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THE STREPSIPTERA PROBLEM: PHYLOGENY OF THE HOLOMETABOLOUS INSECT ORDERS INFERRED FROM 18S AND 28S RIBOSOMAL DNA SEQUENCES AND MORPHOLOGY

MICHAEL F. WHITING,[1] JAMES C. CARPENTER,[2] QUENTIN D. WHEELER,[3] AND WARD C. WHEELER[4]

[1]*Department of Zoology and M. L. Bean Life Science Museum, Brigham Young University, Provo, Utah 84602, USA; E-mail: michael_whiting@byu.edu*
[2]*Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, USA; E-mail: carpente@amnh.org*
[3]*Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853, USA; E-mail: qdw1@cornell.edu*
[4]*Department of Invertebrates, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, USA; E-mail: wheeler@amnh.org*

Abstract.—Phylogenetic relationships among the holometabolous insect orders were inferred from cladistic analysis of nucleotide sequences of 18S ribosomal DNA (rDNA) (85 exemplars) and 28S rDNA (52 exemplars) and morphological characters. Exemplar outgroup taxa were Collembola (1 sequence), Archaeognatha (1), Ephemerida (1), Odonata (2), Plecoptera (2), Blattodea (1), Mantodea (1), Dermaptera (1), Orthoptera (1), Phasmatodea (1), Embioptera (1), Psocoptera (1), Phthiraptera (1), Hemiptera (4), and Thysanoptera (1). Exemplar ingroup taxa were Coleoptera: Archostemata (1), Adephaga (2), and Polyphaga (7); Megaloptera (1); Raphidioptera (1); Neuroptera (sensu stricto = Planipennia): Mantispoidea (2), Hemerobioidea (2), and Myrmeleontoidea (2); Hymenoptera: Symphyta (4) and Apocrita (19); Trichoptera: Hydropsychoidea (1) and Limnephiloidea (2); Lepidoptera: Ditrysia (3); Siphonaptera: Pulicoidea (1) and Ceratophylloidea (2); Mecoptera: Meropeidae (1), Boreidae (1), Panorpidae (1), and Bittacidae (2); Diptera: Nematocera (1), Brachycera (2), and Cyclorrhapha (1); and Strepsiptera: Corioxenidae (1), Myrmecolacidae (1), Elenchidae (1), and Stylopidae (3). We analyzed ~1 kilobase of 18S rDNA, starting 398 nucleotides downstream of the 5′ end, and ~400 bp of 28S rDNA in expansion segment D3. Multiple alignment of the 18S and 28S sequences resulted in 1,116 nucleotide positions with 24 insert regions and 398 positions with 14 insert regions, respectively. All Strepsiptera and Neuroptera have large insert regions in 18S and 28S. The secondary structure of 18S insert 23 is composed of long stems that are GC rich in the basal Strepsiptera and AT rich in the more derived Strepsiptera. A matrix of 176 morphological characters was analyzed for holometabolous orders. Incongruence length difference tests indicate that the 28S + morphological data sets are incongruent but that 28S + 18S, 18S + morphology, and 28S + 18S + morphology fail to reject the hypothesis of congruence. Phylogenetic trees were generated by parsimony analysis, and clade robustness was evaluated by branch length, Bremer support, percentage of extra steps required to force paraphyly, and sensitivity analysis using the following parameters: gap weights, morphological character weights, methods of data set combination, removal of key taxa, and alignment region. The following are monophyletic under most or all combinations of parameter values: Holometabola, Polyphaga, Megaloptera + Raphidioptera, Neuroptera, Hymenoptera, Trichoptera, Lepidoptera, Amphiesmenoptera (Trichoptera + Lepidoptera), Siphonaptera, Siphonaptera + Mecoptera, Strepsiptera, Diptera, and Strepsiptera + Diptera (Halteria). Antliophora (Mecoptera + Diptera + Siphonaptera + Strepsiptera), Mecopterida (Antliophora + Amphiesmenoptera), and Hymenoptera + Mecopterida are supported in the majority of total evidence analyses. Mecoptera may be paraphyletic because *Boreus* is often placed as sister group to the fleas; hence, Siphonaptera may be subordinate within Mecoptera. The 18S sequences for *Priacma* (Coleoptera: Archostemata), *Colpocaccus* (Coleoptera: Adephaga), *Agulla* (Raphidioptera), and *Corydalus* (Megaloptera) are nearly identical, and Neuropterida are monophyletic only when those two beetle sequences are removed from the analysis. Coleoptera are therefore paraphyletic under almost all combinations of parameter values. Halteria and Amphiesmenoptera have high Bremer support values and long branch lengths. The data do not support placement of Strepsiptera outside of Holometabola nor as sister group to Coleoptera. We reject the notion that the monophyly of Halteria is due to long branch attraction because Strepsiptera and Diptera do not have the longest branches and there is phylogenetic congruence between molecules, across the entire parameter space, and between morphological and molecular data.

[Alignment; insect orders; molecular systematics; phylogeny; sensitivity analysis; Strepsiptera; taxon sampling.]

Holometabola (=Endopterygota), consisting of more than half of the world's described animal species (Wilson, 1988) and more than 80% of insect species (Kristensen, 1991), is comprised of the orders Coleoptera (beetles), Raphidioptera (snakeflies), Megaloptera (alderflies, dobsonflies), Neuroptera (sensu stricto = Planipennia; lacewings), Hymenoptera (bees, wasps, and ants), Trichoptera (caddisflies), Lepidoptera (moths and butterflies), Mecoptera (scorpionflies), Siphonaptera (fleas), Diptera (flies), and Strepsiptera (twisted-winged parasites). Although the monophyly of Holometabola and the included orders are relatively well established, relationships among the orders are unclear, and only a few sister-group relationships are unambiguously supported by morphological evidence. A major obstacle in establishing a robust phylogenetic hypothesis for these orders has been the problem of homology assessment across such morphologically diverse and ancient groups, whose radiations date back to the Permian (Hennig, 1981; Kukalová-Peck, 1991). A well-supported hypothesis of phylogenetic relationships for these orders has eluded entomologists for two centuries and remains one of the most basic needs of systematic entomology.

Holometabolous Relationships

Hennig (1981) and Kristensen (1991, 1995) suggested four synapomorphies uniting Holometabola: (1) immatures having larval eyes (stemmata) that do not increase in number in successive instars and are not carried over to adult stages, true ocelli absent, and adult compound eyes developed de novo in the adult (Paulus, 1986); (2) wing rudiments and external genitalia first developing below the body surface, evaginating only in the penultimate (larva–pupa) molt; (3) last immature instars nearly always inactive and nonfeeding (=pupae); and (4) tricondylic coxa–body articulation (Kristensen, 1975; Boudreaux, 1979). Hennig (1969, 1981) recognized the supraordinal groups Neuropteroidea (Megaloptera + Neuroptera + Raphidioptera), Mecopteroidea (Trichoptera + Lepidoptera + Mecoptera + Diptera), Amphiesmenoptera (Trichoptera + Lepidoptera), and Antliophora (Diptera + Mecoptera), although he did not specify relationships among these groups. The position of Strepsiptera and Siphonaptera—two "highly derived" groups—was problematic, and Hennig presented evidence to associate them with several different orders. Ross (1965) suggested a sister-group relationship between Hymenoptera and the other holometabolous insect orders. Boudreaux (1979) divided Holometabola into "Coleopterida" (Coleoptera + Strepsiptera) and "Telomerida" (remaining orders), although the characters supporting this division have been called into question (Kinzelbach, 1971; Kristensen, 1975; Baccetti, 1989; Kathirithamby et al., 1993).

The most widely accepted notion of insect ordinal relationships is attributable to Kristensen's extensive reviews of insect phylogeny (1975, 1981, 1991, 1995). In his most recent work, Kristensen (1995) divided Holometabola into three major clades: Neuropterida (=Hennig's Neuropteroidea) + Coleoptera, Hymenoptera + Mecopterida, and Mecopterida (=Hennig's Mecopteroidea) (Fig. 1). Kristensen (1995) considered the monophyly of Amphiesmenoptera and Mecopterida well established but had some reservations in placement of Hymenoptera as sister group to Mecopterida.

Strepsiptera Problem

The "Strepsiptera problem" (Kristensen, 1981) remains the most enigmatic question in ordinal-level insect phylogenetics. The Strepsiptera are a small (549 species; Kathirithamby, 1989) monophyletic order of insects with extremely modified morphological and life history features associated with their insect parasitoid lifestyle. Adult strepsipteran females are neotenic and lack antennae, mouthparts, eyes, wings, legs, and genitalia. Adult male Strepsiptera are morphologically extremely derived. Some of their unusual features include antennae bearing lateral flabellar segments, compound eyes with 15–150 ommatidia separated by strips of cuticle or setae, mandi-

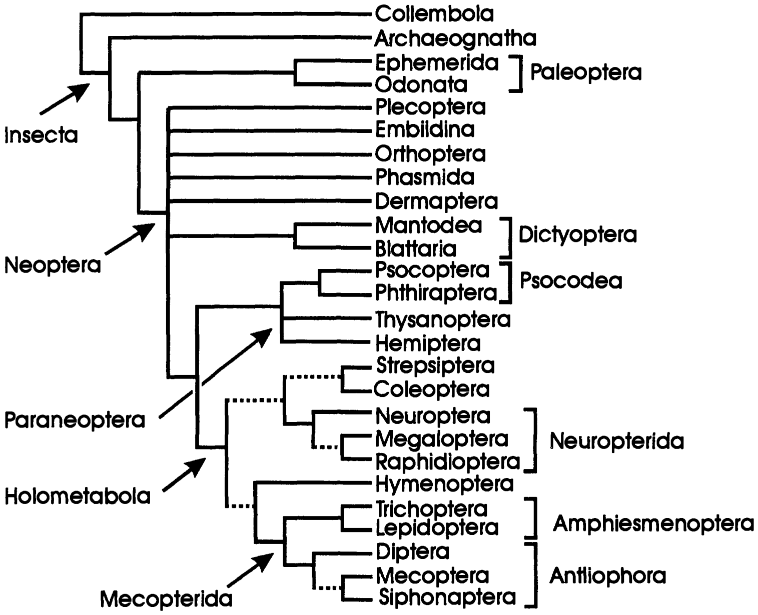


FIGURE 1. Kristensen's (1991) phylogeny of insect orders based on morphology, including common supraordinal names. Dotted lines mark areas of questionable relationships.

bles that function as sensory organs and bear setae, absence of a trochanter in the fore and middle legs, absence of a tentorium, and forewings reduced to structures that resemble the halteres of dipterans. There are at least 25 synapomorphies supporting the monophyly of Strepsiptera (Hennig, 1969; Kinzelbach, 1971; Kathirithamby, 1989). This perplexing amalgamation of morphological reduction in the females and extreme modification in the males, combined with unusual biology and larval characteristics, has challenged systematic placement of this group for over two centuries.

Strepsiptera were first recorded by Rossi (1793), who described *Xenos vesparum* and placed it in Hymenoptera near Ichneumonidae. Kirby (1802) described *Stylops melittae* from an andrenid bee but failed to associate his species with Rossi's species. Latreille (1809) moved *Xenos vesparum* to the tribe Phthiromyae within Diptera, and later Kirby (1815) provided the first diagnosis of the anomalies of these insects and proposed the order Strepsiptera. Lamarck (1816) placed these species within the dipteran family Rhipidoptera, and then Latrielle (1817) removed them from Diptera and placed them within their own order, Rhipiptera. By the end of the 19th century, Strepsiptera had been placed between Odonata and Ephemerida, Hymenoptera and Lepidoptera, Suctoria (Siphonaptera) and Diptera, and again within Diptera (Pierce, 1909).

More recently, phylogenetic placement of Strepsiptera has revolved around three major hypotheses: inclusion within Coleoptera, placement as sister group to Coleoptera, and placement outside of Holometabola. Lameere (1900), Kolbe (1901), and Ganglbauer (1903) placed Strepsiptera within Coleoptera but were uncertain as to its position relative to other beetle families. Arnett (1963), Crowson (1960, 1981), and Ross et al. (1984) placed Strepsiptera as the family Stylopidae within Coleoptera. Crowson (1960, 1981) favored placement of Stylopidae within Lymexeloidea based upon a questionable scenario requiring soft plant boring as a prerequisite to insect endoparasitism. The most popular polyphagan placement for Strepsiptera is as sister group to Rhipiphoridae, based on presumed similarity of the rhipiphorid reduced elytron and strepsipteran forewing, flabellate antennae, hypermetamorphosis with a triungulin stage, and insect endoparasitism (Crowson, 1960). However, closer examination of these characters reveal that these similarities are based upon erroneous interpretations of strepsipteran morphology and biology (Kathirithamby, 1989; Stehr, 1987; Pix et al., 1993).

Handlirsch (1903), Boerner (1904), and Shipley (1904) placed Strepsiptera as an independent order closely allied to Coleoptera. Kinzelbach (1971, 1990) and Kathirithamby (1989) concurred with this hypothesis but noted that this relationship is supported by a single character: the ability to power flight with the hind wings (posteromotorism). The interpretation of presence of a gula and absence of the prothoracic notopleural suture as a Coleoptera–Strepsiptera synapomorphy (Crowson, 1954, 1960) is not tenable because Strepsiptera are primitively hypognathous (Kinzelbach, 1990) and lack a gula (Kinzelbach, 1971; Kathirithamby, 1989). The interpretation of the strepsipteran forewing as a reduced and modified elytron does not hold up under close scrutiny because the wing does not possess the characteristics of elytron morphology (Kathirithamby, 1989) or function (Pix et al., 1993).

Kristensen (1991) suggested that Strepsiptera may belong outside of Holometabola based on the presence of external wing buds on the second instar larvae and the possession of larval stemmata (Kinzelbach, 1990; Kathirithamby, 1989). However, it is not clear whether these are carried over to the adult stage as in nonholometabolous insects or regenerated during pupation as in Holometabola. Neither of the characters argue specifically against the placement of Strepsiptera within Holometabola, however, because they may be the retention of (or reversion to) a plesiomorphic condition. Research on spermatozoa (Baccetti, 1989; Kathirithamby et al., 1993) has demonstrated the uniqueness of these structures in Strepisptera but does not argue for any particular phylogenetic placement. Because of these unresolved morphological questions, Kristensen (1991) gave "these strangely aberrant insects" a tenative placement as Neoptera *incertae sedis*.

Molecular Evidence

There have been a few attempts to establish relationships within Holometabola through the use of molecular data. Wheeler (1989) found tentative support for the clades Neuroptera + Coleoptera, Holometabola, and Insecta based on a limited sample of sequence and restriction map data. Liu and Beckenbach (1992) sequenced the mitochondrial cytochrome oxidase II gene for 13 insects, 7 representing holometabolous taxa. Under both their phenetic and parsimony analyses, Holometabola were paraphyletic, and the only group congruent with ordinal level morphology was the termite–cockroach clade.

Carmean et al. (1992) assessed holometabolan relationships by sequencing a portion of 18S ribosomal DNA (rDNA). They analyzed 17 sequences representing six holometabolous insect orders (Hymenoptera: 10 sequences, Neuroptera: 2, Mecoptera: 1, Siphonaptera: 1, Diptera: 2, and Coleoptera: 1), one insect outgroup (aphid), and two noninsect arthropods (brine shrimp and bird spider). In their bootstrap consensus tree, Holometabola are paraphyletic because Diptera are placed outside of the clade including the aphid and other holometabolous orders (Fig. 2a). The authors suggested that this "misleading result" could be explained by long-branch attraction (Felsenstein, 1978) between the aphid and flies, and consequently they excluded Diptera from any subsequent analyses. From subset analyses of eight taxa, the authors concluded that Hymenoptera are sister group to Mecopterida, which in turn are sister group to Neuroptera.

Pashley et al. (1993) sequenced multiple conserved regions of 18S rDNA from Holometabola and one outgroup. Although they sampled more holometabolous orders than had any previous researchers, they did not sequence Strepsiptera and Mega-

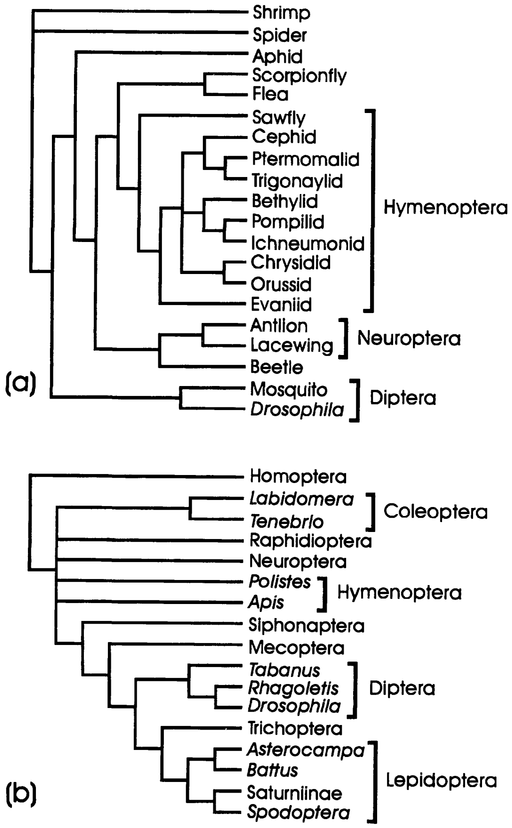


FIGURE 2. Prior phylogenetic hypotheses for Holometabola based on molecular data. (a) Carmean et al.'s (1992) bootstrap consensus tree (bootstrap values not included on tree) with Diptera placed outside of Holometabola. (b) Pashley et al.'s (1993) strict consensus of 10 most-parsimonious trees with monophyletic Amphiesmenoptera and Mecopterida; dipteran taxa within Mecopterida.

loptera, used few exemplars from each order, and relied on a single outgroup sequence (aphid) and so could not test for the monophyly of Holometabola. Their analysis supported a monophyletic Amphiesmenoptera and Mecopterida (Fig. 2b). In their analysis, the dipteran sequences are not attracted to the aphid sequence.

MATERIALS AND METHODS

Specimens Examined

Taxa were selected for sequencing based on previous hypothesis of relationships within and between orders, with an emphasis on those groups whose phylogenetic placement is most problematic (Table 1). Eighteen outgroup taxa from 14 insect orders were sequenced in an attempt to provide rooting for Holometabola and to test adequately for holometabolan monophyly. These outgroup sequences represent all major nonholometabolous lineages within the insects, with the bulk of them from Paraneoptera (Hemiptera + Thysanoptera + Phthiraptera + Psocoptera), the hypothesized sister group to Holometabola (Kristensen, 1995). Sequences were generated from every holometabolous order. Within each order, an effort was made to select at least one representative from major suborders and multiple representatives from the larger and more diverse lineages. Three of the four coleopteran suborders are represented: Archostemata (1 sequence), Adephaga (2), and Polyphaga (7). Within Neuroptera, the three major superfamilies are present: Mantispoidea (2 sequences), Hemerobioidea (2), and Myrmeleontoidea (2). Representatives from half of the mecopteran families, two major flea lineages (Pulicoidea, Ceratphylloidea), and two major trichopteran lineages (Limnephiloidea, Hydropsychoidea) and three exemplars from Lepidoptera were sequenced. Because the sister-group relationship between Lepidoptera and Trichoptera is considered well established (Kristensen, 1995), fewer exemplars were sequenced from these groups. For Hymenoptera, we have representatives of Symphyta and Apocrita, and within Apocrita we have Parasitica and Aculeata. Dipteran sequences originated from Nematocera, Brachycera, and Cyclorrhapha, and six sequences originate from four strepsipteran families. Although fewer 28S sequences were generated in this study, they still represent all the major groups as outlined above. Important taxa we were unable to include in this collection are exemplars from Mengenillidae (Strepsiptera) and Nannochoristidae (Mecoptera).

To this collection of sequences were added all applicable GenBank sequences (as of March 1995). To be considered applicable, the sequences must sufficiently overlap the regions already sequenced to avoid the in-

TABLE 1. List of insect taxa used in the analysis and GenBank accession numbers (where available).

			GenBank accession		18S regions[a]				
Order	Family	Species	18S	28S	A	D	B	C	28S
Collembola	Hypogastruridae	*Hypogastrura* sp.	Z26765		X	X	X	X	
Archaeognatha	Machilidae	*Trigoniopthalmus alternatus*	U65106	U65166	X	X	X	X	X
Ephemerida	Ephemerellidae	*Ephemerella* sp.	U65107	U65167	X	X	X	X	X
Odonata	Calopterygidae	*Agrion maculatum*	U65108	U65169	X	X	X	X	X
	Libellulidae	*Libellula pulchella*	U65109	U65168	X	X	X	X	X
Plecoptera	Perlodidae	*Megarcys stigmata*	U65110	U65170	X	X	X	X	X
	Perlodidae	*Cultus decisus*	U65111	U65171	X	X	X	X	X
Blattodea	Blaberidae	*Blaberus* sp.	U65112		X	X	X	X	
Mantodea	Mantidae	*Mantis religiosa*	U65113	U65172	X	X	X	X	X
Dermaptera	Labiduridae	*Labidura riparia*	U65114		X	X	X	X	
Orthoptera	Acrididae	*Melanoplus* sp.	U65115	U65173	X	X	X	X	X
Phasmatodea	Phasmatidae	*Anisomorpha buprestoides*	U65116		X	X	X	X	
Embiidina	Oligotomidae	*Oligotoma saundersii*	U65117	U65174	X	X	X	X	X
Pscoptera	Psocidae	*Cerastipsocus venosus*	U65118		X	X	X	X	
Phthiraptera	Menoponidae	*Dennyus hirudensis*	U65119		X	X	X	X	
Hemiptera	Aphidae	*Acyrthosiphon pisum*	X62623		X	X	X	X	
	Notonectidae	*Buenoa* sp.	U65120	U65176	X	X	X	X	X
	Saldidae	*Saldula pallipes*	U65121	U65175	X	X	X	X	X
	Miridae	*Lygus lineolaris*	U65122	U65177	X	X	X	X	X
Thysanoptera	Thripidae	*Taeniothrips inconsequens*	U65123		X	X	X	X	
Coleoptera	Cupedidae	*Priacma serrata*	U65124	U65178	X	X	X	X	X
	Carabidae	*Colpocaccus posticatus*	U65125	U65179	X	X	X	X	X
	Dytiscidae	*Cybister fimbriolatus*	U65126	U65180	X	X	X	X	X
	Scarabaeidae	*Xyloryctes faunus*	U65127	U65181	X	X	X	X	X
	Elateridae	*Octinodes* sp.	U65128	U65182	X	X	X	X	X
	Lampyridae	*Photuris pennsylvanicus*	U65129		X	X	X	X	
	Rhipiphoridae	*Rhipiphorus fasciatus*	U65130	U65183	X	X	X	X	X
	Meloidae	*Meloe proscarabaeus*	X77786		X	X	X	X	
	Tenebrionidae	*Tenebrio molitor*	X07801	U65184	X	X	X	X	X
	Cerambycidae	*Tetraopes tetropthalmus*	U65131	U65185	X	X	X	X	X
Megaloptera	Corydalidae	*Corydalus cognatus*	U65132	U65186	X	X	X	X	X
Raphidioptera	Raphidiidae	*Agulla* sp.	U65133	U65187	X	X	X	X	X
Neuroptera	Berothidae	*Lolomyia texana*	U65134	U65188	X	X	X	X	X
	Mantispidae	*Mantispa pulchella*	U65135	U65189	X	X	X	X	X
	Hemerobiidae	*Hemerobius stigmata*	U65136	U65190	X	X	X	X	X
	Chrysopidae	*Chrysoperla plorabunda*	L10183		X	X	X		
	Myrmeleontidae	*Myrmeleon immaculatus*	U65137	U65191	X	X	X	X	X
	Myrmeleontidae	*Myrmeleon* sp.	L10182		X	X	X		
Lepidoptera	Pyralidae	*Galleria mellonella*	U65138	U65198	X	X	X	X	X
	Papilionidae	*Papilio troilus*	U65139	U65199	X	X	X	X	X
	Noctuidae	*Ascalapha odorata*	U65140	U65200	X	X	X	X	X
Trichoptera	Hydropsychidae	*Hydropsyche sparna*	U65141	U65201	X	X	X	X	X
	Limniphilidae	*Pycnopsyche lepida*	U65142	U65202	X	X	X	X	X
	Leptoceridae	*Oecetis avara*	U65143	U65203	X	X	X	X	X
Mecoptera	Bittacidae	*Bittacus strigosus*	U65144	U65204	X	X	X	X	X
	Bittacidae	*Bittacus chlorostigmus*	L10184		X	X	X		
	Boreidae	*Boreus coloradensis*	U65145	U65205	X	X	X	X	X
	Meropeidae	*Merope tuber*	U65146	U65206	X	X	X	X	X
	Panorpidae	*Panorpa latipennis*	U65147	U65207	X	X	X	X	X
Siphonaptera	Pulicidae	*Ctenocephalides canis*	U65148	U65208	X	X	X	X	X
	Hystrichopsyllidae	*Hystrichopsylla schefferi*	L10185		X	X	X		
	Ceratophyllidae	*Orchopeas leucopus*	U65149	U65209	X	X	X	X	X
Hymenoptera	Cephidae	*Hartigia cressonii*	L10173		X	X	X		
	Orussidae	*Orussus thoracicus*	L10174		X	X	X		
	Tenthredinidae	*Hemitaxonus* sp.	U65150	U65192	X	X	X	X	X
	Tenthredinidae	*Periclista linea*	L10172		X	X	X		
	Trigonalidae	*Bareogonalos canadensis*	L10176		X	X	X		
	Evaniidae	*Evania appendigaster*	L10175		X	X	X		

TABLE 1. Continued.

			GenBank accession		18S regions[a]				
Order	Family	Species	18S	28S	A	D	B	C	28S
	Ichneumonidae	*Ichneumon* sp.	L10178		X	X	X		
	Ichneumonidae	*Ophion* sp.	U65151	U65193	X	X	X	X	X
	Pteromalidae	*Mesopolobus* sp.	L10177		X	X	X		
	Chrysididae	*Caenochrysis doriae*	L10179		X	X	X		
	Bethylidae	*Epyris sepulchralis*	L10180		X	X	X		
	Pompilidae	*Priocnemus oregana*	L10181		X	X	X		
	Mutillidae	*Dasymutilla gloriosa*	U65152	U65194	X	X	X	X	X
	Vespidae	*Apoica* sp.	U65153	U65195	X	X	X	X	X
	Vespidae	*Monobia quadridens*	U65154	U65196	X	X	X	X	X
	Vespidae	*Polistes fuscatus*	U65155	U65197	X	X	X	X	X
	Vespidae	*Polistes dominulus*	X74762		X	X	X		
	Formicidae	*Camponotus ligniperda*	X73270		X	X	X		
	Formicidae	*Chalepoxenus muellerianus*	X73271		X	X	X		
	Formicidae	*Doronomyrmex kutteri*	X73274		X	X	X		
	Formicidae	*Leptothorax acervorum*	X73235		X	X	X		
	Formicidae	*Temnothorax recedens*	X73273		X	X	X		
	Formicidae	*Harpagoxenus sublaevis*	X73272		X	X	X		
Diptera	Tipulidae	*Tipula* sp.	U65156	U65210	X	X	X	X	X
	Drosophilidae	*Drosophila melanogaster*	M21017	U65211	X	X	X	X	X
	Asilidae	*Laphria* sp.	U65157	U65212	X	X	X	X	X
	Bombyliidae	*Mythicomyia atra*	U65158		X	X	X	X	
Strepsiptera	Corioxenidae	*Triozocera mexicana*	U65159		X	X	X	X	
	Myrmecolacidae	*Caenocholax fenyesii*	U65160	U65213	X	X	X	X	X
	Elenchidae	*Elenchus japonica*	U65162	U65214	X	X	X	X	X
	Stylopidae	*Crawfordia* n.sp.	U65163	U65215	X	X	X	X	X
	Stylopidae	*Xenos pecki*	U65164	U65216	X	X	X	X	X
	Stylopidae	*Xenos vesparum*	X77784		X	X	X	X	

[a] See Figure 3.

troduction of large amounts of missing data. Pashley et al.'s (1993) sequences were excluded because they had less than 50% overlap with our sequences and are missing the 18S D region and a portion of the C region (Fig. 3), which contain many of the characters important for phylogenetic resolution. The 18S sequence for *Aedes albopictus* was removed from the analysis because it appears to be replete with sequencing artifacts. (Upon alignment with all other insect sequences, positions 642, 885, 905–908, 930, 936, 999, 1008, 1009, 1024, 1054, 1059, 1065, 1088, 1094, 1101, 1102, 1114, 1117, 1118, 1123–1125, 1130, 1131, 1158–1163, 1189, 1230, 1281, 1284–1288, 1320–1324, 1329, and 1357 do not appear to be insect sequence and are typically single indels in regions highly conserved in all other insects; positions 712–788 and 834–841 are also highly suspect [position numbers relative to GenBank X57172]). There were 26 18S sequences and 1 28S sequence added to give a total of 85 18S and 52 28S sequences in the molecular data sets.

Amplification and Sequencing of Ribosomal DNA

Total genomic DNA was isolated from fresh, ETOH-preserved, and dried insect 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+ hr 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 step was replaced by purification of 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

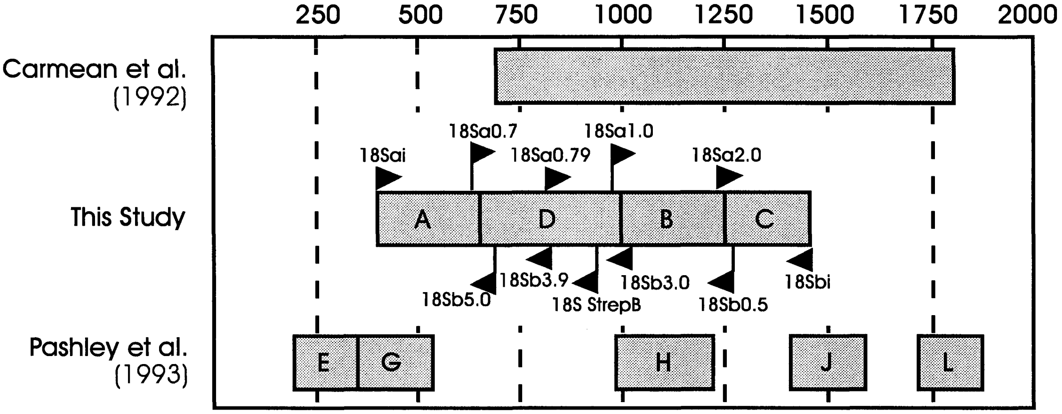


FIGURE 3. Regions of insect 18S rDNA sequenced in this study compared with those sequenced in other studies. Regions are labeled according to the respective authors' nomenclature, and the position of 18S primers used in our study are presented. Position numbers are relative to the sequence for *Drosophila melanogaster* (Tautz et al., 1988).

(PCR) amplification with conserved primers (Table 2). For most 18S sequences, the entire region was amplified and sequenced with internal primers (Fig. 3). If DNA was degraded, sets of primers flanking the A, D, and B + C regions were used to amplify smaller fragments with the program 94°C denaturation (1 min), 50°C annealing (1 min), and 72°C extension (1.5 min) for 35 cycles (Perkin-Elmer Cetus 9600 cycler). Because Strepsiptera have large insert regions in the 18S D fragment with a secondary structure resistant to denaturation, the PCR denaturation times were doubled on every cycle. For 28S, the amplified region corresponds to the D3 expansion segment of 23 S-like ribosomal RNA segment (Michot and Bachellerie, 1987; Michot et al., 1990). Magnesium concentrations had to be decreased for the DNA from aquatic and semiaquatic insects, presumably because they retain heavy metals in their tissues, which interferes with the PCR reactions. Potential insect host contamination in Strepsiptera was avoided by sequencing the free-living males and designing a primer specific to Strepsiptera. Every set of PCR reactions included negative controls to screen for contaminated reagents and amplification products. If PCR product yield was low or particularly difficult to direct sequence, it was ligated to a vector

TABLE 2. Primer sequences (5′ to 3′) used to generate the 18S and 28S rDNA sequences. Positions for 18S are based on the sequence for *Drosophila melanogaster* (Tautz et al., 1988).

Primer	Sequence	Position
18S ai	CCTGAGAAACGGCTACCACATC	398
18S b5.0	TAACCGCAACAACTTTAAT	627
18S a0.7	ATTAAAGTTGTTGCGGTT	609
18S b3.9	TGCTTTRAGCACTCTAA	856
18S a0.79	TTAGAGTGCTYAAAGC	840
18S b3.0	GACGGTCCAACAATTTCACC	1007
18S StrepB	CATACTGTCGARMTAT	≈932
18S a1.0	GGTGAAATTCTTGGACCGTC	988
18S b0.5	GTTTCAGCTTTGCAACCAT	1222
18S a2.0	ATGGTTGCAAAGCTGAAAC	1202
18S bi	GAGTCTCGTTCGTTATCGGA	1421
28S a	GACCCGTCTTGAAACACGGA	
28S b	TCGGAAGGAACCAGCTACTA	

and transformed into a host bacterial cell (Invitrogen, TA cloning kit). The cells were grown and the product removed and sequenced following the manufacturer's protocols. Four to six clones were sequenced to screen for possible variation due to artifacts of amplification or cloning.

The 18S rDNA sequencing was carried out 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.), and the accompanying reagents following standard protocols (Hillis et al., 1990). For the 28S samples, sequencing was carried out with the PRISM cycle sequencing kit (ABI) and run on the ABI 373A automated sequencer. In all cases, complementary strands of all fragments were independently amplified and sequenced to assure accurate results. If complementary strands disagreed, the product was reamplified and sequenced to resolve any discrepancies.

Morphological Characters

Quantitative cladistic analysis has not previously been applied to morphological data in the study of holometabolan relationships. Hennig (1969, 1981), Boudreaux (1979), Kristensen (1975, 1981, 1991, 1995), and others based their phylogenetic conclusions on morphology without a formal parsimony analysis of character data. Moreover, all previous molecular studies have simply compared molecular trees with a morphological topology without considering how conflict within the morphological data may influence the interpretation of molecular data. This study presents the first published morphological matrix and the first attempt to combine directly molecular and morphological evidence for insect interordinal relationships.

Our morphological matrix was derived from the literature, chiefly from the work of Kristensen (1975, 1981, 1991, 1995), Hennig (1969, 1981), and Boudreaux (1979). The matrix is a compilation of all ordinal-level phylogenetically informative characters for the holometabolous insect orders and insect outgroups, and as such these characters represent what is considered to be the ground-plan states for each order. We did not attempt to code morphological characters for resolution of relationships below the ordinal level because the determination of these relationships is not the thrust of this paper. The matrix includes many, but by no means all, of the ordinal autapomorphies for each insect order. The morphological data were combined with the molecular data by extrapolating the ordinal scores to each sequenced exemplar. Hence, all resolution within orders is entirely the result of the molecular data. This methodology biases our results by making it less likely that the monophyly of an order will be rejected. However, this bias is not problematic because the monophyly of the holometabolous insect orders is generally not disputed.

Alignment

The 18S and 28S sequences were aligned using the multiple alignment program MALIGN (parallel version 1.93, Wheeler and Gladstein, 1994). This parsimony-based program selects among all possible multiple alignments by determining the order of sequence accretion that minimizes the phylogenetic cost for a given set of parameter values. Algorithmic alignment was preferred over manual alignment to avoid introducing bias based on preconceived notions of phylogeny and to assure optimal alignments. The heuristic algorithm "Build" with SPR branch swapping on multiple alignments was performed on 10 Hewlett-Packard workstations operating in parallel (change cost = 3, gap cost = 5, leading and trailing gap cost = 8). A change/gap cost ratio of 3:5 was selected because this ratio minimizes incongruence among aligned data sets in arthropods (Wheeler, 1995). The leading and trailing gap costs were set to 8 to cause the flanking primer regions to align. Based on the initial results of alignment, the 28S and 18S sequences were subdivided into multiple contiguous fragments, and more rigorous searches were then performed on the variable regions requiring multiple gaps. When the initial alignment presented evidence of a large insertion in a single taxon or subset of taxa, the region was removed to facilitate alignment of positions flanking the insert.

Phylogenetic Analysis

Multiple alignments were analyzed using NONA 1.15 (Goloboff, 1994) and PAUP 3.1.1. (Swofford, 1991). Primer regions were excluded, and all ambiguous nucleotides were treated as missing data. The data sets were analyzed with NONA under the options "mult*10" (10 random addition sequences with TBR swapping), "max" (TBR swapping on the trees found by mult*), and "hold 5,000" (save up to 5,000 trees). Additional swapping on up to 5,000 trees that are up to 10% longer than the shortest tree ("jump") was performed to help the swapper move between multiple "islands" of trees (Goloboff, 1994). If more than 5,000 trees were found, the search was repeated with a value for "hold," which retained the entire set of trees. For the morphology and one representative each of 18S, 28S, total molecular, and total data trees, the minimum and maximum branch lengths were calculated with PAUP. For these trees, Bremer support values (Bremer, 1994) were calculated by importing the set of most-parsimonious trees found by NONA into PAUP and then TBR branch swapping on the trees while constraining nonmonophyly of the group of interest. If Bremer support values were large (>25), the number was recalculated using heuristic search options of PAUP and the smaller value was taken. The number of steps required to force monophyly was calculated in NONA by constraining the monophyly of a group while swapping on all other terminals (force +n; max/) and taking the difference between the tree lengths.

Sensitivity analysis was performed on these data to test the robustness of clades. Sensitivity analysis is based on the premise that there are parameter values essential for data analysis in a phylogenetic context that cannot be empirically determined prior to phylogenetic analysis (Wheeler, 1995). These values might include character weights, transition/transversion ratios, and gap/change ratios. Sensitivity analysis is not concerned with estimating the "true" value of these parameters but rather concentrates on assessing the relative robustness of clades to perturbations of values across a parameter space. If a group appears monophyletic only under a very specific combination of parameter values, less confidence may be placed in the supposition that the data robustly support the monophyly of that group. If, however, a group appears monophyletic under a wider range and combination of parameter values, more confidence may be placed in the conclusion that the data support the monophyly of that clade. In this analysis, we attempted specifically to determine the influence of gap and character weighting schemes, regions of sequence alignments, different methods of combining data, and the effect of combining multiple data sets on the robustness of holometabolous insect clades.

It has been suggested that only those regions of an alignment that can be unambiguously aligned by eye should be used in phylogenetic reconstruction because these regions are more likely to reflect true homology statements among nucleotides, particularly for deeper phylogenetic relationships (Dixon and Hillis, 1993; Van de Peer et al., 1993; Smothers et al., 1994). To determine the influence of presumed alignment conservation on nodal stability, the 18S and 28S alignments were divided into conserved and variable regions. The conserved regions correspond roughly to those that can be aligned unambiguously by eye (or regions that do not change under a wide range of alignment parameter values). The variable regions correspond to those that required more aggressive alignment routines. For 18S, the variable regions are positions 281–361 and for 28S they are 47–59, 88–118, 135–179, and 198–220 (Appendices 1, 2). In the "conserved" analyses, the variable regions were excluded during phylogenetic reconstruction; in the "entire" analyses all regions were used. Characters marking the positions of major insertions were treated as missing data in the entire analyses. Recoding these shared insert regions into multistate nonadditive characters and appending them to the data matrices does not change tree topology.

Data sets relying on multiple genes often have unequal numbers of sequences because certain taxa are only present for a subset of genes. These data sets may be combined either by removing the taxa that have not been sequenced for all gene regions (merging) or by introducing missing values for the absent sequence region (splicing; Nixon and Carpenter, 1996). Purging a data set of taxa with many missing values may reduce the total number of most-parsimonious trees found because taxa with many missing values may attach themselves to multiple positions, resulting in decreased resolution in the consensus. However, purging missing values may also have the negative effect of removing taxa that may be critical for polarity determinations. We have examined the effects of both methods of data combination in this analysis.

Matrices were generated for the conserved and entire regions of 18S and 28S and were then combined with the corresponding regions in 18S and 28S (e.g., 18S conserved + 28S conserved = molecular conserved) by the methods of merging and splicing. Each of the molecular matrices were then combined with morphological data to form a total evidence matrix (Kluge, 1989). Finally, every data set was analyzed with gaps treated as missing, given the same weight as nucleotide data, and given twice the weight of nucleotide data (the 2:1 weighting approximates the gap/change ratio used during alignment). For the simultaneous analysis of all data sets (=total evidence analysis; Nixon and Carpenter, 1996), morphology data were given the same or twice the weight of nucleotide changes. This procedure yielded 48 matrices, which were analyzed using NONA (Goloboff, 1994) with the same approximate searches as outlined above. The strict consensus of the set of most-parsimonious trees from each matrix was calculated and used as the tree of reference in the sensitivity analyses. The morphological matrix is given in Appendix 3 and tree statistics are given in Appendix 4.

Incongruence among the 18S, 28S, and morphology data sets was tested by calculating the difference between the length of trees from the combined data set and the sum of the lengths of trees from the partitioned data set (the incongruence length difference [ILD]; Mickevich and Farris, 1981; Farris et al., 1994). The advantage of ILD over topology-based measures is that it is character based and can take into account the relative support for a particular topology. The ILD was tested for statistical significance against a distribution of ILD values that was generated by randomly partitioning the combined data set into subsets the size of the original partitions. Each test consisted of 10,000 random partitions. The calculation of these values and tests for significance were automated by using the "arn" program of Farris et al. (1994), and test statistics were adjusted for multiple tests using the Bonferroni correction (Holm, 1979; Rice, 1989).

RESULTS

Sequence Alignment

Multiple alignment of the 18S data produced 1,116 nucleotide positions with 24 inserts; alignment of the 28S data produced 398 positions with 14 inserts (Appendices 1, 2). Of these positions, 671 for 18S and 290 for 28S contained phylogenetically informative base substitutions and/or gaps (excluding primers and insert regions). Of the 18S informative characters, two base substitutions and seven gap characters have identical distributions throughout the taxa. Of the 28S informative characters, four base substitutions and no gap characters have identical distribution throughout the taxa.

Of the 18S inserts, 6 are autapomorphic for individual taxa (inserts 1, 6, 8, 9, 14, 24), 2 are aligned at the generic level (18, 22), 10 are aligned at the ordinal level (2, 3, 12, 13, 16, 17, 19, 20, 21, 23), and 5 are aligned at the interordinal level (4, 5, 10, 11, 15). The two inserts that appear phylogenetically informative at the interordinal level within Holometabola (11, 15) are entirely congruent with relationships supported in all 18S analyses. The majority of the 18S inserts occur in the 5′ portion of the D fragment, beginning at position 330 and extending as far as position 385, although Strepsiptera and Diptera each have an insert starting at position 268 (these inserts correspond to loop regions in the secondary structure of the molecule).

Strepsiptera have another clearly defined insert region at positions 497–520 (insert 23). Although the primary alignment of this insert appears ambiguous, the secondary structure is well supported with long stems, and the secondary structure appears conserved at least among the more morphologically derived strepsipteran taxa (Fig. 4). Insert 23 is unique in that multiple classes of inserts occur within a single strepsipteran individual. Nucleotides outside of the insert region were identical from clone to clone, but within the insert there were many differences in sequence length and nucleotide composition. We found two major classes of inserts in the more derived Strepsiptera: the "long" and "short" inserts of *Xenos* and *Caenocholax*. Stylopidae (*Crawfordia* and *Xenos*) have longer stems and a higher percentage of AT matches than do the more basal taxa (*Triozocera* and *Caenocholax*; see Fig. 4). In *Xenos pecki*, the long insert (386 bp) is extremely AT rich (92%), and different clones showed variation in the string length of A's and T's involved in stem pairing. The short insert is 340 bp long and lacks the AT-rich regions (44%). In *Caenocholax*, the long insert is 126 bp, the short is 97 bp, and neither is AT rich. The sequence from *Xenos vesparum* (364 bp) is AT rich (89%) and probably homologous to the long insert of *X. pecki*. More careful sequencing of this taxon should yield the shorter insert.

Of the 28S inserts, five are autapomorphic for individual taxa (inserts 3, 5, 9, 10, 11), seven are aligned at the ordinal level (1, 2, 4, 7, 8, 12, 13), and two are aligned at the interordinal level (6, 14). The two inserts aligned at the interordinal level support phylogenetic relationships that are entirely congruent with relationships supported in all 28S analyses. Once again, Strepsiptera have a large insert region within the 28S sequences.

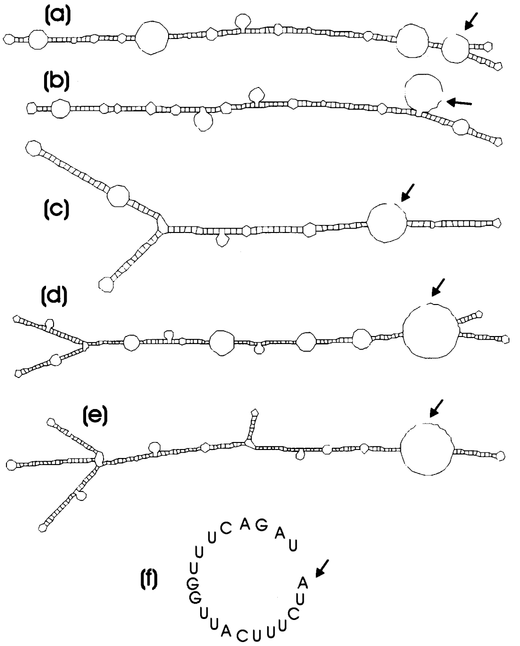


FIGURE 4. Secondary structures for strepsipteran 18S rDNA insert 23. This insert is expanded (232–394 bp) in Strepsiptera and forms long thermostable stems but is a simple loop in all other insects (21–25 bp). The more derived Strepisptera (Stylopidae: *Crawfordia* and *Xenos*) have longer stems and a higher percentage of AU matches than do the more basal taxa (*Triozocera* and *Caenocholax*). Structure computation was based on thermodynamic stability at 37°C using the default heat curve calculations as implimented in RNAdraw 1.0 (Matzura, 1995). Arrows mark the 5′ end of the insert. Number of base pair matches are given. (a) *Triozocera mexicana* (−294.807 kJ): 48 GC, 23 AU, 12 GU. (b) *Caenocholax fenyesi* (−280.487 kJ): 44 CG, 26 AU, 15 GU. (c) *Crawfordia* n. sp. (−206.712 kJ): 16 CG, 54 AU, 15 GU. (d) *Xenos vesparum* (−202.19kJ): 12 CG, 102 AU, 2 GU. (e) *Xenos pecki* (−247.954 kJ): 10 CG, 134 AU, 2 GU. (f) *Drosophila melanogaster* (0 kJ): no matches.

Data Set Incongruence

Significance tests using the "arn" program of Farris et al. (1994) with a Bonferroni correction indicate that for 2 of 24 comparisons, there is sufficient evidence to reject congruence relative to the alternative hypothesis of data set incongruence (Table 3; α < 0.002). The only cases of incongruence are found when the entire alignment of the 28S data is combined with the morphological data. There is no evidence to suggest that 18S and morphological data are incongruent; these comparisons result in α values of 1.0. Overall, these tests suggest that for most data set comparisons there is insufficient evidence to reject the hypothesis of congruence and that most of the incongruence appears to originate from the entire 28S alignment.

Phylogenetic Relationships

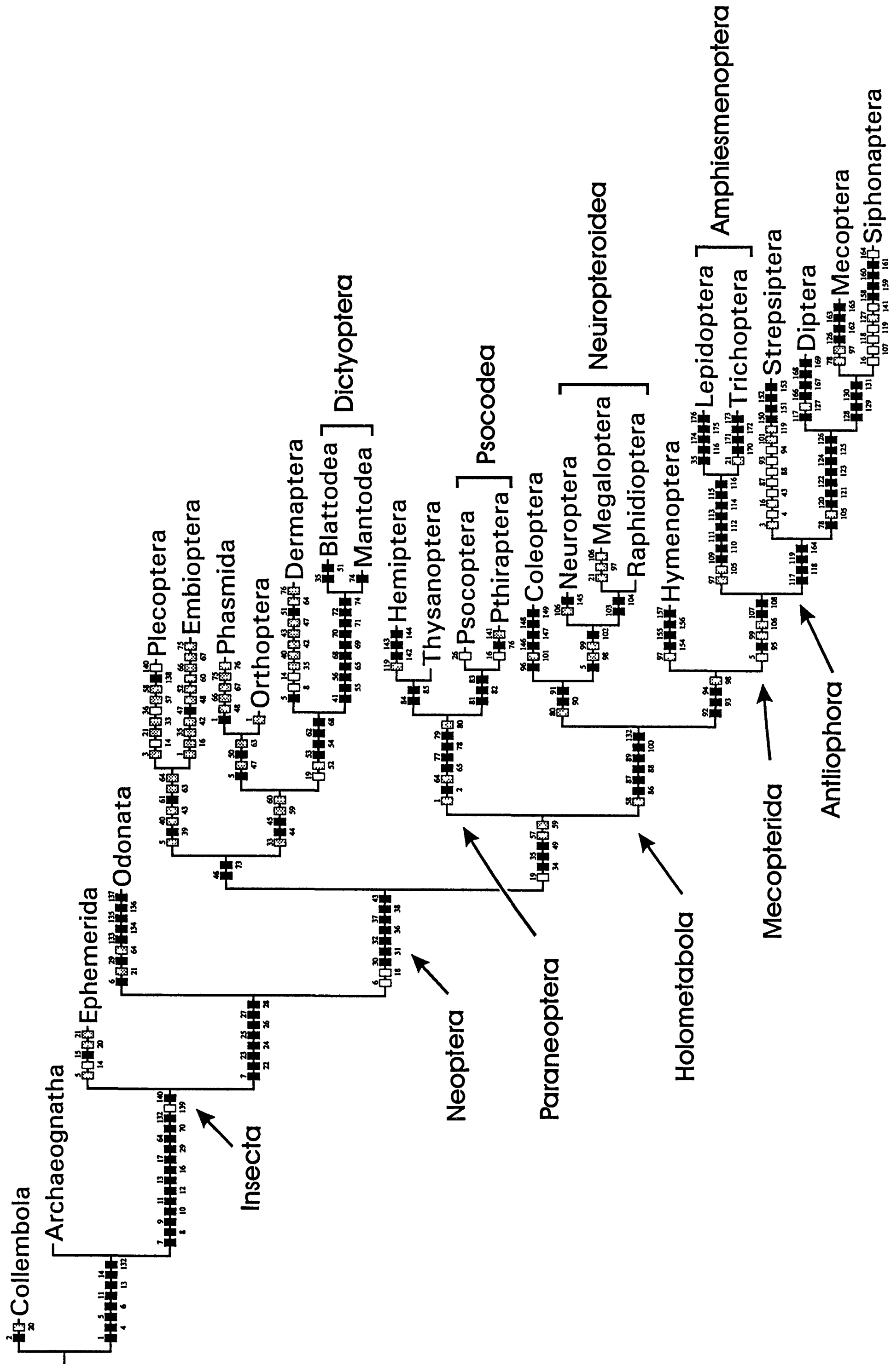
Parsimony analysis of the morphological data with all characters weighted equally generated one most-parsimonious tree of 279 steps, a consistency index (CI) of 0.74, and a retention index (RI) of 0.82 (Fig. 5). The relationships within Holometabola are congruent with those of Kristensen (1995) except for the placement of Strepsiptera as sister to (Diptera + (Mecoptera + Siphonaptera)). This relationship is supported by 4 nonhomoplastic character changes under a modified DELTRAN optimization and 10 nonhomoplastic and 1 reversal character under a modified ACCTRAN optimization (Fig. 6a; Nixon, 1995). The difference in these branch lengths is due to the different manner in which these methods optimize the states coded as missing in Strepsiptera and Siphonaptera. The relationships among the nonholometabolous neopterans do not conflict with Kristensen's hypothesis except for the paraphyly of Paleoptera (Ephemerida + Odonata), with Ephemerida as the more basal clade. Forcing the Strepsiptera as sister group to Coleoptera increases the length of the tree by five steps by adding one extra step to characters 5, 80, 95, 117, 188, and 164 (all homoplastic on the branch subtending Strepsiptera) and removing a step from character 101 (Fig. 6b; modified DELTRAN). Flight by posteromotorism (character 101) is the only morphological character supporting Coleoptera + Strepsiptera when these taxa are forced together.

Parsimony analysis of the entire 18S alignment with gaps coded as missing yielded 162 trees of 1,965 steps (CI = 0.41, RI = 0.63), the strict consensus of which is given in Figure 7. This tree was rooted to *Hypogastrura*. Among the outgroups, the 18S data support the monophyly of Odonata, Plecoptera, Heteroptera, Dictyoptera, and Psocodea. The basal placement of *Trigoniopthalmus* and the placement of Paleoptera as sister group to Neoptera is congruent with Kristensen's hypothesis (1991, 1995). Holometabola are monophyletic and sister group to the clade including Hemiptera and Thysanoptera, members of Paraneoptera. Paraneoptera are paraphyletic because of the more basal placement of

TABLE 3. Results of tests for data set incongruence using "arn" (Farris et al., 1994). Both the conserved and entire alignments were tested. Autapomorphic and uninformative characters were removed prior to performing the test, and for each test the repetition number for determining the null distribution was set at 10,000. For the two combination methods, spliced was used with 85 taxa and merged was used with 52 taxa.

Data set	Gaps weighted	Alpha value[a]
Total		
Entire spliced	?	0.079
	1	0.576
Entire merged	?	0.592
	1	0.012
Conserved spliced	?	1.000
	1	1.000
Conserved merged	?	1.000
	1	0.017
Molecular		
Entire spliced	?	1.000
	1	0.033
Entire merged	?	0.022
	1	0.004
Conserved spliced	?	1.000
	1	0.371
Conserved merged	?	0.061
	1	0.056
18S + morphology		
Entire spliced	?	1.000
	1	1.000
Conserved spliced	?	1.000
	1	1.000
28S + morphology		
Entire spliced	?	0.001*
	1	0.001*
Conserved spliced	?	0.006
	1	0.006

[a] Asterisks mark those values that reject the hypothesis of data set congruence.


Collembola
Archaeognatha
Ephemerida
Odonata
Plecoptera
Embioptera
Phasmida
Orthoptera
Dermaptera
Blattodea
Mantodea
Dictyoptera
Hemiptera
Thysanoptera
Psocoptera
Pthiraptera
Psocodea
Coleoptera
Neuroptera
Megaloptera
Raphidioptera
Neuropteroidea
Hymenoptera
Lepidoptera
Trichoptera
Amphiesmenoptera
Strepsiptera
Diptera
Mecoptera
Siphonaptera
Insecta
Neoptera
Paraneoptera
Holometabola
Mecopterida
Antliophora

Psocodea, and with this one exception, the overall rooting of the tree appears appropriate relative to the position of Holometabola. All orders within Holometabola are monophyletic except for Coleoptera and Mecoptera. The polyphagous beetles are monophyletic, but the basal *Priacma* (suborder Archostemata) and *Colpocaccus* (suborder Adephaga) are not associated with Polyphaga but rather form a sister group with Megaloptera + Raphidioptera (this clade is so commonly encountered in subsequent analyses that it will be abbreviated as MRPC). The other adephagan, *Cybister*, is associated with Polyphaga instead of *Colpocaccus*. The paraphyly of Mecoptera is due to the placement of *Boreus* as sister group to Siphonaptera. The monophyly of Megaloptera + Raphidioptera, Mecoptera + Siphonaptera, and Amphiesmenoptera is congruent with Kristensen's hypothesis (1991, 1995); however, Kristensen's Mecopterida and Neuropterida + Coleoptera are not supported in this analysis. The 18S data strongly support the placement of Strepsiptera as sister group to Diptera (hereinafter called Halteria). The root branches of Diptera and Strepsiptera have the greatest lengths and Bremer support values, although these are comparable to those of Trichoptera and Lepidoptera, which form Amphiesmenoptera, a group considered well established based on morphological data (Kristensen, 1991, 1995).

Parsimony analysis of the entire 28S alignment with gaps weighted as 2 and rooted to *Trigoniopthalmus* yielded 12 trees of 1,404 steps (CI = 0.36, RI = 0.62), the strict consensus of which is given in Figure 8. Among the outgroups, this analysis supports the monophyly of Plecoptera, Odonata, and Heteroptera, although the relationships among these groups are only partially congruent with morphology. Neoptera are paraphyletic because the *Mantis* and *Oligotoma* sequences are sister group to Odonata. *Melanoplus* and the Plecoptera sequences group with Heteroptera and, rather than Paraneoptera, form the sister group to Holometabola. Holometabola, and all included orders, are monophyletic except for Coleoptera and Mecoptera. As was seen in the 18S analysis, mecopteran paraphyly is due to the placement of *Boreus* as sister group to Siphonaptera. Coleopteran paraphyly, however, is due to the placement of *Colpocaccus*, rather than the MRPC grouping as described in the 18S analysis, at the base of Holometabola. *Priacma* is sister group to the remaining beetles, and Polyphaga are paraphyletic because *Cybister* is nested within the group. The 28S data are congruent with the other data sets in supporting the monophyly of Mecoptera + Siphonaptera, Megaloptera + Raphidioptera, Amphiesmenoptera, and Halteria. Again, Amphiesmenoptera and Halteria are composed of orders with long branches and high Bremer support values. The smaller CI and RI values for 28S relative to 18S indicate a greater degree of internal character conflict, especially when the smaller number of taxa and characters for the 28S is taken into consideration.

The combined molecular data were analyzed by scoring the taxa absent in the 28S data set with missing values for the 18S data (splicing) and combining the data sets. The complete 28S and 18S alignments were included, gaps were treated as missing characters, and the tree was rooted to *Hypogastrura*, and the analysis resulted in 168 trees of 2,939 steps (CI = 0.39, RI =

←

FIGURE 5. Insect morphology tree with mapped characters (length = 279, CI = 0.74, RI = 0.82). All characters were weighted equally, and the analysis generated one most-parsimonious tree. Mapped characters were optimized using a modified DELTRAN optimization (Nixon, 1995). Numbers next to boxes refer to character numbers as given in Appendix 3. ■ = nonhomoplastic change; □ = homoplastic change; □ = reversal. Bremer support values for holometabolous relationships are Amphiesmenoptera: 9; Holometabola: 6; Neuropteroidea: 3; Mecopterida + Hymenoptera, Mecopterida, and Antliophora: 2; remaining: 1. This tree is congruent with that of Kristensen (1991) except for the placement of Strepsiptera as sister group to (Diptera + (Mecoptera + Diptera)) and a paraphyletic Paleoptera (Odonata + Ephermerida).

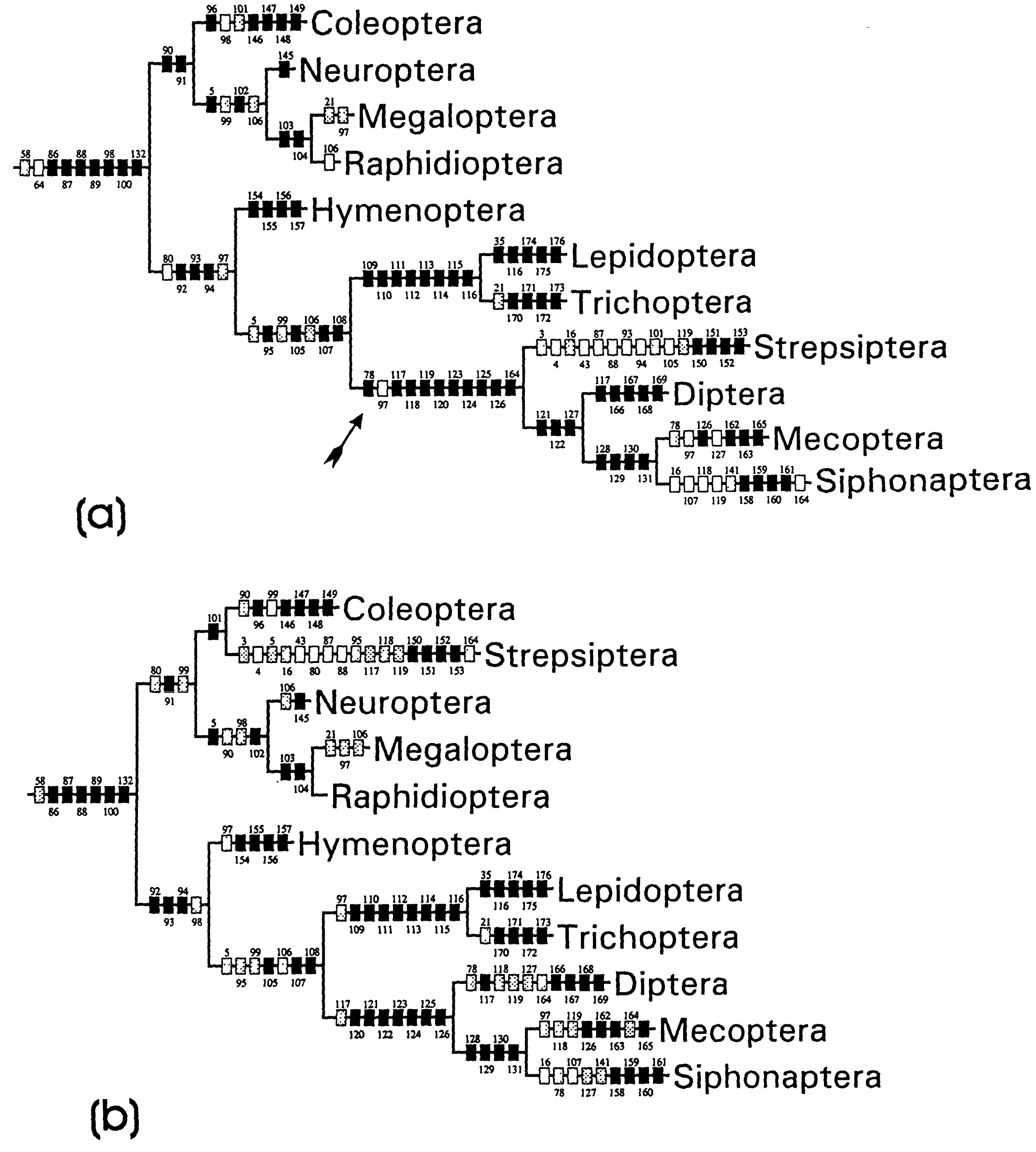


FIGURE 6. Holometabolous portion of morphology tree. Characters were optimized using a modified DELTRAN optimization (Nixon, 1995). Numbers next to boxes are the character numbers as given in Appendix 3. ■ = nonhomoplastic change; □ = homoplastic change; □ = reversal. (a) Characters mapped under a modified ACCTRAN optimization (Nixon, 1995). This optimization yields a tree with 10 nonhomoplastic characters and 1 character reversal supporting the antliophoran node including Strepsiptera (arrow), in contrast to the 4 nonhomoplastic characters supporting the same node under modified DELTRAN optimization (Fig. 5). This difference is a result of how the missing values in Strepsiptera and Siphonaptera are optimized. (b) Strepsiptera forced as sister group to Coleoptera (length = 284, CI = 0.73, RI = 0.81). All characters were weighted equally, and the analysis generated one most-parsimonious tree. Forcing Strepsiptera into this position adds one step to characters 5, 80, 95, 117, 188, and 164 (all homoplastic on the branch subtending Strepsiptera) and removes a step from character 101 (relative to Fig. 5).

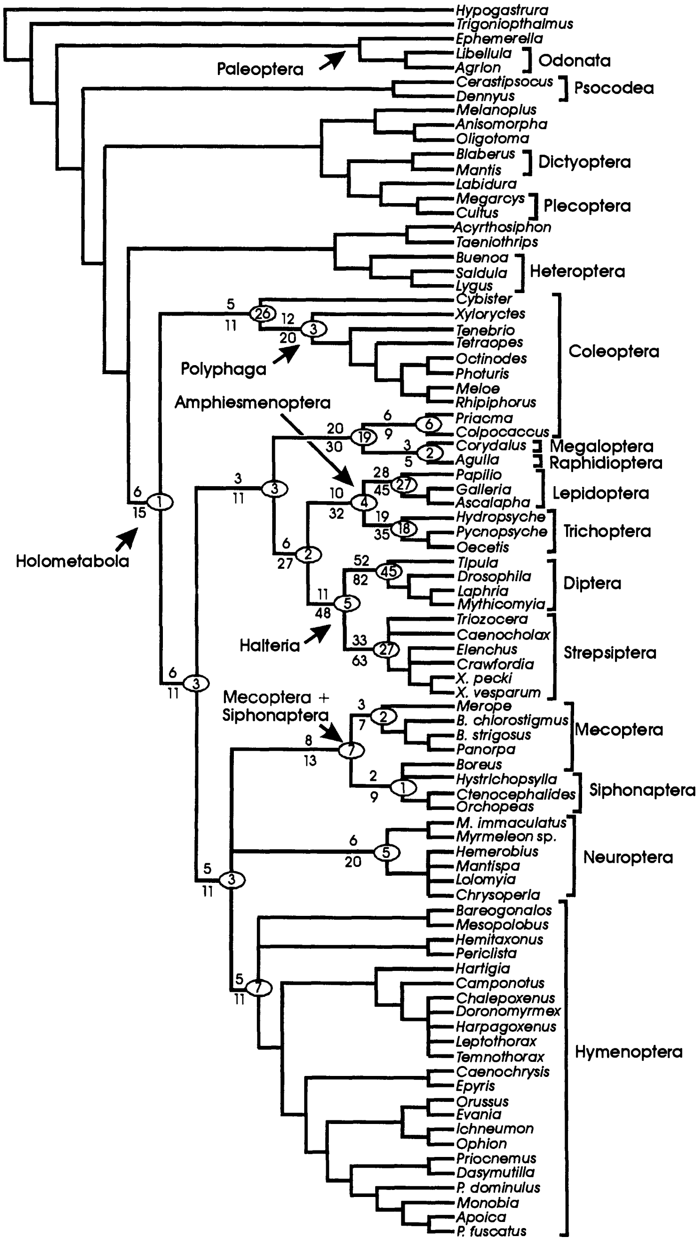


Figure 7. Insect 18S tree (length = 1,965, CI = 0.41, RI = 0.63). This is the strict consensus of 162 trees with gaps coded as missing. The entire portion of the 18S alignment was used in the analysis. Numbers above and below branches are maximum/minimum branch lengths; circled numbers are Bremer support values. The alignment is presented in Appendix 1.

0.61), the strict consensus of which is presented in Figure 9. This analysis supports the monophyly of Odonata, Paleoptera, Psocodea, Heteroptera, Plecoptera, and Dictyoptera. Psocodea are again placed basally and do not group with Hemiptera and Thysanoptera, and the sister group to Holometabola is a clade composed of Ple-

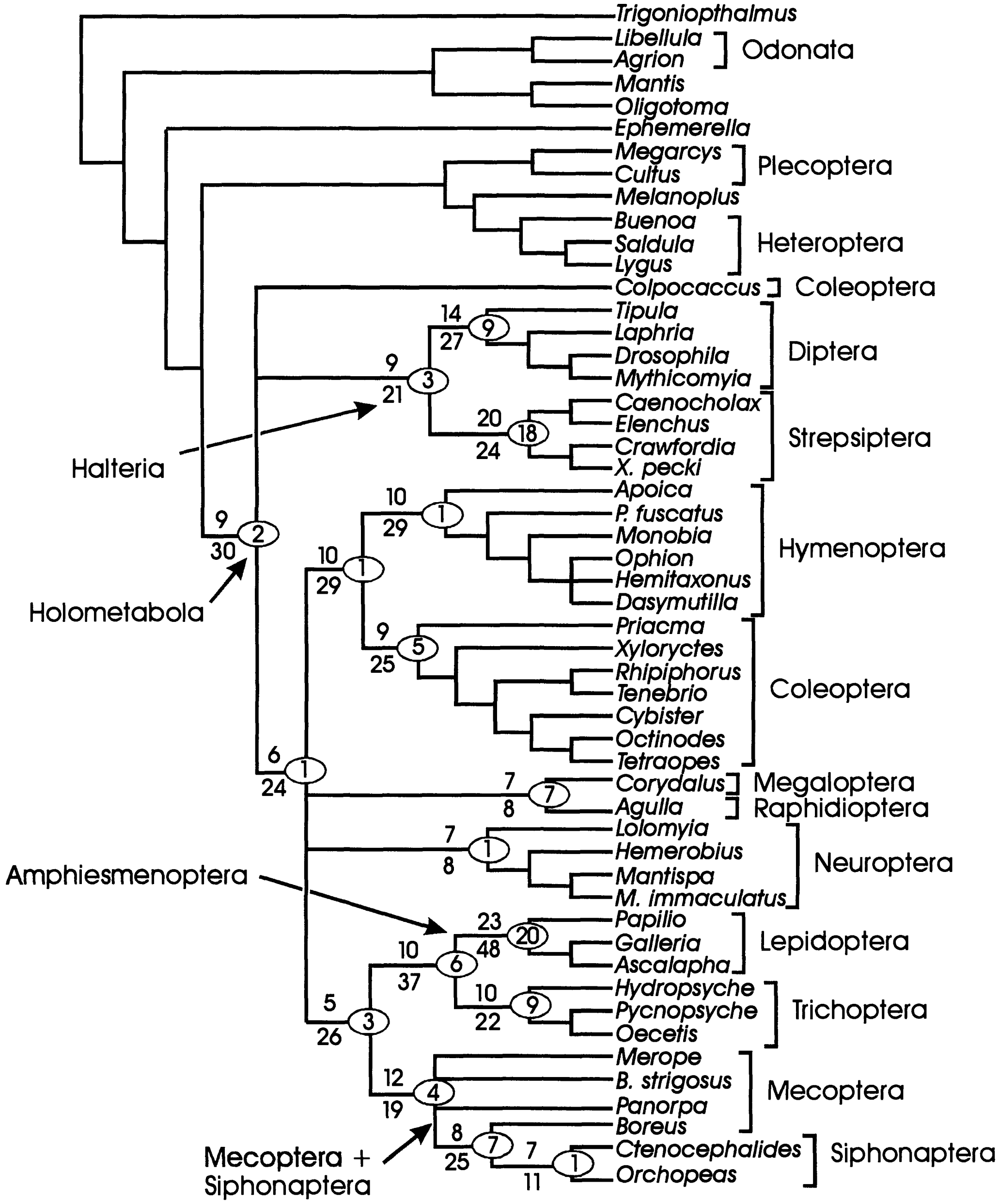


FIGURE 8. Insect 28S tree (length = 1,404, CI = 0.36, RI = 0.62). This is the strict consensus of 12 most-parsimonious trees with a gap weight of 2. The entire portion of the 28S alignment was used in the analysis. Numbers above and below branches are maximum/minimum branch lengths; circled numbers are Bremer support values. The alignment is presented in Appendix 2.

coptera, Dictyoptera, and Dermaptera. Holometabola are monophyletic, and all orders within Holometabola are monophyletic except for Mecoptera and Coleoptera. Again, the paraphyly of Mecoptera is due to the grouping of *Boreus* as sister group to Siphonaptera, and the paraphyly of Coleoptera is due to the presence of MRPC.

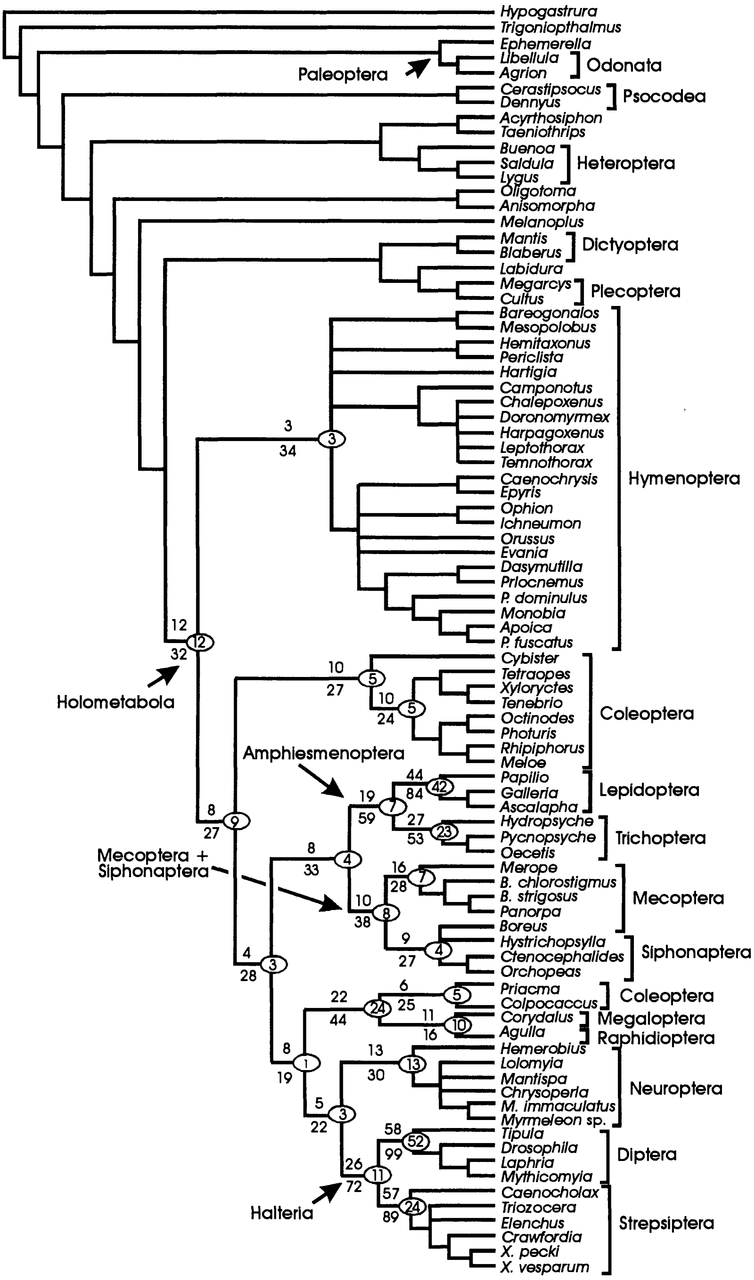


FIGURE 9. Insect molecular tree (length = 2,939, CI = 0.39, RI = 0.61). This is the strict consensus of 168 trees with gaps treated as missing. The entire portions of the 28S and 18S alignments were used in the analysis, and taxa not sequenced for 28S were given missing values prior to data set combination (splicing). Numbers above and below branches are maximum/minimum branch lengths; circled numbers are the Bremer support values.

This combined molecular analysis supports the monophyly of Halteria, Mecoptera + Siphonaptera, Megaloptera + Raphidioptera, and Amphiesmenoptera. Again, the monophyly of the orders comprising Halteria and Amphiesmenoptera is well supported with large branch lengths and Bremer support values. Neuroptera are sister group to Halteria, which, as a clade, are sister group to MRPC. Hymenoptera are the most basal holometabolous order.

A simultaneous analysis of all data was accomplished by scoring each taxon with the morphological data for the order to which it belongs and then combining these data with the spliced molecular data set. Gaps were treated as missing values, nucleotide and morphological characters were weighted equally, and the tree was rooted to *Hypogastrura*. Parsimony analysis resulted in 10 trees of 3,339 steps (CI = 0.42, RI = 0.67), the strict consensus of which is presented in Figure 10. Among the outgroups, this analysis supports the monophyly of Odonata, Dictyoptera, Plecoptera, Psocodea, Hemiptera, Heteroptera, Neoptera, and Paraneoptera. Relationships among these outgroups are congruent with our morphological tree except for the placement of Psocodea as sister group to Thysanoptera (rather than as sister group to Thysanoptera + Hemiptera), Dermaptera as sister group to Plecoptera (rather than Dictyoptera), and Embioptera as sister group to Phasmida (rather than Plecoptera). Paraneoptera are sister group to Holometabola, and Holometabola are a well-supported clade. All orders within Holometabola are monophyletic except for Mecoptera and Coleoptera. As seen in previous analyses, *Boreus* groups with the fleas, and the paraphyly of Coleoptera is due to MRPC. This simultaneous analysis supports the monophyly of Siphonaptera + Mecoptera, Megaloptera + Raphidioptera, Amphiesmenoptera, and Halteria. In addition, Mecopterida and Antliophora (with the inclusion of Strepsiptera) are both monophyletic, and Hymenoptera is sister group to Mecopterida. Once again, the Bremer support values and branch lengths for Amphiesmenoptera and Halteria are large. The placement of Amphiesmenoptera as sister group to Antliophora is congruent with our morphological analyses.

Sensitivity Analysis

Matrices for the sensitivity analysis were generated and analyzed as described above. Results from the sensitivity analyses are given in Figures 11–13, the consensus trees are shown in Figure 14, and tree statistics are presented in Appendix 4. For interordinal comparisons of topologies, if all terminals of an order were monophyletic in the strict consensus tree, the multiple terminals were replaced by the ordinal name at the node subtending those terminals. Where the representatives of an order are unresolved, the node subtending the order is illustrated by a thick bar in the figures. Paraphyletic orders are represented by an asterisk next to the name of the order, with the positions where the terminals appear on the tree labeled. A majority rule (>50%) consensus of each of these resulting sets of trees was taken. For example, the consensus tree for 18S (Fig. 14) is the majority-rule consensus of trees in Figures 11a–f. Numbers on the nodes (nodal values) represent the percentage of times a clade is monophyletic across the sensitivity analyses and were computed by dividing the number of times a group is monophyletic by the sum of the number of times it is monophyletic, paraphyletic, and polyphyletic. Unresolved groupings were ignored in this calculation because it is not clear whether they should be considered congruent or incongruent with the hypothesis of monophyly.

18S data.—In these analyses (Figs. 11a–f), all holometabolous orders are monophyletic (or unresolved) except for Coleoptera and Mecoptera (for the same reasons as discussed above) and one instance of hymenopteran paraphyly (Fig. 11c). The monophyly of Halteria, Amphiesmenoptera, Polyphaga, Mecoptera + Siphonaptera, Megaloptera + Raphidioptera, *Priacma* + *Colpocaccus*, and MRPC is supported in all 18S analyses. When only the con-

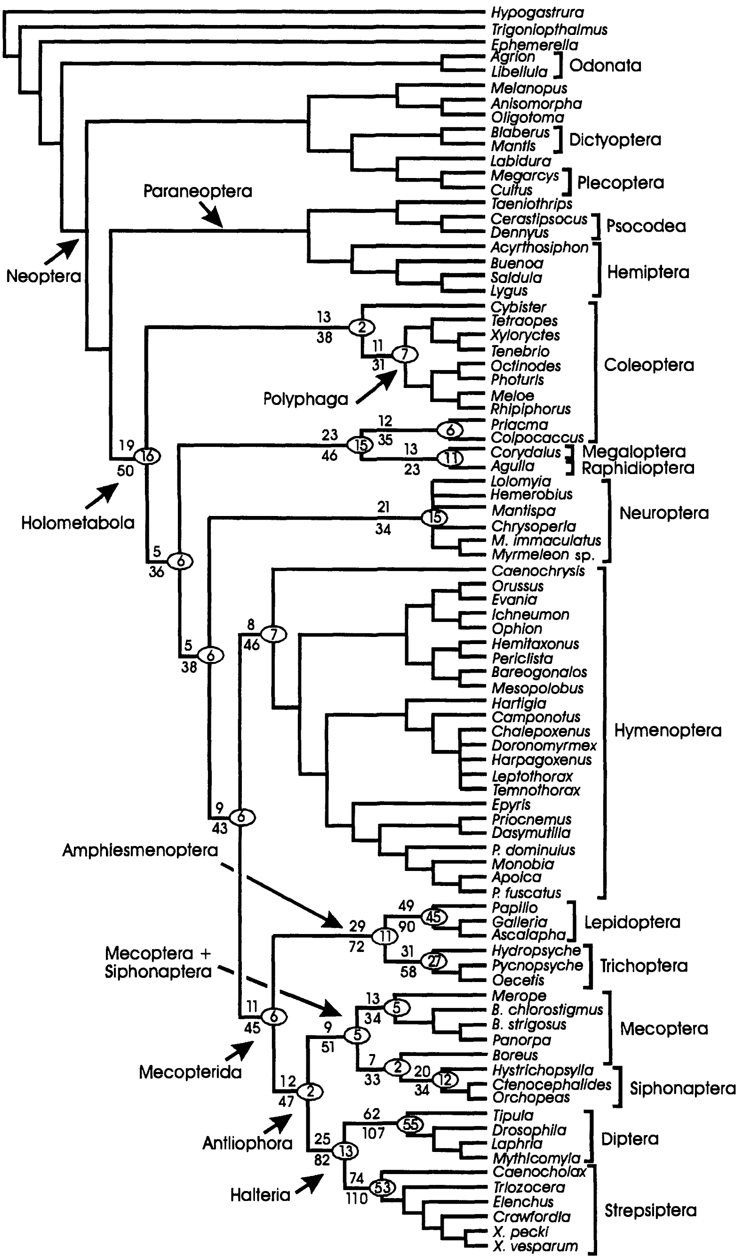


FIGURE 10. Tree from simultaneous analysis of all insect data (length = 3,339, CI = 0.42, RI = 0.67). This is the strict consensus of 10 most-parsimonious trees. The complete 18S and 28S alignments were used in this analysis, gaps were coded as missing, morphological characters were weighted by 1, and taxa not sequenced for 28S were given missing values prior to combination with the morphological data (splicing). Numbers above and below branches are maximum/minimum branch lengths; circled numbers are Bremer support values.

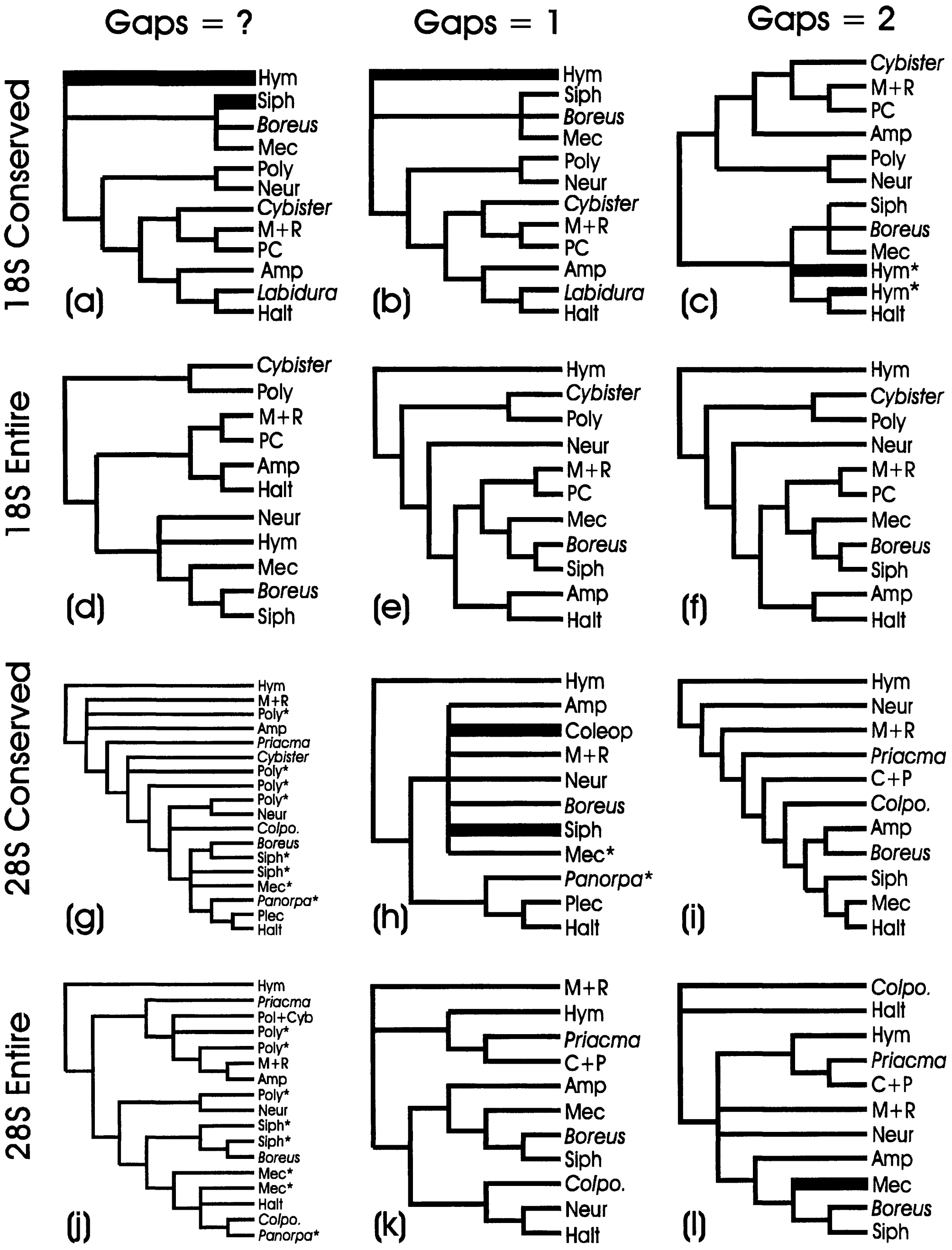


FIGURE 11. Results of sensitivity analysis for 18S (a–f) and 28S (g–l) matrices for holometabolous insect relationships. Sensitivity parameters are alignment region (conserved or entire) and gap weighting scheme (missing [?], 1, or 2). Relationships among outgroups are not included. Unresolved clades are shown as thick bars, and paraphyletic groups are marked by asterisks. Amp = Amphiesmenoptera (Lepidoptera + Trichoptera); *Colpo.* = *Colpocaccus*; Halt = Halteria (Diptera + Strepsiptera); Hym = Hymenoptera; M+R = Megaloptera + Raphidioptera; Mec = Mecoptera excluding *Boreus*; Neur = Neuroptera (sensu stricto = Planipennia); PC = *Priacma* + *Colpocaccus*; Plec = Plecoptera; C+P = *Cybister* nested in Polyphaga; Poly = Polyphaga; Pol + Cyb = Polyphaga + *Cybister*; Siph = Siphonaptera. Tree statistics are given in Appendix 4.

served portion of the alignment is included in tree reconstruction, the outgroup *Labidura* is placed within Holometabola as sister group to Halteria (Figs. 11a, 11b), *Cybister* is sister group to MRPC, and Neuroptera is sister group to Polyphaga. When the entire portion of the alignment is included in tree reconstruction, *Cybister* is sister group to Polyphaga, MRPC is sister group to Mecoptera + Siphonaptera, and Halteria is sister group to Amphiesmenoptera. *Boreus* is sister group to Siphonaptera with the entire alignment and unresolved with respect to Mecoptera and Siphonaptera with the conserved alignment.

28S data.—In all 28S analyses, Strepsiptera, Diptera, Lepidoptera, Trichoptera, Hymenoptera, Halteria, Amphiesmenoptera, and Megaloptera + Raphidioptera are monophyletic (Figs. 11g–l). Holometabola are paraphyletic in two analyses because of the grouping of Plecoptera with Halteria (Figs. 11g, 11h). When gaps are coded as missing, Polyphaga, Mecoptera, and Siphonaptera are paraphyletic (Figs. 11g, 11j). When only the conserved regions of the alignment are included in the tree reconstruction, Hymenoptera are basal to the other holometabolous orders; when the entire alignment is used, Hymenoptera are placed either basally in Holometabola (Fig. 11j) or as sister group to (*Priacma* + (Polyphaga + *Cybister*)). *Boreus* is placed within Siphonaptera (Figs. 11g, 11j), as sister group to Siphonaptera (Figs. 11k, 11l), or as sister group to Amphiesmenoptera (Fig. 11i) or is unresolved (Fig. 11h). *Panorpa* is sister group to Plecoptera + Halteria (Figs. 11g, 11h) and *Colpocaccus* (Fig. 11j); in the remaining analyses it groups with the other mecopteran taxa. Unlike with the 18S data, *Priacma* is never sister group to *Colpocaccus*, and although Megaloptera + Raphidioptera are monophyletic, the MRPC clade is not supported. *Priacma* is generally placed near the other beetles, but *Colpocaccus* does not group with the other beetles, and its position changes in each analysis, probably in part because of its unusual sequence, which includs AT-rich regions (e.g., 28S insert 5, Appendix 3).

Combined molecular data.—All combined molecular analyses support the monophyly of Diptera, Strepsiptera, Halteria, Megaloptera + Raphidioptera, Mecoptera (excluding *Boreus*), Mecoptera + Siphonaptera, Neuroptera, Lepidoptera, Trichoptera, Amphiesmenoptera, *Priacma* + *Colpocaccus*, and MRPC (Fig. 12). There are two instances of holometabolan paraphyly due to the placement of *Labidura* as sister group to Halteria (Figs. 12a, 12b); this result parallels that of the 18S analyses under the same parameter values (Figs. 11a, 11b). The one instance of siphonapteran paraphyly (Fig. 12a) is due to the 28S data and is congruent with the results of that analysis (Fig. 11g). Hymenoptera are sister group to Halteria when gaps are weighted as 2, are unresolved basally when gaps are weighted as 1, and are the most basal order when gaps are coded as missing, although Hymenoptera are paraphyletic in one analysis (Fig. 12a). *Boreus* is sister group to Siphonaptera in all analyses except that of the merged conserved molecular data, where it is sister group to Mecoptera (Figs. 12h, 12i) or unresolved (Fig. 12g); but even when Siphonaptera are paraphyletic (Fig. 12a), *Boreus* is associated with a flea sequence. Amphiesmenoptera is sister group to (Mecoptera + (Siphonaptera + *Boreus*)) in all analyses except one (Fig. 12c), where it is sister group to MRPC. *Cybister* is placed as sister group to Polyphaga in most analyses, although it is unresolved twice (Figs. 12g, 12h) and sister group to MRPC twice (Figs. 12a, 12b).

Total data.—The two molecular and the morphological data sets were combined into "total" data sets by splicing and merging as explained above. In addition to the parameter values used in the other sensitivity analyses, the morphological characters were given a weight of 1 (trees on the left side of the taxon names in Fig. 13) or 2 (trees on the right side). All 24 simultaneous analyses of the total data set support the monophyly of Strepsiptera, Diptera, Halteria, Lepidoptera, Trichoptera, Amphiesmenoptera, Megaloptera + Raphidioptera, *Colpocaccus* + *Priacma*, and Mecopterida. Within Mecopterida, Antli-

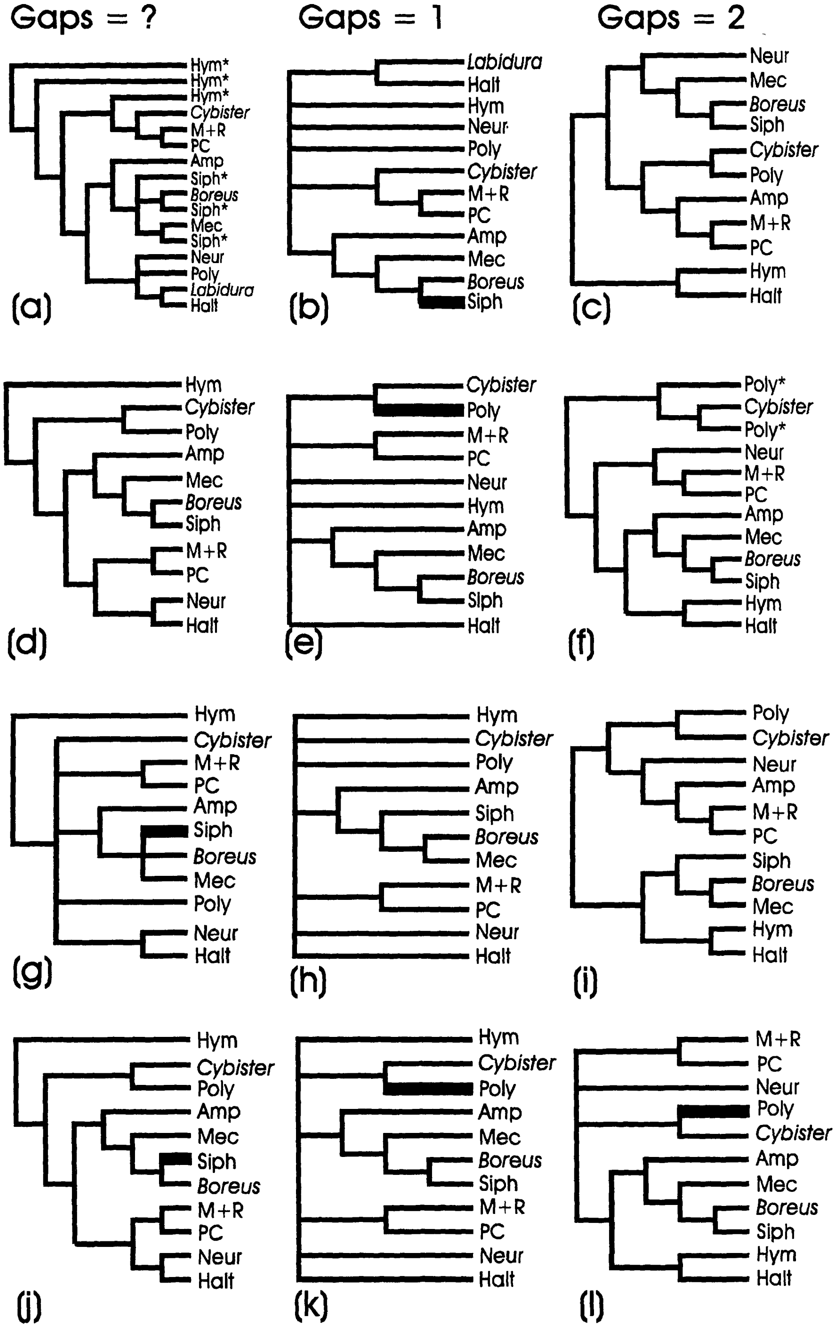


FIGURE 12. Results of sensitivity analysis of combined molecular data for holometabolous relationships. Sensitivity parameters are alignment region (conserved or entire), gap weighting scheme (missing [?], 1, or 2), and method of data set combination (merged or spliced). Relationships among outgroups are not included. Unresolved clades are shown by thick bars, and paraphyletic groups are marked by asterisks. Amp = Amphiesmenoptera (Lepidoptera + Trichoptera); Halt = Halteria (Diptera + Strepsiptera); Hym = Hymenoptera; M+R = Megaloptera + Raphidioptera; Mec = Mecoptera excluding *Boreus*; Neur = Neuroptera (sensu stricto = Planipennia); PC = *Priacma* + *Colpocaccus*; Poly = Polyphaga; Siph = Siphonaptera. Tree statistics are given in Appendix 4.

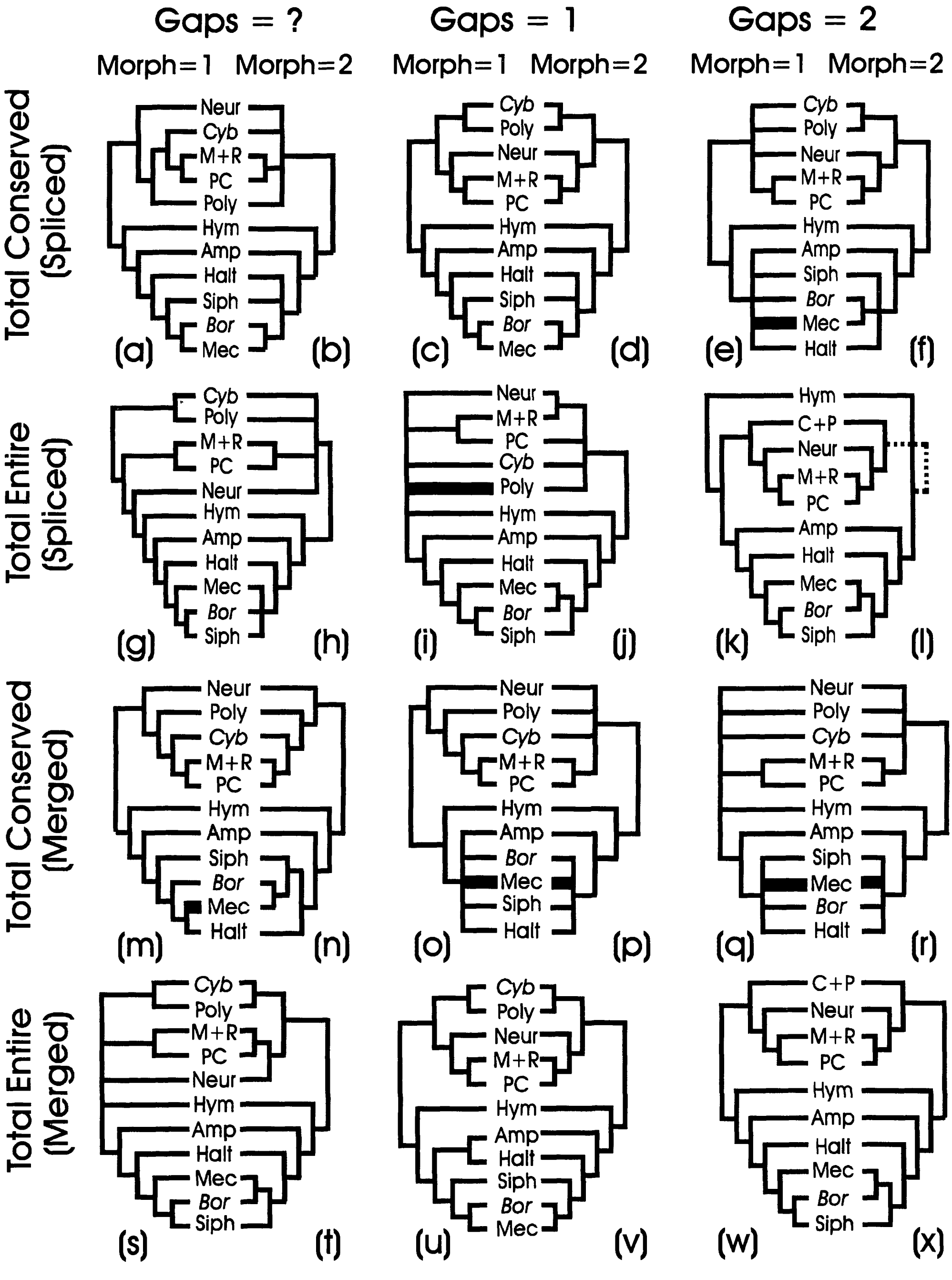


FIGURE 13. Results of sensitivity analysis from the simultaneous analysis of all insect data. Sensitivity parameters are alignment region (conserved or entire), gap weighting scheme (missing [?], 1, or 2), method of data set combination (merged or spliced), and weight of morphological data (1 [left trees] or 2 [right trees]). Relationships among outgroups are not included. Unresolved clades are shown as thick bars. Amp = Amphiesmenoptera (Lepidoptera + Trichoptera); *Bor* = *Boreus*; *Cyb* = *Cybister*; Halt = Halteria (Diptera + Strepsiptera); Hym = Hymenoptera; M+R = Megaloptera + Raphidioptera; Mec = Mecoptera excluding *Boreus*; Neur = Neuroptera (sensu stricto = Planipennia); PC = *Priacma* + *Colpocaccus*; C+P = *Cybister* nested in Polyphaga; Poly = Polyphaga; Siph = Siphonaptera. For tree l the group ((PC, M+R)Neur)C+P) is the most basal clade. Tree statistics are given in Appendix 4.

ophora are monophyletic in every analysis except one (Fig. 13u), where Amphiesmenoptera are sister group to Halteria. In most analyses, Halteria are sister group to Mecoptera + Siphonaptera. *Boreus* is sister group to Siphonaptera when the entire alignment region is included in the reconstruction and morphology is weighted as 1 (except for Fig. 13u). Under all other combinations of parameter values, *Boreus* is placed as sister group to Mecoptera (i.e., most basal member of Mecoptera) or unresolved with respect to Mecoptera and Siphonaptera. Hymenoptera is sister group to Mecopterida in all analyses except one (Fig. 13k), where it is basal to the remainder of Holometabola. Mecoptera + Siphonaptera (Fig. 13m), Coleoptera + Neuropteroidea (Fig. 13g), and MRPC (Fig. 13j) are each paraphyletic in one analysis.

Sensitivity consensus trees.—Trees that summarize results of the sensitivity analysis are presented in Figure 14. The greater resolution and higher frequency values in the 18S summary tree as compared with the 28S data indicate that, overall, there are more clades identical in the 18S analysis than in the 28S analysis. The greater sensitivity of the 28S data to parameter perturbations may be due to greater internal conflict among the characters, although the fact that the 28S data set consists of fewer taxa across a shorter length of sequence may also influence sensitivity. When the 18S and 28S data are combined, the combined molecular topology is congruent with the 18S topology and is more resolved. With the exception of the basal placement of Hymenoptera, the 28S topology is also congruent with but much less resolved than the molecular topology. The 18S data force the monophyly of MRPC for any analysis that includes 18S (with one exception, Fig. 13j). When the morphological data are added to the molecular data, the resulting topology is far more resolved than the molecular topology. This topology from the total data is congruent with the morphology tree (Fig. 5) except for the placement of Strepsiptera as sister group to Diptera and the monophyly of MRPC. The total data summary tree disagrees with the prior analyses in placing *Boreus* as sister group to Mecoptera (i.e., as the basal member of Mecoptera) rather than as sister group to Siphonaptera. This placement results because when the morphological data are given a weight of 2 there are sufficient mecopteran autapomorphies to force the monophyly of Mecoptera; if the morphology were only given a weight of 1 in the sensitivity analyses, the summary tree would place *Boreus* as sister group to Siphonaptera with a nodal value of 56.

In every sensitivity analysis, Strepsiptera, Diptera, Halteria, Trichoptera, Lepidoptera, Neuroptera, Amphiesmenoptera, and Megaloptera + Raphidioptera are monophyletic. This result suggests that confidence can be placed in the conclusion that the data presented in this study truly support these relationships. In most analyses, Hymenoptera, Siphonaptera, Mecoptera (excluding *Boreus*), Siphonaptera + *Boreus* + Mecoptera, *Priacma* + *Colpocaccus*, Polyphaga, MRPC, and Holometabola are monophyletic. The most borderline case is the position of *Boreus*, which moves between Siphonaptera and Mecoptera as discussed above.

Taxon Removal

The paraphyly of Coleoptera, Neuropterida, and Neuropterida + Coleoptera is due to the strongly supported MRPC clade in the analyses that include the 18S data. For these taxa, the 18S sequences are nearly identical for the regions sequenced (average distance = 0.01975), and even insert regions that are typically highly variable among orders (e.g., 18S insert 11) are identical across these taxa. To be certain this identity was not an artifact of amplification or sequencing, the 18S sequences for these taxa were generated multiple times from independent PCR products generated from different genomic extractions. There are base differences in the 18S sequences and marked differences in the 28S sequences, indicating that the genomic DNAs do not appear to be contaminated with the same foreign DNA. This result is surprising because the Coleoptera/Neuropterida split is presumed to be one of the oldest diver-

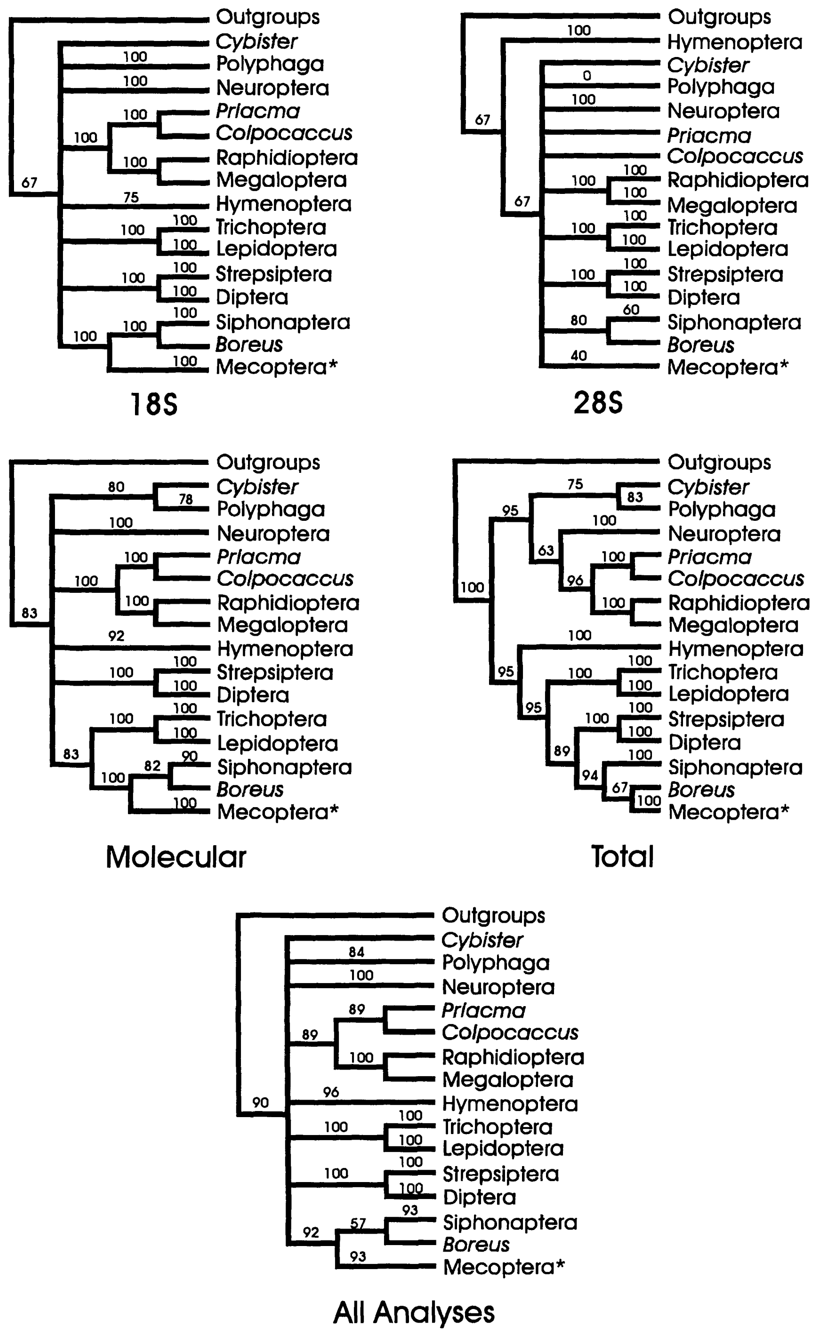


FIGURE 14. Sensitivity analysis consensus trees. Majority rule consensus trees were calculated for the sensitivity analysis trees presented in Figures 11–13. Nodal values represent the percentage of times a particular node is present in the sensitivity analysis; as calculated by $m/m + p$, where m = number of times a clade is monophyletic and p = number of times it is paraphyletic and polyphyletic. Mecoptera excludes *Boreus* (denoted by an asterisk).

gences within Holometabola (Kukalová-Peck, 1991), and it is remarkable that the nucleotide diversity between these two orders is less than that between other orders assumed to be of more recent origin (such as in Amphiesmenoptera). These results clearly indicate that the 18S molecule is not behaving in a clocklike manner in the insects and that this is a case of evolutionary stasis for 18S in these taxa.

If the MRPC clade appears to be preventing the monophyly of Coleoptera and Neuropterida, what happens when the taxa comprising this clade are removed prior to phylogenetic analysis? This question was investigated by rerunning the 18S, combined molecular, and total data sets generated for the sensitivity analyses in three additional ways: (1) with *Priacma* and *Colpocaccus* removed (PC), (2) with *Agulla* and *Corydalus* removed (M+R), and (3) with *Priacma, Colpocaccus, Agulla,* and *Corydalus* removed (MRPC). Because the 28S data do not support MRPC, the results of the removal of these taxa were not investigated. Trees were constructed using the same phylogenetic searching routines as outlined above, and their overall topology is described here in comparison with the trees generated from the all-taxa sensitivity analyses.

18S data.—When *Priacma* and *Calpocaccus* were removed from the 18S data sets, *Agulla* + *Corydalus* became sister group to Neuroptera (=Neuropterida) in four analyses (conserved gaps = 2; entire gaps = ?, 1, 2) and was unresolved with respect to Neuroptera in one analysis (conserved gaps = ?), and in one case the relative topology was unaltered (conserved gaps = 1). The removal of these taxa does not change the relationships of other orders, with three exceptions: (1) *Cybister* becomes sister group to Polyphaga (conserved gaps = 2), (2) Neuropterida becomes sister group to (Mecoptera (*Boreus* + Siphonaptera)) (entire gaps = 1), and (3) Coleoptera becomes the most basal taxon, followed by Neuroptera then Hymenoptera (entire gaps = 2). These results suggest that 18S provides some support for neuropterid monophyly when these two beetle taxa are removed, and the other relationships in the tree are only slightly sensitive to the deletion of these taxa.

When the *Agulla* and *Corydalus* sequences are deleted from the 18S analyses, MRPC collapses to *Priacma* + *Colpocaccus,* and this clade remains in the same relative position as MRPC (conserved gaps = ?, 1, 2; entire gaps = 1) or collapses to the base of Holometabola to give a paraphyletic Coleoptera (entire gaps = ?, 2). All other relationships are congruent or unresolved with respect to the all-taxa analyses except for a paraphyletic Hymenoptera (conserved gaps = ?) and Coleoptera becoming the most basal taxon, followed by Neuroptera and then Hymenoptera (entire gaps = 2; same topology as when the beetles were removed). Polyphaga + Neuroptera is present in the conserved analyses, and Polyphaga are placed at the base of Holometabola and just basal to Neuroptera in the entire analyses. These results suggest that the 18S data do not provide much support for a monophyletic Coleoptera, even with the removal of the megalopteran and raphidiopteran taxa.

Removal of all four sequences from the 18S data sets results in more drastic changes in topology. Halteria are placed as sister group to Psocodea (conserved gaps = 2) or at the base of the insects (conserved gaps = ?), Hymenoptera are paraphyletic (conserved gaps = 1) or nested further within Holometabola with Coleoptera at its base (entire gaps = 1, 2), and Polyphaga and Neuroptera are paraphyletic (conserved gaps = ?, 1, 2).

Combined molecular data.—When *Priacma* and *Colpocaccus* were deleted from the molecular spliced analyses, Neuropterida became monophyletic, except for in two analyses when *Agulla* and *Corydalus* form a clade in the same position as MRPC (conserved gaps = 1; entire gaps = ?). Other relationships in these trees are sensitive to the deletion of these beetle taxa: Holometabola are unresolved (conserved gaps = ?) or paraphyletic (conserved gaps = 1), primarily because of the movement of Halteria to the outgroup; Amphiesmenoptera become sister group to Mecoptera + Siphonaptera (conserved gaps = 2), and Hymenoptera + Halteria moves to the base of the tree (entire gaps = 2). The deletion of *Priacma* and *Colpocaccus* from the merged molecular data does not change relative topology; hence Neuropterida remain paraphyletic (conserved gaps = ?, 1, 2; entire gaps = ?), although they are once unresolved (entire gaps = 1) and once monophyletic (entire gaps = 2). These results suggest that the combined molecular data are less supportive of a monophyletic Neuropterida than are the 18S data alone, presumably because the 28S data do not support this grouping.

When *Agulla* and *Corydalus* are deleted from the molecular spliced analyses, Coleoptera are unresolved (conserved gaps = ?), monophyletic (entire gaps = 2), or paraphyletic (conserved gaps = 1, 2; entire gaps = ?, 1). Holometabola collapse in one instance (conserved gaps = ?) or are paraphyletic due to Halteria grouping with Psocodea (conserved gaps = 1). The clade *Priacma* + *Colpocaccus* becomes the most basal clade in two analyses (conserved gaps = 1; entire gaps = 1), and Hymenoptera are unresolved rather than paraphyletic (conserved gaps = ?). For the molecular merged data, removal of these taxa does not change relative topology, except for one case of a monophyletic Neuropterida (entire gaps = 2). These results suggest that there is little evidence from the combined molecular data to support the monophyly of Coleoptera.

When all four taxa are deleted from the combined molecular analyses (whether spliced or merged), most relationships remain the same or are less resolved than in the all-taxa analyses. One exception is the placement of Halteria in the outgroup in three analyses (conserved gaps = ?, 1, 2). The clade Amphiesmenoptera + Mecoptera + *Boreus* + Siphonaptera is present in all analyses, and this result is in agreement with the all-taxa analyses.

Total data.—Removal of *Colpocaccus* and *Priacma, Agulla* and *Corydalus,* and all four taxa from the simultaneous analyses of the total data results in trees largely congruent with the all-taxa analyses. The major exception is that in all partial-taxa analyses, the monophyly of Coleoptera and the monophyly of Neuropterida are supported (in contrast to the all-taxa analyses where there is never support). Relationships among the remaining orders can be described in terms of four fully resolved general topologies (Figs. 15a–d) and three partially resolved general topologies (Figs. 15e–g; Table 4). In most cases (72%), Coleoptera and Neuropterida are sister groups. The placement of Coleoptera as the most basal taxon (topology b) is supported only in the spliced data sets of the entire alignment, most frequently when *Corydalus* and *Agulla* are removed (six times) and less frequently when *Priacma* and *Colpocaccus* are removed (twice) and when all four taxa are removed (three times). In most cases (93%), Hymenoptera are placed as sister group to Mecopterida, in agreement with our morphological analysis and that of Kristensen (1975, 1991, 1995).

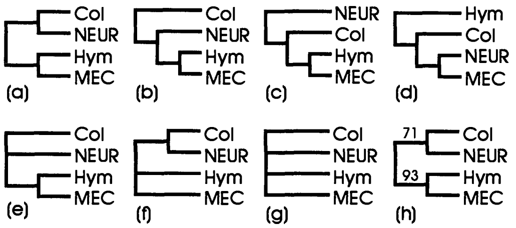


FIGURE 15. Results of removing various insect taxa from the total data sensitivity matrices. Analysis parameters are given in Table 4. The analyses resulted in four general topologies for relationships among major holometabolous groups (a–d) and three less resolved topologies (e–g), with the majority rule consensus given in h. Coleoptera and Neuropterida are always monophyletic. Col = Coleoptera; NEUR = Neuropterida (=Neuroptera + Raphidioptera + Megaloptera); MEC = Mecopterida (=Trichoptera + Lepidoptera + Siphonaptera + Mecoptera + Diptera + Strepsiptera); Hym = Hymenoptera.

Overall, these results suggest (1) the presence of the MRPC clade is masking some molecular evidence for a monophyletic Neuropterida and less evidence for a monophyletic Coleoptera; (2) the total data analysis with the deletion of these taxa most frequently supports ((Coleoptera + Neuropterida) + (Mecopterida + Hyme-

TABLE 4. Results of removing various insect taxa from the total data sensitivity matrices. The analysis resulted in four general topologies (a–d) and three less resolved topologies (e–g) for relationships among major holometabolous groups. Topologies are given in Figure 15.

	Gap weights[a]					
	?		1		2	
Taxa removed from analysis	M = 1	M = 2	M = 1	M = 2	M = 1	M = 2
Agulla and *Corydalus*						
Spliced						
Conserved	a	a	f	a	a	a
Entire	b	b	b	b	b	b
Merged						
Conserved	a	a	a	a	a	a
Entire	e	e	e	a	a	e
Priacma and *Calpocaccus*						
Spliced						
Conserved	g	a	d	a	a	a
Entire	b	b	d	g	g	a
Merged						
Conserved	d	a	g	a	a	a
Entire	d	a	d	a	a	a
Calpocaccus, Agulla, Priacma, and *Corydalus*						
Spliced						
Conserved	e	e	a	a	a	a
Entire	b	b	a	a	b	a
Merged						
Conserved	a	a	a	a	a	a
Entire	c	a	c	a	a	a

[a] Morphological characters (M) were given a weight of 1 or 2.

noptera)); and (3) clades present on the sensitivity consensus trees (Fig. 14) are also present in the analyses with the MRPC taxa removed. The relationships among the other orders are more sensitive to the removal of *Agulla* and *Corydalus* than to the removal of *Priacma* and *Colpocaccus,* presumably because the beetles are well represented by other sequences but Megaloptera and Raphidioptera are not. The spliced analyses are more sensitive to the removal of these taxa than are the merged analyses, which may be the result of an increase in the relative amount of missing data in the spliced analyses.

Discussion

Holometabolous Relationships

Holometabola.—The monophyly of Holometabola was tested with 19 insect sequences and 1 entognath outgroup sequence. Our results provide strong evidence for the monophyly of Holometabola. Although the individual 18S and 28S Bremer support values calculated for Holometabola are rather low (1 and 2, respectively), in the combined molecular analysis and the total data analysis these values are relatively high (12 and 16, respectively). The same trend is seen in branch lengths, with the shortest branch from the 18S analysis (minimum of 6) and the longest from the analysis of all data (maximum of 50). Of the 48 all-taxa sensitivity analyses, Holometabola are paraphyletic in only five instances. In three cases when 18S is included in the analysis, the *Labidura* sequence is placed as sister group to Halteria (Figs. 11a, 11b, 12a); in two cases when 28S is included in the analyses, *Megarcys* + *Cultus* (Plecoptera) is placed as sister group to Halteria (Figs. 11g, 11h). We do not think these few cases argue very strongly against the monophyly of Holometabola because this paraphyly occurs under very specific parameter values that

TABLE 5. Average percentage of extra steps required to enforce group monophyly with each insect data set. The actual number of steps required to force monophyly was calculated in NONA by constraining the monophyly of a group while swapping on all other terminals (force +n; max/) and taking the difference between tree lengths. Exact counts of extra steps are given in Appendix 4.

Forced groupings	No. constraints	18S	28S	Molecular	Total[a] M = 1	Total[a] M = 2	Average % steps
Strepsiptera in Polyphaga							
Conserved	1	0.76	0.44	1.04	0.96	1.22	1.08
Entire	1	0.65	1.31	0.83	0.88	0.94	0.88
Strepsiptera + Coleoptera							
Conserved	3	1.38	0.13	0.86	0.60	0.94	0.88
Entire	3	1.97	1.51	1.55	1.17	0.89	1.26
Monophyletic Coleoptera							
Conserved	1	2.18	0.43	2.21	1.40	0.12	1.27
Entire	1	1.17	0.91	0.80	0.41	0.16	0.53
Monophyletic Neuropterida							
Conserved	1	1.33	0.09	1.09	0.59	0.12	0.63
Entire	1	1.02	0.17	0.74	0.49	0.16	0.48
Coleoptera + Neuropterida							
Conserved	3	1.42	0.16	1.30	0.59	0.12	0.71
Entire	3	1.35	0.97	1.00	0.54	0.16	0.63
Monophyletic Mecoptera							
Conserved	1	0.33	0.07	0.23	0.05	0.00	0.12
Entire	1	0.09	0.68	0.18	0.04	0.00	0.10
Monophyletic Mecopterida							
Conserved	1	0.10	0.16	0.06	0.05	0.00	0.06
Entire	1	0.15	0.26	0.14	0.00	0.00	0.06

[a] Morphological characters (M) were given a weight of 1 or 2.

must include only the conserved portions of the alignment in the analysis. Moreover, the placement of the Plecoptera and *Labidura* sequences relative to the other outgroup taxa is highly sensitive to parameter values of tree reconstruction, hence they are behaving somewhat as "wildcard" taxa on the tree, even when placed outside of Holometabola (Nixon and Wheeler, 1992). Overall, the relationships among the outgroup taxa are mostly congruent with those based on morphology, and the rooting for Holometabola appears appropriate (Kristensen, 1995). Because the sampling of outgroup taxa was not as exhaustive as sampling of the ingroup, we had no expectation of full congruence. A more exhaustive study of nonholometabolous insect relationships is in preparation.

Neuropterida.—The monophyly of Neuropterida is never supported in our all-taxa sensitivity analyses. A higher percentage of steps is required to force monophyly for the 18S data (1.33% [conserved analysis] and 1.02% [entire analysis]; Table 5) than for the 28S data (0.09% [conserved analysis] and 0.17% [entire analysis]; Table 5); most of these additional steps are required to break up MRPC. There is some indication from the partial-taxa analyses that 18S provides evidence for neuropterid monophyly when *Priacma* and *Colpocaccus* are removed. In agreement with Kristensen (1991, 1995) and Achtelig (for summary, see Hennig, 1981), our results appear to strongly support the monophyly of Megaloptera + Raphidioptera; this clade is present in every analysis and is also supported by 28S insert 6. Because our analysis only included a single exemplar from both orders, we are unable to address the question of megalopteran paraphyly (see Kristensen, 1995). Our results support the monophyly of Neuroptera, which were monophyletic in every analysis. In addition, some of the largest inserts for 18S (insert 13) and 28S (inserts 2, 7, 12) occur in this group, and these inserts could be considered further synapomorphies for these groups. In all the analyses, the *Myrmeleon* species cluster together, and the other Neuroptera are generally unresolved with respect to *Myrmeleon*.

Coleoptera.—Our all-taxa analyses never support a monophyletic Coleoptera. In the 28S analysis, coleopteran paraphyly is primarily due to the disassociation of *Colpocaccus* with the other beetles. Polyphaga are either unresolved or paraphyletic in these analyses because of the nesting of *Cybister* within the other beetles (Figs. 11i, 11k, 11l) or the multiple placements of the beetles on the tree (Figs. 11g, 11j). In all the analyses including the 18S data, coleopteran paraphyly is due to MRPC. The average percentages of extra steps required to force a monophyletic Coleoptera (Table 5) for 18S are 1.17 (entire analyses) and 2.18 (conserved analyses) compared with 0.91 (entire) and 0.43 (conserved) for 28S. Even when *Agulla* and *Corydalus* are removed from the analyses, Coleoptera are paraphyletic in the majority of analyses.

Although the molecular data do not support monophyletic Coleoptera, there is strong support for monophyletic Polyphaga. In the 18S analyses, Polyphaga are generally monophyletic and associated with either Neuroptera (Figs. 11a–c) or the adephagan *Cybister* (Figs. 11d, 11e). The molecular analyses and the simultaneous analyses reflect what is seen in the 18S analyses: Polyphaga are monophyletic (except Fig. 12a) and most commonly sister group to *Cybister*. The 18S insert 12 also has synapomorphies for Polyphaga.

Coleoptera + Neuropterida.—This clade was not supported in any of the all-taxa analyses (the percentage of extra steps required to force monophyly ranges from 0.16 to 1.42 [Table 5]) but was occasionally supported when *Colpocaccus*/*Priacma* or *Agulla*/*Corydalus* were removed and was supported 74% of the time when all four taxa were removed from the data set (Fig. 15). It is intriguing that the basal beetles are sister group to Megaloptera + Raphidioptera in all analyses that include the 18S data. These basal taxa, which have retained primitive morphological features (such as vein remnants in the elytra of *Priacma*), may have also retained the primitive Coleoptera–Neuropterida nucleotide states for 18S. Hence, the similarity between these taxa might be attributed to symplesiomorphy rather than synapomorphy. The more derived Coleoptera and Neuroptera are not grouped with their more basal counterparts, but this may be a result of sampling: Coleoptera are an enormously diverse group, and although Neuroptera are less speciose, their 18S sequences are more autapomorphic than those found in most insects.

Hymenoptera.—Hymenoptera were the most well-represented order in terms of the overall number of sequenced exemplars. In nearly all analyses (96%, Fig. 14), Hymenoptera are monophyletic, the branch lengths and Bremer support values are fairly high (Fig. 10), and they share 18S insert 19. Some of the relationships within Hymenoptera are congruent with other phylogenetic hypotheses: ants are always monophyletic, ichneumonid wasps are always monophyletic, tenthredinid sawflies are usually monophyletic, and vespid wasps are usually monophyletic, although the two *Polistes* species are not sister taxa.

Our analyses do not support a definitive placement for Hymenoptera. For 28S, 17 of 24 analyses (including the partial-taxa analyses) place Hymenoptera at the base of Holometabola, but for 18S and the combined molecular data the support is weaker: 4 of 24 and 14 of 48 analyses support this placement. When only the combined molecular data are considered, the placement of Hymenoptera is quite sensitive to the analytical parameters, and this clade is placed in different positions across the combined molecular sensitivity analyses. In the simultaneous analyses of all data, Hymenoptera are sister group to Mecopterida in 82 of 96 analyses, in accord with the morphological tree.

Mecopterida.—The molecular evidence for a monophyletic Mecopterida (Trichoptera + Lepidoptera + Diptera + Siphonaptera + Mecoptera) is sparse, even with the inclusion of Strepsiptera. This group is never present in any of the 28S or combined molecular analyses and is only present in the 18S partial-taxa analyses when gaps = 2 and the entire alignment region is included. This grouping is present in our morphology tree (Fig. 5) and supported in all of the total data analyses with the inclusion of Strepsiptera (Fig. 12).

Amphiesmenoptera.—Under every set of parameters used in the analyses, Trichoptera, Lepidoptera, and Amphiesmenoptera are monophyletic. These groups are supported by long branch lengths and high Bremer support values, with the highest values occurring in Lepidoptera. The 18S insert 16 supports the monophyly of Lepidoptera; 18S insert 17 and 28S insert 13 support the monophyly of Trichoptera. Amphiesmenoptera are considered the best supported sister-group pair among insect orders (Hennig, 1969, 1981; Kristensen, 1995), and both the 18S and 28S data are entirely congruent with this hypothesis.

Antliophora.—The monophyly of Antliophora (Siphonaptera + Mecoptera + Diptera; with the inclusion of Strepsiptera) is not supported by the molecular data but is supported in nearly all simultaneous analyses (Fig. 14). The Mecoptera + Siphonaptera clade is monophyletic in nearly all analyses, and this clade has relatively large branch lengths and Bremer support values. The 18S insert 15 is a striking synapomorphy for this group in that the last 13 bases are identical across these taxa. Overall, our data appear to support strongly the monophyly of Mecoptera + Siphonaptera.

Siphonaptera are monophyletic in every 18S and simultaneous analysis but are paraphyletic in two 28S analyses (Figs. 11g, 11j) because of the grouping of *Boreus* with *Ctenocephalides* and in one combined molecular analysis (Fig. 12a) because of the groupings of *Boreus* + *Ctenocephalides* and *Orchopeas* + other mecopteran taxa. The monophyly of Mecoptera has been disputed, particularly in regard to the placement of Boreidae ("Neomecoptera"; Hinton, 1958) and Nannochoristidae (Wood and Borkent, 1989; Kristensen, 1995). Our analyses present some evidence for the exclusion of boreids from Mecoptera (or the inclusion of Siphonaptera as subordinate within Mecoptera). *Boreus* is never placed within Mecoptera (see Willman, 1987) but is found as sister group to *Ctenocephalides*, sister group to Siphonaptera, or sister group to the remaining Mecoptera (i.e., the most basal member). In two 28S analyses and one combined molecular analysis, *Boreus* is placed as sister group to *Ctenocephalides* and Siphonaptera are paraphyletic. The 18S, 28S, and combined molecular analyses most frequently place *Boreus* as sister group to Siphonaptera (Fig. 14). In the simultaneous analyses, *Boreus* + Siphonaptera occurs 5 times, *Boreus* + remaining Mecoptera occurs 12 times, and *Boreus* is unresolved 7 times. The morphological data include three mecopteran autapomorphies that force *Boreus* as the most basal mecopteran member when morphology is weighted more than 1. The percentage of extra steps required to force a monophyletic Mecoptera is greatest for the 28S entire and 18S conserved analyses (Table 5), but this percentage is relatively small, indicating that a monophyletic Mecoptera is only a few steps away from the shortest tree. The hypothesis that Siphonaptera may be phylogenetically subordinate within Mecoptera is also supported by the recent finding that they share with Boreidae a suite of ovariole characters (Kristensen, 1995). *Boreus* aside, the remaining Mecoptera are monophyletic in every analysis except for the grouping of *Panorpa* with Plecoptera + Halteria (Figs. 11g, 11h) and *Colpocaccus* (Figs. 11j) in three of the six 28S sensitivity analyses. Across the remainder of the analyses, the most basal member of Mecoptera is almost always *Merope*, followed by the *Bittacus* sequences and then *Panorpa*.

Halteria.—The difficulty in placing Strepsiptera among the other insect orders has been discussed. In every sensitivity analysis, Strepsiptera, Diptera, and Strepsiptera + Diptera are monophyletic. The monophyly of these orders is supported by large Bremer support values and long branch lengths, and there can be no doubt that the molecular data support this relationship. Strepsiptera and Diptera have large insertion regions in the same positions for both the 18S (inserts 2 and 3, 20 and 21) and 28S (inserts 4 and 8) alignments. These results agree with those of Chalwatzis et al. (1995), who found *Xenos vesparum* associated with *Drosophila* + *Aedes* in a seven-taxon analysis of 18S rDNA sequences. The average percentage of extra steps required to place Strepsiptera within Polyphaga or as sister group to Coleoptera was calculated; it requires an increase in tree length of approximately 1% to force the monophyly of these assemblages (Table 5). Our analyses do not support a placement of Strepsiptera near Rhipiphoridae as Crowson (1960) suggested, nor do they support a placement as sister group to Coleoptera.

For Diptera, *Tipula* is always the most basal taxon, and the trichotomy of *Laphria–Drosophila–Mythicomyia* is inconsistently resolved across the sensitivity analyses. For Strepsiptera, the stylopid clade (*Crawfordia* (*X. pecki* + *X. vesparum*)) is supported in every analysis, and *Caenocholax* is the most basal strepsipteran taxon. Because a formal phylogenetic analysis of groups within Strepsiptera is still forthcoming, it is not clear whether these relationships are congruent with morphology.

Only one morphological character associates Strepsiptera with Coleoptera: flight motored by the hind wings (posteromotorism). All other characters suggested to support such an association (e.g., insect endoparasitism, planidial larvae, gula, prothoracic notopleural sutures, absence of a telomere, and wing venation; Crowson, 1960; Boudreaux, 1979; Kukalová-Peck and Lawrence, 1993) have been thoroughly examined and rejected (Kathirithamby, 1989; Kinzelbach, 1990; Kristensen, 1991; Whiting and Kathirithamby, 1995). Likewise, Strepsiptera do not possess any of the supraordinal characters of Coleoptera–Neuropterida, as this hypothesis would entail. However, some morphological evidence supports the placement of Strepsiptera within the supraordinal groups to which Diptera belong. The majority of characters supporting a monophyletic Mecopterida (characters 104–106; Appendix 3) are inapplicable to Strepsiptera because the larval mouthparts and associated musculature are too severly reduced to be scored. The lack of an ovipositor (even in the partially free-living Mengenillidae; Kathirithamby, 1989) and the absence of the outer tergal coxal remotor muscle (Kristensen, 1995) are characters that Strepsiptera share with Mecopterida. According to Kristensen (1995), Strepsiptera lack the insertion of the pleural muscle on the first axillary sclerite, the presence of which is considered a mecopterid synapomorphy.

Many of the characters supporting Antliophora (characters 118, 121–124; Appendix 3) are likewise inapplicable to Strepsiptera because of the morphological reduction of the larvae and adults. Strepsiptera do share with Antliophora the slender mandibles with weak anterior articulations (Kristensen, 1995) and prelabium (prementum) without endite lobes and associated muscles (Kristensen, 1991) but do not have a pleural ridge/scutum muscle insertion on the posterior notal wing process (Kristensen, 1995). In addition, in male Antliophora, abdominal segment IX is ringlike, enlarged, and fused along the pleuron. Kristensen (1991) treated the fusion of the gonopod bases above and below the phallic apparatus as an autapomorphy for the order Mecoptera, but this fusion clearly is also present in Strepsiptera (Kinzelbach, 1971). All nematocerous Diptera have this character, which may be the basal condition in Diptera (Wood and Borkent, 1989), although Kristensen (1995: 104) contended that "it remains uncertain whether the male segment IX was 'ringlike' in the dipteran groundplan." In Siphonaptera, sternum IX is modified to form an L-shaped clasping organ, and tergum IX is modified into a complex clasping organ consisting of a pair of manubria and articulating claspers that occupies the posterior tip of the abdomen and encloses the genitalia (Dunney and Mardon, 1991).

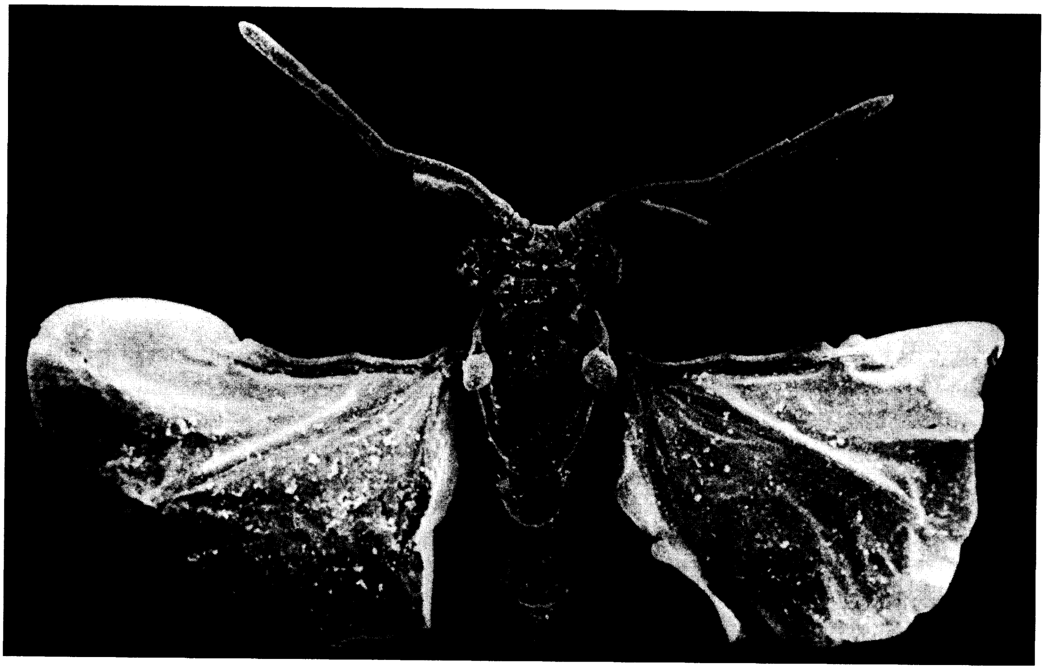


FIGURE 16. Scanning electron mircorgraph, dorsal view, *Caenocholax fenyesi* Pierce (40×). The forewings of male Strepsiptera are modified into structures that morphologically and functionally resemble the halteres of Diptera.

This character may be an autapomorphic modification of the enlargement of abdominal segment IX, which is seen in the other antliophoran orders. If so, this character supports the monophyly of Antliophora inclusive of Strepsiptera. Currently, there is more morphological evidence for the placement of Strepsiptera with the antliophoran orders than for an association with Coleoptera.

The most striking similarity between Diptera and Strepsiptera involves the microstructure and function of the dipteran halteres (reduced metathoracic wings) and strepsipteran pseudohalteres (Fig. 16; reduced mesothoracic wings). Kathirithamby (1989) challenged the long-held notion that pseudohalteres are modified elytra and listed a number of similarities between halteres and pseudohalteres. Pix et al. (1993) concluded that Strepsiptera use their pseudohalteres as gyroscopic balancing organs during flight in the same manner as Diptera, and our observations of Strepsiptera in flight agree with this conclusion. Whiting and Wheeler (1994) hypothesized that a homeotic mutation could be responsible for the apparent shift of the halteres from the metathorax in Diptera to the mesothorax in Strepsiptera. Research into the development of the strepsipteran thoraces is currently underway to test for this suggested homeotic shift.

Long-Branch Attraction

Whiting and Wheeler (1994) concluded that 18S rDNA data support the monophyly of Strepsiptera and Diptera and suggested implications of this phylogenetic conclusion for the role of homeosis in the evolution of Strepsiptera. Carmean and Crespi (1995) argued that halterian monophyly is an artifact of long-branch attraction (Felsenstein, 1978); they demonstrated that Strepsiptera and Diptera have a higher substitution rate than any other taxa included in their phylogenetic analysis and that these two taxa are well supported as sister groups in that analysis. There are four reasons why we believe that long-branch attraction is not a plausible explanation for the grouping of Strepsiptera and Diptera in our phylogeny.

First, 28S and 18S are congruent in strongly supporting the monophyly of Halteria; thus the occurrence of long-branch attraction would need to be postulated for both molecules. The majority of ordinal relationships on the molecular trees are congruent with other hypotheses of insect phylogeny, particularly in the mecopterid portion of the tree. Strepsiptera and Diptera are always monophyletic, and if long-branch attraction were a problem these orders occasionally would be paraphyletic because of the random grouping of an individual strepsipteran sequence with an individual dipteran sequence. Halteria are often positioned within Mecopterida (even in the Carmean and Crespi [1985] tree), and this grouping is also congruent with the morphological data. Hence there appears to be some signal in these data that is not masked by long-branch attraction and that allows ordinal monophyly (Strepsiptera and Diptera) and supraordinal placement (Mecopterida) congruent with that indicated by morphology.

Second, the branch lengths for Diptera, Strepsiptera, and Halteria are comparable to those of other insects groups in this analysis. For instance, the 18S branch lengths for Diptera (52–82) and Strepsiptera (33–63) are not far out of range of those for Lepidoptera (28–45) and Trichoptera (19–35); the branch lengths for Halteria (11–48) and Amphiesmenoptera (10–32) are even more comparable (Fig. 7). For 28S, the situation is reversed: in Lepidoptera the branch length (23–48) is greater—and with higher Bremer support—than that in Diptera (14–27) and Strepsiptera (20–24); likewise the branch length for Amphiesmenoptera (10–37) is greater than that for Halteria (9–21). This trend occurs throughout the sensitivity analyses regardless of whether the entire or only the conserved portions of the alignment are used for tree reconstruction. The mapping of characters on a tree generated from the analysis of 18S + 28S (conserved alignment, gaps = ?, merged data sets) and on a total evidence analysis tree (conserved alignment, gaps = ?, morphology = 1; Fig. 17) demonstrates that a portion of these branch lengths consists of nonhomoplastic characters. The molecular data for these trees are taken only from the unambiguous regions of the sequence alignment and are thus conservative estimates of relationships. The two orders comprising Amphiesmenoptera are considered to have the most firmly established sister-group relationship among all insect orders (Kristensen, 1995). Thus, if the association of the amphiesmenopteran sequences is also due to long-branch attraction, it is fortuitous that it is congruent with morphology.

Third, the greatest sequence diversity between any two taxa is not between Strepsiptera and Diptera. A pairwise percent difference for 18S and 28S was computed by considering only those alignment positions with any nucleotide variation to determine whether any two sequences appeared saturated relative to each other (data not shown). The result indicates that the greatest distance between any two taxa for 18S is between *Tipula* and *Lygus* (0.287) and for 28S is between *Lygus* and *Galleria* (0.300). Because the suspected long-branch attraction is between two orders, the average distance between a single order and all other orders was calculated for the 18S data. Diptera have the greatest average distance relative to all other orders (133.81/530 base changes), but the average number of base changes for Strepsiptera (96.26) is within three base changes of the values for Phthiraptera (99.11), Thysanoptera (96.51), Lepidoptera (96.13), Siphonaptera (95.38), Collembola (95.33), and Epheremoptera (95.27). Thus, in terms of simple average distance calculations, the substitution rate for Strepsiptera is not uniquely high relative to that for other taxa. This point is further confirmed by computing the average number of base changes for 18S between Diptera and all other orders. Strepsiptera rank somewhere in the middle, with 13 orders having higher distance values and 8 orders having lower distance values. Hence relative to Diptera, there are 13 other or-

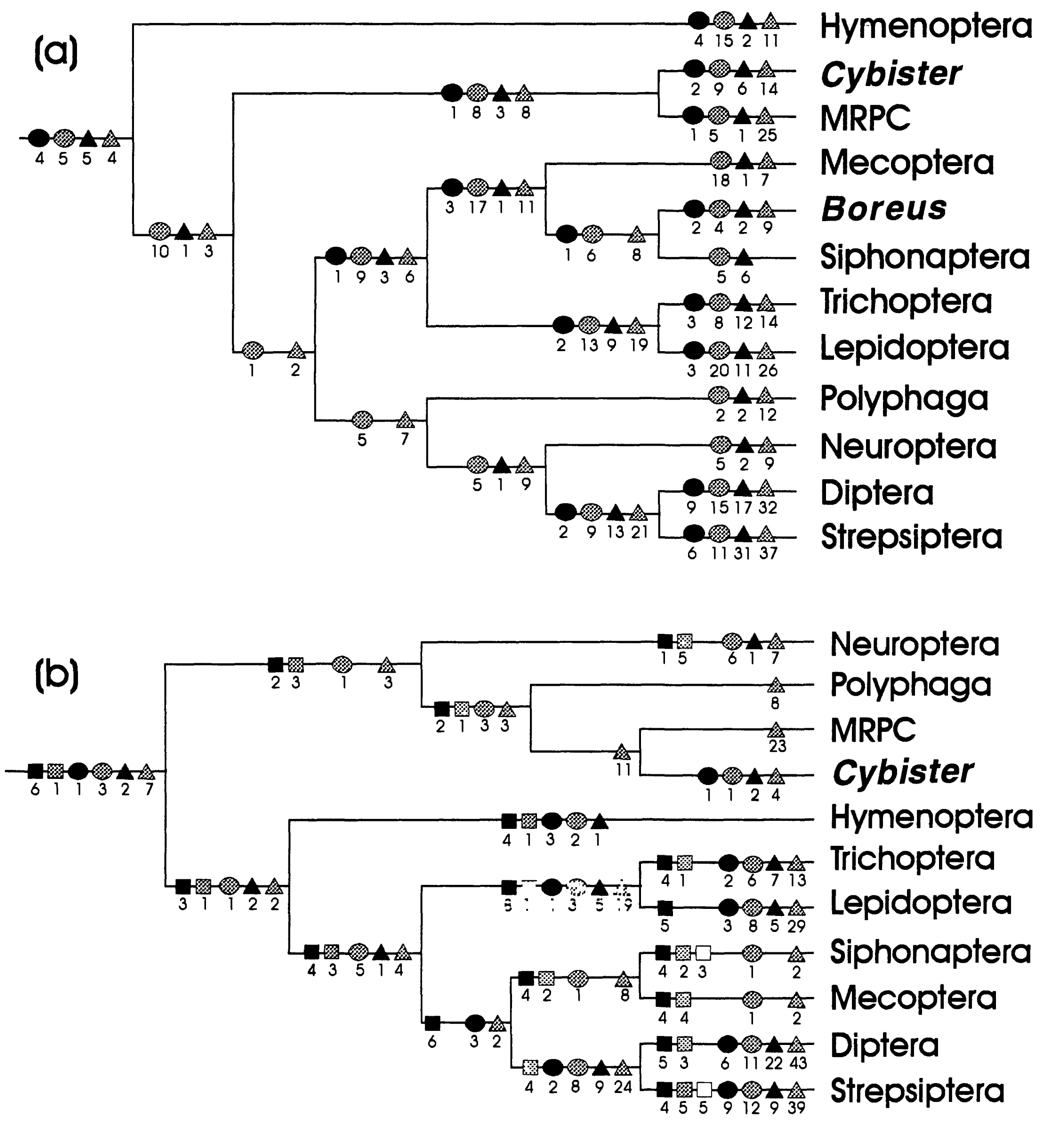


FIGURE 17. Summary character mapping of molecular (a) and total evidence (b) trees for Holometabola. The molecular tree is the holometabolous portion of the strict consensus (conserved alignment, 18S + 28S, merged, gaps = ?). The total evidence tree is the holometabolous portion of the strict consensus (conserved alignment, 28S + 18S + morphology, merged, gaps = ?, morphological characters = 1). Symbol shapes on the nodes refer to the data set from which a character originated: □ = morphology; ○ = 28S; △ = 18S. Coloring represents homoplastic changes (shaded), reversals (open), and nonhomoplastic changes (solid). Numbers beneath symbols represent the number of times that class of characters was present on a node. Characters were mapped using a modified DELTRAN optimization (Nixon, 1995).

ders with higher substitution rates than Strepsiptera.

Fourth, Carmean and Crespi (1995) argued that Strepsiptera and Diptera have uniquely high substitution rates relative to the other sequences, but the number of taxa sampled in their analysis was small: 10 ingroup taxa and 2 outgroup taxa. Representatives of Lepidoptera, Trichoptera, Megaloptera, and Raphidioptera were not included. Strepsiptera were represented by a single species, Diptera were represented by *Drosophila* and the apparently flawed *Aedes* sequence, and sampling for the rest of Mecopterida consisted of a single scorpionfly sequence and a flea sequence. Other holometabolous 18S sequences available at the time of their analysis, including ones generated by Carmean et al. (1992), were inexplicably excluded from their analysis. Thorough taxon sampling is important in this context because it reduces branch lengths (Swofford and Olsen, 1990), whereas the undersampling of taxa artificially inflates branch lengths. By including multiple representatives of each order and by sampling the basal members of Strepsiptera and Diptera, we have reduced the relative distance between the terminals in our phylogeny and have found other instances of insects with high substitution rates.

A point that is often missed in long-branch attraction discussions is that relative rates of substitution are influenced by phylogeny, and thus we should not be surprised to find cases of sister groups that have high rates of nucleotide substitution; shared elevated rates could indeed be evidence of shared history. The supposition that the clades best supported by character data are the ones we should be most suspicious of has the strange result of entailing an inverse relationship between phylogenetic evidence and phylogenetic conclusions. The large amount of molecular evidence supporting the monophyly of Halteria and Amphiesmenoptera can be taken at face value as indicative of well-supported sister-group relationships and not as foibles of the data or analytical method.

Conclusions

There are three things unique to this study. The first is the reliance on multiple independent data sources for phylogenetic inference of holometabolous relationships. By generating two molecular data sets and producing the first morphological matrix for these orders, we have compiled the largest and most comprehensive body of evidence on holometabolan interordinal relationships. The second unique aspect is the broad and thorough selection of exemplars for sequencing. Our study is the first to include exemplars from every holometabolan order, with multiple representatives from most of the major subclades and a very broad range of outgroup taxa. Other critical taxa need to be added to this study, i.e., exemplars of Nannochoristidae (Mecoptera) and Mengenillidae (Strepsiptera) and perhaps a more thorough survey of Nematocera.

Third, we tested the robustness of the phylogenetic conclusions to the assumptions used in the data analysis by performing sensitivity analyses on multiple parameters: the influence of gap costs, methods of data set combination, partitioned versus combined data sets, and the relative weights of morphological and molecular characters. Other parameters may also prove influential in interpreting these data. For instance, ranges of gap/nucleotide cost ratios, transition/transversion biases, and alignment by presumed secondary structure may result in different statements of putative homology during alignment. We anticipate, however, that variation in these other parameters would only alter the more variable regions of the alignment and that the phylogenetic results primarily from the conserved regions are not sensitive to the alignment parameters.

The summary of our best estimate of holometabolan relationships is given in Figure 18. Halteria (Diptera + Strepsiptera), Amphiesmenoptera (Trichoptera + Lepidoptera), Megaloptera + Raphidioptera, and Holometabola are strongly supported monophyletic assemblages. Further, Mecopterida, Antliophora, and Neuropterida probably are monophyletic, although the character support is not as strong as in the previous groupings. All holometabolan orders appear monophyletic, with the possible exception of Mecoptera with regards to *Boreus*, which may actually be the sister group to Siphonaptera (i.e., Siphonaptera are subordinate within Mecoptera). The groups that are rather am-

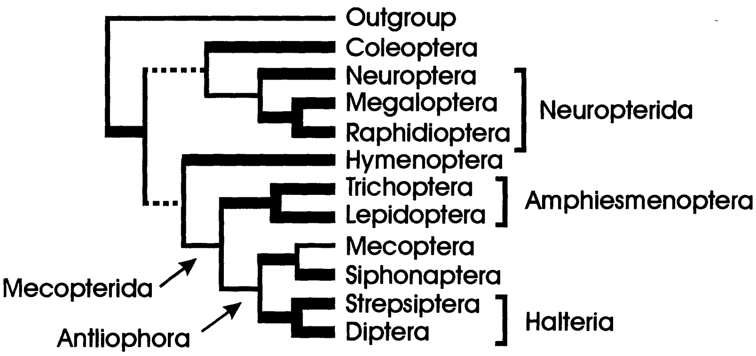


FIGURE 18. Overall conclusions regarding holometabolous insect phylogenetic relationships. Thick lines subtend nodes that strongly support monophyletic groups, thin lines subtend nodes for relatively well-supported monophyletic groups, and dashed lines subtend nodes that are still questionable.

biguously placed in our analyses are Hymenoptera, Coleoptera, and Neuropterida. Hymenoptera is probably the sister group to Mecopterida, although placement at the base of Holometabola is still a possibility. Neuropterida and Coleoptera certainly sit outside of Mecopterida, and there is some morphological and some molecular evidence that these two are sister groups, but they also could be placed as pectinate on the tree, with Coleoptera as (probably) the more basal order. Sequencing more genes from a wider selection of taxa and a reevaluation of the morphological characters promises to provide a more thorough understanding of insect ordinal relationships. It is somewhat ironic that our data support a phylogenetic placement for Strepsiptera that was first suggested in the early 1800s but has long since been abandoned by entomologists.

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REFERENCES

ACHTELIG, M. 1975. Die Abdomenbasis der Neuropteroidea (Insecta, Holometabola). Zoomorphologie 82:201–242.

ACHTELIG, M. 1978. Entwicklung und Morphologie der inneren und äusseren weiblichen Genitalorgane der Kamelhalsfliegen (Neuropteroidea: Raphidioptera). Entomol. Ger. 4:140–163.

ADAMS, P. A. 1958. The relationship of the Protoperlaria and the Endopterygota. Psyche 65:115–127.

ARNETT, R. H. 1963. The beetles of the United States. Catholic Univ. American Press, Washington, D.C.

BACCETTI, B. 1989. The spermatozoan of Strepsiptera (Insecta) and its value for the systematic position of the group. J. Submicrosc. Cytol. Pathol. 21:397–398.

BIRKET-SMITH, J. 1971. The abdominal morphology of *Povilla adusta* Navas (Polymitarcidae) and of Ephemeroptera in general. Entomol. Scand. 2:139–160.

BOERNER, C. 1904. Zur Systematik der Hexapoden (Strepsiptera). Zool. Anz. 27:511–533.

BOUDREAUX, H. B. 1979. Arthropod phylogeny with special reference to insects. John Wiley & Sons, New York.

BREMER, K. 1994. Branch support and tree stability. Cladistics 10:295–304.

CARMEAN, D., AND B. J. CRESPI. 1995. Do long branches attract flies? Nature 373:666.

CARMEAN, D., L. S. KIMSEY, AND M. L. BERBEE. 1992. 18S rDNA sequences and holometabolous insects. Mol. Phylogenet. Evol. 1:270–278.

CHALWATZIS, N., A. BAUR, E. STETZER, R. KINZELBACH, AND F. K. ZIMMERMANN. 1995. Strongly expanded 18S rRNA genes correlated with a peculiar morphology in the insect order of Strepsiptera. Zoology 98:115–126.

CHAPMAN, R. N. 1918. The basal connections of the tracheae of the wings of insects. Pages 27–51 *in* The wings of insects (J. H. Comstock, ed.). Cornell Univ. Press, Ithaca, New York.

CHAUDONNERET, J. 1950. La morphologie céphalique de *Thermobia domestica* (Packard). Ann. Sci. Nat. (Zool.) 12:145–302.

CROWSON, R. A. 1954. The classification of families of British Coleoptera. Superfamily 19: Stylopidae (order Strepsiptera). Entomol. Mon. Mag. 90:57–63.

CROWSON, R. A. 1960. The phylogeny of Coleoptera. Annu. Rev. Entomol. 5:111–134.

CROWSON, R. A. 1981. The biology of Coleoptera. Academic Press, London.

DENIS, J. R., AND J. BITSCH. 1973. Morphologie de la tête des insectes. Traité Zool. 8:1–593.

DIXON, M. T., AND D. M. HILLIS. 1993. Ribosomal RNA secondary structure: Compensatory mutations and implications for phylogenetic analysis. Mol. Biol. Evol. 10:256–267.

DUNNEY, G. M., AND D. K. MARDON. 1991. Siphonaptera. Pages 125–140 *in* The insects of Australia: A textbook for students and research workers, 2nd edition (I. D. Naumann, P. B. Carne, J. F. Lawrence, E. S. Nielsen, J. P. Spradberry, R. W. Taylor, M. J. Whitten, and M. J. Littlejohn, eds.). CSIRO and Melbourne Univ. Press, Melbourne.

FARRIS, J. S., M. KÄLLERSJÖ, A. G. KLUGE, AND C. BULT. 1994. Testing significance of incongruence. Cladistics 10:315–320.

FELSENSTEIN, J. 1978. Cases in which parsimony or compatibility methods will be positively misleading. Syst. Zool. 27:401–410.

FORBES, W. T. M. 1943. The origin of wings and venational types in insects. Am. Midl. Nat. 29:381–405.

FORD, N. 1923. A comparative study of the abdominal musculature of orthopteroid insects. Trans. R. Can. Inst. 14:207–319.

FRANCOIS, J. 1969. Anatomie et morphologie céphalique des protoures. Mem. Mus. Natl. Hist. Nat. Paris Ser. A (Zool.) 49:1–444.

FRANCOIS, J. 1970. Squelette et musculature céphalique de *Campodea chardardi* Condé (Diplura: Campodeidae). Zool. Jahrb. Anat. 87:331–376.

GANGLBAUER, L. 1903. Die neueren Classification der Koleopteren nach Sharp, Lameere, und Kolbe. Münch. Koleopterol. Z. 1:272–306.

GILES, E. T. 1963. The comparative external morphology and affinities of the Dermaptera. Trans. R. Entomol. Soc. Lond. 115:95–164.

GOLOBOFF, P. A. 1994. NONA program and documentation. Fundación e Instituto Miguel Lillo, Tucumán, Argentina.

GÜNTHER, K., AND K. HERTER. 1974. Dermaptera (Ohrwürmer). Handb. Zool. 4:1–158.

HAMILTON, K. G. A. 1971. The insect wing, part I. Origin and development of wings from notal lobes. J. Kans. Entomol. Soc. 44:421–433.

HANDLIRSCH, A. 1903. Zur Phylogenie der Hexapoden (Strepsiptera). Sitzungsber Akad. Wiss. Wien. 112:717–738.

HENNIG, W. 1969. Die Stammesgeschichte der Insekten. Krammer, Frankfurt am Main, Germany.

HENNIG, W. 1981. Insect phylogeny. Academic Press, New York.

HILLIS, D. M., A. LARSON, S. K. DAVIS, AND E. A. ZIMMER. 1990. Nucleic acids III: Sequencing. Pages 318–372 *in* Molecular systematics, 1st edition (D. M. Hillis and C. Mortiz, eds.). Sinauer, Sunderland, Massachusetts.

HINTON, H. E. 1958. The phylogeny of the panorpoid orders. Annu. Rev. Entomol. 3:181–206.

HOLM, S. 1979. A simple sequentially rejective multiple test procedure. Scand. J. Stat. 6:65–70.

ILLIES, J. 1968. Ephemeroptera (Eintagsfliegen). Handb. Zool. 4(2)2/5:1–63.

JAMIESON, B. G. M. 1987. The ultrastructure and phylogeny of insect spermatozoa. Cambridge Univ. Press, Cambridge, England.

KATHIRITHAMBY, J. 1989. Review of the order Strepsiptera. Syst. Entomol. 14:41–92.

KATHIRITHAMBY, J., M. CARCUPINO, AND M. MAZZINI. 1993. Comparative spermatology of four species of Strepsiptera and comparison with a species of primitive Coleoptera (Rhipiphoridae). Int. J. Insect Morphol. Embryol. 22:459–470.

KINZELBACH, R. K. 1971. Morphologische Befunde an Fächerflüglern und ihre phylogenetische bedeutung (Insecta: Strepsiptera). Zoologica 119(1/2):1–256.

KINZELBACH, R. K. 1990. The systematic position of Strepsiptera (Insecta). Am. Entomol. 36:292–303.

KIRBY, W. 1802. *Stylops*. Monogr. Apum Angliæ 2: 112–113.

KIRBY, W. 1815. Review. Bull. Soc. Philomanth. 62–64.

KLUGE, A. J. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). Syst. Zool. 38:7–25.

KOLBE, H. J. 1901. Vergleichend-morphologische Untersuchungen an Koleopteren nebst Grundlagen zu einem System und zur Systematik derselben. Arch. Naturgesch. 67:89–150.

KRISTENSEN, N. P. 1975. The phylogeny of hexapod "orders." A critical review of recent accounts. Z. Zool. Syst. Evolutionsforsch. 13:1–44.

KRISTENSEN, N. P. 1981. Phylogeny of insect orders. Annu. Rev. Entomol. 26:135–157.

KRISTENSEN, N. P. 1991. Phylogeny of extant hexapods. Pages 125–140 *in* The insects of Australia: A textbook for students and research workers, 2nd edition (I. D. Naumann, P. B. Carne, J. F. Lawrence, E. S. Nielsen, J. P. Spradberry, R. W. Taylor, M. J. Whitten, and M. J. Littlejohn, eds.). CSIRO, Melbourne Univ. Press, Melbourne.

KRISTENSEN, N. P. 1995. Fourty [sic] years' insect phylogenetic systematics. Zool. Beitr. N. F. 36:83–124.

KUKALOVÁ-PECK, J. 1978. Origin and evolution of insect wings and their relation to metamorphosis, as documented by the fossil record. J. Morphol. 156: 53–126.

KUKALOVÁ-PECK, J. 1985. Ephemeroid wing venation based upon new gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects. Can. J. Zool. 63:933–955.

KUKALOVÁ-PECK, J. 1991. Fossil history and the evolution of hexapod structures. Pages 141–179 *in* The insects of Australia: A textbook for students and research workers, 2nd edition (I. D. Naumann, P. B. Carne, J. F. Lawrence, E. S. Nielsen, J. P. Spradberry, R. W. Taylor, M. J. Whitten, and M. J. Littlejohn, eds.). CSIRO, Melbourne Univ. Press, Melbourne.

KUKALOVÁ-PECK, J., AND J. F. LAWRENCE. 1993. Evolution of the hind wing in Coleoptera. Can. Entomol. 125:181–258.

LAMARCK, J. B. 1816. Les Rhipidoptères, Histoire naturelle des animaux sans Vertébres 3:348–352.

LAMEERE, A. 1900. Note pour la classification des Coléoptères. Annu. Soc. Entomol. Belg. 44:370–377.

LATREILLE, P. A. 1809. (Placed *Stylops* in Diptera, Tribe III, Phthiromyae). Genera Crust. Insect. 4:388.

LATREILLE, P. A. 1817. Rhipiptera, Cuvier's Règne Animal. Insectes. Rev. Ger. Mag. Entomol. 3:356–359.

LAUTERBACH, K. E. 1972. Die morphologischen Grundlagen für die Entstehung der Entognathie bei den apterygoten Insekten in phylogenetischer Sicht. Zool. Beitr. 18:25–69.

LIU, H., AND A. T. BECKENBACH. 1992. Evolution of the mitochondrial oxidase II gene among 10 orders of insects. Mol. Phylogenet. Evol. 1:41–52.

LOMBARDO, C. A. 1973. On the presence of two coxal organs in Pterygota insects. Monit. Zool. Ital. N.S. 7:243–246.

MAKI, T. 1938. Studies of the thoracic musculature of insects. Mem. Fac. Sci. Agric. Taihoku Imp. Univ. 24: 1–344.

MATSUDA, R. 1965. Morphology and evolution of the insect head. Mem. Am. Entomol. Inst. 4:1–334.

MATSUDA, R. 1970. Morphology and evolution of the insect thorax. Mem. Entomol. Soc. Can. 76:1–431.

MATZURA, O. 1995. RNAdraw, version 1.0. Department of Medical Biophysics, Karolinska Institute, Solna, Sweden.

MICHOT, B., AND J. P. BACHELLERIE. 1987. Comparisons of large sub-unit rRNAs reveal some eukaryotic specific elements of secondary structure. Biochimie 69:11-23.

MICHOT, B., L. H. QU, AND J. P. BACHELLERIE. 1990. Evolution of large sub-unit rRNA structure: The diversification of divergent D3 domains among major phylogenetic groups. Eur. J. Biochem. 188:219-229.

MICKEVICH, M. F., AND J. S. FARRIS. 1981. The implications of congruence in *Menidia.* Syst. Zool. 30:351–370.

MICKOLEIT, G. 1973. Über den ovipositor der Neuropteroidea und Coleoptera und seine phylogenetische Bedeutung (Insecta, Holometabola). Z. Morphol. Tiere 74:37-64.

MILLER, P. L. 1962. Spiracle control in adult dragonflies (Odonata). J. Exp. Biol. 39:513–535.

MINET, J., AND T. BOURGOIN. 1986. Phylogenie et classification de Hexapodes (Arthropoda). Cah. Liason 63:23–28.

MOULINS, M. 1969. Etude anatomique de l'hypopharynx de *Forficula auricularia* L. (Insecte, Dermaptère): Téguments, musculature, organes sensoriels et innervations. Interpretation morphologique. Zool. Jahrb. Anat. 86:1–27.

NIXON, K. C. 1995. Clados, version 1.49.5. Cornell Univ., Ithaca, New York.

NIXON, K. C., AND J. M. CARPENTER. 1996. On simultaneous analysis. Cladistics (in press).

NIXON, K. C., AND Q. D. WHEELER. 1992. Extinction and the origin of species Pages 119–143 *in* Extinction and phylogeny (M. J. Novacek and Q. D. Wheeler, eds.). Columbia Univ. Press, New York.

PASHLEY, D. P., B. A. MCPHERON, AND E. A. ZIMMER. 1993. Systematics of holometabolous insect orders based on 18S ribosomal RNA. Mol. Phylogenet. Evol. 2:132–142.

PAULUS, H. F. 1986. Comparative morphology of the larval eyes of Neuropteroidea. Proc. Int. Symp. Neuropterol. 2:157-164.

PIERCE, W. D. 1909. A monographic revision of the twisted winged insects comprising the order Strepsiptera (Kirby). Bull. U.S. Natl. Mus. 66:1–217.

PIX, W., G. NALBACH, AND J. ZEIL. 1993. Strepsipteran forewings are haltere-like organs of equilibrium. Naturwissenschaften 80:371–374.

POONAWALLA, Z. T. 1966. The respiratory system of adult Odonata. Part 1. The spiracles. Ann. Entomol. Soc. Am. 59:807–809.

RÄHLE, W. 1970. Untersuchungen an Kopf und Prothorax von *Embia ramburi* Rimsky-Korsakow 1906 (Embioptera, Embiidae). Zool. Jahrb. Anat. 87:248–330.

RICE, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

ROSS, H. H. 1965. A textbook of entomology, 3rd edition. John Wiley & Sons, New York.

ROSS, H. H., A. C. ROSS, AND J. R. P. ROSS. 1984. A textbook of entomology, 4th edition, John Wiley & Sons, New York.

ROSSI, P. 1793. Observations sur un nouveau genre d'insecte voisin des Ichneumons. Bull. Soc. Philomanth. 1:49.

SCUDDER, G. G. E. 1961. The comparative morphology of the insect ovipositor. Trans. R. Entomol. Soc. Lond. 113:25–40.

SHAROV, A. G. 1957. Types of insect metamorphosis and their relationship. Entomol. Obozr. 36:569–576.

SHAROV, A. G. 1966. Basic arthropodan stock with special reference to insects. Pergamon Press, Oxford, England.

SHIPLEY, A. E. 1904. The orders of insects (Strepsiptera). Zool. Anz. 27:259–262.

SMOTHERS, J. F., C. D. VON DOHLEN, L. H. SMITH, AND R. D. SPALL. 1994. Molecular evidence that the myxozoan protists are metazoans. Science 265: 1719–1721.

SNODGRASS, R. E. 1933. Morphology of the insect abdomen. Part II. The genital ducts and the ovipositor. Smithson. Misc. Coll. 89:1–148.

STEHR, F. W. 1987. The immature insects. Kendall/ Hunt, Dubuque, Iowa.

STOBBART, R. H. 1956. A note on the tracheal system of Machilidae. Proc. R. Entomol. Soc. Lond. A 31: 34–36.

SWOFFORD, D. L. 1991. PAUP: Phylogenetic analysis using parsimony, version 3.3.1. Illinois Natural History Survey, Champaign.

SWOFFORD, D. L., AND G. J. OLSEN. 1990. Phylogeny reconstruction. Pages 411–501 *in* Molecular systematics, 1st edition (D. M. Hillis and C. Mortiz, eds.). Sinauer, Sunderland, Massachusetts.

TAUTZ, D., J. M. HANCOCK, D. A. WEBB, C. TAUTZ, AND G. A. DOVER. 1988. Complete sequences of the rRNA genes of *Drosophila melanogaster*. Mol. Biol. Evol. 5:366–376.

THORNE, B. L., AND J. M. CARPENTER. 1992. Phylogeny of the Dictyoptera. Syst. Entomol. 17:253–268.

TILLYARD, R. J. 1928. The larva of *Hemiphlebia mirabilis* Selys (Odonata). Proc. Linn. Soc. N.S.W. 53:193–206.

VAN DE PEER, Y., J. M. NEEFS, P. DE RIJK, AND R. DE

WACHTER. 1993. Reconstructing evolution from eukaryotic small-ribosomal-subunit sequences: Calibration of the molecular clock. J. Mol. Evol. 37:221–232.

WHEELER. W. C. 1989. The systematics of insect ribosomal DNA. Pages 307–321 *in* The hierarchy of life. Molecules and morphology in phylogenetic analysis (B. Fernholm, K. Bremer, and H. Jörnvall, eds.). Elsevier, Amsterdam.

WHEELER, W. C. 1995. Sequence alignment, parameter sensitivity, and the phylogenetic analysis of molecular data. Syst. Biol. 44:321–331.

WHEELER, W. C., AND D. L. GLADSTEIN. 1994. MALIGN, version 1.93. American Museum of Natural History, New York.

WHITING, M. F., AND J. KATHIRITHAMBY. 1995. Strepsiptera do not share hind-wing venational synapomorphies with the Coleoptera. J. N.Y. Entomol. Soc. 103:1–14.

WHITING, M. F., AND W. C. WHEELER. 1994. Insect homeotic transformation. Nature 368:696.

WILLMAN, R. 1987. The phylogenetic system of the Mecoptera. Syst. Entomol. 12:519–524.

WILLMAN, R. 1989. Evolution und phylogenetisches system der Mecoptera (Insecta: Holometabola). Abh. Senckenberg. Naturforsch. Ges. 544:1–153.

WILSON, E. O. 1988. The current state of biological diversity. Pages 3–18 *in* Biodiversity (E. O. Wilson, ed.). National Academy Press, Washington, D.C.

WOOD, D. M., AND A. BORKENT. 1989. Phylogeny and classification of the Nematocera. Pages 1333–1370 *in* Manual of Nearctic Diptera, Volume 3 (J. F. McAlpine and D. M. Wood, eds.). Agriculture Canada, Ottawa.

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APPENDIX 1

18S ALIGNMENT WITH APPENDED INSERTS

The 85 taxa were aligned using MALIGN (parallel version 1.93; Wheeler and Gladstein, 1994). The heuristic algorithm "Build" with SBR branch swapping on multiple alignments was performed (change cost = 3, gap cost = 5, leading and trailing gap cost = 8). Primer regions were included in the alignment but were subsequently excluded in phylogenetic analyses. Variable alignment regions (positions 281–361) were excluded from phylogenetic analyses in the conserved tree reconstructions. When the initial alignment presented evidence of a large insertion in a single taxon or subset of taxa, the region was removed to facilitate alignment of positions flanking the insert. Symbols in the alignment (other than standard nucleotide codes) refer to insertions appended after the alignment.

	18S ai 100▼
Hypogastrura	CCTGAGAAACGACTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGG-AGGTAGTGACGAAAAATAACGATACGGAACTCA
Trigoniopthalmus	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCACGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACAATACGGGACTCA
Ephemerella	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Agrion	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCCCAAATTACCCACTCCCGGAACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Libellula	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Megarcys	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Cultus	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Blaberus	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Mantis	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Labidura	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCAGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Melanoplus	CCTGAGAAACGGCTACCACATCCTAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Anisomorpha	CCTGAGAAACGGCTACCACATCCTAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Oligotoma	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Cerastipsocus	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCAGATCGGGGAGGTAGTGACGAAAAATAACGATGCAGAACTCA
Dennyus	CCTGAGAANCGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATGCAGAACTCT
Acyrthosiphon	CCTGAGAAACGGCTACCACATCCAAGGCCGGCAGCAGGCGCGCAAATTACCCACTCC-GGAACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Buenoa	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCACGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACAAAAAATAACGATACGGGACTCA
Saldula	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCACGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACAAAAAATAACGATACGGGACTCA
Lygus	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCACGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACAAAAAATAACGATACGGGACTCT
Taeniothrips	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAGATAACGATGCAGGACTCT
Priacma	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCCCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Colpocaccus	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Cybister	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Xyloryctes	CTTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Octinodes	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Photuris	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Meloe	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Rhipiphorus	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Tenebrio	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Tetraopes	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Corydalus	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Agulla	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Lolomyia	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Mantispa	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Hemerobius	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Chrysoperla	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
M.immaculatus	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Myrmeleon	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Galleria	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCT
Papilio	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Ascalapha	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCT
Hydropsyche	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Pycnopsyche	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCG
Oecetis	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCG
B.strigosus	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCTCGCAAATTACCCACTCCCAGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
B.chlorostigmus	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Boreus	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Merope	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Panorpa	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCTCGGCACGAGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Ctenocephalides	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Hystrichopsylla	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Orchopeas	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Hartigia	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Orussus	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Hemitaxonus	CCTGAGAAACGGCTACCACATCTAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCAGCGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Peridista	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Bareogonalos	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Evania	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Ichneumon	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Ophion	CCTGAGAAACGGCTACCACATCTAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Mesopolobus	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Caenochrysis	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Epyris	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Priocnemus	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Dasymutilla	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGTCGAAAAATAACGATACGGGACTCA
Apoica	CCTGAGAAACGGCTACCACATCTAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
Monobia	CCTGAGAAACGGCTACCACATCTAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
P.fuscatus	CCTGAGAAACGGCTACCACATCTAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAAAAATAACGATACGGGACTCA
P.dominulus	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Camponotus	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Chalepoxenus	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Doronomyrmex	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Harpagoxenus	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Leptothorax	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Temnothorax	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Tipula	CCTGAGAAACGGCTACCACATCTAAGGAAGGCAGCAGGCGCGTAAATTACCCAATCCCAGCACGGGGAGGTAGTGACGAAAAATAACAATACAGGACTCA
Laphria	CCTGAGAAACGGCTACCACATCTAAGGAAGGCAGCAGGCGCGTAAATTACCCACTCCCAGTACGGGGAGGTAGTGACGAAAAATAACAATACAGGACTCA
Mythicomyia	CCTGAGAAACGGCTACCACATCTAAGGAAGGCAGCAGGCGCGTAAATTACCCACTCCCAGCACGGGGAGGTAGTGACGAAAAATAACAATACAGGACTCA
Drosophila	CCTGAGAAACGGCTACCACATCTAAGGAAGGCAGCAGGCGCGTAAATTACCCACTCCCAGCTCGGGGAGGTAGTGACGAAAAATAACAATACAGGACTCA
Triozocera	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCACGCAAATTACCCACTCCCAGCACGGGGAGGTAGTGACGATAAATAACGATCCGGGACTCT
Caenocholax	CCTGAGAAACGGCTACCACATCTAAGGAAGGCAGCAGGCACGTAAATTACCCAATCCCAGCACGGGGAGGTAGTGACGAAAAATAACAATCCGGAACTCA
Elenchus	CCTGAGAAACGGCTACCACATCTAACGAAGGCAGCAGGCGCGCAAATTACCCACTCCCAGCACGGGGAGGTAGTGACGATAAATAACGATACGGAACTCT
Crawfordia	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGATAAATAACGATCCGGAACTCT
X.pecki	CCTGAGAAACGGCTACCACATCTAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGATAAATAACGATCCGGAACTCA
X.vesparum	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX

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                                                                                                                    200▼
Hypogastrura        --TAC-GAGGCTCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCTATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Trigoniopthalmus    --TCC-GAGGCCCCGTAATTGGAATGAGTACACTTTAAATCCTTT-AACGAGTATCTATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Ephemerella         --TCC-GAGGCCCCGTAATCGGAATGAGAACACTTTAAATCTTTT-AACAAGTACCTAATGGAGGGCAAGTCTGGTGCCAGCAGTCGCGGTAATTCCAGC
Agrion              --TCC-GAGGCCCCGTAATCGGAATGAGAACACTTTAAATCCTTT-AACGAGGATCTATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Libellula           --TCC-GAGGCCCCGTAATCGGAATGAGAACACTTTAAATCCTTT-AACGAGGATCTATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Megarcys            --TCC-GAGGCCCCGTAATCGGAATGAGCACAACTTAAATACTTT-AACGAGTATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Cultus              --TCC-GAGGCCCCGTAATCGGAATGAGCACAACTTAAATACTTT-AACGAGTATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Blaberus            --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGTATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Mantis              --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGTATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Labidura            --TCC-GAGGCCCCGTAATCGGAATGAGCACACTTTAAATACTTT-AACAAGTATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCTGCGGTAATTCCAGC
Melanoplus          --TCC-CAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGTATCTATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Anisomorpha         --TGC-CAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGTATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Oligotoma           --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGTATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Cerastipsocus       -ATCC-GAGGCTCTGCAATCGGAATGGGTACACTCTAAATCATTT-AACGAGTATCAATTGGAGGACAAGTCTGGTGCCAGCACCCGCGCTAATTCCAGC
Dennyus             -ATAATGAGGCTCTGCAATCGGAATGAGAAGACTCTAAATCATTT-ACCGAGTATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Acyrthosiphon       --TCC-GAGGCCCCGTAATCGGAATGAGAACACTTTAAAACCTTTAAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Buenoa              --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACAAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Saldula             --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAACCCTTT-AACCAGGATCTATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAACTCCAGC
Lygus               --TAT-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACAAGGATCCATTGAAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Taeniothrips        --TCT-GAGGCCCTGTAATCGGAATGACTACACTTTAAATCCTTT-AACGAGTATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Priacma             --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGACCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCCGCGTAATTCCAGC
Colpocaccus         --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGACCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Cybister            --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAA-TCCAGC
Xyloryctes          --TCC-GAGGCCCCGTAATCGGAATGAGTACACTCTAAACCCTTT-AACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Octinodes           --TCC-GAGGCCCCGTAATCGGAATGAGCACACTTTAAATCCTTT-AACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Photuris            --TCC-GAGGCCCCGTGATCGGAATGAGCACACTTTAAATCCTTT-AACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Meloe               --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AGCAAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Rhipiphorus         --TCC-GAGGCCCGGTAATCGGAATGAGTACACTTTAAATCCTTT-AACAAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Tenebrio            --TCC-GAGGCCCCGTAATCGGAATGAGTACACTCTAAACCCTTT-AACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Tetraopes           --TCC-GAGGCCCCGTAATCGGAATGAGTACACTCTAAACCCTTT-AACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Corydalus           --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGACCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Agulla              --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGACCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Lolomyia            --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTAGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Mantispa            --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Hemerobius          --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGACCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Chrysoperla         --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
M.immaculatus       --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Myrmeleon           --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Galleria            --TAC-GAGGCCTCGTAATCGGAATGAGTACACTTTAAATATTTT-AACGAGGAACAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Papilio             TATCC-GAGGCCTCGTAATCGGAATGAGTACACTTTAAATCCTTT-GACGAGGAACAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTACTTCCAGC
Ascalapha           --TAC-GAGGCCTCGTAATCGGAATGAGTACACTTTAAATATTTT-AACGAGGAACAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Hydropsyche         --TCC-GAGGCCTCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Pycnopsyche         --TCC-GAGGCCTCGTGATCGGAATGATTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Oecetis             --TCC-GAGGCCTCGTGATCGGAATGATTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
B.strigosus         --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTA-TACAAGGAACAATTGGAGGGCAAGTCTGGTGCCAGCAGCTGCGGTAATTCCAGC
B.chlorostigmus     --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Boreus              --TCC-GAGGCCCCGTAATCGGAATGAGTACACCTTAAATCCTTT-AACGAGGACCCATTAGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Merope              --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Panorpa             --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Ctenocephalides     --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCTATTAGAGGGCCAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Hystrichopsylla     --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Orchopeas           --TCC-GAGGCCCCGTAATCGGAATGAGTACACT------CCTTT-AACGATTAACAATTGGAGGGCAAGCCTGGTGCCAGCAGCCGCGGTAACCCCAGC
Hartigia            --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Orussus             --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Hemitaxonus         --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Peridista           --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Bareogonalos        --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Evania              --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Ichneumon           --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCNATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGNTAATTCCAGC
Ophion              --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Mesopolobus         --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Caenochrysis        --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Epyris              --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Priocnemus          --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACAAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Dasymutilla         --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCATCAGCCGCGGTAATTCCAGC
Apoica              --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Monobia             --TCC-GAGGCCCTGTAATCGGAATGAGTACACTTTAAATCCTTT-AACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
P.fuscatus          --TCC-GAGGCCCCGTAATCGGAATGAGTACACTTTAAATCCTTT-AACAAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
P.dominulus         XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXCAGCAGCCGCGGTAATACCAGC
Camponotus          XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXCAGCAGCCGCGGTAATACCAGC
Chalepoxenus        XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXCAGCAGCCGCGGTAATACCAGC
Doronomyrmex        XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXCAGCAGCCGCGGTAATACCAGC
Harpagoxenus        XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXCAGCAGCCGCGGTAATACCAGC
Leptothorax         XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXCAGCAGCCGCGGTAATACCAGC
Temnothorax         XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXCAGCAGCCGCGGTAATACCAGC
Tipula              -ATCC-GAGGCCCTGTAATTGGAATGAGTACACTTTAAATCCTTT-AACAAGGAACAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Laphria             TATCC-GAGGCCCTGTAATTGGAATGAGTACACTTTAAATCCTTT-AACAAGGACCAATTGGAGGGCATGTCTGGTGCCAGCAGCCGCG-TAACTCCAGC
Mythicomyia         TATTC-GAGGCCCTGTAATTGGAATGAGTACACTTTAAATACTTT-AACAAGGACCTATTGGAGGGCAAGTCTGGTGCCAGCAGCTGCGGTAATTCCAGC
Drosophila          TATCC-GAGGCCCTGTAATTGGAATGAGTACACTTTAAATCCTTT-AACAAGGACCAATTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Triozocera          TT--A-GAGTTTCCGTAATCGGAATGAGTACAGTTTAGGTCCTTT-AACGAGGAACAAGTGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Caenocholax         AA--C-GAGTTTCCGAAATTGGAATGAGTACAATTTAAAAACTTT-AACGAGGAGCAAATGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Elenchus            AA--T-GAGTTTCCGTGATCGGAATGAGTGTAATTTAAATCCTTA-TACGAGGAGCAAATGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
Crawfordia          AA--T-GAGTTTCCGTAATCGGAATGAGCACAATTTAAATCCTTT-AACGAGGAGCAAATGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
X.pecki             AA--T-GAGTTTCCGTAATCGGAATGAGTACAATTTAAAAGCGTT-AGCAAGTATCAAATGGAGGGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGC
X.vesparum          XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXCAGCAGCCGCGGTAATACCAGC
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                                                                                                                    300▼
                                 ┌───18S a0.7───┐                                  ┌─Variable Region─
Hypogastrura        TCCAATAGCGTATATTAAAGTTGTTGTGGTTAAAAAGCTCGTAGTTGGATCTCGGTTT-CAGATGGGCGGTGCAC-CTTG-----CGGTGTTT-ACTGTC
Trigoniopthalmus    TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAGAAGCTCGTAGTTGGATCTGGGTCG-CGGGCAGTCGGTTCAC--TTGC----CGGTGTAC-ACTGAC
Ephemerella         TCCATTGGCGTATXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXGATCTGTGTAT-CGGACGGTCGGTT---CGCCGCTCG-CGGTGTTTGACTGAC
Agrion              TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAA-GCTCGTAGTCGGAGGTGTGTCT-CGGACGGTCGGTT---CGCCGCTTGTCGGTGCTCAACTGGC
Libellula           TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCGGAGGTGTGTCT-CGGACGGTCGGTT---CGCCGCTTGTCGGTGCTCAACTGGC
Megarcys            TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGGACTTGTGTCC-CACGCCGTCGGTTCGTCGCCCGTCGACGTAACCGCACGGTT
Cultus              TCCXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Blaberus            TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCGGACTTGTGTCA-CACGCTGCCGGTTCACCGCCCGT---CGGTGTTTAACTGGC
Mantis              TCCAATAGCGTATXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Labidura            TCCAATAGCGTATAATAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAAGTTGTGAAT-CGCACTGTTGGTGCACCAATTTT---CGGTGTTTAACTTAC
Melanoplus          TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGGATTTGTGTCC-CACGCTGTTGGTTCACCGCCCGT---CGGTGTTTAACTGGC
Anisomorpha         TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGGATTTGTGTCC-CACGCTGTCGGTTCACCGTTCGT---CGGTGTTTAACTGGC
Oligotoma           TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGGATCTGTGTCT-CACGCTGTCGGTTCACCGCCCGT---CGGTGTTTAACTGGC
Cerastipsocus       TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGGATCTGTGXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Dennyus             TCCAATAGCGTATXXXXXXXXXXXXXXXXXXXNAAAAGCTCGTAGTTGGACCTGTGTTTCGCGCTGTCGGTTCACCGCCCGT---CGGTGCATAACTGGC
Acyrthosiphon       TCCAATCGCGTATATTAAAGTTATTGCGGTTAAAAAGCTCGTAGTCGGATCTGTGTCT^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^
Buenoa              TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGCAGTTGGTTCTGTGTCC-CGCGCTGTCGGTTCACCGCCTGC---CGGTGC--AACTGGC
Saldula             TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGGTTTTGTGTCC-CACGCTGTTGGTTCACTGCCTGT---CGGTGC--AACTGGC
Lygus               TTCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGGTTCTGCGTGC-CACGCTGTCGGTTCGCCGCCTGC---CGGTGT--AACTGGC
Taeniothrips        TCCAATAGCGTATXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXTGTCC-CACGCTGTCGGTTCACCGCCCGT---CGGTGCCAAACTGGC
Priacma             TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCGAATTTGTGTCT-CGCACTGTCGGTTCACCGCCCG----CGGTGCT-AACTGGC
Colpocaccus         TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATTTGTGTCT-CGCACTGTCGGTTCACCGCCCG----CGGTGCT-AACTGGC
Cybister            TCCTATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTCT-CGCGCTGTCGGTTCACCGTCCG----CAGTGTTAAACTGGA
Xyloryctes          TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCGAACTTGTGTCC-CGCGCCGGCGGTTCATCGTTCG----CGGTGTTTAACTGCC
Octinodes           TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCGAATCTGTGTCC-CGCGCCGCCGGTTCGTCGCTCG----CGGCGTTTAACTGGC
Photuris            TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCGAAATTGTGTCC-TCGGCCGCCGGTTCGTCGT-CG-----GA-C-C-AACTGCG
Meloe               TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCGAATTTGTGTCT-CATGCCGCTGGTTCATCGTTCG----CGGTGTA-AACTGGC
Rhipiphorus         TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCGAATTTGTGTCC-CACACCGCTGGTTCATCGTTCG----CGGTGTT-AACTGGC
Tenebrio            TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCGAATCTGTGTCC-CGCGCCGCCGGTTCATCGTTCG----CGGTGTT-AACTGGC
Tetraopes           TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCGAATCTGTGTCC-CGCGTCGCCGGTTCATCGTCCG----CGGTGTT-AACTGGC
Corydalus           TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATTTGTGTCT-CGCACTGTCGGTTCACCGCCCG----CGGT-CT-AACTGGC
Agulla              TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATTTGTGTCT-CGCACTGTCGGTTCACCGCCCG----CGGT-CT-AACTGGC
Lolomyia            TCTAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGCCGAATCTGTGTCT-CACACTGTCGGTTCACCGCTCG----CGGTGTTCAACTGGC
Mantispa            TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCGAATTTGTGTTC-CACACTGTTGGTTCACCGCTCG----CGGTGTTTAACTGGC
Hemerobius          TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCAATTTTGTGTCC-CACACTGTCGGTTCACCGCTCG----CGGT----AACTGGC
Chrysoperla         TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCGAATCTGTGTCC-TACACTGTTGGTTCAATGCTCG----CATTGTTTAACTAGC
M.immaculatus       TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAACGTTCGTAGTTGAACTTGTGTCA-XXXXXXXXXXXXXXXXXXXXXX----XXXXXXXXXXXXXXX
Myrmeleon           TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCGAATTTGTGTCC-TACACTGTCGGTTCACCGCTCG----CGGTNTTTAACTGGC
Galleria            TCCAATAGCGTATACTAAAATTGTTGCGGTTAAAAAGCTCGTAGTTGCATTTGTGCGC-CGCGCTGTCGGTGCCACGCATC----CGGC-TAT-ACTGAC
Papilio             TCCAATAGCGTATACTAAAATTGTTGCGGTTAAAAAGCTCGTAGTTGCATTTGTGCGC-CGCGCTGTCGGTGCCACGCTTC----CGGC-TAT-ACTGAC
Ascalapha           TCCAATAGCGTATACTAAAATTGTTGCGGTTAAAAAGCTCGTAGTTGCATTTGTGCGC-CGCGCTGTCGGTGCCACGCATC----CGGC-TAT-ACTGAC
Hydropsyche         TCRAATAGCGTATACTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAAATTGTGTCC-AGCGCGGTCGGTCTACCGAATG----CGG--TACGACAGGC
Pycnopsyche         TCCAATAGCATATACTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAAATTGTGTCC-TGCGGTGTCGGTCTACCGAATG----CGG--TACGACAGGC
Oecetis             TCCAATAGCGTATACTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAAATTGTGYCC-GGCGGCGTCGGTCTACCGATTG----CGG--TACGACAGGC
B.strigosus         TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGATGTTGAATTTGTATTC-CATACTGTTGGTACACCGCTCG----CTGC-TT-AACTAGC
B.chlorostigmus     TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATTTGTGTTC-CACACTGTTGGTTCACCGCTCG----CGTT-TT-AACTGGC
Boreus              TCTAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTGCTAGTTGAATCTGTGTGC-CACACTGTCGGTTCACCGCTCG----CTGT-TT-AACTGGC
Merope              TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTCC-CACACTGTCGGTACACCGCTCG------GC-TT-AACTGGC
Panorpa             TCTAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGATGTTGAATTTGTGTCC-CATACTGTCGGTTCACCGCTCG----CTGT-TT-AACTGGC
Ctenocephalides     TCTAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTCC-CACACTGTCGGTTCACCGCTCG------GC-TTCAACTGGC
Hystrichopsylla     TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTCC-CACACTGTCGGTTCACCGCTCG----C-GTGTTCAACTGGC
Orchopeas           TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAGTCTGTGTCC-CACACTGTCGGTTCACCGCTCG------GC-TCCAACTGGC
Hartigia            TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTCC-CACGCTGTCGGTTCATCGCTCG----CGGTGTTTAACTGGC
Orussus             TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTGT-CACGCTGTCGGTTCATCGCTCG----CGGTGTTT-ACTGAC
Hemitaxonus         TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTCC-CACGCTGCCGGTTCGCCGCTCG----CGGTGTTTAACTGGC
Peridista           TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTCC-CACGCTGCCGGTTCGCCGCTCG----CGGTGTTTAACTGGC
Bareogonalos        TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTGC-CACACTGTCGGTTCATCGCTCG----CGGTGTTTAACTGGC
Evania              TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTCT-CACGCTGTCGGTTCACCGCTCG----CG-TGCTC-ACTGAC
Ichneumon           TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTGT-CACGATGTTGGTTCACCGCTCG----CGNT-TTTAACTAGC
Ophion              TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTGT-CACGATGTTGGTTCACCGCTCG----CGGT-TTT-ACTAGC
Mesopolobus         TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTGC-CACGCTGTCGGTTCATCGCTCG----CGATGTTTAACTGAC
Caenochrysis        TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATTTGTGTGC-CACACTGTCGGTGCACCGCTCG----CGTCGC--AACTGGC
Epyris              TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTGC-CACAATGTCGGTCCTCCGCTCG----CGTGGTT--ACTTGC
Priocnemus          TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTGC-CACACTGTCGGTACACCGCTCG----CGT--CTT-ACTGAC
Dasymutilla         TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTAT-CACACTGTCGGTACACCGCTCG----CGGTGTTT-ACTGAC
Apoica              TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGT-TTT-CACACTGTCGGTTCACCGCTCG----CGGTGTTT-ACTGGC
Monobia             TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTTT-CACACTGTCGGTTCACCGCTCG----CGGTGTTT-ACTGGC
P.fuscatus          TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTTT-CACACTGTCGGTTCACCGCTCG----CGGTGTTT-ACTGGC
P.dominulus         TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTTT-CACACTGTTGGTTCACCGCTCG----CGGTGTTT-ACTGGC
Camponotus          TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTCG-CACACCGTCGGTTCACCGCTCG----CGGTGTTTAACTGGC
Chalepoxenus        TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTCG-CACACCGTCGGTTCACCGCTCG----CGGTGTTTAACTGGC
Doronomyrmex        TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTCG-CACACCGTCGGTTCACCGCTCG----CGGTGTTTAACTGGC
Harpagoxenus        TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTCG-CACACCGTCGGTTCACCGCTCG----CGGTGTTTAACTGGC
Leptothorax         TCCAATAGCGTAAATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTCG-CACACCGTCGGTTCACCGCTCG----CGGTGTTTAACTGGC
Temnothorax         TCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTGTCG-CACACCGTCGGTTCACCGCTCG----CGGTGTTTAACTGGC
Tipula              TCCAATAGCGTATATTAAAGTTGTTGCGGTTA-AACGTTCGTAGTTGAACTTGTGTCA-AGCACAGGTGG==============================
Laphria             TCCAATAGCGTATATTAAAGTTGTTGCGGTTA-AACGTTCGTAGTTGAATTTGTGCTC-CATACGGGTAG==============================
Mythicomyia         TCCAATAGCGTATATTAAAGTTGTTGCGGTTA-AACGTTCGTAGTTGAATTTGTGCTT-CAAACGGGTAG==============================
Drosophila          TCCAATAGCGTATATTAAAGTTGTTGCGGTTA-AACGTTCGTAGTTGAACTTGTGCTT-CATACGGGTAG==============================
Triozocera          TCCATTAGTATATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTATCC-CATACTGTCAA``````````````````````````````
Caenocholax         TCCATTAGTATATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCGATTTTGTATCT-CGTACTTTCGA``````````````````````````````
Elenchus            TCCATTAGCATATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCGAATCTGTATCT-CGGCGTGTCAG``````````````````````````````
Crawfordia          TCCATTAGCATATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGAATCTGTATCT-CATACTGTCAG``````````````````````````````
X.pecki             TCCATTAGTATATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTCGAATCTGTATCT-CATCATGTCAG``````````````````````````````
X vesparum          TCCATTAGCATATATTAAAGTTGTTGCGTTTAAAAAGCTCGTAGTTGAATCTGTATCT-CATCATGTCAG``````````````````````````````
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                   ——————————————————Variable Region ——————————————————┐                  400▼
Hypogastrura       TGTTT------GGA--CGATTTTCTTGGT((((((((((((((((((((((((((((((((TGGTT-CTCTTAATCGAGTGCCTTGAGTGGCCAACACG-
Trigoniopthalmus   TGG-CCC----GGA--CGT-CCTGTCGGT((((((((((((((((((((((((((((((((TGGTG-CTCTTCACTGAGTGTCTTGGGTGGCCGACACG-
Ephemerella        CGGTT-C----GGA--CGT-CATGCCGGTGGGACC\\\\\\\\\\\\\\\CTTACCCTCCGCGATG-TTCTTAACCGAGTG-GTCGGTGGGCCGGCACG-
Agrion             CGGT-CC----RGA--CGT-ACTGCCGGWGGGGCC\\\\\\\\\\\\\\\TTATCCTTCCTTGGTC-CTCTTCACCGAGTGCCTTGGTGGGCCGGCACG-
Libellula          CGGT-CC----GGA--CGT-CCTGCCGGTGGGGCT\\\\\\\\\\\\\\\TTATCCTTACGTGGTC-CTCTTCATTGAGTACCTTGTTGGGCCGGCACG-
Megarcys           ATGTGA-GTG-GGA--CGT-CCAGCCGGT)))))))))))))))))))))TTACTCCGTCTCGGTG-CTCTTAATCGAGTGTCTTGACGGGCCGGCTCG-
Cultus             XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXCGGTG-CTCTTAATCGAGTGTCTTGACGGGCCGGCTCG-
Blaberus           ATGCA-CGTGCTGA--CGT-CCTGCCGGTGGCCCA<<<<<<<<<<<<<<<ATA-CCCCTCGTGGTG-CTCTTAACCGAGTGTCTCGATGGGCCGGCACG-
Mantis             XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Labidura           ATGTTGC-AAT--T--CGT-CCAGTCAGTGGGATA<<<<<<<<<<<<<<<TTCACCCATTACGGTG-CTCTTTACTGAGGG---AGA-GGG---TGACG-
Melanoplus         ATGTATCGTG-GGA--CGT-CCTGCCGGTGGGGCG<<<<<<<<<<<<<<<AAATCCTACCGCGGTG-CTCTTTACCGAGTGTCGAGGTGGGCCGGCACG-
Anisomorpha        ATGC-CCGTGCGGA--CGT-CCTGCCGGTGGATGC<<<<<<<<<<<<<<<NAATCCTACCGCGGTG-CTCTTCACCGAGTGTCGAGGTGGGCCGGCACG-
Oligotoma          AT-----GTCCGGA--CGT-CCTGCCGGTGGATGG<<<<<<<<<<<<<<<AAATCCTACTGCGGTG-CTCTTTA-TGAGTGTCACTGTAGGCCGGCACG-
Cerastipsocus      XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXG-
Dennyus            AGT--CCGCG-GAA--CGT-CCTGCCGGT[[[[[[[[[[[[[[[[[[[[[AAACCCTGTCGCGATG-CTCTTTACCGAGTGTCGAGGCGGGCCGGNAAG-
Acyrthosiphon      ^^^^^^^^^^^^^^^^^^^^^^^^^CGGTGTCCCG::::::CCTACTCCAATCTTGCTGCGCGGTG-CTCTTCACCGAGTGCCGTGGCGGGCCGACACG-
Buenoa             ATG--CCGCG-GGA--TGT-CCTGTCGGTGGAGGT]]]]]]CCGCCGATTCAATCCTGCCGCGGTG-CTCTTCACTGAGTGTCGAGGTAGGCCGACACG-
Saldula            ATG--TCGTG-GGA--TGT-CCTGTCGGTGGCGTC]]]]]]TCGCCGACTCAATCCTG-C-CGGTG-CTCTTCACTGAGTGTCGAGGTAGGCCGACACG-
Lygus              ATG--CCGTG-GCA--TGT-CCTGTCGGTGGCGTT]]]]]]TCGCCTACTCTATCCTACCTAGGTG-CTCTTCACCGAGTGTCGAGGTAGGCCGACACG-
Taeniothrips       GTG--TCGCG-GAA--CGT-CATGCCGGTGGGGTG]]]]]]TCGAGT-CGGAATCCCGCTGCGGTG-CTCTTCATTGAGTGTCGAGGTGGGCCGGCACG-
Priacma            ATGTT-TGTG-AGA--CGT-CCTGCCGGTGGATGG///////////////AAATCCTGTCGA--AA-TCCTGTCGGGTGTGTCGAGGCGGGCCGGCACG-
Colpocaccus        ATGTT-TGTG-AGA--CGT-CCTGCCGGTGGATGG///////////////AAATCCTGTCGA--AA-TCCTGTCGCGAGTGTCGAGGCGGGCCGGCACG-
Cybister           ACGTT-CGCG-AGA--CGT-CCTGGCGGTGGCCAC{{{{{{CCGACTT--TAATCCTACTTCGGTG-CTCTTTACCGAGTGTCGA-GTGGGCCGGCACG-
Xyloryctes         GTGT-CCGTG-GGA--CGT-CCTGCCGGTGGACTT{{{{{{CCAACTT-CAAATCCCACCGCGGTG-CTCTTTACCGAGTGTCGAGGTGGGCCGGCACG-
Octinodes          GTGTTACGCG-GGA--CGT-CCTGCCGGTGGGCTT{{{{{{CCAACTTGCGAATCCCGCCGCGGTG-CTCTTCGCTGAGTGTCGAGGCGGGCCGGCACG-
Photuris           -CG-G-CACC-TGA--CGT-CCAGCCGGT------{{{{{{---------------------GGGTG-CTCTTAACCGAGTGTCCAGGCGGGGGCGCAAC
Meloe              --GTGACATG-GGA--CGT-CCTGCCGGTGGGTTT{{{{{{CCTATA---TAATCCTGCGGCGTTG-CTCTTAATCGAGTGTCGAGGTGGGCCGGCTCA-
Rhipiphorus        --GTTTTGTG-GGA--CGT-CCTGCCGGCGGACTT{{{{{{CCAATT---TAATCCTGCCGCGTTG-CTCTTCATTGAGTGTCGAGGTGGGCCGGCACT-
Tenebrio           --GTGCCGCG-GGA--CGT-CCTGCCGGTGGGCTT{{{{{{CCAACT---CAATCCCGCCGCGGTG-CTCTTCGTTGAGTGTCGAGGTGGGCCGGCACG-
Tetraopes          --GTT-CCGG-GGA--CGT-CCTGCCGGAGGGCTT{{{{{{CCGACT---CAATCCCGCCGCGGTG-CTCTTCACTGAGTGTCGAGGTGGGCCGGCACG-
Corydalus          ATGTT-TGTG-AGA--CGT-CCTGCCGGTGGATGG///////////////AAATCCTGTCGGGGTG-CTCTTAATTGAGTGTCGAGGCGGGCC-G---G-
Agulla             ATGTT-TGTG-AGA--CGT-CCTGCCGGTGGATGG///////////////AAATCCTGTCGGGGTG-CTCTTAATTGAGTGTCGAGGCGGGCC-G---G-
Lolomyia           ATGTTATGTG-AGA--CGT-CCTACCGGTGGGTGG!!!!!!CCCCAATTGCAATCCTGT-CCGGTC-CTCTTAATTGAGTGTCGAGGTGGCCCGGTACG-
Mantispa           ATGTTATGTG-GAA--CGT-CCTACCGGTGGATGG!!!!!!ATCCTATTGCAATCCCGTCGCGGTG-CTCTTAATTGAGTGTCGAGGTGGCCCGGTACG-
Hemerobius         ATGTTATGTG-G-A--CGT-C-TACCGGTGGGTGG!!!!!!CCCCAATTACAATCCCGTCGCGGTC-CTCTTAATTGAGTGTCGAGGTGGGCC-G---G-
Chrysoperla        ATGTTATGTG-GGA--CGT-CCTACCGGTGGGTGG!!!!!!CCCCAATTGCAATCCCGTCGCGGTG-CTCTTAATTGAGTGTCGAGGTGGGCCGNTACG-
M.immaculatus      XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX-
Myrmeleon          ATGTTTTGTG-GGA--CGT-CCTACCGGT@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@CGGTG-CTCTTAATTGAGTGTCGAGATGGGCCGGTACG-
Galleria           ACGTTT-GCG-GAA--CGT-ATCGTCGGTGAGC}}}}}}}}CCAACT-CAAAATCCTATCGCGGTG-CTCTTCGGTGAGTGTCGAGGTGGGCCGACAAT-
Papilio            ACGTCT-GCG-GAA--CGT-ATCGTCGGTGAGC}}}}}}}}CCAACT-CAAAATCCTATCGCGGTG-CTCTTCGGTGAGTGTCGAGGTGGGCCGACAAT-
Ascalapha          ACGTCT-GCG-GAA--CGT-ATCGTCGGTGAGC}}}}}}}}CCAACT-CAAAATCCTATCGCGGTG-CTCTTCGGTGAGTGTCGAGGTGGGCCGACAAT-
Hydropsyche        ACGTCT-GCG-GG---CTT-CTCGCCGGT$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$-
Pycnopsyche        ACGTCT-GCG-GGG--CTT-CTCGCCGGT$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$-
Oecetis            GCGTCT-GCG-GA---CTT-CTCGCCNNN$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$-
B.strigosus        ACGTCT-A-G-GAA--TGT-YTTACCGGTGGT+++++++++CCAAATTATAAATCCTATTGCGGTG-CTCTTAATCGAGTGTCGTTATAGGCCGGTACG-
B.chlorostigmus    ATGTCT-GTG-GAA--CGT-CCTACCGGTGGG+++++++++CCAAATAACAAATCCTATCACGGTG-CTCTTAAACGAGTGTCGGGATGGGCCGGTACG-
Boreus             ATGTCTTGTG-GGA--CGT-CCTACCGGTGGGC########CCAACT-CAAAATCCTACCACGGTG-CTCTTTACCGAGTGTCGAGGTGGGCCGGTACG-
Merope             ATGTCTTGTG-GGA--CGT-CCTACCGGTGGGT########CCAACT-AAAAATCCTATCACGGTGCCTCTTTACCGAGTGTCGAGATGGGCCGGTACG-
Panorpa            ATG-CT-ATG-GGA--CGT-CCTATCGGTGGGT########CCAACT-CAAAATCTCATCACGGTG-CTCTTAAACGAGTGTCGAGGTGGGCCGATACG-
Ctenocephalides    ATGTCT-GTG-GGA--CGT-CCTACCGGTGGGC########CCAACT-CAAAATCCTACCACGGTG-CTCTTCACCGAGTGTCGAGGTGGGCCGGTACG-
Hystrichopsylla    ATGTCT-GTG-GGA--CGT-CCTACCGGTGGGC########CCAACT-CAAAATCCTACCACGGTG-CTCTTCACCGAGTGTCGAGGTGGGCCGGTACG-
Orchopeas          ATGTCT-GTG-GGA--CGT-CCTACCGGTGGGC########CCAACT-CAAAATCCTACCACGGTG-CTCTTCACCGAGTGTCGAGGTGGGCCGGTACG-
Hartigia           ATGA-CTGTG-GGA--CGT-CCTACCGGTGGGCTT%%%%%%CCAACT--AATATCCCATCGCGGTG-CTCTTTACCGAGTGTCGAGGTGGGCCGGTACG-
Orussus            ATGA-C-GTG-GGA--CGT-CCTACCGGTGGGCTC%%%%%%CCAACT--AATATCCCATCGCGGTG-CTCTTCACTGAGTGCCGAGGTGGGCCGGTACG-
Hemitaxonus        ATGATT-GTG-GGA--CGT-CCTACCGGTGGGCTT%%%%%%CCAACT--AATATCCCATC-GGGTG-CTCTTCACTGAGTGTCGAGGTGGGCCGGAACGT
Peridista          ATGATT-GTG-GGA--CGT-CCTACCGGTGGGCTT%%%%%%CCAACT--AATATCCCATCGCGGTG-CTCTTCACTGAGTGTCGAGGTGGGCCGGTACG-
Bareogonalos       ATGATT-GTG-GGA--CGT-CCTACCGGTGGGCTT%%%%%%CCAACT--AATATCCCATCGCGGTG-CTCTTAACCGAGTGTCGAGGTGGGCCGGTACG-
Evania             ATG--CCGTG-GTA--CGT-CCTACCGGTGGGCTT%%%%%%CCAGTC--GATATCCCGTCACGGTG-CTCTTCACTGAGTGTCGAGGTGGGCCGGTACG-
Ichneumon          ATG--CCGTG-AGA--CGT-CCTACCGGTGGGCTT%%%%%%CCAACT--AATATCCCATCGCGGTG-CTCTTTATTGAGTGTCGAGGTGGGCCGGTACG-
Ophion             ATG--CCGTG-AGA--CGT-CCTACCGGTGGGCTT%%%%%%CCAACT--AATATCCCATC-GGGTG-CTCTTCACTGAGTGTCGAGATGGGCCGGAACGT
Mesopolobus        ATGATT-GTG-GGA--CGT-CCTACCGGTGGGCTT%%%%%%CCAGCT--AATATCCCATCGCGGTG-CTCTTTACCGAGTGTCGAGGTGGGCCGGTACG-
Caenochrysis       ATGTA--GTG-GGA--CGT-CCTATCGGTGAACTC%%%%%%TTCTCC--AA-ATCCTATCGCGGTG-CTCTTCACTGAGTGTCGAGATGGGCCGATACG-
Epyris             ATCA-C-GTG-GGA--CGT-CCTACCGGTGGCTTC%%%%%%CCAACT--AATATCCCATCGCGGTG-CTCTTCATTGAGTGTCGAGGTGGGCCGGTACG-
Priocnemus         ACGAT--GTG-GGA--CGT-CCTACCGGTGGGCTT%%%%%%CCAACT-ATACATCCCATCGCGGTG-CTCTTCATTGAGTGTCGAGGTGGGCCGGTACG-
Dasymutilla        ACGAT--GTG-GTA--CGT-CCTACCGGTGGGCTT%%%%%%CCAGCT--AACATCCCTTCACGGTG-CTCTTCATCGAGTGTCGCGTTGGGCCGGTACG-
Apoica             ATGAT--GTG-GGA--CGT-CCTACCGGTGGACTT%%%%%%CCAAAT--AATATCCCATC-GCGTG-CTCTTCATTGAGTGTCGAGATGGGCCGGTACGG
Monobia            ATGAT--GTG-GGA--CGT-CCTACCGGTGGGCTT%%%%%%CCAACT--AATATCCCATC-GCGTG-CTCTTCACTGAGTGTCGAGATGGGCCGGTACGT
P fuscatus         ATGAT--GTG-GGA--CGT-CCTACCGGTGGGCTT%%%%%%CCAACT--AATATCCCATC-GCGTG-CTCTTCATTGAGTGTCGAGATGGGCCGGTACGT
P.dominulus        ATGAT--GTG-GGA--CGT-CCTACCGGTGGGCTT%%%%%%CCAACT--AATATCCCATCGCGGTG-CTCTTCATTGAGTGTCGAGATGGGCCGGTACG-
Camponotus         GTGAT--GTG-GGA--CGT-CCTACCTGTGGGCTT%%%%%%CCAACT--AATATCCCGTCGCGGTG-CTCTTTACTGAGTGTCGAGTCGGGCCGGTACG-
Chalepoxenus       GTGAT--GTG-GGA--CGT-CCTACCGGTGGGCTT%%%%%%CCAACT--AATATCCCGTCGCGGTG-CTCTTTACTGAGTGTCGAGTCGGGCCGGTACG-
Doronomyrmex       GTGAT--GTG-GGA--CGT-CCTACCGGTGGGCTT%%%%%%CCAACT--AATATCCCGTCGCGGTG-CTCTTTACTGAGTGTCGAGTCGGGCCGGTACG-
Harpagoxenus       GTGAT--GTG-GGA--CGT-CCTACCGGTGGGCTT%%%%%%CCAACT--AATATCCCGTCGCGGTG-CTCTTTACTGAGTGTCGAGTCGGGCCGGTACG-
Leptothorax        GTGAT--GTG-GGA--CGT-CCTACCGGTGGGCTT%%%%%%CCAACT--AATATCCCGTCGCGGTG-CTCTTTACTGAGTGTCGAGTCGGGCCGGTACG-
Temnothorax        GTGAT--GTG-GGA--CGT-CCTACCGGTGGGCTT%%%%%%CCAACT--AATATCCCGTCGCGGTG-CTCTTTACTGAGTGTCGAGTCGGGCCGGTACG-
Tipula             =TG-C--TA-T-GA--CGT-ATTACTG-T&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&TAGTGCCTCTTTACCGAGTGCTGGTCTGGGCCGGTACT-
Laphria            =TGTTATGCG---AG-CGT-ATTACCGGT&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&CAGTG-CTCTTTACCGAGTGTTGTTGTGGGCCGGTACA-
Mythicomyia        =TGTAT-GTG---AG-CGT-ATTACCGGT&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&CAGTG-CTCTTTGCTGAGTGCGGTTGTGGGCCGGTACT-
Drosophila         =TGTAT-G-T--AAG-CGT-ATTACCGGT&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&TAGTG-CTCTTAAACGAGTGTTATTGTGGGCCGGTACT-
Triozocera         `TGTAT-G-G--GATATGC-A-CGCTGGC*********************************************************TCAGGCCAGCGAT-
Caenocholax        `TGTAC-G-A--GATATAT-A-GACTGGT*********************************************************TCGGGCCGGCGAA-
Elenchus           `CGCAT-G-A--GATATAA-A-TATTGGT*********************************************************TTAGACCAATAAA-
Crawfordia         `TGTAT-G-A--GATATAA-A-TATCGGT*********************************************************TTAGACCGATAAA-
X.pecki            `TGTAT-G-A--GATATAA-A-TACTGGT*********************************************************TTAGACCAGTAAA-
X.vesparum         `TGTAT-G-A--GATATAA-A-TACTGGT*********************************************************TTAGACCAGTAAA-
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                                    ┌──18s a0.79──┐                                                                    500▼
Hypogastrura         TTTACTTTGAAAAAATTGGAGTGCTCAAAGCAGGC----GC-TAC-A-GCCTGAACATTA--GTGCATGGAATAATGGAATAGGATCTCGGTTCTATTTC
Trigoniopthalmus     TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---AGT-G-T-C-GCCTGAATGTTCG-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Ephemerella          TTTACTTTGAACAAATTTGAGTGCTCAAAGCAGGC---CTTATGT-T-GCCTGGAAACTGT-GTGCATGGAATAATGAAAGAGGACCTTGGTTCTATTTG
Agrion               TTTACTTTGAACAAATTAGAGTGCTCAAAGCAGGC---CGTTGGT-C-GCCTGAATACTGT-GTSCATGGAATAATGGAATAGGACCTCGGTTCCATTTT
Libellula            TTTXXXXXXXXXXXXTTAGAGTGCTCAAAGCAGGC---CGTTGGTACAGCCTGAATACTGT-GTGCATGGAATAATAGAATAGGACCTCGGTTCCATTTT
Megarcys             TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---CAATTGC-T-GCCTGAATATTGT-GTGCATGGAATAATGGAATAGGATCTCGGTTCTATTTT
Cultus               TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---CAATTGC-T-GCCTGAATATTGT-GTGCATGGAATAATGGAATAGGATCTCGGTTCTATTTT
Blaberus             TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---AGC-ATC-C-GCCTGAATACTGA-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Mantis               XXXXXXXXXXXXXXXTTAGAGTGCTTAAAGCAGGC---AGC-ATC-C-GCCTGAATACCGA-GTGCATGGAATAATGGAANAGGACCTCGGTTCTATTTT
Labidura             TTTACTTTGAACAAATTAGAGTGCTTAAAAGAGGC---AT---TA-T-GCCTGAATATTGT-GTGCATGGAATAATAGAATAAGACCTCGGTTCTATTTT
Melanoplus           TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---AA--GCC-C-NCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Anisomorpha          TTTACTTTGAACAAATTAGAGTGCTCCCACCAGGC---AGTGGCC-T-GCCTGAATATTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Oligotoma            TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---AGT-GCT-TAGCCTGAATGCTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Cerastipsocus        TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---CTTCAAT-T-GCC-GAAAACTGT-GTGCATGGAATAATATAATAGGACCGCGGTTCTATTTT
Dennyus              TTTACTTTGAACAAATTTGAGTGCTCAAAGCAGGC---ACGTGAACGGGCTTGAAAAATGT-GCGCATGGAATAATGGAATAGGACCGCGGTTCTATTTT
Acyrthosiphon        TTTACTTTGAACAAATTAGAGTGCTCAAAGCAGGC---TCGAATCIG-CCCTGAATACTGG-TCGCATGGAATAATGGAACAAGACCTCGGT;;;;;;;,
Buenoa               TTTACTTTGAACAAATTAGAGTGCTCAAAGCAGGC---TGAATTC-C-GCCTGGATA-TTG-TTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Saldula              TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TGAAT-C-CAGCCAGAATA-GTG-GTGCATGGAATAATAGAACAGGACCTTGGTTCTATTCT
Lygus                TTTACTTTGAACAAATTAGAGTGCTCAAAGCAGGC---TGAAATCTCTGCCTGAATA-GTG-GTGCATGGAATAATAAAACAGGACCTTGGTTCTATTTT
Taeniothrips         TTTACTTTGAACAAATTTGAGTGCTCCAAGCAGGA---TTTCT-C---GCCTGAAGA-TAA-GTGCATGGAATAATAGAATAGGACTTCGGTTCTATTTT
Priacma              TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TAAATTAAT-GCCTGAATAATTA-GTGCATGGAATAATAGAACAGGACCTTGGTTCTATTTT
Colpocaccus          TTTACTTTGAACAAATTAGAGTGCTCAAAGCAGGC---TAAATTAAT-GCCTGAATAATTA-GTGCATGGAATAATAGAACAGGACCTTGGTTCTATTTT
Cybister             TTTACTTTGAACAAATTAGAGTGCTCCAAGCAGGC---TAAAACTTC-GCCTGAATACTGT-GTGCATGGAATAATGGAACAGGACCTCGGTTCTATTTT
Xyloryctes           TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TAAAACTTT-GCCTGAATACTGT-GTGCATGGAATAATAGAATAGGACCTCGGTTCTATTTT
Octinodes            TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TAAAACTTC-GCCTGAATACAAT-CTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Photuris             GTTACTTTGAACAAATTAAAGTGCTTAAAGCAGGC---TAAAT-TCC-GCTCGCATACACG-C-GCATGGAATAATCGAATAGGACCTCCGTTCTATTTT
Meloe                TTTACTTTGAACAAATTAAAGTGCTTAAAGCAGGC---TAAAATTTT-GCCTGAATA-TGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Rhipiphorus          TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TAAAATTTT-GCCTGAATACTGT-GTGCATGGAATAATAGAATAGGACCTCGGTTCTATTTT
Tenebrio             TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TAAAACTTC-GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Tetraopes            TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TAAAATTTC-GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Corydalus            TTTACTTTGAAGAAATTAGAGTGCTTAAAGCAGGC---TAA-TTAAT-GCCTGAATAATTA-GTGCATGGAATAATAGAACAGGACCTTGGTTCTATTTT
Agulla               TTTACTTTGAAGAAATTAGAGTGCTTAAAGCAGGC---TAA-TTAAT-GCCTGAATAATTA-GTGCATGGAATAATAGAACAGGACCTTGGTTCTATTTT
Lolomyia             TTTACTTTGAGCAAATTAGAGTGCTTAAGGCAGGC---TAAAATTTC-GCCTGAATATTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Mantispa             TTTACTTTGAACAAATTAGAGTGCTTAAGGCAGGC---TAAAATTTT-GCCTGAATATTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Hemerobius           TTT-CTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TAAAATTTT-GCCTAAATATTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Chrysoperla          TTTACTTTGAACAAATTAGAGTGCTTAAGGCAGGC---TCAAATTTT-GCCTGAATATTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
M.immaculatus        TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---T>>>>>>>>-GCCTGAATATTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Myrmeleon            TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---T>>>>>>>>-GCCTGAATATTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Galleria             TTTACTTTGAACAAATTAGAGTGCTCAAAGCGGGC---CAAAATGCT-GCNTGAATATTTC-GTGCATGGAATAATAGAATATGATCTCGGTTCTATTTT
Papilio              TTTACTTTGAACAAATTAGAGTGCTCAAAGCGGGC---CAAAATGCG-GCCTGAATATTTC-GTGCATGGAATAATAGAATATGATCTCGGTTCTATTTT
Ascalapha            TTTACTTTGAACAAATTAGAGTGCTCAAAGCGGGC---CAAAATGCG-GCNTGAATATTTC-GTGCATGGAATAATAGAATATGATCTCGGTTCTATTTT
Hydropsyche          TTTACTTTGAACAAATTAGAGTGCTCAAACGGGGC---TGACTCTCG-GCCTGAATATTGT-GYGCATGGAATAATRGAATAGGACCTCGGTTCAATTTT
Pycnopsyche          TTTACTTTGAACAAATTAGAGTGCTCAAACGGGGC---TAACTCTCG-GCCTGAATATTGT-ACGCATGGAATAATAGAATAGGACCTCGGTTCAGTTTT
Oecetis              TTTACTTTGAACAAATTAGAGTGCTCAAACGGGGC---TAACACNCG-GCCTGAATATTGT-ACGCATGGAATAATAGAATAGGACCTCGGTTCTGTTTT
B.strigosus          TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TAATCTC---GCCTGTATATTAT-GTGCATGGAATAATAAAATAGGACCTCGGTGCTATTTT
B.chlorostigmus      TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TTATATTT--GCCTGAATATTAT-GTGCATGGAATAATAGAATAGGACCTCGGTTCTATTTT
Boreus               TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---AAATTTC---GCCTGAATATTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Merope               TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TAAATTTT--GCCTGAATATTCT-GTGCATGGAATAATGGAATAGGACCTCGTTTCTATTTT
Panorpa              TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TAATCTC---GCCTGTATATTGT-GTGCATGGAATAATAGAATAGGACCTCGTTTCTATTTT
Ctenocephalides      TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TNNNTC----GCCTGAATATTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Hystrichopsylla      TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TCATTT----GCCTGAATATTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Orchopeas            TTTACTTTGAACAAATTAGAGTGCTTAAAGCAG-C---TCATTC----GCCTGAATATTCT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Hartigia             TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TACCTTC---GCCTGAATACTGC-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Orussus              TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TGTCTTC---GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Hemitaxonus          TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TATTTTC---GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Peridista            TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TATTTTC---GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Bareogonalos         TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TATTTTC---GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Evania               TTTACTTTGAACAAATTAGAGTGCTCAAAGCAGGC---TAACTTT---GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Ichneumon            TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TAACTTC---GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Ophion               TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TATTTTC---GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Mesopolobus          TTTACTTTGAACAAATTAGAGTGCTCAAAGCAGGC---TATGTTC---GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Caenochrysis         TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TATCTTC---GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Epyris               TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TACTTTC---GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Priocnemus           TTTACTTTGAACAAATTAAAGTGCTTAAAGCAGGC---TACTCTC---GCCTGAATATTCT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Dasymutilla          TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TAGCCTC---GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Apoica               TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TAGCCTC---GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Monobia              TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TAGCTTC---GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
P fuscatus           TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TAGCCTC---GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
P.dominulus          TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TAGCCTC---GCCTGAATACTGT-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Camponotus           TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TACCTTC---GCCTGAATACTGC-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Chalepoxenus         CTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TATCCTC---GCCTGAATACTGC-GTGCATGGAA-AATGGAATAGGACCTCGGTTCTATTTT
Doronomyrmex         CTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TATCCTC---GCCTGAATACTGC-GTGCATGGAAAAATGGAATAGGACCTCGGTTCTATTTT
Harpagoxenus         TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TATCCTC---GCCTGAATACTGC-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Leptothorax          TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TATCCTC---GCCTGAATACTGC-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Temnothorax          TTTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TATCCTC---GCCTGAATACTGC-GTGCATGGAATAATGGAATAGGACCTCGGTTCTATTTT
Tipula               ATTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---CATTTGT---GCCTGAATATTCT-CTGCATGGAATAATGGAATAAGACGTCTGTTCTATTTT
Laphria              ATTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TTCAAAT---GCCTGAATATTTT-GTGCATGGAATAATGGAATAAGACCTCTGTTCTACTTT
Mythicomyia          ATTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TACAATT---GCCTGAATATTTT-GTGCATGGAATAATGGAATAAGACCTCTGTTCTACTTT
Drosophila           ATTACTTTGAACAAATTAGAGTGCTTAAAGCAGGC---TTCAAAT---GCCTGAATATTCT-GTGCATGGGATAATGAAATAAGACCTCTGTTCTGCTTT
Triozocera           ATTACTTTGAACAAATTAGAGTGCTTAAAGCAGGCAAATTTATAT---GCCTTGAATATCG-CAGCATGGAATAATAGAATATGATCTCGGTACCG~~~~
Caenocholax          ATTACTTTGAACAAATTAGAGTGCTTAAAGCAGGCAAATTTATAT---GCCTTGAATATCG-CAGCATGGAATAATAGAATATGATCTCGGTACCG~~~~
Elenchus             ATTACTTTGAACAAAXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Crawfordia           ATTACTTTGAACAAATTAGAGTGCTTAAAGCAGGCAAATTTATAT---GCCTTGAATATGATCAGCATGGAATAATAGAATATGATCTCGATACTG~~~~
X pecki              ATTACTTTGAAGAAATTAGAGTGCTTAAAGCAGGCAAATTTATAT---GCCTTGAATATAA-CAGCATGGAATAATAGAATATGATCTCGATACTG~~~~
X.vesparum           ATTACTTTGAACAAATTAGAGTGCTTAAAGCAGGCAAATTTAAAT---GCCTTGAATATAA-CAGCATGGAATAATAGAATATGATCTCGATACTG~~~~
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Hypogastrura         GTTGGCTTTCGGAG-T----C--GAGGTAATGATTAATAGGACAGAC-GGGGGCATTCGTACTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Trigoniopthalmus     GTTGGTTTTCGGAA-C----TT-GAGGTAATGATTAACAGAAACAGAC-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Ephemerella          GGGGGCTTTCTGAA-C----TC-GAGGTAATGATTAACAGGGACAGAC-GGGGGCATTCGTTTTGCGACGTTAGAGGTGAAATTCTTGGACCGTCCCAAG
Agrion               GTTGGTTTTCAGAA-C----TC-GAGGTAATGATTAATAGGGACGGAC-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Libellula            GTTGGTTTTCAGAA-C----TC-GAGGTAATGATTAATAGGGACGGAC-GGGGGCATTCGTATTGCGA-GTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Megarcys             GTTGGTTTTCTGAA-C----CA-GAGATAATGATTAATAGAGACTGAC-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Cultus               GTTGGTTTTCTGAA-C----CA-GAGATAATGATTAATAGAGACTGGC-GGGGGCATTGCTATTGCGAGCTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Blaberus             GTTGGTTTTCGGAATC----CCCGAGGTAATGATCAATAGGGACAGAC-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Mantis               GTTGGTTTTCGGAATC----CCCGAGGTAATGATCAATAGGGACAGAC-GGGGGCATTCGTATTTCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Labidura             GTTGGTTTTCTGAA-C----CA-GAGGTAATGATTGATAGGAACGGAC-GGGGGCATTCGTATTGAGAGCTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Melanoplus           GTTGGTTTTCGGAA-C----CC-GAGGTAATGATTAATAGGGACAGGC-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Anisomorpha          GTTGGTTTTCGGAA-C----TT-GAGGTAATGATTAATAGGGACAGAC-GGGGGCATTCGTATTNCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Oligotoma            GTTGGTTTTCGGAG-C----CC-GAGGTAATGATTAATAGGAACXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXGGTGAAATTCTTGGACCGTCGCAAG
Cerastipsocus        GTTGGTTTTCAGAA-T----CC-GAGGTAATGATTAATAGGGACTGGC-GGGGGCATTAGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Dennyus              GTTGGTTTACGGAATT---TCT-GCGGTAATGATTAATAGGGTCGGAC-GGGGGCATTGGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCNNAAG
Acyrthosiphon        ;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;GAGACGGGC-GGGGGCATTCGTACCGAGACGTTAGAGGTGAAATTCTTGGACCGTCTCGAG
Buenoa               GTTGGTTTTCGGAA-T----CC-GAGGTAATGATCAATATGGACAGAC-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Saldula              GTTGGTTTTCGGAA-T----CC-AAGGTAATGATCAATAAGGACAGAC-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Lygus                GTTGGTTTTAGGAA-T----CC-AAGGTAATGATCAATAAGGACAGAC-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Taeniothrips         GTTGGTTTTCGGAA-C----CA-GAAGCTTCGATTAATGGAGACAGGC-GGGGGCATTCGTATTACGACGTTAGAGGTGAAATTCTTGGACCGTCGTAAG
Priacma              GTTGGTTTTCGGAA-C----CCCAAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Colpocaccus          GTTGGTTTTCGGAA-C----CCCAAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Cybister             GTTGGTTTTAGGAA-C----CCCGAGGTAATGATTAATAGGAACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Xyloryctes           GTTGGTTTTCGGAA-C----TCCGAGGTAATGATTAATAGGAACGGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Octinodes            GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGAACGGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Photuris             GTTGGTTTTTGGAA-C---ACGCGAGGTAATGATCAATGGGGGCGGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Meloe                GTTGGTTT-AGGAA-C----AC-GAGGTAATGATTAATAGGAACGGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAG
Rhipiphorus          GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGAACGGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Tenebrio             GTTGGTTTTCGGAA-T----TTTGAGGTAATGATTAATAGGAACGGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Tetraopes            GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGAACGGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Corydalus            GTTGGTTTTCGGAA-C----CCCAAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Agulla               GTTGGTTTTCGGAA-C----CCCAAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Lolomyia             GTTGGTTTTCGGAA-C----TCCGAGGTAATGATTAATACGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Mantispa             GTTGGTTTTCGGAA-C----TCCGAGGTAATGATTAATACGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Hemerobius           GTTGGTTTTCGGAA-C----TCCGAGGTAATGATTAATACGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Chrysoperla          GTTGGTTTTCGGAA-C----TCCGAGGTAATGATTAATACGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
M.immaculatus        GTTGGTTTTCGGAA-GTTTTCCGAGGTAATGATTAATACGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Myrmeleon            GTTGGTTTTCGGAA-GTTTTCCGAGGTAATGATTAATACGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Galleria             GTTGGTTTTCAGAA-C----TCCGAGGTAATGATTAATAGGGATAACT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Papilio              GTTGGTTTTCAGAA-C----TCCGAGGTAATGATTAATAGGGATAACT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Ascalapha            GTTGGTTTTCAGAA-C----TCCGAGGTAATGATTAATAGGGANAACT-GGGGGCATGGTGAAATTCT-TGGATCGGTGAAATTCTTGGACCGTCGCAAG
Hydropsyche          GTTGGCTTTCTGAC-C----CCAGAGGTAATGATTAATAGGGACAACT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Pycnopsyche          GTTGGCTTTCTGAT-A----CCAGAGGTAATGATTAATAGGGACAACT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Oecetis              GTTGGCTTTCTGAT-A----CCAGAGGTAATGATTAATAGGGACAACT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
B.strigosus          GTTGGTTTTCGGAA-T----TCCGAGGTAATGATTAATAGAGACAACT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
B.chlorostigmus      GTTGGTTTTCGGAA-C---CCCCGAGGTAATGATTAATAGGGACAACT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Boreus               GTTGGTTTTCGGAA-C----TCCGAGGTAATGATTAATAGGGACAACT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Merope               GTTGGTTTTCGGAA-G----CTCGAGGTAATGATTAATAGGGACAACT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Panorpa              GTTGGTTTTCGGAA-T----TCCGAGGTAATGATTAATAGGGACAACT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Ctenocephalides      GTTGGTTTTCGGAA-T----TCCGAGGTAATGATTAATAGGGACAACT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Hystrichopsylla      GTTGGTTTTCGGAA-C----TCCGAGGTAATGATTAATAGGGACAACC-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Orchopeas            GTTGGTTTTCGGAA-C----TCCGAGGTAATGATTAATAGGGACAACT-GGGGGCATTCGTATTGCTACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Hartigia             GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Orussus              GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Hemitaxonus          GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Peridista            GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Bareogonalos         GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Evania               GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Ichneumon            GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Ophion               GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Mesopolobus          GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Caenochrysis         GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Epyris               GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Priocnemus           GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Dasymutilla          GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Apoica               GTTGGTTTTCGGAA-C----ACCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Monopia              GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
P fuscatus           GTTGGTTTTCGGAA-C----ACCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
P.dominulus          GTTGGTTTTCGGAA-C----TCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Camponotus           GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Chalepoxenus         GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Doronomyrmex         GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Harpagoxenus         GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGAGAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Leptothorax          GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCATATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Temnothorax          GTTGGTTTTCGGAA-C----CCCGAGGTAATGATTAATAGGGACAGAT-GGGGGCATTCGTATTGCGACGTTAGAGGTGAAATTCTTGGACCGTCGCAAG
Tipula               CATTGGTTTTTRGA-T----CAAGACGTAATGATTAATAGAAGCAGTT-GGGGGCATTAGTATTACGGCGCGAGAGGTGAAATTCTTGGACCGTCGTAAG
Laphria              CATTGGTTTTTAGA-T----CAAGAGGTAATGATTAATAGAAGCAGTT-GGGGGCATTAGTATTACGACGCGAGAGGTGAAATTCTTGGACCGTCGTAAG
Mythicomyia          CATTGGTTTTTAGA-T----CAAGAGGTAATGATTAATAGAAGCAGTT-GGGGGCATTAGTATTACGACGCAGAGGGTGAAATTCTTGGACCGTCGTAAG
Drosophila           CATTGGTTTTCAGA-T----CAAGAGGTAATGATTAATAGAAGCAGTTTGGGGGCATTAGTATTACGACGCGAGAGGTGAAATTCTTGGACCGTCGTAAG
Triozocera           ~~~~~~~~~~~~~~~~~~~~ATCGAGATAATGATTAATAGAGACGGAT-GGGGGCATTCGTACTACGACGCTAGAGGTGAAATTCTTGGACCGTCGTAAG
Caenocholax          ~~~~~~~~~~~~~~~~~~~~ATCGAGATAATGATTAATAGAGACGGAT-GGGGGCATTCGTACTACGACGCTAGAGGTGAAATTCTTGGACCGTCGTAAG
Elenchus             XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXGGTGAAATTCTTGGACCGTCGTAAG
Crawfordia           ~~~~~~~~~~~~~~~~~~~~ATCGAGATAATGATCAATAGAGACGGAT-GGGGGCATTCGTACTACGACGCTAGAGGTGAAATTCTTGGACCGTCGTAAG
X.pecki              ~~~~~~~~~~~~~~~~~~~~ATCGAGATAATGATCAATAGAGACGGAT-GGGGGCATTCGTACTACGAGGCTAGAGGTGAAATTCTTGGACCGTCGTAAG
X.vesparum           ~~~~~~~~~~~~~~~~~~~~ATCGAGATAATGATCAATAGAGACGGAT-GGGGGCATTCGTACTACGACGCTAGAGGTGAAATTCTTGGACCGTCGTAAG
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Hypogastrura        ACGAACTACTGCGAAAGCATTTGCCAAGAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Trigoniopthalmus    ACGGGCTAGTGCGAAAGCATTTGCCAAGAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Ephemerella         ACGGACCGATGCGAAAGCGTTTGCCAAGAATGTTTTCGC-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATTAGATACCGCCCTAGTTCTAACCAT
Agrion              ACGAACCGATGCGAAAGCATTTGCCAAGAACGTTTTCGT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Libellula           ACGAACCGATGCGAAAGCATTTGCCAAGAACGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Megarcys            ACGAACATAAGCGAAAGCATTTGCCAAGAAAGCTTTCTT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Cultus              ACGAACATAAGCGAAAGCATTTGCCAAGAAAGCTTTCGT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Blaberus            ACGGACCGAAGCGAAAGCATTTGCCAAGAATGTTTTCTC-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Mantis              ACGGACCGAAGCGAAAGCATTTGCCAAGAATGTTTTCTC-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Labidura            ACGGACAGAAGCGAAAGCATTTGCCAAGAACGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Melanoplus          ACGAAGCGAAGCGAAAGCATTTGCCAAGTATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Anisomorpha         ACGAACCTAAGCGAAAGCATTTGCCATGAGTGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Oligotoma           ACGGACCTAAGCCAAAGCATTTGCCAAGAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Cerastipsocus       ACGAACCTAAGCGAAAGCATTTGCCAAGGATGCTTCCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Dennyus             ACGAACGAAAGCGAAAGCATTTGCCAAGAACGCTTTCAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTGACCGT
Acyrthosiphon       ACGAACTGACGCGAAAGCATTTGCCAAGTACGTTCTCGTATGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACTGT
Buenoa              ACGGACTAGAGCGAAAGCATTTGCCAAGTATGTCTTAGT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Saldula             ACGTACTAAAGCGAAAGCATTTGCCAAGAATGTCTTAAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Lygus               ACGACCGAGAGCGAAAGCATTTGCCAAGTATGTCTTGAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Taeniothrips        ACGAACTGAAGCGAAAGCATTTGCCAAGGATGTTCTCGT-TGATCAAGAACGAAAGTCAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTGACCAT
Priacma             ACGGACTAAAGCGAAAGCATTTGCCAAAGATGTTTTCAT-TAATCAAGAACGAAAGTCAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTGACCAT
Colpocaccus         ACGGACTAAAGCGAAAGCATTTGCCAAAGATGTTTTCAT-TAATCAAGAACGAAAGTCAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTGACCAT
Cybister            ACGGACTAAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTCAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTGACCAT
Xyloryctes          ACGGACTAAAGCGAAAGCATTTGCCAAAAACGCTTTCAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGTCCTAGTTCTAACCAT
Octinodes           ACGGAGAGTAGCGAAAGCATTTGCCAAAAACGCTTTCAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Photuris            CAAGACTTAAGCGAAAGCATTTGCCAAAAACGCTTTCAT-CGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Meloe               ACGAACATAAGCGAAAGCATTTGCCAAAAACGTTTTCAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Rhipiphorus         ACGGAGAGTAGCGAAAGCATTTGCCAAAAACGCTTTCAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Tenebrio            ACGGACAAAAGCGAAAGCATTTGCCAAAAACGCTTTCAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Tetraopes           CAAGACAGAAGCGAAAGCATTTGCCAAAAACGCTTTCAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Corydalus           ACGGACTAAAGCGAAAGCATTTGCCAAAGATGTTTTCAT-TAATCAAGAACGAAAGTCAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTGACCAT
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Lolomyia            ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTGAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Mantispa            ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTGAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Hemerobius          ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTGAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Chrysoperla         ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTGAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
M.immaculatus       ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTGAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Myrmeleon           ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTGAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Galleria            ACGAACATCAGCGAAAGCATTTGCCAAAGGTGTTTTCAT-CAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATTAGATACCGCCCTAGTTCTAACCGT
Papilio             ACGAACATCAGCGAAAGCATTTGCCAAAGGTGTTTTCAT-CAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATTAGATACCGCCCTAGTTCTAACCGT
Ascalapha           ACGAACATCAGCGAAAGCATTTGCCAAAGGTGTTTTCAT-CAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATTAGATACCCGCCTAGTTCTAACCGT
Hydropsyche         ACGGACTAAAGCGAAAGCATTTGCCAAAGGTGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATTAGATACCGCTGTAGTTCTAACCAT
Pycnopsyche         ACGGACTAAAGCGAAAGCATTTGCCAAAGGTGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATTAGATACCGCTGTAGTTCTAACCAT
Oecetis             ACGGACTAAAGCGAAAGCATTTGCCAAAGGTGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATTAGATACCGCTGTAGTTCTAACCAT
B.strigosus         ACGTACATAAGCGAAAGCATTTGCCAAATGTGTTTTCAT-CAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
B.chlorostigmus     ACGGACAGAAGCGAAAGCATTTGCCAAATGTGTTTTCAT-CAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
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Merope              ACGTACAGAAGCGAAAGCATTTGCCAAATGTGTTTTCAT-CAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Panorpa             ACGGACAGAAGCGAAAGCATTTGCCAAATGTGTTTTCAT-CAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Ctenocephalides     ACGGACAGAAGCGAAAGCATTTGCCAAATGTGTTTTCAT-CAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Hystrichopsylla     ACGGACAGAAGCGAAAGCATTTGCCAAATGTGTTTTCAT-CAATCAAGAACGAAAGTTAGAGGCTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Orchopeas           ACGGACAGAAGCGAAAGCATTTGCCAAATGTGTTTTCAT-CAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Hartigia            ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGANACCGCCCTAGTTCTAACCAT
Orussus             ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Hemitaxonus         ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCTT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Peridista           ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCTT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Bareogonalos        ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Evania              ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Ichneumon           ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Ophion              ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Mesopolobus         ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Caenochrysis        ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Epyris              ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Priocnemus          ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Dasymutilla         ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Apoica              ACGAACGGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Monobia             ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
P.fuscatus          ACGAACTGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
P.dominulus         ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Camponotus          ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Chalepoxenus        ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Doronomyrmex        ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Harpagoxenus        ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Leptothorax         ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Temnothorax         ACGGACAGAAGCGAAAGCATTTGCCAAAAATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Tipula              ACTAACATAAGCGAAAGCATTTGCCAAAGATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Laphria             ACTAACTTAAGCGAAAGCATTTGCCAAAGATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Mythicomyia         ACTAACTTAAGCGAAAGCATTTGCCAAAGATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Drosophila          ACTAACTTAAGCGAAAGCATTTGCCAAAGATGTTTTCAT-TAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Triozocera          ACGAACTGAAGCGAAAGCGTTTGTCAAAAACGTTTTCAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Caenocholax         ACGAACTGAAGCGAAAGCGTTTGTCAAAAACGTTTTCAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
Elenchus            ACGAACTGAAGCGAAAGCGTTTGTCAAAAATGTTTTCAT-TGATCAAGAACGAAAGTTAGAGGCTCGAAGACGATTAGATACCGTCCTAGTTCTAACCAT
Crawfordia          ACGAACTGAAGCGAAAGCGTTTGTCAAAAACGTTTTCAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
X.pecki             ACGAACTGAAGCGAAAGCGTTTGTCAAAAACGTTTTCAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
X.vesparum          ACGAACTGAAGCGAAAGCGTTTGTCAAAAACGTTTTCAT-TGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCAT
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Hypogastrura	AAACGATGTCGACCGGCGATCCGTCGTCGTTAATATTA-AT-GA-CTCGACGGGCAGCCT-CCGGGAAACCAGAGTGTTTGGATTCCAGGGGGAGTATGG
Trigoniopthalmus	AAACGATGCCAGCCAGCGATCCGCCGAAGTTCCT-CCA-AT-GA-CTCGGCGGGCGGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Ephemerella	AAACGATGTCAGCCAGCGATGCGCCGATGTTCCT-CCG-AT-GA-CACGGCGCGCAACTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Agrion	AAACGATGCCAGCTAGCCATCCGCCGAAGTTCCT-TCT-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTCTTGGGTTCCGGGGGAAGTATGG
Libellula	AAACGATGCCAGCCAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTCTTGGGTTCCGGGGGAGGTATGG
Megarcys	AAACGATGCCAACTAGCGATCCGCCGGTGTTCCT-CCG-AT-GA-CCCGGCGGGCAGCTT-CCGGGAAACCAAAGTGTTTGGGTTXXXXXXXXXXXNNGG
Cultus	AAGCGATTACCTCCGGTGTTCCGCCGATGATCCG-NNN-AT-GA-CCCGACGGGCXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Blaberus	AAACGATGCCAGCCAGCAATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Mantis	AAACGATGCCAGCCAGCAATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Labidura	AAACGATGCCAGCCAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTTAGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Melanoplus	AATCGATGCCAGCCAGCGATCCGCCGCAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCCT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Anisomorpha	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCXXXXXXXXXXXXXXXXXXXXXXXX
Oligotoma	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Cerastipsocus	AAACGATGCCAGCCAGCGATCCGTCGACGTTCCT-TTT-AT-GA-CTCGACGGGCAGCTT-CCGGGAAACTAAAGCATTTGGGTTCCGGGGGAAGTATGG
Dennyus	AAACGATGCCAGCTGGCGATCCGTCGTTGTTCCT-TGG-AT-GA-CTCGACGGGCAGCCT-CCGGGAAACCAAAGCGTTTGGGTTCCGGGGGTAGTATGG
Acyrthosiphon	AAACGATGCCAGCTAGCGATCCGCCGGCGTTTCA-TTA-AC-GA-CCCGGCGGGCAGCTT-CCGGGAAACCGAAGCTTTTCGGTTCCGGGGGAAGTATGA
Buenoa	AAACGATGCCAGCCAGCGATCCGCCGATGTTCCT-CCG-AT-AG-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Saldula	AAACGATGTCAGCCAGCGATCCGCCGACGTTCAT-TGA-AT-GG-CTCGGCGGGCAGCTT-CCCGGAAACGAAAGCTTTCGGGTTCCGGGGGAAGTATGG
Lygus	AAACGATGCCAGCCAGCGATCCGCCGATGTTCCT-CCG-AT-GA-CTCGGCGGGGAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Taeniothrips	AAACGATGTCAACTAGCAATTTGCCCAAGGTTCT-CTG-AT-GC-CTGGGCAAGCGGCTT-CCGGGAAACCAAAGTTTTTCGATTCCGGGGGAAGTATGG
Priacma	AAACGATGCCAGCTAGCGATCCGCCAAAGTTCCT-CCG-AT-GA-CTTGGCGGGTAGCTT-TCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Colpocaccus	AAACGATGCCAGCTAGCGATCCGCCAAAGTTCCT-CCG-AT-GA-CTTGGCGGGTAGCTT-TCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Cybister	AAACGATGCCAGCTAGCGATCCGCCGACGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Xyloryctes	AAACGATGCCAGCTAGCGATCCGCCGTCGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Octinodes	AAACGATGCCAGCTAGCGATCCGCCGACGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Photuris	AAACTATGCCAGCTAGCGATCCGCCGAAGTTACT-TCT-AC-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTCGGGTTCCGGGGGAAGTATGG
Meloe	AAACGATGCCAGCCAGCGATCCGCCGATGTTCCT-CCG-AT-GA-CTCGGCGGGGAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Rhipiphorus	AAACGATGCCAGCTAGCGATCCGCCGACGTTCCT-CAT-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Tenebrio	AAACGATGCCAGCTAGCGATCCGCCGACGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Tetraopes	AAACGATGCCAGCTAGCGATCCGCCGACGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Corydalus	AAACGATGCCAGCTAGCGATCCGCCAAAGTTCCT-CCG-AT-GA-CTTGGCGGGTAGCTT-TCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Agulla	AAACGATGCCAGCTAGCGATCCGCCAAAGTTCCT-CCG--T-GA-CTTGGCGGGTAGCTT-CGGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Lolomyia	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCTT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Mantispa	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Hemerobius	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCGTTTGGGTTCCGGGGGAAGTATGG
Chrysoperla	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT--CG-AT-GA-CTCGGCGGGCAGCXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
M.immaculatus	AAACGATGCCAGCTAGCGATCCGCCAAAGTTCCT-CCG-AT-GA-CTTGGCGGGCAGCTT-CCGGGAAACCAAAGCATTTGGGTTCCGGGGGAAGTATGG
Myrmeleon	AAACGATGCCAGCTAGCGATCCGCCAAAGTTCCT-CCG-AT-GA-CTTGGTGGGCAGCXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Galleria	AAATNATGTCATCTAGCGATCCGCCGACGTTACT-ACA-AT-GG-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGATTTTGGTCTCCGGGGGA-GTATGG
Papilio	AAATNATGTCATCTAGCGATCCGCCGACGTTACT-ACT-AT-GG-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGATTTTGGACTCCGGGGGA-GTATGG
Ascalapha	AAATNATGTCATCTAGCGATCCGCCGACGTTACT-ACA-AT-GG-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGATTTTGGTCTCCGGGGGA-GTATGG
Hydropsyche	AAATGATGCCAGCTAGCGATCCGCCGAAGTTCCT-TCG-AT-TAACCCGGTGGGCAGCTC-CCGGGAAACCAAAGCTTTCGGGCTCCGGGGGCAGTATGG
Pycnopsyche	AAATGATGCCAGCCAGCGATCCGCCGAAGTTTCT-TAATTT-TAACCCGGTGGGCAGCTC-CCGGGAAACCAAAGCTTTCGGGCTCCGGGGGCAGTATGG
Oecetis	AAATGATGCCAGCCAGCGATCCGCCGAAGTTTCT-TAATCT-TAACCCGGTGGGCAGCTC-CCGGGAAACCAAAGCTTTCGGGCTCCGGGGGCAGTATGG
B.strigosus	AAACGATGCCAACTAGCGATCCGCCGAAGTCCCT-ATG-TT-GA-CTCGGTGGGCAGCTT-CTGGGAAACCAAAGTTTTTGGGTTCCGGGGGAAGTATGG
B.chlorostigmus	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT--CG-AT-GA-CTCGGCGGGCAGCXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Boreus	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Merope	AAACGATGCCAGCTAGCGATCTGCGCACGTTCCT-CCG-AT-GA-CTCGGTAGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Panorpa	AAACGATGCCAGCTAGCGATCCGCCAAAGTTCCT-CCG-AT-GA-CTTGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Ctenocephalides	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Hystrichopsylla	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT--CG-AT-GA-CTCGGCGGGCAGCXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Orchopeas	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Hartigia	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CNG-AT-GA-CTCGGCGGGCAGCXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Orussus	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CNG-AT-GA-CTCGGCGGGCAGCXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Hemitaxonus	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Peridista	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Bareogonalos	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Evania	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CNG-AT-GA-CTCGGCGGGCAGCXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Ichneumon	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Ophion	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Mesopolobus	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Caenochrysis	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Epyris	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Priocnemus	AAACGATGCCAGCCAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Dasymutilla	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Apoica	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCT-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Monobia	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
P.fuscatus	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
P.dominulus	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGACGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Camponotus	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Chalepoxenus	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Doronomyrmex	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Harpagoxenus	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Leptothorax	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGG
Temnothorax	AAACGATGCCAGCTAGCGATCCGCCGAAGTTCCT-CCG-AT-GA-CTCGGCGGGCAGCTT-CCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAACTATGG
Tipula	AAACGATGCCAGCTAGCAATTGGATGGAGCTACT-TAT-AT-GG-CTCTTTCAGTCGCTTTCCGGGAAACCAAAGCTTTTGGGCTCCGGGGGAAGTATGG
Laphria	AAACGATGCCAGCTAGCAATTGGGTGTAGCTACT-ACT-AT-GG-CTTTCTCAGTCGCTTCCCGGGAAACCAAAGCTTTTGGGCTCCGGGGGAAGTATGG
Mythicomyia	AAACGATGCCAGCTAGCAATTGGGTGTAGCTACT-TTT-AT-GG-CTTTCTCAGTCGCTTCCCGGGAAACCAAAGCTTTTGGGCTCCGGGGGAAGTATGG
Drosophila	AAACGATGCCAGCTAGCAATTGGGTGTAGCTACT-TTT-AT-GG-CTCTCTCAGTCGCTT-CCGGGAAACCAAAGCTTTTGGGCTCCGGGGGAAGTATGG
Triozocera	AAACGATGCCGACTAGCGATCCGTCGATGTTCAT-TTAAATTGA-CTCGACGGGCAGCTT-CCGGGAAACCAAAGTTTTTGGGTTCCGGGGGAAGTATGG
Caenocholax	AAACGATGCCGACCAGCGATCCGYCGATGTTCAT-TTAAATTGA-CTCGACGGGCAGCTT-CCGGGAAACCAAAGTTTTTGGGTTCCGGGGGAAGTATGG
Elenchus	AAACTATGCCGACTAGTGATCCGTCGATGTTCAT-TTAAATTGA-CTCGACGGGCAACTT-CCGGGAAACCAAAGTTTTTAGGTTCCGGGGGAAGTATGG
Crawfordia	AAACGATGCCGACCAGCGATCCGTCGATGTTCAT-TTAAATTGA-CTCGACGGGCAGCTT-CCGGGAAACCAAAGTTTTTGGGTTCCGGGGGAAGTATGG
X.pecki	AAACGATGCCGACCAGCGATCCGTCGATCTTCAT-TCAAATTGA-CTCGACGGGCAGCTT-CCGGGAAACCAAAGTTTTTGGGTTCCGGGGGAAGTATGG
X.vesparum	AAACGATGCCGACCAGCGATCCGTCGATGTTCAT-TCAAATTGA-CTCGACGGGCAGCTT-CCGGGAAACCAAAGTTTTTAGGTTCCGGGGGAAGTATGG

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Hypogastrura	TTGCAAAGCTGAAACTTAAAAGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAATCTCACCAGGCCCGGA
Trigoniopthalmus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Ephemerella	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Agrion	TTGCAAAGCTCAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGGTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Libellula	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTTACCAGGCCCAGA
Megarcys	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Cultus	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Blaberus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Mantis	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Labidura	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Melanoplus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Anisomorpha	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Oligotoma	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Cerastipsocus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGCGCACCACCAGGAGTGCAGCCTGCGGCTTAATTTGACTCAACACGGGAAATCTCACCAGGCCCAGA
Dennyus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCTTGCGGCTTAATTTGACTCAACACGGGAAAACTCACCAGGCCCAGA
Acyrthosiphon	TTGCAAAGTTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCGCCAGGCCCGGA
Buenoa	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Saldula	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Lygus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCAGGA
Taeniothrips	TTGCAAAGCTGAAACXXXXXXXXXXXXXXXXXXXXXXXCCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAATCTCACCAGGCCCGGA
Priacma	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Colpocaccus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Cybister	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGTTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Xyloryctes	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Octinodes	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Photuris	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Meloe	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Rhipiphorus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCG-CTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Tenebrio	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Tetraopes	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Corydalus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Agulla	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Lolomyia	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Mantispa	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Hemerobius	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Chrysoperla	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
M immaculatus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Myrmeleon	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Galleria	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAATCTCACCAGGCCCGGA
Papilio	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAATCTCACCAGGCCCGGA
Ascalapha	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAATCTCACCAGGCCCGGA
Hydropsyche	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTNACCAGGCCCAGA
Pycnopsyche	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTCGACTCAACACGGGAAAACTCACCAGGCCCGGA
Oecetis	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAAACTCACCACGCCCRGA
B.strigosus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
B.chlorostigmus	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Boreus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTTACCAGGCCCAGA
Merope	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Panorpa	TTGCAAAGTTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Ctenocephalides	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACTACAAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGTCCGGA
Hystrichopsylla	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Orchopeas	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGATCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGGAACCTCACCAGGCCCAGA
Hartigia	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Orussus	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Hemitaxonus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Peridista	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Bareogonalos	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Evania	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Ichneumon	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Ophion	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Mesopolobus	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Caenochrysis	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Epyris	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Priocnemus	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Dasymutilla	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCCGA
Apoica	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Monobia	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
P.fuscatus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTG-AGC-TGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
P.dominulus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA
Camponotus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Chalepoxenus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Doronomyrmex	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Harpagoxenus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Leptothorax	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Temnothorax	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCAGA
Tipula	TTGCAAAGCTTAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCTTGCGGCTTAATTTGACTCAACACGGGGAAACTTACCAGGTCCGAA
Laphria	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAAACTTACCAGGTCCGAA
Mythicomyia	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAAACTTACCAGGTCCGAA
Drosophila	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAAACTTACCAGGTC-GAA
Triozocera	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCTTGCGGCTTAATTTGACTCAACACGGGAAATCTCACCAGGCCCGGA
Caenocholax	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGTACCACCAGGAGTGGAGCTTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGTCAGGA
Elenchus	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCTTGCGGCTTAATTTGACTCAACACGGGAAATCTCACCAGGCCCAGA
Crawfordia	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCTTGCGGCTTAATTTGACTCAACACGGGAAATCTCACCAGGCCCGGA
X.pecki	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCTTGCGGCTTAATTTGACTCAACACGGGAAATCTCACCAGGCCCGGA
X.vesparum	TTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCTTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCCGGA

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Hypogastrura	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTCAGGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Trigoniopthalmus	CACTGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-AGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Ephemerella	CATCGGAAGGTTTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGCGCGAXXXXXXXXXXXXXXXXXX
Agrion	CACCGGTAGGATTGACAGAATAAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGG-GCGATTTGTCTGGTTAATTCCG
Libellula	CACCGGTAGGATTGAC-GATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGG-GCGATTTGTCTGGTTAATTCCG
Megarcys	CACTGGAAGGATTGACAGATTGATAGCTCTTTCTTGATTC-AGTGGATGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Cultus	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Blaberus	CACCGGGAGGATTGACAGATTGATAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Mantis	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Labidura	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAACGATTTGTCTGGTTAATTCCG
Melanoplus	CACCGGAAGGATTGACAGATTGATAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Anisomorpha	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Oligotoma	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Cerastipsocus	CACCAGGTGGATTGACAGATTGAGAGCTCTTTCTTGATTT-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Dennyus	CACTGAGAGGATTGACGGATTGACAGCTCTTTCTTGATTC-AGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATCCCX
Acyrthosiphon	CACCGGAAAGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATCTGTCTGGTTAATTCCG
Buenoa	CATTGGAAGGATTGACAGATTGATAGCTCTTTCTTGATTC-AGTGGGTAGTGGTGCATGGCCGTTCTTAGTTGGTGGAACGATTTGTCTGGTTAATTCCG
Saldula	CATTGGAAGGATTGACAGATTGATAGCTCTTTCTTGATTC-AGTGGGTAGTGGTGCATGGCCGTTCTTAGTTGGTGGAACGATTTGTCTGGTTAATTCCG
Lygus	CATTGGAAGGATTGACAGATTGATAGCTCTTTCTTGATTC-AGTGGGTAGTGGTGCATGGCCGTTCTTAGTTGGTGGATCGATTTGTCTGGTTAATTCCG
Taeniothrips	CACTGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-AGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Priacma	CACTGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-AGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Colpocaccus	CACTGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-AGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Cybister	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Xyloryctes	CACCGGAAGGATTGACAGATTGACAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Octinodes	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Photuris	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Meloe	CACTGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-AGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Rhipiphorus	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Tenebrio	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Tetraopes	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Corydalus	CACTGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-AGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Agulla	CACTGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-AGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Lolomyia	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Mantispa	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGTTTAATTCCG
Hemerobius	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Chrysoperla	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
M.immaculatus	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Myrmeleon	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Galleria	CACCGGAAGGATTGACAGATTAACAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Papilio	CACCGGAAGGATTGACAGATTAACAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Ascalapha	CACCGGAAGGATTGACAGATTAACAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Hydropsyche	CACYGGAAGGATTGACAGATTGACAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGYGATTTGTCTGGTTAATTCCG
Pycnopsyche	CACTGGAAGGATTGACGGATTAACAGCTCTTTCTCGATTC-GGTGGGTGGTGGTGCATGGCCGCTCTTAGTTGGTGGAGCGATTTGTCAGGTTAATTCCG
Oecetis	CACTGGAAGGATTGACRGATTAACAGCTCTTTCTCGATTC-GGTGGGTGGTGGTGCATGGCCGCTCTTAGTTGGTGGAGCGATTTGTCAGGTTAATTCCG
B.strigosus	CACTGGAAGGATTGACAGATTAAGAGCTCTTTCTTGATTC-AGTGGTTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGTGATTTGTCTGGTTAATTCCG
B.chlorostigmus	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Boreus	CACTGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGYGATTTGTCWGGTTAATTCCG
Merope	CACTGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-AGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Panorpa	CACTGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-AGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Ctenocephalides	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Hystrichopsylla	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Orchopeas	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGAGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATCTGTCTGCTTTATTCCG
Hartigia	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Orussus	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Hemitaxonus	CACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Peridista	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Bareogonalos	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Evania	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Ichneumon	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Ophion	CACCGGAAGGATTGACAGATTGACAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Mesopolobus	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Caenochrysis	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Epyris	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Priocnemus	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
Dasymutilla	CACCGGAAGGATTGACAGATTGATAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Apoica	CACCGGAAGGATTGACAGATTGATAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Monobia	CACCGGAAGGATTGACAGATTGATAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
P.fuscatus	CACCG-AA-GATTGACAGATTGATAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
P.dominulus	CACCGGAAGGATTGACAGATTGATAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Camponotus	CACCGGAAGGATTGACAGATTGATAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Chalepoxenus	CACCGGAAAGATTGACAGATTGATAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Doronomyrmex	CACCGGAAAGATTGACAGATTGATAGCTCTTCCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTGTGGTTAATTCCG
Harpagoxenus	CACCGGAAGGATTGACAGATTGATAGCTCTTCCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTGTGGTTAATTCCG
Leptothorax	CACCGGAAGGATTGACAGATTGATAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Temnothorax	CACCGGAAGGATTGACAGATTGATAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Tipula	CATAAATGAGTAAGACAGATTAATAGCTCTTTCTCGAATC-TATGGGTGGTGGTGCATGGCCGTTCTTAGTTCGTGGAGTGATTTGTCTGGTTAATTCCG
Laphria	CATAAATGAGTAAGACAGATTGATAGCTCTTTCTCGAATC-TATGGGTGGTGGTGCATGGCCGTTCTTAGTTCGTGGAGTGATTTGTCTGGTTAATTCCG
Mythicomyia	CATAAATGAGTAAGACAGATTGATAGCTCTTTCTCGAATC-TATGGGTGGTGGTGCATGGCCGTTGTTAGTTCGTGGAGTGATTTGTCTGGTTAATTCCG
Drosophila	CATAAGTGTGTAAGACAGATTGATAGCTCTTTCTCGAATC-TATGGGTGGTGGTGCATGGCCGTTCTTAGTTCGTGGAGTGATTTGTCTGGTTAATTCCG
Triozocera	CACCGAAAGGATTGACAGATTAATAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Caenocholax	CACTGATAGGATTGACAGATTGATAGCTCTTTCTTGATTC-AGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
Elenchus	CACCGAAAGGATTAACAGATTAATAGCTCTTTTTTAATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCTATCTGTCTGGTTAATTCCG
Crawfordia	CACCGAAAGGATTGACAGATTAATAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
X.pecki	CACCGAAAGGATTGACAGATTAATAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG
X.vesparum	CACCGAAAGGATTGACAGATTAATAGCTCTTTCTTGATTC-GGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCG

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	18S bi
Hypogastrura	ATAACGAACGAGACTC
Trigoniopthalmus	ATAACGAACGAGACTC
Ephemerella	XXXXXXXXXXXXXXXX
Agrion	ATAACGAACGAGACTC
Libellula	ATAACGAACGAGACTC
Megarcys	ATAACGAACGAGACTC
Cultus	XXXXXXXXXXXXXXXX
Blaberus	ATAACGAACGAGACTC
Mantis	ATAACGAACGAGACTC
Labidura	ATAACGAACGAGACTC
Melanoplus	ATAACGAACGAGACTC
Anisomorpha	ATAACGAACGAGACTC
Oligotoma	ATAACGAACGAGACTC
Cerastipsocus	ATAACGAACGAGACTC
Dennyus	XXXXXXXXXXXXXXXX
Acyrthosiphon	ATAACGAACGAGACTC
Buenoa	ATAACGAACGAGACTC
Saldula	ATAACGAACGAGACTC
Lygus	ATAACGAACGAGACTC
Taeniothrips	ATAACGAACGAGACTC
Priacma	ATAACGAACGAGACTC
Colpocaccus	ATAACGAACGAGACTC
Cybister	ATAACGAACGAGACTC
Xyloryctes	ATAACGAACGAGACTC
Octinodes	ATAACGAACGAGACTC
Photuris	ATAACGAACGAGACTC
Meloe	ATAACGAACGAGACTC
Rhipiphorus	ATAACGAACGAGACTC
Tenebrio	ATAACGAACGAGACTC
Tetraopes	ATAACGAACGAGACTC
Corydalus	ATAACGAACGAGACTC
Agulla	ATAACGAACGAGACTC
Lolomyia	ATAACGAACGAGACTC
Mantispa	ATAACGAACGAGACTC
Hemerobius	ATAACGAACGAGACTC
Chrysoperla	XXXXXXXXXXXXXXXX
M.immaculatus	ATAACGAACGAGACTC
Myrmeleon	XXXXXXXXXXXXXXXX
Galleria	ATAACGAACGAGACTC
Papilio	ATAACGAACGAGACTC
Ascalapha	ATAACGAACGAGACTC
Hydropsyche	ATAACGAACGAGACTC
Pycnopsyche	ATAACGAACGAGACTC
Oecetis	ATAACGAACGAGACTC
B.strigosus	ATAACGAACGAGACTC
B.chlorostigmus	XXXXXXXXXXXXXXXX
Boreus	ATAACGAACGAGACTC
Merope	ATAACGAACGAGACTC
Panorpa	ATAACGAACGAGACTC
Ctenocephalides	ATAACGAACGAGACTC
Hystrichopsylla	XXXXXXXXXXXXXXXX
Orchopeas	ATAACGAACGAGACTC
Hartigia	XXXXXXXXXXXXXXXX
Orussus	XXXXXXXXXXXXXXXX
Hemitaxonus	ATAACGAACGAGACTC
Peridista	XXXXXXXXXXXXXXXX
Bareogonalos	XXXXXXXXXXXXXXXX
Evania	XXXXXXXXXXXXXXXX
Ichneumon	XXXXXXXXXXXXXXXX
Ophion	ATAACGAACGAGACTC
Mesopolobus	XXXXXXXXXXXXXXXX
Caenochrysis	XXXXXXXXXXXXXXXX
Epyris	XXXXXXXXXXXXXXXX
Priocnemus	XXXXXXXXXXXXXXXX
Dasymutilla	ATAACGAACGAGACTC
Apoica	ATAACGAACGAGACTC
Monobia	ATAACGAACGAGACTC
P.fuscatus	ATAACGAACGAGACTC
P.dominulus	ATAACGAACGAGACTC
Camponotus	ATAACGAACGAGACTC
Chalepoxenus	ATAACGAACGAGACTC
Doronomyrmex	ATAACGAACGAGACTC
Harpagoxenus	ATAACGAACGAGACTC
Leptothorax	ATAACGAACGTGACTC
Temnothorax	ATAACGAACGAGACTC
Tipula	ATAACGAACGAGACTC
Laphria	ATAACGAACGAGACTC
Mythicomyia	ATAACGAACGAGACTC
Drosophila	ATAACGAACGAGACTC
Triozocera	ATAACGAACGAGACTC
Caenocholax	ATAACGAACGAGACTC
Elenchus	ATAACGAACGAGACTC
Crawfordia	ATAACGAACGAGACTC
X.pecki	ATAACGAACGAGACTC
X.vesparum	ATAACGAACGAGACTC

```
INSERT 1 ^^^
Acyrthosiphon  GGACGGTGCC GGACCACCCT GGCGGTCCGT CGTGTCGCGG CCGGCCGTGT CGCGGGACCA


INSERT 2 === Diptera
Tipula         TACAACCG-TAACTG-GGTTCGTACATCATCTTGA
Laphria        TACAACTATTAATATTGGTTTGTACATTACCTT-A
Mythicomyia    TACACCTA-AAATATTGGTTCGTACATTACCTTTT
Drosophila     TACAACTTACAATTGTGGTTAGTACTATACCTTTA


INSERT 3 ``` Strepsiptera
Triozocera     -TCG-TTCGTAATTT-AATTTGCGTGGTTTGA---CAT-T-T-TT
Caenocholax    -ATT-CCCGCGATTT-TATTCGTGTGGTTTTT-GTTAT-T-TAAT
Elenchus       -TCGTTTAGTAATTTAAATATATTAAATTTGA-GTGACAATT-TT
Crawfordia     CTCG-CTCGTAATTT-AATTTATGCAGTTTGATTTGAC-A-T-TT
X.pecki        -TCG-CTCGTAATTT-AATTTATGTAGTTTGATTTGAC-A-T-TT
X vesparum     -TCG-CTCGTAATTT-AATTTATGTAGTTTGATTTGAC-A-T-TT


INSERT 4 ((( Basal Hexapods
Hypogastrura     TCGTTCA
Trigoniopthalmus ATGTCCT


INSERT 5 \\\ Basal Insects
Ephemerella    TCGGCGCACGGTTCCGTAA
Agrion         ---GCG--AGGCTCCG---
Libellula      ---GTAAAAGGCTCCG---


INSERT 6 )))
Megarcys       ATGTGAGTGG GACGTCCAGC CGGTGGGTCG NCAGGTCGTG AGCTATGCTG GCCGCGCCCC TTGGCGGTTC CATATCATGG CCGCGTCGTG
               GNGTGTGTCG GGAGGTGTTT GTGTCGNNCG TTCGCGTTCG TCGAAGNATC GCCTGGCCCG NCAATAAAAC GGCGCTGTGT TGTGGGGACC
               GTCTCTCACT CAGGGTGTCG CTGTGTCGGC GCACACGGTG CCGGACCCCA TG


INSERT 7 <<< Orthopteroids
Blaberus       AGCCGGGAGCTCTTGGTGCGAGTCCCTCCAGGGTCTCCGCCTCGAACCCGGTCTCTGGGGAGGGSCT-ACTC
Labidura       TG--GTATG-TAATAGTTTGCTTTCGTTCTT-TTCTAAAGGCGGAATGCAG-CTATTGTCAGCCTTTCTCTT
Melanoplus     AGC-CGAAG-GC--GC-GCG-G-CCG-CCTT-G-CGCGTGCCCGTGCGTCC-CGAGGCGGA-CCCCG-T-TG
Anisomorpha    -----GG---Y----C-GA----CCG-T--GGG-C-C-TC-TGGT-C---------------------T--G
Oligotoma      -----TN---N----G-GT----CCG-T------C-A-AC--G-T-C---------------------A--T


INSERT 8 [[[
Dennyus        TGGCATATCC TCGGTTCGGG AATTCCGCAG TTCTCGTCCG TGTCTTGCTT ACTCGCGTCA GCCCTAGGTC CGGGTCGGGT TATTTCTCCG
               TTCGGTCCGG TCCGTGGATA CTCAAAGGGA CTCAGTCCCG GGGTTTCACG GCTCCCGGNC GCGGGAAGTG CCTCCCCCCT AGGGTGCGAG
               GAGTTGCGGC GGCGAGTCGG GTCTCGGACT TACGGGGGCC AAAATTTCGC TGTGACCCAG CG


INSERT 9  :.
Acyrthosiphon  TCGGCGCGGT CGCCGTCGCG CTCGTCAGCC GTCTCGGGGT GTTAGTTACC GGCACGTCGG CCGGACGTAT TGTCGGCAGG CGGACACGTG
               TCGTGCTTCC GGCCCGCCGT CGCGGCCACG CGTCGCGCGG CCGTCGGTGT TCGACGACGG CGGCCGA


INSERT 10 ]]] Hemipteroids
Buenoa         CGTGACCCACGGCG-CGTCCAGGCTCGT-CT-CAGGGC-CG-AAAC-G-CGCCGATG-TGTGTCAGG
Saldula        CGGG-GTCT--TCG-GA-CAAG-TGCC--CT-C-GGGT-GC-TTTC---CGTCGTTC-TT-C--CGG
Lygus          CGGGAGCCTCGTCTAGGTGACGGCCCTTGCCACAAGCTTGGTGTCCGGAGGCCGGGGGTATACTCGT
Taeniothrips   TCAG---CT--GCG-GG-TT-T-CG-G--CT-C-GCAT-GC-GG-C---CGCCGAG--TA-A----T


INSERT 11 /// Megaloptera, Raphidioptera, Basal Coleoptera
Priacma        TACGTAATAGTTGAGGTCTTTACGGATTTCTTCTATTGCTCATCCGACTTTTT
Colpocaccus    TACGTAATAGTTGAGGTCTTTACGGATTTCTTCTATTGCTCATCCGACTTTTT
Corydalus      TACGTAATAGTTGAGGTCTTTACGGATTTCTTCTATTGCTCATCCGACTTTTT
Agulla         TACGTAATAGTTGAGGTCTTTACGGATTTCTTCTATTGCTCATCCGACTTTTT

INSERT 12 {{{ Coleoptera
Cybister       GCGGGGCGTTTCCGTAAGGTTGCGTCTC-GCGTC-
Xyloryctes     A------G--CCCTCTCGG--GGG-CG--GT----
Octinodes      A------G--CCCGCGA----GGG-CG--GC----
Photuris       A------C--TACGAAC----TCG-CT--ACG---
Meloe          A------G--CTCCTAAGG--GGG-CG--GC----
Rhipiphorus    A------G--CTTGCAA----AAG-CG--GT----
Tenebrio       A------G--CTCGTGA----GGG-CG--GC----
Tetraopes      A--GCTCG--CAAGGGCGG-CCCAACTCAATCCCG
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INSERT 13 ''' Neuroptera
Lolomyia       TGTAAATTATTGTTATTATCTTTGCCCCTGTATATTGTTGTATGCACCAATGTGTCTGTGTATGACGTATGTTAATATGCTGTTATCAGTATCGGCTATA
Mantispa       TGTTTGAAATTATTGTTCT-TCACCGCACGTATGTGGCT-CAGGCAATTATGTGTTACTACATATTCGCTGCCAGCTTAATTTTATTA-T-TGGGTTCGA
Hemerobius     T----------------------G----T------G----------CT---GT---A-TG--------C-----GTAT--T-T--------------AG-
Chrysoperla    T--A-------------C----AG---AT------T----------AT---GT---A-TA--------A----AGTATA-T-T--T---T-------AG-

Lolomyia       TGAAAAACGATTATATTTCATACACACACACATTTATTAGCTGGTGTATGTGTGTGTGCGCGCATTATACATATGTTAATAGCATTTGTGTGTGCGTGTA
Mantispa       TGT-T-GTTATTGTGTATTATGG-C-CTCTCAT--AT-ACAT-AT-TATGTGT-TATTAAA-C-TC-TGT-T-TCTTAATTGCATAT-T-TATGC-TATA
Hemerobius     T-----G-T-T-GT----C-T------T-G--T--A----CT----------------C-----TC--AC-T-T-----------------G--------
Chrysoperla    T-----G-T-T-AT----TAT------T-T-ATTTA----ATG---------------CA----TT--ATATAT-----------------AT---T-T-

Lolomyia       TCACACTGCACCGGGCTGATTTATTGGCGTGTGGAAAAATTATTTTCCAATTTTGATATGCGTCAGATTTGATATACACGCATATATATACATGCCCATA
Mantispa       TGGGCCATATTTATTATGAT-AACACGCG-GACCTCCAATAATAAGTAAACC-GG-T-TGAGTTGGATTT--TGTG-AT-TAT-TGTGT-G-TGCACATT
Hemerobius     T-------AT---G--TG-T-G-C-------TG--C-----A---TT------G--------T-A-A-------------G-T----G--C-T-----T-
Chrysoperla    T-----T-AT---T-ATG-T-AATT------TG-TC-G-T-A-A-GT------G--T-T---T-A-A---------C-C-G-TA-A-GT-G-T-----TT

Lolomyia       CGCCACTTGGATTCAAATGTATATTATACGTATATGCAGTTGGGTGGATAATATACATCAAATAATTTGCCGTAAGTGTTTAGCCGTGAAGAACGGCGGC
Mantispa       -A-AA-TTG--TTCTGTTGTTCATG-TGCG-ATTTGT-G-TGTGTTGA-ACGTT-GAT-AA-T--TTTACCGTAAGTGTTTAGCCGTTAAGAGCGGCGGC
Hemerobius     -A-------------G-----C------CG--T---------G----A-A-GA---------------AC-G---C-G----GC----A-G---------
Chrysoperla    -A-------------A-----C------CG--T---------T----A-A-GA---------------GC-G---GTG----GC----A-G---------

Lolomyia       A-GC
Mantispa       AGGC
Hemerobius     ---C
Chrysoperla    ---C


INSERT 14 @@@  (note this sequence is highly suspect)
Myrmeleon sp.  GGTGAGGTAT AAATTATATA TTGTACAATA TAGTTATAAA TAAAAATTAT ACACTTGTAT TTTTATTTAA ATTTTTATTT TATGGGTAAN
               TAATNAAAAT GTTATTTTGT TTTTGTGTAT AATATTATAT TTATTTTTTT NAATTTATAT GTATATATAT AAATATTATA NTTTGNNTTT
               TTTTTACNTT GNAAAATTNA AAGTATACNT ANGAAAANNN NNNNNNTATT NGGNGCTNCA TANTATNCCN ATTN


INSERT 15 ###  Mecoptera Siphonaptera
Boreus          TTAGCCCGTCAAAAGGCGGC
Merope          TTAGCCCGTCAAACGGCGGC
Panorpa         -TAGCCCGTAAAAAGGCAAC
Ctenocephalides TTAG--CGTCAAAAGGCGGC
Hystrichopsylla ---GCACGTCAAAAGGCGGC
Orchopeas       --AGCCCGTCAAAAGGCGGC


INSERT 16 }}}  Lepidoptera
Galleria       CGGCGGTAAAAGGGCGCTCAATA
Papilio        CGCCGGTAATAGGGCGTTCAATA
Ascalapha      CGGCGGTAATAGGTCGTTCAATA


INSERT 17 $$$ Trichoptera
Hydropsyche    GTGTTTCCCGCCGGTGCGTGTCGGTCGTCCCTCACGGTCTGGCCGTCTCGTTTGGCGGACGTTGCGCTG
Pycnopsyche    GCGTCCACCGCCGGCGTGTGTCGGTCG-GCCTCACGGTCTGGCCGTCTCGTTTGGCGGACGTTGCGCTG
Oecetis        GCGTTTTCCGCCGATGCGAGTCGGTCGTCCCTCGCGGTCTGGCCGTCTCGTTTGGCGGACGTTGCGCTG


INSERT 18 +++ Bittacus
B.strigosus     ATCATGTTCACCCCACGATTTGTAGTAAACTACTAGTGCGAATGGTGACTGAC
B.chlorostigmus GTC--GTTTACCCCA-G--TTGAGGTAAA--ACT-TTTC--TGGGGGAC-GGC


INSERT 19 %%% Hymenoptera
Hartigia       AGCTCC-TCACGGGG--GGCGGC
Orussus        AGCCCC-TTTC-AGA--GGCGGT
Hemitaxonus    AG---C-TCTC--GG--GGCGGC
Peridista      AGC-CC-TCTC--GG--GGCGGC
Bareogonalos   AG--CC-TTTC--GG--GGCGGT
Evania         AGCTTC-CTGCGGGC--GGCGG-
Ichneumon      AGCTCT-TCGC--GG--GGCGGT
Ophion         AGCTCT-TAAC--AG--GGCGGT
Mesopolobus    AG---C-CGTA--AC--GG-GT-
Caenochrysis   AG---C-CCTC--CG--GGCGN-
Epyris         CGTCCT-CTTC-GAG--GGCGAG
Priocnemus     AGCTTTGCCTTGTGCTTGGCGGT
Dasymutilla    AG--CC-CCTT--GG--GGCGGC
Apoica         GG--CC-CCT---GG--GGCGGT
Monobia        AG--CT-TTTC--GG--GGCGGT
Pfuscatus      AG--CC-CTTC--GG--GGCGGT
Pdominulus     AG--CT-CTTC--GG--GGCGGT
Camponotus     AG--CC-TCGCGAGG--GGCGGC
Chalepoxenus   AG--CC-TCGCGAGG--GGCGGC
Doronomyrmex   AG--CC-TCGCGAGG--GGCGGC
Harpagoxenus   AG--CC-TCGCGAGG--GGCGGC
Leptothorax    AG--CC-TCGCGAGG--GGCGGC
Temnothorax    AG--CC-CCGCGAGG--GGCGGC
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INSERT 20 &&& Diptera
Tipula         --AGTG-------GC-AT-A-A-AC---GTAA--G-T-T-TAT----CCGC-G-T--AATAAATCTAAAT
Laphria        GGAGTTCTAATATATATTTATTTTCATATTATTTGTTATAAATATATATAACTCCTATTTAAACCTGCTT
Mythicomyia    GGAGTT-TTA-ATGC-TGCGTGTGCTT-CACATTG-T-AGTAT-T-GGCTCCTATTAAAAAAACCTGCTT
Drosophila     GGAGTTCTTATATGTGATTAAATACTT-GTATTTTT-CATATGT-TCCTCCTATT-TAAAAACCTGCTT
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INSERT 21 *** Strepsiptera
Triozocera     GGGTTAC---CGGT-ACGTGTCGGTAAGCCGTGTACA-A-T-AAA-AC-G-G-CA---CA-CTGCTGCGTTG-C-CTTTGCGC-A-A-G-TGC-----A-
Caenocholax    GGATGTT---TAG--A-A-ATCGTT-TGC--T-TATA-G---ACG-AC-G-G--A---CA-TCTGTTCG-CG-C-TATTCATC-G-A-T-TTC----GA-
Elenchus       GGATTTTAAGTAATCAAA-ATAAAA-ATTCATTTTTTTTGTATATAATCGATACAAAATAATTTTTTTTATTAAATATAAATATTTATAGAAAAAATGAT
Crawfordia     GGATTTT---T---CAAG-GTTTTT-TTCG-TATAGTGGCG-TTT-CT-T-TTCGA--T--TCGTTTTT-TTGCGTTTCGAAA-A-A-AGTGC-T-T-C-
X.pecki        GGATTTT---T---CAAA-ATTGAA-ATT--TATTTT-T-T-TAT-AT-T-TA-T---T--T-TATTAT-AA-A-TATAAATT-A-A-A-TGA-T---A-
X.vesparum     GGATTTT---T---CAAA-ATTGAA-TTT--TATTTA-T-T-TAT-AT-T-TTGG---T--T-TTTTTT-TT-T-TTTCAAAA-A-A-A-AAA-T---C-

Triozocera     --C---GTTG--CG-C-AC--TT-TG-CGTGTGA-A---CGGATGCTTGCGCATTGTACG-GCAACGTGTGTGC-C-G-TGTGCGCA-CACCGA-TCGT-
Caenocholax    --T---ATTC--AA-T-AC--GA-TG-GGT-TTA-G---GATTTAATTTCGCA--GCAGT-GTAAAATGTTT-C-A-A-TTACGTTA-CTATTT-TCG--
Elenchus       TTTTTTTAATGGAAAAATTTCAAAATTATTGCAAATTTATTTTTGCTCTAAATTGTAAAAAATATATTGTTACATAAAATTAGATATTTATAAAATTTAC
Crawfordia     T-A-G-AAAT--TA-A-TC-CTTAAA-ATC-CGA-T--ATGGTAGTTTTAAAAA-AAAATCGAAAAAATTTTCACA-G-TTT-ATTT-AGTCGA-TTTT-
X.pecki        --A---TTTT--CA-A-TT--TTAAA-ATT-CGA-T--ATAATAATTTTTAATT-AAAAAAGTTTATTTTTT-A-A---TTA-AAAA-AATATT-TTTT-
X.vesparum     --A---ATAT--AA-A-TT--AT-AT-AGT--AA-T---TTTCGATTTTAAAAT-TCGATATAATAATTTTT-A-A---TCA-AAAA-AGTTTA-TCGA-

Triozocera     C---AG-T--G-TC--C----CG-A--T-GGCGAC-G-GATTCGA-TTA--GC-T-TCGAACTCGTA-TCGCAT-TC-TG-ATC-GAAACTCGT-G----
Caenocholax    C---TG-T--T-TG--T----GA-A--A-TGC-TT-A-AATTCGA-TTG--TA-T-TCTAAA-C-TA-T-GAAG-AA-AG-CGT-TGCGGTCAG-A----
Elenchus       TCAAATCAATAGTGGAGAAATTTTTTCTCATTATTGAAAAATTTTATTAAATAATTAAAAAAAAAGTTAA-TTAATTAATTTATTTTAATTAATTAATAAT
Crawfordia     T---AG-AA-A-TG-AG----GATT--A-ATTGAA-AATTTTTTT-TGA--TT-A-ATCATTTC-GT-T-TTTA-AAGTG-ATT-AAATAAATGAA-T-T
X.pecki        T-A-AT-AA-T-TG-AT---TTTTT--T-TTTAAA-AAAAAACTT-TTT--TA-T-TAAAAAAA-TT-T-TTTT-TA-T--TTT-AAAA-AATT------
X.vesparum     A-A-AT-AA-A-TG--T----TATT--T-TTTAAT-AATAAATTT-TTT--TT-A-AAAAATTT-TT-A-TAAA-AA-A--ATT-AACTTTTTTCG-A--

Triozocera     C-C-C--GATC-G-T-C-T-CG-TGTG-CC--GGC---T-T-C--G-TTGTG-TGCAC--AC-GTGAC-CGTGC--A-C-AAAACT-C-T-G--
Caenocholax    G-A-T--GC-A-A-T-T-T-CG-TAAA-AA--GAA---T-T-C--G-GT-TG-T-CGC--GC--T--C--GTTT--T-C-G-G-CT---T-G--
Elenchus       TTTTTTATTTTAAATAATTTATTTAATTATCGTAAAAATATTTTGTATTCTAATAAAAATTATGTTATTTTTATAATGCATAA-TTTTTTGATT
Crawfordia     TTT-T--TT-C-T-T-T-T--T-TAAA-AC--TAA---T-T-A--TATTCTAATGAAA--AAT-TAATT-TTTT--T---TAA-AA-----A--
X.pecki        T-A-C--TT---A-A-A-T--T-AAAA-TT--TAA---T-T-A--TATTCTAATAAAA-TTAT-TTTTT-GTAA--T---T-T-TT-----A--
X.vesparum     TAA-C--TT---T-T-A-T--T-AAAT-AT--TAA---T-T-A--TATTCTAATAAAA-TTAT-TTAAACGTAA--T---T-T-TT-----A--
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INSERT 22 >>> Myrmeleon
M.immaculatus  TTAAAATTTAAATAGT
Myrmeleon      TTAAAATTTAAATAGT
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INSERT 23 ~~~ Strepsipters
X.vesparum         TTTAAAAAAGAAAATTTTTTTCTGATTTTTT-T-T-T-T-T-TTAA-AT-GA-TTAGAAAAA-AAATAAAAATTGG-CTTAAAGAAATAAA-TAATTTTA
X.pecki[long]      TTTAAAAAA-AGTTTTTTTTTTTTATTTTATATAAAAAAAAAAATAAAATTGGCTTAAAGAAATAAATAAAAATTTTACTTAAAATTTTTCACAAAAAAAA
X.pecki[short]     GG-------G--TGCTTAAAGC-AG----G-CA-A-A-T-T-T-AT-ATG-C-CTTGAA-T-AT---AA-C-A-GC-ATG---GAA-T-AA-TA-GAATA
Caenocholax[long]  TT----------TT--G-TTT--GA----A-AT-T-G-GCT-T-AA-AGG-G-CTAGATAAAAC-GGAAACG-GTT-CGG---ATGCTCGGGCACGGTAC
Caenocholax[short] TT----------T---G-TTT---A----A--T---G-T-T-T--T--T----CTT-AT----C----------TT-CGG---ATA---GA--A----A-
Crawfordia         TT----------TCC-GATTTC-GA----A-AA-G-G-G-G-A-AT-CTT-T-TTTGAA-A-AT---TA-T-T-GG-CTT---AAA-G-AAGTA-AATAA
Triozocera         TT----------TTC-G-TTT--GA----A-AT-T-G-GCT-T-AA-AGG-G-CTAGATAAAACCGGAAACGTGTT-CGG---ATGCTCGGGCACGGTAC

X.vesparum         CTTAAAA-AAA-AA-G-ATTTTTTTTTTTTTTTTGA-T-TTATACAAAAATAGTAAAATTTCTTATCGT-TGCAAAAATT-A-TATTTAAATTTTTTTAA
X.pecki[long]      ATTAACA-AAATAATTCATGTATTGTTGCAATAAAAAAAAATTTTTTTTGTTAAAAAAAATTTTTTTTTTCTTAAAAAAAAGATTACAAAAAAACTATTAA
X.pecki[short]     --TG-AT-CTC-GA-T-AC-T-GT--TTAA--AAAA--AG-TT-TTTT-TT-TT----TT----AT--T--TAAGCCGAA-T-TCCAG-C-A-C----A-
Caenocholax[long]  C-GGGCACATC-GA-C-GCCTAGTG-TGCAC-TCCG-TCG-ACGCATA-AC-GGAA--CG-C--GT-GTG-CAATTCGTA-TCTACGTAC-G-C-C-TA-
Caenocholax[short] --GG-CA-ATT-TT-C-G--T--T--TG-A--T--G-----A---A-A--T-G-----CG-----T------AAG-CGTA-T-T--GT---G------A-
Crawfordia         --TA-CA-TTT-GA-G-AT-T-TT--TTCG--TAAA--AA-TC-TAAA-AG-GT----TT-----T--T--TC-G--GAA-A-TC-AT-C-G-C----A-
Triozocera         C-GGGCACATC-GA-C-GCCTAGTG-TGCAC-TCCG-TCG-ACGCATA-AC-GGAA--CG-C--GT-GTG-CAATTCGTA-TCTACGTAC-G-C-C-TA-

X.vesparum         TTTTTGTATTTTTTTTTTTAATAAAAAAAAAAT-AACAAA-AACTATTTACAATTTTTTTTTTAAAAAAA--A--ATAATTTTGTAAATAGAAAATTTAAA
X.pecki[long]      TAATTTTTTTTTTTATTAAAAAAAAAAAAAAATTAATTAA-TAGTATAAAAAATTTTTTTTAAAAATTTTTATTATAATTATTTTTTTTTGCATTCAAA
X.pecki[short]     TGGCGG-CC-----G--TTACTAGTG-G-A-T-C-CGAGCTCGG-TAC-C-A-A-G-C-T-T-G-ATGC--AT-A-GCTTGAGTATCTATAG---T-ATC
Caenocholax[long]  GTGCTG-CG-----A--ATACGAGCG---C---T-CACGTGCCG-GTC-CGA-A-T-G-C-G---A-GC--ACCG-GCGTCACTA-AAATGG---T-GTG
Caenocholax[short] G-GC-G-A------A--AT--GAAAT-------T--G-G--CT---T----A-A-----------A-GT-----G---G-CA--A-AGTTGG-----GAA
Crawfordia         TTTC---C------G--AAAGAAATG---A-T-T-TTAGTTATC-GA--C-A-A-T-T-T-T-G-A-GA--AT-G-AATTTTTTCGAAATTG--TT-GTC
Triozocera         GTGCTG-CG-----A--ATACGAGCG---C---T-CGCGTGCCG-GTC-CGA-A-T-G-C-G-G-A-GC--ACCG-GCGTCACTA-AAATGG---T-GTG

X.vesparum         AACTTTTTTGCATC-C-ATAACGTTAAGAAAATTTTTTTTTTTG-TTAAAAAAAAATAAT-TTCTTTTTTTTAAGAATTTATTTCGACAGTATG
X.pecki[long]      AACAATTATGAATAATAATTTTGTTAAAAAAAAAATTTTTTTTGTTTTTTTTTGTGTTTTAAAAAAAATTTTAAGAATTTATTTCGACAGTATG
X.pecki[short]     -A-CC-TA--AATA-C--GTTGGCGT--AA--T---------------CATGGT-CA-TA--G-CTG-T-T-T---C-T-G-TGT-GAATTGTT-
Caenocholax[long]  CA-TCGTTT-AGTA-TC-GTGTGTGCCCGA--T-----------G---CAA-CT-CG-AA--T--TA-T-T-T---A---G-CTC-GACGGTAT-
Caenocholax[short] -A-TC-TT--A-AA-T--GA-T-T-T------T---------------C-T--T--------T--T--T-G-T---C-----CAC-GACAGTAT-
Crawfordia         GA-AA-AT--CGTC-T--TTTGGATT-GAA--T---------------AAATTT-CA-GA--G--TA-T-T-T---A-T---TTC-GACAGTAT-
Triozocera         CA-TCGTTT-AGTA-TC-GTGTGTGCCCGA--T-----------G---CAA-CT-CG-AA--T--TA-T-T-T---A---G-CTC-GACGGTAT-
```

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INSERT 24 ;;;
Acyrthosiphon  CCCGCGCATC TCCGCCCTTC GCGGGACGCG CGAAATCGCC TCCGGGGCGT TTCCGTGCGC GGGCCGCCGG GCCGCGGGCG CCAGTCGCCC
              GCGCGTCCCG CCGGGCCGGT TTTCGGGACC GGAGGTAATG ATCAACA
```

Appendix 2
28S Alignment with Appended Inserts

The 52 taxa were aligned using MALIGN (parallel version 1.93; Wheeler and Gladstein, 1994). The heuristic algorithm "Build" with SBR branch swapping on multiple alignments was performed (change cost = 3, gap cost = 5, leading and trailing gap cost = 8). Primer regions were included in the alignment but were subsequently excluded in phylogenetic analyses. Variable alignment regions (positions 47–59, 88–118, 135–179, 198–220) were excluded from phylogenetic analyses in the conserved tree reconstructions. When the initial alignment presented evidence of a large insertion in a single taxon or subset of taxa, the region was removed to facilitate alignment of positions flanking the insert. Symbols in the alignment (other than standard nucleotide codes) refer to insertions appended after the alignment.

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                                                                                                                      100▼
                    ┌────28S ai──────┐                           ┌─Variable─┐                                ┌─Variable─
Trigoniopthalmus    GACCCGTCTTGAAGCAAGGAGTCTAACATGTGCGCGAGTCATTGAG-CGTGA-------CTAAACTCAAAGGCGCAATGAAAGTGAA-GGTT-C-G-CGC
Ephemerella         GACCCGTCTTGAAGCAAGGAGTCTAACATGTGCGCGAGTCATTGGG-TCCCAC------TTACACCCAAAGGCGTATTGAACGAAAA-GG-C-C-G-T-C
Libellula           GACCCGTCTTGAAGCAAGGAGTCTAACATGCGCGCGAGTCGTTGGG'CTCCG-------CTAAACCCATAGGCGCAATGAAAGTGAA-GGTT-T-C-C-C
Agrion              GACCCGTCTTGAAGCAAGGAGTCTAACATGCGCGCGAGTCGTTGGG'CTCCG-------CTAAACCCATAGGCGCAATGAAAGTGAA-GG-C-C-G-C-C
Megarcys            GACCCGTCTTGAACCACGGAGTCTAACATGTACGCGAGTTATTGGG-CTCG-CA-----ATAAACCCAAAAGCGAAATGAAAGTAAA-GGTCGC-GGCGC
Cultus              GACCCGTCTTGAACCACGGAGTCTAACATGTACGCGAGTCATTGGG-ACCG-CA-----ATAAACCTAAAGGCATAATGAAAGTAAA-GGTCGC-GGCGC
Mantis              GACCCGTCTTGAACCACGGAGTCTAACATGTGCGCGAGTCACTGGG-AACCA-------CTAAACCCAGAGGCGCAATGAAAGTG-G-GG---C-G-G-C
Melanoplus          GACCCGTCTTGAACCACGGAGTCTAACATGTGCGCGAGTCATTGGG-CT-G-TA-----CGAAACCTAAAGGCGTAATGAAAGTGAA-GGT--CTC-G-C
Oligotoma           GACCCGTCTTGAACCACGGAGTCTAACATGTGCGCGAGTCATTGGG-TTCGRYAG----CGAAACCCAGAGGCACAGTGAAAGTGAA-GG-C-T-G-C-T
Saldula             GACCCGTCTTGAACCACGAAGTCTAACGTGTGCGCGAGTCATTGGG-T--G--------AAAAACCTAAAGGCGTAATGAAAGTAAA-GG---G-G-A-C
Buenoa              GACCCGTCTTGAACCACGAAGTCTAACATGTGCGCGAGTCGTTGGG-CTCGTTTTT---CGAAACCCAAAGGCTTAATGAAAGTGAA-GG---A-A-G-C
Lygus               GACCCGTCTTGAACCACGGAGTTTAGCGTGTGCGCGAGTCATTGGG-T--G--------TCAAACCTAAAGGCGTAATGAAAGTGAA-GG---A-A-A-C
Priacma             GACCCGTCTTGAACCACGGAGTCTAGCATGCGCGCGAGTCATTGGG-A--CTCT-----CTAAACCTAAAGGCTGAATGAAAGTGAA-GGT--C-C-G-C
Colpocaccus         GACCCGTCTTGAACCACGGAGTCTAGCATGTGCGCAAGTCATTGGG-TA-TTTAT--A-ATAAACCTAAAGGCGTAATGAAAGTGAA%%%%%%%%%%%%%
Cybister            GACCCGTCTTGAACCAAGGAGTCTAGCATGTGCGCGAGTCATTGGG-A--ACAT-----CTAAACCTAAAGGCGCAATGAAAGTGAA-GGTT-C-C-G-C
Xyloryctes          GACCCGTCTTGAACCAAGGAGTCTAGCATGTGCGCGAGTCATTGGG-A--CTCTA--A-CGAAACCTAAAGGCGTAATGAAAGTGAA-GGT--T-C-G-C
Octinodes           GACCCGTCTTGAACCAAGGAGTCTAGCATGTACGCGAGTCATTGGG-TG-CGATT--GTCTAAACCCAAAGGCGAAATGAAAGTGAA-AG-C-G-C-G-C
Rhipiphorus         GACCCGTCTTGAACCACGGAGTCTAGCATGTACGCAAGTCATTGGG-AA-ATAA-----TTAAACCTAAAGGCGTAGTGAAAGTAAA-GGT--T-T-G-C
Tenebrio            GACCCGTCTTGAACCAAGGAGTCTAGCATGCACGCAAGTCATTGGG-AC-ATGA-----TTAAACCTAAAGGCGTAATGAAAGTGAA-AG-T-C-C-G-C
Tetraopes           GACCCGTCTTGAACCACGGAGTCTAGCATGTGCGCGAGTCATTGGG-AC-ATAA-----CTAAACCTAAAGGCGCAATGAAAGTGAA-GG-T-C-C-G-C
Corydalus           GACCCGTCTTGAACCACGGAGTCTAGCATGTGCGCGAGTCAGTGGG-AG-C-G-A----ATAGACCCACGGGCGTAATGAAAGTAAC^^^^^^^^^^^^^
Agulla              GACCCGTCTTGAACCACGGAGTCTAGCATGTGCGCTAGTCAGTGGG-AA-C-G-A----CTAAACCCACGGGCGTAATGAAAGTGAA^^^^^^^^^^^^^
Lolomyia            GACCCGTCTTGAACCACGGAGTCTAGCATGTGCGCAAGTCATTGGG@TT-G-T-A----TGAAACCCAAAGGCGTAATGAAAGTGAA>>>>>>>>>>>>>
Mantispa            GACCCGTCTTGAACCAAGGAGTCTAGCATATGCGCAAGTCATTGAG@AT-T-T-A----TGAAACTCAAAGGCGAAATGAAAGTAAA>>>>>>>>>>>>>
Hemerobius          GACCCGTCTTGAACCACGGAGTCTAGCATGTACGCAAGTCATTGGG@TT-T-T-A----TGAAACCCAAAGGCGTAATGAAAGTAAA>>>>>>>>>>>>>
M.immaculatus       GACCCGTCTTGAACCACGGAGTCTAGCATGTGCGCAAGTCATTGGG@TT-T-T-A----TGAAACCCAAAGGCGAAATGAAAGTAAA>>>>>>>>>>>>>
Hemitaxonus         GACCCGTCTTGAACCACGGAGTCTAACATGTGCGCGAGTCATTGGG-A--CAC------GCAAACCTAAAGGCGAAATGAAAGTGAA-GG---T-C-A-G
Ophion              GACCCGTCTTGAACCACGGAGTCTAACATGTGCGCGAGTCATTGGG-TA-CTC------TGAAGCCTAAAGGCGCAATGAAAGTGAA-GG---T-C-G-G
Dasymutilla         GACCCGTCTTGAACCACGGAGTCTAACATGTGCGCGAGTCATTGGG-A--TAA------ACAAACCTAAAGGCGAAATGAAAGTGAA-AG---T-C-G-G
Apoica              GACCCGTCTTGAACCACGGAGTCTAACATGTGCGCGAGTCATTGGG-A--CTG------CGAAACCTAAAGGCGCAATGAAAGTGAA-GG---T-C-G-C
Monobia             GACCCGTCTTGAACCACGGAGTCTAACATGTGCGCGAGTCATTGGG-A--TAG------TAAAACCTAAAGGCGCAATGAAAGTGAA-GG---T-C-G-G
P.fuscatus          GACCCGTCTTGAACCACGGAGTCTAACATGTGCGCGAGTCATTGGG-A--CTC------TAAAACCTAAAGGCGCAATGAAAGTGAA-GG---T-C-G--
Galleria            GACCCGTCTTGAACCACGGAGTCTAGCATGTGTGCGAGTCATTGAG-AT-TTACATCA-CTAAACTGAAAGGCACAACGAAAGTGAA-GG-CGC-G-C-G
Papilio             GACCCGTCTTGAACCACGGAGTCTAGCATGTGTGCGAGTCATTGAG-TT-ATG--T---ATAAACTGAAAGGCGTAACGAAAGTGAA-GG-CGC-G-C-G
Ascalapha           GACCCGTCTTGAACCACGGAGTCTAGCATGTATGCGAGTCATTGAG-AT-A-A------TAAAACTGAAAGGCGCAACGAAAGTGAA-GG-CGC-G-C-G
Hydropsyche         GACCCGTGTTGAACCACGGAGTCTAGCATGCGCGCGAGTCATTGGG-AW-T-T--Y---GTAAACCCAGAGGCGCAATGAAAGTGAACAG-C-G-C-C-G
Pycnopsyche         GACCCGTGTTGAACCACGGAGTCTAGCATGTGCGCGAGTCATTGGG-AA-C-AC-T-G-ATAAACCCAGAGGCGAAATGAAAGTGAAAGG-C-C-G-C-C
Oecetis             GACCCGTCTTGAACCACGGAGTCTAGCATGTGCGCGAGTCATTGGG-AC-C-ATGT-A-CTAAACCCAGAGGCGCAACGAAAGTGAAAGA-CGG-A-G-C
B.strigosus         GACCCGTCTTGAACCACGGAGTCTAGCATGTGYGCAAGTCATAGGG-TT-T-T------TAAAACCTAAAGGCGAAATGAAAGTAAA-GA---G-A-C**
Boreus              GACCCGTCTTGAACCACGGAGTCTAGCATGTGCGCGAGTCATTGGG-AA-A-T-A----CAAAACCTAAAGGCGCAATGAAAGTAAA-GG---T-T-C-G
Merope              GACCCGTCTTGAACCACGGAGTCTAGCATGTGCGCAAGTCATTGGG-AT-A-T-A----CAAAACCTAAAGGCGAAATGAAAGTAAA-GATT-C-A-C-T
Panorpa             GACCCGTCTTGAACCACGGAGTCTAGCATGTGCGCAAGTCATTGGG-AC-T-T-A----ATAAACCTAAAGGCGTAATGAAAGTAAA-GATT-C-A-C-C
Ctenocephalides     GACCCGTCTTGAACCACGGAGTCTAGCATGTGCGCGAGTCATTGGG-AA-A-T-A----CAAAACCTAAAGGCGCAATGAAAGTAAA-GG---T-T-C-G
Orchopeas           GACCCGTCTTGAACCACGGAGTCTAGCATGTGCGCAAGTCATTGGG-AA-T-C-A----CAAAACCTAAAGGCGTAATGAAGGTGAA-GG---T-T-C-G
Tipula              GACCCGTCTTGAACCACGGAGTCTAGTATATGTGCGAGTCATTGGG-C--T-T------TTAAGCCTAAAGGCATAATTAACGTAAC&&&&&&&&&&&&&
Laphria             GACCCGTCTTGAACCACGGAGTCTAACATGTGTGCAAGTCATTGGG-TA-T-A------TAAAACCTAAAGGCATAATTAACTTAAC&&&&&&&&&&&&&
Drosophila          GACCCGTCTTGAACCAAGGAGTCTAACATATGTGCAAGTTATTGGG-A--T--------ATAAACCTAATAGCGTAATTAACTTGAC&&&&&&&&&&&&&
Mythicomyia         GACCCGTCTTGAACCACGGAGTCTAACATGTGTGCAAGTCAATGGG#A--A--------TGAAACCTAAAGGCGACATTAACTTAAC&&&&&&&&&&&&&
Caenocholax         GACCCGTCTTGAACCACGGAGTCTAACAAGTGTGCGAGTTATTGGT$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$
Elenchus            GACCCGTCTTGAACCACGGAGTCTAACAATTGTGCGAGTTATTGGT$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$
Crawfordia          GACCCGTCTTGAACCACGGAGTCTAACAAGTATGCGAGTTATTGGT$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$
X.pecki             GACCCGTCTTGAACCACGGAGTCTAACAAGTATGCGAGTTATTGGT$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$
```

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INSERT 1 '''  Odonata
Libellula      TCGGACACG
Agrion         TCGGACACG

INSERT 2 @@@ Neuroptera
Lolomyia       ---AATAAAACATTTTTTCATCGGAATGTATATAAT-
Mantispa       ---ACTAAAACATTTTTTCATCGGAATGTATATAAA-
Hemerobius     AATAATAT-GTATTTTTTCATCGGAATATATATGATA
M.immaculatus  ---AATAAAATATTTTTTCATTGAAATATTAATAAA-

INSERT 3 ###
Mythicomyia  TATATAATCA TTTTACTATG ATTGTATATT TAA
```

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                                                                                                           200▼
                      ───Variable───┐                ┌──────────Variable──────────┐                   ┌
Trigoniopthalmus     A--TTTT-G---G-CCGAACCGAGGGGAGATCCG-C-GGT--CGCT--TCGCG-C---G--GCC--CG-------G--CGCATCCCCGGGGCGTCTCGTC
Ephemerella          ---CTCC-G--CG-T-CGGCTGAGGGAAGATGGG-C-G-T---C-C--GCTCG-C---G--G-G-CGC---C---C--CGCATTCCCGGGGCGTCTC(((
Libellula            ---TTCG-C---G-G-G-ACCGAGGGAGGACGGA-G-G-C---T-C--TT-CG-C---G--GAG--GC--TC---C--CGCACTCCCGGGGCGTCTGATT
Agrion               ---TTCT-G---G-T-G-GCCGAGGGAGGACGGG-G-T-C--GTTC--GCGCG-CTCCG--GCG-CGC-GTCGGTCCCCGCACCCCCGGGGCGTCTGATC
Megarcys             A--AGCC-C---G-GCCCAAAGAGGGGAGATGTC-C-G-A--GT-A--TATAA-A---A--T-T--GA--A-GGAC--CGCATCCCCGGGGCGTCTCG-T
Cultus               A--AGCC-C---G-GCCCACAGAGGGGAGATGTC-C-G-T--GG-CG-TCCCT-A---G--TGT-CGCCGACGGAC--CGCATCCCCGGGGCGTCTCG-T
Mantis               ---TTCG-T---G-C-C-GCCAAGGGAGGATGGC-T-C-T--CCTC------A-A-C-G--GGG--GA----G-CC--CGCACTCCCGGGGCGCCCC)))
Melanoplus           ---CTTG-C---G-C-GGGCCGAGGGAGGATGGG-G-C-T-TCCCCGCCCTTACA-C-G--GGG-CGG--T-GGCCTCCGCACTCCCGGGGCGTCTCG-T
Oligotoma            ---CTAG-G---G-T-A-GCCGAGGGAGGATGGA-G-C-A--GGC-------A-T-T-G--TCC--GG------CTTCCGCACTCCCGGGGCGTCTCA-C
Saldula              ---T-CT-G-----T-C-CCTTAGGGAAGATGGG-A-G-A--AGTACCTTC-G-A-A-G--TTG-CTC------CC--CGYATTCCCGGGGCGTCTCT-T
Buenoa               ---T-TG-GAACGCT-T-TCCTAGGGAGGATGAC-C-G-T--GTCAGCCCG-A-A-AAG--GCG-GCG----G-TC--CGCACTCCCGGGGCGTCTCT-T
Lygus                ---T-TT-G-----T-T-TTTGAGGGAGGATGGG-T-T-A--GGTACCTTT-T-TTAAA--GGA-CCG----G-CCT-CGCACTCCCGGGGCGTCTCT-A
Priacma              ---CTCGTT---G-C-GGACCGAGGGAGGATGGC-C-G-C--GTTG---C-GG-CG--T---CG--GC------TC--CGCACTCCCGGGGCRTCTCTCG
Colpocaccus          %%%%%%%%%%%%%%%%%%%%%%AGGGAAGATGGG-T-A-A--CG-T--T-ATTTT---G--TTA--CC-------T--CGCATTCCCGGGGCGTCGCGTA
Cybister             ---CTCG-A---G-C-GGACCGAGGGAGGATGGG-CGG-C--GGGC--TT-TT-GT-ACG--TC--GC------CT--CGCACTCCCGGGGCGTCTCGCA
Xyloryctes           ---CTTG-C---G-C-GAACTGAGGGAGGATGGA-CGG-T--CCTT---C-GA-GG--C---CG--TC-------C--CGCACTCCCTGGGCGTCTCGTT
Octinodes            ---CTCG-C---G-C-GGGCTTAGGGAGGATGGG-CGA-A--GCGA--TT-CG-TTCGTGTGTA--GC------CC--CGCACTCCCGGGGCGTCTCGTT
Rhipiphorus          ---CTCG-T---G-C-TTACCGAGGGAGGATGAG-TAT-A--ACTA---A-GG-TT-AT---T---GC------TC--CGCACTCCCGGGGCGTTTCATT
Tenebrio             ---CTAG-C---G-C-GGACTCAGGGAGGATGGG-TGG-T--CCTC---T-GT-GG-AC---C---GC------CT--CGCACTCCCGGGGCGTCTCGTT
Tetraopes            ---CTCG-C---G-C-GGACCGAGGGAGGATGGA-CGG-TCCGCGC--TTTCG-CGCGCG-GCC--GC------CC--CGCACTCCCGGGGCGTCTCGTT
Corydalus            ^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^GCACTCCCGGAGCGTCTCGTT
Agulla               ^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^^GCACTCCCGGAGCGTCTCGTT
Lolomyia             >>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>GCACTCCCGGGGCGTCTT+++
Mantispa             >>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>GCATTCCTAGGGCGTCTT+++
Hemerobius           >>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>GCACTCCCGGGGCGTCTT+++
M.immaculatus        >>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>GCACTCCCAGGGCATCTT+++
Hemitaxonus          ---C-CT-A-----G-C-GCTGACCGAGGGAGGA-T-G-G--GCCG---C-G--T---C---A---CG------AT--GGCACTCCCGGGGCGTCTCGTT
Ophion               ---C-CT-Y-----G-C-GCCGACCGAGGGAGGA-T-G-G--GYCG---C-G--T---C---A---CG------AT--GGCACTCCCGGGGCGTCTCGTT
Dasymutilla          ---C-CT-A-----G-C-TCCAACCGAGGGAGGA-T-G-G--GCCG---C-G--T---T---A---CG------AT--GGCACTCCCGGGGCGTCTCGTT
Apoica               ACCTACT-A-----A-G-GTCGACCGAGGGAGGA-T-G-G--GCCG---C-G--T---T---AG--CG-------C--GGCACTCYCGGGGCGTCTCGTT
Monobia              ---C-TT-C-----G-C-GTCGACCGAGGGAGGA-T-G-G--GCCG---C-G--C---T---A---CG------AC--GGCACTCCCGGGGCGTCTCGTT
P.fuscatus           ---TACT-A-----A-G-GTCGACCGAGGGAGGA-T-G-G--GCCG---C-GT-T---T---A---CG-------C--GGCACTCCCGGGGCGTCTCGTT
Galleria             ---CTCG-C--CG-C-GCGCTCAGGGAGGATGGA-G-C-GTCGG-T---C-TA-GG-TCG--TCGCTC-------T--CGCACTCCCGAGGCGTCTCGTT
Papilio              ---CTAG-C--CG-C-GCGCTCAGGGAGGATGGA-G-C-GTCGG-T---CGTT-CGATCG--GC-CTC-------T--CGCACTCCCGAGGCGTCTCGTT
Ascalapha            ---CTAG-C--CG-C-GCGCTCAGGGAGGATGGA-G-C-TTCGA-T---C-TA-GG-TCG--TA-CTC-------T--CGCACTCCCGAGGCGTCTCGTT
Hydropsyche          ---CTTC-G---G-T-GGCCGCAGGGAAGATGGC-G-G-C-CGG-T---A-CG-C--CCG--TC-CGC-------C--CGCATTCCCGAGGCGTTTC===
Pycnopsyche          ---CTCG-A---G-CCGGTCGCAGGGAAGATGCGCG-G-G-CGTCG---T-CA-G--ACG--CC-CCG-------C--CGCATTCCCGAGGCGTTTC===
Oecetis              ---CTCG-C---GCTCCGTCCCAGGGAAGATGCGCG-C-A-CGTCT---C-CG-C--ACG--TG-CCG-------C--CGCATTCCCGAGGCGTTTC===
B.strigosus          ******G-G-----G-T-G--GAGGGAAGATGTG-T-A-A-TCT-A---TCAT-A--TT---AA--CA-------C--CGCACTCCCGGRATGTCTCA-A
Boreus               ---CTTA-A---G-T-GAACTCAGGGAAGACGGA-T-C-G-CGT-C---TCGA-T--GC---GA--TC-------C--CGCACTCCCGGGGCGTCTCACT
Merope               ---TTTG-T---G-T-T-TCTAAGGGATGATGGG-T-T-G-TGC-C---ACAA-T--AT---AA--CC-------C--CGCAATCCCGGGACGTCTCATT
Panorpa              ---TACC-C-AAG-T-GAATTTAGGGAAGATGTA-T-A-A-TCC-T---A-AT-G--AT---TG--TA-------C--CGCATTCCCAGGACGTCTCATA
Ctenocephalides      ---CTTA-A---G-T-GAACTGAGGGATGACGGA-C-C-G-CATCT---ACGG-AT-GC---GT--GC-------T--CGCAATCCCGGGGCGTCTCACT
Orchopeas            ---CTTA-T---G-C-GGACTGAGGGATGATGGT-T-G-G-CAT-T---ACGG-A--GC---AA--AC-------T--CGCAATCCCGGGGCGTCTTACT
Tipula               &&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&TTCATCCATGGGCGTTTT///
Laphria              &&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&TCCATCCCGGGACGTTCT///
Drosophila           &&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&ACAATCCCGGGGCGTTCT///
Mythicomyia          &&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&&ACAATCCCGGGGCGTTCC///
Caenocholax          $$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$GCAATCATTGAATATTCA///
Elenchus             $$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$GCAATCATTGAATATTTT///
Crawfordia           $$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$GCAATCACTGAATATTTA///
X.pecki              $$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$$GCAATCACTGAATATTTT///
```

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INSERT 4 $$$   Strepsiptera
Caenocholax     C--TAAA-AC-AATGTGACT--T-GAGTT-T-T-G-T-T-A-CTCT---AT-TTT-AA---G---T----TTTT-GG-TT-T-TA--A-T-T-CA-AA-A
Elenchus        C--TAAA-A--AATGTG--T----G-------------C-A--T-T----T-TTT----------T----TY-------C----A--A-T-A--A-AA-A
Crawfordia      A--GTGT-TT-TTCGTTA-T--T-G-GTT-T-T---T-C-G-GTCG---AA-TTG-AA---G---T----TCTT--T-TC-G-GA--G-G-A-TG-GA-T
X.pecki         AAATTTTTATCAATTTTTCTTTTTTACTTTTCTTTTTTTTTTGTTTTTTAAATTTTAAATAGAAATAAAATTTTTTGCTTGTATACCGTTTTTTGCGTGT

Caenocholax     A-AGAGAATAGCGGCGGCGGCTTCTCAAGTACA-T-TA-AACTAAAT-A-A-AAAC-TAAAAGC--AA-AATGAAA-GTGAAAAGAAAG-A-A--C-AGA
Elenchus        A-ATCGNAAAA-A-ATT-A-TTT-TAAAA-CCA-A--A-AGCGAAAT-G-A-AAG--TAATTG---AA-A-TG----GTGGAN-TAAT--T----T-TTC
Crawfordia      A-ATTCGATCG-GGATTTAATATCGAAAATTTT-T-TA-TAGAATTT-G-A-AAAC-CAAAAGC--AC-AATGAAA-GTGAAAAAAGTG-A-A--T-TTG
X.pecki         ATATTTTTAAAAAAATTTTGTTTTTTTTTTTTAATTTAAAAAAAAAATAAAAAAAAAGAAAAAGATTAAGAATTAATTGTAAATAAAATTTAAAAACCAAA

Caenocholax     AGCATT-GTG----TAA---TAA-C---GTGTTTTGGTTTTTC-TA-AAATGATGAGATCGATTT--G-CT--GC--TGCTTTGAA-AA-AAGC--G-A-
Elenchus        TCCATT-TCA-----AA---TGA-T---GA-A-AT-TGTAGAC--A-AAGT-A--AAATTTATTT--T-AT------T--TTT-AT-CT-ATT-----A-
Crawfordia      TCGGGT-TCG----TTT---GGA-T---TTGAGAAATTCACTT-TA-AAGTGATGAAATTTTTTTCAGTCTT-GCA-CGCGCAGCAGCAGCAGCT-G-CT
X.pecki         AGCATAAGCAAAAGTAAAAAGAAATAAATATTTTTATTTATTTTTTGGAGTGATGAAATTTTAAAAAAAAAAAGAAATG-GAAAAAAATTTTTTTTCCT

Caenocholax     C-G--A-A-A-A-A-G-A--GATC
Elenchus        -----A----------------TT
Crawfordia      GTGT-G-AGAGCGGCGGAATGATT
X.pecki         TTTTTTTAAAGA-AAAAAAAAATT
```

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                   ——Variable——┐                                                                             300▼
Trigoniopthalmus   CG-CATT-TACGCGG-TG-AGGCGCACCTAGAGCGCACACGTTGGGACCCGAAAGATGGTGAACTATGCCTGGCCAGGACGAAGCCAGGGGAAACCCTGG
Ephemerella        ((((((((((((((((((((GGCGCACCCAGAGCGCACACGTTGGTACCCGAAAGATGGTGAACTATGCCTGGCCAGGACGAAGCCAGGGGAAACCCTGG
Libellula          CC-TCTG-CTTGAGG-GA-AGGCGCACCCAGAGCGCACACGTTGGGACCCGAAAGATGGTGAACTATGCCTGGCCAGGACGAAGTCAGGGGAAACCCTGA
Agrion             CC-TCAT-CGCGAGG-GG-AGGCGCACCCAGAGCGCACACGTTGGGACCCGAAAGATGGTGAACTATGCCTGGCCAGGACGAAGTCAGGGGAAACCCTGA
Megarcys           TG-TCAT-TGCGACACAGTAGGCGCACCCAGAGCGTACACGTTGGGACCCGAAAGATGGTGAACTATGCCTGGCCAGGTCGAAGTCAGGGGAAACCCTGA
Cultus             TG-TCAT-TGCGACACAGTAGGCGCACCCAGAGCGTACACGTTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGTCGAAGTCAGGGGAAACCCTGA
Mantis             ))))))))))))))))))))GGCGCACTCTGAGCGTACACGTTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Melanoplus         CC-TCAT-TGCGAGG-TG-AGGCGCACCTAGAGCGTACACGTTGGGACCCGAAAGATGGTGAACTATGCCTGGCCAGGACGAAGTCAGGGGAAACCCTGA
Oligotoma          CC-TCAT-TGCGAGG-AG-AGACGCACCTAGAGCGTACACGTTGGGACCCGAAAGATGGTGAACTATGCCTGGCCAGGACGAAGTCAGGGGAAACCCTGA
Saldula            TC-TCAT-TGCGAGT-GG-AGGCGCACCTAGAGCGCACACGTTGGGACCCGAAAGATGGTGAACTATGCCTGGCCAGGACGAAGCCAGGGGAAACCCTGG
Buenoa             TC-TC-T-TACGAGT-GG-AGGCGCACCCAGAGCGTACACGTTAGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGCCAGGGGAAACCCTGG
Lygus              TC-TCAT-TGCGAGA-GG-AGGCGCACCTAGAGCGTACACGCTGATACCCGAAAGATGGTGAACTATGCCTGGCCAGGACGAAGCCAGGGGAAACCCTGG
Priacma            GCCTCAT-TGCGAGG-CG-AGGCGCACCCAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Colpocaccus        -C-TTAT-TGCAAGT-TG-CGGCGCACCAAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Cybister           -C-TCAT-CGCGAGG-CG-AGGCGCACCACGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Xyloryctes         -C-TCAT-AGCGAGA-AG-AGGCGCACCAAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Octinodes          -C-TCAT-TGCGAGA-AG-AGGCGCACCTAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGCAACCCTGA
Rhipiphorus        -C-TCAT-TGCGAGA-AG-AGGCGCACCTAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Tenebrio           -C-TCAT-TGCGAGA-AG-AGGCGCACCAAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Tetraopes          -C-TCAT-CGCGAGA-AG-AGGCGCACCAAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Corydalus          -C-TCAT-CGCGAGA-CG-AGGCGCATCCGGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Agulla             -C-TCAT-CGCGAGA-TG-AGGCGCATCGAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Lolomyia           ++++++++++++++++AG-AGGCGCACCTAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Mantispa           ++++++++++++++++AG-AGGCGCACCCAGAGCGTATACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Hemerobius         ++++++++++++++++AG-AGTCGCACCTAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
M.immaculatus      ++++++++++++++++AA-AGGCGCACCTAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Hemitaxonus        -C-TCAT-TACGAGA-AG-AGGCGCACCCAGAGCGTACACGTTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Ophion             -C-TCAT-TGCGAGA-AG-AGGCGCACCCAGAGCGTACACGTTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Dasymutilla        -C-TCAT-TGCGAGA-AG-AGGCGCACCCAGAGCGTACACGTTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Apoica             -C-TCAT-TGCGAGA-AG-AGGCGCACCCAGAGCGTACACGTTGGGACCCGAAAGATGGTGGACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Monobia            -C-TCAT-TACGAGA-AG-AGGCGCACCCAGAGCGTACACGTTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
P.fuscatus         -C-TCAT-TGCGAGA-AG-AGGCGCACCCAGAGCGTACACGTTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGACGAAGTCAGGGGAAACCCTGA
Galleria           TCC-AATCCGTGA-A-TGTGGGCGCGCTCTGAGCGCAGATGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGTCGAAGTCAGGGGAAACCCTGA
Papilio            TCC-AATCTGTGA-A-TGTAGGCGCGCTCTGAGCAGAGATGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGTCGAAGTCAGGGGAAACCCTGA
Ascalapha          TCC-AATCTGTGA-A-TGCAGGCGCGCTCTGAGCATAAATGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGTCGAAGTCAGGGGAAACCCTGA
Hydropsyche        ==============A-TCGAGACGCACTGAGAGCGCGCACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGTCGAAGTCAGGGGAAACCCTGA
Pycnopsyche        ==============A-TCGAGACGCACTGAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGTCGAAGTCAGGGGAAACCCTGA
Oecetis            ==============A-TCGAGACGCACTGAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGTCGAAGTCAGGGGAAACCCTGA
B.strigosus        -----AT-TGCGA-T-TAGAGGCGTACCTAGAGCATACACGCTGCGACCCGAAAGATGGTGAACTATGCCTGGTCAGGTGGAAGTCAGGGGAAACCCTGA
Boreus             C--TCAT-TGCGA-G-AAGGGGCGCACCCAGAGCGTACACGCTGGGACCCGAAAGGTGGTGATCTATGCCTGGTCAGGTCGAAGTCAGGGGAAACCCTGA
Merope             C--TCAT-TGCGA-G-TAGAGGCGTACCTAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGTCGAAGTCAGGGGAAACCCTGA
Panorpa            T--TCAT-TGCGA-A-TAGAGGCGTACCAAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGTCGAAGTCAGGGGAAACCCTGA
Ctenocephalides    C--TCAT-TGCGA-G-AAGAGGCGCACCCAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGTCGAAGTCAGGGGAAACCCTGA
Orchopeas          C--TCAT-TGNGA-G-AAGAGGCGCACCAAGAGCGTACACGCTGGGACCCGAAAGATGGTGAACTATGCCTGGTCAGGTCGAAGTCAGGGGAAACCCTGA
Tipula             //////////AG-T-TA-AAGCGTACTGTAAGCATATATACTGTGACCCGAAAGATGGTGAACTATACCTGATCAGGTCGAAGTCAGGGGAAACCCTGA
Laphria            //////////AA-C-TA-GAGCGTACCTTGAGCATATATGTTGTGACCCGAAAGATGGTGAACTATACCTGATCAGGTTGAAGTCAGGGGAAACCCTGA
Drosophila         //////////AA-C-TG-GAACGTACCTTGAGCATATATGTTGTGACCCGAAAGATGGTGAACTATACTTGATCAGGTTGAAGTCAGGGGAAACCCTGA
Mythicomyia        //////////AA-C-TG-GAGCGTACCTTGAGCATATATGTTGTGACCCGAAAGATGGTGAACTATACCTGATCAGGTTGAAGTCAGGGGAAACCCTGA
Caenocholax        //////////AGGT-CG-GAATATATCAAGAGCATACTTGTTGGGACCCGAAAGATGGTGAACTATACCTGGCCAGGATGAAGTCAGGAGAAATTCTGA
Elenchus           //////////TAGT-CG-AAATATATCAAGAGCATAATTGTTGGGACCCGAAAGATGGTGAACTATACCTGGCCAGGGTGAAGTCAGGAGAAATTCTGA
Crawfordia         //////////CAGT-CG-AAATATATCAAGAGCATACTTGTTGGGACCCGAAAGATGGTGAACTATACCTGGCCAGGATGAAGTCAGGAGAAATTCTGA
X.pecki            //////////AAGT-CG-AAATATATCAAGAGCATACTTGTTGGGACCCGAAAGATGGTGAACTATACCTGGCCAGGATGAAGTCAGGAGAAATTCTGA
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INSERT 5 %%%
Colpocaccus      TATATATAAT ATTTATATTA TTTTATAAA

INSERT 6 ^^^     Megaloptera + Raphidioptera
Corydalus        AGAACGGACGTCCGCGCGCTCACGCGCGCTCTCGTCCG-ACGTACGGGAGGATGCGCGCGTCCGTCGTCGGGGCGTACTACTCTCTTCGATCGACGCGGC
Agulla           GCGTCGTTCGTGCGCGCGCGCTCG-TCGCGCGCGTACGTTCGACCGAGGGAAGATACGCGTACG-C-TACGTGCG--CGAAAATGTG-TAT-AACGTA-C

Corydalus        GCGCGCC
Agulla           GCG-T-C

INSERT 7 >>>     Neuroptera
Lolomyia         TATTATTAATTGTTTTGCGGAATTTATT-TTTATGTT-GCAAATTAAATAATAAAGGGAAGATATATTTGTATTATGTATTAAATATC
Mantispa         -ATG-TTATATAAT----ATATT-G-CA-AA-ATGTA-TGG-TATT--GCA-TAAGGGAAGATATATTTTTACTATGTGTTAAATATC
Hemerobius       -TGG-TTAATTATT----GGCTT-CACG-GC-CTTTAGTTGTTAAAAATCA-TAAGGGAGGATATATTTAAATTATGTATTAAATGTC
M.immaculatus    -ATAATTTTTTATTTGG-AAATTTYTTT-TTTATTTA-TGAATACAAAAATTTGAGGGAGGATATATTTTAATTATGTATTGAATATC

INSERT 8 &&& Diptera
Tipula           TA--A-TATATGGGATTACATGTG-A--T-T-GT-ATA--TAATT----
Laphria          TGTTA-TATATGGGATCATATATATATATATGTTTATT-ATATATATAT
Drosophila       TA--A-TA-ATGGGATTAGTTTTTTAGCTAT-TT-ATAGCTAATTA-AC
Mythicomyia      TGTTATTACATGGGATGA-ATATATTT-TCTGAA-ATA-TGAAATATAC
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                                                                                                  ┌─────28S b1──────┐
Trigoniopthalmus    TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAGCTTGGTATAGGGGCGAAAGACTAATCGAACC-AT-C-GTAGCTGGTTCCTTCCGA
Ephemerella         TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACTAATCGAACC-AT-C-GTAGCTGGTTCCTTCCGA
Libellula           TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAGCTGGGTATAGGGGCGAAAGACTAATCGAACC-AT-C-GTAGCTGGTTCCTTCCGA
Agrion              TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAGCTGGGTATAGGGGCGAAAGACTAATCGAACC-AT-C-GTAGCTGGTTCCTTCCGA
Megarcys            TGGAGGACCGTAGCGATTCTGACGTGCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACTAATCGAGCATCT-TAGTAGCTGGTTCCTTCCGA
Cultus              TGGAGGACCGTAGCGATTCTGACGTGCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACTAATCGAGCATCT-TAGTAGCTGGTTCCTTCCGA
Mantis              TGGAGGTCCGCAGCGATTCTGACGTGCAAATCGATCGTCAGAGCTGCCTATAGGGGCGAAAGACTAATCGAACC-AT-TAGTAGCTGGTTCCTTCCGA
Melanoplus          TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAGCTGGGTATAGGGGCGAAAGACTAATCGACCA-CT-TAGTAGCTGGTTCCTTCCGA
Oligotoma           TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Saldula             TGGAGGTCCGCAGCGATTCTGACGTGCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACTAATCGAACA-CT-TAGTAGCTGGTTCCTTCCGA
Buenoa              TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACTAATCGAACA-CT-TAGTAGCTGGTTCCTTCCGA
Lygus               TGGAGGTCCGCAGCGATTCTGACGTGCAAATCGATCGTCGGAGCTGGGTTTAGGGGCGAAAGACCAATCGAACA-CT-TAGTAGCTGGTTCCTTCCGA
Priacma             TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Colpocaccus         TGGAGGTCCGCAGCGATTCTGACGTGCAAATCGATCGCATGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Cybister            TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGA-CC-ATCTAGTAGCTGGTTCCTTCCGA
Xyloryctes          TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGA-CC-ATCTAGTAGCTGGTTCCTTCCGA
Octinodes           TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGA-CC-ATCTAGTAGCTGGTTCCTTCCGA
Rhipiphorus         TGGAGGTCCGTAGCAATTCTGACGTGCAAATCGATTGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGA-CC-ATCTAGTAGCTGGTTCCTTCCGA
Tenebrio            TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGA-CC-ATCTAGTAGCTGGTTCCTTCCGA
Tetraopes           TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGA-CC-ATCTAGTAGCTGGTTCCTTCCGA
Corydalus           TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-GTCTAGTAGCTGGTTCCTTCCGA
Agulla              TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-GTCTAGTAGCTGGTTCCTTCCGA
Lolomyia            TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Mantispa            TGGAGGTTCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Hemerobius          TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
M.immaculatus       TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Hemitaxonus         TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Ophion              TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Dasymutilla         TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Apoica              TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Monobia             TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
P.fuscatus          TGGAGGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Galleria            TGGAGGACCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Papilio             TGGAGGACCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Ascalapha           TGGAGGACCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Hydropsyche         TGGAGGACCGTAGCGATTCTGACGTGCAAATCGATCGTCTGAACTGGGTATAGGGGCGAAAGACTAATCGAACT-ATCTAGTAGCTGGTTCCTTCCGA
Pycnopsyche         TGGAGGACCGAAGCGATTCTGACGTGCAAATCGATCGTCCGAACTGGGTATAGGGGCGAAAGACTAATCGAACT-ATCTAGTAGCTGGTTCCTTCCGA
Oecetis             TGGAGGACCGAAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACT-ATCTAGTAGCTGGTTCCTTCCGA
B.strigosus         TGGAGGACCGTAGCGATTCTGACGTGCAAATCGATCGTTCGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Boreus              TGGAGGACCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Merope              TGGAGGACCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Panorpa             TGGAGGACCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Ctenocephalides     TGGAGGACCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGGGGCGAAAGACTAATCGAACA--TCTAGTAGCTGGTTCCTTCCGA
Orchopeas           TGGAGGACCGTAGCGATTCTGACGTGCAAATCGATCGTCGGAACTGGGTATAGCGGCGAAAGACTAATCGAACA--TCTAGTAGCTGGTTCCTTCCGA
Tipula              TGGAGGATCGTAGCAGTTCTGACGTGCAAATCGATTGTCAGAATTGGGTATAGGGGCGAAAGACCAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Laphria             TGGAAGACCGAAACAGTTCTGACGTGCAAATCGATTGTCAGAATTGGGTATAGGGGCGAAAGACCAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Drosophila          TGGAAGACCGAAACAGTTCTGACGTGCAAATCGATTGTCAGAATTGAGTATAGGGGCGAAAGACCAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Mythicomyia         TGGAAGACCGAAACAGTTCTGACGTGCAAATCGATTGTCAGAATTGGGTATAGGGGCGAAAGACCAATCGAACC-ATCTAGTAGCTGGTTCCTTCCGA
Caenocholax         TGGAGGTCCGAAGCGATTCTGACGTGCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACTAATCGACCC-ATCTAGTAGCTGGTTCCTTCCGA
Elenchus            TGGAGGCCCGTAGCGATTCTGACGTGCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACTAATCGACCC-ATCTAGTAGCTGGTTCCTTCCGA
Crawfordia          TGGAAGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACTAATCGACCC-ATCTAGTAGCTGGTTCCTTCCGA
X.pecki             TGGAAGTCCGTAGCGATTCTGACGTGCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACTAATCGACCC-ATCTAGTAGCTGGTTCCTTCCGA
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INSERT 9 *** Bittacus
B.strigosus      TTATATATATATATAT

INSERT 10 ((( Ephemeroptera
Ephemerella      GTGCTACCGTCGCTCGTCGGCGG

INSERT 11 ))) Mantodea
Mantis           GGCTTCGGCCGTG

INSERT 12 +++ Neuroptera
Lolomyia         A-T-ATTAC-TAT-A-TA--G-A-TATT-AATTTGTAGTTTG--T-CTC-GTGTGTGTGTGTGTGTGTCC-C-TTGTGCATTC-TCGC-ACGCGCGCACG
Mantispa         AATTATTATATTTGAATAACGGAGTTTTTAATGTCTCGACGGCATATTCAGTGTAAGTGTAGGTTTTTCGGAATTATAACTGCCTGTCTATGTGTTCGGG
Hemerobius       A-T-ATT-T-ATT-C-TT------TT---A-T------A----------------T-T-T-T-T-------A-T----CAAT--A-T---T------G--
M.immaculatus    A-T-ATT---ATT-C-TTA-----TA---A-T------T----------------A-T-T-T-T-------A-T----AATT--T-T---T------A--

Lolomyia         C-TCTACAGAATATAAT-G-TTC-TATATAGT
Mantispa         CGTGTACATTGGCTTGTCGATTCGTTTATAAT
Hemerobius       ---------A----AAT-G------A-AT-A-
M.immaculatus    ---------T----TAT-G------A-AT---

INSERT 13 === Trichoptera
Hydropsyche      GAGAAATGCCCCCGTGCGATT
Pycnopsyche      GAGAAA-GCCCCCGTGCGATT
Oecetis          GAGAAA-GTCACCGTGCGATT

INSERT 14 ///   Halteria
Tipula           -A--A--T-CAACTC---A-----T-A-TT-G-C--T----T-------AT--GT---T--T-T-A--T-GA-----G-TT-AA
Laphria          ATATA-GT-TATGCA-TTT-----T-A-AT-A-T-ATT--TTA-T--ATATT-ATA--T--ATG-C--CTCT--A--A-CT-AG
Drosophila       ATATA-GT-TATGTA---T-------A-AT-G-T-ATA---T--T---TAT--AT---T--A-G-C--CTCT--A--A-CT-GG
Mythicomyia      AT-CA-GT-TATGTA-TAG---A-T-T-GT-G-T-ATG-CTTC-G--GCATGCACAT-TT-ATG-C--CTCT--A--A-CT-GG
Caenocholax      GGACACGTGTTTTTTGTTGGCGACTGATGACGGAGATGGCGCAAGTTGTTTTCGT-TGTTGTTGTCAGCTGTTCACGAGGTCGG
Elenchus         GG--A--C--ACGTA---T-----T-ATAT-T-T--T----T-----A-AT--AT---T--T-T-A--T-GT--A--G-TC-GA
Crawfordia       GG--A--C--ACGTA---A-------A-AT-T-T--T----C-----G-A---AT---T--T-T-A--C-GC--A--G-TC-GA
X.pecki          GA-CA--CGTAATTT---T-----T-TCTT-A-A--T----T-----G-AT--AT---T--T-T-A--C-GA--A--G-TC-GA
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APPENDIX 3
MORPHOLOGICAL DATA

The following morphological data have been compiled from various sources, but especially from Hennig (1981), Kristensen (1975, 1981, 1991, 1995) and Boudreaux (1979), including recent contributions by Kukalová-Peck (1978, 1985) and Minet and Bourgoin (1986). The multistate characters were treated as additive, unless specified as nonadditive in the list below. These ordinal-level characters were extrapolated to each sequenced exemplar in the total evidence analyses. The data matrix is provided in Figure A1.

Character List

1. *Cerci.*—Absent (0); present, originating from appendages of 11th abdominal segment (1); simplified (2); unsegmented (3) [nonadditive] (Hennig, 1981). Simplified form has no more than two segments (Kristensen, 1981).
2. *Malphigian tubules.*—Developed, many (>6) (0); lost (1); four (2) [nonadditive] (Kristensen, 1975).
3. *Anterior tentorium.*—Present (0); reduced (1) (Kristensen, 1975; Boudreaux, 1979).
4. *Posterior tentorium.*—Absent (0); bearing arms (1); arms fused (2). The posterior arms are fused together, forming a single transverse apodeme in the ectognath insects (Kristensen, 1975; Boudreaux, 1979).
5. *Ovipositor.*—Absent (0); present (1); vestigial (2 valve pairs) (2); modified (3); fused (4) [nonadditive]. The ovipositor is composed of valvulae from abdominal venter VIII + IX. The modified condition in this case refers to reduction in the second valvulae, the third valvulae serving as the functional components of the ovipositor (Boudreaux, 1979; Kristensen 1981).
6. *Caudal filament.*—Absent (0); present, long (1); short (2). The third single caudal filament (paracerus, terminal filament) was considered 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 (Boudreax, 1979; similar structures in Plecoptera and Dermaptera are of arguable homology).
7. *Mandibular articulation.*—Monocondylic (0); dicondylic (1); anterior articulation fixed (2). A monocondylous mandible is found in Archaeognatha, two articulations being synapomorphic for Thysanura and all pterygote orders (Hennig, 1981). Kukalová-Peck (1985) discussed the difference in the anterior articulation among pterygotes.
8. *Gonangulum in ovipositor base.*—Absent (0); present (1). Presence of a distinct gonangulum in the ovipositor base is taken as synapomorphic for Dicondylia (see summary by Hennig, 1981).
9. *Origin of ventral mandibular and maxillary (stipital) adductors.*—On endoskeletal plates (0); on tentorium (1) (Chaudonneret, 1950; see also Kristensen, 1975).
10. *Fulturae.*—Present (0); absent (1) (Francois, 1969, 1970).
11. *Postoccipital ridge.*—Absent (0); internal ridge lateral only (1); continuous (2) (Lauterbach, 1972; see Kristensen, 1975).
12. *Tracheal commisures and connectives.*—Not developed in abdomen (0); developed in abdomen (1) (Stobbart, 1956; see Kristensen, 1981).
13. *Amniotic cavity.*—Absent (0); open (1); closed (2) (Kristensen, 1991).
14. *Median fusion (at least basal part) of male penes.*—Absent (0); present (1) (Kristensen, 1975).
15. *Paired female genital openings.*—Absent (0); present (1). Kristensen (1975) characterized these as "retained" in Ephemerida and "lost" in Odonata and Neoptera, but they are not present in other hexapods (Snodgrass, 1933; Boudreaux, 1979).
16. *Two pairs of wings.*—Absent (0); present (1); absent in adult females (2). "Wings" constitutes a suite of characters. Also, there are 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).
17. *Two coxal proprioreceptor organs.*—Absent (0); present (1) (Lombardo, 1973, as cited by Hennig, 1981: note 132).
18. *Basal wing brace.*—Absent (0); present (1). Anastomosis of CuP and anterior anal vein (Kukalová-Peck, 1985).
19. *Media stem.*—Absent (0); present (1). Basal fusion of MA and MP (Kukalová-Peck, 1985).
20. *Superlinguae.*—Absent (0); present (1). Well developed in ephemerid nymphs. Reports in Dermaptera (Giles, 1963) appear actually to represent nonhomologous structures (Moulins, 1969), as may also be true of the lateral hypopharyngeal lobes of primitive Odonata (Tillyard, 1928; see Kristensen, 1975). Boudreaux's (1979) contention that superlinguae do not occur in Entognatha is not true of the ground plan (Kristensen, 1981).
21. *Habitat of nymphs.*—Terrestrial (0); aquatic (1).
22. *Subimago.*—Present (0); absent (1). This character was questioned by Sharov (1957; see also Kristensen, 1975; Hennig, 1981), who suggested that a protoperlarian had a subimago stage. Illies (1968) and Kristensen (1975), 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 (but see Kukalová-Peck, 1978).
23. *Tracheation.*—Anterior only (0); arch (1). 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

	1 5 10 15 20 25 30 35 40 45 50 55 60
Collembola	0101000?000000000??100?000000?0???000000000000000?00??000?00
Archaeognatha	10021100001011000??000?000000?0???000000000000000?00??000?00
Ephemerida	1002011?11212011111110000000100000000000000??000000000000000
Odonata	1002122111212101111011111111200000000000000??000000000000000
Plecoptera	1012002?1121200110101111111111?11000111100200100000000001100
Blattodea	100210211121210110000111111111111031110010111100002111110011
Phasmida	300230211121210110100111111111111001110000111110100000000011
Mantodea	100210211121210110000111111111111001110010111100000111110011
Dermaptera	100220201121200110000111111111?1102111010121111000111100001?
Orthoptera	200230211121210110100111111111111001110000111110010000000011
Embioptera	2002002?1121210210100111111111?10021111101200121000100000001
Psocoptera	020210211121210110000111011111110111110000100000100000001010
Pthiraptera	02021021112121001??001?111111?1???111100001??0001?00??001?10
Hemiptera	020210211121210110000111111111110111110000100000100000001010
Thysanoptera	020210211121210110000111111111110111110000100000100000001010
Coleoptera	100210211121210110000111111111110111110000100000100000001110
Megaloptera	100240211121210110001111111111110111110000100000100000001110
Raphidioptera	100240211121210110000111111111110111110000100000100000001110
Neuroptera	100240211121210110000111111111110111110000100000100000001110
Lepidoptera	1002002?1121210110000111111111110141110000100000100000001110
Trichoptera	1002002?1121210110001111111111110111110000100000100000001110
Mecoptera	1002002?1121210110000111111111110111110000100000100000001110
Siphonaptera	1002002?112121001??001?111111?1???111100001??0001?00??001?10
Hymenoptera	100210211121210110000111111111110111110000100000100000001110
Diptera	1002002?11212101100001111111111???1111000010?000100000001110
Strepsiptera	1010002??1212102100001111??111?10111110000000000010000000?110

	61 65 70 75 80 85 90 95 100 105 110 115 120
Collembola	0000000000000000000000000000000000000000?00000000?0000000000
Archaeognatha	0000000000000000000000000000000000000000?00000000?0000000000
Ephemerida	000100000100000000000000000000000000000000000000000000000000
Odonata	000200000100000000000000000000000000000000000000000000000000
Plecoptera	101200000100100000000000000000000000000000000000000000000000
Blattodea	010110021211110000000000000000000000000000000000000000000000
Phasmida	001101100100101100000000000000000000000000000000000000000000
Mantodea	010110021211120000000000000000000000000000000000000000000000
Dermaptera	010200010100100100000000000000000000000000000000000000000000
Orthoptera	001100000100100000000000000000000000000000000000000000000000
Embioptera	101201100100101000000000000000000000000000000000000000000000
Psocoptera	000220000100000011111100000000000000000000000000000000000000
Pthiraptera	0002200001000002111111100000000000000000?00000000?0000000000
Hemiptera	000220000100000011110001100000000000000000000000000000000020
Thysanoptera	000220000100000011110001100000000000000000000000000000000000
Coleoptera	000100000100000000010000011111100001000110000000000000000000
Megaloptera	000100000100000000010000011111100000111101110100000000000000
Raphidioptera	000100000100000000010000011111100000011101110000000000000000
Neuroptera	000100000100000000010000011111100000011101000100000000000000
Lepidoptera	000100000100000000000000011110011110111100001111111111120000
Trichoptera	000100000100000000000000011110011110111100001111111111110000
Mecoptera	000100000100000000000000011110011110111100001111000000001111
Siphonaptera	000100000100000002000000011110011110011100?000?1010?000000?001
Hymenoptera	000100000100000000000000011110011100110100000000000000000000
Diptera	000100000100000002000000011110011110011100001111000000002111
Strepsiptera	0001000001000000?00000001001 0??001?0?1110000???00000000112?

FIGURE A1. Data matrix for 176 insect morphological characters.

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              121 125  130  135  140  145  150  155  160  165  170  175
              |   |    |    |    |    |    |    |    |    |    |    |
Collembola    00000000000000000010000000000000000000000000000000000000
Archaeognatha 00000000000100000010000000000000000000000000000000000000
Ephemerida    00000000000200000001000000000000000000000000000000000000
Odonata       00000000000211111001000000000000000000000000000000000000
Plecoptera    00000000000200000100000000000000000000000000000000000000
Blattodea     00000000000200000001000000000000000000000000000000000000
Phasmida      00000000000200000001000000000000000000000000000000000000
Mantodea      00000000000200000001000000000000000000000000000000000000
Dermaptera    00000000000200000001000000000000000000000000000000000000
Orthoptera    00000000000200000001000000000000000000000000000000000000
Embioptera    00000000000200000001000000000000000000000000000000000000
Psocoptera    00000000000200000001000000000000000000000000000000000000
Pthiraptera   00000000000200000001100000000000000000000000000000000000
Hemiptera     00000000000200000001011100000000000000000000000?00000000
Thysanoptera  00000000000200000001000000000000000000000000000000000000
Coleoptera    00000000000300000001000001111000000000000000000000000000
Megaloptera   00000000000300000001000000000000000000000000000000000000
Raphidioptera 00000000000300000001000000000000000000000000000000000000
Neuroptera    00000000000300000001000010000000000000000000000000000000
Lepidoptera   00000000000300000001000000000000000000000000000000000111
Trichoptera   000000000003000000010000000000000000000000000000?1111000
Mecoptera     11111201111300000001000000000000000000000111100000000000
Siphonaptera  ??111111111300000001100000000000000001111000000000000000
Hymenoptera   00000000000300000001000000000000011110000000000000000000
Diptera       11111110000300000001000000000000000000000001011110000000
Strepsiptera  00????0??0030000000100000000011110000000000001000?00000000
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FIGURE A1. Continued.

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). For alternative interpretations, see papers cited by Kristensen (1975).

24. *Posterior tracheation of leg.*—Absent (0); present (1). Kristensen (1975) pointed 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 ground plan for Ephemerida.
25. *Direct spiracular musculature.*—Absent (0); present (1). In odonates and neopterans, muscles insert directly on the sclerotized spiracular lip (Miller, 1962; Poonawalla, 1966). In contrast, Ephemerida have no direct spiracular muscles but in their place use compression through contraction of dorsoventral body wall muscles (Ford, 1923; Birket-Smith, 1971) (see Kristensen, 1975; Boudreaux, 1979, citation of Maki [1938] on presence in Zygentoma).
26. *Tentorio-lacinial muscle.*—Present (0); absent (1). Ephemerida are the only pterygotes with this muscle. Its presence is probably plesiomorphic, because a similar muscle is found in Archaeognatha. However, this muscle is not known to be present in Zygentoma. Odonata and Neoptera do not have this muscle, and if it is part of the pterygote ground plan then it supports their sister-group status (see Matsuda, 1965; Kristensen, 1975).
27. *Tentorio-mandibular muscles.*—Several bundles (0); one (1). Never more than one in Odonata and Neoptera. More bundles may be retained in Ephemerida according to Matsuda (1965) and Kristensen (1975).
28. *Loss of pterothoracic muscles.*—No (0); yes (1). Second phragma-tergum II, profurcasternum-mesobasalare, furca-first axillary muscles are present in Ephemerida (and Zygentoma) but not in Odonata or Neoptera (Matsuda, 1970; Hamilton, 1971; see Kristensen, 1975).
29. *Sperm transfer.*—Indirect (0); copulation (1); indirect, using claspers (2) [nonadditive] (Boudreaux, 1979).
30. *Wing flexion.*—Absent (0); present (1). A pleural muscle inserted on the third 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).
31. *Third valvulae forming sheath.*—Absent (0); present (1). In all Neoptera with a functional ovipositor, the third valvulae (=gonoplacs of Scudder, 1961) are primarily developed along the full length of the ovipositor, forming a protective sheath for the first and second valvulae. Absent in Odonata (Kristensen, 1975), Ephemerida, etc.
32. *Anal furrow.*—Absent (0); present (1). Forbes (1943) pointed out that an anal furrow separates

the anal lobe from the anterior portion of wing (see Hennig, 1981).

33. *Enlarged hind-wing vannus.*—Small (0); enlarged (1). This character refers to the size of the anal fan of the hind wings (Kristensen, 1981).
34. *Jugal bar.*—Absent (0); present (1). This character describes whether or not a sclerotization (=jugal bar) is present on the jugum (Kristensen, 1981).
35. *Ocelli.*—Present (0); absent in immatures (1); absent in adults (2); median ocellus absent (3); median ocellus absent in adults (4) [nonadditive] (Kristensen, 1975).
36. *Metameric testes ducts.*—Present (0); absent (1) (Kristensen, 1975).
37. *Male gonocoxopidites IX.*—Articulated (0); not articulated (1). Retention of articulated male gonocoxopodites IX is unique to grylloblattids within Neoptera (Kristensen, 1975).
38. *Metaspina.*—Present (0); absent (1). Reported by Kristensen (1975) to be retained within Grylloblattaria.
39. *Phallomeres.*—Normal (0); reduced (1). Male phallomeres are said to be reduced, in conjunction with the formation of secondary intromittent organs from the eversible ejaculatory duct (Kristensen, 1981).
40. *Male styli.*—Expressed (0); supressed (1). The suppression of male styli was suggested by Boudreaux (1979) to be accompanied by the formation of accessory clasping organs "from various sources" (!).
41. *Segmental arteries.*—Absent (0); present (1) (Kristensen, 1975; Boudreaux, 1979).
42. *Female broodcare behavior.*—Absent (0); present (1).
43. *Trochantin.*—Absent (0); present (1); trochantin–episternal sulcus present (2). This character involves the separation of the trochantin and episternum by a sulcus or membranous line (Kristensen, 1981).
44. *Sclerotization of forewing.*—Membranous (0); sclerotized (1). The forewings are said to be "more or less sclerotized" (see Kristensen, 1981).
45. *Vannus pleated.*—No (0); yes (1) (Kristensen, 1981).
46. *Two cervical sclerites.*—No (0); yes (1). This character is problematic (Kristensen, 1981). 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, because its precise distribution therein is not cited).
47. *Prognathy.*—Absent (0); present (1); gula present (2) [nonadditive]. Sometimes said to be synapomorphic in embiids and dermapterans, but earwigs do not have a gula, whereas webspinners do (Kristensen, 1991).
48. *Dorsal paraglossa flexor.*—Normal (0); "aberrant," "peculiar" (1) (Rähle, 1970; see Kristensen, 1975).
49. *Phallic rudiments produce gonopods.*—No (0); yes (1) (Boudreaux, 1979).
50. *Prominent precostal field.*—Absent (0); present (1) (Kristensen, 1981).
51. *Discoid pronotum.*—Absent (0); present (1); enlarged (2) (Kristensen, 1981).
52. *Pleural sutures.*—Not slanting forward (0); slanting forward (1) (Boudreaux, 1979).
53. *Indirect wing muscles.*—Developed (0); reduced (1). Pterothoracic modifications include reduction of the postnota and phragmata, associated with reduction of dorsolongitudinal and tergosternal indirect wing muscles. Functions of these muscles are, instead, assumed by direct wing depressors and tergopleural-tergocoxal muscles, respectively (see Boudreaux, 1979).
54. *Metathoracic tergosternal wing elevators.*—Present (0); weak or suppressed (1). It has been suggested (see Kristensen, 1981:147) that the initial stage of reduction of the dorsolongitudinal wing depressors and the loss of the metathoracic tergosternal wing elevators may be synapomorphies of Dermaptera and Dictyoptera. Kristensen, however, considered these conditions to be independently derived in these two orders, and variation within each may call this character into serious question.
55. *Coxa conical, backwards directed.*—No (0); yes (1) (Boudreaux, 1979).
56. *Phallomeres.*—Symmetrical (0); asymmetrical (1) (Kristensen, 1981).
57. *Shape of mesotrochantin "holometabolan."*—No (0); yes (1) (Ross, 1965; see also Kristensen, 1975:11).
58. *First branch of Cu.*—Not grooved (0); grooved (1). Adams (1958) suggested several possible synapomorphies shared by Plecoptera and Holometabola. These synapomaorphies are, collectively, largely based on Adams's conception of the holometabolan ground plan and thus are controversial. Although Adams suggested several characters in this regard (few-branched weak stem of posterior branch of M, grooved first branch of Cu, distribution of microtrichiae 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 ground plan (probably neopteran, for some characers not in list above). One representative character from Adams is registered here (see Kristensen, 1975).
59. *Separate coxopleuron.*—Yes (0); no (1) (Kristensen, 1975).
60. *Several male accessory glands arranged in cluster.*—No (0); yes (1) (Kristensen, 1975).
61. *Median ventral excurrent ostia in dorsal vessel.*—Absent (0); present (1) (Kristensen, 1975).
62. *Mesothoracic basisternal fold.*—Absent (0); present (1) (Kristensen, 1975).
63. *Premental lobes.*—Free (0); fused (1). This character from Hennig was considered by Kristensen (1981) to have evolved probably 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 because Kristensen believed them to be divergent (see Kristensen, 1975:13).

64. *Tarsi.*—Not subdivided (0); 5-segmented (1); 3-segmented (2) (Kristensen, 1975).
65. *Sternum I.*—Developed (0); reduced (1); absent (2) (Kristensen, 1975).
66. *Dorsal flexor of paraglossae.*—Absent (0); present (1). This refers to a secondary, dorsal flexor of the paraglossae, probably derived from one of the extrinsic prelabial muscles (Kristensen, 1975).
67. *Second profurca–spinasternal muscle.*—Absent (0); present (1). This muscle is in addition to the primitive profurca–spinasternal muscle and has a more oblique course, with posterior insertion on anterior part of (furca+) spinasternum. Kristensen (1975) considered a similar muscle in phasmids clearly convergent.
68. *Female sternum VII.*—Small (0); large (1); forming vestibulum (2). "Dictyopteran" female postabdominal structure. According to Günther and Herter (1974) and Hennig (1981), there exists a unique structural configuration of the female postabdomen in Dermaptera and Dictyoptera (=Blattaria + Mantodea + Isoptera). The genitalia have a vestibulum formed by enlargement of sternum VII and shortening of ovipositor valves (Kristensen, 1975).
69. *Sex determination.*—XX/XY (0); XX/XO (1) (see Thorne and Carpenter, 1992).
70. *Corporotentorium.*—Absent (0); present (1); perforation through which circumesophageal connectives pass (2) (Kristensen, 1975).
71. *Anterior teeth of proventriculus forming ring of strongly sclerotized teeth.*—Absent (0); present (1) (Kristensen, 1975).
72. *Proventriculus teeth with secondary denticles.*—Absent (0); present (1) (see Thorne and Carpenter, 1992).
73. *Tarsal plantulae.*—Absent (0); present (1) (Minet and Bourgoin, 1986).
74. *Ootheca.*—Absent (0); present (1); ootheca hardened after deposition (2) (see Thorne and Carpenter, 1992).
75. *First axillary sclerite attached close to scutal margin.*—Absent (0); present (1) (Kristensen, 1975).
76. *Sperm axoneme sheaths.*—Absent (0); present (1); two dense sheaths surround the inner and outer singlets (2) (Jamieson, 1987).
77. *Abdominal ganglia.*—Unconcentrated (0); one (1). A so-called "concentrated" nerve cord exists in paraneopterans that is defined as consisting of only two or fewer discrete abdominal ganglia (see Kristensen, 1981:148–150).
78. *Lacinia.*—Broad (0); slender rod (1); stylets (2) [nonadditive] (Kristensen, 1981). For information on lacinial stylets, see Kristensen (1975).
79. *Flagella of spermatozoa.*—One (0); two (1) (Kristensen, 1981).
80. *Gonangulum fused with tergum IX.*—No (0); yes (1) (Kristensen, 1981).
81. *Cibarium.*—Absent (0); present (1). This character is stated as a "unique complement of sclerotizations in the cibarium," attributed to Denis and Bitsch (1973) by Kristensen (1981).
82. *Ovarioles.*—Telotrophic or panoistic (0); polytrophic (1) (Kristensen, 1981).
83. *Basal part of antennal flagellomeres with rupture-facilitating cuticular modification.*—Absent (0); present (1) (Kristensen, 1981).
84. *Mandibles.*—Broad (0); stylettiform (1) (Kristensen, 1981).
85. *Sclerotized rings between antennal flagellomeres.*—Absent (0); present (1) (Kristensen, 1981).
86. *Metamorphosis.*—Incomplete (0); complete (1) (Kristensen, 1981).
87. *Larval eyes.*—Carried over to adult (0); not carried over to adult (1) (Kristensen, 1981, 1991, 1995; Paulus, 1986).
88. *Wing rudiments.*—Evaginated prior to penultimate molt (0); evaginated at larval–pupal molt (1) (Kristensen, 1981, 1991, 1995).
89. *Appearance of external genitalia.*—Prior to penultimate molt (0); penultimate molt (1) (Kristensen, 1981, 1991, 1995).
90. *Cruciate cervical muscles.*—Present (0); absent (1) (Kristensen, 1981, 1991).
91. *Female genitalia.*—First valvulae (gonopohyses 8) developed and separate, second valvulae (gonopophyses 9) discrete, cerci articulated (0); first valvulae strongly reduced and fused, second valvulae not discrete, cerci not articulated (1) (Kristensen, 1981, 1991).
92. *Pretarsal claw of larval leg.*—Paired (0); unpaired (1) (Kristensen, 1981, 1991, 1995).
93. *Silk secretion from larval labial glands.*—Absent (0); present (1) (Kristensen, 1981, 1991, 1995).
94. *Eruciform larvae.*—Absent (0); present (1) (Kristensen, 1981). Kristensen (1991) expressed doubts about this character because primitive Mecoptera (Nannochoristidae) and some primitive Amphiesmenoptera are prognathous.
95. *Outer tergo-coxal remotor muscle.*—Present (0); absent (1) (Kristensen, 1995).
96. *Telomere.*—Present (0); absent (1). This character describes the transverse division of the male gonopod ("paramere") into basimere and telomere (Boudreaux, 1979; Kristensen, 1981). Gonopods are absent in Strepsiptera (Kristensen, 1991).
97. *Abdominal limb buds.*—Repressed (0); "derepressed" (1) (Boudreaux, 1979). Kristensen (1981) rejected a single "derepression" event for megalopteran, hymenopteran, and panorpid larval prolegs.
98. *Gastric caeca.*—Present (0); lost (1) (Kristensen, 1981).
99. *Meron.*—Absent (0); present (1) (Boudreaux, 1979). Kristensen (1981) suggested that the presence of a demarcated meron is probably a ground plan state for Holometabola and that its loss in Hymenoptera and Coleoptera is probably secondary.
100. *Cryptosterny.*—Absent (0); present (1) (Kristensen, 1981).
101. *Flight by posteromotorism.*—No (0); yes (1) (Kristensen, 1981, 1991, 1995).
102. *Intrinsic musculature in (fused) third valvulae.*—Absent (0); present (1) (Mickoleit, 1973; Kristensen, 1981, 1991).

103. *Connection of metepimeron to an apophysis-bearing postepimeron pertaining to abdominal segment I.*—Weakly or not connected (0); firmly connected (1) (Achtelig, 1975, 1978; Kristensen, 1991).
104. *Reinforcement of tergum II acrotergite.*—Absent (0); present (1). The reinforcement of the acrotergite accommodates the origin of strong polyintersegmental muscles. See Kristensen (1991); his source was Achtelig (1975, 1978).
105. *Pleural muscle inserted on first axillary sclerite.*—No (0); yes (1) (Kristensen, 1981, 1991).
106. *Larval stipes.*—Entire (0); transversely divided (1) (Kristensen, 1981, 1991).
107. *Larval cranial cardo-promotor, stipitolacinial, and stipitogalaeal muscles.*—Present (0); absent (1) (Kristensen, 1981, 1991).
108. *Cranial antagonist of the primitive craniolacinial muscle in larva.*—Absent (0); present (1) (Kristensen, 1981, 1991, 1995).
109. *Female heterogamety.*—Absent (0); present (1) (Kristensen, 1981, 1991, 1995).
110. *Double Y-shaped fusion of anal veins.*—Absent (0); present (1) (Kristensen, 1975, 1981, 1991).
111. *Achiasmatic oogenesis.*—Absent (0); present (1) (Kristensen, 1975).
112. *Preholocentric chromosomes.*—Absent (0); present (1) (Kristensen, 1975).
113. *Pterothoracic furcal arms fused with epimeron.*—Absent (0); present (1) (Kristensen, 1975).
114. *Pair of glands opening on sternum V.*—Absent (0); present (1) (Kristensen, 1975).
115. *Outer accessory filaments of sperm flagellum very stout (ca. 300 Å diameter).*—Thin (0); stout (1) (Kristensen, 1975).
116. *Vestiture on wing surfaces between veins.*—Absent (0); dense vestiture of long setae (1); scales (2) (Kristensen, 1975).
117. *Daggerlike mandible with anterior articulation reduced.*—Absent (0); present (1); articulation lost (2) (Kristensen, 1975, 1991, 1995).
118. *Prelabium without endite lobes/ligula and associated muscles.*—No (0); yes (1) (Kristensen, 1975, 1981, 1991).
119. *Labial palp segments.*—Five (0); two (1); absent (2) (Kristensen, 1975, 1991, 1995).
120. *Tentorial muscles of prelabium.*—Present (0); lost (1). This refers to loss of some primitive labial muscles that are retained in the amphiesmenopteran ground plan (see Kristensen, 1975:34, 1981:153).
121. *Structure of posterior notal wing articulation.*—Not modified (0); modified (1) (Kristensen, 1975, 1991, 1995).
122. *Pleural ridge/scutum muscle inserting on posterior notal wing process.*—No (0); yes (1) (Kristensen, 1975, 1991, 1995).
123. *Transverse muscle between profurcal arms.*—Absent (0); present (1) (Kristensen, 1975, 1991).
124. *Lateral labral retractor.*—Present (0); absent (1) (Kristensen, 1975, 1991).
125. *Tentorial adductors of cardo in larva.*—Present (0); absent (1) (Kristensen, 1975). Hinton (1958) recorded this muscle as present for the mecopteran family Boreidae, and Willman (1989) rejected this character for Antliophora (see Kristensen, 1991).
126. *Hypopharyngeal muscles in larva.*—Present (0); retractor of hypopharynx and ventral dilator of salivarium absent (1); loss of mouth-angle retractors and dorsal dilator of salivarium (2) (Kristensen, 1975, 1981).
127. *Larvae.*—Podous (0); apodous (1) (Kristensen, 1975, 1991). This refers to thoracic and/or prolegs.
128. *Extrinsic labral muscles.*—Present (0); absent (1) (Kristensen, 1975, 1991).
129. *Proventriculus with specialized type of cuticular processes, acanthae.*—Absent (0); present (1) (Kristensen, 1975, 1991).
130. *Flagellum of spermatozoon coiled around straight axial mitochondrion.*—Absent (0); present (1) (Kristensen, 1975, 1991).
131. *Procoxa with condylus fitting pleural concavity.*—No (0); yes (1) (Kristensen, 1991).
132. *Coxa–body articulation.*—None (0); pleural, mobile (1); pleural, fixed (2); tricondylic (3) [nonadditive] (Kristensen, 1975; Boudreaux, 1979).
133. *Larval labium.*—Not prehensile (0); prehensile (1). A well-known autapomorphy of Odonata. Most of the following ordinal autapomorphies, which are also familiar, are not referenced; however Kristensen's (1991) listing may be consulted.
134. *Posterior tracheal larval gills.*—Absent (0); present (1) [Odonata].
135. *Lateral cervical sclerite in three pieces.*—No (0); yes (1) [Odonata].
136. *Pteropleura tilted backward with notum small.*—No (0); yes (1) [Odonata].
137. *Male accessory copulatory organs.*—Absent (0); present (1) [Odonata].
138. *Tufted larval tracheal gills.*—Absent (0); present, lateral (1) [Plecoptera].
139. *Eversible vesicle on abdominal segment I.*—Absent (0); present (1) (Kristensen, 1981).
140. *Transverse stipital muscle.*—Present (0); absent (1) (Kristensen, 1981).
141. *Vertebrate ectoparasites.*—No (0); yes (1) [Pthiraptera and Siphonaptera].
142. *Labium ensheathing mandibular and maxillary stylets.*—No (0); yes (1) [Hemiptera].
143. *Maxillary palpi lost.*—No (0); yes (1) [Hemiptera].
144. *Maxillary and mandibular stylets piercing/sucking.*—Absent (0); present (1) [Hemiptera].
145. *Larval piercing-sucking tubes.*—Absent (0); present (1) [Neuroptera].
146. *Elytra.*—Absent (0); present (1) [Coleoptera].
147. *Abdominal segments VIII and IX telescoped.*—No (0); yes (1) [Coleoptera].
148. *Abdominal sterna I and II membranous.*—No (0); yes (1) [Coleoptera].
149. *Mesothorax and metathorax fused.*—No (0); yes (1) [Coleoptera].
150. *Insect endoparasitism.*—Absent (0); present (1) [Strepsiptera].
151. *Forewing "halteres."*—Absent (0); present (1) [Strepsiptera].
152. *Antennae flabellate.*—No (0); yes (1) [Strepsiptera].

153. *Male eyes protruding, with ommatidia seperated by cuticle and setae.*—No (0); yes (1) [Strepsiptera].
154. *Hamuli.*—Absent (0); present (1) [Hymenoptera].
155. *Notocoxal muscles.*—Present (0); absent(1) [Hymenoptera].
156. *Volsella.*—Absent (0); present (1) [Hymenoptera].
157. *Venom production by female accessory gland.*—Absent (0); present (1) [Hymenoptera].
158. *Male antennae serving as accessory clasping organs.*—No (0); yes (1) [Siphonaptera].
159. *Ctenidium on prothorax.*—Absent (0); present (1) [Siphonaptera].
160. *Salivary channels in lacinial stylets.*—No (0); yes (1) [Siphonaptera].
161. *Body laterally compressed.*—No (0); yes (1) [Siphonaptera].
162. *Clypeus and labrum fused.*—No (0); yes (1) [Mecoptera] (Kristensen 1975, 1981).
163. *Stylar organ of the male claspers.*—Absent (0); present (1) [Mecoptera] (Willmann, 1987).
164. *Male abdominal segment IX ringlike.*—No (0); yes (1). See Kristensen (1975), Wood and Borkent (1989), Kinzelbach (1990). For an alternative interpretation, see Kristensen (1995).
165. *Spermathecal opening separate from gonopore.*—No (0); yes (1) [Mecoptera].
166. *Halteres.*—Absent (0); present (1) [Diptera].
167. *Hypopharynx styletlike.*—No (0); yes (1) [Diptera].
168. *Labial palpi forming labellum.*—No (0); yes (1) [Diptera].
169. *Larval spiracles without closing apparatus.*—No (0); yes (1) [Diptera].
170. *Larvae apneustic, respiration epidermal.*—No (0); yes (1) [Trichoptera].
171. *Anal prolegs.*—Absent (0); present (1) [Trichoptera].
172. *Larval antennae papillae.*—No (0); yes (1) [Trichoptera].
173. *Adult labium and hypopharynx fused.*—No (0); yes (1) [Trichoptera].
174. *Abdominal tergum X bilobed.*—No (0); yes (1) [Lepidoptera].
175. *Corporotentorium with median posterior process.*—No (0); yes (1) [Lepidoptera].
176. *Ventral nerve cord solid.*—No (0); yes (1) [Lepidoptera].

APPENDIX 4. Tree statistics for the sensitivity analyses of insect data.

							No. extra steps[e]						
Analysis	Alignment	Gaps[a]	Length	No. trees[b]	CI[c]	RI[d]	A	B	C	D	E	F	G
18S	Conserved	?	1,571	5,032	42	64	12	26	34	28	26	3	4
		1	1,711	4,022	44	65	13	24	36	22	25	2	6
		2	1,848	504	45	66	14	21	42	18	22	0	7
	Entire	?	1,965	162	41	63	10	38	21	21	28	4	1
		1	2,257	18	43	63	10	38	21	21	28	4	1
		2	2,542	104	43	65	19	49	27	26	29	4	2
28S	Conserved	?	406	84	45	69	13	5	13	3	5	6	3
		1	424	180	45	69	11	3	11	3	4	2	2
		2	437	4	46	70	10	2	9	1	3	4	0
	Entire	?	938	8	36	59	17	19	10	3	9	5	10
		1	1,179	4	36	60	9	16	9	2	11	2	7
		2	1,404	12	36	62	20	18	13	1	14	2	7
Molecular													
Spliced	Conserved	?	2,008	40	42	64	17	22	39	21	24	1	6
		1	2,170	6,452	42	64	21	15	42	22	24	2	5
		2	2,323	20	43	65	25	16	45	23	24	3	7
	Entire	?	2,939	168	39	61	21	46	30	21	32	5	8
		1	3,492	1,476	39	62	21	45	22	23	8	3	8
		2	4,016	72	40	63	32	51	24	25	30	4	6
Merged	Conserved	?	1,520	12	48	68	15	23	44	20	25	0	2
		1	1,632	2	50	69	19	19	38	19	27	1	4
		2	1,738	1	51	69	20	18	39	18	25	0	3
	Entire	?	2,304	6	44	64	22	47	30	23	38	6	6
		1	2,751	28	43	64	25	46	23	23	29	4	5
		2	3,176	18	43	64	31	51	19	21	26	3	1
Morphology = 1													
Spliced	Conserved	?	2,401	756	46	72	17	12	29	12	12	0	0
		1	2,561	96	47	72	21	10	31	13	13	0	0
		2	2,718	3,564	48	72	25	10	33	14	14	2	2
	Entire	?	3,333	10	42	67	23	37	15	16	18	0	2
		1	3,883	332	42	67	30	38	13	13	18	0	2
		2	4,413	12	42	67	43	44	15	18	19	0	3
Merged	Conserved	?	1,818	24	52	73	19	13	28	13	13	3	3
		1	1,935	3	53	73	21	22	30	16	16	0	0
		2	2,045	5	54	74	24	10	31	13	13	1	1
	Entire	?	2,613	8	47	68	26	39	18	17	19	0	1
		1	3,060	1	46	68	27	37	14	17	17	0	0
		2	3,485	2	46	68	33	45	13	19	20	0	1
Morphology = 2													
Spliced	Conserved	?	2,760	78	50	76	28	23	2	2	2	0	0
		1	2,920	42	50	76	32	26	3	3	3	0	0
		2	3,078	966	51	76	37	30	5	5	5	0	0
	Entire	?	3,701	72	45	72	31	28	12	12	12	0	0
		1	4,247	18	45	71	35	32	1	1	1	0	0
		2	4,778	72	45	71	43	37	9	9	9	0	0
Merged	Conserved	?	2,101	6	55	77	27	24	4	4	4	0	0
		1	2,220	12	56	77	28	27	2	2	2	0	0
		2	2,331	4	57	77	34	29	3	3	3	0	0
	Entire	?	2,898	3	50	72	30	32	5	5	5	0	0
		1	3,347	12	49	71	34	32	8	8	8	0	0
		2	3,783	4	48	70	39	38	8	8	8	0	0

[a] Gaps were coded as missing (?) or were weighted by 1 or 2.

[b] Number of most-parsimonious trees.

[c] CI = consistency index.

[d] RI = retention index.

[e] A = to place Strepsiptera in Polyphaga; B = to force Strepsiptera sister group to Coleoptera; C = to force Coleoptera monophyly; D = to force Neuropteroidea monophyly; E = to force Coleoptera sister group to Neuropteroidea; F = to force Mecopterida monophyly; G = to force Mecoptera monophyly.