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Phylogeny and classification of armored scale insects (Hemiptera: Coccoomorpha: Diaspididae)

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Abstract

Armored scale insects (Hemiptera: Coccomorpha: Diaspididae) are major economic pests and are among the world's most invasive species. Here we describe a system of specimen and identification management that establishes a basis for well-vouchered molecular identification. We also present an expanded Bayesian phylogenetic analysis based on concatenated fragments of 4 genetic loci: the large ribosomal subunit (28S), elongation factor-1 alpha (EF-1 α), cytochrome oxidase I and II (COI-II), and the small ribosomal subunit (16S) of the primary endosymbiont, *Uzinura diaspidicola* (Bacteroidetes: Flavobacteriales). Our sample includes 1,389 individuals, representing 11 outgroup species and at least 311 described and 61 undescribed diaspidid species. The results broadly support Takagi's 2002 classification but indicate that some revisions are needed. We propose a revised classification recognizing 4 subfamilies: Ancepaspidinae Borchsenius, **new rank**, Furcaspidinae Balachowsky, **new rank**, Diaspidinae Targioni Tozzetti, and Aspidiotinae Westwood. Within Aspidiotinae, in addition to the existing tribes Aspidiotini Westwood, Parlatoriini Leonardi, Odonaspidini Ferris, Leucaspidini Atkinson, and Smilacicolini Takagi, we recognize as tribes Gymnaspidini Balachowsky, **new rank**, and Aonidiini Balachowsky, **new rank**. Within Diaspidinae we recognize the 2 tribes Lepidosaphidini Shimer and Diaspidini Targioni Tozzetti, and within Diaspidini we recognize three subtribes: Diaspidina Targioni Tozzetti, Fioriniina Leonardi, and Chionaspidina Brues & Melander. We regard Kuwanaspidina Borchsenius as a junior synonym of Fioriniina, Thysanaspidini Takagi as a junior synonym of Leucaspidini, and Protodiaspidina Takagi and Ulucocinae Takagi as junior synonyms of Chionaspidina. To clarify the composition of the higher taxa we describe 2 new genera for Australian species heretofore misplaced in the genus *Ancepaspis* Ferris: *Brimblecobia* Normark (Aonidiini) and *Hendersonaspis* Normark (Leucaspidini). We also propose many additional minor modifications to the taxonomy of Diaspididae, including the following new combinations, revived combinations, and replacement names: *Aonidia edgerleyi* (Mamet), **new combination** (from *Bigymnaspis* Balachowsky); *Aonidomytilus espinosai* Porter, **revived combination** (from *Porterinaspis* González); *Aspidiotus*

badius (Brain), **new combination** (this and the next 5 *Aspidiotus* species all from *Aonidia* Targioni Tozzetti); *Aspidiotus biafrae* (Lindinger), **new combination**; *Aspidiotus chaetachmeae* (Brain), **new combination**; *Aspidiotus laticornis* (Balachowsky), **new combination**; *Aspidiotus rhusae* (Brain), **new combination**; *Aspidiotus sclerosus* (Munting), **new combination**; *Brimblecobia asperata* (Brimblecombe), **new combination** (this and the next 5 *Brimblecobia* species all from *Ancepaspis*); *Brimblecobia longicauda* (Brimblecombe), **new combination**; *Brimblecobia magnicauda* (Brimblecombe), **new combination**; *Brimblecobia reticulata* (Brimblecombe), **new combination**; *Brimblecobia rotundicauda* (Brimblecombe), **new combination**; *Brimblecobia striata* (Brimblecombe), **new combination**; *Cooleyaspis pseudomorpha* (Leonardi), **new combination** (from *Dinaspis* Leonardi); *Cupidaspis wilkeyi* (Howell & Tippins), **new combination** (from *Paracupidaspis* Howell & Tippins); *Cupressaspis isfarensis* Borchsenius, **revived combination** (this species, the next 2 species in *Cupressaspis* Borchsenius, **revived genus**, and the next 9 species in *Diaspidiotus* Cockerell all from *Aonidia*); *Cupressaspis mediterranea* (Lindinger), **revived combination**; *Cupressaspis relictata* (Balachowsky), **new combination**; *Diaspidiotus atlanticus* (Ferris), **new combination**; *Diaspidiotus marginalis* (Brain), **new combination**; *Diaspidiotus maroccanus* (Balachowsky), **new combination**; *Diaspidiotus mesembryanthemae* (Brain), **new combination**; *Diaspidiotus opertus* (De Lotto), **new combination**; *Diaspidiotus shastae* (Coleman), **new combination**; *Diaspidiotus simplex* (Leonardi), **new combination**; *Diaspidiotus visci* (Hall), **new combination**; *Diaspidiotus yomae* (Munting), **new combination**; *Diaspis arundinariae* (Tippins & Howell), **new combination** (from *Geodiaspis* Tippins & Howell); *Duplachionaspis arecibo* (Howell), **new combination** (this and the next 10 *Duplachionaspis* MacGillivray species all from *Haliaspis* Takagi); *Duplachionaspis asymmetrica* Ferris, **revived combination**; *Duplachionaspis distichlii* (Ferris), **revived combination**; *Duplachionaspis litoralis* Ferris, **revived combination**; *Duplachionaspis mackenziei* McDaniel, **revived combination**; *Duplachionaspis milleri* (Howell), **new combination**; *Duplachionaspis nakaharai* (Howell), **new combination**; *Duplachionaspis peninsularis* (Howell), **new combination**; *Duplachionaspis spartinae* (Comstock), **revived combination**; *Duplachionaspis texana* (Liu & Howell) **new combination**; *Duplachionaspis uniola* (Takagi), **new combination**; *Duplachionaspis mutica* (Williams) (from *Aloaspis* Williams), **new combination**; *Epidiaspis doumtsopi* (Schneider), **new combination** (from *Diaspis* Costa); *Fiorinia ficicola* (Takahashi), **new combination** (from *Ichthyaspis* Takagi); *Fiorinia macroprocta* (Leonardi), **revived combination** (this and the next 2 species of *Fiorinia* Targioni Tozzetti all from *Trullifiorinia* Leonardi); *Fiorinia rubrolineata* Leonardi, **revived combination**; *Fiorinia scrobicularum* Green, **revived combination**; *Genaparlatoria pseudaspidiotus* (Lindinger), **revived combination** (from *Parlatoria*); *Greeniella acaciae* (Froggatt), **new combination** (this and the next 4 *Greeniella* Cockerell species all from *Gymnaspis* Newstead); *Greeniella cassida* (Hall & Williams), **new combination**; *Greeniella grandis* (Green), **new combination**; *Greeniella perpusilla* (Maskell), **new combination**; *Greeniella serrata* (Froggatt), **new combination**; *Hendersonaspis anomala* (Green), **new combination** (from *Ancepaspis*); *Hulaspis bulba* (Munting), **new combination** (this and the next *Hulaspis* Hall species both from *Andaspis* MacGillivray); *Hulaspis formicarum* (Ben-Dov), **new combination**; *Lepidosaphes antidesmae* (Rao in Rao & Ferris), **new combination** (this and the next 19 species all from *Andaspis*); *Lepidosaphes arcana* (Matile-Ferrero), **new combination**; *Lepidosaphes betulae* (Borchsenius), **new combination**; *Lepidosaphes citricola* (Young & Hu), **new combination**; *Lepidosaphes conocarpi* (Takagi), **new combination**; *Lepidosaphes crawi* (Cockerell), **revived combination**; *Lepidosaphes erythrinae* Rutherford, **revived combination**; *Lepidosaphes incisor* Green, **revived combination**; *Lepidosaphes indica* (Borchsenius), **new combination**; *Lepidosaphes kashicola* Takahashi, **revived combination**; *Lepidosaphes kazimiae* (Williams), **new combination**; *Lepidosaphes laurentina* (Almeida), **new combination**; *Lepidosaphes maai* (Williams & Watson), **new combination**; *Lepidosaphes mackieana* McKenzie, **revived combination**; *Lepidosaphes micropori* (Borchsenius), **new combination**; *Lepidosaphes punicae* Laing, **revived combination**; *Lepidosaphes quercicola* (Borchsenius), **new combination**; *Lepidosaphes recurrens* (Takagi & Kawai), **new combination**; *Lepidosaphes viticis* (Takagi), **new combination**; *Lepidosaphes xishuanbanna* (Young & Hu), **new combination**; *Lepidosaphes giffardi* (Adachi & Fullaway), **new combination** (from *Carulaspis* MacGillivray); *Lepidosaphes garciniae* (Young & Hu), **new combination** (this and the next 2 species all from *Ductofrontaspis* Young & Hu); *Lepidosaphes huangyangensis* (Young & Hu), **new combination**; *Lepidosaphes jingdongensis* (Young & Hu), **new combination**; *Lepidosaphes recurvata* (Froggatt), **revived combination** (from *Metandaspis* Williams); *Lepidosaphes ficicola* Takahashi, **revived combination** (this and the next 2 species all from *Ungulaspis* MacGillivray); *Lepidosaphes pinicolous* Chen, **revived combination**; *Lepidosaphes unguolata* Green, **revived combination**; *Lepidosaphes serrulata* (Ganguli), **new combination** (from *Velataspis* Ferris); *Lepidosaphes huyoung* Normark, **replacement name** for *Andaspis ficicola* Young & Hu; *Lepidosaphes tangi* Normark, **replacement name** for *Andaspis schimae* Tang; *Lepidosaphes yuanfeng* Normark, **replacement name** for *Andaspis keteleeriae* Yuan & Feng; *Leucaspis illicitana* (Gómez-Menor), **new combination** (from *Aonidia*); *Lopholeucaspis spinomarginata* (Green), **new combination** (from *Gymnaspis*); *Melanaspis campylanthi* (Lindinger), **new combination** (from *Aonidia*); *Mohelnaspis bidens* (Green), **new combination** (from *Fiorinia*); *Parlatoria affinis* (Ramakrishna Ayyar), **new combination** (this and the next 4 *Parlatoria* species all from *Gymnaspis*); *Parlatoria ficus* (Ramakrishna Ayyar), **new combination**; *Parlatoria mangiferae* (Ramakrishna Ayyar), **new combination**; *Parlatoria ramakrishnai* (Green), **new combination**; *Parlatoria sclerosa* (Munting), **new combination**; *Parlatoria bullata* (Green), **new combination** (from *Bigymnaspis*); *Parlatoria leucaspis* (Lindinger), **new combination** (this and the next species both from *Cryptoparlatoria* Lindinger); *Parlatoria pini* (Takahashi), **new combination**; *Parlatoria tangi* Normark, **replacement name** for *Parlatoria pini* Tang; *Pseudoparlatoria bennetti* (Williams), **new com-**

bination (from *Parlagena* McKenzie); *Pseudoparlatoria chinchonae* (McKenzie), **new combination** (from *Protodiaspis* Cockerell); *Pseudoparlatoria larreae* (Leonardi), **revived combination** (from *Protargionia* Leonardi); *Quernaspis lep-ineyi* (Balachowsky), **new combination** (from *Chionaspis*); *Rhizaspidiotus nullispinus* (Munting), **new combination** (from *Aonidia*); *Rolaspis marginalis* (Leonardi), **new combination** (from *Lepidosaphes*); *Salicicola lepelleyi* (De Lotto), **new combination** (from *Anotaspis* Ferris); *Tecaspis giffardi* (Leonardi), **new combination** (from *Dinaspis*); *Trulliflorinia geijeriae* (Froggatt), **new combination** (from *Fiorinia*); *Trulliflorinia nigra* (Lindinger), **new combination** (from *Crypthemichionaspis* Lindinger); and *Voraspis olivina* (Leonardi), **new combination** (from *Lepidosaphes*).

Key words: Coccoidea, DNA barcoding, evolution, nomenclature, Sternorrhyncha, taxonomy

Introduction

Armored scale insects comprise the most diverse family of scale insects, with over 2600 species (García Morales *et al.* 2016). They are significant economic pests (D.R. Miller & Davidson 2005), and are among the most invasive insects in the world (D.R. Miller *et al.* 2005). Many aspects of the biology of armored scale insects are unusual. There is extreme sexual dimorphism: males have 5 instars, including 2 pupa-like quiescent stages, and the adults are winged, active, non-feeding, and short-lived; females have 3 instars, and the adults are morphologically reduced, non-motile, feeding, and much longer-lived. Males undergo paternal genome elimination (PGE): in some species, the paternal genome is present in all of the male's tissues in heterochromatic form and is only eliminated from his sperm (late PGE), but in 2 different clades, comprising the majority of armored scale species, the paternal genome is eliminated early in development and the male is haploid (early PGE) (Andersen *et al.* 2010; Brown 1965). Other unusual features of armored scale insect genetic systems include regular chimerism, involving the inclusion of polar body genomes in polyploid bacteriocytes (Brown 1965; Normark 2005), and frequent origins of parthenogenesis (Normark 2003; Normark & Johnson 2011; Ross *et al.* 2013). Males have extremely unusual sperm, each cell having dozens of microtubules (Paoli *et al.* 2015; Robison 1990; Ross & Normark 2015). Females continue to grow as adults, something insects are usually regarded as unable to do (Hill *et al.* 2011). Armored scale insects include some of the most highly polyphagous species in the world, feeding on over 100 families of host plants (García Morales *et al.* 2016; Normark & Johnson 2011; Peterson *et al.* 2015). They feed on the contents of individual cells, and unlike other scale insects do not excrete any honeydew (Washington & Walker 1990). Their primary endosymbiont, *Uzinura diaspidicola*, has the smallest genome of any bacterium that serves as its host's sole nutrient-providing endosymbiont (Sabree *et al.* 2013).

The identification of armored scale insects is an important and challenging practical problem, particularly at plant quarantine inspection. Armored scales are extraordinarily invasive, in part because they are very small, cryptic, and nearly ubiquitous associates of woody plants. Plant quarantine inspectors therefore frequently encounter armored scales on imported fruits, nursery stock, and other plant material. Identification of these insects generally requires specimens to be cleared, stained and mounted on microscope slides, and usually only one life stage, the adult female, is identifiable to species. There is no global key to armored scale insects. Many areas (e.g. South America, Australia, and most of Asia) lack regional keys; others (e.g. North America, Africa, Europe) require the use of keys that are increasingly out-of-date (Balachowsky 1953, 1954, 1958; Ferris 1942; Hall 1946). Given the training, library, and labor required for the morphological identification of scale insects, there has been a great deal of interest in their molecular identification (Campbell *et al.* 2014; Ramasubramanian *et al.* 2015; Rugman-Jones *et al.* 2009).

Accurate molecular identification requires a reference collection of DNA sequences that are reliably linked to accurate species names. For scale insects, this in turn requires a system for the combined molecular and morphological preparation and management of specimens and information, and an extensive collection of well-mounted, well-identified voucher specimens from which DNA has been extracted and sequenced. Our laboratory has developed a specimen management system, and a voucher collection, that can serve as the basis for reliable molecular identification of armored scale insects, as we describe below.

The most recent published global classification of armored scale insects is Borchsenius' catalogue (Borchsenius 1966), which is now over 50 years old. It was influenced by Ferris's (1942) taxonomy of the Nearctic fauna, and especially by Balachowsky's (1954, 1958) taxonomy of the Palearctic and African faunas. Since Borchsenius, the leading diaspidid taxonomist has been Sadao Takagi. Takagi revised the higher-level taxonomy of

Diaspididae in 1969 and again in 2002 (Takagi 1969, 2002), and has described a substantial fraction of the world's genera and species, but he has worked almost exclusively with the Asian fauna and has never published a complete classification of the armored scale genera. Other significant regional works since Borchsenius have included Brimblecombe (1959a) on Queensland, Williams & Watson (1988) on the tropical Pacific islands, Danzig (1993) on much of the Palearctic, and Henderson (2011) on New Zealand.

In the last decade or so, the first estimates of the phylogeny of Diaspididae based on molecular data have been published (Andersen *et al.* 2010; Morse & Normark 2006). To date, these have had a minimal effect on the classification. Some of the taxonomic decisions made by Henderson (2011), Schneider *et al.* (2013), and Normark *et al.* (2014) reflect the molecular phylogeny estimate, but the widely accepted higher classification has remained unchanged. For instance, Takagi (2011) retained the genera *Furchadaspis* MacGillivray, *Pseudoparlatoria* Cockerell, *Situlaspis* MacGillivray, and *Protargionia* Leonardi in the tribe Diaspidini, subtribe Diaspidina, despite the availability of contrary molecular evidence (Andersen *et al.* 2010; Morse & Normark 2006). Here we present an expanded molecular phylogenetic estimate for Diaspididae, and this time we explicitly address its implications for taxonomy and offer a revised classification of the armored scale insects.

Materials and methods

Lot numbers and prep numbers. Each vial of scale insect specimens was assigned a lot number, consisting of a letter followed by 4 digits. For specimens that we collected ourselves, each lot number represents scale insects collected from a single host individual. This is typically also the case for vials sent to us by others, although some of these may be more heterogeneous. Each specimen selected for preparation was assigned a prep number, consisting of the lot number followed by a letter; for instance, D2004B is an individual from lot D2004.

DNA extraction. Each specimen was subjected to a joint molecular/morphological preparation protocol that resulted in genomic DNA from a single specimen and a permanent slide-mount of its cuticle. Total genomic DNA was isolated using the Qiagen DNeasy Blood & Tissue kit (Qiagen, Valencia, California, U.S.A.). To facilitate digestion, each insect was punctured with a 000 insect pin before being placed in the lysis solution. After an overnight digestion, individual cuticles were retrieved from the lysate using a wide-mouthed micropipette tip and stored in water at 4°C for later slide mounting. The remainder of the Qiagen protocol was followed, except that at the first elution only 60 µl of Buffer AE was used.

Slide mounting. If not fully cleared, cuticles were placed in 10% potassium hydroxide at room temperature overnight or until cleared, and gently squeezed with a spatula to remove any remaining tissue contents. Specimens were then passed through a staining and dehydration series consisting of: distilled water, 5 min; double stain (BioQuip, Rancho Dominguez, California, U.S.A.), 5 min or until adequately stained; 70% ethanol, 5 min; 100% ethanol, 5 min; clove oil, 5 min or longer. Each cuticle was then mounted individually on a microscope slide using Canada balsam thinned with HistoClear II (National Diagnostics Corporation, Lake Geneva, Wisconsin, U.S.A.), covered with a coverslip, and cured for 2 months at 45–50°C. With a few exceptions, all slides and DNA samples are retained by the University of Massachusetts Insect Collection. The exceptions are several type specimens of recently described species, which are distributed to other museums (Normark *et al.* 2014; Vea *et al.* 2013), and a synoptic collection of Panamanian material deposited in the Museo de Invertebrados G. B. Fairchild (MIUP), Panama City, Panama.

Slide grading and morphological identification. Each slide was examined and classified by life stage. Adult females were graded by quality as LQV, MQV or HQV (low, medium, or high quality voucher). LQV specimens failed to display the characters necessary for species-specific identification (ID). MQV and HQV specimens were identified to species if possible. A list of identifiers and the institutions whose resources they used are given in Table 1. If a particular specimen was lost or unidentifiable, it was often assigned a "lot ID" based upon the identity of other individuals from the same lot (that is, collected at the same time from the same host). In a few cases, if both direct ID and lot ID are unavailable, a field ID may be given.

PCR. Polymerase chain reaction (PCR) was performed to amplify regions of the mitochondrial genes cytochrome *c* oxidase I and II (COI–II), the nuclear protein-coding gene elongation factor-1 alpha (EF-1α) the D2 and D3 expansion segments of the large subunit ribosomal RNA (28S), and a segment of the small ribosomal subunit of the primary endosymbiont, *Uzinura diaspidicola* (16S), as described in Gruwell *et al.* (2007). Details

about amplification primers and PCR protocols are provided in Table 2. We used either GoTaq Green, GoTaq G2 hot-start polymerase (Promega Corporation, Madison, Wisconsin), or Takara Ex Taq (TBUSA Laboratories Inc., Mountain View, California) for standard PCR amplification. PCR products were visualized using 1.5% agarose gel electrophoresis with SYBR Safe (Life Technologies, Carlsbad, California) ultraviolet stain. Amplification products were purified with an ExoSAP-IT PCR Product Clean-Up enzyme digest (Affymetrix, Cleveland, Ohio, U.S.A.) and sequenced directly using an ABI-3130XL Genetic Analyzer at the University of Massachusetts Genomics Resource Laboratory.

TABLE 1. Individuals who have identified scale insect individuals or lots for this project. Abbreviated collection names are defined in Table 3.

Full name	Abbreviation	Primary collection and library consulted
Yair Ben-Dov	Y.B.D.	Agricultural Research Organization, Bet Dagan, Israel
Lucia E. Claps	L.E.C.	Instituto Lillo, Tucumán, Argentina
John Donaldson	J.D.	Queensland Department of Primary Industries, Indooroopilly, Queensland, Australia
John W. Dooley III	J.W.D.	APHIS-PPQ, South San Francisco, California, U.S.A.
Ilya Gavrillov	I.G.	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia
Uri Gerson	U.G.	Hebrew University of Jerusalem, Israel
Raymond J. Gill	R.J.G.	California Department of Food and Agriculture, Sacramento, California, U.S.A.
Penny J. Gullan	P.J.G.	Australian National University, Canberra, Australia
Rosa C. Henderson	R.C.H.	Landcare Research, Auckland, New Zealand
Greg Hodges	G.H.	Florida State Collection of Arthropods, Dept. of Agriculture and Consumer Services, Gainesville, Florida, U.S.A.
Marc Kenis	M.K.	CABI Switzerland
Takumasa Kondo	T.K.	Auburn University Coccoidea Collection, Auburn, Alabama, U.S.A.
Ferenc Kozár	F.K.	Plant Protection Institute, Hungarian Academy of Sciences, Budapest, Hungary
Douglass R. Miller	D.R.M.	NMNH
Benjamin B. Normark	B.B.N.	UMEC
Scott A. Schneider	S.A.S.	UMEC
Megumi Shoubu	M.S.	Moji Plant Protection Station, Ministry of Agriculture Forestry and Fisheries of Japan & Faculty of Agriculture, Kyushu University, Fukuoka, Japan
George Stathas	G.S.	Technological Educational Institute of Peloponnese, Greece
Ian C. Stocks	I.C.S.	Florida State Collection of Arthropods, Dept. of Agriculture and Consumer Services, Gainesville, Florida, U.S.A.
William Tang	W.T.	APHIS-PPQ, Miami, Florida, U.S.A.
Gillian W. Watson	G.W.W.	California Department of Food and Agriculture, Sacramento, California, U.S.A.

Sequence assembly and alignment. Sequence fragments were assembled and edited using Sequencher 4.9 (Gene Codes Corporation, Ann Arbor, Michigan). For EF-1 α , introns were removed prior to phylogenetic analysis. For 28S, sequences were aligned using PASTA (Mirarab *et al.* 2015); hypervariable regions were identified by eye and removed prior to phylogenetic analysis. The data set includes 1389 individual specimens, each of which is represented by a 28S sequence. These include 1373 specimens from our laboratory and an additional 16 specimens sequenced by other laboratories and obtained via GenBank. The aligned and concatenated matrix had 3717 nucleotide sites as characters, of which 979 were from 28S (all 1389 individuals). Amplification of other loci was less consistent and there are some missing data for each of these: COI-II (728 individuals, 747 aligned nucleotide sites), EF-1 α (801 individuals, 675 aligned nucleotide sites), and *Uzinura* 16S (711 individuals, 1316 aligned nucleotide sites).

TABLE 2. PCR primers and annealing temperatures, from Gruwell *et al.* (2007) and Andersen *et al.* (2010). Before thermal cycling begins, all PCR reactions start with a single 2-minute denaturation at 95°C. Each subsequent cycle consists of a 30s denaturation at 95°C, a 1-minute annealing step with temperature given below, and a 2-minute extension at 72°C. After thermal cycling is completed, all PCR reactions end with a single 5- or 10-minute extension at 72°C. Primer sequences are given from 5' to 3'.

Gene Region	Forward Primer	Reverse Primer	Annealing temperature profile
16S	S30 Buch16S Proteobacteria GGC GGC AAG CCT AAC ACA TGC AAG TCG	A547 Buch16 Proteobacteria CC CTC CGT ATT ACC GCG GCT GCT GGC	30–35 cycles at 54°C
	S791 Buch16S Proteobacteria CAG GAT TAG ATA CCC TGG TAG TCC	A958 Buch16S Proteobacteria CCA CCG CTT GTG CGG GCC CCC GTC	
	s688DIASP Diaspididae Bacterioidetes GGAATGTA TGGTGTAGCGGTGAAATGC	A1096 Buch16S Proteobacteria CGA GCT GAC GAC AGC CAT GCA GCA CC	
		A1446 Buch16S Proteobacteria CTC CCA TGG TGT GAC GGG CGG TGT G	
28S	28s_s3660 GAG AGT TMA ASA GTA CGT GAA AC	a1271DIASP Diaspididae Bacterioidetes CATTGTAGCACGTGTAGCCCAAG 28s_a335 TCG GAR GGA ACC AGC TAC TA	58–48°C, -1°C/3 cycles + 11 cycles @ 48°C
EF-1 α	EF-1 α (a) (amplification/sequencing) GAT GCT CCG GGA CAY AGA G EF-SEQF (internal sequencing) ATG CCG TGG TTC AAG GGA TGG	EF2rod (amplification/sequencing) ATG TGA GCG GTG TGG CAA TCC AA EF-SEQR (internal sequencing) AGC TTC GTG GTG CAT TTC	58–42°C, -2°C/3 cycles + 11 cycles @ 42°C
COI- COII	C1-j-2753ywr GTA AAC CTA ACA TTT TTY CCW CAR CA	C2-n-3362 CCA CAA ATT TCT GAA CAT TGA CC	35 cycles at 47°C

Checking for identification errors. The scale insect identifiers we consulted for this project (Table 1) usually preferred to have a series of specimens when making an identification. One reason for this is that specimens vary in their morphological traits, and another reason is that specimens vary in the visibility of those traits to the investigator. The usual way to obtain a series of putatively conspecific specimens is to take them from the same host plant in the same collecting event—they may still constitute a mix of different species, but it is likely that many will be conspecific and that this will be fairly obvious. Here we checked for identification errors using an additional method for grouping specimens into series of putative conspecifics: we used preliminary phylogenetic analyses of each locus and assumed that individuals with highly similar allele sequences were likely to be conspecific. Sequence similarity is a criterion for grouping individuals that does not depend on their having been collected at the same time or from the same host, but that likewise creates a loose expectation of shared species identity, and thus likewise expands the set of potentially relevant specimens available to the identifier.

Trees resulting from preliminary analyses of each gene region were examined and, in cases where individuals assigned to different species shared similar sequences, those individuals were re-examined by one of the identifiers (B.B.N.). Specimens whose phylogenetic position seemed anomalous were also re-examined, and their phylogenetic positions were compared across different loci. For some specimens the identification was revised at this stage. In cases where the morphology seemed inconsistent with a phylogenetic analysis, such that we suspected error in the association between the morphological specimen and one of the sequences, that sequence was excluded from the analysis. If multiple loci were affected, such that we suspected error in the association between the morphological specimen and the DNA sample, the identification in our database was changed to "problem_n" (where n was a unique identifier assigned to that anomaly) and all sequences from that individual were excluded.

Model selection. We calculated the fit of available evolutionary models to each data partition in jModelTest 2.1.9 (Darriba *et al.*, 2012) and compared models using the Bayesian Information Criterion (BIC) and Akaike Information Criterion (AIC). There was only one discrepancy between the models selected by BIC and AIC, for the model best fitting 16S. In this case, we chose the model with the best likelihood score (from BIC). Models were specified as follows: GTR+I+G for 16S, 28S, and COI-II (each codon position); TVM+I+G for EF-1 α (each codon position). The base tree used for likelihood calculations was estimated using BIONJ. The best fitting models were implemented in all subsequent analyses.

Phylogenetic analysis. Bayesian Markov chain Monte Carlo analyses were initiated in BEAST 1.8.4 (Drummond *et al.* 2012), with a Yule tree prior assuming a constant rate of speciation per lineage. A concatenated analysis of all 4 loci for all 1389 individuals was performed for 50 million generations. Preliminary analyses only appeared to approach stationarity within the final 5 million generations. A consensus tree was drawn from the final 5 million generations, and then used as a starting tree for subsequent phylogenetic analyses.

Final analyses were run in MrBayes 3.2.6 (Ronquist *et al.* 2012) using Metropolis-coupled Markov chain Monte Carlo (MC³) methods. These analyses were completed with support from the Cyberinfrastructure for Phylogenetic Research (CIPRES) Science Gateway 3.3 and Extreme Science and Engineering Discovery Environment (XSEDE) computational resources (M. Miller *et al.* 2010; Towns *et al.* 2014). The concatenated dataset was analyzed by conducting 2 independent runs concurrently with 4 chains each (3 hot, 1 cold, with temperature set to 0.035 to allow for sufficient chain mixing). The analysis ran for an additional 50 million generations, sampling parameters every 10,000 generations. To better assess convergence, each chain began with a slightly different starting tree that introduced 50 random perturbations to the topology of the consensus tree derived from preliminary analysis. Parameters were unlinked across data partitions to accommodate site-specific rate heterogeneity.

Stationarity was reached within the first 10 million generations as determined by visualizing the likelihood-by-generation plot, the potential scale reduction factors (PSRF \approx 1.0), ESS posterior values ($>$ 200), and standard deviations of split frequencies (\sim 0.02). Convergence was further assessed by reviewing the parameter log files in Tracer v1.6 (Rambaut *et al.* 2018) and posterior tree distributions in AWTY (Wilgenbusch *et al.* 2004). The first 12.5 million generations were discarded as burnin, leaving a posterior distribution of 3,750 sampled trees from each run used to build a consensus. Trees were then viewed in FigTree 1.4.2 (Rambaut 2009).

To assess the agreement in phylogenetic signal between loci, we focused on a reduced subset of 279 samples for which all 4 loci were successfully sequenced. For each locus, we inferred a phylogeny of these core samples using the same BEAST parameters as used in the full dataset for that locus. We then mapped these locus-specific results onto the topology of the full concatenated tree (pruned down to include only the 279 core samples) by using

the treeAnnotator program in the BEAST package to summarize the proportion of times each node in the pruned concatenated tree appeared in the sample of output trees for each locus, representing the posterior support for each node at each locus.

Revising the classification of Diaspididae. From a study of the literature we inferred the current classification, defined as the classification of Borchsenius (1966) as modified by Takagi (many publications, especially Takagi 2002) and others. An earlier estimate of the current classification was given in Appendix 3 of Andersen (2009) and reflected in the discussion of Andersen *et al.* (2010). For the genera that appear in our tree, we reassigned those genera to higher taxa so as to render the higher taxa monophyletic, while otherwise preserving so far as possible the classification of Takagi (2002). For all the genera that do not appear in our tree, we examined the best available illustrations or descriptions of their type species and re-evaluated their taxonomic positions in light of the revised diagnoses of higher taxa. For 2 highly problematic genera (*Aonidia* Targioni Tozzetti and *Gymnaspsis* Newstead), we examined the best available illustrations and descriptions of all the species, along with type specimens held at BMNH and NMNH (Table 3), in order to re-evaluate their taxonomic positions.

TABLE 3. Abbreviations of the names of museum collections referred to in this paper

Abbreviation	Collection
BMNH	The Natural History Museum, London, U.K.
NMNH	National Museum of Natural History. Cocomorpha collection held at Agricultural Research Service, Beltsville, Maryland, U.S.A.
QM	Queensland Museum, Brisbane, Australia
UMEC	University of Massachusetts Entomology Collection, University of Massachusetts Amherst, Amherst, Massachusetts, U.S.A.

Material included in analysis. In the locality data below, 2 collecting sites are abbreviated as follows: "SL crane" = Colon: Parque Nacional San Lorenzo canopy crane, 9.2811°N, 79.9744°W; "LH crane" = Sarawak, Lambir Hills National Park Canopy Crane, 4.1964°N, 114.040°E. Collectors and identifiers given as initials below are listed in Table 1 or are authors of this paper. Lot numbers followed by multiple letters represent multiple individual prep numbers, for instance D2434ABC represents the three individuals D2434A, D2434B, and D2434C. All individuals directly identified to species (with an ID rather than a LotID or FieldID) are adult females unless otherwise indicated. Names with "ud" followed by 4 digits in place of a specific epithet represent undescribed species. Names with "UG" followed by 4 digits in place of the genus name represent undescribed genera. Some of the records (generally those where the locality is given only as a country) represent quarantine interceptions. The great majority of the specimens are retained at UMEC (Table 3). Holotypes and paratypes of new species are distributed to collections in the countries of origin and other collections as the new species are described.

CONCHASPIDIDAE: *Conchaspis near lepagei* D3008A (ID B.B.N.), Panama: SL crane, 21.viii.2010, ex *Tapirira guianensis* Aubl., coll. G.E.M., B.B.N. *Fagisuga triloba* Lindinger D0560A (lotID L.E.C.), Argentina: Rio Negro: El Bolsón, Cerro Piltriquitrón, 41.97°S, 71.47°W, 17.ii.2003, ex *Nothofagus antarctica* (G. Forst.) Oerst., coll. L.E.C., P. Zamudio, L. Díaz-Briz, L. Guardia Claps.

PSEUDOCOCCIDAE: *Planococcus citri* (Risso) D1142A (fieldID B.B.N.), U.S.A.: CA: Los Angeles: Hayes Avenue, 31.1092°N, 118.1876°W, 28.x.2006, ex *Citrus* sp., coll. B.B.N. **Undetermined pseudococcid** D1022, Mexico: Tamaulipas: Gomez Farias, 23.02°N, 99.15°W, 13.iii.2005, coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N.

ASTEROLECANIIDAE: *Bambusaspis miliaris* (Boisduval) D0320 (lotID D.R.M.), U.S.A.: FL: Davie: UF Ft. Lauderdale Research & Education Center, 26.0842°N, 80.2380°W, 20.xi.2002, coll. D.R.M., R.J.G., T.K., B. Sello, M.E. Gruwell, B.B.N.

COCCIDAE: *Ceroplastes stellifer* (Westwood) D4191A (fieldID B.B.N.), Panama: Colon: SL crane, ex *Tovomita longifolia* (Rich.) Hochr., 21.vi.2012, coll. G.E.M. & B.B.N. *Paralecanium* sp. D0764B (lotID D.R.M.), Australia: QLD: Cedar Creek, 21.viii.2004, coll. G.E.M.

ERIOCOCCIDAE: *Cryptococcus fagisuga* D580F (fieldID M.K.), Georgia: Batumi Botanical Garden, 41.965°N, 41.708°W, 24.vi.2003, ex *Fagus orientalis* Lipsky, coll. M.K.; D0181 (lotID B.B.N.), Canada: Nova Scotia: Waverley. *Gossyparia spuria* (Modeer) D0063 (fieldID D.R.M.), U.S.A.: CA: UC Davis campus,

17.v.2001, ex *Ulmus crassifolia* Nutt., coll. D.R.M. & B.B.N. *Ovaticoccus californicus* D0787A (ID D.R.M.), U.S.A.: UT, Beaver Dam Mts, 2 km E Welcome Spring, 37.093°N, 113.941°W, 18.xi.2004, ex *Yucca brevifolia* Engelm., coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N. *Pseudochermes fraxini* (Kaltenbach) D0074E (LotID F.K.), Hungary, 20vi.2001, coll. F.K.

HALIMOCOCCIDAE: *Comstockiella sabalis* (Comstock) D0972A (lotID B.B.N.) U.S.A.: Florida, Sixmile Rd., 27.8483°N, 80.9088°W, 13.xii.2005, ex *Sabal palmetto* (Walter) Lodd. Ex Schult. & Schult. f., coll. R. A. Gwiazdowski, M.E. Gruwell; D1019A (ID B.B.N.) Mexico: Tamaulipas, Gomez Farias, 13.iii.2005, ex undet. Areaceae, coll. M.E. Gruwell, B.B.N., R. A. Gwiazdowski; D1969C (ID D.R.M.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk, 29.7113°N, 82.456°W, 20.ii.2010, coll. A.O.; D1971D (ID G.W.W.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk, 29.7113°N, 82.456°W, 20.ii.2010, ex *Sabal minor* (Jacq.) Pers., coll. I.C.S.; D1995A (ID G.W.W.) U.S.A.: Florida, Havens Island, 29.1639°N, 83.0272°W, 21.ii.2010, ex *Sabal palmetto*, coll. A.O.; D1998A (ID G.W.W.) U.S.A.: Florida, Cedar Key, 29.1513°N, 83.0488°W, 21.ii.2010, ex *Rhapis excelsa* (Thunb.) A. Henry, coll. A.O.; D2838B (ID B.B.N.) U.S.A.: Florida, 1.0 mi N CR 18, off 441 W side, Mikesville, 24.iii.2010, ex *Sabal palmetto*, coll. W.W. Bailey; D2860B (ID B.B.N.) U.S.A.: Florida, Payne's Prairie State Park, 23.v.2010, ex *Sabal palmetto*, coll. I.C.S. ***Thysanococcus pandani*** Stickney D0468 (lotID R.J.G.), U.S.A.: Hawaii, Hana, quarantine interception at Los Angeles, 13.iii.2003, ex *Pandanus tectorius* Parkinson, coll. Burton.

DIASPIDIDAE: *Achorophora ud4411* D4411D (ID B.B.N.) Malaysia: LH crane, 6.viii.2013, ex *Dipterocarpus globosus* Vesque, coll. G.E.M. ***Acutaspis agavis*** (Townsend & Cockerell) D2774A (ID B.B.N. query) Colombia: Buga-Valle, Bosque del Vinculo, 3.8166°N, 76.2833°W, 3.i.2006, ex *Agave* sp., coll. T.K.; D3721A (ID B.B.N.) U.S.A.: California, El Cajon, 18.v.2012, ex *Agave* sp., coll. C. Betschart. ***Acutaspis albopicta*** (Cockerell) D0701A (ID B.B.N.) Mexico: Quintana Roo, Akumal, 19.v.2004, ex *Cocos* sp., coll. G.E.M.; D1009A (ID B.B.N.) Mexico: Tamaulipas, Ciudad Victoria, Facultad de Agronomia, 12.iii.2005, coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N. ***Acutaspis morrisonorum*** Kosztarab D1937A (ID D.R.M.) U.S.A.: Florida, San Felasco Hammock Preserve State Park, 29.796°N, 82.455°E, 18.ii.2010, ex *Pinus palustris* Mill., coll. A.O. ***Acutaspis perseae*** (Comstock) D1917A (ID B.B.N.) U.S.A.: Florida, Gainesville, back of UFL Dept. Agri. & Cons. services, 29.6333°N, 82.366°E, 17.ii.2010, ex *Sabal minor*, coll. I.C.S.; D3980A (ID B.B.N.) Panama: SL crane 13.vi.2012, ex *Ocotea ira* Mez & Pittier, coll. G.E.M., B.B.N. ***Acutaspis reniformis*** (Cockerell) D3040B (ID D.R.M.) Panama: SL crane, 23.viii.2010, ex *Tapirira guianensis*, coll. G.E.M., B.B.N.; D3089A (ID D.R.M.) Panama: SL crane, 25.viii.2010, ex *Jacaranda copaia* (Aubl.) D. Don, coll. G.E.M.; D4170A (ID B.B.N.) Panama: SL crane, 20.vi.2012, ex *Dendropanax arboreus* (L.) Decne. & Planch., coll. G.E.M., B.B.N.; ***Acutaspis scutiformis*** (Cockerell) D0541A (lotID R.J.G.) Colombia: Ultraroma, Calle 97 No. 11 A 52, 23.vii.2003, ex *Laurus nobilis* L., coll. J. Ferguson. ***Acutaspis* sp.** D3058B Panama: SL crane, 24.viii.2010, ex *Marila laxiflora* Rusby, coll. G.E.M., B.B.N. ***Alioides ud1138*** D1138DEF (ID B.B.N.) Australia: Western Australia, Stirling Range: Camel Lake Nature Reserve, 4.7 km along Salt River Rd from Formbey S Rd, 34.34166°S, 118.016°E, 20.ix.2005, ex *Melaleuca* sp., coll. L.G. Cook. ***Anamefiorinia casuarinae*** (Maskell) D2041D (lotID J.D.) Australia: Queensland, St. Lucia: UQ Campus, 27.50033°S, 153.012°E, 8.v.2007, ex *Casuarina glauca* Sieber ex Spreng., coll. B.B.N. ***Anceaspis edentata*** (Ferris) D5256BD (ID B.B.N.) U.S.A.: Arizona, near Vail, 19.iv.2015, ex *Senegalia greggii* (A. Gray), coll. M.E. Irwin. ***Anceaspis anomala*** (now ***Hendersonaspis anomala***) D2111B (ID B.B.N.) Australia: New South Wales, 28.99008°S, 152.068°E, 2.vi.2007, ex *Acacia* sp., coll. J.C. Andersen, B.B.N. ***Anceaspis near anomala*** (now ***Hendersonaspis near anomala***) D2089A (ID D.R.M.) Australia: Queensland, 28.0145°S, 150.334°E, 31.v.2007, ex *Acacia harpophylla* F. Muell. ex Benth., coll. J.C. Andersen, B.B.N.; D2131A (ID D.R.M.) Australia: Queensland, 27.72971°S, 150.350°E, 31.v.2007, ex *Acacia harpophylla*, coll. J.C. Andersen, B.B.N. ***Andaspis formicarum*** Ben-Dov [now ***Hulaspis formicarum*** (Ben-Dov), **new combination**] D3660A (ID B.B.N.) South Africa: Eastern Cape, East London, 26.iii.2012, ex *Ficus* sp., coll. K. Cole. ***Andaspis punicae*** (Laing) [now ***Lepidosaphes punicae*** Laing, **revived combination**] D0346B (ID D.R.M.) U.S.A.: Florida, Homestead: 25.5004°N, 80.4456°W, 22.xi.2002, coll. B. Sello, M.E. Gruwell, B.B.N. ***Andaspis crawii*** (Cockerell) [now ***Lepidosaphes crawii*** (Cockerell), **revived combination**] D3216B (ID B.B.N.) Japan: Kyushu, Mt. Konosu, 33.5561°N, 130.383°E, 23.xi.2010, coll. A.O. ***Anoplaspis maskelli*** Morrison & Morrison D0870D (lotID R.C.H.) New Zealand: NZAK: Hunua Ra, Massey Track, 6.ii.2005, ex *Metrosideros* sp., coll. R.C.H. ***Anoplaspis metrosideri*** (Maskell) D0923B (ID D.R.M.) New Zealand: NZAK, Karekare, The Tunnel, 1.v.2005, ex *Metrosideros excelsa* Gaertn., coll. R.C.H. ***Anzaspis cordylinidis*** (Maskell) D0874B (ID B.B.N.) New Zealand:

NZFD/SL, north of Manapouri, 225m, 16.ix.2004, ex *Leptospermum scoparium* J.R. Forst. & G. Forst., coll. Hill, G.M. Gutsell, & H. Edmonds. *Anzaspis ud2116* D2116AB (ID B.B.N.) Australia: New South Wales, 28.83933°S, 152.095°E, 2.vi.2007, ex *Allocasuarina littoralis* (Salisb.) L.A.S. Johnson, coll. J.C. Andersen, B.B.N. *Aonidia lauri* (Bouché) D2757C (ID B.B.N.) Slovenia: Nova Gorica, 45.9546°N, 13.652°E, 2.v.2010, ex *Laurus nobilis*, coll. G. Seljak. *Aonidia paradoxa* Lindinger D2052A (ID B.B.N.) Australia: Queensland, 28.72545°S, 150.994°E, 30.v.2007, ex *Casuarina* sp., coll. J.C. Andersen, B.B.N.; D2063A (lotID B.B.N.) Australia: New South Wales, 28.49883°S, 150.566°E, 30.v.2007, ex *Casuarina* sp., coll. J.C. Andersen, B.B.N.; D2084A (ID B.B.N.) Australia: Queensland, 27.85433°S, 150.080°E, 31.v.2007, ex *Casuarina* sp., coll. J.C. Andersen, B.B.N. *Aonidia shastae* (Coleman) [now *Diaspidiotus shastae* (Coleman), **new combination**] D0796A (ID D.R.M.) U.S.A.: Utah, 13 km E Hurricane, on Rte. 59; on Little Plain at foot of Little Creek Mountain, 37.1172°N, 113.1645°W, 19.xi.2004, ex *Juniperus virginiana* L., coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N.; D0809A (ID D.R.M.) U.S.A.: Utah, 13 km E Hurricane, on Rte. 59; on Little Plain at foot of Little Creek Mountain, 37.1172°N, 113.1645°W, 19.xi.2004, ex *Juniperus virginiana*, coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N.; D0881B (lotID B.B.N.) U.S.A.: California, Rte. 138, 1.4 mi W San Bernardino Co. line, 16.vi.2005, ex *Juniperus* sp., coll. M.E. Gruwell; D1841B (ID B.B.N.) Mexico: Tamaulipas, Ciudad Victoria: Centro Universitario, 12.iii.2005, ex undet. Cupressaceae, coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N.; D2526B (ID D.R.M. query) U.S.A.: Maryland, 18.viii.2009, ex *Juniperus* sp., coll. J. Wu. *Aonidiella aurantii* (Maskell) D0011AD (ID D.R.M.), D0012A (fieldID R.J.G.) U.S.A.: California, Sacramento: 16th & O, 17.v.2000, ex *Laurus nobilis*, coll. R.J.G., B.B.N.; D0290A (LotID L.E.C.) Argentina: Tucumán, Yerba Buena, 30.xii.2001, ex *Citrus limon* (L.) Osbeck, coll. L.E.C.; D0617A (ID B.B.N.) Turkey: Adana, Çukorova University, 37.0611°N, 35.358°E, 20.iv.2004, ex *Laurus nobilis*, coll. B.B.N., G.E.M., M.E. Gruwell; D1424A (ID D.R.M.) New Zealand (possibly originated elsewhere), intercepted in quarantine in Australia 17.vii.2006, ex *Citrus* sp. (AQIS N115934); D2498B (ID B.B.N.) Greece: Crete, 8.iv.2010, ex *Citrus* sp., coll. M.E. Gruwell; D2662AB (lotID J.W.D.) South Africa: 12.xi.2009, ex *Encephalartos cycadifolius* (Jacq.) Lehm., coll. M. Tomkins; D2921A (ID B.B.N.) Greece: Peloponnesus, Kalamata, 24.i.2007, ex *Citrus* sp., coll. G. Stathas; D3764A (ID B.B.N.) Mexico, 23.v.2012, ex *Citrus* sp., coll. J. Moore; D3766A (ID B.B.N.) Mexico, 1.iii.2012, coll. T. Clerc; D3767A (ID B.B.N.) Mexico, 1.ii.2012, ex *Persea americana* Mill., coll. T. Clerc; D3768A (ID B.B.N.) Mexico, 25.xi.2011, ex *Citrus* sp., coll. J. Moore; D3769A (ID B.B.N.) Mexico, 15.iii.2012, ex *Citrus* sp., coll. Z. Jordan; D3770A (ID B.B.N.) Mexico, 4.i.2012, ex *Citrus* sp., coll. P. Sullivan; D3771A (ID B.B.N.) Mexico, 15.ii.2012, ex *Citrus x paradisi* Macfad., coll. T. Clerc; D3774B (ID B.B.N.) Mexico, 12.i.2012, ex *Citrus x paradisi*, coll. T. Clerc; D3776A (lotID J.W.D.) Mexico, 23.v.2012, ex *Citrus* sp., coll. T. Clerc; D3778A (ID B.B.N.) Mexico, 7.iii.2012, ex *Citrus* sp., coll. T. Clerc; D3786A (ID B.B.N.) Mexico, 27.iii.2012, ex *Citrus* sp., coll. P. Sullivan. *Aonidiella citrina* (Coquillett) D0137A (ID D.R.M. query) Saudi Arabia: Taif, 7.iv.2001, ex *Olea europaea* L., coll. A. Ajlan; D0533A (lotID R.J.G.) France, Nice, 18.vi.2003, ex *Ruscus* sp., coll. J. Davey. *Aonidiella comperei* McKenzie D3391A (ID B.B.N.) Brazil: Rio de Janeiro, 10.iv.2011, ex *Carica papaya* L., coll. J. Wagner. *Aonidiella inornata* McKenzie D3707A (ID B.B.N.) Japan: Kyushu, Abura Mt., 33.5716°N, 130.358°E, 16.v.2012, ex *Podocarpus macrophyllus* (Thunb.) Sweet, coll. A.O. *Aonidiella orientalis* (Newstead) D0495B (ID D.R.M.) Trinidad & Tobago: Trinidad, Orange Grove Road, Trincity, 17.viii.2001, ex *Cocos* sp., coll. J. Irish, E. Holder; D3517B (ID B.B.N.) Mexico, 21.xii.2010, ex *Azadirachta indica* A. Juss., coll. Laurie E Ortiz; D3788A (lotID W. Tang) Haiti, 7.i.2012, ex *Mangifera indica* L., coll. E.G. Camero; D3800A (ID B.B.N.) Cuba, 12.v.2012, ex *Psidium guajava* L., coll. M.A. Duque. *Aonidiella* sp. D2660A (ID B.B.N.) Canada: British Columbia, 19.i.2010, ex *Citrus reticulata* Blanco, coll. M.S. Hicks. *Aonidiini undet* sp. D2135A Australia: Queensland, 28.0145°S, 150.334°E, 31.v.2007, ex *Acacia harpophylla*, coll. J.C. Andersen, B.B.N. *Aonidomytilus ceanothi* (Ferris) D0028E (ID B.B.N.) U.S.A.: California, Del Puerto Canyon: Frank Raines County Park, 21.v.2000, ex *Ceanothus* sp., coll. D.J. Williams, D.R.M., P.J. Gullan, R.J.G., B.B.N.; D0885C (ID B.B.N.) U.S.A.: California, Whitewater canyon, 3 mi S trout hatchery, 16.vi.2005, coll. B.B.N.; D2684A (ID B.B.N.) U.S.A.: California, Del Puerto Canyon Rd., 37.3862°N, 121.4536°W, 21.v.2010, ex *Ceanothus palmeri* Trel., coll. A.O.; D2704A (ID B.B.N.) U.S.A.: California, 37.5127°N, 120.1035°W, 22.v.2010, ex *Ceanothus palmeri*, coll. A.O.; D2708AB (ID B.B.N.) U.S.A.: California, 37.7582°N, 120.2504°W, 22.v.2010, ex *Ceanothus palmeri*, coll. A.O., B.B.N., A. Krewinski; *Porterinaspis espinosai* (Porter) [now *Aonidomytilus espinosai* (Porter), **revived combination**] D0263B (LotID L.E.C.) Argentina: Tucumán, El Rodeo (entre Tafi del Valle y El Mollor), 17.xii.2001, ex *Baccharis* sp., coll. L.E.C., P. Zamudio. *Aspidaspis arctostaphyli* (Cockerell & Robbins) D1183C (lotID B.B.N.) U.S.A.: Nevada, Red Rock Canyon NCA: Lost Creek/Willow Springs, 19.xii.2008, ex

Arctostaphylos sp., coll. J.W.D.; D1188A (ID D.R.M.) U.S.A.: Nevada, Red Rock Canyon NCA: Lost Creek/Willow Springs, 19.xii.2008, ex *Arctostaphylos* sp., coll. J.W.D.; D2687C (ID B.B.N.) U.S.A.: California, Del Puerto Canyon, 37.3926°N, 121.4497°W, 21.v.2010, ex *Arctostaphylos* sp., coll. A. Krewinski. ***Aspidaspis densiflorae*** (Bremner) D2725A (ID B.B.N.) U.S.A.: California, 38.1647°N, 120.4224°W, 23.v.2010, ex *Quercus chrysolepis* Liebm., coll. A.O., B.B.N. ***Aspidaspis florenciae*** (Coleman) D2400B (ID B.B.N.) U.S.A.: California, 36.3666°N, 120.91°E, 4.ix.2006, ex *Pinus sabiniana* Douglas ex D. Don, coll. R. A. Gwiazdowski. ***Aspidiella hartii*** (Cockerell) D1423A (ID D.R.M.) New Zealand (possibly originated elsewhere), intercepted in quarantine in Australia 17.vii.2006 (AQIS N115097), ex *Dioscorea* sp.; D1166B (ID B.B.N.) Ghana: Accra, 17.vi.2005, coll. G.E.M.; D3546B (ID B.B.N.) Thailand, 22.viii.2011, ex *Hedychium* sp., coll. N. Pyle; D3641A (ID B.B.N.) Nigeria, 10.xii.2011, ex *Dioscorea* sp., coll. A. Hanna; D3772A (ID B.B.N.) Thailand, 5.vi.2012, ex *Curcuma* sp., coll. J.D. Alvarado. ***Aspidiella sacchari*** (Cockerell) D0571C (lotID B.B.N.) Mexico: Jalisco, Puerto Vallarta, 31.xii.2003, coll. G.E.M.; D0955AB (ID B.B.N.) U.S.A.: Florida, Belle Glade, 26.6751°N, 80.67°W, 12.xii.2005, ex *Cynodon dactylon* (L.) Pers., coll. M.E. Gruwell; D3737AC (ID B.B.N.) U.S.A.: Florida, Jacksonville, 8369 Cross Timbers Dr. W, 17.v.2012, ex *Stenotaphrum secundatum* (Walter) Kuntze, coll. E. Harlow. ***Aspidiotini undet sp.***, (all 2nd-instar females) D0950A Mexico: Tamaulipas, 23.084°N, 99.128°W, 16.iii.2005, ex *Taxodium* sp., coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N.; D1020 Tamaulipas, Rio Sabinas, 15.iii.2005, ex *Taxodium* sp., coll. M.E. Gruwell. ***Aspidiotus cryptomeriae*** Kuwana D1102D (ID B.B.N.) U.S.A.: Maryland, Silver Spring, 39.0666°N, 79.9833°W, 7.vi.2006, ex *Tsuga canadensis* (L.) Carrière, coll. D.R.M.; D3132A (ID B.B.N.) Japan: Osaka, Osaka Botanical Garden, 5.iv.2005, ex *Tsuga sieboldii* Carrière, coll. S. Lyon. ***Aspidiotus destructor*** Signoret D0496A (lotID B.B.N.) Trinidad & Tobago: Trinidad, Caroni, 16.viii.2001, ex *Cocos* sp., coll. J. Irish, E. Holder; D0703A (ID B.B.N.) Mexico: Quintana Roo, Tulum, 19.v.2004, coll. G.E.M.; D0705A (ID B.B.N.), D0707A (ID G.W.W.) Mexico: Quintana Roo, Akumal, 19.v.2004, ex *Cocos* sp., coll. G.E.M.; D1120D (ID B.B.N.) Belize, Calcutta, 18.363°N, 88.4365°W, 3.vi.2000, ex *Hibiscus cannabinus* L., coll. M.E. Schauff, R. Sapin, D.R.M.; D1156C (ID D.R.M.) Ghana, Accra, 7.vi.2005, ex undet. Arecaceae, coll. G.E.M.; D3045A (ID D.R.M.) Panama: SL crane, 23.viii.2010, ex *Oenocarpus mapora* H. Karst., coll. G.E.M., B.B.N. ***Aspidiotus elaeidis*** Marchal D3519A (ID B.B.N.) South Africa: Western Cape, Vermont, 25.vi.2011, ex *Syzygium cordatum* Hochst., coll. J.H. Gilimee. ***Aspidiotus excisus*** Green D3028B (ID D.R.M.) Panama: SL crane, 23.viii.2010, ex *Tocoyena pittieri* (Standl.) Standl., coll. G.E.M., B.B.N. ***Aspidiotus hedericola*** Leonardi D0595A (ID B.B.N.) Turkey: Adana, Seyhan River, 1 km N Stone Bridge, 18.iv.2004, ex *Hedera helix* L., coll. B.B.N., M.E. Gruwell; D0620A (ID D.R.M.), D0620B (ID B.B.N.) Turkey: Adana, Adana city center, 21.iv.2004, ex *Acacia* sp., coll. T.K. ***Aspidiotus nerii*** Bouché D0008A (lotID B.B.N.) U.S.A.: California, Sacramento: State Capitol, 38.6°N, 121.4833°W, 17.v.2000, ex *Hedera helix*, coll. R.J.G., B.B.N.; D0009A (fieldID R.J.G.) U.S.A.: California, Sacramento: State Capitol, 38.6°N, 121.4833°W, 17.v.2000, ex *Hedera helix*, coll. R.J.G., B.B.N.; D0018A (lotID B.B.N.), D0019A (ID D.R.M.) U.S.A.: California, Davis: D St. between 2nd & 3rd, 19.v.2000, ex *Berberis* sp., coll. D.R.M.; D0022C (ID B.B.N.) U.S.A.: California, Stebbins Cold Canyon Reserve, 20.v.2000, ex *Arctostaphylos* sp., coll. P.J. Gullan, B.B.N.; D0045AC (lotID B.B.N.) U.S.A.: California, Folsom, 24.iv.2000, ex *Arctostaphylos* sp., coll. M. Smith; D0103B (ID B.B.N.) Italy, Veneto: Padova, 15.iii.2001, coll. G. Pellizzari; D0404B, D0405A (lotID LM Provencher) Italy, Sicily; D0406B (lotID B.B.N.) U.S.A.: California, San Diego Zoo, 31.xii.2001, ex *Pittosporum* sp., coll. L.M. Provencher; D0408AB (lotID L.M. Provencher) U.S.A.: California, Vacaville, 27.viii.2002, ex *Nerium oleander* L., coll. L.M. Provencher; D0409C South Africa, Nelspruit, 19.iii.2001, coll. J. Daneel; D0418C Israel, Rehovot, 10.ix.2000, ex *Pittosporum undulatum* Vent., coll. U. Gerson; D0430A (lotID R.J.G.) U.S.A.: California, Veronica, Penngrove, Passanisi Nursery, 10.v.2000, ex *Schefflera* sp., coll. R.J.G.; D0462B (ID B.B.N.) U.S.A.: California, Davis, UC Davis campus, 38.5333°N, 121.75°W, 16.vi.2003, ex *Nerium oleander*, coll. T.K.; D0493 (lotID R.C.H.) New Zealand: AK, Auckland, New Lynn, 12.xii.2000, ex *Trachycarpus fortunei* (Hook.) H. Wendl., coll. N.A. Martin; D0504L (lotID L.M. Provencher) U.S.A.: Florida, Homestead, ex *Cucurbita* sp., coll. H. Glenn; D0505DE (lotID L.M. Provencher) Italy, Amalfi, ex *Citrus* sp., coll. A. Garrona; D0630A (ID B.B.N. query) Turkey: Osmaniye, Karatepe-Aslantas National Park, 37.2947°N, 36.248°E, 24.iv.2004, coll. T.K., M.E. Gruwell; D0761ACF (ID B.B.N.) Australia: Queensland, Cedar Creek, south of Beenleigh, 21.viii.2004, ex *Lomandra* sp., coll. G.E.M.; D0865A (ID B.B.N.) New Zealand, NZAK: Auckland domain, 12.iii.2005, ex *Rhopalostylis sapida* H. Wendl. & Drude, coll. R.C.H.; D2145F (ID B.B.N.) Portugal, Tróia, 38.4657°N, 8.8733°W, 28.ix.2007, coll. B.B.N., G.E.M., J. Wu, M.E. Gruwell, J.C. Andersen; D2149C (ID D.R.M.) Portugal, Tróia, 38.4657°N, 8.8733°W, 28.ix.2007, coll. B.B.N., G.E.M., J. Wu, M.E.

Gruwell, J.C. Andersen; D2163A (ID D.R.M.) Portugal, Galegos, 39.3624°N, 7.3277°W, 29.ix.2007, coll. M.E. Gruwell, J.C. Andersen, J. Wu; Bouché D2171AC (lotID B.B.N.) Portugal, Oeiras, 38.6955°N, 9.3178°W, 26.ix.2007, ex *Olea europaea*, coll. T.K., M.E. Gruwell; D2436B (ID B.B.N.) U.S.A.: Massachusetts, 42.4666°N, 71.4666°W, 31.v.2009, coll. J.C. Andersen; D2496B (ID B.B.N.) Greece: Episkopi, 3.iv.2010, ex *Ceratonia siliqua* L., coll. C.J. Hodgson; D2871B (ID B.B.N.) Italy, 2.vi.2010, ex *Olea europaea*, coll. M. Tomkins; MD028A (ID B.B.N.), MD028B (lotID R.C.H.) New Zealand, Banks Peninsula, Prices Valley Reserve, 3.xi.2005, coll. N.A. Martin. *Aspidiotus pothos* Takagi D3221B (ID B.B.N.) Japan: Kyushu, Mt. Konosu, 33.5561°N, 130.383°E, 23.xi.2010, coll. A.O. *Aspidiotus ud0043* D0043D (lotID B.B.N.) Australia: ACT, Canberra, Black Mt., Aust. Nat. Bot. Gardens, 35.28333°S, 149.1°E, 19.i.2001, ex *Macrozamia lucida* L.A.S. Johnson, coll. P.J. Gullan, S.R. Donaldson; D2102ABCDEFJK (ID B.B.N. query) Australia: New South Wales, 28.92436°S, 151.199°E, 1.vi.2007, ex undet. mistletoe, coll. J.C. Andersen, B.B.N. *Aulacaspis alisiana* Takagi D2434ABC, D2435AB (lotID D.R.M.) U.S.A.: Hawaii, Panaewa: UH Exp. Station, 22.v.2009, ex *Nephelium lappaceum* L., coll. C. Hirayama. *Aulacaspis crawii* (Cockerell) D3360B (ID B.B.N. query) Hong Kong, Lady Clementi's Ride, Aberdeen Reservoir, 26.ii.2011, ex *Dendrotrophe frutescens* (Champ. ex Benth.) Danser, coll. C.S.K. Lau. *Aulacaspis difficilis* (Cockerell) D0375AE (LotID MS) Japan, Izuhara Town, Tshushima Is., 28.iv.2001, ex *Elaeagnus macrophylla* Thunb., coll. M.S.; D2474B (ID B.B.N.) Japan: Kyushu, Kakinoura Island, 33.0166°N, 129.566°E, 19.iii.2010, ex *Elaeagnus macrophylla*, coll. A.O. *Aulacaspis distylii* Takahashi D0384AC (lotID MS) Japan, Susami Town, Wakayama Pref., 5.v.2001, ex *Distylium racemosum* Siebold & Zucc., coll. M.S. *Aulacaspis nitida* Scott D1173A (lotID B.B.N. query) Mexico, quarantine interception at Los Angeles 19.vi.2005, ex *Mangifera indica*. *Aulacaspis rosae* (Bouché) D0395ABC (lotID MS) Japan: Honshu, Sendai City, 22.viii.2001, ex *Rubus palmatus* Thunb., coll. MS; D1433A (ID D.R.M.) Belize, Corozal, 3.vi.2000, ex *Hibiscus* sp., coll. M.E. Schauff, R. Spain, D.R.M. *Aulacaspis rosarum* Borchsenius D1804D (ID D.R.M.) Korea: Youngjusa, Gyeonggi-do, 21.iv.2006, ex *Rosa hybrida* L., coll. S.J. Suh. *Aulacaspis spinosa* (Maskell) D0376 (lotID MS) Japan: Izuhara Town, Tshushima Is, 28.iv.2001, ex *Smilax china* L., coll. MS. *Aulacaspis tubercularis* Newstead D0225CD (ID D.R.M.) Colombia: Valle del Cauca, Cali, 30.xii.2001, ex *Mangifera indica*, coll. T.K.; D1180ABC (ID B.B.N.) Haiti, quarantine interception 6.vi.2008, ex *Mangifera indica*; D2952A (ID B.B.N.) Colombia, 19.vi.2010, ex *Mangifera indica*, coll. N. Rodriguez. *Aulacaspis vitis* (Green) D4354A (ID B.B.N. query) South Africa, Nelspruit, 0.i.1900, ex *Mangifera* sp., coll. T. Grove. *Aulacaspis yabunikkei* Kuwana D2472A (ID B.B.N.) Japan: Kyushu, Mt. Konosu, 33.5566°N, 130.383°E, 16.iii.2010, ex *Cinnamomum tenuifolium* (Makino) Sugim., coll. A.O.; D2473C (ID B.B.N.) Japan: Kyushu, Mt. Konosu, 33.5566°N, 130.383°E, 16.iii.2010, ex *Cryptomeria japonica* (Thunb. ex L. f.) D. Don, coll. A.O. *Aulacaspis yasumatsui* Takagi D0242A (LotID T.K.) U.S.A.: Florida, Miami: Old Cutler Rd., 7.v.2002, ex *Cycas revoluta* Thunb., coll. Tom Weissling; D0304ABC (ID B.B.N.) U.S.A.: Florida, Ft. Lauderdale, 19.xi.2002, ex undet. Cycadales, coll. T.K.; D0307A (lotID B.B.N.) U.S.A.: Florida, Davie: Univ. of FL Ft. Lauderdale Research & Education Center, 26.0841°N, 80.238°W, 20.xi.2002, ex undet. Cycadales, coll. D.R.M., R.J.G., T.K., B. Sello, M.E. Gruwell, B.B.N.; D0992A (ID D.R.M.) U.S.A.: Florida, Davie, 26.0846°N, 80.2378°W, 18.xii.2005, ex undet. Cycadales, coll. T.K.; D1092C (lotID GH) China, 22.x.2004, coll. R. Nguyen; D1093A (lotID GH) U.S.A.: Florida: Gainesville lab colony, 22.x.2004, coll. R. Nguyen; D1833A (ID B.B.N.) Vietnam, Nhatrang, 25.iii.2006, coll. R. Nguyen; D5050B (ID B.B.N.) Indonesia: Sulawesi, Manado, 7.vii.2013, ex *Cycas* sp., coll. R. Muniappan. *Carulaspis giffardi* (Adachi & Fullaway) [now *Lepidosaphes giffardi* (Adachi & Fullaway), **new combination**] D1203A (ID B.B.N.) U.S.A.: Hawaii, Kahana, Maui, 11.i.2006, ex undet. Bambusoidea, coll. M.E. Gruwell. *Carulaspis juniperi* (Bouché) D0107ABCD, D0108C (ID B.B.N.) U.S.A.: Massachusetts, UMass Amherst campus, 9.xi.2000, ex *Juniperus* sp., coll. L.M. Provencher; D0241A (lotID B.B.N.) U.S.A.: Massachusetts, UMass Amherst campus, 28.v.2002, ex *Juniperus* sp., coll. B.B.N., B. Sello; D0403A U.S.A.: Massachusetts, UMass Amherst campus, 20.v.2003, ex *Juniperus* sp., coll. G.E.M., B.B.N. *Carulaspis minima* (Signoret) D0014 (lotID B.B.N.) U.S.A.: California, Davis, UC Davis campus, 17.v.2000, ex *Juniperus* sp., coll. D.R.M.; D0354A (ID D.R.M.) U.S.A.: California, Rohnert Park, 38.3333°N, 122.7723°W, 27.viii.2001, ex undet. Cupressaceae, coll. L.M. Provencher, G. Oullette; D0458A (ID D.R.M.) U.S.A.: California, Davis, UC Davis campus, 38.5333°N, 121.75°W, 16.vi.2003, ex *Juniperus* sp., coll. T.K.; D0463AB (ID B.B.N.) U.S.A.: California, Davis, UC Davis campus, 38.5333°N, 121.75°W, 16.vi.2003, ex *Sequoia sempervirens* (D. Don) Endl., coll. T.K.; D1014A (ID B.B.N.) Mexico: Tamaulipas, Ciudad Victoria, Centro Universitario, 12.iii.2005, ex undet. Cupressaceae, coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N.; D1208B (ID B.B.N.) U.S.A.: California, Merced City, near Bear Creek, 15.i.2006, ex *Juniperus* sp., coll. M.E. Gruwell; D2146A (ID D.R.M.)

Portugal, Tróia, 38.4657°N, 8.8733°W, 28.ix.2007, ex *Juniperus* sp., coll. B.B.N., G.E.M., J. Wu, M.E. Gruwell, J.C. Andersen. ***Carulaspis* sp.** D0005A (fieldID R.J.G.) U.S.A.: California, Sacramento: State Capitol, 38.6°N, 121.4833°W, 17.v.2000, ex undet. Cupressaceae, coll. R.J.G., B.B.N.; D0015A (fieldID D.R.M.) U.S.A.: California, Davis, UC Davis campus, 38.5333°N, 121.75°W, 17.v.2000, ex *Juniperus* sp., coll. D.R.M. ***Chentraspis unilobis*** (Maskell) D2139BC (ID B.B.N.) Australia: Northern Territory, Alice Springs, 23.73188°S, 133.870°E, 24.vii.2007, ex *Callistemon* sp., coll. B.B.N. ***Chionaspis americana*** Johnson D0833AD (ID B.B.N.) U.S.A.: Texas, Anzalduas County Park, 26.1333°N, 98.3166°W, 20.iii.2005, coll. B.B.N.; D2181A (ID B.B.N.) U.S.A.: Massachusetts, Granby, 42.2371°N, 72.4621°W, 10.x.2007, ex *Ulmus rubra* Muhl., coll. B.B.N.; D2427A (ID D.R.M.) U.S.A.: Massachusetts, Westfield, 42.1359°N, 72.7961°W, 7.v.2009, ex *Ulmus rubra*, coll. K. Robare; D5242EH (lotID B.B.N.) U.S.A.: Florida, Inglis, 29.1166°N, 82.7666°W, 21.ii.2015, ex *Ulmus americana* L., coll. B.B.N., B. Denno. ***Chionaspis brachycephalon*** Vea D1718A (ID IM Vea) Mexico: Mexico, Hwy 95 South of Tres Marias, 19.0166°N, 99.2586°W, 1.ix.2007, ex *Pinus pseudo-strobus* Brongn., coll. R. A. Gwiazdowski, D. Gernandt; D1765AB (ID IM Vea) Mexico: Durango, Restaurante “Los Pinos, Navios, 23.8833°N, 105.0333°W, 24.ix.2007, ex *Pinus cooperi* C.E. Blanco, coll. R. A. Gwiazdowski, A.G. Arévalo. ***Chionaspis etrusca*** Leonardi D0606A (ID B.B.N.) Turkey: Adana, Çukorova University, 37.0611°N, 35.358°E, 20.iv.2004, ex *Tamarix* sp., coll. B.B.N., G.E.M., M.E. Gruwell; D0687ABCDE (lotID I.G.) Russia, Astrachan, 10.v.2004, ex *Tamarix* sp., coll. I.G.; D0810B (ID B.B.N.) U.S.A.: Utah, Smithsonian Butte Rd, north slope, 37.1166°N, 113.1183°W, 19.xi.2004, ex *Tamarix* sp., coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N.; D0811A (ID B.B.N.) U.S.A.: Utah, St George: Las Palmas condominiums, 37.0833°N, 113.6166°W, 20.xi.2004, ex *Tamarix* sp., coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N.; Leonardi D2528A (ID D.R.M.) U.S.A.: Maryland, 19.viii.2009, ex *Tamarix* sp., coll. J. Wu. ***Chionaspis gleditsiae*** Sanders D0932A (lotID B.B.N.) U.S.A.: Massachusetts, UMass Amherst campus, 42.3833°N, 72.5166°W, 31.viii.2005, ex *Gleditsia triacanthos* L., coll. R. A. Gwiazdowski, J.C. Andersen. ***Chionaspis heterophyllae*** Cooley D0570B (lotID B.B.N.) U.S.A.: Massachusetts, UMass Amherst campus, 42.3833°N, 72.5166°W, 17.ii.2004, ex *Pinus* sp., coll. B.B.N.; D0933AB, D0934A (ID B.B.N.) U.S.A.: New Jersey, Pasadena Wildlife Management Area along route 539, 1st left after crossing route 72, 39.8272°N, 74.3666°W, 10.ix.2005, ex *Pinus rigida* Mill., coll. R. A. Gwiazdowski; D0941A (ID B.B.N.) U.S.A.: Connecticut, Middletown Rest Stop along Route 91 north, 41.5531°N, 72.7333°W, 11.ix.2005, ex *Pinus nigra* J.F. Arnold, coll. R. A. Gwiazdowski; D0973A (lotID B.B.N.) U.S.A.: Florida, Sixmile Rd., 27.8508°N, 80.8666°W, 13.xii.2005, ex *Pinus elliotii* Engelm., coll. R. A. Gwiazdowski; D0977A (ID B.B.N.) U.S.A.: Florida, Ten Mile Rd., 27.9666°N, 80.9584°W, 13.xii.2005, ex *Pinus elliotii*, coll. R. A. Gwiazdowski; D1081A (ID B.B.N.) U.S.A.: North Carolina, Schenck Memorial Forest, 35.8166°N, 78.7166°W, 12.ii.2006, ex *Pinus taeda* L., coll. B.B.N., C. Stumpf, B. Wiegmann; D1510AB (ID B.B.N.) U.S.A.: Georgia, Route 86 15 mi south of Atlanta, 33.5666°N, 84.5333°W, 10.viii.2006, ex *Pinus taeda*, coll. R. A. Gwiazdowski; D1820C (ID B.B.N.) U.S.A.: Florida, Sanibel Island, 26.4333°N, 82.0833°W, 25.iii.2007, coll. L. Wiley, M. Jones; D1941DEF (lotID J.W.D.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk., 29.7166°N, 82.453°E, 18.ii.2010, ex *Pinus palustris* Mill., coll. A.O.; D2441B (ID B.B.N.) U.S.A.: Florida, Cedar Key, 29.1513°N, 83.0488°W, 21.ii.2010, ex *Pinus elliotii*, coll. I.C.S. ***Chionaspis kosztarabi*** Takagi & Kawai D1950A (ID D.R.M. query) U.S.A.: Florida, Gainesville, San Felasco Hammock State Preserve, 29.7166°N, 82.453°E, 18.ii.2010, ex *Celtis* sp., coll. A.O. ***Chionaspis lepineyi*** Balachowsky [now ***Quernaspis lepineyi*** (Balachowsky), **new combination**] D0075A (LotID FK) Hungary, 23.vi.2001, ex *Quercus* sp., coll. FK. ***Chionaspis nyssae*** Comstock D0939A (ID B.B.N.) U.S.A.: New Jersey, Richard Stockton College Campus (RSC), 39.4833°N, 74.5333°W, 10.ix.2005, ex *Nyssa sylvatica* Marshall, coll. R. A. Gwiazdowski; D1109B (ID B.B.N.) U.S.A.: Maryland, Beltsville, USDA Facility, 39.0166°N, 76.9166°W, 7.vi.2006, ex *Nyssa* sp., coll. B.B.N.; ***Chionaspis ortholobis*** Comstock D2524A (ID D.R.M.) U.S.A.: Maryland, 18.viii.2009, ex *Salix* sp., coll. J. Wu; D2524B (lotID D.R.M.) U.S.A.: Maryland, 18.viii.2009, ex *Salix* sp., coll. J.W.; D2713B (ID B.B.N.) U.S.A.: California, Arnold, 38.2191°N, 120.37°W, 23.v.2010, ex *Ceanothus integerrimus* Hook. & Arn., coll. A.O., B.B.N. ***Chionaspis pinifoliae*** (Fitch) D0053A, D0054A (ID B.B.N.) U.S.A.: California, Gold Run, I-80 exit, 39.1666°N, 120.8518°W, 12.v.2001, ex *Pinus* sp., coll. D.J. Williams, D.R.M., B.B.N.; D0126B (ID B.B.N.) U.S.A.: California, 8 km NW Quincy, 40.01°N, 120.9833°W, 19.x.2000, ex *Pinus* sp., coll. P.J. Gullan; D0147A, D0148A (lotID B.B.N.), D0148B (ID B.B.N.) U.S.A.: Massachusetts, Amherst, UMASS, Morrill North, 42.3833°N, 72.5166°W, 11.iii.2000, ex *Pinus* sp., coll. L.M. Provencher; D0355B (ID B.B.N.) U.S.A.: California, Rohnert Park, 38.3333°N, 122.7723°W, 27.viii.2001, ex *Pinus* sp., coll. L.M. Provencher, G. Oullette; D0465ABC (ID B.B.N.) U.S.A.: California, outside Lassen Nat'l Park, 40.3833°N,

121.5166°W, 20.vi.2003, ex *Pinus contorta* Douglas ex Loudon, coll. E. Babendreier, R. A. Gwiazdowski, G.E.M., B.B.N.; D0798A, D0799A (ID B.B.N.) U.S.A.: Utah, Smithsonian Butte Rd, 100m N crest, 37.1166°N, 113.1246°W, 19.xi.2004, ex *Pinus monophylla* Torr. & Frém., coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N.; D0889ABCD (ID B.B.N. query) U.S.A.: California, Alta Sierra, 39.1333°N, 121.0666°W, 19.vi.2005, ex *Pinus ponderosa* P. Lawson & C. Lawson, coll. L.G. Cook; D0931A (ID B.B.N.) U.S.A.: New Jersey, Rutgers Marine Science Field Station, Dormitory, 39.5833°N, 74.3333°W, 20.viii.2005, ex *Pinus caribaea* Morelet, coll. R. A. Gwiazdowski; D0945A (ID B.B.N.) U.S.A.: Vermont, Perkins Pier, Burlington, 44.4666°N, 73.2166°W, 22.ix.2005; D1148A (ID B.B.N. query) U.S.A.: California, Angeles Nat'l. Forest: Sycamore Flat Campground, 29.x.2006, ex *Pinus attenuata* Lemmon, coll. R.F. Luck, R. Stouthamer, D. Normark, B.B.N.; D1402A (ID B.B.N.) U.S.A.: California, Mountain Gate: Shasta Lake Visitors' Center, 40.7376°N, 122.3333°W, 2.viii.2006, ex *Pinus* sp., coll. B.B.N.; D1404AB (ID B.B.N.) U.S.A.: Washington, 11 mi NW Leavenworth: Tumwater Campground, 16.viii.2006, ex *Pinus ponderosa*, coll. B.B.N., R.D. Normark; D1415B (ID B.B.N.) U.S.A.: Washington, 1 mi SE Plain, 16.viii.2006, ex *Pinus ponderosa*, coll. B.B.N., RD Normark; D1417B U.S.A.: Washington, 1 mi SE Plain, 16.viii.2006, ex *Pseudotsuga menziesii* (Mirb.) Franco, coll. B.B.N., RD Normark; D1418AB (ID B.B.N.) U.S.A.: Washington, 5 mi NW Plain, 16.viii.2006, ex *Pinus contorta*, coll. B.B.N., RD Normark; D1419A (ID B.B.N.) U.S.A.: Washington, 5 mi NW Plain, 16.viii.2006, ex *Pinus ponderosa*, coll. B.B.N., RD Normark; D1774B (ID B.B.N.) Mexico: Sonora, Hwy 2 W of Cananea, 31.0166°N, 110.3666°W, 5.x.2007, ex *Pinus leiophylla* Schiede ex Schltdl. & Cham., coll. R. A. Gwiazdowski T. R. Van Devender, L. Van Devender; D2246A (ID G.W.W.) U.S.A.: Oregon, Cascade Locks, 45.6833°N, 121.8898°W, 18.iii.2008, ex *Pseudotsuga menziesii*, coll. R. A. Gwiazdowski; D2668A (ID B.B.N.) U.S.A.: Nevada, Red Rock Cyn. Pine Crk. Cyn., 2.iii.2010, ex *Pinus* sp., coll. J.W.D.; D2671A (ID B.B.N.) U.S.A.: California, Gold Run Rest Area, 39.1666°N, 120.851°W, 22.iii.2010, ex *Arctostaphylos* sp., coll. J.W.D.; D2714AB (lotID B.B.N.) U.S.A.: California, Arnold, 38.2261°N, 120.3695°W, 23.v.2010, ex *Pinus ponderosa*, coll. B.B.N., A Krewinski; D2723AB (ID B.B.N.) U.S.A.: California, 38.1980°N, 120.3662°W, 23.v.2010, ex *Pinus ponderosa*, coll. AO, B.B.N.; D2753AB (ID B.B.N.) U.S.A.: Massachusetts, Montague, 42.521°N, 72.5208°W, 19.vii.2010, ex *Tsuga canadensis*, coll. B.B.N., A. Krewinski, AO, & R. Carlton; D2853A (ID B.B.N.) U.S.A.: California, Bishop, 10.viii.2009, coll. BD Denno, D.R.M. ***Chionaspis salicis*** (Linnaeus) D0662AB (lotID B.B.N.) Sweden: Ångermanland, Dekarsön, Fläderbacken, 6.viii.2004, ex *Vaccinium* sp., coll. B.B.N.; D2903A (ID B.B.N.) Hungary: Budapest, 24.viii.2001, ex *Populus* sp., coll. FK. ***Chionaspis salicisnigrae*** (Walsh) [junior synonym of *Chionaspis salicis* (Linnaeus)] D1695A (ID B.B.N.) U.S.A.: Wisconsin, Wisconsin, 13.vii.2007, coll. J. Lund. ***Chionaspis sonoreae*** Veá D1781AC (ID IM Veá) Mexico: Sonora, Yecora, 28.3666°N, 108.9333°W, 8.x.2007, ex *Pinus engelmannii* Carrière, coll. R. A. Gwiazdowski T. R. Van Devender, L. Van Devender. ***Chionaspis* sp.** D1717B Mexico: Mexico, Hwy 95 South of Tres Marias, 19.0166°N, 99.259°W, 1.ix.2007, ex *Pinus pseudostrabus*, coll. R. A. Gwiazdowski, D. Gernandt; D1735A Mexico: Queretaro, Hwy 120 south of Pinal de Amoles, 21.0833°N, 99.6833°W, 6.ix.2007, ex *Pinus cembroides* Zucc., coll. R. A. Gwiazdowski, J. Rull; D1776B Mexico: Sonora, ~12 km E of Yecora, 28.3666°N, 109.0333°W, 7.x.2007, ex *Pinus herrerae* Martínez, coll. R. A. Gwiazdowski, T.R. Van Devender, L. Van Devender; D1782B Mexico: Chihuahua, Hwy 16 near Sonora Border, 28.4333°N, 108.5166°W, 8.x.2007, ex *Pinus discolor* D.K. Bailey & Hawksw., coll. R. A. Gwiazdowski, T.R. Van Devender, L. Van Devender. ***Chionaspis torreyanae*** Veá D2238A (ID B.B.N.) U.S.A.: California, Santa Rosa Island, 33.9833°N, 120.0166°W, 23.i.2008, ex *Pinus torreyana* Parry ex Carrière, coll. C. Greene. ***Chionaspis wistariae*** Cooley D0386AB (lotID MS), Saga Pref.: Hyushu Highway Yamaura Parking Area, 4.viii.2001, ex *Wisteria floribunda* (Willd.) DC., coll. M.S. ***Chortinaspis subchortina*** (Laing) D2445C (ID D.R.M.) U.S.A.: Florida, Cedar Key, 29.1383°N, 83.0308°W, 21.ii.2010, ex *Distichlis spicata* (L.) Greene, coll. B.B.N. ***Chortinaspis ud0265*** D0265 (lotID B.B.N.) Argentina: Jujuy, Humahuaca, 12.ii.2002, coll. L.E.C. ***Chrysomphalus aonidum*** (Linnaeus) D0300AC (lotID B.B.N.) U.S.A.: Florida, Ft. Lauderdale: Port Everglades: Broward County Convention Center, 26.0980°N, 80.1219°W, 19.xi.2002, ex *Liriope* sp., coll. B.B.N., B. Sello, M.E. Gruwell; D0368A (ID B.B.N.) U.S.A.: Florida, 23.x.2000, ex *Citrus* sp., coll. G. Oulette; D1021A (ID B.B.N.) Mexico: Tamaulipas, Ciudad Victoria, Facultad de Agronomía, 12.iii.2005, ex undet. Areaceae, coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N.; D1195A (ID D.R.M.) Thailand, intercepted in quarantine in Australia (AQIS 93919); D2858B (lotID B.B.N.) U.S.A.: Florida, 6779 Palmero Way, West Palm Beach, 17.v.2010, ex *Citrus* sp., coll. P. DeLaConcepcion. ***Chrysomphalus dictyospermi*** (Morgan) D2032A (ID JD) Australia: Queensland, St. Lucia, 27.49858°S, 153.004°E, 6.v.2007, ex *Corymbia trachyphloia* (F. Muell.) K.D. Hill & L.A.S. Johnson, coll. B.B.N.; D3022B (ID B.B.N.) Panama: Colon, at base of crane (Parque Nacional San Lorenzo

Canopy Crane), 9.2811°N, 79.9744°W, 23.viii.2010, coll. G.E.M., B.B.N.; D3061CDF (lotID B.B.N.) Panama: SL crane, 24.viii.2010, ex *Brosimum utile* (Kunth) Oken, coll. G.E.M., B.B.N.; D3078A (ID B.B.N.) Panama: SL crane, 25.viii.2010, ex *Socratea exorrhiza* (Mart.) H. Wendl., coll. G.E.M.; D3984A (ID B.B.N.) Panama: SL crane, 14.vi.2012, ex *Pouteria reticulata* (Engl.) Eyma, coll. G.E.M., B.B.N.; D4003ADFGH (ID B.B.N.) Panama: SL crane, 15.vi.2012, ex *Carapa guianensis* Aubl., coll. G.E.M., B.B.N.; D4013B (ID B.B.N.) Panama: SL crane, 15.vi.2012, ex *Socratea exorrhiza*, coll. G.E.M., B.B.N.; D4192A (ID B.B.N.) Panama: SL crane, 21.vi.2012, ex *Socratea exorrhiza*, coll. G.E.M., B.B.N.; D4455A (lotID B.B.N.) Malaysia: LH crane, 7.viii.2013, ex *Palaquium* sp., coll. G.E.M., B.B.N., D.A.P.; D4456A (ID B.B.N. query) Malaysia: LH crane, 7.viii.2013, ex *Blumeodendron calophyllum* Airy Shaw, coll. G.E.M., B.B.N., D.A.P. **Chrysomphalus near pinnulifer** D4479A (ID B.B.N.) Malaysia: LH crane, 8.viii.2013, ex *Endiandra* sp., coll. G.E.M., D.A.P. **Chrysomphalus pinnulifer** (Maskell) D0122A (lotID B.B.N.) Kenya, Nairobi: ICIPE, 1.22098°S, 36.895°E, 24.v.2001, coll. W.A. Overholt; D1181B (ID B.B.N.) Malaysia, quarantine interception at San Francisco, 16.xii.2008, ex *Podocarpus* sp.; D4405A (ID B.B.N.) Malaysia: LH crane, 6.viii.2013, ex *Ctenolophon parvifolius* Oliv., coll. G.E.M.; D4452A (ID B.B.N.) Malaysia: LH crane, 7.viii.2013, ex *Xanthophyllum brevipes*, coll. G.E.M., B.B.N., D.A.P. **Clavaspidotus apicalis** Takagi D5047ABC (ID B.B.N.) Indonesia: Sulawesi, Fakpak Barat, 22.vi.2013, ex *Citrus* sp., coll. E. Benson. **Clavaspis coursetiae** (Marlatt) D2686AB (ID B.B.N.) U.S.A.: California, Del Puerto Canyon Rd., 37.3862°N, 121.4536°W, 21.v.2010, ex *Ceanothus palmeri*, coll. A.O.; D2690A (ID B.B.N.) U.S.A.: California, 37.3926°N, 121.4497°W, 21.v.2010, ex *Cercocarpus betuloides* Nutt. coll. A.O.; D2694A (ID B.B.N.) U.S.A.: California, 37.3862°N, 121.4536°W, 21.v.2010, ex *Ceanothus* sp., coll. A.O.; D2701C (lotID B.B.N.) U.S.A.: California, 37.4559°N, 120.0743°W, 22.v.2010, ex *Rhamnus crocea* Nutt., coll. A.O.; MD003A (ID D.R.M.) U.S.A.: Arizona, Cave Creek Recreation Area: Go John Trail, 21.iv.2006, ex *Castela emoryi* (A. Gray) Moran & Felger, coll. G.E.M., T.K. **Clavaspis covilleae** (Ferris) D0877ABC (ID B.B.N.) U.S.A.: California, Cameron: intersection of Rte. 58 & Pacific Crest Trail, 35.0833°N, 118.3102°W, 16.vi.2005, ex *Prunus fasciculata* (Torr.) A. Gray, coll. B.B.N. **Clavaspis herculeana** (Cockerell & Hadden) D2040B (ID JD) Australia: Queensland, St. Lucia, 27.49858°S, 153.004°E, 6.v.2007, ex *Corymbia trachyphloia*, coll. B.B.N.; D3727A (ID B.B.N.) Thailand, 24.v.2012, ex *Plumeria rubra* L., coll. J.D. Alvarado. **Clavaspis near covilleae D0833C** (ID B.B.N.) U.S.A.: Texas, Anzalduas County Park, 26.1333°N, 98.3166°W, 20.iii.2005, coll. B.B.N. **Clavaspis texana** Ferris D0838A (ID B.B.N.) U.S.A.: Texas, Anzalduas County Park, 26.1384°N, 98.3262°W, 20.iii.2005, coll. B.B.N. **Clavaspis ud0274** D0274B (ID B.B.N.) Argentina: Neuquen, PN Lanin: Seccional Lago Puelo, 12.ii.2003, ex *Embothrium coccineum* J.R. Forst. & G. Forst., coll. L.E.C., P. Zamudio, L. Díaz-Briz, & L. Guardia Claps. **Clavaspis ud3510** D3510A (ID B.B.N. query) Ecuador, 24.x.2010, ex *Persea americana*, coll. D. Vallejo. **Coccomytilus convexus** (Maskell) D2123A (ID JD) Australia: New South Wales, 28.64578°S, 152.036°E, 2.vi.2007, ex *Acacia falcata* Desf., coll. J.C. Andersen, B.B.N. **Comstockaspis perniciosus** (Comstock) D2068AB (ID JD) Australia: New South Wales, 28.65488°S, 150.199°E, 30.v.2007, ex *Eucalyptus populnea* F. Muell., coll. J.C. Andersen, B.B.N.; D2110A (ID B.B.N.) Australia: New South Wales, 29.01385°S, 151.706°E, 1.vi.2007, ex *Eucalyptus* sp., coll. J.C. Andersen, B.B.N. **Crypthemichionaspis nigra** Lindinger [now *Trulliflorinia nigra* (Lindinger), **new combination**] D2057A (ID B.B.N.) Australia: Queensland, near Yelarbon, 28.49883°S, 150.566°E, 30.v.2007, ex *Acacia harpophylla*, coll. J.C. Andersen, B.B.N.; D2080A (ID B.B.N.) Australia: Queensland, 27.91948°S, 149.715°E, 31.v.2007, ex *Acacia leiocalyx* (Domin) Pedley, coll. J.C. Andersen, B.B.N. **Cryptoparlatoria leucaspis** Lindinger [now *Parlatoria leucaspis* (Lindinger), **new combination**] D0397C (ID D.R.M.) Japan: Kyushu, Fukuma Town, 28.ix.2001, ex *Quercus acutissima* Carruth., coll. M.S.; D3714A (ID B.B.N.) Japan: Kyushu, Tokinokura Vinegar Cellar, 33.3571°N, 130.816°E, 28.v.2012, ex *Chamaecyparis obtusa* (Siebold & Zucc.) Endl., coll. A.O. **Cupidaspis beshearae** Howell & Tippins D2661AB (ID B.B.N.) U.S.A.: Nevada, Red Rocky Canyon, Willow Springs, 36.1573°N, 115.4932°W, 16.i.2009, ex *Juniperus* sp., coll. J.W.D. **Cupidaspis cupressi** (Coleman) D0030B (ID D.R.M.) U.S.A.: California, Del Puerto Canyon: Frank Raines County Park, 21.v.2000, ex *Juniperus californica* Carrière, coll. D.J. Williams, D.R.M., P.J. Gullan, R.J.G., B.B.N.; D0797AC (ID B.B.N.) U.S.A.: Utah, 500m W Smithsonian Butte, on Smithsonian Butte Rd., 37.1164°N, 113.1068°W, 19.xi.2004, ex *Juniperus virginiana*, coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N.; D1189A (ID D.R.M.) U.S.A.: Nevada, Pine Creek Canyon, 36.1279°N, 115.4742°W, 16.i.2009, ex undet. Cupressaceae, coll. J.W.D.; D2663A (ID B.B.N. query) U.S.A.: Nevada, Red Rocky Canyon btw. Icebox Canyon & Pine Crk., 36.1391°N, 115.4723°W, 23.xii.2009, ex *Juniperus* sp., coll. J.W.D. **Dactylaspis ud0296** D0280A (lotID B.B.N.) Argentina: Chubut, PN Lago Puelo: Costa del Lago, 16.ii.2003, ex *Myrceugenia exsucca* (DC.) O. Berg, coll. L.E.C., L. Díaz-Briz; D0287A (lotID B.B.N.) Argentina:

Chubut, PN Lago Puelo: Costa del Lago, 16.ii.2003, ex *Luma apiculata* (DC.) Burret, coll. L.E.C., L. Díaz-Briz. **Dactylaspis ud0296** D0296AC (lotID B.B.N.) Argentina: Chubut, PN Lago Puelo: Sendero Rio Azul, 16.ii.2003, ex *Myrceugenia exsucca*, coll. L.E.C., P. Zamudio, L. Díaz-Briz, L. Guardia Claps. **Davidsonaspis aguacatae** (Evans, Watson, & Miller) D3784A (ID B.B.N.) Mexico, 27.i.2012, ex *Persea americana*, coll. T. Clerc. **Davidsonaspis ud3919** D3919A (ID B.B.N. query) Panama: SL crane, 12.vi.2012, ex *Tovomita longifolia*, coll. G.E.M., B.B.N. **Diaphoraspis compacta** Brimblecombe D2044A (ID JD) Australia: Queensland, Bribie Island, 27.01666°S, 153.116°E, 13.v.2007, ex *Casuarina glauca*, coll. B.B.N. **Diaphoraspis incisa** Brimblecombe D2104A (lotID D.R.M.) Australia: New South Wales, Little Oak Creek at Bruxner Hwy., 29.18531°S, 151.323°E, 1.vi.2007, ex *Casuarina cunninghamiana* Miq., coll. J.C. Andersen, B.B.N. **Diaphoraspis** sp., 1 2nd-instar female D0814A (ID B.B.N. query) Australia: New South Wales, 20 km SW of Merriwa, 32.26666°S, 150.1°E, 28.viii.2004, ex *Casuarina* sp., coll. P.J. Gullan. **Diaspidid undet sp.** D0302BC U.S.A.: Florida, Ft. Lauderdale: Port Everglades: Broward County Convention Center, 26.0980°N, 80.1219°W, 19.xi.2002, ex *Liriope* sp., coll. B.B.N., B. Sello, M.E. Gruwell; D0324C U.S.A.: Florida, Davie: Univ. of FL Ft. Lauderdale Research & Education Center, 26.0841°N, 80.238°W, 20.xi.2002, ex *Citrus* sp., coll. D.R.M., R.J.G., T.K., B. Sello, M.E. Gruwell, B.B.N.; D0344A U.S.A.: Florida, Homestead: Univ. of FL Tropical Research & Education Center, 25.5076°N, 80.5008°W, 22.xi.2002, coll. B. Sello, M.E. Gruwell, B.B.N.; D0507A U.S.A.: Florida, Vanna Tropicals, 8120 SW 178th St., Miami, 33157, 28.vii.2003, ex *Dimocarpus longan* Lour., coll. V. Rodriguez; D0531A U.S.A.: Massachusetts, Tanglewood, 42.3333°N, 73.3581°W, 0.i.1900, coll. L.M. Provencher; D0599A Turkey: Adana, Çukorova University, 37.0611°N, 35.358°E, 20.iv.2004, ex *Nerium oleander*, coll. B.B.N., G.E.M., M.E. Gruwell; D0600A (ID B.B.N.) Turkey: Adana, Seyhan River, Center of Adana, from Stone Bridge northwards ~1km, 18.iv.2004, coll. B.B.N., M.E. Gruwell; D0601A Turkey: Adana, Seyhan River, Center of Adana, from Stone Bridge northwards ~1km, 18.iv.2004, ex *Laurus nobilis*, coll. B.B.N., M.E. Gruwell; D0602A Turkey: Adana, Çukorova University, 37.0611°N, 35.358°E, 21.iv.2004, ex *Pinus* sp., coll. T.K.; D0607A Turkey: Adana, Çukorova University, 37.0611°N, 35.358°E, 20.iv.2004, ex *Melia azadirachta* L., coll. B.B.N., G.E.M., M.E. Gruwell; D1774A Mexico: Sonora, Hwy 2 W of Cananea, 31.0166°N, 110.3666°W, 5.x.2007, ex *Pinus leiophylla*, coll. R. A. Gwiazdowski, T.R. Van Devender, L. Van Devender; D0608A Turkey: Adana, Çukorova University, 37.0611°N, 35.358°E, 20.iv.2004, ex *Platanus* sp., coll. B.B.N., G.E.M., M.E. Gruwell; D0697A Argentina: Chaco, PN Chaco, Sendero Peatonal, 31.x.1996, ex *Glandularia peruviana* (L.) Small, coll. L.E.C., P. González, P. Zamudio; D0700A Mexico: Quintana Roo, Akumal, 19.v.2004, coll. G.E.M.; D0761BD Australia: Queensland, Cedar Creek, south of Beenleigh, 21.viii.2004, ex *Lomandra* sp., coll. G.E.M.; D0768A Australia: Queensland, Lone Pine Koala Sanctuary, 27.53458°S, 152.969°E, 22.viii.2004, ex *Casuarina* sp., coll. G.E.M.; D0771A Australia: Queensland, Lone Pine Koala Sanctuary, 27.53458°S, 152.969°E, 22.viii.2004, ex *Acacia* sp., coll. G.E.M.; D0782C Australia: Queensland, Cape Tribulation Canopy Crane, 25.viii.2004, ex *Syzygium gustavioides* (F.M. Bailey) B. Hyland, coll. P.J. Gullan; D0850A South Africa, Gifberg Pass, 31.76666°S, 18.766°E, 2.i.2005, ex *Maytenus oleoides* (Lam.) Loes., coll. P.J. Gullan; D1088AB U.S.A.: California, 0.8 km NW Quincy, 40.00°N, 120.98°W, 19.x.2000, coll. P.J. Gullan; D1757AB Mexico: Jalisco, ~9 km NW of Tapalpa, 20.0333°N, 103.8513°W, 19.ix.2007, ex *Pinus lumholtzii* B.L. Rob. & Fernald, coll. R. A. Gwiazdowski, L.M. Gonzalez-Villareal; D1937B U.S.A.: Florida, San Felasco Hammock Preserve State Park, 29.796°N, 82.455°E, 18.ii.2010, ex *Pinus palustris*, coll. A.O.; D2004BCGKL Australia: Tasmania, 43.39033°S, 147.261°E, 25.i.2007, ex *Acacia verticillata* (L'Hér.) Willd., coll. B.B.N.; D2007ABC Australia: Queensland, Maijala National Park, Browsers Rd, 26.ii.2007, coll. B.B.N.; D2011A Australia: Queensland, Maijala National Park, Browsers Rd, 26.ii.2007, coll. R.D. Normark; D2029A Australia: Queensland, Mt. Glorious, 27.31666°S, 152.75°E, 28.iv.2007, ex *Alectryon subcinereum* Radlk., coll. B.B.N.; D2053A Australia: Queensland, near Yelarbon, 28.66895°S, 150.858°E, 30.v.2007, ex *Casuarina* sp., coll. J.C. Andersen, B.B.N.; D2074A Australia: Queensland, 28.49348°S, 150.103°E, 31.v.2007, ex *Casuarina* sp., coll. J.C. Andersen, B.B.N.; D2079B Australia: Queensland, 28.41808°S, 149.890°E, 31.v.2007, ex *Casuarina* sp., coll. J.C. Andersen, B.B.N.; D2081A Australia: Queensland, 27.9205°S, 149.928°E, 31.v.2007, ex *Acacia* sp., coll. J.C. Andersen, B.B.N.; D2128B Australia: Queensland, 28.8445°S, 151.339°E, 30.v.2007, coll. J.C. Andersen, B.B.N.; D2185F (LotID P. Moran) France, Vingrau, 42.7833°N, 2.850°E, 28.x.2007, ex *Arundo donax* L., coll. A. Kirk; D2203B Mexico: Baja California, Hwy 2 south of Juarez, 32.5741°N, 116.0833°W, 15.x.2007, ex *Pinus quadrifolia*, coll. R. A. Gwiazdowski, C. Callaway; D2401A U.S.A.: California, Monterey, 36.5833°N, 121.8833°W, 5.ix.2007, ex *Pinus radiata* D. Don, coll. R. A. Gwiazdowski; D2653B Ukraine, 13.i.2010, ex *Crataegus pinnatifida* Bunge, coll. M. Tomkins; D3017C (lotID B.B.N.) Panama:

SL crane, at base of crane, 23.viii.2010, coll. G.E.M., B.B.N.; D3026A Panama: SL crane, 23.viii.2010, ex *Tapirira guianensis*, coll. G.E.M., B.B.N.; D3704A Japan: Kyushu, Heiwa Sanso, 33.5566°N, 130.383°E, 13.v.2012, ex *Podocarpus macrophyllus*, coll. A.O.; D4205A Panama: SL crane, 21.vi.2012, ex *Dendropanax arboreus*, coll. G.E.M., B.B.N.; D4449AB Malaysia: LH crane, 7.viii.2013, ex *Durio lanceolatus* Mast., coll. G.E.M., B.B.N., DAP. **Diaspidinae undet sp.** D0317B (ID B.B.N.) U.S.A.: Florida, Davie: Univ. of FL Ft. Lauderdale Research & Education Center, 26.0841°N, 80.238°W, 20.xi.2002, ex *Bauhinia* sp., coll. D.R.M., R.J.G., T.K., B. Sello, M.E. Gruwell, B.B.N. **Diaspidiotus aesculi** (Johnson) D2706A (ID B.B.N.) U.S.A.: California, 37.5172°N, 120.1050°W, 22.v.2010, ex *Salix* sp., coll. A.O. **Diaspidiotus ancylus** (Putnam) D1855A (ID D.R.M.) U.S.A.: Michigan, Benton Harbor, 11.viii.2009, ex *Vaccinium* sp., coll. N. Hahn; D1944A (ID G.W.W.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk., 29.7166°N, 82.453°E, 18.ii.2010, ex *Smilax bona-nox* L., coll. L. Buss; D2187A (ID B.B.N. query) U.S.A.: Maine, Portage, 29.xi.2007, ex *Pinus resinosa* Aiton, coll. G. Boettner; D2191ABF (ID B.B.N. query) U.S.A.: Massachusetts, Manchester-By-The-Sea, 9.iii.2010, ex *Tsuga canadensis*, coll. Artemis Roehrig; D2501B (ID B.B.N.) U.S.A.: Virginia, Blandy Farm, 42.0666°N, 72.8333°W, 6.viii.2009, ex *Euonymus* sp., coll. J. Wu; D2502AC (ID D.R.M.) U.S.A.: Virginia, Blandy Farm, 42.0666°N, 72.5333°W, 6.viii.2009, ex *Cornus officinalis* Siebold & Zucc., coll. J. Wu; D2510B (ID B.B.N.) U.S.A.: Virginia, 13.viii.2009, ex *Cornus alternifolia* L.f., coll. J. Wu. **Diaspidiotus degeneratus** (Leonardi) D0001B (lotID B.B.N.) U.S.A.: California, Sacramento: State Capitol, 38.6°N, 121.4833°W, 17.v.2000, ex *Camellia* sp., coll. R.J.G., B.B.N. **Diaspidiotus fraxini** (McKenzie) D0808A (ID D.R.M.) U.S.A.: Utah, Virgin: Hwy 9, Zion River Resort RV Park & Camping, 37.2040°N, 113.1789°W, 19.xi.2004, ex *Fraxinus velutina* Torr., coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N. **Diaspidiotus gigas** (Thiem & Gerneck) D0688A (lotID IG) Russia: Voronezh, Voronezh, 22.v.2004, ex *Populus nigra* L., coll. I.G. **Diaspidiotus hunteri** (Newell) D0035A, D0036A (ID D.R.M.) U.S.A.: California, Del Puerto Canyon: Frank Raines County Park, 21.v.2000, ex *Ribes* sp., coll. D.J. Williams, D.R.M., P.J. Gullan, R.J.G., B.B.N. **Diaspidiotus juglansregiae** (Comstock) D0511AB (ID B.B.N.) U.S.A.: California, Jo-Dan Farms, 26550 Pabesu Rd., Murrieta, 92562, 29.vii.2003, ex *Fraxinus* sp., coll. M. Lahti; D2929A (ID B.B.N.) U.S.A.: California, Yuba City, 24.vi.2010, ex *Juglans* sp., coll. J. Hasey. **Diaspidiotus liquidambaris** (Kotinsky) D1079A (ID G.W.W.) U.S.A.: North Carolina, Schenck Memorial Forest, 35.8166°N, 78.7166°W, 12.ii.2006, ex *Quercus alba* L., coll. B.B.N., C. Stumpf, B. Wiegmann; D1106E (ID B.B.N.) U.S.A.: Maryland, Beltsville, USDA Facility, 39.0166°N, 76.9166°W, 7.vi.2006, ex *Liquidambar styraciflua* L., coll. D.R.M. **Diaspidiotus mcombi** McKenzie D1916A (ID D.R.M.) U.S.A.: Florida, Gainesville, back of UFL Dept. Agri. & Cons. services, 29.6333°N, 82.366°E, 17.ii.2010, ex *Pinus taeda*, coll. I.C.S. **Diaspidiotus osborni** (Newell & Cockerell) D2176A (ID B.B.N.) U.S.A.: Massachusetts, Granby: Harris St., 42.3003°N, 72.4745°W, 10.x.2007, ex *Ostrya virginiana* (Mill.) K. Koch, coll. B.B.N. **Diaspidiotus sp.** D2182A U.S.A.: Massachusetts, Granby, 42.2371°N, 72.4621°W, 10.x.2007, ex *Cornus alternifolia*, coll. B.B.N. **Diaspidiotus uvae** (Comstock) D0836A (ID B.B.N. query) U.S.A.: Texas, Anzalduas County Park, 26.1362°N, 98.3314°W, 20.iii.2005, ex *Parkinsonia aculeata* L., coll. M.E. Gruwell; D1844E (ID B.B.N. query) U.S.A.: Texas, Granjeno, 26.1359°N, 98.3314°W, 20.iii.2005, ex *Parkinsonia aculeata*, coll. M.E. Gruwell; D2534C (ID D.R.M.) U.S.A.: West Virginia, 25.viii.2009, ex *Salix* sp., coll. J. Wu. **Diaspidiotus zonatus** (Frauenfeld) D2159AB (ID D.R.M.) Spain, San Pedro, 39.3832°N, 7.2808°W, 29.ix.2007, ex *Quercus suber* L., coll. G.E.M. **Diaspis boisduvalii** Signoret D0143 (lotID B.B.N.) U.S.A.: Massachusetts, Amherst, 15.iii.2001, ex *Cattleya* sp., coll. L.M. Provencher; D2840B (ID B.B.N.) U.S.A.: Florida, 21840 SW 258th St., Homestead, 24.iii.2010, ex *Cymbidium* sp., coll. H. Glenn; D3017A (ID D.R.M.) Panama: SL crane, at base of crane, 23.viii.2010, coll. G.E.M., B.B.N.; D3025A (ID D.R.M.) Panama: SL crane, 23.viii.2010, ex *Tapirira guianensis*, coll. G.E.M., B.B.N.; D3035B (ID B.B.N.) Panama: SL crane, 23.viii.2010, ex *Tapirira guianensis*, coll. G.E.M., B.B.N.; D4275A (ID B.B.N.) Panama: SL crane, 20.vi.2012, ex *Marila laxiflora*, coll. G.E.M., B.B.N. **Diaspis coccois** Lichtenstein D0536AD (lotID R.J.G.) U.S.A.: California, Gardena, ABC Nursery Inc., 424 East Gardena Blvd., 21.vii.2003, ex *Cocos* sp., coll. B. Smith; D3009A (ID B.B.N.) Panama: SL crane, 21.viii.2010, ex *Tapirira guianensis*, coll. G.E.M., B.B.N. **Diaspis doumtsopi** Schneider [now *Epidiaspis doumtsopi* (Schneider), new combination] D3669E (ID B.B.N.) Cameroon, Evoudoula, 28.iv.2012, ex *Mangifera* sp., coll. A. Doumtsop. **Diaspis echinocacti** (Bouché) D0259BC (lotID L.E.C.) Argentina: Tucumán, Tucumán, 26.iii.2002, coll. A. Chalup; D0289AB (lotID L.E.C.) Argentina: Tucumán, Ticucho, 11.i.2002, ex *Opuntia ficus-indica* (L.) Mill., coll. L.E.C., P. Zamudio, L. Díaz-Briz; D0896D (lotID G.W.W.) Mexico: Tamaulipas, 23.3570°N, 99.0012°W, 18.iii.2005, ex *Opuntia* sp., coll. R. A. Gwiazdowski; D1002A (ID D.R.M.) U.S.A.: Texas, Granjeno, 26.1383°N, 98.3262°W, 20.iii.2005, ex *Opuntia* sp., coll. R. A. Gwiazdowski; D2759B (ID B.B.N.) U.S.A.: California, Tustin,

6.ii.2010, ex *Opuntia* sp., coll. N. Nisson. ***Diaspis manzanitae*** (Whitney) D0046A (lotID B.B.N.) U.S.A.: California, Nr. Three Rivers, Mineral King Rd., 36.4666°N, 118.85°W, 30.iii.2001, ex *Arctostaphylos viscida* Parry, coll. P.J. Gullan; D0127AB (ID D.R.M.) U.S.A.: California, 3 mi. S Grass Valley, 39.1833°N, 121.05°W, x.2000, coll. P.J. Gullan; D2652A (ID B.B.N.) U.S.A.: California, Hwy Int. Gold Run RA (I-80), 22.iii.2010, ex *Arctostaphylos* sp., coll. J.W.D.; D2652BC (ID B.B.N.) U.S.A.: California, Hwy Int. Gold Run RA (I-80), 22.iii.2010, ex *Arctostaphylos* sp., coll. J.W.D. ***Diaspis parasiti*** McKenzie D0884C (ID B.B.N.) U.S.A.: California, Whitewater canyon, 3 mi S trout hatchery, 16.vi.2005, ex *Phoradendron californicum* Nutt., coll. LG Cook. ***Diaspis* sp.** D0313AB U.S.A.: Florida, Davie: Univ. of FL Ft. Lauderdale Research & Education Center, 26.0841°N, 80.238°W, 20.xi.2002, ex *Cattleya* sp., coll. D.R.M., R.J.G., T.K., B. Sello, M.E. Gruwell, B.B.N. ***Dinaspis chiriquiensis*** Ferris D3010A (ID B.B.N. query) Panama: SL crane, 21.viii.2010, ex *Tapirira guianensis*, coll. G.E.M., B.B.N.; D4200A (ID B.B.N. query) Panama: SL crane, 21.vi.2012, ex *Tapirira guianensis*, coll. G.E.M., B.B.N. ***Duplachionaspis displicata*** Munting D3506B (ID B.B.N.) South Africa: Western Cape, Vermont, 19.vii.2011, ex *Aloe* sp., coll. J.H. Giliomee. ***Duplachionaspis divergens*** (Green) D0309BCE (lotID B.B.N.) U.S.A.: Florida, Davie: Univ. of FL Ft. Lauderdale Research & Education Center, 26.0841°N, 80.238°W, 20.xi.2002, ex Poaceae undet., coll. D.R.M., R.J.G., T.K., B. Sello, M.E. Gruwell, B.B.N.; D1124B (ID D.R.M.) U.S.A.: Florida, Naples, 14.v.2002, ex Poaceae undet., coll. S.D. Krueger, J.F. Miller, D.R.M.; D1125B (lotID B.B.N.) U.S.A.: Florida, Pembroke Pines (near Ft. Lauderdale), 8.v.2002, ex *Tripsacum dactyloides* (L.) L., coll. M. Quintanilla, J.F. Miller, D.R.M.; D2863A (lotID I.C.S.) U.S.A.: Florida, 10360 SW 118th St., Miami, 11.vi.2010, ex *Cymbopogon* sp., coll. O. Garcia. ***Duplachionaspis sicula*** (Lupo) D0623ABC (lotID D.R.M.) Turkey: Nevsehir, Fairy Chimneys forest, between Ürgüp & Zelke, 38.6725°N, 34.885°E, 23.iv.2004, coll. T.K. ***Dynaspidiotus abietis*** (Schrank) D2673A, D2674AB (ID B.B.N.) Greece: Peloponnesus, Taygetus Mt., 14.iv.2010, ex *Abies cephalonica* Loudon, coll. G. Stathas. ***Dynaspidiotus apachea*** (Ferris) D1753AB (lotID D.R.M.) Mexico: Jalisco, Haciendas la Herradura, 20.7666°N, 103.6718°W, 18.ix.2007, ex *Pinus oocarpa* Schiede ex Schldtl., coll. R. A. Gwiazdowski, L.M. Gonzalez-Villareal; D1774CD (ID B.B.N.) Mexico: Sonora, Hwy 2 W of Cananea, 31.0166°N, 110.3666°W, 5.x.2007, ex *Pinus leiophylla*, coll. R. A. Gwiazdowski, T.R. Van Devender, L. Van Devender; D1783AB (ID B.B.N.) Mexico: Sonora, Hwy 16 E of intersection Hwy 117, 28.4205°N, 109.0833°W, 9.x.2007, ex *Pinus oocarpa*, coll. R. A. Gwiazdowski, T.R. Van Devender, L. Van Devender; D2404AB (ID B.B.N.) Mexico: Sonora, Hwy 16 near Chihuahua border, 28.3666°N, 108.7563°W, 8.x.2007, ex *Pinus oocarpa*, coll. R. A. Gwiazdowski, T.R. Van Devender, L. Van Devender; D2408A (ID B.B.N.) Mexico: Sonora, Hwy 16, 28.3666°N, 109.0166°W, 7.x.2007, ex *Pinus* sp., coll. R. A. Gwiazdowski, T.R. Van Devender, L. Van Devender. ***Dynaspidiotus britannicus*** (Newstead) D1401AE (ID B.B.N.) U.S.A.: Washington, Seattle: 4th Ave N & Garfield St., 1.viii.2006, ex *Hedera helix*, coll. B.B.N. ***Dynaspidiotus californica*** (Coleman) D0026AB (lotID B.B.N.) U.S.A.: California, Del Puerto Canyon: Frank Raines County Park, 21.v.2000, ex *Pinus* sp., coll. D.J. Williams, D.R.M., P.J. Gullan, R.J.G., B.B.N.; D0055A (lotID B.B.N.) U.S.A.: California, Gold Run, I-80 exit, 39.1666°N, 120.8518°W, 12.v.2001, ex *Pinus* sp., coll. D.J. Williams, D.R.M., B.B.N.; D0454A (fieldID) U.S.A.: California, Cold Creek Canyon parking lot, 38.5097°N, 122.0959°W, 15.vi.2003, ex *Pinus sabiniana*, coll. G.E.M., B.B.N.; D1176AB (fieldID) U.S.A.: Nevada, Reno, 28.iv.2008, ex *Pinus* sp., coll. L. Norris, J.B. Knight; D1403A (lotID B.B.N.) U.S.A.: California, Mountain Gate: Shasta Lake Visitors' Center, 40.7376°N, 122.3333°W, 2.viii.2006, ex *Pinus* sp., coll. B.B.N.; D2210A U.S.A.: California, Hwy 138 between route 2 & 15, 34.3537°N, 117.5166°W, 16.x.2007, ex *Pinus monophylla*, coll. R. A. Gwiazdowski, C. Callaway; D2217AB U.S.A.: California, near Wonoga Peak, 36.52°N, 118.0833°W, 20.x.2007, ex *Pinus monophylla*, coll. R. A. Gwiazdowski, S. Graves; D2655A (lotID J.W.D.) U.S.A.: California, 36.1574°N, 115.4919°W, 23.xii.2009, ex *Pinus* sp., coll. J.W.D.; D2680C (ID B.B.N.) U.S.A.: California, 37.5882°N, 121.6122°W, 21.v.2010, ex *Pinus coulteri* Lamb. ex D. Don, coll. A.O.; D2682B (ID B.B.N.) U.S.A.: California, 37.5355°N, 121.5631°W, 21.v.2010, ex *Pinus coulteri*, coll. A.O.; D2691A (ID B.B.N.) U.S.A.: California, Del Puerto Canyon Rd., 37.3926°N, 121.4497°W, 21.v.2010, ex *Pinus coulteri*, coll. A. Krewinski. ***Dynaspidiotus rhodesiensis*** (Hall) D3521A (ID B.B.N. query) Uganda, Kampala, Makerere Univ., M.U.R.I.K., 27.vii.2011, ex *Coffea* sp., coll. R. Muniappan. ***Dynaspidiotus* sp.** D0979A U.S.A.: Florida, 27.5666°N, 80.8166°W, 13.xii.2005, ex *Pinus palustris*, coll. M.E. Gruwell, R. A. Gwiazdowski; D1105AB U.S.A.: Maryland, Beltsville, USDA Facility, 39.0166°N, 76.9166°W, 7.vi.2006, ex *Pinus virginiana* Mull., coll. M.E. Gruwell; D1938A U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk., 29.7974°N, 82.454°E, 18.ii.2010, ex *Pinus palustris*, coll. A.O.; D2669A U.S.A.: Nevada, Red Rock Canyon, Willow Springs, 1.iii.2010, ex *Pinus* sp., coll. J.W.D. ***Dynaspidiotus tsugae*** (Marlatt) D0822AD (ID B.B.N.), D0822B (ID D.R.M.)

Japan, Kami Kochi: Shimizu Tunnel, 18.viii.2004, ex *Tsuga diversifolia* (Maxim.) Mast., coll. S. Lyon. ***Dynaspidiotus* ud1932** D1932B (ID D.R.M. query) U.S.A.: Florida, Gainesville, UFL Hort. Sci. Dept. Res. Citrus Grove, 29.6333°N, 82.358°E, 18.ii.2010, ex *Pinus elliottii*, coll. I.C.S., B.B.N., A.O., L. Buss. ***Epidiaspis gennadii*** (Leonardi) D0603B (ID B.B.N.) Turkey: Adana, Çukurova University, 37.0611°N, 35.358°E, 21.iv.2004, coll. T.K.; D0626C (ID B.B.N.) Turkey: Osmaniye, Karatepe-Aslantas National Park, 37.2947°N, 36.248°E, 24.iv.2004, ex *Pistacia* sp., coll. B.B.N., G.E.M., M.E. Gruwell; D2755AC (ID B.B.N.) Slovenia: Nova Gorica, 45.9666°N, 13.633°E, 24.iv.2010, ex *Pistacia terebinthus* L., coll. G. Seljak. ***Epidiaspis leperii*** (Signoret) D0060A (lotID B.B.N.) U.S.A.: California, Lake Solano, 13.v.2001, ex *Heteromeles arbutifolia* (Lindl.) M. Roem., coll. D.J. Williams, D.R.M., B.B.N. ***Epidiaspis* ud4380** D4380B (ID B.B.N. query) Uganda, Kibale National Park, Kanyawara Biological Station, 12.viii.2012, coll. J.B. Wright. ***Eudinaspis calchaquensis*** Claps D0256ADE (LotID L.E.C.) Argentina: Salta, Entre San Carlos y Dique La Dársena, 12.xii.2001, ex *Capparis atamisquea* Kuntze, coll. L.E.C., P. Zamudio. ***Eulaingia stenophyllae*** (Laing) D2129A (ID JD) Australia: Queensland, 28.41808°S, 149.890°E, 31.v.2007, ex *Acacia* sp., coll. J.C. Andersen, B.B.N. ***Ferrisidea magna*** (Ferris) D0880BC (ID B.B.N.) U.S.A.: California, Cameron: intersection of Rte. 58 & Pacific Crest Trail, 35.0833°N, 118.3102°W, 16.vi.2005, ex *Lycium cooperi* A. Gray, coll. M.E. Gruwell. ***Fiorinia externa*** Ferris D0299A (fieldID) U.S.A.: Massachusetts, Amherst, 0.25 miles N. town Center, UMASS, 26.ix.2002, ex *Tsuga canadensis*, coll. M.E. Gruwell; D2990A (ID B.B.N.) Japan: Kobe, Kobe Botanical Garden, 10.v.2006, *Pseudotsuga* sp., coll. K. Abell. ***Fiorinia fioriniae*** (Targioni Tozzetti) D3422A (ID B.B.N.) South Africa: Western Cape, Stellenbosch, 9.vi.2011, coll. J.H. Giliomee. ***Fiorinia geijeriae*** Froggatt [now ***Trullifiorinia geijeriae*** (Froggatt), **new combination**] D2066A (ID B.B.N.) Australia: New South Wales, 28.62166°S, 150.218°E, 30.v.2007, ex *Geijera parviflora* Lindl., coll. J.C. Andersen, B.B.N.; D2091A (ID B.B.N.) Australia: New South Wales, 28.64541°S, 150.392°E, 1.vi.2007, ex *Geijera parviflora*, coll. J.C. Andersen, B.B.N.; D2093A (ID B.B.N.) Australia: New South Wales, 28.64541°S, 150.392°E, 1.vi.2007, ex *Geijera parviflora*, coll. J.C. Andersen, B.B.N. ***Fiorinia hymenanthis*** Takagi D0387BCD (lotID D.R.M.) Japan: Kyushu, Mt. Hiko, 20.iv.2001, ex *Rhododendron heptamerum* Balf. f., coll. M.S. ***Fiorinia pinicola*** Maskell D2494C (ID B.B.N.) Japan: Kyushu, Hirao Sanso Park, 33.5666°N, 130.383°E, 26.iii.2010, ex *Camellia* sp., coll. A.O. ***Fiorinia* sp.** D4590D Malaysia: LH crane, 10.viii.2013, ex *Gironniera hirta* Ridl., coll. B.B.N., G.E.M. ***Fiorinia theae*** Green D0250AC (LotID T.K.) U.S.A.: Alabama, Auburn University, 19.iii.2002, ex *Camellia japonica* L., coll. T.K.; D1960C (ID B.B.N.) U.S.A.: Florida, Gainesville, San Felasco Nursery, 29.7166°N, 82.466°E, 19.ii.2010, ex *Camellia* sp., coll. I.C.S.; D2857B (ID B.B.N.) U.S.A.: Florida, 2792 CR 564, Bushnell, 10.v.2010, ex *Camellia sasanqua* Thunb., coll. H. Alfred. ***Fiorinia vacciniiae*** Kuwana D0374A (lotID D.R.M.) Japan, Izuhara Town, Tshushima Is., 27.iv.2001, ex *Eurya japonica* Thunb., coll. M.S.; D2453A (ID B.B.N.) Japan: Honshu, Kawasaki, 35.5666°N, 139.606°E, 14.iii.2010, ex *Osmanthus fragrans* (Thunb.) Lour., coll. A.O. ***Fissuraspis ulmi*** (Hoke) D5242B (ID B.B.N.) U.S.A.: Florida, Inglis, 29.1166°N, 82.7666°W, 21.ii.2015, ex *Ulmus americana*, coll. B.B.N., B. Denno. ***Froggatiella penicillata*** (Green) D0773C (ID D.R.M.) Australia: Queensland, Brisbane South Bank Parklands, 22.viii.2004, coll. G.E.M.; D1121AB (ID D.R.M.) U.S.A.: California, Costa Mesa, Scala Nursery, 14.viii.2002, ex *Bambusoidea* undet, coll. N. Nisson, L. Fernandez, J.F. Miller, D.R.M.; D2936A (ID B.B.N.) U.S.A.: Arizona, 5.vi.2010, ex *Bambusoidea* undet, coll. O'Sullivan. ***Froggatiella* ud4353** D3735A (ID B.B.N.) U.S.A.: Florida, N. Fort Myers, 17430 Durrance Rd., 26.7166°N, 81.7833°W, 6.x.2011, ex *Bambusa* sp., coll. M. Brodie, R. Blaney; D4340A (ID B.B.N.) U.S.A.: Florida, Punta Gorda: Bamboo Farm 25370 Zemel Rd (Block 44033), 26.8000°N, 82.0166°W, 9.xi.2011, ex *Bambusa* sp., coll. R. Blaney; D4341A (ID B.B.N.) U.S.A.: Florida, Punta Gorda: Bamboo Farm 25370 Zemel Rd (Block 44033), 26.8000°N, 82.0166°W, 9.xi.2011, ex *Bambusa* sp., coll. R. Blaney. ***Furcaspis biformis*** (Cockerell) D0813AB, D1031A (LotID T.K.) Jamaica, Ocho Rios, 4.ix.2003, ex *Pedilanthus* sp., coll. D.J. Williams, T.K. ***Furcaspis capensis*** (Walker) D3507A (ID B.B.N.) South Africa, Aberdeen, 18.vii.2011, ex *Aloe ferox* Mill., coll. N. Landman. ***Furcaspis cladii*** (Maskell) D1136C (lotID B.B.N.) Australia: Western Australia, nr Mt. Ragged camp site, 33.458°S, 123.455°E, 11.ix.2005, ex *Leptospermum* sp., coll. L.G. Cook. ***Furcaspis douglorum*** Okusu & Normark D3018C (ID B.B.N.) Panama: SL crane, 23.viii.2010, ex *Brosimum utile*, coll. G.E.M., B.B.N.; D3045B (ID B.B.N.) Panama: SL crane, 23.viii.2010, ex *Oenocarpus mapora*, coll. G.E.M., B.B.N. ***Furchadaspis zamiae*** (Morgan) D0455A (fieldID) U.S.A.: California, Davis, UC Davis campus, 38.5333°N, 121.75°W, 16.vi.2003, ex undet. Cycadales, coll. M.E. Gruwell, G.E.M., B.B.N.; D2940A (ID B.B.N.) U.S.A.: California, Rancho Santa Margarita, 8.vi.2010, ex *Cycas revoluta*, coll. Cortes. **Genus AB ud2098** D2098A (ID JD) Australia: New South Wales, 28.82416°S, 150.685°E, 1.vi.2007, ex *Eucalyptus* sp., coll. J.C.

Andersen, B.B.N. *Greeniella capitata* Brimblecombe D2009AB (lotID B.B.N.) Australia: Queensland, Maijala National Park, Browers Rd, 26.ii.2007, coll. R.D. Normark; D2046AB (ID B.B.N.) Australia: Queensland, Maijala NP, 27.32718°S, 152.764°E, 20.v.2007, coll. B.B.N. *Greeniella ud4454* D4454A Malaysia: LH crane, 7.viii.2013, ex *Dryobalanops aromatica* C.F. Gaertn., coll. G.E.M., B.B.N., D.A.P. *Gymnaspis aechmeae* Newstead D0235C (LotID T.K.) U.S.A.: Alabama, Auburn University, 28.ii.2002, coll. T.K.; D0315AB (lotID B.B.N.) U.S.A.: Florida, Davie: Univ. of FL Ft. Lauderdale Research & Education Center, 26.0841°N, 80.238°W, 20.xi.2002, ex undet. Bromeliaceae, coll. D.R.M., R.J.G., T.K., B. Sello, M.E. Gruwell, B.B.N.; D1906D (ID B.B.N.) U.S.A.: Florida, Gainesville, 4700 SW, 56th Dr., 16.ii.2010, ex undet. Bromeliaceae, coll. I.C.S. *Gymnaspis* sp. D3086A (ID B.B.N.) Panama: SL crane, 25.viii.2010, ex *Calophyllum longifolium* Willd., coll. G.E.M. *Haliaspis spartinae* (Comstock) [now *Duplacionaspis spartinae* (Comstock), **revived combination**] D2442A (ID B.B.N.) U.S.A.: Florida, Cedar Key, 29.152°N, 83.0493°W, 21.ii.2010, ex *Spartina alterniflora* Loisel., coll. A.O.; D2909A (ID B.B.N.) U.S.A.: New Jersey, Saltmarsh, 39.6752°N, 74.5403°W, 13.ix.2006, ex *Spartina patens* (Aiton) Muhl., coll. B.B.N. & R. A. Gwiazdowski. *Hemiberlesia andradae* Okusu & Normark D3069ABCDEF (ID B.B.N.) Panama: SL crane, 24.viii.2010, ex *Carapa guianensis*, coll. G.E.M., B.B.N. *Hemiberlesia candidula* (Cockerell) MD004A (ID D.R.M.) U.S.A.: Arizona, Entrance to Ramsey Canyon, corner Ramsey Canyon Road & Desert Storm Road, 22.iv.2006, ex *Prosopis juliflora* (Sw.) DC., coll. G.E.M., T.K. *Hemiberlesia cyanophylli* (Signoret) D0893ABC (ID B.B.N.) U.S.A.: California, Davis: UC Davis campus, in greenhouse, 23.vi.2005, ex *Theobroma cacao* L., coll. T.K. *Hemiberlesia flabellata* Ferris D1714B (ID D.R.M.) Mexico: Mexico, Distrito Federal, 19.3166°N, 99.1833°W, 31.viii.2007, ex *Pinus patula*, coll. R. A. Gwiazdowski, D. Gernandt; D1717A (ID B.B.N.) Mexico: Mexico, Hwy 95 South of Tres Marias, 19.0166°N, 99.259°W, 1.ix.2007, ex *Pinus pseudostrobus*, coll. R. A. Gwiazdowski, D. Gernandt; D1731B (ID B.B.N.) Mexico: Hidalgo, Hwy 85 N of Zimapan, 21.0333°N, 99.1166°W, 5.ix.2007, ex *Pinus teocote* Schltdl. & Cham., coll. R. A. Gwiazdowski, J. Rull. *Hemiberlesia lataniae* (Signoret) D0007 (lotID B.B.N.) U.S.A.: California, Sacramento, State Capitol grounds, 17.v.2000, ex *Hedera helix*, coll. R.J.G., B.B.N.; D0038AB (lotID B.B.N.) U.S.A.: California, W Sacramento, I-5 exit, 21.v.2000, ex *Ceanothus* sp., coll. D.J. Williams, D.R.M., P.J. Gullan, R.J.G., B.B.N.; D0066 (lotID R.C.H.) New Zealand: AK, Auckland, Glen Eden, 12.v.2001, ex *Rosa* sp., coll. R.C.H.; D0461A (ID B.B.N.) U.S.A.: California, Davis, UC Davis campus, 38.5333°N, 121.75°W, 16.vi.2003, ex undet. Rosaceae, coll. T.K.; D0766B (ID B.B.N.) Australia: Queensland, Lone Pine Koala Sanctuary, 27.53458°S, 152.969°E, 22.viii.2004, ex *Banksia robur* Cav., coll. G.E.M.; D0830A (ID B.B.N.) Argentina: Corrientes, Estancia Buena Vista, 30.xii.2004, ex *Nerium oleander*, coll. B.B.N.; D0994A (ID B.B.N.) U.S.A.: Florida, Davie, 26.0846°N, 80.2378°W, 18.xii.2005, ex undet. Arecaceae, coll. T.K.; D1017AB (lotID B.B.N.) Mexico: Tamaulipas, 1 km N Gomez Farias town center, 18.iii.2005, ex *Heliconia* sp., coll. M.E. Gruwell; D1718B (ID B.B.N.) Mexico: Mexico, Hwy 95 South of Tres Marias, 19.0166°N, 99.2586°W, 1.ix.2007, ex *Pinus pseudostrobus*, coll. R. A. Gwiazdowski, D. Gernandt; D2022A (lotID B.B.N.) Australia: Queensland, Mt Glorious, 27.31666°S, 152.75°E, 28.iv.2007, ex *Acacia melanoxylon* R. Br., coll. B.B.N.; D2760A (ID B.B.N.) Mexico: San Jose, 7.vii.2010, ex *Persea americana*, coll. J. Powers; D3773A (ID B.B.N.) Mexico, 5.i.2012, ex *Persea americana*, coll. T. Clerc; D3777A (ID B.B.N.) Mexico, 6.i.2012, ex *Persea americana*, coll. P. Sullivan; D3781A (ID B.B.N.) Mexico, 23.v.2012, ex *Citrus x paradisi*, coll. J. Moore; D4334A (ID B.B.N.) Cuba, 2.v.2012, ex *Annona cherimola* Mill., coll. M. Flores; D4343A (ID B.B.N.) U.S.A.: Florida, Pembroke Pines: 130 N University Dr (Block # 43746), 14.viii.2012, ex *Beaucarnea recurvata* Lem., coll. S. Alspach. *Hemiberlesia mendax* McKenzie D0555A (ID B.B.N.) Argentina: La Pampa, Santa Rosa, 8.ii.2003, ex *Euonymus japonicus* Thunb., coll. L.E.C., P. Zamudio, L. Díaz-Briz, Guardia Claps. *Hemiberlesia musae* Takagi & Yamamoto D2957A (ID B.B.N.) Brazil, 17.vi.2010, ex *Persea americana*, coll. E. Camero; D4149A (ID B.B.N.) Panama: SL crane, 20.vi.2012, ex *Brosimum utile*, coll. G.E.M., B.B.N. *Hemiberlesia near palmae* D3088A (ID D.R.M.) Panama: SL crane, 25.viii.2010, ex *Abarema barbouriana* (Standl.) Barneby & J.W. Grimes, coll. G.E.M. *Hemiberlesia palmae* (Cockerell) D0246A (LotID T.K.) Colombia: Valle del Cauca, Cali, 9.iii.2002, ex undet. Bromeliaceae, coll. T.K.; D0947A (ID D.R.M.) Mexico: Tamaulipas, 23.066°N, 99.1605°W, 16.iii.2005, ex *Ficus* sp., coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N.; D1186A, D1187B (ID D.R.M.) Malaysia, intercepted at San Francisco 16.xii.2008, ex *Podocarpus* sp; D2499A (ID B.B.N.) Fiji: Viti Levu, Suva, University of S.P. campus, 13.ix.2009, coll. C.J. Hodgson; D3058A (ID D.R.M.) Panama: SL crane, 24.viii.2010, ex *Marila laxiflora*, coll. G.E.M., B.B.N.; D4183A (ID B.B.N.) Panama: SL crane, 18.vi.2012, ex *Cespedesia macrophylla* Seem., coll. G.E.M., B.B.N. *Hemiberlesia popularum* (Marlatt) D0801A (ID D.R.M.) U.S.A.: Utah, Coal Pits Wash at Hwy 9, 37.1706°N, 113.0813°W, 19.xi.2004, ex *Baccharis salicifolia* (Ruiz & Pav.) Pers., coll. M.E.

Gruwell, R. A. Gwiazdowski, B.B.N.; D2724A (ID B.B.N.) U.S.A.: California, 38.1743°N, 120.399°W, 23.v.2010, ex *Ceanothus integerrimus*, coll. A.O. ***Hemiberlesia rapax*** (Comstock) D0271 (lotID L.E.C.) Argentina: Chubut, PN Lago Puelo: Sendero Mirador, 1.xii.2001, ex *Discaria articulata* (Phil.) Miers, coll. L.E.C., L. Díaz-Briz; D0298A (LotID L.E.C.) Argentina: Mendoza, Entre El Sosneado & Laguna Niña Encantada, 23.xi.2001, ex *Colliguaya* sp., coll. L.E.C., L. Díaz-Briz; D2142A (ID B.B.N.) Portugal, Oeiras, 38.6955°N, 9.3178°W, 27.ix.2007, ex *Acacia* sp., coll. M.E. Gruwell; D2143C (ID B.B.N.) Portugal, Oeiras, 38.6955°N, 9.3178°W, 27.ix.2007, ex *Nerium oleander*, coll. M.E. Gruwell; D2173B (ID D.R.M.) Portugal, Oeiras, 38.6955°N, 9.3178°W, 26.ix.2007, ex *Cercis* sp., coll. T.K., M.E. Gruwell. ***Hemiberlesia* sp.** D0998A (ID B.B.N.) Mexico: Tamaulipas, 23.0841°N, 99.1316°W, 16.iii.2005, coll. R. Van Driesche. ***Hemiberlesia* ud0288** D0288A (lotID B.B.N.) Argentina: Jujuy, Humahuaca, camino a Aparzo, 14.ii.2002, coll. L.E.C. ***Hemiberlesia* ud4001** D3025B (ID D.R.M. query), D3035A (ID B.B.N. query) Panama: SL crane, 23.viii.2010, ex *Tapirira guianensis*, coll. G.E.M., B.B.N.; D3033A (ID B.B.N. query) Panama: SL crane, 23.viii.2010, ex *Poulsenia armata* (Miq.) Standl., coll. G.E.M., B.B.N.; D3038A (ID B.B.N. query) Panama: SL crane, 23.viii.2010, ex *Apeiba aspera* Aubl., coll. G.E.M., B.B.N.; D4001AB (ID B.B.N. query) Panama: SL crane, 15.vi.2012, ex *Terminalia amazonia* (J.F. Gmel.) Exell, coll. G.E.M., B.B.N.; D4153A (ID B.B.N.) Panama: SL crane, 20.vi.2012, ex *Virola multiflora* (Standl.) A.C. Sm., coll. G.E.M., B.B.N. ***Hemigymnaspis* ud3973** D3973H (ID B.B.N.) Panama: SL crane, 14.vi.2012, ex *Perebea xanthochyma* H. Karst., coll. G.E.M., B.B.N.; D4038BD (ID B.B.N.) Panama: SL crane, 14.vi.2012, ex *Maquira guianensis* Aubl., coll. G.E.M., B.B.N.; D4292A (ID B.B.N.) Panama: SL crane, 21.vi.2012, ex *Tovomita longifolia*, coll. G.E.M., B.B.N. ***Howardia biclavis*** (Comstock) D0229ABC (LotID T.K.) Colombia: Valle del Cauca, Cali, 29.xii.2001, ex *Solanum* sp., coll. T.K.; D0344CE (ID B.B.N.) U.S.A.: Florida, Homestead: Univ. of FL Tropical Research & Education Center, 25.5076°N, 80.5008°W, 22.xi.2002, coll. B. Sello, M.E. Gruwell, B.B.N.; D0958A (ID B.B.N.) U.S.A.: Florida, Belle Glade, 26.6751°N, 80.67°W, 12.xii.2005, coll. M.E. Gruwell. ***Ichthyaspis ficicola*** (Takahashi) [now ***Fiorinia ficicola*** (Takahashi), **new combination**] D0391ABD (lotID D.R.M.) Japan: Ryukyu Islands, Kunigashira Village, 4.ix.2001, ex *Ficus oxyphylla* Miq., coll. M.S. ***Ischnafiorinia bambusae*** (Maskell) D3313B (ID B.B.N.) Hong Kong, Bowen Rd., 17.ii.2011, ex *Bambusa vulgaris* Schrad. ex J.C. Wendl., coll. C.S.K. Lau. ***Ischnaspis longirostris*** (Signoret) D0230 (lotID B.B.N.) Colombia: Valle del Cauca, Cali, 29.xii.2001, ex *Bauhinia purpurea* L., coll. T.K.; D1845B (ID B.B.N.) Mexico: Tamaulipas, 23.066°N, 99.1605°W, 16.iii.2005, ex *Ficus* sp., coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N.; D4262A (ID B.B.N.) Panama: SL crane, 20.vi.2012, ex *Guatteria dumetorum* R.E. Fr., coll. G.E.M., B.B.N. ***Kuwanaspis hikosani*** (Kuwana) D1900A (ID D.R.M.) U.S.A.: Florida, Gainesville, 4700 SW, 56th Dr., 16.ii.2010, ex *Arundinaria* sp., coll. I.C.S.; D1901AC (ID B.B.N.) U.S.A.: Florida, Gainesville, 4700 SW, 56th Dr., 16.ii.2010, ex *Arundinaria* sp., coll. I.C.S.; D2468BE (ID B.B.N.) Japan: Kyushu, Mt. Konosu, 33.5566°N, 130.383°E, 16.iii.2010, ex *Sasa* sp., coll. A.O. ***Kuwanaspis howardi*** (Cooley) D4838IJ (ID D.R.M.) Malaysia: Sarawak, Lambir Hills NP, 4.1964°N, 114.040°E, 17.viii.2013, ex *Bambusoidea* undet, coll. G.E.M., B.B.N., D.A.P. ***Kuwanaspis pseudoleucaspis*** (Kuwana) D0723A (ID D.R.M.) New Zealand, NZAK: Glen Eden, 19.ix.2004, ex *Phyllostachys bambusoides* Siebold & Zucc., coll. R.C.H.; D2670A (ID D.R.M.) Netherlands, 7.v.2009, ex *Fargesia* sp., coll. F. Orozco. ***Kuwanaspis* sp.** D4840A Malaysia: Sarawak, Lambir Hills NP, 4.1964°N, 114.040°E, 17.viii.2013, ex *Bambusoidea* undet, coll. G.E.M., B.B.N., D.A.P. ***Kuwanaspis takahashii*** Takagi D0398AB (lotID MS) Japan: Kyushu, Ibusuki City, Kagoshima Pref., 13.x.2001, ex *Pleioblastus simonii* (Carrière) Nakai, coll. M.S. ***Kuwanaspis vermiformis*** (Takahashi) D4838A (ID B.B.N. query), D4840D (ID D.R.M. query) Malaysia: Sarawak, Lambir Hills NP, 4.1964°N, 114.040°E, 17.viii.2013, ex *Bambusoidea* undet, coll. G.E.M., B.B.N., D.A.P. ***Labidaspis myersi*** (Green) D0645A (lotID R.C.H.) New Zealand, NZAK, Waitakere Range, Fairy Falls Track, 16.v.2004, ex *CollospERMUM hastatum* (Colenso) Skotts., coll. R.C.H. ***Lepidosaphes beckii*** (Newman) D0270 (LotID L.E.C.) Argentina: Tucumán, Yerba Buena, 30.xii.2001, ex *Citrus limon*, coll. L.E.C.; D5054A (ID B.B.N.) Indonesia: Sulawesi, Pakpak Barat, 22.vi.2013, ex *Citrus* sp., coll. E. Benson. ***Lepidosaphes chinensis*** Chamberlin D3310A (ID B.B.N.) China, on nursery stock, 10.ii.2011, coll. B. Oliver. ***Lepidosaphes euryae*** (Kuwana) D2475A (ID B.B.N. query) Japan: Kyushu, Kakinoura Island, 33.0166°N, 129.566°E, 19.iii.2010, coll. A.O. ***Lepidosaphes gloverii*** (Packard) D0266B (LotID L.E.C.) Argentina: Tucumán, Yerba Buena, 30.xii.2001, ex *Citrus limon*, coll. L.E.C.; D0343B (ID D.R.M.) U.S.A.: Florida, Homestead: Univ. of FL Tropical Research & Education Center, 25.5076°N, 80.5008°W, 22.xi.2002, coll. B. Sello, M.E. Gruwell, B.B.N.; D0899B (ID D.R.M.) Mexico: Tamaulipas, Gomez Farias, 12.iii.2005, ex *Citrus* sp., coll. M.E. Gruwell, R. A. Gwiazdowski; D1923A (ID D.R.M.), D1926A (ID J.W.D.) U.S.A.: Florida, Gainesville, UFL Hort. Sci. Dept. Res. Citrus Grove, 29.6333°N,

82.358°E, 18.ii.2010, ex *Citrus* sp., coll. I.C.S., B.B.N., A.O., L. Buss; D1948A (ID B.B.N.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk., 29.7166°N, 82.452°E, 18.ii.2010, ex *Symplocos tinctoria* (L.) L'Hér., coll. A.O. ***Lepidosaphes granati*** Koroneos D0622D (ID D.R.M.) Turkey: Nevsehir, Göreme ("Cappadoccia), 22.iv.2004, ex *Crataegus* sp., coll. T.K. ***Lepidosaphes japonica*** (Kuwana) D1869A (ID D.R.M.) Japan: Honshu, small roadside shrine, *Adelges tsugae* holotype host tree, 10.v.2009, ex *Tsuga sieboldii*, coll. K. Abell. ***Lepidosaphes laterochitinsa*** Green D2651A (ID D.R.M.) Malaysia, 20.i.2010, ex *Dracaena massangeana* Rodigas, coll. Natahsa Pyle; D3380BC (lotID GA Evans) Costa Rica, 13.ix.2010, ex *Sansevera* sp., coll. M. Roman. ***Lepidosaphes newsteadi*** (Šulc) D0614A (lotID B.B.N.) Turkey: Adana, Çukurova University, 37.0611°N, 35.358°E, 20.iv.2004, ex *Pinus* sp., coll. B.B.N., G.E.M., M.E. Gruwell. ***Lepidosaphes pallida*** (Maskell) D0724A (ID D.R.M.) New Zealand, NZAK, Mt. Albert summit, 24.vii.2004, ex *Cryptomeria japonica*, coll. R.C.H.; D2473AD (ID D.R.M.) Japan: Kyushu, Mt. Konosu, 33.5566°N, 130.383°E, 16.iii.2010, ex *Cryptomeria japonica*, coll. A.O.; D2483C (ID B.B.N.) Japan: Kyushu, Kawahara Ooike, 32.5666°N, 129.733°E, 20.iii.2010, ex *Cryptomeria japonica*, coll. A.O.; D3705A (ID B.B.N.) Japan: Kyushu, Heiwa Sanso, 33.5566°N, 130.383°E, 13.v.2012, ex *Podocarpus macrophyllus*, coll. A.O. ***Lepidosaphes pini*** (Maskell) D0812AB (ID D.R.M.) U.S.A.: Massachusetts, Amherst, UMass, Student Union Bldg., 24.xi.2004, ex *Pinus* sp., coll. R. A. Gwiazdowski. ***Lepidosaphes piniphila*** Borchsenius D1182A (ID D.R.M. query) Malaysia, quarantine interception at San Francisco, ex *Cupressus* sp., coll. S. Jarman (interception APWCA083532636007). ***Lepidosaphes pinnaeformis*** (Bouché) D0373AD (lotID D.R.M.) Japan: Kyushu, Hisayama Town, Fukuoka Pref., 17.iv.2001, ex *Persea thunbergii* (Siebold & Zucc.) Kosterm., coll. M.S. ***Lepidosaphes pseudotsugae*** Takahashi D0823B (ID B.B.N.) Japan, Onsen: Mt. Manza, 18.viii.2004, coll. S. Lyon; D1870A (ID D.R.M.) Japan: Honshu, 25.v.2009, ex *Tsuga diversifolia*, coll. K. Abell; D1871A (ID B.B.N.) Japan: Honshu, Mt. Hakoda, Ishikua peak, south facing slope, 15.v.2009, ex *Tsuga diversifolia*, coll. K. Abell. ***Lepidosaphes rubrovittata*** Cockerell D3036A (ID D.R.M.) Panama: SL crane, 23.viii.2010, ex *Tapirira guianensis*, coll. G.E.M., B.B.N. ***Lepidosaphes smilacis*** Takagi D2492A (ID B.B.N. query) Japan: Kyushu, Kawahara Ooike, 32.5666°N, 129.733°E, 24.iii.2010, ex *Camellia* sp., coll. A.O.; D2492B (ID B.B.N.) Japan: Kyushu, Kawahara Ooike, 32.5666°N, 129.733°E, 24.iii.2010, ex *Camellia* sp., coll. A.O.; D3223B (ID B.B.N. query) Japan: Kyushu, Mt. Wakasugi, 33.6216°N, 130.533°E, 23.xi.2010, coll. A.O. ***Lepidosaphes* sp.** D1167E Ghana, Busco Arboretum, 6.2633°N, 0.4655°W, 19.vi.2005, ex *Citrus limon*, coll. G.E.M.; D1168C Ghana, Busco Arboretum, 6.2633°N, 0.4655°W, 19.vi.2005, ex *Theobroma cacao*, coll. G.E.M.; D2039A Australia: Queensland, St. Lucia: UQ Campus, 27.50033°S, 153.012°E, 8.v.2007, ex *Casuarina glauca*, coll. B.B.N. ***Lepidosaphes tokionis*** (Kuwana) D5046A (ID B.B.N.) Indonesia: Sulawesi, Manado, 27.vi.2013, ex *Croton* sp., coll. R. Muniappan. ***Lepidosaphes ud2005*** D2005C (ID B.B.N.) Australia: Tasmania, 43.39033°S, 147.261°E, 25.i.2007, ex *Monotoca* sp., coll. B.B.N. ***Lepidosaphes ud3538*** D3538A (ID B.B.N. query) Indonesia: Sulawesi, Mekongga, 1700m alt. helipad site, 5.vii.2011, coll. L.S. Kimsey. ***Lepidosaphes ud4835*** D4835AD (ID B.B.N.) Malaysia: Sarawak, Lambir Hills NP, 4.1964°N, 114.040°E, 16.viii.2013, coll. G.E.M., D.A.P., B.B.N. ***Lepidosaphes ulmi*** (Linnaeus) D0624A (lotID B.B.N.) Turkey: Nevsehir, Göreme, 38.6426°N, 34.831°E, 23.iv.2004, ex *Juglans* sp., coll. B.B.N., G.E.M., C.J. Hodgson; D0637AC (lotID D.R.M.) Turkey: Osmaniye, Osmaniye, 37.0565°N, 36.195°E, 24.iv.2004, ex *Rosa* sp., coll. G.E.M., T.K.; D1406BC (ID D.R.M.) U.S.A.: Washington, 11 mi NW Leavenworth: Tumwater Campground, 16.viii.2006, ex *Cornus stolonifera* Michx., coll. B.B.N., R.D. Normark; D1407AB (ID D.R.M.) U.S.A.: Washington, 11 mi NW Leavenworth: Tumwater Campground, 16.viii.2006, ex *Acer circinatum* Pursh, coll. B.B.N., R.D. Normark; D1408B (ID B.B.N.) U.S.A.: Washington, 11 mi NW Leavenworth: Tumwater Campground, 16.viii.2006, ex *Salix* sp., coll. B.B.N., R.D. Normark; D1412A (ID B.B.N.) U.S.A.: Washington, 11 mi NW Leavenworth: Tumwater Campground, 16.viii.2006, ex *Alnus sinuata* (Regel) Rydb., coll. B.B.N., R.D. Normark; D1416C (ID B.B.N.) U.S.A.: Washington, 1 mi SE Plain, 16.viii.2006, ex *Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem., coll. B.B.N., R.D. Normark; D2413B (ID D.R.M.) U.S.A.: Massachusetts, Granville, 42.0758°N, 72.846°W, 7.v.2009, ex *Betula papyrifera* Marshall, coll. K. Parks; D2521A (ID D.R.M.) U.S.A.: Pennsylvania, 21.viii.2009, ex *Cornus stolonifera*, coll. J. Wu; D2523A (ID B.B.N.) U.S.A.: Pennsylvania, 21.viii.2009, ex *Amelanchier alnifolia*, coll. J. Wu; D2746B (ID B.B.N.) U.S.A.: Massachusetts, Montague, 42.5155°N, 72.5133°W, 19.vii.2010, ex *Fagus grandifolia* Ehrh., coll. B.B.N., A. Krewinski, A.O., R. Carlton; D2747A (ID B.B.N.) U.S.A.: Massachusetts, Montague, 42.5178°N, 72.494°W, 19.vii.2010, ex *Acer rubrum* L., coll. B.B.N., A. Krewinski, A.O., R. Carlton; D2750A (ID B.B.N.) U.S.A.: Massachusetts, Montague, 42.5181°N, 72.4935°W, 19.vii.2010, ex *Acer rubrum*, coll. B.B.N., A. Krewinski, A.O., R. Carlton. ***Lepidosaphes yanagicola*** Kuwana D0750ADE (ID B.B.N.) U.S.A.:

Massachusetts, Amherst: W. Slope Mt. Norwotock @ 750 ft. elevation; Metacomet-Monadnock Trail & Robert Frost Trail; at border with Town of Granby, 3.x.2004, ex *Tilia americana* L., coll. B.B.N.; D2728C (ID B.B.N.) U.S.A.: Massachusetts, Amherst, 42.3875°N, 72.5221°W, 27.v.2010, coll. R. A. Gwiazdowski. ***Leucaspis cordylinidis*** Maskell D0648A (lotID R.C.H.) New Zealand, NZAK, Auckland, New Lynn, Lynn mall, 5.vii.2004, ex *Cordyline australis* Hook. f., coll. N.A. Martin. ***Leucaspis lowi*** Colvée D0689A (lotID I.G.) Russia, Voronezh, 21.v.2004, ex *Pinus sylvestris* L., coll. I.G. ***Leucaspis morrisoni*** (Brittin) D0650A (lotID R.C.H.) New Zealand, NZAK, University of Auckland [city campus], 4.vi.2004, coll. C. Inglis. ***Leucaspis ohakunensis*** Brittin D0039D (lotID B.B.N.) New Zealand, To, Ohakune, 39.41666°S, 175.383°E, 18.xii.2000, ex *Pseudopanax arboreus* (L. f.) K. Koch, coll. P.J. Gullan; D0040ABC (lotID B.B.N.) New Zealand, Dry Lake at Rotokuru Ecol. Reserve, 39.43333°S, 175.516°E, 18.xii.2000, ex *Pseudopanax arboreus*, coll. P.J. Gullan; D0658A (lotID R.C.H.) New Zealand, NZAK, Waitakere Range, Destruction Gully Track, 19.vi.2004, ex *Cyathodes juniperina* Druce, coll. R.C.H. ***Leucaspis podocarpi*** Green D0735D (ID D.R.M.) New Zealand, NZMC, Lincoln, Canterbury Agricultural Research Centre, 21.viii.2004, ex *Podocarpus totara* G. Benn. ex D. Don, coll. N.A. Martin. ***Leucaspis pusilla*** Löw D0596BC, D0597C (lotID B.B.N.), D0596D, D0597D (ID B.B.N.) Turkey: Adana, Çukurova University, 37.0611°N, 35.358°E, 19.iv.2004, ex *Pinus* sp., coll. B.B.N., G.E.M., M.E. Gruwell; D0625D (ID B.B.N.), D0628A (lotID B.B.N.) Turkey: Osmaniye, Karatepe-Aslantas National Park, 37.2947°N, 36.248°E, 24.iv.2004, ex *Pinus nigra*, coll. B.B.N., G.E.M., M.E. Gruwell; D2172B (ID D.R.M.) Portugal, Oeiras, 38.6955°N, 9.3178°W, 26.ix.2007, ex *Pinus* sp., coll. T.K., M.E. Gruwell; D2195A (ID B.B.N.) Greece: Crete, Near Aredena, 35.2243°N, 24.039°E, 8.iv.2010, ex *Pinus brutia* Ten., coll. B.B.N., M.B. Kaydan. ***Leucaspis signoreti*** Targioni Tozzetti D0633AC (lotID B.B.N.) Turkey: Osmaniye, Karatepe-Aslantas National Park, 37.2947°N, 36.248°E, 24.iv.2004, ex *Pinus nigra*, coll. C.J. Hodgson. ***Leucaspis ud0647*** D0647A (lotID R.C.H.) New Zealand, AK, Titirangi, Ngaio Rd., 13.vi.2004, ex *Dacrydium cupressinum* Sol. ex G. Forst., coll. R.C.H. ***Leucaspis ud0652*** D0729A (lotID R.C.H.) New Zealand, NZAK: Titirangi, 21 Ngaio Rd., 27.vii.2004, ex *Dacrydium cupressinum*, coll. R.C.H. ***Leucaspis ud0660*** D0660A (lotID R.C.H.) New Zealand, NZAK, Waitakere Range, Manukau Bar View Walk, 19.vi.2004, ex *Melicoccus ramiflorus* J.R. Forst. & G. Forst., coll. R.C.H.; D0730A (lotID R.C.H.) New Zealand, NZAK: North Piha, 11.vii.2004, ex *Phormium tenax* J.R. Forst. & G. Forst., coll. R.C.H. ***Leucaspis ud0725*** D0731ABD (lotID R.C.H.) New Zealand, NZMC, Lincoln, Canterbury Agricultural Research Centre, 21.viii.2004, ex *Podocarpus totara*, coll. N.A. Martin. ***Leucaspis ud0728*** D0728AB (lotID R.C.H.) New Zealand, NZAK: Titirangi, 21 Ngaio Rd., 27.vii.2004, ex *Dacrydium cupressinum*, coll. R.C.H. ***Lindingaspis floridana*** Ferris D0335A (fieldID D.R.M.), D0338B (ID G.W.W.) U.S.A.: Florida, Davie: Univ. of FL Ft. Lauderdale Research & Education Center, 26.0841°N, 80.238°W, 21.xi.2002, coll. B. Sello, M.E. Gruwell, B.B.N.; D4456B (ID B.B.N.) Malaysia: LH crane, 7.viii.2013, ex *Blumeodendron calophyllum*, coll. G.E.M., B.B.N., D.A.P. ***Lindingaspis rossi*** (Maskell) D0738B (ID D.R.M.) New Zealand, NZAK, Auckland, Carbine Rd, 26.vii.2004, coll. C. Inglis; D0753ABC (ID B.B.N.) Australia: New South Wales, 5 km NW Molong, 33.06666°S, 148.816°E, 13.viii.2004, ex *Styphelia* sp., coll. C. Unruh; D0828B (ID D.R.M. query) Argentina: Buenos Aires, Hurlingham, Hurlingham Club, 23.xii.2004, ex *Nerium oleander*, coll. B.B.N.; D2073A (ID JD) Australia: Queensland, 28.49926°S, 150.193°E, 31.v.2007, ex *Geijera parviflora*, coll. J.C. Andersen, B.B.N.; D2127A (ID B.B.N.) Australia: Queensland, Girraween NP: Dr. Roberts carpark, 28.82866°S, 151.973°E, 2.vi.2007, coll. J.C. Andersen, B.B.N. ***Lineaspis striata*** (Newstead) D0593ABC (lotID B.B.N.) Turkey: Adana, Seyhan River, Center of Adana, from Stone Bridge northwards ~1km, 18.iv.2004, ex undet. Cupressaceae, coll. B.B.N., M.E. Gruwell; D2199A (ID B.B.N.) Greece: Episkopi, 3.iv.2010, ex *Cupressus sempervirens* L., coll. C.J. Hodgson; D2497A (ID B.B.N.) Greece: Crete, Apta, 1.iv.2010, coll. C.J. Hodgson. ***Lopholeucaspis cockerelli*** (Grandpré & Charmoy) 3 2nd-instar females D3002AB, D3007A (ID B.B.N. query) Panama: SL crane, 21.viii.2010, ex *Brosimum utile*, coll. G.E.M., B.B.N.; 1 adult female D3530A (ID B.B.N.) U.S.A.: Hawaii, 21.viii.2011, coll. J. Wagner. ***Lopholeucaspis japonica*** (Cockerell) D1107B (ID D.R.M.) U.S.A.: Maryland, Beltsville, USDA Facility, 39.0166°N, 76.9166°W, 7.vi.2006, ex *Malus* sp., coll. D.R.M. ***Maskellanna ud0781*** D0781BD Australia: Queensland, Cape Tribulation Canopy Crane, 25.viii.2004, ex *Syzygium sayeri* (F. Muell.) B. Hyland, coll. G.E.M. ***Maskellia globosa*** Fuller D0751A (lotID PJG) Australia: Queensland, Goondiwindi tourist park, 15.viii.2004, ex *Eucalyptus populnea*, coll. N.B. Hardy. ***Megacanthaspis actinodaphnes*** Takagi D0401A, D0402B (lotID MS), D0401E (ID B.B.N.) Japan, Takayama Town, Kagoshima Pref., 14.iv.2002, ex *Litsea acuminata* Litsea acuminata, coll. M.S. ***Melanaspis bromiliae*** Leonardi D0254A (lotID T.K.) U.S.A.: Alabama, Auburn University, 1.iv.2002, ex *Ananas comosus* (L.) Merr., coll. P. Tyler. ***Melanaspis inopinata*** (Leonardi) D0603A (ID B.B.N.), D604A (lotID B.B.N.) Turkey:

Adana, Çukurova University, 37.0611°N, 35.358°E, 21.iv.2004, coll. T.K.; D0631B (ID B.B.N.) Turkey: Osmaniye, Karatepe-Aslantas National Park, 37.2947°N, 36.248°E, 24.iv.2004, ex *Cercis* sp., coll. T.K., ME Gruwell; D0636C (ID B.B.N.) Turkey: Osmaniye, Karatepe-Aslantas National Park, 37.2947°N, 36.248°E, 24.iv.2004, ex *Pistacia* sp., coll. B.B.N., G.E.M. ***Melanaspis madagascariensis*** Mamet D1886ABC (ID Y.B.D.) Madagascar: Toliara, Tsimanam Petsotsa, Mitoho, 6.4 km 77 ENE Efoetse, 24.05°S, 43.766°E, 22.iii.2002, ex undet Euphorbiaceae, coll. B. Fisher; D1889ABD (lotID Y.B.D.) Madagascar: Toliara, Forêt Mîte, 20.7 km 29 WNW, 23.51666°S, 44.116°E, 3.iii.2002, ex undet Euphorbiaceae, coll. B. Fisher. ***Melanaspis obscura*** (Comstock) D0249ABD (ID B.B.N.) U.S.A.: Alabama, Auburn University, 17.iii.2002, ex *Quercus palustris* Münchh., coll. T.K.; D0251C (LotID T.K.) U.S.A.: Alabama, Auburn University, 19.iii.2002, coll. T.K.; D0982A (ID D.R.M.) U.S.A.: Florida, 27.2993°N, 80.6439°W, 14.xii.2005, ex *Quercus chapmanii* Sarg., coll. M.E. Gruwell; D2844A (ID B.B.N.) U.S.A.: Florida, Natural Area Dr next to Entomology & Nematology Bldg., Gainesville, 26.iii.2010, ex *Quercus shumardii* Buckley, coll. L. Buss. ***Melanaspis odontoglossi*** (Cockerell) D3089B Panama: SL crane, 25.viii.2010, ex *Jacaranda copaia*, coll. G.E.M. ***Melanaspis smilacis*** (Comstock) D1984B (ID B.B.N.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk, 29.7095°N, 82.4551°W, 20.ii.2010, ex *Smilax* sp., coll. A.O. ***Melanaspis* sp.** D1888AB Madagascar: Toliara, Bevazoa, 12.7 Km, 287 W, 25.53666°S, 49.15°E, 17.ii.2002, ex undet Euphorbiaceae, coll. B. Fisher. ***Melanaspis tenebricosa*** (Comstock) D0247A (LotID T.K.) U.S.A.: Alabama, Auburn University, 17.iii.2002, ex *Acer rubrum*, coll. T.K. ***Melanaspis ud0276*** D0264C (ID B.B.N.) Argentina: Jujuy, Humahuaca, camino a Aparzo, 14.ii.2002, coll. L.E.C.; D0272C (ID B.B.N.) Argentina: Jujuy, entre Maimar & Tilcara, 13.ii.2002, coll. L.E.C.; D0275G, D0276E (ID B.B.N.) D0297A (lotID B.B.N.) Argentina: Jujuy, Humahuaca, 12.ii.2002, coll. L.E.C.; D0291A (lotID B.B.N.) Argentina: Jujuy, Humahuaca: entrada a Huella, 14.ii.2002, coll. L.E.C., P. Zamudio, L. Díaz-Briz, P. Cabrera. ***Melanaspis ud3977*** D3977F (ID B.B.N.) Panama: SL crane, 13.vi.2012, ex *Ocotea ira*, coll. G.E.M., B.B.N. ***Melissoaspis fisheri*** Ben-Dov D1885ADF (lotID Y.B.D.), D1885BCE (ID Y.B.D.) Madagascar: Toliara, Forest Bealoka, 14.6 km 329 NNW Amboasary, 24.95°S, 46.266°E, 8.ii.2002, ex undet Euphorbiaceae, coll. B. Fisher; D1895A (ID Y.B.D.) Madagascar: Toliara, Forêt Mîte 20.7 km 29 WNW, 23.51666°S, 44.116°E, 27.iii.2002, ex undet Euphorbiaceae, coll. B. Fisher; D1897A (lotID Y.B.D.), D1897CD (ID Y.B.D.) Madagascar: Toliara, Andohahela National Park, Manantalinjo, 7.6 km 99 E Hazofotsy, 24.81666°S, 46.616°E, 16.i.2002, ex undet Euphorbiaceae, coll. B. Fisher; D2733B (lotID B.B.N.), D2733C (ID B.B.N.) Madagascar: Toliara, Reserve Prive Berenty, Foret de Bealoka, Mandrare River, 24.95416°S, 46.266°E, 3.viii.2002, coll. B. Fisher. ***Metandaspis recurvata*** (Froggatt) [now ***Lepidosaphes recurvata*** (Froggatt), **revived combination**] D5286AEFK (ID B.B.N. query) Australia: Queensland, 27.71666°S, 150.352°E, 26.vii.2014, ex *Acacia harpophylla*, coll. B.B.N., D.A.P. ***Microparlatoria fici*** (Takahashi) D5053A (ID B.B.N.) Indonesia: Sulawesi, Manado, 30.vi.2013, ex *Ficus* sp., coll. R. Muniappan. ***Microparlatoria ud5020*** D5020G (ID B.B.N.) Malaysia: LH crane, 21.viii.2013, ex *Shorea laxa* Sloot., coll. B.B.N., D.A.P. ***Mimeraspis ud2101*** D2101D (ID B.B.N.) Australia: New South Wales, 38.911°S, 150.960°E, 1.vi.2007, ex *Acacia spectabilis* A. Cunn. ex Benth., coll. J.C. Andersen, B.B.N. ***Mimeraspis ud5345*** D5345AE (ID B.B.N. query) Australia: Queensland, Daintree Rainforest Observatory Canopy Crane, 16.24666°S, 145.433°E, 1.viii.2014, ex *Cleistanthus myrianthus* (Hassk.) Kurz, coll. G.E.M., B.B.N., DAP. ***Mitulaspis funtumiae*** (Newstead) D2941A (ID B.B.N.) Malaysia: Kuala Lumpur, 18.vi.2009, ex *Nerium oleander*, coll. Hanifah; D3287A (lotID G.W.W.) Malaysia: Kuala Lumpur, 18.vi.2009, ex *Nerium oleander*, coll. Hanifah. ***Monaonidiella* sp.** D2109A Australia: New South Wales, 29.01385°S, 151.706°E, 1.vi.2007, ex *Ozothamnus diosmifolius* (Vent.) DC., coll. J.C. Andersen, B.B.N. ***Monaonidiella ud2056*** D2056B (ID B.B.N.) Australia: Queensland, near Yelarbon, 28.49883°S, 150.566°E, 30.v.2007, ex *Acacia harpophylla*, coll. J.C. Andersen, B.B.N. ***Morganella conspicua*** (Brain) D1874A (ID B.B.N.), D1874B (ID Y.B.D.), D1874C (lotID Y.B.D.) Madagascar: Toliara, Forêt Anja Polo, 21.4 km 325° NW Amboasary, 24.93333°S, 46.216°E, 7.ii.2002, ex undet Euphorbiaceae, coll. B. Fisher; D1879A (ID Y.B.D.) Madagascar: Toliara, Forêt Mîte, 20.7 km 29 WNW, 23.51666°S, 44.116°E, 3.iii.2002, ex undet Euphorbiaceae, coll. B. Fisher; D1881AD (ID Y.B.D.) Madagascar: Toliara, L. Bonano to Iganaro, 25.03333°S, 46.983°E, 1.x.2001, coll. D.O. Burgh; D1891A (ID B.B.N.) Madagascar: Toliara, Andohahela, 1.7 km, 61 ENE Tsimelahy, 24.93333°S, 46.65°E, 20.i.2002, ex undet Euphorbiaceae, coll. B. Fisher; D1898AB (ID Y.B.D.) Madagascar: Toliara, Andohahela National Park, Manantalinjo, 7.6 km 99 E Hazofotsy, 24.81666°S, 46.616°E, 16.i.2002, ex undet Euphorbiaceae, coll. B. Fisher. ***Morganella longispina*** (Morgan) D0393B (ID B.B.N.) Japan, Sasaguri Town, Fukuoka Pref., 17.ix.2001, ex *Acer palmatum* Thunb., coll. M.S.; D2654A (ID B.B.N.) China, 14.i.2010, ex *Magnolia* sp., coll. N. Pyle. ***Mycetaspis personata*** (Comstock) D0228A (LotID T.K.) Colombia: Valle del Cauca,

Cali, 30.xii.2001, ex *Ficus* sp., coll. T.K.; D1116ABC (ID B.B.N.) Belize, Jones Lagoon, near Belize City, 8.vi.2000, coll. D.R.M.; D3079B (ID D.R.M.) Panama: SL crane, 25.viii.2010, ex *Socratea exorrhiza*, coll. G.E.M.; D3733A, D3734AB (ID B.B.N.) U.S.A.: Florida, Miami, SW 104th St & SW 112th Ave, 17.iv.2012, ex *Ficus microcarpa* L.f., coll. M. Igarza; D3798A (ID B.B.N.) Ecuador, 30.x.2011, ex *Mangifera indica*, coll. M.M. Pineda. ***Mycetaspis ud1006*** D1006A (ID D.R.M.) Mexico: Tamaulipas, Alta Cima, 23.0608°N, 99.1981°W, 15.iii.2005, ex *Pouteria* sp., coll. R. A. Gwiazdowski. ***Mycetaspis ud3051*** D3051A (ID B.B.N. query) Panama: Colon, at base of crane (Parque Nacional San Lorenzo Canopy Crane), 9.2811°N, 79.9744°W, 23.viii.2010, ex *Aphelandra sinclairiana* Nees ex Benth., coll. G.E.M., B.B.N. ***Myrtophila pseudadnatae*** Brimblecombe D1139B (ID D.R.M.) Australia: South Australia, 4 km SW Streaky Bay (on Flinders Hwy heading towards Pt. Lincoln), 32.81666°S, 134.233°E, 6.x.2005, ex *Melaleuca lanceolata* Otto, coll. L.G. Cook. ***Neoleonardia alata*** (Froggatt) D2069A (ID JD) Australia: New South Wales, 28.65488°S, 150.199°E, 30.v.2007, ex *Eucalyptus pupulnea*, coll. J.C. Andersen, B.B.N. ***Neoleonardia extensa*** (Maskell) D2055A (ID B.B.N.) Australia: Queensland, near Yelarbon, 28.64306°S, 150.799°E, 30.v.2007, ex *Eucalyptus* sp., coll. J.C. Andersen, B.B.N. ***Neomorgania eucalypti*** (Maskell) D2096B (ID D.R.M.), D2096CD (ID B.B.N.) Australia: New South Wales, 28.82416°S, 150.685°E, 1.vi.2007, ex *Acacia conferta* A. Cunn. ex Benth., coll. J.C. Andersen, B.B.N. ***Neoparlatoria yunnanensis*** Young D2933A, D3262A (ID B.B.N.) Hong Kong, Wan Chai Gap Rd, 6.iii.2009, ex *Cyclobalanopsis neglecta* Schottky, coll. C.S.K. Lau; D3263A (lotID B.B.N.) Hong Kong, Bowen Road, 14.ii.2009, ex *Cyclobalanopsis myrsinifolia* (Blume) Oerst., coll. C.S.K. Lau. ***Nikkoaspis shiranensis*** Kuwana D0642AB, D0643D (ID B.B.N.) Japan: Hokkaido, Sapporo: Hokkaido University, 6.vi.2004, ex *Sasa palmata* (hort. ex Burb.) E.G. Camus, coll. S. Takagi. ***Oceanaspidiotus spinosus*** (Comstock) D0385A (lotID D.R.M.), D0385D (ID D.R.M.) Japan: Honshu, Matsudo City, 17.vii.2001, ex *Ilex crenata* Thunb., coll. K. Tabuchi; D3799A (ID B.B.N.) Peru, 24.iv.2012, ex *Cydonia oblonga* Mill., coll. M. Pizarro. ***Octaspidiotus multipori*** (Takahashi) D0381D (ID D.R.M.), Japan: Nara Pref.: Ryujin Hongu Rindo, 4.v.2001, ex *Illicium anisatum* L., coll. M.S. ***Octaspidiotus subrubescens*** (Maskell) D2133A (ID JD) Australia: Queensland, near Yelarbon, 28.64306°S, 150.799°E, 30.v.2007, ex *Eucalyptus* sp., coll. J.C. Andersen, B.B.N. ***Odonaspis greenii*** Cockerell D0321A (ID D.R.M.) U.S.A.: Florida, Davie: Univ. of FL Ft. Lauderdale Research & Education Center, 26.0841°N, 80.238°W, 20.xi.2002, coll. D.R.M., R.J.G., T.K., B. Sello, M.E. Gruwell, B.B.N.; D4875C, D4882BCDL (ID B.B.N. query) Malaysia: Sarawak, Lambir Hills NP, 4.1964°N, 114.040°E, 19.viii.2013, ex *Bambusoidea* undet, coll. G.E.M., B.B.N., D.A.P. ***Odonaspis litorosa*** Ferris D1018A (ID B.B.N.) Mexico: Tamaulipas, Gomez Farias, 13.iii.2005, coll. M.E. Gruwell, B.B.N., R. A. Gwiazdowski; D1023A (ID B.B.N.) Mexico: Tamaulipas, Bocatomo Dos, 2 km downstream Nacimiento de Rio Frio, 17.iii.2005, ex *Bambusoidea* undet, coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N. ***Odonaspis minima*** Howell & Tippins [now ***Hyparrheniaspis minima*** (Howell & Tippins), **new combination**] D2768A (ID B.B.N.) U.S.A.: Hawaii, Kula, 3.vii.2010, ex *Bambusoidea* undet, coll. E. Reznts. ***Odonaspis ruthae*** Kotinsky D5083AE (ID B.B.N. query) U.S.A.: Florida, Miami, 25.5729°N, 80.4705°W, 12.ii.2014, ex *Pennisetum* sp., coll. C. Millan. ***Odonaspis saccharicaulis*** Zehntner D2848A (ID B.B.N.) U.S.A.: Texas, Texas. HWY 2, 17.vii.2009, coll. B. Denno, D.R.M. ***Odonaspis tapahensis*** Aono D4841ABCD, D4842CD (ID B.B.N.) Malaysia: Sarawak, Lambir Hills NP, 4.1964°N, 114.040°E, 17.viii.2013, ex *Bambusoidea* undet, coll. G.E.M., B.B.N., D.A.P. ***Opuntiaspis carinata*** (Cockerell) D4238C (ID B.B.N.) Panama: SL crane, 22.vi.2012, ex *Perebea xanthochyma*, coll. G.E.M., B.B.N. ***Opuntiaspis philococcus*** (Cockerell) D4328C (ID B.B.N.) Mexico, 13.i.2012, ex *Opuntia* sp., coll. S. Ballesteros. ***Pallulaspis ephedrae*** Ferris D0878CD (lotID B.B.N.), D0878E (ID B.B.N.) U.S.A.: California, Cameron: intersection of Rte. 58 & Pacific Crest Trail, 35.0833°N, 118.3102°W, 16.vi.2005, ex *Ephedra viridis* Coville, coll. R. A. Gwiazdowski. ***Paracupidaspis wilkeyi*** Howell & Tippins [now ***Cupidaspis wilkeyi*** (Howell & Tippins), **new combination**] D2720C (ID B.B.N.) U.S.A.: California, 38.1980°N, 120.3662°W, 23.v.2010, ex *Calocedrus decurrens* (Torr.) Florin, coll. A.O., B.B.N. ***Parlatoareopsis chinensis*** (Marlatt) D0344D (ID D.R.M.) U.S.A.: Florida, Homestead: Univ. of FL Tropical Research & Education Center, 25.5076°N, 80.5008°W, 22.xi.2002, coll. B. Sello, M.E. Gruwell, B.B.N. ***Parlagena bennetti*** Williams [now ***Pseudoparlatoria bennetti*** (Williams), **new combination**] D1854A (ID D.R.M.) Honduras, Roatan, vi.2009, ex *Cocos nucifera* L. ***Parlatoareopsis ud4503*** D4503D (ID B.B.N. query) Malaysia: LH crane, 8.viii.2013, ex *Shorea kunstleri* King, coll. G.E.M., D.A.P. ***Parlatoareopsis ud5035*** D5035ABCEFH (ID B.B.N. query) Malaysia: LH crane, 23.viii.2013, ex *Shorea beccariana* Burck, coll. B.B.N., D.A.P. ***Parlatoria blanchardi*** (Targioni Tozzetti) D0136 (lotID B.B.N.) Saudi Arabia: Hofuf, Al-Hasa, 16.v.2001, ex *Phoenix dactylifera* L., coll. A. Ajlan; D0358A (ID B.B.N.) Israel, Negev, 13.ix.2000, coll. U.G.; D1872A (ID D.R.M.) Egypt, quarantine interception 18.ix.2009,

ex undet Arecaceae; D3199B (ID B.B.N.) Egypt, 14.ix.2010, ex *Phoenix* sp., coll. L. Schroeder. ***Parlatoria camelliae*** Comstock D0002AB (lotID D.R.M.), D0002D (ID D.R.M.) U.S.A.: California, Sacramento: State Capitol, 38.6°N, 121.4833°W, 17.v.2000, ex *Camellia* sp., coll. R.J.G., B.B.N.; D0378A (lotID D.R.M.), D0378D (ID D.R.M.) Japan: Wakayama Pref.: Ryujin Hongu Rindo, 4.v.2001, ex *Pieris japonica* (Thunb.) D. Don ex G. Don, coll. MS; D1955A (ID D.R.M.) U.S.A.: Florida, Gainesville, San Felasco Nursery, 29.7166°N, 82.466°E, 19.ii.2010, ex *Cleyera japonica* Thunb., coll. B.B.N.; D1961B (ID B.B.N.) U.S.A.: Florida, Gainesville, San Felasco Nursery, 29.7166°N, 82.466°E, 19.ii.2010, ex *Osmanthus fragrans* (Thunb.) Lour., coll. I.C.S.; D2452A (ID D.R.M.), D2495C (ID B.B.N.) Japan: Honshu, Kawasaki, 35.5666°N, 139.606°E, 14.iii.2010, ex *Camellia japonica*, coll. A.O. ***Parlatoria cinerea*** Doane & Hadden D3367A (ID B.B.N.) Dominican Republic, intercepted in quarantine 5.xii.2010, ex *Citrus limetta* Risso. ***Parlatoria crypta*** McKenzie D0139A (ID D.R.M.) Saudi Arabia, Taif, 7.iv.2001, ex *Nerium oleander*, coll. A. Ajlan; D0366A (ID D.R.M.), D0366BC (ID B.B.N.) Saudi Arabia, Hofuf, Al-Hasa, 12.v.2001, ex *Nerium oleander*, coll. A. Ajlan. ***Parlatoria fluggeae*** Hall D2665ACD (ID B.B.N.). D2665B (ID G.W.W.) Germany, 15.vi.2009, ex *Adenia globosa* Engl., coll. J. Alvarado. ***Parlatoria fulleri*** Morrison D0748C (ID B.B.N.) New Zealand, NZAK, Avondale, 20.vii.2004, ex *Griselinia littoralis* (Raoul) Raoul, coll. R.C.H. ***Parlatoria oleae*** (Colvée) D0609AB (lotID B.B.N.), D0609C (ID B.B.N.) Turkey: Adana, Çukorova University, 37.0611°N, 35.358°E, 20.iv.2004, ex *Malus* sp., coll. B.B.N., G.E.M., M.E. Gruwell; D0611B (ID B.B.N.) Turkey: Adana, Çukorova University, 37.0611°N, 35.358°E, 20.iv.2004, ex *Asimina* sp., coll. B.B.N., G.E.M., M.E. Gruwell. ***Parlatoria pergandii*** Comstock D0258 (lotID L.E.C.) Argentina: Tucumán, San Miguel de Tucumán, 3.i.2002, ex *Citrus aurantium* L., coll. L.E.C.; D0261B (ID B.B.N.) Argentina: Tucumán, Yerba Buena, 30.xii.2001, ex *Citrus limon*, coll. L.E.C.; D0490A (ID B.B.N.) Spain, Seville, Plaza de España, 18.xi.2000, coll. L.M. Provencher; D1839C (ID B.B.N.) Mexico: Tamaulipas, Gomez Farias, 12.iii.2005, ex *Citrus* sp., coll. M.E. Gruwell, B.B.N., R. A. Gwiazdowski; D2656A (ID B.B.N.) Canada (possibly originated elsewhere), quarantine interception 14.i.2010, ex *Citrus reticulata*, coll. S. Settlege; D2667A (ID B.B.N.) quarantine interception from unknown source (APSWA100056857002), ex *Citrus reticulata*. ***Parlatoria proteus*** (Curtis) D0757AB (lotID B.B.N.), D0757C (ID B.B.N.) Australia: Queensland, Cedar Creek, south of Beenleigh, 21.viii.2004, ex *Vanda* sp., coll. G.E.M.; D0956A (ID B.B.N.) U.S.A.: Florida, Belle Glade, 26.6751°N, 80.67°W, 12.xii.2005, coll. M.E. Gruwell, R. A. Gwiazdowski; D2664A (ID G.W.W.) Thailand, 10.i.2010, ex *Dracaena sanderiana* Sander, coll. N. Pyle; D3719A (lotID G.W.W.) Hong Kong, Sham Shui Po, 18.ii.2012, ex *Osmanthus fragrans*, coll. C.S.K. Lau. ***Parlatoria pseudaspidotus*** Lindinger [now ***Genaparlatoria pseudaspidotus*** (Lindinger), **revived combination**] D0538AC (lotID R.J.G.) Mexico: Sinaloa, Ahome; Benito Juarez #10, 19.vii.2003, ex *Mangifera indica*, coll. Sklingenmeier; D3177A (ID B.B.N.) Mexico, 8.ix.2010, ex *Mangifera indica*, coll. P. Sullivan; D3184A (lotID J.W.D.) Mexico, 7.ix.2010, ex *Mangifera indica*, coll. P. Sullivan; D3724A (ID B.B.N.) Mexico, 12.viii.2011, ex *Mangifera indica*, coll. P. Sullivan. ***Parlatoria* sp.** D2649A (lotID) U.S.A.: Washington, Port Int. fr. unknown, 6.i.2010, ex *Citrus aurantium*, coll. M. Hicks; D4489AB Malaysia: LH crane, 8.viii.2013, ex *Mussaendopsis beccariana* Baill., coll. G.E.M., D.A.P. ***Parlatoria theae*** Cockerell D0392AB (lotID D.R.M.), D0392E (ID D.R.M.) Japan, Sasaguri Town, Fukuoka Pref., 17.ix.2001, ex *Acer palmatum*, coll. M.S.; D2455A (ID J.W.D.) Japan: Honshu, Kawasaki, 35.5666°N, 139.606°E, 14.iii.2010, ex *Zanthoxylum piperitum* DC., coll. A.O. ***Parlatoria ziziphi*** (Lucas) D1835A (lotID B.B.N.) Malaysia, quarantine interception in Australia 25.v.2003, ex *Citrus aurantifolia* Swingle; D1899C (ID D.R.M.) Haiti, 10.ix.2008, coll. J.W.D.; D2657A (ID B.B.N.) Haiti, 23.ii.2010, ex *Citrus* sp., coll. S. Huang; D2672A (lotID) U.S.A.: Hawaii, Tropical Plantation, Waikapu, 15.ix.2009, ex *Citrus* sp., coll. C. Young, M. Fukada; D2925B (ID B.B.N.) Greece, 18.i.2007, ex *Citrus* sp., coll. G. Stathas; D3183A (ID B.B.N.) Bangladesh, 27.viii.2010, ex *Citrus limon*, coll. T. Gary; D3198A (ID B.B.N.) Haiti, 9.viii.2010, coll. S. Huang. ***Parrottia ud4999*** D4999A (ID B.B.N.) Malaysia: LH crane, 21.viii.2013, ex *Santiria laevigata* Blume, coll. B.B.N., D.A.P. ***Pelliculaspis celtis*** McDaniel D0843A (ID D.R.M.) U.S.A.: Texas, Anzalduas County Park, 26.1360°N, 98.3308°W, 20.iii.2005, ex *Sideroxylon celastrinum* (Kunth) T.D. Penn., coll. B.B.N. ***Pellucidaspis epiphytidis*** (Maskell) D0743BC (ID B.B.N.) New Zealand, NZAK: North Piha, 11.vii.2004, coll. R.C.H.; D0929A (ID B.B.N.) New Zealand, NZAK, Waitakere Range, Fairy Falls Track, 31.vii.2005, ex *Collospermum hastatum*, coll. R.C.H.; MD019A (ID B.B.N.) New Zealand: BR, Punakaiki, Bullock Creek, 7.xii.2005, coll. R.C.H. ***Pentalaminaspis minuta*** (Kotinsky) D5032C (ID B.B.N.) Malaysia: LH crane, 23.viii.2013, ex *Shorea fallax* Meijer, coll. B.B.N., D.A.P.; D5034C (ID B.B.N.) Malaysia: LH crane, 23.viii.2013, ex *Shorea beccariana*, coll. B.B.N., D.A.P. ***Phaulomytilus striatus*** (Maskell) D2059C (ID B.B.N.) Australia: Queensland, near Yelarbon, 28.49883°S, 150.566°E, 30.v.2007, ex *Acacia harpophylla*, coll. J.C. Andersen,

B.B.N.; D2060B (ID D.R.M.) Australia: New South Wales, 28.49883°S, 150.566°E, 30.v.2007, ex *Casuarina* sp., coll. J.C. Andersen, B.B.N.; D2113B (ID D.R.M.) Australia: New South Wales, 28.96575°S, 152.084°E, 2.vi.2007, ex *Casuarina cunninghamiana*, coll. J.C. Andersen, B.B.N. ***Phaulomytilus ud2079*** D2079A (lotID B.B.N.) Australia: Queensland, 28.41808°S, 149.890°E, 31.v.2007, ex *Casuarina* sp., coll. J.C. Andersen, B.B.N. ***Pinnaspis aspidistrae*** (Signoret) D0267 (lotID L.E.C.) Argentina: Tucumán, San Miguel de Tucumán, 3.i.2002, ex *Citrus aurantium*, coll. L.E.C.; D2535A (ID B.B.N.) U.S.A.: West Virginia, 25.viii.2009, ex *Ziziphus* sp., coll. J. Wu; D2537A (ID B.B.N.) U.S.A.: West Virginia, 25.viii.2009, ex *Dicksonia* sp., coll. J. Wu; D2939A (ID B.B.N.) U.S.A.: Florida, Riverview, 9.vi.2010, ex *Ophiopogon* sp., coll. N. McNair. ***Pinnaspis buxi*** (Bouché) D0243 (lotID B.B.N.) Colombia: Valle del Cauca, Cali, 11.iii.2002, ex undet Marantaceae, coll. T.K. ***Pinnaspis caricis*** Ferris [junior synonym of ***Pinnaspis aspidistrae*** (Signoret)] D0539A (ID B.B.N.) U.S.A.: Hawaii, Hana; Virginia Trimbel Tropical Flowers & Foliage, SR Box 36-A, 17.vii.2003, ex *Heliconia* sp., coll. C. Moen. ***Pinnaspis hikosana*** Takagi D0388D (lotID MS), D0388E (ID B.B.N.) Japan: Kyushu, Mt. Hiko, 20.iv.2001, ex *Cornus macrophylla* Wall., coll. M.S. ***Pinnaspis piperis*** Takagi D0389ACF (lotID MS), D0389G (ID B.B.N.) Japan: Ryukyu Islands, Naha City, 1.ix.2001, ex *Piper kadsura* (Choisy) Ohwi, coll. M.S. ***Pinnaspis*** sp. D0706A (ID B.B.N.) Mexico: Quintana Roo, Akumal, 19.v.2004, ex *Hibiscus* sp., coll. G.E.M. ***Pinnaspis strachani*** (Cooley) D0248A (lotID T.K.), D0248C (ID B.B.N.) Colombia: Valle del Cauca, Cali, 11.iii.2002, ex *Hibiscus rosa-sinensis* L., coll. T.K.; D0390AE (lotID B.B.N.), D0390D (ID B.B.N.) Japan, Saibara Town, Okinawa Pref., 2.ix.2001, ex *Hibiscus* sp., coll. M.S.; D0551A (ID D.R.M.) U.S.A.: Florida, 23.x.2000, ex *Murraya paniculata* (L.) Jack, coll. G. Oulette; D0704A (ID B.B.N.) Mexico: Quintana Roo, Tulum, 19.v.2004, coll. G.E.M.; D0946A (ID B.B.N.) Mexico: Tamaulipas, 23.0662°N, 99.1610°W, 16.iii.2005, coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N.; D1161B (ID B.B.N. query) Ghana, Shai Hills, 12.vi.2005, ex *Mangifera indica*, coll. G.E.M., T.K.; D1162B (ID D.R.M. query) Ghana, Accra, 7.vi.2005, ex *Hibiscus* sp., coll. T.K.; D2864AB (ID B.B.N.) U.S.A.: Florida, 343 Columbus St., Sebastian, 15.vi.2010, ex *Hibiscus rosa-sinensis*, coll. M. Perez; D2944A (lotID G.W.W.) U.S.A.: Florida, Miami, 19.vii.2010, ex *Dracaena marginata* Lam., coll. N. McNair; D2948A (ID B.B.N.) Panama, 23.vi.2010, ex *Annona* sp., coll. V. Lopez; D2955A (ID B.B.N.) Bolivia, 14.vi.2010, ex *Annona cherimola*, coll. D. Lorenzo; D3638A (ID B.B.N.) U.S.A.: California, Vista, 12.i.2012, coll. A. Romo. ***Pinnaspis uniloba*** (Kuwana) D0542A (ID B.B.N.) U.S.A.: Hawaii, Honolulu, 7770 Kalohelani Pl., 22.vii.2003, coll. G. Onuma. ***Poliaspis callitris*** Laing D0752ABC (lotID B.B.N.), D0752D (ID B.B.N.) Australia: New South Wales, 5 km NW Molong, 33.06666°S, 148.816°E, 13.viii.2004, ex *Callitris endlicheri* (Parl.) F.M. Bailey, coll. C. Unruh. ***Poliaspis exocarpi*** Maskell D2035B (ID B.B.N.) Australia: Queensland, Mt. Glorious, 27.31666°S, 152.75°E, 28.iv.2007, ex *Cordyline petiolaris* (Domin) Pedley, coll. B.B.N. ***Poliaspis floccosa*** Henderson D0661B (ID B.B.N.) New Zealand, NZAK, Auckland, Glen Eden, 16.vi.2004, ex *Phormium tenax*, coll. R.C.H. ***Poliaspis media*** Maskell D0649A (lotID R.C.H.), D0649C (ID B.B.N.) New Zealand, NZAK, Waitakere Range, Destruction Gully Track, 19.vi.2004, ex *Coprosma arborea* Kirk, coll. R.C.H.; D0659A (lotID R.C.H.) New Zealand, NZAK, Waitakere Range, Destruction Gully Track, 19.vi.2004, ex *Leucopogon fasciculatus* A. Rich., coll. R.C.H.; D0857A (lotID R.C.H.) New Zealand, NZMC: Banks Peninsula, Menzies Bay, 4.i.2005, ex *Coprosma propinqua* A. Cunn., coll. R.C.H.; D0862A (ID B.B.N.) New Zealand, NZNC: Arthurs Pass, Devils Punchbowl T.K., 26.x.2004, ex *Coprosma* sp., coll. NA Martin; D0922A (ID B.B.N.) New Zealand, NZTO, Napier-Taupo Rd, (SH5), Okoeke Strm bridge rest area, 21.iv.2005, ex *Coprosma tenuifolia* Cheeseman, coll. N.A. Martin; D0924A (ID B.B.N.) New Zealand, NZNC, Arthurs Pass, Dobsons Nature Trail, 11.v.2005, ex *Hebe subalpina* Hebe subalpina, coll. N.A. Martin. ***Poliaspis syringae*** Laing D2017B (ID B.B.N.) Australia: Queensland, Orchid Beach, 24.95°S, 153.3°E, 20.iii.2007, ex *Persoonia virgate* R. Br., coll. B.B.N.; D2099A (ID B.B.N.) Australia: New South Wales, 28.82416°S, 150.685°E, 1.vi.2007, ex *Jacksonia scoparia* R. Br., coll. J.C. Andersen, B.B.N.; D2124A (ID B.B.N.) Australia: New South Wales, 28.6314°S, 152.008°E, 2.vi.2007, ex *Jacksonia scoparia*, coll. J.C. Andersen, B.B.N. ***Poliaspis ud0776*** D0776D (ID B.B.N.) Australia: Queensland, Nypipamee NP, near entrance, 23.viii.2004, coll. G.E.M., E.V. Freund. ***Poliaspis ud2021*** D2021AB (ID B.B.N.) Australia: Queensland, Mt Glorious, 27.31666°S, 152.75°E, 28.iv.2007, coll. B.B.N. ***Poliaspis ud2100*** D2100D (ID B.B.N.) Australia: New South Wales, 28.90175°S, 150.816°E, 1.vi.2007, ex *Melichrus urceolatus* R. Br., coll. J.C. Andersen, B.B.N. ***Poliaspis wilga*** (Leonardi) D2065AC (ID B.B.N.) Australia: New South Wales, 28.62166°S, 150.218°E, 30.v.2007, ex *Eremophila mitchellii* Benth., coll. J.C. Andersen, B.B.N. ***Poliaspoides leptocarpi*** (Brittin) D2732A (lotID R.C.H.), D2732B (ID B.B.N.) New Zealand: Ak, Tahuna Torea Nature Reserve, 7.ix.2009, ex *Apodasmia* sp., coll. R.C.H. ***Prodiaspis tamaricicola*** (Balachowsky) D0605A (lotID B.B.N.) Turkey: Adana, Çukorova

University, 37.0611°N, 35.358°E, 20.iv.2004, ex *Tamarix* sp., coll. B.B.N., G.E.M., M.E. Gruwell; D2196A (ID B.B.N.) Greece: Crete, Near Aredeia, 35.2243°N, 24.039°E, 8.iv.2010, ex *Tamarix* sp., coll. B.B.N., M.B. Kaydan. ***Prodigiaspis* ud0281** D0281A (lotID L.E.C.) Argentina: Neuquen, San Martin de los Andes: Lago Lolog, 27.xi.2001, ex *Chusquea culeou* E. Desv., coll. L.E.C., L. Díaz-Briz. ***Protargonia larreae* Leonardi** [now ***Pseudoparlatoria larreae* (Leonardi), new combination**] D0260A (ID D.R.M.) Argentina: Tucumán, Entre Ampimpa & Amaicha del Valle, 15.xii.2002, ex *Larrea divaricata* Cav., coll. L.E.C., P. Zamudio. ***Pseudaonidia corbetti* Hall & Williams** D4575A (ID D.R.M.) Malaysia: LH crane, 9.viii.2013, coll. B.B.N., DAP. ***Pseudaonidia dentata* Brimblecombe** D2058A (ID JD) Australia: Queensland, near Yelarbon, 28.49883°S, 150.566°E, 30.v.2007, ex *Acacia harpophylla*, coll. J.C. Andersen, B.B.N. ***Pseudaonidia duplex* (Cockerell)** D0965A (ID B.B.N.) U.S.A.: Florida, 27.5666°N, 80.8166°W, 13.xii.2005, ex *Lyonia* sp., coll. R. A. Gwiazdowski; D0966A (ID B.B.N.) U.S.A.: Florida, 27.5666°N, 80.8166°W, 13.xii.2005, ex *Vitis* sp., coll. M.E. Gruwell; D0969A (ID B.B.N.) U.S.A.: Florida, Sixmile Rd., 27.8483°N, 80.9088°W, 13.xii.2005, ex *Cornus foemina* Mill., coll. R. A. Gwiazdowski; D1912A (ID B.B.N.) U.S.A.: Florida, Gainesville, back of UFL Dept. Agri. & Cons. services, 29.6333°N, 82.366°E, 17.ii.2010, ex *Smilax* sp., coll. B.B.N.; D1945A (ID B.B.N.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk., 29.7166°N, 82.453°E, 18.ii.2010, ex *Quercus hemisphaerica* W. Bartram ex Willd., coll. A.O.; D1958CD (ID B.B.N.) U.S.A.: Florida, Gainesville, San Felasco Nursery, 29.7166°N, 82.466°E, 19.ii.2010, ex *Loropetalum chinense* (R. Br.) Oliv., coll. I.C.S.; D1959C (ID B.B.N.) U.S.A.: Florida, Gainesville, San Felasco Nursery, 29.7166°N, 82.466°E, 19.ii.2010, ex *Loropetalum* sp., coll. B.B.N.; D1992A (ID G.W.W.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk., 29.7095°N, 82.4546°W, 20.ii.2010, ex *Acer negundo* L., coll. A.O. ***Pseudaonidia paeoniae* (Cockerell)** D4400A (ID B.B.N.) Japan, 18.xi.2013, ex *Rhododendron indicum* (L.) Sweet, coll. M. Tomkins. ***Pseudaonidia trilobitiformis* (Green)** D0337C (ID B.B.N.) U.S.A.: Florida, Homestead: Univ. of FL Tropical Research & Education Center, 25.5076°N, 80.5008°W, 21.xi.2002, coll. B. Sello, M.E. Gruwell, B.B.N.; D0340 (lotID B.B.N.) U.S.A.: Florida, Homestead, 22.xi.2002, coll. B. Sello, M.E. Gruwell, B.B.N.; D0345A (ID B.B.N.), D0347A (lotID B.B.N.) U.S.A.: Florida, Homestead, 25.5004°N, 80.4456°W, 22.xi.2002, coll. B. Sello, M.E. Gruwell, B.B.N.; D1094B (ID B.B.N.) Puerto Rico, Mayaguez, 18.ii.2006, ex *Ixora coccinea* L., coll. L.M. Provencher; D1110BC (ID B.B.N.) Belize: Cay Caulker, Belize District, 4.vi.2000, coll. D. Myerdirk; D1164B (ID B.B.N.) Ghana, 13.vi.2005, coll. G.E.M.; D3006A (ID D.R.M.) Panama: SL crane, 21.viii.2010, ex *Brosimum utile*, coll. G.E.M., B.B.N.; D3053A (ID D.R.M.), D3053B (lotID D.R.M.) Panama: SL crane, 24.viii.2010, ex *Brosimum utile*, coll. G.E.M., B.B.N.; D3797A (ID B.B.N.) Haiti, 21.vii.2011, coll. S. Jimenez. ***Pseudaulacaspis biformis* Takagi** D0380D (ID B.B.N.), Japan: Nara Pref.: Ryujin Hongu Rindo, 4.v.2001, ex *Illicium anisatum*, coll. M.S.; D3716A (ID B.B.N.) Japan: Kyushu, Mt. Yufu, 33.2666°N, 131.383°E, 22.v.2012, coll. A.O. ***Pseudaulacaspis brimblecombei* Williams** D0741D (ID D.R.M.) New Zealand, NZAK, Glen Eden, 17.vii.2004, ex *Telopea speciosissima* (Sm.) R. Br., coll. R.C.H.; D2003A (lotID B.B.N.), D2003BC (ID B.B.N. query) Australia: Tasmania, 43.36666°S, 147.216°E, 25.i.2007, ex *Exocarpos cupressiformis* Labill., coll. B.B.N.; D2004AI (ID B.B.N. query) Australia: Tasmania, 43.39033°S, 147.261°E, 25.i.2007, ex *Acacia verticillata*, coll. B.B.N.; D2010A (lotID B.B.N.) Australia: Queensland, Maiala National Park, Browers Rd, 26.ii.2007, coll. R.D. Normark; D2026A (ID B.B.N.) Australia: Queensland, Mt. Glorious, 27.31666°S, 152.75°E, 28.iv.2007, ex *Cordyline petiolaris*, coll. B.B.N.; D2115AC (ID B.B.N. query) Australia: New South Wales, 28.96575°S, 152.084°E, 2.vi.2007, coll. J.C. Andersen, B.B.N.; D2118ACD (ID B.B.N. query) Australia: New South Wales, 28.83933°S, 152.095°E, 2.vi.2007, ex *Exocarpos cupressiformis*, coll. J.C. Andersen, B.B.N.; D2650A (lotID J.W.D.) U.S.A.: Hawaii, Ag. Res. Ctr., 16.ix.2009, ex *Protea* sp., coll. C. Young, M. Fukada; D3271A (ID D.R.M.) U.S.A.: Hawaii, Waikapu, 10.iii.2009, ex *Leucospermum praemorsum* E. Phillips, coll. T. Pieslak. ***Pseudaulacaspis celtis* (Kuwana)** D2491AD (ID D.R.M.), D2491B (lotID D.R.M.) Japan: Kyushu, Lake Daija, 32.2333°N, 129.983°E, 23.iii.2010, coll. A.O. ***Pseudaulacaspis cockerelli* (Cooley)** D0146BC (ID B.B.N.) U.S.A.: Florida, Ft. Pierce, Indian Rv., 25.viii.2001, ex *Nerium oleander*, coll. G. Oulette; D0221AB (lotID B.B.N.) China: Beijing Shi, Beijing (in warmhouse), 10.v.2001, ex *Chrysalidocarpus lutescens* H. Wendl., coll. San'an Wu; D0339A (ID G.W.W.) U.S.A.: Florida, Homestead: Univ. of FL Tropical Research & Education Center, 25.5076°N, 80.5008°W, 21.xi.2002, coll. B. Sello, M.E. Gruwell, B.B.N.; D0400D (ID D.R.M.) Japan, Kagoshima City, Kagoshima Pref., 14.x.2001, ex *Aucuba japonica* Thunb., coll. M.S.; D0535ABC (ID B.B.N.) U.S.A.: Florida, Miami, Pine Island Nursery; 16300 SW 184th St., 20.vi.2003, ex *Mangifera indica*, coll. Regis; D0537A (lotID R.J.G.) U.S.A.: California, Gardena, ABC Nursery Inc., 424 East Gardena Blvd., 21.vii.2003, ex *Cocos* sp., coll. B. Smith; D1200AB (ID B.B.N.) U.S.A.: Hawaii, Baby Beach, Lahaina, 11.i.2006, ex undet. Areaceae, coll. M.E.

Gruwell; D1201A (ID D.R.M.), D1201B (ID B.B.N.) U.S.A.: Hawaii, Baby Beach, Lahaina, 11.i.2006, ex *Nerium oleander*, coll. M.E. Gruwell; D1903A (ID B.B.N.) U.S.A.: Florida, Gainesville, 4700 SW, 56th Dr., 16.ii.2010, ex *Serenoa repens* (W. Bartram) Small, coll. I.C.S.; D1904A (ID B.B.N.) U.S.A.: Florida, Gainesville, 4700 SW, 56th Dr., 16.ii.2010, ex *Trachycarpus fortunei*, coll. I.C.S.; D1910A (ID B.B.N.) U.S.A.: Florida, Orlando area: Disney Animal Kingdom: East Savannah Circle: Lake Buena Vista, 16.ii.2010, ex *Magnolia grandiflora* L., coll. G. Warden; D1934AB (ID B.B.N.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk., 29.7912°N, 82.456°E, 18.ii.2010, ex *Magnolia grandiflora*, coll. G. Hodges; D1953A (ID B.B.N.), D1953B (lotID B.B.N.) U.S.A.: Florida, Gainesville, San Felasco Nursery, 29.7166°N, 82.466°E, 19.ii.2010, ex *Dianella* sp., coll. I.C.S.; D1954A (ID B.B.N.) U.S.A.: Florida, Gainesville, San Felasco Nursery, 29.7166°N, 82.466°E, 19.ii.2010, ex *Magnolia grandiflora*, coll. I.C.S.; D1963C (lotID B.B.N.) U.S.A.: Florida, Gainesville, San Felasco Nursery, 29.7166°N, 82.466°E, 19.ii.2010, ex *Elaeagnus ebbingei* Door., coll. I.C.S.; D1970B (ID B.B.N.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk, 29.7113°N, 82.456°W, 20.ii.2010, ex *Ilex opaca* Aiton, coll. I.C.S.; D1974C (ID G.W.W.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk, 29.7113°N, 82.456°W, 20.ii.2010, ex *Gelsemium sempervirens* (L.) J. St.-Hil., coll. I.C.S.; D1976A (ID B.B.N.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk, 29.7115°N, 82.4556°W, 20.ii.2010, ex *Ilex* sp., coll. B.B.N.; D1981B (ID G.W.W.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk, 29.7095°N, 82.455°W, 20.ii.2010, ex *Smilax auriculata* Walter, coll. I.C.S.; D1983A (ID G.W.W.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk, 29.7095°N, 82.4551°W, 20.ii.2010, ex *Smilax* sp., coll. I.C.S.; D1985A (ID B.B.N.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk, 29.7096°N, 82.4553°W, 20.ii.2010, ex *Magnolia grandiflora*, coll. B.B.N.; D1987B (ID G.W.W.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk, 29.7688°N, 82.453°E, 20.ii.2010, ex *Ilex* sp., coll. A.O.; D1989B (ID G.W.W.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk, 29.7684°N, 82.453°E, 20.ii.2010, ex *Ilex* sp., coll. A.O.; D1991A (ID G.W.W.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk., 29.7657°N, 82.453°E, 20.ii.2010, ex *Magnolia grandiflora*, coll. A.O.; D2034A (ID B.B.N.) Australia: Queensland, St. Lucia: UQ: Goddard Bldg., 7.v.2007, ex undet. *Arecaceae*, coll. B.B.N.; D2447A (ID J.W.D.) U.S.A.: Florida, Cedar key, 29.1786°N, 83.0215°W, 21.ii.2010, ex *Magnolia grandiflora*, coll. I.C.S.; D2450A (ID B.B.N.) U.S.A.: Florida, Cedar key, 29.1786°N, 83.0215°W, 21.ii.2010, ex *Diospyros virginiana* L., coll. I.C.S.; D2839A (ID B.B.N.) U.S.A.: Florida, 6481 SW 27th St, Miramar, 24.iii.2010, ex *Mangifera indica*, coll. C. Sargeant; D2855A (ID B.B.N.) U.S.A.: Florida, Waldo Rd, Gainesville, 22.iv.2010, ex *Dietes bicolor* (Steud.) Klatt ex Sweet, coll. A. Silagyi, L. Whilby; D2942A (ID B.B.N.) U.S.A.: Florida, Goulds, 12.vii.2010, ex *Butia* sp., coll. L. Centoni. ***Pseudaulacaspis difissata*** Brimblecombe D2043A (ID B.B.N.) Australia: Queensland, Bribie Island, 27.01666°S, 153.116°E, 13.v.2007, ex *Banksia serrata* L.f., coll. B.B.N. ***Pseudaulacaspis eugeniae*** (Maskell) D0744B (ID B.B.N.), D0744C (lotID R.C.H.) New Zealand: AK, Auckland, Mt. Albert Research Centre, 30.vii.2004, ex *Acca sellowiana* (O. Berg) Burret, coll. R.C.H.; D2018A (ID B.B.N.) Australia: Queensland, Isla Gorge NP, 25.18333°S, 149.966°E, 12.iv.2007, coll. B.B.N. ***Pseudaulacaspis grandilobis*** (Maskell) D2122A (lotID D.R.M.), (ID D.R.M. query) Australia: New South Wales, 28.77595°S, 152.089°E, 2.vi.2007, ex *Banksia integrifolia* L.f., coll. J.C. Andersen, B.B.N. ***Pseudaulacaspis hillii*** (Laing) D2050A (ID B.B.N.) Australia: Queensland, 28.72546°S, 151.339°E, 30.v.2007, ex *Casuarina* sp., coll. J.C. Andersen, B.B.N.; D2061B (ID B.B.N.) Australia: New South Wales, 28.49883°S, 150.566°E, 30.v.2007, ex *Casuarina* sp., coll. J.C. Andersen, B.B.N.; D2086B (ID B.B.N.) Australia: Queensland, 27.85433°S, 150.080°E, 31.v.2007, ex *Casuarina* sp., coll. J.C. Andersen, B.B.N.; D2134A (ID B.B.N.) Australia: Queensland, 28.41808°S, 149.890°E, 31.v.2007, ex *Casuarina* sp., coll. J.C. Andersen, B.B.N. ***Pseudaulacaspis miyakoensis*** (Kuwana) D3642A (ID B.B.N. query) Jamaica, 7.xii.2011, ex *Mentha* sp., coll. A. Hanna. ***Pseudaulacaspis momi*** (Kuwana) D1832D (ID D.R.M.) Japan, Wakayama, 34.05°N, 135.516°E, 8.v.2009, ex *Tsuga sieboldii*, coll. K. Abell. ***Pseudaulacaspis pentagona*** (Targioni Tozzetti) D0372A (lotID D.R.M.) Japan: Kyushu, Ureshino Town, Saga Pref., 10.iv.2001, ex *Camellia sinensis* (L.) Kuntze, coll. J. Abe; D0372D (ID D.R.M.) Japan: Kyushu, Ureshino Town, Saga Pref., 10.iv.2001, ex *Camellia sinensis*, coll. J. Abe; D0634B (ID B.B.N.) Turkey: Osmaniye, Karatepe-Aslantas National Park, 37.2947°N, 36.248°E, 24.iv.2004, ex *Salix* sp., coll. G.E.M.; D0981C (ID B.B.N.) U.S.A.: Florida, Bluefield Rd., 27.2993°N, 80.6439°W, 14.xii.2005, ex *Asclepiadoidea* undet., coll. B.B.N.; D1962A (ID D.R.M.) U.S.A.: Florida, Gainesville, San Felasco Nursery, 29.7166°N, 82.466°E, 19.ii.2010, ex *Osmanthus fragrans*, coll. I.C.S.; D2959A (ID B.B.N.) Singapore, 5.viii.2010, ex *Plumeria rubra*, coll. M. Tomkins; D3736A (ID B.B.N.) U.S.A.: Florida, Miami, 18020 SW 216th St, 15.v.2012, ex *Kalanchoe blossfeldiana* Poelln., coll. H. Cruz-Escoto; D3762A (ID B.B.N.) Cameroon, Diongo, 4.7666°N, 9.483°E,

23.ii.2009, ex *Manihot esculenta* Crantz, coll. A. Doumstos; D4347AB (ID B.B.N.) U.S.A.: Florida, Miami, 18540 SW 187th Ave, 7.ix.2012, ex *Morus alba* L., coll. H. Cruz-Escoto. ***Pseudaulacaspis prunicola*** (Maskell) D0377A (lotID D.R.M.), (ID D.R.M.) Japan: Honshu, Hidaka Town, 3.v.2001, ex *Prunus* sp., coll. M.S.; D0550AB (ID D.R.M.) U.S.A.: Massachusetts, UMASS, Student Union, 22.v.2001, ex *Syringa reticulata* (Blume) H. Hara, coll. L.M. Provencher. ***Pseudaulacaspis simplex*** Takagi D3717B (ID B.B.N.) Japan: Kyushu, Mt. Yufu, 33.2666°N, 131.383°E, 22.v.2012, ex *Zelkova serrata* (Thunb.) Makino, coll. A.O. ***Pseudaulacaspis*** sp. D2105A, D2106A (ID B.B.N.) Australia: New South Wales, 29.02371°S, 151.499°E, 1.vi.2007, ex *Eucalyptus melanophloia* F. Muell., coll. J.C. Andersen, B.B.N. ***Pseudaulacaspis ud0041*** D0041AB (lotID B.B.N.) Australia: ACT, Canberra, Black Mt., Aust. Nat. Bot. Gardens, 35.26666°S, 149.143°E, 19.i.2001, ex *Eucalyptus elaeophloia* Chappill, Crisp & Prober, coll. P.J. Gullan, S.R. Donaldson. ***Pseudaulacaspis ud2020*** D2020B (lotID B.B.N.) Australia: Queensland, Mt Glorious, 27.31666°S, 152.75°E, 28.iv.2007, coll. B.B.N. ***Pseudaulacaspis ud2038*** D2038BC (ID B.B.N.) Australia: Queensland, Brisbane River at Indooroopilly Golf Course, 27.5075°S, 152.999°E, 8.v.2007, ex *Casuarina glauca*, coll. B.B.N.; D2103A (ID B.B.N.) Australia: New South Wales, Little Oak Creek at Bruxner Hwy., 29.18531°S, 151.323°E, 1.vi.2007, ex *Casuarina cunninghamiana*, coll. J.C. Andersen, B.B.N. ***Pseudaulacaspis ud2114*** D2114A (ID B.B.N.) Australia: New South Wales, 28.96575°S, 152.084°E, 2.vi.2007, ex *Casuarina cunninghamiana*, coll. J.C. Andersen, B.B.N.; D2120A (ID B.B.N.) Australia: New South Wales, 28.8195°S, 152.092°E, 2.vi.2007, ex *Casuarina* sp., coll. J.C. Andersen, B.B.N.; D2121A (ID B.B.N.) Australia: New South Wales, 28.8195°S, 152.092°E, 2.vi.2007, ex *Casuarina equisetifolia* L., coll. J.C. Andersen, B.B.N. ***Pseudischnaspis bowreyi*** (Cockerell) D1012A (ID B.B.N.) Mexico: Tamaulipas, source of the Rio Frio, 17.iii.2005, ex undet. Areaceae, coll. M.E. Gruwell, R. A. Gwiazdowski. ***Pseudodiaspis ud0282*** D0282B (ID B.B.N.) Argentina: Jujuy, entre Maimar & Tilcara, 13.ii.2002, coll. L.E.C. ***Pseudodonaspis mollyae*** Henderson D0856C (ID B.B.N.) New Zealand, NZNN: L. Sylvester, road below hut, 10.i.2005, ex *Chionochloa australis* (Buchanan) Zotov, coll. G.L. Henderson, R.C.H. ***Pseudoparlatoria lentigo*** Ferris D3723A (ID B.B.N. query) Mexico, 31.iii.2012, ex *Chamaedorea* sp., coll. Hagos. ***Pseudoparlatoria mammata*** (Ferris) D3001B (ID D.R.M.) Panama: SL crane, 21.viii.2010, ex *Brosimum utile*, coll. G.E.M., B.B.N.; D3018A (ID B.B.N.), D3018B (ID D.R.M.) Panama: SL crane, 23.viii.2010, ex *Brosimum utile*, coll. G.E.M., B.B.N.; D3022AC (ID B.B.N.) Panama: SL crane, at base of crane, 23.viii.2010, coll. G.E.M., B.B.N.; D3061A (ID B.B.N.) Panama: SL crane, 24.viii.2010, ex *Brosimum utile*, coll. G.E.M., B.B.N.; D4148A (ID B.B.N.) Panama: SL crane, 20.vi.2012, ex *Brosimum utile*, coll. G.E.M., B.B.N. ***Pseudoparlatoria parlatorioides*** (Comstock) D0897B (ID B.B.N.) U.S.A.: Texas, Anzalduas County Park, 26.1333°N, 98.3166°W, 19.iii.2005, ex *Zanthoxylum fagara* (L.) Sarg., coll. M.E. Gruwell; D0975B (ID B.B.N.) U.S.A.: Florida, Sixmile Rd., 27.8508°N, 80.8666°W, 13.xii.2005, ex *Sabal palmetto*, coll. M.E. Gruwell; D1973D (lotID B.B.N.) U.S.A.: Florida, Gainesville, San Felasco Ham. Pres. St. Pk, 29.7768°N, 82.453°E, 20.ii.2010, ex *Smilax* sp., coll. B.B.N.; D3054A (ID D.R.M.) Panama: Colon, Parque Nacional San Lorenzo Canopy Crane, 9.2807°N, 79.6410°W, 24.viii.2010, ex *Virola sebifera* Aubl., coll. G.E.M., B.B.N.; D3194B (ID B.B.N.) Jamaica, 14.ix.2010, coll. W. Rodriguez-Rosado. ***Pseudoparlatoria punctata*** Ferris D4023E (ID D.R.M.) Panama: SL crane, 16.vi.2012, ex *Inga chocoensis* Killip ex T.S. Elias, coll. G.E.M., B.B.N. ***Pseudoparlatoria*** sp. D1001A (ID B.B.N. query) Mexico: Tamaulipas, 16.iii.2005, coll. R. Van Driesche, D3049A (ID B.B.N.) Panama: Colon, Parque Nacional San Lorenzo Canopy Crane, 9.2807°N, 79.9746°W, 23.viii.2010, ex *Manilkara chicle* (Pittier) Gilly, coll. G.E.M., B.B.N. ***Pseudoparlatoria ud0269*** D0269A (lotID B.B.N.) Argentina: Salta, Entre Cafayate & El Paso, 16.xii.2001, ex *Senna* sp., coll. L.E.C., P. Zamudio; D0295A (lotID B.B.N.) Argentina: Tucumán, Entre Amaicha del Valle & Santa María, 15.xii.2001, ex *Senna* sp., coll. L.E.C., P. Zamudio. ***Pseudoparlatoria ud4144*** D3023ACD (ID D.R.M.) Panama: Colon, at base of crane (Parque Nacional San Lorenzo Canopy Crane), 9.2811°N, 79.9744°W, 23.viii.2010, ex *Aphelandra sinclairiana*, coll. G.E.M., B.B.N. ***Pseudoparlatoria ud4190*** D4190A, D4287A (ID B.B.N. query) Panama: SL crane, 21.vi.2012, ex *Tovomita longifolia*, coll. G.E.M., B.B.N. ***Quernaspis quercus*** (Comstock) D0031A (lotID B.B.N.) U.S.A.: California, Del Puerto Canyon: Frank Raines County Park, 21.v.2000, ex *Quercus douglasii* Hook. & Arn., coll. D.J. Williams, D.R.M., P.J. Gullan, R.J.G., B.B.N.; D2679B (ID B.B.N.) U.S.A.: California, 37.6221°N, 121.6568°W, 21.v.2010, ex *Quercus* sp., coll. AO; D2693A (ID B.B.N.) U.S.A.: California, 37.4191°N, 121.3721°W, 21.v.2010, ex *Quercus* sp., coll. A. Krewinski; MD008A (ID D.R.M.) U.S.A.: Arizona, Oak flat campground, 23.iv.2006, ex *Quercus emoryi* Torr., coll. G.E.M., T.K. ***Radionaspis indica*** (Marlatt) D3258B (ID B.B.N.) Mexico, 15.viii.2010, ex *Mangifera indica*, coll. Smith; D3312A (ID B.B.N.) Mexico, 11.ii.2011, ex *Mangifera indica*, coll. Hamilton; D3637A (ID B.B.N.) Ecuador, 21.i.2012, ex *Mangifera indica*, coll. Zenkus. ***Rhizaspidiotus dearnessi*** (Cockerell)

D0883A (ID B.B.N.) U.S.A.: California, Rte. 138, 1.4 mi W San Bernardino Co. line, 16.vi.2005, coll. R. A. Gwiazdowski; D1993A (ID G.W.W.) U.S.A.: Florida, Havens Island 1, 29.1639°N, 83.0272°W, 21.ii.2010, ex *Borrhichia frutescens* (L.) DC., coll. I.C.S.; D1994A (ID B.B.N.) U.S.A.: Florida, Havens Island, 29.1639°N, 83.0272°W, 21.ii.2010, ex *Sarcocornia perennis* (Mill.) A.J. Scott, coll. I.C.S.; MD002AB (ID B.B.N.) U.S.A.: Arizona, Go John Trail, Cave Creek Recreation Area, 21.iv.2006, ex Rhamnaceae undet, coll. G.E.M. ***Rhizaspidiotus donacis*** (Leonardi) D2183ABE (LotID P. Moran), D2183D (ID B.B.N.) Spain, Sanlúcar, 37.3833°N, 6.2513°W, 2.xi.2007, ex *Arundo donax*, coll. A. Kirk; D2184BC (ID B.B.N.) Spain, La Rijana, 36.7583°N, 3.3833°W, 29.ix.2007, ex *Arundo donax*, coll. P.J. Moran; D2185BD (ID B.B.N.), D2185G (LotID P. Moran) France, Vingrau, 42.7833°N, 2.850°E, 28.x.2007, ex *Arundo donax*, coll. A. Kirk; D2186AB (ID B.B.N.), D2186C (ID D.R.M.) Spain, Alicante, 38.4666°N, 0.4666°W, 10.xi.2007, ex *Arundo donax*, coll. A. Kirk. ***Rolaspis compositae*** Hall D3653A (ID B.B.N. query) South Africa: Western Cape, Dwarsrivier, Clanwilliam, 26.ii.2012, ex *Euryops* sp., coll. N. Landman. ***Rolaspis incisa*** Munting D3558A (ID B.B.N. query) South Africa: Western Cape, Duikerfontein Farm, Clanwilliam, 32.01666°S, 18.859°E, 6.i.2012, ex *Leucospermum praemorsum*, coll. J.H. Giliomee. ***Rolaspis lounsburyi*** (Cooley) D3554B (ID B.B.N. query) South Africa: Western Cape, Potberg, De Hoop Nature Reserve, 6.xii.2011, ex *Osyris speciosa* (A.W. Hill) J.C. Manning & Goldblatt, coll. J.H. Giliomee. ***Rolaspis whitehilli*** (Hall) D4385A (ID B.B.N.) South Africa: Western Cape, Karoo National Park, 11.iv.2013, ex *Euphorbia mauritanica* L., coll. J.H. Giliomee. ***Rugaspidiotus arizonicus*** (Cockerell) MD005B (ID B.B.N.) U.S.A.: Arizona, Huachuca City, 22.iv.2006, ex *Prosopis juliflora*, coll. G.E.M., T.K. ***Rutherfordia major*** (Cockerell) D0514ABC (lotID B.B.N.) U.S.A.: Florida, 14330 SW 51st St, Miami, 33175, 13.viii.2003, ex *Dimocarpus longan*, coll. R. Toruno; D1111AB (ID B.B.N.) Belize, Calcutta, 18.363°N, 88.4365°W, 3.vi.2000, coll. M.E. Schauff, R. Sapin, D.R.M.; D2531A (ID B.B.N.) U.S.A.: Maryland, 17.viii.2009, ex *Acer rubrum*, coll. J. Wu; D2533A (ID B.B.N.) U.S.A.: Maryland, 25.viii.2009, ex *Acer saccharum* Marshall, coll. J. Wu. ***Sadaotakagia ud4992*** D4802A (ID B.B.N.) Malaysia: Sarawak, Lambir Hills NP Canopy Walkway, 14.viii.2013, ex undet gen, coll. G.E.M., D.A.P., B.B.N. ***Selenaspis articulatus*** (Morgan) D0510A (lotID R.J.G.) U.S.A.: Florida, Miami, 3030 NW 72 Ave, Miami, 30.vii.2003, coll. R. Toruno; D1158A (ID D.R.M.) Ghana: Western, Ankasa NP, Nkwanta camp, 5.2761°N, 2.639°W, 8.vi.2005, ex *Ficus* sp., coll. G.E.M.; D1160A (ID D.R.M.) Ghana: Western, Ankasa NP, Nkwanta camp, 5.2761°N, 2.639°W, 8.vi.2005, coll. G.E.M.; D3015AB (ID B.B.N.) Panama: Colon, PN San Lorenzo, 9.2799°N, 79.9753°W, 21.viii.2010, ex *Annona muricata* L., coll. G.E.M., B.B.N.; D3028A (ID B.B.N.) Panama: SL crane, 23.viii.2010, ex *Tocoyena pittieri*, coll. G.E.M., B.B.N.; D3059AB (ID B.B.N.) Panama: SL crane, 24.viii.2010, ex *Citrus* sp., coll. G.E.M., B.B.N.; D3061EG (ID B.B.N.) Panama: SL crane, 24.viii.2010, ex *Brosimum utile*, coll. G.E.M., B.B.N.; D3064AB (ID B.B.N.) Panama: SL crane, 24.viii.2010, ex *Carapa guianensis*, coll. G.E.M., B.B.N.; D3072A (ID B.B.N.) Panama: SL crane, 24.viii.2010, ex *Nectandra purpurea* (Ruiz & Pav.) Mez, coll. G.E.M., B.B.N.; D3076A (ID B.B.N.) Panama: SL crane, 25.viii.2010, ex *Virola multiflora*, coll. G.E.M.; D3085A (ID B.B.N.) Panama: SL crane, 25.viii.2010, ex *Calophyllum longifolium*, coll. G.E.M.; D3978A (ID B.B.N.) Panama: SL crane, 13.vi.2012, ex *Apeiba tibourbou* Aubl., coll. G.E.M., B.B.N.; D3982AB (ID B.B.N.) Panama: SL crane, 13.vi.2012, ex *Dussia* sp., coll. G.E.M., B.B.N.; D4018C (ID B.B.N.) Panama: SL crane, 14.vi.2012, ex *Chrysophyllum argenteum* Jacq., coll. G.E.M., B.B.N.; D4116A (ID B.B.N.) Panama: SL crane, 19.vi.2012, ex *Cespedesia macrophylla*, coll. G.E.M., B.B.N.; D4173A (ID B.B.N.) Panama: SL crane, 20.vi.2012, ex *Guatteria dumetorum*, coll. G.E.M., B.B.N.; D4185A (fieldID) Panama: SL crane, 19.vi.2012, ex *Mortoniendron anisophyllum* (Standl.) Standl. & Steyerl., coll. G.E.M., B.B.N.; D4198A (ID B.B.N.) Panama: SL crane, 21.vi.2012, ex *Sloanea meianthera* Donn. Sm., coll. G.E.M., B.B.N.; D4199A (ID B.B.N.) Panama: SL crane, 21.vi.2012, ex *Tapirira guianensis*, coll. G.E.M., B.B.N.; D4203A (ID B.B.N.) Panama: SL crane, 21.vi.2012, ex *Apeiba aspera*, coll. G.E.M., B.B.N.; D4229C, D4230A (ID B.B.N.) Panama: SL crane, 22.vi.2012, ex *Poulsenia armata*, coll. G.E.M., B.B.N.; D4259B (ID B.B.N.) Panama: SL crane, 22.vi.2012, ex *Guatteria dumetorum*, coll. G.E.M., B.B.N.; D4331B (ID B.B.N.) Trinidad & Tobago, 21.xi.2011, ex *Citrus paradisi*, coll. F.I. Morales. ***Selenaspis kamerunicus*** Lindinger D1168E (ID B.B.N.) Ghana, Busco Arboretum, 6.2633°N, 0.4655°W, 19.vi.2005, ex *Theobroma cacao*, coll. G.E.M. ***Serenaspis minima*** (Maskell) D0657AB (lotID R.C.H.) New Zealand, NZAK, Waitakere Range, Manukau Bar View Walk, 19.vi.2004, ex *Melicytus ramiflorus*, coll. R.C.H. ***Silvestraspis uberifera*** (Lindinger) D4489C (ID D.R.M.) Malaysia: LH crane, 8.viii.2013, ex *Mussaendopsis beccariana*, coll. G.E.M., D.A.P. ***Sishanaspis ud4977*** D4491A (ID B.B.N.) Malaysia: LH crane, 8.viii.2013, ex *Drypetes* sp., coll. G.E.M., D.A.P.; D4493BCDE (ID B.B.N.), D4493G (lotID B.B.N.) Malaysia: LH crane, 8.viii.2013, ex *Shorea quadrinervis* Slooten, coll. G.E.M., D.A.P.

Situlaspis yuccae (Cockerell) D0788A (ID D.R.M.) U.S.A.: Utah, Beaver Dam Mtns., 2 km E Welcome Spring, 37.0932°N, 113.9410°W, 18.xi.2004, ex *Yucca brevifolia*, coll. M.E. Gruwell, R. A. Gwiazdowski, B.B.N.; D1126B (ID B.B.N.) U.S.A.: Arizona, Tempe, Arizona State University, 23.viii.2002, ex *Hedera helix*, coll. D. Mills, C. Baptista, J.F. Miller, D.R.M.; D3257A (ID B.B.N.) U.S.A.: California, Calexico, 30.xi.2010, coll. L. Arellano; D4390 (ID B.B.N.) Mexico, intercepted 8.vii.2013, ex *Yucca rostrata* Engelm. ex Trel. ***Stramenaspis kelloggi*** (Coleman) D1519A (ID B.B.N.) U.S.A.: Arizona, Chiricahua Mountains, 31.9138°N, 109.2333°W, 18.viii.2006, ex *Pinus cembroides*, coll. R. A. Gwiazdowski; D2202A (ID B.B.N. query) Mexico: Baja California, Hwy 2 south of Juarez, 32.4666°N, 116.1166°W, 15.x.2007, ex *Pinus quadrifolia* Parl. ex Sudw., coll. R. A. Gwiazdowski, C. Callaway; D2204A (ID D.R.M.) Mexico: Baja California, 32.5507°N, 116.0333°W, 15.x.2007, ex *Pinus monophylla*, coll. R. A. Gwiazdowski, C. Callaway. ***Stramenaspis* sp.** D2203A (ID D.R.M.) Mexico: Baja California, Hwy 2 south of Juarez, 32.5741°N, 116.0833°W, 15.x.2007, ex *Pinus quadrifolia*, coll. R. A. Gwiazdowski, C. Callaway; D2850AB U.S.A.: Arizona, Papogo Springs Road, 4.3 mile S Sonoita., 20.vii.2009, ex *Pinus edulis* Engelm., coll. E.E. Grissell, B. Denno, D.R.M. ***Suturaspis crataegi*** (Bodenheimer) D4356B (ID B.B.N.) Afghanistan : Herat, Herat, 10.x.2012, ex *Prunus* sp., coll. R. Wick. ***Symeria phyllocladi*** Henderson MD015AB (ID B.B.N.) New Zealand, NZAK: Hunua Ra, Mangatangi, Workman T.K., 2.i.2006, ex *Phyllocladus* sp., coll. R.C.H.; ***Symeria pyriformis*** (Maskell) D0067 (lotID R.C.H.) New Zealand: AK, Auckland, Glen Eden, 12.v.2001, ex *Rosa* sp., coll. R.C.H.; D0068A (lotID R.C.H.) New Zealand, NN, North-west Nelson, Heaphy Track, 17.v.2001, ex *Weinmannia racemosa* L.f., coll. N.A. Martin; D0651A (lotID R.C.H.) New Zealand, NZAK, Waitakere Range, Turanga, Rd, Spraggs Bush, 9.vi.2004, ex *Dacrydium cupressinum*, coll. S. Joshee. ***Targionia fabianae*** Leonardi D0273AC (lotID B.B.N.) Argentina: Neuquen, Rahueco, 25.xi.2001, ex *Junellia spathulata* (Gillies & Hook.) Moldenke, coll. L.E.C., L. Díaz-Briz; D0277B (lotID L.E.C.), D0277C (ID D.R.M.) Argentina: Neuquen, Entre Rahueco & El Cholar, 25.xi.2001, ex *Colliguaya* sp., coll. L.E.C., L. Díaz-Briz. ***Thysanaspis litseae*** Takagi D0399AC (lotID MS) Japan: Kyushu, Ibusuki City, Kagoshima Pref., 13.x.2001, ex *Litsea japonica* (Thunb.) Juss., coll. M.S. ***Thysanaspis ud5253*** D5253ABDG (ID B.B.N.) U.S.A.: Florida, Key Largo: nr. Curry Hammock St. Park, 22.x.2014, ex *Avicennia germinans* (L.) L., coll. B. Denno, D.R.M. ***Thysanoflorinia nephelii*** (Maskell) D1089A (ID B.B.N.), D1089BC (lotID G. Hodges) U.S.A.: Florida, Naples: Garden District, 4202 Tamiami Trail N, 6.i.2006, ex *Dimocarpus longan*, coll. S. Krueger; D2879A (ID B.B.N.) U.S.A.: California, Santa Ana, nursery, 18.v.2010, ex *Dimocarpus longan*, coll. J. Rivas; D3290B (lotID G.W.W.) Thailand, intercepted in quarantine 11.viii.2009, ex *Dimocarpus longan*. ***Trulliflorinia acaciae*** (Maskell) D0653A (lotID R.C.H.) New Zealand, NZNN, Nelson, Tahunanui Beach Reserve, 12.v.2004, ex *Acacia floribunda* (Vent.) Willd., coll. B.H. Doherty; D0754B, D0755ABC, D0756A (ID B.B.N.), D0754C (lotID B.B.N.) Australia: Queensland, Cedar Creek, south of Beenleigh, 21.viii.2004, ex *Acacia* sp., coll. G.E.M.; ***Trulliflorinia acaciae*** (Maskell) D2028B (ID JD) Australia: Queensland, Mt Glorious, 27.31666°S, 152.75°E, 28.iv.2007, ex *Acacia melanoxylon*, coll. B.B.N.; D2119A (lotID JD) Australia: New South Wales, 28.8195°S, 152.092°E, 2.vi.2007, ex *Acacia penninervis* Sieber ex DC., coll. J.C. Andersen, B.B.N. ***Trulliflorinia ud2130*** D2130A (ID B.B.N.) Australia: Queensland, 27.72971°S, 150.350°E, 31.v.2007, ex *Acacia harpophylla*, coll. J.C. Andersen, B.B.N. **UG3995 ud3995** D3995B (ID B.B.N.) Panama: SL crane, 15.vi.2012, ex *Protium panamense* (Rose) I.M. Johnst., coll. G.E.M., B.B.N. **UG4163 ud4163** D4163C (ID B.B.N.) Panama: SL crane, 20.vi.2012, ex *Poulsenia armata*, coll. G.E.M., B.B.N. **UG4409 ud4409** D4402A (ID B.B.N. query) Malaysia: LH crane, 6.viii.2013, ex *Shorea* sp., coll. G.E.M.; D4409AB (ID B.B.N. query) Malaysia: LH crane, 6.viii.2013, ex *Shorea curtisii* Dyer ex King, coll. G.E.M. ***Umbaspis regularis*** (Newstead) D3389A (ID B.B.N.) Mali: Segou, Niono, 23.iii.2011, ex *Khaya* sp., coll. R. Muniappan. ***Unachionaspis signata*** (Maskell) D0379CE (lotID M.S.) Japan, Mt. Ando, Wakayama Pref., 4.v.2001, ex *Sasamorpha borealis* (Hack.) Nakai, coll. M.S.; D0641B (ID D.R.M.) Japan: Hokkaido, Sapporo: Hokkaido University, 6.vi.2004, ex *Sasa palmata*, coll. S. Takagi. ***Unachionaspis tenuis*** (Maskell) D0852A (lotID D.R.M.), D0852D (ID D.R.M.) Japan, Tenri-Naka, 14.i.2005, coll. T.K.; D2469B (ID D.R.M.) Japan: Kyushu, Mt. Konosu, 33.5566°N, 130.383°E, 16.iii.2010, ex *Sasa* sp., coll. A.O. ***Unaspis citri*** (Comstock) D1171A (ID B.B.N.) Mexico: Tamaulipas, Gomez Farias, 13.iii.2005, ex *Citrus* sp., coll. E. Ruiz-Cancino, B.B.N.; D3294A (ID B.B.N.) U.S.A.: Florida, Dundee, 28.xii.2010, ex *Citrus reticulata*, coll. A.O., B.B.N.; D3368A (ID B.B.N.) Dominican Republic, intercepted 7.xii.2010, ex *Citrus limon*. ***Unaspis euonymi*** (Comstock) D0076B (lotID FK), D0076EF (ID B.B.N.), Hungary, 20.vi.2001, coll. FK; D0140C (ID B.B.N.) U.S.A.: Massachusetts, UMASS, 8.xi.2000, ex *Euonymus* sp., coll. R. Childs; D0252DE (ID B.B.N.) U.S.A.: Alabama, Auburn University, 22.iii.2002, ex *Euonymus* sp., coll. T.K. ***Unaspis* sp.** D2658A (ID B.B.N.) China, 11.i.2010, ex *Citrus reticulata*, coll. D.R.

Dunlop. *Unaspis yanonensis* (Kuwana) D2666A (ID B.B.N.), border interception from unknown location, 28.xii.2009, ex *Citrus reticulata*, coll. C. Zins. *Velataspis cornigera* Ferris D3042A (ID B.B.N.), D3042B (ID D.R.M.) Panama: SL crane, 23.viii.2010, ex *Tapirira guianensis*, coll. G.E.M., B.B.N. *Velataspis dentata* (Hoke) D0971A (ID B.B.N.), D0971B (lotID B.B.N.) U.S.A.: Florida, Sixmile Rd., 27.8483°N, 80.9088°W, 13.xii.2005, ex *Cornus foemina*, coll. B.B.N. *Velataspis ud1000* D1000A (ID D.R.M.) Mexico: Tamaulipas, 23.0661°N, 99.161°W, 16.iii.2005, coll. M.E. Gruwell. *Xerophilaspis prosopidis* (Cockerell) D0887AB (ID B.B.N.), D0887C (lotID B.B.N.) U.S.A.: California, 100m S Laguna Dam, 17.vi.2005, ex *Prosopis velutina* Wootton, coll. L.G. Cook; MD005A (ID D.R.M.) U.S.A.: Arizona, Huachuca City, in front of post office, 22.iv.2006, ex *Prosopis juliflora*, coll. G.E.M., T.K.

Results

Our sample of 1,389 specimens (the "full dataset") included 11 outgroup species and at least 372 species of Diaspididae, of which 311 have been described (about 12% of the described species in the family) and 61 are as yet undescribed, based on morphological criteria. This included type species of 75 genera as heretofore defined (about 18% of the total of 421 genera of Diaspididae), and representatives of 36 other genera. Thus we have sampled species of 111 genera (26% of the total described). Sequences have been deposited in GenBank under accession numbers KY218908–KY221826.

Results of the phylogenetic analysis of the concatenated data set of all 1,389 specimens are shown in Figs. 1–15 and Figs. S1–S5. The comparison across loci for the core set of 279 specimens (the "core dataset") is shown in the supplementary information in Fig. S6. A list of specimens that had previously been misidentified is given in Table 4. Information about the monophyly of genera from which multiple species were sampled is given in Table 5, and a summary of support for higher taxa is given in Table 6. The revised classification is presented in Tables 7 and 8.

Our analysis strongly supports a few clades that correspond roughly to higher taxa as defined by Takagi (2002), especially in the subfamily Diaspidinae Targioni Tozzetti. A clade that largely corresponds to Diaspidinae is supported by all 4 loci for the core dataset of 279 specimens and by 100% posterior probability for the full concatenated dataset of 1,389 specimens (the "full dataset") (Table 6, Figs. 1, S6).

The same level of strong support (Table 6, Figs. 2, S6) is seen for the subtribe Diaspidina Targioni Tozzetti (excluding *Furchadaspis*), the subtribe Chionaspidina Brues & Melander (excluding *Unaspis* MacGillivray), and the subtribe Fioriniina Leonardi (including members of the subtribe Kuwanaspidina Borchsenius). Our analysis is consistent with the monophyly of each of the tribes Diaspidini Targioni Tozzetti and Lepidosaphidini Shimer, approximately as defined by Takagi (2002), though these clades are supported by fewer loci (Table 6, Fig. S6), and their composition is modified slightly (Figs. 2, 4–6).

In Aspidiotinae Westwood, the only traditionally recognized higher taxon that was strongly supported across our analyses was the tribe Leucaspidini Atkinson (as defined by Borchsenius (1966), thus including the members of the tribe Thysanaspidini Takagi), which was supported by 3 of the 4 loci for the core dataset and 100% posterior probability for the full dataset (Table 6, Figs. S6, 3, 13). Two other clades that received support from a majority of the loci for the core dataset (Table 6, Fig. S6) are: (1) a clade including the genera *Gymnaspis* Newstead and *Hemigymnaspis* Lindinger, here interpreted as constituting a tribe Gymnaspidini Balachowsky, **new rank**, supported by 3 of 4 loci for the core dataset with 100% posterior probability in the full dataset (Fig. 3); and (2) a clade comprising the "core Aspidiotini" sensu Andersen *et al.* (2010), here interpreted as constituting the tribe Aspidiotini Westwood, supported by all 4 loci for the core dataset, with 50% posterior probability in the full dataset (Figs. 3, S1–S5). Excluded from this concept of Aspidiotini are a number of genera that have traditionally been placed in that tribe, in the subtribes Pseudoaonidiina Balachowsky and Aonidiina Balachowsky, whose males have late paternal genome elimination and whose females usually have pores near the anterior spiracles. In the full dataset, these genera form a clade with a posterior probability of 99% (though it was not supported by any locus in the core dataset), and we recognize it as constituting a tribe Aonidiini Balachowsky, **new rank**. As for the 2 other sampled tribes of Aspidiotinae, Parlatoriini Leonardi and Odonaspidini Ferris, our results neither strongly support nor strongly refute their monophyly. In the analysis of the full dataset, Parlatoriini is monophyletic but with a low posterior probability (64%), while Odonaspidini forms an unresolved polytomy. Each of these tribes is supported

by only 1 of 4 loci in the core dataset. The subfamily Aspidiotinae as a whole is supported as monophyletic by the full dataset (97% posterior probability), though its monophyly is not supported by any locus in the core dataset.

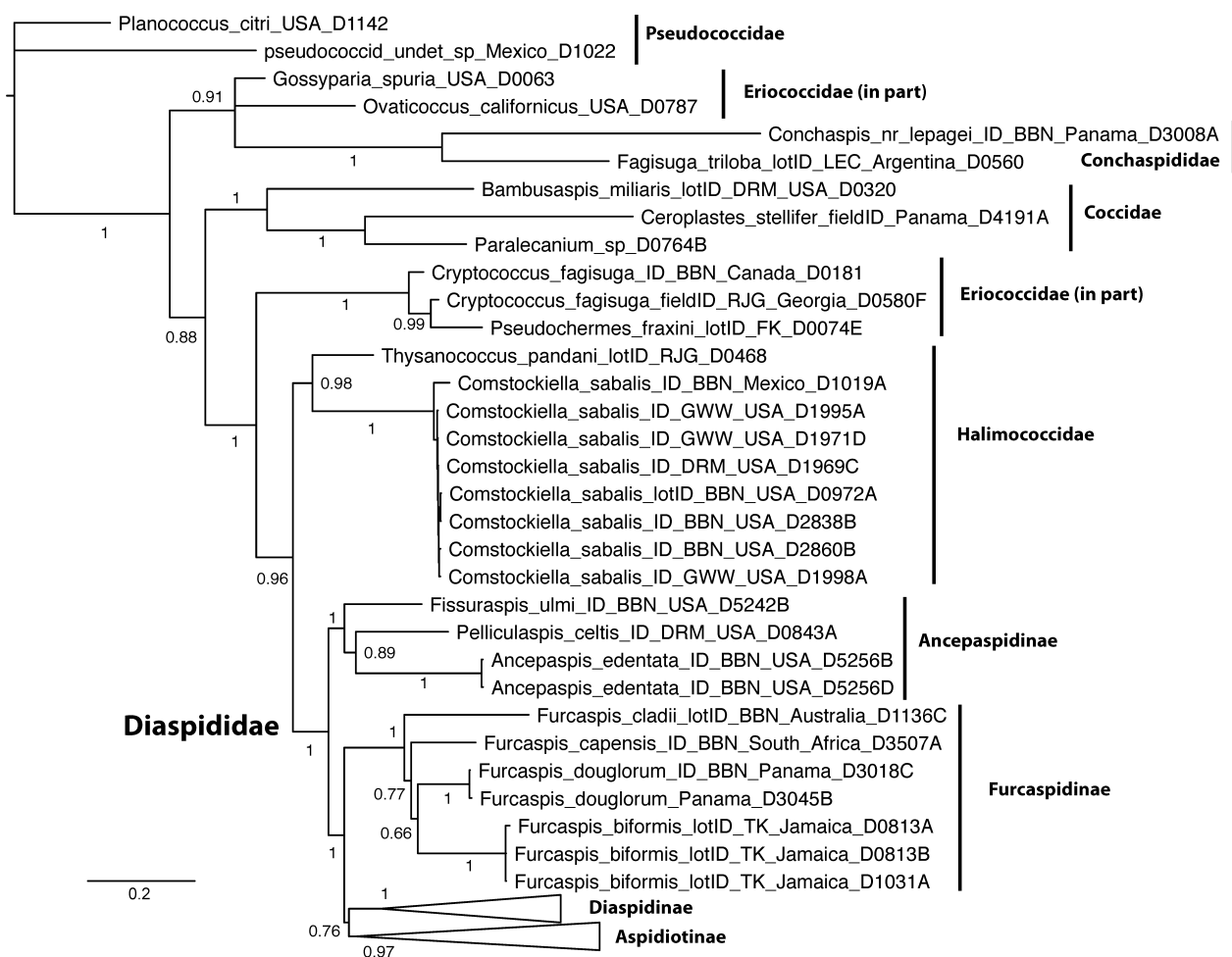


FIGURE 1. Phylogenetic relationships of Diaspididae: outgroups, Ancepaspinae and Furcaspinae. This tree, resulting from a Bayesian analysis of 4 loci, includes 5 outgroup families and shows the relationships of the 4 diaspidid subfamilies under the proposed new classification, as well as relationships of sampled taxa within Ancepaspinae and Furcaspinae. The 2 larger subfamilies of Diaspididae, Diaspidinae and Aspidiotinae, are depicted here with triangular placeholders and shown in more detail in Figs. 2–15 and S1–S5. Note that *Comstockiella*, traditionally placed in within Diaspididae in the monotypic subfamily Comstockiellinae, is here depicted as a member of Halimococcidae. **Figures 1–15 and S1–S5** represent the results of the Bayesian analysis of all 4 loci. Taxon names consist of the species name, the type of identification, the name or initials of the identifier, the country of origin, and the prep number. Identifiers are listed in Table 1. ID = identification based on morphological examination of that specimen itself on a microscope slide; lotID = identification based on morphological examination of 1 or more other specimens of the same series on a microscope slide; fieldID = identification in the field. Values given for internodes are posterior probabilities. Posterior probabilities under 0.5 and most of those within species have been omitted to reduce clutter. Species names are given as the combinations used prior to this study; for species transferred to new genera (Table 9), the new generic assignment is given at the end of the species name. Undescribed species are designated as "ud" followed by a number.

In addition to these clades within Diaspidinae and Aspidiotinae, 2 other distinct clades fall outside both subfamilies in the full dataset: (1) representatives of *Ancepaspis* Ferris, *Fissuraspis* Ferris, and *Pelliculaspis* Ferris; and (2) the genus *Furcaspis* Lindinger. Although these taxa are largely missing from the core dataset, their monophyly and their separation from Diaspidinae and Aspidiotinae are robustly supported by the full dataset (posterior probability 100%) and a previous study also found these taxa to fall outside of the major subfamilies (Andersen *et al.* 2010). Here we recognize these clades as 2 new subfamilies, Ancepaspinae Borchsenius, **new rank** and Furcaspinae Balachowsky, **new rank**. Ancepaspinae comprises tiny pupillarial forms restricted to the New World (that is, to the Nearctic + Neotropical regions); it does not include the Australian species heretofore assigned to *Ancepaspis*, which are transferred to new genera in different tribes, described below. The genera of

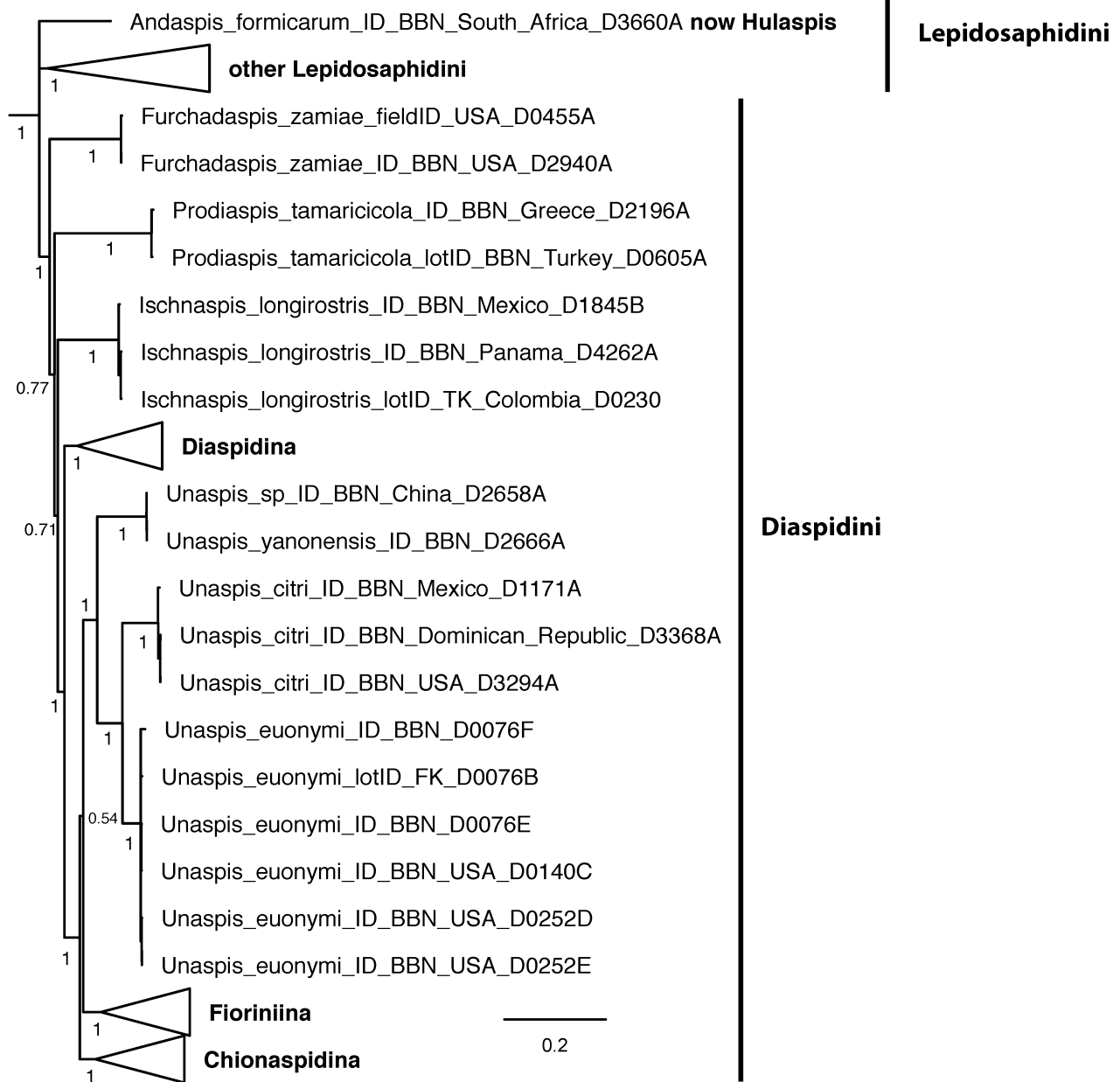


FIGURE 2. Phylogeny of Diaspidinae, whose relationship to the other subfamilies of Diaspididae is shown in Fig. 1. Triangular placeholders are used to represent 4 large clades, whose phylogeny is shown in one or more subsequent figures: other Lepidosaphidini (Figs. 4–6), Diaspidina (Fig. 7), Fioriniina (Figs. 8–10), and Chionaspidina (Fig. 11). For the present we regard *Furchadaspis*, *Prodiaspis*, and *Ischnaspis* as Diaspidini incertae sedis, and we regard *Unaspis* as a member of Chionaspidina. For further explanation of the analysis and notation, see the caption to Fig. 1.

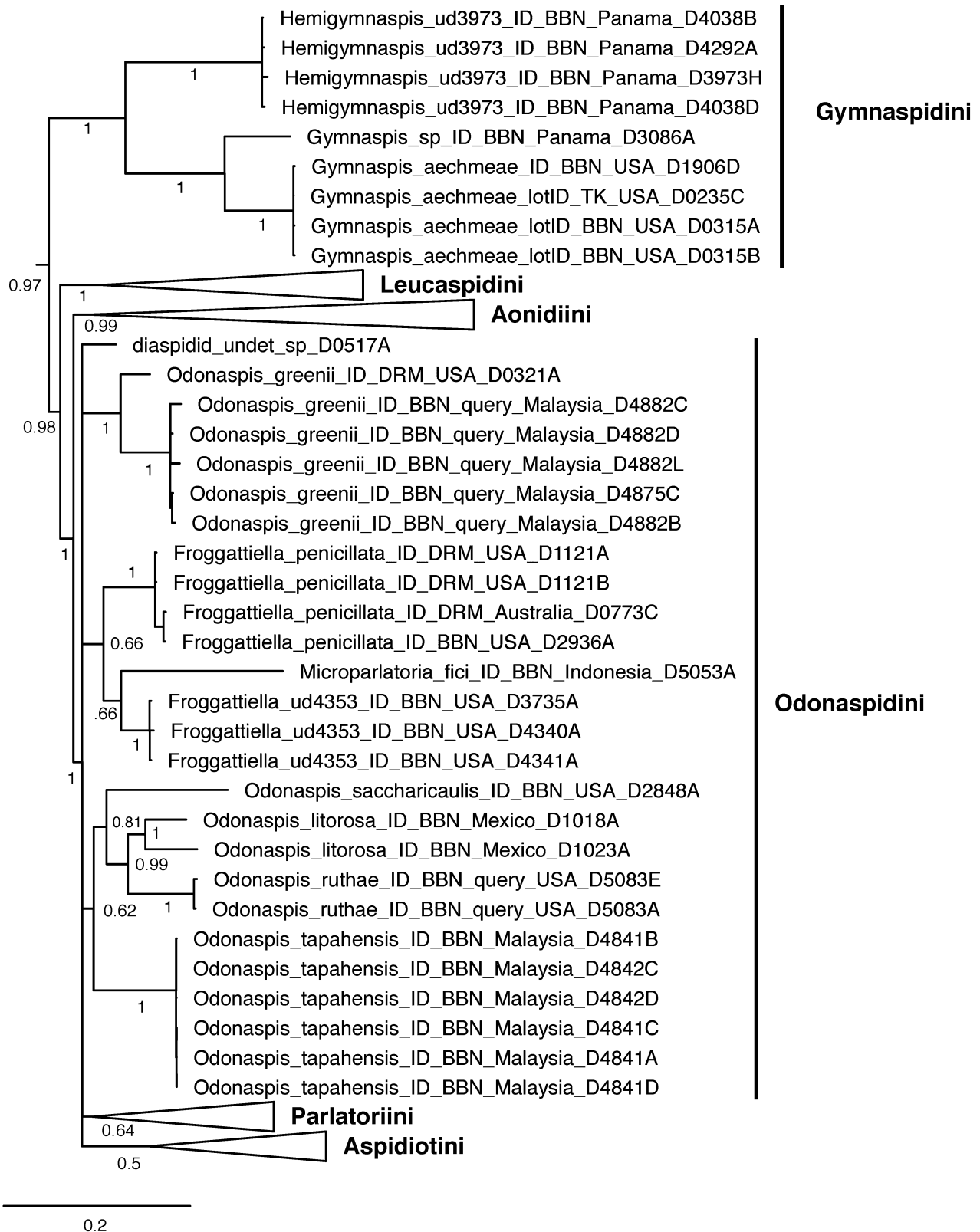


FIGURE 3. Phylogeny of Aspidiotinae, whose relationship to the other subfamilies of Diaspididae is shown in Fig. 1. Triangular placeholders are used to represent 4 tribes, whose phylogeny is shown in one or more subsequent figures: Leucaspidini (Fig. 13), Aonidiini (Fig. 14), Parlatoriini (Fig. 15), and Aspidiotini (Figs. S1–S5). For Gymnaspidini and Odonaspidini, all sampled individuals are shown. For further explanation of the analysis and notation, see the caption to Fig. 1.

TABLE 4. Previously misidentified sources of DNA sequences, with corrected names.

Prep number	GenBank accession numbers	Corrected name	Previous, incorrect name	Reference giving incorrect name (see footnotes)	Reference in which error was first corrected (see footnotes)	Notes
D0326A	JX677917	The specimen cannot be identified based on morphology, so the correct morphology-based ID is "undet. sp."; based on the DNA sequence, the likely source of the DNA is <i>Pinnaspis aspidistrae</i> (Signoret).	<i>Unaspis citri</i> (Comstock)	G	This paper (misidentification discovered by Hang Dao, pers. comm. 22.x.2014)	No voucher cuticle exists for individual D0326A, so no direct morphological ID is possible. The name <i>Unaspis citri</i> was apparently a field ID by one of the original collectors.
D0625A	DQ145357, DQ145469	The specimen cannot be identified based on morphology, so the correct morphology-based ID is "undet. sp."; based on the DNA sequences, the likely source of the DNA is <i>Rhizaspidiotus donacis</i> (Leonardi).	<i>Leucaspis pusilla</i> Löw	A	"An unidentified member of the Aspidiotini" in D	The voucher specimen for this DNA and 4 other voucher specimens from this lot were identified as <i>Leucaspis pusilla</i> by B.B.N., consistent with the host (<i>Pinus</i>). All 3 loci of another individual from the lot, D0625D, cluster with other <i>L. pusilla</i> within <i>Leucaspis</i> ; but 28S and EF-1 α of D0625A cluster with <i>Rhizaspidiotus donacis</i> . The source of this DNA (by mislabeling or contamination) was most likely lot D0600, a sample of <i>R. donacis</i> from <i>Arundo donax</i> in Adana, Turkey.
D0028A	DQ145305, DQ145417	<i>Aonidomytilus ceanothi</i> (Ferris)	<i>Chionaspis ortholobis</i> Comstock	A, G	B, D	No voucher cuticle exists for individual D0028A so no direct morphological ID is possible. <i>C. ortholobis</i> was an early, inexpert ID by BBN. <i>A. ceanothi</i> is a lot ID by D.R. Miller. Both adult specimens identified from this lot are <i>A. ceanothi</i> , and 2 others are second-instar exuviae consistent with <i>A. ceanothi</i> . <i>A. ceanothi</i> is also the best-corroborated molecular ID, based on 4 different lots at 28S, and fewer lots for EF-1 α and COI-II.
D0344A, D0507A, D0514A, D0514B	GQ425010, GQ424861, GQ425026, GQ425027, GQ425028,	<i>Rutherfordia major</i> (Cockerell)	<i>Palinaspis quohogiformis</i> (Merrill)	A, B, C, D	This paper	The single most egregious series of ID errors our laboratory has made and the most persistent ID mystery. No voucher cuticles exist for these individuals, so no direct morphological ID is possible. <i>P. quohogiformis</i> was a field ID of D0344. Of 8 individuals later microscopically examined from lot D0344, 2 were <i>Howardia biclavis</i> (Comstock), 2 were <i>Pinnaspis strachani</i> (Cooley), 2 were second-instar <i>Parlatoreopsis chinensis</i> (Marlatt), and 2 were unidentifiable first-instar nymphs. Lots D0507 and D0514 were both identified as <i>Howardia biclavis</i> by R.J. Gill; between these 2 lots our lab has only 1 identifiable voucher specimen and it (D0514C) is <i>Rutherfordia major</i> . Thus <i>R. major</i> is a lotID for D0514AB. <i>R. major</i> is also the best-corroborated molecular ID of these specimens based on shared haplotypes with identified specimens of D1111, D2531, and D2533.

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TABLE 4. (Continued)

Prep number	GenBank accession numbers	Corrected name	Previous, incorrect name	Reference giving incorrect name (see footnotes)	Reference in which error was first corrected (see footnotes)	Notes
D0041A	GQ403810, GQ325550, GQ424967, GQ424841	an undescribed species, referred to here as <i>Anzaspis</i> ud0041	<i>Chionaspis ethelae</i> Fuller	A, B, G	" <i>Pseudanulacaspis</i> sp." in D	No voucher cuticles exist for these individuals, so no direct morphological ID is possible. Several good specimens of lot D0041 have been studied, and they appear to represent an undescribed species. " <i>C. ethelae</i> " was an early, inexperienced ID by B.B.N.
D0374A	DQ145329, DQ145441, DQ873234, DQ868822	<i>Fiorinia vacciniiae</i> (Kuwana)	<i>Fiorinia euryae</i> Kuwana	A, B, C, D	This paper	No voucher cuticle exists for this individual, so no direct morphological ID is possible. This lot was originally identified as <i>F. euryae</i> by Megumi Shoubu. Only a single identifiable adult voucher specimen exists from this lot (D0374D), and was identified as <i>F. vacciniiae</i> by D.R. Miller. <i>F. vacciniiae</i> is also a 28S-based molecular ID for these specimens, based on shared haplotype with D2453A, although the molecular ID picture is complicated by the very similar haplotypes found in a lot of <i>F. hymenanthidis</i> (D0387).
D0075A	GQ424972, DQ145307, DQ145419	<i>Quernaspis lepineyi</i> (Balachowsky), new combination	<i>Chionaspis salicis</i> (Linnaeus)	A	" <i>Chionaspis lepineyi</i> " in B, C, D	No voucher cuticle exists for this individual, so no direct morphological ID is possible. Other individuals from this lot have been identified as <i>Quernaspis lepineyi</i> by F. Kozár and BBN. " <i>C. salicis</i> " was an editing error.
D0390A	DQ145376, DQ145488, GQ425020, DQ873260, DQ868848	<i>Pinnaspis strachani</i> (Cooley)	<i>Pinnaspis hibisci</i> Takagi	A, B, C, D, G	This paper	No voucher cuticle exists for this individual, so no direct morphological ID is possible. This lot was originally identified as <i>P. hibisci</i> by Megumi Shoubu. Only a single identifiable adult voucher specimen exists from this lot (D0390D), and was identified as <i>P. strachani</i> by B.B.N. Gene trees for 3 loci place the members of this lot with other <i>P. strachani</i> specimens within the <i>P. aspidistrae</i> complex.
D0309B	DQ145338, DQ145450	<i>Duplacionaspis divergens</i> (Green)	<i>Haliaspis asymmetrica</i> (Ferris)	A, G	C, D	No voucher cuticle exists for this individual, so no direct morphological ID is possible. " <i>H. asymmetrica</i> " was an early, inexperienced ID by B.B.N. <i>D. divergens</i> is more recent lot ID by B.B.N. It is also the molecular ID, based on 3 lots for 28S and 2 lots for EF-1 α .
D0623A, D0623B	DQ145321, DQ145320, DQ145433, DQ145432, GU349091, GQ425042, GQ425041, DQ873231, DQ868819	<i>Duplacionaspis sicula</i> (Lupo)	<i>Duplacionaspis noaeae</i> (Hall)	A, C, D, F, G	This paper	Cuticles of these specimens are retained as vouchers. " <i>D. noaeae</i> " was an early, inexperienced ID by B.B.N. D0623B and other individuals from this lot were later identified as <i>D. sicula</i> by D.R. Miller.

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TABLE 4. (Continued)

Prep number	GenBank accession numbers	Corrected name	Previous, incorrect name	Reference giving incorrect name (see footnotes)	Reference in which error was first corrected (see footnotes)	Notes
D0836A	GQ403870, GQ325445	<i>Diaspidiotus uvae</i> (Comstock)	<i>Abgrallaspis colorata</i> (Cockerell)	C, D, E	H	This lot consists of a single high-quality specimen. "A. colorata" was a 2007 ID by B.B.N, influenced by the presence of supernumerary peritubular pores on 1 side. When the specimen was found to share haplotypes (at 28S & EF-1 α with a specimen identified by D.R. Miller as <i>D. uvae</i> , the specimen was re-examined by B.B.N. and found to be more consistent with <i>D. uvae</i> than <i>A. colorata</i> .
D0532	No sequence	Undet. sp.	<i>Ancepaspis edentata</i> (Ferris)	C	This paper	" <i>A. edentata</i> " was an optimistic field ID. Morphological or molecular corroboration of the ID is still lacking.
D2063A, D2084A	GQ403925, GQ403917, GQ325486, GQ325485, GQ424928	<i>Aoniida paradoxa</i> Lindinger	<i>Greeniella</i> sp.	D	I	Cuticles of these specimens are retained as vouchers and are consistent with Lindinger's illustrations of <i>A. paradoxa</i> .
D0273A, D0273C	GQ424997, GQ424996, GQ325476, DQ145427, DQ145315	<i>Targionia fabianae</i> Leonardi	<i>Diaspidiotus</i> sp <i>undesc</i> #3 (refs A, E), <i>Diaspidiotus</i> sp nov (ref D)	A, D, E	J	No voucher cuticle exists for these individuals, so no direct morphological ID is possible. Four identifiable mounted voucher specimens are in hand for this lot (D0273DEFG). Of these, 3 are <i>T. fabianae</i> and 1 is an undescribed species of <i>Melanaspis</i> . The DNA sequences support an ID of <i>T. fabianae</i> .

^AMorse and Normark (2006)^BGruwell *et al.* (2007)^CGruwell *et al.* (2009)^DAndersen *et al.* (2010)^ERugman-Jones *et al.* (2010)^FGwiazdowski *et al.* (2011)^GRoss *et al.* (2013)^HNormark *et al.* (2014)^IMullen *et al.* (2016)^JSchneider *et al.* (2018)

TABLE 5. Monophyly vs. non-monophyly of genera for which multiple species were sampled for this project, based on the full concatenated analysis for 1389 specimens. A few genera (*Aonidomytilus*, *Lepidosaphes*, *Diaspis*, *Fiorinia*, *Cupidaspis*, *Duplachionaspis*) change their monophyly status as a result of the changes implemented in this paper (Table 9). To avoid redundancy with Schneider *et al.* (2018), the genera of Aspidiotini have not been included here.

Genus	Species sampled (described species sampled)	Monophyletic heretofore? (monophyletic as modified in this paper?)	Fig.	Notes
<i>Furcaspis</i> Lindinger	4 (4)	yes (yes)	1	
<i>Unaspis</i> MacGillivray	3 (3)	yes (yes)	2	
<i>Opuntiaspis</i> Lindinger	2 (2)	yes (yes)	4	
<i>Velataspis</i> Ferris	3 (2)	no (no)	4	The 2 sampled described species form 1 clade, <i>V. cornigera</i> Ferris + <i>V. dentata</i> (Hoke). An undescribed species that keys out to <i>Velataspis</i> , <i>V. ud1000</i> , forms a separate clade whose phylogenetic position is poorly resolved.
<i>Pseudoparlatoria</i> Cockerell	6 (4)	no (no)	5	Discussed under "Notes on Higher Taxa", Lepidosaphidini.
<i>Phaulomytilus</i> Morrison & Morrison	2 (1)	yes (yes)	6	
<i>Lepidosaphes</i> Shimer	22 (18)	no (yes)	6	Discussed under "Notes on Higher Taxa", Lepidosaphidini.
<i>Epidiataspis</i> Cockerell	4 (3)	no (no)	7	<i>Diaspis dountisopi</i> Schneider is here treated as a species of <i>Epidiataspis</i> . It fits the morphological definition of <i>Epidiataspis</i> but was placed in <i>Diaspis</i> due to a misleading preliminary DNA analysis. The following are nested within <i>Epidiataspis</i> : <i>Pseudodiaspis ud0282</i> , <i>Carulaspis</i> MacGillivray.
<i>Diaspis</i> Costa	5 (4)	no (no)	7	The genera <i>Epidiataspis</i> , <i>Umbaspis</i> MacGillivray, and <i>Carulaspis</i> MacGillivray are nested within <i>Diaspis</i> . <i>D. coccois</i> Lichtenstein is here considered a synonym of <i>D. boisdavallii</i> Signoret. Regarding <i>D. dountisopi</i> , see note under <i>Epidiataspis</i> , above.
<i>Rolaspis</i> Hall	4 (4)	yes (yes)	8	
<i>Fiorinia</i> Targioni Tozzetti	6 (6)	no (yes)	8	Discussed under "Notes on Higher Taxa", Fioriniina.
<i>Pseudaulacaspis</i> MacGillivray	16 (13)	no (no)	8, 10	Discussed under "Notes on Higher Taxa", Fioriniina.
<i>Unachionaspis</i> MacGillivray	2 (2)	yes (yes)	9	
<i>Kuwanaspis</i> MacGillivray	6 (6)	no (no)	9	<i>Nikkoaspis</i> Kuwana is nested within <i>Kuwanaspis</i> .
<i>Anzaspis</i> Henderson	2 (1)	no (no)	10	<i>Anzaspis</i> is polyphyletic, popping up repeatedly within Australian " <i>Pseudaulacaspis</i> ".
<i>Poliaspis</i> Maskell	9 (6)	yes (yes)	10	
<i>Cupidaspis</i> MacGillivray	2 (2)	no (yes)	11	Discussed under "Notes on Higher Taxa", Chionaspidina.

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TABLE 5. (Continued)

Genus	Species sampled (described species sampled)	Monophyletic heretofore? (monophyletic as modified in this paper?)	Fig.	Notes
<i>Pinnaspis</i> Cockerell	6 (6)	yes (yes)	11	<i>P. caricis</i> Ferris is here considered a synonym of <i>P. aspidistrae</i> (Signoret), following Nakahara (1979). Although our results suggest that the 2 may be different species, the results are also consistent with the hypothesis that <i>P. aspidistrae</i> is simply highly variable both genetically and morphologically. A study of <i>Pinnaspis</i> using methods better suited to species delimitation will be necessary to resolve the question.
<i>Chionaspis</i> Signoret	15 (15)	no (no)	11, 12	Discussed under "Notes on Higher Taxa", Chionaspidina.
<i>Megacanthaspis</i> Takagi	2 (2)	yes (yes)	12	
<i>Aulacaspis</i> Cockerell	12 (12)	no (no)	12	<i>Aulacaspis</i> comprises 3 clades: (a) a core clade of true <i>Aulacaspis</i> , including the type species <i>A. rosae</i> (Virey) along with <i>A. nitida</i> Scott, <i>A. rosarum</i> Borchsenius, <i>A. vitis</i> (Green), <i>A. tuberculatis</i> Newstead, <i>A. alisiana</i> Takagi and <i>A. yasumatsui</i> Takagi; (b) <i>A. yabumikikei</i> Kuwana, sister to <i>Duplachionaspis</i> MacGillivray; and (c) a clade comprising <i>A. crawii</i> (Cockerell), <i>A. spinosa</i> (Maskell), <i>A. distylii</i> Takahashi and <i>A. difficilis</i> (Cockerell), which is sister to <i>Chionaspis</i> + <i>Duplachionaspis</i> + <i>A. yabumikikei</i> .
<i>Duplachionaspis</i> MacGillivray	3 (3)	no (yes)	12	Discussed under "Notes on Higher Taxa", Chionaspidina.
<i>Leucaspis</i> Signoret	14 (7)	no (no)	13	Discussed under "Notes on Higher Taxa", Leucaspidini.
<i>Lopholeucaspis</i> Balachowsky	2 (2)	yes (yes)	13	
<i>Thysanaspis</i> Ferris	2 (1)	yes (yes)	13	
<i>Neoleonardia</i> MacGillivray	2 (2)	yes (yes)	14	
<i>Anoplaspis</i> Leonardi	2 (2)	yes (yes)	14	
<i>Aonidia</i> Targioni Tozzetti	2 (2)	no (no)	14, 20	Discussed under "Notes on Higher Taxa", Aonidiini.
<i>Pseudaonidia</i> Cockerell	5 (5)	no (no)	14	The 5 sampled species of <i>Pseudaonidia</i> are scattered in 3 places across the Aonidiini—the type species, <i>P. duplex</i> (Maskell), forms a clade with <i>P. trilobitiformis</i> (Green) and <i>P. paeoniae</i> (Cockerell). If <i>Pseudaonidia</i> is interpreted as paraphyletic, it includes the type species of <i>Eulaingia</i> Brimblecombe and <i>Neomorgania</i> MacGillivray, along with species assigned to <i>Myrtophila</i> Brimblecombe, <i>Diaphoraspis</i> Brimblecombe, <i>Mimeraspis</i> Brimblecombe, <i>Gomphaspidiotus</i> Borchsenius & Williams, <i>Achorophora</i> Brimblecombe and <i>Parrottia</i> MacGillivray.
<i>Mimeraspis</i> Brimblecombe	2 (0)	no (no)	14	Two undescribed species tentatively assigned to <i>Mimeraspis</i> are adjacent but non-monophyletic in the tree of Aonidiini.
<i>Parlatoria</i> Targioni Tozzetti	11 (11)	no (no)	15	Discussed under "Notes on Higher Taxa", Parlatoriini.

Ancepspidinae, here regarded as comprising *Ancepspis*, *Fissuraspis*, *Pelliculaspis*, *Anotaspis* Ferris, *Costalimaspis* Lepage, and *Nicholiella* Ferris, were traditionally placed in Diaspidinae, but their affinities were always enigmatic (Andersen *et al.* 2010; Brown & McKenzie 1962). Furcaspidinae contains only the genus *Furcaspis*, which was traditionally placed in Aspidiotini, but again was long recognized as having unusual features that made its placement problematic (Davidson & Miller 1977; Williams *et al.* 2006). For details, see "Notes on Higher Taxa", below.

A few of the higher taxa recognized by Takagi (2002) are nested within other higher taxa in our tree: Thysanaspidini (*Thysanaspis* Ferris) within Leucaspidini, Prodiaspidina (*Megacanthaspis* Takagi) within Chionaspidina, and Kuwanaspidina (*Kuwanaspis* MacGillivray, *Nikkoaspis* Kuwana) within Fioriniina. All these taxa are characterized by striking modifications of the pygidial margin: loss of lobes (*Thysanaspis*, *Megacanthaspis*) or the appearance of fringed plates in place of gland spines (*Megacanthaspis*, *Kuwanaspis*, *Nikkoaspis*). Takagi had interpreted these as primitive character states of relictual taxa, but our phylogenetic analysis shows that they are relatively recently derived character states occurring within widespread taxa, and accordingly we sink the higher taxa that were based on them (Thysanaspidini, Prodiaspidina, and Kuwanaspidina).

TABLE 6. Support for higher taxa and clades. The names refer to the higher taxa as they are defined in this paper.

Taxon or clade	Posterior probability in concatenated 1389-specimen analysis	Number of loci supporting clade in separate 279-specimen analyses	Notes on 279-specimen analyses
Ancepspidinae	100%	not tested	only a single taxon included
Furcaspidinae	100%	not tested	not included
Diaspidinae	100%	4/4	
Lepidosaphidini	not a clade	1/4	<i>Hulaspis</i> not included; thus analysis does not discriminate between support for Lepidosaphidini with and without <i>Hulaspis</i> .
Lepidosaphidini excluding <i>Hulaspis</i>	100%	1/4	See note on Lepidosaphidini, above.
Diaspidini	100%	2/4	
Diaspidini excluding <i>Furchadaspis</i> , <i>Prodiaspis</i> , and <i>Ischnaspis</i> .	100%	2/4	<i>Prodiaspis</i> and <i>Ischnaspis</i> not included
Diaspidina	100%	4/4	
Fioriniina	100%	4/4	
Chionaspidina	not a clade	not a clade	
Chionaspidina excluding <i>Unaspis</i>	100%	4/4	
Aspidiotinae	97%	0/4	
Gymnaspidini	100%	3/4	
Leucaspidini	100%	3/4	
Aonidiini	99%	0/4	
Odonaspidini	not a clade	1/4	Only 2 species of <i>Odonaspis</i> .
Parlatoriini	64%	1/4	
Aspidiotini	50%	4/4	

Discussion

It is now widely accepted that classification should reflect phylogeny. But a classification is also a practical tool; in the case of armored scale insects, one of the great practical challenges researchers face is simply to identify the

specimens. The adult female is the life stage that is most commonly noticed and collected for identification, and the classification we have inherited is one that groups together species whose adult females are similar. In most groups of organisms, these 2 purposes of systematics—reflecting history and facilitating identification—largely complement each other. Morphological characters can be used to infer both the history of a group and the identity of specimens, with similarity usually indicating close relationship. To some degree this holds true for armored scale insects as well, as indicated by the rough correspondence between the inferred phylogenetic tree and the higher level classification—family, subfamilies, tribes, and subtribes—but at the level of genera, the correspondence between the phylogeny and the classification starts to break down. Although some morphologically defined genera are monophyletic, more are non-monophyletic (Table 5).

So how should we revise the generic classification to better reflect phylogeny? A case could be made that all diaspidids should be placed in the single genus *Diaspis* Costa. This would accurately reflect their phylogenetic position, nested deep within the family Eriococcidae (Cook *et al.* 2002; Gullan & Cook 2007). It would also reflect the recency and rapidity of their diversification, as indicated for instance by their lack of any sequence diversity in their small ribosomal subunit (18S) (Cook *et al.* 2002; B. B. Normark and G. Colby unpubl. data). Alternatively, a case could be made that the present system, with genera defined typologically by morphological characters of the adult female, is a practical one for identification and that any radical reorganization would have large practical costs without compensating practical benefits. We advocate a course between these extremes, and call for thoroughgoing, but incremental, revision of the genus-level classification, leading eventually to a natural classification with fewer genera, accompanied by practical tools for species-level identification.

Schneider *et al.* (2018) point out that many early-branching lineages of Aspidiotini are morphologically similar species of the genus *Aspidiotus* Bouché. They argue that the common ancestor of Aspidiotini probably resembled a typical *Aspidiotus* species, and that the other genera of Aspidiotini are modifications of an *Aspidiotus*-like morphology. Given this, and given the rampant artificiality of most of the other genera of Aspidiotini (Schneider *et al.* 2018), the best solution may be to regard the entire tribe Aspidiotini as consisting of a single genus *Aspidiotus*. Similar patterns are seen in other tribes of Diaspididae (Figs. 8, 10, 11, 12, 15) and a similar logic could be applied: all members of Parlatoriini could go into *Parlatoria* Targioni Tozzetti, all members of Chionaspina into *Chionaspis* Signoret, and all members of Fioriniina into *Fiorinia* Targioni Tozzetti (which would become the senior synonym of the radically paraphyletic genus *Pseudaulacaspis* MacGillivray). A few tribes—notably Lepidosaphidini and possibly also Aonidiini—show a different pattern of diversification, and may accommodate more genera. We believe that this would represent a reasonable endpoint towards which diaspidid taxonomy should evolve, but there are reasons to proceed cautiously. First, the present system of specimen identification is based on keying adult females to genus, and until better tools are available, for instance interactive keys, or at least artificial dichotomous keys that do not depend upon generic identity (Miller & Davidson 2005), it would impose an impractical hardship on identifiers to toss out the current system of genera wholesale. Second, for some genera, the current tribal placement is uncertain (Table 8); thus their generic placement under a system with fewer genera would have a high probability of being erroneous. It is better if such taxa carry names that reflect the uncertainty of their taxonomic placement. Finally, the enormous species diversity of Diaspididae, and the extraordinary morphological distinctness of many of the groups of species, seem to demand a rich system of names for taxa. It makes sense to work with the current system of generic names, and towards a more natural system of such names, with the expectation that one day many of them will be demoted to subgenera, or infragenera, or species groups. Table 8 shows the present system of generic names; Table 9 lists new combinations; Table 10 lists replacement names; and Table 11 lists new synonymies.

It has been our aim to be as comprehensive and explicit as possible in proposing the classification of diaspidid genera shown in Table 8. Some of the placements are backed up with molecular evidence but many more are not. The classification offered in Table 8 doubtless contains many errors, and is presented as a hypothesis, in the spirit of Francis Bacon's aphorism that truth emerges more readily from error than from confusion (Devey 1902). The keys offered below illustrate the typical ground plans of the higher taxa and should work in most cases, but will fail for some unusual taxa. It is important to recognize that we are still early in the process of making sense of diaspidid diversity. Explicit matrices of morphological characters for all life stages, and further sampling of genera and species for DNA characters, are needed to test and improve upon the outline presented here.

Keys

AF = adult female; **AM** = adult male; **2F** = second-instar female; **2M** = second-instar male; **CR** = crawler (first-instar nymph); **M** = male (any stage). L1 = first pair of pygidial lobes (trullae), occurring on abdominal segment VIII; L2 = second pair of pygidial lobes, occurring on segment VII; L3 = third pair of pygidial lobes, occurring on segment VI. When a range of values is given, followed by one or more values in parentheses, e.g. 0–3 (0), the figure in parentheses gives the modal or most commonly-occurring value or values, unless otherwise noted. Many references were consulted in the preparation of these keys; particularly important were Howell & Tippins's (1990) account of immature forms and Ghauri's (1962) account of adult males.

Key to groups of scale insects that secrete a waxy scale cover

- 1 **AF** legs well-developed; antenna multisegmented; anus at posterior extremity of body; scale cover without exuviae of immature stages; often with submarginal multilocular pores on abdomen Conchaspidae
- **AF** legs absent or rudimentary; antenna 1-segmented; anus dorsal; scale cover usually incorporating exuviae of immature stages; pores on abdomen, if present, usually 5-locular, medial or submedial, restricted to perivulvar area 2
- 2 **AF** dorsal and ventral ducts of abdomen with inner extremity 8-shaped; abdominal segments V–VIII separate, or abdominal segments IV–VIII fused to form a pygidium; margin of abdomen without lobes, plates, or gland spines; perivulvar pores, if present, in 6 groups, with anteriormost pore groups on abdominal segment IV; dorsal and ventral ducts of abdomen similar, very narrow; not permanently enclosed within the sclerotized cuticle of 2F (non-pupillarial); waxy scale cover with or without exuviae of immature stages; **M**, if present, wingless and diploid, with half of the chromosomes heterochromatic; on palms, Nearctic and Neotropical, introduced to Palearctic 3
- **AF** dorsal and ventral ducts of abdomen with inner extremity 1- or 2-barred, not 8-shaped; abdominal segments V–VIII fused to form a pygidium; margin of abdomen often with lobes, plates, or gland spines; perivulvar pores, if present, usually in 5 or 4 groups, all on abdominal segment VI, rarely with supernumerary pore groups on abdominal segment V; dorsal ducts often wider than ventral ducts; permanently enclosed within the sclerotized cuticle of 2F (pupillarial) or not (non-pupillarial); waxy scale cover, when present, incorporating exuviae of immature stages; **M**, if present, winged or wingless, haploid or diploid, with or without heterochromatic chromosomes; on palms and many other hosts, worldwide Diaspididae; see key to subfamilies.
- 3 **AF** waxy scale cover incorporating exuviae of immatures; abdominal segments IV–VIII not fused, membranous, with margins of segments VI–VIII each convex, thus posterior margin of body coarsely crenate reflecting segmental structure; anterior spiracle without associated pores; antenna with a single seta; ducts much shorter than narrowest dimension of prepupillary abdominal segments; dorsal ducts few, scattered, not arranged in duct furrows; setae on body margin small, inconspicuous; anus submarginal, situated more than 2 anal diameters posterior of vulva, less than 1 anal diameter from body margin; perivulvar pores absent; **M** unknown; **CR** antenna annulated for most of its length, segmentation obscure; marginal setae modified into rugose cylinders; Neotropical *Xanthophthalma*, 1 species: *Xanthophthalma concinnum* Cockerell & Parrott. Not a true diaspidid; here tentatively regarded as a non-pupillarial member of Halimococcidae.
- **AF** waxy scale cover without exuviae of immatures; abdominal segments IV–VIII fused, forming a pygidium, moderately sclerotized on dorsum, with margins of segments VI–VIII not convex, posterior margin of body crenulate with >1 crenulation per body segment; anterior spiracle with associated pores; antenna with 3–4 setae; ducts longer than narrowest dimension of prepupillary abdominal segments; dorsal ducts arranged in longitudinal rows in relatively unsclerotized duct furrows, each furrow containing a double row of duct orifices; setae on body margin large, conspicuous; anus situated in center of pygidium, less than one anal diameter posterior of vulva, more than 5 anal diameters from body margin; perivulvar pores present in 6 groups, anteriormost groups situated on abdominal segment IV; **M** wingless and diploid, with half of the chromosomes heterochromatic; **CR** antenna without annulations, clearly 6-segmented; marginal setae simple; Nearctic and Neotropical, introduced to Palearctic *Comstockiella*, 1 species: *Comstockiella sabalis* (Comstock). Not a true diaspidid; here regarded as a non-pupillarial member of Halimococcidae.

Key to subfamilies of Diaspididae

- 1 **AF** permanently enclosed within sclerotized cuticle of 2F (pupillarial); without plates or gland spines; ducts absent or minute; perivulvar pores, when present, forming a horizontal band anterior to vulva; antenna multisetose (rarely unisetose); with 0–3 (usually 0) pairs of pygidial lobes; median lobes, when present, roughly quadrate, with serrate to notched apical margin (sometimes appearing bilobed); body size minute (0.4–0.8 mm long); **2F** body margin without plates; with or without gland spines; with or without ducts—when marginal ducts present, these are 2-barred and often short and wide (barrel-shaped); **CR** abdominal segments III–VI each with 2 submedian setae (1 dorsal, 1 ventral); head without dorsal ducts; abdominal segment II with a submedian dorsal duct; **M** diploid, with half of the chromosomes heterochromatic; antenna 6-segmented, without annulations; Nearctic and Neotropical. ANCEPASPIDINAE

- **AF** permanently enclosed within the sclerotized cuticle of 2F (pupillarial) or not (non-pupillarial); usually with gland spines, or plates, or both; ducts usually present, often large; perivulvar pores, when present, usually in 4–5 groups, some pores situated posterolaterad of vulva; antenna unisetose or (less commonly) multisetose; with 0–5 (usually 1–3) pairs of pygidial lobes; median lobes various, but never appearing bilobed; body size various (0.4–3 mm long); **2F** body margin with or without plates; with or without gland spines; usually with ducts, which may be 1- or 2-barred and of various sizes and shapes; **CR** abdominal segments III–VI each with 1 submedian seta, which may be dorsal or ventral; head with or without dorsal ducts; if submarginal dorsal ducts are absent from head, abdominal segment II lacks a submedial dorsal duct; **M** haploid, without heterochromatic chromosomes or (less commonly) diploid, with half of the chromosomes heterochromatic; antenna 5- or 6- segmented, with or without annulations; widespread. 2
- 2 **AF** antenna with 3–8 setae; plates distinctive, consisting of a dorsoventrally thickened portion that appears bifurcate or trifurcate and a thinner marginal portion stretched between the tines; without fringing on plates and without gland spines; without pores near posterior spiracle; first 3 pygidial lobes similar in shape, unilobular, without notches; dorsal ducts very thin, resembling ventral microducts; **M** diploid, with half of the chromosomes heterochromatic; circumtropical, extending to temperate regions of South Africa and Australia, and in greenhouses FURCASPIDINAE
- **AF** antenna unisetose or (less commonly) multisetose; plates, when present, of uniform thickness and often fringed; with or without gland spines; with or without pores near posterior spiracle; lobes various; ducts various, dorsal ducts often wider than ventral microducts; **M** haploid, without heterochromatic chromosomes or (less commonly) diploid, with half of the chromosomes heterochromatic; widespread 3
- 3 **AF** usually with fringed plates and without gland spines; L2 and L3, when present, unilobular; ducts 1- or 2-barred; orifices of marginal macroducts, if oblong, with long axis usually parallel to body margin; pores by anterior spiracle present or absent, when present usually 5-locular; **2F** usually with fringed plates; L2 unilobular; **CR** abdominal segment II with submedian dorsal duct; abdominal segments III–VI without dorsal submedian setae; abdominal segments IV–VI each without ventral submedian seta; head and mesothorax each with submarginal or submedial dorsal duct; terminal segment of antenna with 2 apical setae; tarsus with seta near base of claw; tarsus and tibia fused or separated by a septum; **AM** midcranial ridge with dorsal branches reduced; tubercular ocelli present; pronotal ridges present; abdomen without dorsal setae on segments IV–VII; **M** haploid without heterochromatic chromosomes or diploid with half of the chromosomes heterochromatic; widespread. ASPIDIOTINAE
- **AF** usually without fringed plates and with gland spines; L2 usually bilobular, L3 bilobular or unilobular; ducts usually 2-barred; orifices of marginal macroducts, if oblong, with long axis oblique or perpendicular to body margin; pores by anterior spiracle usually present, usually 3-locular; **2F** usually without fringed plates; L2 usually bilobular; **CR** abdominal segment II without submedian dorsal duct; abdominal segments III–VI each with dorsal submedian seta; abdominal segments IV–VI each with ventral submedian seta; head and mesothorax without submarginal or submedial dorsal ducts; terminal segment of antenna with 1 apical seta; tarsus with or without seta near base of claw; tarsus and tibia separated by a septum; **AM** midcranial ridge with dorsal branches present; tubercular ocelli absent; pronotal ridges absent; abdomen with dorsal setae on segments IV–VII; **M** haploid, without heterochromatic chromosomes; widespread DIASPIDINAE

Key to tribes of Diaspidinae

- 1 **AF** usually without gland spines between L1; marginal macroducts usually the same size as, or only slightly larger than, dorsal macroducts; pores near anterior spiracle almost always present, trilocular; **2M** usually with tricarinate scale cover and distinctly different from 2F, with more dorsal ducts and often having modified ducts unlike those seen in females; **CR** with a single submedian dorsal duct on each segment of thorax; without seta on tarsus. DIASPIDINI
- **AF** usually with gland spines between L1; marginal macroducts usually distinctly larger than dorsal macroducts; pores near anterior spiracle trilocular, quinquelocular, or absent; **2M** scale cover not tricarinate, similar to 2F; **CR** without submedian dorsal ducts on thorax; with seta on tarsus. LEPIDOSAPHIDINI

Key to subtribes of Diaspidini

- 1 **AF** L1 usually not joined by a zygois; often with a marginal or submarginal macroduct, or a pair of gland spines, between L1; **AM** prosternum with lateral ridges absent; without pair of spots ("larval eyes") on gena; **2M** ducts sometimes paired but not tightly clustered along invaginations in body margin; all ducts simple, consisting of the main duct only, without additional narrow tubes. DIASPIDINA
- **AF** L1 often joined by a zygois; without a macroduct or pair of gland spines between L1 (rarely with a single fused gland spine between L1); **AM** prosternum with lateral ridges present; with or without pair of spots ("larval eyes") on gena; **2M** ducts often tightly clustered along invaginations in body margin, or some ducts with 1–2 narrow tubes in addition to the main duct 2
- 2 **AF** without setae between L1; zygois between L1 often with rounded basal sclerosis; **AM** with pair of spots ("larval eyes") on gena; **2M** without marginal clusters of ducts; marginal ducts sometimes complex, each duct with 1–2 thin tubes parallel to the main duct ("frame ducts"). CHIONASPIDINA
- **AF** usually with setae between L1; zygois between L1 strap-like, without basal sclerosis; **AM** without pair of spots ("larval

eyes") on gena; **2M** pygidial margin often with invaginations lined with tightly clustered ducts; without complex "frame ducts"
 FIORINIINA

Key to tribes of Aspidiotinae

- 1 **AF** without pores near anterior spiracle; ducts 1-barred; without a reticulate sclerotized pattern on pygidial dorsum; **M** haploid or diploid; worldwide 2
- **AF** usually with pores near anterior spiracle (a few minute pupillarial species lack these pores); ducts 1- or 2-barred; with or without a reticulate sclerotized pattern on pygidial dorsum; **M** diploid, with half of the chromosomes heterochromatic; almost exclusively native to Old World (Oriental, Afrotropical, Australasian & Palearctic regions), widely introduced. 3
- 2 **AF** antenna with a single seta; plates usually flat and pectinate, rarely minute and cylindrical; **2F** L3, if present, unilobular; **AM** pronotal ridge interrupted medially; **M** haploid: widespread; on many hosts. ASPIDIOTINI
- **AF** antenna with 2–4 setae; plates conical, with either flat pectinate wing-like projections, or minute terminal filamentous projections; **2F** L3 present, bilobular; **AM** pronotal ridge entire; **M** diploid, with half of the chromosomes heterochromatic: Neotropical, introduced to Europe and U.S.A.; on many hosts, common on Bromeliaceae and Myrtaceae GYMNASPIDINI
- 3 **AF** without pygidial lobes or plates; all dorsal duct orifices minute, same size as ventral duct orifices; often with pores by posterior spiracle; non-pupillarial; **CR** without septum between tibia and tarsus; on grasses and *Smilax* L. 4
- **AF** often with pygidial lobes and plates; dorsal duct orifices usually larger than ventral duct orifices; usually without pores by posterior spiracle; pupillarial or non-pupillarial; **CR** with or without septum between tibia and tarsus; on many hosts. 5
- 4 **AF** antenna with a single seta; widespread, on grasses. ODONASPIDINI
- **AF** antenna with more than 1 seta; Oriental region, on *Smilax* SMILACICOLINI
- 5 **AF** pupillarial, remaining permanently enclosed within cuticle of 2F; antenna with 2 or more setae; ducts, if present, 2-barred; body usually elongate; body margin not indented between thoracic segments; a few quinquelocular pores often present submarginally on venter of prepygidial abdominal segments; often with a cluster of ducts or duct tubercles on venter near anterior spiracle LEUCASPIDINI
- **AF** usually non-pupillarial; antenna with 1 or more setae; ducts, if present, 1- or 2-barred; body usually only slightly longer than broad; body margin sometimes indented between thoracic segments; without pores on prepygidial abdominal segments; usually without a cluster of ducts or duct tubercles on venter near anterior spiracle, though sometimes with a few duct tubercles on submargin of prothorax 6
- 6 **AF** without duct tubercles; with 1-barred ducts; reticulate pattern of sclerotization often present on dorsum of pygidium; body sometimes completely sclerotized at maturity; body margin in some cases strongly indented between thoracic segments AONIDIINI
- **AF** often with duct tubercles on ventral submargin of thoracic or prepygidial segments; with 2-barred ducts; without reticulate pattern of sclerotization on dorsum of pygidium; all or part of body usually remaining membranous; body margin entire, or only slightly indented between thoracic segments PARLATORIINI

NOTES ON HIGHER TAXA

Family DIASPIDIDAE Targioni Tozzetti

Cited as: Diaspididae (Balachowsky 1942; Brown & McKenzie 1962; Brues & Melander 1932; Ferris 1957; Takagi 1969, 2002). The rank of family and name Diaspididae have been standard since about 1960. Before then, many authorities treated the armored scale insects as a lower-ranking taxon, usually called Diaspidinae (Balachowsky 1948; Ferris 1936, 1942; MacGillivray 1921; Maskell 1887) or Diaspinae (Berlese & Leonardi 1898; Lindinger 1913; Morgan 1888) and usually construed as a subfamily or tribe. Several other names were also applied in the past: Lepidosaphidae (Shimer 1868), Diaspidae (Maskell 1879), Diaspites (Targioni Tozzetti 1868), Diaspidina (Atkinson 1886), Diaspina (Douglas 1887). For an exhaustive list of references to these older names, see Borchsenius (1966), but note that several of the names listed by Borchsenius are merely vernacular plurals, the equivalent of "diaspidids" (or, less correctly, "diaspids") in English: French *diaspides*, Italian *diaspiti* and *diaspini*, German *Diaspinen*, Spanish *diaspidos*.

Diagnosis: **AF** with abdominal segments V–VIII fused, forming a pygidium; exuviae of immature stages present, incorporated into waxy scale cover or enclosing adult female; margin of pygidium often with lobes (trullae), plates (pectinae), or gland spines; pores, if present, 3- or 5-ocular (rarely 4-ocular), restricted to perivulvar or perispiracular areas, rarely with a few pores on head or prepygidial abdominal segments; vulva a simple aperture; dorsal ducts 1- or 2-barred, often wider than ventral ducts; antenna 1-segmented, often with 1 seta; legs absent or (rarely) reduced to sclerotized spurs; eyes rudimentary or absent. **2F** similar to adult female, but

lacking vulva and usually with glandular system (ducts, plates, and gland spines) relatively less developed; in pupillarial species (those in which the adult female remains permanently enclosed within the sclerotized cuticle of 2F), the glandular system of 2F may be relatively more developed than AF. **CR** motile; legs with tibia and tarsus partially to completely fused; antenna with 4–6 segments. **AM** lacking functional mouthparts; wings present or absent; if wings present, hind wings modified into hamulohalteres; head and thorax closely associated, forming cephalothorax; tentorium absent; pores and ducts completely lacking. **2M** usually similar to 2F but with more wax ducts; in some tribes 2M is distinctly different from 2F, with modified duct types (Diaspidini) or with additional pygidial appendages (Odonaspidini); **M** haploid or diploid, with or without heterochromatic chromosomes.

Remarks: Diaspididae is a distinctive family of scale insects and for a century there has been little disagreement about its composition (Ben Dov & German 2003). The few points of controversy have concerned some unusual genera that have been alternately included or excluded from Diaspididae, especially *Ancepaspis*, *Comstockiella* Cockerell and *Xanthophthalma* Cockerell & Parrott. *Ancepaspis* was excluded by Ferris (1942), but included by Brown & McKenzie (1962) and subsequent authors (Borchsenius 1966; Williams 1969a). Here we show that it forms a clade with species whose identity as diaspidids has never been questioned (*Fissuraspis* Ferris and *Pelliculaspis celtis* McDaniel), and that this clade is sister to the remaining Diaspididae (Fig. 1). We also provide evidence that *Comstockiella* is not a diaspidid, but is more closely related to Halimococcidae (Fig. 1).

TABLE 7. A synopsis of the proposed classification of Diaspididae. "New World" means the Western Hemisphere (Neotropical + Nearctic). "Old World" means the Eastern Hemisphere (Palearctic + Afrotropical + Oriental + Australasian).

Ancepaspidinae (New World, 6 genera)
Furcaspidinae (Pantropical, 1 genus)
Diaspidinae
Lepidosaphidini (cosmopolitan, 103 genera)
Diaspidini
Diaspidina (cosmopolitan except Australasia, 13 genera)
Fioriniina (almost exclusively Old World, 64 genera)
Chionaspidina (cosmopolitan except South America, 48 genera)
Aspidiotinae
Gymnaspidini (Neotropical, 3 genera)
Leucaspidini (almost exclusively Old World, 11 genera)
Aonidiini (Old World, mostly Australasian and Oriental, 36 genera)
Smilacicolini (Oriental, 1 genus)
Odonaspidini (mostly Oriental, 5 genera)
Parlatoriini (mostly Oriental, 25 genera)
Aspidiotini (cosmopolitan, 88 genera)

Subfamily ANCEPASPIDINAE Borchsenius, new rank

Cited as: Ancepaspidini (Borchsenius 1965, 1966). A recommendation to recognize a separate tribe based on *Ancepaspis* was made by Brown & McKenzie (1962) on the basis of both the morphology and the genetic system, but Borchsenius was the first to form the name and describe the new tribe.

Diagnosis: Minute pupillarial bark-encrusting species. **AF** without plates or gland spines; ducts absent or minute; antenna with multiple setae (rarely with 1 seta); with or without pores near anterior spiracle, without pores near posterior spiracle; perivulvar pores, when present, forming a horizontal band anterior to vulva; with 0–3 (usually 0) pairs of pygidial lobes; L1, when present, quadrate, apical margin serrate to notched; L2 unilobed or bilobed; L3 unilobed. **2F** without fringed plates; with or without gland spines; with 0–3 pairs of pygidial lobes; with or without ducts—when marginal ducts present on second-instar female, these are 2-barred and often short and wide (barrel-shaped). **CR** antenna 6-segmented; with septum between tibia and tarsus; tarsal seta present; submedial dorsal seta present on abdominal segments I–VII; submedian dorsal duct present on abdominal segment II (Stickney, 1934). **AM** wingless, with clavate antenna (in 2 species of *Ancepaspis*—AM not described for other genera). **2M** scale elongate, white, with terminal exuviae; microscopic characters not described. **M** diploid, with half of chromosomes heterochromatic.

Distribution: Nearctic and Neotropical, U.S.A. (Arizona and Georgia) to Brazil (São Paulo).

Included genera: *Ancepaspis*, *Anotaspis*, *Costalimaspis*, *Fissuraspis*, *Nicholiella*, *Pelliculaspis*.

Remarks: For *Ancepaspis*, *Fissuraspis*, and *Pelliculaspis*, there is direct molecular evidence that they form a clade (Fig. 1), sister to the rest of Diaspididae. Inclusion of the other 3 genera—*Nicholiella*, *Costalimaspis*, and *Anotaspis*—is less certain. The strongest case can be made for *Nicholiella*. In describing the genus, Ferris (1941a) opined that it was "connected" with *Fissuraspis* and *Pelliculaspis* and considered the possibility "that the three genera should be united". *Costalimaspis* resembles *Fissuraspis* and *Pelliculaspis* in having multisetose antenna, pores by the anterior spiracles, and second-instar female with gland spines and marginal 2-barred dorsal ducts. *Costalimaspis*, *Fissuraspis*, and *Ancepaspis* also share late paternal genome elimination (Brown 1965), which excludes them from the subfamily Diaspidinae that in some respects they otherwise resemble. The placement of *Anotaspis* is much more speculative. Ferris (1941a) noted its "featurelessness" and speculated that it might be related either to *Ancepaspis* or to *Radionaspis* Ferris. The type species of *Anotaspis*, *A. particula* Ferris, is known only from Panama. Thus, biogeographically, the New World group Ancepaspidinae is a more plausible connection than *Radionaspis*, which belongs to the strictly Old World tribe Parlatoriini.

Our results show that the Australian species *Ancepaspis anomala* (Green) is actually a member of Leucaspidini, sister to the clade of New Zealand Leucaspidini (Fig. 22). Below, we transfer it to a new genus, *Hendersonaspis* Normark, **gen. n.** The other Australian species that have been placed in *Ancepaspis* (*A. longicauda* Brimblecombe, *A. magnicauda* Brimblecombe, *A. reticulata* Brimblecombe, *A. rotundicauda* Brimblecombe and *A. striata* Brimblecombe) we transfer to the new genus *Brimblecombia* Normark, **gen. n.**, described below, in the tribe Aonidiini. The African species *Anotaspis lepellei* De Lotto more closely resembles the Old World genus *Salicicola* Lindinger than the Neotropical type species of *Anotaspis*, having pores by the anterior spiracles (absent in *A. particula*), and with the second-instar nymph having short 2-barred ducts (without ducts in *A. particula*) and patchy sclerotization of the pygidium (uniform in *A. particula*). Here we transfer *A. lepellei* to *Salicicola*, as *Salicicola lepellei* (De Lotto), **new combination**. The Asian genera *Nudachaspis* MacGillivray and *Protancepaspis* Borchsenius & Bustshik are transferred to the tribe Diaspidini, subtribe Fioriniina, based on characters of second-instar nymphs: the second-instar male of *Protancepaspis torreyae* Takagi & Kawai has duct clusters characteristic of Fioriniina (Takagi & Kawai 1973), while the second-instar female of *Nudachaspis fodiens* (Green) has pygidial lobes resembling those of *Pseudaulacaspis* (Green 1899).

Subfamily FURCASPIDINAE Balachowsky, new rank

Cited as: Furcaspidina (Balachowsky 1956, 1958; Borchsenius 1965, 1966; Williams *et al.* 2006).

Diagnosis: **AF** non-pupillarial, secreting a scale cover; antenna with 3–8 setae; without pores near posterior spiracle; first 3 pygidial lobes similar in shape, unilobular, without notches; additional lobes absent or low and inconspicuous; dorsal ducts very thin, resembling ventral microducts; with distinctive plates, consisting of a dorsoventrally thickened portion that is bifurcate or trifurcate and a thinner portion that is stretched between the tines; without fringing on plates and without gland spines; with or without duct tubercles. **2F** similar to **AF** in lobes, plates and ducts. **CR** not described. **AM** without tubercular ocellus; with dorsal setae on all abdominal segments (Davidson & Miller 1977). **2M** not described. **M** diploid, with half of chromosomes heterochromatic.

Distribution: Circumtropical, extending to temperate regions of South Africa and Australia. The type species, *Furcaspis bififormis*, is a widely introduced greenhouse pest, but the subfamily is otherwise absent from the Nearctic and Palearctic regions except for Mexico, Florida, and Japan.

Included genus: *Furcaspis*.

Remarks: Williams *et al.* (2006), in a recent revision of this group, treated it as a subtribe of Aspidiotini. Adult females superficially resemble those of Aspidiotini in having a subcircular body shape, with plates and unilobular lobes along the pygidial margin, and most strikingly in having paraphyses that resemble those of *Melanaspis* Cockerell and related genera. But *Furcaspis* has long been recognized as having unusual features not found in any other Aspidiotini, including multisetose antennae and (in several species) 3-locular pores near the anterior spiracle. The phylogenetic analysis by Andersen *et al.* (2010) placed it outside of the major clades of armored scale insects, but its precise position was poorly resolved. Our results here (Fig 1) have resolved its position as sister to a clade containing all the other Diaspididae except Ancepaspidinae. An excellent revision with a key to all the species was provided by Williams *et al.* (2006), and a slight amendment to the key was given by Normark *et al.* (2014).

Subfamily DIASPIDINAE Targioni Tozzetti

Cited as: Diaspidinae (Takagi 2002).

Diagnosis: **AF** usually without fringed plates and with gland spines; L2 usually bilobular, L3 bilobular or unilobular; dorsal ducts usually 2-barred, short, barrel-shaped; orifices of marginal macroducts, if oblong, with long axes oblique or perpendicular to body margin; pores usually present by anterior spiracle, usually 3-locular. **2F** usually without fringed plates; L2 usually bilobular. **CR** abdominal segment II without submedian dorsal duct; abdominal segments III–VI each with dorsal submedian seta; abdominal segments IV–VI each with ventral submedian seta; head and mesothorax without submarginal or submedial dorsal ducts; terminal segment of antenna with 1 apical seta; tarsus and tibia separated by a septum. **AM** without tubercular ocellus; pronotal ridges absent; dorsal lateral branches of midcranial ridge well developed; prescutum subquadrate; dorsal setae present on all abdominal segments. **2M** resembling 2F but with more dorsal ducts and often with distinctive duct types not found in other life stages. **M** haploid, without heterochromatic chromosomes.

Included genera: *Gramenaspis* MacGillivray, *Parafiorinia* MacGillivray, and the genera listed in the tribes below.

Distribution: Cosmopolitan.

Remarks: Our study supports a concept of Diaspidinae almost identical to that of Takagi (2002). The most surprising members of the subfamily are *Poliaspoides leptocarpi* and *Hyparrheniaspis minima* (Howell & Tippins), **new combination**, discussed below under Lepidosaphidini and Fioriniina respectively.

TABLE 8. A proposed classification of the genera of Diaspididae. Authors of higher taxa are from Williams (1969a) and Takagi (2002).

Subfamily ANCEPASPIDINAE Borchsenius

GENERA: *Ancepaspis* Ferris 1920, *Anotaspis* Ferris 1941, *Costalimaspis* Lepage 1937, *Fissuraspis* Ferris 1937, *Nicholiella* Ferris 1941, *Pelliculaspis* Ferris 1941

Subfamily FURCASPIDINAE Balachowsky

GENUS: *Furcaspis* Lindinger 1908

Subfamily DIASPIDINAE Targioni Tozzetti

Tribe LEPIDOSAPHIDINI Shimer

GENERA: *Acanthomytilus* Borchsenius 1947, *Adiscodiaspis* Marchal 1909, *Allantomytilus* Leonardi 1898, *Ambigaspidis* MacGillivray 1921, *Andaspis* MacGillivray 1921, *Annulaspidis* Ferris 1938, *Antakaspidis* Mamet 1959, *Aonidomytilus* Leonardi 1904, *Balaspis* Hall 1946, *Bayuraspidis* Takagi 2003, *Berlesaspis* MacGillivray 1921, *Caia* Williams 1963, *Coccomytilus* Leonardi 1898, *Crassaspis* Ferris 1941, *Cryptaspidus* Lindinger 1910, *Cynodontaspis* Takagi 1962, *Dactylaspis* Ferris 1937, *Daraspis* Hall 1946, *Dentaspis* MacGillivray 1921, *Diaspidistis* Hempel 1900, *Dinaspis* Leonardi 1911, *Discodiaspis* Koronéos 1934, *Emmereziaspidis* Mamet 1941, *Eucleaspis* Munting 1968, *Eudinaspis* Lizer & Trelles 1942, *Exuviaspidis* Ferris 1941, *Faureaspis* Munting 1968, *Felixiella* Almeida 1973, *Ferreroaspis* Kozár 1983, *Ferrisidea* Borchsenius 1965, *Fulaspidis* Balachowsky 1952, *Galeomytilus* Takagi 1995, *Galeraspis* Mamet 1939, *Gynandraspidis* Balachowsky & Matile-Ferrero 1980, *Hexandaspis* Takagi 2003, *Hovaspis* Mamet 1954, *Howardia* Berlese & Leonardi 1898, *Hulaspidis* Hall 1946, *Imerinaspidis* Mamet 1959, *Kandraspidis* Mamet 1959, *Koroneaspis* Bodenheimer 1943, *Lapazia* Ferris 1921, *Leonardianna* MacGillivray 1921, *Lepidosaphes* Shimer 1868, *Madagaspidis* Mamet 1950, *Madaparlaspidis* Mamet 1962, *Mancaspis* Ferris 1941, *Maskellanna* MacGillivray 1921, *Mauritiaspidis* Mamet 1939, *Melayumytilus* Takagi 1992, *Mempelaspidis* Takagi 2000, *Mercetaspidis* Gómez-Menor 1927, *Mimusaspis* Mamet 1942, *Mitraspidis* Ferris 1941, *Mitulaspidis* MacGillivray 1921, *Mohelnaspis* Šulc 1937, *Neoischnaspis* Fonseca 1969, *Neoparlaspidis* Hempel 1934, *Neopinnaspis* McKenzie 1949, *Neopseudoparlatoria* González 2015, *Niveaspis* MacGillivray 1921, *Notandaspis* Williams & Brookes 1995, *Operculaspis* Laing 1925, *Opuntiaspidis* Cockerell 1893, *Osiraspis* Hall 1928, *Palauaspis* Beardsley 1966, *Pallulaspidis* Ferris 1937, *Pandanaspidis* Mamet 1967, *Paradiaspis* Lahille 1919, *Paraepidiaspidis* Balachowsky 1956, *Paraleucaspis* Mamet 1954, *Parandaspis* Mamet 1967, *Parapandanaspidis* Mamet 1967, *Paraparlagenia* Mamet 1959, *Phaulomytilus* Leonardi 1898, *Poliaspoides* MacGillivray 1921, *Praecocaspis* Ferris 1942, *Primaspis* Howell 1995,

Prodigiaspis Ferris 1941, *Pseudodonaspidis* Henderson 2011, *Pseudoleucaspis* Mamet 1939, *Pseudoparlatoria* Cockerell 1892, *Pudaspis* Hall 1946, *Ramachandraspis* Rao 1953, *Rugaspidiotinus* Balachowsky 1953, *Rugpapaspidis* Ben-Dov 1991, *Sakaramyaspis* Mamet 1954, *Santubongia* Takagi 2003, *Saotomaspidis* Balachowsky 1973, *Scleromytilus* Hall 1946, *Scytalaspis* Ferris 1955, *Serrataspidis* Ferris 1955, *Situlaspidis* MacGillivray 1921, *Stramenaspis* Ferris 1937, *Symeria* Green 1929, *Torosaspis* Ülgentürk & Kozár 2012, *Triaspidis* MacGillivray 1921, *Triraphaspis* Balachowsky 1954, *Tulefiorinia* Mamet 1959, *Velataspidis* Ferris 1937, *Vinculaspidis* Ferris 1942, *Xerophilaspis* Cockerell 1897, *Youngus* Özdikmen 2011

Tribe DIASPIDINI Targioni Tozzetti

Subtribe DIASPIDINA Targioni Tozzetti

GENERA: *Bantudiaspidis* Hall 1928, *Carulaspidis* MacGillivray 1921, *Chilesaphes* González 2015, *Credodiaspidis* MacGillivray 1921, *Cryptodiaspidis* Lindinger 1909, *Diaspidis* Costa 1828, *Diaulacaspis* Takahashi 1942, *Epidiaspidis* Cockerell 1899, *Incisaspidis* MacGillivray 1921, *Leptodiaspidis* Takagi 2011, *Pseudodiaspidis* Cockerell 1897, *Thysanofiorinia* Balachowsky 1954, *Umbaspis* MacGillivray 1921

Subtribe FIORINIINA Targioni Tozzetti

GENERA: *Achionaspis* Takagi 1970, *Adiscofiorinia* Leonardi 1906, *Africaspidis* MacGillivray 1921, *Albastaspis* MacGillivray 1921, *Anzaspis* Henderson 2011, *Asymetraspis* MacGillivray 1921, *Augulaspidis* MacGillivray 1921, *Bayokaspis* Takagi 2003, *Chimania* Munting 1970, *Chlidaspis* Borchsenius 1949, *Collubia* Munting 1968, *Contigaspidis* MacGillivray 1921, *Cooleyaspis* MacGillivray 1921, *Coronaspidis* MacGillivray 1921, *Crockeraspis* Takagi 2000, *Dentachionaspis* MacGillivray 1921, *Epifiorinia* Takagi 1970, *Finaspis* Hall 1929, *Fiorinia* Targioni Tozzetti 1868, *Formosaspis* Takahashi 1932, *Fraseraspis* Takagi 1999, *Fusilaspidis* MacGillivray 1921, *Getulaspidis* Balachowsky 1954, *Heimaspidis* Balachowsky & Ferrero 1967, *Himalaspis* Takagi 2007, *Hyparrheniaspidis* Ghabbour & Hamon 1998, *Inchoaspis* MacGillivray 1921, *Ischnafiorinia* MacGillivray 1921, *Keralaspis* Takagi 2007, *Kulatinganaspis* Takagi 2003, *Kuwanaspis* MacGillivray 1921, *Laingaspis* Borchsenius & Williams 1963, *Ledaspis* Hall 1946, *Lineaspis* MacGillivray 1921, *Magnospinus* Munting 1970, *Mammata* Munting 1969, *Mayonia* Takagi 2003, *Medangaspis* Takagi 1999, *Moraspidis* Hall 1946, *Multispinaspidis* Munting 1969, *Namibia* Munting 1969, *Nanhaiaspis* Takagi & Martin 2010, *Nikkoaspis* Kuwana 1928, *Nudachaspis* MacGillivray 1921, *Parachionaspis* MacGillivray 1921, *Pellucidaspis* Henderson 2011, *Poliaspidis* Maskell 1880, *Protancepaspidis* Borchsenius & Bustshik 1959, *Pseudaulacaspis* MacGillivray 1921, *Relhaniaspidis* Munting 1970, *Rolaspis* Hall 1946, *Rutherfordia* MacGillivray 1921, *Salaspis* Hall 1946, *Sclopetaspis* MacGillivray 1921, *Singapuraspis* Takagi 2003, *Sinistraspis* MacGillivray 1921, *Tecaspis* Hall 1946, *Tenuiaspidis* MacGillivray 1921, *Trichomytilus* Leonardi 1898, *Tsimbazaspis* Mamet 1962, *Unachionaspis* MacGillivray 1921, *Voraspidis* Hall 1946, *Xiphuraspidis* Borchsenius & Williams 1963, *Yomaspidis* Munting 1968

Subtribe CHIONASPIDINA Brues & Melander

GENERA: *Afiorinia* Takagi 1970, *Amphisoma* Takagi 1995, *Anaimalaia* Takagi 1995, *Aulacaspis* Cockerell 1893, *Balachowskiella* Kaussari 1955, *Cameronaspis* Takagi, Pong & Ghee 1988, *Chionandaspis* Takagi 2008, *Chionaspis* Signoret 1868, *Cupidaspis* MacGillivray 1921, *Damaia* Takagi 2003, *Dungunia* Takagi 1993, *Duplachionaspis* MacGillivray 1921, *Duplaspis* Goux 1937, *Fijifiorinia* Williams & Watson 1988, *Greenaspis* MacGillivray 1921, *Guineaspis* Balachowsky 1952, *Guizhoaspis* Young 1986, *Hemiaspidis* MacGillivray 1921, *Hybridaspis* Green 1926, *Kuchingaspis* Takagi 2005, *Kyphosoma* Takagi 1993, *Larutaspis* Takagi 2005, *Marchalaspis* MacGillivray 1921, *Megacanthaspis* Takagi 1960, *Myrtaspis* Takagi 1999, *Narayanaspis* Takagi 1998, *Neochionaspis* Borchsenius 1974, *Neoquernaspis* Howell & Takagi 1981, *Pentacicola* Takagi 1993, *Pinangaspis* Takagi 2003, *Pinnaspis* Cockerell 1892, *Protodiaspidis* Cockerell 1898, *Quernaspis* Ferris 1937, *Semonggokia* Takagi 2003, *Serenaspis* Henderson 2011, *Serrachionaspis* Young 1986, *Shansiaspidis* Tang 1981, *Sinoquernaspis* Takagi & Tang 1982, *Sphaeroceraspidis* Balachowsky & Ferrero 1965, *Takagiaspidis* Varshney 2002, *Takahashiaspidis* Takagi 1961, *Tamuraspidis* Takagi 1989, *Tanaparlatoria* Mamet 1962, *Thoa* Takagi 1993, *Trullifiorinia* Leonardi 1906, *Ulucooccus* Takagi, Pong & Ghee 1990, *Unaspis* MacGillivray 1921, *Yuanaspis* Young 1986

DIASPIDINI INCERTAE SEDIS

GENERA: *Furchadaspidis* MacGillivray 1921, *Gadaspis* Borchsenius 1949, *Ischnaspis* Douglas 1887, *Nimbaspis* Balachowsky 1952, *Prodiaspidis* Young 1984, *Pygalataspidis* Ferris 1921, *Roureaspidis* Takagi 1997, *Trischnaspis* Ben-Dov 1974

DIASPIDINAE INCERTAE SEDIS

GENERA: *Gramenaspis* MacGillivray 1921, *Parafiorinia* MacGillivray 1921

Subfamily ASPIDIOTINAE Westwood

Tribe GYMNASPIDINI Balachowsky

GENERA: *Gymnaspis* Newstead 1898, *Hemigymnaspis* Lindinger 1943, *Lindingeria* MacGillivray 1921

Tribe LEUCASPIDINI Targioni Tozzetti

GENERA: *Anamefiorinia* Leonardi 1906, *Gomezmenoraspis* Balachowsky, *Hendersonaspis* Normark (gen. n.), *Labidaspis* Borchsenius & Williams 1963, *Leucaspis* Targioni Tozzetti 1868, *Lopholeucaspis* Balachowsky, *Mongrovaspis* Bodenheimer 1951, *Namaquea* Munting 1969, *Salicicola* Lindinger 1905, *Suturaspis* Lindinger 1909, *Thysanaspis* Ferris 1955

Tribe AONIDIINI Targioni Tozzetti

GENERA: *Achorophora* Brimblecombe 1957, *Acontonidia* Brimblecombe 1957, *Agrophaspis* Borchsenius & Williams 1963, *Alioides* Brimblecombe 1958, *Anoplaspis* Leonardi 1898, *Aonidia* Targioni Tozzetti 1868, *Aspidonymus* Brimblecombe 1957, *Brimblecombia* Normark (gen. n.), *Diaphoraspis* Brimblecombe 1957, *Diaspidopus* Brimblecombe 1959, *Diastolaspis* Brimblecombe 1959, *Dichosoma* Brimblecombe 1957, *Duplaspidiotus* MacGillivray 1921, *Eugreeniella* Brimblecombe 1958, *Eulaingia* Brimblecombe 1958, *Fernaldanna* MacGillivray 1921, *Genaparlatoria* MacGillivray 1921 (revived genus), *Gomphaspidiotus* Borchsenius & Williams 1963, *Greeniella* Cockerell 1897, *Icaraspidiotus* Takagi 2000, *Loranthaspis* Cockerell & Bueker 1930, *Maskellia* Fuller 1897, *Mimeraspis* Brimblecombe 1957, *Myrtophila* Brimblecombe 1957, *Neoleonardia* MacGillivray 1921, *Neomorgania* MacGillivray 1921, *Paraonidia* MacGillivray 1921, *Parrottia* MacGillivray 1921, *Pentalaminaspis* Smith-Pardo, Evans & Dooley 2012, *Protomorgania* Dooley & Evans 2012, *Pseudaonidia* Cockerell 1897, *Pseudotargionia* Lindinger 1912, *Rhopalaspis* Matile-Ferrero & Foldi 2018, *Sadaotakagia* Ben-Dov 2003, *Semelaspidus* MacGillivray 1921, *Tsimanaspis* Mamet 1959

Tribe SMILACICOLINI Takagi

GENUS: *Smilacicola* Takagi 1969

Tribe ODONASPIDINI Ferris

GENERA: *Batarasa* Takagi 2009, *Circulaspis* MacGillivray 1921, *Dicirculaspis* Ben-Dov 1988, *Froggattiella* Leonardi 1900, *Odonaspis* Leonardi 1897

Tribe PARLATORIINI Leonardi

GENERA: *Aleucaspis* Takagi 1977, *Annonogena* Takagi 2008, *Arivonimaspis* Mamet 1962, *Benaparlatoria* Balachowsky 1953, *Cryptoparlatoeopsis* Borchsenius 1947, *Doriopus* Brimblecombe 1960, *Kochummenaspis* Takagi 2003, *Leptaspis* Hardy & Williams 2018, *Ligaspis* Takagi 2002, *Mangaspis* Takagi & Kondo 1997, *Microparlatoria* Takahashi 1956, *Mixaspis* Takahashi 1932, *Neoleucaspis* Green 1926, *Neoparlatoria* Takahashi 1932, *Neparla* Takagi 1987, *Parlagena* McKenzie 1945, *Parlaspis* McKenzie 1945, *Parlatoeopsis* Lindinger 1912, *Parlatoria* Targioni Tozzetti 1868, *Porogymnaspis* Green 1916, *Proceraspis* MacGillivray 1921, *Radionaspis* Ferris 1942, *Silvestraspis* Bellio 1929, *Sishanaspis* Ferris 1952, *Tamilparla* Takagi 1987

Tribe ASPIDIOTINI Westwood

GENERA: *Acanthaspidiotus* Borchsenius & Williams 1963, *Acutaspis* Ferris 1941, *Affirmaspis* MacGillivray 1921, *Africonidia* McKenzie 1947, *Anaspidiotus* Borchsenius & Williams 1963, *Anastomoderma* Beardsley 1966, *Aonidiella* Berlese & Leonardi 1896, *Aspidaspis* Ferris 1938, *Aspidiella* Leonardi 1898, *Aspidioides* MacGillivray 1921, *Aspidiotus* Bouché 1833, *Avidovaspis* Gerson & Davidson 1974, *Banahaooa* Takagi 2003, *Bigymnaspis* Balachowsky 1958, *Brainaspis* MacGillivray 1921, *Capricornaspis* Balachowsky 1971, *Cephalaspidiotus* Takagi 2003, *Chentraspis* Leonardi 1897, *Chinaspis* Gómez-Menor Ortega 1954, *Chortinaspis* Ferris 1938, *Chrysomphalus* Ashmead 1880, *Clavaspidiotus* Takagi & Kawai 1966, *Clavaspis* MacGillivray 1921, *Comstockaspis* MacGillivray 1921, *Crassaspidiotus* Takagi 1969, *Crenulaspidiotus* MacGillivray 1921, *Cryptaspidiotus* Lindinger 1910, *Cryptophyllaspis* Cockerell 1897, *Cryptoselenaspidus* Lindinger 1910, *Cupressaspis* Borchsenius 1962 (revived genus), *Davidsonaspis* Normark 2014, *Diaonidia* Takahashi 1956, *Diaspidiotus* Cockerell 1897, *Dynaspidiotus* Thiem & Gerneck 1934, *Entaspidiotus* MacGillivray 1921, *Eremiaspis* Balachowsky 1951, *Eugreeniella*

Brimblecombe 1958, *Genistaspis* Bodenheimer 1949, *Gonaspidiotus* MacGillivray 1921, *Greenoidea* MacGillivray 1921, *Helaspis* McKenzie 1963, *Helenococcus* Liu & Howell 1977, *Hemiberlesia* Cockerell 1897, *Hypaspidiotus* Takahashi 1956, *Lindingaspis* MacGillivray 1921, *Marginaspis* Hall 1946, *Megaspidiotus* Brimblecombe 1954, *Melanaspis* Cockerell 1897, *Melissoaspis* Ben-Dov 2010, *Mesoselenaspis* Fonseca 1969, *Monaonidiella* MacGillivray 1921, *Morganella* Cockerell 1897, *Murataspis* Balachowsky & Richardeau 1942, *Mycetaspis* Cockerell 1897, *Neoclavaspis* Brimblecombe 1959, *Neoselenaspis* Mamet 1958, *Nigridiaspis* Ferris 1941, *Obtusaspis* MacGillivray 1921, *Oceanaspidiotus* Takagi 1984, *Octaspidiotus* MacGillivray 1921, *Palinaspis* Ferris 1941, *Paranewsteadia* MacGillivray 1921, *Paraselenaspis* Mamet 1958, *Phaspis* Ben-Dov 1975, *Phaulaspis* Leonardi 1897, *Pseudischnaspis* Hempel 1900, *Pseudoselenaspis* Fonseca 1962, *Pygidiaspis* MacGillivray 1921, *Reclavaspis* Komosinska 1965, *Remotaspidiotus* MacGillivray 1921, *Rhizaspidiotus* MacGillivray 1921, *Rugaspidiotus* MacGillivray 1921, *Rungaspis* Balachowsky 1949, *Sahasaspis* Balachowsky 1951, *Sakalavaspis* Mamet 1954, *Schizaspis* Cockerell & Robinson 1915, *Schizentaspis* Mamet 1958, *Selenaspidopsis* Nakahara 1984, *Selenaspis* Cockerell 1897, *Selenediella* Mamet 1958, *Selenomphalos* Mamet 1958, *Spinaspidiotus* MacGillivray 1921, *Sudanaspis* Chou 1985, *Suluspis* Takagi 2007, *Taiwanaspidiotus* Takagi 1969, *Targionia* Signoret 1869, *Unaspidiotus* MacGillivray 1921, *Varicaspis* MacGillivray 1921

Transfer to ACLERDIDAE Cockerell

Mammilla Wu 2011

Transfer to HALIMOCOCCIDAE Brown & McKenzie

Comstockiella Cockerell 1896, *Xanthophthalma* Cockerell & Parrott 1899

Tribe LEPIDOSAPHIDINI Shimer

Cited as: Lepidosaphidini (Borchsenius 1966; Takagi 2002). Subsumes Antakaspidini Mamet (Borchsenius 1966).

Diagnosis: **AF** body usually elongate; usually with gland spines; usually with sclerotized pygidial lobes; marginal ducts of pygidium often larger than other dorsal ducts; often with gland spines between L1. **2F** similar to AF. **CR** with tarsal seta; without dorsal ducts on thorax. **AM** postoccipital ridge produced posteriorly into a median process; anterior arms of postoccipital ridge meeting medially; with 2 pairs of tentorial pits. **2M** scale cover simple, not tricarinate; microscopic characters similar to 2F, with a few more dorsal ducts.

The tribe Lepidosaphidini is a large and morphologically heterogeneous group and it may not be possible to define a simple suite of adult female characters that always permit recognition of the tribe. Most species of Lepidosaphidini have elongate adult females with gland spines between L1 and enlarged ducts along the pygidial margin, but there are a number of exceptions. So far as is known, the crawler lacks thoracic dorsal ducts, whereas these are present in most other species of Diaspidinae.

Included genera: A complete list is given in Table 8.

Distribution: Cosmopolitan.

Remarks: Our phylogenetic analysis finds support for a large clade (labelled "other Lepidosaphidini" in Fig. 2 and shown in detail in Figs. 4–6) that corresponds closely to the tribe Lepidosaphidini as traditionally conceived. Our analysis provides direct evidence that this clade includes the type species of 11 genera whose membership in Lepidosaphidini has never been questioned (*Mitulaspis* MacGillivray, *Eudinaspis* Lizer & Trelles, *Pallulaspis* Ferris, *Opuntiaspis* Cockerell, *Stramenaspis* Ferris, *Velataspis* Ferris, *Phaulomytilus* Leonardi, *Symeria* Green, *Coccomytilus* Leonardi, *Metandaspis* Williams, and *Porterinaspis* González), along with non-type species of 8 other non-controversial genera of Lepidosaphidini (*Aonidomytilus* Leonardi, *Ferrisidea* Borchsenius, *Dinaspis* Leonardi, *Prodigiaspis* Ferris, *Dactylaspis* Ferris, *Andaspis* MacGillivray, *Maskellanna* MacGillivray, and *Lepidosaphes* Shimer; for *Lepidosaphes* our sample includes 18 described species, including type species of the currently synonymized genera *Pinomytilus* Borchsenius, *Eucornuaspidis* Borchsenius, and *Mytilaspis* Targioni Tozzetti).

The Lepidosaphidini clade we recovered also includes representatives of other genera whose placement has historically been less clear. One of these is *Howardia* Berlese & Leonardi. *Howardia* was placed in Diaspidini by Balachowsky (1954) and Borchsenius (1966) but was understood to be as a member of Lepidosaphidini by Williams (1960) and Takagi (1992); its first-instar nymph was also described by Howell & Tippins (1990) as more



FIGURE 4. Phylogeny of the tribe Lepidosaphidini (Diaspidinae), excluding *Hulaspis*. This is the clade labelled "other Lepidosaphidini" in Fig. 2, and its relationship to the other lineages of Diaspidinae is shown in that figure. Two clades are represented here by triangular placeholders, and an expanded view of the phylogeny of each can be seen in a subsequent figure: *Pseudoparlatoria sensu lato* (Fig. 5) and *Lepidosaphes* + Australian Lepidosaphidini (Fig. 6). For the rest of the tribe, all sampled individuals are shown. For further explanation of the analysis and notation, see the caption to Fig. 1.

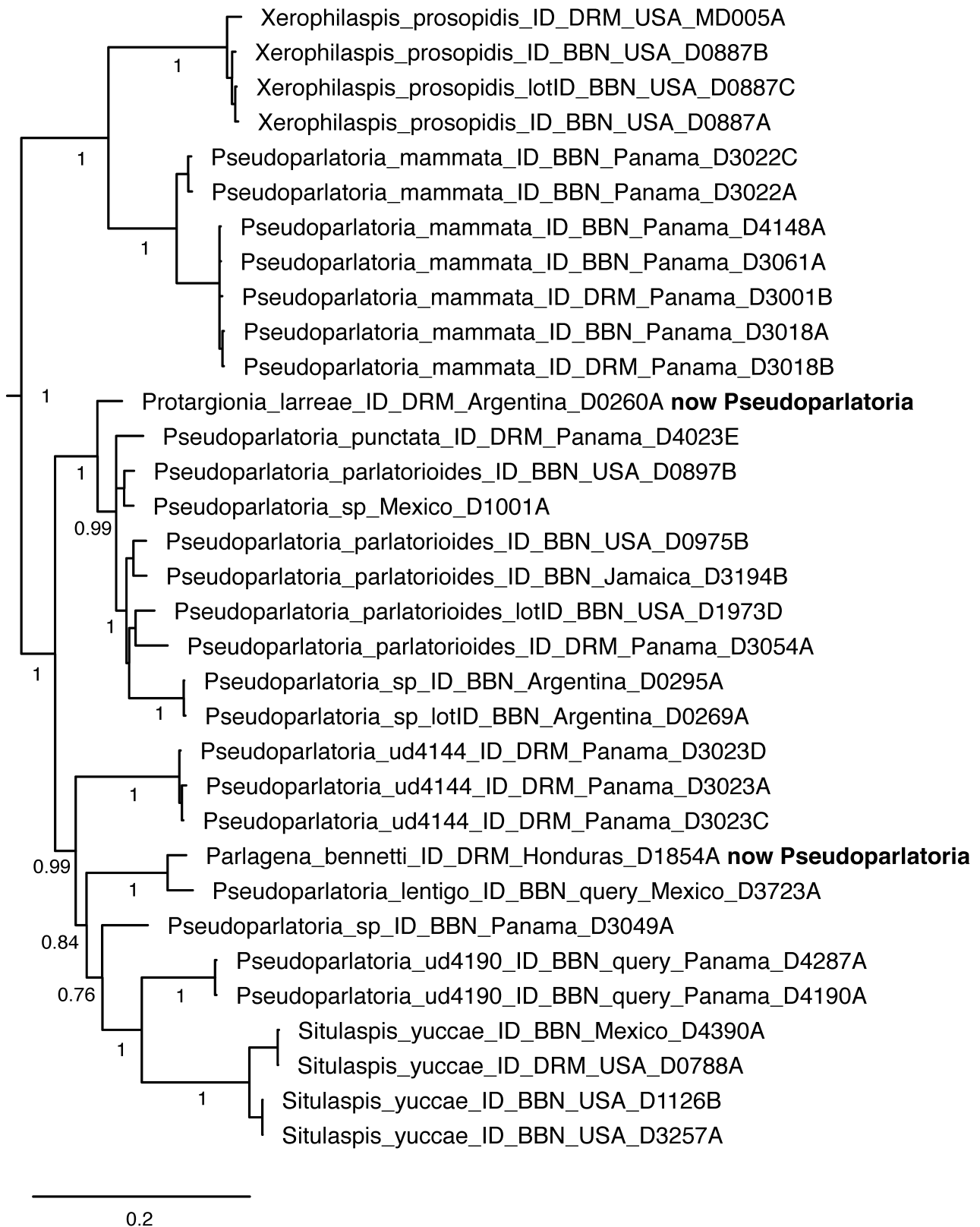


FIGURE 5. Phylogeny of *Pseudoparlatoria* Cockerell and allies (Diaspidinae: Lepidosaphidini). This figure shows the phylogeny of the clade labeled "*Pseudoparlatoria* sensu lato" in Fig. 4. For further explanation of the analysis and notation, see the caption to Fig. 1.

similar to that of Lepidosaphidini than Diaspidini, having a seta on the tarsus near the base of the claw. Williams' (1960) recognition that *Howardia* belonged in Lepidosaphidini was occasioned by his description of a new species

with an elongate body shape, *H. stricklandi* Williams. The type species of *Howardia*, *H. biclavis*, has a turbinate body shape that is more typical of Diaspidina and unusual within Lepidosaphidini.

Our phylogeny shows that *Howardia* is just one example of a general trend: shorter-bodied Lepidosaphidini have been systematically misclassified. Most of these occur within a single clade of New World species, marked as "*Pseudoparlatoria sensu lato*" on Fig. 4 and shown in detail in Fig. 5. The clade is dominated by species of *Pseudoparlatoria*, and also includes the type species of the genera *Xerophilaspis* Cockerell and *Protargionia*, along with non-type species of *Situlaspis* and *Parlagena* McKenzie. All of them are relatively short-bodied, in contrast to the elongate bodies that characterize most Lepidosaphidini species. Takagi (2011) regarded *Pseudoparlatoria*, *Situlaspis*, and *Protargionia* as members of Diaspidina. *Parlagena* has generally been regarded as belonging to Parlatoriini (Borchsenius 1966; McKenzie 1945; Williams 1969b), though a recent molecular study by Gruwell *et al.* (2016) has placed *P. bennetti* Williams in Diaspidinae, consistent with the results presented here. In spite of this heterogeneity of taxonomic treatment, the adult females of all these species are similar, with body less than twice as long as broad; barrel-shaped, 2-barred dorsal ducts submarginally on the pygidium and most prepygidial abdominal segments; rounded L1; bilobed L2; and perivulvar pores. Most strikingly, they all lack pores by the anterior spiracle, whereas all other non-pupillarial members of the subfamily Diaspidinae have such pores. Besides the relatively broad body shape, the morphological feature that seems to have generated the most confusion is the pair of gland spines between L1. The genus *Pseudoparlatoria* characteristically has a pair of broad-based gland spines in this position, described in Ferris's (1942) key as forming a "fish tail-shaped structure"; in all of the species in this clade that have been placed in genera other than *Pseudoparlatoria*, this structure is lost or poorly developed. In *Protargionia larreae* and *Parlagena bennetti*, the gland spines between L1 are very short and broad (Claps 2000; Kondo *et al.* 2015; Williams 1969b) and can appear absent in some specimens (Williams 1969b). In *Situlaspis yuccae*, L1 are close-set and the gland spines between them are minute (D. R. Miller & Davidson 2005); indeed, Ferris's (1936) illustration of this species omits these gland spines. *Parlagena bennetti* resembles the type species of *Parlagena*, *P. inops* McKenzie, in its turbinate body shape; in the distribution of barrel-shaped, 2-barred dorsal ducts; and in the minute gland-spine like structures between L1. But it differs in several characters that often separate higher taxa: *P. inops* has marginal macroducts oriented parallel to the body margin (marginal macroducts absent in *P. bennetti*), pores by the anterior spiracles (absent in *P. bennetti*), and unilobed L2 (bilobed in *P. bennetti*). *Parlagena bennetti* is also (still, nearly 50 years after its first description) known only from the New World, like the other members of this clade, whereas all other *Parlagena* species are exclusively Asian. Williams (1969b) stated that the placement of *P. bennetti* in the genus *Parlagena* was "tentative" and was based largely on advice from M.S.K. Ghauri regarding the affinities of the adult male. In light of the phylogeny (Fig. 5), it seems possible that Ghauri may have erroneously associated an unrelated (Parlatoriini) male with this species. As for *Xerophilaspis prosopidis*, it is a pupillarial species, and like many such species it is highly modified and unusual, lacking any dorsal ducts and having unilobed L2. Nonetheless, it resembles other members of this clade in lacking pores by the anterior spiracle.

In light of this molecular and morphological evidence, we transfer 2 species to *Pseudoparlatoria*, as follows: *Pseudoparlatoria bennetti* (Williams), **new combination**, and *Pseudoparlatoria larreae* (Leonardi), **new combination**. Both species are phylogenetically nested well within the genus *Pseudoparlatoria* (Fig. 5) and morphologically they are essentially typical *Pseudoparlatoria* species except that the gland spines between L1 are shorter than usual, and except that *P. bennetti* lacks marginal macroducts. This action renders the monotypic genus *Protargionia* a synonym of *Pseudoparlatoria* (Table 11).

For the present we take no nomenclatural action regarding *Situlaspis* or *Xerophilaspis*, as these are morphologically more distinctive, they are more distantly related to the core group of *Pseudoparlatoria* species, and the *Pseudoparlatoria* species to which they are more closely related are themselves morphologically distinctive. For instance, in our tree (Fig. 5) *Xerophilaspis prosopidis* is sister to *Pseudoparlatoria mammata* (Ferris), a species with a body shape strikingly different from the simple turbinate shape typical of most *Pseudoparlatoria* species. *Pseudoparlatoria mammata* has a laterally expanded mesothorax, strikingly produced margins of the metathorax and abdominal segment I, and an overall sclerotization of the body. These characters caused Ferris to place this species, with a few others, in a separate genus, *Malleolaspis* Ferris. Wolff (2008) synonymized *Malleolaspis* with *Pseudoparlatoria*, an action that implies, given the phylogeny (Fig. 5), that *Situlaspis* and *Xerophilaspis* should also be synonyms of *Pseudoparlatoria*, which would then be recognized as a morphologically heterogeneous genus united by the absence of perispiracular pores. Alternatively, a

morphologically homogeneous and monophyletic *Pseudoparlatoria* could be preserved, but this would require resurrection of the genus *Malleolaspis*.

The morphological distinctiveness of *Pseudoparlatoria* sensu lato enables us to recognize likely members based on morphology alone, even when we have not sampled the DNA. The group appears to be Neotropical and Afrotropical. Several apparent pupillarial members of the clade were included by Borchsenius in the Xerophilaspidina: *Hovaspis* Mamet, *Neoparlaspis* Hempel, and *Vinculaspis* Ferris. Other genera that appear to belong to this clade are *Diaspidistis* Hempel (Wolff & Claps 2010), *Felxiella* Almeida, *Mancaspis* Ferris, *Neopseudoparlatoria* González, *Paradiaspis* Lahille, and *Sakaramyaspis* Mamet. We also regard *Protodiaspis chinchonae* McKenzie as a species of *Pseudoparlatoria* that lacks perivulvar pores—*Pseudoparlatoria chinchonae* (McKenzie), **new combination**—a view similar to that expressed by Takagi (1993). Possibly also related to this clade is a morphologically diverse radiation of mostly Malagasy species with pygidium resembling that of *Pseudoparlatoria* but with pores near the anterior spiracles, including the genera *Cryptaspidus* Lindinger, *Emmereziaspis* Mamet, *Imerinaspis* Mamet, and *Paraleucaspis* Mamet.

Another species that our phylogeny unexpectedly placed in Lepidosaphidini was *Carulaspis giffardi* Adachi & Fullaway. As in the case of *Pseudoparlatoria*, this species was heretofore thought to be a member of Diaspidina; indeed, it was originally described in *Pseudoparlatoria* (Adachi & Fullaway 1953), before being moved by Borchsenius (1966) into *Carulaspis* MacGillivray. This species is known only from *Araucaria* Juss. in Hawaii and New Caledonia, and the available evidence suggests it is native to New Caledonia. Our phylogeny (Fig. 7) places this species within the genus *Lepidosaphes*. It is sister to a group of Australian species, which in turn is sister to the remaining species of *Lepidosaphes*. Re-examining specimens of *Carulaspis giffardi* with this phylogenetic placement in mind, it is striking that they do, indeed, fit the characters of the genus *Lepidosaphes* in all respects except for their turbinate body shape. It is also clear from the phylogeny that this species is only remotely related to the 2 genera in which it has heretofore been placed. We therefore now regard it as *Lepidosaphes giffardi* (Adachi & Fullaway), **new combination**.

There are several other taxa entangled with *Lepidosaphes*. The most complex of these is *Andaspis*. The 3 nominal species of *Andaspis* we sampled fall in 3 different places in our tree: 1 as an isolated lineage subtending the base of the Diaspidinae (Fig. 2) and 2 within *Lepidosaphes* (Fig. 5). The isolated lineage is *Andaspis formicarum*, an ant-associated species from South Africa. In several characters it differs from most other species of *Andaspis* and instead resembles the African genus *Hulaspis* Hall, having forked gland spines, each L1 with a pair of parallel basal scleroses resembling paraphyses, and a rounded sclerosis present at base of L2. Accordingly, we transfer it to that genus as *Hulaspis formicarum* (Ben-Dov), **new combination**. We also transfer from *Andaspis* another South African species with the same characters: *Hulaspis bulba* (Munting), **new combination**. We regard *Hulaspis* as a member of Lepidosaphidini. This is its traditional placement (as well as the traditional placement of *Andaspis formicarum*); its membership in Lepidosaphidini is neither supported nor refuted by our phylogenetic analysis, in which its relationship to Lepidosaphidini is unresolved (Fig 2).

Another group of *Andaspis* species are those that belong in *Lepidosaphes*. The 2 *Andaspis* species in our tree that fall within *Lepidosaphes*, *A. crawii* and *A. punicae*, closely resemble other *Lepidosaphes* species but have enlarged, close-set, roughly triangular L1. Such lobes are functionally associated with cutting through the plant epidermis, and similar lobes have arisen convergently in several different lineages of diaspidids in species that "burrow" into plant tissues (Takagi 2003). The phylogeny (Fig. 6) shows that *Andaspis*-like L1 have evolved convergently multiple times within *Lepidosaphes*. Consequently, we transfer 20 species of *Andaspis* to the genus *Lepidosaphes* (Table 9).

The third and final group of *Andaspis* species are those that, while they closely resemble *Lepidosaphes* in most characters, have a robust basal sclerosis of L1 that is not found in any species of *Lepidosaphes*. This group includes the type species, *A. hawaiiensis* (Maskell), and 21 other species. It is possible that these also belong in *Lepidosaphes* but we do not have DNA samples from any member of this group, and for the present we regard the 22 species with this character as constituting the genus *Andaspis*: *A. hawaiiensis* (Maskell), *A. artocarpi* Borchsenius, *A. brevicornuta* Hamilton & Williams, *A. conica* Hamilton & Williams, *A. glutae* Takagi, *A. halli* Rao, *A. laingi* Rao, *A. leucophleae* Rao, *A. makilingensis* Takagi, *A. meliae* (Green), *A. naracola* Takagi, *A. novaecaledoniae* Hamilton & Williams, *A. nothofagi* Hamilton & Williams, *A. numerata* Brimblecombe, *A. ornata* Hamilton & Williams, *A. piceae* Takagi & Kawai, *A. raoi* (Borchsenius), *A. retrusa* Williams, *A. rutae* Tang, *A. tokyoensis* Takagi & Kawai, *A. vandrae* (Rutherford), and *A. yunnanensis* Ferris.

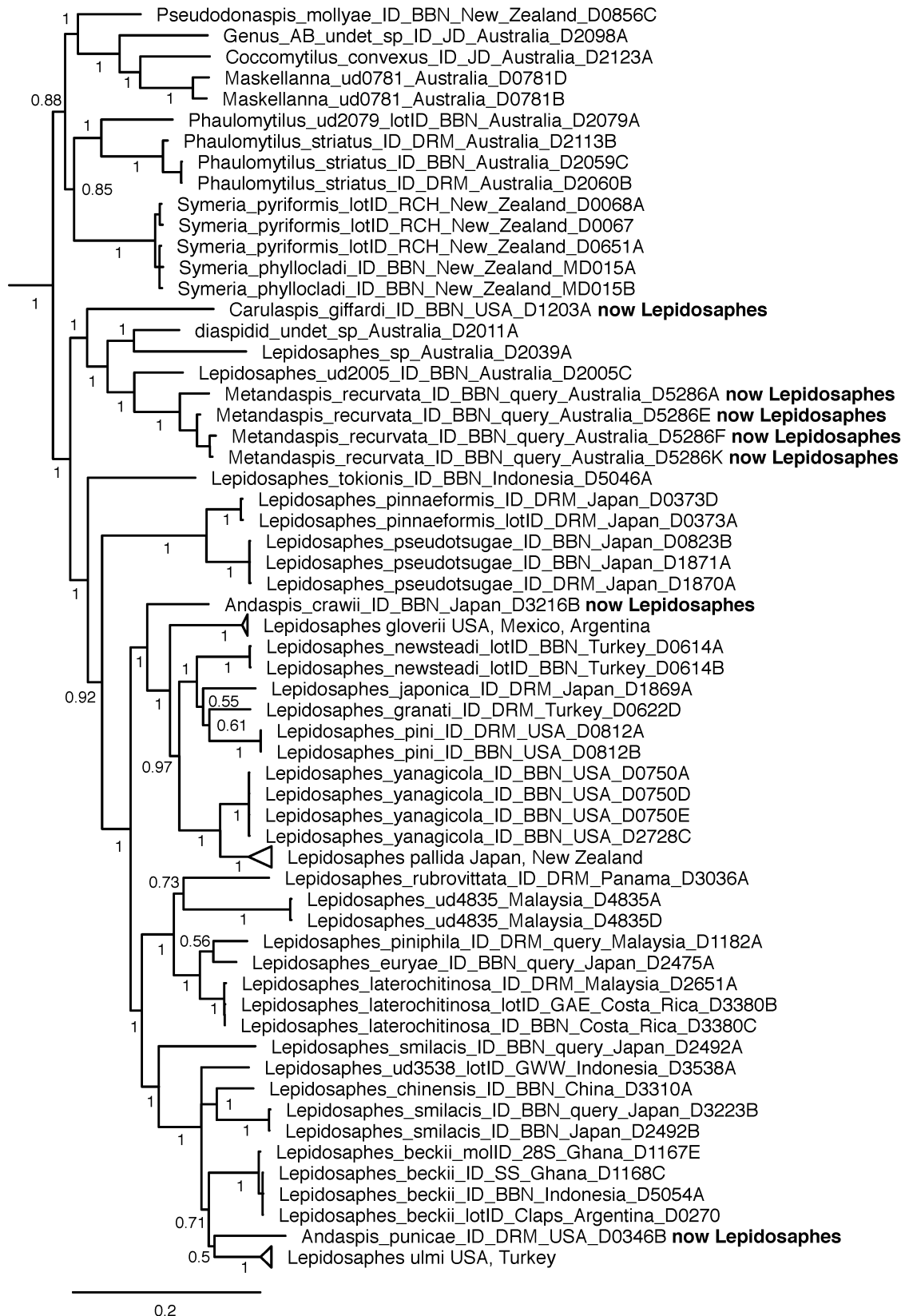


FIGURE 6. Phylogeny of *Lepidosaphes* Shimer and allies (Diaspidinae: Lepidosaphidini). This figure shows the phylogeny of the clade labeled "*Lepidosaphes* + Australian Lepidosaphidini" in Fig. 4. We have condensed the figure somewhat by representing 3 well-sampled species with triangular placeholders rather than listing all the individuals sampled. For further explanation of the analysis and notation, see the caption to Fig. 1.

Another traditionally recognized genus that falls phylogenetically within *Lepidosaphes* is *Ungulaspis* MacGillivray. The undescribed species we have designated *Lepidosaphes* ud4835 possesses the defining characters of *Ungulaspis*—abdominal segments with highly produced margins, with gland spines at the apices (Williams 1971)—and this species, too, is nested well within *Lepidosaphes* (Fig. 6). We therefore regard *Ungulaspis* as another synonym of *Lepidosaphes* (Tables 9, 11). A similar view may be implicit in Miller *et al.*'s (2006) use of the combination *Lepidosaphes pinicolous* Chen in place of *U. pinicolous*.

A slightly more problematic case is represented by *Metandaspis*. This is a monotypic Australian genus whose only species, *M. recurvata*, is nested within *Lepidosaphes*, in the Australasian clade that also includes *L. giffardi* and that constitutes the sister-group of the remaining *Lepidosaphes*. What is more problematic about *Metandaspis* is that it is morphologically more distinctive, lacking the large marginal macroducts ("megaducts" of Balachowsky) that characterize all other species of *Lepidosaphes*. This is one of several examples of a striking autapomorphy within a relatively homogeneous group of armored scales—the genus *Ichthyaspis* Takagi within *Fiorinia*, discussed below under Fioriniina, provides another example. To place diaspidid classification on a more natural footing it is necessary to place such taxa in the groups in which they actually belong—thus we need to sink *Metandaspis* into *Lepidosaphes* as *Lepidosaphes recurvata* (Froggatt), **revived combination**, even though this disrupts the traditional basis for recognizing *Lepidosaphes*.

TABLE 9. Summary of new and revived combinations. For authors of genera, see Table 8. For more complete nomenclatural history of species, see ScaleNet (García Morales *et al.*, 2016). For further discussion of each case, see Notes on Higher Taxa.

New or revived combination	Genus in which species has previously been placed	Higher taxon in which species is now placed
<i>Aonidia edgerleyi</i> (Mamet), new combination	Bigymnaspis	Aonidiini
<i>Aonidomytilus espinosai</i> Porter, revived combination	Porterinaspis	Lepidosaphidini
<i>Aspidiotus badius</i> (Brain), new combination	Aonidia	Aspidiotini
<i>Aspidiotus biafrae</i> (Lindinger), new combination	Aonidia	Aspidiotini
<i>Aspidiotus chaetachmeae</i> (Brain), new combination	Aonidia	Aspidiotini
<i>Aspidiotus laticornis</i> (Balachowsky), new combination	Aonidia	Aspidiotini
<i>Aspidiotus rhusae</i> (Brain), new combination	Aonidia	Aspidiotini
<i>Aspidiotus sclerosus</i> (Munting), new combination	Aonidia	Aspidiotini
<i>Brimblecambia asperata</i> (Brimblecombe), new combination	Ancepaspis	Aonidiini
<i>Brimblecambia longicauda</i> (Brimblecombe), new combination	Ancepaspis	Aonidiini
<i>Brimblecambia magnicauda</i> (Brimblecombe), new combination	Ancepaspis	Aonidiini
<i>Brimblecambia reticulata</i> (Brimblecombe), new combination	Ancepaspis	Aonidiini
<i>Brimblecambia rotundicauda</i> (Brimblecombe), new combination	Ancepaspis	Aonidiini
<i>Brimblecambia striata</i> (Brimblecombe), new combination	Ancepaspis	Aonidiini
<i>Cooleyaspis pseudomorpha</i> (Leonardi), new combination	Dinaspis	Fioriniina
<i>Cupidaspis wilkeyi</i> (Howell & Tippins), new combination	Paracupidaspis	Chionaspidina
<i>Cupressaspis isfarensis</i> Borchsenius, revived combination	Aonidia	Aspidiotini
<i>Cupressaspis mediterranea</i> (Lindinger), revived combination	Aonidia	Aspidiotini
<i>Cupressaspis relictata</i> (Balachowsky), new combination	Aonidia	Aspidiotini
<i>Diaspidiotus atlanticus</i> (Ferris), new combination	Aonidia	Aspidiotini
<i>Diaspidiotus marginalis</i> (Brain), new combination	Aonidia	Aspidiotini
<i>Diaspidiotus maroccanus</i> (Balachowsky), new combination	Aonidia	Aspidiotini
<i>Diaspidiotus mesembryanthemae</i> (Brain), new combination	Aonidia	Aspidiotini
<i>Diaspidiotus opertus</i> (De Lotto), new combination	Aonidia	Aspidiotini
<i>Diaspidiotus shastae</i> (Coleman), new combination	Aonidia	Aspidiotini

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TABLE 9. (Continued)

New or revived combination	Genus in which species has previously been placed	Higher taxon in which species is now placed
<i>Diaspidiotus simplex</i> (Leonardi), new combination	Aonidia	Aspidiotini
<i>Diaspidiotus visci</i> (Hall), new combination	Aonidia	Aspidiotini
<i>Diaspidiotus yomae</i> (Munting), new combination	Aonidia	Aspidiotini
<i>Diaspis arundinariae</i> (Howell & Tippins), new combination	Geodiaspis	Diaspidina
<i>Duplachionaspis arecibo</i> (Howell), new combination	Haliaspis	Chionaspidina
<i>Duplachionaspis asymmetrica</i> Ferris, revived combination	Haliaspis	Chionaspidina
<i>Duplachionaspis distichlii</i> (Ferris), revived combination	Haliaspis	Chionaspidina
<i>Duplachionaspis litoralis</i> Ferris, revived combination	Haliaspis	Chionaspidina
<i>Duplachionaspis mackenziei</i> McDaniel, revived combination	Haliaspis	Chionaspidina
<i>Duplachionaspis milleri</i> (Howell), new combination	Haliaspis	Chionaspidina
<i>Duplachionaspis mutica</i> (Williams), new combination	Aloaspis	Chionaspidina
<i>Duplachionaspis nakaharai</i> (Howell), new combination	Haliaspis	Chionaspidina
<i>Duplachionaspis peninsularis</i> (Howell), new combination	Haliaspis	Chionaspidina
<i>Duplachionaspis spartinae</i> (Comstock), revived combination	Haliaspis	Chionaspidina
<i>Duplachionaspis texana</i> (Liu & Howell), new combination	Haliaspis	Chionaspidina
<i>Duplachionaspis uniolae</i> (Takagi), new combination	Haliaspis	Chionaspidina
<i>Epidiaspis doumtsopi</i> (Schneider), new combination	Diaspis	Diaspidina
<i>Fiorinia ficicola</i> (Takahashi), new combination	Ichthyaspis	Fioriniina
<i>Fiorinia macroprocta</i> (Leonardi), revived combination	Trullifiorinia	Fioriniina
<i>Fiorinia rubrolineata</i> Leonardi, revived combination	Trullifiorinia	Fioriniina
<i>Fiorinia scrobicularum</i> Green, revived combination	Trullifiorinia	Fioriniina
<i>Genaparlatoria pseudaspidiotus</i> (Lindinger), revived combination	Parlatoria	Aonidiini
<i>Greeniella acaciae</i> (Froggatt), new combination	Gymnaspis	Aonidiini
<i>Greeniella cassida</i> (Hall & Williams), new combination	Gymnaspis	Aonidiini
<i>Greeniella grandis</i> (Green), new combination	Gymnaspis	Aonidiini
<i>Greeniella perpusilla</i> (Maskell), new combination	Gymnaspis	Aonidiini
<i>Greeniella serrata</i> (Froggatt), new combination	Gymnaspis	Aonidiini
<i>Hendersonaspis anomala</i> (Green), new combination	Ancepaspis	Leucaspidini
<i>Hulaspis bulba</i> (Munting), new combination	Andaspis	Lepidosaphidini
<i>Hulaspis formicarum</i> (Ben-Dov), new combination	Andaspis	Lepidosaphidini
<i>Hyparrheniaspis minima</i> (Howell & Tippins), new combination	Odonaspis	Fioriniina
<i>Lepidosaphes antidesmae</i> (Rao in Rao & Ferris), new combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes arcana</i> (Matile-Ferrero), new combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes betulae</i> (Borchsenius), new combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes citricola</i> (Young & Hu), new combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes conocarpi</i> (Takagi), new combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes crawi</i> (Cockerell), revived combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes erythrinae</i> Rutherford, revived combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes ficicola</i> Takahashi, revived combination	Ungulaspis	Lepidosaphidini
<i>Lepidosaphes garciniae</i> (Young & Hu), new combination	Ductofrontaspis	Lepidosaphidini

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TABLE 9. (Continued)

New or revived combination	Genus in which species has previously been placed	Higher taxon in which species is now placed
<i>Lepidosaphes giffardi</i> (Adachi & Fullaway), new combination	Carulaspis	Lepidosaphidini
<i>Lepidosaphes huangyangensis</i> (Young & Hu), new combination	Ductofrontaspis	Lepidosaphidini
<i>Lepidosaphes incisor</i> Green, revived combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes indica</i> (Borchsenius), new combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes jingdongensis</i> (Young & Hu), new combination	Ductofrontaspis	Lepidosaphidini
<i>Lepidosaphes kashicola</i> Takahashi, revived combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes kazimiae</i> (Williams), new combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes laurentina</i> (Almeida), new combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes maai</i> (Williams & Watson), new combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes mackieana</i> McKenzie, revived combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes micropori</i> (Borchsenius), new combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes pinicolous</i> Chen, revived combination	Ungulaspis	Lepidosaphidini
<i>Lepidosaphes punicae</i> Laing, revived combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes quercicola</i> (Borchsenius), new combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes recurrens</i> (Takagi & Kawai), new combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes recurvata</i> (Froggatt), revived combination	Metandaspis	Lepidosaphidini
<i>Lepidosaphes serrulata</i> (Ganguli), new combination	Velataspis	Lepidosaphidini
<i>Lepidosaphes ungulata</i> Green, revived combination	Ungulaspis	Lepidosaphidini
<i>Lepidosaphes viticis</i> (Takagi), new combination	Andaspis	Lepidosaphidini
<i>Lepidosaphes xishuanbannae</i> (Young & Hu), new combination	Andaspis	Lepidosaphidini
<i>Leucaspsis illicitana</i> (Gómez-Menor), new combination	Aonidia	Leucaspidini
<i>Lopholeucaspsis spinomarginata</i> (Green), new combination	Gymnaspsis	Leucaspidini
<i>Melanaspsis campylanthi</i> (Lindinger), new combination	Aonidia	Aspidiotini
<i>Mohelnaspsis bidens</i> (Green), new combination	Fiorinia	Lepidosaphidini
<i>Parlatoria affinis</i> (Ramakrishna Ayyer), new combination	Gymnaspsis	Parlatoriini
<i>Parlatoria bullata</i> (Green), new combination	Bigymnaspsis	Parlatoriini
<i>Parlatoria ficus</i> (Ramakrishna Ayyer), new combination	Gymnaspsis	Parlatoriini
<i>Parlatoria leucaspsis</i> (Lindinger), new combination	Cryptoparlatoria	Parlatoriini
<i>Parlatoria mangiferae</i> (Ramakrishna Ayyer), new combination	Gymnaspsis	Parlatoriini
<i>Parlatoria pini</i> (Takahashi), new combination	Cryptoparlatoria	Parlatoriini
<i>Parlatoria ramakrishnai</i> (Green), new combination	Gymnaspsis	Parlatoriini
<i>Parlatoria sclerosa</i> (Munting), new combination	Gymnaspsis	Parlatoriini
<i>Pseudoparlatoria bennetti</i> (Williams), new combination	Parlagena	Lepidosaphidini
<i>Pseudoparlatoria chinchonae</i> (McKenzie), new combination	Protodiaspsis	Lepidosaphidini
<i>Pseudoparlatoria larreae</i> (Leonardi), revived combination	Protargonia	Lepidosaphidini
<i>Quernaspsis lepineyi</i> (Balachowsky), new combination	Chionaspsis	Chionaspidina
<i>Rhizaspidotus nullispinus</i> (Munting), new combination	Aonidia	Aspidiotini
<i>Rolaspis marginalis</i> (Leonardi), new combination	Lepidosaphes	Fioriniina
<i>Salicicola lepellei</i> (De Lotto), new combination	Anotaspis	Leucaspidini
<i>Tecaspsis giffardi</i> (Leonardi), new combination	Dinaspsis	Fioriniina
<i>Trullifiorinia geijeriae</i> (Froggatt), new combination	Fiorinia	Chionaspidina
<i>Trullifiorinia nigra</i> (Lindinger), revived combination	Crypthemichionaspsis	Chionaspidina
<i>Voraspsis olivina</i> (Leonardi), new combination	Lepidosaphes	Fioriniina

Regarding *Lepidosaphes*, a few other improvements are possible for taxa we did not collect, based on morphology. The genus *Ductofrontaspis* Young & Hu is defined by an unusual character, the presence of disk pores on the head, but the members of the genus are otherwise clearly referable to the genus *Lepidosaphes*. For instance, the type species *Ductofrontaspis huangyangensis* Young & Hu is morphologically very close to *Lepidosaphes euryae* (Kuwana), sharing very similar characters of the pygidial margin and a similar distribution of small dorsal ducts, with simple eyes and lacking cicatrices. It seems clear that disk pores on the head is a character that has arisen within the genus *Lepidosaphes*, and therefore that *Ductofrontaspis* should be regarded as a synonym of *Lepidosaphes*, **new synonymy**. The resulting new combinations are given in Table 9.

Another species that we find belongs in *Lepidosaphes* based on morphology is *Velataspis serrulata* Ganguli; the placement of this Indian species in the Neotropical genus *Velataspis* has always been biogeographically anomalous. The conical tubercles along the frontal margin that were apparently the basis of this generic assignment are seen in several other species of *Lepidosaphes*, such as *L. coreana* Borchsenius and *L. ogasawaraensis* Kawai; hence we regard this species as *Lepidosaphes serrulata* (Ganguli), **new combination**. We also find, based on morphology, that 2 putative New World species of *Lepidosaphes* are synonyms of species that are native to the Old World: *L. boguschi* McDaniel is a synonym of *Lepidosaphes punicae* Laing, **revived combination, new synonymy**; and *L. caribaeae* Williams & Miller is a synonym of *Lepidosaphes rubrovittata* Cockerell, **new synonymy**.

Perhaps the most morphologically distinctive and surprising inclusions in Lepidosaphidini in our phylogeny are 2 New Zealand species that resemble Odonaspidini or Smilacicolini, having abundant small dorsal ducts. One is the monotypic genus *Pseudodonaspis* Henderson, and the other is the even more *Odonaspis*-like species *Poliaspoides leptocarpi*. *Pseudodonaspis* feeds on grasses, like *Odonaspis*; *Poliaspoides leptocarpi* feeds on the grass-like Restionaceae. Morphologically similar to both of these is the Nearctic species *Rugaspidiotinus nebulosus* (Ferris). As discussed above, it was not included in this study but we have unpublished data from 2 loci that place it in Lepidosaphidini.

Our sample includes 2 species traditionally placed in *Aonidomytilus*: *A. espinosai* and *A. ceanothi*. The first of these is the type species of the recently erected monotypic genus *Porterinaspis* (Gonzalez 2016), which was distinguished from *Aonidomytilus* by longer gland spines and a more anterior position of the anus. Here *Porterinaspis* is regarded as a synonym of *Aonidomytilus*, **new synonymy**. There exist Nearctic species of *Aonidomytilus*, such as *A. sabatius* Tippins and *A. solidaginis* (Hoke), that have even longer gland spines than *A. espinosai*; both of these also have an anus further anterior than that of *A. espinosai*, as do *A. durus* Ferris, *A. insulanus* Ferris, *A. hyperici* Ferris, *A. variabilis* Ferris and *A. leovalenciae* Balachowsky. Thus we regard these as characters that vary within the genus *Aonidomytilus*, a view supported by the results of this DNA study, which shows a close relationship between *A. espinosai* and *A. ceanothi*.

Our sample also includes what have heretofore been considered 2 species of *Symeria*: *S. pyriformis* (Maskell) and *S. phyllocladi* Henderson. Henderson (2011) described these species as morphologically very similar, but with *S. phyllocladi* having a line of submedial-submarginal ducts on abdominal segment VII and a different host association. We found no sequence differences between the 2 species. *Symeria pyriformis* is already known to be a morphologically variable species that often has different numbers of ducts on different hosts (Henderson 2005, 2011). We infer that *S. phyllocladi* represents a host-induced phenotype of *S. pyriformis* and regard it as a synonym of that species, **new synonymy**.

Our phylogeny leaves the geographic origins of Lepidosaphidini unclear. Many of our samples come from the New World and the Australasian region, and lineages from both regions are involved in a polytomy at the base of the clade (Fig. 4); meanwhile our only African lineage falls slightly outside the clade (Fig. 2, *Hulaspis formicarum*). However, both included Eurasian lineages (the Oriental *Mitulaspis* and the Oriental + Palearctic lineage of *Lepidosaphes*) are nested within the Australasian clade, suggesting that Lepidosaphidini colonized Eurasia via the Australasian region. (In the discussion of biogeographic patterns, here and below, we ignore recent human-assisted colonization events and focus on those ancient enough to have given rise to endemic taxa in the invaded region.) But our sketch of the biogeography of Lepidosaphidini is highly sensitive to biased and inadequate sampling and will no doubt evolve in the future as more taxa are added to the phylogenetic analysis.

We do not recognize any subtribes of Lepidosaphidini. The phylogenetic analysis suggests that the characters on which the subtribes have been based (e.g. the presence of plates for Mempelaspina and the form of the pygidial lobes for Andaspidina Balachowsky) tend to arise repeatedly, and that Lepidosaphidina Shimer, as traditionally recognized, is paraphyletic with respect to the other subtribes.

In Table 8 we have sought to present a complete list of the genera of Lepidosaphidini, not only those discussed above for which we have direct molecular evidence. Many of the genera we have included have previously been recognized as members of Lepidosaphidini and we expect their inclusion to be uncontroversial (Balachowsky, 1968; Borchsenius, 1966; Takagi, 1969, 1995, 2000, 2003; and Ülgentürk & Kozár, 2011): *Acanthomytilus* Borchsenius, *Allantomytilus* Leonardi, *Bayuraspis* Takagi, *Berlesiaspis* MacGillivray, *Caia* Williams, *Cynodontaspis* Takagi, *Daraspis* Hall, *Ferreroaspis* Kozár, *Fulaspis* Balachowsky, *Galeomytilus* Takagi, *Hexandaspis* Takagi, *Koroneaspis* Bodenheimer, *Lapazia* Ferris, *Mauritiaspis* Mamet, *Melayumytilus* Takagi, *Mempelaspis* Takagi, *Mercetaspis* Gómez-Menor, *Mimusaspis* Mamet, *Mitraspis* Ferris, *Mohelnaspis* Šulc, *Neopinaspis* McKenzie, *Niveaspis* MacGillivray, *Notandaspis* Williams & Brookes, *Palauaspis* Beardsley, *Parandaspis* Mamet, *Paraparlagena* Mamet, *Paraepidiaspis* Balachowsky, *Pandanaspis* Mamet, *Parapandanaspis* Mamet, *Santubongia* Takagi, *Scleromytilus* Hall, *Scytalaspis* Ferris, *Saotomaspis* Balachowsky, *Torosaspis* Ülgentürk & Kozár, *Triaspidis* MacGillivray, and *Triraphaspis* Balachowsky. It has been over 50 years since the last complete classification of the genera of Diaspididae (Borchsenius 1966). A number of genera described since then have never been formally classified, including some whose inclusion in Lepidosaphidini should be non-controversial, such as *Neoischnaspis* Fonseca and *Gynandraspis* Balachowsky & Matile-Ferrero. But other included genera have not previously been suggested as members of Lepidosaphidini, and their inclusion here may surprise some readers. We have already mentioned *Poliaspoides* MacGillivray and *Rugaspidotinus* Balachowsky, which lack pygidial appendages and were once placed in the subtribe Rugaspidotina Balachowsky, a taxon long understood by Takagi (1995) to be artificial. Another "rugaspidotine" recently recognized as a member of Lepidosaphidini is *Prodigiaspis riverae* (Cockerell), a Chilean species that was described in *Aspidiotus* in 1905 and languished in that genus until it was recognized as species of *Prodigiaspis* by González (2016)—a conclusion that we also arrived at, independently. Based in part on the examples of these unusual species, we have rather speculatively placed into Lepidosaphidini a number of other genera, some of which were previously placed in Rugaspidotini: *Leonardianna* MacGillivray and *Praecocaspis* Ferris (these 2 genera represent New World species lacking perispiracular pores that may fall within *Pseudoparlatoria* sensu lato), *Adiscodiaspis* Marchal, *Ambigaspis* MacGillivray, *Annulaspis* Ferris, *Antakaspis* Mamet, *Balaspis* Hall, *Crassaspis* Ferris, *Dentaspis* MacGillivray, *Discodiaspis* Koronéos, *Eucleaspis* Munting, *Exuviaspis* Ferris, *Faureaspis* Munting, *Galeraspis* Mamet, *Kandraspis* Mamet, *Madaparlaspis* Mamet, *Madagaspis* Mamet, *Operculaspis* Laing, *Osiraspis* Hall, *Primaspis* Howell, *Pseudoleucaspis* Mamet, *Pudaspis* Hall, *Ramachandraspis* Rao, *Rugpauaspis* Ben-Dov, *Serrataspis* Ferris, and *Youngus* Özdikmen.

At least 1 species that heretofore has been placed in the genus *Fiorinia* (Diaspidini: Fioriniina) has gland spines between L1 and clearly belongs in Lepidosaphidini: *Mohelnaspis bidens* (Green), **new combination**.

TABLE 10. Replacement names.

Replacement name	Name replaced	Notes
<i>Lepidosaphes huiyoung</i> Normark	<i>Andaspis ficicola</i> Young & Hu	The replaced name became a junior homonym of <i>L. ficicola</i> Takahashi when the species was transferred to <i>Lepidosaphes</i> .
<i>Lepidosaphes tangi</i> Normark	<i>Andaspis schimae</i> Tang	The replaced name became a junior homonym of <i>L. schimae</i> Kawai when the species was transferred to <i>Lepidosaphes</i> .
<i>Lepidosaphes yuanfeng</i> Normark	<i>Andaspis keteleeriae</i> Yuan & Feng	The replaced name became a junior homonym of <i>L. keteleeriae</i> Ferris when the species was transferred to <i>Lepidosaphes</i> .
<i>Parlatoria tangi</i> Normark	<i>Parlatoria pini</i> Tang	Transfer of <i>Cryptoparlatoria pini</i> Takahashi to <i>Parlatoria</i> made the replaced name a junior homonym of <i>Parlatoria pini</i> (Takahashi), new combination

Tribe DIASPIDINI Targioni Tozzetti

Diagnosis: **AF** without fringed plates (except in some bamboo-feeding species), with gland spines; L2 bilobular; ducts 2-barred; long axes of orifices of marginal macroducts usually oblique or perpendicular to body margin; pores by anterior spiracle usually present, usually 3-locular; marginal macroducts usually the same size as, or only slightly larger than, dorsal macroducts. **2F** similar to **AF**. **CR** without seta on tarsus. **AM** postoccipital ridge not produced posteriorly into a median process; anterior arms of postoccipital ridge separated by a distance equal to or

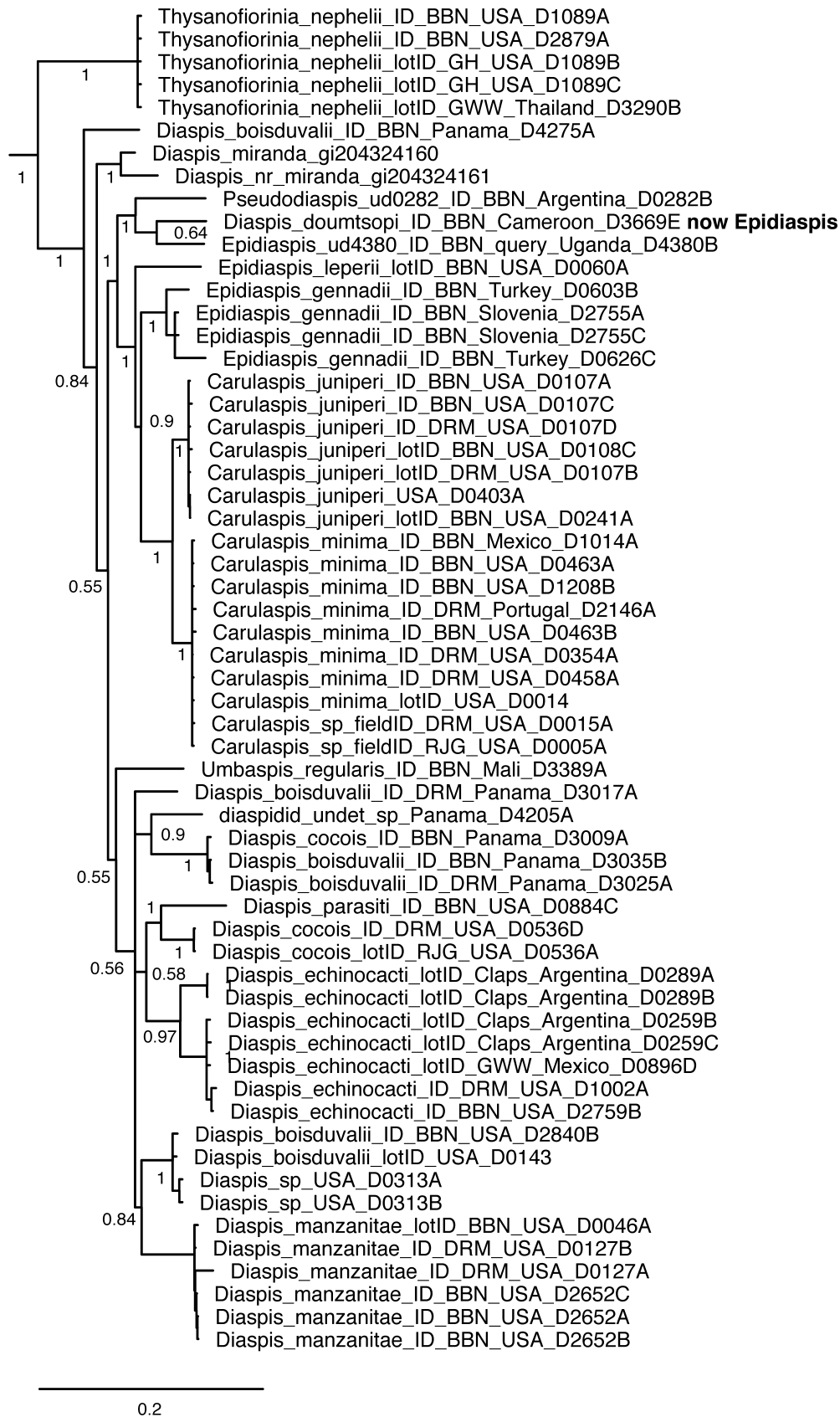


FIGURE 7. Phylogeny of the subtribe Diaspidina (Diaspidinae: Diaspidini), whose relationship to other Diaspidini is shown in Fig. 2. For further explanation of the analysis and notation, see the caption to Fig. 1.

greater than their own length; with 1 pair of tentorial pits. **2M** usually with tricarinate scale cover and distinctly different from 2F, with more dorsal ducts and often having modified ducts unlike those seen in females.

This tribe is notable for the marked sexual dimorphism of the second-instar nymph. Male scale covers in the field often have 3 distinctive ridges or carinae, and on a microscope slide second-instar males often have distinctive ducts not seen in other life stages; these differ between the subtribes as described below.

Included genera: *Furchadaspis* MacGillivray, *Gadaspis* Borchsenius, *Ischnaspis* Douglas, *Nimbaspis* Balachowsky, *Prodiaspis* Young, *Pygalataspis* Ferris, *Roureaspis* Takagi, *Trischnaspis* Ben-Dov, and the genera listed in the subtribes below.

Distribution: Cosmopolitan.

Tribe DIASPIDINA Targioni Tozzetti

Cited as: Diaspidina (Takagi 2002, 2011).

Diagnosis: **AF** L1 usually not joined by a zygotis; often with a marginal or submarginal macroduct, or a pair of gland spines, between L1. **AM** antennal scape with 1 ventral seta; terminal antennal segment with 8–16 simple setae and 2 ventral knobbed setae; prosternum with lateral ridges absent; tegula with 0–3 setae. **2M** ducts sometimes paired but not tightly clustered along invaginations in body margin, not complex with narrow tubes in addition to the main duct.

Included genera: A complete list is given in Table 8.

Distribution: Cosmopolitan except Australasia; widely introduced.

Remarks: Our phylogenetic analysis finds support for a clade (labelled "Diaspidina" in Fig. 2 and shown in detail in Fig. 7) that corresponds approximately to the subtribe Diaspidina as defined by Takagi (2011). The main difference from Takagi's concept of the subtribe is that 4 genera included by Takagi in Diaspidina are removed to elsewhere in the classification, as discussed above: *Pseudoparlatoria*, *Situlaspis*, and *Protargionia* (to Lepidosaphidini), along with *Furchadaspis* (to Diaspidini *incertae sedis*). Our analysis provides direct evidence that this clade includes the type species of 5 genera: *Diaspis*, *Umbaspis* MacGillivray, *Epidiaspis* Cockerell, *Carulaspis*, and *Thysanoflorinia* Balachowsky, along with a non-type (undescribed) species of *Pseudodiaspis* Cockerell (Fig. 7).

In addition to these sampled genera, our proposed list of the genera of Diaspidina (Table 8) includes the other genera placed in this subtribe by Takagi (2011): *Bantudiaspis* Hall, *Diaulacaspis* Takahashi, *Incispaspis* MacGillivray, and *Leptodiaspis* Takagi. We also include in this subtribe 2 pupillarial African genera omitted by Takagi (*Credodiaspis* MacGillivray and *Cryptodiaspis* Lindinger), based on the close similarity of the pygidial fringe of the second-instar females to those of *Diaspis*, along with the recently described genus *Chilesaphes* González, agreeing with González (2016) that it is close to *Diaspis*. We follow Takagi (2011) in regarding *Geodiaspis* Tippins & Howell as a synonym of *Diaspis*. Takagi did not actually form the new combination, so to clarify this synonymy we form it here: *Diaspis arundinariae* (Howell & Tippins), **new combination**.

In our results (Fig. 7), the only sampled Oriental lineage, *Thysanoflorinia nephelii*, is sister to the rest of the subtribe (representing the New World, Africa and the Palearctic). We also find that *Diaspis doumtsopi* falls outside of the genus *Diaspis* and instead is more closely related to species of *Epidiaspis*. This actually accords with morphology, as *D. doumtsopi* has only 1 pair of sclerotized pygidial lobes and keys out as *Epidiaspis* in Hall's (1946) key. Its original generic assignment was based on a preliminary molecular analysis that indicated it was more closely related to *Diaspis* than to *Epidiaspis*—an assessment now shown by this more complete analysis to have been erroneous. Accordingly, here we reassign it as *Epidiaspis doumtsopi* (Schneider), **new combination**.

Subtribe FIORINIINA Leonardi

Cited as: Fioriniini (Borchsenius 1966), Fioriniina (Takagi 2002). Subsumes Kuwanaspina (Borchsenius 1966; Takagi 1999b, 2002).

Diagnosis: **AF** L1 often joined by a strap-like zygotis; usually with a pair of setae between L1; without a macroduct or pair of gland spines between L1. **AM** antennal scape without setae; terminal antennal segment with capitate seta at apex and 14–23 simple setae; prosternum with lateral ridges present; tegula with 2–6 setae. **2M** pygidial margin often with invaginations lined with tightly clustered ducts.

Included genera: A complete list is given in Table 8.

Distribution: Cosmopolitan except New World; widely introduced.

Remarks: Our phylogenetic analysis finds support for a clade, labelled Fioriniina in Fig. 2 and shown in detail in Figs. 8–10, that largely corresponds to Takagi's concept of the subtribe Fioriniina, except that it includes within it his subtribe Kuwanaspidina (Takagi 1999b, 2002; Takagi *et al.* 1988) and 2 genera (*Lineaspis* MacGillivray, *Ichthyaspis* Takagi) that he had placed in Chionaspidina (Takagi 1970, 2007). We have direct molecular evidence that this clade includes the type species of the genera *Fiorinia*, *Pseudaulacaspis*, *Lineaspis*, *Ichthyaspis*, *Poliaspis* Maskell, *Anzaspis* Henderson, *Ischnafiorinia* MacGillivray, *Rolaspis* Hall, *Rutherfordia* MacGillivray, *Pellucidaspis* Henderson, *Kuwanaspis*, *Nikkoaspis*, and *Unachionaspis* MacGillivray, and that it also includes the species heretofore called *Odonaspis minima* Howell & Tippins, which we are calling *Hyparrheniaspis minima* (Howell & Tippins), **new combination**. As mentioned in the Discussion, species of *Pseudaulacaspis* are scattered phylogenetically throughout the tribe. Several of the other genera also closely resemble *Pseudaulacaspis*, such as *Poliaspis*, *Rutherfordia*, *Rolaspis*, *Anzaspis*, and *Pellucidaspis*. The genus *Fiorinia* consists of pupillarial species and for that reason was placed by Borchsenius (1966) in a different tribe from *Pseudaulacaspis* and the other non-pupillarial genera listed here. But species of *Fiorinia* nonetheless bear a detailed similarity to those of *Pseudaulacaspis*, with fewer dorsal ducts but a similar pygidial fringe and very similar second-instar nymphs, allowing Takagi (1969) and Howell & Tippins (1973) to recognize the close relationship of these other genera to *Fiorinia*. From within this clade of morphologically similar species there have arisen several lineages of such morphological novelty that their relationship to this subtribe is difficult to discern.

The largest such lineage is a clade of grass-feeding species, consisting, in our sample, of the genera *Kuwanaspis*, *Nikkoaspis*, *Unachionaspis*, and *Hyparrheniaspis* Ghabbour & Hamon (Figs. 8, 9). *Kuwanaspis* and *Nikkoaspis* were placed in a separate subtribe Kuwanaspidina by both Borchsenius (1966) and Takagi (1999b). Members of Kuwanaspidina have fringed plates like members of the subfamily Aspidiotinae, causing Takagi (2002) to view them as a relatively primitive subtribe of Diaspidini, but our phylogeny makes it clear that their unusual features are convergently derived rather than primitive. *Unachionaspis* and *Hyparrheniaspis* species lack these plates. Takagi (1970) suggested a close relationship between *Unachionaspis* and *Kuwanaspis*, but in a later, more detailed study of Kuwanaspidina (Takagi 1999b) he excluded *Unachionaspis* from membership in the subtribe. Our phylogeny of this clade (Fig. 9.), which has the structure (*Unachionaspis* (*Hyparrheniaspis* (*Kuwanaspis* (*Nikkoaspis*))) provides evidence that the grass-feeding habit preceded the convergent evolution of fringed plates. Although the adult females of Kuwanaspidina are unusual, Howell & Tippins (1973; 1990) discerned the close relationship of *Kuwanaspis* to *Fiorinia* and *Pseudaulacaspis* based on the tightly clustered ("communal") ducts of the second-instar male.

The most surprising element in this clade—and indeed perhaps in all of Diaspidinae—is the species we are calling *Hyparrheniaspis minima* (Howell & Tippins). Until now, this species has been placed in the genus *Odonaspis*, in a different subfamily (Aspidiotinae), though it had always been recognized as a highly unusual member of that genus (Howell & Tippins 1978). We sampled several species of *Odonaspis* (Fig. 3) and our results show that *H. minima* is phylogenetically distant from that genus. Here we transfer it to the genus *Hyparrheniaspis*, a heretofore monotypic genus whose type species is known from the same geographical region (S-E U.S.A.) from the same host family (Poaceae). The 2 species of *Hyparrheniaspis* share a lack of pygidial appendages, turbinate body shape, clusters of submarginal ducts on every thoracic and abdominal segment, and multiple submedial ventral microducts on all body segments. These same features are found in both the adult female and second-instar male of both species. Indeed, the submarginal duct clusters found in the adult female of *Hyparrheniaspis* resemble the cluster ducts typical of the second-instar male of Fioriniina and may be homologous with them. The species and genus are also biogeographically enigmatic, seeming to represent the only New World lineage of the subtribe Fioriniina. The genus is known only from coastal Florida (*H. campbelli* Gabbour & Hamon) and adjacent Georgia (*H. minima*). It has been reported from native and African grasses and possibly represents an introduction from Africa, which has a rich fauna of Fioriniina.

In addition to this large grass-feeding clade, there are 3 other morphologically novel lineages that we find belong in Fioriniina. All are monotypic genera and their phylogenetic placement can be seen in Fig. 8: (1) *Ischnafiorinia bambusae*, (2) *Ichthyaspis ficicola*, and (3) *Lineaspis striata*. *Ischnafiorinia bambusae* is a pupillarial species. Like many such (compare *Xerophilaspis prosopidis*, discussed above under Lepidosaphidini) it has a somewhat simplified adult female, without pygidial appendages apart from minute L1, and without dorsal

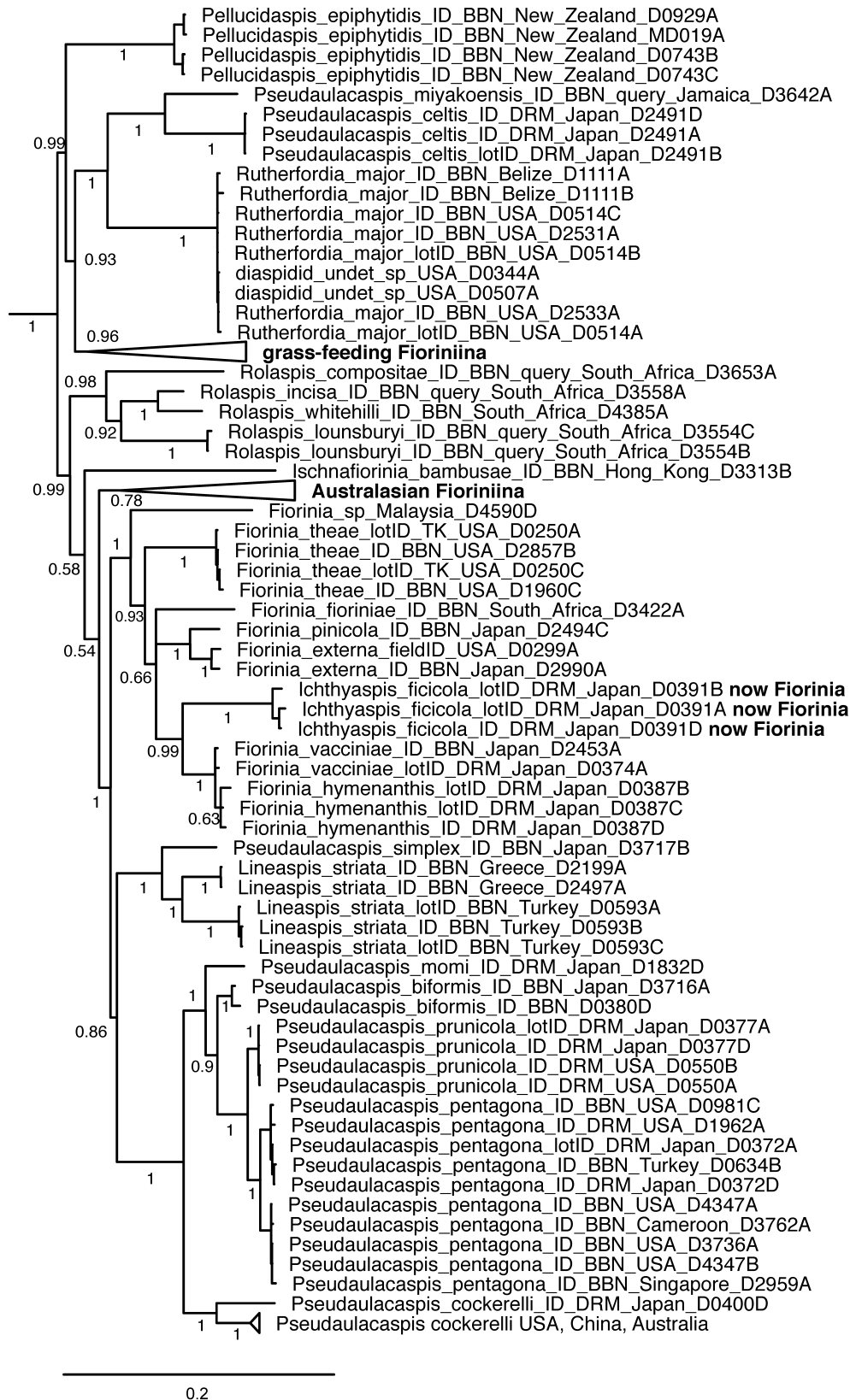


FIGURE 8. Phylogeny of the subtribe Fioriniina (Diaspidinae: Diaspidini), whose relationship to other Diaspidini is shown in Fig. 2. Two clades represented by triangular placeholders are shown in detail in subsequent figures: grass-feeding Fioriniina (Fig. 9) and Australasian Fioriniina (Fig. 10). To save space, a third triangular placeholder is used to represent 37 individuals of *Pseudaulacaspis cockerelli* (Cooley). For further explanation of the analysis and notation, see the caption to Fig. 1.

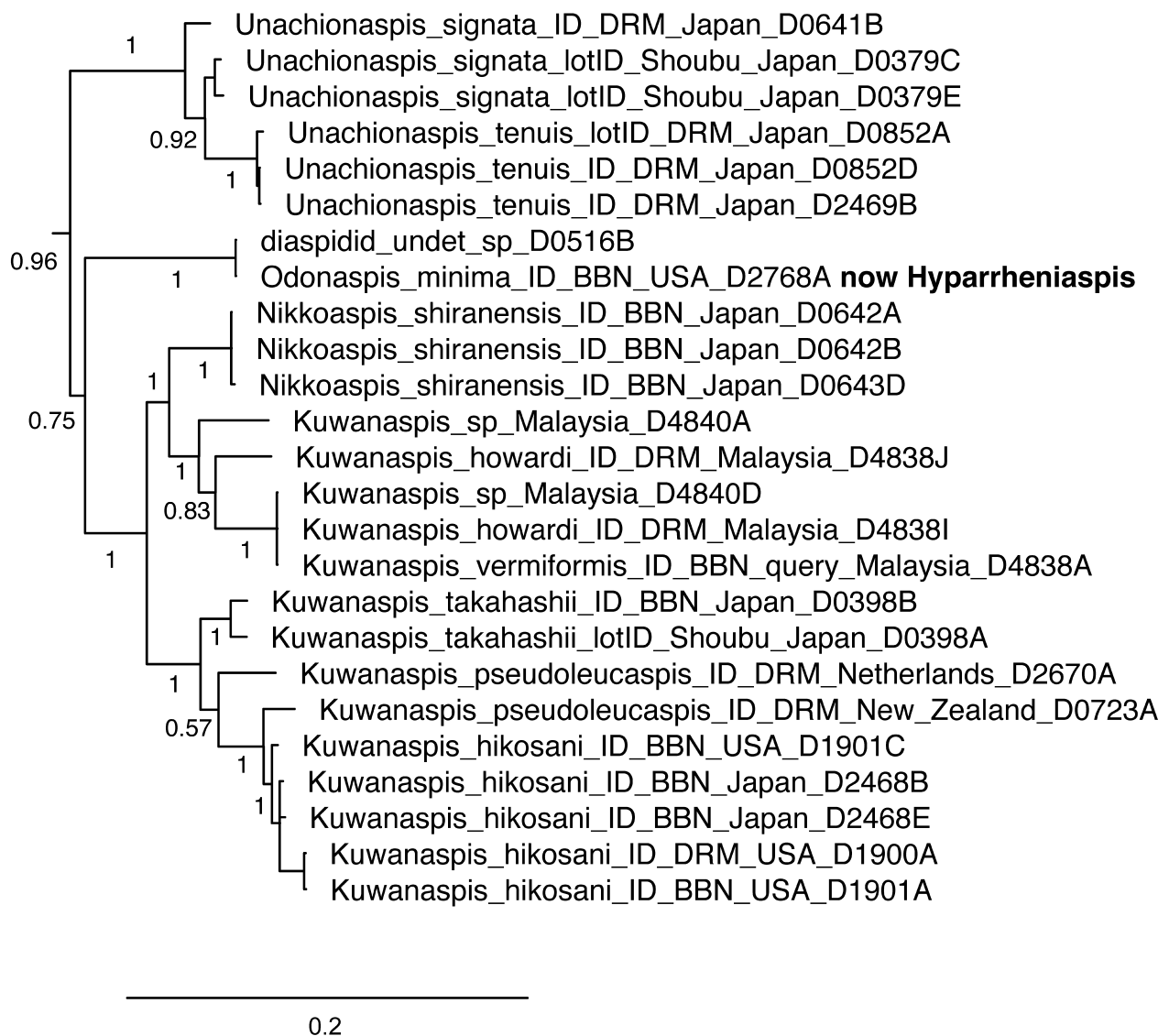


FIGURE 9. Phylogeny of the grass-feeding clade of Fioriniina, including species heretofore placed in Kuwanaspina (Diaspidinae: Diaspidini: Fioriniina). This figure shows the phylogeny of the clade labeled "grass-feeding Fioriniina" in Fig. 8. For further explanation of the analysis and notation, see the caption to Fig. 1.

ducts. Borchsenius placed this species in his tribe Parlatoriini, subtribe Gymnaspina, but there are some morphological characters that indicate it belongs in Diaspidinae, such as 3-locular pores near the anterior spiracles and the second-instar female having 2-barred marginal macroducts whose orifices are oriented longitudinally. *Ichthyaspis ficicola* is another pupillarial species, but unlike *Xerophilaspis* and *Ischnafiorinia*, *Ichthyaspis* arises within a large clade of pupillarial species (the genus *Fiorinia*). While most species of *Fiorinia* are similar to each other, differing in characters such as lobe shape, number of marginal ducts, and presence or absence of a process between the antennae, *Ichthyaspis ficicola* is strikingly different, having lost all pygidial lobes and gland spines, and instead having the apex of the pygidium modified into a rounded fishtail structure. One character that does resemble *Fiorinia* is the series of quasi-marginal ducts on each side of the pygidium, resembling those of *F. hymenanthis*, to which this species is closely related. These are presumably homologous to the marginal ducts of *Pseudaulacaspis*, but tend to be some slight distance from the margin in *Fiorinia*, including *Ichthyaspis ficicola*. Despite its strange aspect, this species is deeply nested within the genus *Fiorinia* and we need to recognize it as an unusual species of that genus: *Fiorinia ficicola* (Takahashi), **new combination**. *Lineaspis striata* is not a pupillarial species. It is unusual in having small L1 and large inner lobules of L2. A distantly related diaspidid genus (*Cupidaspis* MacGillivray) on the same host taxon (Cupressaceae) has converged on a similar phenotype. *Cupidaspis* was considered a synonym of *Lineaspis* by Ferris (1936), Balachowsky (1954), and Borchsenius

(1966) but was resurrected by Howell & Tippins (1977) based on a few characters including the lack of a seta on the antenna. Here we show that *Lineaspis* and *Cupidaspis* are in different subtribes: whereas *Lineaspis* is in Fioriniina, *Cupidaspis* is in Chionaspidina (Fig. 11), where Takagi had placed *Lineaspis*. It is intriguing that similar phenotypes have convergently evolved in different lineages on the same distinctive host family, though the functional significance of the phenotype is unclear.



FIGURE 10. Phylogeny of Australasian Fioriniina species (Diaspidinae: Diaspidini: Fioriniina). This figure shows the phylogeny of the clade labeled "Australasian Fioriniina" in Fig. 8. It includes the great majority of Australasian Fioriniina species, but note that it does not include *Pellucidaspis*, which apparently colonized Australasia independently (Fig. 8). For further explanation of the analysis and notation, see the caption to Fig. 1.

Our phylogeny (Fig. 8) is consistent with a biogeographic scenario in which Fioriniina originated in Asia, with at least 2 invasions of Australasia (by *Pellucidaspis* and by the ancestor of the clade labelled "Australasian Fioriniina" in Fig. 8) and at least 1 invasion of Africa, but again, more intensive collecting, particularly in Africa, may change this picture.

Many of the genera we have included in this subtribe should be uncontroversial, but others are more speculative. In addition to the genera discussed above, we accept several other genera that Takagi has placed in this subtribe: *Achionaspis* Takagi, *Crockeraspis* Takagi, *Sinistraspis* MacGillivray, *Epiflorinia* Takagi, *Heimaspis* Balachowsky & Ferrero, *Africaspis* MacGillivray, *Bayokaspis* Takagi, *Chlidaspis* Borchsenius, *Fraseraspis* Takagi, *Kulatinganaspis* Takagi, *Mayonia* Takagi, and *Singapuraspis* Takagi (Takagi 1970, 2000, 2003). We also assign to this tribe the other genera Takagi assigned to Kuwanaspidina (*Xiphuraspis* Borchsenius & Williams, *Coronaspis* MacGillivray, *Medangaspis* Takagi), along with a genus that Takagi & Martin (2010) tellingly thought might belong to either Fioriniina or Kuwanaspidina (*Nanhaiaspis* Takagi & Martin), and 2 thought to be close to *Lineaspis* (*Himalaspis* Takagi, *Keralaspis* Takagi) (Takagi 2007). A number of other assignments should also be relatively uncontroversial based on fairly obvious similarity to a typical fioriniine body plan reflected in genera such as *Pseudaulacaspis*, *Poliaspis*, and *Rolaspis*, including setae between L1: *Albastaspis* MacGillivray, *Asymetraspis* MacGillivray, *Augulaspis* MacGillivray, *Cooleyaspis* MacGillivray, *Dentachionaspis* MacGillivray, *Finaspis* Hall, *Fusilaspis* MacGillivray, *Getulaspis* Balachowsky, *Inchoaspis* MacGillivray, *Ledaspis* Hall, *Mammata* Munting, *Salaspis* Hall, *Tecaspis* Hall, *Trichomytilus* Leonardi, *Tsimbazaspis* Mamet, and *Voraspis* Hall. As mentioned above under Ancepaspidinae, 2 genera with highly modified adult females are here classified as Fioriniina based on characters of the second-instar nymphs: *Nudachaspis* and *Protancepaspis*. We also more speculatively include here a number of more or less unusual genera that might belong in Lepidosaphidini or Chionaspidina, but that seem to resemble the genera of Fioriniina in their region: in Australasia, *Laingaspis* Borchsenius & Williams; in the Oriental region, *Adiscofiorinia* Leonardi and *Formosaspis* Takahashi; in Africa, *Chimania* Munting, *Collubia* Munting, *Contigaspis* MacGillivray, *Magnospinus* Munting, *Moraspis* Hall, *Multispinaspis* Munting, *Namibia* Munting, *Parachionaspis* MacGillivray, *Relhaniaspis* Munting, *Sclopetaspis* MacGillivray, *Tenuiaspis* MacGillivray, and *Yomaspis* Munting.

Four species that Leonardi (1913, 1914) described in *Lepidosaphes* or *Dinaspis* (Lepidosaphidini) have setae, rather than gland spines, between L1 and clearly belong in Fioriniina rather than Lepidosaphidini. Here we reassign these species as follows: *Cooleyaspis pseudomorpha* (Leonardi), **new combination**; *Tecaspis giffardi* (Leonardi), **new combination**; *Rolaspis marginalis* (Leonardi), **new combination**; and *Voraspis olivina* (Leonardi), **new combination**.

Subtribe CHIONASPIDINA Brues & Melander

Cited as: Chionaspidini (Borchsenius 1966), Chionaspidina (Howell & Tippins 1990; Takagi, 2002). Subsumes Ulucoccinae (Takagi 2002) and Protodiaspidina (Takagi, 1995, 1999b, 2000, 2002, 2003).

Diagnosis: **AF** L1 often joined by a zygosis, this often having a medial basal scleritis with a rounded anterior end; without setae or gland spines or marginal macroduct between L1 (although rarely with a single fused gland spine between L1). **AM** antennal scape without setae; terminal antennal segment with capitate seta at apex and 8 or fewer simple setae; prosternum with lateral ridges absent; tegula with 0–3 setae. **2M** without marginal clusters of ducts; marginal ducts sometimes complex, with 1–2 thin tubes parallel to the main duct ("frame ducts").

Included genera: A complete list is given in Table 8.

Distribution: Cosmopolitan except South America; widely introduced.

Remarks: Our phylogenetic analysis finds support for a clade (labelled "Chionaspidina" in Fig. 2 and shown in detail in Figs. 11–12) that corresponds approximately to the subtribe Chionaspidina as defined by Howell & Tippins (1990). This concept of Chionaspidina is similar to that of Takagi (2002), except that it also includes the genera that Takagi places in the subtribe Protodiaspidina (Takagi 1995, 1999b, 2000, 2002, 2003) and the subfamily Ulucoccinae (Takagi, 2002), and excludes the genera *Ichthyaspis*, *Lineaspis*, *Himalaspis*, and *Keralaspis*, which are discussed under Fioriniina.

There is direct molecular evidence that this clade includes the type species of the genera *Chionaspis*, *Aulacaspis* Cockerell, *Pinnaspis* Cockerell, *Quernaspis* Ferris, *Haliaspis* Takagi, *Serenaspis* Henderson,

Trulliflorinia Leonardi, *Crypthemichionaspis* Lindinger, *Cupidaspis*, *Paracupidaspis* Howell & Tippins, and *Megacanthaspis*, and at least non-type species of *Duplachionaspis* MacGillivray. Of these genera, Takagi placed *Chionaspis*, *Aulacaspis*, *Pinnaspis*, and *Quernaspis* in Chionaspidina (Takagi 1970, 1999a, 2002) and *Megacanthaspis* in the Protodiaspidina (Takagi 1999b). The other sampled genera that appear in this clade in the phylogeny are not explicitly classified by Takagi. In the classification of Borchsenius (1966), the non-pupillarial genera *Duplachionaspis* and *Haliaspis* were in Chionaspidini and the pupillarial genera *Trulliflorinia* and *Crypthemichionaspis* were in Fioriniini. The genera *Cupidaspis*, *Serenaspis*, and *Paracupidaspis* were not recognized by Borchsenius (1966), but he placed the type species of *Cupidaspis* and *Serenaspis* in Chionaspidini. The type species of *Paracupidaspis* was described more recently (Howell & Tippins 1981) but has always been regarded as a close relative of *Cupidaspis* and presumably would have been placed in Chionaspidini in Borchsenius' system as well.

The non-monophyly of several genera (Table 5), including the radical non-monophyly of the genus *Chionaspis*, indicates that revisionary work is required. Most of the needed work is beyond the scope of this article, but we can make a few nomenclatural adjustments to repair some of the more egregious errors. Of all the species of *Chionaspis*, the one that we found to be most phylogenetically distant from the type species is *Chionaspis lepineyi*. In our tree this species is sister to *Quernaspis quercus* (Comstock) (Fig. 11), and we are calling it *Quernaspis lepineyi* (Balachowsky), **new combination**. It is also phylogenetically closer to *Cupidaspis* and *Serenaspis* than to any other species of *Chionaspis*. An alternative solution to the misclassification of *C. lepineyi* would have been to resurrect the monotypic genus *Marchaliella* Bodenheimer, which it once constituted (Bodenheimer, 1951). With this approach, there would be 4 genera in what Takagi & Tang (1982) called the *Quernaspis* group: *Quernaspis* in North America, *Neoquernaspis* and *Sinoquernaspis* in Central and Eastern Asia, and *Marchaliella* in the western Palearctic. All feed on Fagaceae and have fused or appressed L1; but we prefer not to further multiply the genera of Diaspididae except where necessary. Balachowsky (1954) noted the similarity of *Q. lepineyi* to *Q. quercus*, which it resembles in having a reduced outer lobule of L2 and in having L3 replaced by a low, slightly sclerotized serration of the body margin; it even more closely resembles *Q. quercicola* Takagi & Howell, in having L1 closely appressed at the base, rather than fused. Like the other species of *Quernaspis*, its hosts are oaks (*Quercus* L.).

Cupidaspis wilkeyi (Howell & Tippins), **new combination**, has heretofore been regarded as constituting the monotypic genus *Paracupidaspis*; however, we find that it is phylogenetically nested within the genus *Cupidaspis* (Fig. 11). In the original description of *Paracupidaspis*, the authors wrote ". . . we examined specimens which had a remarkable resemblance to *C. beshearae*. Closer study of the specimens has convinced us that the similarity is superficial and that they were a new species and not referable to *Cupidaspis*. . ." (Howell & Tippins, 1981). Our molecular study includes both described species of *Cupidaspis*, and finds that *Paracupidaspis wilkeyi* is more closely related to *C. beshearae* than *C. beshearae* is to *C. cupressi* (Coleman) (Fig. 11). This refutes the hypothesis that the remarkable resemblance to *C. beshearae* was superficial.

The subtribe Chionaspidina includes a clade of pupillarial Australasian species, heretofore assigned to the genera *Trulliflorinia*, *Crypthemichionaspis*, and *Fiorinia*, which we regard as comprising a single genus *Trulliflorinia* (Fig. 11). *Trulliflorinia nigra* (Lindinger), **revived combination**, has until now comprised the monotypic genus *Crypthemichionaspis* Lindinger. Ferris was undecided about whether *Crypthemichionaspis* should be synonymized with *Trulliflorinia*. He tentatively opined that they were synonyms (Ferris 1936) and then tentatively reversed himself pending further study (Ferris 1941b). The molecular evidence supports the case for synonymy. This clade also includes the species *Trulliflorinia geijeriae* (Froggatt), **new combination**, which has until now been placed in the genus *Fiorinia*. *T. geijeriae* is morphologically very similar to *T. nigra* and may be a synonym; both names are retained here pending further study of possible cryptic diversity. Note that the genus *Trulliflorinia* is apparently strictly Australasian and should not include the Asian species that have been placed in it. These species all have setae between L1—or between the positions of L1 in the case of *Fiorinia macroprocta* (Leonardi), **revived combination**—and belong in Fioriniina rather than Chionaspidina. *F. macroprocta* resembles *F. ficicola* (Takagi) in having lost the pygidial lobes in the adult female, though it retains typical *Fiorinia*-like lobes in the second-instar nymph. *Fiorinia rubrolineata* Leonardi, **revived combination**, and *F. scrobicularum* Green, **revived combination**, are both fairly typical species of *Fiorinia* in terms of the appearance of L1. *Trulliflorinia* is sister to the genus *Pinnaspis*, with which it shares appressed or fused L1 subtended by a median sclerosis. Indeed if one keys out a member of *Trulliflorinia* and ignores the fact that it is pupillarial, it will key out as *Pinnaspis* (Brimblecombe 1959a).

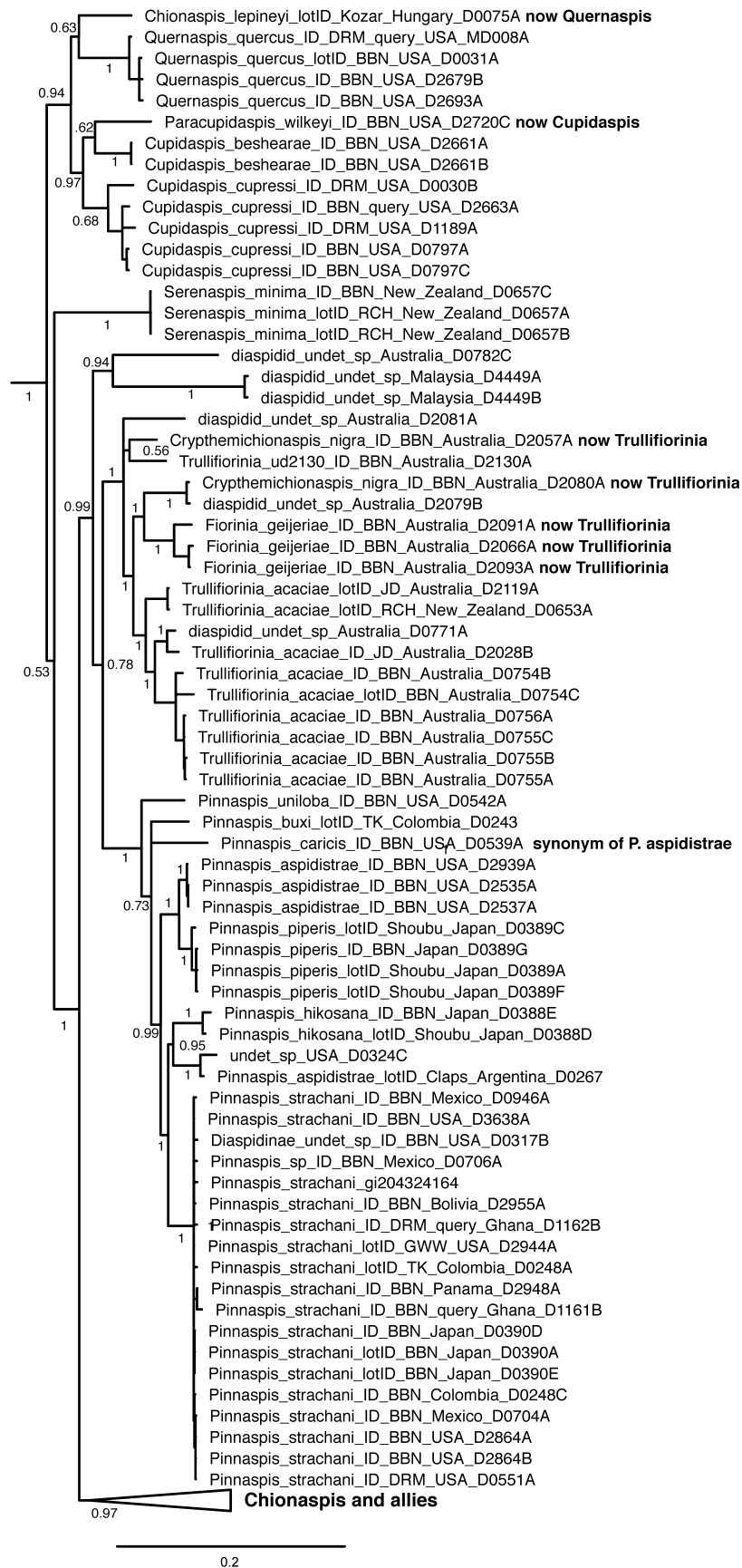


FIGURE 11. Phylogeny of the subtribe Chionaspidina (Diaspidinae: Diaspidini), whose relationship to the other Diaspidini is shown in Fig. 2. One clade is represented by triangular placeholder labelled "*Chionaspidina* and allies". Its phylogeny can be seen in Fig. 12. For further explanation of the analysis and notation, see the caption to Fig. 1.

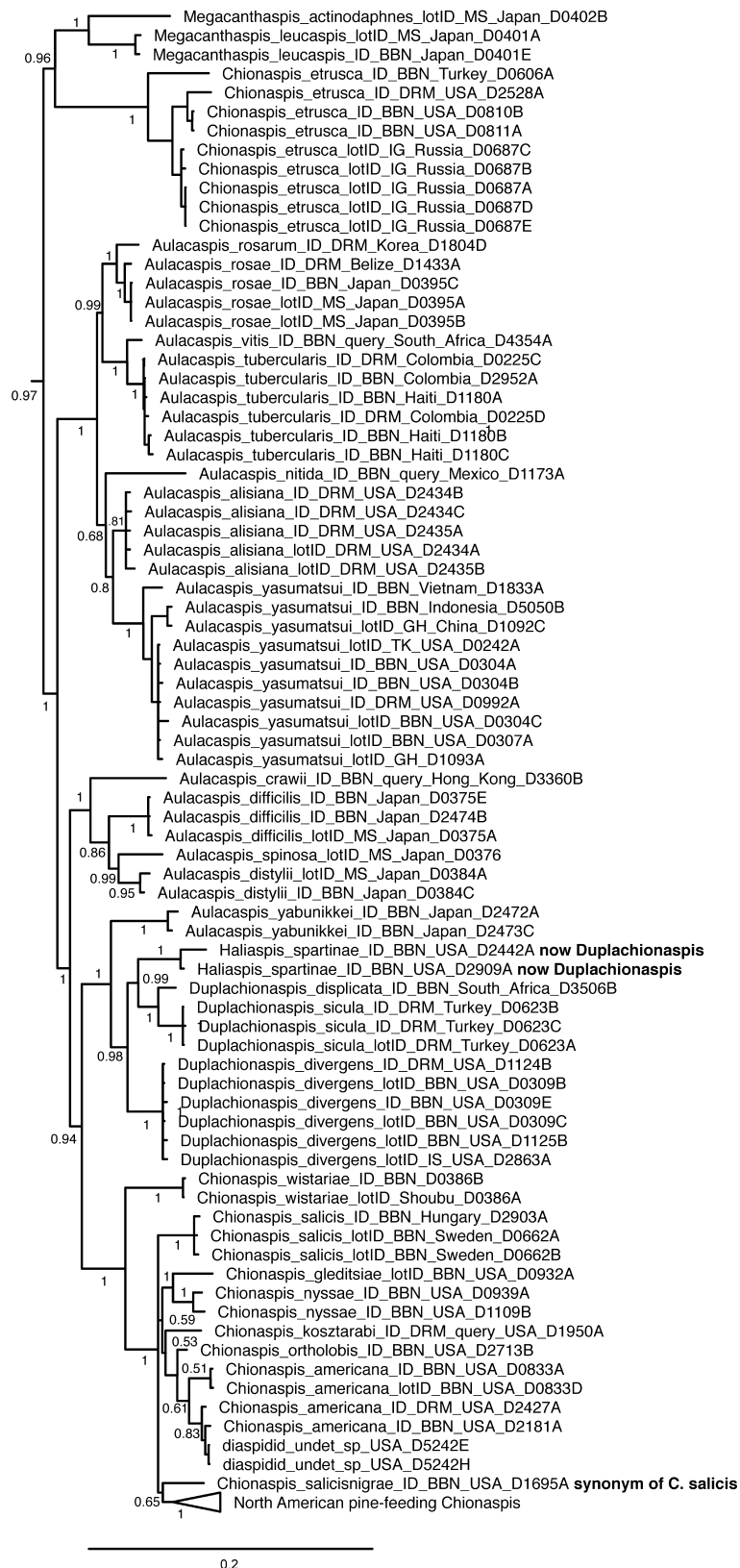


FIGURE 12. Phylogeny of *Chionaspis* Signoret and allies (Diaspidinae: Diaspidini: Chionaspina). This figure shows the phylogeny of the clade labeled "Chionaspis and allies" in Fig. 11. To save space, a triangular placeholder labelled "North American pine-feeding Chionaspis" represents 70 individuals of North American pine-feeding species, including *C. pinifoliae* (Fitch), *C. heterophyllae* (Cooley), *C. brachycephalon* Vea, *C. sonoreae* Vea, and *C. torreyanae* Vea. A more complete analysis and discussion of this clade can be found in Gwiazdowski *et al.* (2011) and Vea *et al.* (2013). For further explanation of the analysis and notation used here, see the caption to Fig. 1.

Duplachionaspis spartinae (Comstock), **revived combination**, is the type species of the genus *Haliaspis*. Our analysis shows that this species is phylogenetically nested within the genus *Duplachionaspis* (Fig. 12). Indeed, this species was regarded as a species of *Duplachionaspis* until Takagi (1963) erected a new genus for it and a few other North American species on the grounds that they had enlarged setae on the venter and an invagination on the head of the first-instar crawler. Our results indicate that these characters arose within the genus *Duplachionaspis*. Accordingly, we regard *Haliaspis* as a synonym of *Duplachionaspis* (Tables 9, 11).

Takagi's work implies that Chionaspidina is of Asian origin and our phylogeny is consistent with that. There appear to have been at least 3 ancient invasions of the Australasian region (by *Serenaspis*, by a pupillarial lineage including *Trulliflorinia*, and by a third lineage represented here by only a single unidentified specimen), and at least 4 ancient invasions of North America (by *Quernaspis* and *Cupidaspis*, and by lineages of *Chionaspis* and *Duplachionaspis*). Again, this picture may change with greater sampling, particularly in Africa.

With respect to the classification of genera that we have not sampled for DNA, several of the genera we have listed as members of Chionaspidina (Table 8) are ones that Takagi explicitly or implicitly placed in the subtribe: *Aflorinia* Takagi, *Amphisoma* Takagi, *Cameronaspis* Takagi, Pong, & Ghee, *Chionandaspis* Takagi, *Damaia* Takagi, *Kuchingaspis* Takagi, *Larutaspis* Takagi, *Myrtaspis* Takagi, *Narayanaspis* Takagi, *Neochionaspis* Borchsenius, *Neoquernaspis* Howell & Takagi, *Pinangaspis* Takagi, *Semonggokia* Takagi, *Sinoquernaspis* Takagi & Tang, *Takagiaspis* Varshney, and *Takahashiaspis* Takagi. *Unaspis* was sampled for DNA but its position is unresolved in our tree, so we defer to the traditional classification and retain it in Chionaspidina, as did Takagi.

TABLE 11. Summary of new synonymies of genera and species. For further discussion of each case, see Notes on Higher Taxa.

Junior synonym	Senior synonym	Higher taxon
<i>Porterinaspis</i> González	<i>Aonidomytilus</i> Leonardi	Lepidosaphidini
<i>Lepidosaphes boguschi</i> McDaniel	<i>Lepidosaphes punicae</i> Laing	Lepidosaphidini
<i>Lepidosaphes caribaeae</i> Williams & Miller	<i>Lepidosaphes rubrovittata</i> Cockerell	Lepidosaphidini
<i>Ductofrontaspis</i> Young & Hu	<i>Lepidosaphes</i> Shimer	Lepidosaphidini
<i>Metandaspis</i> Williams	<i>Lepidosaphes</i> Shimer	Lepidosaphidini
<i>Ungulaspis</i> MacGillivray	<i>Lepidosaphes</i> Shimer	Lepidosaphidini
<i>Protargionia</i> Leonardi	<i>Pseudoparlatoria</i> Cockerell	Lepidosaphidini
<i>Symeria phyllocladi</i> Henderson	<i>Symeria pyriformis</i> (Maskell)	Lepidosaphidini
<i>Geodiaspis</i> Tippins & Howell	<i>Diaspis</i> Costa	Diaspidina
<i>Paracupidaspis</i> Howell & Tippins	<i>Cupidaspis</i> MacGillivray	Chionaspidina
<i>Aloaspis</i> Williams	<i>Duplachionaspis</i> MacGillivray	Chionaspidina
<i>Haliaspis</i> Takagi	<i>Duplachionaspis</i> MacGillivray	Chionaspidina
<i>Crypthemichionaspis</i> Lindinger	<i>Trulliflorinia</i> Leonardi	Chionaspidina
<i>Ichthyaspis</i> Takagi	<i>Fiorinia</i> Targioni Tozzetti	Fioriniina
<i>Cryptoparlatoria</i> Lindinger	<i>Parlatoria</i> Targioni Tozzetti	Parlatoriini

Other genera that we place in Chionaspidina were placed by Takagi in Protodiaspidina or Ulucoccinae, based on the reduced features of the adult females, but the immature forms of many species have characters otherwise found only in Chionaspidina: modified ducts (frame ducts) in the second-instar males and suranal ducts in the crawlers (Takagi, 1995). These led Howell & Tippins (1990) to regard *Protodiaspis* as belonging to Chionaspidina. The molecular evidence showing that *Megacanthaspis* is nested within Chionaspidina (Fig. 12) strongly suggests that these characters provide good evidence of a relationship to Chionaspidina, supporting Howell & Tippins' (1990) view. Accordingly we regard Chionaspidina as including all the genera that Takagi placed in Protodiaspidina (*Animalaia* Takagi, *Dungunia* Takagi, *Kyphosoma* Takagi, *Pentacicola* Takagi, *Protodiaspis* Cockerell, *Thoa* Takagi) and Ulucoccinae (*Ulucoccus* Takagi, Pong, & Ghee). We also include in Chionaspidina several genera not classified by Takagi but that Borchsenius (1966) placed in Chionaspidini—*Balachowskiella* Kaussari, *Duplaspis* Goux, *Greenaspis* MacGillivray, *Guineaspis* Balachowsky, and *Marchalaspis*

MacGillivray—along with genera described from China by Tang (1981) and Young (1986) that have never been formally classified, but that lack setae and gland spines between L1 and generally resemble Chionaspidina—*Shansiaspis* Tang, *Yuanaspis* Young, *Serrachionaspis* Young, and *Guizhoaspis* Young. We also include a series of genera that have not previously been placed in Chionaspidina but that have appressed or fused L1 with a median sclerosis, resembling *Trulliflorinia* and *Pinnaspis*. Three are Australasian and we suspect that they are close relatives of *Trulliflorinia*: *Fijiflorinia* Williams & Watson, *Hybridaspis* Green, and *Hemiaspidis* MacGillivray. Surprisingly, a genus from Madagascar, *Tanaparlatoria* Mamet, also fits the characteristics of this group, bearing a particular resemblance to *Hybridaspis*, and we include it as well. We also include the genus *Sphaeroceraspis* Balachowsky & Ferrero, which Balachowsky & Ferrero (1965) compared to *Protodiaspis* and placed with chionaspiform Diaspidini.

The monotypic genus *Aloaspis* Williams we regard as a synonym of *Duplachionaspis*, **new synonymy**. In most respects it resembles the members of a southern African radiation of *Duplachionaspis* onto species of *Aloe* L. and other dryland plants; our sample includes *D. displicata* Munting, from *Aloe*, which is nested well within *Duplachionaspis* (Fig. 12). *Duplachionaspis mutica* (Williams), **new combination**, differs from the other species in this group by lacking gland spines and by having ducts on the abdominal segment VII, the characters on which Williams based the genus *Aloaspis*; but these are likely to be autapomorphies within this species group, rather like the reduction of gland spines in "*Protargionia*" *larreae* and "*Parlagena*" *bennetti* within *Pseudoparlatoria*.

Subfamily ASPIDIOTINAE Westwood

Cited as: Aspidiotinae (Takagi 2002). Subsumes Leucaspidae and Odonaspidinae (Borchsenius 1966).

Diagnosis: **AF** without gland spines; usually with fringed plates; L2 and L3, when present, unilobular; orifices of marginal macroducts, if oblong, with long axes usually parallel to body margin; pores by anterior spiracle 5-locular or absent, rarely 3-locular. **2F** with or without fringed plates; L2 unilobular. **CR** abdominal segment II with submedian dorsal duct; abdominal segments III–VI with or without dorsal submedian setae; abdominal segments IV–VI each without ventral submedian seta; head and mesothorax each with submarginal or submedial dorsal duct; terminal segment of antenna with 2 apical setae; tarsus with seta near base of claw; tarsus and tibia fused or separated by a septum. **AM** usually with tubercular ocellus; pronotal ridges present; dorsal lateral branches of midcranial ridge absent; prescutum transverse or triangular; dorsal setae usually absent from abdominal segments IV–VII. **2M** similar to 2F. **M** diploid with half of chromosomes heterochromatic or haploid without heterochromatic chromosomes.

Included genera: See Table 8 and the individual tribes, below.

Distribution: Cosmopolitan.

Remarks: Our results (Fig. 3) support Takagi's (2002) concept of the subfamily Aspidiotinae, subsuming the former subfamilies Leucaspidae and Odonaspidinae recognized by Borchsenius (1966). This also coincides with the set of taxa Howell & Tippins call "Group I" in their discussion of immature forms (Howell & Tippins 1990).

Tribe GYMNASPIDINI Balachowsky, new rank

Cited as: Gymnaspidae (Balachowsky 1958; Borchsenius 1966).

Diagnosis: **AF** antenna with 2–3 setae; without pores near anterior spiracle; plates conical, with either flat pectinate wing-like projections, or minute terminal filamentous projections; **2F** L2 unilobular, L3 bilobular. **CR** antenna with 6 segments, terminal segment annulated; septum present between tibia and tarsus; tarsal seta present; submedial dorsal seta present on abdominal segments I–VI. **AM** without tubercular ocellus; distance between anterior arms of postoccipital ridge equal to or greater than the length of each arm; antennal scape with 1 dorsal seta; antennal pedicel with reticulation and with 3 setae; terminal antennal segment with 1 ventral knobbed seta; prosternum with lateral ridges; prescutum transverse; prescutal setae present; scutellar setae absent; dorsal setae present on all abdominal segments. **2M** not described. **M** diploid, with half of the chromosomes heterochromatic. The best source of morphological information on the life stages in this tribe is Davidson & Miller (1977).

Although the type species, *G. aechmeae*, has a simplified pupillarial adult female remarkably free of cuticular

ornamentation, its few characters nonetheless differ markedly from those of Parlatoriini, in which it was traditionally placed; these include multisetose antenna (unisetose in Parlatoriini) and pores near anterior spiracle absent (present in Parlatoriini). In the immature stages, the crawler has a septum between the tarsus and tibia (absent in Parlatoriini), and the second-instar nymph has an unusual combination of unilobed L2 and bilobed L3 (both unilobed in Parlatoriini).

Included genera: *Gymnaspis*, *Hemigymnaspis*, *Lindingeria* MacGillivray.

Distribution: Neotropical. The type species, *G. aechmeae*, has been introduced on cultivated plants to many areas in the Nearctic and Palearctic, and to Hawaii. The view that *G. aechmeae* is Oriental in origin (Ferris, 1937a; D.R. Miller *et al.* 2005) is without foundation, since it has never been recorded from the Oriental region or anywhere in the Old World tropics.

Remarks: The genus *Gymnaspis* and subtribe Gymnaspidina have historically included many pupillarial parlatoriines and other small, subhemispherical ("fleyspeck") pupillarial species, which helps to account for the erroneous impression of an Oriental origin for the type species.

Our phylogenetic analysis (Fig. 3) provides evidence for the existence of a clade that includes the type species of *Gymnaspis* and an undescribed species of *Hemigymnaspis*. Most authorities have placed *Gymnaspis* in Parlatoriini and *Hemigymnaspis* in Aspidiotini (Borchsenius 1966; Davidson & Miller 1977). Indeed, Lindinger (1934), Ferris (1942), and Borchsenius (1966) all placed the type species of *Hemigymnaspis* within the genus *Melanaspis* Cockerell. But Lindinger (1943), who named and described the genus *Hemigymnaspis*, recognized its affinity with *Gymnaspis*, mentioning the bilobed L3 of the second-instar nymph. Davidson (1972) resurrected the genus *Hemigymnaspis* and Davidson & Miller (1977) noted several characters in which it differs from all Aspidiotini other than *Furcaspis* (now in Furcaspidae). We also include the genus *Lindingeria*, based on morphology, as evidenced by Lindinger's (1910) illustrations. Its second-instar nymph has unilobed L2 and bilobed L3. The pygidial fringe of the adult female resembles that of the type species of *Hemigymnaspis*, with conical, fringed plates. The similarity between the type species of what are now the genera *Hemigymnaspis* and *Lindingeria* was noted by Lindinger (1934).

The genus *Gymnaspis* has heretofore been perhaps the most heterogeneous genus of Diaspididae, including pupillarial species whose true affinities appear to lie in 4 different tribes. In the interest of clarifying the composition of the various tribes, the 16 species that until now have been placed in *Gymnaspis* are reassigned as follows. Three species have the distinctive bilobed L3 in the second-instar nymph and are retained in *Gymnaspis*: *G. aechmeae*, *G. clusiae* Lindinger, and *G. sculpta* Hempel. One species belongs in *Lopholeucaspis* Balachowsky (Leucaspidini), based on the marginal pattern of lobes, plates and tubercles: *Lopholeucaspis spinomarginata* (Green), **new combination**. Of the others, 5 are transferred to *Parlatoria* and 5 to *Greeniella* Cockerell, based mostly on the pygidial fringe of the second-instar nymphs in type material in the NHM. The new combinations are listed in Table 9.

Tribe LEUCASPIDINI Atkinson

Cited as: Leucaspidini (Borchsenius 1966; Takagi 2002); subsumes Thysanaspidini (Takagi 2002).

Diagnosis: **AF** pupillarial, remaining permanently enclosed within cuticle of 2F; antenna with 2–6 setae; ducts, if present, 2-barred; body usually elongate; a few 5-locular pores sometimes present submarginally on venter of prepygidial abdominal segments; often with a cluster of ducts or duct tubercles on venter near anterior spiracle. **2F** with unilobular lobes, fringed plates, and 2-barred marginal macroducts with orifices parallel to margin. **CR** antenna with 5 segments, terminal segment annulated; without septum between tibia and tarsus; abdominal segment III with submedian dorsal seta, segments IV–VI each without submedian dorsal seta. **AM** postoccipital ridge with anterior arms triangular in shape; distance between anterior arms greater than the length of each arm; antennal pedicel with reticulation and with 2–6 setae; terminal antennal segment with 2 ventral knobbed setae; prosternum with lateral ridges; prescutum transverse; scutum with median protuberances present; prescutal setae absent; scutellar setae absent; total number of setae on trochanters 12; dorsal setae present on all abdominal segments (Nada & Mohammad, 1984). **2M** resembling 2F but with more dorsal ducts and sometimes with disc pores on abdominal segments. **M** diploid, with half of chromosomes heterochromatic.

Included genera: A complete list is given in Table 8.

Distribution: Almost exclusively Old World; widely introduced.

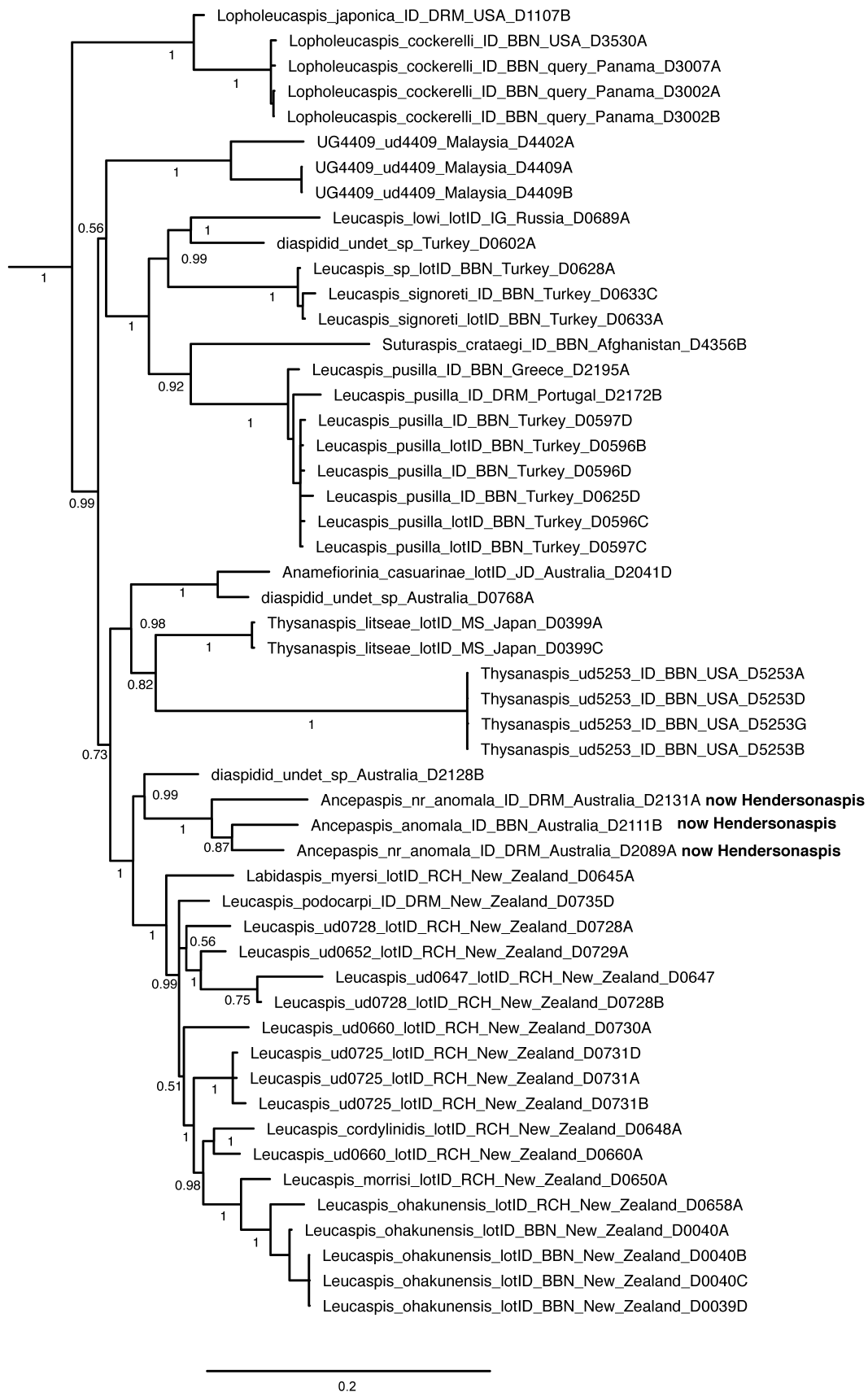


FIGURE 13. Phylogeny of the tribe Leucaspini (Aspidiotinae), whose relationship to other Aspidiotinae is shown in Fig. 3. UG4409 is an undescribed genus. For further explanation of the analysis and notation, see the caption to Fig. 1.

Discussion: Our phylogenetic analysis provides evidence for the existence of a clade (labelled Leucaspidini on Fig. 3 and shown in detail in Fig. 13) that includes the type species of the genera *Leucaspis* Targioni Tozzetti, *Lopholeucaspis*, *Anamefiorinia* Leonardi, *Labidaspis* Borchsenius & Williams, and *Hendersonaspis*, **gen. n.**, and that also includes at least non-type species of *Suturaspis* Lindinger and *Thysanaspis*. Of these, the genera *Leucaspis*, *Lopholeucaspis*, *Anamefiorinia*, and *Suturaspis* were placed in Leucaspidini by Borchsenius (1966), Takagi (1969) and Takagi & Moghaddam (2005). *Thysanaspis* was placed by Borchsenius (1966) in Leucaspidini and by Takagi (2002) in a separate tribe Thysanaspidini. *Labidaspis* is a monotypic New Zealand species, lacking pygidial appendages in the adult female, which was not mentioned by Takagi but that Borchsenius (1966) placed in Parlatoriini, subtribe Gymnaspidina. The type species of *Hendersonaspis* was placed by Borchsenius (1966) in Diaspidinae, tribe Ancepaspidini, and was regarded as *incertae sedis* by Takagi (1969). Thus this clade corresponds fairly closely to both Borchsenius's and Takagi's concepts of the tribe Leucaspidini, except that it also includes a few aberrant taxa that have lost pygidial appendages.

More sampling is necessary to sort out the biogeographic history of Leucaspidini. Our phylogeny is consistent with a scenario in which Leucaspidini originated in Asia, with 1 clade invading the Palearctic and 2 lineages invading the Australasian region. Puzzlingly there is also an undescribed species of *Thysanaspis* found on mangroves in Florida, U.S.A. ("*Thysanaspis_ud5253*" on Fig. 13); it is not clear whether this is a recent introduction of a species not yet found in its native Old World range, or a native New World species representing an ancient dispersal event.

Much revisionary work is needed in Leucaspidini. It is clear from the phylogeny (Fig. 13) that the New Zealand species of *Leucaspis* should be assigned to a different genus (unless the entire tribe is to be regarded as a single genus). R.C. Henderson was working on this group when she died in 2012; hopefully her work can be carried forward. Even the Palearctic species of *Leucaspis* do not quite form a monophyletic clade; the group comprising Palearctic *Leucaspis*—represented by *L. pusilla*, *L. signoreti*, and *L. lowi*—is paraphyletic with respect to the species *Suturaspis crataegi*.

Three of the other genera we have assigned to Leucaspidini were recognized by both Borchsenius and Takagi as belonging to the tribe: *Gomezmenoraspis* Balachowsky, *Mongrovaspis* Bodenheimer, and *Salicicola*. The other included genus, *Namaquea* Munting, post-dates Borchsenius's catalogue and has not been discussed by Takagi; Munting's (1969) description of the genus placed it in Leucaspidini due to the transverse macroduct orifices in the adult female and the unilobulate L2 in the second-instar nymph.

Tribe AONIDIINI Balachowsky, new rank

Cited as: Aonidiina (Balachowsky 1948, 1958; Borchsenius 1965, 1966). Subsumes Pseudaonidiina (Borchsenius 1966; Takagi 2003).

Diagnosis: **AF** with 1 or more pores near anterior spiracle (absent in a few pupillarial species); antenna with 1 seta; without duct tubercles; with 1-barred ducts; reticulate pattern of sclerotization often present on dorsum of pygidium; body sometimes completely sclerotized at maturity; body margin in some cases strongly indented between thoracic segments. **2F** similar to AF, with fewer dorsal ducts. **CR** antenna with 5 segments, terminal segment annulated; septum present between tibia and tarsus; abdominal segments III–VI each without submedian dorsal seta. **2M** similar to 2F, with more dorsal ducts. **AM** not described. **M** diploid, with half of chromosomes heterochromatic.

Included genera: A complete list is given in Table 8.

Distribution: Australasian, Oriental, and Afrotropical, with a few Palearctic species; absent from the New World; introduced worldwide.

Remarks: Our phylogenetic analysis provides evidence for the existence of a clade (labelled Aonidiini on Fig. 3 and shown in detail in Fig. 14) that includes the type species of the genera *Aonidia*, *Pseudaonidia* Cockerell, *Pentalaminaspis* Smith-Pardo, Evans, & Dooley, *Genaparlatoria* MacGillivray (**revived genus**), *Anoplaspis* Leonardi, *Neoleonardia* MacGillivray, *Eulaingia* Brimblecombe, and *Neomorgania* MacGillivray, and at least non-type species of *Alioides* Brimblecombe, *Greeniella*, *Gomphaspidiotus* Borchsenius & Williams, *Diaphoraspis* Brimblecombe, *Mimeraspis* Brimblecombe, *Myrtophila* Brimblecombe, *Achorophora* Brimblecombe, and *Parrottia* MacGillivray. This clade corresponds largely to the subtribe Pseudaonidiina sensu Borchsenius

(Borchsenius 1966); Takagi referred some taxa to this subtribe (Takagi 2000, 2003), though he did not formally include it in his system (Takagi 2002). The clade also includes some species of Aonidiina, including the type species of that subtribe, *Aonidia lauri* Bouché. *Aonidia* is an older name than *Pseudaonidia*, so the correct name of the tribe is Aonidiini. Many species heretofore included in Aonidiina are apparently pupillarial Aspidiotini. The tribe is largely Australasian and Oriental; the type species is one of very few Palearctic representatives. Our phylogeny resolves 3 Australasian clades and 3 Oriental clades but leaves unclear whether one of these areas is ancestral to the other (Fig. 14).

One species nested well within the tribe is *Genaparlatoria pseudaspidiotus* (Lindinger), **revived combination**. This species has been treated by most authors as a species of *Parlatoria* (Ferris 1936; García Morales *et al.* 2016), though previous molecular results have already shown that it is only distantly related to that genus (Andersen *et al.* 2010; Morse & Normark 2006). The genus *Genaparlatoria* differs from *Parlatoria* in having a sclerotized prosoma (Williams & Watson 1988). Closely related to *Genaparlatoria* is *Pentalaminaspis minuta* (Kotinsky), which until recently (Smith-Pardo *et al.* 2012) was classified within Aspidiotini as a species of *Chrysomphalus* Ashmead. Molecular and morphological evidence for the inclusion of *Brimblecobia*, **gen. n.**, in Aonidiini is discussed below under the description of that genus.

With respect to the genera for which we have no molecular data, many of those that we have included in the tribe were placed by Borchsenius in the subtribe Pseudaonidiina: *Acontonidia* Brimblecombe, *Aspidonymus* Brimblecombe, *Diastolaspis* Brimblecombe, *Dichosoma* Brimblecombe, *Duplaspidiotus* MacGillivray, *Paraonidia* MacGillivray, *Pseudotargionia* Lindinger, and *Semelaspidus* MacGillivray. Takagi (2000) recognized Pseudaonidiina as a subtribe of Aspidiotini and seemed to largely accept Borchsenius' concept of the composition of the subtribe, though he did not explicitly enumerate the genera he thought that it contained. Two genera that Takagi did explicitly assign to Pseudaonidiina were *Duplaspidiotus* and *Icaraspidiotus* Takagi (Takagi 2000). Other recently described genera were not formally classified by Borchsenius or Takagi but are easily placed in Aonidiini (and would have been placed in Pseudaonidiina by either Borchsenius or Takagi) due to the combination in the adult female of pores by the anterior spiracle and a deeply incised thorax: *Sadaotakagia* Ben-Dov and *Protomorgania* Dooley & Evans.

Pseudaonidiina was a largely well-defined taxon, as conceived by both Borchsenius and Takagi, and almost all its members are here accepted into Aonidiini. (The exception is *Operculaspis*, which has 3-locular perispiracular pores, 2-barred ducts, and multiple antennal setae; Ferris (1937b) placed it in Diaspidini and we regard it as a member of Lepidosaphidini, possibly near *Howardia*.) But the subtribe Aonidiina is another matter. Like other pupillarial taxa, Aonidiina as recognized by Borchsenius was a highly artificial, polyphyletic assemblage of many unrelated pupillarial forms that shared small body size and approximately circular body form. Much more work will be required to definitively sort out these species. Based on our limited sample it appears that a particularly useful morphological character is the presence or absence of pores by the anterior spiracle: in our sample, all members of the Aspidiotini lack such pores, while most members of the Aonidiini have them (although they are missing in a few species in the genera *Greeniella* and *Eugreeniella* Brimblecombe). Based partly on this character, beyond the 3 genera we have sampled (*Aonidia*, *Greeniella*, *Maskellia*), we retain only 1 genus of Borchsenius' Aonidiina in Aonidiini as here defined: *Maskellia* Fuller. We do include in Aonidiini a few genera with perispiracular pores that Borchsenius placed in a different subtribe of Aspidiotini (Aspidiotina, where he also placed *Neoleonardia*, which our phylogeny places in Aonidiini): *Diaspidopus* Brimblecombe, *Loranthaspis* Cockerell & Bueker, and *Tsimanaspis* Mamet.

Some of the species that our phylogeny places in Aonidiini have broad marginal macroducts whose orifices are oriented nearly perpendicular to the body margin, and these were all previously placed in the subfamily Diaspidinae (Borchsenius 1966): *Anoplaspis metrosideri* (Maskell), *A. maskelli* Morrison & Morrison, and *Alioides* sp. In the case of *Anoplaspis* species, the resemblance to Diaspidinae is further enhanced by the elongate body form; hence we include in Aonidiini the genus *Fernaldanna* MacGillivray, which resembles these genera and like *Anoplaspis* was placed by Borchsenius in Lepidosaphidini.

Finally we include a monotypic, pupillarial, Australasian genus that Borchsenius (1966) placed in Gymnaspidina, but that lacks the distinctive characters of Gymnaspidini as here defined and instead has second-instar nymphs that resemble those of *Aonidia lauri*, with L3 unlobed and flat, fringed plates: *Agrophaspis* Borchsenius & Williams.

The type genus of this tribe, *Aonidia*, has historically been highly heterogeneous, including species from 3 different tribes. In this it resembles *Gymnaspis*, the type genus of Gymnaspini. To clarify the boundaries between tribes, it is useful to examine the species of *Aonidia* and seek to reassign them more accurately. Of the 3 nominal species of *Aonidia* we sampled for DNA characters, 1 was a North American species that turned out to be deeply nested within the *Diaspidiotus ancyclus* complex in the tribe Aspidiotini, and we are now calling it *Diaspidiotus shastae* (Coleman), **new combination**. The other 2, *Aonidia lauri* and *A. paradoxa*, belong to Aonidiini (Fig. 14). As *A. lauri* is the type species, this group should be regarded as the true genus *Aonidia*. This pair of species does not constitute a monophyletic group—the clade that includes them also includes the genera *Neoleonardia*, *Anoplaspis*, and *Alioides*—but sampling is poor, and a more complete and nuanced revision is beyond the scope of this work.

Among the species of *Aonidia* that we have not sampled for DNA, 1 appears to belong in the tribe Leucaspini: *Leucaspis illicitana* (Gómez-Menor Ortega), **new combination**, and a total of 20 species apparently belong in Aspidiotini. For 3 of these, we revive the genus *Cupressaspis* Borchsenius to accept *Cupressaspis isfarensis* Borchsenius, **revived combination**; *Cupressaspis mediterranea* (Lindinger), **revived combination**; and *Cupressaspis relictata* (Balachowsky), **new combination**. These species all have 2 pairs of well-developed lobes and apically fringed, quadrangular plates; they are found on Cupressaceae in the southern Palearctic and Eritrea. For the other species we are transferring to Aspidiotini, we are not segregating them into pupillarial genera but are instead placing them as best we can in genera that are mostly non-pupillarial. It is clear from the phylogenetic evidence that pupillarial habit is highly labile and that it is necessary for taxonomists to tolerate variation in this character within genera—a point well illustrated by the deep nesting of the pupillarial species *Diaspidiotus shastae* within the *Diaspidiotus ancyclus* complex (Fig. S5)—if we are ever to have a manageable number of monophyletic genera. On this basis, we assign species erstwhile in *Aonidia* to the same genera we would assign them to if they were not pupillarial. In Table 9 we list 16 new combinations for these species in the genera *Aspidiotus*, *Diaspidiotus* Cockerell, *Melanaspis*, and *Rhizaspidotus* MacGillivray. The remaining species are retained in *Aonidia* for the present.

Tribe SMILACICOLINI Takagi

Cited as: Smilacicolini (Takagi 2002).

Diagnosis: **AF** antenna with 6–8 setae; without marginal appendages; with many small dorsal ducts. **2F** of various forms; may resemble **AF** (no pygidial appendages, many small dorsal ducts) or **2M** (unilobed L1 & L2, fringed plates, wider dorsal macroducts) or may have modified wide dorsal ducts with an 8-shaped structure at the inner end. **CR** antenna with 6 segments, without annulations; with septum between tibia and tarsus; with dorsal submedial seta on each of abdominal segments III–VI. **AM** not described. **2M** with unilobed L1–L3 and fringed plates; dorsal ducts much wider than those of adult female; gland tubercles present on thorax; resembling **AF** of *Parlatoria* but with multisetose antenna. Smilacicolini resembles Odonaspini but the adult female and second-instar nymphs may be distinguished by the multisetose antenna, and the crawler by the septum between the tibia and tarsus.

Included genus: *Smilacicola* Takagi.

Distribution: Oriental.

Discussion: This is the only tribe that we have not sampled for DNA. We defer to Takagi (2002) in recognizing it.

Tribe ODONASPIDINI Ferris

Cited as: Odonaspidinae (Borchsenius 1966), Odonaspini (Takagi 2002).

Diagnosis: **AF** without pygidial lobes or plates; all dorsal duct orifices minute, same size as ventral duct orifices; antenna with 1 seta; often with pores by posterior spiracle; non-pupillarial; **2F** similar to **AF** but with fewer ducts. **CR** antenna with 5 segments, terminal segment annulated; without septum between tibia and tarsus; without dorsal submedial setae on abdominal segments III–VI. **AM** not described. **2M** of diverse forms in different

species; some are similar to 2F; many others have large dorsal macroducts, sclerotized lobes, and fringed plates, strongly resembling AF of Parlatoriini. See Aono (2009) for an extensive survey of the immature forms.

Included genera: *Odonaspis* Leonardi, *Circulaspis* MacGillivray, *Dicirculaspis* Ben-Dov, *Froggattiella* Leonardi, and *Batarasa* Takagi.

Distribution: Warm regions of the Old World, especially the Oriental region; widely introduced. There are several species described only from the New World; it is not clear whether these are Old World introductions yet to be discovered in their native range, or represent ancient instances of rare dispersal from the Old World. Some may represent convergent origins of an odonaspidine-like morphology—like *Hyparrheniaspis minima*—but this is clearly not the full explanation, as our phylogeny shows the North American species *Odonaspis litorosa* to be deeply nested within a clade of other, mostly Asian, *Odonaspis* species (Fig. 3).

In most armored scale insects, the dorsal and ventral surfaces are very different, with most wax ducts opening on the dorsal surface, where they secrete a tough scale cover; but most grass-feeding species are different. Adult females in grass-feeding species are often tucked between stem and leaf-sheath, with neither surface exposed to the elements; consequently the functional distinction between the dorsal and ventral surfaces is often lost, and both surfaces in grass-feeders are richly covered with small ducts. We see this in Odonaspidini (the name *Odonaspis*, literally tooth-shield, describes the dorsoventrally symmetrical structure that results); we also see something similar in grass-feeding species of Aspidiotini, such as *Aspidiella sacchari* and *Rhizaspidotus donacis*. Given the potential for convergent evolution, an *Odonaspis*-like morphology might evolve more than once. Takagi & Kondo (1997) wrote, "it is assumed that the tribe Odonaspidini originated from the Parlatoriini", which makes it sound as though Odonaspidini should be nested within a paraphyletic Parlatoriini. Given all this, we expected that we might see multiple origins of an *Odonaspis*-like morphology within Parlatoriini. But we don't see evidence of this. In our phylogeny the relationships of Odonaspidini are not fully resolved (Fig. 3) but they are largely consistent with (i.e., they do not refute) the possibility that Odonaspidini is monophyletic. Figure 3 shows an unresolved polytomy of 6 lineages: 3 lineages of Odonaspidini, 1 unidentified species, and the tribes Parlatoriini and Aspidiotini (each of which is only weakly supported as monophyletic). A single species that is usually placed in Parlatoriini, *Microparlatoria fici*, is nested within Odonaspidini, within the genus *Froggattiella* (Fig. 3), though with very low posterior probability.

Pending more complete sampling and better phylogenetic resolution, we have adhered to the traditional composition of Odonaspidini as set out by Borchsenius (1966) and expanded by Ben-Dov (1988) and Takagi (2009); thus, besides the genera we have sampled for DNA, we also include the genera *Batarasa*, *Circulaspis*, and *Dicirculaspis*.

Tribe PARLATORIINI Leonardi

Cited as: Parlatoriini (Borchsenius 1966; Takagi 2002).

Diagnosis: **AF** body usually turbinate; antenna with 1 seta; with pores near anterior spiracles, these usually 5-locular (rarely 3-locular); often with duct tubercles on submarginal venter of thoracic or prepygidial segments; with 2-barred ducts; without reticulate pattern of sclerotization on dorsum of pygidium; all or part of body usually remaining membranous; body margin entire, or only slightly indented between thoracic segments. **2F** similar to adult female but with fewer ducts. **CR** antenna with 5 segments, terminal segment annulated; without septum between tibia and tarsus; abdominal segment III with submedian dorsal seta, segments IV–VI without dorsal seta. **AM** postoccipital ridge with anterior arms triangular; distance between anterior arms equal to or greater than the length of each arm; antennal scape with 1 dorsal seta; antennal pedicel without reticulation and with 0–2 setae; terminal antennal segment with 1 ventral knobbed seta; prosternum with lateral ridges; prescutum triangular; scutum without protuberances; prescutal setae present; scutellar setae present; total number of setae on trochanters 4; dorsal setae present on abdominal segments I–III only. **2M** similar to 2F but with a few more dorsal ducts. **M** diploid, with half of chromosomes heterochromatic.

Included genera: A complete list is given in Table 8.

Distribution: Warm regions of the Old World; widely introduced.

Discussion: Our phylogenetic analysis provides evidence for a clade (labelled Parlatoriini on Fig. 3 and shown in detail in Fig. 15) that includes the type species of *Parlatoria*, *Radionaspis* Ferris, and *Cryptoparlatoria*

Lindinger, and at least non-type species of *Silvestraspis* Bellio, *Neoparlatoria* Takahashi, *Sishanaspis* Ferris, *Parlatorespis* Lindinger, and *Microparlatoria* Takahashi. A second species of *Microparlatoria* was placed outside of Parlatoriini, within Odonaspidini (Fig. 3), though with very weak support. And a non-type species of another genus usually placed in Parlatoriini—*Parlagena*—was nested within Lepidosaphidini; we are now calling it *Pseudoparlatoria bennetti*, as discussed above under Lepidosaphidini. The type species of *Parlagena* differs from that species in crucial characters—having pores by the anterior spiracles and marginal macroducts with sclerotized orifices oriented parallel to the body margin—and we retain the genus in Parlatoriini.

According to our phylogenetic analysis (Fig. 15), the type species of the genus *Parlatoria*, *P. proteus* (Curtis), is more closely related to the type species of the genus *Cryptoparlatorespis*, *C. leucaspis* Lindinger, than it is to any other sampled species of *Parlatoria*. Thus it is clear that any monophyletic concept of *Parlatoria* that includes any significant fraction of its current species will have to include the type species of *Cryptoparlatorespis*. This is 1 of several examples of our finding that the pupillarial habit is a labile character in Diaspididae and that taxonomists should accept that it can vary within a genus. Accordingly, we regard *Cryptoparlatorespis* as a synonym of *Parlatoria*, **new synonymy**. This yields the following new combinations: *Parlatoria leucaspis* (Lindinger), **new combination**, and *Parlatoria pini* (Takahashi), **new combination**. The latter species becomes the senior homonym of *Parlatoria pini* Tang, which requires a placement name, for which we propose *Parlatoria tangi* Normark, **replacement name**.

With respect to the genera we have not sampled for DNA, most of the genera we have included have been recognized as members of Parlatoriini by Takagi (1969, 1987, 2002, 2003, 2008) and Takagi & Kondo (1997), or by Borchsenius & Williams (1963): *Aleucaspis* Takagi, *Annonogena* Takagi, *Benaparlatoria* Balachowsky, *Doriopus* Brimblecombe, *Kochummenaspis* Takagi, *Ligaspis* Takagi, *Mangaspis* Takagi & Kondo, *Mixaspis* Takahashi, *Neoleucaspis* Green, *Neparla* Takagi, *Parlagena*, *Parlaspis* McKenzie, *Parlatorespis*, *Porogymnaspis* Green, and *Tamilparla* Takagi. We also include *Arivonimaspis* (which has a fairly typical parlatoriine pygidial fringe), *Cryptoparlatorespis* Borchsenius and *Leptaspis* Hardy & Williams (which have reduced characters due to the pupillarial habit but are consistent with Parlatoriini), and *Proceraspis* MacGillivray (which has similarities to *Parlatorespis* in the pygidial fringe, especially the scleroses at the positions of L2).

Tribe ASPIDIOTINI Westwood

Cited as: "core Aspidiotini" (Andersen *et al.* 2010). The concept of Aspidiotini used by Borchsenius (1966), Takagi (2002), and other authors (Balachowsky 1958; Ben Dov & German 2003; Davidson & Miller 1977) differs by also including the genera that here are placed in Furcaspidae and Aonidiini.

Diagnosis: **AF** usually with fringed plates; without pores by anterior spiracles; antenna with 1 seta; with 1-barred ducts. **2F** similar to adult female, but with fewer ducts. **CR** antenna with 5 segments, terminal segment annulated; with septum between tibia and tarsus; abdominal segments III–VI each without submedian dorsal seta. **AM** postoccipital ridge with anterior arms irregular in shape; distance between anterior arms less than the length of each arm; antennal scape without setae; antennal pedicel with reticulation and with 2–6 setae; terminal antennal segment with 2 ventral knobbed setae; prosternum without lateral ridges; prescutum transverse; scutum with median protuberances present; prescutal setae absent; scutellar setae absent; total number of setae on trochanters 5–6; dorsal setae present on abdominal segments I–II only. **2M** similar to 2F, but with a few more dorsal ducts. **M** haploid. Adult females that lack pores by the anterior spiracles but that have fringed plates and/or 1-barred ducts generally belong to this tribe. This is the only tribe of Aspidiotinae with haploid males (early paternal genome elimination).

Included genera: A complete list is given in Table 8.

Distribution: Cosmopolitan.

Remarks: A detailed discussion of the phylogeny and taxonomy of this tribe is given in Schneider *et al.* (2018).

Here we discuss a single small genus relevant to clarifying which species belong in which tribe. Like the genera *Gymnaspis* and *Aonidia*, the genus *Bigymnaspis* is a heterogeneous assemblage of small pupillarial species; there are only 3 species in the genus, but each appears to belong in a different tribe. The type species, *Bigymnaspis bilobis* (Green & Laing), known from Tanzania, belongs in Aspidiotini: it lacks pores by the anterior spiracles and

the second-instar nymph has a pygidial fringe typical of Aspidiotini. *Bigymnaspis edgerleyi* (Mamet), known from Madagascar, has pores near the anterior spiracle and cannot be retained in Aspidiotini. It resembles the type species of *Aonidia* in the pygidial fringe of the second-instar nymph and several other characters, and we transfer it to that genus: *Aonidia edgerleyi* (Mamet), **new combination**. As for *B. bullata* (Green), known from tropical Asia, Green (1896) discussed its detailed resemblance to *Parlatoria* in the second-instar nymph, and here we transfer it to that genus: *Parlatoria bullata* (Green), **new combination**.

DESCRIPTIONS OF NEW GENERA

Hendersonaspis Normark, gen. n.

Type species: *Protodiaspis anomala* Green 1915. Type depository: BMNH (Table 3). Syntypes examined.

Additional species: None.

Type material examined: BMNH. 12 slides with a total of 19 AF, 23 2F, 2 CR. left label: "AUSTRALIA / S. Morang, Dixon / On Acacia sp. / Coll. C. French / 109 / BM 1940, 180." (7 slides; 8th slide the same but last line "BM 1953.754"). Right label: "Ancepaspis / anomala Green / Type material / Mounted from Green / collection 5/iv/54 / D. J. Williams, det. " (5 slides) or "Ancepaspis / anomala Green / Second stage [female] / Type material / D. J. Williams" (3 slides). One slide with oval label "Co-type" and other label "Protodiaspis / anomala / Green / on Acacia / S Morang, Dixon. / Australia / Coll. C. French, No. 109"; another slide identically labelled but first label circular, reading "TYPE", and second label with "(TYPE)" inserted before "Green"; 2 other slides labelled identically to these but without the first label with "(nymphal pellicles" inserted on a separate line after "Green". NMNH (Table 3). 10 slides with a total of 8 AF, 1 2F, 4 2M, 8 CR, 1 male pre-pupa, 2 male pupae, and 1 AM. All 10 slides with left label "Ancepaspis anomala / (Green) / [Type Mat.] / [On Acacia sp. / Australia / Ex Coll. E.E.G.] / Stickney Coll. Rec'd 1937", and right labels having various pencilled notes.

Additional material examined. NMNH. Australia: Canberra: CSIRO, on *Acacia decurrens*; 22.viii.1972, coll. L.M. Russell, J. Banks (1 slide with a total of 3 2F). UMEC (Table 3). Australia: Queensland, 28.4988°S, 150.5662°E, 30.v.2007, ex *Acacia harpophylla*, coll. J.C. Andersen, B.B.N. (D2059AD). Australia: Queensland, 28.0145°S, 150.334°E, 31.v.2007, ex *A. harpophylla*, coll. J.C. Andersen, B.B.N. (D2089A). Australia: New South Wales, 28.9901°S, 152.068°E, 2.vi.2007, ex *Acacia* sp., coll. J.C. Andersen, B.B.N. (D2111B). Australia: Queensland, 27.7297°S, 150.350°E, 31.v.2007, ex *A. harpophylla*, coll. J.C. Andersen, B.B.N. (D2131A). Australia: Queensland, 27.6172°S, 150.5003°E, 26.vii.2014, ex *A. harpophylla*, coll. D.A.P., B.B.N. (D5284IJ, D5285E, D5309I, D5310IJ). Australia: Queensland, 28.6858°S, 151.1606°E, 27.vii.2014, ex *Acacia* sp., coll. D.A.P., B.B.N. (D5294AFG).

Description (based on type material at BMNH): **AF** (Fig. 16) pupillarial, remaining enclosed in the cuticle of 2F; body membranous, widest at metathorax; anus at anterior end of pygidium; postanal portion of pygidial dorsum heart-shaped, acute posteriorly, with single pair of appressed, lightly sclerotized or membranous lobes; 1 pair of intermediate marginal ducts opening at bases of lobes; 2 additional pairs of intermediate marginal ducts present on segment 7; no other ducts apparent on pygidium. With a few 5-locular pores present near each anterior spiracle; posterior spiracles without associated pores. With clusters of ventral ducts on thorax, on either side of mouthparts. Antenna with 1 stout, short seta. **2F** (Fig. 17) without pygidial appendages, broadest in thoracic region, progressively narrowing posteriorly; cuticle eventually forming sclerotized puparium with "caudal valve" (Stickney, 1934), a hinged semicircular plate formed from the venter of abdominal segment VIII, "through which the larvae make their escape" (Green, 1915); surface of plate with reticulate pattern submarginally. **2M** (Fig. 18) without pygidial appendages, though with serrated, slightly sclerotized areas along pygidial margin resembling rudimentary lobes; with large ducts in segmental rows on both surfaces of abdomen, more abundant and regularly arranged on venter than on dorsum; large ducts also present on ventral submargin of meso- and metathorax; with a cluster of small ventral ducts laterad of mouthparts.

Diagnosis: Although the adult female has relatively few features, the acute, heart-shaped pygidium is distinctive. *Hendersonaspis* differs from *Ancepaspis* in having pores near the anterior spiracle (absent in *Ancepaspis*). Stickney (1934) considered the relationship of *A. anomala* to the American species of *Ancepaspis*, and concluded that *A. anomala* was "quite different" from the type and the other American species in numerous

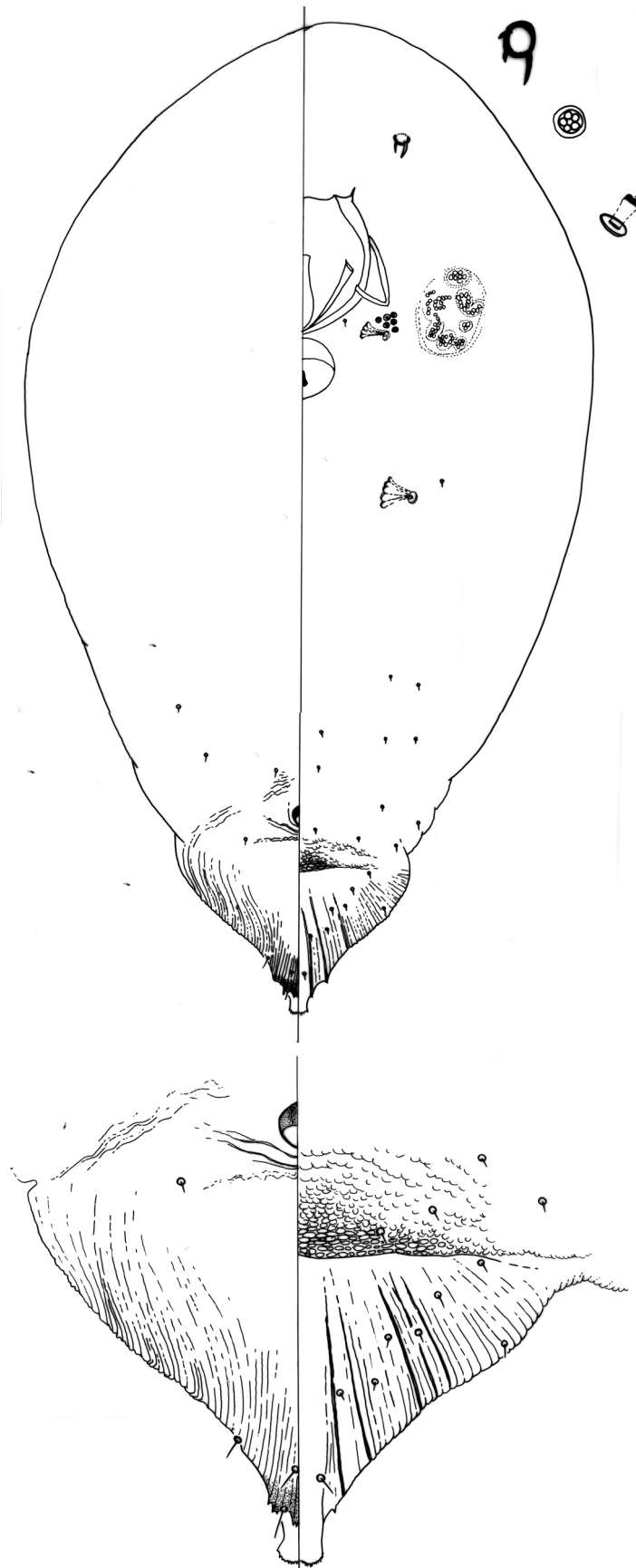


FIGURE 16. *Hendersonaspis anomala* (Green), adult female, illustrated from type material. The dorsal surface is shown on the left and the ventral surface on the right. Below the main figure is an enlarged image of the pygidium. To the upper right of the main figure are enlarged images of an antenna, a perispiracular pore, and a ventral thoracic duct.

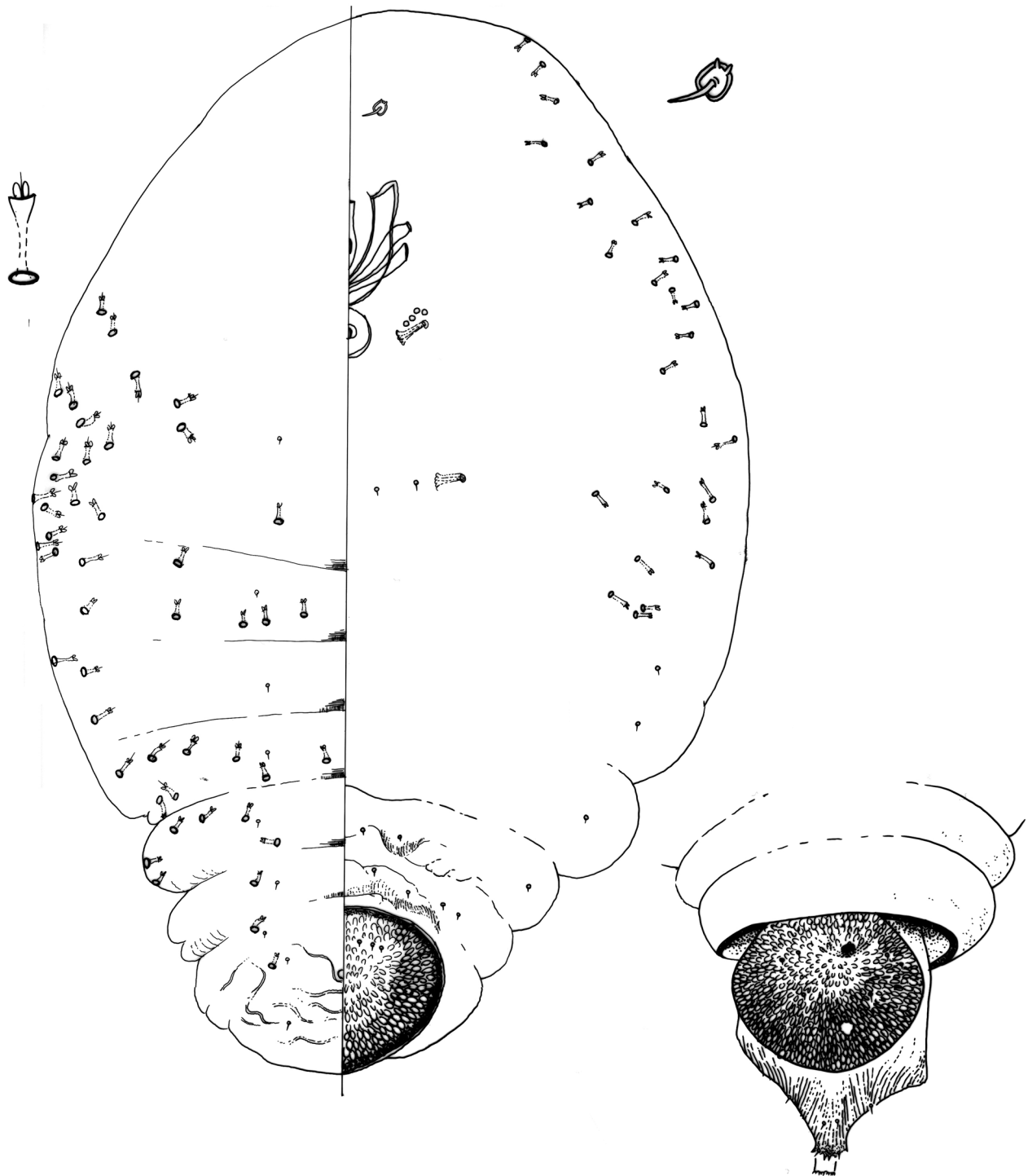


FIGURE 17. *Hendersonaspis anomala* (Green), second-instar female, illustrated from type material. The dorsal surface is shown on the left and the ventral surface on the right. The small figure to the lower left shows a ventral view of the pygidium of the puparium (sclerotized cuticle of the second-instar female) with the caudal valve open and the pygidium of the adult female protruding. The other small figures show enlarged images of an antenna and a dorsal duct.



FIGURE 18. *Hendersonaspis anomala* (Green), second-instar male, illustrated from type material. The dorsal surface is shown on the left and the ventral surface on the right. The small figures on the margins show enlarged images of an antenna, a small thoracic ventral duct, and a larger abdominal dorsal duct.

characters, including: possessing "typical diaspidid" ducts in all life stages; first-instar nymph with distinct pygidium; different position and segmentation of caudal valve in second-instar female, the valve in *A. anomala* being entirely ventral and restricted to segment VIII; and male having filiform antennae and well-developed wings (Stickney, 1934).

Etymology: The name of the genus is formed from *Henderson*, for the New Zealand entomologist Rosa C. Henderson + *aspis*, the Greek word for shield. It is a feminine noun. The name honors Henderson's magisterial work on New Zealand Diaspididae, including a major work on New Zealand Leucaspidini tragically left unfinished due to her untimely death in 2012.

Affinities: It is clear from molecular evidence (Fig. 13) that *Hendersonaspis* is a member of the tribe Leucaspidini. Due to the loss of all pygidial appendages, the affinities of the genus are underdetermined by morphological characters. Nonetheless, most of the characters that are present are typical of the tribe Leucaspidini, in particular the 5-ocular pores by the anterior spiracle, pupillarial habit, elongate body shape, and ventral duct clusters laterad of the mouthparts.

Remarks: Green described the type species, *H. anomala*, placing it in the genus *Protodiaspis*. Ferris (1920) moved the species to a new genus, *Ancepaspis*, typified by *A. tridentata* Ferris of the arid southwest U.S. and northwest Mexico. The genus *Ancepaspis*, so defined, had an unusual geographic distribution, occurring in western North America, eastern Australia, and nowhere else. Our results (Fig. 13) show that *H. anomala* is nested within the tribe Leucaspidini, sister to the New Zealand Leucaspidini, and phylogenetically distant from a strictly New-World *Ancepaspinae*.

***Brimblecobia* Normark, gen. n.**

Type species: *Ancepaspis rotundicauda* Brimblecombe 1959b. Type depository: Queensland Museum, Brisbane, Australia. Holotype and paratype examined.

Additional species: *Ancepaspis asperata* Brimblecombe, *Ancepaspis longicauda* Brimblecombe, *Ancepaspis magnicauda* Brimblecombe, *Ancepaspis reticulata* Brimblecombe, *Ancepaspis striata* Brimblecombe.

Type material of type species examined: *Brimblecobia rotundicauda* (Brimblecombe), **new combination**. QM (Table 3): Moggill, Sept. 1943, ex *Casuarina cunninghamiana* Miq., coll. A.R. Brimblecombe (holotype and paratype, T5780, T5781).

Other material examined: *Brimblecobia rotundicauda*. UMEC. Australia: Queensland: St. Lucia, UQ campus, 27.4992°S, 153.0133°E, 8.v.2007, ex *Casuarina glauca* Sieb., coll. B.B.N. (D2036A). *Brimblecobia asperata* (Brimblecombe), **new combination**, QM, Australia: Queensland: Tugun, May 1953, ex *C. littoralis* Salisb., coll. A.R. Brimblecombe (holotype and paratype, T5776, T5777). *Brimblecobia longicauda* (Brimblecombe), **new combination**, QM, Australia: Queensland: Marmor, Oct. 1955, ex *C. glauca* Sieb., coll. A.R. Brimblecombe (holotype and paratype, T5768, T5769). UMEC. Australia: Queensland: St. Lucia, UQ campus, 27.4992°S, 153.0133°E, 8.v.2007, ex *C. glauca*, coll. B.B.N. (D2036BF); Australia: Queensland: St. Lucia, UQ campus, 27.5003°S, 153.0121°E, 8.v.2007, ex *C. glauca*, coll. B.B.N. (D2042A). *Brimblecobia magnicauda* (Brimblecombe), **new combination**, QM, Australia: Queensland: Tara, Aug. 1957, ex *Acacia harpophylla* F. Muell. ex Benth., coll. A.R. Brimblecombe (holotype and paratype, T5770, T5771). UMEC. Australia: Queensland: 28.6858°S, 151.1606°E, 27.vii.2014, ex *A. decurrens*, coll. B.B.N., D.A.P. (D5295E). *Brimblecobia reticulata* (Brimblecombe), **new combination**, QM, Australia: Queensland: Pikedale, Oct. 1954, ex *C. luehmanni* R.T. Baker, coll. A.R. Brimblecombe (holotype and paratype, T5778, T5779). *Brimblecobia striata* (Brimblecombe), **new combination**, QM, Australia: Queensland: Tara, Aug. 1957, ex *A. harpophylla* F. Muell. ex Benth., coll. A.R. Brimblecombe (holotype and paratype, T5782, T5783).

Description: **AF** (Figs. 19, 20) pygidium without lobes, plates, or gland spines; ducts few, minute, duct openings difficult to see. Apex of pygidium in most species with flat, spatulate margin and with 3–5 conspicuous longitudinal sclerotized ridges or folds. With 5-ocular pores near anterior spiracles (but these apparently missing in 1 species, *B. longicauda*). Antenna with 1 seta. Adult female sclerotized at full maturity.

Diagnosis: Whereas *Ancepaspis* species are pupillarial, *Brimblecobia* species are not; neither does *Brimblecobia* appear to secrete a scale cover. When we collected *Brimblecobia rotundicauda* and *B. longicauda* around Brisbane in May 2007, they were naked, heavily sclerotized, gravid adult females on twigs of *Casuarina*.

Nakedness—the lack of either a puparium or scale cover—is a highly unusual habit for an armored scale insect; yet Brimblecombe (1959b) reported that the adult females were membranous. This discrepancy between our observations and Brimblecombe's may be due to his having collected in a different season (August through October). *Brimblecombia* species also differ from *Ancepaspis* species in having pores by the anterior spiracles. In the Australian fauna, *Brimblecombia* species are distinctive among non-pupillarial species for their lack of lobes, plates, gland spines, and ducts, and for the distinctive sculpturing of the pygidium, usually including a flat, sclerotized plate projecting from the posterior margin, and often including multiple longitudinal striae consisting of sclerotized cuticular folds.

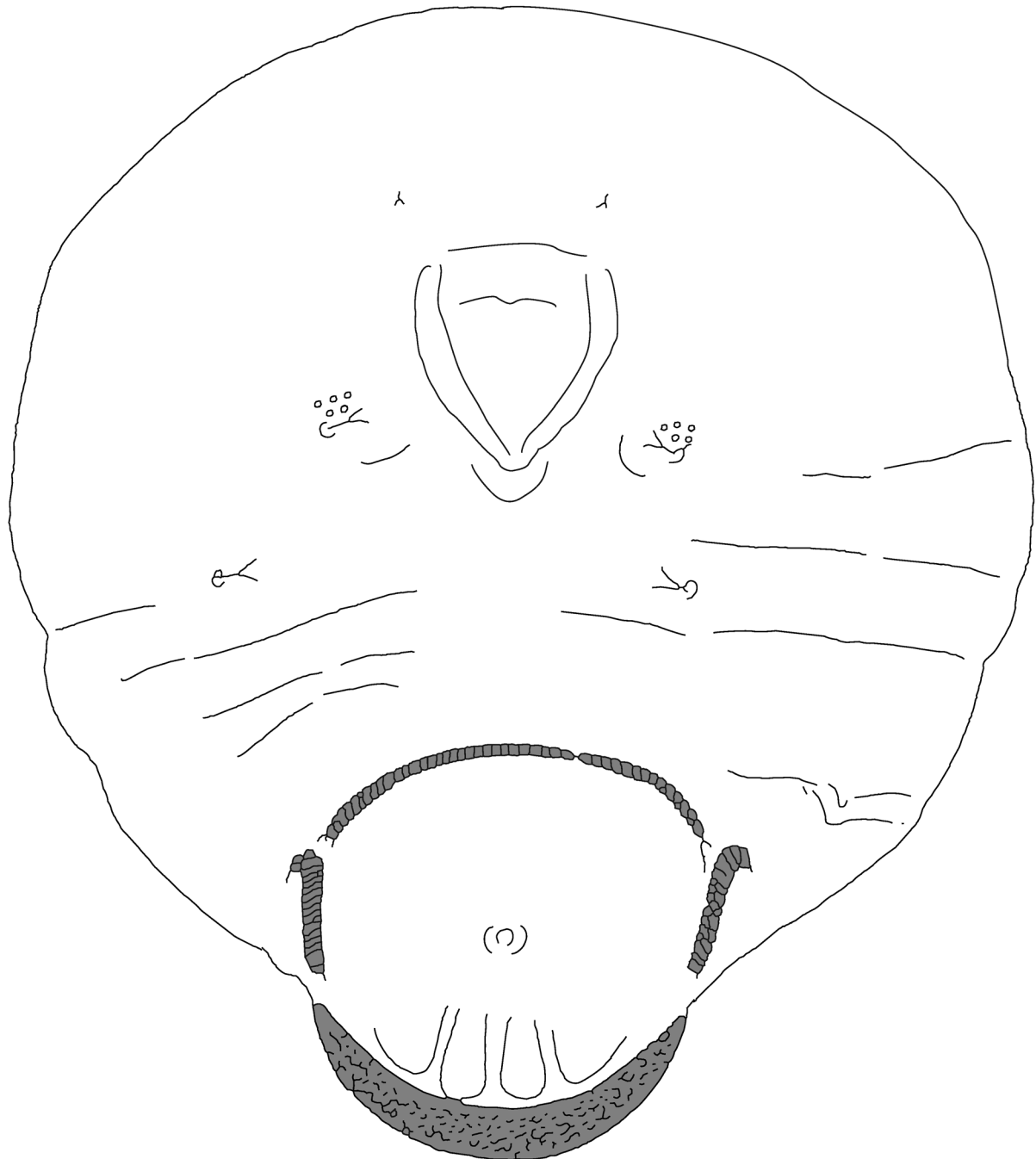


FIGURE 19. *Brimblecombia rotundicauda* (Brimblecombe), adult female, ventral surface. Adapted from Brimblecombe (1959b).

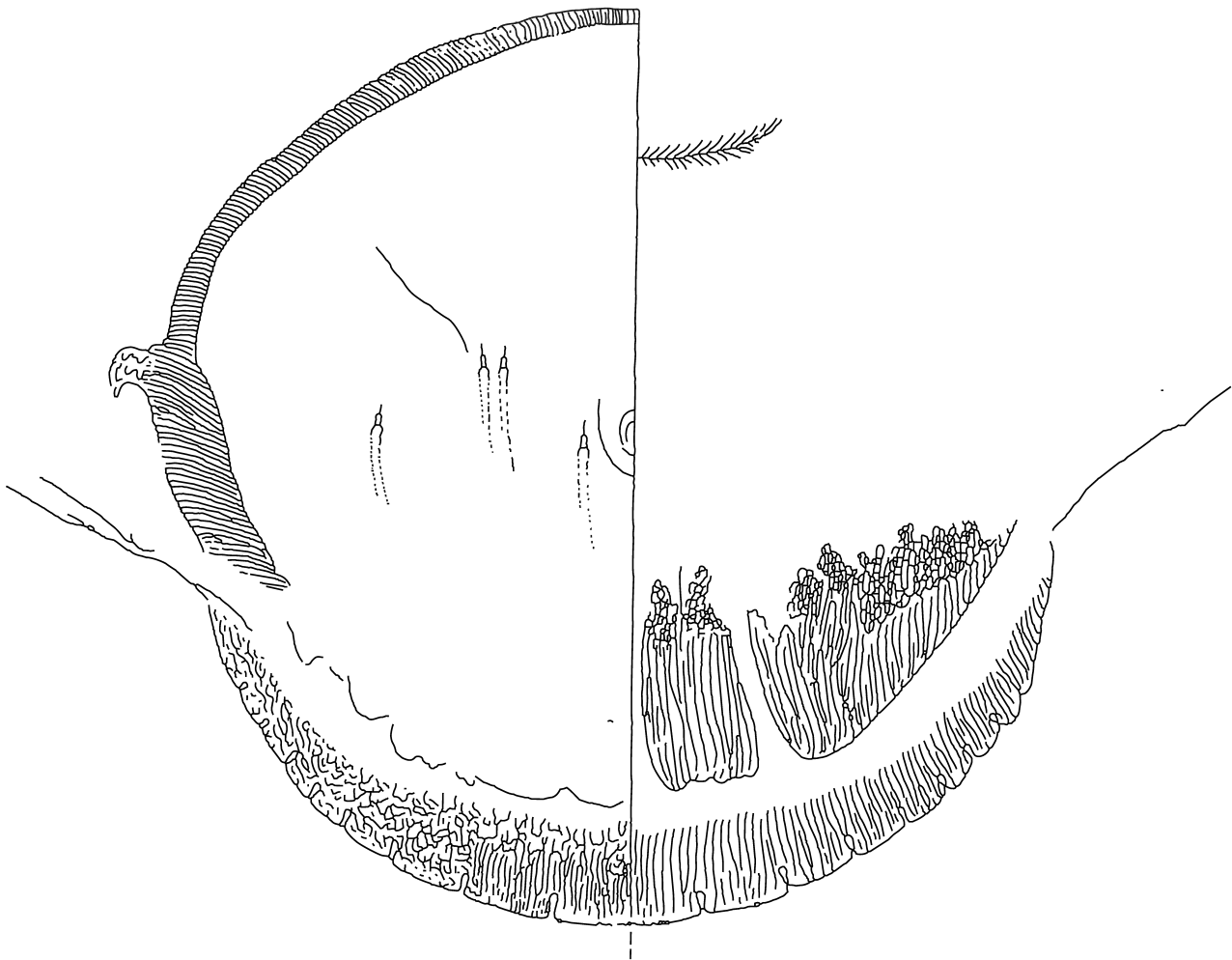


FIGURE 20. *Brimblecombia rotundicauda* (Brimblecombe), adult female pygidium. Adapted from Brimblecombe (1959b). The dorsal surface is shown on the left and the ventral surface on the right.

Etymology: *Brimblecombia* is a feminine noun. The genus is named for A.R. Brimblecombe, who described all of its constituent species, in honor of his crucial work on Australian Diaspididae. The key he included in his 1959 Ph.D. dissertation makes it possible to identify most of the Diaspididae of Queensland, and many from elsewhere in Australia. Unfortunately it was never published, but copies may be purchased from the University of Queensland library (<https://web.library.uq.edu.au/library-services/other-libraries/ordering-copies-uq-theses>). The title is "Studies of the Coccoidea in Queensland: with particular reference to the Diaspididae" and the UQ thesis number is 645. The critical volume to order is Volume 1.

Affinities: *Brimblecombia* is a member of the tribe Aonidiini. Evidence for this is discussed below.

Remarks: Brimblecombe did not give a full explanation for why he placed these species in *Ancepaspis*. He remarked that some of them "resemble" *Ancepaspis edentata*, apparently referring to the sclerotized pygidial margin; very small anus; few, minute ducts; lack of perivulvar pores; and overall shape. Phylogenetic analyses of both EF-1 α and COI-II placed *B. rotundicauda* within the tribe Aonidiini, sister to *Diaphoraspis compacta* Brimblecombe (B.B.N. and A.O., unpublished data; this species was not included in the concatenated phylogenetic analysis presented here because we did not obtain 28S sequences for it.) *Brimblecombia* shares with related Aonidiini a number of features, including: pores by anterior spiracles (absent in *Ancepaspis*), a single antennal seta (multiple in most *Ancepaspis* species, including *A. edentata*), non-pupillarial (*Ancepaspis* is pupillarial), and derm of adult female sclerotized at maturity (membranous in *Ancepaspis*). In addition, the most common host of *Brimblecombia*, like that of *Diaphoraspis* and related Australian Aonidiini, is *Casuarina* (though 1 species, *B. magnicauda*, is found on *Acacia*, like some North American *Ancepaspis* species).

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