8 Sampling, groundplans, total evidence and the systematics of arthropods

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8.1 INTRODUCTION

The outline of arthropod relationships was clearly and firmly established by Snodgrass (1938) (Figure 8.1). All work on these taxa since then concerns the support for, and discussion of the basic groups he delineated. Although the efforts of Tiegs, Manton, and Anderson (Tiegs and Manton, 1958; Manton, 1964, 1973, 1979; Anderson, 1979) to incorporate functional morphology and observational embryology diverted discussion from Snodgrass' basic principles, the field has returned to the apportionment of variation so productive in the past.

Since Snodgrass, arthropod systematics has seen two fundamental advances: synapomorphy and DNA. Technical innovation has presented molecular genetic data in immense quantity, and the theoretical advances of Hennig (1966) have offered the framework for their interpretation. Although the cladistic paradigm allows (some might say requires) simultaneous analysis of morphological and molecular data, this combination of evidence is rarely attempted (Wheeler *et al.*, 1993). This is due, in part, to the sampling problems of molecular studies (reviewed by Wheeler, 1997) and the use of groundplans and single-character analysis in morphological work (see papers of Walossek and Boxshall, 1997, this volume).

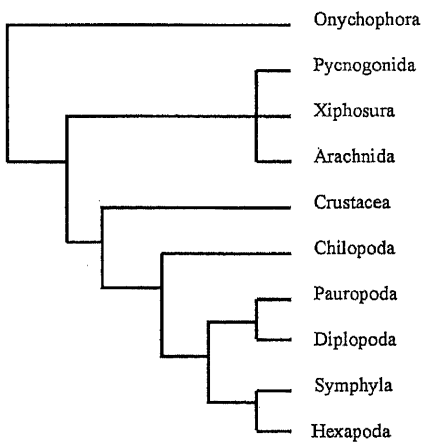

Figure 8.1 Phylogeny of the extant arthropods. (After Snodgrass, 1938.)

The discussion presented here is based on two analytical notions. First, that large, diverse samples of taxa are better able to recover the phylogenetic pattern of higher taxa; and second, that diverse types of information (characters) offer more robust indicators of phylogeny than single systems or sources of data. This is the kernel of the 'total evidence' approach (Kluge, 1989).

Although 'total' evidence is something of a misnomer, the concept – that all evidence currently available be used simultaneously – is hard to deny. This does not mean or imply that no new data could be gathered which would overturn the results, just that, for now, this is the best we can do. Hence data from hard and soft-part anatomy, behaviour, development, molecular sequence and gene organization are included in my analysis. If we combine information from behaviour, anatomy and development, it is difficult to see why we should exclude molecular characters from the data set (Kraus and Kraus, 1994). It seems illogical to reserve or segregate organismal variants *a priori*, because we cannot know which features are informative and congruent without simultaneous analysis. Lastly, although not examined here, there is the question of accommodating our knowledge of extinct taxa with molecular systematics. Unless data are combined, the overwhelming majority of creatures which have ever lived – the fossil ones – will be excluded from integration with living taxa.

Another motivation for my analysis comes from desire to employ better samples of lower taxa to arrange higher groups. The fundamental questions of arthropod phylogenetics concern the interrelationships of four lineages: chelicerates, crustaceans, myriapods and hexapods. Of these, the monophyly of the Myriapoda is most frequently questioned. Each of these lineages has been divided into constituent lower taxa

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('orders'), which though not equivalent in any sense, reflect the cladistic diversity of the groups. Where possible, samples have been used from each of these and relevant outgroups. This should help to augment the quality of groundplan estimates for higher taxa through cladistic sampling.

Although most recent analyses have accepted the monophyly of the Arthropoda and even the basic split between chelicerates on one side and mandibulates (crustaceans, myriapods and hexapods) on the other, argument persists within the Mandibulata. Recent molecular work (Field *et al.*, 1988; Turbeville *et al.*, 1991; Freidrich and Tautz, 1995; Garey *et al.*, 1996; Giribet *et al.*, 1996) (Figure 8.2) has pointed to a Hexapoda + Crustacea grouping as opposed to the more traditional Tracheata (Hexapoda + Myriapoda). As pointed out earlier (Wheeler *et al.*, 1993), molecular data point to the Crustacea + Hexapoda group while morphological analysis offers near uniform support for Tracheata (but see Dohle, 1997, this volume). Some morphological analyses even present the 'Myriapoda' as paraphyletic with respect to the hexapods showing the Labiata as Hexapoda grouped with the Symphyla, Pauropoda and Diplopoda to the exclusion of the Chilopoda (Pocock, 1893; Snodgrass, 1938; Kraus and Kraus, 1994). The status and sister group relations of the myriapods form the main thrust of the following analysis.

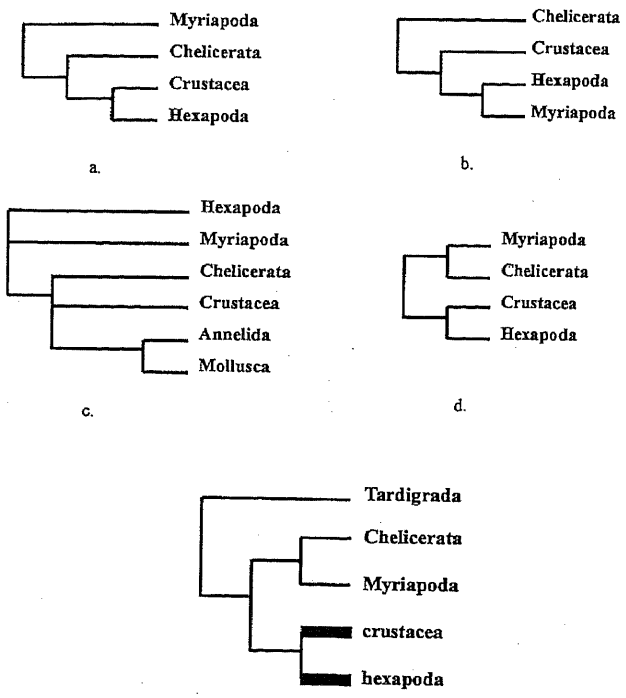

Figure 8.2 Molecular phylogenies of the Arthropoda. (a) Field *et al.* (1988); (b) Abele *et al.* (1989); (c) Lake (1990); (d) Turbeville *et al.* (1991); and (e) Giribet *et al.* (1996). The cladogram of Garey *et al.* (1996) resembles that of Giribet but contains no myriapodan sample and places a branchiopod in an unresolved clade with the hexapod and crustacean taxa. Taxa in lower case (and with thicker lines) are not monophyletic.

8.2 THE DATA SET

8.2.1 CHARACTERS

In attempting to include as much data as possible, characters were garnered from both morphological and molecular sources. The analysis of non-sequence data from variants among and between higher taxa resulted in 90 defined lineages (Table 8.1). These include five outgroup (Mollusca, Polychaeta, Clitellata, Onychophora and Tardigrada), 13 chelicerate, 35 crustacean, four myriapod and 33 hexapod taxa. These lineages were defined by variation in the 552 non-sequence characters. Of these, 121 concerned relationships among arthropod taxa at the highest level (from a variety of sources), 96 concerned chelicerate interrelationships [mainly derived from the work of Weygolt and Paulus (1979), Yoshikura (1975) and Schultz (1990)], 248 bore on the hexapod orders [from a variety of sources, mainly Hennig (1981), Kristensen (1995) and Boudreaux (1979)] and 87 concerned the crustaceans (entirely from Emerson and Schram, 1997, this volume). For these 90 lineages, 45% of the entries were missing or inapplicable – an unfortunately high number. Most of these are due to the inapplicability of ingroup variation characters in non-ingroup taxa (e.g. wing venation in worms).

The molecular characters are drawn from three sources (see data on web site). The first are mitochondrial gene order characters of Boore *et al.* (1995) which are included in the non-sequence data (i.e. morphology, behaviour, etc.). The other molecular sources are the small (18S) and large (28S) ribosomal subunit DNAs. Although the entirety of each locus has been sequenced for many taxa, only the middle 1200 bases of the small and a central 400 bases of the large subunit were used. This is due to the large amount of missing data that would exist for most of the taxa if the entire genes were included in the analysis. Even so, approximately 23% of the molecular observations were missing. The regions used were limited to those which had been sequenced for 50% of the taxa. For this reason, the data of Ballard *et al.* (1992) were also not included.

8.2.2 TAXA

Of the 90 morphologically defined lineages, 31 of these taxa are currently unavailable as sequence data (one chelicerate – palpigrades; two myriapods – pauropods and symphylans; and 26 crustacean lineages; Table 8.1). Most of the remaining lineages are represented by two sequenced taxa resulting in 136 terminal taxa for analysis. Those taxa

Table 8.1 Taxa used in the study

Higher group	*Taxon*	*18S rDNA*	*28S rDNA*
Mollusca			
Cephalopoda	*Loligo pealei*	Wheeler	ND
Polyplacophora	*Lepidochiton cavernae*	Wheeler	ND
Annelida			
Polycheata	*Glycera* sp.	Wheeler	ND
Oligocheata	*Lumbricus terrestris*	Wheeler	ND
	Tubifex sp.	Freidrich	Freidrich
Hirudinea	*Haemopis marmorata*	Wheeler	ND
Onychophora			
Peripatoidae	*Peripatus trinitatis*	Wheeler	ND
Peripatopsidae	*Peripatoides novozealandia*	Wheeler	ND
Tardigrada	*Macrobiotus hufelandi*	Giribet	ND
Chelicerata			
Pycnogonida	*Anoplodactylus portus*	Wheeler	Hayashi
	Anoplodactylus lentus	Hayashi	Hayashi
	Colosendeis sp.	Hayashi	Hayashi
Xiphosura	*Limulus polyphemus*	Wheeler	Hayashi
Scorpiones	*Centruroides hentsii*	Wheeler	Hayashi
	Androctonus australis	Hayashi	Hayashi
	Hadrurus arizonensis	Hayashi	Hayashi
	Paruroctonus meaensis	Hayashi	Hayashi
Araneae	*Peucetia viridans*	Wheeler	Hayashi
	Gea heptagon	Hayashi	Hayashi
	Erypelma californica	Freidrich	Freidrich
	Thelechoris striatipes	Hayashi	Hayashi
	Heptathelia kimurai	Hayashi	Hayashi
	Liphistius bristowei	Hayashi	Hayashi
Palpigrada	Morphology only	ND	ND
Psuedoscorpiones	*Americhenernes* sp.	Hayashi	Hayashi
Solifugae	*Chanbria regalis*	Hayashi	Hayashi
Opiliones	*Vonones ornata*	Hayashi	Hayashi
	Leiobunum sp.	Hayashi	Hayashi
Acari	*Amblyomma americanum*	Hayashi	Hayashi
	Rhiphicephalus sanguineus	Hayashi	Hayashi
	Tetranychus urticae	Hayashi	Hayashi
Ricinulei	Ricinoididae (juvenile)	Hayashi	Hayashi
Amblypygi	Amblypygid sp.	Hayashi	Hayashi
Thelyphonida	*Mastogoproctus giganteus*	Wheeler	Hayashi
Schizomida	*Trithyreus pentapeltis*	Hayashi	Hayashi
Crustacea			
Nectiopoda	Morphology only	ND	ND
Stomatopoda	Morphology only	ND	ND
Anaspidacea	Morphology only	ND	ND
Bathynellacea	Morphology only	ND	ND
Lophogastrida	Morphology only	ND	ND
Mysida	Morphology only	ND	ND
Mictacea	Morphology only	ND	ND
Isopoda	Morphology only	ND	ND
Amphipoda	Morphology only	ND	ND
Cumacea	*Diastylis* sp.	Kim	ND
Tanaidacea	Morphology only	ND	ND
Spelaeogriphacea	Morphology only	ND	ND
Thermosbaenacea	Morphology only	ND	ND
Euphausiacea	Morphology only	ND	ND
Amphionidacea	Morphology only	ND	ND
Dendrobranchiata	Morphology only	ND	ND
Caridea	Morphology only	ND	ND
Euzygida	Morphology only	ND	ND

Table 8.1 (continued)

Higher group	*Taxon*	*18S rDNA*	*28S rDNA*
Reptantia	*Callinectes* sp.	Wheeler	Hayashi
	Procambarus leonensis	Spears	ND
Leptostraca	Morphology only	ND	ND
Cephalocarida	Morphology only	ND	ND
Notostraca	Morphology only	ND	ND
Anostraca	*Artemia salina*	Nelles	Freidrich
	Branchinecta packardi	Spears	ND
Conchostraca	Morphology only	ND	ND
Cladocera	*Bosmina longirostris*	Kim	ND
Ostracoda	Podocopid sp.	Spears	ND
	Stenocypris major	Kim	ND
Mystacocarida	Morphology only	ND	ND
Branchiura	*Argulus nobilis*	Abele	ND
	Porocephalus crotali	Spears	ND
Tantulocarida	Morphology only	ND	ND
Copepoda	*Calanus pacificus*	Spears	ND
Rhizocephala	Morphology only	ND	ND
Ascothoracida	Morphology only	ND	ND
Acrothoracica	*Trypetesa lampas*	Spears	ND
Thoracica	*Balanus* sp.	Wheeler	Hayashi
	Calantica villosa	Spears	ND
	Octolasmis lowei	Spears	ND
Facetotecta	Morphology only	ND	ND
Myriapoda			
Chilopoda	*Scutigera coleoptrata*	Wheeler	Hayashi
	Lithobius sp.	Freidrich	Freidrich
Diplopoda	*Spirobolus* sp.	Wheeler	Hayashi
	Polyxenus sp.	Freidrich	Freidrich
	Megaphyllum sp.	Freidrich	Freidrich
Pauropoda	Morphology only	ND	ND
Symphyla	Morphology only	ND	ND
Hexapoda			
Collembola	*Psuedochorutes*	Freidrich	Freidrich
	Podura aquatica	Carpenter	Carpenter
Protura	*Nipponentomon* sp.	Carpenter	Carpenter
Diplura	*Metajapyx* sp.	Carpenter	Carpenter
	Campodea tillyardi	Carpenter	Carpenter
Archeognatha	*Petrobius brevistylus*	Freidrich	Freidrich
	Trigoniopthalmus alternatus	Whiting	Whiting
Zygentoma	*Lepisma* sp.	Carpenter	Carpenter
	Thermobius domestics	Carpenter	Carpenter
Ephemeroptera	*Stenonema* sp.	Carpenter	Carpenter
	Ephemerella sp.	Whiting	Whiting
Odonata	*Libellula pulchella*	Wheeler	Whiting
	Calopteryx sp.	Carpenter	Carpenter
Plecoptera	*Megarcys stigmata*	Whiting	Whiting
	Cultus decisus	Whiting	Whiting
Embiidina	*Oligotoma saundersii*	Whiting	Whiting
	Clothoda sp.	Carpenter	Carpenter
Grylloblatta	*Grylloblatta* sp.	Carpenter	Carpenter
Dermaptera	*Forficula auricularia*	Carpenter	Carpenter
	Labia sp.	Carpenter	Carpenter
	Labidura riparia	Whiting	Whiting
Isoptera	*Reticulotermes virginiana*	Carpenter	Carpenter
Blattaria	*Blaberus* sp.	Carpenter	Carpenter
Mantodea	*Mantis religiosa*	Wheeler	Whiting
Orthoptera	*Ceuthophilus* sp.	Carpenter	Carpenter
	Melanoplus sp.	Whiting	Whiting

Higher group	*Taxon*	*18S rDNA*	*28S rDNA*
Phasmida	*Timema californica*	Carpenter	Carpenter
	Phyllium sp.	Carpenter	Carpenter
Pthiraptera	*Dennyus hirudensis*	Whiting	Whiting
Thysanoptera	*Taeniothrips inconsequens*	Whiting	Whiting
Psocodea	*Cerastipsocus venosus*	Wheeler	Whiting
Hemiptera	*Saldula pallipes*	Wheeler	Whiting
	Buenoa sp.	Wheeler	Whiting
Coleoptera	*Priacma serrata*	Whiting	Whiting
	Calpocaccus posticatus	Whiting	Whiting
Neuroptera	*Lolomyia texana*	Whiting	Whiting
Megaloptera	*Corydalus cognatus*	Whiting	Whiting
Raphidiodea	*Agulla* sp.	Whiting	Whiting
Hymenoptera	*Hemitaxonus* sp.	Whiting	Whiting
	Ophion sp.	Whiting	Whiting
Lepidoptera	*Papilio troilus*	Wheeler	Whiting
	Galleria mellonella	Whiting	Whiting
Trichoptera	*Leptocerus* sp.	Whiting	Whiting
	Pycnopsyche sp.	Whiting	Whiting
Mecoptera	*Nannochorista neotropica*	Carpenter	Carpenter
	Boreus coloradensis	Whiting	Whiting
Siphonaptera	*Ctenocephalides canis*	Whiting	Whiting
	Hystrichopsylla schefferi	Whiting	Whiting
Strepsiptera	*Crawfordia n.* sp	Whiting	Whiting
	Xenos pecki	Whiting	Whiting
Diptera	*Laphria* sp.	Whiting	Whiting
	Tipula sp.	Whiting	Whiting

Abele= Abele *et al.* (1989); Giribet = Giribet *et al.* (1996); Hendriks = Hendriks *et al.* (1988); Freidrich = Freidrich and Tautz (1995); Hayashi = Wheeler and Hayashi (unpublished); Kim= Kim *et al.* (1993); Nelles = Nelles *et al.* (1984); Sharp = Sharp and Li (1987); Spears= Spears *et al.* (1994); Tautz = Tautz *et al.* (1988); Wheeler = Wheeler *et al.* (1993); Whiting = Whiting *et al.* (in press); ND = no data; Carpenter = Wheeler, Whiting, Wheeler, and Carpenter (in press).

without sequence data were placed on the basis of morphology alone with the molecular data coded as missing. This resulted in an overall level of missing data of approximately 29%.

8.3 ANALYSIS

8.3.1 MORPHOLOGICAL

Morphological characters were analysed using Goloboff's (1995) parsimony-based NONA (version 1.1). These searches used 'tbr' branch swapping on 50 random addition sequences.

8.3.2 MOLECULAR

Phylogenetic analysis of molecular sequence data (18S and 28S rDNA) were performed via direct optimization of sequences (Wheeler, 1996), without the intermediate step of multiple alignment, using MALIGN (Wheeler and Gladstein, 1992, version 2.7 on a dedicated cluster of workstations). As with the morphological data, 'tbr' type branch swapping was employed and 50 random addition sequences attempted. For this analysis, an insertion–deletion cost of 2 : 1 was used and a transversion : transition ratio of 2 : 1. These values, though somewhat arbitrary, have been shown to optimize character congruence in other arthropod studies (Wheeler, 1995, 1997). Insertion–deletion events were treated independently and included as phylogenetic information (Wheeler, 1993). Other investigators (Friedrich and Tautz, 1995) have used similar parameter values – though rarely gaps. The choice of these parameters, however, can affect the outcome of phylogenetic analysis (Wheeler, 1995), hence the robustness of these results awaits further appraisal.

8.3.3 TOTAL EVIDENCE

When the morphological and molecular data were combined to create 'total evidence' cladograms, morphological character transformations were assigned the same weight as insertion–deletion events. Otherwise, all weighting was equal, in other words, morphological (552) and molecular

(~1400) characters were employed without regard to source. The combined data were analysed in the same manner as described for the molecular data alone.

8.4 RESULTS

Phylogenetic analysis of morphological (non-sequence) characters yielded 87 most parsimonious cladograms of length 1204 with a C.I. of 0.55 and an R.I. of 0.85 (Figure 8.3). The molecular (18S and 28S) data alone produced a single tree at weighted length 10599 (Figure 8.4). Combined data yielded a single tree at 16079 weighted steps (Figure 8.5) The most parsimonious cladogram forced to link crustaceans and hexapods to the exclusion of myriapods had a length of 16167 steps – 88 steps longer (0.55 %; Figure 8.6). The comparison of the individual morphological and molecular analyses to the combined data produces 4.13% additional homoplasy (ILD of Mickevich and Farris, 1981), showing a low level of character incongruence between the main sources of data.

8.5 CONCLUSIONS

The most salient conclusion from this study is that as far as these data are concerned, the Tracheata are monophyletic as are the Labiata = (Hexapoda + ((Diplopoda + Pauropoda) + Symphyla)) with the myriapods relegated to paraphyly. There are three factors which bear on the confidence which can be placed on this result: analytical robustness, missing data, and missing – that is, extinct – taxa.

The robustness of these results is unknown. The analysis performed here is based on a specific set of assumptions which include an insertion–deletion cost of twice that of transversions, a transversion cost twice that of transitions, and non-sequence character change equal in cost to insertion–deletion events. Although these values are similar to those used in other studies (Freidrich and Tautz, 1995; Wheeler, 1995), the consistency of phylogenetic results under varying parameter values is unknown, but may be important. This is especially pertinent given the small differential in support between the Tracheata scheme and Crustacea + Hexapoda.

Missing data may have an insidious effect on phylogenetic analysis (Nixon and Davis, 1991; Platnick, 1991). In situations of ambiguity or high levels of missing data, these defects are unpredictable. Although additional sequencing effort will remove some missing values, most of the non-sequence missing values cannot be established. This is because many 'missing' values are inapplicabilities, that is, no corresponding feature or attribute can be identified in a taxon. For instance, cheliceral features in myriapods or wing-vein characters in Onychophora can never be appropriately coded. However, given that these features do not, in general, affect the relative placement

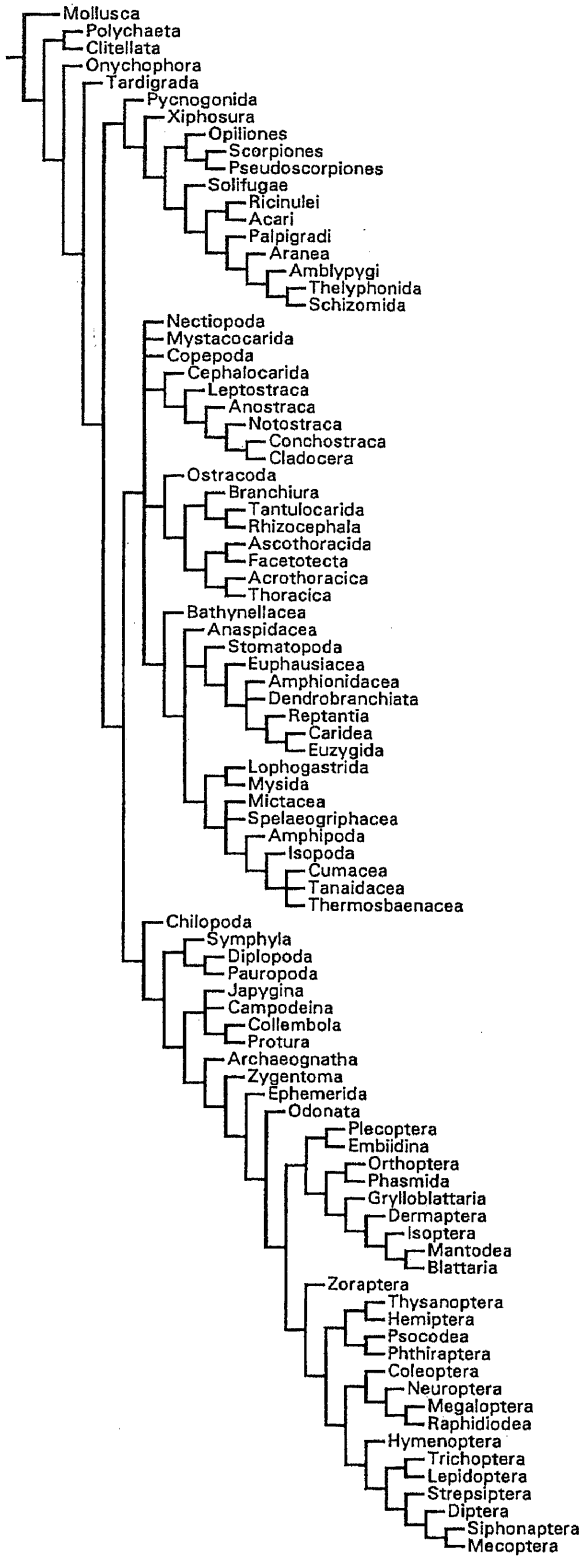

Figure 8.3 Cladogram of arthropod lineages based on the 552 non-sequence characters of tables published on web site. There were 87 equally parsimonious representations of the 90 taxa found at a length of 1204, a C.I. of 0.55, and an R.I. of 0.85.

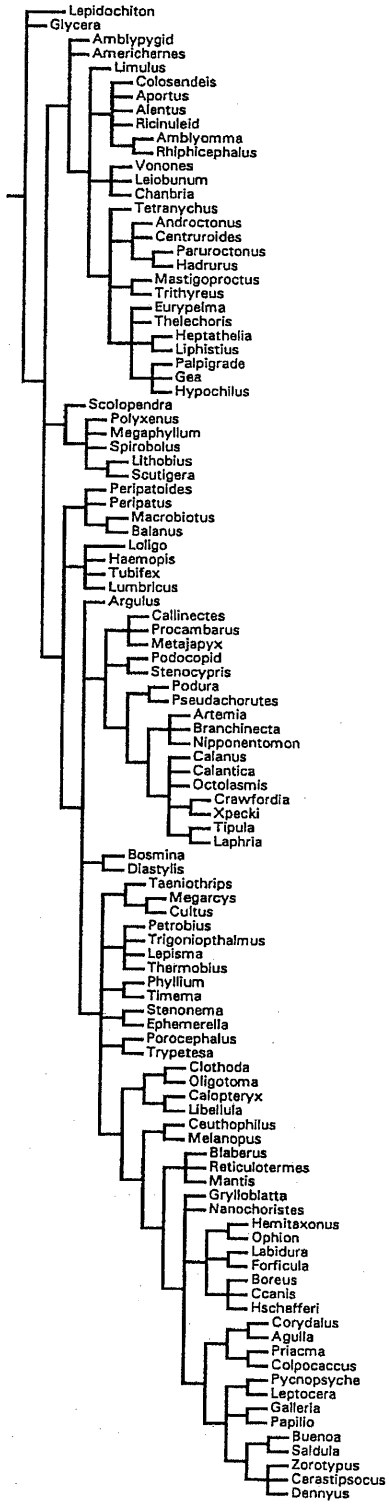

Figure 8.4 Cladogram of sampled arthropod lineages based solely on molecular sequence information. The cladogram of 106 taxa is based on approximately 1000 bp of 18S rDNA and 350 bp of the 28S rDNA. The total weighted length is 10 599 weighted steps, given insertion–deletion events weighted twice transversions and transversions twice transitions.

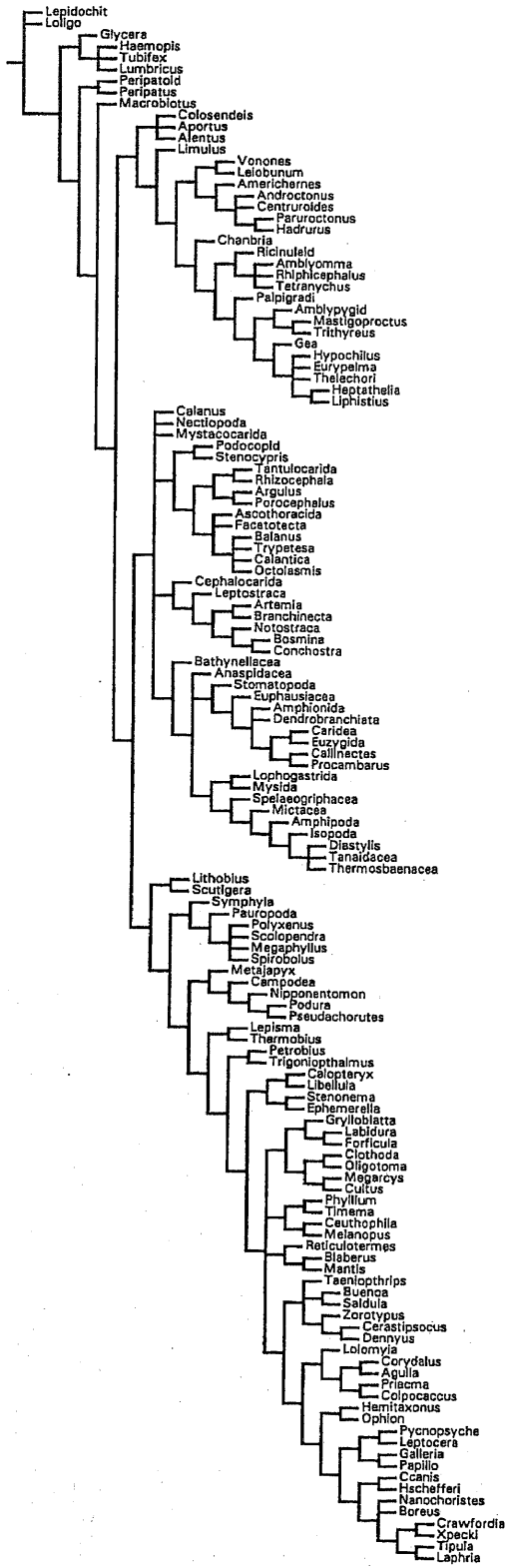

Figure 8.5 Total evidence cladogram of arthropod lineages. Combined data for 136 terminals yielded a single cladogram at 16 079 weighted steps. Non-sequence changes were weighted equally with insertion deletion events. Other weights were as in Figure 8.5

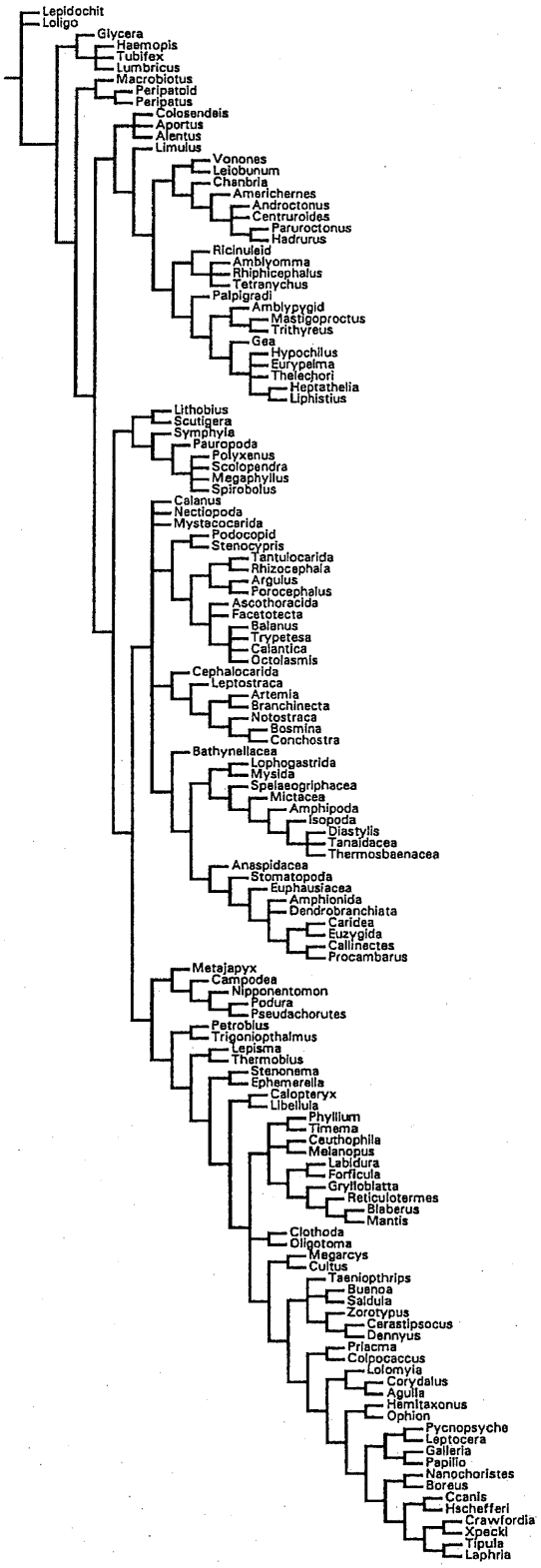

Figure 8.6 Cladogram of arthropod lineages with Hexapoda + Myriapoda. This most parsimonious cladogram forced to contain Hexapoda + Crustacea has a length of 16 167 weighted steps. Analysis as in Figure 8.5.

of higher taxa, the morphological results are most likely stable.

The final and perhaps most important problem is the estrangement between molecular characters and Palaeozoic taxa. Given the little we yet know about arthropod diversity in the distant past, it is nonetheless clear that crown chelicerates are but a small sample of a single lineage of arachnates. Furthermore, no matter how adept we become at extracting nucleic acid information from fossilized samples, it is unlikely we will ever be able to gather the quantities of sequence data which present themselves in living creatures. Anomalocarids and orsten crustaceans (whatever their phylogenetic position) are likely to be crucial to understanding arthropod diversity; a diversity which cannot be seen, much less understood by molecular data. All need not be lost, however, since nucleic acid-based phylogenies have converged (more or less) on arthropod and mandibulate monophyly. The current disagreements centre on myriapods versus crustaceans and hexapods. Interestingly, basal mandibulate and tracheate groups are those least represented in the fossil record. DNA data offer a huge amount of information which will flesh out the skeleton of arthropod systematics, and should be informative within Chelicerata, Mandibulata and Tracheata, but cannot comment on basal lineages long gone. Nucleic acids offer a huge wealth of characters which are unavailable in many taxa – inapplicability writ large – hardly the panacea claimed by some.

Even given the limitations described here, these data reflect the wealth of information on arthropod relationships. Studies which do not include **all** of this information are limited. They do not even attempt to encompass or explain natural variation, usually ignoring either morphological or molecular data. This distinction is unnecessary. The sum of these data points strongly toward a monophyletic Arthropoda and Mandibulata. Although less firmly, Tracheata and Labiata are also supported. These conclusions, especially the labiate clade, require further investigation.

What has been added to Snodgrass (1938) is a greater diversity of information, DNA sequences, internal and external anatomy. The incorporation of extinct lineages remains problematical. We have a coherent picture of extant arthropods, but the simultaneous resolution of extant and extinct lineages is still at a preliminary stage of investigation (Briggs and Fortey, 1989; Wills *et al.*, 1995; see also Zrzavý *et al.*, 1997, this volume). In summary, the combined analysis performed here yielded the scheme of relationships (Mollusca + (Annelida + (Onychophora + (Tardigrada + (Chelicerata + (Crustacea + (Chilopoda + ((Symphyla + (Pauropoda + Diplopoda)) + Hexapoda)))))))).

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