1 Reassessing the phylogenetic position of the epizoic

2 earwigs (Insecta: Dermaptera)

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8 Abstract

9 Dermaptera is a relatively small order of free-living insects that typically feed on
10 detritus and other plant material. However, two earwig lineages – Arixeniidae and
11 Hemimeridae -- are epizoic on *Cheiromeles* bats and *Beamys* and *Cricetomys*
12 rats respectively. Both of these epizoic families are comprised of viviparous
13 species. The monophyly of these epizoic lineages and their placement within
14 dermapteran phylogeny has remained unclear. A phylogenetic analyses was
15 performed on a diverse sample of 47 earwig taxa for five loci (18S rDNA, 28S
16 rDNA, COI, Histone 3, and Tubulin Alpha I). Our results support two independent
17 origins of the epizoic lifestyle within Dermaptera, with Hemimeridae and
18 Arixeniidae each derived from a different lineage of Spongiphoridae. Our
19 analyses places *Marava*, a genus of spongiphorids that includes free-living but
20 viviparous earwigs, as sister group to Arixeniidae, suggesting that viviparity
21 evolved prior to the shift to the epizoic lifestyle. Additionally, our results support
22 the monophyly of Forficulidae and Chelisochidae and the paraphyly of
23 Labiduridae, Pygidicranidae, Spongiphoridae, and Anisolabididae.

24

Keywords

Dermaptera

Evolution

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1. Introduction

During the evolution of insects, there have been multiple shifts from free-living forms to forms that are parasitic or epizoic on vertebrate hosts. Examples include fleas (Siphonaptera) derived from a mecopteran lineage (Whiting, 2002; Misof et al., 2014), various lineages of lice derived from troctomorph booklice (Yoshizawa & Johnson, 2006; Johnson et al., 2004), and multiple lineages within what are predominantly free living insect orders, including bed bugs (Cimicidae), bat bugs (Polyctenidae), and various beetle lineages (e.g., *Platypsyllus castoris* Ritsema, 1869 on beaver hosts, *Leptinus americanus* LeConte, 1866 on small rodents, and *Trichillium brachyporum* Askew, 1971 on three-toed sloth) (Ratcliffe, 1980; Peck, 1982). One of the most intriguing examples of an apparent shift from free living to epizoic lifestyle involves two families of earwigs, Hemimeridae and Arixeniidae.

Dermaptera (earwigs) is a small but ancient order of polyneopterous insects. Earwigs are typically identified by their prominent forceps-like cerci on their

abdomen (Fig.1). These cerci serve a variety of functions including wingfolding, predation, defense against predation, and possibly in sexual selection, as there is a tremendous variation in the morphology of this feature and sexual dimorphism (Haas et al., 2000). Dermaptera includes approximately 2200 extant species of earwigs within 11 families, distributed worldwide (Sakai, 1982; Popham, 2000; Deem, 2012). Earwigs range from 5mm to 55mm in length (Rentz & Kevan, 1991), though the endemic and presumably extinct Saint Helena earwig (*Labidura herculeana* (Favricius, 1798)) reached the massive length of 84 mm (Brindle, 1970).

The majority of earwigs are free-living and commonly found in confined, damp areas feeding on detritus and other plant material. Some species, including the widely distributed European earwig (*Forficula auricularia*, Linnaeus, 1758) are active predators and scavengers. Earwigs are unusual for non-social insects in that they exhibit maternal care, with the mother protecting eggs from predators by regularly cleaning them to reduce fungal growth. The mother will assist the first instar nymphs as they hatch and will continue to tend them through the first instar by feeding them regurgitated food and fending off predators (Staerckel & Koelliker, 2008; Suzuki & Kitamura, 2005).

The chief reproductive strategy in earwigs is oviparity, where eggs are deposited in a safe habitat and embryogenesis takes place. During embryogenesis, the embryos use reserved material (yolk, protein, lipids) stored during oogenesis and

are surrounded by protective coverings, the vitelline envelope and the chorion (Tworzydło et al., 2013). The epizoic forms exhibit viviparity, where the embryonic development takes place within the body of the mother and the mother provides nourishment for the embryos (Tworzydło et al., 2013). In the case of *Arixenia esau* Jordan, 1909, the most thoroughly studied of the epizoic forms, embryological development takes place within the mother's body in two distinct compartments: the terminal ovarian follicle and the uterus (Tworzydło et al., 2013). Variation in reproductive strategies across earwigs as a whole is poorly known, but forms of viviparity have been documented in three non-epizoic earwig species belonging to the family Spongiphoridae. In *Chaetospania borneensis* (Dubrony, 1879), viviparity was documented by observing embryos in different stages of development within the mother's body (Kocarek, 2009). Observations by D. Matzke have shown that *Sphigolabis hawaiiensis* (de Bormans, 1882) is also viviparous (Schneider & Klass, 2013). In *Marava arachidis* (Yersin, 1860), a form of viviparity (ovoviviparity) was documented by observing females that deposit their eggs with developed embryos, and the first instar nymphs emerge from the eggshells 10-20 minutes after deposition (Herter 1943, 1965; Patel & Habib, 1978). Like viviparity, ovoviviparity embryogenesis largely occurs within the body of the mother. However, ovoviviparous embryos develop by utilizing reserved materials within the egg rather than taking nutrients directly from the mother (Tworzydło et al., 2013).

93 Although the majority of earwigs are free-living, two earwig families –
94 Hemimeridae and Arixeniidae – require a mammal host to survive. Throughout
95 the dermapteran literature, the terms epizoic and ectoparasitic have been used
96 interchangeably to refer to the relationship between the earwigs and their host.
97 The term epizoic, however, is more accurate as there is no evidence that these
98 insects adversely affect their mammal host. Hemimeridae and Arixeniidae are
99 morphologically distinct from free-living Dermaptera and rather distinct from each
100 other (Fig. 1). Both families are wingless, blind or with reduced eyes, have filiform,
101 segmented cerci, and are viviparous (as discussed above); features presumably
102 associated with their shift to the epizoic lifestyle. The relationship of these
103 families to each other and to the free-living earwigs remains controversial.
104 Consequently, it is unclear whether these morphological modifications and
105 features associated with their epizoic lifestyle evolved once or were derived in
106 two independent lineages, and it is unclear from which group of free-living
107 earwigs the epizoic forms were derived.

108

109 Hemimeridae contains eleven described species placed within two genera:
110 *Hemimerus* and *Araeomerus* (Nakata & Maa, 1974). Hemimerids are relatively
111 small (5mm to 15mm) and inhabit the fur of giant murid rats in Africa.
112 Hemimerids have short, broad legs with grooves that allow them to cling to the
113 host and specialized mouthparts for scraping dead skin and fungus from their
114 host (Nakata & Maa, 1974). *Araeomerus* is found in the nest of long-tailed pouch
115 rats (*Beamys*) and *Hemimerus* is found on giant *Cricetomys* rats (Nakata & Maa,

1974). *Araeomerus* are found more often in the burrows and nests of *Beamys* rat than on the rat itself, while *Hemimerus* less frequently leaves its host.

Arixeniidae is less closely associated with their host than *Hemimeridae*, spending much of their time on the cave walls and guano of the bats. *Arixeniidae* contains five species in two genera and are associated with the naked bat genus *Cheiromeles* located in Indonesia, the Philippines and the Malay Peninsula (Nakata & Maa, 1974). Species within *Arixenia* are found in the skin folds and gular pouch of Malaysian hairless bulldog bats (*Cheiromeles torquatus*), apparently feeding on the bat body or glandular secretions (Nakata & Maa, 1974). The genus *Xeniaria* has powerful mandibles and specialized mouthparts for the mastication of food; this genus associates more closely with the bat's guano than with the host (Nakata & Maa, 1974).

Three extant suborders have traditionally been recognized within *Dermaptera*: *Hemimerina*, *Arixeniina*, and *Forficulina*, with the latter suborder containing the vast majority of the species, which are the free-living forms (Giles, 1963; Sakai, 1982; Rentz & Kevan, 1991; Haas & Kukalova-Peck, 2001). Popham (1985) considered *Arixeniidae* to be a family within *Forficulina* and sistergroup to *Spongiphoridae*. Klass (2001) described synapomorphies associated with female genitalia and the immobilization of terga supporting placement of hemimerids within *Forficulina*.

139 In a reclassification of Dermaptera, Engel and Haas (2007) placed all extant
140 Dermaptera within the suborder Neodermaptera. Neodermaptera was divided
141 into two infraorders: Protodermaptera and Epidermaptera, the latter of which
142 include the epizoic forms. These authors placed Hemimeridae within the
143 superfamily Hemimeroidea in the parvorder Paradermaptera. They placed
144 Arixeniidae within the superfamily Forficuloidea in the parvorder Eteodermaptera,
145 demonstrating their recognition that these epizoic forms appear to be distinct
146 lineages that are not sister group to each other. These authors emphasize that
147 the placement of these epizoic groups still remains a difficult question and that
148 higher-level classification of Dermaptera depends upon finding a well-supported
149 placement for these groups.

150
151 Jarvis et al. (2005) performed the first molecular analysis of dermapteran
152 relationships based on three loci (18S, 28S, and H3) for 32 earwig taxa. In their
153 analysis, they found that their single *Hemimerus* exemplar was placed as sister
154 to Chelisochidae + Forficulidae, though this relationship was poorly supported
155 and the molecular data for this taxon were not complete. Kocarek et al. (2013)
156 built upon the Jarvis et al. (2005) study by adding two additional epizoic taxa
157 (*Hemimerus hansenii* Sharp, 1895 and *Arixenia esau* Jordan, 1909) to the Jarvis
158 et al. dataset for the same genes. In a Bayesian analysis, they recovered
159 Hemimeridae as sister to Forficulidae and Arixeniidae as sister to Chelisochidae,
160 with moderate amounts of support (Posterior Probabilities of 0.83 and 0.82
161 respectively). Our reanalysis of Kocarek et al.'s data (below) suggests that this

result is not robust, and our data reveal a different solution. Consequently, the origin of the epizoic lineages and the phylogenetic relationships among the earwigs as a whole remains an open question. Both of these molecular analyses were limited in that they did not include Plecoptera among the outgroups, an order which may be sister group to Dermaptera (Yoshizawa & Johnson, 2005; Ishiwata et al., 2011; Wan et al., 2012; Letsch & Simon, 2013).

The purpose of this work is to report the most comprehensive analysis to date on earwig phylogenetic relationships, with an expanded sampling of ingroup and outgroup taxa and additional molecular loci. We use these data to address the following questions: 1) Is there a single origin or multiple origins of the epizoic lifestyle in earwigs? 2) From which group or groups did the epizoic forms arise? 3) What are the higher-level relationships among the free-living dermapteran families?

2. Materials and Methods

Our taxon sampling included a total of 47 ingroup taxa representing 9 of the 11 extant dermapteran families (Table 1), including Forficulidae (9 spp.), Pygidicraniidae (4 spp.), Chelisochidae (4 spp.), Spongiphoridae (12 spp.), Anisolabidae (6 spp.), Labiduridae (6 spp.), Apachyidae (1 sp.), Hemimeridae (3 spp.), and Arixeniidae (2 exemplars.). Two relatively obscure and restricted families are missing from our analysis (Karschiellidae and Diplatyidae) as we were unable to acquire specimens suitable for DNA extraction. However,

Diplatyidae is placed within the superfamily Pygidicrinoidea, and this superfamily is represented in our analysis by four pygidicranid exemplars. A total of 19 outgroup taxa were selected from throughout Polyneoptera, Odonata, and Ephemeroptera, and the tree was rooted to Ephemeroptera. Misof et al. (2014) suggested that Zoraptera may be sister group to Dermaptera, though this result was poorly supported, and directly contradicts subsequent analyses which point out genomic anomalies within Zoraptera (Matsumura et al., 2015). When we included three zorapteran exemplars (supplemental fig. 5), they exhibited a very long branch and grouped with Dictyoptera. The difficulties of placing Zoraptera among the polyneopterous insects have been discussed elsewhere (Matsumura et al., 2015), and it is likely that they may act as a random root for this analysis (Wheeler, 1990). Consequently, Zoraptera was excluded from our analysis. All specimen vouchers are deposited in the Insect Genomics Collection, M. L. Bean Museum, Brigham Young University.

Specimens were preserved in 100% ethanol and stored at -80⁰ C. Muscle was removed from the thorax or leg and DNA was extracted using the Qiagen DNeasy Blood and tissue kit (Qiagen Inc., Valencia, California, U.S.A.) following the standard protocol provided by the manufacturer. Five loci (2 ribosomal DNA, 1 mitochondrial, and 2 nuclear protein-coding) commonly used in insect phylogenetic studies were used for this analysis (Colgan et al., 1998; Svenson and Whiting, 2004, 2009; Whiting, 2002; Wild and Maddison, 2008). These include the 28S ribosomal subunit (28S rDNA, ~ 2.4 kb), the 18S ribosomal

subunit (18S, ~ 2.0 kb), Cytochrome c Oxidase Subunit I (COI, ~ 600 bp),
Histone 3 (H3, ~ 350 bp) and Tubulin Alpha I (TUBA, ~ 350 bp). Genes were
sequenced and amplified using oligonucleotide primers from Integrated DNA
Technologies (San Diego, CA). PCR protocol was previously described for H3
(Colgan et al., 1998), 28S and 18S (Whiting, 2002), COI (Svenson and Whiting,
2009), and TUBA (Buckman et al., 2013). PCR was performed using 25 ul
reactions with Platinum taq DNA polymerase (Invitrogen, Carlsbad, CA). For 28S
and 18S ribosomal genes, 1.25 ul of water was replaced with DMSO. Gene
amplification parameters were as follows: 2 min. at 94°C and 35 cycles of 30 s. at
94°C, 30 s. at 46-58°C, and 45-120 s. at 72°C, with a final extension at 72°C for
7 min. with specific annealing temperature and extension times by gene. All
reactions were run on GeneAmp® PCR system 9700 (Applied Biosystems,
Foster City, CA). 2% agarose gel electrophoresis using ethidium bromide was
used to confirm amplification and test for contamination of PCR product.
Products were cleaned with PrepEase® purification plates (USB Corporation,
Cleveland, OH) following manufacturer's instructions. Products were sequenced
with BigDye chain terminating chemistry and fractioned on the ABI 3730xl
(Applied Biosystems Inc.) at the Brigham Young University DNA Sequencing
Center (Provo, UT).

Contigs were assembled and edited using Sequencher V.4.9 (GeneCodes 2006),
and Geneious Pro 5.6.3 (Biomatters LTD. 2012) and submitted to GenBank.
Protein coding genes were uploaded into MEGA V5 (Kumar et al., 2008).

Nucleotide sequences were translated into amino acid sequences and after the correct reading frame was determined, alignment was conducted using the default parameters in MUSCLE (Edgar, 2004). Sequences were then back translated to nucleotides for further phylogenetic analyses. Amino acid sequences were highly conserved throughout the taxa, making the final DNA alignments unambiguous. Ribosomal genes were aligned using the E-INS-I algorithm and default settings in MAFFT V6 (Kato et al., 2005) available through the online server at <http://mafft.cbrc.jp/alignment/server/>. Alignments of the individual ribosomal sequences were also conducted using MUSCLE (Edgar, 2004) to determine the sensitivity of the data to the alignment methods. Because ribosomal genes can be difficult to align due to the multiple conserved regions flanked by the variable expansion regions, we tested the sensitivity of the ribosomal alignments via GBLOCKS v0.91b (Castresana, 2000) using the server at http://molevol.cmima.csic.es/castresana/Gblocks_server.html. Two parameters were selected: (1) allow for smaller final blocks and (2) allow gap positions within the final blocks.

Maximum Likelihood (ML) and Bayesian analysis (BI) methods were used to reconstruct trees. The concatenated dataset was partitioned by gene for the ML and BI searches. JModelTest (Posada, 2008) determined GTR+I+G as the best fit model for gene partition. Maximum likelihood searches were conducted using RAxML V7.0.3 (Stamatakis, 2006) implemented on the supercomputer resources available at BYU (<https://marylou.byu.edu>). Bootstrap support was calculated

with 1000 bootstrap replicates. Bayesian inferences using flat priors were performed with MrBayes v1.3.2 (Ronquist & Huelsenback, 2003) on the BYU supercomputing resources. Two independent runs of 20 Markov Chain Monte Carlo (MCMC) were run for 200 million generations and sampled every 5000 generations. Tracer V1.5 (Rambaut & Drummond, 2003) was used to view the progress of the Bayesian run and to determine the adequate level to “burn-in”. The Shimodaira-Hasegawa (SH) test was performed to test the statistical significance of multiple origins for the the epizoic lifestyle (Shimodaira & Hasegawa, 1999).

In order to test the robustness of Kocarek et al.’s (2013) topology to alignment of the ribosomal genes, we repeated Kocarek et al.’s analysis from the alignments provided at TreeBase using the parameters reported by these authors. Additionally, we obtained the gene sequences used by these authors from GenBank and aligned using MAFFT v6 (Kato et al., 2005) following the parameters listed above. We also obtained Kocarek et al.’s data for the ribosomal genes from GenBank and tested the sensitivity of their ribosomal alignments via GBLOCKS v0.91b (Castresana, 2000). Alignments have been deposited on TreeBase and are available at (<http://purl.org/phylo/treebase/phylows/study/TB2:S18838>).

3. Results

3.1 Alignment

Our total alignment resulted in 6281 aligned positions including 2249 bp from 18S, 2921 bp from 28S, 475 bp from COI, 336 bp from H3, and 300 bp from Tuba. Alignments of 18S and 28S using MAFFT and Gblocks found no noticeable topological difference between the resulting trees, suggesting that our phylogenetic results are not sensitive to alignment. Expansion regions of 18S and 28S were included in the MAFFT alignment.

3.2 Phylogenetic Analysis

Trees were constructed via Bayesian and Maximum Likelihood methods. The Akaike's Information Criterion (AIC) in JModeltest (Posada, 2008) found a six-parameter model, Gamma distribution, and proportion of invariable sites (GTR + I + G) as the best-fit model of sequence evolution for each partition. The Bayesian analysis had an average log score of -63115.5514 over the two runs. The best RAxML tree recovered a log score of -64235.311257 and was almost identical to the topology derived from the Bayesian analysis, with a few differences in the deeper nodes. The Bayesian tree is given in Figure 2. The SH test refutes the null hypothesis that there is only a single origin of the epizoic lifestyle in earwigs ($P=0.002$), thus supporting our finding that there are two independent origins of this lifestyle.

3.3 Phylogenetic Relationships

Dermaptera was recovered as a well-supported monophyletic group that is sister to Plecoptera. Within Dermaptera, we recovered four families as monophyletic

with high support values (bootstrap >75 and PP >95): Hemimeridae, Arixeniidae, Chelisochidae, and Forficulidae. The monophyly of Apachyidae, a small family of earwigs containing two genera and 16 described species with a distribution from Africa to New Guinea (Popham, 2000), could not be confirmed as only one exemplar was included in this analysis. Hemimeridae is placed as sistergroup to a clade of spongiphorids and Arixeniidae as sister to a different spongiphorid *Marava feae* (Dubrony, 1879).

Spongiphoridae was recovered as polyphyletic and members of this family occupy five positions on the tree. *Marava feae* (Dubrony, 1879) is placed as sister to Arixeniidae, a clade consisting of three *Irdex* spp. + *Auchenomus forcipatus* Ramamurthi, 1967 is placed as sister to Hemimeridae, a clade of three species -- *Spongovostox* sp., *Chaetospania thoracica* (Dohrn, 1867), and *Paralabella fruehstorferi* (Burr, 1897) -- was recovered, and two spongiphorid species (*Nesogaster aculeatus* (de Bormans, 1900) and *Labia* sp.) are placed at the base of Anisolabidae.

Regarding the overall phylogeny of Dermaptera, four families were recovered as paraphyletic: Labiduridae, Anisolabididae, Pygidicranidae, and Spongiphoridae. Labiduridae formed a well-supported clade, but include an anisolabidid (*Parisolabis* sp.) and a spongiphorid (*Sphingolabis* sp.) nested in the apex of this clade. Anisolabididae is paraphyletic due to the placement of *Parisolabis* within Labiduridae and the placement of one anisolabidid species at the base of the

tree. The remaining Anisolabididae, consisting of four taxa (*Euborellia femoralis*,
Cacinopehorinae sp. *Anisolabididae* sp. 2, and *Thakalabis* sp.) form a well-
supported group. Pygidicranidae was recovered as paraphyletic as in previous
studies (Colgan et al., 2003; Haas & Kukalova-Peck, 2001; Kamimura, 2004;
Jarvis et al., 2005; Kocarek et al., 2013). However, the two pygidicranid
subfamilies Echinomatinae and Pygidicraninae were recovered as
monophyletic with high PP and bootstrap support, in agreement with Jarvis et al.
(2005) and Kocarek et al. (2013). Note that the relatively basal placement of
Pygidicranidae relative to the other dermapteran groups is in agreement with the
classification of Engel and Haas (2007).

3.4 Reanalysis of Kocarek et al. (2013)

Kocarek et al. (2013) generated sequences for two epizoic taxa (*Arixenia esau*
Jordan, 1909 and *Hemimerus hansenii* Sharp, 1895) and added these to the
Jarvis et al. (2005) molecular data set, which originally consisted of three genes
(18S, 28S, and H3). Kocarek et al. (2013) did not obtain 28S and H3 sequence
for their hemimerid exemplar nor H3 for their arixeniid exemplar. It is possible
that missing data played a role in how these taxa were placed in their tree.
Kocarek et al. (2013) recovered Arixeniidae as sister group to Chelisochidae and
Hemimeridae as sister group to Forficulidae with high posterior probability. These
authors provided us with the data matrix they used in this study and we
recovered their reported topology. However, in constructing this matrix, large
sections of the ribosomal genes were deleted. Thus, we were thus interested in

the robustness of their results to a reanalysis of all the underlying genetic data. We downloaded the ribosomal genes from GenBank and aligned using MAFFT v6 according to the parameters listed above. The alignment was tested using GBlocks to gauge whether there was any justification for excluding regions of the ribosomal alignment. GBlocks analysis suggested that the alignment of the sequences was robust and GBlocks did not remove the regions excluded by these authors. Trees were constructed with Mr.Bayes using a script provided by Kocarek et al. (2013). Based on this new matrix, we confirmed that their data supports Arixeniidae + Chelisochidae, albeit with poor support values (posterior probability of 0.69). However, we were unable to confirm Hemimeridae + Forficulidae since Hemimeridae was placed unresolved in a polytomy consisting of four groups (Supplemental Figure 3). Given the missing genes in their analysis and the manual exclusion of data, it appears that their placement of these epizoic taxa is not particularly robust.

4. Discussion

Our understanding of phylogenetic relationships among Dermaptera is still in its infancy and only now is a basic understanding of the pattern of diversification of this group taking form. Our analysis is the first to include Plecoptera among the outgroups in rooting a molecular tree to estimate dermapteran phylogeny. We recovered Plecoptera + Dermaptera, a result that is congruent with recent analyses that included more extensive data (Misof et al., 2007; Yoshizawa & Johnson, 2005; Ishiwata et al., 2011; Wan et al., 2012; Letsch & Simon, 2013).

Relationships among the remaining outgroups, including a monophyletic Phasmatodea, Embioptera, Grylloblattodea, Orthoptera, Dictyoptera, and Odonata suggest that these data are providing reasonable signal to correctly root relationships within Dermaptera.

The new classification of Dermaptera proposed by Engel and Haas (2007) placed four families (Forficulidae, Spongiphoridae, Arixeniidae, and Chelisochidae) as part of a superfamily Forficuloidea. It is clear that Forficuloidea is not monophyletic based on this analysis, confirming suspicions of paraphyly for this group based on a series of morphological characters associated with ovariole structure (Bilinski et al., 2014). Our work supports the monophyly of Forficulidae and Chelisochidae, but the remaining free-living families appear paraphyletic. While our findings agree with Koracek (2013) that Arixeniidae and Hemimeridae do not form a monophyletic clade of epizoid dermapterans, our results disagree in the details of where these independent lineages arose.

The non-monophyly of Hemimeridae and Arixeniidae suggests that morphological characters associated with an epizoid lifestyle were derived independently and represent two independent shifts to the epizoid lifestyle. It is probable that at least some of these morphological features may be pedomorphic (Engel and Haas, 2007). For instance, the lack of wings and the presence of segmented cerci are both explained via pedomorphism.

Hemimerids lack eyes entirely and are certainly blind. Arixeniids have reduced eyes and it is unclear to what level or whether they have even retained visual acuity. Although, it is likely they still maintain sensitivity to light given that other parasitic insects with reduced eyes have retained vision (e.g., fleas, Taylor, 2005).

While both groups have specialized mouthparts for grazing on their host, the details of these modifications are different. Within Arixeniidae, there is a large degree of variation between the mouthparts of *Xeniaria* and *Arixenia*. *Xeniaria* have large mouthparts and large, powerful mandibles for mastication; while *Arixenia* have much smaller mouthparts modified for brushing (Nakata & Maa, 1974). This difference in mouthparts has been attributed to their disparity in diet and may explain why both groups are often found within the same bat roost (Nakata & Maa, 1974). Hemimeridae have small mouthparts for grazing the skin and fungus found on the epidermis of the host (Nakata & Maa, 1974). Between the two genera within Hemimeridae there is not a large degree of variation in biology, although it is hypothesized from the small number of *Araeomerus* that have been found that it is less closely associated with its host and may feed on plant material (Nakata & Maa, 1974).

It is clear that Spongiphoridae as currently constituted is a catch-all group that is polyphyletic, supporting findings based on ovariole structure (Bilinski et al., 2014) and further suggested by work on the female genitalic track (Schneider & Klass,

2013). Interestingly, both Hemimeridae and Arixeniidae were recovered as sister to two different lineages of Spongiphoridae. Our analysis recovered *A. esau* Jordan, 1909 as sister to *Marava feae* (Dubrony, 1879), the latter species belongs in the subfamily Spongiphorinae. While we do not know the reproductive strategy of this species, its congener *Marava arachidis* (Yersin, 1860) is ovoviviparous, a specialized form of viviparity where embryogenesis takes places largely within the mother's body and the first instars hatch a few minutes after the eggs are laid. *A. esau* shows interesting features that can be interpreted as adaptations to viviparity (Tworzydło, 2013).

We found Hemimeridae to be sister to a clade consisting of three *Irdex* spp. + *Auchenomus forcipatus* Ramamurthi, 1967. Within Spongiphoridae, *Irdex* belongs to the subfamily Spongiphorinae and *Auchenomus* belongs to the subfamily Sparattinae. The ovariole structure of *Irdex* has been characterized, and found to be very different from the ovariole structure of *Chaetospania* belonging to the subfamily Sparattinae (Bilinski et al., 2014). *Chaetospania borneensis* (Dubrony, 1879) is known to be viviparous (Kocarek, 2009). It appears hemimerids may also derive from a different spongiphorid lineage that has developed viviparity.

Viviparity in free-living earwigs, which is thought to be a strategy to protect offspring from fungal infestations (Kocarek, 2009), may have facilitated the transition to the epizoic lifestyle. Viviparity allows these epizoic forms to

continually live and associate with the host, removes the need to leave or find a new host, and protects the eggs from damage or predation. What is intriguing is that there were two transitions to epizoic lifestyles during the evolution of earwigs and that each transformation may have come from a free-living lineage that developed viviparity as a precursor to this transformation. These results suggest that changes in the reproductive strategy of earwigs may have been a driver in the evolution and diversification of this group. Further work is required to better decipher the phylogenetic pattern of diversification within this fascinating group.

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Glossary

Viviparous: Bringing forth live young that have developed inside the body of the parent

Ovoviviparous: A form of viviparity in which eggs are stored within the body of the parent, nutrients are obtained from the yolk and reserve materials stored by the mother during oogenesis.

Epizoic: Living on the exterior of a host animal.

Synapomorphy: a characteristic present in an ancestral species and shared exclusively with its evolutionary descendants.

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Figures

Figure 1-Diversity within Dermaptera

Nala lividipes (Labiduridae) **B.** *Elaunon bipartitus* (Forficulidae) **C.** *Chaetospania thoracica* (Spongiphoridae) **D.** *Cranopygia ophthalmica* (Pygidicranidae) **E.** *Hemimerus talpoides* (Hemimeridae) **F.** *Arixenia esau* (Arixeniidae). **G.** Mandible of *H. talpoides* which are modified for scraping skin and fungus of their rat host.

H. Mandibles of *A. esau* which are modified for feeding on skin and gland secretions.

Figure 2

662 Bayesian tree. Posterior Probabilities over 90 are indicated. Family relations
663 within Dermaptera are labeled by color.

664

665

685 **Tables**

686 **Table 1**

687 Taxon included in this analysis and GenBank accession numbers

Figure

Figure 2

Family	Subfamily	Species
Anisolabididae	Carcinophorinae	<i>Euborellia femoralis</i> (Dohrn, 1863) (DM17)
Anisolabididae	Carcinophorinae	<i>sp.</i> (DM49)
Anisolabididae	Carcinophorinae	<i>Thakalabis</i> sp. (DM16)
Anisolabididae	Parisolabiinae	<i>Parisolabis</i> sp. (DM43)
Anisolabididae	Parisolabiinae	<i>Parisapsalis spryi</i> Burr, 1914
Anisolabididae		<i>sp.1</i> (DM22)
Anisolabididae		<i>sp.2</i> (DM26)
Apachyidae	Apachyinae	<i>Dendroiketes novaeguineae</i> Boeseman, 1954 (D
Arixeniidae		<i>Arixenia esau</i> Jordan, 1909
Arixeniidae	Arixeniidae	<i>Arixenia esau</i> Jordan, 1909 (DM60)
Chelisochidae	Chelisochinae	<i>Chelisoches morio</i> (Fabricius, 1775) (DM12)
Chelisochidae	Chelisochinae	<i>Chelisoches annulatus</i> Burr, 1906 (DM13)
Chelisochidae	Chelisochinae	<i>Proreus duruoides</i> Hebard, 1993 (DM52)
Chelisochidae		<i>sp.</i> (DM28)
Forficulidae	Cosmiellinae	<i>Acanthocordax papuanus</i> Gunther, 1929 (DM25)
Forficulidae	Ancistrogastrinae	<i>Ancistrogaster</i> sp.
Forficulidae	Forficulinae	<i>Doru spiculiferum</i> (Kirby, 1891) (DM03)
Forficulidae	Forficulinae	<i>Elaunon bipartitus</i> (Kirby, 1891) (DM50)
Forficulidae	Forficulinae	<i>Forficula</i> sp. (DM05)
Forficulidae	Forficulinae	<i>Forficula auricularia</i> Linnaeus, 1758
Forficulidae	Opisthocosminae	<i>Eparchus biroi</i> (Burr, 1902) 1 (DM06)
Forficulidae	Opisthocosminae	<i>Eparchus biroi</i> (Burr, 1902) 2 (DM15)
Forficulidae	Opisthocosminae	<i>Opisthocosmia tenuis</i> Rehn, 1936 (DM08)
Forficulidae	Opisthocosminae	<i>Paratimomenus</i> sp. (DM09)
Forficulidae	Skendylinae	<i>Cosmiella</i> sp. (DM47)
Hemimeridae	Hemimerinae	<i>Hemimerus</i> sp. (DM29)
Hemimeridae	Hemimerinae	<i>Hemimerus hansen</i> Sharp, 1895
Hemimeridae	Hemimeridae	<i>Hemimerus talpoides</i> (DM59)
Labiduridae	Labidurinae	<i>Forcipula clavata</i> Liu, 1946 (DM07)
Labiduridae	Labidurinae	<i>Forcipula decolyi</i> de Bormans, 1900 (DM19)

0.2

Hemimerus talpoides

Arixenia esau