations: *A*, antennal segment; *b*, postfrontal endoskeletal bar; *C*, postoral head segment; *dam*, dorsoanterior extrinsic limb muscle mass; *dmm*, dorsomedial extrinsic limb muscle mass; *dpm*, dorsoposterior extrinsic limb muscle mass; *dlm*, dorsal longitudinal muscle; *dva*, anteriorly descending dorsoventral muscle; *dvp*, posteriorly descending dorsoventral muscle; *dvv*, ventrally descending dorsoventral muscle; *e*, esophagus; *fb*, frontal endoskeletal bar; *fdm*, frontal dilator muscles of esophagus (hypothetical); *h*, hypostoma; *hom*, horizontal muscle; *i*, intestine; *itm*, intertergal membrane; *m*, metastoma; *mac*, macula; *mca*, mouth cavity; *s*, stomach, *T*, thoracic segment; *tah*, articulating half ring of thoracic tergite; *tar*, axial ring of thoracic tergite; *tpa*, tergal posterior apodeme; *vam*, ventroanterior extrinsic limb muscle mass; *vdm*, ventral dilator muscles of esophagus; *vlm*, ventral longitudinal muscle; and *vpm*, ventroposterior extrinsic limb muscle mass.

3) The paired coxal endites in *Triarthrus* define an uninvaginated food groove of the same sort that is associated with the mechanical transport of food material in cephalocarid and phyllocarid crustaceans (*21, 22*). In this one respect, and probably in others, *Triarthrus* had a similar trunk limb food collection mechanism. Such mechanisms, found only in crustaceans, and shown by Sanders (*22*) to be phyletically conservative among the most primitive groups, are an important link between Trilobita and Crustacea. The implication that *Triarthrus* likewise fed on particulate detritus is borne out by the structure of the mouthparts and digestive tract and by the finding of fossilized gut contents, clouds of fine particulate pyritic material emanating from the anus in one specimen and from the ruptured gut in another; this was revealed in streoscopic radiographs.

Cryptolithus appears to have a food groove similar to that in *Triarthrus*; but owing to severe deformation of specimens of other well-known species, the conformation of limb bases has not been made clear.

4) Coxal endites of postoral head limbs in *Triarthrus*, the first (C_1) in particular, are developed as gnathobasic gripping jaws (Fig. 1). This weakly developed masticatory mechanism, if that is what it may be called, is not specialized in any direction toward gnathobasic masticatory mechanisms of crustaceans and chelicerates, and is altogether unlike the whole-limb masticatory mechanisms found in uniramians (*8*).

5) The skeletomusculature of *Triarthrus* is basically similar to that found in the most primitive crustaceans, namely, cephalocarids, notostracan branchiopods, and phyllocarids (*23*) (Fig. 2). The paired dorsal longitudinal muscles (dlm) form a sheet of parallel fibers along the top of the body cavity. The paired ventral longitudinal muscles (vlm) are two parallel bundles, segmental blocks of which are inserted end to end on transverse bars (fb, b) of the probably tendinous ventral endoskeleton. Lateral longitudinal muscles and body wall muscles, characteristics of primitive uniramians (*24*), are absent. Except in the first two limb-bearing head segments (A, C_1), the dorsal and ventral parts of the musculature are linked by sets of dorsoventral muscles (dva, dvp, dvv) that fall into the pattern of a box truss.

Horizontal muscles (hom) extend laterally from the ends of endoskeletal bars, where the dorsoventral muscles are also attached, to the ventral integument. The ladder-like series of bars in the ventral endoskeleton are anchored to the ventral integument by this means (hom) and by thin, paired connecting ligaments that descend from each bar.

Functional similarities in the limb mechanisms of locomotion and feeding are probably the underlying causes of the detailed anatomical similarities that *Triarthrus* shows to primitive crustaceans. In this context, the anatomical similarities suggest a common ancestry for Trilobita and Crustacea.

As revealed in the skeletomusculature of *Triarthrus*, the distinctive structure of the trilobite head is largely a reflection of scant specialization of head segments over the pattern of trunk segments—an extremely primitive feature (*3*). From the antennal segment posteriorly along the thorax, all segments contain similar elements of the longitudinal muscles and endoskeleton (Fig. 2). Cephalization of three postoral segments and formation of a fused head tergum over them have taken place with otherwise little modification of the primitive pattern of these segments. In *Cryptolithus*, as in *Triarthrus*, the ventral endoskeleton extends into the preoral part of the head in essentially unmodified condition, suggesting a similarly high degree of serial homology of segments even though in body form *Cryptolithus* is superficially more specialized.

6) The trilobite digestive system includes a J-shaped gut and extensive digestive glands in the head region. The finding of the digestive tract in *Phacops, Triarthrus*, and *Crytolithus* (*14–16*) confirms that, as suspected (*25*), the mouth is posteriorly directed (the feature that gives the gut its J-shape). In *Triarthrus*, the posteriorly directed mouth cavity (mca, an atrium oris) opens between two sternites, the hypostoma (h, a "labrum") and metastoma (m, a small sternite belonging to the C_1 segment) (Fig. 1). The esophagus (e; the pharynx cannot be distinguished from it in fossils) loops around the first endoskeletal bar in passing into the stomach (or stomachs), which lies in the anterior part of the head. The stomach passes into the intestine (i) well within the head. Extensive digestive glands strongly resembling the ramified digestive gland in the horseshoe crab, *Limulus*, a chelicerate, are present in the lateral regions of the head in *Triarthrus*. As indicated by ramified markings on the dorsolateral parts of the head tergum in many trilobites, this digestive gland was characteristic of the Trilobita (*26*). The basic structure of the digestive system links trilobites with both crustaceans and chelicerates, which primitively have the same conformation of the gut and glands, but distinguishes them from uniramians, which primitively have a more or less terminal mouth, a feature appropriate to food collection by head limbs rather than trunk limbs, and which lack extensive digestive glands (*2, 6, 8*).

From the anatomy of adults, it is impossible to tell whether trilobites, like other arthropods, have a segment anterior to the antennal segment; for that embryonic segment is typically limbless and suppressed in adults. Though the point has remained controversial even for modern arthropods studied embryologically, a similar preantennal (or precheliceral) segment appears to be present in the head of all modern forms except onychophorans (*27*). The fact that the trilobite gut (e, s) loops around the endoskeletal bar (fb) at the front of the antennal segment (A) might suggest that this segment was formed behind the mouth region in embryonic development. In all probability, this interpretation is incorrect. In no known arthropod does the first segment form behind the mouth region. Moreover, the arrangement of segmental ganglia and commissures of the nervous system with respect to the gut in modern arthropods (a very conservative feature) gives reason to believe that the first segment formed in front of the mouth region even in the most primitive arthropods. The configuration of the gut and the endoskeleton in the trilobite probably represents a secondarily developed accommodation between the two systems that does not reflect the primary segmentation of the body.

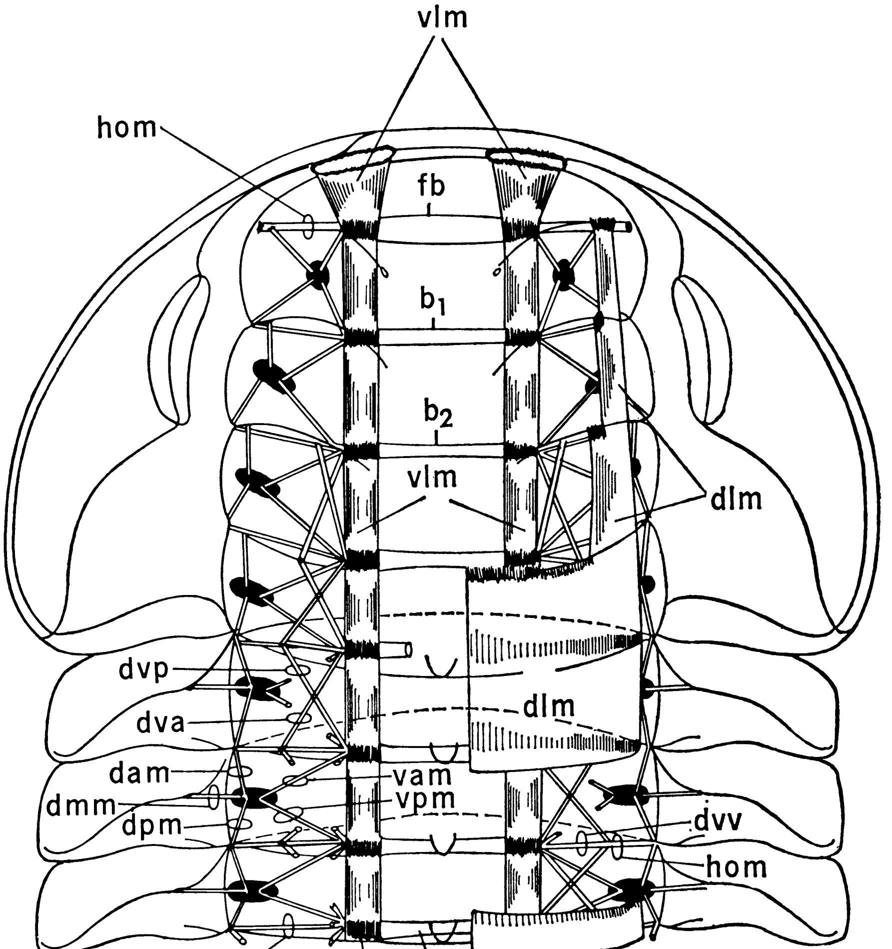

Fig. 2. Dorsal view of the head and first three thoracic segments of the Ordovician trilobite *Triarthrus eatoni* (Hall) showing the musculature. This part of the animal is at most 1 cm long. Abbreviations are as in Fig. 1.

The Relationships of Trilobites

The Trilobita are characterized as a distinct class-level arthropod group in having the head comprised of one preoral limb-bearing segment with a uniramous antenna and three postoral segments bearing biramous limbs little differentiated from trunk limbs which together served in a gnathobasic food ingestion mechanism.

Trilobites link together the Trilobita-Crustacea-Chelicerata (TCC) as a natural group with a common ancestry at a very primitive, trilobite-level grade of organization (*28*) (Fig. 3). As enumerated, trilobites show the characteristics of both Crustacea and Chelicerata in their very primitive body plan, but show none of the characteristics of Uniramia. The TCC are united as a distinct group by possession of these evolutionarily conservative features: (i) a primitively multiramous limb, (ii) a gnathobasic food ingestion mechanism, (iii) primitively, a posteriorly direct mouth, and (iv) digestive glands in the head region that are often quite extensive. Differences in details imposed upon the basic similarities in the structure of postoral limbs and in the construction of the food ingestion mechanism indicate that the three groups diverged from a common ancestor that had these features developed in more generalized fashions. General similarities in the anatomical underpinnings of the trunk limb food collection mechanism likewise indicate divergence of trilobites and crustaceans from a common ancestor. The common ancestor for the TCC group probably had this sort of feeding mechanism, the predaceous feeding mechanisms of chelicerates having evolved subsequently. The trilobite condition, setting an upper limit on the degree of specialization, the common ancestor probably occupied the same extremely primitive organizational grade. Though this ancestor would probably be classed as a "trilobitoid" if found, it should have much the same body construction as a trilobite.

Trilobites suggest the very primitive and generalized plan from which the crustacean and chelicerate conditions can be derived. The essential features of the crustacean head, including the diagnostic features of Crustacea, can be derived from the condition in trilobites by fusion of an additional segment to the head posteriorly (trilobite T$_1$, crustacean second maxillary), movement of an additional segment to a preoral position in the adult (trilobite C$_1$, crustacean second antennal), and further differentiation of head segments with reduction and specialization of what then would be the first postoral limb (trilobite C$_2$, crustacean mandible) to a gnathobasic mandible. These changes follow along the general evolutionary trend among arthropods toward cephalization through segmental specilization (*3*). These same changes are seen in the development of the crustacean nauplius larva toward more advanced stages (*22, 29, 30*). The nauplius larva is similar to the adult *Triarthrus* in that the second antenna, the apparent homolog of the first postoral limb (C$_1$) in the trilobite, is likewise postoral and bears a finger-like enditic process that extends to the side of the mouth cavity. The developmental sequence for the crustacean head begins from a very trilobite-like condition. The head in adult as well as naupliar cephalocarid crustaceans conforms beautifully to the derived condition. The derivation explains why the second maxilla conforms so precisely to the pattern of trunk limbs, which is perhaps the most obvious feature distinguishing cephalocarids as the most primitive living crustaceans (*22, 23*).

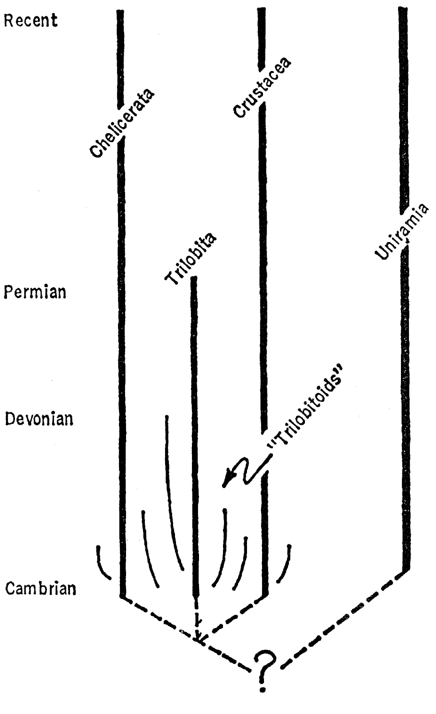

Fig. 3. A phylogenetic tree for the major groups of arthropods. Known geologic ranges are shown as solid, vertical lines. Inferred relationships are indicated by dashed lines. The major groups diverged rapidly around 600 million years ago near the beginning of the Cambrian. Did the Trilobita-Crustacea-Chelicerata and the Uniramia share a common ancestor that was itself an arthropod? Are the Arthropoda not one phylum but two?

Evolution of the chelicerate condition probably involved radical adaptation of a trilobite-like body plan for predaceous feeding. Yet if the cheliceral segment corresponds to the trilobite antennal segment (*27*), preoral segmentation would appear to have remained the same. Radical changes would have been involved in the formation of the chelicerate prosoma ("cephalothorax") through cephalization of three more segments than are present in the trilobite head. Yet the biramous trilobite limb as found in *Triarthrus*, with its large basendite and seven-segmented telopod ("walking leg" exclusive of the coxa), appears to be an ideal, unspecialized precursor for legs in *Limulus* and, with its feathery exite ("gill branch"), for the gills of *Limulus* as well (*12*).

The Origin of Arthropods

Trilobites delineate a dichotomy between the TCC group and the Uniramia that extends virtually to the origin of the Arthropoda. In their low degrees of cephalization and specialization of postoral segments, trilobites stand close to the condition to be expected for an ancestor of all arthropods. Yet they have only the most basic features in common with uniramians—metameric segmentation and presumably a hemocoelic body cavity and a sclerotized cuticle. While being more advanced than trilobites in having the three head segments strongly differentiated among themselves and in relation to trunk segments, onychophorans, the most primitive uniramians, occupy a more primitive grade of arthropodization in lacking development of the cuticle as an exoskeleton. Evolution along the two general trends toward progressive specialization of segments (*3*) and toward arthropodization itself (*7*), had proceeded to much different degrees even at these most primitive organizational levels. Though the Cambrian protonychophoran *Aysheaia* comes a little closer to the condition expected for some common ancestor (*31*), the TCC group and the Uniramia appear to be separated by differences of kind in the anatomy of the locomotory, feeding, and digestive systems even at this exceedingly primitive level of organization.

The contrasts between TCC and Uniramia suggest that arthropodization occurred independently in the two groups, with hard sclerites having appeared at somewhat more advanced organizational levels among uniramians, as suggested by Manton (*2*). The idea is further borne out by the gradient in degrees of arthropodization among uniramians demonstrated by Manton (*7*). The arthropod exoskeleton has probably evolved not once, as supposed in traditional phylogenies (*3–5*), not basically thrice as proposed by Tiegs and Manton (*6*), but essentially twice (*32*).

From what is actually known of the evolutionary history of arthropods, the dichotomy between TCC and Uniramia can be explained either in terms of separate evolutionary origins or in terms of profound divergence from a common ancestral group near the beginning of the Cambrian. Newly recognized embryological similarities between annelids and arthropods (*9*) suggest that indeed both groups originated from the same soft-bodied, segmented, worm-like animals that existed some 600 million years ago. Perhaps several groups of these primordial worms became arthropodized, just as advanced polychaete annelids have tended to become arthropodized (*33*). But only two major lineages, TCC and Uniramia, persisted and greatly diversified. Arthropods continued to diversify, with separate groups becoming progressively isolated from one another through extinction of primitive intermediates and subsequent specialization among survivors. Going back to the beginning, where would one draw the line between "arthropod" and "nonarthropod" necessary for deciding whether the ultimate common ancestor of TCC and Uniramia was itself an arthropod when one would be considering a group of extinct, soft-bodied animals that one would probably never see nor recognize in the fossil record? This is probably an impossible question. Hence it should be practically impossible to determine whether or not the Arthropoda represent one phylum or several. The answer becomes a matter of opinion. What is more important is that we work out the relationships among the known arthropod groups and, recognizing the uncertainties, interpret their patterns of evolution (Fig. 3).

One circumstantial argument for arthropods having a common origin is that the dichotomy between the TCC group and the Uniramia falls very nearly between the primitively marine and primitively terrestrial branches of Arthropoda, as if their differences were due largely to divergent adaptations for their different types of environment. The one important exception to the generalization that uniramians are primitively terrestrial is *Aysheaia*, the earliest and most primitive uniramian, which comes from a marine deposit. Perhaps some quintessentially primitive arthropod group of which onychophorans are the last somewhat specialized survivals bridged the gap between TCC and Uniramia near the beginning of the Cambrian.

Why Did Arthropods Become Fossilizable?

One of the mysteries in the history of life has been why hard parts of a variety of invertebrate animals, trilobites among the first, should appear rather suddenly in the fossil record near the base of the Cambrian. The problem has attracted much speculation. The immediate driving force behind the evolution of hard parts has been variously suggested to have been demand for supporting skeletons coupled perhaps with evolutionary increase in adult size (*34*), or demand for protection from the first large predators (*35*). Both factors have been invoked in explaining the appearance of fossilizable invertebrates as a direct reflection of an evolutionary explosion (*36*) set off perhaps by the evolution of sexual reproduction (*37*) or the evolution of heterotrophic nutrition and "consumer-oriented" ecological communities (*38*). Arthropods did not become readily fossilizable until their body mechanical system became arthropodized. How and why did this change take place?

The continuum in degrees of arthropodization among uniramians (*7*) suggests how the transition to arthropodization took place. Starting from a soft-bodied, onychophoran-like condition, supporting function was progressively shifted from the hemocoel, originally a hydrostatic skeleton, to the cuticle, which became an exoskeleton (*7*). There was thus a shift in the principle of operation of the body mechanical system.

The body mechanical system in *Triarthrus* combines both an internal hydrostatic skeleton and an exoskeleton, and thus gives indications of its origin from a nonarthropodized condition. Dorsally, the armored tergal exoskeleton forms a framework for attachment of body and limb muscles (Fig. 2). Ventrally, the endoskeleton, not the thin sternal cuticle, forms the corresponding framework. Internal hydrostatic pressure would appear to have been necessary as an antagonist for body muscles in maintaining the telescoping of the loosely articulated thoracic tergites (tar over tah, Fig. 1). The role of hydrostatic pressure has been demonstrated both anatomically and experimentally in similarly constructed cephalocarid crustaceans (*23*). For the trilobite, just as for primitive uniramians (*7*), the hemocoel can be hypothesized to have been the primitive supporting organ.

Energetic efficiency, much more than protection against predators, may have been the adaptive advantage behind the evolution of the exoskeleton. In the TCC group, the evolution of limb mechanisms for locomotion and feeding in an aqueous medium, mechanisms based on precise and coordinated movement of precisely formed parts in a concerted pattern, may have demanded maintainence of shape in body and limb parts and joints. This objective could have been achieved more economically through strengthening of the cuticle than through use of a complex body wall musculature as found in onychophorans. Development of the cuticle as an exoskeleton would have allowed loss of the body wall musculature, simplification of the body and limb musculature, and concentration of lines of muscular action across hinge joints. Inasmuch as onychophorans attain lengths over 10 centimeters, the size of rather large trilobites, and inasmuch as typical arthropod adults are no more than a tenth this long, size itself would not seem to have been the most important factor behind the transition. The reason why trilobites became arthropodized at such an early phyletic stage in segmental specialization may be related to the evolution of mechanisms, such as trunk limb feeding mechanisms, that are exclusively geared to an aqueous medium.

The idea that an armored exoskeleton evolved in trilobites primarily as protection against predators and parasites leaves much to be desired. Like olenellid trilobites of the earliest Cambrian, *Triarthrus* could not fully enroll.

Whether or not enrollment actually provided protection against predators, enrollment in olenellid trilobites and *Triarthrus* could not have served to protect the limbs and ventral integument in any special way. The difference in thickness and stiffening between the dorsal and ventral sides can be explained simply in body mechanical terms. Beyond the trilobite problem, the predation theory does not well explain the appearance of hard parts in Early Cambrian merostome chelicerates (*39*) which, to judge from close living relatives, were the first larger predators to appear in the fossil record.

Summary

While the question of whether the Arthropoda represent more than one phylum of animals is debatable, the jointed exoskeleton, a fundamental feature of arthropods, evolved independently in two groups that shared a worm-like common ancestor. The two major branches of Arthropoda, the primitively marine TCC and the primitively terrestrial (with one exception) Uniramia, independently arrived at arthropodization as the solution to the same problems of adaptation of the body mechanical system. New discoveries on trilobite anatomy show the unity of TCC as a group that shared a trilobite-like ancestor near the beginning of the Cambrian. With change in the constituency of Arthropoda through geologic time, the ways in which it would be categorized as a taxonomic group have also changed. The seeming isolation of the major modern arthropod groups is in large part an artifact of extinction of primitive intermediate forms such as trilobites which, in the Early Paleozoic, made the Arthropoda more diverse in basic modes of body organization than the group is at present.

The appearance of fossilizable hard parts in arthropods resulted from shift in supporting function from the body cavity, primitively a hydrostatic skeleton, to the cuticle, which came to be strengthened in becoming an exoskeleton. Energetic efficiency, more than protection from predators or evolutionary size increase in itself, was probably the impetus behind the transition. On the scale provided by the general evolutionary trend toward progressive specialization of segments, TCC became arthropodized at earlier stages than did Uniramia. Among TCC, the shift may have been driven by the evolution of locomotory and feeding mechanisms that were exclusively geared to an aqueous medium.

References and Notes

1. The taxonomic ranking of the major arthropod groups is controversial. For convenience, Crustacea and Chelicerata are herein called superclasses. Uniramia, of debatable status, include superclasses Onychophora, Myriapoda, and Hexapoda. Superclasses Tardigrada, Pentastomida, and Pycnogonida are minor groups. See S. M. Manton, in *Treatise on Invertebrate Paleontology*, R. C. Moore, Ed. (Univ. of Kansas Press, Lawrence, 1969), part R (Arthropoda 4), p. R3.
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17. An extensive account of *T. eatoni* (Hall), with full documentation, is found in J. L. Cisne, thesis, University of Chicago (1973). The *Triarthrus* specimens were made famous by C. E. Beecher (*18*) [*See* J. L. Cisne, *Ecology* **54**, 137 (1973); *Postilla No. 160* (1973)].
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19. *Phacops*, *Asteropyge*, *Triarthrus*, and *Cryptolithus* have three pairs of postoral head limbs (*14–16*), which suggests that only three postoral head segments were present, not four as thought by Beecher (*18*). The body musculature in *Triarthrus* provides evidence that three and only three segments were present behind the mouth, contrary to Beecher's (*18*) and Bergstrom's (*15*) interpretations from external anatomy. *Olenoides serratus* (Rominger) probably has three postoral head limbs (H. B. Whittington, *Foss. Strata*, in press). Raymond (*4*) stated that he actually observed only three pairs of postoral head limbs in *Cryptolithus* and *Isotelus* spp. The established idea that trilobites categorically have four postoral head segments stems from Beecher's (*18*) interpretation of *Triarthrus*. Unfortunately, because of postmortem deformation effects that he could not adequately study with the techniques available to him, and because of the small number of specimens that he had time to meticulously prepare, Beecher counted the first pair of thoracic limbs as a fourth pair of postoral head limbs. Størmer's (*12*) interpretation of *Ceraurus pleurexanthemus* Green, which is based on small parts of three specimens and which draws heavily on an analogy with Beecher's interpretation of *Triarthrus*, appears to perpetuate the error. Three pairs of lateral glabellar furrows and a single occipital furrow are characteristic of the trilobite head tergum [H. B. Whittington, *Biol. Rev. (Camb.)* **32**, 421 (1957)]. These furrows correspond to areas of attachment of major body muscles in *Triarthrus* and hence would appear to mark segmental boundaries, as has long been supposed. The frontal glabellar lobe is preantennal, the first lateral glabellar lobe is antennal, and so forth.
20. D. L. Bruton, *Foss. Strata*, in press; C. P. Hughes, *ibid.*, in press; A. M. Simonetta, *Monit. Zool. Ital.* **69**, 172 (1962); *ibid.* **71**, 97 (1963); *ibid.* **72**, 215 (1964); *Palaeontogr. Ital.* **66**, 35 (1970); in preparation; H. B. Whittington, *Geol. Surv. Can. Bull. No. 209* (1971); *Foss. Strata*, in press.
21. H. G. Cannon, *Trans. R. Soc. Edinb.* **55**, 355 (1927).
22. H. L. Sanders, *Mem. Conn. Acad. Arts Sci.* **15** (1963).
23. R. R. Hessler, *ibid.* **16** (1964).
24. S. M. Manton, personal communications; *Zool. J. Linn. Soc.* **53**, 257 (1973).
25. → N. Eldredge, *J. Paleontol.* **45**, 52 (1971).
26. H. J. Harrington, in *Treatise on Invertebrate Paleontology*, R. C. Moore, Ed. (Univ. of Kansas Press, Lawrence, 1959), part O (Arthropoda 1), p. O38.

→ S. M. Manton, *Phil. Trans. R. Soc. Lond. Ser. B* **233**, 483 (1949); *Biol. Rev. (Camb.)* **35**, 265 (1960).

28. While Trilobita-Crustacea-Chelicerata may be an awkward name for the group, it seems too early to propose a better name (such as Multiramia) for it. The TCC group may form only part of a still more inclusive natural group into which a variety of other primitively marine groups may also fall.
29. W. T. Calman, in *A Treatise on Zoology*, E. R. Lankester, Ed. (Black, London, 1909), vol. 7, fasc. 3, pp. 1–28.
30. W. Garstang and R. Gurney, in *Evolution: Essays Presented to Professor Goodrich*, G. R. De Beer, Ed. (Oxford Univ. Press, Oxford, 1938), p. 271.
31. G. E. Hutchinson, *Proc. U.S. Natl. Mus.* **78** (11) (1930); *Am. J. Sci.* **267**, 1062 (1969).
32. In making this generalization, pycnogonids can reasonably be included with TCC as chelicerate allies. Tardigrades and pentastomids, though usually included in Arthropoda, are scarcely arthropodized. Whether or not arthropodization might have occurred independently in a variety of primitive Paleozoic forms such as arthropleurids remains an open question—and a problem with the generalization.
33. R. B. Clark, *Dynamics in Metazoan Evolution* (Oxford Univ. Press, Oxford, 1964), pp. 118–164; E. J. W. Barrington, *Invertebrate Structure and Function* (Houghton Mifflin, Boston, 1967), pp. 98–111.
34. D. Nicol, *J. Paleontol.* **41**, 1397 (1966).
35. G. E. Hutchinson, in *Oceanography*, M. Sears, Ed. (AAAS, Washington, D.C., 1961), p. 85.
36. P. E. Cloud, *Evolution* **2**, 322 (1948); in *Evolution and Environment*, E. T. Drake, Ed. (Yale Univ. Press, New Haven, 1968), p. 1.

→ J. W. Schopf, B. N. Haugh, R. E. Molnar, D. F. Satterthwaite, *J. Paleontol.* **47**, 1 (1973).

38. S. M. Stanley, *Proc. Natl. Acad. Sci. U.S.A.* **70**, 1486 (1973).
39. L. Størmer, in *Treatise on Invertebrate Paleontology*, R. C. Moore, Ed. (Univ. of Kansas Press, Lawrence, 1955), part P (Arthropoda 2), p. P4; J. Bergstrom, *Geol. Foren. Stockh. Forh.* **90**, 489 (1968).

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