

Phylogeny of earwigs (Insecta: Dermaptera) based on molecular and morphological evidence: reconsidering the classification of Dermaptera

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Abstract. Dermaptera (earwigs) is a cosmopolitan order of insects, the phylogenetic relationships of which are poorly understood. The phylogeny of Dermaptera was inferred from large subunit ribosomal (28S), small subunit ribosomal (18S), histone-3 (H3) nuclear DNA sequences, and forty-three morphological characters. Sequence data were collected for thirty-two earwig exemplar taxa representing eight families in two suborders: Hemimeridae (suborder Hemimerina); Pygidicranidae, Anisolabididae, Labiduridae, Apachyidae, Spongiphoridae, Chelisochidae and Forficulidae (suborder Forficulina). Eighteen taxa from ten additional orders were also included, representing Ephemeroptera, Odonata, Orthoptera, Phasmoda, Embiidina, Mantodea, Isoptera, Blattaria, Grylloblattodea and Zoraptera. These data were analysed via direct optimization in poy under a range of gap and substitution values to test the sensitivity of the data to variations in parameter values. These results indicate that the epizoic *Hemimerus* is not sister to the remaining Dermaptera, but rather nested as sister to Forficulidae + Chelisochidae. These analyses support the paraphyly of Pygidicranidae and Spongiphoridae and the monophyly of Chelisochidae, Forficulidae, Anisolabididae and Labiduridae.

Introduction

Dermaptera (earwigs) is an insect order comprised of 1784 extant described species, 182 genera, and eleven families (Sakai, 1982). The monophyly of this group is well supported by the forcepslike, unsegmented cerci present in adults that are used to assist in predation, mating and wing folding (Haas *et al.*, 2000) and also by the presence of holocentric chromosomes (Rentz & Kevan, 1991). Wings, if present, are highly specialized: forewings are short and toughened into tegmina, and hindwings fold into an intricate fanlike conformation, mostly covered by the tegmina (Haas *et al.*, 2000). The earwig body is elongate and somewhat dorsoventrally flattened, usually 15–20 mm in length, with a muscular telescoping abdomen.

The European earwig *Forficula auricularia* is a cosmopolitan species, having become an agricultural pest on

every continent except Antarctica (Sakai, 1987). The black earwig *Chelisoches morio* and the small earwig *Labia minor* are also widespread and common earwig species. Most earwigs are found in confined, damp areas, such as underneath stones, bark, fallen logs, or in leaf litter. However, two enigmatic lineages of earwigs, Arixeniidae and Hemimeridae, have evolved into nearly ectoparasitic lifestyles on mammals, although the origin and relationship of these lineages to free-living earwig lineages are unknown (Giles, 1963; Nakata & Maa, 1974).

Unlike most insects, earwigs exhibit maternal brood care (Rentz & Kevan, 1991). Earwig females typically fashion a burrow in a confined space, such as under a rock or under the bark of a tree, where eggs are deposited. After deposition, females remain in the burrow, protecting the eggs from destruction, predation and mould, generally not emerging from their burrows until after the eggs have hatched (Rentz & Kevan, 1991). Free-living earwigs exhibit maternal brood care, and maternal brood care has been suspected for epizoic lineages, but has yet to be documented (Nakata & Maa, 1974).

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Taxonomy

Three suborders have traditionally been recognized within Dermaptera: Forficulina (free-living earwigs), Arixeniina (found on molossid bats) and Hemimerina (found on murid rats). Whereas the monophyly of each epizoic lineage is well established, their relationship to the free-living groups is controversial. Hemimerina is comprised of two genera (*Hemimerus* and *Araeomerus*) and eleven species. Hemimerine earwigs are commensal inhabitants of the fur of giant murid rats of the genera *Beamys* and *Cricetomys* in sub-Saharan Africa. These earwigs are small (5–15 mm in length) and are found in large numbers in the fur of their hosts (Nakata & Maa, 1974). Synapomorphies supporting the monophyly of Hemimerina are associated with adaptations to epizoic life on *Beamys* and *Cricetomys* murid hosts. These include short, broad legs, specialized grooves on the legs that allow them to adduct their legs close to the body, loss of wings and eyes, and straight, narrow cerci. The mouthparts are specialized for grazing and brushing dead skin and fungus off their rat hosts, which may be beneficial to the host (Nakata & Maa, 1974).

The suborder Arixeniina is comprised of two genera, *Arixenia* and *Xeniaria*, and five species. These earwigs are associated with *Cheiromeles* and possibly other bat genera in Indonesia, the Philippines and the Malay peninsula (Nakata & Maa, 1974). Bat earwigs feed on dead skin and gland secretions of their hosts, but are less closely associated with their hosts than are Hemimerina, often being found on guano in caves and trees. Arixeniine earwigs are remarkably large (body up to 25 mm in length), with long legs. Synapomorphies include the absence of wings, eyes reduced, and the presence of thin, pubescent cerci that presumably serve a sensory function.

The majority of earwig species are placed in the suborder Forficulina, which contains a wide variety of diverse lineages (Sakai, 1987). Members of Forficulina range in length from 5 mm in many spongiphorids to 55 mm in the anisolabidid *Titanolabis colossea* (Rentz & Kevan, 1991). Some forficuline taxa have complex wings and specialized wing-locking mechanisms on their tegmina, whereas others are wingless, as in many anisolabidids (Haas, 1995). Forficuline earwigs are particularly diverse in tropical areas, but are also found in other climates on all continents except Antarctica (Sakai, 1987). Forficulina includes nine families: Anisolabididae (= Carcinophoridae), Apachyidae, Chelischidae, Diplatyidae, Forficulidae, Karschiellidae, Labiduridae, Pygidicranidae and Spongiphoridae (= Labiidae) (Sakai, 1982).

Whereas the suborder Forficulina is commonly treated as monophyletic (Sakai, 1982; Rentz & Kevan, 1991; Haas, 1995), this has never been tested formally in a phylogenetic analysis. Indeed, the most recent systematic research on Dermaptera has neglected the epizoic lineages altogether, due to a lack of fresh specimens for DNA work (Wirth *et al.*, 1998; Colgan *et al.*, 2003) and the absence of wings for venational characters (Haas, 1995; Haas & Kukalova-Peck, 2001). Morphological characters supporting Forficu-

lina have been presented, such as paired subocular sulci, joined tormae, complete epistomal sulcus, occipital sulcus running from eyes to posterior aspect of head, dorsal surface of hypopharynx asymmetrical, reduced terga XIII and IX in females, and strongly developed cerci (Giles, 1963). However, these characters may be plesiomorphic, and the unique hemimerid and arixeniid characters may be independently derived, a result of an epizoic lifestyle. Dermaptera is the only insect order for which epizoic lineages are given such a high rank, distinct from the free-living lineages. In other insects (e.g. Leptinidae in Coleoptera, Polycetenidae in Hemiptera, Nycteribiidae in Diptera) it is recognized that each parasitic lineage is a specialized group derived from a free-living lineage within that order. Clearly, the placement of the epizoic lineages within Dermaptera ought to be clarified to understand basic patterns of earwig diversification.

Phylogenetic hypotheses

The phylogenetic placement of Dermaptera among the other insect orders is controversial. Dermaptera is one of the neopteran orders referred to collectively as 'Polyneoptera', which also includes Orthoptera, Phasmida, Embiidina, Plecoptera, Mantodea, Blattodea, Isoptera, Grylloblattodea, Zoraptera (Boudreaux, 1979; Wheeler *et al.*, 2001) and the newly described Mantophasmatodea (Klass *et al.*, 2002). Relationships among Polyneoptera are not well understood (Kristensen, 1991), and the relationship of Dermaptera to the other orders is in question (Kukalova-Peck & Peck, 1993; Rasnitsyn, 1998; Terry & Whiting, unpublished data). Wheeler *et al.* (2001) placed Dermaptera in an unresolved clade that included Grylloblattodea, Zoraptera and Dictyoptera. Beutel & Gorb (2001) presented a phylogeny in which Dermaptera was sister to Embiidina, which in turn was sister group to Zoraptera + Paraneoptera + Holometabola. A recent analysis of molecular and morphological data on an extensive sampling of Polyneoptera and other insect orders suggests that Dermaptera is sister group to Zoraptera (Terry & Whiting, unpublished data), a small order of insects that exhibit gregarious behaviour (Smithers, 1991). Synapomorphies for a Dermaptera and Zoraptera sister-group relationship are few, however: absence of ocelli and thigmotactic behaviour.

Whereas extensive research has been performed on earwig morphology, with heavy emphasis on wing and genital features (Popham, 1961; Giles, 1963; Nakata & Maa, 1974; Matsuda, 1976; Sakai, 1987; Rentz & Kevan, 1991; Haas & Wootton, 1996; Haas *et al.*, 2000; Popham, 2000; Haas & Kukalova-Peck, 2001), phylogenetic relationships among earwig taxa are poorly understood. Popham (1965, 1985, 2000) presented a classification for Dermaptera based on characters of the reproductive anatomy, primarily consisting of male external genitalia. Although he produced a large number of detailed drawings of genitalia, abdomen, and other structures, no formal character analysis was conducted to derive his phylogeny (Fig. 1a). Popham (1965, 1985) considered Arixeniina to be sister to Spongiphoridae,

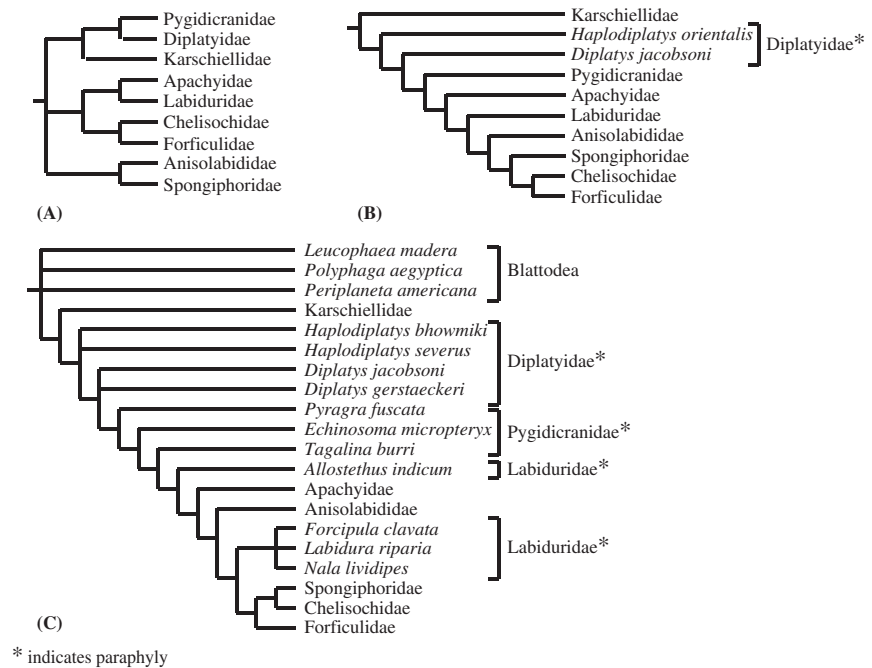


Fig. 1. Previous phylogenetic hypotheses for relationships within Dermaptera based on morphology. a, Popham (2000), an intuitive phylogeny; b, Haas (1995), a phylogenetic analysis of twenty-four morphological characters; c, Haas & Kukulova-Peck (2001), a phylogenetic analysis of forty-five morphological characters.

placed Karschiellidae, Pygidicranidae and Diplatyidae as sister to the remainder of Dermaptera, and proposed the relationship of (Forficulidae + Chelisochidae) + (Labiduridae + Apachyidae) (Popham, 2000). Popham's (2000) hypothesis has not generally been accepted, as it was based on an informal analysis rather than a cladistic treatment of coded characters.

Karyotype characters have not solved this question, as chromosome count varies from $2n = 10$ to $2n = 37$ within Forficulina (Sakai, 1987; Sakai *et al.*, 1988), Arixeniina is $2n = 7$ (White, 1971) and Hemimerina is $2n = 60$ (White, 1972).

Haas (1995) performed the first quantitative phylogenetic analysis of Dermaptera, using morphological characters derived from ten forficuline earwig taxa representing all nine recognized forficuline families and three blattid outgroups. Neither Hemimerina nor Arixeniina were included in this analysis. He compiled a matrix of twenty-four characters, coding the characters in previous studies (Verhoeff, 1902; Zacher, 1911; Burr, 1914; Giles, 1963; Popham, 1965, 1985; Steinmann, 1986, 1989, 1990, 1993) and augmenting these with several novel characters. These data support the placement of Karschiellidae as sister to the remainder of Dermaptera, with Diplatyidae as paraphyletic, and Spongiphoridae as sister to Forficulidae + Chelisochidae (Fig. 1b).

Haas & Kukulova-Peck (2001) expanded on the Haas (1995) matrix by adding additional wing structure and venational characters and additional taxa. They analysed these data in a matrix of forty-three characters for seventeen earwig taxa and three blattid outgroup species. Four diplatyid species, three pygidicranid species and four labidurid species were coded at the species level, whereas Karschielli-

dae, Apachyidae, Anisolabididae, Carcinophoridae, Spongiphoridae, Chelisochidae and Forficulidae were coded at the family level. Hemimerina and Arixeniina were not included in the analysis. This was the first analysis to specifically test the monophyly of Pygidicranidae and Labiduridae. Their data indicated paraphyletic Diplatyidae, Pygidicranidae and Labiduridae. Chelisochidae and Spongiphoridae were supported as sister taxa, and this clade was sister to Forficulidae. This study included the largest sampling of taxa and morphological characters of any study to date (Fig. 1c).

Three molecular studies on Dermaptera have provided some additional insight into earwig phylogeny. Wirth *et al.* (1999) sequenced 684 bp of cytochrome oxidase II across six dermapteran species; four forficulid species, one labidurid species and one anisolabidid species were included. Two orthopterans, one blattid and an odonate were also included, and the tree was rooted to the odonate. A neighbour joining analysis of these data (Wirth *et al.*, 1999) supported a monophyletic Forficulidae whose sister group was Labiduridae, and with Anisolabididae as sister to Forficulidae + Labiduridae (Fig. 2a).

Guillet & Vancassel (2001) reconstructed a phylogeny of fifteen earwigs in four families based on 411 bp of 16S mitochondrial ribosomal sequence. Their exemplars included two labidurids, one chelisochid, one spongiphorid and eleven forficulid representatives, including five *Forficula auricularia* exemplars. Two orthopterans were included as outgroups. The phylogeny presented from parsimony analysis indicated a monophyletic Forficulidae (Fig. 2b), sister to a (Labiduridae + Chelisochidae) + Spongiphoridae clade (Guillet & Vancassel, 2001)

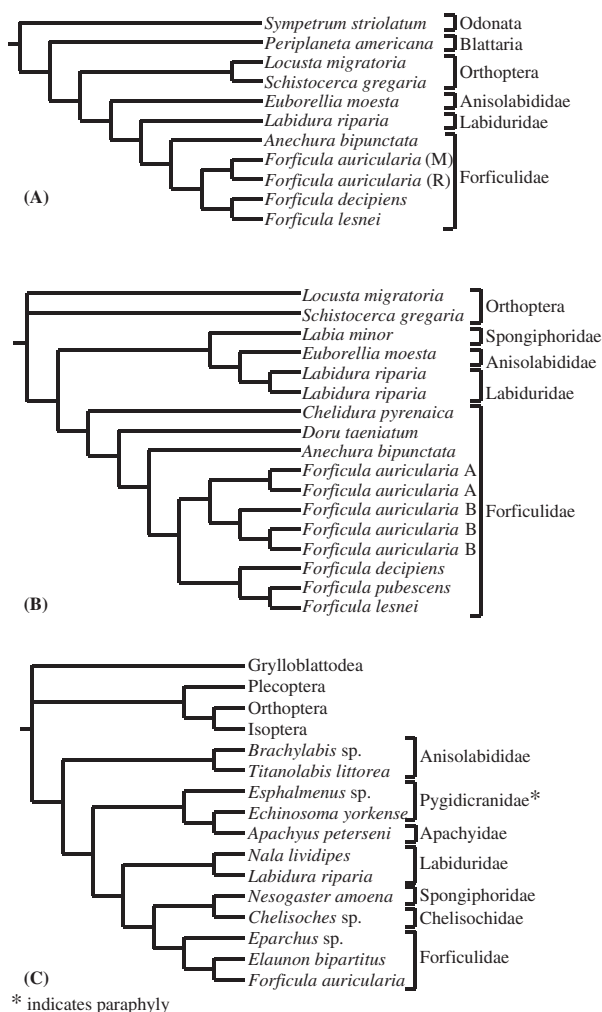


Fig. 2. Previous phylogenetic hypotheses for relationships within Dermaptera based on molecular data. a, Wirth *et al.* (1999), a phylogenetic analysis of 684 bp of cytochrome oxidase II; b, Guillet & Vancassel (2001), a phylogenetic analysis of 411 bp of 16S; c, Colgan *et al.* (2003), a phylogenetic analysis of cytochrome oxidase I, 16S, 18S and 28S.

Colgan *et al.* (2003) included the widest selection of exemplars and phylogenetic markers to date. Their analysis included twelve dermapteran taxa representing seven families and four outgroup taxa. They generated partial sequences from cytochrome oxidase I, 16S, 18S and 28S, aligned the data in CLUSTAL W (Thompson *et al.*, 1994), and reconstructed a tree using parsimony in PAUP*. Their analyses supported Anisolabididae as sister to the remainder of Dermaptera, paraphyletic Pygidicranidae with respect to Apachyidae, and Labiduridae as sister group to Spongiphoridae + (Forficulidae + Chelisochidae). Labiduridae, Anisolabididae and Forficulidae each were found to be monophyletic, and Pygidicranidae was paraphyletic with respect to Apachyidae (Fig. 2c).

Given that prior morphological and molecular studies have provided incomplete and conflicting phylogenies for Dermaptera, the aim of this study was to provide a detailed molecular and morphological analysis that included a greater diversity of taxa than previous studies. The specific goals of this study were to (1) test the monophyly of Forficulina by including Hemimerina, (2) test the monophyly of Diplatyidae, Pygidicranidae and Labiduridae as suggested by Haas & Kukalova-Peck (2001) and Colgan *et al.* (2003), (3) test the monophyly of each family, and (4) establish the basic pattern of phylogenetic relationships among the families.

Materials and methods

Thirty-two earwig taxa, representing two of the three sub-orders, eight of the eleven families and sixteen of the forty-five subfamilies, were included in this analysis (Table 1). Specimens from three families – Arixeniidae, Karschiellidae and Diplatyidae – were unavailable for this analysis. Earwig specimens were collected in North America, Papua New Guinea, Africa, Australia and Southeast Asia. Specimen vouchers are deposited in the Insect Genomics Collection, Brigham Young University. Sequences from Guillet & Vancassel (2001) and Wirth *et al.* (1999) were not included because their taxa and characters did not overlap with those used in the present study. Colgan *et al.* (2003) sequenced portions of 18S and 28S in their study, but as they sequenced regions largely different from those generated in this study (maximally 25%), their data were not included in this analysis.

Eighteen exemplars from ten orders of insects besides Dermaptera were included in the analysis, across eight 'polyneopteran' orders, Odonata and Ephemeroptera (Table 2). Two species were included from each of the orders except for single species in Zoraptera and Ephemeroptera,

Table 1. Taxa sampled in this analysis relative to the diversity of Dermaptera.

	Genera			Species		
	Sampled	Total	%	Sampled	Total	%
Hemimeridae	1	2	50	1	11	9
Arixeniidae	0	2	0	0	5	0
Pygidicranidae	3	19	16	4	165	2
Anisolabididae	3	27	11	3	381	1
Labiduridae	2	6	33	5	71	7
Apachyidae	1	2	50	1	17	6
Spongiphoridae	4	35	11	6	451	1
Chelisochidae	3	14	21	4	93	4
Forficulidae	7	67	10	8	438	2
Karschiellidae	0	2	0	0	13	0
Diplatyidae	0	6	0	0	139	0
Total	24	182	13	32	1784	2

Table 2. Taxa include in this analysis and GenBank accession numbers.

Family	Subfamily	Genus	Species	18S	28S	H3
Anisolabididae	Carcinophorinae	<i>Euborellia</i>	<i>femoratis</i>	AY707326, AY707349	AY707373, AY707393, AY707414	AY707429
Anisolabididae	Carcinophorinae	<i>Thekalabis</i>	sp.	AY707325, AY707348	AY707372, AY707392, AY707413	AY707428
Anisolabididae			sp.	AY707328, AY707351	AY707375, AY707395, AY707416	AY707431
Apachyidae	Apachyinae	<i>Dendroiketes</i>	<i>novaequinae</i>	AY521839	AY521758, AY521759, AY521760	–
Chelisoehidae	Chelisoehinae	<i>Chelisoehes</i>	<i>morio</i>	AY121133	AY125273	AY125220
Chelisoehidae	Chelisoehinae	<i>Chelisoehes</i>	<i>annulatus</i>	AY707323, AY707346	AY707370, AY707390, AY707411	AY707426
Chelisoehidae	Chelisoehinae	<i>Proneus</i>	<i>duruoides</i>	AY707363	AY707384, AY707404	AY707439
Chelisoehidae			sp.	AY521841	AY521764, AY521765	–
Forficulidae	Cosmiellinae	<i>Acanthocordax</i>	<i>papuanus</i>	AY707331, AY707354	AY707378, AY707398, AY707419	–
Forficulidae	Forficulinae	<i>Doru</i>	<i>spiculiferum</i>	AY121131	AY125272	–
Forficulidae	Forficulinae	<i>Elauon</i>	<i>bipartitus</i>	AY707338, AY707361	AY707382, AY707402	AY707438
Forficulidae	Forficulinae	<i>Forficula</i>	sp.	AY521836	AY521752	AY521703
Forficulidae	Opisthocosminae	<i>Eparchus</i>	<i>biroi</i>	AY707324, AY707347	AY707371, AY707391, AY707412	AY707427
Forficulidae	Opisthocosminae	<i>Eparchus</i>	<i>biroi</i>	AY521837	AY521753, AY521754, AY521755	–
Forficulidae	Opisthocosminae	<i>Opisthocosmia</i>	<i>tenius</i>	AY707321, AY707344	AY707425	–
Forficulidae	Opisthocosminae	<i>Paratimomenus</i>	sp.	AY707322, AY707345	AY707410	–
Hemimeridae	Hemimerinae	<i>Hemimerus</i>	sp.	AY707334, AY707357	AY707381, AY707422	–
Labiduridae	Labiduridae	<i>Forcipula</i>	<i>clavata</i>	AY707320, AY707343	AY707369	–
Labiduridae	Labiduridae	<i>Forcipula</i>	<i>decolyi</i>	AY707327, AY707350	AY707374, AY707394, AY707415	AY707430
Labiduridae	Labiduridae	<i>Labidura</i>	<i>riparia</i>	AY707333, AY707356	AY707380, AY707400, AY707421	AY707435
Labiduridae	Nalinae	<i>Nala</i>	<i>tenuicornis</i>	AY707336, AY707359	AY707401	AY707436
Labiduridae	Nalinae	<i>Nala</i>	<i>lividipes</i>	AY707339, AY707362	AY707383, AY707403	–
Pygidicranidae	Echinosomatinae	<i>Echinosoma</i>	sp.	AY121132	–	AY125219
Pygidicranidae	Echinosomatinae	<i>Echinosoma</i>	<i>micropteryx</i>	AY707330, AY707353	AY707377, AY707397, AY707418	AY707433
Pygidicranidae	Pygidicraninae	<i>Cranopygia</i>	<i>ophthalmica</i>	AY707340, AY707364	AY707385, AY707405	AY707440
Pygidicranidae	Pygidicraninae	<i>Tagalina</i>	sp.	AY521838	AY521756, AY521757	AY521704
Spongiphoridae	Labinae	<i>Labia</i>	sp.	AY521840	AY521761, AY521762, AY521763	–
Spongiphoridae	Nesogastrinae	<i>Nesogaster</i>	<i>aculeatus</i>	AY707335, AY707358	–	–
Spongiphoridae	Sparattinae	<i>Auchenomus</i>	<i>forcipatus</i>	AY707329, AY707352	AY707376, AY707396, AY707417	AY707432
Spongiphoridae	Sparattinae	<i>Auchenomus</i>	sp.	AY707337, AY707360	–	AY707437
Spongiphoridae	Spongiphorinae	<i>Ir-dex</i>	sp.1	AY707365	AY707386, AY707406	AY707441
Spongiphoridae	Spongiphorinae	<i>Ir-dex</i>	sp.2	AY707366	AY707387, AY707407	AY707442

Table 2. Continued.

Order	Family	Genus	Species	18S	28S	H3
Ephemeroptera	Baetidae	<i>Baetis</i>	sp.	AY338695	AY338652	AY338619
Blattaria	Blaberidae	<i>Gromphadorhina portentosa</i>		AY121129	AY125270	AY125216
Blattaria	Cryptoceridae	<i>Cryptocercus</i>	<i>punctulatus</i>	AY521829	AY521738, AY521739	AY521698
Embiidina	Oligotomidae	<i>Oligotoma</i>	<i>nigra</i>	AY121134	AY125274	AY125221
Embiidina	Teratobiidae	<i>Teratobia</i>	sp.	AY121135	AY125275	AY125222
Grylloblattodea	Grylloblattidae	<i>Galloisiana</i>	sp.	AY707341, AY707367	AY707388, AY707408, AY707423	AY707443
Grylloblattodea	Grylloblattidae	<i>Grylloblatina</i>	<i>djakonovi</i>	AY707342, AY707368	AY707389, AY707409, AY707424	AY707444
Isoptera	Hodotermitidae		sp.	AY521853	AY521779, AY521780	–
Isoptera	Termitidae	<i>Nasutitermes</i>	sp.	AY121140	AY125280	AY125226
Mantodea	Mantidae	<i>Prohierodula</i>	sp.	AY521858	AY521787	AY521709
Mantodea	Mantoididae	<i>Mantoida</i>	<i>schraderi</i>	AY491138	AY491259	AY491371
Odonata	Aeschnidae	<i>Anax</i>	<i>junius</i>	AY338719	AY338676	AY338639
Odonata	Gomphidae	<i>Ophiogomphus</i>	<i>severus</i>	AY121143	AY125283	AY125228
Orthoptera	Rhaphidophoridae	<i>Ceuthophilus</i>	<i>utahensis</i>	AY521870	AY521800	AY521720
Orthoptera	Tridactylidae	<i>Ellipses</i>	<i>minutus</i>	AY338723	AY338679	AY338641
Phasmida	Heteronemiidae	<i>Gratidia</i>	<i>longikawiensis</i>	AY121166	AY125306	AY125249
Phasmida	Pseudophasmatidae	<i>Paraphasma</i>	<i>rufipes</i>	AY121160	AY125300	AY125244
Zoraptera	Zorotypidae	<i>Zorotypus</i>	sp. nov.	AY521891	AY521824	AY521733

and trees were rooted to Ephemeroptera (Wheeler *et al.*, 2001; Ogden & Whiting, 2003).

All specimens were preserved in 100% ethanol and stored at -80°C . The thorax or leg of insect specimens was dissected for extraction of genomic DNA with Qiagen DNeasy[®] Tissue Kit (Qiagen Inc., Valencia, California, U.S.A.). Small subunit nuclear ribosomal RNA (18S, ~2000 bp), large subunit nuclear ribosomal RNA (28S, ~2400 bp), and histone-3 protein-coding gene (H3, 376 bp) were amplified using AmpliTaq Gold[®] DNA Polymerase (Applied Biosystems, Foster City, California, U.S.A.). Primer sequences used in amplifying and sequencing 18S and 28S are given in Whiting (2002), with additional primers listed in Table 3. The temperature profile employed for amplification of 18S by polymerase chain reaction (PCR) was 95°C for 12 min, 94°C for 1 min, 50°C for 1 min, 72°C for 1 min, with the latter three steps repeated thirty-five times, followed by 72°C extension for 7 min. The other genes were amplified with identical temperature profiles except for a 55°C annealing temperature for 28S and a 52°C annealing temperature for H3. Ribosomal genes were amplified in overlapping pieces of 300–1000 bp, and H3 was amplified in its entirety.

PCR products were examined via agarose gel electrophoresis and purified using Gene Clean[®] III (Qbiogene Inc., Carlsbad, California, U.S.A.). Sequencing of purified PCR products was performed using BigDye[™] v3.0 (Applied Biosystems). Sequencing reactions were purified using Sephadex[™] G-50 gel filtration medium (Amersham Biosciences Corp., Piscataway, New Jersey, U.S.A.) and fractionated on an ABI PRISM[®] 377 or ABI PRISM[®] 3100 Genetic Analyser (Applied Biosystems).

Primary sequence data were assembled using SEQUENCHER[™] 4.1 (Gene Codes Corp., Ann Arbor, Michigan, U.S.A.), and complementary strands were assembled to verify the identity of the sequences. Large expansion regions exist in dermapteran 18S and 28S ribosomal DNA, through which sequencing was difficult. Thus, portions of 18S and 28S are not included, due to the lack of complementary sequences. We sequenced 697 bp from the 5' end of 18S (regions V1, V2, V3, 100 bp of V4 *sensu* De Rijk *et al.*, 1992) and 1080 bp from the 3' end of 18S (including 50 bp of V4 and V5–V8), for a total of 1777 bp of 18S. We sequenced 632 bp from the 5' end of 28S (including D2 *sensu* De Rijk *et al.*, 1994), a 360 bp region in the middle of the gene (including D4) and 266 bp from the 3' end (the region flanking D7b), for a total of 1254 bp of 28S. H3 sequences were all 376 bp long.

In total, forty-three morphological characters, as described in Haas & Kukalova-Peck (2001), were included in this analysis. These characters were coded for the taxa not present in the original Haas & Kukalova-Peck (2001) matrix. Characters were based on hindwing morphology and wing articulation (twenty-four characters), thorax and tegmina (seven), legs and abdomen (nine), and male genitalia (three). The morphological matrix is available as supplementary material.

Table 3. The primers used, in addition to those in Whiting (2002).

Primer name	Sequence (5'→3')
18S 1F	TACCTGGTTGATCCTGCCAGTAG
18S 2F	AGGGTTCGATTCCGGAGAGGGAGC
18S b2.9	TATCTGATCGCCTTCGAACCTCT
28S Road 1a	CCCSCGTAAYTTAGGCATAT
28S Road 2a	TCATGCACCTTGGCAAGTCC
28S Road 3a	AGTACGTGAAACCGTTCAGG
28S Road 4a	GGAGTCTAGCATGTGYGCAAGTC
28S Road 6a	GGCGAAAGGGAATCYGGTTC
28S Road 6b	AACCRGATTCCCTTTCGCC
28S Road 4b	CCTTGGTCCGTGTTTCAAGAC
28S Road 3b	CCYTGAACGGTTTCACGTACT
Hex AF	ATGGCTCGTACCAAGCAGACGGC
Hex AR	ATATCCTTGGGCATGATGGTGAC

Analysis

Initial alignments were performed in SEQUENCHER™ 4.1 software (Gene Codes Corp.) by manually aligning conserved domains. The 18S and 28S sequences were partitioned and analysed via direct optimization, as implemented in POY 3.0.11 (Wheeler *et al.*, 2003). The datasets were partitioned according to conserved regions to allow for efficient heuristic analysis in POY (Giribet, 2001) and reduced ambiguity in reconstructing the implied alignment (Wheeler 2003). This resulted in eleven regions of 18S of 81–232 bp and ten regions of 28S of 37–262 bp. The 18S partitions corresponded to regions as defined in De Rijk *et al.* (1992), except that 112 bp of V2 was included with V1, V4 was divided into two regions, 25 bp at the end of V4 was included with all of V5, and 27 bp of V9 was included in the V8 region. The ten 28S partitions corresponded to De Rijk *et al.* (1994), but was also subdivided further, with four 28S partitions between the 5' end and D2; the first 209 bp of D2; just downstream from D3; D4; D5; and a small portion adjacent to and downstream from D7b.

POY analyses were executed on a Dell desktop computer with a Pentium 4 processor at 2.8 GHz with 1.0 GB RAM under the following commands: '-weight 1 morph.txt -impliedalignment -fitchtrees -noleading -norandomizeoutgroup -sprmaxtrees 1 -tbrmaxtrees 1 -maxtrees 5 -holdmaxtrees 50 -slop 5 -checkslop 10 -replicates 10 -multirandom -treefuse -fuselimit 10 -fusemingroup 5 -fusemaxtrees 100 -numdriftchanges 30 -driftspr -numdriftspr 10 -drifttbr -numdrifttbr 10 -slop 10 -checkslop 10 -molecularmatrix 111.txt -seed -1'.

In order to explore the sensitivity of this dataset to variation in parameter values, analyses were performed under sixteen gap:transversion:transition parameter sets (Wheeler *et al.*, 2001). Morphological changes were weighted equal to the highest value of the other parameters. Although these parameter sets represent only a few of the possible combination of parameter values that could be explored, they are biologically plausible

and cover the portion of the search space under which the character data are often most congruent (Wheeler, 1993; Ogden & Whiting, 2003; Svenson & Whiting, 2004).

One hundred random addition replicates and the same heuristic search strategies as described above were performed in POY for the entire dataset with gap cost, transition cost, and transversion cost set to 1 (=1:1:1 analysis). Prior analyses on other insect groups indicate that the 1:1:1 cost results in the greatest character congruence (Ogden & Whiting, 2003; Whiting *et al.*, 2003; Svenson & Whiting, 2004; Terry & Whiting, 2004), and there are strong theoretical reasons for using unity of costs under parsimony (Grant & Kluge, 2003). This implied alignment is available as supplementary material.

Bootstrap values were calculated in PAUP* 4.0b10 (Swofford, 2002) using the implied alignment. Although an implied alignment is produced in the same manner as a multiple alignment, it can still be used similarly to a typical alignment in calculating support. However, support values may tend to be higher than would be expected when analysing the data when aligned via other methods, as direct optimization biases the implied alignment towards the optimal tree (De Laet & Wheeler, 2003; Wheeler, 2003). We performed 1000 nonparametric bootstrap replicates, with ten random additions performed during each replicate in PAUP. Partitioned Bremer supports (Baker & DeSalle, 1997) were calculated in PAUP (Swofford, 2002) using constraints compiled in TREEROT v.2c (Sorenson, 1999). Twenty random addition replicates were performed for tree searches on each node.

Results

The mean uncorrected pairwise divergence for all sequences was 9.29%, for 18S 6.85%, for 28S 13.61% and for H3 16.38%.

A total evidence analysis performed under the 1:1:1 parameter set resulted in one most-parsimonious tree of length 5208 with consistency index = 0.5363 and retention index = 0.7636 (Fig. 3). The 1:1:1 tree supports a monophyletic Dermaptera and places it as sister to Zoraptera. Our analysis places *Echinosoma*, a pygidicranid genus, as sister to the remaining dermapteran taxa. This analysis indicates that Hemimeridae is sister to Forficulidae, rendering the Forficulina paraphyletic. The tree also indicates that Forficulidae, Chelisoichidae, Labiduridae and Anisolabididae are monophyletic, whereas Spongiphoridae and Pygidicranidae are paraphyletic.

Summing the partitioned Bremer support values for each gene and the morphology demonstrated that 46.8% of the phylogenetic signal was derived from 18S, 39.2% from 28S, 9.9% from H3 and 4.2% from morphology (Table 4). Normalizing the sum of partitioned Bremer support values by dividing by the number of parsimony

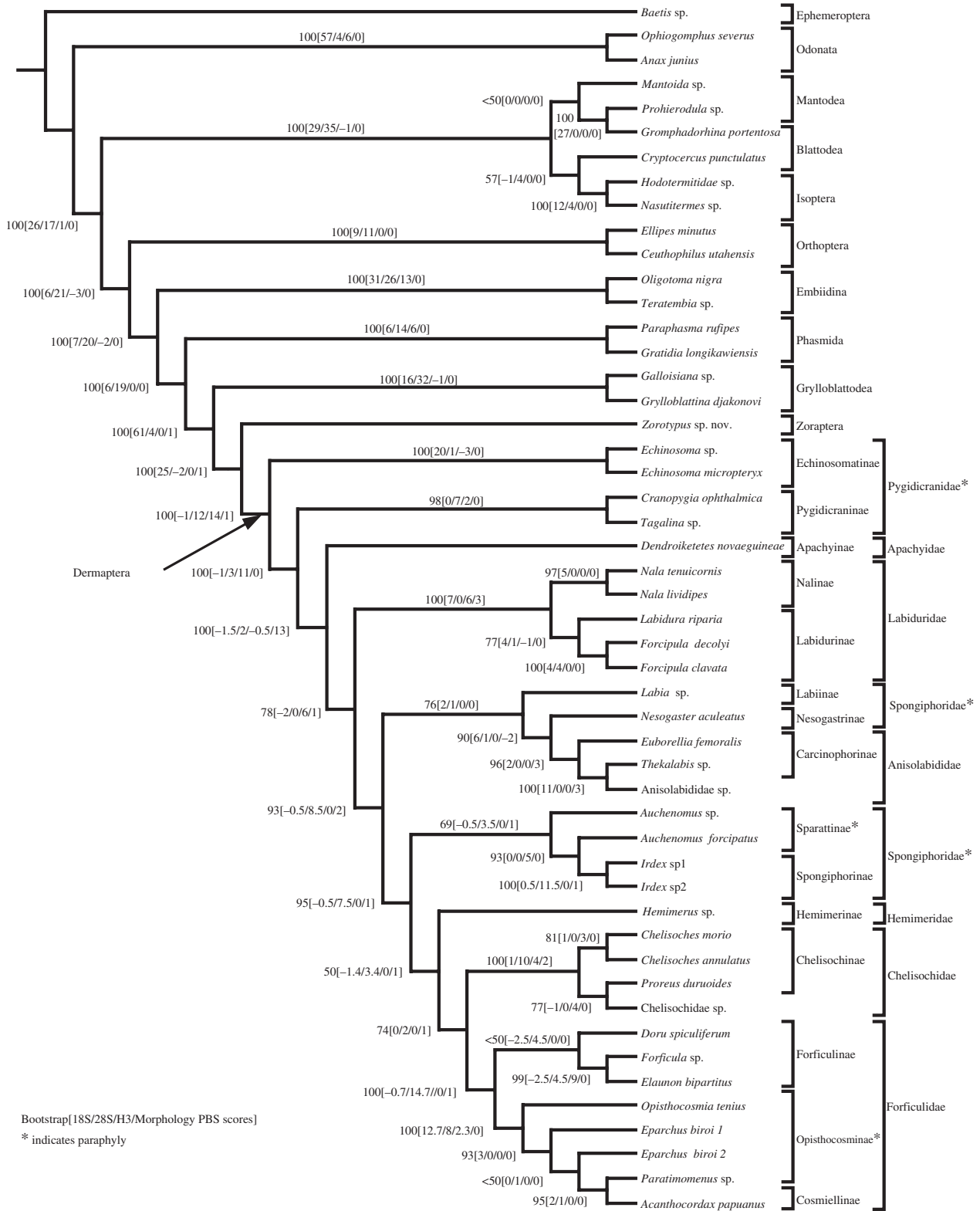


Fig. 3. This single most-parsimonious tree of length 5208 is from a phylogenetic analysis of 18S, 28S, histone-3 and morphological data in *POY*. The implied alignment from this analysis was reanalysed in *PAUP*, weighting gaps, transversions, transitions, and morphological changes as equal, obtaining a consistency index of 0.5363 and a retention index of 0.7636.

Table 4. Partitioned Bremer support (PBS) values compared with parsimony informative (PI) characters.

	18S	28S	Histone-3	Morphology	Total
Sum of PBS values	383.1	321.1	80.8	34.0	819.0
Percentage of total Bremer	46.8	39.2	9.9	4.2	100.0
No. of PI chars	470	529	132	34	1165
PBS/PI chars	0.815	0.607	0.612	1.000	0.703

informative characters within each partition gives an indication of the amount of signal derived per unit character within each partition. For instance, even though morphology provided only thirty-four of the 819 partitioned Bremer support units, each character provided a single partitioned Bremer support unit as contrasted with 28S, which provided on average 0.607 units per parsimony informative character.

Bootstrap values were relatively high across the tree, with only twelve of the forty-seven nodes having a value less than 90%. Interordinal relationships had the highest support according to this measure, all with values of 100 with two exceptions. Within Dermaptera, bootstraps varied across the nodes much more, with both high and low values across the tree.

A topology summarizing the results from the sensitivity analysis is shown in Fig. 4. Each node of this topology has a parameter landscape depicting the parameter values under which a particular relationship is monophyletic or not. For instance, Chelisochidae is monophyletic for all direct optimization cost parameter values investigated, whereas the monophyly of Forficulinae is supported under a narrower range of parameters. Overall, these results suggest that the ordinal and family-level relationships within the phylogeny are more sensitive to fluctuations in parameter values than are relationships within families and among species. Nodes that are robust to perturbations in parameter values tend to correlate with nodes with high bootstrap and Bremer values.

Discussion

These analyses support a monophyletic Dermaptera with high bootstrap and Bremer support values, and this relationship is not sensitive to the parameters investigated. The 1:1:1 analysis supports Dermaptera as sister group to Zoraptera, in agreement with a more extensive analysis that sampled 'polyneopteran' and 'palaeopteran' orders in greater detail (Terry & Whiting, unpublished data). This sister-group relationship has been suggested in other studies (Giles, 1963; Kamp, 1973; Wheeler *et al.*, 2001). This disagrees with Beutel & Gorb (2001), who placed Dermaptera as sister to Embiidina; although the latter group has been

shown to be sister to Phasmatodea based on molecular and morphological information (Whiting *et al.*, 2003). However, the sensitivity analysis indicates that Dermaptera + Zoraptera is somewhat unstable, being found in six of the sixteen parameter combinations, with five alternative placements found under other parameter combinations.

In all analyses, the suborder Forficulina is paraphyletic with *Hemimerus* nesting within Forficulina. This result runs counter to the classification of Popham (1985), who treated Hemimerina as sister group to Forficulina and even suggested that they should be placed in their own order. It is very clear that *Hemimerus* nests somewhere within Forficulina, although the exact placement is not well supported. The analysis that treats parameter values as unity (Fig. 3) places *Hemimerus* as sister to Forficulidae + Chelisochidae, although the bootstrap and Bremer support values for this position are relatively low, and the sensitivity analysis is not particularly robust.

Giles (1963) suggested that Forficulina and Hemimerina are closely related, based on the characters of twisted anterior tentorial arms, cylindrical paraglossae, and reduced terga VIII and IX. Given that the morphological characters used to support the monophyly of Forficulina are nothing more than plesiomorphic characters for Dermaptera, we suggest that the definition of Forficulina be expanded to include Hemimeridae. There is no evidence to suggest that hemimerids should be given separate ordinal status, as Popham (1961) suggested. Therefore, we suggest discontinuing the use of the term Hemimerina, as it is one of many lineages derived from within Forficulina.

Within Dermaptera, our analyses support a sister-group relationship between the pygidicranid subfamily Echinomatinae and the remainder of Dermaptera. This relationship is somewhat sensitive to parameter selection, although there are relatively high bootstrap and Bremer support values supporting this node. Haas & Kukalova-Peck (2001) placed karschiellids and diplatyids as sister groups to the remainder of Dermaptera. These taxa were absent from this analysis, but our results agree with these authors in placing Echinomatinae as sister to the remainder of Dermaptera. These analyses further support the paraphyly of Pygidicranidae, in agreement with other recent studies (Haas & Kukalova-Peck, 2001; Colgan *et al.*, 2003). We found that two pygidicranid subfamilies – Echinomatinae and Pygidicraninae – are monophyletic and supported by relatively high bootstrap and Bremer support values. Additional analyses that include diplatyids and karschiellids will be required to test the basal dermapteran node as outlined by Haas & Kukalova-Peck (2001).

Forficulidae, Chelisochidae, Labiduridae and Anisolabididae are each consistently recovered as monophyletic families under nearly the full range of parameter value combinations, and high bootstrap and Bremer support values also confirm this. Partitioned Bremer support values indicate that morphology supports the monophyly of all four of these families. In addition, Chelisochidae receives support from all three gene regions, Labiduridae is supported by 18S and H3,

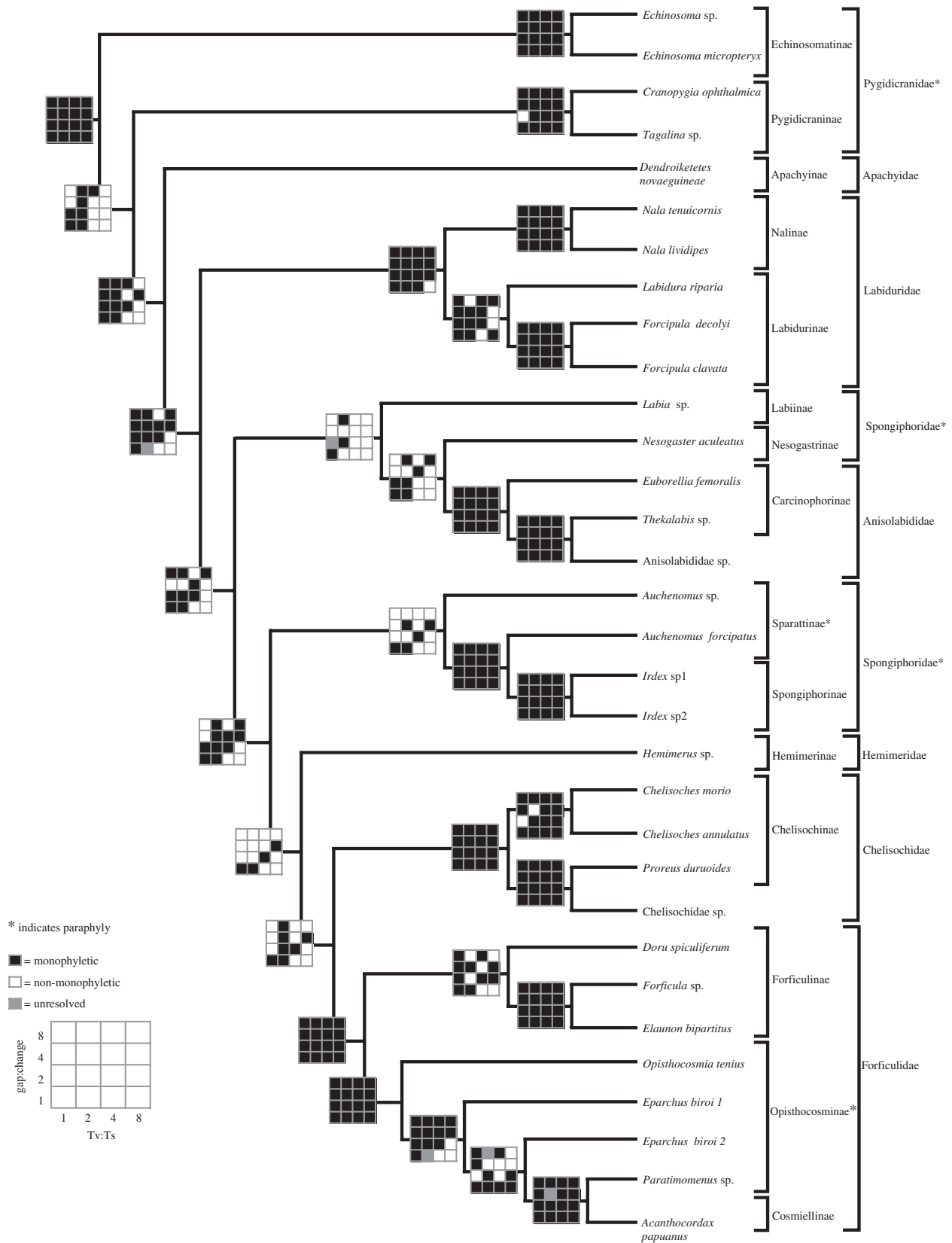


Fig. 4. Portion of the tree from Fig. 3 showing Dermaptera only, with sensitivity analysis results indicated in grid format on each node.

Anisolabididae by 18S and Forficulidae by 28S. Each family also exhibits unique morphological synapomorphies: the second tarsomere in forficulids is lobed and very wide, chelisochid second tarsomeres are lobed and narrow, and anisolabidids, which are typically wingless, have dilated abdomens. Labidurid males have genitalia with one medial lobe directed forward and the other backward. Within Forficulidae, the subfamily Forficulinae is monophyletic, although this is only moderately supported. The forficulid subfamily Opisthocosminae is paraphyletic due to Acanthocordax, a member of Cosmiellinae, nesting within it. However, the monophyly of Opisthocosminae + Cosmiellinae is very well supported and stable across all parameters. The labidurid subfamily Nalinae is monophyletic across all parameter sets. Labidurinae has low bootstrap and Bremer support values, but is monophyletic in twelve parameter set values. Haas & Kukalova-Peck (2001) found congruent results in Labiduridae (*Allostethus* nested outside of Labiduridae, but this taxon was absent from our sampling).

These analyses suggest that Spongiphoridae is not a monophyletic group, but rather consists of three distinct lineages. Two lineages are sister to Anisolabididae, and one clade is sister to the Chelisochidae + Forficulidae + Hemimeridae clade. No parameter combination resulted in a monophyletic Spongiphoridae. These results underscore the fact that there are no reliable morphological synapomorphies supporting Spongiphoridae, and that this family appears to be a grab bag of taxa. Furthermore, within the Spongiphoridae, Spartinae appear to be paraphyletic, suggesting that future revisionary work is needed. Note that previous studies failed to include multiple spongiphorid exemplars and thus were not able to detect this gross paraphyly.

Apachyidae, which has at times been placed as a subfamily within Pygidicranidae, is placed at a position sister to the remainder of Dermaptera with the exclusion of Echinomatinae and Pygidicraninae. High bootstrap and Bremer support values indicate reasonable support for this placement. Under some parameter values, apachyids shift position, but they are always placed near the pygidicranids. Colgan *et al.* (2003) placed Apachyidae within Pygidicranidae. Haas & Kukalova-Peck (2001) placed the labidurid *Allostethus indicum* in the position our apachyids is in. We did not have this taxon in our analysis, but otherwise Haas & Kukalova-Peck's (2001) placement of Apachyidae is congruent with our topology.

Conclusions

These results suggest that the phylogeny of Dermaptera is not fully congruent with current dermapteran classification. Our work strongly supports the monophyly of extant Dermaptera and further indicates that one of the two epizoic lineages was derived from within Dermaptera. In addition, the paraphyly of Spongiphoridae and Pygidicranidae indicates that additional work is needed to discover how many distinct lineages are present in their phylogeny. Other studies have also suggested that

some dermapteran families are paraphyletic (Haas & Kukalova-Peck, 2001; Colgan *et al.*, 2003). We regard this analysis to be preliminary in the sense that some critical taxa were missing and that additional molecular markers are needed to support some relationships better. We also feel that significant progress has been made towards establishing a reliable phylogeny of Dermaptera.

Supplementary material

The implied alignment and morphological matrix are available at: <http://www.blackwellpublishing.com/products/journals/suppmat/SEN/SEN276/SEN276sm.htm>

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