Arthropod Fossils and Phylogeny, Gregory Edgecombe (Editor), 1998, Columbia University Press, New York, 347 p. (Hardcover $125.00) ISBN: 0-231-09654-2.

There is something about writing on arthropod phylogeny that brings out the worst in people.

J.W. Hedgepeth

The above gem was reintroduced 17 years ago in an article surveying the crustacean fossil record (Schram, 1982). Although this observation is just as true today as it was then, there has been improvement: modern versions of these tendentious and occasionally abrasive disagreements at least are more explicit. Edgecombe's edited volume, Arthropod Fossils and Phylogeny, extends this theme, but also follows in the tradition of two important and scholarly precursors, Arthropod Phylogeny (Gupta, 1979) and Arthropod Relationships (Fortey and Thomas, 1997). A new treatment is deemed necessary since Arthropod Relationships makes clear that major disagreements about how to analyze arthropods and the nature of their relationships is as contentious as ever. Arthropod Fossils and Phylogeny also gives us the stürm und drang of arthropod relationships.

Even if the tenor of the debate has not improved, there have been advancements in the quality and types of evidence and approaches that have been brought to bear on the subject. Consider the recent plethora of analytical techniques for estimating phylogenies both within the morphological and biomolecular research programs, the inclusion of fossil and extant data, addition of larval and adult characters, the diversity of algorithms for establishing relatedness, and incessant discoveries of new biomolecules and morphologies for intertaxal comparisons. Of course, if that is not enough, on the other side of the problem are arthropods themselves. The Arthropoda is the most speciose macroscopic group of organisms of all time, possessing a bewildering range of morphology that encompasses the more familiar trilobites, lobsters, tarantulas, and beetles. This phenomenal range in body plans applies not only to the fossil record, such as the bi-

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zarre "funnies" of the Burgess Shale (as my former mentor Jack Sepkoski once referred to them), but also many extant arthropod representatives equally stretch our sensibilities of what a conventional arthropod should look like. Arthropods include organisms as different as barnacles, butterflies, fluke-like pentastomids (Abele et al., 1992), and some parasitoid insects that are perennially worm-like. Many phylogeneticists would include tardigrades and possibly velvet worms as well. Perhaps the problem with arthropod phylogeny is that there is a double dose of trouble: a multitude of techniques are available to exercise on an immensely multifarious phylum.

Although this context may be unduly gloomy, there are a few bright lights. I have identified several recurring and inter-related themes that the 16 authors of the volume's seven chapters mostly can agree on. While some of these themes are not expressed or supported in every chapter, they collectively transcend the background level of argumentation because they emerge at the ends of these chapters as important conclusions. The first seven themes involve substantive methodological issues, and the subsequent five are results concerning arthropod phylogeny.

(1) Fossils, combined with modern taxa, are essential for phylogenetic analyses. Data sets based exclusively on extant representatives, or alternatively only on fossils, provide inaccurate results for phylogeny reconstruction (an exception, of course, are clades that are wholly extinct, but they too should be linked at coarser levels to extant lineages). For example, as pointed out by Walossek and Müller in Chapter 5, stem-group fossils may possess synapomorphies no longer expressed in their extant descendants and, thus, are essential for establishing early developmental features that are largely inaccessible today. Also, recent discoveries have increased the range of known taxa, preservational types, and sampled environments and have significantly narrowed the gap between the quality of modern and fossil morphological evidence. Data now are available for three-dimensionally and soft-part-preserved embryos, larval instars, and taxa as obscure as pentastomids. Sampling paleoenvironments such as the benthic flocculant zone has markedly increased the range of morphologies and taxa available for examination. It is in this context that Wheeler's presentation of "total evidence" in Chapter 1 is difficult to grasp since "total" in his analysis excludes crucial fossil material.

(2) Arthropod data-sets are still significantly incomplete in terms of the total range of potentially available taxa and characters. For example, important unsequenced taxa could provide crucial data toward resolving or expanding relationships that are too poorly known morphologically. Wills and colleagues in Chapter 2 indicate that molecular studies have sampled too few representatives across arthropods to yield repeatable phylogenies. Moreover, some of this incompleteness is conditioned by the lack of computational power inherent in the analysis of larger data sets. Schram and Hof, in Chapter 6, term this general deficiency of data as the "vraagteken effect," and note that the absence of critical information results in unstable phylogenies.

(3) Arthropods have significant homoplasy, confounding phylogenetic analyses. Consistency indices of 0.5 and lower are typical for more taxonomically inclusive studies. Bergström and Hou in Chapter 4—probably the most heterodox contribution of all—cite the recurring problem of a mosaic pattern of character distribution as being a critical issue that needs to be addressed before further progress can be made in arthropod phylogeny. Elevated arthropod homoplasy is frustrating for those ferreting out phylogenies and undoubtedly reflects a developmental program that allows for major subelement transpositions within modular and segmental organisms. Thus, subelements can be often transposed, resulting in unique combinations of appendage type or body segments, yet retaining conservative similarities of the larger constituent clade. Such complications undoubtedly have spurred the application of the multitude of techniques mentioned above.

(4) The issue of what are the character-based limits of modern taxa is as relevant as ever. This issue is particularly important when it is applied to fossil arthropod taxa that incorporate some but not all of the characters found in their crown-group descendants, as discussed by Schram and Hof for the Crustacea and by Selden and Dunlop for opilionid Arachnida in Chapter 7. One solution is a relaxation of the definition of a crown group, which typically is based on modern taxa, to include reasonably those fossil stem lineages that are phylogenetically close, the collection of which are monophyletic at a coarser level. The alternative—which has resulted in much confusion regarding arthropod problematica addressed in this volume—is to propose an inordinate number of unfathomable stem-groups and plesions left in phylogenetic limbo.

(5) There remains confusion regarding the establishment of initial ground-plan characters of a basal taxon prior to phylogenetic analysis of its constituent lineages. Constructing a ground pattern (to use Walossek and Müller's term) or a hypothetical ancestor (Ramsköld and Chen's similar term in Chapter 3) for determining the primitive spectrum of plesiomorphic and synapomorphic characters is an alternative to selecting an appropriate fossil or credible outgroup that ideally would reveal the same plesiomorphies and synapomorphies of interest. But relevant fossil material is frequently unavailable. The major contrast to using ground patterns, appropriate fossils, or hypothetical ancestors is to arrive at hypotheses from extant taxa, such as computer-based analyses of unordered molecular data. Such analyses, even if combined with morphological data, according to Walossek and Müller, neglect the contingency that evolution has on morphology. Thus, a resulting trajectory of character-state change must be evaluated sequentially, from the bottom-up, and not post hoc at the terminal twigs of a highly-branched tree. Krzeminski (1992) has introduced an example of this approach in an analysis of the Mesozoic phylogeny of dipteran insects.

(6) The current state of the art involves multiple approaches, constant experimentation and introduction of new analytical techniques. Because of the proliferation of such approaches, alternatives, for example, no longer include just parsimony versus consensus approaches, but more appropriately which consensus technique will be used: majority rule, strict consensus, or others? In fact, journals such as Cladistics and Systematic Biology now contain a high fraction of contributions devoted solely to the introduction and discussion of such techniques.

(7) The translation of cladograms into classifications is probably unwarranted at this time. This is because of the ongoing problems mentioned above and even uncertainties about some basic arthropod homologies. Evidence for this, as mentioned above, are major and persistent difficulties in obtaining reasonably stable cladograms of the same taxa by different researchers.

This volume presents six other developments that encapsulate major conclusions regarding internal arthropod relationships and the phyletic integrity of the entire clade. When these issues are discussed, there is agreement among the contributors of this volume on the following issues.

(1) Arthropods are almost undoubtedly monophyletic. The term Euarthropoda is typically applied to this clade and includes the Tracheata (Myriapoda + Hexapoda) and Schizoramia. The Schizoramia encompasses the extinct Marellomorpha, the Arachnomorpha (including trilobitomorph and chelicerate clades), and the Crustacea. Tardigrades are probably arthropods as a sister-group to the Euarthropoda, although lobopodan onychophorans, "great appendage" anomalocaridids, and Opabinia with a median and frontal grasping claw are best considered as more distantly related, protarthropodan lineages (but see Ballard et al., 1992). Manton's speculative scenario of profound arthropod polyphyly (summarized in her 1977 book) is insightful functional morphology but it has not withstood the test of many subsequent and varied phylogenetic analyses.

(2) Enigmatic Cambrian taxa of arthropodan affinities are not as weird as once thought. These taxa, such as Burgessia, Marella, Naraoia, Sidneyia and Waptia, form basal lineages comprising either (1) an extensive pectinate series that terminates in a crown group, the Crustacea (indicated by Schram and Hof and suggested by Walossek and Müller and by Bergström and Hou), or (2) a larger group of four principal clades within the Arachnomorpha, with each of the three larger clades characterized by a pectinate but highly pruned topology (indicated by Wills and colleagues). Although the position within the Arthropoda of these Cambrian taxa is significantly different in these two sets of studies, the successive acquisition of apomorphies by these Cambrian taxa is a key common feature. Their possession of at least some of the characters found in subsequently-derived crustaceans or arachnomorphs make them appear less "bizarre." Interestingly, a Paleozoic clade of high phylogenetic distinctiveness, the Marellomorpha, consists of Burgess Shale and Hunsrück Slate taxa that are probably

associated with basal arachnomorphs. Also, Ramsköld and Chen document a diverse, Early to Middle Cambrian lobopodan clade consisting of at least 15 species, including the famed Hallucigenia, with appreciable higher-rank cladogenetic structure.

(3) The concept of the "Uniramia" survives. I once thought that the Uniramia was a dead idea. The polyramy hypothesis advocated by Kukalova-Peck (1992), which advocates that each body segment of primitive arthropods had polyramous limbs and that biramy and uniramy are derived conditions, has been questioned directly by Walossek and Müller and implicitly by some of the other authors. These authors posit that ancestral arthropods bore basipods with two rami, an inner endopod and an outer, often leaf-like, exopod, both modified for diverse functions in crustaceans and largely missing in chelicerates and tracheates. Bergström and Hou extend this issue, stating that Cambrian material supports the view that ancestral arthropods had only one unsegmented exopod per body segment, and that biramy and polyramy, as illustrated in exites of Paleozoic insects, is derived.

(4) The Crustacea is monophyletic and the best-supported monophyletic clades of crustaceans are the Phyllopoda, Maxillopoda, and Malacostraca. Surprisingly, there was agreement among the four studies that analyzed ostensible "crustacean" forms that the Crustacea is a monophyletic clade, contrary to significant recent evidence. In the detailed analysis by Schram and Hof limited only to crustacean forms and a myriapod/hexapod outgroup, the Phyllopoda, two major clades of Maxillopoda, and Malacostraca (minus phyllocarids) were deemed monophyletic. These results are largely consistent with Walossek and Müller's views. Interestingly, forms from the Cambrian Burgess Shale and the Orsten Fauna constitute a separate clade between crown-group Crustacea and a noneuarthropod out-group, reminiscent of the Marellomorpha of Wills and colleagues. The counterintuitive result of a sister-group relationship between isopods and amphipods also was presented.

(5) A position of the Hexapoda within the Crustacea is not supported. Ironically, the one major arthropod subclade not analyzed in this volume is the Tracheata, also known as the Atelocerata or Antennata, and consisting of the Myriapoda (millipedes, centipedes and relatives) and the Hexapoda (insects and a few basal groups). However, tracheates were included as data in three of the chapters, in conjunction with evaluations of major relationships within the Arthropoda. Several recent molecular-based analyses (Averof and Akam, 1995; Friedrich and Tautz, 1995) and evidence from developmental biology (Panganiban et al., 1995; Popadic et al., 1996) have placed the Hexapoda within their fellow "mandibulates", the Crustacea—an idea that was first suggested at the turn of the century based on external morphological considerations and subsequently abandoned. Wheeler's total evidence approach (modern data only) and the comprehensive analysis by Wills and colleagues (modern and fossil data), however, indicate that the Hexapoda is joined with the Myriapoda as the monophyletic Tracheata, which supports considerable evidence from traditional studies of morphology. Curiously, the two chapters that analyzed all major arthropod groups, including tracheates, reached different conclusions. Will's cladistic analyses lodged tracheates between the more derived crustaceans, arachnomorphs, and marellomorphs and the more primitive lobopods, tardigrades, and anomalocaridids. Alternatively Wheeler's cladistic analysis and a phenetic study by Wills and colleagues placed tracheates as a terminal clade whose closest relatives are crustaceans, and more distantly, chelicerates, supporting the clade Mandibulata. However, as other authors in this volume have shown, the integrity of the Mandibulata evaporates when fossils are included.

Edgecombe states on the first page that this volume was inspired by two topical issues. "One is an explosion of research on high-level phylogeny of the Arthropoda. The other is a rekindling of interest in the role fossils play in phylogenetic analysis." The contributions in this volume certainly address these two aims. However, this is a volume that may rankle participants within the various ongoing arthropod debates. For those of us who are removed from current skirmishes of methodology and lack interest in the increasingly powerful armamentaria of cladistic algorithms, but are interested in basic questions of how did the most successful macroscopic clade of all time achieve dominance on this planet, this volume is highly recommended. If one can get though the unavoidable but often dreadful arthropod terminology—there frequently is terminological incongruity from chapter to chapter—this volume presents generally cutting-edge summaries of considerable fascination in aggregate. This is a fast-moving field and most of the conclusions in this volume would have been unanticipated even five years ago. Who would have thought that many Burgess Shale taxa would have been accommodated within modern crustacean or arachnomorph subgroups? Or that lobopodan protarthropods were so disparate at higher taxonomic levels during the Cambrian, and that the recent Onychophora is only a surviving remnant? Or that the position of the tracheates within the Arthropoda remains as unresolved as ever? With a bit of patience, this book will not bring out the worst in people.

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