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Arthropod Cladistics: Combined Analysis of Histone H3 and U2 snRNA Sequences and Morphology

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Morphological, developmental, ultrastructural, and gene order characters are catalogued for the same set of arthropod terminals as we have scored in a recent study of histone H3 and U2 snRNA sequences (D. J. Colgan *et al.*, 1998, *Aust. J. Zool.* 46, 419–437). We examine the implications of separate and simultaneous analyses of sequence and non-sequence data for arthropod relationships. The most parsimonious trees based on 211 non-sequence characters (273 apomorphic states) support traditional higher taxa as clades, including Mandibulata, Crustacea, Atelocerata, Myriapoda, and Hexapoda. Combined analysis of morphology with histone H3 and U2 sequences with equal character weights differs from the morphological results alone in supporting Progoneata + Hexapoda (= Labiophora) in favor of a monophyletic Myriapoda, resolves the entognathous hexapods as a grade, and supports pycnogonids as sister group to Eucheliceratа (rather than as basal euarthropods). Monophyly of Chelicerata (including pycnogonids), Mandibulata, Crustacea, Progoneata, Chilopoda, and Hexapoda is maintained under a range of transition/transversion and third codon weights, whereas Atelocerata and Myriapoda/Labiophora do not withstand all sensitivity analyses.

INTRODUCTION

Despite a flurry of research activity in recent years, the interrelationships between and within the major clades of arthropods remain a contentious issue. The monophyletic status of the Arthropoda is one of the few points of widespread consensus, although a few workers (e.g., Fryer, 1996) still endorse the view (Anderson, 1973; Manton, 1977) that arthropods are a polyphyletic group. Reviews of major competing hypotheses for the relationships between chelicerates, crustaceans, myriapods, and hexapods, as well as the status of Onychophora and Tardigrada relative to the euarthropods, have been outlined by Wheeler *et al.* (1993), Wills *et al.* (1995, 1998), Regier and Shultz (1997), and Zrzavý *et al.* (1997), among others. To briefly summarize these issues, ongoing controversy concerns the status of

- a clade composed of Crustacea, Myriapoda, and Hexapoda (the Mandibulata hypothesis) or crustaceans alternatively grouping with the Chelicerata (the TCC or Schizoramia hypothesis);
- Crustacea as a monophyletic group, a paraphyletic grade to other mandibulates, or a paraphyletic grade to hexapods (the Pancrustacea hypothesis; Zrzavý *et al.*, 1997);

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• Myriapoda as either a monophyletic or a paraphyletic group;
• myriapods as a sister or basal paraphylum to Hexapoda (the Tracheata or Atelocerata hypothesis), a sister group to Chelicerata, or a basal group of euarthropods;
• pycnogonids as either sister group to Chelicerata or basal within the Euarthropoda; and
• Onychophora or Tardigrada as most closely related to other arthropods.

Ambiguity or disagreement is also found when considering recent ideas concerning relationships *within* the major groups. Crustacean phylogeny has proven especially recalcitrant, with significant discordance between recent cladograms (Spears and Abele, 1997; Wills, 1997; Schram and Hof, 1998). In addition to the pycnogonid problem, chelicerate phylogeny is most complicated by competing schemes of relationship between the arachnid orders (Weygoldt and Paulus, 1979, versus Shultz, 1989, 1990; see Wheeler and Hayashi, 1998; Weygoldt, 1998). A major controversy in hexapod phylogeny is the mono-, para-, or polyphyly of the Entognatha, i.e., whether the Diplura, if themselves a clade, are more closely related to Collembola and Protura or to the Insecta (Kukalová-Peck, 1991; Štys *et al.*, 1993; Kristensen, 1997; Bitsch and Bitsch, 1998).

The objective of this study is to evaluate competing hypotheses of arthropod relationships based upon morphological and molecular evidence. We employ a broader taxonomic sample than has been used in most prior molecular work and consider genes that have not previously been examined in relation to arthropod phylogeny. Sequence data are derived from histone H3 and the small nuclear RNA U2 (Colgan *et al.*, 1998). In order to subject these sequence data to simultaneous analysis with morphological evidence, the same taxonomic sample is scored for anatomical, developmental, ultrastructural, and gene order characters. This serves to compile much of the classical evidence and puts this evidence in a form by which it can be evaluated for its most parsimonious cladograms.

Previous DNA sequencing studies of arthropod phylogeny have concentrated on ribosomal RNA cistrons—particularly 12S (Ballard *et al.*, 1992), 18S (Wheeler *et al.*, 1993; Friedrich and Tautz, 1995; Giribet *et al.*, 1996; Spears and Abele, 1997; Giribet and Ribera, 1998), and 28S (Friedrich and Tautz, 1995; Wheeler, 1998), although the nuclear genes ubiquitin (Wheeler *et al.*, 1993), elongation factor-1α, and RNA polymerase II (Regier and Shultz, 1997, 1998) have also been considered. In a forthcoming study in collaboration with W. C. Wheeler and G. Giribet, we will integrate histone H3 and U2 sequence data with other available sequences and include fossils for morphological codings. The present synthesis limits the data pool to morphological characters and extant taxa in order to minimize the effects of missing data (morphology being the only data set for which all of the terminals sequenced for H3 and U2 are currently scored). For some characters, alternative interpretations based on fossils are noted.

MATERIALS AND METHODS

Taxonomic Sampling

The deficiencies of taxonomic sampling in early molecular analyses were well summarized by Wheeler *et al.* (1993), and some of these flaws have persisted in subsequent work. The essential problem is that too few exemplars have been examined in most studies to adequately sample the enormous taxonomic diversity of the Arthropoda. An empirical demonstration of the need for rigorous sampling is shown by work on 18S rDNA, the most exhaustively sampled gene for arthropods. Previous indications of a chelicerate–myriapod grouping (Friedrich and Tautz, 1995; Giribet *et al.*, 1996; Spears and Abele, 1997) are rejected in favor of Chelicerata as sister to Mandibulata with the inclusion of additional taxa, such as pycnogonids and more euchelicerates (Giribet and Ribera, 1998).

Where possible, we have avoided assuming ancestral (ground plan) character states for the taxa that we have scored, using a more explicit exemplar method (Yeates, 1995). We have selected several representatives within each putative major clade of the Arthropoda-and in particular focused on groups that have been regarded as nearly basal in previous investigations. Such taxa are most likely to provide an estimate of plesiomorphic characters within the clade. Some such exemplars may, in fact, be highly autapomorphic, but sampling several putatively basally derived taxa within each clade would be expected to counter this problem. Sampling has been notably deficient for myriapods, a situation we attempt to address by including all five extant

chilopod orders, diplopod representatives from the two most basally derived lineages (fide Enghoff, 1984), a pauropod and a symphylan.

Coding

For gross anatomical characters codings are based on the particular species that was sequenced in the molecular analyses. Were the same procedure applied to most of the developmental, histological, and ultrastructural (e.g., sperm) characters, very few of these could be scored and a large amount of previous work would go unused in this analysis. To use a broader range of developmental and histological characters, some assumptions of monophyly have been made. For example, embryological data available for any chilopod species have been coded for the representative of the same order (Scutigeromorpha, Lithobiomorpha, Scolopendromorpha, Geophilomorpha) used in our analysis. The same practice has been applied within the following groups: Peripatidae, Peripatopsidae, Pauropoda, Symphyla, Penicillata and Pentazonia. Developmental and sperm characters for *Tricholepidion* have been scored based on other Zygentoma.

Some characters (e.g., those dealing with gene expression and mitochondrial gene arrangements) have been examined in few arthropod taxa. We have included these characters because they have featured prominently in recent debates, such as the crustacean–hexapod (= Pancrustacea) hypothesis, and should therefore be used in the analysis if these hypotheses are to appraised via character congruence. These characters must be scored as missing data for most terminals. Some minimal assumptions of monophyly were made to code at least a three-taxon statement (e.g., coding the sole pterygote, an ephemeropteran, for data from other pterygotes; coding the hoplocarid *Kempina* for data involving eumalacostracans; and coding *Epicyliosoma* for chilognathan millipedes).

Character definition obviously requires strict application of a homology scheme between metameres that transcends differences in tagmosis between major groups. Where a character may be informative within a particular group (e.g., presence or absence of a limb on the first opisthosomal somite in Chelicerata) we have made attempts to present an alternative definition that can be more generally applied (presence or absence of limb on the eight metamere). Segmental homologies for euarthropods as outlined by Schram (1978, Table 2), based on the neural innervation scheme of Bullock and Horridge (1965), are followed in this work with the exception of Trilobita (which, while not coded as a terminal, figure in some character discussions). The trilobite antenna is regarded as homologous with the (deutocerebral) antennule of crustaceans (Müller and Walossek, 1986), the first biramous limb pair of trilobites with the antenna, the second pair with the mandible, and so on. An alternative homology scheme for chelicerates has been advanced by Damen *et al.* (1998) and Telford and Thomas (1998) based on expression domains of *Hox* genes. These workers consider the chelicera homologous with the antennule (see Wheeler *et al.*, 2000, for commentary on this reinterpretation).

Homologies of appendage podomere characters across the arthropods are an ongoing problem. Although many authors have attempted to demonstrate pan-arthropodan podomere homologies (e.g., Sharov, 1996; Brusca and Brusca, 1990), these attempts have been flawed because inappropriate taxa were used for comparison. The fundamental crustacean limb bears scant resemblance to that of atelocerates. This point is clearly shown by the alleged stem-lineage crustaceans (Walossek and Müller, 1990)—or stem-lineage mandibulates (Lauterbach, 1988; Wägele, 1993; Moura and Christoferssen, 1996)—in which the paucisegmented endopod defies podomere homologies with atelocerates or chelicerates. In characters for which some homologies are dubious, we have scored states only for those taxa in which we are confident of homologies (e.g., within the Atelocerata or Chelicerata). An "uncertain" coding has been used for other taxa.

Except where indicated or where larval or embryological characters are specifically involved, we have restricted decisions of homology to adults. For example, although the nauplii of the branchiopods scored in this analysis (*Branchinella* and *Triops*) have biramous antennae, the adults do not; therefore, we have scored this character state as absent for these taxa.

Outgroups

The selection of outgroups for rooting arthropod trees highlights ongoing controversies in protostome

phylogeny. The classical hypothesis that Annelida is the closest relative of Arthropoda (the Articulata hypothesis) has found support in some cladistic analyses based on morphological and developmental characters (Rouse and Fauchald, 1995; Nielsen *et al.*, 1996). An alternative to this is the Eutrochozoa hypothesis, in which annelids are allied with molluscs and arthropods are more closely related to kinorhynchs and nematodes (Eernisse *et al.* 1992). The latter grouping, with the addition of the priapulids and nematomorphs, finds support in 18S rDNA sequence data and has been named Ecdysozoa (Aguinaldo *et al.*, 1997; Giribet and Ribera, 1998). As our principal goal is examining relationships within the Euarthropoda, we have included several onychophorans (including representatives of both families, the Peripatidae and the Peripatopsidae) and a tardigrade. All recent work identifies these groups as appropriate outgroups for the euarthropods. We have also coded annelids, which accommodates the Articulata hypothesis, but caution that the interpretation of some characters in onychophorans and tardigrades will differ from trees in which aschelminth Ecdysozoa were used as outgroups. Given that 18S phylogenies agree with results obtained here with respect to tardigrades and onychophorans as parts of the first and second outgroup branches, respectively, to the Euarthropoda (Fig. 1 in Giribet and Ribera, 1998), resolution and character interpretations within Euarthropoda should be unaffected by more distant outgroups.

Analytical Methods

The morphological data set consists of 211 characters with 273 apomorphic states in total, with one constant character. The latter (character 33, crustacean cardioactive peptide) was included in our data because it has been accorded some significance in other studies (Wägele, 1993), despite being uninformative at the level of our sampling. Two characters involving mitochondrial gene order were included. Multistate characters were treated as unordered except for characters 5, 17, 25, 54, 87, 108, 144, and 155. In each of these, evidence for homology of state 1 and state 2 is compelling, and a transformation series (0–1–2) can be posited. The data were analyzed with Portable PAUP for Windows, version 4.0b2 (Swofford, 1999). Heuristic multiple parsimony searches employed 10 iterations of random stepwise addition of the taxa, uninformative characters ignored. Tree-space searches (cf. Swofford, 1993:104, as in Reid, 1996) were performed using 100 random addition sequence replicates with three trees sampled per iteration (nchuck = 3, chuckscore = 1). All trees found by this procedure were then branch-swapped using tree bisection–reconnection to check for shorter resolutions and to fill out tree space. Bremer support (Bremer, 1994) was calculated using MacClade test version 4.0b7 (Maddison and Maddison, 1999) to automatically generate the PAUP* command file with negative constraints. The authors hold differing opinions on the merits of bootstrapping as a measure of support; we provide bootstrap values for comparison with Bremer support. Bootstrapping used 100 randomized (with replacement) character samples, with each bootstrap sample using the heuristic search options addseq = random, nreps = 10, nchuck = 10, chuckscore = 1. Each bootstrap sample could contain no more than 100 trees, thus reducing iteration bias.

Laboratory and analytical techniques for histone H3 and snRNA U2 sequences are described elsewhere (Colgan *et al.*, 1998). In the present study, we subjected these data to a range of weighting schemes to assess the effects of these parameters on congruence between data sets as well as cladogram sensitivity (Wheeler, 1995; Wheeler and Hayashi, 1998). Congruence between data partitions is measured by incongruence length difference (ILD; Mickevich and Farris, 1981), based on individual partition and combined analyses run using the heuristic parameters addseq = random, nreps = 100, nchuck = 3, chuckscore = 1. Significance of partition incongruence (Farris *et al.*, 1994) was tested with the partition homogeneity test as implemented in PAUP*; *hompar* heuristic options used were nbest = 3, allswap = yes, addseq = asis.

For H3, the arthropods have 151 variable sites in 327 aligned bases, of which 139 are informative. Thirty-one of 109 first-base positions are variable, with 4 that are uninformative. The third-base positions have 106 variable sites (105 informative). Only 14 second-base positions are variable and only 7 of these are informative. Therefore, most of the informative sites are in the H3 third position, although these sites may be saturated (Colgan *et al.*, 1998). The aligned U2 data, 133 bases total, have 53 informative characters, with 64 constant and 16 variable characters that are uninformative. Taxa for which only one of the two sequences were obtained are as follows: *Lithobius, Mecistocephalus,*

Campodea, Petrobiinae, *Hutchinsoniella* (histone H3 sequence only; U2 missing), *Derocheilocaris*, *Limulus*, and *Macrobiotus* (U2 sequence only; H3 missing). Colgan *et al.* (1998) tested sensitivity to alternative methods of data combination, analyzing with all terminals for which either sequence was available as well as with only those taxa with both sequences ("spliced" and "merged" analyses of Nixon and Carpenter, 1996). The former approach, of more inclusive taxonomic sampling, yielded much more explicit results (Fig. 1) and is employed in the present study.

As argued by Allard and Carpenter (1996), equal weighting (one morphological state change equal to one base change, transitions equal to transversions, all codon positions equally weighted) is the obvious and appropriate starting point for simultaneous analysis. To examine the sensitivity of the combined results to different analytical parameters for the molecular characters, we varied the weights of transitions and of the third-codon position in the H3 sequences. Higher homoplasy rates for third codon positions in protein genes and for transitions are well known (Philippe *et al.*, 1996; Yoder *et al.*, 1996). Many systematists have advocated the downweighting or elimination of the third codon to decrease putatively negative effects of this homoplasy (see citations in Wenzel and Siddall, 1999). Fractional weightings, implemented by PAUP*, were used to vary the H3 third-codon weightings and the transitions in transversion / transition step matrices. Tranversions therefore always had a weight of 1, while transitions and the H3 third codon had weights varying between 1 and 0. This procedure allowed the morphological characters and putatively less homoplastic DNA characters to retain equal weights in all tests. We did not explore different partition weights. No reason exists to suspect "swamping" of one partition by another. The morphology and DNA data sets were nearly equal in their strength, morphology having 210 parsimony informative characters while H3 and U2 together have 192 informative sites.

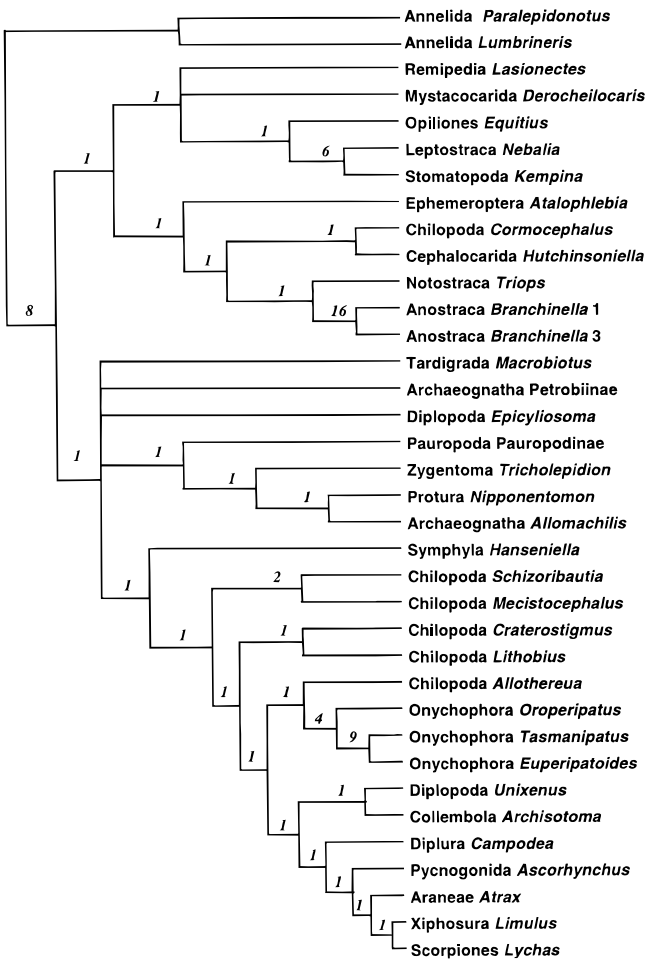


FIG. 1. Strict consensus of 14 shortest cladograms based on histone H3 and U2 sequences (Colgan *et al.*, 1998). Length 1376 steps, CI 0.27, RI 0.40. Bremer support is shown at nodes.

MORPHOLOGICAL CHARACTERS

1. Non-migratory gastrulation: 0, absent; 1, present. Anderson (1973) described the unique pattern of gastrulation in onychophorans, and this character has been accepted as an autapomorphy for Onychophora (Monge-Nájera, 1995).

2. *Engrailed* expressed in mesoderm patterning: 0, absent; 1, present. Zrzavý and Štys (1995) surveyed "compartment-like patterning" in the mesoderm of annelids and arthropods, as marked by *engrailed* expression. Limited data are available to indicate the absence of such mesodermal patterning in some insects and crustaceans versus its presence in at least some chilopods, onychophorans, and annelids. Despite the preponderance of missing data, this character is included as a target for future investigation.

3. Early cleavage: 0, spiral; 1, total cleavage with radially oriented position of cleavage products; 2, intralecithal cleavage. A wide range of euarthropods share

early total cleavage without oblique spindles, which Scholtz (1997) suggested is an autapomorphy of Euarthropoda. We have coded for the most closely related proxy in groups identified by Scholtz as possessing this derived cleavage pattern.

4. Annelid cross cleavage pattern: 0, absent; 1, present. Annelida and Echiura share a distinctive blastomere pattern, with a cross formed by blastomere cells $1a^{112}$–$1d^{112}$ (Rouse and Fauchald, 1995).

5. Blastokinesis: 0, absent; 1, amniotic cavity open; 2, amniotic cavity closed. Insect embryology is uniquely characterized by the division of the dorsal extra-embryonic ectoderm into an amnion and a serosa, termed blastokinesis (Anderson, 1973). We follow Whiting *et al.* (1997) in regarding the closed amniotic cavity of Dicondylia as a modification of the open (Larink, 1983) amniotic cavity of Archaeognatha (i.e., the character is ordered).

6. Blastoderm cuticle: 0, absent; 1, present. Anderson (1973) identified a thin, highly resistant blastoderm cuticle beneath the chorion as shared by Progoneata and lacking in Chilopoda. Blastoderm cuticle is also present in Collembola, Diplura, Archaeognatha, and Zygentoma (Anderson, 1973:180), so the character is a potential synapomorphy for Labiophora, though distinction from blastoderm cuticle in Xiphosura (Anderson, 1973:370) would be required.

7. Ectoteloblasts: 0, absent; 1, present, arranged in ring. Ectoteloblasts are specialized stem cells that give rise to the ectoderm of most postnaupliar segments in Cirripedia and in Malacostraca (Gerberding, 1997). They are absent in branchiopods (Gerberding, 1997) and are lacking only in Amphipoda among the Malacostraca (Dohle and Scholtz, 1988; present in Leptostraca and Stomatopoda coded here fide Weygoldt, 1994). Malacostracan ectoteloblasts are characterized by their circular or semi-circular arrangement at the anterior border of the blastopore (Weygoldt, 1994).

8. Head lobes (paired semicircular lobes that give rise to the lateral eyes and lateral parts of the protocerebrum): 0, absent; 1, present. Scholtz (1997) regarded head lobes as a synapomorphy of onychophorans and euarthropods, with no corresponding structure in annelids. Although Scholtz (1997) did not address this character in tardigrades, total cleavage and the lack of a germ band stage in tardigrades mean that structures comparable to the head lobes of germ band embryos are absent, although the prominent dorsolateral lobes of the tardigrade brain indicate that "head lobes" would form during neurogenesis (R. Dewel, pers. comm., 1998).

9. Fat body: 0, absent; 1, fat body cells develop from vitellophages in yolk; 2, fat body cells develop from walls of mesodermal somites. The presence of a cephalic storage organ, the fat body, has been identified as an atelocerate synapomorphy (Boudreaux, 1979). Anderson (1973) made a distinction between vitellophagal fat body cells (Symphyla + Pauropoda + Diplopoda) and an origin of the fat body in the mesoderm (Chilopoda + Hexapoda). Dohle (1980) upheld this distinction and employed the former condition as evidence for monophyly of the progoneate myriapods. A partial uncertainty coding (states 1 or 2, but not 0) is employed for several taxa in which a fat body is present but its embryological origin is unknown.

10. Fate map ordering of embryonic tissues: 0, presumptive mesoderm posterior to presumptive midgut; 1, presumptive mesoderm anterior to midgut; 2, mesoderm midventral, cells sink and proliferate, midgut internalizes during cleavage; 3, mesoderm diffuse through the ectoderm; 4, midgut develops from anterior and posterior rudiments at each end of midventral mesoderm band. Fate map patterns follow Anderson (1973, 1979). Available data for pycnogonids include a diversity of patterns (Schram, 1978) but some species conform most closely to the chelicerate pattern and have been coded as such.

11. Epimorphic development: 0, absent; 1, present. Several arthropod groups have been diagnosed by epimorphosis, hatching with the complete complement of segments (e.g., Epimorpha within Chilopoda; Diplura + Insecta fide Kraus, 1997). This character exhibits considerable homoplasy within Arthropoda but serves as a synapomorphy for several clades.

12. Nauplius larva or egg nauplius: 0, absent; 1, present. The nauplius is a "short head" (Walossek and Müller, 1997) swimming larva that has only three pairs of limbs (antennule, antenna, mandible), each of which has a generalized morphology. The naupliar antenna has a proximal enditic process ("naupliar process") that acts as a food-pushing device in the absence of a gnathal lobe on the mandible. Some authors (e.g., Fryer, 1992, 1996) have suggested that the nauplius is the primordial crustacean form, although even Cambrian fossils well known to be crustaceans (Walossek, 1993) show clearly that the nauplius is only a transient

larval stage. Absence of a nauplius cannot be meaningfully interpreted for terrestrial arthropods, and we have opted for an inapplicable coding (cf. Wägele, 1993:278).

13. Pupoid stage: 0, direct hatching; 1, motionless stage after hatching, pupoid remains encased in embryonic cuticle. Anderson (1973) summarized evidence for a pupoid stage in Chilopoda, Diplopoda, and Pauropoda. Dohle (1997), however, identified a pupoid stage as confined to diplopods and pauropods. We recognize the peripatoid and fetoid stages of Epimorpha (Chilopoda) as character 181.

14. Sclerotization of cuticle into hard, articulated exoskeleton: 0, absent; 1, present.

15. Cuticle containing α-chitin and protein: 0, absent; 1, present (Weygoldt, 1986). The composition of the chitin in tardigrade cuticle is not known with certainty (Dewel and Dewel, 1997). α-chitin is, however, shared by euarthropods (but not pentastomids), onychophorans, and non-arthropod Ecdysozoa (Priapulida; see Schmidt-Rhaesa *et al.*, 1998, for citations).

16. Exocuticular cones: 0, absent or moderately developed; 1, extensively developed in cuticle of head. Manton (1965) identified cuticular specializations for flexibility and strength as synapomorphies of the Geophilomorpha, linking these to the burrowing habits of the clade. Exocuticular cones are especially well-developed in the head and maxilliped. They are absent in "anamorphic" chilopods and much less extensively developed in scolopendromorphs than in geophilomorphs (Manton, 1965).

17. Ectodermal cilia: 0, present in many tissues; 1, present in photoreceptors and sperm; 2, present in sperm only. We follow Wheeler *et al.* (1993, their character 65) in scoring this as an ordered multistate character.

18. Tendon cells with tonofilaments penetrating epidermis: 0, absent; 1, present. Boudreaux (1979) and Wägele (1993) acknowledged tonofilaments as a euarthropod synapomorphy, and Dewel and Dewel (1997) confirmed their absence in onychophorans and tardigrades.

19. Molting with ecdysone: 0, absent; 1, present. Molting is frequently evoked as a synapomorphy of Panarthropoda (e.g., Weygoldt, 1986), although it has alternatively been suggested to be a plesiomorphy for a broader group that also includes nematodes, nematomorphs, priapulids, kinorhynchs, and loriciferans (Aguinaldo *et al.*, 1997; Schmidt-Rhaesa *et al.*, 1998) but excludes annelids. Ecdysone-like steroidal hormones induce and control molting in non-arthropod Ecdysozoa (see nematode citations in Schmidt-Rhaesa *et al.*, 1998) as well as in Arthropoda.

20. Ecdysial suture pattern: 0, transverse rupture between head and trunk; 1, dorsal longitudinal ecdysial suture; 2, marginal ecdysial suture; 3, rupture at stylus apparatus. States 0–2 were used by Zrzavý *et al.* (1997). Boudreaux (1979) regarded ecdysis at the head–trunk contact (state 0) to be diagnostic of Myriapoda and dorsal longitudinal ecdysis (state 1) to be diagnostic for Hexapoda. Snodgrass (1952:269) specified that the latter pertained to Insecta in particular, whereas Collembola and Protura have a head–trunk ecdysial split (Kaufman, 1967:16). R. Dewel (pers. comm., 1998) indicates that tardigrades molt at the stylus apparatus.

21. Resilin protein: 0, absent; 1, present. Weygoldt (1986) indicated that the spiral protein resilin is known only from euarthropods and onychophorans. Nielsen (1995), however, mapped resilin onto the tree as a euarthropod synapomorphy, indicating its absence in tardigrades and onychophorans.

22. Molting gland: 0, absent; 1, present. Wägele (1993) cited a molting gland as a diagnostic character of Mandibulata. This was based on a proposed homology between the Y-organ of Malacostraca and the prothoracic gland of insects. Wägele noted that such molting glands in insects and crustaceans are hypodermal derivations of the second maxilla and are absent in chelicerates. An alleged ecdysial gland in some chilopods (Lithobiomorpha, Seifert and Rosenberg, 1974; glandula capitis in Scutigeromorpha, Seifert, 1979) may be homologous. Evidence for an ecdysial gland has not been found in other myriapods (Tombes, 1979) except for polyxenid millipedes (glandula perioesophagealis, Seifert, 1979). The restriction of the Y-organ to Malacostraca within the Crustacea (Fingerman, 1987) is problematic for the homology of these glands. Studies of branchiopods have not discovered similar molting glands although molting hormones appear to be present (Martin, 1992).

23. Bismuth staining of Golgi complex beads: 0, not staining; 1, staining. Locke and Huie (1977) observed Golgi beads to stain with Bismuth in various euarthropods and tardigrades, but not in Onychophora, Annelida, Mollusca, Nematoda, or Platyhelminthes. Due to the depauperate taxonomic sampling for this character, we have coded with the following proxies examined

by Locke and Huie (1977): undetermined isopod and *Orconectes* for *Kempina*, undetermined polydesmoid for *Epicyliosoma*, and representatives of four pterygote orders for *Atalophlebia*.

24. Metanephridia with sacculus with podocytes: 0, absent; 1, present. While metanephridia are probably plesiomorphic for arthropods (Fauchald and Rouse, 1997), the sacculus and podocytes are novel nephridial structures for onychophorans and euarthropods, lacking in tardigrades (Nielsen, 1997; Schmidt-Rhaesa *et al.*, 1998). Absence of nephridia in pycnogonids is coded following King (1973) and Clarke (1979).

25. Distribution of segmental glands: 0, on many segments; 1, in at most the last four cephalic segments and first two post-cephalic segments; 2, on second antennal and maxillary segments only. Definition of the basic euarthropod distribution of segmental glands, a reduction from that in Onychophora, follows Weygoldt (1986). We have not attempted to define all variants of segmental gland distribution within Euarthropoda, and state 1 above is an artificial grouping. A more advanced reduction in Crustacea, restricted to the antennal and maxillary segments, has been regarded as a crustacean synapomorphy (Lauterbach, 1983, 1986). Walossek and Müller (1990:410) considered remipedes (Schram and Lewis, 1989) and anostracans to deviate from this state in possessing additional cephalic segmental glands, but Wägele (1993) dismissed these as integumental glands and embryonic mesodermal cells, respectively.

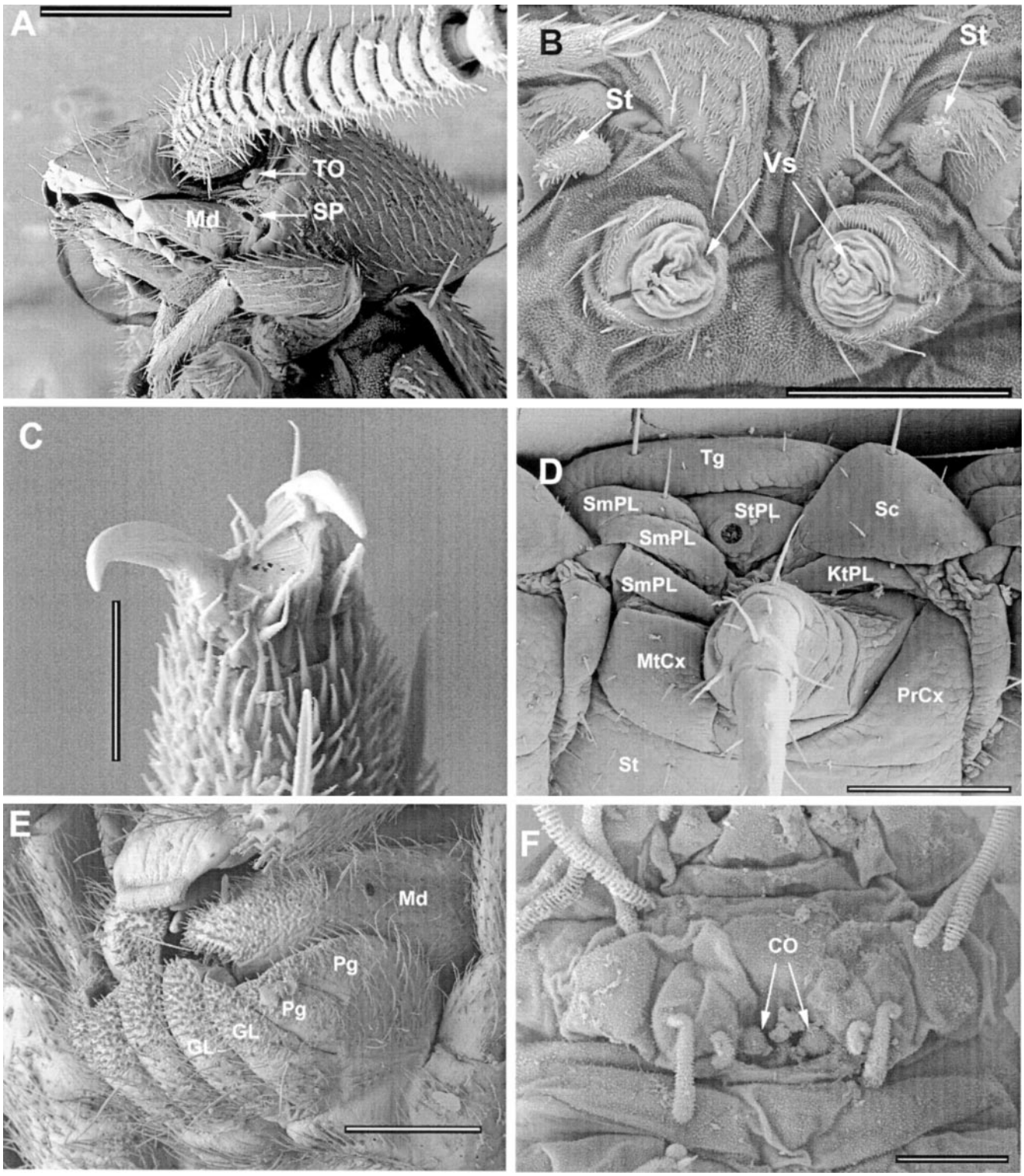
26. Tömösváry organ ("temporal organs" at side of head behind insertion of antennule): 0, absent; 1, present. Homology of Tömösváry organs (Fig. 2A) across the Myriapoda has been widely accepted (Snodgrass, 1952), but relationships to similarly positioned structures in hexapods are contentious. François (1969), for example, homologized the pseudocellus of Protura with Tömösváry organs, whereas Tuxen (1959) regarded them as antennal vestiges on the basis of musculation. The postantennal organs of Collembola may also be homologous (Haupt, 1979). We have scored the temporal organs of Ellipura as homologous with those of Myriapoda, following Haupt (1979) and Bitsch and Bitsch (1998). The homologue of the Tömösváry organ in *Craterostigmus* is a ringed organ set on a triangular sclerite lateral to the clypeus (Fig. 50 in Shear and Bonamo, 1988; Fig. 2 in Dohle, 1990). The form and positioning of this organ are comparable to the Tömösváry organ in Lithobiomorpha (Henicopidae).

27. Salivary gland reservoir: 0, absent; 1, present. Monge-Nájera (1995) identified a salivary gland reservoir as an onychophoran autapomorphy.

28. Malpighian tubules formed as endodermal extensions of the midgut: 0, absent, 1, present. Shultz (1990) claimed that endodermal Malpighian tubules are unique to Arachnida and, despite their absence in some ingroup taxa (such as Opiliones), resolved them as an arachnid autapomorphy. Atelocerate Malpighian tubules, in contrast, are extensions of the ectodermal hindgut (see character 29). The non-homology of these structures is generally recognized, and we have accordingly coded them as separate characters.

29. Malpighian tubules formed as ectodermal extensions of the hindgut: 0, absent; 1, single pair of Malpighian tubules at juncture of midgut and hindgut; 2, multiple pairs of tubules at anterior end of hindgut. The presence of Malpighian tubules in Collembola is dubious (Clarke, 1979; Bitsch and Bitsch, 1998), while Protura have several pairs of papillae behind the midgut–hindgut junction (see character 30). Distinct conditions can be recognized within the myriapods and the ectognath hexapods and serve as the basis for states 1 and 2 above. The origin of insect Malpighian tubules (whether ectodermal or entodermal) is controversial

FIG. 2. (A–C) *Hanseniella* n. sp. (Symphyla), Mt. Colah, NSW, Australia. (A) Lateral view of head, showing mandibular base plate (Md), Tömösváry organ (TO), and spiracle (SP). (B) Ventral view of trunk, showing styli (St) and eversible vesicles/coxal sacs (Vs). (C) Pretarsal claws. (D) *Schizoribautia* n. sp. (Chilopoda, Geophilomorpha), Sydney, NSW, Australia. Lateral view of trunk, showing ventral confluence of procoxa (PrCx) and metacoxa (MtCx) and elaboration of pleurites, including scutellum (Sc), stigmatopleurite (StPL), and small pleurites (SmPL) between tergite (Tg) and sternite (St). (E) *Allomachilis froggatti* (Archaeognatha), Kiama, NSW, Australia. Ventrolateral view of head, showing division of labial glossae (GL) and paraglossae (Pg). (F) Pauropodinae, 3 km N of Weldborough, Tasmania, Australia. Ventral view of posterior part of head, collum segment, and anterior part of first leg-bearing trunk segment, showing collum organs (CO) variably interpreted as vesicles (Tiegs, 1947) or appendage vestiges (Kraus and Kraus, 1994). Scale bars: A and E, 200 m; B and D, 100 m; F, 20 m; C, 10 m.



(Dohle, 1997). One or a small pair of supernumerary Malpighian tubules is present in some chilopods (Prunescu and Prunescu, 1996). The so-called Malpighian tubules of eutardigrades are not in contact with cuticle and as such do not appear to be ectodermal in origin (Møbjerg and Dahl, 1996).

30. Form of ectodermal Malpighian tubules: 0, elongate; 1, papillate. The Malpighian tubules are elongate in myriapods and most hexapods, Bitsch and Bitsch (1998, their character 14) interpreting this as the basal state for Atelocerata. Bitsch and Bitsch coded the very similar papillae of Protura and Campodeina as homologous, a procedure adopted here.

31. Neck organ: 0, absent; 1, present. Martin and Laverack (1992) have reviewed the so-called dorsal organ or neck organ (Walossek, 1993) of crustaceans. The term "neck organ" is preferred for this structure so as to avoid confusion with the region of extra-embryonic ectoderm that is commonly called a "dorsal organ" in many groups of arthropods (Fioroni, 1980).

32. Hemocyanin: 0, absent; 1, present. Codings for the presence of hemocyanin follow Gupta (1979). In pycnogonids, hemocyanin is only found dissolved in the plasma (Arnaud and Bamber, 1987), without cyanocytes *sensu* Gupta. Some remipedes have large hemocyanin crystals scattered throughout the head and swimming appendage tissue (J. Yager, pers. comm., 1998). Within Chilopoda, Scutigeromorpha have hemocyanin as the oxygen transport molecule (Mangum *et al.*, 1985) versus gaseous exchange between the tracheae and the tissues in Pleurostigmophora (Hilken, 1997). Hemocyanin is lacking in hexapods (Beintema *et al.*, 1994).

33. Crustacean cardioactive peptide in neurosecretory cells of nervous system: 0, absent; 1, present. Wägele (1993) documented the similarity in the sequence of this nonapeptide in insects and eumalacostracans and proposed it as a mandibulate synapomorphy, although no evidence was presented to confirm its absence in chelicerates or its presence in myriapods. Missing data render this character entirely ambiguous, but we include it to encourage further investigation.

34. Subcutaneous hemal channels in body wall: 0, absent; 1, present. Presence is unique to Onychophora (Brusca and Brusca, 1990; Monge-Nájera, 1995).

35. Hemocoel: 0, absent; 1, present. Disintegration of the coelomic cavities, resulting in the body cavity being used as a hemocoel or mixocoele, is a shared derived character of onychophorans, tardigrades, and euarthropods (Weygoldt, 1986).

36. Dorsal heart with segmental ostia and pericardial sinus: 0, absent; 1, present. The dorsal, ostiate heart and pericardial sinus / septum are shared by Onychophora and Euarthropoda, but absent in tardigrades and pauropods. We have not coded with the assumption that these absences are due to miniaturization.

37. Arterial blood supply to limbs: 0, absent; 1, limbs receive blood from a supraneural artery; 2, limbs receive blood from a subneural artery. Most atelocerates lack an arterial blood supply to the legs. Clarke (1979) identified different patterns of arterial branching in malacostracan crustaceans and in many chelicerates.

38. Slit sensilla: 0, absent; 1, present. Slit sensilla are small clefts or slits in the cuticle, used in detecting compressional forces acting on the exoskeleton (Shultz, 1990). They have been recognized as a synapomorphy for Arachnida, but are (doubtfully) present in the extinct Eurypterida (Dunlop and Braddy, 1997).

39. Neuroblasts: 0, absent; 1, present. The identity and relative positions of cell types in the central nervous system exhibit impressive similarities between insects and some malacostracan crustaceans (for which *Kempina* is coded as a proxy). Certain chilopods have different patterns of segmental neurons (Whitington *et al.*, 1993), and neuroblasts, the precursor cells of the embryonic ganglia, are variably described as lacking (Osorio and Bacon, 1994; Zrzavý and Štys, 1994) or present (*Scutigera*: Knoll, 1974). Since recent treatments (e.g., Gerberding, 1997) consider myriapod ganglia to develop without neuroblasts, we are reluctant to accept Knoll's (1974) interpretation of *Scutigera*. *Scutigera* appears to have some larger cells in the neurogenic area but the asymmetric division that characterizes neuroblasts is not shown (G. Scholtz, pers. comm., 1999). Dohle (1997) indicated that onychophoran and chelicerate ganglion formation resembles that of centipedes and millipedes. Weygoldt (1998:68) likewise observed that the nervous system in chelicerates and myriapods arises by invagination. We have coded *Euperipatoides* and *Epicyliosoma* as proxies because details of neurogenesis are unknown for most taxa considered in this analysis. Gerberding (1997) showed that Cladocera have cells with the characteristics of neuroblasts and that their morphology is identical to that in Malacostraca; branchiopods in the present study are thus coded as having neuroblasts. Neuroblasts have been reported

in single spider and scorpion species (Whitington and Bacon, 1997). The absence of cells with the characteristics of neuroblasts in pauropods, symphylans, and diplopods in older studies was noted by Whitington and Bacon (1997), and absence in these groups is coded based on these data. Insect and crustacean neuroblasts differ in that the former delaminate from the surface and form a separate layer, whereas the latter lie superficially (Gerberding, 1997).

40. Globuli cells: 0, confined mainly to brain, in massive clusters; 1, making up majority of neuropil and ventral layer of ventral nerve cord. Schürmann (1995) recognized that onychophorans are specialized relative to annelids and other arthropods in that globuli cells are the main cell type in the brain and also form a massive ventral layer in the ventral nerve cord.

41. Corpora allata: 0, absent; 1, present. Corpora allata are present in insects, proturans, collembolans, and diplurans (Cassagnau and Juberthie, 1983) and are regarded as a hexapod apomorphy (Wägele, 1993).

42. Intrinsic secretory cells in protocerebral neurohemal organ: 0, absent; 1, present. Gupta (1983) reviewed the distribution of intrinsic secretory cells in neurohemal organs, assuming that the presence of these cells was a derived state. This character has been coded based on the state of the primary protocerebral neurohemal organ: the sinus gland in some crustaceans, the cephalic gland in symphylans, the cerebral gland in chilopods, Gabe's organ in diplopods, the corpora cardiaca in hexapods, Schneider's Organ I in spiders, and the stomatogastric ganglia of scorpions (see papers in Gupta, 1983). The state in *Tricholepidion* is coded based on information from lepismatids (Cassagnau and Juberthie, 1983).

43. Enlarged epipharyngeal ganglia: 0, absent; 1, present. Protura and Collembola share specialized masses of sensory and secretory cells in the epipharyngeal region (François, 1969; Kristensen, 1991).

44. Ganglia of pre-esophageal brain: 0, protocerebrum; 1, protocerebrum and deutocerebrum; 2, protocerebrum and tritocerebrum; 3, proto-, deuto-, and tritocerebra. A tripartite brain has been proposed as a synapomorphy for Mandibulata (Brusca and Brusca, 1990) or a character uniting tardigrades and euarthropods (Nielsen, 1995). The most recent assessment of homologies of the tardigrade brain, however, suggests that its components (dorsal and ventral cones, internal cirrus, and their respective ganglia) are homologous only to the protocerebrum of arthropods and not to the deutocerebrum or tritocerebrum (Dewel and Dewel, 1996). Furthermore, the incorporation of the tritocerebrum into a pre-esophageal brain is not shared by all crustaceans; Walossek and Müller (1997) showed that the brain includes the proto- and deutocerebral segments only in Entomostraca, such as branchiopods. Coding for this character recognizes a distinction between the "bipartite" brain of Entomostraca (and Leptostraca fide Calman, 1909) and that of Chelicerata (including Pycnogonida) in that the latter is classically considered to lack the deutocerebrum (state 2 above). Fossil taxa alter the interpretation of this character from that based on extant taxa alone. Instead of regarding the absence of the deutocerebrum (and its appendage pair, the first antenna) in chelicerates as a primitive absence, fossils allied to Chelicerata indicate it to be a secondary reduction/loss. Taxa such as the Devonian *Cheloniellon*, which is closely allied to chelicerates (Stürmer and Bergström, 1978; Dunlop and Selden, 1997), possess a flagelliform first antenna, as do most other early Arachnata (Edgecombe and Ramsköld, 1999). The alternative homology scheme suggested by *Hox* gene expression (Damen *et al.*, 1998; Telford and Thomas, 1998) equates states 1 and 2.

45. Ganglia of post-oral appendages fused into single nerve mass. 0, absent; 1, present. Zrzavý *et al.* (1997) coded fusion of anterior ganglia as a synapomorphy for pycnogonids and euchelicerates. We do not regard the fusion of the palp and oviger nerves to the subesophageal ganglion in pycnogonids (Fig. 12 in Arnaud and Bamber, 1987) to be as reliable an apomorphy as the fusion of all post-oral, cephalic, limb-bearing segments to the subesophageal nerve mass in euchelicerates. The coding used here is thus at the same level of generality as Moura and Christofferson's (1996) citation of fusion of post-cephalic ganglia into a subesophageal mass (eucheliceratе apomorphy). An additional state might be recognized for arachnids, which fuse abdominal ganglia to the nerve mass (Wegerhoff and Breidbach, 1995).

46. Prostomium: 0, forms acron; 1, clearly demarked by a distinct groove. The separation of the prostomium was regarded by Rouse and Fauchald (1997) as an annelid synapomorphy. We follow Rouse and Fauchald in coding its absence (inapplicability) in Onychophora, although some workers consider the prebuccal head

region of onychophorans to include an acron (de Haro, 1998).

47. Cephalon composed of one pair of preoral appendages and three pairs of postoral appendages: 0, absent; 1, present. The composition of the fundamental euarthropod head has considered information from fossils as well as extant taxa. Weygoldt's (1986) proposal that the basic euarthropod cephalon included four pairs of post-oral appendages is in conflict with well-known paleontological data (e.g., three pairs of post-oral biramous limbs in trilobites). Walossek's (1993) contention that the crown-group euarthropod cephalon is composed of preoral antennae and an additional three pairs of limbs is corroborated by *engrailed* expression in crustaceans and insects, in which an *engrailed* stripe on the first maxillary segment indicates the original posterior limit of the head (Scholtz, 1997).

48. Cephalic kinesis: 0, absent; 1, present. Cephalic kinesis, defined as movable ophthalmic and antennular segments and an articulated rostrum (Kunze, 1983), is shared by the Leptostraca and the Stomatopoda but not other Crustacea. The Mystacocarida have an articulated antennular segment, but lack compound eyes and a rostrum; whether this arrangement is homologous with cephalic kinesis is uncertain.

49. Flattened head capsule, with head bent posterior to the clypeus: 0, absent; 1, present. Dohle (1985) and Shear and Bonamo (1988) emphasized the peculiar construction of the flattened head capsule of Pleurostigmophora, with the clypeal region of the head becoming ventral and the mouth pushed backward. Manton (1965) alternatively regarded the flattened head capsule as a basal apomorphy for Chilopoda and considered the head of Scutigeromorpha to be secondarily domed to accommodate the enlarged mandibles. Manton's interpretation is unparsimonious.

50. Reduced lateral expansion of head shield (head of adults rounded, capsule-like): 0, absent; 1, present. In Anostraca, the lateral expansions of the head shield are developed only in the hatching nauplius (Walossek, 1993; Walossek and Müller, 1998).

51. Two primary pigment cells in ommatidium: 0, two corneagenous cells lacking pigment grains; 1, two corneagenous cells contain pigment grains. Paulus (1979) homologized a pair of corneagenous cells in Crustacea with the two primary pigment cells of hexapods. Scoring for this character is restricted to those taxa with two corneagenous cells, part of the alleged mandibulate eye (see character 55).

52. Lateral compound eyes: 0, absent; 1, simple lens with cup-shaped retina; 2, stemmata with rhabdom of multilayered retinular cells; 3, faceted; 4, onychophoran eye. The inclusion of fossil taxa will modify the inferred basal state for several groups from that coded here based on extant representatives. Compound eyes (state 3) are present in fossil scorpions (Sissom, 1990) and diplurans (Kukalová-Peck, 1991), whereas extant taxa possess states 1 and 0, respectively. Fossil diplopods have been considered to have compound eyes (Kraus, 1974), though Spies (1981) interpreted them as pseudofaceted; extant Chilognatha have stemmata (state 2). Rather than coding the pseudofaceted eye of Scutigeromorpha as an uninformative autapomorphy, we follow Paulus (1979, 1986, 1989) in interpreting this eye as a modification of myriapod stemmata (state 2) based on ultrastructural similarities. Myriapod lateral eyes possess a rhabdom composed of two (Scutigeromorpha and Polyxenida) or many (Pleurostigmophora and Chilognatha) layers of retinular cells. Paulus (1986) considered the layering of the rhabdom as a probable synapomorphy for Myriapoda, noting a similar construction only in the larval eyes of certain insects.

53. Compound eyes medial margins: 0, separate; 1, medially contiguous. The medial coalescence of the compound eye has been treated as a shared derived character of the Archaeognatha (Hennig, 1981; Kristensen, 1991). The approximation of the antennal bases in archaeognathans is regarded as a correlated character (cf. Kraus, 1997), an effect of a medial repositioning of cephalic structures.

54. Optic neuropiles: 0, no chiasmata; 1, one chiasma (between lamina ganglionaris and medulla); 2, two chiasmata (between lamina ganglionaris and medulla / between medulla and lobula). The presence of two chiasmata between the neuropiles in some malacostracans and in insects has been cited as evidence for a sister group relationship between these taxa (Osorio *et al.*, 1995) or as defining a clade of Malacostraca, Remipedia, and Atelocerata (Moura and Christoffersen, 1996). However, the Leptostraca have only one chiasma in the optic lobe (Elofsson and Dahl, 1970), and Collembola have only two neuropiles (Paulus, 1979). An ordered coding recognizes a homology between the chiasma between the lamina ganglionalis and medulla in all taxa possessing chiasmata.

55. "Mandibulate" eye (two corneagenous cells, four Semper cells, cone with four parts, retinula with eight cells): 0, absent (variable, higher number of parts); 1, present. Despite some variation in precise numbers of subunits within crustacean and hexapod eyes, Paulus (1979, 1989) postulated that a ground pattern (state 1 above) could be interpreted for the common ancestor of these clades. Attempts to interpret myriapod stemmata as a modified mandibulate ommatidium (Paulus, 1986, 1989) have been unconvincing.

56. Median eyes fused to naupliar eyes: 0, absent; 1, present. Naupliar eyes are the median eyes of Crustacea, and the close association of the median eyes to form a functional unit has been proposed as a crustacean synapomorphy (Lauterbach, 1983; Weygoldt, 1986; Kraus, 1997). Naupliar eyes are not, however, present in all the crustacean taxa we have scored. Although Eloffsen (1966) dismissed pan-crustacean homologies in the naupliar eyes, Paulus (1979) did not regard the differences between those types with everse and inverse sensory cells as so fundamental as to disallow homology, and we concur. This character is scored as inapplicable for myriapods (lacking median eyes).

57. Number of median eyes: 0, none; 1, four; 2, two; 3, three. Paulus (1979) summarized evidence for four median eyes being a general condition in Euarthropoda. This number is reduced to two within Chelicerata. The lack of median eyes in Myriapoda has been interpreted as a synapomorphy (Boudreaux, 1979), whereas Kraus and Kraus (1994) cited the loss of median eyes as occurring independently in Chilopoda and in Progoneata. Knoll (1974) described two "frontal ocelli" in the embryo of *Scutigera*, but these transform into gland-like organs, rendering homology with median eyes improbable.

58. Inverted median eye: 0, absent; 1, present. In arachnids, the retina cells develop from an inverted invagination of the epidermis (Paulus, 1979).

59. Bulbous bothriotrichs: 0, absent; 1, present. Bothriotrichs (= trichobothria) are complex mechanoreceptors developed in several terrestrial arthropod groups. They have distinctive modifications in polyxenid millipedes, pauropods, and symphylans, notably a hair that forms a basal bulb (Haupt, 1979). This character has been proposed as a synapomorphy of Progoneata (Kraus and Kraus, 1994), although this requires that loss of trichobothria is a reversal in chilognathan millipedes (Enghoff, 1984).

60. Arthropod sensillae: 0, absent; 1, present. Mechano- and chemosensory sensillae of a characteristic structure are identified in tardigrades (R. Kristensen, 1981), onychophorans, and euarthropods (Nielsen, 1995). These are composed of one or a few primary receptor cells usually with a modified cilium surrounded by tormogen, trichogen, and thecogen cells.

61. Oral papillae with slime glands and adhesive glands: 0, absent; 1, present. Oral papillae and their associated glands are unique to Onychophora (Brusca and Brusca, 1990). The slime glands may be modifications of the crural glands (character 208) that are developed in a variable number of legs (Storch and Ruhberg, 1993).

62. Dorsolateral folds in buccal cavity: 0, absent; 1, present. Rouse and Fauchald (1997) observed dorsolateral buccal folds to be an annelid synapomorphy.

63. Mouth direction: 0, anteroventral; 1, posterior. A posteriorly directed mouth has been proposed as a characteristic feature of the TCC or schizoramian group (Cisne, 1974). This condition is present in xiphosurids, whereas the anteroventral orientation of the mouth is regarded as an arachnid synapomorphy (Shultz, 1990). It is acquired in ontogeny, modified from a posteriorly directed state in the embryo of arachnids.

64. Labrum: 0, absent; 1, present, originating from bilobed anlage. Partial covering of the mouth by a labrum is observed in all euarthropods except for the pycnogonids (Sharov, 1966; King, 1973). Scholtz (1997) recognized a labrum originating from bilobed anlage as a euarthropod synapomorphy.

65. Fleshy labrum: 0, absent; 1, present. Walossek and Müller (1990) recognized an apomorphic character complex in the mouth region of crown-group Crustacea. This consists of a fleshy labrum that forms the cover of the atrium oris, with setulate, brush-like sides. A sternum with humped paragnaths (Fig. 3A) is also part of the crustacean labral complex as defined by Walossek and Müller (1990), although paragnaths are less pronounced in some crustaceans (e.g., Cephalocarida and Mystacocarida).

66. Entognathy (overgrowth of mandibles and maxillae by cranial folds): 0, absent; 1, present. Entognathy in the broad sense (mouthparts overgrown by cranial folds) occurs to varying degrees in onychophorans, pauropods, and chilopods, as well as the hexapodan Entognatha (Manton, 1964). This character is scored to recognize more detailed similarities of the latter

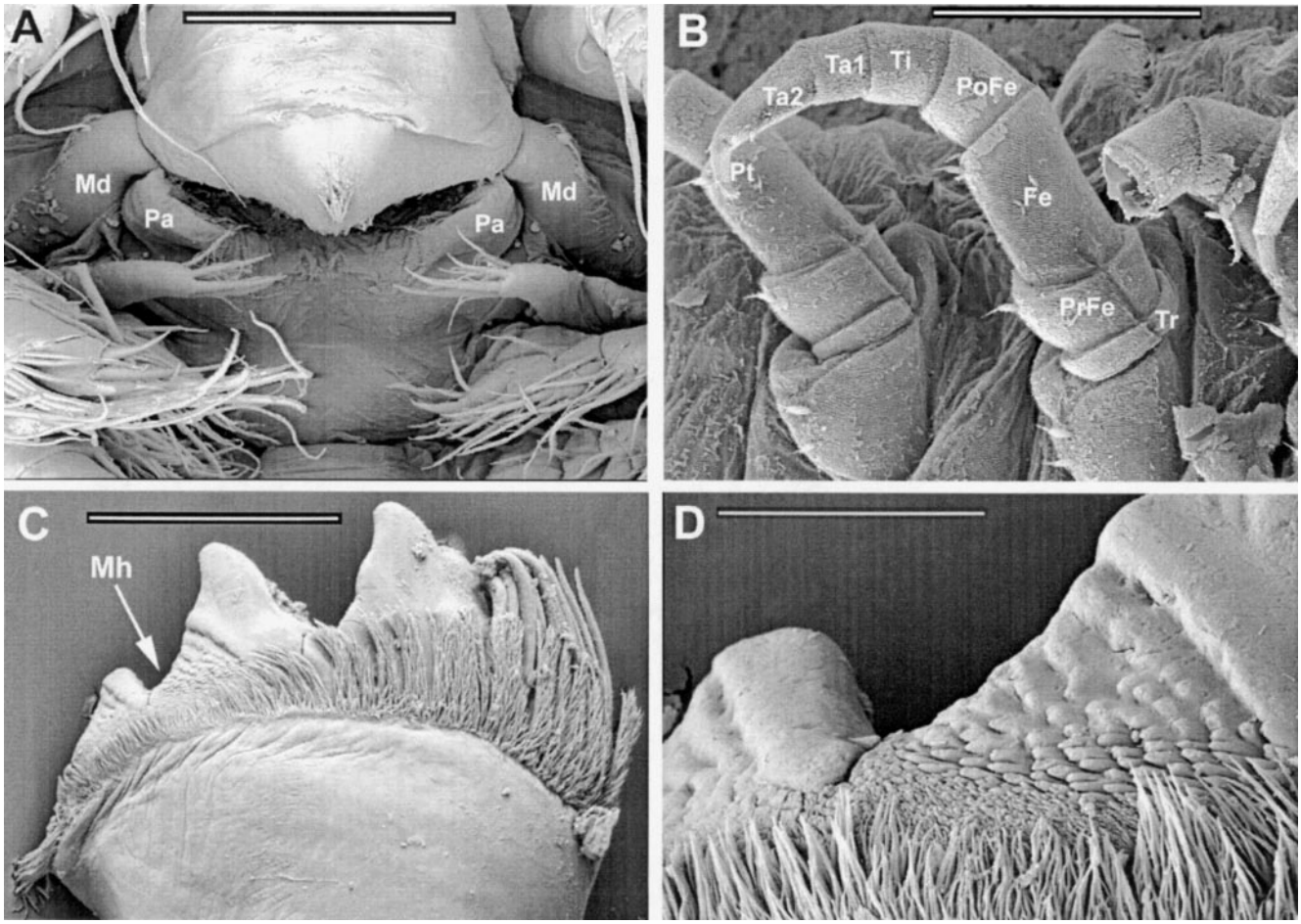


FIG. 3. (A) *Hutchinsoniella maracantha* (Cephalocarida), Buzzard's Bay, Massachusetts. Ventral view of head, showing paragnaths (Pa), mandibles (Md), and labrum. (B) *Unixenus mjobergi* (Diplopoda, Penicillata), Mt. Tom Price, Western Australia. Ventrolateral view of a trunk leg, with trochanter (Tr), prefemur (PrFe), femur (Fe), postfemur (PoFe), tibia (Ti), first tarsomere (Ta1), second tarsomere (Ta2), and pretarsus (Pt) identified following Manton (text and Fig. 3 in 1956). (C and D) *Paralamyctes* n. sp. (Chilopoda, Lithobiomorpha), Mt. Keira, NSW, Australia. Gnathal lobe of mandible, showing molar hooks (*sensu* Kraus, 1997) at base of teeth. Scale bars: A, 100 m; B and C, 200 m; D, 50 m.

(Bitsch, 1994, p. 114, and references therein). The oral folds in Entognatha are joined together ventrally and are united behind with the postlabium. Inclusion of fossil taxa, in particular the Carboniferous japygid *Testajapyx* (Kukalová-Peck, 1987), which is not fully entognathous, will force homoplasy on the tree.

Moura and Christoffersen (1996) suggested that the internalization of the mandible into a preoral buccal cavity (atrium oris) is a synapomorphy of the Remipedia and the Atelocerata. Although Schram and Lewis (1989) identified a specialized atrium oris in the remipedes as being different from that of all other crustaceans, this feature does not particularly resemble that of the Atelocerata; the mouth field is posteroventrally directed, similar to other Crustacea (see above). Further, paragnaths are external to the atrium oris, rather than the atelocerate situation in which the hypopharynx is internal to the preoral cavity. The lacinia mobilis, another mandibular character cited by Moura and Christoffersen (1996) as a remipede–atelocerate–malacostracan synapomorphy, is not employed here. A lacinia mobilis is lacking in basal Malacostraca (Leptostraca and Hoplocarida, being restricted to Eumalacostraca—Walossek, 1993), and its very scattered occurrence in Hexapoda also questions its presence at the basal node for hexapods (Kristensen, 1997).

67. Sclerotic sternum formed by antennal to maxillulary sternites: 0, absent; 1, present. Fusion of particular

cephalic sternites into a sclerotic sternum is shared by the crown group of Crustacea (Walossek and Müller, 1998) and is more generally shared with the fossil taxon Phosphatocopina according to Walossek (1999). Shultz (1990) regarded an unsegmented intercoxal plate in the prosomal sternum (the endostoma of Xiphosura) as the plesiomorphic state for arachnids. Neither the segmental composition nor the morphology of this plate suggests homology with fusion of sternites in crustaceans. The post-hypostomal cephalic sternum of Trilobita is composed of separate sternal sclerites (Chen *et al.*, 1997).

68. Clypeolabrum and labium mobility: 0, free; 1, immobile. Kukalová-Peck (1991) identified immobility of the clypeolabrum and labium as a shared derived character of the Ellipura.

69. Triradiate pharyngeal lumen: 0, absent; 1, present. Dewel and Dewel (1997) suggested that the triradiate pharynx of tardigrades may be plesiomorphic, being similarly developed in aschelminths. This argument has been elaborated by Schmidt-Rhaesa *et al.* (1998), who illustrated a triradiate lumen in Onychophora and nematodes. We code the "introverted Y" pharynx of pycnogonids (Schmidt-Rhaesa *et al.*, 1998) as triradiate.

70. Stomothecae: 0, absent; 1, present. Shultz (1990) defined stomothecae as expanded coxal endites that form the wall of the pre-oral chamber in some arachnids (here scorpions and opilionids). Weygoldt (1998) interpreted Paleozoic scorpions as lacking stomothecae and questioned the homology of these endites.

71. Post-cephalic filter-feeding apparatus with sternitic food groove: 0, absent; 1, present. Walossek (1993, 1995) emphasized a character complex associated with filter feeding as an apomorphy of the Branchiopoda.

72. Antennular rami: 0, uniramous; 1, multiramous. Multiramy, defined as two or more rami attached distally to distinct basal podomeres (peduncle), is found in the Malacostraca, including the Leptostraca, in which the antennula is biramous, and the Stomatopoda, in which it is triramous. The later condition is considered to be derived from the basal malacostracan biramous state (Kunze, 1983). The Remipedia have biramous antennulae, but lack defined basal podomeres, and their modification of the first head limb is not considered homologous with that of the malacostracan antennule.

73. Antennula size: 0, long, flagelliform; 1, only few segments. Branchiopoda scored in this analysis have highly reduced antennulae, while most other crustaceans and atelocerates have long, flagelliform antennules.

74. Antennular apical cone sensilla: 0, absent; 1, present. Unique to Diplopoda is a cluster of cone-shaped sensillae on the distal antennomere of the antennula (Enghoff, 1984). The cluster usually consists of four sensillae.

75. Antennule lacking extrinsic muscles, with Johnston's organ in scapus: 0, absent (antennule musculated, lacking Johnston's organ); 1, present. As recognized by Imms (1939), the flagelliform, unmusculated antenna is unique to Insecta (N. Kristensen, 1981, 1991, 1997).

76. Sclerotized bridge between antennule: 0, present; 1, absent. Absence of a sclerotized bridge between the antennae is distinctive for Geophilomorpha within the Chilopoda (Dohle, 1990). Fusion of the antennal lobes of the deutocerebrum in Geophilomorpha (Minelli, 1993) may be an expression of the same character complex.

77. Antennular circulatory vessels: 0, antennular vessels joined with dorsal vessel; 1, antennular and dorsal vessels separate; 2, antennular vessels absent. Pass (1991) provided a review of antennular circulatory vessels in arthropods. Insecta are defined by the separation of the antennular vessels and the dorsal vessel versus the connection of the dorsal vessel and antennular vessels in Diplura, Myriapoda, and Malacostraca. Data for Crustacea are limited (Pass, 1991). Collembola and Pauropoda lack antennular vessels.

78. Appendage on third (tritocerebral) head segment: 0, unspecialized; 1, antenna; 2, intercalary appendage absent; 3, chelifore or chelicera. Several major groups of arthropods are defined by conditions of the appendage of the third metamere. The plesiomorphic state is that observed in fossil groups such as trilobites, in which this post-antennular limb is undifferentiated from other cephalic limbs (or, for that matter, from trunk limbs). Crustaceans uniquely possess a second antenna, atelocerates have suppressed this somite (such that embryonic limb buds in some taxa are its maximal expression—Anderson, 1973), and chelicerates have the chelicera in this position.

79. Antennal exopod: 0, present; 1, absent. Fossil arachnomorphs (e.g., trilobites) demonstrate that a biramous second cephalic limb is not restricted to Crustacea (as would appear to be the case based on extant taxa alone). In some crustacean taxa, the exopod is expressed only as a scale (Stomatopoda and Eumalacostraca) while others have a more general flagellate exopod. The Notostraca and Anostraca have an antennal exopod in their larval stages, but not as adults. Other branchiopods, however, have biramous antennae as adults.

80. Antennal naupliar protopod: 0, short; 1, long. Sanders (1963) contrasted the length of the antennal protopod in branchiopod nauplii with that in other crustaceans. The branchiopod condition (state 1) may be characterized as a protopod exceeding 50% of the length of the naupliar antenna.

81. *Distal-less* expressed in mandible: 0, present (including transient expression in embryo and in palp); 1, absent in all ontogenetic stages. Manton's (1964) argument that atelocerate mandibles are the tips of "whole limbs," whereas crustacean mandibles arise as coxal gnathobases has been recast (Panganiban *et al.*, 1995; Popadić *et al.*, 1996) and then rejected (Popadić *et al.*, 1998; Scholtz *et al.*, 1998) by work on *Distal-less* expression, which indicates that mandibles are uniformly gnathobasic. As in other characters involving gene expression, taxonomic sampling is limited. We have scored the character for Anostraca (using *Artemia* for *Branchinella*), Malacostraca (using *Mysidopsis, Orchestia, Armadillidium, Asellus*, and *Porcellio* for *Kempina*), and chilognathan millipedes (using *Oxidus* and *Glomeris* for *Epicyliosoma*). Rather than coding inapplicability for Chelicerata, the high, continuous expression of *Distal-less* in all prosomal limbs of the spider *Achaearanea* (coded for *Atrax*; Popadić *et al.*, 1998) is used as evidence that state 0 pertains to non-mandibulates. The absence of *Distal-less* expression in all ontogenetic stages pertains only to Hexapoda [coded for Collembola, Zygentoma, and several groups of Pterygota based on Popadić *et al.* (1998) and Scholtz *et al.* (1998)].

82. Mandible (gnathobasic appendage of third limb-bearing metamere is main feeding limb of adult head): 0, absent; 1, present. Snodgrass (1950) and Manton (1964) assumed opposite positions on the significance of mandibles in arthropods. The former emphasized their fundamental similarity between crustaceans and atelocerates, whereas the latter regarded their differences as violating the possibility of a single origin. Defenses of the homology of mandibles are offered by Weygoldt (1986) and Wägele (1993), the latter regarding the embedding of the mandible between the labrum and the hypopharynx to form a "chewing chamber" as evidence for homology. The pattern of reduced *Distal-less* expression through ontogeny that is observed in the mandibles of crustaceans and myriapods (expression completely suppressed in hexapods) reinforces the homology of mandibles (Popadić *et al.*, 1998).

83. Mandibular base plate forming side of head: 0, absent; 1, present. Mandibular structure and function are similar in Symphyla and Diplopoda (Snodgrass, 1950). In each of these groups, the proximal part of the mandible, the base plate, is a prominent component in the side of the head capsule (Fig. 2A), such that muscular abduction of the mandible is abandoned (Manton, 1979a). Instead, the mandible abducts by the anterior tentorial apodeme ("swinging tentorium") pushing on the sides of the gnathal lobes. This style of abduction in symphylans and diplopods is associated with a greater degree of muscular independence of the gnathal lobe than in chilopods. Though Boudreaux (1979) employed a movable, articulated mandibular endite (so-called gnathal lobe) as a myriapod synapomorphy, we cannot identify a convincingly homologous expression of a gnathal lobe in pauropods and chilopods.

"Molar hooks" is another mandibular gnathal feature that we have not yet incorporated. Kraus (1997) claimed these to be an atelocerate synapomorphy, but reversed (absent) in Diplura and Dicondylia. We are unaware of critical evaluation of the homology of this feature, e.g., whether similar processes in Crustacea are possible homologues, but confirm the presence of molar hook-like structures on mandibular teeth in Chilopoda (Figs. 3C and 3D).

84. Second (anterior) mandibular articulation with the cranium: 0, absent; 1, present. N. Kristensen (1975, 1981), among many others, noted that a dicondylic articulation of the mandible defined a clade uniting all insects to the exclusion of Archaeognatha.

85. Mandibular scutes: 0, absent; 1, present (mandible composed of two to five moveable scutes). The chilopod mandible is unique, even among other myriapod taxa with segmented mandibles (symphylans and diplopods), in that it is fragmented into a series of

scutes. This structure has been posited as a synapomorphy of Chilopoda (Boudreaux, 1979).

86. Mandibular palp: 0, present (appendage of third limb-bearing cephalic metamere with telopod); 1, absent throughout ontogeny; 2, present in larva, absent in adult. The lack of a mandibular palp is frequently evoked as a synapomorphy of Atelocerata by workers who have defended a monophyletic Mandibulata (e.g., Weygoldt, 1986; Kraus, 1997). The presence or absence of a mandibular palp is, however, variable within Crustacea. We recognize three states to account for ontogenetic change in the presence or absence of a mandibular palp in crustaceans.

87. Posterior tentorial apodemes: 0, absent; 1, tentorial arms; 2, metatentorium. Posterior tentorial apodemes are lacking in myriapods. Manton (1964) regarded the anatomy, connections, and associated muscles of the posterior tentorial arms in Collembola and Diplura as indicating homology with the fused posterior tentorial bar (metatentorium) of Insecta. An ordered coding recognizes the fused state (metatentorium) as a modification of separate tentorial arms.

88. Anterior tentorial arms: 0, absent; 1, developing as ectodermal invaginations; 2, developing in gnathal pouch. The tentorial cephalic endoskeleton is restricted to atelocerates. Snodgrass (1950) regarded the anterior tentorial arms of Myriapoda as homologous with those of Insecta, in which they likewise arise as cuticular (ectodermal) invaginations. Some workers (summarized in Matsuda, 1965) have considered homologous elements to be lacking in the Entognatha, in which the comparable structures (the so-called fulturae) originate within the gnathal pouch. Others, such as Manton (1964), emphasize the similarities of anterior tentorial arms throughout the Atelocerata. We have followed Manton (1964) in recognizing their absence in campodeids.

89. Swinging tentorium: 0, absent; 1, present. Abduction of the mandible in most Myriapoda is achieved by movements of the anterior tentorial arms (Manton, 1964). This condition is unique to myriapods. Mandibular movements are, however, solely muscular in Geophilomorpha and Scutigeromorpha (Manton, 1965).

90. Suspensory bar from mandible: 0, absent; 1, present. An articular rod (Snodgrass, 1950) or suspensory bar (Boudreaux, 1979) is present in the posterior mandibular attachment in all orders of chilopods except the Geophilomorpha. A similar rod, a thickening of the lateral pouch wall, forms the posterior support of the mandible in Ellipura (Snodgrass, 1950). This similarity reflects the apparently independent development of entognathy in Chilopoda and Ellipura.

91. Complete postoccipital ridge: 0, absent; 1, present. Snodgrass (1935) described a postoccipital ridge as the internal aspect of the postoccipital suture, which is often produced into apodemal plates on which are attached the dorsal prothoracic and neck muscles of the head. A complete postoccipital ridge (N. Kristensen, 1981) or dorsally complete postoccipital suture (Kristensen, 1997) is cited as a synapomorphy of Dicondylia.

92. Salivary glands: 0, absent; 1, arise as ectodermal invaginations on second maxilla/labium; 2, arise as mesodermal segmental organs of the first maxillae. Anderson (1973) recognized two patterns of development for salivary glands in Atelocerata. In chilopods and hexapods, the salivary glands form as ectodermal invaginations of the second maxillary or labial segment. In Progoneata, salivary glands are mesodermal segmental organs of the maxillary segment.

93. Opening of maxillulary salivary glands: 0, pair of openings at the base of the second maxillae; 1, one median opening in the midventral groove of the labium; 2, one median opening in the salivarium, between the labium and the hypopharynx. Bitsch and Bitsch (1998, their character 8) identified distinctive positions of ducts of the salivary glands in Entognatha (state 1) and Insecta (state 2). Coding is restricted to those taxa with salivary glands of ectodermal origin on the second maxillae/labium (chilopods and hexapods; character 92, state 2).

94. Maxillae on fourth limb-bearing metamere: 0, absent; 1, present. All extant mandibulates have the appendage of the fourth metamere specialized as a mouthpart, a maxilla. This character is sometimes combined with maxillary development on the succeeding limbs as a mandibulate synapomorphy (e.g., Brusca and Brusca, 1990, among others). Discussion under character 102 indicates that first and second maxillae must be evaluated separately.

95. Mx1 precoxal segment: 0, absent; 1, present. Boxshall (1997) suggested that definition of a precoxa in the maxillulary (mx1) protopod is restricted to the Remipedia and taxa traditionally grouped as Maxillopoda, including the Mystacocarida. Moreover, these two taxa have a maxillula made of a seven-segmented

uniramous stenopodium (exopod lacking; endopod of four segments).

96. Mx1 with medially directed lobate endites on the basal podomere, possibly consisting of a precoxa and coxa: 0, no lobate endites; 1, two endites; 2, one endite. Crustaceans are unique in the presence of medially directed lobate endites on a number of appendages. Boxshall (1997) summarized information on endite configurations on the crustacean first maxilla (maxillule). Separate states are recognized for malacostracans (one basal endite) and for the cephalocarids, remipedes, and mystacocarids (two basal endites). Extant branchiopods are coded as inapplicable − due to the reduction of the maxillulae, but fossil taxa such as *Rehbachiella* (Walossek, 1993) indicate that the plesiomorphic branchiopodan state is 2. Walossek (1993, 1999) recognized this similarity in maxillulary endite configurations as grounds for separating Entomostraca and Malacostraca.

97. Maxillary plate [basal parts of fifth limb-bearing metamere (second maxilla or labium) medially merged, bordering side of mouth cavity]: 0, absent; 1, present. Kraus and Kraus (1994) cited this morphology as a synapomorphy for Labiophora (Progoneata + Hexapoda = Labiata of Snodgrass, 1938). They contrasted it with the situation in chilopods, in which the first maxillae border the mouth. The maxillary plate corresponds to Snodgrass' (1938) concept of a labium, which he also regarded as synapomorphic for Labiophora. Kraus and Kraus' (1994, 1996) argument is dependent on their interpretation that the diplopod and pauropod gnathochilarium is composed of two pairs of appendages, first and second maxillae, a claim developed earlier by Verhoeff and upheld by Kraus and Kraus based on external morphology. Dohle's (1997) counterarguments, including the complete lack of limbs on the mx2 segment in embryos, innervation by a single pair of ganglia, and muscles being those of a single segment, are accepted in our codings of maxillary characters. Dohle (1997) concluded that the lower lip of Dignatha is composed of the appendages of the first maxillary segment and the intervening sternite alone. Scholtz *et al.* (1998) strengthened Dohle's interpretation by demonstrating the lack of *Distal-less* expression on the postmaxillary segment in diplopods.

98. Mx1 palps: 0, present (telopod present on appendage of fourth metamere); 1, absent. The absence of maxillary palps has been cited as a synapomorphic character for Progoneata (Kraus and Kraus, 1994; Kraus, 1997). An ambiguity, however, is the interpretation of the minute lateral cone on the so-called stipes of symphylans, which has been cautiously homologized with a vestigial palp (e.g., Snodgrass, 1952). The evidence is not especially compelling, and we have coded the palp as absent in Symphyla. Presence of a palp in polyxenids follows Shear (1997).

99. Hypertrophied maxillary palp: 0, absent; 1, present. Kristensen (1997) regarded a maxillary palp larger than the thoracic locomotory limbs as a possible autapomorphy for the Archaeognatha. This character recognizes the size of the palp rather than its pronounced segmentation (the latter being regarded by Kukalová-Peck, 1997, as evidence for the most plesiomorphic limb segmentation in any extant arthropod).

100. Mx1 divided into cardo, stipes, lacinia, and galea, with similar musculation and function: 0, absent; 1, present. Manton (1964) observed the structure and function of the maxilla to be similar throughout the Hexapoda, and there is little question that details are apomorphic. While the same descriptive terminology is employed for the units of the first maxilla in symphylans, Manton noted significant differences in details of musculature and function from those in hexapods. Characteristic of the hexapod maxilla are the cardo bearing a strong point of articulation with the cranium, the principal retractor–adductor to the lacinia inserting on the cranium, and muscle XI (following the homology scheme of Manton, 1964) from the cardo being a principal protractor. Tuxen's (1959) study of Diplura concluded that the structure of the maxilla in this group was most similar to that in Ellipura, but also noted that the entognathan maxilla closely resembled that of other hexapods.

101. Gnathochilarium including intermaxillary plate: 0, absent; 1, present. Pauropods and diplopods have classically been united based on the maxillary structures, developed as a gnathochilarium. Kraus and Kraus (1996) have, however, disputed the view that pauropods and polyxenid diplopods possess a true gnathochilarium. Our coding recognizes the traditional hypothesis.

102. Second maxillae on fifth metamere: 0, appendage developed as trunk limb; 1, well-developed maxilla differentiated as mouthpart; 2, vestigial appendage; 3, appendage lacking. Second maxillae are lacking in some crown-group Crustacea (notably Cephalocarida),

in which the corresponding appendage may retain the structure of a trunk limb. Suppression of the second maxilla, being largely a pedestal for the maxillary gland (state 2), is coded for branchiopods. The complete absence of limbs on the second maxillary segment is shared by pauropods and diplopods (following Dohle, 1997; see discussion of character 97).

103. Egg tooth on second maxilla: 0, absent (no embryonic egg tooth on cuticle of fifth limb-bearing metamere); 1, present. Dohle (1985) proposed that an egg tooth on the second maxilla is an autapomorphy of Chilopoda.

104. Coxae of mx2 medially fused: 0, absent (coxae of fifth metamere not fused); 1, present. Pleurostigmophoran chilopods share a medial fusion of the coxae of the second maxilla, a condition regarded as synapomorphic (Dohle, 1985; Shear and Bonamo, 1988).

105. Linea ventralis: 0, absent; 1, present. Kristensen (1991) and Kraus (1997) postulated that the median groove in the posterior / ventral surface of the head in Ellipura, the linea ventralis, was a synapomorphy. It extends from the openings of the labial glands to the neck membrane in Protura and back to the preabdominal ventral tube in Collembola.

106. Divided glossae and paraglossae: 0, undivided pair of glossae and paraglossae; 1, glossae and paraglossae bilobed. Kristensen (1991) noted that bilobed ligular elements (Fig. 2E) were a "peculiarity" of the archaeognathan labium, but was uncertain whether they provided an autapomorphy for Archaeognatha. *Campodea* is coded as missing data because the ligulae are fused. Protura is coded with the assumption that the inner and outer labial lobes (Fig. 40B in Matsuda, 1976) are the glossae and paraglossae, respectively. Ephemeroptera is scored for the state of the ligulae in nymphs (Fig. 49A in Matsuda, 1976), the character being inapplicable for adults.

107. Direct articulation between first and fourth articles of telopodite of maxilliped: 0, absent (first and fourth articles of telopodite of sixth metamere lack a common hinge); 1, present. Characters 107–114 pertain to various conditions of the maxilliped (forcipule) in Chilopoda. States in other arthropods are based on the appendage of the homologous (sixth limb-bearing) metamere. The common hinge between the articles of the maxilliped telopodite is a classic character for Epimorpha (Scolopendromorpha and Geophilomorpha), as recognized by Attems (1926) and maintained in more recent cladistic analyses (Kraus, 1997, and references therein). A Jurassic geophilomorph that appears to have complete second and third articles of the maxilliped telopodite (Fig. 4 in Schweigert and Dietl, 1997) requires confirmation; if correctly documented, this character exhibits homoplasy (see also Borucki, 1996, for absence of this articulation in *Cryptops* and *Dicellophilus*).

108. Coxosternite of maxilliped sclerotized in midline: 0, coxae separated medially, with sternite present in adult; 1, coxosternal plates meeting medially, with flexible hinge; 2, coxosternal plates meeting medially, hinge sclerotized and nonfunctional. Shear and Bonamo (1988) coded the condition of the maxilliped coxosternum in Chilopoda as a multistate character. They (1988:9) regarded the medially sclerotized condition shared by *Craterostigmus* and Epimorpha as apomorphic based on serial homology (fusion makes the maxillipeds less like the following trunk legs). Dohle (1990) drew the same interpretation of this state as a synapomorphy for that group, whereas Ax (1999) considered the separate coxosternal plates of Scutigeromorpha to be an autapomorphy. Scutigeromorpha have a sternite present in adults (Fig. 91a in Manton, 1965) and coxae are separated medially, as in outgroups (Symphyla and Hexapoda). In Scolopendromorpha, the sternal contribution to the coxosternite is expressed only in early ontogeny (Manton, 1965:324). Medial coalescence (state 1, Lithobiomorpha) and sclerotization of the hinge (state 2, *Craterostigmus* + Epimorpha) are thus coded as states of an ordered character, as suggested by Shear and Bonamo (1988).

109. Maxilliped coxosternite deeply embedded into cuticle above second trunk segment: 0, not embedded; 1, embedded. Manton (1965) identified features of the maxillipeds in Craterostigmomorpha and Epimorpha associated with strengthening their proximal attachment. Among these is the embedding of the coxosternum into cuticle beneath the succeeding trunk segment.

110. Maxilliped segment with pleurite forming a girdle around coxosternite: 0, small lateral pleurite; 1, large girdling pleurite. This character has been coded only for atelocerates (other arthropod taxa lack pleurites on the first trunk segment), the apomorphic state being restricted to certain chilopods. In Craterostigmorpha and Epimorpha, the pleurite of the maxilliped

segment envelopes the coxosternite (Manton, 1965; = "Spange" of Attems, 1926).

111. Sternal muscles truncated in Maxilliped segment, not extending into head: 0, sternal muscles extended into head; 1, sternal muscles truncated. Manton (1965) observed that the truncation of the sternal muscles in the maxilliped segment distinguishes craterostigmomorph and epimorph chilopods from scutigeromorphs and lithobiomorphs. The latter condition, with the sternal muscles extending into the head, is shared by pauropods and symphylans (Manton, 1966) and collembolans and proturans (Manton, 1972) and is thus regarded as plesiomorphic. Because of uncertainties in drawing homologies with muscles in crustaceans and chelicerates, this character is coded for atelocerates only.

112. Maxilliped tooth plate (anteriorly projecting, serrate coxal endite): 0, absent; 1, present. The toothplate is employed by scolopendromorph centipedes as a "can opener" in stabbing prey. The same type of endite is present in in the Craterostigmomorpha (Manton, 1965; Dohle, 1990) and the Devonian *Devonobius* (Shear and Bonamo, 1988).

113. Maxilliped poison gland: 0, absent; 1, present. This character describes the modification of the first pair of trunk limbs in chilopods into a fang with a poison gland.

114. Maxilliped distal segments fused as a tarsungulum: 0, separate tarsus and pretarsus; 1, tarsus and pretarsus fused as tarsungulum. Borucki (1996) recognized the fused tarsungulum in the maxilliped of pleurostigmorphoran chilopods as a synapomorphy for that group, in contrast to the articulated tarsus and pretarsus in scutigeromorphs.

115. Oblique muscle layer in body wall: 0, absent; 1, present. An oblique muscle layer, with fibers organized in a chevron pattern (Storch and Ruhberg, 1993), is a specialization of Onychophora.

116. Longitudinal muscles: 0, united sternal and lateral longitudinal muscles; 1, separate sternal and lateral longitudinal muscles, with separate segmental tendons. The division of the longitudinal muscles into separate sternal and longitudinal bands serves to unite craterostigmomorph, scolopendromorph, and geophilomorph chilopods (Manton, 1965). Taxa lacking lateral longitudinal muscles (e.g., *Campodea*; Manton, 1972) have been coded as inapplicable. Coding is restricted to atelocerates.

117. Superficial pleural muscles: 0, absent; 1, present. Within the Chilopoda, Epimorpha and Craterostigmomorpha share details of pleural musculature. These include the presence of the superficial pleural muscles pam.1, pam.2, and ptm of Manton (1965). The homology of these with muscles in other arthropod groups is questionable, so we have not coded this character for most taxa.

118. Crossed, oblique dorsoventral muscles: 0, absent; 1, present. Boudreaux (1979) interpreted the crossed, oblique dorsoventral muscles in crustaceans, myriapods, and hexapods as a mandibulate synapomorphy. A similar configuration has been reconstructed for trilobites (Cisne, 1981), but additional evidence is needed to corroborate this character. We regard Cisne's (1981) photographs of *Triarthrus eatoni* in which these muscles are shown in the accompanying drawings as suggestive but not certain. Confirmation of a "box truss" arrangement of dorsoventral muscles in trilobites, a branch from the chelicerate stem lineage, would weaken this character as a synapomorphy for Mandibulata, allowing it to be resolved as a basic euarthropod feature. Codings for *Epicyliosoma* and *Atalophlebia* are entered as uncertain because the trunk musculature (for Chilognatha and Pterygota) is greatly modified. Serial dorsoventral muscles are lacking in pycnogonids and onychophorans (Firstman, 1973), rendering this character inapplicable for those taxa. The dorsoventral suspensors of the endosternum and the abdominal dorsoventral muscles of chelicerates lack the crossed, oblique arrangement of mandibulates.

119. Deep dorsoventral muscles in the trunk: 0, absent; 1, present. Manton (1965) identified a complex of dorsoventral muscles (dvc muscles in her terminology) that pass upward to the trunk tergites in epimorphic chilopods. They are absent in "anamorphic" chilopods. As for character 117, a limited range of taxa are coded due to uncertain homologies. Polarity can, however, be provided by Manton's (1966) observation that deep dorsoventral trunk muscles are lacking in Symphyla.

120. Circular body muscle: 0, present; 1, suppressed. Lack of circular body wall muscle is shared by tardigrades and euarthropods. We code the similarity without assuming that the former is due to miniaturization (Dewel and Dewel, 1997).

121. Discrete segmental cross-striated muscles attached to cuticular apodemes: 0, absent; 1, present. Brusca and Brusca (1990) and Nielsen (1995) cited

cross-striated muscles as a synapomorphy to unite tardigrades with euarthropods.

122. Abdominal muscles: 0, straight; 1, twisted. This character describes one aspect of abdominal modifications associated with jumping in Archaeognatha. Manton's (1972) description of abdominal skeletomusculature in *Petrobius* noted such modifications as twisted, rope-like dorsal muscles and deep oblique muscles in the abdomen and strong development of the abdominal tendon system. Modifications of the endoskeleton and tergum, such as greatly overlapping abdominal tergites that slide over one another dorsally, are part of the same character complex (Kristensen, 1997). Kukalová-Peck (1991) claimed that the abdominal rope muscles of archaeognathans are a plesiomorphy because they are "shared with Crustacea." Such muscles are in fact present in a small portion of crustacean diversity and in none of the crustaceans considered here.

123. Stomach in the foregut: 0, absent; 1, present. Malacostracan crustaceans (Leptostraca and Stomatopoda in this analysis) share an expanded anterodorsal chamber, divided into a cardiac and a pyloric region adjacent to anterior caecae of the midgut (Dahl, 1987). The Leptostraca lack the more complicated filter plates found in the Stomatopoda (Kunze, 1981, 1983) and Eumalacostraca, but have the same basic arrangement with variation in the size of the digestive caecae (Schram, 1986). Klass (1998) documented detailed similarities in the proventriculus of Decapoda and Zygentoma, but considered only derived taxa (Reptantia).

124. Gut caecae: 0, absent; 1, present along the midgut; 2, restricted to the anterior part of the midgut. Clarke (1979) summarized information on gut caecae in arthropods. The 16 so-called caecae of *Campodea* (Clarke, 1979), being positioned at the anterior end of the hindgut, are coded here as papillate Malpighian tubules.

125. Proctodeal dilation: 0, posterior section of hindgut simple, lacking a dilation; 1, proctodeum having a rectal ampulla with differentiated papillae. Bitsch and Bitsch (1998, their character 12) homologized the rectal ampulla in *Campodea* and the rectal ampullae of Insecta.

126. Peritrophic membrane: 0, absent; 1, present. Clarke (1979) documented the distribution of a peritrophic membrane in the gut, noting its presence in onychophorans, myriapods, and hexapods [except for Protura (Bitsch and Bitsch, 1998); Snodgrass (1935) noted its presence in Collembola] as well as some crustaceans, including branchiopods (Martin, 1992) and stomatopods (Kunze, 1983). It is absent in tardigrades, chelicerates, and pycnogonids.

127. Radiating, tubular diverticula with intracellular final phase of digestion: 0, absent; 1, present. Snodgrass (1952) united euchelicerates (xiphosurids and arachnids) with pycnogonids on the shared presence of their radiating, tubular diverticula and acknowledged Schlottke's (1933) observation that the final phase of digestion is intracellular, in the walls of these diverticula.

128. Prosoma and opisthosoma: 0, absent; 1, present. Chelicerate tagmosis is uniquely defined by a prosoma bearing six locomotory and feeding appendages and an opisthosoma composed of, maximally, 12 somites (see Dunlop and Selden, 1997, for discussion of a putative 13th opisthosomal somite in scorpions). Stürmer and Bergström (1981) described a seventh prosomal limb in a fossil xiphosurid, although Dunlop and Selden (1997) considered this limb opisthosomal.

129. Transverse furrows on prosomal carapace corresponding to margins of segmental tergites: 0, absent; 1, present. Shultz (1990) identified segmental furrows on the prosomal carapace as a synapomorphy for the arachnid clade Dromopoda, within which some taxa possess discrete segmental sclerites.

130. Opisthosomal lamellae: 0, absent; 1, book gills; 2, enclosed to form book lungs. The opisthosomal respiratory lamellae of chelicerates are regarded as homologous with the exopod lamellar setae in early fossil Arachnata (Walossek and Müller, 1997, 1998). This homology is most obvious for the book gills of Xiphosura. The lamellate book lungs of scorpions have long been recognized as homologous with book gills (Lankester, 1881), a view maintained by more recent work on fossil scorpions (Selden and Jeram, 1989).

131. Appendage on first opisthosomal segment: 0, appendage present on eighth limb-bearing metamere; 1, appendage absent on eighth metamere. Shultz (1990) cited the lack of an appendage on the first opisthosomal segment as a derived character of arachnids. The homologous segment in xiphosurids bears a limb, the chilaria. Outgroup evidence (e.g., from trilobites) suggests that the absence of a limb on this trunk segment is apomorphic.

132. Capillary chaetae: 0, absent; 1, present. Chaetae

are absent in arthropods, and it is uncertain whether this absence is a reversal or plesiomorphic (Rouse and Fauchald, 1995; Eibye-Jacobsen and Nielsen, 1996), the position of the chaetate Echiura being problematic. Annelids share a distinctive chaeta form (Rouse and Fauchald, 1997).

133. Lobopods with pads and claws: 0, absent; 1, present.

134. Paired ventrolateral appendages with distal claws: 0, absent; 1, present.

135. Articulated limbs with intrinsic muscles: 0, absent; 1, present. Nielsen (1995) considered the presence of articulated limbs with intrinsic muscles to be a synapomorphy uniting tardigardes and euarthropods to the exclusion of onychophorans. Monge-Nájera (1995) and Schmidt-Rhaesa *et al.* (1998) questioned the homology of sclerotized limbs between tardigrades and euarthropods, distinguishing the former as telescopic and the latter as jointed, whereas Dewel and Dewel (1997) noted that telescopic limbs are present only in arthrotardigrades. Brusca and Brusca (1990) stated that tardigrade limb musculature is entirely extrinsic as in onychophorans, but our observations confirm Nielsen's (1995) coding of intrinsic muscles.

136. Fundamentally biramous post-antennular limbs (endopod and exopod): 0, absent; 1, present. The homology of the limb rami (endopod and exopod) and the basis in stem-group crustaceans and stem-group chelicerates (e.g., trilobites) have been argued by Walossek (1995) and extended to xiphosurids (Walossek and Müller, 1997, 1998). The alleged homology of minute thoracic styli in hexapods such as Archaeognatha and the exopod of Crustacea or fossil arachnates (e.g., Delle Cave and Simonetta, 1991; Bitsch, 1994) is unconvincing, and we see no compelling evidence for an exopod in Hexapoda. Fryer (1996) has drawn the same conclusion.

137. Abdomen (limb-free somites between the terminal segment and limb-bearing trunk segments, posterior to expression domain of *Ubx*, *abdA*, and *abdB*): 0, absent; 1, present. Evidence from *Hox* genes provides insights into the homologies of tagmata and forms the basis for not coding hexapod and crustacean "thoraxes" (characters 138 and 139) as homologous. Expression of the *Hox* genes *Antp, Ubx, abdA*, and *abdB* has led to the proposal that the crustacean "thorax" or pereion is homologous to the hexapod thorax and abdomen (Averof and Akam, 1995; Deutsch, 1997). Grenier *et al.* (1997) found this *Hox* gene set throughout the Panarthropoda, including Onychophora. Crustacea uniquely possess a limbless abdomen, which does not express *Ubx* and *abdA* (Grenier *et al.*, 1997, and references therein). The crustaceans coded here all have a morphologically defined limbless abdomen, except for the Malacostraca and the Remipedia. While a series of limbless abdominal somites has been cited as an autapomorphy for Entomostraca (Walossek, 1999), Scholtz (1995) showed that *Engrailed* expression extends to additional embryonic segments within the telson of malacostracans. We interpret these somites as the homologue of the abdomen of entomostracans.

138. Pereion tagmosis: 0, one locomotory tagma; 1, two locomotory tagmata. Following from the identity of the crustacean pereion in character 137, the malacostracan pleon is identified as a second set of thoracic segments (Walossek, 1999). Number of somites in the pereion of different crustacean taxa (see Fig. 12,13 in Walossek and Muller, 1997) is expressed in the coding of variable gonopore positions (character 187) rather than as a separate character.

139. Thorax with three limb-bearing segments: 0, absent; 1, present.

140. Diplosegments: 0, absent; 1, present. The fusion of trunk segments into diplosegments is considered a diplopod synapomorphy (Dohle, 1980; Enghoff, 1984; Kraus and Kraus, 1994). Other myriapod taxa, as well as Ellipura within the Hexapoda, have been described as having "diplosegmentation trends" (Zrzavý and Štys, 1994), but are readily distinguished from the pattern in diplopods, a point strongly emphasized by Manton (1974).

141. Endosternum (ventral tendons fused into prosomal endosternum): 0, absent; 1, present. Euchelicerates are distinct in the modification of the intersegmental tendon system. In the prosoma, the ventral tendons are consolidated into a plate, the endosternum, which is suspended by the dorsoventral muscles (Boudreaux, 1979). Firstman (1973) additionally ascribed a role for fusion of perineural vascular membrane in the endosternum. Homology between Dohrn's membrane (horizontal vascular septum) in pycnogonids and the endosternum has been suggested (Firstman, 1973); the coding used here recognizes a restricted definition of the endosternum.

142. Tergal scutes extend laterally into paratergal folds: 0, absent; 1, present. Paratergal folds (paranotae) have been upheld as a basal synapomorphy for Euarthropoda (Boudreaux, 1979; Wägele, 1993). They are lacking or reduced in myriapods, a condition that has been interpreted as an apomorphic reversal (Boudreaux, 1979).

143. Paramedian sutures: 0, absent; 1, present. Paramedian sutures (Manton, 1965) are a pair of lineations along the tergum and sternum in epimorphic chilopods. Attems (1926) cited this character ("Längsnähten") as a defining character of Epimorpha.

144. Intercalary sclerites: 0, absent; 1, developed as small rings; 2, developed as pretergite and presternite. Well sclerotized intercalary tergites and sternites are present in Craterostigmorpha and Epimorpha (Chilopoda). Weaker sclerotizations occur in the corresponding positions in Lithobiomorpha. A correlated character (dependent on the presence of intercalary sternites) is the anchoring of the tendon of the sternal longitudinal muscles on the intercalary sternite in these chilopods (Manton, 1965). Dohle (1985) indicated that division of the tergites and sternites into pre- and metatergites and pre- and metasternites was autapomorphic for the Geophilomorpha. Manton (1965) demonstrated that the muscles of the pretergites are more independent of those of the metatergites than are those of other chilopods with intercalary sclerites, and related this to the burrowing habits of the geophilomorphs. The intercalary sclerites of Symphyla (Manton, 1966) are tergal only and not coded as homologous with those of chilopods.

145. Trunk heterotergy: 0, absent; 1, present (alternating long and short tergites, with reversal of lengths between seventh and eighth walking-leg-bearing segments). Borucki (1996) recognized special heterotergy as a synapomorphy of the Chilopoda, with a homologous alternation in long and short tergites between post-maxillipedal segments 7 and 8 in all ingroup taxa except the Geophilomorpha. Heterotergy in nonchilopods (such as Symphyla) does not share this precise segmental homology.

146. Pleurites: 0, absent; 1, present. Manton (1979b) identified a unique construction of the pleuron in hexapods and myriapods, including the presence of pleural sclerotizations (pleurites). Coding is restricted to those taxa with a tergum and sternum (the pleuron is otherwise inapplicable).

147. Procoxal and metacoxal pleurites surround coxa: 0, pleurites absent or incompletely surrounding coxa; 1, procoxa and metacoxa surround coxa. The chilopod orders Scolopendromorpha and Geophilomorpha are united by the pronounced development of pleurites around the leg base (Fig. 2D). The metacoxa is a large sclerotization in the scolopendromorphs (see Figs. 48 and 49 in Manton, 1965), unlike *Craterostigmus* (Fig. 74 in Manton, 1965) or the "anamorphic" chilopods.

148. Elongate coxopleurites on anal legs: 0, absent; 1, present. Formation of coxopleurites on the last leg-bearing segment was cited by Kraus (1997) as a synapomorphy for *Craterostigmus* and Epimorpha s.s. Defined as such, this character is actually present in all chilopods, which invariably have pleurites fused to the coxa to form a single basal leg sclerite on the anal leg segment. The apomorphy that Kraus (1997) may have been describing as "coxopleurites" is their enhanced differentiation in *Craterostigmus* and Epimorpha. In scutigeromorphs and lithobiomorphs, the anal leg coxopleurite is shorter than that of Epimorpha, with the former condition more closely resembling the bases of preceding legs.

149. Pleuron filled with small pleurites: 0, absent; 1, present. Geophilomorphs (Fig. 2D) have an elaboration of pleurites (including the so-called scutellum, katopleure, and stigmatopleurite and a few more small pleurites) that fill the pleuron except for the pleural furrow (*sensu* Manton, 1965).

150. Longitudinal muscles attach to intersegmental tendons: 0, absent; 1, present. The intersegmental tendon system of euarthropods was reviewed by Boudreaux (1979). Absence of such tendons in pycnogonids is scored following Boudreaux.

151. Coxopodite with gnathobasic endite lobes medially: 0, absent; 1, present. Gnathobasic feeding was identified as a common feature of crustaceans and chelicerates (Manton, 1964) and was used to support the TCC group (Cisne, 1974). As discussed under character 81, gnathobasic endites / gnathobasic feeding is also shown in the mandible of myriapods and hexapods (Scholtz *et al.*, 1998). Endites have been posited as synapomorphic for Euarthropoda (Wägele and Stanjek, 1995).

152. Coxal swing: 0, coxa mobile, promotor–remotor swing between coxa and body; 1, coxa with limited mobility, promotor–remotor swing between coxa and

trochanter. Arachnids differ from xiphosurids (and other arthropods) in the anchoring of the coxa on the prosoma, with promotor–remotor swing shifted distally to the coxa–trochanter joint rather than the coxa–body joint.

153. Coxopodite articulation: 0, arthrodial membrane; 1, pleural condyle; 2, sternal condyle; 3, sternal and pleural condyles; 4, internal plate. Manton (e.g., 1972) attributed much importance to the nature of coxal articulation within the Atelocerata. She contrasted the myriapod condition (coxa with a condylic articulation ventrally, on the sternum) with that observed in most insects (coxa articulating dorsally, on a pleurite). Unique conditions are recognized for Collembola, in which an internal suspensory system is developed (Manton, 1972), and Protura, which possess sternal as well as pleural condyles. In primitive crustacean taxa as well as early fossil arachnomorphs (Chen *et al.*, 1997), the coxopodite (= basis) joins the body in arthrodial membrane rather than a condylic joint. Arachnids are scored as missing data for this character due to their immobile coxal attachment (character 152).

154. Separation of coxae of trunk legs: 0, coxae separated laterally; 1, coxae in close approximation mid ventrally. The close medial setting of the trunk coxae serves as a synapomorphy for Diplopoda (cf. Manton, 1956:155).

155. Coxal vesicles: 0, absent; 1, present on numerous trunk segments; 2, restricted to first abdominal segment (modified as *Ventraltubus*). Dohle (1980) reviewed the distribution of coxal vesicles (or eversible sacs) in Atelocerata. He noted their variable positioning in different progoneate and hexapod taxa and did not conclude that they provided sound evidence for a monophyletic group. Kraus and Kraus (1994), however, listed coxal vesicles together with styli as a synapomorphy uniting progoneates and hexapods, whereas Moura and Christoffersen (1996) cited a stylus and eversible vesicles as an atelocerate synapomorphy (but did not acknowledge their absence in Chilopoda). Matsuda (1976) distinguished between eversible sacs of appendicular nature (e.g., the single pair of sacs at the end of the *Ventraltubus* on the first abdominal segment in Collembola and Protura) and those that appear to have extra-appendicular origins. The latter include the vesicles of Symphyla (Fig. 2B), which arise on the "ventral organs" associated with ganglion formation (Tiegs, 1940), these being segmental thickenings of the embryonic ventral ectoderm. It can thus be validly questioned whether "coxal vesicles" should be regarded as broadly homologous. Although Tiegs (1947) regarded a pair of organs of the collum of pauropods (Fig. 2F) as vesicles, this homology is contentious; Kraus and Kraus (1994) suggest that they are vestigial appendages. Vesicles are present on numerous trunk segments in symphylans and some groups of diplopods (not the representatives considered here) and on numerous abdominal segments in Diplura, Archaeognatha, Zygentoma, and *Tricholepidion*. In contrast, the confinement of vesicles to the first abdominal segment in Ellipura is regarded here as a synapomorphy (state 2) and a modification of state 1. The character is accordingly ordered.

156. Styli: 0, absent; 1, present. Styli have a close association with coxal vesicles / eversible sacs in some atelocerate taxa, for example, Symphyla (see discussion under character 155 and Fig. 2B). However, styli and vesicles do not covary phylogenetically; Ellipura possess vesicles but lack styli. As such we treat these as separate characters (cf. Dohle, 1980) rather than a single feature (Kraus and Kraus, 1994). Evidence for styli in chilopods is contentious, the only evidence being Heymons' (1901) description of a coxal spur on embryonic appendages of *Scolopendra*, which has been upheld as being in a position comparable to the coxal stylus of machiloids (Matsuda, 1976). A further distinction could be made between taxa having styli on numerous abdominal / trunk segments in both sexes and those that have more restricted distributions of styli (e.g., on the ninth segment of the adult males only in Ephemeroptera).

157. Trochanter distal joint: 0, mobile; 1, short, ringlike trochanter lacking mobility at joint with prefemur. The very short trochanter in chilopods is part of a proximal region of the leg specialized to facilitate a rapid backstroke (Manton, 1965). Associated with the shortening of the trochanter in chilopods is immobility at its distal joint with the prefemur. Arthropods lacking stenopodial legs, such as most Crustacea, are scored as missing data for this character because the homologues of the myriapodan trochanter and prefemur cannot be identified with reasonable confidence.

158. Origin of pretarsal depressor muscle: 0, pretarsal depressor originates on tarsus; 1, pretarsal depressor originates on tibia or patella. Previous workers have cited a relatively distal point of origination of

the pretarsal depressor as an apomorphic character, as occurs in atelocerates as well as in arachnids (Shultz, 1990). The latter condition may be polarized by the more distal origination of this muscle in pycnogonids and in xiphosurids (originating in the tarsus). However, the general significance of this character across the Arthropoda is rendered ambiguous by the imprecision with which it can be coded for most primitive crustaceans.

159. Pretarsal levator muscle: 0, present; 1, absent (depressor is sole pretarsal muscle). Snodgrass (1952) recognized a single pretarsal muscle, a depressor, as a synapomorphy uniting myriapods and hexapods.

160. Antennal and mandibular protopod composed of basis and coxa: 0, absent; 1, present. Although variably interpreted, the proximal limb region of Crustacea possesses unique structure, as is most generally distributed on the antenna and mandible. Our coding accommodates Walossek and Müller's (1990, 1992, 1998) hypothesis that the coxa of Crustacea is a novel element, developed from a proximal endite that is more generally shared by Cambrian fossils.

161. Tracheae / spiracles: 0, absent; 1, pleural spiracles; 2, spiracles at bases of walking legs, opening into tracheal pouches; 3, single pair of spiracles on head; 4, dorsal spiracle opening to tracheal lungs; 5, open-ended tracheae with spiracle on third opisthosomal segment; 6, many spiracles scattered on body. Defined as ectodermal tubes with a chitinous intima and respiratory function (Dohle, 1997), tracheae are present in arachnids and onychophorans as well as Atelocerata. Dohle (1997), Kraus (1997), and Hilken (1998) take the diversity in tracheal position and structure in Atelocerata to imply four to seven independent originations of tracheae in that group alone. Given that all of these lineages are sister groups in Kraus' (Fig. 22.3 in 1997) and Hilken's (Fig. 37 in 1998) cladograms, the idea that their shared ancestors lacked tracheae is unparsimonious. We have not, however, forced a broad homology of tracheae, acknowledging the weakness of primary homology (Hilken, 1998). Codings of states correspond to Dohle's (1997) and Hilken's (1998) hypotheses of tracheal origins except for coding the pleural tracheae of insects and chilopods as a shared state based on similarities in position, branching, and helical taenidia (Kaufman, 1967). Studied representatives of Collembola and Protura lack tracheae and are thus coded for absence; we have not attempted to code for the peculiarities of tracheae in other collembolans and proturans (Xué *et al.*, 1994). Within the Pauropoda, Hexamerocerata share a peculiar spiracle position with diplopods, opening into tracheal pockets that function as apodemes (Kraus and Kraus, 1994). Dohle (1997) emphasized that these similarities provide strong evidence for a common origin. A ground-plan coding is used for Pauropoda to avoid loss of this information, despite the exemplar pauropod studied here lacking tracheae.

162. Longitudinal and transverse connections between segmental tracheal branches: 0, tracheae not connected; 1, tracheae connected. Tracheal commissures and connectives have been recognized as a synapomorphy for Epimorpha within Chilopoda (Manton, 1965) and for Dicondylia within Insecta (N. Kristensen, 1981). Hennig (1981) stated that tracheal connectives are more general across Insecta, also being present in Archaeognatha. Our coding follows Bitsch and Bitsch (1998, their character 15), not accepting that the variably developed connections of Archaeognatha are reliably homologous. Coding for characters 162–164 is restricted to chilopods and hexapods with pleural spiracles.

163. Pericardial tracheal system with chiasmata: 0, dendritic tracheae; 1, long, regular pipe-like tracheae with specialized molting rings. Manton (1965) documented numerous modifications of the tracheal system in Geophilomorpha. These include distinctive pericardial tracheae and a median dorsal atrium, as well as chiasmata between the anastomoses (Hilken, 1997).

164. Abdominal spiracles: 0, present (pleural spiracles on posterior part of trunk); 1, absent on first abdominal segment; 2, absent on all abdominal segments. Štys and Bilinski (1990) stated that the absence of abdominal spiracles is a synapomorphy for campodeids and Ellipura (versus a primitive presence of abdominal spiracles in japygids and insects). To evaluate this character at a more general level it is necessary to homologize the hexapod abdomen with the posterior region of the trunk in myriapods. Evidence from chilopods conforms to Štys and Bilinski's (1990) polarity (presence of posterior trunk spiracles plesiomorphic). Archaeognatha lack a spiracle on the first abdominal segment alone, and this has been regarded as an autapomorphy (Hennig, 1981; Kristensen, 1991, 1997).

165. Collum: 0, absent (appendages of sixth limb-bearing metamere not reduced); 1, present. Diplopods

possess a limbless first postcephalic metamere, the collum. Pauropods have, at most, minute vestiges of limbs on this segment (Kraus and Kraus, 1994).

166. Paddle-like epipods: 0, absent; 1, present. Hessler (1992) suggested that epipods on cephalocarid, branchiopod, and malacostracan (leptostracan) trunk limbs were an apomorphy uniting these crustacean taxa into a clade, Thoracopoda.

167. Trunk limbs with lobate endites formed by folds in limb bud: 0, absent; 1, present. Morphogenesis of branchiopod trunk limbs indicates that "phyllopodous" limbs in that group arise from early, radical repatterning compared to Leptostraca, in which the developing limbs preserve fundamentally biramous structure (Williams, 1999).

168. Patella / tibia joint: 0, free; 1, fused. Due to uncertain identity of the atelocerate patella / tibia joint in other arthropods (and its likely absence in taxa presumed to lack a patella), coding for this character is restricted to Atelocerata. Kristensen (1991) cited "tight union of the patella and the tibia" as a hexapod autapomorphy. This is one expression of the six-segmented leg that is considered a novelty for Hexapoda (Kristensen, 1997; Willmann, 1997).

169. Patellotibial joint: 0, dorsal monocondylar articulation; 1, bicondylar articulation. A bicondylar articulation of the patella and tibia defines a subset of Arachnida (Shultz, 1989, 1990). Because homology of the chelicerate patella in other arthropod taxa is uncertain (the patella being widely regarded as lost in extant arthropods other than chelicerates, e.g., Boudreaux, 1979), we have restricted coding of this and other patellar characters (170–171) to the Chelicerata.

170. Femoropatellar joint: 0, transverse dorsal hinge; 1, bicondylar articulation. Shultz (1990) recognized a bicondylar articulation between the femur and the patella as a synapomorphy for the arachnid taxon Dromopoda.

171. Origin of posterior transpatellar muscle: 0, arises on distodorsal surface of femur, traverses femoropatellar joint ventral to axis of rotation, receives fibers from wall of patella; 1, arises on distal process of femur, traverses femoropatellar joint dorsal to axis of rotation, does not receive fibers from patella. The transpatellar muscle corresponds to muscle 7 of Shultz (1989), who noted that its origin in opilionids, scorpions, pseudoscorpions, and solifugids was distinctive within Arachnida.

172. Pretarsal claws: 0, paired; 1, unpaired. Unpaired pretarsal claws have been upheld as a synapomorphy for Protura and Collembola (N. Kristensen, 1981), although it has alternatively been speculated that a single median claw could be the basal state for Hexapoda (Bitsch, 1994) and paired claws a synapomorphy of Insecta (Kraus, 1997). We have scored all myriapods except Symphyla (Fig. 2C) as having unpaired claws based on the condition of the median claw, although accessory claws are commonly paired (chilopods) or a lateral accessory claw may combine with the median claw to simulate pairing (pauropods; Fig. 7b in Kraus and Kraus, 1994). Although comparisons have been made with the malacostracan dactylus in an attempt to determine the basal state for this character in atelocerates (e.g., Bitsch, 1994) pretarsal claws are lacking in most Crustacea (and all taxa coded herein), and this character is scored as uncertain.

173. Tarsus segmentation: 0, not subsegmented; 1, subsegmented. Segmentation of the tarsus into tarsomeres has been cited as an apomorphy for several clades within the Arthropoda (e.g., Chilopoda and Arachnida fide Boudreaux, 1979; Insecta fide N. Kristensen, 1981, 1991). Shear *et al.* (1998) conclude that diplopods have a unitary tarsus except for instances of secondary subdivision. We have scored the tarsus as subdivided in diplopod exemplars (e.g., Penicillata; Fig. 3B) following the podomere homologies of Manton (text–Fig. 3 in 1956).

174. Pretarsal claw(s) articulation: 0, on pretarsal base; 1, on distal tarsomere. The articulation of the pretarsal claws on the distal tarsomere has been proposed as an insect apomorphy (Boudreaux, 1979; Kristensen, 1997).

175. Abdomen 11 segmented: 0, absent; 1, present. The segmental composition of the hexapod abdomen has received extensive debate (see Matsuda, 1976). We follow Kristensen (1997) in defining the abdomen as being composed of 11 true segments and a telson, noting that the alternative interpretation (12 segments) would receive the same codings.

176. Annulated caudal filament: 0, absent; 1, present. Abdominal segment XI (or XII; see character 175) is modified as an annulated caudal filament in Archaeognatha, Zygentoma, and primitive pterygotes (Ephemeroptera) and has accordingly been cited as an insect synapomorphy (Kukalová-Peck, 1991; Kristensen, 1997).

177. Natatory pleopods: 0, absent; 1, present. Malacostracan crustaceans (Leptostraca and Stomatopoda in this analysis) share posterior trunk limbs differentiated into biramous natatory limbs, with only one basal podomere prior to the rami (Calman, 1909). This podomere is typically referred to as the sympod or protopod.

178. Abdominal segment XI modified as cerci: 0, absent; 1, present. Cerci are absent in Ellipura (Kristensen, 1991), although Kukalová-Peck (1991:150) referred to their presence in Protura. In addition to segmental homology, cerci in Diplura and Insecta have a modified, fused condylic base; this has been cited as evidence in favor of a dipluran sister group to insects (Kukalová-Peck, 1991).

179. Articulate furcal rami: 0, absent; 1, present. Walossek and Müller (1992) recognized a pair of articulated furcal rami as a shared derived character for the crown-group level of Crustacea.

180. Egg cluster guarded until hatching: 0, absent; 1, female coils ventrally around cluster; 2, female coils dorsally around egg cluster. A distinctive style of maternal care is shared by Craterostigmomorpha and Epimorpha (Manton, 1965; Dohle, 1985). Dohle (1985) and Borucki (1996) upheld geophilomorph monophyly based on the habit of the female to coil with the dorsum against the eggs versus the sternum against the eggs in *Craterostigmus* and Scolopendromorpha.

181. Peripatoid and fetoid stages protected by mother: 0, absent; 1, present. Brood care (character 180) in Epimorpha is extended to the first two postembryonic stadia (Dohle, 1985).

182. Female gonopod used to manipulate single eggs: 0, absent; 1, present. Ax (1999) treated the usage of the female gonopod in egg manipulation and the laying of single eggs as two independent autapomorphies of his taxon Gonopodophora (= Lithobiomorpha + Scutigeromorpha). Single-segmented gonopods are identified in Geophilomorpha, but are lacking in Scolopendromorpha and *Craterostigmus* (Prunescu, 1996). Absence of gonopods renders the character broadly inapplicable; most instances of gonopods outside Chilopoda (e.g., Diplopoda) cannot be homologized with those of chilopods.

183. Female abdomen with ovipositor formed by gonapophyses of segments VIII and IX: 0, absent; 1, present. The ovipositor is cited as an insect synapomorphy (Kristensen, 1997).

184. Gonangulum sclerite fully developed as ovipositor base, articulating with tergum IX and attached to first valvula / valvifer: 0, absent; 1, present. A putative synapomorphy for Dicondylia (N. Kristensen, 1981, 1997), this character is applicable only to those taxa with an ovipositor (character 183).

185. Elongate dorsal gonad: 0, absent; 1, present. This is a euarthropod–tardigrade–onychophoran character, with the annelids having segmental gonads.

186. Penes: 0, absent; 1, present. "Penes" refers to a pair of narrow appendages behind the second trunk leg pair in diplopods and pauropods, bearing the male gonopore at their tips (Dohle, 1980, 1997; Kraus and Kraus, 1994).

187. Male gonopore location: 0, posterior end (opisthogoneate); 1, somite 19; 2, somite 11 (6th pereion segment); 3, somite 9; 4, somite 8 (first opithosomal segment); 5, behind legs of somite 8 (second pair of trunk legs); 6, somite 13 (8th pereion segment); 7, somite 17 (12th pereion segment); 8, somite 16; 9, on multiple leg bases. An alleged remipede–atelocerate clade was based in part on placement of the gonopore on the last (preanal) body segment (Moura and Christoffersen, 1996). This is, however, not true of remipedes unless Moura and Christoffersen's hypothesis that a unique common ancestor of these taxa had precisely 15 trunk segments is accepted. This character is coded to recognize varied states of "progoneaty" in chelicerates, crustaceans, and myriapods. We acknowledge that state 0 includes additional variation (e.g., male gonopore behind the 11th abdominal segment in Protura, at the posterior margin of the 8th abdominal segment in Diplura, behind the 9th abdominal segment in insects). Gonopore position and numbers are variable in annelids (reviewed by Fauchald and Rouse, 1997); our coding for pycnogonids is agnostic concerning multiple gonopores being an arthropod plesiomorphy (cf. Sharov, 1966). Given the nephridial association of polychaete gonoducts, homology is unlikely. Furthermore, some pycnogonids possess a single pair of gonopores (Clarke, 1979).

188. Female gonopore position: 0, on same somite as male; 1, two segments anterior to male; 2, seven segments anterior to male. States 1 and 2 recognize the separation of male and female gonopores in Malacostraca and Remipedia, respectively. Within Hexapoda, Entognatha have male and female gonopores on the same segment (Matsuda, 1976), whereas in Insecta the

female gonopore is generally located behind the seventh abdominal sternite and the male on the ninth segment.

189. Embryonic gonoduct origin: 0, gonoduct arising as a mesodermal coelomoduct; 1, gonoduct arising as a secondary ectodermal ingrowth; 2, gonoduct arising in association with splanchnic mesoderm. The developmental origin of the gonoducts was traced by Anderson (1973). Specialized conditions were described for progoneate myriapods, in which the gonoduct is a secondary ectodermal ingrowth, and hexapods, in which it arises in association with splanchnic mesoderm. Additional apomorphic states can likely be defined within state 0. Tardigrades are scored as unknown; although the gonads have been described as arising from the posterior pair of coelomic pouches, Dewel *et al.* (1993:171) considered this inadequately established.

190. Genital atrium with looped deferens duct: 0, absent; 1, present. The deferens duct in Chilopoda is looped near its opening (Fig. 5 in Prunescu, 1996). This character is scored only for those taxa with an unpaired, opisthogoneate deferens duct.

191. Lateral testicular vesicles linked by a central, posteriorly extended deferens duct: 0, absent; 1, present. Prunescu (1996) described an apomorphic testicular system in *Craterostigmus* and epimorphic chilopods, in which the vasa efferentia emanate from both ends of the testes. Additional information is present in vesicle shape (spindle-shaped in scolopendromorphs and geophilomorphs; Dohle, 1985) and number (single in geophilomorphs, pseudometameric in *Craterostigmus* and Scolopendromorpha) but has not been coded here due to inapplicability to most taxa.

192. Testicular follicles with pectinate arrangement: 0, absent (elongated testicular sac or sacs); 1, several pectinate follicles present. State 1 corresponds to a basal apomorphy for Insecta in the analysis of Bitsch and Bitsch (1998, their character 24). Coding is restricted to panarthopods (taxa with an elongate dorsal gonad; character 185).

193. Spermatophore web: 0, absent; 1, present. Dohle (1985) indicated that lithobiomorph, scolopendromorph, and geophilomorph chilopods spin a web for the deposition of the spermatophore. While the web has been documented in few chilopod taxa, web spinning can be coded based on the "Spinngriffel" structure (so-called penis). Dohle (1990:77) identified this structure in *Craterostigmus*. The web material is probably produced by accessory glands of which Pleurostigmophora have two pairs and Scutigeromorpha (which do not produce a web) have a single, rudimentary pair (Brunhuber and Hall, 1970).

194. Sperm dimorphism: 0, absent; 1, present (microsperm and macrosperm). Although ultrastructural evidence for sperm dimorphism is best known for Scolopendromorpha (Jamieson, 1986), it is consistent with sperm of two sizes in all other chilopod orders except Geophilomorpha (Jamieson, 1987; Carcupino *et al.*, 1999). Such dimorphism is elsewhere known in Symphyla.

195. Acrosomal complex in sperm: 0, bilayered (filamentous actin perforatorium present); 1, monolayered (perforatorium absent); 2, acrosome absent; 3, periacrosomal material present. Codings for the presence of a performatium in the sperm are based on Baccetti and Dallai (1978), Baccetti *et al.* (1979), Jamieson (1987, 1991), and Alberti (1995). Baccetti *et al.* (1979) particularly regarded the loss of the perforatium to be a shared derived character of Myriapoda. Jamieson (1987) cited the presence of periacrosomal material (state 3 above) as an insectan apomorphy.

196. Centrioles in sperm: 0, proximal and distal centrioles present, not coaxial; 1, coaxial centrioles; 2, single centriole; 3, centrioles absent. Wirth (1984) identified the presence of two coaxial centrioles in all flagellate sperm (state 1 above) as an autapomorphy of the Chelicerata. The doublet centrioles of malacostracans (*Kempina*) are not regarded as homologous with state 0.

197. Centriole adjunct: 0, absent; 1, present. A wide zone of dense material around the connecting piece of the sperm, the centriole adjunct, was regarded by Jamieson (1987) as an autapomorphy of atelocerates, but lost in Entognatha. However, Dallai *et al.* (1992) record the presence of a centriole adjunct in Protura. In those taxa lacking a centriole (character 196, state 3), we have coded this character as inapplicable.

198. Sperm "accessory bodies" developed from the centriole: 0, absent; 1, present. Kristensen (1991) followed Jamieson (1987) in regarding one to three crystalline accessory bodies flanking the axoneme as a synapomorphy of Insecta.

199. Cristate, noncrystalline mitochondrial derivatives in sperm: 0, absent; 1, present. Jamieson (1987) identified two elongate mitochondrial derivatives as a

ground-plan synapomorphy of Hexapoda, interpreting their absence in Protura as a reversal.

200. Supernumary axonemal tubules (peripheral singlets): 0, absent; 1, present, formed from the manchette; 2, present, formed from axonemal doublets. A 9 + 2 arrangement of axonemal tubules was regarded by Baccetti (1979) as plesiomorphic for arthropods, and this condition is widespread. Insects and campodeids share a 9 + 9 + 2 pattern, a state also found in onychophorans. Dallai and Afzelius (1993) revealed different origins for the hexapod and onychophoran states, which we accordingly code separately.

201. Axonemal endpiece "plume": 0, endpiece not extended; 1, endpiece extended, plume-like. Jamieson (1986) postulated that chilopods and pauropods shared derived characters in sperm structure. In particular, he proposed that an expanded endpiece of the axoneme, the so-called plume, unites these taxa. Data reviewed by Jamieson (1987) confirm the presence of the plume in Scolopendromorpha, Geophilomorpha, and Lithobiomorpha and Mazzini *et al.* (1991) indicate that it is present in Scutigeromorpha (*Scutigera*) as well.

202. Spiral ridge in sperm: 0, absent; 1, present. Chilopod sperm possess several modifications, including a spiral ridge on the nucleus (various references cited by Dohle, 1985).

203. Sperm flagellum: 0, present; 1, absent. Štys and Bilinski (1990) proposed that immotile sperm are a synapomorphy for Ellipura/Parainsecta. This condition is also observed throughout the Diplopoda and has been regarded as a synapomorphy for that group (Enghoff, 1984). Many Crustacea also have aflagellate, immotile sperm, including the Branchiopoda and Malacostraca.

204. Ovary shape: 0, sac- or tube-shaped, entire; 1, divided into ovarioles; 2, ovarian network. Štys and Bilinski (1990) observed the lack of subdivision of the ovary into ovarioles as a distinctive state in campodeids, proturans, and collembolans. Broader comparison (Štys *et al.*, 1993), however, indicates that the lack of metameric ovarioles in these taxa, in contrast to their development in Japygina and Insecta, is certainly a plesiomorphic state. Makioka (1988) regarded the looped ovary of ticks as approximating the basal state for Euchelicerata. Xiphosura and Scorpiones share a complex, network-like ovary (Fig. 4 in Makioka, 1988).

205. Location of ovary germarium: 0, germarium forms elongate zone in the ventral or lateral ovarian wall; 1, germarium in the terminal part of each egg tube; 2, single, median mound-shaped germarium on the ovarian floor. Bitsch and Bitsch (1998, their character 21) contrasted an allegedly myriapod-like position of the gonial tissue in Collembola with its apical position in the ovariole in all other hexapods. State 0 is known for euchelicerates, pycnogonids, onychophorans, chilopods (*Lithobius*), and some crustaceans (Anostraca); state 1 is present in Notostraca and some Malacostraca (data summarized by Makioka, 1988). An apical germarium is also in Mystacocarida (Boxshall and Defaye, 1996:416), Cephalocarida (Hessler and Elofsson, 1996:278), and Tardigrada (Dewel *et al.*, 1993:171). Progoneate myriapods share a distinctive median, mound-shaped germarium (state 2 above), which is observed in symphylans, pauropods, and polyxenid diplopods (Yahata and Makioka, 1994, 1997). We follow Yahata and Makioka's (1994) interpretation that the germarium is lost in chilognathan diplopods (which instead have paired germ zones on the ovarian wall as the sites of oogonial proliferation and oocyte growth) and code this character as inapplicable for that group.

206. Site for oocyte growth: 0, in ovarian lumen; 1, on outer surface of ovary, in hemocoel, connected by egg stalk. Mandibulate-type (state 0) and chelicerate-type (state 1) oocyte growth patterns follow descriptions by Makioka (1988) and Ikuta and Makioka (1999). The mandibulate pattern was identified in pycnogonids, but a reinterpretation of the pedal space containing the growing oocytes suggests that the oocytes protrude from the ovarian surface into the hemocoel and are stalked as in chelicerates (Miyazaki and Makioka, 1991). The chelicerate pattern is shared by Onychophora according to Makioka (1988).

207. Coxal organs: 0, absent; 1, present. Rosenberg (1982, 1983a,b) investigated the histology of organs associated with the coxal pores in pleurostigmophoran chilopods. Dohle (1985) and Shear and Bonamo (1988) accepted the homology of these coxal organs and we concur, based on detailed ultrastructural similarity. From an ecological scenario, Prunescu (1996) interpreted the lack of coxal organs as a secondary loss in scutigeromorphs, but this is unparsimonious.

208. Crural glands: 0, absent; 1, present. Monge-Nájera (1995) cited crural glands as a synapomorphy for onychophorans.

209. Stalked sperm drops: 0, absent; 1, present.

Schaller (1979) reviewed spermatophores in Arthropoda. Stalked sperm drops in campodeids, collembolans, and symphylans exhibit considerable similarity in form.

210. Mitochondrial DNA arrangement with $tRNA^{L(UUR)}$ between COI and COII: 0, absent; 1, present. Boore *et al.* (1995, 1998) cited a relocation of $tRNA^{L(UUR)}$ as a shared derived character of hexapods and crustaceans (branchiopods and a eumalacostracan), lacking in diplopods, *Lithobius*, *Limulus*, an onychophoran, a tardigrade, and outgroups. We have coded for *Atalophlebia*, *Branchinella*, *Kempina*, and *Epicyliosoma* as proxies, based on these observations.

211. Mitochondrial DNA arrangement 1-rRNA/$tRNA^{L(CUN)}$/NDI: 0, absent; 1, present. Limited taxonomic sampling (Boore *et al.*, 1995) suggests that this

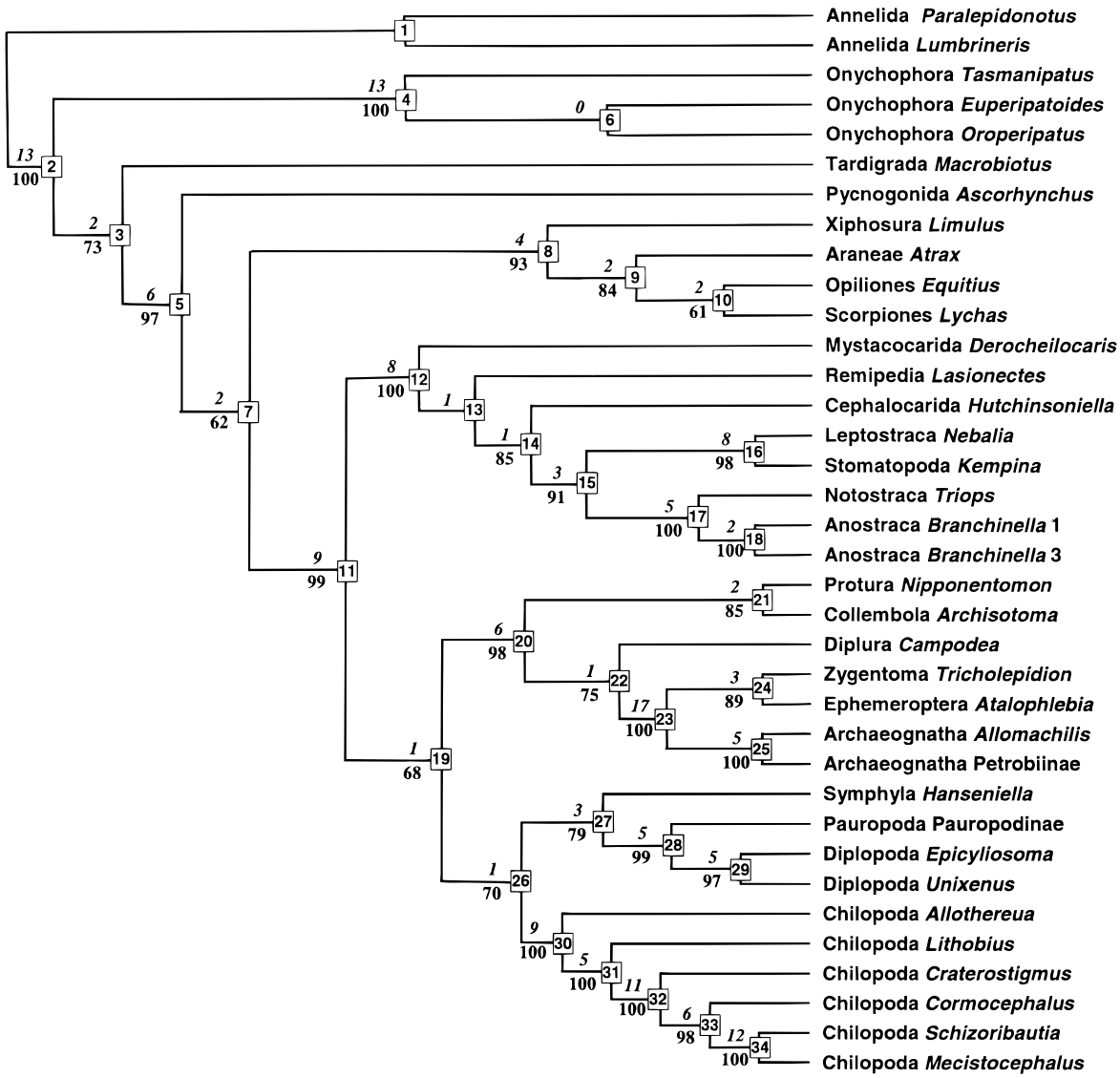


FIG. 4. Shortest fully resolved cladogram for 211 morphological characters in Table 1. Length 410 steps, CI 0.67, RI 0.86. Bremer support is shown in italics above each branch and bootstrap support below each branch. Character optimizations for internal nodes (1–34, in boxes) and terminals are listed in Table 2.

character is restricted to Mandibulata. Boore *et al.* (1995) suggested several other putative synapomorphies for Euarthropoda based on mitochondrial DNA arrangements. We have not employed these characters because information was not presented for myriapods and onychophorans.

RESULTS

Phylogenetic Analysis of Morphological Data

Two shortest trees of 410 steps (CI 0.67, RI 0.86) are retrieved with the analytical parameters described above (Fig. 4; see also Tables 1 and 2). The only instance of ambiguity concerns the internal relationships of Onychophora, for which none of the characters provides unambiguous resolution. Tree topology mirrors the results of our principal sources for character data: chelicerate relationships are as in Shultz (1990), hexapods as in Kristensen (1997), progoneates as in Kraus (1997), and chilopods as in Dohle (1985) and Borucki (1996). Noteworthy components include the following:

(1) Tardigrades are weakly supported as sister group to euarthropods (uptree of Onychophora), as suggested by Nielsen (1995), Dewel and Dewel (1996, 1997), and Wheeler (1997). Apomorphic transformations are the loss of circular body wall muscle (120:1), cross-striated muscles attaching at cuticular apodemes (121:1), articulated limbs with intrinsic muscles (135:1), and Bismuth staining of Golgi beads (23:1). This hypothesis accommodates some of the complex apomorphies shared by Onychophora and Euarthropoda, such as the ostiate heart (36:1) and metanephridia with sacculi (24:1), by allowing that their absences in tardigrades are due to miniaturization.

(2) Pycnogonids fall to the base of Euarthropoda (cf. Zrzavý *et al.*, 1997) rather than as sister group to Chelicerata. Two steps separate these rival hypotheses. The basal position for pycnogonids is effected by absences of nephridia (24:0), a labrum (64:0), intersegmental tendons (150:0), and gnathobasic endite lobes (151:0). Interpreting pycnogonids as chelicerates forces these absences to be due to loss.

(3) Mandibulata is supported, with nine steps required to force nonmonophyly. Mandibles (82:1), maxillae as functional mouthparts (94:1), crossed dorsoventral muscles (118:1), and a mitochondrial DNA arrangement with $tRNA^{L(CUN)}$ between rRNA and NDI (211:1) serve as unreversed mandibulate synapomorphies. Oocytes developing in the ovarian lumen (206:0) is an unreversed mandibulate synapomorphy with the present taxonomic sampling, though Ikuta and Makioka (1999) indicate that some maxillopodan crustaceans display state 1 for this character. An ecdysial split between the head and the trunk (20:0) and a peritrophic membrane (126:1) are also optimized as basal apomorphies for Mandibulata. As noted in discussion of character 118, trilobites show some evidence for crossed dorsoventral muscles, indicating that this character may be more general (basal state for Euarthropoda). If the pattern of reduced *Distal-less* expression in the mandible through ontogeny (Popadić *et al.*, 1998; Scholtz *et al.*, 1998) is coded as a separate character, support for Mandibulata is further increased.

(4) Crustacea is a monophyletic group (Bremer support of 8), with Entomostraca a grade. Unreversed crustacean synapomorphies in all optimizations are segmental glands confined to the antennal and maxillary segments (25:2), a fleshy labrum (65:1), a sclerotic sternum (67:1), two medially directed, lobate endites on mx1 (96:1), protopods composed of the basis and a coxa (160:1), and a limb-free abdomen behind the expression domain of *Ubx*, *abdA*, and *abdB* (137:1); furcal rami (179:1) are also a basal apomorphy for Crustacea in all optimizations. Unreversed apomorphies with delayed transformation are the nauplius larva (12:1) and second antennae (78:1); the frequent assumption that these characters must be symplesiomorphies for Mandibulata or Pancrustacea is challenged below. Several characters optimized as crustacean synapomorphies are, however, more convincingly reinterpreted as symplesiomorphies when fossil groups are considered. Among these are a posteriorly directed mouth (63:1), an antennal exopod (79:0), biramous limbs (136:1), and paratergal folds (142:1). All of these states are shared by trilobites and a range of other stem-lineage chelicerates (Edgecombe and Ramsköld, 1999). Inclusion of extinct terminals would thus be expected to optimize these characters as basal states for Euarthropoda.

TABLE 1

Morphological Characters

Character Number (10)							1	2	3	4	5	6	7	8	9
Character Number	12	3	45678	9	0	1	2345678901234567890123456789012345678901234567890123456789012345678901234567890123456	7	8	9	0	1	2	3	4	5	6	7890123456789
Annelida *Paralepidonotus*	01	0	10000	0	0	0	0000-000-000000000-00?00000000-00010----0----0-000100-0--0-0--------------	-	00-0-0-------
Annelida *Lumbrineris*	01	0	10000	0	0	0	0000-000-000000000-00?00000000-00010----0----0-000100-0--0-0--------------	-	00-0-0-------
Onychophora *Tasmanipatus*	11	2	00001	0	0	1	-001-101100?100100-00?11100?10-000-0----4--0-0-011000-0--1-0------0?--0---	-	00-0-0-0-----
Onychophora *Oroperipatus*	1?	2	00001	0	0	1	-001-1011000100100-00?11100?10-000-0----4--0-0-011000-0--1-0------0?--0---	-	00-0-0-0-----
Onychophora *Euperipatoides*	11	2	00001	0	0	1	-001-101100?100100-00?11100010-000-0----4--0-0-011000-0--1-0------0?--0---	-	00-0-0-0-----
Tardigrada *Macrobiotus*	0?{01}		00001	?	?	1	000?-10130010-00?0-0??01000?00-000?0----0----0-010000-0--1-0------0?--0---	-	00-0-0-0-----
Chilopoda *Craterostigmus*	??	?	?????{12}?			0	-?11021101??111001000?01100?00?03001010-2--0-0-010001000-0-00000?2--?10-1	1	0111-101-0000
Chilopoda *Schizoribautia*	??	?	?????{12}?			1	-011121101??110001000?01100?00103001010-0----0-010001000-0-00000102--?10-0	1	0100-101-0000
Chilopoda *Mecistocephalus*	??	?	?????{12}?			1	-011121101??110001000?01100?00103001010-0----0-010001000-0-00000102--?10-0	1	0100-101-0000
Chilopoda *Lithobius*	??	?	??0?1{12}?			0	-011021101l?111001000?01100?00103001010-2--0-0-010001000-0-00000002--?10-1	1	0111-101-0000
Chilopoda *Allothereua*	0?	2	00001{12}0			0	-011021101l?111001001?01110000103001000-2-00-0-010001000-0-00000002--?10-1	1	0101-101-0000
Chilopoda *Cormocephalus*	01	2	00001	2	0	1	-011021101??110001000?01100000103001010-2--0-0-010001000-0-00000002--?10-1	1	0111-101-0000
Symphyla *Hanseniella*	0?	1	00001	1	3	0	-011021101O?111001000?01100000003001000-0----0-110001000-0-00000002--?11-0	1	0110-2-1-011-
Pauropoda Pauropodinae	0?	1	00101	1	3	0	-111021101??11100100??01000000?03001000-0----0-110001000-0-00000022--?10-0	1	0110-2-1-001-
Diplopoda *Epicyliosoma*	0?	1	00101	1	3	0	-111021101?111001000?01100000003001000-2--0-0-010001000-0-00010002--011-0	1	0110-2-1-001-
Diplopoda *Unixenus*	0?	1	00101{12}3			0	-111021101l?11100100??01100000003001000-2--0-0-110001000-0-00010?2--?11-0	1	0110-2-1-0000
Diplura *Campodea*	0?	2	00101	2	3	1	-011021l?1??11000210??01100?00003001000-0----0-01000101000-00000002--?1000	1	10000111-0100
Protura *Nipponentomon*	??	?	?????	?	?	0	-?11021101??11100210??01100?01013001000-0----0-01000101010-0------2--?1000	1	12010111-0100
Collembola *Archisotoma*	0?	1	00101	2	3	0	-011021101??111000-00?01100?01113001000130010100100010101O-00000022--11000	1	12010111-0100
Zygentoma *Tricholepidion*	0?	2	02101	2	4	1	-011021111?110002000?01100101103001000130210300100010000O-00001012--11010	1	21001121-0100
Archaeognatha *Allomachilis*	??	?	?????{12}4			1	-011021111??11000200??01100?01?03001000131210300100010000O-00001012--?1000	1	21000121-0101
Archaeognatha Petrobiinae	0?	2	01101	2	4	1	-011021111??110002000?01100?01?03001000131210300100010000O-00001012--?1000	1	21000121-0101
Ephemeroptera *Atalophlebia*	00	2	02?01	2	4	1	-011021111111110002000101100101103001000130210300100010000O-00001012--11010	1	21001121-0100
Cephalocarida *Hutchinsoniella*	??	?	?????	0	?	0	1011021101??120000-0??01100?00?01001000-0----0-010011101-0-000000?100?10-0	2	00-0-0-101000
Remipedia *Lasionectes*	??	?	?????	0	?	0	1?11021101??120000-01?011?0?00?01001000-0----0-010011101-0-000000?10??10-0{12}		00-0-0-111000
Mystacocarida *Derocheilocaris*	??	?	?????	0	?	0	1011021101??120000-00?01100?00?01001?00-0---010010011101-0-000000?100?10-0	0	00-0-0-111000
Leptostraca *Nebalia*	0?	2	0?011	0	?	0	1011021101l?120000-1??01120?00?0100110003011-0-010011101-0-010000011-?10-0	0	00-0-0-102000
Notostraca *Triops*	??	?	?????	0	?	0	1011021121O?120000-10?01100100?0100100003001110010011101-0-101000?111?10-0	2	00-0-0-10-01-
Anostraca *Branchinella 1*	0?	1	00001	0	1	0	1011021101O?120000-10?01100100001001001030011300100111O1-0-101000?111010-0	2	00-0-0-10-01-
Anostraca *Branchinella 3*	0?	1	00001	0	1	0	1011021101O?120000-10?01100100001001001030011300100111O1-0-101000?111010-0	2	00-0-0-10-01-
Stomatopoda *Kempina*	00	2	00011	0	1	0	1011021101111120000-11101120100003001100030211300100111O1-0-010000010?010-0	0	00-0-0-102000
Xiphosura *Limulus*	0?	2	00101	0	2	1	0011021121011100000-01?01110?00002101--0-3000020010011000-000----0-31-?0---	0	00-0-0-0-0000
Pycnogonida *Ascorhynchus*	0?	1	0000?	0	2	(01)	0011021121010-0000-01?01100?00?02001--0-0---010010000-0?-1-0------31-?0---	0	00-0-0-0-0000
Opiliones *Equitius*	0?	2	00001	0	?	1	-011021121O?110000-0??011?1?00102101--0-0---021010001000-010------31-?0---	0	00-0-0-0-0000
Scorpiones *Lychas*	0?	2	00001	0	?	1	-011021121O?110010-01?01111100102101--0-1--0021010001000-010------31-?0---	0	00-0-0-0-0000
Araneae Atrax	0?	2	00001	0	2	1	-011021121O?110010-01?01111100102101--0-1--0021010001000-000------31-00---	0	00-0-0-0-0000

Character Number (10)	10	11	12	13	14	15	16	17	18	19	20	21
Character Number	01234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901											
Annelida *Paralepidonotus*	----------------0----000-0000--0-1000-0-000--------00---00----0-------------00-0000-0-00?00-0-00000000000---0000?											
Annelida *Lumbrineris*	----------------0----000-0000--0-1000-0-000--------00---00----0-------------00-0000-0-00?00-0-00000000000---0000?											
Onychophora *Tasmanipatus*	---------------1----000-0010--00011000-000--------00---00----6---000----0--00-0000-0-10000-0000220001000001010??											
Onychophora *Oroperipatus*	---------------1----000-0010--00011000-000--------00---00----6---000----0--00-0000-0-10000-0000?200010000001010??											
Onychophora *Euperipatoides*	---------------1----000-0010--00011000-000--------00---00----6---000----0--00-0000-0-10000-0000220001000001010??											
Tardigrada *Macrobiotus*	---------------0--0?110-0000--0-001100-0000-------00---00----0---000----?--00-0000-0-1000?-00000??00000001?0000?											
Chilopoda *Craterostigmus*	001?1--0211111101111110000?00-00001100-0000011101011020001110100000000???10000-0010-0-1000?1101??????????0??10???											
Chilopoda *Schizoribautia*	00111--1211101101111110000100-00001100-0000120111111020001110111000000???10000-002100-1000?1101012100011100??100??											
Chilopoda *Mecistocephalus*	00111--1211101101111110000100-00001100-0000120111111020001110111000000???10000-002100-1000?1101012100011100??100??											
Chilopoda *Lithobius*	00111--0100001100010110000100-00001100-0000001100011020001110100000000???11000-000010-1000?1001112100011000010000?											
Chilopoda *Allothereua*	00110--0000001000010110000100-00001100-0000001100011020001110400-0000???11000-000010-1000010001?2100011100??000??											
Chilopoda *Cormocephalus*	00111--1211111101111110000100-00001100-0000111111011020001110110000000???11000-0011-0-1000011011121000110??100??											
Symphyla *Hanseniella*	001000-00-0000000010110000100-00001100-0000000100011020110110103---0000???00000-0000-0-10501-0001120000000020001??											
Pauropoda Pauropodinae	013----0--000000001?110000?00-00001100-00000000-0-110200001102---1000???11000-0000-0-11501-0000220001000200002?											
Diplopoda *Epicyliosoma*	013----0--0?00000???110000100-00001100-0100000100011021000110 2---1000???11000-0000-0-11501-000012000--010-000001											
Diplopoda *Unixenus*	013----0--0?0000001?110000100-00001100-0100000100011121000110 2---1000???11000-0000-0-11501-000013-00--010200002?											
Diplura *Campodea*	101000?00-0?0000-?1?110001100-00001100-1000000100011020110110100200 01???00010-1000-001000?0000003-0120000100 01??											
Protura *Nipponentomon*	101?01000-000000?0??110000000-00001100-1000000100011030200110 0---0001???10010-0000-001000?00000?31000-0101000???											
Collembola *Archisotoma*	101001?00-0000001?1?110010100-00001100-1000000100011040200110 0---0001???10000-0000-0010002000000020010-01000001??											
Zygentoma *Tricholepidion*	101000000-0?00000?1?110021100-00001100-1001000100011010010110110000001???01111-1000-1110012001003211120001100002?											
Archaeognatha *Allomachilis*	101?00100-0?00000?1?111021100-00001100-1001000100011010110110100100 01???01111-1000-101001?0010????????????1100002?											
Archaeognatha Petrobiinae	101000100-0?00000?1?111021100-00001100-1001000100011010110110100100 01???01111-1000-101001?0010032111200011000002?											
Ephemeroptera *Atalophlebia*	101000000-0?00000???110021100-00001100-1001000100011010010110110000001???01111-1000-1110012001000200 12-0111000011											
Cephalocarida *Hutchinsoniella*	000?0--00---00?0?-1?110020?00-00001111000010000---1100000??010---010?????0?0000100-0-1020?-000003-0000000100002?											
Remipedia *Lasionectes*	001?0--00---00?0?-1?110010?00-00001111?000010000---1100000??010---000?????0?0000100-0-1012?-000003-0000000??0001?											
Mystacocarida *Derocheilocaris*	001?0--00---00?0?-1?110000?00-00001111000010000---1100000??010---000?????0?0000100-0-1030?-000003-0000000100002?											
Leptostraca *Nebalia*	00100--00---00?0?-1?110120?00-00001111100010000---1100000??010---010???????0010100-0-10610-000022000--010?0000??											
Notostraca *Triops*	002?0--00---00?0?-1?110020100-00001111000010000---1100000??010---011?????0?0000100-0-10800-000022000--01010000??											
Anostraca *Branchinella 1*	00200--00---00?0?-1?110020100-00001111000010000---1100000??010---011?????0?0000100-0-10700-000022000--0100000011											
Anostraca *Branchinella 3*	00200--00---00?0?-1?110020100-00001111000010000---1100000??010---011?????0?0000100-0-10700-000022000--0100000011											
Stomatopoda *Kempina*	00100--00---00?0?-1?110120100-00001111100010000---1100000??010---000?????0?0010000-0-10610-00000??00--010?000011											
Xiphosura *Limulus*	-0000--00---0000?-0?110010011010001110-00110000---1100000000000---000?00000?00-0000-0-1040?-000001000000020100000											
Pycnogonida *Ascorhynchus*	-0000--00---0000?-??110010011-00001100-00000000---000000000000---000????11?00-0000-0-10900-000020000000001000??											
Opiliones *Equitius*	-0000--0----0000?-0?110010011101001100-00100000---111-00001005---000?11101?00-0000-0-1040?-0000020000-010010002?											
Scorpiones *Lychas*	-0000--0----0000?-0?110010011121001100-00110000---111-00001000---000?11101?00-0000-0-10400-000001000000020100002?											
Araneae *Atrax*	-0000--0----0000?-0?110010011021001100-00100000---111-00001005---000?00001?00-0000-0-10400-0000?10000-010010002?											

Note. See text for characters and states.

(5) Atelocerata (= Myriapoda + Hexapoda) is favored over Pancrustacea (= Crustacea + Hexapoda), though one additional step collapses the atelocerate clade.

(6) Myriapoda (= Chilopoda + Progoneata) is favored over Labiophora (= Progoneata + Hexapoda), but Bremer support for Myriapoda is weak (one step). Dohle (1997) remarked that no positive characters have been proposed in support of myriapod monophyly (as opposed to absence/loss characters like absence of median eyes, paratergites, and scolopidia). Manton's (1964) characterization of mandibular movements, in particular the so called swinging tentorium (89:1), provides a "presence" apomorphy, though only with accelerated transformation. A monolayered acrosomal complex in the sperm (195:1) is a myriapod synapomorphy under all optimizations. With delayed transformation, Tömösváry organs (26:1), a single pair of Malpighian tubules (29:1), and ectodermally derived anterior tentorial arms (88:1) are myriapod apomorphies, whereas accelerated transformation regards them as basal apomorphies for Atelocerata. We are reluctant to accept the absence of neuroblasts as a myriapod apomorphy (39:0) until the validity of purported neuroblasts in chelicerates is confirmed. The coding strategy employed here does not optimize stemmata with a multilayered rhabdom (52:2) as a myriapod synapomorphy, though this is affected by blindness in pauropods and symphylans;

(7) Within the Hexapoda, Diplura is sister group to Insecta (cf. Kukalová-Peck, 1991; Kraus, 1997) rather than sister group to Ellipura, i.e., "Entognatha" is a paraphyletic group.

Simultaneous Analysis

Analysis of the morphology, H3, and U2 data with equal weighting yields two trees of 1916 steps (see Fig. 5 for consensus, Fig. 6 for the alternative resolutions within Crustacea and Hexapoda). Taxonomic congruence with the morphological trees is high, and disagreement is limited to the following taxa:

(1) Pycnogonids are sister group to Euchelicerata with the combined data, rather than sister to Euarthropoda. Four steps are needed to collapse the pycnogonid/euchelicerate clade. This relationship of pycnogonids and euchelicerates is expected to be strengthened by the addition of fossil taxa as terminals.

TABLE 2
Apomorphies for Branches on Fig. 4, with Delayed Transformation

Node 1 to node 2: **4**, 1 ⇔0; **8**, 0 ⇔1; **11**, 0 ⇔1; **15**, 0 ⇔1; **17**, 0 ⇔1; **19**, 0 ⇔1; **35**, 0 ⇔1; **60**, 0 ⇔1; **62**, 1 ⇔0; **69**, 0 ⇔1; **132**, 1 ⇔0; **134**, 0 ⇔1; **185**, 0 ⇔1
Node 2 to node 3: **23**, 0⇒1; **120**, 0⇒1; **121**, 0⇒1; **135**, 0⇒1
Node 2 to node 4: **1**, 0⇒1; **3**, 0→2; **24**, 0⇒1; **27**, 0⇒1; **34**, 0⇒1; **36**, 0→1; **40**, 0⇒1; **52**, 0⇒4; **61**, 0⇒1; **115**, 0⇒1; **126**, 0⇒1; **133**, 0⇒1; **161**, 0⇒6; **196**, 0→2; **200**, 0⇒1; **208**, 0⇒1
Node 3 to node 5: **10**, 0→2; **14**, 0⇒1; **17**, 1⇒2; **18**, 0⇒1; **20**, 1→2; **21**, 0⇒1; **36**, 0→1; **44**, 0⇒2; **46**, 1→0; **47**, 0⇒1; **78**, 0⇒3
Node 3 to Tardigrada *Macrobiotus*: **20**, 1→3; **205**, 0⇒1
Node 4 to node 6: **195**, 0→2
Node 5 to node 7: **3**, 0→2; **24**, 0⇒1; **25**, 0→1; **39**, 0→1; **64**, 0⇒1; **69**, 1⇒0; **150**, 0⇒1; **151**, 0⇒1
Node 5 to Pycnogonida *Ascorhynchus*: **3**, 0→1; **32**, 0→1; **57**, 0⇒1; **124**, 0→1; **127**, 0→1; **172**, 0→1; **173**, 0→1; **187**, 0⇒9; **195**, 0⇒2
Node 7 to node 11: **11**, 1⇒0; **20**, 2⇒0; **82**, 0⇒1; **94**, 0⇒1; **102**, 0⇒1; **118**, 0⇒1; **126**, 0⇒1; **128**, 1⇒0; **206**, 1⇒0; **211**, 0⇒1
Node 7 to node 8: **32**, 0→1; **37**, 0⇒1; **45**, 0⇒1; **57**, 0⇒2; **124**, 0→1; **127**, 0→1; **141**, 0⇒1; **187**, 0⇒4; **196**, 0→1
Node 8 to node 9: **38**, 0⇒1; **42**, 0⇒1; **58**, 0⇒1; **131**, 0⇒1; **152**, 0⇒1; **158**, 0→1; **173**, 0→1
Node 8 to Xiphosura *Limulus*: **6**, 0⇒1; **52**, 0→3; **63**, 0⇒1; **130**, 0→1; **136**, 0⇒1; **142**, 0⇒1; **204**, 0⇒2
Node 9 to Araneae *Atrax*: **28**, 0→1; **52**, 0→1; **130**, 0→2; **161**, 0→5; **203**, 0→1
Node 9 to node 10: **70**, 0⇒1; **129**, 0⇒1; **169**, 0⇒1; **170**, 0⇒1; **171**, 0⇒1
Node 10 to Scorpiones *Lychas*: **28**, 0→1; **52**, 0→1; **130**, 0→2; **142**, 0⇒1; **204**, 0⇒2
Node 10 to Opiliones *Equitius*: **161**, 0→5; **196**, 1⇒2; **203**, 0→1
Node 11 to 12: **12**, 0→1; **25**, 1⇒2; **44**, 2→1; **63**, 0⇒1; **65**, 0⇒1; **67**, 0⇒1; **78**, 3→1; **79**, 1→0; **96**, 0⇒1; **136**, 0⇒1; **137**, 0⇒1; **142**, 0⇒1; **160**, 0⇒1; **179**, 0⇒1; **196**, 0→3; **205**, 0→1
Node 11 to node 19: **9**, 0⇒2; **10**, 2→3; **22**, 0→1; **44**, 2→3; **78**, 3→2; **86**, 0⇒1; **92**, 0⇒1; **146**, 0⇒1; **153**, 0⇒2; **158**, 0→1; **159**, 0⇒1; **196**, 0→2
Node 12 to Mystacocarida *Derocheilocaris*: **57**, 0⇒1; **187**, 0→3
Node 12 to node 13: **86**, 0⇒2; **210**, 0→1
Node 13 to node 14: **95**, 1⇒0; **124**, 0→2; **166**, 0⇒1
Node 13 to Remipedia *Lasionectes*: **32**, 0→1; **124**, 0→1; **187**, 0→1; **188**, 0⇒2
Node 14 to Cephalocarida *Hutchinsoniella*: **102**, 1⇒0; **187**, 0→2
Node 14 to node 15: **10**, 2→1; **31**, 0⇒1; **52**, 0⇒3; **55**, 0→1; **56**, 0→1; **196**, 3⇒2; **203**, 0⇒1
Node 15 to node 16: **7**, 0⇒1; **22**, 0→1; **37**, 0⇒2; **48**, 0⇒1; **54**, 0⇒1; **72**, 0⇒1; **86**, 2⇒0; **96**, 1→2; **123**, 0⇒1; **138**, 0⇒1; **177**, 0⇒1; **187**, 0→6; **188**, 0⇒1
Node 15 to node 17: **71**, 0⇒1; **73**, 0⇒1; **79**, 0→1; **80**, 0→1; **98**, 0⇒1; **102**, 1⇒2; **167**, 0⇒1; **195**, 0→2
Node 16 to Leptostraca *Nebalia*: **79**, 0→1; **195**, 0→2
Node 16 to Stomatopoda *Kempina*: **2**, 1→0; **32**, 0→1; **44**, 1⇒3; **54**, 1⇒2; **57**, 0→3; **166**, 1⇒0; **179**, 1⇒0
Node 17 to node 18: **3**, 2→1; **50**, 0⇒1; **57**, 0→3; **187**, 0→7; **205**, 1⇒0
Node 17 to Notostraca *Triops*: **20**, 0⇒2; **57**, 0→1; **187**, 0→8
Node 19 to node 20: **6**, 0⇒1; **51**, 0→1; **55**, 0→1; **81**, 0⇒1; **87**, 0⇒1; **93**, 0→1; **97**, 0⇒1; **100**, 0⇒1; **139**, 0⇒1; **155**, 0⇒1; **168**, 0→1; **189**, 0⇒2
Node 19 to node 26: **26**, 0→1; **29**, 0→1; **39**, 1⇒0; **88**, 0→1; **195**, 0⇒1
Node 20 to node 21: **26**, 0→1; **41**, 0→1; **43**, 0⇒1; **66**, 0→1; **68**, 0→1; **88**, 0⇒2; **90**, 0⇒1; **105**, 0⇒1; **155**, 1⇒2; **172**, 0→1; **203**, 0⇒1

TABLE 2—*Continued*

Node 20 to node 22: **11**, 0⇒1; **29**, 0→2; **125**, 0⇒1; **156**, 0⇒1; **161**, 0→1; **175**, 0→1; **178**, 0⇒1; **199**, 0→1; **200**, 0⇒2; **205**, 0→1
Node 21 to Collembola *Archisotoma*: **3**, 2→1; **42**, 0⇒1; **52**, 0⇒3; **57**, 0⇒1; **77**, 0→2; **116**, 0→1; **124**, 0⇒1; **153**, 2→4; **199**, 0→1; **209**, 0→1
Node 21 to Protura *Nipponentomon*: **29**, 0→2; **30**, 0→1; **126**, 1⇒0; **153**, 2→3; **175**, 0→1; **196**, 2→3; **197**, 0→1; **205**, 0→1
Node 22 to Diplura *Campodea*: **30**, 0→1; **66**, 0→1; **164**, 0⇒2; **196**, 2→3; **209**, 0→1
Node 22 to node 23: **5**, 0⇒1; **10**, 3⇒4; **20**, 0→1; **41**, 0→1; **52**, 0⇒3; **54**, 0→2; **57**, 0⇒3; **75**, 0⇒1; **77**, 0⇒1; **87**, 1⇒2; **88**, 0→1; **93**, 1⇒2; **124**, 0⇒2; **142**, 0⇒1; **153**, 2⇒1; **173**, 0→1; **174**, 0⇒1; **176**, 0⇒1; **183**, 0⇒1; **188**, 0⇒1; **192**, 0⇒1; **204**, 0⇒1
Node 23 to node 24: **5**, 1⇒2; **42**, 0→1; **84**, 0⇒1; **91**, 0⇒1; **155**, 1⇒0; **162**, 0⇒1; **184**, 0⇒1
Node 23 to node 25: **53**, 0⇒1; **99**, 0⇒1; **106**, 0⇒1; **122**, 0⇒1; **164**, 0⇒1
Node 24 to Ephemeroptera *Atalophlebia*: **2**, 1→0; **203**, 0⇒1; **210**, 0→1
Node 24 to Zygentoma *Tricholepidion*: **195**, 0→3; **197**, 0→1; **198**, 0→1
Node 25 to Archaeognatha Petrobiinae: **195**, 0→3; **197**, 0→1; **198**, 0→1
Node 26 to node 27: **3**, 2→1; **9**, 2⇒1; **59**, 0⇒1; **89**, 0→1; **92**, 1⇒2; **98**, 0⇒1; **187**, 0⇒5; **189**, 0⇒1; **205**, 0→2
Node 26 to node 30: **10**, 3⇒0; **42**, 0⇒1; **52**, 0⇒2; **85**, 0⇒1; **90**, 0⇒1; **103**, 0⇒1; **113**, 0⇒1; **145**, 0⇒1; **157**, 0⇒1; **172**, 0→1; **190**, 0→1; **194**, 0→1; **197**, 0→1; **201**, 0→1; **202**, 0⇒1
Node 27 to node 28: **6**, 0⇒1; **13**, 0⇒1; **101**, 0⇒1; **102**, 1⇒3; **161**, 0→2; **165**, 0⇒1; **172**, 0→1; **173**, 0→1; **186**, 0⇒1
Node 27 to Symphyla *Hanseniella*: **22**, 1⇒0; **83**, 0→1; **97**, 0⇒1; **155**, 0⇒1; **156**, 0⇒1; **161**, 0→3; **194**, 0→1; **209**, 0⇒1
Node 28 to node 29: **52**, 0⇒2; **74**, 0⇒1; **83**, 0→1; **140**, 0⇒1; **154**, 0⇒1; **203**, 0⇒1
Node 28 to Pauropoda Pauropodinae: **36**, 1⇒0; **77**, 0⇒2; **146**, 1⇒0; **195**, 1⇒2; **201**, 0→1
Node 29 to Diplopoda *Epicyliosoma*: **59**, 1⇒0
Node 29 to Diplopoda *Unixenus*: **98**, 1⇒0; **152**, 0⇒1; **196**, 2⇒3
Node 30 to Chilopoda *Allothereua*: **32**, 0⇒1; **37**, 0⇒1; **161**, 0→4; **173**, 0→1
Node 30 to node 31: **49**, 0⇒1; **89**, 0→1; **104**, 0⇒1; **108**, 0⇒1; **114**, 0⇒1; **161**, 0→1; **193**, 0⇒1; **207**, 0⇒1
Node 31 to Chilopoda *Lithobius*: **173**, 0→1
Node 31 to node 32: **108**, 1⇒2; **109**, 0⇒1; **110**, 0⇒1; **111**, 0⇒1; **116**, 0⇒1; **117**, 0⇒1; **119**, 0⇒1; **144**, 0⇒1; **148**, 0⇒1; **180**, 0⇒1; **191**, 0⇒1
Node 32 to Chilopoda *Craterostigmus*: **112**, 0→1
Node 32 to node 33: **11**, 0⇒1; **26**, 1⇒0; **107**, 0⇒1; **143**, 0⇒1; **147**, 0⇒1; **162**, 0⇒1; **181**, 0⇒1
Node 33 to Chilopoda *Cormocephalus*: **112**, 0→1; **173**, 0→1
Node 33 to node 34: **16**, 0⇒1; **52**, 2⇒0; **76**, 0⇒1; **85**, 1⇒0; **89**, 1⇒0; **90**, 1⇒0; **144**, 1⇒2; **145**, 1⇒0; **149**, 0⇒1; **163**, 0⇒1; **180**, 1⇒2; **182**, 1→0; **194**, 1⇒0

Note. Branch: **character**, change. See text for character numbers. Open arrows indicate unambiguous transitions. Single-lined arrows indicate transitions assigned to a branch in some, but not all, optimizations.

Notably, the Devonian pycnogonid *Palaeoisopus* (Bergström *et al.*, 1980) possesses some apparent apomorphies for Chelicerata (styliform telson; anus situated ventrally at base of telson) lacking in extant pycnogonids.

(2) Ingroup resolution for Euchelicerata differs, with opilionids rather than xiphosurids identified as the basal branch. The absence of H3 sequence for *Limulus* may be a factor influencing this result.

(3) With the combined data, cephalocarids either are the sister group of the remaining crustaceans or are the sister group of the Branchiopoda. Combination resolves remipedes as more closely related to mystacocarids than to the other crustacean exemplars. This result, albeit weakly supported (Bremer support 1), conforms to a hypothesis advanced by Boxshall (1997) that remipedes are closely allied to Maxillopoda.

(4) Labiophora rather than Myriapoda is favored in the combined analysis, though support is weak (Bremer support 1).

(5) Protura ally with Insecta rather than other "Entognatha," and Ellipura is rejected. Support for Hexapoda is weakened by the sequence characters. Insect monophyly is endorsed, though support is decreased (Bremer support 4) relative to the morphological data on their own (Bremer support 17). A proturan–insect group is the most strongly supported clade in Hexapoda when the data are combined.

Combination provides unambiguous resolution of relationships between the onychophorans, with the peripatopsids united to the exclusion of the peripatid. This result is significant because peripatopsid monophyly is difficult to defend on morphological grounds. Since the main distinguishing features of the families (Reid, 1996) involve characters that are inapplicable to outgroups (alternative states for onychophoran autapomorphies), molecular synapomorphies are valuable. Simultaneous analysis provides strong support for Peripatopsidae (Bremer support of 9).

Taxa for which support is increased by combination are (with Bremer support based on morphology alone versus combined) Onychophora (13 to 18), Crustacea (8 to 13), Malacostraca (8 to 14), Branchiopoda (5 to 15), Atelocerata (1 to 3), Chilopoda (9 to 13), Pleurostigmophora (5 to 7), Epimorpha (6 to 7), Geophilomorpha (12 to 19), Dignatha (5 to 6), and Dicondylia (3 to 4). Concerning major arthropod clades, the increased support for the monophyly of Crustacea is most noteworthy.

Table 3 summarizes the results of the sensitivity analysis, while Fig. 7 depicts components that are resolved in all weighting regimes for transitions and transversions and third-codon positions as specified above.

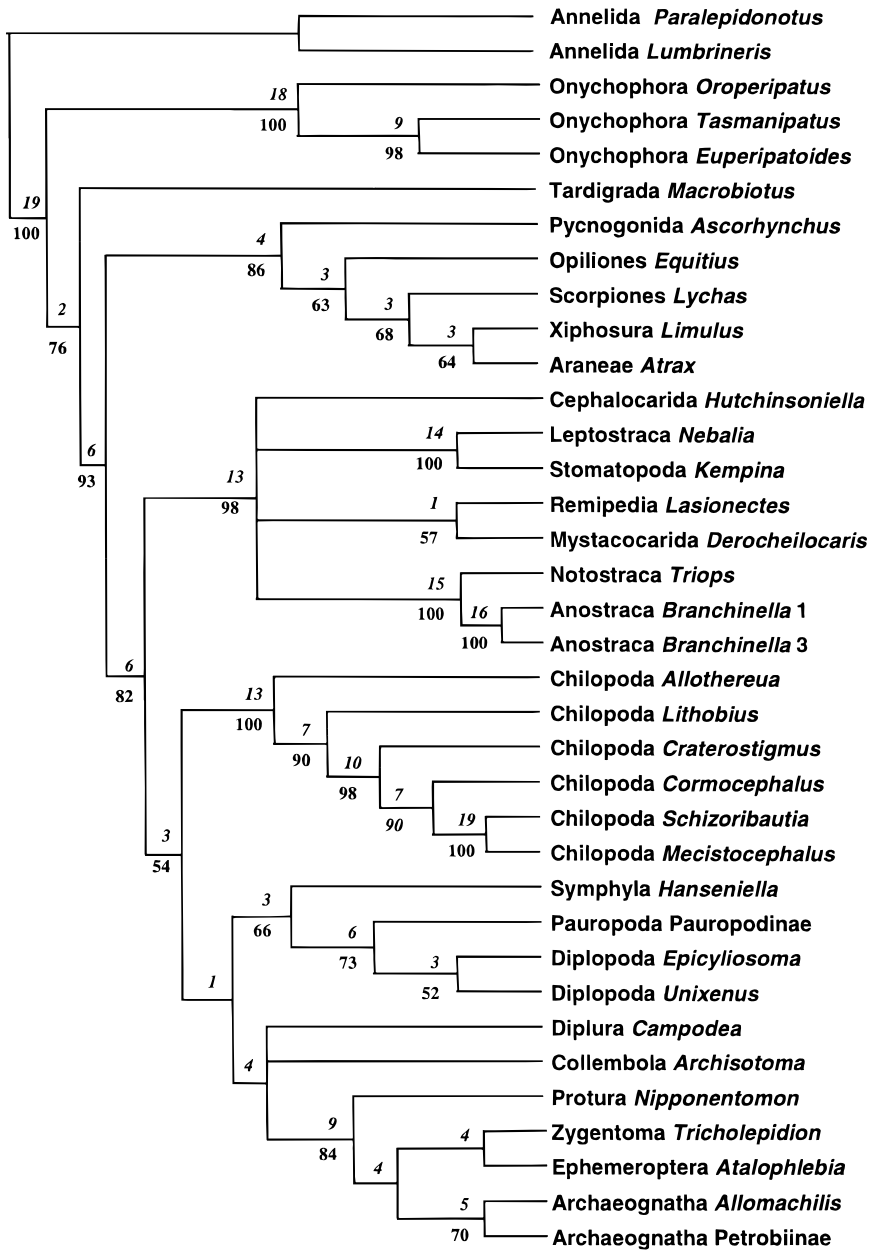


FIG. 5. Strict consensus of two shortest cladograms based on simultaneous analysis of all data (morphology, histone H3, and U2) with equal character weights. Length 1916 steps, CI excluding uninformative characters 0.34, RI 0.52. Bremer support is shown in italics above each branch and bootstrap support below each branch (missing values for the latter are less than 50%).

Only 35 unique cladograms were found in all of the weighting experiments, indicating that many major groups (Onychophora, Chelicerata, Crustacea, Progoneata, Chilopoda, Hexapoda, Insecta) withstand testing in a simultaneous analysis regime. Ingroup relationships for Progoneata and Chilopoda are identical to those in morphological trees as well as to equally weighted simultaneous analysis trees. Mandibulata is supported in all analyses, but Atelocerata and Myriapoda/Labiophora are rejected in some weighting regimes.

Maximum congruence between each partition as measured by ILD values is approached with a transition-to-transversion ratio of 2.5:1 and the third codon

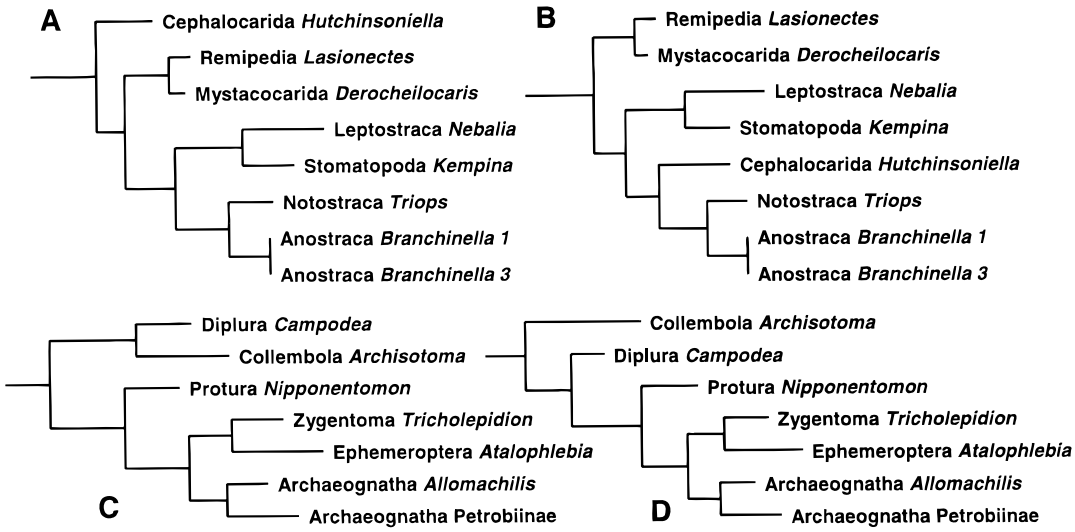


FIG. 6. Alternative shortest resolutions for Crustacea and Hexapoda based on simultaneous analysis of all data (morphology, histone H3, and U2) with equal character weights. A and C are parts of one cladogram, B and D parts of the other.

in H3 downweighted to 0.18 (Table 3). The consensus of the two most parsimonious trees with minimal incongruence (ILD 0.0853) is shown in Fig. 8. Analyses with transition-to-transversion ratios of 2:1 to 2.5:1 and third codon weights of 0.12–0.25 all yield the same two most parsimonious trees, identical to those producing Fig. 8.

Comparing minimal ILD trees with those produced without weighting, we note only minor differences in topology. The minimal ILD trees group cephalocarids with remipedes or mystacocarids, rather than exclusively grouping the latter two. This topology, with Crustacea having a basal split into one clade that includes cephalocarids, remipedes, and mystacocarids and another that includes branchiopods and malacostracans, is similar to Wilson's (Fig. 1 in 1992) phylogeny. The other difference between minimal ILD and equally weighted trees is a resolution within Hexapoda in the former that is more congruent with morphological signal (identical to Fig. 4). In the minimal ILD trees, Ellipura is sister to Diplura + Insecta, although this component is weakly supported.

If transitions and the H3 third codons are both weighted zero (thus dismissing the majority of the molecular evidence), the ILD is slightly less than that obtained by the equally weighted data set. The three trees obtained, however, are substantially different to the unweighted analysis; they are, hardly surprisingly, similar to the morphology trees. Still, the inclusion of even this reduced set of sequence characters has some important phylogenetic effects, moving the Pycnogonida to sister group of the chelicerates (with ingroup resolution for Eucheliceratа as in the morphology-only trees, with Xiphosura basal). Other differences from the morphology trees include the unambiguous monophyly of the Peripatopsidae and division of the crustaceans into two clades grouping cephalocarids, remipedes, and mystacocarids separately from the branchiopods and malacostracans.

DISCUSSION

Cladograms retrieved by sequence data sets, considered as individual partitions or in combination with each other, can appear anomalous if topology is evaluated without consideration of support. As noted by Colgan *et al.* (1998), anomalous nodes are weakly supported (i.e., Bremer support of 1) in the histone H3 and U2 snRNA data (Fig. 1), whereas the sequences offer stronger support for several clades that are widely recognized based on morphological data, such as Malacostraca, Branchiopoda, and Onychophora. Combining the two molecular data sets allowed more morphologically based groups to be retrieved than were found

TABLE 3
Weightings for DNA Transitions and Third-Codon Position in H3, with Resultant Lengths for Combined Analysis (C) and Each Partition (P) and ILD Values

Transversion transition ratio	Transition weight	H3 3rd codon weights	Combined analysis (C)	H3 analysis (P_2)	U2 analysis (P_3)	Individual partitions (ΣP)	ILD $(C - \Sigma P)$ / C
2.50	0.4	0.18	870.40	213.35	172.80	796.15	0.0853
2.00	0.5	0.18	906.34	230.36	188.50	828.86	0.0855
2.50	0.4	0.25	917.85	256.40	172.80	839.20	0.0857
2.00	0.5	0.25	958.00	277.25	188.50	875.75	0.0859
2.50	0.4	0.12	829.74	175.21	172.80	758.01	0.0864
2.00	0.5	0.12	862.06	188.98	188.50	787.48	0.0865
2.00	0.5	0.33	1017.04	330.29	188.50	928.79	0.0868
2.50	0.4	0.33	972.07	304.85	172.80	887.65	0.0868
4.0	0.25	0.18	816.11	186.46	148.75	745.21	0.0869
4.0	0.25	0.12	780.57	153.91	148.75	712.66	0.0870
4.0	0.25	0.25	857.56	223.94	148.75	782.69	0.0873
4.0	0.25	0.33	904.62	266.24	148.75	824.99	0.0880
1.3	0.75	0.18	995.28	270.74	226.50	907.24	0.0885
1.3	0.75	0.25	1057.31	327.25	226.50	963.75	0.0885
1.3	0.75	0.33	1128.21	391.65	226.50	1028.15	0.0887
2.0	0.50	0.50	1142.50	442.50	188.50	1041.00	0.0888
2.5	0.40	0.50	1087.30	407.70	172.80	990.50	0.0890
1.3	0.75	0.12	942.10	221.52	226.50	858.02	0.0892
1.3	0.75	0.50	1278.88	527.25	226.50	1163.75	0.0900
4.0	0.25	0.50	1004.50	354.88	148.75	913.63	0.0905
10.0	0.10	0.18	760.96	158.84	123.20	692.04	0.0906
10.0	0.10	0.12	730.91	131.43	123.20	664.63	0.0907
10.0	0.10	0.25	796.03	190.63	123.20	723.83	0.0907
4.0	0.25	0.00	709.50	86.25	148.75	645.00	0.0909
2.0	0.50	0.75	1325.50	606.12	188.50	1204.62	0.0912
2.5	0.40	0.75	1255.50	558.05	172.80	1140.85	0.0913
10.0	0.10	0.00	670.80	76.30	123.20	609.50	0.0914
1.3	0.75	0.75	1496.00	722.75	226.50	1359.25	0.0914
2.5	0.40	0.00	748.00	96.60	172.80	679.40	0.0917
2.0	0.50	1.00	1505.50	768.50	188.50	1367.00	0.0920
2.0	0.50	0.00	773.50	103.50	188.50	702.00	0.0924
∞	0.00	0.00	645.00	68.00	106.00	584.00	0.0946
1	1.00	0.75	1665.50	835.75	262.00	1507.75	0.0947
∞	0.00	0.12	697.80	115.52	106.00	631.52	0.0950
1	1.00	0.12	1021.96	252.56	262.00	924.56	0.0953
∞	0.00	0.18	724.20	139.12	106.00	655.12	0.0954
1	**1.00**	**1.00**	**1917.00**	**1061.00**	**262.00**	**1733.00**	**0.0960**
10	0.10	0.75	1044.53	406.43	123.20	939.63	0.1004
1	1.00	0.00	898.00	134.00	262.00	806.00	0.1024
∞	0.00	1.00	1082.00	443.00	106.00	959.00	0.1137

Note. Sorted according to increasing ILD. Weightings in the top part all produced the same two trees as the lowest ILD. In all cases, the morphology data set (P_1) supported the shortest tree length of 410 steps. To ease comparison, the equal weighted case is in boldface.

when each gene was analyzed in isolation (Colgan *et al.*, 1998). This emergence of signal, coupled with theoretical defense of simultaneous analysis as the obvious extension of the parsimony criterion (Nixon and Carpenter, 1996), led us to combine data from different sources. The simultaneous analysis cladograms largely express the morphological signal; this in itself can hardly be regarded as objectionable given that the homology hypotheses incorporated into the morphological data set are the results of hundreds of years of

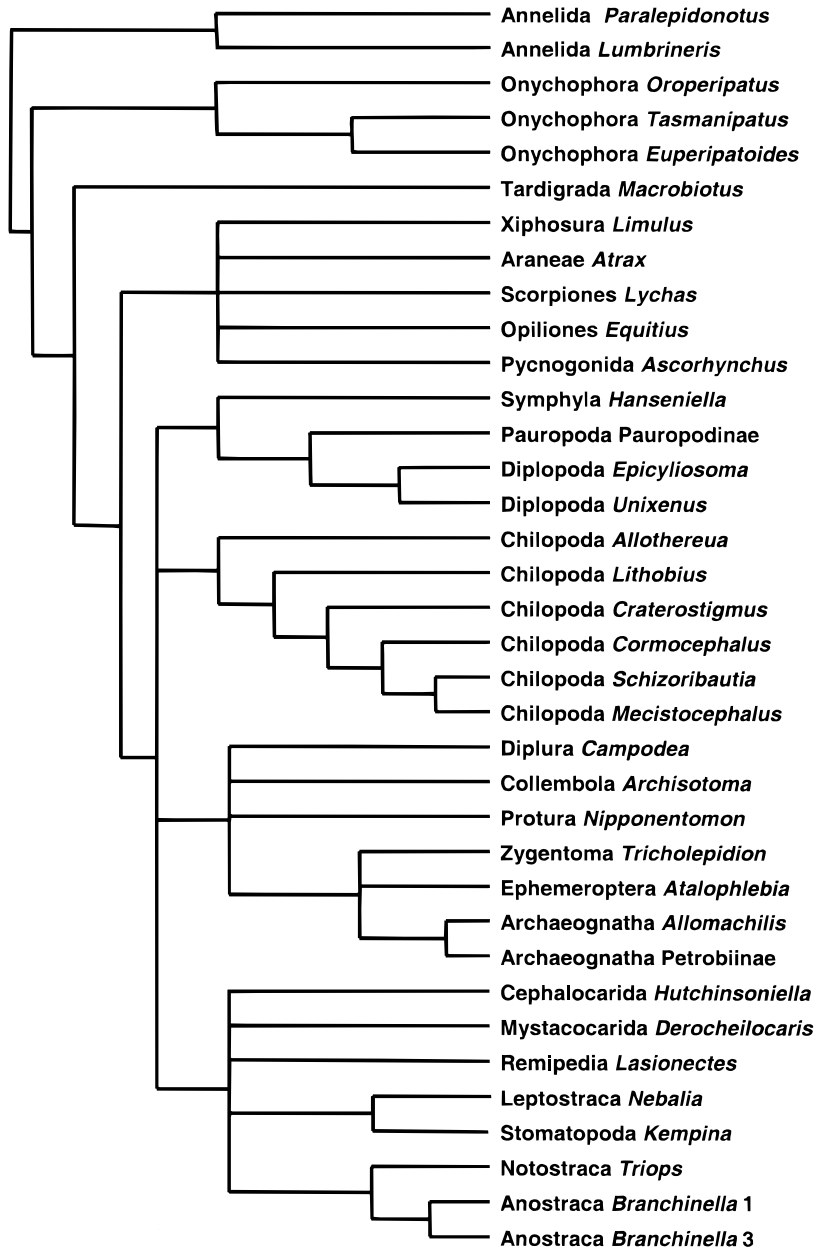


FIG. 7. Strict consensus of 35 minimum-length cladograms from simultaneous analysis under all weighting parameters in Table 3.

intensive study. Still, the addition of the sequence characters is sufficient to overturn some morphological hypotheses (e.g., pycnogonids as basal euarthropods; Myriapoda as a clade) in favor of rival schemes (pycnogonids as chelicerates; myriapods as a grade) that also have morphological support.

Advocates of the so-called conditional combination approach (Huelsenbeck *et al.*, 1996), finding significant incongruence between partitions, contend that sets of trees produced by each data set be considered in isolation, with unique explanations for their implied relationships. We observe significant incongruence between the three partitions in this study. Applying an ILD test (Farris *et al.*, 1994) with 100–1000 replicates in

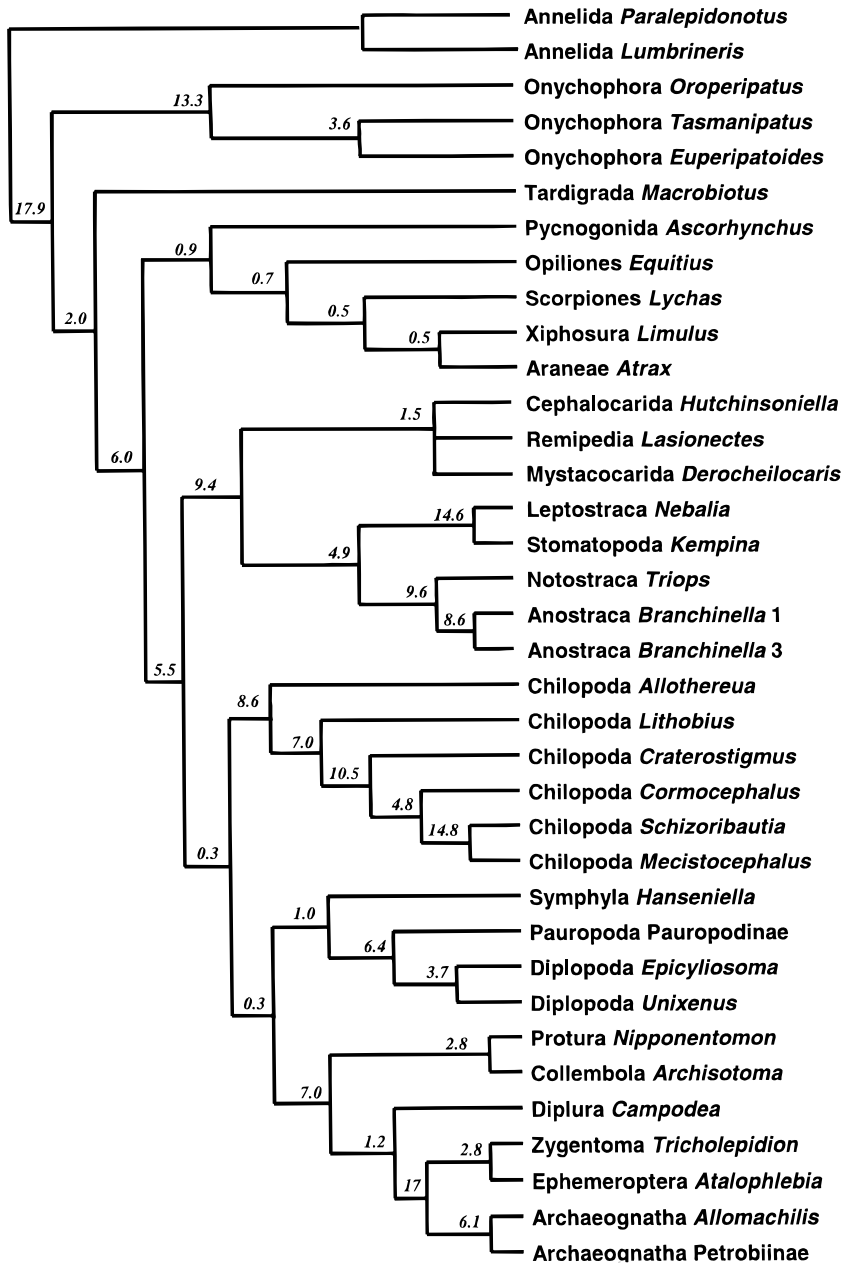


FIG. 8. Strict consensus of two shortest cladograms with minimum incongruence between morphology, H3, and U2 (lowest ILD in Table 3). Bremer support is shown at nodes.

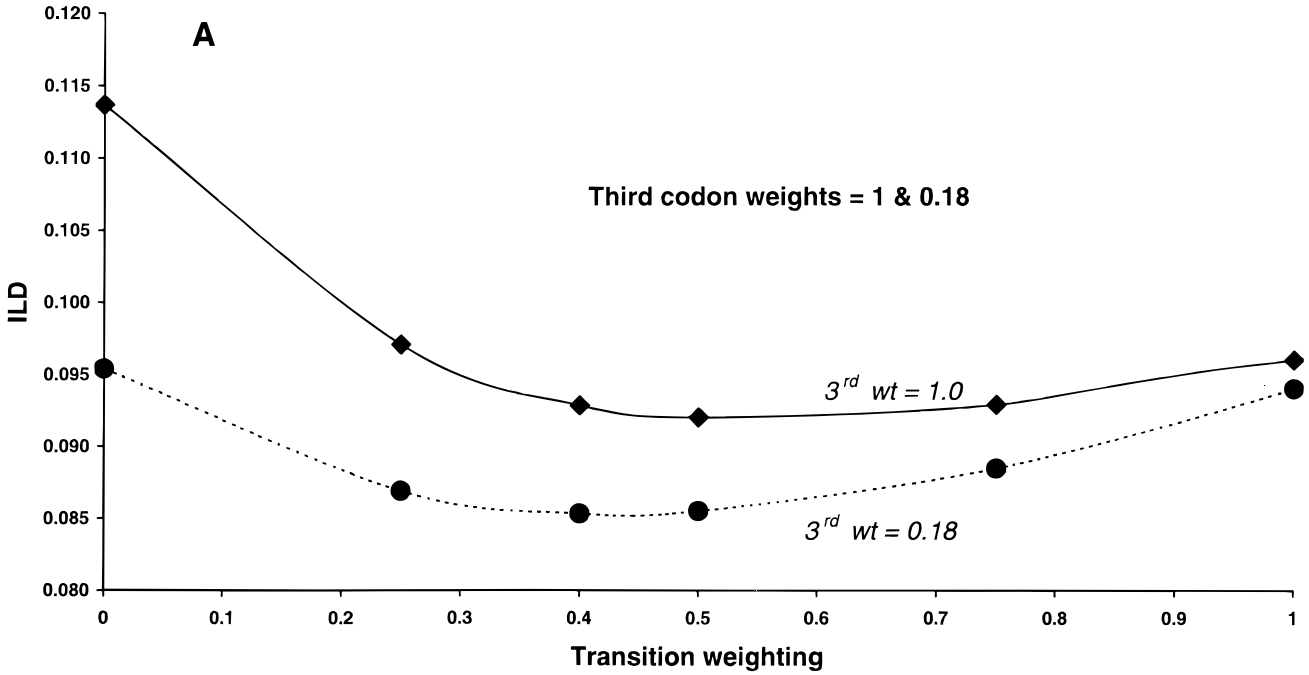
the partition homogeneity test implemented in PAUP*, each pairwise comparison of H3, U2, and morphology, as well as the three-way comparison, is significantly incongruent ($P < 0.01$) even under the minimally incongruent weights for the sequence characters defined in Table 3. An alternative to simultaneous analysis, a consensus of the trees from each of the three partitions, yields but a single component (the leptostracan and stomatopod united as Malacostraca). This underwhelming result is obviously a less insightful response to the question "What do the data at hand say about arthropod phylogeny?" than the cladograms in Figs. 4–8.

If differential weighting is used at all, minimizing

partition incongruence provides a route to selecting optimal weights under a parsimony criterion (Wheeler and Hayashi, 1998). Deleting, or changing the weights of one of the data partitions without adjusting the others can substantially increase incongruence between the partitions (see Figs. 9A and 9B). Deleting *all* allegedly suspect data could be construed as an alternative to equal weighting of consistent and inconsistent characters alike, on the grounds that the ILD is decreased. This procedure, however, is retrogressive because fewer data are being used rather than more; the very data that we wish to explain are being discarded. Downweighting third codons in particular has been questioned as appropriate for the problem it purports to solve (i.e., more homoplasy) because synapomorphic characters are downweighted along with homoplastic ones (Allard *et al.*, 1999; Källersjö *et al.*, 1999). A philosophy that maximizes the number of tests of phylogenetic hypotheses requires that more than just the ILD be considered when examining congruence between data partitions. If *character* congruence is given precedence over partition congruence, one returns to the stance of Allard and Carpenter (1996) that equal weighting should be favored.

Simultaneous analysis of histone H3, snRNA U2, and morphological characters supports the Mandibulata hypothesis. The alternative TCC or Schizoramia grouping of crustaceans and chelicerates requires at least 6 extra steps on trees with equal character weights (length 1922 versus 1916). A sister-group relationship between Crustacea and Hexapoda is more parsimonious than TCC, but is still at least three steps longer than cladograms with myriapods as sister group to hexapods (using equal character weights). However, addition of 18S sequence data to the sample would be expected to strengthen a crustacean / hexapod grouping (see Giribet and Ribera, 1998). Atelocerata cannot be regarded as strongly supported by our data; Bremer support is 1 based on morphology and 3 based on all data, and the group collapses in the sensitivity analysis (Fig. 7). While a crustacean / hexapod sister group relationship warrants closer investigation, the hypothesis that Crustacea is a basal grade to Hexapoda is strongly opposed by our data. The basal branch establishing crustacean monophyly is one of the longest internal branches for the Arthropoda, though, as discussed above, a number of apparent crustacean synapomorphies are rendered plesiomorphic when extinct taxa such as trilobites are considered. Arrangements with Hexapoda nested *within* Crustacea are grossly unparsimonious. Any position for Hexapoda within the Crustacea (e.g., sister to Malacostraca) adds at least 28 steps. A recurring theme in recent considerations of arthropod phylogeny has been a dearth of synapomorphies for Crustacea (Lauterbach, 1983; Wägele, 1993). This view has invited speculation that Crustacea is a paraphyletic group (Averof and Akam, 1995; Moura and Christoffersen, 1996). However, an impressive suite of crustacean apomorphies has been compiled by Walossek (1999), most of which are employed in the present analysis. We encourage opponents of crustacean monophyly to demonstrate that these characters are present in insects. Some characters observed only in Crustacea, notably the nauplius larva and second antennae, have been dismissed as probable ground-plan characters for all mandibulates (e.g., Regier and Shultz, 1997:910). We adopted a neutral coding of the nauplius (making it inapplicable to atelocerates rather than absent). No direct observational evidence exists to indicate that hexapods or myriapods ever had a nauplius or that the suppressed limb of the intercalary segment was previously an antenna; these interpretations, while plausible, are entirely *ad hoc*.

Allying the hexapods with eumalacostracans (sister to the stomatopod) adds 48 *ad hoc* instances of homoplasy; a eumalacostracan–insect sister-group relationship adds at least 45 steps. That Eumalacostraca and Insecta share some complex and impressive similarities is indisputable, but we caution that interpreting these as synapomorphies carries a high cost. The arrangement of optic neuropiles (character 54, state 2) provides an example. Forcing synapomorphy between this state in eumalacostracans and insects requires that Malacostraca and Hexapoda (as well as Atelocerata and Crustacea) be dismissed as monophyletic groups (because of plesiomorphic states in Leptostraca and Collembola). Malacostracan monophyly is, however, supported by such characters as the pattern of tagmosis (138:1, 187:6), detailed correspondences in the ectoteloblasts (7:1), gut structure (123:1), and pleopod structure and function (177:1). Hexapod monophyly is supported by unique thoracic tagmosis (139:1), eye ultrastructure (51:1), the pattern of *Distal-less* expression in the mandible (81:1), maxillary structure (100:1), posterior tentorial apodemes (87:1), leg segmentation (168:1), and the gonoduct origin (189:2); corpora allata (41:1) and paired,



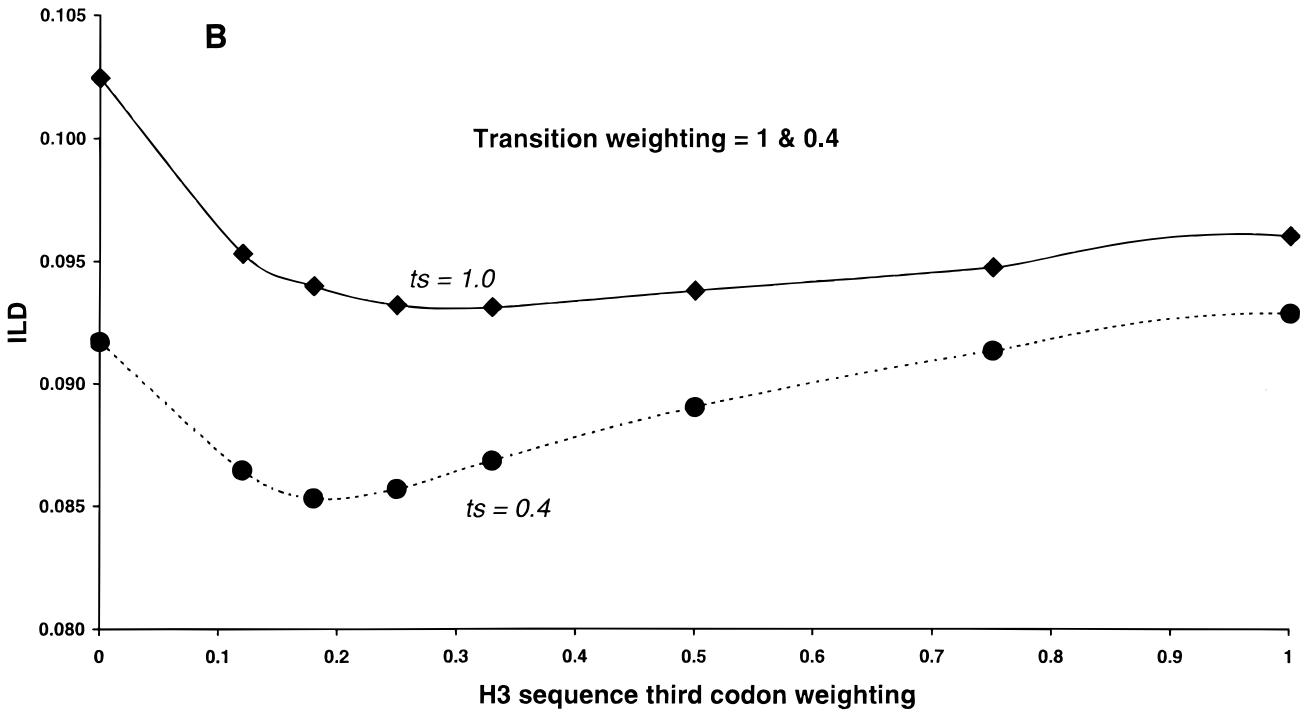


FIG. 9. Relationship between weightings in Table 3 and ILD. (A) Transition weights versus ILD. (B) H3 third-codon weights versus ILD.

elongate mitochondrial derivatives in the sperm (199:1) are additional hexapod synapomorphies with accelerated transformation. Several of the purported synapomorphies between eumalacostracans and insects pertain to sensory/nervous structure (e.g., optical neuropiles, pattern of ganglion development). The most parsimonious cladograms in this study would explain similarities confined to insects and eumalacostracans as convergent. More comprehensive sampling of non-malacostracan crustaceans, entognathous hexapods, and a broader range of myriapods is needed to clarify the systematic implications of malacostracan–insect similarities.

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