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A Phylogenetic Analysis of Armored Scale Insects, Based Upon Nuclear, Mitochondrial, and Endosymbiont Gene Sequences

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A PHYLOGENETIC ANALYSIS OF ARMORED SCALE INSECTS, BASED UPON NUCLEAR, MITOCHONDRIAL, AND ENDOSYMBIONT GENE SEQUENCES

A Thesis Presented

By

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DEDICATION

To Monique Stillger-Walker.

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ABSTRACT

A PHYLOGENETIC ANALYSIS OF ARMORED SCALE INSECTS, BASED UPON NUCLEAR, MITOCHONDRIAL, AND ENDOSYMBIONT GENE SEQUENCES.

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Armored scale insects (Hemiptera: Diaspididae) are among the most invasive insects in the world. They have unusual genetic systems, including diverse types of paternal genome elimination (PGE) and parthenogenesis. Intimate relationships with their host plants and bacterial endosymbionts make them potentially important subjects for the study of co-evolution. Also, in some groups, the adult female never sheds the second instars cuticle, and remains within its confines, a habit referred to as the pupillarial habit. Here we expand upon recent phylogenetic work (Morse and Normark 2006) by analyzing a partitioned dataset including armored scale and endoysmbiont DNA from one hundred and twenty three species of armored scales, represented by two hundred and fifty-four samples. Included were fragments of the nuclear protein-coding gene Elongation Factor 1α (EF1α), the D2 and D3 expansion segments of the large subunit ribosomal RNA gene 28S, and a region of mitochondrial DNA encompassing the 3' portion of cytochrome oxidase I (COI), and the 5' portion of cytochrome oxidase II (COII). Ribosomal 16S from the primary bacterial endosymbiont *Uzinura diaspidicola* was amplified as well. Two versions of our dataset were analyzed due to concerns over the possible effects of missing data. The first version (the full dataset) contained all 254 taxa, with every taxon having at least both the 28S and EF1α fragments. The second version (the core dataset) had only the 113 taxa for which all four fragments were available. Maximum parsimony, maximum likelihood, and Bayesian analyses were run on both versions of the dataset, as well as individually for each fragment. We find that our results were consistent across methods, and between the two versions of the dataset. It appears that including missing data had little effect on topology. Our results mirror that of the classic taxonomy, however we reconstruct a general lack of monophyly at the subfamily, tribal, and subtribal levels. Within the two major subfamilies, we reconstruct that the same developmental pathway has evolved independently. We reconstruct independent replacements of the pupillarial habit with the scale cover, followed by independent origins of early PGE. In each case there appears to be increased diversity in clades associated with the scale cover and early PGE. In light of this apparent increase we propose a new adaptive scenario under which early PGE may have evolved – the removal of male-killing paternal chromosomes. We also reconstruct the ancestor to the armored scales to Australasian in origins, and to have an ancestral diet breath that includes members of the Rosids and/or Monocot plant groups.

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CHAPTER 1

A PHYLOGENETIC ANALYSIS OF ARMORED SCALE INSECTS, BASED UPON NUCLEAR, MITOCHONDRIAL, AND ENDOSYMBIONT GENE SEQUENCES.

Introduction

Scale insects (superfamily Coccoidea) are a diverse group of mostly sap sucking insects, with at least 30 families and around 8000 species (Gullan and Cook 2007). Female scale insects have simplified morphology, with the head, thorax and abdomen fused, and none have any trace of wings. Like their sister group the aphids (superfamily Aphidoidea) and other members of the Hemipteran suborder Sternorrhyncha, scale insects harbor vertically transmitted endosymbionts that are believed to help synthesize amino acids missing from their diet (Buchner 1965; Gruwell et al. 2007; Gruwell et al. 2004). Most of these insects also have an unusual haplodiploid genetic system in which the paternal chromosomes in males are heterochromatic and unexpressed throughout postembryonic development, and are eliminated during spermatogenesis (Brown 1965).

The most diverse family of scale insects is Diaspididae, the armored scales, with over 2400 species (Miller and Davidson 2005; Miller and Gimpel 2008). Traditionally, the armored scales have been regarded as the most derived family of scale insects due to the extreme modification of adult female morphology, with the complete loss of legs and the reduction of eyes and antennae (Balachowsky 1948). In some species, the adult female never sheds the second instar's derm and spends her entire life within its confines, a developmental mode known as the pupillarial habit (Howell and Tippins 1990). Many armored scales have a derived system of paternal genome elimination in which the paternal chromosomes in males are completely eliminated during embryogenesis (Brown 1965).

Armored scales have colonized every continent except Antarctica, and are among the most invasive insects in the world. Fully 40% of the species found in the United States were introduced (Miller et al., 2005). In addition, the armored scales are among the most polyphagous insects known, with some species feeding on over 100 families of plants (Ben-Dov 2008; McClure 1990; Miller and Gimpel 2008). Local adaptation to genotypes of individual hosts has been inferred for some armored scale insects, even within polyphagous species (Glynn and Herms 2004; Hanks and Denno 1994). Their invasive potential, small size, and difficulty of identification make armored scales a major problem for plant quarantine workers around the world (Burger and Ulenberg 1990). Recently, results of molecular-phylogenetic studies have been applied successfully to the problem of molecular identification of invasive armored scales (Edwards et al. 2008).

The study of these important and bizarre insects suffers from the lack of information about their phylogeny. Though many classifications of armored scale insects have been proposed (Ben-Dov and German 2003), the first quantitative attempt to infer the relationships of armored scales was a phenetic analysis of male morphological characters for 26 species by Ghauri (1962). Much of this data was later reanlyzed using principle component and principle coordinate analyses (Boratyński and Davies 1971; Davies 1981; Davies and Boratyński 1979). Miller (1990) reported preliminary results of a cladistic analysis of 70 morphological characters for 33 taxa. This matrix was later analyzed in conjunction with molecular data by Morse *et al.* (2005) for 28 species. The most thorough analysis to date was by Morse and Normark (2006), who examined 112 specimens in 89 species. Here we expand upon the molecular dataset from Morse and Normark (2006), by increasing the number of specimens to 254, in 123 species. We also add two new gene regions, both of which are maternally transmitted: COI-COII from the mitochondrial DNA (Provencher et al. 2005), and 16S ribosomal DNA from the primary endosymbiont *Uzinura diaspidicola* (Flavobacteria; Bacteroidetes) (Gruwell et al. 2007). Gene sequences from vertically transmitted primary endosymbionts have been widely used to reconstruct phylogeny in other groups of sternorrynchan insects, especially aphids (Lozier et al. 2008; Lozier et al. 2007; Martinez-Torres et al. 2001; Simon et al. 2003; Simon et al. 1996).

We use a combination of molecular markers from different genomic regions to estimate the phylogeny of armored scales, and we compare our estimated phylogeny to the existing classification. We use our results to infer the evolutionary history of the pupillarial habit and the mode of paternal genome elimination, and we estimate the extant species diversity of key clades. We also discuss the evolution of host plant affiliations and of biogeography.

Methods and Materials

Taxa examined

One hundred and twenty-three species of armored scales were sampled in this analysis, represented by two hundred and fifty-four samples. The majority of samples are from the USA, Australia, Argentina, and Japan. Specimens were either directly frozen at

–80°C, or were preserved in 100% ethanol then stored at –20°C. Tribal designations followed Morse and Normark (2006). Subtribal designations are based on a combination of the work of Borchsenius (1966) with more recent updates to armored scale taxonomy by Takagi (1969; 2002; Takagi et al. 1997). We have tried to adhere to Takagi's classification whenever possible, however he has not published a complete classification to the subtribal level, and has commented mostly on the tribe Diaspidini. Also, Takagi has not recognized subtribes within the tribe Aspidiotini, therefore the subtribal classification presented by Borchsenius was used for this tribe, and for armored scale genera not discussed by Takagi. Five different tribes of Diaspididae were included as well as one tribally unplaced species (*Prodiaspis tamaricicola),* and one outgroup taxon (*Thysanococcus pandani* of the family Halimococcidae). Species names were updated according to the ScaleNet database (Ben-Dov 2008; Miller and Gimpel 2008). A complete list of collection information is available in Table 1.

DNA sequences

Nucleic acids were isolated from specimens using the Qiagen DNeasy Blood & Tissue Kit (Qiagen, Valencia, California), with the following modifications. For fresh specimens, the insect was placed in the cap of a 1.5ml Eppendorf tube with 2μl of Buffer ATL. Microscope cover glass was broken into small fragments slightly larger than the insect. Using sterilized forceps, the cover glass was placed on top of the insect, and downward pressure was applied to force the body contents out. The cover glass was rinsed with 20μl of Buffer ATL, and then disposed of. Samples were sometimes stored frozen for several days before 160μl Buffer ATL was added to bring the volume to 180μl as per Qiagen's protocol. For insects preserved in 100% ethanol, the insect was punctured using a 000 pin, and air dried before being placed in 180μl of Buffer ATL. The Qiagen protocol was followed in both methods until the elution, for which only 40μl of Buffer AE was used. For all specimens, the cuticle was saved for mounting on a microscope slide, and vouchers are maintained in the University of Massachusetts Insect Collection.

Fragments of the nuclear protein-coding gene Elongation Factor 1α (EF1α), the D2 and D3 expansion segments of the large subunit ribosomal RNA gene 28S, and a region of mitochondrial DNA (mtDNA) encompassing the 3' portion of cytochrome oxidase I (COI), and the 5' portion of cytochrome oxidase II (COII) were amplified. For the EF1α and 28S fragments we used the protocols and primers reported in Morse and Normark (2006) except that for EF1α we used *Takara Ex Taq™* (Takara Bio Inc., Otsu, Japan). For COI-COII we used the protocols and primers reported in Provencher *et al.* (2005), except that we used *Takara Ex Taq™* . Ribosomal 16S from the primary bacterial endosymbiont *Uzinura diaspidicola* was amplified using primers and protocols reported in Gruwell *et al.* (2007).

Products from PCR reactions were visualized using 1.5% agarose gels, and stained with SYBRsafe™ (Invitrogen, Carlsbad, California). PCR products were cleaned either using a MinElute kit (Qiagen), a Qiaquick kit (Qiagen), or Exo SAP-IT enzymatic digestion (USB Corporation, Cleveland, Ohio). Sequencing was performed on a 3730 DNA Analyzer (Applied Biosystems, Foster City, California) either at Brigham Young University in Provo, Utah, or at Yale University in New Haven, CT. Sequences were edited using Sequencher 4.2 (Gene Codes Corporation, Ann Arbor, Michigan).

Alignments of EF1α and COI-COII were trivial because no insertions or deletions were present in the coding regions. Four introns were identified and excluded from EF1α using the starting and ending nucleotides (GT-AG). The tRNA normally present in insects between COI and COII was absent in all sampled individuals, as previously reported for *Aspidiotus nerii, Hemiberlesia lataniae, and Aonidiella aurantii* (Provencher et al. 2005). In its place was a short (2 to 41 bp) intergenic spacer that was excluded from the analysis. Due to high levels of variation observed in both the introns of EF1α and the intergenic spacer between COI and COII, these sections were excluded from the analysis. Alignments of ribosomal 28S and 16S were performed using Clustal X v.2.0.3 (Larkin et al. 2007). GenBank accession numbers are shown in Table 1.

Phylogeny construction

Two versions of our dataset were analyzed. The first version (the full dataset) contained all 254 taxa. All 254 taxa had both the 28S and EF1α gene fragments, although some individuals were missing some or both of the other gene fragments. The second version (the core dataset) had only the 113 taxa for which all four gene fragments were available. Maximum parsimony, maximum likelihood, and Bayesian analyses were run on both versions of the dataset, as well as on the individual gene fragments.

Maximum parsimony analyses were run in PAUP (Swofford 2003) using the Wrap-ratchet algorithm through the CIPRES portal (Warnow 2008). Duplicate trees were discarded, and trees were filtered to include only the most parsimonious trees. These trees were then used as the starting trees for a heuristic search with max trees set to 100,000. Bootstraping was performed using 250 pseudo-replicates, each with ten random-addition starting trees as in Morse and Normark (2006). Maximum likelihood as well as maximum likelihood bootstrap analyses were performed in RAxML (Stamatakis et al. 2008), using the GTR+I+G model. Bayesian analyses were also run following Morse and Normark (2006), with the following eight data partitions: EF1α 1st, 2nd, and 3rd codon positions; COI-COII 1st, 2nd, and 3rd codon positions; 28S; and 16S. For each analysis, four chains were run for 5,000,000 generations at a temperature of 0.2. Chains were sampled every 1,000 generations, with a burn-in of 10,000 generations.

Character mapping

For each identifiable species in our dataset we scored the following four characters: pupillarial vs. non-pupillarial (Howell and Tippins 1990; Stickney 1934), early vs. late paternal genome elimination (Brown 1965; Gavrilov 2007; Nur 1990a; Nur 1990b), biogeographic regions (Ben-Dov 2008; Miller and Gimpel 2008), and host clades. The host clades used were; Ferns and Allies, Gymnosperms, Basal Angiosperms, Magnoliid Complex, Monocots, Basal Tricolplates, Core Tricoplates, Rosids, and Asterids. To score host clades we obtained the host family records from Scalenet (Ben-Dov 2008; Miller and Gimpel 2008), corrected these names using the Angiosperm Phylogeny Website (Stevens 2001 onwards), and grouped into clades using the phylogeny presented in Judd *et al.* (2002). For complete character matrices, see Appendix 1. These characters were mapped onto the phylogeny using parsimony in Mesquite (Maddison and Maddison 2007).

Results

After concatenation of all fragments, the full version of the dataset included 254 taxa and 3490 aligned nucleotide sites. For the parsimony analysis, there were 1500 parsimony informative sites, and an overall tree length of 17023. The core version of the dataset included 113 taxa and 3374 sites. There were 1300 parsimony informative sites, and an overall tree length of 11315. Tree scores for all 27 analyses can be seen in Table 2. One interesting result was that five species (*Chionaspis etrusca, Leucaspis lowi, Neoleonardia extensa, Peliculaspis celtis,* and *Pseudaonidia trilobitiformis*) had the alternative start codon ATT for COII, recently reported in Coleoptera (Dobler and Müller 2000). These species also had extremely short intergenic spacers, 2-4 base pairs in length. The comparison of the Bayesian trees from the full and core versions of the dataset found that only 11 nodes were in conflict (Appendix 2). In each case these represented a switch between two adjacent nodes.

The results from the Bayesian analysis of the full dataset can be seen in Figure 1. Of the nodes on this tree, 64% were well supported by all three methods of anlaysis (MP and ML ≥ 75 bootstrap support, BI ≥ 90 posterior probability); 79% of nodes were supported by two methods, and only 21% of nodes were present in the Bayesian topology alone. There were several instances where the analyses of individual gene partitions were in conflict with the topology of the concatenated tree. In total there were eight such nodes in conflict (see open symbols on Figure 1). Four of them received high support from the respective gene fragment (dark open symbols on Figure 1), and four received moderate support (grey open symbols on Figure 1).

Monophyly of taxonomic groups

We find that neither of the major subfamilies of the Diaspididae is perfectly monophyletic as currently constituted. Node A (Figure 1) roughly corresponds to the subfamily Diaspidinae, including the tribes Diaspidini and Lepidosaphidini, except that it also contains a species generally considered a member of the Aspidiotinae (*Palinaspis quohogiformis*) and does not include the species *Pelliculaspis celtis*. The subfamily Aspidiotinae (clades G and E, together with *Gymnaspis, Maskellia* and *Furcaspis*) appears to be paraphyletic with respect to Diaspidinae. Relationships among the major clades of Aspidiotinae are very poorly supported.

At the tribal level, a rough correspondence can be drawn between the tree and the classification, though none of the tribes sampled is perfectly monophyletic as currently constituted. Node C largely corresponds to the tribe Diaspidini, but it also includes species usually assigned to the tribes Aspidiotini (*Palinaspis quohogiformis*) and Lepidosaphidini (*Ischnaspis longirostris*), as well as a tribally unplaced species (*Prodiaspis tamaricicola*). Node D corresponds to the tribe Lepidosaphidini, except that it also includes a number of xeric-habitat New World species that have traditionally been placed in the tribe Diaspidini (*Eudinaspis calchaquensis, Protarigionia larreae, Pseudoparlatoria sp., Situlaspis yuccae, and Xerophilaspis prosopidis)*. The tribes Parlatoriini and Aspidiotini appear to be more radically non-monophyletic and interdigitated with each other, though the relationships among their component clades are very poorly resolved in our analysis. The largest of these component clades (Node F) includes the majority of sampled individuals and species of the tribe Aspidiotini, including all sampled species known to have early paternal genome elimination. The two species sampled that were once assigned to the obsolete tribe Rugaspidiotini (Takagi 1995; Takagi et al. 1997), namely *Prodiaspis tamaricicola* and *Poliaspoides formosana,* appear to be distantly related members of the tribe Diaspidini.

The tribe Leucaspidini (Node E) is nearly monophyletic as currently constituted except for the inclusion of a species usually assigned to the Parlatorini (*Labidaspis myersi*). This finding differs from the findings of Morse and Normark (2006), where the tribe was reconstructed as polyphyletic. In that study, specimen D0625A (identified as *Leucaspis pusilla*) was reconstructed as closely related to the type species of the tribe Aspidiotini, while the placement of specimens D0039A and D0040A (*Leucaspis ohakunensis*) more closely mirrored traditional placements of the tribe. Upon further sampling individuals from lot D0625, other representatives of the species *Leucaspis pusilla*, and increasing the total number of species sampled in this tribe, we find that the tribe Leucaspidini formed a distinct clade, and that the DNA from D0625A must have come not from *Leucaspis pusilla*, but from a yet-unidentified member of the Aspidiotini.

None of the well-sampled subtribes is perfectly monophyletic as currently constituted (Figure 2). Some are radically polyphyletic, such as Aonidiina (*Maskellia* and *Greeniella*) and Gymnaspidina (*Gymnaspis* and *Labidaspis*). However, some of the clades in our estimated phylogeny correspond fairly closely with recognized subtribes. In the tribe Diaspidini, we find closely related clades corresponding roughly to the subtribes Chionaspidina, Diaspidina (Clade K), and Fioriniina sensu Takagi (Clade J). In the tribe Aspidiotini, we find a clade (Clade L) that corresponds roughly to the subtribe Pseudaonidiina. Its affinities to the core Aspidiotini (Clade F) vs. Parlatoriini remain unresolved. Another sampled subtribe of Aspidiotini, Furcaspidina, is more distantly related to other aspidiotines and is discussed below under *Taxonomic implications*.

Character mapping

In our reconstruction, the pupillarial habit is the ancestral condition of the armored scales (Figure 3). We find two independent losses of this habit, one at Node G, and one at Node H. Our reconstruction also shows multiple reversions to the pupillarial state, one within Aspidiotinae, and several within Diaspidinae. The Australian species *Trullifiorinia acaciae* and *Crypthemichionaspis nigra* have been classified as belonging to the subtribe Fioriniina based on their shared character of being pupillarial. We find no support from the molecular data for that placement, instead finding strong evidence that *Trullifiorinia* and *Crypthemichionaspis* form a clade within the subtribe Chionaspidina. We find two independent origins of early paternal genome elimination (Figure 3), one in Aspidiotinae (Clade F), and the other at the base of Diaspidinae (Clade A), with no reversions.

The ancestral armored scale we reconstruct to be Australasian (Figure 5), with the two major subfamilies having radiated in separate biogeographic regions. Clade A roughly corresponds to the subfamily Diaspidinae, which we reconstruct as Palearctic in origin. A clade (Clade G) comprising the majority of Aspidiotinae is reconstructed as Australasian. Host use is reconstructed to be highly variable within the armored scales (Figure 6). The ancestor to the armored scales may have fed on rosids and/or monocots, and the majority of nodes reflect reconstructed diets that include rosids. There also appear to be several examples of host shifts, including a monocot (bamboo) feeding clade (Clade I) that includes the subtribe Kuwanaspidina.

Discussion

According to our reconstructions the ancestral armored scale insect was pupillarial with late paternal genome elimination (PGE). There were two independent origins of the scale cover, each of which was followed by an origin of early PGE (Figure 3). One of these early PGE clades (Clade A) comprises the great majority of sampled members of the subfamily Diaspidinae. Using the existing subtribal classification (see details below) we estimate that this clade comprises about 1270 described species. The other early PGE clade (Clade F) comprises the majority of the sampled members of the tribe Aspidiotini, and we estimate its diversity at 650 described species. These two clades comprise the great majority (79%) of diaspidid diversity. The total number of armored scale species lying outside of these clades is approximately 510. Thus, regardless of any other details of tree topology, each of the origins of early PGE was associated with an increased diversification rate (Mitter et al. 1988), although with only two origins, this is not a statistically significant result. Our best estimate of this history in the context of species diversity is presented in Figure 4. To arrive at the diversity estimates we compiled a catalog of armored scale insects according to the best available classification (Appendix 3). This consisted of Borchsenius' (1966) catalog as modified according to the opinions of Takagi (1969; 2002; Takagi et al. 1997). Each of these character systems – the pupillarial habit vs. the armored scale cover and late vs. early PGE -- is unique to armored scale insects. Below we discuss their evolution and offer some speculations on how they may have affected diversification.

Pupillarial habit

Most arthropods, including most members of the insect order Hemiptera, molt several times during their life cycle, resulting in a series of instars of increasing size. Armored scales are sexually dimorphic both in the number of instars and in the modes of development observed between the two sexes. Males have an essentially holometabolous mode of development, with a winged adult preceded by two non-feeding instars, termed the prepupa and pupa. Females have fewer instars, and a hemimetablous mode of development, with wingless adults resembling immature forms. In most species of armored scales females have two complete molts, however in pupillarial species females have only a single complete molt. In both pupillarial and nonpupillarial armored scales at the end of the second larval instar, apolysis occurs and results in a third instar, the adult female. In pupillarial armored scales, ecdysis does not occur. Thus, the adult female spends her entire life within the confines of the second instar's cuticle. Pupillarial females increase in size only once, between the first and second larval instars, and thus represent a peculiar case: female development is more similar to male development in that the male prepupa also develops inside the test of the last larval instar.

Adult females of non-pupillarial armored scale insects are not enclosed in the cuticle of the second instar, but they are enclosed in a structure that incorporates the cuticle, namely the scale. In addition to the cuticles of the first and second instars the scale consists of secreted wax filaments cemented together by an anal excretion (Foldi 1990a; Foldi 1990b). Females actively sculpt the scale by characteristic movements of their bodies. Females in the Aspidiotini (Clade F) typically pivot in nearly complete circles about their mouthparts, producing nearly circular scale covers, whereas the movements of females in the Diaspidinae (Clade A) are typically much more restricted, producing elongate scale covers (Foldi 1990a; Foldi 1990b). The few cases of non-pupillarial armored scales that lack scale covers are all associated with ants, which apparently remove the waxy secretions from the insects (Ben-Dov 1978; Ben-Dov 1990; Ben-Dov and Matile-Ferrero 1984). The absence of any free living armored scales with "naked" adult females suggests that the enclosure of the adult female either by the second instar cuticle or by the scale cover is essential for preventing desiccation or some other function.

The taxonomy of pupillarial scale insects is notoriously problematic. Much of the traditional classification of armored scales is based upon characters of the adult female, which are often radically simplified in the pupillarial forms. Most of the tribes of armored scale insects include one subtribe into which the pupillarial forms are traditionally placed: Aonidiina within Aspidiotini, Gymnaspidina within Parlatorini, and Xerophilaspidina within Diaspidini. Although we have sampled only a few representatives of these pupillarial subtribes, our findings suggest that they are radically polyphletic, a result that will not surprise any scale insect systematist. In making the diversity estimates shown in Figure 4 we have assumed that all unsampled members of these pupillarial subtribes are primitively pupillarial and have late PGE, an assumption that is conservative with respect to the hypothesis that the origins of early PGE have spurred diversification.

Our results indicate that the pupillarial habit is ancestral within the Diaspididae (Figure 3) as previously suggested by both Brown (1965) and Miller (1990). Although this is the most parsimonious reconstruction, Takagi (1969) has hypothesized that there have been multiple ancient origins of the pupillarial habit, and that pupillarial species are more resistant to extinction than species with a scale cover – a scenario that could also account for the pattern we observe.

Paternal Genome Elimination

The majority of extant scale insects (Sternorrhyncha: Coccoidea) have a sexual system in which the paternal copy of chromosomes in males are heterochromatized; this system is referred to as paternal genome elimination (PGE) (Brown 1965; Gavrilov 2007; Normark 2003). Therefore while males develop from fertilized eggs, the paternal set of chromosomes is never passed on. In the family Diaspididae, there exist two different systems of PGE. In the first system, also found in many other families of scale insects, the paternal chromosomes are heterochromatinized early in embryogenesis but are not eliminated until spermatogenesis (late PGE). In the second, the paternal chromosomes are eliminated during embryogenesis (early PGE) (Brown 1965; Normark 2003). Early PGE appears to have contributed to the diversity of armored scale insects as the two clades in which it has developed greatly outnumber their sister clades. Taking at face value the apparent link between origins of early PGE and increased diversification rate

(Figure 4), below we outline a few scenarios by which early PGE might promote diversification.

Adaptive scenarios

Of course one possibility is that there is no causal connections between origins of early PGE and enhanced diversification. With only two origins we cannot reject this null hypothesis. Nur (1990a) hypothesized an adaptive advantage of early PGE, simply based on not paying the cost of replicating unexpressed DNA. Recent discussions of the evolution of PGE have invoked genetic conflict between maternal and paternal chromosomes (Brown 1962; Haig 1993; Herrick and Seger 1999; Normark 2004). Herrick and Seger (1999) interpret the origin of early PGE from late PGE as a maternal strategy for more reliably preventing expression and transmission of paternal chromosomes. If early PGE indeed stabilizes the outcome of maternal-paternal genetic conflict, it could have an adaptive advantage at the organismal level. In Herrick and Seger's model the only adaptive phenotype for expressed paternal chromosomes is transmission to offspring. But there may be other adaptive phenotypes for paternal chromosomes. Under PGE paternal chromosomes are maternally transmitted. In principle, they may avail themselves of any of the strategies of maternally transmitted elements to enhance their own transmission. For instance, selection ought to favor paternal chromosomes that have a male-killing phenotype. If so, early PGE, which removes paternal chromosomes from males, ought to confer an organism-level adaptive advantage.

Both origins of early PGE take place in lineages that have evolved a scale cover. The origin of the scale cover removes a constraint on the size and fecundity of the adult female, allowing her to grow much larger than the second instar female. Because armored scale females do not move, and because they feed on the contents of parenchyma cells, which can be locally exhausted, they may soon encounter another constraint on their size and fecundity, due to resource limitation. Of the adaptive scenarios discussed above, resource limitation plays a role both in Nur's hypothesis of physiological costs, and in our hypothesis of male-killing paternal chromosomes. Resource limitation plays no obvious role in Herrick and Seger's model based on transmission genetics. Under Herrick and Seger's model there would seem to be no causal connection between the origin of the scale cover and the subsequent origin and diversification of early PGE, but under the other adaptive scenarios discussed above, this sequence of evolutionary events, which is repeated twice in armored scale insects, may be causally related.

Biogeography

Armored scale insects are successful pests worldwide. In spite of the biology of armored scales and their obvious difficulties in dispersal, these small insects have been able to colonize almost the entire world (except Antarctica). Our geographic sampling has included all inhabited continents, but has not been exhaustive, or random. Our sampling is best in the USA, Australia, Japan, and Argentina, and we have almost nothing from Africa, or continental Asia. Our observations on the biogeographical implications of our results are therefore tentative. We reconstruct the ancestral armored scale to be of Australasian origin (Figure 5), and the two major subfamilies of armored scales appear to have evolved in separate biogeographic regions. Node A roughly represents the subfamily Diaspidinae, which appears from our evidence to be Palearctic in origin. The majority of the subfamily Aspidiotinae (Node G) appears to be Australasian, with a subsequent radiation into the Nearctic. Many of the species of both of these subfamilies are highly invasive and globally distributed. It appears that the two major subfamilies developed in geographic isolation, and have since undergone many dispersal events.

Evolution of host use

The arms race between plants and herbivores has been hypothesized to be one of the driving forces of speciation in insects through the creation of new adaptive zones (Ehrlich and Raven 1964). Recently the interaction between insects and their hosts have been explored using phylogenetics (Janz et al. 2001; Janz and Nylin 1998; Janz et al. 2006; Kelley and Farrell 1998; Nosil and Mooers 2005). The ancestral armored scale might have fed on monocots and/or rosids (Figure 6), and the ability to feed on rosids is reconstructed to the majority of nodes with many species also feeidng on the closely related asterids. We find several possible examples of adaptation to new adaptive zones, namely at the subtribal (Node J), and tribal levels (Node E). However, our sampling was not exhaustive nor random, and includes many of the most invasive and polyphagous species of armored scales. Due to the extreme amount of diversity displayed in diet breadth, especially in these polyphagous species, it is difficult to comment on host associations at the family level. However, while local adaptation may occur at the species, or even subtribal level, the extreme diversity displayed in host range suggests that selection in this family has maintained a generalist lifestyle. This may be a necessary adaptation driven by the fact that these insects have very little control over their own dispersal, and the random nature in which they colonize hosts.

Taxonomic implications

Pelliculaspis celtis

One of the more interesting results from the analysis is the placement of *Pelliculaspis celtis*: subfamily Diaspididinae, tribe Xerophilaspidina. Included in our analysis is the type species of the Xerophilaspidina (*Xerophilaspis prosopidis*), which we found to be closely related to other New World species in the tribes Lepidosaphidini and Diaspidini. According to our analysis, *Pelliculaspis celtis* is distantly related -- it does not belong within the subfamily Diaspdinae -- and is sister to all other sampled armored scales. Another unusual feature of *Pelliculaspis celtis*, though not included in this analysis, is an extremely long intron (235 bp) in EF1α, over twice as long as the same intron in other diaspidid species (79-101 bp).

Ferris (1941) established the genus *Pelliculaspis* after collecting specimens (*P. durapyga,* and *P. pellita*) in Panama that, while similar to the genera *Fissuraspis* and *Nicholiella*, in his opinion didn't belong to any described genus. All three of these genera are pupillarial and have a reduction of pores and ducts in the adult female. *Nicholiella* has late PGE (Brown 1965) and the others have never been studied cytologically. All have been placed in the problematic subtribe Xerophilaspidina, discussed above. There are several differences that distinguish *Pelliculaspis celtis* from the other members of *Pelliculaspis*, and from other members of the subfamily Diaspidinae. *Pelliculaspis celtis* differs from other members of *Pelliculaspis* in the number of pygidial lobes, segments of antennae, and the absence of macroducts and gland spines in the second instar stage (McDaniel 1972). The lack of the last two is especially significant, for they are two of the diagnostic characters of the subfamily Diaspidinae, and further highlight the peculiarity of this species. *Pelliculaspis celtis* also bears some resemblance to the unusual armored scale genus *Ancepaspis*, which has sometimes been placed in its own tribe, the Ancepaspidini, and sometimes has been considered not to belong to Diaspididae. The adult females of both *Pelliculaspis celtis* and *Ancepaspis* have significant posterior constrictions of their body, and the second instar's pygidium lacks macroducts, gland spines, and lobes, and perivulvar pores. All together it should not be surprising that *Pelliculaspis* are only distantly related to other sampled armored scales, but a good deal of further sampling will be necessary to clarify its true affinities.

Furcaspis

The subtribe Furcaspidina, traditionally included in the tribe Aspidiotini, has recently been revised to include the single genus *Furcaspis* (Williams et al. 2006) with 28 species. In our results *Furcaspis* is sister to the subfamily Diaspidinae. Although this is somewhat surprising, *Furcaspis* does share several morphological characters with Diaspidinae and not with other Aspidiotini. These include: six antennal segments in first instar, gland spines in first instar, two complete dorsal abdominal lines in first instar, mid cranial ridge with long lateral arms in males, pores associated with anterior spriacle in adult females, and multisetose antennae in adult females (D.R. Miller and B.B. Normark, unpublished data). Probably this group belongs in an expanded Diaspidinae.

Conclusions

Relatively few morphological characters are available for armored scale classification. High levels of convergent evolution have caused errors in tribal designations (Takagi 1995; Takagi et al. 1997). The fact that two characters unique to armored scales – the "armored" scale syndrome, and early PGE – are both examples of convergent evolution highlights the problems in determining homology in this group, and provides a possible explanation for historical taxonomic difficulties.

Both origins of early PGE take place in lineages that have evolved a scale cover. Due to the immobility of armored scale females, resource limitation likely constrains growth and fecundity. Therefore an adaptive scenario for the evolution of early PGE, and the apparent increased diversification rate of early PGE armored scales, should take into account resource limitation. Both in Nur's hypothesis of physiological costs, and in our hypothesis of male-killing paternal chromosomes, resource limitation may have driven the evolution of early PGE.

Table 1. Insect collection vouchers and GenBank accession numbers by taxon.

				Gen Bank Accession Numbers			
Species	Voucher	Source	Type Sp.	28S	EF1α	16S	COI-COII
HALIMOCOCCIDAE:							
Thysanococcus pandani Stickney	D0468C	USA:HI		DQ145391.2	DQ145503.1	GQ424871	
DIASPIDIDAE:							
ASPIDIOTINAE:							
Tribe Aspidiotini:							
Abgrallaspis colorata (Cockerell)	D0836A	USA:TX		GQ325445[d]	GQ403870[d]		
Abgrallaspis cyanophylli (Signoret)	D0893B	USA:CA	x	GQ325446[d]	GQ403883[d]		
Abgrallaspis degenerata (Leonardi)	D0001	USA:CA		DQ145286.2	DQ145398.1	DQ868797.1	GQ424957
Aonidiella citrinia (Coquillett)	D0533A	France		GQ325448[d]	GQ403826[d]	GQ424872	
Aonidiella aurantii (Maskell)	D0012	USA:CA	x	DQ145288.2	DQ145400.1	GQ424836	
	D0290	Argentina		DQ145289.2	DQ145401.1	DQ868798.1	DQ119748
Aspidiella sacchari (Cockerell)	D0571	Mexico	x	DQ145368.2	DQ145480.1	DQ868839.1	
Aspidiotus destructor Signoret	D0496A	Tinidad & Tobago		DQ145293.2	DQ145293.2	DQ145405.1	
Aspidiotus cf. nerii	D0043A	Australia		DQ145296.2	DQ145408.1	DQ868800.1	DQ119750.1
Aspidiotus nerii Bouché	D0022A	USA:CA	x	DQ145292.2	DQ145404.1	GQ424838	GQ424960
	D0045A	USA:CA	x	DQ145294.2	DQ145406.1	GQ424842	GQ424968
	D0409C	South Africa	x	DQ145297.2	DQ145409.1		DQ119752.1
	D0493	New Zealand	x	DQ145295.2	DQ145407.1	DQ868861.1	DQ119758.1
	D0599A	Turkey		GQ325510	GQ403833	GQ424877	GQ425035
	D2102A	Australia	x	GQ325450[d]	GQ403931[d]	GQ424940	GQ425099
Chrysomphalus aonidum (Linnaeus)	D0300	USA:FL	x	DQ145309.2	DQ145421.1	DQ868810.1	GQ425007
Chrysomphalus dictyospermi (Morgan)	D0122A	Kenya		DQ145310.2	DQ145422.1	GQ424845	GQ424974
	D2032A	Australia		GQ325463[d]	GQ403902[d]	GQ424913	
Clavaspis covilleae (Ferris)	D0877A	USA:CA		GQ325464[d]	GQ403876[d]	GQ424893	GQ425071
	D0877C	USA:CA		GQ325465[d]	GQ403877[d]	GQ424894	GQ425072
Clavaspis herculeana (Cockerell & Hadden)	D2040B	Australia	x	GQ325466[d]	GQ403907[d]	GQ424918	
Clavaspis texana Ferris	D0838A	USA:TX		GQ325467[d]	GQ403871[d]	GQ424891	GQ425069

Diaphoraspis compacta Brimblecombe	D2044A	Australia		GQ325472	GQ403910		GQ425088
Diaspidiotus gigas (Thiem & Gerneck)	D0688A	Russia		GQ325473[d]	GQ403853[d]		GQ425054
Diaspidiotus osborni (Newell & Cockerell)	D2176A	USA:MA		GQ325474[d]	GQ403944[d]	GQ424950	
Diaspidiotus perniciosus (Comstock)	D2068A	Australia		GQ325475[d]	GQ403920[d]	GQ424931	GQ425094
Diaspidiotus sp. undesc. #1[a]	D0288A	Argentina		DQ145313.2	DQ145425.1	DQ868813.1	GQ425001
Diaspidiotus sp. undesc. #2[a]	D0265	Argentina		DQ145314.2	DQ145426.1	GQ424853	GQ424990
Diaspidiotus sp. undesc. #3[a]	D0273A	Argentina		DQ145315.2	DQ145427.1		GQ424996
	D0273C	Argentina		GQ325476[d]	GQ403818[d]		GQ424997
Furcaspis biformis (Cockerell)	D1031A	Jamaica	x	GQ325481	GQ403885		
Furcaspis sp.	D0813B	Jamaica		GQ325482	GQ403866	GQ424889	
Greeniella capitata Brimblecombe	D2046B	Australia		GQ325484[d]	GQ403911[d]	GQ424922	
Greeniella sp.	D2063A	Australia		GQ325485	GQ403917	GQ424928	
	D2084A	Australia		GQ325486	GQ403925		
Hemiberlesia lataniae (Signoret)	D0007	USA:CA		DQ145339.2	DQ145451.1	GQ424835	GQ424959
	D0038	USA:CA		DQ145340.2	DQ145452.1	DQ868814.1	GQ424963
	D0038B	USA:CA		GQ325487[d]	GQ403808[d]		
	D0066	New Zealand		DQ145341.2	DQ145453.1	GQ424843	DQ119749
	D0766B	Australia		GQ325488[d]	GQ403864[d]	GQ424887	GQ425065
Hemiberlesia palmae (Cockerell)	D0246A	Colombia		DQ145342.2	DQ145454.1	DQ868815.1	
Hemiberlesia rapax (Comstock)	D0271	Argentina	x	DQ145343.2	DQ145455.1	GQ424855	GQ424995
	D0298A	Argentina	x	DQ145344.2	DQ145456.1	GQ424859	GQ425006
Lindingaspis rossi (Maskell)	D0753A	Australia		GQ325505[d]	GQ403858[d]		GQ425059
	D0753B	Australia		GQ325506[d]	GQ403859[d]		GQ425060
	D2073A	Australia		GQ325507[d]	GQ403922[d]	GQ424933	
Maskellia globosa Fuller	D0751A	Australia	x	DQ145358.2	DQ145470.1	DQ868834.1	
Melanaspis bromiliae (Leonardi)	D0254A	USA:AL		DQ145360.2	DQ145472.1	DQ868835.1	
Melanaspis obscura (Comstock)	D0251C	USA:AL	x	GQ325511[d]	GQ403817[d]	GQ424850	GQ424985
Melanaspis sp. undesc. #1[a]	D0264A	Argentina		DQ145361.2	DQ145473.1	GQ424852	GQ424989
Melanaspis sp. undesc. #2[a]	D0297A	Argentina		DQ145362.2	DQ145474.1	GQ424858	GQ425005
	D0275	Argentina		DQ145363.2	DQ145475.1	DQ868836.1	GQ424998
Melanaspis tenebricosa (Comstock)	D0247A	USA:AL		DQ145364.2	DQ145476.1	GQ424849	
Mycetaspis personata (Comstock)	D0228	Colombia	x	DQ145366.2	DQ145478.1	DQ868838.1	

Neoleonardia alata (Froggatt)	D2069A	Australia		GQ325512[d]	GQ403921[d]	GQ424932	
Neoleonardia extensa (Maskell)	D2055A	Australia	x	GQ325513	GQ403915	GQ424926	GQ425089
Nuculaspis californica (Coleman)	D0026A	USA:CA		DQ145322.2	DQ145434.1	GQ424839	GQ424961
	D0026B	USA:CA		GQ325515[d]	GQ403807[d]		
	D0055A	USA:CA		DQ145323.2	DQ145435.1	DQ868820.1	GQ424971
Nuculaspis tsugae (Marlatt)	D0822A	Japan		GQ325516[d]	GQ403867[d]		
Oceanaspidiotus spinosus (Comstock)	D0385A	Japan		DQ145287.2	DQ145399.1	GQ424864	
Octaspidiotus multipori (Takahashi)	D0381	Japan		DQ145365.2	DQ145477.1	DQ868837.1	GQ425017
Octaspidiotus subrubescens (Maskell)	D2133A	Australia	x	GQ325517[d]	GQ403943[d]	GQ424949	GQ425105
Palinaspis quohogiformis (Merrill)	D0344A	USA:FL	x	DQ145369.2	DQ145481.1	GQ424861	GQ425010
	D0514A	USA:FL	x	DQ145370.2	DQ145482.1	DQ868840.1	GQ425027
	D0514B	USA:FL	x	DQ145348.2	DQ145460.1		GQ425028
Pseudaonidia dentata Brimblecombe	D2058A	Australia		GQ325541	GQ403916	GQ424927	GQ425092
Pseudaonidia trilobitiformis (Green)	D0337	USA:FL		DQ145381.2	DQ145493.1	DQ868850.1	GQ425008
	D0340C	USA:FL		DQ145382.2	DQ145494.1	GQ424860	GQ425009
	D0347A	USA:FL		DQ145383.2	DQ145495.1	GQ424862	GQ425011
Selenaspidus articulatus (Morgan)	D0510A	USA:FL	x	DQ145389.2	DQ145501.1		
Targionia fabianae Leonardi	D0277B	Argentina		DQ145390.2	DQ145502.1		
Tribe Leucaspidini							
Anamefiorinia casuarinae (Maskell)	D2041D	Australia	x	GQ325445	GQ403908	GQ424919	
Leucaspis cordylinidis Maskell	D0648A	New Zealand		GQ325493	GQ403843		
Leucaspis lowi Colvée	D0689A	Russia		GQ325494	GQ403854		GQ425055
Leucaspis morrisi (Brittin)	D0650A	New Zealand		GQ325495	GQ403845		GQ425047
Leucaspis ohakunensis Brittin	D0039D	New Zealand		DQ145355.2	DQ145467.1	DQ868796.1	GQ424964
	D0040B	New Zealand		DQ145356.2	DQ145468.1		GQ424965
	D0040C	New Zealand		GQ325496	GQ403809	GQ424840	GQ424966
	D0658A	New Zealand		GQ32597	GQ403849		GQ425051
Leucaspis pusilla Löw	D0597C	Turkey		GQ325498	GQ403831		
	D0597D	Turkey		GQ325499	GQ403832	GQ424876	
	D0625D	Turkey		GQ325500	GQ403838		GQ425043
Leucaspis signoreti Signoret	D0633A	Turkey		GQ325501	GQ403839		GQ425044
Leucaspis sp. undesc. #1[b]	D0647	New Zealand		GQ325502	GQ403842		

Leucaspis sp. undesc. #2[b]	D0660A	New Zealand		GQ325503	GQ403851		
Leucaspis sp. undesc. #3[b]	D0728A	New Zealand		GQ325504	GQ403855		GQ425056
Tribe Parlatoriini							
Gymnaspis achmeae Newstead	D0235C	USA:AL	x	DQ145335.2	DQ145447.1	DQ868795.1	
	D0315A	USA:FL	x	DQ145336.2	DQ145448.1		
	D0315B	USA:FL	x	DQ145337.2	DQ145449.1		
Labidaspis myersi (Green)	D0645A	New Zealand	x	GQ325489	GQ403841	GQ424882	
Parlatoria blanchardi (Targioni Tozzetti)	D0136	Saudi Arabia		GQ325518	GQ403813		
Parlatoria camelliae (Comstock)	D0002A	USA:CA		GQ325519	GQ403805		GQ424958
	D0002B	USA:CA		DQ145371.2	DQ145483.1	DQ868841.1	GQ424956
Parlatoria crypta McKenzie	D0139A	Saudi Arabia		GQ325520	GQ403814	GQ424846	
Parlatoria oleae (Colvée)	D0609B	Turkey		GQ325521[d]	GQ403834[d]	GQ424879	GQ425037
	D0609C	Turkey		GQ325522	GQ403835		GQ425038
Parlatoria pergandii (Comstock)	D0258	Argentina		DQ145372.2	DQ145484.1	DQ868842.1	GQ424987
Parlatoria pseudaspidiotus Lindinger	D0538	Mexico	x	DQ145334.2	DQ145446.1	DQ868824.1	
Parlatoria proteus (Curtis)	D0757A	Australia		GQ325523	GQ403862		GQ425063
	D0757B	Australia		GQ325524	GQ403863		GQ425064
Parlatoria theae Cockerell	D0392A	Japan		DQ145373.2	DQ145485.1	DQ868843.1	GQ425021
DIASPIDINAE:							
Tribe Diaspidini							
Aulacaspis difficilis (Cockerell)	D0375	Japan		DQ145298.2	DQ145410.1	DQ868801.1	
Aulacaspis distylii Takahashi	D0384	Japan		DQ145299.2	DQ145411.1	DQ868802.1	
Aulacaspis rosae (Bouché)	D0395A	Japan	x	GQ325451	GQ403823	GQ424867	GQ425022
	D0395B	Japan	x	GQ325452	GQ403824	GQ424868	GQ425023
Aulacaspis spinosa (Maskell)	D0376	Japan		DQ145367.2	DQ145479.1	GQ424863	GQ425015
Aulacaspis yasumatsui Takagi	D0242	USA:FL		DQ145300.2	DQ145412.1	DQ868803.1	GQ424982
Carulaspis juniperi (Bouché)	D0241	USA:MA	x	DQ145303.2	DQ145415.1	DQ868804.1	GQ424981
	D0403A	USA:MA	x	DQ145301.2	DQ145413.1	GQ424870	GQ425024
Carulaspis minima (Targioni Tozzetti)	D0014B	USA:CA		DQ145302.2	DQ145414.1	GQ424837	
Chionaspis americana Johnson	D0833A	USA:TX		GQ325454	GQ403869		GQ425068
	D2181A	USA:MA		GQ325453	GQ403945	GQ424951	
Chionaspis etrusca Leonardi	D0606	Turkey		DQ145397.2	DQ145509.1	DQ868858.1	GQ425036

	D0687A	Russia		GQ325455	GQ403852		GQ425053
Chionaspis heterophyllae Cooley	D0933A	USA:NJ		GQ325456	GQ403884	GQ424897	GQ425075
Chionaspis lepineyi Balachowsky	D0075	Hungary		DQ145307.2	DQ145419.1	DQ868809.1	GQ424972
Chionaspis pinifoliae (Fitch)	D0006B	USA:CA		GQ325457	GQ403806		
	D0054A	USA:CA		GQ325458	GQ403811		GQ424970
	D0126B	USA:CA		GQ325459	GQ403812		GQ424975
	D0355B	USA:CA		GQ325460	GQ403822		GQ425012
	D0531	USA:MA		DQ145306.2	DQ145418.1	DQ868807.1	GQ425030
	D0889A	USA:CA		GQ325461	GQ403881		
	D0889D	USA:CA		GQ325462	GQ403882		GQ425074
Chionaspis wistariae Cooley	D0386A	Japan		DQ145308.2	DQ145420.1	DQ868808.1	GQ425018
Crypthemichionaspis nigra Lindinger	D2080A	Australia		GQ325468	GQ403924	GQ424935	
Crypthemichionaspis sp.	D2091A	Australia		GQ325469	GQ403927	GQ424936	GQ425096
Crypthemichionaspis sp.	D2093A	Australia		GQ325470	GQ403928	GQ424937	GQ425097
Crypthemichionaspis sp.	D2066A	Australia		GQ325471	GQ403919	GQ424930	
Diaspis boisduvalii Signoret	D0143	USA:MA		DQ145316.2	DQ145428.1	GQ424847	GQ424976
Diaspis coccois Lichtenstein	D0536A	USA:CA		DQ145317.2	DQ145429.1	DQ868816.1	GQ425031
Diaspis echinocacti (Bouché)	D0289	Argentina	x	DQ145318.2	DQ145430.1	DQ868817.1	GQ425002
	D0289B	Argentina	x	GQ325477	GQ403819		GQ425003
Diaspis manzanitae Whitney	D0046	USA:CA		DQ145319.2	DQ145431.1	DQ868818.1	GQ424969
Duplachionaspis divergens (Green)	D0309	USA:FL		DQ145338.2	DQ145450.1	DQ868825.1	
	D0309C	USA:FL		GQ325478	GQ403821		
Duplachionaspis noaeae (Hall)	D0623	Turkey		DQ145320.2	DQ145432.1	DQ868819.1	GQ425041
	D0623B	Turkey		DQ145321.2	DQ145433.1		GQ425042
Epidiaspis leperii (Signoret)	D0060	USA:CA		DQ145324.2	DQ145436.1	DQ868860.1	
Eudinaspis calchaquensis Claps	D0256A	Argentina		DQ145325.2	DQ145437.1	GQ424851	GQ424986
Fiorinia euryae Kuwana	D0374A	Japan		DQ145329.2	DQ145441.1	DQ868822.1	
Fiorinia externa Ferris	D0299	USA:MA		DQ145330.2	DQ145442.1	DQ868823.1	
Fiorinia hymenanthis Takagi	D0387A	Japan		DQ145331.2	DQ145443.1	GQ424866	GQ425019
Fiorinia theae Green	D0250A	USA:AL		DQ145332.2	DQ145444.1	DQ868859.1	
	D0250C	USA:AL		GQ325480	GQ403816		GQ424984
Furchadaspis zamiae (Morgan)	D0455A	USA:CA	x	DQ145333.2	DQ145445.1	DQ868846.1	GQ425025

Ichthyaspis ficicola (Takahashi)	D0391	Japan	x	DQ145349.2	DQ145461.1	DQ868827.1	
Kuwanaspis takahashii Takagi	D0398A	Japan		DQ145351.2	DQ145463.1	DQ868830.1	
Lineaspis striata (Newstead)	D0593B	Turkey	x	GQ325508	GQ403829	GQ424874	GQ425033
	D0593C	Turkey	x	GQ325509	GQ403830	GQ424875	GQ425034
Megacanthaspis leucaspis Takagi	D0401A	Japan		DQ145359.2	DQ145471.1	GQ424869	
Nikkoaspis shiranensis Kuwana	D0642A	Japan	x	GQ325514	GQ403840	GQ424881	GQ425045
Pelliculaspis celtis McDaniel	D0843A	USA:TX		GQ325525	GQ403872	GQ424892	GQ425070
Pinnaspis sp.	D2130A	Australia		GQ325528	GQ403942		
Pinnaspis aspidistrae (Signoret)	D0267	Argentina		DQ145374.2	DQ145486.1	DQ868845.1	GQ424992
Pinnaspis buxi (Bouché)	D0243	Colombia	x	DQ145375.2	DQ145487.1	DQ868847.1	GQ424983
Pinnaspis dysoxyli (Maskell)	D0657A	New Zealand		GQ325526	GQ403847		GQ425049
	D0657C	New Zealand		GQ325527	GQ403848		GQ425050
Pinnaspis hibisci Takagi	D0390A	Japan		DQ145376.2	DQ145488.1	DQ868848.1	GQ425020
Pinnaspis piperis Takagi	D0389A	Japan		DQ145377.2	DQ145489.1	DQ868849.1	
Pinnaspis strachani (Cooley)	D0248A	Colombia		DQ145378.2	DQ145490.1		
Pinnaspis uniloba (Kuwana)	D0542A	USA:HI		GQ325529	GQ403828		GQ425032
Poliaspis sp.	D2021A	Australia		GQ325533	GQ403897	GQ424908	GQ425085
Poliaspis sp.	D2021B	Australia		GQ325534	GQ403898	GQ424909	GQ425086
Poliaspis sp.	D2035B	Australia		GQ325535	GQ403904	GQ424915	
Poliaspis sp.	D2065A	Australia		GQ325536	GQ403918	GQ424929	GQ425093
Poliaspis argentosis Brittin	D0659A	New Zealand		GQ325530	GQ403850		GQ425052
Poliaspis media Maskell	D0649A	New Zealand	x	GQ325531	GQ403844	GQ424883	GQ425046
	D0857	New Zealand	x	GQ325532	GQ403875		
Poliaspis syringae Laing	D2099A	Australia		GQ325538	GQ403930	GQ424939	
	D2124A	Australia		GQ325539	GQ403939	GQ424948	GQ425104
	D2017B	Australia		GQ325537	GQ403894	GQ424905	GQ425083
Poliaspoides formosana (Takahashi)	D0516B	USA:CA	x	GQ325540	GQ403825		GQ425029
Pseudaulacaspis cockerelli (Cooley)	D0221A	China		DQ145384.2	DQ145496.1	DQ868851.1	
	D0221B	China		GQ325543	GQ403815		GQ424977
	D0537A	USA:CA		GQ325544	GQ403827	GQ424873	
	D2034A	Australia		GQ325545	GQ403903	GQ424914	
Pseudaulacaspis difissata (Brimblecombe)	D2043A	Australia		GQ325546	GQ403909	GQ424920	GQ425087

Pseudaulacaspis eugeniae (Maskell)	D2038B	Australia		GQ325547	GQ403905	GQ424916	
	D2038C	Australia		GQ325548	GQ403906	GQ424917	
	D2103A	Australia		GQ325549	GQ403932	GQ424941	
Pseudaulacaspis pentagona (Targioni Tozzetti)	D0372	Japan	x	DQ145385.2	DQ145497.1	DQ868852.1	GQ425013
Pseudaulacaspis prunicola (Maskell)	D0377	Japan		DQ145386.2	DQ145498.1	DQ868853.1	GQ425016
Pseudaulacaspis sp.	D0041A	Australia		GQ325550	GQ403810	GQ424841	GQ424967
Pseudaulacaspis sp.	D0041B	Australia		DQ145304.2	DQ145416.1	DQ868805.1	
Pseudaulacaspis sp.	D2003A	Australia		GQ325551	GQ403886	GQ424898	GQ425076
Pseudaulacaspis sp.	D2003B	Australia		GQ325552	GQ403887	GQ424899	GQ425077
Pseudaulacaspis sp.	D2004A	Australia		GQ325553	GQ403888	GQ424900	GQ425078
Pseudaulacaspis sp.	D2010A	Australia		GQ325542	GQ403892	GQ424903	
Pseudaulacaspis sp.	D2026A	Australia		GQ325553	GQ403899	GQ424910	
Pseudaulacaspis sp.	D2050A	Australia		GQ325555	GQ403912	GQ424923	GQ425090
Pseudaulacaspis sp.	D2105A	Australia		GQ325558	GQ403933	GQ424942	GQ425100
Pseudaulacaspis sp.	D2115A	Australia		GQ325556	GQ403935	GQ424944	GQ425101
Pseudaulacaspis sp.	D2118A	Australia		GQ325557	GQ403936	GQ424945	GQ425102
Pseudoparlatoria sp.	D0269A	Argentina		DQ145387.2	DQ145416.1	GQ424854	GQ424993
Quernaspis quercus (Comstock)	D0031A	USA:CA	x	DQ145388.2	DQ145500.1	DQ868854.1	
Situlaspis yuccae (Cockerell)	D0788A	USA:UT	x	GQ325559	GQ403865	GQ424888	GQ425066
Trullifiorinia acaciae (Maskell)	D0653A	New Zealand	x	GQ325560	GQ403839	GQ424884	GQ425048
	D2028B	Australia	x	GQ325561	GQ403900	GQ424911	
	D2119A	Australia	x	GQ325562	GQ403937	GQ424946	
Unachionaspis signata (Maskell)	D0379	Japan	x	DQ145392.2	DQ145504.1	DQ868856.1	
Unaspis euonymi (Comstock)	D0076			DQ145393.2	DQ145505.1	DQ868855.1	GQ424973
Xerophilaspis prosopidis (Cockerell)	D0887C	USA:CA	x	GQ325588	GQ403880	GQ424896	
Tribe Lepidosaphidini							
Aonidomytilus ceanothi (Ferris)	D0028A	USA:CA		DQ145305.2	DQ145417.1	DQ868806.1	GQ424962
	D0885C	USA:CA		GQ325449	GQ403879		GQ425073
	D0263	Argentina		DQ145290.2	DQ145402.1	DQ868799.1	GQ424988
	D0279	Argentina		DQ145291.2	DQ145403.1	GQ424856	GQ424999
Dactylaspis sp. undesc.[a]	D0287	Argentina		DQ145311.2	DQ145423.1	DQ868811.1	
	D0296A	Argentina		DQ145312.2	DQ145424.1	DQ868812.1	

	D0280A	Argentina		DQ145394.2	DQ145506.1	DQ868857.1	
Eulepidosaphes pyriformis (Maskell)	D0067	New Zealand	x	DQ145326.2	DQ145438.1	DQ868821.1	
	D0068	New Zealand	x	DQ145327.2	DQ145439.1	GQ424844	
Ferrisidea magna (Ferris)	D0880C	USA:CA		GQ325479	GQ403878	GQ424895	
Howardia biclavis (Comstock)	D0229	Colombia	x	DQ145345.2	DQ145457.1	DQ868826.1	GQ424978
	D0229C	Colombia	x	DQ145346.2	DQ145458.1	GQ424848	GQ424979
	D0507A	USA:FL	x	DQ145347.2	DQ145459.1	DQ868828.1	GQ425026
Ischnaspis longirostris (Signoret)	D0230	Colombia	x	DQ145350.2	DQ145462.1	DQ868829.1	GQ424980
Lepidosaphes beckii (Newman)	D0270	Argentina		DQ145352.2	DQ145464.1	DQ868831.1	GQ424994
Lepidosaphes gloverii (Packard)	D0266B	Argentina		DQ145353.2	DQ145465.1	DQ868832.1	GQ424991
Lepidosaphes newsteadi (Šulc)	D0614A	Turkey		GQ325490	GQ403836		GQ425039
	D0614B	Turkey		GQ325491	GQ403837	GQ424880	GQ425040
Lepidosaphes pinnaeformis (Bouché)	D0373A	Japan		DQ145354.2	DQ145466.1	DQ868833.1	GQ425014
Lepidosaphes pseudotsugae Takahashi	D0823B	Japan		GQ325492	GQ403868	GQ424890	GQ425067
Prodigiaspis sp undesc[a]	D0281A	Argentina		DQ145379.2	DQ145491.1	DQ868793.1	GQ425000
Protargionia larreae Leonardi	D0295	Argentina	x	DQ145380.2	DQ145492.1	DQ868794.1	GQ425004
Genus AB sensu John Donaldson[c]	D2098A	Australia		GQ325483	GQ403929	GQ424938	GQ425098
Diaspidinae incertae sedis							
Prodiaspis tamaricicola (Malenotti)	D0605A	Turkey	x	DQ145396.2	DQ145508.1	GQ424878	
DIASPIDIDAE UNDETERMINED							
undetermined	D0291	Argentina		GQ325563	GQ403820	GQ424857	
undetermined	D0625A	Turkey		DQ145357.2	DQ145469.1		
undetermined	D0752A			GQ325564	GQ403856	GQ424885	GQ425057
undetermined	D0752B			GQ325565	GQ403857	GQ424886	GQ425058
undetermined	D0755A			GQ325566	GQ403860		GQ425061
undetermined	D0755B			GQ325567	GQ403861		GQ425062
undetermined	D0850			GQ325568[d]	GQ403873[d]		
undetermined	D0852			GQ325569	GQ403874		
undetermined	D2004B	Australia		GQ325554	GQ403889	GQ424901	GQ425079
undetermined	D2007A	Australia		GQ325571	GQ403890		GQ425080
undetermined	D2007C	Australia		GQ325572	GQ403891	GQ424902	GQ425081

undetermined	D2011A	Australia	GQ325573	GQ403893	GQ424904	GQ425082
undetermined	D2018A	Australia	GQ325574	GQ403895	GQ424906	GQ425084
undetermined	D2020B	Australia	GQ325575	GQ403896	GQ424907	
undetermined	D2029A	Australia	GQ325576	GQ403901	GQ424912	
undetermined	D2052A	Australia	GQ325577	GQ403913	GQ424924	
undetermined	D2053A	Australia	GQ325578	GQ403914	GQ424925	GQ425091
undetermined	D2079B	Australia	GQ325579	GQ403923	GQ424934	GQ425095
undetermined	D2089A	Australia	GQ325580	GQ403926		
undetermined	D2109A	Australia	GQ325581	GQ403934	GQ424943	
undetermined	D2122A	Australia	GQ325582	GQ403938	GQ424947	GQ425103
undetermined	D2128A	Australia	GQ325583	GQ403940		
undetermined	D2128B	Australia	GQ325584	GQ403941		
undetermined	D2131A	Australia	GQ325585	GQ403804		
undetermined	MD0002A	USA:AZ	GQ325586[d]	GQ403946[d]	GQ424952	
undetermined	MD0002B	USA:AZ	GQ325587[d]	GQ403947[d]	GQ424953	

Sequences whose accession numbers begin with the prefix DQ were previously reported in Morse and Normark (2006). Those beginning with GQ were obtained for this study, except those marked with a superscipt d, which were previously published.

An x in the column "Type sp." indicates a generic type species (Ben Dov 2009, Miller and Gimpel 2009).

[a] These species are to be described by Lucia Claps, Instituto Lillo, Argentina.

[b] These species are to be described by Rosa Henderson, Landcare Research, New Zealand.

[c] This individual represents an undescribed genus, according to John Donaldson, who recently retired from the Queensland Department of Primary Industries (QDPI) in Indooroopilly, Australia. Other putative members of this genus are in the QDPI collection, labeled "Genus AB".

[d] Sequence previously reported in: Rugman-Jones, P.F., J.C. Andersen, J.G. Morse, B.B. Normark, and R. Stouthamer. Submitted. Molecular phylogenetic placement of the recently described armored scale insect *Abgrallaspis aguacatae* and several congeners (Hemiptera: Diaspididae). Annals of the Entomological Society of America.

Table 2. Tree Scores from Maximum Parsimony (MP), Maximum Likelihood (ML), and Bayesian (BI) analyses

		254				113				
		28S	EF1α	28S&EF1α	All	28S	EF1α	COI-COII[*]	16S	All
MP	# Characters	892	693	1585	3490	798	693	733	1150	3374
	# p. inform	381	269	650	1500	286	256	482	276	1300
	# Trees	100,000	100,000	100,000	100,000	2430	362	47	100,000	18
	Tree-length	2794	4188	7101	17023	1504	2248	5972	1366	11315
	C.I.	0.268	0.136	0.186	0.193	0.361	0.208	0.182	0.403	0.234
	R.I.	0.825	0.757	0.782	0.714	0.8	0.719	0.543	0.798	0.665
ML	Optimization likelihood	-15035.648	-19681.98	-35464.749	-83233.907	-8492.3541	-11108.967	-24138.892	-9132.2412	-56207.619
	Tree-length	4.55626	4.712603	4.7125	6.022282	1.843314	2.169196	9.667045	0.95184	2.506758
BI	Standard Deviation		0.021002	0.01708	0.01753		0.007131	0.014311		0.008284
	LnL Run1 (or web)	-18453.838	-19459.786	-35040.871	-78970.08	-10251.052	-10770.522	-23980.168	-10564.783	-53010.428
	LnL Run2		-19440.944	-35027.34	-78882.686		-10792.93	-23983.248		-52998.946

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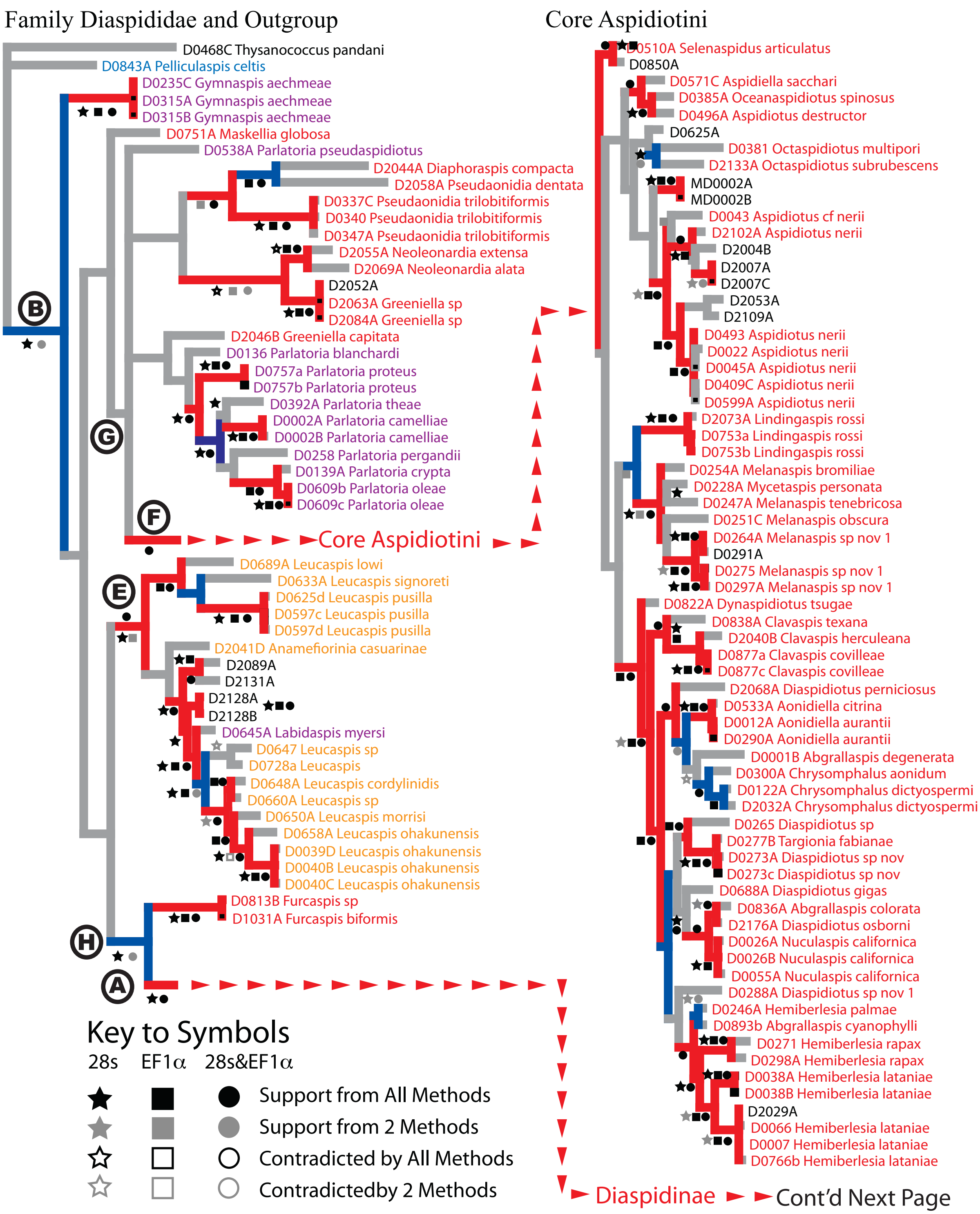
[*] Five species (*Chionaspis etrusca, Leucaspis lowi, Neoleonardia extensa, Peliculaspis celtis,* and *Pseudaonidia trilobitiformis*) had the alternative start codon ATT for COII, recently reported in Coleoptera (Dobler, S. and J.K. Müller. 2000. Resolving phylogeny at the family level by mitochondrial cytochrome oxidase sequences: phylogeny of carrion beetles (Coleoptera, Silphidae). Molecular Phylogenetics and Evolution 15:390-402). These species also had extremely short intergenic spacers, 2-4 base pairs in length.



Family Diaspididae and Outgroup

Core Aspidiotini

Figure 1. Bayesian majority rule consensus of full dataset.
Red lines indicate support from all three methods of reconstruction. Blue lines indicate support from two methods. Grey lines represent nodes present in the Bayesian tree, but unsupported by the other analyses. Symbols indicate results from separate analyses of 28S and EF1α. The criterion for support is a Bayesian posterior probability of ≥ 90, and for Maximum Parsimony or Maximum Likelihood a bootstrap of ≥ 75.

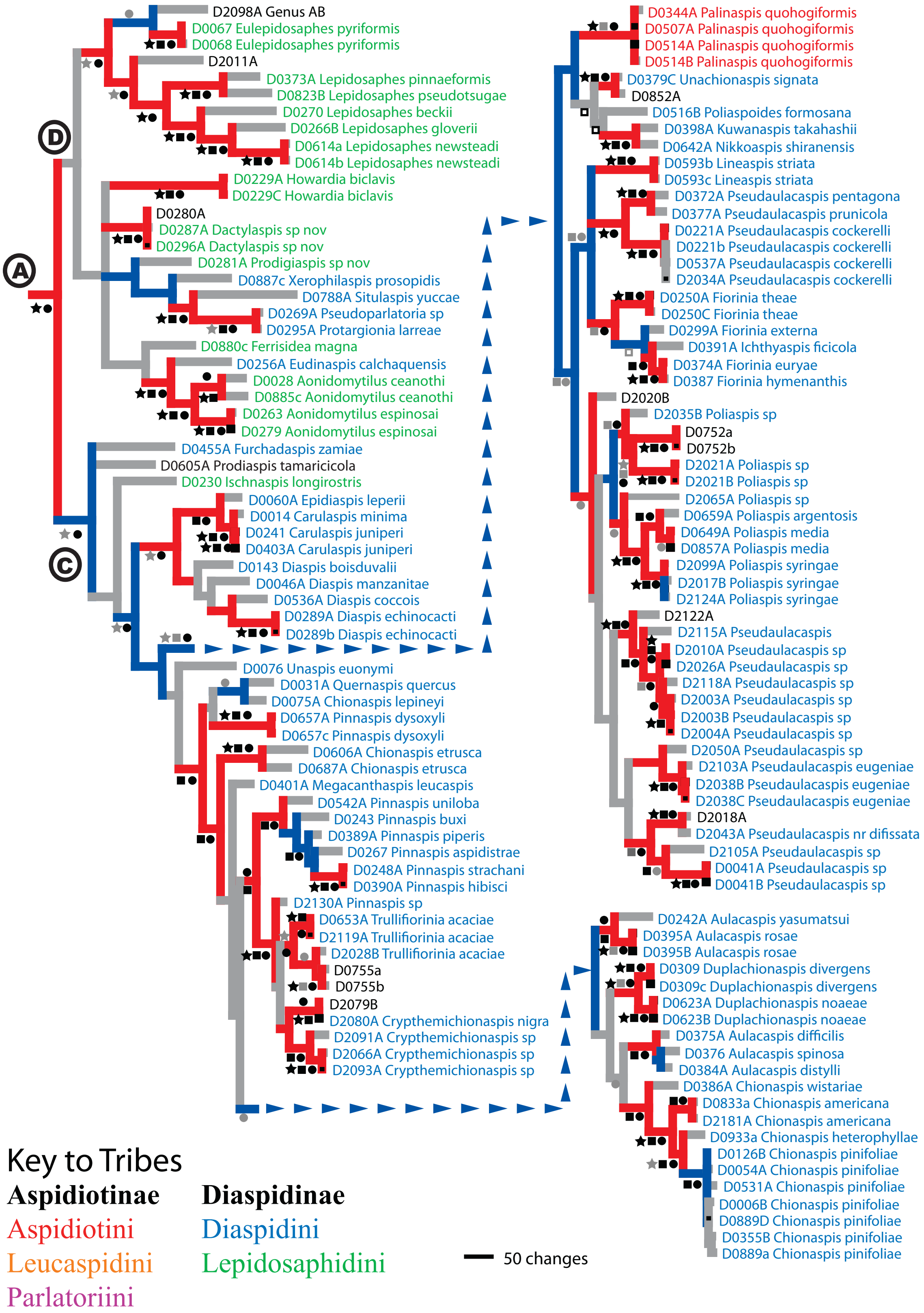


Figure 1. Bayesian majority rule consensus of full dataset.
Continued from previous page.

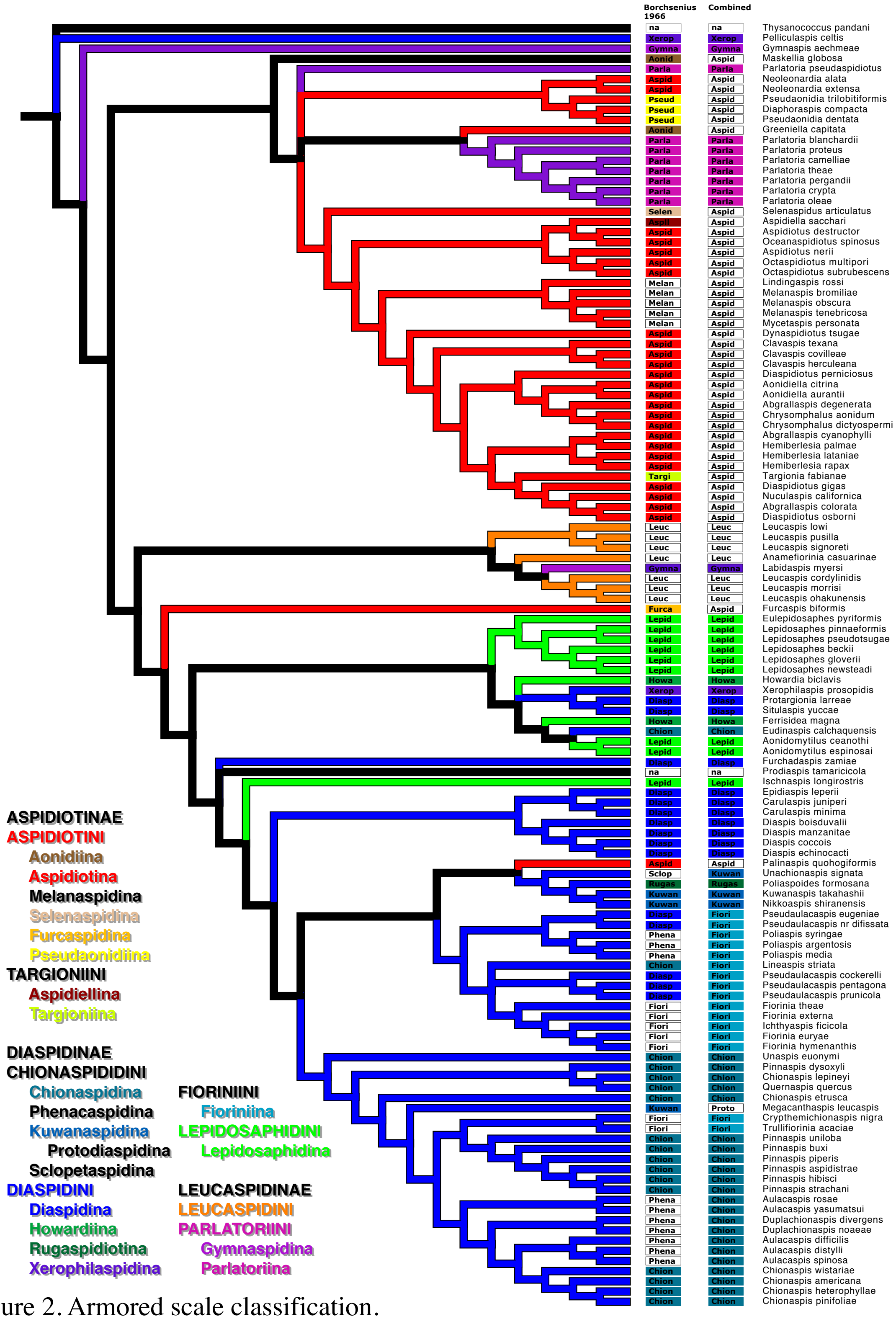


Figure 2. Armored scale classification.

The results presented in Figure 1 were pruned to remove unidentified specimens and so each species is here represented by a single terminal. Branches are colored by tribal designation. Boxes included subtribe abbreviations, and are colored according to key. Boxes not colored are either subtribes not recognized by Takagi, or represent tribes.

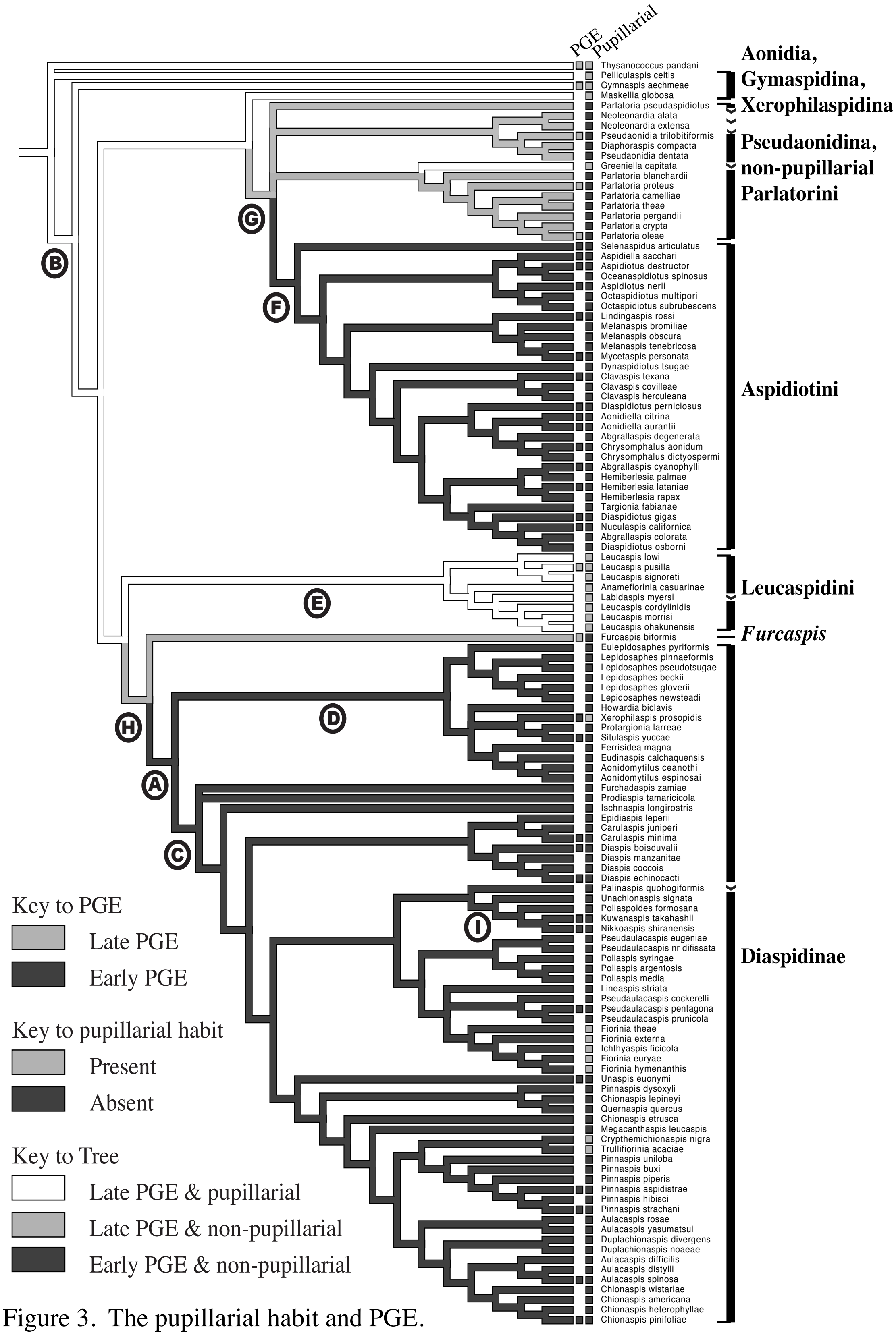


Figure 3. The pupillarial habit and PGE.
Ancestral reconstructions of the pupillarial habit, and of the forms of PGE were mapped onto Figure 2, using Mesquite (Maddison and Maddision 2007). Discontinuous vertical lines represent non-exclusive groupings.

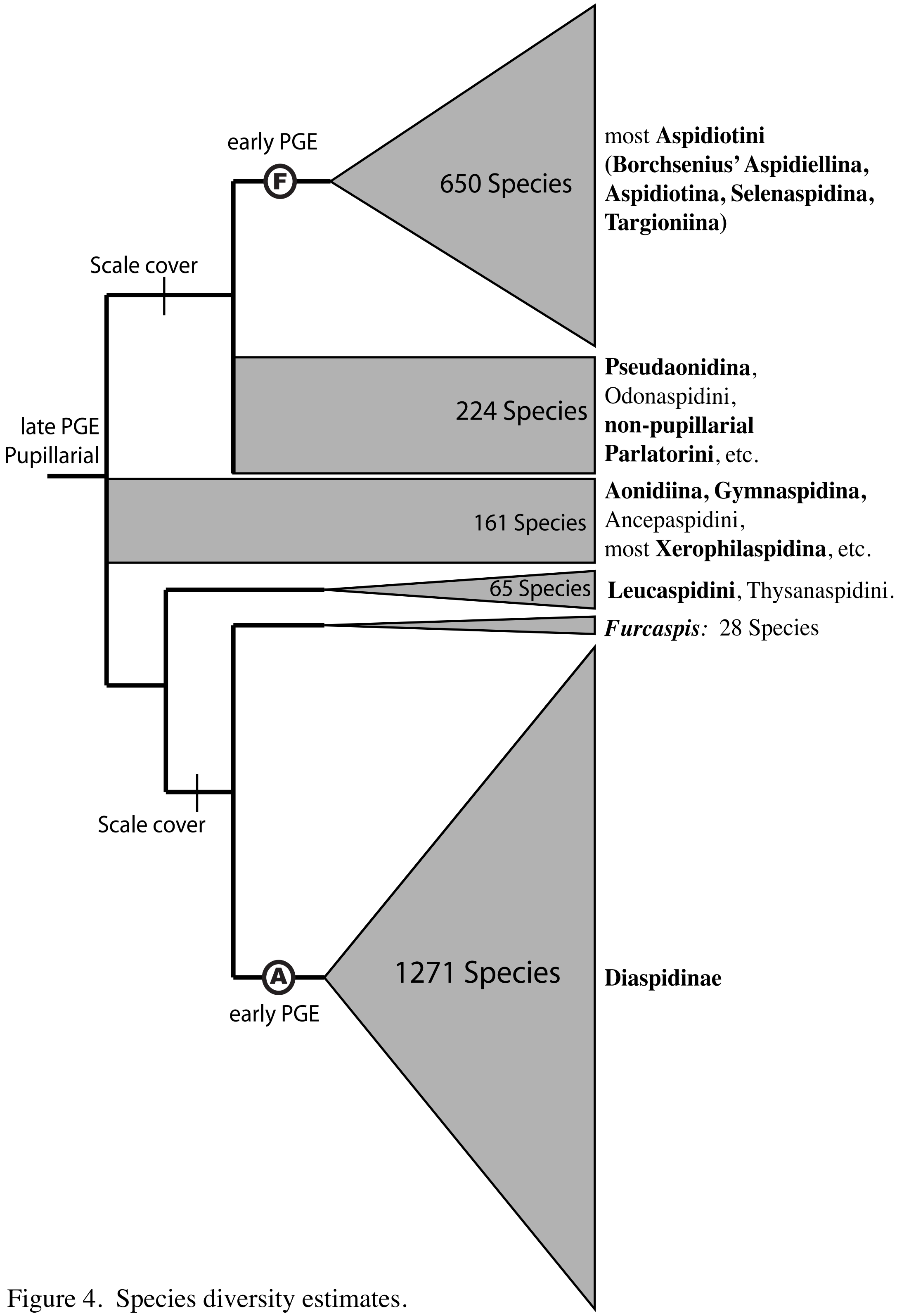


Figure 4. Species diversity estimates.
A simplified version of our results representing the major patterns observed in Figure 3. Taxonomic groups in bold represent those surveyed in our analysis. The height of each group represents the relative proportion of species we expect to be found in that group. The letters represent the clades presented in Appendix 3

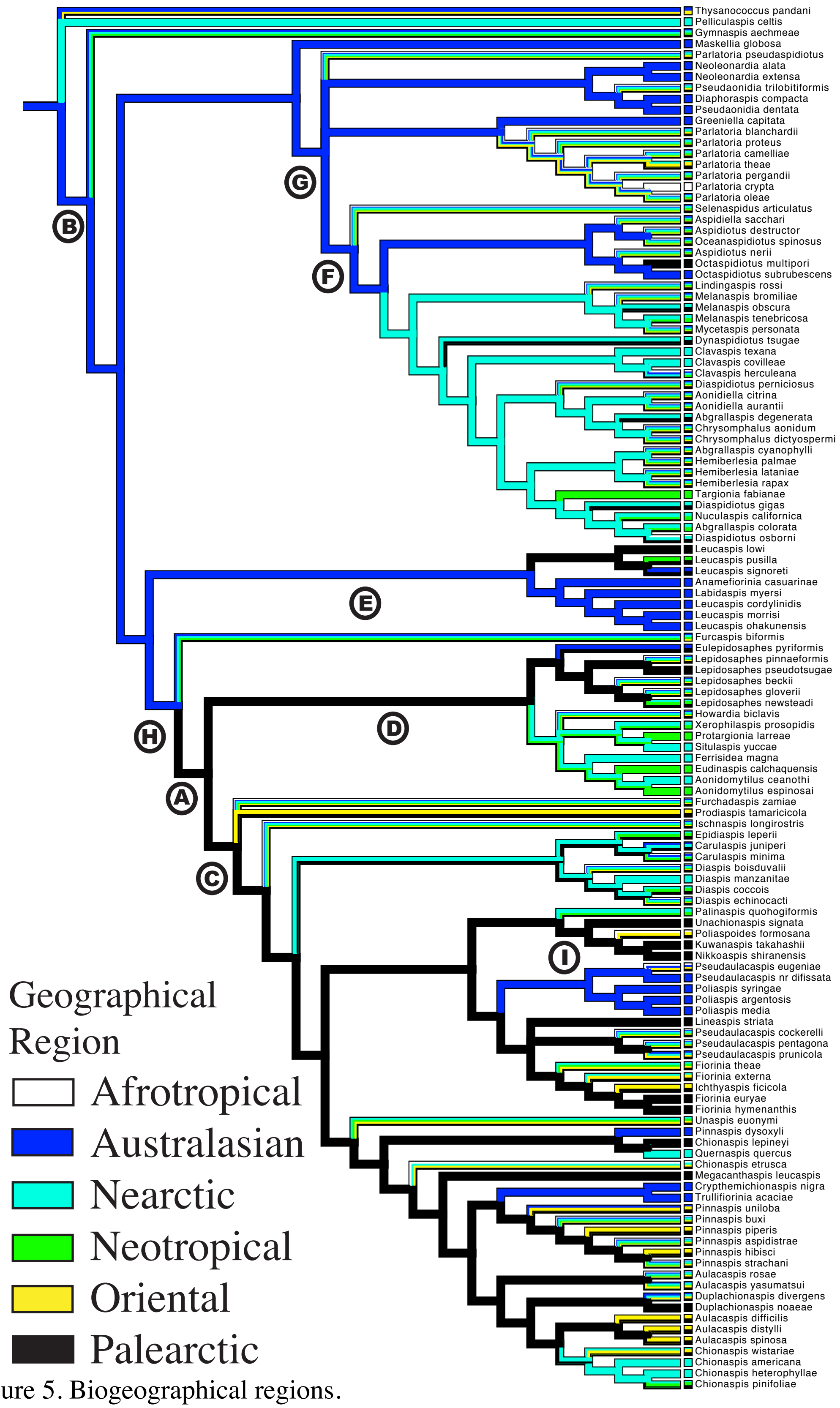


Figure 5. Biogeographical regions.
Geographical ranges were mapped onto Figure 2 using parsimony reconstruction of ancestral states as implemented in Mesquite (Maddison and Maddison 2007).

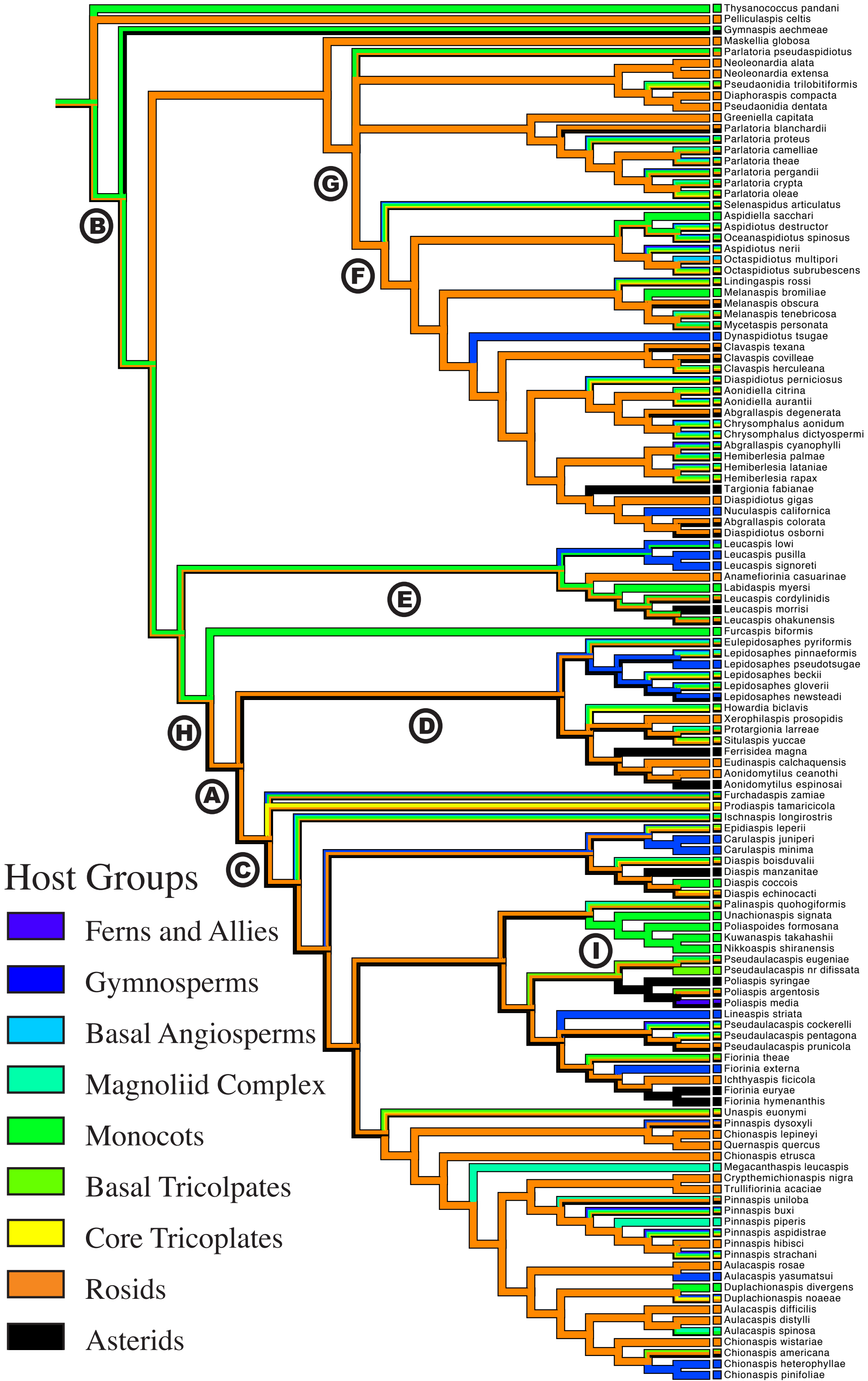


Figure 6. Ancestral diet breadth.
Host groups were mapped onto Figure 2 using parsimony reconstruction of ancestral states as implemented in Mesquite (Maddison and Maddison 2007).

APPENDIX 1

CHARACTER STATES USED IN ANCESTRAL STATE RECONSTRUCTIONS.

Species	Pupillarial	PGE	Host Groups	Geographical Range
Abgrallaspis colorata	0	?	8,9	2,3
Abgrallaspis cyanophylli	0	0	1,2,4,5,6,8,9	0,1,2,3,4,5
Abgrallaspis degeneratus	0	?	8,9	2,5
Anamefiorinia casuarinae	1	?	8	1
Aonidiella aurantii	0	0	2,4,5,6,7,8,9	0,1,2,3,4,5
Aonidiella citrina	0	0	4,5,6,7,8,9	0,1,2,3,4,5
Aonidomytilus ceanothi	0	?	8	2
Aonidomytilus espinosai	0	?	9	3
Aspidiella sacchari	0	0	5	0,1,2,3,4,5
Aspidiotus destructor	0	0	2,4,5,6,7,8,9	0,1,2,3,4,5
Aspidiotus nerii	0	0	1,2,4,5,6,7,8,9	0,1,2,3,4,5
Aulacaspis difficilis	0	?	8	4,5
Aulacaspis distylli	0	?	8	4,5
Aulacaspis rosae	0	?	8	0,1,2,3,4,5
Aulacaspis spinosa	0	0	4,5	4,5
Aulacaspis yasumatsui	0	?	2	1,2,3,4,5
Carulaspis juniperi	0	?	2	1,2,5
Carulaspis minima	0	0	2	0,1,2,3,5
Chionaspis americana	0	?	6,8,9	2
Chionaspis etrusca	0	?	8	0,2,4,5
Chionaspis heterophyllae	0	?	2	2
Chionaspis lepineyi	0	?	-	5
Chionaspis pinifoliae	0	0	2	2,3,5
Chionaspis wistariae	0	?	8	2,4,5
Chrysomphalus aonidum	0	0	2,3,4,5,6,7,8,9	0,1,2,3,4,5
Chrysomphalus dictyospermi	0	?	2,3,4,5,6,7,8,9	0,1,2,3,4,5
Clavaspis covilleae	0	?	8,9	2
Clavaspis herculeana	0	?	4,6,7,8,9	0,1,2,3
Clavaspis texana	0	0	8,9	2
Crypthemichionaspis nigra	1	?	8	1
Diaphoraspis compacta	0	?	8	1
Diaspidiotus gigas	0	0	8	2,5
Diaspidiotus osborni	0	?	8,9	0,2,5
Diaspidiotus perniciosus	0	0	2,4,5,6,7,8,9	0,1,2,3,4,5
Diaspis boisduvalii	0	0	4,5,7,8,9	0,1,2,3,4,5
Diaspis coccois	0	?	5	2,3,5
Diaspis echinocacti	0	0	7,8,9	0,1,2,3,4,5
Diaspis manzanitae	0	?	9	2
Duplachionaspis divergens	0	?	5	1,2,3,4,5

Duplachionaspis noaeae	0	?	2,7,8	5
Dynaspidiotus californicus	0	0	2	2,3
Dynaspidiotus tsugae	0	?	2	2,5
Epidiaspis leperii	0	?	2,6,7,8,9	2,3,5
Eudinaspis calchaquensis	0	?	8	3
Eulepidosaphes pyriformis	0	?	2,4,5,8,9	1,5
Ferrisidea magna	0	?	9	2
Fiorinia euryae	1	?	9	5
Fiorinia externa	1	?	2	2,4,5
Fiorinia hymenanthis	1	?	9	5
Fiorinia theae	1	?	5,6,8,9	2,3,4,5
Furcaspis biformis	0	1	5	1,2,3,4
Furchadaspis zamiae	0	?	2,5,8,9	0,1,2,3,4,5
Greeniella capitata	1	?	8	1
Gymnaspis aechmeae	1	1	5,9	1,2,3,5
Hemiberlesia lataniae	0	0	1,4,5,6,7,8,9	0,1,2,3,4,5
Hemiberlesia palmae	0	?	2,4,5,6,8,9	0,1,2,3,4,5
Hemiberlesia rapax	0	?	4,5,6,7,8,9	0,1,2,3,4,5
Howardia biclavis	0	?	4,5,6,7,9	0,1,2,3,4,5
Ichthyaspis ficicola	1	?	8	4,5
Ischnaspis longirostris	0	?	2,4,5,6,8,9	0,1,2,3,4,5
Kuwanaspis takahashii	0	0	5	5
Labidaspis myersi	1	?	5	1
Lepidosaphes beckii	0	?	2,4,5,6,7,8,9	0,1,2,3,4,5
Lepidosaphes gloverii	0	?	2,4,5,6,8,9	0,1,2,3,4,5
Lepidosaphes newsteadi	0	?	2,9	2,3,5
Lepidosaphes pinnaeformis	0	?	2,3,4,6,8,9	0,1,2,3,4,5
Lepidosaphes pseudotsugae	0	?	2	5
Leucaspis cordylinidis	1	?	5,8,9	1
Leucaspis lowi	1	?	2,5	5
Leucaspis morrisi	1	?	9	1
Leucaspis ohakunensis	1	?	5,8,9	1
Leucaspis pusilla	1	1	2	3,5
Leucaspis signoreti	1	?	2	1,5
Lindingaspis rossi	0	0	2,5,6,7,8,9	0,1,2,3,4,5
Lineaspis striata	0	?	2	5
Maskellia globosa	1	?	8	1
Megacanthaspis leucaspis	0	?	4	5
Melanaspis bromiliae	0	?	5	0,1,2,3,4,5
Melanaspis obscura	0	?	8,9	2,5
Melanaspis tenebricosa	0	?	4,6,8,9	2,3
Mycetaspis personata	0	0	4,5,8,9	0,1,2,3,4,5
Neoleonardia alata	0	?	8	1
Neoleonardia extensa	0	?	8	1

Nikkoaspis shiranensis	0	0	5	5
Oceanaspidiotus spinosus	0	?	2,4,5,6,8,9	0,1,2,3,4,5
Octaspidiotus multipori	0	?	3,8	5
Octaspidiotus subrubescens	0	?	2,5,6,7,8,9	1
Palinaspis quohogiformis	0	?	4,6,8,9	2,3
Parlatoria blanchardii	0	?	8,9	0,1,2,3,4,5
Parlatoria camelliae	0	?	4,6,8,9	0,1,2,3,4,5
Parlatoria crypta	0	?	4,5,8,9	0
Parlatoria oleae	0	1	4,5,6,7,8,9	0,1,2,3,4,5
Parlatoria pergandii	0	?	2,5,6,8,9	0,1,2,3,4,5
Parlatoria proteus	0	1	2,4,5,6,8,9	0,1,2,3,4,5
Parlatoria theae	0	?	2,4,6,8,9	2,4,5
Pelliculaspis celtis	1	?	8	2
Pinnaspis aspidistrae	0	0	1,2,4,5,6,7,8,9	0,1,2,3,4,5
Pinnaspis buxi	0	?	1,2,4,5,6,8,9	0,1,2,3,4,5
Pinnaspis dysoxyli	0	?	2,8,9	1
Pinnaspis hibisci	0	?	8	4,5
Pinnaspis piperis	0	?	4	4,5
Pinnaspis strachani	0	0	1,2,4,5,6,7,8,9	0,1,2,3,4,5
Pinnaspis uniloba	0	?	4,8,9	1,4,5
Poliaspis argentosis	0	?	6,8,9	1
Poliaspis media	0	?	1,9	1
Poliaspis syringae	0	?	9	1
Poliaspoides formosana	0	?	5	0,4,5
Prodiaspis tamaricicola	0	?	7,8	4,5
Protargionia larreae	0	?	4,5,8,9	3
Pseudaonidia dentata	0	?	8	1
Pseudaonidia trilobitiformis	0	1	4,5,6,7,8,9	0,1,2,3,4,5
Pseudaulacaspis cockerelli	0	?	1,2,4,5,6,7,8,9	0,1,2,3,4,5
Pseudaulacaspis eugeniae	0	?	4,5,6,8,9	0,1,4,5
Pseudaulacaspis nr difissata	0	?	6	1
Pseudaulacaspis pentagona	0	0	2,4,5,6,7,8,9	0,1,2,3,4,5
Pseudaulacaspis prunicola	0	?	8,9	1,2,4,5
Quernaspis quercus	0	?	8	2
Selenaspidus articulatus	0	0	2,4,5,7,8,9	0,1,2,3,4,5
Situlaspis yuccae	0	0	5,6,7,8,9	2
Targionia fabianae	0	?	9	3
Thysanococcus pandani	0	1	5	1,4
Trullifiorinia acaciae	1	?	8	1
Unachionaspis signata	0	?	5	5
Unaspis euonymi	0	0	5,6,7,8,9	2,3,4,5
Xerophilaspis prosopidis	1	0	8	2,3

Key To Characters

PGE

0	Early
1	Late

Pupillarial

0	Absent
1	Present

Geographical region

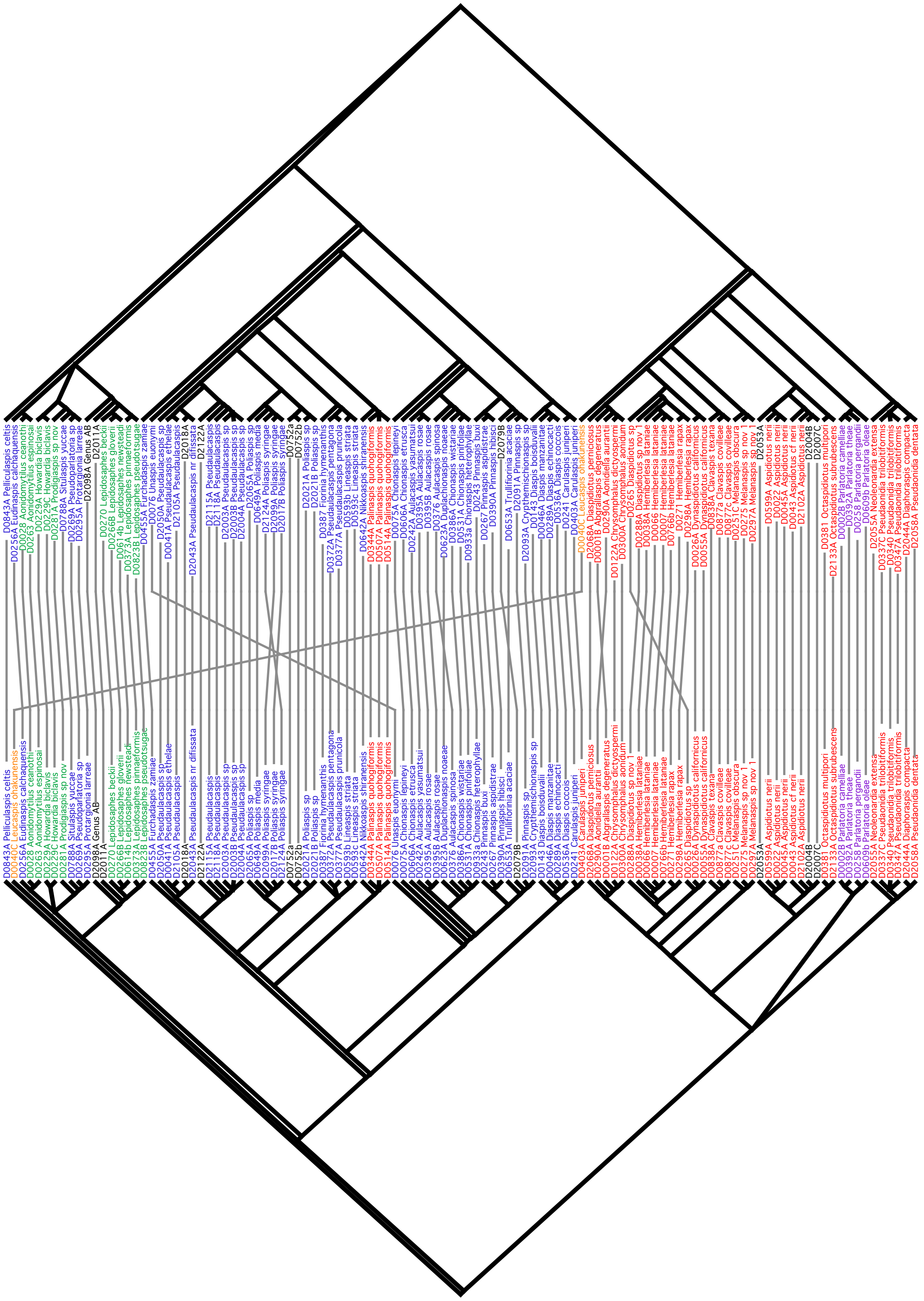
0	Afrotropical
1	Australasian
2	Nearctic
3	Neotropical
4	Oriental
5	Palaearctic

Host Group

0	Lyophytes
1	Ferns_and_Allies
2	Gymnosperms
3	Basal_Angiosperms
4	Magnoliid_Complex
5	Monocots
6	Basal_Tricolpates
7	Core_Tricoplates
8	Rosids
9	Asterids

APPENDIX 2

THE EFFECT OF MISSING DATA ON PHYLOGENETIC ACCURACY.



The 254 taxa full analysis (bottom) is compared with the 113 taxa core analysis (top).

APPENDIX 3

ARMORED SCALE CLASSIFICATION

	Author	Pupillarial	Clade	# species	Type in study	# species in study	Classifications
Aspidiotinae							
Aspidiotini							
Aonidiina							
Aonidia	Targioni Tozzetti	1	LPGE-Pup	43			Aspidiotinae, Aspidiotini, Aonidiina : Borchsenius Aspidiotini : Takagi
Cryptaspidiotus	Lindinger	1	LPGE-Pup	3			Aspidiotinae, Aspidiotini, Aonidiina : Borchsenius
Diaonidia	Takahashi	1	LPGE-Pup	2			Aspidiotinae, Aspidiotini, Aonidiina : Borchsenius Aspidiotini : Takagi
Felixiella	Almeida	1	LPGE-Pup	1			
Greeniella	Cockerell	1	LPGE-Pup	13		1 (2)	Aspidiotinae, Aspidiotini, Aonidiina : Borchsenius Parlatoriini : Takagi
Maskellia	Fulller	1	LPGE-Pup	1	x	1	Aspidiotinae, Aspidiotini, Aonidiina : Borchsenius
Phaulaspis	Leonardi	1	LPGE-Pup	1			Aspidiotinae, Aspidiotini, Aonidiina : Borchsenius
Aspidiellina							
Aspidiella	Leonardi		F	8	x	1	Aspidiotinae, Targioniini, Aspidiellina : Borchsenius
Eremiaspis	Balachowsky		F	2			Aspidiotinae, Targioniini, Aspidiellina : Borchsenius
Remotaspidiotus	MacGillivray		F	8			Aspidiotinae, Targioniini, Aspidiellina : Borchsenius
Rhizaspidiotus	MacGillivray		F	11			Aspidiotinae, Targioniini, Aspidiellina : Borchsenius
Stringaspidiotus	MacGillivray		F	1			Aspidiotinae, Targioniini, Aspidiellina : Borchsenius
Tollaspidiotus	MacGillivray		F	1			Aspidiotinae, Targioniini, Aspidiellina : Borchsenius
Aspidiotina							
Abgrallaspis	Balachowsky		F	18	x	3	Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Acanthaspidiotus	Borchsenius & Williams		F	1			
Acutaspis	Ferris		F	18			Aspidiotinae, Aspidiotini, Melanaspidina : Borchsenius
Africonidia	McKenzie		F	5			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Anaspidiotus	Borchsenius & Williams		F	1			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Anastomoderma	Beardsley		F	1			
Aonidiella	Berlese et Leonardi		F	32	x	2	Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius Aspidiotini : Takagi

Aspidaspis	Ferris	F	7			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Aspidioides	MacGillivray	F	1			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Aspidiotus	Bouché	F	82	x	2	Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Avidovaspis	Gerson & Davidson	F	1			
Banahaoa	Takagi	F	1			Aspidiotini, Aspidiotina : Takagi
Cephalaspidiotus	Takagi	F	1			Aspidiotini, Aspidiotina : Takagi
Chentraspis	Leonardi	F	1			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Chinaspis	Gómez-Menor Ortega	F	1			Aspidiotinae, Aspidiotini, Melanaspidina : Borchsenius
Chortinaspis	Ferris	F	15			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Chrysomphalus	Ashmead	F	17	x	2	Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius Aspidiotini : Takagi
Clavaspidiotus	Takagi & Kawai	F	3			
Clavaspis	MacGillivray	F	18		3	Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Crenulaspidiotus	MacGillivray	F	12			Aspidiotinae, Aspidiotini, Melanaspidina : Borchsenius
Cryptophyllaspsis	Cockerell	F	3			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Diaspidiotus	Cockerell	F	89		3 (6)	Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Diclavaspis	Balachowsky	F	3			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Dynaspidiotus	Thiem & Gerneck	F	25		2	Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Gonaspidiotus	MacGillivray	F	3			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Greenoidea	MacGillivray	F	1			
Helaspis	McKenzie	F	1			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Hemiberlesia	Cockerell	F	33	x	2	Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius Aspidiotini : Takagi
Hypaspidiotus	Takahashi	F	2			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Lindingaspis	MacGillivray	F	24		1	Aspidiotinae, Aspidiotini, Melanaspidina : Borchsenius Aspidiotini : Takagi
Loranthaspis	Cockerell & Bueker	F	1			Aspidiotinae, Aspidiotini, Melanaspidina : Borchsenius
Marginaspis	Hall	F	2			Aspidiotinae, Aspidiotini, Melanaspidina : Borchsenius
Megaspidiotus	Brimblecombe	F	1			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Melanaspis	Cockerell	F	63	x	4 (7)	Aspidiotinae, Aspidiotini, Melanaspidina : Borchsenius
Monaonidiella	MacGillivray	F	4			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Morganella	Cockerell	F	6			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius Aspidiotini, Aspidiotina : Takagi

Murataspis	Balachowsky & Richardeau	F	2			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Mycetaspis	Cockerell	F	8	x	1	Aspidiotinae, Aspidiotini, Melanaspidina : Borchsenius
Neoclavaspis	Brimblecombe	F	2			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Neoleonardia	MacGillivray	LPGE-Scale	5	x	2	Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Nigridiaspis	Ferris	F	1			Aspidiotinae, Aspidiotini, Melanaspidina : Borchsenius
Obtusaspis	MacGillivray	F	3			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Octaspidiotus	MacGillivray	F	15	x	2	Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius Aspidiotini : Takagi
Palinaspis	Ferris	A	5	x	1	Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Phaspis	Ben-Dov	F	1			
Pseudischnaspis	Hempel	F	2			Aspidiotinae, Aspidiotini, Melanaspidina : Borchsenius
Pygidiaspis	MacGillivray	F	1			Aspidiotinae, Aspidiotini, Melanaspidina : Borchsenius
Reclavaspis	Komosinska	F	2			
Rungaspis	Balachowsky	F	3			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Saharaspis	Balachowsky	F	1			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Sakalavaspis	Mamet	F	2			Aspidiotinae, Aspidiotini, Melanaspidina : Borchsenius
Schizaspis	Cockerell & Robinson	F	1			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Spinaspidiotus	MacGillivray	F	2			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Sudanaspis	Chou	F	1			
Taiwanaspidiotus	Takagi	F	2			Aspidiotini : Takagi
Tsimanaspis	Mamet	F	1			Aspidiotinae, Aspidiotini, Melanaspidina : Borchsenius
Unaspidiotus	MacGillivray	F	1			Aspidiotinae, incertae sedis, : Borchsenius
Varicaspis	MacGillivray	F	1			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Furcaspidina						
Furcaspis	Lindinger	*Furcaspis*	28	x	1	Aspidiotinae, Pseudaonidiini, Furcaspidina : Borchsenius
Pseudaonidiina						
Achorophora	Brimblecombe	LPGE-Scale	2			Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius
Acontonidia	Brimblecombe	LPGE-Scale	1			Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius
Aspidonymus	Brimblecombe	LPGE-Scale	1			Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius
Diaphoraspis	Brimblecombe	LPGE-Scale	3		1	Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius
Diaspidopus	Brimblecombe	LPGE-Scale	1			Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius

Diastolaspis	Brimblecombe	LPGE-Scale	1		Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius
Dichosoma	Brimblecombe	LPGE-Scale	1		Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius
Duplaspidiotus	MacGillivray	LPGE-Scale	18		Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius
Eulaingia	Brimblecombe	LPGE-Scale	1		Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius
Gomphaspidiotus	Borchsenius & Williams	LPGE-Scale	1		Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius
Icaraspidiotus	Takagi	LPGE-Scale	1		Aspidiotini, Pseudaonidiina : Takagi
Mimeraspis	Brimblecombe	LPGE-Scale	2		Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius
Myrtophila	Brimblecombe	LPGE-Scale	4		Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius
Neomorgania	MacGillivray	LPGE-Scale	1		Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius Aspidiotini : Takagi
Operculaspis	Laing	LPGE-Scale	1		Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius
Paraonidia	MacGillivray	LPGE-Scale	1		
Parrottia	MacGillivray	LPGE-Scale	1		Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius
Pseudaonidia	Cockerell	LPGE-Scale	18	2	Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius Aspidiotini : Takagi
Pseudotargionia	Lindinger	LPGE-Scale	13		Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius
Sadaotakagia	Ben-Dov	LPGE-Scale	1		
Semelaspidus	MacGillivray	LPGE-Scale	4		Aspidiotinae, Pseudaonidiini, Pseudaonidiina : Borchsenius
Selenaspidina					
Entaspidiotus	MacGillivray	F	4		Aspidiotinae, Aspidiotini, Selenaspidina : Borchsenius
Mesoselenaspidus	Fonseca	F	1		
Neoselenaspidus	Mamet	F	5		Aspidiotinae, Aspidiotini, Selenaspidina : Borchsenius
Paraselenaspidus	Mamet	F	2		Aspidiotinae, Aspidiotini, Selenaspidina : Borchsenius
Pseudoselenaspidus	Fonseca	F	1		Aspidiotinae, Aspidiotini, Selenaspidina : Borchsenius
Schizentaspidus	Mamet	F	2		Aspidiotinae, Aspidiotini, Selenaspidina : Borchsenius
Selenaspidopsis	Nakahara	F	2		
Selenaspidus	Cockerell	F	29 x	1	Aspidiotinae, Aspidiotini, Selenaspidina : Borchsenius
Selenediella	Mamet	F	1		Aspidiotinae, Aspidiotini, Selenaspidina : Borchsenius
Selenomphalos	Mamet	F	2		Aspidiotinae, Aspidiotini, Selenaspidina : Borchsenius Aspidiotini : Takagi
Targioniina					
Genistaspis	Bodenheimer	F	1		Aspidiotinae, incertae sedis, : Borchsenius

Targionia	Signoret		F	14		1	Aspidiotinae, Targioniini, Targioniina : Borchsenius
subtribe incertae sedis							
Crassaspidiotus	Takagi		F	1			Aspidiotini : Takagi
Oceanaspidiotus	Takagi		F	5		1	Aspidiotini : Takagi
Leucaspidini							
Anamefiorinia	Leonardi	1	LPGE-Pup	2	x	1	Leucaspidinae, Leucaspidini, na : Borchsenius Leucaspidini : Takagi
Anotaspis	Ferris	1	LPGE-Pup	2			Leucaspidinae, Leucaspidini, na : Borchsenius "any reliable idea has not yet been proposed" : Takagi
Chimania	Munting		LPGE-Pup	1			
Faureaspis	Munting		LPGE-Pup	1			
Galeraspis	Mamet	1	LPGE-Pup	1			Leucaspidinae, Leucaspidini, na : Borchsenius
Gomezmenoraspis	Balachowsky	1	LPGE-Pup	1			Leucaspidinae, Leucaspidini, na : Borchsenius Leucaspidini : Takagi
Leucaspis	Targioni Tozzetti	1	LPGE-Pup	31		5 (8)	Leucaspidinae, Leucaspidini, na : Borchsenius Leucaspidini : Takagi
Lopholeucaspis	Balachowsky	1	LPGE-Pup	6			Leucaspidinae, Leucaspidini, na : Borchsenius Leucaspidini : Takagi
Mongrovaspis	Bodenheimer	1	LPGE-Pup	1			Leucaspidinae, Leucaspidini, na : Borchsenius Leucaspidini : Takagi
Namaquea	Munting	1	LPGE-Pup	1			
Neoleucaspis	Green	1	LPGE-Pup	1			Leucaspidinae, Leucaspidini, na : Borchsenius Parlatoriini : Takagi
Paraleucaspis	Mamet	1	LPGE-Pup	5			Leucaspidinae, Leucaspidini, na : Borchsenius
Pseudoleucaspis	Mamet	1	LPGE-Pup	2			Leucaspidinae, Leucaspidini, na : Borchsenius
Radionaspis	Ferris	1	LPGE-Pup	1			Leucaspidinae, Leucaspidini, na : Borchsenius "any reliable idea has not yet been proposed" : Takagi
Salicicola	Lindinger	1	LPGE-Pup	6			Leucaspidinae, Leucaspidini, na : Borchsenius
Odonaspidini							
Annulaspis	Ferris		LPGE-Scale	2			Odonaspidinae, na, na : Borchsenius
Berlesaspidiotus	MacGillivray		LPGE-Scale	2			
Circulaspis	MacGillivray		LPGE-Scale	4			Odonaspidinae, na, na : Borchsenius Odonaspidini : Takagi
Dicirculaspis	Ben-Dov		LPGE-Scale	2			
Froggattiella	Leonardi		LPGE-Scale	3			Odonaspidinae, na, na : Borchsenius
Leonardianna	MacGillivray		LPGE-Scale	1			Odonaspidinae, na, na : Borchsenius

Odonaspis	Leonardi		LPGE-Scale	30			Odonaspidinae, na, na : Borchsenius Odonaspidini : Takagi
Parlatoriini							
Gymnaspidina							
Agrophaspis	Borchsenius & Williams	1	LPGE-Pup	1			Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius Parlatoriini : Takagi
Bigymnaspis	Balachowsky	1	LPGE-Pup	3			Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius Parlatoriini : Takagi
Cryptoparlatorea	Lindinger	1	LPGE-Pup	2			Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius Parlatoriini : Takagi
Cryptoparlatoreopsis	Borchsenius	1	LPGE-Pup	7			Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius
Doriopus	Brimblecombe	1	LPGE-Pup	1			Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius
Emmereziaspis	Mamet	1	LPGE-Pup	2			Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius
Eugreeeniella	Brimblecombe	1	LPGE-Pup	1			Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius Parlatoriini : Takagi
Formosapis	Takahashi	1	LPGE-Pup	4			Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius Diaspidini : Takagi
Gymnaspis	Newstead	1	LPGE-Pup	14	x	1	Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius Parlatoriini : Takagi
Ischnafiorinia	MacGillivray	1	LPGE-Pup	3			Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius
Labidaspis	Borchsenius & Williams	1	LPGE-Pup	1	x	1	Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius
Lindingeria	MacGillivray	1	LPGE-Pup	1			Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius
Mixaspis	Takahashi	1	LPGE-Pup	1			Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius Parlatoriini : Takagi
Neoparlatoria	Takahashi	1	LPGE-Pup	7			Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius Parlatoriini : Takagi
Porogymnaspis	Green	1	LPGE-Pup	5			Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius Parlatoriini : Takagi
Sakaramyaspis	Mamet	1	LPGE-Pup	1			Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius
Silvestraspis	Bellio	1	LPGE-Pup	2			Leucaspidinae, Parlatoriini, Gymnaspidina : Borchsenius Parlatoriini : Takagi
Parlatoreopsidina							
Benaparlatoria	Balachowsky		LPGE-Scale	1			Leucaspidinae, Parlatoriini, Parlatoreopsidina : Borchsenius Parlatoriini : Takagi
Microparlatoria	Takahashi		LPGE-Scale	2			Leucaspidinae, Parlatoriini, Parlatoreopsidina : Borchsenius Parlatoriini : Takagi
Paraparlagena	Mamet		LPGE-Scale	1			Leucaspidinae, Parlatoriini, Parlatoreopsidina : Borchsenius
Parlagena	McKenzie		LPGE-Scale	4			Leucaspidinae, Parlatoriini, Parlatoreopsidina : Borchsenius Parlatoriini : Takagi

Parlaspis	McKenzie		LPGE-Scale	1			Leucaspidinae, Parlatoriini, Parlatoreopsidina : Borchsenius Parlatoriini : Takagi
Parlatoreopsis	Lindinger		LPGE-Scale	6			Leucaspidinae, Parlatoriini, Parlatoreopsidina : Borchsenius Parlatoriini : Takagi
Sishanaspis	Ferris	1	LPGE-Pup	2			Leucaspidinae, Parlatoriini, Parlatoreopsidina : Borchsenius Parlatoriini : Takagi
Parlatoriina							
Parlatoria	Targioni Tozzetti		LPGE-Scale	68	x	7	Leucaspidinae, Parlatoriini, Parlatoriina : Borchsenius Parlatoriini : Takagi
Madaparlaspis	Mamet		LPGE-Scale	1			
subtribe incertae sedis							
Neparla	Takagi		LPGE-Scale	1			Parlatoriini : Takagi
Tamilparla	Takagi		LPGE-Scale	1			Parlatoriini : Takagi
Ligaspis	Takagi		LPGE-Scale	2			Parlatoriini : Takagi
Kochummenaspis	Takagi		LPGE-Scale	1			Parlatoriini : Takagi
Mangaspis	Takagi & Kondo		LPGE-Scale	1			Parlatoriini? : Takagi
Tanaparlatoria	Mamet		LPGE-Scale	1			
Smilacicolini							
Smilacicola	Takagi		LPGE-Scale	3			Smilacicolini : Takagi
Thysanaspidini							
Thysanaspis	Ferris	1	LPGE-Pup	3			Leucaspidinae, Leucaspidini, na : Borchsenius Thysanaspidini : Takagi
Tribe incertae sedis							
Cryptoselenaspidus	Lindinger		LPGE-Scale	1			Aspidiotinae, incertae sedis, : Borchsenius
Paranewsteadia	MacGillivray		LPGE-Scale	1			Aspidiotinae, incertae sedis, : Borchsenius
Comstockiellinae							
Comstockiellini							
Comstockiella	Cockerell		LPGE-Scale	1			Aspidiotinae, Comstockiellini, na : Borchsenius ? "genera incertae sedis" : Takagi
Diaspidinae							
Ancepaspidini							
Ancepaspis	Ferris	1	LPGE-Pup	11			Diaspidinae, Ancepaspidini, na : Borchsenius ? "genera incertae sedis" : Takagi
Nudachaspis	MacGillivray	1	LPGE-Pup	1			Diaspidinae, Ancepaspidini, na : Borchsenius

Protancepaspis	Borchsenius & Bustshik	1	LPGE-Pup	2			Diaspidinae, Ancepaspidini, na : Borchsenius
Antakaspidini							
Antakaspis	Mamet		LPGE-Scale	1			Diaspidinae, Antakaspidini, na : Borchsenius
Diaspidini							
Augulaspidina							
Asymetraspis	MacGillivray		A	1			Diaspidinae, Chionaspidini, Augulaspidina : Borchsenius
Augulaspis	MacGillivray		A	5			Diaspidinae, Chionaspidini, Augulaspidina : Borchsenius Diaspidini : Takagi
Dentachionaspis	MacGillivray		A	10			Diaspidinae, Chionaspidini, Augulaspidina : Borchsenius Diaspidini : Takagi
Getulaspis	Balachowsky		A	1			Diaspidinae, Chionaspidini, Augulaspidina : Borchsenius
Mammata	Munting		A	1			
Moraspis	Hall		A	1			Diaspidinae, Chionaspidini, Augulaspidina : Borchsenius Diaspidini : Takagi
Rolaspis	Hall		A	17			Diaspidinae, Chionaspidini, Augulaspidina : Borchsenius Diaspidini, the Rolaspis group : Takagi
Salaspis	Hall		A	1			Diaspidinae, Chionaspidini, Augulaspidina : Borchsenius
Tecaspis	Hall		A	11			Diaspidinae, Chionaspidini, Augulaspidina : Borchsenius Diaspidini, the Rolaspis group : Takagi
Voraspis	Hall		A	6			Diaspidinae, Chionaspidini, Augulaspidina : Borchsenius Diaspidini, the Rolaspis group : Takagi
Yomaspis	Munting		A	1			
Yuanaspis	Young		A	1			
Chionaspidina							
Afiorinia	Takagi	1	A	1			Diaspidini, Chionaspidina : Takagi
Albastaspis	MacGillivray		A	1			Diaspidinae, Chionaspidini, Phenacaspidina : Borchsenius
Amphisoma	Takagi		A	1			Diaspidini, Chionaspidina : Takagi
Aulacaspis	Cockerell		A	91	x	5	Diaspidinae, Chionaspidini, Phenacaspidina : Borchsenius Diaspidini, Chionaspidina? : Takagi
Balachowskiella	Kaussari		A	1			Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius
Cameronaspis	Takagi, Pong & Ghee		A	4			Diaspidini, Chionaspidina : Takagi
Chionandaspis	Takagi		A	3			Diaspidini, Chionaspidina : Takagi
Chionaspis	Signoret		A	79		6	Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius Diaspidini, Chionaspidina : Takagi
Cooleyaspis	MacGillivray		A	1			Diaspidinae, Chionaspidini, Phenacaspidina : Borchsenius

Cupidaspis	MacGillivray	A	2			Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius
Damaia	Takagi	A	1			Diaspidini, Chionaspidina : Takagi
Diaulacaspis	Takahashi	A	2			Diaspidinae, Chionaspidini, Phenacaspidina : Borchsenius Diaspidini, Diaspidina : Takagi
Duplachionaspis	MacGillivray	A	35		2	Diaspidinae, Chionaspidini, Phenacaspidina : Borchsenius Diaspidini : Takagi
Duplaspis	Goux	A	1			Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius Diaspidini : Takagi
Eudinaspis	Lizer & Trelles	A	2		1	Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius
Greenaspis	MacGillivray	A	6			Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius Diaspidini, ? Fioriniina or Chionaspidina : Takagi
Guineaspis	Balachowsky	A	1			Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius
Guizhoaspis	Young	A	1			
Haliaspis	Takagi	A	11			Diaspidinae, Chionaspidini, Phenacaspidina : Borchsenius
Inchoaspis	MacGillivray	A	2			Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius
Kuchinaspis	Takagi	A				
Laingaspis	Borchsenius & Williams	A	1			Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius
Larutaspis	Takagi	A				
Ledaspis	Hall	A	9			Diaspidinae, Chionaspidini, Phenacaspidina : Borchsenius
Lineaspis	MacGillivray	A	3	x	1	Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius Diaspidini : Takagi
Madagaspis	Mamet	A	4			Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius
Magnospinus	Munting	A	1			
Marchalaspis	MacGillivray	A	1			Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius
Myrtaspis	Takagi	A	4			Diaspidini, Chionaspidina? : Takagi
Narayanaspis	Takagi	A	1			Diaspidini, Chionaspidina? : Takagi
Neochionaspis	Borchsenius	A	1			Diaspidinae, Chionaspidini, Sclopetaspidina : Borchsenius Diaspidini, ? Chionaspidina : Takagi
Neoquernaspis	Howell & Takagi	A	11			Diaspidini, Chionaspidina : Takagi
Pinangaspis	Takagi	A	1			Diaspidini, Chionaspidina : Takagi
Pinnaspis	Cockerell	A	41	x	7 (8)	Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius Diaspidini, Chionaspidina : Takagi
Poliaspis	Maskell	A	10	x	3 (6)	Diaspidinae, Chionaspidini, Phenacaspidina : Borchsenius
Proceraspis	MacGillivray	A	1			Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius
Quernaspis	Ferris	A	3	x	1	Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius Chionaspidini : Takagi

Semonggokia	Takagi	A	1			Diaspidini, Chionaspidina : Takagi
Serrachionaspis	Young	A	1			
Shansiaspis	Tang	A	2			
Sinoquernaspis	Takagi & Tang	A	1			
Tenuiaspis	MacGillivray	A	1			Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius
Trichomytilus	Leonardi	A	1			Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius
Unaspis	MacGillivray	A	18		1	Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius Diaspidini : Takagi
Diaspidina						
Alioides	Brimblecombe	A	1			Diaspidinae, Diaspidini, Diaspidina : Borchsenius
Bantudiaspis	Hall	A	2			Diaspidinae, Diaspidini, Diaspidina : Borchsenius
Carulaspis	MacGillivray	A	7	x	2	Diaspidinae, Diaspidini, Diaspidina : Borchsenius Diaspidini : Takagi
Diaspidistis	Hempel	A	2			Diaspidinae, Diaspidini, Diaspidina : Borchsenius
Diaspis	Costa	A	57	x	4	Diaspidinae, Diaspidini, Diaspidina : Borchsenius Diaspidini, Diaspidina : Takagi
Epidiaspis	Cockerell	A	14	x	1	Diaspidinae, Diaspidini, Diaspidina : Borchsenius Diaspidini : Takagi
Eucleaspis	Munting	A	2			
Furchadaspis	MacGillivray	A	1	x	1	Diaspidinae, Diaspidini, Diaspidina : Borchsenius
Geodiaspis	Tippins & Howell	A	1			Diaspidini, Diaspidina : Takagi
Imerinaspis	Mamet	A	1			Diaspidinae, Diaspidini, Diaspidina : Borchsenius
Incisaspis	MacGillivray	A	1			Diaspidinae, Diaspidini, Diaspidina : Borchsenius
Malleolaspis	Ferris	A	2			Diaspidinae, Diaspidini, Diaspidina : Borchsenius Diaspidini, Diaspidina : Takagi
Mancaspis	Ferris	A	2			Diaspidinae, Diaspidini, Diaspidina : Borchsenius
Parachionaspis	MacGillivray	A	1			Diaspidinae, Diaspidini, Diaspidina : Borchsenius
Protargionia	Leonardi	A	1			Diaspidinae, Diaspidini, Diaspidina : Borchsenius
Pseudodiaspis	Cockerell	A	3			Diaspidinae, Diaspidini, Diaspidina : Borchsenius Diaspidini, Diaspidina : Takagi
Pseudoparlatoria	Cockerell	A	32		1	Diaspidinae, Diaspidini, Diaspidina : Borchsenius Diaspidini : Takagi
Serrataspis	Ferris	A	1			Diaspidinae, Diaspidini, Diaspidina : Borchsenius
Situlaspis	MacGillivray	A	5	x	1	Diaspidinae, Diaspidini, Diaspidina : Borchsenius Diaspidini, Diaspidina : Takagi
Takahashiaspis	Takagi	A	1			Diaspidinae, Diaspidini, Diaspidina : Borchsenius

Umbaspis	MacGillivray		A	2			Diaspidinae, Diaspidini, Diaspidina : Borchsenius
Yunnanaspis	Young		A	1			
Fioriniina							
Adiscofiorinia	Leonardi	1	A	3			Diaspidinae, Fioriniini, na : Borchsenius
Africaspis	MacGillivray		A	18			Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius Diaspidini, Fioriniina : Takagi
Bayokaspis	Takagi		A	1			Diaspidini, Fioriniina : Takagi
Chlidaspis	Borchsenius		A	2			Diaspidinae, Chionaspidini, Augulaspidina : Borchsenius Diaspidini, ?Fioriniina : Takagi
Crockeraspis	Takagi		A	1			Diaspidini, Fioriniina : Takagi
Crypthemichionaspis	Lindinger	1	A	1	x	1	Diaspidinae, Fioriniini, na : Borchsenius
Epifiorinia	Takagi		A	1			
Exuviaspis	Ferris	1	A	1			Diaspidinae, Fioriniini, na : Borchsenius
Fijifiorinia	Williams & Watson		A	2			
Fiorinia	Targioni Tozzetti	1	A	66		4	Diaspidinae, Fioriniini, na : Borchsenius Diaspidini, Fioriniina : Takagi
Fraseraspis	Takagi		A	1			Diaspidini, Fioriniina : Takagi
Heimaspis	Balachowsky & Ferrero		A	1			Diaspidini, Fioriniina : Takagi
Hybridaspis	Green	1	A	1			Diaspidinae, Fioriniini, na : Borchsenius
Ichthyaspis	Takagi		A	1	x	1	Diaspidini : Takagi
Kulatinganaspis	Takagi		A	1			Diaspidini, Fioriniina : Takagi
Mayonia	Takagi		A	1			Diaspidini, Fioriniina : Takagi
Parafiorinia	MacGillivray	1	A	1			Diaspidinae, Fioriniini, na : Borchsenius
Pseudaulacaspis	MacGillivray		A	65	x	6 (?)	Diaspidinae, Diaspidini, Diaspidina : Borchsenius Diaspidini, Fioriniina : Takagi
Rutherfordia	MacGillivray		A	3			Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius Diaspidini, Fioriniina : Takagi
Singapuraspis	Takagi		A	1			Diaspidini, Fioriniina : Takagi
Sinistraspis	MacGillivray		A	1			Diaspidinae, Chionaspidini, Phenacaspidina : Borchsenius Diaspidini, Fioriniina : Takagi
Thysanofiorinia	Balachowsky	1	A	2			Diaspidinae, Fioriniini, na : Borchsenius Diaspidini, Diaspidina : Takagi
Trullifiorinia	Leonardi	1	A	5	x	1	Diaspidinae, Fioriniini, na : Borchsenius
Tulefiorinia	Mamet	1	A	1			Diaspidinae, Fioriniini, na : Borchsenius
Kuwanaspidina							

Coronaspis	MacGillivray		A	3			Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius Diaspidini, Kuwanaspidina : Takagi
Kuwanaspis	MacGillivray		A	20		1	Diaspidinae, Chionaspidini, Kuwanaspidina : Borchsenius Diaspidini, Kuwanaspidina : Takagi
Medangaspis	Takagi		A	1			Diaspidini, Kuwanaspidina : Takagi
Nikkoaspis	Kuwana		A	7	x	1	Diaspidinae, Chionaspidini, Kuwanaspidina : Borchsenius Diaspidini, Kuwanaspidina : Takagi
Unachionaspis	MacGillivray		A	3	x	1	Diaspidinae, Chionaspidini, Sclopetaspidina : Borchsenius Diaspidini : Takagi
Xiphuraspis	Borchsenius & Williams		A	2			Diaspidinae, Chionaspidini, Kuwanaspidina : Borchsenius Diaspidini, Kuwanaspidina : Takagi
Phenacaspidina							
Protodiaspidina							
Anaimalaia	Takagi		A	1			Diaspidini, Protodiaspidina? : Takagi
Dungunia	Takagi		A	1			Diaspidini, Protodiaspidina : Takagi
Kyphosoma	Takagi		A	3			Diaspidini, Protodiaspidina : Takagi
Megacanthaspis	Takagi		A	5		1	Diaspidinae, Chionaspidini, Kuwanaspidina : Borchsenius Diaspidini, Protodiaspidina : Takagi
Pentacicola	Takagi		A	3			Diaspidini, Protodiaspidina : Takagi
Protodiaspis	Cockerell		A	16			Diaspidinae, Diaspidini, Rugaspidiotina : Borchsenius Diaspidini, Protodiaspidina : Takagi
Thoa	Takagi		A	1			Diaspidini, Protodiaspidina : Takagi
Sclopetaspidina							
Aloaspis	Williams		A	1			Diaspidinae, Chionaspidini, Sclopetaspidina : Borchsenius
Balaspis	Hall		A	1			Diaspidinae, Chionaspidini, Sclopetaspidina : Borchsenius Diaspidini : Takagi
Contigaspis	MacGillivray		A	14			Diaspidinae, Chionaspidini, Sclopetaspidina : Borchsenius Diaspidini : Takagi
Gadaspis	Borchsenius		A	4			Diaspidinae, Chionaspidini, Sclopetaspidina : Borchsenius
Sclopetaspis	MacGillivray		A	3			Diaspidinae, Chionaspidini, Sclopetaspidina : Borchsenius Diaspidini : Takagi
Xerophilaspidina							
Costalimaspis	Lepage	1	LPGE-Pup	1			Diaspidinae, Diaspidini, Xerophilaspidina : Borchsenius ? "genera incertae sedis" : Takagi
Credodiaspis	MacGillivray	1	LPGE-Pup	1			Diaspidinae, Diaspidini, Xerophilaspidina : Borchsenius
Cryptaspidus	Lindinger	1	LPGE-Pup	1			Diaspidinae, Diaspidini, Xerophilaspidina : Borchsenius
Cryptodiaspis	Lindinger	1	LPGE-Pup	2			Diaspidinae, Diaspidini, Xerophilaspidina : Borchsenius

Fissuraspis	Ferris	1	LPGE-Pup	1			Diaspidinae, Diaspidini, Xerophilaspidina : Borchsenius ? "so abberant that its taxonomic position cannot be suggested" : Takagi
Hovaspis	Mamet	1	LPGE-Pup	1			Diaspidinae, Diaspidini, Xerophilaspidina : Borchsenius
Neoparlaspis	Hempel	1	LPGE-Pup	1			Diaspidinae, Diaspidini, Xerophilaspidina : Borchsenius
Nicholiella	Ferris	1	LPGE-Pup	2			Diaspidinae, Diaspidini, Xerophilaspidina : Borchsenius ? "genera incertae sedis" : Takagi
Pelliculaspis	Ferris	1	LPGE-Pup	3		1	Diaspidinae, Diaspidini, Xerophilaspidina : Borchsenius
Vinculaspis	Ferris	1	LPGE-Pup	9			Diaspidinae, Diaspidini, Xerophilaspidina : Borchsenius
Xerophilaspis	Cockerell	1	A	1	x	1	Diaspidinae, Diaspidini, Xerophilaspidina : Borchsenius
subtribe incertae sedis							
Achionaspis	Takagi		A	2			Diaspidini : Takagi
Dentaspis	MacGillivray		A	8			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius Diaspidini : Takagi
Namibia	Munting		A	3			
Primaspis	Howell		A	1			
Roureaspis	Takagi		A	1			Diaspidini, ? : Takagi
Tamuraspis	Takagi		A	1			Diaspidini : Takagi
Tsimbazaspis	Mamet		A	1			
Lepidosaphidini							
Coccomytilina							
Allantomytilus	Leonardi		A	2			Diaspidinae, Lepidosaphidini, Coccomytilina : Borchsenius
Coccomytilus	Leonardi		A	2			Diaspidinae, Lepidosaphidini, Coccomytilina : Borchsenius Lepidosaphedini, Coccomytilina : Takagi
Dactylaspis	Ferris		A	7		3?	Diaspidinae, Lepidosaphidini, Coccomytilina : Borchsenius Lepidosaphidini : Takagi
Finaspis	Hall		A	1			Diaspidinae, Lepidosaphidini, Coccomytilina : Borchsenius
Hemaspidis	MacGillivray		A	1			Diaspidinae, Lepidosaphidini, Coccomytilina : Borchsenius
Mauritiaspis	Mamet		A	2			Diaspidinae, Lepidosaphidini, Coccomytilina : Borchsenius
Melayumytilus	Takagi		A	1			
Mitulaspis	MacGillivray		A	2			Diaspidinae, Chionaspidini, Chionaspidina : Borchsenius Lepidosaphidini, Coccomytilina : Takagi
Mohelnaspis	Sulc		A	6			Diaspidinae, Lepidosaphidini, Coccomytilina : Borchsenius
Prodigiaspis	Ferris		A	1			Diaspidinae, Lepidosaphidini, Coccomytilina : Borchsenius

Scleromytilus	Hall	A	2			Diaspidinae, Lepidosaphidini, Coccomytilina : Borchsenius
Triaspidis	MacGillivray	A	2			Diaspidinae, Lepidosaphidini, Coccomytilina : Borchsenius
Howardiina						
Ambigaspis	MacGillivray	A	1			Diaspidinae, Diaspidini, Howardiina : Borchsenius
Ferrisidea	Borchsenius	A	3		1	Diaspidinae, Diaspidini, Howardiina : Borchsenius
Howardia	Berlese et Leonardi	A	3	x	1	Diaspidinae, Diaspidini, Howardiina : Borchsenius Lepidosaphidini, Howardiina : Takagi
Hulaspis	Hall	A	3			Diaspidinae, Diaspidini, Howardiina : Borchsenius
Kandraspis	Mamet	A	1			Diaspidinae, Diaspidini, Howardiina : Borchsenius
Multispinaspis	Munting	A	2			
Paradiaspis	Lahille	A	1			Diaspidinae, Diaspidini, Howardiina : Borchsenius
Paraepidiaspis	Balachowsky	A	2			Diaspidinae, Diaspidini, Howardiina : Borchsenius Diaspidini : Takagi
Praecocaspis	Ferris	A	1			Diaspidinae, Diaspidini, Howardiina : Borchsenius
Pudaspis	Hall	A	1			Diaspidinae, Diaspidini, Howardiina : Borchsenius Diaspidini : Takagi
Lepidosaphidina						
Acanthomytilus	Borchsenius	A	14			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius Lepidosaphedini : Takagi
Andaspis	MacGillivray	A	43			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius Lepidosaphidini, Lepidosaphidina : Takagi
Anoplaspis	Leonardi	A	2			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Aonidomytilus	Leonardi	A	16		1	Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius Lepidosaphedini : Takagi
Bayuraspis	Takagi	A	1			Lepidosaphidini, Lepidosaphidina : Takagi
Berlesaspis	MacGillivray	A	1			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Caia	Willliams	A	1			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Cynodontaspis	Takagi	A	2			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius Lepidosaphedini : Takagi
Daraspis	Hall	A	1			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Dinaspis	Leonardi	A	11			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Ductofrontaspis	Young & Hu	A	3			
Eulepidosaphes	Borchsenius & Williams	A	1	x	1	Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Fernaldanna	MacGillivray	A	1			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Fulaspis	Balachowsky	A	4			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius

						Lepidosaphedini : Takagi
Gynandraspis	Balachowsky & Matile-Ferrero	A	1			
Hexandaspis	Takagi	A	1			Lepidosaphidini, Lepidosaphidina : Takagi
Insulaspis	Mamet	A				Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Ischnaspis	Douglas	A	7	x	1	Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Koroneaspis	Bodenheimer	A	2			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Lapazia	Ferris	A	2			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius Lepidosaphedini : Takagi
Leonardaspis	Leonardi	A	1			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Lepidosaphes	Shimer	A	160		5	Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius Lepidosaphidini, Lepidosaphidina : Takagi
Maskellanna	MacGillivray	A	1			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Mercetaspis	Gómez-Menor	A	13			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Metandaspis	Williams	A	2			Diaspidinae, Lepidosaphidini, Coccomytilina : Borchsenius
Mimusaspis	Mamet	A	2			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Mitraspis	Ferris	A	1			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Neopinnaspis	McKenzie	A	3			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius Lepidosaphedini : Takagi
Niveaspis	MacGillivray	A	12			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Notandaspis	Williams & Brookes	A	2			
Opuntiaspis	Cockerell	A	3			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius Lepidosaphedini : Takagi
Palauaspis	Beardsley	A	1			
Pallulaspis	Ferris	A	5			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius Lepidosaphedini : Takagi
Pandanaspis	Mamet	A	1			
Parandaspis	Mamet	A	1			
Parapandanaspis	Mamet	A	1			
Phaulomytilus	Leonardi	A	1			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Santubongi	Takagi	A	1			Lepidosaphidini, Lepidosaphidina : Takagi
Saotomaspis	Balachowsky	A	1			
Scrupulaspis	MacGillivray	A	2			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Scytalaspis	Ferris	A	1			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Stramenaspis	Ferris	A	1			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius

Symeria	Green	A	2			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius
Triraphaspis	Balachowsky	A	3			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius Lepidosaphedini : Takagi
Trischnaspis	Ben-Dov	A	2			
Ungulaspis	MacGillivray	A	3			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius Lepidosaphedini : Takagi
Velataspis	Ferris	A	7			Diaspidinae, Lepidosaphidini, Lepidosaphidina : Borchsenius Lepidosaphedini : Takagi
Mempelaspidina						
Mempelaspis	Takagi	A	1			Lepidosaphidini, Mempelaspidina : Takagi
Rugaspidiotina						
Adiscodiaspis	Marchal	A	1			Diaspidinae, Diaspidini, Rugaspidiotina : Borchsenius
Crassaspis	Ferris	A	2			Diaspidinae, Diaspidini, Rugaspidiotina : Borchsenius
Discodiaspis	Koronéos	A	6			Diaspidinae, Diaspidini, Rugaspidiotina : Borchsenius
Nimbaspis	Balachowsky	A	3			Diaspidinae, Diaspidini, Rugaspidiotina : Borchsenius
Osiraspis	Hall	A	1			Diaspidinae, Diaspidini, Rugaspidiotina : Borchsenius
Poliaspoides	MacGillivray	A	3	x	1	Diaspidinae, Diaspidini, Rugaspidiotina : Borchsenius Rugaspidiotini : Takagi
Pygalataspis	Ferris	A	1			Diaspidinae, Diaspidini, Rugaspidiotina : Borchsenius Diaspidini, ? : Takagi
Ramachandraspis	Rao	A	1			Diaspidinae, Diaspidini, Rugaspidiotina : Borchsenius
Rugaspidiotinus	Balachowsky	A	3			Diaspidinae, Diaspidini, Rugaspidiotina : Borchsenius Rugaspidiotini : Takagi
Rugaspidiotus	MacGillivray	A	3			Diaspidinae, Diaspidini, Rugaspidiotina : Borchsenius Lepidosaphidini : Takagi
Rugpapuaspis	Ben-Dov	A	1			
subtribe incertae sedis						
Galeomytilus	Takagi	A	1			Lepidosaphidini : Takagi
Ferreroaspis	Kozár	A	1			
Tribe incertae sedis						
Gramenaspis	MacGillivray	A	1			Diaspidinae, incertae sedis, : Borchsenius
Prodiaspis	Young	A	2	x	1	Diaspidini/Lepidosaphedini : Takagi
Relhaniaspis	Munting	A	1			

Ulucoccinae				
Ulucoccus	Takagi, Pong & Ghee	0	2	Ulucoccinae : Takagi
Xanthophthalminae				
Xanthophthalma	Cockerell et Parrott	0	1	Xanthophthalminae Phoenicococcidae : Takagi
incertae sedis				
Acanthaspidiotus	Green	F		Aspidiotinae, Aspidiotini, Aspidiotina : Borchsenius
Neoischnaspis	Fonseca	LPGE-Pup	1	
Aleucaspis	Takagi	LPGE-Pup	1	
Helenococcus	Liu & Howell	LPGE-Pup	1	
Totals				
LPGE-Pup	226			
Furcaspis	28			
LPGE-Scale	224			
A	1271			
F	650			

Clade letters represent the clades presented in Figure 4. Clade LPGE-Pup corresponds to individuals that are either late PGE and Pupillarial, or ones where we were uncertain about their placement. Clade *Furcaspis* corresponds to the genus *Furcaspis*. Clade LPGE-Scale corresponds to members of the subfamily Aspidiotinae that have lost the pupillarial habit, but retained the late PGE system. Clade A corresponds to the majority of the subfamily Diaspidinae, and Clade F corresponds to the majority of the tribe Aspidiotini. Both of these clades have the early PGE system. The number of species in each genus represented in our study is indicated. In the case where the molecular results suggest that unidentified individuals may belong to a genus, we have used parentheses to indicate the possible increased number of species sampled.

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