The Phylogeny of the Extant Hexapod Orders

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Morphological and molecular data are marshalled to address the question of hexapod ordinal relationships. The combination of 275 morphological variables, 1000 bases of the small subunit nuclear rDNA (18S), and 350 bases of the large subunit nuclear rDNA (28S) are subjected to a variety of analysis parameters (indel and transversion costs). Representatives of each hexapod order are included with most orders represented multiply. Those parameters that minimize character incongruence (ILD of Mickevich and Farris, 1981, *Syst. Zool.* 30, 351–370), among the morphological and molecular data sets are chosen to generate the best supported cladogram. A well-resolved and robust cladogram of ordinal relationships is produced with the topology (Crustacea ((Chilopoda Diplopoda) ((Collembola Protura) ((Japygina Campodeina) (Archaeognatha (Zygentoma (Ephemerida (Odonata ((((Mantodea Blattaria) Isoptera) Zoraptera) ((Plecoptera Embiidina) (((Orthoptera Phasmida) (Grylloblattaria Dermaptera)) ((((Psocoptera Phthiraptera) Thysanoptera) Hemiptera) ((Neuropteroidea Coleoptera) (((((Strepsiptera Diptera) Mecoptera) Siphonaptera) (Trichoptera Lepidoptera)) Hymenoptera)))))))))))))). © 2001 The Willi Hennig Society

INTRODUCTION

The phylogenetic arrangement of the higher groups of insects has been contentious since the time of Linnaeus. The 32 (or so) extant hexapod "orders" comprise perhaps the most diverse and ubiquitous animals on earth. Great progress has been made through the rigorous analysis of anatomical features exemplified by Snodgrass (1933, 1935, 1938) and the epistemological revolution brought about by Hennig (1966). This tradition continues through the critical synthetic work of Kristensen (1975, 1981, 1991, 1995, 1998). Most recently molecular sequence data have offered additional information (Wheeler, 1989; Carmean *et al.* 1992; Whiting and Wheeler, 1994; Pashley *et al.* 1995; Whiting *et al.* 1997), at times in monstrous quantity. This study attempts to integrate these novel molecular data with the anatomical and behavioral features examined over the past two centuries.

The lineages commonly referred to as orders are not to be taken as equal in any sense; they are after all arbitrary taxonomic levels. Almost all are well supported as monophyletic units (the few exceptions—e.g. Diplura—are not treated homogeneously here). Only

extant lineages are discussed here even though extinct taxa could (in principle) be accommodated via morphological analysis. Although extinct lineages may affect our notions of character polarity and phylogenetic arrangement, the present analysis is limited to standing diversity.

TAXONOMIC BACKGROUND

The phylogenetics of hexapods has been developed over centuries (millennia if Aristotle is included), and many of the characters and groups recognized today have their scientific origin in early work. Our discussion of insect taxonomy is centered on several groupings or problem areas—outgroups, apterous insects (entognathans and thysanurans), paleopterans, polyneopterans, paraneopterans, and neuropteroid and panorpoid holometabolous insects.

Outgroups

Historically, the myriapods have been promoted as the sister-group of the hexapods. In fact, the "Myriapoda" have been proposed to be paraphyletic with respect to hexapods with the Chilopoda (centipedes) excluded from the Labiata (Pauropoda, Diplopoda, Symphyla, and Hexapoda—Pocock, 1893; Snodgrass, 1938; Kraus and Kraus, 1994). As tracheate synapomorphies the loss of the mandibular palpus, ectodermal Malpighian tubules (Weygoldt, 1986), the pretarsal segment of leg (dactylopodite) with only a single muscle (Snodgrass, 1952), and pretarsal claws (potentially "paired" Hennig, 1969) have been proposed in addition to tracheae and the intercalary segment. The labiate clade is supported by a maxillary plate where the mouth cavity is bordered by the second maxillae and the presence of coxal vesicles. Furthermore, Snodgrass (1938) proposed that the Symphyla were closer to the hexapods than other labiate myriapods, though he admitted problems with this view concerning the position of the genital openings. Some recent molecular studies of arthropods have proposed the Crustacea as sister-group to the Hexapoda, relegating a monophyletic Myriapoda to the base of the Mandibulata (Friedrich
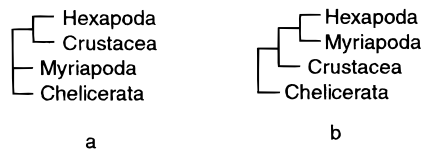

FIG. 1.   Arthropod relationships after (a) Friedrich and Tautz (1995) and (b) Wheeler *et al.,* (1993a).

and Tautz, 1995) (Fig. 1a). This pattern had been seen before (Wheeler *et al.* 1993a), but the signal is not strong enough to overwhelm tracheate synapomorphies in "total evidence" analysis (Wheeler *et al.* 1993a; Wheeler, 1998a, b) (Fig. 1b). Here we use the chilopod and diplopod lineages of the myriapods as well as two crustacean representatives as outgroups for the hexapods.

"Aptera"

The historical division between the winged Pterygota and wingless "Aptera" was established by Aristotle and maintained through Aldrovanus' (1602) habitat-based system, the metamorphosis systems of Swammerdam (1669) and Ray (1710; Ray and Willughby, 1710), and to Linnaeus (1735, 1738). Later, Latreille (1809, 1817) erected the "Thysanura," which included those apterous hexapods that we now recognize as basal (as opposed to the derived apterous forms such as fleas, which Linnaeus included in the Aptera). The naturalness of Aptera was attacked by Snodgrass (1938; Fig. 2). Snodgrass recognized the unique aspect of the internal mouthparts of the Collembola, Protura, and Diplura as being formed in a similar way from the outgrowth and formation of the *plicae orales.* Furthermore, he noted the presence of the ovipositor and posterior tentorium of the Thysanura and pterygote insects. Among the Insecta *sensu stricto,* the variation
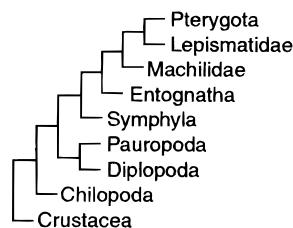

FIG. 2.   Basal hexapod relationships after Snodgrass (1938).

in mandibular articulation and further tentorial specialization suggested to Snodgrass that the Thysanura themselves were heterogeneous with the machiloids (Archaeognatha) basal with respect to the lepismatoids (Zygentoma) and their sister-taxon the Pterygota. Except for the question of *Tricholepidion* (Wygodzinsky, 1961), this scheme of basic hexapod diversification has held up to scrutiny. It should also be noted that Börner (1904) recognized some of these distinctions in his classification (Archaeognatha vs Zygentoma), but it seems clear that the distinction he made on the variation in mouthparts was more of gestalt than specific character argumentation, since he referred to the Zygentoma as intermediate, binding the Archaeognatha with the Pterygota. Kukalová-Peck (1991; Fig. 3) has rejected the placement of the Diplura with the other entognathous insects, placing them based on an ad hoc notion of character polarity (internal mouthparts as primitive, even though no other taxa possess them) and appeals to fossil specimens of less than consensual affinity (i.e., *Testajapyx*). These issues have been analyzed by Kristensen (1998) as well supporting dipluran monophyly and their placement within the Entognatha. Hennig (1969) discussed the Entognatha and added novel observations of his own. His analysis upheld the basic scheme of Snodgrass (1938) and elaborated it by specifying the affinities between the Collembola and the Protura based on reduced antennae and the lack of abdominal spiracles (Fig. 4). The Ellipura (Collembola + Protura) were also supported by Hennig (1953). Perhaps most importantly, Hennig placed insect systematics (in fact all systematics) on the firm epistemological
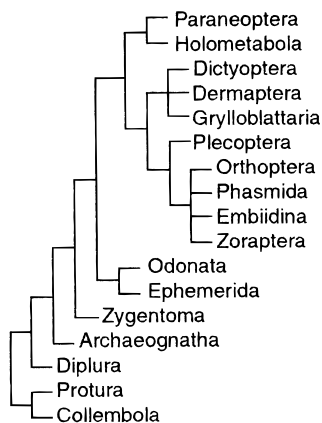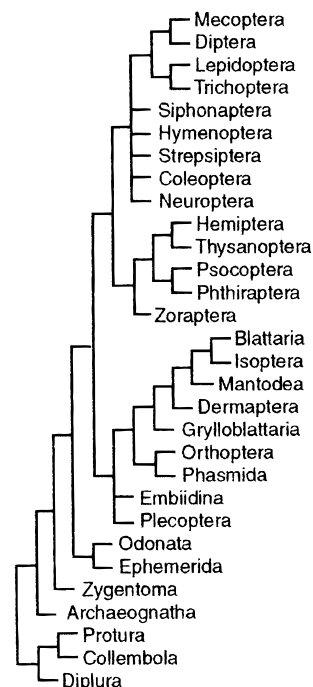

FIG. 4. Hexapod relationships after Hennig (1969).

grounds we rely on today. His interpretation of Snodgrass' observations forms the foundation of all subsequent analysis of insect phylogeny.

"Paleoptera"

The basal Pterygota present an interesting problem. The salient feature of the Pterygota—wings—varies in the structure of the axillary sclerites, which articulate the wings to the body. In the Neoptera, the arrangement of these structures allows the wings to fold back. In the Ephemerida and Odonata, this is not possible. Additionally, intercalary veins are uniquely present in these latter two orders. Since the wing veins are specific to wings, and the outgroup is wingless, this particular feature is inherently unpolarizable and hence of limited utility. In principle other winged taxa outside the extant Paleoptera might allow the proper comparisons. Kukalová-Peck (1978, 1985, 1991) has made the argument that these two wing features are synapomorphies for these taxa based on her interpretation of certain fossils. However, in addition to being outside the brief of this discussion of extant taxa, her reasoning is, at times, hard to follow. The fine structure (and number)

FIG. 3. Hexapod relationships after Kukalová-Peck (1991).

of axillary sclerites is difficult to determine in many of the fossils in the best of circumstances. Hence, Kukalová-Peck's polarization scheme requires verification.

Hennig (1953) initially favored breaking up the Paleoptera, uniting Odonata and Neoptera, but later changed his view to one of monophyly (Hennig, 1969). He based this union on four putative synapomorphies: aquatic larvae, fusion of the inner lobes of the maxillae, intercalary veins, and "bristle-like" antennal flagella. Sharov (1966) also supported this view. After Hennig, both possibilities were proposed for paleopteran affinities (Fig. 5). Boudreaux (1979) united the ephemerids with the Neoptera, resurrecting the Opisthoptera of Lemche (1940). He based his arrangement on three characters: powerful dorso-longitudinal wing depressor muscles, folding pattern of the nymphal wing pads, and direct transfer of sperm from male to female. Kristensen (1975, 1981) criticized Boudreaux's characters, describing them as plesiomorphic, autapomorphic, or homoplastic, and treated Paleoptera as an evolutionary grade, joining the Odonata and Neoptera. In supporting Börner's (1904) Metapterygota, Kristensen cited seven derived characters: suppression of imaginal molts, tracheation of wings and pterothoracic legs from their own and the following segment, insertion of occlusar muscles directly on spiracular sclerites of abdominal spiracles, veins R and RS with common stem, unpaired female gonopore, suppression of superlingulae, and loss of several cephalic and thoracic muscles. Kristensen's critical discussions of evidence bearing on the Paleoptera certainly place great doubt on their

monophyly and add strength to the argument for Odonata + Neoptera, but his more recent statements have not been so sanguine (Kristensen, 1991).

Polyneoptera

The Neoptera have been consistently divided into three sections: orthopteroid insects (Polyneoptera), hemipteroid insects (Paraneoptera), and those creatures with complete metamorphosis (Holometabola). The most questionable (vis à vis monophyly) and heterogeneous is certainly the Polyneoptera. These 10 orders (Plecoptera—stoneflies, Embiidina—web spinners, Orthoptera—grasshoppers and kin, Phasmatodea—walking sticks, Grylloblattaria—ice bugs, Dermaptera—earwigs, Mantodea—mantises, Isoptera—termites, Blattaria—roaches, and the enigmatic Zoraptera) have been allied in almost all possible combinations. There is no consensus, with disagreement centered about three foci of discontent—Plecoptera, Embiidina, and Zoraptera.

Linnaeus (1735, 1st ed.) initially had the orthopteroid lineages split between his Coleoptera and Hemiptera but later grouped the *"Forficula," "Blatta,"* and *"Gryllus"* in the Coleoptera (1758, 10th ed.). Somewhat more recently, Martynov (1925, 1938) proposed that the Plecoptera together with the other orthopteroid orders (Paurometabola) were monophyletic, together forming the Polyneoptera. The single character for this grouping seems to be an enlarged vannus of the hind-wing. Although there is some detailed similarity in this structure within the Polyneoptera, it is not present in the Embiidina and even if so may still be part of the neopteran ground plan (Kristensen, 1975). The lack of this feature in web spinners certainly seems to be a derived loss based on reduction of the other veins, due to the peculiar wing articulation system, and the frequent aptery in this group. Hennig (1953, 1969; Fig. 4) was undecided with respect to a monophyletic Paurometabola with Embiidina potentially its basal-most member. Boudreaux (1979, Fig. 6) supported a similar grouping, but with the stoneflies (Plecoptera) and web spinners (Embiidina) as sister-taxa forming the Plecopterida. Kristensen pointed out that Boudreaux's synapomorphies (suppression of phallomeres and abdominal styli, male clasping organs from 10th abdominal tergum, and reduction of Rs and M veins) are not obviously homologous within the Polyneoptera.
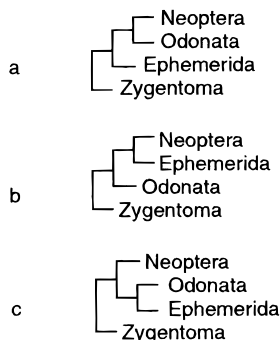

FIG. 5. Paleopteran relationships after (a) Hennig (1953) and Kristensen (1975), (b) Boudreaux (1979), and (c) Hennig (1969) and Kukalová-Peck (1991).
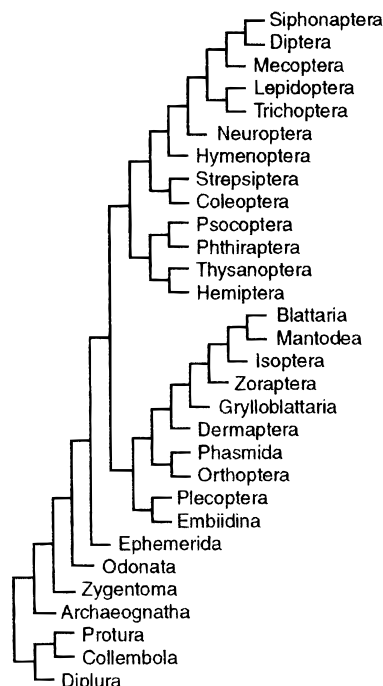
FIG. 6.   Hexapod relationships after Boudreaux (1979).

Planoneoptera was erected by Ross (1965) and endorsed by Hamilton (1971, 1972) to unite the Plecoptera with the Eumetabola (i.e., Paraneoptera + Holometabola) based on a "modification" of the trochantin. The remaining Paurometabola were then relegated to the Pliconeoptera. In this case, a derived fan-like folding of the hind wing vannus is postulated for the Pliconeoptera (= Paurometabola). However, even if this attribute is synapomorphous for this group, its absence might be primitive, removing support for the Planoneoptera specifically or for uniting the Plecoptera with anything in particular. Adams (1958) proposed a variant of this by uniting the stoneflies solely with the Holometabola, based on perceived similarities between Plecoptera and sialid Megaloptera. This hypothesis rests largely on two points: first that the fossil Lemmatophoridae are actually ancestral Plecoptera, which is doubtful (Carpenter, 1966; Hennig, 1969; Kristensen, 1975), and second that the megalopteran characters Adams cited are part of the ground plan of the Holometabola, which is also doubtful (Kristensen, 1975).

An additional scheme of plecopteran affinities is also based on several plesiomorphies. In this arrangement, the Plecoptera are proposed to be the sister-group of the remaining Neoptera. Hennig (1969) cited several uniquely primitive attributes concerning the embryonic yolk band (Sharov, 1966) and prothoracic sclerites (Snodgrass, 1935). Kristensen regarded these as uninformative due to a similar coxopleuron in the Embiidina and general misinterpretations of the order of germ band formation in the Plecoptera and Zygentoma. He did offer the primitive characters of nymphal tail filaments and seminal duct arrangement, noting, however, that other orthopteroid groups maintain distinct plesiomorphies at least as striking.

The Embiidina have been placed near the base of the Polyneoptera (Hennig, 1969), sister-group to the Plecoptera (Boudreaux, 1979), sister-group to the phasmids (Rähle, 1970), and within an "orthopteroid" assemblage including Orthoptera, Phasmatodea, and Zoraptera (Kukalová-Peck, 1991). The Zoraptera are poorly understood and as a result also have been bounced around. Hennig (1969) placed them within the Paraneoptera (hemipteroids), whereas Boudreaux (1979) placed them with the Dictyoptera (based on the "fontanelle") and Kukalová-Peck (using wing venation) allied them with embiids and Orthoptera. The homologies implicit in both these models have been criticized by Kristensen (1981, 1995). Additionally, Zoraptera and Embiidina have been proposed to be sister-taxa by Minet and Bourgoin (1986), based on tibial structural and muscular similarities. The placements of these orders are unclear, to say the least.

The Dictyoptera (Isoptera, Mantodea, and Blattaria) have long been thought to be monophyletic (Hennig, 1969). There has been a notion that the highly social termites were really derived roaches or at least the two orders were sister-taxa. Hennig cited the loss of the median ocellus and several wing venation patterns to support this clade. Hennig himself was agnostic as to whether the Isoptera were a subordinate clade of the Blattaria, making the latter paraphyletic. Kristensen (1975, 1981, 1991, 1995) supported this view in his visits to the question. Boudreaux (1979) added the Zoraptera as sister-group to the Dictyoptera based on the putative homologies of the fontanelle. Kristensen (1981) derided this feature as obviously nonhomologous. Thorne and Carpenter (1992) added many new observations and suggested that mantids and roaches were sister-taxa. The molecular sequence data of DeSalle *et al.* (1992)

supported this in their simultaneous analysis. Kristensen (1995) questioned this result and changed character codings in the matrix of Thorne and Carpenter in a way that was as he (p. 123) put it: "obviously subjective." The effect of his recoding was that no conclusions were well supported.

In addition to the problems of interrelationship among the Polyneoptera, their monophyly has been questioned on several occasions. Hennig (1969) suggested (with great reservations) that the Plecoptera might be the sister-group of the remainder of the Neoptera (but drew the tree as unresolved) and certainly thought the Zoraptera were allied with the Paraneoptera. Kukalová-Peck (1991) has suggested that the blattoid orders were sister-group to the Eumetabola. Most recently, Štys and Biliński (1990) and Büning (cited in Kristensen, 1995) proposed the "Meroista," consisting of the Dermaptera and the Eumetabola with the Plecoptera as the sister-group of that assemblage.

Paraneoptera

The hemipteroid insects—"Psocoptera" (book lice, which are probably paraphyletic; Lyal, 1985), Phthiraptera (biting and sucking lice), Thysanoptera (thrips), and Hemiptera (true bugs, plant hoppers, and their allies)—have most frequently been allied as a group with the Holometabola to form the Eumetabola. Although, as Kristensen (1995) points out, this group has achieved wide acceptance, the characters originally presented by Hennig, the absence of ocelli in immatures (but Zoraptera, which have them, must be excluded) and a reduced number of Malpighian tubules (basal Hymenoptera do not show this), are not without problems. Hamilton (1972) proposed that a sclerotization of the jugum—jugal bar—joins the Paraneoptera and Holometabola. Boudreaux (1979) renamed the group "Phalloneoptera" after an observation of Snodgrass (1957). He stated that the origin of gonopods from "phallic rudiments" is novel and not homologous with that of other insects (coxopodite + stylus). Kristensen criticized this logic based on the notion that the structures are more broadly distributed, no matter how they develop. Büning (cited in Kristensen, 1995) has added ovariole traits to eumetabolan support.

The Paraneoptera themselves (exclusive of the Zoraptera—more properly referred to as the Acercaria of Börner, 1904) were initially characterized by Hennig (1969; Fig. 4) as having lacinial stylets, four or fewer Malpighian tubules, a single abdominal ganglion, and lacking both sternum I and cerci. Kristensen (1981) added two more characters—spermatozoa with two flagella and the fusion of the gonangulum with tergum IX. Within the Paraneoptera/Acercaria are two lineages. The first is the Psocoptera, which is most likely paraphyletic with respect to the Phthiraptera (Lyal, 1985); thus the two orders are united by Lyal under the name Psocodea. The other side of the Paraneoptera consists of the Thysanoptera + Hemiptera. Hennig supported this group on the basis of the transformation of the maxillary laciniae into stylets. The name Condylognatha for this clade is derived from Börner, but this delineation actually goes back to Linnaeus' definition of the Hemiptera (1758, *Alae Superiores semicrustaceae,* 10th edition). Although the character support is weak (as for the Eumetabola) the group is generally accepted. Büning (cited in Kristensen, 1995) has proposed an ovariole character to support Condylognatha but also discussed two features that would link the Psocodea and Thysanoptera (sperm ultrastructure and aspects of the cibarial dilator).

Holometabola

The insects that display complete development and metamorphosis have been accepted as monophyletic for some time. Certainly Swammerdam (1737) had an inkling of this in his Metamorphic System with Coarctate (Diptera), Complete (Hymenoptera, Coleoptera, and Lepidoptera), and Incomplete (Neuroptera, Orthoptera, and Hemiptera) lineages. Hennig (1969) cited three synapomorphies: endopterygoty (imaginal disks), holometaboly (pupal stage), and an articulating joint in the coxa. Hamilton (1972) added the observation of a unique type of wing flexion where the wing is folded over the plica jugalis as opposed to the plica vannalis. Later, Kristensen (1975, 1981) mentioned as a possibility the *de novo* genesis of the imaginal compound eye after the larval eye is broken down.

Within the Holometabola, the fundamental distinction supported by Hennig (1969, 1981, Fig. 4) really concerned only the Neuropteroidea (Neuroptera *s.s.* + Megaloptera + Raphidioptera), Coleoptera, Hymenoptera, and the Mecopteroidea (Diptera, Siphonaptera, Mecoptera, Lepidoptera, and Trichoptera). Hennig

supported their monophyly, but with unclear relationships. Kristensen (1975) argued that the main holometabolan division was between Neuropteroidea + Coleoptera on one side and the Hymenoptera and Mecopteroidea on the other. The support for Coleoptera + Neuropteroidea, as delineated by Kristensen (1981, 1995; Fig. 7), comes from three sources—absence of cervical cruciate muscles, a specific modification of the female terminalia, and unique, multilayered monoaxonal stemmata. The Hymenoptera + Mecopteroidea are characterized by an unpaired tarsal claw of the larval leg (Snodgrass, 1935), silk secretion from labial glands, and eruciform larvae. Boudreaux (1979) placed the Coleoptera (and Strepsiptera discussed below) as the sister-group to the remaining Holometabola forming the Telomerida. The noncoleopteran taxa were then proposed to be united on a division of the male gonopod into a "basimere" and "telomere," "derepression" of abdominal limb buds, and the loss of gastric caeca. Kristensen (1981) dismissed these features as based on questionable homology statements and overly narrow
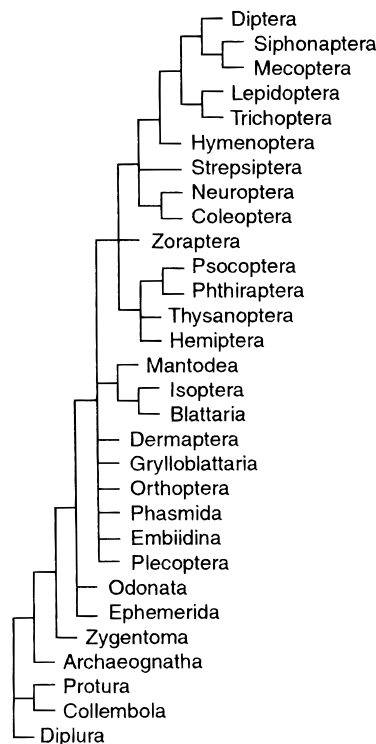
distributional assumptions of certain features. The Hymenoptera have also been proposed as the basal member of the endopterygotes (Ross, 1965). This argument is based on the maintenance of a three-valve ovipositor. At best this is a solitary feature.

The mecopteroid orders are characterized (Kristensen, 1981) by the insertion of pleural muscle on the first axillary sclerite, divided larval stipes, larval maxillary and labial muscle losses, and the presence of a unique cranial muscle in the larvae. Within this group, the Amphiesmenoptera (Trichoptera + Lepidoptera) form an ironclad clade (Kristensen, 1995) with a large list of synapomorphies, starting with female heterogamety and Y-shaped fusion of the anal veins. The remaining orders (Antliophora = Siphonaptera + Diptera + Mecoptera) have been allied in various ways since the inclusion of the Siphonaptera by Kristensen (1975), uniting them on the basis of the larval mouthparts and possibly the sperm pump itself. The fleas have been proposed to be allied with Diptera (Matsuda, 1965) due to their similar apodous larvae and the lacinial stylets. Kristensen (1975) doubted this and suggested that the Mecoptera are a more logical sister-taxon, citing muscular, nervous, and sperm structure similarities. The spermatozoan structure is regarded as most convincing with a novel arrangement of the axial mitochondrion and flagellum. Recently, Whiting and Wheeler (1994), Whiting *et al.* (1997), and Whiting (1998b) have urged the inclusion of the Strepsiptera in the Antliophora (Fig. 8). Although usually allied with the Coleoptera (based on posteromotorism) or even included within the Coleoptera, Whiting and Wheeler (1994) placed them as sister-group to the Diptera by employing analysis of ribosomal DNAs. They also pointed to morphological features of the Strepsiptera more in common with panorpoid insects than beetles. These ideas are discussed in depth by Kristensen
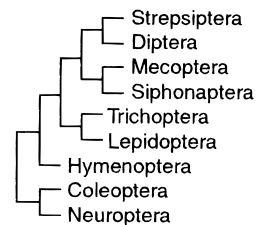

FIG. 7. Hexapod relationships after Kristensen (1995).

FIG. 8. Holometabolan relationships after Whiting and Wheeler (1994) and Whiting *et al.* (1997).

(1995), who questioned the homology of several of these characters and the relative importance of others. Detailed description of character codings for Strepsiptera were described in Whiting (1998b). Kukalová-Peck and Lawrence (1993) also supported a Coleoptera–Strepsiptera clade defined by a series of wing venation features. These homologies and even the observations themselves are questioned by Whiting and Kathirithamby (1995) in their critique. Kukalová-Peck (1998) responded by rejecting all of Whiting and Kathrithamby's interpretations and cited two additional venational characters to support Strepsiptera + Coleoptera. However, her interpretations are highly suspect, and since she has failed to provide any primary data to support her claims on wing venation (unlike Whiting and Kathirithamby, 1995), her characters are of questionable phylogenetic utility.

Other molecular analyses and reanalyses (Carmean *et al.* 1992; Pashley *et al.* 1993; Whiting and Wheeler, 1994; Carmean and Crespi, 1995; Whiting *et al.* 1997; Huelsenbeck, 1997, Whiting 1998a, b) have concentrated on holometabolan relationships. Carmean *et al.* (1992) suggested that the Diptera lay outside of other holometabolous insects. The results of Pashley *et al.* (1993) were more in line with traditional views, supporting the Amphiesmenoptera and Mecopteroidea. They also placed the Diptera as sister-group to the Lepidoptera and Trichoptera. The main area of disagreement, as mentioned above, has concerned the sister-group relationship between the Diptera and the Strepsiptera (= "Halteria"). Criticisms surround the notion of "long-branch attraction" and the presumed inability of parsimony to adequately account for rate heterogeneity. In a reanalysis of the limited Carmean and Crespi (1995) data, Huelsenbeck (1997) argued that Strepsiptera + Diptera was an artifact of long-branch attraction. Whiting (1998a) suggested that the meager sampling in the Carmean and Crespi (1995) data set and the unconventional trees generated by Huelsenbeck (1997) for other portions of holometabolan phylogeny were indications that his results were spurious. This has been confirmed by Siddall and Kluge (1997) and Siddall and Whiting (1999). In fact, in a reanalysis of the Whiting *et al.* (1997) data set, Huelsenbeck (1997) found that for 18S rDNA, maximum-likelihood analysis (incorporating parameters for rate heterogeneity) does indeed support Diptera + Strepsiptera, though not with the strength of support that Huelsenbeck

deems significant. Hwang *et al.* (1998) generated a more complete sequence of 28S for a single strepsipteran species, but failed to include even a reasonable number of exemplar taxa in their study. Their poor sampling strategy and ad hoc arguments have led to particularly specious conclusions, neither supporting nor refuting the Strepsiptera + Diptera clade. It is clear that the morphological and molecular analyses to date support the Halteria clade.

In this study, we attempt to integrate these and other morphological studies with molecular sequence data, through sampling each of the hexapod orders and explicitly combining morphological and molecular data in a total evidence (Kluge, 1989) or simultaneous analysis (Nixon and Carpenter, 1996a) context. Only in this way can the corroborating and conflicting observations sort themselves into all-encompassing schemes for all the data.

DATA

Taxa

In order to assess basal conditions and variation within groups, where possible, multiple representatives of hexapod lineages were examined. This netted 122 samples to represent the orders and 6 outgroup representatives for a total of 128 terminal taxa (Table 1). All ordinal lineages are represented, and most are represented by multiple taxa.

The three sources of data used in this study are anatomy and sections of both the small (18S rDNA) and the large subunit nuclear ribosomal DNAs (28S rDNA).

Morphology

The morphological data matrix was derived from literature sources and resulted in 275 variables (Table 2 and Appendix 1). The primary sources for this information were Snodgrass (1935, 1938), Hennig (1953, 1969, 1981), Kristensen (1975, 1981, 1995), Boudreaux (1979), and Kukalová-Peck (1991, and others). These characters were scored as ground-plan or presumed basal conditions in the 34 extant ordinal lineages and outgroup taxa; that is, the orders were treated as summary terminals (Nixon and Carpenter, 1996a). No attempt was made to score these features for the actual

TABLE 1
Taxa Used in the Study

Higher group	Taxon	18SrDNA	28SrDNA
Crustacea			
Maxillopoda	*Balanus* sp.	Wheeler	Hayashi
Malocostraca	*Callinectes* sp.	Wheeler	Hayashi
Myriapoda			
Chilopoda	*Scutigera coleoptrata*	Wheeler	Hayashi
	Lithobius forficatus	Friedrich	Friedrich
Diplopoda	*Spirobolus* sp.	Wheeler	Hayashi
	Megaphyllum sp.	Friedrich	Friedrich
Hexapoda			
Collembola	*Pseudachorutes* sp.	Friedrich	Friedrich
	Crossodonthina koreana	Hwang	ND
	Hypogastrura dolsana	Hwang	ND
	Podura aquatica	Here	Here
	Lepidocyrtus paradoxus	Soto-Adames	ND
Protura	*Acerentulus traegardhi*	Here	Here
Diplura	*Metajapyx* sp.	Here	Here
	Campodea tillyardi	Here	Here
Archaeognatha	*Petrobius brevistylis*	Friedrich	Friedrich
	Trigoniophthalmus alternatus	Whiting	Whiting
Zygentoma	*Lepisma* sp.	Here	Here
	Thermobius domestica	Here	ND
Ephemerida	*Stenonema* sp.	Here	Here
	Ephemerella sp.	Whiting	Whiting
	Heptagenia diabasia	Wheeler2	ND
Odonata	*Libellula pulchella*	Wheeler	Whiting
	Agrion maculatum	Whiting	Whiting
	Calopteryx sp.	Here	ND
Plecoptera	*Megarcys stigmata*	Whiting	Whiting
	Cultus decisus	Whiting	Whiting
	Agnetina sp.	Here	Here
	Paragnetina media	Here	Here
	Agnetina capitata	Here	Here
	Mesoperlina pecircai	Aleshin	ND
Embiidina	*Oligotoma saundersii*	Whiting	Whiting
	Clothoda sp.	Here	Here
Grylloblattaria	*Grylloblatta* sp.	Here	Here
Dermaptera	*Forficula auricularia*	Here	Here
	Labia sp.	Here	Here
	Labidura riparia	Whiting	Whiting
Isoptera	*Reticulotermes virginicus*	Here	ND
	Anopliotermes sp.	Here	Here
Blattaria	*Blaberus* sp.	Here	Here
	Gromphadorhina portentosa	Here	ND
Mantodea	*Mantis religiosa*	Wheeler	Whiting
Orthoptera	*Ceuthophilus* sp.	Here	ND
	Melanoplus sp.	Whiting	Whiting
	Warramaba picta	Wheeler2	ND
Phasmida	*Timema californica*	Here	Here
	Phyllium sp.	Here	Here
	Anisomorpha buprestoides	Whiting	Here
Zoraptera	*Zorotypus snyderi*	Here	Here
Phthiraptera	*Dennyus hirudensis*	Whiting	Whiting
Thysanoptera	*Taeniothrips inconsequens*	Whiting	Whiting
Psocoptera	*Cerastipsocus venosus*	Wheeler	Whiting

TABLE 1—*Continued*

Higher group	Taxon	18SrDNA	28SrDNA
Hemiptera	*Oncometopia orbana*	Wheeler3	Here
	Tibicen sp.	Wheeler3	Here
	Saldula pallipes	Wheeler3	Whiting
	Buenoa sp.	Wheeler3	Whiting
	Belostoma flumineum	Wheeler3	ND
	Lygus lineolaris	Wheeler3	Here
	Oncopeltus fasciatus	Wheeler3	ND
Coleoptera	*Cybister fimbriolatus*	Whiting	Whiting
	Xyloryctes faunus	Whiting	Whiting
	Octinodes sp.	Whiting	Whiting
	Photuris pennsylvanicus	Whiting	Whiting
	Rhipiphorus fasciatus	Whiting	Whiting
	Meloe proscarabaeus	Whiting	Whiting
	Tenebrio molitor	Whiting	Whiting
	Tetraopes tetropthalmus	Whiting	Whiting
Neuroptera	*Lolomyia texana*	Whiting	Whiting
	Mantispa pulchella	Whiting	Whiting
	Hemerobius stigmata	Whiting	Whiting
	Chrysoperla plorabunda	Carmean	ND
	Myrmeleon immaculatus	Whiting	Whiting
	Myrmeleon sp.	Carmean	ND
Megaloptera	*Corydalus cognatus*	Whiting	Whiting
	Sialis hamata	Here	Here
Raphidiodea	*Agulla* sp.	Whiting	Whiting
Hymenoptera	*Hartigia cressonii*	Carmean	ND
	Orussus thoracicus	Carmean	ND
	Hemitaxonus sp.	Whiting	Whiting
	Periclista linea	Carmean	ND
	Bareogonalos canadensis	Carmean	ND
	Evania appendigaster	Carmean	ND
	Ichneumon sp.	Carmean	ND
	Ophion sp.	Whiting	Whiting
	Mesopolobus sp.	Carmean	ND
	Caenochrysis doriae	Carmean	ND
	Epyris sepulchralis	Carmean	ND
	Priocnemus oregana	Carmean	ND
	Dasymutilla gloriosa	Whiting	Whiting
	Apoica sp.	Whiting	Whiting
	Monobia quadridens	Whiting	Whiting
	Polistes fuscatus	Whiting	Whiting
	Polistes dominulus	Chalwatzis	ND
	Camponotus ligniperda	Baur	ND
	Chalepoxenus muellerianus	Baur	ND
	Doronomyrmex kutteri	Baur	ND
	Leptothorax acervorum	Baur	ND
	Temnothorax recedens	Baur	ND
	Harpagoxenus sublaevis	Baur	ND
Lepidoptera	*Papilio troilus*	Wheeler	Whiting
	Galleria mellonella	Whiting	Whiting
	Ascalapha odorata	Whiting	Whiting
Trichoptera	*Oecetis avara*	Whiting	Whiting
	Hydropsyche sparna	Whiting unpub.	Whiting unpub.
	Pycnopsyche lepida	Whiting	Whiting

TABLE 1—*Continued*

Higher group	Taxon	18SrDNA	28SrDNA
Mecoptera	*Nannochorista neotropica*	Whiting unpub.	Whiting unpub.
	Nannochorista dipteroides	Whiting unpub.	Whiting unpub.
	Boreus coloradensis	Whiting	Whiting
	Boreus californicus	Whiting unpub.	Whiting unpub.
	Merope tuber	Whiting unpub.	Whiting unpub.
	Bittacus pilicornis	Whiting unpub.	Whiting unpub.
	Bittacus strigosus	Whiting	Whiting
	Panorpa isolata	Whiting unpub.	Whiting unpub.
	Panorpa helena	Whiting unpub.	Whiting unpub.
Siphonaptera	*Craneopsylla minerva*	Whiting unpub.	Whiting unpub.
	Megarthroglossus divisius	Whiting unpub.	Whiting unpub.
	Acanthopsylla rothschildi	Whiting unpub.	Whiting unpub.
	Atyphloceras echis	Whiting unpub.	Whiting unpub.
	Orchopeas leucopus	Whiting	Whiting
Strepsiptera	*Triozocera mexicana*	Whiting	Whiting
	Caenocholax fenyesi	Whiting	Whiting
	Elenchus japonica	Whiting	Whiting
	Xenos vesparum	Chalwatzis	ND
	Xenos pecki	Whiting	Whiting
	Crawfordia n. sp	Whiting	Whiting
Diptera	*Laphria* sp.	Whiting	Whiting
	Tipula sp.	Whiting	Whiting
	Drosophila melanogaster	Tautz	Whiting
	Mythicomyia atra	Whiting	ND

Note. Hendriks denotes Hendriks *et al.,* (1988); Friedrich denotes Friedrich and Tautz (1995); Hayashi denotes Wheeler and Hayashi (1998); Tautz denotes Tautz *et al.* (1988); Wheeler denotes Wheeler *et al.* (1993a); Whiting denotes Whiting *et al.* (1997); ND, no data; Soto-Adames denotes Soto-Adames and Robertson (unpublished results); Aleshin denotes Aleshin *et al.* (unpublished results); Chalwatzis denotes Chalwatzis *et al.* (unpublished results); Baur denotes Baur *et al.* (1993); Hwang denotes Hwang *et al.* (1995); Wheeler denotes Wheeler (1989); Wheeler3 denotes Wheeler *et al.* (1993b). Whiting unpub. denotes Whiting (unpublished results). Genbank Accesion Nos. AF28676, AF286286, AF286287, AF286291, AF338256–267, AF354681–703.

species level taxa employed in molecular analysis. A subset of these characters, for holometabolan taxa, was presented in Whiting *et al.* (1997).

Molecular Data

Approximately 1000 bases of the 18S rDNA and 350 bases of the 28S rDNA were determined as described by Whiting *et al.* (1997). The small subunit sequences of some taxa have been published previously and were included. All of the areas within the contiguous segments of DNA were used with the exception of a single insertion region where there was no corresponding sequence in a majority of taxa. Total genomic DNA was isolated from fresh, ETOH-preserved, and dried specimens by homogenization in an extraction buffer (10 mM Tris, 25 mM EDTA, 0.5% SDS, 100 mM NaCl, 0.1 mg/ml proteinase K). After 12+ h of incubation with agitation at 55°C, the DNAs were cleaned with a standard series of phenol/chloroform extraction followed by ethanol precipitation and resuspension in water. If tissues were rare, the precipitation was replaced by purifying the supernatant in separation columns (Centricon 100) to increase the total DNA yield and quality. Double-stranded template suitable for sequencing was prepared for 18S and 28S rDNA via polymerase chain reaction (PCR) amplification with conserved primers (Whiting *et al.* 1997). For most 18S sequences, the entire 1-kb region was amplified and sequenced with internal primers. 18S rDNA sequencing was carried out by using ^{35}S-ATP, the primers used for PCR amplification and internal primers, the modified T7 DNA polymerase Sequenase (version 2.0, U.S. Biochemical Corp.; the accompanying reagents following standard protocols), and with the PRISM cycle sequencing kit (ABI) and run on the ABI 373A automated sequencer. In all cases, complementary strands of all

TABLE 2

Morphological Character Matrix

```
              1                                                                                           100
Crustacea     111000100010000000000001000000200-0-000000-00000000-0000000--0000000-000-00--20000-0000--0000-0-000
Chilopoda     00001101110001110000000000000-005000010000002000000000000000000--00000000000-00--20000-0000--0000-0-000
Diplopoda     000111010101-0001110000000000-005000010000200200000000000000000--00000000000-00--2000000000--0000-0-000
Japygina      00000101110110000001111211111-12101000000011100000000000000000--20000000001-00--2000000001--0000-0-000
Campodeina    00000101110110000001111211111-1210111000000110000000000000000000--200-0000001-00--2000000001--0000-0-000
Collembola    000001011101100000011221101012121110111110600100000000000000--100-0000001-00--20-0000001--0000-0-000
Protura       0000010111011000000011111110001-221201?111110-101000000000000000--000-0000001-00--2000000000--0000-0-000
Archaeognatha 0000010111011000000111111111030322120000120121101000101100--00000000001-00--0000000001--0000-0-000
Zygentoma     0000010111011000000111111111000032312000012012111111112121000--00000110001-00--0000000001--0000-0-000
Ephemerida    0000010111011000000111111111000032322000016012011111121201111111100000010000000000000000000000000000
Odonata       0000010111011000000111111111000032312000012012122111212101111011111112000000000000000000000000000000
Plecoptera    00000101110010000001111111111000032312000001?1120021-11212001101011111111111-11000111100020010000000000
Embiidina     00000101110010000001111111210003231200001401200021-112121021010011111111111-10021111110112001210001000
Grylloblattaria 00000101110010000001111111111000032312000012012102111112121001--00111111111-1---2100000001--1000-11101
Dermaptera    00000101110010000001111111111000032312000013012202021-112120011020011111111111-11021110101021111100011110
Mantodea      00000101110010000001111111111000032312000015012102111212101102001111111111111110011001111000001111
Blattaria     00000101110010000001111111111000032312000015012102111212101102001111111111111031110010011110000021111
Isoptera      00000101110010000001111111111000032312000001?01210211112121011020011111111111111031110001010010000011111
Orthoptera    00000101110010000001111111210003231200001401230211112121011010011111111111110011100001111100100000
Phasmida      00000101110010000001111111310003231200001501230211112121011010011111111111110011100001111110100000
Zoraptera     00000101110010000001111111110033231200001?0120021-112121011040011111111111-1010111010110000000011101
Psocodea      00000101110010000001111111010004323120000011?01210211112121011030011111111111110111₽1000001000001000000
Phthiraptera  00000101110010000001111111010004323120000011?0121021111212100--001111111111-1---1111000001--0001-00000
Thysanoptera  00000101110010000001111111010004323120000011?01210211112121011030011111111111101111100000100001000000
Hemiptera     00000101110010000001111111010004323120000011?01210211112121011030011111111111101111100000100001000000
Megaloptera   00000101110010000001111111110003231200001?01240211112121011030111111111111110111110000010000010000000
Raphidiodea   00000101110010000001111111110003231200001?01240211112121011030011111111111110111110000010000010000000
Neuroptera    00000101110010000001111111110003231200001?01240211112121011030011111111111110111110000010000010000000
Coleoptera    00000101110010000001111111110003231200001?01210211112121011030011111111111110111110000010000010000000
Strepsiptera  00000101110010000001111111110003231200001?1100021-?12121021030011111??111-1011111000000000001000000
Hymenoptera   00000101110010000001111111110003231200001?01210211112121011030011111111111101111100000100001000000
Siphonaptera  00000101110010000001111111110003231200001?01200-1-112121001--00111111111-----1111000001--0001-00000
Mecoptera     00000101110010000001111111110003231200001?0120-021-112121011030011111111111-101?111000001000001000000
Diptera       00000101110010000001111111110003231200001?0120021-112121011030011111111111----1111000010-0001000000
Trichoptera   00000101110010000001111111110003231200001?0120021-112121011030111111111111-1011111000001000001000000
Lepidoptera   00000101110010000001111111110003231200001?0120021-112121011030011111111111-1014111000001000001000000
```

TABLE 2—*Continued*

```
                101                                                                                      200
Crustacea       00-00000000000000000000000000000000000001000010000000000000000000000000000000000000000000000000000000
Chilopoda       00-00000300000000000000000000000000001000010000000000000000000000000000000000000000000000000000000000
Diplopoda       00-00000000000000000000000-000000000001000010000000000000000000000000000000040000000000000000000000
Japygina        00-00000000000000000000000000000000000000000000000000000000000000000000000001110000000000000000000
Campodeina      00-00000000000000000000002000000000000000000000000000000000000000000000001110000000000000000000
Collembola      00-00000000000000000000002000000001000000000000000000000000000000000000001002001111000000-0000
Protura         00-00000000000000000001000101000000100000000000000000000000000000000002002110000000000000000
Archaeognatha   00-00000000000000000000000000000000000000000000000000000000000000000003003000001110000000000
Zygentoma       00-00100100000000000000000000000000000000000000000000000000000000000003003000000001100000000
Ephemerida      000000010000000100000000000000000000000000000000000000000000000000000400300000000001111000
Odonata         000000020000000100000000000000000000000000000000000000000000000000000040030000000000000111
Plecoptera      011001012000000010010000000000000000000000000000000000000000000000000400300000000000000000
Embiidina       000011012011000100100000000000000000000000000000000000000000000000000400300000000000000000
Grylloblattaria 10-10000100011001001-0000000000000000000000000000-000000000000000000000400300000000000000000
Dermaptera      0001-010200000101001000100000200000000000000000000000000000000000000400300000000000000000
Mantodea        10011010110000212111020000000000000000000000000000000000000000000000400300000000000000000
Blattaria       10011010110000212111110000000000000000000000000000000000000000000000400300000000000000000
Isoptera        00011010110000202101100000000000000000000000000000000000000000000000400300000000000000000
Orthoptera      00011001100011001001000000000000000000000000000000000000000000000000400300000000000000000
Phasmida        00011001101100001001001100000000000000000000000000000000000000000000400300000000000000000
Zoraptera       0101000030000000100000001000000000000000000100000000000000000000000400300000000000000000
Psocodea        0101000022000000100000002111121000000000000000010000000000000000000400300000000000000000
Phthiraptera    01-10000220000001000-002211112100000000000000010000000000-00000000000400300000000000000000
Thysanoptera    0101000022000000100000002111010110000000000000010000000000000000000400300000000000000000
Hemiptera       0101000022000000100000002111030110000000000000010000000000000000002000000000000400300000000-00000000
Megaloptera     011100001000000010000000000010?0001111110000111201101000000000000000000500300000000000000000
Raphidiodea     011100001000000010000000000010300011111100001120111000000000000000000500300000000000000000
Neuroptera      01110000100000001000000000010000111111000011201000100000000000000000500300000000000000000
Coleoptera      011100001000000010000000000010?00011111100010002100000000000000000500300000000000000000
Strepsiptera    0-110001000000010000000-000?00010010??00?0?1210000???100000000112?00-???0??00500300000000-00000000
Hymenoptera     011100001000000010000000000020001111001110110200000000000000000500300000000000000000
Siphonaptera    01-10000100000001000-00002000?0-0111100111001120000-1-110-000000-001--11111111150030000000000000000
Mecoptera       011100001000000010000000000?0001111001110111200001111100000000111111111201111500300000000000000000
Diptera         011100001000000010000002000000011110011001120000111110000000211111111111000050030000000000000000
Trichoptera     0111000010000000100000000000200011110011101120000111111111111000000000500300000000000000000
Lepidoptera     011100001000000010000000000020001111001110111200001111?11111112000000000000500300000000000000000
```

TABLE 2—*Continued*

```
                201                                                                        275
Crustacea       000000010000000000000000000000001000000000000000000000000000000000000000000
Chilopoda       000000010000000000000000000000001000000000000000000000000000000000000000000
Diplopoda       000000010000000000000000000000001000000000000000000000000000000000000000000
Japygina        000000010000000000000000000000000000000000000000000000000000000000000000000
Campodeina      000000010000000000000000000000000000000000000001000000000000000000000000000
Collembola      0000000100000000000000000000000000000000000000000000000-000000000-00
Protura         000000010000000000000000000000000000000000000000000000000010000000000000000
Archaeognatha   000000010000000000000000000000000000000000000000000000000100000000000000000
Zygentoma       000000010000000000000000000000000000000000000000000000010000000000000000000
Ephemerida      000000001000000000000000000000000000000000000000000000000000000000000000000
Odonata         110000000100000000000000000000000000000000000000000000000000000000000000000
Plecoptera      001000000000000000000000000000000000-0000000000000000000000000000000000000
Embiidina       000111000100000000000000000000000000-0000000000000000000000000000000000000
Grylloblattaria 0000001-1000000000000000000000000000000000000000000000000000000000000000000
Dermaptera      000000001110000000000000000000000000-0000000000000000000000000000000000000
Mantodea        000002000101110000000000000000000000000000000000000000000000000000000000000
Blattaria       000000000100011000000000000000000000000000000000000000000000000000000000000
Isoptera        000001001010000011100000000000000000000000000000000000000000000000000000000
Orthoptera      000000000100000000110000000000000000000000000000000000000000000000000000000
Phasmida        000000000100000000011100000000000000000000000000000000000000000000000000000
Zoraptera       000000000100000100000001000000000000-0000000000000000000000000000000000000
Psocodea        000000000100000000000000000000000000000000000000000000000000000000000000000
Phthiraptera    00000000-1000000000000001111000000000000000000000000000000000001000000000000
Thysanoptera    000000000100000000000000001111000000000000000000100000000000000000000000000
Hemiptera       000000000100000000000000000001110000000000000000000000000000000-00000000
Megaloptera     000003000100000000000000000000011000000000000000000000000000000000000000000
Raphidiodea     000000000100000000000000000000001111000000000000000000000000000000000000000
Neuroptera      000000000100000000000000000000000010000000000000000000000000000000000000000
Coleoptera      000000000100000000000000000000000001111000000000000000000100000000000000000
Strepsiptera    000000000100000000000000000000000000-0000000011110000000000010000-00000000
Hymenoptera     000000000100000000000000000000000000000000000000000111100000000000000000000
Siphonaptera    00000000-10000000000000000100-00000000-000000000000000001111000000000000000
Mecoptera       000000000100000000000000000000-0000000000000000000000000001111000000000000
Diptera         000000000100000000000000000000-0000000000000000000000000001011110000000
Trichoptera     000000000100000000000000000000-00000000000000000000000000000000-1111000
Lepidoptera     000000000100000000000000000000-00000000000000000000000000000000000000111
```

Note. Characters 20–27, 29, 30, 32, 38–40, 42, 45, 46, 48–61, 63–71, 73–78, 80–91, 93–108, 110–125, 127–129, 131–179, 181, 182, 184–205, 208–275 were treated as additive (ordered).

fragments were independently amplified and sequenced to ensure accurate results. If complementary strands disagreed, the product was reamplified and sequenced to resolve any discrepancies.

PHYLOGENETIC METHODS

The character data were analyzed using parsimony to elucidate efficiently Hennigian synapomorphy schemes (Hennig, 1966). That is, the simplest or most parsimonious result was taken to be the best summary representation of variation in the studied taxa. This was accomplished in two ways. The morphological data on their own were examined using Goloboff's (1999) parsimony program NONA. TBR branch swapping was performed, and 20 random addition sequences and 200 "Ratchet TBR" replicates (Nixon, 1999) were employed to search for solutions.

The molecular data were analyzed with POY (Gladstein and Wheeler, 1997) to construct phylogenetic hypotheses directly. This is performed by optimizing the nucleic acid sequences without the intervening step of multiple sequence alignment (Wheeler, 1996). When total evidence analysis was performed, the morphological characters received weights corresponding to the indel cost. If indels were weighted 4, transversions 2, and transitions 1, the morphological character data were weighted 4. Leading and trailing gaps were weighted one-half internal gaps. This scheme of assigning equal weights to character data and indel events yielded most congruent results in a

TABLE 3

Cladogram Lengths and Incongruence Values for Analyses of Parameter Sets

Gap cost ratio	Transversion cost ratio	Length combined	Length 18S + 28S	Length Morph	Length 18S	Length 28S	ILD combined	ILD 18S vs 28S	ILD MOL vs Morph	Scaled ILD combined	Scaled ILD 18S vs 28S	Scaled ILD Mol vs Morp
1	1	10,861	9,676	968	6,417	3,007	0.0432	0.0260	0.0200	0.0310	0.0277	0.0146
1	2	9,150	7,981	968	4,805	2,928	0.0491	0.0311	0.0220	0.0318	0.0305	0.0145
1	4	16,615	14,459	1,936	7,983	5,949	0.0450	0.0364	0.0132	0.0286	0.0373	0.0086
1	8	30,294	25,992	3,872	14,012	10,708	0.0562	0.0489	0.0142	0.0337	0.0479	0.0087
1	∞	27,364	22,870	3,872	12,136	9,494	0.0680	0.0542	0.0227	0.0386	0.0513	0.0132
2	1	6,516	5,439	968	3,586	1,682	0.0430	0.0314	0.0167	0.0247	0.0320	0.0098
2	2	13,163	11,003	1,936	5,774	4,647	0.0612	0.0529	0.0170	0.0340	0.0499	0.0097
2	4	23,617	19,187	3,872	9,701	8,283	0.0746	0.0627	0.0236	0.0385	0.0554	0.0125
2	8	44,479	35,346	7,744	17,484	15,430	0.0859	0.0688	0.0312	0.0429	0.0592	0.0160
2	∞	41,280	32,232	7,744	15,328	14,280	0.0952	0.0814	0.0316	0.0450	0.0669	0.0154
4	1	10,117	7,897	1,936	4,299	2,934	0.0937	0.0841	0.0281	0.0432	0.0669	0.0133
4	2	19,822	14,989	3,872	7,155	6,776	0.1019	0.0706	0.0485	0.0469	0.0557	0.0229
4	4	36,602	26,718	7,744	12,249	12,270	0.1185	0.0823	0.0585	0.0516	0.0610	0.0261
4	8	70,240	50,094	15,488	22,345	23,152	0.1318	0.0918	0.0663	0.0556	0.0655	0.0288
4	∞	67,080	46,656	15,488	20,128	21,848	0.1434	0.1003	0.0736	0.0586	0.0687	0.0309
8	1	17,651	12,644	3,872	5,686	5,866	0.1262	0.0864	0.0643	0.0532	0.0612	0.0278
8	2	32,437	22,010	7,744	9,336	10,477	0.1504	0.0998	0.0827	0.0598	0.0654	0.0338
8	4	61,885	40,724	15,488	16,447	19,680	0.1660	0.1129	0.0917	0.0637	0.0707	0.0362
8	8	120,733	77,469	30,976	30,660	38,081	0.1741	0.1127	0.1018	0.0655	0.0679	0.0394
8	∞	117,504	74,192	30,976	28,264	36,800	0.1827	0.1230	0.1050	0.0672	0.0719	0.0398
16	1	30,194	19,332	7,744	7,621	9,503	0.1764	0.1142	0.1033	0.0661	0.0679	0.0398
16	2	57,176	35,143	15,488	13,052	17,771	0.1900	0.1229	0.1145	0.0684	0.0688	0.0423
16	4	111,319	67,101	30,976	23,855	34,258	0.1997	0.1339	0.1190	0.0703	0.0726	0.0431
16	8	219,552	130,161	61,952	45,295	66,880	0.2069	0.1382	0.1250	0.0721	0.0734	0.0449
16	∞	215,960	125,808	61,952	42,656	65,536	0.2122	0.1400	0.1306	0.0729	0.0722	0.0462

previous study (Wheeler and Hayashi, 1998). For all analyses, as with the morphological data alone, TBR branch swapping was performed with 128 random addition sequences and 25 Ratchet TBR replicates (Nixon, 1999).

Since phylogenetic results can depend critically on the assumptions made to perform the analysis (Wheeler and Gladstein, 1992–1996, 1994; Wheeler, 1995), multiple analyses were performed to examine the effect of variation in two parameters on phylogenetic outcome. These parameters, insertion:deletion cost (indel) and transversion:transition ratio (TvTi), were varied and data sets were analyzed together as well as separately. The indel cost was applied as the relative cost of the insertion or deletion of a base versus a base change. In other words, if an indel ratio of 2:1 were specified, two base changes would be taken as equal in cost to a single insertion or deletion event. When the overall cost of a phylogenetic topology is determined, the weighted sum of the events is minimized. The analyses performed here varied the relative indel cost from equal to base substitutions to 2, 4, 8, and 16 times as costly (if the transversions and transitions were weighted unequally, the indel cost was set in relation to the transversion cost). Analogously, the transversion:transition weights are specified and employed identically except that instead of a final 16:1 ratio, a transversion-only scheme (transition cost = 0, hence made no contribution to cladogram length) was used. With a transversion:transition cost ratio of 1, all base substitutions are treated equally, whereas a ratio of 4:1 would count four transitions as equal to a single transversion. In all cases where morphological data were included, character transformations for morphology were weighted as equal to the indel cost.

The five ratios were used for both the insertion:deletion cost and transversion:transition cost, resulting in 25 sets of assumptions and 100 phylogenetic results (Table 3). In each case, the character incongruence was calculated (ILD of Mickevich and Farris, 1981) for the combinations of molecular, morphological, and total analyses (Table 3; Fig. 9). A rescaled ILD (RILD for want of a better acronym; Wheeler and Hayashi, 1998) was also calculated for each analysis. This value is derived along the lines of the retention index by normalizing homoplasy levels with respect to maximum and minimum possible levels of incongruence. Where

the ILD is calculated by dividing the difference between the overall tree length and the sum of its data components,

$$\text{ILD} = (\text{Length}_{\text{Combined}} - \text{Sum Length}_{\text{Individual Sets}})/\text{Length}_{\text{Combined}},$$

the rescaled value uses the same numerator but the denominator is the difference between the maximum tree length from the combined data (on an unresolved bush) and the minimum (sum of the individual lengths):

$$\text{RILD} = (\text{Length}_{\text{Combined}} - \text{Sum Length}_{\text{Individual Data}})/(\text{Max Length}_{\text{Combined}} - \text{Sum Length}_{\text{Individual Sets}}).$$

The benefit of this rescaled index is that it does exhibit the trivial minimum (0) as data set weights become increasingly disproportionate.

MORPHOLOGICAL RESULTS

Phylogenetic analysis of the 275 morphological variables yielded four equally parsimonious cladograms of length 484 (CI = 0.71, RI = 0.83; Fig. 10). These cladograms differed in the status of the Entognatha as monophyletic or paraphyletic with the Diplura sister-group to the remaining Insecta and the placement of the Plecoptera + Embiidina as sister-group to the Orthoptera + Phasmida or at the base of the Polyneoptera. The characters that are cited and plotted in Fig. 10 as supporting groups are those that are independent of optimization. They do not include other features that may ambiguously optimize to the base of a clade; hence the cited features are a conservative set. Complete character descriptions and citations are in Appendix 1.

Hexapoda

The features that are apomorphic to the Hexapoda depend, to some extent, on the disposition of the Diplura. Whether this group is monophyletic or not, the hexapods are characterized by a maxillary plate

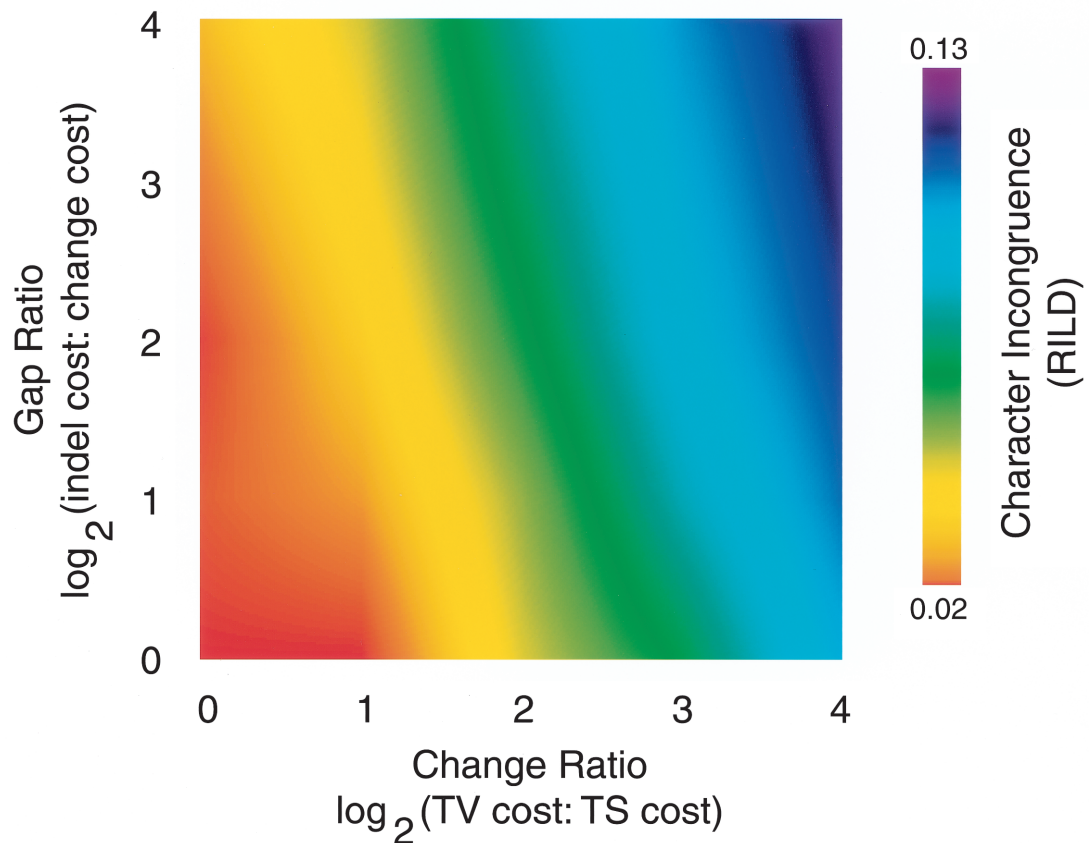# Rescaled Character Incongruence Among Data Sets

FIG. 9.   Sensitivity plot for rescaled character incongruence (RILD) of Table 3. The axes are the analysis parameters of indel:transversion cost ratio and transversion:transition cost ratio. Red denotes low character incongruence among data sets, blue denotes high incongruence.

[character 13], tagmosis with distinct thorax and abdomen [20], hexapody [21], 6-segmented limbs (Collembola are 5-segmented with a tibio-tarsus) [22], 11-segmented abdomen plus a telson (Collembola again vary with a 6-segmented abdomen) [23], jointed knee [24], second maxillae fused to form a labium [25], epimorphic segmental growth (Protura show anamorphic) [27], two primary pigment cells in ommatidia (Protura and Diplura are blind, but the eyes of Collembola cause this feature to be optimized to the base of the hexapods) [29], the presence of a trochantin (absent in Protura, Ephemerida, Odonata, and Strepsiptera) [88], and the presence of an arolium (absent in paleopterans) [73].

Entognatha

The consensus cladogram does not contain this group. When the Entognatha are supported, the group is united by entognathy [30] and loss of compound eyes (but with dispersed ocelli in Collembola) [31]. When the Diplura are treated as sister-group to the Insecta, these two taxa are united by the presence of cerci originating from appendages of the 11th abdominal segment (absent in the Paraneoptera and simplified in some polyneopterans) [28] and the paired pretarsal claw of the larval leg (lost in Hymenoptera + Mecopteroidea) [140].
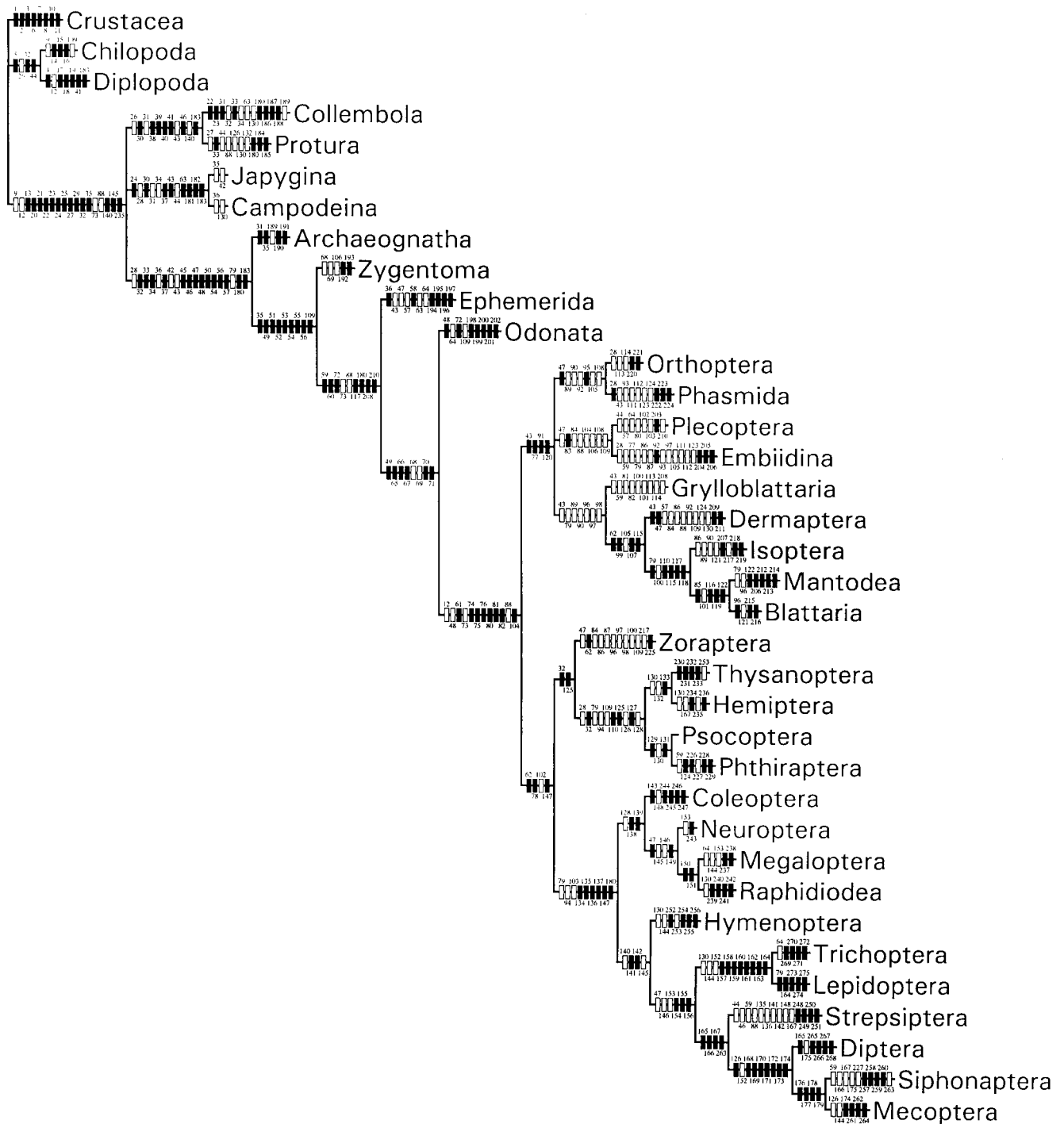
FIG. 10. Hexapod relationships based on the 275 morphological characters described in Table 2 and Appendix 1. This is the strict consensus of four equally most parsimonious cladograms of length 484 (CI = 0.71, RI = 0.84). The solid boxes represent nonhomoplastic changes and the open squares represent homoplastic changes in the numbered characters. Optimizations and figure using CLADOS (Nixon, 1995) defaults.

Ellipura

The Protura and Collembola are united by (presumably) secondary postantennal organs [26], extreme entognathy with labium obliterated [30], linea ventralis [38], enlarged epipharyngeal ganglia [39], entognathous position of the pseudocommissure of stomatogastric nervous system [40], coiled and immotile sperm [41], posterior tentorium with separate arms [46], and a terminal gonopore [183].

Diplura

The characters supporting monophyly are interlocking superlinguae [63], terminal mandibular teeth [181], and a unique femoral–tibial pivot [182].

Insecta

Synapomorphies of the insects with external mouthparts are well-developed Malpighian tubules [32], annulated antennae [33], two pretarsal claws articulated with tarsus [37], antennal circulatory organs with separate ampullary enlargements (many missing observations though) [43], presence of Johnston's organ [45], posterior tentorial arms fused [46], ovipositor (several modifications in the higher Neoptera) [47], caudal filaments (lost in Neoptera) [48], dicondylic femoro-tibial articulation [50], presence of a postoccipital ridge [54], amniotic cavity [56], median fusion of male penes [57], and ocelli present in all stages (lost in immatures in Eumetabola) [79].

Dicondylia

Synapomorphies for the Zygentoma and pterygote insects are dicondylic mandibular articulation (later modified in Metapterygota—but the character is additive) [49], presence of a distinct gonangulum in the ovipositor base [51], origin of the ventral mandibular and maxillary adductors on the tentorium [52], fulturae [53], continuous postoccipital ridge [54], tracheal commissures and connectives developed in abdomen [55], closed amniotic cavity [56], and five segmented tarsi (further reduced to three and two segmented in some taxa—this character relates to the placement of *Tricholepidion*—see Appendix 1) [109].

Pterygota

The winged insects are characterized by two pairs of wings (although wings may be lost in higher neopteran taxa) [59], two coxal proprioreceptor organs [60], sperm transfer through copulation (claspers in Odonata) [72], a corporotentorium [117], coxa–body articulation that is pleural and fixed [180], the lack of an eversible vesicle on abdominal segment I (present in grylloblatids) [208], and the presence of a transverse stipital muscle (lost in Plecoptera) [210].

Metapterygota (Börner, 1904)

The characters supporting the monophyly of the Odonata and Neoptera are the fixation of the anterior mandibular articulation [49], lack of a subimago [65], anterior and posterior trunks are fused into an arch in the wing and leg tracheae [66], posterior tracheation of the pterothoracic leg [67], a single bundle of tentorio-mandibular muscles [70], and the loss of some pterothoracic muscles [71].

Neoptera

Features that are apomorphic for the Neoptera are the absence of coxal vesicles and styli [12], absence of a caudal filament [48], absence of a basal wing brace [61], characteristic wing flexion derived from a muscle insertion on the third axillary sclerite [74], third valvulae forming a sheath over the first and second ovipositor [75], presence of an anal furrow on wing [76], non-metameric testis ducts [80], the male gonocoxopodites IX are not articulated (with the exception of the Grylloblattaria) [81], absence of metaspina (again reversed in Grylloblattaria) [82], and the absence of a separate coxopleuron (reversed in Plecoptera + Embiidina) [104].

Polyneoptera

Synapomorphies of the orthopteroid insects include the enlarged hind-wing vannus (not in Embiidina and inapplicable in the Grylloblattaria) [77], presence of two cervical sclerites [91], and tarsal plantulae [120]. Within the Polyneoptera, the Plecoptera and Embiidina are united by a shared lack of an ovipositor (this is

also true of Zoraptera, Ephemerida, and some Holometabola) [47], reduced phallomeres [83], suppressed male styli (also in Zoraptera) [84], trochantin with an episternal sulcus (also in Dermaptera) [88], and median ventral excurrent ostia in dorsal vessel (also in lepismatoids) [106]. Synapomorphies for the Orthoptera + Phasmida are a uniquely modified ovipositor [47], prognathy (also in Dermaptera) [92], and a prominent precostal field [95]. The dictyopteran–dermapteran–grylloblatid lineage is united by a discoid pronotum (lost in mantids and also present in Zoraptera) [96], forward slanting pleural sutures (also present in embiids and Zoraptera) [97], and reduction in the indirect wing muscles (again also present in Zoraptera) [98]. The synapomorphies of the Dermaptera + Dictyoptera are the MA + R fusion of the forewing media (but inapplicable for grylloblattids) [62], weak or suppressed metathoracic tergosternal wing elevators [99], mesothoracic basisternal fold [107], and female sternum VII enlarged (forms a vestibulum in the Dictyoptera—additive character) [115]. The Dictyoptera are supported by a reduced sternum I [110], female sternum VII formed into a vestibulum [115], perforated corporotentorium [117], and the anterior teeth of proventriculus forming a ring of strongly sclerotized teeth [118]. The synapomorphies of the mantids and roaches include the presence of segmental arteries [85], asymmetrical phallomeres (also in grylloblattids) [101], XX/XO sex determination [116], proventriculus teeth with secondary dentricles [119], and ootheca [122].

Eumetabola

Synapomorphies for this group include R + M forewing media fusion [62], presence of a "jugal bar" [78], a "holometabolan" type mesotrochantin [102], and cryptosterny [147].

Zoraptera + Paraneoptera

This group is characterized by the number of Malpighian tubules (six or four) [32] and the concentration of abdominal ganglia into one or two masses [125].

Paraneoptera

Features that unite these taxa are the absence of cerci [28], four Malpighian tubules [32], absence of sternum I [110], one concentrated abdominal ganglion [125], lacinial stylets [126], and spermatozoa with two flagella [127]. Within the Paraneoptera, the Psocodea ("Psocoptera" + Pthiraptera) are supported by a cibarium [129] and the basal part of the antennal flagellomeres without rupture-facilitating cuticular modification [131]. The synapomorphies of the Condylognatha (Thysanoptera + Hemiptera) include stylettiform mandibles [132] and sclerotized rings between the antennal flagellomeres [133].

Holometabola

The endopterygote insects are united by their shared grooved first branch of Cu (also in Plecoptera; inapplicable in Siphonaptera) [103], complete metamorphosis [134], larval eyes not carried over into the adult (not true of Strepsiptera) [135], wing rudiments evaginated at larval–pupal molt [136], appearance of external genitalia at the penultimate molt [137], cryptosterny [147], and tricondylic coxa–body articulation [180].

Neuropteroidea + Coleoptera

These taxa are jointly characterized by cruciate cervical muscles [138] and unique female genitalia characterized by strong reduction and fusion of the first valvulae, the second valvulae not discrete, and the cerci not articulated [139].

Hymenoptera + Mecopteroidea

The synapomorphies for this lineage include unpaired pretarsal claw of the larval leg [140], silk secretion from larval labial glands (not in Strepsiptera though probably inapplicable) [141], and eruciform larvae [again not in Strepsiptera, Nannochoristidae, and some basal Lepidoptera (Kristensen, 1991)] [142].

FIG. 11. Total evidence cladogram of hexapod relationships that minimizes total character incongruence among all data. This cladogram is a strict consensus of the 132 cladograms derived from the combined morphological, 18S rDNA, and 28S rDNA data. Each morphological character transformation was weighted 2, as were insertion:deletion events. Transition and transversion events each were weighted 1. This minimum tree length of 6516 weighted steps was generated and diagnosed using the optimization-alignment procedure of Wheeler (1996) implemented in POY (Gladstein and Wheeler, 1997).
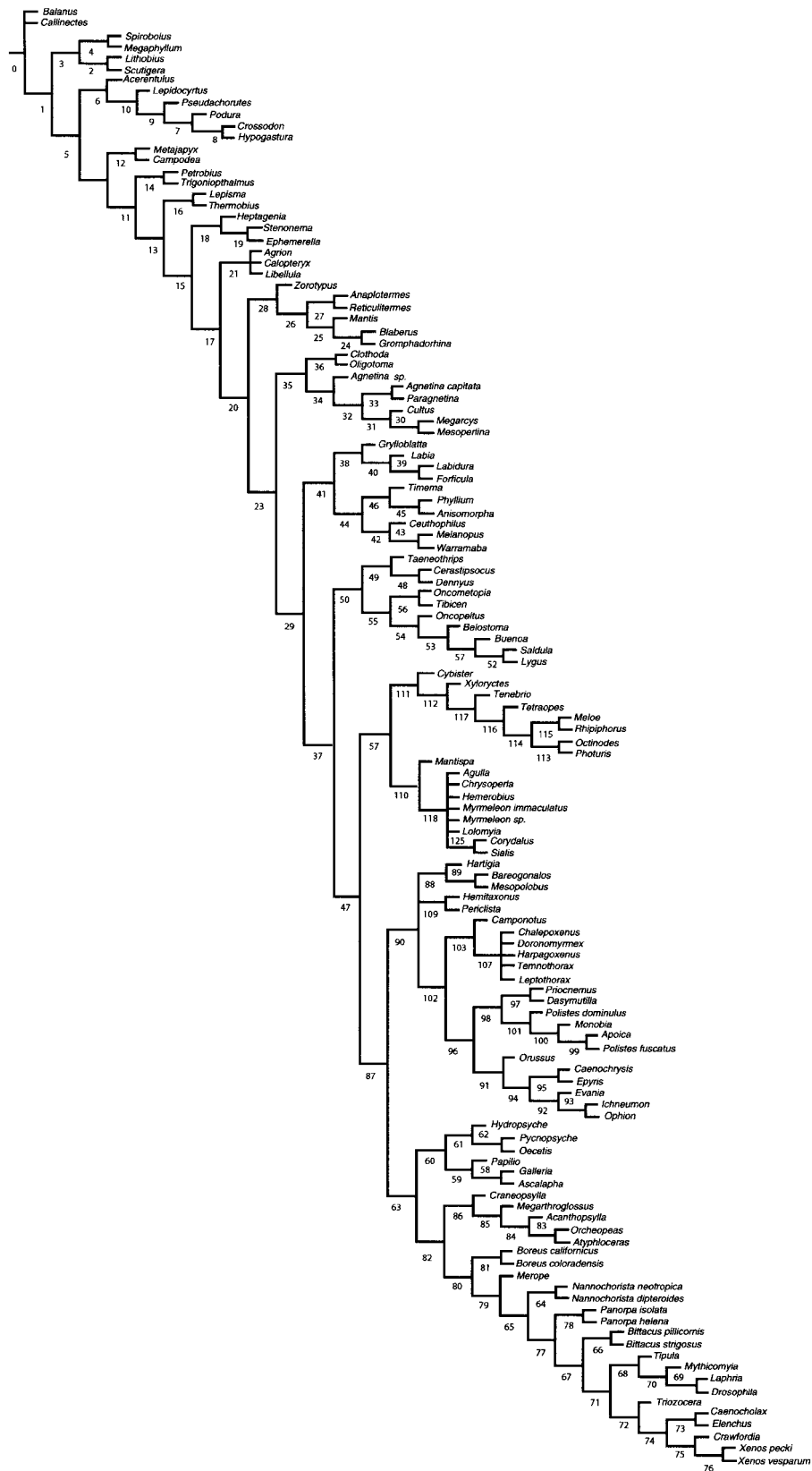
Mecopteroidea

The Amphiesmenoptera and Antliophora are united
by the absence of an ovipositor (but this condition
occurs in Zoraptera, Embiidina, Plecoptera, Ephemer-
ids, and Entognatha) [47], the presence of a meron (but
also present in Neuropteroidea) [146], a divided larval
stipes (also in the Neuroptera s.s. and Megaloptera)
[153], the loss of some labial and larval muscles [154],
a cranial antagonist of the primitive craniolacinial mus-
cle in larvae [155], and the absence of the outer pteroth-
oracic tergocoxal remoter [156].

Amphiesmenoptera

Characters that unite this group include female het-
erogamety [157], double Y-shaped fusion of anal veins
[158], achiasmatic oogenesis [159], preholocentric chro-
mosomes [160], pterothoracic furcal arms fused with
epimeron [161], pair of glands opening on sternum V
[162], outer accessory filaments of sperm flagellum
very stout [163], and vestiture on wing surfaces be-
tween veins of long setae or scales [164].

Strepsiptera + Antliophora

This group is supported by a dagger-like mandible
with anterior articulation reduced (secondarily lost in
Diptera and Siphonaptera) [165], only a single endite
lobe present in maxilla and none in labium (not in
Siphonaptera) [166], reduction in labial palp segments
(again not in Siphonaptera) [167], and a ring-like male
abdominal segment IX (not in Siphonaptera, but see
Whiting, 1998b) [263].

Antliophora

Synapomorphies of this taxon include the loss of the
prelabial tentorial muscles [168] and modified poste-
rior notal wing articulation (but inapplicable in Si-
phonaptera) [169]. For a description of these features
in Strepsiptera see Whiting (1998b).

Siphonaptera + Mecoptera

This clade is united by the absence of extrinsic labral
muscles [176], proventriculus with specialized type of
cuticular processes (acanthae) [177], flagellum of sper-
matozoon coiled around straight axial mitochondrion
[178], and completely fused nervi corporis cardiaci
[179].

MOLECULAR RESULTS

The total (morphological + 18S + 28S), molecular
(18S + 28S), and morphological and combined molecu-
lar (18S + 28S) analyses achieved minimum incongru-
ence with different transformation cost parameter val-
ues (Table 3). The total, combined analysis achieved
minimum character incongruence when indel (and
morphological character transformations) cost was
twice that of base substitutions and transitions equal
to transversions (Fig. 11), while the molecular analysis
(18S versus 28S) was at minimum incongruence with
indels, transitions, and transversion all equal (Fig. 12a),
and morphological versus molecular (18S + 28S)
achieved optimal character agreement when indels
(and morphological changes) were equal to transver-
sions, but transitions had only one quarter the weight
of transversions (Fig. 12b).

Both the small (18S rDNA) and the large (28S rDNA)
analyses contain groups clearly not supported by any
other source of evidence (Figs. 13 and 14). Of a total
of 30 "orders," 23 were sampled more than once. The
28S data alone supported only 10 of these as monophy-
letic clades. The 18S rDNA data performed (by this
measure) slightly better, presenting 18 monophyletic
orders. When the molecular data were combined, again
18 of the 23 were supported. Of the remainder, 3 (Mec-
optera, Phasmida, Hymenoptera) were paraphyletic
and 2 (Diplura and Neuropteroidea) had two origins.
When the morphological and molecular data were ana-
lyzed together, 22 of 23 orders were monophyletic
(Mecoptera remain paraphyletic). If ordinal member-
ship (really a morphological congruence criterion) is
used to measure the behavior of combining data, then
the combination of sources of information is clearly
positive.

The main outlines of the ordinal relationships based
solely on molecular information are in broad agree-
ment with morphological schemes with several excep-
tions. On the side of concordance are the basal positions
of the Entognatha, the paraphyly of the Thysanura and

FIG. 12. Combined molecular analysis (18S rDNA and 28S rDNA data) cladogram that minimized character incongruence between the molecular data sets (a) and morphological versus combined molecular data (b). For cladogram a, each insertion:deletion event was weighted 1 as were transitions and transversions. The cladogram is a strict consensus of three cladograms of length 5302 weighted steps. For cladogram b, each insertion:deletion event was weighted 4, transitions were weighted 1, and transversions were weighted 4. The cladogram is a strict consensus of four cladograms of length 16,615 weighted steps. Optimization and computational implementation as in Fig. 11.
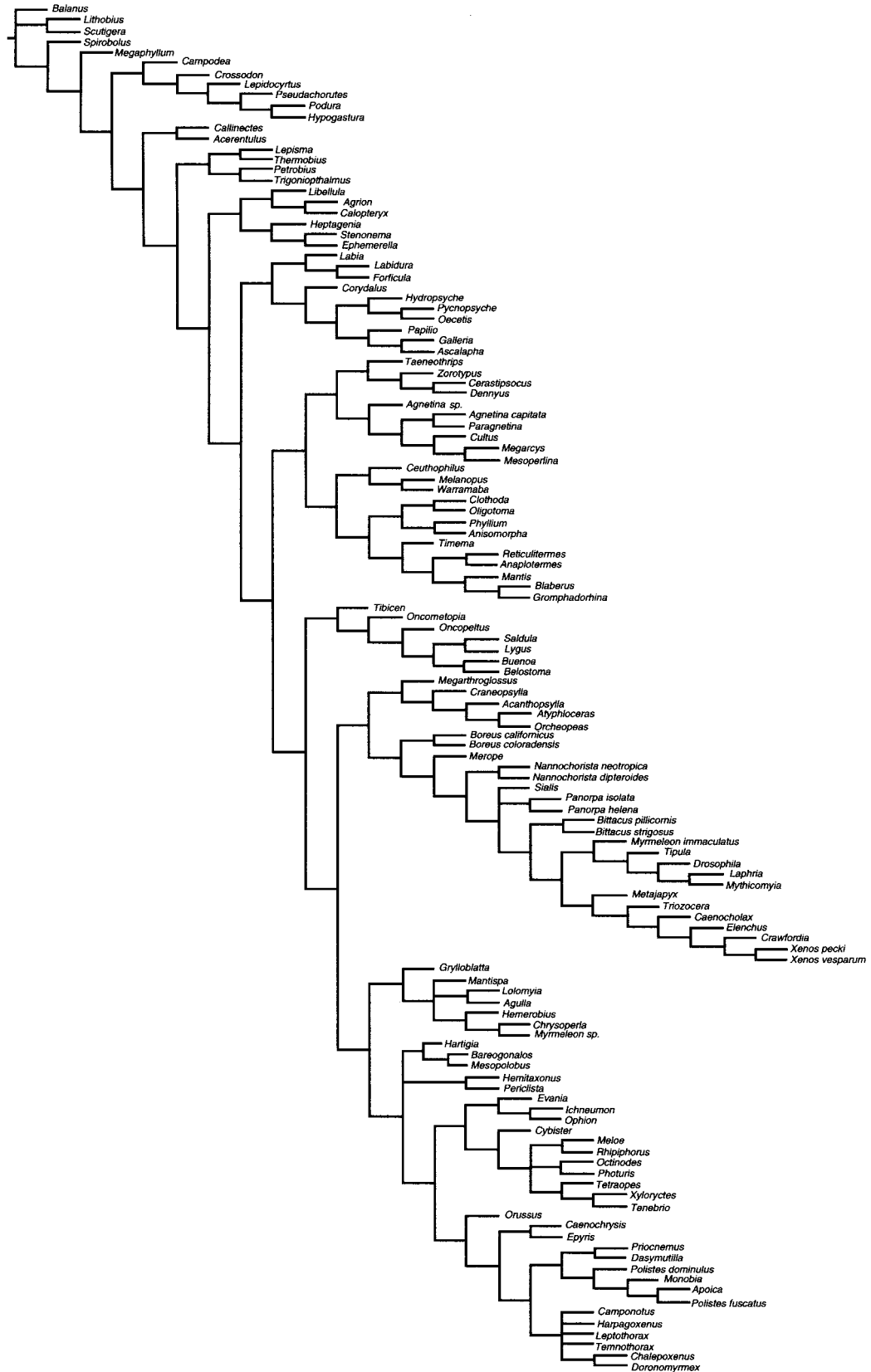
FIG. 13.   Consensus cladogram for the 18S rDNA data at analysis parameters of minimum incongruence. Each insertion:deletion event was weighted 1. Transition and transversion events were each weighted 1. The two constituent cladograms lengths are 6428 weighted steps. Optimization and computational implementation as in Fig. 11.

"Paleoptera," the monophyly of the Dictyoptera and Heteroptera, and the grouping of Diptera + Strepsiptera. Other aspects of the molecular results less concordant with morphological results are four placements: the grylloblattids and Plecoptera coming within the Holometabola, the Zoraptera as sister-group to the Amphiesmenoptera, and the scattering of the Neuropteroidea. The placement of these groups was neither weakly nor strongly supported compared to other molecular groupings. Interestingly, the trees supported by different data sets were not that unparsimonious when other sources of information were optimized on them (Table 4). As an example, the combined molecular data only required 1.05% more steps to optimize the total evidence result and 5.37% for the morphological data alone.

COMBINED ANALYSIS RESULTS

Overall, the simultaneous analyses (morphology + 18S + 28S) where morphological character changes and indels were weighted twice base substitutions (morphological changes = 2, indels = 2, transversions = 1, and transitions = 1) exhibited the lowest levels of character incongruence (Table 3, Fig. 11). This group of analyses was also remarkably stable (Fig. 15). Most of the variations in the cladograms are due to differences between those analyses with indels treated as equally costly to base changes and those where indels are more expensive.

This cladogram, however, is not one of the four most parsimonious results of the morphological analysis alone. The morphological characters in this total evidence analysis were weighted equal to indels. For comparison "all equal" weighting was applied to the data (morphology = indel = transversion = transition) (Fig. 16).

Detailed levels of morphological character change can be seen in Fig. 17. Here, we concentrate on those arrangements that arise from the minimum incongruence combined analysis. All reported character changes are optimization independent.

Diplura + Insecta

The combined analysis strongly supports monophyly of the Diplura + Insecta. With a Bremer support

of 17 weighted steps (out of a tree length of 6516), the group is supported by two unequivocal morphological synapomorphies, the presence of cerci [28] and the paired pretarsal claw of the larval leg [140]. In addition, there were one unequivocal transition in the 18S rDNA data and two unequivocal transversions and an insertion in the 28S rDNA data.

Zoraptera + Dictyoptera

There are four morphological synapomorphies for this clade. These are the presence of a discoid pronotum [96] (modified in Blattaria but absent in Mantodea), forward slanting pleural sutures [97] (but also present in Embiidina, Grylloblattaria, and Dermaptera), a reduction in the indirect wing muscles [98] (also seen in in the Grylloblattaria and Dermaptera), and a modified coxa [100] (also in the Grylloblattaria). Unambiguous molecular support comes from four transitions, one transversion, and two insertions in the 18S and four additional transitions and six transversions in the 28S. The overall Bremer support value of 23 weighted steps arises entirely from the combination of data. None of the constituent data sets support this group alone.

(Plecoptera + Embiidina) + (((Gryllobattaria + Dermaptera) + (Orthoptera + Phasmida)) + Eumetabola)

No morphological synapomorphies map to this clade. The small ribosomal DNA data show a single transversion and a single deletion, while the 28S data show a transition, two transversions, and three deletions. The overall Bremer support was 10 weighted steps, again arising entirely from the combination of data.

((Gryllobattaria + Dermaptera) + (Orthoptera + Phasmida)) + Eumetabola

No morphological synapomorphies map to this clade. The 18S rDNA data support this group with two transversions, a single transition, an indel, and a molecular change that could be one of several types. The overall Bremer support was only two weighted steps arising entirely from the combination of data.
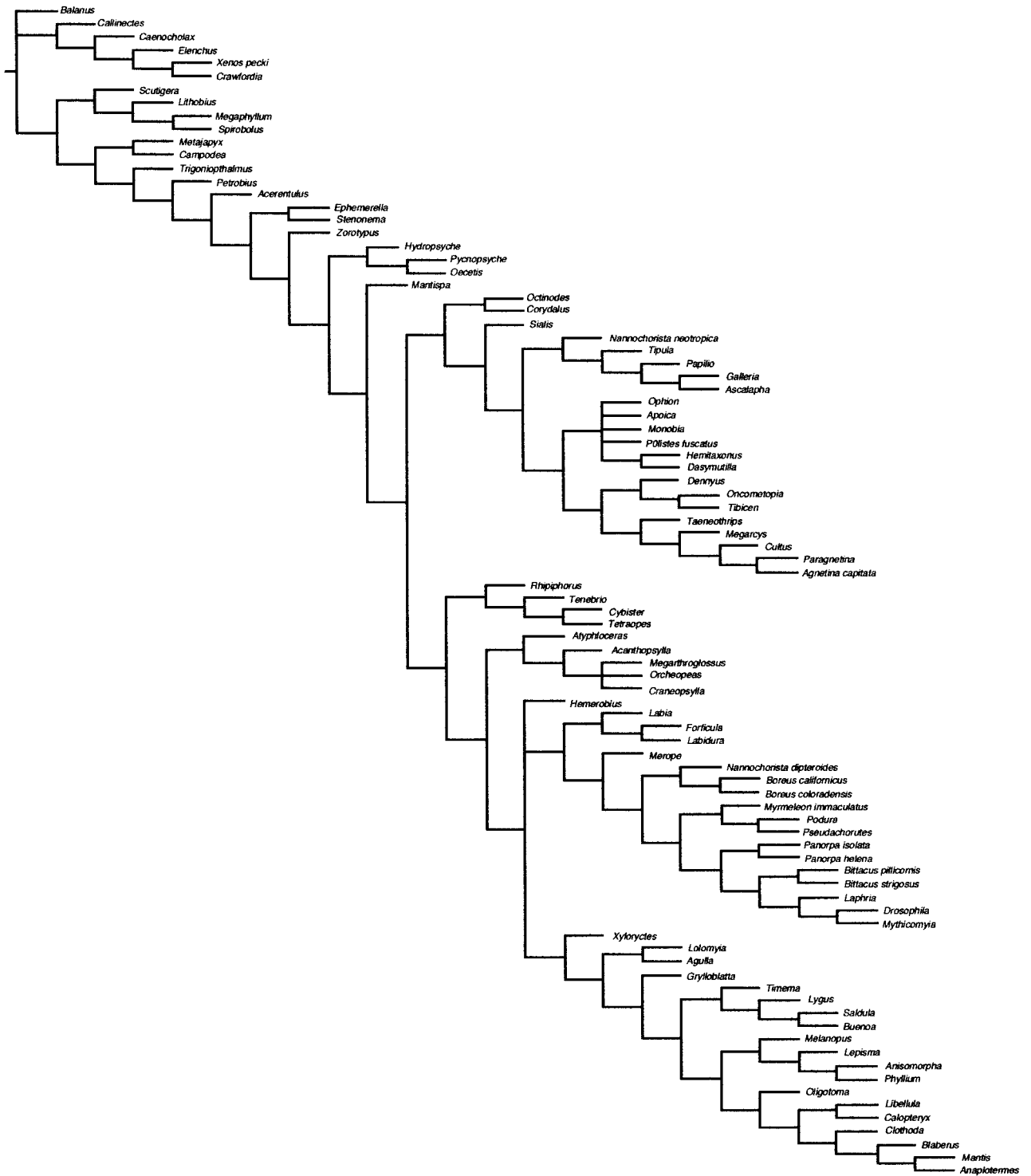
FIG. 14.   Minimum length cladogram for the 28S rDNA data at analysis parameters of minimum incongruence. Each insertion:deletion event was weighted 1. Transition and transversion events each were weighted 1. The single cladogram length is 3026 weighted steps. Optimization and computational implementation as in Fig. 10.

TABLE 4
Comparison of Cladogram Lengths Derived from Data Partitions

	Cladogram			
Data set	Combined	18S + 28S	Morphology	18S
Combined	—	8.06%	8.07%	12.80%
18S + 28S	1.05%	—	11.70%	3.50%
Morphology	5.37%	65.50%	—	78.10%
18S	2.47%	1.19%	8.70%	—
28S	6.84%	6.18%	27.80%	20.00%

Note. Since the 28S data are a subset of the 18S and morphological data sets (fewer taxa), diagnosing other cladograms with 28S data alone is uninformative.

(Thysanoptera + Psocodea)

There are no morphological synapomorphies that map to this clade, but it has very strong molecular support. In the 18S rDNA data, 10 transitions and 4 transversions characterize the clade. The 28S presents 4 transitions, 6 transversions, and a single deletion. The Bremer support is 10 weighted steps.

(Mecoptera + (Strepsiptera + Diptera))

This clade is supported by two unequivocal morphological changes, the presence of a single endite lobe on the maxilla and none on the labium [166], and ringlike male segment IX [263]. The molecular support is weak with a single 18S transition and a single 28S transition. The Bremer support is 13 weighted steps.

(Bittacidae + (Strepsiptera + Diptera))

The paraphyly of the Mecoptera has no support from morphological variation but this node has 32 unequivocal molecular changes defining the node. The 18S rDNA present 5 transitions, 10 transversions, and 5 indels, while the 28S data yield 5 transitions, 6 transversions, and one change of unknown type. This clade has a Bremer support of 18 weighted steps.

(Strepsiptera + Diptera)

There are no unequivocal morphological synapomorphies for this group, but there are 43 unequivocal

molecular changes: 8 transitions, 8 transversions, and 7 indels in the 18S and 6 transitions, 8 transversions, and 6 indels in the 28S. The Bremer support for this clade is 44 weighted steps.

STABILITY

Support for all groups is dependent on the analytical assumptions we make. The notion of stability or sensitivity (sensu Wheeler, 1995) embraces this idea. In the analysis performed here, insertion:deletion costs and transversion:transition ratios were varied, and the effects on phylogenetic arrangements were determined. As mentioned above, the area of maximum agreement among the various sources of data is found when gaps were weighted twice that of base substitutions and transitions and transversions treated equally (Table 3 and Fig. 15a). Some of the groups described at this maximum character agreement (or minimum incongruence) are not generally supported (over a wide variety of parameter values). To examine this, the consensuses of various combinations of individual results were constructed.

The first sample was created to determine which groups are constant, invariantly supported over all combinations of analysis parameters tested. To do this, the strict consensus was constructed over the 25 combined evidence analyses. Forty-seven groups (out of a possible 126 nontrivial) were present no matter how extreme the analysis conditions (Fig. 15a). These constant groups include all the orders (including Diplura) with the exception of the Mecoptera and Neuropteroidea. Of the higher clades, included are Hexapoda, Insecta, Dicondylia, Pterygota, Metapterygota (Odonata + Neoptera), Paraneoptera, Holometabola, and Halteria (sensu Whiting and Wheeler, 1994). Many of these groups are unexceptional. The placement of the Odonata with the Neoptera in all situations along with other more basal and derived distinctions is strong support for Kristensen's (1975) hypothesis. This same level of confidence is placed in the union of the Strepsiptera and Diptera, agreeing with several earlier analyses (Whiting and Wheeler, 1994; Whiting *et al.* 1997). A consensus cladogram displaying all those clades present in greater than half the analyses shows more resolution (Fig. 15b)—not surprisingly—with 97
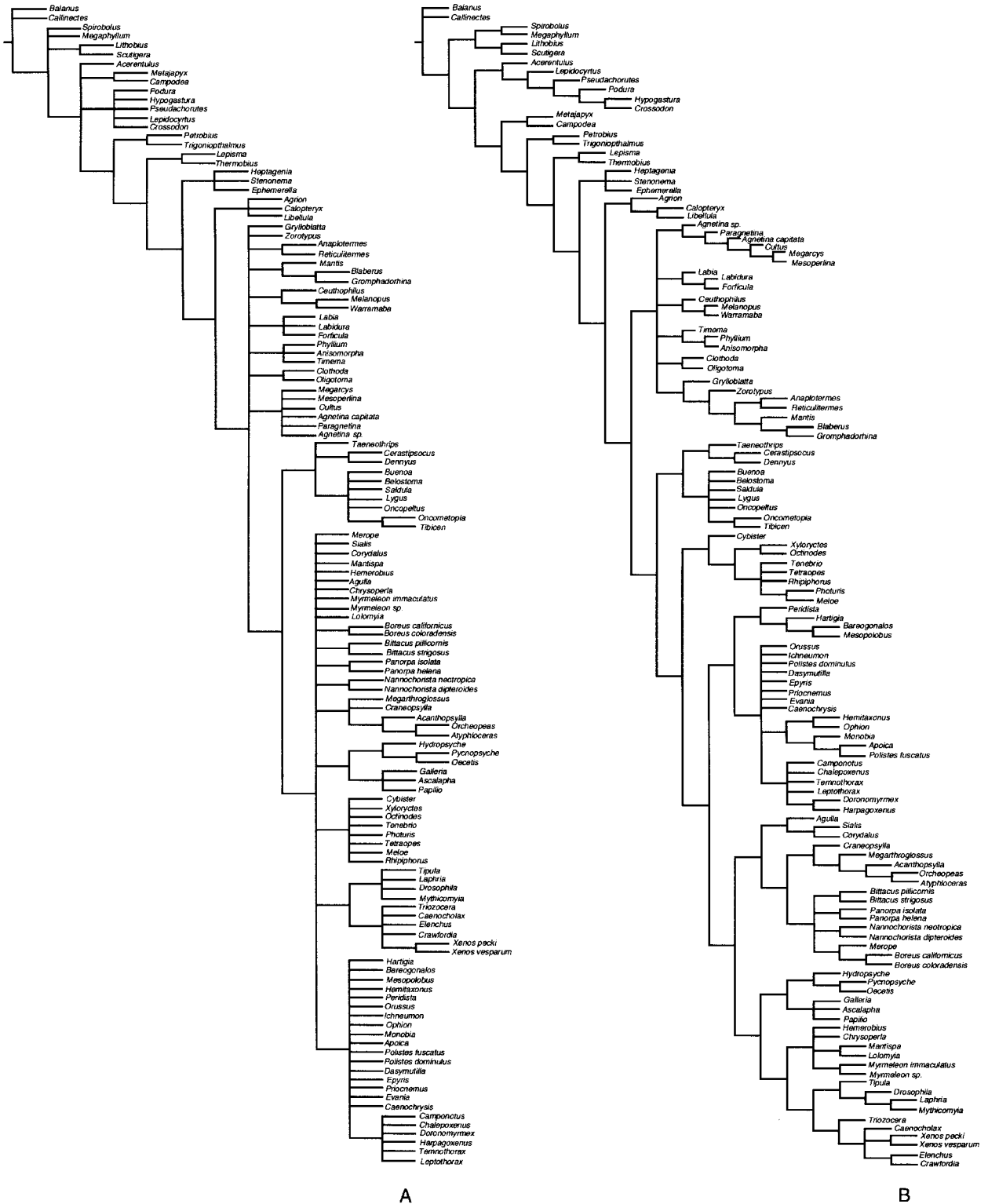
FIG. 15. Consensus cladograms for total evidence analyses over all (25) analysis parameter sets (Table 3). (a) Strict consensus; (b) 50% compromise tree (Nixon and Carpenter, 1996b).
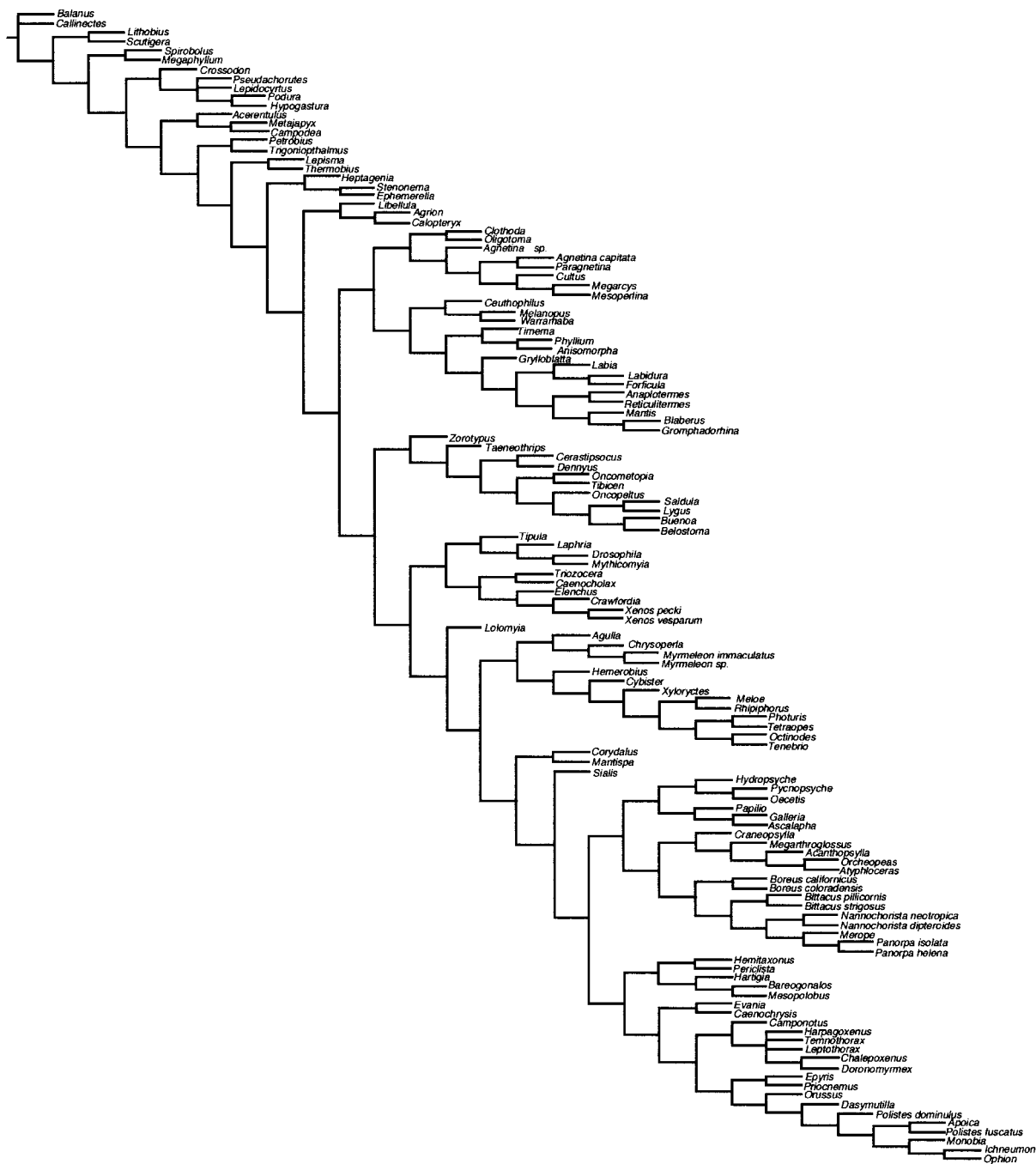
FIG. 16. Strict consensus cladogram of two equally parsimonious cladograms based on total evidence analysis of hexapods where all character transformations were weighted equally (1). This cladogram is derived from the combined morphological, 18S rDNA, and 28S rDNA data. Each morphological character transformation was weighted 1, as were insertion:deletion, transition, and transversion events. The two constituent cladograms lengths were 10,861 weighted steps. Optimization and computational implementation as in Fig. 10.
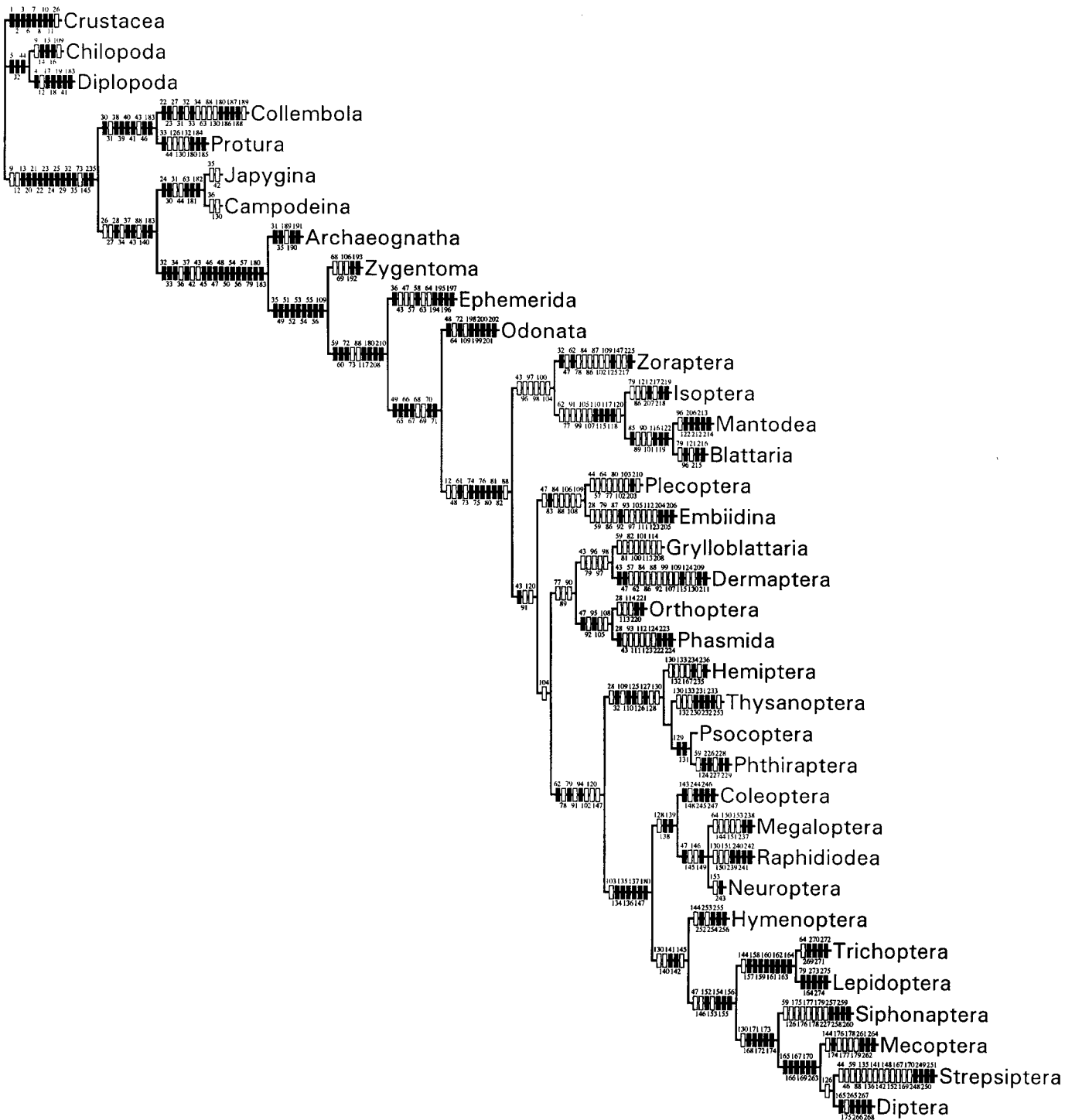
FIG. 17. Morphological characters described in Table 2 and Appendix 1 optimized on the minimal incongruence ordinal cladogram of Fig. 11. This cladogram has a length of 504 steps for the morphological characters alone. The solid boxes represent nonhomoplastic changes and the open squares represent homoplastic in the numbered characters. Optimizations and figure using CLADOS (Nixon, 1995) defaults.

resolved clades. Other supported groups include the Mecoptera (96%) and some of the more traditional higher taxa: Ellipura (64%), Neoptera (100%), Mecoptera + Siphonaptera (96%), Amphiesmenoptera (100%), an enlarged Polyneoptera (Zoraptera + orthopteroids—72%), and Eumetabola (100%). The surprising placement of the Zoraptera with the Dictyoptera (72%) is in the same polyneopteran placement as the most favored tree. In agreement with the most congruent topology, the Diplura are placed with the Insecta (à la Kukalová-Peck) in 68% of the analyses. There were four major placements in the majority rule consensus of all analyses that disagreed with the most congruent topology. These were the monophyly of the Polyneoptera (including Zoraptera), the monophyly of the Mecoptera (96% paraphyletic with respect to Halteria in the most congruent tree), the Siphonaptera + Mecoptera (96%), and the division of the Coleoptera + Neuropteroidea. These 96% figures for disagreeing clade placements mean that the result in the most congruent tree is present in only that one result; i.e., all other analyses yielded a different (and constant) result. Clearly, these placements in the favored topology are highly unstable.

Another examination of the robustness of the 115 clades present in the most congruent cladogram was performed through comparing the "best" result to those with indel costs and transversion:transition cost ratios adjoining the most congruent. In this case, parameter sets adjacent to an indel cost of 2:1 and transversion:transition of 1:1 are the four results based on an indel cost of 1:1 and TvTi of 1:1, an indel cost of 2:1 and TvTi of 2:1, and that based on an indel cost of 4:1 and TvTi of 1:1 (Fig. 18). A great deal of resolution is lost with only 54 groups supported over these five parameter sets. The Polyneoptera are hit especially hard.

Overall, the relationships among the Polyneoptera, the status of the Mecoptera, and the placement of the Neuropteroidea are least robust to parameter variation. Roughly one-third of the groups in the most congruent "best" cladogram are uniformly present, no matter what analysis assumptions were made. These included basal Hexapoda, Paraneoptera, and the Strepsiptera + Diptera.

SUPPORT

The degree of character support for each resolved node in the most congruent cladogram is summarized in Table 5. Not surprisingly, Bremer (1994) support values and branch lengths show a scattered correlation (Fig. 19). When individual Bremer supports are compared among the morphological, 18S, and 28S data, the numbers are not additive. An example of this would be Dictyoptera. The small subunit (18S) data yield a Bremer value of 6 steps, the large subunit (28S) data yield 0 steps (there was another topology of equal length for these data), and the morphology data yield -2 weighted steps (there was another topology 2 steps shorter for the morphology alone). These values sum to 4, whereas the actual total support is much higher at 35 steps. The reason these numbers are not additive is that the ordered hierarchies of tree lengths are not identical for these data sets. The second best (or best) cladograms for the 18S data are not necessarily the same for the 28S or morphology. The interaction of these data sets potentiates the support—a phenomenon seen only in combined analyses.

In terms of Bremer values, the most supported taxa in the analysis are several of the hexapod orders. Ranging down from a high of 81 steps (on a 6516-step cladogram), the highest support values were for the Strepsiptera (81 steps), Trichoptera (79), Diptera (68), Dermaptera (59), Lepidoptera (57), Embiidina (45), Ephemerida (43), and Collembola (34). The most supported superordinal clade was the Insecta at 48 steps. Other highly supported taxa were Neoptera (44), Strepsiptera + Diptera (44) and Amphiesmenoptera (Lepidoptera + Trichoptera) (40). The least supported order was the Hemiptera at 6 steps, while the lowest supported higher taxa was the Hymenoptera + Mecopteroidea (2).

DISCUSSION

Of the more than 30 ordinal relationships proposed in this analysis, several merit special attention: the status of the Diplura and Mecoptera, relationships within Dictyoptera, the placement of the Zoraptera, and the
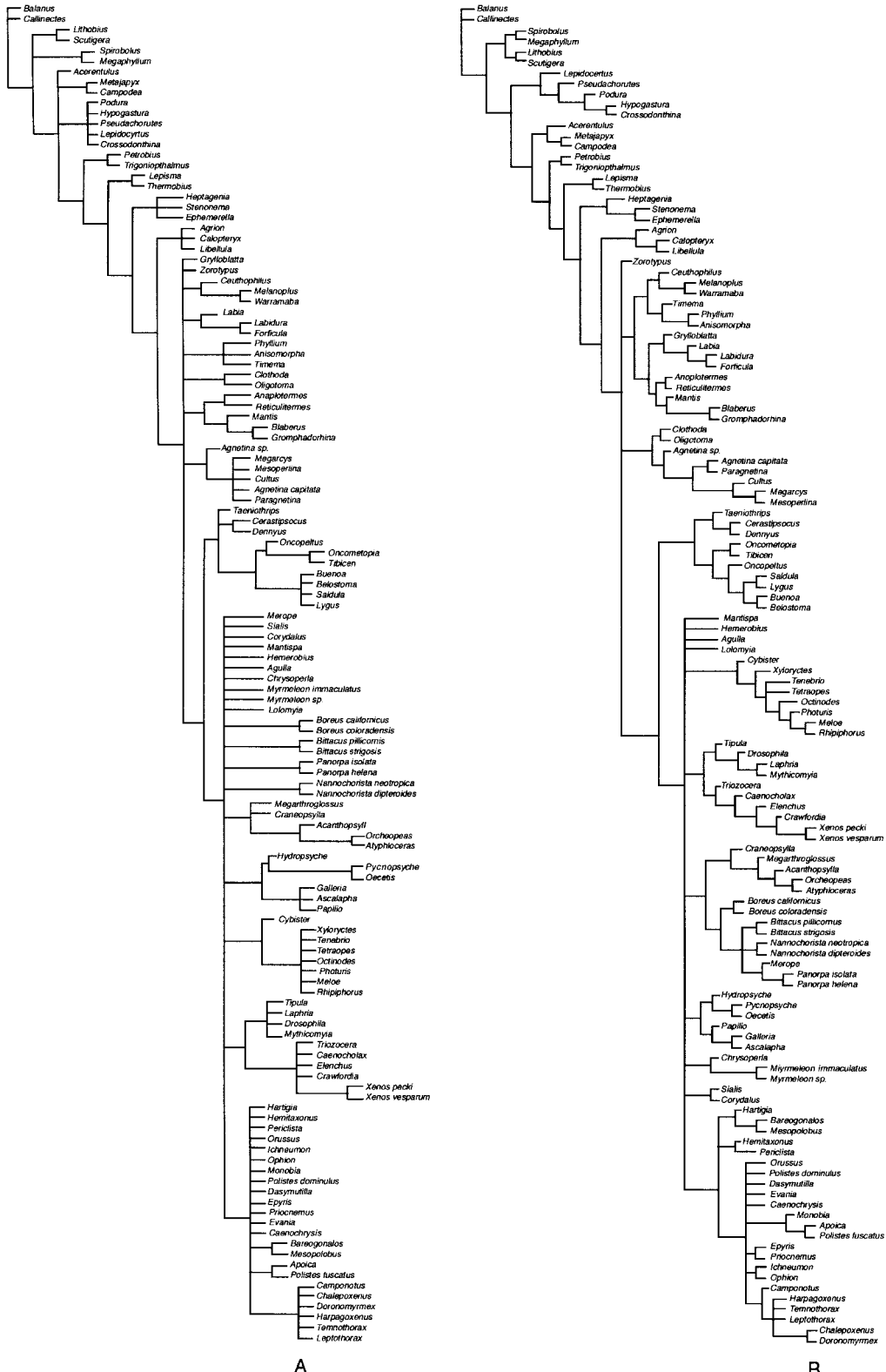
FIG. 18.   Consensus cladograms for the three total evidence analyses analysis parameter sets adjacent to the minimal incongruence set (morphology = indel = transversion = transition = 1; morphology = indel = 4, transversion = 2, transition = 1; morphology = indel = 4, transversion = 1, transition = 1). (A) Strict consensus, (B) 50% compromise tree (Nixon and Carpenter, 1996b).

TABLE 5

Bremer Support and Branch Length Values for Least Incongruent Cladogram

Node[a]	Combined data Bremer	18S Bremer	28S Bremer	Morphology Bremer	Minimum branch length	Maximum branch length
0	35	9	−8	16	40	101
1	29	−2	−7	18	36	98
2	19	10	−11	8	31	47
3	17	−5	0	6	24	63
4	27	−1	0	12	32	57
5	17	−5	−8	4	9	64
6	18	−2	−5	4	48	115
7	3	3	0	0	6	10
8	2	2	0	0	3	3
9	5	−2	0	0	12	60
10	34	10	−8	14	58	139
11	48	3	−8	28	50	112
12	27	1	0	8	29	119
13	31	−2	−8	16	28	53
14	14	7	−5	6	20	38
15	38	3	−8	10	29	59
16	11	5	−4	6	17	114
17	15	3	−8	2	25	51
18	43	14	−7	22	41	79
19	5	5	−2	0	8	81
20	44	3	−8	16	33	81
21	29	9	−2	12	28	78
23	10	−1	−8	−6	12	40
24	7	0	0	4	7	42
25	21	−1	0	−4	19	33
26	35	6	0	−2	41	90
27	9	3	0	0	9	109
28	23	−1	−6	−6	28	65
29	2	−1	−9	−6	7	32
30	1	1	−3	0	1	16
31	10	3	−3	0	10	20
32	6	6	−6	0	9	73
33	2	1	−5	0	3	8
34	31	9	−9	12	34	94
35	18	−2	−9	10	19	37
36	45	4	0	18	47	60
37	16	−3	−9	2	15	35
38	24	−3	−7	−6	18	49
39	25	8	0	0	23	33
40	59	15	0	18	66	91
41	13	−3	−8	−4	13	40
42	15	4	−5	8	17	35
43	2	0	−5	0	4	20
44	8	−2	−8	2	12	24
45	10	2	−3	0	16	21
46	19	−2	−8	16	25	39
47	26	0	−6	8	32	55
48	10	4	−9	2	23	100
49	10	0	−3	−4	26	56
50	18	−1	−9	14	31	60
51	4	0	−6	−4	2	6
52	6	5	−7	−4	12	17
53	15	14	−7	−4	9	28
54	16	2	−7	10	19	34
55	6	−2	0	−4	20	49
56	5	−9	−8	−2	10	135
57	1	0	−6	−4	9	17

TABLE 5—*Continued*

Node[a]	Combined data Bremer	18S Bremer	28S Bremer	Morphology Bremer	Minimum branch length	Maximum branch length
58	16	4	0	0	6	8
59	57	25	0	10	60	86
60	40	1	−2	12	45	69
61	79	29	0	8	70	102
62	14	10	0	0	26	37
63	15	−9	−8	4	28	61
64	4	1	−8	0	8	21
65	15	−1	−8	−10	8	23
66	14	7	−1	0	33	69
67	18	1	0	−10	37	86
68	68	25	0	0	82	155
69	6	−2	0	0	9	16
70	28	1	−1	0	34	92
71	44	1	−1	−10	68	133
72	81	37	0	20	90	180
73	12	−3	0	4	7	48
74	15	1	0	4	13	89
75	13	6	0	4	12	24
76	9	0	0	4	10	71
77	8	−2	0	−10	14	55
78	16	12	0	0	21	50
79	3	−2	−8	−10	7	19
80	13	−2	−8	−2	16	26
81	15	9	0	0	15	23
82	26	−7	−6	0	34	59
83	6	5	−8	0	8	9
84	1	0	−8	0	1	4
85	18	−2	−8	0	4	5
86	28	−1	−8	8	25	30
87	2	−9	−8	4	10	33
88	1	−3	−8	0	2	3
89	1	−3	−8	0	1	2
90	15	−5	−8	10	21	40
91	1	1	−7	0	1	9
92	1	1	−7	0	1	3
93	4	4	−7	0	5	5
94	2	2	−7	0	2	10
95	1	1	−7	0	3	4
96	2	1	−7	0	3	4
97	3	2	−5	0	5	11
98	3	2	−5	0	3	6
99	8	2	−2	0	6	13
100	7	7	−4	0	9	18
101	2	2	−5	0	2	17
102	2	−3	−7	0	5	10
103	7	5	−6	0	8	10
107	1	1	−6	0	1	1
109	3	0	−6	0	3	6
110	21	−1	−8	6	48	95
111	22	−1	−2	8	21	31
112	9	3	−2	0	10	13
113	3	1	−2	0	7	24
114	3	1	−2	0	3	7
115	6	4	−1	0	8	23
116	1	0	−2	0	5	8
117	2	0	−2	0	6	11
118	16	−9	−8	−2	7	28
125	27	−9	−4	8	67	242

TABLE 5—*Continued*

Terminal taxon	Minimum branch length	Maximum branch length
Balanus	102	160
Callinectes	39	91
Lithobius	23	35
Scutigera	26	30
Spirobolus	49	63
Megaphyllum	50	73
Acerentulus	145	242
Podura	7	8
Crossodonthina	23	24
Hypogastrura	7	8
Pseudachorutes	7	29
Lepidocyrtus	21	36
Metajapyx	41	194
Campodea	77	226
Petrobius	78	101
Trigoniophthalmus	24	34
Lepisma	18	55
Thermobius	11	16
Heptagenia	5	6
Stenonema	34	55
Ephemerella	27	60
Agrion	7	11
Calopteryx	12	25
Libellula	15	47
Blaberus	0	37
Gromphadorhina	5	87
Mantis	26	40
Anoplotermes	1	78
Reticulotermes	0	47
Zorotypus	193	233
Megarcys	2	21
Mesoperlina	3	3
Cultus	17	88
Agnetina capitata	15	176
Paragnetina	13	15
Agnetina sp.	14	69
Clothoda	21	133
Oligotoma	11	57
Grylloblatta	47	145
Labidura	2	2
Forficula	8	9
Labia	19	29
Ceuthophilus	5	55
Melanoplus	6	8
Warramaba	8	10
Phyllium	5	12
Anisomorpha	5	73
Timema	25	28
Cerastipsocus	29	143
Dennyus	56	137
Taeniothrips	68	193
Buenoa	22	28
Saldula	28	34
Lygus	41	44
Belostoma	8	13
Oncopeltus	18	21
Oncometopia	6	52

TABLE 5—*Continued*

Terminal taxon	Minimum branch length	Maximum branch length
Tibicen	20	50
Galleria	8	11
Ascalapha	19	23
Papilio	9	13
Hydropsyche	14	29
Pycnopsyche	11	17
Oecetis	21	29
Cybister	28	33
Xyloryctes	16	20
Octinodes	11	33
Photuris	66	68
Meloe	24	25
Rhipiphorus	13	31
Tetraopes	12	20
Tenebrio	12	13
Agulla	38	75
Corydalus	25	33
Sialis	4	66
Mantispa	24	30
Chrysoperla	10	50
Hemerobius	43	61
Myrmeleon mmaculatus	54	266
Myrmeleon sp.	4	60
Lolomyia	44	130
Tipula	53	88
Laphria	23	44
Drosophila	44	65
Mythicomyia	31	57
Triozocera	15	84
Caenocholax	77	99
Elenchus	53	73
Crawfordia	24	60
Xenos pecki	7	60
Xenos vesparum	7	345
Hartigia	3	42
Bareogonalos	2	38
Mesopolobus	3	39
Orussus	4	41
Evania	6	44
Ichneumon	2	45
Ophion	10	11
Caenochrysis	8	46
Epyris	7	45
Priocnemus	10	46
Dasymutilla	11	19
Apoica	10	15
Polistes fuscatus	11	14
Monobia	4	12
Polistes dominulus	4	308
Camponotus	2	306
Chalepoxenus	2	308
Doronomyrmex	0	306
Harpagoxenus	1	307
Temnothorax	1	305
Leptothorax	2	306
Hemitaxonus	14	20
Periclista	1	39

TABLE 5—*Continued*

Terminal taxon	Minimum branch length	Maximum branch length
Orchopeas	12	51
Atyphioceras	11	15
Acanthopsylla	9	11
Megarthroglossus	7	32
Craneopsylla	4	7
Nannochorista neotropica	49	58
Nannochorista dipteroides	13	21
Bittacus pillicornis	15	22
Bittacus strigosus	8	18
Panorpa isolata	4	4
Panorpa helena	2	2
Merope	22	56
Boreus californicus	3	4
Boreus coloradensis	3	3

[a] Node numbers are from Fig. 11.

sister-taxon relationship between the Strepsiptera and the Diptera.

Štys and Biliński (1990) questioned the monophyly of the Diplura, citing the metameric nature of the ovarioles. They suggested that the Diplura were paraphyletic, with the Campodeina as sister-group to the Ellipura. The morphological data presented here unambiguously support their monophyly but are ambiguous with respect to their sister-group. When the molecular data are combined with the morphology, there is unequivocal support for the Diplura—both molecular data and morphological data show positive Bremer support for their placement as sister-group to the Insecta. Furthermore, results from all 25 parameter sets supported both monophyletic Diplura and Insecta + Diplura when all data were combined.

The scheme of Thorne and Carpenter (1992) for the Dictyoptera is upheld in these analyses. In 25 of the 25 simultaneous analyses (100% for all data), the Mantodea + Blattaria clade is supported. Furthermore, each of the 18S, 28S, and combined molecular data sets supports a Mantodea + Isoptera clade. There is no support from either the molecular or the morphological data for Blattaria + Isoptera.

The potential paraphyly of the Mecoptera has been discussed in an earlier analysis by Whiting *et al.* (1997). In their analysis, the genus *Boreus* was placed as sister to the siphonapteran sample. The analyses presented here do not show this pattern. In our enlarged sample,

the Mecoptera are again paraphyletic under the analysis parameters that yielded the most congruence among morphological, 18S rDNA, and 28S rDNA data. The paraphyly here was with respect to the Strepsiptera + Diptera clade. This result, however, was highly assumption-dependent. All other assumption sets supported a monophyletic Mecoptera and its sister-group relationship with a monophyletic Siphonaptera ((Mecoptera + Siphonaptera) + (Diptera + Strepsiptera)) in concert with the results of Whiting *et al.* (1997). Clearly, the status of the Mecoptera requires further analysis.

The Zoraptera have been allied with many taxa, but most recently as sister-group to the Holometabola (Rasnitsyn, 1998). Almost all analyses place the Zoraptera within the Polyneoptera and usually (in 72% of analyses) as sister-group to the Dictyoptera. In all other cases save one (such as where indel and transversion ratio are both set to unity), the Zoraptera are placed in a group with other orthopteroids. The single exception did place the Zoraptera with the Paraneoptera. These results are more in concordance with the results of Boudreaux (1979; although the character basis is different) and Minet and Bourgoin (1986), who placed the Zoraptera within the Polyneoptera. The orthopteroids themselves are not supported as monophyletic in the most congruent hypothesis. This (lack of) support must be regarded as weak, however, given that most (72%)
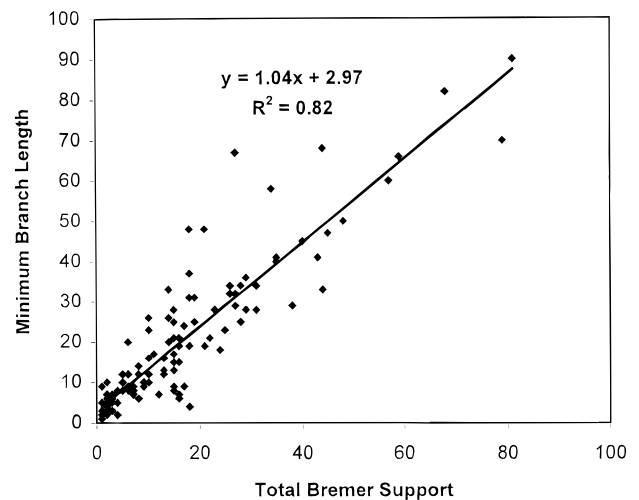

FIG. 19. Regression of minimum branch length (as reported by POY) on total evidence Bremer support values. This cartoon is not meant to be a statistical statement, but a picture of overall correlation among these support measures.

analysis parameters support Polyneopteran monophyly. The support for the break between the Zoraptera + Dictyoptera is stronger (in character and Bremer support) than the break between these "lower" Neoptera and the ((Orthoptera + Phasmida) + (Grylloblattaria + Dermaptera)) group. This is an area that requires further analysis to confirm or refute these results.

The analyses here support Coleoptera unequivocally. In Whiting *et al.* (1997), this was not the case. Since the publication of that work, we have determined that several sequences *(Priacma, Colpocaccus, Agulla,* and *Corydalus)* were coleopteran contaminants. The sequences presented here are new and the disturbing results regarding the Neuropteroidea and Coleoptera have vanished.

Perhaps the most striking result of Whiting and Wheeler (1994) and Whiting *et al.* (1997) is the union of the Strepsiptera and Diptera. All 25 simultaneous analyses performed here confirm this group. Additionally, each measure of conviction (optimization-independent changes, Bremer support, and parameter sensitivity) showed high levels of support for this clade. There are still many internal features characteristic of the mecopteroid orders that have not been examined in the Strepsiptera (e.g., muscle insertions) and of course there are additional sources of molecular information to be gathered. These new sources of information may force a reappraisal of this relationship. For now, however, the best-supported hypothesis for these taxa is unequivocally that the Strepsiptera and Diptera are sister-taxa.

These phylogenetic relationships are summarized in Fig. 20.

CONCLUSION

The scheme of higher relationships presented here represents the most consistent statement of higher hexapod taxa made to date. The phylogenetic statements are based on the ensemble behavior of morphological, behavioral, and two sources of molecular information. These historical relationships are strongest with regard to basal insect, and paraneopteran and holometabolan alliances. They are weakest with regard to the status of the Polyneoptera and Mecoptera.

Certainly, this phylogenetic picture may be revised with new data. The inclusion of extinct taxa (e.g., *Testajapyx,* Paleodictyoptera) could well affect polarity and putative homology statements throughout the morphological matrix, suggesting new relationships among the extant taxa. New sources of molecular information not linked to the rDNA cluster may also yield novel patterns of relationship. It is not the purpose of this analysis to state that these relationships are complete, correct, and fixed, but rather that this is the best notion of hexapod relationships given our current state of knowledge.

APPENDIX 1: MORPHOLOGICAL CHARACTER DESCRIPTIONS

[1] Nauplius larva
  0, Absent
  1, Present
  Schram (1986).
[2] Number of Antennae
  0, Single pair (I and intercalary segment)
  1, Two pairs (I and II)
  Schram (1986).
[3] Median eyes fused to naupliar eyes
  0, Absent
  1, Present
[4] Palps on first and second maxillae
  0, Present
  1, Absent
  Brusca and Brusca (1990).
[5] Median eyes
  0, Present
  1, Absent
  Weygoldt and Paulus (1979).
[6] Tracheae
  0, Absent
  1, Present.
[7] Fundamentally biramous postantennal appendages.
  0, Absent
  1, Present
  Schram (1986).
[8] Ordering of fate map tissues
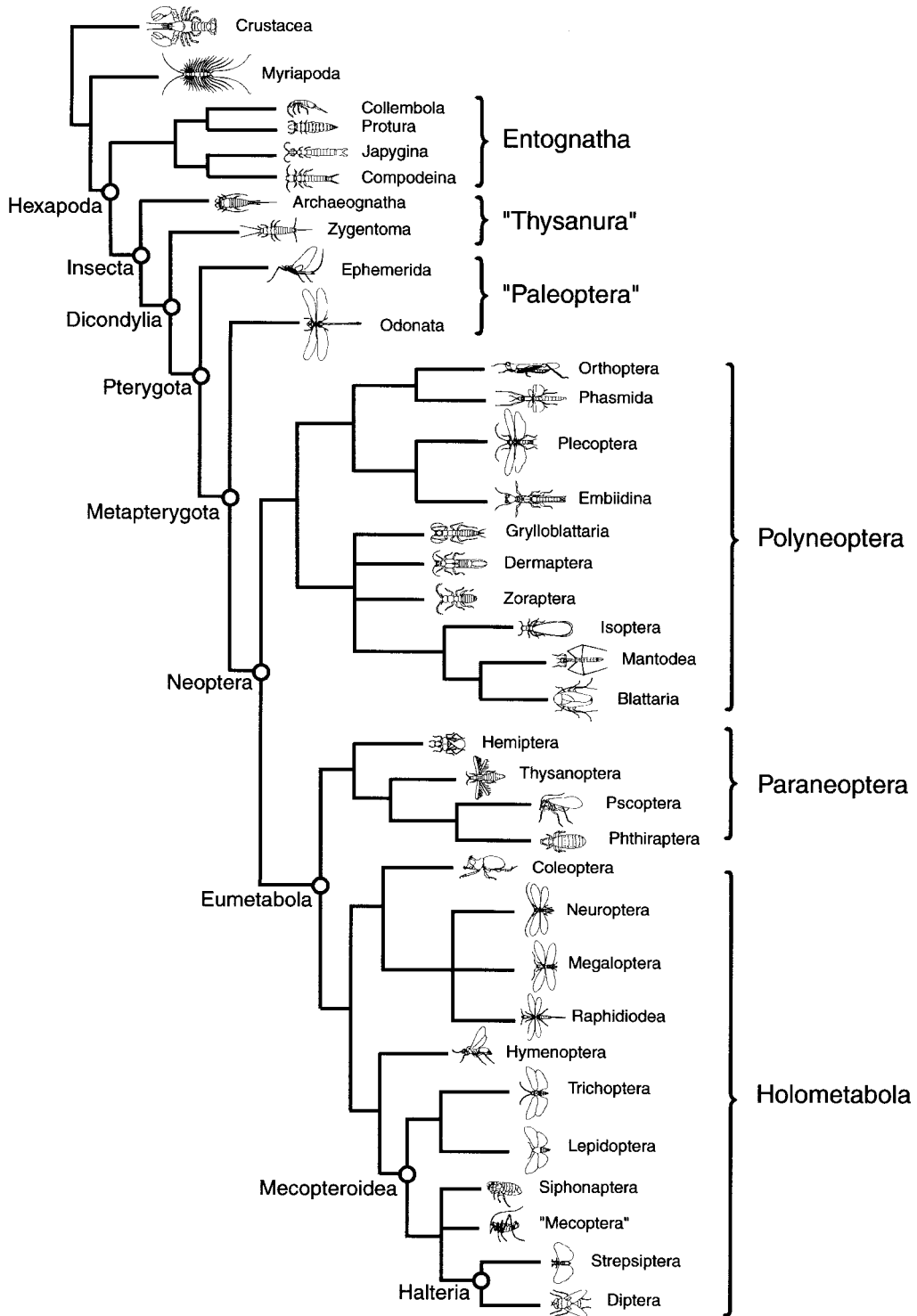 0, Anterior (stomodaeum–midgut–mesoderm) posterior

FIG. 20.   Summary cladogram of hexapod relationships based on the discussion and data presented here.

1, Anterior (midgut–mesoderm–stomodaeum) posterior

Anderson (1979); Schram (1978).

[9] Pretarsal segment of leg (dactylopodite) with only a single muscle

0, Absent

1, Present

Snodgrass (1952).

[10] Pretarsal claws (perhaps paired)

0, Absent

1, Present

Hennig (1981).

[11] Unique crustacean limb segmentation pattern based on a shared coxa–basis muscular arrangement.

0, Absent

1, Present

Boxshall (1998).

[12] Coxal vesicles styli

0, Absent

1, Present

Kraus and Kraus (1994).

[13] Maxillary plate–mouth cavity bordered by IInd maxillae

0, Absent

1, Present

Kraus and Kraus (1994).

[14] Appendages of first postcephalic segment transformed into maxillipedes

0, Absent

1, Present

Kraus and Kraus (1994).

[15] Specialization in the ventral border of the mouth cavity

0, Absent

1, Present

Kraus and Kraus (1994).

[16] Stemmata

0, Absent

1, Present

(Scutigeromorph eyes are "pseudocompound;" Paulus, 1979) Kraus and Kraus (1994).

[17] Diplosegments

0, Absent

1, Present

Kraus and Kraus (1994).

[18] Antennae with four sensory cones in distal segment

0, Absent

1, Present

Kraus and Kraus (1994).

[19] First postcephalic segment into collum

0, Absent

1, Present

Kraus and Kraus (1994).

[20] Tagmosis: thorax, abdomen

0, Without distinct thorax and abdomen

1, With distinct thorax and abdomen

Hennig (1981, p. 97).

[21] Thoracic segmentation

0, Thorax not divided into three segments

1, Hexapody.

[22] Locomotory limbs

0, Locomotory limbs 7-segmented

1, Locomotory limbs 6-segmented

2, Locomotory limbs 5-segmented

(Collembola tibiotarsus)

Tibia and tarsus fused, at least on 2nd and 3rd pairs of legs (Hennig, 1981, p. 103). The tibio-tarsal articulation is supposedly well developed in Protura (Prell, 1913, and Tuxen, personal communication, cited by Kristensen, 1975, p. 5). Kukalová-Peck (1987) suggested that the hexapod leg was primitively 11-segmented, a suggestion discounted by Bitsch (1994) and Willmann (1998).

[23] Abdominal segmentation

0, Abdomen with >12 segments

1, Abdomen consists of 11 segments + telson (=12)

2, 6 segments (Collembola)

Hennig (1981) treated reduction of number of abdominal segments initiated as a synapomorphy of Collembola and Protura, but Kristensen (1975) questioned the usefulness of this comparison.

[24] Jointed "knee"

0, "Knee" comprising additional segment

1, "Knee" comprising joint

Manton (cited in Tuxen, 1970; cf. Kristensen, 1975).

[25] Labium

0, Second maxillae not fused

1, Second maxillae fused.

[26] Postantennal organs

0, Present

1, Absent

Kristensen (1991); Kukalová-Peck (1991).

[27] Segmental growth

0, Anamorphic

1, Epimorphic.

[28] Cerci

0, Absent

1, Present, originating from appendages of 11th abdominal segment

2, Simplified

3, Unsegmented

Hennig (1981, p. 98). Simplified form has no more than two segments (Kristensen, 1981, p. 146).

[29] Pigment cells in ommatidia

0, With four primary pigment cells in ommatidia

1, With two primary pigment cells in ommatidia

Kristensen (1975).

[30] Entognathy

0, Mouthparts not retracted into pocket in head

1, Head retracted into head capsule

2, Labium obliterated

Tuxen (1959, 1970); Lauterbach (1972); Kristensen (1975, p. 4); Hennig (1981, p. 101). Entognathy actually refers to a suite of characters that may or may not be fully correlated. There exist single and double internal pockets, internal struts that may or may not correspond to parts of the tentorium in ectognathous insects, and movement in the plane of articulation of the mandible and maxilla within the entognaths, with partial (at least in terms of function) reversal in certain Collembola. See, e.g., discussion by Hennig (1981, pp. 101–102). Further, Janetscheck (1970), Manton (1964, 1972), and Kraus (1998) have suggested polyphyletic origins of entognathy at least as seen in Collembola and Diplura.

[31] Compound eye

0, Developed

1, Dispersed (Collembola)

2, Lost (Protura)

3, Apposite (Archaeognatha)

Nonadditive.

Eyes are stated to be present in a fossil dipluran by Kukalová-Peck (1987), but Bitsch (1994) questioned the attribution of this fossil to Diplura.

[32] Malpighian tubules

0, Developed, many (>6)

1, Reduced

2, Lost

3, 6

4, 4

Nonadditive.

Kristensen (1975, p. 5) stated that papilliform organs in Protura seem to be remnants of Malpighian tubules (Janetschek, 1970). Denis (1949) discussed corresponding structures in Diplura.

[33] Antennal segmentation

0, Developed

1, Reduced (at most 4 segments)

2, Pseudoculi

3, Annulated (scape with muscles, apical flagellum without muscles)

Nonadditive.

Hennig (1981, pp. 102, 109). Kristensen (1975) questioned Hennig's synapomorphy interpretation for Ellipura; is it reasonable to compare well-developed, short Collembola antennae with absence of antennae in Protura?

[34] Sperm centriole adjunct

0, Present

1, Absent

2, Forming 1–3 "accessory bodies"

Nonadditive.

Jamieson (1987).

[35] Tracheal system

0, Present

1, Reduced (abdominal spiracles absent, Hennig 1981, p. 103)

2, Segment 8 with spiracle, segment 1 without (Archaeognatha)

3, Segment 8 with spiracle

Nonadditive.

Hennig (1981, p. 103); Kristensen (1991, p. 130).

[36] Sperm flagellum axoneme

0, Filaments arranged $9 + 2$

1, $9 + 9 + 2$

2, $9 + 9 + 0$

Nonadditive.

Protura have a number of arrangements ($9 + 0$, $12 + 0$, $14 + 0$), but also $9 + 9 + 2$ (Kristensen, 1995, citing Yin *et al.* 1985). The $9 + 2$ filament arrangement in the sperm flagellum is also seen in Mecoptera–Aphaniptera (Baccetti, 1970, cited in Kristensen, 1975).

[37] Pretarsal claws

0, Two

1, One

2, Two, articulated with tarsus

Nonadditive.

Hennig (1981, p. 103); Kristensen (1975, p. 5); Boudreaux (1979).

[38] Linea ventralis

0, Absent

1, Present

François (1969) noted the presence of a furrow in the labial region of the head capsule (Kristensen, 1975, p. 5).

[39] Epipharyngeal ganglia

0, Small

1, Enlarged

François (1969); Kristensen (1975, p. 5).

[40] Position of pseudocommisure of stomatogastric nervous system

0, Without entognathous position

1, With entognathous position

François (1969); Kristensen (1975, p. 5).

[41] Spermatozoa

0, Motile

1, Coiled and immotile

2, Uncoiled and immotile

Boudreaux (1979, p. 150).

[42] Ovary

0, Nonmetameric

1, Metameric

Štys *et al.* (1993).

[43]Antennal circulatory organs

0, Originating from dorsal vessel

1, Originating from aorta anteriorly

2, Separate, ampullary enlargments

3, Ampullae pusatile, compressors

4, Ampullae pusatile, dilators

5, Transverse muscle with intersecting muscles

6, Lacking

Nonadditive.

Pass (1991).

[44] Anterior tentorium

0, Tentorium present

1, Tentorium reduced

2, Movable (Myriapoda)

Nonadditive.

Kristensen (1975, p. 5); Boudreaux (1979).

[45] Johnston's organ

0, Absent

1, Present

The development of the Johnston's organ (Snodgrass, 1935) in the second segment (pedicel) explains the absence of muscles therein, supporting the argument that the pedicel is a true (ancestrally musculated) segment as opposed to an annulation of the third segment (i.e., the flagellum), see, e.g., Hennig (1981, p. 110).

[46] Posterior tentorium

0, Absent

1, Arms

2, Arms fused

The posterior arms are fused together, forming a single transverse apodeme in the ectognath insects.

[47] Ovipositor

0, Absent

1, Present

2, Vestigial (two valve pairs)

3, Modified

4, Fused

Nonadditive.

Composed of valvulae from abdominal venter VIII + IX. The modified condition in this case refers to reduction in the second valvulae, and the third valvulae serving as the functional components of the ovipositor (Boudreaux, 1979; Kristensen, 1981, p. 146).

[48] Caudal filament

0, Absent

1, Present, long

2, Short

The third single caudal filament (paracerus, terminal filament) is held by Kristensen (1975) to be a synapomorphy of the Insecta. Sharov (1966) suggested that a long, flagellate telson was present in ancestral myriapods and that it was lost in the entognaths. Kristensen considered Sharov's proposition as entirely unfounded. The filament is suppressed in Neoptera (Boudreaux, 1979; similar structures in Plecoptera and Dermaptera are of arguable homology).

[49] Mandibular articulation

0, Monocondylic

1, Dicondylic

2, Anterior articulation fixed

A monocondylous mandible is found in Archaeognatha, two articulations being synapomorphic for the Zygentoma and all pterygote orders (Hennig, 1981, p. 112). The homology of dicondyly in Pterygota and Zygentoma has been questioned by Beier and Tuxen (1970). However, Chaudonneret (1950) has described a lepismatoid head in sufficient detail to suggest that it is indeed homologous to the condition in pterygotes (see Kristensen 1975, p. 6). Kukalová-Peck (1985) discussed the difference in the anterior articulation among ptergotes.

[50] Femoro-tibial articulation

0, Moncondylic

1, Dicondylic

Sharov (1966, cited in Hennig, 1981, p. 112) argued this character is synapomorphic for Dicondylia. Manton (1972) stated that this dicondyly occurs also in Archaeognatha, and Boudreaux (1979, p. 267) characterized Archaeognatha as "barely dicondylic." This character is thus synapomorphic for Insecta, not Dicondylia as argued by Sharov and Hennig.

[51] Gonangulum in ovipositor base

0, Absent

1, Present

Presence of a distinct gonangulum in the ovipositor base is taken as synapomorphic for the Dicondylia (Scudder, 1957, cited in Kristensen, 1975, p. 6). This structure effects the movements of the two pairs of gonapophyses relative to each other. According to Scudder (1961), it evolved from the second gonocoxa (see summary by Hennig, 1981, p. 112). An alternative view of its origins was held by Sharov (1966), but as Hennig (1981) stated, it is synapomorphic in either event and unique to the Dicondylia. Bitsch (1994), however, stated that a rudimentary gonangulum is present in Archaeognatha.

[52] Origin of ventral mandibular and maxillary (stipital) adductors

0, On endoskeletal plates

1, On tentorium

Chaudonneret (1950); see also Kristensen (1975, p. 6).

[53] Fulturae

0, Present

1, Absent

François (1969, 1970).

[54] Postoccipital sulcus and ridge

0, Absent

1, Internal ridge lateral only

2, Continuous

Lauterbach (1972); see Kristensen (1975, p. 6).

[55] Tracheal commissures and connectives

0, Not developed in abdomen

1, Developed in abdomen

Stobbart (1956, cited in Kristensen (1981, p. 6).

[56] Amniotic cavity

0, Absent

1, Present, open

2, Closed

Closed temporarily by cellular plug (Zygentoma) or continuous amniotic membrane (Kristensen, 1991;

p. 130). In Archaeognatha the blastodermal folds were considered never to close entirely beneath the embryo (Sharov, 1966; see Kristensen, 1975, p. 6). This was not maintained by Kristensen (1981, p. 139), but Kristensen (1991, p. 130) returned to the interpretation.

[57] Median fusion (at least basal part) of male penes

0, Absent

1, Present

Kristensen (1975, p. 7).

[58] Paired female genital openings

0, Absent

1, Present

Kristensen (1975, p. 9) characterized these as "retained" in Ephemerida, "lost" in Odonata and Neoptera, but they are not present in other hexapods (Snodgrass, 1933; Boudreaux, 1979, p. 133).

[59] Two pairs of wings

0, Absent

1, Present

2, Absent in females

"Wings" constitutes a suite of characters. It would be reasonable to note also synapomorphic similarities of the complicated basal articulation of the wing, the venation of the wing (including the archedictyon irregular network of cross-veins), and the flight muscles, adding several characters to the monophyly of Pterygota [whether or not Kukalová-Peck's (1985) homologies are adopted]. The best substantiated hypothesis for the origin of wings remains that they are developed from paranotal lobes (Bitsch, 1994).

[60] Two coxal proprioreceptor organs

0, Absent

1, Present

Lombardo (1973), as cited by Hennig (1981, p. 124, note p. 132).

[61] Basal wing brace

0, Absent

1, Present

Anastomosis of CuP and anterior anal vein (Kukalová-Peck, 1985).

[62] Forewing media fusion

0, Absent

1, Basal fusion of MA and MP

2, Fusion of MA and R

3, Fusion of R and M

4, Fusion of R with M and Cu

Nonadditive.

Kukalová-Peck (1985); Kukalová-Peck and Peck (1993).

[63] Superlinguae

  0, Absent

  1, Present

  2, Interlocking

Well developed in ephemerid nymphs.

Reports in Dermaptera (Giles, 1963) appear actually to represent nonhomologous structures (Moulins, 1969). This may also be true of the lateral hypopharyngeal lobes of primitive Odonata (Tillyard, 1928; see Kristensen, 1975, p. 9). Boudreaux's (1979, p. 200) contention that superlinguae do not occur in Entognatha is not true of the groundplan (Kristensen, 1981, p. 141).

[64] Aquatic habitat of nymphs

  0, No, terrestrial

  1, Yes.

[65] Subimago

  0, Present

  1, Absent

This has been questioned by Sharov (1957; see also Hennig, 1981, p. 130, and Kristensen, 1975, p. 7), who suggested that a protoperlarian had a subimago stage. Illies (1968) and Kristensen, however, questioned this interpretation of the fossil record and doubted that the fossils believed to be subimagos are actually so. Instead they may represent different species or sexes or morphs. However, see Kukalová-Peck (1978).

[66] Tracheation

  0, Anterior only

  1, Arch

In Odonata and Neoptera each wing, like each leg, is supplied with an anterior tracheal trunk from the corresponding segmental spiracle and a posterior trunk from the spiracle behind. The two alar trunks are almost always fused to form a complete arch in the wing base, and the leg trunks are similarly fused. In most ephemerids, only the anterior alar trunk is present; the arrangement is similar to the tracheization of the paranotal lobe in Zygentoma (Kristensen, 1975, p. 8). For alternative interpretations, see citations in Kristensen (1975).

[67] Posterior tracheation of pterothoracic leg

  0, Absent

  1, Present

Kristensen (1975, p. 8) points out that the similar condition reported in *Epeorus* by Chapman (1918) involves a very small trachea and even if posterior may not correspond to the groundplan for Ephemerida.

[68] Direct spiracular musculature

  0, Absent

  1, Present

In odonates and neopterans, muscles insert directly on the sclerotized spiracular lip (Miller, 1962; Poonawalla, 1966). In contrast, Ephemerida have no direct spiracular muscles, closure by compression through contraction of dorsoventral body wall muscles (Ford, 1923; Birket-Smith, 1971). See Kristensen (1975, p. 9), Boudreaux (1979, p. 200; citation of Maki, 1938, on presence in Zygentoma).

[69] Tentorio-lacinial muscle

  0, Present

  1, Absent

Ephemerida are the only pterygotes with this muscle. Its presence is probably plesiomorphic, since a similar muscle is found in Archaeognatha. However, it is not known to be present in Zygentoma. Odonata and Neoptera do not have this muscle, and if it is part of the pterygote groundplan, then it supports their sister-group status. See Matsuda (1965); Kristensen (1975, p. 9).

[70] Tentorio-mandibular muscles

  0, Several bundles

  1, One

Never more than one in Odonata and Neoptera. More bundles may be retained in Ephemerida according to Matsuda (1965); Kristensen (1975, p. 9).

[71] Loss of some pterothoracic muscles

  0, No

  1, Yes

Second phragma-tergum II, profurcasternum-mesobasalare, furca-first axillary muscles are present in Ephemerida (and Zygentoma), but not in Odonata or Neoptera (Matsuda, 1970, and Hamilton, 1971; see Kristensen 1975, p. 9).

[72] Sperm transfer

  0, Indirect

  1, Copulation

  2, Indirect, using claspers

  Nonadditive.

  Boudreaux (1979).

[73] Arolium

  0, Absent

  1, Present

Minet and Bourgoin (1986; also Kristensen, 1995) suggested that presence of an arolium is a synapomorphy of Neoptera, but it is present in apterygotes.

[74] Wing flexion

0, Absent

1, Present

A pleural muscle inserted on the 3rd axillary sclerite permits the wing to be flexed over the back. The basal articulation of the wing is complex and might be divided into several characters, such as described by Hennig (1981, p. 158).

[75] Third valvulae forming sheath

0, Absent

1, Present

In all Neoptera with a functional ovipositor, the 3rd valvulae (= gonoplacs of Scudder, 1961) are primarily developed along the full length of the ovipositor forming a protective sheath for the 1st and 2nd valvulae. Absent in Odonata (Kristensen, 1975, p. 9), Ephemerida, etc.

[76] Anal furrow

0, Absent

1, Present

Forbes (1943) pointed out that an anal furrow separates the anal lobe from the anterior portion of wing. See Hennig (1981, p. 159).

[77] Enlarged hind-wing vannus

0, Small

1, Enlarged

This character refers to the size of the anal fan of the hind-wings (Kristensen, 1981, p. 143).

[78] Jugal "bar"

0, Absent

1, Present

Whether or not a sclerotization (= jugal bar) is present on the jugum (Kristensen, 1981; p. 143).

[79] Ocelli

0, Present

1, Absent in immatures

2, Absent in adults

3, Median ocellus absent

4, Median ocellus absent in adults

Nonadditive.

Variable within Mecoptera (Byers, 1991).

[80] Metameric testis ducts

0, Present

1, Absent

Kristensen (1975).

[81] Male gonocoxopodites IX

0, Articulated

1, Not articulated

Retention of articulated male gonocoxopodites IX is unique to grylloblattids within the Neoptera (Kristensen, 1975).

[82] Metaspina

0, Present

1, Absent

Reported by Kristensen (1975, p. 17) to be retained within Grylloblattaria.

[83] Phallomeres

0, Normal

1, Reduced

Male phallomeres said to be reduced, in conjunction with the formation of secondary intromittent organs from the eversible ejaculatory duct (Kristensen, 1981).

[84] Male styli

0, Expressed

1, Suppressed

The suppression of male styli is suggested by Boudreaux (1979) to be accompanied by the formation of accessory clasping organs "from various sources" (!).

[85] Segmental arteries

0, Absent

1, Present

Kristensen (1975); Boudreaux (1979).

[86] Female brood-care behavior

0, Absent

1, Present.

[87] Hypertrophy of metathoracic tibia depressor, and femur

0, Absent

1, Present

Minet and Bourgoin (1986) suggested that hypertrophy of the metatibial musculature, and the femora, is a synapomorphy of Embiidina and Zoraptera.

[88] Trochantin.

0, Absent

1, Present

2, Trochantin–episternal sulcus present

This character involves the separation of the trochantin and episternum by a sulcus or membranous line (Kristensen 1981, p. 145). Boudreaux (1979) argued that the trochantin of Zygentoma was nonhomologous with that of Pterygota ("pseudotrochantin") but Kristensen (1995) dismissed this.

[89] Sclerotization of fore-wing

    0, Membranous

    1, Sclerotized

The fore-wings are said to be "more or less sclerotized." See Kristensen (1981, p. 145).

[90] Vannus pleated

    0, No

    1, Yes

Kristensen (1981, p. 145).

[91] Two cervical sclerites

    0, No

    1, Yes

This character is problematic (Kristensen 1981, p. 145). Once offered as a synapomorphy of "Orthopterodida," it is also present in embiids, "some" Plecoptera (coded here as present for stoneflies), and "some" Holometabola (here not coded as present for holometabolans, since its precise distribution therein is not cited).

[92] Prognathy

    0, Absent

    1, Present

    2, Gula present

    Nonadditive.

Sometimes said to be synapomorphic in embiids and dermapterans, but earwigs do not have a gula, while web spinners do (Kristensen, 1991, p. 145).

[93] Dorsal flexor of paraglossa

    0, Normal

    1, "Aberrant," "peculiar"

    Rähle (1970); see Kristensen (1975).

[94] Gonopod morphogenesis from phallic rudiments

    0, Absent

    1, Present

    Boudreaux (1979).

[95] Prominent precostal field

    0, Absent

    1, Present

    Kristensen (1981, p. 146).

Note: Blackith and Blackith (1968), based on phenetic and Camin-Sokal analysis of 92 characters for 13 orthopteran taxa, suggested that Orthoptera is not monophyletic and that Ensifera and/or Caelifera may have closer relationships to other orders than they do to one another. The evidence for this was discussed, and largely dismissed, by Kristensen (1981, p. 146). In any event, reanalysis of Blackiths' data matrix using parsimony results in the orthopterans appearing as a monophyletic group.

[96] Discoid pronotum

    0, Absent

    1, Present

    2, Enlarged (Blattaria)

    See Kristensen (1981, p. 147).

[97] Pleural sutures

    0, Not slanting forward

    1, Slanting forward

    Boudreaux (1979).

[98] Indirect wing muscles

    0, Developed

    1, Reduced

Pterothoracic modifications include reduction of the postnota and phragmata, associated with reduction of dorso-longitudinal and tergosternal indirect wing muscles. Functions of these muscles are, instead, assumed by direct wing depressors and tergopleural–tergocoxal muscles, respectively. See Boudreaux (1979, pp. 207–208).

[99] Metathoracic tergosternal wing elevators

    0, Present

    1, Weak or suppressed

It has been suggested (see Kristensen, 1981, p. 147) that the initial stage of reduction of the dorso-longitudinal wing depressors and the loss of the metathoracic tergosternal wing elevators may be synapomorphies of Dermaptera and Dictyoptera. Kristensen, however, thinks that these are likely independently derived in these two orders and variation within each may call this character into serious question.

[100] Coxa conical, backward-directed

    0, No

    1, Yes

    Boudreaux (1979).

Flight muscle reductions in grylloblattids were suggested by Boudreaux to indicate relationship with Zoraptera and Dictyoptera (i.e., mantids, blattids, isopterans); however, Kristensen (1981, p. 148) noted that similar reductions are numerous in wingless pterygotes including Orthoptera.

[101] Phallomeres

    0, Symmetrical

    1, Asymmetrical

    See Kristensen (1981, p. 147).

Phallic rudiments in grylloblattids were reported not to be horizontally split during ontogeny as they

are in dictyopterans, Orthoptera, Phasmida, and some Plecoptera.

[102] Shape of mesotrochantin "holometabolan"

   0, No

   1, Yes

   Ross (1965); see also Kristensen (1975, p. 11).

[103] First branch of Cu

   0, Not grooved

   1, Grooved

Adams (1958) suggested several possible synapomorphies shared by Plecoptera and Holometabola. These are, collectively, largely based on Adams' conception of the holometabolan groundplan and are by no means uncontroversial. Although Adams suggested several characters in this regard (few-branched weak stem of posterior branch of M; grooved first branch of Cu; distribution of micro-trichiae on wing surfaces; tendency for coalescence of S and anterior branch of M; etc.) all have been questioned by Hennig, Kristensen, and others because they are vague, imprecise, or apparently part of a broader groundplan (probably neopteran, for some characters not in list above). One representative character from Adams is registered here (see Kristensen, 1975, p. 11).

[104] Separate coxopleuron

   0, Yes

   1, No

   See Kristensen (1975, p. 12).

[105] Several male accessory glands arranged in cluster

   0, No

   1, Yes

   See Kristensen (1975, p. 11).

[106] Median ventral excurrent ostia in dorsal vessel

   0, Absent

   1, Present

   See Kristensen (1975, p. 13).

[107] Mesothoracic basisternal fold

   0, Absent

   1, Present

   See Kristensen (1975, p. 13).

[108] Premental lobes

   0, Free

   1, Fused

This character from Hennig was said by Kristensen (1981) to be likely to have evolved more than once. It is coded here as an apomorphy found in orthopteroids (as contended by Hennig) and as also occurring in

plecopterans and embiids as noted by Kristensen (1981). It is not coded for blattopteroid taxa, since Kristensen believes them to be divergent (see Kristensen, 1975, p. 13).

[109] Tarsi

   0, Not subdivided into 5 tarsomeres

   1, Subdivided into 5 tarsomeres

   2, 3-segmented

   3, 2-segmented

See Kristensen (1975, p. 14). Kristensen (1975, p. 6) suggested that a smaller number in archaeognaths is primitive and is secondary in Zygentoma. The 5-segmented condition occurs in the zygentoman genus *Tricholepidion,* leading Kristensen to suggest that this condition is lost in other zygentomans, but is primitively absent in Archaeognatha. An alternative interpretation might be that this genus is sister-group to the pterygotes and that Zygentoma as now recognized is paraphyletic. It is interesting to note in this regard that Hennig (1981, p. 119) cited little evidence for the monophyly of Zygentoma (= Thysanura s. str.). Further, the 5-segmented tarsi of *Tricholepidion* could be interpreted as synapomorphic with pterygotes as could the absence (loss?) of scales of the body. In light of this evidence, it could be argued that the presence of ocelli in *Tricholepidion* is plesiomorphic and that loss of ocelli defines a monophyletic group defined as Zygentoma minus *Tricholepidion.* For a detailed discussion of *Tricholepidion* and these characters, see Wygodzinski (1961).

[110] Sternum I

   0, Developed

   1, Reduced

   2, Absent

   See Kristensen (1975, p. 14).

[111] Dorsal-flexor of paraglossae

   0, Absent

   1, Present

This refers to a secondary, dorsal flexor of the paraglossae, probably derived from one of the extrinsic prelabial muscles (see Kristensen, 1975, p. 14).

[112] Second profurca-spinasternal muscle

   0, Absent

   1, Present

This muscle is in addition to the primitive profurca-spinasternal muscle and has a more oblique course with posterior insertion on the anterior part of (furca +) spinasternum. Kristensen (1975, pp. 14–15)

thinks that a similar muscle in phasmids is clearly convergent.

[113] Proventricular "neck," before anterior enlarged portion (Kristensen, 1975, p. 18).
 0, Absent
 1, Present.

[114] Open-ended chambers formed by development of secondary segments of dorsal diaphragm and enclosing the paired excurrent ostia (Nutting, as cited by Kristensen, 1975, p. 18).
 0, Absent
 1, Present.

[115] Female sternum VII
 0, Small
 1, Enlarged
 2, Vestibulum
 "Dictyopteran" female postabdominal structure. According to Günther and Herter (1974) and Hennig (1981), there exists a unique structural configuration of the female postabdomen in the Dermaptera and Dictyoptera (= Blattaria + Mantodea + Isoptera). The genitalia have a vestibulum formed by enlargement of sternum VII and shortening of ovipositor valves (Kristensen, 1975, p. 17). Kristensen considered the reduction in the two groups to be so different that their origin from a common state was questionable.

[116] Sex determination
 0, XX/XY
 1, XX/XO
 See Thorne and Carpenter (1992).

[117] Corporotentorium
 0, Absent
 1, Present
 2, Perforation through which circumesophageal connectives pass
 See Kristensen (1975, p. 19).

[118] Anterior teeth of proventriculus forming ring of strongly sclerotized teeth
 0, Absent
 1, Present
 See Kristensen (1975, p. 19).

[119] Proventriculus teeth with secondary denticles
 0, Absent
 1, Present
 See Thorne and Carpenter (1992).

[120] Tarsal plantulae
 0, Present
 1, Absent

Minet and Bourgoin (1986).

[121] Forewing Sc
 0, Long
 1, Short
 Kristensen (1975, p. 19); see Thorne and Carpenter (1992).

[122] Ootheca
 0, Absent
 1, Present
 2, Ootheca hardened after deposition (Mantodea)
 See Thorne and Carpenter (1992).

[123] First axillary sclerite attached close to scutal margin
 0, Absent
 1, Present
 Kristensen (1975, p. 21).

[124] Sperm axoneme sheaths
 0, Absent
 1, Present
 Two dense sheaths surround the inner and outer singlets
 Jamieson (1987).

[125] Abdominal ganglia
 0, Unconcentrated
 1, Two
 2, One
 A so-called "concentrated" nerve cord exists in paraneopterans that is defined as consisting of only two discrete abdominal ganglia or fewer (see Kristensen, 1981, pp. 148–150).

[126] Lacinia
 0, Broad
 1, Slender rod
 Kristensen (1981, pp. 149–150); on lacinial stylets see Kristensen (1975, pp. 32–35).

[127] Flagella of spermatozoa
 0, Single
 1, Two
 Kristensen (1981, pp. 149–150).

[128] Gonangulum fused with tergum IX
 0, Free
 1, Fused
 Kristensen (1981, pp. 149–150).

[129] Cibarium
 0, Absent
 1, Present
 This character is stated as a "unique complement

of sclerotizations in the cibarium," attributed to Denis and Bitsch (1973) by Kristensen (1981, pp. 149–150).

[130] Ovarioles
0, Panoistic
1, Neopanoistic
2, Polytrophic
3, Telotrophic
Nonadditive.
See Štys and Biliński (1990, Table 1).

[131] Basal part of antennal flagellomeres without rupture-facilitating cuticular modification
0, Absent
1, Present
Kristensen (1981, pp. 149–150).

[132] Mandibles
0, Broad
1, Stylettiform
Kristensen (1981, pp. 149–150).

[133] Sclerotized rings between antennal flagellomeres
0, Absent
1, Present
Kristensen (1981).

[134] Metamorphosis
0, Incomplete
1, Complete
Kristensen (1981).

[135] Larval eyes
0, Carried over to adult
1, Not carried over to adult
Kristensen (1981).

[136] Wing rudiments
0, Evaginated prior to penultimate molt.
1, Evaginated at larval–pupal molt
Kristensen (1981). We have coded Strepsiptera for state 0 because Kristensen (1991, 1995) reports that strepsipteran larvae possess wing buds prior to the penultimate molt. However, this is probably not the ground plan condition for Strepsiptera, because members of the basal-most family Mengenillidae lack wing buds prior to this molt (Kinzelbach, 1971). For a discussion of the homology of the penultimate molt across Strepsiptera and an alternate coding see Whiting (1998b).

[137] Appearance of external genitalia
0, Prior to penultimate molt
1, At penultimate molt
Kristensen (1981).

[138] Cruciate cervical muscles
0, Present
1, Absent
Kristensen (1981).

[139] Female genitalia
0, First valvulae developed, separate; second valvulae discrete; cerci articulated
1, First valvulae strongly reduced, fused; second valvulae not discrete; cerci not articulated
Kristensen (1981).

[140] Pretarsal claw of larval leg
0, Paired
1, Unpaired
Kristensen (1981).

[141] Silk secretion from larval labial glands
0, Absent
1, Present
Kristensen (1981). This character has not been reported from Strepsiptera, but it is likely to be inapplicable.

[142] Eruciform larvae
0, Absent
1, Present
Kristensen (1981). Kristensen (1991) later expressed doubts about this character because primitive Mecoptera (Nannochoristidae) and some primitive Amphiesmenoptera are prognathous. Strepsipteran larvae are planidial and are scored for state 0.

[143] Telomere
0, Present
1, Absent
This character describes the transverse division of the male gonopod ("paramere") into basimere and telomere (Boudreaux, 1979; Kristensen, 1981). Because the male gonopod is absent in Strepsiptera (Kristensen, 1991; Kathirithamby, 1991), Boudreaux (1979) incorrectly assigned this state to Strepsiptera.

[144] Abdominal limb buds
0, Repressed
1, "Derepressed"
Boudreaux (1979).

[145] Gastric caeca
0, Present
1, Lost
Kristensen (1981).

[146] Meron
0, Absent
1, Present

Boudreaux (1979); Kristensen (1981).

[147] Cryptosterny

0, Absent

1, Present

Kristensen (1981).

[148] Flight by posteromotorism

0, No

1, Yes

Kristensen (1981). This is the only supposed synapomorphy between Coleoptera and Strepsiptera. Kukalová-Peck and Lawrence (1993) suggested a number of synapomorphies in the hind-wing venation, but these have been discounted (Whiting and Kathirithamby, 1995; Whiting, 1998b). Kukalová-Peck (1998) disagrees with our interpretation of wing venation and suggested two additional characters, but failed to document any of her characters that appear likewise untenable.

[149] Intrinsic musculature in (fused) third valvulae

0, Absent

1, Present

Kristensen (1981).

[150] Pecularities of abdominal base

0, Absent

1, Present

This character was reported by Kristensen (1981), but not discussed in detail. His source was Achtelig (1975, 1978).

[151] Pecularities of female genitalia

0, Absent

1, Present

This character was reported by Kristensen (1981), but not discussed in detail. His source was Achtelig (1975, 1978).

[152] Pleural muscle inserted on first axillary sclerite

0, No

1, Yes

Kristensen (1981, p. 153).

[153] Larval stipes

0, Entire

1, Divided

Kristensen (1981, p. 153).

[154] Some larval maxillary and labial muscles lost

0, Present

1, Absent

Kristensen (1981, p. 153).

[155] Cranial antagonist of the primitive craniolacinial muscle in larva

0, Absent

1, Present

Kristensen (1981, p. 153; 1995).

[156] Outer pterothoracic tergocoxal remotor

0, Present

1, Absent

Kristensen (1975, 1981, 1995).

[157] Female heterogamety

0, Absent

1, Present

Kristensen (1975, p. 32).

[158] Double Y-shaped fusion of anal veins

0, Absent

1, Present

Kristensen (1975, p. 32).

[159] Achiasmatic oogenesis

0, Absent

1, Present

Kristensen (1975, p. 32).

[160] Preholocentric chromosomes

0, Absent

1, Present

Kristensen (1975, p. 32).

[161] Pterothoracic furcal arms fused with epimeron

0, Absent

1, Present

Kristensen (1975, p. 32).

[162] Pair of glands opening on sternum V

0, Absent

1, Present

Kristensen (1975, pp. 32–33).

[163] Outer accessory filaments of sperm flagellum very stout (ca. 300 Å in. diameter)

0, Thin

1, Stout

Kristensen (1975, p. 33).

[164] Vestiture on wing surfaces between veins

0, Absent

1, Dense vestiture of long setae

2, Scales

Kristensen (1975, p. 33).

[165] Dagger-like mandible with anterior articulation reduced

0, Absent

1, Present

2, Lost

Kristensen (1975, p. 34).

[166] Only one endite lobe present in maxilla and none in labium

    0, No

    1, Yes

    Kristensen (1975, p. 34).

[167] Only two labial palp segments present

    0, No

    1, Yes

    Kristensen (1975, p. 34).

[168] Tentorial muscles of prelabium

    0, Present

    1, Lost

    This refers to loss of some primitive labial muscles that are retained in the amphiesmenopteran ground plan (Kristensen, 1975, p. 34; 1981, p. 153).

[169] Structure of posterior notal wing articulation

    0, Not modified

    1, Modified

    See Kristensen (1975, p. 34; 1995).

[170] Pleural ridge/scutum muscle inserting on posterior notal wing process.

    0, No

    1, Yes

    Kristensen (1975, p. 34; 1995).

[171] Transverse muscle between profurcal arms

    0, Absent

    1, Present

    Kristensen (1975, p. 34).

[172] Lateral labral retractor

    0, Present

    1, Absent

    Kristensen (1975, p. 35).

[173] Tentorial adductors of cardo in larva

    0, Present

    1, Absent

    Kristensen (1975, p. 35).

[174] Hypopharyngeal muscles in larva

    0, Present

    1, Retractor of hypopharynx and ventral dilator of salivarium absent

    2, Loss of mouth-angle retractors and dorsal dilator of salivarium

    Kristensen (1975, p. 35; 1981, p. 154).

[175] Larvae

    0, Podous

    1, Apodous (thoracic and/or prolegs)

    Kristensen (1975, p. 35).

[176] Extrinsic labral muscles

    0, Present

    1, Absent

    Kristensen (1975, p. 35).

[177] Proventriculus with specialized type of cuticular processes, acanthae

    0, Absent

    1, Present

    Kristensen (1975, p. 35).

[178] Flagellum of spermatozoon coiled around straight axial mitochondrion

    0, Absent

    1, Present

    Kristensen (1975, p. 35).

[179] Two nervi corporis cardiaci in each side

    0, Free (or partially fused)

    1, Fused completely

    Kristensen (1975, p. 35).

[180] Coxa–body articulation

    0, Ventral

    1, None

    2, Dicondylic

    3, Pleural, mobile

    4, Pleural, fixed

    5, Tricondylic

    Nonadditive.

    Kristensen (1975); Boudreaux (1979).

[181] Mandibular teeth

    0, Lateral

    1, Terminal (Diplura),

[182] Thoracic legs

    0, Without trochanteral femur-twisting muscles

    1, With such muscles, femur–tibia pivot unique (Diplura)

    Kristensen (1991, p. 129).

[183] Gonopore

    0, Diverse trunk segments

    1, Abdominal segment IX (Diplura)

    2, Terminal (Ellipura and Chilopoda)

    3, Abdominal segment VIII (female; secondarily on VII or IX), X (male)

    4, Between II and III trunk legs

    Nonadditive.

    Boudreaux (1979).

[184] Legs I

    0, Not sensory

    1, Sensory (Protura).

[185] Digestion

    0, Extracellular

1, Intracellular (Protura).

[186] Collophore

0, Absent

1, Present (Collembola).

[187] Furcula

0, Absent

1, Present (Collembola).

[188] Tendinous struts

0, Absent

1, Present, anchoring cuticle (Collembola).

[189] Cleavage

0, Superficial

1, Total (Collembola)

Also found in Archaeognatha, although of short duration (Kristensen, 1995, p. 88, citing Machida *et al.,* 1990).

[190] Mandibular molar area and pick

0, Absent

1, Present (Archaeognatha).

[191] Jumping by abdominal push

0, Absent

1, Present (Archaeognatha).

[192] Apical segment of labial palp

0, Narrow

1, Widened.

[193] Sperm conjugation

0, Absent

1, Present

(Zygentoma).

[194] Paired larval gills

0, Absent

1, Present, lateral (Ephemerida).

[195] Male forelegs clasping

0, Absent

1, Present (Ephemerida).

[196] Male styli IX

0, Not claspers

1, Claspers (Ephemerida).

[197] Imaginal lifespan

0, Normal, feeding

1, Shortened, nonfeeding (Ephemerida).

[198] Larval labium

0, Not prehensile

1, Prehensile (Odonata).

[199] Posterior tracheal larval gills

0, Absent

1, Present (Odonata).

[200] Lateral cervical sclerite in three pieces

0, No

1, Yes (Odonata).

[201] Pteropleura tilted backward with notum small

0, No

1, Yes (Odonata).

[202] Male accessory copulatory organs

0, Absent

1, Present (Odonata).

[203] Tufted larval tracheal gills

0, Absent

1, Present, lateral (Plecoptera).

[204] Tarsal silk gland

0, Absent

1, Present (Embiidina).

[205] Male cerci functioning in copulation

0, No

1, Yes (Embiidina).

[206] Lateral cervical sclerites fragmented

0, No

1, Two pieces (Embiidina)

2, Four pieces (Mantodea)

[207] Eusociality

0, Absent

1, Present (Isoptera)

Nonadditive.

[208] Eversible vesicle on abdominal segment I

0, Absent

1, Present (Grylloblattaria)

Fused eversible sacs on venter I, forming a peculiar structure (Kristensen 1981, p. 144).

[209] Forewings truncate

0, No

1, Yes (Dermaptera).

[210] Transverse stipital muscle

0, Present (Plecoptera)

1, Absent.

[211] Metathoracic and abdominal sternum I fused

0, No

1, Yes (Dermaptera).

[212] Prothorax and procoxae elongated

0, No

1, Yes (Mantodea).

[213] Forelegs raptorial

0, No

1, Yes.

[214] Compound eyes enlarged

0, No

1, Yes (Mantodea).

[215] Thoracic desclerotization
  0, Absent
  1, Present (Blattaria).

[216] Clypeofrontal sulcus
  0, Present
  1, Suppressed (Blattaria).

[217] Moniliform antennae
  0, Absent
  1, Present (Isoptera, Zoraptera).

[218] Wing autotomy
  0, Absent
  1, Present (Isoptera).

[219] Symbiotic gut zooflagellates
  0, Absent
  1, Present (Isoptera).

[220] Pronotum overlapping propleuron
  0, Absent
  1, Present (Orthoptera).

[221] Hindlegs modified for jumping
  0, Absent
  1, Present (Orthoptera).

[222] Pronotal repellant gland
  0, Absent
  1, Present (Phasmida)
  Kristensen (1975, p. 23).

[223] Abdominal dorso-ventral short and parallel
  0, Absent
  1, Present (Phasmida)
  Kristensen (1975, p. 23).

[224] Mesenteron appendices
  0, Absent
  1, Present (Phasmida)
  Kristensen (1975, p. 23).

[225] Subgenital plate of female formed by sternum VIII
  0, No
  1, Yes (Zoraptera)

Subgenital plate of female formed by enlarged sternum VII and reduction of ovipositor and location of gonopore behind sternum VII (Kristensen, 1975, p. 15). These were reported by Hennig as synapomorphies of dermapterans and blattopteroideans, but are questioned by Kristensen.

[226] Head flattened and prognathous
  0, No
  1, Yes (Phthiraptera).

[227] Vertebrate ectoparasites
  0, No
  1, Yes.

[228] Supraesophageal ganglion displaced backward
  0, No
  1, Yes (Phthiraptera).

[229] Dorsal tentorial arms lost
  0, No
  1, Yes (Phthiraptera).

[230] Right mandible
  0, Present
  1, Absent (Thysanoptera).

[231] Conelike beak
  0, Absent
  1, Present (Thysanoptera).

[232] Labrum ensheathing stylets
  0, No
  1, Yes (Thysanoptera).

[233] Wings straplike, fringed
  0, No
  1, Yes (Thysanoptera).

[234] Labium ensheathing stylets
  0, No
  1, Yes (Hemiptera).

[235] Maxillary palpi lost
  0, No
  1, Yes (Hemiptera).

[236] Maxillary and mandibular stylets piercing/sucking
  0, Absent
  1, Present (Hemiptera).

[237] Respiratory abdominal filaments
  0, Absent
  1, Present (Megaloptera).

[238] Elongate larval stipes
  0, Absent
  1, Present (Megaloptera).

[239] Ovipositor highly elongated, with secondary basal union
  0, No
  1, Yes (Raphidiodea).

[240] Neck elongate
  0, No
  1, Yes (Raphidiodea).

[241] Pronotum extended
  0, No
  1, Yes (Raphidiodea).

[242] Third tarsomere bilobed
  0, No
  1, Yes (Raphidiodea).

[243] Larval piercing–sucking tubes
  0, Absent
  1, Present (Neuroptera).
[244] Elytra
  0, Absent
  1, Present (Coleoptera).
[245] Abdominal segments VIII and IX telescoped
  0, No
  1, Yes (Coleoptera).
[246] Abdominal sterna I and II membranous
  0, No
  1, Yes (Coleoptera).
[247] Mesothorax and metathorax fused
  0, No
  1, Yes (Coleoptera).
[248] Insect endoparasitism
  0, Absent
  1, Present (Strepsiptera).
[249] Forewing "halteres"
  0, Absent
  1, Present (Strepsiptera).
[250] Antennae flabellate
  0, No
  1, Yes (Strepsiptera).
[251] Male eyes protruding
  0, No
  1, Yes (Strepsiptera).
[252] Hamuli
  0, Absent
  1, Present (Hymenoptera).
[253] Haplodiploidy
  0, Absent
  1, Present (Hymenoptera).
[254] Volsella
  0, Absent
  1, Present (Hymenoptera).
[255] Venom production by female accessory gland
  0, Absent
  1, Present (Hymenoptera).
[256] Notocoxal muscles
  0, Present
  1, Absent (Hymenoptera).
[257] Male antennae serving as accessory clasping organs
  0, No
  1, Yes (Siphonaptera).
[258] Prothoracic ctenidium
  0, Absent

1, Present (Siphonaptera).
[259] Salivary channels in lacinial stylets
  0, No
  1, Yes (Siphonaptera).
[260] Body laterally compressed
  0, No
  1, Yes (Siphonaptera).
[261] Clypeus and labrum fused
  0, No
  1, Yes (Mecoptera)
  Kristensen (1975, p. 35; 1981, p. 154).
[262] Tentorio-mandibular muscles
  0, Present
  1, Absent (Mecoptera)
  Kristensen (1981, p. 154).
[263] Male abdominal segment IX ringlike, enlarged and fused on pleuron
  0, No
  1, Yes
  See Kristensen (1975), Wood and Borkent (1989), Kinzelbach (1990), and Whiting (1998b). It is possible that the complex clasping organ in Siphonaptera is an autapomorphic modification of this character state as seen in other antliophoran orders (discussed in Whiting, 1998b).
[264] Spermathecal opening separate from gonopore
  0, No
  1, Yes (Mecoptera).
[265] Halteres
  0, Absent
  1, Present (Diptera).
[266] Hypopharynx styletlike
  0, No
  1, Yes (Diptera).
[267] Labial palpi forming labellum
  0, No
  1, Yes (Diptera).
[268] Larval spiracles without closing apparatus
  0, No
  1, Yes (Diptera).
[269] Larvae apneustic, respiration epidermal
  0, No
  1, Yes (Trichoptera).
[270] Anal prolegs
  0, Absent
  1, Present (Trichoptera).
[271] Larval antennae papillae
  0, No

1, Yes (Trichoptera).

[272] Adult labium and hypopharynx fused

0, No

1, Yes (Trichoptera).

[273] Abdominal tergum X bilobed

0, No

1, Yes (Lepidoptera).

[274] Corporotentorium with median posterior process

0, No

1, Yes (Lepidoptera).

[275] Ventral nerve cord solid

0, No

1, Yes (Lepidoptera).

ACKNOWLEDGMENTS

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